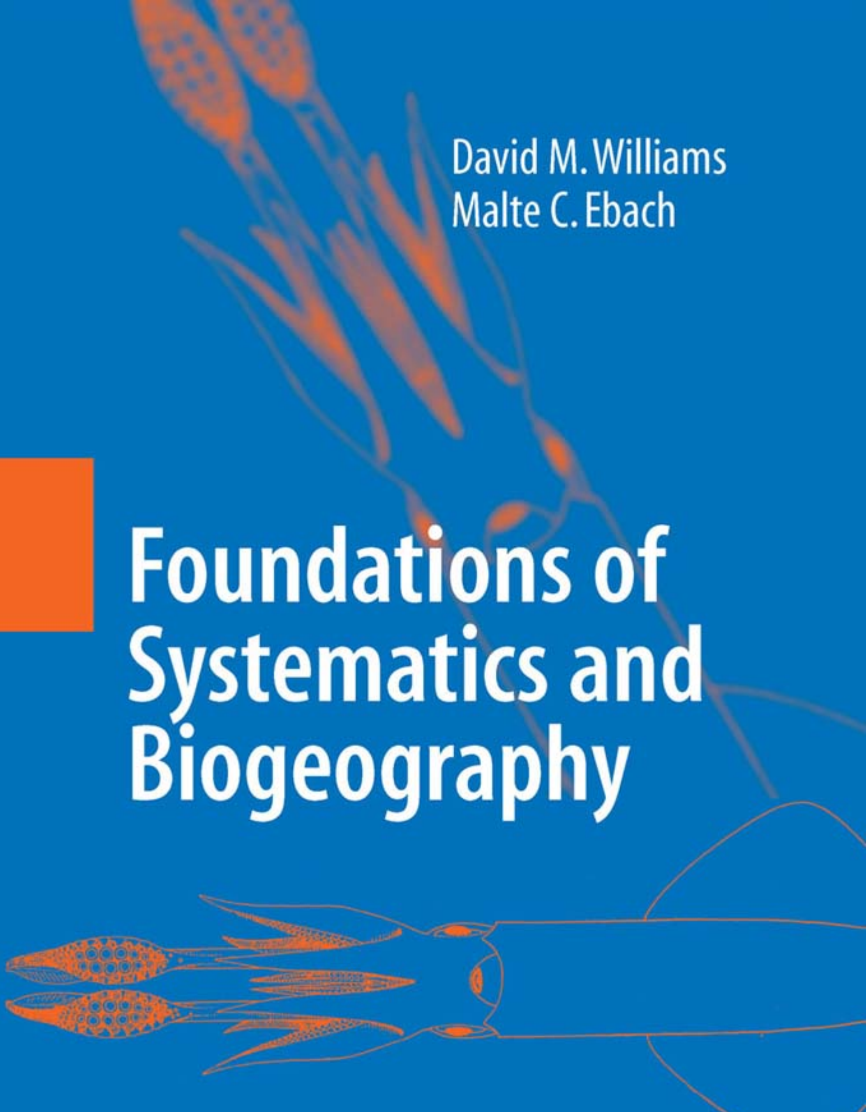
David M. Williams
Malte C. Ebach

# Foundations of Systematics and Biogeography



Springer

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David M. Williams · Malte C. Ebach

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Foreword by Gareth Nelson

Springer

David M. Williams
Dept. Botany
Natural History Museum
Cromwell Road
London SW7 5BD
United Kingdom

Malte C. Ebach
Botanischer Garten und
Botanisches Museum Berlin-Dahlem
Freie Universität Berlin
Königin-Luise-Str. 6–8
14191 Berlin
Germany

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*Dedicated to*
*Agnes Arber (1879–1960)*
*Adolf Naef (1883–1949)*
*Léon Croizat (1894–1982)*
*Lars Brundin (1907–1993)*
*Rainer Zangerl (1912–2004)*
*Colin Patterson (1933–1998)*
*Ronald H. Brady (1937–2003)*

# Foreword

> “But where shall wisdom be found? and where is the place of understanding?”
>
> Job 28: 12

Where, indeed? Today in systematics and biogeography, DNA is revered as the source of all. One reads for example of the “unlovable mass of nucleotide sequence characters that are the foundation of virtually all well-supported phylogenetic trees” (Palmer et al. 2004:1443); and "Much of the improved understanding derived from new genetic data and allows us to date important evolutionary events and, in some cases, to trace the actual geographic routes travelled by early peoples over the earth" (Orr 2006:18). Such assessment says nothing of the long history of human effort in systematics and biogeography, as if that were now rendered irrelevant by modern biology and its techniques of reading DNA sequences and of their computer-assisted phylogenetic analysis.

Two generations ago palaeontology was similarly revered. Then one could read for example that for mammals “Their fossil record is unequalled and allows an almost magical view into the past” (Darlington 1957:320; reaffirmed by Briggs 1974:249). Today’s attitude towards DNA is much the same except that there is no “almost” about it. A lesson from the past, a sense of proportion widely overlooked, is Blackwelder’s (1977:115) dictum that “New types of data are potentially of great importance, but they do not replace other types except in problem cases.” His perspective grew from consideration of overblown claims offered for the “new kinds of data” of his time: chromosomes, behaviour, serology, genetics, a list that today would be augmented by organelles, membranes, nucleic and amino acids, genomics, proteomics, etc. Even so, the abiding reality remains: “there is no such thing as magic.” And, alas, to Job’s queries there are no easy answers.

In 1813 AP de Candolle observed (p. 68) that in earlier times “the plant that one botanist considered related to some other would later be far removed from it by another botanist, with neither opinion capable of being proven either true or false.” For this dilemma he saw the remedy to be “the natural method,” which took all characters into consideration and relied on character congruence for support of one opinion and refutation of another. His view prevails to the present, but its focus was improved by Hennig’s (1949) distinction between primitive and advanced characters – his plesio- and apomorphies – that is the basis of the modern discussion of cladistics.

The present volume broadens the discussion by incorporating the pre-Hennigian German literature from Goethe, Haeckel, Naef et al. – what in the anglophonic world is usually dismissed as the romanticism of “German idealistic morphology” (Levit and Meister 2006). Through the ageless eyes of the “modern synthesis” the broadening must seem to approach Marx’s (1852) apotheosis of The Past: “The tradition of all dead generations weighs like a nightmare on the brains of the living” – *Die Tradition aller toten Geschlecter lastet wie ein Alp auf dem Gehirne der Lebenden*.

Nightmares notwithstanding, nothing for long, it seems, can safely be ignored.

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Gareth Nelson
School of Botany
University of Melbourne
Victoria 3010
Australia

# Prologue

The views expressed in this book are an amalgamation of the works of several 18th, 19th- and 20th-century comparative biologists, notably Johann Wolfgang von Goethe, Louis Agassiz, Geoffroy St. Hilaire, Richard Owen, Adolf Naef, Rainer Zangerl, and Gareth Nelson. In one sense this book is simply an anthology of their studies on *homology* and *classification*, as expounded in such classic studies as *Die Metamophose der Pflanzen* (Goethe 1790), *Essay on Classification* (Agassiz 1857, 1859) *Idealistische Morphologie* (Naef 1919), and *Systematics and Biogeography: Cladistics and Vicariance* (Nelson & Platnick 1981), ideas that form the basis of a comparative biology for the 21st century.

In another sense, the intention behind writing this book was to explode some myths currently part of biology and reassert—and restate—the principal aims of comparative biology, especially in relation to evolutionary studies. The prevailing attitude of many systematists and biogeographers has led to conflicting ideas being combined under an apparent evolutionary synthesis (Mayr & Provine 1980). In order to alert prospective students of comparative biology to the dangers and pitfalls involved in systematics and biogeography, this book intends to provide three principal messages:

1. Biological classifications and explanatory mechanisms are separate entities. Classifications form either artificial or natural groups, the latter being discovered through *homology* and *monophyly*, the former simply assertions, imposed rather than discovered.
2. Most, if not all, concepts of homology originated prior to the work of Charles Darwin, a fact that emphasises the rich, varied, and valuable work of 18th to 19th-century anatomists—the history of its development a subject still not exhausted.
3. The underlying concept for all of comparative biology is *relationship*—neither "similarity" nor "genealogical hypotheses of descent" are sufficient.

These three messages echo the work of the last three centuries of comparative anatomy, most recently expressed in Gareth Nelson and Norman Platnick's book *Systematics and Biogeography* (1981), now over 25 years old. *Systematics and Biogeography* was the first book of the 20th century to provide a historical account of the ideas behind the emerging cladistic revolution.

Nelson & Platnick's book was not the only attempt at a summary of methods for classifying organisms. Two very different books appeared that covered, in part at least, the history of comparative biology: *Phylogenetic patterns and the evolutionary process* (Eldredge & Cracraft 1980) and *Phylogenetic Systematics* (Wiley 1981). Both of these books interpret what amounts to the same history discussed in *Systematics and Biogeography* but adopt a mechanistic approach rather than what might be called the descriptive or pattern approach.

The appearance of these three books, all stemming from the same institution (the American Museum of Natural History), at the same time, interpreting the same history in three different ways, implies a conflict of interpretation—and some viewed the immediate aftermath as a ”war” between methodologies, documented by historians biased towards a particular viewpoint—that of mechanisms (see Hull 1988). The “war” of interpretation would have made far more sense if all sides had noticed that each was influenced by a different part of that same history—interpretation did not in any fundamental sense differ at the level of methodology but at the level of intention.

Posing the question, “Why study comparative biology?” yields two very different answers, if any positive answer is given at all. One sees virtue in classifying organisms (Nelson & Platnick 1981), the other sees virtue in explaining that classification (Eldredge & Cracraft 1980). Oddly, it is a third group, those who wished to mingle classification and explanation, where confusion has been most mischievous, exemplified by Wiley (1981)—it is, thus, perhaps no coincidence that Wiley intended his book to be regarded as an update of one foisted on a previous generation, one buried in the ”modern synthesis” as an explanation for organismic diversity (Mayr 1969). Only after consideration of the significant incompatibility—or the fundamental clash between classification and explanation—can the enterprise of classification begin to progress. At present, it has stagnated.

The “war” between explanation and classification is rarely discussed, most preferring the more conventional world of explanation—possibly because there is a belief that explanation conveys greater meaning than classification.

We felt that by recording some history, along with some interpretation, we were able to understand the numerous—and reoccurring—disagreements between comparative biologists: A history that clearly separates the differing intentions of its practitioners does not exist. One detailed history of the more recent period does exist: David Hull's *Science as a Process* (Hull 1988; but also see Craw 1992). Even Hull's title suggests a viewpoint from the outset, presenting a “process-orientated” reading of history. We present the missing version—the version based on pattern and on classification.

David M. Williams and Malte C. Ebach,
*London, Paris & Berlin, November 2006*

# Acknowledgments

The ideas we explore in this book are, like most dynamic and exciting fields of enquiry, continually changing and developing. Since the book's inception, some six years ago, biogeography and systematics have both undergone dramatic changes, especially with the accumulation of massive amounts of molecular data and the plethora of new methodologies for its analysis. The entire scientific landscape has altered since the Cladistic revolution began some 40 years ago, starting in the mid- to late 1960s. We felt it was necessary to examine not just the immediate past of our subject but to explore some of the lost avenues of research in its more distant past, with the desire to show that data are not now necessarily the major source of problem solving, many conceptual issues are outstanding. This volume represents the combined work of our investigations and insights into the foundations of systematics and biogeography over a working partnership spanning 6 years. The content of this book summarises several key works, most notably, Williams (2004, 2006), Ebach (2005) and Williams and Ebach (2004, 2006) (with permission).

The *Foundations of Systematics and Biogeography* would not have been possible without valued, and at times heated, debates with many of our colleagues. While we are grateful to them all for putting up with our constant quest for their input and tolerance of our insistence, we would especially like to thank Mark Carine, Peter Forey, Juan J. Morrone, Gary Nelson, Lynne R. Parenti, and Robert Scotland. We would also like to thank Bob Press, Johannes Vogel, and René Zaragüeta for assisting with these preoccupations when, perhaps, we should have been dealing with more pressing matters.

Finally, and naturally, we wish to thank Lorraine Williams and Caitlin Hulcup, who had to witness not only the birth and subsequent growing pains involved in the writing of this book but also its rather prolonged adolescence.

# Contents

# Chapter 1
# Introduction: Systematics, Evolution, and Classification

> "The theory of evolution has a simple answer for the main question formulated above: natural systematics can be explained by the assumption that existing forms are the descendants of species which developed from a common ancestor in each group by continuous change and division of species, in a process comparable to the branching of a genealogical tree. *The question how a natural system has been obtained is not explained, nor do genealogists deal with it in detail*." (Naef 1921–23: 6, from the English translation; Naef 1972a: 12, italics ours)

> "I respect faith, but doubt is what gives you an education."
> (Wilson Mizner)

Today phylogenetic studies are struggling under the weight of their own ingenuity. It is no longer sufficient simply to find the tree or cladogram that best summarises the available data (evidence), but it has become necessary to substantiate that claim by attaching a measure or index of "goodness". Of techniques there are plenty: bootstrapping, jack-knifing, decay indices, homoplasy indices, various support measures, *ad nauseum*. Each developed to offer some kind of "confidence" in the nodes and branches of the particular phylogenetic tree recovered—and the numbers derived from applying these methods adorn every published phylogenetic tree, giving it the appropriate aura of "mathematical", "statistical" respectability. Of course, methods to "reconstruct" these phylogenies have had considerable effect, such that there are now methods dealing with too many data, not enough data, data of the wrong kind, data of the right kind, taxa of the wrong kind, taxa of the right kind, too many trees, not enough trees, trees of the wrong sort, trees of the right sort, no trees at all, *ad nauseum*. The creators of this "movement", if it is such, now have a ready supply of manuals to examine, confirming when and where such techniques might be applied and what benefits they offer the "comparative biologist", "evolutionist", "systematist", "phylogeneticist" (Salemi & Vandamme 2003, Semple & Steel 2003, Felsenstein 2004, Sakhar 2006). Felsenstein notes in the preface to his book, "Phylogenies . . . have been around for over 140 years, but statistical, computational, and algorithmic work on them is barely 40 years old" (Felsenstein 2004: xix). Putting those 40 years to one side for the moment, what might be the relevance of the first 100 years, if any? What might we still learn from history? While this book presents a critique of current methodology, it is situated among developments made during those ignored 100 years —and before.

Not too long ago it would have been readily agreed by systematists that there were three, and only three, approaches to classification, each referred to as a particular "school": "gradistics" (an eclectic approach, more often called "evolutionary systematics"), "phenetics", and "cladistics" (e.g., Hull 1970, 1988). Each of these schools was characterised by a particular approach. To simplify, "phenetics" advocated grouping by overall or raw similarity, "cladistics" advocated grouping by shared derived characters (by "synapomorphy"), and "gradistics" advocated grouping by a consideration of both overall similarity and synapomorphy. All three "schools" discussed their approach relative to phylogeny, its discovery, and representation; phylogeny being understood as a complete system of ancestor-descendant relationships. "Phenetics" advocated recognising groups on the basis of percentage similarity, for the most part ignoring phylogenetic considerations; "cladistics" advocated recognising groups strictly on the basis of recency of common ancestry; and "gradistics" advocated recognising groups on the basis of both common ancestry as well as a measure of anagenesis (represented by some measure of overall similarity). While all three approaches received considerable discussion in the 1970s and 1980s, we concentrate on cladistics and its development—in many of its various guises.

Of cladistics, conventional wisdom usually places its origin with the studies of the German entomologist Willi Hennig (1913–1976; Schmitt 2001), especially his English language book *Phylogenetic Systematics* (Hennig 1966a; see also Hennig 1965), a revision, rather than a translation, of his earlier book (Hennig 1950, Schmitt 2001). The spread, advocacy, and popularity of cladistics are usually associated with the rise of a new generation of systematic biologists (and palaeontologists) in the late 1960s and early 1970s, primarily working in the United States and Great Britain (Hull 1988), but also in many parts of Europe (France, Denmark, Belgium, etc.). Perusal of the recently published compendium *Assembling the Tree of Life* (Cracraft & Donoghue 2004) reveals many citations to that effect. A more considered history of cladistics is provided later. We begin by introducing key issues inherent to understanding the discipline as it relates to biology as a whole and evolutionary biology in particular.

## 1.1 The Evolution of "Cladistics"

### *1.1.1 What Is Cladistics?*

> "How often misused words generate misleading thoughts." (Spencer 1879)

> "Hennig, in fact, never used the word [cladistic], which was coined by his critics (Mayr, Sokal, Darlington, Simpson et al.), who argued that Hennig's philosophy was hopelessly narrow-minded and, therefore, deserves to receive a special name. Alas! The critics never seemed quite to understand what they were criticizing to begin with."
>
> (Nelson 1979: 13)

Relevant to any discussion of cladistics is an examination of its definition, a term having a tortured and convoluted history.[1] While definitions have limited appeal in achieving clarity, it is worth dwelling on the conflicting meanings, if for no other reason than to grasp how and why the present understanding is so ambiguous. Even though Willi Hennig is often assumed to have introduced the subject, he never used the word "cladistic" or "cladogram".[2] "Cladogram" originated with Mayr (1965) and Camin & Sokal (1965), "cladistic" being coined somewhat earlier by Rensch (1958) and Cain & Harrison (1960), both of whom derived their usage from Huxley (1958). Mayr's intention was to characterise and christen Willi Hennig's approach to classification, with the desire to distinguish it from "other" phylogenetic methods:

> . . . [t]o prevent further confusion [with other so-called 'phylogenetic' methods], I shall call this [Hennig's approach] the cladistic approach, in conformance with the terminology proposed by Rensch (1960) (cladogenesis) and by Cain and Harrison (1960). (Mayr 1965: 78)

Mayr suggested a few properties of a cladogram (Figure 1.1), such that "the ordinate gives the estimated time, the abscissa degree of difference" (Mayr 1965: 81; cf. Mayr 1969: 255).

It was George Gaylord Simpson who corrected Mayr, suggesting that "A cladogram on Hennig's principles shows only the succession of dichotomies; Mayr (1969) is mistaken in saying that a cladogram according to Hennig has time on the ordinate and degree of difference on the abscissa" (Simpson 1975: 14). Mayr changed his definition accordingly: "[a] cladogram is a dendrogram depicting the branching of the phylogenetic tree without respect to rates of divergence" (Mayr 1978: 85) and later: "[A cladogram is] a dendrogram based on the principles of cladism; a strictly genealogical dendrogram which features the branching points of phyletic lineages but in which rates of evolutionary divergence are not considered" (Mayr & Ashlock 1991: 411), and finally arriving at the view that a cladogram was an ". . . inferred branching pattern of a phylogenetic tree" (Mayr 1997a: 306).

It was, however, Camin & Sokal who first suggested branching as a factor:

> By cladistic relationships we mean evolutionary branching sequences among taxonomic units without regard to the phenetic similarities among them or to an absolute time scale [and] [w]e suggest the term *cladogram* to distinguish a cladistic dendrogram from a phenetic one which might be called a *phenogram*. (Camin & Sokal 1965: 311; italics in original)

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[1] For those interested, the following references are guides to the literature. These few papers by no means cover the subject in any general way: they all speak from particular points of view (Edwards 1996, Sneath 1995, Farris & Kluge 1997, Tassy 1996a, Felsenstein 2001, 2004)

[2] Hennig did, however, use the word "clade". His usage (e.g., Hennig 1966a: 159, 223) is interesting for a number of reasons, of which the most significant is that he was not quoting Huxley (1958) but Cuenot (1940: 24), who was using the term "clade" in the sense of a unit of classification. The origin of Cuenot's usage can be traced back to Haeckel, who used it as a category of classification (Haeckel 1866; for Cuenot, see Tassy & Barriel 1995; for Haeckel, see Williams 2006 [2007]). When Hennig uses "cladistics", "cladistic analysis", "cladogram", etc., he enclosed the words in quotation marks to indicate that these are words used by other persons (Hennig 1974).

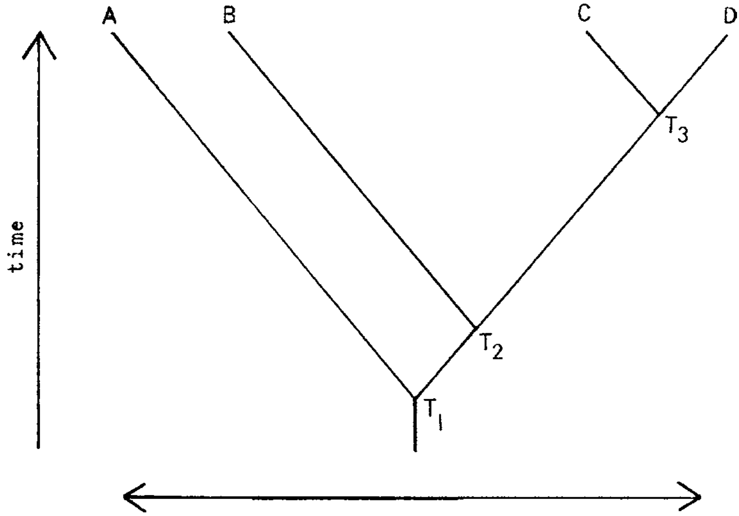

**Fig. 1.1** After Mayr (1969: 256, Fig. 10.17). "A cladogram. The branching points at $T_1$, $T_2$, and $T_3$ determine the classification of the taxa A, B, C, and D", reproduced with permission of The MacGraw-Hill Companies

While it was clear that Mayr had Hennig's work in mind, [3] Camin & Sokal, being interested in all kinds of numerical methods for the "reconstruction" of phylogenetic relationships and classifications, considered a more general view. [4]

Sneath & Sokal, continuing with their (Camin & Sokal's) numerical perspective, elaborated on the definitions of "cladogram" and "cladistic relationship":

> Cladistic relationship can be defined as—and represented by—*a branching (and occasionally anastomosing) network of ancestor-descendant relationships*. These treelike networks expressing cladistic relationships are called *cladograms*.... (Sneath & Sokal 1973: 29; italics in original)[5]

To some, then, "cladograms" were considered to be one kind of representation of ancestor-descendant relationships—a genealogy.

Others were somewhat confused, as their understanding differed significantly from the critics.[6] What, then, *is* a cladogram? Speaking with one voice—or so it

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[3] "Typical representatives of this school [cladistics] are Hennig (1950) and Kiriakoff (1959)" (Mayr 1965: 78).

[4] Camin & Sokal (1965: 311) cited several different methods including an early effort using "parsimony" (Doolittle & Blomback 1964), maximum likelihood (Edwards & Cavalli-Sforza 1964), and compatibility (Wilson 1965).

[5] Later Sneath subdivided "kinds" of cladograms such that "cladistic relationships, *sensu originale*, shown by cladograms, *sensu originale*, can be measured in several ways: (a) as only the order of branching or number of branches passed between OTU's is a *topocladogram*; (b) as the time at each node (a *chronocladogram*); (c) as a minimal (phenetic) evolutionary distance between each node (*orthocladogram*); and (d) as actual (unknown, but phenetic) evolutionary distance between each node (*holocladogram*)" (Sneath 1983: 28–29; see also Sneath 1975: 360).

[6] Nelson, for instance, noted "... with regret that discussions of these matters [cladistics and its

seemed—the "cladists" stated clearly that a cladogram is a *synapomorphy scheme*,[7] an idea that originated with Schlee (1969). Such a statement invites further questions: What, then, is *synapomorphy*? How is it discovered? We return to these issues later as they occupy the core of this book, as it is the core of comparative biology.

As far as we can establish, the terms "cladistic" and "cladogram" were first given a *cladistic* treatment and interpretation by Nelson (1978a, 1979, and Nelson & Platnick 1981):

> . . . a cladogram . . . is merely a branching diagram that summarizes general knowledge about the kinds and relationships of organisms. (Nelson 1978a: 108)

"Cladogram" can be understood as a general term for any kind of branching diagram or hierarchical classification.

That view did not, of course, satisfy everyone. Sneath (1982), in a detailed review of Nelson & Platnick's (1981) book, objected to the definition:

> The greatest confusion is caused by the word 'cladogram'. Nelson and Platnick most often mean a diagram of nested synapomorphies (nested shared derived character states). This is not the original meaning of a formalized phylogenetic tree (Mayr 1965; Camin & Sokal 1965). But they use the word also for diagrams that are neither of these . . . A cladogram in their preferred sense, therefore, is referred to here for clarity as a synapomorphogram. (Sneath 1982: 209; see also Sneath 1983: 30)

Thus, Sneath wished to see the word "cladogram" *sensu* Nelson restricted to his new—but rather cumbersome—term "synapomorphogram". Rohlf & Sokal elaborated:

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meaning], particularly in this journal [*Systematic Zoology*], has been partly confused, because the critics of 'cladistics' have had the habit of defining its key concepts in a narrow and objectionable fashion, presumably for the purpose of more easily refuting them" and "[I]f I remember correctly, the avowed purpose of the early pheneticists was not to temper the supposedly rigid demands of 'cladistics'. At that time 'cladistics' was a word not even defined in its currently *abused* sense" (Nelson 1978a: 105; emphasis added). Farris made similar protestations: "Most proponents of other schools prefer to refer to the Hennigian school approach as 'cladistic'. Sneath and Sokal (1973), Mayr (1974), and Michener (1978) all seem to have about the same attitude on this matter. They define 'cladistic' to refer only to the branching pattern of evolution (as it indeed was originally intended), and they emphasize that 'cladistic' classification represents only that branching pattern: that it does not represent any information about characters ('adaptiogenetic' information of Mayr)" (Farris 1979: 488).

[7] ". . . Anyone familiar with Hennig's work, however, knows that Hennig did include character information in his hierarchies – that is why they are termed '*synapomorphy schemes*'." (Farris 1979: 488–489; emphasis added); "Their [Sneath and Sokal 1973] adherence to such a belief [as stated in the texts above] suggests either simple ignorance or deliberate disregard of a very large body of literature dating from about 1950, in which classificatory schemes—recently termed 'cladograms'—are formed on the basis of shared derived characters. To a remarkable degree this literature has been explicit in its intended goal of producing '*synapomorphy schemes*'. " (Schuh & Farris 1981: 335; emphasis added); "In a cladogram, the branch point represents the generality of supposedly true statements ('synapomorphies') that can be made about the terminal taxa. . . . In short a cladogram is *a synapomorphy scheme*. . . . " (Nelson 1979: 8, footnote 1; emphasis added) "But a cladogram is hardly a phylogeny in the usual sense. Instead, it is a summary of the pattern of homologies, *a synapomorphy scheme*, or, at best, a hierarchical classification." (Patterson 1982a: 56; emphasis added)

> Cladistic relationships by the definition we employ *must* involve evolutionary branching sequences. Thus we interpret a synapomorphy scheme, by a Hennigian cladist who does not proceed to make inferences about the genealogy of the OTUs being studied, as a special kind of phenetic relationship. (Rohlf & Sokal 1981: 463, emphasis added; cf. Nelson 1992)

According to the critics, then, cladistics had to be either a special kind of phenetics (with no evolutionary connotations) or a special kind of evolutionary systematics (with very particular evolutionary connotations)! Regardless of these varied interpretations, Nelson's usage remains the more general and appropriate, allowing hierarchical schemes of relationship to be understood and interpreted in terms of their branching. Any and every tree, as well as any and every classification, can and does have a hierarchical component—what we will refer to as its **cladistic aspect** or **cladistic parameter** following Nelson (1979: 12; Nelson & Platnick 1981: 318–319). This parameter is directly related to the notion of synapomorphy, itself a derivation of the older terms "homology" and "taxon" (see Chapter 7), which in turn relate to the notion of a **unit of systematics** (Chapters 2, 3, 7, 8 & 12). Thus, if it is accepted that homology = taxon (= unit of systematics = cladistic parameter), matters are simplified. It is with the exploration of the **cladistic parameter** that this book is largely concerned. We will refer to this approach as **Cladistics** (with a capital C) to distinguish it from the varied interpretations given above—cladistic, with a small c, refers to particular mathematical methodologies (parsimony, compatibility, etc.) and is related more closely to the concerns of the numerical systematists.

The Cladistic parameter is a property of all methods based on specified relationships. Biogeographic cladograms—*areagrams*—are another example, where the Cladistic parameter was noted by Nelson (1978c: 294, footnote 87) in an essay on the history of biogeography but first hinted at by Rosen (1975), after an earlier illustration of a geographical cladogram (Rosen 1974a), documented more explicitly in Rosen (1978: 160) and in Platnick & Nelson (1978).

### *1.1.2 What Is Cladistics—Again?*

> "I've been shooting in the dark too long, when something's not right,
> it's wrong." (Bob Dylan 1976)

Early on, Felsenstein (1982, 1984), a population geneticist (Slatkin 1995), developer of numerical (phenetic) methods as applied to phylogeny (Felsenstein 2004), and promoter of R.A. Fisher's "statistical" perspective on science (Felsenstein 1988), suggested avoiding the word "cladistic" altogether because of its apparent ambiguity (see below). He introduced a different way of looking at the problem:

> Cladistics is a term with two distinct meanings. In one, it implies acceptance of a cladistic position on classification, the view that groups in the classification system should be monophyletic. In its other meaning, it signifies an interest in reconstructing phylogenies, without regard to how the classification system is set up. … The question of how to construct classifications and how to reconstruct phylogenies are logically separable, so that it would

> be better to avoid the word *cladistics* altogether. (Felsenstein 1984: 169; but see Felsenstein 1983: 315 for a slightly different view and Felsenstein 2004: 145–146 for more dogmatic statements)

Felsenstein's usage follows that of other numerical systematists, uniting one of the two versions of "cladistics" with a very specific method of analysis (parsimony) and the other version with a very specific method of classification (monophyly). The notion that cladistics might have two separate meanings originated with Ernst Mayr:

> There is little argument between cladists and evolutionary taxonomists about the cladogram that results from cladistic analysis. The argument arises over the relationship of such a cladogram to the classification. Cladists argue that a one-to-one relationship exists between cladogram (phyletic diagram) and classification. ... The evolutionary taxonomist, on the contrary, believes that a mere branching pattern cannot convey nearly as much information as an evolutionary classification that takes additional processes of evolution into consideration. (Mayr 1974: 98)

Mayr & Ashlock recently summarised their understanding of the distinction:

> 1 Cladistic analysis, or the reconstruction of the branching sequence of phylogeny through an analysis of synapomorphic characters, a method also adopted by many non-cladists ...
> 2 Cladistic classification, or the delimitation of taxa and their ranking in a Linnean hierarchy based on the principle of holophyly [=monophyly] (Mayr & Ashlock 1991: 208).

Separating cladistic analysis ("the reconstruction of the branching sequence of phylogeny") from cladistic classification ("the delimitation of taxa and their ranking in a Linnean hierarchy") meant that one might choose to focus upon each as a distinct and separate endeavour. Cladistic analysis, however conceived, represents a method of discovery. Cladistic classification, however conceived, represents a procedure for naming "things" discovered.

Yet the idea that cladistics was concerned with "the reconstruction of the branching sequence of phylogeny" was something Mayr borrowed from the numerical systematists, as Cladistics (noting the capital C) was concerned with classification and the evidence available to support any particular branching structure—the specific sets of relationships.

In Felsenstein's view, because cladistics was successful in its quest for an unambiguous approach to classification but not unique in finding the method for discovering the "phylogeny" upon which that classification should be based, the proper focus for future study should rest with explorations of method, implementing some notion of phylogenetic reasoning. Whatever value there might have been in this shift (see below), the focus did indeed move towards "method"—and with a vengeance. What method was best, and under what circumstances? Perhaps a different method was required for each different set of circumstances. But how many different circumstances are admissible—or even possible? How many permutations of change could be imagined? Few? Many? This ambiguity allowed Felsenstein (and many others) to interpret "phylogeny reconstruction" in terms of various underlying models of "change" implicit in the reconstruction method—which he did, under "a probabilistic model of evolutionary change" (Felsenstein 1983: 328; Felsenstein 1979, 2004). Felsenstein successfully moved the central focus of systematics—discovering relationship among taxa—to “phylogeny reconstruction” —tracing paths of ancestry and descent—and ultimately away from classification (Felsenstein 2004).

“Phylogeny reconstruction” is rendered possible only by examining various suites of methods each said to be dependent upon a different model of change. Oddly, all methods are applied to what we will refer to as phenetic data (see Chapter 8), the “phenetic similarities” of Camin & Sokal (1965: 311).

More recently, Felsenstein claimed that classification, if anything at all, is irrelevant (Felsenstein 2004: 145), a viewpoint previously articulated by O’Hara:

> During the early years of cladistics, in the 1960s and 1970s, the mismatch between cladistically reconstructed phylogenies and traditional classifications gave rise to a great deal of controversy over the relation between trees and classifications, but this controversy has today almost completely withered away. *This is because more and more systematists have come to realize that in the evolutionary world the notion of classification as an object of systematics can be largely dispensed with*. The point of systematics in an evolutionary world ought not to be the construction of classes, but the reconstruction of history (De Queiroz 1988, O’Hara 1988[a]), and the analogy of systematics to classification is in fact a relict of the pre-evolutionary period, when living diversity was viewed ahistorically. (O’Hara 1994:14, italics ours)

O’Hara’s words are a puzzling and idiosyncratic summary of recent history: *Classification as an object of systematics can be largely dispensed with*. Consider Norman Platnick’s (2001: 5) words: “Back in the early days of the cladistics wars, it was fashionable in some circles to see classification as a serious problem for phylogeneticists. The problem, of course, was imaginary.”

From other remarks in Felsenstein’s book *Inferring Phylogenies* (2004), one may understand him to be a *good* evolutionist, maybe even a *good* Darwinian (Felsenstein 1986), certainly a committed population geneticist (Slatkin 1995). It is odd, then, that Felsenstein understands cladistic analysis as *bad* (or at least not that good) and cladistic classification as *good*, while fellow evolutionist and Darwinian Ernst Mayr understands cladistic analysis as *good* but cladistic classification as *bad*. As Felsenstein understands cladistics in its narrow sense (that is, as a parsimony *algorithm*), one might interpret his words as a critique of that parsimony algorithm, rather than of Cladistics. Mayr understood cladistic classification as *bad* primarily because he could perhaps sense what might become of phylogeny (as traditionally conceived) should paraphyletic groups be eliminated (Nelson 1989a)—groups commonly thought to be equated with ancestors (see below). Yet, an even stranger viewpoint comes from other evolutionists and Darwinians. The Phylocodists (De Queiroz 1988, De Queiroz & Gauthier 1992) have spent some considerable time promoting the notion that biological nomenclature and classification requires reform (even when some claim its *irrelevancy;* see O’Hara’s remarks above), and they understand cladistic classification as *good*—but for very peculiar reasons (see critiques in *Botanical Review* 69[1]). Thus, Phylocodists (De Queiroz 1988), Gradists (Mayr 1974, Mayr & Bock 2002), and Numerical Systematists (and whatever O’Hara might be) all see themselves as evolutionists and most probably Darwinians, yet their views conflict in an absolute sense—as well as conflicting with each other (De Queiroz 1988, O’Hara 1988).

Something is evidently wrong.

## 1.2 Cladistic Analysis

Classification to one side (for the moment), phylogenetics is now a vastly complex and, apparently, mathematical subject (Semple & Steel 2003, Felsenstein 2004, Hall 2004, Gascuel 2005). It seems appropriate to revisit some basic tenets, to try and recover what qualitative analysis is being lost in the current haste to refine "techniques".

### *1.2.1 Cladograms and Trees*

> "The arguments between the two schools of phylogeny reconstruction—cladistics and evolutionary taxonomy—are most obvious in the comparison of cladograms and trees." (Forey 1982: 119)

Consider the branching diagram in Figure 1.2.

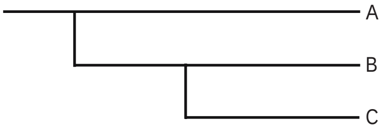

**Fig. 1.2** Branching diagram—A(BC)

What phylogenetic statements are possible for relationships among taxa A, B, and C?

1. A is ancestral to B.
2. B is ancestral to C.
3. A is ancestral to C.
4. C is ancestral to B.

Each of these alternatives can be represented with a further diagram (Figure 1.3).

**Fig. 1.3** Linear arrangement of character [states], for options 1–4 above

Alternatively,

1. A is sister species to C, which is ancestral to B.
2. A is sister species to B. which is ancestral to C.
3. A is ancestral to both B and C.

Each of these alternatives can be represented with a diagram (Figure 1.4).

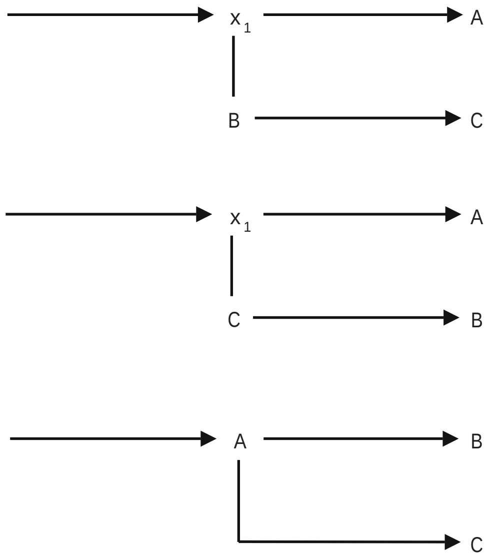

**Fig. 1.4** Branching diagrams for options 1–3 above

In spite of these various kinds of explanation of phylogenetic relationships among taxa A, B, and C, one general statement will suffice:

1. B and C are more closely related to each other than they are to A.

This statement is equivalent to one diagram, the cladogram (Figure 1.2). The scheme is summarised in Figure 1.5.

Thus, phylogenetic trees and cladograms differ in that the former is based on various speculations concerning the direct ancestral-descendant relationship in an

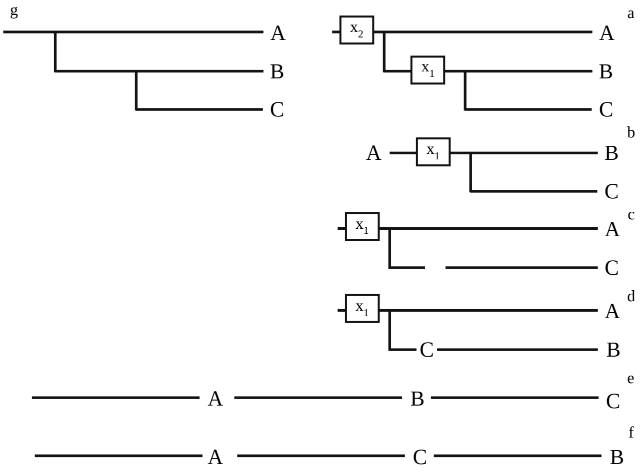

**Fig. 1.5** Cladograms and trees. Trees a–f derived from Cladogram g; see Forey (1992: 125, Fig. 8.1)

effort to produce a "complete" phylogenetic tree—"complete" in the sense that as many ancestor-descendant relationships as possible are recognised, while the cladogram simply describes a general statement of relationship. In spite of any similarity of appearance, it is vital to grasp the fact that phylogenetic trees and cladograms are radically different.

It may be that the similarity in appearance of phylogenetic trees and cladograms has been the major cause for misleading interpretations (see below). It is of significance that because they are both branching diagrams they have nodes at the junction between two or more closely related taxa. Nodes on phylogenetic trees are often said to represent an ancestor, hypothetical or otherwise, or a character-state change (or complex) that relates particular transformation series, yielding the ancestral characters of the ancestral taxa, real or hypothetical.

That nodes and their meaning are significant relates to another issue discussed in further detail later: paraphyly. Paraphyly might be thought of as a consequence of "tree" thinking. Thus, an assumed lineage (ghost lineage, Norell 1993) traced through stratigraphic time with a sequence of fossils, for example, such as the now much discredited lineage sequence of horses, beginning in the Eocene with *Hyperion*, is based on a linear transformation of characters dictated primarily by their stratigraphic position (Figure 1.6).

While such schemes are rarely produced today to represent the phylogenetic history of any organism, there are many such trees published that purport to identify ancestral characters (or their states) at the nodes of the trees, as if Richard Owen's archetype (Chapter 9) might now spring to life via the nodes of phylogenetic trees rather than through fossil remains.

From the perspective of a cladogram, the single node in A(BC), for example, represents the relationship between B and C when compared to A. That node derives

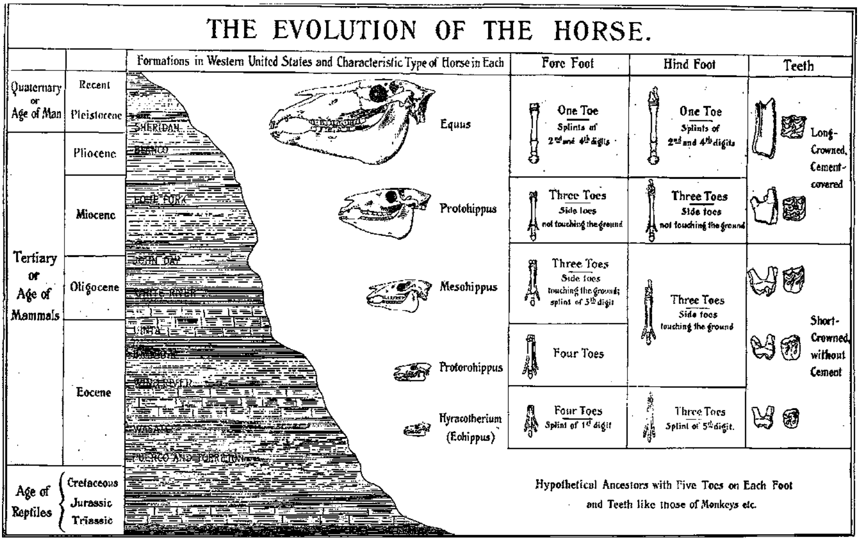

**Fig. 1.6** "The Evolution of the Horse", after Matthew (1913: 36)

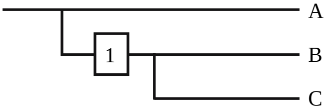

**Fig. 1.7** Branching diagram with node

its support from evidence, supplied either by a morphological character (state 1, relative to 0) or a molecular character (nucleotide A at position 616 on Cytochrome *c* relative to nucleotide G). Thus, node 1 in the cladogram in Figure 1.7 can be read as 0(11) or G(AA), directly relating evidence to node—or even, directly relating taxon to homology (see later).

### *1.2.2 Cladograms and Evidence*

In a retrospective on developments in cladistics, Patterson wrote:

> Much of the hundreds of pages on systematic theory and method published by morphologists during the last 20 years is embroidery on and exploration of Brundin's [1968] message; or more precisely, given the sister group as the target, it explores the concept of synapomorphy, the relation that should find the target. (Patterson 1989: 472)

Brundin's message was to "search for the sister group" (Brundin 1968); Patterson's message was to "explore the concept of synapomorphy, the relation that should find the target." Beyond these simple statements lay a welter of baggage. The topic of how to implement Hennig's ideas contributed to the "hundreds of pages on systematic theory", but one might see these contributions as part of the numerical taxonomy literature, or the phenetic experiment, the "school" that originally advocated ignoring phylogeny altogether as, according to them, such things could not be discovered (see Felsenstein 2004: 123).

Cladistic analysis may be simply stated: "... interpret the distribution of homologies parsimoniously" (Patterson 1981a: 448, Patterson 1983a: 19, Platnick 1982: 283).

That phrase begs two questions:

1. What are homologies?
2. What is parsimony?

We address these questions later (Chapters 7 & 8), but first we present a short account of the analytical part of Cladistics. Here we are concerned with the analysis of cladograms rather than trees, first called **component analysis** by Nelson & Platnick (1981; see Nelson 1979) (Chapter 11).

While Nelson & Platnick's (1981) book may be interpreted as a discourse on the general principles of Cladistics, relatively little attention has been paid to the methodology they discussed, with the possible exceptions of Rod Page's work on consensus trees (Page 1987) and biogeography (Page 1990a, 1990b), Nobihira Minaka's studies on the logic underlying tree diagrams (Minaka 1987, 1990, 1997), and Sneath's book review (Sneath 1982).

Branching diagrams (cladograms) can be understood in terms of their "parts", the nodes and tips. Nelson (1979; Nelson & Platnick 1981) refers to the tips of a cladogram as **terms** and the nodes of a cladogram as **components**, hence component analysis refers to the analysis of branching diagrams. A component may be thought of in the same way as "synapomorphy" or "homology"; as support for a particular node on a particular branching diagram. Nelson & Platnick took a more general approach to the definition of synapomorphy, calling it "a unit of resolution" (Nelson & Platnick 1981: 142) and defining a component as "a statement of general synapomorphy" (1981: 169) and "a unit of information" (1981: 169).

**Synapomorphy** is the evidence that support nodes on a cladogram. A cladogram may thus be understood in terms of nodes with groups of characters equivalent to components and "statements of general synapomorphy".

A component may be understood as analogous to the "evolutionary hypotheses" of compatibility analyses (Estabrook et al. 1976); that is, "single character" branching diagrams. Likewise, homology statements, as sets and subsets, might also be seen as branching diagrams (Patterson 1982a; see Chapters 7 & 8). Thus, it is, and was, possible to see component analysis (and compatibility analysis) as consensus techniques, methods designed to find commonality among a set of different branching diagrams. And indeed that was the case:

> Its [component analysis] major weakness [and *fatal flaw*] is that it relies on consensus techniques. (italics ours; Wiley 1988: 524; see also Brooks & McLennan 1991: 196)

The claim that component analysis was "fatally flawed" and has no connection with parsimony was refuted by Page (1990a). However, most critiques of component analysis were made within the study of biogeography. It seemed that few have considered any analytical connection between biogeography and systematics in the context of component analysis (with the exception of Morse & White 1979).

In a lengthy review of Nelson & Platnick's (1981) book, Sneath discussed the construction of cladograms:

> One inexplicable omission is that there is no discussion of two well known, cogent strategies for reconstructing phylogenies. The first is the construction of trees on the basis of minimum evolutionary change (minimum-length trees, e.g., Wagner trees). The second is construction of trees showing minimum incompatibilities between characters (in the sense of fewer parallel or backward changes, e.g., character compatibility trees). The second method is close conceptually to parsimony of conflicting synapomorphies. (Sneath 1982: 210)

Sneath recognised that the methodology presented in Nelson & Platnick was not that of the more conventionally accepted version of cladistic parsimony (i.e., parsimony and Wagner trees). Sneath (1982: 211) attempted to render what he understood of the methodology in Nelson & Platnick (1981) into algorithmic form, which he called "the rule of D". The name arose simply because some of the hypothetical data presented in Nelson & Platnick's examples included a problematic fourth taxon 'D'. After discussing two possibilities, Sneath returned to a previous suggestion that there might indeed be "reversals" present in the data (e.g., true synapomorphies might mislead), which in turn led him once again back to the issue of whether character states should have been considered "primitive" or "derived" in the first place:

> . . . should one have been searching all along for the most parsimonious trees irrespective of judgements primitive or derived states? This last strategy . . . implies that one should use techniques such as that of Camin and Sokal (1965) and others derived from it. (Sneath 1982: 212)

By “others derived from it [Camin and Sokal]”, one assumes Sneath was referring to Wagner parsimony algorithms. That component analysis was understood to be problematic for characters and taxa stemmed from the view that binary matrices and binary data were the only source for deriving the cladograms. In Chapter 11 we challenge that view and present a way forward for component analysis.

## 1.3 Cladistic Classification

### *1.3.1 Cladistic Classification and Phylogeny*

Cladograms and trees relate directly to classification, in spite of those who have attempted to speak out against any consistency (Brummitt 1996, 1997, 2002). Two examples are provided here. The first was published by Newell in 1956 and discussed in Nelson & Platnick (1981: 144–148, Newell 1956). The second was published by Daniele Rosa (1918, 1931) and discussed in Nelson et al. (2003).

*Example 1: Figure 1.8a after Newell (1956: 68, Fig. 2a*)—The diagram Newell published is said to represent “an assumed real history of a group of species evolving through time (vertical axis), known from samples of specimens at four different time levels (A, B, C, D)” (Newell 1956: 68, Nelson & Platnick 1981: 144, plate legend for Figure 2.77). This diagram is similar to many published at that time purporting to represent a “real history of a group of species” (Lam 1936; see also Cavalier-Smith 1998: Figs. 1.1 and 2), the kind of representation favoured by many palaeontologists during the mid-1950s to the mid-1960s.

If the relationships of species 1–13 could be accurately determined with synapomorphies and represented as a cladogram, it would be as in Figure 1.8.b.

The details of Figure 1.8.b suggest that evidence is available for each node supporting terminal taxa distal to it. Thus, for node *g* there are synapomorphies for

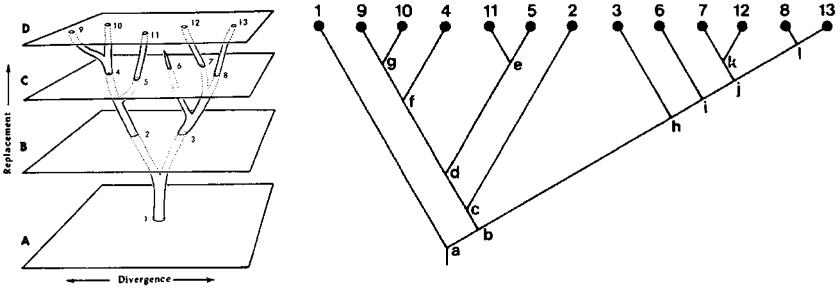

**Fig. 1.8** a. After Newell (1956: 68, Fig. 2), reprinted with permission of the Systematics Association, London; b. After Nelson & Platnick (1981: 144, Fig. 2.78), reprinted with permission of Gareth Nelson and Norman Platnick

species 9 and 10, for node *f* there are synapomorphies for species 4, 9, and 10, and so on. To understand the diagram in Figure 1.8a as a phylogenetic tree rather than a cladogram, the branch points (nodes) can be interpreted as speciation events. A speciation event implies a process—that something has occurred at node *f* to give rise to species 9 and 10. The idea might be captured in the notion that their ancestor resides at node *f*. If such an ancestor is unknown, it can be postulated as (or assumed to be) a hypothetical entity. If known—and Figure 1.8a suggests the ancestor is species 4—then it might be better placed at node *f* rather than as sister to both 9 and 10. Even so, from a classificatory sense, how might one group these species? It seems almost intuitive that there would be a group including species 9, 10, and ancestral species 4. This may be arrived at regardless of what is or is not known of species 4 and its true phylogenetic relationship to species 9 and 10. Thus, irrespective of the number and kind of branches and the status of the species (ancestor or descendant), the evidence that relates the three (their synapomorphies) is equal to the group itself (4 + 9 + 10). Sneath & Sokal (1973) discuss a similar situation but present conflicting classifications. The only reason their classifications conflict is the struggle they clearly have with placing a known ancestor—a struggle of evidently misplaced effort (Nelson & Platnick 1981: 151). One might understand contemporary comment (Brummitt 2003) more readily when views such as the following are kept in mind:

> The cladogram, in effect, satisfies the concern about futile theorizing . . . [as most of that effort] belongs to the three-step process of deriving a tree from a cladogram. (Nelson & Platnick 1981: 151)

*Example 2: Figure 1.9 after Rosa (1918: 137–138, 1931: 174–175, reproduced in Croizat 1976: 825, Lam. 72, Fig. 165A; Nelson & Platnick 1981:325, Fig. 4.34; Luzzatto et al. 1997: Fig. 2; Luzzatto et al. 2000: Fig. 2; Vergata 2001: 239–240 and Nelson et al. 2003:296)* —Rosa's tree "represents the connections of affinity between the species of a group, such as they would be if the species were the result of dichotomous speciation. . . . Having before us 32 terminal species, represented by the black dots above, we would be able to make four groups (such as genera): A, B, C, D" (Rosa 1918: 138–139; translated in Nelson et al. 2003: 295). Rosa's tree represents a particular kind of "phylogenetic" tree, different to that of Newell's. Rosa's tree is similar to one illustrated by Hennig (1966a: 214, Fig. 64; reproduced in Croizat 1976: 825, lam. 72, Fig. 165B) and, more recently, Brummitt (2002: Fig. 1.1).

Rosa explained:

> It is clear that, even without paleontological knowledge of the connections, an adequate knowledge of the morphology of these species would suffice to indicate that genus B is more closely related to genus A than to genus C; and that, before grouping the 32 species into four genera, it would be necessary to group them into two 'supergenera' or subfamilies: AB and CD. And within each genus it would be possible also to recognize subgenera and even smaller groups of more closely related species.
>
> If this scheme corresponds to reality, one may conclude that the distinction between groups of equal taxonomic rank cannot be arbitrary; and also that the distinctions are not caused by gaps in the system, gaps produced by extinction. Even in the absence of extinction, the distinctions would be quite clear. And while it might be arbitrary to consider group A a genus, no good systematist would ever combine some species of group C with AB, and the other species of group C with D. (Rosa 1918: 138–139)

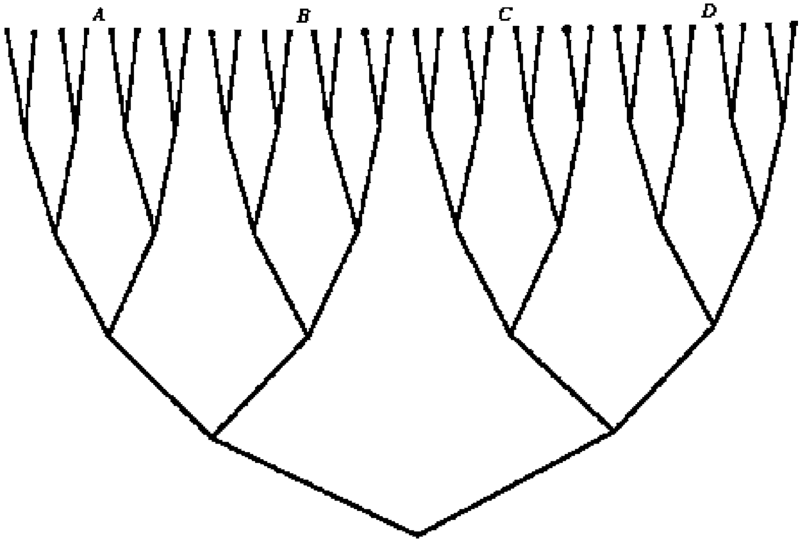

**Fig. 1.9** After Rosa (1918: 138, 1931: 174)

Thus, even an alternative phylogenetic tree, with hypothetical instead of real ancestors (Newell's species 4, 9, and 10), exact classification is possible, if not obvious.

One might imagine further, even more complex scenarios of species evolution, further complex trees, even those not even treelike but "Rings of Life" (Figure 1.10; after Rivera & Lake 2004: Fig. 3) or "networks" (Figure 1.10b; Doolittle 1999). Classification in each case becomes relatively obvious, leaving the impression that whatever "phylogeny" is supposed to add, it seems not to amount to much in terms of enhancing our understanding of the relationships among taxa in any greater detail.

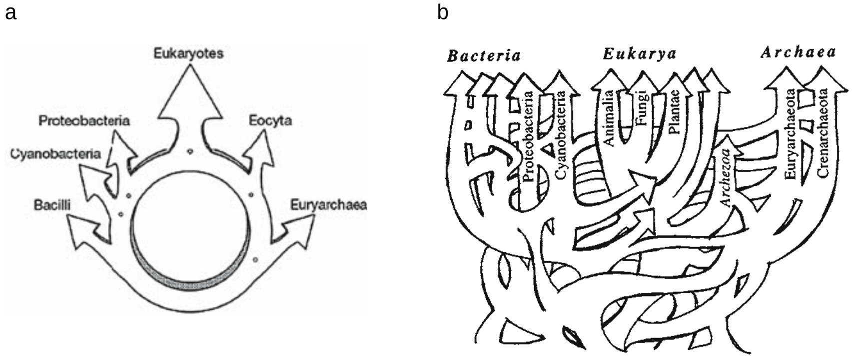

**Fig. 1.10** a. After Rivera & Lake (2004, reprinted with permission: Fig. 3); b. After Doolittle (1999, reprinted with permission)

### *1.3.2 Cladistic Classification and the Perils of Paraphyly*

> "What do invertebrates, apes, and barbarians have in common? … Invertebrates are non-vertebrate animals; apes, non-human anthropoids; barbarians, non-Greek humans, whose diverse languages, to the ears of the ancient Greeks, all sounded like "bar-bar-bar"—even perhaps like the bleating of sheep." (Nelson 2007)

Groups in cladograms that share congruent apomorphic character-states are called "natural" or **monophyletic**. In cases where non-monophyly occurs, certain "groups" are considered either **paraphyletic** (Hennig 1962: 35; see Schmitt 2001: 331) or **polyphyletic** (Hennig 1950) (Figure 1.11).

Paraphyletic groups occur if a part of an assumed monophyletic group is more closely related to another group (Nelson 1971a: 472). Polyphyletic groups occur when taxa either closely or distantly related are scattered throughout an assumed monophyletic group (Nelson 1971a: 472). Hennig first referred to paraphyly in a footnote:

> Diese handliche Bezeichnung habe ich kürzlich für die auf Symplesiomorphie begründeten Gruppenbildungen … eingeführt. (Hennig 1962: 35, footnote 1; "This handy designation I use for groups based by symplesiomorphy", our translation)

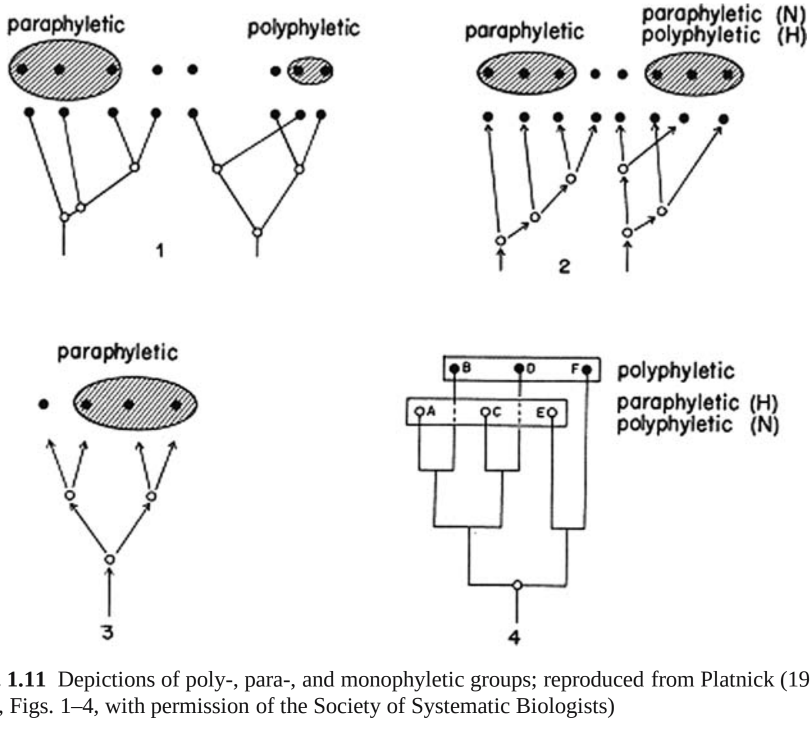

**Fig. 1.11** Depictions of poly-, para-, and monophyletic groups; reproduced from Platnick (1977a: 196, Figs. 1–4, with permission of the Society of Systematic Biologists)

At first, then, it was understood that paraphyletic groups resulted from grouping by symplesiomorphy (Hennig 1962, 1965), a synapomorphy shared with a more remote ancestor. Logically, paraphyletic groups result from character-states in a “group” that are “uniquely derived but reversed” (Farris 1974: 554). Polyphyletic groups, however, have diverse relationships, attributed to the existence of a multitude of different ancestors with no direct relationship to homology (Hennig 1950, 1966). Paraphyletic and polyphyletic groups are *explanations* for collections of terminals that have non-congruent homologies; paraphyletic groups are non-groups or “timeless abstractions” (Brundin 1972: 110; Patterson 1978a: 220; Patterson 2002: 19; also see Ebach & Williams, 2004). Nevertheless, paraphyletic and polyphyletic groups have been *given* historical explanations (Hennig 1950, 1962). The traditional viewpoint (and one that, rather remarkably, seems to be gaining favour all over again) is that paraphyletic groups are, or nearly are, equivalent to ancestors. If paraphyletic groups are non-groups, and non-groups are ancestors, then such entities can play no part in classification, are impossible to discover, and have no relevance beyond giving a measure of reality to a particular theory of origin, whatever that theory might be. Nevertheless, it is still common to read of non-birds giving rise to birds, non-humans giving rise to humans (Nelson 1989b, Nelson et al. 2003) in the belief that “Evolution is paraphyly all the way” (Brummitt 2002: 40; see also Cavalier-Smith 1998: 210, Figs. 1.1 and 1.2; cf. Nelson et al. 2003, Ebach & Williams 2004, Reif 2005). If “Evolution is paraphyly all the way”, then there is a real problem to be addressed. That problem may relate to either “evolution” itself or “paraphyly”. We suggest it resides with the latter, the non-existence of paraphyletic groups, these non-groups as ancestors and the lack of credibility given to the almost obvious notion that “from nothing, nothing comes” (Nelson et al. 2003: 297). The study of evolution need not be pursued only by a search for the origin of things—especially from non-things (Chapter 13).

Paraphyly and polyphyly are explanations for non-groupings, or more accurately, excuses for the absence of monophyly. Therefore, the contradictory terms “paraphyletic groups” and “polyphyletic groups” are both more accurately and simply termed “non-monophyletic” (Ebach & Williams 2004).

## 1.4 Overview

We noted that a few decades ago three different schools of systematics were recognised: Evolutionary Systematics (Gradistics), Phenetics and Cladistics. Nelson & Platnick (1984) suggested an alternative characterisation. As Evolutionary Systematics (Gradistics) and Phenetics shared a desire to retain paraphyletic groups, both were best characterised as Darwinian systematics, in the sense that they retained a necessity for non-groups, so often associated with ancestors (Patterson 1977):

> ... from the phenetic standpoint ... such groups are necessary to depict nature in its static aspect; from the evolutionary standpoint ... such groups are necessary to depict nature in its dynamic, or transformational, aspect. (Nelson & Platnick 1984: 156)

Nevertheless, the defence of Darwinian systematics, however conceived, continues to garner controversy (Nelson 1974, Padian 1999, Mayr & Bock 2002, Padian 2004, Ghiselin 2004). Is it fair, or indeed just, to name the approach to classification that continues to include non-groups (paraphyletic groups) Darwinian? Some would answer "no" (e.g., De Queiroz 1988). Rather than debate the issue afresh, we cite a passage from Agassiz that might help focus further discussion:

> It is not that I hold Darwin himself responsible for these troublesome consequences. In the different works of his pen, he never made allusion to the importance that his ideas could have for the point of view of classification. It is his henchmen who took hold of his theories in order to transform zoological taxonomy. The different incarnations of that influence is felt on the general conceptions of Palaeontology and more directly on those of Zoology. . . . (Agassiz 1869: 375; our translation)[8]

Agassiz was referring to Ernst Haeckel, Darwin's first henchman (Williams 2006 [2007]). Yet the point seems clear even today, that it is Darwin's latter-day henchmen (De Queiroz 1988, Mayr & Bock 2002) who have taken hold of his theories in order to transform zoological taxonomy, even when the generations are separated and differ in their attempted transformation (De Queiroz 1988, Mayr & Bock 2002; cf. Wheeler 2004). Cladistics was one attempt to check these excesses (or abuses) of classificatory illusions.

We also noted that any and every tree and any and every classification have a hierarchical component best referred to as its **Cladistic Parameter** (Nelson 1979: 12; Nelson & Platnick 1981: 318–319). Such a parameter excludes non-groups, those that are polyphyletic and paraphyletic. We suggest that once coupled with evidence that offers support for the cladistic parameter, one might reasonably explore the notion of a **unit of systematics**. We also suggest that once evidence is coupled with the idea of a cladistic parameter, it is relatively easy to appreciate that homology (evidence) = taxon (cladistic parameter)—and matters of both classification and phylogeny are thereby simplified. Thus, if

homology = evidence

and

taxon = the Cladistic Parameter,

then, evidence, the cladistic parameter and the unit of systematics, may equate directly with the notion of relationship, most economically summarised as

A and B are more closely related to each other than they are to C.

---

[8] The extract is taken from a chapter, one of three, Agassiz added to the 1869 French translation of his *Essay on Classification*, under the title of *De l'espèce et de la Classification en Zoologie* (Agassiz 1869).This new chapter outlines many of the difficulties Agassiz had with the notion of evolution as it affected classification (see Morris 1997).

**Cladistics** (with a capital C) is the study of relationships, those pertaining to taxa and the areas they occupy. Such a viewpoint sees the study of evolution as the search for meaningful, repeated relationships rather than the origin of this or that "thing". The rest of this book explores these issues further.

# Chapter 2
# Systematics as Problem-Solving

## 2.1 The Problem

Systematics is primarily concerned with problem solving. This might seem an obvious statement, yet the majority of those interested in systematics and phylogeny approach the subject as being concerned with “inferences ”, “reconstructions”, or “estimations”, as captured in the title of the most comprehensive systematics text available, *Inferring Phylogenies* (Felsenstein 2004). To treat systematics as addressing a problem or set of problems, rather than an exercise in “reconstruction” or “inference”, admits to the possibly of testable solutions and offers a way to *evaluate* data such that they can be considered either relevant or irrelevant. It admits to the possibility of discovering taxonomic or geographic relationships rather than imposing them. The general problem may be phrased as follows: “What are the interrelationships among organisms?"

## 2.2 The Solutions

For any particular problem, the number of terminal taxa (a collection of organisms grouped together, either species or groups of species) is specified from the outset; and it is their interrelationships that are to be discovered. For any specified number of terminal taxa, there are a finite number of possible solutions when results are presented as hierarchical branching diagrams or classifications. That a hierarchical branching diagram is utilised has significance only inasmuch as it is the graphic representation of a specific relation or set of relationships, which is one way of depicting the Cladistic Parameter. Any solution will suggest that, among the taxa being considered, some are more closely related to each other than they are to the remainder, thus creating new taxa corresponding to the newly discovered node uniting them. For example, among four taxa the total number of possible solutions is 26 (Table 2.1). Of those 26, 15 are fully resolved (all inter-relationships are solved—two nodes are identified), 10 partially resolved (only some inter-relationships are solved—one node is identified), and 1 completely unresolved (no inter-relationships are solved—which is not really a solution) (Table 2.1). Consider the first solution

**Table 2.1** All 26 solutions (cladograms) for a four-taxon (A–D) problem: 15 two-node solutions, 10 one-node solutions, and one unresolved “solution”

| Two-Node Cladograms | One-Node Cladograms | | Unresolved Cladogram |
|---|---|---|---|
| A(B(CD)) | AB(CD) | A(BCD) | ABCD |
| A(D(BC)) | AC(BD) | B(ACD) | |
| A(C(BD)) | AD(BC) | C(ABD) | |
| B(D(AC)) | BC(AD) | D(ABC) | |
| B(A(CD)) | BD(AC) | | |
| B(C(AD)) | CD(AB) | | |
| C(D(AB)) | | | |
| C(B(AD)) | | | |
| C(A(BD)) | | | |
| D(C(AB)) | | | |
| D(B(AC)) | | | |
| D(A(BC)) | | | |
| (CD)(AB) | | | |
| (AC)(BD) | | | |
| (AD)(BC) | | | |

in column 1, Table 2.1: A(B(CD)). The notation A(B(CD)) can be represented as a branching diagram (Figure 2.1). The diagram has two nodes, one uniting C and D (Figure 2.1a, node 2), the other uniting B, C, and D (Figure 2.1a, node 1). Each node might be named in a taxonomic hierarchy, such that BCD is a genus and CD a subgenus. Reference below to branching diagrams, hierarchical classifications, solutions, or cladograms all share the same meaning as a summary of relationships.

For a four-taxon problem, any of the solutions in Table 2.1 are possible, inasmuch as the nodes from each union receive support from relevant data. In the

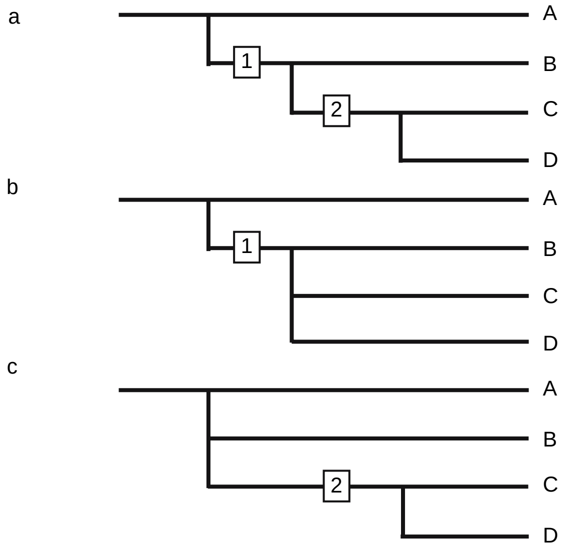

**Fig. 2.1** a–c: Cladograms of four taxa. (a) A–D with two nodes, BCD and CD; (b) A–D with one node, BCD; (c) A–D with one node, CD

case of a four-taxon problem (A–D), if all available data support only groups CD and BCD, then the problem is relatively trivial (Figure 2.1a)—the only creditable solution being A(B(CD)). Finding solutions becomes more complex when data conflict rather than simply accumulate—that is, when data support alternative solutions (see Chapter 11). Mere accumulation of data—no matter how large that accumulation might be—is insignificant if it all points to the same solution. We discuss conflicting data in more detail below, but at present we focus only on non-conflicting data.

Some cladograms in Table 2.1 might be considered partially resolved (Table 2.1, columns 2 and 3). For example, cladogram A(BCD) has one node resolved, leaving the possibility of further resolution (Figure 2.1b, node 1). The addition of more non-conflicting data may result in a second node being resolved. There are three possibilities:

| A(BCD) |
|---|
| 1 A(B(CD)) |
| 2 A(C(BD)) |
| 3 A(D(BC)) |

These possibilities are achieved by finding support for the extra node contained within BCD; that is, any of the three smaller groups CD, BD, and BC. These smaller groups nest within the larger group, BCD.

The cladogram AB(CD) also has one node resolved, leaving the possibility of further resolution (Figure 2.1c, node 2). Addition of more non-conflicting data may result in another node being resolved. There are three possibilities:

| AB(CD) |
|---|
| 1 A(B(CD)) |
| 2 B(A(CD)) |
| 3 (AB)(CD) |

This does not exhaust all possible solutions. The CD group may be retained but can *include* within either A or B providing a further four solutions:

| AB(CD) |
|---|
| 4 A(C(BD)) |
| 5 A(D(BC)) |
| 6 B(C(AD)) |
| 7 B(D(AC)) |

To allow for these possibilities requires some flexibility. If the cladogram AB(CD) is considered to be two separate statements of *relationship*, rather than a group, then it remains possible that only one is found to be true. The two separate statements of relationships are A(CD) and B(CD). If both A(CD) and B(CD) are indeed true—that is, receive support from further non-conflicting data, then the only possible overall solution is AB(CD). If only A(CD) is found to be true, five further solutions are possible:

| A(CD) |
|---|
| 1 A(B(CD)) |
| 2 B(A(CD)) |
| 3 (AB)(CD) |
| 4 A(C(BD)) |
| 5 A(D(BC)) |

If only B(CD) is found to be true, five further solutions are possible:

| B(CD) |
|---|
| 1 A(B(CD)) |
| 2 B(A(CD)) |
| 3 (AB)(CD) |
| 6 B(C(AD)) |
| 7 B(D(AC)) |

As solutions 1–3 are common to each series, there is a total of seven possible solutions (Table 2.2). In Table 2.2, cladograms 1–3 correspond to what Nelson & Platnick (1980) call **Interpretation 1**, based on the interpretation that C and D are more closely related to each other than either is to A or B (Nelson & Platnick 1980). That is, C + D remain each other's closest relatives. Interpretation 1 is analogous to **Assumption 1** in biogeographical problems (Platnick 1981, Nelson & Platnick 1981, Humphries & Parenti 1999). Cladograms 1–7 correspond to what Nelson & Platnick (1980) called **Interpretation 2**, based on the assumption that C and D are more closely related to each other than *either of them* is to A and/or B (Nelson & Platnick 1980). Interpretation 2 is analogous to **Assumption 2** in biogeographic problems (Platnick 1981, Nelson & Platnick 1981, Humphries & Parenti 1999).

## 2.3 Discovering Solutions

Taxonomic problems change as data accumulate and additional terminal taxa become relevant. In spite of arguments to the contrary (e.g., Graybeal 1998), increasing the number of taxa simply changes the nature of the problem (Platnick 1977b: 440). For example, with one additional taxon, a four-taxon problem with 26 possible solutions becomes a five-taxon problem with 236 possible solutions. With more terminal taxa, the number of solutions increases at an alarming rate (Table 2.3). [1]

If increasing the number of taxa changes only the magnitude of the problem, then progress in systematics is limited to three options:

1. The acquisition of new data (characters)
2. Re-examination of data (characters) already studied
3. Consideration of data (characters) representation

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[1] The mathematical formula for this progression is given in Felsenstein (1978).

**Table 2.2** All possible cladograms for four taxa relative to the cladogram AB(CD). Solutions 1–7 can be found with more non-conflicting data.

| *Character AB(CD)* | |
|---|---|
| **All possible cladograms for four taxa** | **Solution of Nelson & Platnick (1980)** |
| **Two-node trees** | |
| 1.B(A(CD)) | Interpretations 1 & 2 |
| 2.A(B(CD)) | Interpretations 1 & 2 |
| 3.(AB)(CD) | Interpretations 1 & 2 |
| 4.A(D(BC)) | Interpretation 2 |
| 5.A(C(BD)) | Interpretation 2 |
| 6.B(C(AD)) | Interpretation 2 |
| 7.B(D(AC)) | Interpretation 2 |
| 8.C(D(AB)) | |
| 9.C(B(AD)) | |
| 10.C(A(BD)) | |
| 11.D(C(AB)) | |
| 12.D(B(AC)) | |
| 13.D(A(BC)) | |
| 14.(AC)(BD) | |
| 15.(AD)(BC) | |
| **One-node trees** | |
| 16.A(BCD) | |
| 17.B(ACD) | |
| 18.C(ABD) | |
| 19.D(ABC) | |
| 20.AB(CD) | **Original Character** |
| 21.CD(AB) | |
| 22.BD(AC) | |
| 23.BC(AD) | |
| 24.AD(BC) | |
| 25.AC(BD) | |
| 26.(ABCD) | |

**Table 2.3** Relationship between numbers of terminal taxa (T) and numbers of possible cladograms (solutions). Figures given for T = 3 to T = 10

| T | Cladograms |
|---|---|
| 3 | 4 |
| 4 | 26 |
| 5 | 236 |
| 6 | 2,752 |
| 7 | 39,208 |
| 8 | 660,032 |
| 9 | 1,281,892 |
| 10 | 282,137,824 |

These three options exhaust all possibilities (Platnick 1977b, Patterson 1981a). The first option is straightforward. In the last two decades, for example, the primary source of new data has been DNA nucleotides, having a profound effect on studies in phylogeny and classification (Cracraft & Donoghue 2004). Yet systematists working on a wide range of organisms continue to find new and unknown non-molecular character systems (e.g., Smith & Stockley 2005). Regardless of their source, new data are always welcome.

The second option above deals directly with the issue of re-investigating characters already known—or characters assumed to be known—to verify or confirm their internal consistency. Thus, many comparative biologists are occupied with the same question: Is this identified "part" of one organism really the same as that "part" in another organism? A recent example is the "parts" of turtles (Lee 1996, 1997, Rieppel 1996, DeBraga & Rieppel 1997; see Vickaryous & Hall 2006). The pectoral girdle of turtles is a highly derived structure among primitive reptiles and turtles. The endochondral shoulder girdle (scapulocoracoid) in primitive reptiles consists of a scapula (lacking anterior processes) and two discrete coracoids, anterior and posterior (Figure 2.2). In Pareiasaurs the scapulocoracoid consists of a scapula with an anterior, acromion-like process, and two discrete corcoids (anterior and posterior). The acromion-like process has been interpreted as a "flange of scapula". In turtles, there is a well-developed flange to the scapula. There are conflicting propositions of "sameness" concerning the "flange of scapula": Either the flange is understood to be a modified anterior coracoid, hence the flange of the scapula in Pareiasaurs is a unique character (an autapomorphy) (Lee 1998), or the anterior coracoid has been lost in turtles and the flanges in Pareiasaurs and turtles are really the "same" (homologous and synapomorphic) (Rieppel 1996). Each interpretation may produce different relationships (Lee 1996, 1998, Rieppel 1996).

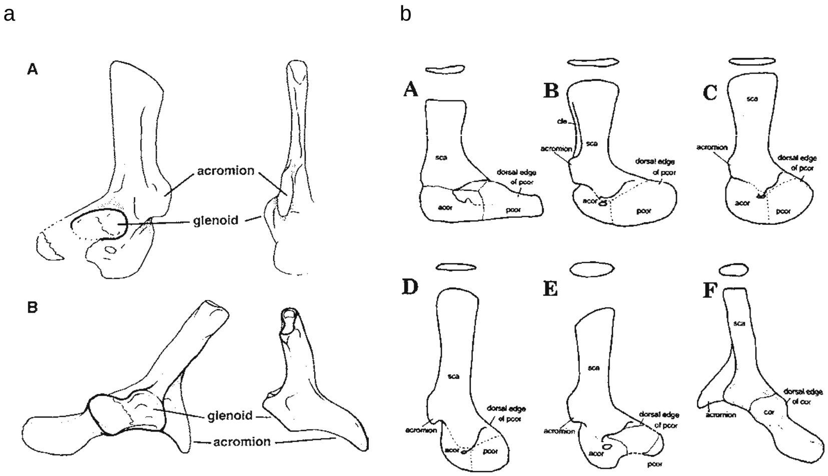

**Fig. 2.2** Two illustrations of the turtle shoulder girdle. (a) From Lee (1997: 234, Fig. 12); (b) from De Braga & Rieppel (1997: 303, Fig. 2), reproduced with permission of Blackwell Publishing.

Identifying the shared "parts" of organisms remains very much a central task of systematic investigations.[2] Resolution of such issues leads to a greater understanding of the organisms in question. The "parts", when identified, are usually referred to as **homologues**. Comparison of various parts of organisms is often understood as determining their homology. Below we develop the notion that the homologue taken alone is the part, while **homology** is the *relationship* derived from the parts. This distinction, only recently appreciated, is of central significance. It is directly linked to the third possibility above, that of data representation.

The notion that homology is discovered had led some systematists, primarily those interested in numerical methods, to suggest a fourth option for progress:

4. Examination of the method to discover "congruent" distribution of characters

Here we might consider Felsenstein's comment that "… statistical, computational, and algorithmic work on them [phylogenetic trees] is barely 40 years old" (Felsenstein 2004: xix). Remarkably, that 40 years has not produced a consensus—nor even attempted to—or even found agreement concerning what might best be achieved from "statistical, computational, and algorithmic work". Felsenstein's book is a good example, as he suggests no preference for the very many methods he summarises, leaving the reader to ponder the general usefulness of these past 40 years' endeavour. Still, of methods there are plenty, spawning an industry that shows no sign of abating—again, the general idea seems to be that the more methods available, the better the chance of discovering … well, discovering what? This question is something we concern ourselves with below.

Homology is considered indispensable to systematic enquiry and is understood as "…the most important principle in comparative biology" (Bock 1974: 386, Patterson 1982a: 22). Be that as it may, we believe that the following question remains unanswered, or at least has not hitherto been fully articulated. Relative to the Cladistic Parameter, is there a "unit" of classification or a "unit" of phylogeny, derivable from our understanding of homologues (the parts of organisms) and, ultimately, of homology (their relationship)?

The idea that there might be a basic "unit" for classification (and phylogeny) will be either appealing or irrelevant, depending on one's point of view (cf. Jardine 1969a: 44, Colless 1972). To offer some focus on the formation of this point of view, we first provide a historical account of the archetype (Ebach 2005, Chapter 3), exploring a concept that has engendered much discussion but little clarity. We then discuss the development of the concept of homology to illustrate that, as we understand the issue, there always were **two** central concepts in comparative biology, one regarding "homologues", the other "homology". That the two concepts have become inextricably intertwined with each other over the last 150 years is significant, as we shall demonstrate (Williams 2004).

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[2] A major source of concern in molecular systematics is their alignment, bringing the sequences of nucleotides into line with each other. In one sense, this operation is the same as that which morphologists regularly use. Any two sequences, if there are mismatches, differ in certain areas and their alignment is not at all straightforward.

# Chapter 3
# The Archetype

## 3.1 The Dynamic Organism: *Bildung*

“Morphology”, a term coined by Johan Wolfgang von Goethe (1749–1832), “… may be said to include the principles of structured form and the formation and transformation of organic bodies … it arranges them, sometimes in groups and sometimes in sequence, according to the forms that are sought out and recognized” (Goethe 1995: 57, 1999b). Morphology, then, is the study of living form, the interactions of its parts, forming not only the basis of comparative biology but also the foundations of systematics and biogeography. Morphology explores the concept of form. The type or *gestalt* is the *morphotype* (Zangerl 1948) on which classifications are ultimately based. One specimen, or in cases of poor preservation (fossil or Recent) several specimens, is used to “define” the particular taxon. The *gestalt* is simply the morphological features that characterise the taxon in question. Any variations—colour, size, sex—are auxiliary and added on to the description of the type as and when such are discovered. The concept of a type is to provide a general example of the *gestalt* of the taxon to which all other taxa are compared. For Goethe, the *gestalt* was a static object and not a meaningful representation of form (Stephenson 1995).

Goethe proposed a means by which to experience form. The *gestalt* was too fixed—it did not include developmental, behavioural, or any other characteristics that the organism displayed during its lifetime. For Goethe, the type was not a true representation of form, but simply a snapshot of the taxon during one phase of its life. Although Goethe’s objections to the type may sound simple, they sparked investigations into a new way with which to generalise form.

Prior to Goethe, the *gestalt* was equated with the *Bauplan* of each organism. All Mammals have hair, certain skeletal structures, and other histological characteristics. Despite this, only one individual would be selected to represent all the different variations of the same form, becoming a “blueprint” for nature and the type its most perfect or prime example. For Goethe, no “perfect” specimen existed. Instead, *all* specimens were perfect and *all* were different manifestations of the same form—the type being just one example. Goethe refuted the teleological argument that one form can be “more perfect” due to its having specialised organs, or “less perfect” because it has organs that appear to fulfil no particular function, thereby becoming dismissed as the remnants of a "higher", more developed form:

> Every creature is its own reason to be. All its parts have a direct effect on one another, a relationship to one another, thereby constantly renewing the circle of life; thus we are justified in considering every animal physiologically perfect. Viewed from within, no part of the animal is a useless or arbitrary product of the formative impulse (as so often thought). (Goethe 1995: 121)

Goethe uses the word *Bildung*, the formation or development of form from the embryo or seed, all the way through to the fully grown adult, including all the pathology and variations.[1] *Bildung* can only reach full recognition within the observer's mind, thus causing several practical problems as well as a philosophical challenge. To appreciate Goethe's concept of type and his goal of seeing the *Bildung* of a form, it is not enough to draw or point to one particular specimen. From the outset, our attention needs to be inclusive of all specimens at all stages along the continuum of their form. Clearly, this presents a practical difficulty for those used to a numerical, quantitative approach to classification. The real challenge, however, is posed by our ability to recognise the inclusion of the taxonomist in the classificatory process. Before Goethe, the taxonomist was viewed as being separate from the taxonomy being undertaken. Indeed, this position persists as being part of the standard criterion for an investigation to be regarded as "properly scientific". In the Cartesian/dualistic world-view inherited from 18th-century science, it is supposed that we are subjective observers, rather than active participants, in relation to various phenomena. The recognition of our inclusion in the experience of the phenomenon breaks down the dualistic barrier between man and nature. Goethe's simple idea of *Bildung* represents a philosophical upheaval that started the field of phenomenology in philosophy and informed the biological science of morphology, later to become the basis of systematics.

## 3.2 The Beginnings of Comparative Biology: Goethe's Archetype

In his essay, "A Fortunate Encounter", Goethe recounts a conversation in 1794 with his acquaintance Friedrich Schiller (1759–1805; Thomas 2004):

> I gave an enthusiastic description of the metamorphosis of plants, and with a few characteristic strokes of the pen I caused a symbolic plant to spring up before his eyes. [. . . ] But when I stopped he shook his head and said, "That is not an observation from experience. That is an idea." (Goethe 1995: 20)[2]

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[1] "But if we look at these *Gestalten*, especially the organic ones, we will discover that nothing in them is permanent, nothing is at rest or defined-everything is in flux of continual motion. This is why German frequently and fittingly makes use of the word *Bildung* [formation] to describe the end product and what is in process of production as well" (Goethe 1995: 63).

[2] From *Fortunate Encounter* (Goethe 1995: 18).

Schiller's reply at the time reflected the dualistic or Kantian view of the world; namely, that "to see" is literally to see things as individual units that follow one another in a linear progression through time. Goethe's major contribution to Natural philosophy is his challenge to this Kantian world-view. Instead, he experienced parts in Nature by observation, treating the individual parts as components of his perception of organismal wholeness.

Goethe could see the "Symbolic Plant", simply by collecting all the parts that he has experienced by observation and categorically describing them as "relationships" rather than as "things". That is, each part is related to the whole in some way. Seeing relationships does not suggest that Goethe could be described as a Lamarckian or Darwinian (or even some precursor evolutionist). Rather, it identifies the *historical* basis of comparative biology as observing and discovering relationships. Natural selection, for example, is a concept that acts as an explanatory rule or mechanism: a thought that Goethe never entertained. The confusion surrounding Goethe's term *Metamorphosis* has led many to suspect that Goethe was indeed entertaining evolutionary ideas. If Goethe's metamorphosis was to mean "evolution" of any kind, it would simply be confined to ontogeny—that is, development. Evidence of this can be found in Goethe's concept of *Metamorphosis*. Natural objects, such as observed in the development of leaves, provide no evidence of the developmental route those changes have taken. *Metamorphosis* is the observation of the different states related by their form (morphology) rather than by their place with a particular series. Goethe's *Metamorphosis* and *Archetype* were the first steps towards the modern concept of homology,[3] which here is termed **urhomology.** This concept was to allow the development of idealistic morphology (Chapter 5) as well as Darwinian thought in the latter half of the 19th century.

## 3.3 Visualizing the Archetype

The brilliance of Goethe's *Morphology* was viewing organisms as whole life cycles, appreciating all developmental forms and variations and how they are related.[4] This viewpoint allowed the exploration of relationships between different organisms. Organisms share particular parts and can therefore be compared, allowing the discovery of natural groups. Comparing shared characteristics was the underlying rationale for Goethe's *Comparative Biology*: to "teach us what parts are common to all animals [organisms], and how these parts differ. The idea must govern the whole—it must abstract the general picture in a genetic way".[5]

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[3] Similar parts related to each other in some way follow a non-linear progression.

[4] "In observing objects of nature, especially those that are alive, we often think the best way of gaining an insight into the relationship between inner nature and the effects they produce is to divide them up into their constituent parts" (Goethe 1995: 63).

[5] "Genetic" may be translated as an "unbroken succession" (Miller in Goethe 1995: 331, footnote 4), that is to "arrange things in order" (Goethe 1995: 73).

Goethe's *Archetype*, however, represents all known individual wholes and their parts.[6] The Archetype theoretically represents the *Urphenomenon* in comparative biology, the progression or "movement" of form, such as the changing shape of an ivy leaf compared to the "movement" of unspecialised to specialised forms within a whole "being" or taxon. The *urphenomenon* is restricted to actual experiences, such as ontogeny, the transgression of darkness into light, an object coming into being and into experience. The archetype, however, serves as the theoretical and historical alternative to the *urphenomenon* in that the changes appear to take place (as in a transformation series or *Umbildung*) but are transitions that cannot be witnessed. Instead, parts can be recognised, such as forearms in different organisms because the form "moves" (in our mind's eye, so to speak) as it "appears" in other individuals.

