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# Cladograms can reconstruct phylogenies: an example from the fossil record

B. MICHAUX

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A phylogenetic analysis of Recent and fossil species of the genus *Amalda* (Gastropoda) was undertaken. The resulting cladogram is compared with the phylogeny implied by stratigraphic evidence. The two phylogenies are in broad agreement, and both suggest that the subgenus *Alocospira* should be elevated to generic rank. The status of the subgenus *Gracilispira* is uncertain on both cladistic and stratigraphic grounds. Of the two remaining subgenera, only *Baryspira* is unequivocally monophyletic. *Gemaspira* and *Baryspira* are sister taxa in the cladistic analysis. However, stratigraphic evidence strongly suggests that *Gemaspira* is a paraphyletic group. The implied sister-group relationship is interpreted as resulting from coding procedures which assumed no transformation series between states of a multistate character. Clearly, stratigraphic evidence implies that the synapomorphies linking *Baryspira* spp. are transformations from (rather than being independent of) the synapomorphies linking *Gemaspira* spp. This underlines the importance of deducing the correct transformations linking multistate characters in attempting to reconstruct phylogenies. In this case the transformation series implied are counter-intuitive. It is concluded that cladistic analysis of morphological characters has the potential to reconstruct phylogenies provided the correct transformation series are known. These, it is argued, can be obtained through a study of the dynamics of form development.

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THE SUBFAMILY Ancillinae is a group of marine gastropods that live from bathyal depths to intertidal environments in both tropical and warmer temperate seas of the Indo-west Pacific. There are approximately one hundred extant species and subspecies (Kilburn, 1981a). The basis for the modern classification of this group was given by Chavan (1965), subsequently revised by Kilburn (1981b). Kilburn, based on a proposed evolutionary sequence, included the following genera: *Olivula* Conrad 1832; *Turrancilla* von Martens 1903; *Ancillista* Iredale 1936; *Anolacia* Gray 1857; *Amalda* H. & A. Adams 1853; *Eburna* Lamarck 1801; *Ancillarina* Bellardi 1882; *Ancilla* Lamarck 1799.

Kilburn (1981b) referred to *Olivula* as a west Tethyan genus (type species *Ancillaria staminea* from the North American Eocene) with numerous plesiomorphic characters including absence of spire callus. *Turrancilla*

consists of a small complex of species inhabiting deep water from the continental slope to bathyal depths throughout (?) the Indo-west Pacific. It is of interest to note that a subantarctic species (*Ancillaria longispira* Strebel 1908), which Kilburn (1981b) places in this genus, is found in South Georgia. *Ancillista* covers a small number of species found in tropical waters; formerly thought to be endemic to Australia, it was recently recorded off Mozambique (Kilburn & Jenner, 1977). *Anolacia* is a tropical genus restricted to the east African coast and adjacent islands. The genera *Eburna* and the extinct *Ancillarina* are problematical as so few details are available. *Ancilla* is another tropical genus of the western Indian Ocean (plus one Brazilian species) which has been revised recently by Kilburn (1981a).

*Amalda* is the largest ancilline genus and has two centres of distribution; a smaller western group of species found around southern Africa (Kensley, 1973; Kilburn, 1975, 1977), and a larger eastern group found

in Japan (Habe, 1961; Kira, 1967), east and south-east Australia (MacPherson & Gabriel, 1962), the Kermadec Islands (Powell, 1967), and New Zealand. Many species of this genus are found in temperate regions, which is unusual for this subfamily, although *Turrancilla* spp. must also be tolerant of reduced temperatures. The taxonomy of extant and Tertiary New Zealand *Amalda* was revised by Olson (1956). He recognized six subgenera within the taxon *Baryspira* (= *Amalda* of Chavan, 1965): *Baryspira* s.s. Fischer 1833; *Gemaspira* Olson 1956; *Spinaspira* Olson 1956; *Alocospira* Cossmann 1899; *Gracilispira* Olson 1956; *Pinguispira* Olson 1956. These subgenera are illustrated in Fig. 1.

Subsequent work by Ponder (1968) and Beu (1970) has led to a revision of Olson's classification. Both these authors have rejected *Pinguispira* as a valid subgenus, Ponder noting that shell differences are only minor, and that there are no differences in the radula and operculum. Indeed, *Amalda* (*Pinguispira*) *depressa* has been classified by some authors as a subspecies of *Amalda* (*Baryspira*) *australis*, although Michaux (1987) has shown them to be valid biological species. Beu (1970) has also rejected *Gemaspira*, synonymising it with *Baryspira* s.s. An important contribution to our knowledge of this group was Ponder's (1968) recognition that the radula of the Australian *Alocospira edithae* is pectinate like that of the New Zealand gracilispirid *Amalda novaezelandiae*. Radulae of the Australian *Alocospira marginata* group are tricuspid and resemble those of modern *Baryspira*. Beu commented on the similarity of Australian and New Zealand Tertiary *Alocospira* spp., which he felt are more closely related to each other than are the Australian Tertiary to modern Australian alocospirids. Details of the genetics and distribution of modern New Zealand *Amalda* are given by Michaux (1987).

## Methods

The approach used throughout this work is termed phylogenetic systematics, and is based on the work of Hennig (1966). Two important methodological problems of phylogenetic

analysis are determining character polarities, and arranging monophyletic groups into hierarchical sets on the basis of the distribution of shared-derived characters in the data.

### *Character polarity*

The decisions concerning plesiomorphy and the related question of how to order the remaining states in a transformation series are crucial for phylogenetic reconstruction. Outgroup analysis (Easterbrook, 1977; Watrous & Wheeler, 1981; Maddison *et al.*, 1984) and the ontogenetic method (Nelson, 1978) are the two most widely used methods for determining character state polarity. Full reviews of these and other methods for determining character state polarity are given in Crisci & Stuessy (1980) and Stevens (1980).

*Outgroup analysis.* 'For a given character with two or more states within a group, the state occurring in related groups is assumed to be the plesiomorphic state.' (Maddison *et al.*, 1984, p. 83). When only one outgroup is used the application of this method is unproblematical. However, when a number of outgroups are used this method may not be directly applicable, because characters states can vary among outgroup taxa. Because using more than one outgroup is clearly the better option, there have been a number of methods developed to resolve this problem. The simplest solution is to designate the commonest state in the outgroup as plesiomorphic (e.g. Arnold, 1981). An alternative and more rigorous approach has been suggested by Maddison *et al.* (1984). They determine the character states for the 'outgroup node', which are then used to determine the polarity of the ingroup states. The logic behind this argument is that the 'outgroup node' represents a hypothetical taxonomic unit (HTU) that is directly ancestral to the ingroup and is, by definition, entirely plesiomorphic relative to the ingroup.

