INFORMATION TO USERS

This reproduction was made from a copy of a document sent to us for microfilming. While the most advanced technology has been used to photograph and reproduce this document, the quality of the reproduction is heavily dependent upon the quality of the material submitted.

The following explanation of techniques is provided to help clarify markings or notations which may appear on this reproduction.

1. The sign or “target” for pages apparently lacking from the document photographed is “Missing Page(s)”. If it was possible to obtain the missing page(s) or section, they are spliced into the film along with adjacent pages. This may have necessitated cutting through an image and duplicating adjacent pages to assure complete continuity.

2. When an image on the film is obliterated with a round black mark, it is an indication of either blurred copy because of movement during exposure, duplicate copy, or copyrighted materials that should not have been filmed. For blurred pages, a good image of the page can be found in the adjacent frame. If copyrighted materials were deleted, a target note will appear listing the pages in the adjacent frame.

3. When a map, drawing or chart, etc., is part of the material being photographed, a definite method of “sectioning” the material has been followed. It is customary to begin filming at the upper left hand corner of a large sheet and to continue from left to right in equal sections with small overlaps. If necessary, sectioning is continued again—beginning below the first row and continuing on until complete.

4. For illustrations that cannot be satisfactorily reproduced by xerographic means, photographic prints can be purchased at additional cost and inserted into your xerographic copy. These prints are available upon request from the Dissertations Customer Services Department.

5. Some pages in any document may have indistinct print. In all cases the best available copy has been filmed.

University Microfilms International
300 N. Zeeb Road
Ann Arbor, MI 48106
Schaferman, Steven Dale

PALEOBIOSYSTEMATICS OF THE ARTISCINAE LINEAGES (MIocene Radiolaria) AND THE IMPLICATIONS FOR BIOSTRATIGRAPHY, BIOSYSTEMATIC ANALYSIS, AND THE TEMPO AND MODE OF EVOLUTION

Rice University

Ph.D. 1983

University Microfilms International 300 N. Zeeb Road, Ann Arbor, MI 48106
PLEASE NOTE:

In all cases this material has been filmed in the best possible way from the available copy. Problems encountered with this document have been identified here with a check mark

1. Glossy photographs or pages ✓
2. Colored illustrations, paper or print
3. Photographs with dark background
4. Illustrations are poor copy
5. Pages with black marks, not original copy
6. Print shows through as there is text on both sides of page
7. Indistinct, broken or small print on several pages
8. Print exceeds margin requirements
9. Tightly bound copy with print lost in spine
10. Computer printout pages with indistinct print
11. Page(s) ________ lacking when material received, and not available from school or author.
12. Page(s) ________ seem to be missing in numbering only as text follows.
13. Two pages numbered ________. Text follows.
14. Curling and wrinkled pages
15. Other __________________________
RICE UNIVERSITY

PALEOBIOSYSTEMATICS OF THE ARTISCINAE LINEAGES
(MIOCENE RADIOLARIA) AND THE IMPLICATIONS FOR
BIOSTRATIGRAPHY, BIOSYSTEMATIC ANALYSIS,
AND THE TEMPO AND MODE OF EVOLUTION

by

STEVEN DALE SCHAFFERSMAN

A THESIS SUBMITTED
IN PARTIAL FULFILLMENT OF THE
REQUIREMENTS FOR THE DEGREE

DOCTOR OF PHILOSOPHY

APPROVED, THESIS COMMITTEE:

Richard E. Casey, Professor of Geology
Chairman

Dr. John A. S. Adams, Professor of Geology

Dr. Frank M. Fisher, Professor of Biology

HOUSTON, TEXAS

APRIL, 1983
PALEOBIOSYSTEMATICS OF THE ARTISCINAE LINEAGES
(MIOCENE RADIOLARIA) AND THE IMPLICATIONS FOR
BIOSTRATIGRAPHY, BIOSYSTEMATIC ANALYSIS,
AND THE TEMPO AND MODE OF EVOLUTION

ABSTRACT

Species (single lineages) of two clades (extended lineages) of the polycystine radiolarian subfamily Artiscinae were studied to determine their pattern of evolutionary change in Miocene tropical pelagic sediments. Morphometric measurements were made on specimens from 43 closely-spaced samples from a continuous stratigraphic sequence in DSDP core 9-77B, eastern equatorial Pacific. The samples are at approximately 165,000 year intervals through a 7.1 m.y. period.

For this study, a new method of biosystematic analysis was formulated to deal with fossil organisms that are suspected to exhibit gradual anagenetic change through time. First, a stratophenetic analysis is performed to discover and eliminate continuous plesiomorphic characters which undergo anagenesis and stasisgenesis; this procedure leaves apomorphic characters of two types: punctuated continuous characters and new discrete characters. These apomorphic characters, the result of cladogenesis, are used to identify speciation events and, by using synapomorphies, perform a cladistic analysis which results in a classification. A type 1 genealogy can be inferred from the cladogram a type 2 genealogy is derived from stratigraphic data. Combining a type 2 genealogy with a stratophenogram results in a phylogeny. Three types of lineages and three types of extinction are defined to enable unequivocal interpretation of microevolutionary and macroevolutionary processes and patterns.
Evolution in the artiscins is both punctuated and gradual: the *Ommartus tetrathalamus* clade and the *O. hughesi* clad both contain gradually-changing characters, but in both clades descendants are separated from ancestors by cladogenetic events and the appearance of apomorphic characters. Other characters reveal stasis. Previous authors arbitrarily subdivided single continuous characters undergoing anagenesis to delimit artiscin species, but this practice is typological and ignores species variability and important apomorphic characters. For these reasons, the species *Cannartus laticonus* and *O antepenultimus* are synonymized with *O penultimus*. Furthermore, the character of polar caps is not homologous between the two artiscin lineages; in the *O hughesi* lineage, caps develop from the spongy column, not as an extension of the cortical shell. Since anagenetic phyletic change in the artiscins controls macroevolutionary change to an extent equal to cladogenetic punctuated change, there is no reason to adopt a punctuated model over a gradual one for this taxon. However, artiscin classification must be radically revised in light of the monophyletic lineages (clades) delimited by cladistic analysis. Furthermore, the implications of this study make clear the necessity to rely solely on material, non-evolutionary data for biostratigraphic purposes. Lineage-zones and phyletic-biohorizons are invalid because they require a specific evolutionary model and method of phylogenetic inference, neither of which can apriori be assumed to be correct.
ACKNOWLEDGMENTS

A number of individuals deserve my thanks for their assistance during the course of my research and preparation of this dissertation. I am extremely grateful to Dr. Richard Casey for his unfailing assistance, concern, and patience during the many years this study was in progress. Dr. Casey served as my dissertation committee chairman, and I will remember and benefit from the personal example he set of hard work and emphasis upon empirical data for success in the profession of science. I also wish to thank Dr. John Adams and Dr. Frank Fisher for serving on my research committee and reviewing my dissertation. My stratophenetic data were plotted by Mrs. Pam Gray. The final stratophenograms and other figures were drafted by Mr. Dale Schulze. The photographs were printed by Ms. Kathy Hallett from plates prepared by me. The dissertation was typed and reproduced with the financial assistance of my employer, Tenneco Oil Exploration and Production. I am very grateful for Tenneco's help in completing this project.

Finally, sample preparation expenses and two years of graduate student tuition and stipend were paid by a grant to Dr. Richard Casey from the Donors of the Petroleum Research Fund administered by the American Chemical Society. I thank them for their financial support of my research.
# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Introduction</td>
<td>1</td>
</tr>
<tr>
<td>Purpose and scope of the study</td>
<td>1</td>
</tr>
<tr>
<td>Methods of the study</td>
<td>16</td>
</tr>
<tr>
<td>Core location and correlation of samples</td>
<td>16</td>
</tr>
<tr>
<td>Sample preparation</td>
<td>27</td>
</tr>
<tr>
<td>Morphometrics and statistics</td>
<td>28</td>
</tr>
<tr>
<td><strong>Biosystematics, paleontology, and evolution</strong></td>
<td>39</td>
</tr>
<tr>
<td>Methods of biosystematic analysis</td>
<td>39</td>
</tr>
<tr>
<td>Models of evolution and phylogenetic inference</td>
<td>63</td>
</tr>
<tr>
<td>Fossil species and speciation</td>
<td>80</td>
</tr>
<tr>
<td>Evolutionary species and fossil lineages</td>
<td>80</td>
</tr>
<tr>
<td>Modes of speciation</td>
<td>99</td>
</tr>
<tr>
<td>Types of extinction</td>
<td>107</td>
</tr>
<tr>
<td>Evolutionary relationships and systematics</td>
<td>111</td>
</tr>
<tr>
<td>Review of examples in the recent literature</td>
<td>131</td>
</tr>
<tr>
<td><strong>Results and interpretation of the biosystematic analysis of</strong></td>
<td>145</td>
</tr>
<tr>
<td>the Miocene Artiscinae</td>
<td></td>
</tr>
<tr>
<td><strong>Biosystematic analysis</strong></td>
<td>145</td>
</tr>
<tr>
<td>Stratophenograms and alternative interpretations</td>
<td>145</td>
</tr>
<tr>
<td>Cladistic analysis</td>
<td>206</td>
</tr>
<tr>
<td>Genealogical analysis</td>
<td>214</td>
</tr>
<tr>
<td>Phylogenetic analysis</td>
<td>218</td>
</tr>
<tr>
<td>Topic</td>
<td>Page</td>
</tr>
<tr>
<td>------------------------------------------------------------</td>
<td>------</td>
</tr>
<tr>
<td>The tempo and mode of evolution</td>
<td>220</td>
</tr>
<tr>
<td>Evolutionary change within the artiscin lineages</td>
<td>220</td>
</tr>
<tr>
<td>Punctuation versus gradualism</td>
<td>222</td>
</tr>
<tr>
<td><strong>Implications for biostratigraphy</strong></td>
<td>224</td>
</tr>
<tr>
<td>The use of evolutionary theory in biostratigraphy</td>
<td>224</td>
</tr>
<tr>
<td>Lineage-zones and phyletic-biohorizons in biostratigraphy</td>
<td>243</td>
</tr>
<tr>
<td><strong>Introduction</strong></td>
<td>243</td>
</tr>
<tr>
<td>Critique of lineage-zones and phyletic-biohorizons</td>
<td>245</td>
</tr>
<tr>
<td>Lineage-zones and planktonic foraminifera</td>
<td>266</td>
</tr>
<tr>
<td>Lineage-zones and radiolaria</td>
<td>285</td>
</tr>
<tr>
<td>Critique of idiosyncratic evolutionary theory in radiolarian taxonomy and biostratigraphy</td>
<td>310</td>
</tr>
<tr>
<td><strong>Summary of major conclusions</strong></td>
<td>324</td>
</tr>
<tr>
<td><strong>References</strong></td>
<td>329</td>
</tr>
</tbody>
</table>
# LIST OF FIGURES

<table>
<thead>
<tr>
<th>FIGURE</th>
<th>PAGE</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Illustration of the traditional interpretation of artiscin genealogy</td>
<td>15</td>
</tr>
<tr>
<td>2. Core location and migration track map</td>
<td>17</td>
</tr>
<tr>
<td>3. Geologic cross-section of DSDP Site 9-77</td>
<td>18</td>
</tr>
<tr>
<td>4. Correlation of radiolarian index-species with the paleomagnetic and absolute time scales</td>
<td>22</td>
</tr>
<tr>
<td>5. Comparison of the artiscin biohorizons in DSDP Core 9-77 B of Goll versus Westberg and Riedel</td>
<td>24</td>
</tr>
<tr>
<td>6. Artiscin skeletal measurements for morphometric and biosystematic analysis</td>
<td>31</td>
</tr>
<tr>
<td>7. Six types of evolutionary diagrams used in systematic biology</td>
<td>46</td>
</tr>
<tr>
<td>8. Two diagrams to illustrate monophyly, paraphyly, and polyphyly</td>
<td>56</td>
</tr>
<tr>
<td>9. Models of evolution, gradual versus punctuated</td>
<td>67</td>
</tr>
<tr>
<td>10. Two diagrams illustrating subdivision of successional species (paleospecies)</td>
<td>93</td>
</tr>
<tr>
<td>11. Photomicrographs of <em>Ommatartus penultimus</em></td>
<td>149</td>
</tr>
<tr>
<td>12. Photomicrographs of <em>Ommatartus penultimus</em></td>
<td>151</td>
</tr>
<tr>
<td>13. Photomicrographs of <em>Ommatartus penultimus</em> and <em>O. tetrathalamus</em></td>
<td>153</td>
</tr>
</tbody>
</table>
14. Photomicrographs of *Ommatartus petterssoni*. 155
15. Photomicrographs of *Ommatartus petterssoni* and *O. hughesi*. 157
16. Stratophenogram of artiscin total length 163
17. Stratophenogram of artiscin cortical shell length 165
18. Stratophenogram of artiscin cortical shell width 167
19. Stratophenogram of artiscin spongy column length 169
20. Stratophenogram of artiscin spongy column width 171
21. Stratophenogram of artiscin polar cap length 173
22. Stratophenogram of artiscin polar cap width 175
23. Stratophenogram of artiscin polar cap length ÷ spongy column length 177
24. Stratophenogram of artiscin spongy column length ÷ total length 179
25. Stratophenogram of artiscin cortical shell length ÷ total length 181
26. Stratophenogram of artiscin polar cap width ÷ cortical shell width 183
27. Stratophenogram of artiscin polar cap length ÷ cortical shell length 185
28. Stratophenogram of artiscin spongy column width ÷ polar cap width 187
29. Stratophenogram of artiscin spongy column width ÷ cortical shell width 189
30. Alternative interpretations of the artiscin spongy column width stratophenogram 194
31. Alternative interpretations of the artiscin polar cap length stratophenogram 196
32. Alternative interpretations of the artiscin polar cap length ÷ cortical shell length stratophenogram 198
33. Alternative interpretations of the artiscin spongy column width ÷ polar cap width stratophenogram 200
34. Alternative interpretations of the artiscin spongy column width ÷ cortical shell width stratophenogram 202
35. A cladogeny of five species of the Artiscinae 208
36. The artiscin cladogram with apomorphies and plesiomorphies indicated 210
37. A type 1 genealogy of five species of the Artiscinae 215
38. A type 2 genealogy of five species of the Artiscinae 217
39. Four major types of biozones 253
40. Model of gradual planktonic foraminifer evolution 260
41. Illustrations of the Globorotalia fohsi subspecies 268
42. Chart of the Globorotalia fohsi lineage-zones 270
43. Two diagrams illustrating the "evolutionary limits" of Riedel and Sanfilippo 293
44. The tropical Cenozoic radiolarian biozonation of Riedel and Sanfilippo 311
LIST OF TABLES

<table>
<thead>
<tr>
<th>TABLE</th>
<th>PAGE</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. List of DSDP core 9-77B samples</td>
<td>19</td>
</tr>
<tr>
<td>2. Summary of range-limit data from DSDP 9-77B studies</td>
<td>26</td>
</tr>
<tr>
<td>3. Sampling and methodological criteria for testing evolutionary hypotheses</td>
<td>40</td>
</tr>
</tbody>
</table>
INTRODUCTION

Purpose and Scope of the Study

The availability of stratigraphically long-ranging and hiatus-free sequences of pelagic sediment in deep sea cores has markedly increased in recent years due to the activity of the Deep Sea Drilling Program and similar ocean sampling programs using piston cores. Such deep sea cores offer relatively complete and continuous records of the evolutionary history of testate microplankton, primarily radiolarians, planktonic foraminifera, and calcareous nannoplankton. The importance of such sedimentary records is obvious, for it is possible to use this material to examine the morphologic change a species undergoes during evolution at intervals measured in ecologic time rather than at intervals of geologic time as has been the case in the past. The increased interest in evolutionary patterns as seen in the fossil record, and paleontologists' new awareness of their discipline's potential for significant additions to evolutionary theory, can well be served by study of microfossils in cored pelagic sediments.

The purpose of this study is to investigate, document, and interpret the pattern, and perhaps the process, of evolution as seen in the fossil record of the Artiscinae, a subfamily of radiolarians that has an excellently-preserved Miocene evolutionary record. In past decades, this task would appear to be relatively straightforward: an investigator would merely identify the fossil species, genera, or higher taxa, locate them stratigraphically against a relative time scale,
connect them by lines of descent in the pattern that appeared most appropriate, and then explain the pattern by whatever theory of evolution the investigator happened to believe in. Significantly, by this method it was quite possible to both identify species and perceive their phylogenetic relationships by simple observation, since evolution could be "seen" in the fossil record by any competent and knowledgeable investigator. Furthermore, it was quite possible to explain any phylogenetic pattern by any theory of evolution, since, historically, this is exactly what was done. This method of investigation and interpretation is still being practiced today by many paleontologists.

Today, however, paleontologists are aware that the goals and methods of science require more rigor in the performance of a phylogenetic investigation. We are not at liberty to examine the pattern and process of evolution visible in the fossil record by the methods and assumptions of previous years. Today, a new awareness of the nature of scientific method permits new hypotheses about evolutionary process and pattern and requires a carefully thought-out theoretical framework in the formulation and testing of these hypotheses. Also today, because of this new awareness, evolutionary science and biosystematics are in a state of extreme controversy and transition. These are the reasons why the present study is not an easy task. It is necessary today to consider our theoretical assumptions and methods as well as the empirical evidence before claiming an increase in scientific knowledge about any aspect of evolution.

Both biosystematics and macroevolutionary theory are in a state of marked change. Both are undergoing a scientific revolution or
renaissance of major importance to any biosystematist who wishes to study and classify organisms. More importantly, the relationship of fossil organisms in taxonomic and evolutionary theory is even more problematic than that of living organisms. Today we have conflicting models of speciation, models of phylogeny, methods of phylogenetic inference, and methods of classification. The recent availability of fossil material capable of being sampled at relatively fine stratigraphic intervals therefore appears at a time of extreme controversy, and its availability will either increase or remove some of the confusion which surrounds many of the issues. This paper is an attempt to examine some of those issues in light of recently gained knowledge concerning evolutionary change in microfossils sampled at short stratigraphic intervals in thick and complete sedimentary sequences.

Another purpose of this paper is to investigate the use of evolutionary theory in biostratigraphy. Biostratigraphy has been practiced since the beginning of the 19th century, its principles have been proposed and modified at various times during its history, and these principles have recently been stated in the International Stratigraphic Guide (Hedberg, 1976). The American Stratigraphic Code is soon to be revised (Oriel and Weiss, 1979), and it would be well to examine again the principles of biostratigraphy involving the use of lineage-zones, as enunciated in the Guide, for possible revision. To this end I will examine the work of micropaleontologists who deal with biostratigraphic zonations of microfossils, and see how the existence of excellently-preserved and finely-sampled material from complete and
continuous sedimentary sections has influenced their perception of the nature of the evolutionary process and led to adoption of idiosyncratic biostratigraphic and taxonomic concepts and practices.

In the last few years an immense literature has appeared which discusses the new concepts, principles, and theory of biosystematics. A paleontologist or biostratigrapher unfamiliar with the material may find terminology in the present paper difficult to understand, so I have taken care to define some commonly used but ambiguous terms. That this must be done is unfortunate, for the current controversy has ironically muddled terminology at the same time it has clarified scientific thinking. Only someone familiar with the bulk of the literature and of the history of biosystematic revision will be able to wade without slipping through the morass of overly-generalized claims, ill-conceived arguments, ignored criticism, subjective interpretations, and aimless polemic found in the current literature, all fashioned out of idiosyncratic definitions attached to commonly-used terms and subtle distinctions of meaning which escape all but the initiated.

The success of the Deep Sea Drilling Program is by now too well known to require major discussion. Its major contribution so far has been to obtain stratigraphic and sedimentologic data which have massively corroborated the theory of plate tectonics. However, for the purposes of evolution and biosystematics the DSDP has exciting potential which has not yet been properly exploited. The DSDP cores have given us thick, continuous, and undisturbed sedimentary sequences that can be sampled, if desired, at millimeter intervals (one meter intervals are more common). Cores are geographically distributed throughout the
world's oceans and occur in all major ecological regions and biogeographical realms. The cores sometimes extend stratigraphically throughout the entire Cenozoic. The cores contain an abundant and well-preserved oceanic biota of testate microzooplankton, microphytoplankton, and nannophytoplankton. Three of these groups, the foraminifera, radiolarians, and coccolithophores, are useful for biostratigraphic zonation and evolutionary studies because they are extremely abundant, they evolved rapidly, they are geographically widespread, their hard skeletons ensure their preservation under many conditions, they are easily sampled and prepared for study, and their skeletons permit the measurement of numerous morphometric characters and thus allow quantitative studies. The appeal of a group of organisms with such attributes is obvious, since one doesn't have to worry about stratigraphic control, stratigraphic gaps, or numbers of specimens. The presence of such fossilizable organisms in DSDP and piston cores means that we can examine the complete evolutionary and biogeographical records of a few taxonomic groups living in the pelagic regions of the ocean. This should result in the preparation of numerous studies investigating evolutionary processes and patterns.