To Goethe's chagrin, Schiller called his archetype an "idea" rather than an observation based on experience.[7] The archetype, in Goethe's sense, was not an imagined idea, something based on certain principles that can be traced or predicted by models. Rather, it was a concept based on experience (see Brady 1998). Through our experience of objects in the natural world, the observer relates the qualities of the objects. In doing so, the observer is able to recognise the natural world as a series of relationships. Such appreciation of relationships provides the way in which natural objects can be meaningfully distinguished.

Consider the act of comparing a cat with a dog. The observer immediately relates both "objects" and their qualities as "catness" and "dogness". Despite their differences, cats and dogs share many characteristics in common. It is, of course, possible to compare any two objects, listing how they are the same and how they differ. The list gains meaning only when a third object is introduced to compare the qualities of the relationships. Comparing a cat with a dog, for example, requires the introduction of a third creature to act not just as a reference point but also as a standard with which to orient the comparisons. For example, it is meaningful to observe ways in which a cat shares greater relationship with a panther than it does to a dog—the same cat-like forms "appear" in the panther. It is not possible to meaningfully compare a cat with a dog unless another creature is present (or present from previous experience in our mind's eye): "Thus we will not hesitate to suggest a third thing, intermediate between the two…" (Goethe 1995: 124). Goethe—probably for the first time—clearly *articulates* the Cladistic Parameter required to understand relationships (Nelson & Platnick 1981).

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[6] In a letter to Herder written in Naples on May 17, 1787, Goethe writes, "The primordial plant [the archetype] is turning out to be the most marvellous creation in the world, and nature itself will envy me because of it. With this model and the key to it an infinite number of plants can be invented, they do not exist, they *could* exist, and are not mere artistic or poetic shadows and semblances, but have an inner truth and necessity. The same law will be applicable to every other living thing" (Goethe 1989: 256).

[7] Goethe's reply, "Then may I rejoice that I have ideas without knowing it, and can even see them with my own eyes," reflects his inner resentment at the Kantian and Newtonian "idea" of the mechanization of Nature (Brady 1998: 59). This frustration is expressed in his *Theory of Colour*: "In his view mathematics had its place but not in interpreting the Natural world: But the false application of the mathematical method has undoubtedly harmed this science [physics] as well; here and there we will find this fact grudgingly admitted" (Goethe 1995: 272).

The same principle of observing and experiencing organisms by way of relationship also applies to the archetype. It is the complete catalogue of characteristics that makes a plant, a plant and a mammal, a mammal. An archetype may be visualised in our mind's eye or discovered from new specimens, such as fossils. *Archaeopteryx* is a classic example in that it has both "reptilian" and avian characteristics, but is not an archetype. The archetype, although able to be seen in our mind's eye by the known forms that appear in other individuals, does not exist as an individual organism: We make sense of archetype by relating the parts. Therefore, *Archaeopteryx* relates avian wings with other birds that together are part of the "Bird Archetype".

It is therefore not surprising that Schiller calls Goethe's Archetype an idea. Towards the end of the 18th century, natural history was becoming increasingly mechanical under the Cartesian ruse that organisms are no more than machines that serve some universal purpose. The archetype was seen as a disorganised jumble of parts (Arber 1946), no more than Nature's scrap heap, with no purpose and no function, serving only as an idea—and a clumsy one at that. But by relating the archetype to our observations, classification is even more confounding, as *relationship* does not in fact imply a process of succession but rather the appearance and recognition of form within the whole.

## 3.4 Metamorphosis

Goethe's *Metamorphosis* may be translated as "transformation" or "development". Goethe evidently did not mean "metamorphosis" in the evolutionary sense of the transformation of parts of one organism into the parts of another. Jaeger (1814 in Arber 1946) clearly pointed this out: The term "transformation" is symbolic, a figure of speech. Transformations outside the phenomenon themselves are not observed, acting merely as explanatory mechanisms. In fact, Goethe never directly referred to a mechanism or "forming force", or *Bildungstrib* (see Steigerwald 2002: 299) as was so common at the time. Metamorphosis stems from *Bildung* and can thus be defined as formation, "movement" or "development".[8]

Ontogeny, the development of form within a single organism, is an observable phenomenon. The process is *ahistorical*, inasmuch as it may be repeated in our mind's eye in either direction—that is to say, ontogeny is not confined to strict linear transformation. If an embryo is observed growing, for example, it is not as a step-by-step progression. One cannot split the process of development into individual, discrete stages; there are no "compartments" with strictly defined barriers. Instead, form "moves" from one "shape" to another, from egg to embryo. The change in form is recognised in the same way an old school friend is recognised many years later.

Goethe described three forms of metamorphosis: **regular**, **irregular,** and **accidental**. Regular metamorphosis is the development of the seed to the fruit and back

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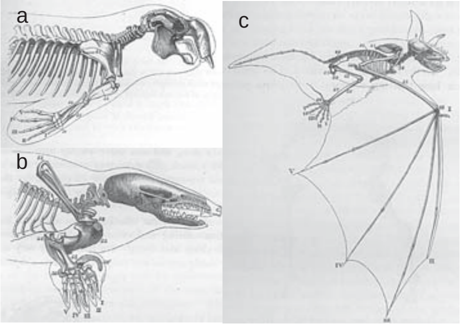
[8] Brady also suggests that the "metamorphic relation does not depend upon direction" (Brady 1998: 106). Direction in metamorphosis is akin to transformation.

**Fig. 3.1** Homologues from various animals (sea-cow, mole, and bat respectively), after Owen (1849: Figs 1–3)



to the seed again, thus forming a continual ontogenetic cycle (a life cycle). Irregular metamorphosis is the development of the seed to a non-fruiting flower. It is irregular as the process is not cyclic, as flowers do not give rise to seeds. Accidental metamorphosis is the cross fertilization of plants that leave hybrids, again not forming a regular cycle.

The development of regular, irregular, and accidental metamorphosis has been mistaken as an early precursor to evolutionary development biology (evo-devo).[9] Goethe's science of description, which includes an active involvement of the mind's eye, has been confused as hypotheses or speculations about different explanatory mechanisms.

The parts that make up the archetype can be compared to the homologues of the 19th-century anatomist, Richard Owen (1804–1892) (Chapter 9). A homologue is simply a part of an organism, *not a relationship*. It may occur in many different manifestations, all related by way of their structure. A homologue such as the wing of an insect does not share the same basic structure as that of a gorilla's forearm, the bat's wing, and the whale's fin: It is not a further manifestation of the same form and considered "non-homologues" (see Figure 3.1 and Chapter 7).

## 3.5 Urhomologie

Goethe did not formalise the notion of homology nor did he predict species evolution; he balked at the idea of a "Natural system (as opposed to *the* Natural method)", which he called "a contradictory expression" (Goethe 1995: 43). Nature was indeed made up of natural forms that (by way of their relationships) would lead to a natural classification. Linneaus' system offered no such thing for Goethe:

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[9] Enrico Coen (1999) believes that the ABC model to explain the development of mutant flowers is similar to Goethe's *accidental metamorphosis*. The confusion in Coen's argument is that Goethe described abnormalities as a non-linear process that does not follow the regular development from seed to fruit to seed. These abnormal or accidental forms were not considered to be part of the normal process of flower development. Coen argues that abnormalities are part of a linear or molecular progression between species.

> I have always held it impossible to treat one genus like another. I would say there are genera with a character which is expressed throughout all their species; we can approach them in a rational way. (Goethe 1995: 43)

The relationship between the parts (homologues) was the key to understanding whole organisms and distinguishing individual species from within the archetype. Organisms share relationships that can be represented in a real archetype, the *ur-animal* or *ur-plant*. Such was Goethe's conviction that such organisms existed (a viewpoint he later revised), prompting him to mount a search during his Italian journey (Goethe 1995: 214).[10]

## 3.6 Relating the Ideal Organism

An ideal organism, in Goethe's view, is one that has diverse homologues. Less ideal or "complete" animals, for instance, have a lower diversity of parts and therefore they all look similar. Urhomologies can trace the archetype through various organisms and their homologues (Goethe 1995: 118–119), creating a successive progression from least to most ideal organism. Figure 3.2 is a reconstructed Goethean Archetype using five hypothetical organisms (A–E) made up of four homologues each. Moving up the graph from the least ideal to the most ideal, the homologues become more diverse (that is, more dissimilar). Note that the homologues in the least ideal organism do not resemble those in the most ideal although they are still the same structure.[11] In Figure 3.2 the taxa are related by their homologues:

> Although a plant or tree seems to be an individual organism, it undeniably consists only of separate parts which are alike and similar to another and to the whole. (Goethe 1995: 64)

It is not immediately possible to compare taxon A—a more ideal organism—with taxon E, a less ideal organism, as they share no similar characteristics. In fact, once again, comparisons between A and E, as Goethe suggested, require a "third thing intermediate to the two", such as taxon B. Thus, taxon A would be deemed more closely related to taxon B than it is to E based on homologue *f*, establishing a specific relationship based on homology $c(f, f)$.[12] Goethe never fully pursued the concept of homology although it is integral to his idea of the archetype. Thus, we

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[10] Palermo, Tuesday, April 17, 1787: "Confronted with so many kinds of fresh new forms, I was taken again by my old fanciful idea: might I not discover the primordial plant amid this multitude? Such a thing must exist, after all! How else would I recognize this or that form as being a plant, if they were not all constructed according to one model?" (Goethe 1989: 214).

[11] Goethe realised that the differences between the most and least ideal taxa may result in no common homologues: "... the human being cannot serve as the archetype for the animal, nor the animal for the human being. Thus we will not hesitate to suggest a third thing, intermediate between the two..." (*Goethe* 1995: 124).

[12] A homology statement is that taxa A and B are more like each other than they are to taxon E. Similarly, we can say that taxon E is more like taxon D than C based on the homology $b(a, a)$ and that C than is more like D than it is to B based on the homology $c(b, b)$.

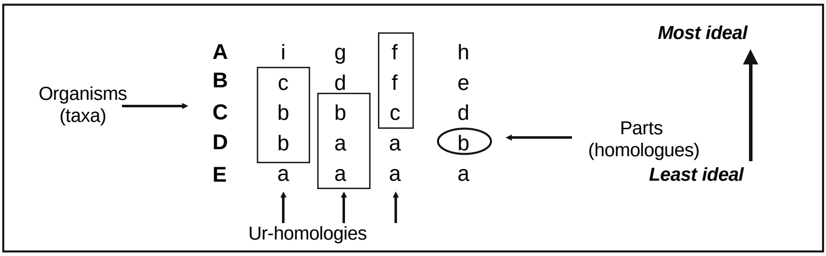

**Fig. 3.2** The *urhomology*. Goethe's Archetype and Metamorphosis translated into a table of relationships (urhomologies) based on similarity of homologues

have created the term urhomology, as Goethe's primary idea can be considered a precursor to the modern notion of homology—an idea analogous to *urfaust* (see Petsch in Goethe 1987, Goethe 1999a), the earliest surviving draft manuscript of *Faust* (1773–1775) that accompanied Goethe in his move from Frankfurt to Weimar in November 1775.[13]

## 3.7 Transformation and Goethe's Archetype

Goethe never considered the archetype to be either ancestral or primitive. Homologues did not adhere to an ordered sequence. In Figure 3.2, for example, homologue *a* does not, and would not, transform into homologue *b*: They are related, but in a non-linear way.

Without linear transformation between the "parts", the archetype could not qualify as an ancestor. Rather, it is the representative of a natural group. Goethe's archetype can be compared to a monophyletic group (Chapter 7). That is, a group of organisms most closely related by virtue of their shared homologues, by way of the relation of homology. The archetype is a generic creature, a "mammal" that represents all mammal characteristics or *mammal-ness*. The archetype contains urhomologies that relate the more perfect mammals more closely to each other than the less perfect ones. Humans would be grouped with the great apes based on urhomologies. The archetype is not an individual organism, as Goethe suspected, but a group of closely related forms. In modern parlance it would be equivalent to a **monophyletic clade** *sensu* Hennig (Chapter 5).

Today, comparative biology still uses Goethe's urhomology concept to make statements of relationship based on similarity. Adolf Naef, and other "ideal" morphologists such as Joseph Kälin and Rainer Zangerl, recognised the significance of Goethe's non-linear succession, metamorphosis, archetype, and urhomology as a way of finding natural relationships and allowing the testing of existing classifications (Chapter 5).

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[13] Erich Schmidt discovered the draft in 1887 as an untitled manuscript that he later published with annotations (see Schmidt 1915).

The cladistic revolution (Chapter 6) was made possible by theoretical developments of Goethe’s urhomology via the idealistic morphologists of the early 20th century (Chapter 5). Nevertheless, the concepts of homology and archetype had already been absorbed into the transformationalist literature, notably those who followed Darwin, Ernst Haeckel, in particular, misreading Goethe’s work.

# Chapter 4
# Ernst Haeckel and *Systematische Phylogenie*

*E pur si muove*.[1]

## 4.1 Ernst Haeckel and Darwin

Darwin's *Origin of Species* overwhelmed Ernst Haeckel (1834–1919). He started to lecture on Darwin in 1863, shortly after he had read Heinrich Bronn's translation, giving his first public lecture on the subject at the age of 29 to the 38th meeting of the *Society of German Naturalists and Physicians* in Stettin (Haeckel 1863). Haeckel used the title *Über die Entwicklungstheorie Darwin's*,[2] which yields various translations: "On Darwin's theory of development" (Nyhart 1995: 129), suggesting that evolution is a form of development, while an alternative, "On Darwin's theory of evolution" (Hoβfeld & Olsson 2003: 296), avoids the interpretative issues altogether. But as Nyhart (1995: 129) points out, Haeckel could easily have used the more appropriate *Descendenztheorie* for "evolution"—a word he was to use later (Haeckel 1868). Nevertheless, Haeckel began by dividing the world neatly into righteous Darwinists ("Development and progress!"—"Entwickelung und Fortschritt!") and intransigent conservatives ("Creation and species!"—"Schöpfung und Species!") (Haeckel 1863: 18[3]).

Slowly recovering from the sudden death of his wife in early 1864 (Weindling 1989: 319, Desmond 1994: 349, Richards 2004, 2005), Haeckel began assembling

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[1] The Italian phrase *E pur si muove* translates as *And yet it moves.* Galileo Galilei was supposed to have whispered these words after recanting his view that the Earth did indeed move around the sun.

[2] Richards (2005: 1) provides a newspaper account of the event, where the reporter writes of the "huge applause [that] followed this exciting lecture". The lecture was later reprinted, with minor amendments, in a collection of articles (Haeckel 1906); the amended version was reprinted in Heberer (1968).

[3] Haeckel later wrote more inflammatory expressions of his "battle": "On the one side spiritual freedom and truth, reason and culture, evolution and progress stand under the bright banner of science; on the other side, under the black flag of hierarchy, stand spiritual slavery and falsehood, irrationality and barbarism, superstition and retrogression" (Haeckel 1874: xiii–xiv).

what eventually became *Generelle Morphologie,* an enormous book containing all his ideas, a book that would spew "fire and ash over the enemies of progress, and radically alter the intellectual terrain in German biological science" (Richards 2005). *Generelle Morphologie* had its origin in lecture notes taken by his students, the book being written in 1865–1866, finally published towards the end of 1866 (Ulrich 1967, 1968, Uschmann 1967a). It was to be a union of the ideas of Goethe, Lamarck, and Darwin. Yet *Generelle Morphologie* was not well received; its failure to impress was explained by Radl thus: "The German professors treated the book as a belated offshoot of the long discarded *Naturphilosophie*, and paid little attention to it" (Radl 1930: 122–123). Regardless of its contemporary impact, one remains impressed with Haeckel's sense of commitment in promoting Darwin's cause: two thirds of the way down the title page of both volumes, ranged to the right in small capitals, were printed the words "E pur si muove".

Its critical failure notwithstanding, Haeckel immediately embarked upon another project to render his ideas more accessible. He was again lecturing on Darwin in 1867–1868; these lectures formed the basis of *Natürliche Schöpfungsgeschichte* (1868), his first popular book, which was to summarise and simplify the complexities of *Generelle Morphologie*. It was *Natürliche Schöpfungsgeschichte* that had the greater impact on German science as well as the general public via its various translations (Nordenskiöld 1936: 515).

## 4.2 Haeckel's Genealogical Oaks and Stick "Trees"

> "While the booming of guns at the Battle of Königgrätz in 1866 announced the demise of the old Federal German Diet and the beginning of a new splendid period in the history of the German Reich, here in Jena the history of the phylum [*Stammesgeschichte*] was born." (Volkmann 1943: 85; translation in Gasman 1971 [2004]: 18)

> "… whatever hesitation may not unfrequently be felt by less daring minds, in following Haeckel in many of his speculations, his attempt to systematise the doctrine of Evolution and to exhibit its influence as the central thought of modern biology, cannot fail to have a far-reaching influence on the progress of science." (Huxley 1878: 744)

While none of Haeckel's genealogical trees appears in *The Hierarchy of Life* (Fernholm et al. 1989), a book whose aim was to "… summarise the progress we have made towards a tree of life ... a goal hardly attempted since Haeckel" (Patterson 1989: 486), one of his illustrations does grace the cover of its successor, *Assembling the Tree of Life* (Cracraft & Donoghue 2004). Not surprisingly, the editors chose the *Monophyletischer Stammbaum der Organismen*, or the monophyletic tribe of organisms, a reproduction of the first plate in Haeckel's *Generelle Morphologie* (Haeckel 1866) and reproduced in many basic texts on systematic biology. Another of Haeckel's trees is found in the introductory essay to *Assembling the Tree of Life*

(Cracraft & Donoghue 2004: Fig. 1.2, taken from Haeckel 1866, the inset of Taf. VII), as one of four believed to have contributed most to the developing views on how best to represent the living world (the other three diagrams are from Darwin 1859: 160–161, Zimmermann 1931: 1004, Fig. 179, and Hennig 1966a: 91). These four trees are seen to collectively mark the passage of the birth of "phylogenetics", from Darwin via Haeckel, Zimmermann, and finally Hennig to its present "maturity", in the algorithms of the numerical taxonomists (Cracraft & Donoghue 2004: 1–3)—a journey from *Systematische Phylogenie* to *Phylogenetic Systematics*. That depiction may well be an oversimplification (see, for example, Richards 1992), yet Haeckel remains, if not the father, then at least the midwife of phylogenetic trees. In the hands of Haeckel, the union of Darwin, Bronn, and Schleicher (see below) produced many "fruitful offspring", mostly in the form of trees representing the genealogical relations among organisms, their phylogenetic history.

## 4.3 Heinrich Georg Bronn: Trunks and Twigs

*Natura doceri*.[4]

In 1850 the Paris *Académie des Sciences* offered a prize to anyone satisfactorily answering a question posed concerning the fossil record and what it represents of the changing life that inhabits the Earth and has inhabited it in the past. The task was to present an essay

> . . . to study the laws of the distribution of fossil organisms in the different sedimentary strata according to the order of their supposition; to discuss the question of their successive or simultaneous appearance or disappearance; to examine the nature of the relations between the present and the former states of the organic world. (*Comptes-Rendus* 30: 257–260, 1850; translation from Rudwick 1972 [1985]: 219, Nelson 1989b: 64; see also introduction to Bronn 1859a: 81 and Laurent 1997)

The opportunity offered by the *Académie des Sciences* reflects a lingering interest in the notion of the transformation of species, inspired, if not initiated, by Lamarck in the early 1800s (Laurent 1987, 2001). The award, a gold medal to the value of 3000 francs, was announced in 1857 (*Comptes-Rendus* 44: 167–169, 1857) and presented to the eminent palaeontologist Heinrich Georg Bronn (1800–1862; portrait in Burkhardt et al. 1993: opposite p. 89 and Seibold and Seibold 1997: 521, Abb. 2); Bronn would be first to translate Darwin's *Origin of Species* into German. The prize-winning essay was first published in its original German in 1858 as *Untersuchungen über die Entwickelungs-Gesetze der organischen Welt* (Bronn 1858), a full French translation not appearing until a few years later, in 1861 (Bronn 1861). On the title page of each full edition were the words *Natura doceri*, "Being taught by nature", a phrase that would have appealed to Louis Agassiz (Winsor 1991). An English and French translation of the concluding section, "On the Laws

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[4] Translated from the Latin as "Being taught by nature".

of Evolution of the Organic World during the Formation of the Crust of the Earth", was published a few months prior to Darwin's *Origin of Species* (Bronn 1859a, 1859b).

Bronn's monograph included a great many summary diagrams derived from the fossil record of various groups of animals, diagrams similar to Agassiz's (compare Figures 4.1 and 4.2). Bronn noted that such systems could be generalised by a branching diagram, relating various groups of animals to each other, which he included (Figure 4.3 reproduced from Bronn 1861: 900 after Bronn 1858: 481; see also the cover of Bowler 1976 and his plate X, Uschmann 1967b: 15, Bowler 1988 [1992]: 55, and Craw 1992: 69, Fig. 1A, for other reproductions):

> Veut-on représenter cet état de choses par une figure, il faut se figurer le système comme un arbre, où la position plus ou moins élevée des branches correspond à la perfection relative de l'organisation, d'une manière absolue et sans tenir compte de la position plus ou moins élevée des rameaux sur la même branche. (Bronn 1861: 899, 1858: 481)

The tree has a main trunk, with a number of main branches, A through G, including invertebrates, fishes, reptiles, birds, mammals, and man. A further series of subsidiary branches are labelled with lowercase letters—*a* to *m*—representing species at different levels of development and time of appearance in the geological record—this diagram was to have some influence on Haeckel. The design of Bronn's tree is much like many of Haeckel's, whether the *Stammbaum* is Oak-like (Figure 4.4) or stick-like (Figure 4.5).

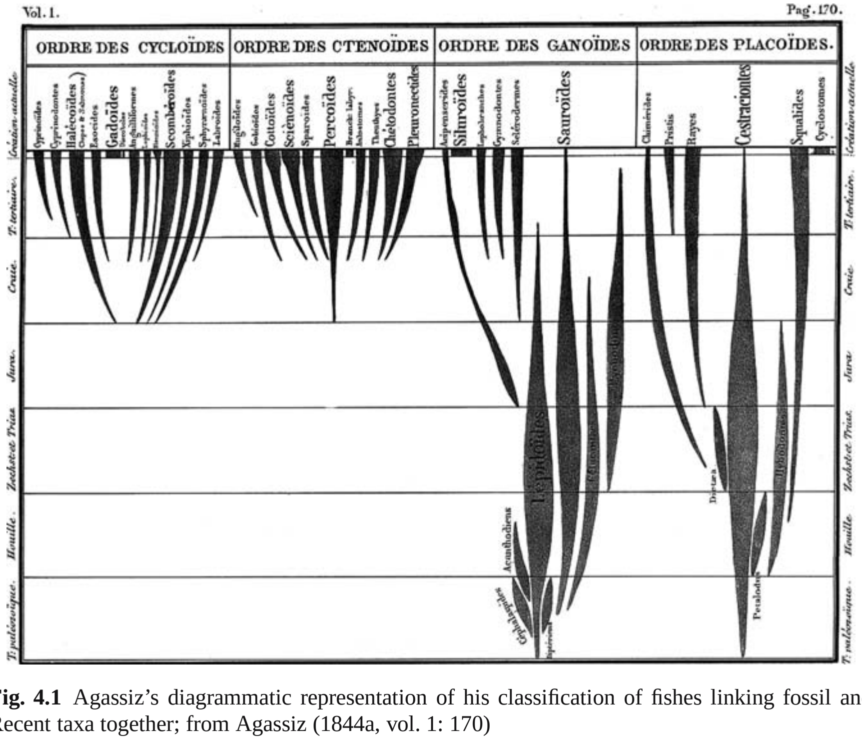

**Fig. 4.1** Agassiz's diagrammatic representation of his classification of fishes linking fossil and Recent taxa together; from Agassiz (1844a, vol. 1: 170)

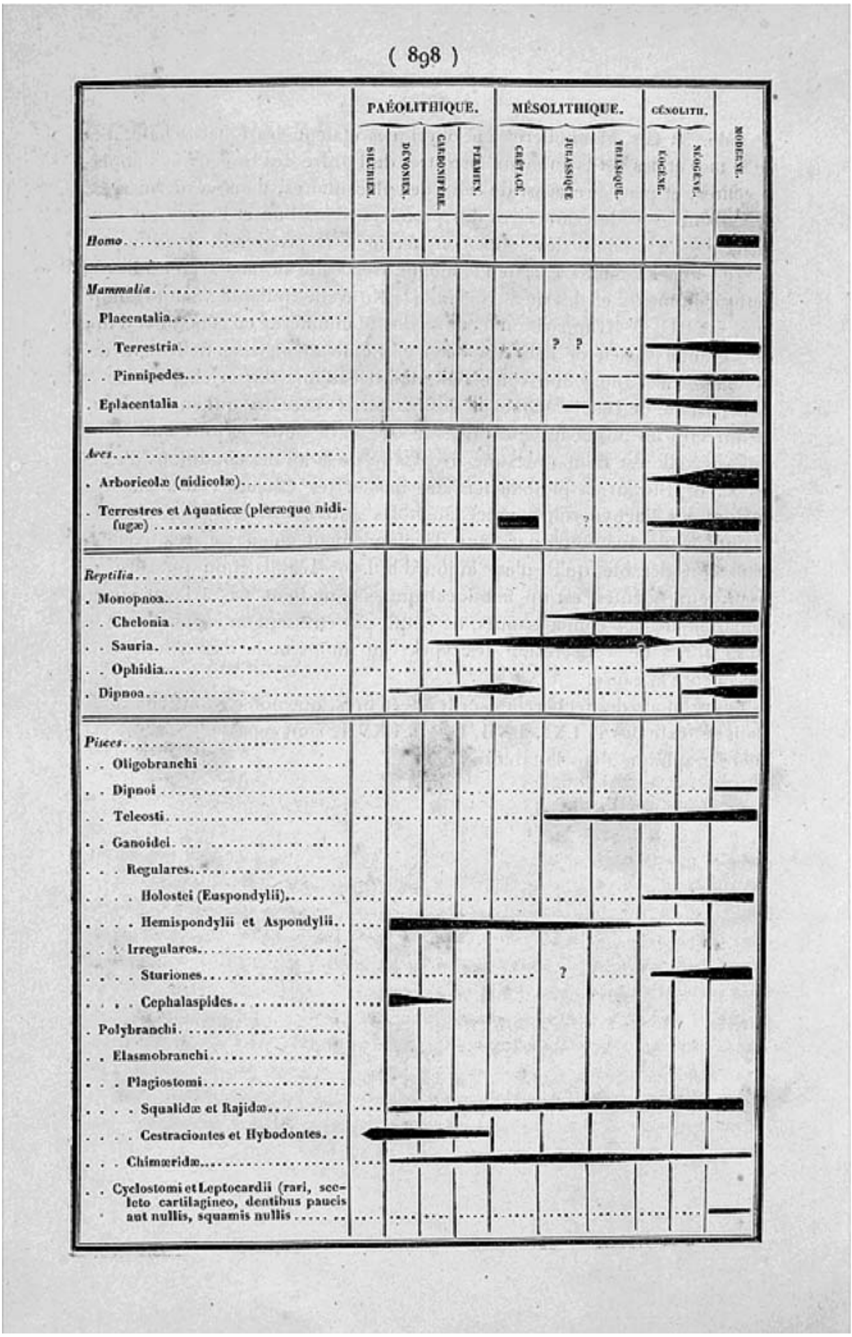

**Fig. 4.2** Summary diagram of the fossil record of various groups of animals, after Bronn (1861: 900 after Bronn 1858: 481); compare with Agassiz (Fig. 4.1)

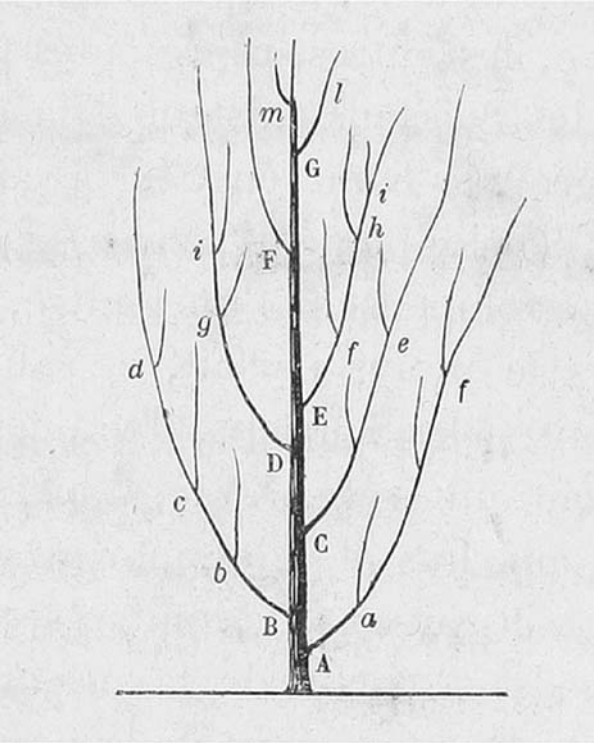

**Fig. 4.3** Tree diagram from Bronn (1861: 900; see also Bronn 1858: 481)

Bronn argued that the fossil remains recorded in various strata showed the replacing of earlier groups of organisms with later ones, the later groups better adapted to local environments. Bronn maintained that the fossil remains showed conclusively a constant progress from the early simple forms of life to the more complex ones. Yet, he also concluded that the fossil record does not allow direct access to the successive appearance of the various species and, more significantly, does not provide any proof of the transmutation of species (Baron 1961, Junker 1991, Laurent 1997, Seibold & Seibold 1997). Interestingly, Bronn noted that to distinguish between species' fixity or their transformation amounts to a commitment of belief, the problem of distinguishing between the two was beyond empirical resolution (Bronn 1858). Bronn returned to this theme when he added an additional chapter to the German translation of Darwin's *Origin of Species* (Bronn 1860), the version that was read by Haeckel (Richards 2005).

Haeckel began reading the German translation of Darwin's *Origin* in the summer of 1860, returning to it in November 1861 (Richards 2004). Encouraged by Darwin,[5] Bronn added his own 15th chapter outlining some of the difficulties he

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[5] Although see the comments in Burkhardt et al. (1993: 102–103 and 407–409, especially footnote 1).

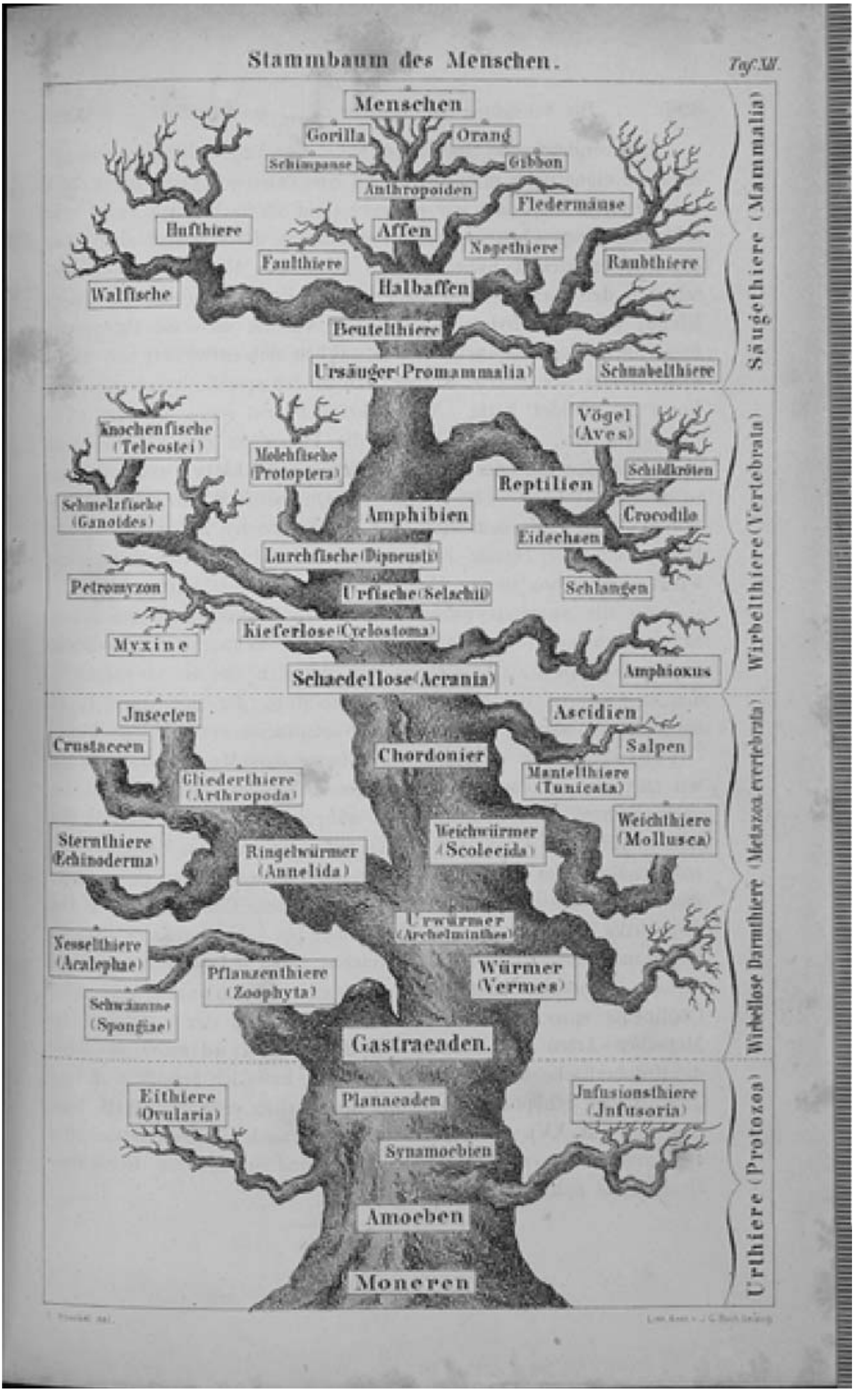

**Fig. 4.4** Haeckel's Oak-like *Stammbaum*

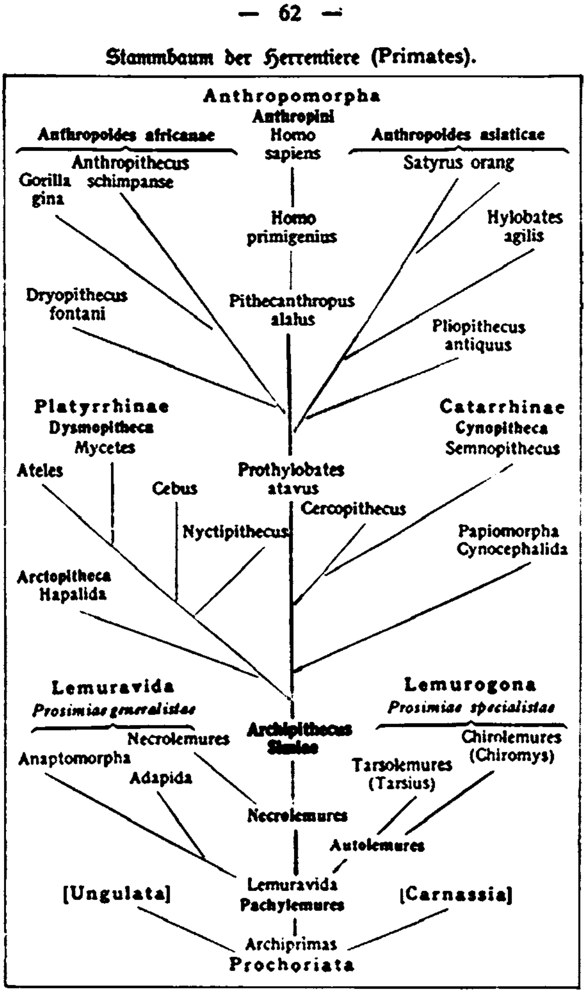

**Fig. 4.5** Haeckel's stick-like *Stammbaum*

had with Darwin's thesis. Bronn's additional chapter had a significant impact on Haeckel—and German evolutionary thinking from thereon (Junker 1991). For while Bronn states his enthusiasm for Darwin's general thesis, he suggests that it remains simply a hypothesis, one "possible scenario of life's history" (Richards 2005):

> We have therefore neither a positive demonstration of descent nor—from the fact that [after hundreds of generations] a variety can no longer be connected with its ancestral form (*Stamm-Form*)—do we have a negative demonstration that this species did not arise from that one. What might be the possibility of unlimited change is now and for a long time will remain an undemonstrated, and indeed, an uncontradicted hypothesis. (Bronn 1860: 502, 1861: 533; translation from Richards 2005)

Haeckel saw a way of solidifying Darwin's suggestions of the genealogical connection of all organisms by marrying the systematic arrangement, as revealed by the hierarchical “natural system”, with a graphic representation of genealogy, a pedigree of species, such that visually, as well as positively, Haeckel could provide both an account of, as well as a depiction of, which species gave rise to others. Thus, for Haeckel, of course, his genealogies *did* represent the transformationist view, graphically and literally. Haeckel also required some independent evidence, a way of tackling Bronn’s objections. He found that in other trees, those of his linguist friend August Schleicher.

## 4.4 Schleicher, Linguistics & Trees

The linguist August Schleicher (1821–1868) worked at Jena University, becoming a good friend of Ernst Haeckel. Haeckel insisted that Schleicher read Darwin’s *Origin* (Koerner 1989, Alter 1999, Di Gregorio 2002, Richards 2004). Schleicher did and was immensely impressed, responding almost immediately by publishing an open letter to Haeckel, *Die Darwinische Theorie und die Sprachwissenschaft* (Schleicher 1863; later translated as *Darwinism tested by the Science of Language* and published posthumously in 1869). Schleicher argued that contemporary languages had also undergone a process of change, not too dissimilar from that which Darwin suggested for organisms: Evolutionary theory *confirmed* language descent, rather than suggesting it. Schleicher had already anticipated such a development, as is evident from his 1860 book and the earlier 1853 article (Schleicher 1853, 1860): “these assumptions [the origins of an Indo-European language family], deduced logically from the results of previous research, can best be depicted by the image of a branching tree” (Schleicher 1853: 787, translation from Koerner 1987: 112). In *Die Darwinische Theorie*, Schleicher referred to the tree Darwin provided in the *Origin*, noting that it was a purely hypothetical construct, containing no real species, either at the tips or at the nodes. This he compared to a tree he had constructed, one depicting the Indo-European languages and included as a figure appended to the 1863 essay (Figure 4.6; reproduced from Schleicher 1863; also in Alter 1999: 75, Fig. 4.1). As early as 1850, Schleicher suggested using a tree-like diagram (a *Stammbaum*) for representing the development of languages, publishing the first in 1853 (Figure 4.7; Schleicher 1853) and another in 1860 (Schleicher 1860). Schleicher has received credit for introducing the tree as a graphic way of representing the genealogies of languages (Richards 2002a; although see Koerner 1987 and Traub 1993 for further details). Schleicher’s three trees have a modern language named at each tip with the branches and nodes labelled for their common origin (Figure 4.7). Thus, in both the 1853 and 1860 trees, there are branches for the Persian and Hindu languages, for example, linked by a node labelled Hindu–Persian (Schleicher 1853) or Asiatic (Hindu–Persian) (Schleicher 1860). Schleicher was convinced that the evolution of languages provided definitive evidence for the evolution of man and a way of tracing their development. He referred the problems of identifying transitional organisms from few fossil remains, noting that there were far more linguistic fossils than there were geological fossils (Richards 2002a), a view that Haeckel later echoed:

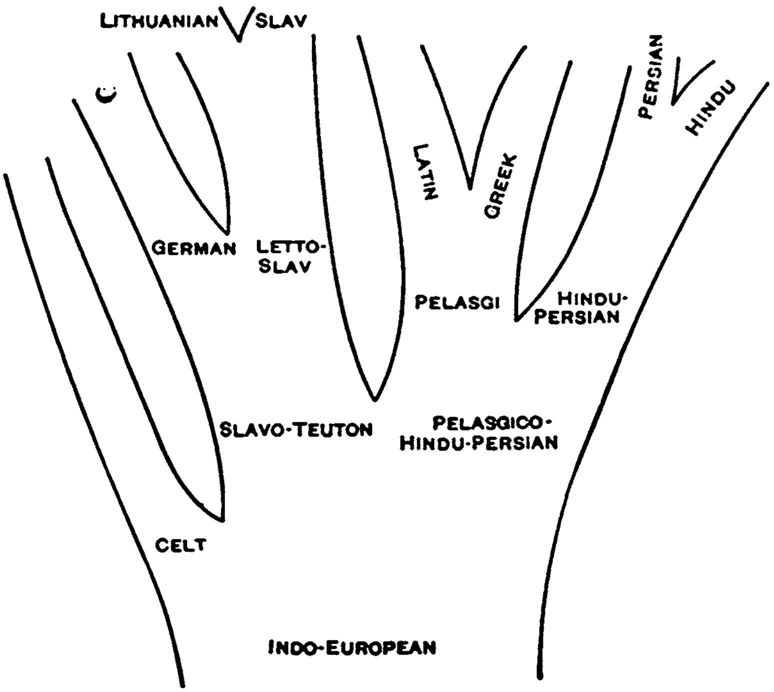

**Fig. 4.6** Schleicher's *Stammbaum*

> The former [philology] can .. adduce far more direct evidence than the latter [geology], because the palaeontological materials of Philology, the ancient monuments of extinct tongues, have been better preserved than the palaeontological materials of Comparative Zoology, the fossil bones of vertebrates. . . . (Haeckel 1879: 24[6])

In his second contribution to the evolution of man, *Ueber die Bedeutung der Sprache für die Naturgeschichte des Menschen*, Schleicher criticises the available morphological evidence for relating various humans as superficial, and suggests that language provided a "higher criterion, an exclusive property of man" (Schleicher 1865: 18–19; translation from Richards 2002a). Schleicher's arguments for linguistic superiority are remarkably similar to those now offered by DNA sequence data, today's universal "higher criterion".

As Richards notes:

> . . . Schleicher's greatest and lasting contribution to evolutionary understanding may simply be the use of a *Stammbaum* to illustrate the descent of languages. . . . Haeckel quite obviously took his inspiration from his good friend Schleicher. And Haeckel's *Stammbäume* have become models for the representation of descent ever since. (Richards 2002a)

And as Alter states more boldly: ". . . the historical significance of their friendship is enormous" (Alter 1999: 117). Schleicher died at 48 years old in 1868,

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[6] In 1859 and 1863 a two-volume work entitled *Essai de paléontologie linguistique* was published by Adolphe Pictet, a distance relative of the palaeontologist François Jules Pictet (Wells 1987: 47–48).

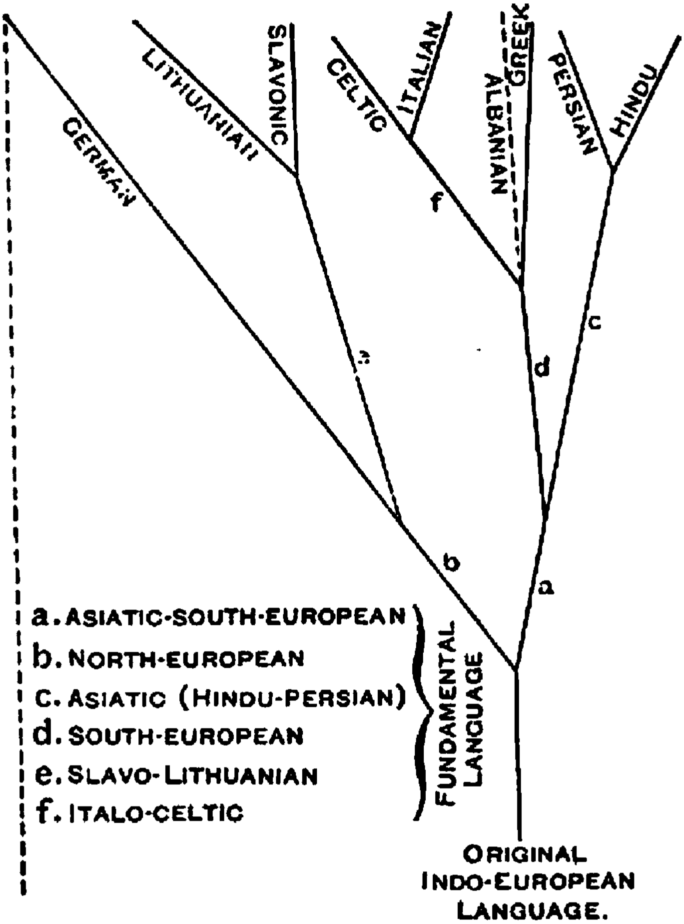

**Fig. 4.7** Schleicher's *Stammbaum*

two years after Haeckel published his great work (Haeckel 1866). Haeckel would later include a tree of the "Pedigree of the Indo-Germanic languages" in many of his books, beginning with the second German edition of *Natürliche Schöpfungsgeschichte* (1870: 625) and all subsequent editions, both German and English, of *Anthropogenie* (e.g., Figure 4.8 after *The Evolution of Man* 1883, II: 23).

## 4.5 Haeckel and Palaeontological Truth

Haeckel was able to evaluate the palaeontological evidence provided by Bronn, as well as utilise the graphic representations provided by both Bronn and Schleicher. That is, a union of palaeontology and genealogy would illustrate Darwin's views exactly—or so it seemed.

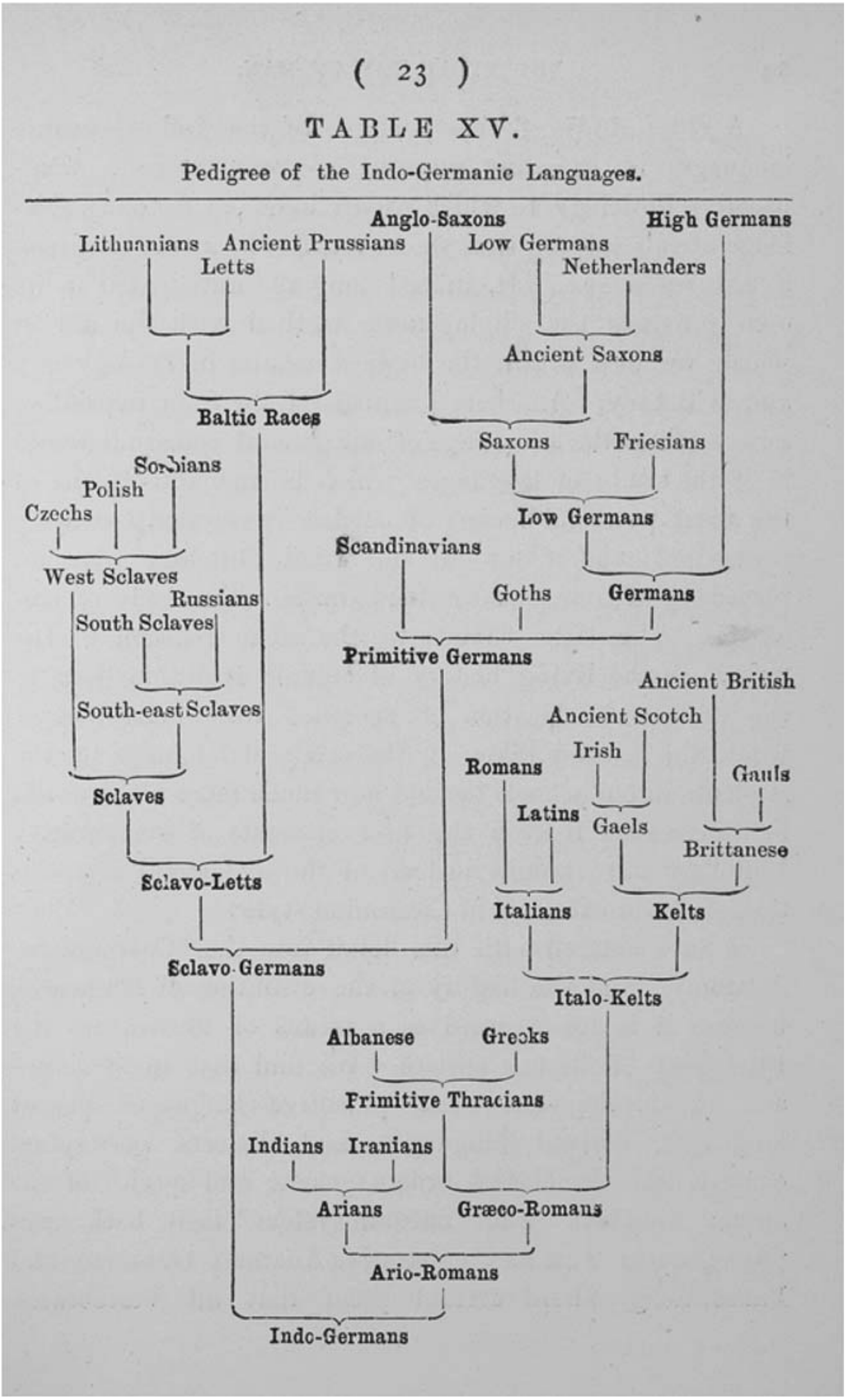

**Fig. 4.8** Haeckel's tree relating languages

Haeckel coined the word “phylogeny” (Haeckel 1866, I: 57, II: 301: “Generelle phylogenie oder Allegemeine Entwickelungsgeschichte der organischen Stämme”) for what he later described as the “tribal history, or ‘palaeontological history of evolution”’, adding for precision, “Phylogeny includes palaeontology and genealogy” (Haeckel 1874: 710, 1883, II: 460; see Haeckel 1866, II: 305). With palaeontology firmly in mind as the prime source of evidence for genealogy, Haeckel speculated on the role of individual development:

> This palaeontological history of the development of organisms, which we may term *Phylogeny*, stands in the most important and remarkable relation to the other branches of organic history or development, I mean that of individuals, or Ontogeny. On the whole, the one runs parallel to the other. In fact, the history of individual development, or Ontogeny, is a short and quick recapitulation of palaeontological development, or Phylogeny, dependent on the laws of Inheritance and Adaptation. (Haeckel 1876: 10–11)

Regardless of any truths in this assertion, classifications, if understood “properly”, should represent the phylogenetic relationships of organisms—one (genealogy) being derived from the other (classification). Haeckel connected classification directly with the “facts of palaeontology”, facts that even then were variously interpreted especially as they related to issues of “transformation” (see Bronn above). Haeckel had early on made some efforts to convert the “natural system” of classification into a genealogical scheme, in the first part of his monograph on the *Radiolaria*, in a table entitled *Genealogische Verwandtschaftstabelle der Familien, Subfamilien und Gattungen der Radiolarien* (Haeckel 1862: 234[7]). The 1862 monograph had its origins in Haeckel’s earlier *Habilitationschrift* studies (Haeckel 1860, 1861), where he described many new genera and species. Although at that time he pondered their genealogical relationships, he resisted any mention of how Darwin’s ideas might influence classification. Nevertheless, along with the “genealogical” table, the 1862 monograph included a footnoted discussion on Darwin’s *Origin* (Haeckel 1862: 231–232).

Haeckel’s *Generelle Morphologie* was published in two volumes; the second included a *Systematische Einleitung in die allgemeine Entwickelungsgeschichte*, a detailed description and classification of all life, with 8 plates depicting various *Stämmbaume* or pedigrees, the first diagrams of their kind (Haeckel 1866, “mit acht Genealogischen Tafeln”; listed in Table 4.1). *Generelle Morphologie* appeared in just one edition and was never translated,[8] although a condensed German-language edition was eventually published 40 years later (Haeckel 1906), excluding the 8 *Stämmbaume*, and Heberer (1968; see also Uschmann 1967a and Ulrich 1967, 1968)

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[7] Haeckel’s monograph was finally completed in 1888 (Haeckel 1862, 1888). In between times, he presented a series of genealogies and charts capturing the interrelationships of various Radiolarian groups derived from the Challenger material (Haeckel 1887) and presenting a final summary in the form of a chart and diagram in Systematische Phylogenie (Haeckel 1894: 207–208; see Aescht 1998).

[8] Not for want of trying. Every effort was made by Huxley to translate the book, finally deciding that it was “too profound and too long” (from Darwin in Desmond 1982: 155). Richards (2005) deals with this episode in detail.

**Table 4.1** Figures in Haeckel's *Generelle Morphologie, Systematische Einleitung in die allgemeine Entwickelungsgeschichte* (1866)

| *Generelle Morphologie, Systematische Einleitung in die allgemeine Entwickelungsgeschichte* (1866) | |
|---|---|
| Taf. I | Monophyletischer Stammbaum der Organismen |
| Taf. II | Stammbaum des Pflanzenreichs |
| Taf. III | Stammbaum des Coelenteraten oder Acalephen (Zoophyten) |
| Taf. IV | Stammbaum des Echinodermen palaeontologisch begründet |
| Taf. V | Stammbaum des Articulaten (Infusorien, Würmer und Arthropoden) |
| Taf. VI | Stammbaum des Mollusken (Molluscoiden und Otocardien) |
| Taf. VII | Stammbaum des Wirbelthiere palaeontologisch begründet |
| Taf. VIII | Stammbaum des Säugethiere mit Inbegriff des Menschen |

published large extracts for a collection of Haeckel's work celebrating the 100th anniversary of its publication.[9]

In five of Haeckel's plates (Table 4.2, Tafs III, IV, V, VI, and VII) there are two trees per plate, a larger, more detailed tree with many of the nodes named and a smaller inset, presumably representing the morphological relationships. Two of the five (Table 4.2, Tafs IV and VII) include explicit palaeontological eras ("palaeontologisch begründet") appended to the axis of the main tree, which has been interpreted as adding common descent to the fossil record (Patterson 1983b: 8).

*Natürliche Schöpfungsgeschichte* went through 12 editions, the text and illustrations being modified accordingly. The first German edition has 8 plates, different from those published in *Generelle Morphologie* (Table 4.1). In all of the later editions (8th–12th), the pedigrees, *Stämmbaume,* and genealogies are represented in a simpler format, as charts within the text (e.g., Figure 4.5), the "branches" becoming simple lines directly connecting taxon names, the lines relating taxa specified in an accompanying synoptic table (*Systematiche Übersichten*).

The second through seventh editions have only four plates (Table 4.2 ), while the eighth and ninth editions have but a single plate (Table 4.2).[10] Three of the plates in the second to seventh editions are reproductions from the first edition. Of the eight plates in the first edition, plates II and VI are said to be "palaeontologisch begründet"; these are the retained plates for the second to seventh editions, both included in the English editions (Table 4.2 ). The fourth plate, however, is unique and was not published in the first edition. It represents Haeckel's tree of humans and their wanderings, *Hypothetische Skizze des monophyletischen Ursprungs und der Verbreitung der 12 Menschen-Species von Lemurien aus ü ber die Erde*. Although

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[9] Heberer (1968) includes reproductions of only Taf. I-III, V-VIII, noting "Es Folgen auf den Seiten 269–274 den acht genealogosichen Tafeln, die dem Bd. 2 der "Generelle Morphologie" von Haeckel beigegeben wurden, die Nrn. I, II, III, IV, VI, VIII. Massgebliche Fachleute haben dazu bemerkt, man müsste mit Erstaunen feststellen, dass Haeckel schon damals die phylogenetischen Beziehungen der Ogranismen in wesentlichen Zügen richtig erfasst habe" (Heberer 1968: 268). Although Haeckel's genealogical trees have been reproduced on many occasions, Papavero et al. reproduce all eight (1997a: 254–261) taken from the second French edition of *Natürliche Schöpfungsgeschichte, Histoire de la Creation....*

[10] We have examined the first, second, fifth, seventh, eighth, and ninth editions.

**Table 4.2** Figures included in the various editions of Haeckel's *Natürliche Schöpfungsgeschichte*

| | |
|---|---|
| ***Natürliche Schöpfungsgeschichte (1868) First Edition*** | |
| Taf. I | Einstämmiger oder monophyletischer Stammbaum der Organismen |
| Taf. II | Einheitlicher oder monophyletischer Stammbaum des Pflanzenreichs palaeontologisch begründet |
| Taf. III | Einstämmiger oder monophyletischer Stammbaum des Thierreichs |
| Taf. IV | Historisches Wachsthum der jechs Thierstämme. Siehe die Erflärung |
| Taf. V | Stammbaum des Oliedfüsser oder Arthropoden |
| Taf. VI | Einheitlicher oder monophyletischer Stammbaum des Wirbelthierstammes palaeontologisch begründet |
| Taf. VII | Stammbaum der Säugethiere mit Inbegriff des Menschen |
| Taf. VIII | Stammbaum der Menschen-Arten oder Classen |
| ***Natürliche Schöpfungsgeschichte (1870, Second Edition–1879, Seventh Edition)*** | |
| Taf. IV | Einheitlicher oder monophyletischer Stammbaum des Pflanzenreichs palaeontologisch begründet |
| Taf. V | Historisches Wachsthum der sechs Thierstämme |
| Taf. XII | Einheitlicher oder monophyletischer Stammbaum des Wirbelthierstammes palaeontologisch begründet |
| Taf. XV | Hypothetische Skizze des monophyletischen Ursprungs und der Verbreitung der 12 Menschen-Species von Lemurien aus über die Erde |
| ***Natürliche Schöpfungsgeschichte (1889, Eighth Edition–1898, Ninth Edition)*** | |
| Taf. XX | Hypothetische Skizze des monophyletischen Ursprungs und der Verbreitung der 12 Menschen-Species von Lemurien aus über die Erde |
| ***The History of Creation,or the Development of the Earth and Its Inhabitants by the Action of Natural Causes (1876)*** | |
| Taf. V | Single-stemmed monophyletic pedigree of the vegetable kingdom based on palaeontology |
| Taf. VI | Historical growth of the six great stems of animals |
| Taf. XIV | Single or monophyletic pedigree of the stem of the back-boned animals based on palaeontology |
| Taf. XV | Hypothetical sketch of the monophyletic origin and the extension of the 12 races of Man from Lemuria over the Earth |

modified in subsequent editions, it is the only plate that survives through to at least the ninth edition.

For the English translation of *Natürliche Schöpfungsgeschichte*, *The History of Creation, or the Development of the Earth and Its Inhabitants by the Action of Natural Causes* ("…or, as Professor Haeckel admits it would have been better to call his work, 'The History of the Development or Evolution of Nature'," Huxley 1869: 13), the first to third editions (adapted and translated from the second through seventh German editions) have just four plates (see above) but many synoptic tables (Table 4.2 ). Among those four plates is the *Hypothetical Sketch of the Monophyletic Origin and the Extension of the 12 Races of Man from Lemuria over the Earth*[11] (Haeckel 1876: Taf. XV, Fig. 7) (see Chapter 13 for a fuller discussion of this figure).

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[11] Haeckel seems to have made an error on the figure legend, as the diagram is supposed to be of the 12 species of man, rather than races, of which Haeckel recognised 36 (Haeckel 1876: 308–309). Comparison with the German editions suggests the error was in the translation as the word *Menschen-Species* is used.

*Systematische Phylogenie* (1894–1896) was Haeckel's final attempt to document the genealogical relationships for all of Life, some 26 years after his *Generelle Morphologie*. *Systematische Phylogenie* did indeed contain many pedigrees, but the "oak-trees" of the *Generelle Morphologie* had disappeared, leaving just a series of stylised line drawings, similar to those from later editions of *Natürliche Schöpfungsgeschichte*, where taxa either link directly to each other or descend from one another. Each *Stammbaum* is accompanied by a *System* (Table 4.2 ).

Towards the end of his life, Haeckel returned to the theme of evidence derived from the "three great records"—his threefold parallelism which represented the data to support his pedigrees:

> The first rough drafts of pedigrees that were published in the *Generelle Morphologie* have been improved time after time in the ten editions of my *Naturaliche Schopfungsgeschichte* (1868–1902) (English translation, *The History of Creation*, London, 1876). A sounder basis for my phyletic hypotheses, derived from a discriminating combination of the three great records—morphology, ontogeny, and palaeontology—was provided in the three volumes of my *Systematische Phylogenie* (Berlin, 1894–1896). (Haeckel 1909)

Yet even while acknowledging the efficacy of the "threefold" evidence, he continued to rely heavily on palaeontology:

> ... The task of phylogeny is to trace the evolution of the organic stem or species—that is to say, of the chief divisions in the animal and plant world, which we describe as classes, orders, etc.; in other words, it traces the genealogy of species. It relies on the facts of palaeontology, and fills the gaps in this by comparative anatomy and ontogeny. (Haeckel 1904: 97)
>
> The three most valuable sources of evidence in phylogeny are palaeontology, comparative anatomy, and ontogeny. Palaeontology seems to be the most reliable source, as it gives us tangible facts in the fossils which bear witness to the succession of species in the long history of organic life. (Haeckel 1904: 393)

Haeckel's interest in "creating" ancestors was hindered by the lack of paleontological "facts", but that did not stop him creating "missing ancestors modelled on living embryos" (Desmond 1994: 349) or from the paraphyletic non-groups of systematics. The reliance on palaeontology, of course, set the scene for nearly all phylogenetic research during the following 100 years, a programme that eventually split at its seams once the concept of relationship was clarified and understood (Hennig 1966a). The cladistic revolution could set about reforming palaeontology (Nelson 1969c, Patterson 1977) and, as a consequence, comparative biology (Williams & Ebach 2004). If certain aspects of early 20th-century German morphology had been acknowledged and understood, the revolution in palaeontology might not have been necessary ("The issue would never have been raised unless it was made necessary by the over-zealous advocation of a purely palaeontological approach", Nelson & Platnick 1984: 156, Nelson 1989b: 71, Nelson 2004; Williams & Ebach 2004; see Chapter 6). Nevertheless, it is important to recognise that the majority of Haeckel's genealogical trees were representations of linear schemes of relationships, taxa "giving rise" to other taxa and paraphyletic groups not so much created (many were) but *retained and explained* in terms of evolutionary relationships, relative to a particular model of change, a model still invoked today to account for paraphyly and its apparent significance in evolutionary studies (Mayr & Bock 2002).

# Chapter 5
# The German Development of Morphology: From Ernst Haeckel to Willi Hennig

> "But there remains a largely untold story about the significance of morphology and comparative anatomy (also minimized in the Modern Synthesis)." (Love 2003: 309)

> "... for the whole of the huge and profound thought collected in the field of morphology, from Goethe to Remane, has virtually been cut off from modern biology (Remane 1952; 2nd edition 1971, no English version). It is not taught in American universities. Even the teachers who could teach it have disappeared." (Riedl 1978: 352; but see Kaplan 2001)

## 5.1 Post-Haeckelian Systematics

Morphology after Darwin became distinctly different from the programme Richard Owen envisaged. Inspired by Haeckel's *Generelle Morphologie der Organismen* (1866), the possibility of documenting, explaining, and representing the origin and diversification of life on Earth blossomed into an active research programme, linking all organisms by their phylogenetic relationships, the study of their parts becoming "evolutionary morphology" (Gegenbaur 1874, 1878) rather than the old "idealistic morphology" of Owen. Haeckel, of course, created the word "phylogeny" (Haeckel 1866: 57), defining it as the "history of paleontological development of organic beings" (Haeckel 1874: 18; translation from Tassy 1996b: 57; see Chapter 4). Hinged on the assumed efficacy of the biogenetic law ("ontogeny recapitulates phylogeny"), Haeckel "promoted it [phylogeny] by analogy with ontogeny" (Patterson 1983b: 1). To represent "the whole of phylogeny", Haeckel (1876: 314) employed the metaphor of a branching tree, a metaphor acquired with the help of Heinrich Bronn and August Schleicher (Chapter 4). Armed with analogies and metaphors the search for the one true tree of life, the one true genealogy, began (Chapter 4).

For Haeckel's biogenetic law to succeed, the course of phylogeny needed to be mirrored sufficiently accurately by ontogeny. As Patterson (1983b) noted, the assumed relationship covered by Haeckel's biogenetic law rapidly fell into disfavour. How could the course of ontogeny be known to mirror phylogeny when no actual phylogenies were available for comparison? The demand, then, was to discover phylogenies without the use of the biogenetic law so that they could then be compared directly with the ontogenetic transformations observed for the features (their parts—their homologues) of organisms and the correlation examined. That task fell to the palaeontologists, who claimed to be able to recreate actual lineages ("pedigrees") from the stratigraphic succession of fossil remains, as "Stratigraphic succession is the only source that has ever been offered for actual ancestor-descendant series" (Patterson 1983b: 14). A shift occurred from the use of Haeckel's biogenetic law as a guide to the phylogenetic succession of organisms, to palaeontology and the succession of fossils in preserved sequences.

Many palaeontologists working in the early 1900s became convinced that they could read evolution directly from the rocks. Thus, palaeontology claimed special and privileged knowledge with respect to phylogeny and constituted *the* fundamental method for its discovery. While the notion was never really quantified by Anglo-American palaeontologists (but see Gingerich 1979), the ideas were discussed by European morphologists; for example, Naef referred to "Das Primat der paläontologishcen Präzedenz" (Naef 1919: 28), "The primacy of paleontological precedence" (Naef 1921–1923: 19; translation from Naef 1972a: 22), the basic idea was that a "good" stratigraphic succession of fossils was required before phylogenetic "trends" might be discovered—once a good fossil record was found, a true phylogeny was near to hand. As Patterson was to later remark, "By about 1960 palaeontology had achieved such a hold on phylogeny reconstruction that there was a commonplace belief that if a group had no fossil record its phylogeny was totally unknown and unknowable" (Patterson 1987a: 8)—and while that viewpoint seems to have not completely disappeared—"The stratigraphic sequence of fossils is the truth, it may not be the whole truth, but it is certainly nothing but the truth" (Paul 2001: 16, Paul 1992, Foote 1996; cf. Forey 2004)—by the beginning of the 1970s, that 100-year-old grip was failing (Chapter 6).

Nevertheless, with respect to homology and taxa, there was early resistance to Haeckel's "phylogenetic" vision, particularly among German morphologists, primarily motivated by a critique of Haeckel's recapitulationist version of the biogenetic law (Nyhart 1995, Breidbach 2002). A new generation of post-Haeckelian morphologists attempted to expand and develop Richard Owen's "homological anatomy" research programme, but within a phylogenetic context (Naef 1917, 1919, 1927, Jacobshagen 1924, 1925, 1927, Kälin 1933, 1936, 1941, 1945, Zangerl 1948, Remane 1952). The desire was to separate morphological principles from phylogenetic speculation. As Lubosch noted, there was a "young generation of comparative anatomists, the first to vouch for the independence of comparative anatomical research" (Lubosch 1931: 60; our translation), and, according to Trienes, the group had "enough weight to constitute an actual movement" (Trienes 1989: 24). More recently, Coleman suggested that "The history of comparative anatomy that Lubosch wrote for the first volume of Bolk's *Handbuch der vergleichenden Anatomie der Wirbeltiere* seems to the pragmatic eye to be a never-never land of morphology" (Coleman 1980: 178).

## 5.2 After Haeckel: Spemann and Homology

In the mid-1950s Richard Goldschmidt (1878–1958), the *bête noire* of the modern synthesis (Dietrich 1995), was encouraged to publish his memoirs, which duly appeared as a series of short biographical vignettes of zoologists he encountered during the first half of his career (Goldschmidt 1956, 1966; he later wrote a "proper" autobiography, posthumously published, Goldschmidt 1960). Goldschmidt was the perfect person for informed reminiscences, having met and interacted with many different German zoologists, from the elderly and famous Ernst Haeckel through to the curious enigma of Paul Kammerer. Among these encounters, Goldschmidt was present when Hans Spemann (1869–1941) gave his lecture for the professorship of the University of Rostock, "a small and unimportant chair . . . " (Goldschmidt 1956: 10). Goldschmidt and Spemann were both candidates for the position; Spemann was successful. Goldschmidt attributed part of Spemann's success to a presentation he gave a year earlier "on the problem of homology". Spemann's account contrasted the discovery of homology from the perspective of the then new science of "experimental embryology" with "the old-fashioned phylogenetic morphology":

> In the discussion he [Spemann] was violently assailed by some of the more old-fashioned colleagues, especially the nasty and aggressive Plate. Spemann had tried to derive ideas from results of experimental embryology while his opponents introduced the old-fashioned phylogenetic morphology and refused to even understand the logic of Spemann's arguments. (Goldschmidt 1956: 11)

After Spemann became Associate Director of the Kaiser Wilhelm Institute of Biology at Berlin-Dahlem in 1914, he published his thoughts on homology in a lengthy essay in the *Die Kultur der Gegenwart* series (Spemann 1915)—which happened to include a chapter by the "nasty and aggressive Plate" (Plate 1914; see Levit & Hoßfeld 2006). Spemann's essay began with a historical perspective, dividing the history of the homology concept into three periods: The first he called "idealistic", founded on the works of such people as Goethe, Geoffroy St. Hilaire, and, towards the close of this period and perhaps indicating to Spemann its finale, Richard Owen. The second period he called "historical", based on the re-interpretations of the "natural system" (archetype to ancestor, see Chapter 7) made by people such as Darwin, Haeckel, Lankester, and Gegenbaur (Russell 1916), who Spemann saw as its main practitioners. The third period, the one he was attempting to usher in, Spemann called the "causal-analytical" period, based on *Entwicklungsmechanik*, a discipline he was helping to develop (Nyhart 2002). As Laubichler has recently noted, "Spemann was reacting against the then widespread fashion of deriving phylogenies based on comparative anatomical and embryological data that relied heavily on what he defined as the historical concept of homology (phylogenetic and ontogenetic continuity)" (Laubichler 2000: 777). Spemann's essay was to be much discussed and cited among morphologists for many years to come, but rarely was the "the old-fashioned phylogenetic morphology" simply defended. The German approach to morphology (and homology) was to develop in its own direction.

## 5.3 Adolf Naef and "Systematische Morphologie" (Systematic Morphology)

In the early 1900s a new generation of scientists—mostly from Germany—tackled anew the issues of morphology, especially from the perspective of "evolutionary morphology", a discipline made significant by Haeckel and Gegenbaur (Breidbach 2006). Among these the most notable were Adolf Naef (Boletzky 1999, 2000) and Joseph Kälin (Anonymous 1966). Both of these men were firm in their rejection of the phylogenetic ("historical") homology concept—but, equally, they were firm in their rejection of Spemann's causal-analytical concept. Naef, in particular, wanted to understand the working of "natural systematics" by investigating the basics of the subject, examining its rudiments, so to speak:

> For decades, phylogenetics lacked a valid methodological basis and developed on the decayed trunk of a withering tradition rooted in the idealistic morphology and the systematics of pre-Darwinian times. There was talk of systematic "tact" and morphological "instinct", terms which were felt rather than understood and consequently insufficient to form the frame of a science which required sound definitions and clearly formulated principles. (Naef 1921–1923: 6–7, from the English translation, Naef 1972a: 12)

Adolf Naef (1883–1949) was Swiss by birth, born on May 1, 1883. He studied at the University of Zürich, under the guidance of Arnold Lang (1855–1914), "A former Professor of the Jena University and close friend of Ernst Haeckel, but definitely not a 'fervent disciple"' (Boletzky 2000: xi, 1999, Levit and Meister 2006: 292–296; for portraits of Naef see Boletzky 1999, 2000 and Ghiselin and Groeben 2000, Fig. 8; for Arnold Lang see Hescheler 1915, Haeckel 1916). Naef visited the Zoological Station at Naples in 1908, shifting his studies from other molluscs to the squid *Loligo vulgaris*, completing his dissertation on that animal, publishing his results just a year later (Naef 1909). He remained in Naples until 1916 and returned in the mid-1920s to continue his study on cephalopods, the results eventually published in the *Fauna und Flora des Golfes von Neapel und der Angrenzenden Meers-Abschitte* (*Fauna e Flora del Golfo di Napoli*) series (Naef 1921–1923, 1928), both, after a long period of time, eventually translated into English (Naef 1972a, 1972b, 2000). He became Professor at the University of Zagreb in 1922, and Professor of Zoology at the University of Cairo in 1927.

Prior to the publication of the first part of his cephalopod monograph, Naef published two short studies explaining in detail the principles behind "Systematische Morphologie" (Naef 1917, 1919—the 1919 study, *Idealistische Morphologie und Phylogenetik*, was originally intended to be part of the first monograph, Naef 1921–1923; see translation 1972a: 11). These two works had their origin in Naef's first research topics, the marine molluscs. Between the two parts of the cephalopod monograph (1921–1928), Naef completed a study on fossil coleoid cephalopods (Naef 1922, which has recently been translated; Naef 2004). Practically all of Naef's subsequent publications dealt with vertebrates, but all within the "Systematische Morphologie" he outlined at the beginning of his career (Naef 1931a, b, 1933).

Naef began studying Molluscan morphology (Naef 1911, 1913), coupling these studies with a critical examination of Haeckel’s “biogenetic law” (Naef 1913: 333; 1917, 1920, 1928). Haeckel’s theory was supposed to meld phylogenetic reasoning with ontogenetic development, thereby explaining phylogeny—or at least providing a tool for biologists to directly discover (and confirm) historical relations. Naef firmly rejected Haeckel’s biogenetic law and proposed a “systematic morphology” (first discussed in Naef 1913: 344) as

> Phylogenetic and natural systematics deal with the same factual material, and although each has different basic concepts, both disciplines can be united in a single concept because their objects are so similar. I have therefore proposed the name “systematic morphology” for this concept (Naef 1913). … It is intended to show that there is an inner relationship between natural systematics and (comparative) morphology. (Naef 1921–1923: 7, from the English translation, Naef 1972a: 12)

Naef’s “systematic morphology” was a stripped-down version of comparative biology, taking much from Richard Owen’s 19th-century “homological anatomy”, the attempt to discover precise relationships among taxa by comparing the parts of organisms—homologues or namesakes. Naef found the basis of these views in Goethe, whom he read differently to Haeckel (Chapter 3, Breidbach 2003). Naef’s contribution developed and elaborated a structural concept of homology that was dependent neither on embryology, “phylogenetic homology”, nor any other causal-analytical processes. He also wished to explore the relationship between systematics and morphology, that is, to demonstrate the relationship between conclusions (taxa) and evidence (homologues). Sadly, the developments and progress made by this group of morphologists went largely unnoticed in the Anglo-American literature, except for the occasional dismissive remark.[1]

Many of Naef’s ideas, from the vantage point of the 21st century, appear remarkably modern.[2] For example, he wrote of the “Ideal genealogical tree” (Naef 1921–1923: 13, Fig. 2, from the English translation, Naef 1972a: 17, Naef 1919: 20, Text-fig. 2; see Figure 5.1a, b—compare this tree with those in Chapter 1, Figure 1.8), suggesting that the “only way to achieve this is if the typical relationships are thoroughly worked out, i.e., if the genealogical tree is the result of a comparative morphological study” (Naef 1921–1923: 13, from the English translation, Naef 1972a: 17).

This tree was compared to a scheme of taxonomic categories (Figure 5.1b), noting that “Conventional systematics with its hierarchy of classes, orders, families, etc. should express the typical relationships of the genealogical tree” (Naef 1921–1923: 15, Fig. 3, from the English translation, Naef 1972a: 19, Fig. 3; Naef

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[1] Simpson (1961), Mayr (1969); current commentary treats Naef more fairly: Trienes (1989), Boletzky (1999), Breidbach (2003), Willmann (2003), but see Starck (1980) and the closing remarks in Hoßfeld & Olsson (2003: 300).

[2] The following text is based on the English translations of Naef (1921-1923, 1928) (1972a, 1972b, and 2000, respectively). Naef retained his ideas almost intact from 1913 onwards, many of the same diagrams appearing in subsequent works. Although his 1917, 1919, and the two 1931 studies are best known, they do not deviate significantly from principles outlined in the 1921-1923, 1928 monographs. A discussion of Naef’s publications can be found in Williams & Ebach (submitted).

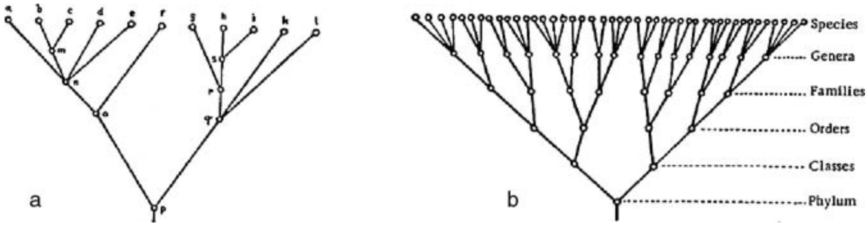

**Fig. 5.1a, b** After Naef (1919), see text for explanation

1919: 47, Text fig. 3; see Figure 5.1b). Naef concludes with a discussion of problems in classification, which need not concern us here, except to note that Naef advocated the necessity of classifying only monophyletic groups:

> With adequate knowledge of the phylogeny, one rule would suffice; "to place in a systematic group always all such forms which are derived from a common ancestor". (Naef 1911: 152; translation from Bieler 1992: 311)

And as Reif noted:

> Naef betont wie die Kladisten und die transformierten Kladisten daß nur im strengen Sinne monophyetische Gruppen verwendet werden können, daß Schwestergruppen zu koordinieren seien und daß es keine objektiven Anhaltspunkte für die Ranghöhe von Taxa gebe. (Reif 1998: 417, "Naef stressed, that like Cladists and transformed cladists only in the strict sense can monophyletic groups be used and that co-ordinated sister groups do not give objective reference points for the rank of taxa", our translation)

Although there is a *direct* relationship between a genealogical tree and a classification, Naef's interpretation of the nodes on respective trees is clear:

> Here it must be made very clear that I am absolutely not opposed to the theory of heredity. That theory was our starting point and is our ultimate destination. But I consider the theory to be incomplete and in need of further development. A more profound development of systematic morphology may further improve knowledge of phylogeny, which actually depends on morphology. One should not commit the error of believing that searching for "relationships of form" and for ancestors is one and the same thing! (Naef 1922: 4, from the translation in Naef 2004: 4)

Finding the genealogical tree, Naef outlined his notion of "morphological primacy": "… the type occupies a prominent place within the 'group' or systematic category which it characterizes. This position may be named the 'morphological primacy' of the type" (Naef 1921–1923: 19, from the English translation, Naef 1972a: 22). The type is a "tertium comparationis"[3] (Naef 1921–1923: 37, from the English translation, Naef 1972a: 37). One might define "tertium comparationis" (the third aspect of comparison—"the quality that two things which are being compared have in

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[3] "The morphotype is not a hypothetical ancestral condition, but rather a methodological tool, serving as a tertium comparationis whenever structures in different taxa belonging to the group are compared, an operation quite similar, in principle, to using a standard length (e.g., the standard meter) for measuring (=comparing) one unknown distance with another" (Zangerl 1948: 56); see also Zangerl et al. (1998: 56).

common. It is the point of comparison which prompted the author of the comparison in question to liken someone or something to someone or something else in the first place" (Wikipedia defintion[4]).

Naef outlined seven criteria, three of major significance, four "auxiliary" (Naef 1921–1923: 19–23, from the English translation, Naef 1972a: 22–27). The three major criteria are

1. The primacy of systematic precedence
2. The primacy of ontogenetic precedence
3. The primacy of palaeontological precedence

The primacy of systematic precedence reiterates a general understanding of comparative biology, "that a character typical for an entire group of forms has to be considered also typical for the sub-groups, provided it occurs in them" (Naef 1921–1923: 19, from the English translation, Naef 1972: 22). The idea rested with similarity of plan and with homology, defined by Naef as

> If two organisms are constructed according to the same plan, we consider a given part of the one homologous to a given part of the other, provided that both parts are represented by one in the common plan. (Naef 1928: 6, from the English translation, Naef 2000: 7; see also Naef 1926)

This concept Naef found useful in ontogeny, where he identified "homologous stages",

> If two organisms develop according to the same plan, we consider a given stage of one as homologous to a given stage of the other, provided both stages are represented in the common ontogenetic plan. (Naef 1928: 7, from the English translation, Naef 2000: 8)

Thus, the primacy of ontogenetic precedence "follows from the general experience that the degree of similarity between morphological related organisms increases at the beginning of development" (Naef 1921–1923: 19, from the English translation, Naef 1972a: 23). Naef noted that this allowed the idea that "only homologous stages permit, strictly speaking, discussion about homologous parts" (Naef 1928: 8, from the English translation, Naef 2000: 8; see Figure 5.2).

The primacy of palaeontological precedence "was not clearly formulated by the idealistic morphology" (Naef 1921–1923: 22, from the English translation, Naef 1972: 25). Nevertheless, Naef elaborates, with comments on the incompleteness of the fossil record ("The gaps in the paleontological picture") and the lack of agreement between palaeontological sequences and systematic sequences, yet comments that "both the ontogenetic and paleontological data strongly support our systematic-morphological concept. Mainly because of them the 'natural system' appears as a formulation of facts which must and can be explained…" (Naef 1921–1923: 22, from the English translation, Naef 1972: 25).

The auxiliary principles were

4. The primacy of typical correlations
5. The primacy of complete development

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[4] http://en.wikipedia.org/wiki/Tertium_comparationis.

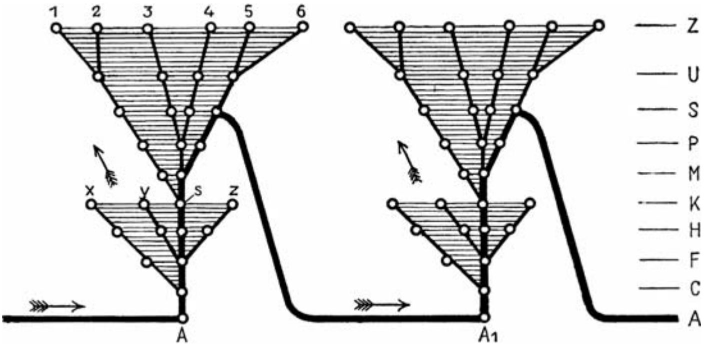

**Fig. 5.2** After Naef (1913: 351, Fig. 2, Naef 1928: 8, text figure 1; see English translation, Naef 2000: 8, text figure 1)

6. The primacy of monomorphous development of homonomous parts
7. The primacy of monomorphous structures in individuals of the same species

Earlier, Naef (1919) outlined six criteria, three major, three auxiliary:

I. Das Primat der ontogenetischen Präzedenz
II. das Primat der paläontologische Präzedenz
III. das Primat der systematischen Präzedenz
IV. das Primat der typischen Korrelation
V. das Primat der vollständigen Entwicklung
VI. das Prinzip des morphologischen Mittelwertes (Naef 1919: 26–33).

It was the 1919 series of criteria that attracted attention, focus being placed more on the auxiliary criteria, especially "das Primat der typischen Korrelation" (the primacy of typical correlations) and "das Prinzip des morphologischen Mittelwertes", the first becoming associated with congruence, the second with "transformations" via "morphologischen Mittelwertes" (Chapter 8).

Naef returned to the three major parameters of "precedence" (systematic, palaeontological, ontogenetic), discussing them in terms of "phylogenetic evidence" (Naef 1921–1923: 31–37, from the English translation, Naef 1972a: 32–36). For Naef, of least significance is the evidence from palaeontology, which "does not provide direct evidence for a line of descent. ... From the phylogenetic aspect, paleontology is thus placed at a disadvantage with respect to ontogenetics, in which morphological relationships can be interpreted historically as natural and coherent connections" (Naef 1921–1923: 33, from the English translation, Naef 1972a: 33). Thus, a measure of understanding is obtained from the ontogenetic trajectories of characters, a viewpoint that was eventually called "Naef's theorem" but seems related to ideas of Goethe (Løvtrup 1978: 350; see Chapter 10 and Figure 5.3 and Chapter 3 for Goethe).

Adolf Remane, in his *Die Grundlagen des natürlichen Systems, der vergleichenden Anatomie und der Phylogenetik* (1952; see also Remane 1955, 1961),

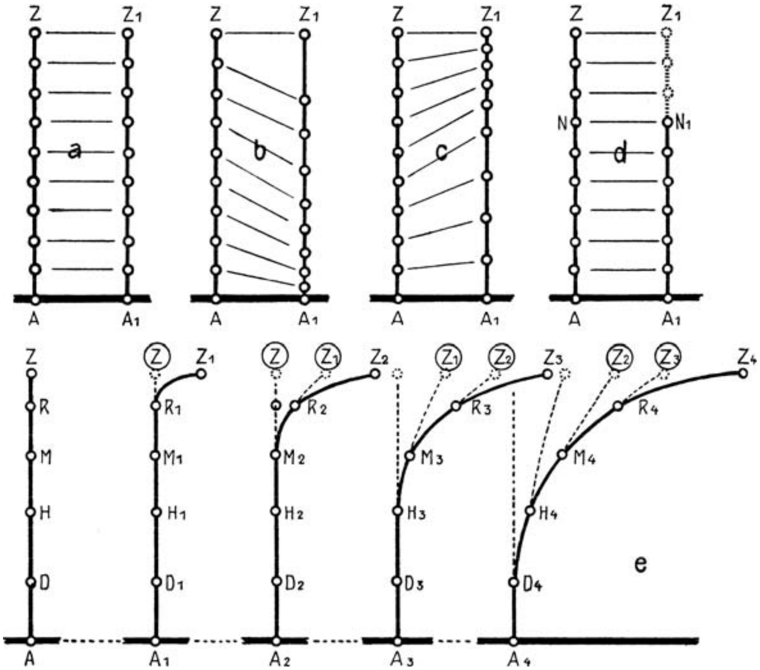

**Fig. 5.3** After Naef (1913: Fig. 3 and Naef 1917: 36, Fig. 3)

discussed criteria of homology, which have received a good deal of attention.[5] Remane proposed three principal (main) criteria ("Hauptkriterien", Remane 1952: 63) and three auxiliary criteria ("Hilfskriterien", Remane 1952: 64), discussed in greater detail in Chapter 8. Here it is of note that Remane's criteria, while much like Geoffroy-St. Hilaire's *Principle of Connections* and *Principle of Composition*, grew from Naef's statements of morphological precedence—Remane's criteria having much in common with Patterson's tests of homology (Patterson 1982a, 1988a; see Chapter 8).

Of Naef's work, Reif offered the following:

> . . . a close look at Naef's methodology shows that it forms the basis of a Darwinian, structuralist morphology, rather than a mystical speculative typology. (Reif 1998: 413; translated by Boletzky 2000: xi)

And Boletzky summarised:

> . . . as far as Naef is concerned, his careful reassessment of "idealist morphology" should not be taken as the sole content of his method! (Boletzky 2000:xi; Boletzky 1999)

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[5] Hennig (1950: 172, 1953: 11, 1966a: 94), Kiriakoff (1954a), Simpson (1961: 93), Sokal (1962), Eckhart (1964), Sattler (1964, 1984: 338), Bock (1969, 1974, 1977, 1989), Hagemann (1975), Riedl (1978: 34, 1983: 211, 1989: xiv), Wiley (1981: 131), Froebe (1982: 25), Kaplan (1984: 54, 2001), J. Remane (1985: 169-170, 1989), Rieppel (1986: 198), Ax (1987: 160), Sluys (1989), Mayr & Ashlock (1991: 143), Donoghue (1992: 172), Schmitt (1995: 428), Hazspruner (1998: 335).

Naef died on May 11, 1949. His passing went virtually unnoticed save a brief mention in *Revue Suisse de Zoologie* (1950: 451) and a notice in the Swiss newspaper *Neue Zürcher Zeitung* (1949[6]).

Just a few months after his death, on a different continent, the book *Genetics, Paleontology & Evolution* (Jepson et al. 1949) was published, a contribution Mayr often spoke of as expressing the solid foundation of the modern synthesis (Mayr & Provine 1980). In that book, D. Dwight Davis contributed a chapter, "Comparative anatomy and the evolution of vertebrates" (Davis 1949; see Davis 1960). Davis included a short paragraph on "The Neo-Classicists", noting that the "neo-classical school of idealistic or 'pure' morphology, led by Jakobshagen, Naef, and Kälin, has returned to the non-phylogenetic type concept of Goethe" (Davis 1949: 65). Davis offers a perfunctory description of the work of these men, "Certainly the interpretation of homology that Kälin has developed is far more logical than the recent crop of illogical and poorly thought-out suggestions by non-morphologists" (Davis 1949: 66; see also Ghiselin 2006: 314).

