

Hierarchy Theory as the Formal Basis of Evolutionary Theory

Science attempts to provide a truly universal language through which to describe the world. The problem is that, as an unfortunate result of ever increasing specialisation, science can become fragmented into different factions with different approaches and different standards for evaluating methods. The fragmentation of scientific language that can result from specialisation is detrimental to the course of science. Each of the factions is impoverished, in that the true depth of implications held by particular facts are not explored. Creative hypotheses are not developed because that would lead the investigator outside his chosen faction. I suggest that the unity of science does not rest in key facts specifically, but in the adoption of a single formal language that is common across different fields. There is no such formal language for biology. Among other things, this hinders the teaching of biology. Too many people are put off by the number of seemingly unconnected facts they have to learn and the general lack of first principles. Fragmentation in science manifests itself as a fragmentation in the language science uses. That language blocks creativity by denying expression of certain research questions, and indeed denying questions of broader philosophical significance. Science, as a search for knowledge rather than just the provider of technology, then becomes divorced from society in general, seeming of little relevance to the rest of reality.

Thompson (1989) views scientific theories simply as interpreted formal systems. A theory has a purely formal basis and becomes a scientific theory proper when a particular interpretation is placed upon it. Thompson (1989) gives a very useful example to illustrate this view of theories. The theory of physical space was challenged indirectly through a challenge on its formal basis. There was no direct challenge, at the empirical level, on the predictions of the theory itself, though these predictions were extended. One of Euclid's postulates, the parallel postulate, was found not to be derivable from the other axioms. Two new systems of curved geometry resulted: hyperbolic geometry and spherical, or Riemannian, geometry. Einstein's theory of general relativity has

Riemannian, rather than Euclidean, geometry as its formal basis, adopting a picture of space as curved.

To discover the formal basis of an existing scientific theory, to provide a formalisation or systematisation, is to elucidate the connections between different parts of the theory. The philosophy of science tells us that *formal simplicity* is one criterion of a good, sound theory (see Goodman, 1959). This contrasts with the empirical simplicity criterion of Popper (1959). From a formal standpoint, a sound theory is well connected; the theory has firm, clear relationships among its parts. If we believe that theories should be tested through hypothetico-deductive logic, as Popper (1959) requires, then how can we test the predictions if we are not sure quite what implications an observation has for the theory as a whole? The practical benefit to be gained from providing a formalisation of a scientific theory is to clarify the relationships between parts of the theory. Particular observations will have unforeseen relevance to areas of the theory outside their normal province. For example, if we say that the properties of a constrained developmental system enable punctuational changes, then we might predict that the cases in which gradual evolution has been observed involve changes which, developmentally, are not significantly constrained. An understanding of the formal basis of a theory will also clarify the particular aims of different approaches to the theory and enable a choice between models.

It is the aim of this paper to propose a formalisation of evolutionary theory which permits a solution of certain controversies in systematics and evolution. The particular controversy I have in mind is whether the nature of the empirical results of cladistics is at odds with what would be expected from a Darwinian theory of evolution, as Nelson and Platnick (1984) argue, or can be reconciled with such a theory. The formal system I choose to facilitate this analysis is the theory of hierarchically organised systems. I do not wish to discuss the many ways in which the concept of hierarchy has been used in systematics, but rather to work from first principles. A hierarchy is defined as a system of communication, where entities are defined by the extent to which they constrain or filter

information they receive (Allen and Starr, 1982: 11, 37). Organisms are hierarchies of constraint; elements of the phenotype differ in the extent to which they constrain genetic information.

Information flows two ways through a hierarchy, out into the environment and back again (Allen and Starr, 1982: 8-9). On the outward journey of the gene, the constraints of the developmental system produce the characteristic form of the organism. On the homeward journey of the gene, the phenotype acts as a hierarchy of selective constraints, favouring or reducing the chance of the different items of genetic information being passed on to the next generation.

A striking prediction of a hierarchical formalisation of evolutionary theory is that there should exist a biological principle of complementarity equivalent to that found in quantum physics (Pattee, 1978).

My original interest in hierarchy theory came with the thought that this principle might be equivalent to the notion of complementarity suggested by Rieppel (firstly in 1984) for systematics. I now deepen the treatment of hierarchy theory which followed from that thought (Wood, 1994), extending and modifying my conclusions.

To justify that hierarchy theory is an appropriate formal system, it is important to show that the concept of constraint is applicable to the living organism. The first part shows the relationship between concepts of homology and developmental constraint from the viewpoint of systematics. The second part provides a description of cladistic analysis that lays the groundwork for the justification of complementarity in the final part. The third part takes the theme of morphological stability as a route into an evolutionary discussion of developmental constraint and its counterpart, adaptational constraint. The fourth and final part shows that there are two complementary aspects of evolutionary history, and a different approach should be used to reconstruct each one. The two approaches differ as to the source of data, method of generating data, model of evolution assumed and form of results produced. It is in this context that cladistics finds its place alongside Darwinian approaches to studying evolutionary history, and a fragmentation in the language of science is closer to being healed.

Nelson's concept of homology

Nelson (1989) has suggested that instead of taxa being seen as groups of units, such as species or organisms, they should be seen as relationships. A taxon is a relationship inherited by organisms, and a homology, then, is a relationship inherited by parts of organisms. 'Conceived as relationships, taxa and homologies do not literally descend from one another. Taxa come into being with organisms that literally descend' (Nelson, 1989: 281). Through descent with modification, Nelson concludes, organisms and parts of organisms accumulate inherited phylogenetic relationships (cf. Nelson, 1989: 281-282). Descent with modification results in a phylogenetic hierarchy of organisms with inherited relationships.

Nelson's (1989) concept of homology, combined with a hierarchical perspective, is a powerful tool for evolutionary theory. It disposes of the criticisms that have been advanced against the historical concept of homology. For example, Wagner (1989b) lists four criticisms of the historical concept (the first and fourth are in fact the same):

(1,4) Lack of continuity

'Only replicators like genes pass on their own structure to their descendants directly. Morphological structures are not replicators ... The notion of continuity of descent is not problematic for genes but is less clear for organs' (Wagner, 1989b: 55-56).

'Conceived as relationships, taxa and homologies do not literally descend from one another' (Nelson, 1989: 281). Morphological homologies are inherited by parts of the organism's phenotype, and it is the organisms themselves that literally descend. Continuity of descent is possible only for elements of the genotype, but not for elements of the phenotype.

(2) Lack of individuality

'In the simplest case phylogenetic homology is a one-to-one mapping from the characters of one species onto characters of another species. A one-to-one mapping implies that in each species all characters can be recognised individually' (Wagner, 1989b: 57).

The organism, from a hierarchical perspective, is neither an undecomposable whole, nor a fully decomposable 'composite of atoms'. Organisms are *near-decomposable* (see Simon, 1962, 1973; Koestler, 1967: 64-65; Allen and Starr, 1982: 70-74). How does one make sense of elements that, in comparisons across a variety of organisms, cannot be recognised individually? The simple answer is not to focus on one level in the hierarchy as a naive perspective would dictate, but to proceed with the examination at the next level, that of the whole series of elements.

(3) Variability of development

'Phylogenetically homologous characters need not share common pathways of ontogenetic development' (Wagner, 1989b: 58). Between species, the origin of cellular material, the precise sequence of events or specific inducers, have all been found to vary.

If homology is seen as a relationship inherited by parts of organisms, then the variable development of those parts is no longer problematic.

Having discussed problems with the historical concept of homology, Wagner (1989b) proposes an alternative, a biological concept of homology: 'Structures from two individuals or from the same individual are homologous if they share a set of developmental constraints, caused by locally acting self-regulatory mechanisms of organ differentiation. These structures are thus developmentally individualised parts of the phenotype' (Wagner, 1989b: 62). Below I shall elaborate how the elements of Wagner's biological definition are embraced by Nelson's (1989) concept of homology.

We have said that homologies are relationships inherited by parts of organisms. However, in hierarchy theory the contrast between wholes complete in themselves and fragmentary, dependent parts is regarded as an illusion. Whether an entity appears as a part or a whole simply depends on the point of view of the observer: from a more inclusive level, the entity appears as a part, from a less inclusive level, as a whole. Constituent 'elements' of an organism are thus simultaneously autonomous wholes and dependent parts, they are *holons* in the sense of Koestler (1967): 'Every holon has the dual tendency to preserve and assert its individuality as a quasi-autonomous whole; and to function as an integrated part of an (existing or evolving) larger whole. This polarity between the

self-assertive and integrative tendencies is inherent in the concept of hierarchic order; and a universal characteristic of life. The self-assertive tendencies are the dynamic expression of holon wholeness, the integrative tendencies of its partness' (Koestler, 1967: 343). The distinctiveness of an element, the fact that we can recognise its identity across numerous organisms, derives from its wholeness, the tendency of a holon to assert itself. If an element cannot be recognised individually, this lack of distinctiveness emphasises the partness of the holon, its tendency to integrate itself among other elements as part of a larger whole, such as a series. The following passage by Bateson may be interpreted in this light: 'The phenomenon of serial resemblance is in fact an expression of the capacity of repeated parts to vary similarly and simultaneously. In proportion as in their variations such parts retain this capacity the relationship is preserved, and in proportion as it is lost, and the parts begin to vary independently, exhibiting differentiation, the relationship is set aside' (Bateson, 1894: 569). When elements of a series vary similarly and simultaneously they cannot be recognised as distinct. They remain parts integrated into the larger whole, the series. When elements differentiate, they become individually recognisable and thus assert themselves as wholes distinct in themselves. To reiterate: whether an element appears as a part or a whole depends on context. Armed with this insight it is possible to extend Nelson's (1989) concept of historical homology to include serial, or more generally, iterative homology. Nelson could equally well be referring to a series of elements. Hence, the iterative homology of a set of parts is imparted to them through the inheritance of the embracing singular homology. The 'scaleness' of the scales of a fish, in virtue of which the individual scales are iteratively homologous, is inherited in the same way as the singular homology 'possessing scales'. It does not matter that the scales of a fish are not individually recognisable. The logical necessity of this position was realised many years ago by Hubbs: 'If we admit the homology between any scale x of an individual trout and any scale, say y of a salmon, and between this scale y in the salmon and scale z in the trout, then how can we logically deny that homology exists between scales x and z on the body of the same trout!' (Hubbs, 1944: 294).

