

Institute for Christian Teaching  
Education Department of Seventh-day Adventist

**DEALING WITH DEEP PHYLOGENIES  
FROM A CHRISTIAN PERSPECTIVE**

By

**David L. Cowles, Ph.D.**

**670-09 Institute for Christian Teaching  
12501 Old Columbia Pike  
Silver Spring, MD 20904 USA**

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Ever since Darwin published the “Origin of Species”, evolutionary trees have been a powerful tool for supporting the evolutionary model of deep phylogeny, the idea that all living things are descended from a common ancestor. A tree is a quick, diagrammatic way to illustrate postulated lines of descent and and compacts a multitude of evolutionary arguments down into a simple, easy to understand, apparently compelling package. When presented by a respected scientist, such trees carry with them an aura of authority and I believe they have been an important factor in the widespread current acceptance of macroevolution through deep time. In this paper I examine the types of data and reasoning processes that go into construction of these trees from the perspective of a scientist who accepts the Biblical story of creation. I will emphasize what we as creation scientists can profitably learn from such trees, and will also point out assumptions and limitations used during their construction that can be enlightening when confronted with their conclusions.

The science which specializes in postulating the relationships among living things, including construction of evolutionary trees, is called Systematics. The science of naming different groups and species is called Taxonomy. Although these two disciplines are not exactly the same, in practice there is broad overlap between the two and in this paper I will treat them as the same. The goal of most systematists and taxonomists is not only to simply categorize or classify species, but for the classification to accurately represent the pattern by which they believe the species evolved in the past. Such a system of classification is called a “phylogeny” and is illustrated by an evolutionary tree called a “phylogenetic tree”. The goal of systematists while constructing phylogenetic trees is to arrange the groups (branches) so that every group includes all the species which are united by having a common ancestor, and to include no species which do not share that ancestor. Such a group is called a monophyletic group. Other types of groupings, which systematists want to avoid, include polyphyletic groups, in which the members do not all share the same ancestor, and paraphyletic groups, which do not include all the species descended from the common ancestor (Figure 1).

Over the years, the methods and logic used for phylogenetic trees have changed. Early trees were not much more than rough sketches illustrating a scientist’s general hypothesis for how things might be related. More modern trees, however, are based on much more rigorous criteria, and many of them are actually constructed mathematically by computers. Whatever the method, phylogenetic trees may make use of many types of data including morphology, known fossils, biogeographic ranges, gene frequencies, and protein and DNA sequences. In the following sections I will discuss the main types of phylogenetic trees extant today. To make simple illustrations of the methods used, I will base the trees exclusively on morphology. The organisms I will use are a hypothetical group of organisms called caminalcules (Sokal 1983a, b) (Figure 2).