Apart from Davis' contribution, most English-speaking biologists were made aware of the ideas of Jakobshagen, Naef, and Kälin (especially the latter two) from a paper by the palaeo-herpetologist Rainer Zangerl (1912–2004) (Zangerl 1948, but see Sokal 1962 and Kuhlenbeck 1967 [1966]; biographical details for Zangerl can be found in Richardson & Turnbell 1981 and Schultze 2005). Zangerl never changed his views on the importance of morphology as a science independent of phylogenetic "speculation", and throughout his life continued to stress the importance of the work Joseph Kälin (Zangerl 1948, Zangerl et al. 1998: 56, and pers. comm., 2003: "The comparative morphological method furnishes the data for our evolutionary conclusions"). As Zangerl stressed:

> It may again be pointed out that neither Naef, nor Kälin, nor this writer intend to advocate a return to pre-evolutionary thinking, or to suggest that morphological results should be considered as ends in themselves. All of these writers firmly confess to an evolutionary outlook. (Zangerl 1948: 352) . . . [Their work] merely attempts to separate phylogenetic thinking from morphological thinking, and put both on a sounder basis. (Zangerl 1948: 371)

The works of Naef, and especially Kälin, were ably summarised in Zangerl (1948), a contribution of which Ernst Mayr, who was editor of the journal *Evolution* at the time of its publication, thought "would serve 'no good purpose' to continue with that 'discussion"' (Cain 1994: 420, 2003[7]). Rainer Zangerl's paper was all

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[6] The notice read: "Adolf Naef +. B. P. On 11 May Prof. Dr. Adolf Naef, Professor of Zoology at the University of Cairo, passed away in his 66th year after a serious illness. A pupil of Arnold Lang, Naef first studied cephalopods. His monograph of this group of animals is of fundamental importance. It served as starting point for an excellent study of fossil [coleoid] cephalopods. Subsequently Naef expanded his studies to cover vertebrates. His works on general questions in biology are of very great significance, especially as expressed in his book 'Idealistic morphology and phylogenetics'. The untimely death of Adolf Naef takes away one of the leading researchers in the field of comparative anatomy." Translation kindly provided by Sigurd von Boletzky.

[7] Jean Hough offered a critique of the Zangerl paper. Mayr's response was as follows (November 14, 1949): "I greatly regret the fact that you did not get in touch with me when you started working on your answer to Zangerl. I then could have given you a little information on the history of that paper, as well as on the editorial policy of Evolution. I might have explained to you that Zangerl's

but strangled at birth, its development stifled and the most prominent members of these morphologists were paid little, if any, attention. Zangerl and Davis were to work together for a short while—translating Willi Hennig's *Phylogenetic Systematics* from German to English (Schmitt 2001).

Yet in spite of any consensus on the evolutionary process in the 1940s and 1950s—real or apparent—Erik Stensiö and Erik Jarvik, two influential palaeoichthyologists, would continue their stunning morphological work, gaining inspiration from the studies of Adolf Naef (their relevance is documented in Chapter 6).

## 5.4 Konrad Lorenz, Homology, and Systematics

Some 25 years after Spemann's account of homology, another German, Konrad Lorenz (1903–1989), wrote on the subject, somewhat indirectly at first, through a comparative study of the Anatinae (a group of birds that include the dabbling ducks; Lorenz 1941[8]). In this work, Lorenz published what has since been recognised as one of the first modern "phylogenetic schemes", first published as a fold-out table in Lorenz (1941); the same diagram was later reproduced in the English translation as a single figure with the names of the birds added to the tips of the tree (Lorenz 1953). It is the latter diagram that is usually reproduced (Craw 1992, Fig. 3c and Willmann 2003: 475, Fig. 8—see Figure 5.4).

The purpose of Lorenz's diagram was to indicate the characters (homologues) that united various taxa at different levels in their phylogenetic development. Lorenz's diagram was not too dissimilar from the more well-known argumentation schemes made popular by Willi Hennig (for example, Hennig 1957: 66, Abb. 9; see Chapter 8, Fig. 8.1). On more than one occasion, Lorenz acknowledged his debt to the concept of homology (Lorenz 1947, 1950, 1953) and, indeed, to comparative biology as a whole (Lorenz 1950, Müller 2001). Lorenz had adapted what he considered to be a version of the "old phylogenetic homology", and reaped rewards from its application to behavioural characteristics in birds. In what may have been one of Lorenz's last published articles, he wrote

> I had the benefit of a very thorough instruction in the methodological procedure of distinguishing similarities caused by common descent from those to parallel adaptation. …

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paper was published only very reluctantly and very specifically to place on the record the minor opinion of the typologists. It was agreed by the members of the Editorial Board that it would serve no good purpose to continue the discussion after the publication of the Zangerl paper because all of its statements had been more than sufficiently answered by previous papers. In fact, the timing of the Zangerl paper, after the earlier publications of Hubbs, Simpson, Haas and others served to bring out the ludicrous anachronism of the Zangerl paper. As far as Evolution is concerned, the essential point is that any further discussion of the typological homology concept would not be a contribution either to the factual repertoire or the theory of evolution." Mayr's comment on the "minor opinion of the typologists" seems even more significant given that his efforts to document taxonomists' use of essentialism and typology are now construed as "wrong and harmful in its basic message" (Winsor 2003).

[8] The English translation appeared in 1953 (Lorenz 1953).

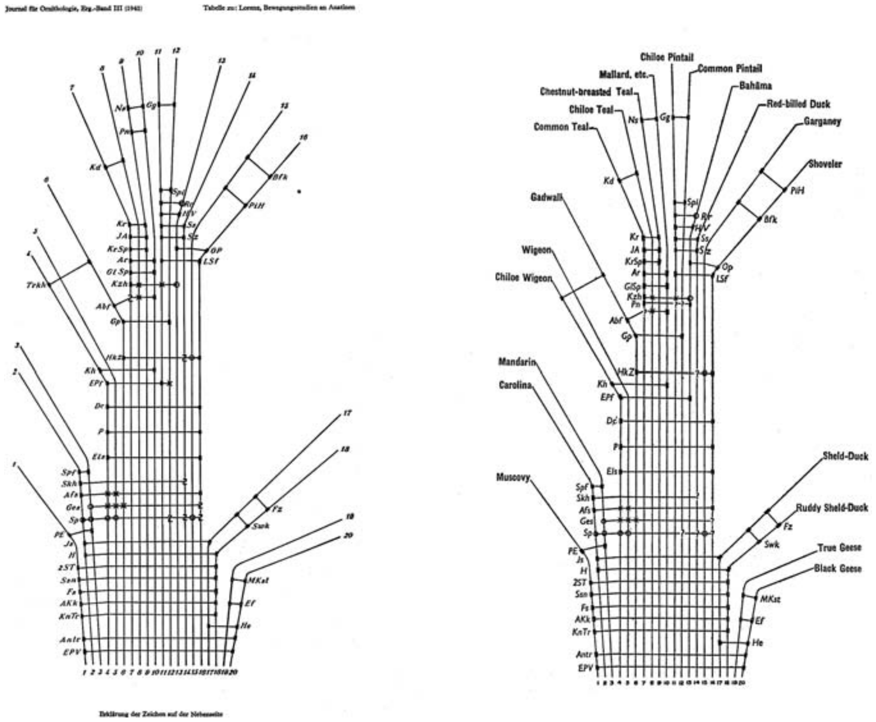

**Fig. 5.4** (a) After Lorenz (1941). (b) After Lorenz (1953)

> Perhaps I should mention here that this procedure has led me to the discovery which I personally consider to be my own most important contribution to science. Knowing animal behavior as I did, and being instructed in the methods of phylogenetic comparison as I was, I could not fail to discover that the very same methods of comparison, the same concepts of analogy and homology, are as applicable to characters of behavior as they are in those of morphology. (Lorenz 1974: 231)

Lorenz's article appeared in the journal *Science*. It was a translated (and slightly modified) text of a lecture he delivered in Stockholm, on December 12, 1973, on receiving the Nobel Prize in Medicine or Physiology, nearly 40 years after Hans Spemann had received the same prize (in 1935). Significant developments in biology appear to be marked by developments in the concept of homology.

## 5.5 Willi Hennig and the Resurrection of Transformational Systematics

A little while after Zangerl had published his "ideal morphology" summary (Zangerl 1948), two significant German books were published: Willi Hennig's *Grundzuge einer Theorie der phylogenetischen Systematik* (1950) and Adolf Remane's *Die Grundlagen des natürlichen Systems, der vergleichenden Anatomie und der*

*Phylogenetik* (1952). According to Rupert Riedl, "Remane's absolutely decisive contribution [Remane 1952], however, was never translated. The fault must have lain in the mistrust that people in 'modern countries' brought to the 'old morphology"' (Riedl 1983: 211, Zachos & Hoßfeld 2001, 2006, Hoßfeld et al. 2003). For George Gaylord Simpson Remane's book was "... another exceptionally valuable book on taxonomy in general" (Simpson 1961: 93). Given Mayr's antipathy to German morphology ("Morphology is nothing but German idealistic philosophy", Mayr in Riedl 1983: 206), it is not surprising that early on Kiriakoff felt the need to note of Hennig's (1950) work: "It is a pity that modern phylogenetic systematics seems to be quite unknown in the United States" (Kiriakoff 1959: 118), a sentiment soon echoed by Sokal & Sneath (1963: 21) and, later, by Nelson (1973a: 451; see also Nelson 1970).

In spite of its remarkable influence, Remane's book remains untranslated. Hennig's *Grundzuge einer Theorie der phylogenetischen Systematik* ("Perhaps the most important nonavailable book during the past two decades for English-speaking people...", Bock 1968: 646) was never translated, but the revised and expanded English version (Hennig 1966a) was to have a remarkable impact on comparative biology (Schmitt 2001).

Naef wrote disparagingly (see quote above from Naef 1921–1923: 7, from the English translation, Naef 1972a: 12, 1919: 25; that is, without approval, contrary to Willmann's [2003: 462], interpretation of Zimmermann 1953: 403; see also Breidbach and Jost 2006: 20) of "systematic 'tact' and morphological 'instinct"' as explanations of discovery, words echoed later by Lorenz, who wrote of the "Classifying Instinct" (Lorenz 1941: 198 "systematische Taktgefühl", perhaps better translated as something similar to Naef's "systematic tact"; Lorenz 1953: 1) and that "the 'classifying instinct' does all this without the man who possesses it needing to analyse it himself. However, only when the analysis is accomplished does his performance become science" (Lorenz 1941: 198, 1953: 2; see Chapter 3). Both Naef and Lorenz understood that while systematics did indeed seem to work (relationships of organisms were apparent), the question they addressed was how. Another man, Willi Hennig (Schmitt 2001), was drawn to the protestations of Naef and Lorenz, citing them both, almost on the same page of his first book on systematics (Hennig 1950: 188); Hennig, like Naef, set himself the task of discovering exactly how systematics worked (Hennig 1950; see also Rieppel 2003a: 179).

Hennig included a discussion of "recapitulation", Haeckel's version of the threefold parallelism, and commented on Sewertzoff's 1931 book (Sewertzoff 1931;[9] Hennig 1950: 335, 1966a: 96). Remane's (1952) homology criteria resemble Hennig's "rules" (Schmitt 2001), which in turn resemble Naef's criteria of "morphological primacy", also discussed with reference to Haeckel's threefold parallelism; Hennig borrowed from both Naef and Remane (Hennig 1953, 1966a).

Like much German biology during the middle of the 19th century, it was almost drenched in complex philosophy. Kälin's *Ganzheitliche Morphologie und*

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[9] Ghiselin wrote of Sewertzoff's book that "His analysis included a magisterial treatment of the ontogeny-phylogeny issue, which justified Haeckel but accounted for the many exceptions to the biogenetic law" (Ghiselin 1980: 189; see Levit et al. 2004).

*Homologie* (*Integrated Morphology and Homology*) (Kälin 1941), for example, begins with many complex philosophical issues, much of which is difficult, if not impossible, to translate accurately into English. Rieppel (2003a) noted similar passages in Hennig's major works, even passages that have been rendered into English and appear in his most popular books (Hennig 1966a). Nevertheless, Hennig's task can be understood better if it is perceived as an attempt to replace the notions of systematic morphology with a concept of transformation, applied to characters, rather than taxa, as Haeckel did (this is discussed further in Chapter 8).

The concept of transformation was popularised by Haeckel, via his aphorism "ontogeny recapitulates phylogeny". Von Baer, like Schelling and other *Naturphilosophen* of the 19th century, was concerned with understanding the archetype. As with most scientists working at that time on development (ontogeny), propositions of mechanisms and processes dominated their studies. The need at the time to adopt a model for the development of form and to explain the gestalt archetype between different forms helped secure a concept of transformation (Chapter 3). If the unspecialised structures in an embryo can develop into specialised structures in an adult, then why not a less ideal taxon develop into a more ideal one? The concept of the archetype changed from that of a blueprint encompassing all forms, to that of a primitive organism from which all others may be derived.

A change in the gestalt archetype also meant that concepts of homology had to change. Owen's primary form, the gestalt archetype, adopted by Darwin, was the precursor to the evolutionary ancestor. And the transformations between the homologues of organisms led to the concept of evolutionary transformations. Goethe's archetype, too idealistic and complex for evolutionary biology, was quickly forgotten in the Anglo-American literature. Instead, it flourished in the German literature, almost as a defiant gesture against Ernst Haeckel.

Haeckel, a self-proclaimed "monist", was in fact perhaps the greatest dualist in German biology. His misreading of Goethe and rapid acceptance of Darwinism made his ideas and work anathema to many European systematists. Louis Dollo (1857–1931) and Othenio Abel (1875–1946), for example, continued Goethe's idea of a specialised hierarchy that related two organisms to a third—the archetype or *tertium comparationis*. Dollo's concept of Spezialisationskreuzungen is a direct reference to Goethe's trend from the less to the most ideal taxon (see Nelson 2004; Chapter 3).

Via the concept of character phylogeny, Hennig attempted to introduce the concept of transformation into homology, where before it resided in the taxa described (*homologues*, the evidence; *taxa*, the conclusions). The cladistic revolution that took place soon afterwards collided head on with the transformational version of homology perpetuated by Darwin and Haeckel in the 19th century and by the Modern Synthesis in the early 20th century. The task of solving systematic problems of relationships was turned on its head. Transformational notions of homology conflicted with the concept of homology as relationship (between different manifestations of the same structure). In order to investigate this conflict further and gauge its significance, it was important to discover—if such was possible—a unit of relationship, the analytical equivalent of the *tertium comparationis*.

The history of Haeckel's legacy, Naef's criticism of it, and the continued use of transformational studies led to perhaps the greatest intellectual battle in systematics since the Geoffroy St. Hilaire–Cuvier debate in the mid-19th century. The battle is a direct result of interpreting what was to become Naef's *tertium comparationis,* namely relationship as similarity, relationship, or descent. This conflict started with a simple branching diagram, a structure that has become symbolic for two very different fields within comparative biology, phylogenetics and pattern cladistics.

## 5.6 A Postscript on Naef's Criteria: Patterson's Homology Testing

From a cladistic perspective, Patterson (1982a: 37) summarised the two prevailing approaches to homology testing, both summaries of Naef's criteria (see Chapter 8):

1. **The Similarity Test.** Homologies may be rejected because of "dissimilarity": "... shared similarity is the *only valid empirical test of homology*" (Bock 1977: 882).
2. **The Congruence Test.** Homologies may be rejected because they fail to specify a group resolved by other homologies: "Hypotheses of homology may be tested with other hypotheses of homology" (Wiley 1974: 240, Wiley 1981: 130, 138).

For Patterson, however, the difference rested not with the relative importance of the two tests, but with the result of their combination. In all, Patterson suggested three tests to discover homology: similarity, conjunction, and congruence. If all three tests are passed, homology is effectively discovered. Failing one or more of these tests yields "relations" that differ from homology but might still be useful for systematics. Patterson presented the three tests as a series of comparisons giving a total of eight possible relations: homology, homonomy, the complement relation, two homologies, parallelism, multiparallelism,[10] convergence, and multiconvergence[11] (Table 5.1). Of these relations, he considered only the first four—those that pass the congruence test—useful for systematics as they identify, "define", or diagnose particular taxa.

Rieppel (1988: 59–60) modified Patterson's tests, by omitting the conjunction test, reducing the number of relations to four. He presented his revised scheme in the form of a flowchart (Rieppel 1988: 60, Fig. 5.4). It is presented here in tabular form (Table 5.2).

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[10] Patterson suggested "homeosis" as the relation that passed only the similarity test. In his 1988 paper, the term "homeosis and multiple parallelism" was used (Patterson 1988a: 606, Table 2). We will use the general term "multiparallelism" except where it is necessary to be more specific (cf. Patterson 1988a: 611, Table 3).

[11] Patterson suggested the presence of an endoparasite as an example of a relation that might fail all three tests (Patterson 1982a: 48). In his 1988 paper, he substituted "endoparasitism and multiple convergence" for the relation that failed all three tests (Patterson 1988a: 606, Table 2). We use the general term "multiconvergence", except where it is necessary to be more specific (cf. Patterson 1988a: 611, Table 3).

**Table 5.1** Patterson's three tests (after Patterson 1982a, Table II: 47; modified with reference to Patterson 1988a, Table 3: 611). Patterson (1982a: 48) added, "Endoparasitism is entered with a query as the relation which fails all three tests."[a] indicates those relations useful for systematics. Relations in the first column are for morphology, and those in the last column are relations for molecules

| Relation | Congruence | Similarity | Conjunction | Relation |
|---|---|---|---|---|
| Homology [a] | Pass | Pass | Pass | Orthology [a] |
| Homonomy [a] | Pass | Pass | Fail | Paralogy [a] |
| Complement [a] | Pass | Fail | Pass | Complement [a] |
| Two homologies [a] | Pass | Fail | Fail | Two orthologies [a] |
| Parallelism | Fail | Pass | Pass | Xenology |
| Multiparallelism | Fail | Pass | Fail | Paraxenology |
| Convergence | Fail | Fail | Pass | Convergence |
| Multiconvergence | Fail | Fail | Fail | — |

Rieppel's scheme adds a new category, one that has been encountered many times in the past. The issue is best summed up by the following question: Can there be a neutral term for comparisons prior to testing? Here it is only necessary to reiterate Rieppel's conclusions: Initial conjectures of homology are called "topographical correspondences". Therefore, prior to testing, all comparisons would simply be called "topographical correspondences" and become either homology (congruent correspondences) or homoplasy (incongruent correspondences) after analysis.

Rieppel understood "topographical correspondence" to be equivalent to the pre-evolutionary use of the term "homology", which Lankester suggested dropping altogether. Rieppel acknowledged Lankester's (1870a) efforts. Lankester's ideas can also be presented in tabular form to allow direct comparison to Rieppel's scheme (Table 5.3).

Rieppel's and Lankester's schemes are comparable—up to a point. For Lankester, the arbiter between applying the term "homology" and "homogeny" is whether the similarities can be explained by common ancestry: If common ancestry is understood as the cause, the relation is homogeny; if not, the relation is homoplasy.

For Rieppel, the arbiter for sorting "similarities" is not a cause but a further test, congruence. Congruent "similarities" are explained by common ancestry:

> Homology is a conjecture of inheritance from a common ancestor. (Rieppel 1996: 1395)

The shift in emphasis is towards methods of discrimination of the initial comparisons, whatever those comparisons might be called. The shift de-emphasised what "basic data" might be—a general unit of systematics—to the analysis of those data relative to however congruence might be implemented.

**Table 5.2** After Rieppel (1988: 65)

| Relation | Congruence | Similarity |
|---|---|---|
| Homology | Pass | Pass |
| Homoplasy | Fail | Pass |
| "Topographic correspondence" | Pass/Fail | — |
| Non-homology | — | Fail |

**Table 5.3** After Lankester(1870a; but see Spemann 1915[12]). Lankester offered neither a term for comparisons that failed any similarity "test" nor a term for those that passed any similarity "test"

| Relation | Common Ancestry | Similarity |
|---|---|---|
| Homogeny | Pass | Pass |
| Homoplasy | Fail | Pass |
| "Homology" | Pass/Fail | Pass |
| — | — | Fail |

Patterson's tests can be adapted to this tabular form by removing the conjunction test and adding in a column for a neutral, pre-analysis term for the data (Table 5.4). Once again, it seems of crucial significance to be clear about what is being tested; What are these initial conjectures?

Comparisons can be made among the three schemes (Table 5.5).

The distinction between convergence and non-homology and parallelism and homoplasy is of no significance here. The significant aspect is the additional category noted as "homology" in Patterson and "topographic correspondence" in Rieppel but with no equivalent in Lankester. That extra category has surfaced many times since Lankester's work (Table 5.6).

### 5.6.1 The Similarity Test

Most commentators, including Patterson, suggested that "similarity" is not really a test but a way of suggesting which particular homologues are worthy of testing. This viewpoint suggests that only the two remaining parameters (conjunction and congruence) function as tests. Below we suggest that "similarity" does indeed function as a test of sorts and its use, relative to the modern preoccupation with character *x* taxon data matrices, leads to some unexpected consequences.

Rieppel (1988) and De Pinna (1991) both concluded that because testing by similarity occurs prior to character matrix construction, those comparisons that fail the similarity "test" have no effect on any subsequent analysis, as these "comparisons" are simply excluded from further consideration:

> . . . only those characters which pass the test of similarity are of potential interest in phylogeny reconstruction. (Rieppel 1988: 65)
> Characters do not exist before similarity considerations. (De Pinna 1991: 377)

**Table 5.4** Patterson's test in relation to Table 5.2

| Relation | Congruence | Similarity |
|---|---|---|
| Homology | Pass | Pass |
| Parallelism | Fail | Pass |
| "Homology" | Pass/Fail | Fail |
| Convergence | Fail | Fail |

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[12] The tripartite scheme of a generic "homology" with two derivative terms seems to have been first suggested by Spemann (1915) but with a different intention.

**Table 5.5** Comparisons among Lankester's, Patterson's, and Rieppel's "tests"

| Lankester (1870a) | Patterson (1982a) | Rieppel(1988) |
|---|---|---|
| Homogeny | Homology | Homology |
| Homoplasy | Parallelism | Homoplasy |
| — | "Homology" | Topographic correspondence |
| — | Convergence | Non-homology |

Thus, by definition, every comparison that is entered into a character *x* taxon matrix is understood to have passed the similarity test, no matter how crude that test might have been. This observation casts Patterson's test in a different light.

If the relations that pass the similarity test alone are listed, then, for morphology, it would be impossible to discriminate among homology, homonomy, parallelism, and multiparallelism (Table 5.7); and for molecules, it would be impossible to discriminate among orthology, paralogy, xenology, and paraxenology (and pleurology).

Discriminating between homology and homonomy may not be that problematic, as most cases of homonomy are readily recognisable and dealt with easily (e.g., multiple "copies" of leaves). Discriminating between orthology and paralogy might seem equally simple, as multiple occurrences of the same (or similar) genes are relatively easy to note. The more significance case of discriminating between homology and parallelism is dealt with under the congruence test.

If similarity is considered an irrelevant test, then Patterson's remaining two categories (conjunction and congruence) alone are available to discriminate between relations (Table 5.8). The role of the conjunction test is relatively straightforward (see below); therefore, it does seem that only the congruence test is of significance.

With the similarity test omitted, convergence and parallelism are indistinguishable. Patterson's distinction between parallelism (and multiparallelisms) and convergence (and multiconvergence) was that the former passed the similarity test, the latter did not. Interestingly, for molecular data, Patterson concluded that

**Table 5.6** Comparison between terms used for "similarity" and "congruence" (see Table 8.4)

| | "Similarity" "Generic" Term | Common Ancestry [= "Congruence"] | Independent |
|---|---|---|---|
| Pre-Cladistic | | | |
| Cope (1868) | Homology | Heterology | |
| Lankester (1870a) | Homogeny | Homoplasy | |
| Mivart (1870) | Homology | Evolutionary homogeny | |
| Haeckel (1872) | "Homology" | Homophyly | Homomorphy |
| Boyden (1943) | Structural homology | Homology | Non-homology |
| Hubbs (1944) | Homology | Independent homologies | |
| Moment (1945) | Homophyly | Heterophyly | |
| Boyden (1947) | Structural correspondence | Homology | Non-homology |
| Florkin (1962) | Isology | Homology | |
| Bock (1963) | Homology | Non-homology | |
| Hunter (1964) | Paralogy | Homology | |
| Meyer-Abich (1964) | Homology | Isophyly | |
| Jardine (1967) | "Homology" | Phylogenetic homology | |
| Jardin (1969b) | Topographic homology | Phylogenetic homology | |

**Table 5.7** Relations passing the similarity test

| Relation (Morphology) | Similarity | Relation (Molecules) |
|---|---|---|
| Homology | Pass | Orthology |
| Homonomy | Pass | Paralogy |
| Parallelism | Pass | Xenology |
| Multiparallelism | Pass | Paraxenology; Pleurology |

> . . . if there is no deceptive similarity to cause molecular convergence, there is no deceptive similarity to cause the kind of mistake that would occupy the last row in table 5.3 [our Table 5.1, last row]. (Patterson 1988a: 611)

The key here is "deceptive similarity". Patterson (1988a: 611) suggested that similarity in molecular data was a statistical concept, as the ability to be rather precise about the degree of similarity between two (or more) lengths of sequence data can be quantified. No such quantification is available for morphological data, in spite of those who might speak on its behalf and those who continue to search for it (MacLeod & Forey 2001). One might imagine that to distinguish between Patterson's parallelism and convergence, similarity would need to be examined *after* analysis as well as before, forcing the systematist to re-examine the information more carefully, "checking and re-checking the data" (Hennig 1966a). Although this is a worthwhile exercise, we would be surprised if a certain amount of incongruence (conflict) did not remained.

If the relations are listed that pass only the similarity test, then it is impossible to discriminate among the complement relation, two homologies (two orthologies), convergence, and multiconvergence (Table 5.9). Initially, it might seem peculiar to contrast the complement relation with convergence. Yet the complement relation fails because of a presence-absence dichotomy—something (a presence) cannot be compared with nothing (an absence), whereas convergence simply fails to satisfy any kind of comparison. Both might seem meaningless comparisons in the first place.

As De Pinna & Rieppel stress, admitting characters into a matrix acknowledges they have passed the similarity test and as a consequence any incongruent similarities are rated as parallelisms or multiparallelisms (following Patterson's nomenclature). After a detailed discussion, Rieppel concluded that relations that fail the similarity test could easily be lumped together as "non-homology" and discarded

**Table 5.8** Relations passing the congruence test

| Relation (Morphology) | Congruence | Relation (Molecules) |
|---|---|---|
| Homology | Pass | Orthology |
| Homonomy | Pass | Paralogy |
| Complement | Pass | Complement |
| Two homologies | Pass | Two orthologies |
| Parallelism | Fail | Xenology |
| Multiparallelism | Fail | Paraxenology pleurology |
| Convergence | Fail | [Convergence] |
| Multiconvergence | Fail | — |

**Table 5.9** Relations failing the similarity test

| Relation (Morphology) | Similarity | Relation (Molecules) |
|---|---|---|
| Complement | Fail | Complement |
| Two homologies | Fail | Two orthologies |
| Convergence | Fail | [Convergence] |
| Multiconvergence | Fail | — |

prior to analysis (Table 5.5; Rieppel 1988: 68). Non-homology is often thought of as parallelism (and multiparallelisms) and convergence (and multiconvergence)—or at least similarities not attributable to common ancestry.

Patterson considered two relations (the complement relation and two homologies) that failed the similarity test but remain useful for systematics. In morphology, the relations that fail the similarity test are the "complement relation", "two homologies", "convergence", and "multiconvergence" (Table 5.10), while three relations fail in molecules, "the complement relation", "two orthologies", and "convergence" (the entry for "multiconvergence" was left blank by Patterson 1988a: 622, Table 5.3). Of the four morphological relations, two, the complement relation and two homologies (or two orthologies), were interpreted as useful for systematics because they may subsequently pass the congruence test.

### 5.6.2 The Complement Relation

Patterson described the complement relation as follows:

> The complement relation, which passes the congruence test but fails the similarity test, is the presence of a homology versus its absence. If there is no secondary reversion, this relation is congruent with other homologies, which explains why it has the same value to the systematist as homology. (Patterson 1982a: 46)

Even a cursory examination of published data matrices reveals that characters conforming to Patterson's complement relation frequently occur.

> The complement relation … only passes the conjunction test if the organism is viewed at one time … since most homologies present later in life are absent in the zygote. (Patterson 1982a: 48)

How can such characters be explained in the light of the similarity test? A first obvious point is that the complement relation is not homology:

**Table 5.10** Patterson's tests with relations that fail the similarity test. The upper two relations pass the congruence test and are understood as useful for systematics. (After Patterson 1982a: Table II: 47; modified with reference to Patterson 1988a, Table 3: 611; Patterson 1982a: 48.)

| Relation (Morphology) | Congruence | Conjunction | Relation (Molecules) |
|---|---|---|---|
| Complement | Pass | Pass | Complement |
| Two homologies | Pass | Fail | Two orthologies |
| Convergence | Fail | Pass | [Convergence] |
| Multiconvergence | Fail | Fail | — |

> The complement relation is presence of a homology versus its absence (absence complements presence, the two states constituting a whole with no other possible condition) . . . (Patterson 1988a: 606)

Viewed this way, some of the difficulties in interpretation become clear, as revealed in an exchange between Mabee (1993) and Patterson (1994a). Mabee suggested that

> Many binary characters are recognized with two states: presence or absence. The evolutionary interpretation of ontogenetic characters that are conceived with these alternative states relies on making hypotheses of homology between structures that are absent. (Mabee 1993: 207)

Patterson responded:

> That view of a character [absence + presence], does entail "making hypotheses of homology between structures that are absent" .. . . . On the alternative view, that presence is a character and absence is merely absence or symplesiomorphy (unless or until incongruence shows some "absence" to be presence in disguise) this problem does not arise; the relation between presence and absence is not homology but the complement relation . . . . (Patterson 1994a: 181[13])

Patterson is clear: "the *relation* between presence and absence is not homology". Clarification may be achieved if "homologue"—understood as a part of an organism—is substituted for homology. Thus, Patterson's earlier statement might be rendered clearer if an appropriate substitution is made:

> The complement relation is the presence of a *homologue* versus its absence (absence complements presence, the two states constituting a whole with no other possible condition). . .

This presents a revised question. Given the presence of a homologue, what is its complement? First, however, one needs to examine how relations might be hypothesised in the first place.

Take feathers as an example. It would seem there are two legitimate propositions that could be made concerning the distribution of feathers. First, we could observe that only particular kinds of animals have forelimbs with feathers. Such a proposition is based on detailed comparisons of various kinds of feathers from various kinds of animals. This would suggest that "feathers" characterise a group of organisms that have been called birds. What is the relation? "Feathers" characterise those particular organisms (birds) relative to all other living organisms. Thus, the complement relation is inherently hierarchical—it cannot be otherwise:

| | Birds | Other Animals |
|---|---|---|
| Feathers | Present | Absent |

If feathers are considered to be a homologue and no complement to feathers is recognised, then the character might be represented by

| | Birds | Other Animals |
|---|---|---|
| Feathers | Present | ? |

---

[13] ". . . presence is always a subset of absence" (Patterson in Fisher 1994: 148).

The meaning of the question mark can be read as “homologue not yet known”. Is there a real difference between “no feathers – feathers” and “unknown homologue – feathers”? In other words, is the “absence” of a homologue to feathers, rather than it being unknown, significant? To be sure, non-birds really do not have feathers. But some non-birds have scales, which have been considered as homologues of feathers:

| Birds | Some other Animals |
|---|---|
| Feathers | Scales |

It might be that each hypothesis differs in its generality: Scales and feathers are specific homologues; feathers coupled with an unknown homologue are less specific; absence of feathers is less specific than an unknown homologue. This might suggest that the complement relation is similar to homology but differs by being considerably less specific with respect to one of the homologous states. It might be better to think of presence-absence characters as “unbounded”, in the sense that for a particular homologue, its complement homologue is as yet unknown but presumably does exist (Nelson 1994).

With respect to modern character matrix construction, what becomes of simple binary (presence + absence) characters? The only possible way to subject all characters to the congruence test is to assume that *all* “complement” characters actually specify homologous relations with both the “absent” and “present” aspects being treated as the whole character, both parts having possible evidential significance (this has been explored by Williams & Siebert 2000 and Scotland 2000a). It appears that while the complement relation is not homology, applying the congruence test to these kinds of characters makes it so, and the “absent” part of the character may become informative and explained as a “reversal”. This sense casts doubt on some of the implications of the congruence test—at least as implemented with current computer programs.

### *5.6.3 Two Homologies*

Patterson stated that

> The “two homologies” relation is that between two unreversed homologies with the inclusion relation . . . such as notochord and feathers, or heart and ear ossicles. (Patterson 1982a: 48)

The significant point here is the inclusion relation (see Chapter 11). This specifies that one feature is nested within another (Figure 11.8; after Patterson 1982a: Figs. 1B and C). Of these relations, Patterson (1982a: 38) wrote

> Suppose that a homology specifying X has been identified. . . . Other homologies may relate to X in five ways . . . X as part of non-X (Fig. 1B, i.e. they include X); part of X (Fig. 1C; i.e. included within X) . . . B and C are consistent (congruent) with the original hypothesis, for they stand in hierarchic relationship to it. They corroborate X as part of an ordered system, but do not yet provide any real test of it. (Patterson 1982a: 38)

The first point seems to be that the "two homologies" relation allows comparison to be made between any two features—but then Patterson's ideas on recognising homology allow this. Yet as these kinds of comparisons eventually fail the similarity test, why then were they compared in the first place?

These examples highlight one use of the conjunction test, in that if either feature does not co-occur in the same organism, then the comparisons would be examples of convergence, as dissimilar features failing the congruence test would make the relation convergence. Thus, it would seem that "two homologies" would only be recognised after analysis, when each homologue fits to a separate part of the tree. In other words, these initial comparisons would then be seen as a pair of complement relations (Table 5.11).

Patterson (1982a) noted two further instances:

(1) "The relation between two homologies of this sort, one of which is reversed (lost or suppressed), such as heart and hindlimb, comes out as convergence, since the comparison is incongruent with those homologies resolving the loss or suppression" (Patterson 1982a: 48).
(2) "The relation between two homologies with the exclusion relationship . . . , such as plant tracheids and insect trachae, comes out as convergence" (Patterson 1982a: 48).

Example (1) is instructive, as it involves the absence of a feature. This will be discussed later. Example (2) is the exclusion relationship illustrated in Patterson:

> Other homologies may relate to X in five ways. . . . They may specify part of non-X. . . . The first of these categories (A) is irrelevant to the status of the original homology. Patterson (1982a: Fig.1A, reproduced here as Figure 11.8)

Thus, the exclusion relationship with "two homologies" is also really a pair of complement relations. It is of interest that Scotland's (2000b) "paired homologies" are really more like Patterson's "two homologies" rather than homology (Chapter 12).

Nelson, perhaps inadvertently, suggested another example:

> Mammals, for example, are said to be amniotes with hair and mammary glands — two among many mammalian synapomorphies associated with the node leading to mammals. What is the relationship, if any, between hair and mammary glands? (Nelson 1994: 132)

One point of view might be that there is no relation between hair and mammary glands, that the two, as homologues, fail the similarity test. Hair and mammary glands would also fail the conjunction test as they both co-occur in the same organisms. But given our current understanding of mammals, they would both pass the congruence test. In relation to each other, they

**Table 5.11** The Complement Relation

| Complement | 0 –> 1 | |
|---|---|---|
| Two homologies | | |
| | Complement (1) | 0 –> 1 |
| | Complement (2) | 0–> 2 |

> . . . are consistent (congruent) with the original hypothesis [hair = mammalian synapomorphy], for they [hair + mammmary glands] stand in hierarchic relationship to it. (Patterson 1982a: 39)

In his later paper on homology, Patterson (1988a) seemed to cast doubt on homologising such different features. But as Nelson says:

> Homology (orthology) between these two features [hair and mammary glands] would be universally denied, as if there were no relationship at all. Both are epidermal derivatives, and each has homologues in other vertebrates and in other organisms as well (feathers and scales are possible homologues of hair, and sundry epidermal glands are possible homologues of mammary glands). (Nelson 1994: 133)

Nelson's suggestion seems to imply that at some level all characters may be homologues of other characters and that any distinction between parts of organisms (homologues) and the tree of taxa (relationships of organisms) is illusory.

### *5.6.4 The Conjunction Test*

Patterson described the conjunction test thus:

> If two structures are supposed to be homologous, that hypothesis can be conclusively refuted by finding both structures in one organism. (Patterson 1982a: 38)

Patterson noted that "most transformational homologies are not subject to this test" (Patterson 1982a: 38). Patterson did not discuss the idea further, only noting in his later paper that

> Conjunction is the name I gave to a test that will disprove homologies as "anatomical singularities." (Patterson 1988a: 605; "anatomical singularities" referred to Riedl's term for homologies—Riedl 1978: 52)

The purpose behind the conjunction test was to separate out those features that might usually be called serial homology (Owen 1843), iterative homology (Ghiselin 1976), or homonomy (Riedl 1978; see Chapter 10). Patterson's test does not require an examination of causes—the source of the problem, as, for example: "Structures within a single individual may correspond because they are manufactured in the same way" (Roth 1988: 4). Thus, for persons such as Roth, the cause—what is responsible for the "manufacture" of similar structures—is the guide to all kinds of homology.

What of those categories that fail the conjunction test? Of the eight categories, four will fail the test: homonomy, two homologies, multiparallelism, and multiconvergence. Of interest are the first two categories, as they pass the congruence test. Two homologies are discussed elsewhere as a category that fails the similarity test. Thus, homonomy will pass the similarity test as well as the congruence test and might appear, at first glance, to be synonymous with serial homology. Patterson noted that homonomy is best thought of as mass homology or "anatomical plurals", following Riedl's (1978: 38) terminology, noting that "serial homology, like transformational homologies, appears to be an untestable version of homonomy"

(Patterson 1982a: 48). Patterson's example was somewhat contrived. He suggested that if an angel was discovered with wings and arms, then homologising the two forelimbs would fail the conjunction test, as both wings and arms co-exist in the angel (see Figure 7.2). De Pinna (1991) suggested that the decision as to which features were homologues or not ultimately rested on the optimisation criterion employed. From a taxic perspective, the decision would rest on possible groups.

In Table 5.12a, neither bird wings nor "angel" wings are considered homologues of each other, nor of arms. Thus, the only group suggested is the three mammals plus the "angel": Bird (Angel, Mammals).

In Table 5.12b, the bird wings—but not the "angel" wings—are considered homologues of mammalian limbs (indicated by a "2" such that "angel" wings = modified arms). Thus, the only group suggested is the three mammals plus the bird: Angel (Bird, Mammals). The "angel" wings are independent homologies and the bird wings are "modified" limbs.

In Table 5.12c, both bird wings and "angel" wings are considered homologues of mammalian limbs. Thus, no group is recognised beyond "angels" plus birds plus mammals. Yet this approach might be thought of as unusual, as both the "angel" wings and the mammalian limbs co-exist. Does that deny any homology between the two? Not necessarily. As Patterson's tests reveal, in this case, the "angel" wings and the mammalian limbs fail only the conjunction test, passing both the similarity test and the congruence test; failing only the conjunction test denies that they are

**Table 5.12** Data from De Pinna (1991). The numbers of taxa are the same as De Pinna suggests simply so that optimisation procedures can be clarified

| (a) | | | (b) | | |
|---|---|---|---|---|---|
| | Wings | Arms | | Wings | Arms |
| Angel | 0 | 1 | Angel | 1 | 1 |
| Mammal 1 | 0 | 0 | Mammal 1 | 0 | 1 |
| Mammal 2 | 0 | 0 | Mammal 2 | 0 | 1 |
| Mammal 3 | 0 | 0 | Mammal 3 | 0 | 1 |
| Bird | 1 | 0 | Bird | 0 | 2 |

| (c) | | | (d) | | | |
|---|---|---|---|---|---|---|
| | Wings | | Arms | | Wings | Arms |
| Angel | 0 | 1 | Angel | 0 | 1 | 0 |
| Mammal 1 | 0 | 0 | Mammal 1 | 0 | 0 | 1 |
| Mammal 2 | 0 | 0 | Mammal 2 | 0 | 0 | 1 |
| Mammal 3 | 0 | 0 | Mammal 3 | 0 | 0 | 1 |
| Bird | 1 | 0 | Bird | 1 | 0 | 0 |

| (e) | | | |
|---|---|---|---|
| | Forelimbs | Wings | Arms |
| Angel | 1 | 1 | 1 |
| Mammal 1 | 1 | 0 | 1 |
| Mammal 2 | 1 | 0 | 1 |
| Bird 1 | 1 | 1 | 0 |
| Bird 2 | 1 | 1 | 0 |

homologues (*sensu* Patterson) but that they are homonomes (or homotypes *sensu* Owen). Thus, bird wings are homologues and "angel" wings are homonomes.

In Table 5.12d, bird wings and "angel" wings are homologues of each other, but neither are homologues of mammalian limbs. Thus, two groups are revealed, one of "angel" plus bird and the other the three mammals.

Whatever permutations might be possible, the only way such data can be usefully compared is as two complement relations relative to each other or homologues relative to mammalian limbs. The data in Table 5.12a–d suggest two conflicting groups, "angels" + mammals and "angels" + birds. The two groups conflict; hence, one might suspect that one group (one character) is incorrect and dismiss that group (or character) as informative. Alternatively, one might view one of the groups (or characters) as wrong but the "similarities" correct and in need of interpretation; that is, rather than deciding which group is "false" ("angels" + mammals; "angels" + birds), one may decide which character is "false" (wings of angels + wings of birds: homologues; wings of angels + wings of birds: homoplasies).

Yet the two complement relations specifically deny any homology between wings and arms. A relation could be added to represent forelimbs. But doing so denies the relation between "wings" and "arms", as they are now both free to be independent. Hence, we return to homology as a relation between features (homologues) (Table 5.12e).

### *5.6.5 The Congruence Test*

Testing by congruence is now almost universally understood as the major arbiter in discriminating homology from non-homology (Patterson 1982a,[14] 1988a, Rieppel 1988, 1994, De Pinna 1991; but see Bock 1977; Haszprunar 1998, and Schmitt 1995). Wiley's comment here is relevant. The test of homology

> ... is to hypothesise that the supposed homology is a synapomorphy. (Wiley 1974: 235)

And as

> ... synapomorphies are the *only* properties of monophyletic groups, tests of a hypothesis of homology must be other hypotheses of homology—other synapomorphies. (Patterson 1982a: 38)

Therefore, one may propose a group by proposing a synapomorphy and test that group by the correspondence (or congruence) of other synapomorphies. In this case congruence is the method said to separate, sort, or discriminate the "true" homologies from the "false". By "true" and "false", we do not mean relative to an actual phylogeny but relative to their support for a particular and specified relationship.

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[14] Patterson (1988a) took a different view for molecular data where he understood similarity as a more powerful test than congruence. The implications are relevant for some of the topics discussed here.

**Table 5.13** Patterson's congruence test (after Patterson 1982a: Table 4.7; Patterson 1988a, Table 3: 611)

| Relation | Congruence |
|---|---|
| Homology | Pass |
| Homonomy | Pass |
| Complement | Pass |
| Two homologies | Pass |
| Parallelism | Fail |
| Multiparallelism | Fail |
| Convergence | Fail |
| Multiconvergence | Fail |

The congruence test yields four relations that remain useful for systematics. These relations are discussed elsewhere. The most significant aspect in removing the congruence test is that no meaningful distinction can be made between parallelism and homology, the two relations that pass the similarity test (Compare Table 5.13 and 5.14; Table 5.14, with other relations omitted).

Interestingly, when Patterson extended his tests to molecular data, they revealed some issues of general interest. Removal of the congruence test in molecular data leaves orthology and xenology indistinguishable, the molecular equivalents of homology and parallelism, respectively. Patterson suggested that xenology *was* a form of homology, as a general explanation was available relative to common ancestry by invoking horizontal transfer. Yet the reason behind the proposal of xenology as homology was their similarity:

> The interesting difference between parallelism in comparative morphology and xenology in molecular comparisons is that parallelism is usually regarded as nonhomology (because of incongruence), whereas xenology *is* regarded as homology (because of similarity). (Patterson 1988a: 612)

Patterson's (1988a) later account of homology might lead to the conclusion that, rather than congruence and similarity, it is the appeal to common ancestry that makes xenology explainable as a plausible version of homology (or, as Patterson later said, while a variety of homoplasy, xenology is a "peculiar kind of homology"; see below). In 1994, Patterson was somewhat more guarded recognising the explanation for xenology relative to its discovery:

**Table 5.14** Comparison of Patterson's (1982a, 1988a) categories with the congruence test removed. For comparison, both morphological and molecular relations have been included

| Morphology | | |
|---|---|---|
| **Relation** | **Similarity** | **Conjunction** |
| Homology | Pass | Pass |
| Parallelism | Pass | Pass |
| Molecules | | |
| **Relation** | **Similarity** | **Conjunction** |
| Orthology | Pass | Pass |
| Xenology | Pass | Pass |

> These two varieties [of homology] (xenology, plerology) share a common feature, unexpected or incongruent similarity. Compared with their analogues in morphology, they are varieties of homoplasy (Patterson, 1988a, Table 5.3). . . . In xenology, the incongruent similarity is explained as a peculiar kind of homology, incorporation in the host genome of a fragment of an alien genome, a sort of molecular endoparasitism" (Patterson 1994b: 187)

It seems that while xenology may have a plausible explanation, parallelism usually does not (although Patterson did explore the many possible explanations that have been offered for morphological parallelism—ideas subsequently attaining some revival). Oddly enough, ideas explaining parallelisms have had, and continue to amass, a huge literature, devoted to the possible explanations for "the recurrence of similarity" (Sanderson & Hufford 1996). We have no intention of reviewing this literature here (but for modern examples, see Gosliner & Ghiselin 1984, Sluys 1989, Brooks 1996, DeSalle et al. 1996). A viewpoint emerging again is that a distinction between homology and parallelism need not necessarily be quite so well defined (see below and Roth 1984: 14, Wagner 1989: 55, 66).

Viewed from an alternative perspective, parallelism seems to be nothing more than another term (or explanation) for recognising but not resolving character conflict. In other words,

> . . . there has been a practise of long standing to explain character conflict, . . . but these notions seemed to offer no exact solution to the problem of conflicting characters, and no significant aid to judgment. (Nelson 1996: 13)

The notions Nelson refers to are "character combination, underlying synapomorphy, inside parallelism, orthogenesis, and whatnot . . . "—the list may be extended by adding parallelisms (cf. Brooks 1996), or homoplasy in general.

### 5.6.6 Rejection of Patterson's Tests

With respect to the validity of the congruence test, dissenting voices suggest that it merely depends on

> . . . testing homologies by correlation with other homologies or by the distribution of the features in groups of organisms and thus do not provide tests of independent homologous features; these tests must be rejected for these purposes. (Bock 1989: 336; Schmitt 1995 and Haszprunar 1998, seem to agree; see also Neff 1986: 116 and Bryant 1989: 217)

Early on, Bock rejected Remane's 3rd—6th criteria, leaving only the first two aspects of similarity:

> Generally accepted criteria used to recognise homologous features include morphological similarity, position in the body, relationship to other features, similar ontogenetic development, and so forth. (Bock 1969: 416, 1974: 388, 1989: 337–338)

Ax (1987: 161) discussed Remane's criteria, also rejecting all but the first two (he rejected the word "criteria" as well):

> In formulating independent hypotheses about the existence of homologous features in different organisms, there is only one source of data (well known though it may be)—this is similarity or agreement between features in the taxa compared. (Ax 1987: 161)

Schmitt (1995: 429) noted that Remane's first two criteria are "simply denotations of different kinds of similarity." He also noted that Remane's 5th and 6th criteria are merely complements, both referring to unobservable "phylogenetic relationships" and concurred with Bock (above) that the 3rd–6th criteria "are not independent empirical tests since they depend on other statements on homology." Schmitt suggests, as does Bock (1989), that this reasoning renders Patterson's congruence test invalid.

Haszprunar extended Remane's criteria (Haszprunar 1998: 335, Table 5.3, "Criteria of Homology"), referring to his three principal criteria as "Position-Structure"[15] and the three auxiliary criteria as "Patterns of Characters". Haszpruner recognised character congruence as a criterion of homology rather than a test, in much the same way that Remane initially suggested (see also Mayr & Ashlock 1991: 144).

Bock's critique is an interesting one. He concludes that the similarity test is the only one with any force, but it is of low resolving power (Bock 1974, 1989). Patterson, when discussing molecular homology, came to a similar conclusion because he could find possible causes for some "peculiar kinds of homology" and because of the possibility of conflicting but "true" gene trees, which in turn may suggest conflicting "phylogenies". The essence of the matter is conflict: distinguishing between "homology" and "parallelism" rather than simply just naming them as different.

The differences may be summarised as a conflict in the relative importance of "similarity" and "congruence" (Donoghue 1992: 176, Donoghue & Sanderson 1994: 398), a subject that may have no resolution beyond mere argument.

Here it is worth remembering that Remane's criteria and Patterson's test are versions of Naef's criteria. And that such discussions are destined to be interminable, as Naef, Remane, and Patterson are struggling with the concept of similarity and its meaning relative to taxa. We suggest Nelson cut this particular Gordian Knot by proposing that homology is concerned with relationships, a view we expand below.

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[15] Haszprunar adds one significant item to "Position-Structure", "The character always shows the same *developmental pattern*" (Haszprunar 1998: 335, Table 3. We return to this topic later). He also adds a third group called "Function and Ecology", which we will not consider further.

# Chapter 6
# Pattern Cladistics

> “A spectre is haunting palaeontology—the spectre of cladism.”
> (Campbell 1975: 86)

> “The issue would never have been raised unless it was made necessary by the over-zealous advocation of a purely palaeontological approach.”
> (Nelson and Platnick 1984: 156, Nelson 1989b: 71, 2004)

> “I’ve heard that Gareth J. Nelson, curator of herpetology at the American Museum of Natural History, is a creationist. Do you know if this is true?”
> (TalkOrigins Archive, June 1998)

It is tempting to start this chapter with a discourse on “history” and “truth”, two concepts related in a complex way. Reserving that discussion for another time, we begin by simply noting that much nonsense and many inaccuracies have been written on the subject of pattern cladistics—even cladistics in general—from the point of view of its history (Hull 1988), its meaning (Felsenstein 2004), and its aims (Mayr 1982a, Ridley 1986, Donoghue 2001), among other things. Characterised as occurring during “the years of conflict” (Funk 2001), the accounts of the development of cladistics are seen as part of a battle, even war (Hull 1988), among persons of different persuasions. Even religious fervour has been invoked (Grene & Depew 2004), all of which has caused certain commentators to appear startled that scientists can ever be passionate about their work (Donoghue 2001, Felsenstein 2001), Felsenstein going as far as to suggest that such behaviour “would not be condoned in other, more mature, fields of science” (Felsenstein 2004: xix; cf. White 2001). Maturity of disciplines and persons to one side, that correspondents to TalkOrigins live in a fantasy world primarily of their own making should come as no great surprise. Nevertheless, that some scientists create imaginary worlds is a little worrying (Dawkins 1986, Ridley 1986, Hull 1988, Felsenstein 2004; see Winsor 2003 and Provine 2005 on Ernst Mayr); one might, *pace* Felsenstein, dwell on the meaning of maturity in relation to some of these authors’ contributions. Our concern here is that the record be set straight with respect to Cladistics, or at the very least it be rendered a little more accurate.

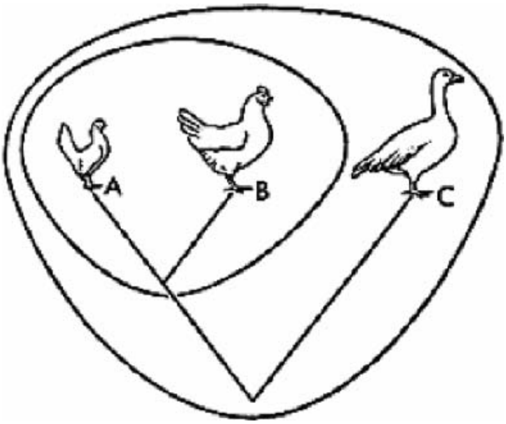

**Fig. 6.1** After Patterson (1980a, Fig. 1: 234)

Many years after the "modern" development of cladistics, Colin Patterson (1933–1998; see Bonde 1999, Fortey 1999, Nelson 2000, Forey et al. 2000) wrote a popular account for *The Biologist*, the journal of the Institute of Biology, London (Patterson 1980a). A precise and clear account was presented, with a few basic axioms.[1]

1. Features shared by organisms (homologies) manifest a hierarchical pattern in nature.
2. This hierarchical pattern is economically expressed in branching diagrams, or cladograms.
3. The nodes in cladograms symbolise the homologies shared by the group of organisms grouped by the node, so that a cladogram is synonymous with a classification (our Figure 6.1).

Alternative axioms have been suggested, existing ones modified. Panchen (1992: 181), for example, stripping them down to just two:

1. The formation of groups rather than lineages.
2. The formation of nested sets based on homologies

Thus, requirements for successful systematic studies could be captured by the requirement of characters and groups, the latter represented by classifications (Chapter 2).

Patterson related his account to "the new theory ... [of] ... 'transformed cladistics' and the transformation away from evolutionary theory" (Patterson 1980a: 239). "Transformed cladistics" was used to describe a generalised version of cladistics, somewhat removed from the *Phylogenetic Systematics* of Willi Hennig (see below) but nevertheless part of the general evolution of ideas (Platnick 1979). In another popular account, this time for the British science magazine *The New Scientist*, Patterson noted that developments in cladistics arose as a response to "critics like Mayr, in particular Mayr (1974)" (Patterson 1982b: 304—some further commentary on

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[1] An axiom is a sentence or proposition that is taken for granted as true, and serves as a starting point for deducing other truths.

Mayr 1974 is offered below). Again, Patterson referred to this modified version as "transformed cladistics", following Norman Platnick (see Ebach et al. 2007). Patterson had used "pattern analysis" at the *Palaeontological Association'*s Silver Jubilee meeting in 1979 (Peter Forey 2002, pers. comm.). This revised and streamlined version of cladistics was the focus of the "salmon-lungfish-cow" debate (Gardiner et al. 1979; for more details see below). Later Patterson began to use "*pattern cladistics"* when dealing with general issues relevant to systematics, classification, and evolution (Patterson 1988b, 1989).

Yet it was John Beatty, a philosopher and critic, who first applied "Pattern cladistics" in print:

> Let's call the former subgroup [of cladists], of which Wiley is a member, the "phylogenetic" cladists, in recognition of their adherence to Hennig's original goal of phylogenetic systematics. And let's call the latter group the "pattern" cladists. I will get to the reason for that reference shortly. (Beatty 1982: 27; see Patterson 1988b: 77)

Beatty's reasoning for the label "pattern cladistics", however, was based on the understanding that this subgroup of cladists wanted *nothing* to do with evolution:

> What they mean by that is that no evolutionary suppositions are necessary to discover the sort of "pattern" that they hypothesize/assume is characteristic of the living world. (Beatty 1982: 29)

Beatty based most of his understanding on a lecture Patterson gave to the 2nd Annual Meeting of the Willi Hennig Society, a presentation that was never published in its entirety, although parts have appeared in other papers (e.g., Patterson 1982a), and was summarised in the account of the meeting (Fink 1982). The pertinent comment from Patterson's talk is as follows:

> I think the goals and assumptions of cladistics can be dealt with very simply and briefly, because they are the same thing, and boil down to one statement. The assumption of cladistics is that there is a single pattern in nature—one pattern, or one order, or one hierarchy, whatever you want to call it. And the goal of cladistics is to find that pattern. I don't think it makes much difference whether one believes the pattern is there to be found or discovered, or whether one regards it as hypothetical. But I prefer to regard it as real and discoverable. So the goal is to find the pattern and the assumption is that there is one to be found. We find the pattern through homologies, which Hennig divided into symplesiomorphies and synapomorphies. I don't believe that distinction is necessary any longer, and I prefer to equate homology, synapomorphy and taxonomic character—all have one thing in common—they are hypotheses of grouping. Homologies, comparisons implying grouping, can be thought of as relations that are discoverable, or as hypotheses—I prefer to think of them as hypotheses—so to me the pattern we are looking for is real, and hypotheses of homology are how we discover it. (Patterson 1981b: 1[2])

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[2] The presentation Beatty quoted from was never published in its entirety. Beatty had access to a tape of the talk (Beatty, pers. comm.), the same tape being used as the basis for Fink's report (Fink 1982, Fink, pers. comm.). However, that tape no longer exists (Beatty, pers. comm., Fink, pers. comm.) and no transcript has been discovered. Among Patterson's papers in the Natural History Museum, London is his hand-written account of the lecture he prepared for presentation. This extract has been taken from that text. Patterson was known to prepare carefully worded accounts of his lectures, learn the words, and give his presentations more or less word for word (Forey, pers. comm.). Therefore, it seems his text would be a fairly faithful representation of what he said in Ann Arbor at the 2nd Willi Hennig Meeting in 1982.

Of course, elsewhere in his presentation Patterson talks of evolution in relation to cladistics, but from the perspective of the subject matter above, the statements seem clear enough. Of further significance is a comment reported by Kluge:

> Their [pattern cladists] chosen rule is not parsimony but a belief that there is one pattern in nature (C. Patterson, pers. comm.; see also Patterson 1982: 41). (Kluge 1984: 29, footnote 2; Patterson refers to his view as "modern cladistics" in Patterson (1982a: 62); that manuscript was submitted in May 1980, sometime before Beatty's paper)

Similar to Patterson's concerns, Nelson & Platnick wrote:

> We would, however, have discovered an element of pattern ... an element of a different kind than the observations that we accumulate. The element of pattern can be restated in a taxonomic or systematic form: *there is a group, including A and B, but excluding C*. Now there is a place—an accumulation, if you like—for information of that kind, and that is systematics in its traditional guise. (Nelson & Platnick 1981: 32; our italics)

Axioms, however clear and focused, might, then, seem largely irrelevant. The essence of cladistics (if not all of "systematics in its traditional guise") is captured by a single phrase:

There is a group, including A and B, but excluding C.

Therefore, we identify pattern cladistics as Cladistics (with a capital C) to distinguish it from the varied interpretations the subject has received.[3] This relates Cladistics directly to the Cladistic Parameter, the estimate of relationships among taxa (see Chapter 1).

In spite of the simplicity of this discovery, several persons saw no need to differentiate "kinds" of cladists (Farris 1985), while others saw some value in appropriate labels (Brooks & Wiley 1985; Kluge 1985). Critical responses to Beatty's (1982) paper came from Platnick (1982), Patterson (1982c), and Brady (1982). Later, when reviewing further contributions to the debate from Brooks & Wiley (1985) and Kluge (1985), Nelson noted that

> ... the real substance of the papers is not analysis but philosophy and sociology—that the substance is the cause, not the result, of the analysis. ... What of the substance, then? It concerns "pattern cladistics", which the authors distinguish from "phylogenetic cladistics", among which they include themselves. It is as if the authors perceive two natural taxa and now attempt to specify defining characters. (Nelson 1985a: 39)

Nelson closed with these comments:

> ... I do not regard this present manuscript as a defense of "pattern cladistics", nor do I recognize anything covered by that term, as used by Beatty, Brooks and Wiley, and Kluge, as worth a defense. (Nelson 1985a: 41)

Nevertheless, Cladistics did not spring *de novo* in the mid-1970s or late-1960s as an aberrant form of Hennig's *Phylogenetic Systematics* (Ridley 1986), nor as

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[3] Other designations for "kinds" of cladistics include phylogenetic cladistics and process cladistics, as well as those who persist in identifying the subject as equivalent to parsimony analysis. The latter deserves further attention, which we undertake below.

a new-fangled and much mangled version of it (Ereshefsky 2001), but from best practise as enunciated by many systematists, taxonomists—even evolutionists and geneticists—during the last 140 years of "systematics in its traditional guise". We may ask, What can be learnt from these previous generations? A Cladistic perspective offers some insight into this question.

At this stage one may rightly wonder what any of the above has to do with palaeontology and the spectre that apparently haunted it (Campbell 1975: 86; see also Campbell 1993, no relation). Below we attempt to tell that story, or at least part of it, so other systematists may absorb something of the history of their discipline and hopefully learn, as we have, from the experience.

## 6.1 Preamble

Many understand Cladistics to have its beginnings with Willi Hennig's *Phylogenetic Systematics* (Hennig 1966a; see also Hennig 1950, 1953, 1957, 1965) and Lars Brundin's exposition and promotion (Brundin 1966, 1968). An alternative history sees its beginnings with Sokal & Sneath (1963), being developed further by its successor, Sneath & Sokal (1973), reaching "maturity" with Felsenstein (2004). While there is much of merit in Sokal & Sneath's book (1963), they deal primarily with "cladistics" (with a small c), describing a methodology closely linked to parsimony as part of the numerical pursuit of phylogeny reconstruction (see Chapter 11). The history of Cladistics, as much as it is understood as an extension of general systematic endeavour, extends much further back, probably to the beginnings of science (Nelson & Platnick 1981, Papavero et al. 1995a–c, 1997b). Of the two major figures in the 20th century's development of cladistics, Hennig and Brundin, Lars Brundin should indeed be considered especially influential—influence we believe has yet to be appreciated fully and appropriately recognised.

Brundin's promotion of Hennig's *Phylogenetic Systematics* was of especial importance to the Stockholm palaeo-ichthyological community (Brundin 1968), where it rapidly blossomed, primarily because it allowed the discovery of solutions to outstanding problems in systematic ichthyology (Nelson 1971b; Greenwood et al. 1973).

David Hull's (1988) account of the development of *Phylogenetic Systematics* has attracted much attention, yet his narrative seriously misrepresented progress in systematic biology during the 1900s, fictionalising the development of Cladistics and interpreting it from a neo-Darwinian point of view. Rather than an uninvolved and impartial historian, Hull seems to have held as an objective to demonise what he identifies as *pattern cladistics* (see above). It is therefore not unsurprising that Hull concentrates his account on the latter half of the last century—beginning in 1950 with Hennig's *Grundzüge einer Theorie der phylogenetischen Systematik*, all but ignoring the first half of that century, missing or trivialising major developments in morphology. An appreciation of the significance of Adolf Naef and other European morphologists working between 1910 and 1950 with their attempt to develop, in Naef's words (1913: 344), a "systematic morphology" (Systematische

Morphologie), is notably lacking. It is especially remiss that Hull fails to note the many critiques of Ernst Haeckel's work, as Haeckel can be safely named the founder of genealogical (phylogenetic) studies, particularly as he coined the word "phylogeny" (see Chapter 4). Hull mingles the history of numerical taxonomy with the history of cladistics simply because—or so it seems—the former group were a useful source of salacious gossip (Farris & Platnick 1989: 310).

Hull rejects the notion of *Science as a Pattern*, stating that

> If anything, processes are more fundamental to science than patterns. The importance that I place on process is reflected in the title of this book. It is *Science as a Process* not *Science as a Pattern*. (Hull 1988: 241; original italics)

Hull embraces a transformational view of the world that in spite of his training as a philosopher and historian of science is an exceedingly narrow viewpoint (see also Lennox 2001). The history of Cladistics may be understood as more complex than Hull's account, yet at the same time surprisingly straightforward in its achievements.

Earlier (Chapter 5) we discussed the rise of neo-idealistic or systematic morphology as a reaction to Ernst Haeckel's Darwinian excesses, the latter's work succinctly summed up by Russell (1916: 248) as "a medley of dogmatic materialism, idealistic morphology, and evolutionary theory. ..." Russell continued that "It was scarcely modern even on its first appearance, and many regarded it, not without reason, as a belated offshoot of *Naturphilosophie*." Developments between Richard Owen's clarifications of homologues and homology (Chapter 7), Adolf Naef's critiques of Haeckel, evolutionary morphology, and the biogenetic law (Chapter 5), and Erik Stensiö's achievements, led—albeit indirectly—to what we understand Cladistics to be; in fact, what we understand Systematics to be. A modern interpretation of Cladistics, and the view that shone through from the young palaeo-ichthyology community of the 1960s, has its source in Stockholm but its inspiration in biogeography.

## 6.2 Discovering Léon Croizat

In the autumn of 1962, the 25-year-old ichthyologist Gareth Nelson took William Gosline's (1915–2002) Zoogeography course at the University of Hawai'i (Nelson, pers. comm.). Nelson was at the University of Hawai'i to undertake a PhD with Gosline as his supervisor; Gosline was a student of George Myers at Stanford (Nelson & Ladiges 2001: 399). Some 18 years before Nelson's arrival, Gosline had published a controversial contribution to fish geography (Gosline 1944), a paper considered to be critical of prevailing notions explaining the geographical distributions of fishes. Those prevailing notions were set in place by Myers (1938), who followed William Diller Matthew (1915) and his Northern dispersal paradigms (see below). Many years later Myers changed his mind in favour of "drift as an explanation of the geographical distribution of fishes" (Nelson & Ladiges 2001: 400). This change of heart was first presented at the 1966 meeting of the *American Society of Ichthyologists and Herpetologists*, an occasion that impressed the young Nelson (pers. comm.).

Gosline would never embrace Cladistics, as exemplified in its computerised form; he never embraced Cladistics in its Hennigian form either, but this may simply have been because he saw its central proposition as a restatement of an idea already well known and ably articulated:

> Ridewood (1904), Hennig (1966[a]), and a host of others have pointed out that relationships cannot satisfactorily be determined on the basis of ancestral characters. (Gosline 1969: 214; see Nelson 1971b: 368; for further commentary on Ridewood see Hilton and Forey 2005)

In the early 1960s, Darlington's *Zoogeography*, *The Geographical Distribution of Animals* would have been one of the primary textbooks for teaching biogeography, alongside similar contributions from the Modern Synthesis era (Mayr 1963, Simpson 1953, 1965), all more or less founded upon Matthew's *Climate and Evolution* (Matthews 1915), "one of the most seminal or heuristic studies of paleogeography and historical biogeography" (Simpson 1978: 272). Matthew's view was that life originated in the north in various centres of origin, each allowing dispersal of organisms to the south, towards Africa, through southeast Asia to Australia and across the Bering land bridge into North America, and then on down through South America. These ideas have their origin with Ernst Haeckel (Chapter 13; see below for Matthew) and are represented in his various diagrams of humans dispersing around the globe from Paradise (Nelson & Ladiges 2001: 397, Williams 2006 [2007]), although Haeckel had humans emerging from a Southern Paradise (see Chapter 5 for a general discussion of Haeckel and Chapter 13 for a discussion of Haeckel's "migrating-humans" diagrams). Indeed, Matthew published a diagram similar to Haeckel's, with humans panning out over the globe, but having a different, more vague point of origin (Figure 6.2). Haeckel's view on dispersal, centres of origin, and their significance prompted him to provide another neologism, *chorology* (see Chapter 13).

Darlington's book, and Matthew's legacy—ultimately Haeckel's interpretation of Darwin—would have been considered received wisdom in the mid-1960s, with many admirers and few dissenters.

Léon Croizat (1894–1982), a French-Italian naturalist who spent time working at the New York Botanical Gardens and eventually left the U.S. in 1947 to spend his final years as a botanist in Coro, Venezuela,[4] attacked Darlington's "pearls" of biogeographic wisdom in several weighty tomes: *Manual of Phytogeography* (Croizat 1952), *Panbiogeography* (1958), and *Space*, *Time*, *Form* (1964). Croizat's position was ably summarised by the phrase "Life and Earth evolved together" (Croizat 1964: ii)—as opposed to the more or less random effects of chance dispersal advocated by Darlington.

Gosline used Croizat's *Panbiogeography* (Croizat 1958) as part of his Zoogeography course, saying little about its content but describing Croizat as a "superb screwball" (Nelson, pers. comm.). Léon Croizat, upset with prevailing notions in biogeography, was something of a revolutionary figure, studying "biogeography in the grand manner" (Nelson, pers. comm.). Croizat not only proposed a

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[4] For biographical and bibliographical information, see Nelson (1973e), Craw (1984a, b), Craw & Heads(1984), Zunino (1992), Llorente et al. (2000), Morrone (2000), Colacino & Grehan (2003), and Pahnke & Danova (2003).

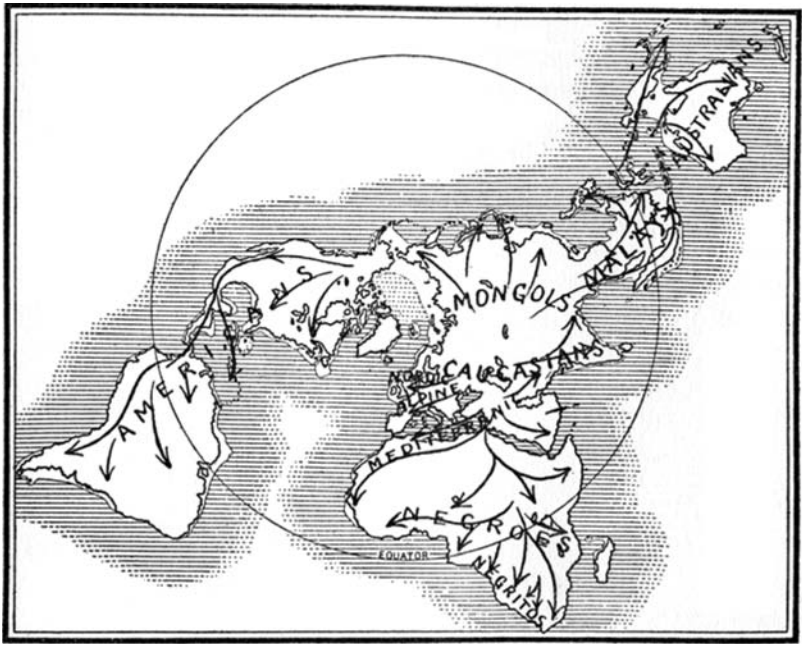

**Fig. 6.2** Matthew's picture of humans dispersing. After Matthew (1915)

new approach to biogeography but in doing so challenged the entire Darwinian paradigm. For species origin, he proposed a version of orthogenesis developed from an interpretation of Daniele Rosa's *Hologenesis*, a process preferable to Darwin's *natural selection* as evolution's primary creative force (Rosa 1918, 1931, reprinted in Vergata 2001; see Colosi 1944, reprinted in Vergata 2001; Croizat 1976: 609–613, 824–828, Luzzatto et al. 1997, 2000, Zunino 2004[5]). In any case, mechanisms to one side, Gosline had said enough in his Zoogeography class to encourage Nelson to read the three large volumes of Croizat's *Panbiogeography* (Croizat 1958) and to begin to recognise that, whatever one's views on biogeography happened to be, it was clearly a troubled discipline.

## 6.3 Erik Stensiö, Vertebrate Palaeontology, and the Birth of Cladistics

After completing his PhD in Hawai'i, Nelson eventually went to the Paleozoological Department of the Swedish Museum of Natural History in Stockholm, home to Erik Helge Andersson Stensiö (1891–1984)[6] and Erik Jarvik (1907–1998), two brilliant

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[5] Croizat dedicated *Space, Time, Form* to Rosa; for a portrait of Rosa, see the cover illustration of *Zoologia, The Italian Journal of Zoology* 61(2), 1994.

[6] He was born in the village of Stensjö in Döderhult and took his surname from his place of origin.

and innovative palaeo-ichthyologists (see Cloutier 2004: Fig. 6.3 for a group portrait including Stensiö, Jarvik, and Nelson; see Patterson 1990 and Nelson & Chang 1986 for biographical details on Stensiö). Stensiö founded what became known as the Stockholm School of studies in vertebrate structure and evolution. Nelson split his post-doctoral time between the British Museum (Natural History)—now the Natural History Museum—in London and the Paleozoological Department in Stockholm. Once again it was William Gosline who provided Nelson with the enthusiasm for investigating this work—Stockholm become a "Mecca" (according to Rex Parrington; see below) for any aspiring, young palaeo-ichthyologist (Nelson 1969a: 64, 1973a: 825; see also Wake 1970: 95, Patterson 1990: 374, Janvier 1996: 316). Why Stockholm?

Erik Stensiö received his PhD and a lectureship in palaeontology from Uppsala University in 1921, becoming professor and keeper of the Zoopalaeontological

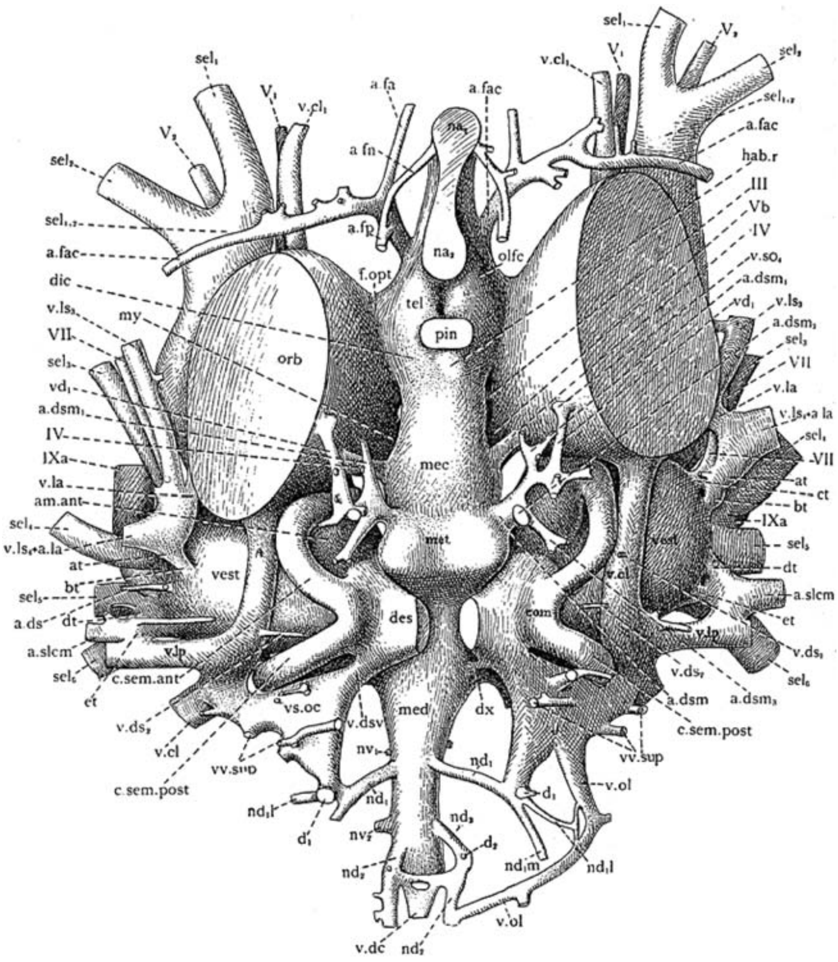

**Fig. 6.3** Diagram of homologies from a fossil Cephalaspid brain. After Stensiö (1927)

(later Palaeozoological) Department of the Swedish Museum of Natural History in Stockholm in 1923, remaining there all his working life, retiring 36 years later in 1959. His speciality was the anatomy and evolution of “lower” vertebrates, studying placoderms and their relationships to modern sharks. Much of his work was based on material collected from Spitzbergen during a series of expeditions (1912, 1913, 1915, and 1916), which resulted in monographs considered to be among “the greatest works in palaeontology ever published” (Colin Patterson’s opinion, Fortey 1999: 369). Stensiö examined placoderms in great detail, using three-dimensional models of their skulls to reveal the canals for nerves, arteries, and veins, revealing a character system previously hidden from sight as well as understanding (Figure 6.3). He considered placoderms to be true-jawed fishes most closely related to modern-day sharks. Like Adolf Naef, a few years before (Chapter 11, Figure 11.10), Stensiö summarised the complexities of morphological homologues with simple branching diagrams relating taxa (Figure 6.4).

After Stensiö retired, Erik Jarvik, who worked on the “four-legged” fish, *Ichthyostega*, succeeded him. Jarvik completed his PhD in 1942, participated in Säve-Söderbergh’s 1932 Greenland expedition, eventually being appointed Assistant Palaeontologist in the Department of Palaeozoology of the Swedish Museum of Natural History in 1937, succeeding Stensiö in 1960 and finally retiring in 1972.[7]

Some few years after he retired, Jarvik published his monumental summary on vertebrate morphology, *Basic Structure and Evolution of Vertebrates* (Jarvik 1980). The book was published in two volumes, weighing in at over 1000 pages and 500 illustrations, representing a detailed account of more than 40 years of “the most interesting and provocative work in morphology” (Patterson 1981c: 432). In a review of Jarvik’s book, Patterson noted that

> Vertebrate morphology is not a fashionable subject. … The heyday … was over by about 1920, when it seemed that the comparative anatomy and embryology of vertebrates were

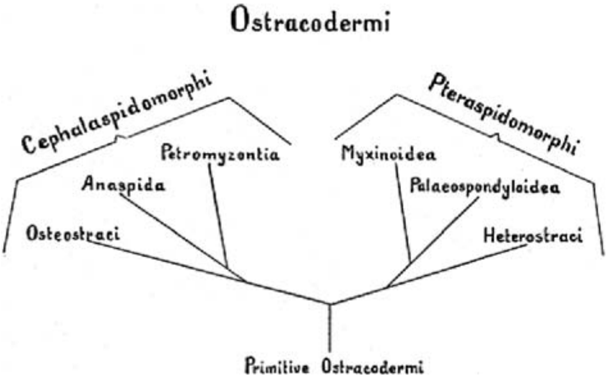

**Fig. 6.4** Diagram of Ostracoderm relationships from Stensiö (1927)

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[7] Jarvik published his final paper in 1996, appropriately a monograph on the anatomy of *Ichthyostega*, finishing a career that spanned 54 years. He died on January 11, 1998, at the age of 90.

> well enough understood for the framework of morphology to be permanent, so attention could be turned to newer fields. … Then in 1921 Erik Stensiö published the first of a series of brilliant monographs, analyzing fossil lower vertebrates in an entirely new way. (Patterson 1981c: 431)

Perhaps with these few words it is possible to understand why Adolf Naef's progress in morphological theory made little impact, as he was publishing during the decades (1910–1930) when morphology was out of fashion. Maybe Naef's work was seen as irrelevant to a field that was finished, having discovered all it possibly could (Chapter 5), a refrain not uncommon in today's "genomic" world (Scotland et al. 2003). Nevertheless, Stensiö, and later Jarvik, did study new characters and character systems and made them relevant to general questions of relationships within the "lower vertebrates" (Figure 6.5). Stensiö's and Jarvik's work was sufficient stimulus for a new generation of palaeo-ichthyologists to explore their subject afresh. Data could now be utilised to support or refute relationships among the "lower" vertebrates, a strategy not embraced by many of their Anglo-American colleagues, who bowed to the apparent weight and authority of the stratigraphic record as arbiter in determining relationships. Romer, for example, had this to say of Stensiö's work:

> This *geological sequence*, first clearly established by Heintz in 1931…, seemed to most workers an *evolutionary sequence* as well, … Stensiö … comes to a conclusion … startlingly different … but acceptance of … this … thesis makes it necessary to assume that the geological record presents the arthrodires *upside down. This is difficult to believe.* (Romer 1968: 31–32; italics ours)

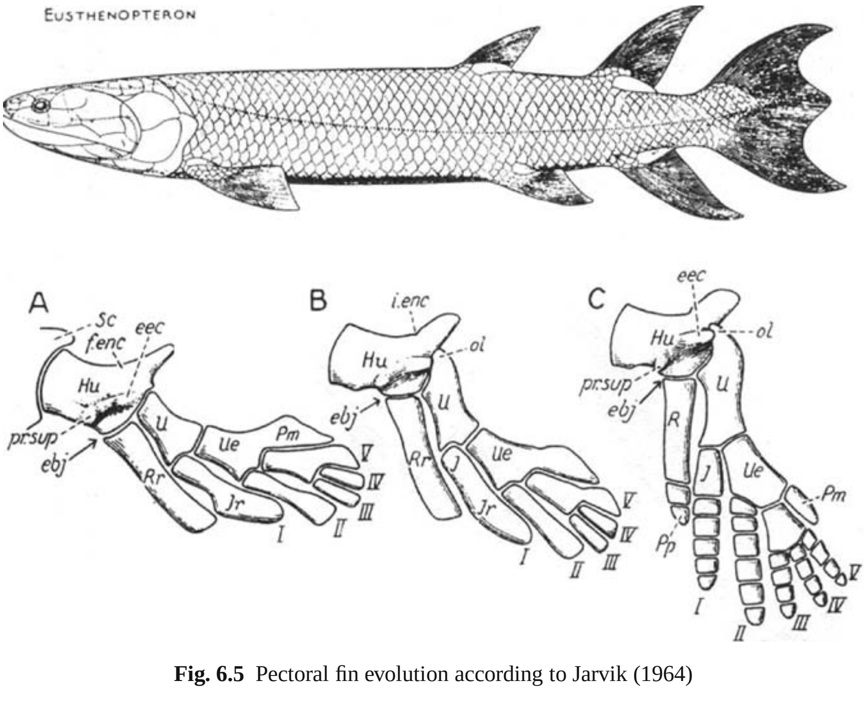

**Fig. 6.5** Pectoral fin evolution according to Jarvik (1964)

The “geological sequence” of arthrodires was an “evolutionary sequence”, one “clearly established”. Stensiö‘s data contradicted this sequence; therefore, it is “difficult to believe”. That belief system, of course, was established earlier by Haeckel (Chapter 4) and, via Henry Fairfield Osborn, was generalised by William Diller Matthew:

> No one carries a more solid conviction of the truth of evolution than the field palaeontologist ... he has seen it himself ineffaceably inscribed in the records of the past. (Matthew 1926: 454)

George Gaylord Simpson, Matthew’s successor, dutifully followed:

> The leadership among the group of Matthewsians has now somewhat naturally fallen to George Gaylord Simpson, who succeeded Matthew in the position of Curator in charge of Vertebrate Paleontology at the American Museum in 1944. (Schmidt 1955: 780, see Nelson & Ladiges 2001: 397)

Simpson gave strength to the entire edifice:

> ... fossils provide the soundest basis for evolutionary classification. ... In some large groups (for example, mammals), ... classifications have come to depend more on fossils than on recent animals. (Simpson 1961: 83)

It was Lars Brundin who eventually challenged that notion, in prose that still shines for its sparkling clarity:

> ... when the classification of mammals has “come to depend more on fossils than on recent animals”, that is in reality not a demonstration of the overwhelming importance of the fossils ... but a sign of fateful misconception of phylogenetic relationships ... (Brundin 1966: 27)

This “fateful misconception” refers to the overlooked yet all-important aspect of taxon interrelationships, how they might be determined, discovered, and expressed.

## 6.4 Lars Brundin, Vertebrate Palaeontology, and the Growth of Cladistics: “An Unlikely Place to Find Enlightenment”

Lars Brundin (1907–1993) was employed at the same institution as Jarvik and Stensiö. He had been working on chironomid midges since 1936 but had evidently been giving a lot of thought to palaeontology, as “young visitors to the Swedish Museum of Natural History were often stimulated by Lars Brundin’s comments on the method and concepts used by palaeontologists for the reconstruction of evolutionary trees” (Janvier 1996: 317). Among those young visitors was Gareth Nelson.

Brundin’s interest in biogeography developed because he saw that the explanations for the distributions of organisms in the Southern Hemisphere were many and usually contradictory, with far-fetched dispersal scenarios being offered as explanations. Brundin discovered the theoretical writings of fellow dipterist Willi Hennig and found in *Grundzüge einer Theorie der phylogenetischen Systematik*, Hennig’s first book (Hennig 1950), and subsequent publications (Hennig 1953, 1957, 1960, 1966a, 1966b), a method that allowed the discovery of relationships among organisms on the basis of evidence from characters—a method that would provide the necessary historical dimension for an understanding of the geographical distribution of organisms that did not require fossils at all, let alone a "complete" or "near complete" record:

> Hennig's epoch-making ideas went largely unnoticed for several years, but for my part there was no doubt that I had found the toolnecessary for a successful analysis of the history behind the Antarctic vicariance pattern. (Brundin in Wanntorp 1993: 362, Page 1989a: 473)

With this tool, over 30 years of accumulated data on midges, and approaching 60 years of age, Brundin published what is perhaps the most significant monograph of the 20th century: *Transantarctic Relationships and Their Significance, as Evidenced by the Chironomid Midges* (Brundin 1966), "... a model for all systematists. It combines painstaking detail with a clearly articulated theoretical framework" (Page 1989a: 473).

Brundin's influence became exceptional, especially among a new generation of palaeontologists (Patterson 1981b: 8, 1981d). As Patterson noted many years later:

> He [Gareth Nelson] arrived in London in April 67, the week before I got back from New York, and when I saw him he told me that there was something new in the Library that might interest me. It was this, Lars Brundin's 500-page monograph on chironomid midges, at first sight an unlikely place to find enlightenment. The Museum datestamp—17th April 1967—fixes the week when I first saw it. I don't know if anyone reads Brundin these days, but he was my first introduction to Hennig and phylogenetic systematics, what we now call cladistics. The first fifty pages of this are still a wonderfully clear and strong statement of Hennig's ideas. I was bowled over by it and became an instant convert. (Patterson 1995, partly cited in Nelson 2000: 14–15; see also Patterson 1981d: 195; Brundin's introduction has recently been reprinted in Lomolino et al. 2004, and translated into French in Goujet and Matile 1978 and Goujet et al. 1990: 31–60)

It may be that no one reads Brundin today, though they might still do with profit (Williams & Ebach 2004). Not surprisingly, as Brundin weighed in against "authorities" such as Darlington, Mayr, and Simpson (Brundin 1965, 1966, 1968, Fittkau 1994: 5), reaction from those quarters was vigorous and hostile. Many years later, Brundin offered a comment on this reception:

> That criticism was often based on unwarranted misunderstandings by those who for no good reason considered themselves experts ... (Brundin in Wanntorp 1993: 365)

In a Royal Society Biographical Memoir, Colin Patterson wrote that "... if there were a Nobel Prize in his field Stensiö would have won it ... " (Patterson 1990: 373). Nevertheless, as such a prize was lacking, "his colleagues in Stockholm organized the fourth Nobel Symposium in his honour." That symposium, published in 1968 (Ørvig 1968), included a lengthy exposition of Hennig's ideas by Brundin (Brundin 1968). In short, this was a Nobel Prize presentation that was to eventually benefit the entire systematics community (see Janvier 1996: 315–318). It was Tor Ørvig who suggested Brundin as a speaker, gaining permission for him to deliver an unscheduled talk concerning Hennig's principles of *Phylogenetic Systematics*. Jarvik, not surprisingly, and like Gosline (above), saw nothing new:

> Of course, when assessing relationships primitive characters must be disregarded. Only unique specialisations can be used; these, however, must be weighed with care. It is not with cladistic terms but through comparative studies of extinct and extant vertebrates that phylogenetic knowledge increases. (Jarvik 1981: 384)

Hennig's concern with distinguishing primitive from derived characters was generally considered to be of some significance—but not particularly original to him, having a long history (some examples are captured in Nelson & Platnick 1981: 325–238[8]). It might, then, strike many as odd that among the numerical systematists (cladistic or otherwise) such issues—distinguishing primitive from derived characters —became the stuff of nightmares, obsessing almost everyone who played with numbers. Such concerns seem to suggest that the "excursion into futility" that Herbert Ross understood phenetics to be descending into might well be extended to numerical taxonomy in general, even in its phylogenetic disguise (Ross 1964; see Chapter 11).

