HOMOLOGY
The Novartis Foundation is an international scientific and educational charity (UK Registered Charity No. 313574). Known until September 1997 as the Ciba Foundation, it was established in 1947 by the CIBA company of Basel, which merged with Sandoz in 1996, to form Novartis. The Foundation operates independently in London under English trust law. It was formally opened on 22 June 1949.

The Foundation promotes the study and general knowledge of science and in particular encourages international cooperation in scientific research. To this end, it organizes internationally acclaimed meetings (typically eight symposia and allied open meetings, 15-20 discussion meetings, a public lecture and a public debate each year) and publishes eight books per year featuring the presented papers and discussions from the symposia. Although primarily an operational rather than a grant-making foundation, it awards bursaries to young scientists to attend the symposia and afterwards work for up to three months with one of the other participants.

The Foundation's headquarters at 41 Portland Place, London W1N 4HN, provide library facilities, open every weekday, to graduates in science and allied disciplines. The library is home to the Media Resource Service which offers journalists access to expertise on any scientific topic. Media relations are also strengthened by regular press conferences and book launches, and by articles prepared by the Foundation's Science Writer in Residence. The Foundation offers accommodation and meeting facilities to visiting scientists and their societies.

Information on all Foundation activities can be found at http://www.novartisfound.org.uk
Contents

This symposium is based on a proposal made by Adam Wilkins
Editors: Gregory R. Bock (Organizer) and Gail Cardew

B. K. Hall  Introduction  1

A. L. Panchen  Homology — history of a concept  5
  Discussion  18

D. B. Wake  Homoplasy, homology and the problem of 'sameness' in biology  24
  Discussion  33

R. L. Carroll  Homology among divergent Paleozoic tetrapod clades  47
  Discussion  61

G. B. Müller and S. A. Newman  Generation, integration, autonomy: three steps in
  the evolution of homology  65
  Discussion  73

F. Galis  On the homology of structures and Hox genes: the vertebral column  80
  Discussion  91

J. R. Hinchliffe and E. I. Vorobyeva  Developmental basis of limb homology in
  urodeles: heterochronic evidence from the primitive hynobiid family  95
  Discussion  105

R. A. Raff  Larval homologies and radical evolutionary changes in early
  development  110
  Discussion  121

G. P. Wagner  A research programme for testing the biological homology
  concept  125
  Discussion  134

A. Meyer  Homology and homoplasy: the retention of genetic programmes  141
  Discussion  153
CONTENTS

G. F. Striedter  Homology in the nervous system: of characters, embryology and levels of analysis 158
Discussion 170

H. W. Greene  Natural history and behavioural homology 173
Discussion 182

G. A. Wray  Evolutionary dissociations between homologous genes and homologous structures 189
Discussion 203

E. Abouheif  Establishing homology criteria for regulatory gene networks: prospects and challenges 207
Discussion 222

P. W. H. Holland  The effect of gene duplication on homology 226
Discussion 236

B. K. Hall  Summary 243

Index of contributors 246

Subject index 248
Participants

E. Abouheif  Department of Ecology and Evolution, State University of New York at Stony Brook, Stony Brook, NY 11794-5245, USA

M. Akam  University Museum of Zoology, Downing Street, Cambridge CB2 3EJ, UK

R. L. Carroll  Redpath Museum, McGill University, 859 Sherbrooke St. West, Montreal, Canada H3A 2K6

P. Donoghue  School of Earth Sciences, University of Birmingham, Edgbaston, Birmingham B15 2TT, UK

F. Galis  Institute for Evolutionary and Ecological Sciences, University of Leiden, PO Box 9516, 2300 RA Leiden, The Netherlands

H. W. Greene  Museum of Vertebrate Zoology and Department of Integrative Biology, University of California, Berkeley, CA 94720-3101, USA

B. K. Hall *(Chair)*  Department of Biology, Dalhousie University, Halifax, Nova Scotia, Canada B3H 4J1

J. R. Hinchliffe  Institute of Biological Sciences, University of Wales, Aberystwyth, Wales SY23 3DA, UK

N. D. Holland  Marine Biology Research Division, Scripps Institution of Oceanography, La Jolla, CA 92093-0202, USA

P. W. H. Holland  School of Animal and Microbial Sciences, The University of Reading, Whiteknights, Reading RG6 6AJ, UK

T. C. Lacalli  Department of Biology, University of Saskatchewan, Saskatoon, Saskatchewan, Canada S7N 5E2

J. Maynard Smith  School of Biological Sciences, University of Sussex, Falmer, Brighton BN1 9QG, UK
A. Meyer  Department of Biology, University of Konstanz, 78457 Konstanz, Germany