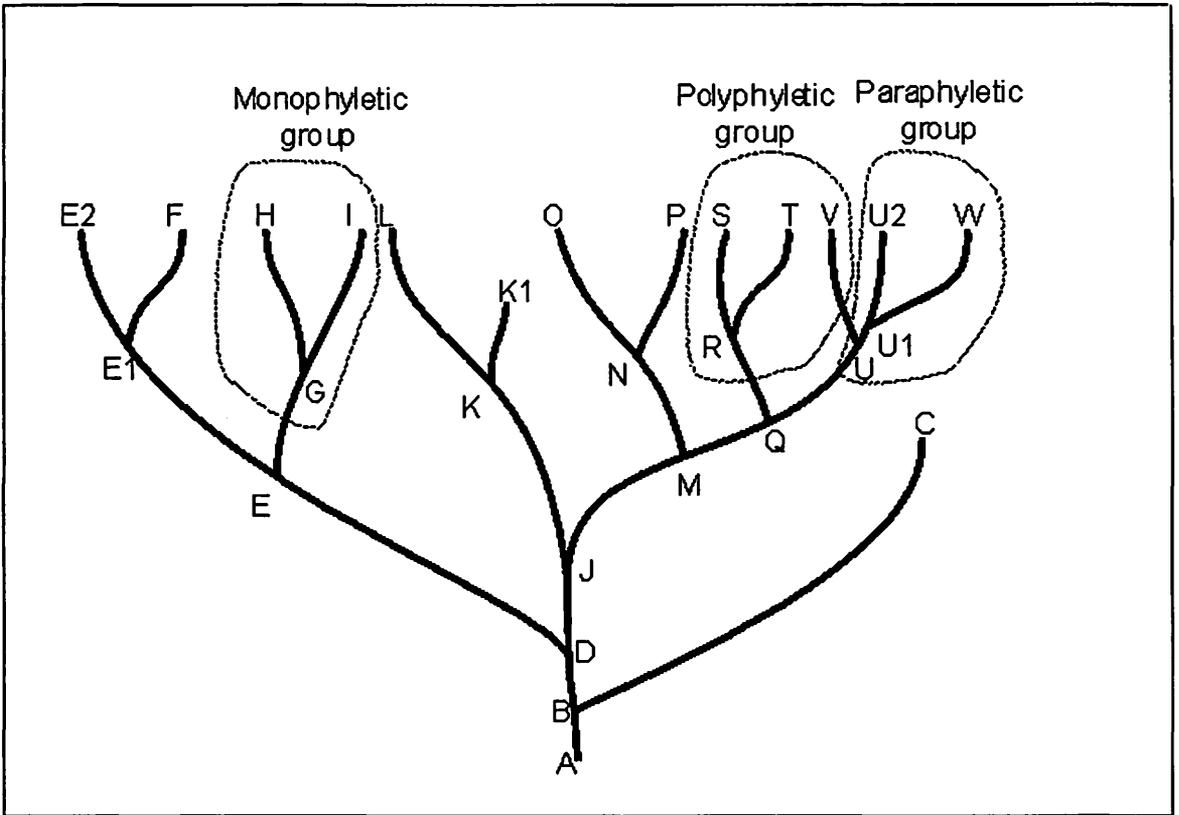


Figure 1: A sample of a phylogenetic tree, with some terms identified.

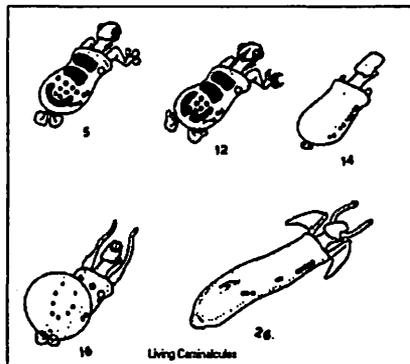


Figure 2: Sample Caminalcules

**Method 1: Phyletics:** The traditional technique used by systematists is an intuitive one, called phyletics or evolutionary taxonomy (Brusca and Brusca 1990). This technique makes heavy use of the reasoning power and evolutionary assumptions of the systematist. The scientist makes judgements as to what they think the ancestor must have looked like (based either on hypothetical considerations or on fossils), then makes educated guesses about what sequence of changes may have taken place through time as the ancestor evolved into the descendants. Hypotheses are made about what changes are more likely to have taken place, and the tree is arranged accordingly. The result is a tree of species, showing hypothetical changes through time. The lengths of the branches represent the degree of change (for example, the development of eyes would likely be considered a larger change than the change of large spots to small spots). The horizontal distance between branches sometimes suggests how different groups are from one another. For example, for the group of species shown in Figure 2, the evolutionary taxonomist may generate a phyletic tree such as that shown in Figure 3.