Patterson (1982) describes a contrast between transformational and taxic homology. According to Patterson, taxic homology is the relation that specifies hypotheses of grouping. Nelson's (1989) concept of homologies as relationships is also taxic. Transformational homology is rooted in the concept of ideal or material transformation from a common precursor, and thus subsumes both idealistic and evolutionary concepts of homology. We compare structures with the supposed precursor in the common archetype or common ancestor to judge whether they are homologous. Patterson regards serial homology as a form of transformational homology (Patterson, 1982: 48). He is forced therefore to deny that taxic homologies are repetitive: '... homologies are anatomical singulars (Riedl, 1978, p.52), structures of which there is only one, or a bilateral pair, per organism' (Patterson, 1987: 9). But there is a fudge here, which is nonetheless admirably declared by Patterson: how can a repetition of structures across the main axis of the animal be logically distinguished from any other form of repetition? Ghiselin (1976) legitimately calls the homology between members of a bilateral pair 'antimeric homology' (Ghiselin, 1976: 139). If this concept is construed transformationally, then we must envisage that structures on the two sides of the animal trace back to single structures in an ancestral one-sided animal! No, iterative homology and historical homology are, as Van Valen (1982) perceived, aspects of the same phenomenon. But that phenomenon is taxic not transformational homology. The concept of transformational homology applies only to the genotype, where material continuity of descent is possible.

If organisms are near-decomposable, they do not consist wholly of individually recognisable parts. We have parts in a context, for example, one element among several of a series. This element, for example the axis vertebra of tetrapods, may later assert itself, weakening its integration into the rest of the series, and become individualised. We can extend the notion of 'parts in a context' in more general terms to the issue of characters versus character states. The character is not simply an abstraction but provides the biological context for its character states. We might take the palatine bone as a character and thus differences in the shape and orientation of the palatine boss and prong reflect evolutionary changes within this context. Character concepts of this 'either/or' sort therefore

comprise an aspect of similarity (homogeneity) and aspects of difference (heterogeneity). Teleost fishes are all to some extent homogeneous, since they all have a recognisable palatine (within the context of the palatopterygoquadrate arch), but are also heterogeneous in the extent to which parts of the palatine are developed. 'Presence/absence' characters are simpler. They represent the expression or suppression of the self-assertive tendency of the holon, the acquisition or loss of its individuality. To sum up, character states are designed to document changes in the individualisation of parts of organisms, changes in the balance between similarity and difference, between the integrative and self-assertive tendencies of those parts.

The insight of Nelson (1989) into taxic homology also provides a useful characterisation of Wagner's concept of individualisation: through descent with modification, parts of organisms accumulate inherited taxic homologies, and thus become increasingly individualised. If we remember that 'parts of organisms' can refer to 'series of parts' we can see how the individualisation and differentiation of a particular part of a series involves the inheritance of at least one taxic homology unique to it alone. Wagner repeatedly cites an excellent example of individualisation of members of a series, namely the thorax of insects (Wagner, 1986: 151; 1989a: 1162; 1989b: 63). He says that the thorax most probably arose as a differentiation of segments 7, 8 and 9 in the annelid-like ancestors of insects. However, the thorax as an entity in itself is not homologous to the corresponding segments in annelids or centipedes for example. 'The thorax is the unit differentiated from the rest of the body in terms of appendages and internal anatomy, a condition not found in centipedes' (Wagner, 1986: 151; 1989a: 1162; 1989b: 63). The thorax represents, in the terms of Rieppel (1994), a unique condition of form, or in other words, a new autonomous whole irreducible to its parts.

The thorax has become individualised from the other bodily segments; at the same time the thorax serves to "individuate" the taxon Insecta (in the sense of von Baer, 1828; see Rieppel, 1994: 90). But we must be clear with our language here. Is it the acquisition of the new assertive holon that individuates the new taxon? Not exactly, since a taxic homology is a relation among holons: organismic holons are homologues related by particular homologies (Nelson, 1994: 120). Why is it

that we recognise the thorax, in fact? The thorax, as a self-assertive whole, creates its own environment of constraint for its parts (Allen and Starr, 1982: 51), so that these parts do not vary in such a way as to undermine the individuality of the whole. It is possible for such a trend to be reversed, for the balance to swing from heterogeneity back to homogeneity. For example, the prootic and epiotic of reptiles lost their separate individualities and fused to form the mammalian petrosal, which then in its turn has followed its own path of differentiation.

If we say that the thorax is a part which is homologous throughout the insects, then we imply a continuity of descent between the thorax of the ancestral insect and that of the descendant insects. But as Wagner (1989b) points out, continuity of descent is possible only for aspects of the genotype not the phenotype. What we see conserved throughout the insects is the developmental constraint that preserves the individuality of the thorax. The thorax as taxic homology is a developmental constraint inherited by an insect's parts. Indeed, *any similarity that we see across organisms can be considered as a shared developmental constraint*. It is the business of phylogenetic systematics, namely cladistic analysis, to decide the cause of this sharing (Rieppel, 1992, 1994). The cause of the shared developmental constraint is deduced from the overall relationship of the particular constraint to other constraints. The relationship between one character state and other states for a particular study group may be either congruence, in which case the constraint is homologous, or incongruence, in which case the constraint is homoplastic. This judgment of ultimate, historical cause is made without concern for the proximate causes of the constraint in terms of particular developmental mechanisms.

Cladistic analysis as a process of creation and discovery

Nelson (1989) refers to cladistics as a discovery procedure. Nelson's intention in bringing the term to systematics appears partly to emphasise the empirical claims of cladistics: 'For Nelson (1989), empirical notions require a "discovery procedure" such as cladistics' (Rieppel, 1991: 93).

Relationships that cannot be discovered by cladistics, for example, that between an ancestral species and its descendant species, are deemed non-empirical by Nelson (1989). Let us investigate the richer significance of Nelson's term and delve down to its roots in semiotics, the theory of signs (see, for example, Dunsby and Whittall [1988: Part IV] where the theory is applied to music). If we wish to discover the meaning of a message, such as a passage of music or a phrase of spoken language, then we need two things: (1) a code, by which we are able to interpret the message, i.e. discover its meaning; and (2) a discovery procedure, by which we discover the code. If we apply this to systematics, then the message is equivalent to a study group of organisms. The code is the means by which we bring meaning to the study group, in terms of meaningful features (similarities) and meaningful similarities (homologies). The code therefore represents the specific characters and the specific hierarchy that comprises them. The discovery procedure is the means of discovering the code, the specific characters and hierarchy. The methodological rules of Rieppel (1988a, b) thus form the discovery procedure of cladistics. The code consists of rules for the interpretation of the structures of the study group, rules in a different sense, namely that of Pattee (1978). Pattee's rules will have great significance when we come to discuss the principle of complementarity, but for the time being we will discuss rules in Rieppel's sense.

Nelson (1979) divides cladistic analysis into three stages. The fundamental stage of character analysis (Nelson discussed only component analysis) involves the collection of representative specimens of the species to be studied. In the derivative stage characters are conceptualised and the character states for particular species recorded. The general stage involves the use of a parsimony algorithm to generate a cladogram and to discover the defining characters of groups. In moving from one stage to the next the focus of the analysis shifts. Three focal contexts can therefore be described, corresponding to a particular stage of the analysis.

Each stage of character analysis involves a different kind of character pattern. A fundamental pattern is the holomorphology of a species (see next section). It consists of the observed features of all

morphological variants of the species, which are at this stage not yet conceptualised. A derivative pattern is a pattern of constraint, or similarity, shared by a number of species. A general pattern describes the pattern of homologies inherited by organisms. Sharing is meaning in the derivative context, and congruence, the nested hierarchical relationship between derivative patterns, is meaning in the general context.

