DETERMINATION OF PHYLOGENETIC RELATIONSHIPS BETWEEN FORAMINIFERAL SUBORDERS: A CLADISTIC APPROACH

by

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ABSTRACT

A morphological data matrix of 10 characters for 1 suborder of the Euamoebae and 15 suborders of foraminifera is designed to determine the phylogenetic relationships among the suborders of the Foraminiferida. Each character has a minimum of 2 states and a maximum of 7 states. Ordered versus unordered character state trees (CST's) for wall composition and wall ultrastructure are developed to evaluate the evolution of the foraminifera by focusing on Loeblich and Tappan's interpretations of relationships among foraminiferal suborders and on an evaluation of possible character changes. The computer packages MacClade 3.0, and PAUP 3.1 are utilized to analyze the coded data set under the criteria of unordered (Fitch) parsimony and mixed ordered and unordered (General) parsimony. A 50% majority consensus solution for 2,104 trees (mixed ordered and unordered parsimony) is described. An optimal ordered parsimony tree (OPT) of subordinal foraminiferal phylogeny chosen from among the multiple equally parsimonious cladograms is proposed. Techniques of tree building and tree comparison are objectively evaluated. Problems with homoplasy and assumptions of character polarity are discussed. The evolutionary scheme for the foraminifera produced by Tappan and Loeblich is interpreted within a cladistic framework and compared with the parsimonious results of this study. Parsimony analyses suggest that the suborders Involutinina and Robertinina, characterized by a calcareous aragonitic wall composition, are monophyletic and associated with the Fusulinina, not Textulariina. Ordered and unordered parsimony hypothesizes that Rotaliina and Globigerinina are closely related to the sister group of Spirillinina, which is a monophyletic group with calcareous calcite shells. There is no evidence that Fusulinina is not monophyletic. This research indicates the utility of a systematic cladistic approach to the determination of phylogenetic relationships between foraminiferal suborders.

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CHAPTER I INTRODUCTION

The Aims of This Chapter

This chapter aims to introduce the nature and organization of this work. To such an end, we shall first look at the concept of Foraminiferida and then move into a brief examination of three conventional approaches to foraminiferal classification. After that, the cladistic approach, which has been followed in this study, will be outlined. Finally, the purposes of my research and the organization of this thesis will be stated.

The Working Definition: Foraminifera

Foraminifera, as defined by Loeblich and Tappan in their 1987 monograph on foraminiferal genera, "are protozoans that generally construct a test by incremental additions, commonly a separate chamber each time, and each new chamber covering a preceding aperture to allow cytoplasmic continuity through the test and contact with the external environment."

As a reliable indicator of paleoceanographic and tectonic events, the order Foraminiferida (Protozoa, Sarcodina), including both extant and extinct forms, is amongst the most significant economic micropaleontological tools. It is also worth noting that, due to its profuse variety and easy availability, this order presents abundant fossil data to document the diverse evolutionary radiations in the fossil record. However, despite over 200 years of research, the natural phylogeny of foraminifera, in large part, remains an enigma. With these words, I shall naturally turn our attention to the conventional approaches to foraminiferal classification.

The Conventional Approaches

Three conventional approaches to both family and subordinal foraminiferal classification can be identified, each depending on a different cognizance. They have been tabulated as follows:

Table 1. Conventional approaches to foraminiferal classification and representative researchers

	Family Classification	Subordinal Classification
Phenetics	d'Orbigny.....1826-1852 Williamson.....1858 Reuss.....1861 Carpenter.....1862 Glaessner.....1945	Reuss.....1861 Carpenter.....1862 Jones.....1876
Evolutionary Taxonomy	Schwager.....1876 Neumayr.....1887 Lister.....1903 Mayr.....1969 Hofker.....1972 Adams..... 1978 Blow.....1979	Brady.....1884 Loeblich and Tappan, 1964, 1987
Phylogeny	Rhumbler.....1897 Cushman.....1909, 1933 Galloway.....1933	Tappan and Loeblich, 1988 Loeblich and Tappan, 1989

The tabular analysis above, by presenting some representative researchers in each area, appears to indicate a progressive relationship among different approaches, since it points to a chronological difference among them. The research profiles listed above indicate that the pheneticists were the earliest researchers in this field, and that those regarded as

phylogeneticists characterize the present generation of researchers. The tabulated data also show that investigation into foraminiferal family classification began much earlier than that on subordinal classification. (For a detailed discussion on the history of the classification of foraminifera, refer to Cifelli and Richardson 1990.)

The phenetic approach, based on a descriptive framework of classification, groups similarly structured taxa together, with the focus on structural similarity in determining taxonomic relationship. As Wiley (1981) observes, phenetics is utilized to "group individuals into taxa on the basis of an estimate of overall similarity," and those who argue for this approach maintain that "grouping by overall similarity results in stable and natural classifications."

In one sense, phenetics can be described as an attempt to apply an empirical classification method to taxonomic studies. However, phenetics seems to represent only a small step from traditional systematics in that at its philosophical core is the desire to assess the general similarity of the organisms to be classified. It should also be recognized though that grouping taxa according to overall similarity ignores the results of parallel or convergent evolution (Wiley et al. 1991). Therefore, the phenetic approach may result in misinterpretation or miscomprehension of evolutionary history (for discussion, refer to Scott-Ram, 1990).

As an alternative to the phenetic approach, evolutionary taxonomy, now regarded as "classical systematics" methodology, focuses on a few characters that help denote common ancestry and emphasizes amount of devergent change, i.e. autapomorphies (for discussion, refer to Myar, 1969, Simpson, 1959 and 1961, Wiley, 1981). This method of classification draws from phenetics, though the significance of some plesiomorphic characters is emphasized and the importance of cladogenesis ignored. In fact, evolutionary taxonomy presents a balance of autapomorphies (character uniqueness) and plesiomorphies, both of which are necessary for reconstructing the phylogenetic history and classification of taxa.

Conventional evolutionary taxonomic approach (classical systematics) has played an important role in the way that foraminiferal evolution has been studied. However, high order taxonomic classifications by using this approach is deemed to be more intuitive because the method employs character weighting. Weighted characters are selected according to often quite different opinions of various researchers. In consequence, this method fails to properly evaluate the evolutionary significance of the groups classified in that it is unknown whether the results, often skewed by personal opinion or intuition, represent the true situation in nature. Hull (1964) pointed out: "Phylogeny is not a fact to be discovered, but an abstraction that is inferred almost exclusively from morphological, genetic, paleontological and other types of evidence and is not observed directly."

To provide an alternate approach, some taxonomists developed a methodology called the phylogenetic approach. As successors to the practitioners in the evolutionary taxonomic field, the phylogeneticists advanced the opinion that classification should be done with a view to reflect evolutionary history as closely as possible. Therefore phylogeneticists like Rhumbler (1897), Cushman (1909 and 1933), Galloway (1933), Tappan and Loeblich (1988), and Loeblich and Tappan (1989) employed some strictly evolutionary -- a few unclearly derived apomorphies, but not cladistic -- principles in the area of family and suborder classification to judge phylogenies, and sought to form a classification by finding taxa genealogues rather than by resorting to intuition.

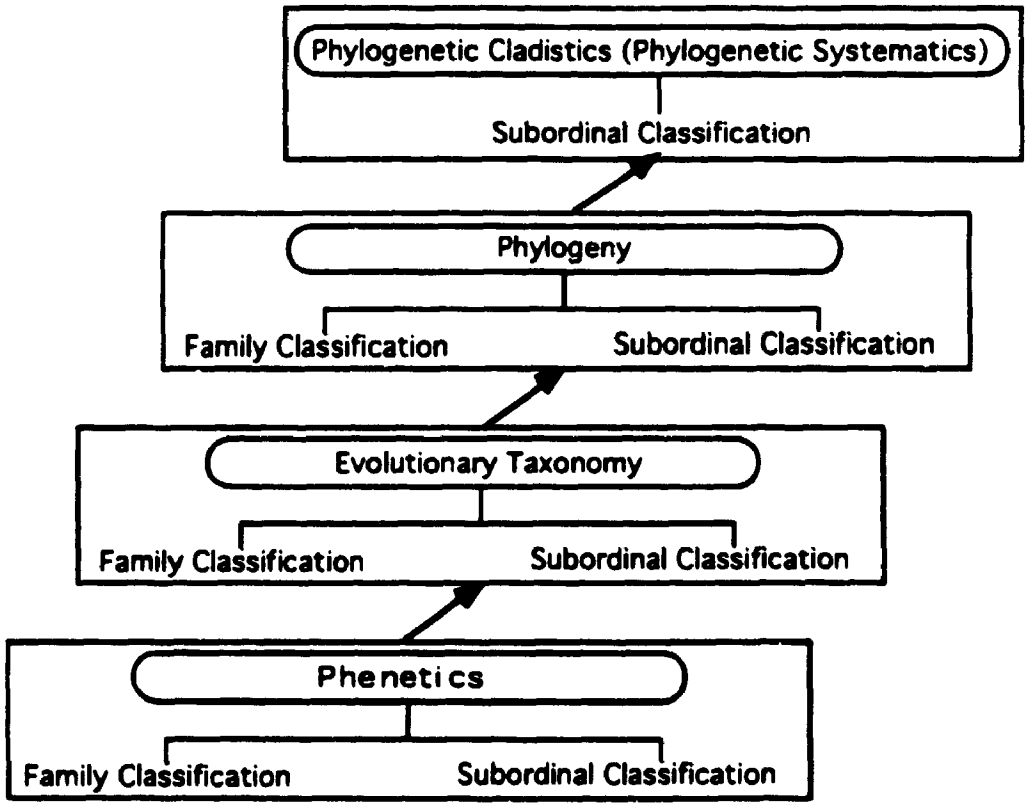
Classifications using this phylogenetic scheme have been widely accepted by researchers with varying degrees of success and have become very popular in many fields of biology and paleontology. In reality, some practitioners of this approach have turned their attention to the synapomorphic messages gleaned in their data sets.

For instance, the subordinal classification of foraminifera proposed by Tappan and Loeblich (1988) and Loeblich and Tappan (1989) suggests the emphasis of a few morphologic characters (e.g. test mineralogy and microstructure) that are believed to be

importantly informative in apomorphic clues. Their subordinal foraminiferal classification has become the standard model, which has been invoked by most micropaleontologists ever since its development.

At this point, I will introduce another approach to classification based on *phylogenetic cladistics* or *phylogenetic systematics* as developed by Hennig (1965 and 1966, later defined by Wiley, 1981). As a rigid methodology for phylogenetic analysis, the cladistic approach aims to analyze historically common ancestral relationships among groups of taxa by defining shared derived apomorphic characters (i.e. the emphasis of synapomorphies). It is the rank order that is important, not the unique qualities of the characters, nor the importance of novelties or overall similarities due to adaptive convergence. In this sense, the cladistic approach signifies the most recent development of foraminiferal classification.

The evolution of classificatory approach in the studies of foraminifera can be graphically represented as follows:



Although the cladistic techniques are commonly used in other disciplines (e.g. Entomology; for detail, see Heraty et al. 1994), it has not been utilized for subordinal classificatory research on foraminifera prior to the present study.

The Purposes of This Study

The purpose of this study is fourfold: 1) to re-analyze the baseline phylogenetic classification scheme as proposed by Tappan and Loeblich (1988) and Loeblich and Tappan (1989); 2) to determine the character similarity and hierarchy of all the 15 suborders of foraminifera by choosing shared derived characteristics and attampting to avoid characters that exhibit convergence during foraminiferal evolution; 3) to compare the monophyletic groups emerging from the collected data with their longevity; and 4) to propose a new cladistic model at the subordinal level for foraminifera. Meanwhile, this article is also intended to demonstrate the goals, methods and dynamic features of the cladistic approach as applied in foraminiferal phylogenetic reconstruction. It is my hope that the subordinal phylogenetic model for the foraminifera presented in this work offers a testable hypothesis for the application of evolutionary information crucial to the interpretation of foraminiferal ecology/paleoecology, fossilizable molecular biology and biochemistry.

To achieve the above purpose, I shall begin with a historical overview (Chapter II), where the history of foraminiferal classification will be reviewed. The theoretical background of cladistics will be delineated in Chapter III. In Chapter IV, the nature of the dataset and the types of character analysis utilized will be outlined. Chapter V presents my reconstruction of the parsimonious hypotheses of phylogeny in the realm of foraminiferal research, while Chapter VI functions to expound certain meaningful analysis results and subsequent assumptions with some concluding remarks. In Chapter

VII. I will summarize my conclusions as established from all the facts having emerged in this investigation.

CHAPTER II PREVIOUS RESEARCH

The Aims of This Chapter

This chapter aims to present a historical review of what has been accomplished by previous researchers in the area of foraminiferal classification. In reality, as will be shown later in this chapter, much work has been done in this area. Cladistic studies of plesiomorphic and apomorphic characters at the subordinal level have never been attempted though. To show this, a short retrospect will be offered in the following regards: 1) the family classification based on phenetics, evolutionary taxonomy or phylogenetics; 2) the subordinal classification based on phenetics, evolutionary taxonomy or phylogenetics.

It has to be pointed out that much weight will be put on Tappan and Loeblich's (1988) and Loeblich and Tappan's (1989) phylogenetic scheme when I discuss phylogenetic subordinal classification. Because their classificatory scheme is regarded as the standard model in the field, it is selected as the subject to be tested in this work.

Phenetic Classification of Foraminiferal Families

Pheneticists (d'Orbigny, 1826 and 1852; Williamson, 1858; Reuss, 1861; Carpenter, 1862; Glaessner, 1945) made in-depth studies of virtually all aspects of foraminifera and through their collective efforts laid much of the groundwork for family classification. They examined, in detail, chamber arrangement, wall textures, internal structures, and shell forms.

The most representative researcher in this area is d'Orbigny (1826 and 1852), who constructed 5 families in his *Tableau Methodique* (1826) and thus provided the earliest classification of foraminiferans as a distinct group. D'Orbigny also constructed a set of 100 models of foraminifera to illustrate the features of all of his "genera and subgenera, and even the principle species of the order of Foraminifera" (d'Orbigny, 1826).

One of d'Orbigny's major achievements was the classification of the "Foraminifera" as a separate order within the class Cephalopoda. The essential characters selected by d'Orbigny to isolate the foraminifera from other cephalopods were: their internal shell, their lack of a siphon, their final closed chamber; and the presence of one or many apertures to provide a means of communication between chambers.

D'Orbigny also observed the external shell, tiny head and pseudopodia of the foraminiferal animal on live specimens. He interpreted the pseudopodia as numerous minute tentacles. It was this interpretation that induced d'Orbigny to retain the order Foraminifera in the class Cephalopoda.

Although d'Orbigny fundamentally was in error as to the nature of foraminifera, his phenetic approach laid the groundwork for modern foraminiferal classification. D'Orbigny (1852), for instance, recognized a large number of families in 7 orders. D'Orbigny's familial categories were based on the single character of plan of growth or chamber arrangement -- a highly variable character. For instance, the elongate spiral or serial *Bulimina* was grouped together with the trochospiral *Rotalia* and the planispiral *Nonionina* in the family Turbinoidae. His classification also required that these variants be placed in separate families. In a few words, it should be evident that d'Orbigny's classification was very simple: families were defined on merely one external feature.

Phenetic Classification of Foraminiferal Suborders

Among pheneticists involved in subordinal classification (Reuss, 1861; Carpenter, 1862; Jones, 1876), there was agreement on a major, two-fold breakdown based on the

presence or absence of pores and an additional subdivision based on wall composition.

In his history of foraminiferal classification, Cifelli and Richardson (1990) reported the remarkable coincidence with which Reuss (1861) and Carpenter (1862) "should produce a classification essentially the same in its major features." According to Cifelli and Richardson, Reuss and Carpenter subdivided the order Reticularia into two primary groups: the "Sub-Orders" Imperforata and Perforata. Their classifying criterion was the presence or absence of pseudopodial pores in the test wall. Carpenter (1862) considered plan of growth to be anessentially worthless character for "separating the great primary divisions of Foraminifera".

Carpenter (1862) regarded porosity as a factor of greater systematic value to consider in classification than plan of growth. He thought that porosity similarity is very important. Reuss (1861) provided for a clearer separation between the arenaceous and imperforate forms. In their imperforate suborder, Reuss and Carpenter distinguished a calcareous group, which they placed in the family Miliolidae, and an arenaceous group, which they placed in the family Lituolidae.

Jones' (1876) three suborders -- the Imperforata, Arenacea and Perforata -- were based on wall texture and represented a reversion to Williamson's (1858) porcellaneous, agglutinated and hyaline subdivisions.

Family Classification based on Evolutionary Taxonomy

The research in this area can be clearly illustrated by Schwager's work (1876). As mentioned earlier in Chapter I, conventional evolutionary taxonomy has played an important role in the way that foraminiferal evolution has been studied. Nevertheless, because of its emphasis on character weighting, this classification method is more intuitive than data-oriented. With brief diagnoses, the format of Schwager's classification was so simple and formalistic that it reads like a key designed to be a

practical guide to the families and genera of foraminifera. His classification of about 17 families represented a fundamental physiological condition of the foraminifera, as Cifelli and Richardson (1990) observe, "was very brief and concise." However, Schwager seemed to intend his classification scheme to be provisional and thus to provide more than just a key. He meant it to be "closest to nature as possible." Schwager thought that it was immediately evident that natural relationships were interfered if morphologically similar forms with different wall textures were grouped together. He also recognized that the arenaceous miliolids remained a problem but made no provision for them in his classification.

The classification made by evolutionary taxonomists (e.g. Schwager, 1876; Neumayr, 1887; Lister, 1903; Mayr, 1969; Hofker, 1972; Adams, 1978; Blow, 1979) were more concerned with wall texture and composition. The more recent classifications were more natural and were thus preferable to the system presented by Carpenter.

Subordinal Classification based on Evolutionary Taxonomy

Brady (1884) made a great advance in the field of foraminiferal classification. His monograph of 814 pages and 115 plates reported 10 families of foraminifera collected during the world-wide expedition of H. M. S. *Challenger.*

As for Brady's work, Cifelli and Richardson (1990) comment: "The classification that Brady established to deal with the huge, world-wide fauna at his disposal, would be generally followed for probably a more extended period of time than any other classification before or since. His notes on the geographic and bathymetric distribution of species allowed for insight into the ecology of benthic foraminifera and his study of tow-net material brought planktonic foraminifera into focus for the first time."

Brady recognized that many species and even genera in some families differed in details of morphology as well as in habit, though closely related by an array of

intermediate modifications. He realized that many of these forms should be distinguished and nominated. In a criticism of Reuss' (1861) inclusion of the arenaceous types in the suborder Imperforata, Brady pointed out that examples of arenaceous forms with porous tests were too numerous and varied to be discarded as mere exceptions. However, since Brady recognized no groupings of subordinal or superfamilial rank, he arranged his families in numerical order, grading them from the most primitive family (Gromidae) to the most structurally advanced family (Nummulinidae).

In practice, most of the families he proposed (e.g. Textularinidae, Lagenidae and Globigerinidae) were later elevated to suborders (Loeblich and Tappan, 1964 and 1987). Loeblich and Tappan (1964 and 1987) put more emphasis on wall composition and wall ultrastructure, and tried to pinpoint the homologous relationships among these characters.

Family Classification based on Phylogenetic Approach

By basing classification on evolutionary taxonomy, phylogeneticists (Rhumbler, 1897; Cushman, 1909 and 1933; Galloway, 1933) expected to find taxa genealogues that reflected evolutionary history as closely as possible. As a phylogeneticist, Rhumbler built up an evolutionary scheme of 9 foraminiferal families. According to Rhumbler, the evolutionary development in foraminifera was the reverse of recapitulation, with the early types of test representing the descendent rather than the ancestral stage, except for the prolocular area. The distal end of the test represented the most primitive stage of development and eventually becomes discarded in the course of phylogeny. One reason he gave for this conclusion was that in the course of foraminiferal ontogeny, a change in growth plan proceeds from more complex to simple and not the reverse.

In Rhumbler's view, the chief factor in foraminiferal development was adaptation to resist mechanical stress through selection of more compact test forms. He regarded the biserial, triserial and spiral forms as increasingly more resistant to breakage than the

uniserial forms. The reversal of the usual order of ontogenic development was attributed to the greater delicacy of the small chambers in the early types of test. In the later stages of growth, the greater bulk of protoplasm present in the expanded chambers could compensate for a weaker type of chamber form. Rhumbler used a number of examples to illustrate his point, including the development of coiled taxa within different families.

Phylogenetic Classification of Suborders

Most of the work on the phylogenetic classification of foraminiferal suborders was carried out by Loeblich and Tappan (1987) and Tappan and Loeblich (1988). They identified 3,620 genera, divided into 12 suborders (Allogromiina, Carterinina, Fusulinina, Globigerinina, Involutinina, Lagenina, Miliolina, Robertinina, Rotaliina, Silicoloculinina, Spirillinina, Textulariina). Furthermore, Loeblich and Tappan (1989) proposed a revision to the number of agglutinated suborders and increased the total number of suborders from 12 to 15. Four agglutinated suborders, including Astrorhizina, Haplophragmiina, Trochamminina and Textulariina, were derived from subdivision Textulariina (Tappan and Loeblich, 1988).

Loeblich and Tappan (1989) also defined the suborder Astrorhizina to include monothalamous agglutinated taxa. The suborder Haplophragmiina was revised to include multilocular agglutinated taxa with alveolar walls. The suborder Trochamminina was proposed to include taxa with organic cement and simple agglutinated walls. The Textulariina was now restricted to multilocular taxa with agglutinated walls of low-magnesium calcite. In the short time since this publication, this classification has become the standard in the field. Nonetheless, it should be mentioned here that their phylogenetic scheme is not unquestionable, and as with all previous systematic analysis, subject to revision. With this said, we shall move on to examine the phylogenetic scheme suggested by Tappan and Loeblich.

Tappan and Loeblich's Phylogenetic Scheme

Despite the long history of foraminiferal systematics, the development of a comprehensive classification that clearly identifies monophyletic lineages and their phylogeny has largely eluded researchers. A subordinal classification scheme (Tappan and Loeblich, 1988, and Loeblich and Tappan, 1989) outlined the evolutionary trends for the 15 foraminiferal suborders and became the basis of the previous phylogenetic model (Figure 1).

Tappan and Loeblich (1988) considered the Allogromiina, characterized by a membranous organic coating, as the most primitive suborder. They point out: "In summary of the subordinal phylogenetic development suggested, two major lineages may have arisen from Allogromiina. An increase in the proportion of foreign particles in the proteinaceous wall by some Allogromiina could have led to the evolution of the fully agglutinated test as in Textulariina although their firmer tests have produced a much better fossil record." They suggest that the walls of textulariinids are characterized by a calcareous groundmass cementing the agglutinating particles together, and that small quantities of adventitious material present in the tests of some Allogromiina and the organic inner lining or proteinaceous cement of many Textulariina indicate their close relationship. They also believe that primitive Fusulinina (Archaesphaeridae) probably arose from a similarly globular allogromiid: "Fusulinina probably arose directly from Allogromiina in the Late Silurian with development of the capability to secrete walls of amorphous or spicular calcium carbonate. Again, this is represented as a higher group." [Note: Murray (1973) also pointed out that the low-magnesium calcite equidimensional crystals comprising the test cement are enveloped in an organic sheath that can be aggregated into bundles of rods].

Tappan and Loeblich (1988) note: "Biomineralization of calcite occurs in some Textulariina, hence as greater emphasis on the deposition of calcium carbonate as aragonite led from Trochamminidae to Duostominidae (Robertinina), some of which also

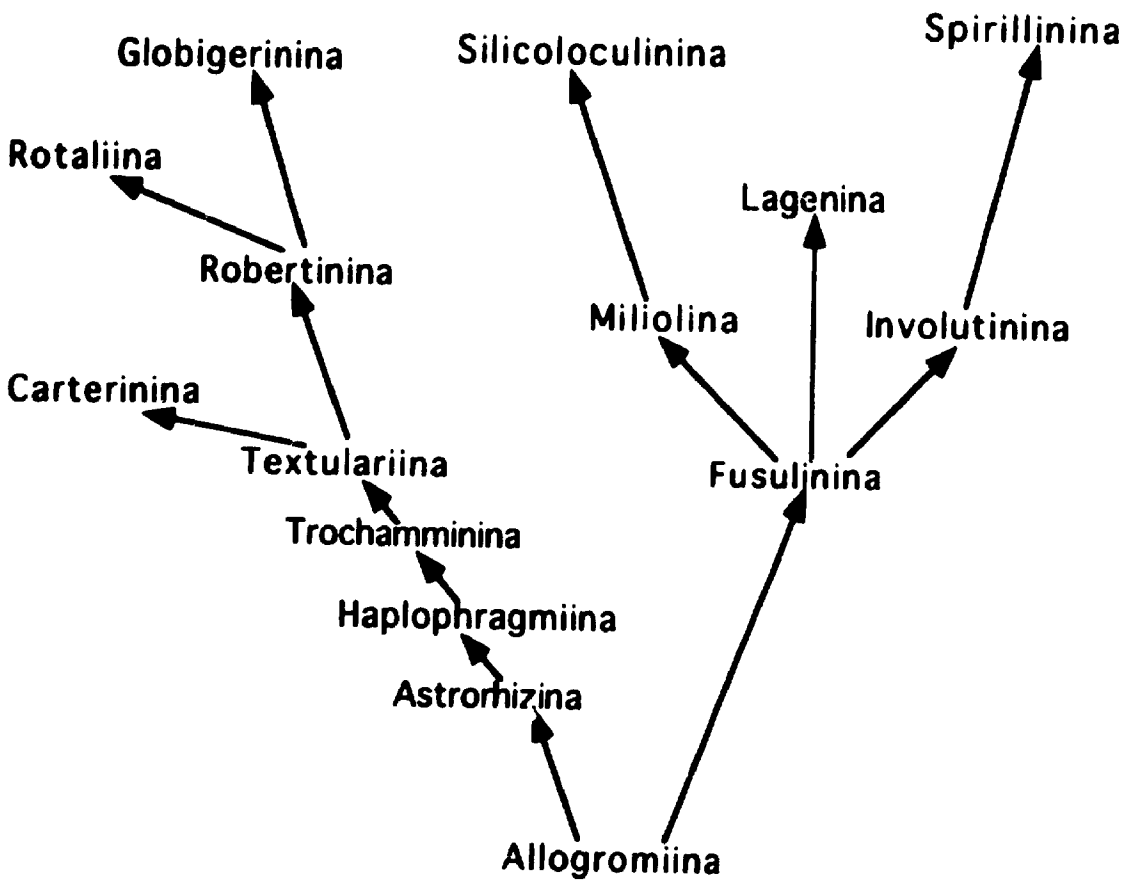


Figure 1. Evolution of the suborders of the Foraminiferida after Tappan and Loeblich (1988), and Loeblich and Tappan (1989).

may utilize adventitious material in their tests, or as calcite leading much later from Trochamminidae to Carterinina." They declare that the suborder Carterinina is characterized by an organic inner lining and by rodlike calcitic spicular in the outer layer, and that this similarity of these spiculars to those found in Textulariina may indicate a close association between related groups.

According to Tappan and Loeblich (1988), the aragonitic Robertinina, which appeared in the Middle Triassic and are characterized by low trochospiral chambers, are more advanced than Involutinina (Permian) and perhaps closely related to Trochamminina (Textulariina). Tappan and Loeblich state that by Jurassic time, primitive Robertinina gave rise to the more advanced aragonitic Robertinina, and in turn to the calcitic Rotaliina and Globigerinina.

Tappan and Loeblich (1988) suggest that since the porcellaneous walls of Miliolina are constructed of high-magnesium calcite, they may have been derived from similarly microgranular-calcite-walled fusulinids. They also suggest: "Since the general plan of growth in the Silicoloculinina is identical to that of Miliolina they are probably closely related,...the monogeneric Silicoloculinina characterized by a biomineralized wall of opaline silica are a late offshoot from the Miliolina."

By the end of the Paleozoic, Fusulinina gave rise to Lagenina, and its tubular enrolled phenotypes gave rise to the aragonitic Involutinina (Tappan and Loeblich, 1988). Tappan and Loeblich (1988) suggest that Involutinina in turn gave rise to the calcitic Spirillinina by the Late Triassic.

Unfortunately, this subordinal foraminiferal classification scheme has some potential problems. It gives rise to some questions as to where the real common ancestor of subordinal foraminiferal groups lies based on the synapomorphies, how the agglutinated groups are related, and whether their subordinal deviation sequence reflects the natural phylogenetic history.

Concluding Remarks

All the above approaches concentrate on one or a few aspects so that it is difficult to build up a dependable classificatory foundation for future studies. These studies also clearly imply the need for a cladistic classification of foraminifera at the subordinal level. With all this addressed, we shall now turn to erect a theoretical framework for this taxonomic investigation. This is the work to be accomplished in Chapter III.

CHAPTER III THEORETICAL FRAMEWORK

The Aims of This Chapter

In the previous chapter, the different classification approaches of certain representative researchers were looked at. This chapter will serve to lay down a theoretical framework for the cladistic exploration carried out in this study. For this purpose, a set of important concepts and associated terms will be defined, including characters, homoplasy, transformation series, CSN, CST, and monophyletic groups. Attention then will be turned to relating some broader notions that function as vital nodes on the theoretical framework for this study. Among these notions, special weight will be put on character coding, cladograms, tree length, *CI* and *RI*, and consensus techniques. The first two are indispensable for the type of character state judgment to be made later, and the rest essential for the tree analysis unfolded in Chapter V. In so doing, I will seek to develop a method of analysis appropriate to subordinal classification of foraminifera.

Characters and Associated Terms

The value of any judgment about hierarchical relationships between organisms has to be determined by character analysis. Consequently, the term *character* is undoubtedly vital to any research in the discipline of bioecology and biogeography. As for this term and the concepts associated with it, the following terminological distinctions will be followed in this work.

Wiley (1981) provides a comprehensive definition of *character*:"a morphological feature consisting of an internal or external observable attribute". (As for the discussion

on morphological characters, refer to Duncan and Stuessy, 1984.) A character can be observed as a set of alternative conditions, termed as *character states*, which can evolve from one to another (Maddison and Maddison, 1992).

The concept of *character* as referred to in systematic investigations normally concerns the sphere of evolution, thus generating variant terms: *ancestral character*, *plesiomorphic character*, *descendant* or *derived character*, *apomorphic character*, *synapomorphic character*, *phylogenetic character*, *homologous character*, *nonhomologous* or *homoplastic character*, *structural character* and *functional character*.

An evolutionary novelty (i.e. an inherited change of an old character to a new one) generally evolves from a previously existing character that relates an ancestor with its descendant. (See Scott-Ram, 1990 for observations on ancestor-descendant relationships.) The previously existing character mentioned here is normally referred to as an *ancestral character*, or more precisely, termed a *plesiomorphic character*. The new character resulting from an evolutionary novelty is usually mentioned as a *descendant* or *derived character*, or termed an *apomorphic character*. Within the context of a phylogenetic group, a character state derived within the group is called an *apomorphy*, whereas an ancestral character state featuring the most recent common ancestor of the group is called a *plesiomorphy*.

A *synapomorphic character* is a homologous character found in two or more taxa that share a common ancestor. Maddison and Maddison (1992) propose an explicit definition of both *synapomorphy* and a related term *autapomorphy*: "A derived character state shared by members of a group is a *synapomorphy* of the members of the group, and an *autapomorphy* of the group."

When defining *phylogenetic character* (a broad concept of synapomorphy), Wiley (1981) remarks that characters of this type contain the features of two or more organisms "hypothesized to be homologues" (i.e. homologous traits; I will return to the term *homologue* in later paragraphs). He continues to observe that a *phylogenetic character*

shared by two or more organisms suggests a phylogenetically significant relationship between these organisms. *Phylogenetic characters*, as he finally comments, "are expected to be similar from organism to organism at a level of similarity set by the investigator, but because of evolutionary divergence, we do not always expect phylogenetic characters to exhibit detailed similarity."

A *homologous character*, sometimes called *homologue*, entails the concept of *homology*, which has been defined by many researchers (e.g. Hennig, 1966; Boyden, 1973; Hecht and Edwards, 1977; Eldredge and Cracraft, 1980; Van Valen, 1982; Patterson, 1982). Bock (1974 and 1989) provides the following definition: "A feature (or condition of a feature) in one organism is homologous to a feature (or condition of a feature) in an another organism if the two features (or conditions) can be traced phylogenetically to the same features or conditions in the immediate common ancestor of both organisms." His definition looks somewhat meticulous. Here, Bock seems to avoid mentioning similarity so as to distinguish homologous resemblance from convergent likeness. Actually, Van Valen's (1982) definition of *homology* as similarity by virtue of common ancestry is simpler and also acceptable.

Considering all this, a *homologous character* can be defined as an attribute of an organism with the similarity to an attribute of another organism that can be traced phylogenetically to the same attribute observable in common ancestry. In this sense, *ancestral character*, *plesiomorphic character*, *descendant* or *derived character*, *apomorphic character*, *synapomorphic character* and *phylogenetic character* can all be classified as *homologous characters*.

It should be added that the term *homologue*, apart from its meaning of *homologous character*, can also be used to refer to homologous relationships, organs or structures. Consider the meanings of *homologue* occurring in the following statement by Wiley (1981): "Homologues are probable between characters of two organisms which share other characters of sufficient complexity to be judged homologous by the major

criteria...perhaps even more interesting is the situation where rather dissimilar structures can be homologues because of their special qualities." Clearly, the first term *homologues* connotes the homologous relation between characters, whereas the second denotes homologous structures.

A *nonhomologous* or *homoplastic character* is a similar character shared by two taxa without meeting the criteria of common ancestor (Wiley et al. 1991). As defined by Maddison and Maddison (1992), a character state having evolved more than once in different branches of the tree is called *homoplasy*. Since convergences and parallelisms, or homoplasies, evolve independently, they confuse the interpretation of relationships between taxa and create problems with the identification of homologous characters by investigators. Homoplastic characters or homoplasies therefore provide no evidence of common ancestry.

Parallel reversals can occur several times during development of individual lineages although superficially they look like homologous characters. For instance, when studying Protozoan animals, such as foraminifera, we could not use the complex array of tests as a means to identify homologous arrangements merely because they repeatedly appear so many times in the independent groups. Much of this research is an attempt to apply cladistics in spite of this apparent problem and to seek out real homologous characters by eliminating character reversals during adaptable convergence.

To go deeper, homoplasies can be sorted into two types: *structural character* and *functional character*. According to Wiley (1981), *structural characters* are two attributes similar in basic structure so that parts are directly comparable; and functional characters are traits similar in detailed function in such a way that parts may be appropriate to functional comparison. At the biochemical level, this means that both the structural character and the functional character may be exactly similar but not phylogenetic or homologous.

Transformation Series, Character State Polarity and Character State Order

The term *transformation series* can be defined as a group of homologous character states. A transformation series, if ordered, serves to distinguish the path of possible evolution, but not necessarily the direction of the path. To determine a transformation series, we must know both *character state polarity* and *character state order* (Mickevich, 1982).

Character state polarity specifies which of two or more homologous character states is plesiomorphic or apomorphic (i.e. *primitive* or *derived* in earlier researchers' terms; see Patterson, 1982). Polarity is decided by using outgroup comparison (Farris, 1973 and 1982). *Character state order* is the relative relationship of the states to each other (=state adjacency, Wheeler, 1990).

Ordered transformation series and polarized transformation series need to be differentiated from each other. Ordered transformation series are those having only two homologous characters. All transformation series of this type, as Wiley et al. (1991) reported, "are automatically ordered but not necessarily polarized." Polarized transformation series are those with the direction of character evolution already specified. In other words, they are polarized in that the relative apomorphy and plesiomorphy of characters have been determined. A transformation series can be both ordered and polarized, or unordered but polarized.

Binary Transformation Series

A binary transformation series is a transformation series of two directly homologous character states. It consists of a plesiomorphy (code "0") and its single derived homologue (code "1") (Wiley et al. 1991).

Multistate Transformation Series and Associated Terms

What we term as a *multistate transformation series* actually refers to a transformation series having more than two different homologous character states. Such series are observable when we work on a large group, or even a small group that has undergone considerable evolution. A multistate transformation series poses a hypothesis as to which states of a character evolve directly into which other states (Hennig, 1966). Some researchers nominate it as a character phylogeny or a character tree (e.g. Lipscomb, 1992). A multistate transformation series normally contains a plesiomorphic character and several apomorphic character states.

When the character has just two states, there is only one possible character state order; the order can be ambiguous in multistate transformation series (Lipscomb, 1990; Mickevich, 1982). If a multistate transformation series is unordered, several paths might be possible. Therefore, the ordering of multistate transformation series is of considerable significance for reconstructing character evolutionary history. There are two ways to order multistate transformation series: 1) by distributing character states with *ordered characters*; and 2) by distributing character states with *unordered characters*.

The concepts of *ordered character* and *unordered character* need to be clarified. An *ordered character* hypothesizes a specific pathway with regard to the evolutionary relationships observed among the character states. It is a restrictive statement that restricts other possible assumptions of character state order. An *unordered character*, optimized by the Fitch minimum mutation model (Fitch, 1971), also makes a peculiar announcement about evolutionary relationships between individual character states and their distances. However, unlike an ordered character, an unordered character presents unrooted transformation series, which accounts for the change from one state to any other state in one step (Fitch parsimony; Fitch, 1971; and Hartigan, 1973). Thus, any change, either from 0 to 1, or from 0 to 6, or from 5 to 7, is counted as one step. The polarity of unordered characters is allowed to reverse freely.

Generally, for ordered character states, morphological structures are likely to undergo changes (i.e. *ordered state hypothesis* or *ordered change*) in the course of evolution, so that extreme character states are linked by a series of intermediate states. Ordered changes are counted as the absolute value of the difference between their state numbers ("Wagner parsimony"; see Farris, 1969 and 1970; Swofford and Maddison, 1987).

Hauser and Presch (1991) suggest that hypotheses concerning character state order are more informative than those based on the studies of unordered character states. They, after examining 27 data sets, observed that ordering characters may increase (or restrict) the number of equally parsimonious trees as well as increase tree resolution.

However, the ordering of multistate characters to present transformation series can be problematic. If multistate characters are ordered, the distance between non-neighboring states always covers more than one step in a linear transformation series. Generally, this distance contains more than one step in the reticulate and branched forms (Wiley et al. 1991). That is, the ordering of characters is based on the presupposition that the distance of character state change is equal to 1 between adjacent states (i.e. 0<->1=1 step) or covers more than one step between non-adjacent states (i.e. 0<->2=2 steps). In consequence, the number of alternative assumptions about orders rejected increases with the comparatively larger number of states presented by a multistate character, and the number of steps covered in an ordered character state tree will be higher than that of steps displayed by an unordered character state tree.

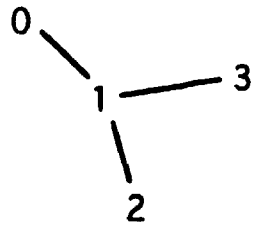
On the other hand, ordering multistate transformation series, as mentioned earlier, is of phylogenetic significance, since it helps reconstruct evolutionary relationships between individual character states. Unordered multistate characters, which do not specify such relationships, may result in producing more equally parsimonious trees because linkages between character states for different taxa are broken.

A Priori and *A Posteriori* Hypotheses

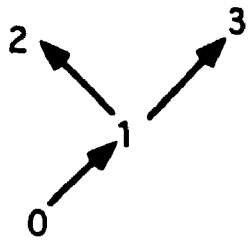
Ordering a character may be based on two types of hypotheses about character state transformation: a *priori* hypotheses and *a posteriori* hypotheses. The former are hypotheses advanced before examining the relationships between characters. They serve to produce a character state network (i.e. CSN). The latter are those developed after evaluating the congruence between characters. They function to present a character state tree (i.e. CST).

CSN (Character State Network) and CST (Character State Tree)

To distinguish CSN from CST, Wilkinson (1992) might be cited: "A character state network (CSN=data matrix) is an *a priori* hypothesis of the relationships between the states of a character without regard to polarity or direction." Clearly, what Wilkinson calls *character state network* is an unrooted or unordered character state diagram:



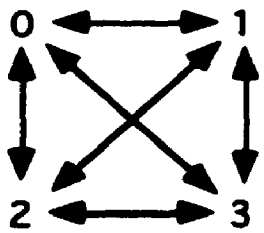
Unlike a CSN, a CST is often used to postulate character phylogeny by polarizing transformation series. Accordingly, it is normally rooted (for relevant discussion, see Camin and Sokal, 1965; Farris, 1970; Estabrook, 1984; Mickevich and Weller, 1990):



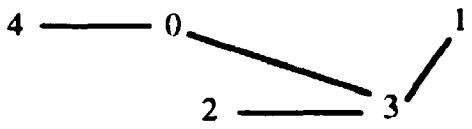
The above example shows how a CST differs from the linear ordering of character transformation. The transformation series represented by the example is both ordered and polarized so that not only the relationships but also the direction of evolution are specified.

A CST can be the result of an iterative procedure to determine the best corroborated transformation by means of reciprocal cladogram illumination (Mickevich and Weller, 1990). This procedure continues until all transformation series used in the construction of the tree are identical to the cladogram characters. In general, multiple paths existing between character states in a partially ordered CST are said to be ambiguous, while those in a fully ordered CST are considered unambiguous. Yet, discussing CST in terms of ambiguity recalls Swofford's (1990) claim that a CST imposes a "partial order" on the character states. In contrast, Hauser and Presch (1991) argue that CST's are fully ordered, and that the connections between character states in a tree might be neither completely unambiguous nor completely ambiguous.

When inferring a phylogeny for a certain group, we might wish to know how a particular trait of interest evolved along the lineages of this phylogeny. For example, we hypothesize pathways of change for the character states of an organism so that the ancestral lineage of the organism has state 0, with a later lineage evolving to state 1, and then to state 2, and so on. If character state changes could be presented in an unordered character state graph -- the equivalent of a CSN, it should be postulated that pathways allow every state to be connected directly to any other state. That is, the change between any two states involves only one step:

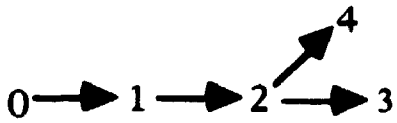


The graph shown above provides us with a binary relationship model, since only one line is traversed between any two character states. A typical CSN would display a random evolutionary model below: (For the convenience of exemplification, state 4, though not discussed, is added in the following graphs.)



Conversely, in a CST, possible pathways can be inferred to simulate the direction of character state evolution. Suppose that a direct change from state 0 (i.e. ancestral character state) to state 3 is available with some evidence from the real-world data. It might as well be inferred that the ancestral character state ignored intermediate states 1 and 2 on its pathway to state 3. This can be considered evolutionarily cost-effective (only 1 step was covered). See the diagram below, where a CST is depicted to represent our inference:

It should be added that our evidence might not be strong enough to fully verify our first inference. This means that other pathways are not impossible. Our second inference then can be expressed in a different CST, which points out the possibility that state 0 reaches state 3 via states 1 and 2:



Presumably, such CST's directly show the hypothesized history of character state change. If interpreted alternatively, as we have to admit, a CST displays only the model of the possible evolutionary pathways. Of the above two graphic methods, obviously

CST is more appropriate for our purposes in that it helps produce the possible-pathway model. Supposing that the history of character state change were already known, using CST as an assumption would be almost meaningless in reconstructing character evolution. Instead, a CST suggestive of possible pathways functions importantly "as an assumption to constrain (but not completely specify) our conclusions about character evolution" (Maddison and Maddison, 1992). Hence lies the reason for character state trees to be utilized as the major graphic expressions in this work.

Character Coding

Before a collection of data can be used in computer-based analysis, the data need to be coded in a form acceptable to visualize the proposed changes and to the computer program to be used. Character codes are the numerical names of particular character stages. A character can be coded in descriptive values (e.g. "triangular", "spherical", "hexagonal"; "agglutinated", "calcareous", "siliceous"), or in numeric values (0, 1, 2, 3, 4, 5).

Maddison and Maddison (1992) notice that a numeric character may be coded into discrete (continuous) values for convenience "with certain ranges of values grouped together as one state." On the other hand, they also observe some seemingly discrete characters, which may have ambiguously separated states. Anyhow, decisions made in coding the character should be made with flexibility because it will have an effect on all later stages of phylogenetic analysis.

Obviously, attempts to use certain assumptions (coding characters) about character evolution often require special coding methods in order to facilitate the processing of these assumptions.

In her discussion of transformation series analysis, Mickevich (1982) recognized two primary types of multistate characters, additive (ordered) and non-additive

(unordered). When represented as a variable, an additive character has a linear sequence of states and therefore conforms to the strict definition of an ordinal variable. A non-additive variable has states ordered in a branching pattern, not in a single linear sequence, and therefore is not an ordinal variable. For clarity, we refer to those characters (variable/internodes) as ordinal and branched respectively. We use additive and non-additive to describe coding methods.

It might be helpful to mention that 10 accompanying characteristics sorted out from the typical alternative features of the Foraminiferida and Euamoebae, and their 47 character states, as collected from literature, were compiled for coding (Table 2). (For detail, see Chapter IV.)

To reflect coding results, a data matrix is designed (Tables 3a-b). In the data matrix, transformation series are listed in columns and taxa displayed in rows, indicative of how plesiomorphies relate to their apomorphies. As mentioned earlier, such state codes as "1", "2", "3" and so on stand for derived homologous character states (apomorphies) and the state code "0" the plesiomorphy. A character ontogeny will occur with its state codes on the tree.

Numeric coding of cladistic data can be multistate (sequential numbering), additive binary, or non-additive binary (0, 1 designations only). The use of multistate coding reflects the advent of computer programs that can handle such data. In this study, which is a cladistic investigation into multistate transformation series, the multistate coding is utilized to break one character into a number of character states, each represented by its own column of information. For instance, membranaceous walls, organic walls, organic agglutinated walls, calcareous agglutinated walls, aragonitic walls and siliceous walls are all considered as different states of wall composition (i.e. chartacter 3); thus, they are coded in sequential numbers from 0 to 6. State 0 *membranaceous walls* is employed as the referential state, or simply plesiomorphic state, while the other states are given as apomorphic states.

Character / State	0	1	2	3	4	5	6	7
1. Shell	Absent	Present						
2. Pseudopodia	Lobose /Filose	Granuloreticulose						
3. Wall composition	Membranaceous /Proteinaceous	Organic	Organic Agglutinated	Calcareous Agglutinated	Calcitic	Aragonitic	Siliceous	Secreted Spicular in Organic Groundmass
4. Wall ultrastructure	Tectinous	Simple Agglutinated	Alveolar Canaliculate Agglutinated	Microgranular	Porcellaneous	Hyaline Monolamellar	Hyaline Bilamellar	
5. Test perforation	Absent	Present						
6. Test shape	Spherical	Radiate	Fusiform	Pyriform /Ovate /Globular	Elongate	Trochoid		
7. Number of chambers	Unilocular	Multilocular						
8. Chamber arrangement	Simple planispiral	Uniserial	Multiserial	Planispiral Involute /Evolute	Low or High Trochospiral	Milioline		
9. Chamber shape	Globular /Ovate	Fusiform	Palmate	Discoidal	Conical	Lenticular /Tubular		
10. Surface sculpture	Smooth /Pillared	Ribbed /Costate /Reticulate	Fissured /Pitted /Nodose	Peripherally Keeled	Planktic-Spinous	Punctate /Rugose /Hispid		

Table 2. Character and character states examined (after Loeblich and Tappan, 1964 & 1987).

Table 3a. Data matrix comprising coded character (1-5) states describing subordinal foraminiferal phylogeny.

	Taxon	1 Shell	2 Pseudopods	3 Wall composition	4 Wall ultrastructure	5 Test perforation
1	Euamoebae	0	0	0	0	0
2	Allogromiina	1	1	1	0	0
3	Astrorhizina	1	1	2	1	0
4	Haplophragmiina	1	1	2	2	0
5	Trochamminina	1	1	2	1	0
6	Textulariina	1	1	3	1	0
7	Fusulinina	1	1	4	3	0
8	Involutinina	1	1	5	5	1
9	Miliolina	1	1	4	4	0
10	Silicoloculinina	1	1	6	4	0
11	Lagenina	1	1	4	5	1
12	Rotaliina	1	1	4	6	1
13	Globigerinina	1	1	4	6	1
14	Robertinina	1	1	5	5	1
15	Spirillinina	1	1	4	5	1
16	Carterinina	1	1	7	1	0

Transformation Series

Table 3b. Data matrix comprising coded character (6-10) states describing subordinal foraminiferal phylogeny.

	Taxon	6 Test Shape	7 Number of chambers	8 Chamber arrangement	9 Chamber shape	10 Surface sculpture
1	Euamoebae	0	0	0	0	0
2	Allogromiina	0/3	0	0	0	0
3	Astrorhizina	0/1/3	0	0	0	0
4	Haplophragmiina	0/3/5	1	2/4	0	2
5	Trochamminina	3/5	1	2/4	0	2
6	Textulariina	3/4	1	1/2	0	0/2
7	Fusulinina	2	1	3	0/1	0/2
8	Involutinina	0/3	1	3	5	0
9	Miliolina	0/2/3/4	1	5	0/1/3/4/5	0/2
10	Silicoloculinina	0/3/4	1	5	4/5	0/2
11	Lagenina	3/4	0/1	0/1/3	0/2/5	0/1/3
12	Rotaliina	0/3/4/5	1	2/3/4	0/3/4/5	0/3/5
13	Globigerinina	0/3/4/5	1	2/3/4	0	4/5
14	Robertinina	0/3	1	3/4	0	0/3
15	Spirillinina	0/5	1	4	4/5	0/3
16	Carterinina	0/5	1	3/4	0/4	0/2
	Transformation Series					

The multistate numeric coding used in this research can be identified as of two types: ordered numeric coding and unordered numeric coding. The former type specifies the order of derivation reflected in the relationships between different character states, whereas the latter type simply signifies the plesiomorphic attribute of state 0 and the apomorphic quality of the other states. The former type is clearly exemplified in the coding of characters 3 and 4, and the latter type is mostly applied in coding characters 6, 8, 9 and 10.

Additive binary coding was recommended by Farris (1972 and 1973), and Kluge (1985) because it preserves the form and direction of character state changes. To suit our analytic purposes, we have also exploited this method to code certain characters with merely binary states: e.g. characters 2 and 7. The order of character state changes is indicated in the coding of this sort. For instance, ***multilocular chambers*** are coded as state 1 to be differentiated from the plesiomorphic state ***unilocular chambers*** (i.e. state 0). Here the relation of derivation is clearly suggested.

Non-additive binary coding discards form and direction of character state changes. When characters are coded in a non-additive binary fashion, each state is treated as a nominal attribute, present or absent. Consequently, treating each state as a nominal variable denies order and relationship among the states. For this reason nominal variables seem invalid for cladistic analysis. Nevertheless, viewed in another perspective, this coding method may be used to avoid such embarrassing problems as ambiguity arising from parallel character state relations that are not clear at all. This is illustrated by the coding treatment implemented for characters 1 and 5, each of which presents two states that can only be nominally identified (i.e. present or absent).

It might be informative to note that apart from the methods mentioned above, other coding methods are possible. O'Grady and Deets (1987), and O'Grady et al. (1989) introduce certain methods in their monograph on coding multistate characters: additive binary coding, redundant linear coding, nonredundant linear coding and internal rooting.

Yet, the selection of coding methods has to be determined by the needs emerging from our research.