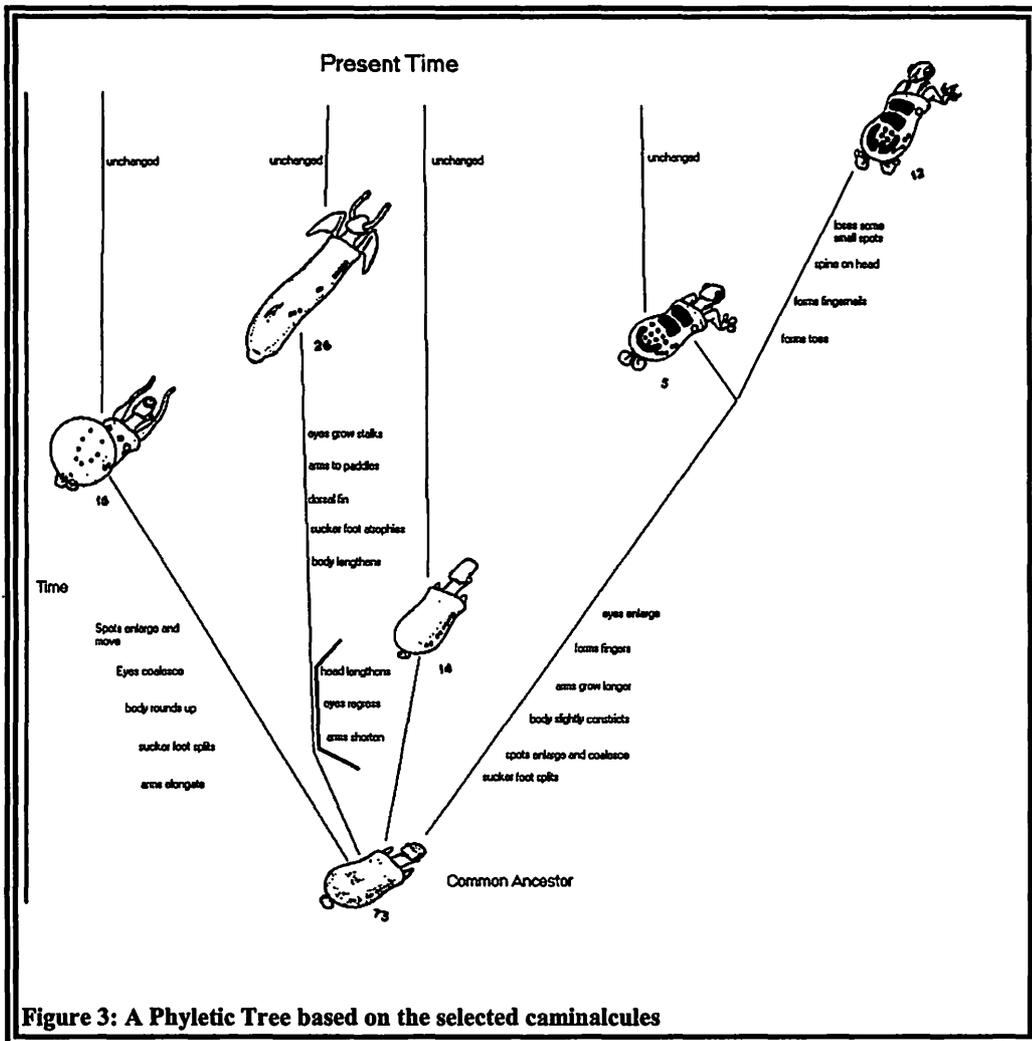


Figure 3: A Phyletic Tree based on the selected caminalcules

In Figure 3 there are four lines of descent from #73 which is the common ancestor. A variety of changes occurred along each line of descent. Species 5 and 12 are more closely related to each other than to any of the others because they are on the same branch. The rest of the species, though, are no more closely related to one another than they are to the ancestor, that is, they are widely evolutionarily separated from one another. Species which are depicted lower in the tree evolved from the ancestor more quickly than those shown higher in the tree. Some species are thought to have evolved quickly then to have remained nearly unchanged for a long period of time. This is known as evolutionary stasis and is shown by lines drawn from the species up to the present time.

**Method 2: Phenetics:** All of the early phylogenetic trees were phyletic trees, and they are still widely used today. However, as the science of systematics matured many criticized the evolutionary taxonomy (phyletics) approach because it is based so largely on subjective opinion and may involve circular reasoning (one is likely to arrive at an evolutionary tree which supports the evolutionary scenario you assumed took place to begin with). In reaction to these problems, a second approach was developed which attempts to minimize bias. Phenetics (or numerical taxonomy) makes no initial assumptions about what evolutionary steps might have taken place in the past, nor does it try to decide which traits might take longer to evolve than others. For example, losing a spot may be treated as just as important as forming an eye. No distinction is made between fossil and living species. Phenetics simply tries to establish a rigorously quantitative description of all the species involved by listing as many characters as possible for all the species, then counting how many differences there are between each species pair and generating distance measures among them. The pair most similar (nearest distance) is grouped together first, then the next most similar pair (or individual to the first pair), etc. The result is a phenogram or cluster diagram, in which the relative similarities of all the species are graphed. The longer the branch length connecting two species on the phenogram, the more distantly related they are assumed to be. The organizing basis for this approach is that we do not know beforehand what the branching pattern was, and any guesses we make may simply bias our result. Therefore the phenetic approach is to consider as many characters as possible and let the characters dictate the branching pattern. Hopefully the sheer number of characters will swamp out any distortions caused by differences in evolutionary rates, convergence, selection, etc.

Let's look at an example using our sample caminalcules: First a pheneticist would make a table of all the characters they could measure on the species. We will use 5 characters. They list the state of each character, and assign a value to each. Values might be "0" for absence & "1" for presence; "1" for short, "2" for medium, and "3" for long; etc. (Table 1).

| Character | State              |             |               |              |              |               |
|-----------|--------------------|-------------|---------------|--------------|--------------|---------------|
|           | Length/Width Ratio | Description | Short         | Long         |              |               |
| Value     |                    | 1           | 2             |              |              |               |
| Eyes      | Description        | Absent      | Present       |              |              |               |
|           | Value              | 0           | 1             |              |              |               |
| Arms      | Description        | Short       | Long          | With Paddles | With fingers | Fingers/Nails |
|           | Value              | 1           | 2             | 3            | 4            | 5             |
| Eystalks  | Description        | Absent      | Present       |              |              |               |
|           | Value              | 0           | 1             |              |              |               |
| Spots     | Description        | Only small  | Small + Large |              |              |               |
|           | Value              | 1           | 2             |              |              |               |

