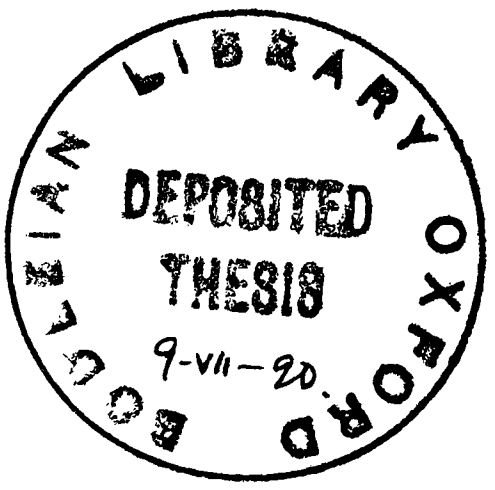
NATURAL CLASSIFICATION

AND THE REALITY OF HIGHER TAXA

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ABSTRACT

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NATURAL CLASSIFICATION AND THE REALITY OF HIGHER TAXA

Many generations of taxonomists have struggled with the self-appointed task of constructing a 'natural' classification of biological organisms. Advocates of the cladistic school of classificatory methodology have in recent years made insistent claims that the cladistic method of phylogenetic reconstruction provides the sought-for, unique, natural classification. Especially, they have claimed that the taxa delineated by cladistic methodology are of radically different status from other kinds of taxon. Adopting and extending a philosophical innovation which categorizes biological species as individuals rather than classes, they assert that cladistic taxa are 'real entities', and other kinds of taxon merely 'subjective' or 'convenience' classes whose existence should not be recognized in formal classifications.

Having outlined the present situation as regards rival taxonomic philosophies, and some of its historical background, the thesis examines this attempt to recategorize taxa as individual-like entities, and finds it wanting. The properties of species which render them regardable as individuals do not readily extend to more inclusive levels, or, if they do, are not readily restricted solely to cladistic taxa. Cladistic systematization, in moving away from the notion of a taxon as a class of similar entities, may cease to convey the information expected of a classification system. The practice of biology requires a more flexible and more stable taxonomy than can be provided by strict adherence to cladistic rules, and taxa are better regarded as 'historical classes', delineated neither by pure unanalysed similarity nor by logical transformation of hypotheses of phylogenetic relationship, but by a considered pragmatic synthesis of the two, employing the notion of convexity as a criterion of acceptability.

Parable

There was once a philosopher of that school called the Cladists; and a young man came to the philosopher and said: "Sir, tell us of the diversity of living things." And the philosopher pointed to a tree and said: "The Tree of Life is an individual, for it is an unique instance of the action of Nature. Its diverse branches are also individuals, for they are objectively delineated segments of the genealogical nexus." The philosopher then took a knife, and cut off a branch from the tree. "This cut" he said, "signifies Synapomorphy, for it divides off a natural taxon." The young man took the branch, and cut off a twig. "So this also is a natural taxon," he said, holding up the twig which he had cut off. "Of course!" replied the philosopher. "And what of this one?" asked the young man, holding out the branch from which he had cut the twig. "That" said the philosopher, "is unnatural and subjective. It does not exist." The young man scratched his head, and then with the knife he made himself a staff of the branch, and took it with him to lean upon. "For something that does not exist," he said, "it carries a lot of weight."

from "The Philosopher's Tail"

by J. H. Marshall (1987)

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Unapologetic Apologia

Theoretical problems seem inevitably to have turned into philosophical problems. I am a zoologist by education, not a philosopher, and much of this thesis therefore represents a somewhat tentative exploration of unfamiliar territory: for inadequacies in philosophy I can only crave indulgence. However, I make no apology for attempting such an exploration, for

> the growth of understanding can be just as luxuriant in the shadowy hedgerows between fields of enquiry as it is in the virgin soil at the frontiers of knowledge.

Nor do I apologise for conducting my discussion from a definite standpoint: the reputation of Oxford zoology rests partly on "work of unabashed advocacy" (Dawkins 1982:1). I have tried to provide an antithesis to some theses of contemporary cladistics, which might contribute to an eventual pragmatic synthesis between phylogenetic and traditional taxonomy; otherwise, I might reluctantly claim to have supported cladistics by failure to refute it!

CHAPTER ONE

*

INTRODUCTION

*

Classification and Perceptions of Naturalness

"Things are similar: this makes science possible. Things are different: this makes science necessary."
Levins & Lewontin (1985:141)

"Nothing can happen in the field of animal taxonomy to rouse our concern."
Douglas (1966:73)

$ 1.1 Classification and the Problem of Naturalness

Classification can be broadly described as the sorting of things into groups, whose members possess some kind of attribute in common (Pratt 1977). The process of classification simplifies any complex assemblage by allowing that not only identical entities, but those which are similar, may, in at least some respects or for some purposes, be treated as equivalent (Rosch & Lloyd 1978). The result is a more or less ordered information system - a classification - devised for the use of those with an interest in the information contained, thus reduced to manageable proportions (Ivanovskiy 1977, McArthur 1986), by encapsulating generalizations concerning the members of groups or classes. Such ordering of knowledge is fundamental to science, indeed, to thought itself (Humphrey 1984, Atran 1985).

> A classification is a systematic set of classes, a class being regarded as a conceptual grouping of things ... by virtue of particular resemblances that in some way or other associate them together.... We cannot think about the world ... unless we divide it into classes. Needham (1979:3)

Certainly, for biology perhaps even more than for many other areas of research, it has always been one of the most basic scientific concerns, as

> the mode of classification adopted gives any study its basic categories and thus structures it at the most fundamental level of all. Pratt (1977)

> Conceivably a system of nomenclature might exist that would be independent of classification. Such a nomenclature would supply a name to each individual. As soon, however, as we assert that certain individuals are essentially alike, ...we are linking nomenclature with taxonomy. Swingle (1934)

Taxonomy (from the Greek taxis arrangement + nomia principles) is the science of classificatory method and of classifications and their categories.

In considering the classification of the natural world, two questions

in particular arise. Firstly, are there 'natural kinds' to which the class-concepts which we delineate correspond? Secondly, is there a single correct classification?

The ultimate basis for the notion that there might be natural categories, and the search for them, is surely our persistent perception of discrete and apparently objective groupings (cf. Atran 1985). Even the most primitive of human languages have words for different kinds of animal and plant, and more than one modern scholar has sought enlightenment concerning the problem of natural classification by investigating the class-concepts implicit or explicit in the vocabularies of the world's peoples (Diamond 1966, Gould 1979, Briggs & Walters 1984:255). It was from this starting-point that the first attempts were made to outline the underlying criteria for the scientific distinction and delineation of biological groups.

> The method then that we must adopt is to attempt to recognize the natural groups, following the indications afforded by the instincts of mankind, which led them for instance to form the class of Birds and the class of Fishes...
>
> Aristotle **de Partibus Animalium** I 643b [tr. Ogle (1912)]

Aristotle himself did not apparently construct a classification of animals (hence the difficulty of reconstructing it from his biological treatises): partly, perhaps, because he was more interested in collecting examples for discussions of causality; partly, perhaps, because his biological work was left unfinished (hence possibly some inconsistency of the latter with his philosophical work on categories)(Atran 1985, Balme 1987, Temple 1988). Even so, the untutored instincts of mankind have in many instances got considerably beyond the class of Birds and the class of Fishes: much work in folk classification or 'ethnozoology' has focused on the sophisticated systems of vernacular names which are found in the languages of various hunting tribes. Such 'pre-scientific' peoples have an

intimate knowledge of the bewildering diversity of nature which surrounds them, and frequently recognize a large number of categories, sometimes including sibling species so subtly different as scarcely to be separable by the professional taxonomist, often organized, or at least organizable, into sets of varying inclusiveness in the manner of formal taxonomy. Comparison with the categories of scientific taxonomy reveals some considerable degree of congruence.

> Objective biological discontinuities recognised by primitive man are, for the most part and with explainable exceptions, identical at some level with those recognised by western science. Berlin (1973)

Here some have seen grounds for affirming the existence of natural kinds: the consensus is an indicator of the objective reality of groups which are consistently perceived by observers of nature.

> I believe that these findings... can be interpreted as support for the view held by the few remaining conservative taxonomists concerning the 'reality of species'* and are contrary to the relativistic position I once espoused myself (Berlin et al 1966). Berlin (1973)

Not only species are at issue; folk taxonomies often recognise groupings corresponding to supra-specific taxa, even if the level at which the systems correspond is variable: Navaho 'genera', for example, match up to Linnaean families (Morris 1979). Berlin's argument could thus also be interpreted as giving affirmative answers to both the questions of natural classification, supporting 'taxonomic realism' at one or both levels - the reality of higher groups, and of a single natural classification, towards which our perceptions converge.

Some have minimized the comparison on the grounds that the Linnaean hierarchy itself is simply another folk taxonomy:

---

* In fact, probably rather fewer biologists now regard the species as a purely artificial unit (though how they do regard it is still a matter of contention [Rosenberg 1985 ch.7]: see also ch. 2).

> The initial discoveries in the modern era that extensive and precise taxonomies exist among illiterate primitives originally occasioned surprise bordering on incredulity in some quarters. But it is increasingly recognised that the similarity to Linnean taxonomy of the folk taxonomies discovered by ethnographers and ethnobiologists need not cause surprise, since Linnean taxonomy is simply that particular folk taxonomy with which Western Europeans are most familiar. Kay (1971)

Kay sees the Linnaean system as merely making formally explicit the taxonomic principles implicit both in primitive taxonomic systems and in the vulgar taxonomies of the European languages, which themselves represent universal principles of classification and nomenclature. The correspondences are then not between an ideal scientific taxonomy and various imperfect folk systems but between more or less sophisticated folk taxonomies of the same relative standing. Berlin's hope that:

> correspondences... might reveal aspects of the natural world which are in some sense 'natural' and which are apparently perceived as the same by persistent observers of nature everywhere... Berlin (1973)

is only half borne out - the correspondences reveal the similarity of the 'persistent observers of nature', but not thereby the similarity of the 'aspects of the natural world' they are observing. Rather than telling us anything about the external reality of species or higher taxa, as Berlin claimed, comparison of the findings of biosystematics and ethnography reveals only universals of human mental structure (cf. Briggs & Walters 1984:256).

This conclusion still stands even though Linnaean taxonomy is better regarded as qualitatively different from folk taxonomy. Kay's presentation would not be happily accepted by most scientific taxonomists, who would deny (possibly vociferously) that they were simply applying the principles of folk taxonomy, in however sophisticated a manner. Anthropologists (e.g. Kesby 1979, Rambo 1982) agree:

> The many-tiered, refined Linnaean taxonomy is unusual to the point of uniqueness. Kesby (1979)

It is not simply a matter of the obvious difference between the maximum of around five ranks in the hierarchies of folk taxonomies (such as that of the Rangi people studied by Kesby, or the Tzeltal studied by Berlin) and the twelve to twenty or more discriminated by professional taxonomists. Ellen (1979), in criticizing comparisons such as that of Berlin (1973), points out that the imposition of the taxonomic structure of Linnaean systematics on folk systems is often inappropriate, as the actual structure of classifications can vary very widely, and need not conform to the framework of the taxonomic hierarchy with bounded units in a relationship of hierarchical inclusion (cf. also Conklin quoted in Rinnert 1979, Kemp 1985a, David Nash, pers. comm.), even if such a classification might be the most semantically informative (Johnson-Laird 1988:241, 246; Mickevitch & Platnick 1989). Here Ellen reaches a fundamental disagreement with the entire thrust of Kay's paper, which tries to show that 'taxonomic structure' is universal.

Yet the problem with Berlin's comparison is that it need not mesh with external biological reality at all. Whether Linnaean taxonomy is placed alongside or above folk taxonomies, the comparison itself will not contribute to an assessment of the objective reality of taxa. If the Linnaean taxonomy is taken as an absolute against which folk taxonomies can be measured, then the reality of scientific taxa would thus have been tacitly assumed, and the comparison merely assesses the ability of various peoples to recognise those taxa marked off as real by Linnaean taxonomists; such an assessment says nothing about the actual existence of those groups.

Moreover, the comparisons, especially at higher taxonomic levels, rarely bear close inspection: Navaho primary taxa such as na't'agi dinee and na'nagi dinee ('flying people' and 'crawling people') have no taxonomic equivalent, nor do many English vernacular 'genera' such as 'moth', 'fly', 'mushroom' etc. (Dupré 1981). As Briggs & Walters (1984) remark:

> Correspondence between folk names and 'Linnaean species' is especially close with higher animals, less close with angiosperms and relatively poor with 'lower' organisms, whether animals or plants. Common sense dictates that 'any fool can recognise a tiger', but it does not follow that we should recognise, say, the several species of Hypericum from each other... Briggs & Walters (1984:256)

What are delineated are the readily recognizable groups:

> The species [or genera: see Berlin (1986)] in any one restricted geographic region ... tend to represent highly perceptually distinct discontinuities, Berlin (1978:17)

but where they don't, they are not recognized (Dupré 1981, Atran 1985).

Even Aristotle was aware that intuitively delineated taxa do not necessarily coincide with the apparently naturally existing groups which the careful and systematic observer may discern: there are, as he remarked, no common names for the taxa which he characterized as "blooded" and "bloodless" (de **Partibus Animalium** I 642b [tr. Peck (1961)]). There is a certain tension between 'those categories which naturally exist' and 'those categories which one naturally recognizes'. Can this tension be resolved? I return to the questions mentioned above: are there natural kinds; is there one correct classification?

Many systematic biologists have posed these questions in one way or another, and in one way or another many more have answered them, implicitly or explicitly. Some, making reference to the Divine order (e.g. Cuvier: Enç 1976) or, more recently, to the course of phylogenetic history (e.g. Hennig 1966), have answered both in the affirmative, asserting that there is one correct classification whose categories are determined by groupings which exist independently of the classifier (a position that Dupré (1981) calls 'taxonomic realism'); others, making reference to the blurring of boundaries consequent on continuous gradual evolution, or to a more general nominalist philosophy, have answered both negatively, asserting that our categories are purely subjective impositions on the world, and therefore

that classifications can never have grounds for being considered uniquely correct: they can only be optimal (which I suppose might be called 'taxonomic nominalism').

Arising from this dichotomy, there is a deep ambiguity, in a biological context, of the term 'natural'. Advocates of a particular systematic philosophy often show a tendency to define 'naturalness' so that it coincides with what they consider as 'usefulness' (unless they reject the term as altogether too ambiguous - thus Ridley 1986, Ax 1987 - or stoutly assert that their classifications are artificial but none the worse for that - as does Charig 1982)(see §3.1 for further discussion of uses of the term 'natural'). The significant breach is between those who treat naturalness as an 'objective' reality, pertaining to the outside world, and those who treat it as an operational or 'subjective' term, pertaining to language and cognition*. Those who take the latter view often equate 'natural' with 'general' classification (Gilmour 1940, Heywood 1964, Stace 1980, 1989).

A **general** or 'general-purpose' classification is frequently defined as one in which members of classes possess many attributes in common, and a **special** classification as one based on a few attributes of special interest for a particular purpose (Gilmour & Turrill 1941, Berlin et al. 1966, Stace 1980, 1989). In the taxonomic debates of the eighteenth and early nineteenth centuries this distinction underlay the split between so-called 'natural' taxonomists (systematists) and 'artificial' taxonomists+

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* The distinction is characterized by Ruse (1987) as being between Aristotelian and Lockean philosophies of natural kinds.

+ The most famous 'artificial' taxonomy was the Sexual System of Linnaeus, which divides plants into classes by the anatomy of their female floral organs, and then into orders by that of the male. Aristotle, incidentally, recommends 'natural' classification (de **Part. Anim.** I 643b [tr. Peck 1961]):

> The proper course is ... to take the animals according to their groups ... marked off by <u>many differentiae</u>.

(methodists) (Kirby & Spence 1826). Another, somewhat similar, distinction may be drawn between **monothetic** classification, in which at each level the classes are based on a single feature common to all members, and **polythetic** classification, in which classes are formed whose members possess at least some of a number of features in combinations which may be disjunct or overlap between classes (Sokal & Sneath 1963, Sokal 1966, Needham 1979, Greig-Smith 1980; compare 'cluster-concept' of philosophers q.v. Kripke 1980).

Simple taxonomic controversies arise wherever there is a conflict between two or more proposed classifications - in other words, where two attributes or groups of attributes produce special classifications which are incongruent, i.e. incapable of simple conflation into a single more general classification. Such problems are not restricted to biological classification - the librarian is familiar with the problem of choosing between principles of classification in order to reduce complex relationships of similarity to a manageable number of dimensions (Broadfield 1946). The librarian's aim, however, is simply a usable or useful classification: no-one suggests that there might be a "natural" way to classify books. Adherence to the Dewey or Universal Decimal Classification is purely by convention, for convenience.

It is because of the supposition that there might be a classification uniquely correct in its categories that the problem of resolving taxonomic incongruity assumes particular importance. Sometimes resolution is to be sought at the level of empirical observation; the more widespread and fundamental debate in systematics arises from the conflict between general principles of classification and methods of resolving taxonomic conflict. The search for criteria which will resolve incongruences to reveal the elusive natural classification has frustrated taxonomists ever since the

fourth century BC when Aristotle started the whole business on the shores of Assos and Lesbos.

The conflict between two notions of 'natural' classification, reflecting the diverse demands of objectivity and utility, has been traced by various writers, including Nelson & Platnick (1981), who illustrate it with a quotation from their predecessor, von Sachs (I expand the extract somewhat):

> Systematic botany, as it began to develop in the seventeenth century, contained within itself from the first two opposing elements; on the one hand the fact of a natural affinity indistinctly felt ... and on the other the desire ... of arriving by the path of clear perception a classification of the vegetable kingdom which should satisfy the understanding. These two elements of systematic investigation were entirely incommensurable; it was not possible by the use of arbitrary principles of classification which satisfied the understanding to do justice ... to the instinctive feeling for natural affinity which would not be argued away... But a new departure dates from Linnaeus himself, since he was the first who clearly perceived the existence of this discord... This state of things finally ceased [!] with the appearance of Darwin's first and best book ... in 1859. Garnsey & Balfour (1890)

However, "entirely incommensurable" appears an over-pessimistic analysis: presumably if we could satisfy our understanding of the nature of 'natural affinity', then we would have the possibility of fulfilling both criteria.

> Darwinian evolution opened up the prospect .. that the hierarchy of taxonomic classification might be adjusted to reflect [the] tree of descent. Bisby (1988)

Unfortunately, though, the application of Darwin's theory to classification is controversial: Darwin's own characteristically ambiguous suggestions (Kohn 1989) have been used as proof texts by various schools of thought (Ghiselin 1985b): there is no agreed Darwinian mandate.

$ 1.2 The Competing Systematic Philosophies

There is as yet no consensus as to the most appropriate method for producing a general zoological* classification, and the argument has sometimes degenerated into polemics or even politics, especially when dedicated advocates of the newer forms of taxonomy are involved (Ghiselin 1984a, Atran 1985, Hull 1985, Kemp 1985a). The dispute is usually of little direct concern to the 'person at the bench', and even less to the 'person in the field'; yet despite the sceptical lack of interest in systematics shown by much of the general zoological community, taxonomy provides much of the conceptual framework within which the study of biology is necessarily conducted, and philosophical shifts in systematics can significantly affect (and be affected by) the way in which biologists view their subject matter (Enç 1976, Patterson 1988).

The competing contemporary systematic methods and their accompanying philosophies+ offer alternative ways of dealing with the problem of taxonomic incongruence. I shall regard them as divisible into four basic schools, under the following names: evolutionary taxonomy, phenetics, cladistics, and transformed cladistics; and here append thumbnail sketches of the four.

---

* No plant now knew the stock from which it came
Andrew Marvell (in Wain 1986)
'The Mower Against Gardens'

Botanists have slightly different disagreements, as they do not always have the same kinds of problems, and I shall restrict my discussion to the debate among animal systematists unless the interest-value of examples and arguments outweighs my reluctance to delve into the tangled forest of plant taxonomy.

+ I exclude from present consideration the persistent but eccentric systems based on mystical, cosmological, or numerological principles (e.g. Kolisko 1977; see also Knight 1981, Nelson & Platnick 1981).

$ 1.2.1 Evolutionary taxonomy

> If a species ... is the result of a process [this] must be taken into account when we attempt to determine its likeness or unlikeness to other species. T.H. Huxley (1875)

> The recognition and delimitation of 'natural entities' implies a consideration of relationship and phylogeny. Maguire (1943)

Evolutionary taxonomy (occasionally called by various other names such as 'phyletics' [Stuessy 1987], or 'omnispective' [Blackwelder 1964] or 'eclectic taxonomy' [Minkoff 1983, Patterson 1988]) represents to some extent a continuation of the practice of taxonomy before Darwin's time, combined with a developing theoretical basis in evolutionary theory. The gradual incorporation of Darwinian evolutionary theory into the essentially typological Linnaean system produced a confusion as to what the aims of taxonomy actually were, but evolutionary taxonomists generally suppose that the most natural and most useful classification is one which reflects the course of evolutionary history and groups together organisms with a shared genetic heritage,* taking note of

> degrees of divergence, relative amounts of diversification and recency of common ancestry, etc. Hull (1985)

Evolutionary considerations tend to provide grounds for judgements of the relative taxonomic importance of similarities which might be used for the characterization of groups: grounds which will be to some extent **ad hoc** by necessity, owing to the unique situation of each taxon.

This fairly pragmatic method forms the basis of most standard modern

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* Although there has been some attempt to suggest genetic criteria which might provide a feature on which a monothetic classification might be based ('genes in common', 'inferred amount of shared genotype': Pratt 1972), they would be unlikely to provide uncontentious systems, for even had we the information, its significance is complex and not well understood (Joysey 1988, Knapp 1988) - for example, to inadvertently include a transposable element or proviral sequence in a genetic taxonomy would be like including characters of their tapeworms in a classification of mammals.

classifications, and its principles were expounded by Simpson (1945, 1951, 1961) and Mayr et al. (1953). However, Bigelow (1956) drew attention to an incongruity in Mayr's and Simpson's presentation of the principles underlying the 'new systematics' of the 1950s - an incongruity between their often explicit ideal of 'monophyletic' classification based on recency of common ancestry, and their actual tendency towards a largely pragmatic classification which in many cases appeared to give the priority to simple overall similarity (see also Michener 1957, Ehrlich 1958). This plurality of criteria, though carefully acknowledged and expounded by Simpson (1961) and (more adequately) by Mayr (1969), seemed to jeopardize the coherence of the resulting taxonomy: many neo-Darwinian systematists sought greater 'objectivity' for taxonomy as a science, mistrusting the tendency of traditional taxonomists to treat it as an art, relying on intuitive judgements and a conventionalist approach to taxonomic consensus. Seeking independently repeatable methods, in order to be able to claim 'correctness' for their taxonomies, they moved toward two radically opposed positions, upholding either overall similarity or recency of common ancestry as the fundamental taxonomic criterion; so arose the phenetic and cladistic methodologies, the key texts of which are respectively Sokal & Sneath's "Principles of Numerical Taxonomy" (1963) and Hennig's "Phylogenetic Systematics" (1966 [Eng. ed.]). Proponents of both these methods (which might be described somewhat hyperbolically as 'non-evolutionary' and 'hyper-evolutionary' taxonomy) criticise evolutionary taxonomy for its reliance on the taxonomist's judgement and its lack of clearly stated principles, though the vast explosion of systematic debate has forced a much more careful and coherent exploration and exposition of evolutionary taxonomy by its adherents (e.g. Ashlock 1971, 1974, Mayr 1981, 1988, Stuessy 1987).

$ 1.2.2 Phenetics

> Cuvier's classification is purely morphological; it is an attempt to enunciate the facts of structure ... in a series of propositions of which the most general are the definitions of the largest groups. T.H. Huxley (1875)

The most basic criterion of the pre-evolutionary 'natural' taxonomists, grouping things together more or less closely according to the overall similarity of their appearance, is effectively inherited and formalized by modern phenetic methods, which are based on the principle of overall similarity. This principle aims to construct the most general classification by grouping together those organisms which are most similar, according to a quantitative estimate or coefficient of similarity, frequently making use of computerized techniques of cluster analysis, etc. The method was intended to achieve objectivity by its rejection of any kind of 'weighting' of characters thought to be biologically significant, i.e. by excluding any recourse to biological theory until a general-purpose classification had been constructed.