The fact is, however, that to date very few such studies have appeared. Here we must distinguish between two types of evolutionary studies of planktonic microfossils in deep-sea cores, the first being common abut almost valueless for evolutionary insight, and the second being uncommon but of considerably more usefulness. The first type of evolutionary study is aptly termed a "lineage study" by Haq (1978, p. 97). He states that "these studies involve a close scrutiny of all taxa
(usually at the specific or generic level) within a family..." and that "from such detailed study trends in the modification of structural features with time can be easily discerned." This may be true, but the end result of a "lineage study" is not a cladogram or a morphometric diagram of changes of characters through time, but rather a family tree or phylogram with the ranges or occurrences of species depicted and phyletic lines connecting ancestors to descendents within "lineages". Invariably, the exact process which leads from discerning "the modification of structural features" to inferring ancestral-descendent relationships is not stated. And well it is not, for the process is actually an unstateable and untestable mixture of the investigator's personal understanding of the evolutionary process, subjective taxon determination and ranking of characters, subjective phylogenetic inference of ancestral-descendent relationships, and authoritarian presentation of these as "suggested lineages." I say authoritarian because even though the lineages are "suggested," they are often tacitly presented as verified fact and are utilized in biostratigraphic zonations which other investigators must then use or at least consider. Some examples of such studies are Gartner (1969), Haq (1973), Riedel and Sanfilippo (1971b, 1978; these are best illustrated in Kling, 1978), and Berggren (1968, 1971). While these studies certainly have biostratigraphic value, since they closely examine and identify morphologic changes which can be used in biozonations, they have little biosystematic value, being for the most part speculative and suggesting further, more rigorous, investigations.
The second type of evolutionary study using planktonic microfossils from complete sedimentary sequences involves the use of morphometric measurements of specimens sampled at closely-spaced intervals. These types of data are precisely what are required for an adequate evolutionary study which purports to identify species, recognize lineages, and infer phylogenetic relationships. The studies make optimum use of a deep sea core's potential, for they explicitly and quantitatively examine morphologic change through time without engaging in subjective and untestable phylogenetic statements. The only examples of this type of study known to me are Kellogg (1975a, 1975b, 1980, Kellogg and Hays, 1975), Lazarus, Hays and Prothero (1979, 1982), Malmgren and Kennett (1980, 1981), and Schafersman (1978, 1980). These will be reviewed later.

The study of the fossil record for the distinct purpose of providing unique information about the evolutionary process and evolutionary patterns is entering a new period of increased activity. Previously, fossils were studied almost solely for taxonomic, biostratigraphic, and paleoecologic purposes. Paleontologists have in recent decades interpreted the evolutionary patterns of fossils from the standpoint of neontological concepts. This became the practice because early speculations about evolution on the part of paleontologists, using their knowledge of fossils but excluding or lacking knowledge of the neontological evolutionary process, were almost invariably misguided or subsequently shown to be wrong. The reasons are that early twentieth century paleontologists were basically geologists and stratigraphers and lived in an age when evolutionary theory was itself developing amid many
controversies. Thus, many of the early paleontological hypotheses about evolution have not held up (orthogenes is being a particularly relevant example). Thus, later paleontologists, following the lead of G. G. Simpson, interpreted many features and patterns of the fossil record in terms of the synthetic theory of evolution, adaptation, and other neontological processes. Today, the situation is different. Many modern paleontologists are much more knowledgeable about evolution and are now attempting to use the fossil record as an independent source of data about evolutionary processes and patterns. Some recent hypotheses conflict with the current synthetic theory of evolution and are leading to the theory's possible revision. A major purpose of the present study is to examine and test some of these hypotheses.

One of the many important new hypotheses is that evolution viewed on a geological time scale is punctuational rather than gradual as long believed. Another hypothesis is that the extrapolation of microevolutionary processes may not necessarily be the total cause of macroevolution (the synthetic theory has always maintained that microevolutionary mechanisms are totally responsible for macroevolutionary changes). Some now believe that differential species selection, not individual natural selection, is the primary force in macroevolution. A third hypothesis that is ingrained in paleontology is that speciation occurs by anagenesis as well as cladogenesis: Do species originate by gradual transition? Does anagenesis occur at all? One problem with these three hypotheses is that they have not been adequately tested by a skeptical investigator. The present study does test these hypotheses and considers the alternatives in light of
morphometric statistical data obtained from two Miocene radiolarian lineages of artiscins. Specifically, the problems investigated are:

1. Is the pattern of evolution punctuational or gradual?
2. Does differential mortality of species (extinction) lead to macroevolutionary change?
3. Do species form by cladogenesis (splitting), anogenesis (gradual transformation), or both?
4. How much evolutionary change occurs by anagenesis and how much by cladogenesis?
5. Is microevolution visible in the fossil record and does it influence or control macroevolution? If so, to what degree?

After initiation and during the course of the investigation, it became apparent that other problems stood in the way of obtaining the necessary significant results to answer the above evolutionary questions. Most of these new problems were hidden and unrecognized by previous micropaleontological researchers: they involved, for the most part, errors in logic, theory, and scientific method. Because of these errors, much of the possibility of utilizing the microfossil record to investigate evolution would be lost if the problems were ignored. Furthermore, the opportunity to investigate and improve our research methods presented itself. The new problems appeared in two significant areas: biosystematic analysis and biostratigraphy.

Briefly, certain methods of taxonomy (specifically, phylogenetic inference and phylogeny construction) and biostratigraphy (specifically, lineage-zones and phyletic-biohorizons) are theoretically invalid because they necessarily assume a particular mode or process of
evolution to accomplish their ends. The tropical radiolarian biozonation is replete with idiosyncratic phyletic-biohorizons which mark many of the boundaries of the interval zones. It is quite easy to show that the evolutionary assumptions which must be invoked to establish these zones are untenable and thus the zones are theoretically improper, although they may still work if one wishes to adopt precisely the same evolutionary presuppositions as the zones' authors. The same evolutionary assumptions are used to create phylogenies which are equally invalid and unsubstantiated. A primary goal of this study, therefore, is to stress that scientific knowledge is a mixture of both data and interpretation, and the latter necessarily requires a theory in which to view the data. Micropaleontology labors under the mistaken view that data alone is sufficient for scientific advancement; this erroneous view has perforce led many workers to ignore the theory which must underly all of their interpretations and conclusions. The result is that many seemingly established principles in radiolarian and other planktonic microfossil biostratigraphy and biosystematics are actually untenable and unsubstantiated.

It is obviously necessary to weed out these authoritarian and mistaken concepts and assumptions from biostratigraphic, biosystematic, and evolutionary theory in order to objectively pursue the major goal of the dissertation: the investigation of planktonic microfossil evolutionary patterns and processes. Thus, the dissertation is a work of scholarship as well as science: the theories and assumptions underlying our understanding and interpretation of fossil data by biosystematic and biostratigraphic methods are thoroughly examined and
evaluated before new data is interpreted under their influence. Only then can one examine pure morphometric statistical data and draw proper conclusions from it.

The present study, therefore, was expanded from an investigation of evolutionary process and pattern visible in an exceptionally complete and finely-sampled fossil record to a study which, in addition, examines the scientific theoretical structure which permits correct interpretation of the evolutionary phenomena. In particular, in addition to the evolutionary problems listed earlier, I wished (needed) to first solve other theoretical problems in biosystematics (species definition, taxonomy, phylogenetic inference, etc.) and biostratigraphy (the relationship of evolution to biostratigraphy and the concept of evolutionary-based biozones and biohorizons). Some of the questions and problems are as follows:

Biosystematics:

1. What is a fossil species? How does one recognize and delimit a species?
2. How does speciation occur? Is the answer to this question necessary to recognize and delimit species?
3. What is the best method to perform a biosystematic analysis? If the taxa are fossils, should the method be different?
4. How does one organize and utilize morphologic, stratigraphic, and geographic data in species identification and biosystematic analysis? Which data is necessary or appropriate for the construction of cladogenies, genealogies, phylogenies, and scenarios?
5. Anagenetic evolution can be studied in the fossil record. What is the relationship of this to stratigraphic correlation, cladogenetic and phylogenetic analysis, and models of evolution?

6. What is the best method to classify fossil organisms?

Biostratigraphy:

1. What is the theory of biostratigraphy? Has it ever been examined, or is it merely assumed?

2. What criteria do we use for the definition of biozones and biohorizons?

3. What is the relationship of evolution to biostratigraphy? Are lineage-zones and phyletic-biohorizons valid within biostratigraphical theory?

4. Is a biozonation based on a model of the evolutionary process more reliable than one which isn't?

I want to again emphasize that it is essential to first discuss these largely theoretical problems before examining and interpreting new data, because data do not speak for themselves. I will reach quite different conclusions about planktonic microfossil evolution and taxonomy than previous workers, not only because my data is better data or newer data, or because my data was specifically collected to test certain distinct problems, but because I will interpret my data in an entirely new theoretical framework which I demonstrate to be methodologically superior and scientifically more valid than earlier theoretical frameworks. I consider my theoretical work, which is original in a great many respects, to be equal in importance to the original data I collected and interpreted.
Figure 1 shows the current interpretation of the evolution of two Miocene to Holocene artiscin lineages. The figure is from Kling (1978, p. 237) and is based on the work of Riedel and Sanfilippo (1977, 1978, and references therein). The artiscins are a subfamily of polycystine radiolarians that dwell in shallow, equatorial waters of the world's oceans. They have been extremely well-studied by Riedel, Sanfilippo, and Kellogg, and it is felt that their evolutionary relationships have been correctly worked out to be that shown in Figure 1. I don't believe this to be the case, however, and the present study will attempt to document and defend my new interpretations. This study examines only two lineages of one subfamily in detail so as to hopefully exhaust all the interpretive problems mentioned above. It is my feeling that such a theoretical study is necessary to examine the underlying assumptions and taxonomic methods that are commonly implicitly invoked by microfossil taxonomists and biostratigraphers, yet never defended explicitly by these same workers.
FIGURE 1
Illustration of the Traditional
Interpretation of Artiscin Genealogy

The identity of each species is as follows: (30) Cannartus tubarius,
(31) C. violina, (32) C. mammiferus, (33) C. laticonus, (34) C. petterssoni,
(35) Ommatartus hughesi, (36) O. antepenultimus, (37) O. penultimus,
(38) O. avitus, (39) O. tetrathalamus. The figure is reproduced from
Kling (1978, p. 237) and is based on the work and evolutionary
Methods of the Study

Core Location and Correlation of Samples

DSDP Core 9-77B was chosen for this study for a number of reasons. First, its location on the equator and its spreading history entirely within the equatorial region (Figure 2) ensure that its Tertiary pelagic sediments will be thick and continuous. The DSDP site report on this core (Hays and others, 1972) indicate that it is an essentially complete and undisturbed section from the late Eocene to the present (Figure 3). Thus, no gaps in the fossil record from samples of this core were expected. Second, the site report and the description of radiolarians from this core (Goll, 1972) both indicate that preservation of the radiolarian microfauna (and other planktonic microfaunas and nannofloras) is excellent. Thus, this core provides an excellent stratigraphic section to collect fossils for an evolutionary study. It is believed that no better complete fossiliferous section exists in the world, although others equally as good certainly occur. Only a single core was used in this study because of the impossibility of correlating the samples with other cores with the precision needed; this point is discussed in more detail later. The samples used in this study are listed in Table 1.
FIGURE 2. Site location and spreading history of DSDP Core 9-77. The migration track shows the location of the site in millions of years before the present.
<table>
<thead>
<tr>
<th>Sample Designation</th>
<th>Number of Specimens</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. 8/1/ 25-27</td>
<td>10</td>
</tr>
<tr>
<td>2. 9/1/ 25-27</td>
<td>10</td>
</tr>
<tr>
<td>3. 10/1/ 25-27</td>
<td>29</td>
</tr>
<tr>
<td>4. 10/2/ 75-77</td>
<td>17</td>
</tr>
<tr>
<td>5. 10/3/125-127</td>
<td>19</td>
</tr>
<tr>
<td>6. 10/5/125-127</td>
<td>15</td>
</tr>
<tr>
<td>7. 11/1/148-150</td>
<td>10</td>
</tr>
<tr>
<td>8. 12/1/ 25-27</td>
<td>19</td>
</tr>
<tr>
<td>9. 12/2/ 77-79</td>
<td>20</td>
</tr>
<tr>
<td>10. 12/3/125-127</td>
<td>15</td>
</tr>
<tr>
<td>11. 12/5/125-127</td>
<td>20</td>
</tr>
<tr>
<td>12. 13/1/ 25-27</td>
<td>20</td>
</tr>
<tr>
<td>13. 13/2/ 73-75</td>
<td>20</td>
</tr>
<tr>
<td>14. 13/3/125-127</td>
<td>10</td>
</tr>
<tr>
<td>15. 13/5/125-127</td>
<td>17</td>
</tr>
<tr>
<td>16. 14/1/ 25-27</td>
<td>20</td>
</tr>
<tr>
<td>17. 14/2/ 73-75</td>
<td>30</td>
</tr>
<tr>
<td>18. 14/3/125-127</td>
<td>20</td>
</tr>
<tr>
<td>19. 14/5/125-127</td>
<td>20</td>
</tr>
<tr>
<td>20. 15/1/ 25-27</td>
<td>19</td>
</tr>
<tr>
<td>21. 15/2/ 73-75</td>
<td>24</td>
</tr>
<tr>
<td>22. 15/3/125-127</td>
<td>32</td>
</tr>
<tr>
<td>23. 15/5/125-127</td>
<td>17</td>
</tr>
<tr>
<td>24. 16/1/ 25-27</td>
<td>10</td>
</tr>
<tr>
<td>25. 16/2/ 73-75</td>
<td>24</td>
</tr>
<tr>
<td>26. 16/3/125-127</td>
<td>20</td>
</tr>
<tr>
<td>27. 16/5/125-127</td>
<td>23</td>
</tr>
<tr>
<td>28. 17/1/ 24-26</td>
<td>12</td>
</tr>
<tr>
<td>29. 17/2/ 68-70</td>
<td>20</td>
</tr>
<tr>
<td>30. 17/3/125-127</td>
<td>19</td>
</tr>
<tr>
<td>31. 17/5/125-127</td>
<td>21</td>
</tr>
<tr>
<td>32. 18/1/ 20-22</td>
<td>12</td>
</tr>
<tr>
<td>33. 18/2/ 73-75</td>
<td>14</td>
</tr>
<tr>
<td>34. 18/3/125-127</td>
<td>16</td>
</tr>
<tr>
<td>35. 18/5/125-127</td>
<td>20</td>
</tr>
<tr>
<td>36. 19/1/ 25-27</td>
<td>14</td>
</tr>
<tr>
<td>37. 19/2/ 73-75</td>
<td>13</td>
</tr>
<tr>
<td>38. 19/3/125-127</td>
<td>13</td>
</tr>
<tr>
<td>39. 19/5/125-127</td>
<td>14</td>
</tr>
<tr>
<td>Sample Designation</td>
<td>Number of Specimens</td>
</tr>
<tr>
<td>-------------------</td>
<td>---------------------</td>
</tr>
<tr>
<td>40. 20/1/ 25-27</td>
<td>14</td>
</tr>
<tr>
<td>41. 20/3/125-127</td>
<td>22</td>
</tr>
<tr>
<td>42. 20/5/ 25-27</td>
<td>22</td>
</tr>
<tr>
<td>43. 21/1/ 23-25</td>
<td>13</td>
</tr>
</tbody>
</table>

Note: The full designation of a sample would be 9/77B/18/3/125-127, in which 9 is the DSDP leg, 77B is the core site, 18 is the core number (each core is 9m in length), 3 is the core section number (each section is 1.5m in length), and 125-127 is the depth in cm in the section.
The very few past efforts at performing statistical studies of microfossil evolution have almost invariably plotted the samples locations against depth in core. For reasons discussed later, this study will plot samples against absolute age on an interval time scale. For piston cores which have a paleomagnetic record preserved within the sediment, it is a straightforward task to determine the absolute age. DSDP cores, on the other hand, are subject to a great deal of disturbance by the rotating drill bit, and the paleomagnetic record is irremediably distorted as it enters the core barrel. Therefore, some other method was necessary to determine the absolute ages of the samples in DSDP Core 9-77B. The only other method available is to correlate the core with the absolute time scale by using the information contained in Theyer, Mato, and Hammond (1977). These authors examined an overlapping series of piston cores by taking closely spaced samples, recording the contained radiolarian index fossils, and plotting these data against the paleomagnetic record and absolute time scale of the piston cores (Figure 4). In order to assign absolute time dates to my DSDP core, one needs to assume that the first and last appearance datums (empirical morphological biohorizons) of the radiolarian species are isochronous throughout a small region of the equatorial Pacific Ocean. Despite its universal use in biostratigraphy, this is actually a porr assumption, but it must nevertheless be made. The method used here is purely empirical and is thought to be reasonably accurate. It suffers, of course, from the same lack of precision as any biostratigraphical correlation, but is permissible in this case because the goal is only to assign reasonably accurate absolute age dates to the samples, not to
FIGURE 4. Correlation of the ranges of radiolarian index species and biozones with the paleomagnetic time scale. Figure is from Theyer, Mato, and Hammond (1978, p. 389).
combine samples from separate cores to statistically measure geographic variability. This latter task requires more precision than the method possesses.

There were some problems in correlating the piston cores and Core 9-77B, however. The problems involve the two most pervasive difficulties of biostratigraphic correlation: (1) different species delimitation by different authors, and (2) the actual non-isochroneity (diachroneity) of index species vertical ranges from different locations. These problems are discussed in a later section with regard to biostratigrapher's attempts to overcome them. As a final conclusion, it can only be stated that the absolute ages against which samples will be plotted are only reasonably accurate. Further accuracy and refinement of evolutionary studies of planktonic microfossils in thick pelagic sedimentary sequences will await the full utilization of hydraulic piston coring in the Deep Sea Drilling Project.

Another problem in correlating the samples from 9-77B to the paleomagnetic time scale was the difficulty in species range-limit determination in the core. For example, refer to Figure 5 which illustrates the disparity of the depths of vital artiscin species range-limits between two authorities, Westberg and Riedel (1978) and Goll (1972), in the same core studied here. Most of the morphologic first appearance and last appearance datums agree, but some don't. The difference can be explained easily by different authors identification and delimitation of the species. A more glaring discrepancy is the widely different levels of the "evolutionary" species limits which actually mark the biozone boundaries by definition. Westberg and Riedel
FIGURE 5. Comparison of the artiscin biohorizons in DSDP Core 9-77B.
closely follow the instructions of Riedel and Sanfilippo (1970, 1972) to find this biohorizon in the core. Goll, on the other hand, misinterpreted or ignored the instructions and placed the biohorizons at the level of first morphological appearance, so all of his zonal boundaries are too low relative to the correctly located biohorizons. The problem of locating an "evolutionary" biohorizon will be discussed in great detail in a later chapter. For correlating from 9-77B to the paleomagnetic time scale of the piston cores, the problem is irrelevant (but only if one recognizes the problem, understands why it occurs, and avoids its consequences) because simple morphological range limits alone are sufficient to perform the correlation. The bizonation itself is not needed. Table 2 contains a summary of the absolute ages taken from Theyer and others (1978) and the range limits of Westberg and Riedel (1978), Goll (1972), and this study.