Initial reaction to Hennig's and Brundin's work, by those who had every reason to try and understand it, was indeed hostile (e.g., Darlington 1970, Mayr 1974, Simpson 1975). More recent reaction has been one of indifference (Semple & Steel 2003, Felsenstein 2004), as if their work was simply insignificant and irrelevant for today's numerical sophistication. It is no coincidence that the same persons who see no difference between the value offered by primitive or derived characters (the numerical systematists) are those who ignore the history of cladistics (see Chapter 11).

## 6.5 Lars Brundin and Léon Croizat: Conflict over Origins

Brundin discovered Croizat in the early 1960s. Giuseppe Colosi (1892–1975) (Colosi 1956, 1961: 361) had already linked Hennig and Croizat via the work of Daniele Rosa (1857–1944; for Colosi, see Pardi 1977). Impressed with the "blazing sermon" (Brundin 1966: 61; see Brundin 1981) delivered in *Panbiogeography* (Croizat 1958), Brundin contacted Croizat and a friendship developed. Ironically, this took place at the same time as Brundin was reading Hennig, whom Croizat apparently loathed (Croizat 1976, 1978). The biogeographic problems of the Southern Hemisphere facing Brundin were illuminated by the work of both Croizat and Hennig, both of whom proposed solutions, albeit rather different ones. Croizat often commended Brundin's various chironomid studies (Croizat 1968a: 7, 9 ["Brundin est auteur d'une splendide monographie ... de la partie australe d'un groupe d'insectes..."], 10, 1968b: 227, 233–234, 1968a:142, although see Croizat 1982: 293–294). Nevertheless, whenever Brundin discussed Hennig's work, Croizat had no hesitation in commenting negatively (Croizat 1976: 584, 1978, 1982, 1984). That negativity stemmed from a number of issues, including the belief that Hennig was a Nazi (Platnick & Nelson 1988: 415, Morrone 2000: 46; see also Heads 2005c: 106), an accusation that appears to be unfounded (Schmitt 2001: 320),[9] to

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[8] Rieppel (2006) has recorded Tschulok's comments (1922: 197): "The distinction of primitive and derived conditions of form is a *conditio sine qua non* for the reconstruction of phylogenetic trees."

[9] "Er geriet bei Kriegsende (Mai 1945) als Mitglied des Malaria-Lehrtrupps I in Lignano (am Golf von Triest, Oberitalien) in britische Kriegsgefandenschaft, aus der er erst inm Herbst 1945 entlassen wurde (Entlassung aus dem Heeresdienst im Oktober). Er war nicht Mitglied der NSDAP (Dok. 4). Die-wahrscheinlich auf den Begründer der 'PanBiogeographie', Leon Croizat,

the assertion that Hennig was entirely unoriginal, plagiarising many of his ideas, primarily from Daniele Rosa (Croizat 1976, 1978, 1984; see Colosi 1956, 1961, and above). Croizat himself acknowledged Rosa as an early and significant influence (1960, 1964).

Brundin, like Croizat, saw the possibilities of a deeper, more reasonable understanding of evolution through biogeography rather than palaeontology (Brundin 1988: 366). Brundin promoted biogeography as a means of achieving a more profound understanding of evolution, as the interrelationships of organisms could be meaningfully interpreted in their spatial (geographical) dimension more readily than in their temporal dimension (Brundin 1988: 345). Thus, data and their interpretation were more accessible than simply searching for earlier and earlier fossils, splitting more and more rocks, to reveal an ever more unreliable fossil record.

The unlikely marriage between palaeo-ichthyology and neo-entomology began its courtship in Stockholm and was a relationship borne from "a criticism original with Brundin, of vertebrate palaeontology and its involvement with biogeography" (Nelson 2000: 16; see also Page 1989a: 473 and Nelson 2004). It is of significance that while both Lars Brundin and Gareth Nelson adopted and utilised ideas developed by Croizat and Hennig, a more comprehensive understanding of different approaches to biogeography for biologists and palaeontologists, respectively, during the middle of the 20th century has become hopelessly muddled—it too a subject now "infected" by the enthusiasm of numerically minded taxonomists. We return to this subject later, but first we deal with a few significant events in the Cladistic revolution that occurred in London and New York, both misrepresented (or misunderstood) by David Hull (1988).

## 6.6 The London Reaction: A Salmon, a Lungfish, a Cow, and the Vertebrate Palaeontologists

> "Halstead altered my opinion, which I now see as hopelessly naïve, of scientists as dispassionate seekers after truth. He showed that scientists can be no different from politicians; winning the argument is more important than truth, self-gratification is more important than public good, hence all that nonsense about Marxism." (Miles, pers. comm.)

> "Great is the power of steady misrepresentation; but the history of science shows that fortunately this power does not long endure." (Darwin 1872: 421)

Since 1953 the Annual Symposium of Vertebrate Palaeontology and Comparative Anatomy has been held in either the UK or France. A record of these events is currently being compiled (www.svpca.org), the ninth meeting (1960) being the first documented (as of October 4, 2006). That event is recorded with a

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züruckgehenden-Geruchte, Willi Hennig sei Nationalsozialist gewesen sind haltlos" (Platnick & Nelson 1988).

group photograph, which includes George Gaylord Simpson (1902–1984), Alfred Sherwood Romer (1894–1973), and David Meredith Seares (D.M.S.) Watson (1886–1973), the *crème de la crème* of post–WWII palaeontologists. The 16th meeting (1967), held at Queen Elizabeth College London, is commemorated with a series of photographs, including a young Alan Charig and Brian Gardiner (of whom, more later), among others. There is a gap in the record from 1967 to 1982, from the 16th to the 31st meeting. For those whose inspiration comes from organisms other than vertebrates, the 16th meeting's programme appears somewhat erudite, contributions seemingly as obscure and non-controversial as any other get-together of biologists or palaeontologists: "Neuromasts, lateral lines and dermal bones" (T.S. Westoll), "The Late Devonian freshwater fishes from Mt Howitt, Victoria, Australia" (J.A. Long), "On the coelacanth air-bladder" (K.A. Josey), and "Sub-Holostean fishes from Monte San Giorgio" (J.A. Griffith), among the contributions. But if one jumps ahead to the 35th (1986) meeting, the programme seems altogether of broader interest, including a session chaired by Colin Patterson with presentations such as "The paraphyly of plesions" (R.P.S. Jefferies) and "Are palaeontological scenarios proper science?" (T.S. Kemp). If one examines the "Group Photo" for this symposium, in the second row, standing next to each other are Colin Patterson (1933–1998) and Lambert Beverly Halstead (1933–1991).

For the growth and development of cladistics—especially in London and the UK— the crucial year is not yet marked by any items of interest, captured only by a note that the 26th symposium was held in 1978 at Reading University, UK, a symposium organised by Lambert Beverly Halstead. This symposium sparked a debate that had lasting consequences for systematics, classification, and evolutionary studies—as well as Museum science and exhibitions.

Halstead was born in Pendleton, Lancashire. He studied geology at the University of Sheffield in 1952, eventually undertaking a PhD at the Zoology Department of University College London during the years of 1955 to 1963, guided by Professor D.M.S. Watson. It was here he became friends with Brian Gardiner (Sarjeant 1993). He settled (of sorts) at the Geology Department, Reading University. Always a provocative and controversial man, he managed to pick many fights with many people, as well as taking up and defending causes he believed were just (Sarjeant 1993). The exhibition policy at the Natural History Museum in London at the start of the 1970s and its link with cladistics was one such cause.

Halstead recorded some of the events of the 26th symposium in the journal *Nature*:

> Palaeontologists did not reckon on the ingenuity of certain colleagues, who not only succeeded in applying it [cladistics] to fossil fishes, but managed to convert others to this new system. (Halstead 1978b: 759)

The reference to success was the *Interrelationships of Fishes* symposium organised by Colin Patterson, Humphry Greenwood, and Roger Miles (all of the Natural History Museum in London) and the resulting book, published by The Linnean Society (Greenwood et al. 1973). Of this book, Patterson noted some years later:

> Our excuse was to produce a Festschrift for two honorary Foreign members of the Linnean, two Swedish heroes … Erik Stensiö [and] Erik Jarvik … but our hidden agenda was cladistics, to get as many major groups of fishes as possible worked over in the new cladistic framework. … We didn't manage to raise a complete cast of cladists but I think this was the first multi-author volume, anywhere in biology, in which the overall message is cladistics. *It has a certain historical significance*. (Patterson 1995: 6; italics added[10])

Stensiö and Jarvik ("two Swedish heroes") were the figureheads for the "Stockholm school" of palaeo-ichthyology (see above).

### 6.6.1 Two Schools and Extinct Fishes

> "The issue was summed up for many by R. Parrington's (University of Cambridge) exasperated exclamation that according to the cladists a lungfish is more closely related to a cow than a salmon to which Colin Patterson (British Museum (Natural History)) answered, 'Yes, I cannot see what is wrong in that'." (Halstead 1978b: 760)

And so "a special session was set aside for the topic [cladistics] to be debated at the 26th Symposium of Vertebrate Palaeontology and Comparative Anatomy held in September at the University of Reading" (Halstead 1978b: 759). It was this session that prompted Rex Parrington's (1905–1981) "exasperated exclamation" concerning the relationships of the salmon, lungfish, and cow. Nor was this Parrington's first outburst:

> I remember the Nobel Symposium IV in June 1967. Humphry Greenwood and Rex Parrington FRS were sitting together on the bus back to the hotel. Rex was remonstrating with Humphry on his earlier comment, also Colin's [Patterson], favourable to Jarvik, which Parrington took as implied criticism of Parrington. (Nelson, pers. comm.)

It was at the 4th Nobel Symposium *Current problems of lower vertebrate phylogeny* where Brundin presented his summary of Hennig's ideas (Brundin 1968).

Parrington was educated at Sidney Sussex College, Cambridge, receiving lectures on zoology from Hans Gadow and Sir Clive Forster-Cooper, the former a student of Ernst Haeckel, one-time employee of the British Museum and Cambridge University Museum, and author of *The Wanderings of Animals* (1913), the latter eventually becoming the 6th Director of the Natural History Museum, London in 1938. Parrington settled at the University Museum of Zoology in Cambridge in

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[10] This fact was not lost on reviewers: "To an astonishing degree, the present volume exhibits the influence on fish systematics of the entomologist Hennig's (1966) thoughts, as pointed out by Nelson (1972) [1973]" (Bonde 1974: 563); "... the subject matter is united by an approach to classification and relationships heavily influenced by the phylogenetic systematics of Willi Hennig. This book is the first one on fish classification to show extensively this influence and the resulting implications concerning the future of fish classification are far-reaching and important" (Weitzman 1975: 331). Years later, Nelson was to write, "I can't imagine that history developing in the absence of that first volume ..." (Nelson, 2000: 19).

1927, remaining for the next 41 years, becoming its director when Forster-Cooper moved to London. In 1960 Parrington was offered the position of Director of the Natural History Museum, but declined due to ill health. He retired from Cambridge in 1970 with the intention of giving up "his palaeontology" (Charig 1990: 268) but continued to publish on the subject until his death in 1981.

It was Parrington who organised the first Annual Symposium of Vertebrate Palaeontology and Comparative Anatomy: "The 'Father' of this Symposium was, without doubt, Rex Parrington" (Charig 1990: 367).

It was said of Parrington that he founded a "school" (Charig 1990), initially composed of Alan Charig, "Fuzz" Crompton, Barry Cox, Alec Panchen, Arthur Cruickshank, Tom Kemp, and Anne Warren (née Howie):

> These seven students, once they obtained their doctorates, all helped to produce a third and even fourth "generation" of vertebrate palaeontologists and comparative anatomists. Together they constitute a "Parrington school" that must have had a beneficial impact upon the worldwide development of the science. (Charig 1990: 367; see Joysey & Kemp 1972, a book worth comparing with Greenwood et al. 1973)

Thus, so it seems, the stage was set for clashes between members of the "Parrington school" and the "Stockholm school"—disagreements had been simmering for some years.

In his first swipe at the cladists, Halstead noted that "An example of this process [dealing with evidence for and against particular cladograms] was illustrated by the cladograms prepared by P. Janvier … on agnathans and B. Gardiner … on choanichthyans both of which were demolished within hours of their being proposed" (Halstead 1978b: 760), statements that caused some surprise (Gardiner et al. 1979). In a further letter, Halstead clarified his view, suggesting that "Janvier's agnathan cladogram was a reflection of Stensiö's mistaken notion of the myxinoid affinities of the heterostracans, which has been firmly rejected by workers in the field … " (Halstead et al. 1979: 176). Halstead cited two of his own papers. Janvier responded with a summary of the problem and the characters considered indicative of the relationships of these animals. Yet this part of the *Nature* correspondence must have been something of a puzzle to those who had no in-depth understanding of the background to the controversy concerning these primitive fishes (Janvier 1979). Nevertheless, some years later Janvier and Blieck wrote:

> When a student, L.B. Halstead … heard of the heterostracan controversy, which ranged the "Swedish school" (Stensiö and his disciples) against the "Anglo-American school" (Watson, White, Westoll, Romer, Stetson), and he became interested. (Janvier & Blieck 1993: 92)

And this was something of an issue in the "Halstead–Natural History Museum" conflict:

> The school that Stensiö founded came to be called "the Stockholm school", an epithet that probably originated with A.S. Romer For.Mem.R.S. (1894–1973), a near contemporary of Stensiö, and his transatlantic counterpart as the master of vertebrate palaeontology. The views of the Stockholm school would be contrasted, in debate, with those of the "Anglo-Saxon school", generally meaning the British and North Americans. An assessment of the Stockholm school attributed to Romer is "brilliant descriptive work but bizarre conclusions" (Nelson 1973). (Patterson 1990: 374)

It was not just the relationships of these fishes that was controversial but their mode of origin and dispersal, of which more later.

### *6.6.2 A Salmon, a Lungfish, a Cow, and Some Vertebrate Palaeontologists*

> "For some, cladistics has become more of a creed than a tool. 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: 35)

It was Brian Gardiner's presentation that provoked the salmon, lungfish, cow exchange. In response to Halstead's published jibe concerning their relationships (Halstead 1978b), seven palaeontologists responded (most having at one time or another been part of or associated with the "Stockholm school"). "The debate on cladism has smouldered in specialist journals for over a decade," the seven began, "and we are glad that Halstead has brought it to *Nature* . . . " (Gardiner et al. 1979: 175). Of the problem posed, "If experienced comparative anatomists can disagree on so simple a question, either there is revolution in the air, or words are being used in different ways" (Gardiner et al. 1979: 175)—as it happened, both were true: words were being used differently and revolution was in the air. The difference between the two viewpoints (Halstead and Gardiner) is best appreciated by examination of the diagrams each used to illustrate relationships (compare Figures 6.6a–c with d).

Gardiner et al. presented three cladograms that expressed all possible relationships among the salmon, lungfish, and cow (Figure 6.6a). Of the three diagrams Gardiner et al. remarked that

> . . . *a* [Figure 6.6a] was the preferred solution of the cladists . . . *c* [Figure 6.6c] was the preferred solution of Parrington and Halstead . . . when evolutionary systematists prefer cladogram *c*, they mean that lungfish and salmon are more similar than lungfish and cows. And in preferring cladogram *a*, cladists mean that they infer that lungfish and cows shared a more recent common ancestor than lungfish and salmon. This inference is drawn from the fact that lungfish and cows share derived characters . . . not found in salmon. (Gardiner et al. 1979: 175–176; ellipses represent omitted references)

Thus, the differences in approach are concerned with whether similarities or relationships were the focus of attention. A further point was made:

> Overall similarity may be modernised or dignified by calling it "genes in common" or "shared genotypes", yet when we do have information on genes . . . the biochemists present their information in the form of cladograms, and use the same genealogical concept of relationship as Hennigians. (Gardiner et al. 1979: 176)

The idea that "genes in common" would be of significance was introduced by Mayr (1965: 79), without any knowledge that such would be the case—in 1965

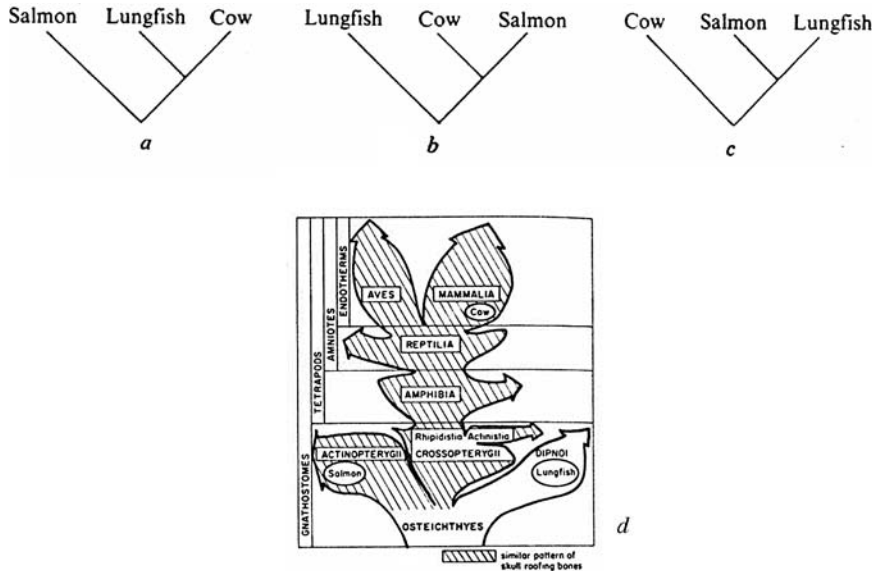

**Fig. 6.6** Contrasting illustrations from the *Nature* salmon–lungfish–cow debate. Figure 6.6a–c after Gardiner et al. (1979); Figure 6.6d after Halstead et al. (1979), reproduced with permission

relevant information was significant only for its absence.[11] Nevertheless, Mayr's claim was the impetus needed to provoke an examination of genes, an exploration that led Patterson into the further reaches of homology as more molecular data became available (Patterson 1980a, 1981d: 198, 2002; see also Rosen 1974b: 447, Sokal 1975: 259, and below, Section 6.6.3).

The cladists' response (Gardiner et al. 1979) was published simultaneously with a further comment from Halstead et al. (1979: 176[12]), which added to the obscurity

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[11] "The consistent failing of Mayr in his synthesis endeavors, however, was his understanding of genetics" (Provine 2005: 412).

[12] Halstead, Errol White, and Giles T. MacIntyre authored the response in *Nature*. Halstead drafted the ms, with a revised version that included MacIntyre as an author. This revised version (Halstead & MacIntyre) is virtually identical to the published document. Errol White appears not to have had any input. Oddly enough, the reference is missing from his bibliography (Stubblefield 1985). Prior to publication, the revised manuscript was sent to a number of persons for comment: Charig, Panchen, Parrington, Savage, Thulborn, Underwood, Westoll, and White (data from mss and correspondence in the Cain collection held in the American Philosophical Society).

So what part did White and MacIntyre play? According to Colin Patterson, White was simply added by "passive participation due to Halstead's machinations" (Nelson, pers. comm.). Oddly, White's affiliation is given as The Department of Geology, University of Reading, rather than the Natural History Museum. White was retired from the Natural History Museum by then. When Halstead wrote an obituary for Errol White (The Times, January 22, 1985: 16), he mentions that "In 1971 he [White] became attached to the Geology Department of Reading University, where he continued his researches until the end of 1984."

For MacIntyre it may have been a result of his participation in the 26th Symposium of Vertebrate Palaeontology and Comparative Anatomy, where Halstead (1978b) noted that "Where complete sequences from species to species or, as G. MacIntyre (Queen's College, New York) demonstrated, from genus to genus can be demonstrated ....."

of the debate: “The cladists simply omit the possibility that none of the three pairings shared a more recent common ancestor, than any of the others, but rather were all derived from a pre-existing common stock. . . . ” Inspection of Halstead’s diagram illustrates the obscurity with which taxon relationships were once hidden and the vagaries surrounding the interpretation of such diagrams (Figure 6.6b).

These letters “provoked a large correspondence” (*Nature* 280: 541, August 16, 1979), but only a few were published (Panchen 1979,[13] Fink & Wiley 1979, Crowson 1979, Janvier 1979). The relationships among these three animals (Salmon, lungfish and cow) quickly disappeared from public view.[14] Two years later other matters seemed more pressing.

### *6.6.3 Exhibitions and Cladistics*

While Halstead’s 1978 Annual Symposium of Vertebrate Palaeontology and Comparative Anatomy “Cladistics” session was a fire that didn’t require much stoking, extra fuel came from Roger Miles, when he gave an account of the new exhibition policy of the British Museum (Natural History) (summarised in Miles 1978, accompanied by a response from Halstead 1978a). That battle had been brewing for some time, as “The new exhibition schemes at the British Museum (Natural History) and the consequent changes in the more traditional exhibits have caused some consternation amongst interested scientists,” as a *Nature* editorial comment chose to view it (*Nature* 275, page 682, October 26, 1981).

The origins of the Natural History Museum’s exhibition policy date back to Frank Claringbull’s (1911–1990) reign as its 10th director (Stearn 1998). Frank Claringbull began his directorship in 1968, retiring just 8 years later in 1976:

> On appointment as Director of the Natural History Museum in 1968 he took up the challenge to modernize the museum with characteristic energy and by his retirement in 1976 the museum had begun to acquire a widely acclaimed new style. (McKie 1991: 974)

Not “widely acclaimed” by all. One action that displeased many scientists, both within and outside the Museum, was that Claringbull removed “ownership” of the galleries from the Science Department Keepers (and effectively from the scientists) and eventually, in January 1975, created a Department of Public Services, which had direct responsibility for the style and content of any new exhibitions. To make matters worse, the palaeo-ichthyologist Roger Steele Miles was appointed its first Head—Miles was of the “Stockholm school” of palaeo-ichthyology, spending time with Stensiö and Jarvik, and a cladist to boot.

Relevant events began a few years earlier. In 1972 a panel of 13 Museum scientific staff were asked to review the exhibition policy of the Museum, presenting,

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[13] Panchen did not attend the 1978 symposium.

[14] A more private academic battle was fought after the publication of Rosen et al. (1981), including a hostile seven-page review from Jarvik (1981; see Forey et al. 1991). The example still crops up in popular books to illustrate the simplicity of cladistics (e.g., Thompson 1991, Weinburg 1999, Gee 2000).

in February 1973, an internal paper entitled "A proposal for a new approach to the visiting public". Claringbull's group suggested that a new exhibition scheme should be set up to present aspects of "modern biology" that were understandable to a more general (and modest) audience. More general, that is, than the old-style galleries, designed, so it was believed, for the learned few rather than the interested public (the latter was of more interest to Richard Owen and his "Index Museum"). There were to be four main themes: "*Man*; *Ecology*; *Life Processes and Behaviour*; *Evolution and Diversity*".[15] By the end of 1972, there were outlines for the content of the first three themes—*Man; Ecology; Life Processes and Behaviour*. The fourth theme—*Evolution and Diversity*—was to become a contentious bear-pit.

Miles had chaired the panel for the third theme—*Life Processes and Behaviour*—and during 1973, as *Evolution and Diversity* was being tackled, Miles was seconded from the Palaeontology Department to oversee the development of the three completed themes. Text for the outline of *Evolution and Diversity* was eventually finished in October 1973 (Anonymous 1973). Events moved fast. By 1974, Human Biology, the first concrete project related to the *Man* theme, was in development; by 1975 Miles had become head of the new Department of Public Services; two years later, in 1977, *The Hall of Human Biology* opened to the public, followed quickly by the second project, *Introducing Ecology* in 1978; *Dinosaurs and Their Living Relatives* occupied the main hall of the building in 1979, and *Man's Place in Evolution* opened in 1980. Within six years the public galleries of the Museum were completely transformed.

It was the last two exhibitions that galvanised Halstead into action: "Both the new exhibits are simply vehicles for the promotion of a system of working out relationships known as cladistics" (Halstead 1980a: 208). The context for the remarks, perhaps, was that the exhibitions portrayed cladistics rather than the "evolution" of these groups, apparently so well known.

### *6.6.4 Mammals and More "Dinosaur" Cladistics*

While never one of the main focal points for discussion in *Nature* (or even elsewhere), events surrounding the Fossil Mammal exhibitions were crucial components. Policies and outlines, discussions and progress, all seemed to be part of some sinister plot. Donovan, then head of University College London, Department of Earth Sciences (1966–1982), wrote a lengthy letter in the New Year edition of

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[15] The schemes were outlined in the *Report on the British Museum (Natural History) 1972–1974*: 73 (1975); both Halstead's and Miles' 1978 contributions to *Nature* contained summaries, followed, a few years later, by a contribution from Southwood & Hedley (1981), the former, at that time, chairman of NHM trustees, the latter director, succeeding Claringbull in 1976; see also Clarke & Miles (1980).

*Nature* (Donovan 1981[16]). After briefly reviewing the Museum's past exhibition strategy, he noted that

> Eventually a policy seemed to emerge, exemplified by the new Fossil Mammal exhibit opened in 1972 in what was the old Fossil Mammal Gallery. In place of the dramatic long vista past mounted skeletons of fossil elephants, the continuity of the gallery was broken up and its original architectural character subdued, though some of the detail is visible. Scientifically the new exhibit is much better than the old one, with a great deal of information on the animals and on the rocks from which they came, attractively displayed. As Halstead has pointed out, everyone, from a specialist to a child, can get something out of it. (Donovan 1981: 105)

The Fossil Mammal exhibition opened in phases, the first was the section on the Pleistocene era, developed by Alan Charig, head of amphibians, reptiles, and birds in the Natural History Museum, opened in July 1970 (*Report on the British Museum (Natural History) 1969–1971*: 70, 1972, "representing about one-third of the proposed total gallery"; Milner 1997); the remaining sections opened on July 14, 1972, completing the exhibition (*Report on the British Museum (Natural History) 1972–1974*: 73, 1975). Roger Hamilton wrote a critique of the gallery in the *New Scientist*, "Even the most conscientious non-specialist visitor will find difficulty in coming to terms with the subject matter" (Hamilton 1980: 336). "I feel free," he continued, "to make these criticisms because this gallery was largely the result of my own work and occupied most of my time during 1970–1972" (Hamilton 1980: 336, the article was published posthumously). The conflict between Halstead's views and those of Hamilton was not lost on Museum exhibition staff (Alt 1980: 18).[17]

Roger Hamilton (1945–1979) died young. He joined the Natural History Museum in London as a palaeontologist and as part of his job was given the Tertiary section of the new Fossil Mammal exhibition to supervise. When his time with the gallery redevelopment was completed, in 1972, he returned to the palaeontology department as head of the Fossil Mammal section. He remained its head for two years until he was transferred to the Department of Public Services as Roger Miles' deputy in 1975 (Fifield 1979, Wybrow 1980).

Alan Charig (1927–1997) was one of Parrington's seven (see above), studying Triassic archosaurs under his supervision. He took a post in invertebrate palaeontology at the Natural History Museum in 1957, moving to fossil reptiles and birds in 1961, retiring in 1987 (Milner 1997). Among other things, he was a great populariser of science, writing and presenting *Before the Ark*, a 10-part series on vertebrate palaeontology for the BBC television series in 1974. A book accompanied the series (Charig & Horsfield 1975). Charig published a second popular book, *A New Look at*

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[16] Many years later Donovan wrote a short account of Cladistics and Phylogenetic Systematics for the Palaeontological Association Newsletter (Donovan 2003). He wished to promote the view offered by Bechly (2000) that computerised cladistics was equivalent to "pattern cladistics", both being devoid of meaning. He also notes along the way that Patterson's AMNH talk (see 6.6.9) was "disastrous". Donovan's confusion of ideas is one of the reasons we started this book. There is, of course, no relationship between computerised cladistics and "pattern cladistics".

[17] The whole exhibition was eventually moved to make way for *Introducing Ecology* in 1978.

*Dinosaurs* (1979), which "had even greater impact and was translated into several different languages" (Milner 1997: 67).

During his short life, Hamilton was a regular contributor to the popular science weekly *New Scientist*, reviewing books and exhibitions. *Dinosaurs and Their Living Relatives* (British Museum (Natural History 1979)), an exhibition that Hamilton worked on, opened in the autumn of 1979:

> Although the dinosaur skeletons are the most obvious feature of the exhibition, there is also a series of displays which show the visitors how scientists attempt to discover relationships between organisms, either living or fossil, and explain modern views about the evolutionary history of the dinosaurs and their relationships with living animals. (*Report on the British Museum (Natural History) 1978–1980*: 67, 1981)

Charig was not involved in this exhibition (Halstead 1984a[18]).

In the March 1979 issue of the *New Scientist*, Roger Hamilton reviewed Charig's *A New Look at Dinosaurs*, framing his remarks in the context of the soon-to-open Museum exhibition *Dinosaurs and Their Living Relatives*. Hamilton began with compliments. Then using Museum exhibition styles, he contrasted various ways of explaining what dinosaurs are to a largely non-professional audience, contrasting the setting out of their relationships with "the alternative, 'ecological', approach" (Hamilton 1979: 888). The "ecological" approach was captured by phrases such as

> "*Tyrannosaurus rex* was the largest flesh eater of all time; the ceratopsians were the very first palm wine drinkers; *Ornithomimus* may have eaten eggs." All very interesting, but not inspiring and without any structure. Certainly not anything a modern scientist would be proud of! (Hamilton 1979: 888)

"In contrast," he continued,

> . . . a treatment of the relationships of the dinosaurs can rely on specimens and objective interpretations from them. It is an approach that has not been attempted before, either in book or exhibition form. This was the approach we chose. (Hamilton 1979: 888)

Hamilton then proceeded to present a succinct and clear account of cladistics using dinosaur relationships as examples (an account every bit as clear and concise as Patterson's article in *The Biologist*, 1980a):

> So the birds are closely related to some animals that we call dinosaurs. . . . This means that the classical idea of the dinosaurs (Dinosauria) is only tenable if the birds are included. But we cannot validate the group Saurischia and cannot establish relationships with the *Ornithischia*. Therefore, as Charig suggests, it may be necessary to include the crocodiles and pterosaurs which would make the Dinosauria and Archosauria synonymous. Not much future in this: the group Dinosauria seems to be taxonomically extinct. (Hamilton 1979: 889)

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[18] Halstead reviewed Charig's book: "There is an important section on the principles of classification as well as of the dinosaurs themselves, which are straightforward and sensible discussions of the issues involved and which contrast dramatically with the approach to dinosaurs which now adorn the Central Hall of the Natural History Museum. It is certainly curious that the Natural History Museum should publish ... an excellent book by their dinosaur expert and yet should simultaneously put on display an exhibit, with which Alan Charig had no connection ..." (Halstead 1979a: 10). Halstead also reviewed *Dinosaurs and Their Living Relatives* with his usual barbed comments (Halstead 1979b).

The book that accompanied the *Dinosaurs and Their Living Relatives* exhibition included a guide to working out animal relationships, a primer in cladistic techniques.[19] While Charig may have suggested such relationships among dinosaurs in his book, he was neither a cladist nor particularly fond of the new exhibits—especially his exclusion from their creation—and was not about to embrace the "extinction" of dinosaurs, albeit in name only. It was evident that the new boys were beginning to instruct the palaeontologists of the past in their science. Charig did respond to the cladists (Charig 1980, 1982), but like so many at the time (Halstead included), he chose to address what he imagined was a schism between Hennigian cladists and transformed cladists, the latter being "neither Hennigian, phylogenetic, nor cladistic. . . " (Charig 1980: 19).

As if to rectify matters, in 1984 the Yorkshire Museum, UK, mounted a new dinosaur exhibition, entitled *A New Look at Dinosaurs*, based on Charig's book, his input, and support from the ever-present Halstead: "Here is what a museum exhibition is all about," he wrote. "As a Northerner, I am proud that the North has so convincingly exposed the trendy nonsense that has recently infected one of our most revered national institutes, not by calling them but actually showing them how things should be done, by bloody well doing it" (Halstead 1984a).

### *6.6.5 Creationism, Marxism, Gradualism . . . "Isms multiply when ideologies collide" (Moore 2001: 36)*

In his first letter to *Nature* concerning the Museum exhibitions, Halstead began to include his views on evolution and its workings: "Evolution is a gradual process that takes place over time and man simply imposes on it his own arbitrary system of classification" (Halstead 1978b: 760). Two years later, the booklet for *Man's Place in Evolution* (1980[20] (British Museum (Natural History))) provided Halstead with evidence for misdeeds:

> According to the stated assumptions of cladistics none of the fossil species can be ancestral by definition. This presents the public for the first time with the notion that there are no actual fossils directly antecedent to man.

And for obvious special effect, he added,

> What the creationists have insisted on for years is now being openly advertised by the Natural History Museum. (Halstead 1980a: 208)

Halstead then posed a question:

> The questions that should arise in everyone's mind are: what is this all about, what is going on and what is behind it all? The answers can be found by reading the literature of cladistics.

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[19] A second edition was published in 1985. According to the rear book jacket,"The methods of working out relationships, on which this book is based, have been clarified and simplified."

[20] The second edition was published in 1991, very much the same style and content as the first, although slightly updated. To account more fully for the fossil material, a companion booklet, *Our fossil relatives: More about Man's place in evolution* (Stringer & Grey 1983), was published.

> The tenor of this is seen in its abuse of E. Mayr and G.G. Simpson, and indeed of Charles Darwin himself, because of their firm adherence to the concept of gradualism and to the idea that the processes that can be observed at the present day, when extrapolated into the past, are sufficient to explain changes observed in the fossil record. (Halstead 1980a: 208)

Then, as if that was not enough to goad even the meekest of *Nature* readers, Halstead contrasted the gradual evolution of the Neo-Darwinians (Mayr, Simpson, Darwin) with the episodic evolution he associated with Marxism:

> If the cladistic approach becomes established as the received wisdom, then a fundamentally Marxist view of the history of life will have been incorporated into a key educational system of this country. (Halstead 1980a: 208)

Thus, creationism, anti-Darwinism, and Marxism were all thrown in as necessary components, or conclusions, of cladistic thinking. The immediate response highlighted the ludicrous nature of comparing scientific theories with political ones (Hugh-Games 1980, Rothman 1980, Marks 1980). Patterson's reply was succinct:

> He [Halstead] sees a necessary connection between cladistics and one view of the evolutionary process, but as cladistic literature makes plain, there is no such connection. Cladistics is not about evolution, but about the pattern of character distribution in organisms, or the recognition and characterisation of groups. (Patterson 1980b: 430)

Halstead's further response (1981a see also 1981b and 1981c) was to isolate Patterson as a "transformed cladist" (as did Charig), not the kind whose ideas are represented in the Museum's displays, which, according to Halstead, are "Hennigian". Thus, Halstead could continue to link "punctuated equilibrium" theory (a recent proposal for saltational, episodic evolution) to cladistics via Cracraft (1979), linking that to Marxism via Gould & Eldredge (1977[21]), the whole fermented union being dealt with at length in other papers (Halstead 1981b, 1983[22]). Halstead's ideas relate by association rather than logic. In any case, Nelson offered a different perspective:

> Knowing Halstead to be usually of good cheer and judgement, I am led to suspect that not all is as it might seem—that the root of his dislike is not to be found brewing in a pot pourri of punctuated equilibria, Marxism, scholastic death, etc. Rather, his dislike may stem, as seems to me, from a sense of loss of "the fossil record"—the ultimate source of truth of evolution as rendered by a professional class of fellow-specialists. (Nelson 1981: 627)

### *6.6.6 Halstead and Evolution*

Halstead was indeed a very conventional palaeontologist, at least by the post-war Anglo-American standards:

> My approach as a palaeontologist may seem naive, it is first to examine the fossil record and being initially trained as a geologist, I am able to add a further naivety by looking at

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[21] Their paper did include a brief account on Marxism and gradualism in a section entitled *Towards a General Philosophy of Change* (Gould & Eldredge 1977: 145).

[22] Halstead was keenly aware of a political dimension, contributing many articles to the *Freethinker, New Humanist,* and the *Salisbury Review*.

> fossils in the order in which they appear in the rocks. One of the curious features of the fossil record is that wherever a palaeontologist finds himself, it is obvious that evolution has taken place somewhere else. This is such a commonplace experience that it calls for explanation. (Halstead 1983: 249[23])

Some years later, Halstead elaborated:

> One of the common experiences of all paleontologists is that one rarely finds examples of gradual evolution in the rocks one studies. This is the experience that undoubtedly stimulated the theory of punctuated equilibria. In many instances a zonal succession of species can be documented, which are clearly closely related, but seem to be unchanged in one formation only to be replaced by a similar but significantly advanced representative of the same group. Such a situation typifies the succession of pteraspid ostracoderms described by White in the Welsh borderlands [78].[24] I described a comparable succession in the Old Red Sandstone of Scotland with psammosteid ostracoderms [79].[25] (Halstead 1991: 41)

Pteraspid ostracoderms are heterostracans, the animals that caught Halstead's imagination in his student days (see above). Early in his career Halstead had determined something of their evolution:

> Within the same environment, significant differences can be seen between the faunas which succeed one another in time. For example, in the Dittonian the various species of *Pteraspis* which follow one another are quite distinct, and show no evidence of evolution from one species to another, there being no intermediate forms, while other heterostracans and cephalaspids generally appear at particular horizons only, and are replaced by entirely different forms. This individuality can best be explained by postulating a series of immigrations to the Anglo-Welsh province, such as was suggested by Westoll when discussing White's paper (1946), as the presence of some of the same genera and species in such distinct provinces as Podolia and Spitzbergen can only be accounted for by a faunal interchange via the sea. (Allen & Tarlo[26] 1963: 151)

Even earlier, he insists,

> Most probably there was a centre of evolution elsewhere from which waves of migration took place into the Anglo-Welsh area, and from the evidence so far available, this centre appears to have been in the Arctic. (Tarlo 1962: 153)

And in 1967:

> There is no doubt that the Baltic province was an evolutionary centre for the psammosteids and that from it there were waves of migration to other provinces. Indeed this pattern appears to be fairly general throughout the fossil record. Briggs (1966) has shown that with the living shore fishes, .... (Tarlo 1967: 1237)

Briggs' 1966 paper was the influential "Zoogeography and Evolution", which apparently provided further evidence for a dispersalist model of evolution by calling

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[23] And further, "Detailed family trees of the horse and elephant and many groups of invertebrates such as the ammonites (shelled relatives of the squids) became classics, since detailed successions of forms preserved in successive layers of strata provided clear proof of gradual evolution through time of particular lineages" (Halstead 1982b: 95–96).

[24] 78 is the reference to White (1950).

[25] 79 is the reference to Tarlo (1961).

[26] Halstead had at first taken his stepfather's name, Tarlo. Thus, all his papers up to 1967 had that surname. After 1968 he used his born name, Halstead (Sarjeant 1993).

to attention “the presence of an evolutionary center in the Indo-West Pacific” for shore fishes (Briggs 1981). Briggs (1981) reviewed the history of the centre of origin concept, which, he noted, began with Darwin and his single centres of creation (Darwin 1859), eloquently captured by Ernst Haeckel as “… the distribution of the great majority of animals and vegetable species in regard to which the *single origin of every species in a single locality*, in its so-called ‘central point of creation,’ can be considered as tolerably certain” (Haeckel 1925: 367), encouraged by Adams (1902), developed by Matthew (1915), and, of course, solidified with Darlington (1957). Briggs studied under George Sprague Myers (1905–1985[27]) at Stanford University, which—intellectually at least—connected Halstead’s views on the evolutionary process directly to that of the New York School (“W.D.Matthew (1871–1930), K.P. Schmidt (1890–1957), G.G. Simpson (1902–1984), J. Darlington, Jr (1904–1983) and G.S. Myers (1905–1985)”, Nelson & Ladiges 2001: 389).

Frank H.T. Rhodes, a palaeontologist who eventually became president of Cornell University in 1977, retiring in 1995, wrote a review on “the course of evolution” in 1966. Here he noted:

> Furthermore, many faunal sequences are interrupted by migration. The fossil record contains striking illustrations of the importance of this as an explanation of discontinuity. Simpson (1953: 364) has shown the effect of this in phylogenetic reconstruction of horses, based respectively on faunas collected from North America and Eurasia. In the latter case the few known fossil representatives could suggest saltationary development, but the completely transitional North American sequences show the “discontinuous” European series to be occasional migrants from the mean evolutionary stream. (Rhodes 1966: 32)

Halstead thought highly of Rhodes’ paper: “A quarter of a century after Rhodes survey, we are back to the very position presented to us in his lecture of 1964”, a position captured by waves of migration from certain centres of “creation”:

> From such evolutionary centres waves of migration can be traced to other regions and it is this phenomenon that is responsible for many of the gaps and missing links in the fossil record. … Whenever there is a complete geological sequence in a major evolutionary centre, evolution can be demonstrated to be a gradual process. Classic examples are Devonian jawless vertebrates from the Baltic region, horses in the Tertiary of North America and, more recently, the studies of the evolution of primitive adapid primates, again in North America. (Halstead 1989: 217)

The Devonian jawless vertebrates from the Baltic region refer, of course, to Halstead’s heterostracans and their dispersal (Figure 6.7).

Of course, as Nelson perceived early on in the *Nature* correspondence (1981), and as he and other palaeo-ichthyologists learned a decade and half before these events, when the role of palaeontology is questioned then for some, it was the same as questioning evolution, even our very knowledge of it. Of course, the issue *did* eventually become about evolution, at least its Neo-Darwinian explanation.

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[27] It was Myers’ paper on Fresh-water Fishes and West Indian Zoogeography (Myers 1938) that was a stimulus for Gosline and his comments on fish biogeography (Gosline 1944).

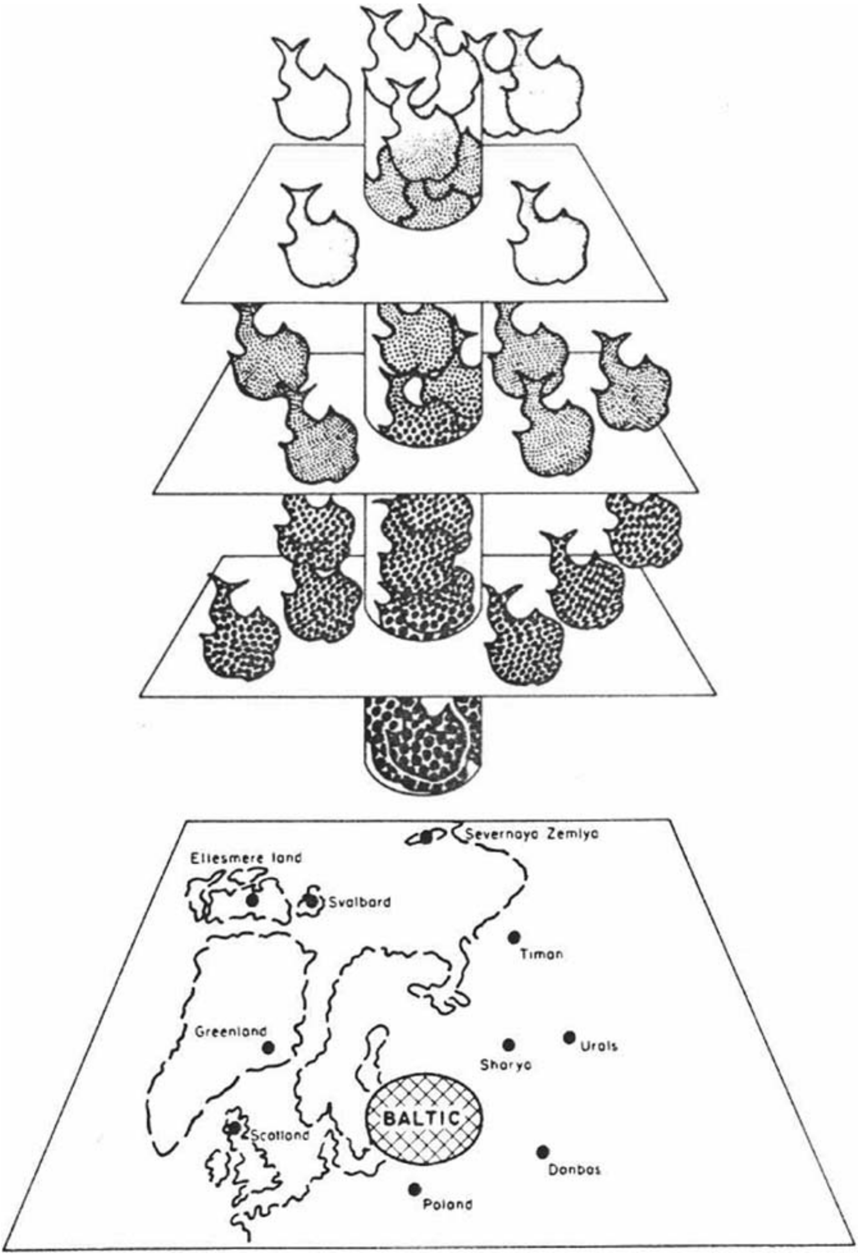

**Fig. 6.7** From Halstead (1983: Fig. 6: 254), "Diagram to illustrate successive migrations of psammosteds to give impression of evolutionary discontinuities in all regions except the Baltic"; diagram also appears in Halstead 1982a: 82 and 1991, Fig. 3: 44.

Halstead died tragically in a car accident in May 1991. Among those present at the funeral was his old friend Colin Patterson (Sarjeant 1993: 55, Patterson 1991a, 1991b[28]).

### *6.6.7 More Creationism*

> "But some of the letters carried the implication that many distinguished zoologists, and especially palaeontologists, had given up believing in evolution, and this is a matter which does deserve the attention of all scientists." (Huxley 1982a: 141)

Halstead's final riposte in the *Nature* correspondence confirmed his status as a palaeontologist of the "older" kind—and repeated his assertion of the connection between cladistic ideas and creationist notions (Halstead 1981d).

> Whatever view is taken of my linking hypothesis, this does not in any way affect the factual account of what has been happening at the museum. (Halstead 1981d: 404)

In all, *Nature* published four editorials: *Darwin's death in South Kensington* (February 26, 1981), *How true is the theory of evolution?* (March 12, 1981), *Does creation deserve equal time?* (*Nature*, May 28, 1981), and *Cladistics and evolution on display* (*Nature*, July 23, 1981) (Anonymous 1981a–d). It is quite likely that Sir John Maddox, editor of *Nature* during 1972–1995, wrote the pieces, a man who delighted in stirring the pot, regardless of his expertise.[29] The first two editorials were designed to force Museum scientists to declare themselves on their stand towards the theory of evolution. The first few sentences from *How true is the theory of evolution?* began:

> So is Darwin's theory of evolution a fact, a pack of lies or something in between? This is the question prompted by the two letters with which the British Museum (Natural History) has broken its long silence over *the rights and wrongs of* cladistics *and other matters. . . .* (Anonymous 1981a; our italics)

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[28] Other Natural History Museum (London) palaeontologists were just as enthusiastic about defending their science. A notable palaeobotanist was Chris Hill. Hill wrote many articles on the subject of palaeontology and cladistics (Hill 1981a, b, Hill & Camus 1986, Hill & Crane 1982), even going so far as naming a fossil plant from the Wealden (Lower Cretaceous), southern England, *Bevhalstia pebja* (Hill 1996). Hill became good friends with David Hull.

Charig had also outlined his view on "The role of vertebrate palaeontology in modern zoology" (Charig 1966), similar to those of Halstead et al.

[29] Maddox was married to Brenda, a home affairs correspondent for the *Economist*. It is believed she also had strong views about the Museum, hoping that it would stay as a Victorian building with an Edwardian display (see Anonymous 2006). Brenda Maddox went on to write many highly acclaimed biographies: *Nora: The Life of Mrs James Joyce* (2000), *The Married Man: A Life of D.H. Lawrence* (1994), *George's Ghosts: A New Life of W B Yeats* (1999), *Rosalind Franklin: The Dark Lady of DNA* (2003), *Freud's Wizard: The Enigma of Ernest Jones* (2006), and an early biography of Margaret Thatcher, Maggie: The First Lady (1994).

The article proceeded to detail some legal issues surrounding one particular Creationist battle in San Diego, California, underway at that time. Surprisingly (or maybe not, with the benefit of hindsight), the articles continues:

> Cladistics, a technique of classification, is in no sense inconsistent with the theory of evolution. Indeed, on the face of things, cladistic systems of classification should be more easily accommodated with the theory of evolution than those based on species. Cladism, therefore, is irrelevant to this journal's quarrel with the Natural History Museum, *at least as now defined*. (Anonymous 1981a)

"At least as now defined ... the rights and wrongs of ... other matters"—the clarity of those phrases, lost in the welter of other prose, is the focus—matters linked in the mind of Halstead and, without missing a beat, echoed by the editor of *Nature*. As one commentator observed, the battle became The Natural History Museum versus *Nature*, rather than with Halstead (Schafersmann 1985), with Sir Andrew Huxley stepping into the breach (Huxley 1982a, b, Anonymous 1981e).

### *6.6.8 Karl Popper and Cladistics*

It was Roger Miles who bought the ideas of Karl Popper into cladistics, with his contribution to the *Interrelationships of Fishes* book (Miles 1973[30]). As summed up by Bonde in his review of the book:

> With a background in Popper's (e.g., 1972) philosophy of empirical science, Miles (also 1974 [1975]) disregards positive or confirmatory evidence for hypotheses of relationships and acknowledges the "conclusiveness of disproof" of such characters. To that end shared advanced characters (Hennig's synapomorphies) are used not as evidence for one specific phylogenetic hypothesis, but rather to disprove alternative hypotheses. Hypotheses of relationships are thus tested by the distribution of characters. (Bonde 1974: 563)

This interpretation was contrasted with that of the contributions of Nelson and Patterson in the same book, who used shared characters as positive evidence. Miles' interpretation was exemplified in the "salmon, lungfish, cow" debate, in the display of competing diagrams (see Figure 6.6a). Since those early days, discussion concerning the interpretation of Popper's ideas and their relevance to systematics has continued unabated (Farris et al. 2001, De Queiroz & Poe 2001, Kluge 2001, Faith & Trueman 2001, Rieppel 2003b, Helfenbein & DeSalle 2005 for a small sample of the more recent contributions).

Miles applied his understanding of Popper to exhibition design (Miles & Tout 1978) and to an interpretation of evolution, both of which had an impact on the *Origin of Species* exhibition, which fired up Halstead and Nature yet again, prompting the editorial *How true is the theory of evolution?* (Anonymous 1981b); Patterson had referred to Popper in his book *Evolution* (Patterson 1978b; see the second edition, published 1999), while Nelson & Platnick (1981) added Popper to their primary

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[30] Popper's ideas had been noted before in connection with phylogenetic reconstruction (Ghiselin 1966: 210–211) and many other contributions to *Systematic Zoology*.

influences. A much fuller account of Popper's influence on the Natural History Museum exhibition controversy is given by Schafersman (1985). Here it is worth simply recording one of his conclusions:

> . . . I fail to see why cladistics needs any philosophical support, for its scientific success will be judged by its ability to provide useful, natural, and predictive classifications of organisms. (Schafersman 1985: 196)

Perhaps one aspect remains "true", connected with distinguishing between natural and artificial classifications, with natural classifications having "an empirical connection that allows for falsification" (Nelson 1983: 490). That is, data speak for or against any particular classification.

### *6.6.9 Even More Creationists: "Remember, Remember the 5th of November, Gunpowder, Treason and Plot . . . "*

The words above are from a verse commemorating an episode in English history. On November 5, 1605, Guy Fawkes attempted to blow up the Houses of Parliament in a plot to assassinate King James I. Before a match could be struck, Fawkes was caught, tried as a traitor, and sentenced to death. As his crime was treason, he was not simply hung but "drawn and quartered". In England, remembering the event (or non-event) has become a tradition. Every November 5, effigies of Guy Fawkes are burnt on bonfires, with grand firework displays, the original purpose to provide a warning to those who might chose such a route to effect changes to the establishment.

Although the editors of *Nature* called a halt to the Museum correspondence with their final editorial, *Cladistics and evolution on display* (Anonymous 1981d), the tale was to take another turn on a different November 5, 1981, this time overseas at the American Museum of Natural History (AMNH) with a presentation by Colin Patterson to the Systematics Discussion Group entitled "Evolutionism and Creationism" (Patterson 2002). That talk gained a certain amount of notoriety (see Bethell 1985, 1986a, 1986b):

> Well, just log on to the Google web search engine . . . and type in "Colin Patterson" and wait for hundreds of sites to appear. After about one hour you may have scratched the surface and read countless quotes and innumerable misquotes taken from this talk, seemingly supporting the case for creation "science" and excavating the bedrock of evolutionary theory. These web sites are continuing to appear—perpetuating this message. (Forey 2002)

A little after the presentation, Patterson hinted at events that followed:

> It is a pity that the tape-recorder allows others to give the permanence of print to verbal explorations. Beatty's printed quotes from one such talk do less harm than extracts from another in the current creationist literature, but in both cases I would have preferred a chance to approve what is published. (Patterson 1982c: 285; see above for comments on Beatty)

And later Patterson wrote:

> Unfortunately, and unknown to me, there was a creationist in my audience with a hidden tape recorder. A transcript of my talk was produced and circulated among creationists,

> and the talk has since been widely, and often inaccurately, quoted in creationist literature. (Patterson 1994b: 174)

The presentation was finally published in 2002, taken from Patterson's detailed lecture notes (Patterson 2002).

Given the context of controversies in the late 1970s and early 1980s, the presentation is notable for its conspicuous lack of any reference to palaeontology. The word does not appear in the text. It also lacks any reference to Popper. Primarily, the presentation deals with relationships, how they're discovered and represented, and how, given the then emergence of nucleotide sequence data, they can be found from sources of evidence independent of morphology (and the related areas of palaeontology and ontogeny). Secondarily, the presentation was directed at Ernst Mayr and his recent paper in *Science* (Mayr 1981). In other words, Patterson was following up and becoming enmeshed in the problem of "genes in common", the notion Mayr floated that would apparently serve the purpose of discovering the "true" relationships among organisms. "If you remember," said Patterson in the November 5 presentation,

> . . . in his [Mayr, 1969: 256, Fig. 10.17, reproduced here as Figure 1.1] 1969 book and his 1974 [Mayr, 1974: 103, Fig. 1 (left), reproduced here as Figure 6.8] anti-cladist paper, the diagram looked like this [see Figure 1.1 and compare with Figure 6.8]. Mayr was trying to put some precision into evolutionary systematics, and said "let A be the common ancestor of BCD, and suppose that the genome of B has deviated by 15% from the ancestral genome A, C has diverged from A by 10%, and D has evolved rapidly and diverged from A by 70% of the genome, entering a new adaptive zone." Then, he said, "We should be quite wrong to classify C with D, its nearest relative by common ancestry, because relationship means the inferred amount of shared genotype, not the inferred recency of common ancestry—here B + C share 75% of the ancestral genotype, whereas C and D share only 30%." (Patterson 2002: 19)

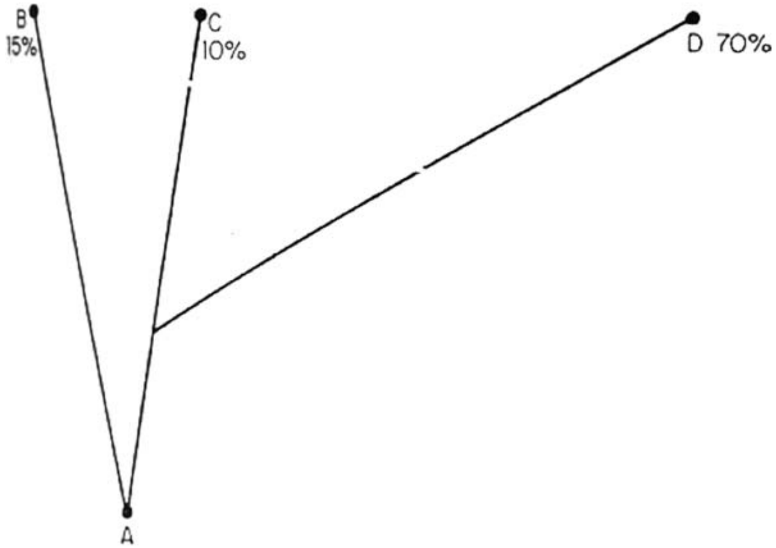

**Fig. 6.8** Reproduced from Mayr (1974: 103, Fig. 1, left) with permission of Blackwell Publishing

Patterson explored Mayr's example, concluding

> If you remember, Mayr published this diagram, with proportions of genome in it, in 1974 [Figure 6.8, Mayr 1974: 103, Fig. 1 (left)], when there were very few samples of genomes available in the form of protein or nucleic acid sequences, and he offered no examples that should conform to it—the bird crocodile one, and the man ape one. Well, since 1974 we've had abundant samples of the genome in man and apes, and far from matching this diagram, it turns out that chimps and man differ by only about 1% of the molecular genome. So Mayr's prediction was falsified there. As I said before, falsification is never absolute, and in this case I suggested that there are three possible things that might be false here—the genome data, the diagram, or the claims about evolution. (Patterson 2002: 23[31])

Patterson then examined the first 896 base pairs sequenced from the primate mtDNA (Brown et al. 1982), concluding

> So what about this tree and the numbers on the branches, and so on—where do they come from? Well, they don't pop out of the data, so I suppose they come from massaging the data with a theory—or with a computer programme based on a theory; and the theory is evolutionary theory, descent with modification. So what does the tree tell us about—is it telling us something about nature, or something about evolutionary theory—I'll leave you to decide. (Patterson 2002: 27)

In retrospect, it is clear that Patterson's critique concerns the numerical manipulation of data, the other "cladistics" (see below) that was then rising—less than silently—from the ashes of phenetics.

Patterson's reasoning arose from his study of homology. In 1981 in a presentation to Museum of Comparative Zoology, Harvard, a little after the AMNH presentation, Patterson related the origins of the task:

> Last year [1980] I was asked to write a paper on homology for a Systematics Association symposium on "Problems of Phylogeny Reconstruction" [Patterson 1982a]. I accepted because I had always felt that the concept of homology raised vague problems that I had tried to kick back under the rug, but I wondered how on earth there could be anything to say about homology, a relation that has been under discussion for well over 150 years. Anyway, I began reading and thinking and writing, and eventually came to the conclusion that homology, phylogeny and evolution, which had previously seemed to be concepts of successively greater generality—*homology*, least general, *evolution* most general, *phylogeny* in between—seemed to be all the same thing. I found that the least general concept, homology, was the easiest to comprehend, and the problems that remained were not really with homology but with phylogeny and evolution, two concepts that I had previously taken for granted. So I ended up feeling at home with homology, but full of doubt about where phylogeny and evolution were concerned. So I became an agnostic about evolution. Perhaps I'm coming out of that phase now, but I will try to take you along part of that road I travelled, hopefully not into the abyss of agnosticism or nihilism.[32]

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[31] These details were presented as part of Patterson's "Significance of fossils in determining evolutionary relationships" paper (Patterson 1981d: 197–199).

[32] More recently Stephen Wood remarked that "My Ph.D. supervisor, Ken Joysey, commissioned this paper [Patterson 1982a] from Patterson. He hoped that, forced to consider the question of homology, Patterson would give up the pattern approach he had adopted from Nelson and Platnick. Instead, Joysey relates, 'Patterson gave up evolution'!" (Wood 2003).

Homology, as Naef had discovered some 50 years before (Chapter 5), was the key. On another occasion, Patterson had been more explicit, contrasting evolution with creationism:

> … let's concentrate on the strong points of evolution. What are they? One way to find out is to go round asking biologists. If you do that, not that I've done enough to pretend I've got a valid sample, you find an odd thing—that people never cite their own field. For example, ask palaeontologists—they're likely to cite genetics or molecular biology; ask geneticists, they're likely to cite palaeontology; ask molecular biologists, they're likely to cite something quite different like mimicry. There seems to be some sort of a problem here, if professionals always choose the bit of biology they don't really know about. This situation reminds me of a comment on the fossil record attributed to Bev Halstead—in the days before he became the spokesman for the establishment. He said that wherever you looked at the fossil record, evolution always seemed to be going on somewhere else—in other words, wherever you specialised, you failed to find evolution—it seems to be just the same with other disciplines, if specialists always direct you elsewhere.

The reference to Halstead relates to the view (detailed above) that "It is the experience of palaeontologists that the fossil record shows that evolution always takes place somewhere else" (Halstead 1981b: 13). That comment, like most things, has a history.

In a review of Stanley's *Macroevolution: Pattern and Process* (Stanley 1979), Patterson (1980c: 6) wrote, "Sylvester-Bradley (1971: 2) quotes, with approval, a remark attributed to Halstead: 'Evolution always occurs somewhere else"'; Sylvester-Bradley's actual phrase was that "In our present context, phylogenetic evolution has a characteristic of particular importance. I have heard it described best by Dr. L.B. Halstead in a lecture. 'Evolution,' he said, 'always occurs somewhere else"' (Sylvester-Bradley 1971: 2). The origins of Halstead's views are detailed above.

Still, the spur to study molecular data meaningfully was developing—and in the context of systematics and homology and what that might offer the study of relationships and, ultimately, the study of evolution. Patterson (1982a: 48) mentioned molecules in passing in the first homology paper but was more expansive later:

> There is one class of phylogenies, or X-trees, that does differ from ontogeny: molecular phylogenies, derived from nucleotide or protein sequence data. The transformations postulated in molecular phylogenies are gene duplications and changes in nucleotides that are nowhere matched in ontogeny … molecular sequences are linear, or one-dimensional, and do not themselves display hierarchical organisation. (Patterson 1983b: 26)

Patterson had previously come to realise that ontogeny was not just a guide to assessing homologues but the only sure way that character transformations could be discovered. Without ontogeny, what would provide orientation for nucleotides?

> In building phylogenies from homologous sequences, methods such as parsimony (minimum evolution), compatibility or likelihood … must be used to link the sequences by hypothetical ancestral sequences. Different methods (assumptions) may give different phylogenies from the same data …; that is, the tree topology and the ancestral sequences hypothesised are assumption dependent. This means that hierarchical structure is not inherent in comparative sequence data … but is imposed by the investigator. (Patterson 1983b: 26)

No amount of methodological tweaking would remove that problem: "hierarchical structure is not inherent in comparative sequence data."

Patterson pursued the meaning of molecular data in a number of other papers, in particular how the notion of homology might relate to sequences (Patterson 1988a; see also Patterson 1987a, 1988b, 1989, 1994b), but just two months before his death, Patterson offered the following to a *New Scientist* report:

> By 1990, I would have had no hesitation—if you can get the money, get the sequencing done; that's the way to go. ... Now I'd say that if the organisms you are working on have a good set of characters, stick with the morphology—you get into much deeper trouble with the molecular data. (Patterson in Lewin 1998: 39)

Molecular data are the data of choice: Almost all systematic studies have some nucleotide component. That the problems have been ignored seems puzzling.

## 6.7 The Beginnings in New York: Fossils and Reform

> "... Gary Nelson joined Donn Rosen in New York in October 1967, and began the campaign of argument and persuasion that eventually turned the American Museum of Natural History into the world's leading institute of systematics, or a hotbed of crazy cladists, depending on your point of view." (Patterson 1995)

Nelson did indeed join the American Museum of Natural History in New York as an Assistant Curator for Ichthyology in 1967. During this early period he continued his assault on palaeontology (Nelson 1969a, c, Nelson in Williams & Ebach 2004) but also began to develop the field of historical biogeography (Nelson 1969d).

In 1969, Nelson was invited to give a lecture to the scientific staff of the American Museum of Natural History, New York, by the then director, Dr James Oliver. Nelson addressed the issue of the paleontological method, the idea that there might be a "pure paleontology" (Romer 1968: 90), a discipline devoted to recovering the ancestor–descendant relationships that were apparently preserved directly in the stratigraphic record. The seeds of the critique were sown in this 1969 presentation (see also Nelson 1970: 375) although Nelson had briefly tackled the subject earlier (Nelson 1969c: 528, 531, 1969a: 23, 1970: 375; see also Nelson 1969b: 65). A short account of problems with the palaeontological method appeared in 1973 (Nelson 1973d and see Nelson 1973b), and five years later this was followed by a more fully developed critique, which included an outline the role biogeography might play in a more comprehensive comparative biology (Nelson 1978b).

Brundin (above) wrote of Simpson's "fateful misconception of phylogenetic relationships". Simpson's misconception might be remedied by a more succinct statement of relationship, following Hennig's principle, here summarised by Brundin: "the study of phyletic relationships is the search for sister groups" (Brundin 1965: 497, 1966: 18). This articulates an idea that was to focus the reform of palaeontology. The principle may be accurately and simply captured in one of Hennig's early diagrams (in Chapter 8, Figure 8. 6.6, after Hennig 1957: 66, Fig. 8; but see also Hennig 1966a: 91, Fig. 22 and Hennig 1950: 103, Fig. 23). The main part of the diagram shows the interrelationships among three taxa, A, B, and C. Two taxa, B and C, are united by a synapomorphy, a shared derived feature (the black bars) that links two branches. In Hennig's diagram, homology (synapomorphy) expresses a relationship such that the group (BC) and the character (synapomorphy) are one and the same thing, the issue being clarified by Patterson (1982a). Hennig's diagram may be contrasted with that one published earlier by Kälin (Figure 6.9, after Kälin 1941, Fig. 6.2; see also Kälin 1936, 1941, 1945, and Chapter 5). Missing from Kälin's formulation is an explicit concept of relationship and the direct association of homology with taxon, a view that has since been called "taxic" (Eldredge 1979; Patterson 1982a) but is better associated with the more general idea of the Cladistic Parameter and Cladistics (Nelson 2004). Hennig's concept of relationship, simply put, is that B and C are more closely related to each than they are to A, with evidence supplied by homologies (synapomorphies).

Although Hennig made the concept of relationship explicit, it had been evident in systematic biology for some time (Nelson & Platnick 1981, Craw 1992) as previously articulated by, for example, Daniele Rosa:

> ... even without palaeontological knowledge of the connections, an adequate knowledge of the morphology of these species would suffice to indicate that genus B is more closely related to genus A than to genus C. (Rosa 1918: 137–138; translation from Nelson et al. 2003: 295)

And Walter Zimmermann:

> We say that the plant or organs B and C are more closely related to each other than with A. (Zimmermann 1931: 989; translation from Donoghue & Kadereit 1992: 78, which includes reproductions of Zimmermann's "cladograms", see Donoghue & Cracraft 2004: Fig. 1.3)

Of course, this simple concept of relationship allowed (all) organisms to be studied from a historical point of view without (necessary) recourse to fossils or ancestors. Abandoning the fixation on ancestors, the palaeontologists' claim to have the only "voice in the discussion of evolutionary problems" (Zangerl 1948: 358) became, once and for all, void.

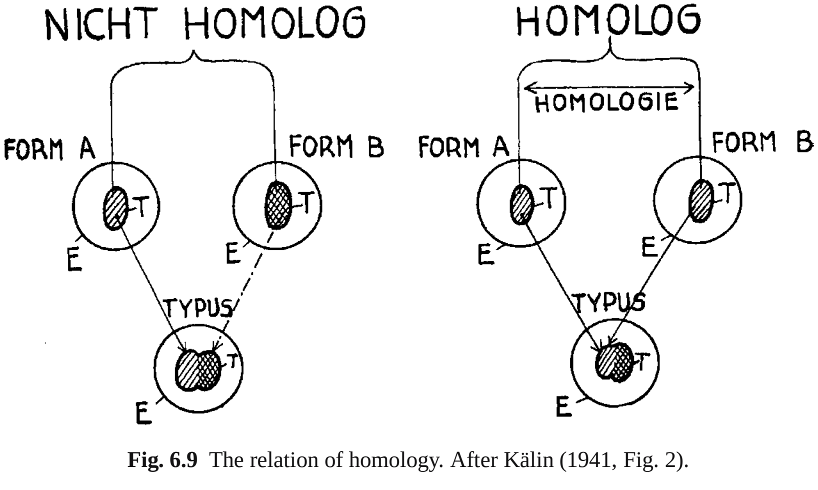

**Fig. 6.9** The relation of homology. After Kälin (1941, Fig. 2).

The cladistic revolution of the 1960s and 1970s tackled the issue of palaeontology and its role in discovering and depicting phylogeny, by calling into question the central significance of ancestors and their discovery—the factor added in by Haeckel many years previously. While it was acknowledged that the remains of organisms found in the rocks (however well preserved) required understanding, they were "… data in search of interpretation" (Nelson 1978b: 329). This viewpoint had already been well expressed by a previous generation of palaeo-ichthyologists, beginning with Stensiö (Patterson 1981c: 431), who was influenced by Adolf Naef and his systematic morphology. However, interpretation, wrote Patterson, is achieved via the "homology theorem … the essential part of the principles of morphology" (Patterson 1983b: 15, Riedl 1978: 32). And that homology theorem had been worked over—"thrashed out" might be more appropriate—by the previous generation of German morphologists (Chapter 5). We see, then, that Hennig's synapomorphy may be viewed as a refined concept of homology (Patterson 1982a, Williams 2004), and Cladistics, above all, is concerned with how the evidence (homologues) and their propositions (homology – relationships) generate the result (a classification) (Williams 2004).

The cladistic revolution really would not have been necessary if not for "the over-zealous advocation of a purely palaeontological approach." As a consequence, two ideas that had lain dormant for some years was bought into the open: that primitive characters were useless for classification; precision concerning relationships required three things, namely the relationship between two taxa or characters and a third. The cladistic revolution also rediscovered and developed the relevance of homology and its connection with discovering relationship, not simply in its application to morphology (Patterson 1982a) but to biogeography as well (Craw 1983: 437, Nelson 1994: 135). Yet of all those discoveries (or rediscoveries), it was perception that the ideas of Croizat could be united with the ideas of Brundin (Hennig) for biogeographical studies that was the most inspirational aspect—in effect, it was the statement of a new and profound way of looking at problems of evolution, posing them in terms of classification.

It was this task that Nelson set himself, unconsciously or otherwise.

## 6.8 New York Collaborations: Distributions and Historical Biogeography

Nelson's interest in historical biogeography was to influence fellow ichthyologist Donn E. Rosen and entomologist Norm Platnick, both at the American Museum of Natural History, the latter having come to Hennig's work via Petr Wygodinsky (Farris & Platnick 1989). The union among these three helped to bring about the field of **Vicariance** or **Cladistic Biogeography**(see Nelson & Rosen 1981).

Nelson's starting point was Brundin's application of Hennig's method to biogeographical problems. The problem Nelson was facing was not the availability of fossil groups or even efforts to find hypothetical ancestors but the very reverse: Palaeo-ichthyologists had vast numbers of fossil groups that appeared to have no immediate, living descendants. All the fossil groups were "equal", so to speak, and their relationships established without knowledge of “ancestral” condition; Stensiö and Jarvik had already pointed the way, noting specific characters and how they were shared among specimens. Unlike Brundin, Nelson *began* by discovering relationships without claiming to know either the ancestors or the ancestral conditions.

Brundin provided the framework for historical biogeography by adding schemes of phylogenetic relationships to species distributions, yielding a biogeography that was at once both evolutionary and historical, with no reliance on fossils or even a fossil record. Brundin used Hennig’s phylogenetic trees to plot the distributional history of monophyletic groups of organisms (Figure 6.10; Brundin 1966).

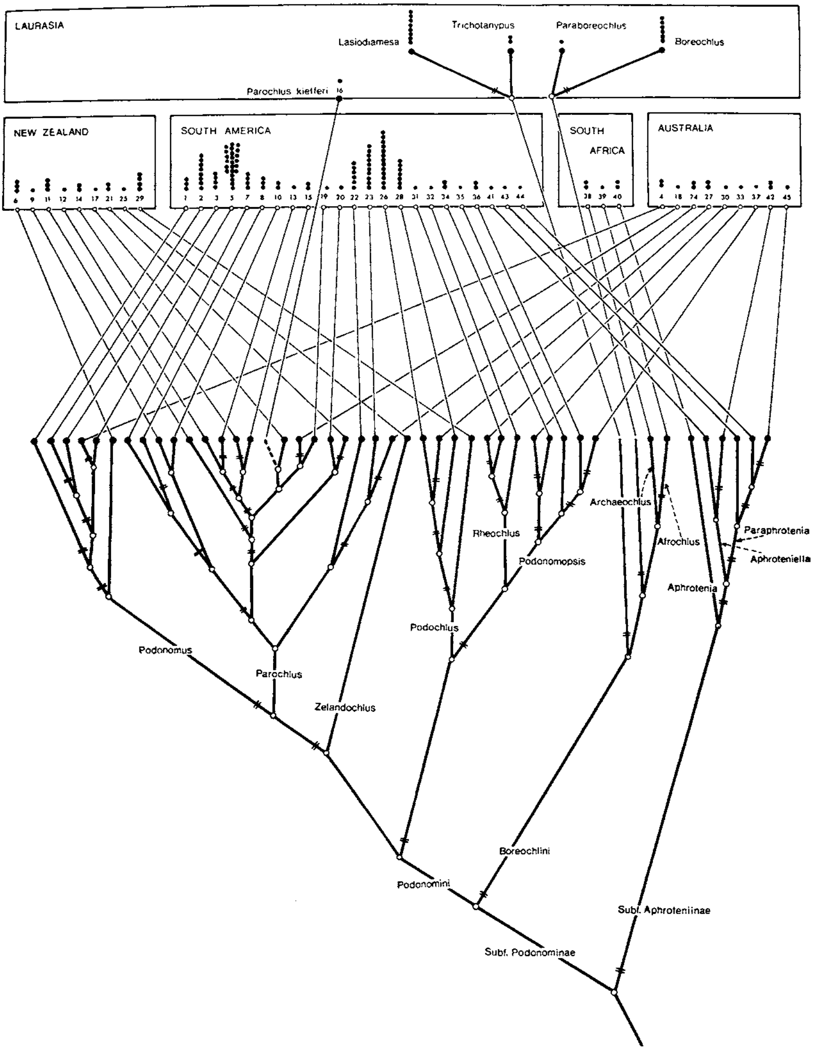

**Fig. 6.10** Transantarctic midge relationships. From Brundin (1966)

In each cladogram, the most basal organisms were supposedly those nearest the ancestor in both space and time. Each node on the tree acted as a hypothetical ancestor for each group, and the further towards the top of the tree the more derived the taxa were. For the organisms, the direction of dispersal was hypothesised as moving away from the particular centre of origin, those places inhabited by the most basal or plesiomorphic species. Brundin called this the *Progression Rule* (Brundin 1966[33]), an idea that remains the main principle behind phylogeographic interpretation (Parenti 2006). In spite of Nelson's enthusiasm for Brundin's work, he had doubts concerning the progression rule (Nelson 1975). For Nelson, all his species were of similar age and could not have moved from a shared "centre of origin". In fact, all the taxa at the branches were equivalent to modern taxa and modern distributions. No matter how they were related, a taxon's place in a hierarchy could not be indicative of the position of any "centre of origin". Nelson recognised that the *morphotypes* at the nodes of cladograms were hypothetical and

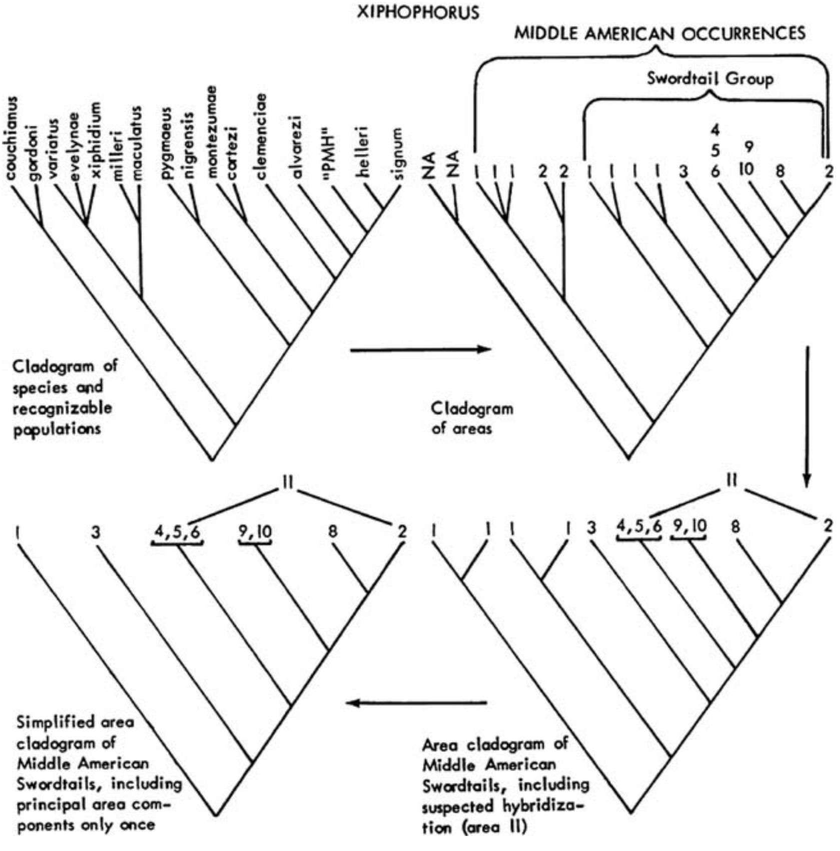

**Fig. 6.11** Cladograms and areagrams for species of *Xiphophorus;* after Rosen (1979).

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[33] First discussed in Hennig (1960; translation in Hennig 1966b).

therefore could present many different scenarios of dispersion and vicariance—all equally valid. The "centre of origin" was unknown and would remain so, no matter how old or "primitive" looking the organism might be—it could never be established whether or not they were really the oldest or indeed the actual ancestor. Following Croizat, Nelson criticised the search for origins, whether ancestral taxa or areas, a viewpoint that was misunderstood by many "conventional" biologists and a viewpoint that was misinterpreted by other cladists (for more on origins, see Chapter 13).

The first major study that implemented the ideas behind vicariance biogeography was that of Rosen (1978; see also Rosen 1979)—a study that became a landmark in biogeography, with literally hundreds of papers interpreting and reinterpreting his data. In terms of original monographs, Rosen's killifish study is perhaps second only to Brundin's midges (see above) for significance to 20th-century comparative biology (Nelson et al. 1987).

Rosen based his study on the killifishes of Central America, species in the genera *Heterandria* and *Xiphophorus*. After discovering the relationships between the two groups of fishes, Rosen used the taxon cladograms to construct what he called **Reduced Area Cladograms** (RAC). Rosen replaced the names of the species (terminal taxa) with the areas they occupied, thus forming a **Taxon-Area Cladogram** (TAC). The resulting TAC's from *Heterandria* and *Xiphophorus* were reduced to represent the smallest statements of relationship of each and then combined to form a general pattern. That common pattern indicated vicariant relationships; that is, each taxon was considered to be isolated from its sister by a vicariance event, by geographical isolation (Figure 6.11).

## 6.9 The Two Cladistics

What was significant about Rosen's biogeographical studies was that they could explain patterns of distribution without having to conjure up intricate dispersal scenarios. Yet some systematists misinterpreted Rosen's work on a numbers of points. Wiley, for example, considered the possibility that hypothetical ancestors *could* be interpreted as real taxa if enough evidence—from characters and their distribution—pointed in that direction (Engelmann & Wiley 1977).

Wiley was to vigorously promote Hennig's views, retaining the name *Phylogenetic Systematics*, as if he, rather than anyone else, was valiantly preserving Hennig's work in its original and pristine form. Beatty christened this approach Phylogenetic Cladistics (Beatty 1982: 27). Yet this viewpoint is no more phylogenetic than the viewpoint adopted by the pattern cladistics; hence, we refer to Wiley's viewpoint as **Process Cladistics**. Process cladistics relates directly to developments in numerical taxonomy, rather than anything Hennig may or may not have done. Those developments attempted to retain—albeit buried within various algorithms—the evolutionary model of the New York dispersalist school. After all, some cladists have understood the union of numerical taxonomy (phenetics) with Hennig's notion of characters ("transformation series") as the real revolution in systematics (Andersen 1999, 2001, Mitter 1999, Schmitt 2003), as if real progress in Hennig's ideas required a computerised version that would reinvent—or codify—the palaeontological method (optimisation—the progression rule) to grasp finally how and why systematics does work (Nelson 2004).

One might best understand this development by a consideration of the early work of Farris and Kluge, the former being part of the early numerical taxonomy movement (Farris 1966, 1967), the latter an intellectual descendant of Simpson (Kluge 1971, 1977) (for more details on the numerical episode, see Chapter 11). Nevertheless, the split between the two kinds of cladists might be likened to the last great "dichotomous" battle between Geoffroy St. Hilaire and Georges Cuvier (Appel 1987), its significance of similar import.

Pattern cladistics was—and still is—a reaction against transformational "phylogenetics", be that of taxa (Ernst Haeckel) or characters (Willi Hennig, numerical cladists, etc.). In general, literature that opposed pattern cladistics primarily suggested it was *non-phylogenetic*, even *non-evolutionary*, a reaction stemming from the apparent loss of paraphyletic groups, ancestors, and centres of origin, as if these factors defined what it is to be *evolutionary* (Halstead's derived model). Others suggested that the loss of evolutionary *interpretations* for paraphyletic groups, ancestors, and centres of origin rendered the study of organisms and their relationships sterile, seeing it as a denial of evolution (Dawkins 1986, 2004, Ridley 1986), rather than embracing the immense and very real possibilities provided by a classificatory perspective. And others, who deal with unrooted trees (real phenetics) and character transformations (Kluge & Farris 1999, Felsenstein 2004, Donoghue 2001), understood it to be *phenetic* and *idealistic*, a view proposed initially by those who really should have known better (Hull 1988).

Pattern cladistics is the re-establishment of a non-transformational methodology for discovering the relationships among organisms and the areas they occupy—a classificatory perspective.

## 6.10 Overview

Reviewing progress in systematics during the 1960s–1980s seems fraught with dead-ends, pointless polemics, and, on reflection, issues of no great moment. Nevertheless, while systematics was threatened with revolution, evolution—as understood at that time—was a target. A target inasmuch as the collective theories designed to explain why there are so many organisms, how they have come to be what they are, and where they are, were becoming so close a part of the method, that it was rendering the subject of systematics immune to real discovery.

Of the controversy, a recent popular book on The Natural History Museum in London put it this way:

> Outside scientific circles the controversy may have seemed little more than a minor spat between academics. Yet, in its way, this was the greatest upheaval in our understanding of evolution since Darwin. (Thackray & Press 2001: 114)

In effect, the “Parrington school” had an intellectual heritage directly inherited from Haeckel, Matthew, and Simpson (the Anglo-American palaeontological tradition), while the “Stockholm school” arose (mostly) from those who critiqued Haeckel, the early post-Darwinian ideal morphologists, and the works of Adolf Naef in particular (Chapter 5, Olsson 2003, 2005, Olsson et al. 2005: 150), who rejected the biogenetic law as well as the palaeontological approach as an arbiter of schemes of relationships. The two “schools”—if they can be referred to as such—divided and maintained almost separate existences during the inter-war years (the 1920s to the 1950s). Their meeting again, in the 1960s, was a clash between two post-Darwinian (and pro-evolutionary) ideologies, a clash that had been postponed for more than half a century, perhaps even going unrecognised by the larger community, ignoring the complex development of evolutionary theories in post–World War II Europe in deference to the hegemony of the modern synthesis.

With respect to molecular data, Morris Goodman, reflecting on his early years in molecular systematics, wrote:

> The earlier maximum parsimony studies from my laboratory and those by Walter Fitch had an impact on the emerging field of cladistics. In this connection, Donn Rosen, Gareth Nelson, and Colin Patterson in their foreword to the 1979 reissue of Hennig’s *Phylogenetic Systematics* singled out two papers (Goodman 1976, Fitch 1977) as representative of molecular cladistics. Rosen, Nelson, and Patterson pointed out that molecular cladistics was based on amino acid and nucleotide sequences and that it was a method of cladistics which was independently developed but integratable with Hennig’s approach. (Goodman 1996: 274)

We believe Goodman is mistaken in equating “maximum parsimony” with “the emerging field of cladistics”; development of “phylogenetic algorithms” was part of numerical systematics, not cladistics as related to the palaeontological critique. The words of Gardiner et al. are worth repeating: Molecular systematists “use the same genealogical concept of relationship as Hennigians” (Gardiner et al. 1979: 176). Similarities between Goodman’s approach and those of the cladists resided in how they portrayed relationships, not the methods by which they could be discovered (Figure 6.12).

Indeed, Ernst Mayr, in the same paper in which he claimed that “genes-in-common” were the guide to “true” relationships, suggested that “… it may force him [any cladist] to place *Homo* and the African apes (*Pan*) in one family and the orang (*Pongo*) in another family, as was indeed proposed by Goodman (1963)” (Mayr 1965: 78).

It may be useful to note that during the long, tortuous, and circuitous correspondence in *Nature* (as well as in *The Biologist*, the *Museums Journal*, and elsewhere) not one numerical taxonomist (cladist, pheneticist, or phylogeneticist) made any contribution.[34]

Cladistics, then, offered a focused critique of the palaeontological method and, by implication, the evolutionary paradigm attached to that viewpoint; cladistics

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[34] An exception was a paper by Martin in *The Biologist* (Martin 1981). Martin’s paper was a response to those of Patterson (1980a) and Charig (1980), where he suggested that it was worth paying attention to the differences between classification and phylogenetic reconstruction–an issue that was to later become of some significance.

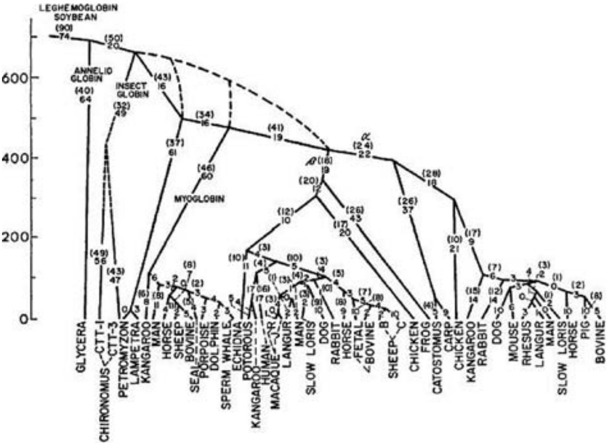

**Fig. 6.12** Tree from Goodman & Moore (1973, Fig. 1: 511), "Maximum parsimony tree of forty seven more adequately sequenced globins." Reproduced with permission

offered a critique of numerical methods, in the context of the analysis of molecular data—with optimisation if not mimicking then closely resembling the evolutionary viewpoint buried in the palaeontological method; cladistics offered a positive and dynamic way forward—the union of Form (morphology, ontogeny, palaeontology, molecules) with Space (areas); cladistics confirmed the fact that comparative biology was dependent on an understanding—an exploration—of homology.

Thus, Cladistics—if not all of systematics—depends almost exclusively on homology. The rest seems almost irrelevant.

# Chapter 7
# Homologues and Homology

> "In the early part of the nineteenth century there was a complex semantic web around words signifying relationships and resemblances—words such as 'primitive', 'type', 'essence', 'organization', 'symmetry', and 'analogy'. From this web emerged the term 'homology'. . . ."
>
> (Stevens 1984a: 78)

## 7.1 The Search for the Unit of Classification

One of the earliest and certainly the most well-known depiction of homologues is Pierre Belon's famous figure illustrating the comparable parts of a human and bird skeleton (Belon 1555, Pls. 40 and 41[1]). Belon's figures immediately convey to the reader which parts are to be considered the same even though they might appear (superficially) different. To assist the reader, Belon labelled comparable parts of each skeleton with the same symbols (Figure 7.1).

In 1849, Richard Owen provided another excellent visual representation of homologues included as frontispiece to his book *On the Nature of Limbs*—his illustration being remarkably similar to that of Belon (Owen 1849, reproduced in Stevens 1998: Cover illustration, Williams 2004: Fig. 9.1; Figure 7.2a).