Hennigian Methodology

Hennig's (1966) auxiliary principle is: Never assume convergence or parallel evolution, but always assume homology in the absence of contrary evidence. In reality, convergences are facts of nature and are rather common in some groups. His grouping rule is: Synapomorphies are evidence for common ancestral relationships, whereas symplesiomorphies, convergences, and parallelisms are useless for evidencing common ancestry. His inclusion/exclusion rule is: The information from two transformation series can be combined into a single hypothesis of relationship if that information allows for the complete inclusion or the complete exclusion of groups that were formed by the separate transformation series. Overlap of groupings leads to the generation of two or more hypotheses of relationship because the information cannot be directly combined into a single hypothesis.

Cladograms

The basis of phylogenetic systematics is the use of derived (apomorphic) characters to reconstruct the common ancestry for the classification of taxa. Phylogeneticists therefore describe the procedure of reconstructing phylogeny in terms of building phylogenetic trees based on one or more characters (note: they differ from CST's that are basically the phylogeny of an individual character).

A cladogram is a phylogenetic tree that presents a relative time axis and the particular implications of an ancestry. In this sense, it serves as a hypothesis of character state changes for a given group of taxa. When building a cladogram, the researcher often

attempts to discover the common ancestry among the taxa under study by inferring a phylogeny as a presupposition of evolutionary relationships. In most cases, a cladogram is intended for the reconstruction of a hierarchical scheme of monophyletic group relationships. Occasionally, "it is purely a depiction of the derived characters shared by taxa with no necessary connotation of common ancestry or relative time axis." (Wiley et al. 1991)

Monophyletic Groups

A *monophyletic group* (i.e. monophyly) is a group of taxa containing an ancestral taxon (known or hypothesized) and all of its descendant taxa. A major problem is to determine which groups are monophyletic, and which two groups are more closely related to each other than to any other taxon in any given array of taxa. Therefore, the term *monophyletic groups* needs to be further defined. Clarifying the concept of monophyly may aid in confining the usage of the term *monophyletic group*. Members of monophyletic groups acting as an independent evolutionary unit share a common ancestry not found within any other taxa placed outside the group. To put it more simply, a group of organisms is monophyletic if its single most recent common ancestor is not shared by organisms not included in the group. The designation *monophyletic group*, as a consequence, should be restricted to the groups whose most recent common ancestors are unique to them. A monophyletic group is also called a *clade*, a natural taxon.

Ingroup, Outgroup and Sister Groups

In Wiley and other's (1991) terms, an *ingroup* is the group of interest. To be further clarified, it is the set of taxa actually under study. In other words, the *ingroup* is a set of groups (i.e. taxa) often assumed to be monophyletic and investigated as the focus of

interest (Maddison and Maddison, 1992). (See also Duncan and Stuessy, 1984 for the defining of the ingroup criterion.)

An *outgroup* is any group of taxa involved in an analysis but not included in the taxa studied as the focus of interest. Outgroups are normally used for comparative purposes to polarize homologous character states. They are brought into studies to provide a larger phylogenetic context for determining the root of the ingroup or ancestral states (Farris, 1972, 1977 and 1982; Watrous and Wheeler, 1981; Maddison et al. 1984, Maddison, 1991).

Maddison and Maddison (1992) suggest using outgroups as a clade attached to the stem coming down from the ingroup so that "the character states ancestral for the ingroup are estimated on the basis of the states and interrelationships of the outgroup." As outgroup relationships are uncertain, uncertainty about ancestral states occurs. An outgroup is normally introduced into a comparative analysis as value 0 to represent the plesiomorphic character transformation series. (For discussion of the deficiencies of the outgroup comparison method of character analysis, see Watrous and Wheeler, 1981, Wheeler, 1986)

A *sister group* is a taxon or a set of taxa genealogically most close to the ingroup. The ancestor of the ingroup cannot be its sister because the ancestor is a member of the group. (For more discussion, see Duncan and Stuessy, 1984.)

Tree Length and Associated Terms

Changes of character states marked along the branches of a cladogram represent attempts to depict evolution and to track the development of characters for different lineages.

The sum of the number of character state changes on each branch or internode of a tree for one character is referred to as the number of steps for that character, and the

summed cost of all character state changes on a tree is the tree length. Simply, each character state change is equal to 1 step, and on any tree the tree length is representative of the total amount of character state changes (steps) for all characters. Generally, character states should be counted if they have a substantial contribution to make in the reconstruction of the phylogeny. In the formula, the total tree length is calculated as the sum of the number of steps for the individual characters multiplied by their respective weights (Maddison and Maddison, 1992):

$$\text{Tree-length} = \sum_{i=1}^{n} w_i s_i$$

where w_i is the weight applied to character i, and s_i is the number of steps for the individual characters.

Parsimony

Trees are built using the "principle of parsimony." Parsimony methods search for minimum-length trees -- i.e. the fewer the changes to be accounted for, the better the result. It does guide us to choose some hypotheses over others. The constraints determined by the investigation determine the trees developed using parsimony methods.

Unordered (Fitch) parsimony is characterized by the treatment of multistate characters as unordered. Ordered (Wagner) parsimony treats multistate characters as ordered. Mixed (General) parsimony is a mixed ordered and unordered parsimony which reflects the investigator's assumptions of the evolution of certain characters. Dollo's parsimony permits each derived or apomorphic character state to originate only once (Wiley, 1981 and Wiley et al. 1991).

Parsimony is used to search for the optimal tree or "best set of trees" that explain the data in the simplest manner, and the shortest tree presents the optimal hypothesis of unknown common ancestral relationships for the taxa analyzed. In this study, methods of

unordered (Fitch) and mixed ordered and unordered (General) parsimony are chosen to build phylogenetic trees.

PAUP and MacClade

PAUP (Phylogenetic Analysis Using Parsimony, Version 3.1) is a data-analyzing program for building phylogenetic trees and inferring phylogenies from discrete character data in the principle of maximum parsimony (Swofford and Begle, 1993). MacClade (Version 3.0) is a character-state-sorting program to explore drawing and interacting with trees (Maddison and Maddison, 1992). It serves to search character state changes in the tree as the output from PAUP.

Computer Algorithms

Several different algorithms have been developed to find the shortest tree under the assumption of parsimony. The Wagner algorithm based on Wagner Groundplan Divergence Analysis was developed independently of the Hennig argumentation algorithm (Wiley et al. 1981) The operational analysis can be briefly exemplified with the following example selected from part of the data matrix of this study (see Table 3):

Sample date matrix for Wagner definitions

Taxon	Characters				
	1	2	3	4	5
E	0	0	0	0	0
A	1	1	2	1	0
H	1	1	2	2	0

1) A particular character (Y) of a particular taxon (H) is defined as Y(H, *i*), where *i* is *i*th character in a vector of *i* characters.

2) The vector of characters for a particular taxon is defined as $\sum Y(H, i)$. For example, the character vector for H is:

$$\sum Y(H, i) = 1\ 1\ 2\ 2\ 0;$$

3) The difference (D) between two taxa is the sum of the absolute differences between their characters:

$$D(H, A) = \sum |Y(H, i) - Y(A, i)|.$$

We calculate this in the following manner:

$$\begin{aligned} D(H, A) &= \sum |Y(H, i) - Y(A, i)| \\ &= |1 - 1| + |1 - 1| + |2 - 2| + |2 - 1| + |0 - 0| \\ &= 1; \end{aligned}$$

4. The interval (INT) of a taxon is the length of the line between that taxon and its ancestor. For example, the interval of H is

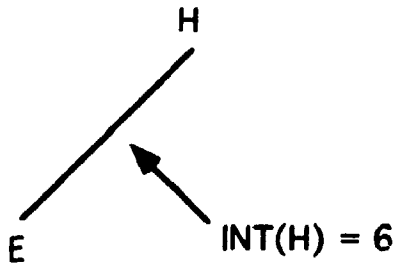
$$INT\ (H) = D[H, ANC(H)],$$

where INT (H) is the interval of taxon H, ANC (H) is the hypothetical ancestor of H, and D[H, ANC(H)] is the path length distance of H to its ancestor (E).

Calculating interval H:

$$\begin{aligned} INT(H) &= D[H, E] \\ &= \sum |Y(H, i) - Y(E, i)| \\ &= |1 - 0| + |1 - 0| + |2 - 0| + |2 - 0| + |0 - 0| \\ &= 6 \end{aligned}$$

(Note: 2 steps longer than if using unordered characters, i.e. 2 - 0 = 1). The interval is therefore shown graphically below.



Graphic representation of INT(H) of the Wagner algorithm

Now, we implement the Wagner algorithm in a concise step (from Kluge and Farris, 1969): 1) specify an ancestor or outgroup; 2) calculate D for each taxon within the ingroup to the ancestor/outgroup; 3) search for the next taxon that has the next smallest D to the ANC (the taxon) or sister group; and 4) create the interval that has the smallest D with the taxon selected in step 3. The following formula shows the computation of D (taxon, interval):

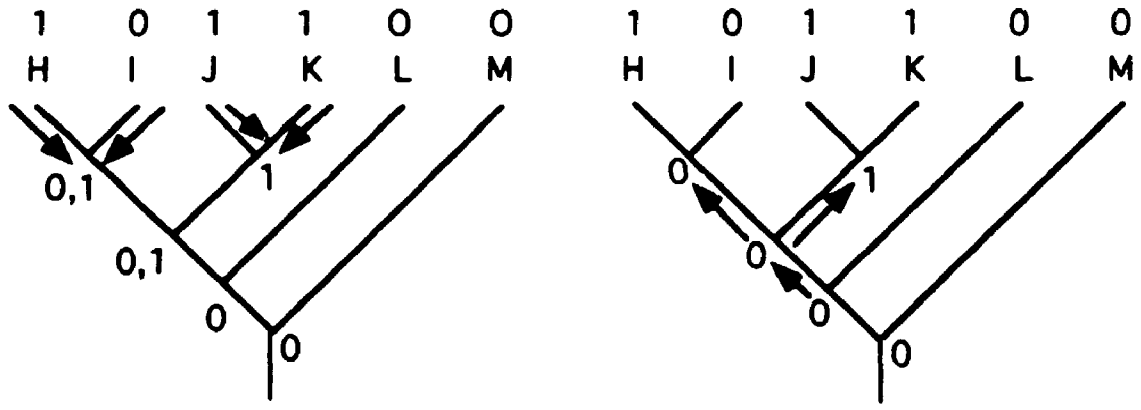
$$D[H, INT(A)] = \frac{D(H, A) + D[H, ANC(A)] - D[A, ANC(A)]}{2}$$

5) Select the taxon by constructing a hypothetical ancestor for the two taxa. The character vector of the ancestor, and thus its position along the interval, is computed by taking the median value of the existing taxon, its ancestor, and the added taxon. 6) Repeat for each remaining taxon along step 3.

ACCTRAN and DELTRAN

Although a tree can be built with the Wagner algorithm, it does not guarantee that the individual characters assigned to the ancestors (hypothesis) are optimal for a given tree topology. Trees produced during tree construction usually bring about alternate interpretations for the distributions of homoplasies. Farris (1970) then provided an algorithm for optimizing these distributions because he suggested that characters showing no homoplasy are optimized. ACCTRAN and DELTRAN (Swofford and Maddison, 1987), as two basic types, are therefore designed to operate the most parsimonious character for each branch of the tree under the general optimality criterion.

ACCTRAN means that the procedure accelerates the evolutionary transformation of a character, pushing it down the tree as far as possible (Farris, 1970). "Two pass" algorithm (Maddison et al. 1984, Maddison, 1991) is one of these procedures. "Downward pass" assigns characters to nodes in a pass from the terminal branches to the root, then "upward pass" reviews these assignments from reversals. This process can be broken down into four phases (e.g. binary transformation series) according to Farris (1970), Swofford and Madison (1987), and shown in a simple diagram below:



(a) The downward pass (b) The upward pass

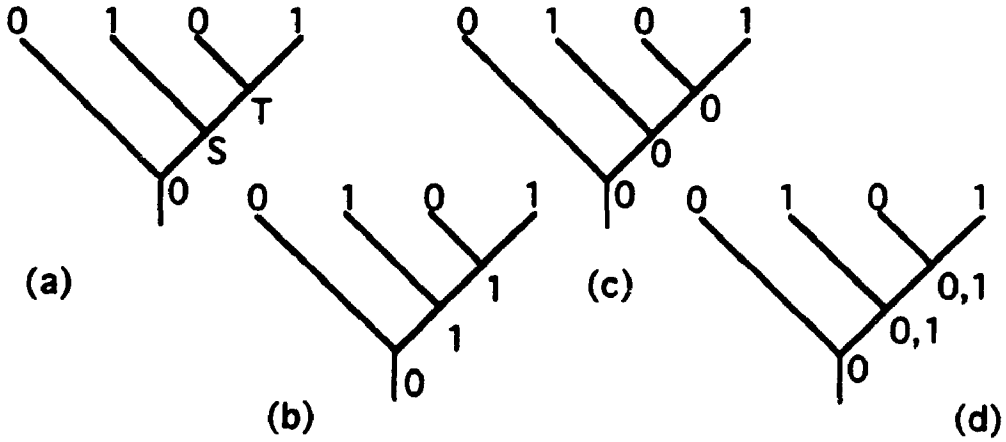
1) the tree is set up with labelling terminal taxa and their ancestor;

2) the downward pass (a); assign character states toward the ancestral root node from the beginning of the terminal taxa; label the identical node if two taxa have the same character states, or label their common majority nodes if two taxa have different character states;

3) label ancestral root nodes (character states);

4) the upward pass (b). Reevaluate these assignments in a pass from the root to the terminals. Label the lower number if two taxa have different character states, or label the same node if two taxa have more than one equal character states. ACCTRAN is therefore a special way by which characters or character states are optimized on a given tree topology.

According to the other example below, when we optimize the ancestral nodes S and T on a tree (a), two equally parsimonious trees (b: ACCTRAN tree and c: DELTRAN tree) are possible. ACCTRAN is also a means of looking at character evolution.



If two trees are combined into one tree (d), ancestor S or T has a state set 0, 1 rather than just 1 (b) or 0 (c). This set (0, 1) is termed the most parsimonious resolution (MPR). The analytical procedure is a -> d via b and c depending on our hypothesis.

DELTRAN delays the transformation of a character on a tree. If there is no ambiguity, both ACCTRAN and DELTRAN will yield the same results (Wiley, 1991).

CI (Consistency Indices) and *RI* (Retention Indices)

Synapomorphies provide the best evidence for estimating common ancestral relationships on the tree. Evaluating the performance of each character originally coded as a synapomorphy is carried out by calculating a consistency index (*CI*). The *CI* of a character is the reciprocal of the number of times that a character appears on the tree. According to Maddison and Maddison (1992), the *CI* for all characters on a tree is the minimum possible tree length divided by the observed tree length. To be exact, it is the weighted sum of the minimum conceivable number of evolutionary steps for each character of the n characters divided by the weighted sum of the observed number of steps for each character:

$$\text{Tree CI} = \frac{\sum_{i=1}^{n} w_i m_i}{\sum_{i=1}^{n} w_i s_i}$$

where w_i is the weight applied to character i.

This formula is the same as Kluge and Farris' *CI* (1969): c (*CI*) = m/s (where s denotes the actual number of steps on a given topology and m is the minimum number of steps possible). Data sets with no homoplasy for a given tree topology are expected to have a *CI* of 1.0. That is, if groups are consistent (congruent) with those proposed by other homologies, then transformation series are supported. If the character fits the tree poorly or shows homoplasy, the *CI* decreases (<1.00).

The amount of homoplasy can also be expressed as a fraction of possible homoplasy. This fraction can be done by the retention index (*RI* or r) (Farris, 1989). Retention index measures the fitness of the characters on the tree and defines the fraction of apparent synapomorphy to actual synapomorphy:

$$r=1-d=\frac{[(g-m)-(s-m)]}{(g-m)}=\frac{(g-s)}{(g-m)}$$

where d [d=h/(g-m)] is the distortion coefficient representing the fraction of possible homoplasy, and h (h=s-m) shows extra steps as homoplasy. The g denotes the greatest amount of change that the character may require on any tree. The g-m is the greatest possible value associated with the amount of homoplasy. The maximum value of g is equal to the maximum number of steps possible (=# of taxa) for a character that shows no congruence (autapomorphic) on a given tree topology.

Consensus Techniques

The distribution of the shortest length and higher *CI* or *RI* value for a given tree sketches the "best" phylogenetic signal of character evolution via computer algorithm. As mentioned earlier, computer simulations dealing with the "best tree" from phylogenetic information can create multiple equally parsimonious trees for a set of topologically different trees under various conditions. With the realization that multiple equally parsimonious cladograms might exist for a given data set (Mickevich, 1978), classification in such instances becomes problematic.

Multiple equally parsimonious solutions are not our ideal result, because: 1) trees showing the same common ancestral relationships have different character interpretation; and 2) different tree topologies represent different views of the common ancestry. For

systematics or biogeography, equally parsimonious trees that differ in character interpretations but have identical topologies do not affect any subsequent analysis. Different tree topologies might affect the interpretation of evolutionary mechanisms because they lead to different views of common ancestral relationships.

Consensus trees (Adams, 1972; Nelson, 1978 and 1979, Nelson and Platnick, 1981), which are one possible solution for grouping different trees into a single tree, were developed for producing a "compromise classification" (Adams, 1972) between cladograms produced from different data sets or form multiple parsimonious trees for one data set. A consensus tree is not a phylogeny (Miyamoto, 1985), but rather a statement integrating topologies common in all resolved trees. Consensus trees are thus a tool for the measurement of unambiguous resolution in each data set. This tree, representing the information on grouping shared by all the competing cladograms, might be viewed as a "conservative" classification (Carpenter, 1988).

Strict consensus trees also provide possible resolution for all monophyletic groups common to competing trees (Sokal and Rohlf, 1981).

The 50% majority consensus trees (Margush and McMorris, 1981; Swofford, 1990, Swofford and Olsen, 1990, Swofford and Begle, 1993) are based on the hypothesis that a few topologically distinct trees may be competing with the majority of tree topologies (resulting in the collapse of nodes in a Strict consensus). These trees can be used to explore discrepancies among multiple choice, and to check conflicts within the original trees.

Such trees may be logically consistent with each other. The 50% majority consensus trees are therefore suitable to combine more than half of topologically different but equally parsimonious trees into a single tree. A series of internodes, usually shown on the branch of a given tree, represent the percentage of the trees with these branches that show support for that node (>50%).

Optimal Tree

How do we select the optimal tree? To answer this question, we must review the phylogenetic techniques. A computer algorithm identifies the shortest length of trees for a given data set. The final topology that is driven by the search for the shortest path determines the tree length. As mentioned earlier, tree length is calculated by summing the number of character changes along each branch of the tree (Wiley et al. 1991). The shortest length based on the shortest number of steps for all of the data denotes the "best pathway" of evolution, because evolution is believed to choose the shortest road. Therefore, the optimal tree is the tree of shortest length chosen from the multiple equally parsimonious trees; it is the closest set to the 50% Majority-rule consensus result and selected through a series of comparisons.

Concluding Remarks

In this chapter, we have defined some theoretical elements to be applied in judging character states, categorizing groups, plotting character state trees and tracing phylogenetic relationships. In working out some definitions and related theoretical assumptions, I have documented some views from established researchers in relevant areas. It has been recognized that theories are indispensable for the classification of foraminiferal suborders. Furthermore, I am aware that the construction of classification is closely associated with the reconstruction of evolutionary relationships. The classification with splits between them will end up with misinterpretation and fallacy.

With these words, we are now in a position to examine the data (coding) matrix built on our material and theoretical framework, which will bring us to Chapter IV.

CHAPTER IV CHARACTER ANALYSIS

The Aims of This Chapter

In Chapter III, a theoretical framework was laid down for the main work to be confronted in this and the following chapters. Two subsequent recognitions are that theories are important for the classification of foraminiferal suborders, and that the classification of this sort should not be separated from the reconstruction of evolutionary relationships.

The primary goal of this chapter is to introduce the characters used in coding the matrix. The characters and their states for the data matrix, one suborder of Euamoebae (as outgroup) and fifteen recognized suborders of the Foraminiferida are presented. The subordinal classification will be reported by describing and analyzing all alternative conditions (character states). In the recognition achieved in the previous chapter, it might be helpful to point out that our discussion and categorization would be conducted according to an extensive understanding of character evolution.

Material

In order to provide morphologic evidence for the subordinal groups and for cladistic analyses, 10 accompanying characteristics sorted out from the typical alternative features of the Foraminiferida and Euamoebae, and their 47 character states, as collected from literature, were compiled (see Table 2).

Character states are a set of alternative conditions, including ancestral conditions (plesiomorphies) and descendant conditions (apomorphies). These alternatives might be homologous or convergent conditions. Characters were sorted into two groups: Group 1 includes four sets of internal adult characters (1-4); Group 2 comprises six sets of conservative external infantile or adult characters (5-10). Each set of characters consists of one ancestral state (plesiomorphy) and a series of descendant states (apomorphies). These internal and external morphological features and their alternative conditions (states) are a reflection of the unicellular nature of the foraminifera and include features having evolved for the facilitation of cytoplasmic movement, intercameral communication, types of test construction and mode of feeding and habitat. All these major external and internal characters will be examined and morphologically categorized according to an extensive understanding of character state evolution.

These alternative conditions with each suborder have been coded in a data matrix (see Table 3a-b) as discussed in Chapter III.

Foraminiferal suborders (Loeblich and Tappan, 1964, 1987 and 1989, Tappan and Loeblich, 1988) under consideration include the following (in alphabetical order): Allogromiina, Astrorhizina, Carterinina, Fusulinina, Globigerinina, Haplophragmiina, Involutinina, Lagenina, Miliolina, Robertinina, Rotaliina, Silicoloculinina, Spirillinina, Textulariina and Trochamminina. Euamoebae are used as an outgroup for the analysis of phylogenetic polarity.

Character Analysis

The initial decisions on the plesiomorphic or apomorphic attributes of character states were made prior to the analysis. To this end, it was decided to build up a framework to reveal how these different conditions might have related to one another. I

shall now define all alternative conditions (states) of the 10 characters used in the analysis (e.g. Tables 2 and 3) by distinguishing their plesiomorphic and apomorphic attributes.

1. Shell (or Test)

There are two states of shell, absent (state 0) and present (state 1). The primary components of Protozoa protoplasm are water (H_2O), large molecules containing carbon atoms of the carbohydrates, lipids (fats), and proteins. The physical arrangement contributes potentialities for complex chemical activity by increasing the number of interactions between many kinds of molecules. Euamoebae usually include star-like protists with stiffened temporary extensions of the cell body without a firm shell. The shell-less (state 0) Euamoebae were probably similar in form to the common ancestor of the foraminifera.

Within the Protozoa, the earliest fossil record consists of the hard remains of dead foraminifers. Foraminifera, with a shell (state 1) of organic matter and adhering particles around the body, seem to have been derived from Euamoebae. Therefore, the presence of a distinct hard shell is an apomorphy both in the extant and extinct foraminifera. The test might have originated with Allogromiina as characterized by an organic shell (Loeblich and Tappan, 1964 and 1987) and was then passed to descendant taxa. The formation of agglutinated, calcareous and siliceous shells in most suborders of the Foraminiferida is most likely apomorphic for the order.

2. Pseudopodia

Rigid pseudopodia function in the capture and digestion of food, and also help with test construction (Loeblich and Tappan, 1964). The type of pseudopodia characterizing the suborders being analyzed can be divided into three distinct groups

(Loeblich and Tappan, 1987), the Lobosa and Filosa (state 0) and Granuloreticulosa (state 1). Euamoebae (i.e., *Acanthamoeba, Amoeba, Astramoeba, Cashia, Cochliopodium, Hartmanella, Mayorella, Saccamoeba, Thecamoeba, and Vannella*), which are rhizopod amoebae with one or more broad pseudopodia, and may have short, stubby, filose subpseudopodia or lobose pseudopodia (state 0) emerging from a larger pseudopodial region (Patterson and Hedley, 1992).

Granuloreticulose pseudopods (state 1) are characteristic of all foraminiferal suborders (Loeblich and Tappan, 1964). These relatively rigid pseudopodia help to anchor the specimens in soft sediment, allowing them to stand erect. "In highly spinose planktonic species, these pseudopodia extend along the radiating spines and the protoplasmic granules appear to stream up and down their surface" (Loeblich and Tappan, 1964). According to Loeblich and Tappan (1964), granuloreticulose pseudopods originated from filose pseudopodia or lobose pseudopodia with a gradual (progressive) change through geological time or sudden (eruptive) change in a short reproductive cycle. Thus, lobose and filose are regarded as the plesiomorphic character state and granuloreticulose pseudopods as the apomorphic character state.

3. Wall Composition

Wall composition has been used as a basis of foraminiferal classification since the 18th century, and remains an important criterion (Loeblich and Tappan, 1964, 1987 and 1989, Tappan and Loeblich, 1988) for the interpretation of foraminiferal phylogeny. Based on the previous model proposed by Tappan and Loeblich (1988), wall compositions within the foraminifera range from primitive membranous walls to agglutinated fragments held in various matrixes, to calcareous and siliceous walls. Thin single-chambered species that are easily deformable as membranous/proteinaceous (state 0) are regarded as plesiomorphic.

The organic (state 1) material (chitinous, chitinoid, pseudochitinous, keratinous and proteinaceous or tectinous) in the tests of some suborders such as Allogromiina is a primitive apomorphic feature, because no matter how complex the wall composition may be in the agglutinated or calcareous shell, the internal organic cyst remains unchanged. The secreted spicular in organic-groundmass (state 7) may have originally reacted with calcareous matter. As it is unrelated to true organic material, it might be apomorphic.

In organic agglutinated (state 2) and calcareous agglutinated (state 3) walled taxa, the degree of selectivity of the foreign matter utilized for wall construction varies. The type of foreign particles utilized in test construction depends on the binding ability of the organic cement and to some extent on the local environment. For example, agglutinated foraminifera in siliciclastic facies may utilize siliciclastic grains including quartz grains, various heavy minerals and clay minerals to build up their tests, and in carbonate facies these same species cement the calcareous materials consisting of carbonate fragments or organic debris and tests of small organisms such as radiolarians, coccoliths or fragments of molluscan shells to form their shells.

Many species with these types of test are known in fossil and extant faunas, but owing to their derived or apomorphic features they are scarce in the phylogenetic record. The gross mineralogical composition of secreted calcitic chamber walls (Todd, 1950) -- calcitic walls (state 4), offers little scope for biometrical apomorphic analysis, as significant variation occurs only at subordinal levels.

According to Wood et al. (1946), hyaline calcareous perforate walls (state 4) are often composed of prisms of calcite crystals (hexagonal crystal forms of $CaCO_3$). These crystals have their principle axis perpendicular to the surface of the shell or with their c-axes normal to the spherical surface as indicated by the characteristic black cross under polarized light. These calcareous crystals were utilized to build walls overlying the organic sheath, and are considered apomorphic.

Quantitative analyses of aragonitic (state 5) (orthorhombic form of $CaCO_3$) benthic foraminiferal shells reveal marked interspecific variation that is attributed to changes in calcareous tests. This variation is not specification but allotropy substance of calcium carbonate. The variety of derived calcareous foraminifera also rely upon changes in the ratio of Mg/Ca in saturation and precipitation of sea water with time. These biochemical features may provide discriminatory synapomorphic information about calcareous groups not observable in phenetic or evolutionary taxonomic analyses. Siliceous walled (state 6) foraminifers are considered to be more advanced than foraminifera with walls of calcareous composition. Forms with siliceous walls are more likely to come from deeper marine environments under the carbonate compensation depth (CCD). Therefore, the siliceous walls are suggested to be autapomorphic, and derived from calcareous matter.

4. Wall Ultrastructure

Wall ultrastructures were classified into seven states (Loeblich and Tappan, 1964, 1974 and 1987): tectinous (state 0), simple agglutinated (state 1), alveolar canaliculate agglutinated (state 2), microgranular (state 3), porcellaneous (state 4), hyaline monolamellar (state 5) and hyaline bilamellar (state 6). The simple tectinous structure is a plesiomorphic characteristic of amoebae from which the other complex structures have subsequently developed.

Simple agglutinated tests (state 1) are partially formed organically, but also contain a varying proportion of extraneous matter. For example, the alveolar canaliculate agglutinated ultrastructure (state 2) is considered as a complex derivation of simple non-canaliculate agglutinated types and is also considered as apomorphic. Some of these forms are known to have a simple layering of smoothly finished inner wall and coarser-grained covering with alveolar canaliculate openings (Loeblich and Tappan, 1974).

These openings may have evolved from irregular tubules as tiny perforations or from branching or anastomosing alveolae within the walls of simple agglutinated types.

Microgranular tests (state 3) consist of very tiny calcite crystals and are not comparable with grain size of the surrounding matrix; therefore, it is apomorphic. The granularity seems to be a characteristic of the shell itself deriving from its tectinous origin rather than from agglutinated particles on the sea floor.

Most porcellaneous tests (state 4) (high-magnesium-calcite) contain 6.0-16.0 per cent $MgCO_3$ (according to the data record of Loeblich and Tappan, 1974) and are characterized by an opaque three-layer wall (smooth or with pits in the inner wall and outer wall, random crystal middle layer). This structure appears to be homogeneous to the microgranular test made up of a three-layer wall (lower keriotheca, upper keriotheca and tectum).

The similarity between alveolar-microgranular and alveolar-porcellaneous structures implies iterative (sequential character state change with time) evolutionary divergence. The non-allotropic porcellaneous shells characteristic of both Miliolina and Silicoloculinina are treated as homologous. The tests of the agglutinated, microgranular and porcellaneous type are nonlamellar, with each chamber being added independently.

The hyaline calcareous forms have lamellar walls, with each new chamber added to overlap earlier formed chambers. This wall ultrastructure may be homologous to microgranular tests because the new chamber commonly attaches to the previously formed test so that little overlap or layering occurs, while porcellaneous calcareous walls lack this distinct feature. Hence, the hyaline monolamellar wall ultrastructure (state 5) is apomorphic.

The hyaline bilamellar shell (state 6), and so-called "three-layered septa" (i.e. rotaliid septa and bilamellar septa of the Globigerinina), may have evolved from the double-layered septa of the monolamellar shell (i.e. Lagenina) and are autapomorphic.

5. Test Perforation

Test perforation can be identified in two states, absent (state 0) and present (state 1). Paleozoic groups, including organic, simple agglutinated and primitive microgranular tests, are characterized by the absence of perforation (Loeblich and Tappan, 1964). The agglutinated foraminifera are known to have a simple layering characterized by a smoothly finished inner wall, coarser-grained central portion and finer-grained non-perforate surface covering.

Most microgranular tests consist of very tiny calcite crystals which are subangular and tightly packed in the absence of a perforated wall. Reytlinger (1966) divided Paleozoic smaller foraminifers into six groups, one of which had dark micrograined walls with very fine calcite grains and fin perforations, implying that the earliest perforations occurred with the microgranular types.

The porcellaneous wall was described as "an opaque calcareous substance having a porcellaneous aspect, and the absence or presence of perforations in the wall for extrusion of pseudopodia" (Loeblich and Tappan, 1964). Distinct pores have characterized hyaline foraminiferal tests since the Early Mesozoic. All pores on the ventral surface of tests are clearly visible under high magnification and are probably glandular in nature.

Wood et al. (1946) systematically examined hundreds of species from many families under polarized light and found that most hyaline tests have perforate radial microstructures and in a few families perforate granular microstructures prevailed. These pores may function by helping the test secrete wastes or may aid in reproduction during nuclei expansion (Loeblich and Tappan, 1964). It is thought that certain types of organic sheaths, consisting of pseudochitinous, keratinous and proteinaceous tests without perforation and giving the reaction of a carbohydrate, are the most plesiomorphic character state. Hence, such basal organic layer are known to be present in primitive perforate tests that became calcified perforata after foreign matter was added.

Calcified imperforate microgranular tests probably gave rise to imperforate porcellaneous tests. In turn, imperforate porcellaneous tests gave rise to perforate porcellaneous types, and calcified perforate microgranular tests gave rise to hyaline perforate tests. (For detailed analysis, refer to Loeblich and Tappan, 1964 and 1987.) Therefore, perforate wall ultrastructure is presumed to be homologous to perforate microgranular form. In conclusion, the absence of scattered minute openings is considered to be a plesiomorphic trait, since pores are characteristic of many varied groups. The presence of pores is an apomorphic trait.

6. Test Shape (Including Test Cross-section)

Unlike other characters, test shape and cross-section are clearly derived from one to another. Undoubtedly, a spherical test shape (state 0) and circular cross-section should be plesiomorphic because within almost all suborders of the foraminifera, many species are characterized by such a state as juveniles. Test form is mechanically accounted for on the basis of surface tension of the protoplasm, environmental changes, apertural position and volume and shape of previous chambers. Radiating (state 1) and fusiform (state 2) morphologies may result from combinations of various spherical test types. Pyriform, ovate and globular (state 3) or elongate (state 4) and trochoid (state 5) shapes may be homologous to biformed, or triformed tests. All shapes are homologous.

7. Number of Chambers

Unilocular (state 0) foraminifera are regarded as plesiomorphic and an increased number of chambers-multilocular (state 1) are apomorphic. However, some genera and species of the unilocular Lagerida are thought to be derived from multilocular ancestors. Based on taxonomic revisions by Patterson and Richardson (1987 and 1988) more new

genera of the unilocular Lagenina have been recognized. They found that hyaline calcareous unilocular foraminifera have become much more diverse over their evolutionary history.

8. Chamber Arrangements

Chamber arrangements are extremely varied in multilocular tests. According to the form of the chamber itself simple planispiral chamber arrangements (state 0) are regarded as plesiomorphic. The development of multiserial arrangements (state 2) may connect with the division of uniserial tests (state 1). The planispiral involute or evolute tests (state 3) and milioline tests (state 5) are probably derived from simple planispiral tests. High trochospiral tests (state 4) evolved from the low trochospiral ones (state 4). These chamber arrangements may be apomorphic. This complexity of chamber arrangements results in radiate adaptations and the evolutionary divergence of foraminifera.

9. Chamber Shape

The array of body shapes is deemed here to have repeatedly arisen from an ovate and globular shape (state 0). The ovate or globular shape is considered to be plesiomorphic because in infancy most shells have this form. Other shapes, including fusiform (state 1), palmate (state 2), discoidal (state 3), conical (state 4) and lenticular or tubular (state 5) shapes, together with some irregular shapes, are considered to be apomorphic. Although these morphologic features may represent dimorphism between sexual and asexual generations in the life cycle, they do not affect the definition of apomorphic character states. The major types of globular-shaped benthic and planktic foraminifera, identified in trochospirally-coiled taxa, are apomorphic.

These structures, found in various lineages of Cretaceous or Cenozoic planktic foraminifera, are fundamentally more advanced than other chamber-shape morphologies characteristic of benthic forms. Apomorphic chamber states contribute to the analysis by positing relationships between classified benthic and planktic foraminiferal groups.

10. Surface Sculpture

The ornamentation of non-perforate foraminifera is generally smooth or characterized by pillars on the shell surface. The simple smooth or pillared test (state 0) is therefore considered to be plesiomorphic. Various sculpted modifications found in hyaline foraminifera such as ribbed/costate(ridges)/reticulate (state 1), or fissured/pitted /nodose (state 2), or planktic-spinous (state 4), and punctate/rugose/hispid (state 5) surfaces, are suggested to be ascribable to one another and are possibly apomorphic. Norris (1991) found that planktic forams are characterized by five types of peripherally keeled structure. He suggests that similar genetic rules for keel construction may have been inherited repeatedly from unkeeled common ancestors since the same type of keel structure evolved independently in closely related lineages. Thus, a peripherally keeled (state 3) surface sculpture is apomorphic.

Concluding Remarks

We have covered a lot of ground in this chapter. For the purpose of reconstructing phylogeny, it may be useful to bring together all the threads in the form of parsimony trees. This is what the next chapter is to achieve.

CHAPTER V RECONSTRUCTION OF PHYLOGENY

The Aims of This Chapter

In the last chapter, we examined the data matrix and feel the need to sort out all the threads with parsimony trees. In this chapter, two types of parsimony trees will be used to interpret and evaluate the phylogenetic attributes of various character states involved in the evolution of foraminiferal suborders: mixed-parsimony trees (i. e. mixed ordered-parsimony trees) and unordered-parsimony trees. The focus of discussion will be on the former. An optimal tree will be chosen as the new model for the reconstruction of phylogeny in the area of subordinal foraminiferal classification. The optimal tree is to be selected through a series of comparisons, especially that between the Tappan-Loeblich tree and the mixed-ordered-parsimony tree developed in this chapter.

Ordered Versus Unordered Character State Trees

In order to determine whether or not there is any evidence in favor of interpreting foraminiferal phylogeny as "natural", I have focused on the combined morphologic and cladistic phylogenetic analysis of 16 suborders between this study and the relevant work by Tappan and Loeblich (1988) and Loeblich and Tappan (1989) under the assumptions of unordered and mixed parsimony (i.e. mixed ordered and unordered parsimony).

Mixed parsimony is an important hypothetical approaches for reconstructing phylogeny. To put this approach to use, the first step is to select characters that can be ordered. Selecting characters that are in an ordered range might be helpful to further determine phylogenetic relationships among the taxa. The decision on ordered character

state trees (CST's) designed from unordered clues, was dependent on *a priori* hypotheses about pathways that character state changes might adopt (ordered transformation series). Mapping ordered character states on a cladogram led to new interpretations of the data by placing a constrained measure on character state changes.

Character 3 (wall composition) and 4 (wall utrastructure) are sensitive to assumptions about transformation series. In order to ascribe the polarity of character states for different foraminiferal taxa, two CST's (CST1 for character 3 and CST2 for character 4) were hypothesized, by focusing on a dissection of Tappan and Loeblich's (1988) and Loeblich and Tappan's (1989) tree, and on more concrete ideas of earlier researches from literature sources (Hull, 1964 and 1980; Loeblich and Tappan, 1964, 1974 and 1987; Hofker, 1972; Adams, 1972 and 1978). Both character transformation series (i.e. CST1 and CST2) are processed and shown in binary ordered tree form.

CST1 shown in Figure 2 presents a hypothesis of an evolutionary sequence of wall composition (character 3). Membranous or proteinaceous walls (state 0) possibly gave rise to organic walls (state 1), organic walls (state 1) gave rise to two independent apomorphic character states featuring organic agglutinated walls (state 2) and calcitic walls (state 4); in turn, organic agglutinated walls (state 2) gave rise to calcareous agglutinated walls (state 3) and to walls characterized by secreted spicular in an organic groundmass (state 7); and aragonitic (state 5) and siliceous walls (state 6) were successively derived from calcitic walls (state 4).

CST2 (Figure 3) is the transformation series proposed for wall ultrastructure (character 4). The evolutionary pathway of wall ultrastructure seems to indicate that: tectinous walls (state 0) are the oldest type of walls; alveolar canaliculate agglutinated walls (state 2) evolved from tectinous walls (state 0) via a simple-agglutinated-structure stage (state 1); the appearance of microgranular ultrastructure (state 3) that also evolved from tectinous walls (state 0) represents an important evolutionary step, from which

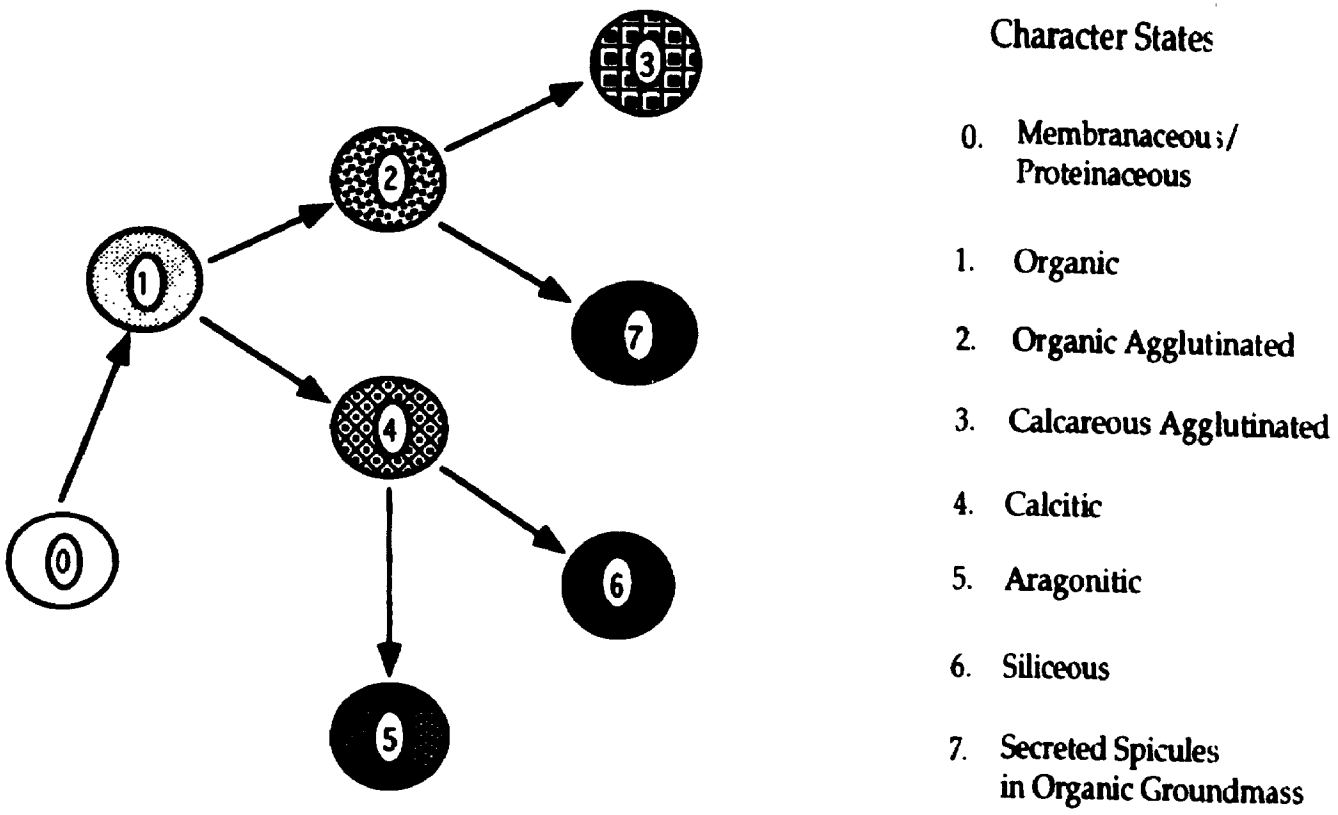
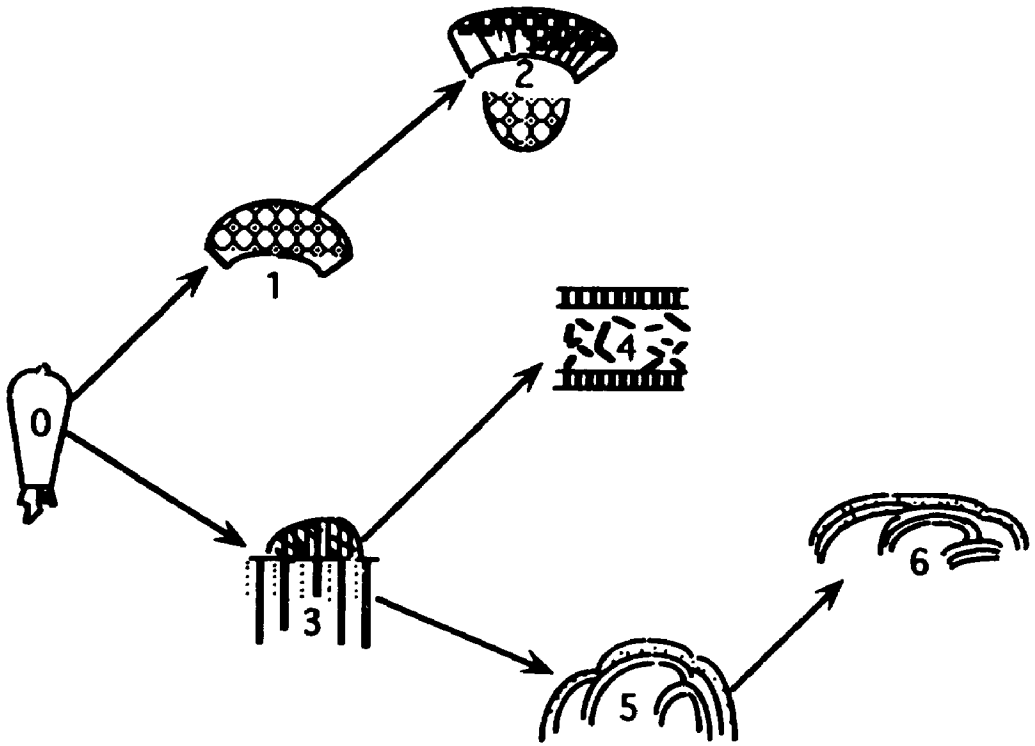


Figure 2. Character state tree 1 (CST1) -- Various foraminiferal wall compositions (character 3) described as character states. Arrows indicate proposed evolutionary trends in wall evolution (after Loeblich and Tappan, 1964, and Tappan and Loeblich, 1988).



Character State

0. Tectinous
1. Simple agglutinated
2. Alveolar canaliculated agglutinated
3. Microgranular
4. Porcellaneous
5. Hyaline monolamellar
6. Hyaline bilamellar

Figure 3. Character state tree 2 (CST2) -- Various foraminiferal wall ultrastructures (character 4) described as character states. Arrows indicate proposed evolutionary trends in wall ultrastructure evolution (after Loeblich and Tappan, 1964, and Tappan and Loeblich, 1988).

porcellaneous walls (state 4) and hyaline monolamellar walls (state 5) evolved; in turn, hyaline monolamellar walls (state 5) gave rise to hyaline bilamellar walls (state 6).

Mixed Ordered and Unordered (General) Parsimony

For ordered parsimony to be carried out, two CST's (i.e. ordered characters 3 and 4) and eight CSN's (unordered transformation series, characters 1-2 and 5-10) were adopted and equally weighted (weight=1). Data were processed using heuristic methods of PAUP. Heuristic searches were made using closest stepwise additional sequences, and various numbers of initial trees held during tree building. As a consequence, 2,104 equally parsimonious trees were obtained (see Appendix I). No additional sets of tree topologies were obtained through use of a variety of heuristic procedures. The most parsimonious trees were yielded tree length=31; *CI*=0.828; *RI*=0.889.

The 50% Majority-rule consensus result from the 2,104 trees (Figure 4: OPT1) provides evidence of group relationships and using the percentage values of those trees with major node-supporting branches. A series of circled numbers (e.g. (72) and (100); i.e. 72% or 100%) are marked on the tree to show the percentage of trees that demonstrate character support for that branch.

The 50% Majority-rule consensus tree seems to reveal several supposed monophyletic groups. The clade of Astrorhizina group, including Carterinina, Trochaminina, Haplophragmiina and Textulariina, is supported by 99% of the trees. The clade of Carterinina group, including Trochaminina, Haplophragmiina and Textulariina, is supported by 56% trees. The clade of Trochaminina, Haplophragmiina and Textulariina is supported by 81% trees.

The ingroup of Haplophragmiina and Textulariina is supported by 100% trees. The clade of Fusulinina group (Fusulinina, Miliolina, Silicoloculinina, Involutinina, Robertinina, Lagenina, Spirillinina, Rotaliina and Globigerinina) is supported by 100%

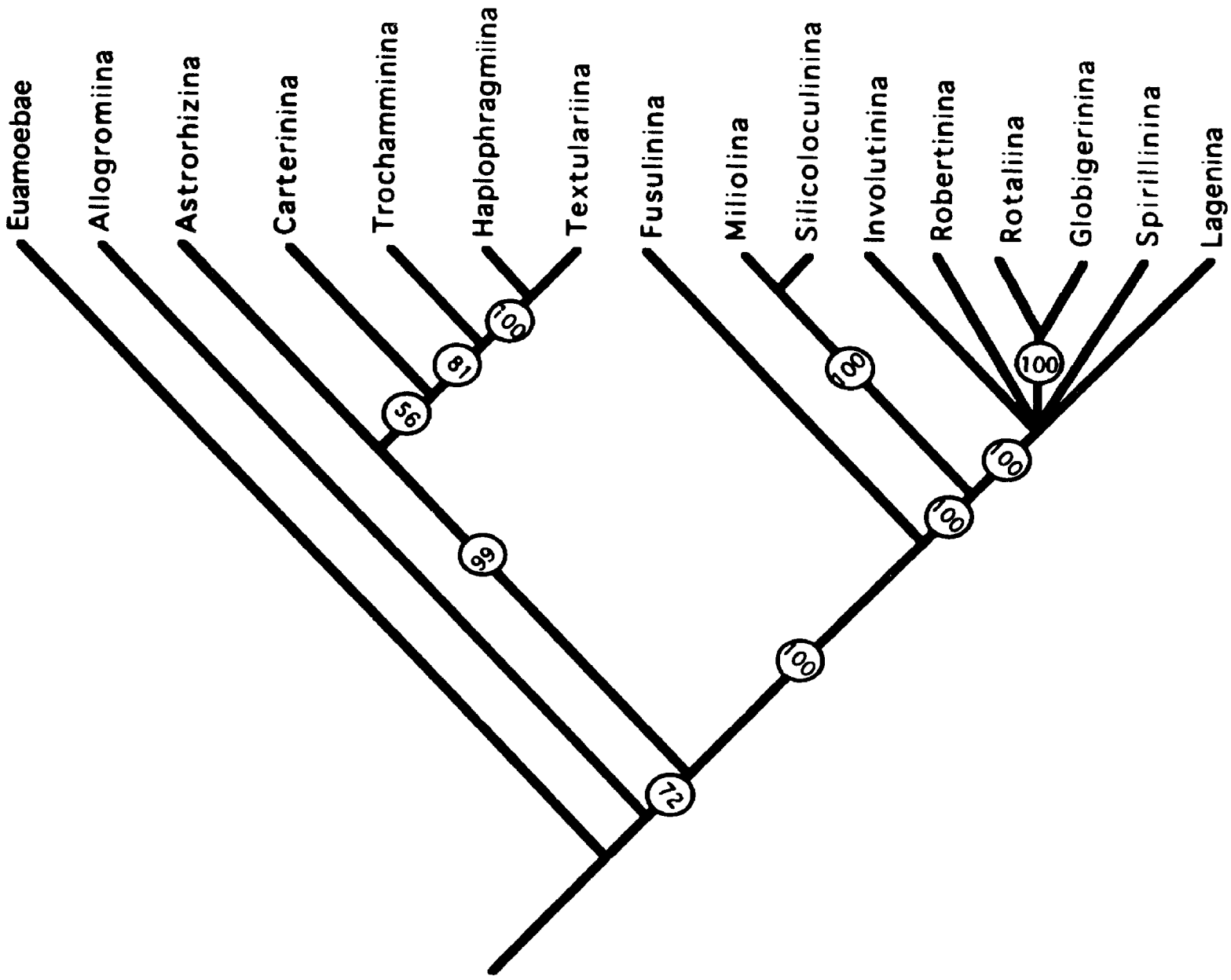


Figure 4. OPT 1 (Ordered Parsimony Tree 1)-- 50% Majority-rule consensus result based on analysis of 2,104 trees (mixed ordered and unordered parsimony). The circled values on the tree indicate the percentage of trees with branches that support that node (>50%).

trees. Miliolina and Silicoloculinina, Involutinina-Robertinina and Lagenina-Spirillinina, Rotaliina and Globigerinina, each pair being an ingroup, are supported respectively by 100% trees bearing the relevant branch. Since there seems to be more evidence (>50% trees) indicating that close relationships exist within each clade identified, the monophyletic groups may have arisen at an atypically rapid pace during geological time.