The last problem to consider is that van Andel and others (1975) contains two correlations of site 9-77B with an absolute time scale (Appendix 3, p. 27 and Appendix 4, p. 1 and 14). The two don't agree very closely at all, and neither agrees with the correlation using the data of Theyer and others (1978), which is the one used in this study. The lack of agreement is unfortunate, but characteristic. Van Andel and others (1975) explicitly discuss their method of determining absolute chronology and the errors which necessarily accompany the method (p. 110-113). They state (p. 110) that the practice of specifying ages in "millions of years rather than in terms of zone names...has many advantages as long as its limitations are clearly understood." They adopt the absolute time scale of Berggren (1972) as the basis for their
<table>
<thead>
<tr>
<th></th>
<th><em>O. laticonus</em></th>
<th><em>O. antepenultimus</em></th>
<th><em>O. penultimus</em></th>
<th><em>O. petterssoni</em></th>
<th><em>O. hughesi</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Goll (1972)</td>
<td>25/5-6 to 17/1-2</td>
<td>18/2-3 to 12/2-3</td>
<td>17/3-4 to 8/4-5</td>
<td>20/5-6 to 15/1-2</td>
<td>18/4 to 14/4-5</td>
</tr>
<tr>
<td>Westberg and</td>
<td>22/6 to 14/6</td>
<td>17/6 to 13/2</td>
<td>16/6 to</td>
<td>20/2 to 17/1</td>
<td>18/2 to 14/4</td>
</tr>
<tr>
<td>Riedel (1978)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Schafersman</td>
<td>22/1 to 15/1</td>
<td>18/2 to 13/2</td>
<td>16/5 to</td>
<td>20/5 to 17/1</td>
<td>18/3 to 14/5</td>
</tr>
<tr>
<td>(this study)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Theyer, Mato,</td>
<td>13.5 to 9.5</td>
<td>10.7 to 5.5</td>
<td>8.8 to</td>
<td>11.2 to 9.5</td>
<td>10.7 to 8.8</td>
</tr>
<tr>
<td>&amp; Hammond (1978)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Embley and</td>
<td></td>
<td></td>
<td></td>
<td>11.2 to (e 10.1)</td>
<td>to 8.8</td>
</tr>
<tr>
<td>Johnson (1980)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Johnson and</td>
<td></td>
<td></td>
<td></td>
<td>12.1 to (e 10.8)</td>
<td>to 8.65</td>
</tr>
<tr>
<td>Wick (1982)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**TABLE 2.** Comparison of range-limit data of Miocene artiscins of various authors. The data from Goll, Westberg and Riedel, and Schafersman are of the morphologic range-limits of the artiscin species from DSDP Core 9-77B. The data from Theyer and others, Embley and Johnson, and Johnson and Wick are of the absolute ages of the morphologic and evolutionary range-limits (in m.y.) derived from correlation with the paleomagnetic time scale.
correlation. This time scale was correlated by Berggren with the biozonation of Riedel and Sanfilippo (1971b) by inspection of the literature. Since Van Andel and others (1975) simply adopt Goll's (1972) radiolarian zonal determination for core 9-77B, and since Goll's determination is wrong as explained above, this can account for the lack of agreement between Van Vandel and others (1975) and Theyer and others (1978) for absolute age dates of core 9-77B. I have not been able to determine, however, why Van Andel and others (1975) contains two different absolute age time scales for this core. This problem does not affect the present study, however.

Sample Preparation

Samples were taken from core 9-77B at 1 meter intervals. Each sample was approximately 10 cc and consisted of white, buff, tan, or brown ooze. Samples were selected at 9 m intervals from the entire core (upper Eocene to present) for a long-range evolutionary study (not reported here), and at 2 m intervals from section 10 to 21 (middle and upper Miocene) for the detailed evolutionary study reported here. Some day, samples may be selected from 10 cm or finer intervals to study evolution in ecological time, but the 2 m interval used in this study is a sufficient first investigation, since no previous study has used such fine sampling (43 samples) over such a long time period (7.1 my) to look explicitly at evolutionary change. Some authorities state that the rotating drill bit disturbs the sediment so much, even throughout a 9 m length core, that it is impermissible to sample DSDP cores at fine intervals for detailed statistical studies. This objection was ignored.
Each sample was split into two parts: one part was archived and the other washed through a 63 μm screen sieve to remove the silt and clay size particles. The residue was again split into two parts: one fraction was saved for future examination of planktonic foraminifera, while the other part was prepared for siliceous microfossil analysis. The sample was boiled in water and H₂O₂ (hydrogen peroxide) to disagreegate the ooze and destroy any organic material. Later, HCl (hydrochloric acid) was added to dissolve any remaining calcium carbonate in the sample. The end result was an accumulation of pure siliceous radiolarians and diatoms. Two or three strew slides of each sample were prepared with Permount as the mounting medium and a cover slip. Each slide was prepared to insure a sufficient concentration or density of radiolarian skeletons for observation. This sometimes required repeated drying of the sample on the slide and adding more fossil material before the strewn material mount was covered by permount and the cover slip. After preparation, the slides were stored flat in slide trays.

**Morphometrics and Statistics**

Two types of morphological characters are used in biosystematics, (1) continuous and (2) discrete, discontinuous, or meristic. Continuous characters can be measured; discrete characters can be itemized and, if necessary, counted. As discussed in more detail later, certain characters can gradually transform by anagenetic evolution (anagenesis), while other characters can disappear or new characters appear by cladogenetic evolution (cladogenesis). The third alternative is that
characters can exhibit no change at all; this is stasigenetic evolution (stasis). Of course, the same character can be involved in all three types of evolution; for example, it can remain unchanged for awhile, then gradually change shape or size for a time, and then quickly alter or disappear into a new character, different in some degree from the ancestral state. We can think of morphological features as characters or character states; the latter category implies that a group or sequence of characters are related by origin and are differentiated by evolution through time. We can also describe characters or character states as derived (apomorphic) or ancestral (plesiomorphic).

Figure 6 illustrates the radiolarian characters which are measured in the present study. These are all continuous characters which can and do exhibit evolutionary change in size or shape. These taxa also possess a number of discrete characters that will be identified and analyzed during cladogram construction later in the study.

Traditionally, the most obvious discrete and continuous characters have been used in taxonomy for species delimitation and classification. Subtle characters were usually ignored and left unstudied. The reason for this is that the sheer number of plant and animal species necessitated reliance upon the obvious characters for efficiency. Therefore, many important apomorphic characters have been neglected, and the taxonomic data base probably does not contain sufficient information on character distribution and degree of apomorphy and plesiomorphy to adequately analyze cladistic and genealogical relationships and test hypotheses about evolutionary processes and patterns. Thus, a study such as this one must restudy specific monophyletic groups and explicitly identify, measure, and analyze as many of the groups'
Four arsiscin species are illustrated in the figure with an indication of the linear measurements made on each specimen by an eyepiece micrometer. Six separate measurements were made on specimens in the Ommatartus tetrathalamus lineage (top row), while five measurements were made on specimens in the O. hughesi lineage (bottom row). From these measurements, a calculation was used to determine two test dimensions for use in statistical calculations. The measurements are indicated below.

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Formula</th>
</tr>
</thead>
<tbody>
<tr>
<td>total length</td>
<td>C</td>
</tr>
<tr>
<td>cortical shell length</td>
<td>A</td>
</tr>
<tr>
<td>spongy column length</td>
<td>(C-B)/2</td>
</tr>
<tr>
<td>polar cap length</td>
<td>(B-A)/2</td>
</tr>
<tr>
<td>cortical shell width</td>
<td>F</td>
</tr>
<tr>
<td>spongy column width</td>
<td>D</td>
</tr>
<tr>
<td>polar cap width</td>
<td>E</td>
</tr>
</tbody>
</table>
taxonomic characters as necessary to reach satisfactory conclusions about taxonomic relationship and evolution. Of course, every taxonomist has felt his conclusions were satisfactory, but in fact, the degree of reliability of any conclusion is a function of the rigor of the method as well as the quality of the data. An investigator's method is heavily influenced by the theoretical underpinnings he holds concerning the nature of science. If, for example, he believes that taxonomy is an art and biostratigraphy is merely a matter of authority, then he will choose a method to analyze his taxonomic data that is consistent with these beliefs. Although the final conclusions may be satisfactory in his eyes, anyone holding a different view of the scientific method in, for example, taxonomy and biostratigraphy, will undoubtedly disagree. Therefore, if there is disagreement about method and theory (which is certainly the case in the present study), it is imperative to discuss these problems before submitting data to analysis and conclusions to scientific scrutiny.

Rather than assume that gradual anagenetic change doesn't occur or isn't important, as some investigators have done, such change was measured. Actually, all important potential continuous characters were measured to determine whether they exhibited stasis or change. As discussed later, this information was useful for two major purposes: (1) to ascertain the continuity of any suspected gradual change through time to eliminate the discontinuities associated with speciation, and (2) to allow the construction of phylogenies (which combine cladogenetic, genealogical, and anagenetic information) that permit the determination of amount of evolution and help test the two models of evolution, punctuation and gradualism. Obviously, if stasis and discontinuous
(cladogenetic) change far outweigh gradual anagenetic change, then the punctuational model is a better hypothesis of the evolutionary process than the gradualistic model.

Continuous characters shown in Figure 6 were measured under the compound microscope at 250X magnification. An eyepiece micrometer was used to perform the measurements. This micrometer was carefully calibrated to a stage micrometer and all measurements were converted to micrometers ($\mu$m) by the calculator programs used to perform the statistical analyses. Measurements could be made to 2.5 significant digits; this precision was carried forward in all calculations and graphs. Usually about twenty specimens were measured in each sample. Sometimes more than thirty were measured, but never less than ten. A number of statistical programs, written specifically for this study and using a Texas Instruments TI-58 calculator and PC-100A printer, were used to reduce the data to the following statistics: mean, standard deviation, standard error (of the mean), and 95% confidence limits using a one-tail t-statistic at .05 significance (Zar, 1974). The statistics are plotted against an interval time scale in millions of years on the traditional vertical axis by using Hubbs and Rubbs (1953) diagrams. These diagrams conveniently depict mean, standard deviation, 95% confidence limits, range, and number of samples in a highly legible format. The diagrams are oriented horizontally to have the time scale as a vertical axis and to permit the draftsman to draft these relatively tedious figures in the most efficient manner (horizontally). Furthermore, this is the standard form and thus allows ease of comparison with trends of other authors. Such diagrams are termed stratophenograms (Gingerich, 1976b).
Although both Malmgren and Kennett (1981) and Lazarus and others (1982) use a vertical time axis, the papers by Kellogg (1975a, 1975b, and 1980) unfortunately use a horizontal time axis. This makes interpretation and comparison difficult. Furthermore, both Kellogg and Malmgren use "depth in core" as the time axis, not millions of years. Not only does this make comparison with other authors impossible, it is theoretically invalid, since sedimentation rate cannot be assumed to be constant, and therefore the spacing of the measurements on the stratophenograms may be inaccurate and allow misinterpretation of gradual trends, punctuation, and stasis.

The most common form of Hubbs and Hubbs diagrams plot range as a single horizontal line, standard deviation as a thin horizontal rectangle, 95% confidence interval as a thin, solid horizontal rectangle within the standard deviation rectangle, and mean as a short vertical line or narrow triangle. The morphology of radiolarians is so plastic, however, that ranges plotted on stratophenograms by the Hubbs and Hubbs representation would be extremely long lines that would clutter the diagram. Therefore, the ranges are omitted in the stratophenograms constructed for this study. Here, the single horizontal line represents standard deviation, the thin horizontal rectangle the 95% confidence limits, and the thin triangle the mean. Kellogg's papers, Malmgren and Kennett, and Lazarus and others also omit ranges. All authors plot the mean and the 95% confidence interval, which is a necessity, and Lazarus and others (1982) also plot the standard deviation in a stratophenogram similar to that utilized in this study. The studies by Lazarus and others (1980, 1982) and Schafersman (1978, 1980, 1982, this study) are the only ones which present stratophenetic data in a proper format that
permits comparison with other authors and confidently allows interpretation of gradual trends, punctuation, and stasis without assuming that the sedimentation rate was constant throughout the interval studied.

There are certain rules that must be followed to interpret Hubbs and Hubbs stratophenogram. These are spelled out in Simpson and others (1960, pg. 350-355). They note that it is popularly thought that if the 95% confidence intervals of two different samples do not overlap, then the sample means are significantly different at the 5% level. However, the authors point out that this impression is false, since there is no general correspondence between overlap of the 95% confidence intervals and the t-test for the difference of two means (the reason why is explained below). In fact, the intervals may overlap markedly despite a significant difference between the means at the 5% level and, conversely, means which are not significantly different may have nonoverlapping intervals. The correspondence between overlap and significance depends upon the relative sample sizes and standard errors of the two samples, but Simpson and others (1960, p. 353) provide a few general rules.

1. If the confidence interval for one sample includes the observed mean for another sample, the two means are certainly not significantly different.

2. If the confidence intervals for two samples are nearly equal in length and these intervals are clearly nonoverlapping, the difference between the samples is significant.

3. As a corollary of (2), if both means are arbitrarily assigned confidence intervals equal in length to the larger of the two
intervals, and if there is no overlap of these intervals, then the means are significantly different.

Phyletic and phylogenetic morphologic trends are not generated by an independent events process, such that a dependent variable is totally controlled by an independent variable. Therefore, an evolutionary trend's slope cannot be statistically tested against other slopes or against a null hypothesis (slope equals zero) by commonly-used methods. That is, two-sample statistical tests can be used when the two samples are independent -- independence implying that each datum in one sample is in no way associated with any datum in the other sample (Zar, 1974, p. 121). Therefore, such tests as Student's t, F test (variance ratio test), and others cannot be used to test the difference between two evolutionary trends or samples. Evolutionary trends are a Markov process (Raup, 1977; Raup and Schopf, 1978) which produces a sequence of events such that each event is partly dependent on the outcomes of preceding events and partly dependent on a random process acting at the time of the event itself. Thus, a Markov process is one which has a "memory" that constrains each new event; the memory, of course, is the genetic inheritance which each species or population receives from its immediate ancestor. There is, however, an analytical method which can be used to determine if the trend is real (i.e. caused by a determinable process) or random. Raup (1977) and Raup and Schopf (1978) have used equations provided by Feller (1968) to assess the relevant probabilities of an observed trend being, in fact, a random walk. This test, the only one available to test the evolutionary trends of monophyletic taxa which exhibit anagenesis, is a valuable supplement to simple observation and
interpretation. As Raup and Schopf (1978) make quite clear, many random patterns are strikingly counter-intuitive and may appear to be deterministic. This test, used by Kellogg (1980) for example, is not used here because simple inspection indicates that the trends described in this study would fail the test.

As previously mentioned, discrete or noncontinuous characters can be identified, tabulated, and, if appropriate, counted; they cannot be measured. Examples of these characters include the presence, absence, or number of spines, polar caps, skeleton segments, ornaments, etc., or the quality of a morphological feature, such as its texture (porous or spongy), shape (square, spherical, elongate), robustness (heavy or thin-shelled, fragile or robust), and ornamentation (heavily or simply ornamented). The taxonomic significant of any character, discrete or continuous, with regard to its usefulness in constructing a tree of nested evolutionary novelties, ancestral-descendant relationships, or amount of phyletic change, is at first a matter of judgement of the taxonomist. Many authors believe that this is all that is necessary in taxonomy, but in the present study a method of biosystematic analysis is followed which uses as many of the characters as possible and tests them in a cladogram. New characters of the known taxa, or new taxa with new characters, must invariably refute or corroborate an existing cladogram. This method is one which discourages authoritarian decisions on the part of the taxonomist, but still gives free reign to his ability, imagination, and energy in the search for new characters and new relationships.

When dealing with fossils, as opposed to extant organisms, it is very desirable to examine two aspects of characters: (1) the time or
stratigraphic level of first and last appearance, and (2) whether the appearance (or transition from one character state to another) is rapid or slow and gradual. These matters will concern discrete and continuous characters differently. For example, a discrete character is either present or not; it cannot appear slowly and gradually if it has taxonomic significance which defines a species. On the other hand, individuals within a species population may possess the discrete character or not if the character has no presumed taxonomic significance. Also, some individuals may possess a discrete character half in one character state and half in another; this occurrence is not as impossible as it sounds. If we consider continuous characters in this regard, it is obvious that individuals may exhibit a variety of measurements of these characters, so we must measure a sample of a population to determine the mean character measurement for a species. Taxonomically significant continuous characters, unlike taxonomically significant discrete characters, can appear either slowly and gradually or rapidly in a punctuated fashion. Therefore, the speed of transition of a character into another, as well as the type of character, will determine which evolutionary process and model is correct. All of these points must be kept in mind when analysing characters by any biosystematic method.
BIOSYSTEMATICS, PALEONTOLOGY, AND EVOLUTION

Methods of Biosystematic Analysis

Earlier we had spoken of the desirability of using a single deep sea core for evolutionary studies, because the temporal relationships of the enclosed microfossil taxa were determinable solely by superposition, and needn't rely on using the same or different taxa for correlation purposes. However, for many reasons, it is desirable to extend the study to additional cores. What are these reasons? Table 3 synthesizes methodological criteria necessary for testing evolutionary hypothesis. Eldredge (1974) and Gould and Eldredge (1977) both explicitly state that samples should derive from all available areas in the depositional basin to study the geographic variability of species over their entire preserved range. They caution against confining a study to local sections or a single core. There are, however, at least three silent assumptions accompanying this advice. First, they assume that a single section or core will not contain specimens exhibiting the total range of variability, whereas I believe that a valid argument can be made for the widespread mixing of oceanic specimens of planktonic microorganisms as they settle through the water column during the weeks and months required. Specimens of surface-dwelling microorganisms over a wide geographic range will mix before settling at any one spot. I am not arguing that the complete range of the species population will be present in any single core, only that under some circumstances, such as with planktonic organisms, the necessity of sampling a wide geographic area is tempered because a single core can contain an adequate sample of
TABLE 3. Sampling and Methodological Criteria Necessary for Testing Evolutionary Hypotheses in Paleontology

Eldredge (1974) and Gould and Eldredge (1977):

1. Population samples should be closely spaced and span a considerable segment of geologic time.

2. Samples should be derived from all available areas in the depositional basin to study the geographic variability of species over their entire preserved range. Do not confine a study to local sections or single cores.

3. Samples should be sufficiently large and analyzed by a proper method of phylogenetic inference which adequately and realistically grasps the phylogenetic relationships among samples.

4. The phylogenetic patterns of all members of a fauna or assemblage should be studied, not just the ones which exhibit phyletic change. Remember, stasis is data, and most forms do not show any evolutionary change throughout their stratigraphic range.

The model of punctuated equilibria predicts that in local sections one would observe either sudden transition from ancestor to descendent (punctuation) or stasis within individual taxa (equilibrium). Since fossil morphological breaks in a stratigraphic section can usually be attributed equally well to either punctuation by allopatic speciation or to an imperfect depositional record, the model can best be tested by observing the relative frequency of stasis or gradual directional change. We believe the former overwhelmingly predominates.

Gingerich (1976a, 1976b, 1977):

1. The stratigraphic sections being studied must be completed, or sufficiently overlapping that a relatively complete composite section can be constructed.

2. The stratigraphic sections must be subdivided into units representing significantly less time than that separating the evolutionary events being studied, the more finely divided the better.

3. The samples from each level must be treated as "biological" species, i.e. the number of species at each level must be based on the number of (inferred) reproductively isolated evolutionary lineages indicated for that level rather than on the total number of morphotypes present. A typological species concept must not be used.

Gaps in the fossil record (periods of nondeposition or erosion), coarse stratigraphic sampling of a continuous record (insufficiently divided stratigraphic section), or typological analysis of the fossils (using a typological species concept), would all yield a pattern of "punctuated equilibria" as an artifact of methodology.
the entire population whose statistics will not be significantly different from statistics of samples taken to explicitly sample the entire range of the population. This possibility deserves to be tested, of course.

The second silent assumption with the advice to sample a wide geographic area is that we need to know the total range of spatial variation (actually, a statistical estimate of it) for the purpose of testing an evolutionary hypothesis. Here we must be explicit. If one wishes to test the hypothesis of allopatric speciation of a species in geologic time by analysis of the stasis or transformation of characters through time, then the assumption is valid. But what if one wishes to test taxic relationships among species, such as cladogenetic or genealogical hypotheses? What if one wishes to use characters analyzed for their plesiomorphic and apomorphic states among the taxa of interest? These are also evolutionary hypotheses, but knowledge of the complete temporal and spatial variation is not here a requirement. It is only the undue attention paid to the transformation of characters (the transformational outlook) rather than to the origin of species (the taxic outlook) that has allowed sweeping generalizations that we must know the complete spatial and temporal variation to perform an evolutionary study properly. Of course, Eldredge himself (1979b) first distinguished the transformational and taxic approaches to study of fossil evolution. Cracraft (1979, p. 28) incorrectly identifies (although he cites Eldredge, 1979b) the transformational approach as an "adherence to a gradualistic philosophy," when, in fact, it can equally be identified with the search for stasis in continuous characters to justify the punctuational model of speciation. I think the
"transformational approach" is more correctly identified as a belief that evolution is largely a matter of genetic change within species populations for intraspecific adaptational reasons, while the "taxic approach" is a belief that evolution is largely a matter of genetic change between species populations for interspecific reasons controlling differential species survival. I, however, do not wish to characterize the transformational approach as injurious to biosystematic investigations, since it is extremely useful in many cases, such as classification construction and testing evolutionary hypotheses of character transformation or stasis in geologic time at the phylogenetic or scenario level of investigation. I only wish to point out that the taxic approach is advantageous to testing evolutionary hypotheses at the cladogenetic level, and here a reliance upon "total variation" over a wide geographic area is not required.