Next, the pheneticist rates each of the animals according to each of the characteristics, like this:

| Character          | Caminalcules     |                          |                |                |                  |                |
|--------------------|------------------|--------------------------|----------------|----------------|------------------|----------------|
|                    | 5                | 12                       | 14             | 16             | 26               | 73             |
| Length/width ratio | Short (1)        | Short (1)                | Short (1)      | Short (1)      | Long (2)         | Short (1)      |
| Eyes               | Present (1)      | Present (1)              | Absent (0)     | Present (1)    | Present (1)      | Present (1)    |
| Arms               | With fingers (4) | With fingers & nails (5) | Short (1)      | Long (2)       | With paddles (3) | Short (1)      |
| Eystalks           | Absent (0)       | Absent (0)               | Absent (0)     | Absent (0)     | Present (1)      | Absent (0)     |
| Spots              | Large (2)        | Large (2)                | Only small (1) | Only small (1) | Only small (1)   | Only small (1) |

Once this table is created, it is used to make a table of distances. There are several ways to do this, but we will use the simple method of adding all the (absolute values of) the distances. This

is called the Manhattan distance. For example, Caminalcule 5 (score 1,1,4,0,2) differs from Caminalcule 12 (score 1,1,5,0,2) by  $(1-1=0)+(1-1=0)+(5-4=1)+(0-0=0)+(2-2=0) = 1$  unit. Here is the table of distances for our sample Caminalcules based on the 5 characters above:

|    | Caminalcule |    |    |    |    |    |
|----|-------------|----|----|----|----|----|
|    | 5           | 12 | 14 | 16 | 26 | 73 |
| 5  | 0           |    |    |    |    |    |
| 12 | 1           | 0  |    |    |    |    |
| 14 | 5           | 6  | 0  |    |    |    |
| 16 | 3           | 4  | 2  | 0  |    |    |
| 26 | 4           | 5  | 5  | 3  | 0  |    |
| 73 | 4           | 5  | 1  | 1  | 4  | 0  |

Next the pheneticist starts the phenogram by joining together those Caminalcules which are the most similar. We note that Caminalcules 5&12 are only 1 unit apart [if any are 0 units apart they would be considered to be one species, or more characters would be added to the matrix so they can be distinguished]. Rules are made for ties and for groups which may be inconsistent distances apart (such as Caminalcules 14, 16, & 73). The phenogram is begun by linking together the closest individuals at the distance that separates them (Figure 4):

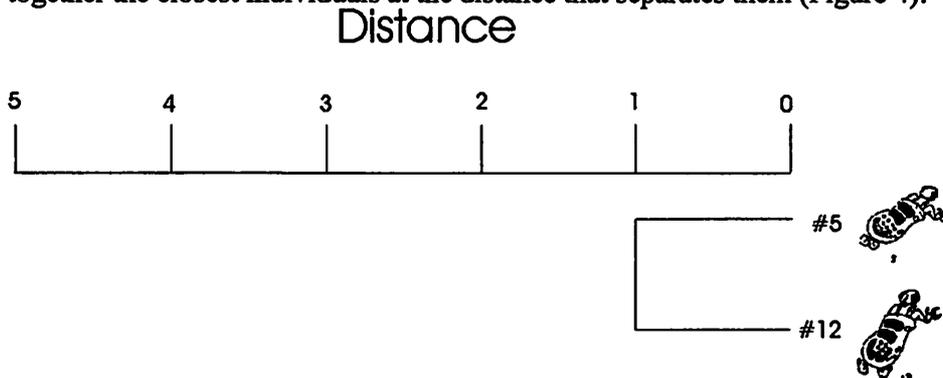


Figure 4: The first linkage in the phenogram. Caminalcules 5 and 12 are linked together at a distance of 1 arbitrary unit.

After joining the individuals they are henceforth treated as a group, with characteristics that are the average for the group. The distance between the linked group and all other individuals can then be calculated, and the individuals with the shortest distance linked again. This starts a

repeating process. Twigs, then larger branches are added as successive groups are linked until an entire tree is constructed (Figure 5).