For characters with more than two states, the remaining states may be left equivalent or ordered into a transformation series. A transformation series assigns relative apomorphy to states. This implies a closer degree of relatedness for taxa which have character states directly connected to each

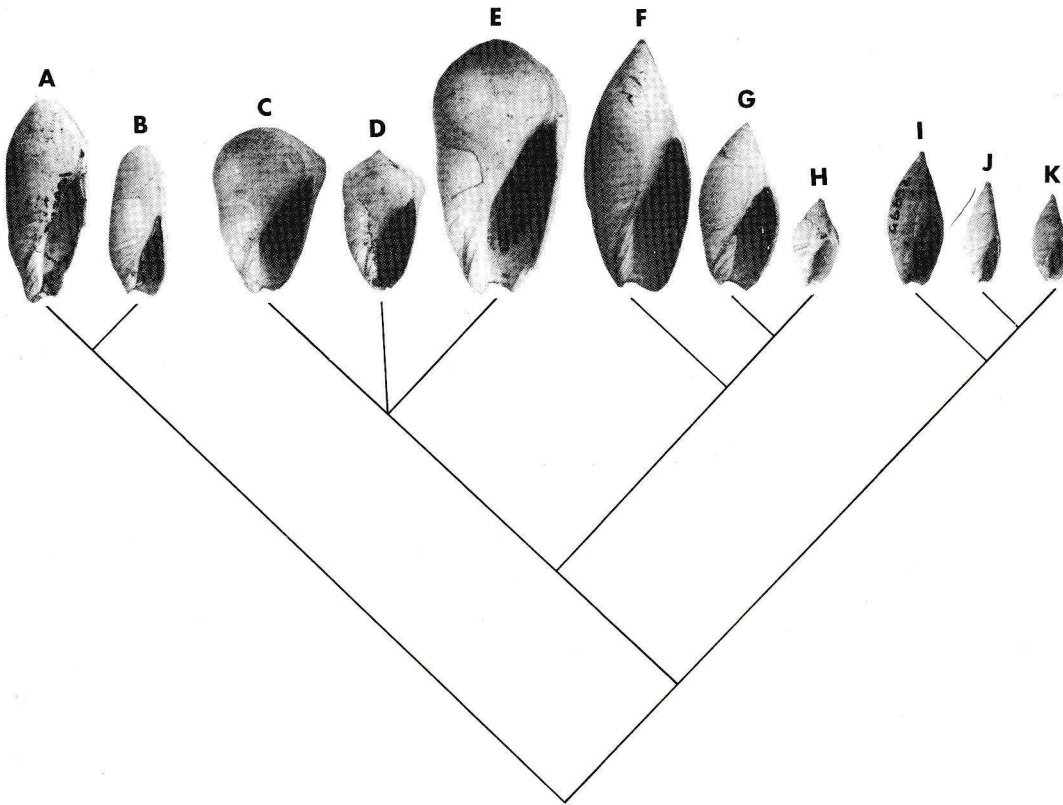


Fig. 1. Illustration of the major shell-types, and their proposed relationships based on character analysis. All are natural size. A. *Alocospira subhebera* (Pliocene), B. *Alocospira hebera* (L. Miocene); C. *Amalda (Spinaspira) stortha* (M. Miocene), D. *A. (S.) pakaurangiensis* (L. Miocene), E. *A. (Gemaspira) platycephala* (L. Miocene); F. *A. (Baryspira) mucronata* (Pleistocene), G. *A. (B.) australis* (Pleistocene), H. *A. (B.) depressa* (Pleistocene); I. *A. (Gracilispira) morgani* (U. Eocene), J. *A. (G.) gigartoides* (L. Miocene), K. *A. (G.) novaezelandiae* (Pleistocene).

other in the transformation series, and may lead to greater resolution of relationships within the group. Transformation series can be deduced from developmental evidence (discussed below), or by Transformation Series Analysis (Mickevich, 1982).

*Ontogenetic method.* '... given an ontogenetic character transformation, from a character observed to be more general to a character observed to be less general, the more general character is primitive and the less general advanced.' (Nelson, 1978 p. 327). Nelson (1978) argues that all methods of character polarity assessment are dependent on the orderliness of ontogeny, and that it is preferable to go directly to this source for information on character state polarity. Despite Nelson's restatement of Haeckel's biogenetic law, the practical application is the

same — a character state found in the juvenile stage of one species is the primitive condition when found in the adult stage of another species. The utility of this law is clearly dependent on the assumption that development is an 'unfolding' process, and that changes in ontogenetic sequences are primarily by terminal addition. Heterochrony, or the alteration in timing of developmental events, is a process that can violate this assumption (Gould, 1977). After a neotenic event a juvenile state is retained in the adult of a derived species. This state would be wrongly regarded as plesiomorphic.

A more serious criticism of the literal reading of developmental sequences is given in Alberch (1985). Whilst he agrees with Nelson that development is an ordered process and central to systematics, he argues that the

Character	States
Terminal appendage to penis	0 = absent 1 = present
Metapodium	0 = divided 1 = undivided
Fasciolar band	0 = divided 1 = undivided
Primary callus	0 = covers entire shell 1 = broad band free
Spire callus	0 = forms false sutures 1 = sutures free 2 = glaze-like
Parietal callus	0 = absent or restricted to paries 1 = present
Operculum	0 = small or absent 1 = fills aperture
Foot	0 = large 1 = small
Columella pillar	0 = straight with no lirae 1 = twisted and lirate

Character distribution matrix				Manhattan distance matrix					
OTU	Character				T	An	Am	Anc	PI
<i>Turrancilla</i>	1234	5	6789	T	X	8	6	6	-
<i>Ancillista</i>	1101	010	0001	An		X	6	6	-
<i>Amalda</i>	1111	001	1100	Am			X	6	2
<i>Ancilla</i>	0000	001	0000	Anc				X	2

Table 1. Characters and characters states used for the manual computation of the Wagner tree.

basis for understanding homology (and hence constructing reliable phylogenies) is to be found in the developmental *processes* that generate the various states, rather than through a study of the states themselves. Alberch (1985) maintains that form is generated by the interaction of a set of (physicochemical) rules with initial and boundary conditions defined by the specific environment in which an embryo develops. The different forms generated by alterations to various parameters may be independent solutions that are not related linearly to each other. Similar views have also been expressed by Goodwin (1982a, 1982b) and Webster & Goodwin (1982). Such forms *could* be arranged in a linear sequence (see Murray's results reported in Alberch, 1985), which may then be arranged in a transformation series. This would be erroneous because the states *are* unordered. Alberch is not suggesting that no character states are causally related, but that it should not be assumed automatically.