Holomorphologies

Consider the following passage from Beckner (1959). Here he discusses the view of the 'New Systematics' that the biological species is real, whereas higher taxa are not: '... the whole species is, so to speak, bound together in a network, the strands of the net representing potential crosses. These strands are largely confined within the limits of one species. The essential point is that the relation between mates is a biological, dynamic, causal, or if one prefers, real and objective relation ... The relations between the members of higher taxa are not biological, not dynamic, not causal, and in this sense not real and objective; they are historical relations (in so far as the taxa are based upon phylogeny) and relations of abstract morphological similarity' (Beckner, 1959: 67-68). Beckner's discussion agrees with that of Wiley, where he says that taxa are not individuals but historical groups of species (Wiley, 1980: 78; 1981: 75). This view recognises that higher taxa have a class-like quality, but holds to the most obvious evolutionary understanding of taxa as historical entities.

Taking Beckner's view, it is not necessary to limit ourselves to a species concept rooted in interbreeding. According to Eldredge and Salthe (1984: 189) species owe their existence to the production of new entities of like kind from old. This ability of cohesion or 'more-making' (Eldredge, 1985: 144) shows species construed in this way to be individuals. Eldredge and Salthe's definition is in line with the concept of species advocated by Nelson and Platnick (1981: 11), as populations of self-perpetuating organisms: 'In many groups of organisms, for example, we can distinguish samples representing males and females; or eggs, larvae, pupae, and adults. We find,

however, that males do not produce other males, or larvae other larvae, so that these samples, by themselves, have no independent existence in nature. Thus the concept of species must include a criterion of self-perpetuation: males and females together; eggs, larvae, pupae, and adults together; form self-perpetuating species.' This 'extended biological' species concept is a very intuitive one. Without the concept it is impossible to speak of an aberrant specimen, a unrepresentative sample, or even of comparable semaphoronts (Hennig, 1966; see Nixon and Wheeler, 1990: 219).

Kluge (1988: 57) has drawn attention to the view of Danser (1950: 118), a typologist, that life cycles as a whole should be classified: 'His reason for doing so was simple - it is only natural to think of organisms in their entirety'. This empirical process of ontogeny is the basis of Hennig's (1966) concept of holomorphy: 'The holomorphy of an organism is the total spectrum of characters exhibited by that organism during its lifetime' (Wiley, 1981: 12). The reason for studying the holomorphy of an organism is obvious. A consideration of whole life cycles will reveal that characters absent in late ontogeny are nonetheless present in early ontogeny. For example, the relationship of tunicates with vertebrates was revealed by the discovery of a notochord in the tunicate larval stage.

Wiley has generalised Hennig's concept to apply to species, as well as to organisms: 'The holomorphy of a species is the total spectrum of the holomorphy of the individuals comprising that species' (Wiley, 1981: 12). The introduction of the concept of species holomorphy is a natural one, taking into account the processes of ontogeny and tokogeny through which biological populations maintain themselves in nature. However, the concept of species holomorphy derives principally from the observation that a particular organism may not display the representative characters of the self-perpetuating population to which it belongs. Wiley (1981: 119) gives various examples. Alternation of generations in both animals and plants produces complex holomorphologies. A single organism of the sporophyte or gametophyte generation of a moss cannot qualify as a fundamental unit of systematics, since alone it does not form a self-

perpetuating population. Mosses must be classified by means of characters from both generations. The caste system found in social insect yields both reproducing and non-reproducing organisms. Each shows a different suite of characters.

The tension between creation and discovery

Cladistics, if it is a discovery procedure in the sense of semiotics, is a way of discovering and communicating meanings. If we examine an excellent discussion of the nature of communication provided by McCabe (1987), then a tension is exposed between aspects of creation and aspects of discovery in cladistics. The same tension exists within cladistics that is present in all forms of linguistic communication.

‘All life at any level is a matter of communication. Every organism is an organism by virtue of its power of communication. What makes a human body human is that it is involved in linguistic communication’ (McCabe, 1987: 118). An animal’s environment is organised in terms of the relevance of the parts of that environment to the animal’s activities and needs. The fruits of the animal’s exploration turn the animal’s environment into its world. An animal’s world is organised through its body and its senses, they make the world meaningful to it. ‘To share in the interpretation of a world and the response to it is to communicate ... the animal’s body is the means of creating or discovering meaning in the environment and thereby turning the environment into a world’ (McCabe, 1987: 119). An animal is therefore able to ‘realise’ meanings in its world, in the sense of ‘to discover’ and ‘to make real’ (McCabe, 1987: 120). Meanings are therefore found to be ‘real’ (discovered) and at the same time made to be ‘real’ (created). An object has meaning and significance if it has a role in the business of living (McCabe, 1987: 119).

Classifying organisms must be done for pragmatic reasons: to divide up the world into manageable parts to facilitate communication. As human beings we partake in linguistic communication by

sharing meanings by means of media which we have created ourselves (McCabe, 1987: 120), and these include formal scientific classifications. Classifications are created as tools in linguistic communication, but nevertheless involve discoveries about the world.

The creation-discovery cycle

Resolution of the tension between creation and discovery is made particularly clear by Checkland and Scholes (1990). They realise that our interactions with the world are cyclical. The cyclic nature of cladistic analysis was described by Hennig (1966) in his famous phrase ‘reciprocal illumination’, referring to the checking and re-checking of hypotheses. The cyclic illumination of the world that takes place during cladistic analysis has been highlighted recently by Kluge (1991). Human observers create the linguistic tools for understanding organisms. Furnished with these tools, they are able to give nature a proper interrogation and discover her secrets. Cladistic analysis involves a cycle of interrogation and response, of creation and discovery. Cladistic analysis is not simply a discovery procedure, but indeed represents what might be called a ‘creation/discovery procedure’.

The legend to Checkland and Scholes (1990: figure 2.1) describes the essence of cyclic illumination: ‘The world interpreted in terms of ideas whose source is the world itself.’ This diagram (modified in the light of Checkland and Scholes, 1990: figures 1.1 and 1.3) is reproduced as Figure 1. The ideas we have abstracted from the world influence further perception. The ideas, in a sense, create a new perception of the world. This new perception can then lead to the abstraction of further ideas which themselves create a new perception, and so the cycle of creation and discovery continues.

Ideas abstracted from the world are not simply arbitrary or conventional. Even if sanctioned by consensus, they cannot mould the world to any form we wish. Comparing the ideas we have abstracted with future perceptions a discrepancy may be found. The error is not in the world but in our ideas about the world. These ideas must be adjusted and corrected. If this is not possible then

they must be abandoned. Figure 2 (Checkland and Scholes, 1990: figure 1.3 modified in the light of figures 1.1 and 2.1) therefore more clearly expresses the empirical element of cyclic illumination.

So far no distinction has been made between public and private ideas and concepts, between objective and subjective knowledge. We have two worlds, as it were, the perceived world and the world of 'experience based knowledge' (Checkland and Scholes, 1990: 3). In the context of soft systems analysis, where Checkland and Scholes introduce these ideas, human concepts derived from the world must be taken as given. The task is then to use them constructively to alter the problem situation and modify them if necessary. In science, however, we ask for ideas and concepts that are derived by some explicit means, a methodology, that is open to public scrutiny and logical analysis (Ziman, 1968). Figure 2 may therefore be modified so as to represent science to yield Figure 3 (cf. Checkland and Scholes, 1990: figure 2.2).

Figures 4 and 5 describe cladistic analysis as a system of cyclic illumination. Figure 4A shows the derivative stage, that is character conceptualisation. Character concepts are tested against further specimens, and if found not to be applicable are modified or abandoned. Features seen in available specimens are extrapolated in the assumption that they are representative for the holomorphology of the species. Factors of ontogeny and tokogeny (e.g. differential growth, sexual dimorphism) are taken into account in this extrapolation. It can be seen that the attempt to form character concepts can result in the falsification of species concepts. Figure 4B shows how the derivative stage can feed back on the fundamental stage. Specimens supposedly of the same species may fall outside the range of variation expected for its holomorphology. Specimens supposedly of different species may fall within the range of variation expected for a single holomorphology. In other words, all differences between the two specimens from the supposedly different species can be explained as caused by the processes of ontogeny and tokogeny by which biological populations maintain themselves in nature.

Figure 5A describes the general stage, that is the use of a parsimony algorithm to generate a set of cladograms from the data available. This involves the decision that particular states comprise particular taxa. Such a decision may be checked by reexamining specimens of the species inferred to have inherited the taxon to see if the specimens exhibit the characters that comprise the taxon. This may reveal that erroneous decisions have been made for those species. Figure 5B shows that it is in assessing the results of a cladistic analysis that the general stage feeds back on the derivative stage. Two of the simplest criteria are chosen for sake of example, firstly, comparison with the worker's own intuitive assessment of the study group and secondly, comparison with the views of other workers. An initial intuition may indicate that a taxon is incorrectly placed. Attention would be directed to characters which influence the taxon's placement and these may be found to be poorly conceptualised. On the other hand the intuition may encourage a search for further characters that the supposedly related species exhibit which may then be brought to bear on the problem of its relationships. In order to deal with the challenge presented by the views of other workers, it may be possible to include their data in the analysis, or to alter conceptualisations of certain characters which they have also observed but perhaps in a better sample of taxa.