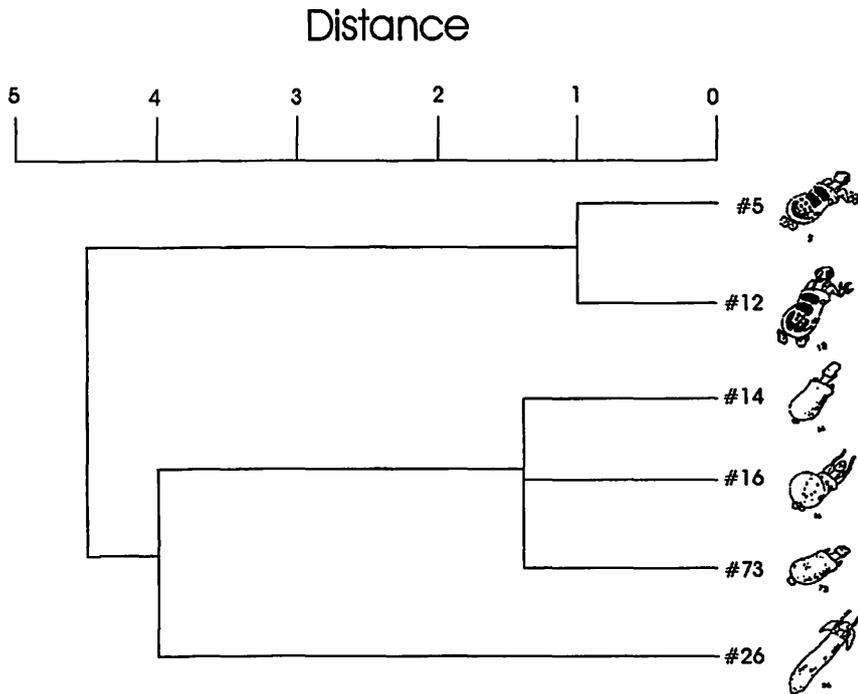


Figure 5: The completed phenogram. All species are linked together at the distance they are from the next nearest species. As in all phenograms, the distances are in arbitrary units. Note that the distances among species cluster 14-16-73 is ambiguous so they are all grouped together. Species 26 would be considered most similar to the ancestor since it is found on the lowest branch of the tree.

In a phenogram, the relative length of the arms represents how similar different groups are to one another (the shorter the arm the more similar they are). The overall arm lengths in the phenogram, however, are of arbitrary units relevant only to the specific phenogram and should not be compared to the arm lengths on another phenogram unless both phenograms were constructed using exactly the same criteria. The relative separation of species perpendicular to the arms and the relative order in which the species are depicted on the diagram are arbitrary and convey no information except for the fact that species which are linked by short arms will automatically be found close to one another due to the way the diagram is constructed. The species or group attached most closely to the “base” of the tree is usually considered to be most similar to the ancestor; for example in the tree above the ancestor would have been similar to Caminalcule 26.

Some of the features which were considered as strengths of phenetics have also been criticized as weaknesses. For example, the fact that phenetics essentially ignores what is thought to be known about the evolutionary history of a group (for example, not forcing the root of the tree to be in

some known other group or in a fossil) is thought by many to be a weakness. Part of the pheneticist's response has been that this approach is on purpose—that if a group is truly rooted in some other group, or if a fossil is truly an ancestor then careful quantification of all the known information about the group should reveal this on its own without arbitrarily distorting the tree to place its root at a predetermined spot. Critics have countered that phenograms can't always reliably find the root because the logic is backward—pheneticists are trying mathematically to climb “down” the tree from the branch tips, while the tree is assumed to have been constructed from the roots upward through time. Climbing “down” the tree can be a different process from climbing “up” the tree, as anyone who has climbed many trees or rescued cats from them can testify. Phenetics has also been criticized for weighting all characters equally, since logic would seem to indicate that some changes should be more difficult than others. (Many modern applications of phenetics do use different weights for different changes but this of course risks introducing bias to the calculations). Phenetics has also been criticized because it has trouble recognizing convergent evolution (two species looking similar because they have been subjected to similar selection factors rather than because they are related—for example marsupial vs placental moles), and it is vulnerable to distortion by different intensities of natural selection acting on different branches.

Today, phenograms are constructed by sophisticated computer programs using elaboration of a general technique called “cluster analysis” and a variety of different methods for measuring the distances between the species. For an example see Figure 1 in Giribet et al. (2001).

**Method 3: Cladistics:** Cladistics is a comparatively new phylogenetic technique which retains much of the mathematical rigor of phenetics while conforming more directly to the best-accepted paradigm for how genetic changes take place in populations. It also allows the root of the tree to be placed in some known group or fossil. The central theme of cladistics is that the only features that can be used to compellingly infer the evolutionary descent of a species are the features that they share in common with some similar group, but that other, more distantly related groups do not have. Accordingly, cladistics is a process of determining descent by means of shared, derived characteristics (synapomorphies). It tries to construct a tree of descent by starting with the features of some predetermined root (consisting of a fossil thought to be the ancestor or of a group which is believed to be closely related but not part of the group). This root is called the “outgroup”. Cladistics then repeatedly divides the group of descendant species into two smaller groups (clades) based on the sharing of characters different from that of the ancestor (synapomorphies). The resulting tree is called a cladogram (Figure 6). Each branch of the cladogram is defined by one or more synapomorphies which are found on one and only one branch of the tree. The branching points are thought to represent actual species, either still alive or most often extinct, which had characteristics as defined by the cladogram. For example, in Figure 6 branchpoints A, B, C, and probably others are assumed to represent actual species which existed whether or not such species or their fossils can be found today. The length of the branches and the direction in which the branches project have no meaning other than convenience in drawing the tree. Characters which two or more groups share but which the suspected ancestor also shared are called symplesiomorphies (shared ancestral characteristics) and are thought to have no value in determining the pattern by which the tree should branch. Autapomorphies are characters which only one species possesses. They are useful only for

constructing the finest branches of the tree which divide individual species. Example: Fig. 22.20 in Brusca and Brusca (2003).