The third hidden assumption is probably the most important of all. Knowledge of temporal and spatial character variation is necessary for phylogenetic reconstruction of fossil organisms to investigate evolutionary patterns. The procedure for obtaining data about spatial variation assumes that the many local sections or cores required by such an investigation can be correlated not only with each other, but with absolute time on an interval time scale. The ability to correlate the cores with each other on an ordinal time scale will only allow a genealogical reconstruction that results in a tree exhibiting ancestral-descendent relationships, but such a tree is not sufficient to show all evolutionary patterns. Amount of change through time, which, among other things, a phylogram purports to show, cannot be shown except with an absolute time framework. Of course, anagenetic change has often
been illustrated on relative time scales by many workers, but this information is not very valuable. Anagenetic change must be illustrated on an interval time scale if the phylogeny is to have comparative scientific value. Precise correlation of local sections or cores over a wide area onto an interval time scale is difficult or impossible to achieve in almost all cases; therefore, knowledge of the total temporal and spatial variation cannot be obtained for most analyses.

Perhaps at this point it would be wise to discuss some of the terms used in the foregoing paragraph. Great advances have been made in recent years in clarifying biosystematical concepts and methods of phylogenetic inference. Eldredge (1979a; Eldredge and Tattersall, 1975) has identified three stages or levels of complexity in biosystematical analysis: cladogeny, phylogeny, and scenario. The three stages result in the construction (hypothetical reconstruction) of diagrams depicting each of these: cladogram, phylogenetic tree, and scenario. Extending the analysis from one level to the next necessitates adding ad hoc assumptions and untestable hypotheses. Nevertheless, this may be done if desired and if the investigator is aware of the theoretical difficulties involved. The explicit identification of these levels of complexity has done much to advance our understanding, but unfortunately the dissection by Eldredge is incomplete. There are actually four levels of complexity in biosystematical analysis, and the confounding of two of these has resulted in more confusion than any other error in the modern discussion and criticism of biosystematic analysis.

The first and last, cladogenetic and scenario, levels of Eldredge are nonproblematic and acceptable as he presents them. However, I would term his last level a "narrative explanation" and reserve the term
"scenario" for the actual diagram. The cladogram which results from a cladogenetic analysis is "a branching diagram depicting the pattern of shared similarities thought to be evolutionary novelties ('synapomorphies') among a series of taxa" (Eldredge, 1979a, p. 167). The scenario resulting from a narrative explanation is a "phylogenetic tree with an overlay of adaptational narrative" (Eldredge, 1979a, p. 168). Eldredge, however (and he is surely not alone in this), ignores the significant difference between a genealogical tree (family tree) and a phylogenetic tree (phylogram). Eldredge's definition for his phylogenetic tree is actually that of a family tree which results from a genealogical analysis: "a diagram depicting the actual pattern of ancestry and descent among a series of taxa." A true phylogenetic tree, which for evolutionary taxonomists is a major goal of systematics and which precedes a classification, is a diagram depicting the history of evolution, both cladogenetic and anagenetic, among a series of taxa. This is done by taking a family tree and extending or shortening the length of the branches and the angle with which they radiate from a stem. Phylogenetic trees are presumably the basis for all classifications of evolutionary taxonomists and contain both cladogenetic (branching evolution) and anagenetic (progressive evolution) information. Illustrations and definitions of these four stages or levels of complexity are presented in Figure 7.

The most important feature of these four levels of biosystematic analysis is the time framework within which each falls. This single feature is largely responsible for the scientific applicability of cladistics and the suspicion with which we now view evolutionary taxonomy. A cladogeny is constructed within a timeless framework;
FIGURE 7. This figure illustrates six types of evolutionary diagrams frequently used in systematic biology and paleontology. Each diagram depicts taxonomic or evolutionary relationships among five species (labeled A through E).

CLADOGENY. A **cladogeny** is the pattern created by the distribution of derived (apomorphic) characters among the recognized taxa. A **cladogram** depicts a cladogeny, which hypothesizes the distribution of shared derived (synapomorphic) characters among the taxa. There are two slightly different types of cladograms, both illustrated here. The more common form (the larger cladogram) does not indicate hypothetical ancestors at the nodes of the branching network. Such hypothetical ancestors are unnecessary in practice and often don't exist in fact, since a terminal species could be the ancestor of its sister species. Hypothetical ancestor represented by open circles at nodes (the smaller cladogram) can be either of the two terminal (sister) species or a third unknown species. In fact, a long-ranging terminal species could exist from node to node far down into the cladogram, although if a taxonomist inferred that this is indeed the case and plotted the species at these nodes, the diagram would no longer be a cladogram, but would become a genealogical tree. Therefore, any terminal species can be the ancestor of any or all of the other terminal species, but the extreme difficulty of inferring the ancestral-descendant relationships of the species, and the constant problem of undiscovered ancestral species, has led cladists to perform taxonomic classifications at the level of the cladogeny and
to ignore the other types of evolutionary diagrams shown here except for special purposes. Note that cladograms are not plotted within time or morphology axes; the lengths and angles of the cladogram's branches are meaningless, and no specific pattern of ancestry and descent or branching sequence is indicated.

**TYPE 1 GENEALOGY.** If one decides, by inference from some set of data, which of the species is ancestral to others, and brings certain terminal species down to nodes formerly occupied by open circles, one has constructed a genealogy of the simplest (first) type. The problem here is that a large number of type 1 genealogies, only one of which could be correct, can be derived from a single cladogram. For example, both genealogies shown here are consistent with the original cladogeny, and many other examples are possible, especially if unknown ancestors are invented and stationed at the various nodes. A genealogy is the pattern of ancestry and descent among the recognized taxa. A genealogical or family tree depicts a genealogy, so the two diagrams depicted are two different trees (we will assume the larger is correct). Such trees have a polarity from old to young, that is, they lie on an ordinal (relative) time scale, as shown in the figure. The branch nodes indicate the pattern of ancestry and descent, but the length and angle of the branches are meaningless. Since numerous assumptions, not discussed here, are needed to proceed from a cladogram to a family tree, type 1 genealogies are often speculative and highly subject to modification, and are thus not a reliable basis by which to classify organisms.
TYPE 2 GENEALOGY. A more specialized type of genealogy utilizes stratigraphic data derived from the fossil record. Type 2 genealogies are commonly found in paleontological publications, and are often constructed solely from fossil phenetic and stratigraphic data without the necessary preliminary steps of a cladistic analysis and a type 1 genealogical inference. Type 2 genealogies require additional assumptions over those of type 1 genealogies, for example, that the stratigraphic and fossil records are relatively complete. A type 2 genealogy may be plotted against an interval (absolute) time scale, as in this figure, or against an ordinal time scale with units such as biozones or chronostratigraphic stages. By this point in a biosystematic analysis (which proceeds from cladogram to type 1 tree to type 2 tree to phylogram to scenario) we are searching for patterns to examine the tempo and mode of evolution that can only be recognized by constructing nonrigorous diagrams higher than cladograms. Also, please note that type 2 genealogies are frequently plotted against rock thickness or against lithostratigraphic units, although these trees are practically useless for comparative purposes. Furthermore, the horizontal axis for both type of genealogies is dimensionless and does not indicate degree or type of morphologic change.

STRATOPHENOGRAM. A stratophenogram is a plot of a morphometric datum (measurement of a univariate character, bivariate ratio, or multivariate factor) of one species (single lineage) or higher monophyletic taxon (clade) against an interval time scale. In other words, a stratophenogram shows phenetic data plotted against stratigraphy, hence the
name. Stratophenograms plotted against rock thickness (core or measured section length) or against an ordinal time scale are essentially useless for comparative work and are useful for recognizing only the most generalized phyletic patterns. A rigorous stratophenogram must be plotted against an interval time scale to be valuable in the investigation of evolutionary tempo and mode. In some cases it is necessary to construct stratophenograms before performing cladistic analysis, so that both static and gradually changing characters may be recognized and avoided in the subsequent cladistic analysis. Such characters are ancestral (plesiomorphic) and might appear to the investigation to be derived if an evolving lineage is not completely sampled and plotted by stratophenograms. Some paleontologists derive classifications directly from stratophenograms without performing a cladistic analysis; this practice is not theoretically valid and should be discouraged.

PHYLOGENY. A phylogeny is probably the most controversial of all evolutionary patterns, since it seeks to represent the pattern of branching, ancestry, descent, and divergence (progression along a branch) of the recognized taxa. It seeks to illustrate the entire evolutionary history of the taxa: all cladogenetic, anagenetic, and ancestral-descendant relationships. A phylogeny is depicted by a phylogenetic tree or phylogram, a diagram by which the lengths and angles of branches (single lineages) convey anagenetic information in addition to the cladogenetic and genealogic information conveyed by the splitting branches and the location and sequence of the branch nodes. Anagenesis, also called phyletic evolution, is progressive evolution
within a single branch (lineage). This component of evolutionary change is distinguished from cladogenesis, the splitting of lineages which yields the other component of evolutionary change. The appearance of a phylogram depends heavily on the author's preferred models of evolution and speciation. For example, the quite atypical example illustrated here assumes a punctuated model of evolution: that speciation occurs at a tempo that would appear instantaneous on a geologic time scale. The assumption of a gradualistic model, on the other hand, would result in a phylogram that shows species gradually splitting and diverging from one another, with no dashed lines between species to indicate a speciation event. Such phylograms have appeared in the paleontological literature for decades, because the gradualistic model of evolution was universally held. A second assumption about evolution implicit in the figured phylogram is that a single lineage (ancestral-descendant sequence of populations) remains a single species, no matter what amount of gradual divergent evolution (anagenesis) occurs. Thus, species C remains one species for 6.5 units of time, whereas its great degree of progressive change (in a character, ratio, or factor) during this time would lead most paleontologists to divide it into two or more paleospecies or chronospecies, i.e. arbitrarily subdivided parts of a gradually changing lineage, so that the phylogram would show ancestral species gradually transforming into new descendant species.

A rigorous phylogeny utilizing fossil data is simply a combination of a type 2 genealogy and stratophenograms of each species (taxon) in the genealogy. It should be obvious that a phylogeny, which purports to
express the type and amount of evolutionary divergence (anagenesis) by the lengths and angles of the branches, is essentially useless for such a purpose unless it is constructed within an interval or ratio time scale and morphometric unit scale that accurately presents such anagentic data. The phylogeny illustrated here is therefore an ideal that has yet to be reached in the systematic paleontologic literature. All published phylograms are really quasi-phylograms that are nonrigorous, speculative diagrams that omit the interval scale axis, the morphometric scale axis, or both. They are simply the result of an author's subjective belief about a fossil group's evolutionary history, and the obvious difficulty of anyone else reaching the same phylogeny by examining the same data makes the construction of phylograms a futile practice in authoritarianism. The reader should be aware that the cladist literature frequently confounds genealogies and phylogenies by calling both family trees and phylogenetic trees simply "trees." For some reason, modern cladistic taxonomists tend to discount the occurrence of anagentic evolution, so the possibility of constructing phylogenies is ignored, and the term is frequently used interchangably with genealogy. Obviously, if anagenesis doesn't occur, genealogies would be phylogenies.

SCENARIO. A scenario is simply an annotated phylogram that strives to present an environmental or adaptive explanation for every cladogenetic event (speciation, in the strict sense used here) and anagentic change or stasis. A scenario depicts a narrative explanation, a history of evolution of the recognized taxa with an adaptational and environmental
narrative explanation for every gradual change, episode of speciation, or extinction event. Now that stasis is recognized to be an important attribute of a lineage, this also must be explained. It is not unusual for different paleontologists to propose the same environmental explanation for both speciations and extinctions, different adaptive explanations for evolution of the same species or the different evolutionary histories of two sympatric species, and different modes of speciation for similar species, all depending on which circumstances the paleontologist wishes to consider. The problem with all these explanations is that they are highly generalized extrapolations of microevolutionary neontological processes, which are themselves often poorly understood and controversial, to the fossil record on the basis of a few facts. Such sanguine extrapolation ignores the numerous hidden assumptions and ad hoc hypotheses these explanations entail. Thus, scenarios have justifiably been described as "fairy tales."
cladograms have no time scale. A typical cladogram is illustrated in Figure 7. Since a cladogram is timeless, fossil and living synapomorphies can be depicted together and hypothetical descendant taxa can be inserted the same way as additional fossil and living taxa. A cladogram represents a universal hypothesis capable of scientific testing by empirical falsification, and not a hypothesis limited in some way and thus unfalsifiable because not all conditions are known for a proper test. Subsequent levels of biosystematical analysis require additional assumptions and thus impair the unambiguous falsifiability of the hypothesis.

A good example of the usefulness and theoretical superiority of cladistics involves the cladistic definition of monophyly (sensu Hennig, 1966; holophyly of Ashlock, 1971). Bonde's (1977) definition is precise: "A monophyletic group includes (only) a species and all its descendents." Monophyly was long understood to refer to a taxon possessing a nearest common ancestor, but the new cladistic definition requires that the taxon contain both the common ancestor (stem) species and all the descendent species (not just some of them). This made the concept of clade internally consistent, so that all clades could be analyzed by the same unbiased techniques without resorting to apriorisms and ad hoc hypotheses necessary if clades were to be arbitrarily divided. The new definition of monophyly has met with much criticism and misunderstanding on the part of evolutionary taxonomists, who would prefer the old, less rigorous definition. Unfortunately, the old definition allows ambiguity to creep in whenever phyla are analyzed, so it must be abandoned. Platnick (1979) recounts how Bergstrom (1979) criticized the cladistic concept of monophyly as follows: "Since the
definition is not related to the present time level, all future descendants have to be included. A living group and its ancestors, therefore, do not constitute a monophyletic group, unless it will become extinct without leaving any future descendants." It should not be difficult to see that the descendants of the living group can certainly be included in the monophyletic group, and that they should be. The living group could just as easily be a fossil group, and its descendants would then be excluded if we follow Bergstrom's philosophy. The concepts of paraphyly and polyphyly are as controversial as monophyly. Figure 8 explains the correct distinction among these terms.

The step from a cladogram to a family tree is simply to recognize ancestral-descendent relationships and choose which taxa to move down to the ancestral position of branch nodes or to recognize an unknown ancestor at branch nodes. Figure 7 illustrates this procedure. Of course, a number of possible family trees can be constructed for any one cladogram. The distinguishing characteristics of a family tree is that the time scale is relative: we know the sequence of events and can plot them on an ordinal scale. As discussed by Gaffney (1979) and Eldredge (1979a), among others, the route from cladogram to family tree necessitates the invocation of an assumption concerning the evolutionary mechanism, i.e. the nature of the evolutionary event which links ancestral-descendant taxa and allows their recognition (as ancestor and descendant), an assumption that character reversals do not take place and an assumption that the fossil record is complete. Cladogenetic analysis and subsequent classification do not require the postulation of ancestral-descendent relationships. As clearly explained by Englemann and Wiley (1977) and Cracraft (1979), by the cladistic method it is
FIGURE 8. These two diagrams will help illustrate the definitions of monophyly, paraphyly, and polyphyly. The upper diagram is a cladogram which cladistically relates the eight recognized taxa in the example; the lower diagram is a specialized type of phylogram which portrays a number of additional items: a single genealogy (one of many which could be extracted from the cladogram), hypothetical ancestors, and a representation of the amount of morphological divergence that has occurred through time. From the cladogram, we would unhesitatingly recognize that CD, EF, GH, BCD, A-D, E-H, and A-H are monophyletic taxa. A monophyletic taxon is a group that includes a common ancestor and all of its descendants. Since these eight taxa (we will call them species) are all that we have discovered, and we have used many shared derived (synapomorphic) characters to produce the cladogram, we assume that, for each of the monophyletic taxa, either one of the known species in the taxon is the common ancestor or the actual but unknown common ancestral species has not been discovered.

In the lower phylogram, seven hypothetical ancestral species are shown. Let us assume that this phylogram accurately depicts the actual phylogeny of the species and their extended lineages. Note that species B has diverged considerably from its sister taxon CD and converged toward species A, and that species F has diverged from its sister species E and converged on taxon GH. An evolutionary taxonomic analysis which uses such phenetic information as shared ancestral (sympleisomorph) and uniquely derived (autapomorphic) characters without a rigorous cladistic analysis could result in a classification
containing the paraphyletic taxa AB, ABC, and GFH, and the polyphyletic taxa DE, A-E, and D-H. A paraphyletic taxon is a group that includes a common ancestor and some but not all of its descendants. Paraphyletic taxa AB and ABC include common ancestor 2, but ABC leaves out descendant D and AB leaves out both C and D. Paraphyletic taxon GFH includes common ancestor 5, but omits descendant E. A polyphyletic taxon is a group in which the most recent common ancestor is assigned to some other group and not to the group itself. Polyphyletic taxa DE, A-E, and D-H all possess 1 as the most recent common ancestor, but this ancestor would be assigned to either paraphyletic taxon ABC or GFH if the polyphyletic taxa were accepted.

Both evolutionary and cladistic taxonomists agree that polyphyletic taxa are unnatural, but unlike cladists, evolutionary taxonomists accept paraphyletic taxa as natural. The Class Reptilia is an excellent example of such a paraphyletic taxon. The reptiles are a grade characterized by many shared ancestral characters. In the diagram, paraphyletic taxon GFH could represent the reptiles, with F being the dinosaurs, E being the birds, and G and H being some other reptiles. Monophyletic taxon EF would group the dinosaurs and birds together, since they share a common ancestor that other reptiles do not share. Although the amount of morphological divergence between E and F is immense, a cladistic classification which logically emerges solely from recency of common ancestry is better in many ways than one which arbitrarily separates related groups by subjective criteria of degree of morphologic change.
impossible to unambiguously falsify the hypothesis that A is the ancestor of B, because no possible test can rigorously show that A and B do not share a common unknown ancestor. Therefore, specifying an ancestral-descendant relationship requires abandonment of the cladistic method, a solution that clearly is no scientific solution. As I will show later, the excellent evolutionary history of microfossils contained in deep sea cores seemingly allows the unambiguous inference of ancestral-descendent relationship of certain taxa, and yet their recognition is theoretically unjustified and taxonomically useless. To see this requires an understanding of the new evolutionary species concept that will be explained later.

The concept of a family tree which expresses genealogical (ancestral-descendant) relationships would be straightforward if such trees were not called phylogenetic trees by cladists. Eldredge (1979a, p. 182) states that "the reconstruction of patterns of ancestry and descent...are expressed in diagrams called phylogenetic trees." A phylogenetic tree is actually correctly defined as a diagram reconstructing the pattern of a phylogeny, not a pattern of genealogy (ancestry and descent). Gaffney (1979, p. 87) states that "Phylogeny is the geometric pattern of ancestry and descent among organisms; that is, it is the genealogy of life." This statement well illustrates the cladists' confusion over the meaning of phylogeny. Why must the genealogy of life be called anything other than a genealogy? Cladists often distinguish a "genealogy of individuals" from "phylogeny of species or higher taxa. However, a genealogy expresses the ancestral-descendent relationships of individuals, which I believe includes species. Gaffney agrees, as I do, that "clades are
monophyletic units of whatever magnitude" (Huxley, 1958, p. 27), that species are "individuals" (Ghiselin, 1974; Hull, 1976), and that "logically a clade, just like a species, can be treated as an individual" (Bonde, 1977, p. 757). A genealogy can be constructed for any clade, whether of individuals or species; it does not need a different name depending on the type of clade.

Of course, the whole problem of the cladist concept of "phylogeny" extends back to Hennig (1966). Subsequent cladists have adopted his idiosyncratic definition of phylogeny, which is restricted to only the branching (genealogical) component. Mayr (1974, p. 101) discusses this criticism in detail, and I must agree with Mayr. A phylogeny is a history of life, not a genealogy of life. Phylogenetic trees are diagrams "which by the lengths and angles of their branches convey far more information than a cladogram" (Mayr 1974, p. 101). I would, of course, insert the word "untestable" in front of the word "information" in this quote. The use of the terms phylogenetic and relationship in their restricted cladistic sense only obscures the evolutionary problems with which we must grapple. Phylogeny has long been understood to express both the branching between and the progression within monophyletic taxa, i.e. both cladogenetic and anagenetic evolution. Gaffney (1979, p. 80) may believe that "phylogenetic systematics" is an "unusually apt term" for the cladistic method, but I must disagree. I think it is an obfuscation. Readers of Cracraft and Eldredge (1979) are apt to be confused by the restricted cladistic definitions given both "phylogenetic" and "monophyletic;" the new definition given "monophyly" is justified, however, since the previous definitions of the term (of which there are many) were confused and ill-conceived, for a
"monophyletic taxon" by previous definitions could be arbitrarily delimited by a taxonomist to mean almost anything. This is not true of the word "phylogenetic," however, since it has always been used to refer to all relationships of the history of life and we already have different terms for the restricted relationships, such as ancestral-descendant, cladogenetic, and anagenetic.