Species and general taxa

To refer to the entities discovered by cladistic analysis as 'higher taxa', 'supraspecific taxa', 'monophyletic groups', or 'historical groups' is to rely on a group concept of taxa and on the notion of focal, or hierarchical, level which that embodies. Traditionally then, general taxa are seen as groups of species, i.e. existing at a higher hierarchical level than the species. However, if a general taxon is seen as a relationship inherited by species, then the traditional descriptions are inapplicable. Species are fundamental taxa, they exist in the fundamental realm. General taxa cannot be groups of species, since general taxa and species exist in different realms. General taxa are not groups of species, they are relationships inherited by species. It follows that a cladogram, as a diagram of the pathways of morphological inheritance, is not a hierarchy of groups within groups. But such a

diagram may be treated as isomorphic to a diagram of set membership, that is, to a cladogram in the sense of Nelson (1979) and Friday (1994). Here the historical meaning of the diagram is omitted, and the diagram simply represents a hierarchical classification. A phenogram may be treated as a diagram of set-membership, but is not supposed to be isomorphic to a diagram of the pathways of morphological inheritance since it does not embody a concept of taxic homology. I have suggested elsewhere (Wood, 1995), that the terms monophyletic, paraphyletic and polyphyletic should only be applied to cladograms when they are treated as hierarchical classifications.

Nelson and Platnick (1981: 12) conclude their discussion of the nature of species with the following definition: 'the smallest detected samples of self-perpetuating organisms that have unique sets of characters.' However, this definition implies an operational method of detection and that species are the smallest groups detected by this method. However, we may ask then, what are the entities that have been analysed to arrive at this conclusion? If we say that species are the terminal entities of cladistic analysis then we enter a circular argument: this conclusion must be based on a cladistic analysis that justifies them as such. Vrana and Wheeler (1992) conclude instead that individual organisms are the terminal entities of analysis, and that a limit to resolution (at which divergent evolution is said to be replaced by reticulation) must be discovered empirically: 'Certainly it might be a consistent and useful definition if the term "species" always applied to that level below which reticulation occurred. The caveat is that there is no way to know this prior to analysis, thus in many cases applying the term by this definition must be a statement of blind faith' (Vrana and Wheeler 1992: 69). Vrana and Wheeler do not, however, address the issue of focal context. By discussing whether or not species are the smallest taxa definable (by general character states), species are treated as general taxa. The special place of species is not due to them being general taxa at the lowest possible hierarchical level. A species concept is needed in order to assess the variety of specimens needed for a representative sample of fundamental patterns. And no fundamental patterns, no general pattern. No species, no cladistic analysis.

Nixon and Wheeler (1990) agree with me: 'In addition to the traditional roles of describing, naming, and classifying the kinds of living things, systematists also must recognise the biological entities that can be analysed using cladistics' (p. 213). They advocate a 'phylogenetic' species concept, after Cracraft (1983), that can be implemented prior to cladistic analysis (p. 217). Nixon and Wheeler give the following definition: 'the smallest aggregate of populations (sexual) or lineages (asexual) diagnosable by a unique combination of character states in comparable individuals (semaphoronts)' (p. 218). The use of epithet 'phylogenetic' is rather puzzling here, since their concept of 'population' is based on 'genealogical (not phylogenetic) relationships of its component individuals' (pp. 218-219). Awkward cases, where individuals lack the characteristics of their species, can be resolved by observing the genealogies of these individuals directly: 'Such individuals probably would not be identifiable as members of the species except by direct association with other individuals of the species that bear diagnostic characters. The (comparable) offspring of such individuals would bear the diagnostic characters of the species, indicating that the parents did not lack the characters of the species' (p. 219). Genealogy is indeed a process by which biological populations maintain themselves in nature. If directly observable genealogical relationships may indeed aid in the assignment of individual organisms to species. I suggest that we may use our knowledge of the characteristic effects of particular biological processes in assigning organisms to species, even if those processes may not be directly observable in the species we are dealing with. For example, Merrett and Marshall (1981) were led to synonymise two species of the deep sea fish genus *Coryphaenoides*, namely *C. colon* and *C. zaniophorus*. The two species were found at the same capture station. Smaller individuals were found to have the characteristic proportions of *C. zaniophorus* and the larger individuals the characteristic proportions of *C. colon*. They conclude that the differences between the two are explicable as allometric variation within a single species. Given the recognised phenomenon of allometric growth, the combinations of character states found in *C. colon* and *C. zaniophorus* fall within the range expected for the holomorphology of a single species.

Stability and constraint

The theme of stability is common to all the ground-breaking accounts of hierarchy theory. The parable of the two watchmakers, first presented by Simon (1962: 470), provides a clear statement of this theme and has been variously adapted by Koestler (1967: 45-47) and Allen and Starr (1982: 49-51). Simon describes two watchmakers, named Hora and Tempus (Koestler renames them Bios and Mekhos, and Allen and Starr provide a factual analogue of the fictional Hora). Both Hora and Tempus make watches that consist of 1000 parts. However, Hora manufactures his watches in subassemblies of 10 parts each, whereas Tempus assembles his watches part after part. The subassemblies that Hora has discovered are *stable*. They do not fall apart when Hora leaves them to cope with disturbances, such as the telephone ringing. But for Tempus only the completed watch is stable. A disruption at any stage except the final one requires him to start from scratch again. Hora's strategy is superior for dealing with environmental disturbances, caused by customers ringing the workshop, since the use of stable subassemblies minimises the effect of those disturbances. Watches built by Hora as a hierarchy of subassemblies will come to predominate in the market at the expense of the watches of Tempus.

Simon (1962) draws two conclusions from his watchmaker parable, in order to emphasise the importance of hierarchical structure. Similar conclusions are reached by Dawkins (1976, 1989a,b). Through his popular writings Dawkins has gained something of a reputation as a reductionist and arch-adaptationist. He has advocated the gene not the individual as the level of selection (Dawkins, 1982, 1989b) and natural selection as the creative force in evolution (Dawkins, 1986). It may then seem strange to find that he has adopted some of the language, and the conclusions, of hierarchy theory.

(1) In nature only the stable survive. Survival of the stable is a generalisation of survival of the fittest (Simon, 1962: 471). Thus, the rule of the survival of the stable extends into the inanimate, as well as to animate (Simon, 1962: 479).

‘Darwin’s “survival of the fittest” is really a special case of a more general law of *survival of the stable*. The universe is populated by stable things. A stable thing is a collection of atoms that is permanent enough or common enough to deserve a name ... The things that we see around us, and which we think of as needing explanation - rocks, galaxies, ocean waves - are all, to a greater or lesser degree, stable patterns of atoms’ (Dawkins, 1989b: 12). ‘The earliest form of natural selection was simply a selection of stable forms and a rejection of unstable ones’ (Dawkins, 1989b: 13).

(2) ‘Among possible complex forms, hierarchies are the ones that have time to evolve’ (Simon, 1962: 473).

Dawkins (1976) discusses Simon’s argument in the context of a hierarchical approach to animal behaviour and suggests that it also applies to the nervous system. He summarises Simon’s principle as follows: ‘that the evolution of statistically “improbable assemblies proceeds more rapidly if there is a succession of intermediate stable subassemblies. Since the argument can be applied to each subassembly, it follows that highly complex systems which exist in the world are likely to have a hierarchical architecture”’ (Dawkins, 1976: 16; Dawkins, 1982: 251).

Dawkins (1989b) points out, however, that we cannot expect complex organisms to arise through the simple heat agitation processes that brought about the stable inanimate forms (Dawkins, 1989b: 14). What is required are special molecules, called *replicators*, which are able to hold information and pass it on to future generations. Selection then accumulates beneficial modifications and complex forms are built up. Elsewhere he provides a second condition: ‘It is that there must be an embryology; the genes must influence the development of a phenotype; and the replicators must be able to wield some phenotypic power over their world, such that some of them are more successful at replicating themselves than others’ (Dawkins, 1989a: 202).

We may reflect on these two requirements by considering how we might go about defining a living organism. Cairns-Smith (1982) divides definitions of life into two classes: genetic and teleonomic. Genetic definitions concern the properties of organisms that we would expect as prerequisites for an

evolutionary process, namely some sort of replicating molecule that can act as a hereditary material. Teleonomic definitions concentrate on the products of evolution, namely elaborately integrated wholes, apparently contrived, exhibiting a high degree of cooperation between their parts. Cairns-Smith shows that it is the definition of Waddington (1968: 3) that provides the link between these two classes of definition: living things take part in the long-term processes of evolution. Thus organisms that are beyond the ability to reproduce are products of the long-term processes of evolution, although no longer active participants. The very first organisms on earth are at the beginning of those long-term processes, although not yet possessing the high degree of apparent design typical of later forms.

The genetic and teleonomic definitions of life relate to the dual aspect of every organism. The hereditary material embodies the organism's genotype, the messages replicated from generation to generation. The organism's subtly cooperating parts are its phenotype. Organisms generate more organisms of like kind and set up cycles of self-generation. Heritable variation results from imperfections in the replication of genetic information. Changes accumulate in the genotype, which in turn manifest themselves in the phenotype of the organism. The cycles of self-generation thus have a direction, a history, as a result of these accumulated changes. Descent with modification thus requires a logical separation of genotype and phenotype: a genotype to perpetuate change, a phenotype to manifest it.