In his diagram, Owen numbered the parts. The numbers correspond to equivalent bones, a numbering system he used in many of his subsequent publications dealing with vertebrate anatomy (Figure 7.2b). Yet he also named the parts, such that, for example, part 51 is called the scapula. His ultimate aim was to name (and number) all the comparable parts of the vertebrate skeleton.

Illustrations like those provided by Belon and Owen continue to appear in morphological studies, the style, form, and presentation having changed little, usually

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[1] Belon (1555: plates 40 and 41; reprinted in Cole (1944 [1975]: 8), Zimmermann (1967: 68, abb. 3); Kluge (1971: 4, Fig. 1–1, 1977: 4, Fig. 1.1), Bonde et al. (1985 [1996]: 92), Ellenius (1993: 381, Fig. 2), Panchen (1994: 43, Fig. 8, 1999: 6, Fig. 1), Zunino & Colomba (1997: 67, Fig. 7.2), Minelli (1999: 88), Goujet (2000: 46), Rieppel & Kearney (2002: 71, Fig. 2; redrawn in Singer 1931: 87 [1950: 87; 1959: 91]), Boyden (1973: Fig. 4.1), and Papavero et al. (1995a: 145, for a small sample).

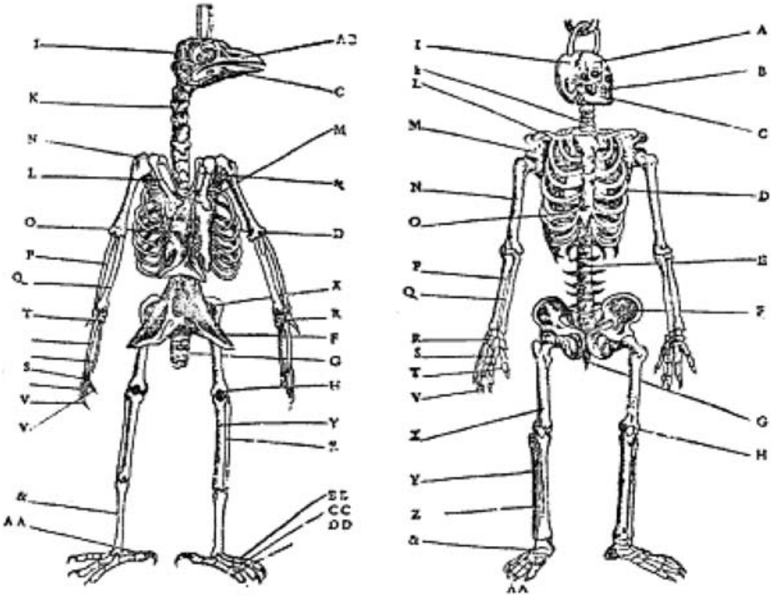


**Fig. 7.1** Illustration reproduced from Belon (1555)

with names (or abbreviations) in place of numbers (Figure 7.3a), but numbers remaining acceptable (Figure 7.4). Today, numbers are usually assigned after the parts have been named, when a data matrix is created (Figure 7.5; see later).

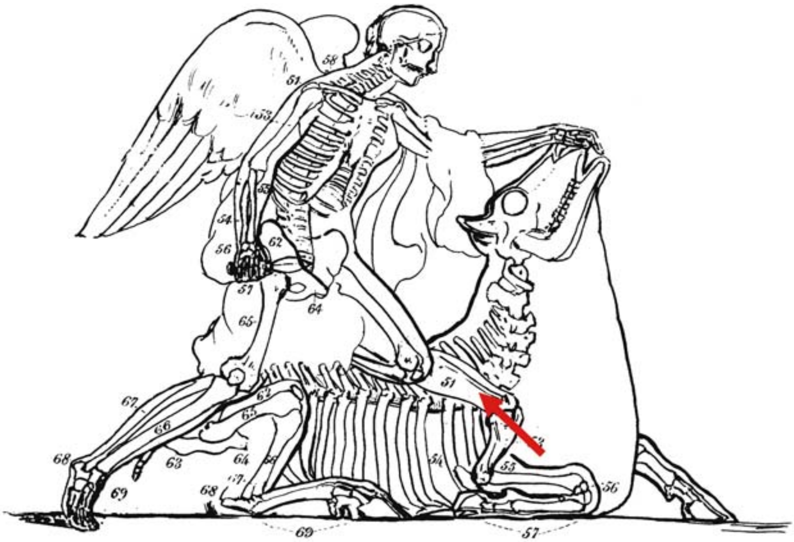
Thomas Henry Huxley commented on Belon's diagram in his retrospective account of Richard Owen's scientific contributions:

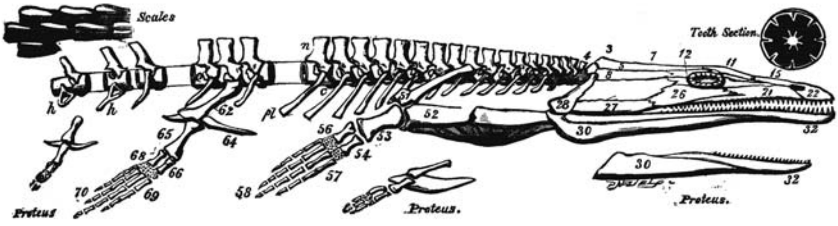
> The old French naturalist Belon, who must have been a good deal of an artist, and illustrated his book "L'Histoire de la Nature des Oyseaux", with many "naifs portraicts", initiated this way of dealing with anatomy [… the artistic fashion …, Huxley 1894: 287]. The skeleton of a bird is set beside that of a man, and the reader is left to draw the obvious conclusion as to their "unity of organisation". A child may see that skull "answers" to skull; spinal column to spinal column; ribs to ribs; breast bone to breast bone; wings to arms; and legs to legs, in the two. (Huxley 1894: 287–288)

Colin Patterson echoed Huxley's words some 100 years later:

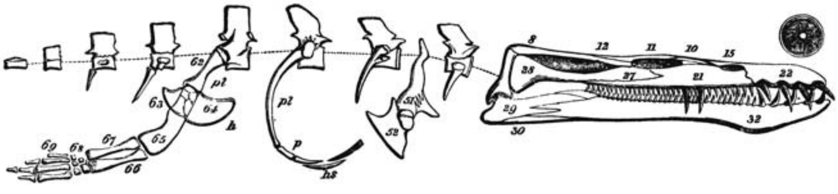
> When a child learns to recognise birds, the criteria used are, at root, the same as those used by the scientist: the feathers, beak and wings, and so on are "the same" in a sparrow and a swan, whereas the wings of a beetle or the beak of a turtle do not make those creatures birds—the "sameness" is different or inessential; technically it is analogy rather than homology. (Patterson 1987b: 235)

For Huxley and Patterson—100 years apart—recognising homology is child's play. Patterson (1988a: 605) later referred to Owen's (1849: 71) view that "useful" or "essential" similarities indicate the "namesake or 'homologue'." If the task of discovering the parts of organisms identified as "namesakes" were self-evident, then





Apateon or Archegosaurus (Carboniferous).



Nothosaurus (Trias).

**Fig. 7.2** a. Illustration reproduced from Owen's *On the Nature of Limbs*—frontispiece. b. From Owen's "Cyclopedia" article (Owen 1859a)

the business of systematics would have come to a happy conclusion many years ago. But one lesson learned over the past 100 years is that such comparisons are not necessarily simple nor do they necessarily point to the same conclusion. That is, some comparisons turn out to be "true", others "false". Patterson (1994: 62) compared what he referred to as two kinds of homology, contrasting "homology in

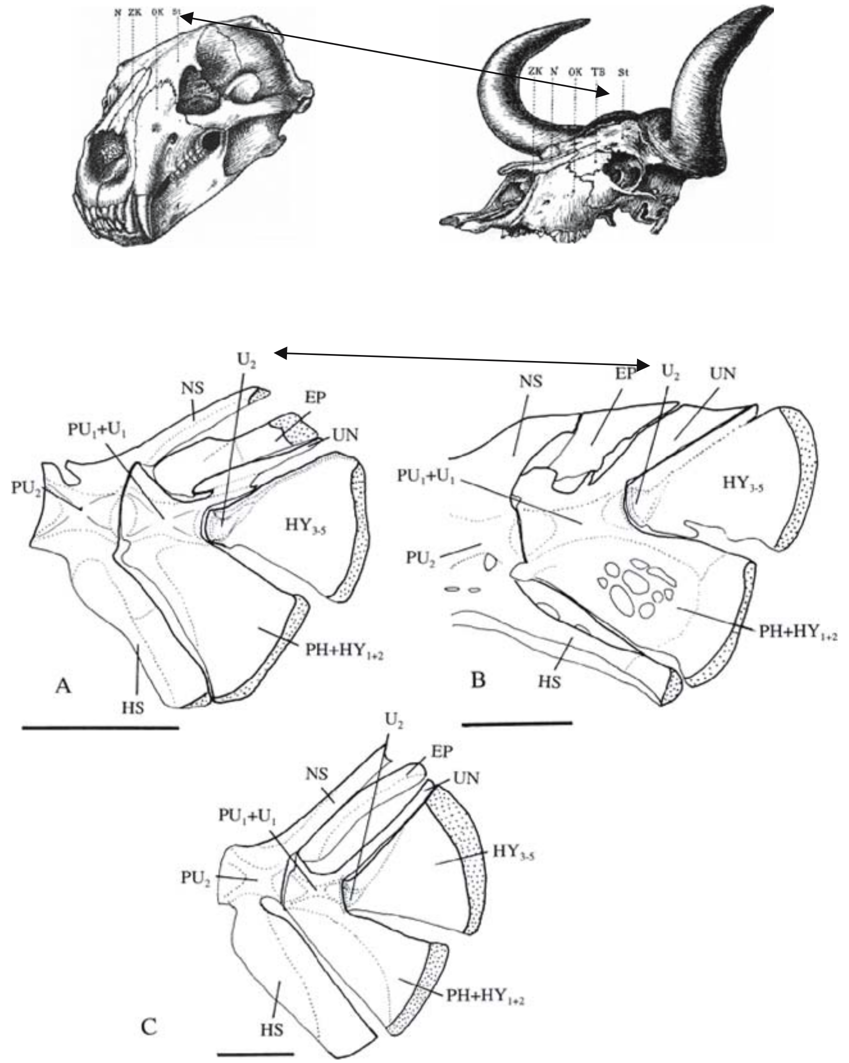


**Fig. 7.3** a. After Jacobshagen (1927), *Zur Reform der allgemeinen vergleichenden Formenlehre der Tiere,* Figs. 88 and 89. b. After De Pinna & Ng (2004). Courtesy of the American Museum of Natural History

the classical sense of ‘naming of parts”’ (Patterson 1994: 62) with the “… narrower, cladistic sense of discriminating homology from homoplasy” (Patterson 1994: 63). This implies two distinct operations, one dealing with the comparison of parts, the other dealing with methodology, the sorting of the parts. In this section we deal with the first aspect, the “naming of parts”. We begin by examining the work of Richard Owen and some of his contemporaries.

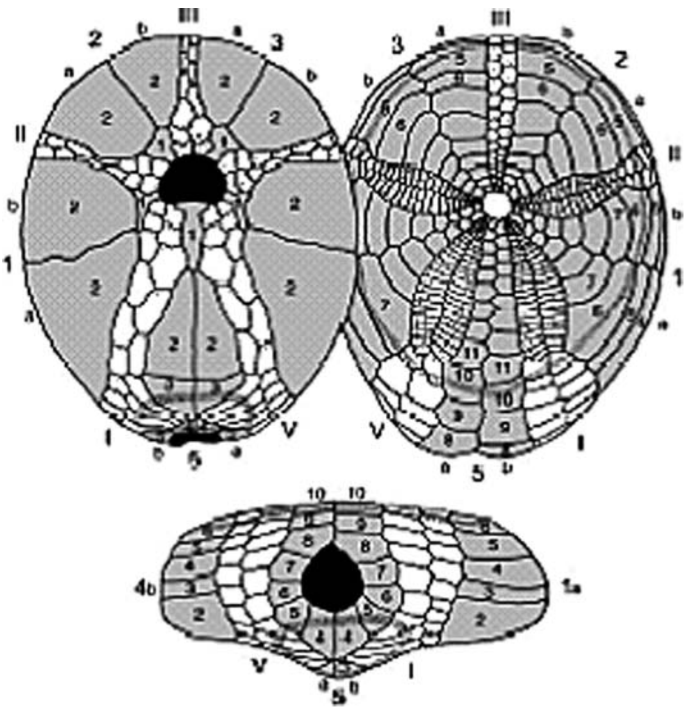


**Fig. 7.4** Fasciole pathways in spatangoid echinoids. After Smith & Stockley (2005 Fig. 3), with permission of Blackwell Publishing Inc

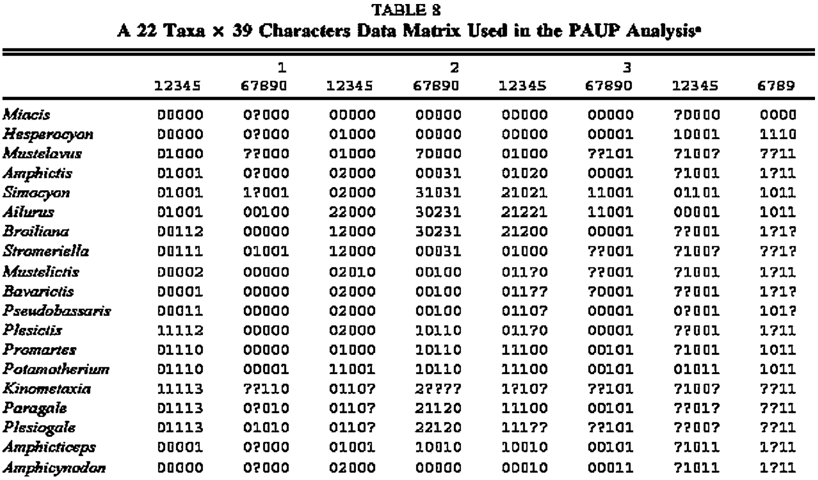


TABLE 8

A 22 Taxa × 39 Characters Data Matrix Used in the PAUP Analysis[a]

| | | 1 | | 2 | | 3 | | |
|---|---|---|---|---|---|---|---|---|
| | 12345 | 67890 | 12345 | 67890 | 12345 | 67890 | 12345 | 6789 |
| *Miacis* | 00000 | 0?000 | 00000 | 00000 | 00000 | 00000 | 70000 | 0000 |
| *Hesperocyon* | 00000 | 0?000 | 01000 | 00000 | 00000 | 00001 | 10001 | 1110 |
| *Mustelavus* | 01000 | 7?000 | 01000 | 70000 | 01000 | 7?101 | 7100? | 7?11 |
| *Amphictis* | 01001 | 0?000 | 02000 | 00031 | 01020 | 00001 | 71001 | 1?11 |
| *Simocyon* | 01001 | 1?001 | 02000 | 31031 | 21021 | 11001 | 01101 | 1011 |
| *Ailurus* | 01001 | 00100 | 22000 | 30231 | 21221 | 11001 | 00001 | 1011 |
| *Brailiana* | 00112 | 00000 | 12000 | 30231 | 21200 | 00001 | 7?001 | 1?1? |
| *Stromeriella* | 00111 | 01001 | 12000 | 00031 | 01000 | 7?001 | 7100? | 7?1? |
| *Mustelictis* | 00002 | 00000 | 02010 | 00100 | 01170 | 7?001 | 71001 | 1?11 |
| *Bavarictis* | 00001 | 00000 | 02000 | 00100 | 0117? | 70001 | 7?001 | 1?1? |
| *Pseudobassaris* | 00011 | 00000 | 02000 | 00100 | 0110? | 00001 | 0?001 | 101? |
| *Plesictis* | 11112 | 00000 | 02000 | 10110 | 01170 | 00001 | 7?001 | 1?11 |
| *Promartes* | 01110 | 00000 | 01000 | 10110 | 11100 | 00101 | 71001 | 1011 |
| *Potamotherium* | 01110 | 00001 | 11001 | 10110 | 11100 | 00101 | 01011 | 1011 |
| *Kinometaxia* | 11113 | 7?110 | 0110? | 2???? | 1?10? | 7?101 | 7100? | 7?11 |
| *Paragale* | 01113 | 0?010 | 0110? | 21120 | 11100 | 00101 | 7?01? | 7?11 |
| *Plesiogale* | 01113 | 01010 | 0110? | 22120 | 1117? | 7?101 | 7?00? | 7?11 |
| *Amphicticeps* | 00001 | 0?000 | 01001 | 10010 | 10010 | 00101 | 71011 | 1?11 |
| *Amphicynodon* | 00000 | 0?000 | 02000 | 00000 | 00010 | 00011 | 71011 | 1?11 |

**Fig. 7.5** A data matrix with numbers, after Wang et al. (2005). Courtesy of the American Museum of Natural History.

## 7.2 Homologues and Analogues

Richard Owen's first clear distinction between "homologue" and "analogue" appeared as concise, simple definitions in the glossary appended to his *Lectures on Comparative Anatomy* (1843):

> Analogue. A part or organ in one animal which has the same function as another part or organ in a different animal. (Owen 1843: 374)
>
> Homologue. The same organ in different animals under every variety of form and function. (Owen 1843: 379)[2]

When one compares parts of a skeleton, bones that correspond are to be considered "homologues", as they are thought to be "the same thing" or "namesakes":

> The corresponding parts in different animals being thus made namesakes, are called technically "homologues". (Owen 1847a: 173, 1848: 6)
>
> . . . a bone in the skeleton of a dog, a horse, a mole, and a platypus, is proved to be the same or answerable bone to the one called "scapula" in man, and is called by the same name; and when the answerable bone can be traced through birds, reptiles and fishes, where it is similarly recognised and indicated,—determined, in short, to be the namesake or "homologue" of the human scapula . . . . (Owen 1849: 71)
>
> A "homologue" is a part or organ in one organism so answering to that in another as to require the same name. . . . A "homologue" is the same part or organ in different animals under every variety of form and function. (Owen 1866: xii)

Homologues are therefore parts of organisms (Nelson 1989c: 282, Nelson 1994: 104).

## 7.3 Homology and Analogy

While the idea of "homologues" or "namesakes" as parts of organisms seems straightforward, the concept of "homology" is complex. Owen made clear that homology specifies a particular kind of *relation* rather than just the part. Owen did not claim priority for this general understanding or for the use of the term "homology", writing that:

> I have always felt and stated that I was merely making known the meaning of a term introduced into comparative anatomy long ago, and habitually used in the writings of the philosophical anatomists of Germany and France. (Owen 1846: 526)

He did, however, suggest that he had advanced the idea by distinguishing different kinds of homology relationships and giving them meaning:

---

[2] Owen repeated the definitions in some of his later works (Owen 1847a: 175, 1848: 7). In one of these later texts the definition of homologue differs slightly from the earlier work: "A part or organ in one animal which has the same function as a part or organ in *another* animal" (Owen 1866: xii; our italics).

> I have gone perhaps a little further than Oken and Geoffroy [the philosophical anatomists of Germany and France referred to above] in defining kinds of “homology”, which appeared to me to be three, viz. “general”, “serial”, and “special”. (Owen 1846: 526)

By “further”, Owen was referring to the work of Geoffroy St. Hilaire, who was the creator of the “Theory of Analogues” (Figure 7.6), ‘analogue’ being Geoffroy’s term for homology.[3]

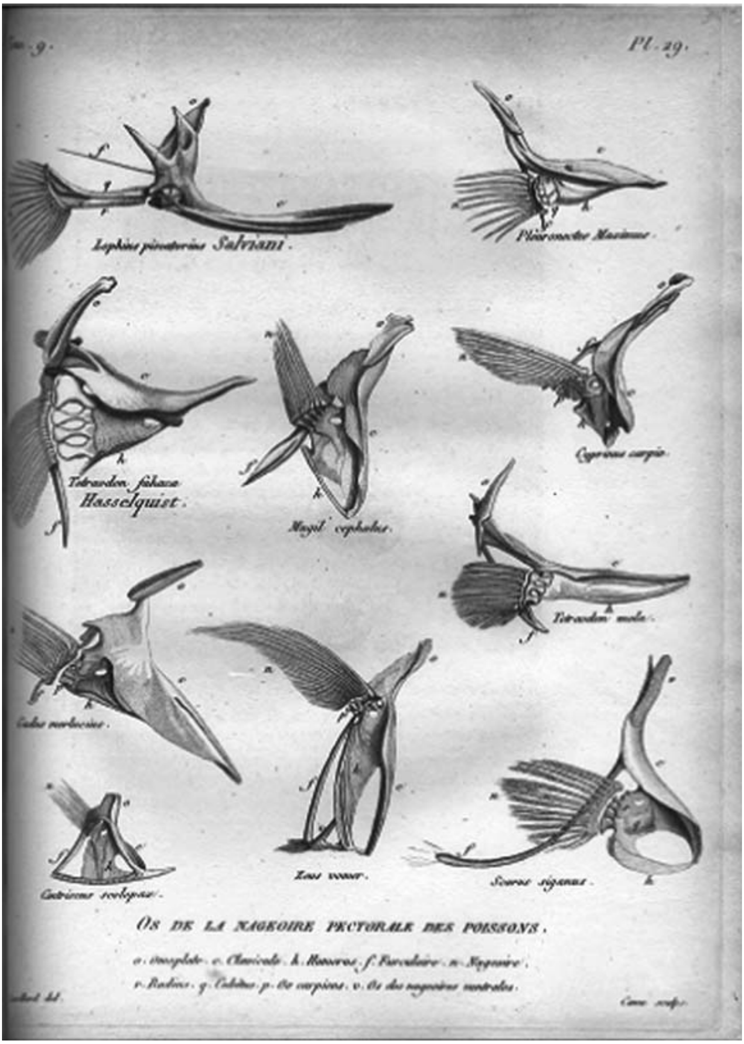


**Fig. 7.6** Illustration of homology from St. Hilaire (1818).

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[3] St. Hilaire’s work, and the controversy surrounding it in the 1830s, has been covered in various ways (Lubosch 1918, Appel 1987, Corsi 1988, Le Guyader 2003). The significance of this episode is central to this book, but dealing with it adequately is beyond its scope. Nevertheless, we see St.

## 7.4 Homology

Owen's best-known and detailed description of "homology" and "analogy", as opposed to the stark definitions of "homologue" and "analogue", appeared in his book *Archetype and Homologies of the Vertebrate Skeleton* (Owen, 1847a,[4] 1848). In this book (and an earlier short summary, Owen 1846) Owen described the three kinds of homology, "general", "special", and "serial":

> Relations of homology are of three kinds: the first is that above defined [special homology], viz. The correspondency of a part or organ, determined by its relative position and connections, with a part or organ in a different animal; the determination of which homology indicates that such animals are constructed on a common type . . . . (Owen 1847a: 175, 1848: 7)
>
> General homology was described as "A higher relation of homology is that in which a part or series of parts stands to the fundamental or general type, and its enunciation involves and implies a knowledge of the type on which a natural group of animals, the vertebrate for example, is constructed." (Owen 1847a: 175, 1848: 7)
>
> . . . any given part of one segment may be repeated in the rest of the series, just as one bone may be reproduced in the skeletons of different species, and this kind of repetition or representative relation in the segments of the same skeleton I call "serial homology". (Owen 1847a: 175, 1848: 7)

Owen's "special homology" ("the correspondency of a part or organ") was determined by various, well-known criteria:

> These relationships [homologies] are mainly, if not wholly, determined by the relative position and connection of the parts, and may exist independently of form, proportion, substance, function, and similarity of development. (Owen 1847a: 174, 1848: 6, 1866: vii)

While Owen stressed that homologies were "mainly, if not wholly" dependent upon comparisons, their meaning was somewhat more complex, as "the determination of homology indicates that such animals are constructed on a common type . . . ":

> I take for granted that it is generally known, as it is universally admitted by competent anatomists and naturalists, that these limbs or locomotive members, which, according to their speciality of form, have received the above special names, are answerable or "homologous" parts: that the arm of the Man is the fore-leg of the Beast, the wing of the Bird, and the pectoral fin of the fish. This special homology has been long discerned and accepted; but the general homology of the parts or their relations to the vertebrate Archetype, in short their "Bedeutung" or essential nature, is not generally known. (Owen 1849: 3)

Owen refers to the special homology of forelimbs as being well known but their meaning ("Bedeutung", "signification" or "meaning", Owen 1849: 3) not generally

---

Hilaire's as a precursor to much sensible systematic endeavour, in spite of his occassional flights of fancy.

[4] Owen first presented his work as a report to the British Association for the Advancement of Science in September 1846. Owen gave two reports, one "On the Homologies of the Bones Collectively Called 'Temporal' in Human Anatomy" and "On the Vertebrate Structure of the Skull". The report was published in 1847; the book, a combination of the two lectures, was published a year later in 1848 (Owen 1847a, 1848).

known or understood. By “well known”, Owen is referring to the identities of the homologues (“homologous parts”), the bones themselves, but meaning is elucidated only by a consideration of their general homology. The key to Owen’s understanding of homology is the archetype, the point of reference from which all the parts have been subsequently “modified”, or derived. Matters might be simplified if Owen’s criteria were understood as applying to the recognition of structures considered “homologues” rather than the relation of homology. In this way criteria may be understood as useful for establishing the “sameness” of different parts, for establishing which parts are indeed homologues (Chapter 8).

## 7.5 Homotype

Further to this understanding is Owen’s distinction between special and serial homology, both based on the same criteria of discovery, differing only in that serial homology “repeats” in a single organism:

> It will, of course, be obvious that the humerus is not “the same bone” as the femur of the same individual in the same sense in which the humerus of one individual or species is said to be “the same bone” as the humerus of another individual or species ... it is not its namesake, not properly, therefore, its homologue. I propose, therefore, to call bones so related serially in the same skeleton “homotypes” and to restrict the term “homologue” to the corresponding bones in different species .... (Owen 1847a: 333)
>
> If it be admitted that the general type of the vertebrate endo-skeleton is rightly represented by the idea of a series of essentially similar segments succeeding each other longitudinally from one end of the body to the other, such segments being for the most part composed of pieces similar in number and arrangement, and though sometimes extremely modified for special functions, yet never so as to wholly mask the typical characters,—then any given part of one segment may be repeated in the rest of the series, just as one bone may be reproduced in the skeletons of different species, and this kind of repetition or representative relation in the segments of the same skeleton I call “serial homology”. As, however, the parts can be namesakes only in a general sense ... I call such serially related or repeated parts “homotypes”. (Owen 1848: 7–8)[5]

---

[5] Terminology is complex. Owen’s homotypy has gained numerous synonyms over time, homonomy being one still commonly used. Homonomy was first used by Bronn (1858); Remane (1952) provided an extensive discussion on the subject, as does Simpson (1961: 93). Homonomy seems to be an accepted alternative to Owen’s “serial homology”: “When it is said to repeat, in its vertebra or natural segment of the skeleton, the body of the sphenoid bone, the body of the atlas, and the succeeding vertebrate bodies or centrums, its *serial homology* is indicated” (Owen 1846: 526). Opinion diverges over whether serial homology really is a kind of homology. For example, Ghiselin wrote, “Finding correspondences between, say, fingers and toes, or between organs on the left and right side of the body, is one kind of homologizing. Among these, Owen named only one kind. This was ‘serial homology’, the correspondence between equivalent units in metameres-for example, between humerus and femur. He left the others unnamed, and did not provide a general term for all such corresponding elements in the same organism. ... The repeated parts are formed in much the same way in their embryological development and they have the same ‘plan’, but we are not sure why. At any rate, more is involved than community of evolutionary descent. The correspondence nonetheless seems to be something fundamental in the organization of the animals, not superficially like analogy; hence, it is not inconsistent to continue calling it “homology” (Ghiselin 1976: 135,

Thus, appropriate comparisons between parts of organisms are first "homologues". If further comparisons are made with the other parts of the same organism, then repeated "homologues" are "homotypes". Thus, a vertebra is a homologue; the repeated parts, the vertebrae, when compared, are homotypes. Thus, any "namesake" can be both a homologue and a homotype. Riedl neatly captured the idea by distinguishing "anatomical plurals" (homotypes) from "anatomical singulars" (homologues) (Riedl 1978: 52).

## 7.6 Analogy

To demonstrate the meaning of analogy, Owen referred to the "Dragon", *Draco volans*:

> Its forelimbs being composed of essentially the same parts as the wings of a bird are homologous with them; but the parachute being composed of different parts, yet performing the same function as the wings of a bird, is analogous to them. . . . But homologous parts may be, and often are, also analogous parts in a fuller sense, viz. As performing the same functions . . . the pectoral fin of the flying fish is analogous to the wing of the Bird, but, unlike the wing of the Dragon, it is also homologous with it. (Owen 1847a: 175[6])

An analogue is thus "defined" solely in terms of function: legs are for walking, wings are for flying. In this sense, homology and analogy may be applied in four possible permutations. Boyden, for example, tabulated examples of each relative to the forelimb of man (Boyden 1943: 231; Table 7.1).

**Table 7.1** Relations of analogy and homology with reference to the human forelimb (after Boyden 1943: 231).

| | Homologous | Non-homologous |
|---|---|---|
| **Analogous** | (a) Forelimb of man<br>(b) Forelimb of monkey | (a) Forelimb of man<br>(b) Cheliped of crayfish |
| **Non-analogous** | (a) Forelimb of man<br>(b) Wing of bird | (a) Forelimb of man<br>(b) Gill of crayfish |

---

Smith 1967: 101). Ghiselin proposed the more refined "iterative homology". Earlier Boyden suggested that "Homology is a genetic phenomenon and both serial and special homology are based upon mechanisms which involve the interaction of genes and cytoplasm, but serial homology or homotypy (Owen's meaning) has no direct bearing upon problems of genetic relationship, whereas special homology bears directly upon the analysis of racial descent" (Boyden 1943: 240; see also Haas & Simpson 1946). Finally, Holmes (1980: 49), citing Simpson (1961: 93) for use of the term "homonomy", also noted that "Acceptance of the term 'serial homology' would necessitate a definition of the unqualified term 'homology' so broad as to be relatively meaningless, since it would have to encompass very different concepts" (Holmes 1980: 49-50). Regardless of these diverse opinions, here we are simply trying to separate the parts of organisms from the relation they indicate, if any.

[6] Also in Owen (1848: 7, 1866: xii; see also Owen 1846: 526).

Boyden’s permutations make clear that while both relations are based upon homologues, the actual relation is determined by other factors such that it was quite possible for homologues to be both homologous and analogous. The forelimb of man and monkey are derived from the “same” part; they also perform the same function, whereas the forelimb of man and the forelimb of a bird are homologous but not analogous.

## 7.7 The Conceptual Split: Owen’s Archetype and the Path to Transformation

Although Owen adopted the term *archetype,* he never accepted Goethe’s version (Chapter 3), despite stumbling on the same conclusion Goethe did, of urhomologies and their importance. Neither did Goethe’s concept of *Bildung* establish itself in the minds of the French or English anatomists, who were concerned with descriptions and identification of organisms rather than establishing relationships.

Owen’s archetype was the “lowest common denominator of the vertebrate class, describing the vertebrate as essentially a string of vertebrae” (Richards 2002b: 443). The archetype worked so as to include all the primitive forms that can be related to more developed or derived forms in higher taxa—thus, we might call Owen’s version a **Gestalt Archetype**. The gestalt archetype, differing from Goethe’s Archetype, denotes the start of a transformational taxonomic hierarchy. Forms that had specialised manifestations of structures found in the gestalt archetype are simple forms *transformed* into specialised structures in higher or more developed groups, such as mammals (Chapter 3).

Owen’s concept of the homologue was that of one “primitive” structure transforming into more specialised (“advanced”) structures. Thus, the forearm of a gorilla, the wing of a bat, and the fin of a dolphin are but different manifestations of the same structure (or part), indicated in the archetype diagram (Figure 7.7). Owen’s transformation differs from Goethe’s metamorphosis in that it proposed a linear progression or succession of transformations. The problem with Owen’s General Homology was that the structures could not be related to each other in order to discover “homology” as a relationship. The same is true for modern transformational series that concentrate entirely on parts (Chapter 10). In Owen’s case the homologues formed a structure that, in turn, when added together with all the

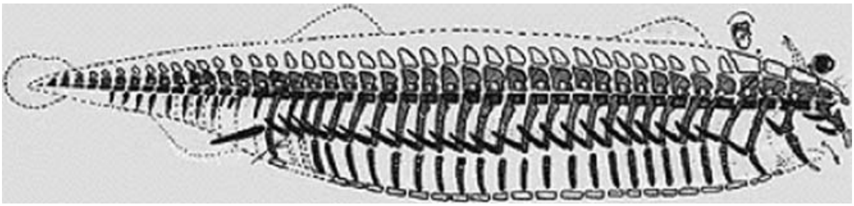

**Fig. 7.7** Owen’s archetype (after Owen, 1847a, 1848).

other transformed or developing parts, formed a multitude of wholes. Owen's gestalt archetype was a *bauplan* or a starting point that led to different expressions (*gestalten*). In this sense, organisms that showed both underdeveloped and ideal parts were considered to be intermediate forms in a progression along a supposed "transformation series", whatever explanation is given to that transformation.

There are, however, certain similarities between Goethe's and Owen's archetypes. Homologues, in Owen's view—the parts of the gorilla forearm, the parts of the bat wing—could be related to each other *without* referring to the gestalt archetype. These were Owen's *special homologies* (noted above), similar to Goethe's urhomologies. Missing from both Goethe's and Owen's archetypes was the notion of any evolutionary transformation, from "primitive" to "derived" conditions. For Goethe, metamorphosis was about observed phenomena; for Owen, any transformation between forms would imply evolution (in the general sense), something he was not prepared to accept during the early part of his career.

The prevailing theme taken up by 20th- and 21st-century historians and philosophers of science is to divide biologists into those who classified organisms (or their parts) with evolutionary or non-evolutionary ideas. Owen, demonised as a creationist, did not see the necessity for evolutionary mechanisms when classifying organisms or even understanding their morphology. Whether one form evolved into another did not and would not change how they might be classified (Agassiz held the same view). Goethe too saw no point in creating hypotheses about how things came to be. Experience of the phenomenon was what mattered most. Any move beyond the phenomenon means leaving the field of morphology as well as the realm of rigorous science based in observation. Continued attempts to cast Goethe as an evolutionist—or at least someone who was not far from discovering evolution (see Richards 2002b)—is an attempt to allow a consideration of pre-evolutionary comparative biologists into the field of evolutionary biology under its particular paradigm. As will be clear from the following chapters of this book, the notion of transformation between organisms and their ancestral and biogeographical origins does not help to further our understanding of morphology and classification—a view that was most likely shared by both Owen and Goethe.

We deal further with homology and transformation in Chapter 10.

## 7.8 Parts and Their Meaning

Owen offered an explanation of anatomical form in terms of its derivation from a common archetype, enabling homologies to be determined from "immutable positional criteria", as a consequence asserting the primacy of form (homology) over function (analogy) (Padian 1995). But it was made clear by Owen that homology and analogy were to be considered different *kinds* of comparisons rather than opposites to be contrasted; Owen never intended "homologue" and "analogue" to be antonyms (or "antitheses" as Strickland misunderstood; Strickland 1846: 35, Panchen 1994: 39; many modern authors make the same mistake, e.g., Blaisdell 1992: 40), even though they have frequently been used in that sense (Ghiselin 1976).

Thus, it is important to concentrate on and remember the difference between homologue and homology. Owen made it clear that “homologue” referred to comparable parts of organisms, while “homology” referred to a “relationship” derived from the homologues. To determine homology, one must first discover the homologues (the “namesakes”).

# Chapter 8
# Discovering Homologues

## 8.1 Homologues and Criteria

Even a rudimentary glance at Belon's famous diagram (Chapter 7, Figure 7.1) is apt to provoke the question: What, if anything, led Belon to make these particular comparisons? (Rieppel 1988: 35). Are there criteria, guidelines, to judge the reality of homologues? Much has been said about the role of similarity in establishing homologues, as "… without similarity, we should not even dream of homology" (Stevens 1984b: 403, Rieppel & Kearny 2002). While similarity seems almost an absolute necessity, it can be, and sometimes is, relatively vague, not meaning the same thing as "identity":

> Although homology is not identity, comparisons passing the similarity test do so by virtue of an abstracted identity or 1:1 correspondence, which may be as general as that common to the hyomandibular of a shark and the stapes of a mouse or as precise as that between the stapes of two mice. (Patterson 1988a: 605, Hall 1994: 7, Cartmill 1994: 118, footnote 2)

Nevertheless, as Patterson noted, criteria do seem necessary to guide the discovery of parts worth comparing, summarising what has been acknowledged for many years as useful: for comparison of "fixed" (static) entities, the parts as revealed by detailed examination of specimens, for comparison of dynamic entities, the notion that "ontogenetic transformations" establish homology—the latter Patterson considered to be the most important:

> The similarity evaluated may be of any kind (topographic, ontogenetic, histological, etc.), but "the mode of development itself is the most important criterion of homology" Nelson, 1978: 335 (Patterson 1982a: 38, Nelson 1994: 108)
>
> Topographic correspondence and ontogenetic transformations are the usual criteria, and correspondences that pass such tests merit the same name …. (Patterson 1988a: 605)

The most detailed discussion of criteria is still that found in Adolf Remane's book *Die Grundlagen des natürlichen Systems, der vergleichenden Anatomie und der Phylogenetik, Theoretische Morphologie und Systematik I.* (1952; see also Remane 1955, 1961 see Chapter 5). Riedl noted that for homology "everything essential was said by Goethe, among the early morphologists, and by Remane, among the modern ones" (Riedl 1978: 23).[1]

To determine homologues, Remane suggested a total of six criteria, three principal ("Hauptkriterien", Remane 1952: 63) and three auxiliary ("Hilfskriterien", Remane 1952: 64) criteria.[2]

His three principal criteria are

1. ***The positional criterion.*** "Homology can be recognised by similar position in comparable systems of features" (Remane 1952: 33; translation from Riedl 1978: 34 and Ax 1987: 160).
2. ***The structural criterion.*** "Similar structures can be homologized, without reference to similar position, when they agree in numerous special features. Certainty increases with the degree of complication and of agreement in the structures compared" (Remane 1952: 46; translation from Riedl 1978: 46 and Ax 1987: 160).
3. ***The transitional criterion, "Stetigkeitskritium".*** "Even dissimilar structures of different position can be regarded as homologous if transitional forms between them can be proved so that, in considering two neighbouring forms, the conditions under headings (1) and (2) are fulfilled. The transitional forms can be taken from the ontogeny of the structure or can be true systematically intermediate forms" (Remane 1952: 49; translation from Riedl 1978: 34 and Ax 1987: 160).

His three auxiliary criteria are

1. ***The general conjunctional criterion.*** "Even simple structures can be regarded as homologous when they occur in a great number of adjacent species" (Remane 1952: 64; translation from Riedl 1978: 64 and Ax 1987: 160).
2. ***The special conjunction criterion.*** "The probability of the homology of simple structures increases with the presence of other similarities, with the same distribution among closely similar species" (Remane 1952: 64; translation from Riedl 1978: 64 and Ax 1987: 160).
3. ***The negative conjunctional criterion.*** "The probability of the homology of features decreases with the commonness of occurrence of this feature among species which are not certainly related" (Remane 1952: 64; translation from Riedl 1978: 64 and Ax 1987: 160).

According to some, Remane's criteria simply "… reiterate Geoffroy St. Hilaire's Principle of Connections and Principle of Composition" (Brower 2000: 14, Stevens 2000: 84, Rieppel 1988: 37). Remane's first and second principal criteria bear a close resemblance to the usual descriptions of the "similarity" criteria (Patterson 1982a) as well as Geoffroy St. Hilaire's "Principle of Connections" and "Principle of Composition" see Chapter 5. However, Remane's third principal

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[1] For a varied selection of interpretations see references on page 62, foot note 1.

[2] Our descriptions are taken from Riedl (1978: 34) as he writes, "I shall quote him [Remane] verbatim."

criterion is somewhat different, dealing with "transitional forms". Remane's third criterion and Patterson's "ontogenetic transformations" are dynamic rather than static comparisons—both invoking transformations, the change of one homologue into another. We return to the issue of transformation later, but first we deal with current practise, the "unit" of classification and the data matrix in the context of homologues. Here the recent inventions of numerical taxonomy—both as "phenetics" and "cladistics"—is of some significance.

## 8.2 Homologues and Phenetics

The phenetic episode in systematics and phylogeny began in the late 1950s; after almost disappearing in 1970s, it has now reached something of a crescendo in the early 21st century—albeit disguised as "phylogenetics" (see below). Phenetics is usually discussed in terms of clustering procedures or algorithms available for finding (constructing) trees to summarise data under the principle of "overall similarity":

> Following a suggestion by Mr H.K. Pusey, we shall refer to the arrangement [ = classification] by overall similarity, based on all characters without any weighting (Cain & Harrison 1958) as *phenetic*, since it employs all observable characters (including of course genetic data when available), and that which aims to show the course of evolution as *phyletic*. (Cain & Harrison 1960: 2–3; italics in original)

We depart from that convention and discuss the subject in terms of characters, the evidence, rather than the method. After defining "phenetics" and "phyletics", Cain & Harrison offered explanations for different kinds of similarity in taxonomic characters:

> Similarity due to common ancestry, not to convergence, can be called *patristic*. Closeness of relationship in terms of phyletic lines can be called *cladistic* (cf. the definition of clades by Huxley 1959[3]). Patristic similarity, therefore, is one form of similarity, the other being convergent. "Cladistic" refers to the paths by which a given similarity has been attained. (Cain & Harrison 1960: 3; italics ours)

With respect to whatever basic systematic data (characters) might be, in the first book-length treatment of phenetics, Sokal & Sneath wrote:

---

[3] Julian Huxley offered definitions for "grade" and "clade" based on what he understood as three types of evolutionary process: anagenesis, cladogenesis, and stasigenesis (the first two originally proposed by Rensch 1954; Huxley was introducing the third term). Huxley wrote (1959: 22; italics in original): "It is suggested, therefore, that two terms outside the formal taxonomic categories should be employed, namely *grade* (already widely used) for units of anagenetic advance, and *clade* for monophyletic groups, of whatever magnitude." Huxley's definition is the one that holds today. Nevertheless, Rensch (1954) cited Cuneot, who had borrowed the term "clade" from Haeckel, who used it as a systematic category (see Chapter 4).

> Taxonomic relationships between taxa are to be evaluated purely on the basis of the resemblances existing *now* in the material at hand. The relationships are thus *static* (Michener 1957) or *phenetic*, as we now prefer to call them. (Sokal & Sneath 1963: 55)

In the revised edition of their book *Numerical Taxonomy*, published 10 years later, they wrote:

> Taxonomic relationships are evaluated purely on the basis of the resemblances existing *now* in the material at hand. These phenetic relationships do not take into account the origin of the resemblances found nor the rate at which resemblances may have increased or decreased in the past. (Sneath & Sokal 1973: 9)

Thus, basic systematic data could be interpreted as the "resemblances existing now"—similarities shared between organisms or, as a previous generation might have put it, "essential resemblances".[4] And these resemblances Sneath & Sokal relate to "phenetic relationships". To *explain* these resemblances, Sneath & Sokal, like Cain & Harrison, turned their attention to the relevance or otherwise of common ancestry. "Phenetic" resemblances were considered to include both homologous resemblances (those due to common ancestry) plus homoplastic resemblances (those not due to common ancestry). They also understood homologous similarity to be identical to patristic similarity. Hence, phenetic similarity had two components: patristic + homoplastic.

One of Willi Hennig's insights was to recognise that "resemblances existing now" are of three kinds, rather than two: synapomorphy, meaning a shared derived character; symplesiomorphy, meaning a shared primitive character; and "convergences", meaning superficial or false similarity (Table 8.1 and Figure 8.1).

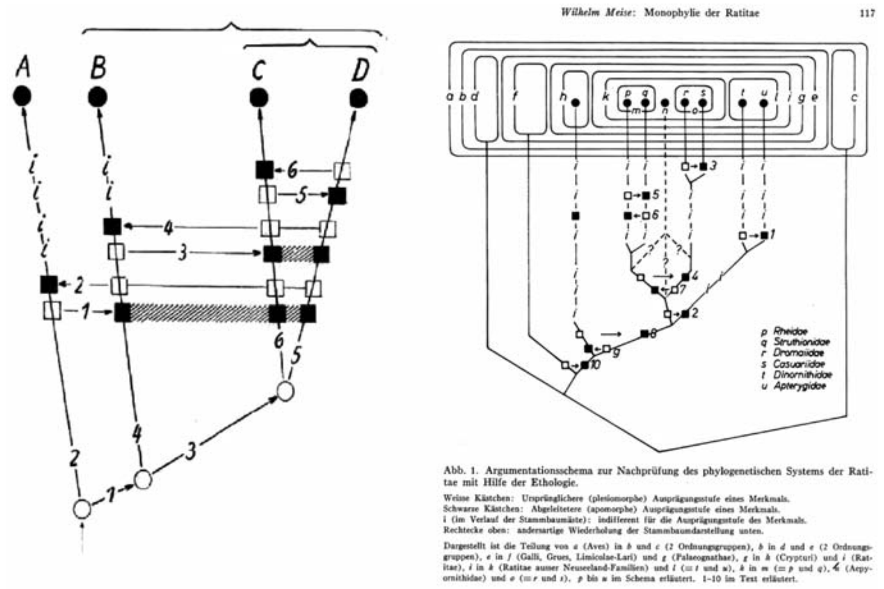
Later, Sokal & Camin (1965) developed the ideas of Cain & Harrison (1960) incorporating some of Hennig's early work (citing Hennig 1950: 176). Sokal & Camin acknowledged that patristic similarity has in fact two components, "primitive patristic similarity" and "derived patristic similarity" (Sokal & Camin 1965: 186). They understood "derived patristic similarity" to be equivalent to Hennig's synapomorphy and their "primitive patristic similarity" to be equivalent to Hennig's sympleisomorphy (Sokal & Camin 1965: 185; see Table 8.2 and also McNeil 1979: 477).

**Table 8.1** Relations of similarity, after Hennig (1966a: 95)

| Similarity | Subdivision | Equivalence |
|---|---|---|
| **Homology** | Apomorphy | Shared derived characters |
| | Plesiomorphy | Shared primitive characters |
| **Homoplasy** | Convergence | Superficial similarity |

---

[4] "When by these considerations we have arrived at the notion of a natural system, composed of natural groups arranged in a determinate order, we may proceed to define *affinity* as *the relation which subsists between two or more members of a natural group*, or in other words, *an agreement in essential characters*" (Strickland 1840: 221).



*Wilhelm Meise*: Monophylie der Ratitae 117

Abb. 1. Argumentationsschema zur Nachprüfung des phylogenetischen Systems der Ratitae mit Hilfe der Ethologie.

Weisse Kästchen: Ursprünglichere (plesiomorphe) Ausprägungsstufe eines Merkmals.
Schwarze Kästchen: Abgeleitetere (apomorphe) Ausprägungsstufe eines Merkmals.
i (im Verlauf der Stammbaumäste): indifferent für die Ausprägungsstufe des Merkmals.
Rechtecke oben: andersartige Wiederholung der Stammbaumdarstellung unten.

Dargestellt ist die Teilung von *a* (Aves) in *b* und *c* (2 Ordnungsgruppen), *b* in *d* und *e* (2 Ordnungsgruppen), *e* in *f* (Galli, Grues, Limicolae-Lari) und *g* (Palaeognathae), *g* in *h* (Crypturi) und *i* (Ratitae), *i* in *k* (Ratitae ausser Neuseeland-Familien) und *l* (≡ *t* und *u*), *k* in *m* (≡ *p* und *q*), 4 (Aepyornithidae) und *o* (≡ *r* und *s*). *p* bis *u* im Schema erläutert. 1–10 im Text erläutert.

**Fig. 8.1** Reproduction of Hennig's diagram (left) and a later version from Meise (1960: 34, Abb. 12), (right)[5].

**Table 8.2** Relations of similarity, after Sokal & Camin (1965: 186)

| **Patristic Similarity** | **Subdivision** | **Description** |
|---|---|---|
| | Primitive | "Classical homology" |
| | Derived | "Parallelisms = homoiology" |

| **Homoplastic Similarity** | **Subdivision** | **Description** |
|---|---|---|
| | Convergence | "Different characters or character states are erroneously coded as homologous" |

---

[5] This diagram was first published in Hennig (1957: 66, Abb. 9). As an explanation of his views on characters, it is often reproduced, sometimes redrawn, sometimes altered. Of significance is its inclusion in *Assembling the Tree of Life* (Donoghue & Cracraft 2004: 3) as one of the four diagrams that, in the authors' view, summarises progress in systematic biology since Darwin; other reproductions of Hennig's figure can be found in Günther (1962: 270, Abb. 1 and 2), Hennig (1965: 106, Fig. 3, 1966a: 91, Fig. 22, 1969: 20, Abb. 2A, 1981: 7, Fig. 2A, 1982: 94, Abb. 22), Mayr (1969: 212, Fig. 10-4), Darlington (1970: Figs. 5 and 6), Nelson (1989a: 284, Fig. 1). The diagram appears in a modified form in a study of the bird genus Gavia (Meise 1960: 34, in Berndt & Meise 1960: 34, Abb. 12; reproduced in Haffer 2003: 125, Abb. 4 describes both the terminal taxa and the characters used for the diagram); see also Schmitt (1996: 22, Abb. 2) for a reproduction of Günther (1974: 944), an argumentation plan for *Tetrigoidea*. Such diagrams are still in use today (e.g., Zangerl et al. 1998: 58, Fig. 36).

Oddly, Sokal & Camin (1965: 186) suggest that "derived patristic similarity" is equivalent to their understanding of parallelism and the related term homoiology.[6] In other words, similarity is considered derived when it originates independently along separate branches ("derived patristic similarity (homoiology, parallelism)"; Sokal & Camin 1965: Fig. 3) as well as derived from the most recent common ancestry ("derived patristic similarity plus divergence"; Sokal & Camin 1965: Fig. 4) (Figure 8.2).

In addition, they understood "convergence" to be simply mistakes in coding characters—"Different characters or character states are erroneously coded as homologous"—which is really mistaken similarity (cf. Patterson 1982a). In their 1973 book, Sneath & Sokal (1973: 39–40) adjusted their terminology to accord with more accepted evolutionary explanations, judging both parallelisms and homoiology to be homoplasious (Table 8.3).

Leaving aside Sokal & Camin's earlier idiosyncratic definitions of "primitive" and "derived" similarity due to or explained by common ancestry was of two sorts. While this might *explain* the various "kinds of similarity", what of those "resemblances existing now" or, as Sneath & Sokal would later express it, the "general resemblances among organisms" (Sneath 1982: 208)?

In their 1973 book, Sneath & Sokal expanded their terminology to include the relatively new term "isology" for "general resemblances among organisms", a neologism coined by the biochemist Marcel Florkin in 1962 for comparisons of similarities among sequences of amino acids:

> It is noteworthy that chemists are increasingly using the term isology (introduced by Florkin 1962), for chemical correspondences (for example the occurrence of cyanides in two organisms) rather than homology, when little is known about their evolutionary origins. (Sneath & Sokal 1973: 76)

Sneath & Sokal were grappling with the homology concept, as Sneath made clear some time later:

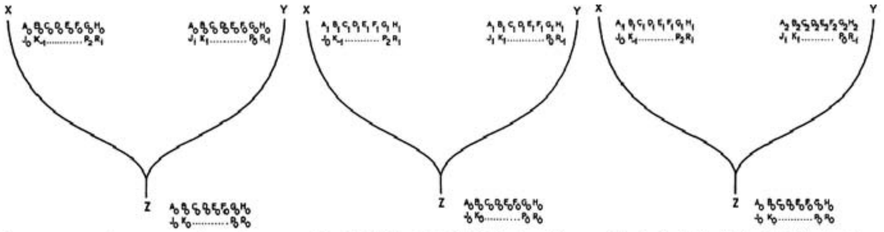


Fig. 2. Primitive patristic similarity between OTU's **X** and **Y**. OTU **Z** is their common ancestor. Capital letters and subscripts refer to characters and character states, respectively.

Fig. 3. Derived patristic similarity (homoiology, parallelism) between OTU's **X** and **Y**. Symbolism as in Figure 2.

Fig. 4. Derived patristic similarity plus divergence between OTU's **X** and **Y**. Symbolism as in Figure 2.

**Fig. 8.2** Reproduction of Camin & Sokal (1965, Figs. 2–4).

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[6] "Homoiology describes a form of homology in which the particular character has been acquired independently by close relatives. It corresponds to the homoiogenesis of Eimer" (Plate 1928: 781; translation from Hennig (1966a: 117); see also Riedl (1978: 36) and Patterson (1982a: 47–48).

**Table 8.3** Relations of similarity, after Sneath & Sokal (1973: 40)

| Patristic Similarity | Subdivision | Description |
|---|---|---|
| | Primitive<br>Derived<br>Derived + primitive | “Classical homology” |

| Homoplastic Similarity | Subdivision | Description |
|---|---|---|
| | Parallelism<br>Homoiology<br>Convergence | “Identical characters or “states, or both, derived from different phyletic lines, or different characters or characters states erroneously coded as homologous” |

> It should be noted that reference has been made to “homologies”. The quotation marks indicate that it is not evolutionary homology that is meant here. A better word is *isology*, merely implying sameness. This is operational homology as used in phenetic work .... (Sneath 1983: 27 and 29)
>
> Evolutionary homologies cannot be recognised from the distribution of character-states in monophyletic groups, *because those groups cannot be constructed until the homologies have first been recognised* . What can be recognised is isology. By rejecting any concept of isology the initial recognition of comparable characters is prevented. (Sneath 1988: 266; italics in original)[7]

Florkin had defined isology as follows:

> The biochemical compounds, molecules or macromolecules, which show signs of chemical kinship, we shall call *isologues*. (Florkin 1966: 6, from a translation of Florkin 1962: 820)

What Florkin meant by isology was the “general resemblances” among proteins and amino acids, resemblances that may or may not have arisen via common ancestry. Florkin contrasted isology with homology, noting that the latter is explained by having “… a common origin and a common line of descent.” Florkin elaborated by adding,

> When we considered the concept of homology …, we defined it as pointing to a common origin, starting from an initial prototype, and we decided that a high degree of isology in the primary structure of proteins, *viz*. in amino acids would be taken as a sign of homology. (Florkin 1966: 43)

Isology, then, appears to be a synonym for what we call “phenetic” characters (see below), a character that simply represents “resemblances existing now”,

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[7] It is worth comparing this sentence with one that appeared earlier: “Synapomorphies [evolutionary homologies, Sneath 1988] cannot be recognized from relationships in trees [distribution of character-states in monophyletic groups, Sneath 1988] because those *trees cannot be constructed until the synapomorphies* [*homologies*, Sneath 1988] *have first been recognized*. What can be recognized are the general resemblances between organisms [is isology, Sneath 1988]” (Sneath 1982: 209; see also Sneath 1995: 287).

regardless of the explanations available—the usual kind of entries found in any data matrix. According to the phenetic viewpoint, to reject the concept of isology was equivalent to rejecting "safe, sure knowledge" (Patterson 1982a). It is sufficient to note that Sneath & Sokal, in various publications after their 1973 book, continued to advocate the use of the term "isology" for "general resemblances"—although Sneath (1995: 287) adopted the term "general homologies" where he would previously have used "isology".

Isology never did gain much usage, cropping up every now and then.[8] "Isologue" is defined in the glossary of Hillis & Moritz (1990) and used in the introductory essay to that volume.[9] Elsewhere, Hillis wrote:

> Wegenez (1987) suggested the substitute jargon *isology* to describe measured percent similarity of aligned sequences (as in "the two genes are 50% isologous"). Use of the term isology would seem to satisfy the desire of using a word that is unfamiliar (and therefore surely important and complex) to describe a familiar and simple concept . . . . (Hillis 1994: 340)

The simple concept Hillis had in mind was similarity.

Hillis' perceptive comment is of significance, as today's data matrices, regardless of interpretation, include entries that are simply similarities—data that eschew *any* notion of homology (as relationship), beyond the idea that the concept must have some kind of similarity component.

## 8.3 Homologues and Cladistics

At about the same time Florkin coined the term "isology", a similar idea occurred to morphologists. The original use of the term "paralogy" in biology—different from its current use in molecular systematics (Fitch 1970, 2000) and biogeography (Nelson & Ladiges 1996)—was coined by Hunter (1964[10]), where a

> "Paralogue"—a part or organ in one animal similar in anatomical structure or microanatomical structure to a part or organ in a different animal. Paralogy, then, refers only to anatomical similarity and has no phylogenetic or functional implications. (Hunter 1964: 604)

As paralogy (*sensu* Hunter) refers "only to anatomical similarity", it is a synonym of isology. Of Hunter's paralogy, De Pinna wrote that ". . . when translated to current

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[8] Minelli (1993: 12, 22) makes a note of it, with the implication that it means identity as opposed to the less exact term "similarity"; Riedl (1978: 37) discusses the term and its relationship to homology ("Isologies of very high accidental improbability can be recognised as homologies"); Schoch (1986: 131) offered a definition ("... chemical similarity or chemical kinship of biological compounds ... Isologues may be homologous or analogous", a definition adopted by Sudhaus & Rehfeld (1992: 75, 89); Wegnez (1987) suggests its resurrection to represent percentage DNA sequence similarity; Patterson (1988a: 622) noted Wegnez's use of the term but added no comment of his own.

[9] The glossary entry remains in the second edition, but Hillis does not refer to it in the revised introduction (Hillis et al. 1996).

[10] For commentary, see Kaplan (1984), Inglis (1966), Van Valen (1982: 308), and De Pinna (1991: 389).

[cladistic] concepts, [it] is equivalent to … ‘shared derived character’ or ‘putative synapomorphy’, i.e. primary homology” (De Pinna 1991: 389). That would seem to suggest that phenetic characters and cladistic characters—at least the concept of “primary homology”—are virtually identical.

Here it is worth recalling what Hennig said of synapomorphy:

> We will call characters and character conditions from which the transformation started … in a monophyletic group plesiomorphous, and the derived conditions … apomorphous …. We will call the presence of plesiomorphic characters in different species symplesiomorphy, the presence of apomorphic characters synapomorphy, always with the assumption that the characters belong to one and the same transformation series. (Hennig 1966a: 89; see Figure 8.3, reproduced from Hennig 1957: 66, Abb. 9)

In the lower part of Hennig’s diagram (Figure 8.3), he illustrates two homologues, a and a’. In the upper part of the diagram, homologue a’ (the black box) is present in taxa B and C but not in A. Thus, homologue a’ is a synapomorphy for the group B + C. At that time an apparent issue was how to distinguish synapomorphies (putative shared derived characters) from “real” shared derived characters—how to go from Hennig’s lower diagram to the upper one. If the arrow is removed from Hennig’s lower diagram (Figure 8.3), then the character is identical to that of a phenetic character.

What, then, is synapomorphy? In Tuomikoski’s words, “ … synapomorphy means agreement in apomorphic characters between two groups and thus also covers the similarity which is due to parallelism, chance similarity, etc.” (Tuomikoski 1967: 139). Tuomikoski’s commentary was initiated by his sensing a difference between Hennig’s (1966a) and Brundin’s (1966) use of the term, as Brundin (1966: 26) had spoken of “true synapomorphy” to distinguish it from the more operational definition of “shared derived character”, only the former distinguishing natural or monophyletic groups, while Hennig, on occasion, wrote that synapomorphy was “common possession of derived characters” (Hennig 1965: 605). Tuomikoski suggested that “… a change in the original sense of the terms synapomorphy would be confusing and a term for ‘true synapomorphy’ would at any rate be needed” (Tuomikoski 1967: 139). Tuomikoski’s viewpoint was echoed by other cladists:

> A term seems to be missing from Hennig’s vocabulary, namely one for the sharing of an apomorphic feature—whether convergent or homologous. The term “synapomorphy” might be used for this more inclusive concept, while the older term homology could be reserved for Hennig’s synapomorphy. (Bonde 1977: 779)

Although “shared derived” characters might be identified (proposed or hypothesised), not all would define or characterise a particular monophyletic group, as a certain number will mislead because of parallelism—or more generally, because of homoplasy. Since Hennig a number of different proposals have been suggested, differing mostly in terminology, but recognising three terms: one apparently neutral, meaning just similarities; and two further terms, one for similarities accepted as due to common ancestry and another for those not accepted. In other words, what was recognised was the need to discriminate homology from homoplasy; a “sorting procedure” was required to form a bridge between neutrality and meaning:

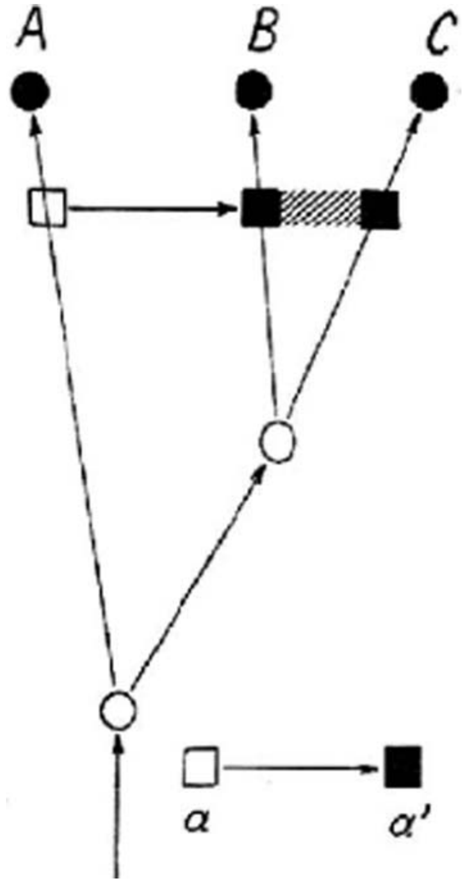


**Fig. 8.3** Reproduction of Hennig's (1957) diagram.

> I emphasise the concept of synapomorphy instead of homology, the former being viewed as an estimator, the latter the parameter. I do so because synapomorphy does not presuppose common ancestry whereas homology does. Homology is dealt with only indirectly by maximum character congruence, the ultimate arbiter of character history. (Patterson 1982, Kluge 1993a: 9, Kluge & Strauss 1985: 258)

If "Homology is dealt with only indirectly by maximum character congruence", then a method is required to sort the things called "synapomorphy" from the things that are to become homology. If "synapomorphy does not presuppose common ancestry", then what does it represent? Does synapomorphy mean just similarities, the raw data? A glance at Table 8.4 suggests that in at least some cases synapomorphy *is* interpreted to represent *similarity* only, something apparently devoid of interfering theory. In any case, it does seem that synapomorphy (or whatever item appears in column 1 of Table 8.4) *is* regarded as a unit of systematics and equivalent to those things entered into a matrix. Thus, there seems no real difference between the concept of a phenetic character, as outlined above, and the data matrix entry—for

**Table 8.4** The nature of resemblances from a post-cladistic viewpoint. For the latter kind of resemblances, homoplasy has been universally adopted (see also Schmitt 1995: 429). For a similar table, see Schuh (2000: 71, Table 4.1) see Table 5.6.

| | "Unknown" Cause | "Known" Cause | |
|---|---|---|---|
| | "Similarity" | Common Ancestry | "Independent" similarities |
| **Sokal & Sneath (1963)** | Isology | — | — |
| **Hunter (1964)** | Paralogy | Homology | — |
| **Brundin (1966)** | Synapomorphy | "True synapomorphy" | Homoplasy |
| **Bonde (1977), Kluge (1991), McKitrick (1994)** | Synapomorphy | Homology | Homoplasy |
| **Gaffney (1979)** | Putative synapomorphy | Synapomorphy | Homoplasy |
| **Farris & Kluge (1979)** | Shared derived character | Synapomorphy | Homoplasy |
| **Rieppel (1980)** | Topographical homology | Phylogenetic homology | Homoplasy |
| **Rieppel (1988)** | "Homology" = topographic correspondence | "Homogeny" = homology | Homoplasy |
| **De Pinna (1991)** | Primary homology | Secondary homology | Homoplasy |
| **Rieppel (1992, 1993, 1994)** | Topological homology | Phylogenetic homology | Homoplasy |
| **Minelli & Schram (1994), Minelli (1996)** | Positional homology | "Phylogenetic" homology | Homoplasy |
| **Brower & Schawaroch (1996)** | "topographic identity" [= transformational homology] | Homology | Homoplasy |

cladists and pheneticists alike. The difference between phenetics and cladistics is, as has always been, the algorithms rather than the basic unit.

## 8.4 The Data Matrix

Nearly all phylogenetic (systematic) studies undertaken include as a first step the creation of a data matrix. The matrix is said to represent data acquired during a particular study. Of systematic data matrices, Sokal & Sneath (1963: 123) wrote: "We adopt the convention used in psychology of arranging data for such an undertaking in the form of an $n \times t$ matrix whose $t$ columns represent the $t$ fundamental entities to be grouped on the basis of resemblances and whose $n$ rows are $n$ unit characters." These are the kinds of data matrices in use today. In their later book, Sneath & Sokal (1973: 114) described the matrix as a table "whose $t$ columns represent the OTU's [terminal taxa] to be grouped on the basis of resemblances and whose $n$ rows are $n$ unit characters" (Figure 8.4). Data matrices are often said to contain the "raw" data

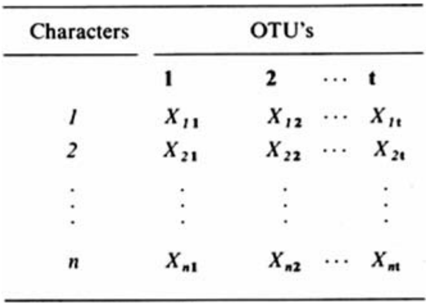


**Fig. 8.4** A data matrix from Sneath & Sokal (1973: 115).

| Characters | OTU's | | | |
|---|---|---|---|---|
| | 1 | 2 | ⋯ | t |
| *1* | $X_{11}$ | $X_{12}$ | ⋯ | $X_{1t}$ |
| *2* | $X_{21}$ | $X_{22}$ | ⋯ | $X_{2t}$ |
| ⋮ | ⋮ | ⋮ | | ⋮ |
| *n* | $X_{n1}$ | $X_{n2}$ | ⋯ | $X_{nt}$ |

(“unit characters”), in the sense that the entries are derived directly from empirical investigation of the various parts of organisms.

In this sense, matrices relate to tables of characters many taxonomists provide in their studies that allow the reader to contrast various parts of the specimens examined and identify those parts considered to be the “same”, the homologues (Figure 8.5).

Consider the following hypothetical matrix with six characters (columns 1–6) and four taxa (rows A–D; Figure 8.6). The intersections of taxon rows and character columns consist of similarities and differences recorded from observations. Similar parts are assigned a code; for the sake of convenience, these are usually a part of a numerical series with 0’s, 1’s, 2’s, etc. These data are often considered neutral—or nearly so—with respect to any grouping. By neutral, we mean that the data are said to have no immediate meaning relative to the groups (or relationships) they may come to represent or support. To achieve an optimal grouping from all the data, some methodology is required to “sort” or “arrange” the “shared similarities”.

This viewpoint implicitly suggests that there can be no such thing as a basic unit of systematics, aside from the concept of a “unit character”, a similarity judgment/interpretation resides in the assumptions of the algorithm used to create groups from the many characters in the matrix. Thus, we understand these kinds of data matrices to embrace the phenetic notion of characters as “unit characters” (Sokal & Sneath 1963). While pheneticists retreated from the thorny issue of separating useful similarities from the useless and advocated grouping by an estimate of overall similarity, their version of a character and its representation in a matrix is identical to that used by numerical “phylogeneticists”, and any differences between approaches reside in the varying methodologies. Thus, we refer to these kinds of data and their representation as **Phenetic Characters** (see Williams and Ebach 2006).

If taxa A and B are scored as 1 and taxa C and D are scored as 2, phenetic data may be alternatively represented as follows:

$$[[A] + [B] + [C] + [D]] .$$

The square brackets represent “potential” rather than specific relationships. What is implied in the notation above is that the relationships might be (AB), or (CD), or (AB)(CD)—or even (A), (B), (C), and (D). An additional implication is that the value or importance of any entry in the matrix (0, 1, etc.) is only realised via a

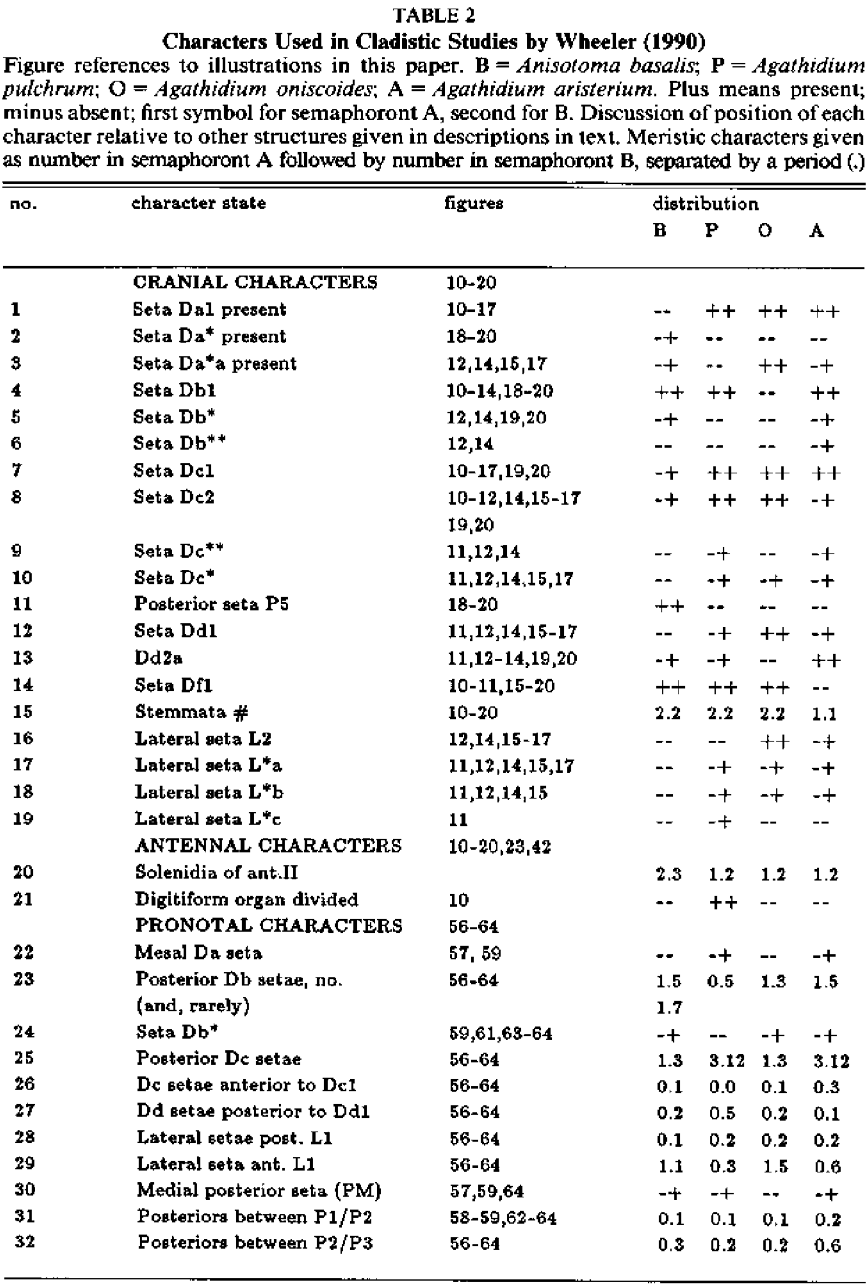


TABLE 2

**Characters Used in Cladistic Studies by Wheeler (1990)**

Figure references to illustrations in this paper. B = *Anisotoma basalis*; P = *Agathidium pulchrum*; O = *Agathidium oniscoides*; A = *Agathidium aristerium*. Plus means present; minus absent; first symbol for semaphoront A, second for B. Discussion of position of each character relative to other structures given in descriptions in text. Meristic characters given as number in semaphoront A followed by number in semaphoront B, separated by a period (.)

| no. | character state | figures | distribution B | P | O | A |
|---|---|---|---|---|---|---|
| | CRANIAL CHARACTERS | 10-20 | | | | |
| 1 | Seta Da1 present | 10-17 | -- | ++ | ++ | ++ |
| 2 | Seta Da* present | 18-20 | -+ | -- | -- | -- |
| 3 | Seta Da*a present | 12,14,15,17 | -+ | -- | ++ | -+ |
| 4 | Seta Db1 | 10-14,18-20 | ++ | ++ | -- | ++ |
| 5 | Seta Db* | 12,14,19,20 | -+ | -- | -- | -+ |
| 6 | Seta Db** | 12,14 | -- | -- | -- | -+ |
| 7 | Seta Dc1 | 10-17,19,20 | -+ | ++ | ++ | ++ |
| 8 | Seta Dc2 | 10-12,14,15-17 19,20 | -+ | ++ | ++ | -+ |
| 9 | Seta Dc** | 11,12,14 | -- | -+ | -- | -+ |
| 10 | Seta Dc* | 11,12,14,15,17 | -- | -+ | -+ | -+ |
| 11 | Posterior seta P5 | 18-20 | ++ | -- | -- | -- |
| 12 | Seta Dd1 | 11,12,14,15-17 | -- | -+ | ++ | -+ |
| 13 | Dd2a | 11,12-14,19,20 | -+ | -+ | -- | ++ |
| 14 | Seta Df1 | 10-11,15-20 | ++ | ++ | ++ | -- |
| 15 | Stemmata # | 10-20 | 2.2 | 2.2 | 2.2 | 1.1 |
| 16 | Lateral seta L2 | 12,14,15-17 | -- | -- | ++ | -+ |
| 17 | Lateral seta L*a | 11,12,14,15,17 | -- | -+ | -+ | -+ |
| 18 | Lateral seta L*b | 11,12,14,15 | -- | -+ | -+ | -+ |
| 19 | Lateral seta L*c | 11 | -- | -+ | -- | -- |
| | ANTENNAL CHARACTERS | 10-20,23,42 | | | | |
| 20 | Solenidia of ant.II | | 2.3 | 1.2 | 1.2 | 1.2 |
| 21 | Digitiform organ divided | 10 | -- | ++ | -- | -- |
| | PRONOTAL CHARACTERS | 56-64 | | | | |
| 22 | Mesal Da seta | 57, 59 | -- | -+ | -- | -+ |
| 23 | Posterior Db setae, no. (and, rarely) | 56-64 | 1.5<br>1.7 | 0.5 | 1.3 | 1.5 |
| 24 | Seta Db* | 59,61,63-64 | -+ | -- | -+ | -+ |
| 25 | Posterior Dc setae | 56-64 | 1.3 | 3.12 | 1.3 | 3.12 |
| 26 | Dc setae anterior to Dc1 | 56-64 | 0.1 | 0.0 | 0.1 | 0.3 |
| 27 | Dd setae posterior to Dd1 | 56-64 | 0.2 | 0.5 | 0.2 | 0.1 |
| 28 | Lateral setae post. L1 | 56-64 | 0.1 | 0.2 | 0.2 | 0.2 |
| 29 | Lateral seta ant. L1 | 56-64 | 1.1 | 0.3 | 1.5 | 0.6 |
| 30 | Medial posterior seta (PM) | 57,59,64 | -+ | -+ | -- | -+ |
| 31 | Posteriors between P1/P2 | 58-59,62-64 | 0.1 | 0.1 | 0.1 | 0.2 |
| 32 | Posteriors between P2/P3 | 56-64 | 0.3 | 0.2 | 0.2 | 0.6 |

**Fig. 8.5** Table with character list from Wheeler (1990 Table 2, p. 8), with permission of the author.

**Fig. 8.6** Data matrix of 4 taxa and 6 characters.

| | Characters | | | | | |
|---|---|---|---|---|---|---|
| Taxa | 1 | 2 | 3 | 4 | 5 | 6 |
| A | 0 | 1 | - | - | - | - |
| B | 1 | 0 | 0 | 1 | - | - |
| C | 1 | 0 | 1 | 0 | 0 | 1 |
| D | 1 | 0 | 1 | 0 | 1 | 0 |

particular algorithm. Thus, the numerical "revolution", such as it is, allowed systematists to switch their efforts from understanding the data (the characters) to producing and using various algorithms designed to "maximise" the potential of *all* characters, however interpreted. Thus, most, if not all, "modern" phylogenetic methodology, no matter how sophisticated the *analytical* techniques, remains rooted in the phenetic notion of "unit characters" (Sokal & Sneath 1963; see Felsenstein 2004: 123 *et seq.)*. There is, of course, much more to homology than similarity and more to phylogenetic studies than algorithms (assumptions).

### *8.4.1 The Matrix: A Short Historical Digression*

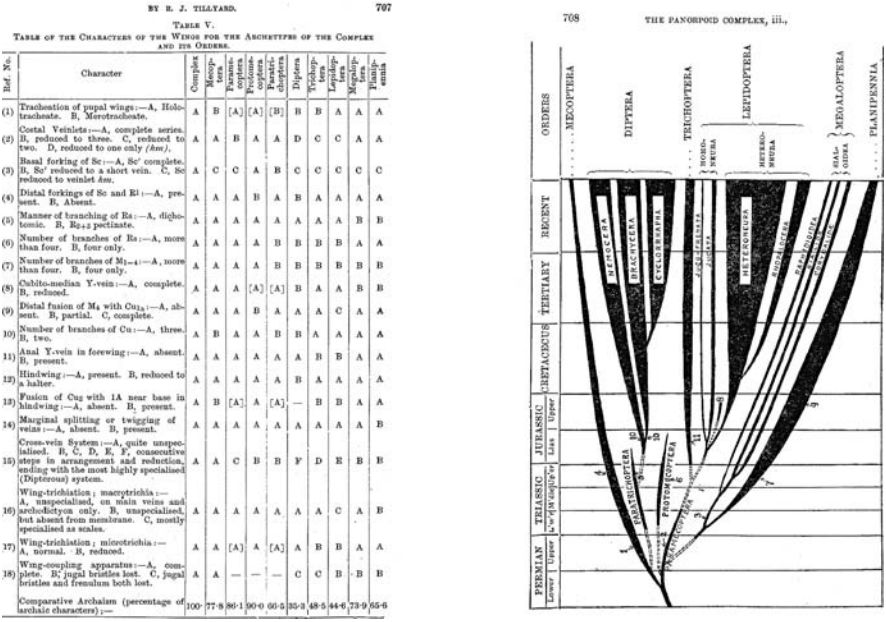
Not all data summaries (tables, charts, matrices, etc.) have been quite so distinctly phenetic as the numerical interventions covered above, those that began in the 1950s but are now commonplace in any systematic study. One example, discussed by Willman (2003), was of some tables presented by Robin John Tillyard (1881–1937; Dunbar 1937). Some have considered Tillyard's work a precursor to the more usual cladistic approach (Craw 1992).

Tillyard presented a series of papers on the phylogenetic utility of wing venation in insects, summarising his data in table form (Tillyard 1919: 705, Table see Figure 8.7, left). Tillyard described his table thus:

> In the Table given, the characters of the wings for the various Archetypes constructed in Sections viii.-xi., [of his paper], and for the Archetype of the whole Complex, are arranged together for comparison. For each character selected, the most archaic condition is indicated by the letter A. This is usually contrasted with a single specialised condition, represented by the letter B. In the case of characters in which a series of evolutionary stages can be recognised, these are represented by the letters A, B, C, . . . , in ascending order of specialisation. (Tillyard 1919: 705)

Tillyard provided a summary phylogenetic tree with characters and taxa plotted against a time scale (Figure 8.7, right).

Tillyard's Table (Figure 8.7, left) might be better viewed as a series of characters with states indicating either their "primitive" or "derived" state. Tillyard further expounded on his manipulation of the data in which he attempted to determine the "Comparative Archaism" for each taxon defined as "*the percentage of archaic*



BY R. J. TILLYARD. 707

TABLE V.

TABLE OF THE CHARACTERS OF THE WINGS FOR THE ARCHETYPES OF THE COMPLEX AND ITS ORDERS.

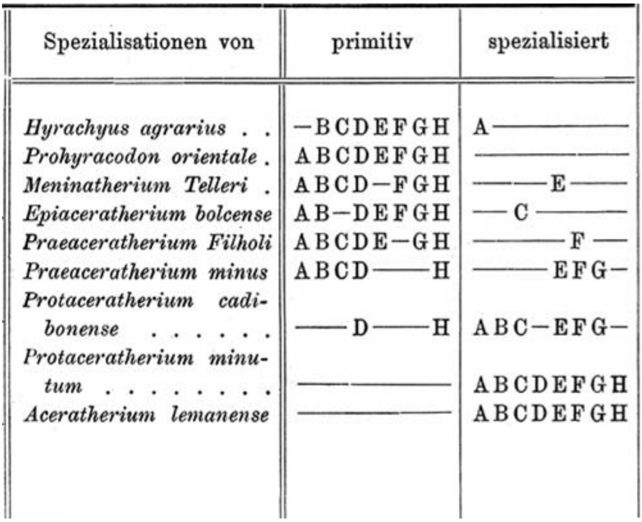
| Ref. No. | Character | Complex | Mecoptera | Paramecoptera | Protomecoptera | Paratrichoptera | Diptera | Trichoptera | Lepidoptera | Megaloptera | Planipennia |
|---|---|---|---|---|---|---|---|---|---|---|---|
| (1) | Tracheation of pupal wings:—A, Holotracheate. B, Merotracheate. | A | B | [A] | [A] | [B] | B | B | A | A | A |
| (2) | Costal Veinlets:—A, complete series. B, reduced to three. C, reduced to two. D, reduced to one only *(hm)*. | A | A | B | A | A | D | C | C | A | A |
| (3) | Basal forking of Sc:—A, Sc′ complete. B, Sc′ reduced to a short vein. C, Sc reduced to veinlet *hm*. | A | C | C | A | B | C | C | C | C | C |
| (4) | Distal forkings of Sc and R1:—A, present. B, Absent. | A | A | A | B | A | B | A | A | A | A |
| (5) | Manner of branching of Rs:—A, dichotomic. B, $R_{2+3}$ pectinate. | A | A | A | A | A | A | A | A | B | B |
| (6) | Number of branches of Rs:—A, more than four. B, four only. | A | A | A | A | B | B | B | B | A | A |
| (7) | Number of branches of $M_{1-4}$:—A, more than four. B, four only. | A | A | A | A | B | B | B | B | B | B |
| (8) | Cubito-median Y-vein:—A, complete. B, reduced. | A | A | A | [A] | [A] | B | A | A | B | B |
| (9) | Distal fusion of $M_4$ with $Cu_{1a}$:—A, absent. B, partial. C, complete. | A | A | A | B | A | A | A | C | A | A |
| 10) | Number of branches of Cu:—A, three. B, two. | A | B | A | A | B | B | A | A | A | A |
| 11) | Anal Y-vein in forewing:—A, absent. B, present. | A | A | A | A | A | A | B | B | A | A |
| 12) | Hindwing:—A, present. B, reduced to a halter. | A | A | A | A | A | B | A | A | A | A |
| 13) | Fusion of $Cu_2$ with 1A near base in hindwing:—A, absent. B, present. | A | B | [A] | A | [A] | — | B | B | A | A |
| 14) | Marginal splitting or twigging of veins:—A, absent. B, present. | A | A | A | A | A | A | A | A | A | B |
| 15) | Cross-vein System:—A, quite unspecialised. B, C, D, E, F, consecutive steps in arrangement and reduction, ending with the most highly specialised (Dipterous) system. | A | A | C | B | B | F | D | E | B | B |
| 16) | Wing-trichiation; macrotrichia:—A, unspecialised, on main veins and archedictyon only. B, unspecialised, but absent from membrane. C, mostly specialised as scales. | A | A | A | A | A | A | A | C | A | B |
| 17) | Wing-trichiation; microtrichia:—A, normal. B, reduced. | A | A | [A] | A | [A] | A | B | B | A | A |
| 18) | Wing-coupling apparatus:—A, complete. B, jugal bristles lost. C, jugal bristles and frenulum both lost. | A | A | — | — | — | C | C | B | B | B |
|  | Comparative Archaism (percentage of archaic characters):— | 100· | 77·8 | 86·1 | 90·0 | 66·5 | 35·3 | 48·5 | 44·6 | 73·9 | 65·6 |

**Fig. 8.7** Table and tree from Tillyard (1919).

*characters retained by the given Archetype*" (Tillyard 1919: 705). To estimate this condition, Tillyard suggested that with "… characters represented by A or B only, A scores 1, B scores nil; for those represented by A, B, C, A scores 1, B 1/2, C nil; for those represented by A, B, C, D, A scores 1, B 2/3, C 1/3, and D nil; and so on" (Tillyard 1919: 706). As Tillyard notes, the archetype of the entire group would receive a score of 100%, as it in theory possesses all the primitive characters. In Tillyard's Table the last column reported the "Comparative Archaism" values. Thus, while Tillyard's method of analysis might be somewhat idiosyncratic by today's accepted protocols, his table of values (characters) cannot be thought of as simply phenetic.

An even earlier version of a non-phenetic table found in Abel (Figure 8.8; see Willman 2003: 468). In this small table Abel distinguishes between "primitiv" and "spezialisiert" character states, with an indication of what condition is found in a particular organism (Abel 1910).

We return to Abel later, but at this stage it is worth considering Hennig's diagram again (Figure 8.3). In the lower part of the diagram there are two homologues, a and a'. As noted above, if the arrow is removed, then the character is identical to that of a phenetic character. In the upper part of the diagram, homologue a' is a synapomorphy for the group B + C, where homologue and taxon are one and the same thing, depicting the monophyly of the group B + C. The latter is equivalent to Patterson's taxic homology, which "is concerned with the monophyly of groups" (Patterson 1982a: 34), an equation that can be derived from Abel's table but not



| Spezialisationen von | primitiv | spezialisiert |
|---|---|---|
| *Hyrachyus agrarius* . . | —BCDEFGH | A——— |
| *Prohyracodon orientale* . | ABCDEFGH | ——— |
| *Meninatherium Telleri* . | ABCD—FGH | ——E—— |
| *Epiaceratherium bolcense* | AB—DEFGH | —C—— |
| *Praeaceratherium Filholi* | ABCDE—GH | ———F— |
| *Praeaceratherium minus* | ABCD——H | ———EFG— |
| *Protaceratherium cadibonense* . . . . . . | ——D——H | ABC—EFG— |
| *Protaceratherium minutum* . . . . . . . . | ———— | ABCDEFGH |
| *Aceratherium lemanense* | ———— | ABCDEFGH |

**Fig. 8.8** Data matrix from Abel (1910).

Tillyard’s (Figures 8.7 and 8.8), thus directly equating homology with systematics, with classification.

Three things appear relevant:

1. The Cladistic notion of “transformation”
2. The Cladistic notion of homologues
3. The Cladistic notion that taxon = homology

# Chapter 9
# Homology and Systematics

## 9.1 Natural Systems, Affinity, and Analogy

In the early part of the 19th century, biologists became interested in the "natural system" of classification and how it might be discovered. Such debate began around the 1820s, petering out, unresolved, in the late 1850s. Central to the debate was the use and meaning of various terms; in particular "affinity" and "analogy", words bought to general attention by the entomologist William Sharp MacLeay (1792–1865). Discussion among zoologists intertwined and overlapped with the views of Richard Owen, although contrasting Owen's use of the words "homology" ("affinity") and "analogy" with that of many zoologists, was not due to confusing and contradictory terminology (Stevens 1984a, 1991) but to some very real differences.