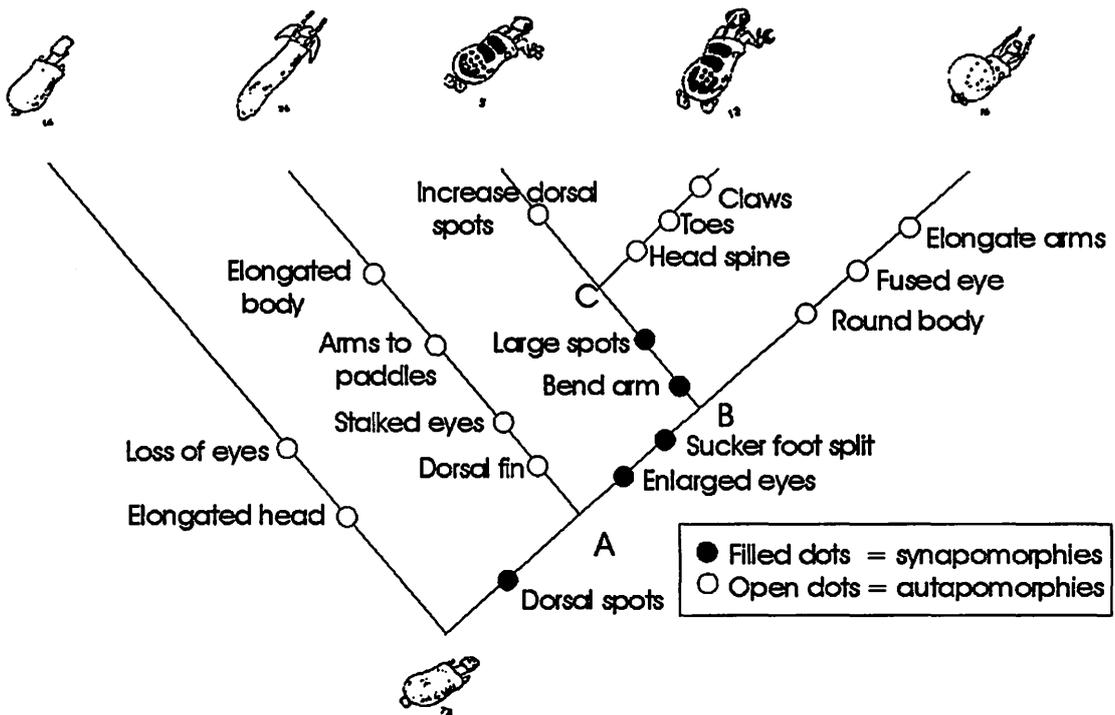


Figure 6: A cladogram of the Caminalcules.

One of the drawbacks of cladistics is that for all but the smallest and simplest groups there are a huge number of possible cladograms that can be constructed. For example, there are at least 34 million possible cladograms which could be constructed for a group of only 10 species (Brusca and Brusca 2003). How does one go about deciding which is the most likely cladogram among this multitude of possibilities while avoiding the subjective nature of phyletic trees? The answer lies in the principle of maximum parsimony, also known as “Occam’s razor”. The principle of maximum parsimony simply says that the simplest scenario is most likely to be the correct one. The changes that would have been required to create the branching patterns of each of the candidate cladograms for a group of species can be counted. The cladogram which involves the least number of changes throughout the entire tree is accepted as the most probable cladogram.

Obviously, given the astronomically large number of possible cladograms which could be constructed for any given group of species, it is not possible to try them all by hand to find which one is the simplest. Sophisticated software programs such as PAUP and PHYLIP exist which use complicated algorithms to construct the trees and find the most parsimonious ones.

## **Strengths and Weaknesses of Phylogenetic Trees, and what Creationists can learn from them:**

1. **Phyletic trees (Phylograms):**
  - a. These are the most intuitive trees but also the most subjective. The majority of trees in popular literature are phyletic trees. They purport to show a great deal of information but the information is usually quite speculative and is subject to the presuppositions of the person who created the tree.
  - b. Phyletic trees are useful as general illustrations of evolutionary ideas, and can be used as starting points for discussions of what information led the author to conclude that the evolutionary relationships the tree depicts actually existed, but they should not be regarded as having any compelling level of objective support.
  
2. **Phenetic trees (Phenograms):**
  - a. These trees are designed to avoid the pitfalls of scientific bias inherent in phyletics and to a lesser extent in cladistics. They can be very useful for rigorously exploring the similarities and differences among a group of species, and if it is valid to assume that the group is monophyletic the diagram can be used to infer what the actual network of relationships and patterns of descent may have been.
  - b. The phenetics approach in general uses the logic that is usually described as “maximum likelihood”. That is, if two species of a group are most similar to each other then it is assumed that they are the most likely to be closely related to each other. This seems like a reasonable beginning assumption if they are monophyletic. “Maximum likelihood” phylogenetic trees often are shaped like a phenogram and use this type of logic, or a combination of phenetic and cladistic techniques. Situations phenetics does not deal with well include convergent evolution, parallel evolution, or differences in the rate of change in different features (due for example to differing intensities of selection or of the relative ease with which a feature is changed). A great deal of work has been done to help maximum likelihood techniques avoid these problems.
  - c. See the note below under cladograms for a discussion of bootstrapping.
  