A. L. Panchen  Department of Marine Sciences, University of Newcastle upon Tyne, NE1 7RU, UK

M. Purnell (Bursar)  Department of Geology, University of Leicester, Leicester LE1 7RH, UK

E. Raff  Indiana Molecular Biology Institute, and Department of Biology, Indiana University, Bloomington, IN 47405, USA

R. A. Raff  Indiana Molecular Biology Institute, and Department of Biology, Indiana University, Bloomington, IN 47405, USA

V. L. Roth  Department of Zoology, Box 90325, Duke University, Durham, NC 27708-0325, USA

G. F. Striedter  Department of Psychobiology and Center for the Neurobiology of Learning and Memory, University of California at Irvine, Irvine, CA 92697, USA

D. Tautz  Zoologisches Institut, Universität München, Postfach 202136, D-80021 München, Germany

G. P. Wagner  Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT 06520-8106, USA

D. B. Wake  Museum of Vertebrate Zoology, University of California, Berkeley, CA 94720-3160, USA

A. Wilkins  Editorial Office, 10/11 Tredgold Lane, Napier Street, Cambridge CB1 1HN, UK

G. A. Wray  Department of Ecology and Evolution, State University of New York, Stony Brook, NY 11794-5425, USA
Introduction

Brian K. Hall

Department of Biology, Dalhousie University, Halifax, Nova Scotia, Canada B3H 4J1

I am delighted to have the opportunity of welcoming the speakers and discussants to what should be an exciting symposium on homology. Although it is presumptuous of me to set the direction that our discussion should take, and even more presumptuous to map the route we will take or to attempt to predict our destination, I will provide some signposts at the beginning of our journey. Whether the route we take or the destination we reach will bear any resemblance to the route and destination suggested remains to be seen. I pose four questions that we are likely to encounter during our deliberations.

What is homology?

Much of the discussion about homology in the past has been mired in semantics. I hope we will not become bogged down in definitional issues but rather hope that, along with David Wake (1994), in an oft-cited review of a volume on homology, we can agree that homology is ‘the central concept for all of biology’ and move on. Despite the importance of homology as the ‘hierarchical basis of comparative biology’ (the subtitle of the volume edited by Hall [1994]) and its central place with evolution in biology, definitions of homology abound. In the same review, and as a result of reading the 1994 book, Wake concluded that: ‘...I found no reason to change my personal definition of homology (which is not worth repeating, since I cannot even convince students in my own lab of the correctness of my position).’

Do biologists need a definition for such a central concept or is it sufficient to know that homology exists and to move on? It is my hope that in this symposium we will move on, each presenting our definition of homology for clarity of discussion, but then moving to the important issues raised by the three other issues posed below. I am sure that definitional issues will arise, but I hope they will not dominate or overwhelm us. From various speakers we will see homology as sameness, identity, synapomorphy, a statement about final structures, a statement about developmental processes and/or about genes, and we will discuss whether homology is (or should be) hierarchical and is (or can be) partial.
Perhaps by the end we may be able to agree, or at the very least comment on:

1. whether having a definition is important or whether the explanatory power of an ill-defined but central concept is sufficient;
2. whether one definition holds for all situations, or whether it is sufficient to just say what we each mean when we invoke homology; and
3. whether multiple definitions are possible, allowable or desirable.

What is the antithesis of homology?

Curiously, given that homology is such a central concept, second only to evolution, non-homology is not the antithesis of homology. Traditionally, homology is contrasted with analogy, as Alec Panchen will discuss in the opening presentation. Both Panchen and Wake will raise the issue of whether homoplasy is a more appropriate antithesis to homology. Homoplasy has variously been viewed as non-homology, a mistake in homology assessment, or the occurrence of similar structures in distantly related organisms. None of these definitions coincides with analogy. I expect that our discussions will bear much more strongly on homoplasy than on analogy than has been the case in past discussions of homology.