To examine character state phylogeny for the available data, one tree has to be selected from 2,104 trees to sort out the main trend of character state changes. Here it should be explained why and how one tree is to be selected. Is it a random choice? The answer is no.

The one tree (single tree) discussed below (Figure 5), is one hypothesis based on character state changes shown in one tree topology of the available 2,104 trees. The tree graphically analyzed in the above-mentioned figure is not chosen randomly, but selected on the basis of the *closest set* to the 50% majority consensus resolution. The single tree has been generated utilizing the present ordering scheme (i.e. CST1 and CST2). It reflects a close similarity to Tappan and Loeblich's (1988) and Loeblich and Tappan's (1989) tree, since the latter has served as the main source of inspiration in the initial work (i.e. ordering of CST's) for the establishment of the former. The single tree to be selected is expected to be the optimal estimate of phylogenetic relationships given the data at hand, but it is problematic that it is only one of many possible solutions. This one tree topology (PAUP output) of the most parsimonious trees, called OPT2 (i.e. the Ordered Parsimony Tree 2), is generated from the OPT1.

The independent character ontogeny (single character/single tree, MacClade output) is illustrated in Figures 6, 7, 8A-8D, which are interpretations of different characters on the one tree topology (i.e. OPT2). The single character/single tree analysis also serves to compare the distribution of character states in the tree (i.e. OPT2, Figure 5) chosen for this study against the tree suggested by Tappan and Loeblich (1988) and

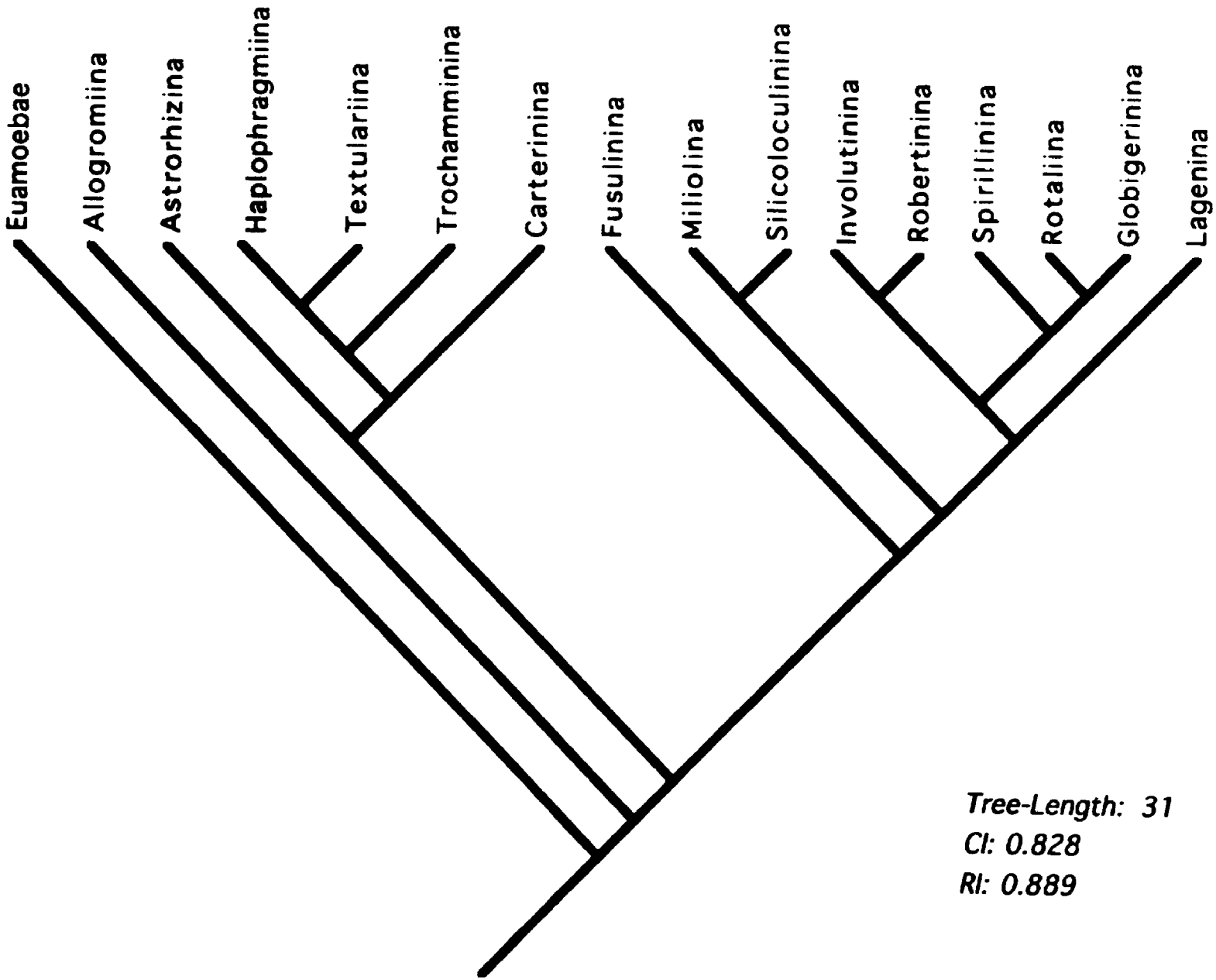


Figure 5. OPT 2 (Ordered Parsimony Tree 2) -- One model for subordinal foraminiferal phylogeny based on one of the most parsimonious tree topologies (mixed ordered and unordered parsimony). This tree closely resembles the 50% Majority-rule consensus result.

Loeblich and Tappan (1989) (i.e. Figure 1). Figure 9 summarizes Figures 6, 7, 8A-8D, indicating the overall character evolutionary trends.

OPT2 (i.e. Figure 5) offers a graphic interpretation of the foraminiferal subordinal phylogeny under consideration. In order to test whether it is advisable for this tree analysis to be examined in comparison with the one tree established by Tappan and Loeblich (1988) and Loeblich and Tappan (1989), and to establish this tree as the optimal estimate of phylogenetic relationships of the group in question, our analyses on ontogenic characters are intended to demonstrate the character changes under discussions.

Figure 6 shows the evolutionary hierarchy of wall composition (character 3) described on OPT2. The tree topology presented in this figure is the same as in Figures 5 and 18b. Numbers labeled on the tree signify character state changes designated along the terminals. The Euamoebae are characterized by plesiomorphic membranaceous/ proteinaceous walls (state 0). Allogromiina are marked by organic walls (state 1). Some members (Astrorhizina, Haplophragmiina and Trochamminina) of Astrorhizina group (Astrorhizina, Carterinina, Trochamminina, Haplophragmiina and Textulariina) share organic agglutinated walls (state 2). Carterinina have an apomorphic state of secreted spicular in organic groundmass walls (state 7). Textulariina have apomorphic calcareous agglutinated walls (state 3). Fusulinina, Miliolina, Lagenina, Spirillinina, Rotaliina and Globigerinina share calcitic walls (state 4). Involutinina and Robertinina share synapomorphic of aragonitic walls (state 5). Silicoloculinina are characterized by an apomorphic siliceous walls (state 6).

Figure 7 illustrates a hypothesis about the evolutionary hierarchy of wall ultrastructure (character 4) occurring in OPT2. Tree topology is the same as in Figures 5 and 19b. Numbers marked on the tree show character state changes listed along the terminals. Euamoebae-Allogromiina are characterized by tectinous walls (state 0). Most members of Astrorhizina group (Astrorhizina, Carterinina, Trochaminina and Textulariina) share simple agglutinated walls (state 1). Haplophragmiina are

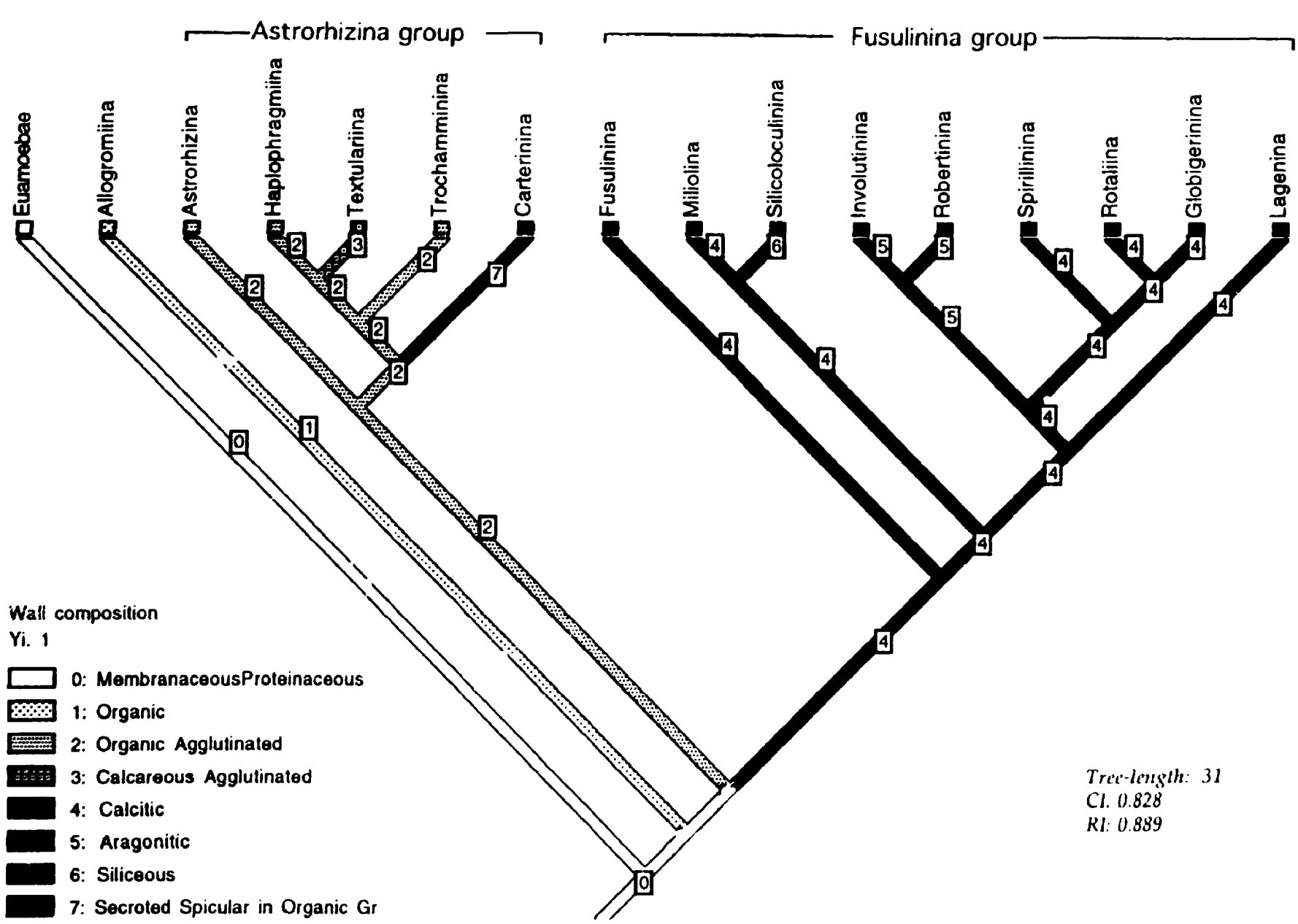


Figure 6. Hypothesis describing evolutionary hierarchy of the foraminiferal suborders illustrates distribution of character 3 (wall composition) on OPT 2. Numbers drawn on the tree show character state changes. This tree topology is the same as in Figures 5 & 18b.

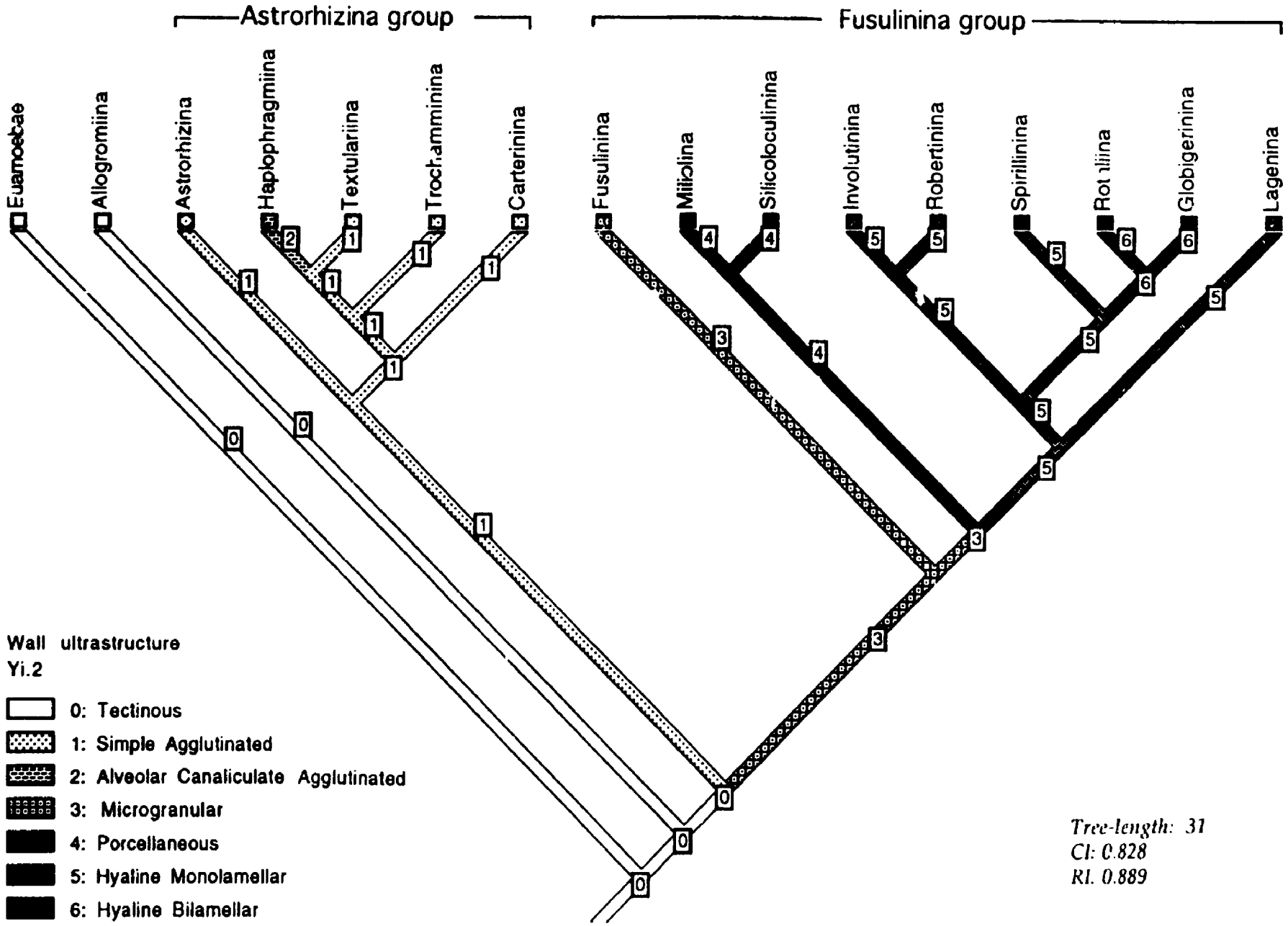


Figure 7. Hypothesis describing evolutionary hierarchy of the foraminiferal suborders illustrates distribution of character 4 (wall ultrastructure) on OPT 2. Numbers drawn on the tree show character state changes. This tree topology is the same as in Figures 5 & 19b.

characterized by apomorphic alveolar canaliculate agglutinated walls (state 2). Fusulinina are characterized by an autapomorphy of microgranular walls (state 3). Miliolina and Silicoloculinina share the synapomorphic porcellaneous walls (state 4). Involutinina, Robertinina, Spirillinina and Lagenina share hyaline monolamellar walls (state 5). Rotaliina and Globigerinina share the synapomorphic hyaline bilamellar walls (state 6).

Figures 8A--8D show the character hierarchies of each unordered transformation for the suborders on one parsimonious solution (i.e. OPT2, Figure 5), including shell (character 1), pseudopodia (character 2), test perforation (character 5), test shape (character 6), number of chambers (character 7), chamber arrangement (character 8), chamber shape (character 9) and surface sculpture (character 10).

Figure 8A:a is a hypothesis of evolutionary hierarchy of shell (character 1) on OPT2, and Figure 8A:b is a hypothesis of evolutionary hierarchy of pseudopodia (character 2) on OPT2. The predetermined outgroup of Euamoebae is characterized by the absence of shell and lobose/filose pseudopods (state 0); other groups are featured by the presence of shell and granuloreticulose pseudopods (state 1).

Figure 8B:a is a hypothesis about the pathways of the test perforation (character 5) change on OPT2: the ancestral lineage of several taxa Euamoebae, Allogromiina, Astrorhizina, Haplophragmiina, Textulariina, Trochamminina, Carterinina, Fusulinina, Miliolina and Silicoloculinina connects the primary state of non-perforation tests (state 0) with a later lineage evolving to perforation tests (state 1), which is shown in other taxa such as Lagenina, Involutinina, Robertinina, Spirillinina, Rotaliina and Globigerinina.

Figure 8B:b is a hypothesis of evolutionary hierarchy of test shape (character 6) on OPT2. The outgroup Euamoebae is characterized by spherical forms (state 0). Allogromiina are characterized by spherical/pyriform test shapes (states 0/3). The spherical/radiating/pyriform test shapes (states 0/1/3) are characteristics of Astrorhizina. Carterinina have spherical/trochoid shapes (states 0/5). Therefore, the state 0 (spherical

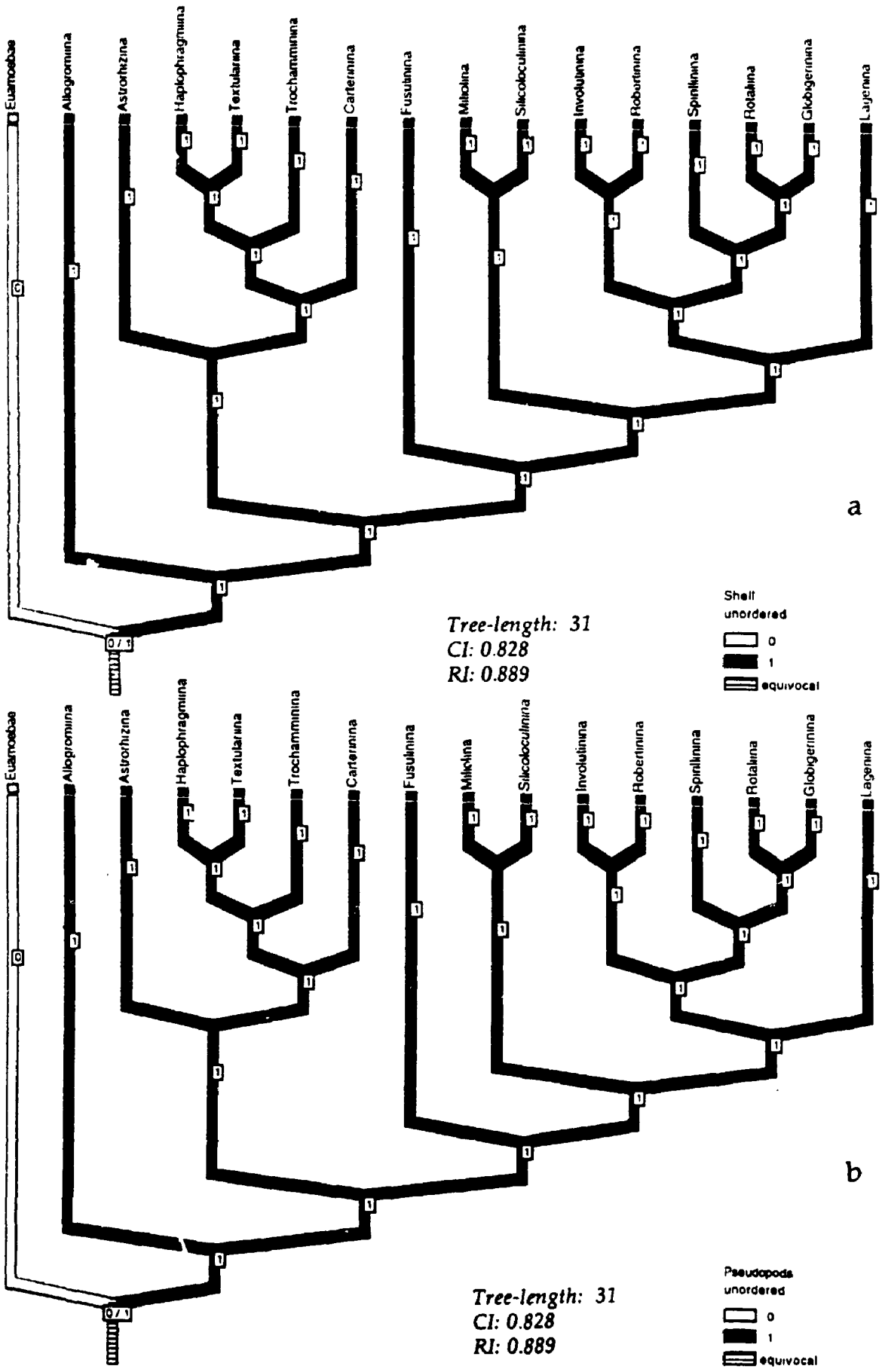


Figure 8A. Hypothesis describing evolutionary hierarchy of the foraminiferal suborders illustrates distribution of character 1 and 2 on OPT2: (a) shell (character 1) and (b) pseudopodia (character 2). Numbers shown on the tree are state codes (see Table 3a).

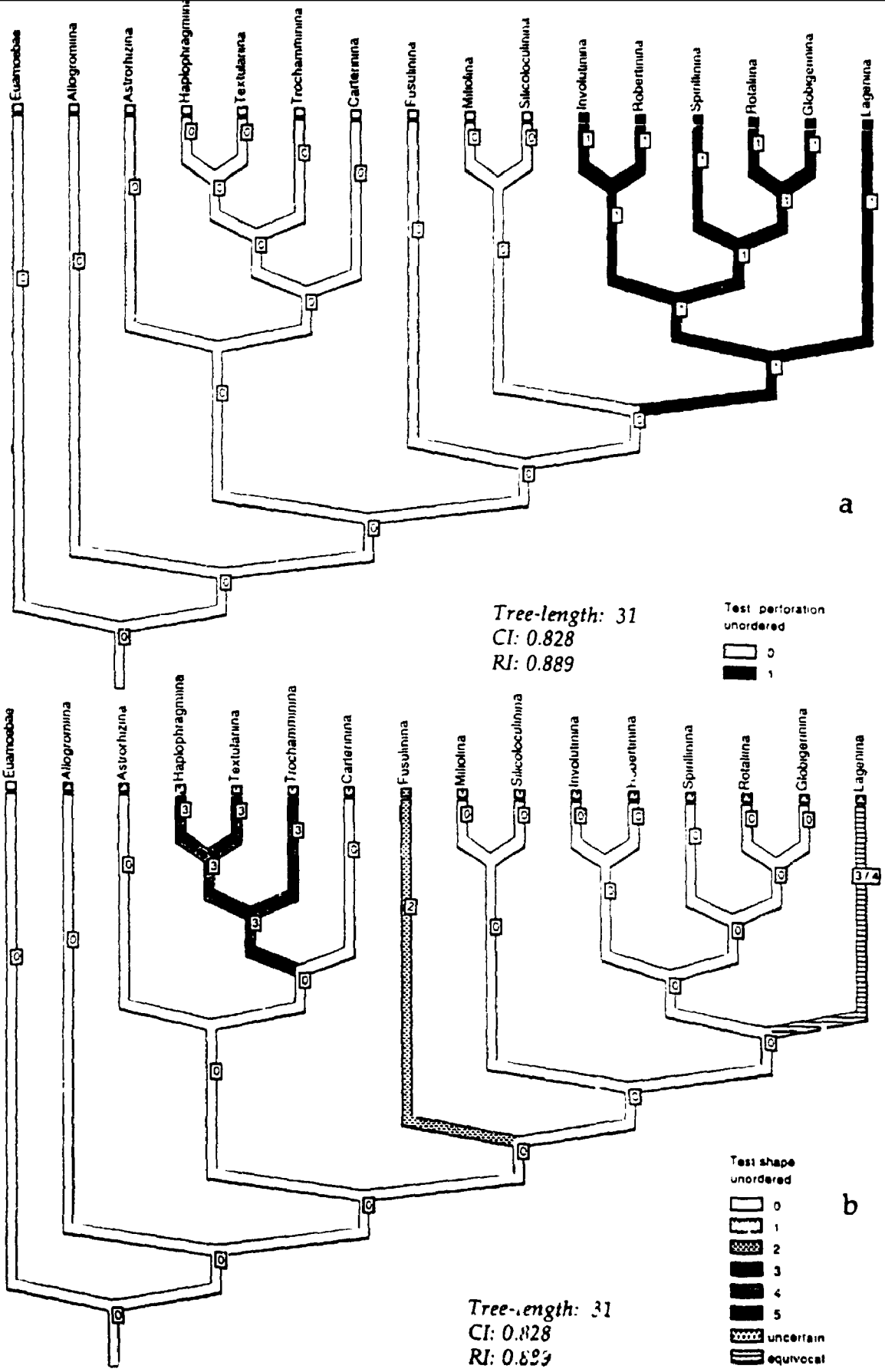


Figure 8B. Hypothesis describing evolutionary hierarchy of the foraminiferal suborders illustrates distribution of character 5 and 6 on OPT2: (a) test perforation (character 5) and (b) test shape (character 6). Numbers shown on the tree are state codes (see Table 3a & 3b).

tests) is their common plesiomorphic character condition. Haplophragmiina have spherical/pyriform/trochoid test shapes (states 0/3/5), Trochamminina have pyriform/trochoid test shapes (states 3/5) and the Textulariina have states of pyriform/elongate test shapes (states 3/4). Thus, state 3 (same legend branches) is the common ancestral state among Trochamminina, Haplophragmiina and Textulariina. The pyriform/elongate test shapes (states 3/4) are characteristic of Lagenina. The spherical/fusiform/pyriform/elongate test shapes (states 0/2/3/4) are the plesiomorphic and apomorphic states of Miliolina, and Silicoloculinina are only characterized by the spherical/pyriform/elongate test shapes (states 0/3/4). MacClade outputs only show the plesiomorphic state 0 (same legend branchches) but not the common apomorphies states 3/4 between Miliolina and Silicoloculinina; states 3/4 are also features of Lagenina. The spherical/pyriform test shapes (states 0/3) are the characteristics of Involutinina and Robertinina. The spherical/trochoid shapes (states 0/5) are apomorphies of Spirillinina. The spherical/pyriform/elongate/trochoid test shapes (states 0/3/4/5) are the common plesiomorphic and apomorphic character states of Rotaliina and Globigerinina. Same legend branches featuring by state 0 indicate that the spherical shape is common plesiomorphy among Involutinina, Robertinina, Spirillinina, Rotaliina and Globigerinina. In fact, both state 0 and state 3 mark the ancestry of Involotinina and Robertinina, while state 5 is the common ancestral state among Spirillinina, Rotaliina and Globigerinina.

Character state changes in chamber numbers (character 7) of OPT2 shown on the Figure 8C:a indicate that Euamoebae, Allogromiina and Astrorhizina exhibit the unilocular feature (state 0), while the other taxa (Haplophragmiina, Textulariina, Trochamminina, Carterinina, Fusulinina, Miliolina, Silicoloculinina, Involutinina, Robertinina, Spirillinina, Rotaliina, Globigerinina and Lagenina) do exhibit the well-developed multilocular feature (state 1). (note: states 0/1 marked under the branches of Astrorhizina and Carterinina are the either ancestral states of the groups by ACCTRAN downward pass labelling).

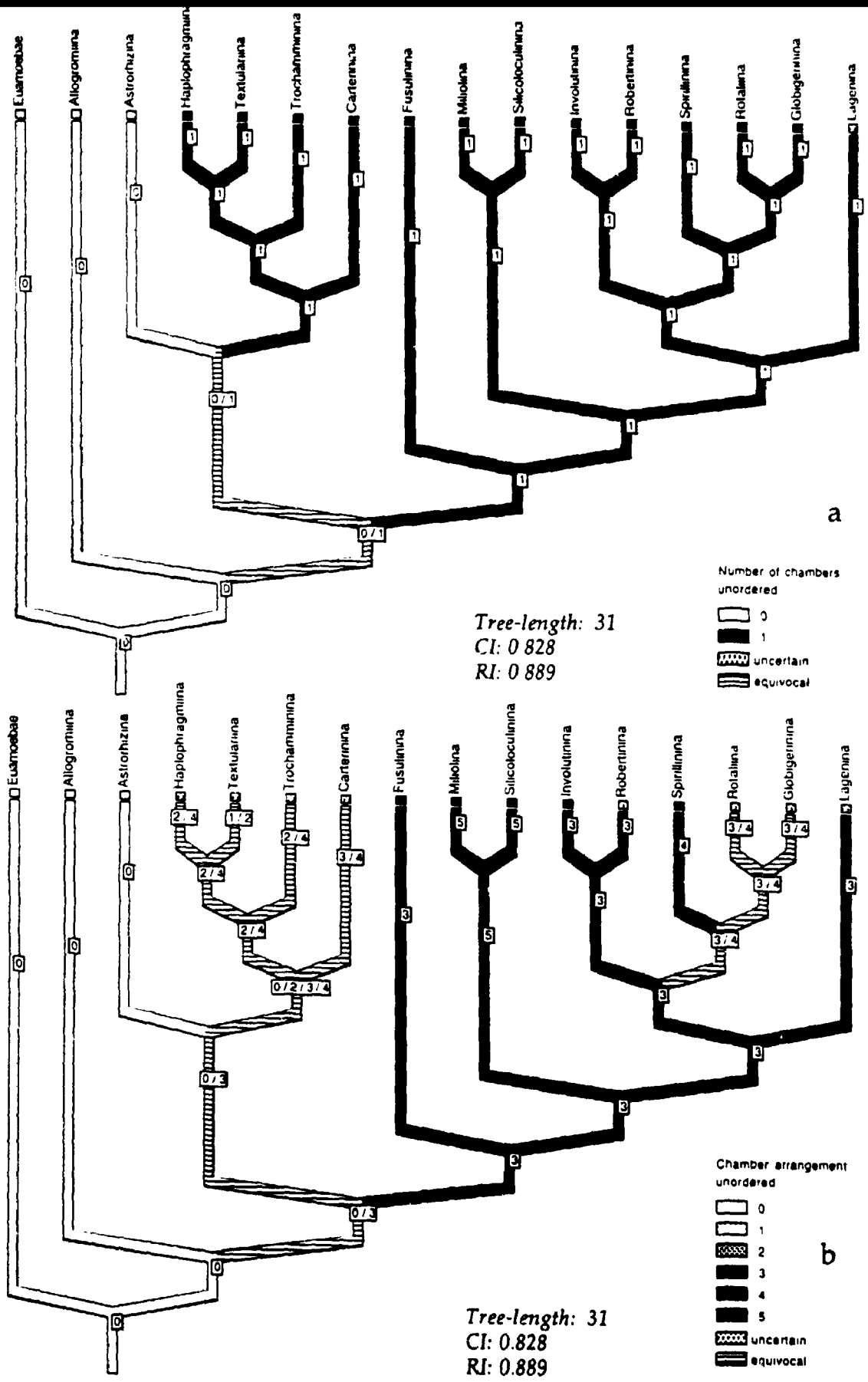


Figure 8C. Hypothesis describing evolutionary hierarchy of the foraminiferal suborders illustrates distribution of character 7 and 8 on OPT2: (a) number of chambers (character 7) and (b) chamber arrangement (character 8). Numbers shown on the tree are state codes (see Table 3b).

Figure 8C:b is an illustration of chamber arrangement (character 8) on OPT2. Euamoebae, Allogromiina and Astrorhizina are characterized by simple planispiral chambers (state 0). Any one of multiserial/trochospiral chambers (states 2/4) just suggests that it may be either the common ancestral state of Trochamminina and Haplophragmiina; Textulariina (states 1/2, uniserial/multiserial) share state 2 with Trochamminina and Haplophragmiina. In addition, the simple planispiral chambers (state 1) are Textulariina's independent character state. Carterinina share trochospiral tests (state 4) with Trochamminina and Haplophragmiina, and their planispiral involute/evolute chambers (state 3) are an apomorphic character state. (note: labels 0/2/3/4 under the branches of Carterinina and Trochamminina are the uncertainty for ancestors of the groups by the ACCTRAN labelling.

Fusulinina are characterized by planispiral involute/evolute chambers (state 3), and the groups Miliolina and Silicoloculinina have milioline chambers (state 5). Involutinina are characterized by planispiral involute/evolute chambers (state 3). Robertinina are marked by planispiral involute or evolute/trochospiral chambers (states 3 and 4). Simple planispiral/uniserial/planispiral involute or evolute chambers (states 0, 1 and 3) are characteristics of Lagenina. Judging from these clues, Fusulinina, Lagenina, Involutinina and Robertinina share an apomorphy -- i.e. state 3. Rotaliina and Globigerinina are characterized by multiserial/planispiral involute or evolute/trochospiral chambers (states 2, 3 and 4). Trochospiral chamber arrangement (state 4) is Spirillinina's characteristic. Thus, state 4 is a common ancestral state among Spirillinina, Rotaliina and Globigerinina.

Figure 8D:a is a hypothesis of the evolutionary hierarchy of chamber shape (character 9) on OPT2. Most taxa have the plesiomorphic character state -- globular/ ovate chamber shape (state 0). Carterinina are characterized by conical chamber shape (state 4). Fusulinina, which present state 0, have fusiform chamber shapes (state 1), Miliolina have globular, ovate, fusiform, discoidal, conical, lenticular or tubular chamber

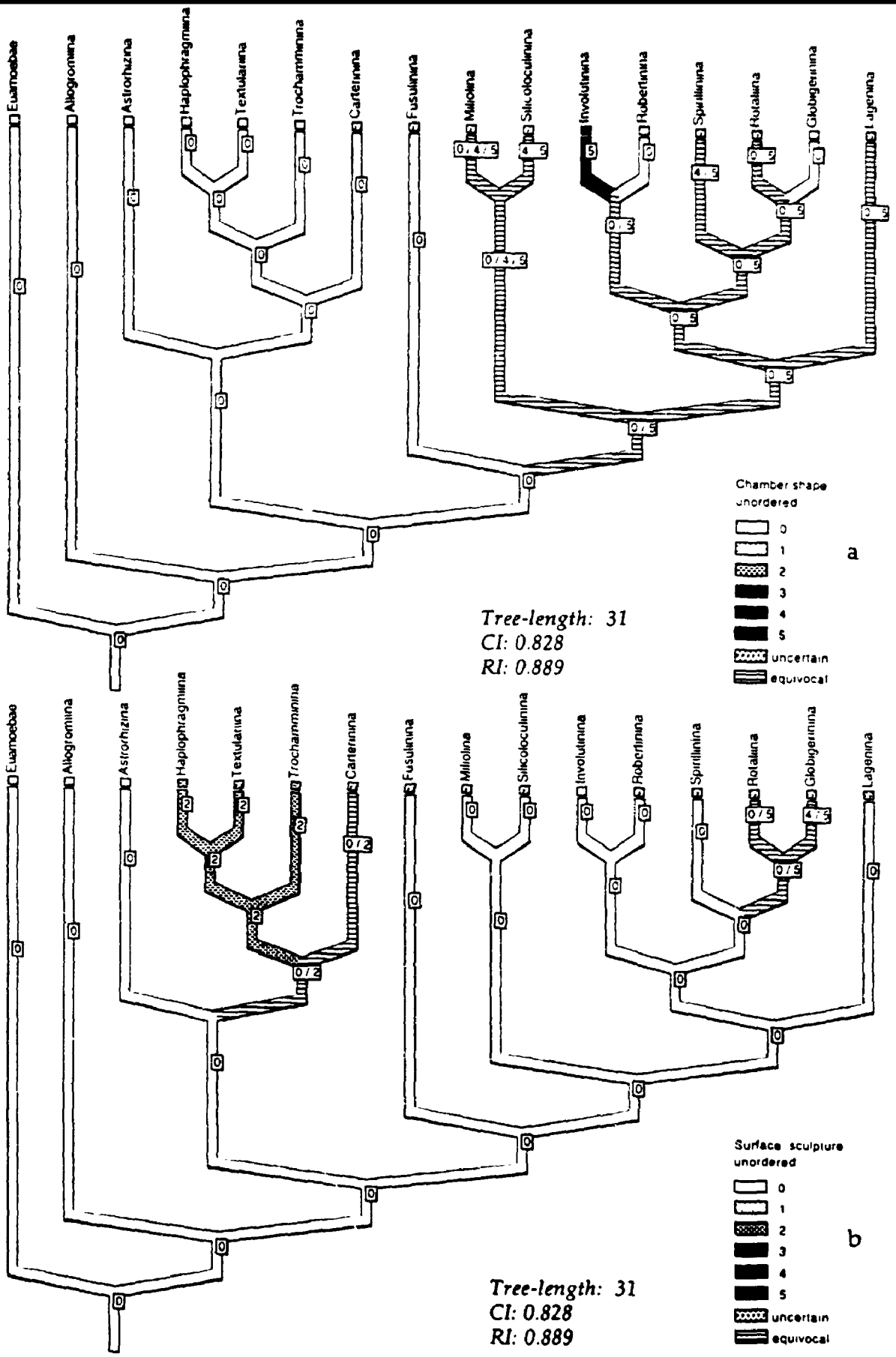


Figure 8D. Hypothesis describing evolutionary hierarchy of the foraminiferal suborders illustrates distribution of character 9 and 10 on OPT2: (a) chamber shape (character 9) and (b) surface sculpture (character 10). Numbers shown on the tree are state codes (see Table 3b).

shapes (states 0, 1, 3, 4 and 5), and Silicoloculinina present conical/lenticular or tubular chamber shapes (states 4/5). Therefore, Miliolina and Silicoloculinina have common ancestry states 4/5, and Fusulinina and Miliolina have state 1. Lenticular or tubular chamber shapes (state 5) are characteristics of Involutinina; Spirillinina are characterized by conical/lenticular or tubular chamber shapes (states 4 and 5); Rotaliina display globular or ovate, discoidal, conical, lenticular or tubular chamber shapes (states 0, 3, 4 and 5). Globigerinina only have state 0, while Lagenina demonstrate globular, ovate, palmate, lenticular or tubular chamber shapes (states 0, 2 and 5). The down pass ACCTRAN lablelling, therefore, marks states 0/5 as their common ancestrial attibutes.

Figure 8D:b illustrates the character state change in surface sculpture (character 10) on OPT2. Most taxa have plesiomorphies of smooth or pillared test surfaces (state 0). Both Textulariina and Carterinina have fissured/pitted/nodose surfaces (states 2). They do share this apomorphy (state 2) with Haplophragmiina and Trochamminina. Fusulinina, Miliolina and Silicoloculinina are characterized by smooth or pillared test surface (state 0) and fissured, pitted or nodose test surfaces (state 2). Involutinina have smooth or pillared surfaces (state 0). Robertinina and Spirillinina, indicative of state 0, have peripherally keel- test surfaces (state 3). Lagenina, having states 0/3, present ribbed, costate or reticulate test surfaces (state 1). ACCTRAN upward pass only labels their common plesiomorphy (i.e. state 0) on the branches. Rotaliina-Globigerinina share punctate, rugose or hispid test surfaces (state 5); Globigerinina also have planktic-spinous ornamentation (state 4) on the test surface. ACCTRAN downward pass therefore labels their common ancestral states (i.e. states 0/5).

It might be helpful to look back at Figures 8A to 8D, which present the marking of character changes with numbers of each suborder. The codes labeled for each suborder in these figures only function to illustrate the character-state-oriented of a suborder in its ontogenic development, without focusing on derived characteristics shared between suborders. ACCTRAN downward pass or upward pass sometimes only labels

the common plesiomorphic character state among taxa in a same legend relm. In the consideration, plesiomophies do not play a very important role in the course of evolution. Despite this fact, it must be noted that the codes in these figures remain indicative of some shared states to be considered later. In practice, these shared character states are phylogenetic evidence that we are looking for (I have generally posed in the earlier paragraphs). Yet, to see this point more clearly, we have to move into the groundplan state codes tabulated in Tables 3c and 3d derived from Tables 3a and 3b, which serve to demonstrate the array of shared derived character states (same legended branches or not) functioning in the character (1-2 and 5-10) evolution of varied suborders.

Following interpretations will be summed up briefly in the possibilities for the group relationships by the shared derived character states for the present 8 characters (1-2 and 5-10) illustrated in the tables, and by the aid of Figure 9. Figure 9 (OPT3) graphically sketches such interpretation for almost all of character state evolution charted on OPT2. This diagram clarifies the relationships between the evolutionary trends of ontogenic shared derived characteristics and that of overall shared derived characteristics between foraminiferal suborders.

Euamoebae as an outgroup are characterized by all plesiomorphic states (state 0), whereas all foraminiferal suborders are characterized by shell presence and granuloreticulose pseudopods (state 1).

Allogromiina have 3 derived character states, i.e. organic walls (state 1 of character 3), shell presence (state 1 of character 1) and granuloreticulose pseudopods (state 1 of character 2).

Astrorhizina have 2 derived states, i.e. organic agglutinated walls (state 2 of character 3), simple agglutinated wall ultrastructure (state 1 of character 4), and 2 inherited states from Allogromiina (state 1 of character 1 and state 1 of character 2). Astrorhizina only share organic agglutinated walls (state 2 of character 3) with Trochaminina and Haplophragmiina.

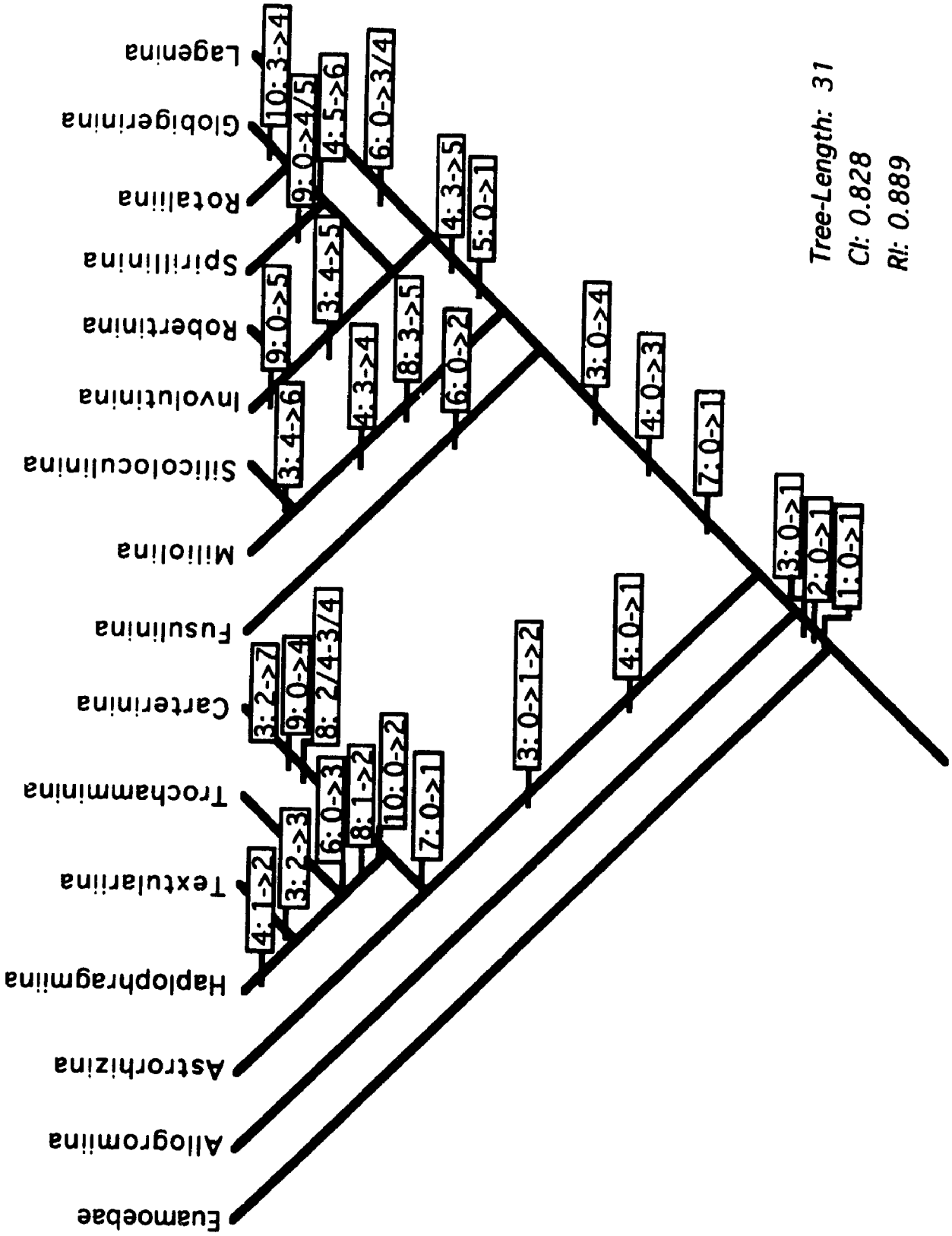


Figure 9. OPT 3 (Ordered Parsimony Tree 3) -- Character state changes on one of the most parsimonious tree topologies (mixed ordered and unordered parsimony) based on Figures 5, 6, 7, 8.

The alveolar canaliculate agglutinated wall ultrastructure (state 2 of character 4) is an apomorphic state of Haplophragmiina.

Trochamminina, Haplophragmiina and Textulariina share 3 derived character states: i.e. pyriform/ovate/globular test shapes (state 3 of character 6), multiserial/trochospiral chamber shapes (state 2 of character 8) and fissured/pitted/nodose test surfaces (state 2 of character 10). Trochamminina and Haplophragmiina also share the trochospiral chamber shape (state 4 of character 8). Calcareous agglutinated walls (state 3 of character 3) are marked as an apomorphic state displayed by Textulariina.

Secreted spicular in organic groundmass walls (state 7 of character 3) are a featuring character state of Carterinina. Carterinina share simple agglutinated wall ultrastructure (state 1 of character 4) with Trochamminina and Textulariina, trochospiral chamber shape (state 4 of character 8) with Trochamminina and Haplophragmiina, and fissured/pitted/nodose surfaces (state 2 of character 10) with Trochamminina, Haplophragmiina and Textulariina.

Fusulinina have some plesiomorphies from Allogromiina, such as non-perforate tests, globular/ovate chamber shape and smooth surface (state 0 of character 5, 9 and 10). However, Fusulinina's calcitic walls (state 4 of character 3), microgranular wall ultrastructure (state 3 of character 4), fusiform test shape (state 2 of character 6) and planispiral involute/evolute chamber shape (state 3 of character 8) are the character states derived from the primitive stage.

Like Fusulinina, Miliolina and Silicoloculinina have multilocular chambers (state 1 of character 7), but the calcitic walls (state 4 of character 3) are a shared character state between Fusulinina and Miliolina. Miliolina and Silicoloculinina have such synapomorphies as porcellaneous wall ultrastructure (state 4 of character 4) and milioline chamber shape (state 5 of character 8). Siliceous walls (state 6 of character 3) are an autapomorphy of Silicoloculinina.

Lagenina share calcitic walls (state 4 of character 3), planispiral involute/evolute chamber shape (state 3 of character 8) with Fusulinina and Involutinina. Lagenina may evolve their hyaline monolamellar ultrastructure (state 5 of character 4) from the microgranular wall ultrastructure (state 3 of character 4) of Fusulinina. Interestingly, hyaline monolamellar ultrastructure is a character state shared by Lagenina, Involutinina, Robertinina and Spirillinina. Meanwhile, Lagenina, Fusulinina, Involutinina, Robertinina, Rotaliina and Globigerinina share planispiral chamber shape (state 3 of character 8).

Involutinina and Robertinina share such synapomorphies as aragonitic walls (state 5 of character 3). They share hyaline monolamellar wall ultrastructure (state 5 of character 4) with Lagenina and Spirillinina, and planispiral involute/evolute chamber shape (state 3 of character 8) with Fusulinina, Lagenina, Rotaliina and Globigerinina. They also share perforate tests (state 1 of character 5) with Lagenina, Spirillinina, Rotaliina and Globigerinina.

Spirillinina share hyaline monolamellar wall ultrastructure (state 5 of character 4) with Involutinina and Robertinina. Spirillinina share the calcitic walls (state 4 of character 3) and the trochospiral chamber shape (state 4 of character 8) with Rotaliina and Globigerinina. These trochospiral chamber shapes (state 4 of character 8) are deemed to be derived character states from Involutinina and Robertinina or Robertinina. Spirillinina share the conical chamber shape (state 4 of character 9) with Miliolina and Silicoloculinina, while the lenticular or tubular chamber shape (state 5 of character 9) of Spirillinina is also characteristic of Lagenina and Rotaliina.

Rotaliina and Globigerinina share such synapomorphies as hyaline bilamellar wall ultrastructure (state 6 of character 4), and have apomorphies like planispiral involute/trochospiral chamber shapes (states 3/4 of character 8) and punctate rugose test surfaces (state 5 of character 10). They share calcitic walls (state 4 of character 3) with all calcareous groups such as Fusulinina, Miliolina, Lagenina and Spirillinina.

So far, we have pointed out that some shared derived character states support groups on the basis of the "groundplan states" (Tables 3c-3d) in order to go deeper in our discussion about character evolution and group relationship. The groundplan states were intended to help search for groups and look at the characters that justify those groups (note: the more important aspect of this work would be the comparison of the parsimony analysis results with the Tappan and Loeblich tree).

Good support (i.e. unique character state assigments in foraminifera or low homoplasy) for certain groups has been given by some characters, such as character 1 (shell), character 2 (pseudopodia), character 5 (test perforation) and character 7 (number of chambers). These characters are found in all members of a terminal taxon. Some characters, exhibiting numerous states within taxa, are not likely to be good characters, such as character 8 (chamber arrangement) and character 9 (chamber shape), especially when we are forced to select the second grounplan states (e.g. Tables 3c-3d) from the first recorded data (e.g. Tables 3a-3b).

These character's attributes offer very poor support (very homoplastic or equivocal characters): they are represented by multiserial chamber arrangement and low or high trochospiral chamber arrangement (states 2 and 4 of character 8, see Figure 8C: b) or conical chamber shapes and lenticular/tubular chamber shapes (states 4 and 5 of character 9, see Figure 8D: a).

However, it should be noted that some multiple state characters (e.g. characters 3 and 4, see Figures 6 and 7), which exhibit one state in terms of single apomorphy within taxa seem to be good characters. The siliceous walls (state 6 of character 3), secreting spicular in organic groundmass walls (state 7 of character 3), aragonitic walls (state 5 of character 3) and bilamellar wall ultrastructure (state 6 of character 4), are autapomorphies in which the natural groups are best identified.

Table 3c. Groundplan of character (1-5) states describing subordinal foraminiferal phylogeny (taken from Table 3a).