In fact, the method has been strongly and to a great extent successfully challenged (e.g. by Johnson 1970 and Pratt 1972; see also Kemp 1985a:144-145; Rosenberg 1985:183-186; Ridley 1986). It is practically impossible to make a totally objective choice between the various phenetic algorithms available, and in principle impossible to divide continuously varying characters non-arbitrarily, or to count the number of characters which an organism possesses. The 'objectivity' of phenetic classification, based on repeatability and independence from taxonomic decision, is thus, at least in part, illusory.

Such problems have led to the abandonment of phenetics as a systematic philosophy by most zoologists, although the techniques of numerical taxonomy continue to be widely used, particularly for classifications of

organisms with entirely obscure histories or many characters of unknown significance. In particular, phenetic methods seem to have lost much less ground in botanical taxonomy (Briggs & Walters 1984, Stace 1989), and also play an important role in the classification (for example) of bacteria (Austin & Priest 1986), or of units other than organisms (such as vegetation types: Greig-Smith 1980). They have also been more controversially adapted to provide phylogenetic data from the similarities between molecules, assessed crudely by immunological cross-reactivity or DNA hybridization, or in a more sophisticated manner by protein or nucleic acid sequencing techniques: there remain immense theoretical problems consequent on this inductive move, especially in the face of increasing doubt concerning the congruence of molecular and organismal phylogenies (see e.g. Joysey 1988, Sarich et al. 1989).

$ 1.2.3 **Cladistics**

> Whatever one may feel about Hennig's philosophy of classification, his elucidation of the role of characters in the reconstruction of the pattern of evolutionary trees (via cladograms), under the Principle of Divergence, is a major achievement. Friday (1987:64)

The cladistic method (also called 'phylogenetic systematics') represents a clarification and formalization of one of the chief tasks of the historical or 'diachronic' biologist: the process of phylogenetic analysis, which attempts to trace the chronological order of evolutionary branching events, and hence in large part the history of life, which is assumed to issue forth as a single, unique, non-overlapping hierarchical genealogy (Kemp 1985a). This is done by means of the logical assessment of **synapomorphies** - characters which are shared by two or more organisms by virtue, so it is deduced, of having been inherited from their most recent

common ancestor. Characters retained from earlier ancestors (symplesiomorphies or 'primitive' characters) and characters derived independently ('homoplasies' acquired by convergent or parallel evolution) or uniquely (autapomorphies) are ignored.

One of the central problems is the assessment of 'polarity' - the direction of the change between two character states which are supposed to have evolved one into the other - and a complex methodology, involving extrapolation from character distribution in related groups ('outgroups') or from ontogenetic sequences, has been elaborated in such detail by so many that I am reluctant to describe it yet again (see Hennig 1966, Wiley 1981a, Ax 1987).

This methodology is widely acknowledged as giving a firm logical basis to phylogenetic reconstruction, within the limits set by the availability of appropriate data (Martin 1981, Charig 1982, Kemp 1985b, Friday 1987, Mayr 1988), though it continues to have its critics. However, its proponents have met with rather more resistance to their contention that the sole duty of the taxonomist is the precise presentation of such phylogenetic branching patterns. If this were the case, then taxonomic categories would become, not indicators of any kind of morphological or phenotypic similarity or distinctness, but purely measures of recency of common ancestry (Barnes et al 1988): this would require that only holophyletic taxa - i.e. clades, containing all descendants of a common ancestor and definable in terms of synapomorphy (see above and $ 1.3 below) - should be accepted in classification (Wiley 1981a, Ax 1987). Most cladists thus effectively assume synonymy between 'phylogenetics' and 'classification', but the adoption of this assumption may prove over-hasty, as many biologists would, now that controversy has made the difference explicit, take a broader view.

> The problem of phylogenetic inference is separate from that of classification because there can only be one set of correct phyletic relationships, but there may be several classificatory systems depending on one's belief concerning the function of classification. Hecht (1976:335)

> Evolutionists [i.e. evolutionary taxonomists] regard production of classifications as a two-step process: cladistic analysis followed by analysis of divergence. Patterson (1982a)

> There are two distinct activities of the taxonomist which are often confused; one is the recognition of phyletic lines and their separation from one another at any moment in time, and the other is the grouping of these phyletic lines according to their 'natural affinities' to produce a natural classification which will show as far as possible the course of evolution in each group. Cain (1956:100)

This distinction between phylogenetics and classification is based mainly on the apprehension that members of a cladistic taxon need not actually exhibit the defining synapomorphy of the group: they need only have (hypothetical) ancestors which did so. This effective disengagement of the process of classification from the process of identification is fundamental to the evolutionary taxonomists' critique of cladism, and it is even beginning to be seriously suggested in cladistic circles:

> Hennig's "phylogenetic system" should be synonymized with "cladogram", not with "classification". Tassy (1988:52).

$ 1.2.4 **Transformed cladistics**

> In pattern cladist terms, the evidence for naturalness, or reality, of a proposed taxon is that all the members share characters otherwise unique to that group of organisms. Kemp (1988b)

The transformed cladistic method (or 'pattern cladism' or 'natural order systematics' [Charig 1982]) was developed in the belief that evolutionary classificatory methods (including Hennigian cladistics) are circular, in that they make **a priori** assumptions about evolutionary processes in order to analyse the observable patterns of diversity, and

then justify the evolutionary theories on the basis of the pattern. To avoid this apparent circularity, the aim of this school is to construct classifications by means of an analysis of the pattern of character distribution without any processual preconceptions (a disengagement of theory and classification shared with the phenetic approach). This is supposed to produce a taxonomy which does not force a particular evolutionary model (or perhaps even the concept of evolution) onto the user of the taxonomy (Patterson 1988), and so can be used in the Popperian manner in attempted falsifications of evolutionary theory. Rather than trying to define class membership on the basis of general or averaged similarity coefficients (the phenetic method), the pattern is treated as a set of discrete characters defining unique groups, in the manner of classical phylogenetic systematists (hence its claim to be a cladistic method), and the aim of the classification is a nesting set of homologies (in Patterson's usage coincident with the synapomorphies of Hennig, an apparent synonymy criticized by Ghiselin 1984a) which define classes operationally equivalent to holophyletic taxa (Patterson 1980, 1988).

In starting from the observable pattern rather than the hypothetical process, pattern cladism takes much the same empirical-cum-positivist approach to systematic philosophy as phenetics, but is much criticized for an inability to justify its method without implicit reference to the evolutionary assumptions it is trying to avoid.

> The time element is the very essence of monophyletic classification. Bigelow (1956)

The system of nesting sets which it produces lacks any kind of explanatory power:

> 'A system of homologies ... is in itself pretty mysterious. It is hard to see in what way it could be said that it explains or interprets the ... phenomena. It organizes them. But what is the role, and what is the nature of this organization?'[D.

> Sperber] In default of an answer to this question, we are open to the charge of having constructed a model without an object.
>
> Needham (1979:59)

> Patterson sees partial rejection of the evolutionary framework as a progression beyond Hennig ('transformed cladism'). One fears that this trend might progress to its logical conclusion, 'transcendental cladism', whose practitioners could proliferate branching diagrams oblivious of biological reality.
>
> Martin (1981:128)

The approach has been comprehensively discussed and to some extent conclusively dismissed by Charig (1982), Ridley (1986), Harré (1987), and Kemp (1988b)(see also Kemp 1985a, Dawkins 1988); but its concepts and arguments have become much confused with those of Hennigian cladistics, a confusion which continues to trap the unwary critic, and there is a tendency for writers who are not taxonomists to use the unqualified term 'cladistics' for the transformed (non-evolutionary) school (Grene 1983, Harré 1987, Peacocke pers.comm.). Charig (1982) and Ridley (1986) provide thorough disentanglements of the two.

$ 1.3 The Terminological Gordian Knot

> Technical phraseology is powerful ... for the propagation either of truth or error.
>
> W. Whewell
> History of the Inductive Sciences

> Debates concerning the theoretical basis of evolution are often couched in a strange language.
>
> Minkoff (1983:364)

Terminological wrangling has on occasion been a source of much amusement to writers on systematic biology and anguish to their readers (Boucot mischievously suggests that cladistics is nothing more than traditional taxonomy overlaid with an obfuscatory jargon), and the possession of its own conceptual vocabulary by each school of thought sometimes makes it difficult to conduct a discussion without either adopting the terms, and tacitly the viewpoint, of one school, or else

inventing yet another vocabulary with no partisan connotations. The latter course of action would in general be frowned upon as merely compounding the problem, were it not for the fact that many of the problems arise from the continued use of a single overt vocabulary by authors intending to express entirely different concepts and opinions. I shall, in the course of the following pages, make some feints towards the Gordian knot, with brief investigations of such words as 'natural', 'individual', 'stable'; but I should here like to go some way towards clearing the ground around a particularly tangled area: the problem of monophyly.

There is an exceedingly complicated history of the use of the term 'monophyly' and its counterparts, 'holophyly', 'homophyly', 'paraphyly' and 'polyphyly', to distinguish various types of biological group according to their phylogenetic implications (Turrill 1942, Ashlock 1971, Farris 1974, Eldredge & Cracraft 1980, Charig 1982, Meacham & Duncan 1987). (The difference is immaterial to phenetic taxonomists who do not take origins into account when delineating taxa.)

The notion of genetic unity is considered central to the notion of monophyly (Greek monos single + phylē stock, race), the contrasting term 'polyphyly' (Greek poly many) implying an assemblage of species of different lineage. Species (or organisms) included within a monophyletic taxon are supposed to have an ancestor in common. But of course, it is usually assumed that all species will share a common ancestor somewhere in the depths of their respective histories (Simpson 1961), so some qualification must be made such that more restricted taxa have more recent ancestors in common, and more inclusive taxa more ancient ancestors. Simpson (1961) defines monophyly in these terms:

> A taxon is monophyletic if it is derived from a single immediately ancestral taxon of its own or lower rank.

However, Simpson's formula, described by Turrill (1942) as the 'taxonomic' definition of monophyly, presents distinct problems. For one thing, it lends rather more significance to taxonomic rank than most taxonomists would find justifiable: categorical rank is usually accepted as a pure convenience rather than any kind of absolute statement about the nature of a taxon. Furthermore, it would allow into the classification groups which are widely rejected because they do in fact contain more than one lineage, albeit developed to some extent in parallel from related ancestors. Simpson was thinking mainly in terms of accommodating such well-established taxa as Mammalia, which he conceived of as containing fossil groups, as well as the ancestors of the present day mammals, which had arisen independently from different therapsid lines and achieved 'mammalness' in parallel (Kemp 1982:293-4, Benton 1988). However, his definition would also allow into the fold taxa such as 'Haemothermia', introduced by Owen to include birds and mammals, and controversially revived by Gardiner (1982), despite the almost universally accepted opinion that birds and mammals do not share a common ancestor closer than the earliest base of the reptiles (Kemp 1982, 1988b): the class Reptilia can be proposed as a single immediately ancestral taxon of equal or lower rank. Moreover, if Reptilia is accepted as a monophyletic taxon on similar grounds as Simpson's Mammalia, birds and mammals could then be derived not only from different reptile ancestors, but different amphibian ancestors, and by extension, different osteichthyean, or even agnathan ancestors, and yet still be classified into a monophyletic taxon.

Turrill (1942) contrasts Simpson's definition with another, which he calls the 'genealogical' use:

> A taxon is monophyletic if it is derived by descent from a single immediately ancestral species.

Most evolutionary taxonomists would accept something close to this. The

term 'ancestral taxon' thus comes to mean only 'the taxon containing the ancestral species'. Even in cases of hybridization or repeated generation of polyploids, the known mechanisms of speciation do not allow for the possibility of a taxon ranked higher than species actually being itself a direct ancestor (Wiley 1981a, Coomans 1983): 'derivation from taxon A' can in all cases be reduced (or expanded) to 'derivation from one or more species in taxon A' (see $ 4.6).

> If [the term 'monophyly'] be used genealogically, any group which has been formed by distinct lineages must be called polyphyletic. Turrill (1942:251)

The phylogenetic systematists, working on the basis of cladograms, in which all taxa are treated for the purpose of analysis as terminal (i.e. not ancestral to each other), proposed a much stricter definition of monophyly based on the nested sets of a cladogram: for cladistics, monophyletic taxa represent clades - discrete branches or subsets of a cladogram defined by a node representing a synapomorphy (and hence a (hypothetical) common ancestor), and including all the terminal taxa which are dependent upon that node (Hennig 1966, Wiley 1981a, Ax 1987). Any other grouping of terminal taxa is arbitrary from the point of view of cladogram topology, and is therefore simply regarded as non-monophyletic, and ignored or explicitly rejected.

Evolutionary taxonomists did not accept this stricter definition of monophyly, which they (after Ashlock 1971) and some cladists (e.g. Lorenzen 1985) termed 'holophyly' (Greek holos entire): they pointed out the important distinction between 'rag-bag' polyphyletic groups based on phenetic or arbitrary criteria (such as 'birds + bats'), and non-holophyletic taxa which are genetically related by descent from a common ancestor, but from which one or more particularly distinct subgroups have been excluded (such as the ape family Pongidae, from which humans and

their precursors are separated as Hominidae). The latter kind of taxon, characterized by a symplesiomorphic or 'patristic' character and termed 'paraphyletic' (Greek para beside: also 'false', because they may be erroneously regarded as holophyletic during phylogenetic analysis), is considered acceptable in principle in classifications by evolutionary taxonomists (Ashlock 1971, Eldredge & Cracraft 1980, Mayr 1981:514, 1988): some of the reasons for this will become apparent during the course of later discussion .

Transformed cladistics, in purging taxonomy of evolutionary assumptions, is forced to redefine monophyly entirely in terms of character distribution - monophyletic groups are those definable by at least a single exclusively shared attribute or group of attributes, which may be referred to a common ancestor, but need not be. This redefinition makes a nonsense of the etymology of the word, and is perhaps an example of a situation where it would be better to make up a new word than to confuse concepts by recasting an old one.*

Another attempted redefinition which I find fundamentally unsatisfactory is that of Oosterbroek (1987), who distinguishes two different types of paraphyletic group on the basis of their inclusion of the sister-groups of excluded sub-taxa, and purloins the term 'polyphyletic' for those which do not completely include such sister-groups. Such a reshuffling leaves no term for polyphyletic groups in the accepted sense: that is, assemblages of distantly related organisms, of distinct lineages, excluding their common ancestor. Its only advantage would seem to be that, in replacing ancestor-based with sister-group-based definitions, it enables cladists (including pattern cladists) to co-opt the

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* Some transformed cladists use 'natural group' in this sense, which begs a lot of questions to be discussed later.

terms and distinguish between different types of non-holophyletic group on a cladogram.

A more useful innovation is the term 'convex' introduced by Estabrook et al. (1976)(see also Estabrook 1978, 1987, Meacham & Duncan 1987, Stuessy 1987), which is equivalent in extent with 'monophyletic' in the broad sense in which it has been used by many evolutionary taxonomists, incorporating both holophyletic and paraphyletic taxa. A convex taxon is one which forms a topologically connected set on a phylogenetic tree. I shall postpone full discussion of this term and the implications of its use to a later chapter ($ 4.8): it has not yet achieved a wide currency, being both recent and unaccepted by most cladists as a valid concept (Wiley 1981b), since it cannot be properly applied to cladograms, but only to phylogenetic trees on which the status of nodes as ancestral species is less equivocal. The criterion of convexity is in effect equivalent to the criterion of acceptability used by many evolutionary taxonomists: a taxon must either be a clade (holophyletic taxon), or else be a clade from which one or more definite subclades have been removed on the grounds of significant (autapomorphous) dissimilarity (Mayr 1988).

I agree with Gould (1980a:112) that the distinction of paraphyly as a concept is important: I shall therefore regard 'holophyly' and 'monophyly' as synonyms, tending to favour 'holophyly', and prefer to distinguish 'paraphyly' rather than subsuming it in 'monophyly' **sensu** Simpson (or confusing it with 'polyphyly' **sensu** Oosterbroek). The important argument between classical evolutionary taxonomy and cladistics concerns the acceptability of paraphyletic taxa, not what they should be called.

$ 1.4 Naturalness Dissected

> The new classificatory systems that are destined to arise will be more natural, in the sense of more truly reflecting nature.
> J.S. Huxley (1942:411)

It is the stated objective of evolutionary systematists to discover and name taxa which have some objective basis in evolutionary history, and the aim of apologists for cladism to demonstrate that only cladistically defined holophyletic groups have such a basis. Wiley (1981a: ch.3) expounds this aim in terms of naturalness, which he carefully separates into three usages (the first three of various mentioned below, which I have distinguished by subscripts):

naturalness$_A$: (Aristotelean naturalness) - natural$_A$ taxa contain members which agree in characters embodying the essence of the group - such characters are necessary and sufficient for membership; the members of such a group may be expected to resemble each other in extra characters.

naturalness$_P$: (phenetic naturalness) - natural$_P$ taxa contain members that resemble each other more closely than they do non-members (thus also Sokal 1966, following Gilmour and the pre-evolutionary 'natural' taxonomists; cf. Heywood 1988).

naturalness$_C$: (cladistic naturalness) - natural$_C$ taxa consist of all the descendants of a single common ancestor, i.e. they are 'strict monophyletic' or holophyletic taxa, and correspond to **clades**.

He then gives a more fundamental realist definition:

naturalness$_R$: ("real" naturalness) - natural$_R$ taxa exist in nature independent of man's ability to perceive them.*

The thrust of the cladistic ontological argument is to equate

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* This, of course, begs philosophical questions of uncertainty about how we can know the world as it would be were we not observing it.

naturalness$_R$ entirely with naturalness$_C$ by demonstrating that holophyly is the only objectively existing taxonomic criterion, and that all other considerations of resemblance, whether in terms of overall or special similarity, are man-made and have no independence of the observer.

$ 1.5 Existence as a Taxonomic Criterion

> Ontological argument: ... argument from the nature of a concept to the existence of whatever instantiates it.
> Collins Concise Dictionary

In its strong form, cladistics claims for holophyletic groups an 'ontological priority' over non-holophyletic groups:

> Paraphyletic groups .. do not have an ancestral species in common only to them. Lacking individuality and reality such groups have no place in a classification intended to be a representation of nature's hierarchy. Brundin (1972)

> As many phylogeneticists have argued, only monophyletic groups **sensu** Hennig (1966) are natural groups with a real existence in nature. Wiley (1979:213)

> Strictly genealogical taxa have a different ontological status from other taxa. Patterson (1987)

Paraphyletic taxa (i.e. monophyletic taxa which are not clades) are non-existent, it is asserted (Patterson 1980, 1982, 1988), and cannot be "meaningful biological entities" (Wiley 1981a, 1981b); they are inadmissible to taxonomies, and as well as (or because of) being unreal, unnatural, non-existent, they are not definable, explanatory or predictive, as the heuristically superior holophyletic groups are.

> Paraphyletic groups have no reality in nature and their use ... is a major obstacle to progress. Bremer & Wanntorp (1978)

I have attempted not to become too entangled in the general debate concerning realism as a philosophy of science. I should like, from a broadly realist (?common-sense = ?woolly-minded) standpoint (cf. $ 6.1), to approach several questions concerning this claim of cladistics: what

'individuality' could mean in this context; whether cladistic methodology delineates the only 'real' groups of animals (or even delineates 'groups' at all); whether other natural biological groups can be recognised, named and used constructively in the business of biology; and whether a realistic approach to biology requires there to be a single general classification which accurately reflects some unique (hierarchical) structure in the outside world. As ontological priority seems more immediately powerful than some form of utilitarian superiority, I shall deal with existence claims (chapter 2) before returning to the theme of the function in biological theory of classificatory groups and of taxonomic language (chapters 3 - 5), and some practical consequences.

CHAPTER TWO

*

NATURALNESS AND INDIVIDUALITY

"Reality is that which, when you stop believing in it, doesn't go away." Dick (1985)

$ 2.1 The Individual Species

> It is a matter of logic to conclude [from the evolutionary insignificance of inter-specific hybridization] that the monophyletic species groups of nature's hierarchy have individuality and reality. Brundin (1972)

The argument over objectivity and naturalness in taxonomy has, perhaps unexpectedly, taken over and extended recent philosophical debate concerning the status of species as 'individuals' rather than 'classes' (as expounded by Brundin [1972], Ghiselin [1974] and others). Apologists for cladistics, such as Wiley, Eldredge, and Ax, assume that entities or individual objects have a better claim to biological 'meaning' or 'reality', and therefore to inclusion in taxonomies, than kinds or classes of similar objects,* and attempt to demonstrate that clades, as well as species, are individual objects and hence natural_R.

> Closed descent communities are not classes, and thus not the artificial product of Man's imagination. Instead they are real, individual-like unities of Nature with a historical continuity. Ax (1987:23)

Eldredge so argues in the context of his 'hierarchy theory', which proposes the 'individuality' of entities at various organisational levels below and above the organismal, of which clades form one level.

The supposition that species are real, i.e. actually exist in nature, was assumed by many pre-Darwinian taxonomists to make them necessarily eternal classes with immutable definitions, thereby implying the fixity of species:

> A **species** is a natural object whose differences from those most nearly related to it had their origins when it came from the hands of the CREATOR; while those that characterize a **variety**, have been produced since that event. Kirby & Spence (1826 iv:396)

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* Some kind of nominalist assumption about the non-existence of anything other than individuals seems often to be made.

(Note that 'related' cannot here mean 'genetically related', but carries some such connotation as 'related, or relatable, by the intellect', as in related concepts.)

The concept of the reality of species was therefore initially rejected by evolutionists along with that of their fixity (Darwin 1872). The subsequent neo-Darwinian position of Mayr and Simpson regarded species-populations as synchronic slices through a temporal continuum which could be divided only arbitrarily by palaeontologists (Simpson 1951:295, 1963, Cracraft 1979)*. Taxonomy was seen as possible only because present-day taxonomists work over such a short timescale, and with an imperfect fossil record:

> They who deny that such a thing as a species exists, concede nevertheless that a botanist or zoologist may reason as if the specific character were constant, because they confine their observations to a brief period of time.
>
> Lyell (1832 ii:2)

However, the empirical work of various recent palaeontologists has apparently supported the so-called 'punctuated equilibrium' view of

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* To cope with (or dispense with) the problem of continuity, cladistic methodology adopts the assumption that speciation must be regarded as occurring only by dichotomous division of a lineage (Kemp 1985a), the 'parent' species being considered extinct at the point of division in favour of two 'daughter-species' (Giray 1976, Ax 1987). This assumption has been strongly challenged, on the grounds that anagenetic speciation (change within a single lineage such that portions of the lineage differ as much or more than separate lineages) may be held to occur. Another strong possibility is the allopatric divergence of peripheral populations to leave a persistent parent species. Such speciation by 'budding' would result in a parent 'paraspecies' which may be quite distinct, but cladistically indefinable as not possessing any unique characters but only plesiomorphous character-states complementary to the autapomorphies of the daughter-species (Vane-Wright pers. comm., Buck 1986, Ackery 1987). At the species level this can be side-stepped on the grounds that species do not need cladistic definition (Ax 1987:23-4), but an analogous situation may arise with genera (see $ 4.5.1). There is obviously more to be worked out on the problem of species-continuity, but Ax (1987) does not succeed in making the cladist's choice of splitting events as determinative of species boundaries (thus equating them with lineages) sound any more than a methodological decision: his willingness to draw this principle out (following Willmann) such that two species which hybridize must also cease to exist, even should the two original populations continue, is almost bizarre in its implications (do parents become different people on the birth of a child?).

evolution (Eldredge & Gould 1972, Gould & Eldredge 1977), which proposes from the fossil evidence that species do not generally undergo constant gradual change but are stable over long periods, and evolve in (geologically) short bursts of relatively rapid evolution, usually by means of allopatric speciation, which produces a new species which may co-exist alongside an old one or replace it by invasion, rather than by sympatric or anagenetic evolution (Eldredge 1971, Cheetham 1986).