What are the levels of homology?

A major reason for Adam Wilkins proposing homology as a topic for a Novartis Foundation Symposium was to discuss homology as a hierarchical concept. The recent finding in genetics in which equivalent (homologous) master genes 'switch on' the development of structures long regarded as non-homologous — the eyes of flies and frogs, for example — has focused attention squarely on the issue of the level(s) of biological organization at which homology should be addressed. We will discuss homology on at least three levels — structural, genetic and behavioural.

Structural homology

The basis for structural homology will be addressed directly by several speakers (Wagner, Striedter, Müller) and indirectly by many others. Is structural homology:

1. related to some aspect of embryonic development that may be embodied in rules of development, developmental programmes or developmental constraints; or
2. related to processes operating at one or more levels of biological hierarchy and involving constraints, epigenetic interactions or networks?
INTRODUCTION

How does structural homology deal with evolutionary changes in development that may obscure homology without rendering the resulting structures non-homologous?

*Genetic homology*

The basis for genetic homology will be addressed in several contexts and I am sure will generate much discussion. Is genetic homology based on:

1. the same genes;
2. the same genes in different animals (discussed by Holland in the context of paralogy and orthology);
3. the same genes that share the same function;
4. the same genes with different functions (discussed by Wray); and/or
5. similar genetic networks (discussed by Abouheif)?

Does the identification of master genes (control, developmental or regulatory genes) require a reassessment of homology?

*Behavioural homology*

Homology has predominantly been used for structures; hence structural homology. It would be more inclusive to speak of phenotypic homology to reflect the fact that other aspects of the phenotype, such as homologous behaviours, can be recognized and analysed. The inclusion of behavioural homology in the programme should serve to remind us that homology is much broader than structural and genetic homology. Homology is the hierarchical basis of comparative biology and that means biology at all levels. The relationship of shared or divergent structural bases to behavioural homology is similar to, and raises the same issues as, the relationship between shared or divergent embryonic development and structural homology. Just as homologous structures can arise from divergent developmental programmes, so homologous behaviours need not share a common structural basis.

**What is the research agenda?**

It is clear from the topics to be covered in this symposium that attention is shifting from arguments over the definition of homology to research agenda that shed light on the essential nature of homology. Numerous speakers will address research agenda in an exciting variety of contexts. These include fossils (Carroll), limb and vertebral column evolution (Galis, Hinchliffe), the nervous system (Striedter), constraints (Wagner), the origin of novelties (Müller), the evolution of early
development (Raff) and behaviour (Greene). I predict that the identification of precisely how homology translates into research programmes in comparative biology — how homology is used and tested — and how research agenda shed light on homology as a central concept in biology, will be an important contribution of this symposium and this volume.

References

Homology — history of a concept

Alec L. Panchen

Department of Marine Sciences, University of Newcastle upon Tyne, NE1 7RU, UK

Abstract. The concept of homology is traceable to Aristotle, but Belon’s comparison in 1555 of a human skeleton with that of a bird expressed it overtly. Before the late 18th century, the dominant view of the pattern of organisms was the scala naturae — even Linnaeus with his divergent hierarchical classification did not necessarily see the resulting taxonomic pattern as a natural phenomenon. The divergent hierarchy, rather than the acceptance of phylogeny, was the necessary spur to discussion of homology and the concept of analogy. Lamarck, despite his proposal of evolution, attributed homology to his escalator naturae and analogy to convergent acquired characters. Significantly, it was the concept of serial homology that emerged at the end of the 18th century, although comparison between organisms became popular soon after, and was boosted by the famous Cuvier/Geoffroy Saint-Hilaire debate of the 1830s. The concepts of homology and analogy were well understood by the pre- (or anti-) evolutionary comparative anatomists before the general acceptance of phylogeny, and they were defined by Owen in 1843. The acceptance of evolution led to the idea that homology should be defined by common ancestry, and to the confusion between definition and explanation. The term ‘homoplasy’, introduced by Lankester in 1870, also arose from a phylogenetic explanation of homology.