Taxon		1	2	3	4	5
		Shell	Pseudopods	Wall composition	Wall ultrastructure	Test perforation
1	Euamoebae	0	0	0	0	0
2	Allogromiina	1	1	1	0	0
3	Astrorhizina	1	1	2	1	0
4	Haplophragmiina	1	1	2	2	0
5	Trochamminina	1	1	2	1	0
6	Textulariina	1	1	3	1	0
7	Fusulinina	1	1	4	3	0
8	Involutinina	1	1	5	5	1
9	Miliolina	1	1	4	4	0
10	Silicoloculinina	1	1	6	4	0
11	Lagenina	1	1	4	5	1
12	Rotaliina	1	1	4	6	1
13	Globigerinina	1	1	4	6	1
14	Robertinina	1	1	5	5	1
15	Spirillinina	1	1	4	5	1
16	Carterinina	1	1	7	1	0
		Transformation Series				

Table 3d. Groundplan of character (6-10) states describing subordinal foraminiferal phylogeny (taken from Table 3b).

	Taxon	6 Test Shape	7 Number of chambers	8 Chamber arrangement	9 Chamber shape	10 Surface sculpture
1	Euamoebae	0	0	0	0	0
2	Allogromiina	0	0	0	0	0
3	Astrorhizina	0	0	0	0	0
4	Haplophragmiina	3	1	2/4	0	2
5	Trochamminina	3	1	2/4	0	2
6	Textulariina	3	1	1/2	0	2
7	Fusulinina	2	1	3	0	0/2
8	Involutinina	3	1	3	5	0
9	Miliolina	3/4	1	5	0/4/5	0
10	Silicoloculinina	3/4	1	5	4/5	0
11	Lagenina	3/4	1	3	0/5	0
12	Rotaliina	5	1	3/4	0/5	0/3/5
13	Globigerinina	5	1	3/4	0	4/5
14	Robertinina	3	1	3	0	0
15	Spirillinina	5	1	4	4/5	0
16	Carterinina	0/5	1	3/4	0	0/2

Transformation Series

Unordered (Fitch) Parsimony: the Aim and Procedure

This method has been used in interpreting the phylogeny of three genera of the Maastrichtian-Danian triserial and biserial planktic foraminifera (MacLeod, 1993). However, it is rarely applied to subordinal foraminiferal classification.

In this work, unordered parsimony was employed for comparative purposes because trees built up on the basis of unordered data do not only rely on *a priori* assumptions and some monophyletic groups may also be provided by using the same supportive data.

First, this approach was introduced into the research in order to see how unordered results may vary with each different approach. It is worthwhile to determine which approach, ordered parsimony or unordered parsimony, is more convincing in disclosing the actual phylogenetic relationships between foraminiferal suborders. Second, this method is used in this study as an attempt to explore the possibilities of integrating both approaches in our phylogenetic studies. It has been the author's intention to exploit the advantages of both methods so that they can complement each other in the research work.

Similar to the mixed ordered one, for unordered parsimony to be carried out, all characters are treated as unordered and also equally weighted (weight=1) before being calculated with the aid of heuristic search methods. Heuristic searches were still made using closest stepwise additional sequences, and various numbers of initial trees held during tree building. As a consequence, 3,980 equally parsimonious trees were obtained (see Appendix II). No additional sets of tree topologies were obtained through use of a variety of heuristic procedures. The most parsimonious trees were 28 steps long with *CI*=0.93 and *RI*=0.92.

Descriptions

A 50% Majority-rule consensus tree (Figure 10) for the 3,980 trees shows our findings from a heuristic methodology about foraminiferal phylogenetic relationships revealed up to the subordinal level. A series of circled numbers (e.g. (57) and (100); i.e. 57% or 100%) marked out on the tree show the percentage of trees with each branch that supports the corresponding node (>50%).

Results indicate that the clade of Haplophragmiina, Trochamminina, Textulariina and Carterinina within Astrorhizina is supported by 100% trees with this branch. The clade of the Fusulinina group (Fusulinina, Involutinina, Lagenina, Rotaliina, Globigerinina, Robertinina, Spirillinina, Miliolina and Silicoloculinina) is supported by 67% trees with this branch. The ingroup consisting of Involutinina, Lagenina, Rotaliina, Globigerinina, Robertinina and Spirillinina is evidenced by 57% of the trees. 72% of the trees support Rotaliina and Globigerinina. The ingroup composed of Miliolina and Silicoloculinina is supported by 100% trees with this branch.

Figure 11, as one solution of character state change model of the most parsimonious tree topologies (3,980), presents one of the closest sets of the 50% Majority-rule consensus result. This cladogram graphically demonstrates character evolutionary patterns by the numbers shown along the terminals. The differences between the ordered tree (i.e OPT3, Figure 9) and the tree produced in this method (unordered parsimony) are quite small. The root of Allogromiina is presented by character state change 1: 0->1 (from shelllessness to shell presence), character state change 2: 0->1 (form lobose/filose pseudopods to granuloreticulose pseudopods), and character state change 3: 0->1 (from membranaceous/proteinaceous walls to organic walls). The root of Astrorhizina is marked by character state change 3: 1->2 (from organic walls to organic agglutinated walls) and character state change 4: 0->1 (from tectinous to simple agglutinated walls). The root of Caterinina is marked by character state change 7: 0->2 (from unilocular to multilocular). The root of the Haplophragmiina

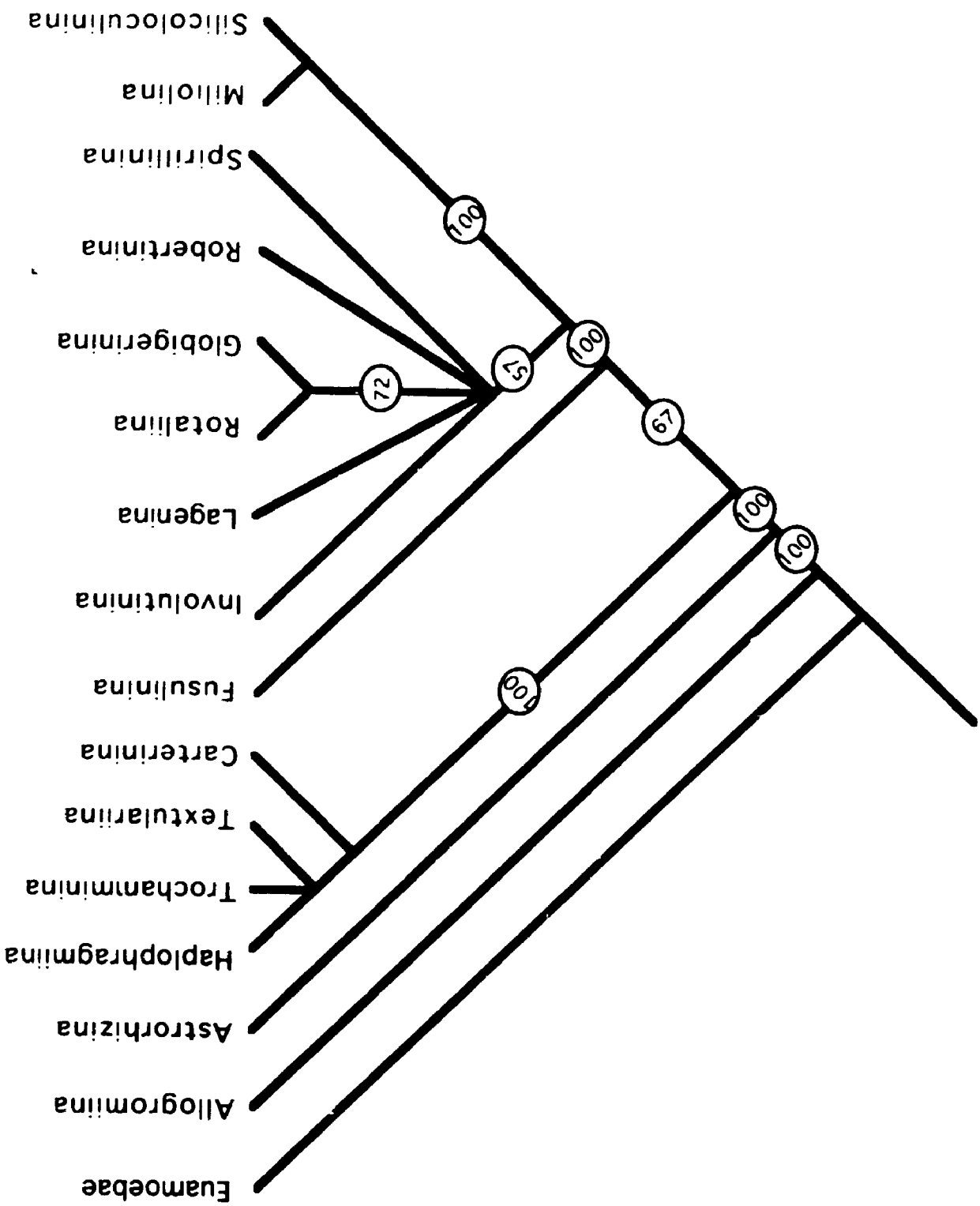


Figure 10. 50% Majority-rule consensus result based on 3,980 trees (unordered parsimony). The circled values on the tree indicate the percentage of the trees with branches that support that node (>50%).

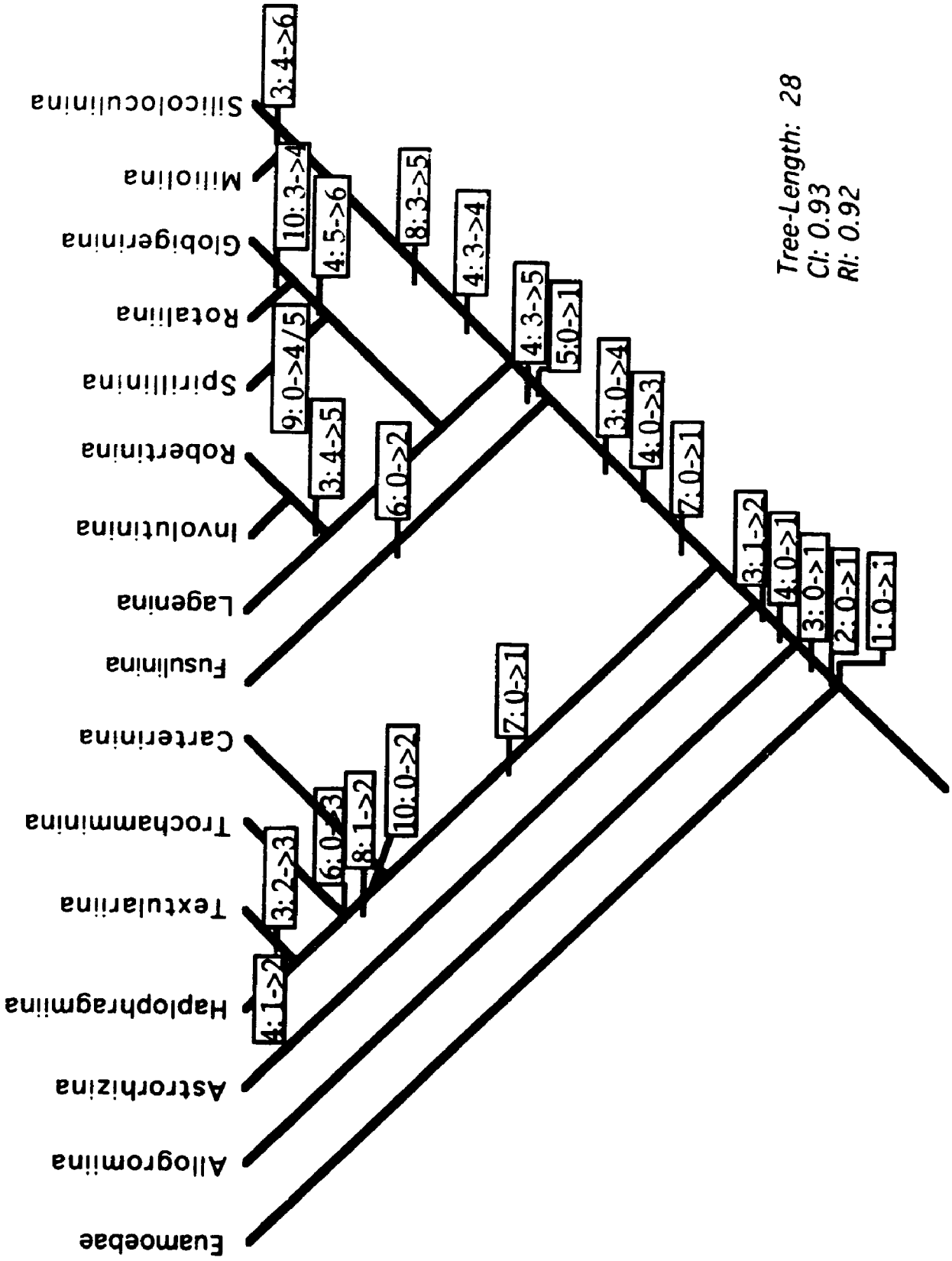


Figure 11. Character state changes on one of the most parsimonious tree topologies (unordered parsimony). This tree closely resembles the 50% Majority-rule consensus result of 3,980 trees.

clade (Haplopgragmiina-Trochamminina-Textulariina) is presented by character state change 6: 0->3 (spherical test shapes to pyriform test shapes), character state change 8: 1->2 (from uniserial chambers to multiserial chambers), and character state change 10: 0->2 (from smooth/pillared surface to fissured, pitted or nodose surface). Alveolar canaliculate agglutinated walls (state 2 of character 4) derived from tectinous walls (character 4: 1->2) are the apomorphic character state of Haplophragmiina, while the calcareous agglutinated walls derived from organic agglutinated walls (character 3: 2->3) are the Textulariina's apomorphic character state.

The ancestral character state changes of the Fusulinina group (Fusulinina, Involutinina, Lagenina, Rotaliina, Globigerinina, Robertinina, Spirillinina, Miliolina and Silicoloculinina) are presented by 3: 0->4 (from membranaceous/proteinaceous to calcitic walls), 4: 0->3 (from tectinous to microgranular wall ultrastructure), and 7: 0->1 (from unilocular to multilocular). The root of Fusulinina is mainly characterized by 6: 0->2 (character state change from spherical to fusiform tests), while microgranular walls (state 3 of character 4) are the apomorphic attributes of Fusulinina.

The ancestral stage of Lagenina and Miliolina-Silicoloculinina are presented by hyaline monolamellar wall ultrastructure derived from microgranular wall ultrastructure (4: 3->4), and their perforate test are derived from their plesiomorphy (5: 0->1). The ingroup of Miliolina and Silicoloculinina mainly feature by milioline test shapes derived from planispiral involute/evolute test shapes (character 8: 3->5), and by porcellaneous wall ultrastructure (character state change 4: 3->4). The siliceous walls (character 3: 4->6) are the apomorphy of Silicoloculinina.

The ingroup of Involutinina and Robertinina is characterized by their synapomorphic aragonitic walls (state 5), which developed from calcitic walls (character 3: 4->5). The conical/lenticular chamber shape (character state change 9: 0->4/5) is characteristic of Spirillinina. The hyaline bilamellar walls (state 6 of character 4) of Rotaliina and Globigerinina may be originated from hyaline monolamellar walls (state 5

of character 4). The planktic-spinous surface sculpture (character 10: 3->4) is the autapomorphic character state Globigerinina.

Tree Comparison: Mixed Parsimony and Unordered Parsimony

What I consider most important are the similarities between the hypothesized hierarchies of taxa established by two parsimonies (i.e. unordered parsimony and mixed parsimony). *Mixed parsimony* refers to the integrative approach in which the ordered and unordered character states are analyzed and used for this study. *Unordered parsimony* is the method for establishing the unordered trees analyzed previously for our comparative purposes. In a broader view, the mixed ordered trees and the unordered trees for 16 subordinal taxa used the same character states but different coding polarity; however, each type of parsimonious tree provided an unalternative hypothesis for character evolution.

The comparison (Figure 12) of the 50% majority consensus trees built up in unordered and mixed ordered schemes shows that, examined after the flipping of certain branches for our comparative purpose, the differences in branching pattern between the two trees are small. Looking back at the pertinent figures, we may confirm the correspondence of most branches of the consensus trees using different methods. Even though few percentage values are similar in both parsimonies, a percentage identical on both trees can be spotted: e.g. the branch of Miliolina and Silicoloculinina is supported by 100% trees drawn out in both methods.

The analysis of the figure view (i.e. Figure 11) has encompassed an impressive array of subordinal foraminiferal phylogeny, all character state changes of certain clades are similar to those shown in the mixed ordered and unordered cladogram commented earlier (Figure 9: OPT3). Most character state changes have been addressed here within an explicitly phylogenetic context; many have been presented here in an unrandom order.

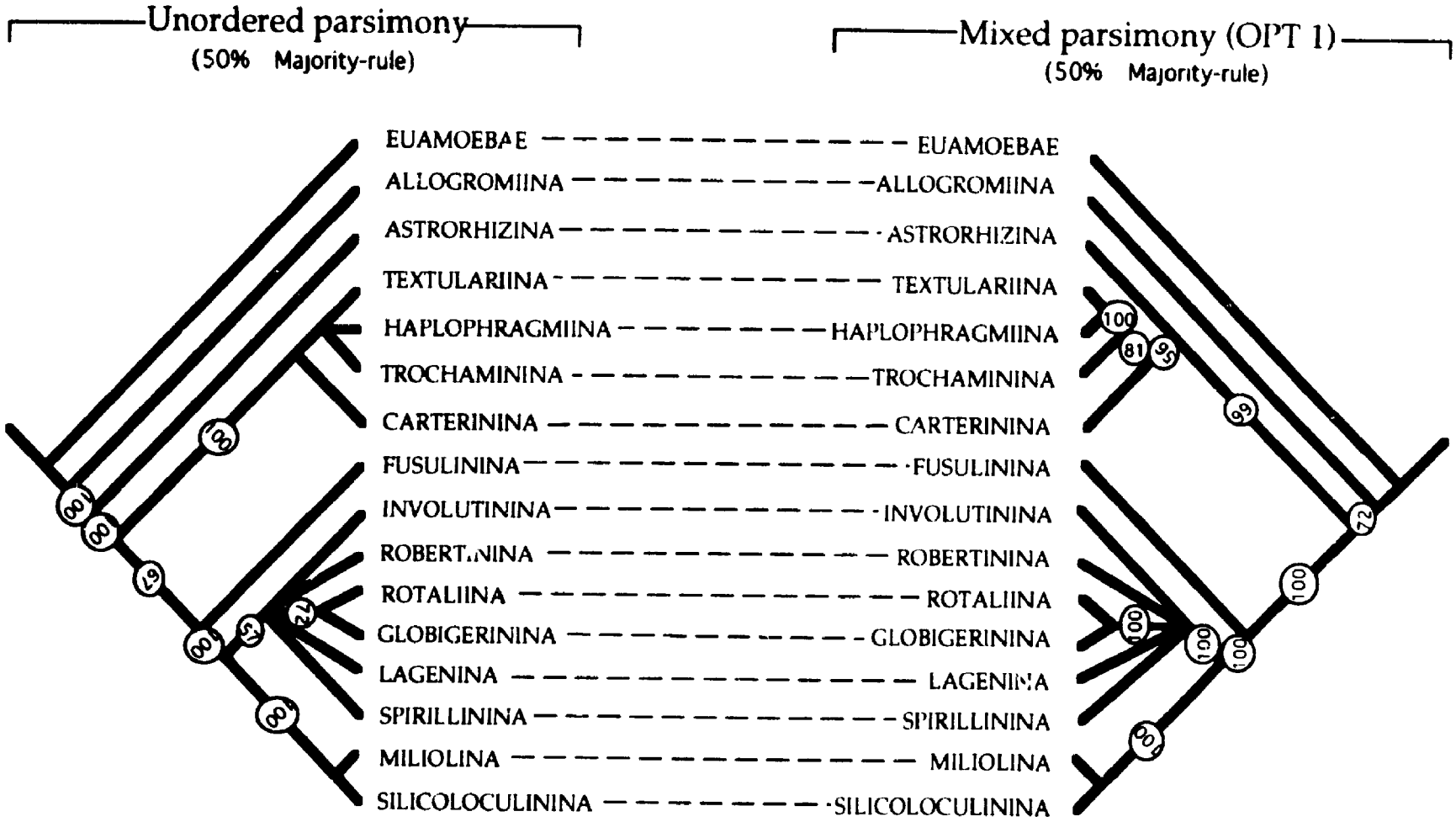


Figure 12. Comparison of unordered and mixed parsimony after branch flipping based on the 50% Majority-rule consensus trees as proposed in this study. The left tree is based on the unordered parsimony, the right tree is based on the mixed ordered and unordered parsimony. Dash lines in the middle suggest that both trees are nearly congruent. The circled values on the tree show the percentage of trees with branches that support that node (>50%).

For example, the clade of Astrorhizhina and the clade of Fusulinina differ considerably in morphologic aspects shown by using both methods. In two parsimonies, Carterinina group are associated with Astrorhizina by a derived apomorphy indicated in wall composition. The clade of Involutinina and Robertinina is found sharing a synapomorphy. The ancestral state of this clade, in turn, joins their older ancestral states common among the calcareous community.

Both parsimonious analyses also result in the specification of the tree branches in which the four suborders (Involutinina, Lagenina, Robertinina and Spirillinina) share the common ancestral states of hyaline monolamellar walls (state 5 of character 4, i.e. 4: 3->5) and perforate tests (state 1 of character 5, i.e. 5: 0->1). Indeed, the nodes that are themselves jointed to the main ingroup of Rotaliina and Globigerinina stand for the derived shared state denoting hyaline bilamellar walls (state 6 of character 4, i.e. 4: 5->6). Though Lagenina and Miliolina positioned on each tree (e.g. Figure 9 or Figure 11) seem to occur in a different array, this common node (3: 0->4) of the two taxa remains to reflect the same evolutionary movement in both trees. Viewed in the two quite similar tree forms, many more derived charactere states appear to have occurred as a series of nodes that are very similar for the definer.

As we know, the tree of the shortest length is the one in which the actual common ancestral relationships between the taxa are best estimated, only if parsimony is used as a way of criticism. The average tree length is 28 for the unordered tree and 31 for the mixed ordered and unordered tree. The ordered parsimony trees (e.g. OPT2 and OPT3) were 3 steps longer than if all characters had been treated as unordered. It seems that the unordered parsimony tree may also reveal certain significant relationships between the taxa classified. Hence, questions, such as how to evaluate the "shortest tree" and how to interpret "shortest length" in different situations (e.g. ordered or unordered), need to be answered.

Tree length can be affected by many factors. Hauser and Presch (1991) made a statistical analysis of ordered and unordered tree length on the basis of a literature search. Among 27 pairs of trees promulgated, they found that most trees (some are exempted) erected in an ordered scheme were longer (including extra step) than those built up in the unordered one, with the minimum distance of 1 step and the maximum distance of 81 steps. Therefore, if the length is used as a viable criterion for parsimony techniques, the ordered parsimony should be considered less preferable to the unordered one, since it lengthens tree length.

In this study, for example, the ordered trees (mixed-parsimony trees) for homoplasitic characters 7 (number of chambers), 8 (chamber arrangement) and 9 (chamber shape) are one step longer than the unordered ones. The *CI* statistics tells us that the particular derived similarity turns out lower *CI* with a little longer tree length (see Appendices I & II):

		Unordered parsimony		Mixed parsimony	
character	state	steps	CI	steps	CI
7	2	1	1.00	2	0.50
8	6	4	1.00	5	0.80
9	6	2	0.50	3	0.33

Although it looks worse here for characters 7, 8 and 9 of mixed parsimony shown in the table above, we should emphasize here that the mixed ordered analysis using mixed-ordered characters (i.e. OPT2 or OPT3) seems to be preferable to the unordered parsimony, if its ordered polarized interpretation about character evolution and restricted tree number are considered since unordered parsimony utilizing unordered character evolution pathways.

Three reasons are considered as follows: First, the tree length produced by the ordered parsimony is a little longer than that by the unordered parsimony because the ordered parsimony remains some ordered pathways (e.g. ordered characters 3 and 4) and

influences the steps of the other characters (e.g. characters 7, 8 and 9). It seems possible that a sort of uncertainty would occur due to the capricious pace of character state in the unordered evolutionary progress. This uncertainty may have caused high levels of instability between character deviation and subordinal foraminiferal phylogeny and may have led to branch collapse. Another possibility is that the flaws underlying the unordered parsimony are such that treating character evolution to the subordinal degree is beyond character evolutionary capacity-oriented. The tree (i.e. cladogram) set up through the ordered method may offer more messages about the order of subordinal foraminiferal evolution than the one based on the unordered parsimony, which provides no more than the depiction of reversible binary relations of one character state with the others.

For another reason, the mixed parsimony restricts the number of equally parsimonious trees to the extent appropriate for broad historical studies on evolution. As is known, a small number of equally parsimonious trees suggest fewer open answers to evolutionary questions, and vise versa; more open answers mean less reliability of the parsimony results and more harassing work in choosing a cladogram (phylogenetic tree) as the paragon for constructing phylogenetic models. It has been seen that 2,104 trees were produced in the ordered parsimony, while 3,980 trees were created in the unordered parsimony: The ordered trees occupy merely 52% of the unordered ones.

Finally, we have chosen to compare the mixed-parsimony tree with Tappan-Loeblich tree on the basis of ordered assumptions for character 3 and 4 -- the weighted character 3 and 4 are based on Tappan and Loeblich tree.

Comparative Evaluation against Tappan and Loeblich's Tree

In order to visualize the properties of Tappan and Loeblich's (1988) and Loeblich and Tappan's (1989) tree (i.e Tappan and Loeblich Tree), and identify the similarities and discrepancies between their tree (i.e. Figure 1) and the tree produced in this study (e.g.

Figure 9: OPT3), both unordered and mixed parsimonies have been adopted to observe character distributions on the Tappan and Loeblich's (1988) and Loeblich and Tappan's (1989) tree. Fifteen suborders, together with Euamoebae as an outgroup, were investigated. The hierarchical branching patterns were analyzed using PAUP (3.1) (see Appendices III and IV). MacClade (3.0) was used to model unordered and ordered characters on the Tappan and Loeblich's (1988) and Loeblich and Tappan's (1989) tree (i.e. Figure 1), which was then compared with the 50% majority tree (i.e. Figure 4: OPT1) based on the data (i.e. Tables 1 and 2a-b) of this study.

The tree using unordered characters (Figure 13) modeled on the Tappan and Loeblich's (1988) and Loeblich and Tappan's (1989) tree (i.e. Figure 1) treats all characters. Its length and relevant values are as follows: Length=32, *CI*=0.800 and *RI*=0.769 (see Appendix III). It is observable that character state changes are not well-ordered-traced on the tree. Due to its evident inconsisdency with CST's on character evolution, this tree is ignored.

Figure 14 (i.e. OTL: the Ordered Tappan and Loeblich Tree) is a mixed ordering tree modeled on the Tappan and Loeblich's (1988) and Loeblich and Tappan's (1989) tree (i.e. Figure 1) by ordering characters 3 (i.e. CST1) and 4 (i.e. CST2). Its length and pertinent values are given as follows: Length=36, *CI*=0.706 and *RI*=0.778 (see Appendix IV). The possible character state evolution trends have been mapped on the tree. All of the character state changes displayed by the same data employed for OPT3 are presented following the Tappan-and-Loeblich model. Due to our focus on the ordered parsimony in this study, it was decided to use this ordered Tappan and Loeblich's (1988) and Loeblich and Tappan's (1989) tree for the comparative analysis of OPT3 (i.e. Figure 9).

There are some best supported clades. The root of Fusulinina group (Fusulinina, Miliolina, Silicoloculinina, Lagenina, Involutinina and Spirillinina) is mainly characterized by calcitic walls (3: 0->4), and microgranular wall ultrastructure (4: 0->3). The clade of Miliolina and Silicoloculinina is supported by synapomorphy porcellaneous

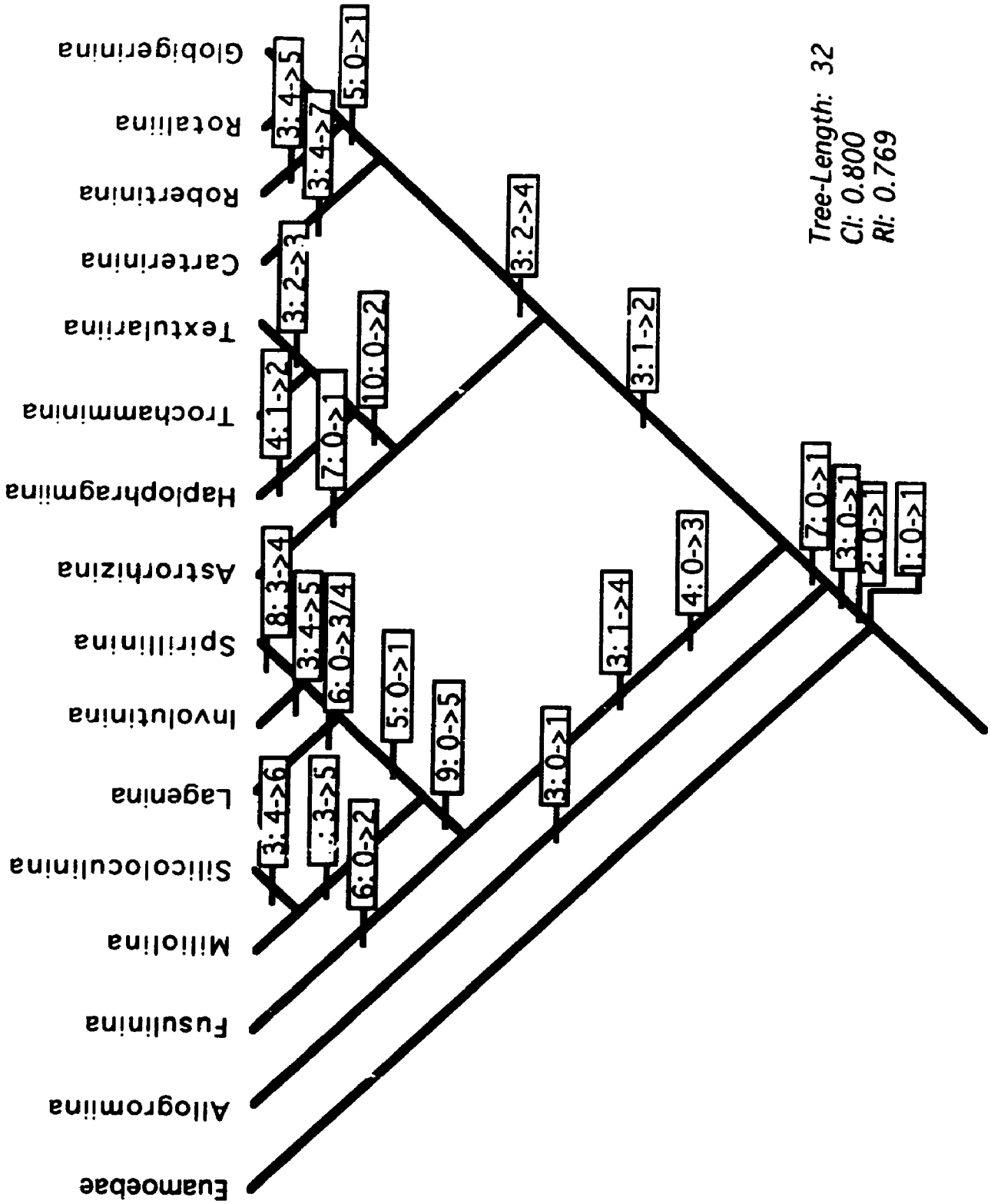


Figure 13. Character state changes in the modelled Tappan and Loeblich tree. Numbers drawn on the tree show character evolutionary trends of unordered parsimony.

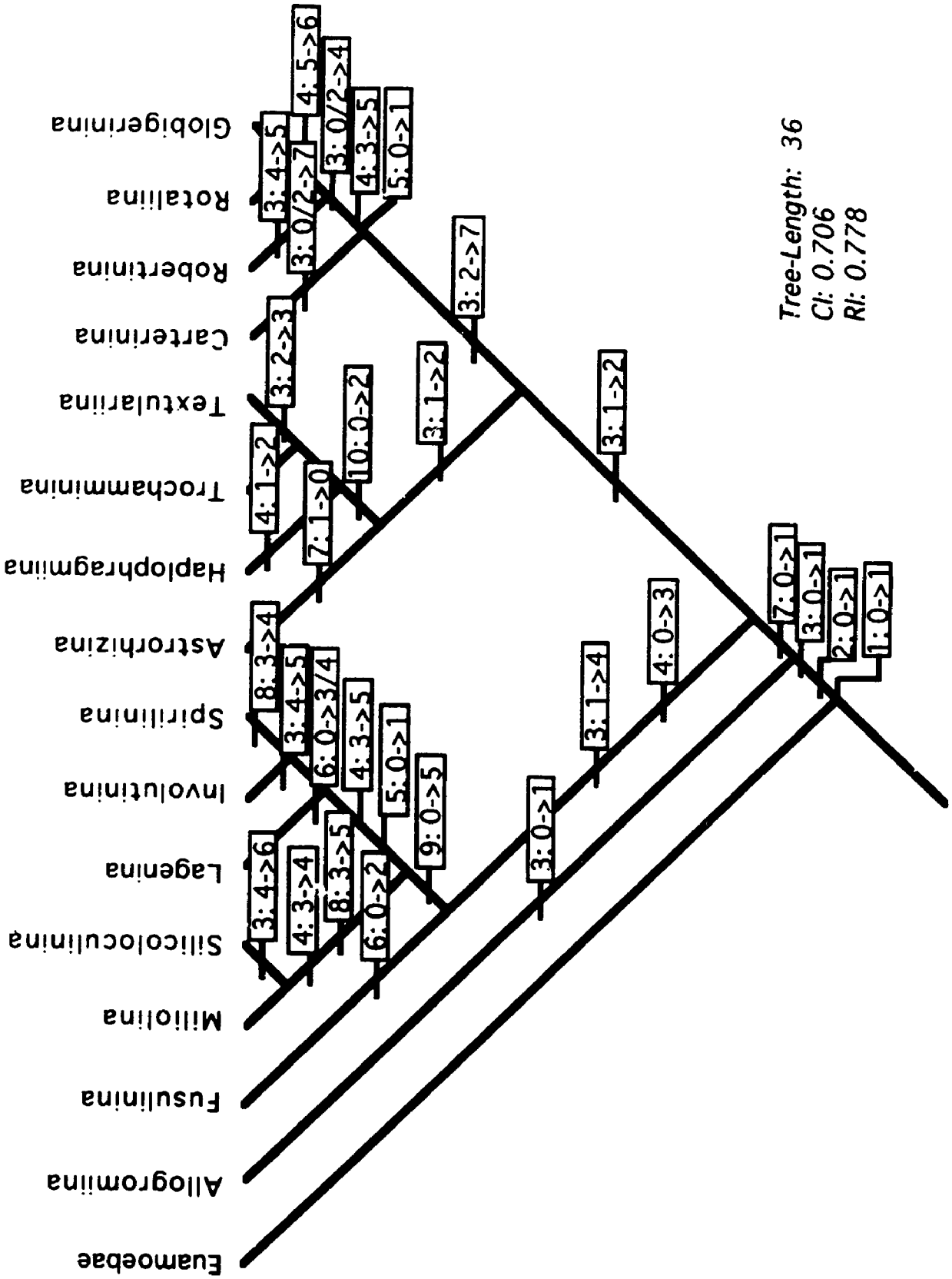


Figure 14. OTL (Ordered Tappan and Loeblich Tree) -- Character state changes on a cladogram based on modelling of the tree (Tappan and Loeblich, 1988, Loeblich and Tappan, 1989). Numbers drawn on the tree show character evolutionary trends (mixed ordered and unordered parsimony).

wall ultrastructure (4; 3->4) and milioline chamber arrangement (8: 3->5), while siliceous walls (3: 4->6) are the autapomorphy of Silicoloculinina. The root of Lagenina-Involutinina-Spirillinina are marked by monolamellar wall ultrastructure (4: 3->5), perforation test (5: 0->1), while the aragonitic walls (3: 4->5) are the apomorphy of Involutinina, Spirillinina are presented by trochospiral chamber arrangement (8: 3->4). The root of the Astrorhizhina group (Astrorhizina, Haplophragmiina, Trochamminina and Textulariina) is represented by organic agglutinated walls (3: 1->2), the unilocular chamber (7: 1-> 0) is a nonadditive code of the clade. The root of the Haplophragmiina-Trochamminina-Textulariina is supported by fissured/pitted/nodose surface sculpture (10: 0->2). The clade of Robertinina-Rotaliina-Globigerinina is supported by some apomorphies -- i.e. calcitic walls (3: 0/2->4), Rotaliina-Globigerinina are characterized by hyaline monolamellar wall ultrastructure (4: 3->5), while Robertinina have aragonitic walls (3: 4->5). Carterinina group are characterized by the autapomorphy -- i.e. the secreted spicular in organic groundmass walls.

Figures 15 and 16 show the distribution of character 3 (wall composition) and character 4 (wall ultrastructure) on the OTL. The two diagrams show that Euamoebae are characterized by plesiomorphies of membranaceous walls (state 0) and tectinous wall ultrastructure (state 0). Organic (state 1) Allogromiina are presented by tectinous wall ultrastructure (state 0). Organic agglutinated (state 2) Astrorhizina and Trochamminina are characterized by simple agglutinated wal ultrastructure (state 1). Organic agglutinated (state 2) Haplophragmiina have alveolar canaliculate agglutinated wall ultrastructure (state 2). Calcareous agglutinated Textulariina have simple agglutinated wall ultrastructure (state 1). Calcareous (state 4) Fusulinina are p:e. nted microgranular wall ultrastructure (state 3). Caicareous (state 4) Miliolina and siliceous (state 6) Silicoloculinina are marked by porcellaneous wall ultrastructure (state 5). Calcitic (state 4) Lagenina and Spirillinina, aragonitic (state 5) Involutinina and Robertinina are represented by hyaline monolamellar wall ultrastructure (state 5). The hyaline bilamellar

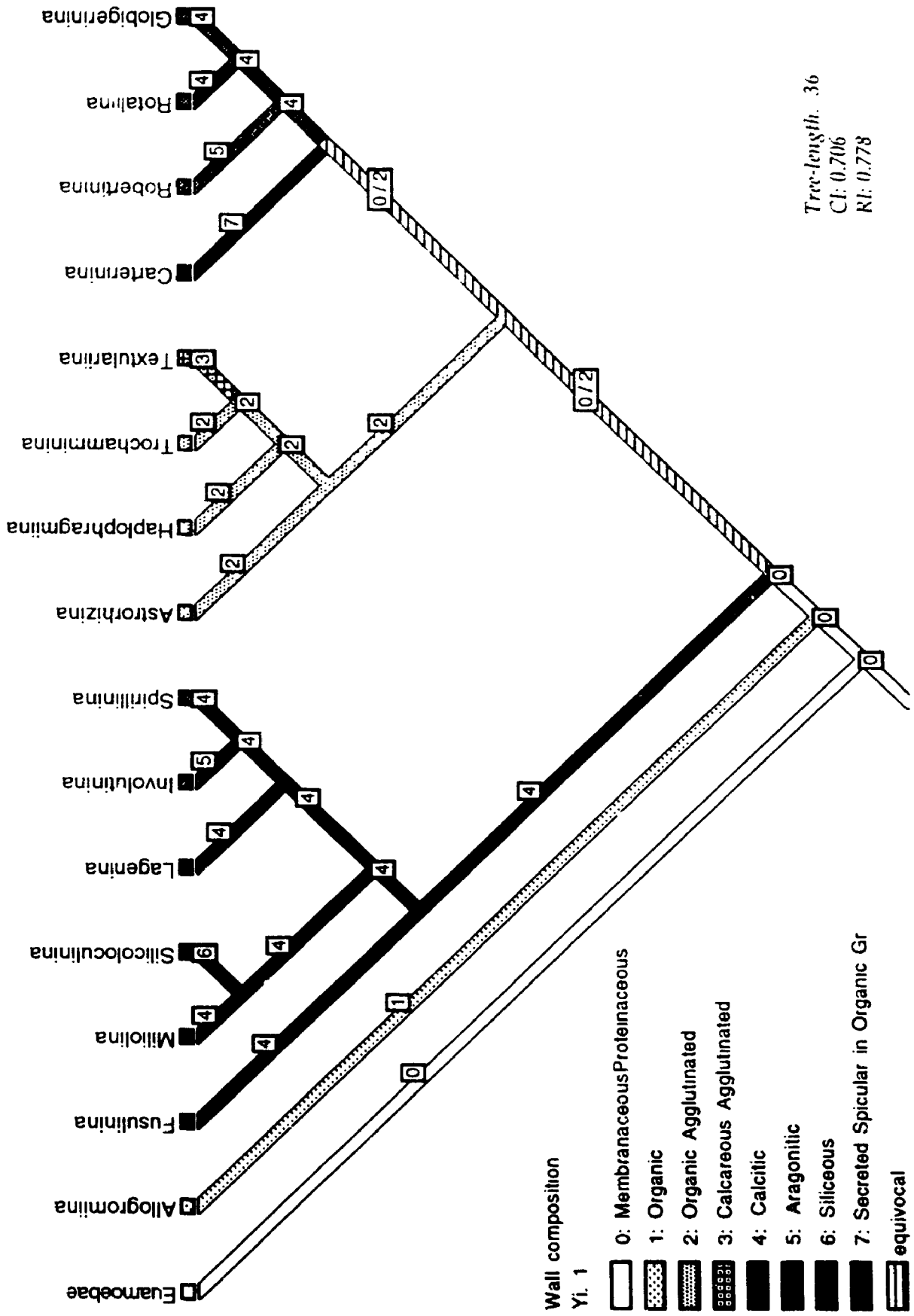


Figure 15. Hypothesis explaining subordinal foraminiferal evolutionary hierarchy of wall composition (character 3) based on the modelled Tappan and Loeblich tree. Numbers drawn on the tree show character state changes. This tree topology is the same as in Figures 14 & 18a.

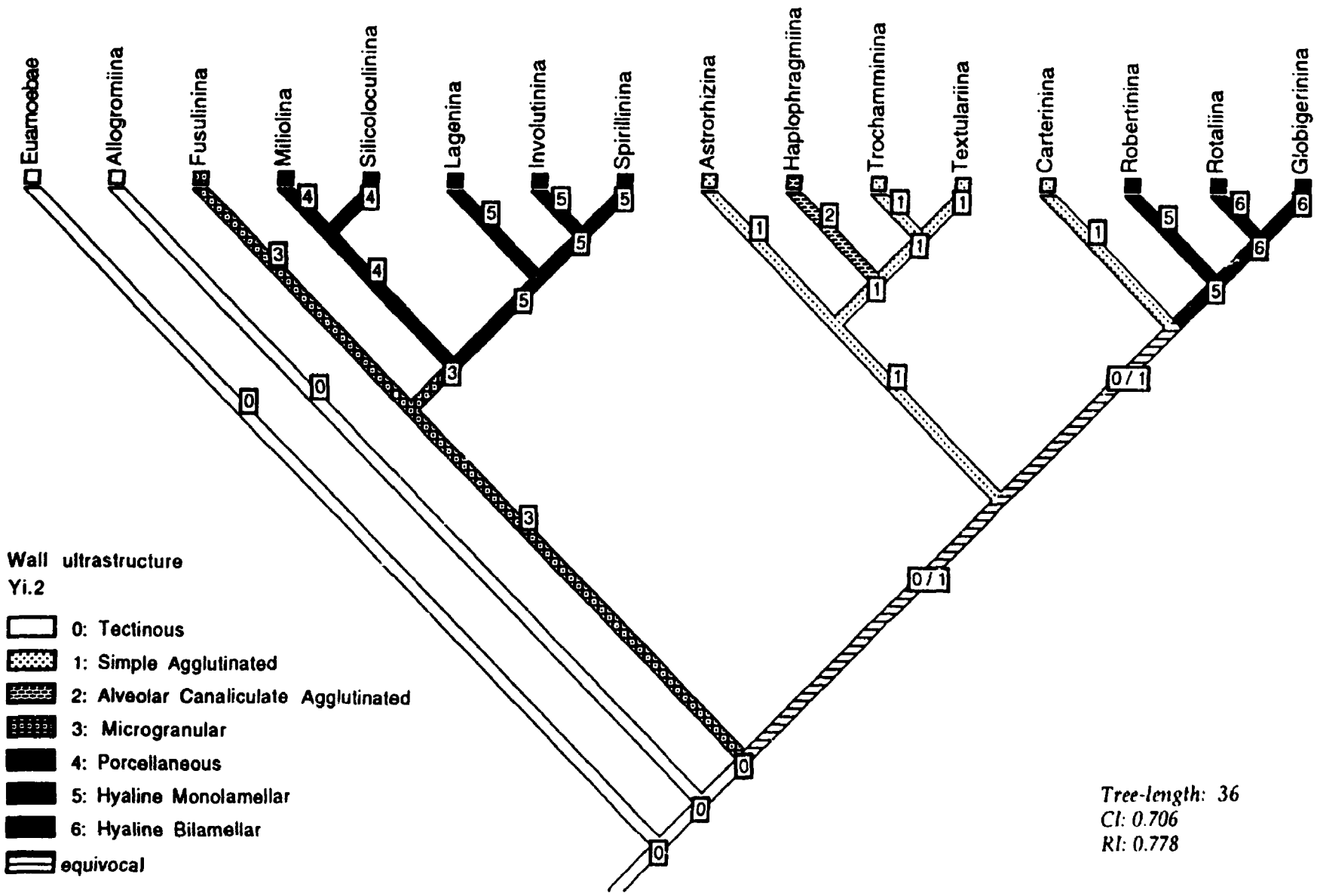


Figure 16. Hypothesis explaining subordinal foraminiferal evolutionary hierarchy of wall ultrastructure (character 4) based on the modelled Tappan and Loeblich tree. Numbers drawn on the tree show character state changes. This tree topology is the same as in Figures 14 & 19a.

wall ultrastructure (state 6) are the features of Rotaliina and Globigerinina.

Nevertheless, certain problems with these trees (i.e. Figures 14, 15 and 16) concern some character state evolutionary reversals incurred. For instance, aragonitic walls (3: 4->5) and monolamellar wall ultrastructure (4: 3->5) are recurrent states on the branches of Robertinina-Rotaliina-Globigerinina and Lagenina-Involutinina-Spirillinina. The perforation test (5: 0->1) occurr on the clades mentioned above twice. These cladograms provide taxon morphological quality but prove to be misleading about synapomorphic character state distribution; thus, it fails to fit CST1 and CST2 well.

The rest transformation series (i.e. characters 1-2 and 5-10) can be seen in Appendix IV.

Comparisons between OPT and OTL

Both mixed ordered analyses (i.e. OPT and OTL) used in the comparative studies conducted for this work have made certain assumptions about character evolution. Comparisons of OPT and OTL were made, assuming that foraminifera underwent a certain evolutionary road.

Ingroup comparisons

The 50% Majority-rule consensus tree OPT1 and one tree OTL were compared (Figure 17). In Figure 17a, the two tree diagrams were compared in original versions. The numbers on OPT1 are node labels indicating percentage consensus. Basically, they are similar in tree topology but are slightly different in some branches.

Figure 17b is a comparative tree diagram with some branches flipped to suit the comparative purpose. Having been flipped, some of the branches in both trees suggest similarity between the two trees in determining monophyletic groups, while some of them

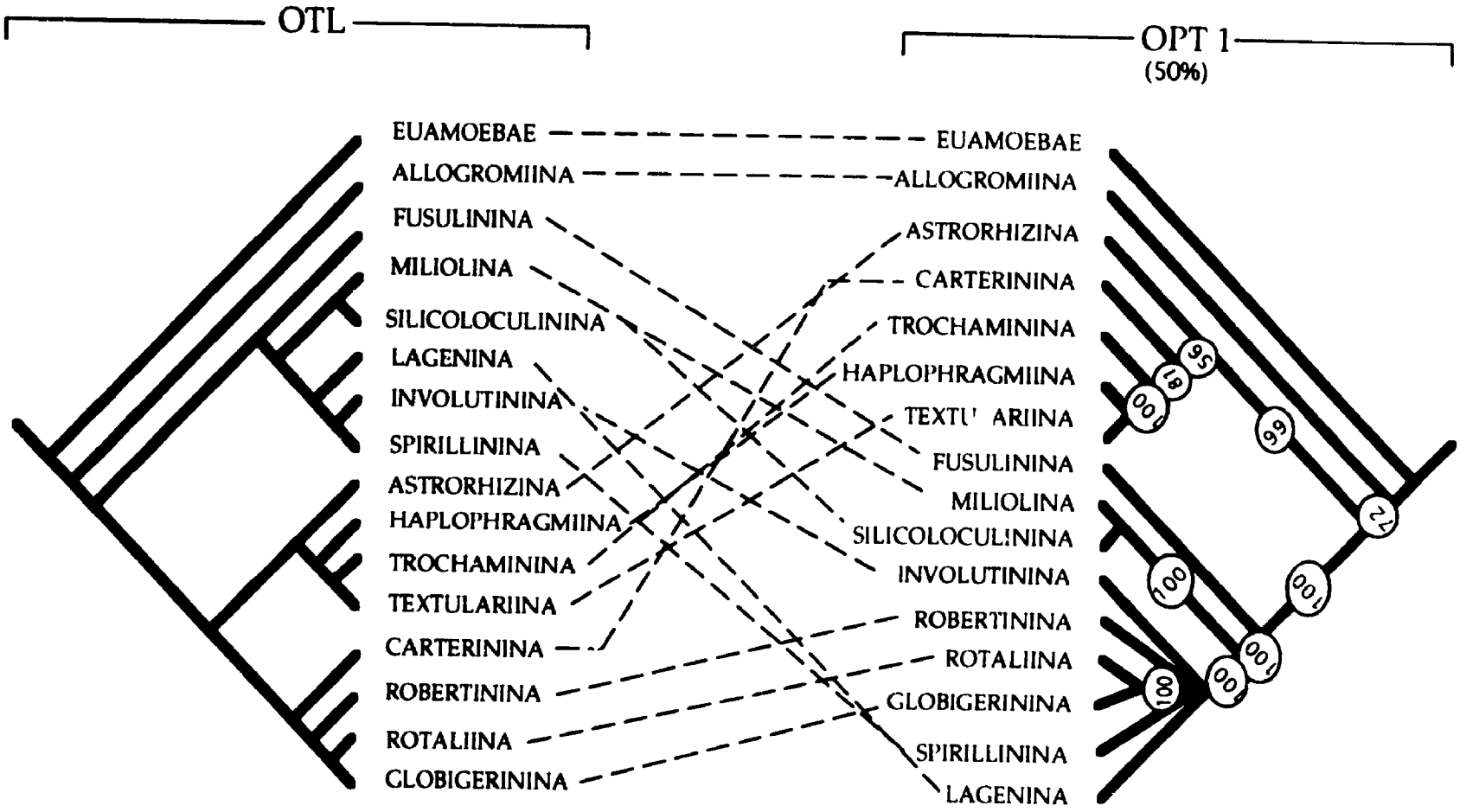


Figure 17a. Comparison of ordered Tappan and Loeblich tree (OTL) and ordered parsimony tree (OPT 1) of 50% Majority-rule consensus. Dashed lines indicate different evolutionary positions of the same suborder utilizing both taxonomic schemes. Numbers on the OPT show the percentage of the trees with branches that support that node (>50%).