Support for this view of speciation varies, as does opinion on how much it really differs from the allopatric quantum speciation allowed for by the 'synthetic' model (Simpson 1944: it bears some resemblance to Berg's 'nomogenetic' theory of the stability of species under the influence of conservative selection and the absence of transitional stages between saltatively originating species [Berg 1926:406]. See also Borgmeier [1957] - apparently a saltationist - who emphasizes species-stability). The 'modern synthesis' of the mid-20th century had shifted from a view of species as groups of similar organisms towards the concept of reproductive species, which are seen as

> groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups. Eldredge (1986a)

Reproduction provides the mechanism of isolation between species and thus the biological world is spatially discontinuous both in terms of reproductive units and, as a natural consequence, in terms of adaptive phenotypic properties:

> Species came to be understood as dynamic reproductive units whose members tend to resemble each other more than they resemble members of other species. Species thus possess a source of internal cohesion, and seem to be real entities, rather than mere whimsically recognised collections of similar organisms. Eldredge (1986a)

The 'neontological species' is thus recognised as a real biological entity which exists of itself in the outside world.

The 'punctuational' view continued this development by analogical extension to the temporal discontinuity observed to exist between allochronous species. The gradualist assumption was of a slowly evolving lineage, a morphological continuum which could be empirically but arbitrarily divided by palaeontologists at stratigraphical discontinuities into chronologically delineated species (Simpson 1951). The emphasis of punctuationists on the interruption of long periods of stasis by rapid punctuational events leads to a picture of distinct stable reproductive communities succeeding one another (Eldredge 1986a, Eldredge & Gould 1988).

> We treat species as "real" units in nature, not as arbitrary elements in a continuum... This "reality" may arise from the conventional dynamic argument of direct interaction by gene flow..; it may also reflect the historical argument that unique, highly homeostatic systems arise during the genetic reorganization that accompanies speciation (thus preserving the basic character of a species even in the absence of gene flow among its demes). Gould & Eldredge (1977)

So the model treats species as coherent entities bounded in space and time, thus meriting application of the term 'individual'.

In fact, the idea of the species as an individual analogous to the organism, and suggestions towards a punctuational model of speciation, had been presented by J.S. Huxley in his book "The Individual in the Animal Kingdom" (1912):

> The existence of a species or race, a procession of similar individuals each descended from a previous one ... leads of necessity to the separation of two distinct kinds of individuality, one belonging to the race, and one to the persons that constitute the race. ...The first constitutes what I shall call species-individuality, or individuality in time, while the other corresponds to our ordinary notions of individuality and, if a special term is needed, may be called simultaneous or spatial individuality.* J.S. Huxley (1912:23)

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* By an over-emphasis of the species-individuality of which we are the parts, it is often said that our bodies are only 'cradles for our germ cells' J.S. Huxley (1912:24)

It is still said, but usually reflects over-emphasis of the sub-organismal rather than the super-organismal level (e.g. Dawkins 1976).

Earlier biologists such as Agassiz had toyed with the idea of species as somehow analogous to individuals (Knight 1981), or even as super-organisms in the manner of insect societies (Gerard 1958), though this was usually regarded as taking things too far.

> The species is not necessarily a particular kind of organism; the species is a kind of population. Camp & Gilly (1943:331)

The effective move of species from the philosophical category of 'class' to that of 'individual' which had been made by Huxley (1912)(and perhaps implicitly by Darwin (1859): Hull 1976) was re-emphasized by Brundin (1972) and Ghiselin (1974 etc.), followed by Hull (1976 etc.), and favourably received (if misinterpreted) by many as a correlate of the increasingly accepted punctuationist model of speciation. It attempts to avoid the problem of species definition by viewing a species not as a natural_A class of organisms grouped together on the basis of necessary and sufficient defining characters (which proves difficult e.g. in the case of sex, age or life-stage dependent differences within species), but as a discrete entity or individual with its own history. That species are in some sense 'individual' was perhaps already implicit in the shift from a 'typological' to a reproductive species concept, and the 'type' system of nomenclature became recognized as designating a name-bearer ('onomatophore') for a variable species, not as identifying a typical example of a class of object (Mayr 1942). Species are made up of components which do not necessarily share defining features but make up a spatio-temporally distinct whole which Ghiselin and others are happy to call an individual. These individuals have their own properties, such as a distinct origin and termination, which allow their construal as units of selection, capable of variation and natural selection in a way analogous to that of the lower selective levels of the gene and the organism (Eldredge & Salthe 1984, Vrba & Eldredge 1984, Vrba & Gould 1986).

$ 2.2 Hierarchy Theory and Higher Individuals

> There is an instance of scientific reflection when complex social wholes are considered as individuals of a higher order, or reversely when that which as a rule is taken to be an individual is considered as an organized community.
> Jeuken (1953:60)

This concept of the species has apparently proved relatively uncontroversial, and seems acceptable to many biologists (if not to philosophers; Ruse 1987). However, the hierarchical model of Eldredge & Salthe (1984) seeks to extend this concept of individuality to other groups in the biological world - to coherent ecological units at various scales, and to clades - i.e. holophyletic higher taxa in the genealogical tree:

> Each of these sorts of entities display the boundaries in space and time characteristic of individuals. Eldredge (1986a)

The 'hierarchy theory' as expounded by Eldredge & Salthe (1984; also Vrba & Eldredge 1984, Eldredge 1985, Vrba & Gould 1986) is a speculative conceptual framework for biology which sets out the biological world in two parallel but interlocked hierarchies - the genealogical and the ecological - arising from the two fundamental kinds of biological process - the reproductive and the 'economic' (Eldredge 1986b). Many of the ideas were anticipated in detail by earlier writers - the theme of hierarchy recurs throughout the history of biology (Barker 1976)*: especially, a conceptual scheme was laid out by R.W. Gerard (1958) and discussed at the 1957 Conference on Concepts of Biology by, among others, Mayr, Sewall Wright, and Simpson:

> We are smack up against the issue of the hierarchical organization of the world... A .. branching seems to occur in

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* In proposing analogies of individuality and selective processes at levels below the organismal, the model echoes the extension of Darwinian theory made by W. Roux ['Der Kampf der Theile im Organismus' Leipzig (1881); see J.S. Huxley (1912)] which sees selection and adaptation occurring at the cellular level (cf. Wright in Gerard 1958:139). It also accommodates the genetic selection models of 'selfish DNA' theory.

> the living domain, above the individual - one direction giving species and higher taxonomic groups; the other, family, community, and higher social systems. Gerard (1958:136)

The current exposition of the scheme was developed partly as a component of the new evolutionary 'synthesis' developed over the last fifteen years or so around the punctuational model of speciation (Eldredge 1971, Eldredge & Gould 1972), which some regard as beyond the capabilities of the neo-Darwinian synthesis to accommodate (Eldredge 1986a: but see Hecht & Hoffman 1986) and which seeks to disengage macro-evolutionary study (of speciation and large scale evolutionary history) from that of micro-evolution (morphological and genetic change at the population level). As well as its obvious direct importance to the study of evolution, the scheme potentially entails profound implications for classificatory philosophy, as in inserting 'monophyletic group' into the hierarchy of individuals it appears to represent a potential justification of cladistic classification on empirical grounds: cladistic taxa are 'really out there'.

The result of viewing not only species but higher groups as entities possessing 'reality and individuality' (as had already been insisted on by Brundin [1972: see also Patterson 1988]) is to render taxonomy a totally 'objectivist' enterprise. If higher taxa are not only theoretical constructs but entities with an actual external existence, then systematics cannot be seen as the classification of organisms into more or less inclusive kinds on the basis of observed similarities, but is the recognition of natural$_C$ groups as spatio-temporal entities. If individual reality is extended exclusively to holophyletic taxa, classification as an activity in biology becomes completely subsumed under phylogeny, with phylogenetic systematics being the only justifiable method (as stated explicitly by Eldredge [1986b] and Patterson [1988] and effectively practised by Ax [1985, 1987]: indeed, Ax [1987:8] wisely

refuses to call his cladistic 'systematization' a classification at all). This would render utilitarian criteria such as predictivity simply inappropriate, as such 'subjective' considerations pale into insignificance beside the objectivity of a 'real' classification. It does offer an uncompromising answer to the question of a correct classification, but threatens to remove direct consideration of similarity from taxonomy entirely, which removal not all would welcome (Charig 1982, Grene 1983).

One immediate problem is that the hierarchical model proposes two types of 'individual' or 'real' group: the genealogical and the ecological. This would seem to suggest that there are two sorts of real biological object - two objective ways of classifying organisms such that the 'groups' they fall into are individual entities with an independent existence in the outside world:

> If you classify the higher collective of individuals by criteria of derivation or origin, then you arrive at a super group of kinship ... If, on the other hand, you arrange the higher group of the collective according to the functional interrelations or living conditions of its members, you arrive at such units as the biotum or ecological niche, and so on. In both of these classifications you are dealing with groups which are on the same level, ... but the units are grouped according to different principles; one is a natural, ecological principle, and the other is a logical principle, which you have to reconstruct from studying the history. ... These grouping principles are not inherent in the natural systems. Weiss in Gerard (1958:185)

There thus remains a potential conflict between two kinds of $natural_R$ classification - but note that while Weiss calls the ecological one 'natural', in contrast to the 'logical' historical one, he does not seem keen to allow either principle inherent $natural_R$ status. Taxonomists who adhere to a strictly genealogical classification on the grounds that only holophyletic groups are real would appear to be challenged by the existence of real groups in the ecological hierarchy, if such there be. I shall have a little to say on ecological groups - a more immediate problem is a terminological confusion concerning the word 'individuality'....

$ 2.3 What is Individuality?

> An organized biological unit relatively independent of other units is considered a biological individual.
>
> Alfred A. Emerson (1939)
> quot. in Jeuken (1953:72)

It would seem necessary to investigate the concept of 'individuality' in this context, and the extent to which it is applicable to biological groups, both higher holophyletic taxa and ecological units. Eldredge & Salthe (1984) may have unduly extended the range of the concept under the influence of the cladistic dogma that only holophyletic taxa are natural, and there is arguably a distinct difference between species (which may be considered as the operative units of taxonomy) and higher taxa, which difference does not allow one easily to regard anything said of species to be "a **fortiori** true of higher taxa" (as Eldredge would have it: pers. comm. 1986, contrary to Eldredge 1971). Certainly the extension, though strongly asserted by Ax (1987) and Patterson (1988), is not supported by Hull (1976), by Splitter (1982), or even, without heavy qualification, by Wiley (1979, 1981) or Vrba & Gould (1986)*.

The attempt to discover criteria by which claims to individuality may be assessed runs into the common difficulty of a word with different meanings in different contexts (Ghiselin 1984b). 'Individual' is a word which may have identical meanings in philosophy and in biology (as, for example, when used of a particular human being), but the range of concepts over which any word's use may extend is dependent on the paradigmatic system or conceptual framework in which it is used - it changes its relationship with words adjacent or opposed in meaning - and the

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* Vrba & Gould (1986) speak explicitly of individuality only for genes, organisms, and species, which they regard as 'entities acting as evolutionary individuals'.

implications of the concept indicated in one field may not carry unambiguously into another. In particular, it may not be the case that the individuality proposed by Ghiselin (1974) is the same as that accepted by Eldredge & Salthe (1984). 'Individual' in the sense of 'organised whole' (see Emerson as quoted above) is so ostensibly a feature of the organismal level of the hierarchy and part of the biologist's basic vocabulary, that it tends to obscure the weaker and more general sense of 'individual' as 'unique referent' or 'particular', the philosophically important contrastive term to 'class' which Ghiselin is apparently concerned to emphasize; and the vagueness of the term 'spatio-temporal continuity' exacerbates the problem. There develops a tendency for biologists and philosophers to talk at cross-purposes, not made wholly explicit in Rieppel's (1986) critique or in Jeuken's (1953) historical study, and leading to Wiley's arrangement of referents into:

> Classes
> Historical entities
> Individuals Wiley (1981a)

which Ghiselin, with no more explanation than the briefly dismissive remark

> it seems to me that the following arrangement is more satisfactory

amends to:

> Classes
> Individuals
> Historical entities
> Integrated wholes Ghiselin (1984a)

If for the moment we take Ghiselin's arrangement as a working scheme, there are two different types of individuality which might be claimed for higher taxa, and the claims will require different criteria for their assessment.

> Among those actual or potential aggregates which meet the criteria of being entities there are some which meet the further and specific criteria of being organic systems.
>
> Campbell (1958: 15-6)

I shall first deal with the claim of higher taxa to be individuals in the sense of organised systems or integrated wholes ($ 2.4)(though I believe few would argue that they were), and then ($ 2.5) investigate the difference between class and 'historical entity' status.

$ 2.4 Taxa as Integrated Wholes?

> Groups [i.e. systems] as entities do not have an epistemological status different from such middle-sized entities as stones and rats, but are apt to be fuzzier, less discrete, less multiply confirmed, and in this sense less real. Campbell (1958:14)

What criteria appear suitable for assessing individuality in the sense of organised entity? What makes us consider an aggregate as a single system? Comparison must be made between putative entities and undisputed exemplars.

> We have evolved in an environment in which the identification of certain middle-sized entities was both useful and anatomically possible. Campbell (1958:17)

> When we want to check on existence, bodies have it over other objects on the score of their perceptibility.
> Quine (1969a)

The most obvious example of a biological individual would seem to be the organism (cf. Rieppel 1986:286), although even this is not as straightforward a supposition as it might be; the problem of apparent levels or orders of individuality was appreciated by the Victorians:

> A zoological individual is constituted either by any single animal as a mammal or bird, which may properly claim the title of a **zoon**, or by any such group of animals as the numerous **Medusae** that have been developed from the same egg, which are to be severally distinguished as **zooids**. Spencer (1864:73) quot. OED

> The term 'zooid' [is] intended to suggest that they are like individuals, and yet are not individuals, in the sense that one of the higher animals is an individual. Huxley (1851:15) quot. OED

Haeckel felt a need to introduce the concepts of 'morphon(t)' and 'bion(t)' to apply respectively to morphologically and physiologically individual (indivisible) units (paralleling later definitions of the species). The notion which seems central is a certain kind of 'indivisibility', that which modern philosophers call 'spatio-temporal continuity' (Wiggins 1980) and which J.S. Huxley (1912:25) calls a 'minimum conception of continuance'. Basically, an individual must have some kind of spatial and temporal coherence as a unit, and distinctness from other such units, a combination I have termed 'discreteness'.

$ 2.4.1 Space and Synchronic Discreteness

The first act of existence is the taking possession of space.
Le Corbusier

The most obvious property of human organisms as paradigm individuals is spatial coherence - they can usually be regarded as discrete entities with a coherent and continuous boundary. They are also generally discontinuous with other individuals, and do not spatially overlap with them. Nevertheless, while internal continuity seems to be a basic feature, the 'non-overlapping' criterion of discontinuity seems by contrast to be rather fuzzy. For humans, at least, individual overlap is rare though it seems to occur in Siamese twins - it could be held to occur in mammalian pregnancy as the mother and foetus maintain an imperfect inter-organism boundary at the placenta. For highly colonial animals, however, the boundaries of any individual may become difficult to determine, and while it remains clear that there are several countable individuals present, they are spatially continuous, and there are regions where it might be correct to regard two overlapping individuals as being present. So it would seem that the

taxonomic criterion of delineating non-overlapping groups, whatever its other justifications, does not originate as a necessary reflection of an empirical discontinuity between 'individuals' at a given hierarchic level, because such discreteness is not always exhibited by organisms.* (The same problem arises at the level of the gene, where individual genes may overlap each other [Lewin 1983:60; Falk 1986], and at that of the community [Austin 1985].) While the axioms of taxonomy require that the world be divided into non-overlapping taxa (and convention demands completeness at the levels of species, genus, family, order, class and phylum), it may in fact turn out that the world can no more be unambiguously divided into a countable number of species than into a countable number of organisms.

> If absolutely discrete boundaries are required for individuals, then there can be no individuals in nature.
>
> Hull (1976:185)

(One is even tempted to suggest that since natural entities have this bemusing tendency to blur at the edges, the exact definability of cladistic taxa militates against their being considered such.)

The analogy used by Ghiselin of a company as an individual points up the fact that spatial contiguity is not required of a coherent individual system: the National Westminster Bank is spread in little bits all over the country, but the telephone lines and computer links maintain the whole as an integrated system.+ J.S. Huxley similarly allows for multiple 'corporate individuals' in his model:

> A man can very well be at one time a member of a family, a race, a club, a nation, a literary society, a church, and an empire. 'Yes, but surely **these** are not individuals,' I seem to hear my

---

* The situation is unfortunately confused by the fact that the constituent 'individuals' in colonial animals are frequently clones.

+ When the Natwest's computer breaks down, the whole no longer functions as a system, but it may be reconstituted without forfeiting continuity, passing in the meantime through a period of different status - perhaps 'historical class' status (see §2.9) - cf. perhaps myxomycete colonies.

> readers' universal murmur ... they **are** individuals ... the tendency towards the formation of closed systems has manifested itself. J.S. Huxley (1912)

Yet all but one of these are system entities whose components interact with each other (the exception being 'race', a biological category with the same mixture of similarity and ancestry relationships as a taxon). The same might be said of ecological communities of various sizes up to the biosphere (again a suggestion made by Huxley), but it could by no means be said of (e.g.) Mammalia, or of any higher taxon, holophyletic or not.*

It might here be noted that the status of ecological units is decidedly controversial: the influential 'individualistic hypothesis' (of Gleason; see Austin 1985) supposes that the components of ecological patterns are unique in their structure and composition and that a rigid typology of communities is therefore impossible, but many ecologists are wary of the suggestion that communities may be seen as individuals in the sense of discrete integrated wholes:

> To consider the community homologous with an organism seems an overstatement of the integrity of the community. In the living world the degree of organization decreases from cell to organism to population to biocoenosis. Daubenmire (1968:243)

In fact, the individualistic hypothesis, that each species is distributed in its own way, and so that no two species have like distributions, tends naturally to be linked with the concept of the ecological continuum,

> in antithesis to the community-unit theory which stated that plant communities are natural units of coevolved species populations forming homogeneous, discrete and recognizable units. Austin (1985)

The debate among ecologists concerning the appropriateness of continuum or community description of ecological patterns continues, but from it transpires the observation that individuality and uniqueness are not by any means the same thing.

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* Except, trivially, of contemporary monotypic taxa coterminous with a species, such as the family Ornithorhynchidae (platypus) or the order Tubulidentata (aardvark).

$ 2.4.2 Emergent Properties

Emergent properties are those properties possessed by an organized group or whole which arise from its higher level organization and are not the simple result of the sum of the properties of its components (Barker 1976). Do higher taxa have emergent properties? Group properties actually fall into two categories (Vrba & Gould 1986) with different implications:

(i) aggregate properties, which are in some respect simply the sum of the inherent characters of the members (e.g. colour in any species is the aggregate of the colour of its constituent individuals; genotype in a human individual is the aggregate of the genes of its constituent somatic cells [Vrba & Gould 1986:218]);

(ii) emergent or organizational properties, which arise from the organization of the constituents (e.g. tissue structures are emergent from cellular organization, population structures from organismal interactions).

(The presence of organization also implies a third type of property: those properties of the constituents which are derived from their group relations and which they therefore cannot possess independently of the group (e.g. family relationships, social hierarchies)[Harré, pers.comm.]).

Aggregate properties are possessed by various kinds of particular aggregation merely by virtue of aggregation: they are class properties. Kemp (1985a) refers to size, rates of origin and of extinction as possible emergent properties of clades, but these are aggregate properties, and would not seem to justify treating clades holistically in a way inapplicable to other aggregations of organisms. It may be possible to talk of groups such as the dinosaurs and the synapsids competing as units, but the units are defined not by their genealogical coherence (both, be it noted, are paraphyletic) but by their 'behavioural consensus' - their common fate. Does common fate characterise taxa as individuals?

$ 2.4.3 Causality and Common Fate

> Elements that move together in the same direction, and otherwise in successive temporal observations share a 'common fate' are more likely to be perceived as parts of the same organization.
> Campbell (1958:17-8)

Common fate is important to the question of individuality mainly because of its role as an indicator of causal relevance. Yet perception of an 'organization' (see quot. above) is not enough to guarantee perception of an 'individual'. For common fate, like emergent properties, can be split between the aggregate and the relational.

An organized individual is characterised by internal relational properties, and the consequent common fate arising from interaction and/or interdependence between components. (So, for example, all the cells in my body move together in roughly the same direction.)

Aggregate properties, including the legacy of a shared history, result in a more contingent common fate arising from similarity. Common fate may indicate not a causal effect of the group on its members, but a statistical effect of the members on the group (Vrba & Gould 1986:220).

In the context of evolutionary process, statements such as the following are made:

> Whereas, natural selection operates upon individuals within populations, a process that can be termed **species selection** operates upon species within higher taxa, determining statistical trends. Stanley (1975:648)

However, the portentous little phrase "operates upon species **within higher taxa**" appears on inspection to mean less than it might. It is introduced as if higher taxa are to be regarded as units with a role in species selection analogous to that of the population in individual selection, but no such analogous role seems to exist. The importance of the population for individual selection is that it represents the genetic pool, the

bounded system of informational interchange between individuals. No such systemic interaction is seriously proposed between species in a higher taxon: Stanley himself tends to treat macroevolution simply as a description, not an explanation involving causal mechanism (Stanley 1979: 192). The analogy does not extend to a demonstration of the functional 'reality' of higher taxa which is, as it were, subliminally suggested. There is a sense in which membership of a higher taxon implies a constraint on the adaptive and evolutionary potential of a species (canalization: Brundin 1972), but this is a historical constraint, not a systemic constraint derived from interaction. Such constraint results in a common fate mediated by (historical) similarity; such similarity might be held to delineate a class.

$ 2.4.4 Time and Diachronic Discreteness

> The very idea of species...is inherently imprecise.
> Ellen (1979:3)

The uncountability of entities at the species level which I have suggested above ($ 2.4.1) is, of course, exactly what palaeontologists such as Simpson confronted in the problem of chronospecies or palaeospecies -

> an unhappy attempt to impose a taxonomy of discontinuous groups on a continuous series. Cain (1956)

It is the discrete locatability in 'morphological space' of most contemporaneous species that convinces of their reality (cf. $ 1.1) and the fuzziness of the boundaries that convinces of their mutability (Darwin 1859). Their temporal discreteness would require an analogy to the fission of reproducing organisms; this, punctuated equilibrium theory seeks to provide. An individual has a discrete beginning and end; this is extended to species by the punctuational stasis model, and the same unique beginning

is shared by all subsequent descendant clades. A monophyletic (holophyletic or paraphyletic) taxon thus differs from a universal class in that it has a historically unique starting point. Even this may not necessarily be a very discrete event - speciation is rarely conceived to be instantaneous, even by punctuationists, whose reluctance to be linked to macromutational or other saltative mechanisms of speciation has led to doubts as to the content of their theory. Indeed, some well known taxonomic tangles arise from apparently incomplete speciation. However, the gradualness of origin does not itself detract from the status of species as individuals (Rieppel 1986). The tracing back to a speciation event - to a founding ancestral population - is the fundamental meaning of 'monophyly' ($ 1.3), and it could even be proposed for hybrid species, which originate in a single event.

Yet this 'temporal locatability' is in a way one-ended. An individual organism may die while some of its constituent cells are still alive; an individual species may 'die' while some of its constituent organisms are still alive (e.g. as isolated males in zoos); - but a higher taxon (whether holophyletic or paraphyletic) 'dies' if and only if all of its constituent species die (cf. Raup 1975, Sepkoski 1987). Its temporal bounding is entirely equivalent to the sum of those of its constituent members and it does not differ in this respect from any arbitrary group of species.

$ 2.5 Extinction and Pseudoextinction

The attempts of macro-evolutionary theorists to deal with clades as units result in the categorical separation of clade and non-clade taxa when discussing extinction.