1999 Homology, Wiley, Chichester (Novartis Foundation Symposium 222) p 5–23

In the novel Moby-Dick Herman Melville (1851) frequently interrupts the narrative of the hunt for the great white whale with assorted facts, anecdotes and soliloquies. Chapter XXXII is devoted to ‘cetology’, including the classification of whales. Melville is in no doubt as to their taxonomic position: despite their mammalian features, they are fish: ‘a whale is a spouting fish with a horizontal tail’ (his italics). He then goes on to give a classification of known whales by size (as ‘Folios’, ‘Octavos’ and ‘Duodecimos’!) as all other known taxonomic characters seem to him inconsistent.

Exactly 300 years before, Pierre Belon (1551) also concluded after detailed study that whales were fish, having seen their heart, lungs, mammary glands etc., and compared them with those of humans. Yet Aristotle had described whales as mammals (Vivipara) in the fourth century B.C. (Aristotle 1945).

One’s first reaction to Belon’s placement of cetaceans among the fish (and also bats among the birds and the hippopotamus as a cetacean!) is either that he was
ignorant of the comparative anatomy involved or perverse to the point of stupidity (Cole 1944). Yet it was also Belon (1555) who produced the famous comparative diagrams of the skeleton of a human and that of a bird, with most of the individual bones correctly homologized (Fig. 1). He claims to have dissected over 200 birds, but he also enumerated all the mammalian features of bats, and did comparative dissections of three species of cetacean. Presumably what was missing in Belon (and in Melville) was not knowledge or intelligence, but a concept of natural classification based on anything other than function and habitat — truly analogy without homology. And yet his human–bird comparison demonstrates the concept of unity of plan which today we always consider essential to the idea of homology.

Most modern biologists associate homology with the fact of evolution. Homologous structures in two different organisms are so recognized because it is proposed that the nearest common ancestor of both had a corresponding structure: indeed definitions of homology frequently involve community of descent. Historically this lacks any backing. The concept of homology was accepted by most comparative anatomists in the first half of the 19th century, based on the idea that there is a natural order of organisms whether explained by evolution or not. Classifications are to be discovered rather than invented.

I suggest that there are in fact four logical (if not strictly chronological) stages in the development of the anatomical concept of homology — other concepts, developmental, molecular and genetic are dealt with later in this book. In the first stage there can be considerable anatomical knowledge, but classification carries with it no necessary idea of a natural order. As with Aristotle and Belon homology and analogy may be recognized, but either, or a mixture of both, may be used as a basis for taxonomy. A fish is what you find on a fishmonger’s slab!

The second stage is the development of criteria for the recognition of homology. Here Belon (1555) may also be invoked, but it is not until the end of the 18th century that the criteria were clearly codified. The French transcendental morphologist Etienne Geoffroy Saint-Hilaire (1772–1844) developed such criteria principally in the first volume of his Philosophie anatomique (Geoffroy Saint-Hilaire 1818). He noted the criterion of similarity, but his main contribution was the principe des connexions. Homologous structures were to be recognized by shared topology, their relationship to surrounding anatomical features.

The third stage is the recognition (hypothesis?) that there is a true natural order, whatever form that may take. Correctly identified homologies are evidence for a particular order, but the a priori assumption of a natural order ‘out there’ implies the possibility of mistaken homologies detected by their non-congruence with the taxonomic pattern produced in the light of other homologies (Patterson 1982). I consider theories as to the nature of this pattern to be of great historical importance.
FIG. 1. Skeletons of a human and a bird to show homologous bones. After Belon (1551) from the original.
and will devote the next section to it. But meanwhile the fourth stage is concerned with ‘mistakes’.

After the publication of *On the origin of species...* (Darwin 1859), systematic biologists were anxious to forge the link between the recognition of homology and the phylogenetic pattern of an irregular tree-like divergent hierarchy emphasized by both Wallace (1855) and Darwin. One of the most enthusiastic advocates of this link was Ray Lankester, and in 1870 he introduced the concept of ‘homoplasy’ for apparent homology not explicable by common ancestry. I will discuss this further below.