Dawkins (1989a) provides an insight into the nature of development through an elaborate thought experiment, aided by a computer program. He is interested in creating 'biomorphs', two dimensional images that evolve according to the two conditions he has outlined above. The phenotype of each biomorph consists of a pattern of pixels on a computer screen. What is the best way to organise the genome that codes for this phenotype? The first idea that suggests itself is to have a gene coding for each pixel: 85,000 genes for each pixel on the Macintosh screen. Any pattern of pixels, any conceivable biomorph, could in theory be generated through gradual change at the level of both the

genes and the overall morphology. 'But only in theory. In practice we'd be waiting till kingdom come ... Our improvements [to the developmental program] will take the form of constraints. Constrained embryologies are improvements over naive pixel-peppering, not because they have greater generality but because they have less. Naive pixel-peppering can produce all possible pictures, including the set that anyone might regard as biological. The problem lies in the astronomical number of nonsense pictures that it can also produce. Constrained embryologies have a restricted set of phenotypes that they can generate, and they will be specified by a smaller set of genes, each gene controlling a more powerful drawing operation than colouring a single pixel' (Dawkins, 1989a: 204-205).

Dawkins (1989a) has realised that, for complex forms to evolve, not only must there be replicators, but the developmental system must be set up in a certain way, specifically, so that it embodies particular *constraints*. The existence of a characteristic set of developmental constraints has the negative result that evolution is canalised along certain pathways. Dawkins shows how he tried to select biomorphs that corresponded to letters of the alphabet, specifically to be able to spell his name in biomorph characters. However, he was unable to generate a 'K' despite all his efforts and he could not remove a tail from the rather triangular 'D' (Dawkins, 1989a: 216).

The conclusions that Dawkins has made on the nature of the developmental system match those arrived at empirically by Goldschmidt (1938, 1940). There is no great divide between their views as you might expect (see Gould, 1980c, on the rehabilitation of Goldschmidt). I identify three points of correspondence between Dawkins and Goldschmidt:

(1) Genetic change causes local changes in the partial processes of development

(Goldschmidt, 1938: 51-52; see also Alberch, 1982: 326)

'Genes don't control small fragments of the body, the equivalent of pixels. Genes control growing rules, developmental processes, and embryological algorithms. Powerful though they are, an important feature of these growing rules is that they are local. There is no grand blueprint for the

whole and when all the local instructions are obeyed together a body eventually results' (Dawkins, 1989a: 206).

(2) Small genetic changes accumulate until a threshold is reached and great potential for rapid macroevolution is released (Goldschmidt, 1940: 396)

Dawkins (1989a) proposes modifications to his basic developmental program. These involve the introduction of a number of genes that regulate the kind of patterns that can be produced. Thus there are genes for various patterns of symmetry or segmentation. These modifications lead to 'opulent flowerings of new emergent properties' defining 'a whole new range of types' (Dawkins, 1989a: 209, 212). Here Dawkins has introduced genes for global patterns. But given his statement in (1) perhaps it is not too much to imagine that these global patterns might in fact be the result of the local interactions as Goldschmidt envisaged.

(3) Hopeful monsters (Goldschmidt, 1940: 390-393)

'I suspect that the first segmented animal was not a dramatically successful individual. It was a freak, with a double (or multiple) body where its parents had a single body. Its parents' single body plan at least fairly well adapted to the species' way of life; otherwise they would not have been parents. It is not, on the face of it, likely that a double body would have been better adapted. Quite the contrary. Nevertheless, it survived (we know this because its segmented descendants are still around), if only (this, of course, is conjecture) by the skin of its teeth' (Dawkins, 1989a: 218). This seems a bizarre scenario, and one that appears to contain a dangerous element of circularity. We reconstruct a hopeful segmented monster to explain the existence of segmented animals and justify that, however unlikely it was, it survived because we have segmented animals here today. The standard objection is that a single monstrous individual is produced easily enough, but how do we arrive at an interbreeding population of monstrosities? Dawkins and Goldschmidt have emphasised the potential of the developmental system to produce sharply discontinuous changes to such an extent that they have brought their theory of macro-evolutionary change to brink of non-Darwinian saltationism.

However, neither Dawkins nor Goldschmidt need do so. An alternative course is provided by their own observations: 'Suppose that a discontinuous change in adult form arises from a small genetic alteration. Problems of discordance with other members of the species do not arise, and the large, favourable variant can spread through a population in Darwinian fashion' (Gould, 1980c: 191).

Gould suggests that the large change in morphology may cause a cascade of related adaptations. A new mode of life will then be opened up through a series of gradual modifications.

Stability and homology

'The most fundamental principle of evolutionary strategy, related to the watchmakers' parable, is the *standardisation* of subassemblies ... Animals and plants are made out of homologous organelles like the mitochondria, homologous organs like the gills and lungs, homologous limbs such as arms and wings. They are the stable holons in the evolutionary flux' (Koestler, 1967: 135, 139). Riedl, in the following passage, reflects similarly on the stability of homologues: 'Actually, every homologue is characterised by the fact that it shows adaptive freedom in only a few directions, but fixation in many others. If this were different, if every character were free to change in every direction, the living world would appear as a random chaotic mixture of patterns, as chaos, and the single relationship left among representatives would not relate to common ancestry but only to common functions, such as analogous limbs, horns, wings, jaws, and so forth' (Riedl, 1977: 354; cf. Alberch, 1982: 315-316). Riedl therefore introduces a concept of morphological stability, or fixation, to account for the fact of homology. Parts of organisms possess a stability which permits us to recognise relationships between them that are not the result of shared function. But stability is also the ability 'to adapt in response to shocks from the environment' (Checkland and Scholes, 1990: 19). Morphological stability is thus adaptability, or *evolvability* (cf. Waddington, 1957: chapter 5). Dawkins (1989a) defines evolvability as follows: 'New embryologies that are evolutionarily fertile tend to be the embryologies that characterise the forms of life that we actually see. As the ages go by, changes in embryology that increase evolutionary richness tend to be self-perpetuating. Notice that this is not the same thing as

saying that embryologies that give rise to good, healthy individual organisms tend to be embryologies that are still with us, although that, too, is no doubt true. I am talking about a kind of higher-level selection, a selection not for survivability but for evolvability' (Dawkins, 1989a: 218). The stable morphologies that we see today are the product of embryologies that were pregnant with evolutionary potential. A stable morphology, although the result of a constrained embryology, shows great evolutionary potential in the few directions open to it.

To sum up, we are apparently provided with two ways of describing the stability of the organism: (1) the organism consists of stable subassemblies, or homologues; (2) the organism's development is set up so that it embodies particular constraints, homologies. However, it is not parts of organisms (homologues) that are inherited from generation to generation. That would imply a material continuity possible only for the genotype. What are conserved through phenotype after phenotype are relationships of constraint (homologies). The inheritance of these relationships from generation to generation maintains the organism as a set of stable subassemblies. The organism's developmental constraints filter out the effects of destabilising genetic mutations, but at the same time make the organism adaptable to future environmental changes.

Hierarchies of constraint

'Hierarchies can be profitably viewed as systems of constraint' (Allen and Starr, 1982: 11). Allen and Starr (1982) discuss constraint in terms of information flow through the hierarchy. They adopt Koestler's metaphor of Janus (Koestler, 1967: 47-49). In the Roman mythology the god Janus had two faces; the Latin for door *ianua* is from the same root. Each holon is thus a doorway through which information enters and departs, flowing down the hierarchy from the environment and flowing up from lower levels of the hierarchy (Allen and Starr, 1982: 9). The position of the holon in the hierarchy is determined by the way in which the holon filters information that it receives. The asymmetry of information exchange produces relations of constraint between holons. Constraining

holons filter out the signal that they receive from constrained holons and remain largely unaffected. Constrained holons receive the signal from constraining holons relatively unfiltered and thus are significantly affected. (This account of constraint and information exchange is derived from Allen and Starr, 1982: 20; cf. Dawkins, 1976: 14).

Signals pass out from the genome and modify the environment to produce the phenotype. This is what we call development. Development is an interaction between the genetic signals and the environment. The dividing line between the phenotype and the environment is not precise: the phenotype 'is a bit of the environment locally modified by the genetic information' (Cairns-Smith, 1982: 80). It is possible to imagine that the phenotype, the manifestation of the effects of the genetic signals, extends into the environment beyond the bounds of the body housing the corresponding genes. This is the essence of Dawkins' idea of the 'extended phenotype' (Dawkins, 1982).