#### Phylogenetic tree construction

Two types of numeric analysis exist for constructing phylogenetic trees from the binary coded data that represent character state distributions between taxa. These two types of analysis are based on the principles of character compatibility and parsimony. Phylogenetic trees may also be constructed by direct inspection of the synapomorphies within the data (e.g. Baverstock *et al.*, 1982), although how conflicting synapomorphy groupings are resolved is not made clear. If the data are well structured, with few conflicts, this approach should yield the same tree as a compatibility analysis (Meacham, 1981). An excellent summary of these two types of analysis, and the range of algorithms which work on these two different principles, is given in Funk & Stuessy (1978) and Buth (1984).

The approach to tree construction used in this study is based on the principle of parsimony. Wagner trees, based on Wagner's

'groundplan' method (Wagner, 1980), and developed by Farris (1970), are constructed by minimizing a distance measure between taxa. The principle of parsimony and other aspects of this tree building technique are best illustrated by reference to a manually computed example.

*A manual computation of a Wagner tree.* The first step prior to phylogenetic analysis of New Zealand *Amalda* is to determine character state polarity by the choice of a suitable outgroup. Three genera of ancillids — *Amalda*, *Turrancilla* and *Ancillista* — have a broad band on the body whorl which is free of callus. This is interpreted as a synapomorphy defining monophyly for this group. *Ancilla*, which has callus over the entire shell, is included as an outgroup. The characters and their states used in this analysis, together with the presence/absence data matrix upon which the analysis is performed, are given in Table 1. The distribution of states among the OTUs (operational taxonomic units) came from Kilburn (1977, 1981a, 1981b).

The method used to compute Wagner trees manually is given in Jensen (1981), and what follows is the application of this method to the example described above. Computation of a Wagner tree starts with the construction of a matrix of Manhattan distances between OTUs. The Manhattan distance between two OTUs is equal to the number of differences in character states between them. This matrix, together with the placement index (PI) for each OTU, are also given in Table 1. An interval is formed between the two most distant OTUs, and the PIs of the remaining OTUs are calculated from this interval (see Fig. 2A).

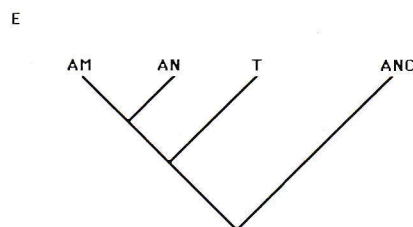
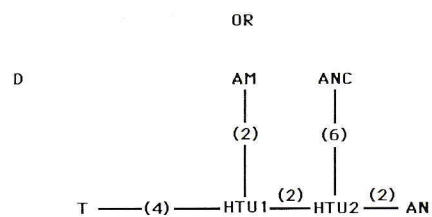
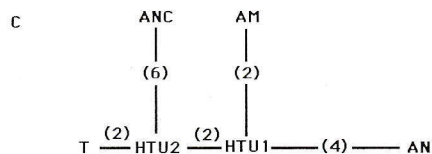
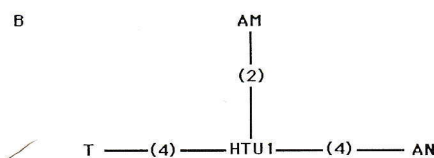
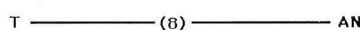
The PI of OTU X is the distance between X and T plus the distance between X and AN minus the distance between T and AN (i.e.  $\text{Int}(T, AN)$ ) all divided by two. For *Amalda* and *Ancilla* these indices are:

$$d(\text{AM}, \text{Int}(T, \text{AN})) = 1/2(6 + 6 - 8) = 2$$

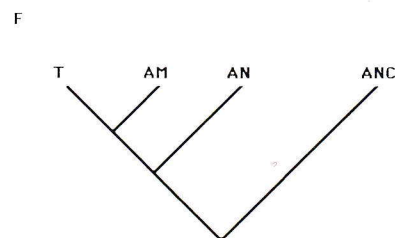
$$d(\text{ANC}, \text{Int}(T, \text{AN})) = 1/2(6 + 6 - 8) = 2$$

The OTU with the greatest PI is then added to the interval. In this particular case the PIs

A Interval *Turrancilla* (T) and *Ancillista* (AN) = 8



Total length = 16. C.I. = 11/16 = 0.69



Total length = 16. C.I. = 11/16 = 0.69

Fig. 2. Stages in the manual construction of Wagner trees (see text for explanation).

are equal and two 'lines' of trees need to be constructed, one adding AM first, the second adding ANC. Only the first 'line' is illustrated in Fig. 2B and following.

At the point where the new OTU is added to the original interval a hypothetical taxonomic unit (HTU) is constructed, which has character states that are the median of the character states of the three surrounding OTUs. The branch lengths are equal to the number of character state differences between the two OTUs at either end of the appropriate interval.

The next OTU is then added to the interval from which it is least distant. This is why these trees are called minimum distance trees, and illustrates one of the uses of the concept of parsimony in tree construction. In the present example, only one OTU remains with three possible positions to which it can be attached. If there was another OTU in the data set there would be five possible positions and so on.

The calculations involved are:

$$\begin{aligned}d(\text{ANC}, \text{Int}(\text{T}, \text{HTU1})) &= 1/2(6 + 6 - 4) = 4 \\d(\text{ANC}, \text{Int}(\text{AM}, \text{HTU1})) &= 1/2(6 + 6 - 2) \\&= 5 \\d(\text{ANC}, \text{Int}(\text{AN}, \text{HTU1})) &= 1/2(6 + 6 - 4) \\&= 4\end{aligned}$$

Two networks are produced (Fig. 2C & D), one of which has *Ancillista* and *Amalda* as sister taxa, the other *Turrancilla* and *Amalda*. The trees formed by rooting these networks are shown in Fig. 2E & F. Both are equally parsimonious, that is both have the same minimum length. If one tree were shorter than the other, the shorter tree would be preferred. In this example, the decision about choice of the appropriate outgroup is equivocal.

The principle of parsimony has been criticized on the grounds that there is no reason to believe that evolution is necessarily parsimonious (e.g. Bock, 1974). There are two related but separate issues regarding the use of parsimony arguments in the construction of Wagner trees, and both will be examined in the light of this criticism.