**The natural order**

The received opinion among most biologists is that Linnaeus inaugurated modern biological classification. This view is enhanced by the fact that the year of publication of the 10th edition of his *Systema naturae* (Linnaeus 1758) is taken as the ‘starting point’ by the International Code of Zoological Nomenclature (Ride et al 1985). Only taxonomic names proposed in or after that year are deemed valid. Similarly the ‘start date’ for the nomenclature of extant Spermophyta (flowering plants and gymnosperms), plus Pteridophyta, is based on Linnaeus’ *Species plantarum* (1753). Furthermore, Linnaeus codified a series of categories, each of a different rank, so that any classification using his methods would result in a divergent hierarchy, with the animal kingdom divided into a number of classes, each class into several orders, orders into genera, and each genus into a number of species. Other intermediate categories were of course added later. Given the resulting hierarchy, homology could be defined as a sharing of features that served to diagnose a taxon at any rank, by their presence in all the species that composed that taxon (taxic homology). But if the concept of homology was (and is) to be regarded as anything other than a convenient instrumental one, the hierarchy must have some reality.

There is evidence that Linnaeus, and probably most of his naturalist contemporaries, did not regard even an imagined perfect classification as representing a natural phenomenon. Through the early part of his career, Linnaeus had been an exponent of the *scala naturae*, the natural relationships of organisms was as a ladder of perfection or elaboration from inanimate objects at the bottom to humankind at the top (Ritterbush 1964). He tried in vain to find a natural linear way to order plants, and compromised by producing an avowedly artificial hierarchical classification, his famous ‘sexual system’ using flower anatomy. Eventually he abandoned the search. Even in 1751 he had suggested that ‘All plants show affinities on all sides, like the territories in a geographical map.’ He had also suggested the analogy of a map in a letter of Johann Matthias Gesner (1691–1761: not to be confused with the great naturalist Konrad von
Gesner, 1516–1565). The map analogy was to be presented pictorially by a German pupil of Linnaeus, Paul Giseke, who edited a posthumous book by his master (Linnaeus 1792) and added a pictorial representation of his own (Fig. 2). Oldroyd (1980) has suggested a comparison between Giseke's figure and a phylogeny sliced through at a time plane, but it seems much more probable to me that a better analogy is the clustering in hyperspace of a modern phenetic taxonomist. The latter implies no hypothesis of homology.

But how could Linnaeus thirst after a *scala naturae* but propose a method of classification that yielded a divergent hierarchy? The answer was that, to him, elucidating the *scala* was a different operation from classification. His method of classification was based on the method of logical division attributed to Plato and Aristotle (Cain 1958, Panchen 1992, chapter 6). A taxon at any level (e.g. species) was characterized by features of the taxon at one rank above (genus) plus features—each a *diafora* (Greek) or *differentia* (Latin)—diagnostic of it: logical division *per genus et differentiam*. To Plato and Aristotle a *genos* (genus) could be a class at any level, from all created things to a small group, animate or not, and an *eidos* (species) one of the subordinate classes into which the *genos* was divided.

Linnaeus gave genus and species an appointed rank, but as with the Greeks, his method was to systematize knowledge rather than to reveal the natural order. If there was any sense in which Linnaeus regarded his taxonomic hierarchy as natural, it is that corresponding to the philosophy of essentialism (Panchen 1992 [p109–117, 337–341], 1994). Any taxon has a reality because its essence is represented by an exclusive list of characters. I have argued that this is to be distinguished from the Idealism of Plato, in which any valid taxon owes its reality to the existence of a Platonic *form* or *idea* corresponding to it. In its final state, in the *Republic* and the *Timaeus*, Plato was to claim not only that his ‘ideas’ were real, but that they were the only real entities (Oldroyd 1986, chapter 1). But before we turn to idealistic morphology, there is more that needs to be said about the *scala naturae*.

**The curse of the *scala naturae***

In his famous series of William James lectures on the *scala naturae*, published as *The great chain of being*, Arthur O. Lovejoy (1936, chapter V) quotes from a letter written by the philosopher Gottfried Wilhelm Leibniz (1646–1716) and published in 1753. In part this reads:

> ... all the orders of natural beings form but a single chain, in which the various classes, like so many rings, are so closely linked to one another that it is impossible for the senses or the imagination to determine precisely the point at which one ends and the next begins—all the species which, so to say, lie
FIG. 2. A two-dimensional clustering of plant families by P. D. Giebe in Linnaeus (1792).
near to or upon the borderlands being equivocal, and endowed with characters which might equally well be assigned to either of the neighbouring species.