We can envisage the phenotype itself as a set of holons which differ in the extent to which they filter genetic signals as they pass out into the environment. Phenotypic holons that exert little constraint on the genome express the genetic signal relatively unfiltered. Phenotypic holons that exert heavy constraint on the genome express the genetic signal significantly filtered. Thus continuous genetic differences between organisms in a population may be expressed as continuous phenotypic differences, if the corresponding genetic signals are relatively unfiltered, or as discontinuities, if the genetic signals are significantly filtered. The accumulation of genetic changes will cause gradual modifications of the phenotype in the first case, but sudden shifts between stable states in the second. In this way phenotypic holons can be said to constrain the dynamics of genetic change. These constraints are properties of the developmental system: they are *developmental constraints*. Genetic signal is filtered in such a way that across individuals, and indeed across species, qualitatively different morphologies are produced. (An understanding of the developmental system in terms of its inherent constraints cannot be derived from the study of a single individual; *contra* Dawkins [1989a: 203].)

If holons are doorways then information passes through them in two directions. If we believe that development is the result of genetic information passing out through a hierarchy of holons into the environment, then there must be a process in which genetic information flows back the other way. I suggest that information flows back from the environment to the genome when organisms reproduce. On their return journey genetic signals pass through a hierarchy of *adaptive constraints*. The position of a phenotypic feature in this hierarchy is determined by the selective or adaptive advantage of that feature. As in the case of development we must think not about a single individual, but a set of individuals, in this case the population. Selective filtering occurs when the population reproduces as a whole to provide the next generation. The predominance of a gene in the next generation is proportional to the strength of the signal arriving from the environment back in the communal genome, or gene pool. Adaptive, i.e. selectively advantageous features amplify the signal, whereas maladaptive features attenuate it. A particular phenotypic feature may filter the signal of many genes. It is also possible that selective filtering of different features is correlated in some way. There is no need to conceive a simple relation between genetic signal and selective constraint. It is on genetic signals that selection acts: genetic signals are selectively filtered. This is the essence of another of Dawkins' ideas: the 'selfish gene' (Dawkins, 1989b). Dawkins has been dubbed a reductionist for advocating the gene as the level at which selection acts. I have shown here that his position is exactly that expected from hierarchy theory.

Homologies are rules of interpretation that make the phenotypes of organisms meaningful.

Homologies are developmental constraints conserved among organisms. Homologies are the rules operating at the phenotypic level that constrain the dynamics of the genetic level (cf. Allen and Starr, 1982: 42). Through descent with modification then, organisms accumulate inherited constraints on their genetic dynamics, or as Riedl (1977) would put it, on their adaptive freedom. The type is the totality of constraints inherited by the organism. The homologies, the parts of the type, are the individual constraints inherited by the parts of the organism. A general taxon or type characterises 'a

set of species sharing a common pattern of constraints and adaptive opportunities ... the key event in the origin of a [general] taxon is a change in the pattern of constraints' (Wagner, 1986: 154-155).

I have described above a 'feedback regulatory cycle' operating between genotype and phenotype, similar to that envisaged by Riedl (1977). In order to explain the stability of homologues over evolutionary time, Riedl saw the necessity of 'feedback loops of cause and effect both from the genome to the phenome and in the *reverse* direction' (Riedl, 1977: 364). This sounds rather puzzling but can be understood in terms of the expectations of hierarchy theory. The dynamics of gene frequencies may be the cause of phenotypic change, but the effects are constrained by the phenotype itself. Thus information flows both ways: from genotype to phenotype in the causal relationship enshrined in the 'central dogma' of molecular biology, and from phenotype to genotype as constraints enshrined in the systems approach (Riedl, 1977; Wagner, 1986). I might even suggest that Riedl's notion of burden, or systemic position, is equivalent to the position in the hierarchy of constraint. Structures of high burden have great stability and are unlikely to be rejected or modified by natural selection (Riedl, 1978: 239).

Dynamical systems theory

Like Dawkins (1989a), Alberch (1982) describes the idea of developmental constraints with the aid of a thought experiment. Consider, for sake of example, that the whole diversity of a phenotype can be expressed in terms of two variables, x and y . The distribution of forms found in nature is not continuous. Instead, phenotypes cluster and certain regions of the xy space remain empty. Now let us take a population of one of the natural forms and breed the population for a large number of generations. The effect of natural selection is eliminated as far as possible, by enforcing random mating and minimising competition. The overall genetic variability of the population can also be increased through the use of mutagens. Score all the new phenotypes in terms of x and y , including teratologies. We will get the same phenotype clusters as before, plus new ones, which will be

naturally lethal or non-functional phenotypes. ‘However, there will still be states that are prohibited by developmental constraints’ (Alberch, 1982: 318). The basic effect of developmental constraints on the apportionment of morphological variation is that ‘a continuous distribution of genotypes can result in a discontinuous distribution of phenotypes’ (Alberch, 1982: 319).

The theoretical framework that Alberch (1982) provides for understanding developmental constraints is dynamical systems theory: ‘Developmental systems are complex non-linear dynamical systems. It is an intrinsic property of such systems that they will fall into a discrete number of stable states, i.e. we should a discrete and bounded distribution of phenotypes. Furthermore, non-linear dynamical systems will exhibit preferred transitions of form’ (Alberch, 1982: 327-328). The analysis of development as a dynamical system enables possible stable states of morphology to be identified and also the preferred transformations between those states. The morphogenetic process is conceived as a set of simple, locally-acting “assembly” rules (Alberch, 1982: 321). Genetic change perturbs the parameters of the developmental system, but as long as the parameters stay within certain limits, the morphology remains unchanged. The morphology is said to be self-regulating or canalised (Waddington, 1957). However, if a particular parameter reaches a threshold value then a sudden shift to a different stable state occurs. This effect is known in the language of dynamical systems theory as ‘bifurcation’. The parameter space for a particular dynamical system is said to have ‘bifurcation boundaries’ at which the global behaviour of the system, such as the resulting morphology, shifts from one stable state to another. Oster and Alberch (1982) describe ‘how the bifurcations in the developmental program acts as a *filter*, giving order to the random mutations in the genome, so as to present natural selection with a small subset of the possible phenotypes’ (Oster and Alberch, 1982: figure 11, legend; my italics). Thus developmental bifurcations ‘filter random mutations, giving them a non-random character’ (Oster and Alberch, 1982: 454).

The view of the developmental process derived from the theory of non-linear dynamical systems is compatible with that provided by hierarchy theory. In fact, they complement each other. On the

phenomenological level, the notion of developmental constraints is left obscure by dynamical systems theory. A phenotype can never be expressed in terms of just two variables. Hierarchy theory, as applied to systematics, clarifies the notion. Homologies are developmental constraints and, through descent with modification, are inherited by parts of organisms. Dynamical systems theory provides the basis of constraint at a deeper level. Developmental bifurcations filter genetic signals, producing variation at the morphological level which is constrained or canalised into particular stable states.

Quantity to quality

Gould (1980b) provides a lucid description of the two proposed modes of macroevolutionary change: gradualism and punctuated equilibria. Gradualism asserts that evolution proceeds by the continuous, gradual change at both the level of the gene and the total morphology. The theory of punctuated equilibria (Eldredge and Gould, 1972; Gould and Eldredge, 1977) asserts that species appear rapidly and then remain stable for the rest of their history. Gradualism is forced to explain the existence of discontinuities in nature as gaps in the preservation of the fossil record. Punctuationism, on the other hand, sees the gaps as real, to be expected by the theory. The theory explains discontinuity in terms of a process of speciation which requires rapid change in both genotype and phenotype in a small population (Gould, 1980b: 183).

The theme of Gould (1980b) is that gradualism has found favour because of the Western preference for slow, orderly transformation. A preference for revolutionary, cataclysmic change belongs to a different tradition, namely the tradition of dialectics derived by Engels from Hegel's philosophy: 'The dialectical laws are explicitly punctuational. They speak, for example, of the "transformation of quantity into quality."' This may sound like mumbo-jumbo, but it suggests that change occurs in leaps following a slow accumulation of stresses that a system resists until it reaches the breaking point' (Gould, 1980b: 184-185). I argue that the concept of a "transformation of quantity into quality" offers an explanation of the existence of discontinuities in nature which does not require reference to

a separate macroevolutionary theory. *Quantitative change at the genetic level gives rise to qualitative change at the morphological level.* Change at the level of the genome may be continuous, but discontinuous at the level of the overall form. If some phenotypic characters do change continuously it is because the corresponding genetic signals are expressed relatively unfiltered. It is these characters that have been studied in genetic experiments that have supposedly demonstrated evolution to be change in gene frequencies. The properties of the developmental system are such that genetic changes, even if copious, small and undirected, can still give rise to specific, large, directed changes of form: 'These [small, genetic] changes can have substantial impact on adult phenotypes because they operate by altering rates of development early in ontogeny, with cascading effects throughout later growth' (Gould, 1980a: 45).

A biological principle of complementarity

Organisms and species comprise aspects of both genotype and phenotype: genome or gene pool and holomorphology respectively. Phylogenetic history can be described as the history of the genotype and the history of the phenotype. There are therefore two different ways of approaching the phylogenetic history of organisms and species, genetic and morphological. The genetic approach takes DNA sequences as the source of its data, since these comprise the genotypic information passed on from generation to generation. All aspects of the phenotype provide the source of data for the morphological approach.