The term 'pseudoextinction' is used by Raup (1975), Stanley (1975), Patterson & Smith (1987) and others to refer to the event that has apparently occurred when an organism or group of organisms is supposed to have disappeared from the fossil record not by termination of the phyletic lineage but by transformation into a different kind of organism. The unreality of this phenomenon is taken by cladists as a methodological assumption (Ax 1987). However, there must in such cases be a 'ceasing-to-be' of some sort: dinosaurs are no longer met with (Hutchinson 1897), and the biologist's common-sense revolts at the prospect of using their name to refer to the rather different, small, feathered archosaur-derivatives which sing in the trees every morning. It is true that, in a meaningful sense, the clade (holotaxon) Trilobita is extinct in a way in which the clade (holotaxon) Archosauria (including Aves and Crocodilia) is not: yet it is equally true that dinosaurs, like trilobites, are a kind of organism which no longer exists; and this is just as much a meaningful biological statement. As the effective extinction of a parataxon,* the phenomenon might be better called 'para-extinction', leaving the prefix 'pseudo-' to false extinction events such as the disappearance of a taxon from the fossil record due to migration or geological discontinuity.

Patterson & Smith (1987) distinguish 'pseudoextinction' from the extinction of clades on the grounds that only clades are real in the first

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* By analogy with the existing words 'paraclade' (Cheetham 1986) and 'paraspecies' (Ackery 1987), I have coined the term 'parataxon' to substitute for the unwieldy 'paraphyletic taxon', and hereafter use it and its obvious counterpart 'holotaxon'. I prefer this to Ax's (1987) terms 'monophylum' and 'paraphylum' (adapted from Hennig, but confusingly suggesting the nomenclatural rank of 'phylum') - although the use of the terms 'parataxon' and 'para-nomenclature' for the quasi-taxonomic categories or form-genera of palaeontologists (Simpson 1961, Rasnitsyn 1977; cf. 'ichnogenus' and 'ichnospecies' for trace-fossils: Bottjer et al 1988) may reduce the acceptability of my suggestion.

place, and can therefore be used as terms in macro-evolutionary analyses. This is disputed by Sepkoski (1987) for reasons similar to mine. That clades are individuals in the 'weak' sense of particulars is accepted by Sepkoski, but he rightly rejects Patterson & Smith's apparent contention that they are therefore system-entities capable of causal agency or unit behaviour in response to evolutionary processes. Clade-taxa are assemblages, and their extinction is an aggregation of the extinction of their components ($ 2.4.4). (It might again be emphasized that 'para-extinction', like extinction, is permanent: it forms the unique termination of an unrepeatable historical class.)

Recent attention in palaeobiology has been focused on the role of abiotic processes in evolutionary history, and the analyses of Sepkoski and others are intended to contribute to the data on long-term periodicity in extinction patterns. In this context, the species is basically the unit of interest, but the fossil record being insufficiently detailed, higher taxa are generally used as a rough guide to species numbers (Jablonski 1984). Simply as aggregates of species grouped for the purpose of mathematical analysis, their status as holotaxa or parataxa may be unimportant - the only important criteria are that such taxa should be of comparable size in terms of species-diversity (not always adequately assessed), and that they should be non-overlapping (to avoid counting species twice). In terms of abiotic factors, exact genealogical relationship is irrelevant.

Yet there are hazards in using higher taxa of any kind in pattern analysis: for example, a mild extinction event which happened to wipe out a large number of monotypic or very restricted taxa of high rank might register as an extinction profile rather more impressively than it ought (Valentine & Walker 1987). Many therefore recommend that species-level data should be used wherever possible to minimize spurious patterns due to

taxonomic inconsistency or peculiarity (Stanley 1979, Culver et al. 1987).

Moreover, the criticism by Patterson & Smith (see also Boucot [1988]) is here justified to the extent that when extinction (i.e. lineage termination) is actually supposed to be the subject of the investigation, the distinction must be made - otherwise a period of rapid evolution among several groups will register as a mass extinction event. If biologists are going to reject the strict logic of cladistics they must not simply take refuge in unclarity of thought, especially since the necessity of care with concepts has been highlighted by the cladistic controversy.

$ 2.6 Selection and Pseudoselection

Of course, biotic explanations can be sought for extinctions, and perhaps more particularly, for survivals. In these cases, the focus of interest is on what it is about a taxon that affected its survival one way or the other: i.e. some character. The units of description will therefore be taxa which share the character/s in question, or rather, the same character state/s: again, their status as holotaxa or parataxa is irrelevant. It is phenotype that 'appears' to the 'view' of the selective process, not genotype or phylogenetic history.

Valentine & Walker (1987), in their model of extinction patterns based on simulation studies, distinguish between 'bloc' extinction of ecological communities regardless of taxonomy (e.g. by wholesale destruction of a complex of habitats), and 'clade' extinction which eliminates taxa which have particular intrinsic properties (i.e. a form of negative selection).

> If .. the presence or absence [of a critical feature] was to some extent a familial characteristic, then .. this would be a clade pattern, with the removal of families dependent on one of their intrinsic properties, not shared by all the members of the orders to which they belonged.

Or, one might add, not shared by all the organisms included in the clade either: descendent subclades differing in their characteristics would, in a cladistic classification, be included, and the pattern of extinction would be blurred; in an evolutionary classification, they might be excluded, thus clarifying that the extinction of a coherent paraclade has occurred. Other simulations of extinction admit paraclades into the analysis explicitly (Cheetham 1986).

It is true that recent developments in evolutionary theory (notably the notions of sorting and hierarchical selection) suppose the pattern of survival and extinction to reflect more than solely the sorting of organismal phenotypes by selection for those phenotypes. There may be a role in models of evolution for selective processes at the genetic level, causing sorting of organisms, or processes at the species level involving characters emergent at that level. However, with respect to higher taxa, these latter are still characters of species (whether aggregate or emergent), which may be shared by several species, that are consequently linked (whether as a holotaxon or a parataxon) by common fate. Groups of species may fall within the scope of a single explanatory description, and be affected by the same causal process, but they do not actually participate in that process as a unit.

> The closed descent community [i.e. clade] .. is .. not subject to the process of evolution. Ax (1987:22)

Patterson & Smith (1987) seem to require a form of 'vitalism' (or 'entelechy': Jeuken 1953) to explain how members of a clade or holotaxon, regardless of similarities and differences, could act as an evolutionary unit. For clades to be 'real units' in macro-evolutionary hypotheses they would be required actually to have properties - system-properties - to which a hypothesis about extinction might refer in its explanation (Hull

1976).* In the absence of any evidence for such properties, it can be concluded that holotaxa function only in macro-evolutionary description, not in macro-evolutionary processes.

> Much of macroevolution is a record that we construct **post hoc** and not a process with mechanisms. Salthe (1975:358)

Clades indubitably exist (in whatever sense one supposes spatially discontinuous, unobservable, theoretical objects to exist); they arise in a speciation event, and cease to be when the last descendant of that event dies. They are not universal classes, since they are characterized only by an 'individual essence' - to be a member is the only criterion of membership. They are not integrated wholes, since members have no connection with each other apart from the simple relationship. They cannot, therefore, be said to have true emergent individual properties, but only the aggregate properties of their constituents considered as a (historical) class: size, duration, rate of growth etc.. As units, they may be the subject of macro-evolutionary hypotheses (concerning 'tempo and mode', rates of speciation = clade production, the longevity of clades), but they are unique instances of the result of evolution, not entities which act as causal agents in the process of evolution. They do not exist as systems, and cannot be treated as entities strictly analogous to species. In many respects they can be treated in the same way as parataxa - as **convex grades**: genealogically connected taxa grouped (even polythetically) by biologically important sets of properties.

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* Some analyses of macroevolutionary pattern by simulation come close to proposing constraints on species arising from membership of higher taxa: e.g. the assumption of correlation (direct or inverse) between diversity and rate of speciation in a higher taxon (Hecht & Hoffman 1986).

$ 2.7 Taxonomy for Animals

> The basic task is to detect ... those genetically independent groups that we call species and that the animals themselves would recognize as constituting 'us' as distinct from 'them'.
> Corbet & Hill (1986)

Unfortunately, because higher groups do not act as units, and do not have any internal interactions of their own, the suggestion above (heard also from Arthur Cain [pers. comm.]) that taxonomists should 'let the animals do their own taxonomy' will work only at the primary level of the species (microtaxonomy [Mayr 1987]). The key to the delineation of species may be the discovery of the means by which conspecific organisms themselves recognize each other as such (Paterson 1985). Nevertheless, no higher level taxonomic method can be simply extrapolated from this. Animals have only to divide the world into a very few taxa - partners, rivals, relatives, edibles, threats, and everything else. Relationship at the super-specific level confers historical similarities, but no systemic interaction. It is true that some animals, and more plants, have networks of intra-generic breeding which muddle the ideal pattern of exclusive and coherent biological species - there is evidence for the importance of a notion of 'congener' among higher vertebrates (such as primates or gregarious birds) with elaborate psychological mechanisms for communication and empathy (Kortmulder 1986) - but this need not be significant in terms of relationship. Reproductive isolation can be seen as an autapomorphy which may subsequently be lost: isolation (or lack of it) between species may be uninformative concerning relationship, linking holo-, para- or polyphyletic species-groups (see e.g. Ackery 1987).

$ 2.8 Historical Groups or Natural Classes?

Wiley, in discussing higher (supraspecific) taxa in terms of Ghiselin's (1974 etc.) class vs. individual distinction, comes to the conclusion which I am in effect proposing - that clades (natural$_C$ taxa) cannot be adequately fitted into the scheme either as classes or as individuals. Classes are supposed to be spatio-temporally unbounded constructs, whereas individuals are restricted to a unique historical location. Wiley and Ghiselin agree that natural$_C$ taxa are not classes in the sense of universals - they have a historical uniqueness which in Ghiselin's terminology is a mark of individuality. Wiley, who identifies the term 'individual' rather more strongly with 'integrated whole', points out that natural$_C$ higher taxa do not have active cohesion due to participation in natural processes (i.e. they lack organizational or system properties) and are therefore somewhat different in character from those indubitably natural$_R$ coherent entities such as organisms or populations (or even species) which behave in some measure as units. They fall into a different category of entity, and he characterizes them as '**historical groups** derived from individuals'.

Whether holophyletic taxa are called individuals after Ghiselin or historical groups after Wiley (or closed descent communities after Ax [1987]), the important point for evolutionary taxonomy is that paraphyletic groups do not qualify. Wiley remarks in his footnote:

> As classes, such groupings cannot be considered natural because the individuals comprising these classes cannot be defined in terms of natural processes. Wiley (1981a:75)

Wiley proceeds on the assumption that only holophyletic (natural$_C$) taxa are 'historical groups' and natural$_R$ taxa.

The interesting introduction here is the idea that natural taxa might

be defined in terms of natural processes. In a later chapter (6) Wiley inserts a broad discussion of types of classification, and in preference to a simple dichotomy between hierarchical and non-hierarchical, or natural and non-natural classifications, he divides them into three major types - classifications in which the units are:

1 - natural classes;

2 - historical groups and individuals;

and 3 - convenience classes;

Type 2 seems to relate straightforwardly to individuals **sensu** Ghiselin, but a new meaning of natural appears to have been invoked to distinguish between the different sorts of class which appear in types 1 and 3. From Wiley's description I have characterized this meaning as:

naturalness$_L$: ("Law of Nature" naturalness) - natural$_L$ classes contain individuals which fit a class definition and "whose origins and behaviour are governed by natural processes" (Wiley 1981a:194).

I believe this concept of naturalness was used by G.G. Simpson (Ridley 1986), and it sheds a new light on Wiley's footnote quoted above. The import of the sentence is not: "These groupings cannot be considered natural because they are classes" but rather: "These groupings do not qualify as natural classes". This begins to undermine the identification of naturalness$_R$ with naturalness$_C$, as it effectively admits that there are ways of being natural without being holophyletic. Natural$_L$ taxa would fit the definition of natural$_R$ taxa: they can be said to exist in nature independently of observation. They are characterized by common fate inasmuch as they are linked causally by shared historical constraints. They could also fall within a loose definition of 'natural kinds' - members are characterized by a relationship of 'appropriate similarity' (Splitter 1982). The cladist must argue either that naturalness$_L$ is insufficient

to qualify a taxon for consideration as $natural_R$, and find a way of including holophyletic ($natural_C$) taxa while excluding paraphyletic taxa which, as candidate $natural_L$ classes, appear to have just as much claim to objective reality ($naturalness_R$): or else, that paraphyletic taxa do not even have a claim to $naturalness_L$ as classes (which Wiley seems to want to do, as evidenced by his footnote above).

My approach in the role of the evolutionary taxonomist is two-pronged. Having questioned the identification of higher taxa as 'individuals', I suggest that they are almost invariably treated by biologists as classes of some sort; and having questioned the assumption that biological reality or objectivity is restricted to 'individuals' and cannot be proposed of classes, I suggest, in effect, that both holophyletic and paraphyletic taxa may be types of $natural_L$ class and may therefore be acceptable in taxonomy as putative $natural_R$ groups.

(This contrasts with the approach of Charig (1982) who accepts the identity of natural groups with clades, and proceeds to argue for the acceptability of paraphyletic groups as artificial taxa. Dupré (1981) and Maggenti (1983) also refer to the artificiality of higher taxa, though it is unclear whether Maggenti means to refer to the groups themselves, or only to the categories ('family', 'order', etc.).)

$ 2.9 Higher Taxa as Historical Classes?

> Having the appropriate past history is necessary for a species to be the species that it is. Hull (1973)

It has been noted that taxa cannot cease to exist while any component survives, and so take on the class-like quality of definitional inclusion, and it is perhaps significant that the criterion of definability creeps

into Wiley's dismissal of paraphyletic taxa (probably under the influence of 'transformed' cladistics). Yet it must also be noted that taxa, holophyletic or otherwise, are assumed to be temporally circumscribed:

> Gold, by virtue of its essence (i.e., its atomic number), cannot become extinct, but at best can become temporarily unavailable, and consequently its properties can be described in terms of general and timeless laws. Not so with particular species taxa that may go extinct and never reappear again.
>
> Rieppel (1986:283-4)

It should be noted that the last phrase here means not "and might never reappear" but "and once extinct can never reappear". Taxa are generally regarded as historically unique and unrepeatable, i.e. subject to permanent extinction. It is therefore not permissible to 're-use' a taxon name* (as Simpson's concept of 'monophyly' would allow) to indicate supposed recurrence as opposed to continuity, as in the notable sentence: "The Archbishop of Paris was murdered in the insurrection of 1848 and murdered again during the Commune of 1871." (**Independent** 3-2-88). Even here, it can be argued that 'Archbishop of Paris' is the name of an individual, but not of an individual man - it names a unique element in a relational framework of bishops in the way that 'the 8.30 express' names an element in the framework of the train service. In both cases, the term also thereby implies a historical class - the class of individuals (men, trains) which have held that relational position. But I begin to be out of my depth and of my present topic.

It can perhaps be argued that a natural_C higher taxon is not best (or at least, not always best) regarded as a unique referent with a proper name, as Ghiselin regards species, but as a quasi-Aristotelean class whose definition includes a historical component. This renders not only the holophyletic historical groups of Wiley - non-integrated individuals of

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* But see Rosenberg's suggestion of the possible repetitive origin of taxa ($ 4.5.1).

Ghiselin - but potentially other taxa with a claim to naturalness$_L$ a distinct kind of class, grouped by shared historical characters. Brundin's (1972) and Wiley's (1981b) simplistic characterization of paraphyletic taxa such as Reptilia as "time-less abstractions", because of their basis in symplesiomorphy (shared primitive characters) rather than in synapomorphy, is entirely inappropriate: paraphyletic taxa are no more "time-less abstractions" than are holophyletic taxa. Naturalness$_L$ is in effect an updated version of naturalness$_A$ - replacing the antique concept of 'essence' with the more modern idea of 'action of natural processes', which is a scientific unpacking of the hidden structures or laws which result in what Aristotle calls essence.*

A holophyletic taxon fits very well the definition of a natural$_L$ class. Evolution is certainly a natural process which results in the production of clades, in accordance with the natural law of divergence from common ancestors. However, the laws of divergence are complemented by the laws of differential divergence, and hence non-clade taxa may have a claim to naturalness$_L$.+ As has been briefly suggested (see discussion at §3.7), the appropriateness of identifying taxonomies wholly with implicit phylogenetic hypotheses is highly debatable: biology has more things to say than that organisms are related to each other. If there is such a thing as taxonomic prediction - reasoning by some logical (though not necessarily

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* Some confusion may have resulted from a misidentification of Aristotle's 'real essence', an abstraction which is real only inasmuch as it is manifest in individual objects, with Plato's 'form', in which reality eternally resides, and which has a kind of 'ontological priority' over its expression in objects. Aristotle was neither a Platonist, nor a thoroughgoing 'essentialist' (**contra** Hull 1967:310; see van der Hammen 1981, Atran 1985, Gotthelf 1985, R. Winch pers.comm.).

\+ It is in fact inadequate to speak of <u>the</u> groups produced by evolution, for at least at levels higher than the species the workings of evolution can be thought of as producing different groupings depending on which aspects of those workings is stressed. Pratt (1972:312)

deductive) route from observation to potential observation by way of connective hypotheses - then genealogy might be regarded as one general connective hypothesis or 'natural law' among others, such as potential laws of form, ontogeny, biochemistry, etc., which describe or determine the properties of organisms.

I would suggest that the reason why species, and indeed organisms, are inadequately encompassed by the term 'class' is their possession of individuality in the strong sense ('species-individuality' of Huxley 1912). They have true relational emergent properties, integrated common fate, participation in processes as a unit - qualities not shared by Wiley's holophyletic 'historical groups'.

> It is what species <u>do</u> which makes them individual, spatio-temporally restricted objects. Rosenberg (1983)
>
> Genera do not do anything. Ghiselin (1987)

This is not to say that higher taxa are arbitrary classes - the result of Wiley's classification of classifications is the admission that there are non-arbitrary class-based classifications, incorporating $natural_L$ classes related to natural processes, distinct from convenience classes. I would prefer to reinstate Wiley's divisions, allowing taxa to feature in an intermediate position, as a subset neither of 'individual' nor of 'class':

> Classes
> Historical entities
> Individuals — Wiley (1981a)
>
> Classes
> Individuals
> Historical entities
> Integrated wholes — Ghiselin (1984a)
>
> Ahistorical ('timeless') classes
> Historical ('finite') classes
> Individuals — Marshall (syn.nov.)

This to some extent subverts the dichotomy between '(universal) class' and

'(particular) individual' which Ghiselin presents; but this may not ultimately be a very useful distinction for biology. Even Quine (1969b) is prepared to subvert it by regarding individuals as classes of one: cf.:

> The class is, of course, a kind of individual.[!]
> Gerard (1957)

> My ontology includes neither pure classes nor pure individuals, both being idealized entities. Colless (1977)

Not all classes are universal, and not all particulars are individual, and the biological world seems dominated by non-universal classes. Taxa fall somewhere in between the categories,* and their characterization as 'historical classes' rescues the **historicity** of biology without sacrificing its explanatory power.

Taxa, as non-system entities, can only play a role in theories as classes (though species, of course, if conceived of as system entities, can play a role as individuals). Yet taxa will not behave as good essentialist (homogeneous) classes with universally covarying characters (Branford 1890, Hull 1973): they are finite and heterogeneous (Elsasser 1981).

Ghiselin's argument about the individuality (particularity) of species is similar to one about individuals used by Grossman (see Wilson 1986), who argues that individuals (Ghiselin - species) are correctly characterized as particulars and incorrectly characterized as bundles of properties (these being thought of as universals and not as particulars located in space and/or time). But Wilson (1986) points out that another way of viewing individuals is as characterized by properties <u>including</u> spatial and temporal ones, which are especially important. (Thus a historical entity which consists of components creates the definition of a class of those

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* The possibility that species might fall into some hybrid category was admitted, though not discussed, by Hull (1976), though both he and (more so) Ghiselin seem to exclude finite classes by insisting that classes are necessarily spatio-temporally unrestricted.

components: I am regardable as **a** class of cells - note, not **the** class of cells.) This echoes my suggestion that natural historical classes are defined by 'particular properties'.

Even then the argument will continue, for Ghiselin too has made a start on the notion of 'particular properties':

> Only recently have I been able to relate my views on homology to those on the individuality of taxa; homologues are parts of a whole, analogues members of a class. Ghiselin (1987)

In other words, just as cladistic taxa are to be regarded as individuals and other taxa as classes, so cladistic synapomorphies are to be regarded as individuals (wholes?!), other characters as classes. The argument about the individuality of characters or properties would seem destined to run virtually in parallel with the discussion of groups. In effect, my position is the same for characters as for taxa - accepting their non-universal nature, but rejecting the suggestion that holophyly provides justification for an ontological separation of synapomorphies (or holophyletic taxa) from other homologies (or paraphyletic taxa).

$ 2.10 Classes and Change

> The continuance of the working of a species as we have defined it would preclude change; but change and the idea of evolution are at the basis of all modern thought. Huxley J.S. (1912:27)
>
> That individuals change is commonplace; that species and other kinds change is a theoretical proposition (the doctrine of organic evolution). Wells (1987)

Universal classes, as Ghiselin (1987 et ubique) does not tire of pointing out, do not evolve*: that is, their definitions cannot change

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* Interestingly, Ax (1987) makes the same point about holophyletic taxa despite not regarding them as classes.

over time; but some classes do change, in the sense that their membership may change over time. Once a definition is made ('the class of dodos') that definition may remain eternally the same ('the class of dodos'), but the class changes in content ('the class of $dodos_{1489}$: containing several hundred live dodos'; cf.'the class of $dodos_{1989}$: Ø'). This seems contrary to Ghiselin's position, which is that:

> an entity can only change if it is an individual. Classes cannot do anything whatever.... Evolution is a kind of change. Therefore anything that evolves must be an individual. Species evolve, therefore species are individuals.
>
> Ghiselin (1987)

and it casts doubt on the idea that persistence through change is a characteristic only of individuals. With historical classes it is not that the definition ('what it is to be a member of the class') changes - just that the historical content of the definition means that after a certain point in time (extinction) it becomes impossible for any newly-originated entity to fulfil the class definition.

Other groups of individuals may fall into this category of 'historical class': certain kinds of asexual population, HeLa cells, Vikings, Ming vases, copies of 'The Hobbit'. It might be better to say that after extinction (or indeed at any time) it is allowable in principle that a member of a historical class could arise independently, but virtually inconceivable in practice. If a million monkeys spent an aeon typing 'Hamlet', the result would indubitably be a copy of 'Hamlet'; thus also a synthetic human being may be counted a member of Homo sapiens. (Cf. Dupré's (1981) argument that if (if) a chicken laid a walnut, we would not call this a chicken, and might show it to be a proper walnut. Note also Rosenberg's polyphyletic species ($ 4.5.1).)

Holophyletic taxa behave timelessly: their definitions in terms of a primaeval synapomorphy never change. Cladistic method effectively attempts

to treat common ancestry as a (directly unobservable) property necessary and sufficient for membership of a group (Ruse 1987). (Transformed cladistics attempts to treat synapomorphies in the essentialist fashion as necessary and sufficient features for membership of a defined class.) As long as a lower taxon (or lower level entity) has the 'essential' property - in this case, that of having originated by divergence from a common ancestor - it falls into the higher taxon by definition: no historically disjunct taxon can share the defining property. However, the taxon contents change over time. Paraphyletic taxa behave similarly, but because their definitions may be framed in terms of actual rather than hypothetical characters, it is possible for members to leave the taxon. It may not be accurate or particularly appropriate to say that taxa evolve (any more than it is to say that they are ancestors; see §1.3), but they certainly change as species cease to be one kind of thing and become another, and so a nomenclatural system may need to allow species to 'leave' higher taxa. Neither type of taxon is ever temporally disjunct: part of the perceived 'essence' of a taxon (perhaps universally and explicitly among evolutionary taxonomists only since Hennig) is historical continuity: convexity.