Most phylogenies in the paleontological literature are really genealogies, sometimes with a little phylogenetic information thrown in. A rigorously constructed phylogeny must possess an absolute time framework plotted on an interval scale, a qualification so difficult to achieve that it is usually ignored. We end up with hybrids that purport to demonstrate definite relationships, but which actually demonstrate little or nothing. The major addition to a phylogram from a family tree is the representation of the amount of progressive (anagenetic) change (indicated by length of a branch) or speed of change (indicated by the branch's angle of attachment) of the taxa in question. Without an absolute (interval) time scale, such branch lengths and branching angles are meaningless. This fact has not been properly appreciated by evolutionary taxonomists (who purport to base their classifications on phylogeny) or paleontologists (who construct most of the phylogenetic trees). The construction or interpretation of a phylogeny without an interval time scale is an exercise in authoritarianism.

The fourth level of a biosystematic analysis is the narrative explanation. Despite the evolutionary taxonomist's claim that his classifications are based on phylogenies, it is easy to demonstrate that they are based on narrative explanations. The general impression that grades are closely tied to anagenesis (i.e. the amount of change in a
clade as revealed in a phylogeny) is false, for grades are a concept that must be described by a narrative explanation. Grades are recognized by adaptive criteria; the "adaptational overlay" (Eldredge, 1979a) of a scenario must be explicitly identified to distinguish grades. Grades are never apparent in a phylogeny alone. And grades, of course, are one of the main features of classification constructed by evolutionary taxonomists (an example would be the Class Reptilia). Eldredge (1979a, p. 193) correctly describes scenarios as "mostly fairy tales constructed of a maze of untestable propositions concerning selection, function, niche utilization, and community integration, and alas, do not generally represent good science." Elements of a narrative explanation do not necessarily have to be reserved for the final stage of analysis; such elements are often inserted in genealogies or phylogenies on an eclectic basis. This practice is interesting, but contains the same hidden assumptions as an acknowledged narrative explanation. Scenarios are thus rarely formally presented as such in the many hybrid forms of genealogical and phylogenetic trees which paleontologists construct, but scenario elements are nevertheless present, especially when an "explanation" is given for the environmental or biological conditions governing the appearance, disappearance, splitting, or diverging (changing along a phyletic branch) that taxa are seen to undergo. Such "explanations" are, of course, based on a myriad of hidden assumptions and ad hoc criteria, usually implicit and unrecognized as part of the hypothesis, and which make the hypothesis untestable. Such practice is common in paleontology among its three primary branches: paleobiosystematics, biostratigraphy, and paleoecology. The attempt to criticize and correct practice in the
first branch has been initiated by a small number of cladist paleontologists and neontologists and is still continuing. This study and two earlier attempts (Schafersman, 1978, 1980) analyze current biostratigraphic practice and thus initiate similar criticism and corrections for biostratigraphy.
Models of Evolution and Phylogenetic Inference

It should now be obvious that a regional or multi-core study of evolutionary processes and patterns that can be represented by a phylogeny requires that absolute time, rather than relative time, be known. This is true because the information about cladogenetic evolution (time of branching) and anagenetic evolution (speed and amount of gradual progressive change through time along each branch) that a phylogram purports to depict is almost useless unless it can be plotted on an interval time scale. Therefore, since a representation of phylogeny by a phylogram should be constructed on an absolute time scale, combining data from various cores or local sections to construct the single phylogram necessitates that the absolute time framework of each core or section used be accurately known. This is true because the synchronicity or lack of it for gradual morphologic change, appearance and disappearance of characters, and origination or extinction of taxa themselves must be precisely correlateable from core to core. Anything less would obviously be invalid. The stratigraphic framework must not rely solely on the fossils of interest and on other fossils, the latter included because (1) no fossils provide absolute time by themselves, and (2) many taxa and zones are defined by phylogenetic or evolutionary criteria.

As we have seen, constructing phylogenies is not a straight-forward task, since numerous hidden apriori assumptions about the nature of the evolutionary process are necessary. Most paleontologists who construct phylogenies have adopted a research strategy and methodology based
squarely on the nature of species and evolution as they understand it. Most paleontologists believe that they can "see evolution in the rocks" and that inferring life's history only requires gathering fossil data from different stratigraphic levels and plotting it; the facts will then speak for themselves. Most paleontologists believe that only they can reconstruct life's history, because only they have the historical fossil data which allow this. Most paleontologists believe that phylogenies based on stratigraphic and morphologic data provide the proper method to identify and classify fossil organisms. I am not so sanguine about any of these beliefs, for I recognize that some methods of taxon discrimination and phylogenetic inference must come between the "data" and the "results," and that unless the methods are explicitly recognized and rigorously evaluated, the "results" are apt to be unanalyzable, untestable, and irreproducible—in short, unscientific. I would agree with the cladists that taxa should be recognized and classified by their synapomorphies, that this historical data is more testable than extrinsic stratigraphic and geographic data, and that subsequent steps in a biosystematic analysis can usually be dispensed with for classification. The question remains: When is it valuable to go beyond a cladogenetic analysis and attempt a genealogical or phlogenetic analysis? What can a phylogeny tell us that is useful?

The major contribution of phylogeny is that it contains information about anagenesis. In fact, many typical paleontological phylogenetic diagrams are really portions of phylogenies in which the inferred anagenetic data is plotted and the cladogenetic and genealogical information has been omitted or given secondary emphasis. This contrasts with the neontological cladists, who consider anagenesis a
secondary evolutionary phenomena and ignore it in practice. In fact, some cladists do not even accept the concept of anagenesis, apparently believing it does not occur in nature. Perhaps this is the reason why they insist on confounding phylogeny and genealogy: phylogenies would be genealogies if anagenesis does not occur and is therefore to be ignored. Nevertheless, anagenesis does occur. Let us be clear exactly what is meant by the word: anagenesis is progressive evolutionary change (not necessarily slow or unidirectional, but necessarily gradual) within a single lineage or branch, i.e. progressive evolutionary change within a taxon. Phyletic evolution is the same thing as anagenesis. Progressive, of course, is not used in the sense of improvement or progress, but refers to progression by a successive series of (imperceptible) steps or stages. Anagenesis is thus any evolutionary change between the branching points of a genealogy; representation of this change in a genealogy changes it into a phylogeny. The punctuational model of evolution maintains that most evolutionary change takes place at the branching point when speciation (sensu stricto) takes place by cladogenesis, but some change may also take place between such points by anagenesis. That is, the punctuational model maintains that the major part of evolutionary change is concentrated in speciation events rather than in phyletic evolution. The previously popular and still widely held gradualistic model of evolution (phyletic gradualism) maintains precisely the opposite, that the major part of evolutionary change is concentrated in phyletic evolution rather than speciation. These two models of evolution are illustrated in Figure 9.

It is widely accepted by systematists that speciation (sensu lato) or, less ambiguously, phyletic transition (Raup and Stanley, 1978,
FIGURE 9
Models of Evolution: Gradual versus Punctuated

The figure illustrates two alternative models of evolutionary change. The graphs are 3-dimensional, with the frequency distribution curves projecting out of the page. Different species are denoted by alternate shading. The model of phyletic gradualism on the left is characterized by uniform, unidirectional, phyletic change with no rate increase at the splitting event. Macroevolutionary trends are produced by additive phyletic evolution, and species are arbitrary subdivisions of a continuous single lineage. In contrast, the model of punctuated equilibria is characterized by episodic phenotypic change, high during speciation, low to absent (stasis) within species. Macroevolutionary trends are caused by the non-random survival of stochastic speciation events (species selection), and species are real, discrete entities with natural, non-arbitrary beginnings and terminations at the single lineage boundaries. The figure is taken from Vrba (1980, p. 62).
p. 103) can occur by phyletic evolution; that is, species can change by anagenesis until they become new species. But the idea that phyletic gradualism necessitates, implies, or even allows new species to form by phyletic evolution (anagenesis) is demonstrably erroneous. This idea is rejected not for lack of supporting evidence or presence of contradictory evidence, but for theoretical constraints placed upon our interpretation of any evidence by adherence to a systematic scientific method. This statement will be clarified later, but for now it is sufficient to note that although anagenesis occurs and may even be a common feature, and although the model of phyletic gradualism may be correct, in neither case should we ascribe speciation, in any sense, to be a result of anagenesis. As will be shown later, species can form only by creation of newly derived characters (apomorphies) by cladogenesis.

Anagenesis (phyletic evolution) must be distinguished from phyletic gradualism: the former is a type or mode of evolution, the latter is a model of hypothesis of evolution. To reject the occurrence of anagenesis because of a disbelief in phyletic gradualism is obfuscation. Gould and Eldredge (1977, p. 141) state:

We find intellectually satisfying (though not necessarily true on that account) the reduction of these supposed processes [anagenesis and cladogenesis] to the single phenomenon of speciation—for, in our model [punctuated equilibria], anagenesis is only accumulated cladogenesis filtered through the directed force of species selection.

Gould and Eldredge are saying that by rejecting phyletic gradualism and adopting punctuation, anagenesis is evolutionary change between species lineages, rather than within species lineages. I would therefore say
that the reduction they find intellectually satisfying is in fact not true. No doubt we often see a directional change between separate species, each species produced by cladogenesis; but this evolutionary change of cladogenesis directed (perhaps) by species selection is not anagenesis: it is a phylogenetic trend. Anagenesis can produce a phyletic trend, but I believe it is incorrect to speak of anagenesis producing any directional change, by itself, on the phylogenetic level. There is a problem in speaking of anagenesis as the type of evolutionary process which produces progressive evolutionary change between species (at the phylogenetic level) as well as, or even more mistakenly, instead of, progressive evolutionary change within a single species (at the phyletic level). Gould and Eldredge are using the term in this sense. Probably no modern evolutionary term has more definitions than anagenesis. Simpson (1953, p. 384) discusses the term in the context of phyletic evolution, although he notes Rensch's (1947) definition to be slightly less general. Here, by the way, Simpson considers splitting and phyletic evolution to be the two modes of evolution (what I call cladogenesis and anagenesis). In 1961, Simpson (p. 201) notes that there is no unequivocal definition for anagenesis. Huxley (1957) and Rensch (1960) have both given it different definitions, neither of which is what is required (in Simpson's estimation). Here he refers to phyletic evolution as "progression," but he includes anagenesis as part of this. Here also is the justification for the subsequent usage of the term to sometimes refer to more than what is now called phyletic evolution, for Simpson (p. 201) suggests that the term should be used "for any kind of change occurring sequentially in a single line of descent (or without reference to any branches that the line may also
have)...." Simpson refers to a figure which shows a straight-line progression of a "lineage." He unfortunately doesn't say what kind of lineage this is (as explained later, there are three kinds), so the problem of obtaining an unequivocal definition of anagenesis is never resolved. Since most workers, mainly paleontologists, have understood Simpson's "lineage" to be either what I call a single lineage (a single species) or an extended lineage (a single line of descent which is traced through many species in a phylogeny), then anagenesis has come to connote progressive change both within a species and a phylogeny. For example, Valentine in Dobzhansky and others. (1977, p. 236) notes that anagenesis "has come to be applied to nearly any kind of evolutionary change ... except for the branching pattern...."

Thus, despite the early implicit, but never quite exact, identification of anagenesis with phyletic evolution, the term has sometimes come to be the mode or type of evolution for progressive change at all levels of taxa and patterns, phylogenetic as well as phyletic. Yet anagenesis in this sense clearly leads to a remarkable contradiction if cladogenesis is indeed the main process of phylogenetic evolutionary change, as the punctuational model predicts. For if the model is true, then most anagenesis in the above sense would be the result of cladogenesis, just as Gould and Eldredge state. This, despite the fact that anagenesis has always been considered the antithesis of cladogenesis. Gould and Eldredge wish to create a synthesis, but at the cost of obscuring the distinctions among evolutionary patterns and processes.

Surely anagenesis cannot exist as a distinct mode of evolutionary change if it can be confounded with cladogenesis. For example, a
phylogenetic trend created largely by cladogenesis would be referred to as an example of anagenesis if we allowed the wider, more inclusive terminology adopted by Gould and Eldredge (1977) and Dobzhansky et al. (1977). Clearly, such a phylogenetic trend should be referred to as an example of cladogenesis (although, quite likely, the trend is a result of both cladogenesis and anagenesis, but the former dominates). We have good reason to restrict anagenesis to change within species (single lineages), because this type of evolutionary change obviously takes place without cladogenesis. Therefore, anagenesis (= phyletic evolution) cannot result in speciation by the creation of new lineages, but only in change of the existing lineage.

Phyletic branches (single lineages), each a species, are distinct entities which may show a progressive directional change along a number of connected single lineages (i.e. along an extended lineage); this change is a phylogenetic trend (rather than a phyletic trend) because the branches of the phylogeny are involved. A phylogenetic trend is therefore defined as an evolutionary trend involving an extended lineage within a phylogeny, i.e. a trend among a number of single lineages resulting from net directional change among the phylogenetic branches. Anagenesis and phyletic evolution are synonyms for a good reason: anagenesis is evolutionary change within phyletic branch, i.e. within a single lineage. A phyletic trend is therefore an evolutionary trend within a single lineage, i.e. a trend within an evolving species that persists through numerous generations and results from net directional change among a number of demes, populations, or subspecies. The vital distinction between a phylogenetic trend and a phyletic trend is that the former always contains cladogenetic evolutionary change while the
latter never does. It is likewise extremely important that an evolutionary trend has always been understood, by the foremost students of paleontology and evolution, to refer to the unidirectional or straight-line morphologic change through time of a path traced through a single lineage or phylogeny which does not completely exhaust (or predetermine!) the evolutionary change the single lineage or phylogeny contains. Simpson (1951, 1953) emphasized that trends did not follow a single phyletic path. He maintained that an "evolutionary trend is sustained, prevailing tendency in [phyletic or] phylogenetic progression" (Simpson, 1953, p. 245); note the word "prevailing" rather than "total." Another definition of trend is one which involves "the majority of related [fractional or single] lineages of a group" (MacGillavry), 1968, p. 72). I have added terms in brackets to emphasize my modern view. Eldredge and Gould (1972, p. 111-112) accept MacGillavry's definition and state that what is most important in a trend is the "long-term, net directional change" rather than the expectation of finding "all events of adaption" following the trend's direction. Their context is phylogenetic, but I point out that the same is true of phyletic trends. Raup and Stanley (1978, p. 335) accept Eldredge and Gould's definition and define a phylogenetic trend as "a net change within a more complex, branching phylogeny." Obviously, the same would be true of a phyletic trend, except that the net change would be within a single lineage. Stanley (1979, p. 182) states that "...observed change represents a net trend in phylogeny..., or a phylogenetic trend." He emphasizes that a phylogeny "includes segments of many lineages, some of which represent evolution in a direction opposite to that of the overall trend ..." (p. 182). Since Stanley's context is
macroevolution, he of course considers only a phylogeny. But I stress that the same would be true of a single lineage, which would include segments of many fractional lineages, some of which might evolve in a direction opposite to that of the overall trend. The prevailing, directional change in a species should no more represent the totality of its evolving subpopulations than does such change in a phylogeny represent the totality of its evolving species. In fact, one of the subpopulations or subspecies may be the one which becomes a new species. My careful distinction between phyletic and phylogenetic trends is only another manifestation of the current scientific insight into the idea that evolution has a number of different levels which contain analogous processes (such as individual selection ad species selection), and it is by a hierarchical system that we will best understand evolution. For example, the evolutionary processes which govern macroevolution may be completely different from, analogous to, or identical to those which govern macroevolution. There are evolutionists who support each of the three cases. A major theme in modern evolutionary paleontological studies is that, at the very least, macroevolution must be "decoupled" from microevolution (e.g. Stanley, 1979). Although this is a fascinating topic, it cannot be examined further in detail within the limits of this paper.

All of the discussion of terminology emphasizes the fact that evolutionary paleontology has grown so fast that new ideas have outstripped the theoretical fundamentals and the old, hazy concepts which heretofore sufficed. The main problems of the latter appear to be (1) a belief that "phyletic" and "phylogenetic" are synonymous, with subsequent confusion whenever these terms appear in a definition or are
used to explain an evolutionary concept; (2) the term "anagenesis" has always been imprecisely defined, although it has long been understood to be the antithesis of cladogenesis; (2) the term "lineage" and the three different types of lineages have never been unambiguously differentiated; (2) the different types of extinction, closely related to the lineage problem, have never received the attention they deserve. The first two problems have already been discussed and, I hope, clarified; the last two problems involving lineages and extinction will be treated in a later section in detail. All of these terminological distinction are of extreme importance, and it is unfortunate that the lack of rigor in previous analyses necessitates their clarification here. Too much confusion and ambiguity has been caused by imprecise definitions in the modern biosystematic literature.

Although we have discussed two modes of evolutionary change in some detail, it is well to remember that phylogeny is characterized by four basic evolutionary modes or processes: (1) evolutionary change between branches caused by the splitting or diversification of single lineages: speciation, cladogenetic evolution, or cladogenesis; (2) evolutionary change within branches caused by progressive change within single lineages (or divergence between sister-group single lineages): phyletic evolution, anagenetic evolution, or anagenesis; (3) equilibrium or persistence without change of single lineages: arrested evolution or stasigenesis; (4) termination of single lineages: extinction. These four basic kinds of evolutionary processes or events are not new: they were listed quite explicity by Simpson (1961, p. 201) and recognized by others before him. If a species is a single lineage (as I maintain and will later demonstrate), the question is which is more important,
evolution between species (cladogenesis) or evolution within species (anagenesis)? Remember, the question is which is more important for evolution, not speciation, since anagenesis cannot by itself result in new species by definition. So, does the bulk of evolutionary change occur by speciation, as asserted by the punctuational model, or by phyletic evolution, as maintained by the gradualistic model? This extremely important question can be answered only by constructing phylogenies; cladogenies by themselves will not suffice. We cannot ignore phylogeny construction because of theoretical difficulties. Furthermore, we should investigate the best methods to construct phylogenies. Eldredge (1979a) now allows phylogeny construction despite his former opposition (Schaeffer, Hecht, and Eldredge, 1972). And well he should, since Eldredge and Gould (1972) and Gould and Eldredge (1977) both discuss, analyze, and criticize constructed phylogenies from the point of view of correctness, relevance, and value, not from the point of view that they should never have been constructed in the first place. In fact, they consider their hypothetical phylogram (Eldredge and Gould, 1972, p. 113, fig. 5-10) to be the first explicit representation of species selection.

Since phylogenies are important and necessary for testing models of macroevolution, how does one construct a valid phylogeny or, more exactly, portion of a phylogeny, since in our valid phylogenies we will always plot anagenetic change and sometimes omit cladogenetic and genealogical data; these later concepts are better expressed by cladograms and formal family trees derived from cladograms. Our phylogeny is simply a plot of change through time, with change expressed by biometric statistical character change and time expressed by absolute
time of an interval scale. First one must decide on the amount of geographic variation in the measured character our phylogenetic analysis will use by choosing to sample a single core or local section, and thus rely on simple superposition as a sample ordering method, or by choosing to perform a regional study and sample a number of geographically-separated cores or sections, and therefore require some means of correlation between samples for valid statistical analysis. Both cases require absolute age assignment, while the second also requires absolute age correlation. I am using the term "absolute age" to mean, at a minimum, the ability to divide the stratigraphic time scale into equal intervals of known duration, that is, an interval scale of equal intervals of time units such as years or millions of years. Of course, the term absolute age usually means the ability to specify the age of the intervals in time units (i.e. a ratio scale), but while this is useful and sometimes possible, it is not strictly necessary for the present purpose of testing evolutionary anagenetic hypotheses. A multi-core regional study to investigate geographic variation is widely believed to be necessary for a valid test. For example, Ager (1973, p. 20) states: "one must clearly study the variation of a species throughout its geographical range, at one moment in geologic time, before one can claim that it has changed into something else." Gould and Eldredge (1977, p. 136) quote this passage with approval, although it clearly implies a transformational, rather than taxic, approach to the study of life's history. The fact is, of course, that precise equal-time-interval correlation of samples from widely spaced cores or sections for valid statistical sampling is an extremely difficult, almost impossible task. For single cores or sections containing a
uniform lithology, equal interval age assignments can be made by assuming constant rate of deposition and obtaining a good estimate of time required to deposit an interval thickness. Of course, compaction must be taken into account if the matrix has been lithified. Needless to say, this is a highly risky assumption. Single stratigraphic sections containing a number of lithologies present additional difficulties. I hope it is clear that the usual method of plotting sample measurements against a stratigraphic section measured in length rather than time invokes a number of major questionable assumptions. Only an independently-determined absolute time chronology allows valid results. This may be obtained in deep sea piston cores by paleomagnetism. Furthermore, if proper biostratigraphic methods are used which avoid the use of evolutionary criteria and other apriori and ad hoc concepts for taxonomy and biohorizon and biozone definition, then the paleomagnetic zonations of individual piston cores may be extended to other cores. Elucidation of such proper biostratigraphic methods is a primary purpose of this paper.