Earlier in the letter Leibniz gives the order in the *scala* (from top to bottom): ‘Thus men are linked with the animals, these with plants and these with fossils, which in turn merge with those bodies which our senses and our imagination represent to us as absolutely inanimate.’ Later, he anticipates the discovery ‘of zoophytes, or plant-animals... creatures which in some of their properties, such as nutrition or reproduction, might pass equally well for animals or for plants...’

Leibniz died early in the 18th century, but as Lovejoy (1936, chapter VI) says ‘Next to the word “Nature”, “the great chain of being” was the sacred phrase of the 18th century, playing a part somewhat analogous to that of the blessed word “evolution” in the late 19th.’ The naturalist most famous for his advocacy of the *scala* (as an *Échelle des Étres*) was the Swiss Charles Bonnet, particularly in his *Contemplation de la Nature* (1764). Ritterbush (1964) has turned Bonnet’s written account into a diagram (Fig. 3).

There are two components in the concept of the *scala* attributed (of course!) to Plato and Aristotle, respectively. Firstly, the idea of ‘plenitude’ or, in other words, that creation is a ‘plenum’: the created world is ‘the best of all possible worlds’ (to quote Leibniz) and in such a creation there are no gaps between entities — any apparent gaps in the *scala* are simply due to our ignorance. The second component is the *scala* itself. Given the gaps, however, there is a justification for producing an hierarchical classification, using the lacunae to delimit the boundaries between groups; but unless such an artificial classification is declared natural by the tenets of essentialism, there can be no natural concept of homology except as a gradual change in any given structure as one progresses up the *scala*.

The *scala* was regarded as a static phenomenon by 18th century philosophers (including scientists), but the introduction of a worked-out theory of evolution did not dispose of it. Lamarck first introduced his evolutionary theory in lectures in 1800, but his original ‘phylogeny’ consisted of an ‘*escalator naturae*’, to coin a phrase. Throughout the history of the habitable earth ‘monas’ was spontaneously generated to evolve through the generations into humans. He admitted the necessity of separate *scalae* for animals and plants and in the immediately following years introduced his theory of ‘the inheritance of acquired characters’ to explain both deviation from the preordained *scala* and the phenomenon of adaptation. What he did not do, even in the principal statement of his theory, the *Philosophie zoologique* (1809), was to abandon the distinction between elucidating the *scala* (‘*distribution general*’, a phrase also used by Bonnet), and ‘*classification*’, i.e. using gaps in our knowledge to produce an hierarchical classification. Chapter I of the *Philosophie zoologique* is entitled ‘On artificial devices in dealing with the productions of nature — how schematic classifications, classes, orders, families,
**MAN**  
monkey  
tortoise  
**QUADRUPEDS**  
crocodile  
sea lion  
sea calf  
hippopotamus  
whales  
**BIRDS**  
amphibious birds  
aquatic birds  
flying fish  
**FISH**  

eels and creeping fish  
water serpents  
**REPTILES**  

crab  
crayfish  
lizard  

e Shellfish  
frog  
lime-secreting worms  
**INSECTS**  
worms  
polyp  
sensitive plants  
trees  
shrubs  
herbs  
lichens  
molds  
mushrooms and agarics  
truffle  
stones composed of layers, fibres, and filaments  
unorganized stones  
**CRYSTALLINE SALTS**  
vitriols  
**SEMIMETALS** [nonmalleable metals]  
**MALLEABLE METALS**  
sulphur and bitumens  
compound earths [pure earths united with oils, salts, sulphurs, etc.]

**PURE EARTH**

**WATER**

**AIR**

**ETHEREAL MATTER**

FIG. 3. *Idée d'une échelle des êtres naturelles*. Diagram from Ritterbush (1964), by permission of the publishers. After the written list of Bonnet (1764).
genera, are only artificial devices.' Lamarck did, however, talk of 'affinities', but rather representing the distance between two species on the *scala* (comparable to the 'taxonomic distance' of modern phenetic classification), than representing homology as it did to later 19th century naturalists such as MacLeay (1821) and Strickland (1846) (see Panchen 1994).