CHAPTER THREE

*

WHAT IS CLASSIFICATION FOR ?

or

Theories, Things, and Kinds of Thing

"Where is the knowledge we have lost in information?"
T.S. Eliot (1934)
'Choruses from "The Rock"'

$ 3.1 The Usefulnesses of Classification

> Arguments on how to deduce the evolutionary tree have spilled over into the original question faced by Linnaeus: how to classify organisms and provide a stable reference system for biologists and naturalists. Bisby (1988a)

Arguments about the relative merits of different taxonomic systems are almost inevitably more or less elaborate variations on the theme of 'usefulness', even when the overt criterion is that of 'naturalness'. Defences of each of the systematic schools adopt various viewpoints on what is useful (often with corresponding definitions of what is natural: $ 1.1), and this thesis will ultimately prove no exception. This is true even of Ridley's (1986) study, which apparently rejects both 'usefulness' and 'naturalness' as criteria in favour of 'objectivity'. He presents the different schools' alternative solutions to incongruence as either objective or subjective, where 'subjective' is taken to be synonymous with 'arbitrary', and 'objective' is expounded as meaning:

> dictated by a theoretical principle ...[which] must specify some discoverable hierarchical property of nature, which it is **desirable** and technically possible for classification to represent. Ridley (1986:3)(emphasis mine)

This seems to beg the question of what is desirable in a classification, and Ridley's study, unlike Mayr's (1981) or Johnson's (1970), fails to ask the initial question: "What is classification for?". (To define objectivity in terms of desirability would in fact be to undermine the exercise from the start.) Particularly, it assumes (against the assertion of Ellen 1979) that classification must be hierarchical, and that classification therefore requires a hierarchical property of nature in order to be objective (cf. Brundin 1972; more or less seriously dissenting views are expressed by Clement 1985 and Kemp 1988b).

There are several types of 'usefulness' which a classification system

may exhibit. Usefulness$_1$ is that of optimized information storage and retrieval, common to all information systems. Usefulness$_2$ is specific to open-ended classifications where the information is incomplete, and is the capacity of the system to incorporate new information without collapsing. Either or both of these may be meant by a taxonomist referring to the criterion of 'stability', though the second is perhaps more fundamental than the first, being dependent less on the user and more on the system and the data which it includes.

Usefulness$_3$ is special to certain open-ended classifications, in which taxonomy has a close relationship with theory. Not only does a taxonomy have to accomodate new data - the taxonomy itself plays a significant part in the production of new data. Biological theories are framed in terms of the taxonomy, and new data arises not only from the discovery of new organisms which must be incorporated into the system, but also from review of the known organisms within the system. This kind of feature of taxonomy is commonly identified as 'predictivity', and I shall deal with it as such for the moment. The types of usefulness may be summed up thus (these are not strict definitions of the terms used):

A classification is a system into which one puts known information.

An informative (useful$_1$) classification allows one to extract the known information.

A stable (useful$_2$) classification allows one to insert previously unknown information.

A predictive (useful$_3$) classification allows one to extract previously unknown information.

Along with some adjunct attribution of naturalness, these form the primary features most commonly ascribed to taxonomies. Predictivity in

particular receives much attention:

> Of all the proposed aims of systematics (e.g. information storage and retrieval, the delimitation of 'real' or 'natural' groups, etc.), one of the most agreed upon aims is predictivity.
> Beatty & Fink (1979:650)

> One of the greatest assets of a sound classification is its predictive value. It permits extrapolation from known to previously unstudied characters. Mayr (1969:7)

> One may argue about the function of classification, but it is generally agreed that the greatest virtue of a classification is predictivity. Patterson (1982)

Predictivity, even when it is not being conflated or confused with informativeness (Stace 1989), is perhaps over-emphasized as a property of taxonomy under the influence of the philosophical supposition (derived mostly from Popper) that any meaningful scientific statement must be a falsifiable hypothesis.

> Popper's falsifiability thesis has assumed the status of a dogma in some evolutionary circles. Culver (1985)

It is, however, debatable to what extent prediction is or should be a property of taxonomies at all ($ 3.6), but in order to discuss this I shall have to disentangle predictivity from a proposed synonymy with stability.

$ 3.2 The Instability of Theory-laden Taxonomy

> There is a strong traditional feeling that stability of some sort is important in classification, especially in regard to nomenclature. Gaffney (1979)

Nelson & Platnick (1981) attempt to defuse arguments about stability by conflating stability and predictivity, on the grounds that they are effectively identical, as "the most stable classification is the one that most successfully predicts the structure of newly acquired data".

The problem with this direct identification is that common usage of the term 'stability' covers two different concepts. Computer taxonomists

working with dendrogram building use 'stability' in a 'usefulness$_2$' sense to refer to the property of a dendrogram of absorbing new information without changing topology. Field entomologists and other creatures of the woods and pastures use 'stability' in a 'usefulness$_1$' sense to refer to that property of an information retrieval system which prevents it from becoming so restructured over time as to make any reference to past work a major exercise in mapping nomenclatural history.* Nelson & Platnick distinguish between stability at the level of binomial nomenclature and at the higher taxonomic levels, and it is true that the quasi-legal and antiquarian aspects of naming play a much lesser part in higher taxon naming. They admit that

> it is obvious that if the names of individual species change very frequently, they will lose much of their usefulness as means of information storage and retrieval.

At the specific level this is a matter for the nomenclatural Commissions, not for the systematic theorists. What many practising biologists also object to is the frequent changing of names at the generic and higher taxonomic levels due to fluctuating phylogenetic opinion, and they do not

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* In many groups, such as wild flowers (Dony et al. 1986), fish (Bailey et al. 1970), invertebrate agricultural pests (Thomas et al. 1968) and moths (Scoble pers. comm.; South 1907, 1909: cf. South 1961), the Latin binomials are so labile that formal lists of common names (even of English binomials: see Dony et al. 1986) have been produced.

> It is a paradox that in a list of common names, the scientific names are the more troublesome. Thomas et al. (1968:1)

> It is to be hoped, and the history of the recent past confirms, that common names may be more stable than scientific names. Bailey et al. (1970:1)

> It is rumoured that some practising taxonomists actively enjoy a state of linguistic uncertainty and the need to learn a new classification with every paper they read, but such clado-masochism (Schaden-Freude 1980) does not appeal to biologists in general or contribute in any significant way to our gradual progress towards a more accurate understanding of evolutionary history. Martin (1981:131)

sympathize with Nelson & Platnick's identification of such nomenclatural fluidity as improvement in the direction of increased predictivity and hence "in the long run, greater stability".

> By far the most tiresome changes arise from what Hawksworth charitably calls "advancement of scientific knowledge", but which are often better described as mere changes of opinion as to where or whether, in an assembly of species, a generic distinction should be placed. Crisp & Fogg (1988)

> From a situation in which Simpson's 1945 classification of the Primates was widely adopted (with only minor modifications) for some 25 years, we have 'progressed' to a situation in which at least 20 radically different classifications of the Primates have been published in the last ten years. In other words, we have progressed from relative linguistic stability and mutual understanding to linguistic anarchy and misunderstanding, and a large measure of the blame must be attached to the Hennigian school. Martin (1981:131)

> [Taxonomists] seem quite unable to understand that instability of nomenclature seriously impairs the value of their work to biology as a whole. Barnett (1986)

It may be the case that "stability and predictive value are not in conflict with one another" (Nelson & Platnick 1981), but the concord is not a necessary one due to their being "one and the same thing" (ibid.); it is a contingent one, where optimizing one tends to optimize the other, if stability is taken only in the '$usefulness_2$' sense. The phylogenetic systematists assume that at higher taxonomic levels the need for basic '$usefulness_1$' stability is overridden by the pure desire for knowledge, and in effect stability ceases to be a concern:

> ...When classifications are presented as biological hypotheses, then we must question the usefulness of stability. ...Temporal stability of classifications often reflects ignorance of relationships and lack of work. I hardly advocate change for its own sake, but the maintenance of names for discarded concepts seems useless and misleading. Gaffney (1979)

> we should always be eager to discard our current classifications in favor of improved ones that have increased predictive value. Nelson & Platnick (1981)

But the 'scientific real world' is full of those rather too "eager to discard our current classifications" while other people are still trying to

use them (see also $ 4.1). The appropriateness of treating classifications as falsifiable theories or hypotheses in the style of Popperian method, as advocated by Gaffney (1979), Coomans (1983) and others, is debatable. A relationship does exist between evolutionary theory and classification (notwithstanding the transformed cladists; Ridley 1986), but in the eyes of many biologists they are complementary not identical (Martin 1981).

> Part of the trouble comes from the romantic confusion of biological classification with evolutionary studies, exemplified by S.J.Gould's words:- 'taxonomies are not neutral hat-racks for the pristine facts of nature. They are theories that create and reflect the deep structure of science and human culture.' Too many taxonomists appear to subscribe to this kind of sentimental codswallop.... Barnett (1986)

In fact, Gould, the victim of the letter quoted above, has himself used the stability argument against cladistics:

> Cladistics produces wildly unbalanced and unstable higher taxa (any change of opinion about branching sequence early in the history of the group forces a recalibration of all ranks). Gould (1980:112)

Stability itself, as Gaffney recognizes, is a contradictory aim when classifications are themselves regarded as hypotheses to be improved by rigorous testing wherever possible. There is a conflict between the stability of any particular classification, and the theoretical stability of a classificatory methodology. Cladists (such as Nelson & Platnick) may be right to suppose that a perfect phylogenetic classification would be stable, but until this ideal is achieved, if it ever can be, cladistic classification - in other words, phylogenetic theory - remains testable and (as Gould remarks) highly revisable. Hence while the ideal classification sought by cladists may be stable, the methodology itself while in action is inherently unstable.

> The advent of cladism has by no means eliminated disagreement between research workers in the interpretation of phylogenetic relationships. Hence, the implacable logic of Hennigian classification requires that there should be as many different

> classifications of the same organisms as there are resecarch workers deriving different inferences from their data!
> Martin (1981:131)

> Almost every conceivable combination and permutation of living and extinct hominids has been proposed by one cladist or another. Lowenstein & Zihlman (1988)

Gaffney complains that stable classifications are not ideally suited to his purpose:

> In the literature, a classification is often the most important, if not the only, way of presenting phylogenetic hypotheses and conclusions of other systematic work. This is unfortunate because the formulation of scientific ideas in a context that imposes stability for traditional purposes breeds the illusion that stability of classifications demonstrates accuracy and depth of understanding. Gaffney (1979)

He seeks "a classification that mirrors a phylogenetic hypothesis (however transitory)" (Gaffney 1979:104). But a classification, it might be argued, is not necessarily the only way of presenting a phylogenetic hypothesis - as Ridley formerly admitted:

> We do need to know phylogenies ..; but we do not need to find them in taxonomy. .. Just as we can extract facts about adaptations from the appropriate literature, we can take phylogenies from the phylogenetic literature. The latter need no more be represented in the taxonomy than the former.
> Ridley (1983:20)

Indeed, because such presentation results in nomenclatural instability, especially if the hypothesis is controversial, it would be better if other methods were found. Moreover, a classification, if not necessarily the means by which a hypothesis is presented, is necessarily the context for such presentation, whether it be phylogenetic or otherwise; evolutionary taxonomists portray cladistics as an attempt to hi-jack the general classification system of biology for a special classification of narrower, purely phylogenetic interest. (As to illusion-breeding, it is often pointed out that the spurious precision of many cladistic analyses results in over-confidence both in the method and in its results). In order to maintain the coherence and stability of biological language, phylogenetic reconstruction must be decoupled from classification (Martin 1981).

$ 3.3 Prediction from Pattern

The 'predictions' presumed to be obtainable from classifications are inductive generalizations of facts established in one or more representative individual members of the group to the remaining members of the group (Pratt 1972, 1977). What is of concern to the biologist, as Mayr (1969, quot. $ 3.1 above) suggests, is to be able to make, from the known characters of a particular organism, some kind of prediction of the properties of an organism not studied, either within the same population of organisms, or within some higher taxonomic unit which includes both organisms.

A fairly crucial problem with predictivity as a criterion for assessing taxonomies is that it can only be directly judged with the benefit of hindsight - only if we had access to all the as-yet-undiscovered information could we decide which taxonomy was going to predict it most reliably! Any attempt to optimize predictivity must therefore be indirect. Two such attempts, the phenetic and the 'transformed cladistic' (the 'information models' of Kemp 1985a), might be described as 'pattern' philosophies , in that they attempt to produce predictive taxonomies simply by so structuring the known information that the resulting distribution pattern can be extrapolated to generate new information.

The basic argument is stated thus by the 'transformed' cladists Nelson & Platnick (1981):

> If we already know that we can make general statements about some properties of a set of organisms (1,2,3,4,5) and about a subset of that set (1,2,3), can we not predict that for other properties that we do not yet know, some may be true of the set (1,2,3,4,5), others may be true of the subset (1,2,3), but none should be true of other incongruent subsets like (3,4,5)?

This Principle of Congruence is the basis for 'pattern prediction' or the

attempt to predict simply by extrapolating information about character distributions. Phenetic prediction is based on a more general version:

> If a classification is based on many correlated features, predictions about the states of other characters in various groupings of the classification should be more successful...
> Sokal (1966)

The phenetic approach to predictivity is based on the definition of natural$_P$ taxa - groups about which the largest number of general statements can be made - and to assert that such taxa will be most predictive (Sokal 1966, Stace 1989). This is in effect a conflation of the concept of a maximally informative ('Gilmour-natural') taxonomy with that of a maximally predictive taxonomy, which would appear ill-justified: does a classification which maximizes the storage of known information necessarily thereby optimize its response to or revelation of new information? To Nelson & Platnick's rhetorical question above I feel constrained to answer "No".

$ 3.4 The Inadequacy of Theory-free Taxonomy

> Arguing from resemblances has led a number of bright minds in silly directions. Pohl (1988)

The pattern approach has been to treat taxonomies as themselves hypotheses, and to interpret prediction solely in terms of character distributions, based on the principles of congruence and parsimony. But parsimony of known character distribution is not a valid criterion of predictivity. Congruence of any number of characters itself tells you nothing about any further characters - only some form of auxiliary or **connective hypothesis** can do this. For example, however many characters are congruent on a most-parsimonious cladogram of mammal species, reliable predictions of coat colour cannot be made on this basis. Parsimony must

operate on the entire range of biological knowledge, and cannot be isolated as a criterion for character distributions. This style of argument is based either on a fallacy - that of extrapolating from statistical or quasi-statistical data - or on a hidden explanatory assumption. If asked to make a prediction of the form: 'What is the probability of a character **c** being possessed by an animal A?' the taxonomist does not simply assess the number of characters held in common by A and known **c**-bearing organisms to come up with some abstract taxonomic probability. If a reliable 'prediction' can be made, it is made in consideration not just of character distributions but in terms of the rest of an organism's biology, and comparison with as many related or unrelated forms as seem relevant.

Analogy might be made with the problem of predicting whether or not the sun will rise tomorrow. Confidence in the sun's appearance in the east tomorrow is not soundly based on a statistical prediction from the number of previous occasions it has risen - this is not a proper inference (H.C. Dawkins pers.comm. 1987), despite the fact that it generates a successful prediction. It is more soundly based in a connective hypothesis which proposes a shared causal framework for instances of the sun's arising - i.e. the science of celestial mechanics.* (In this case statistical inference mimics the predictions of the causal connective hypothesis, but as biological causality is more complex, purely statistical descriptions will be less reliable as behavioural models of the system.) It is not the case that in making successful predictions a hypothesis is necessarily identifying causal mechanisms - Ptolemy's astronomy is often remarked upon as a model which can provide broadly reliable predictions without being correct as regards the fundamental arrangement of things in the universe

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* If we did not know about the Solar System, we should be a little at a loss to know what to make of the diurnal rising of the sun, millenia of observations notwithstanding. Maddox (1988)

that it implies. Usefulness, then, is not truth.

Of course, inference of a quasi-statistical kind may be used and is often the only option where causal mechanisms are presently inaccessible. Entire models can be remarkably coherent and useful despite their apparent lack of causal mechanism; for example, Chinese medicine often succeeds unexpectedly where Western medicine fails, because its root concerns are less with the location of anatomical objects than with the tracking of physiological effects: this results in a kind of phenomenal organ system based (rather obliquely to Western eyes) on practical therapy not dissected anatomy:

> All Zang Fu [elements in the Chinese organ system] refer more to functions than to structures, .. San Jiao is the extreme case - 'San Jiao has a name but no bodily shape'. Ross (1985)

Similar heuristic or descriptive models are used in conventional science, such as, for example, the various polar co-ordinate models of limb development and regeneration (Bryant et al. 1987), and perhaps some of the widely-used ecological models such as that of optimal foraging. Subsequent work using other methods of investigation may clarify the causal mechanisms, as microscopy clarified the microbial theory of disease; but medical science is beginning to suspect that some causal mechanisms (e.g. that of acupuncture) may prove impenetrable at least for the near future. Some physicists suppose that models such as those of quantum theory can only ever be phenomenological (behaviour-mimicking) models. Usefulness is not truth, but it may nevertheless have to be accepted when truth is out of reach. However, science has tended to prefer causal hypotheses to behavioural models where the former are available.

$ 3.5 Predicting and Explaining

Cuvier's method of comparative anatomy can be compared to Ptolemy's astronomy: he and other pre-evolutionary taxonomists (as is pointed out by apologists for transformed cladism) provided successful predictions only from a descriptive or phenomenological system, not from a true theory about the pattern they saw. Naturally this led to problems: Swainson, for example, was fully justified on grounds of congruence and parsimony in moving the thylacine from the marsupials to the carnivores (Knight 1981). Cuvier's placing of this anomalous organism had been based on an incipient typological hypothesis which held some characters (such as tooth structure or possession of a pouch) to be specially significant: only when combined with evolution theory did this typology achieve some coherence, with ancestry and adaptation providing causal explanations of taxonomically pivotal characters.*

Purely arbitrary classification will not support predictions reliably - trustworthy inference requires some hypothesis that will make a causal or explanatory connection between groups. If classifications are expected to be predictive, they must do so by constructing groups based on connective hypotheses: this implies that supposedly non-theoretical classifications such as phenetic or pattern cladistic classifications will not support predictions, or at least, cannot be expected to generate them. Even if classifications are not expected to be predictive ($3.7), but simply

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* Other non-Darwinian classifications occasionally surface, but are generally taken note of only if in tandem with a proposed causal mechanism. Vavilov's 'law of homologous series' is an example of such: his hope for a 'periodic table of form' was perhaps over-optimistic, but "his vision of a predictive morphology, powerful and suggestive," (Gould 1984:192) has prompted serious consideration of such a connective hypothesis. The network classification of Clement (1985), with the suggestion of cross-taxonomic genetic transfer, is perhaps another.

explanatory, then they will similarly have to have inherent compatibility with connective hypotheses of causal mechanism.*

The connective hypotheses most appropriate for biological classification would seem to be those derived from the theory of evolution (Burtt 1964, Ridley 1983, 1986), as it forms a base for most branches of biological science, and is accepted in principle, if not in detail, by all biologists except Biblical fundamentalists. Evolutionary taxonomy, and (evolutionary) cladistics seek in different ways to involve evolutionary theory in classification, not simply to make predictions and hence enable Popperian falsification, but because explaining how animals <u>are</u> necessarily involves explaining how they <u>came</u> to be so.

§ 3.6 <u>Identifying Classes</u>

> Something very much like nothing anyone had seen before came trotting down the stairs and crossed the room.
> 'What is that?' the Duke asked, palely.
> 'I don't know what it is,' said Hark, 'but it's the only one there ever was.' Thurber (1951)

The attempt to move species from the ontological category of 'class' to that of 'individual' seems potentially to constitute a shift of taxonomy from being a nomothetic discipline (seeking law-like statements from repeated instances) to being an idiographic one (descriptive of unique events)(terminology after Windelband, see Crowson 1970:5, Gould 1980a:113), and therefore to change its status as regards predictivity; some palaeontologists were rather hoping that they had managed to make the

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* Stace (1989) expects assignment of an organism to a taxon to be informative, and by extension, predictive about a new organism assigned with some confidence to an existing taxon. However, this predictivity is groundable only in an implicit assumption that there is a connection, not on pure phenetic extrapolation: in other words, phenetic prediction relies on an unstated and therefore unanalysed connective hypothesis.

transition the other way (Raup 1975). As (non-transformed) cladistic apologetic abandons the view that taxa are classes, it abandons the possibility of justifying cladism by demonstrating its capacity for generating law-like statements (Rosenberg 1983, 1985). (Such a move would perhaps be congenial to Ghiselin, who regards the 'methodological individualism' of economics as a example to biologists and interprets Darwinism as entirely concerned with individuals [Ghiselin 1985a].)

It is characteristic of individuals (according to Ghiselin 1966 etc.) that they do not have definitions, as do classes or kinds, but can only be indicated ostensively, by pointing; they are named by 'baptism'. The problem with so viewing taxa is that you can't have a baptism without a baby* - but there is no way of 'getting hold of' or 'pointing to' a taxon in order to name it, except by indicating one of its organismal 'components', and proposing that it is one of a kind (Grene 1983). I do not think that this is simply a problem of scale. I cannot point to a bacterium, but the microscope eliminates this purely mechanical disability; however, even were a 'macroscope' available, species or higher taxa would not be visible as objects. Even the recognition of a clade is critically dependent on its being considered as a class+ - how much more so the generation of putative predictions.

I have taken the (apparently reasonable) position that predictivity, insofar as this is an appropriate word for taxonomies, is a matter of making reliable inductive generalizations between members of a group (following Mayr 1969, Hull 1973, Pratt 1972, 1977). But it is not possible just to extrapolate from the properties of a unique spatio-temporally

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* I do not mean to exclude adult baptism!

+ As noted by Patterson (1987), an uneasy combination with his insistence on the individuality of clades (Patterson & Smith 1987).

delineated individual to those of another; nor is it possible to make inductive generalizations about them **qua** components of an individual at a higher hierarchical level. Unlike members of a class, components of an individual P need not share any features in common whatsoever except for the defining feature of 'componentship of the individual **P**'. Without classes,

> we have only individuals and therefore no possibility of scientific study. Pratt (1977)
>
> Science deals with classes of entities. Hull (1973:70)
>
> Individuals cannot figure in general and timeless scientific laws, but only in particular statements. Rieppel (1986)
>
> Statements about individuals are precisely what laws of nature are not. Ghiselin (1987)

This appears to introduce a problem into the attempt to regard higher taxa as individuals. Even if taxa are individuals, they are predictive (perhaps even informative) only inasmuch as they are classes of their components (i.e. their members). But even if taxa are classes, they are historically locatable and unique , and so do not figure in 'timeless' laws.

Biological taxonomy apparently deals with a kind of class which allows some degree of definition and yet is not 'timeless' in the way that the classes of 'triangles' or 'gold atoms' are timeless.* Rosenberg (1983) asserts that all we can hope for are laws about <u>all</u> species - about the category 'species' - but we are still going to need reliable generalizations about groups of animals even if we are not allowed to consider them laws or law-like statements. Hence I prefer to regard holophyletic (and paraphyletic) taxa as finite or historical classes with, so to speak, a particular historical component to their definition?

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* Here some philosophers of science appear to have come unstuck in trying to formulate a concept of 'natural kind' that will encompass both 'triangles' and 'tigers' (see Dupré 1981 and Splitter 1982 on Putnam and Kripke; Grene, pers. comm.).

$ 3.7 Testing Classifications

Much of the debate about taxonomy has taken as a basic assumption the notion that in order to be scientific, taxonomies must be theories amenable to testing or (in Popperian terms) falsification. However, it is by no means clear that classifications are themselves theories, or need be seen as such. A distinction is made thus by van Dongen & Vossen (1984) between scientific **results**, scientific **concepts**, and scientific **theories**:

> Results are **reliable** or not; results are reliable when essentially similar observations yield similar results... Concepts are **valid** or not; concepts are validated when essentially different observations yield similar conclusions... Theories are **falsified** or not; a theory is falsified when (crucial or too many) discrepancies have been found between the results predicted according to the theory and the actual results.
>
> van Dongen & Vossen (1984:37)

The notion of reproducibility has certainly been thought important: pheneticists sought algorithms that would consistently produce the same result from the same observations in the hands of different taxonomists; cladists sought logical principles that would do the same. The reason for the frequent failure of phenetics, and the controversiality of cladistic classifications, is often that the attempted reproduction of the interpreted observations - that is, of the characters as they have to be perceived in order to fit that classification - does not succeed. Phenetics especially suffers from the arbitrariness of biometric characters such as 'leg longer than 3mm': it attempts to perform mathematical analysis, using algorithms which must be arbitrarily selected, on characters which are only arbitrary abstractions from a continuum of features. Cladistics may suffer from a similar subjectivity involved in selecting character states and synapomorphies, and faces the problem of choosing between radically different dendrograms scarcely separable by

methodological criteria such as a principle of parsimony.