## 9.2 William Sharp MacLeay and "Affinity" and "Analogy"

It would be easy to underestimate W.S. MacLeay's influence on 19th-century natural history, especially classification.[1] If he is remembered at all, it is for what was eventually called the "Quinarian" approach to classification, outlining—if rather briefly—its principles in *Horae Entomologicae* (MacLeay 1819–1821) and some sharply worded papers (MacLeay 1823, 1825,[2] 1830). MacLeay's work was discussed enthusiastically by a number of naturalists in the mid-1800s. Many used his ideas, applying them to different groups of animals (Figures 9.1a and b); the system was discussed (favourably) in the "notorious" *Vestiges of the Natural History of Creation,* which devoted an entire chapter to its explanation (Chambers 1844, Secord

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[1] Biographical details on Macleay can be found in Fletcher (1921), Swainston (1985), and Holland (1996).

[2] MacLeay's 1825 paper contained large sections that first appeared in *Horae Entomologicae*. Most copies of *Horae Entomologicae* were destroyed in a fire at the bookseller's prior to distribution (MacLeay 1830: 434, Winsor 1976: 83), hence it instantly became a rare volume, difficult to track down.

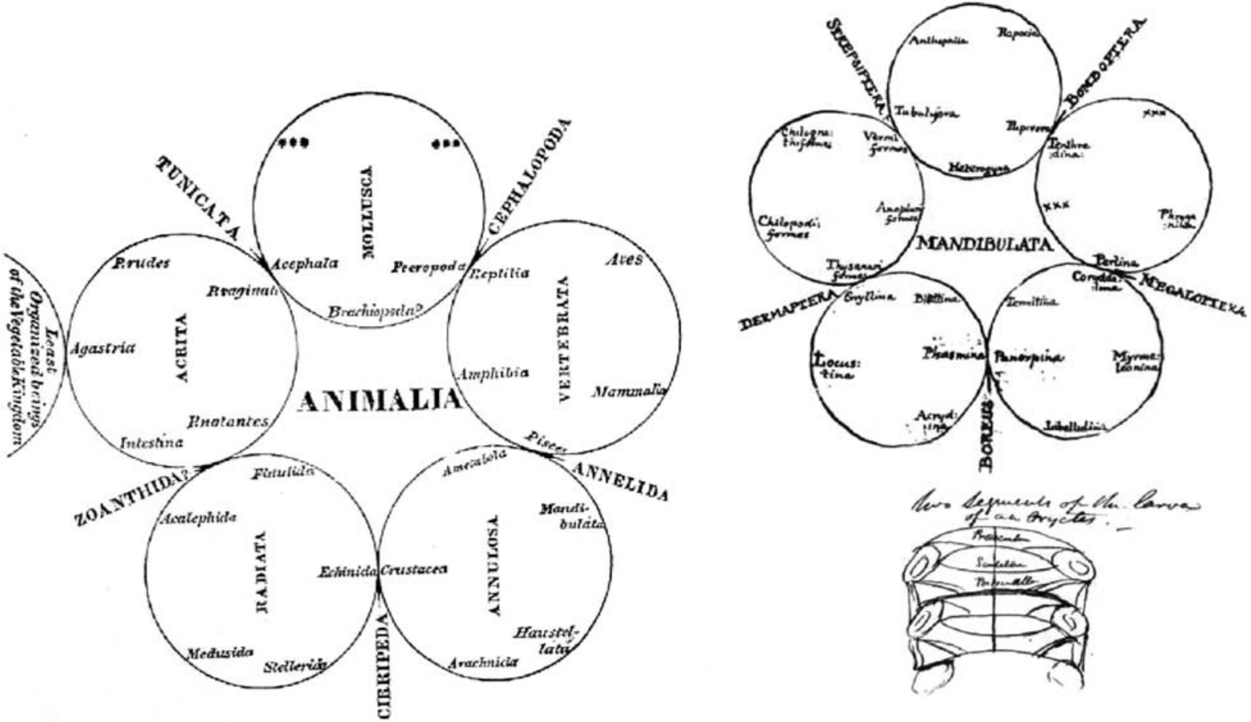

**Fig. 9.1** Two diagrams illustrating Quinarian relationships among certain animals, upper diagram manuscript version held in the Linnean Society of London (reproduced with permission), lower diagram from MacLeay (1821).

1994, 2000), an episode that may have helped kill off any chance MacLeay's ideas would be taken seriously.[3]

MacLeay's approach to classification was said to have been finished in 1845, the beginning of the end occurring at the 10th meeting of the British Association for the Advancement for Science (Strickland 1841a, b), its "deathblow" (Wallace 1855: 188) being struck, again by Strickland, at the 14th meeting of the British Association for the Advancement for Science (Strickland 1845a). The latter was attended by many distinguished scientists and, as reported in the *Athenaeum*,

> One result of it [Strickland's presentation] seems to be, that true affinities of organic structures branch out irregularly in all directions, and that no symmetrical arrangement or numerical uniformity is discoverable in the system of nature when studied independently of preconceived theory. (*Athenaeum* 1845: 851)

Richard Owen was among those present, the *Athenaeum* reporting that "He rejected altogether quinary, circular, and other systems" (*Athenaeum* 1845: 851)—although it remains unclear as to whether Owen rejected not only MacLeay's "system" (Ospovat 1981: 113) but all "systems", including the "maps" presented by Strickland (McOuat 1996). Nevertheless, although various systems were rejected in favour of a branching aspect, MacLeay's affinities and analogies remained empirical realities, an achievement acknowledged by many:

> This mode of studying the Variation of the position of similar parts [homology] has been justly stated by one of our most eminent Naturalist's, Mr. MacLeay, to be one of the most important considerations in Zoology. (Owen 1837[4] in Sloan 1992: 110)
>
> Zoologists had long been aware that certain sets of characters produced an arbitrary or artificial method if employed for classification, while others seemed to lead to a natural system, but the question was involved in obscurity till the time of MacLeay, who was first to give us clear definitions on the distinction between AFFINITY and ANALOGY. (Strickland 1845a: 356)
>
> The ideas that have been broached respecting the affinities and classification of the Mammalia after Cuvier, and which are most remarkable for their novelty and boldness, are those which have emanated from the naturalists of the English Quinary School. The founder and the most talented of this sect—Mr. W.S. MacLeay—thus enunciates his views of the analogies observable between the principal groups of Mammalia, and those into which the class of birds is observable. (Owen 1847a: 242)
>
> To William Sharp MacLeay, author of the "Horae Entomologicae", belongs the merit of first clearly defining and exemplifying, in regard to the similarities observable between different animals, the distinction between those that indicate "affinity" and those that indicate "analogy" or representation. (Owen 1859b: lxvii; see Cain 1984: 12)
>
> We can understand, on these views, the very important distinction between real affinities and analogical or adaptive resemblances. Lamarck first called attention to this distinction, and he has been ably followed by MacLeay and others. (Darwin 1859: 410; the comment remained through to the final edition, Darwin 1872: 373)

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[3] Although discussion of Quinarianism was included up to the third edition of the *Vestiges* (February 1845), it was not in the fifth edition (January 1846), having a minor resurgence in the sixth edition (March 1847).

[4] Owen used some of MacLeay's studies for his early Hunterian lectures (Ospovat 1981: 107, Sloan 1992) and *Cyclopedia* of *Anatomy* articles (Owen 1847b).

T.H. Huxley showed great interest in MacLeay's ideas, exploring their implications for over a decade (Winsor 1976, Desmond 1994, Lyons 1999), writing to MacLeay many years later (November 1851) that "I am every day becoming more and more certain that you were on the right track thirty years ago in your views of the order and symmetry to be traced in the true natural system" (Huxley 1913: 134, Winsor 1976: 93, Swainston 1985: 18).

With the rise of the modern synthesis and the "new" systematics, many 20th-century commentators portrayed MacLeay's ideas as ridiculous, absurd, or "mystical" (Ghiselin 1969: 104, Stresemann 1975: 177, Mayr 1982a: 202). For example, when Gavin De Beer wrote an introduction to the publication of Darwin's *Notebooks on Transmutation of Species*, he noted that

> There would be no need to make mention of such abject nonsense [MacLeay's "system"] were it not for the fact that at the time when Darwin opened his Notebook these notions were current, and, as will be seen, ... , Darwin himself had to struggle through them when considering the problem of affinities between different groups. (De Beer 1960: 29 [5])

With the rise of interest in classification and an appropriate understanding of the history of biology, more sympathetic commentary on MacLeay has been offered.[6] As Desmond (1985: 162) noted, MacLeay's system of classification was never really developed until the zoologist William Swainson mounted his vigorous promotion (Swainson 1834, Farber 1985, Knight 1985, 1986, Gardiner 2001a). Swainson (1835) elaborated and extended MacLeay's work by developing the more numerological parts. And it was Swainson's version—rather than MacLeay's—which gained greater attention. MacLeay, now living in Australia, remained silent for a long while but eventually commented on Swainson's "excesses" in a short paper on the "Natural System of Fishes" (MacLeay 1842).[7]

## 9.3 The *Horae Entomologicae* (MacLeay 1819–1821) and After

It was in the *Horae Entomologicae* that MacLeay first presented his diagram of all known organisms divided into five groups and arranged in a circular system (MacLeay 1821[8]). Every group that was further subdivided was also arranged into a set of five, hence the term "Quinarian" (see Figures 9.1a and b). MacLeay's

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[5] Darwin did indeed struggle with Macleay's "system" (De Beer 1960: 29, Barrett 1960: 256, 286, Smith 1965: 100, Di Gregorio 1981, 1982, 1996, Secord 2000: 430), copying out numerous passages for himself (or at least getting Syms Covington to do so on his behalf, Di Gregorio 1996).

[6] Winsor (1976), Nelson & Platnick (1981), Ospovat (1981), Blaisdell (1982, 1992), Rehbock (1983), Stevens (1984a), Desmond (1985), Knight (1985), Rachootin (1985), O'Hara (1988, 1991), McOuat (1996), and Ritvo (1997).

[7] Swainson's elaborations were noted in several of MacLeay's obituaries: "Speculative ideas, however, of such a general kind, even in the hands of their author, are apt to be carried too far in their application, and, when they fall into those of other speculators of less information and less capacity can hardly fail to be grossly misused" (Busk in Fletcher 1921: 597).

[8] MacLeay's diagrams have been reproduced a number of times: Swainson (1835: 203), Agassiz (1859: 347), Swainston (1985: 14), Gardiner (1985: Fig. 1, 2001a: 2, 2001b: 9), Williams &

"system" was said to be a combination of Cuvier's branching system and Lamarck's linear-progessionist system, leading to the view that a circular arrangement of relationships was most appropriate.

Some years later, Jenyns (1835: 152–153) attempted to clarify MacLeay's method by reducing it to four basic principles:

1. "That all natural groups, of whatever denominations, return into themselves forming circles ...
2. That each of these circular groups is resolvable into exactly five others ...
3. That these five groups always admit of a binary arrangement, two of them being what he [MacLeay] calls typical, the other three aberrant ...
4. That while proximate groups in any circle are connected by relations of affinity, corresponding groups in two contiguous circles are connected by relations of analogy ..."

The first three principles are concerned with the issue of how groups might be represented in a classification, relative to one another, and include the requirement that groups are "resolvable into exactly five ...". Most, if not all, subsequent discussion of Quinarian classification dealt with the numerical aspect of arranging groups of organisms into five. But, as Nelson & Platnick (1981: 110–118) pointed out, that was hardly of any real consequence.[9] The fourth principle itemised by Jenyns differs from the others, as it proposes the means with which to discover the relations among organisms. That is, groups are arranged according to their "analogies" and "affinities", these being discovered through comparisons among organisms (McOuat 1996). MacLeay's illustrations are an attempt to convey both relations of affinity and analogy on the same diagram (Figures 9.1a and b): The groups placed within each circle are related by *affinity* and the circles connect by virtue of *analogy*. Oddly, the meaning and distinction of "affinity" and "analogy", the means for discovering and arranging the groups, rarely figure in recent commentaries (Ghiselin 1969: 104, Stresemann 1975: 177, Mayr 1982a: 202, Farber 1997: 111, but see O'Hara 1991). Stripped of its numerological "mysticism" (which was largely due to Swainson), MacLeay's separation of affinity and analogy had a marked effect on many naturalists (Rachootin 1985). What, then, was MacLeay's contribution to the debate on affinity and analogy?

Like Richard Owen, MacLeay never claimed to be the first to distinguish "affinity" from "analogy" but to have discovered the "nature of the difference" (MacLeay 1821: 363, Jenyns 1835: 156, Ospovat 1981: 105). For affinity, he wrote:

> A natural series of affinity is such as, taking the majority of characters for our guide, shall be found uninterrupted by any thing known, although possibly broken by chasms occasioned by the absence of things unknown. (MacLeay 1821: 401, Ospovat 1981: 104)

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Humphries (2004: 121). The latter three publications reproduce a manuscript version, preserved in the Linnean Society of London and included here as Figure 9.1a.

[9] Surprisingly, a numerical aspect to systematic has been resurrected, albeit unwittingly, on occasion (McNeil 1979, Stevens 1997: 248) with no real outcry from the systematics community.

MacLeay at first refers to the relationships of entire organisms rather than their parts, hence his directive for using as a "guide" the "majority of characters". MacLeay proposed a test for "affinity":

> . . . the test of a relation of affinity is its forming part of a transition continued from one structure to another by nearly equal intervals. (MacLeay 1821: 363, MacLeay 1825: 196)

MacLeay expected the relation of affinity to be circular. That is, if a series of organisms possessed the affinity A-B-C-D, then D would be adjacent to A as well as C. The circular nature of affinities to one side, MacLeay's "test" is significant, as it would be resurrected in one form or another over the next century (Chapter 10).

For analogy, MacLeay wrote:

> A relation of analogy consists in a correspondence between certain parts of the organization of two animals which differ in their general structure. (MacLeay 1821: 363, MacLeay 1825: 196, Winsor 1976: 85)

Analogy, then, was a relation between "certain parts of the organisation" that "differ in their general structure". One might rephrase this, as analogy—for MacLeay—represents features that are not too similar but enough to suggest a correspondence elsewhere in the overall classification. No mention was made of function, as in Owen's version of analogy (see Chapter 7). And as MacLeay imagined, he could represent both relationships in one diagram; A circular arrangement would have seemed both appropriate and suitable.

## 9.4 Westwood's Affinity and Analogy

Another entomologist, John Obadiah Westwood (1805–1893), succinctly captured MacLeay's use of affinity and analogy:

> It is in consequence of the more complete resemblance *in the numerical majority of the essential characters* of the two beings or groups of beings contrasted together, that the relationship becomes one of affinity; while from a resemblance in the *numerical minority* of such essential characters, the relationship is deemed an analogy. (Westwood 1840a: 143)

Westwood's characterisation is an attempt to add a note of exactitude by quantifying the nature of each kind of relationship. Significantly, he added that ". . . these relations [affinity and analogy] are strictly comparative and relative . . . " (Westwood 1840a: 143). The *relative* nature of "affinity" and "analogy" did reflect more accurately MacLeay's meaning, who had later complained to Huxley about such misunderstandings:

> Affinity and analogy "have always been used by me as words expressing *the mode in which relations of resemblances take place* rather than as two kinds of resemblance different in themselves." (Winsor 1976: 84; quotation from a letter from MacLeay to Huxley, March 13, 1849, in Winsor 1976: 92)

Westwood (1840b) further clarified his meaning by stating two aspects to determining "affinity" and "analogy":

> … That relations of analogy and affinity are nothing else than instances of more or less perfect resemblances … [and] … as these relations are absolutely comparative in their nature, it follows that both kinds of relation may exist at the same time between any two animals, according to the animals compared therewith. (Westwood 1840b: 305)

Therefore, while Westwood considered both analogy and affinity to be based on "more or less perfect resemblances" because both relations "are absolutely comparative," they may "exist at the same time" (in much the same way as Owen's homology and analogy; see Chapter 7). According to MacLeay and Westwood, analogy was not to do with function but the framework in which comparisons were made. Thus, Westwood's (and MacLeay's) distinction between "affinity" and "analogy" was not just whether the characters were "essential" or "similar" but concerned both the numerical quantity and the "mode in which the relation of resemblances take place" that determined the nature of the relationship.

As well as noting the relative nature of "affinity" and "analogy", Westwood, like MacLeay, had applied both terms to organisms rather than organs (O'Hara 1991: 258), an aspect that inspired later comment from Strickland:

> … it is not usual to apply the term affinity to the similarities between parts, yet as the similarity between the wholes results from the similarities of their parts, the word affinity may be correctly applied to the one as to the other. (Strickland 1845b: 358)

That is, for Strickland there were two kinds of comparisons (similarities) of which only some will be found "true" ("essential"—affinities), others being "false" ("mere"—analogies). Strickland wrote:

> *Affinity* consists in an essential and physiological agreement in the corresponding parts of organic beings, resulting from a uniformity of plan which pervades the System of Nature. These essential agreements of parts consist rather in a similarity of organic *composition* and of *relative situation*, than of *form*. (Strickland 1845b: 356)
>
> These analogous agreements are equally the result of natural laws, but of laws of a different class from the former [affinities]. (Strickland 1845b: 360)

## 9.5 Strickland's Affinity and Analogy

Hugh Edwin Strickland (1811–1853), who commented on Westwood's propositions, suggested that relationships among groups of organisms indicative of "affinity" are of "natural groups" and are indicated by discovering "essential and important" characters:

> When by these considerations we have arrived at the notion of a natural system, composed of natural groups arranged in a determinate order, we may proceed to define *affinity* as *the relation which subsists between two or more members of a natural group*, or in other words, *an agreement in essential characters* … It is not, however, sufficient, that man should detect those natural groups,—he must also give a definition of their characters,—not of the *superficial* and *arbitrary* ones, but of the *essential* and *important*, and this is often the most difficult part of his task. (Strickland 1840: 221; italics in original)

Thus, for Strickland, "affinity" would be detected from natural groups when their essential characters agreed:

> Hence we see why the idea of a *natural system* is necessary to the definition of *affinity*, for an *artificial system* the characters of the groups are not *essential*, but *arbitrary*, and the relation between the members of such a group would be, not *affinity*, but mere *resemblance* or *analogy*. (Strickland 1840: 221)

Strickland offered no way of detecting the "essential and important" characters, beyond a systematist's "best judgement" (Mayr 1982a: 209; but see below), but did tie them directly to the "natural system" and its creation. Strickland also implies that "analogy" means just "mere resemblance" in contrast to "essential" resemblance for "affinity"—more importantly he is not using either term in the way Westwood does but as indicative of a particular relationship: Affinities discriminate natural groups, analogies do not. Strickland disagreed strongly with Westwood (and MacLeay) over the *relative* nature of affinity and analogy:

> We thus perceive the distinction between affinity and analogy to consist, not in degree, but in kind.... (Strickland 1840: 222)

Strickland's mature view of "affinity" linked three aspects:

1. Parts of organisms
2. Their relations discovered by similarity in composition and position
3. Their relations corresponding to a "uniformity of plan", which provides a focus or framework for their determination

These three factors were more or less identical to those of Richard Owen.

## 9.6 Owen and Strickland on Homology and Analogy

Owen's first extended discussion on homology in *Archetype and Homologies of the Vertebrate Skeleton* included a footnote referring to a recent contribution from Hugh Strickland:

> My ingenious and learned friend Mr. Hugh Strickland has made a strong and able appeal to the good sense of comparative anatomists in favour of the restriction of these terms [homology and analogy] to the senses in which they are here defined [Strickland 1845b: 358, 362]. (Owen 1847a: 175, 1848: 7)

Strickland (1845) had given an account of "affinity" and "analogy" suggesting that

> ... as the relation between equivalent organs is one of real *affinity*, and forms the sole ground on which we assert the affinity of the whole beings, we may introduce the adjective *affine* or *homologous* in place of *analogous*, when referring to structures which essentially correspond in different organic beings. (Strickland 1845b: 358[10])
>
> These [analogies] consist in a similarity of external form and of function connected with it, but without that agreement of essence which constitutes *Affinity*. (Strickland 1845b: 360)

---

[10] Strickland had touched on the subject in his presentation to the 14th *British Association for the Advancement of Science* report (Strickland 1845a: 172, footnote) but at that time considered only the use of the word "affinity". Owen was present at this meeting (Athenaeum 1845: 841).

Owen and Strickland agreed on what constituted homology. Like Owen, Strickland's desire to clarify the words "affinity" and "analogy" was, in part, motivated by the prior tradition of using "affinity", "homology", and "analogy" interchangeably. Owen (1846) further clarified his use of the term "homology", discussing various aspects of its history. He also presented a description of "analogy", which differed from that given by Strickland (Owen 1846, Strickland 1846). As noted above, Owen allowed that comparisons could be at the same time analogous and homologous (the forelimb of man and the forelimb of monkey), analogous and non-homologous (forelimb of man and Cheliped of crayfish), or non-analogous and homologous (forelimb of man and the wing of a bird) (Table 9.1). Owen also understood analogy as relative:

> But "analogy" strictly signifies the resemblance of two things in their relation to a third. . . . (Owen 1849: xii)

In contrast, Strickland understood "resemblances" to be *either* homologous or analogous, with only homologous resemblances of any significance.

## 9.7 Homology and Relationship

We noted above that Woodward used the term "relationship" in two quite different ways, one that simply meant "perfect resemblance", irrespective of what perfect resemblance meant. Woodward's second use of "relationship" is best illustrated by an example (taken from Strickland 1840; Table 9.1, who borrowed the example from Swainson 1835).

Westwood argued that all living beings are "connected" by "affinity" at some level. For example:

> The swallow and the martin are two birds belonging to the same genus (*Hirundo*), and resembling each other in the greatest possible number of their essential characters; they are therefore allied together by an affinity of the first or highest degree. (Westwood 1840a: 143)

Tracing the relationships of organisms would require identification of other affinities but more and more remote than those of the "first or higher degree".[11]

> In like manner the dragon-fly and the bat, as *animals*, must possess a common relation of affinity when compared with *vegetables* (the catch-fly plant [*Dionaea*, Table 9.1] for

**Table 9.1** Comparison for four "organised beings" according to Westwood (1840a)

| Character | Goatsucker | Bat | Dragon-Fly | *Dionaea* | Inorganic Matter |
|---|---|---|---|---|---|
| **Affinity** | Organised | Organised | Organised | Organised | — |
| **Affinity** | Animal | Animal | Animal | — | — |
| **Affinity** | Vertebrate | Vertebrate | — | — | — |
| **Analogy** | | **Bat** | **Dragon-Fly** | | |

---

[11] Blyth (1835) and Waterhouse (1843: 411) developed the idea of a "degree of affinity", linking it directly with the taxonomic hierarchy.

> instance). And even between animals and vegetables as compared with inorganic matter, there must be a relation of affinity founded upon the circumstance of their organized structure. (Westwood 1840a: 144, 1840b: 306)

Affinity, then, was tied exclusively to, and determined by, the nature of the relationship. One might easily comprehend the idea by inspection of Table 9.1. The first taxonomic level includes all "Organised Beings" (the Goatsucker, the Bat, the Dragon-fly and the "catch-fly" plant) but excludes "Inorganic Matter"; the second level includes all "Animals" (the Goatsucker, the Bat, and the Dragon-fly) but excludes the "catch-fly" plant and "Inorganic Matter"; the third taxonomic level includes "Vertebrates" (the Goatsucker, the Bat) but excludes the Dragon-fly, the "catch-fly" plant, and "Inorganic Matter". On the other hand, analogy recognises a different kind of relationship, rather than a different kind of "resemblance":

> Here then we find the bat and the dragon-fly, belonging to different sub-kingdoms of the animal kingdom (or next higher group), and we have already seen that as compared together with reference to the objects of the other next higher group (that is the vegetable kingdom), an affinity exists between them; but if, on the other hand we regard the relations of the bat with any other animal belonging to the same sub-kingdom as itself (*Vertebrata*, the goat-sucker for instance), we find the relation between bat and the dragon-fly to be so comparatively remote, that we term it a relation of analogy. (Westwood 1840a: 144)

Strickland dealt with the same example but focused on a different aspect, primarily because he regarded "affinity" and "analogy" to apply to "equivalent organs" rather than "equivalent organisms". Thus, he considered Westwood's reasoning fallacious, as he had "… not attended to the distinction between essential and non-essential characters" (Strickland 1840: 225). That is, in his view, Westwood did not pay sufficient attention to the nature of the characters considered for each kind of grouping: He did not identify which characters indicate "affinity" and which "analogy"; he did not say what actual characters were required to be a Vertebrate, an Animal, and an Organised Being (Di Gregorio 1987). Strickland advanced his argument by adding another character, "fly-catching", to demonstrate analogy (Table 9.2); even though "fly-catching" is a property of all the organisms in Table 9.2, it does not indicate their affinity. Hence, for Strickland, "… the whole process of classification consists in observing the affinities of structure in different beings, in estimating their importance, and in arranging them according to that estimate" (Strickland 1846: 359).

Consideration of Tables 9.1 and 9.2 suggests that Westwood and Strickland were addressing different aspects of the "natural system". If appropriate modern terminology were to be applied then in the case of groups (organisms), Westwood's argument

**Table 9.2** Comparison for four "organised beings" according to Strickland (1840)

| Character | Goatsucker | Bat | Dragon-Fly | Dionaea |
|---|---|---|---|---|
| **Affinity** | Organised | Organised | Organised | Organised |
| **Affinity** | Animal | Animal | Animal | — |
| **Affinity** | Vertebrate | Vertebrate | — | — |
| **Analogy** | Fly-catching | Fly-catching | Fly-catching | Fly-catching |

is "affinity" = monophyly and "analogy" = non-monophyly; in the case of characters (organs), Strickland's view is "affinity" = homology and "analogy" = non-homology (Table 9.3). Neither view conflicts.

**Table 9.3** Summary of Westwood's and Strickland's views on affinity and analogy

| | Affinity | Analogy |
|---|---|---|
| **Westwood (Groups)** | Monophyly | Non-monophyly |
| **Strickland (Characters)** | Homology | Non-homology |

Owen understood the nature of this distinction:

> "Affinity", as first defined by MacLeay in contradistinction from "analogy", signifies the relationship one animal bears to another in its structure, and is the closer as the similarity of structure is greater. Swainson illustrates this idea by comparing a goatsucker with a swallow and with a bat [cf. Tables 9.1 and 9.2]: with the one its relation is *intimate*, with the other *remote*; the goatsucker has affinity with the swallow, analogy to the bat. (Owen 1859b: ixvii)

Westwood would probably have agreed with Owen's statement, but might have asked, "affinity" as what? This question would have provided a different answer. The goatsucker and the swallow have "affinity" as birds, the goatsucker and the bat have "affinity" as vertebrates. But Owen saw another distinction:

> But the idea of the foregoing intimate relation of entire animals, called "affinity", is different from the idea of the answerable relation of parts of animals called "homology". Animals, however intimately "affined", are never the same in the sense in which homologous parts are so esteemed: they could never be called by the same name, in the way or sense in which a bone, for example, of the fore-limb, is called "humerus" in the goatsucker, swallow, and bat. (Owen 1859b: ixvii)

But why not? The goatsucker, swallow, and bat *are* called the same thing: Vertebrates. Owen and Strickland both tied their understanding of homology (affinity) to the idea of a type, imaginary or otherwise; in Owen's case this became his archetype. Owen tied his understanding of homology to his archetype, and his efforts were to elucidate the archetype for each major group of organisms and for each organ system (Panchen 1994: 36). MacLeay and Westwood tied their understanding of homology (affinity) to the relationship specified by the natural system, to discover all natural groups.

## 9.8 Homology, Analogy, Parts, and Wholes

Owen recognised, as did all other anatomists, that the first stage in effective comparison of organisms was to identify the parts that might reasonably be considered the same, even though they may differ, on the basis of "essential resemblances". The parts are **homologues** and may share relationships of both form and function. For Owen, the determination of precise relationships of form was achieved only through the archetype. These relationships are **homology**. For Owen, the determination of relationships of function was more practical. These relationships are **analogy**. Homology and analogy were not opposites, as both involved discovering the same parts, the homologues.

Strickland also recognised two kinds of comparisons: “essential resemblances”, representing **affinity**, and “non-essential (mere) resemblances”, representing **analogy**. The determination of the relationships of form was achieved only through an understanding of the natural system. Homology and analogy were opposites.

Westwood recognised that while “essential resemblances” were discoverable, their meaning was established only by the relative nature of the comparisons: “Affinity” as what? “Analogous” as what?

These views are summarised in Table 9.4. Column 1 identifies the relevant parts (homologues), recognised by comparisons of one kind or another; column 2 identifies the relationship of form and its applications to either organs (homology) or organisms (monophyly); column 3 identifies the relation of a function and its application to organs (analogy); in the case of Strickland and Westwood, the relation is a negative one, a “non” relation of form.

All authors recognised the importance of “essential resemblances” in discovering homology, regardless of how “essential” was defined. There was, however, disagreement over the meaning of homology as a relation. As Owen’s concept of homology became more widely used, the *relation* of special homology and the *determination* of homologues become blurred, as if the two really were the same. It is more appropriate—in fact, essential—to keep them separate. As Nelson recently wrote: “It should be clear, however, that homology, in general or in particular, is a relationship between homologues … and not simply the homologues themselves” (Nelson 1994: 120).

Subsequent history reveals much discussion on **criteria** for recognising homology, which appear to be criteria for recognising homologues; the difference is significant. If criteria for determining homology are really criteria for determining homologues (“essential resemblances”), how, then, can the relation of homology be studied? Two approaches come to mind:

1. Investigation of the possible causes of the “sameness” of the homologues
2. Investigation of the possible meaning of relationship

**Table 9.4** Comparison of the “systems” of Owen, Strickland, and Westwood

| | “Resemblances” | | |
|---|---|---|---|
| | Criteria “Observation” (Homologues) | Relation Affinity/Homology | Relation Analogy |
| **Owen (1843, 1849)** | “Comparisons” | Relations of form (organs) | Relations of function (organs) |
| **Strickland (1840)** | “Essential resemblances” | Relations of form (organs) | Non relation of form (organs) |
| **Westwood (1840a)** | “Perfect resemblances” | Relations of form (groups) | Non relation of form (Non-group) |

Criteria for discovering homologues, as outlined by Owen, were well known then and have been discussed at length ever since. Yet the notion of homology as a “relation” or “relationship” remained free for interpretation—and, after Darwin, that interpretation mostly took the form of investigating the causal aspect to discover how homologues came into being. For “homology”, Strickland and Owen saw understanding residing in the “uniformity of plan” rather than the “relative relationship” of Westwood and MacLeay.

Perhaps it is not that odd to note Owen’s version prevailed because—ironically—it paved the way for an evolutionary interpretation of the origin of structures, their transformation from one condition to another, by converting the archetype into an ancestor (Russell 1916). The result was that homology assumed a “dynamic” aspect, one of transformation, of change, however conceived. As Bather put it many years later:

> The chief difference that the acceptance of evolution made to morphology was to substitute a rational for a transcendental basis. It changed the meaning of “affinity” (from “resemblance” to “blood-relationship”), but did not suggest a way of detecting affinity. It encouraged phylogenetic speculation without providing a touchstone for the hypothesis. “Ancestral form” was but old “Archetype” writ large, or, more precisely, turned from a professed abstraction into a presumed concrete existence. (Bather 1927: lxxxii, Russell 1936, Amundson 1998)

The search for *the* natural method of classification was never really resolved, effectively being abandoned in favour of other more easily determined “systems” (Nelson & Platnick 1981). Investigations into the discovery of “natural classifications” resurfaced for a short time during the Cladistic “revolution” (Nelson 1979) only to fade yet again, without solution, silently submitting to the onslaught of methodologies from the numerical systematists and the overload of data from DNA sequencing, “witness[ing] the re-emergence, even the vindication, of phenetics as the overall similarity of synapomorphy” (Nelson 2004: 139).

# Chapter 10

# Homology and Transformation

> "'Transformation' naturally refers to real historical processes of evolution, and not to the possibility of formally deriving characters from one another in the sense of idealistic morphology." (Hennig 1966a: 93)
>
> "'Transformation' in this context does not refer to a real process because organs do not become transformed directly into each other. . . ." (Sattler 1984: 390)

## 10.1 The Process of Change

While the general notion of "transformation" between parts of organisms pre-dates Darwinian thought (Appel 1987, Desmond 1989, Laurent 1997, 2001), the idea that some kind of transformation has *actually* occurred between homologues remained attractive. The nature of that "transformation" remains a matter of some debate (Rieppel 1988, Brady 1994a, 1994b, Bang et al. 2002, Scotland 2000b, Laubichler 2000): Transformation has been considered *a hypothesis, a theory*, or even *an observation* that "relates" any two (or more) homologues. In this sense, "relate" is used in the sense of one homologue changing into or becoming another (as in, for example, Figure 10.1).

Although transformation has been considered from a variety of different viewpoints, we have partitioned it into two "kinds": **material transformation** and **logical transformation**.

Material transformation deals with hypotheses of transformation that are considered to result from actual (or possible) mechanisms of change. It may be subdivided into **Phylogenetic Transformation** and **Ontogenetic Transformation**. Both deal with the transformation process relative to time. To many, consideration of the *mechanisms* of transformation is thought to lead to the discovery of the *causal* aspect of change, thus turning sets of homologues (the parts) into the relation homology—that is, to ultimately understanding how one homologue "changes" into another is said to discover the "real" meaning behind similarities among organisms.

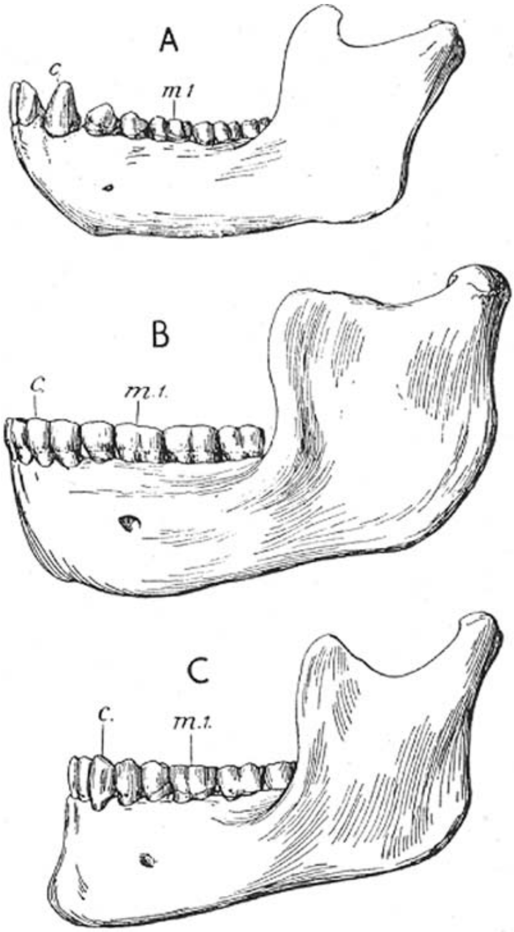

**Fig. 10.1** After Le Gros Clark (1949: 89, Fig. 30, reprinted with permission)

Logical transformation deals with structural identity, in terms of how one might judge and equate various parts of organisms and thereby determine their relationships and the relation of homology at one and the same time.

## 10.2 Material Transformation

### 10.2.1 Phylogenetic (Historical) Transformation

A modern interpretation of historical transformation between homologues was given by Darwin:

> Naturalists frequently speak of the skull as formed from metamorphosed vertebrae; the jaws of crabs as metamorphosed legs, the stamens and pistils of flowers as metamorphosed

> leaves. … Naturalists, however, use such language only in a metaphorical sense; they are far from meaning that during a long course of descent, primordial organs of any kind … have been converted into skulls and jaws. Yet so strong is the appearance of a modification of this nature having occurred, that naturalists can hardly avoid employing language having this plain signification. *On my view these terms may be used literally*.… (Darwin 1859: 438–439, our italics; see Brady 1994a, 1994b)

By "literally", Darwin means that the homologues have changed and skulls are "metamorphosed vertebrae", the jaws of crabs are "metamorphosed legs", the stamens and pistils of flowers are "metamorphosed leaves"; and that the transformation has taken place over long periods of time:

> … 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: 404)

Ernst Haeckel immediately picked up on the importance of Darwin's words for "natural classification" (see later):

> The real relations which unite all and extinct organisms in one or other of the principal groups of the natural system, are genealogical: their relationship in form is blood-relationship.… (Haeckel 1866; translation from Russell 1916: 250)

Homology provides the evidence that reveals the real relations; real relations are genealogical; genealogy is represented in the "principal groups of the natural system". Given this viewpoint, E. Ray Lankester saw the need to redefine homology in terms of phylogenetic change:

> It is less likely to cause confusion if we have a new term than if we amend an old one, which is my reason for not retaining "homology". (Lankester 1870a: 42)

The puzzle was how to *explain* parts of organisms that were considered the same:

> But how can the sameness (if we may use the word) of an organ under every variety of form and function be established and investigated? This is, and always has been, the stumbling-block in the study of homologies without the light of evolutionism.… (Lankester 1870a: 35)

Lankester sought the explanation of "sameness" in history:

> Without doubt the majority of evolutionists would agree that by asserting an organ A in an animal a to be homologous with an organ B in animal α they mean that in some common ancestor γ the organs A and B were represented by an organ C, and that α and β have inherited their organs A and B from γ (Lankester 1870a: 36)

Lankester suggested a new terminology for these relations, proposing "homogeny" for "… structures which are genetically related, in so far as they have a single a representative in a common ancestor …" (Lankester 1870a: 36) and "homoplasy" for "When identical or nearly similar forces, or environments, act on two or more parts of an organism which are exactly or nearly alike, the resulting modifications of the various parts will be nearly or exactly alike" (Lankester 1870a: 39).

Lankester's intention was to rid biology of the word "homology" because of its Platonic associations in the hands of Richard Owen and instead place it in the new historical context.

St. George Mivart, a defender of Owen (Mivart 1893), swiftly replied:

> . . . but I contend that it is desirable to retain the word "homology" also, and that in the very sense Professor Owen gave to it—namely, a close resemblance of parts, to whatever cause that resemblance may be due, whether genetic or otherwise.
>
> Mr. Lankester's terms will be useful additions to be employed when it is possible to determine to which process any given resemblance is due, i.e. whether it is a homogenetic or homoplastic homology. (Mivart 1870: 115)

For homogeny, Mivart identified two different kinds: ancestral and developmental homogeny, the former equivalent to Lankester's homogeny, and the latter for "parts which go through a process of development which is similar in the two individuals" (Mivart 1870: 116).

Mivart thus separated out the two most frequently suggested causes for homology, ontogeny and phylogeny, and left Owen's homology as a generic term simply meaning "the close resemblances of parts". Lankester (1870b) immediately replied to Mivart, stressing that he really meant homogeny to be applied *only* to those similar structures "caused" by ancestry and not to any other kind of cause of similarity. Nevertheless, these exchanges mark the beginning of the obsession with causes of change, with the material transformation between homologues being taken as a given. Of course, it was evident to many early morphologists that transformation *did* occur as organisms, as well as their parts, do indeed develop.

### *10.2.2 Ontogenetic Transformation*

Darwin was quick to incorporate Lankester's new terminology into the sixth edition of the *Origin*:

> But morphology is a much more complex subject than it at first appears, as has lately been well shown in a remarkable paper by Mr. E. Ray Lankester, who has drawn an important distinction between certain classes of cases which have all been equally ranked by naturalists as homologous. He proposes to call the structures which resemble each other in distinct animals, owing to their modification, *homogenous*; and the resemblances which cannot thus be accounted for he proposes *homoplastic*. (Darwin 1872: 385)

The sixth edition of the *Origin*, for the first time, included a glossary, provided by W.S. Dallas.[1] Oddly enough, the glossary included a definition of homology but not homogeny. Part of the glossary definition of homology was

> that relation between parts which results from their development from corresponding embryonic parts.. . . (Darwin 1872: 434[2])

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[1] The glossary was possibly added at the suggestion of Darwin's publishers (Peckham 1959), as the sixth edition was to be a popular, more accessible version (Freeman 1976). Darwin had written "... several readers have complained to me that some of the terms used were unintelligible to them" (Darwin 1872: 430).

[2] The full definition read: "That relation between parts which results from their development from corresponding embryonic parts, either in different animals, as in the case of the arm of man, the foreleg of a quadruped, and the wing of a bird; or in the same individual, as in the case of the fore

This definition is in complete contrast to the passages Darwin rewrote in the *Origin* to accommodate Lankester's homogeny—causing Gavin De Beer, some years later, to exclaim, that "... is just what homology is *not*" (De Beer 1971: 14).

While Lankester was busy adapting homology to fall in line with recent evolutionary thinking, Gegenbaur was undertaking the same in Germany (Gegenbaur 1874). Gegenbaur, a friend of Ernst Haeckel, had recently embraced wholeheartedly the evolutionary perspective for morphological studies, helping to create an evolutionary morphology. While the first edition of his *Grundzüge der Vergleichenden Anatomie* (Gegenbaur 1859) was heavily influenced by a previous generation of "ideal" morphologists, the second edition would be recognised as a classic in evolutionary morphology (Gegenbaur 1874). In this second edition, Gegenbaur wrote that "homology" is the name given

> ... to relations which obtain between two organs which have had a common origin, and which have also a common embryonic history. (Gegenbaur 1874, 1878: 64; see also Hubbs 1944: 305)

Gegenbaur included both a common (historical) origin *and* a common embryonic history to explain the "sameness". The contemporaneous exchanges between Lankester and Mivart characterise a long-running conflict between the role of the two most commonly proposed causes of homology—when understood in terms of actual transformations—ontogeny and phylogeny. And Gegenbaur (as well as Dallas in Darwin's final edition of the *Origin*) managed to mingle (or, perhaps, mangle) both into one single definition of homology.

Yet ontogeny has been seen as a decisive criterion by many commentators over many decades, starting with Geoffroy St. Hilaire, if not earlier. Løvtrup (1978) summarised the general viewpoint with what he named "Naef's theorum", after Adolf Naef, an early 20th-century morphologist (see Chapter 5):

> Morphogenetic processes of an ontogenetic stage through whose modification a following stage arises are to be looked upon as phylogenetically older than those which grew out of them. (Naef 1931b: 15, translated in Holmes 1944: 326, Løvtrup 1978: 350, Wiley 1981, Bonde 1984: 231)
>
> Parts "that have been given a stage of development, with regard to a particular morphotype, remain, with regard to the latter, homologous throughout all subsequent transformations." (Naef 1919, translation in Zangerl 1948: 368)

Naef's comments relate to single characters and their development; thus, it may be understood as an early approach to "character phylogeny" (see below and Chapter 5). Understood as a way of relating homologues, rather than determining some historical connection, "the mode of development itself is the most important criterion of homology" (Nelson 1978b: 335)—as indeed it seems always to have

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and hind legs in quadrupeds, and the segments or rings and their appendages of which the body of a worm, a centipede, &c., is composed. The latter is called serial homology. The parts which stand in such a relation to each other are said to be homologous, and one such part or organ is called the homologue of the other. In different plants the parts of the flower are homologous, and in general these parts are regarded as homologous with leaves."

been. But, as will be seen below, we need to alter one word: “the mode of development itself is the most important criterion of homologues.”

Homology, as a relation, is more than just the homologues (Nelson 2004).

### *10.2.3 Material Transformation and the Conflict of Causes*

In the 1940s, Alan Boyden published an essay commemorating the 100th anniversary of Richard Owen’s original clarification of the term “homology” (Boyden 1943). Boyden appealed for a return to Owen’s original usage, which he (Boyden) understood as an aid to discovering close resemblances or “real” similarity. Boyden understood Owen’s “homology” as being wholly determined by stated criteria—“relative position and connection of the parts”, criteria stated most clearly by Geoffroy St. Hilaire (1818)—representing, in part, the earlier viewpoint of Mivart. Assuming Lankester’s role in this new version of the old debate, Moment responded:

> The basic distinctions among the similarities of plants and animals would rather seem to be those based on (1) developmental, (2) genetical and (3) evolutionary differences. (Moment 1945: 453)

Moment’s intention was the same as Lankester’s: to identify and separate out the different possible causes for “sameness” and to indicate their use as an aid to discovering the real relations among the parts. The only difference between the list presented by Moment and that presented by Mivart is the addition of genetics as a category distinct from evolution—genetics being unknown as a separate discipline in Mivart’s time. Not surprisingly, the basis of Moment’s argument was identical to Lankester’s:

> The word homology had perhaps best be discarded as too charged with metaphysical overtones and a neutral descriptive term like similarity substituted. (Moment 1945: 455)

Like those before him, Moment suggested a new terminology to deal with these different causes (Table 10.1). While Moment’s terminology was somewhat idiosyncratic relative to the use some of these words had previously been put (see Haas & Simpson 1946 and Hubbs 1944, for a review of the more conventional use of these terms), they do provide a way of understanding the nature of the problem as Moment (and others) saw it. That is, in their view, similarities can only really be understood in terms of their cause, be that historical, developmental, or genetical (Table 10.1). And that once those causes were understood, there would, of course, be no need for the term “homology”, which left the cause of “sameness” mysterious and unknown and was best left called simply “similarity”.

**Table 10.1** Causes of homology (after Moment 1945: 455)

| | Causes | | |
|---|---|---|---|
| | **Developmental** | **Genetic** | **Evolutionary** |
| **Similar** | Homodynamic | Homogenetic | Homophyletic |
| **Dissimilar** | Heterodynamic | Heterogenetic | Heterophyletic |

## 10.3 Logical Transformation

> "… the most recent English language literature has almost entirely overlooked the methodological nature of the *concept* [of homology] and dealt primarily with the causality of the *phenomenon*.…" (Zangerl 1948: 362)

Whatever Gegenbaur wrote concerning the twin causes of homology, he, like many others, continued to perform his morphological studies in much the same way as he did before the concept of evolution was accepted; by detailed comparison of the parts and then inferring common descent from those parts deemed the "same" (Russell 1916: 266). Eventually many biologists tired of the excessive "phylogenetic" speculations of Haeckel and Gegenbaur and activated a re-examination of the principles of the pre-Darwinian morphologists. Instrumental in this move was Oscar Hertwig (1906), who claimed to have identified a certain circularity in the evolutionary conception of homology (an argument which was to be much repeated). Hertwig argued from a critique of Haeckel's biogenetic law and suggested that similarities in early development did not necessarily point to common descent—yet neither did similarities when compared otherwise. He suggested returning to the pre-evolutionary viewpoint, that homology was to be regarded as some kind of "special similarity" untainted by any particular theory of cause.

This renewed consideration of pre-evolutionary morphology inspired a new generation of European morphologists who attempted to expand and develop the earlier programme (see Chapter 5). These biologists, perhaps wrongly called "Idealists", developed and enhanced some of the principles outlined by the pre-evolutionary "ideal" morphologists, developing what they called systematic morphology.[3] Zangerl gave a clear account of their views on homology (a viewpoint similar to that of Hertwig):

> … an individual homology between two or more organisms is indicative of neither of these possibilities [common ancestry or homoplasy], but merely postulates a particular relation between the compared parts, a relation that we call homology. (Zangerl 1948: 363)

This viewpoint does indeed bear strong similarity to those of the pre-evolutionary morphologists. Here, we call this approach "logical", as it depends on establishing the relations among the parts rather than determining the causes of any "sameness". Rieppel has proposed something similar:

> The recognition of a character constitutes a conjecture of similarity, establishing a relation between appearances or, in a more practical sense, it corresponds to a group. (Rieppel 1988: 68)

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[3] Most of this work was published in German journals and was to a large extent ignored by the wider world. Elsewhere we cover their ideas in more detail (Chapter 5, a major source of denigration was Mayr 1982a, who helped promote the attitude that much of their thinking was pre- or even non-evolutionary. For more informed commentary see, for example, Blacher 1968, Triennes 1989, Reif 1998, Boletzky 1999).

While Rieppel suggests that characters establish a “relation” between “similarities”, he makes clear an additional property: the correspondence of those “similarities” with a group (a taxon). Much of Rieppel’s later work has focused on quantifying “essential similarity”, or at least attempting to clarify its theoretical basis:

> … that in order to “observe” similarity and therewith pattern in the first place, a theory and method is required about what biologically meaningful similarity is or can be. The “recognition” or conjectures of homologies … depends on the “principe des connexions” of Etienne Geoffroy Saint-Hilaire … i.e. on a fixed map … which provides the frame for the recognition of topographic relationships. (Rieppel 1987: 416; ellipses represent omitted references)

Rieppel’s main point is that

> Something must be added to the observation of similarity which guides this observation (since theory free observation is non-existent) but must be justified outside the context of one character testing the other [i.e., congruence]. (Rieppel 1994: 70)

“Something must be added.” For Rieppel, that something is *topology*, the relation of the parts to the whole (Rieppel 1994)—similar, in some ways, to the views of Naef (1919) and the other systematic morphologists.

## 10.4 Generalised Causes

The connection between homology and developmental biology (or ontogeny) has roots that go deep into history (see above and Hall 1992, 1995, 1998). As a cause of homology, development (and ontogeny) has vied for prominence with the historical interpretation. A recent proposal is Wagner’s “biological homology”:

> The historical homology concept explains why the distribution of homologous characters among recent species forms a set of nested sets, but relies as much on an unexplained notion of sameness as did Owen’s original definition of structural identity. (Wagner 1994: 278)

Wagner distinguished his “biological” concept from the historical concept, the latter being “defined by historical continuity from a common ancestor” (Wagner 1989: 51) and the former as

> Structures from two individuals or from the same individual are homologous if they share a set of developmental constraints, caused by locally acting self-regulating mechanisms of organ differentiation. (Wagner 1989: 62, 1994: 275)

While the historical concept refers to genealogy (common ancestry), the biological concept was created to account for any current biological processes that might explain the “sameness” between homologues.[4]

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[4] Again terminology becomes confusing. Because Wagner’s biological homology relied heavily on development, Hall (1992) suggested “developmental” homology—similar, perhaps, to Kluge’s “ontogenetic” homology (Kluge 1988: 94). It might be fair to regard these three (biological, developmental, ontogenetic) as synonyms.

Roth's papers on homology apparently inspired Wagner's biological homology concept. Roth provided the following definition of homology:

> . . . homology is a correspondence between two or more characteristics of organisms that is caused by continuity of information. (Roth 1988: 2, 1994: 305, Mindell 1991: 897)

Her definition of homology had its origin in two earlier but similar ideas, intended to cover the many different sorts of similarity and their many different kinds of causes:

> . . . homology can be defined, in a quite general way, as correspondence caused by continuity of information. (Van Valen 1982: 305)
> Homologien sind nicht zufallige Ubereinstimmungen komplexer Strukturen, die auf gemeinsamer Information (im Sinne von Instruktion = Information von funktionaler Bedeutung; nach Eigen) beruhen. (Osche 1973, 1975, 1982: 21,[5] Sudhaus 1980)

Van Valen and Osche (and Roth) link two quite different aspects: generalised similarity ("correspondence") and generalised cause.

Wagner's concerns do not differ much from those discussed above. That is, homology might indeed be *explained* by common ancestry, but the remaining "unexplained" part was the mechanism responsible for the "sameness". Investigation of those mechanisms would reveal the "true" nature of homology. If this time around Wagner was Mivart, then Olivier Rieppel was to be Lankester:

> The confusion manifest in the claims put forward by the authors quoted above [Wagner 1989, Minelli & Peruffo 1991] results from a neglect of a concept, available to comparative biology for over a hundred years, and allowing to distinguish homology from homodynamy. (Rieppel 1992: 710)
> . . . homodynamy would correspond to Wagner's (1989) concept of biological homology.. . . (Rieppel 1992: 711)

Rieppel wanted to reserve homology for Wagner's historical homology—with a different terminology, to be sure, but much like Lankester's early account. Yet Rieppel's argument can be turned on himself, and one may declare that there has also been a word available for 100 years distinguishing homology from phylogenetic homology: Moment's (or Haeckel's) homophyly (Table 10.1) or Lankester's homogeny. Indeed, Rieppel had previously suggested that Lankester's terminology might benefit from revival:

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[5] There are two published English translations of Osche's definition of homology: "Homologies are non-random similarities of complex structures which are based on common genetic information (in the sense of instruction)" (Osche 1982: 21, translation from Hazsprunar 1992: 14); "Homologies are non-causal correspondences between complex structures sharing a common informational background" (Osche 1982: 21, translation from Minelli & Peruffo 1991: 432). Osche (1973: 164) provided an earlier definition: "homolog sind ... Strukturen, deren nicht zufallige Ubereinstimmung auf gemeinsamer Information beruht", which Schmitt (1995: 426) translated as follows: "homologous structures whose non-incidental resemblances are based on shared information". Hazsprunar simplified the idea by stating that "Homology can best be defined as a similarity in structure or patterns caused by continuity of information or instruction" (Hazsprunar 1992: 21; see also Collazo & Fraser 1996: 248).

> It would indeed appear advantageous to return to Lankester's (1870) clear-cut terminology, were it not for the universal use, in modern biology, of the term "homology" in an evolutionary context. (Rieppel 1988: 58; see Simpson 1959)

The issue masks much more than simple terminological squabbles. The majority of post-Darwinian arguments developed along one line: attempts to find the causes of the "sameness" of homologues: Lankester (homology explained by common ancestry) versus Mivart (homology is similarity), Moment (homology explained by various causes) versus Boyden (homology is similarity), to Wagner (homology is explained by developmental mechanisms) to Rieppel (homology is explained by common ancestry).

## 10.5 Transformation Revisited

Hennig's views on homology and character phylogeny can be summarised by two steps: First, criteria are used to establish whether features (characters) are sufficiently "similar" to be considered homologues; second, polarities (directions of change) are assigned to those features (Hennig 1953), the latter identified as "character-phylogeny". Hennig's was influenced by the botanist Walter Zimmermann (Hennig 1966a: 95[6]), prefacing his section entitled "Rules for Evaluating Morphological Characters as Indicators of Degree of Phylogenetic Relationship" with a quotation:

> Evolution is a transformation of organisms in form and mode of life through which the descendants become different from their ancestors. (Zimmermann 1953, translation from Hennig 1966a: 88)

In 1934 Zimmermann presented a short summary of his ideas on "character phylogeny":

> Formerly the main aim of phylogenetists was in most cases undoubtedly the "genealogical tree". … *But this research on phylogeny of species is not the only phylogenetical science* … there are phylogenetical assertions which are entirely independent of these great difficulties of the "phylogeny of species". They are the assertions on the "*phylogeny of single characters*". … It must not be forgotten that the causal-phylogenetical problems which are usually discussed under the catch-word of Darwinism-Lamarckism equally do not refer to the more statistically oriented research on "phylogeny of species", but treat questions of a rather kinetically and dynamically oriented research on "phylogeny of single characters". (Zimmerman 1934: 381–382, 384)

Zimmermann referred to the phylogeny of single characters as "semophyletik or Merkmalsphyletik" (1934: 382), a term he first used in 1930 (Zimmermann 1930: 11, 26, 427, Zimmermann 1931: 98, 1001) and characterised by Meeuse as

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[6] Zimmermann's principal works were published in 1930, 1931, 1953, and 1967. For further comment on Zimmermann, see Stevens 1980: 342, Humphries & Chappell 1988, Craw 1992: 74–76, Donoghue & Kadereit 1992: 81–82, Richter & Meier 1994: 215, and Hossfeld 1998: 199, 203–204; Zimmermann's contributions have frequently been ignored in accounts of the development of evolutionary thinking; see Rief (1998: 271).

> Merkmalsphylogenie or semophylesis sensu Zimmerman, “phylogeny of single features”, or organogeny sensu Lam. (Meeuse 1966: 12).
> … all elements forming a single uninterrupted semophylesis … [which is] an evolving sequence of organs. (Meeuse 1966: 40)

The concern of “character phylogeny” (*Merkmalsphylogenie* or semophylesis) is the causal aspects of evolutionary change in individual characters.

When Hennig discussed Remane’s criteria for establishing homology, he noted:

> … all three of his [Remane’s] “principal criteria” are only accessory criteria that we have to use because the real principal criterion—the belonging of the characters to a phylogenetic transformation series—cannot be directly determined. Remane’s second and third principal criteria are in reality only accessory criteria of lower rank that are not usable without the “criterion of sameness of position”. (Hennig 1966a: 94)

That is, to arrange characters in a meaningful series (Remane’s third criterion) requires knowledge of their similarity (Remane’s first and second criteria). To determine Remane’s third criterion, Hennig recommended using evidence from “ontogeny” or “palaeontology”—in other words, to “order” a sequence of characters determined to be similar, additional information is required. After his discussion of Remane’s criteria, Hennig then discussed “character phylogeny” in terms of “transformation series” and the relative terms “apomorphy” and “plesiomorphy”:

> We will call characters and character conditions from which the transformation started … in a monophyletic group plesiomorphous, and the derived conditions … apomorphous. … We will call the presence of plesiomorphic characters in different species symplesiomorphy, the presence of apomorphic characters synapomorphy, always with the assumption that the characters belong to one and the same transformation series. (Hennig 1966a: 89)

Characters belonging to the same transformation series are homologous:

> Different characters that are to be regarded as transformation stages of the same original character are generally called homologous. (Hennig 1966a: 93)

Hennig changed the nature of the problem from discovering homologues (characters) and determining their homology, into one of postulating how a series of homologues may have arisen. As Patterson (1983b: 21) succinctly commented years later, “… [t]he notion of character phylogeny is therefore one of transformation”. The central problem, as Hennig saw it, was how to read the direction of change, how to orient each transformation series—how to determine their polarity.

> If it can be shown that a character is homologous in a series of species, the question arises: In which direction is this transformation series to be read? (Hennig 1966a: 95)

Hennig’s “primitive” and “derived” conditions were linked by some notion of “transformation” allowing further development of the “literal transformation” interpretation, directly developing Darwin’s early suggestion (above).

Others viewed homology in a similar way. Ghiselin (1969) drew attention to what he understood as the relation between homology and similarity (Ghiselin 1966, 1969, 1981: 275, 1984: 217): “Homology is, by definition, correspondence between the parts. … This is what is meant when it is said that homology is not a kind of similarity” (Ghiselin 1969: 148; see also Eckhardt 1964, who also understood homology as correspondence). So what is Ghiselin’s relation of correspondence?

**Table 10.2** Discrimination of similarity and homology, according to Ghiselin. Column a after Ghiselin (1969: 148); the amino acids have been represented by their standard abbreviation and their three base codon added. Column b after Ghiselin (1976: 137); dealing with "entities composed of parts designated by letters ... labelled 1, 2 ,3, and 4 and are arranged according to 'how similar' they are..."

| a) | | b) | |
|---|---|---|---|
| **Peptides** | **Amino Acids** | **Entities** | **Parts** |
| **A** | [DVEMA] | 1 | a-b-c |
| **B** | [DPEMA] | 2 | a-b-d |
| **C** | [DPTMA] | 3 | a-e-d |
| **D** | [GPTMA] | 4 | f-e-d |
| **E** | [GPTY A] | | |
| **F** | [GPTY S] | | |

He presented an example of a series of six peptides each identified by a sequence of five amino acids and arranged in an aligned series (Table 10.2; Ghiselin 1969: 148; similar examples are given in Ghiselin 1976: 137 and 1997: 206).

According to Ghiselin, similarity is the relation between the individual peptides A–F: that is, A is similar to B, B is similar to C, C is similar to D, and so on (Table 10.2, column a). Homology is the relation between the parts. In this case the amino acid moieties, such that A is homologous to F in spite of there being no immediate similarity between them in terms of amino acids: DVEMA is wholly different to GPTYS. Ghiselin's later morphological example, of "entities composed of parts designated by letters ... labelled 1, 2, 3, and 4 and are arranged according to 'how similar' they are...", shows the same relation: Character ("entity") 1 is wholly different to character ("entity") 4 (Table 10.2, column b). For Ghiselin "... homology is neither identity nor synapomorphy; it is correspondence" (Ghiselin 1997: 207). Ghiselin's concerns address the issue of discovering the entities (parts) worth recognising as homologues—in that respect his proposals seem quite reasonable—certainly homologues can be identified as parts that are quite dissimilar. Nevertheless, Roth (1984: 20) and others *do* understand Ghiselin's "correspondence" as a kind of similarity and include both the terms "correspondence" and "similarity" in their criteria for establishing homology (as does Patterson 1988a; see Patterson 1982a and Rieppel 1984). Following Roth, "sameness", "similarity", and "correspondence" might all be thought of as much the same thing. But this oversimplifies the matter. Ghiselin's homology (as correspondence) resembles Remane's third criterion, the transitional criterion (discussed above),[7] and Rolf Sattler equated Remane's third criterion with the morphocline concept.[8]

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[7] "Remane's major criterion of connection through intermediate forms ... is valid if the intermediate forms are intermediate morphological conditions or intermediate developmental sequences." (Bock 1969: 416); "The third criterion permits to extend homologies based on the first and second one [Remane's two 'similarity' criteria]. It is of great value as it allows to establish homologies even between very dissimilar structures" (J. Remane 1983: 268).

[8] "In extreme cases this criterion [intermediate linking forms] leads to the homologization of the extremes of a morphological series (morphocline), even if they have nothing in common ..." (Sattler 1984: 384).

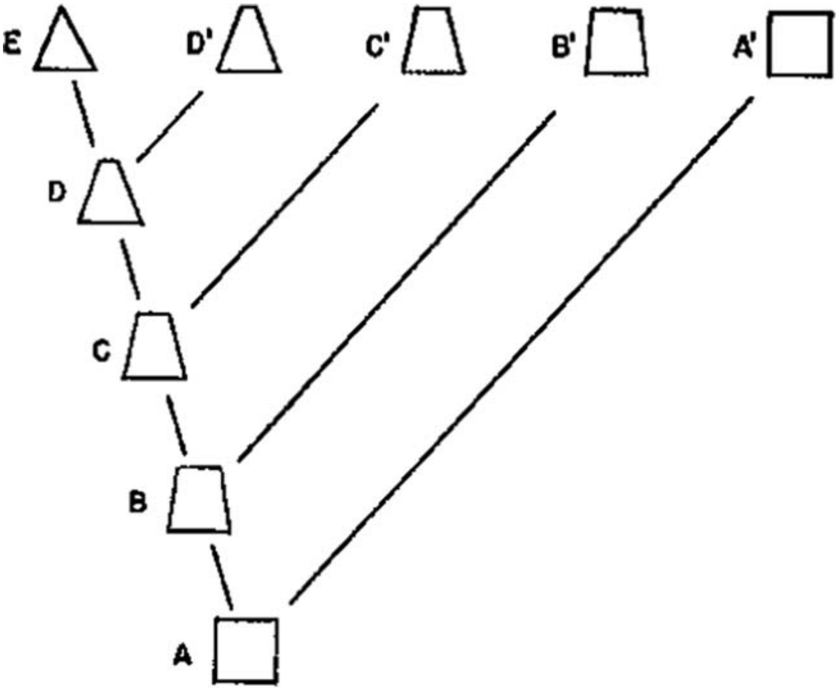

**Fig. 10.2** Diagram of a morphocline (Maslin 1952).

Maslin adopted the term "morphocline" to deal with changes in morphological structures that could be observed through detailed similarity considerations (Fig. 10.2). He used Huxley's (1938, 1939) term "cline"[9] to provide an evolutionary basis to his concept:

> To my knowledge no such term has been coined to describe such morphological clines. I propose, therefore, the term morpho-cline to include not only eco-clines and geo-clines as defined by Huxley but also those discontinuous clines remaining should the populations attain complete species status. (Maslin 1952: 52)[10]

Sattler (1984: 384) presented an example that has here been redrawn alongside one of Ghiselin's (Table 10.3a).

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[9] "Some special term seems desirable to direct attention to variation within groups, and I propose the word *'cline'*, meaning a gradation in measurable characters" (Huxley 1938: 219).

[10] Maslin's use of the "cline" terminology is but one manifestation of numerous suggestions attempting to document the "change" of one feature into another relative to some defined parameter: There have been ecoclines, geoclines, genoclines, chronoclines, ontoclines (Huxley 1938, 1939), choroclines (Simpson 1975), paedomorphoclines, peramorphoclines (Wake & Roth 1989: 373), morphocoenocline (Hohenegger 2006), generalised as phenoclines (Brand et al. 1972: 47; see Ross 1974: 179 and De Jong 1980; for an extensive discussion of the early use of morphocline, see Kluge 1971: 16-25; for historical background of the cline concept, see Winsor 2000, who discusses, among other things, the abandoned alternative term "phenograde").

**Table 10.3a** Discrimination of similarity and homology, after Ghiselin (1984: 384)

| | Properties (A–F) | | | | | |
|---|---|---|---|---|---|---|
| **Characters** | | | | | | |
| **1** | A | B | C | | | |
| **2** | | B | C | D | | |
| **3** | | | C | D | E | |
| **4** | | | | D | E | F |

**Table 10.3b** After Ghiselin (1976) and redrawn from Table 10.2, column a

| | Properties (A–F) | | | | | |
|---|---|---|---|---|---|---|
| **Characters** | | | | | | |
| **1** | A | B | C | | | |
| **2** | A | B | | D | | |
| **3** | A | | | D | E | |
| **4** | | | | D | E | F |

Sattler's example illustrates characters 1–4 composed of various combinations of properties, A–F. With successive changes, character 1 corresponds with character 4 but shares none of its properties; character 1 is composed of properties A, B, and C, and character 4 is composed of properties D, E, and F—they are entirely dissimilar but correspond. Comparison with Ghiselin's example shows that while the "beginning" and "end products" are the same as Sattler's (ABC –> DEF), the "routes" are different. Ghiselin's "correspondence" allows a variety of both similar and dissimilar structures to be usefully compared. In these examples, it can be seen how Remane's third criterion, the related idea of "intermediate" series, and the idea of "homology as correspondence" do indeed bear direct comparison with Maslin's (1952) "morphoclines".

From the perspective of "correspondence" and "sameness", if homology is considered as a series of features related by some process or notion of change, as represented in the diagrams of Ghiselin and Sattler, then they can be rendered dynamic by the simple addition of arrows. The arrows implicitly supply the notion of transformation: that A changes into B, B into C, and so on (Table 10.4).

The attempt to study characters as linear series of correspondences may be impossible, in the sense of having some reasonable empirical basis. The failure lies in the purely phenetic approach to homology, regardless of the fact that the similarities are placed in some specified or unspecified sequence. To some the entire enterprise of discovering "character phylogenies" is irrational and misconceived:

**Table 10.4** Discrimination of similarity and homology with the addition of "transformation" by adding a few arrows

| Characters | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **1** | A | → | B | → | C | | | | | | |
| **2** | | | B | → | C | → | D | | | | |
| **3** | | | | | C | → | D | → | E | | |
| **4** | | | | | | | D | → | E | → | F |

> The reason for a widespread insistence on 1:1 correspondence (i.e. either-or thinking) may be a fallacious transfer of genealogical reasoning to parts of organisms. Disregarding some complexities, we can say that two organisms either have a common ancestor at a certain level or they do not. However, this kind of reasoning does not apply to parts of organisms or characters (or character states) because there is no genealogical relation between parts of characters (and their states). (Sattler 1994: 464)

Sattler's words are of some interest, not least in that others have expressed similar views (Crow 1930, Boyden 1947, Inglis 1966,[11] Rieppel 1979; Hay & Mabberley 1994). The cladistic literature is diverse in its reaction to Hennig's "transformation series" and Maslin's (1952) "morphocline analysis". Some see a close relationship (e.g., Schaeffer et al. 1972: 32, Rieppel 1979, 1980: 84), others have questioned that equation (Gaffney 1979, Farris 1982, Sluys 1983, Wilkinson 1994), but enough have agreed with the equivalence to believe it has some substance (e.g., Pimentel & Riggins 1987: 201, Ax 1987: 134).

Terminology to one side, Ghiselin's "correspondence", Maslin's "morphocline", Zimmermann's "semophylesis", Hennig's "transformation series", and Remane's third criterion are similar if not identical efforts to account for the transformational aspect of single-character phylogenies, or at least to aid in the identification of the sequence in which the various homologues are believed to have changed. In a short history on character phylogeny, Rieppel (1979, 1980: 84) suggested that Louis Dollo (1895: 89) may have been responsible for the first example of "morphocline" analysis, while Panchen (1992) suggests W.S. MacLeay:

> … the test of a relation of affinity [homology] is its forming part of a transition continued from one structure to another by nearly equal intervals. (MacLeay 1821: 363, MacLeay 1825: 196; a passage of sufficient interest to Darwin that he had Syms Covington write it out for his future reference; see Di Gregorio 1996: 110)

MacLeay's "test" is not unlike the suggestions made today in popular "phylogeny" instruction manuals (Figure 10.3).

Nelson (2004) noted Hennig's borrowing from vertebrate palaeontology the term "specialization-crossings", derived from Othenio Abel's *Gesetz der Spezialisationskreuzungen*, a translation of Louis Dollo's *chevauchement des specialisations*. Nierstrasz (1936: figure on p. 674) used *evolution entre-croisée* and presented a figure that Hennig (1950: Fig. 31) reproduced (Figure 10.3). Nelson continued: "Hennig later switched to the term 'heterobathmy'—different steps on a stair … (from the Greek *bathmos*—a step or stair) … ", a term borrowed from Takhtajan (1959:11).

Nelson (2004) noted Hennig's borrowing of "character phylogeny" from botany, a concept that "evolved" into optimisation:

> … optimization does formally derive characters from one another—in an idealistic morphology of all formal transformations imaginable, and their reversals, in the hope that some

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[11] In fact, Inglis identified such "chains of homologies" as similar to those established using ontogeny, but noted that they are "... certainly not phyletic, neither are they phenetic. I suggest that they be called akoluthic" (Inglis 1966: 224). Needless to say, Inglis's rather cumbersome word did not gain favour.

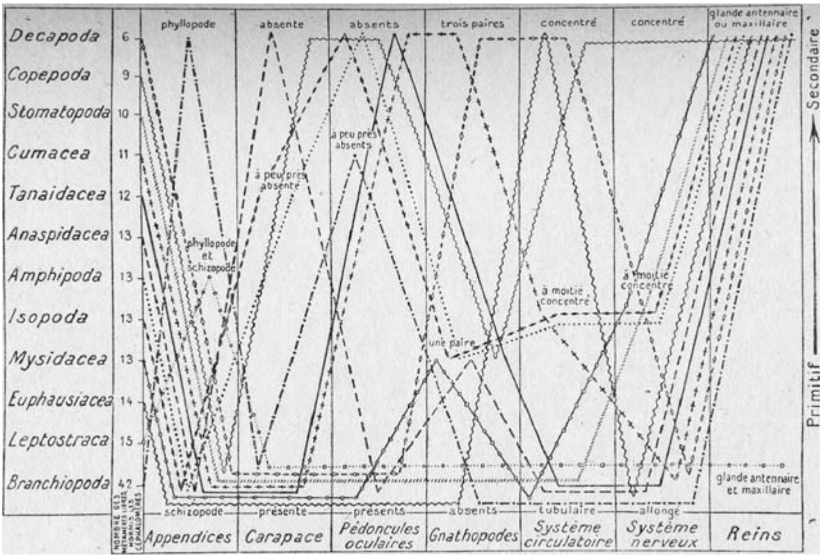
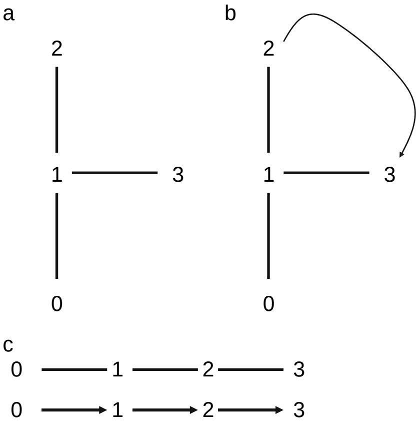


**Fig. 10.3** Reproduction of Nierstrasz's (1936) figure on p. 674 used to illustrate *evolution entre-croisée*. This figure taken from a reproduction in Hennig (1950: Fig. 31)

> might intelligibly reflect, and thereby approximate if not reveal, the "real historical processes of evolution"—whatever those processes might be.

Thus, the task facing systematists became not so much to "establish homologies" and discover relationships but to discover the sequence of "states" and then their "polarities" (as in the sequence between states in Figure 10.4). Systematic practise absorbed this message, as if it really was the central issue and one that might be solved to everyone's satisfaction by some as-yet developed technical innovation. And, like the initial stages of phenetic taxonomy, there were technical innovations aplenty—an endless supply, in fact.

**Fig. 10.4** Three examples of character-state transformations



# Chapter 11
# Character Conflict

“The way one views congruence is a reflection of the way one chooses to express agreement and disagreement among characters.” (De Pinna 1991: 381)

## 11.1 The Problem of Conflict

Probably the first attempt to tackle the issue of conflicting systematic data, at least in its numerical context, was Sokal & Sneath (1963; see also Mayr 1974: Fig. 30.6; our Figure 11.1), who explored what became known as “Hennig’s dilemma” (Felsenstein 1982: 381; or, as Farris & Kluge [1997: 216] preferred, “Felsenstein’s dilemma”):

> It is not clear how Hennig would handle contradictory data. . . . If one counted characters indicating one phyletic arrangement and those indicating another and took the verdict of the majority, this would be in effect employing phenetic affinities to indicate phyletic relations. (Sokal & Sneath 1963: 225–226)

More than 20 years later, Sneath saw no progress or possible resolution:

> Unless all characters are perfectly nested the synapomorphic method fails, because one must prejudge the issue by deciding which exceptions are the false synapomorphies. (Sneath 1988: 266; see also Sneath 1995: 287)

Felsenstein (1982) explored “Hennig’s dilemma” with some examples (Felsenstein 1982: 380; a similar example was presented in Felsenstein 1984: Table 11.1).

Felsenstein noted that

> Hennig takes each character as providing evidence for the existence of one monophyletic group in the phylogeny. (Felsenstein 1982: 380)

Taking just the first four characters in column a of Table 11.1, character 1 suggests the group AC, character 2 suggests the group ACE, character 3 suggests the group BD, and character 4 is uninformative (“makes no real contribution to the phylogeny”, Felsenstein 1982: 380). As a summary of these data, Felsenstein noted that one tree would suffice (Figure 11.2; Felsenstein 1982: Fig. 11.1).

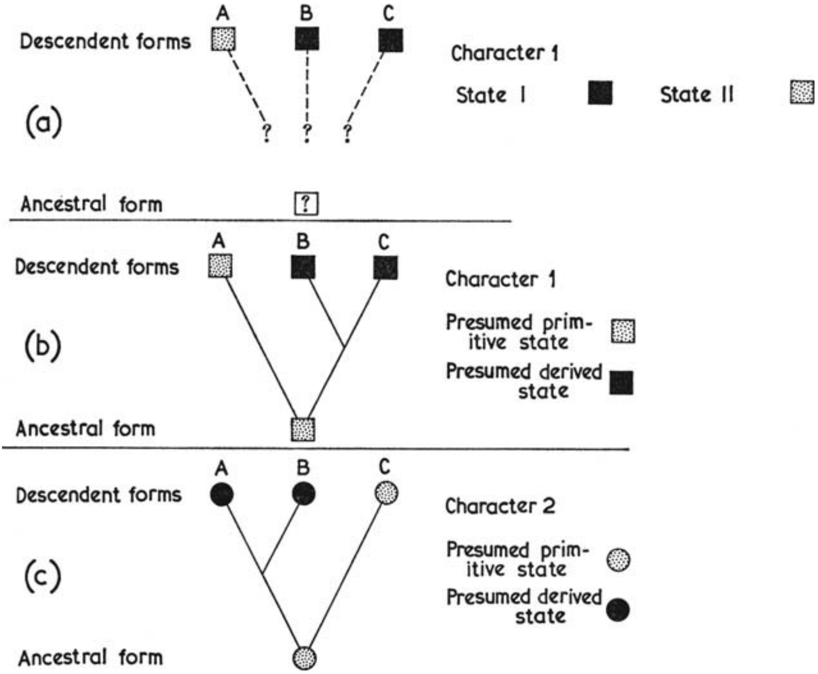


**Fig. 11.1** After Sokal & Sneath (1963: 225, Fig. 8.2)

The addition of characters 5 and 6 results in "Hennig's dilemma" as both these characters suggest the group BCE, which conflicts with the overall summary provided by characters 1–4 (Figure 11.2). Felsenstein noted that

> ... there is no possible phylogeny according to which all of these groups can be monophyletic. Hennig's method works only as long as there is no internal conflict in the data. (Felsenstein 1982: 381)

Although Felsenstein was simply restating the problem outlined by Sokal & Sneath (1963), rather than avoid it he suggested two analytical methods in which character conflict might be resolved: "parsimony" and "compatibility".

Felsenstein characterised "parsimony" as

**Table 11.1** Column a after Felsenstein (1982: 380); column b after Felsenstein (1984: Table 10.1). To follow Felsenstein, "the ancestral state has been called 0 and the derived state 1"

| | a) Example 1: Felsenstein (1982: 380) | | | | | | b) Example 2: Felsenstein (1984: Table 10.1) | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **1** | **2** | **3** | **4** | **5** | **6** | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** |
| **A** | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 |
| **B** | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 |
| **C** | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 |
| **D** | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 |
| **E** | 0 | 1 | 0 | 0 | 1 | 1 | | | | | | | | |

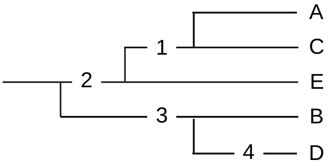


**Fig. 11.2** After Felsenstein (1982: Fig. 1)

> mak[ing] a compromise among the characters, a compromise with which no individual character may be entirely compatible

and "compatibility" as

> find[ing] the phylogeny that is completely compatible with a plurality of characters, even though the remaining characters may be extremely incompatible with it. (Felsenstein 1982: 381)

Felsenstein presented results for parsimony analyses of his example[1] (Figure 11.3). Farris & Kluge explained "parsimony" and "compatibility" in similar terms:

> The distinction is that compatibility methods recognize only perfect correlations—sets of fully congruent characters—whereas the Wagner [parsimony] method more realistically accepts some imperfect correlations, which makes possible a better fit to all available evidence. (Farris & Kluge 1979: 405, Kluge 1984: 28)

Thus, an apparent solution to "Hennig's dilemma" was possible by applying a method. While Farris & Kluge understood their method—and theirs alone—to be an implementation of the discovery of Hennig's synapomorphy, the idea works on data matrices that include only phenetic characters, simple similarities. Even given the apparent inclusion of Hennig's ideas, Kluge & Farris (1969) understood their method—which they initially called "Quantitative Phyletics"—as an *improvement* upon Hennig (see below). Thus, while many understand the Kluge–Farris parsimony algorithm to be equivalent to cladistics, that equation is by no means true.

Relevant to implementation, "cladistics" had an early association with Wagner's (1961) "Ground-Plan Divergence Method",[2] Camin & Sokal's (1965) "parsimony"

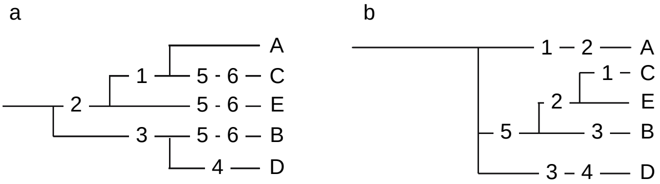


**Fig. 11.3** After Felsenstein (1982: Fig. 2)

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[1] For these data modern parsimony programs find just one tree. These rather more efficient programs were not available to Felsenstein when he offered the example and solutions.

[2] Fitch cites Wagner as a forerunner: "Farris (1970) has explicitly considered the parsimony principle as a part of his method which, like the present method, has its roots in the Wagner tree ..." (Fitch 1971: 406).

method,[3] Wilson's (1965)[4] character "compatibility", as well as Hennig's non-mathematical approach (Hennig 1966a). All these methods of implementation relate in one way or another to "parsimony".

The interconnection among "parsimony", "compatibility", and Hennig's "Phylogenetic Systematics" is significant. To some, Hennig's "Phylogenetic Systematics" and developments in parsimony algorithms are considered one and the same thing (Farris et al. 1970, 1983, Farris & Kluge 1997, Tassy 1992, 1996a, Goujet & Tassy 1994). To others, Hennig's "Phylogenetic Systematics" and developments in compatibility algorithms are considered one and the same thing (Felsenstein 1982,[5] Duncan 1984). And more recently, some have argued that Hennig's "Phylogenetic Systematics" is not the same as either parsimony *or* compatibility (Richardson & Stern 1997,[6] Wägele 1994, 1996: 134–136, Bechly 2000). To complicate matters further, "parsimony" methods now come in a variety of different "kinds", subsumed under the term "generalized parsimony" (Swofford et al. 1996), "compatibility" methods keep re-appearing, and a plethora of "statistical" methods have been formalised as a general set of alternatives (Swofford et al. 1996, 1998, Felsenstein 2004).

Below we consider only parsimony methods, understood in the broadest context.

## 11.2 Cladistic Analysis

> "What is cladistic analysis?" (Nelson 1979: 3)

### *11.2.1 Parsimony*

> "The principle that entities are not to be multiplied beyond necessity."
> (Chambers English Dictionary 1988)

By way of example, consider the simple matrix in Figure 11.2. There are four (1–4) characters distributed among four taxa (A–D); all the data may be explained with reference to any of the 26 possible solutions. Each of the 26 solutions will accommodate the data in different ways.

---

[3] The term "parsimony methods" has become synonymous with "minimum-evolution methods". With this understanding it may be pertinent to credit Edwards & Cavalli-Sforza (1963, 1964) with the first efforts.

[4] Felsenstein (1982: 390) credits Camin & Sokal (1965) with the first numerical representation of compatibility, again testifying further to the complex interconnections; it is worth noting that Wilson (1965: 218) used the term "cladistic" in his paper: "... the present paper together with independent and parallel attempts to formalize cladistic analysis. ..."

[5] "[H]is proposal [Wilson 1965] may be regarded as an analogue of Hennig's method" (Felsenstein 1982: 390).

[6] "An alternative to maximum overall parsimony is to return to an Hennigian approach" (Richardson & Stern 1997: 132).

One way of accounting for the data is to simply count the number of times each character appears on every possible cladogram. Character 1 appears in all the solutions, as it simply denotes an attribute of taxon D. Character 4 appears in all solutions, as it simply denotes the entire group A–D. Character 2 appears in 4 of the 26 solutions, A(B(CD)), B(A(CD), (CD)(AB), and AB(CD). Character 3 also appears in 4 of the 26 solutions, A(B(CD)), A(C(BD)), A(D(BC)), and A(BCD). Both characters 2 and 3 appear together in only one solution, A(B(CD)), suggesting that is the best of all possibilities as it can explain all characters simply and efficiently. The counts embody no more than one version of the principle of parsimony.

Of course, the example is straightforward, in two respects. Different kinds of characters appear only once and no characters conflict. That is, the first parameter relates to strength of evidence, the second to contradictory evidence.

### 11.2.2 Strength of Evidence

Table 11.3 includes a single new observation (character 5). These data support the same solution as the data in the matrix in Table 11.2; character 5 supports the group CD and simply duplicates the information in character 2: Character 5 corroborates character 2.

### 11.2.3 Contradictory Evidence

If more data are bought to bear on the problem, such as characters 6 and 7 in Table 11.4, the situation differs (character 5 has been removed to simplify the example). These data suggest that BCD forms a group (character 3) with CD as a subgroup (character 2) and, *in addition*, that ABC forms a group (character 7) with AB as a subgroup (character 6)—a similar situation to the one explored by Felsenstein above: The evidence from characters 6 and 7 conflicts with the evidence from characters 2 and 3 (Fig. 11.4).

**Table 11.2** Matrix of characters (1–4) for four taxa (A–D)

| | 1 | 2 | 3 | 4 |
|---|---|---|---|---|
| **A** | 0 | 0 | 0 | 1 |
| **B** | 0 | 0 | 1 | 1 |
| **C** | 0 | 1 | 1 | 1 |
| **D** | 1 | 1 | 1 | 1 |

| | 2 | 3 |
|---|---|---|
| **A** | 0 | 0 |
| **B** | 0 | 1 |
| **C** | 1 | 1 |
| **D** | 1 | 1 |

**Table 11.3** (Top) Matrix of characters (1–5) for four taxa (A–D); (bottom) same matrix with uninformative characters (characters 1 and 4) removed

| | 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|---|
| **A** | 0 | 0 | 0 | 1 | 0 |
| **B** | 0 | 0 | 1 | 1 | 0 |
| **C** | 0 | 1 | 1 | 1 | 1 |
| **D** | 1 | 1 | 1 | 1 | 1 |

| | 2 | 3 | 5 |
|---|---|---|---|
| **A** | 0 | 0 | 0 |
| **B** | 0 | 1 | 0 |
| **C** | 1 | 1 | 1 |
| **D** | 1 | 1 | 1 |

There seem to be three alternative solutions:

1. Recognition of group ABC and its subgroup AB (characters 6 and 7 are informative)
2. Recognition of group CD and group AB (characters 2 and 6 are informative)
3. Recognition of group BCD and its subgroup CD (characters 2 and 3 are informative)

Although all three cladograms imply exact *solutions*, these results in fact identify a *problem*; if only one cladogram can be “correct”, which is it? Felsenstein’s point, that it is not possible for all the characters to be placed together on one cladogram, is obviously true. An alternative conclusion is that some of the characters in the matrix might be false. Reducing possible solutions from 26 to 3 might be understood as progress of sorts. However, the results suggest that the problem requires further study and solution, accessible only through the acquisition of more data (characters).

**Table 11.4** (Top) Matrix of characters (1–7, character 5 omitted) for four taxa (A–D)

| | 1 | 2 | 3 | 4 | 6 | 7 |
|---|---|---|---|---|---|---|
| **A** | 0 | 0 | 0 | 1 | 1 | 1 |
| **B** | 0 | 0 | 1 | 1 | 1 | 1 |
| **C** | 0 | 1 | 1 | 1 | 0 | 1 |
| **D** | 1 | 1 | 1 | 1 | 0 | 0 |

| | 2 | 3 | 6 | 7 |
|---|---|---|---|---|
| **A** | 0 | 0 | 1 | 1 |
| **B** | 0 | 1 | 1 | 1 |
| **C** | 1 | 1 | 0 | 1 |
| **D** | 1 | 1 | 0 | 0 |

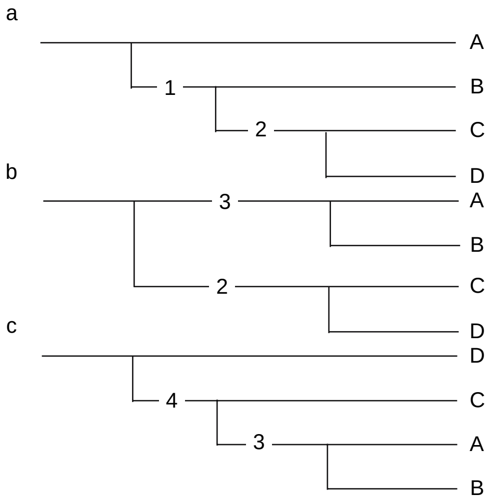

**Fig. 11.4** Three cladograms derived from the matrix in Table 11.4

### *11.2.4 Strength of Evidence and Contradictory Evidence*

Suppose a further seven new characters are discovered (8–14, Table 11.5). One solution offers recognition of the following groups: ABC (characters 7, 8, 13, and 14 are informative) and a subgroup AB (characters 10–12 are informative). These data suggest the following groups:

1. AB(CD) (character 2)
2. A(BCD) (character 3)
3. CD(AB) (characters 6, 10–12)
4. D(ABC) (characters 7, 8, 13, 14)

and the following solutions:

1. AB(CD) + A(BCD) = A(B(CD))
2. AB(CD) + (AB)CD = (AB)(CD)
3. D(ABC) + CD(AB) = D(C(AB))

**Table 11.5** Matrix 4 of 13 characters (1–14, character 5 is omitted) for four taxa (A–D)

| | 1 | 2 | 3 | 4 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **A** | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| **B** | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| **C** | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 |
| **D** | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

| | 2 | 3 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **A** | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| **B** | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| **C** | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 |
| **D** | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

Although there are still conflicting sets of data, the weight of evidence differs in each:

1. AB(CD) × 1 + A(BCD) × 1 = A(B(CD)); total = 2
2. AB(CD) × 4 + (AB)CD × 1 = (AB)(CD); total = 5
3. D(ABC) × 4 + CD(AB) × 4 = D(C(AB)); total = 8

Therefore, the weight of evidence favours solution 3: D(C(AB)).