The *scala naturae* is with us yet! Much talk of 'lower' and 'higher' animals is a symptom of it, as in the palaeontological conceit of an 'age of fish', followed by an 'age of amphibians', 'age of reptiles' and 'age of mammals'. Darwin used to remind himself not to talk of 'higher' and 'lower' animals, and we find Alfred Russel Wallace (1870, chapter IV) debating whether the Papilionidae (swallowtails) are the highest among butterfly families.

**Hierarchy and homology**

The most influential early break with the concept of the *scala naturae* was that of Georges Cuvier (1769–1832). In 1800, in *Lesons d'anatomie comparée*, Cuvier simply divided all animals into nine classes, four vertebrate and five invertebrate, but by 17 years later, Cuvier (1817), in *Le règne animal* . . . , he had settled on his definitive classification of the animal kingdom into four *embranchements*: vertebrates, mollusces, articulates (arthropods and annelids) and radiates (echinoderms, polyps and various other invertebrates). The basis of this classification is Cuvier's principle of subordination of characters, a direct application of his principle of functional correlation (Russell 1916). The dominant characters are those which both have the greatest constancy, but are also of the greatest importance in determining the functioning of the individual animal. The nature of the nervous system defines the four *embranchements*: a single dorsal trunk with an anterior brain in vertebrates, as scattered masses in mollusces, paired ventral nerve cords with segmental ganglia in articulates, no apparent system (to Cuvier) in radiates.

Given the nature of the nervous system (and the circulatory system that correlates well with it) other vital characters—digestion, locomotor system, etc.—are to some extent predetermined to produce a viable organism. According to Cuvier it is idle to seek any what we would call homologies between different *embranchements*. In this view he was disagreeing with his close colleague and erstwhile friend Geoffroy Saint-Hilaire, a disagreement that led eventually to an acrimonious public debate (Appel 1987). Two other apparently contradictory statements arise from Cuvier's taxonomy: (1) that he made no distinction between homology and analogy; and (2) that he enunciated the principle of taxic homology.

To Cuvier, every feature of the anatomy of an animal was to be interpreted in terms of the viable functioning of the whole; every anatomical difference between two organisms was to be given an adaptive explanation. Unity of plan meant
identity of function. But despite this completely teleological approach Rieppel (1988) has argued that to Cuvier homologous characters were those that define taxa. In the terms of modern cladists, taxic homology is synapomorphy (Patterson 1982).

Despite being a colleague in Paris of both Lamarck and Cuvier, Geoffroy Saint-Hilaire worked more in the tradition of the German Naturphilosophen, such as Schelling, Meckel, Oken and Carus. The concept of the archetype, later developed for the vertebrate skeleton (Fig. 4) in a spirit of pure Platonic idealism by Richard Owen (1848, 1849), arose in this group (Rupke 1993). But their inspiration appears to have come from Goethe. Interestingly, Goethe’s principal preoccupation was not with comparison of corresponding organs or structures in two different species (‘special homology’: Owen), or comparison between a particular animal and the archetype (‘general homology’: Owen), but with ‘serial homology’, despite Goethe’s concept of the archetypal plant (Urplantz) and animal (Urtier). It was Goethe who suggested that all the appendages of a plant (leaves, sepals, petals, stamens, cotyledons) were variants on a common theme. Similarly, not only were the vertebrae of a chordate serial homologues, but the vertebrate skull was formed of a series of modified vertebrae.

Serial homology was quite compatible with the scala naturae as was transformational homology, whether attributed to evolution or not, but taxic homology is predicated on a divergent pattern. Karl Ernst von Baer, despite his background in Naturphilosophie, adopted, apparently independently, a pattern of classification similar to Cuvier’s, and claimed that even within one embranchement, the vertebrates, there was a divergent pattern in ontogeny (von Baer 1828). Early stages in different classes looked similar, later ones less so. There was no scala of development. Incidentally, von Baer’s demonstration implied another possible explanation for the phenomenon of homology, apart from teleology, essentialism and Platonic idealism. Organs in different animals were homologous because of gradual divergence in development from a common plan (although to von Baer, only within one embranchement).