Yet these are essentially not tests of the classification, but of the reliability of the observational material on which it is based. True,

> a zoologist, like any scientist, cannot make his observations first and frame his theories afterwards.
>
> Winsor (1976:75)

But I would suggest that classifications in themselves do not make predictions, and so are not theories. Taxonomic 'predictions', if there be such, are made by a connective hypothesis: predictivity (usefulness$_3$) need not be a property of taxonomies themselves at all.

One of the most awkward facts about the attempts to draw predictions from biological classifications is that they are unreliable. Yet nobody really expects them to be reliable. Nobody regards a classification as falsified if an expected correlation does not in fact turn out to be the case. Such correlations are applications of a connective hypothesis: either structural-functional or genealogical. 'Prediction' just seems to be the wrong word to describe the inferences of taxonomists - 'expectation' seems nearer the mark. If an 'expectation', whether it arises from a purely genealogical hypothesis or from a structural or functional correlation, is unfulfilled, it is not the classification which is re-assessed, but the applicability in this instance of the connective hypothesis on which the expectation is based. This is the case for any classification which is not strictly monothetic (not just phenetic ones, as Kemp [1985a] suggests). It even applies to cladistic classifications, in which the classification might be supposed to reflect exactly the applicability of genealogical hypotheses, because the 'expectations' derived from a genealogical hypothesis ('these are all descendants of X so they are expected to have character **d**') are just as likely to be unfulfilled, due to losses, convergences, and especially superimposed

synapomorphies. Only the strictly monothetic classifications of pattern cladists could be treated in this Popperian fashion, and they are therefore even less likely than Hennigian classifications to be stable.

The proposal of a taxon, then, is not a theory which is to be falsified, but as a concept which is to be validated by being found appropriate in several contexts. This is part of what Ruse (1987) appears to mean by a 'consilience of inductions' (the term is Whewell's: see also Ruse 1986). Taxa are rejected, not because they make 'predictions' which are not borne out, but because they cease to be found appropriate in various contexts. A concept which is no longer fruitful, no longer appears to reflect our knowledge of how the world is, is redundant.

$ 3.8 The Duality of Connective Hypotheses

> Genealogy by itself does not give classification since the amount of difference in the several branches or groups, though allied in the same degree in blood to their common progenitor, may differ greatly, being due to the different degrees of modification which they have undergone. Darwin (1859:520)

Current neo-Darwinian evolutionary theory essentially makes a two-fold statement about the pattern of diversity seen in the biological world:

I. Organisms are historically interrelated by genealogical affinity, and so all organisms can in theory be traced back to more or less distant common ancestors. This may be called the Theory of Common Descent (van Dongen & Vossen 1984; Patterson [1987] calls it the 'general' theory of evolution).

II. Organisms are modified during the course of evolution by various evolutionary processes, of which one of the most important is adaptive natural selection (its proportional contribution to evolution being a

subject of debate but its importance being undoubted).

This interlocking of the phylogenetic past with the adaptational present (the "twin game of evolution and natural selection" [Friedberg 1979]) results in a complex pattern of similarities and differences between organisms, which it is the systematist's job to arrange in some kind of order. The structure for classifications proposed by cladistics (i.e. holophyletic phylogenetic classification) contains an embedded genealogical hypothesis. A classic formulation of the principle of this type of classification is the list of the five basic ideas of Hennig given by Wiley (1981a). These include the assertions that

> all other types of relationship (i.e. phenotypic and genetic) are correlated with genealogical descent and thus are best understood within the context of genealogical descent with modification ... the best general classification of organisms is one that exactly reflects the genealogical relationships among these organisms.
>
> Wiley (1981a)

Are these assertions sustainable, or are there ways other than strict genealogy of constructing a general evolutionary classification? Cladists claim that their system is the optimal, and indeed the only objective, classification - at once the most natural and the most useful. Yet it is based on only one of the two components of evolution theory outlined above - the genealogical. Is it inherently logical to analyse the observed results of the two interlocking causal networks of evolution in terms of only one of them, unless it possesses an intrinsic priority? This priority is claimed for genealogy by cladists.

$ 3.9 Grades and Clades - I

> Monophylesis alone will not produce an evolutionary classification.
>
> Heywood (1964)

The fact of evolution is seen by phylogenetic systematists as implying

the priority of genealogy (e.g. Eldredge & Cracraft 1980:12), yet as is noted above, evolution theory proposes more about organisms than the mere fact of historical relatedness. If, as many evolutionists would argue, a prime mover in the generation of biological diversity is the adaptation of organisms by natural selection, then the features of an organism of interest to the ordinary structural or functional biologist (and so perhaps those which s/he might find most usefully expressed or predicted in classifications) are not those it possesses by virtue of ancestry but those it has acquired by natural selection, and even, perhaps, those especially which it has evolved convergently with other organisms undergoing similar selection processes. The fundamental mechanisms and laws by which organisms operate are perhaps to be most clearly seen in those organisms which have independently solved the same problems. Thus it is in convergent not divergent systems that structural and functional predictions can be made without the confusion of incorporating features which are the result of historical accident rather than selective processes. This was the insight behind the theory of nomogenesis, a scarcely popular alternative to orthodox Darwinism developed by Leo S. Berg (1926; see also Calabrese 1976). This theory stressed the convergence of polyphyletic grade-groups of organisms responding to the same selection pressures, and though it is justifiably ignored as an overall evolutionary theory, the notion of the structural 'grade' was advocated by such distinguished (if unfashionable) evolutionists as Julian Huxley and G.G. Simpson.*

If predictive value could be regarded as a valuable criterion for assessment of classifications, then there is no doubt that genealogical

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* In fact, much of Simpson's thought echoes (directly or independently) the ideas of Berg, particularly his conviction of the ubiquity and importance of convergence, a conviction shared by Cain (pers. comm.)(Benton 1988; Bennet-Clark pers. comm.).

classifications will enable 'prediction' of the attributes of organisms, but so will structural or functional classifications not based primarily on genealogy; investigation in comparative anatomy and physiology often proceeds by analogy between similar, even convergently similar, groups. It would seem worth questioning the implicit assumption that classifications constructed directly on structural or functional information are intrinsically less useful than those constructed on genealogical grounds. It can even be argued that gradistic or semi-phenetic classifications, based on the structure and function of organisms, are more likely to yield useful lines of investigation (?predictions) concerning structural and functional features than are genealogical ones (R.J. Pankhurst 1985, pers. comm.). There is a tension between two causal networks: genealogical descent, and consequent prediction by connective hypothesis of homology; and selective processes leading to convergent evolution, and consequent prediction by connective hypothesis of analogy. The Darwinian Principle of Divergence (Darwin 1859: chap.iv; Winsor 1976; Friday 1987) cannot be regarded as a law to be uncritically built into methods, like the properties of macromolecules: it ranks with Dollo's and Von Baer's Laws as a useful but constantly contravened heuristic guide.

The simple assumption that similar groups have a common origin is well known to be unreliable (Tatarinov 1977), and when ignorance requires the assumption to be made, it is used with extreme caution (Hart 1985a).

> A classification based solely on overall phenetic similarity may reflect phylogenetic affinity, but it carries no guarantee to this effect. Joysey in Heywood & McNeill (1964)

However, the converse assumption, that groups with a common origin have similar characteristics, is similarly unreliable: character-informative classification is therefore disengaged from phylogeny (as expounded at length by Bigelow 1956). Knowledge of lineage membership does not give a

reliable guide to possession of characteristics - not even synapomorphous characters, because these are theoretical attributes inferred to belong to the common ancestor, not actual attributes possessed by each member-species of the clade. Phylogenetic method, as much as phenetic method (Sokal & Sneath 1963), does not allow us to insist that all entities in a group have a particular characteristic: it is not essentially essentialist.

The situation with species definitions is analogous: the attributes proposed as characteristic of the species are not necessarily to be inferred as being possessed necessarily by any of the member-organisms of the species. Individual variation within a species means that if an animal is identified as, for example, a member of the marsupial (pouched mammal) species Macropus giganteus (grey kangaroo), one may not therefore predict that it has a pouch - it may be a male; similarly, species variation within a clade will mean that if a species is placed in the class Mammalia, it does not follow that it will possess each of the characters which characterize the clade Mammalia - it may be a species of furless mole-rat or toothless anteater. It could be argued that this analogy is imperfect: in both cases it is organismal characters about which predictions are being sought; yet the same holds if significance is attached to putative species-level characters such as population size, clade longevity or rate of sub-clade production. The resulting indeterminacy of taxon definitions has long been recognized, and is not restricted to holophyletic taxa:

> Whoever has paid the slightest attention to the classification of natural objects, whether plants or animals, must be aware, that if we desire to follow natural principles in forming our groups, - that is, to bring together such species as resemble each other in habit, properties and structure [not simply relying on a special classification by single properties], - it is a vain task to attempt to define, with absolute strictness, the classes into which we are forced to combine them.
>
> Harvey (1849)

> The student has always to bear in mind that he is dealing with definitions which apply not necessarily to every individual in the group defined, but only to the bulk of the members composing it. Branford (1890)

It is this fuzziness of definition which renders the pattern cladist approach to monothetic classification by way of necessary and sufficient essential characters appealing and yet hopelessly out of reach.

CHAPTER FOUR

*

PLURALISM AND PRAGMATISM

"Parmenides said: 'Either **it is** or **it is not.**' Aristotle began to say: 'We must consider the possibility that **it is** and **it is not.**' This is precisely the attitude that man in explaining natural law has to adopt from time to time."

Parker (1967)

"There is no little danger of throwing science into confusion if the taxonomist allows himself to be influenced by merely speculative considerations. The present essay is an attempt ... to draw up a classification of the animal kingdom, which ... may have some chance of permanence, in principle, if not in detail, while the successive phylogenetic schemes come and go."

T.H. Huxley (1875:201)

$ 4.1 Taxonomy in its Social Context

> It is not impossible for an individual to revise his own personal scheme of classifications. But no individual lives in isolation and his scheme will have been partly received from others.
> Douglas (1966:38)

> The taxonomist always has to keep in mind the practical aspect of his job, however great the temptation may be to search for the 'whole truth'.
> Riedl (1972:81)

> Taxonomists are a part of human society. Therefore, any system devised should also be a practical basis for other scientific work, beginning with identification, without which such disciplines as ecology and zoogeography cannot exist.
> Loof (1983)

> When Darwin was faced with new and unfamiliar names for his broad genus Scalpellum he rejected them, commenting that such changes undermined the basis of classification - by which we believe he meant convenience to the body of naturalists.
> Crisp & Fogg (1988)

Taxonomists have recently found themselves on the receiving end of strong criticism from both inside and outside their professional circle by researchers protesting that, in engaging in complex internal argument concerning taxonomic philosophy and the legalistic issues of nomenclature, taxonomists have isolated themselves from the users of taxonomies, who urgently require a general biological taxonomy insofar as such a thing can be provided. Interests such as the theoretical study of evolution and the investigation of phylogeny, which loom large on many systematists' horizons, are less important to the non-specialist consumer than the provision of usable, stable taxa - the nouns in the language of biology - and the development of reliable methods of species identification, separation and information retrieval by biologists, medical researchers and other scientists who are interested in historical (phylogenetic) information only when it tells them something about the present distribution of the features they are studying (Pratt 1977; Martin 1981;

Barnett 1986; Hawksworth & Bisby 1988; Heywood 1988; Pickersgill 1988; Haskell & Morgan 1988).

General classification, if the pheneticists' formulation ($ 1.1) is not accepted, is not easily defined, but is intuitively imagined as a utilitarian classification which satisfies most people most of the time. Stability is a constant concern of working biologists:

> As Linnaeus himself pointed out, the reference system must be such that it does not change as ideas on the interrelationships of particular groups change. Cain (1956)

Patterson (1987) asserts that the most general classification will be the one which makes least appeal to 'special' rather than 'general' theories of evolution, but his distinctions are less than entirely coherent. He regards 'Lamarckian' and 'Darwinian' models as the only two competing general theories of evolution, and natural selection as a special theory alongside neutralism. The only evolutionary input allowable in taxonomy is the bald assumption that evolution has occurred, with the supplementary presumption that it has been consistently divergent (a presumption often made rather too lightly; Friday 1987). Evolutionary taxonomy is criticised by Patterson for appealing to special theories of evolution (such as hypotheses about rates of divergence) in order to recognise the non-existent groups in which it purports to find significance. In fact this is not quite true - evolutionary taxonomy does not require a hypothesis of evolutionary rate in order to justify recognition of a paraphyletic taxon, merely an observation of evolutionary divergence which is regarded as significant.

Ridley (1986), on the other hand, regards the most general classification as the most unambiguous, reflecting the cladistic theme that a particular quality of information is to be preferred to quantity, and that precision is to be sought at the cost of comprehensiveness.

Patterson himself admits that there are two effects of evolution, the phenetic and the cladistic, evolutionary taxonomy attempting to reflect both in some degree rather than ignoring one in order to be unambiguous about the other. If a general classification is to be utilitarian, the best way of assessing it would seem to be to investigate the opinions of the potential utilisers.

Eldredge and Cracraft (1980:1) note that

> ecological and distributional considerations ... lead to different general approaches to the very perception of patterns in the organic world.

One might well add that the same is true of genealogical and adaptational considerations. Yet, as has been pointed out above ($ 3.8), if it is so readily accepted that different patterns can be perceived in the natural world, it does not seem inherently logical to restrict the classification and analysis of these differing patterns to terms derived from only one of them (e.g. cladogenesis, as proposed by Hennig [1966], or teleology, as apparently intended by Berg [1926]), unless it possesses an intrinsic fundamentality with respect to the others. According to Eldredge & Cracraft, valid theories about the origin of non-monophyletic (i.e. non-existent) groups cannot be made, and the recognition of such groups

> distorts not only the information content of the classificatory system, but also our very notions of evolutionary processes.
> Eldredge & Cracraft (1980:13)

This of course runs precisely counter to the arguments of evolutionary taxonomists: that it is a distortion to restrict evolution and classification to cladogenesis (Mayr 1987 et ubique). Is our notion of evolution so radically illuminated by the elimination of non-holophyletic taxa? My earlier discussion of extinction has suggested that this is not necessarily the case: paraclades may be a useful component of the conceptual armoury of the palaeontologist.

$ 4.2 The Conflict of Interests

> It may be said, that, as there can be but one natural system strictly speaking, it is impossible that both these principles can conduct to true results. This would be correct if animals exhibited only one **kind** of relation to each other. But we know that they exhibit more than one ... notwithstanding the opposite nature of these principles, the day may come, in which it will be found possible to reconcile the views to which they have respectively given birth. Jenyns (1837)

> It is notoriously not possible to represent in a series, on a flat surface, [all] the affinities which we discover in nature amongst the beings of the same group.
> Darwin (1859:422)

The Systematics Association conference on 'Prospects in Systematics' in the summer of 1987 saw much discussion of the need for taxonomy to be informative (Hawksworth & Bisby 1988, Bisby 1988), and the external pressure for stability and for a clear guide as to what is actually implied or not implied by the current systems (e.g. by Felsenstein in discussion).

As has already been mentioned, classification plays a central role in theory-making, as it specifies the groups about which theories are to be made, and it may thus significantly affect the way explanations are sought in a particular case. If the concepts appropriate to one causal explanation are built into the taxonomy, then the explanation of patterns produced by processes other than that built into the system of taxonomic terms is to some extent precluded, or at least rendered more complicated a task. So, while gradistic classifications may hinder the macro-evolutionary theorists, cladistic classification may obstruct investigation in other branches of biology. To subsume taxonomy under phylogeny is rather like subsuming anatomy under descriptive embryology (cf. Sewall Wright's classification of biological disciplines - Gerard 1958:107). To insist that anatomical structures must be named and classified only in terms of their ontogenetic origin would be seen by most biologists as frankly silly:

few would deny the existence of the pituitary gland as an entity because it does not have a unitary development.

One might refer again to Barnett:

> Part of the trouble comes from the ... confusion of biological classification with evolutionary studies.
>
> Barnett (1986)

Barnett, under the polemic, is arguing about usefulness - in effect asking that question so singularly avoided in Ridley's study: "What is taxonomy for?" Obviously for Barnett, it is not just about phylogenetic reconstruction. We have come up against the problem of deciding for whom a general biological classification is supposed to be useful. The field of macro-evolutionary and phylogenetic studies is in the process of establishing itself as an area of modern scientific enquiry, but it must expect to need its own vocabulary, and cannot necessarily impose its particular requirements on the whole of biology (especially when those requirements are still not adequately agreed upon; Patterson & Smith 1987, Sepkoski 1987). The complex interweaving of different networks of explanation - different sets of connective hypotheses - makes it important not to tie taxonomy too closely to any one embedded hypothesis. What is needed, in other words, is an imprecise, pluralist, consensus taxonomy. Even if a phylogenetic system were widely adopted, cladists would have to

> concede the right of other ... biologists to set up other systems of categories if we feel that we need them in order to group information adequately.* Grant (1986:541)

> I .. am no longer willing to be told by pheneticists and cladists, and before them by phytochemists and cytotaxonomists, that my work is already outdated and that I should use whatever the newest, trendiest methodology might be.
>
> Buck (1986)

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* Completely non-genetic categories, such as palaeontological 'form-genera', or the ammonoid shell morphology groups used by Saunders & Swan (1984), deliberately independent of conventional taxonomic grouping or phyletic lineages, would not normally be expected to contribute to the framework of taxonomic nomenclature.

$ 4.3 Heuristics and Linguistics

The ontological argument for reality of higher taxa does not in the end produce a justification of cladistics, and Eldredge & Cracraft (1980) do not really recognise it as providing such. The debate concerning the heuristic or epistemological value of different systematic approaches reflects differing opinions regarding the importance or significance in evolutionary models and descriptions of various natural processes and the (?natural$_L$) groupings which result from them. (So it may be that those attracted by theories of neutral evolution such as that of Kimura may tend towards cladistic taxonomy, while those investigating adaptation and selection may not, those dealing with reticulate groups of plant species even less.) The value of a cladistic approach to phylogeny is certainly great, in that it clarifies the logical structure of the process of historical reconstruction; but does the cladistic style of classification by strict common ancestry represent such a valuable tool? Some would argue that it does, and cite as independent corroboration of its value the almost universal adoption of cladistics by linguistic historians (Platnick & Cameron 1977, Patterson 1980).

> It often comes as a surprise to biologists that the predominant method in linguistic classification has been cladistic for well over one hundred years. Hoenigswald & Wiener (1987:xi)

It might be supposed from the above quotation that the field of linguistics represents a possible source of comparison for assessing the potential usefulness of cladistic taxonomies in biology. The terminology of historical linguistics has from the mid-nineteenth century (in particular since the work of August Schleicher: Wells 1987) been loaded with biological metaphors of descent: filiation, parent-, sister- and daughter-languages, and language families or stocks. Schleicher (himself,

not incidentally, also a geologist; MacMahon 1988) constructed branching diagrams (Stammbaume) and compared them with Darwin's family trees; moreover

> Schleicher's diagrams were not mere logical schemata. As he himself explains, 'The length of the lines indicates the amount of time which had elapsed and the distance between them degrees of relationship.' In this respect, Schleicher's trees differed from the traditional tree of Porphyry or Porphyrian scale, which was a purely logical method of exhibiting the series of subaltern genera to which a concept may be assigned.
>
> Percival (1987:6)

It is also undeniable that languages are functional systems, and hence individuals in a strong sense (Ghiselin 1987).

In fact, the evolution of language being at once more apparent (e.g. from old manuscripts, or even in living memory) and less theologically sensitive than that of living organisms, the understood significance of the 'nodes' in the dendrograms shifted from abstract archetype to hypothetical common ancestor more readily in linguistics than in biology: as linguistic monophyly and divergence was rather suggested than excluded by Scripture (see Genesis ch. 11 v. 1 as against ch. 1 v. 25) it was possible even at the dawn of comparative linguistics in 1786 for Sir William Jones to propose common origin as the source of similarities between Sanskrit and the classical European languages (Renfrew 1987:9-10). In the significant year of 1859, Adolphe Pictet set out the basis of a 'linguistic palaeontology' which was ultimately to foster hypotheses not only of linguistic but of ethnic relationships (ibid.:14-15). Does such overwhelming acceptance of cladistic classification by historical linguists give grounds for confidence among biological cladists? I suspect it should not.

Languages and their constituent parts show even more commonly than do organisms (especially plants) the characteristics of parallel evolution

('common development' - Renfrew 1987:104) and reticulate evolution (that is, evolution by borrowing of characters, or even large-scale hybridization, as in Maltese, Yiddish, English; Mithun 1984, Wells 1987). These are the very features which make cladistic analysis not only difficult but also necessarily inaccurate (because they contravene the assumption of divergence). The reconstruction of linguistic history by lexico-statistical methods (i.e. arithmetical comparisons identical in principle with those of phenetic taxonomy: Sokal 1966) or by glottochronology (a form of cladistics - in manuscript studies known as 'stemmatics') runs into the same problems as are encountered by those attempting to construct molecular and organismal phylogenies - rates of evolution cannot be assumed to remain constant, and suitable similarities must be available to be analysed in cladistic terms in order to provide chronological information. Languages also have an important characteristic which separates them from organisms and renders cladistic classification a more useful tool in linguistics than might be the case in zoology: they are arbitrary. No analogue to adaptation, to the environment, or to selection, exists in the history of languages.* There is consequently no criterion of theoretical relevance that might claim to take precedence in classification over that of cladistic (genealogical) significance, where such is discernible. In zoology, however, significance has more to it than the mere carrying of cladistic information.

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* We have no standards (or only the most conjectural) by which to assert that any human language is intrinsically superior to any other, that it survives because it meshes more efficiently than any other with the demands of sensibility and physical existence... No language is demonstrably adaptive... None is concordant with any particular geophysical environment.
Steiner (1975:54-5)

$ 4.4 Theory Making and the Naming of Names

> Things are not quite real until they acquire names and can be classified in some way. Tuan (1977:29)

> Human beings are merely a highly derived subgroup of osteolepiform fishes. Long (1988:44)

The cladistic assertion that the only objective taxa are those marking off clades ('closed descent communities' [Ax 1985a], the 'real individual-like unities of Nature' [Ax 1987:23]), leads inevitably to the conclusion that much of what is written by well-meaning biologists concerning evolutionary history is fallacy, misunderstanding, or plain error. The full force of Ax's logical battery is directed against the unfortunate Kemp (1982) and his discussion of the origin of mammals from reptiles.

> As purely human errors, formulations of this sort do great mischief in the phyogenetic (sic) literature. Ax (1987:220)

However, it is difficult to claim that what Kemp writes is meaningless, or even misleading. For example, a statement is made to the effect that the origin of mammals represents the origin of one vertebrate class from another. Ax, in the spirit of Wiley's condemnation of 'supra-specific ancestors' (Coomans 1983) and of his own insistence on 'closed descent communities', protests that this simply cannot have happened. He ignores the fact that such statements are universally accepted as shorthand forms of longer, more precise statements of the form: "the common ancestor of the mammals (or birds) was derived from an animal which was morphologically and, by inference, genetically similar to those non-mammalian tetrapods called reptiles, and which may therefore be grouped with them in a meaningful taxon".

> Paleontologists often speak of a population, or species, or higher category as being adapted. Kitts (1974:462)

As previously mentioned ($ 1.3), "derived from taxon B" is in most contexts simply a synecdoche for "derived from a single member of taxon B", and I have never met a biologist who did not understand it as such (with the possible exception of Patterson; I never met Simpson!)(so, e.g., Levinton 1988:397 note).