We have seen that single core studies sometimes allow valid phylogeny construction (anagenetic aspect only) with or without necessary assumptions. Obviously, multiple core studies which infer a similar phylogeny, but with a better statistical grasp of regional variation, can require even greater ill-advised assumptions. Not only are we faced with recognizing equal time intervals, but these intervals must be precisely correlated. Although they have been used for this purpose, biozonations by themselves cannot provide the necessary correlation of either absolute age assignment or equal-time-intervals between separate stratigraphic sections. Furthermore, as previously
emphasized, the biozonation must be free of hidden apriori assumptions of the evolutionary mechanism which are so prevalent in some current biostratigraphic systems. Thus, we have two reasons why independent groups of microfossils do not provide "independent" means of correlation similar to that of paleomagnetism for phylogeny construction. First, biozonations provide relative ages while paleomagnetism provides absolute ages (unless, of course, the biozonation has been first correlated with paleomagnetic stratigraphy), and second, the species of the biozonation are defined, identified, and classified, and sometimes the zonal boundaries are defined and delineated, by exactly the same evolutionary criteria of the theory we wish to examine when we test evolutionary hypotheses by constructing phylogenies. When we use paleomagnetism as a basis for an absolute chronological framework, some may object that we are only substituting a physical theory for a biological theory, but I defend this by noting that the paleomagnetic zoneation can be independently tested without recourse to presuming the truth of a particular evolutionary theory, an advantage which does not exist for many biozonations as currently defined and used.

One important method for correlating samples from different areas without relying on either biostratigraphy or paleomagnetism is the practice of lateral tracing of beds. In a single area or basin with a uniform and well-studied depositional history, this method may have some value. The major assumption here, besides recognizing equal age intervals in rocks of different lithology, is the assumption that time transgression by lateral facies change is not a problem. Sometimes, this assumption is valid, but more often it is not. In every case, however, it is important to explicitly recognize it. Usually one can
assume that any age discrepancy due to lithofacies time transgression is of less magnitude than the rate at which morphology changes at evolutionary rates.
Evolutionary Species and Fossil Lineages

No question is as important, or as controversial, in paleontology as "What is a species?" Intuitively, since we are one ourselves, we know that species are real. All taxonomic categories, including species, are artificial groups which we use to classify organisms. All taxa, on the other hand, are artificial in a similar sense except for species. While it is generally understood that taxonomic categories are creations of taxonomists, it was believed that the taxa themselves were somehow "real" natural entities that existed apart from scientific understanding. This belief for all taxa except that of species has now been discarded, since there are no perceivable substantive differences among taxa of genus, family, order, and class, only different degrees of species inclusiveness. The higher taxa have been replaced in theory, although not in nomenclature, by the concept of clade. This transition is a major advance in taxonomic understanding; it has been and still is resisted by many taxonomists, but eventually the new taxonomic attitude will prevail and the traditional Linnean hierarchical system will be revised (Wiley, 1979). Already the practices of neontological taxonomy involving taxon ranking and classification construction have changed tremendously. Similar changes in paleontological taxonomy will follow, just as advances in ecology stimulated fresh approaches in paleoecology. It is a sad tale, but paleontological advancements have always followed, not preceded, revolutions in biological theory and
practice. This theme has been repeated again and again; for example, paleontology adopted evolutionary explanations, the experimental method, the synthetic theory of evolution, and ecological mathematical models and techniques, only after these were developed and utilized by biologists. Whenever paleontologists made interpretations from their data alone, and ignored biological theory and practice, the results were often wrong and subsequently repudiated (an example would be orthogenesis); this happened frequently in the nineteenth and early twentieth centuries, and still occasionally occurs today.

If we assume that species are real, we should consider whether species should be the units of classification, that is, the fundamental natural entities which a classification must discriminate, order, and rank. Since we will assume that our classification must somehow reflect or be consistent with the evolution of organisms (in order for the taxonomic system to be most natural and stable), we first must ask whether species are the units of evolution. This question would be immediately answered in the affirmative by most systematists, including myself, were it not for the critiques of Rosen and Lovtrup. It took decades for the dictum that "populations evolve, not individuals" to be accepted by working taxonomists; but now is it also true that "populations evolve, not species?" Rosen (1978, pl 176-177) concludes that "a species...is a unit of taxonomic convenience, and that the population... is the unit of evolutionary significance." Lovtrup (1979, p. 391) agrees that the "unit of evolution is a population which may range from all to a single member of a terminal taxon." Both of these systematists criticize traditional concepts of species that rely on determination of amount of continuous and discontinuous morphologic
variability contained in species populations. Rosen (1978, p. 176) makes the valid point that species concepts which have in common a requirement for the discovery of discontinuous phenetic variation will ultimately resolve to the concept that a species is what a competent taxonomist says it is. Obviously, such a species concept can't be scientific. For example, if two or more geographically isolated populations show overlapping variation with statistically different means, are these separate populations treated as subspecies within a species, as species within a genus, or ignored by the taxonomist. The treatment usually is a factor of the taxonomist's personal species concept, experience, and training, rather than an objective and repeatable scientific method.

The cladistic solution to this problem is to analyze for apomorphic (both uniquely and shared derived) characters. Thus Rosen (1978, p. 176) considers a population to be "a geographically constrained group of individuals with some unique apomorphic characters." This is a good definition of a population, but what evolutionary significance does geographical constraint have? Depending on circumstances, it may or may not have an effect on apomorphic characters. Since we will use intrinsic apomorphic characters, rather than extrinsic geographic criteria (which we would apriori have to assume we know before we could use them anyway), to analyze characters in populations, it makes sense to delete the words "geographically constrained" from the definition of a population. The definition of a population then reads "a group of individuals with some unique apomorphic characters." But this is the definition of a species. A species is such a population as defined above; continuous and discontinuous variation and geographic
constraintment (and, I might add, stratigraphic constraintment) are ignored in favor of apomorphic characters alone. Therefore, we may conclude that while a population is the "unit of evolutionary significance" or the "unit of evolution," such a population, correctly defined, is in fact a species, so that species are the units of evolution after all. Since the taxon species is the unit of evolution, it makes sense to make the category species the unit of classification. Now, while the category species is a unit of "taxonomic convenience" (in Rosen's words), the taxon species is not. By our taxonomic practice we strive to equate the (artificial) category species with the (natural) taxon species, and if we succeed, the artificiality of taxonomic convenience vanishes. Whether a taxonomist succeeds or not is an empirical question which cannot be answered without real data, a rigorous analysis, and the constant testing, falsification, and corroboration of the scientific method. I believe I have shown, however, that no theoretical difficulties stand in the way of using species, rather than populations, as the unit of classification and evolution.

We have described a species as "a group of organisms with at least one unique apomorphic character." Is this the best definition possible? No, because it lacks recognition of the fact that a species is not a single population, as implied by the definition's derivation from Rosen's population definition, but a sequence of populations with an evolutionary history. By itself, the above definition would serve to identify living species in a classification which only evaluated the cladogenetic history. But if we wish to recognize an anagenetic history, or an ancestral-descendent relationship, or wish to have a
single universal definition for both fossil and living organisms, all of which I believe are necessary, then we must expand the definition to include their possibility.

The need for an evolutionary species definition to serve both paleontology and biology was understood by Simpson. His remarkable definition was a considerable advance over previous definitions and agreed with the speciation concept and taxonomic theory of evolutionary biosystematics. Simpson's definition states: "An evolutionary species is a lineage (an ancestral-descendant sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies" (Simpson, 1961, p. 153). Before we analyze this definition, it would be well to point out that any satisfactory species definition does not mention morphology, although the evidence that the definition is met is largely morphological, especially for fossils. Simpson and all other informed taxonomists recognize this explicitly. For example, the biological species definition emphasized reproductive isolation (lack of interbreeding between populations); for the paleontologist, the inability to test this directly made it impossible to apply this definition. This is the so-called "species problem" in paleontology (see Imbrie, 1957, or Raup and Stanley, 1978, p. 109). But it is impossible to discriminate species of fossil organisms by including in a fossil species only those specimens that would have belonged to a single biological species, identified by morphological criteria, if they had all lived today. As Imbrie (1957, p. 125, 126) points out, the concept of fossil species held by most paleontologists is an inference based on the observed structure of living species. "Morphologic data are never really considered by themselves; their interpretation is always colored
to some degree by prevailing theories on population structure." The inadequacies of the biological species definition are too well-known to require further comment; the discussion above was an example to clarify the notion that the evolutionary species definition requires that we use morphologic data to distinguish lineages which evolve separately and have different evolutionary roles and tendencies, and that such inference from morphologic data is unavoidable.

The first criticism of Simpson's definition of an evolutionary species is the way he wishes the inference from morphologic data to be done. Simpson makes it clear that the evolutionary species is not only consistent with the biological (genetical) species, but helps to clarify it and remove some of its limitations. Thus, the evolutionary species for Simpson is an attempt to produce a "broader theoretical definition that relates the genetical species directly to the evolutionary processes that produce it" (Simpson, 1961, p. 153). As such, the inference of evolutionary species from morphologic data proceeds by estimating genetic discontinuities within the evolutionary processes which Simpson claims we should know. For example, Simpson (1961) states that the best evidence for species discrimination is a demonstration at a sufficient level of statistical confidence that a morphologic discontinuity exists between populations inferred from specimens. Populations placed in separate species are either in separate lineages (contemporaneous or not) between which significant breeding does not occur, or at successive stages in one lineage, but with intervening evolutionary change of such magnitude that populations differ as much as do contemporaneous species. Fossil material, often incomplete, commonly cannot establish the original presence or absence of a morphological
discontinuity. Future fossil discoveries may alter current conclusions about an ostensible discontinuity, so taxonomic inference is heavily dependent on the adequacy of sampling and the completeness of the fossil record. In an earlier paper, Simpson (1943) explains that taxonomic inference varies from the mistaken use of intuition, to the pragmatically valid empiricism of experience, and finally to the use of statistical methods, the most exact and reliable of all. I, however, fail to see how even the last type of taxonomic inference is scientifically valid when we are faced with the authority needed to decide a "sufficient level of statistical confidence," the occurrence or not of "significant breeding," the amount of "intervening evolutionary change of such magnitude that populations differ," the "presence or absence of a morphologic discontinuity" that somehow reflects reproductive and genetic isolation, and the assumptions of completeness of data of morphologic variation, despite the inadequacy of the fossil record. Both Rosen (1978) and Lovtrup (1979) are right in claiming that Simpson's evolutionary species concept is nothing more than the biologic species concept in disguise. Both species concepts are based on an implicit phenetic evolutionary theory heavily dependent on knowing the processes of evolution and speciation in advance and analyzing phenetic variation from this standpoint. I can only point out that such a theoretical basis is untenable, since the assumptions it requires do not permit proper testing and falsification; ad hoc explanations can always be produced, such as "I infer that these two lineages are one species, despite the morphological discontinuity, because part of the stratigraphic record is missing," or "I infer that these two lineages are two species, because of a morphologic discontinuity that suggests
reproductive isolation, and your intermediate specimen is from a
different basin (state, continent) and belongs to the upper (lower)
lineage."

Basing a fossil species concept on apriori assumptions about
evolutionary theory is standard practice among paleontologists. For
example, consider the following:

"The concept of fossil species held by most
paleontologists is largely an inference...based
both on the observed structure of living species
and on a theoretical model of the evolutionary
mechanism...Moreover, descriptions of
species...are inferences drawn from various
sorts of data, including observations on
gographic distribution and ecology as well as
morphology and genetics." (Imbrie, 1957,
p. 125-126)

The questions that are rarely asked about species concept criteria
such as these are: What if our model of the evolutionary mechanism
turns out to be wrong? What if reproductive isolation is not the major
factor in speciation? What if we misjudge the amount of evolutionary
change, geographic disjunction, or ecological separation necessary to
conclude that populations differ enough to call them separate species?
What if morphologic variation does not closely reflect genetic
variation? I conclude that species concepts and definitions should not
be based on any specific evolutionary theory.

The second criticism of Simpson's evolutionary species definition is
the ambiguous nature of the word "lineage." Inexact use of this word
has led to much confusion in the literature, and Simpson's evolutionary
taxonomic concept of lineage has ironically led to typological
practice. Simpson stated the following:
"An evolutionary species is defined as a separate lineage...of unitary role. If you start at any point on the sequence and follow the line backward through time, there is no place where the definition ceases to apply. You never leave an uninterrupted, separate, unitary lineage and therefore never leave the species with which you started.... Such classification is manifestly both useless and somehow wrong in principle. Certainly the lineage must be chopped into segments for purposes of classification, and this must be done arbitrarily...because there is no nonarbitrary way to subdivide a continuous line.... Successive species should be defined as to make the morphological difference between them at least as great as sequential differences among contemporaneous species of the same group or closely allied groups.... Application of this criterion depends heavily on personal judgement and again reminds us that classification is an art." (Simpson, 1961, p. 165)

I suppose that the above quotation fairly represents all of evolutionary taxonomy that needs revision in a paleontological context. I would hope that no science is "arbitrary" or "an art," and if it is, then something needs revision. In all fairness to Simpson, his analysis is quite in line with usual paleontological theory and practice. For example:

"In the course of time one species gradually becomes transformed into another, in which case the kind of biologic discontinuity that separates related contemporaneous species is lacking, and vertical phyletic lines do not naturally fall into series of discreet units.... In an historical sense fossil species do not have natural chronologic boundaries. However, they commonly do have real stratigraphic limits.... Since evolution is continuous, the selection of species limits in a vertical series might be arbitrary.... In theory, the paleontologist should be unable to delimit species vertically since they are continually evolving systems.... If an evolving
lineage continuously occupied an area for long (a condition rarely realized) and if the fossil record of occupancy here were complete (also rare), then the record of each line of descent would be continuous and the delimitation of successive vertical subspecies and species would be arbitrary." (Newell, 1958, p. 67-68).

Wiley (1978, p. 21) satisfactorily criticized Simpson's (and Newell's) evolutionary species concept from the point of view of cladistic analysis. Wiley states: "No presumed separate, single, evolutionary lineage may be subdivided into a series of ancestral and descendent 'species.'" He points out that there is no reason to arbitrarily subdivide the evolutionary continuum, because evolution is composed of two processes: "One, the continuum, ties all of life together. The other, punctuations of the continuum, produces diversity.... Every punctuation of the continuum followed by divergence results in a single evolutionary lineage being split into two or more evolutionary lineages." As Bonde (1975, p. 294) has stated: "This continuum is subdivided in a non-arbitrary way by the speciation process which delimits 'natural' species in the time dimension." Thus, if we analyze for cladogenetic events, rather than for gradual anagenetic change and continuous or discontinuous variation between ancestor and descendent, we can identify the punctuational events and nonarbitrarily subdivide species.

The discussions of both Wiley and Simpson implicitly recognize that lineages may be of different lengths, but unfortunately neither author explicitly comes to grips with this problem. The first attempt to explicitly clarify the distinctions among different lineages was in Schafersman (1978; the distinction was made in the talk, however, not
the abstract). Wiley's (1978, p. 18) revised definition of an evolutionary species is as follows: "A species is a single lineage of ancestral descendent populations or organisms which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate." The only substantive difference between this definition and Simpson's is the addition of the word "single" before lineage. Yet the addition of this word removed decades of ambiguity and arbitrariness from the species concept, and changed it from a largely phenetic concept to a cladistic concept. A lineage is an ancestral-descendent sequence of populations, and as such, it may be of any length from protozoa to man, species to species, or population to population within a species. I maintain that it is necessary to explicitly state which of three different types of lineages one is invoking; I name these types the extended lineage, single lineage, and fractional lineage. A single lineage is a series of all the populations in an ancestral-descendent sequence whose limits are marked by cladogenetic branching points; a fractional lineage is a partial series of such populations; an extended lineage is a sequence of populations that crosses cladogenetic branching points. Thus, an evolutionary species is a single lineage; a fractional lineage is part of and entirely within an evolutionary species and may represent, for example, a subspecies; an extended lineage include populations on both sides of one or more cladogenetic branching points and thus must contain two or more evolutionary species in sequence. A cladogenetic branching point, of course, is the appearance of a new apomorphy (i.e. a uniquely derived character).
Simpson (1961) used the term "extended lineage" at least once (p. 164), although he did not distinguish or define the term; the main problem involves his failure to clearly distinguish a single lineage species from a fractional lineage species because of his toleration of arbitrary subdivision of a lineage to create evolutionary species. Simpson (p. 165) clearly states that an evolutionary species is "a separate lineage...of unitary role"; Wiley also stressed the unitary role of his "single lineage." Unfortunately, Simpson was referring to an arbitrarily-subdivided "segmental species in a lineage" which he called a "successive species" (Simpson, 1961, p. 166). He notes that this is the same as a paleospecies or successional species. Simpson indicates, for example, that "when in a lineage the inferred ranges of observed changing characters for populations...do not overlap, those populations may be placed in different successive species and the division between species drawn approximately midway (in time) between them." Since Simpson (1961, p. 166) believes that a successive species can be viewed as "a segment of an evolutionary species delimited in a certain span of time," we may ask how one kind of species can be a segment of another kind of species? Apparently, an evolutionary species is an ideal species that must be arbitrarily subdivided to give a practical species, the successive species. Thus, Simpson believes that the evolutionary species is the real species, but in paleontology we often must accept an arbitrarily-defined successive species. On page 167, Simpson explicitly shows the subdivision of a single lineage into different successive species (reproduced here as Figure 10); the criterion for subdivision is arbitrary placement of boundaries to create species that differ phenetically to the approximate degree that similar
Two Diagrams Illustrating Subdivision of a Single Lineage to Create Successional Species

Successional species, also known as paleospecies or chronospecies, are arbitrarily discriminated species that must be recognized according to the tenets of evolutionary taxonomy. These diagrams of Simpson (1961, p. 167) and Gingerich (1976b, p. 10) illustrate the concept. Although rarely invoked in practice, the concept of successional species is a manifestation of evolutionary taxonomy's assumption of the model of phyletic gradualism and its reliance upon arbitrary and typological phenetic criteria to identify species without distinguishing plesiomorphic from apomorphic characters or monophyly from paraphyly. Figure 10A shows Simpson's criterion of subdividing a phylogeny into species of approximately equal horizontal and vertical differences. Figure 10B shows Simpson's criterion of range overlap in a single changing lineage. Population 1 exists at time $t_1$ with range $R_1$, while Population 2 exists at time $t_2$ with range $R_2$. According to Simpson, the "corresponding populations are placed in different species, divided arbitrarily at an intermediate time in a population indicated by the dotted curve." In Figure 10C, Simpson shows how a single lineage can be arbitrarily subdivided into two successional species ($C'$) or three successional species ($C''$), at the option of the investigator. Figure D shows Gingerich's illustration of the relationship between "biological species" A, B, and C sampled at time t. Where stasis and disjunct phenetic separation occur, "nonarbitrary morphological
discontinuities are used to infer reproductive isolation on any given time plane." However, when a lineage is changing morphologically through time, the "evolving lineage must be separated at an arbitrary, time-parallel boundary" to separate species. Schafersman (1980) characterized this practice as typological, because it artificially restricts an evolutionary species' natural variation through time. The same artificial restriction on variation horizontally in space, rather than vertically in time, would be universally acknowledged to be typological. Also, there is no reason to assume, and no way to test, the assertion that biological species B and C are indeed reproductively isolated.
living species do. Presence or absence of unique or shared apomorphic characters is ignored. Gingerich (1976b) is a modern paleontologist who retains Simpson's traditional, arbitrary successional species (Figure 10).

Confusion about the three different types of lineages has led a number of workers to mistaken interpretations. For example, Raup and Stanley (1978, p. 313) incorrectly equate the terms chronospecies, successional species, paleospecies, and evolutionary species. There are two different entities here; an evolutionary species is a single lineage whose sequence of populations are bounded by cladogenetic events, and emphatically do not "arise and disappear by phyletic evolution" (= anagenesis) as claimed by Raup and Stanley. This evolutionary mode of formation is reserved for successional species (= paleospecies = chronospecies) which, as previously shown, must be arbitrarily delimited by searched-out phenoetic discontinuous variation and, as argued here, are therefore invalid, since species discrimination by discontinuous morphologic variation cannot be tested.

One of the best examples of the theoretical difference between the traditional evolutionary taxonomic and the cladistic concepts of species discrimination can be illustrated in the following argument by Newell (1956, p. 67-68):

"It seems unrealistic, however, to insist that taxonomic categories are real only if they are separated by discontinuities [Newell refers to stratigraphic gaps or distinct anagenetic morphological discontinuities, but presumably the argument holds for cladogenetic discontinuities involving newly derived characters]. The segments of a phyletic stem are real even if the boundaries are arbitrarily
drawn. [The conclusion that discontinuities must be present to subdivide evolving species], if generally accepted, would invalidate all sorts of man-made classifications. For example, the State of Nebraska is separated from Kansas by an invisible, wholly artificial boundary, but I believe that the good people of both state would join me in thinking that both Nebraska and Kansas are real; they do have 'objective existence.'"