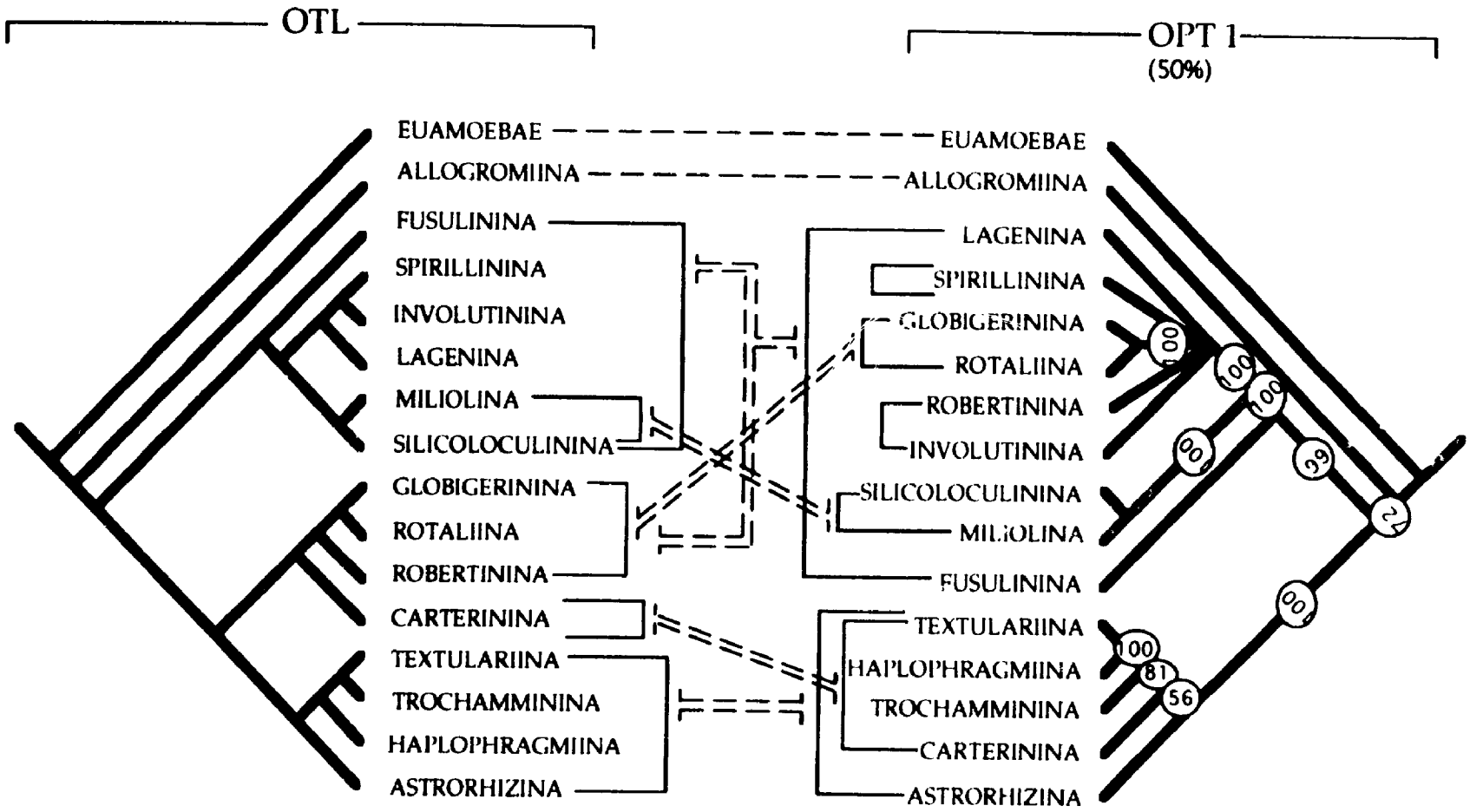


Figure 17b. Comparison of OTL and OPT 1 (50% Majority-rule consensus) after branch flipping (see Figure 17a). This topology allows direct comparison of monophyletic groups. Numbers on the OPT 1 show the percentage of the trees with branches that support that node (>50%).

are considerablely different. For instance, the four groups headed respectively by Astrorizina, Fusulinina, Miliolina and Rotaliina are independently positioned as ingroups (later defined as monophyletic groups in Chapter VI) on both OPT1 (50% Majority-rule) and OTL respectively, though the members of each ingroup on OPT1 are slightly dissimilar from OTL's group members.

The Carternina ingroup (Carterinina, Trochamminina, Haplophragmiina, Textulariina) being monophyletic on OPT1 is positioned just opposite the single taxon of the Carterinina group on OTL. This is the origin of the Carterinina group found in OPT are different from that of the OTL by the character comparison supposed. The Spirillinina group and the Involutinina ingroup (Involutinina and Roberetinina) are assumed to be monophyletic groups on OPT1 but ignored in OTL.

The comparative tree diagrams (Figures 18 and 19) adapted from Figures 6, 7, 15 and 16 show two ontogenic (wall composition and wall ultrastructure) cladogram comparisons. Figures 18a, 18b, 19a and 19b have shown how the ordered character states fit the different tree topologies.

The major discrepancies found between OPT1 and OTL are as follows: 1) the members of calcareous group such as Fusulinina, Miliolina, Silicoloculinina, Lagenina, Involutinina, Spirillinina, Robertinina, Rotaliina and Globigerinina to the multi-taxon in tree-bifid (i.e. OTL) are completely and uniformly separated, while, they are set together on the OPT; 2) in OTL, Involutinina were set apart from Robertinina, but they are inferred to be one composition ingroup (later defined as a monophyletic group in this study) in OPT, as evidenced, for instance, by the presence of aragonitic walls (character 3: state 5).

We quantify these differences with the trees to be the variation of character evolutionary pathways. That is, there may be some clades in the analysis on OPT that are supported by some good characters (unique within foraminiferal groups), while, there

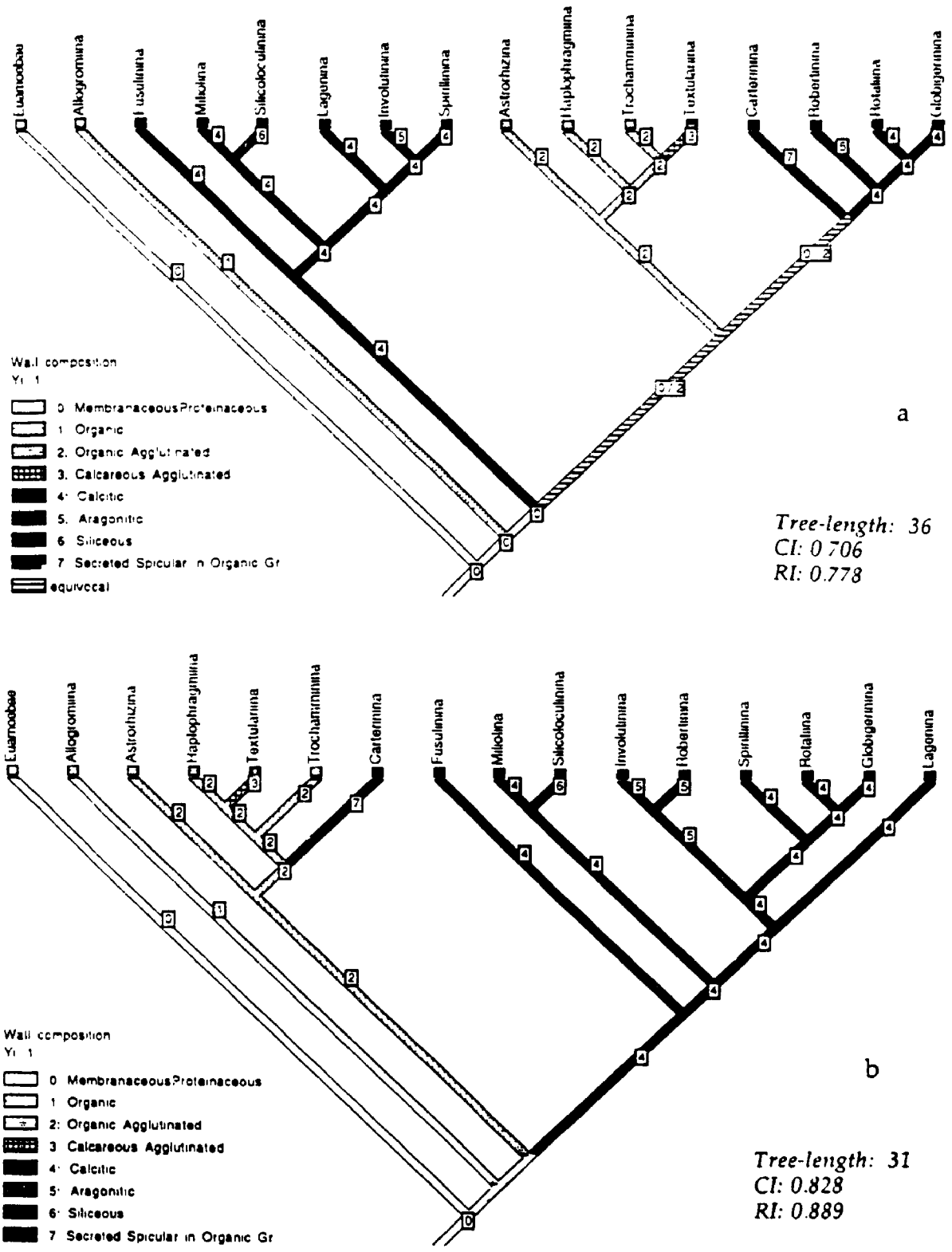


Figure 18. Comparison of evolutionary hierarchy of wall composition (character 3) between (a) tree modelled after Tappan and Loeblich (1988) and (b) the parsimonious results of this study. Circled numbers are states of wall composition. Figure 18a is the same as in Figure 15. Figure 18b is the same as in Figure 6.

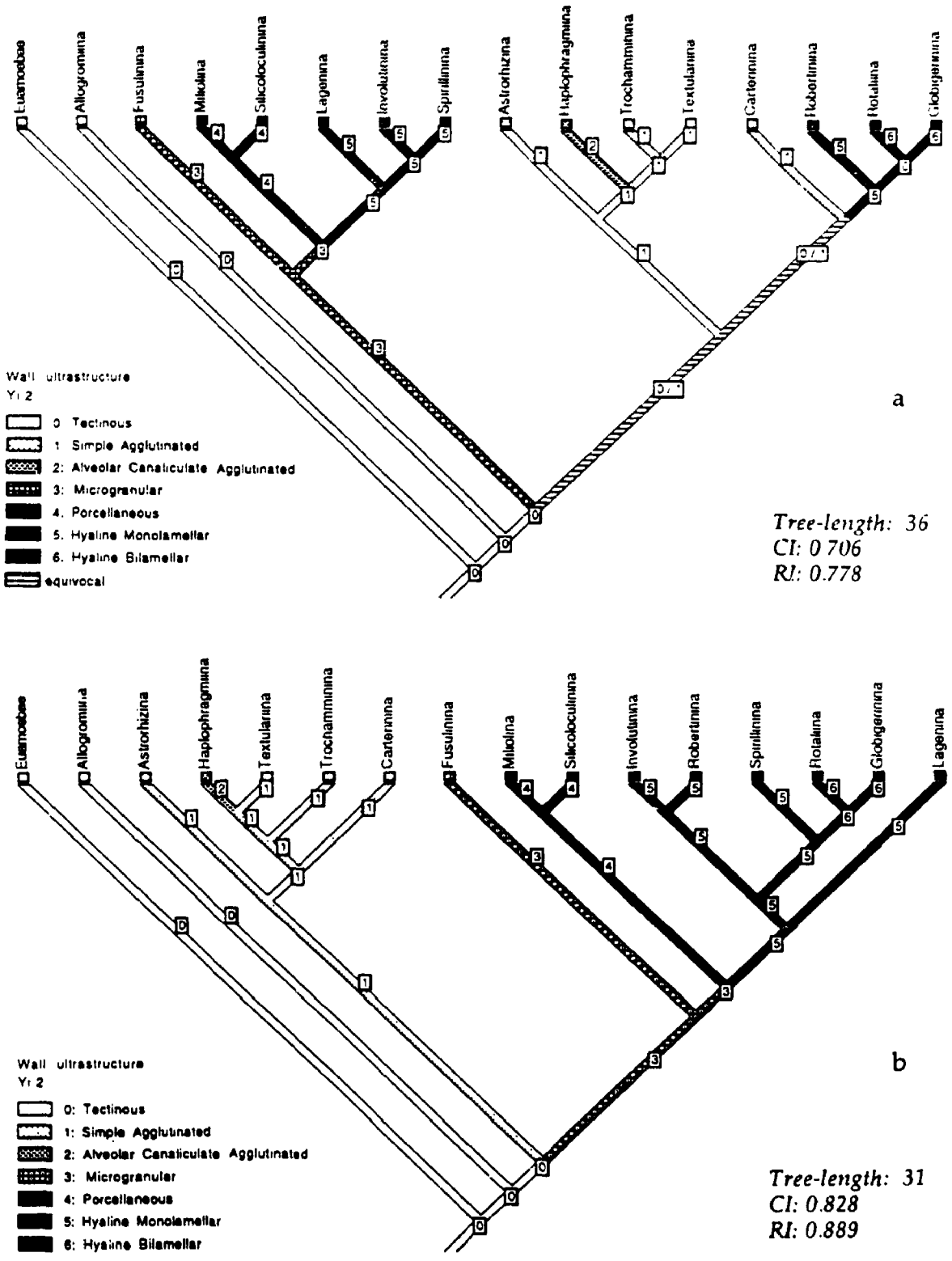


Figure 19. Comparison of evolutionary hierarchy of wall ultrastructure (character 4) between (a) tree modelled after Tappan and Loeblich (1988) and (b) the parsimonious results of this study. Circled numbers are states of wall ultrastructure. Figure 19a is the same as in Figure 16. Figure 19b is the same as in Figure 7.

may be some no good characters (good characters such as phylogenetic characters treated as convergence) that influence the clade building on the OTL. I would recommend that these parallel homoplasies be ordinarily kept in reservation for each iteration until they are no longer disjointed.

Comparisons of *CI* and *RI*

States 4 (calcitic walls) and 5 (aragonitic walls) of character 3 (see Figure 18a) and state 5 (hyaline monolamellar wall ultrastructure) of character 4 (see Figure 19a) are instances of parallel homoplasies in the data of OTL; such character states may not be a good indicator of group relationships. These homoplastic character states (i.e. no good character states) occur twice on the binary-fission tree forms (i.e. OTL) causing the separation of some branches (maybe clades), whereas they occur on the same branches on OPT (e.g. Figures 18b and 19b) only once.

In Figure 14 (i.e. OTL), state 1 of character 5 is also an example of homoplastic convergence, while, in OPT's, such character attributes are the phylogenetic characters (good conditions) which group the closest taxa together. In other words, they occur closely with a common ancestor and are thus homologous according to OPT, but not so in light of OTL.

The development and use of consistency indices underscores the realization that homoplasies are common in divergent taxa. Obviously homoplastic features on OTL are such characters as wall composition (character 3), wall ultrastructure (character 4) and test perforation (character 5) in terms of *CI* values, since the *CI* or *RI* values for these characters on OTL are less than 1.0. Consider the tabular analysis below: (For more details, see Appendices I, II and IV)

Table 4. Comparison of character states, step (s), *CI* and *RI* between OPT and OTL.

CATEGORIES		OPT						OTL		
		ORDERED			UNORDERED			ORDERED		
Character	States	Steps	CI	RI	Steps	CI	RI	Steps	CI	RI
1	2	1	1.00	1.00	1	1.00	1.00	1	1.00	1.00
2	2	1	1.00	1.00	1	1.00	1.00	1	1.00	1.00
3	**8**	**7**	**1.00**	**1.00**	**7**	**1.00**	**1.00**	**10**	**0.30**	**0.50**
4	**7**	**6**	**1.00**	**1.00**	**6**	**1.00**	**1.00**	**9**	**0.30**	**0.50**
5	**2**	**1**	**1.00**	**1.00**	**1**	**1.00**	**1.00**	**2**	**0.50**	**0.80**
6	6	3	0.67	0.50	3	0.67	0.50	3	0.67	0.50
7	2	2	0.50	0.50	1	1.00	1.00	2	0.50	0.50
8	6	5	0.80	0.80	4	1.00	1.00	5	0.80	0.80
9	**6**	**3**	**0.33**	1.00	2	0.50	0.50	**1**	**1.00**	**1.00**
10	6	2	1.00	1.00	2	1.00	1.00	2	1.00	1.00

The *CI* and *RI* values shown here indicate that the linear quantity and quality of the OTL (see Figures 18a and 19a) decrease with more homoplasies than those of the OPT (see Figures 18b and 19b), yielding higher overall consistencies.

The *CI's* for the features, such as character 3 (wall composition), character 4 (wall ultrastructure) and character 5 (test perforation), that are lower on OTL than that on OPT (e.g. mixed ordered parsimony and examplification of unordered parsimony) can be inferred as homoplastic states, including state 4 of character 3 (i.e. calcitic walls), state 5 of character 3 (i.e. aragonitic walls) and state 1 of character 5 (perforation test); they are parallel reversals. The examination of the above table suggests: 1) for the character 3, 7 steps (minimun steps: *CI*=1.00) occur for 8 states on OPT, meaning phylogenetic ordering, while 10 steps (homoplastic convergence: *CI*=0.30) occur for 8 states on OTL --

3 steps longer than that of OPT; 2) for the character 4, on OPT, 6 steps (minimun steps: *CI*=1.00) occur for 7 states (phylogenetic ordering), while 9 steps (homoplastic convergence: *CI*=0.30) occur for 7 states on OTL -- 3 steps longer than that of OPT; 3) for the character 5, 1 step occurs (minimun steps: *CI*=1.00) for 2 states (non-additive) on OPT, while 2 steps (homoplastic convergence: *CI*=0.50) occur for 2 states on OTL -- 1 step longer than that of OPT. The character 9 (chamber shape) is a homoplasric feature in OPT -- 2 steps longer than that of OTL.

The relation formula between CI_{OPT} and CI_{OTL} is concluded below (we suppose that $m_{i\ OPT}$ equals to $m_{i\ OTL}$, i.e. $m_{i\ OPT} = m_{i\ OTL}$, and $w_i = 1$, based on the same state numbers of each character on both trees, and equalized character weighting.):

$$1.00 \geqslant CI_{OPT} = \frac{\sum_{i=1}^{n} S_{i\ OTL}}{\sum_{i=1}^{n} S_{i\ OPT}} CI_{OTL} \geqslant CI_{OTL} = \frac{\sum_{i=1}^{n} S_{i\ OPT}}{\sum_{i=1}^{n} S_{i\ OTL}} CI_{OPT}$$

$$\left(\quad CI_{OPT} = \frac{\sum_{i=1}^{n} w_i m_{i\ OPT}}{\sum_{i=1}^{n} w_i S_{i\ OPT}} ; \quad CI_{OTL} = \frac{\sum_{i=1}^{n} w_i m_{i\ OTL}}{\sum_{i=1}^{n} w_i S_{i\ OTL}} \right)$$

Calculated from the *CI* index inequality above, OPT (e.g. Figures 18b and 19b) produces a consistency index (excluding uninformative characters) of 0.828, indicating that this tree exhibits synapomorphies (83%), with homoplasies (17%). Compared with OTL (e.g. Figures 18a and 19a), which shows a 0.706 consistency index, the percentage of synapomorphies on OPT is 71%, with 29% homoplasies.

It appears to be reasonable to use such consistency or retention indexes in evaluating OTL against our unordered parsimony trees (*CI's* are listed underlying the OPT in Table 4) because assumptions inherent in hypotheses of ordered and unordered

trees render the datasets themselves fundamentally similar (or same) to each other. In addition, different "g" values existing in OPT (two forms) and OTL might control *CI* and *RI* values equally.

Comparisons of tree length

Both trees are built up using the same assumptions and same data. The length of the OTL is 36, while that of the OPT is 31. Their difference in tree length is 5 steps. As mentioned earlier, the tree reconstructed under the same presupposition with the shortest length is the one in which the actual common ancestral relationships between the taxa are best estimated. Therefore, judging from the data available, the OPT is more advisable than the OTL.

To put this another way, the unordered parsimony (underline the OPT in the Table 4) can also be compared to observe the homoplastic variations. The unordered parsimony trees that exhibit a non-sequential character state change have a higher consistency index (0.93) and retention index (0.92) for the whole tree. They also show their shorter tree length (Length=28), which is 3 steps shorter than that of the mixed parsimony, and 8 steps shorter than that of OTL. In addition, unordered OTL has shorter tree length of 32 than ordered one of 36, *CI* (0.800) in unordered OTL (it is not counted in Table 4, see Appendix III) yields higher values than *CI* (0.706) of ordered OTL (note: *RI*=0.769 of unordered OTL is lower than *RI*=0.778 of ordered OTL). It should be noted that ordered characters undergoing sequential character state changes exhibit homoplasies in the intermediate states. This results in a lower *CI* or *RI* and relatively longer tree length for the whole tree. As analyzed so far, investigated in the same manner with the same datasets as done for OPT, OTL produces much longer tree length due to its inadequate determination of the fitness of characters (homoplastic attributes) to the tree topology (e.g. Figures 14, 15 and 16).

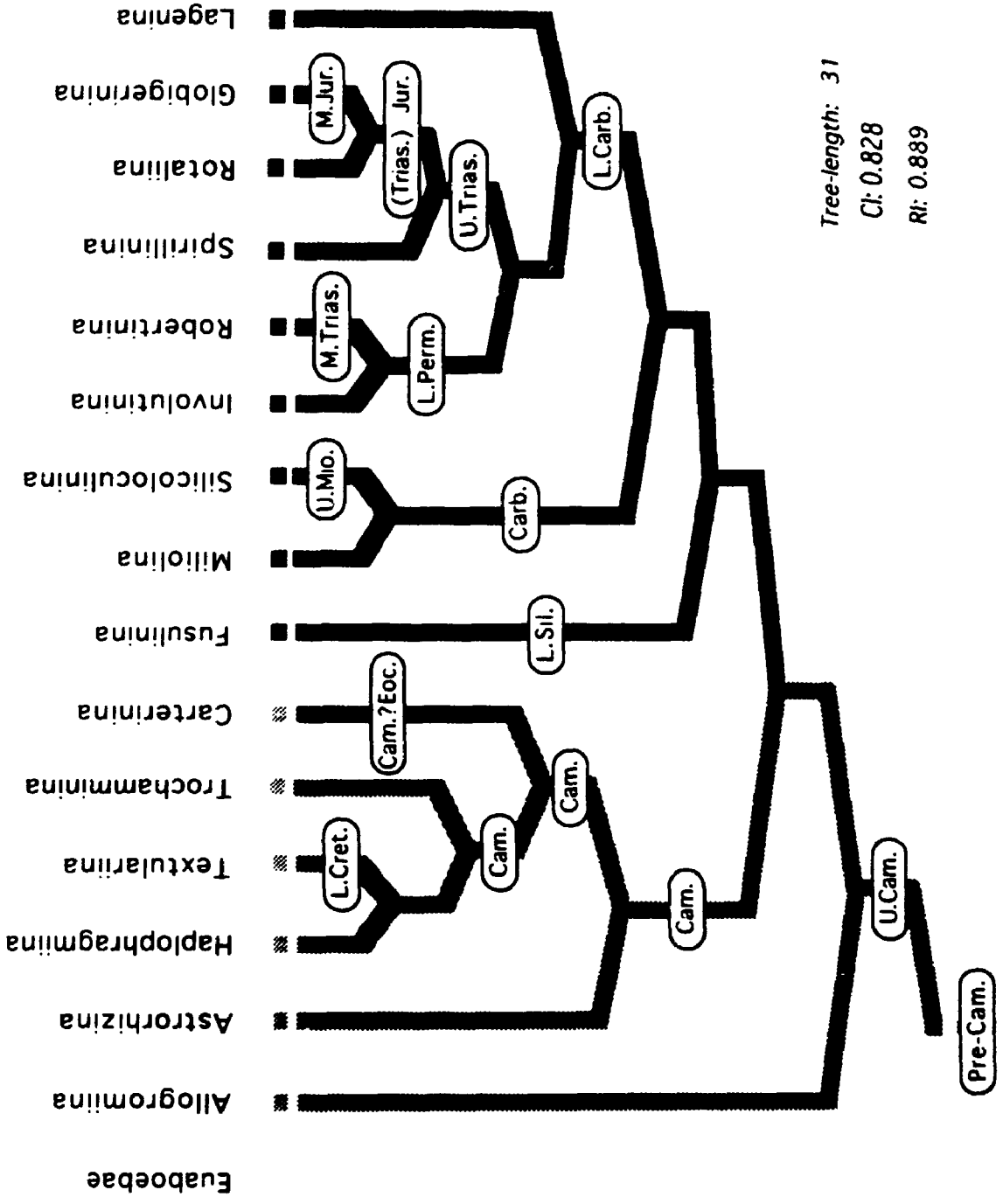


Figure 20. OPT 4 (Ordered Parsimony Tree 4) -- Tree derived from the OPT 3 presents the optimal foraminiferal subordinal phylogeny. Horizontal labels on the branches show the geological origin of each suborder.

Concluding Remarks: Selecting the Optimal Parsimony Tree

The major advantage of OTL seems to lie in its capacity for revealing the polarity of character state changes and relating some natural foraminiferal groups. The disadvantages of OTL are its longer tree length, more homoplasies, lower *CI* and *RI* values, and good characters (unique within foraminiferal groups), which are treated as convergence. What has been discussed so far suggests that both the mixed parsimony and unordered parsimony exploited in this work may offer feasible hypotheses for explaining character evolution in the given data at hand, and that the tree (OPT) established on the mixed parsimony (based on the CST1 and CST2) may be considered as the optimal phylogeny tree in the set of rival trees. On OPT4 (Figure 20, one type of the optimal tree), the geological origin of each suborder has been plotted in order to observe the tree in more perspectives. This tree, to be fully justified as a new model, will be further discussed together with other OPT's in Chapter VI.

CHAPTER VI DISCUSSION

The Aims of This Chapter

Chapter V represents a process of choosing an optimal parsimony tree through a series of comparisons. This chapter serves to expound the phylogenetic relationships between foraminiferal suborders, and delineate certain monophyletic groups in fossil lineages. Before going into any part in detail, the classification criteria will be restated. First, we shall concentrate on defining the root of the phylogenetic tree of foraminiferal suborders. The Euamoebae as the most primitive ancestor of the foraminifera will be assumed. Second, we shall see how the determination of monophyletic groups in the Foraminiferida can be justified. Third, foraminiferal monophyly within the fossil lineages will be sketched. Finally, a few reflections and implications arising from our discussion will be presented as concluding remarks.

Phylogenetic Relationships between Foraminiferal Suborders

The decision on choosing the optimal phylogenetic tree has to rely on the results of a character analysis. Most systematists prefer to take one phylogeny of certain groups as self-evident. Wiley (1981 and 1987), for example, incorporated his optimal tree as an axiom of the phylogenetic system. In reality, there cannot be two trees of the same taxa that are both true to the actual evolutionary process, but there can be two equally possible hypotheses. It is then deduced that different inferences are allowed to trail a certain phylogenetic pattern. The problem is how to postulate on that pattern with any accuracy.

The two hypotheses analyzed in this article were both erected for the conceptual reconstruction of the optimal subordinal foraminiferal phylogeny: OPT and OTL.

Throughout Chapter V, some assumptions about character state changes were made as an endeavor to reconstruct foraminiferal relationships, and one tree (OPT) was sifted out as an argument against the Tappan and Loeblich tree (OTL). The point to be emphasized here is that what underlies the mixed ordering analysis used to set up the optimal phylogenetic tree is the principal approach followed throughout this research: cladistics.

Cladistics, representing classification graphically, uses phylogenetic techniques to infer common ancestry, and excludes polyphyletic groups. The classification using cladistic methods is believed to be an estimate of phylogeny, and hopefully informative regarding the common ancestral relationships of the groups classified. For example, evolutionary taxonomists and early phylogeneticists categorized "wall composition" or "wall ultrastructure" as important featuring characters. Cladistic phylogeneticists inherited these featuring concepts and stratify them to such distinguishing states as shared derived and unshared derived apomorphies. By doing so, they expect to explore the process of shared derived character evolution. The cladistic classification, as we have seen earlier, is capable of producing tree structures that are entirely grouped in a close set with short tree length and high *CI* resolution.

The fact is that Tappan and Loeblich's tree shows noticeable homoplasies for some characters and that their tree length is considerably longer. Their tree seems slightly arbitrary: it might be somewhat intuitive; or it might be phylogenetic.

The cladistic approach followed in this study can provide more feasible solutions to the problems of research on character evolution, and thus may be used to better clarify the questions about common ancestral relationships of the subordinal foraminifers. The following discussions concern a set of OPT's [Figures 5, 6, 7, 8A:a-b, 8B:a-b, 8C:a-b, 8D:a-b, 9 and 20], where the monophyly of the subordinal foraminifera are best defined.

Outgroup --Euamoebae

Assuming that Euamoebae (originating in the Pre-Cambrian) represent the outgroup, the most parsimonious arrangement has been shown in Figures 5, 6, 7, 8A-8D, 9 and 20. The assumption of Euamoebae as the outgroup with plesiomorphic character states is consistent with the morphologic evidence -- i.e. *shelllessness, lobose/filose pseudopods, membranaceous/proteinaceous walls, tectinous wall ultrastructure, non-perforate walls, spherical shape, unilocular chambers, simple chamber arrangement, globular/ovate chamber shape* and *smooth surface*. The plesiomorphic character states of Euamoebae would have been ancestral to the foraminifera. This has been marked as the root of the cladogram.

Allogromiina group

Loeblich and Tappan (1964 and 1987) and Tappan and Loeblich (1988) justifiably consider that Allogromiina are the most primitive foraminiferal suborder due to their chitinous tests; hence, they distinguish the group from other arenaceous taxa. Yet, by delving deeper, we may find that Allogromiina could not be the ultimate ancestor of the Foraminiferida. The shared derived character evidence reported in Chapter V suggests that Allogromiina evolved from Euamoebae through three derived character states --- *shell presence, granuloreticulose pseudopods* and *organic walls*. The kinship between them can be confirmed by Euamoebae's seven plesiomorphies bequeathed to Allogromiina --- *tectinous wall ultrastructure, non-perforate tests, spherical test shape, unilocular chambers, simple planispiral chamber arrangement, globular/ovate chamber shape* and *smooth test surface*. This observation of homologous characters indicates that Allogromiina may have evolved from Euamoebae about 600 million years ago, even though this group has had a poor fossil record. It is a useful second outgroup for the purpose of character state polarization in the cladistic studies.

Astrorhizina group

Astrorhizina are characterized by two derived states (i.e. organic agglutinated walls and simple agglutinated wall ultrastructure), eight inherited states including shell presence and granuloreticulose pseudopods, and some plesiomorphies (state 0 of character 5-10) from Allogromiina. This suborder is characterized by such repeated characters as organic agglutinated walls that link to Carterinina and its own descendants like Trochaminina, Haplophragmiina and Textulariina ingroups.

Besides shell presence and granuloreticulose pseudopods, Astrorhizina share two character states (i.e. non-perforate shells and globular/ovate chamber shape) with Trochaminina, Haplophragmiina and Textulariina; they only share organic agglutinated walls with Trochaminina and Haplophragmiina. Astrorhizina are therefore considered to be the most primitive group with agglutinated walls in the clade (Astrorhizina group). Loeblich and Tappan (1989) have made a similar inference.

Trochamminina, Haplophragmiina and Textulariina share three derived character states -- pyriform/ovate/globular test shapes, multiserial/trochospiral chamber arrangement and fissured/pitted/nodose test surfaces. Haplophragmiina and Trochaminina share organic agglutinated walls, pyriform/ovate/globular test shapes, multilocular, multiserial/low/high trochospiral chamber arrangements, and fissured/pitted/nodose surface sculpture; so they are closely related. The alveolar canaliculate agglutinated wall ultrastructure of Haplophragmiina stands for an apomorphic state and signals their derivation from Astrorhizina and Trochamminina. It suggests that Haplophragmiina are more advanced than Astrorhizina and Trochaminina.

Textulariina share the simple agglutinated wall ultrastructure with Trochaminina and Astrorhizina. The most parsimonious interpretation of Textulariina's calcareous agglutinated walls implicates their autapomorphic attribute: this test morphology must have evolved from the organic agglutinated walls found in the other agglutinated-wall

groups. Textulariina differs from Haplophragmiina and Trochaminina by presenting such apomorphic character states as elongate test shape and uniserial chamber arrangement.

Carterinina group

Loeblich and Tappan (1964) and Tappan and Loeblich (1988) describe Carterinina as being characterized by an organic inner lining similar to those found in Textulariina. OPT3 indicates the plesiomorphies and apomorphies Carterinina inherit or share with Trochamminina, Haplophragmiina and Textulariina; OPT4 presents Carterinina's congruent relationships with Trochamminina, Haplophragmiina and Textulariina. It seems evident that Carterinina inherited homologous non-perforate tests, spherical test shape, globular/ovate chamber shapes and a smooth test surface from Astrorhizina. The secreted spicular on organic groundmass walls in Caterinina may be a derived character state from organic agglutinated walls of Astrorhizina; th· ·efore, Carterinina could be identified as the offspring of Astrorhizina.

If viewed from different perspectives, Carterinina share one apomorphy with Trochamminina and Textulariina (i.e. simple agglutinated wall ultrastructure), three apomorphies with Trochamminina and Haplophragmiina (i.e. simple agglutinated wall ultrastructure, trochoid test shape and trochospiral chamber arrangement), and one apomorphy with Trochamminina, Haplophragmiina and Textulariina (i.e. fissured/pitted/ nodose test surface); consequently, it can be inferred that Carterinina are closely associated to the clade of Trochamminina, Haplophragmiina and Textulariina, especially to Trochamminina. In the Carterinina the conical chamber shape and secreted spicular in the organic groundmass of their test walls can be recognized as autapomorphic character states from the agglutinated-wall groups.

Stratigraphic problems raise the argument as to how Carterinina (earliest fossil record in the Eocene) gave rise to groups with older fossil records (e.g. Trochamminina

and Haplophragmiina, ranging from Cambrian to Holocene; and Textulariina from Early Cretaceous to Holocene). If viewed on OPT's, Carterinina appear to be just a suborder derived from Astrorhizina; in this consideration, the problem with dating Carterinina in the fossil record should be easy to clarify.

There seems to be no clear phylogenetic evidence available to support the classification of Carterinina with Haplophragmiina, Trochamminina and Textulariina as a monophyletic group sharply distinct from Astrorhizina. Carterinina differ from Astrorhizina in their autapomorphic character -- i.e. the secreted spicular in organic groundmass on their walls. Multilocular chambers are found in all suborders other than Astrorhizina and considered homoplastic. Carterinina share an apomorphic state with Haplophragmiina and Trochamminina (i.e. trochospiral chamber arrangement), but not with Textulariina and Astrorhizina, while Haplophragmiina and Trochamminina have the same derived trochoid test shape and fissured/pitted/nodose surface sculpture.

On the basis of the research done for this dissertation, it appears to be justifiable to include Carterinina, Haplophragmiina, Trochamminina and Textulariina in an ingroup designated after Carterinina. Here, it might be assumed that this is a monophyletic group as an autapomorphic member that originated from Astrorhizina.

Furthermore, based on our recognitions, Carterinina and each other suborder of the Carterinina ingroup (i.e. Haplophragmiina, Trochamminina and Textulariina) may have arisen as an independent monophyletic group from Astrorhizina in the Cambrian period.

The third possibility is that Carterinina may have originated from any more primitive ancestor other than Astrorhizina, and might have evolved in parallel with Astrorhizina. However, no sufficient fossil record of Carterinina is available to verify our inferences. This may suggest that Carterinina is merely an underevolved small suborder.

Fusulinina group

As Tappan and Loeblich (1988) point out, Fusulinina probably arose from Astrorhizina. They observe that the Fusulinina group of nine suborders appeared in the Late Silurian with the development of the ability to secrete walls of apomorphous or spicular calcium carbonate. Fusulinina, according to Tappan and Loeblich, inherited some plesiomorphies from Allogromiina, such as non-perforate tests, globular/ovate chamber shapes and smooth test surfaces.

However, as revealed in this study, the calcitic walls, microgranular wall ultrastructure, fusiform test shape and planispiral involute/evolute chamber arrangement of Fusulinina are character states derived from their pre-existing stage, when Allogromiina, Astrorhizina, Trochamminina, Haplophragmiina and Textulariina were rampant (i.e. abundant).

Various calcareous shells found in all fusulinid descendants may have evolved from chitinous schemes with the development of an autapomorphic microgranular ultrastructure. The root stock of the calcareous foraminiferal community evolved during the 213 million year time span, when Fusulinina flourished.

Fusulinina and their descendants (i.e. the Fusulinina group) are a calcareous monophyletic group. Members of this group also share a set of common ancestral states, such as pyriform/ovate test shapes, multilocular and planispiral involute/evolute chamber arrangements, as well as globular or ovate chamber shapes.

These character states are likely to be unique to the Fusulinina group, not shared with any other taxa outside this group (e.g. Astrorhizina group). Such peripherally keeled and punctate surface sculptures are only found in some calcareous suborders within the Fusulinina group. Consequently, the Fusulinina group is a monophyletic group, which may be tracked back to Allogromiina and have evolved parallelly to Astrorhizina.

Miliolina + Silicoloculinina group versus Lagenina group

Miliolina and Silicoloculinina inherited non-perforate tests, a smooth test surface and unilocular chambers from Fusulinina, but calcitic walls are a character state shared by Fusulinina and Miliolina. Miliolina and Silicoloculinina share two phylogenetic features -- porcellaneous wall ultrastructure and milioline chamber shape. It is presumed that the porcellaneous ultrastructure identifiable among both groups is synapomorphic evidence supporting monophyly attribute. The assumption that Silicoloculinina evolved directly from Miliolina has been based on the autapomorphic siliceous compositions somehow evolving from calcitic tests. It might be worth mentioning that some apomorphies of Miliolina and Silicoloculinina are also shared by Spirillinina, which will be discussed later.

The inclusion of Lagenina in the Fusulinina group is made possible by their sharing such character states as calcitic walls. As determined by their partitioning (e.g. OPT3), Lagenina is closely associated to the clade of Fusulinina, Miliolina and Silicoloculinina.

Lagenina's hyaline monolamellar ultrastructure is deemed to have a parallel evolutionary relationship with the porcellaneous walls of Miliolina that evolved from the microgranular shells of Fusulinina. The hyaline monolamellar ultrastructure of Lagenina may be assumed to have evolved from microgranular shells (Fusulinina). With Miliolina, Lagenina not only share calcitic walls, but also unilocular chambers, planispiral involute/evolute chamber arrangement and smooth test surface.

However, in the process of evolution, Lagenina seem to occupy a position distinct from that of Miliolina. Lagenina derived their hyaline monolamellar wall ultrastructure from the microgranular wall ultrastructure of Fusulinina, which Miliolina do not share. Planispiral chambers are shared by Lagenina, Fusulinina, Involutinina, Robertinina, Rotaliina and Globigerinina, signaling the close connections between these suborders. Yet, such chambers cannot be identified among Miliolina. The monolamellar shell,

perforation, palmate chamber shape, ribbed/costate/reticulate surface sculpture and test peripheral keel are the autapomorphic characters of Lagenina, indicative of the possibility that Lagenina evolved as a monophyletic group from Fusulinina and that their evolution was more advanced than that of Miliolina.

Involutinina +Robertinina group

In the past, Involutinina and Robertinina were regarded as loosely related taxa (e.g. Figures 1, 14, 15 and 16, Tappan and Loeblich, 1988). That is, Involutinina were assumed to have been derived directly from Fusulinina due to their overall similarity in wall composition and test shape (i.e. calcareous wall composition and tubular enrolled test shape). In view of their similar test shape and non-perforate shell, Robertinina probably arose from Trochamminina --- "subdivision of Textulariina", in Tappan and Loeblich's (1988) terms. In fact, these homoplastic features are merely the nonhomologous structures caused by adaptable convergence.

OPT3 shows Involutinina and Robertinina as an independent clade: both share highly modified synapomorphies (i.e. aragonitic walls and hyaline monolamellar walls). This independent clade shares one apomorphy with Lagenina and Spirillinina (i.e. hyaline monolamellar wall ultrastructure), one apomorphy with Fusulinina, Lagenina, Rotaliina and Globigerinina (i.e. planispiral involute/evolute chambers), and one with Lagenina, Spirillinina, Rotaliina and Globigerinina (i.e. perforate tests). Both Involutinina and Robertinina inherited such ancestral states as spherical test shape and smooth test surface from their ancestors, Fusulinina and Miliolina; both of them inherited multilocular chambers from their older ancestors. Hence, Involutinina and Robertinina are assumed to be a monophyletic group because their synapomorphies are not shared with other taxa placed outside the group.

Involutinina are characterized by a hyaline perforate aragonitic test with lamellar thickenings that seem to be more homologous to those characterizing microgranular ultrastructures. Generally, their fibrous aragonitic walls are not well preserved, but their recrystallized aragonitic scheme seems to be more homogenous with recrystallized monolamellar walls observed in Lagenina (Loeblich and Tappan, 1964). The wall of Robertinina is characterized by pseudohexagonal or hexagorhombic twins of aragonite and by hyaline perforate microstructure whereby the glassy tests are built or radically arranged (Loeblich and Tappan, 1964). Twinned pseudohexagonal and hexagorhombic aragonite walls have been considered to be more advanced than fibrous aragonitic character and to have independently evolved from the calcitic walls (Loeblich and Tappan, 1964, Tappan and Loeblich, 1988). This suggests that Robertinina may have been derived from Involutinina rather than Textulariina.

Spirillinina group

Spirillinina share at least five apomorphies with Involutinina -- hyaline monolamellar walls, perforate tests, spherical or pyriform/ovate/globular test shapes, lenticular or tubular chamber shapes and a smooth test surface. Spirillinina also share hyaline monolamellar wall ultrastructure with the Involutinina/Robertinina clade; they are the sister group of this clade. The trochospiral chambers and peripherally keeled surface ornamentation of Spirillinina are their derived apomorphies. The trochospiral chambers of Spirillinina are apomorphies derived from globular/ovate chamber shapes featured in Involutinina and Robertinina, and conical/lenticular or tubular chamber shapes of Spirillinina may evolve from Involutinina solely. Therefore, Spirillinina are considered species derived from Involutinina and Robertinina. Spirillinina form the sister group of Rotaliina and Globigerinina due to their sharing of such apomorphies as hyaline calcitic walls, perforate tests, spherical/pyriform/ovate/globular test shapes, multilocular and low

or high trochospiral chamber arrangements. Spirillinina also share two apomorphies with Rotaliina -- i.e. conical and lenticular or tubular chamber shapes, and smooth peripherally keeled ornamentation.

Eventually, the derived character states shared by Spirillinina with Rotaliina or Globigerinina indicate that Spirillinina are a set closer to Rotaliina and Globigerinina than to the Involutinina/Robertinina clade. Considering all this, Spirillinina have to be identified as monophyletic.

Rotaliina + Globigerinina group

Rotaliina (94 families) are characterized by a hyaline bilamellar wall. This type of test, easily recognized due to the thick-walled early chambers and the single bilamellar walls of the final chamber, is assumed to be more advanced than monolamellar wall types, implying that hyaline bilamellar walls might be derived from hyaline monolamellar walls. This has also been recognized by Loeblich and Tappan (1964), Tappan and Loeblich (1988).

Globigerinina (23 families) are planktic foraminifera, living within the water column. This group is closely related to the benthic Rotaliina as they share a series of synapomorphies: i.e. calcitic walls, hyaline bilamellar walls, perforate tests, ovate or globular/elongate/trochoid test shapes, radiate chamber array such as spherical/ pyriform, multiserial/planispiral involute chamber arrangements, and punctate/rugose/ hispid surface sculpture. The planktic spine surface sculpture of Globigerinina is an autapomorphy, which can be traced back to the punctate or hispid ornamentation of Rotaliina.

Rotaliina and Globigerinina also share calcitic walls with Fusulinina, Miliolina, Lagenina and Spirillinina, and inherited perforate tests and multilocular chambers from their older ancestors. Rotaliina and Globigerinina seem to be more associated with

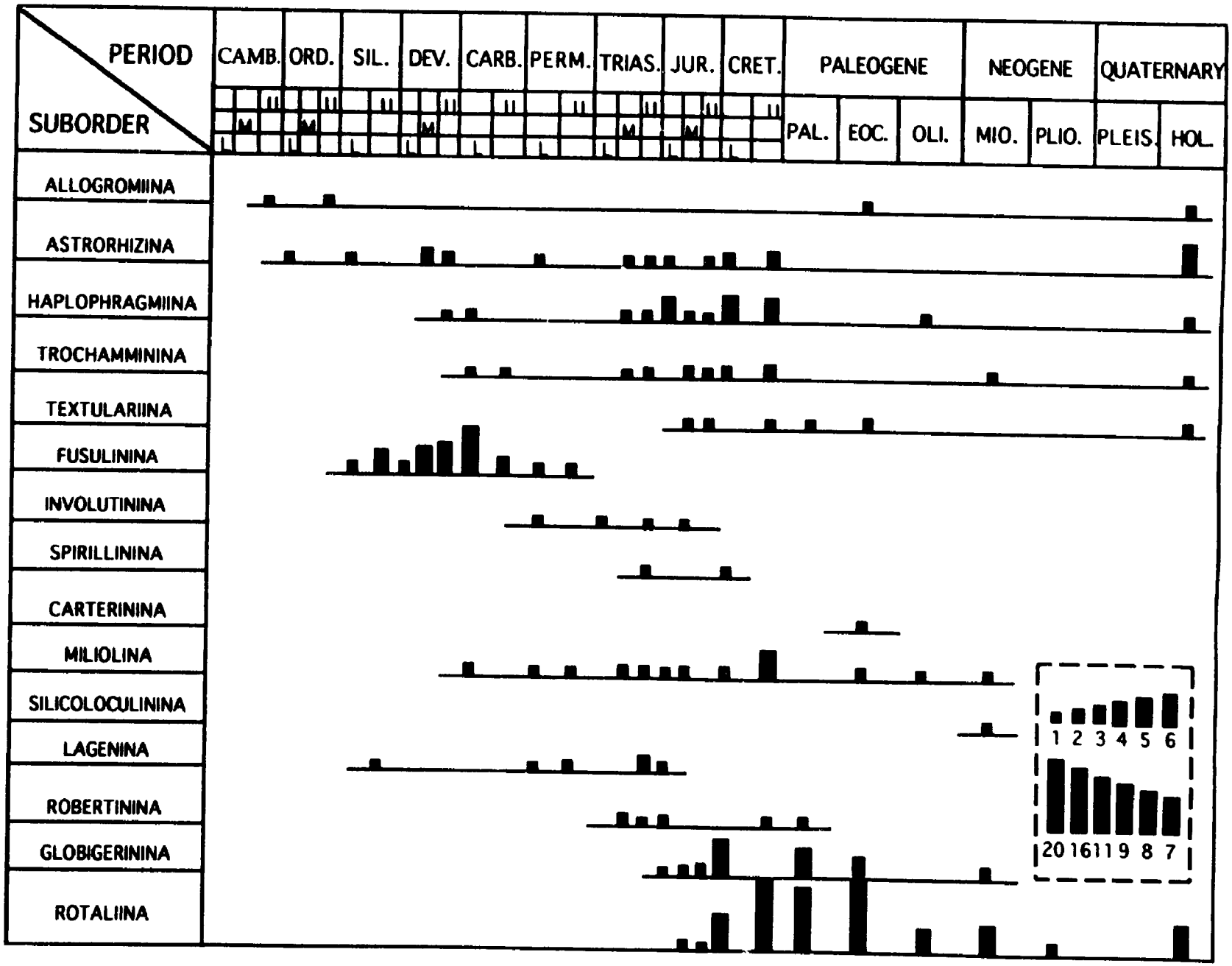
Spirillinina. They share calcitic walls and trochospiral chambers with Spirillinina, and their hyaline bilamellar chambers stem from the latter's hyaline monolamellar wall ultrastructure. Spirillinina then may be considered as the ancestors of Rotaliina and Globigerinina. Considering all this, it should be reasonable to identify Rotaliina and Globigerinina as a monophyletic group.

Monophyletic Groups in Fossil Lineages

The analysis of monophyletic groups in fossil lineages can enhance the use of information on foraminiferal phylogeny. The knowledge of subordinal longevity with their family diversity provides evidence as to ancestral relationships among members of monophyletic groups, especially when detailed results of primitive and derived character analyses are combined with respect to their homologues in the fossil record. Both comparative morphology and fossil lineages of suborders are used extensively here as a basis for deriving phylogenetic inferences. The formation of monophyletic groups represents not only the result of an organic internal biological differentiation, but also the interaction of organisms with the ecological system that they inhabit over long geological time spans. During the Phanerozoic, great changes in the environment (i.e. oceanic circulation, temperature variation, salinity, bioturbidity, nutrient supply, symbionts and eustasy of sea) have taken place. This has ultimately resulted in higher diversification and speciation of monophyletic groups.

Foraminifera have undergone several phases of evolutionary radiation since the Early Cambrian. Loeblich and Tappan (1964), Tappan and Loeblich (1988) and Ross and Haman (1989) plotted the stratigraphic ranges of many of these suprageneric taxa. Table 5, taken from Loeblich and Tappan (1987), and Ross and Haman (1989), is an outline of the family origins of all foraminiferal suborders with their longevity. Agglutinated foraminifera diverged in the Paleozoic greatly increasing in diversity by the Middle to the

Table 5. Distribution of foraminiferal family originations over geologic range of each suborder (modified after Loeblich and Tappan, 1987). Geological time scale after Boggs (1987).



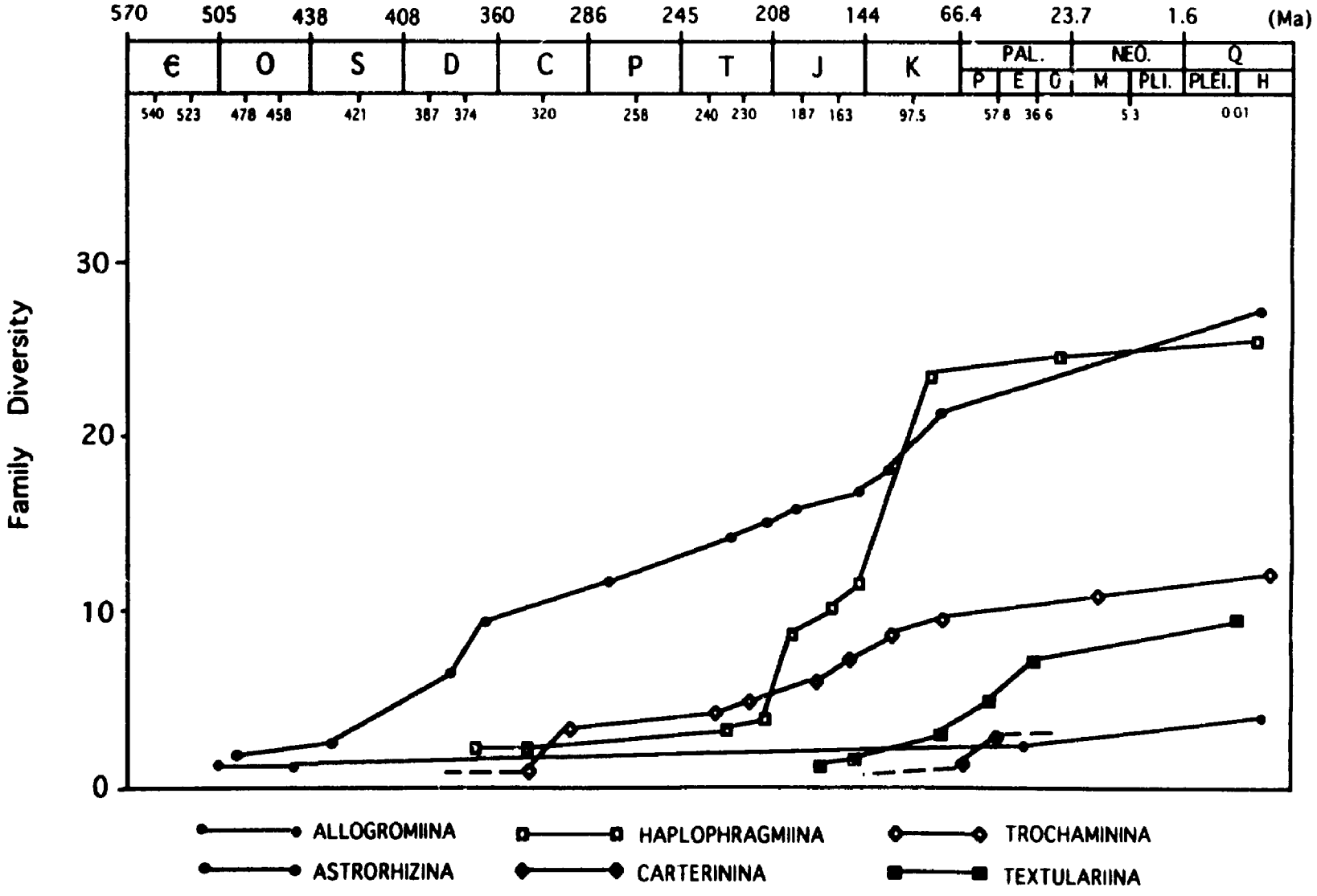
Late Mesozoic. Calcareous benthic foraminifera underwent steady growth in the Paleozoic and increased in the Cenozoic. Family diversity of planktic foraminifera prompted a major diversification during the Late Cretaceous and the Eocene.