Cladistic taxonomy leaves the biologist with a peculiar lack of terminology with which to ask or answer a range of questions.

> "So, Dr Kemp, what kind of animals were the ancestors of the mammals?"
> "Well, they were synapsids - a group of reptiles."

But in Ax's classification (sorry, systematization) the synapsids are included in the mammals, and the reptiles do not exist at all. Cladistic taxa never evolve from other taxa: they are just included in them.

> "So, Dr Ax, what kind of animals were the ancestors of the mammals?"
> "Well, they were members of the mammalian stem-lineage."
> "?"
> "Er, they were amniotes (synapsids, tetrapods, vertebrates)."
> "Yes, but so are mammals. What were they that mammals are different from?"
> "Um, they were non-mammalian amniotes (synapsids, tetrapods, vertebrates)."

What I am attempting to suggest is that if biologists are to talk about evolutionary transformation of organisms - and they are certainly expected to - they need to be able to use names for groups (classes) in the knowledge that they are actually conveying information by using them. Even Eldredge emphasizes that

> a legitimate paleoecology will need to generalize about classes of individuals. quot. in Ghiselin (1987:111)

In particular, the names of paraphyletic groups associated with the stem-lineages of distinct holophyletic grades are not superfluous, as Kemp (1982) clearly recognizes (see also Tassy (1988)). The dismissal of such language as meaningless (an imputation common to much positivist

philosophy) seems to come perilously close to abolishing meaning altogether.

Clades no doubt form an important part of the biologist's conceptual vocabulary. Yet not all biological questions - not even all evolutionary questions - are actually about clades. Cladistic analysis uses characters for their phylogenetic information content, and discards non-synapomorphous character-states, seeking to make classification reflect solely the study of cladogenesis (creation of clades) rather than that of anagenesis (the transformation of characters within lineages); but the rest of the biological world persists in finding characters interesting of themselves.*

> Degree of similarity between groups is ... more than a tool in constructing a classification; it is of interest in itself.
> Greig-Smith (1980:6)

Macro-evolutionary theorists seek to make theories about clades as units, but while from their point of view, 'taxic' theories become paramount (Hecht & Hoffman 1986:28), other 'non-macro' studies still concern themselves with transformational (or micro-evolutionary) history and theory; the dissociation of the two levels of enquiry may even require a two-level taxonomy. Theories about clades may require framing in terms of clades, but theories about organisms may need terms for evolutionary groups other than clades. Even now, there are two classifications available for many groups of organisms: one cladistic, often complex and unwieldy; one more pragmatic, adopting paraphyletic groups where useful, and reflecting the consensus of ignorance rather than the contentions of speculation.

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* Shared interest in characters does not justify the occasional claim of cladists (e.g. Brundin 1972) that evolutionary and phenetic taxonomy are effectively based on the 'same' criteria, for the functional and evolutionary interests of the evolutionary taxonomist are alien to the non-theoretical approach of the pheneticist.

$ 4.5 Parataxa and Informativeness

> The monophyletic ideal demands that the overall similarity between ... 'distantly related' species, as well as the extensive overall differences between them and those species with whom they share a more recent common ancestor, should be disregarded. Overall similarities and differences are usually **not** disregarded in such cases, however.... Monophyletic classification, therefore, is obviously not the ideal of taxonomy. Bigelow (1956)

The systematist or evolutionary theorist is interested in the discovery of facts previously unknown to science; but the applied biologist or specialist researcher needs taxonomy for 'predicting' not just truly novel facts, but facts previously unknown to the investigator - in other words, informativeness is the priority.

Evolutionary taxonomies, as Hull (1985) remarks, are "correlated to phylogeny in a loose kind of impressionistic way".* The evolutionary taxonomist's groups based on shared retention of primitive features are described as being "of dubious cohesion", but this can only be meant in the vaguely abstract sense of "hanging together as a group", since, as Eldredge & Cracraft (1980), Wiley (1981a) and Ax (1987) admit, higher taxa of any status have no direct or 'synchronic' cohesion. Nevertheless, some paraphyletic taxa are in fact of remarkable 'cohesion' as recognised groups, and come unstuck only on the application of the cladistic criterion for taxon-validity. The criticisms of evolutionary classifications often thus reduce simply to protestations that they are, after all, not cladistic classifications (e.g. Ax 1987:188).

Parataxa are retained because of their important role as informative classes; they are almost invariably grades of some kind. Holophyletic taxa

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* Evolutionary taxonomy may be 'impressionistic', but if we are going to borrow analogies from art, we might note that while expressionism is concerned with the self-projection of the observer and his moods and feelings onto the world, impressionism is almost dispassionately objective in its concern to reflect nature as it is observed to be (Reeves 1967)!

may also be grade-groups, of course: Mammalia is an example of a grade-group which is also thought to be a holophyletic taxon (though some, including Simpson, have had their doubts about this because of the failure of attempts to find osteological defining characters for the group - features consistently present in modern forms appear gradually and repetitively in the fossil record of Mammalia and its collaterals [Simpson 1961, Kemp 1982, Kirsch 1984]).

$ 4.5.1 The Persistence of Parataxa

> Only robust classes of objects acquire names.
> Edwards & Cavalli-Sforza (1964)

The use of established parataxa by biologists is not showing too many signs of declining: even the archetypal parataxon Reptilia continues to appear, e.g. in the taxonomic designation of papers in the Journals of the Linnean Society, and in lists of fauna such as Frailey's (1986) of the Tertiary.

Moreover, biologists still consciously construct paraphyletic taxa at a variety of taxonomic levels. For example, Archimerata (= Lophophorata + Echinodermata + Hemichordata: i.e. excluding Chordata) was established by Emig (1976) as "a phylogenetic stage and a natural systematic unit" ("cet assemblage est située à la base de la lignée des Chordata, il est considère comme un stade phylogénétique et une entité systématique naturelle"). This diagnosis is made quite unambiguously, the intention being to unite a series of phyla related by inferred common origin, and which retain a large number of ancestral shared characters derived from that common origin, without decreasing the informativeness of the grouping by including those organisms which have significantly diverged (i.e. the chordates and their

close relatives). Emig indeed finds the informative value of this taxon overwhelming: "nous nous éfforcerons de dégager un concept pour l'ensemble de ces groupes zoologiques".* Margulis (1988) is similarly unambiguous in her championing of the paraphyletic Kingdom Protoctista.

Other probable parataxa in widespread use include two of the three main divisions of annelid, Polychaeta and Oligochaeta:

> The polychaetes are almost universally considered the most primitive annelids ... and the oligochaetes and hirudineans have been derived from the polychaetes. Fauchald (1974)

> The Hirudinea are widely accepted as a derivative from oligochaete stock. Mettam (1985)

and the platyhelminth group Turbellaria:

> All the characteristic features of the 'Turbellaria' (free-living, body covered by a ciliated epidermis, etc.) are plesiomorphies; the 'Turbellaria' without doubt represent a paraphyletic group. Ehlers (1985)

Even authors whose work announces itself to be cladistic in methodology show a tendency to use parataxa in their final conclusions. Hart (1985a, 1985b) presents a Hennigian analysis of the plant genus Lepechinia and gives a cladogram on which proposed sister-group relationships and synapomorphies are clearly indicated. The section Salviifoliae, which had earlier been suggested as a possible sister-group to section Parviflorae, turns out to be paraphyletic: yet Hart refrains from any nomenclatural juggling to break up Salviifoliae into holophyletic subgroups, or to move the species cladistically closer to Parviflorae into that group. In other

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* It is debatable, it must be admitted, whether formal taxon-names are justified at the super-phylum level: the information is perhaps better served by a set of informal group designations (the lophophorates; the arthropods; the deuterostomes) supplemented by diagrammatic evolutionary trees. 'Archimerata' is unlikely to make it as a useful taxon outside the realms of phylum-level phylogenetic studies; for most investigators, the statement "Echinodermata is grouped with Lophophorata in the Archimerata" has little to recommend it over "lophophorates are close relatives of the echinoderms". But see d'Hondt (1989), who recommends the use of 'embranchments' (after Lamarck's 'embranchements') for distinct and delimitable groups of phyla, holophyletic or paraphyletic.

words, he has concluded his phylogenetic analysis with an evolutionary taxonomy. Tassy (1988) similarly includes admitted paraphyletic groups in his classification of proboscideans, as genera in quotation marks, or as stem-groups labelled in a subsidiary fashion on the cladogram: Kemp (1982) also uses this latter convention.

A few examples persist of Simpsonian parataxa where the excluded descendants are placed together in a polyphyletic taxon, on the grounds of both phenetic and presumed underlying (convergent) genetic similarity: oysters in the genus Gryphaea, for example, have apparently arisen independently on several occasions from Ostrea, yet the similarity in form between the various lineages has led to the same name being given to them all (Arkell & Moy-Thomas 1940; Maynard-Smith 1975). Such known polyphyletic taxa are occasionally retained, mainly for the sake of nomenclatural stability or simplicity, even though many evolutionary systematists would now consider such polyphyly extraordinary and unacceptable. Unless such an instance is shown to occur at the species level, it would seem better to avoid such 'horizontal' assemblages; Simpson's definition of monophyly is inadequate and few would now attempt to use it (see §1.3). Nevertheless, Rosenberg does discuss the possibility of polyphyletic species, as might occur with several allochronous yet genetically indistinguishable parthenogenetic hybrid populations of a species such as the lizard Cnemidophorus (Rosenberg 1985:210) - it is this example which poses interesting problems concerning the spatio-temporal restriction of taxa.

Numerous further examples of widely accepted parataxa could be cited: the related heteropteran superfamilies Coreoidea, Pyrrhocoroidea and Pentatomoidea all apparently represent separate clades arising from the paraphyletic stem-taxon Lygaeoidea (Schaefer 1976); so likewise the social

hymenopteran subfamilies Polistinae, Stenogastrinae and Vespinae from the paraphyletic ancestral group Eumeninae, and possibly Apidae from Sphecidae; the marsupial superfamily Macropodoidea may have arisen from within another, the Phalangeroidea (Beveridge 1986)(cf. $4.6).

> Though I agree in considering that the three-toed woodpeckers (Picoides) present terminal developments of the Nearctic representatives of Dendrocopos, I do not see that the theory of their relationship should lead to nomenclatural consequences. Besides, there are sufficient taxonomic [i.e. nomenclatural] reasons for not merging Picoides and Dendrocopos and so avoiding serious nomenclatural inconvenience. Vouss 1977:vii

In this case, the smaller genus, Picoides (2 spp.) takes priority over the larger, Dendrocopos (22 spp.), according to the rules of nomenclature, so amalgamation requires the renaming of the majority of the species in question, as is therefore done by some North American ornithologists. A cladist would have to split the whole of Dendrocopos into small genera to continue (separate) generic recognition of the three-toed woodpeckers.

$ 4.5.2 The Delineation of Parataxa

All the acceptable parataxa mentioned above share a common feature: they are true paraclades - clades defined by common ancestry, from which one or more well-characterized subclades have been excluded.

Because taxa are not strict monothetic classes, loss of single features which typically act as diagnostic features of a group is not usually regarded as sufficient to warrant the removal of a sub-group to a new evolutionary taxon - for example, among mammals, new major subdivisions are not generally proposed simply to accommodate furless variants (the naked mole-rat Heterocephalus), toothless ones (the anteater Myrmecophaga) or those with extraordinary numbers of cervical vertebrae (the sloth Bradypus). What makes a new natural category appropriate is a grade-shift, an innovation which removes a sub-group from a taxon by placing it outside

the focus of the 'consilience of inductions' (Ruse 1987) which renders the taxon a usable scientific concept, or making it the focus of a new and distinct 'consilience' (a new $natural_A$, $natural_L$, temporarily $natural_C$ and perhaps to some degree $natural_P$ taxon)(Van Valen 1971, Schaefer 1976). Though this may represent the breaking out of an apparent evolutionary canalization within the stem-group, it need not necessarily result in the spectacular diversification of an 'adaptive radiation' - very odd yet very restricted grades tend to get placed as abnormal variants at an intermediate level within the stem-taxon (e.g. the placing of Sacculina within Crustacea, and the generic, or sometimes familial, but never sub-ordinal separation of Homo within Primates - though a separate kingdom Psychozoa has been proposed). The important factor is the level at which comparison is thought to be of theoretical significance, at which some analogy or analogies can be drawn between the stem-taxon and the crown-taxon which make the contrast meaningful.

$ 4.6 Parataxa as Contrast-Groups

When an established genus is split to raise the rank of a particularly distinct subgroup, the original genus will become paraphyletic (e.g. Capnura [Plecoptera]: Nelson & Baumann 1987; Dendrocopos [see $ 4.5.1 above]: Vouss 1977) unless the excluded subgroup happens to be the most cladistically plesiomorphous branch. According to the rules of cladistic taxonomy, it must be completely dismembered by raising all the other subgroups to generic status - if this is possible (and the remaining sub-groups may be less easily delineated) it may be useful, or it may simply obscure the contrast-group relation between the parataxon and the crown-taxon. It is this relationship which Hart (1985b) preserves in his taxonomy of Lepechinia ($ 4.5.1).*

The contrast-group relation is a more general version of the relation within successive divisions of a dichotomous classification such as the 'Tree of Porphyry' (Nelson & Platnick 1981; Panchen 1987). Each taxon in a taxonomy belongs to a contrast-set: a group of taxa which are all subsumed under the same immediately superordinate taxon (Kay 1971: though I am not using his particular terminology). In the special case of monotypic (formally 'redundant'+) taxa, the subsumed contrast-set consists of only one taxon: otherwise, for every taxon there is at least one contrast-group.

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* This frequently creates problems for methodological cladists, who may come across a set of genera derived from a coherent and distinct parent 'paragenus', which is not cladistically definable, being characterized by lack of the synapomorphy of the derived species. Ride (1988) proposes that the first element in the binomial should be changed to be of higher rank, to avoid the chaos resulting from generic dismemberment.

+ Examples are numerous: among extant mammalian taxa there are seven monofamilial orders and twenty monospecific families, among which is one monospecific order, Tubulidentata (containing only the aardvark, Orycteropus afer)(Corbet & Hill 1986). Of this molehill - the existence of non-identical sets with identical membership - the logicians have made something of a mountain (Gregg 1954, Simpson 1961).

[Note that this is not simply intended to mean (as e.g. Eldredge & Cracraft [1980] would present it) that for every class 'A' characterized by a feature '**a**' there is a class 'not-A' of elements lacking '**a**'.] The contrast-group, then, generally comes at the same rank in a taxonomy (in a cladistic taxonomy it constitutes the sister-group) and falls into the same class at the next highest rank. So, for example, within Vertebrata, Agnatha may form the contrast-group to Gnathostomata (at the rank of superclass or similar). Dichotomy is not necessarily required - the orders of insect: Hymenoptera, Diptera, Coleoptera, etc., form a set of contrast-groups. It is this relation which is referred to by some as 'taxonomic equivalence': groups bearing the same rank are held to be comparable in some sense (Schaefer 1976). The problem with taxonomic equivalence, as the concept is usually expressed, is that it does not adequately distinguish true contrast-groups [i.e. sub-classes of the same class (in either the general or the zoological sense) - 'direct contrast' in the terminology of Kay (1971)] from merely accidental equivalents (e.g. sub-families in different phyla)(Simpson 1963).

Among taxonomic ranks or categories, only species have any claim to absolute status; the other ranks are purely relative. Genera, for example, are groups of similar related species smaller than (or occasionally co-extensive with) subfamilies:

> There is no objective criterion for determining the limits of genera, it is largely a matter of personal philosophy ... Common sense is of paramount importance. Loof (1983)

Nevertheless, taxa at these ranks do function as informative units, usually (even in cladistic taxonomies) as grades: species in the same higher taxon share some significant feature (Kemp 1988a) or group of features (Maggenti 1983). Insect orders, for example, represent structural ground-plans which remain recognisable to a greater or lesser extent throughout the order.

Their diversification may vary, of course, so that, for example, Diptera are more variable in overall morphology than either the even more numerous Coleoptera or the much scarcer Psocoptera - this fact is itself interesting. It is because the order-names implicitly carry such information, that distinct grade-groups may be excluded from paraphyletic taxa - for example, the Strepsiptera are excluded from Coleoptera, and the Siphonaptera from Diptera (or maybe from Mecoptera; Ross 1974:47) - by evolutionary taxonomists who happily accept the phylogenetic derivation of the 'crown' holotaxon from the 'stem' parataxon.

> When something is firmly classed as anomalous, the outline of the set in which it is not a member is clarified.
>
> Douglas (1966:38)

It might be protested that information is lost in such grouping, but information is lost in any grouping, and there is a distinct difference between the mathematical concept of information, with its connotations of randomness and entropy, and the taxonomic concept of informativeness, which has to take account not only of the information as pure data, but also of the would-be-informed (cf. $ 5.1).*

This does imply, of course, that determination of the ranks of taxa is due mostly to their relationship to other taxa, not by any inherent property or diversity of the organisms.

> If the asteroid [that eliminated the dinosaurs had] missed, the problems of reptile paraphyly would never have arisen, because birds and mammals would have had the same rank as any other amniote subgroup; and cladists would have had much less to talk about.
>
> Gee (1988:506)

But the asteroid didn't miss, the birds and the mammals did undergo dramatic adaptive radiations, and the evolutionary classification which assigns class status to them recognizes the facts of history. Certainly,

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* Hence the aridity and difficulty of application of analyses such as that of Mickevitch & Platnick (1989), who discuss the formal information content of cladograms with varying patterns of branching.

if a significant evolutionary event (a grade-shift) had not occurred, the taxonomy would not be as it is, but taxonomy does not deal primarily with what might have been the case.

$ 4.7 Negative Characters and Plesiomorphies

'Positives' and 'privatives' are not opposed as are contraries
Aristotle **'De categoribus'** X

Some confusion over how contrast-groups are delineated arises from the 'transformed' cladistic philosophy, which in seeking to eliminate evolutionary assumptions from its method, attempts to redefine cladistic terms in non-temporal language, so that 'holophyletic clade characterized by a shared derived character' becomes 'monothetic class defined by an exclusively possessed character'. It can then be argued that only taxa definable by exclusively possessed characters may be accepted; paraphyletic taxa are 'not-A' groups, whose unreality as 'negative' or 'privative' classes can be argued along purely logical lines which date back to Plato: the definition of 'Greeks' does not simultaneously delineate a valid class 'non-Greeks', because the members of the latter class share no feature other than the negative one of not being Greeks (Wiley 1981b).

The problem is that paraphyletic taxa are not necessarily characterized simply by the absence of a positive character defining the crown-group: they may not be 'privative'. For example, two families of midge are recognized, of which one (Chironomidae: the non-biting midges) contains midges with reduced mouthparts, while the other (Ceratopogonidae) has toothed mandibles and maxillary blades. Current theory supposes that the Chironomidae are in fact a sub-clade of Ceratopogonidae, and so have lost features during the course of evolution. The absence of the mouthparts constitutes a synapomorphous character state. From a purely logical point

of view, it is the Chironomidae which are non-definable, being characterized only by lack of the characters present in Ceratopogonidae - they are a 'not-A' group; yet in phylogenetic (sc. evolutionary) terms it is the Ceratopogonidae which are paraphyletic. The negative ('privative') characters are in fact synapomorphies, and the positive characters are symplesiomorphies.* Evolutionary cladistics is able to resolve this in the phylogeny by a method of parsimony linked to the explanatory assumption of character transformation, but without such a hypothesis of character transformation (i.e. evolution), 'pattern cladistics' is hard-pressed to avoid pure phenetics.

The presumption that taxa must be defined as 'A' groups not 'not-A' groups can be extended to ludicrous lengths. Patterson, for example, denies the acceptability of such plesiomorphic (or at least apparently privative) designations as that of Insectivora and makes the somewhat facetious comment:

> May the reader have more success than I did in deciding what organisms fit this description (oppossums, caenolestids, notoryctids, lizards, toads, pitcher plants?).
>
> Patterson (1982:59)

The point to be made here is that even in the basic Tree of Porphyry, the dichotomies are never in the form: 'A' versus 'not-A'; but always: 'Z and A' versus 'Z but not-A'. At each stage of the taxonomy the previous operations are assumed, and the possibility of pitcher plants getting into a taxonomy of mammals is not even remote. In any case, it is frequently possible to restate a privative definition to read as a positive one (instead of 'absence of the derived state' read 'presence of the ancestral state').

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* I have since found this point similarly discussed in Ax (1987).

Patterson (1982) admits the stability and convenience of paraphyletic groups which recognize the occurrence of evolutionary advances, and his argument against evolutionary taxonomy is based on the "crippling disadvantage and unfortunate consequences" of their uncharacterizability (or indefinability; Funk 1986), but as is here shown, this assertion is based on the peculiarly restricted view that a group may be characterized only by positive monothetic definition: in fact, paraphyletic groups may be amenable to very precise definition. As Meacham & Duncan (1987) point out, you do not, as Wiley supposes, have to enumerate all the members of the class Reptilia in order to find its limits: a reptile can be simply recognized as such.

$ 4.8 Grades and Clades - II

> These taxa are indeed real, in the sense that they result from a real evolutionary event, the breaking-through of a progenitor-population into a new adaptive zone, i.e. the attainment of a grade. Schaefer (1976)

I have suggested that not only parataxa but also holotaxa may be best construed as grade-taxa: many holotaxa are coextensive with grade-groups. Even the 'arch-individualist' Eldredge treats Hominidae as a grade:

> By 3 million to 4 million years ago, in Africa, there lived upright bipeds who, if not yet qualifying to be known as human, nevertheless possessed some of those attributes which are unique to our own species in the modern world, and who can at the very least be admitted to our own zoological family, Hominidae. Eldredge & Tattersall (1982:7)

Some holotaxa, however, have proved singularly unsuccessful in their reception by the wider taxonomic community: the vast Hennigian system of Boudreaux, with its unmemorable names for rank upon rank of arthropod clade, seems unlikely to gain any wide acceptance among entomologists. The reason for this seems to be that only those holotaxa which are co-extensive

with some form of grade are meaningful to the biologist.* Truth is not necessarily usefulness: the world is full of potential groupings or distinctions which have no interest whatsoever.

Not all grades are potential taxa, of course (Schaefer 1976). In the course of a critique of sociobiology, Eldredge & Tattersall (1982) claim:

> In their zest for universal generalizations, sociobiologists have violated the cardinal rule of evolutionary biology: explanations of evolutionary history must be made for groups that evolution has produced [but see Pratt 1972: § 2.9].

Looking for common elements in societies is like studying the "taxon" [sharks + porpoises + ichthyosaurs];

> All we learn is principles of hydrodynamics. The group does not exist.

But we will learn more than that from study of convergent evolution. And of course, principles of hydrodynamics may be interesting to the biologist! Nevertheless, hydrodynamics itself is not part of evolutionary theory, but a physical theory with biological applications.

> This type of analysis accomplishes an important task, but it will not tell us why a shark differs from an ichthyosaur or a fish from a whale. Rindos (1986:318)

The group of organisms is a structural grade in some sense, but not a potential evolutionary taxon. The difference has long been recognized

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* One important obstacle stands in the way of any attempt to give a complete picture of the phylogenetic relationships among species: the number of categories needed to show such relationships is so great that the classification would become unwieldy to the point of uselessness.
Schenk & McMasters (1936)

The problem of the numerous different ways in which a cladogram, even when agreed upon, may be converted into a classification, has plagued cladists: Tassy (1988) discusses the problem, showing that arbitrary choices must necessarily be made about which nodes on the cladogram are actually to feature in the formal classification, and at what rank (absolute rank from absolute age or degree of derivation having been long since abandoned as unworkable: Simpson 1961).

between homologous and analogous characters,* the distinction now generally being taken as that between characters with a historical (genetic) continuity and those which are convergently similar (Winsor 1976). Taxonomic recognition in an evolutionary classification is restricted to convex taxa: those which have a historical continuity.