This argument is easily refuted by pointing out that the shapes and boundaries of political entities do not have an evolutionary history and were arbitrarily created by man. In taxonomy we deal with living organisms that reached their present states by natural processes through an evolutionary history. There is nothing arbitrary or man-made about them. Segments of a phyletic stem may be "real" even if the boundaries are arbitrarily drawn, but such segments would not have any scientific value or meaning. Scientists strive to understand nature as it really is, and not to force nature into human preconceptions. It would be fine to use an arbitrary system, such as phenetic taxonomy, to classify inanimate objects, but living objects with an evolutionary history demand a nonarbitrary system which takes the evolutionary history into account. I agree with Wiley (1979, p. 216) that we should "classify by nature's own history of lineage splitting and not the psychologism we impose on nature." In this way we can avoid the excesses of Gingerich (1976, 1979) whose views about evolution are directly related to his species concept (as pointed out by Wiley, 1979, p. 215). Gingerich (1979, p. 48) defines a species as "an arbitrarily divided segment of an evolving lineage that differs morphologically from other species in the same or different lineages." Gingerich explicitly invokes the gradualistic model as the major mode of speciation. Because of these
views, he creates may more typological species than the data warrants (Wiley, 1979). The evolutionary taxonomic practice of arbitrarily delimiting the vertical variation of an evolving lineage to produce a sharply bounded "successive species" is just as typological as arbitrarily delimiting the horizontal variation of an evolving population to produce a sharply bounded "species." This story is ironic because the evolutionary taxonomists were the foremost systematists and paleontologists to criticize the latter practice, yet they explicitly allow the former.

I mentioned previously that Simpson's and Wiley's definition of evolutionary species differ mainly in the latter's addition of the word "single." Wiley may not have meant by this to emphasize in yet another way the unitary evolutionary role of a species, while Simpson's use of the word "lineage" by itself was ambiguous. Nevertheless, Wiley (1978, p. 21) did discuss as a corollary of his definition that evolutionary species (a single lineage) may not be subdivided into successive "species," as Simpson (1961, p. 166) was willing to allow. I here explicitly equate the term "single lineage" to an ancestral-descendent sequence of populations bounded by cladogenetic events (branching points identified by new apomorphous characters) and then logically define the other two types of lineages, the "fractional lineage" and the "extended lineage." However, it seems to me that the rest of Wiley's species definition is really no improvement over Simpson's. I would like to propose the following new definition of an evolutionary species which I believe gets to the bare bones of our current theoretical understanding of a species. I also believe it meets Wiley's five criteria (Wiley, 1978, p. 18) better than Wiley's definition. An evolutionary species is
a single lineage of ancestral-descendent populations whose members share some unique apomorphic character or characters and an individual evolutionary history. This definition eliminates the ambiguous words "tendencies," "role," "identify," and "fate," emphasizes the cladogenetic elements which permit recognition and demarcation of species and clearly specify species' origins, and still allows the recognition and analysis of anagenetic elements within a species' evolutionary history. This definition will be followed throughout the rest of this study.

Note that the definition forbids the arbitrary recognition of ancestral-descendent "species." That is, speciation cannot occur by anagenesis. Although this statement is straightforward enough, its acknowledgement by paleontologists will change paleontological understanding to a considerable degree. The idea that a species can evolve by anagenesis into another species was explicit in all of the quoted passages from Simpson and Newell cited previously. Although the problem arose very infrequently in paleontological practice, the question of where one species ended and the next began was a major theoretical question that generated volumes of discussion and argument. Newell (1956, p. 80) answered the question by concluding that two populations would belong to different subspecies if the difference in the means of a character exceeds 2.56 standard deviations, and two different successive species would differ by 4.0 standard deviations; the species boundary would be drawn midway between such populations. Simpson (1961, p. 165) answered the question by stating that successive species should be so defined so that they are as different as two similar contemporaneous species. Both answers are dependent on the
hidden assumption that the essence of speciation is the gradual (anagenetic) change of one species into another and that such change is reflected in continuous variation in morphology through time. But the essence of speciation is not the gradual change in a character (by anagenesis), but the appearance of a new character (by cladogenesis). It is impossible to answer the question "when does a species change enough to recognize a new species?" because the question itself is meaningless: continuous character change by anagenesis cannot result in a new species because the breaks in the evolutionary continuum which delimit species are discontinuous cladogenetic events. Furthermore, gradually-changing continuous characters are plesiomorphic, not apomorphic. The evolutionary species definition takes these facts into account.

Modes of Speciation

It is interesting to examine the gradual changes in paleontological thinking that have occurred in recent years about the topic of speciation. In the first edition of their excellent paleontology textbook, Raup and Stanley (1971, p. 97) note that there are two types of speciation: "phyletic speciation and geographic speciation. The first is the evolution of one species into another through time." It is useful to quote this section at some length to allow later comparison and discussion about changed views.

"Evolutionary change in the genetic composition of a population may represent either progressive adaptation to constant environmental conditions,
or adjustment to changing environmental conditions. With each succeeding generation, the gap in genetic composition with respect to an arbitrary starting generation is widened. As a population changes, it becomes almost inevitable (statistically) that differences develop that would inhibit individuals expressing the changed phenotype from breeding with individuals or the original ancestral phenotype.

If we think of a chronologic series of populations and choose one of these as an arbitrary starting point, then there will be a point at which the accumulated differences are such that the later populations would be reproductively isolated from the initial population if they were living at the same time. At this point a new species has been formed."

This passage is practically a paean to phyletic gradualism. In contrast, the second edition of *Principles of Paleontology* (Raup and Stanley, 1978, p. 103) treats the subject differently. The authors note that there is "some confusion" about the use of the term *speciation*; it is commonly used as a label for the process by which lineages split (cladogenesis), but paleontologists sometimes use the term to "describe the appearance of a new species by the gradual evolution of an entire lineage." To avoid confusion, they call this second process *phyletic transition*, and define it as "phyletic evolution" which results in "change from one species to another." The authors correctly define phyletic evolution (= anagenesis) as "evolution within an established lineage," although I would substitute the word "single" for "established." Thus, although Raup and Stanley admirably restrict speciation to cladogenesis, they continue to recognize the possibility of new species formation by a process which is not "speciation." This equivocation is not simply presented as something some or a few other
paleontologists believe, for Raup and Stanley implicitly indicate that, although rare, the process does occur. For example, their Figure 5-3 (p. 112) shows the distinction between speciation by cladogenetic events and species-formation (not "speciation") by phyletic evolution. One illustrated species "shows that the rate of phyletic evolution of this species would not have produced a new species...until long after the actual termination of the...lineage. The dashed horizontal bar represents the position where the transition would have been placed subjectively by a taxonomist" if the lineage had not terminated. Again, they state the following (1978, p. 113):

"There is no question that phyletic evolution occurs and that competent taxonomists consider certain well-documented lineages to be divisible into successional species. The extent to which such transitions constitute a taxonomic problem will depend on how frequently they occur. In other words, the severity of the species problem is in large part a question of what percentage of species arise by phyletic transition and what percentage arise by discrete, divergent speciation events."

I agree that there is a problem, but I claim it is not a species problem. The question should be what percent of evolutionary change occurs by phyletic evolution (anagenesis, not phyletic transition) and what percent by speciation events. I believe that Raup and Stanley allowed this equivocation to remain because they were not yet willing to totally reject traditional paleontological concepts and fully embrace the obvious implications of the cladistic and punctuational message:
that species contain unique apomorphies and are thus bounded by cladogenetic events. Perhaps they were correct in doing so, but I hope the third edition of their book will correct what I believe to be an error.

Stanley (1979) addresses this very topic. He correctly (p. 13) identifies the very problem in the question: "...is most evolution in the history of life associated with speciation or is more evolution of the phyletic variety?" His discussion preceding this question explicitly recognizes that the "fundamental question...concerns the relationship between speciation and rate of [phyletic] evolution."

Stanley correctly notes the two extreme possibilities: that either all evolution occurs in association with speciation (cladogenesis), or that "speciation is only incidental to rate of change" and that anagenesis is responsible for evolutionary change. Of course, the true course of any evolutionary change lies somewhere between these extreme possibilities; one goal of paleobiology is to discover what the true course is.

Yet Stanley continues to accept the possibility of phyletic transition (anagenetic species-formation). He claims (p. 17) that the idea that "most entities recognized as species arise through...speciation" is an "incorrect inference" of what "the punctuational model implies." He points out that the punctuational model implies only that speciation is responsible for most of the "net change in a segment of phylogeny," and it is quite possible for this to be true "even if most recognized species have formed by phyletic transition" (Stanley, 1979, p. 17, and Figure 2-5, p. 18). Stanley believes the speciation component of evolution far outweighs the phyletic component in the origin of higher taxa (p. 19). Nevertheless,
since "phyletic evolution represents the fine tuning of adaption," and
since this fine tuning leads to changes within a species, then "quite
often such changes accumulate to the point where, with sufficient data,
a competent paleontologist will demarcate a new chronospecies" (p. 19).

First, let me agree with Stanley that the punctuational model does
not imply that "most entities recognized as species arise
through...speciation;" this is implied by the scientific model, since
only when species are created by speciation (cladogenetic) events are we
inferring the existence of new species by natural processes and not by
human preconceptions we impose upon nature. Only here are we
recognizing new species by definite and explicit natural phenomena
(autapomorphous characters) and not by arbitrary and authoritarian
pronouncements about amount of morphological difference at least as
great as the difference sufficient to recognize a contemporaneous
species of the same or related group. Only here are we dealing with a
rigorous method by which new species are recognized and defined by
criteria which can be tested and taxonomic relationships refined by the
addition of new data (newly discovered autapomorphies and newly
discovered taxa), and not by a procedure whereby no amount of new data
will lead to refined taxonomic relationships in conflict with preferred
patterns, since new autapomorphies can be ignored and newly discovered
taxa can be inserted into pre-existing taxa without regard for
monophyletic affinities. For these reasons, let me disagree with
Stanley that phyletic transition occurs and that chronospecies or
successional species should be recognized.
Let us examine more closely Stanley's justification for the existence of phyletic transition. Very simply, it is the following:

There is no question that phyletic evolution occurs and that competent taxonomists consider certain well-documented lineages to be divisible into successional species. (Raup and Stanley, 1978, p. 113)

Quite often such changes accumulate to the point where, with sufficient data, a competent paleontologist will demarcate a new chronospecies. (Stanley, 1979, p. 19)

Thus we have the authority of competent taxonomists and paleontologists that successional species do, in fact, exist, and they can be demarcated by those competent enough to do so. Leaving aside the obvious criticism of when one knows that "sufficient data" exist to permit recognition of a "well-documented lineage," we may instead examine the concept of the "competent paleontologist." If there are competent paleontologists, there must also be extremely competent paleontologists and, regretfully, incompetent paleontologists. We may argue with the competent paleontologist about the correctness or advisability of his placement of boundaries between different successional species, suggesting, for example, that 40-60% be used rather than 50-50%, or, if more than one character exhibits phyletic evolution, that some other character be used for species differentiation rather than the one chosen. Perhaps one could point out to the competent paleontologist that certain gaps exist in the phyletic trend, making it difficult to so precisely place the boundary as he has done. Or maybe one can question the adequacy of the competent paleontologist's samples of fossil material, or his simple correlations if more than one section is used in the study, since the
amount of morphologic variation through time is at issue here, and these are valid concerns. Yes, there are many items we can question about the competent paleontologist's successional species, and no doubt he can argue quite convincingly in support of his own views. But do we dare question the successional species determinations made by the extremely competent paleontologist, a person who has studied his fossil group for a generation, who has produced dozens of definitive papers, who is widely acknowledged as the foremost authority, who is sometimes called "Mr. ________" (insert the appropriate fossil group in the blank). No, we are inclined to accept this person's successional species without question (at least in print until he's retired). But a sadder case is the successional species determinations of the incompetent paleontologist, for no other paleontologist bothers to accept this person's views (or even to read his papers). The point is: even if the extremely competent paleontologist's successional species determinations are wrong and the incompetent paleontologist's are right, other workers are invariably led to accept the former and ignore the latter, purely on the basis of authority. When one allows a successional species identification using competency as a criterion (as does Stanley), we inevitably must accept authoritarianism as the final arbiter. This is not science, but some sort of religion, bereft of any redeeming analytical or predictive value. What is lacking is the scientific method which allows explicit and unambiguous testing of hypothetical species determinations and the corroborations of those phylotheses which escape falsification. This is all that cladistic taxonomy wishes to promote. Successional species may very well exist in
nature, waiting to be discovered, but we cannot yet discover them by any
any scientific means.

I wish to emphasize that although anagenesis does not result in
speciation, it is incorrect to conclude that anagenesis is unimportant
in evolution or even that it does not exist at all. Apparently, some
cladist taxonomists have reached precisely these conclusions. Although
we no longer have to tolerate ambiguous or arbitrary species concepts,
we still must tolerate a great deal of morphologic variation and
evolutionary change in time and space within as well as between
species. Although the evidence for evolutionary change in time within a
species, i.e. anagenesis or phyletic evolution, is not substantial, what
there is of it is to my mind unequivocal. Although faulty in many
respects, the examples of Gingerich's mammals, Ozawa's fusulinid,
Kellogg's radiolarians, and Malmgren and Kennett's planktonic
foraminifer all present evidence that suggests that anagenesis occurs to
some extent. The question is: To what extent? This is the basis for
the two competing models of evolution, the punctuational model and the
gradualistic model. The former model hypothesizes that the major part
of evolutionary change is concentrated in speciation events; that is,
the change is the result of cladogenesis. The latter model hypothesizes
that the major part of evolutionary change "occurs as phyletic change
within established species" (Raup and Stanley, 1978, p. 327); that is,
the change is the result of anagenesis. Raup and Stanley (1978,
p. 327-330; see also Stanley, 1975) reviewed several kinds of evidence
to decide between these two models, and the punctuational model receives
by far the most support. Eldredge (1971), Eldredge and Gould (1972),
Gould and Eldredge (1977) provide similar analyses. I agree with these
authors on this point, and believe that the punctuational model is a major breakthrough in the science of paleontology. It is clear that the punctuational model and the cladistic taxonomic system provide mutual support for each other and have greatly increased the excitement and theoretical understanding of both paleontology and paleobiosystematics. Cracraft (1979) makes a similar observation. Together, these two ways of looking at fossil species follow the taxic approach advocated by Eldredge (1979b) and Cracraft (1979).

Types of Extinction

Another difficulty with terminology, closely related to the problem of the word "lineage," is the word "extinction." Although extinctions of organisms in geologic time is a frequently investigated topic, competent distinction of different types of extinction began in 1961 when Simpson (1961, p. 201-202) first distinguished "termination" as a special type of extinction. Termination is when taxa die without issue, or at the ending of a lineage in a phylogeny (in context, an extended lineage is implied). This is therefore a special and important case of extinction in general, since a taxon may completely disappear with or without having previously branched off some new species. In fact, the only example Simpson (p. 202) provides for non-termination extinction is when taxa "evolved so far as to be called different taxa of the same rank." Simpson makes no further distinctions.

Both Raup and Stanley (1978, p. 330) and Stanley (1979, p. 13) distinguish between "extinction" and "pseudoextinction" (=phyletic extinction). Pseudoextinction occurs during phyletic evolution, or more
exactly, during phyletic transition, when one successional species (paleospecies or chronospecies) evolves into another; when this occurs, the ancestral successional species becomes pseudoextinct. All other extinction is simply called "extinction," which "will refer only to the termination of a lineage" (Stanley, 1979, p. 13). In the context of the description, "lineage" refers to a single lineage. Note that in this usage it is not specified whether or not the terminated single lineage left any branches or descendant taxa: in either case its end is called extinction. Therefore, Stanley, unlike Simpson, does not distinguish the special case of "termination." When a species speciates (by cladogenesis, not by phyletic speciation or transition), the ancestral species may persist, as might be expected in a "peripheral isolate" model, or it may disappear, as would be assumed in canonical Hennigian "phylogenetic systematics." This latter case is extinction, but of course not termination. If, however, the same ancestral species were to have completely disappeared without having branched off any new species by speciation, Simpson would call this termination but Stanley would still call this just extinction.

It is clear that Simpson and Stanley both systematically distinguished two types of extinction, but the one type they held in common, which they both called simply "extinction," contained different subsets of phenomena in each system. What each distinguished as a distinct type of extinction was subsumed by the other in the general category of "extinction." Therefore, it is clear that there are in fact three types of extinction worthy of discriminating among, and furthermore, each can be directly related to the lineage terminology developed in this paper.
First, there is the extinction of subspecies or successional species, i.e. termination of a fractional lineage; this is called phyletic extinction or pseudoextinction. As previously discussed, successional specia (chronospecies, paleospecies) are not objective biological or evolutionary entities, cannot be recognized without resort to arbitrary criteria, and are thus untestable and therefore to be avoided. Yet the term pseudoextinction is useful when referring to the extinction of a vertical subspecies or the termination of a fractional lineage without a single lineage (evolutionary species). Entities such as subspecies or fractional lineage may be arbitrarily defined, for whatever purpose the systematist desires, without destroying the scientific basis of biosystematics.

Second, there is the extinction of an evolutionary species, i.e. termination of a single lineage; this is called extinction (*sensu stricto*) or orthoextinction (I will retain the use of Greek prefixes which Stanley initiated). Orthoextinction refers only to the extinction of a single known evolutionary species and says nothing about the survival of any single lineages which split from this species prior to or at the orthoextinction event. However, the possibility or actuality of the continuing existence of such cladogenetically-created branches is implied, because otherwise the extinction would be referred to the third type.

Third, there is the extinction of an evolutionary species, or, at the highest level of generality, clade, without issue, i.e. the termination of an extended lineage or a clade of extended lineages; this is called termination or holoextinction. The point about holoextinction
is its completeness: no descendants or cladogenetic branches of an extended lineage or clade remain after holoextinction.

The terms pseudoextinction, orthoextinction, and holoextinction may be used whenever it is necessary to avoid the confusion which the terms extinction or termination alone might cause. Further, the sharp differentiation of the three types of extinction might allow some fruitful hypotheses. For example, Van Valen (1973) stated this conclusion based on examination of many survivorship curves, that rate of extinction for established species was essentially random and did not vary a great deal through time, even in periods of mass extinction. This might suggest that the type, rather than rate, of extinction might be more directly controlled by the environment, and thus, for example, holoextinction is more common during periods of environmental stress than orthoextinction.
Evolutionary Relationships and Systematics

There are two kinds of relationships among species: ancestor-descendant relationships and relationships by common ancestry. The stratophenetic method of Gingerich (1979) and other evolutionary taxonomic methods, such as those of Simpson (1961) and Newell (1956), yield only ancestor-descendant relationships among the samples analyzed. As McKenna and others (1977) point out, it is necessary to assume that such relationships are preserved in the record, and such an assumption is unsupportable. Schaeffer and others (1972) assert that "it is dangerous to assume at the outset that a chronocline is a pure reflection of an ancestral-descendant sequence, no matter how complete the record may seem to be." Thus, for an evolutionary taxonomic analysis it is necessary to recognize ancestral-descendant relationships, but the certainty of knowing these is not strictly justifiable. We may contrast this with cladistic taxonomic analysis which recognizes common ancestry relationships by the possession of shared derived characters (synapomorphies). Once a species speciates, it is no longer a single lineage but a series of two or more single lineages which are separate and independently evolving. These single lineages have no relation to each other except the relationship derived from common ancestry, and it is this relationship which can be analyzed by an unambiguous, nonarbitrary system. One does not have to mix biologic, stratigraphic, and geographic data together in a way which prevents rigorous testing. Instead, the major reason to adopt a cladistic or taxic approach is to avoid all the hidden ad hoc and untestable assumptions which must be taken with any non-cladistic
taxonomic system that implicitly invokes a specific evolutionary theory. For a readily obtainable critique of evolutionary taxonomy and a defense of cladistic taxonomy (so-called "phylogenetic systematics"), see the papers by Cracraft, Gaffney, Eldredge, and Wiley in Cracraft and Eldredge (1979).

At this point, one may object that cladistic taxonomy itself invokes a specific evolutionary theory and is thus no different and assumption-free than evolutionary taxonomy. The critic would assert that cladistic taxonomy assumes that speciation only takes place by a splitting process (cladogenesis) involving allopatric speciation and that anagenesis is irrelevant in evolutionary change, and defines an evolutionary species by a restrictive definition that invokes these assumptions. To answer these criticisms, it is necessary to distinguish between an assumption and a corroborated hypothesis. An assumption does not have the integrity or universal acceptance of an hypothesis which has been corroborated by repeated testing and lack of falsification. Also, an assumption is often adopted ad hoc for expedient reasons, i.e. it is chosen for a particular objective or case at hand rather than for universal application. Evolutionary taxonomy makes use of many corroborated hypotheses, uncorroborated but generally acceptable assumptions, and unacceptable ad hoc assumptions. The aim in science is to base one's model, system, or theory on corroborated hypotheses and to avoid all assumptions which prevent decisive testing of predictions. I believe that the new evolutionary species definition and the cladistic taxonomic system both fulfill this aim better than competing systems.