3. **Cladistic trees (Cladograms):**
  - a. Cladistics seems to conform the most closely to theoretical models of how evolutionary change is thought to take place, and also incorporates carefully thought-out mathematical algorithms to express the relationships. Accordingly, cladistics has become the method of choice for many systematists. Cladograms are very common in the primary scientific literature on systematics.
  - b. Cladograms can be completely confused if lateral gene transfer has taken place among species. Lateral gene transfer may take place in several ways, such as by infection by viruses or by parasites.
  - c. Given the large number of possible cladograms for any given group of species, it is not possible even for computers to exhaustively test all possible trees. Cladistic programs

such as PAUP therefore test a limited number of possibilities and arrive at a tree which represents a “local minimum” of parsimony rather than a “global minimum”. A logical attempt is made to generate the most parsimonious tree of all but for most trees it cannot be completely ruled out that there may be another, untested and very different tree which is more parsimonious.

- d. **Bootstrapping:** Because of the mathematical algorithms involved in their construction, both phenograms and cladograms can be very strongly affected by one or a few unusual species in the tree or by the miscoding of a variable. The structure of the trees is therefore very susceptible to major change depending on exactly what species are included in the tree. To avoid this problem various techniques such as “bootstrapping” are used (Hillis et al. 1996). With bootstrapping, individual species are randomly dropped from the tree and the tree is reconstructed without the species being present. This is done repeatedly and the number of times that particular branches are replicated in the different trees is noted. If a branch is replicated in a large number of the trees it is said to have “high bootstrap support”. A branch with high bootstrap support is one which is strongly supported by data from more than one species. The bootstrap support for each branch is sometimes shown next to the branch as a percentage. A related but slightly different technique is called “jackknifing”.
- e. **Phenetics and Cladistics** are independent methods of arriving at phylogenetic trees. Each has its own strengths and weaknesses. Therefore many studies use both methods and construct trees which are supported by both methods or a combination thereof. These studies generally indicate that they used both “maximum likelihood” and “maximum parsimony” methods and that their trees are “consensus trees”.
- f. Branches of cladograms or phenograms which cannot be unambiguously resolved are often depicted together as many branches coming out from the same point or level. This simply indicates that, given the techniques and characters used, it cannot be determined just what the pattern of branching on that portion of the tree should be. See, for example, Figure 4 in Knoll and Carroll (1999).

#### 4. General:

- a. It should be pointed out that **ALL** these trees are based on one huge and glaring assumption that, if not true, makes every one of the trees invalid. Every tree is based on the assumption that there is an actual evolutionary line of descent from one original ancestor to all the descendants included in the tree (that is, the tree as a whole is monophyletic). If that assumption is not true—if the species shown in the tree are not in fact descended from a common ancestor—then the tree is false regardless of the sophistication of the math and the number of characters used to construct the tree. Furthermore, **ALL** these methods start with this assumption\* and **HAVE NO WAY OF TESTING IT**. The techniques can be used to construct a tree with any collection of objects whether they are in fact related to one another or not. If the tree fits the data very strongly this may be regarded as a stronger **INFERENCE** that the tree is showing some real relationship rather than random matchings, but there is no objective way to test this inference using these methods. Therefore the construction of these trees, even sophisticated trees with a high degree of statistical support, should not be regarded as objective evidence that the species involved are actually descended from a common

ancestor, since the paradigm for constructing the tree never tested any alternative hypotheses.

\*Techniques do exist for inferring whether a group of species is likely to have descended from a particular outgroup or ancestor (the outgroup should be rooted near the base of the tree and all the other species should occur on the other branch) but every rooted tree automatically assumes that a common root does in fact exist. Actually, many of the techniques do not require the identification of a root but they still assume that all the group members are related in some way. See, for example, Figure 1 in Baldauf (2003). Specifying a root adds an additional layer of assumptions to the tree (Swofford et al. 1996).

- b. Gene exchange (lateral or horizontal gene transfer) and other forms of homoplasy (shared features for some other reason than shared descent) can cause havoc with the structure of any of the trees above. In the past horizontal gene transfer was thought to be of almost no importance in deep phylogenies. This has changed for some groups at least, such as bacteria and archaea, in which it has been found that genetically-based trees can be dramatically different from another down to the very roots depending on which genes are used. This has led to the recent conclusion that a great deal of gene exchange has occurred among bacteria and archaea so that the actual phylogenetic trees of these groups may never be reliably constructed. See for example Figure 3 in Doolittle 1999, McInerney and Pisani 2007, and Sorek et al. 2007. An increasing number of similar anomalies in other groups such as plants and animals are being found. This has led to the hypothesis that gene exchange has also occurred in these groups to a much greater extent than previously thought, perhaps via parasites or viruses. Of course, another potential interpretation of these anomalies is that the organisms are not evolutionarily related at all but that the different gene patterns reflect differences that were designed into them originally according to their needs and purposes, with no correspondence to any particular phylogenetic tree.