Figure 21, based on the data from Table 5, shows the frequency of family diversity for each suborder over geological time. The Paleozoic Era is associated with high productivity of both organic and agglutinated tests in both free-living and attached surface dwellers (Figure 21a). Allogromiina diversified slightly since the Late Cambrian. Astrorhizina underwent a great deviation of free-living types after Allogromiina waned in importance in the Early Ordovician. The monophyletic Carterinina group (Carterinina, Trochaminina, Haplophragmiina and Textulariina) may have evolved from the Cambrian. The diversification of Trochaminina occurred in the Early Carboniferous when free-living taxa successfully reappeared in deep water after the extinction of previous surface dwelling types. Family level diversification of Haplophragmiina has tended to be faster than in the Trochaminina since the Late Devonian. Textulariina possibly arose in the Early Cretaceous from a hierarchical agglutinated community within the Haplophragmiina acme-zone.

Given the high quality of the calcareous fossil record (Figure 21b), it has been possible to detect monophyletic relationships. As fusulinids (Silurian to Permian) declined at the end of Paleozoic, there was an accompanying increase of Miliolina and Lagenina during the Late Permian. This implies that Miliolina and Lagenina evolved independently from Fusulinina in the Early Carboniferous. Therefore, Fusulinina and their descendants like Miliolina and Lagenina seem to form a monophyletic group in Carboniferous; the same is also true of the other derivative suborders of Fusulinina.

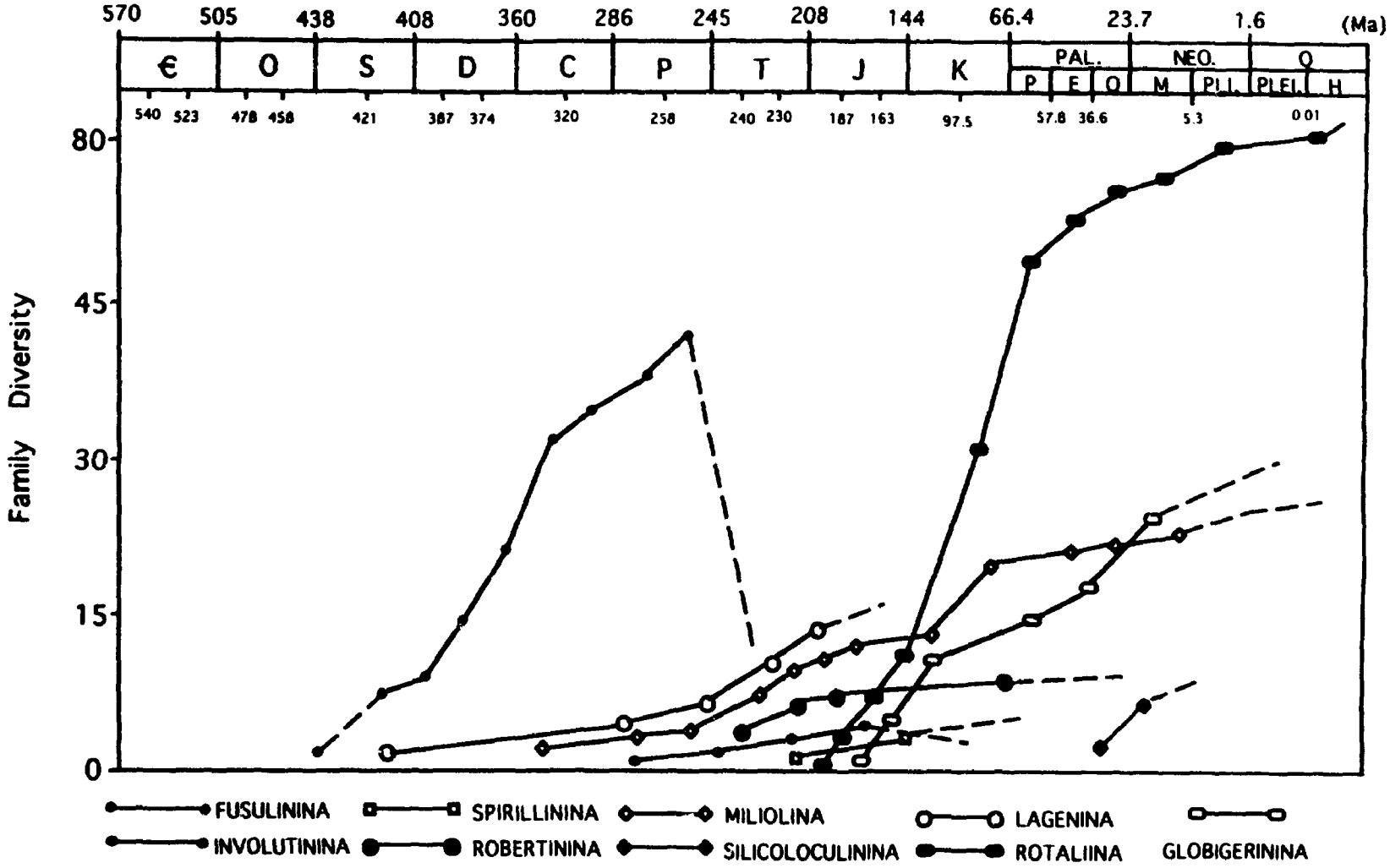
As a member of the Involutinina monophyletic group, aragonitic Robertinina were flourishing in the Middle Triassic with the decrease of Involutinina (Early Permian-Middle Jurassic). They were alternated by the calcareous Spirillinina in the Late Triassic. Rotaliinids, whose first family fossil record was in the Early Jurassic (Ross and Haman,

Figure 21a. Family diversity of organic and agglutinated walled foraminiferal suborders over their geological ranges. Geological time scale after Boggs (1987). Dashed lines indicate the supposed family diversity.



Taken from Table 5

Figure 21b. Family diversity of calcareous walled foraminiferal suborders over their geological ranges. Geological time scale after Boggs (1987). Dashed lines indicate the supposed family diversity.



Taken from Table 5

1989), dominated benthic foraminiferal faunas by the Late Mesozoic and the Cenozoic. This group, as the largest and the most diverse, had a wide affinity with the Spirillinina in the Triassic and Jurassic. Judging from this, evidence of paleoecological divergence over geological time provides confidence in the available morphologic data on the groups. Unlike other taxa, both herbivorous and carnivorous planktic foraminifera show a marked gradient over geological time. They successively diversified into a wide variety of test shapes, chamber arrangements and surface sculpture since the Jurassic. Rotaliina and Globigerinina are monophyletic and were derived from their sister group Spirillinina during the Early Jurassic. This group further diversified during the Cenozoic.

Cenozoic monophyletic groups linked fossil and extant organisms. The appearance of the siliceous shells of Silicoloculinina implicates the recent monophyletic development shared by their sister group Miliolina since the Late Miocene.

Concluding Remarks

In view of these observations, I suggest that all of the available evidence, both on extant and extinct organisms, be taken into consideration when assessing phylogenetic relationships. As one might suppose, an analysis based on incomplete data results in less accurate conclusions. In comparison with similar analysis on extant groups, the fossil record has limitations.

The fossil record is important when trying to interpret evolutionary data. However, evolution is difficult to explain as there is no time axis in phylogenetic clades.

No reputable biologist or geologist today doubts that all species of living organisms evolved from previously existing types under the control of evolutionary processes. Evolution is a vast and complex subject, one that touches upon every phase of biology, from biochemistry and cell physiology to systematics and ecology. (See for

discussion Savage, 1965.) Consequently, in the study of evolution of organisms, it is necessary to take complete information into account.

CHAPTER VII CONCLUSIONS

Subordinal foraminiferal phylogenetic systematics have been studied in detail by utilizing cladistic methods. The results can be summarized as follows:

1. The new model hypothesizes revised taxonomic relationships for foraminifera at the subordinal level. It differs from the previous model proposed by Tappan and Loeblich (1988) and Loeblich and Tappan (1989) in several fundamental aspects:

1) the new classification is built up using a strict cladistic (MacClade 3.0 and PAUP 3.1) approach (coding and organizing characters and their states into a verifiable scheme, and using a parsimony approach for analysis), whereas Tappan and Loeblich's classification is based on the primitive phylogenetic principles (the importance of unique characters);
2) the new classification reflects an optimal hypothesis for foraminiferal subordinal phylogeny established using mixed parsimony with 10 transformation series, including synapomorphies and autapomorphies that are vitally informative for identifying the common ancestry; the taxonomic relationships presented on Tappan and Loeblich's tree rely on the examination of only two significant characters (wall composition and wall ultrastructure);

3) the phylogenetic reconstruction of foraminiferal suborders in this study is supported by *a posteriori* character state trees -- CST1 and CST2 (i.e. wall composition tree and wall ultrastructure tree); the phylogeny proposed by Tappan and Loeblich stems from unordered character state network with character states unpolarized;

4) to achieve accuracy in the analysis for the new model, computer packages -- MacClade (3.0) and PAUP (3.1), were used to assess the data and to produce a number of possible cladograms via statistical algorithms; Tappan and Loeblich's studies for their model were carried out without computer aid;

5) the Loeblich and Tappan tree shows considerable homoplasy for some characters and the tree length is longer than in the new model.

2. Shared derived character states (synapomorphies) are useful for hypothesizing the common ancestral relationships between foraminiferal suborders.

3. Both mixed ordered (General) parsimony and unordered (Fitch) parsimony are likely to offer similarly feasible hypotheses for explaining character evolution in the given data at hand, and the tree established on mixed parsimony may be considered as the optimal phylogeny tree in the set of rival trees since it exhibits CST's. Ordered techniques can also function to decrease equally parsimonious trees from an unordered hypothesis of character state changes. The phylogenetic indifference of unordered parsimony has been perceived.

4. The 50% Majority-rule consensus result is an objective parsimony interpretation in which the monophyletic groups are better defined. The Allogromiina group, the Astrorhizina group, the Carterinina group (Carterinina, Trochaminina,

Haplophragmiina and Textulariina) (or each member of this group such as the Trochaminina group, the Haplophragmiina group, the Textulariina group, the Carterinina group), the Fusulinina group (Fusulinina, Miliolina, Silicoloculinina, Lagenina, Involutinina, Robertinina, Spirillinina, Rotaliina and Globigerinina), the Miliolina group (Miliolina and Silicoloculinina), the Involutinina group (Involutinina and Robertinina), the Spirillinina group and the Rotaliina group (Rotaliina and Globigerinina) are all monophyletic.

5. A series of OPT's was exploited for this work to re-estimate the phylogenetic relationships between foraminiferal suborders. The following points are worth noting (see one type of the optimal tree -- OPT4):

1) Allogromiina (U. Cambrian-Holocene), may have evolved from Euamoebae (outgroup) about 600 million years ago.
2) Astrorhizina (Cambrian-Holocene) are the ancestors of the agglutinated-wall suborders. They may have originated from Allogromiina, or directly evolved from a common ancestor of Foraminiferida -- i.e. Euamoebae in the Cambrian.
3) Carterinina (Cambrian ?, Eocene-Holocene), despite their sparse fossil record, are monophyletic. On the basis of the research done for this dissertation, it appears to be justifiable to include Carterinina, Haplophragmiina, Trochamminina and Textulariina in an ingroup (designated the Carterinina group). It is assumed that this is a monophyletic group that originated from Astrorhizina. The second possibility is that Carterinina and each other suborder of the Carterinina ingroup may have arisen as an independent monophyletic group from Astrorhizina in the Cambrian.

A third possibility is that Carterinina may have evolved from any more primitive ancestor other than Astrorhizina; it might have evolved in parallel with Astrorhizina. A possible reason for the poor fossil record of Carterinina is that they might be an underevolved small suborder.

4) Fusulinina (L.Silurian-U.Permian) may be ancestral to the monophyletic calcareous suborders. The Fusulinina group is monophyletic.

5) Miliolina (Carboniferous-Holocene) and Lagenina (L.Carboniferous-Holocene) may have evolved from Fusulinina in Carboniferous, respectively.

6) Silicoloculinina (U.Miocene-Holocene) that evolved from Miliolina in the Late Miocene; Silicoloculinina and Miliolina belong to one monophyletic group.

7) Involutinina (L.Permian-U.Cretaceous) share synapomorphies with Robertinina (M.Triassic-Holocene). They are likely to be monophyletic since the Middle Triassic.

8) The traditional perception that Spirillinina (U.Triassic-Holocene) were closely related to Involutinina is reasonable. This suborder is monophyletic.

9) Rotaliina (Triassic? L.Jurassic-Holocene) may have had a close relationship with Spirillinina in the Early Jurassic.

10) The planktic Globigerinina, which originated from Rotaliina in the Middle Jurassic, are the phylogenetic sister group of Rotaliina. Globigerinina and Rotaliina are monophyletic.

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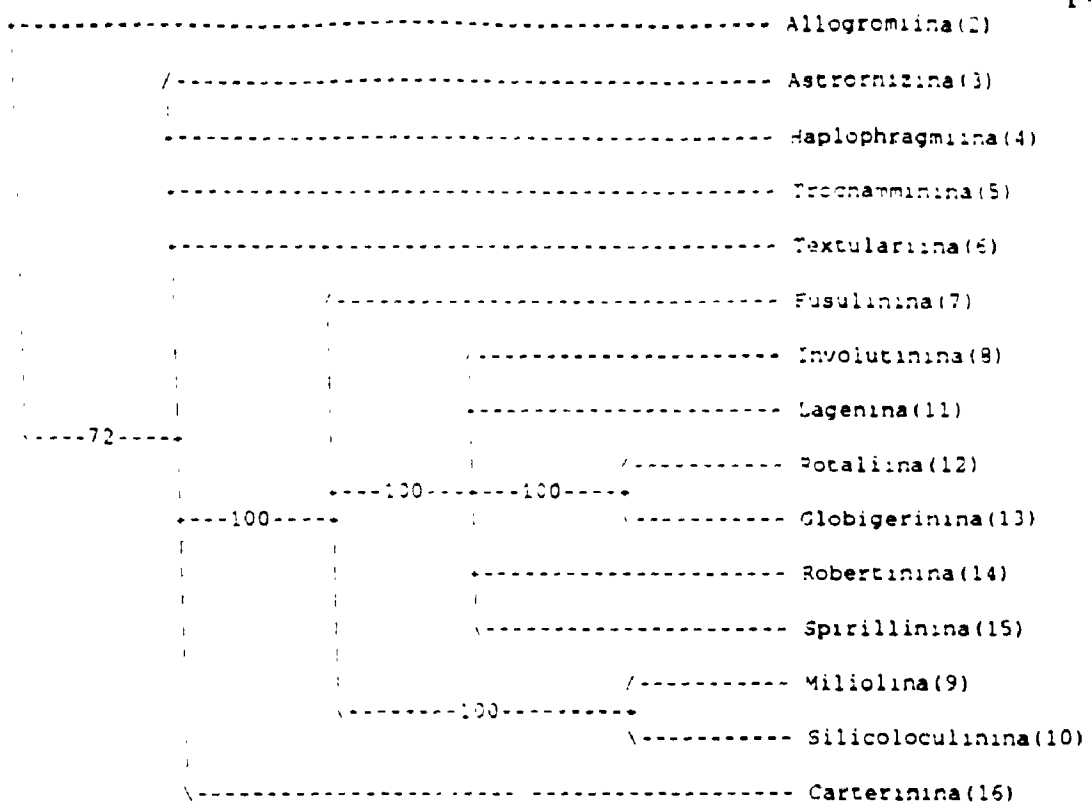
APPENDIX I

Mixed ordered and unordered (General) parsimony (new model).



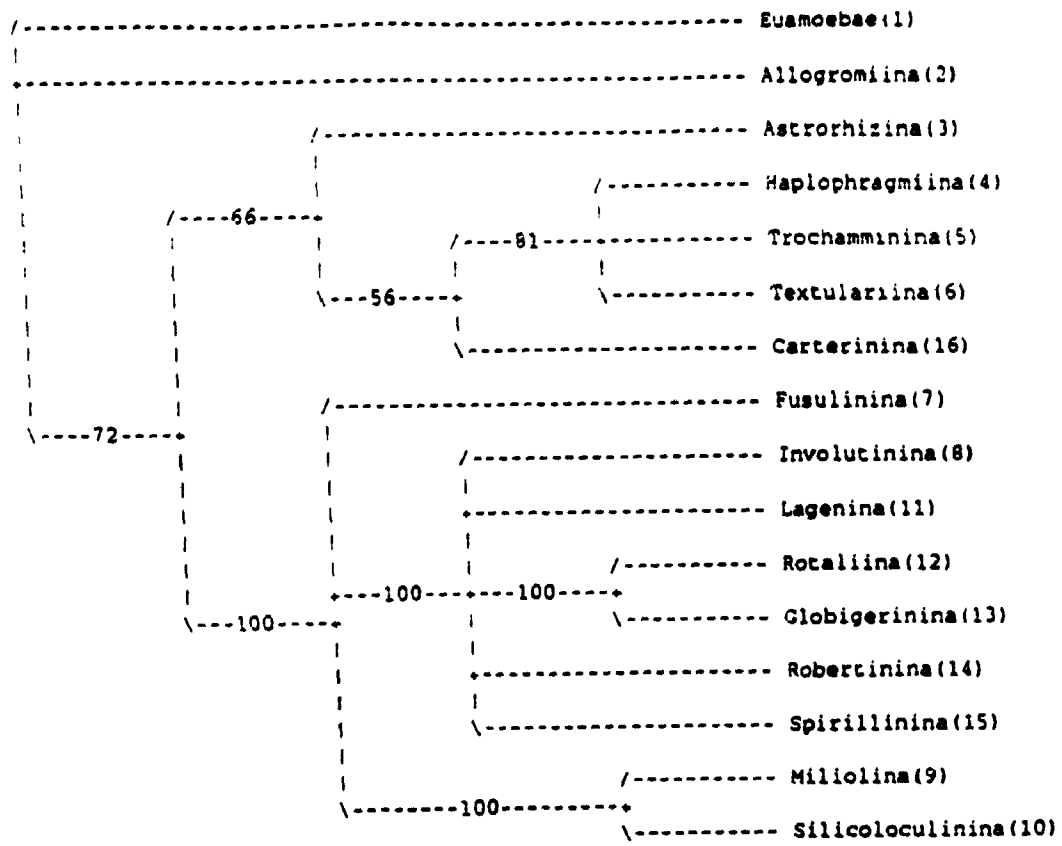
Partitions found in one or more trees and frequency of occurrence:

1234567890123456	Freq
... ..********.	2104
..........**...	2104
.........**	2104
.......*..*****.	2104
...***..........	1714
.**************	1515
.****.........*	1384
...***.........*	1178
......*.....*..	995
......********	966
...**	904
...************	720
..**...........	630
.......*......*.	562
..........***...	444
......**..*****.	400
..........****..	396
...........***..	383
.......*..****..	366
.......*.....**.	315
..****..........	307
......*..*...*.	267
.......*..*..**.	267
..........*...*.	222
.......*..*..*..	222
...***********	198
..........*..*..	180
......**********	174
...*..........*	166
...*.*..........	166
...........**.*.	154
.......*...***..	148
.......*..*.....	132
...........****.	91
.......*...****.	36
.......*...**.*.	9

Partitions found in one or more trees and frequency of occurrence:

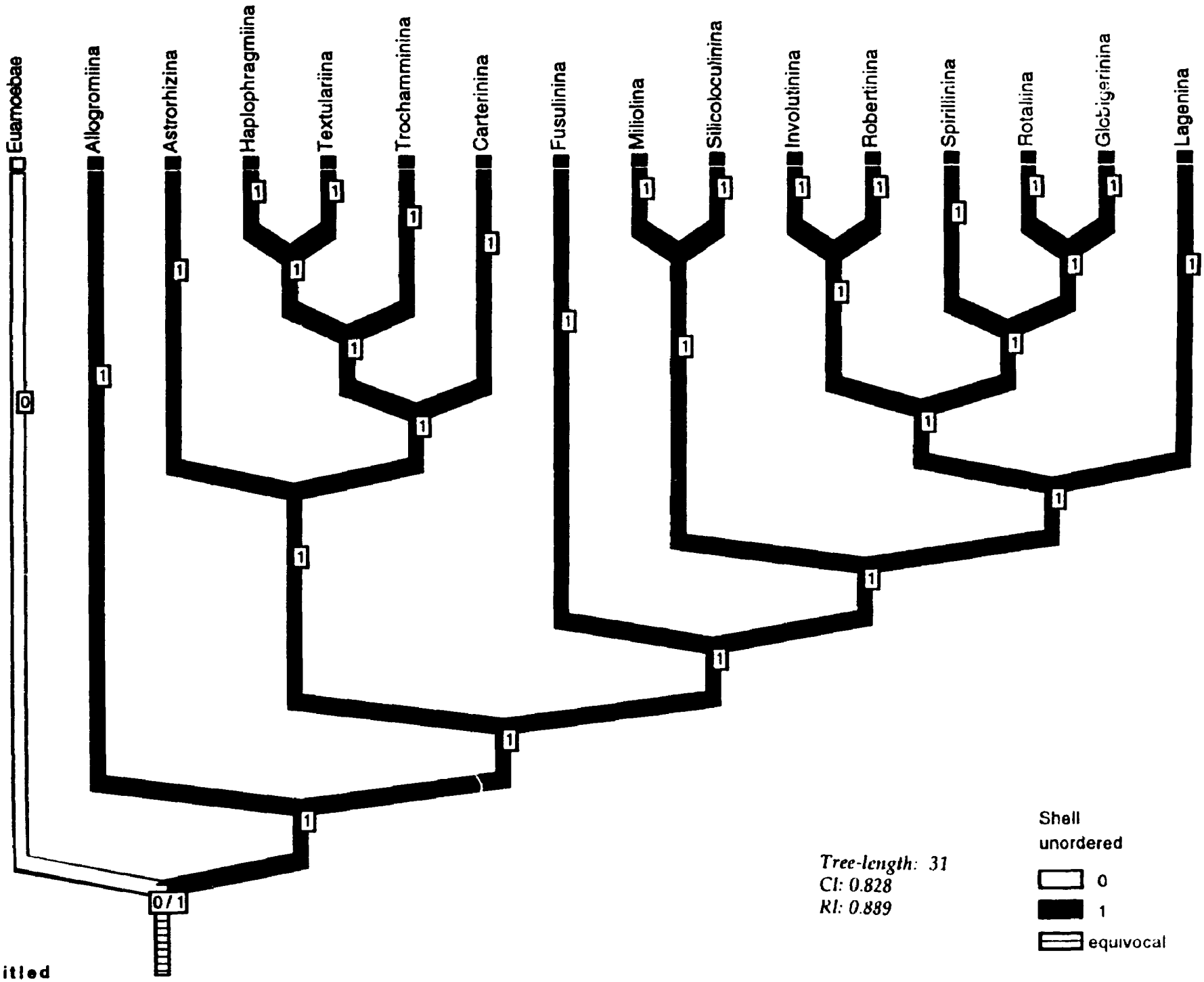
1111111 1234567890123456	Freq
.....•••••••••.	2104
..........••...	2104
........••.....	2104
.......•..•••••.	2104
...•••..........	1714
..••••••••••••••	1515
..••••.........•	1384
...•••.........•	1178
.......•.....•..	995
.......••••••••.	966
....••..........	904
...••••••••••••••	720
...••............	630
........•.....•.	562
..........•••...	444
......••..••••.	400
..........••••..	396
...........•••..	383
.......•..••••..	366
.......•.....••.	315
..••••..........	307
.......•..•...•.	267
.......•..•..••.	267
..........•...•.	222
.......•..•..•..	222
...••••••••••••.	198
..........•..•..	180
......••••••••••	174
...•...........•	166
...•.•..........	166
...........••.•.	154
........•...•••..	148
.......•..•.....	132
...........••••.	61
.......•...••••.	36
.......•...••.•.	9

50% Majority-rule consensus of 2104 trees



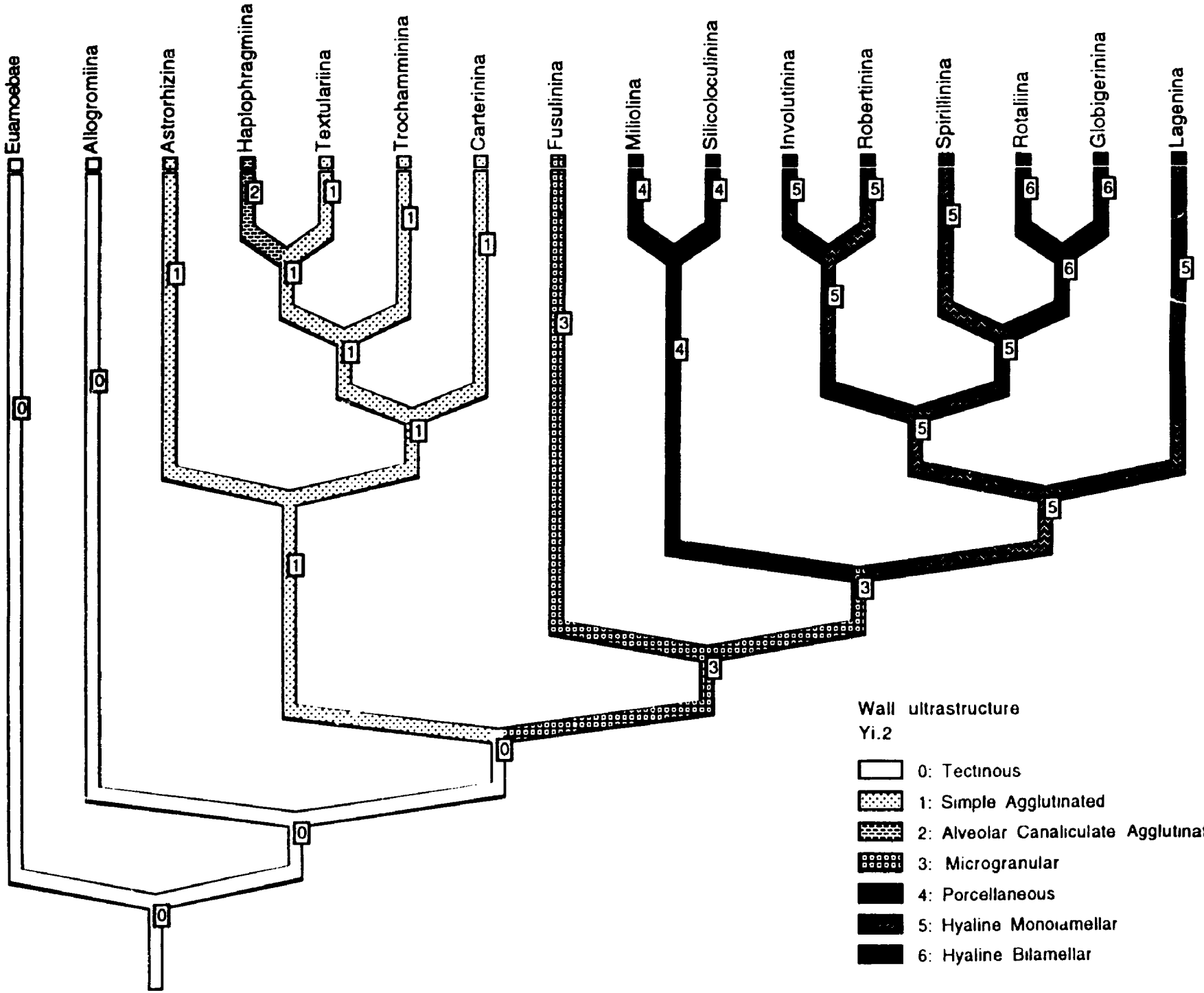
Display of character statistics of new phylogenetic model (Ordered)

Character	Type	Weight	States	Steps	CI	RI
☑ 1. Shell	unordered	1	2	1	1.00	0.0
☑ 2. Pseudopods	unordered	1	2	1	1.00	0.0
☑ 3. Wall composition	Yi. 1	1	8	7	- -	- -
☑ 4. Wall ultrastructure	Yi.2	1	7	6	- -	- -
☑ 5. Test perforation	unordered	1	2	1	1.00	1.00
☑ 6. Test shape	unordered	1	6	3	0.67	0.50
☑ 7. Number of chambers	unordered	1	2	2	0.50	0.50
☑ 8. Chamber arrangement	unordered	1	6	5	0.80	0.80
☑ 9. Chamber shape	unordered	1	6	3	0.33	0.0
☑ 10. Surface sculpture	unordered	1	6	2	1.00	1.00


Euamoebae
Allogromiina
Astrorhizina
Haplophragmiina
Textulariina
Trochamminina
Carterinina
Fusulinina
Miliolina
Silicoloculinina
Involutinina
Robertinina
Spirillinina
Rotaliina
Globigerinina
Lagenina
0
1
0 / 1
Tree-length: 31
CI: 0.828
RI: 0.889
Shell
unordered
0
1
equivocal
Untitled

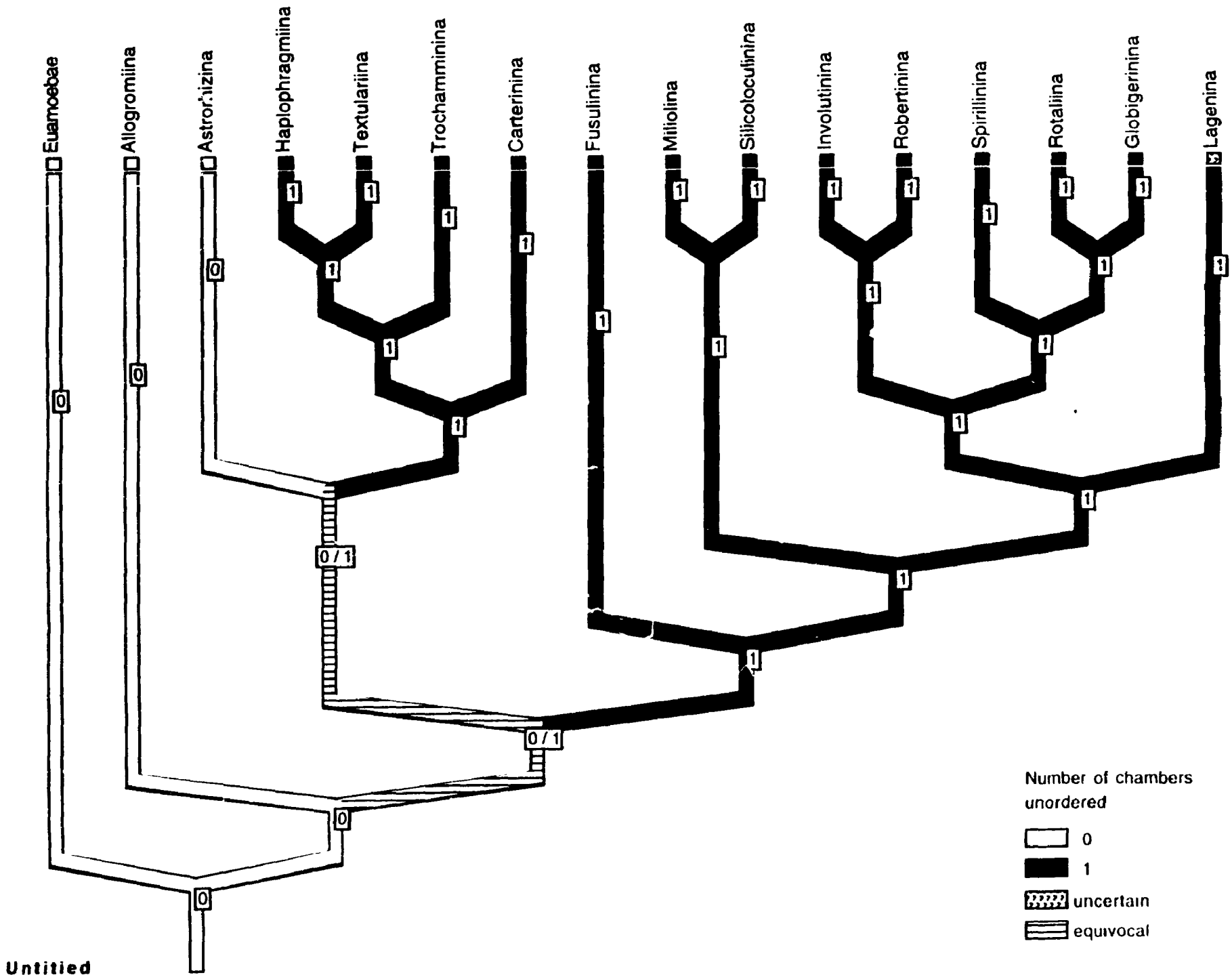
Pseudopods
unordered
0
1
equivocal
Lagenina
Globigerinina
Rotaliina
Spirillinina
Robertinina
Involutinina
Silicoloculinina
Miliolina
Fusulinina
Carterinira
Trochammminina
Textulariina
Haplophragmiina
Astrorhizina
Allogromiina
Euamoebae
0/1
Untitled

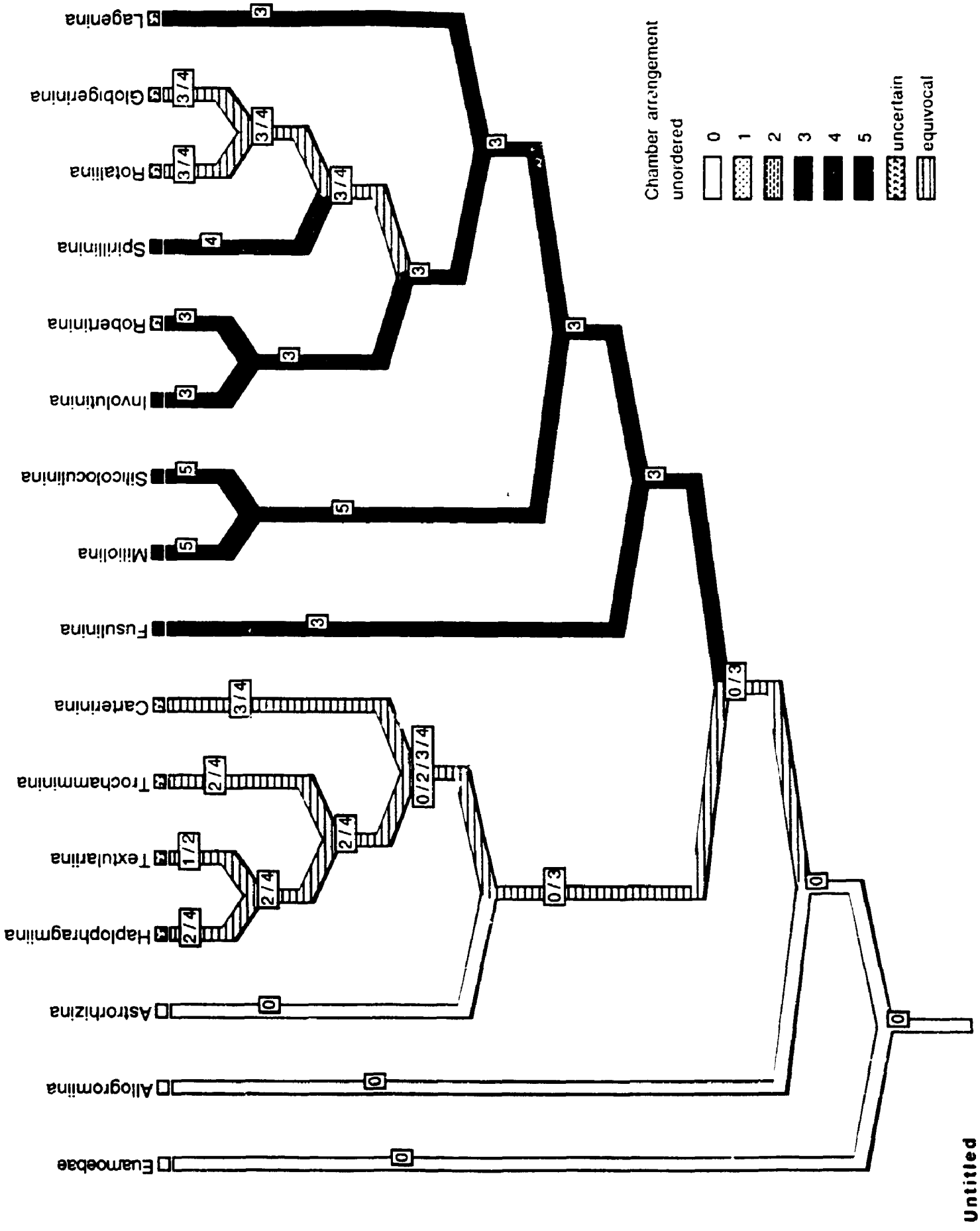
Euamoebae
Allogromiina
Astrorhizina
Haplophragmiina
Textulariina
Trochammiina
Cartertina
Fusulinina
Miliolina
Silicoloculinina
Involutinina
Robertinina
Spirillinina
Rotaliina
Globigerinina
Lagenina
Wall composition
Yi. 1
0: MembranaceousProteinaceous
1: Organic
2: Organic Agglutinated
3: Calcareous Agglutinated
4: Calcitic
5: Aragonitic
6: Siliceous
7: Secreted Spicular in Organic Gr

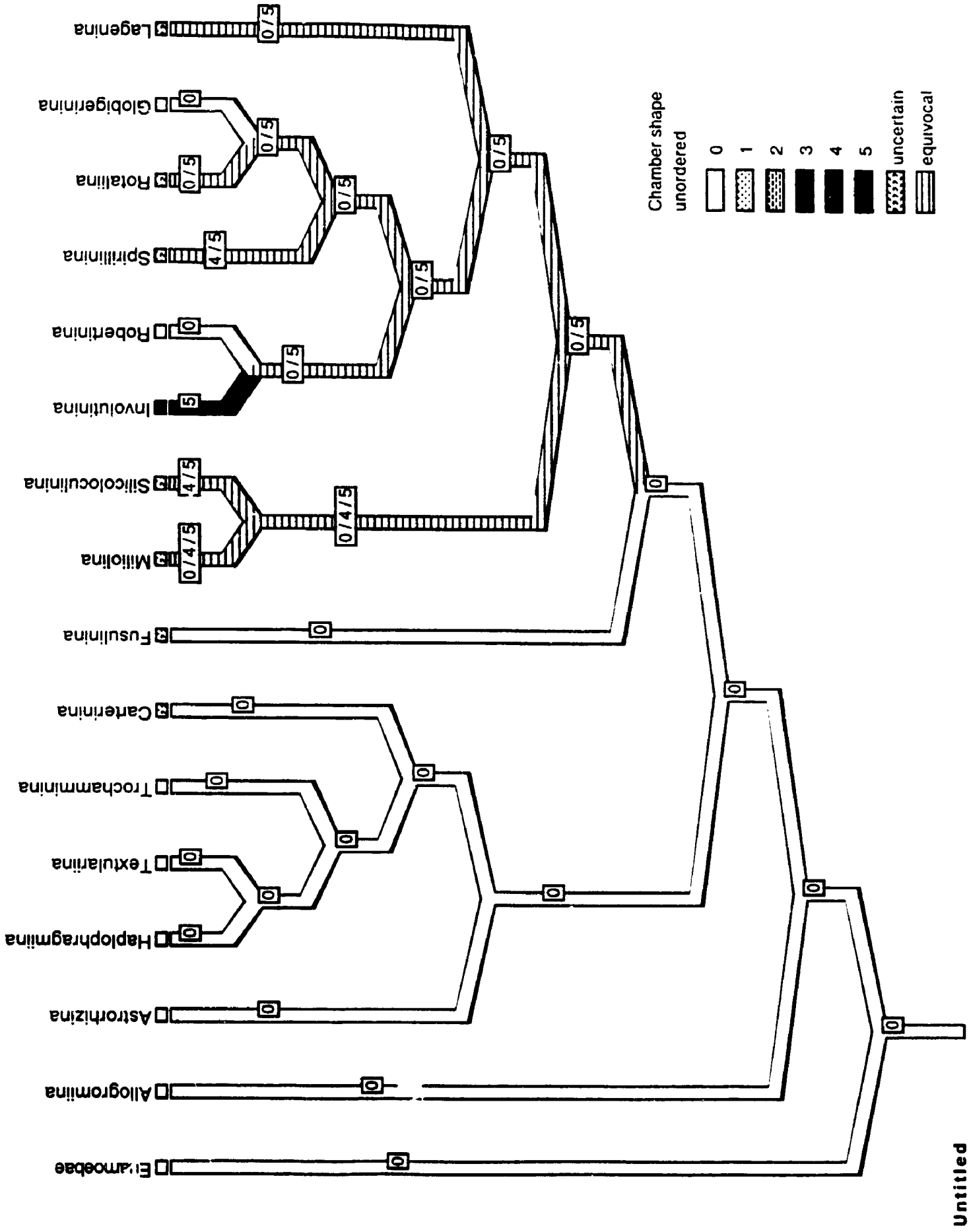

Euamoebae
Allogromiina
Astrorhizina
Haplophragmiina
Textulariina
Trochamminina
Carterinina
Fusulinina
Miliolina
Silicoloculinina
Involutinina
Robertinina
Spirillinina
Rotaliina
Globigerinina
Lagenina
Wall ultrastructure
Yi.2
0: Tectinous
1: Simple Agglutinated
2: Alveolar Canaliculate Agglutinated
3: Microgranular
4: Porcellaneous
5: Hyaline Monolamellar
6: Hyaline Bilamellar

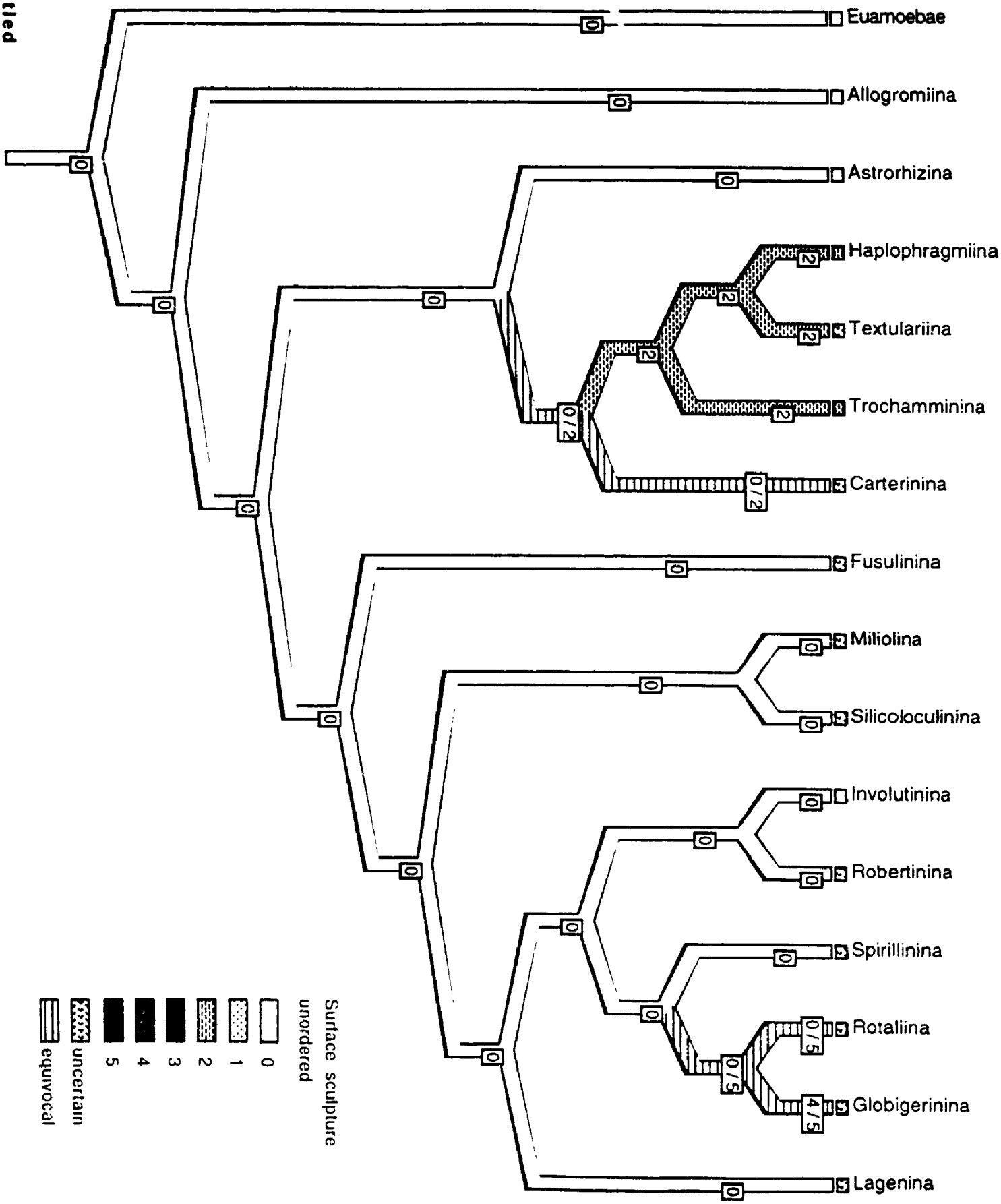
Lagenina
Globigerinina
Rotaliina
Spirillinina
Robertinina
Involutinina
Silicoloculinina
Miliolina
Fusulinina
Carterinina
Trochammininа
Textulariina
Haplophragmiina
Astrorhizina
Allogromiina
Euamoebae
Test perforation
unordered
0
1
Untitled

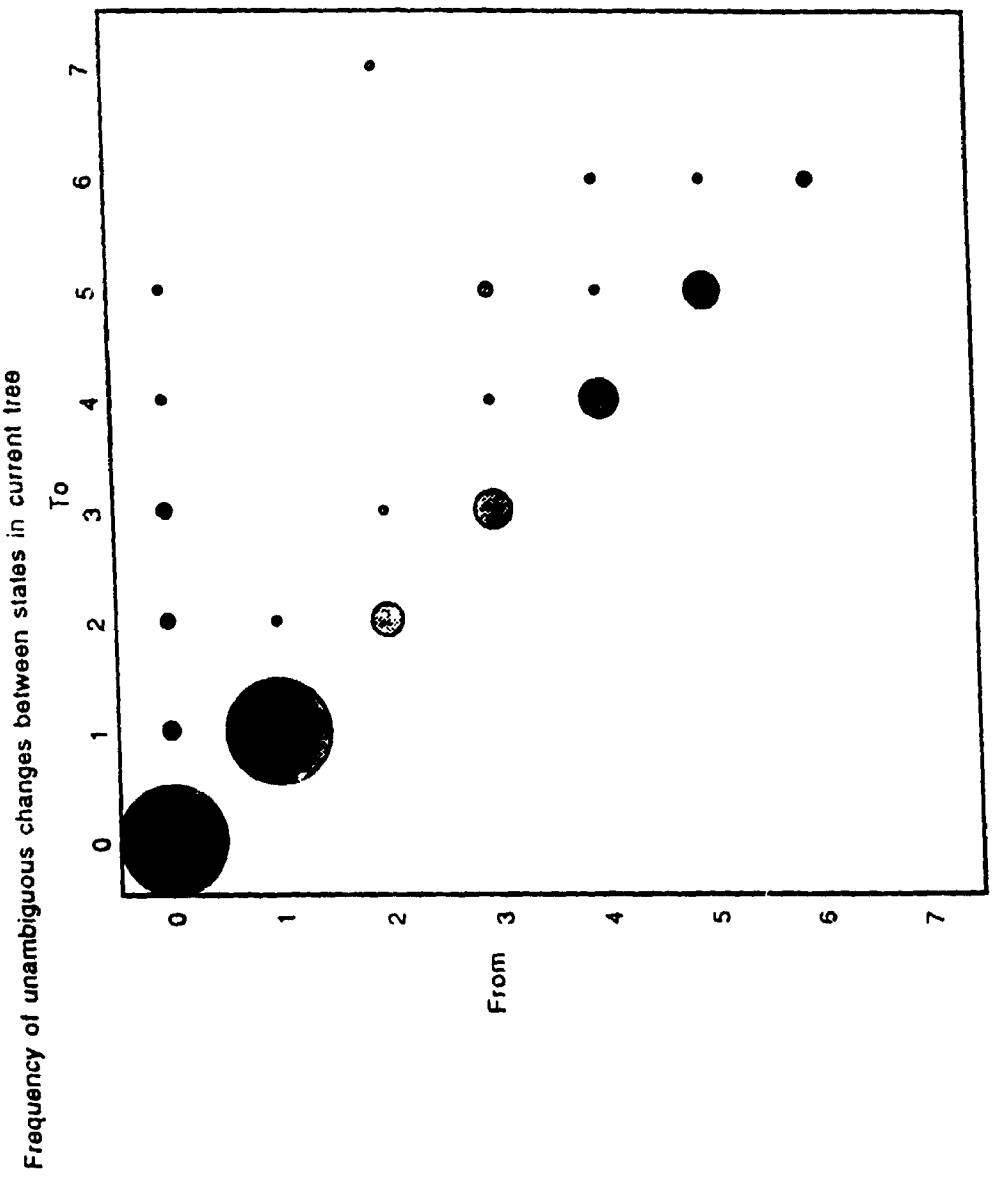
Test shape
unordered
0
1
2
3
4
5
uncertain
equivocal
Lagenina
Globigerinina
Rotaliina
Spirillinina
Robertinina
Involutinina
Silicoloculinina
Miliolina
Fusulinina
Carterinina
Trochammininа
Textulariina
Haplophragmiina
Astrorhizina
Allogromiina
Euamoebae
3/4
Untitled


Euamoebae
Allogromiina
Astrorhizina
Haplophragmiina
Textulariina
Trochamminina
Carterinina
Fusulinina
Miliolina
Silicoloculinina
Involutinina
Robertinina
Spirillinina
Rotaliina
Globigerinina
Lagenina
0 / 1
0 / 1
Number of chambers
unordered
0
1
uncertain
equivocal
Untitled