But post-Origin, the usual explanation of homology was community of descent as a result of evolution. Ray Lankester (1870) decided that the change needed an overhaul of nomenclature. Owen’s (1843) pre-evolutionary definitions, first published in the glossary to his published invertebrate lectures, were:

(1) Analogue: a part or organ in one animal which has the same function as another part or organ in a different animal.
(2) Homologue: the same organ in different animals under every variety of form and function.
FIG. 4. Richard Owen’s archetype of the vertebrate skeleton and its modification in the various classes. After Owen (1848) from the original.
Owen (1848, p.7) was emphatic that the two were not mutually exclusive, indeed to Cuvier they would have been indistinguishable. Lankester’s objection was that the term ‘homologous’ smacked too much of Platonism. ‘Special homology’ (sensu Owen) was to be replaced by ‘homogeny’:

Structures which are genetically related, in so far as they have a single representative in a common ancestor, may be called homogenous. We may trace an homogeny between them, and speak of one as the homogen of the other (his italics).

All other resemblances—‘serial homology’ within a single organism, or analogy between organisms attributed to parallel or convergent evolution, or simple unexplained coincidence—Lankester labelled homoplasy: they were homoplastic. ‘Homogeny’ did not catch on, but ‘homoplasy’ has earned its revival to describe characters incongruent with the pattern of homologies, whether this pattern is interpreted as phylogeny or not.

Since Lankester’s time, the concept of homology has been firmly linked to that of phylogeny, except to some ‘pattern cladists’. But until recently there has been another (partly hidden) assumption. A hypothesis of homology was assumed to be based on a comparison between structures in (usually) adult organisms. Indeed de Beer (1971) produced a little ‘Oxford reader’ tacitly making that assumption and thus pointing out the paradox that obviously homologous structures may have different genotypes, different developmental pathways, different segmental positions and may occur in two different taxa without being ubiquitous in either (Panchen 1994). Now with our greater understanding of molecular biology, we can homologize genes, yet discover that homologous genes need not lead to homologous adult structure (Abouheif et al 1997).

Acknowledgements

I thank Wallace Arthur in particular for his critical reading of the manuscript, and for facilities at the Ecology Centre, University of Sunderland. The Natural History Society of Northumbria allowed photography of their first edition of Belon (1555), and the Robinson Library, University of Newcastle upon Tyne, of Owen’s (1848) archetype. The photographs were taken by the Audiovisual Centre, Newcastle University. Figure 2 was photographed with the kind permission of the Linnean Society. The manuscript was typed at Sunderland by Carolyn Stout.

References

Belon P 1551 L'histoire naturelle de estranges poissons marins. Regnaud Chaudiere, Paris
Belon P 1555 L'histoire de la nature des oyseaux. Guillaume Cavellet, Paris
Bonnet C 1764 Contemplation de la Nature, 2 vols, 1st edn. Marc-Michel Rey, Amsterdam
Cuvier G 1800 Leçons d'anatomie compare de G Cuvier; recueilliies et publiées sous ses yeux par C Duménil, vol I. Bandouin, Paris
Cuvier G 1817 Le règne animal distribué d'après son organisation. Deterville, Paris
Geoffroy Saint-Hilaire E 1818 Philosophie anatomique (vol 1) des organes respiratoires sous le rapport de la determination et de l'identité de leurs pièces osseuses. JB Baillière, Paris
Lankester ER 1870 On the use of the term homology in modern zoology, and the distinction between homogenetic and homoplastic agreements. Ann Mag Nat Hist (series 4) 6:34–43
Linnaeus C 1751 Philosophia botanica. Kiesewetter, Stockholm
Linnaeus C 1753 Species plantarum, exhibentes plantas rites cognitas. Laurentii Salvii, Stockholm
Linnaeus C 1758 Systema naturae per regna tria Naturae, tomus 1, 10th edn. Laurentii Salvii, Stockholm (facsimile Brit Mus NH 1956)
Linnaeus C 1792 Praelectiones in ordines naturales plantarum (edited posthumously by Giseke PD). BG Hoffmann, Hamburg
Lovejoy AO 1936 The great chain of being. Harvard University Press, Cambridge, MA
MacLeay WS 1821 Horae entomologicae: or essays on the annulose animals, vol. 1 part II. S Bagster, London
Melville H 1851 Moby-Dick, or the whale. Harper & Brothers, New York
Oldroyd DR 1986 The arch of knowledge: an introductory study of the history of the philosophy and methodology of science. Methuen, New York