Although this version of counting characters and their fit to each tree is a kind of parsimony, it differs from the usual versions implemented in currently available computer programs (e.g. Farris 1988, Goloboff 1993, Swofford 1990).

### *11.2.5 "Computerised" Parsimony*

The matrix in Table 11.3 can once more serve as an example. Using "computerised" parsimony, unlike the example above, the best cladogram is that with the smallest count rather than the largest; this version of parsimony requires every character to be accounted for on each tree, rather than seeing some characters as true and others as false for any particular solution. Where do the counts come from?

Consider a less parsimonious cladogram A(D(BC)). Characters 1 and 4 are irrelevant as they fit each tree with a count of one. Character 3 fits at the basal node A(BCD) of the solution and hence has a count of one. Character 2 can only fit C and D separately; hence, there is a count of one for each terminal. In other words, rather than determining that some characters are false, *all are considered true in some sense or other and an explanation is required* (Table 11.6).

Such counting procedures may be seen as limiting the usefulness of the data as well as the precision of the solutions. For example, a completely wrong solution, such as B(C(AD)), will have the same count as the completely uninformative "bush", (ABCD).

To achieve solutions, rather than finding some data true and others false, all characters in the matrix are "modified" or "distorted" (Nelson et al. 2003), so they fit a particular cladogram. That modification finds justification in the methodology rather than the data.

**Table 11.6** Character fit for solution A(D(BC))

| Solution | Character1<br>ABC(D) | Character2<br>AB(CD) | Character3<br>A(BCD) | Character4<br>(ABCD) |
|---|---|---|---|---|
| A(D(BC)) | A(D(BC)) | A(D(BC)) | A(D(BC)) | A(D(BC)) |

### *11.2.6 Partial Characters*

Some years ago Sankoff suggested a difference between parsimony and compatibility analyses (compatibility is discussed in more detail below). He noted that

> … maximizing parsimony is equivalent to minimizing the total number of extra steps over all characters. Maximizing compatibility is equivalent to minimizing the number of characters requiring at least one step. (Sankoff in Le Quesne 1975: 426)

Sankoff's comment might be restated in a different way: Compatibility uses only whole binary characters while parsimony uses whole as well as partial binary characters. The view that "synapomorphies" may be derived from partial binary characters was summarised by Farris & Kluge:

> On a tree consistent with a single derivation of some trait, all the similarities in that trait can be applied as synapomorphy. … If a tree requires separate derivations of a trait in two or more groups, then that similarity cannot be applied as synapomorphy, but the similarity within the groups still can be applied, and each additional requirement for an independent origin reduces the similarities that can be applied as synapomorphy. (Farris & Kluge 1986: 300)

Partial binary characters can best be viewed by some examples. For character AB(CD) there is one whole binary character, as (CD) cannot be subdivided further. For the character A(BCD) there are three partial binary characters, as (BCD) can be subdivided into (BC), (BD), and (CD). Therefore, there is potentially more information when the data are subdivided than when they remain whole.

### 11.2.7 Informative Symplesiomorphy

Partial binary characters are not the only way "synapomorphies" might be generated. The distinction between Hennig's "Phylogenetic Systematics" and Kluge & Farris' "Quantitative Phyletics" (Kluge & Farris 1969) was put into sharper focus by Kluge:

**Table 11.7** Whole characters and their partial equivalents

| | Whole Binary Characters | Partial Binary Characters |
|---|---|---|
| AB(CD) | AB(CD) | None |
| A(BCD) | A(BCD) | AB(CD) |
| | | AC(BD) |
| | | AD(BC) |
| A(BCDE) | A(BCDE) | ADE(BC) |
| | | ACE(BD) |
| | | ABC(BE) |
| | | ABE(CD) |
| | | ABD(CE) |
| | | ABC(DE) |
| | | AC(BCD) |
| | | AD(BCE) |
| | | AB(CDE) |
| AB(CDE) | ABC(DE) | ABC(DE) |
| | | ABD(CE) |
| | | ABE(CD) |
| ABC(DE) | ABC(DE) | None |

> The most significant difference between the two approaches concerns the fact that Phylogenetic Systematics estimates only the cladistic parameter and in doing so it uses only derived states. Quantitative Phyletics estimates both cladistics and patristics and it *uses all states, derived and primitive*, in those estimations . . . to ignore similarity based on shared primitive states can lead to significantly different phylogenetic hypotheses.[7] (Kluge 1976: 43; italics ours)

The "most significant difference" concerned matters of implementation relative to "classical" phylogenetic systematics (*sensu* Brundin 1968 and Hennig 1966a); and the "improvements" hinged on the use of "similarity based on shared primitive states". Kluge returned to this apparent "advantage" in a recent critique of three-item analysis where he suggested that

> . . . the transformation [three-item analysis] distorts the original data as evidence for genealogical relationships because symplesiomorphies are no longer available to be tested with congruence for phylogenetic informativeness as evolutionary reversals, i.e. when matching 0s delimit sister-groups. (Kluge 1993b: 251)

Such a view might seem to contradict the classic cladistic assumption of grouping by synapomorphy (not only contradicting cladistics but seemingly a lot of systematics from the past—see Chapter 5)—yet a covering explanation was provided: "evolutionary reversals".[8] Farris & Kluge (1985, 1986, 1997) went to great lengths to document the many instances in Hennig's work where he used "reversals", as if those examples justify the general *manipulation* of data by any particular algorithm. That Hennig used reversals is one thing; that it is the same as modifying (distorting) data is another.

Consider again the character AB(CD). CD cannot be subdivided; hence, there are no partial binary characters. However, if symplesiomorphy may be informative, then the AB portion may be considered possible evidence; hence, another result may be (AB)CD. Thus, almost any evidence may be utilised as potential synapomorphy. Consider the character AB(CDE). There are three partial binary characters: ABC(DE), ABD(CE), and ABE(CD). In addition, there is the AB portion, allowing two further possibilities: (AB)CDE and (AB)(CDE). For the character AB(CDE) there are six possibilities (other examples are given in Table 11.8).

### *11.2.8 Resolving Conflict*

Parsimony resolves conflict not by considering the data—that some homologies might be false—but by adding an assumption-laden methodology (an algorithm).

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[7] "Cladists will assail Kluge for his inclusion of primitive character states in assessing similarity and for his reluctance to adhere to 'cladistic classificatory dogma"' (Moss 1978). See Wilkinson (1991) for an attempt to revive the use of primitive character states in a somewhat different way and the replies of Whiting & Kelly (1995) and Wilkinson (1997).

[8] An argument used also to distinguish Wagner parsimony from Camin-Sokal parsimony (Farris 1970, Farris et al. 1970, Farris & Kluge 1997) and from the monothetic subset method of Marx & Rabb (1970).

**Table 11.8** Whole characters, their partial equivalents, and "symplesiomorphy"

| | Whole Binary Characters | Partial Binary Characters | "Symplesiomorphy" |
|---|---|---|---|
| AB(CD) | AB(CD) | — | (AB)CD |
| A(BCD) | A(BCD) | AB(CD) | — |
| | | AC(BD) | — |
| | | AD(BC) | — |
| A(BCDE) | A(BCDE) | ADE(BC) | — |
| | | ACE(BD) | — |
| | | ABC(BE) | — |
| | | ABE(CD) | — |
| | | ABD(CE) | — |
| | | ABC(DE) | — |
| | | AC(BCD) | — |
| | | AD(BCE) | — |
| | | AB(CDE) | — |
| AB(CDE) | AB(CDE) | ABC(DE) | (AB)CDE |
| | | ABD(CE) | (AB)(CDE) |
| | | ABE(CD) | |
| ABC(DE) | ABC(DE) | — | (AB)C(DE) |
| | | | (AB)CDE |
| | | | (AC)B(DE) |
| | | | (AC)BDE |

To achieve an optimal tree, the data require modification to fit an appropriate solution. That is, data are seen as neutral and only become informative with respect to the implementation of an algorithm—data may be modified according to the program. In short, when phenetic data are used (binary variables), exact solutions are imposed by the algorithm (whatever that might be), rather than an *actual* solution being discovered. This reasoning extends to almost all phylogenetic computer programs available and in use today.

We believe that inspection of the data, rather than more methods (however refined), might allow a way of *discovering* solutions rather than *imposing* them. Two possibilities come to mind:

1. Characters might be considered as components (groups).
2. Characters might be considered as relationships.

## 11.3 The Data Matrix—Again: Components Characters

When entries in a column of a data matrix match (all those that have the numerical value 1, for example), the taxa that share the same value imply a particular group. Thus, in Table 11.2 character 2 suggests the group C + D, written (CD), and character 3 suggests the group B + C + D, written (BCD). Both groups are based on shared similarities—the 1's, in this case. More accurately, the groups are based on shared homologues. These groups have been referred to as **components,** following Nelson's original use of the term: "Cladistic components are branch points. A particular branch point is defined by the branch tips (terminals or terms) to which it leads"

(Nelson 1979: 3). Thus, for character 3 (BCD) is the component. But each column consists of similarities and differences, 0‘s and 1‘s. What is the relationship between the similarities and differences? One answer might be that the entries in each column are the same but different. This last phrase crops up frequently in the systematic literature as a definition, or description, of homology: “A character is ... a theory that two attributes which appear different in some way are nonetheless the same (or homologous)” (Platnick 1979: 542). Components do not to take into account the “difference” aspect, the relationship between the 0 and 1. To deal with the data in its entirety is to note that it implies a **relationship**. There are two kinds of relationship relative to a matrix entry. For character 1 the relationship implied is AB(CD), which means that C and D are more closely related to each other than either is to A or B. This may be called a **maximal relationship**. AB(CD) implies two further relationships, A(CD) and B(CD). These may be called **minimal relationships** or **three-item statements** (Nelson & Platnick 1991). The meaning or explanation of “relationship” is not considered for the moment.

The three matrix elements can be thought of as different kinds of basic “units” of data, differing in what they represent:

a) **Component**: (CD)
b) **Maximal Relationship**: AB(CD)
c) **Minimal Relationship**: A(CD) + B(CD)

Each “unit” might be utilised to achieve an optimal summary for all the data in a matrix. Each “unit” might also be considered as a statement of homology. This allows a significant contrast to be made between the various “units”. Component (CD) is not a statement of relationship but a group; it lacks any reference point. One might say that the component implies the relationship AB(CD). However, when analysed using any particular algorithm, only the CD part is considered of significance. Otherwise, the data really imply [AB][CD], as in phenetic characters (see Chapter 8). Similarly, while AB(CD) does express the relationship and might function as a “unit” of analysis, it is clearly a composite, as it can be broken into further “units”. A(CD) and B(CD) are minimal statements that directly express relationships as well as being capable of functioning as a “unit” in various analyses. They appear to be the “character” equivalent of the cladistic parameter, a further step towards generalising homology as relationship (Fig. 11.5).

### 11.3.1 Compatibility

When “Phylogenetic Systematics” (*sensu* Hennig) was being numericalised, compatibility analysis was understood by some to be the equivalent of “grouping by synapomorphy”, a parsimony approach and directly equivalent to Hennig’s methodology (there was a significant debate on this matter in the pages of the journal *Taxon*[9]).

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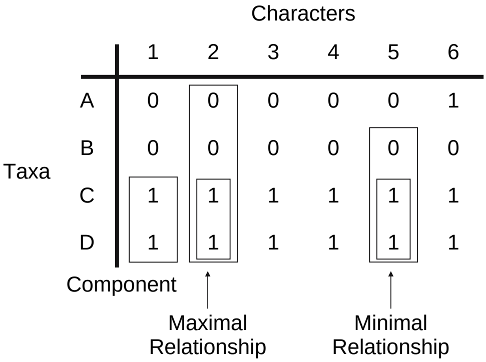
[9] See Duncan (1984, 1986), Farris & Kluge (1985, 1986), Churchill et al. (1985), and Nordal (1987). See also Felsenstein (1982) and Dahlgren & Rassmussen (1983).



| Taxa | 1 | 2 | 3 | 4 | 5 | 6 |
|---|---|---|---|---|---|---|
| A | 0 | 0 | 0 | 0 | 0 | 1 |
| B | 0 | 0 | 0 | 0 | 0 | 0 |
| C | 1 | 1 | 1 | 1 | 1 | 1 |
| D | 1 | 1 | 1 | 1 | 1 | 1 |

**Fig. 11.5** Matrix indicating maximal and minimal relationships and components

Character compatibility analysis is based on the idea that characters specify particular hypotheses of relationship (Figure 11.6, after Estabrook 1972). When two or more character hypotheses are consistent, they are said to be compatible and represent a more robust overall hypothesis. A character that specifies a particular hypothesis of relationship is a synapomorphy. Thus, synapomorphies are identified prior to analysis, the aim being to separate “true” synapomorphies from the “false”. Of interest is that compatibility has been reinvented (or resurrected) several times in the past few years (see below[10]).

Farris & Kluge supplied the most severe critique (Farris & Kluge 1979, 1985, 1986). Essential to their view was Hennig’s meaning of synapomorphy and how that meaning was addressed by various implementations: Initially, at least, “All authors evidently deemed it desirable to be termed ‘Hennigian’ . . . ” (Farris & Kluge 1979: 411).

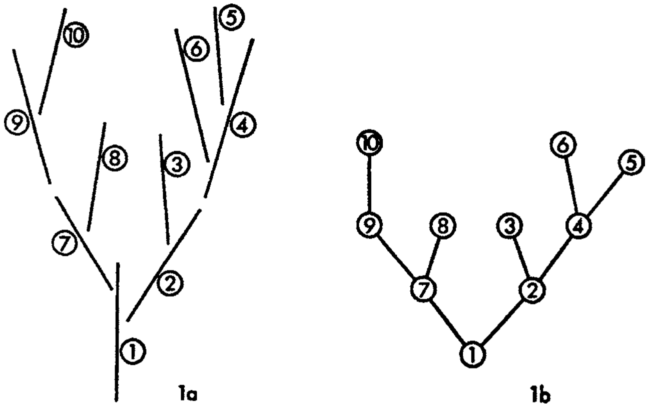


**Fig. 11.6** After Estrabrook (1972, reprinted, with permission, from the *Annual Review of Ecology and Systematics*, 3; ©1972 by Annual Reviews www.annualreviews.org)

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[10] See Lorenzen (1993) and Wägele (1994), for example; cf. Wilkinson (1994).

Although George Estrabrook laid the foundations for a numerical compatibility approach, debate began with Duncan et al. (1980), who provided a discussion of various methods for reconstructing phylogenetic trees. They concluded that no one method was any better than another. With respect to Wagner parsimony, Duncan suggested that

> Fundamental changes to Hennig's method date from Farris et al. (1970) who summarise Hennig's methods in four axioms. ... Synapomorphy in the sense of Farris et al. (1970) is a shared derived character state, regardless of how many times that state evolved. (Duncan 1984: 700)

Also significant to Duncan's claim was that if, as stated in Kluge & Farris' Axiom AI, characters "have a fixed order of evolution", it implies that

> ... shared non-congruent apomorphies *can* be used as synapomorphies on their estimation of phylogenetic relationships. Synapomorphy can be determined by examining character state change in the context of an "appropriately restricted section of the evolutionary tree" for the group under study, whereas Hennig's method holds that determination of synapomorphy is based on examination of character state change in the entire group being analysed. (Duncan 1984: 701)

Thus, the disagreement rested upon whether one examines character congruence in a "restricted section of the evolutionary tree" (Farris et al. 1970: 173) or "examination of character state change in the entire group ...". Originally, Farris et al. (1970) had suggested that

> [o]ne widely known criterion—parsimony—could be used to select trees. This would be in accord with AIV, since on a most parsimonious tree OTUs that share many steps (this is *not* the same as the OTUs' being *described* by many of the same *states*) are generally placed together. (Farris et al. 1970: 176)

According to Duncan, the distinction between "steps" and "states" redefines synapomorphy: "Steps" and "states" were indeed seen as different things. Farris & Kluge's subsequent rebuttals turned on the idea of maximising parsimony, in which case local changes in parts of the tree suggest that the Wagner approach would be *more* parsimonious—that is, steps favour states.

Whatever, compatibility faded fast (at least as it was then recognised) largely due to Duncan and others' insistence that all methods should be judged by their underlying model and each method was only as good as the associated model, a position adopted from Felsenstein:

> Eclecticism in the development and application of cladistic methodology seems warranted at this point in the development of cladistics. Data can be analyzed by selecting methods whose assumptions approximate the appropriate evolutionary model for groups under study, or by choosing methods that suit the nature of the data. (Duncan 1984: 704)

Churchill et al. (1985) came to different conclusions suggesting that Hennig's "scheme of argumentation" was equivalent to Wagner parsimony—or at least both "methods" would find identical trees. Nevertheless, one aspect that was not developed in the debate, and would have profound implications, was the notion that "synapomorphy" could be represented in a treelike form (Figure 11.7). For example:

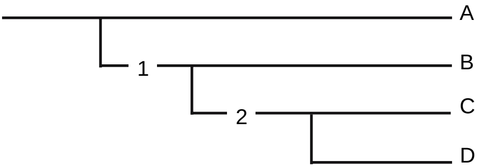

**Fig. 11.7** Cladogram representing the interrelationships among four taxa A–D, with data supporting nodes (components) 1 and 2 (components marked with boxes)

> Character compatibility analysis is an analysis of character-state trees construed as hypotheses of evolutionary relationships to determine whether and how they contradict each other. (Estabrook 1984: 151)

If the above is rephrased, then one might entertain a more general notion:

> Character compatibility analysis is an analysis of *synapomorphy* construed as hypotheses of *taxon* relationships to determine whether and how they contradict each other.

Such a view might be relevant to an understanding and development of component analysis (Nelson & Platnick 1981).

### *11.3.2 Component Analysis (Nelson 1979, Nelson & Platnick 1981)*

To arrive at a solution when more than one component is available requires their combination. Combining components simply notes some aspect that each of the original, individual components shares. To speak of combining components suggests comparison with “consensus techniques”, a suite of methods designed to summarise information from a series of independent cladograms (Swofford 1990). Objections to consensus methods have been raised in favour of a consideration of all the original information, rather than their summary, originally cast in terms of “total evidence” (Kluge 1989), evolving into “simultaneous analysis” (Nixon & Carpenter 1996). However, it would be a mistake to believe that comparison and combination of different cladograms depend upon using *either* matrix methods or “consensus” techniques. *All* analytical methods attempt to discover the optimal cladogram, that which may represent a set of characters, whether those characters are suites of (mini-) cladograms or columns in a matrix (Page 1987, 1989a, b, 1990a, b, c, Nelson & Ladiges 1991a, b, 1992). And both approaches may use “parsimony” in the sense of either maximising or minimising some quantity.

Page (1990a) was the first to draw attention to the two different kinds of method within the component analysis described in Nelson & Platnick (1981; see also Nelson 1979):

1. Component analysis of fundamental cladograms (derived from different data sets), which are combined to yield a general cladogram (summarising the information in the fundamental cladograms) (Nelson 1979; Nelson & Platnick 1981: 305–323)
2. Component analysis of areagrams (derived from taxon cladograms), which are combined to yield a general area cladogram (summarising all the information in the areagrams) (Nelson & Platnick 1981: 410–467)

In fact, Nelson & Platnick (1981) intended component analysis to mean the study of branching diagrams; hence, their book is really a study of component analysis in all its various guises: ancestor-descendant relationships, optimal cladograms, optimal areagrams. While Page determined different methodologies, these should rightly be considered subsets of component analysis in this general sense. Bearing this is mind, we refer to the first kind of component analysis (number 1 above) as **General Component Analysis** and the second (number 2 above) as **Augmented Component Analysis**. General Component Analysis shares operational similarities to Patterson's **General Congruence** and Scotland's (1992) treatment of parsimony. Augmented Component Analysis is somewhat more complex and is dealt with in more detail below.

### *11.3.3 General Component Analysis (Nelson 1979, Nelson & Platnick 1981: 305–323, Page 1989b: 177–180)*

Nelson (1979) outlined a method in which individual cladograms could be combined into a single summary diagram based on the combination of their individual components. Components may share two possible relations: They are either **combinable** or **non-combinable**. Components are combinable when they can be part of the same cladogram (Figure 11.7), non-combinable when they cannot. There are three kinds of combinable components: **exclusion, inclusion,** and **replication.**

a) **Exclusion.** "Components are combinable and exclusive if their definitions are different and non-overlapping" (Nelson 1979: 7, Nelson & Platnick 1981: 312).
b) **Inclusion.** "Components are combinable and inclusive if their definitions are different and overlapping, such that one is included in the other" (Nelson 1979: 8, Nelson & Platnick 1981: 312).

Consider a simple problem, with just four taxa. There are 15 fully resolved solutions and 11 less resolved solutions. With a perfect fit between pairs of components, the systematic problem and its solution are trivial, as each solution is the summary of two different non-conflicting components. For instance, cladogram A(B(CD)) is the combination (or summary) of the components (BCD) and (CD) (example 1 in Table 11.9). The first two combinations—(a) and (b)—are inclusive, as one component is included in the other. The third solution (c) is exclusive, with neither component nested (Table 11.9).

Every triplet combines perfectly with three different pairs. By "perfectly", we mean that all the original data (components) are included in the summary. For instance, (BCD) will combine perfectly with (CD), (BC), and (BD) (first

**Table 11.9** Combinations of various components with (CD)

| | | | | |
|---|---|---|---|---|
| (a) (CD) | + | (BCD) | = | A(B(CD)) |
| (b) (CD) | + | (ACD) | = | B(A(CD)) |
| (c) (CD) | + | (AB) | = | (AB)(CD) |

**Table 11.10** Comparison of all 15 fully resolved cladograms for 4 taxa (A–D) and their respective components

| Cladogram | | Component 1 (Triplet) | | Component 2 (Pair) |
|---|---|---|---|---|
| **A(B(CD))** | = | (BCD) | + | (CD) |
| **A(D(BC))** | = | (BCD) | + | (BC) |
| **A(C(BD))** | = | (BCD) | + | (BD) |
| **B(D(AC))** | = | (ACD) | + | (AC) |
| **B(A(CD))** | = | (ACD) | + | (CD) |
| **B(C(AD))** | = | (ACD) | + | (AD) |
| **C(D(AB))** | = | (ABD) | + | (AB) |
| **C(B(AD))** | = | (ABD) | + | (AD) |
| **C(A(BD))** | = | (ABD) | + | (BD) |
| **D(C(AB))** | = | (ABC) | + | (AB) |
| **D(B(AC))** | = | (ABC) | + | (AC) |
| **D(A(BC))** | = | (ABC) | + | (BC) |
| **(CD)(AB)** | = | (AB) | + | (CD) |
| **(AC)(BD)** | = | (BD) | + | (AC) |
| **(AD)(BC)** | = | (BC) | + | (AD) |

three rows in Table 11.10). Each pair will combine perfectly with three different triplets. For example, (CD) will combine perfectly with (BCD), (ACD), and (AB) (Table 11.10).

c) **Replication.** Components are combinable and replicated if their definitions are the same; one component is replicated exactly by another (Nelson 1979: 8, Nelson & Platnick 1981: 312).

For example, component (BC)—derived from one source—and (BC)—derived from another source—specify the same component, hence replicate. Replicated components might be considered trivial, but they are corroborative and their relative numbers are significant (see above).

d) **Non-combinable**. Components are non-combinable if they cannot be part of the same cladogram because their definitions overlap (Nelson 1979: 8, Nelson & Platnick 1981: 312).

Two (or more) components may not combine at all. For instance, for (CD) and (BD) there is no possible solution that would summarise both components exactly: The two conflict. Possible solutions, such as they are, indicate that there is no common information:

(a) (CD) + (BD) = (BCD)
(b) (CD) + (BD) = (CD) + (BD)

Neither of these options is very useful. They do not resolve the conflict but simply restate it.

e) **Combination Results.** For consensus methods, a general cladogram is constructed from information specified by the set of fundamental cladograms. Components represented in the general cladogram may be divided into three sets: **true, false,** or **ambiguous**—"... by 'true' and 'false' I mean only agreement or disagreement with the general cladogram" (Nelson 1979: 11, Nelson & Platnick 1981: 315).

All combinable components can be understood as "true"—that is, they are true for the summary diagram. For instance, the cladogram A(B(C(DE))) has three true components: (BCDE), (CDE), and (DE). Components excluded from the general cladogram (the non-combinable components) can be understood as "false"—for the cladogram A(B(C(DE))), the component (AB) is false. Components that are "mutually non-combinable" can be understood as "ambiguous". "Mutually non-combinable" means that of two or more components, all cannot be represented in the same general cladogram. Components thought of as "false" or "ambiguous" are of interest as they indicate areas of conflict.

The method was not intended for use in character analysis although Morse & White (1979) briefly noted the idea. The general principles, however, seemed to share a number of points with compatibility or clique methods.

### *11.3.4 Patterson's General Congruence (1980a, 1982a, 1988a, b)*

A method of analysis directly comparable to General Component Analysis was outlined by Patterson (1980a, 1982a, 1988a, 1988b; see also Janvier 1984: 48 for a similar but less detailed account). Patterson called his method "General Congruence" (Patterson 1980a, 1988b: 74).[11] Although he did not state it in terms of component analysis, he did allude to some equivalence: "... this is the basis of pattern cladistics, the analysis of *hierarchically branching diagrams*" (Patterson 1988b: 75; our italics).

Rather than fundamental cladograms, Patterson used characters, the "fundamental cladograms" being individual characters. The equivalence represents the notion of taxic homology, characters that specify groups. Thus, an optimal cladogram is constructed from the combination of characters, with only combinable characters (components) accepted. Patterson's method was a direct outcome of his study on the testing of homology:

> ... as far as I can see, synapomorphies are the *only* properties of monophyletic groups, tests of a hypothesis of homology must be other hypotheses of homology—other synapomorphies. (Patterson 1982a: 38; see also Wiley 1974: 240)

Given a homology specifying one group, Patterson discussed five possible ways in which other homologies might relate to it (Figure 11.8). He used a series of Venn diagrams to illustrate the principle (Patterson 1982a: 39). Later, Humphries & Funk (1984: 331) used a series of branching diagrams to illustrate Patterson's five relations (see also Scotland 1992: 7, Fig. 11.1.4, 2000a: 159, Kitching et al. 1998: 9, Fig. 11.1.6). Below we use the representation in Kitching et al. (1998: 9, Fig. 11.1.6) as a more direct illustration (Figure 11.9).

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[11] Patterson first outlined the procedure in 1980 and gave a fuller explanation in 1988 (Patterson 1980a, 1988b: 74): "I have illustrated the method of general congruence with a small sample of myoglobin sequence data" (Patterson 1980).

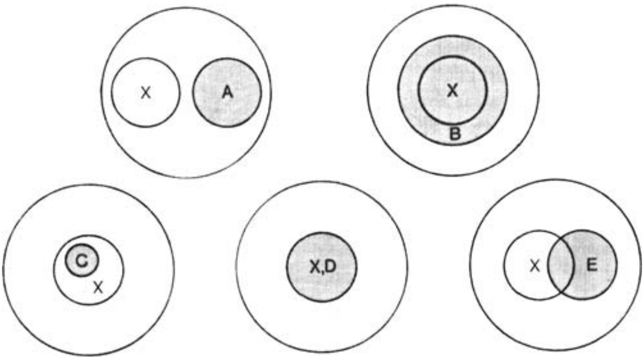


**Fig. 11.8** The five "relations" between homologies. From Patterson (1982a: 39, Fig. 1).

Considering one character (one homology) ABC (Figure 11.9b), a second homology can "relate" it in five ways using set theroy:

(A) It may define a different but non-conflicting group. For instance, if the first "homology" is ABC and the second is DE, they can define different parts of the same set (Figure 11.9c).

(B) It may define a larger group relative to the first "homology". For instance, if the first "homology" is ABC and the second is ABCD, the two do not conflict but define nested parts of the same set (D(ABC)).

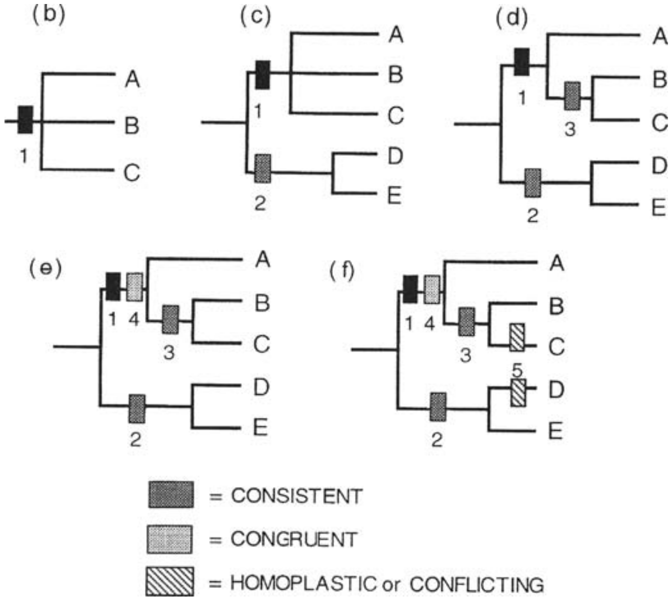


**Fig. 11.9** The five "relations" between homologies. From Kitching et al. (1998: 9, Fig. 1.6)

(C) It may define a smaller group relative to the first “homology”. For instance, if the first “homology” is ABC and the second is AB, the two do not conflict but define nested parts of the same set C(AB).
(D) It may define the same group as the first “homology”; for instance, if the first “homology” is ABC and the second is also ABC.
(E) It may define a different group relative to the first “homology”; for instance, if the first “homology” is ABC and the second is ABD.

Patterson considered the most interesting categories to be (D) and (E), replicated groups and conflicting groups, respectively. He adopted a statistical (or probabilistic) approach to the quantification of replicated versus conflicting “homologies”. The similarities between Patterson’s General Congruence and Nelson’s (1979) Component Analysis should be clear (see also Rosen 1984: 85–88).

### *11.3.5 Consistent and Congruent Characters (Scotland 1992, 1997, Kitching et al. 1998)*

Outlining Patterson’s five “relations”, Scotland (1992: 8) elaborated further on terminology (Table 11.11, column 3) by making a distinction between consistent and congruent characters, the latter being characters that describe exactly the same group, “consistent” for characters that describe different but non-conflicting groups. For example, characters (ABC) and (DE) are consistent, and they can be combined as (ABC)(DE). Kitching et al. (1998: 8) described it like so:

> Since no common taxa are involved the characters can be said to be consistent (strictly “logically consistent”) with one another. (Kitching et al. 1998: 8)

The use of two terms to describe non-conflicting characters was derived from Patterson’s identification of kinds of characters that were of most interest in testing homology. Of these, incongruent and congruent characters are significant because

(1) Incongruent characters suggest an alternative group that contradicts the original.
(2) Congruent characters confirm (or corroborate) the initial homology (and group) and therefore lend increased support.

### *11.3.6 Comparison*

Direct comparison among Nelson’s Component Analysis, Patterson’s General Congruence, and Scotland’s use of consistent and congruent characters can be made (Table 11.11).

Even more clearly, as recently outlined by Nelson & Ladiges (2001: 393), the issue might best be understood in terms of corroboration, consistency, and conflict (Table 11.11, column 4). These few items of relationships cover the problem of analysis almost completely.

**Table 11.11** Comparison of kinds of General Component Analysis and General Congruence

| Nelson(1979) | Patterson(1982a) | Scotland(1992) | Nelson & Ladiges (2001) |
|---|---|---|---|
| **Relation** | **Relation** | **Relation** | **Relation** |
| Exclusion | a) A different group | Consistent | Consistent |
| Inclusion | b) A larger group | Consistent | Consistent |
| | c) A smaller group | | |
| Replication | d) The same group | Congruent | Corroborate |
| Non-combinable | e) Conflicting group | Conflict | Conflict |

### *11.3.7 Component Solutions: Paralogy*

The term "paralogy" is used today to refer to divergent gene trees (Fitch 1970, 2000). Paralogous relationships have been applied to biogeography by Nelson & Ladiges (1996) and palaeontology/biostratigraphy by Zaragüeta et al. (2004) but may be generalised to the analysis of all patterns of relationships (Nelson 1994, Nelson & Ladiges 2001). One might realistically see relevant data for all organisms linked by a basal—and uninformative—paralogous node. For instance, above we noted that data could be expressed as mini-cladograms. Data are not independent in the sense that each may apply to all or some organisms. The presence of RNA unites all organisms; the presence of "flowers" unites some organisms; the same organisms have RNA. Identification of any character (homology) may separate out a particular "subtree" of life. If each character is viewed as a "subtree", then, as in molecular systematics and biogeography, these data either corroborate (suggest the same "subtree") or are consistent with (suggest an alternative but different "subtree") or conflict (suggest an alternative "subtree") with each other.

### *11.3.8 Components and Equivalents*

The cladogram in Figure 11.7 represents the interrelationships among four taxa, A–D. All relationships in this cladogram are specified by two components. Component 1 specifies the group B + C + D (BCD), and component 2 specifies the group C + D (CD); therefore:

component = group.

Each component is equivalent to a node on a cladogram (Figure 11.7, nodes 11.1 and 2); therefore:

component = group = node.

The groups specified by the nodes are equivalent to taxonomic groups, in the sense that A + B + C and A + B may be named taxa; therefore:

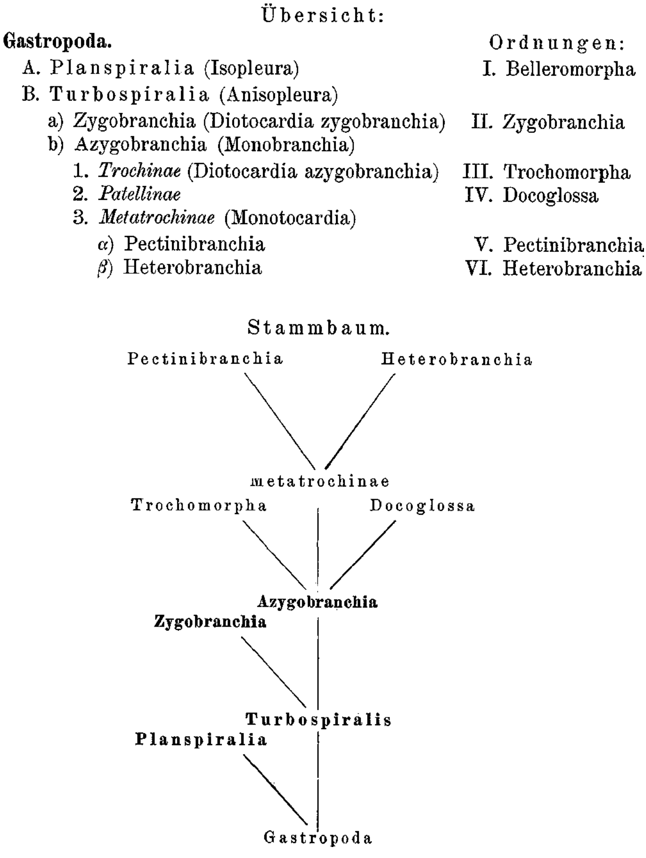
component = group = node = taxon.

Such schemes have been a feature of the past, since trees were used to represent relationships (rather than phylogenies; see Chapter 8). For example, Naef (1911) adopted its use (Figure 11.10), as did Stensiö (Figure 6.4). Naef summarised his conclusions with a written classification and a branching diagram, both being identical (Figure 11.10).

Nelson & Platnick (1981) provided a detailed account of the history of systematics, demonstrating how components might be derived from classifications and diagrams of relationships..

For the cladogram in Figure 11.7, taken together, components 1 plus 2 summarise the interrelationships among taxa A–D. That is, C and D are more closely related to each other than they are to A and B, and B, C, and D are more closely related among themselves than they are to A. The cladogram in Figure 11.7 can be summarised in matrix format as two binary characters (Table 11.12).

The matrix in Table 11.12 has four taxa (rows A–D) and two "characters" (columns 1 and 2). The "characters" in the matrix (Table 11.12) and the components



Übersicht:

| **Gastropoda.** | Ordnungen: |
|---|---|
| A. Planspiralia (Isopleura) | I. Belleromorpha |
| B. Turbospiralia (Anisopleura) | |
| a) Zygobranchia (Diotocardia zygobranchia) | II. Zygobranchia |
| b) Azygobranchia (Monobranchia) | |
| 1. *Trochinae* (Diotocardia azygobranchia) | III. Trochomorpha |
| 2. *Patellinae* | IV. Docoglossa |
| 3. *Metatrochinae* (Monotocardia) | |
| α) Pectinibranchia | V. Pectinibranchia |
| β) Heterobranchia | VI. Heterobranchia |

Stammbaum.

**Fig. 11.10** Reproduction of Naef's diagram and classification, after Naef (1911: 159)

**Table 11.12** Matrix of four taxa (rows A–D) and two "characters" (columns 1 and 2)

| | 1 | 2 |
|---|---|---|
| **A** | 0 | 0 |
| **B** | 1 | 0 |
| **C** | 1 | 1 |
| **D** | 1 | 1 |

of the cladogram (Figure 11.7) match exactly. Shared characters, such as character 1 in Table 11.12, may be considered equivalent to components (Page 1987); therefore,

component = group = node = taxon = shared character.

In a broader sense, as they are based on evidence, components are statements of "general synapomorphy" (Nelson & Platnick 1981: 169) or, more generally, statements of "homology", in as much as the component (homology) specifies a particular group based on evidence. Therefore,

component = group = node = taxon = shared character = homology.

This is the usual way of looking at systematic data. Yet these equations, while of some significance, have no exact relational component. Alternatives are possible, which we explore below.

### *11.3.9 Components as Data*

Representing data relevant to solving systematic problems is most easily appreciated with reference to the usual binary character/cladogram notation. For three taxa there are eight different kinds of characters: Three specify each of the terminals (Table 11.13, characters 1–3), two specify the entire set (Table 11.13, characters 7 and 8), and three discriminate two taxa from among the set of three (Table 11.13, characters 4–6). Characters 7 and 8 are really the same; hence, there are seven kinds of character. Only characters 4–6 are of use in determining relationships.

Binary (matrix) characters can be written as branching diagrams; hence, the data in Table 11.13 can be written as in Figure 11.11.

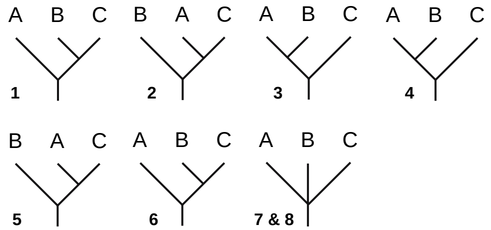


**Fig. 11.11** Series of cladograms for each character

**Table 11.13** Matrix of three taxa (rows A–C) with all eight possible characters (columns 1–8)

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
|---|---|---|---|---|---|---|---|---|
| **A** | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| **B** | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 |
| **C** | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 |

For ease of representation, such cladograms can be written in parenthetical form (Table 11.14).

**Table 11.14** Characters from Table 11.13 written in parenthetical form

| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
|---|---|---|---|---|---|---|---|
| (A)BC | (B)AC | (C)AB | (AB)C | (AC)B | (AC)B | (ABC) | (ABC) |

**Table 11.15** Matrix of 4 taxa (rows A–D) with all 16 possible characters (columns 1–16)

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **A** | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 |
| **B** | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 |
| **C** | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 |
| **D** | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 |

For 4 taxa there are 16 different kinds of characters (Table 11.15). Four specify the terminal taxa (Table 11.15, characters 1–4), 2 specify the entire set (Table 11.15, characters 15 and 16, which are really the same), and 10 discriminate a subset of taxa from the entire set (Table 11.15, characters 5–14). Of those 10, 6 distinguish two from the four (Table 11.15, characters 5–10) and four distinguish three from the four (Table 11.15, characters 11–14).

The binary characters in Table 11.15 may be written as

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
| (A)BCD | (B)ACD | (C)ABD | (D)ABC | (AB)CD | (AC)BD | (AD)BC | (BC)AD |
| 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 |
| (BD)AC | (CD)AB | A(BCD) | B(ACD) | C(ABD) | D(ABC) | (ABCD) | (ABCD) |

These kinds of relationships can be generalised over all numbers of taxa (Table 11.16). Inspection of Table 11.16 shows how different kinds of data increase with increasing numbers of taxa.

## 11.4 Augmented Component Analysis

> "Within systematics, nevertheless, there had been a practice of long standing to explain character conflict, as if conflict itself were evidence of a group, by means of notions such as character combination, underlying synapomorphy,

**Table 11.16** Compilation of all possible characters and all possible cladograms for 3–10 taxa. T = taxa, Ch. Comp. = total number of characters (Ch.) or components (Comp.), subdivided into T = total number of characters and B = binary characters. Binary character values are the sum of all informative characters (components), and total values are the binary character total plus the uninformative characters (components). As an example, for three taxa there are seven kinds of characters, of which three are binary and all of those three are pairs. The four remaining characters are the three for each terminal and one for the entire group. Informative characters (components) = those characters that distinguish groups from the total set. "Cladograms" indicates the total number of cladograms possible from the suite of taxa. Binary = fully resolved cladograms, Total = fully resolved cladograms plus all the partially resolved cladograms. After Felsenstein (1978) and Page (1990a)

| T | Ch.Comp. | | Informative Characters = Components | | | | | | | | Cladograms | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | T | B | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | Binary | Total |
| **3** | 7 | 3 | 3 | | | | | | | | 3 | 4 |
| **4** | 15 | 10 | 6 | 4 | | | | | | | 15 | 26 |
| **5** | 31 | 25 | 10 | 10 | 5 | | | | | | 105 | 236 |
| **6** | 63 | 56 | 15 | 20 | 15 | 6 | | | | | 945 | 2752 |
| **7** | 127 | 119 | 21 | 35 | 35 | 21 | 7 | | | | 10,395 | 39,208 |
| **8** | 255 | 246 | 28 | 56 | 70 | 56 | 28 | 8 | | | 135,135 | 660,032 |
| **9** | 511 | 501 | 36 | 84 | 126 | 126 | 84 | 36 | 9 | | 2,027,025 | 1,281,892 |
| **10** | 1023 | 1012 | 45 | 120 | 210 | 252 | 210 | 120 | 45 | 10 | 34,459,425 | 282,137,824 |

> inside parallelism, orthogenesis, and whatnot, but these notions seemed to offer no exact solution to the problem posed by the conflicting characters, and no significant aid to judgement. There the problem rested for some years." (Nelson 1996: 13)

The second implementation of component analysis in Nelson & Platnick (1981) was concerned with the analysis of relationships rather than determination of groups.

### 11.4.1 The Meaning of Statements of Relationship

Consider the binary character AB(CD). What does it say about the relationships of A, B, C, and D? The answer might seem straightforward: C and D are more closely related to each other than either is to A or B, an interpretation 1 argument (see Chapter 2). But if evidence is presented for relating C and D together, it does not, and cannot, specify the relationships of A or B to either C or D. In simpler terms, AB(CD) is silent with respect to the relationships of A or B. The solution might be represented as a matrix, with the usual 0's and 1's. Thus, AB(CD) might be represented as 00(11). As a matrix entry, one might suggest that, in fact, these data are really ambiguous and solutions depend on further assessment. As a conventional matrix, the data would look like so:

| | |
|---|---|
| **A** | 0 |
| **B** | 0 |
| **C** | 1 |
| **D** | 1 |

The ambiguity might be seen as offering different (possible) solutions. Thus, the matrix might imply the following three alternatives:

| | |
|---|---|
| **1** | AB(CD) |
| **2** | (AB)CD |
| **3** | (AB)(CD) |

The first solution, AB(CD), simply restates the problem; the second, (AB)CD, denies the initial homology statement altogether (or reverses it): that C and D form a group relative to A and B; the third, (AB)(CD), suggests that the initial homology statement is partially misleading. However, as has already been noted above, any homology statement is composed of both the 0‘s and 1‘s in the matrix’s binary equation, and the three solutions above bear no relation to the original evidence—of AB(CD)—as the sum of relationships expressed is ambiguous. Interestingly, the third solution, (AB)(CD), suggests that AB may contribute an extra (spurious) node, in analogous fashion to **Assumption 0** in biogeography (Brooks 1981, Wiley 1988), more or less equated with the invention of data (the extra node).

Augmented Component Analysis operates under the assumption that the original statement of relationship may be broken into its constituent parts, such that AB(CD) is exactly equivalent to A(CD) and B(CD) with one, both, or neither statement true when judged relative to other data. In terms of homology, this means that data may support the homology statement among taxa A, C, and D, or B, C, and D, or both. This viewpoint utilises the smallest unit, what we believe is *the* unit of systematics, the ***three-item statement***, a more or less exact representation of the cladistic parameter and a precisely defined minimal relationship (see above).

In Chapter 2 some solutions were discussed relative to viewing data in different ways. Three-item representation allows more solutions to be considered, even if they do not summarise all the data perfectly. In Chapter 12 we discuss some examples of three-item analysis that improve understanding of relationships.

# Chapter 12
# The Analyses of Relationships

## 12.1 Three-Item Data

Three-item data and their analysis may be viewed as a development of component analysis, originally devised for dealing with the relationships of geographic areas (Nelson & Platnick 1981, Platnick 1981, Ladiges et al. 1992, Nelson & Ladiges 1991a, b; see Nelson 1993: 359 and Nelson 1996: 13). When applied to taxa, the first accounts considered relationships from the perspective of solutions to three-taxon *problems* (Nelson & Platnick 1980 for the early cladogram-three-taxa problem approach and Platnick et al. 1996 for further comment). Three-item data depart from other analytical approaches by considering the "smallest possible unit of relationship", the three-item statement—what we consider to be *the* unit of classification (Chapters 7 and 11). In this sense, component matrices should be understood as variants on *group* representation, while three-item data—an entirely different way of viewing information – represent *relationships* directly. It is based on the understanding that taxon = homology (Nelson 1994). Nelson & Ladiges (1991a: 481) wrote of component approaches in biogeography that, "Our criticism is of component analysis of *groups*", a statement equally applicable to character data (see Platnick 1993).

The three-item approach sees systematic data as reducible to the simplest *relational* form, the three-taxa statement: hence, the statement A(BC), where B and C share a relationship to the exclusion of A based on evidence. Thus, three-item data directly represent the *cladistic parameter*, the common property of all aspects of systematic endeavour (organisms, areas, languages, etc.), probably (implicitly) from the beginnings of systematics (Nelson & Platnick 1981; see Chapter 1).

The details below should be understood as a guide rather than a definitive account. A specific program to implement the analysis of suites of three-item statements has yet to be written.

## 12.2 The Relationship Between Three-Item Statements and Binary Characters

For each binary character the number of possible three-item statements are given by the general formula $(t - n)n(n - 1)/2$, where $t$ = the number of taxa and $n$ = number of taxa with the informative state (Nelson & Ladiges 1992: Table 12.1, reproduced here as Figure 12.1).

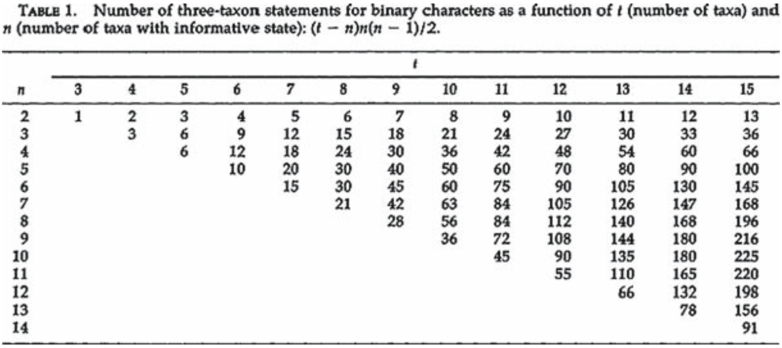


**TABLE 1.** Number of three-taxon statements for binary characters as a function of *t* (number of taxa) and *n* (number of taxa with informative state): $(t - n)n(n - 1)/2$.

| | *t* | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *n* | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 |
| 2 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 |
| 3 | | 3 | 6 | 9 | 12 | 15 | 18 | 21 | 24 | 27 | 30 | 33 | 36 |
| 4 | | | 6 | 12 | 18 | 24 | 30 | 36 | 42 | 48 | 54 | 60 | 66 |
| 5 | | | | 10 | 20 | 30 | 40 | 50 | 60 | 70 | 80 | 90 | 100 |
| 6 | | | | | 15 | 30 | 45 | 60 | 75 | 90 | 105 | 130 | 145 |
| 7 | | | | | | 21 | 42 | 63 | 84 | 105 | 126 | 147 | 168 |
| 8 | | | | | | | 28 | 56 | 84 | 112 | 140 | 168 | 196 |
| 9 | | | | | | | | 36 | 72 | 108 | 144 | 180 | 216 |
| 10 | | | | | | | | | 45 | 90 | 135 | 180 | 225 |
| 11 | | | | | | | | | | 55 | 110 | 165 | 220 |
| 12 | | | | | | | | | | | 66 | 132 | 198 |
| 13 | | | | | | | | | | | | 78 | 156 |
| 14 | | | | | | | | | | | | | 91 |

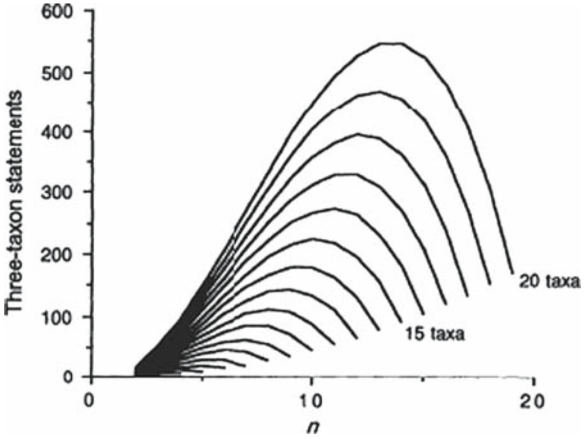


**Fig. 12.1** Table for total statements, $t = 14$, $t = 15$; in the original there was an error where values for $n = 6$ are 120 (not 130) for $t = 14$, and 135 (not 145) for $t = 15$; graph of relationship between $n$ and $t$. After Nelson & Ladiges (1992: Table 12.1 and Fig. 12.1)

When $n > 2$, there is redundancy among the statements and hence not all are independent. The number of independent three-item statements is $(n - 1)(t - n)$, and the absolute value is the ratio of independent statements to total statements, $2/n$ (Nelson & Ladiges 1992). For instance, for five taxa (ABCDE) of which two (DE) have the informative state, the total number of statements is three: A(DE), B(DE), C(DE). The number of independent statements is calculated by $(n - 1)(t - n) = (2 - 1)(5 - 2) = 3$ with an absolute value of $2/2 = 1$: All statements are independent (Figure 12.2).

In words, "independent" means that all the statements are required to accurately reflect the primary hypothesis, in the example above, ABC(DE). Thus, when all three statements are considered together, A(DE) + (B(DE) + C(DE) = ABC(DE); if any two statements are considered, the results differ: A(DE) + B(DE) = AB(DE), where taxon C is missing. However, for five taxa (ABCDE) of which three (CDE) have the informative state, the total number of statements is 6, whereas the number of independent statements is $(n - 1)(t - n) = (3 - 1)(5 - 3) = 4$. The six statements

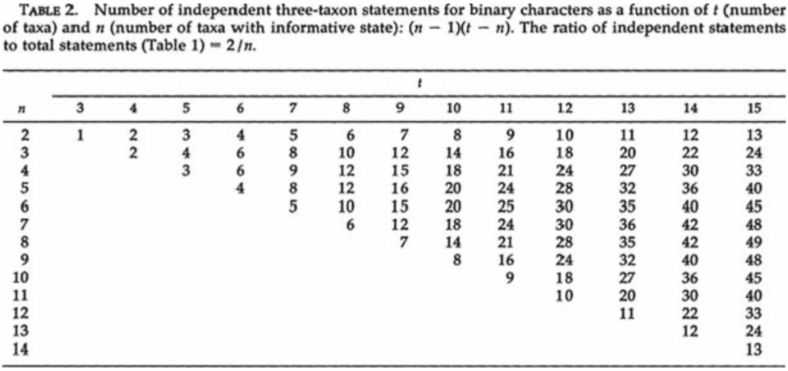


TABLE 2. Number of independent three-taxon statements for binary characters as a function of *t* (number of taxa) and *n* (number of taxa with informative state): $(n - 1)(t - n)$. The ratio of independent statements to total statements (Table 1) = $2/n$.

| | *t* | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *n* | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 |
| 2 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 |
| 3 | | 2 | 4 | 6 | 8 | 10 | 12 | 14 | 16 | 18 | 20 | 22 | 24 |
| 4 | | | 3 | 6 | 9 | 12 | 15 | 18 | 21 | 24 | 27 | 30 | 33 |
| 5 | | | | 4 | 8 | 12 | 16 | 20 | 24 | 28 | 32 | 36 | 40 |
| 6 | | | | | 5 | 10 | 15 | 20 | 25 | 30 | 35 | 40 | 45 |
| 7 | | | | | | 6 | 12 | 18 | 24 | 30 | 36 | 42 | 48 |
| 8 | | | | | | | 7 | 14 | 21 | 28 | 35 | 42 | 49 |
| 9 | | | | | | | | 8 | 16 | 24 | 32 | 40 | 48 |
| 10 | | | | | | | | | 9 | 18 | 27 | 36 | 45 |
| 11 | | | | | | | | | | 10 | 20 | 30 | 40 |
| 12 | | | | | | | | | | | 11 | 22 | 33 |
| 13 | | | | | | | | | | | | 12 | 24 |
| 14 | | | | | | | | | | | | | 13 |

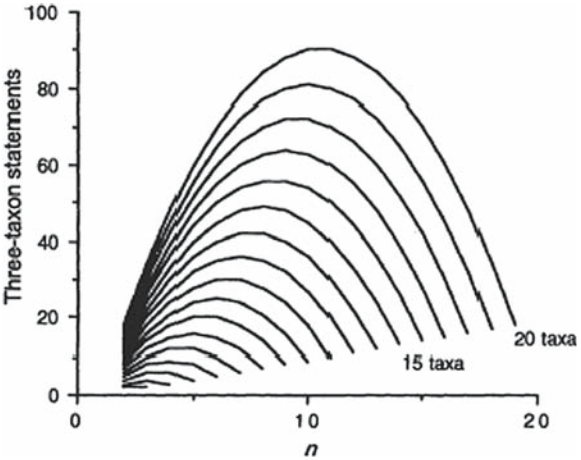


**Fig. 12.2** Table for independent statements, *t* = 14, *t* = 15; graph of relationship between *n* and *t*. After Nelson & Ladiges (1992: Table 12.2 and Fig. 12.2 )

are A(CD) + A(DE) + A(CE) + B(CD) + B(DE) + B(CE) = AB(CDE), one set of three statements corresponding to the relationships of A with CDE, the other set of three statements corresponding to the relationships of B with CDE. When all three statements for the relationships of A are considered together, A(DE) + A(CD) + A(CE) = A(CDE); if any two statements are considered, the solution is the same: A(DE) + A(CE) = A(CDE). The same holds for the relationships of B to CDE. Thus, each suite of three statements may be "fractionally weighted" by 2/3 with the total proportional weight 4/6. Only four statements are required to yield the correct answer, two from each suite, such as A(DE) + A(CE) + B(DE) + B(CE) = AB(CDE). However, all six statements are "true" for the initial observation; hence, no statement can be eliminated and a fractional weight (FW) is applied to compensate (Nelson & Ladiges 1992).

As redundant statements may offer spurious information, one would expect fractionally weighted data to be more precise (Nelson & Ladiges 1994).

## 12.3 The Relationship Between Three-Item Statements and Multi-State Characters

Multi-state characters are conventionally understood as suites of binary characters for the purpose of analysis, but as yet there is no clear consensus on the best way to achieve appropriate conversion for unordered characters (Mickevich 1982, Pimentel & Riggins 1987, Lipscomb 1992—if accurate conversion is possible at all; Meier 1994). Rendering multi-state characters as a series of binary characters (as in the standard approach to additive binary coding; Farris et al. 1970) may include redundant information, and the two representations may not be direct equivalents (Nelson 1993, Purvis 1995). A multi-state character should be more informative (as states are assumed dependent) than the pair of binary characters (which are assumed independent). From the perspective of three-item analysis, a multi-state character is equivalent to a suite of unique three-taxa statements with no statement appearing more than once (Nelson & Ladiges 1992).

## 12.4 Cladogram Length and Three-Item Statements

Once data are assembled as a matrix of three-item statements, they can be “fitted” to a cladogram(s) using any conventional parsimony programs (although this may not be the only way to achieve results; Platnick 1993, Wilkinson 1994b). As in standard parsimony analyses, the optimal tree is the shortest in length.

The relationship between tree length and three-item statements is simple. Tree length ($L$) = accommodated three-item statements + (2 × not accommodated three-item statements) (Nelson 1992: 357, Nelson & Ladiges 1994: 195). Nelson (1993: 262) noted that “ … Hennig86 (and PAUP) efficiently implements three-item analysis because tree length, if not optimization, is *exact*.” Thus, tree length will accurately reflect the fit of statements to tree. For fractionally weighted trees the length is the product of the number of statements and their fractional weight, so shorter trees do not necessarily fit more statements but fit a greater total weight (Nelson 1993, Nelson & Ladiges 1994).

## 12.5 Information Measures: How Good Is a Three-Item Cladogram?

There is a direct relationship between tree length and the number of accommodated three-item statements; hence, parsimony programs are adequate for finding optimal trees with these data. Nelson & Platnick (1991: 358) noted that the *ci* (consistency index) will either be 1.00 (for each statement that fits to a node of any particular cladogram) or 0.50 (when it fits to more than one node) and is rejected as a useful overall measure. However, *ri* (retention index) does scale each statement’s fit correctly and, along with tree length, accurately measures the fit of data to tree.

## 12.6 Minimal Trees

Parsimony analysis of any three-item matrix may yield one or more most parsimonious cladograms—but all may not be minimal. A minimal tree is the shortest tree (in terms of tree length) but with all resolved nodes supported by data (statements). Some parsimony programs will over-resolve trees by adding spurious nodes when missing values (represented with ?), for example, are present (Platnick et al. 1991, Nelson & Ladiges 1993: 112, Table 12.1). Nodes resolved by the inclusion of a question mark will not increase tree length. A minimal tree may be found by inspection of the strict consensus of all the most parsimonious trees (Nelson 1992). If the strict consensus tree is the same length as the original trees, then it is minimal and is the preferred solution. Thus, the "best" (minimal) tree will be that with all nodes supported by data as well as accommodating the greatest number of statements (see Nixon & Carpenter 1996 for similar applications to standard parsimony analyses).

Some simple examples are presented in Table 12.1. The first column of Table 12.1 contains eight examples from Nelson & Ladiges (1991a: Table 12.6), presented as pairs of three-item statements [A(BC) plus one other] for combining; the second–fifth columns are the numbers of trees recovered from analysis implemented using Hennig86 (Farris 1988), NONA, with (+) and without (–) ambiguous optimisations (Goloboff 1993) and Compatibility (implemented using Phylip, Felsenstein 1993), respectively. The sixth column is the "correct" solution (equivalent to the "Assumption 2" solution in biogeography). NONA produces one extra cladogram (a bush and hence not minimal) for examples 5 and 6, three extra non-minimal trees for example 7, and seven extra non-minimal trees for example 8. The protocol for determining minimal trees followed that outlined by Nixon & Carpenter (1996).

Other issues pertaining to minimality are relevant when "combining" statements. For example, the combination of A(BC) and A(DE) produces multiple cladograms with some parsimony programs (Table 12.1): Hennig86 produces 11 cladograms, NONA with ambiguous optimisation active produces 9 and with unambiguous

**Table 12.1** Several simple examples

| Examples | Programs | | | | Minimal Tree |
|---|---|---|---|---|---|
| | Hennig86 | NONA (+) | NONA (–) | Compat. | |
| Four Taxa | | | | | |
| 1. A(BC) + D(BC) | 3 | 1 | 1 | 3 | AD(BC) |
| 2. A(BC) + A(CD) | 3 | 1 | 1 | 3 | A(BCD) |
| 3. A(BC) + C(BD) | 1 | 1 | 1 | 1 | A(B(CD) |
| 4. A(BC) + B(AD) | 1 | 1 | 1 | 1 | (AD)(BC) |
| Five Taxa | | | | | |
| 5. A(BC) + D(CE) | 11 | 11 | 4(3) | 7 | AD(BCE) |
| 6. A(BC) + A(DE) | 11 | 9 | 3(2) | 14 | A(BC)(DE) |
| 7. A(BC) + B(DE) | 7 | 7 | 7(4) | 7 | A(BC)(DE) |
| Six Taxa | | | | | |
| 8. A(BC) + D(EF) | 55 | 47 | 18(11) | 27 | AD(BC)(EF) |

optimisation non-active produces 2: A(BC)(DE) and A(BCDE).[1] These two cladograms differ as the first, A(BC)(DE), has two nodes, and the second, A(BCDE), has one. Intuitively, the one-node cladogram might be assumed minimal, or at least as good as the alternative, A(BC)(DE). However, with the accumulation of more data relevant to this solution, the situation differs.

For the cladogram A(BC)(DE), addition of further non-conflicting statements results in the cladogram A(BCDE). For instance, if A(BE) is added to A(BC) + A(DE), the solution becomes A(BCDE). Conversely, there are no data that could be added to the cladogram A(BCDE) to yield the cladogram A(BC)(DE). Thus, the one-node cladogram, A(BCDE), requires *more* data than the two-node cladogram and the latter, in this sense, is minimal (Nelson & Ladiges 1996). In this respect, cladograms resulting from three-item analysis need closer inspection than simply accepting the suite of most parsimonious trees or, indeed, simply inspecting the strict consensus of all cladograms produced. Such situations help to focus on exactly what data do support nodes in the resulting trees. An appreciation of how three-item analysis deals with increasing resolution with increasing data points again to its greater precision.

Wilkinson (1994b) suggested that "parsimony" analysis of a three-item matrix should yield identical results to a compatibility analysis. In other words, a "correct" solution can be arrived at by the use of either a compatibility program or a parsimony program. Wilkinson (1994b: 222) provided three examples of three-item analysis that violates the "pairwise compatibility theorem" (Fitch 1975). His examples are combinations of pairs of three-item statements drawn from a selection of three:

$$\mathrm{D(AB),\ B(AC),\ C(AD).}$$

Each permutation yields one tree:

$$\begin{gathered}\mathrm{D(AB)} + \mathrm{B(AC)} = \mathrm{D(B(AC))},\\ \mathrm{D(AB)} + \mathrm{C(AD)} = \mathrm{C(D(AB))},\\ \mathrm{B(AC)} + \mathrm{C(AD)} = \mathrm{B(C(AD))}.\end{gathered}$$

With a parsimony program, results are the same (a single cladogram for each combination). Wilkinson concluded that because optimisation of the missing value in each permutation requires a different value each time, the statements are incompatible, and because "… missing entries invalidate the pairwise compatibility theorem … it limits its applicability to three-item statements of the character-based approach to clique analysis" (Wilkinson 1994b: 223).

The logic is the same as applied to implementation using parsimony analysis: Because a *program* does something, the *non-computed* conclusion must be incorrect. Of greater interest is that compatibility programs find the same solution as

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[1] In actual fact, NONA produces three cladograms. The third cladogram, not discussed above, is a collapsed bush.

the parsimony programs. However, if results from the compatibility analyses are compared to those of the parsimony analyses (Table 12.1), then examples 5, 6, and 8 differ in the number of cladograms produced. Examples 2 and 5 do not contain the correct (“Assumption 2”) solution among the results. This appears to suggest that current compatibility programs do not necessarily find minimal trees when used for the analysis of three-item data, in spite of the obvious advantage of their use.

## 12.7 Explanations

For standard binary or multi-state characters, to explain the distribution of 1’s (the apomorphic state) that do not fit to a node, precisely either a “mistaken” homology decision has been made (hence, two separate “origins” of the “character” 1; they are the “same” but not homologous) or else an additional transformation from 1 → 0 (a “reversal”, the 1’s are homologous but one taxon has reverted to the 0 state) in one taxon must be assumed (two steps in each case). These are the basics of optimisation: Characters are distorted to fit the optimal tree under a “step-counting” procedure; both “kinds” of optimisation require character transformation (distortion) to explain its distribution on a tree.

A three-item statement is not a character in this conventional sense, and notions of transformation (and optimisation) simply do not and cannot apply. A three-item statement is the *relationship* implied by a group of two taxa in relation to a third and the statement either will fit a particular tree or will not.

## 12.8 “Reversals”

Consider the following binary matrix (1–3 are characters, A–C are taxa, OG is the outgroup):

|  | 1 | 2 | 3 |
|---|---|---|---|
| OG | 0 | 0 | 0 |
| A | 0 | 0 | 1 |
| B | 1 | 1 | 1 |
| C | 1 | 1 | 0 |

Analysed using a parsimony program, the matrix yields one cladogram, A(BC), based on the exact fit of characters 1 and 2. Character 3 can fit A(BC) in two different ways as represented by cases 1 and 2. For each case, characters 3a and 3b are the “distortions” required to fit character 3 to the optimal tree; both kinds of “distortion” are equal under optimisation (see Chapter 11).

| | Case 1 | | | | Case 2 | | | |
|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3a | 3b | 1 | 2 | 3a | 3b |
| OG | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| A | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| B | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 |
| C | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 |

For case 1, character 3 is understood to "harbour" a reversal, as the data imply that the 0 of taxon C is really derived, thereby forming a character for the entire group, A + B + C, and a unique character (apomorphy) for taxon C.

For case 2, character 3 is understood to harbour two independent apomorphies for taxa A and B(1s), both distortions required to find (and explain) the optimal cladogram.

Three-item analysis finds the same result, A(BC), but has no need to invoke explanations for characters that do not fit the optimal cladogram (character 3): They simply does not fit that particular cladogram; for the purposes of those data and result, character 3 may be thought of as false.

## 12.9 Alternatives to Simulation

Examination, understanding, and testing of various analytical methods—such as parsimony, maximum likelihood, etc.—often employ simulation studies. The basic premise behind each simulation study is to create a particular model of character-state change, construct trees conforming to these parameters, and test programs for their efficiency in recovering trees specified by the parameters. Here we suggest an alternative strategy. Data matrices might be designed such that they include various kinds of character conflict, making it possible to "test" the performance of programs relative to those data. The "test" matrices require design, as there are serious flaws when using random data, for example.

Reasons for not using matrices composed of random data were presented by Goloboff (1991), who suggested the idea of *decisiveness* and illustrated it with reference to matrices that are completely *undecisive*. These were of two classes: (1) matrices of uninformative characters, and (2) matrices of informative characters.

For class (1), Goloboff noted that, for parsimony analyses, "every possible tree, resolved or unresolved, has the same length." For the latter class, "every dichotomous tree has the same length." For a matrix of the latter class, "every possible informative character is found in the matrix in equal numbers." Thus, for the simplest kind, with an outgroup (O) and one character in three taxa, BCD, all possible trees (unresolved and resolved) would have the same length (Table 12.2, columns 1 and 2). Another matrix has an all-zero outgroup (O) and three characters conflicting in all possible combinations of two out of three taxa BCD (Table 12.2, columns 3–6). For this matrix, Goloboff noted that "every one of the three possible dichotomous trees has exactly the same length, 5, a CI of 0.60, and an RI of 0.33."

**Table 12.2** Two example matrices: an all-zero outgroup (O) and one character in three taxa, BCD (columns 1 and 2), an all-zero outgroup (O) and three characters conflicting in all possible combinations of two out of three taxa BCD (columns 3–6)

| | 1 | | 1 | 2 | 3 |
|---|---|---|---|---|---|
| **O** | 0 | **O** | 0 | 0 | 0 |
| **B** | 1 | **B** | 0 | 1 | 1 |
| **C** | 1 | **C** | 1 | 0 | 1 |
| **D** | 1 | **D** | 1 | 1 | 0 |

The two matrices bear some relationship to each other. If the matrix of characters is understood as cladograms (mini-cladograms), then the first matrix has (represents) one unresolved cladogram—O(BCD)—which is equivalent to the three resolved cladograms of the second matrix: OB(CD), OC(BD), OD(BC). Therefore, the matrices are equivalent in that sense as

$$\mathrm{BCD} = \mathrm{B(CD)} + \mathrm{C(BD)} + \mathrm{D(BC)}.$$

However, with a parsimony analysis, O(BCD) has a length of 6, one step longer than each of the three resolved trees.

These two matrices might be enhanced by adding an additional taxon (A), identical to the outgroup (Table 12.3). Here, the first matrix has all possible cladograms relating taxa BCD with length 1: A(BCD), A(B(CD)), A(C(BD)), A(D(BC)) (Table 12.3, column 1). For the second matrix, all resolved cladograms relating taxa BCD have length 5: A(B(CD)), A(C(BD)), A(D(BC)) (Table 12.3, columns 1–3). Tree A(BCD) has length 6, one step longer. The strict consensus of all trees found (6) for the second matrix is not A(BCD) but remains unresolved: ABCD.

**Table 12.3** Two matricies of four taxa relative to the relationship A(BCD).

| | 1 | | 1 | 2 | 3 |
|---|---|---|---|---|---|
| **O** | 0 | **O** | 0 | 0 | 0 |
| **A** | 0 | **A** | 0 | 0 | 0 |
| **B** | 1 | **B** | 0 | 1 | 1 |
| **C** | 1 | **C** | 1 | 0 | 1 |
| **D** | 1 | **D** | 1 | 1 | 0 |

The six trees found for the second matrix (Table 12.3, columns 1–3) include the three resolved trees for taxa BCD and three partially resolved trees: AB(CD), AC(BD), AD(BC). The partially resolved trees together duplicate the matrix and are redundant and irrelevant as AB(CD) is character 1, AC(BD) is character 2, AD(BC) is character 3. If the redundant trees are ignored, then the first and second matrices are equivalent. The three resolved trees yield the strict consensus A(BCD).

Alternatively, the three partially resolved trees—the characters of the second matrix—find the same solution:

| AB(CD) | = | A(CD) | + | B(CD) | | |
|---|---|---|---|---|---|---|
| AC(BD) | = | A(BD) | + | C(BD) | | |
| AD(BC) | = | A(BC) | + | D(BC) | | |
| | | A(BCD) | + | BCD | = | A(BCD) |

This alternative is equivalent to a parsimony analysis of the corresponding three-item matrices (Table 12.4).

For a three-item matrix of the same characters as the first matrix (Table 12.4, columns 1–4), all possible trees relating taxa BCD have length 3 (uniform weighting): A(BCD), A(B(CD)), A(C(BD)), A(D(BC)). For a three-item matrix of the same characters as the second matrix (Table 12.4, columns 5–11), all resolved trees relating taxa BCD, the only trees found for that matrix, have length 8: A(B(CD)), A(C(BD)), A(D(BC)). The strict consensus of the three trees found, A(BCD), has length 9.

These matrices are *undecisive* with respect to relationships among taxa B–D, but are *decisive* with respect to the relationships of taxa BCD to taxon A.

Goloboff noted that "the number of possible different (informative) characters for T taxa (plus a root) is 2T – T – 2. From this it follows that for a matrix to be completely undecisive it must have a number of informative characters equal to (or an exact multiple of) 2T – T – 2". Accordingly, for 3 taxa (B–D), 3 different characters are required; for 4 taxa (B–E), 10 characters; for 5 taxa (B–F), 25 characters; for 6 taxa (B–G), 56 characters; for 7 taxa (B–H), 119 characters; for 8 taxa (B–I), 256 characters; and so on.

It should be clear that random matrices cannot be either completely undecisive or completely decisive—they will always have a signal as long as any one character is duplicated.

The six matrices with such characters are among the 120 analysed previously for groups of taxa B–D through B–I (Nelson 1996). For 114 other matrices with fewer characters, optimisation of three-item matrices assigns equal weight to all resolved trees (3 trees for 3 taxa B–D, 15 trees for 4 taxa B–E, 105 trees for 5 taxa B–F, etc.). Optimisation of standard matrices assigns unequal weight to resolved trees.

The parsimony results from 96 of these 120 matrices found the group B–*n.* relative to A, while 24 did not. In other words, over three-quarters find an informative consensus as a solution—a sufficient number to suspect that matrices of this kind

**Table 12.4** Three-item matrix representation of data in Table 12.3

| | Three-Item Matrices | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 1 | 1 | | 1 | 2 | 3 | 1 | 2 | 3 |
| | A | b | C | | a | b | c | a | b | c |
| **O** | 0 | 0 | 0 | **O** | 0 | 0 | 0 | 0 | 0 | 0 |
| **A** | 0 | 0 | 0 | **A** | 0 | 0 | 0 | ? | ? | ? |
| **B** | ? | 1 | 1 | **B** | ? | 1 | 1 | 0 | 1 | 1 |
| **C** | 1 | ? | 1 | **C** | 1 | ? | 1 | 1 | 0 | 1 |
| **D** | 1 | 1 | ? | **D** | 1 | 1 | ? | 1 | 1 | 0 |

are generally informative. Three-item statements analysis of the same 120 matrices *always* yields the informative consensus.

These kinds of matrices are more efficient in judging performance of both kinds of data and methods of analysis—random data contain a signal, even though they are random.

### 12.9.1 "Nullius in Verba" (Nelson 1996): Outgroups, Polarity, and Data

Further examination of the simplest matrix with conflicting characters is possible. If the parts of the character entries considered to be evidence have the positive numbers (1's) and the lack of evidence has negative numbers (0's), there are several possible ways these data might be represented.

The first example consists of entries with just 1's and 0's. The first data set consists of three "unpolarised" characters (Table 12.4). Considered as homology statements (or groups), the data consist of three positive (1's) groups (BC, BD, and CD) and three negative groups (AD, AC, AB). The positive groups may be considered specific homology statements in that BC are grouped relative to A, BD are grouped relative to A, and CD are grouped relative to A, based on evidence. The negative groups are the residual statements related by a common shared absence. Thus, the negative groups are not really homology statements at all.

| Character | Positive | Negative |
|---|---|---|
| 1 | BC | AD |
| 2 | BD | AC |
| 3 | CD | AB |

To polarise characters, one might consider using either outgroups or ontogeny to provide appropriate values. Values may be either positive or negative. The data set in Table 12.5 has an all-zero outgroup. Thus, the data consist of three positive (1's) components: BC, BD, and CD, which together relate to A as in the summary A(BCD), as BC + BD + CD = A(BCD).

**Table 12.5**

| | 1 | 2 | 3 |
|---|---|---|---|
| A | 0 | 0 | 0 |
| B | 1 | 1 | 0 |
| C | 1 | 0 | 1 |
| D | 0 | 1 | 1 |

| Group | Positive | Negative |
|---|---|---|
| 1 | BC | — |
| 2 | BD | — |
| 3 | CD | — |

The data set in Table 12.6 has an all-positive outgroup (1's), making all the 0 (absent) entries "informative". The data consist of three "positive" (0's) components: AD, AC, and AB. Together they relate no taxa, as AD + AC + AB = ABCD.

| Component | "Positive" | "Negative" |
|---|---|---|
| 1 | AD | — |
| 2 | AC | — |
| 3 | AB | — |

The data set in Table 12.7 consists of three characters "polarised" by an outgroup with all question marks (literally meaning either 0's or 1's, the values are unknown). These data consist of three positive (1's) components (BC, BD, and CD) and three negative components (AD, AC, AB). Together they relate no taxa at all:

$$\begin{aligned} BC + BD + CD &= A(BCD), \\ AD + AC + AB &= (ABCD), \\ A(BCD) + (ABCD) &= (ABCD). \end{aligned}$$

| Component | Positive | Negative |
|---|---|---|
| 1 | BC | AD |
| 2 | BD | AC |
| 3 | CD | AB |

**Table 12.6**

|  | 1 | 2 | 3 |
|---|---|---|---|
| O | 0 | 0 | 0 |
| A | 0 | 0 | 0 |
| B | 1 | 1 | 0 |
| C | 1 | 0 | 1 |
| D | 0 | 1 | 1 |

**Table 12.7**

| O | 1 | 1 | 1 |
|---|---|---|---|
| A | 0 | 0 | 0 |
| B | 1 | 1 | 0 |
| C | 1 | 0 | 1 |
| D | 0 | 1 | 1 |

The data set in Table 12.8 consists of three multi-state characters “polarised” by an all-zero outgroup. The difference between multi-state characters and binary characters might be the information contained in the “uninformative” portion, the 0’s. Consider feathers as one of the characters. The 0 might be taken to mean no feathers, or feathers absent. “Feathers absent” relates the data (feathers) to all life that lacks feathers, which can be represented by a binary character. This, in turn, might suggest that we can postulate a taxon with feathers (birds) but do not know more precisely of its relationships to the rest of life. If our knowledge is rather better and we feel comfortable proposing that feathers relate to lizard scales, then this may now be construed as a multi-state character, with increased complexity (Nelson 1994). The increased complexity suggests that we might discover two taxa, birds (with feathers) and birds + lizards (lizard scales + feathers). Yet the complexity might include ignorance in not knowing which–feathers or lizard scales–is the subset, the homology relative to the set lizard scales plus feathers. In this case it might be seen that both lizard scales and feathers are data in as much as they are real observations. In this (artificial) case, these data consist of six positive (1’s and 2’s) components (BC, BD, CD and AD, AC, AB). Together they relate no taxa at all:

| Component | Positive | Negative |
|---|---|---|
| 1 | AD | — |
| 2 | AC | — |
| 3 | AB | — |
| 4 | BC | — |
| 5 | BD | — |
| 6 | CD | — |

The data set in Table 12.10 consists of binary representation of the multi-state characters from the data set in Table 12.9, or binary representation of “paired homologues” (Scotland 2000b). Thus, if character 1 is feathers and lizard scales, then 1a is the “feather” homologue and 1b is the lizard scale homologue. These data yield six positive and six negative components. In other words, each possible homology statement is supported by both a positive and a negative component. Together they relate no taxa at all:

| Component | Positive | Negative |
|---|---|---|
| 1 | AD | AD |
| 2 | AC | AC |
| 3 | AB | AB |
| 4 | BC | BC |
| 5 | BD | BD |
| 6 | CD | CD |

**Table 12.8**

| O | ? | ? | ? |
|---|---|---|---|
| A | 0 | 0 | 0 |
| B | 1 | 1 | 0 |
| C | 1 | 0 | 1 |
| D | 0 | 1 | 1 |

**Table 12.9**

|  | 1 | 2 | 3 |
|---|---|---|---|
| O | 0 | 0 | 0 |
| A | 2 | 2 | 2 |
| B | 1 | 1 | 2 |
| C | 1 | 2 | 1 |
| D | 2 | 1 | 1 |

**Table 12.10**

|  | 1a | 1b | 2a | 2b | 3a | 3b |
|---|---|---|---|---|---|---|
| A | 0 | 1 | 0 | 1 | 0 | 1 |
| B | 1 | 0 | 1 | 0 | 0 | 1 |
| C | 1 | 0 | 0 | 1 | 1 | 0 |
| D | 0 | 1 | 1 | 0 | 1 | 0 |

With the addition of an all-zero outgroup (Table 12.11), these data yield six positive components, identical to that of the data set in Table 12.10 using multi-state characters. Together they relate no taxa at all.

| Component | Positive | Negative |
|---|---|---|
| 1 | AD | — |
| 2 | AC | — |
| 3 | AB | — |
| 4 | BC | — |
| 5 | BD | — |
| 6 | CD | — |

Examination of these permutations–all possible representations–suggests resolution is achieved using only three-item analysis relating positive occurrences only (Table 12.12). Thus, it can be demonstrated that results are dependent on representation.

**Table 12.11**

|  | 0 | 0 | 0 | 0 | 0 | 0 |
|---|---|---|---|---|---|---|
| A | 0 | 1 | 0 | 1 | 0 | 1 |
| B | 1 | 0 | 1 | 0 | 0 | 1 |
| C | 1 | 0 | 0 | 1 | 1 | 0 |
| D | 0 | 1 | 1 | 0 | 1 | 0 |

**Table 12.12**

| Data Set | Characters | “Root” | Positive Components | Negative Components | Standard Analysis | Three-Item Analysis |
|---|---|---|---|---|---|---|
| a) | Binary | None | 3 | 3 | — | — |
| b) | Binary | Positive | 3 | 0 | — | + |
| c) | Binary | Negative | 3 | 0 | — | — |
| d) | Binary | Pos. + Neg. | 3 | 3 | — | — |
| e) | Multi-state | Positive | 6 | 0 | — | — |
| f) | Multi-state | None | 6 | 6 | — | — |
| g) | Binary | Positive | 6 | 0 | — | — |

### *12.9.2 Precision and Simple Matrices (Platnick et al. 1996)*

Platnick et al. (1996) demonstrated another advantage of three-item data. Using one binary character, such that C and D share the apomorphic state and A and B share the plesiomorphic state, yields (unequivocally) the solution AB(CD). Inspection of all 26 possible cladograms provides an indication of how poorer solutions (non-optimal) compare to the correct solution. When AB(CD) is measured against all the 26 possible solutions, there are two series. Four cladograms have one step, while the remaining 22 have two steps. Examination of the cladograms with two steps implies that, among other things, completely incorrect solutions are as good (or as bad) as some partially correct solutions, even the totally unresolved bush (see also Platnick 1989: 23, Chapter 2).

AB(CD) has two three-item statements, A(CD) and B(CD). Its analysis will, of course, find (unequivocally) the solution AB(CD). If the two statements are measured against all 26 possible solutions, three series, rather than two, are obtained. Four cladograms have 2 steps, 6 have 3 steps, and 16 have 4 steps. Thus, data represented as series of three-item statements are more “precise”, in the sense that they partition possible solutions in a more efficient way.

What, then, is the significance of such partitioning? That lies in the value of different cladograms as more data accumulate. For example, using the standard approach, two of the 26 cladograms explain none of the data. However, using three-item statements, one cladogram includes one statement, A(CD), and hence explains at least some of the data. The value of three-item data is that they are likely to be more sensitive to the accumulation of further data than are the usual binary (phenetic) characters.

Of interest is that the fully resolved solutions selected by the usual binary character approach correspond to the “Interpretation 1” solutions, originally proposed by Nelson & Platnick (1980) for dealing with potential resolution of basal trichotomies. In contrast, the fully resolved solutions selected by the three-item approach correspond to the “Interpretation 2” solutions proposed by Nelson & Platnick (1980), where the close relationship of C and D is maintained, even though A or B is more closely related to either C or D (see Chapter 2). Finally, Interpretations 1 and 2 bear some resemblance to Assumptions 1 and 2 in biogeography, while “secondary” symplesiomorphy, "reversals", and plesiomorphies as "potentially informative" have a certain amount of similarity with Assumption 0 of biogeography, a somewhat questionable protocol as it invents data to allow optimisation to function properly and find optimal trees.

### *12.9.3 Comparison of Cladograms and Single Non-Conflicting Characters*

Any standard binary character can be compared to any other non-conflicting character. Any pair of non-conflicting characters may support (imperfectly) certain combinations of taxa.

Consider all possible permutations of a binary character with nine informative taxa and two uninformative taxa, such as AB(CDEFGHIJK). There are at least 502 informative permutations (this number does not exhaust all possible permutations). A selection from the 502 possibilities can be considered against a cladogram that does not conflict with any of these possibilities.

Consider again the binary character AB(CDEFGHIJK) and a general cladogram expressing exactly the relationship, AB(CDEFGHIJK). If the binary character AB(CDEFGHIJK) is fitted to (mapped onto) the cladogram AB(CDEFGHIJK), it has length 1, *ci* = 100, *ri* = 100; that is, it is an exact fit (Table 12.13a). If the same character AB(CDEFGHIJK) is fitted to (mapped onto) a different general cladogram, ABC(DEFGHIJK), then it has length 2, *ci* = 50, *ri* = 50 (Table 12.13b). If the same character AB(CDEFGHIJK) is fitted to (mapped onto) a further general cladogram, ABCD(EFGHIJK), then it has length 3, *ci* = 33, *ri* = 0 (Table 12.13c). In short, if the binary character AB(CDEFGHIJK) is fitted to (mapped onto) cladograms with group membership decreasing by a single taxon at a time, regardless of the size of the group, the character always report length 3, *ci* = 33, *ri* = 0 (Table 12.13d–h).

Inspection of the retention index (Table 12.13, column 5) shows the amount of grouping information in that character for that particular cladogram. The character AB(CDEFGHIJK) does not conflict with any of the cladograms in the series. Thus, the binary character relates to the majority of the non-conflicting cladograms as if it were totally uninformative (*ri* = 0 for examples c–h). The reason is clear. The 0's

**Table 12.13** A series of cladograms used to fit the single binary character AB(CDEFGHIJK)

| Cladogram | + | Character | Length | *ci* | *ri* |
|---|---|---|---|---|---|
| a) AB(CDEFGHIJK) | + | AB(CDEFGHIJK) | 1 | 100 | 100 |
| b) ABC(DEFGHIJK) | + | AB(CDEFGHIJK) | 2 | 50 | 50 |
| c) ABCD(EFGHIJK) | + | AB(CDEFGHIJK) | 3 | 33 | 0 |
| d) ABCDE(FGHIJK) | + | AB(CDEFGHIJK) | 3 | 33 | 0 |
| e) ABCDEF(GHIJK) | + | AB(CDEFGHIJK) | 3 | 33 | 0 |
| f) ABCDEFG(HIJK) | + | AB(CDEFGHIJK) | 3 | 33 | 0 |
| g) ABCDEFGH(IJK) | + | AB(CDEFGHIJK) | 3 | 33 | 0 |
| h) ABCDEFGHI(JK) | + | AB(CDEFGHIJK) | 3 | 33 | 0 |

in the matrix (the uninformative plesiomorphic values for taxa A and B) eventually become informative and the step count has to include them.

The counts of occurrences (the length in steps) are “explained” by various kinds of “origin” hypotheses. Consider the first example:

| | | | | | |
|---|---|---|---|---|---|
| a) AB(CDEFGHIJK) | + | AB(CDEFGHIJK) | 1 | 100 | 100 |

a) The group CDEFGHIJK is “explained” by homology (1 step).
Consider the second example:

| | | | | | |
|---|---|---|---|---|---|
| b) ABC(DEFGHIJK) | + | AB(C–DEFGHIJK) | 2 | 50 | 50 |

b) C is explained by a unique occurrence (1 step, C is outside the group of the cladogram); DEFGHIJK is explained by homology (1 step, it is inside the group of the cladogram).
Consider the third example:

| | | | | | |
|---|---|---|---|---|---|
| c) ABCD(EFGHIJK) | + | AB(CD–EFGHIJK) | 3 | 33 | 0 |

c) Taxa C and D are explained by unique occurrences (1 step each, both C and D are outside the group of the cladogram); EFGHIJK is explained by homology (1 step, it is inside the group of the cladogram).
Consider the fourth example, when the “process” of optimisation begins to have a distorting effect:

| | | | | | |
|---|---|---|---|---|---|
| d) ABCDE(FGHIJK) | + | AB–(CDEFGHIJK) | 3 | 33 | 0 |

d) Here, the entire group ABCDEFGHIJK is explained by homology (1 step), but A and B are explained by two separate “reversals” (1 step each). No part of the original character is considered synampomorphic and is uninformative.

This explanation applies to every subsequent cladogram is this series regardless of whether they differ. Rather than speak to homology,“reversals”, homoplasy, or any other ad hoc explanation, each cladogram is inextricably bound to the method of optimisation:

| | | | | | |
|---|---|---|---|---|---|
| d) ABCDE(FGHIJK) | + | AB(CDEFGHIJK) | 3 | 33 | 0 |
| e) ABCDEF(GHIJK) | + | AB(CDEFGHIJK) | 3 | 33 | 0 |
| f) ABCDEFG(HIJK) | + | AB(CDEFGHIJK) | 3 | 33 | 0 |
| g) ABCDEFGH(IJK) | + | AB(CDEFGHIJK) | 3 | 33 | 0 |
| h) ABCDEFGHI(JK) | + | AB(CDEFGHIJK) | 3 | 33 | 0 |

In all cladograms from c–h, the binary character AB(CDEFGHIJK) is uninformative, in spite of the fact that it does not conflict with the given cladogram.