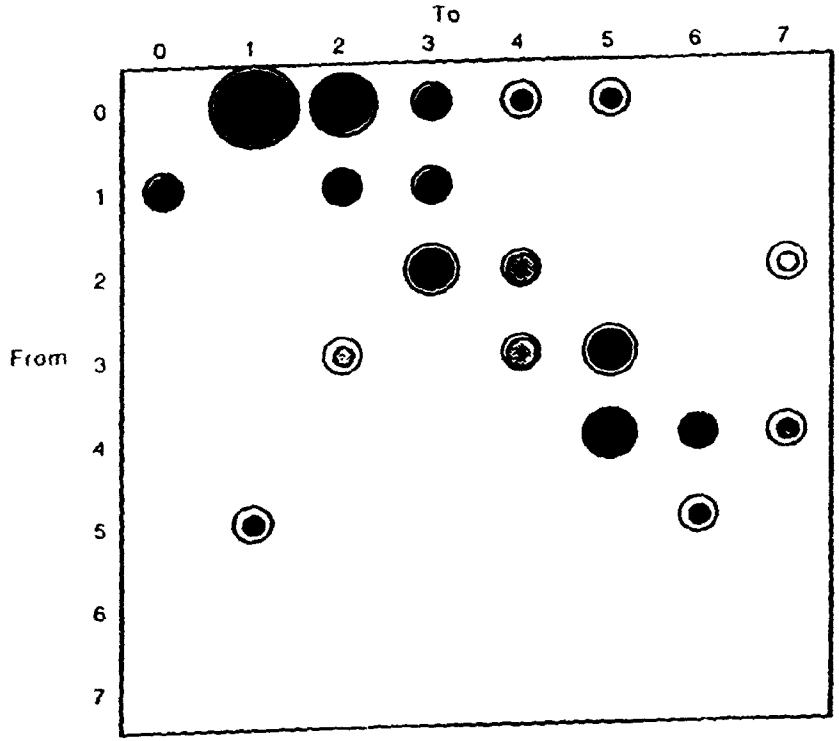

Chamber arrangement
unordered
0
1
2
3
4
5
uncertain
equivocal
Lagenina
Globigerinina
Rotaliina
Spirillinina
Robertinina
Involutinina
Silicoloculinina
Miliolina
Fusulinina
Carterinina
Trochammininа
Textulariina
Haplophragmiina
Astrorhizina
Allogromiina
Euamoebae
Untitled


Chamber shape
unordered
0
1
2
3
4
5
uncertain
equivocal
Lagenina
Globigerinina
Rotaliina
Spirillinina
Robertinina
Involutinina
Silicoloculinina
Miliolina
Fusulinina
Carterinina
Trochammminina
Textulariina
Haplophragmiina
Astrorhizina
Allogromiina
Eiyamoebae
Untitled


Euamoebae
Allogromiina
Astrorhizina
Haplophragmiina
Textulariina
Trochamminina
Carterinina
Fusulinina
Miliolina
Silicoloculinina
Involutinina
Robertinina
Spirillinina
Rotaliina
Globigerinina
Lagenina
0/2
0/2
0/5
0/5
4/5
Surface sculpture unordered
0
1
2
3
4
5
uncertain
equivocal


Frequency of unambiguous changes between states in current tree
To
0
1
2
3
4
5
6
7
From
0
1
2
3
4
5
6
7

Frequency of unambiguous changes between states in stored trees



○ *maximum* unambiguous
● **average** unambiguous
● **minimum** unambiguous

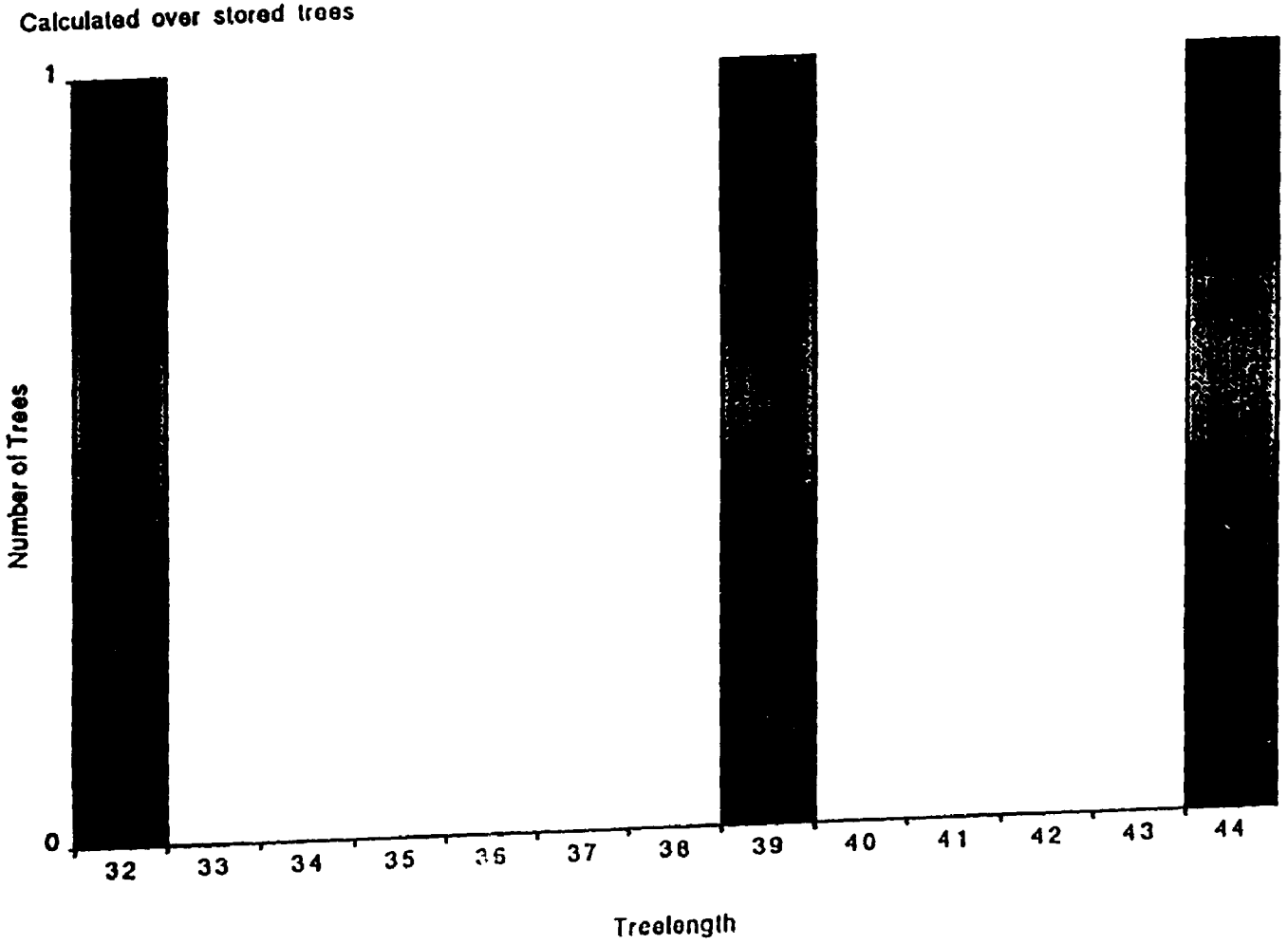


Chart showing that the total treelength is calculated as the sum of the number of steps for the individual characters multiplied by their respective weights.

$$Treelength = \sum_{i=1}^{n} w_i s_i$$

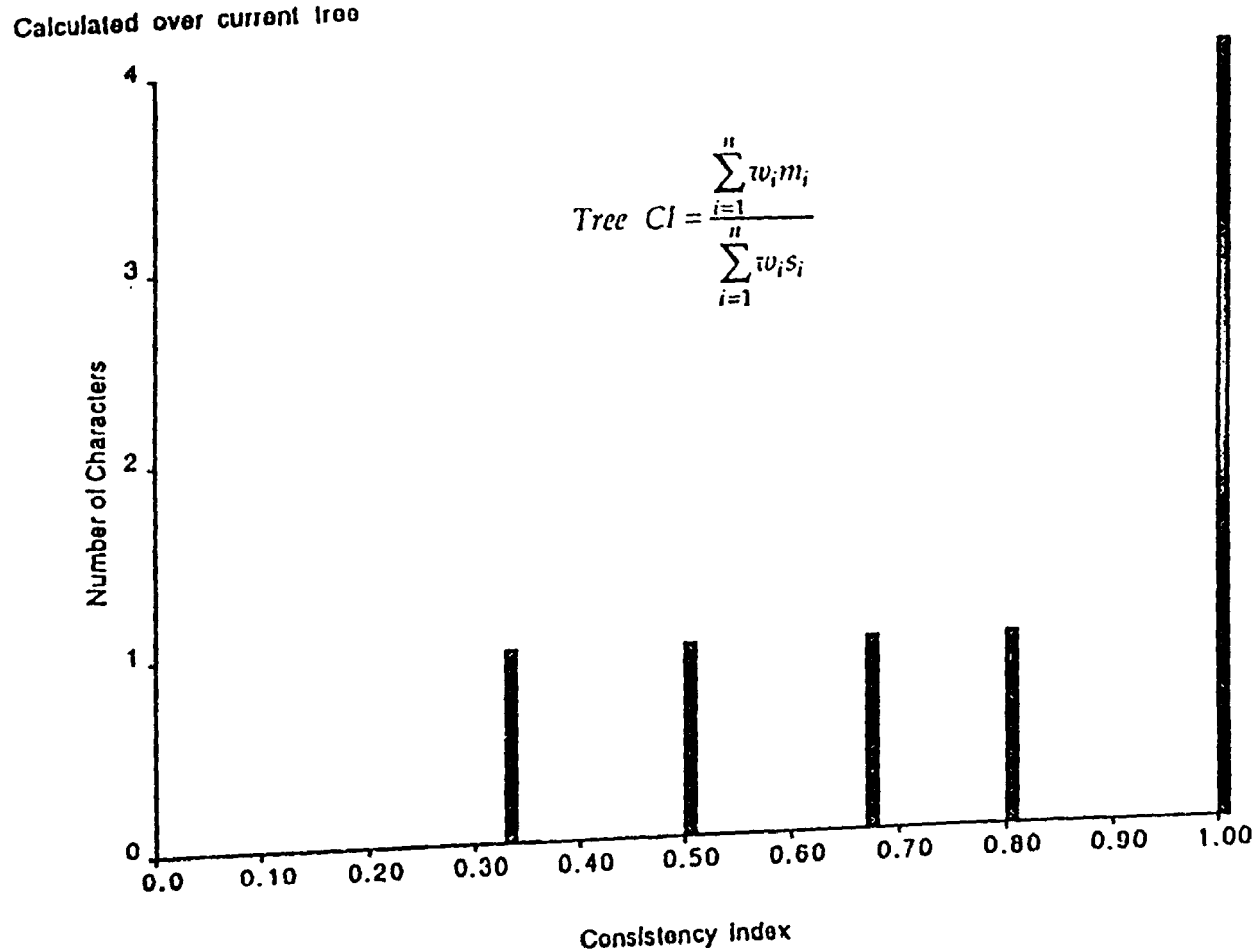


Chart shows that the consistency index (CI) for all characters on a tree is the minimum possible treelength divided by the observed treelength.

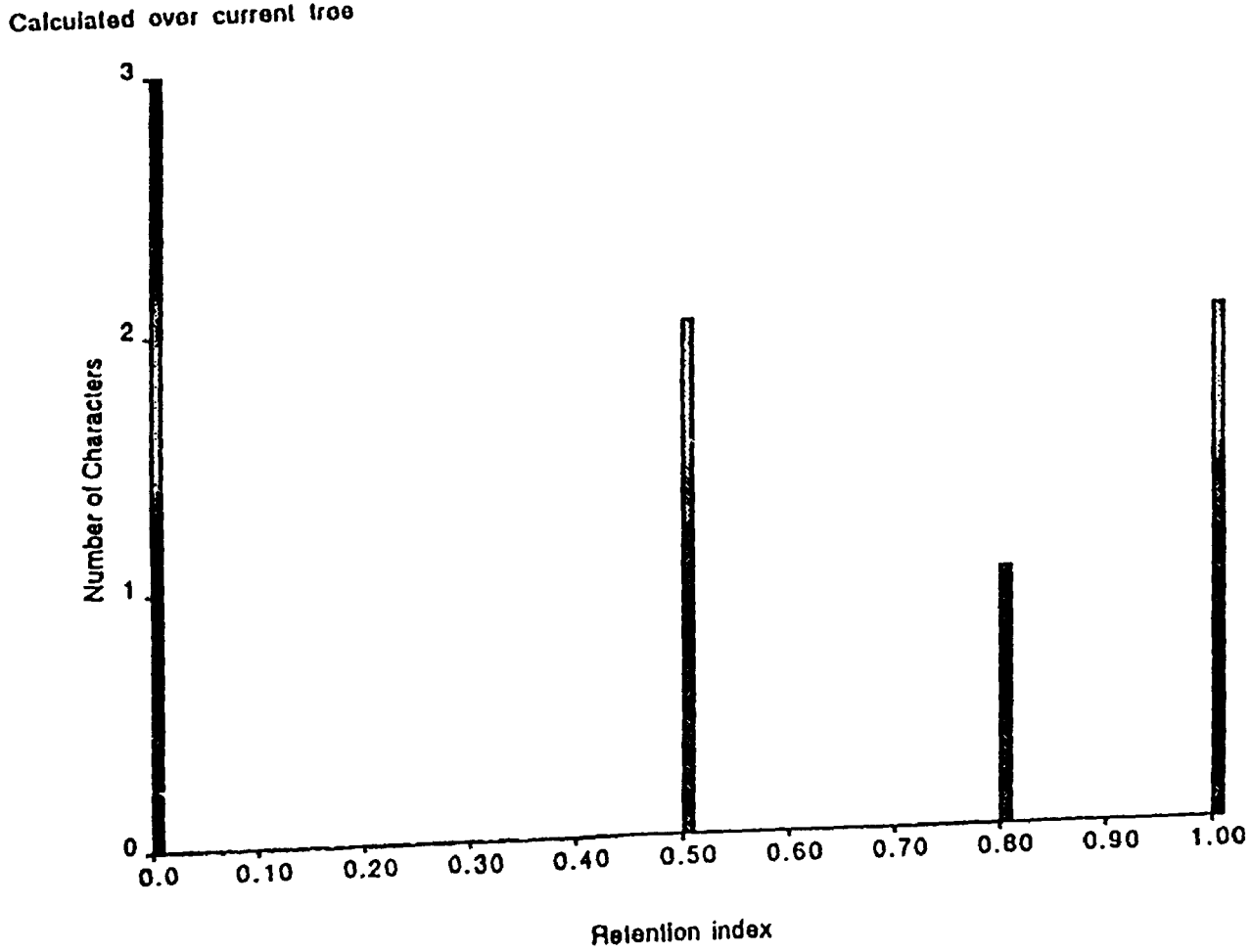


Chart shows that the retention index RI for all characters on a tree is calculated as the (maximum possible treelength-actual treelength)/(Maximum possible treelength- minimum possible treelength).

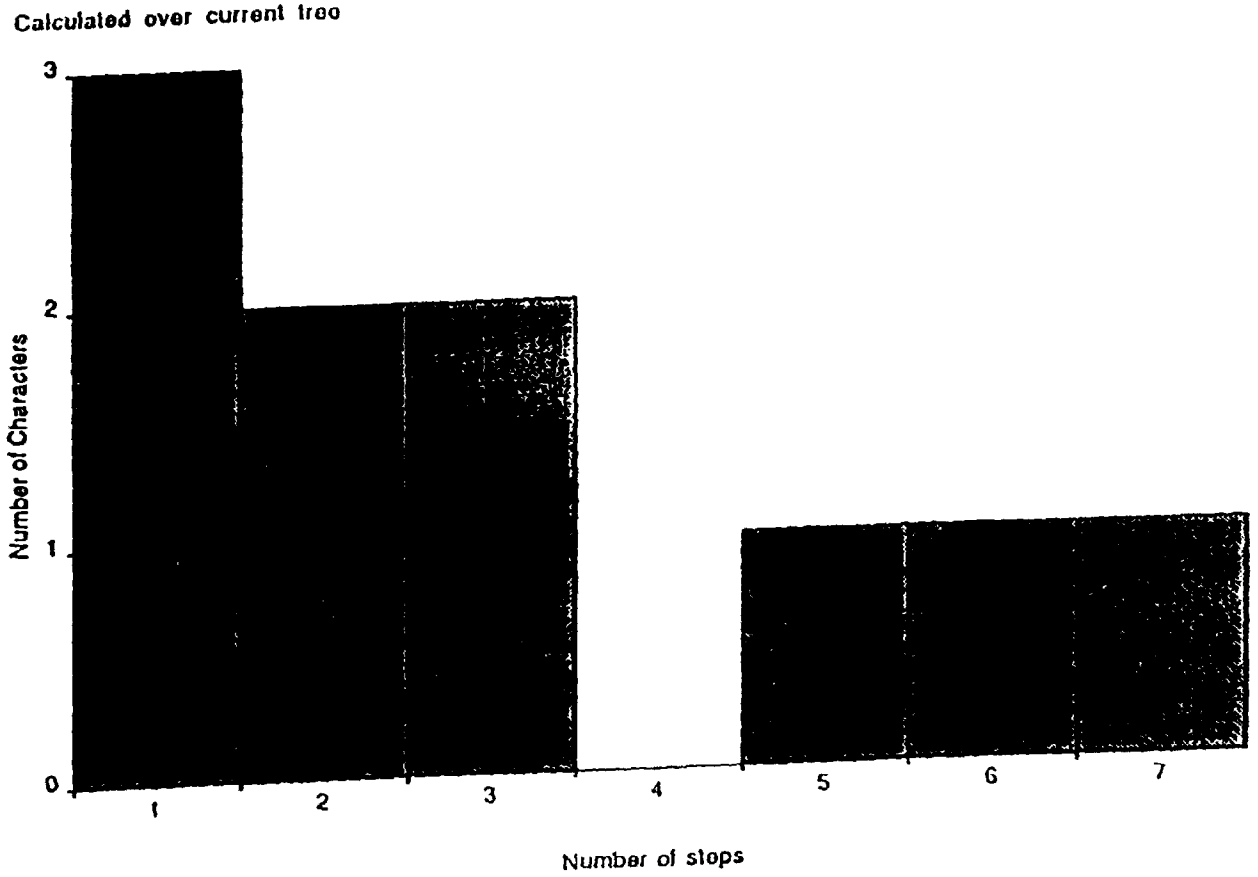
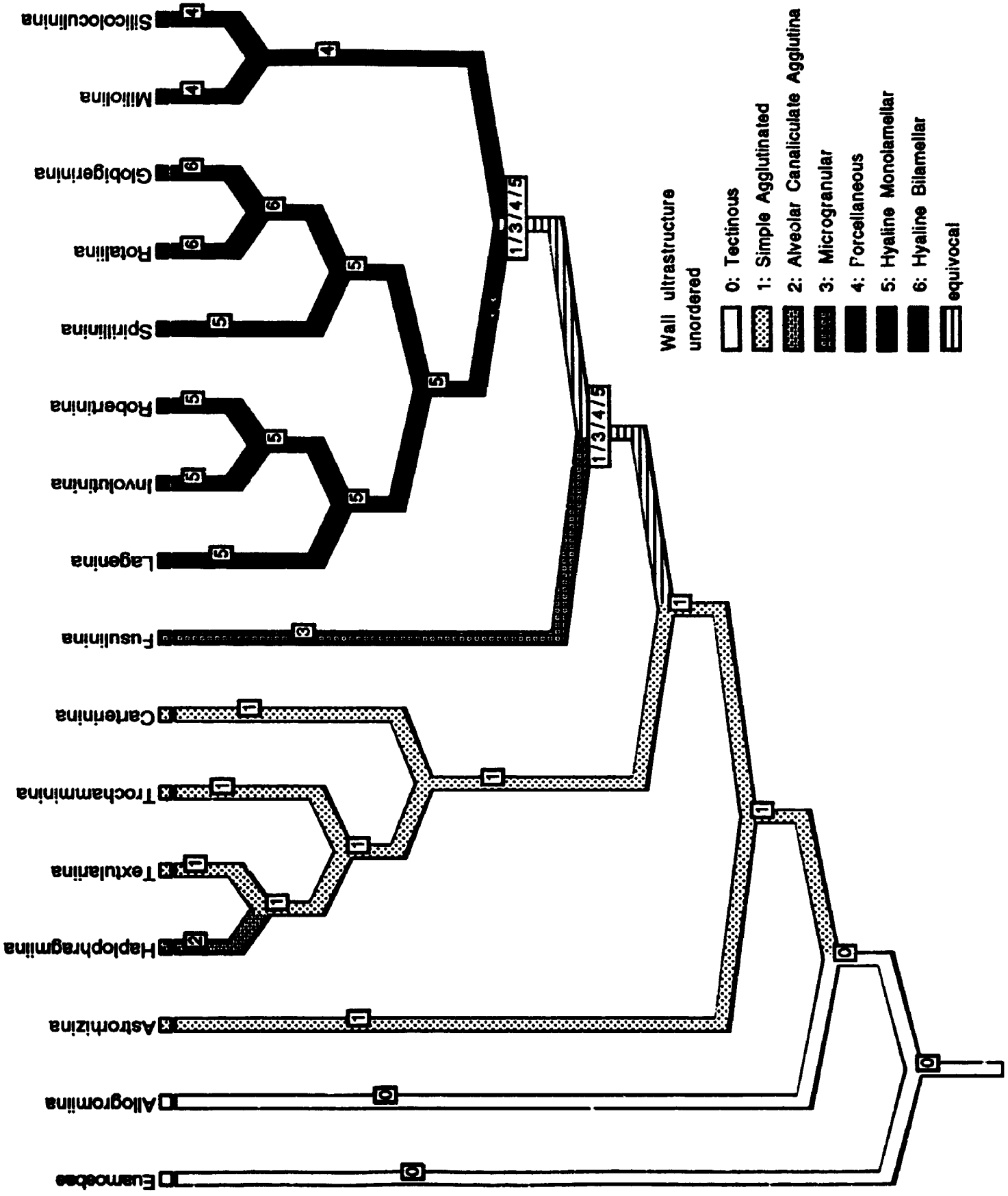
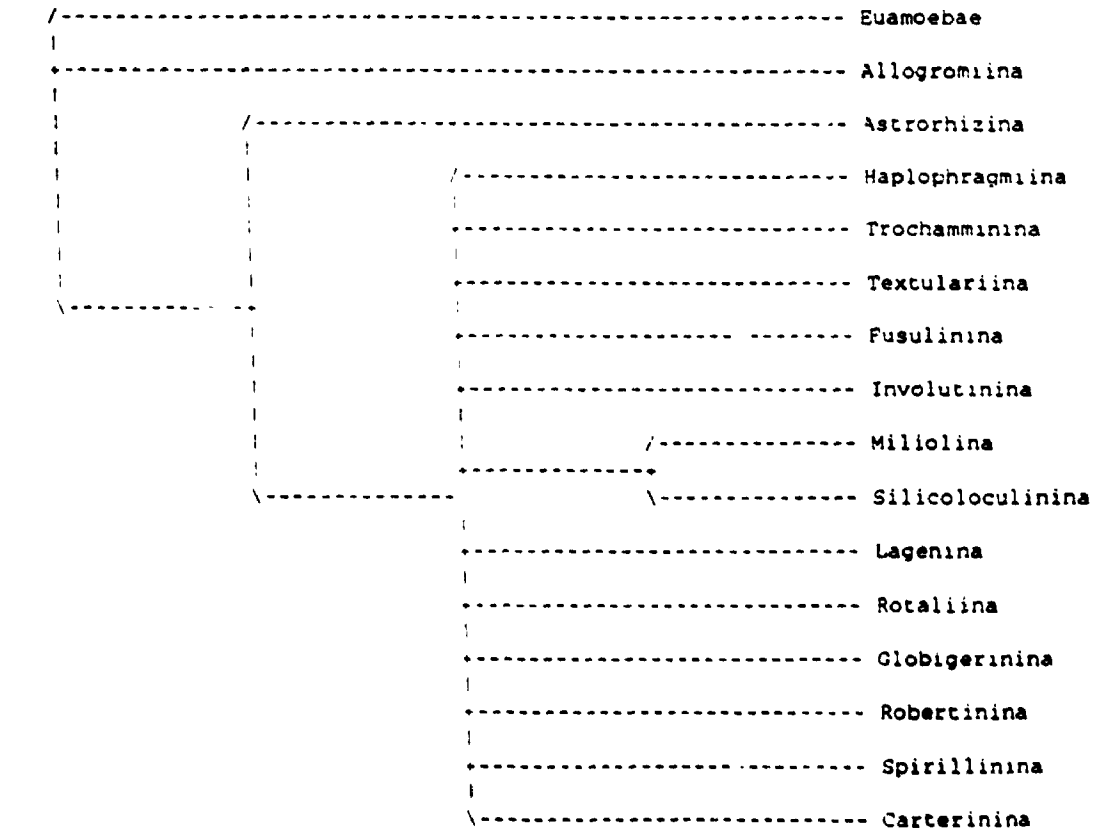


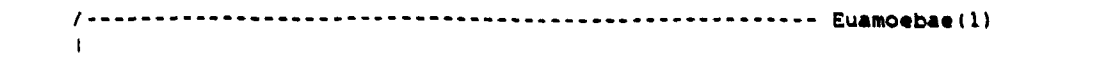
Chart shows most of the changes on the tree are at the first position.

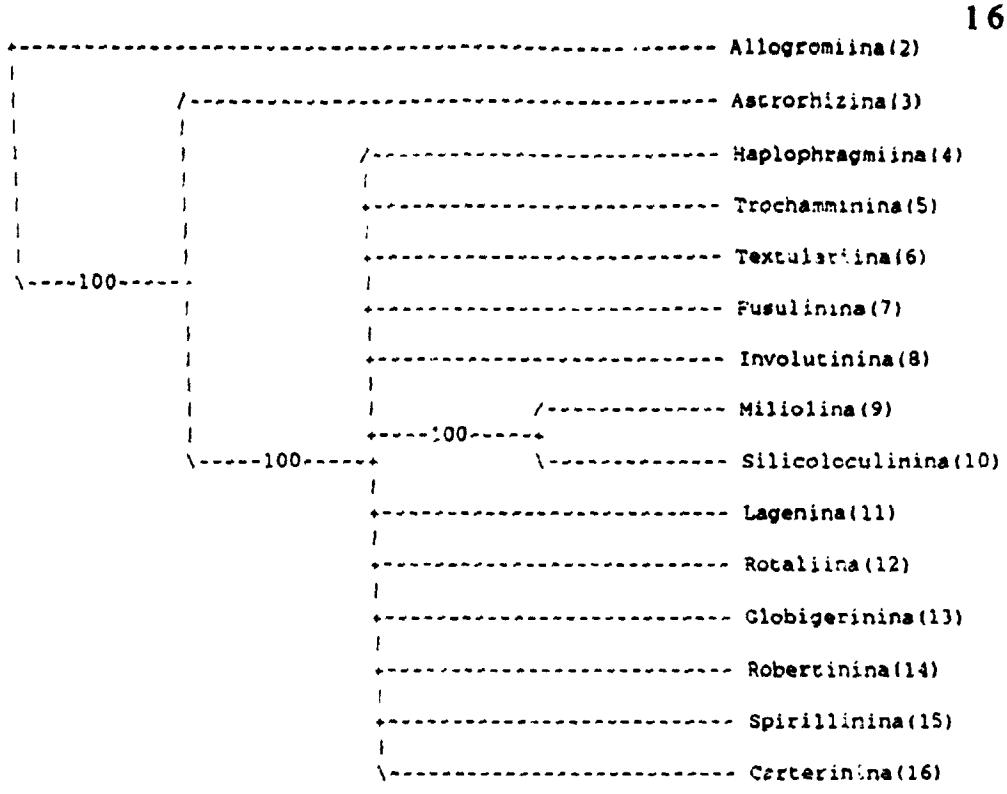

Wall ultrastructure
unordered
0: Tectinous
1: Simple Agglutinated
2: Alveolar Canaliculate Agglutina
3: Microgranular
4: Porcellaneous
5: Hyaline Monolamellar
6: Hyaline Bilamellar
equivocal
Euamoeba
Allogromiina
Astrorhizina
Haplophragmiina
Textulariina
Trochammmina
Carterinina
Fusulinina
Lageniina
Involutinina
Robertinina
Spirillinina
Rotaliina
Globigerinina
Miliolina
Silicoloculinina
1/3/4/5
1/3/4/5

```
Processing of file "Phylo. matrix" begins...

Data matrix has 16 taxa, 10 characters
Valid character-state symbols: 01234567
Missing data identified by '?'
Gaps identified by '-', treated as "missing"

2 trees read from TREES block

Processing of file "Phylo. matrix" completed.

Heuristic search settings:

   Addition sequence: closest
   10 trees held at each step during stepwise addition
   Tree-bisection-reconnection (TBR) branch-swapping performed
   MULPARS option in effect
   Steepest descent option not in effect
   Initial MAXTREES setting = 100
   Branches having maximum length zero collapsed to yield polytomies
   Topological constraints not enforced
   Trees are unrooted
   Multi-state taxa interpreted as uncertainty

Heuristic search completed:

   Total number of rearrangements tried = 5483970
   Length of shortest tree found = 29
   Number of trees retained = 3980
   Time used = 04:34:09.3

3980 trees saved to file 'Phylo. 3980 trees'

Strict consensus of 3980 trees:
```




```
   Semistrict consensus of 3980 trees:
```





Partitions found in one or more trees and frequency of occurrence:

1111111 1234567890123456	Freq
..**********	3980
...**********	3980
........**.....	3980
...***.........	3975
..........**...	2849
......********.	2672
.......********	2250
.......*..*****	2181
......**********	2148
.......*.....*..	1877
....**..... ..	1328
...**..........	1327
.......*..*..**.	1140
..**********	989
.......****..**.	966
.......*......*.	915
...***.........*	843
......**..*****	609
........**....*.	548
.........***...	517
.......*..*...*.	516
.......*.....**.	507
......*.**.....	489
.......***....*.	486
.......****...*.	477
.......*..*..*..	466
.........****..	378
.........*..*..	351
.......*..****..	326
.........*...*.	321
.......*..*.....	309
........**.....*	249
......**..******	240
........***...*.	237
.......*****.**.	237
.......***...**.	234
........***.....	219

```
...........***..     210
.......*..**.**.     192
.......****.....     108
.......****..*..     108
...........**.*.     105
........*...***..     87
........*...****.     60
........***.****.     42
......*****..**.     33
......**..****..     32
......*....**...     27
......*...****..     27
.........**.**.*.     27
........***.**.*.     27
.......*********     27
  .....*...**.*.     27
...........****.     27
......*****..***     12
......*.**....*.      9
......*...***...      9
...*.*.........       9
......****....*.      9
......****...**.      3
.....**********.      1
```

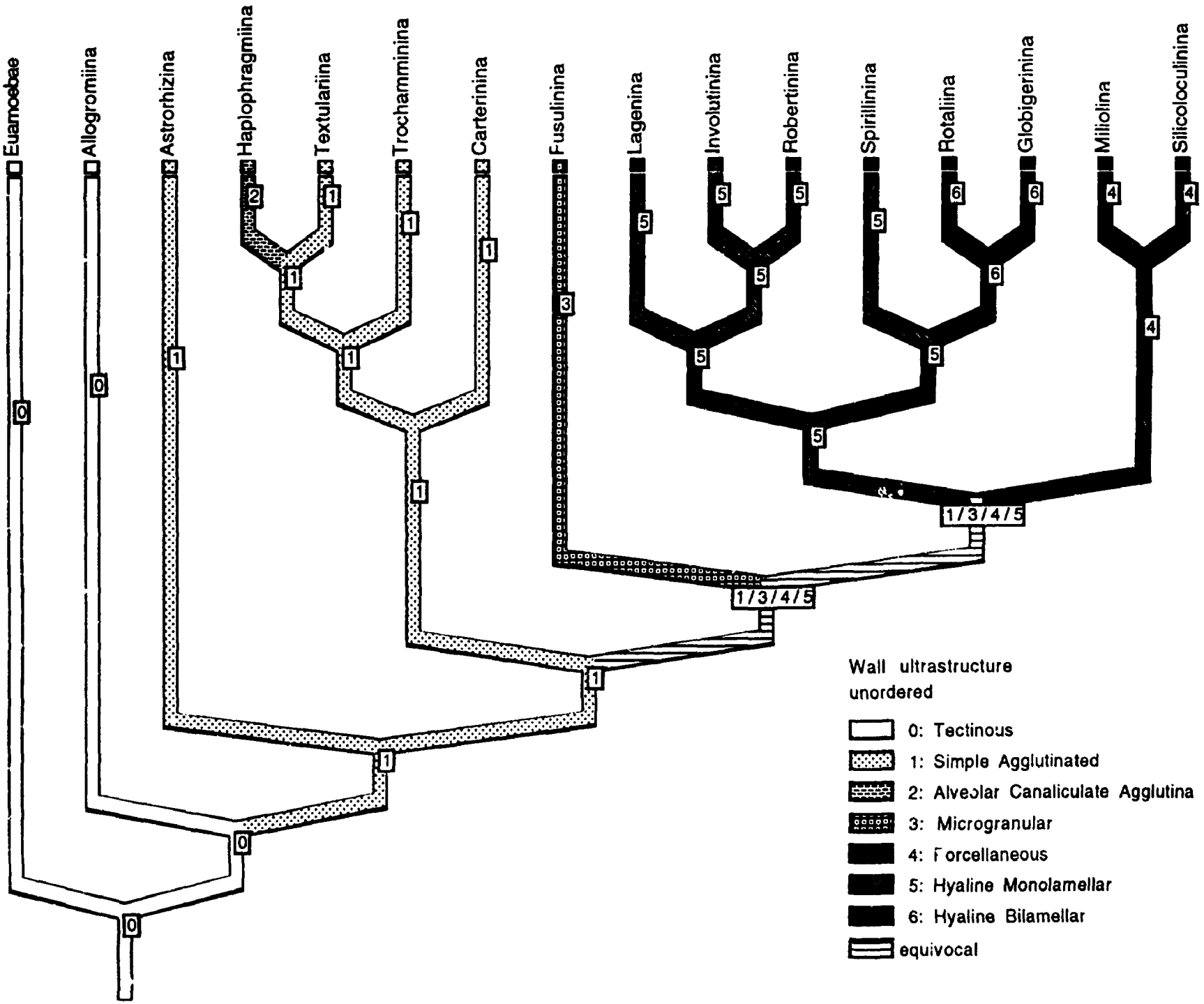
50% Majority-rule consensus of 3980 trees

Display of character statistics of new phylogenetic model (Unordered)

Character	Type	Weight	States	Steps	CI	RI
☑ 1. Shell	unordered	1	2	1	1.00	0.0
☑ 2. Pseudopods	unordered	1	2	1	1.00	0.0
☑ 3. Wall composition	unordered	1	8	7	1.00	1.00
☑ 4. Wall ultrastructure	unordered	1	7	6	1.00	1.00
☑ 5. Test perforation	unordered	1	2	1	1.00	1.00
☑ 6. Test shape	unordered	1	6	3	0.67	0.50
☑ 7. Number of chambers	unordered	1	2	1	1.00	1.00
☑ 8. Chamber arrangement	unordered	1	6	4	1.00	1.00
☑ 9. Chamber shape	unordered	1	6	2	0.50	0.50
☑ 10. Surface sculpture	unordered	1	6	2	1.00	1.00

APPENDIX III

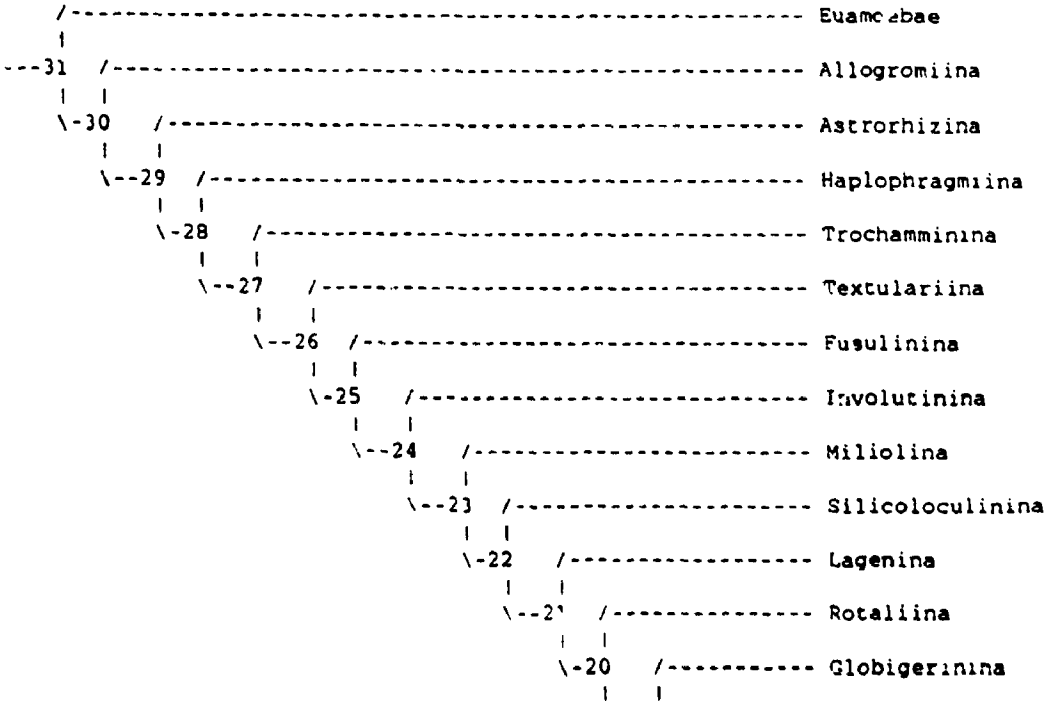
Unordered (Fitch) parsimony (modelled Tappan and Loeblich tree).

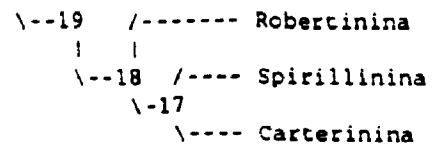

Euamoebae
Allogromiina
Astrorhizina
Haplophragmiina
Textulariina
Trochamminina
Carterinina
Fusulinina
Lagenina
Involutinina
Robertinina
Spirillinina
Rotaliina
Globigerinina
Miliolina
Silicoloculinina
1/3/4/5
1/3/4/5
Wall ultrastructure
unordered
0: Tectinous
1: Simple Agglutinated
2: Alveolar Canaliculate Agglutina
3: Microgranular
4: Porcellaneous
5: Hyaline Monolamellar
6: Hyaline Bilamellar
equivocal

APPENDIX III

Unordered (Fitch) parsimony (modelled Tappan and Loeblich tree).

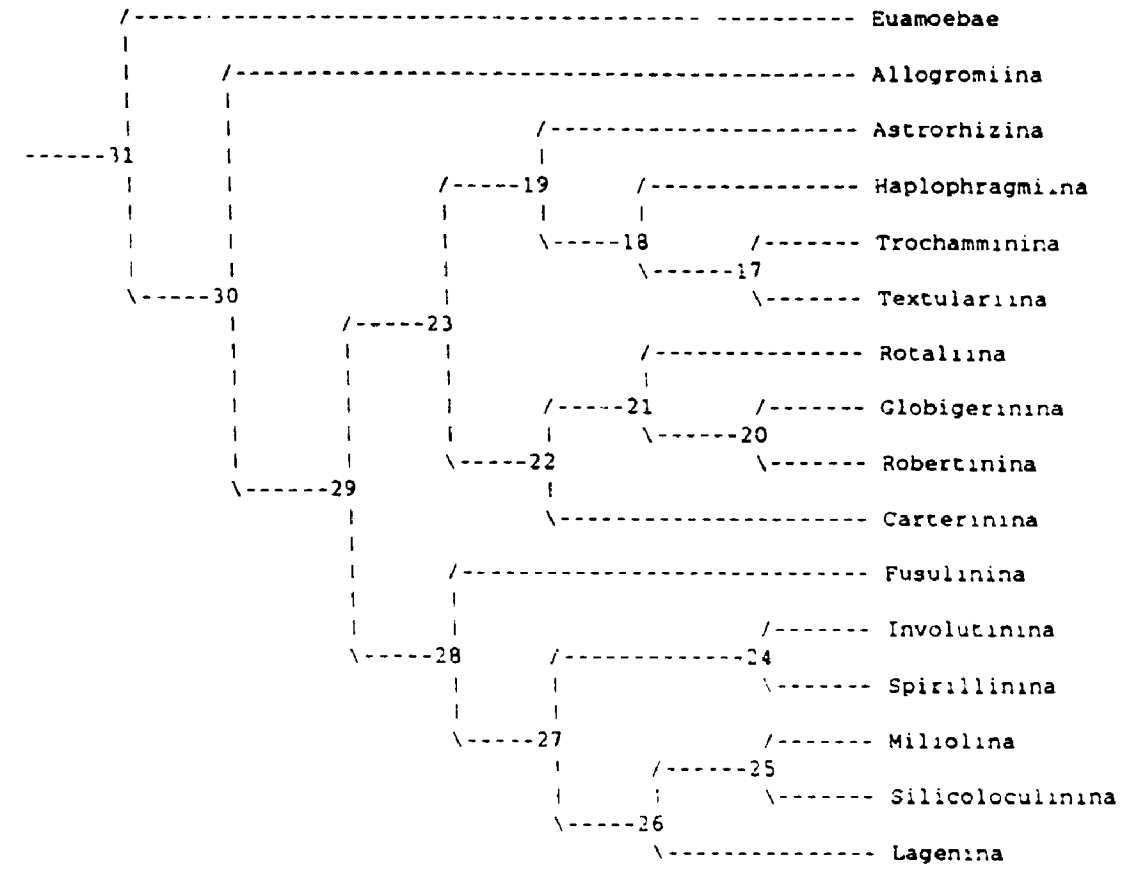
```
Processing of file "Loe.or. 2" begins...

Data matrix has 16 taxa, 10 characters
Valid character-state symbols: 01234567
Missing data identified by '?'
Gaps identified by '-', treated as "missing"

3 trees read from TREES block

Processing of file "Loe.or. 2" completed.

No taxa have been deleted.

No taxa have been assigned to the outgroup.  Outgroup defaults to first
taxon (Euamoebae).

Current status of all characters:

Character        Type      Inform?  Status     Weight    States

1.Shell          Unord        N                  1     01
2.Pseudopods     Unord        N                  1     01
3.Wall compo     Unord        Y                  1     01234567
4.Wall ultra     Unord        Y                  1     0123456
5.Test perfo     Unord        Y                  1     01
6.Test shape     Unord        Y                  1     012345
7.Number of      Unord        Y                  1     01
8.Chamber ar     Unord        Y                  1     012345
9.Chamber sh     Unord        Y                  1     012345
10.Surface sc    Unord        Y                  1     012345

Tree description:

   Character-state optimization: Accelerated transformation (ACCTRAN)

Tree number 1:

Tree length = 37
Consistency index (CI) = 0.703
Homoplasy index (HI) = 0.297
CI excluding uninformative characters = 0.686
HI excluding uninformative characters = 0.314
Retention index (RI) = 0.577
Rescaled consistency index (RC) = 0.405
```





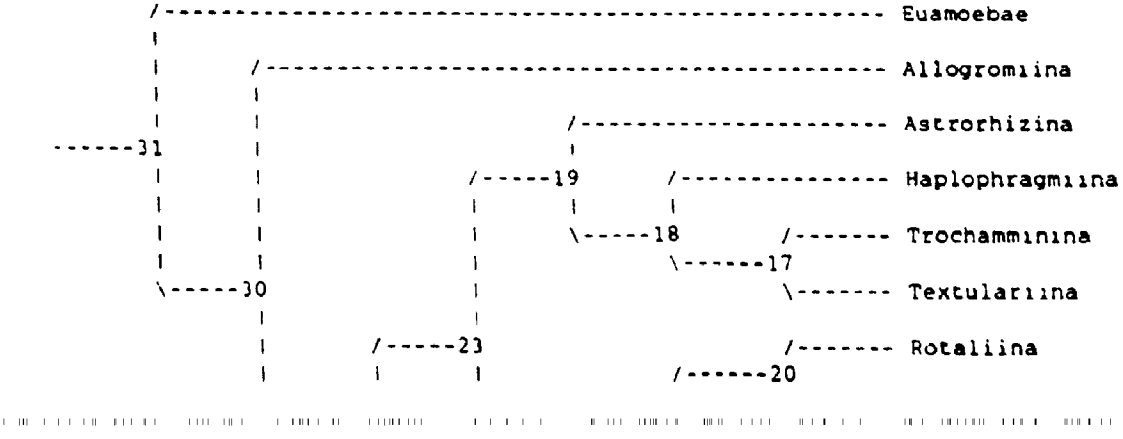
Tree number 2:

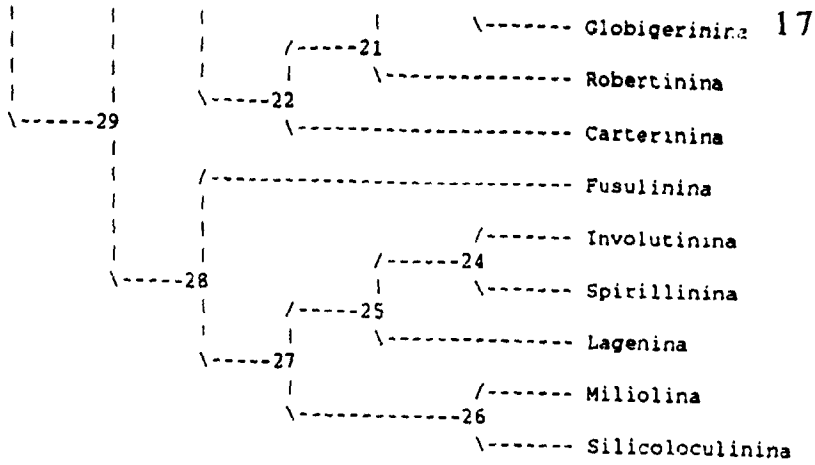
Tree length = 33
Consistency index (CI) = 0.788
Homoplasy index (HI) = 0.212
CI excluding uninformative characters = 0.774
HI excluding uninformative characters = 0.226
Retention index (RI) = 0.731
Rescaled consistency index (RC) = 0.576



Tree number 3:

Tree length = 32
Consistency index (CI) = 0.812
Homoplasy index (HI) = 0.188
CI excluding uninformative characters = 0.800
HI excluding uninformative characters = 0.200
Retention index (RI) = 0.769
Rescaled consistency index (RC) = 0.625

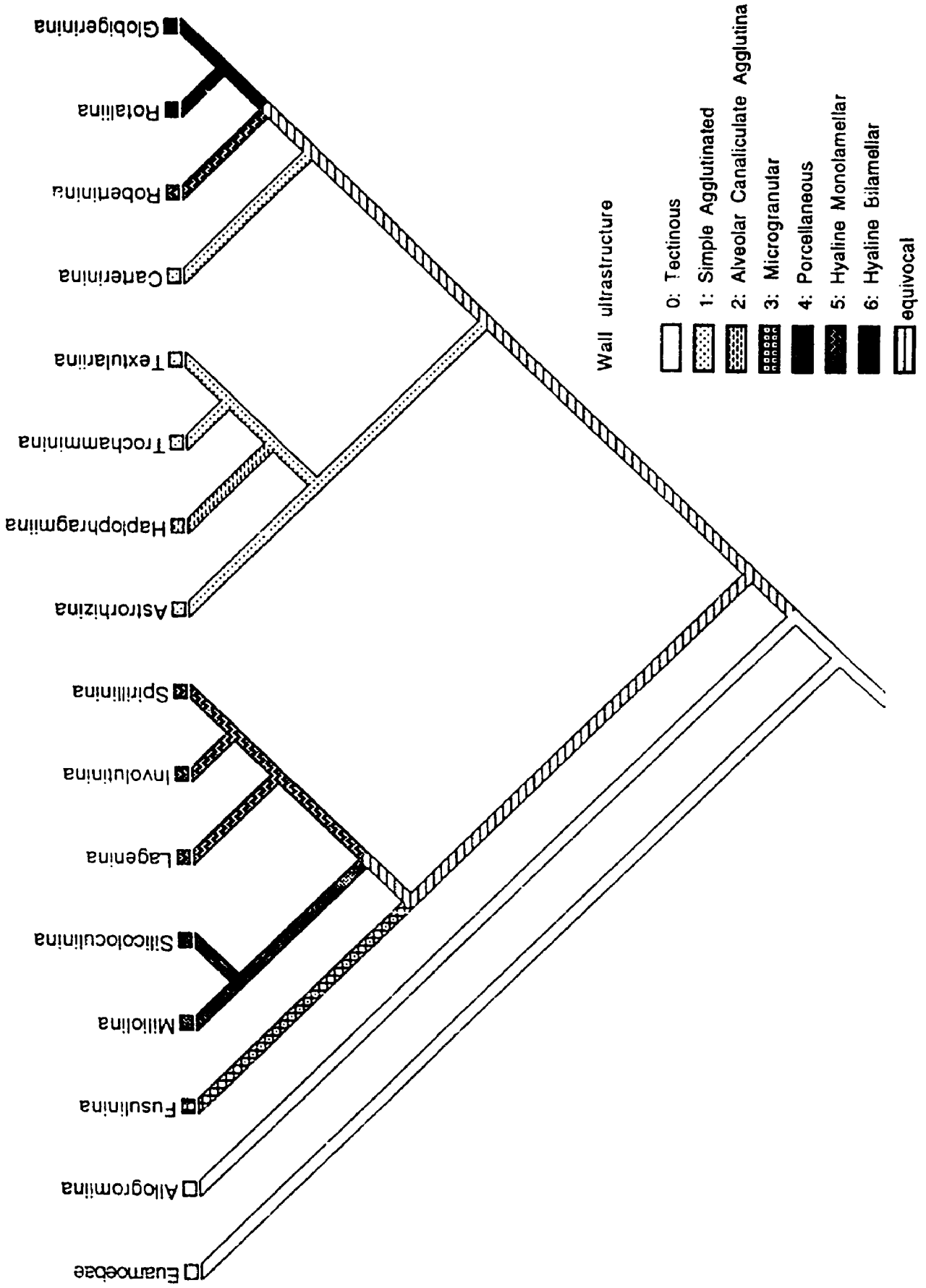



Globigerinina
Robertinina
Carterinina
Fusulinina
Involutinina
Spirillinina
Lagenina
Miliolina
Silicoloculinina

Display of character statistics of previous phylogenetic model (Unordered)

	Character	Type	Weight	States	Steps	CI	RI
☑	1. Shell	unordered	1	2	1	1.00	0.0
☑	2. Pseudopods	unordered	1	2	1	1.00	0.0
☑	3. Wall composition	unordered	1	8	8	0.88	0.67
☑	4. Wall ultrastructure	unordered	1	7	7	0.86	0.83
☑	5. Test perforation	unordered	1	2	2	0.50	0.80
☑	6. Test shape	unordered	1	6	3	0.67	0.50
☑	7. Number of chambers	unordered	1	2	2	0.50	0.50
☑	8. Chamber arrangement	unordered	1	6	5	0.60	0.80
☑	9. Chamber shape	unordered	1	6	1	1.00	1.00
☑	10. Surface sculpture	unordered	1	6	2	1.00	1.00