The first use of the principle of parsimony is in tree construction, and was demonstrated in the above example by the minimal distance criterion for addition of OTUs to the appropriate interval of the growing network.

What happens during this operation is that the position of the OTU is decided by minimizing the incongruities (homoplasies) that result from the OTU's position in the network. This seems an entirely sensible approach considering that the original decision of character state polarity is the basis of this incongruity. It is in this decision that the real assumptions concerning evolutionary process reside. Evolution is not regarded as primarily parsimonious but rather that, given a set of already defined character state polarities, the parsimony criterion is simply a way of minimizing inconsistency.

The second aspect of the application of the principle of parsimony concerns the criterion by which the 'best' tree is chosen. The most parsimonious tree (i.e. the shortest) is taken to be the best estimation of the real phylogeny. The problem here is an argument of degree — is a tree of length 54 better than one of 55? This application of the parsimony principle may either be rejected or accepted in particular cases, depending on the systematist's interpretation of the results. For an interesting discussion of the principle of parsimony, see Johnson (1982).

Finally, this manually computed example of Wagner tree construction illustrates the NP-completeness of Wagner algorithms (Day, 1983). An algorithm which attempts to solve an NP-complete problem cannot simultaneously be efficient and guarantee to find the most parsimonious tree. The basis of this problem is the enormous number of trees generated, even for data sets with modest numbers of OTUs. Short of inspecting all these trees, it is not possible for an algorithm to guarantee producing the most parsimonious solution. PENNY is an algorithm which, by a 'branch and bound' search strategy, indirectly inspects all trees, and does guarantee to find all the most parsimonious solutions. It is useful, however, only for modest size data sets (< 10 OTUs).

There are a number of reasons why so many trees are generated by most data sets. Firstly, the initial interval chosen to start the network construction is done on the criterion of maximal Manhattan distance. If there are a number of pairs of taxa separated by the same (maximal) Manhattan distance, the algorithm

Character	Character states
A. Bulbous protoconch	(0)absent (1)present
B. Margin shape of secondary callus	(0)irregular (1)sigmoidal (2)tongue (3)'v' (4) subhebera-type
C. Maximum extension of secondary callus from aperture	(0)<45° (1)45° (2)90° (3)>90°
D. Width of depressed band	(0)normal (1)wide
E. Ancillid groove	(0)present (1)absent
F. Columella ornamentation	(0)notch is prominent, lirae absent or weakly developed (1)notch present or absent, variable number of strong lirae developed anteriorly
G. Profile of body whorl	(0)inflation slight (1)inflated (2)inflated and strongly retracted to the body whorl (3) straight and sloping anteriorly towards coiling axis (4)straight and parallel to coiling axis
H. Thickness of secondary callus	(0)thin (1)well developed
I. Shape of paries	(0)straight (1)convex (2)concave
J. Denticular projection at posterior of outer lip	(0)present (1)absent
K. Spire height	(0)tall (1)medium (2)short
L. Type of spire	(0)conical (1)mucronate (2)bullet
M. Posterior siphonal groove	(0)absent (1)present
N. Concentric markings on spire	(0)present (1)absent
O. Columella	(0)sinistral twist (1)straight
P. Size*	(0)very small (1)small (2)medium (3)large
Q. Shape*	(0)short spired shells, maximum thickness posteriorly (1)long spired shells, maximum width anteriorly

Table 2. Characters and character states employed in the phylogenetic analysis of New Zealand ancillines.

\* Classes determined by groupings on the first two principal components from morphometric analysis (Michaux, unpublished data).

selects the first pair in the input data set as the initial interval. It is possible that another pair of OTUs would produce a more parsimonious solution. This may be overcome by shuffling the input order of the OTUs in the data set, as recommended by Felsenstein in his documentation for the PHYLIP package. A second source of the problem occurs when there is a tie in the placement index, as occurred in the example above. At every instance of a tie, each OTU has to be

added in all possible permutations. Thirdly, an OTU may be added to a number of intervals on the growing network if its distance from these intervals is equally minimal, and once again, all such permutations have the potential to give different trees. Practically, there is no choice of which type of algorithm to use — it must be efficient — and therefore one has to accept that the most parsimonious tree may not result from the analysis.



## Phylogenetic reconstruction of New Zealand Tertiary and Recent *Amalda*

The characters and character states used in this study are given in Table 2. The distribution of these states among the OTUs is given in Table 3, which represents the presence/absence matrix on which the analysis was performed. Non-additive coding was used in this study, i.e. no transformation series are implied for multistate characters where three or more character states are recognised. Two outgroup OTUs were included, *Turrancilla apicalis* Taki (Japan) and *Ancillista velesiana* Iredale (New South Wales). The analysis was made using the program MIX from Felsenstein's PHYLIP package. Because only one outgroup can be used in this program, and there is uncertainty as to which of these two outgroups is the sister group of *Amalda*, a composite outgroup was formed by the intersection of character states of these two OTUs. The value of 9 for character A represents an unknown outgroup state for this character. Specimens of neither outgroup had a depressed band. The outgroup states for characters D and E (which refer to depressed band characteristics) were derived from figured specimens of other Ancillinae (assuming that the commonest outgroup state is primitive). The analysis was performed four times, each time with a re-ordered data set, and the most parsimonious Wagner tree that was generated is given in Fig. 3. The major features of this tree are:

1. Two monophyletic sister groups are present — *Alocospira* spp. and *Baryspira/Gemaspira/Spinaspira/Gracilispira* spp.
2. Within the larger grouping, two monophyletic groups are present — *Baryspira* and *Gemaspira/Spinispira*.
3. *Gemaspira* and *Spinispira* cannot be separated into two monophyletic groups even when additional characters are added, such as the presence of a keel around the base of the spire.
4. *Gracilispira* is a paraphyletic group. In Eldredge & Cracraft's (1981) terminology, it is a 'not-A group', i.e. *Amalda* that do not belong to either *Baryspira* or *Spinaspira/Gemaspira*.

Relationships within each of these monophyletic groupings have not been shown in this tree. There are two reasons for this. Firstly, only four runs were performed with this data set, and each gave different arrangements of OTUs within the groups. The major features, however, remained unaltered. The data set was far too large, with concomitant lengthy run times (~2 hours), to be able to manipulate it to gain some idea of the most stable arrangement of OTUs within the groups, or even to verify that these major groups were the most parsimonious solutions. Secondly, many of these OTUs have a large percentage of primitive characters which are genealogically uninformative. Nothing can be done about this latter difficulty (bearing in mind that only conchological characters are available in fossils), but a number of techniques are available that overcome the first.