DNA sequences, as genotype, have no ontogeny and exist effectively in only one dimension (Patterson, 1988a: 74; 1988b: 610). Ontogeny is the process by which the information stored as the genotype is translated into the three-dimensional structure of the phenotype (Patterson, 1988a: 94). The genotype can be expressed in simple physical and chemical terms. This is what a nucleotide sequence is. The phenotype cannot be reduced to a physicochemical description if essentials are not

to be lost. Its hierarchical organisation has emergent properties, homologies, which are irreducible to the underlying physics and chemistry.

Tennant (1986) provides an interesting discussion of how it might be possible to define a morphological homology like the gastrula. Is it possible to reduce the homology to a precise definition in physical and chemical terms? We might start by defining the gastrula as certain types of cells in particular topological configurations. A gastrula is thus a hollow ball of cells, where the outer layer of cells is ciliated and the inner layer is unciliated and free to divide. However, in a purely reductionist exercise each cell would have to be described in terms of particular configurations of nuclear, cytoplasmic and membranous components. Each of these components could be reduced to configurations of different sorts of molecules, and so on *ad infinitum*. We might take a different approach and describe the gastrula of each species in terms of its characteristic cell types, and the characteristic rate at which these differentiate. But even with this approach, the term would become complicated and unwieldy. Moreover, the term would lose what Tennant calls its 'open-textured meaning'. A student is taught to recognise a gastrula by being shown an example, probably together with a simple diagram. The student is able to grasp the concept intuitively. Equipped with this knowledge, he is able to apply it even to a previously undescribed species. Any description of the gastrula purely in physical and chemical terms would have to be altered with the discovery of the new example. However, the term itself would survive this extension unchanged. It is Tennant's belief that ultimately morphological homologies will submit to the reductionist exercise. But I think his claim misses the point. The beauty of morphological terms lies in their openness, and the problem with attempts to reduce them is that this openness is lost. The use of character concepts which are open and irreducible characterises the intuitive ability for *pattern recognition* possessed by human beings (see Ziman, 1978). The formulation, learning and application of the concept 'gastrula' all necessarily involve human observers. For this reason morphological characters are observer-dependent or intersubjective: they express knowledge which 'can only be validated and translated into action by the intervention of human minds' (Ziman, 1978: 7).

An analogous process of pattern recognition to that involved in morphological work might well be employed in the generation of nucleotide sequence data. Sequences may be simply aligned by eye, gaps being inserted by inspection to produce the closest visual match between the sequences. But again we may ask, is it possible to replace this intuitive process with a mathematical algorithm embodied in a computer program? Strikingly this problem has been solved by Bishop and Thompson (1986). They were able to carry out alignment of pairs of sequences under a model of evolution that incorporated substitution, deletion and insertion events. The achievement of Bishop and Thompson is of great theoretical importance, even though it is practically limited. It shows that genetic data is fundamentally different from morphological data. Patterson (1988b) discusses the attempts made by Jardine and Jardine (1967) to develop a mathematical means of comparing morphologies. He notes significantly that the computer program they wrote was quickly seen to be 'only an aid' (Jardine, 1970: 332). Patterson links the failure of their attempt to the fact that morphology exists in three dimensions, rather than one. We may link it to the fact that, unlike DNA sequences, morphologies are hierarchically organised.

The genetic approach deals with linear DNA sequences, which are aligned according to a dynamical model of the causal process of evolution, a process assumed to take place independent of the observer. The context of morphology, with its inherent hierarchical organisation, dictates that character concepts are the result of the interpretations made by a community of observers. The morphological approach derives its data through a process of interpretation, similar to that involved in any linguistic communication. Morphological comparisons are governed by a creation/discovery procedure and therefore require an observer. What is important is the code, the means by which we bring meaning to the study group, in terms of meaningful features (similarities) and meaningful similarities (homologies). The code therefore consists of rules for the interpretation of the structures of the study group. What are we to make of the existence of two such different approaches to systematics? Are we to say that one must be more reliable than the other? A principle of complementarity, on the other hand, would argue for 'the necessity of formal incompatibilities in the

dual modes of description, in contrast to the unity and consistency of the classical paradigm of a unified formalism' (Pattee, 1978: 193). Here we may make use of the concept of complementarity introduced into systematics by Rieppel: 'Neither perspective is in itself sufficient to produce a complete explanation of natural phenomena, nor is it possible to reduce one perspective to the other. Observation and explanation may proceed from either point of view, resulting in different appearances subject to alternative explanatory theories. There result alternative and complementary views of a whole which as such remains incomprehensible' (Rieppel, 1988b: 5). Pattee (1978) and Allen and Starr (1982) discuss three heuristic criteria designed to identify instances of true complementarity between two modes of description. I shall show below that each identifies a complementarity between the genetic and morphological approaches to systematics. This conclusion bears out the suggestion made by Pattee (1978: 195) that the basis of a principle of complementarity for biology rests on the distinction between genotype and phenotype.

(1) Structure versus function, laws versus rules (Pattee, 1978: 195-196)

Pattee illustrates the complementarity existing between structure and function using the example of the genetic code. The structure of the DNA can be understood in terms of physical *laws*, whereas its function can only be comprehended in terms of *rules* of interpretation specific to living organisms. The coding relationship between DNA triplet and aminoacid is not reducible to physical laws, but rather to be understood as a property of the whole organism. The two approaches to systematics we have discussed are readily understood in these terms. The genetic approach assumes a process of evolution that, at least for the purpose of the analysis, lawfully governs all sequence alignments over the whole study group. The aim of the approach is to improve the fit between the model and the data. The aim of the morphological approach is to discover rules for the interpretation of biological structure. Thus the underlying aims of the two approaches can be seen to have the character of law or rule respectively. The two approaches are therefore complementary.

(2) Rate-dependent versus rate-independent, dynamic versus linguistic descriptions (Pattee, 1978: 195)

The genetic approach generates its data through the use of a dynamical, necessarily rate-dependent model of evolution. The morphological approach derives its data through a process of interpretation and the results of the interpretation are independent of the rate at which the interpretation is carried out.

(3) Observer-independent versus observer-dependent (Allen and Starr, 1982: 43)

In the genetic approach the alignment of sequences can be carried out effectively independent of the observer. In the morphological approach the formulation of characters inevitably involves the observer's judgment.

Models of change

Statistical methods, which adopt some stochastic model of the evolutionary process, are commonly employed for nucleotide sequences, whereas the cladistic method has been widely used to analyse morphological data. The details of different parsimony methods are provided by Kitching (1992). Kitching also describes the method of generalised parsimony (see Swofford and Olsen, 1990: 463-465; Kitching, 1992: 55-58; also Williams, 1992: 115-119). Here a 'cost' is assigned to each transformation between states. The costs are represented as a square m -by- m matrix, in which the elements, S_{ij} , represent the increase in the length of the cladogram that is associated with the transformation from state i to state j . The value m is the total number of states for the character. Any assumptions about order and weighting, any conceivable character coding in other words, can be incorporated into the appropriate cost matrix. For instance, transformations deemed to be impossible can be given a cost of infinity. Note that in generalised parsimony each character state change has a particular weight associated with it. Parsimony as a general method of placing character states on a cladogram specifies the estimate of the true cladogram as the solution of minimal cost. Each parsimony method has its characteristic cost matrix (see Kitching, 1992: table 4.1). The specific cost matrix is the model of the evolutionary process assumed by the particular parsimony technique.

Mickevich and Weller (1990) make a distinction between transmodal characters and cladogram characters. Transmodal characters they define as based on some evolutionary model, whereas cladogram characters are supposedly model-free, based only on the hierarchy of the cladogram. Buckup (1991) shows, however, that cladogram characters are, indeed, transmodal. Mickevich and Weller's intention is to devise a method of character coding that is independent of assumptions about evolution, in the words of Platnick (1989), 'a method that would allow attributes of the data themselves to determine the ordering...' (p. 23). However, since all characters are transmodal, any method of coding makes more or less explicit assumptions about the evolutionary process.

The assigned weights reflect our assumptions about which state changes are particularly favoured. It is readily apparent, from the language that we use for morphology, that the model of evolution employed in cladistics is deterministic, rather than stochastic (Bishop and Friday, 1985). Indeed, Friday makes the point that stochastic models are unable to deal directly with natural selection, usually characterised as a deterministic force (Friday, 1989: 232; 1994: 211). However, deterministic models deal only with (favoured or unfavoured) directions of change, and thus information about evolutionary rates is lost.

Deterministic and stochastic models are complementary following the criterion developed by Allen and Starr: 'It is worthwhile not only to identify what the two complements achieve, but also to identify what is sacrificed, what is the price paid for the perfect internal consistency of each mode of description' (Allen and Starr, 1982: 62). Information about the forces of natural selection and developmental canalisation are incorporated into deterministic models, but are not explicitly described by stochastic models. Information about the rates of evolution taking place in time are incorporated into stochastic models, but are foreign to deterministic models.