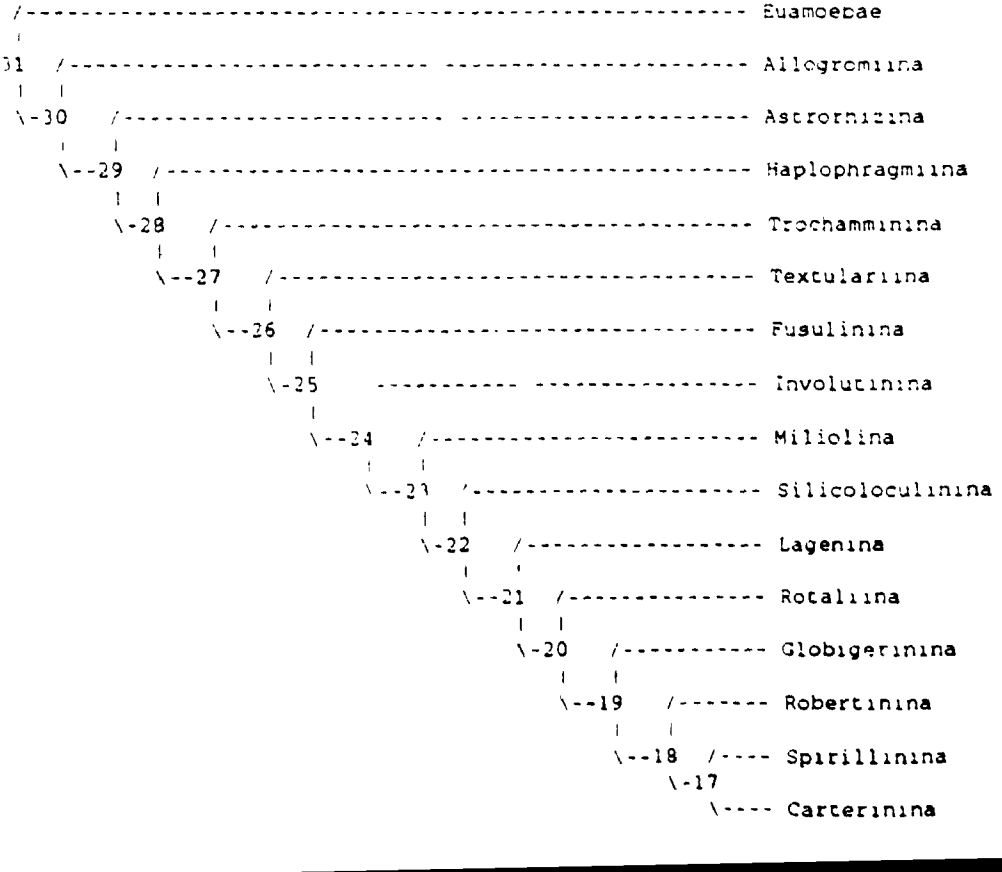
Wall composition
0: MembranaceousProteinaceous
1: Organic
2: Organic Agglutinated
3: Calcareous Agglutinated
4: Calcitic
5: Aragonitic
6: Siliceous
7: Secreted Spicular in Organic Gr
equivocal
Globigerinina
Rotaliina
Robertinina
Carterinina
Textulariina
Trochammininа
Haplophragmiina
Astrorhizina
Spirillinina
Involutinina
Lagenina
Silicoloculinina
Miliolina
Fusulinina
Allogromiina
Euamoebae


Wall ultrastructure
0: Tectinous
1: Simple Agglutinated
2: Alveolar Canaliculate Agglutina
3: Microgranular
4: Porcellaneous
5: Hyaline Monolamellar
6: Hyaline Bilamellar
equivocal
Globigerinina
Rotaliina
Robertinina
Carterinina
Textulariina
Trochammminina
Haplophragmiina
Astrorhizina
Spirillinina
Involutinina
Lageninа
Silicoloculinina
Miliolina
Fusulinina
Allogromiina
Euamoebae

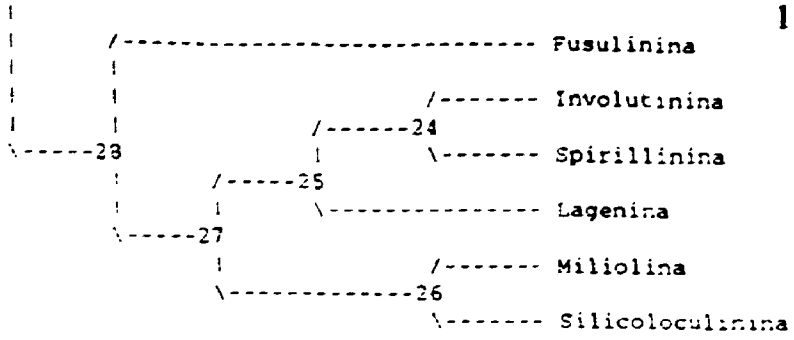
APPENDIX IV

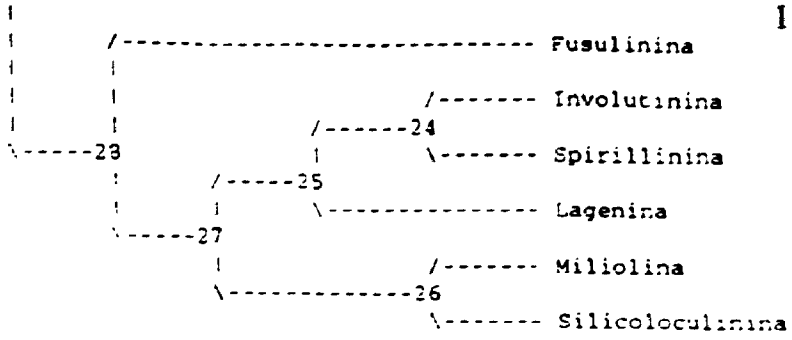
Mixed ordered and unordered (General) parsimony (modelled Tappan and Loeblich tree).

```
Processing of file "Loe.or. 2" begins .

Data matrix has 16 taxa, 10 characters
Valid character-state symbols: 01234567
Missing data identified by '?'
Gaps identified by '-', treated as "missing"

3 trees read from TREES block

Processing of file "Loe.or. 2" completed.

Current status of all characters:

Character        Type      Inform?  Status     Weight    States

1.Shell          Unord        N                  1     01
2.Pseudopods     Unord        N                  1     01
3.Wall compo     Yi. 1        Y                  1     01234567
4.Wall ultra     Yi.2         Y                  1     0123456
5.Test perfo     Unord        Y                  1     01
6.Test shape     Unord        Y                  1     012345
7.Number of      Unord        Y                  1     01
8.Chamber ar     Unord        Y                  1     012345
9.Chamber sh     Unord        Y                  1     012345
10.Surface sc    Unord        Y                  1     012345

Tree description:

   Character-state optimization: Accelerated transformation (ACCTRAN)

Tree number 1:

Tree length = 44
Consistency index (CI) = 0.591
Homoplasy index (HI) = 0.409
CI excluding uninformative characters = 0.571
HI excluding uninformative characters = 0.429
Retention index (RI) = 0.600
Rescaled consistency index (RC) = 0.355
```



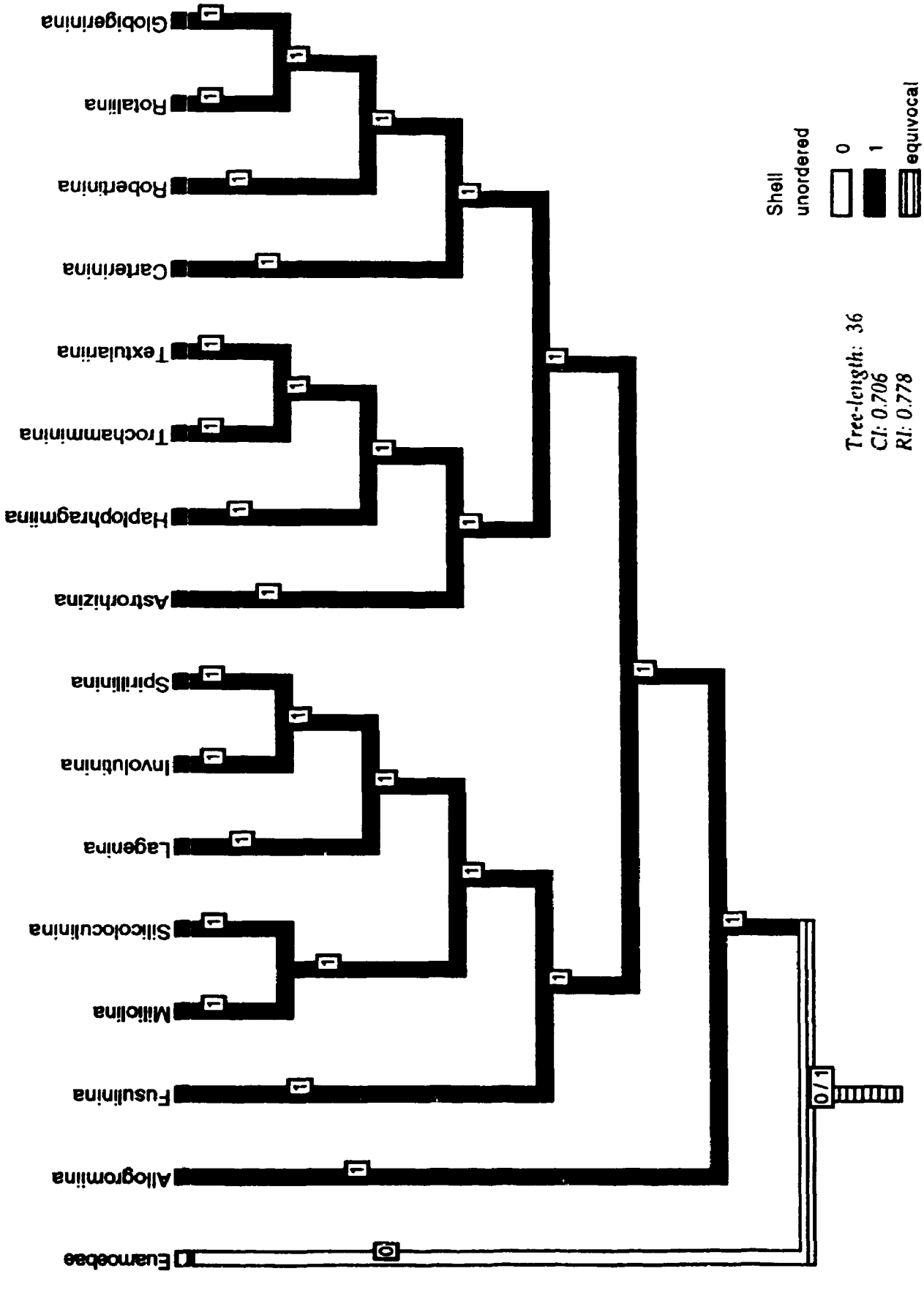
Pseudopods
unordered
0
1
equivocal
Globigerinina
Rotaliina
Robertinina
Carterinina
Textulariina
Trochammminina
Haplophragmiina
Astrorhizina
Spirillinina
Involutinina
Lagenina
Silicoloculinina
Miliolina
Fusulinina
Allogromiina
Euamoebae
0/1
Untitled


Fusulinina
Involutinina
24
Spirillinina
25
Lagenina
27
Miliolina
26
Silicoloculinina


Fusulinina
Involutinina
24
Spirillinina
25
Lagenina
27
Miliolina
26
Silicoloculinina

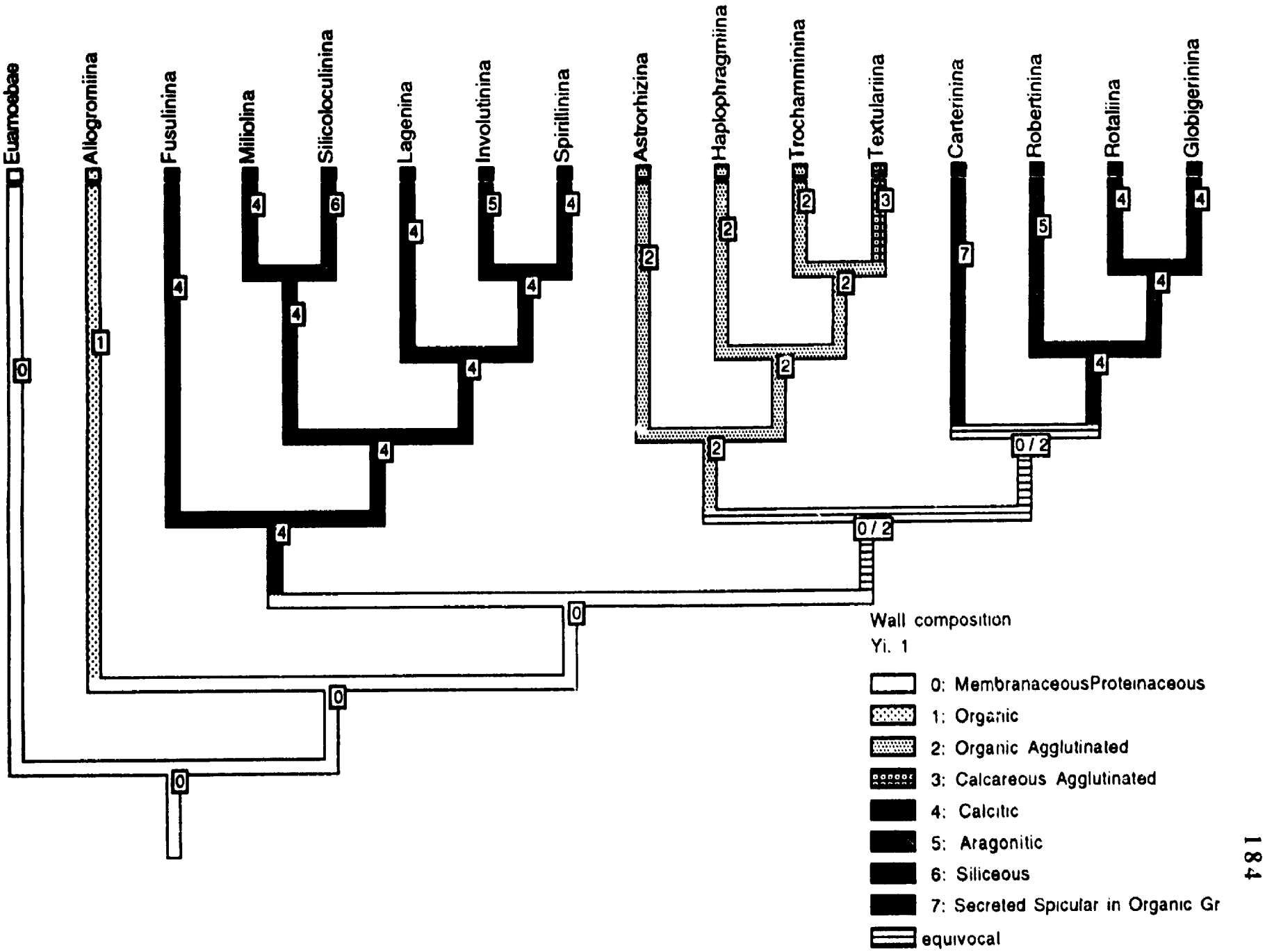
Display of character statistics of previous phylogenetic model (Ordered)

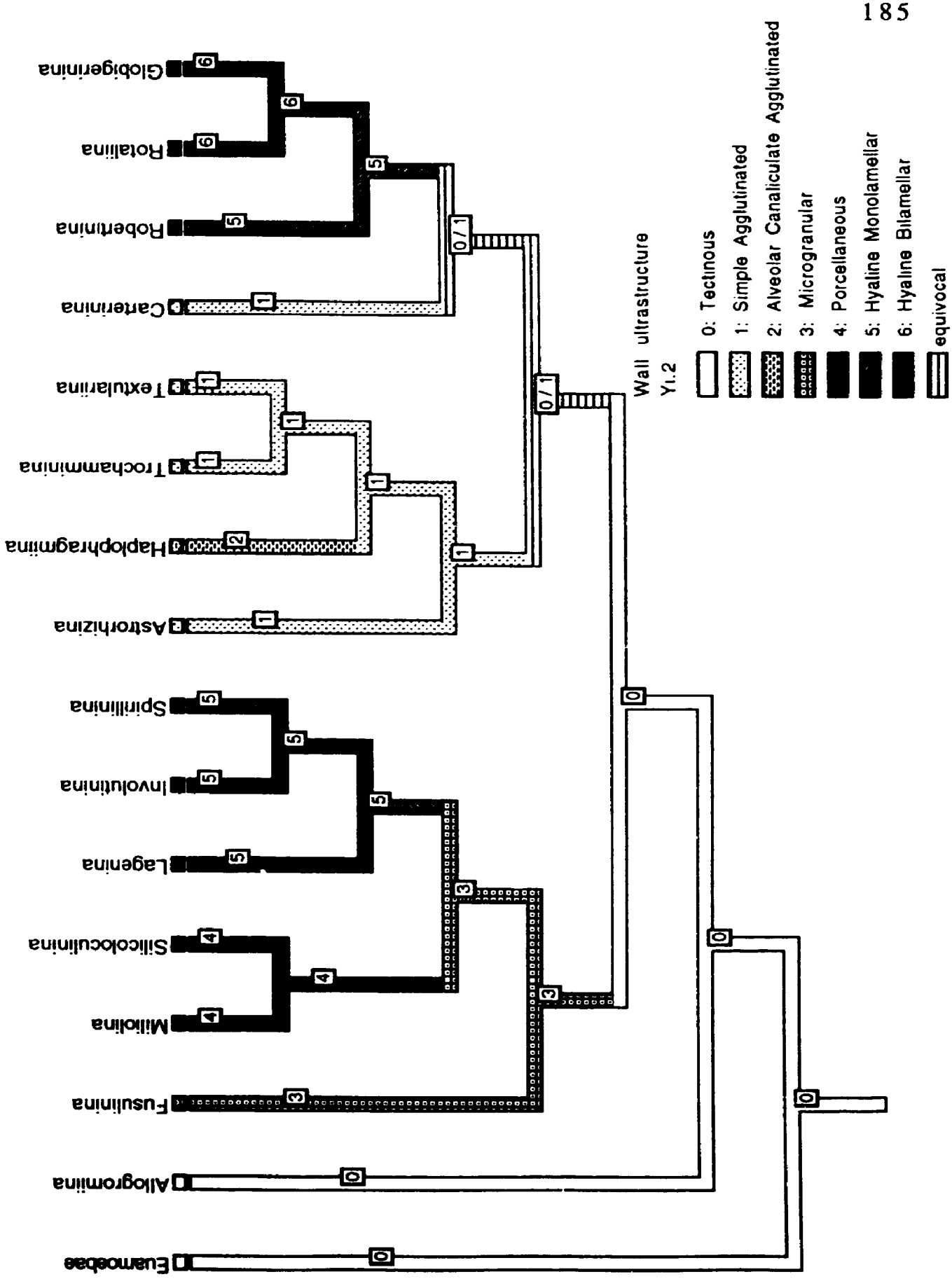
	Character	Type	Weight	States	Steps	CI	RI
☑	1. Shell	unordered	1	2	1	1.00	0.0
☑	2. Pseudopods	unordered	1	2	1	1.00	0.0
☑	3. Wall composition	Yi. 1	1	8	10	- -	- -
☑	4. Wall ultrastructure	Yi.2	1	7	9	- -	- -
☑	5. Test perforation	unordered	1	2	2	0.50	0.80
☑	6. Test shape	unordered	1	6	3	0.67	0.50
☑	7. Number of chambers	unordered	1	2	2	0.50	0.50
☑	8. Chamber arrangement	unordered	1	6	5	0.80	0.80
☑	9. Chamber shape	unordered	1	6	1	1.00	1.00
☑	10. Surface sculpture	unordered	1	6	2	1.00	1.00


Globigerinina
Rotaliina
Robertinina
Carterinina
Textulariina
Trochammminina
Haplophragmiina
Astrorhizina
Spirillinina
Involutinina
Lagenina
Silicoloculinina
Miliolina
Fusulinina
Allogromiina
Euamoebae
0/1
Shell
unordered
0
1
equivocal
Tree-length: 36
CI: 0.706
RI: 0.778
Untitled


Euamoebae
Allogromiina
Fusulinina
Miliolina
Silicoloculinina
Lagenina
Involutinina
Spirillinina
Astrorhizina
Haplophragmiina
Trochamminina
Textulariina
Carterinina
Robertinina
Rotaliina
Globigerinina
0
1
1
1
1
1
1
1
1
1
1
1
1
1
1
1
1
1
1
1
1
1
1
1
1
1
1
1
0 / 1
Pseudopods
unordered
0
1
equivocal

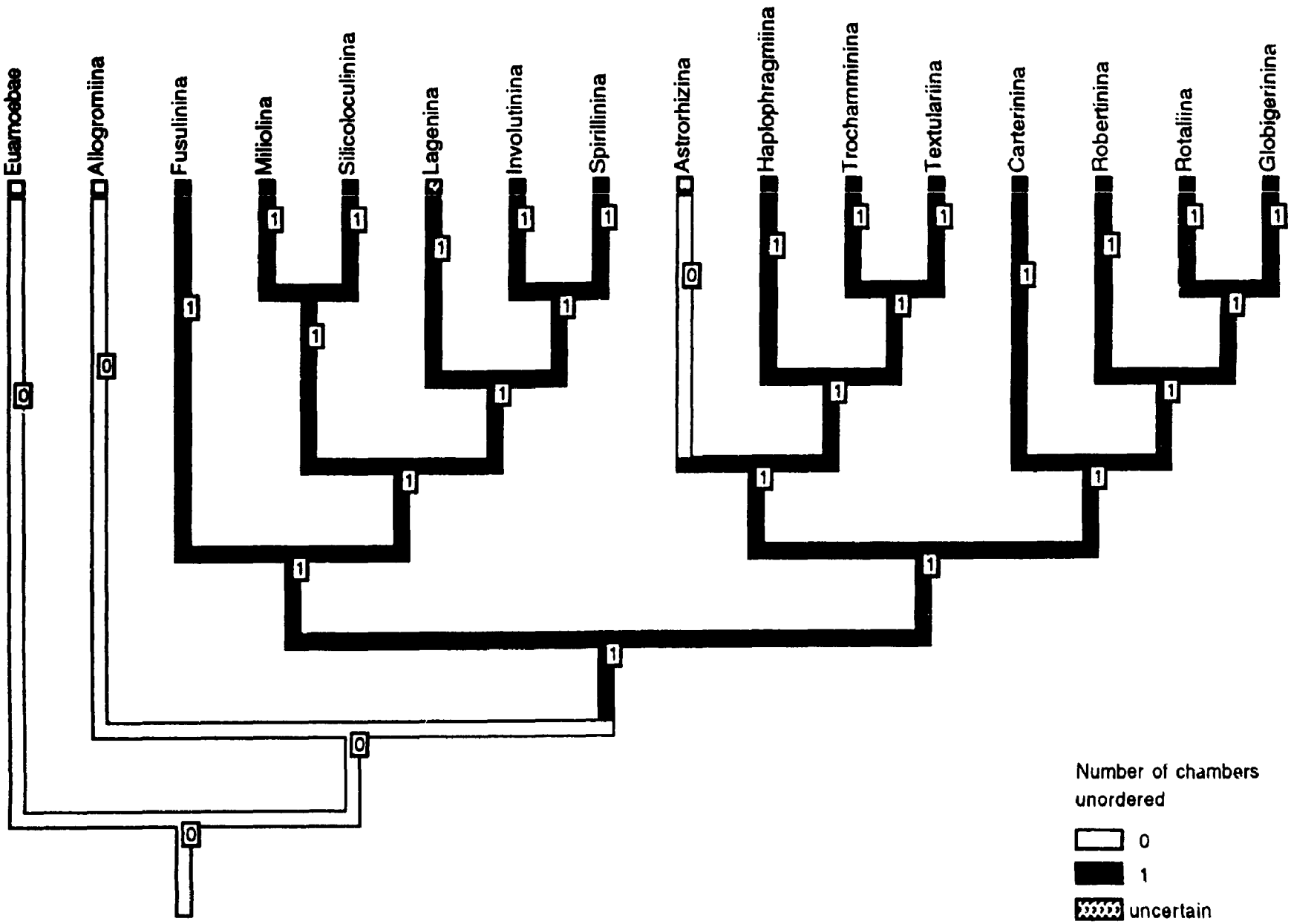
Untitled


Euamoebae
Allogromiina
Fusulinina
Miliolina
Silicoloculinina
Lagenina
Involutinina
Spirillinina
Astrorhizina
Haplophragmiina
Trochamminina
Textulariina
Carterinina
Robertinina
Rotaliina
Globigerinina
Wall composition
Yi. 1
0: MembranaceousProteinaceous
1: Organic
2: Organic Agglutinated
3: Calcareous Agglutinated
4: Calcitic
5: Aragonitic
6: Siliceous
7: Secreted Spicular in Organic Gr
equivocal

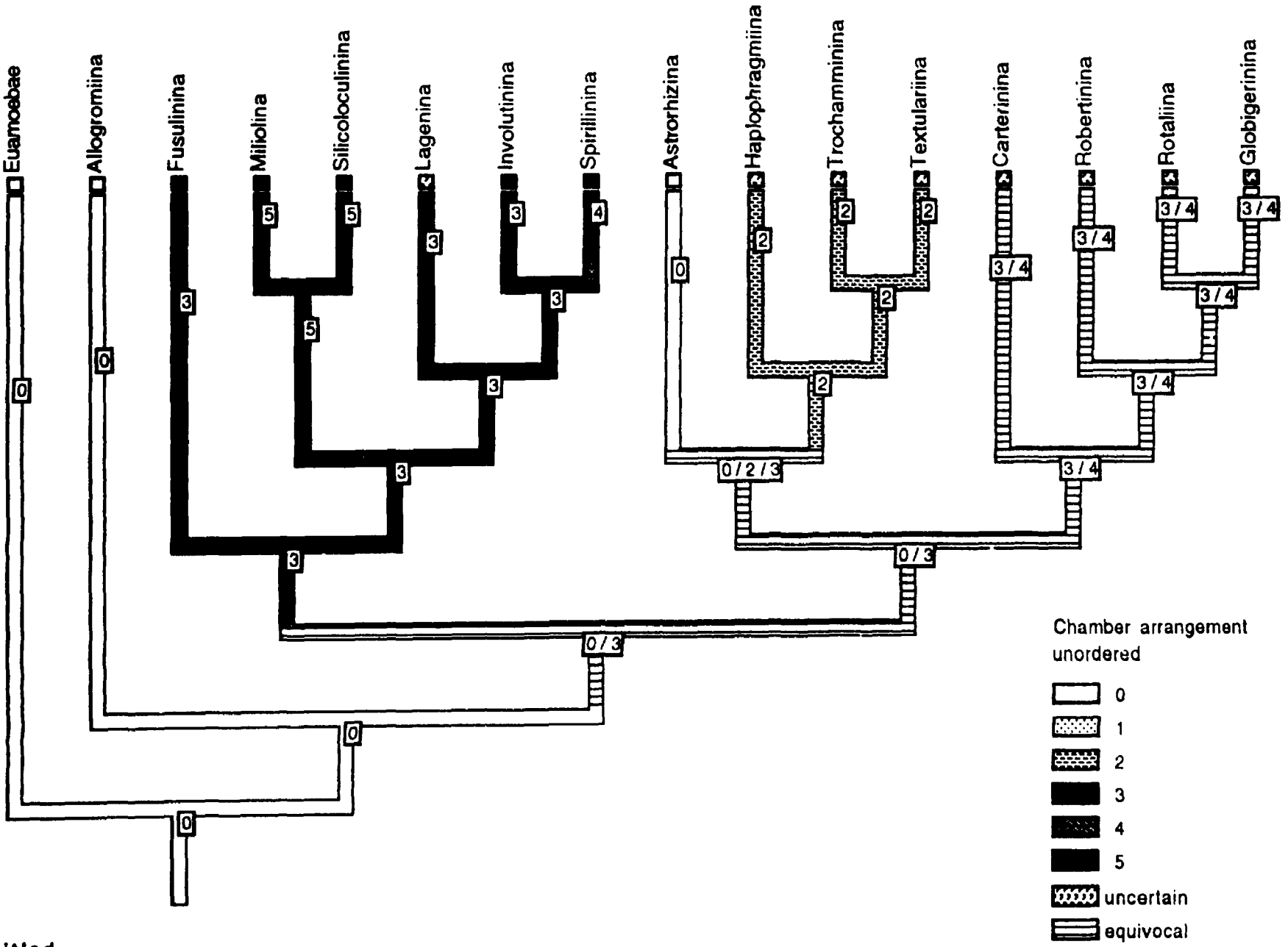

Wall ultrastructure
Y1.2
0: Tectinous
1: Simple Agglutinated
2: Alveolar Canaliculate Agglutinated
3: Microgranular
4: Porcellaneous
5: Hyaline Monolamellar
6: Hyaline Bilamellar
equivocal
Euamoebae
Allogromina
Fusulinina
Miliolina
Silicoloculinina
Lageninа
Involutinina
Spirillinina
Astrorhizina
Haplophragmiina
Trochammininа
Textulariina
Carterinina
Robertinina
Rotaliina
Globigerinina

Test perforation
unordered
0
1
Globigerinina
Rotaliina
Robertinina
Carterinina
Textulariina
Trochammminina
Haplophragmiina
Astrorhizina
Spirillinina
Involutinina
Lagenina
Silicoloculinina
Miliolina
Fusulinina
Allogromiina
Euamoebae
Untitled

Test shape
unordered
0
1
2
3
4
5
uncertain
equivocal
Globigerinina
Rotaliina
Robertinina
Carterinina
Textulariina
Trochammininа
Haplophragmiina
Astrorhizina
Spirillinina
Involutinina
Lagenina
Silicoloculinina
Miliolina
Fusulinina
Allogromiina
Euamoebae
Untitled

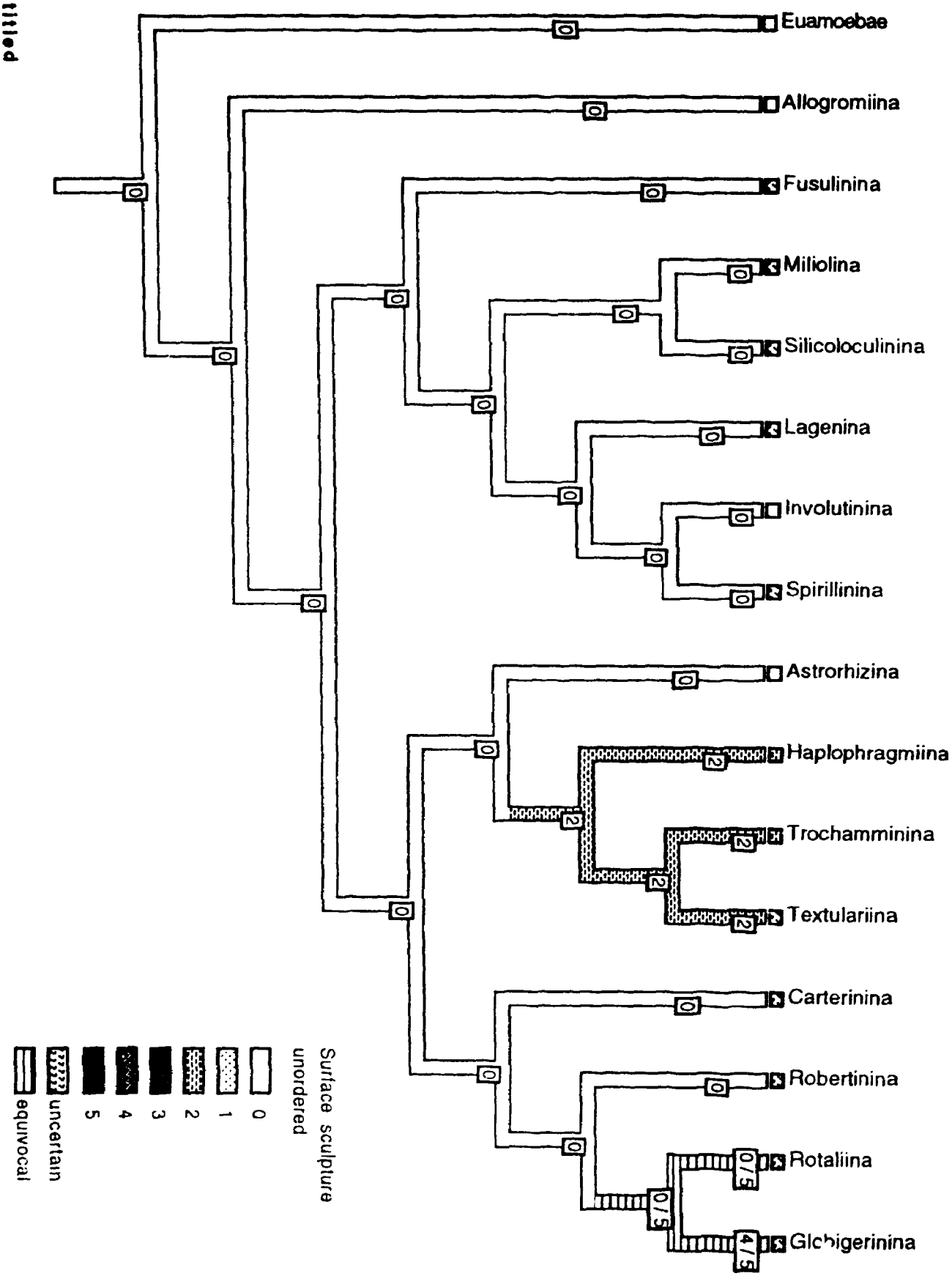

Euamoebae
Allogromiina
Fusulinina
Miliolina
Silicoloculinina
Lagenina
Involutinina
Spirillinina
Astrorhizina
Haplophragmiina
Trochammminina
Textulariina
Carterinina
Robertinina
Rotaliina
Globigerinina
Number of chambers
unordered
0
1
uncertain

Untitled

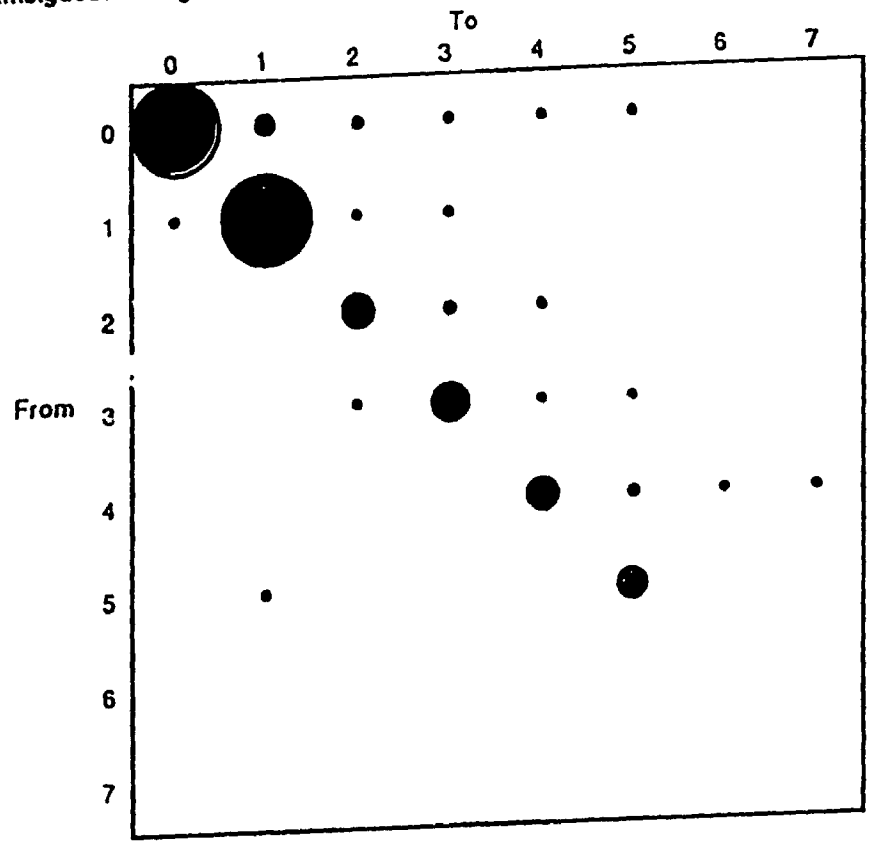

Euamoebae
Allogromiina
Fusulinina
Miliolina
Silicoloculinina
Lagenina
Involutinina
Spirillinina
Astrorhizina
Haplophragmiina
Trochamminina
Textulariina
Carterinina
Robertinina
Rotaliina
Globigerinina
Chamber arrangement
unordered
0
1
2
3
4
5
uncertain
equivocal

Untitled

Chamber shape
unordered
0
1
2
3
4
5
uncertain
Euamoebae
Allogromiina
Fusulinina
Miliolina
Silicoloculinina
Lagenina
Involutinina
Spirillinina
Astrorhizina
Haplophragmiina
Trochammminina
Textulariina
Carterinina
Robertinina
Rotaliina
Globigerinina
Untitled

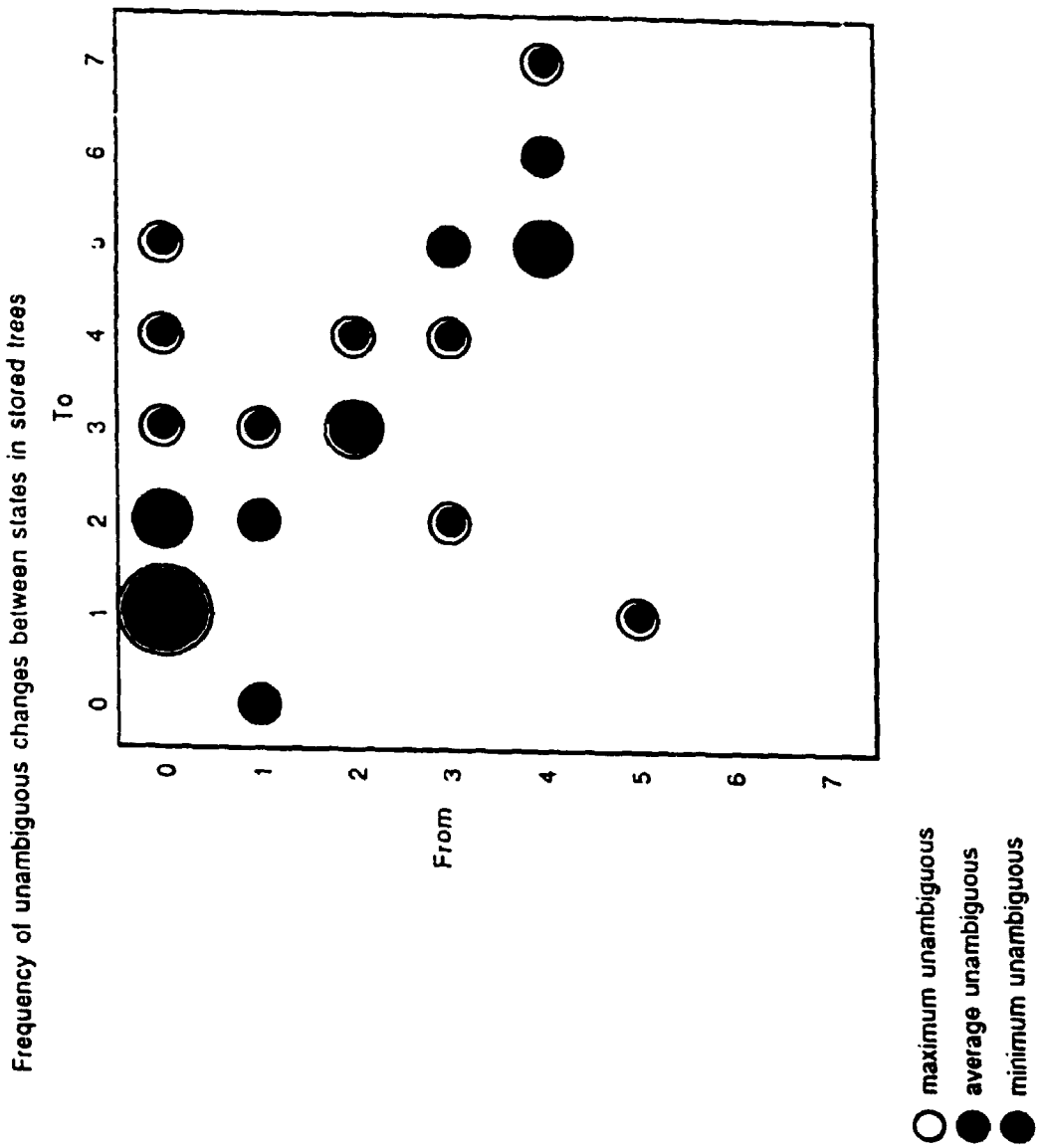

Euamoebae
Allogromiina
Fusulinina
Miliolina
Silicoloculinina
Lagenina
Involutinina
Spirillinina
Astrorhizina
Haplophragmiina
Trochamminina
Textulariina
Carterinina
Robertinina
Rotaliina
Glchigerinina
0 / 5
0 / 5
4 / 5
Surface sculpture
unordered
0
1
2
3
4
5
uncertain
equivocal

Frequency of unambiguous changes between states in stored trees



○ maximum unambiguous
● average unambiguous
● minimum unambiguous

This chart is calculated over all sites (i.e, character 7), coding and non coding, as no characters have been excluded.


Frequency of unambiguous changes between states in stored trees
To
0
1
2
3
4
5
6
7
From
0
1
2
3
4
5
6
7
maximum unambiguous
average unambiguous
minimum unambiguous

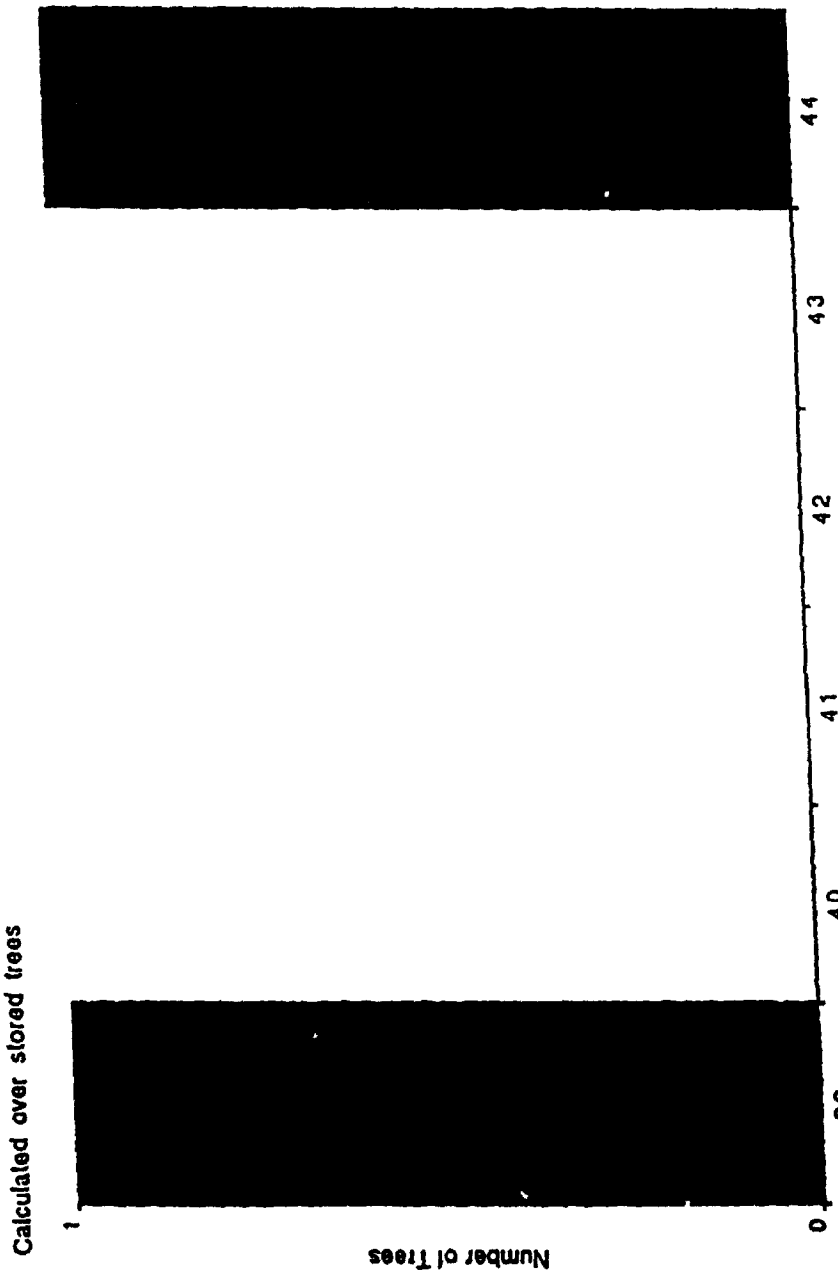


Chart showing that the total treelength is calculated as the sum of the number of steps for the individual characters multiplied by their respective weights.

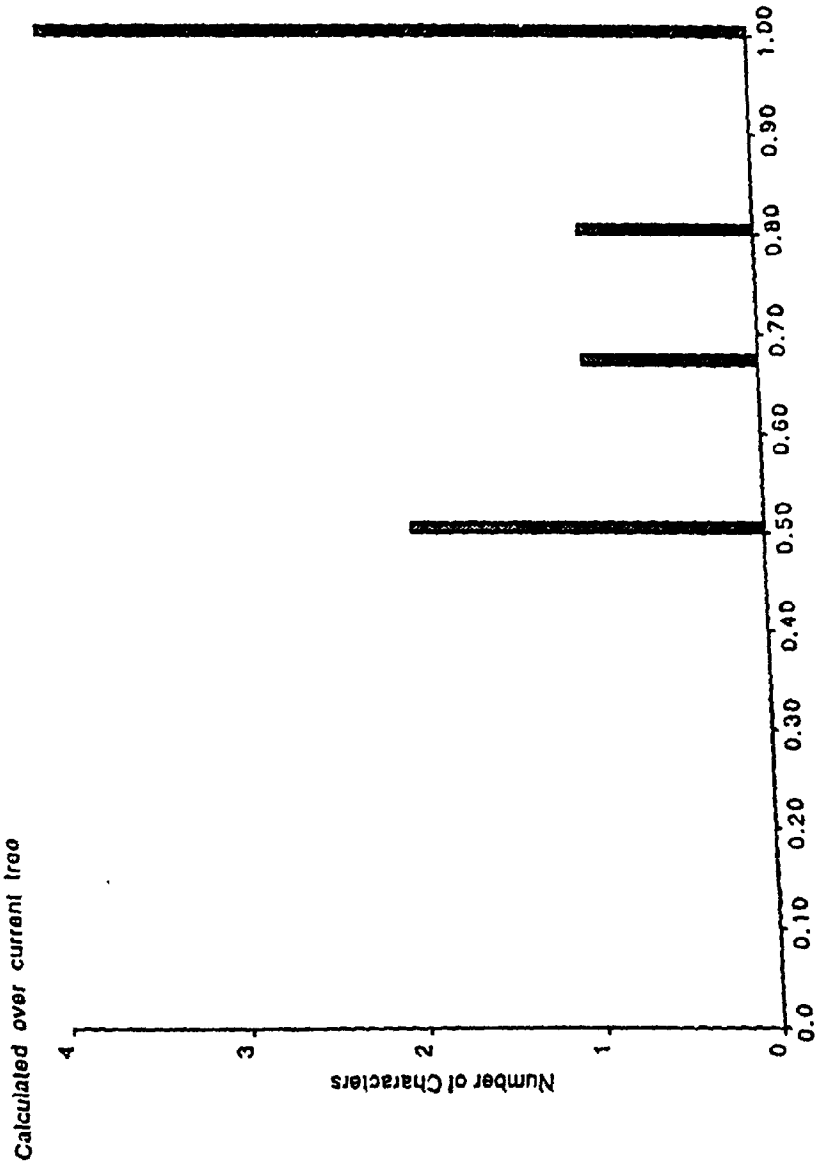


Chart shows that the consistency index (CI) for all characters on a tree is the *minimum* possible treelength divided by the observed treelength.

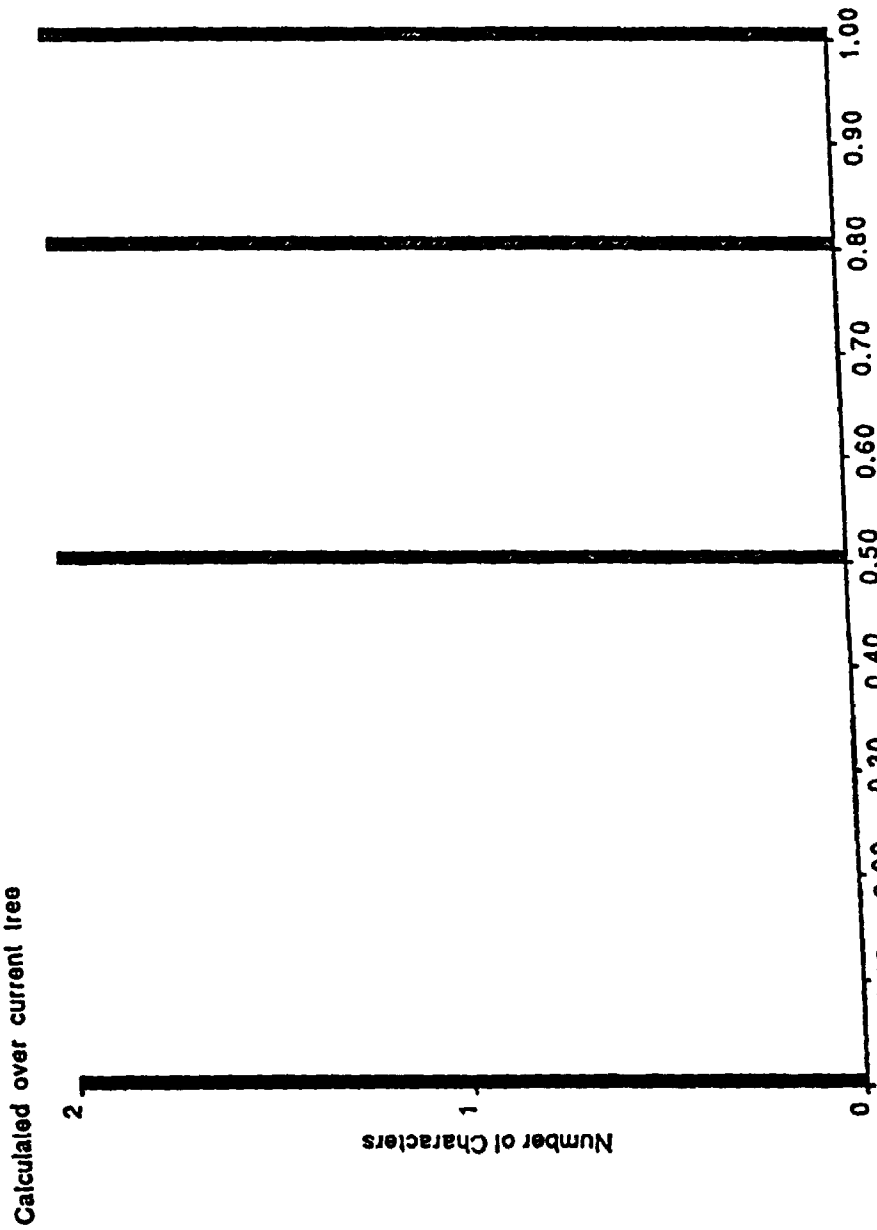


Chart shows that the retention index RI for all characters on a tree is calculated as the (maximum possible treelength-actual treelength)/(Maximum possible treelength- minimum possible treelength).

Chart shows most of the changes on the tree are at the first position.

END

17-1/1-95

FIN