The basic aim of this second stage of analysis was to reduce the size of the data set, without reducing its content. The strategy adopted was to estimate the character states of the ingroup nodes for the three monophyletic groupings identified (nodes 1, 2, and 3 in Fig. 3). This was achieved by running the appropriate data for these groups on PENNY (which guarantees to find the most parsimonious solution). The ancestors of these groups were used as outgroups (nodes 4 and 5 in Fig. 3). The character states of the ancestors were generated during the original analysis by MIX. The data set for *Spinaspira/Gemaspira* generated so many parsimonious trees that no relationships could be reliably deduced from the data. In effect the relationships within this group are totally unresolved. A single most parsimonious tree was generated for *Alocospira* which is shown in Fig. 4A. The composite tree for *Baryspira*, based on three equally parsimonious solutions, is given in Fig. 4B. The character states for each of the three ingroup nodes were generated by PENNY. These are included in the presence/absence matrix given in Table 4 and represent a 'summary' of states for all the OTUs of the respective groups. Inspection of the original data set showed that GBEN/GR and GW/GB had the same character states; therefore GR and GB were removed. The

original data set was thus reduced from 30 to 10 OTUs. It was now possible to examine the

effects of altering the character states of the outgroup taxon.

OTU		Character states																
Characters		A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q
<b>Gracilispira</b>																		
<i>morgani</i>	GM	1	10000	1000	1	0	1	10000	0	010	0	100	100	0	1	1	0010	1
<i>rimuensis</i>	GR	1	01000	0010	0	0	1	10000	1	010	0	100	001	1	1	1	0100	1
<i>gigartoides</i>	GG	1	10000	1000	0	0	1	10000	0	010	0	100	100	0	1	1	0010	1
<i>wairarapaensis</i>	GW	1	10000	1000	0	0	1	10000	0	010	0	100	100	0	1	1	0100	1
<i>brevicula</i>	GB	1	10000	1000	0	0	1	10000	0	010	0	100	100	0	1	1	0100	1
<i>exspata</i>	GE	1	10000	1000	0	0	1	10000	0	010	0	100	100	0	1	1	0100	1
<i>novaezelandiae</i>	GN	1	bb000	0010	0	0	1	10000	0	010	0	100	100	0	1	1	0100	1
<i>benthicola</i>	GBEN	1	01000	0010	0	0	1	10000	1	010	0	100	001	1	1	1	0100	1
<b>Alocospira</b>																		
n. sp.	An	1	10000	1000	0	0	1	00001	1	100	1	100	001	0	9	1	0010	1
<i>hebera</i>	AH	1	00010	0100	0	0	1	00001	0	100	1	100	001	0	0	1	0010	1
<i>subhebera</i>	AS	1	00001	0010	0	0	1	00001	1	100	1	100	001	1	0	1	0010	1
<i>cuppedia</i>	AC	1	10000	1000	0	0	1	00001	0	100	1	100	100	0	0	1	0010	1
<b>Baryspira s.s.</b>																		
<i>australis</i>	BA	1	01000	0010	0	0	1	01000	0	010	0	010	100	0	1	1	0010	1
<i>depressa</i>	BD	1	01000	0010	0	0	1	01000	0	010	0	001	100	1	1	1	0100	9
<i>mucronata</i>	BM	1	01000	0010	0	0	1	01000	0	010	0	100	010	0	1	1	0001	1
<i>oraria</i>	BO	1	01000	0010	0	0	1	00100	0	010	0	100	010	0	1	1	0001	1
<i>erica</i>	BE	1	01000	0010	0	0	1	01000	1	010	0	010	010	0	1	1	0001	1
<i>gladiolaria</i>	BG	1	01000	0010	0	0	1	01000	0	010	0	010	010	0	1	1	0001	1
<i>bathami</i>	BB	1	01000	0010	0	0	1	01000	0	010	0	010	010	0	1	1	0010	1
<b>Gemaspira</b>																		
<i>robusta</i>	GEMR	0	00100	0001	0	1	0	00010	1	001	0	001	100	1	1	1	0001	0
<i>platycephala</i>	GEMP	0	00100	0001	0	1	0	00010	1	001	0	001	100	1	1	1	0001	0
<i>pristina</i>	GEMPR	0	00100	0001	0	1	0	01000	1	001	0	100	100	1	1	1	0001	1
<i>macbeathi</i>	GEMM	0	00100	0001	0	1	0	01000	1	001	0	010	100	1	1	1	0010	1
<i>tirangiensis</i>	GEMT	0	00100	0001	0	1	0	00010	1	001	0	001	100	1	1	0	0001	0
<i>waikaniaensis</i>	GEMW	0	00100	0001	0	1	0	00010	1	001	0	001	100	1	1	1	0010	0
<b>Spinaspira</b>																		
<i>stortha</i>	SS	0	00100	0001	0	1	0	00010	1	001	0	001	100	1	1	1	0010	0
<i>cingulata</i>	SC	0	00100	0010	0	0	0	01000	1	001	0	010	100	1	1	1	0010	1
<i>spinigera</i>	SSP	0	00100	0001	0	1	0	00010	1	001	0	001	100	1	1	1	0010	0
<i>tholiculus</i>	ST	0	00100	0001	0	1	0	00010	1	001	0	001	100	1	1	1	0100	0
<i>pakaurangiensis</i>	SP	0	00100	0010	1	1	0	00010	1	001	0	001	100	0	1	1	0010	0
<i>Turrancilla apicalis</i>		9	10000	1000	9	9	1	10000	0	001	0	100	100	0	1	1	0010	1
<i>Ancillista velesiana</i>		9	10000	1000	9	9	9	01000	0	001	0	100	100	0	1	1	0001	1
Composite outgroup	COG	9	10000	1000	0	0	1	10000	0	001	0	100	100	0	1	1	0010	1

Table 3. Matrix showing the distribution of binary coded character-states among the OTUs. 9 = unknown state, b = both states.