The notion of convexity (mentioned at $ 1.3) has recently come into prominence as a term for taxa which are not polyphyletic, and are thus potentially acceptable in evolutionary taxonomy (Estabrook et al. 1976, Estabrook 1978, 1986, Duncan 1980, Meacham 1980, Meacham & Duncan 1987, Stuessy 1987; see also $ 4.9). Convex taxa form connected sets on a phylogenetic tree, whereas non-convex taxa are topologically disjunct. In other words, all members of a convex taxon are directly related to one another through a sequence of ancestors and descendants. This is not a

* The distinction was originally made in a non-evolutionary context, and 'homology' as used by Owen from the 1840s (replacing the earlier usage of 'affinity' by, e.g., MacLeay the quinarian and T.H. Huxley: Winsor 1976) meant 'essential similarity', conceived in either topographical or embryological terms (cf. Jenyns 1837, T.H. Huxley 1894, Tomlinson 1984a, Aboitiz 1988). Darwin's use of the term varied between typological and evolutionary senses: in The Origin of Species (1859), for example, he refers to

> the swim-bladder...homologous, or 'ideally similar', in position and structure with the lungs of the higher...animals.
>
> Darwin (1859 vi:191)

By contrast, in his book on orchids (1862) he states unequivocally that

> all homologous parts or organs, however much diversified, are modifications of one and the same ancestral organ.
>
> Darwin (1862 vii:288)

Subsequent writers were often ambiguous, and the evolutionary implications of the term were not sufficiently well established to be written into the Oxford English Dictionary (Vol.V: 1899). However, they are now completely dominant in mainstream biology (see Lincoln et al. 1982) except in some respects with reference to 'serial homology' and to the correspondences of molecular sequences (see Fitch 1988). Nevertheless, a few attempts have been made to revive the original ahistorical comparative sense, by writers advocating transformed cladism (Patterson 1980) or a form of idealistic or 'structuralist' comparative morphology (Aboitiz 1988), in which evolutionary concerns are secondary.

totally new idea, but a formal restatement of the long held position that classifications delineate

> genealogical groups of relative internal homogeneity.
> Ashlock (1974)

> So far as we can recognize the natural system, we recognize no taxonomic group which is not genetically continuous with itself. A group which is acceptable under this requirement is legitimately called a natural group. It is not by caprice that we insist that tenable groups be natural: these groups and no others possess a fundamental unity making it worth our while to recognize them. Copeland (1947:346)

Convex taxa are historical classes which are grouped by homologous similarity: an 'appropriate' similarity with a theoretical content which allows the biologist in some sense to say of a homologous character that it is the 'same' character in different organisms. (Barring holistic implications, almost certainly unintended, this is the point made by Ghiselin (1987) - homologous characters are themselves 'particular': see §3.8. One could even be tempted to suggest that when a taxon is recognized, it is not a group of organisms which is named, but a suite of homologous characters - a notion found in some transformed cladistic writings.) The kind of character which characterizes a grade is not an analogy, for it is convex; but it is not necessarily a synapomorphy either, for symplesiomorphies also are homologies. Neither genealogical common ancestry nor general similarity is alone sufficient to delineate a grade-taxon: both the historical and morphological components may be called upon.

Meacham (1986) admits that he is not primarily guided by a fundamental acceptance of the evolutionary taxonomists' position, but by pragmatic considerations arising from the problems of phylogenetic reconstruction. The aim, arising out of the numerical taxonomic method known as compatibility analysis, is to provide a classificatory method in which

knowledge of the directionality (polarity) of character transformations is not absolutely essential: the result is to provide a classification in which paraphyletic groups are explicitly accepted. In such a classification in which convex paraclades are admitted to classification, it will be the case that members of a taxon will be both similar to each other and related to each other.

> It is significant that the members of a higher category [i.e. taxon] can be characterized with respect to habits.
> Schaefer (1976)

> Genera are monophyletic [**sensu** Mayr (1969) **non** Hennig (1966)] units that occupy distinctly different ecological niches or adaptive zones. Glazier (1987)

That similarity is important, if insufficient, for classification is implied by numerous systems of taxa - for example, the family level classification of polychaete annelids. A large majority of polychaete families contain animals with a shared 'life-form' or broad adaptive niche (Sveshnikov 1985). However, in no case is a polyphyletic taxon deliberately created to unite morpho-ecologically similar but genetically unrelated forms: in fact, some effort has been expended in the demotion of the Archiannelida (a small assemblage of mesopsammic worms) from primitive grade-taxon (with the implication of convexity) to mere polyphyletic grade (Fauchald 1974, Nichols & Cooke 1971). The resulting classification might be described as 'gradogenetic' - not simply grouping by overall similarity but taking phylogenetic affinity into account.

Ruse (1987) proposes the 'consilience of inductions' as grounds for asserting the reality of species as natural kinds (not individuals), based on the congruence of 'biological', 'evolutionary', 'morphological' and 'genetic' definitions of the species. He asserts that such consilience does not work for higher taxa, but does not expand. Certainly I would accept that there are no satisfactory definitions of higher <u>categories</u>

analogous to those of the species, but the taxa themselves can often be recognized or re-delineated according to different criteria. Reproductive criteria are obviously inapplicable at supra-specific levels, but the notion that

> there are no measures of morphological difference to coincide with genetic difference, to coincide with evolutionary difference Ruse (1987:240)

is surely pessimistic. Morphological criteria frequently delineate supra-specific taxa (especially genera) with much greater definiteness than species (groups of sibling species being the obvious example) and genetic criteria may behave similarly. As to the evolutionary criterion, if 'unitary evolutionary role' has any meaning for species distinct from genetic exchange and reproductive isolation, then it surely exhibited by grade-taxa of all kinds.

$ 4.9 The Role of Imprecision

> It is part of our human condition to long for hard lines and clear concepts. When we have them we have to either face the fact that some realities elude them, or else blind ourselves to the inadequacy of the concepts. The final paradox of the search ... is that it is an attempt to force experience into logical categories of non-contradiction. But experience is not amenable and those who make the attempt find themselves led into contradiction. Douglas (1966:162)

> Zadeh's principle of incompatibility states that, 'In general, complexity and precision bear an inverse relation to one another in the sense that, as the complexity of a problem increases, the possibility of analyzing it in precise terms diminishes.' Thus 'fuzzy thinking' may not be deplorable, after all... Jain (1980)

Nelson & Platnick (1981) presume that the stability of a classification is effected by its success in predicting the structure of new information, but there seems to be at least one other important feature which renders classifications stable at higher taxonomic levels - that of imprecision. This may sound controversial or even 'unscientific', but it seems to be the critical factor which can prevent classifications from succumbing to the instability characteristic of phylogenetic hypotheses.

As has been suggested above, the treatment of classifications as hypotheses which are to be proposed and rigorously tested by attempted falsification leads to instability, as it is one origin of the production of over-precise classifications which, while being highly testable, are at the same time necessarily highly subject to revision. In the problem of 'general' zoological taxonomy the concept of imprecision may have a role:

> It is always undesirable to make an effort to increase precision for its own sake ... One should never try to be more precise than the problem situation demands.... Popper quoted in Avis (1986)

> The advice "Define your terms" is bad counsel to give to biologists, for ... if definition makes the argument simpler it does so at the expense of truth. Yapp (1951)

Rather than constructing a classification rigidly along the lines of a hypothesis, in the hope that its predictions will be accurate and hence its stability assured (at least temporarily), it should be possible to construct a looser classification which is not itself such a very precise hypothesis, but which is flexible enough to accomodate various explanatory stories without the necessity of restructuring the classification. The resulting stability would be greater than that of a precise classification because it imparts the capacity for incorporation of new information without prejudging what form that information is actually going to take. This dissociates stability - a property of taxonomies - from predictivity - a property of hypotheses.

A methodology for this can be conceived in terms of the classificatory dendrogram, familiar to the cladist and long a part of the armoury of the pheneticist.

> Tree-diagrams have long been used in various areas of research in order to describe, structure, explore and represent various collections of cohesive data. ...The most widely applied tree representation in taxonomy is based on the use of ultrametric trees or dendrograms. Such trees are planted trees, i.e. the apex or root is connected to the leaves by branches valuated in positive numbers. ... Certain specialists (natural scientists, psychologists and linguists) have come to prefer the more general model of tree-analysis. The tree produced by the latter method does not evince a planted, hierarchical structure, but ... is described as a radial tree, similar to the naturalist's phylogenetic trees [sic!]. The model establishes a relationship between proximity (distance criterion) and classification or membership (structure criterion) which provides more information, albeit at the cost of reintroducing at times moderate ambiguity. Juillard & Luong (1988)

Allowing for slight misconceptions regarding phylogeny, this paragraph represents a close parallel in linguistics to the method proposed by Estabrook (1986) and others, in their computer tree-construction method based on the principle of convexity as a taxonomic criterion. This produces 'unrooted' trees ('radial trees') of a kind used in many

biological analyses (e.g. of viral DNA sequences: Penny 1988). If a dendrogram of relationship is produced without determining the root of the tree, then a taxonomy may be derived from it which is framed in terms of convex taxa rather than in terms of nesting holophyletic groups.

The importance of this method (whether the details of the mathematics be controversial or not) is that it makes it possible to propose different phylogenies without necessitating a change in the classification, because the geometry of a tree may be altered without altering its topology. The fact that two taxa are related is then retained in the classification even if the actual nature of the genealogical affinity is debated.*

The result is not simply vagueness, for the delineations may be quite precise, but allows for the kind of indeterminacy akin to the 'open texture' referred to by linguistic philosphers, which recognizes that future borderline cases may occur (Lacey 1986).

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* It is perhaps worth noting, incidentally, the extraordinary attempt of Meacham (1986) to include this system of undirected tree construction within an extended redefinition of the term 'cladistics':

> I acknowledge that, in a sense, the methodology of Hennig is the 'type specimen' of cladistics, but I recommend that use of the term be broadened so that it is no longer restricted to a single methodology. ... The term should apply to a field of study: the scientific endeavour of reconstructing the evolutionary history of biological organisms. Meacham (1986)

The suggestion is patently absurd for three reasons: (i) the term 'phylogenetics' is already available if a counterpart is needed to the ahistorical term 'phenetics'; (ii) transformed cladistics would still remain outside even the broader definition of 'cladistics'; and (iii) the distinction between cladistic and 'phyletic' or 'patristic' evolutionary classifications would be lost.

> The distinctions between plesiomorphy and apomorphy, and paraphyly, are important. ... A definition of cladistics that blurs these concepts, and lumps Meacham with Hennig, would only conceal very real and very fundamental differences.
> Donoghue & Maddison (1986)

CHAPTER FIVE

*

CONCLUSIONS

"Nature doesn't come as clean as you can think it."
Whitehead quoted in Gerard (1957)

"Science must rely on ordinary language as well, because this is the only language in which we can be certain to get hold of the phenomena."
Heisenberg (quoted in Davidson 1985)

$ 5.1 The Place of Similarity in Scientific Discourse

> Kind terms must have their meaning partially determined by intralinguistic relations to other meaningful terms (**valeur**), and partially determined by extralinguistic relations, that is by their referents (**signifies**). Harré 1987:33

My investigation of the use of taxonomic terms has led me to a position concerning their meaning which seems close to that expressed in the above quotation concerning kind terms. Biological theory does not require its terms to refer simply to concrete or ostensible objects, to 'things' which have a unique and verifiable existence in the external world: whether or not a kind of thing can be considered a kind of thing, its name carries a meaning to the biologist, a meaning arising partly from its place within biological language.

The application of the notion of 'individuality' to higher biological groups has come adrift because advocates of the 'individuality hypothesis' have lost sight of the essentially partial nature of the application. This discussion has made it clear that biological individuality is in many respects a matter of degree (cf. Gerard 1957). Species, and to a lesser extent higher groups, can be analogically (or even metaphorically) regarded as individuals, in certain contexts (Jeuken 1953, Bernier 1984); to regard them as ontologically individual in such a way that they cannot be regarded as classes in any sense is perhaps to misunderstand the role of heuristic analogy (or metaphor).

> The tenor of a metaphor is always less than its vehicle. A changing [kind; species; in Wells's context, language] cannot be both a (discrete) succession of living individuals and a (continuous) succession of states of one living individual ... But it may be like a discrete succession and like a continual succession - like the former in some respects and like the latter in others. Wells (1987)

The way you classify your data, and the sorts of questions you want

answers to, depend critically on each other; the sorts of questions you can practically get answers to impose limits on idealistic approaches to taxonomy. There is no set of facts which can be so aranged to give a single, unambiguously natural classification:

> Classification is never a natural undertaking, but carries a range of assumptions with it which in each case have a major role in governing the outcome. Renfrew (1987:297 note)

Cohen (1974) argues that the ontological status of a concept is dependent on the context in which it is placed. Hull (1976) replies that evolutionary theory demands individual species (though not individual higher taxa), and cannot conceive of a taxonomic imperative other than the dictates of evolutionary theory which could require any other status to be considered. I believe I have shown that the practice of taxonomy, even if it cannot be described as a theory, requires taxa, and in some cases perhaps species, to be regarded as classes.

There is a constant conflict of aims and interests (Charig 1982, Levinton 1988). So Patterson claims that non-cladistic taxa are theoretically obstructive for evolutionary theory; Mayr claims that the cladistic system is theoretically obstructive for other biological fields. Evolutionary taxonomy, in leaving the methodology of classification relatively open, allows the asking of different kinds of question about a wide range of groups. Cladistics, on the other hand, insists that we are sometimes asking the wrong questions, because we are framing them in terms of what we, as observers, see (such as paraphyletic groups, adaptations, functions and modes of organization), not what can be inferred to be there (such as lineages, holophyletic taxa, hierarchies of synapomorphy). To some extent, evolutionary taxonomy and the school of zoology it represents stand against both cladistics and phenetics in their search for a totally unambiguous objective way of seeing the universe, and seek to give perhaps

slightly muddled answers to the questions people are actually asking, rather than insisting that they rephrase their questions in a way that can be more precisely, but perhaps less informatively, answered. This is the basis of the protest that cladistics is 'inhuman' (Ridley 1986), and it is notable that the most outspoken exponent of evolutionary taxonomy still starts his objections to cladism with indignation at the counter-intuitive cladistic groupings of vertebrate classes (Mayr 1987 pers. comm.).

I would suggest it to be the case that, despite the theoretical drive towards abandonment of the powerful intuitive notion of similarity (Quine 1969b), classification as a reference system will continue to need similarity in order at the least to maintain a connection with natural language and thus be intelligible to the non-taxonomist (or indeed to the ordinary taxonomist)(cf. Heywood 1988). Anyway, however effective a classification system becomes, it is no substitute for actually knowing what you are talking about - understanding the contents and the limitations of taxonomy.

A tentative analogy might perhaps be drawn with astronomical terminology. Since the Copernican revolution which replaced the geocentric Ptolemaic system with a heliocentric model of the known universe, modern astronomy has removed the centre of the universe even further from the human observer, placing it at the galactic centre, or at the inferred coordinates of the primal event (the Big Bang), or adopting relativistic systems which have no central reference point at all. This conflicts to some extent with conventional language which still operates in terms of the geocentric model:

> "We **live** in one world in which we both see and say that 'the sun rises', and we **think** in another, where we know that the earth revolves around the sun. Conflict exists between the lived world and the known world, between the **percipio** and the **cogito.**"
>
> V. Descombes: quot. Davidson (1985)

Yet it is not only casual star-gazers and astrologers who continue to use geocentric terminology. Despite the non-existence of constellations as theoretically significant entities, they play a key role in the use of language to convey scientific (in this case, astronomical) information (and the biologist who thinks that the members of Reptilia must be a group with no descendents outside the taxon is on an intellectual par with the astronomer who thinks that the stars of Ursa Major must be closer to each other in space than to any other star). The similar irrelevance on a universal scale of events such as planetary occultations does not prevent them from being methodologically useful to an observer who is necessarily observing from his particular standpoint, however sophisticated his analytical tools. Moreover, with the possible exception of the location of the Big Bang, most points in the universe have an equally good (or bad) claim to be the centre.

This may perhaps be objected to as overly subjectivist, asserting the right of human beings to question the universe on their own terms, though this kind of anthropocentric approach to knowledge has started to receive serious attention from scientists in various fields, notably cosmology. I do not wish to draw the same conclusions from this example as Davidson (1985), who advocates a move towards a phenomenalist philosophy of science which ceases to connect the real with the external: few biologists will be in sympathy with this interpretation of scientific activity. Nor is there a similarly obvious pragmatic classification in the biological world, for the astronomers have to deal only with a three-dimensional universe projected on a two-dimensional taxonomic graph - phenetic taxonomy has demonstrated the almost insuperable complexity of attempting to plot the multi-dimensional patterns of biological variation.

It is true that, in some degree, resemblance is in the eye of the beholder. Yet perceived similarity plays a pivotal role in maintaining the informativeness of biological language, a role that is not adequately taken over by theoretical concepts of 'similarity' such as 'inferred genealogical relatedness'.

> Logic does have a place in the creation of scientific discourse, but not at its core. That is formed by semantic structures, and relations of likeness and difference. Harre (1987:4-5)

In groups where there is a scarcity of phylogenetic information, taxa are in effect phenetic constellations of organisms whose relationship in other dimensions has yet to be elucidated, and an eventual classification by cause will be preferred over a classification by effect. Even so, in groups where phylogenetic information is available, it is not necessarily advantageous to recast taxa in terms of phylogenetic theory: even though the Andromeda nebula has been re-classified as a galaxy, it is still in Andromeda; even though it is accepted that the lungfish are close relatives of the tetrapods, they are still fish (Gould 1980a). Astronomy demonstrates the workability of a scheme which distinguishes the useful from the theoretically significant; evolutionary taxonomy can make the stronger claim that what it regards as useful is useful because of its role in realistic theory-making, being theoretically significant in either phylogenetic or functional study.

> Phylogeny and taximetrics come **after** a firm classification on traditional lines - they are, in a sense, **metataxonomies**.
> Burtt (1964)

The limitations of an imprecise or partly subjective taxonomy are easily overcome provided that no simplistic assumptions are made about what information it is that a classification is trying to convey.

There is a fine line to be trodden. On the one hand it is deeply antithetical to the scientific process to propose that constraints or

facilities of language should be allowed entirely to dictate the pattern of enquiry by excluding or accepting concepts on subjective, or even quasi-aesthetic grounds; some pragmatic arguments against cladistics may tend in this direction. On the other hand, scientific language must remain flexible enough to allow for different patterns of enquiry, not excluding names or concepts on the grounds that they do not fit easily with such-and-such an apprehended system.

Scientific, and especially taxonomic, language must be treated not as a window through which the world is directly perceived, but more like an electron microscope, which must be eagerly used and thoroughly mistrusted at one and the same time.

$ 5.2 The Fall of the Ontological Argument

> Nature refuses to be forced into the fetters of a precise system.
> John Ray (quot. Swingle 1934:27)

> Perhaps what I've been leading up to here is a sort of plea for anarchy - I hope I'm not just being subversive here, but a certain amount of anarchy in biological concepts or classifications seems to be a very good thing.
> G.G. Simpson in Gerard (1958:112-3)

The kernel of this thesis is essentially that there are two ways of classifying organisms - by similarity or by origin; that they are both significant in terms of biological theory; and that it is unjustifiable to assert the priority of one over the other on grounds of 'reality', 'naturalness' or 'objectivity'. The ontological argument for cladistics is based on the assertion that phylogenetic relationship alone is real and significant, and similarity, regardless of its cause, genetic or otherwise, is not; the falsity of this assertion overturns the 'strong programme' of cladistic apologetic. The 'weak programme', presenting phylogenetic taxonomy as ultimately the most useful, can be justified only by the test of time. As in the biological world where survival is the only measure of success, so it may be that survival will prove the only ultimate criterion for assessing the merits of classification systems - and chance will no doubt play its part. Yet the selection pressures in the taxonomic 'environment' can be outlined, and they are largely pragmatic not dogmatic, acting on the 'phenotype' of taxonomic practice, not on the 'genotype' of systematic theory. Taxonomies, like animals, are not designed and are not optimal. They grow.

POSTSCRIPT

*

PHILOSOPHICAL COMMITMENT

"The best thing in the sciences is their philosophical ingredient - like life in an organic body. Dephilosophize the sciences and what is left? Earth, air and water."

Novalis quoted in Davidson (1985)

$ 6.1 Philosophical commitment

> Unanimity often indicated the death of a subject, or of freedom of thought. A New Dict. Xtn. Theol.

> A completely unbiased, unprejudiced exploration of nature is a methodological impossibility, as the late Sir Peter Medawar was fond of pointing out. Lewin (1988)

Gaffney (1979:103) laments the fact that throughout the debate in classification, much of the discussion is concerned more with the sociology of science than with the "substantive biological problems". Yet it seems that this will inevitably be the case, as the debate has involved not only a clash of interests between rival theories of speciation and evolutionary mechanism, but a difference of opinion over the extent to which classification should reflect such theoretical concerns. As Gaffney remarks,

> the most important disagreement among systematists concerns the nature of science ... a resolution of this problem is of primary importance.

The disagreement can be presented in many ways, one being as a dichotomy between what I here call 'scientistic' and 'scientific' world views (already hinted at in $ 5.1). The 'scientistic' world view of cladistic (and much other) philosophy sees the field of knowledge as a kind of incomplete library shelf or jigsaw, to which individuals add accumulated data, working out small parts of a pristine and coherent whole which is the 'truth' about the natural world - to such a world view the term 'positivist' may perhaps be partly appropriate. The 'scientific' view (scienti-fic: knowledge-making) sees science in more personal terms as the sharing among the community of scientists of a body of experiential knowledge. Scientists are educated into this community, to produce not simply an in-filling of data, but an extension of or shift in understanding. Scientists do not merely document, they comprehend.

Such a view of science, regarding it as a tradition in which scientists are creatively interacting, is inimical to the idealised vision of a gradual unfolding of absolute truth by an exact methodology. Many practising scientists, even if they give lip service to the rhetoric of the scientistic view, act out the knowledge-making role of creative scientist, attempting to understand their subject personally and to contribute that personal knowledge to the shared deposit (F. Rowe, pers.comm. 1987).

The suggestions just made above reflect not only a divergence in thought between scientists, but between those philosophers of science who have analysed science in logical terms, and those who approach it more historically, giving credence to the notion that scientific progress may be made rationally without strict logic (Harré 1987, Yee 1987) (or on occasion even irrationally [?]).

Parallels in theology may seem unusually irrelevant to a discussion of internal scientific issues, but the nature of the debate in systematics, its virulence and its complexity, and its close connection with philosophy of science, render it more than a simple empirical debate in scientific method. Advocates of methods such as transformed cladism (Patterson) or theories such as punctuated equilibrism (Eldredge and Tattersall) will openly admit that their scientific position is strongly underpinned by a philosophical commitment, to a conscious positivism, or to a Marxian dialectical materialism (Levins & Lewontin 1985). My own standpoint, such as it is, is intended to reflect to a great extent, as far as I perceive it, the "transcendental realism inherent in actual scientific practice." (Tiles 1987). Divergence in this commitment - intellectual, intuitive, temperamental - cannot be resolved by rational argument in scientific terms any more than a basic disagreement in theological presuppositions can be argued out in the language of religion.

No doubt Gaffney is right in his assertion that "a resolution of this problem is of primary importance"; but we can no more suspend biology until we have achieved unanimity of philosophical outlook than we could suspend daily life pending unanimity of political outlook! The philosophers have been debating some of the issues involved for centuries: the biologists may have valuable information and insights to contribute, but they will not solve them overnight. Meanwhile, consensus, or pluralism, is essential in order not to have biology disintegrate as a discipline. Because the systematics debate has plunged into such deep waters, it has become personal and thus acrimonious, and is unlikely to be resolved by rational argument alone. Hennig (like Thomas Aquinas) has elaborated a coherent system of thought, but the cladist (or Thomist) will make no headway by arguing within the system unless his opponent has read and believed. Ernst Mayr is as likely to adopt cladism as Richard Dawkins is to embrace creationism, but then, Dr Dawkins may find a Cambrian fossil man in his back garden, and the cladists may finally and unanimously produce a complete and practical phylogenetic classification.

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ARISTOTLE: see Balme (1972), Ogle (1912), Peck (1961)

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