#### 5. Lessons for Christian scientists:

- a. While phyletic trees are powerful tools to summarize evolutionary arguments, they should not themselves be regarded as evidence for or against deep phylogenies because they are constructed based on the subjective bias of those who created them.
- b. Phenetic trees are very useful in showing the levels of similarity among species, and may be important tools for detecting the relationships among groups of species which truly did evolve from a common ancestor. The assumption that all the species descended from a common root, however, is an assumption used in constructing the trees and so the tree cannot be used as evidence that such a common descent did take place.
- c. Phenetic trees could be potentially useful tools for inferring what groups of species are descended from a common ancestor (part of the same creation "kind") and which are not. It may be reasonable to postulate that related species would cluster together while unrelated species would not. Therefore, if some of the processes named above have not confounded

the relationships, a carefully constructed phenogram of all the species may be expected to show related species clustering close together on short branches which have high bootstrap support, while considerably longer branches may be needed to connect groups of species which are not related to each other, and these branches would likely have low bootstrap support. This concept should be explored in various groups of species to see whether such a pattern can be discerned.

- d. Cladograms are constructed by carefully thought-out evolutionary logic and may have the best chance of depicting patterns of common descent among groups which actually do share common descent. It is interesting to note, by the way, that in order to do this cladograms have had to drop any specific reference to the relative amount of inferred time that may have taken place between branch points. The cladogram simply shows a likely branching pattern without specific inferences of the amount of time this branching may have required (although cladograms are often compared with the fossil record to try to make such inferences). Cladograms may be useful as a secondary method for identifying clusters of common descent, as outlined in point c for phenograms above.
- e. Finally, impressive as the mathematics and logic of phenograms and cladograms may be, it should be remembered that the rooting of these trees is based on assumptions made by the systematist rather than a self-evident feature of the trees themselves. While high bootstrap support may be regarded as evidence for a robust branching relationship and merits further careful attention, the trees themselves do not provide independent evidence that the species are indeed descended from a common ancestor. There is still plenty of room for the polyphyletic model depicted in Genesis.

#### **Literature cited:**

- Baldauf, S.L., 2003. The deep roots of eukaryotes. *Science* 300: 1703-1706
- Brusca, Richard C. and Gary J. Brusca, 1990. *Invertebrates*. 1<sup>st</sup> edition. Sinauer Associates, Inc., Sunderland, MA.
- Brusca, Richard C. and Gary J. Brusca, 2003. *Invertebrates*. 2<sup>nd</sup> edition. Sinauer Associates, Inc., Sunderland, MA.
- Doolittle, W. Ford, 1999. Phylogenetic classification and the universal tree. *Science* 284: 2124-2128
- Giribet, Gonzalo, Gregory D. Edgecombe, and Ward C. Wheeler, 2001. Arthropod phylogeny based on eight molecular loci and morphology. *Nature* 413: 157-161
- Hillis, David M., Barbara K. Mable, and Craig Moritz, 1996. Applications of molecular systematics: the state of the field and a look to the future. pp. 515-543 in Hillis, David M.,

Crag Moritz, and Barbara K. Mable (eds). *Molecular Systematics*, 2<sup>nd</sup> edition. Sinauer Associates, Sunderland, MA

Knoll, Andrew H. and Sean B. Carroll, 1989. Early animal evolution: emerging views from comparative biology and geology. *Science* 284:2129-2137.

McInerney, J. O. and D. Pisani, 2007. Paradigm for Life. *Science* 318: 1390-1391

Sokal, R. R., 1983a. A phylogenetic analysis of the caminalcules. I. The data base. *Systematic Zoology* 32(2): 159-184

Sokal, R. R., 1983b. A phylogenetic analysis of the caminalcules. II. Estimating the true cladogram. *Systematic Zoology* 32(2): 185-201

Sorek, R., Yiwen Zhu, C. J. Creevey, M. P. Francino, P. Bork, and E. M. Rubin, 2007. Genome-wide experimental determination of barriers to horizontal gene transfer. *Science* 318: 1449-1452

Swofford, David L., Gary J. Olsen, Peter J. Waddell, and David M. Hillis, 1996. Phylogenetic inference. pp. 407-514 in Hillis, David M., Crag Moritz, and Barbara K. Mable (eds). *Molecular Systematics*, 2<sup>nd</sup> edition. Sinauer Associates, Sunderland, MA