**Table 12.14** A series of cladograms used to fit the 72 three-item statements derived from the binary character AB(CDEFGHIJK)

| Cladograms | + | Characters | Length | ci | RI[2] | Tot. Stat. |
|---|---|---|---|---|---|---|
| a) AB(CDEFGHIJK) | + | AB(CDEFGHIJK) | 72 | 100 | 100 | 72 |
| b) ABC(DEFGHIJK) | + | AB(CDEFGHIJK) | 88 | 81 | 77 | 56 |
| c) ABCD(EFGHIJK) | + | AB(CDEFGHIJK) | 102 | 70 | 58 | 42 |
| d) ABCDE(FGHIJK) | + | AB(CDEFGHIJK) | 114 | 63 | 41 | 30 |
| e) ABCDEF(GHIJK) | + | AB(CDEFGHIJK) | 124 | 58 | 27 | 20 |
| f) ABCDEFG(HIJK) | + | AB(CDEFGHIJK) | 132 | 54 | 16 | 12 |
| g) ABCDEFGH(IJK) | + | AB(CDEFGHIJK) | 138 | 52 | 8 | 6 |
| h) ABCDEFGHI(JK) | + | AB(CDEFGHIJK) | 142 | 50 | 2 | 2 |

What of three-item representation? For a standard binary character with 9 informative states, there are 72 three-item statements. Thus, for the character AB(CDEFGHIJK), 72 possible statements of relationship may be considered true. Comparison of the same series of characters and cladograms illustrates a sliding scale of fit that is accurately reflected in the tree length, the *ri*, and the total number of statements on the tree (Table 12.14). Note that even with the poorest match, example h, two statements remain true–A(JK) and B(JK)–both reflect the relationships in the data and the cladogram considered.

## 12.10 Summary

Rather than labour the point, the few examples above suggest that an exploration of systematic data, as opposed to the creation of a multitude of models, is a more productive way of determining taxon relationships. In effect, we see the exploration of various weighting schemes ("models") to be a modern preoccupation with artificial systems of classification—it is time to investigate the possibilities of discovering the "natural classification", for organisms, by an inspection of the way data are represented.

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[2] Note that the *ri* actual statements/total statement × 100; e.g., 56/72 × 100 = 77.77.

# Chapter 13
# Biogeographical Relationships, Evolution, and Classification

## 13.1 Prelude

Biogeography is often understood to be part of evolutionary biology, yet an examination of the field reveals two distinct aspects: that historically, evolutionary biology came from, or is a result of, biogeographical studies, and that most, if not all, biogeographers tend to be evolutionary biologists. In order to unravel the history and ontology of biogeography, it is important to understand why biologists undertake distributional studies.

Some of the first naturalists to pose questions concerning the distribution of organisms were the ancient Greeks. Aristotle, for example, believed that climate and geography determined an organism's form:

> In many places the climate will account for peculiarities; thus in Illyria, Thrace, and Epirus the ass is small, and in Gaul and in Scythia the ass is not found at all owing to the coldness of the climate of these countries. (Aristotle *History of Animals*, VIII: 28)

Aristotle listed variations between similar organisms from different areas—such as the bite of scorpions—indicating that organisms, like the landscape, are products of the elements peculiar to a given area.

> Again, locality is an important element in regard to the bite of an animal. Thus, in Pharos and other places, the bite of the scorpion is not dangerous; elsewhere—in Caria, for instances—where scorpions are venomous as well as plentiful and of large size, the sting is fatal to man or beast, even to the pig, and especially to a black pig, though the pig, by the way, is in general most singularly indifferent to the bite of any other creature. If a pig goes into water after being struck by the scorpion of Caria, it will surely die. (Aristotle *History of Animals*, VIII, 29)

A similar idea occurred to the 7th-century Irish monk Augustine, who also noted the distribution of organisms in Ireland in relation to the ebb and flow of the tides (Hofsten 1916). He believed that a sudden drop in sea level offered various organisms a land bridge with which they could cross the Irish Sea.

If both Aristotle's and Augustine's observations are considered steps towards understanding the distribution of organisms, then it would be towards understanding the areas they occupy rather than the mechanisms for their dispersion (for an examination of dispersion, see below).

The discovery of the Americas, and the striking similarities between Old and New World species, brought greater attention to dispersion and its mechanisms. For large mammals, for example, the disjunct distributions were too great, the oceans too deep, and the Earth too static to explain the apparent geographical anomalies. Thus, organisms were responsible for their distribution. Therefore, it was supposed that by only achieving an understanding of the distributional mechanisms of various taxa can their distribution—their biogeography—be understood.

During the 17th century, naturalists turned their attention to the origin of species and their centres of creation. Georges-Louis Leclerc, Compte de Buffon (1707–1788), was the first to offer a method to explain distribution patterns. Buffon was struck by the many resemblances between New and Old World taxa. Eurasian, Indian—even Far East Asian taxa—were known to be both similar and diverse. Their distribution could be easily explained by a consideration of the climate in the areas in which they were found. The Americas, however, were not open to these explanations. If the Earth was static, non-changing, its one land bridge—the Arctic or Bering Strait—provided no easy explanations for the distribution of disjunct tropical species. The failure to explain geographical or inorganic processes, such as sea level changes or erosion of barriers, meant that the organisms themselves had the ability to travel across vast distances. What's more, species from the New and Old World that lived with the same climatic conditions only *appeared* similar. Organisms living in the same environment in the New and Old World formed the same physical attributes but were actually *different* species. Aristotle had been wrong: Similar climates produced similar *looking* characteristics, not the *same* species. Buffon (1761) generalised these observations, suggesting that organisms changed over time to accord with their environment. A cat, if relocated to a hot and humid climate, such as the African plain, will, over time, "become" a lion. Thus, organisms change the farther they are moved away from their centre of origin. Nelson (1978c) called this Buffon's law—still the *prima facie* of modern biogeography.

Thus, in some senses, the history of modern biogeography began with Buffon and was only significantly developed by Augustin Pyramus de Candolle (1788–1841). Candolle was France's foremost botanist—indisputably the father of biogeography (Ebach & Goujet 2006[1]—whose work was read widely, discussed, and, in some cases, translated. In his *Essai Élémentaire de Geographie Botanique* (Candolle 1820), Candolle outlined some principles for understanding the distribution of organisms. It was in this essay that Candolle created *stations* and *habitations*:

> By the term *station* I mean the special nature of the locality in which each species customarily grows; and by the term *habitation*, a general indication of the country wherein the plant is native. (Candolle 1820: 383, translated in Nelson 1978c: 280)

Candolle's habitations and stations—the latter translated into English as *habitat*—represent the beginnings of ecological and historical biogeography, respectively (see Nelson 1978c: 280–281).

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[1] Candolle was the first to produce a biogeographical map. (Lamarck & Candolle 1805; see Ebach & Goujet 2006).

In the late 1860s, historical biogeography became the “geography of morphology”. The maps that Ernst Haeckel drew to illustrate the journeys taken by various humans were applied to many different kinds of organisms and their travels (see below). On the other hand, ecological biogeography appealed to biologists who studied the distribution of populations or individual species, gaining extensive popularity by those who examined the distribution of organisms on islands—possibly following Darwin’s lead in his dealings with the biota of the Galapagos Islands.

Biogeography, as developed by Alfred Russel Wallace and Charles Darwin, may be considered the starting point for ecological biogeography (MacArthur & Wilson 1963), although some now claim Ernst Mayr was if not responsible for that discipline then certainly a precursor (Bock 2004, 2005, Vuilleumier 2005; see Figure 13.1).

Historical biogeography became the domain of palaeontologists, as their focus was interpreting continental distributions over long periods of time. If there

**Fig. 13.1** Map taken from Mayr (1944, Fig. 2), depicting the “route of colonization of *Caprimulgus affinis*”

was a “bone of contention” between these approaches, it rested firmly with the palaeontologists, who claimed to be the only scientists in a position to find, discover, and identify “ancestors”—and once an ancestor was found, its place of origin would thereby be determined. As Patterson noted many years later:

> By about 1960 palaeontology had achieved such a hold on phylogeny reconstruction that there was a commonplace belief that if a group had no fossil record its phylogeny was totally unknown and unknowable. (Patterson 1987a: 8)

And, of course, its biogeographic history would be totally unknown and unknowable too (Patterson 1981a).

The aim of this chapter is to outline the relation biogeographic data may have to other kinds of comparative information, and how that might reflect on the classification of organisms, the classification of the world they occupy, and evolutionary theories. We focus our discussion on the threefold parallelism and its extended meaning.

## 13.2 The Threefold Parallelism: Its Beginning

Tracing the origins of the threefold parallelism—and the “doctrine of recapitulation”, the apparent relation between the results of comparative anatomy (systematics, the “natural system”, classification) and the ontogenetic development of individual organisms—is a formidable task.[2] Notwithstanding Kohlbrugge’s (1911: 448) early attempt—he lists 72 possible candidates, beginning in 1797 with contributions from both Goethe and Autenrieth—and Meyer’s (1935) tentative vision of its origin with Aristotle, one might easily be forgiven for attributing the notion to Louis Agassiz (1807–1873, Agassiz 1844a, Agassiz & Gould 1848; see Marcou 1896, I: 230). While Agassiz acknowledged Tiedemann as the “true” creator of recapitulation[3] as he had noted a relationship among comparative anatomy, development, and the fossil record (Tiedemann 1808: 73, Russell 1916: 255, footnote 3), Agassiz clearly believed he had discovered something, writing “Das ist mein Resultat!” in the margin of his copy of *Natürliche Schöpfungsgeschichte* (1868: 280) against Haeckel’s treatment and interpretation of recapitulation (Gould 1973: 322, 1979: 280). In fact, Agassiz’s concerns were with the inclusion of “geological succession” among other forms of evidence:

> But I may at least be permitted to speak of my own efforts, and to sum up in the fewest words the result of my life’s work. I have devoted my whole life to the study of Nature, and yet a

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[2] See, for example, Kohlbrugge (1911), Russell (1916), Shumway (1932), Meyer (1935, 1936), Lebedkin (1936, 1937), Wilson (1941), Holmes (1944), Oppenheimer (1959), Gould (1977), Mayr (1994), Müller (1998).

[3] [Agassiz] (1860–1862: 245); see Lurie (1960: 286); Tiedemann had taught Agassiz; see Marcou (1896, I: 16), Lurie (1960: 21).

> single sentence may express all that I have done. I have shown that there is a correspondence between the succession of Fishes in geological times and the different stages of their growth in the egg,—this is all. (Agassiz 1862: 52)

Agassiz first wrote of “recapitulation” and its relationship to geology in his *Poisson fossiles* (Part I, 1844a: 81, 102), the relevant passages coming from the first volume. Earlier, Charles Lyell, in the second volume of his *Principles of Geology*, was able to write:

> There is yet another department of anatomical discovery, to which we must not omit some allusion, because it has appeared to some persons to afford a distant analogy, at least, to that progressive development by which some of the inferior species may have been gradually perfected into those of more complex organization. Tieddemann [sic] found, and his discoveries have been most fully confirmed and elucidated by M. Serres, that the brain of the foetus, in the highest class of vertebrated animals, assumes, in succession, the various forms which belong to fishes, reptiles and birds, before it acquires those additions and modifications which are peculiar to the mammiferous tribe. So that in the passage from the embryo to the perfect mammifer, there is a typical representation, as it were, of all those transformations which the primitive species are supposed to have undergone, during a long series of generations, between the present period and the remotest geological era. (Lyell 1832: 62–63 [1991 reprint[4]])

It may well have been Agassiz’s students, friends, and teachers[5] who were responsible for giving more substance to Agassiz’s parallelism (see also Russell 1916: 255). Alpheus Hyatt (1894: 390) and Jules Marcou (1896, II: 126), both students of Agassiz, drew attention to Haeckel’s appropriation,[6] and Bronn, one of Agassiz’s teachers, gave him credit for recognising this particular threefold parallelism, with the inclusion of fossils (Bronn 1858: 103, 1861: 534). The significance of Agassiz’s work was rendered more profound by Joseph Le Conte, another Agassiz student and friend (Le Conte 1903). Writing some 10 years after Agassiz’s death:

> I know that many think with Haeckel that biology was kept back half a century by the baleful influence of Agassiz and Cuvier; but I can not think so. The hypothesis [the evolution hypothesis] was contrary to the facts of science, *as then known and understood.* It was conceived in the spirit of baseless speculation, rather than of cautious induction; of skilful elaboration, rather than of earnest truth-seeking. Its general acceptance would have debauched the true spirit of science. ... The ground must first be cleared . . . and an insuperable obstacle to hearty rational acceptance must first be removed, and an inductive basis laid. (Le Conte 1888: 33, 1905: 33)

Naturally, Le Conte considered Agassiz the person who cleared the ground, as

> . . . the only solid foundation, of a true theory of evolution . . . is found in . . . the method of comparison of the phylogenic and the embryonic succession, . . . and the laws of embryonic development (ontogeny) are also the laws of geologic succession. (Le Conte 1888: 33, 1905: 33)

Le Conte held the view that “no one was reasonably entitled to believe in the transformation of species prior to the publication of the work of Agassiz” (Lovejoy

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[4] The texts differ in subsequent editions.

[5] See Winsor (1991: 35) for a list of Agassiz’s students.

[6] Russell (1916: 255), Gould (1979: 280), Janvier (1996: 313), Williams & Ebach (2004: 691).

1909a: 501; Lurie 1960; see Le Conte 1903: 151). Be that as it may, Haeckel early on embraced the notion of "recapitulation"—or the efficacy of a threefold parallelism providing evidence. As early as 1863 Haeckel wrote for the first time his perception of the threefold parallelism and how together they present the strongest evidence possible for evolution:

> [. . . ] the threefold parallelism between the embryological, systematic, and palaeontological development of organisms, this threefold step-ladder, I think is one of the strongest proofs of the truth of the theory of evolution. (Haeckel 1863: 29; translation modified from Hoßfeld & Olson 2003: 296; also see Heberer 1968: 58)

Later Haeckel was more explicit:

> The laws of inheritance and adaptation known to us are completely sufficient to explain this exceedingly important and interesting phenomenon, which may be briefly designated as the *parallelism of individual, of paleontological and of systematic development*. (Haeckel 1876, I: 313, emphasis in the original; see Haeckel 1872, I: 471 for Haeckel's first note)

Whatever relation might emerge among individual, paleontological, and systematic development (see below), Haeckel did not see a role for biogeography *as primary evidence*, in spite of the fact that Darwin and Wallace required a geographical dimension for the mechanism of species descent they proposed (Richardson 1981). To the contrary, Agassiz's interest in the possibilities of geographical differentiation and its meaning extended his entire career.

## 13.3 Haeckel's *Hypothetische Skizze des monophyletischen Ursprungs und der Verbreitung der 12 Menschen-Species von Lemurien aus über die Erde* and the Concept of Chorology

Of all of Haeckel's genealogical diagrams, the most reproduced is that which first appeared in *Anthropogenie*, Haeckel's popular book on the evolution of Man, a tree that has been identified as *Quercus robur*, the European Oak (Oppenheimer 1987: 127), the illustration still reproduced today, often as the cover illustration for books dealing with some aspect of Darwin's thinking, rather than Haeckel's (e.g., Richards 1987 [1989], Bowler 1988 [1992], Alter 1999). Its popularity may be on account of its depiction of the evolution of man, possibly the first of its kind. The first German edition of *Anthropogenie* (1874) includes five "pedigrees" in all, but this particular tree guides the reader from the bottom to the top, from primitive and insignificant Monads to the crowning glory of Man, successively leading from one to the other up the sturdy trunk, with the rest of "creation" splitting off at various intervals, leaving their ancestors in its wake[7] (see Chapter 4, Figure 4.4).

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[7] Haeckel (1874: Taf. XII, 1883: Taf. XV, 1891: Taf. X; the translated English edition, *The Evolution of Man: A Popular Exposition of the Principal Points of Human Ontogeny and Phylogeny*, first published in 1879, includes the tree, as do all subsequent editions). The number of illustrations in *Anthropogenie* changed with successive editions, like many of Haeckel's books. The 1891 fourth German edition, for example, has two "oak-tree" diagrams, one modified from previous editions

Less well-known is Haeckel's *Hypothetische Skizze des monophyletischen Ursprungs und der Verbreitung der 12 Menschen-Species von Lemurien aus über die Erde* or *Hypothetical Sketch of the Monophyletic Origin and the Extension of the 12 Races of Man from Lemuria over the Earth*, even though it relates to Man. The implications behind the diagram are many but have been discussed by few (Nelson 1983, Kirchengast 1998, Nelson & Ladiges 2001).

The *Hypothetische Skizze* is a departure from those Haeckel previously drew, as it depicts the "species" of man overlain on a map of the world, tracing out the migration route each human "species" (= branch) took, arriving at its current place of habitation. The *Hypothetische Skizze* went through some changes with successive editions of *Natürliche Schöpfungsgeschichte*, the first version appearing in the second edition (Figure 13.2, after Haeckel 1870: Taf. XV) as a half-tone, with the "origin" of man located somewhere between Malay and South West Africa, a place he referred to as "Paradise", a point located out to sea. This particular viewpoint remained until the seventh edition, although the shading of the picture was some-

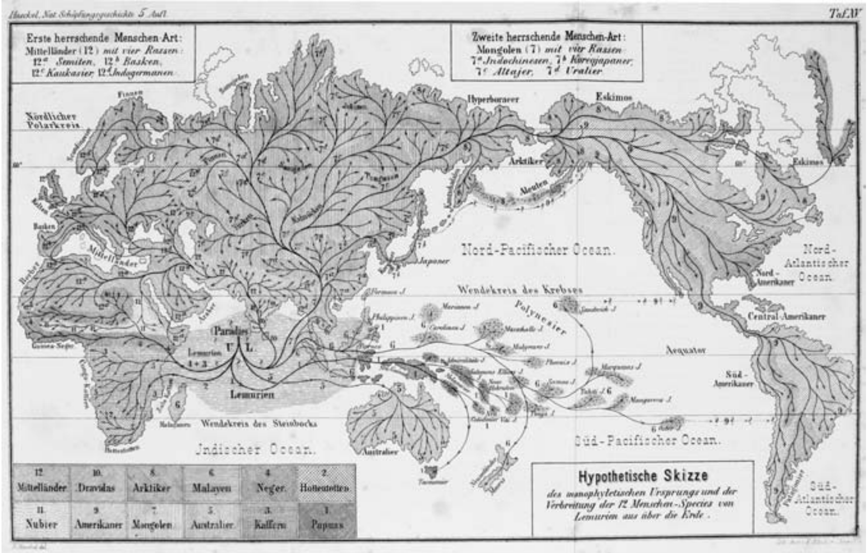

**Fig. 13.2** Reproduction of Haeckel's *Hypothetische Skizze des monophyletischen Ursprungs und der Verbreitung der 12 Menschen-Species von Lemurien aus über die Erde* or *Hypothetical Sketch of the Monophyletic Origin and the Extension of the 12 Races of Man from Lemuria over the Earth*, after Haeckel (1870: Taf. XV). Colour versions were printed in Haeckel (1879: Pl. XV) and the English translation (Haeckel 1876: Taf. XV)

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(Taf. XV, which shifts the "Reptilien" from branch to trunk, descendant to ancestor), the other illustrating the "Palaeontologischer Stammbaum der Wirblthiere" (Haeckel 1891: Taf. XVI). Later English editions (the 1905 edition, for example) lack the familiar oak-tree diagram of Taf. XV. A manuscript version of the tree depicted in Taf. XV is reproduced in Klemm (1969, between pp. 112-113, as well as part of the dust jacket illustration), Gasman (1971 [2004], between pp. 8-9) and on the dust jacket and cover of Richards (1987 [1989]).

what enhanced (Haeckel 1879: Pl. XV). By the eighth edition, this illustration was the only genealogy included as a plate (rather than a diagram in the text), it had been rendered in colour, and "Paradise" had moved on to land (Haeckel 1889: Taf. 20; see Kirchengast 1998: 178, Abb. 2). For the first English edition, the illustration was in colour but "Paradise" remained out at sea (Haeckel 1876: Taf. XV). In each case when readers encounter in the text the table for *Menschen-Arten und Rassen*, they are referred to this diagram.

The notion of humans travelling from their "original point of creation" has probably caused vast problems, not least in how we view ourselves (Bowler 1995). Nevertheless, that they travelled retained a special place in the interpretation of current distributions. William Diller Mathew, for example, in his *Climate and Evolution* (1915)—written while Haeckel was still alive—also drew a map depicting the various routes of humans, stating that most "authorities … today agreed in placing the center of dispersal of the human race in Asia" (Matthew 1915: 41, Fig. 6; reproduced in Lomilino et al. 2004: 244, see Fig. 6.2). The route maps continue, seen in many popular books and articles on human evolution and migration (Finlayson 2005).

The significance of the *Hypothetische Skizze*, human wanderings to one side, is that Haeckel chose it as a graphic representation of *chorology*, a term first proposed in his *Generelle Morphologie* (1868: 286–289, "… chorology is the science of the geographic and topographic spread of organisms",[8] translated) and expanded into a full chapter for *Natürliche Schöpfungsgeschichte* (*History of Creation*):

> I mean *Chorology*, or the theory of the *local distribution of organisms over the surface of the earth*. By this I do not only mean the *geographical* distribution of animal and vegetable species over the different parts and provinces of the earth, over continents and islands, seas, and rivers, but also their *topographical* distribution in a *vertical* direction, their ascending to the heights of mountains, and their descending into the depths of the ocean. (Haeckel 1925: 364)

Haeckel goes on:

> The strange chorological series of phenomena which show the horizontal distribution of organisms over parts of the earth, and their vertical distribution in heights and depths, have long excited general interest. In recent times Alexander Humbolt and Frederick Schouw have especially discussed the geography of plants, and Berghaus, Schmarda, and Wallace the geography of animals, on a large scale … only since Darwin that we have been able to speak of an independent science of Chorology …. (Haeckel 1925: 365–366[9])

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[8] "Unter Chorologie verstehen wir die gesammte Wissenschaft von der räumlichen Verbreitung der Oragnism, von iher geographischen und topographischen Ausdehnung über die Erdoberfläche. Diese Disciplin hat night bloss die Ausdehnung der Standorte und die und die Grenzen der Verbreitungs - Bezirke in horizontaler Richtung zu projiciren, sondern auch die Ausdehnung der Organismen oberhalb und unterhalb des Meeresspiegels, ihr Herabsteigen in die Tiefen des Oceans, ihr Heraufsteigen auf die Höhen der Gebirge in verticaler Richtung zu verfolgen. Im weitesten Sinne gehört mithin die gesammte "Geographie und Topographie der Thiere und Pflanzen" hierher, sowie die Statistik der Organismen, welche diese Verbreitungs-Verhältnisse mathematisch darstellt" (Haeckel 1866: 287).

[9] The various editions of *The History of Creation* have different wordings, but their essence is the same. This passage is the version included in Lomilino et al. 2004: 178-193.

Haeckel states some conditions:

> The most important principle from which we must start in chorology, and of the truth on which we are convinced by due examination of the theory of selection, is that, as a rule, every species has arisen only *once* in the course of time and only in *one* place on the earth—its so-called "centre of creation"—by natural selection ... the distribution of the great majority of animals and vegetable species in regard to which the *single origin of every species in a single locality*, in its so-called "central point of creation", can be considered as tolerably certain. (Haeckel 1925: 367)

Haeckel used the remaining parts of the chapter to discuss the various means of migration species may undergo to travel from their particular centre of creation. He used the idea sparingly in his own work, discussing the vertical and horizontal distributions of species of *Radiolaria* found in the Challenger material (Haeckel 1887) and Australian material he later studied (Haeckel 1893[10]).

Haeckel understood chorology as part of Physiology (" = The Science of Functions"), noting that it was the "science of migrations" (Haeckel 1904: 98, third Table). Physiology (" = The Science of Functions") was contrasted with Morphology (" = The Science of Forms").

## 13.4 The Development of Chorology

According to Uschmann (1972), Haeckel's insistence on the fundamental importance of Darwin's ideas to biology is most apparent in his "ecology" and "chorology", "both concepts have won acceptance" (Uschmann 1972), while for Hoßfeld chorology has "been widely adopted" (Hoβfeld 2004: 84, Stauffer 1957). Interestingly enough, in the various editions of *The History of Creation*, Haeckel appears to contrast regional biogeography (of which more below)—exemplified by the works of Humboldt, Schouw, Berghaus, Schmarda, and Wallace—with chorology. Regional biogeography gained many critics; writing while Haeckel was still alive, Ortmann suggested:

> It is incorrect to regard the creation of a scheme [of regions] of animal distribution as an important feature or purpose of zoogeographical research. Thus we are justified in saying that zoogeographical study, as introduced by Wallace [and Sclater], is not directed in the proper channels [and results in] fruitless discussions on the limits of the zoogeographical regions. (Ortmann 1902a, after Heads 2005c: 87)

Ortmann understood the matter as one of linking the present to the past, along with any necessary changes in the Earth's surface that might have occurred (such a view has recently resurfaced in Donoghue & Moore 2003). Ortmann later, when reviewing the work of Jacobi (1900), noted that he (Jacobi) found "certain parts

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[10] Haeckel included a table of relationships from Haeckel (1866: xii) and tables of "phylogenetische stufenreihe" (on p. xiv).

of the earth's surface" that are "inexplicable by the present conditions" (O[rtmann] 1902b: 158).

With such criticisms, a distinction began to develop between what was eventually described as the static geographical method (regional biogeography) and the dynamic faunal method (chorology), summarised later by Voous:

> The geographical method is static; it tries to define the borders of zoogeographical regions, districts, or provinces. It is part of the classical zoogeography of Philip Lutley Sclater and Alfred Russel Wallace. The faunal method is dynamic; it tries to detect and to describe the far-reaching intergradation of separate faunas throughout the continents. ... This method starts from the conception that there are distinct faunas but no distinct zoogeographic regions. (Voous 1963: 1104)

In an early paper Ernst Mayr made the following comments:

> Eventually it was realised that the whole method of approach—the *Fragestellung*—of this essentially static zoogeography was wrong. Instead of thinking of fixed regions, it is necessary to think of fluid faunas .... (Mayr 1946: 5, 1976 [1997b]: 567)

Later he commented on regions and faunas:

> I shall not rehearse the history of zoogeography in the last 100 years. I shall merely remark that the faunal and historical approach favored by Darwin tended to recede into the background as the geographical approach of Sclater and Wallace came to the fore and as an increasing number of authors expended their energies in trying to determine the borders between geographic regions and in subdividing these regions into subregions and biotic provinces .... (Mayr 1965, 1976 [1997b]: 553)

Mayr continues by noting those who supported the "faunal" approach, citing a paper by Carpenter (1894), an early critic of regions, noting a paper by Dunn, who "... was the pioneer of this concept [dynamic faunas]" (Dunn 1922), finishing with two examples from German ornithologists, Stegmann (1938) and Stresemann (1939) (Mayr 1946: 5,1976 [1997b]: 567–568). Yet, the faunal approach reaches further back than Dunn or German ornithology, back to Haeckel and his chorology. Mayr stated the difference between classical and "modern" biogeographers:

> Classical zoogeography asked: What are the zoogeographic regions of the earth, and what animals are found in each region?
> The modern zoogeographer asks when and how a given fauna reached its present range and where it originally came from; that is, he is interested in faunas rather than in regions. (Mayr 1946: 6, 1976 [1997b]: 569)

In Mayr's "classical" zoogeography, his words clearly reflect not a static approach to the living world but a classificatory one: "to determine the borders between geographic regions and in subdividing these regions into subregions and biotic provinces...". The modern approach, as he outlined it, is more concerned with mechanisms, and dealing with each "lineage" separately, as if they developed independently of each other.

In the immediate past many have attempted to distinguish between different kinds of biogeography, such as ecological and historical biogeography (Humphries &

Parenti 1999[11]). More recently, biogeographers have suggested more subdivisions and more partitions—and, as a consequence, there is less coherence rather than clarity (Crisci et al. 2000, 2003[12]. Given the above, notwithstanding various claims to the contrary, there is a clearer way of distinguishing the subject matter of the geographical distribution of organisms:

> Biogeography is the study of the inter-relationships of areas (classification).
> Chorology is the study of the mechanisms of distribution related to taxon origins.[13]

If it is accepted that biogeography is the study of the inter-relationships of areas and is a problem of classification, then its most significant aspect is the concept of homology, the parameter that poses hypotheses of relationships (Morrone 2004; see below).

For chorology, mechanisms encompass all those so far suggested above, including all aspects of dispersal and vicariance, and whatever other theories relate to attempts to discover any particular taxon's origin.[14] It is not necessary to trace the fortunes of chorology and its changing role, or even to ascertain whether it really did achieve general acceptance—the word is still in use, if not that often, and in quite a variety of different ways (e.g., Huxley et al. 1998), but many "modern" studies do appear to be within that remit (De Queiroz 2005):

> This new view [more oceanic dispersal] implies that biotas are more dynamic and have more recent origins than had been thought previously. . . . The new support for oceanic dispersal

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[11] The beginnings of Ecological Biogeography are attributed to the work of Alphonse Louis Pierre Pyramus de Candolle (1806–1893). Alphonse's father, A.-P. Candolle, sought to classify areas within a taxonomy based on environmental and climatic barriers, as well as their causes. In doing so Candolle (1820) combined an ecological and historical approach to start the first biogeographical classification—in fact Candolle senior coined the term *taxonomy* (Candolle 1813). Alphonse's great endeavour to synthesise plant geography (Candolle 1855) "blurred what Candolle Sr. [Candolle 1820] had made clear, particularly the distinction between ecology (or ecological biogeography) and biogeography (or historical biogeography)" (Nelson 1982: 217–218). We agree with Nelson (1982) that ecological biogeography is simply ecology, but disagree with Nelson (1978c) that a real ecological and historical division exists within biogeography per se. If ecologists choose to use ecological methods and techniques to do biogeography, then their approach is naturally limited (e.g., MacArthur & Wilson 1963, Hubbell 2001). Naturalists throughout the 19th century used both ecological *and* historical elements to classify areas and explain how taxa got to where they are presently found (e.g., Drude 1884, Engler 1879). A.-P. Candolle, for instance, used ecological descriptions—climate, soil types, and environment—as a way of classifying areas in order to build a classification (Lamarck & Candolle 1805; see Ebach & Goujet 2006). The ecological and historical division heightened during the Island Biogeography revolution of the 1960s has most likely caused a political and sociological division, rather than pioneering a new theoretical field. Biogeographers of today, like 19th-century naturalists, were divided between the causes (mechanical explanations) and classifications of organisms and areas, the latter being dismissed by 20th-century evolutionary biologists as irrelevant (see Mayr 1946).

[12] See also Morrone (2005a: Table 1), correction in Morrone (2005b: 1505).

[13] It is possible that chorology is the same as Cain's Areography (Cain 1944), a term Hubbs noted was "of bastard origin and denotes a concept that is sufficiently covered by 'biogeography' and by 'chorology"' (Hubbs 1945).

[14] For another definition, see Aubréville (1970: 450).

> has come primarily from information on the timing of speciation, fueled by the development of improved methods of DNA sequencing and of estimating lineage divergence dates based on molecular sequences. (De Queiroz 2005: 69)

De Queiroz's claim seems too bold. Support for timing of speciation and estimating lineage divergence dates comes from palaeontology, fossils, Haeckel's "significant" data. Nevertheless, De Queiroz essentially embraces what is understood as chorology ("dynamic biotas") rather than biogeography.

It is worth noting that Erwin Stresemann (1889–1972; Haffer et al. 2000), discussed above as an early proponent of dynamic faunal studies, was professor to the young Ernst Mayr, who saw the development of chorology within the German ornithological community of the 1930s (Junker 2003, Bock 2004). According to Mayr, "... Virtually everything in Mayr's 1942 book was somewhat based on Stresemann's earlier publications" (Mayr 1999: 23; see Mayr 1997b). According to Bock, Mayr's "first and last interest in ornithology is biogeography ... ", where he applied "the (then) new ideas for analyzing the biogeography of birds that were advocated by Stresemann (1939)" (Bock 2004: 645, 2005: 10–11; see Bock 1994: 291 and Vuilleumier 2005). According to Haffer et al., "After his high school examinations (Abitur), Stresemann entered the University of Jena in 1908, where he took courses offered by Ernst Haeckel (Haffer et al. 2000: 399–400). In 1931, Stresemann "declared historical morphology as terminated, i.e. phylogenetic or systematic morphology ... in the sense of Ernst Haeckel ... and Max Fürbringer ... " (Haffer et al. 2000: 420).

Stresemann was also professor to Wilhelm Meise (1901–2002) (Haffer 2003: 117; Meise "was primarily a systematist studying problems of geographical variation, hybridisation, and speciation in birds"). Meise nurtured the 19-year-old soon-to-be entomologist, Willi Hennig (Meise & Hennig 1932, 1935, Schmitt 2001, Haffer 2003), who went on to create and develop the chorological method for determining character polarity from geographical distances, a flawed method as it turned out[15] (Figure 13.3). Hennig noted that "The use of the chorological method in zoology has become known particularly through the books of Rensch" (Hennig 1966a: 133; see also Hennig 1950: 192–199 and Kiriakoff 1953, 1954b); Rensch was also a student of Stresemann (Junker 2003).

George Gaylord Simpson seemingly discovered chorological relationships independently, through the use of clines: "Clines may, then, be distinguished according to the variate that is used to define the array [of populations]. In one case the arrangement is geographical and these may be called choroclines, i.e. 'space clines"' (Simpson 1943: 174).

Chorology—in all its variations and permutations—addresses issues that pertain to the origin of things, either taxa or characters, in their geographical dimension. It also relates to processes, the causes of origins—mostly subsumed under two mechanisms: vicariance and dispersal.

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[15] Hennig also coined the words *apochor* and *plesiochor,* related to geographical criteria (Hennig 1950).

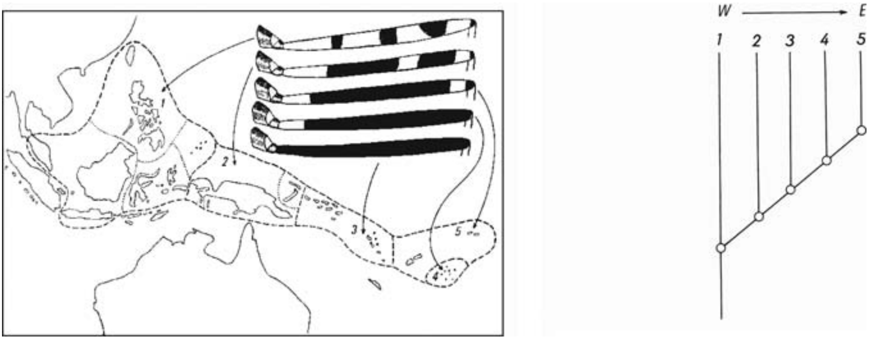

**Fig. 13.3** After Hennig (1966a), to demonstrate the chorological method for determining character polarity from geographical distances

## 13.5 Vicariance Versus Dispersal: Another "False War"

Vicariance and dispersal have been proposed as mechanisms to explain taxon distributions. Dispersalism was founded on the basis that taxa are distributed via physiological adaptation and locomotion on a static earth. Vicariance was proposed in response to the discovery of a dynamic earth, in which organisms are forced to move (i.e., sea level rises) or move unwittingly (i.e., continental drift, etc.). In either case, a mechanism is invoked to explain a fluid, ever-changing biota that inhabits either a static or dynamic inorganic environment. Whatever the mechanism, it does not—nor can it—assist in the discovery of a biotic classification.

The theoretical difference between dispersal and vicariance is that the former is a purely explanatory device for generating biogeographical scenarios, whereas the latter, although also explanatory, is often confused with another mechanism namely, "allopatry" or the process of geographical isolation.

Dispersal is perhaps the most poorly defined mechanism. In one sense, it simply means to "disperse", namely, "to scatter over a wide area; to separate or; to spread" (Collins, *Australian Pocket Dictionary*). Dispersal is a common process to describe the way seed, pollen, or spawn behave when released into the environment. Dispersal is a process, one that describes an event. In biogeography, however, dispersal is a mechanism that explains an observation, namely the distribution of some organisms. Whatever the mechanism of dispersal might be (seeds blown by wind, diatoms transported by ducks, etc.), it highlights its very vague nature and the inability of biogeographers and ecologists alike to define it. Dispersal is at best an ad hoc explanation that is unique to any (and every) given scenario: One person's trilobite may have "dispersed" to an area differently to another's daisy. As a *mechanism*, dispersal provides an excuse, an unknown (and mysterious) one-off event designed to explain an observation. Platnick (1976), in an effort to avoid the confusion between observations and mechanisms, promoted the term "dispersion".

Platnick's "dispersion" is the area to which a taxon moves. The wandering albatross (*Diomedea exulans*), for instance, has a very large area of distribution because it can move over large distances before encountering a barrier (such as a continent).

It is thus possible to note that the wandering albatross "disperses" within its area of distribution—that does not associate the term with a mechanism that causes the bird's isolation. Certainly the albatross may confine its dispersion within a certain region of its vast distributional area, but that does not suggest the biological mechanism that causes its isolation from another population of albatrosses. If the taxon is confined to one region of its distributional area because of some geographical barrier, then it has undergone a "vicariance event", or its distribution has "vicariated".

Nevertheless, a "vicariance event" is as dubious and ad hoc as any "dispersal event". The actual "event" is *unknown* and hypothesised to be the result of an existing or former barrier. Similarly, each vicariance event is unique to the organism or group of organisms that has been affected by geographical isolation. Vicariance, in the sense of a "vicariance event", is impossible to define as every event carries a unique explanation. In order to make "dispersal" and "vicariance" meaningful, it should be defined as a *descriptive* term.

Vicariance—as in a "vicariant pattern" of distributions—is a *descriptive* term employed to describe *one or more geographically isolated or separated taxon*. Like dispersion, it requires no hidden or unknown mechanism. Relative to a classification, the terms "vicariance" and "dispersion" or "dispersal" are descriptive terms, *not* indicators of mechanisms, as currently practised in biogeography today.

Thus, the apparent conflict between those who advocate dispersal and those who advocate vicariance is of little consequence for progress in biogeography. To understand biogeography as a battle for unification between vicariance and dispersal processes is, in short, meaningless. The real task in biogeography is the unification between classification and explanation—a unification that has obsessed biologists since Haeckel and his discussion of chorological "processes".

## 13.6 Origins

> "Our mistake was thinking in terms of origins rather than relationships—Darwin may well be to blame for that preoccupation. Anyway, origins has been a dirty word to me ever since, a symptom either of ignorance or of creationism." (Patterson 1995)
>
> "The origin of taxa, if at all a concrete notion to pursue, lies beyond the empirical horizon of systematics." (De Pinna 1999: 363)

The origin of species (Darwin 1859), if not the origin of taxa (Løvtrup 1987), is a concern that predates Darwin's efforts at explaining the phenomenon. For example, when Arthur Lovejoy surveyed "The Argument for Organic Evolution Before *The Origin of Species*" (Lovejoy 1909a, b), he summarised three possibilities for the origin of species, possibilities that were outlined in a popular, standard account, Gray & Adams' *Elements of Geology* (1852; see also Lyell 1832): (1) successive special creations . . . ; (2) "transmutation, which supposes that beings of the most simple organization having somehow come into existence, the more complex and the higher orders of animals have originated in them by a gradual increase in the complexity of their structures; and (3) *generatio aequivoca* [spontaneous generation] of individuals and species" (Lovejoy 1909a: 500). Gray & Adams opted for the first, successive special creations (the option favoured by Louis Agassiz and Heinrich Bronn). It is not difficult to imagine more possibilities for speculating on the origin of species. Nevertheless, it was clear that somehow the geographical distribution of organisms would if not provide clues, then at least point the way (Hofsten 1916). For various reasons, the single centre of origin became the focus, as "... the simplicity of the view that each species was first produced within a single region captivates the mind" (Darwin 1859: 352).

Exploring species' origin today is much more precise, requiring the identification of a particular centre of origin (Avise 2000; in the past, centres of origin have fluctuated in size; see Croizat et al. 1974: 269, footnote 6), the particular time of origin (Donoghue & Smith 2003), and subsequent migration to other parts of the world (De Quieroz 2005), investigations once considered to be the domain of palaeontology (Matthew 1915) but now more closely associated with various methodologies subsumed under the term "phylogeography" (Excoffier 2004) but still with a palaeontological basis.

The original idea was popularised by Linnaeus, having its own "origin" in the Bible with the notion that each species would begin minimally with two individuals: "If we trace back the multiplication of all plants and animals ... we must stop at one original pair of each species." It was this idea that Darwin captivating:

> Undoubtedly there are many cases of extreme difficulty in understanding how the same species could possibly have migrated from some one point to the several distant and isolated points, where now found. Nevertheless the simplicity of the view that each species was first produced within a single region captivates the mind. He who rejects it, rejects the vera causa of ordinary generation with subsequent migration, and *calls in the agency of a miracle*. It is universally admitted, that in most cases the area inhabited by a species is continuous; and when a plant or animal inhabits two points so distant from each other, or with an interval of such a nature, that the space could not be easily passed over by migration, the fact is given as something remarkable and exceptional. (Darwin 1859: 352)

Darwin may have found the idea, it was questioned, primarily but not exclusively, by vicariance biogeographers (Croizat et al. 1974: 274, Croizat 1981: 503, Patterson 1983a: 14, Croizat 1984: 57–58, Brady 1989: 112, Nelson & Ladiges 2001: 401; Heads 1985, 2005a: 676, 2005b: 74, 2005c: 85, 94, 111). The American ecologist Frederick Clements, early in the 20th century, commented on Darwin's "captivating idea", noting that

> From the very nature of his task, Darwin was forced to assume that species were first produced at one spot. ... This view seems to be little more than inheritance from the special creationists. (Clements 1909: 145)

In his review of the 1979 American Museum of Natural History's vicariance biogeography symposium (Nelson & Rosen 1981), Ernst Mayr (1982b: 619) commented on the various critiques of the single point of origin, noting that "... Darwin's argument was directed against authors like Louis Agassiz, who explained discontinuous distribution of species by multiple independent creations." Darwin did not explicitly mention Agassiz in this context. Nevertheless, Agassiz had indeed written on the subject of centres of origin:

> The greatest obstacles in the way of investigating the laws of the distribution of organized beings over the surface of our globe, are to be traced to the views generally entertained about their origin. There is a prevailing opinion, which ascribes to all living beings upon earth one common centre of origin, from which it is supposed they, in the course of time, spread over wider and wider areas, till they finally came into their present state of distribution. And what gives this view a higher recommendation in the opinion of most men is the circumstance, that such a method of distribution is considered as revealed in our sacred writings. (Agassiz 1850a: 181)

Agassiz, like those before, traced the idea of centres of origin to the Bible, and because he thought otherwise, saw himself in conflict with those "sacred writings", whereas for Darwin, those who disbelieve the "ordinary generation [from a single region] with subsequent migration" requires "the agency of a miracle".

Sacred texts and miracles to one side, Léon Croizat, for example, happily rejected Darwin's "captivating idea". In more recent times Croizat's ideas have had significant representation by Michael Heads, among others (Grehan & Ainsworth 1985), and have been related to what he (Heads) called the "nature of ancestors" (Heads 1985). The notion that characters of ancestors might not be "uniform" relates to Croizat's *polytopism* (= "multiple origins"; Heads 1985: 209; see Croizat 1971 and Aubréville 1969, 1974, 1975a, 1975b), as contrasted by the more usual *monotopic* ancestor, a position Heads (and Croizat) suggested was held by the cladists Willi Hennig and Lars Brundin (Heads 1985). Croizat favoured a polytopic origin for many taxa (Croizat 1971, 1978) rather than the more usual monotopic explanation. Theodor Just, a palaeobotanist, offered the following commentary on polytopic speciation in review:

> This author [Suessenguth 1938] is of the opinion that certain areas can be explained best by assuming the possibility of a polytopic as well as polyphyletic origin, provided the original stock was sufficiently widely distributed. According to this view, several or even many parallel lines are evolving more or less simultaneously in several species and genera. This mode of origin would do away with the problem of large scale migrations and the invariably long spans of time required for such. (Just 1947: 132)

Just continues that "... not a single case is presented by Suessenguth to illustrate this view". But such options were—and still are (Heads 1985)—considered, with vicariance as a covering explanation. Just's account to one side, the idea does not appear too dissimilar to that proposed by Agassiz (whom Croizat does not cite), if primary causes (deities) are disregarded.

This difference—between "polytopism" and "monotopism"—might go some way towards explaining the antagonism between Croizat and the Hennigians, at least with respect to different approaches for the "origin" of taxa (Croizat 1982). If differences of opinion are related to particular "kinds" of origin and these differences in turn relate to particular mechanisms, then one might conceivably see the problem residing, once again, in a model—"polytopism" or "monotopism"—and its explanation—dispersal or vicariance. Oddly enough, given the contrast between Agassiz and Darwin and Croizat and Hennig, for example, evolution in its most general sense seems not to be an issue—it is the idea that one might discover something about a taxon's *origin*.

Agassiz was specific enough concerning the role of geographic distribution:

> ... work ... in the Museum, has already extended to comparisons ... with the view of ascertaining whether there is any probability of tracing a genetic connection between the animals of ... different geographical areas, and how far geographical distribution and specific distinction are primary factors in the plan of creation. It must be obvious that the question of the origin of species is not likely to be discussed successfully before the laws of geographical distribution of organized beings have been satisfactorily ascertained. (Agassiz 1865: 12; Annual report for 1864, cited in Winsor 1991: 81)

His remarks echo those of Candolle's some 45 years earlier:

> All of the theory of geographical botany rests on the particular idea one holds about the origin of living things and the permanence of species. (Candolle 1820: 417, translation in Nelson 1978c: 285)

And Candolle's remarks relate to Lyell's discourse on the origin of species in the second volume of the *Principles of Geology* (Lyell 1832, Nelson 1978c), summaries of which are found in popular books like Gray & Adams' *Elements of Geology* cited above.

When Kinch, in his summary of ideas on the origin of life and the history of biogeography, noted in closing that "The key needed to resolve the biogeographical debate was a credible theory for species origin" (Kinch 1980: 119), he appears mistaken. A credible theory, such models, and their explanation are best set to one side: "The origin of taxa, if at all a concrete notion to pursue, lies beyond the empirical horizon of systematics" (De Pinna 1999: 363). If chorology is about the mechanisms to discover the *origin* of species, and the study of origins is a futile enterprise, then what is left?

As in systematics, there is classification (Nelson & Platnick 1984). And without a classification of areas, what generalities, really, are there to explain?

## 13.7 Realms, Regions, and Provinces

Many early studies on biogeographic regions focused on humans, their place of residence, and how they came to be where they are (Richardson 1981, Browne 1983). Human distribution and evolution were of some significance for Darwin, Desmond, and Moore, noting in Darwin's *Origin*, "the subject pervades the text as a ghostly presence ..." (Moore & Desmond 2004: xiv; see also Cooke 1990).

While most acknowledge Buffon's *Histoire Naturelle* as the first real statements on the geographic distribution of organisms (Nelson 1978c, Browne 1983), it was Eberhard August Wilhelm von Zimmermann's (1743–1815) *Geographische Geschichte des Menschen, und der allgemein verbreiteten vierfüssigen Thiere, nebst einer hieher gehörigen zoologischen Weltcharte* that considered Man as part of that distribution. Zimmermann dealt with the relation of the various "kinds" of humans with their domesticated animals (Zimmermann 1778–1783). Zimmermann's work was not well known; hence, James Cowles Prichard's (1786–1849) *Researches into the Physical History of Mankind* (1813) is often considered the first work to deal with biogeographic regions in relation to man as well as other animals. Prichard considered what areas were repopulated after the flood:

> ... we may divide the earth into a certain number of regions, fitted to become the abodes of particular groupes of animals; and we shall find on inquiry, that each of these provinces, thus conjecturally marked out, is actually inhabited by a distinct nation of quadrupeds [mammals], if we may use that term. (Prichard 1826: 54; see Nelson & Platnick 1981: 518, Kinch 1980: 101)

Prichard published several editions of his *Researches into the Physical History of Mankind*[16] (Augustein 1999), a work described by Moore & Desmond as "a monogenist encyclopedia" (Moore & Desmond 2004: xxx), noting that while Prichard "defended Adamic unity; its arguments rested on a raft of biological, philological and enthnographic fact" (Moore & Desmond 2004: xxvii). Prichard also included six maps illustrating "The natural history of man", depicting the areas occupied by various tribes and ethnic groups. Prichard named seven regions (Table 13.1). As "a monogenist encyclopedia", the book championed the view that the various "races" of man had one origin—were monogenic—and were one species, varieties being the result of environmental effects on waves of migration of humans—that is, humans originated in one place and migrated to other areas (Haller 1970).

One of the first books to deal with the entire animal kingdom and its geographical distribution was William Swainson's *A Treatise on the Geography and Classification of Animals* (1835). Swainson, elaborating on Prichard's work, began his commentary with some objections:

> The objections that may be stated against these [Prichard's] divisions chiefly arise from the author not having kept in view the difference between affinity and analogy, as more particularly understood by modern naturalists. (Swainson 1835: 13)

**Table 13.1** The seven regions recognised by Prichard (1813, I: 53)

1. The Arctic Region of the New and the Old Worlds
2. The Temperate
3. The Equatorial or Tropical
4. The Indian Islands
5. The Islands of New Guinea, New Britain and New Ireland, and those more remote in the Pacific Ocean
6. Australia
7. The Southern extremities of America and Africa

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[16] The second edition of *Researches into the Physical History of Mankind* (1826) is referred to rather than the first (1813) or later editions. The first edition is less explicit on detail, while the later editions were heavily influenced by Lyell (1830-1832). The third edition consisted of five volumes, published between 1836-1847. The book was later renamed *Researches in the History of Mankind*, and later still *Researches in the History of Man, with The Natural History of Man* (1843) published as an abbreviated edition. An edition was reprinted in 1973, with an introduction written by G.W. Stocking (1973).

Swainson's comment is perhaps the first explicit statement relating to geographical homology, even though it is stated in the vernacular of the 19th century, as affinities and analogies. Swainson explained:

> The arctic regions of America, Europe, and Asia indisputably possess the same genera, and in very many instances the same species; and if it should subsequently appear that these regions are sufficiently important in themselves to constitute a zoological province, then it is a perfectly naturally one; for not only are the same groups, but even the same species, in several instances, common to both. But can this be said of the second of these provinces, made to include the temperate regions of three continents? Certainly not. We find, indeed, analogies without end, between their respective groups of animals, but they have each a vast number of peculiar genera; and so few are the species common to all three, that the proportion is not perhaps greater than as 1 to 50. (Swainson 1835: 13)

Between Prichard and Swainson, three significant issues are bought into focus: the notion of distinct geographical regions, the notion of geographical homology, and the notion of the origin of things. Swainson went on to suggest that "natural" geographical regions might very well correspond with "the five recorded varieties of the human species" (Swainson 1835: 14).

For Agassiz, human distribution—as well as the distribution of other organisms—could be captured and understood in a series of realms or *Natural Provinces of Mankind*, areas which harbour collections of organisms, unique to each region (Agassiz 1854: facing p. lxxviii); for Haeckel, human distribution—as well as that of other organisms—was not so much captured by their current place of residence but by their travels (Figure 13.2).

## 13.8 Agassiz's (1854) Geographical Realms: *The Natural Provinces of Mankind*

In the recent compendium of "classic" papers *The Foundations of Biogeography* (Lomolino et al. 2004), Louis Agassiz hardly rates a mention in all its 1400 pages. No contribution of his is included and, as far as can be established, he is referred to only twice and then in passing.[17] Agassiz's words may simply be of no significance or importance today and not part of the inexorable flow of common scientific understanding. Ernst Mayr, never shy of an opinion, offered the following retrospective on Agassiz's geographical writings:

> When Agassiz, in the 1850s, wrote about biogeography, his uncompromisingly fundamentalist interpretation seemed like a throwback to a long past period. (Mayr 1982b: 443)

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[17] The first mention of Agassiz's name is in Sclater's influential 1858 paper (Sclater 1858, paper 9 in Lomolino et al. 2004: 131), where he discusses Agassiz's regions (see p. 10 of this paper); the second mention is in Hart Merriam's paper on biogeographical regions in the U.S. (Merriam & Stejneger 1890, paper 15 in Lomolino et al. 2004: 222, 228), where he mentions Agassiz's "Great Central Province" (p. 222) and in a footnote Agassiz's *Louisiana Fauna* (p. 228).

That view to one side, Agassiz did have a lot to say about the geographical distribution of organisms, particularly in relation to Man (Hofsten 1916: 297–301, Kinch 1980: 102). Agassiz's interest in the geographical distribution of animals and plants began in 1845 (Agassiz 1845a, 1845b, 1846), forming a major part of his ideas on how a Museum display should be constructed (Winsor 1991, 2000).

Rather than simply a throwback, it is possible his contributions to geographical distribution were too closely linked to his shameful views on race and its developing context in mid-19th-century U.S. (Roberts 1982). Agassiz's viewpoint has indeed fallen out of sight, except as an example used to illustrate the misfortunes that come of scientific ideas when given free social, religious, or political reign and interpretation.[18] Nevertheless, beyond "opinion" and "context", Agassiz did have some interesting things to say; the story is worth telling from the geographical viewpoint. Agassiz published a short chapter outlining the zoogeographical regions of the Western hemisphere (Agassiz & Gould 1848), followed by several papers specifically dealing with human distribution (Agassiz 1850a, 1850b, 1854). Agassiz's views on humans, both their origin and unity, changed between 1845 and 1855.

Before moving to his adopted home in the U.S., Agassiz had lectured in Neuchâtel on the geographical distribution of organisms. It was the last in a series of 12 lectures on the "Plan de la Création", the only one that was published (Agassiz 1845a; see also 1845b[19]). The series of lectures was highly publicised; an advertisement from the time illustrates just how much Agassiz relied on the idea of a "parallelism" to explain the "Plan de la Création", these early words showing how he leant more heavily on geography than he would come to do later:

> Suffice it to say that he [Agassiz] intends to show in the general development of the animal kingdom the existence of a definite preconceived plan, successively carried out; in other words, the manifestation of a higher thought,—the thought of God. This creative thought may be studied under three points of view: as shown in the relations which, in spite of their manifold diversity, connect all the species now living on the surface of the globe; in their geographical distribution; and in the succession of beings from primitive epochs until the present condition of things. (Lurie 1960)

It was in these 1845 Neuchâtel lectures that Agassiz first discussed his ideas of "zoological provinces". Agassiz noted that provinces (or regions) could be "defined" by their particular composition of plants and animals as well as by their human inhabitants (Agassiz 1845a). Although Agassiz believed the animals confined to each region were all created within them—*in situ*, so to speak—he understood the races of Mankind to be "one and the same species capable of ranging over the surface of the globe" (Agassiz 1845b: 29). Thus, his early views were distinctly monogenic. In spite of that sentiment, even in his early writings Agassiz had suggested that blacks ("Negroes") had a distinct origin, different from that of whites ("Caucasians"), and the former could not be traced back to the sons of Noah (Lurie 1959,

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[18] See, for example, the different approaches taken to Agassiz and his views on "Mankind" in Roberts (1982: 27–31), Walls (2003: 181–184), and Stephens (2000: 195–211).

[19] Agassiz dealt with geographical distributions in passing prior to 1845, notably in two papers from 1844 (Agassiz 1844b, 1844c) before his first general paper on animals and man (Agassiz 1845a).

1960). Suggesting that both had different origins, while forming part of his general opinion on the creation of all species, departed from the received religious view, of Man created as one. But at that time he did insist that all men belong in one species.

His Neuchâtel geography lecture was given in Boston shortly after Agassiz's arrival in the U.S. He travelled to Philadelphia, the place where he first met blacks and wrote the now-infamous letter sent to his mother detailing his apparent distaste for these "people".[20] Whether as a result of these early meetings or subsequent encounters, when Agassiz eventually lectured on Man in Charleston, he had changed his views, suggesting not only that black and white men were of different origin but of different species, a decidedly polygenic view.

It was in his 1854 book *Types of Mankind* that Agassiz included his coloured map of realms. The map details the eight realms he recognised: Arctic, Asiatic, European, American, African, East-Indian (Malayan), Australian, and Polynesian. The realms and their inhabitants (humans and other animals) are tabulated on a separate fold-out sheet (Agassiz 1854: facing p. lviii), which has a page explaining the contents of the table (Agassiz 1854: lxxvii). The table's explanation expands on the composition of the Realms, each being composed of a series of "faunae" (except the Arctic). The table has eight columns and a variable number of rows; each row corresponds to a human "kind" and a realm. In total there are 67 numbered boxes. For example, column I is the Arctic realm, with nine rows (numbered 1–9); column II is the Mongol realm, with eight rows (numbered 10–17); column III is the "European" realm, with eight rows (numbered 18–25); and so on. Each column has a series of separate illustrations illustrating the "concept" of each realm. For example, in the first box (number 18) of the European realm (the third column) there is an example of European man (in this case illustrated with a portrait of Cuvier [from his 1816 study]; see Winsor 1979: 113), followed by a human skull (box 19) and six other animals (a bear, a stag, an antelope, a goat, a sheep, and an aueroch [an ancient ox]). Only in the Arctic realm (column I, row 9) is there a plant—a reindeer-moss (a lichen). With respect to man, the realms marked on the coloured map are not equivalent to the entries in the table: the Arctic, European, American, Malay, and Australian are the same, whereas the Asiatic realm is "inhabited by Mongols ..." (column II in the table) and the African realm is "inhabited by Nubians, Abyssinians, Foolahs, Negroes, Hottentots, Bosjesmans"; the "Negro" is the example used for column V (the African realm) and the Hottentot is used for the example of column VI, described in the legend of the table as the "Hottentot fauna". The Polynesian realm is not represented in the table at all, but the legend states "inhabited by South-Sea Islanders ..." (Agassiz 1854: lxxvii).

For all its detail, Agassiz's realms do not relate to one another. That is, Agassiz saw regions as problems of definition rather than of discovery—as in discoveries made with the classifications of animals, in spite of the fact he had written a book on the subject (Agassiz 1859).

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[20] This letter has been reproduced on many occasions; see Lurie (1959, 1960).

## 13.9 Regions, Homology, and Relationships

The problem of classification was solved some years ago, or at least a solution was made possible. Appreciation of that solution has dwindled simply because cladistics became confused with a particular method of analysis, as if it were one solution among many, as if in the geographical realm it was but one aspect of chorological investigation. Cladistics is not a method nor a doctrine but a statement about classification and its results, captured by the cladistic parameter (Chapter 2).

The notion of homology in biogeography has been previously tackled, the first detailed statement being Patterson (1981a: 448; see Patterson 1980a: 238, attributed to Platnick & Nelson 1978), which may be summarised as "... in cladistic biogeography homologies are congruent distributions of taxa . . . " (Patterson 1981a: 448, 466, Nelson 1994: 135, Platnick & Nelson 1989: 412); other interpretations are possible (Grehan 1988, Morrone 2001, 2004).

Morrone adopted the concepts of primary and secondary homology (De Pinna 1991), relating each to a particular question and a particular method of analysis (Morrone 2001, 2004). This viewpoint reveals a mistaken notion, one that currently pervades systematics (Chapter 7). Primary homology is related to the phenetic view of similarity, somewhat divorced from a *direct* notion of relationship (Chapter 8). Comparison among organisms reveal homologues; placing those homologues in context allows homology statements to be made—that is, statements of relationship derived from the data and independent of any particular method. In effect, there are no primary or even secondary homology statements; there are simply statements of relationships (homology), some of which turn out to be true, others not. If biogeography concerns classification, then it too deals with relationships.

## 13.10 Sclater, Huxley, and the Classification of Regions

A paper of some significance in the study of regions is Sclater's "On the general Geographical Distribution of the members of the class Aves" (Sclater 1858). Philip Lutley Sclater (1829–1913), a 19th-century British ornithologist, held the view that "each species must have been created within and over the geographical area, which it now occupies," a viewpoint not unlike that of Agassiz. Sclater commented on Agassiz's and Swainson's studies:

> In Mr. Swainson's article in Murray's "Encyclopedia of Geography", and in Agassiz's introduction to Nott and Gliddon's "Types of Mankind", what I consider to be a much more philosophical view of this subject is taken. The latter author, in particular, attempts to show that the principal divisions of the earth's surface, taking zoology for our guide, correspond in number and extent with the areas occupied by what Messrs. Nott and Gliddon consider to be the principal varieties of mankind. The argument to be deduced from this theory, if it could be satisfactorily established, would of course be very adverse to the idea of the original unity of the human race, which is still strongly supported by many Ethnologists in this country. But I suppose few philosophical zoologists, who have paid attention to the general laws of the distribution of organic life, would now-a-days deny that, as a general rule, every species of animal must have been created within and over the geographic area

> which it now occupies. Such being the case, if it can be shown that the areas occupied by the primary varieties of mankind correspond with the primary zoological provinces of the globe, it would be an inevitable deduction, that these varieties of Man had their origin in the different parts of the world where they are now found, and the awkward necessity of supposing the introduction of the red man into America by Behring's Straits, and of colonizing Polynesia by stray pairs of Malays floating over the water like cocoa-nuts, and all similar hypotheses, would be avoided. (Sclater 1858: 131)

Sclater proposed six regions, Palaearctic, Ethiopian, Indian, Australian, Nearctic, and Neotropical, grouped into two series (Table 13.2). Sclater's regions were perhaps the first universally accepted classification of areas, following Candolle's 20 botanical (endemic) regions and Buffon's division of the Old and New Worlds (Nelson 1978c), and although numerous minor modifications were made during the 20th century (i.e., Udavary 1975), the regions are largely in use today.[21]

Huxley (1868) offered another version, retaining Sclater's six regions but grouping them differently, along a North-South divide (Table 13.2). Although Wallace adopted Sclater's regions, he prepared a diagram contrasting Sclater and Huxley's groupings (Wallace 1876, I: 66). Wallace's diagram is similar, in some respects, to the divisions in Table 13.2. While the regions Sclater proposed and Wallace endorsed were discussed almost endlessly in the following years, a significant change occurred some 120 years later. The contrasting classifications of Huxley and Sclater were compared as two cladograms (Figure 13.4; after Nelson & Platnick 1981: Fig. 8.50). The cladogram representing Sclater's scheme (Figure 13.4 left) has two nodes corresponding to Paleogaea and Neogaea; the cladogram of Huxley's scheme (Figure 13.4 right) has two nodes corresponding Arctogaea and Notogaea. In fact, one might say that the classifications disagree over the placement of the Australian and Nearctic region (Table 13.2). In any case, what remained was a problem in classification, not simply a static system that did not work and was of no use. A suitable analogy would be if the classification of land plants was decided by general agreement, and then it was supposed to inform on "greater" issues. Quite simply, classifications of regions became of little use, simply because they were artificial,

**Table 13.2** Comparison of the regions of Sclater (1858) and Huxley (1868)

| Sclater (1858) | Huxley (1868) | |
|---|---|---|
| Paleogaea | Arctogaea | |
| | Palaearctic | Palaearctic |
| | Ethiopian | Ethiopian |
| | Indian | Indian |
| | *Australian* | *Nearctic* |
| Neogaea | Notogaea | |
| | *Nearctic* | *Australian* |
| | Neotropical | Neotropical |

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[21] No universal classifications exist at the level of endemic areas, with the exception of the Nearctic (Merriam 1892), France (Lamarck & Candolle 1805), and the recent work of Juan Morrone in South America.

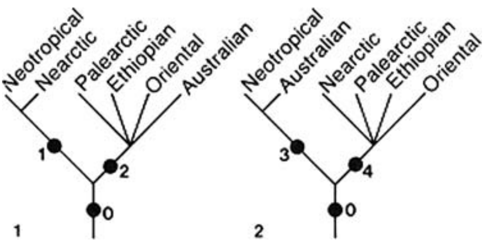

**Fig. 13.4** Contrasting classifications of Huxley's and Sclater's areas relationships, compared as two cladograms, after Nelson & Platnick (1981: Fig. 8.50), with permission

adopted, and agreed upon by fiat. While the study of regions was understood as static, that characterisation seems deliberately obtuse. From this example, and the representation of regions in cladograms, it is best understood as a problem of classification (Chapter 2).

## 13.11 Croizat's Radical Realms: Ocean Basin and Cladograms

Croizat presented a "radical" (Craw & Page 1988: Fig. 12) rearrangement of global realms (regions) (Croizat 1958: Fig. 259; see also Nelson & Ladiges 2001: 393), focusing on five interrelated regions. Craw provided an example of Croizat's approach in a diagram with two cladograms (Figure 13.5; after Craw 1983: Figs. 4A and B and Craw 1988). He included three terminals, North America, New Zealand, and Africa, and presented one diagram of their inter-relationships, some terminal having more than one direct relationship (Craw 1983: Fig. 4A). His other diagram included reticulations, allowing all the terminals to appear only once, but the lines connecting them are duplicated (Craw 1983: Fig. 4B). The nodes of the diagrams were recognised as the Pacific, Indian, and Atlantic oceans (Figure 13.5; after Craw 1983: Figs. 4A and B).

Nelson provided an alternative pair of cladograms to represent Croizat's realms. Nelson's first cladogram (reproduced here as Figure 13.6a) is unresolved, including just the five "regions" Croizat recognised: Atlantic, Austral, Boreal, Indian, and

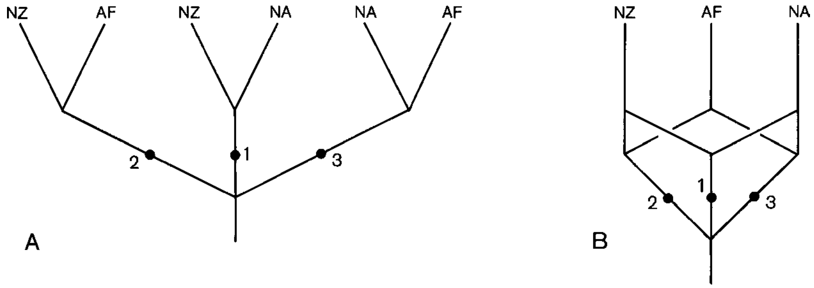

**Fig. 13.5** Example of Croizat's approach in a diagram with two cladograms, after Craw (1983: Figs. 4A and B and 1988). The nodes of the diagrams were recognised as the Pacific, Indian, and Atlantic oceans. Reproduced with permission

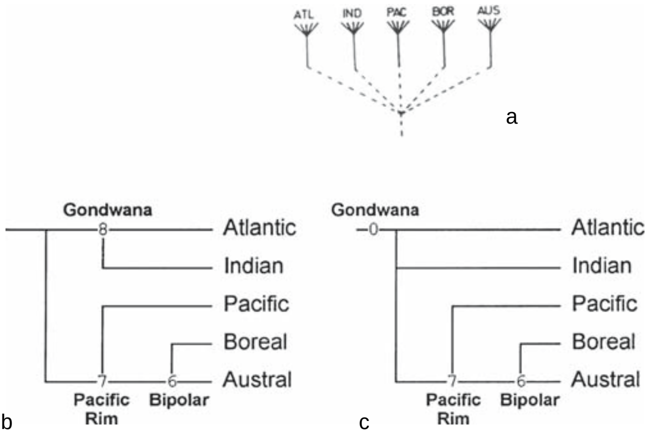

**Fig. 13.6** Alternative pair of cladograms to represent Croizat's realms; (a) after Nelson (1985b: 188). (b) with two nodes worth of resolution, one representing "bipolarity", the other the "Pacific rim" (Nelson 1985b: Fig. 1C, Nelson & Ladiges 2001: Fig. 8B; (c) after Nelson & Ladiges (2001: Fig. 8A) representing Croizat's proposal

Pacific. Nelson (1985b: 188) said of these "regions" that the Atlantic "includes taxa whose subtaxa are differentiated on either side of the tropical Atlantic", the Indian Ocean "similarly includes taxa having species endemic on or along the shores of the tropical Indian Ocean … So … for the tropical Pacific." The Boreal and Austral regions are somewhat different, and "include those taxa commonly termed Holarctic and Antarctic, and together termed bipolar or antitropical" (Nelson 1985b: 188). This cladogram (Figure 13.6a) is uninformative of relationships, the implication being that Croizat represented (or discovered) the "regions" but did not suggest how they might be further interrelated. Nelson's second cladogram (reproduced here as Figure 13.6b) presents two nodes worth of resolution excepting the Gondwana node, one representing "bipolarity", the other the "Pacific rim" (Nelson 1985b: Fig. 13.1C, Nelson & Ladiges 2001: Fig. 8B; see Brooks et al. 1981: Fig. 16, Parenti 1991: Fig. 11; but see Lovejoy 1996, 1997, De Carvalho et al. 2004).

Other representation of Croizat's diagram have been proposed, such as the series of blocks representing "parts" of continents (Figure 13.7; Craw & Page 1988: Fig. 12, Craw 1988: Fig. 13.12, Craw 1989: 537, Fig. 8, Page 1989a: 475, Fig. 5, Grehan 1991: Fig. 13.1, Craw et al. 1999: Figs. 6–13, Humphries & Parenti 1999: Fig. 13.1.14, Grehan 2001, and, in a modified form, Parenti 1991: Fig. 13.1; cf. Craw 1982: 311, Fig. 3). Nelson & Ladiges (2001: Fig. 8A) include another cladogram, representing this novel proposition (Figure 13.5c). Figure 13.5 b and c differ in their understanding of Gondwana.

In earlier times, regions were considered to be units in need of definition (Schmidt 1954, Horton 1973) rather than discovery, as evidenced by the above series of hypotheses. Yet inter-relationships among regions, although not always clear, seem tractable (Cox 2001, Morrone 2002), even if competing systems require evaluation and testing. Ultimately, regions (and their subdivision) may come to represent the living world, in the same way angiosperms, vertebrates, and the many

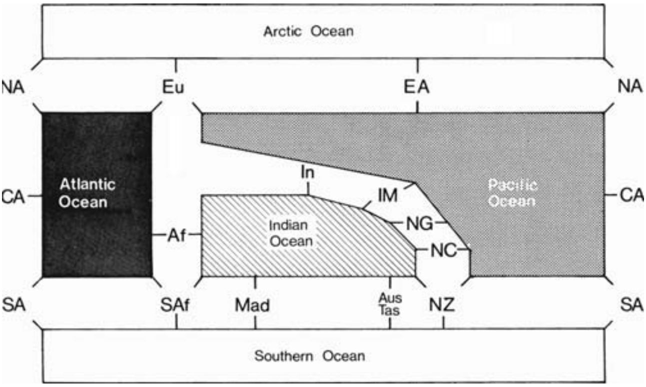

**Fig. 13.7** Representation of Croizat's diagram as "parts" of continents, after Craw & Page (1988: Fig. 12)

other taxa characterised over the years are understood as part of the world we live in, discoveries, actual knowledge.

## 13.12 The Threefold Parallelism: … and Its End

The threefold parallelism meant different things to different people. For Ernst Haeckel, it provided "the strongest proofs of the truth of the theory of evolution", for Louis Agassiz, the strongest evidence for the plan of divine creation. Haeckel developed his threefold parallelism, hinging its usefulness on a version of the biogenetic law and the data provided by palaeontology (Bryant 1995). For Haeckel, geography was not considered direct evidence of anything. Rather, it is circumstantial. Haeckel's efforts to forge a "phylogenetic" system of representation did not go unchallenged, in the first instance by a number of German morphologists, in the second by the cladistic revolution in palaeontology (Williams & Ebach 2004).

Agassiz continued to require further sources of evidence, each drawing him nearer to the explanation of the origin of things, a world-view where the primary cause was hidden from investigation (Rieppel 1988, Janvier 2003)—a cause Agassiz had already identified. The threefold parallelism came and went, eventually receiving its "death-blow" in the hands of Nelson (1978b, although some still see value in its original formulation, Bryant 1995—although Bryant does note the geographical possibility: Bryant 1995: 208). Briefly, Nelson concluded that the "old" threefold parallelism (palaeontology, ontogeny, systematics) has no special meaning or interpretation beyond being interrelated evidence for the classification of organisms; biogeography, the spatial dimension, was the only independent source of data on organisms and their place in the world—and that too was a problem of classification (Nelson 1978c). The issue of classification was solved, to a degree, with the clarification of relationships (Hennig 1966a), something only recently becoming apparent in the context of all kinds of data (Nelson 1994). In a general sense, any parallelism of evidence is concerned with homology or, as we have suggested throughout this book, with a unit of classification.

It might be said that a new threefold parallelism arose from the ashes of the old: Form, the interrelations of palaeontology, ontogeny, systematics—and now molecules; Space—the interrelations of areas (Ebach 1999); and Time, falling out from their interplay (Nelson & Platnick 1981)—time being a discovery rather than an imposition. This reformulation picks up a problem, first stated clearly by Candolle, developed by Prichard, Lyell, Swainson, Agassiz, Sclater (and others), eventually clarified by Nelson & Platnick (1981), who posed the problem in a tractable way. The revived threefold parallelism—systematics, biogeography, geology—does not aim at discovering ancestry, origins, or any matters related to those things as commonly understood from Haeckel to our present state. But it does relate to the tractability of classificatory problems and what that allows us to discover of the world we live in.

## 13.13 Systematic Biogeography: The Rediscovery of Classification

Little can be achieved in systematics without a classification and an established nomenclature; with its lack, communicating results to other biologists would be impossible. Thus, if we speak of the robin, it depends whether we are European (*Erithacus rubecula*), American (*Turdus migratorius*), or Australian (*Petroica*, *Poecilodryas*, *Eopsaltria*, *Melanodryas*, *Tregallasia*)—these are all very different birds. And so biogeography—without a classification at each biotic level, biogeographical areas become a jumble of arbitrary units that vary from person to person, study to study, culture to culture. In spite of this, biogeography continues to survive—largely as an extension of ecology, Haeckel's chorology writ large.

Recently, some palaeobiogeographers have attempted to erect biogeographical classifications based on stratigraphy and "basin analysis" (Westermann 1996, Cecca & Westermann 2001). Using this approach, areas are based on geological and palaeoecological considerations, rather than biotic characteristics.

Westermann's nomenclature, however, is reminiscent of Mayr's objections to Wallace's biogeographical classification, namely the carving up of the Earth to suit current, or in the case of Westermann, preserved distribution patterns of fossils. Westermann's nomenclature, although a noble attempt to establish a classification, is flawed in its use of geology as a unifying theme for biotic areas. A biotic classification is best based on *biotic* elements. As we use taxic characteristics to identify taxa, so it is appropriate to classify biotas using biotic characteristics: taxa and their inter-relationships. In systematics we call these taxic elements "homologues" and the inter-relationships "homologies". Applying this same idea to biotas, discovery of area homologues and area homologies establishes a **Systematic Biogeography**.

### *13.13.1 Area Homology*

Area homologies are best defined as either a geographical (Croizat 1964) or biological (Morrone 2001) *relationship* that corresponds to a unique grouping (see above).

Croizat's area homology is based on geography rather than biotic elements; Morrone's area homology is based on De Pinna's (1991) criterion of homology to areas. In either case, area homology is understood as a relationship based on a twofold similarity constructed by either geographical or biotic proximity. As the basic unit of classification is a three-item relationship (Chapter 7), its application in biogeography is the **three-area relationship**, the smallest biotic characteristic, an **area homologue**. **Area homologies** are simply the patterns "expressed" by area homologues. Just as all mammals are more closely related to each other than to any other animal, based on shared homologues such as mammalian hair, so to any area homologue shared by more than one monophyletic group in which the areas overlap is an area homology. In other words, taxa act as area characteristics to indicate an area homology (see this Chapter, section 13.9). Given that area homology is discovered through the taxic relationships found in multiple monophyletic groups, then the cladograms representing the monophyletic groups can be expressed in terms of area relationships, called **areagrams**. Combination of all area homologues, however, forms a **general areagram**, a statement of relationships that represents all discovered area homologies. Once area homologues and area homologies have been established, there remains a relevant question: What does this say of the biotic area?

### *13.13.2 Defining the Biotic Area: Biotic Morphology or Taxonomy*

It is important to avoid an "area concept" debate in systematic biogeography. The recent interest in quantitative endemic area methods has spurned the equivalent of a "species" concept debate in biogeography (Hausdorf 2002, Linder 2001). To avoid "area concepts", **a culture of biotic morphology is required, a culture that is empirical and independent of explanatory mechanisms**. Areas are like taxa, groups of biota that share closer relationships with each other than they do to another biota. The biogeographer—be it a systematist, ecologist, or naturalist—would gain the same insight as a taxonomist by describing the area in great detail over time. The practise of area morphology is essential in understanding any particular area and its barriers for biogeographical analysis.

### *13.13.3 Towards Area Monophyly*

A systematic biogeography results in a biogeographical classification based on area homologies as represented in a general areagram. A biogeographical classification is the *biotic archetype* or *area monophyly*—a pattern that denotes a process, namely that of a common biotic history. How we choose to interpret this common history is the next and final stage of systematic biogeography.

Before reaching the stage of interpreting the biotic process, existing classifications require study, primarily those stemming from Sclater (1858), and revised classifications proposed, based on patterns of area homologies. In doing so we are able to establish an area nomenclature and taxonomy derived from biotic morphology and taxonomy.

*Biogeographical Nomenclature*. The purpose of Biogeographical Nomenclature is not only to establish a formal descriptive process but also to help provide a *Biogeographical Classification* that captures the area hierarchy.

*Biogeographical Classification*. Endemic biotic areas are the equivalent of taxa in a biogeographical classification. Like taxa, biota share relationships with other biotas based on their area homologues (biotic relationships). Biotic areas are based solely on the monophyletic groups of taxic relationships and, unlike Westermann's Biochlores, are defined by the interaction of the organisms and their inorganic environment. Thus, efforts are directed at discovering whether biota (realms, regions, areas, etc.) are monophyletic. For instance, is the region (land-mass) "Australia", a term commonly used in biogeographical analyses, monophyletic— "Australia" consists of *x* number of biotic areas. Suppose that southeastern Australia is discovered to be more closely related to southern Patagonia, in the Neotropical realm, than it is to any other part of the "Australian" area (land-mass). If this were the case, then "Australia" is evidently non-monophyletic.

If this (hypothetical) example is discovered to be true and Australia is indeed non-monophyletic, then previous biogeographical classification requires reassessment. Without a clear idea of what defines the region "Australia" (as opposed to the land-mass), there is an endless accumulation of different meanings, all corresponding to, or equivalent to, "Australia". Thus, "Australia" has been defined as all areas on the single land-mass except Tasmania (Humphries 1981), all northern areas of the land-mass above 35 degrees latitude (Andersen 1991), all known areas in the Australian land-mass (Seberg 1991), all eastern areas above Tropic of Capricorn (Welzen et al. 2003), and all except New Guinea and Queensland (Wagstaff & Dawson 2000). Rather surprisingly, some authors have used *all* the above definitions in a single analysis to determine "consensus" areagrams (Sanmartín & Ronquist 2004).

Without an established area taxonomy that uses area monophyly to uncover "natural" realms, regions, and areas, terms such as "Australia" remain arbitrary units meaning different things to different people. Without an established taxonomy, we would be unable to compare "Australia" in one analysis to "Australia" in another, as the above examples show.

In order for biogeography to remain a practical and empirical science, it needs to formalise areas, regions, and realms under a systematic hierarchy—possibly one system adopted by all biogeographers, equivalent to the *International Code of Zoological Nomenclature* (ICZN), a code adopted and accepted by all zoologists (as is the *International Code of Botanical Nomenclature* (ICBN)).

Once a taxonomy and systematic hierarchy are established and monophyletic areas, regions, and realms established, we are able to uncover biogeographical patterns that may indicate biotic processes. One method or technique that deals with uncovering such processes is *Area Cladistics* (Ebach 1999, 2003, Ebach & Humphries 2002).

### 13.13.4 Area Cladistics: Interpreting Area Monophyly

The premise of area cladistics is to interpret area relationships (based on area homologies found in general areagrams) as geographical proximity. The assumption that two areas are more closely related to each other than they are to a third and are also geographically closer to one another is not a new concept. The interpretation of the component that signifies the relationship (when compared to a third) as biotic divergence is rather more unique, indicating that two biotas share a similar history both biologically and geographically at some point in time. The component does not mean vicariance or any other mechanism. A component on a general areagram indicates geographical isolation (*sensu* allopatry) not only of the taxa but also of the inorganic areas. In this sense all the elements of the biotic area are interpreted rather than just the shared or common history of the organisms. The areagram also tells us about the history of the inorganic area as well.

Evidence to suggest that components on a general areagram (the combination of many monophyletic areagrams of different taxa that have overlapping areas) denote biotic divergence is based on the fact that no other known observable process would form such patterns. Migrations, for instance, are unique to one type of organism and not necessarily another. Barriers, however, generally can affect a greater number of organisms equally. Area cladistics is a tool that discovers geographical isolation and translates it diagrammatically into biotic maps that outline the past geographical barriers responsible for biotic divergence and subsequent geographical isolation. The mechanisms that have caused the organisms to be isolated (climate change, sea

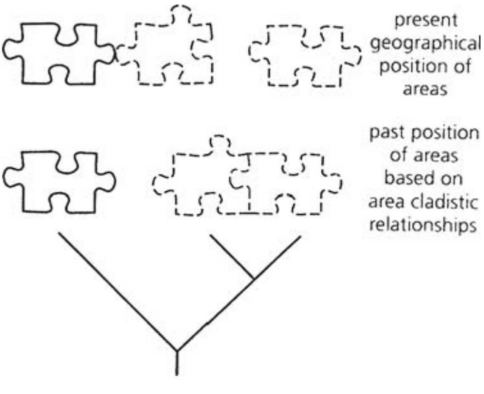

**Fig. 13.8** Area cladistics jig-saw, the "dovetailing" of areas

level rises, etc.) are not discoverable by area cladistics. What can be discovered is whether a barrier was present at one time (Figure 13.8).

General areagrams may also be translated into biotic maps, showing the geographical positions of the biota during the time of divergence. The resultant biotic maps are useful to compare with palaeo-magnetic maps derived from palaeo-magnetic data. The problem with paleo-magnetic data is their inability to measure and uncover palaeo-longitudes. Area cladistics, in collaboration with palaeomagnetic data, will produce palaeo-reconstructions based on reliable empirical data to uncover palaeo-longitude. Recent area cladistic analyses, although producing alternative palaeo-reconstructions, differ from palaeo-magnetic maps in palaeo-longitude not latitude (Ebach & Humphries 2002, Holden 2003). The corroboration between palaeo-magnetic data and general areagrams highlights the importance of biogeography in interpreting geological evolution.

On a dynamic planet, life and Earth clearly do evolve together and systematic biogeography is the most appropriate way to study organisms and their environments (Nelson 1983).

# Epilogue: Pattern Cladistics From Goethe to Brady

Most, if not all, ideas in science are recycled, rediscovered, or rehashed, either surreptitiously, through rereading and rediscovering old works, or simply (commonly?) through lack of knowledge of past achievements. The idea of transformation—that things might change, transform, convert into other things—for instance, has been proposed many times, by both evolutionists and non-evolutionists alike. Yet the notion of transformation is really a myth, a story which many scientists embrace, a story that tells of living things transforming into other living things, with their role to interpret its meaning and mechanism: The fall of Paradise to the untamed wild, the tamed landscape to the Biblical flood, the reigns of monarchs, a kingdom to a republic and the pastoral to the industrial—of transformations there are plenty. A deep desire to uncover what mechanism(s) lie behind these transformations has provided many explanations, from the acquisition of sin after the fall from grace, to God's will, to progress, however construed. The belief that every transformation neatly fits a law or model by which nature abides has shaped our way of thinking. Yet concomitant with such thoughts is the recognition that Nature is complex, and that Nature's complexity obeys no single law or theory that places it neatly into a box. For every law and theory, we are told, there are exceptions, which are given ad hoc explanations. Man may have toiled the soil to shape nature into his or her image of Eden, but complexity does not fit any man-made law. Complexity is in itself a law; all we can do is interact with it and discover its relationships—this is the essence of knowledge.

As Hennigian cladistics gained acceptance by many more systematists between 1981–1990, Ron H. Brady (1937–2003[1]), a historian and philosopher, became interested in the studies of Gareth Nelson, Norm Platnick, and Donn Rosen, all then at the American Museum of Natural History. The connection between Brady's work and that of Nelson is complex (see Brady 1979, 1982, 1985, 1987, 1989, 1994a, 1994b and Ebach 2005).

After meeting the cladists in the early to mid-1980s, Brady wrote a paper entitled "Form and Cause in Goethe's Morphology" (Brady 1987), a work that discussed the development of Goethe's archetype through to modern day. In his article, Brady concluded:

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[1] It remains a surprise that no obituary has yet appeared of Brady.

> The argument that a cladogram is a purely descriptive device has been clearly set forth by Nelson and Platnick, 1981. ... Obviously, on this level we can find no opposition to Goethe's approach. The next interpretive level, that of the tree, does produce such opposition, not because a historical element is introduced, but because the other half—i.e. the a-historical, is not. (Brady 1987: 298)

The dichotomy between tree and cladogram leads back to Goethe and his archetype. Brady may have been the first person to realise the historical significance of Nelson's work: the connection between Goethe's *Morphology* and pattern cladism. Earlier Brady (1982) had defended the position of non-mechanistic explanations in systematics:

> Beatty seems to defend cladists who are willing to interpret their results according to "evolutionary perspectives", but if the strategy of defining characters contradicts those perspectives—and my reading of his [Beatty's] argument suggests this result—any attempt to combine this research strategy with those interpretations would build in a contradiction ... the pattern cladists, by discarding all such explanations, may have the only cladistic position which remains free from internal contradiction. (Brady 1982: 290)

Brady realised the importance of finding patterns first and interpreting them later in the light of known or hypothesised processes. The pattern cladistic interpretation gave cladistics (and systematics in general) a chance to discover processes, thus highlighting the importance of uncovering patterns prior to invoking processes (see Brady 1987). The link between Goethe's archetype and pattern cladism that Brady made is significant for one other reason: homology.

Nelson rarely spoke of homology in terms of archetypes. Homology, in Hennigian terms, is understood to be the transformation of character-states that unite two taxa. The synapomorphy is the homology that contains the homologues and lies in a great chain of being, namely that of the optimisation of character-states on a cladogram. Nelson never accepted this, as can be appreciated by his conversion of nodes to components. If the nodes represent transformational parts that unify two taxa, then components are junctions between two areas that represent a statement of relationship to a third thing. The dismissal of transformations and synapomorphies was revolutionary, something many systematists and biogeographers still fail to accept but was understood as a return to Goethe's way of science for Brady.

A unique aspect of Nelson's approach was to reform palaeontology by resurrecting and modifying Agassiz's threefold parallelism and, as a consequence, reform biogeography. The revolution today is no longer solely about palaeontology but of reforming its legacy—transformation and origins in molecular genetics. The tradition of seeing the world through mechanisms in order to discover patterns has hampered comparative biology since its inception in the 18th century. The revolution for 21st-century systematic biology lies in the work of Nelson and in precise methods, such as three-item analysis. Patterns can only be discovered if we consider it to be the primary aim of biology—s*cience as a pattern* and not *science as a process*.

The role of pattern cladistics today is to realise Nelson's legacy and learn from biogeography, the revolution that changed palaeontology, and reform molecular biology:

> Palaeontology of the past is revived in molecular systematics of the present, in its search for ancestors and centers or origin. (Nelson 2004: 127)

That search—“for ancestors and centers of origin”—was made possible only by assuming that the phylogenetics of today had moved away from the phenetics of yesterday. That seems not to be the case.

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