Cladograms and family trees

The results of the morphological approach to phylogenetic reconstruction are cladograms in the sense of Nelson (1989). As hierarchies of types (Rieppel, 1985) cladograms have no time axis (they are rate-independent) and have no notion of ancestry (instead, inheritance). Taxa revealed through cladistic analysis are not groups consisting of an ancestral species and its descendant species; taxa are relationships inherited by species. Cladograms do not characterise biological species; they are diagrams which summarise relationships of species. A family tree, on the other hand, is 'a simple model of the pathways of genetic transmission' (Bishop and Friday, 1985: 273). A family tree describes the fate (change without splitting, splitting, extinction) of replicator-continua (Lidén, 1990: 184). If the replicators involved are gene pools, as they must be if the organisms being studied reproduce sexually, then the family tree describes the fate of species in their genetic aspect. Gene pool continuity is the material, biological, causal relationship that binds together an ancestral species and its descendant species (cf. Beckner, 1959: 67-68). The tree has concepts of time, ancestry and species which the cladogram lacks. These differences form the basis of the cladogram/tree distinction discovered by Nelson (1976, draft; published in Nelson and Platnick, 1981).

In the genetic approach what really matters are the nucleotide sequences and the tree of highest likelihood. Ideally there is no intermediate stage. The alignment of the sequences should be carried out as an integral part of the phylogenetic analysis. In the morphological approach what is of interest is the code, the set of patterns of constraint (derivative patterns) and the congruence among those patterns, which specifies the hierarchy of homologies (general pattern). The code brings meaning to the multiplicity of fundamental patterns displayed by the species of the study group. In cladistic analysis we move through different focal contexts, and the contrast between derivative and general stages is much more relevant here. In the statistical approach we simply move from the lowest focal level to higher levels, from species to monophyletic groups of species. The statistical approach operates within the fundamental realm, whereas cladistics moves from the fundamental realm to the

general. Conventional concepts of species and higher taxa apply only to the fundamental realm, to family trees. Species and monophyletic groups of species are fundamental taxa. They are individuals, irreproducible wholes united by gene pool continuity among their parts (cf. de Queiroz and Donoghue, 1988; Lidén, 1990). Cladograms, which describe the hierarchy of constraints inherited by species, exist in the general realm.

Stratophenetics and the derivative realm

Nelson and Platnick (1981) do not simply have a dichotomy between cladogram and family tree. They describe first-, second- and third-order trees. In a first-order tree all possible ancestors are named, whereas in the second-order all rejectable ancestors are rejected. For the third-order tree no ancestors are named, since in this ideal case we are considering the tree to be an unbroken continuum. In the genetic approach a tree is seen as 'a simple model of the pathways of genetic transmission' (Bishop and Friday, 1985). No ancestors are named and the focus is instead on the unbroken continuity of genetic transmission. For this reason, I describe the family trees resulting from the genetic approach as third-order, or ideal, trees.

There is an approach to the reconstruction of evolutionary history which attempts to discover possible ancestors. This is the stratophenetic approach (Gingerich, 1979). It assumes that species may be ancestral, and that ancestral species can be discovered through examination of a sufficiently well-preserved fossil record. Cladists have argued that species are to be discovered through cladistic analysis and that they must be considered monophyletic. By definition, then, they cannot be ancestral. Nelson and Platnick (1984) have taken this to mean that the Darwinian theory of evolution, with its emphasis on ancestral species, is wanting. I argue that species are not discovered through cladistic analysis. They are said to be diagnosed by (aut)apomorphies. However, autapomorphies are not relationships, they are differences. So a species diagnosed by an autapomorphy is in fact diagnosed by a morphological gap, which is not in line with cladistic

principles. It is not obvious how a synapomorphy for a species could relate together different life-history stages, different sexes and other morphological variants, such as alternative generations or social castes. A biological (or fundamental) relationship relating these aspects of the species appears to be required first before any cladistic analysis can begin. I suggest that species can only be diagnosed through a consideration of morphological gaps (which is what cladists are doing anyway), together with a consideration of the processes by which biological populations maintain themselves in nature. They exist, in this context, in the derivative realm.

If diagnosed species can be legitimately said to exist in the derivative realm, then there is the possibility that a reconstruction of evolutionary history can also exist there. The fate of morphologically distinct populations could be followed through time with the aid of a well-preserved fossil record. This 'stratophenetic' approach would result in first- and second-order trees, depending on the degree of resolution possible. It is possible that this approach might make use of evolutionary models based on underlying changes in gene frequencies, as described by Felsenstein (1988).

Complementarity applied to natural selection and gradualism

Dynamic and linguistic descriptions are necessary for a complete account of phylogenetic history. This is a logical consequence of Darwin's theory of descent with modification. Descent with modification employs a theory of the organism as both genotype and phenotype, and it is to these two aspects that the dual descriptions apply. Darwin's theory of natural selection can also be described in complementary yet incompatible ways. An account of the stochastic process governing the differential survival of genes from generation to generation provides the dynamic description. An account of the selective benefit of phenotypic traits, and of the patterns of adaptation observable in nature, provides the linguistic description (Allen and Starr, 1982: 57-66). An account of the dynamics of gene transmission acts *a posteriori* as a causal explanation of adaptation: the fit are the ones that have survived. We must remember that the phenotype acts so as to constrain the dynamics

of gene transmission. Adaptation is not therefore reducible to dynamics and in theory may be judged *a priori*, as the selective significance or meaning of the phenotypic feature. The teleological account of adaptation and its mechanistic explanation are equally necessary aspects of the theory of natural selection (Allen and Starr, 1982: 58-59). Description of adaptation is not logically prior to an explanation in terms of genetic dynamics (cf. Brady, 1980). The historical priority in the description of adaptation is because patterns of adaptation, like patterns of organic form, are conspicuous to human observers. As science always begins with observers, it is understandable that investigation of adaptation has generally preceded investigation of its underlying genetic processes.

Complementary aspects of change must be recognised if Darwin's last theory, gradualism, is to be properly understood. Gradual change is to be expected at the genetic level, and at the phenotypic level if there are no significant constraints in the developmental system. The causal explanation of morphological discontinuities, when they occur, is still change in the genotype. We need only propose that the constraints inherent in the developmental system enable a transformation of quantity into quality, from quantitative genetic change to qualitative morphological change.

Summary

In the simple view, a hierarchy consists of a number of structural levels, such as nuclei, atoms, molecules, for which different levels of description are applied for a complete account of the phenomena. In a more sophisticated view, levels in a hierarchy are defined by the descriptions themselves. Each level of a hierarchy requires an alternative description to that which applies to the lower level. Properties emerge at higher levels which cannot be reduced to the behaviour of lower levels. The rules of behaviour of the higher level constrain the dynamics of the lower level. A full account of the hierarchical system is provided by descriptions of both constraints and dynamics. However, it is impossible to reduce one to the other, so the two descriptions are incompatible yet complementary. Descriptions of the organism as genotype and phenotype are alternative,

complementary descriptions of the type expected for hierarchical systems. Complex entities are organised as a hierarchy of stable subassemblies. Indeed, it is only hierarchically organised forms which are able to evolve conspicuous complexity. Organisms and lineages of organisms are able to maintain a stability in the face of environmental perturbations. They consist of stable subassemblies, namely homologous organs. In hierarchy theory, a system is seen as a hierarchy of constraints, each acting on the level below in such a way as either to restrict or amplify the information flowing through the system. The phenotype of an organism is to be regarded as a hierarchy of constraints. These constraints, depending on one's point of view, may be seen as developmental or adaptational and they act so as to maintain the organism as a set of stable subassemblies.

From a hierarchical perspective, cladistic theory is firmly rooted in developmental and evolutionary biology. It is here argued that: (1) The biological basis of homology is developmental constraint.

Homologies are relationships of constraint inherited by parts of organisms. (2) A character's coding expresses a set of assumptions about the process by which it has evolved. The ordering and weights associated with states of a character can never be independent of an evolutionary model. (3)

Cladogram and tree express different kinds of evolutionary relationships. A cladogram is a hierarchy of types, where a type is the totality of constraints (homologies) inherited by a species. Types are not groups of species, but rather relationships of species. A family tree consists of monophyletic groups of ancestral and descendant species.

The realisation that hierarchy theory is the formal basis of evolutionary theory leads to a renewed emphasis on the morphological aspects of Darwin's theories of evolution. (1) Descent with modification. The material continuity between organisms that Darwin envisaged occurs only in respect of their genotypes. Conventional phylogenetic reconstruction of family trees aims at this genetic aspect. However, organisms are both genotype and phenotype. The history of changes in genetic constitution, on the one hand, and developmental constraints, on the other, may be investigated independently. (2) Natural selection may also be described in terms of genetic dynamics

and aspects of constraint. The typical neo-Darwinian, or at least Fisherian, emphasis is on the genetic aspect, neglecting details of the purposive aspect, namely adaptational constraint. A treatment of both mechanistic and teleonomic aspects is necessary for a full account of natural selection. (3) Gradualism. Genetic change may be gradual and continuous, but the properties of the developmental system are such that the phenotypic products of change may emerge discontinuously. The origin of discontinuities in nature need not be ascribed to speciation, but simply the properties of developmental systems.

Complementarity exists at the heart of biology: in the dichotomy between genotype and phenotype, cladogram and tree, and continuity and discontinuity. Hierarchy theory is therefore an appropriate formal system for evolutionary theory, and cladistics an appropriate method of evolutionary systematics.

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