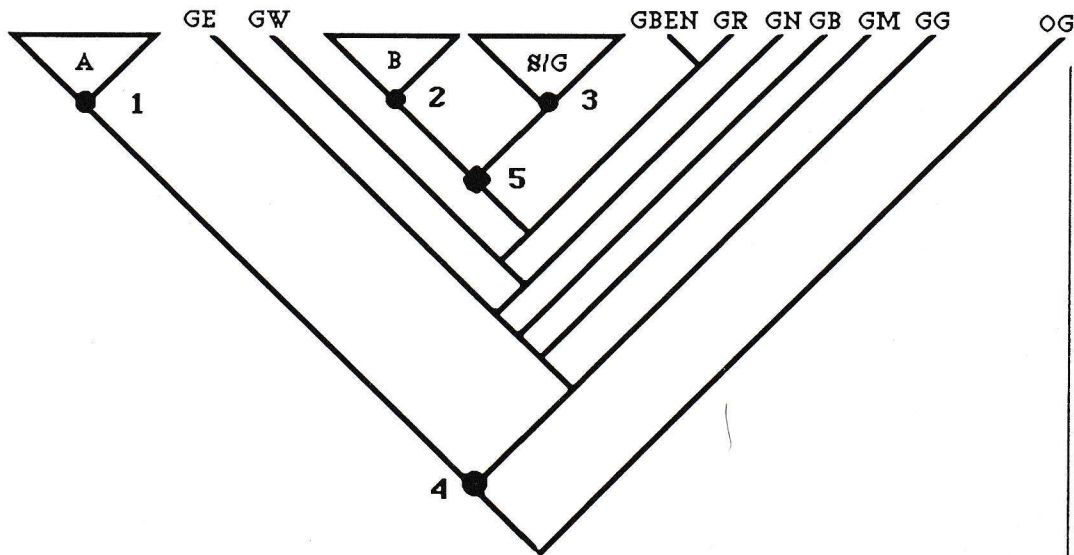


Fig. 3. Initial most parsimonious Wagner tree, C.I. = 0.50. Refer to Table 3 for species abbreviations. A = *Alocospira* ingroup; B = *Baryspira* ingroup; S/G = *Spinaspira*/*Gemaspira* ingroup. 1,2,3 = ingroup nodes; 4,5 = ancestral nodes. Refer to text for details.

Ten runs, each with altered OTU input orders, were performed on MIX. Eight equally parsimonious solutions were obtained, all of which had the major features of the tree in Fig. 3, but differed in the arrangement of the *Gracilispira* spp. Finally, state (1) for character G (profile of body whorl) was designated primitive. The reason for this alteration is that this is the state found in *Ancillista velesiana*. The original coding of state (0) as primitive was based on its occurrence in *Turrancilla apicalis*. As the analysis of sister group relationships performed in the previous section did not resolve which of these two genera is the sister group to *Amalda*, both states were included in separate analyses.

Five runs were performed on MIX, yielding three most parsimonious solutions, one of which resulted in *Gracilispira* forming a monophyletic grouping. The other two trees were similar to the results from the previous analysis and all three showed the major features already outlined. The tree which implies monophyly for *Gracilispira* is shown in Fig. 5.

### Relationship between phylogenies derived from character analysis and stratigraphy

Two interpretations of the phylogeny of the species are shown in Fig. 6B. One of these interpretations (A-F-I) treats the cladogram as a tree which depicts the actual phylogeny of the group. The second (A-E-H) is a construction that uses the relationships implied by the cladogram together with stratigraphic evidence. The stratigraphic ranges of the species are shown in Fig. 6A. International correlations of New Zealand series and stages are given in Table 5. The interpretations concerning aspects of the phylogeny are discussed below in terms of the letters A-I, which are shown in Fig. 6B.

A. The initial split between *Alocospira* and *Amalda* must have occurred prior to the upper Eocene. The interpretation that *Alocospira* n. sp. was derived from *Amalda* (*G.*) *morgani* is rejected because of the occurrence of *Alocospira* spp. in the Australian Tertiary.

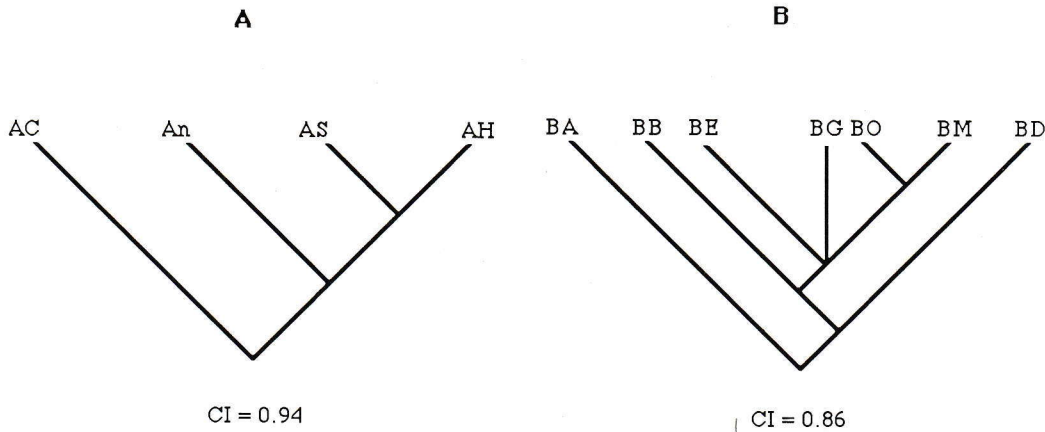


Fig. 4. Composite Wagner trees for A. *Alocospira* B. *Baryspira*. Refer to Table 3 for species abbreviations.

This suggests that the initial split occurred prior to their occurrence in New Zealand and before any extensive opening of the Tasman Ocean. A minimum estimation of divergence time is therefore the Late Cretaceous or Early Paleocene.

B. The relationships among *Alocospira* spp., indicated by character analysis (Fig. 4A), are well supported by stratigraphic evidence. The one area of disagreement is the position of *A. n. sp.* On stratigraphic evidence (which assumes the relative positions of *A. n. sp.* and *A. cuppedia* are correct and not a result of the imperfection of the fossil record), this species must be either the stem species (Hennig, 1966) or the outgroup species with respect to other *Alocospira*. This would result in the reinterpretation of the conic spire of *A. cuppedia* as a reversal, and hence a derived character.

C. A reconstruction for the evolution of *Alocospira* spp. is as follows. At some time prior to the Duntroonian (Ld) two lineages evolved, one of which is recognised by a derived parietal callus margin, and the other by a (derived) reversal to a conic spire. The latter lineage is represented by one species, *A. cuppedia*, which may have evolved through a neotenic change to the ancestral ontogeny, as indicated by juvenile *Alocospira* sometimes showing conic spires. The former lineage split in two (pre-Duntroonian), one branch recognised by a sigmoidal parietal callus margin (*A. electa*) and the other by a V-shaped margin (*A. hebera*). The ontogenetic process through which the parietal callus is developed, and the factors by which it may be transformed, remain unknown. *A. subhebera* appears to have evolved directly from *A. hebera*. The 'common ancestor' did

OTU	Character states
<i>Alocospira</i>	19000090000010000019100110090900100101
<i>Baryspira</i>	10100000100010010000010009999091109919
<i>Spin/Gemaspira</i>	00010000100001010001001001010011100101
GG	11000010000010100000010010010001100101
GBEN	10100000100010100001010010000111101001
GW	11000010000010100000010010010001101001
GM	11000010001010100000010010010001100101
GN	10100000100010100000010010010001101001
GE	11000010000010100000010010010001110001
Outgroup	91000010000010100000010110010001100101

Table 4. Matrix showing the distribution of binary coded character-states among the OTUs which includes the *Alocospira*, *Baryspira*, and *Spinaspira/Gemaspira* ingroup nodes. 9 = unknown state.

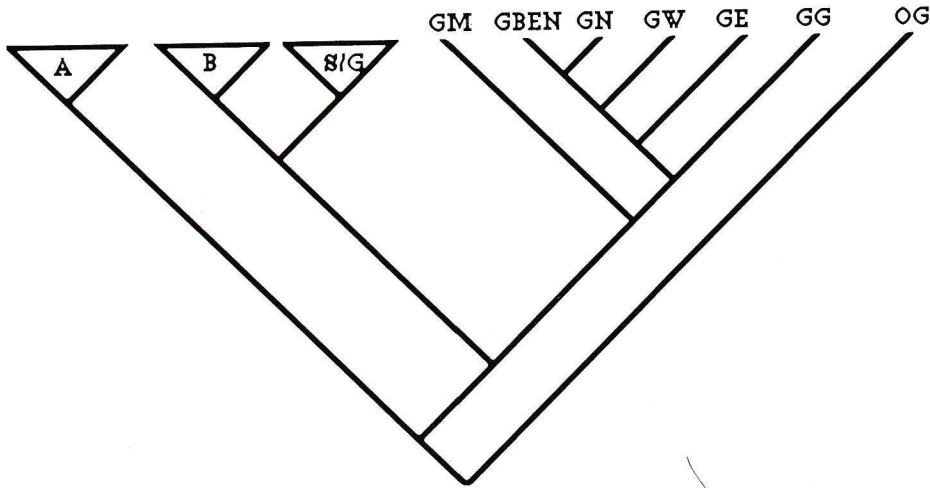


Fig. 5. Most parsimonious Wagner tree with *Gracilispira* as a monophyletic group, C.I. = 0.74. Refer to Table 3 for species abbreviations.

not exist - *A. hebera* remained unchanged after speciation. This can be interpreted as a case of speciation in a peripheral isolate where the ancestral species remained unaltered (Brooks & Wiley, 1986). *A. subhebera* shows gerontic features which presumably evolved by a process involving prolongation of somatic growth relative to sexual maturation. D. The relationships indicated for *Gracilispira* (Fig. 4) are also well supported by stratigraphic evidence, although the relative positions of *Amalda (G.) exspata* and *A. (G.) brevicula / A. (G.) wairarapaensis* should be

reversed on the basis of stratigraphy. In Fig. 6B the relationships indicated are that succeeding species are sister species. This more general statement of relationship is preferred to postulating a direct ancestor-descendant relationship. Direct ancestor-descendant relationships can occur through the anagenic modification of the ancestral species, or through speciation in peripheral isolates. The former process is unproved and unprovable (Bond, 1981; Patterson, 1982; Forey, 1982). The latter is only preferred when stratigraphic evidence indicates that this is a more plausible

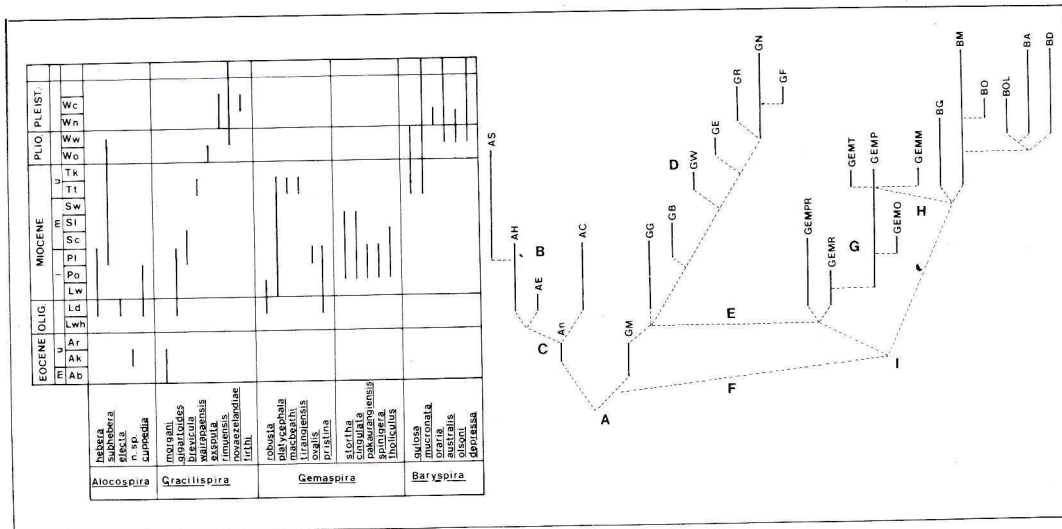


Fig. 6. A. Stratigraphic range of species. B. Proposed phylogenies. Refer to text for explanation.

Series	Stage		Correlation
HAWERA	Post-glacial Several glacial and interglacial stages	H	Holocene
			U. Pleistocene
WANGANUI	Castlecliffian Okehuan Nukumaruian Hautawan Waitotaran Waipipian Opoitian	Wc	M. Pleistocene
		Wk	
		Wn	L.  Pliocene
		Wh	
		Ww	
		Wp	
		W	
TARANAKI	Kapitean Tongaporutuan	Tk	U. Miocene
		Tt	
SOUTHLAND	Waiuan Lillburnian Clifdenian	Sw	M. Miocene
		Sl	
		Sc	
PAREORA	Altonian Otaian	Pl	L. Miocene
		Po	
LONDON	Waitakian Duntroonian Whaingaroan	Lw	U. Oligocene
		Ld	L.
		Lwh	
ARNOLD	Runangan Kaiatan Bortonian	Ar	U. Eocene
		Ak	M. Eocene
		Ab	
DANNEVIRKE	Porangan Heretaungan Mangaorapan Waipawan Teurian	Dp	L. Eocene
		Dh	
		Dm	
		Dw	Paleocene
		Dt	

Table 5. Divisions of the New Zealand Cainozoic (adapted from Fleming (1979, fig. 10))

hypothesis. Thus *A. (G.) firthi* is thought to be a direct descendant of *A. (G.) novaezelandiae*, because to do otherwise would be to hypothesise that *A. (G.) firthi* existed further back in time than there is evidence for at present.

E. The evolution of the *Gemaspira* included the alteration of a *Gracilispira* ontogeny involving prolongation of somatic growth relative to sexual maturation. This is clearly shown by juvenile *Gemaspira* having the same general shell shape as *Gracilispira*. Other growth parameters, such as Raup's (1964) translation of the generating curve down the coiling axis, and the shape of the generating curve (i.e. the aperture shape) were also altered. On stratigraphic evidence this event occurred some time between the Upper Eocene and Duntroonian. The positioning of the split between the two lineages here results in *Gracilispira* becoming a paraphyletic group, unless *A. (G.) morgani* is regarded as the stem species which may be supportable stratigraphically. If the split is hypothesised to have occurred earlier (F), where a sister group relationship between *Gemaspira* and *Gracilispira* is indicated, then *Gemaspira* spp. must have existed from the Eocene. No such fossils have been found but, like all negative evidence, this is inconclusive. Because the shallow marine record of the pre-Duntroonian is not particularly extensive, the relative merits of these alternatives are hard to judge.

G. Stratigraphy does little to clarify the unresolved nature of the species' relationships within *Gemaspira*. The phylogeny indicated in Fig. 6B is only one of a number of possibilities. The group that Olson (1956) called *Spinaspira*, which has been omitted from Fig. 6B, may well have evolved outside the immediate area of Miocene New Zealand, and migrated into this region with the emplacement of the Northland allochthon (Michaux, in prep.). On the basis of character analysis this group cannot be separated as a monophyletic group, but it may well be on geologic and stratigraphic evidence.

H. The evolution of *Baryspira* from *Gemaspira* involved neoteny, interestingly to an ontogenetic system that is intermediate between *Gemaspira* and *Gracilispira*, at least in terms of shell shape and callus development. On stratigraphic grounds this event took place in the Upper Miocene, when *A. (G.) platycephala* is hypothesised to have given rise to a series of species, one of which (*A. (G.) macbeathi*) shows the potential for the development of a baryspirid *Bauplan*. This

interpretation of the evolution of *Baryspira* results in *Gemaspira* becoming a paraphyletic group, a view already advanced by Beu (1970), who suggested that they should be synonymised with *Baryspira*. An alternative interpretation is that both *Gemaspira* and *Baryspira* evolved from a common ancestor sometime prior to the Duntroonian (I). This is a literal interpretation of the results of the phylogenetic analysis, and indicates that *Baryspira* spp. existed considerably earlier than is indicated by stratigraphy. Once again the absence of fossils is inconclusive, but in this case it is difficult to accept, given the good post-Duntroonian marine record, that *Baryspira* spp. existed but have not been found.

## Discussion

Phylogenetic systematics aims at reconstructing the phylogeny of a group, by an analysis of shared-derived characters. In general terms, this type of analysis performed on New Zealand ancilline has given results which are confirmed by stratigraphy. This is despite the simple nature and paucity of the morphological characters available for ancillines, which makes them less than an ideal group for such a test.

In most cladistic studies the fossil evidence is too patchy for any stratigraphic test of the resulting cladograms. In this study, where the fossil record is good, it is possible to identify probable errors in phylogenetic reconstruction. An example of such an error occurs in the relationship between *Baryspira* and *Gemaspira*. Character analysis suggests that *Gemaspira* is a monophyletic group, but stratigraphy suggests strongly that it is not. This implies that the synapomorphies defining *Baryspira* are derived from those of *Gemaspira*, i.e. these sets of characters are not independent, but that the former are derived from the latter. In other words, for cladistic analysis to reconstruct phylogenies character-state trees must be known.

Goodwin (1982a) and Alberch (1985) have argued that particular forms (character-states) can only be understood in terms of the generative principles that give rise to them developmentally. Forms are then related to

each other as solutions to this generative process. The generative process is (locally) universal — the forms are specific solutions produced by altering parameter variables. Webster & Goodwin (1982) have suggested that because of this relationship between forms and the field equation that describes their generation, we should construct 'periodic' taxonomies rather than genealogical ones. Such a taxonomy would arrange biological diversity in a manner analogous to the arrangement of elements in the periodic table. If I am correct in my understanding of Webster & Goodwin (1982), the definition of homology should revert to its original usage as a structural term. Thus an homologous series would be a group of forms generated by a particular field equation, rather than a group of forms related by genealogy.

Redefining homology in structural terms has considerable merit. At present relatedness is recognised by homology, which is itself defined in terms of genealogy. Clearly this situation has an element of circularity in it. However, unlike Webster & Goodwin (1982) who argue that a redefinition of homology requires the construction of a novel taxonomic system, I suggest that viewing homology in a structural sense will allow genealogies to be reconstructed with much greater certainty. Consider the evolution of a species that is also the first member of what can be recognised as a new higher taxon. The characters by which we recognise this new taxon arise during development through the interaction of generative 'rules' with particular contexts. This novel generative process presumably contains ancestral elements together with unique (derived) elements. Subsequent evolution in this taxon will elicit all or some of the potentials inherent in the system.

It seems highly unlikely that all potential character-states of the taxon will be contained within the initial system. If they were, all homologous series would be related as independent solutions and the concept of primitive and derived would be obsolete. If, however, potential emerges as various solutions to the generative process arise, then the formation of one character may depend on a precursor. Thus some states of a multi-state character may be linked, whilst others

are independent. The characters of the first member of the new taxon would be primitive with respect to its descendants, and subsequent homologous characters derived to varying degrees, except when they represent independent solutions to the generative process. In this case one would expect to find a relatively synchronous development of these characters in the fossil record. Thus a developmental analysis of character-state transformations has the potential to be used in reconstructing the genealogical connections between taxa through which these states are distributed.

How then is a cladogram to be regarded? The results and interpretations presented in this contribution suggest that it is an indicator of relationships, and that parts may well represent the 'real' phylogeny. Regarding a cladogram as a strict phylogenetic tree is not supported in this particular case. This is not to imply that this will be so in all cases. If a group was morphologically complex and more importantly, as discussed above, there were developmental data available which could determine character state transformation series, then one would expect the results of cladistic analysis to closely reconstruct the 'real' phylogeny.

The importance of this study, therefore, is not so much in demonstrating that phylogenetic analysis does appear to reconstruct phylogenies with a fair degree of accuracy, but rather in demonstrating where it *doesn't* appear to do so. Only when weaknesses in a method have been identified can that method be improved.

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