As Gaffney (1979, p. 85-86) explains, cladistic taxonomy need rely on only two corroborated hypotheses for operation. These are that
evolution occurs and that new taxa are characterized by new features. The only alternative to the first hypothesis that evolution occurs is that species are immutable and therefore must be uniquely created by some divine or natural process; this alternative is no longer held by scientists or other rational, educated persons. I trust that the second hypothesis is equally well accepted; I would not like to deal with a new material entity that can't be distinguished empirically from a different material entity, although in practice, a new feature may be difficult to defect or even undetectable. If we accept the two hypotheses, cladistic taxonomy becomes possible without any further assumptions about speciation, degree of resemblance, amount of phenetic discontinuity, separation of features in time or space, or any knowledge about the evolutionary process or mechanism. Very simply, the occurrence of evolution implies that, since every individual has at least one parent and this continued back to the first living organism, life has one genealogy. The important thing here is that a genealogy exists, that there is an extremely large number of individual organisms on this genealogy, and that those individuals can be divided into groups (taxa) of different size depending on their shared features. We will designate one such taxon a species and group its population's members on the basis of their mutually possessing at least one uniquely derived feature (autapomorphy). Thus, a species population will possess at least one uniquely derived character (usually more) and different species can be distinguished by the unambiguous presence or absence of such unique apomorphies. A monophyletic species clade (single lineage) cannot be subdivided into two or more successional species, since these new "species" would not be monophyletic, i.e. the last "species" would not
contain the stem taxon and all the earlier "species" would not contain all the descendents. A monophyletic species clade is recognized and defined by the unique apomorphies it possesses; so subdividing it because of some internal anagenetic change (which does not affect apomorphies) which the individual species population's members exhibit does not preserve monophyly and thus is a violation of the species definition. Finally, the presence of shared derived characters (synapomorphies) among different species allows their unambiguous grouping and ranking in a hierarchical sequence.

As can be seen from this analysis, the cladistic taxonomic system does not depend on any speciation model: dichotomous splitting, allopatric, sympatric, or parapatric. It does depend, of course, on the splitting inherent in a genealogy, and the existence of a genealogy follows from the hypothesis that evolution occurs. The analogy of sister groups of an ancestor to the children of parents is precise: both are expressions which support the cladistic criterion that taxon relationships should be analyzed on the basis of common ancestry, because taxon common ancestry is a direct upward extension of sibling common ancestry. Anagenesis is definitely not irrelevant in evolutionary change; it is only irrelevant in analysis of species discrimination, ordering, and ranking for classification purposes. Although anagenesis is restricted to change within a single lineage, there is still a major question about how much anagenesis causes species to change, under what circumstances it operates, and the possibility that it affects some groups of organisms (such as protozoans and Tertiary mammals) more than others. A legitimate question is: Can a new species and its characteristics be more heavily indebted to the
anagenesis which preceded or succeeded its origin than to the cladogenesis which created it? If the answer is yes (and it may very well be yes), then we would want to know the extent this phenomenon occurs in nature. We now see why anagenesis must be limited to evolutionary change within a single lineage, and not additionally used to described progressive change within an extended lineage, because the very real possibility exists that most progressive change in such a long clade is cladogenetic in origin. I point out that we can attempt to answer these questions only by constructing genealogies and phylogenies in addition to cladogenies. Cladists must recognize that anagenesis in species is a phenomenon that must be analyzed; we can ignore it when we analyze character states for cladistic classification, but classification is only one part of biosystematics, and not necessarily the most interesting or important part. For example, paleontologists have traditionally been interested in macroevolution; I believe that a better understanding of all taxonomic issues and problems, not just cladistic examples, should lead to further advances in understanding macroevolution.

Some evolutionary taxonomists, such as Michener (1970), Ashlock (1974), Mayr (1974), and Bock (1975) have acknowledged the priority of an explicit and unambiguous cladistic analysis for classification. However, they insist that an anagenetic analysis must follow to result in a phylogeny, which then is used to deduce the best of several possible classifications. They argue that since evolution is a multi-process phenomenon, and since a classification should be based on the totality of the evolutionary history of taxa, then a classification should utilize and be consistent with all evolutionary processes, i.e.
cladogenesis and anagenesis. Phylograms, not cladograms, therefore should be the basis of classifications. Unfortunately, their argument is not valid. The second premise should specify scientific classifications, and thus the conclusion is that a classification should be based on cladogenesis alone. For it is still not possible to accurately and unambiguously express the anagenetic relationships of taxa, and even if it were, the system of classification and nomenclature presently used would have to be heavily revised into something much more complex to enable unambiguous and explicit representation of both anagenesis and cladogenesis, for, as everyone admits, the Linnean hierarchical system is incapable of precisely expressing both.

Michener (1970) and Ashlock (1974) suggest that the best research strategy is to work for a way to combine both cladogenetic and anagenetic aspects of evolution into classifications, and both believe this goal is possible. I am not so sanguine. Brothers (1975) and Michener (1977) attempted to combine both in taxonomic analyses, but were criticized by Nelson (1978). Reproducibility, objectivity, and testability are major problems which anagenetic analysis must overcome; no doubt modern evolutionary taxonomists such as Ashlock, Michener, and Brothers are striving to discover a method which will take a cladogram and allow explicit, reproducible, objective, nonarbitrary, and testable calculation of amount of anagenesis between monophyletic taxa in a clade. Taxonomic distance coefficients could perhaps be calculated from the apomorphic characters previously elucidated during cladistic analysis. While I believe that such a method will eventually be worked out, I still question its value for two reasons. First, what does the inference of anagenesis (as an evolutionary process) mean from an
evolutionary classification standpoint? The genetic basis of anagenesis is not as straightforward as that of cladogenesis, for while both involve the change of gene frequencies and are thus both processes of evolution, the latter is a decisive rearrangement of the species genetic integration, while the former is a more problematical shift in genetic integration. Thus, the question we may ask is that although the inference of anagenesis is certainly important from an evolutionary standpoint, is it important enough to warrant inclusion in a classification? Second, what does the inference of anagenesis (as taxonomic distance) mean from a methodological standpoint? Anagenesis is inferred from morphological change between or within character states of species, but does this change have an evolutinary basis, i.e. is it anagenesis and not something else, such as migration, ecological replacement, etc.? These latter possibilities must be eliminated before the phenetic change we see is inferred to be anagenesis, but then does anagenesis mean the same thing for different taxa? A taxonomic distance coefficient provides a precise and unambiguous measure of phenetic difference (inferred to be anagenesis) between taxa, but the phenetic difference may not result from or mean the same thing among taxa. Different genes may affect changing morphology of derived characters to different degrees among different taxa depending on circumstances. For example, mutation may be important in one case, or environmental stress due to competition, predation, or change in the physical environment, or perhaps differential timing during ontogeny (heterochrony) controlled by regulatory genes. All of these causes will affect anagenetic change, so how can such change be directly compared by a single type of taxonomic distance measurement? So many variables exist to affect phenotypic
characters that no precise and unambiguous phenetic measurement between taxa will mean the same thing. Therefore, measurement of anagenesis will probably not be useful for taxonomic differentiation except possibly between closely related taxa. Of course, the appearance of new characters (apomorphies) may also be caused by a variety of environmental, mutational, and heterochronic circumstances, but the appearance of new characters among taxa means the same thing for different taxa at all levels, because the rationale for comparison and classification is simply the presence or absence of such characters, the sequence in which they appear, and how they are shared among taxa. This contrasts strongly with anagenetic change within characters, since the rationale for comparison and classification is amount of change, but the amounts can't be directly compared. Thus, a taxonomic system which utilizes both anagenetic and cladogenetic information for classification makes two suspect assumptions: First, one must assume that calculated taxonomic distance on a phylogram derived from a cladogram exactly reflects some genetic change in a taxon, and second, one must assume that the amount of change is directly comparable with amounts of change between other taxa.

The discussion above recognizes my concern about the problems a taxonomist would face if he or she wished to combine anagenetic and cladogenetic information into an inferred phylogeny and to devise methods to represent the results in an unambiguous classification. Undeniably there is more to evolution that just cladistic relationships, but it is better to represent one aspect of phylogeny explicitly and unambiguously than mix up a number of aspects into something which is subjective and ambiguous. Cladistic taxonomy has enough problems
without adding new ones from anagenetic sources. Cladist taxonomists disagree among themselves as much as they disagree with phenetic and evolutionary taxonomists. For example, how does one classify extinct (fossil) species? Some cladists advocate separate classifications or advocate distinguishing extinct taxa by some means. A number of methods (e.g. Patterson and Rosen, 1977) have been proposed to accomplish this. I strongly feel (as does, for example, Farris, 1976) that fossil and living taxa must be treated the same way and analyzed by the same method. For example, a taxon containing birds and crocodiles, as advocated by many cladists, is useless in my opinion, since it is based only on living forms; I would insist that dinosaurs also be included. For different reasons, evolutionary taxonomists also consider such a taxon useless, but they would consider a taxon containing birds and dinosaurs equally useless, whereas I believe this monophyletic taxon has immense explanatory value. Another problem is "knowing" or determining whether a character is apomorphic or plesiomorphic. There are methods for this, but they are by no means foolproof. Some cladists maintain that it is necessary to determine the polarity of a transformation series (morphocline) derived from the cladogram, while others deny this necessity. Does a cladogram represent species or characters? Most cladists now believe, and I concur, that any monophyletic group (clade) can be represented on a cladogram by ignoring clade size and plotting apomorphous characters alone. Of course, species are the most important clades and the ones most often plotted. There is the major problem of dividing monophyletic clades into higher taxonomic units. First one has to justify the need for higher taxonomic categories by showing that they are meaningful and useful. Then one has to devise an explicit,
unambiguous, and objective method to group species clades into higher taxonomic clades without relying on anagenetic criteria, such as major phenetic discontinuities or gaps, which traditionally are used. Such a method has yet to be devised; an alternative would be to deny the meaningfulness and usefulness of higher taxa and then ignore them. Another problem is determining exactly what a fork in a cladogram represents: it certainly represents the emergence of a newly derived character, but does it also represent the splitting of one species into two or the geographic separation of two populations of a single species? As discussed previously, speciation events are inferred by the appearance of autapomorphous characters and a species is defined as possessing at least one such character. Therefore, a cladogram fork represents at least the appearance of both a uniquely derived character and a species; obviously, it may also represent the origin of a higher taxon if these are to be recognized. A final methodological problem is what to do with the ancestral species if it splits, and can it split into one or three new species rather than the two that canonical cladistic theory demands? As discussed previously, dichotomous branching of the cladogram is a necessary methodological procedure and does not imply a dichotomous speciation model; in fact, the best modern speciation model (allopatric speciation) states that peripheral isolate populations split off from the ancestral species population. This model obviously allows any number of new peripheral isolate species to branch from an original species, and it implies that the ancestral species population does not disappear as Hennig (among others) wished us to believe. To repeat: the type of speciation and the nature of the ancestral gene pool before and after splitting are irrelevant to
cladistic analysis. The daughter species (sister taxa) need not diverge after splitting, as Hennig required. Divergence is an amagenetic phenomenon that is, again, irrelevant to cladistic analysis. Hennig is certain to suffer the same fate as Darwin: subsequent workers will revise the entire system he created except for a few essential features.

Possibly, the greatest problem most taxonomists have with cladistic taxonomy is that the system does not require or allow ancestral-descendant relationships to be recognized. This procedural rule is especially hard for paleontologists to follow. Cladistic taxonomists criticize ancestral-descendant relationships for various reasons. First, the standard Linnean classification system cannot represent ancestral-descendant relationships; it hierarchical scheme is suitable for representing only cladistic relationships. Second, in contrast to the ability to establish good sister-group relationships by the use of shared derived characters, there is no unambiguous method to establish ancestral-descendant relationships. Third, any distribution of characters which suggests an ancestral-descendant relationship between two taxa does not eliminate the possibility that one taxon is the sister group of the other and both have an unknown common ancestor. Fourth, the fossil record is inadequate to unambiguously demonstrate that two taxa are ancestor-descendant and not cladistic sister groups, i.e. it is inadequate to allow an unambiguous determination that the common ancestor exists or not. For example, Bonde (1977, p. 770) pointed out that even if one finds that a fossil species exactly conforms to the hypothetical reconstructed ancestor, there is no way of demonstrating that in fact this fossil species actually is representative of the actual ancestral species. These four reasons are interesting because
methods could be devised to make reasons one and two irrelevant, and it is possible to conceive of a fossil record so complete that reasons three and four become irrelevant. Does such a fossil record exist? I believe it does: the record of testate planktonic microfossils in pelagic sediments. However, strictly speaking, even if such excellent information was available, it could not be used in a pure cladistic analysis which eschews stratigraphic data of any kind, even for determining the plesiomorphy or apomorphy of a character or the polarity of a transformation series. Not allowing excellent stratigraphic data in these instances seems to be the height of methodologicalism and perhaps is not justifiable, even when it obviously introduces some subjectivity (e.g. How "excellent" does stratigraphic data have to be before one allows cladistic character information to be inferred from it?). On the other hand, Bonde (1977) allows ancestral-descendant relationships to be hypothesized because they are "bolder" hypotheses than strict cladistic sister group hypotheses. However, Popper's criterion of boldness is fraught with difficulty unless the bolder hypothesis can be tested and falsified as easily as the less bold hypothesis. Popper intended boldness to be directly proportional to ease of falsifiability, yet ancestor-descendant hypotheses may be less falsifiable than sister-group hypotheses, and thus the presumed greater boldness of the former may not actually exist. The entire question of ancestral-descendant relationships in taxonomy remains open and controversial.

We will reach a point in our biosystematic efforts when we wish to know more about an organism than its cladistic relationships, when a classification is a means to an end and not an end to itself. A
cladistic classification can only express the cladogenetic aspects of evolution, and we must accept the cladistic methodological conventions (i.e. strict monophyly, ignoring anagenetic changes, using only intrinsic data, not recognizing ancestral-descendant relations) that make the cladistic analysis work. On the other hand, other aspects of evolution may be worth studying now. Paraphyletic groups such as reptiles are worthy of study as such groups because the concept of grade is important in evolution. Anagenetic change is worthy of study to allow investigation of microevolutionary processes such as the frequency of phyletic gradualism. Phylogenetic trends among extended lineages are worthy of study to help understand macroevolutionary processes, such as the possibility of species selection. All of these are reasons why any complete biosystematic system must recognize anagenesis along with cladogenesis, phylogeny along with cladogeny, grades along with clades, patrastic distance along with cladistic distance, ancestral-descendant relations along with common ancestry (sister group) relations, an adaptive features along with apomorphic/plesiomorphic features. Although we may restrict one aspect of biosystematics (taxonomy) to cladistics, evolution has many additional aspects that require investigation, and even though one aspect may deserve priority, no aspect deserves our sole undivided attention. Evolution has numerous problems that require non-cladistic explanations, and if even our explanations don't have the scientific rigor that cladistic explanations possess, we mustn't therefore cease to discover and hypothesize such explanations, for to do so would be to limit the possibility of increasing our knowledge and understanding. Thus, I suggest that
"phylogenetic systematics" in theory and practice is really "cladistic taxonomy," and is not a complete biosystematic system at all.

The revolution in biosystematics has created a lamentable confusion at the same time it has introduced a new rigor into systematic analysis. For example, I disagree with the criticisms against paleontologists expressed by Nelson (1978, p. 327-331), who states that "paleontologists are the only folk who claim to know the truth of any evolution" in the context of phylogenetic relationships. Nelson takes Stephen Jay Gould to task because Gould (1973, 1976, 1977) expresses his belief that phylogenies can be known, macroevolution proceeds by certain punctuational processes, fossils generally represent the termini of successful branches, fossils provide additional important information in historical reconstructions which modern organisms alone can't provide, and the fossil record is indispensable for formulating phylogenetic hypotheses. Nelson characterizes the fossil record as only "data in search of interpretation" (a characterization with which I wholly agree), but also as the "impressive and authoritative" final arbiter which paleontologists appeal to when they wish to assert the truth of their phylogenetic reconstructions. The tone of Nelson's polemical paper is similar to that of an angry person who has just discovered that science has misrepresented itself to the public all these years, and that it is not a body of absolute truthful knowledge, after all (as the person had been led to believe), but rather (as scientists really knew all the time) is only a method of logical thinking about empirical data that allows a systematic understanding of the universe in a special way. I think that paleontologists understand that phylogenetic reconstructions are only hypotheses and not final "esoteric truth," and
I would not characterize such reconstructions as "superstition," as does Nelson, simply because they utilize fossil and stratigraphic data. It is simply not possible to construct phylogenies without such data, and paleontologists are, or should be, aware of the welter of assumptions that accompany such reconstructions. Certainly Gould understands this; he simply didn't feel the need to elaborate on these problems in papers and books written for popular and general scientific audiences. Phylogenies can be known in a hypothetical sense similar to the hypothetical sense that cladogenies can be known; the notion that the potential falsifiability, and thus the scientific value, of a cladogeny is greater than that of a phylogeny is left unstated. Phylogenies have their own value quite apart from cladogenies, and I reject the cladistic argument that phylogenetic analysis and reconstruction should not be attempted at all. Furthermore, although an explicit cladogenetic analysis should precede a phylogenetic analysis, this procedure is not absolutely necessary, although much of the scientific value of the phylogeny is thereby lost. A classification based on strictly cladogenetic criteria is a means to an end, not an end in itself; evolution proceeds by a number of processes, and the study of evolution cannot afford to ignore all except one of these processes. For example, Gould is interested in macroevolutionary patterns and processes which must perforce be studied at the phylogenetic, rather than cladogenetic, level. For this reason alone, Gould did not deserve Nelson's criticism. The lesser degree (not lack) of potential falsifiability which characterize many of Gould's phylogenetic statements is obvious in comparison with cladogenetic statements, but this merely makes Gould's statements less rigorous, not unscientific. I believe that further work
will make phylogenetic statements more falsifiable, and thus more scientific, although they will never approach the falsifiability of cladogenetic statements.

On the other hand, when paleontologists assert that "the fossil record shows the course of evolution because it shows actual ancestor-descendant sequences," or that" the fossil record...shows actual character transformations," or that given" two different but homologous characters, that character known to be geologically older is the more primitive," then I must agree with Nelson (1978, contains quotes above) that such statements are fallacious. The statements imply a degree of certainty that just doesn't exist. Some paleontologists have defended themselves by saying that the great majority of paleontologists don't make such statements, and that they fully realize the problems and lack of certainty in using stratigraphic data in biosystematic analysis. But I think that Nelson is quite right in believing that the majority of paleontologists, as evidenced by their published work if not by their explicit statements, hold that the "paleontological argument" (the statements quoted above) is valid and not fallacious. I shall show later that, in particular, micropaleontologists and biostratigraphers accept the paleontological argument and devote quite a bit of effort on its behalf to elucidate lineages and phylogenies and to construct biozonations based on the results. Perhaps the statements of the paleontological argument can be modified by adding qualifying adjectives such as: often, in general, may, sometimes, usually, etc. This would certainly disclose a candid degree of uncertainty, but it is not the proper solution, because this method only hides our ignorance rather than eliminates our ignorance. Furthermore, paleontologists would
continue to act as if the qualifying adjectives were not there, and they would not strive to remove the ambiguity and authoritarianism inherent in the paleontological argument. What, then, is the solution?

First, classification of fossil taxa should be based on a cladistic analysis. This rigorous first step is a necessary prelude to further biosystematic analysis, although it may be dispensed with if only a single, species is under examination. Even the idea that some sort of biosystematic analysis, cladistic or otherwise, is necessary for proper scientific classification is foreign to a number of modern biostrati-grapher/micropaleontologists, who continue to typologically classify species on the basis of their stratigraphic utility rather than their biologic attributes. This practice must stop. Second, further analysis with a phylogenetic reconstruction as the goal must explicitly state all proposed relationships which cannot be tested by potential falsification. We will call such untestable relationships assumptions, and term any testable relationship an hypothesis. Therefore, the potential falsification of a statement of relationship is the criterion by which we judge whether it is an assumption or any hypothesis. As discussed previously, we want to build our models or theories with corroborated or uncorroborated hypotheses, and avoid warranted or unwarranted assumptions. The distinction between an assumption being warranted (acceptable) or unwarranted (unacceptable) is usually a matter of subjective judgement among paleontologists, since assumptions are impervious to testing by definition. This subjectivity is one reason to avoid assumptions.

Cladistic relationships in a strict cladogenetic analysis deal only with hypotheses. We wish to know, however, which assumptions we entail
when we go beyond the cladogeny and start to perform a phylogenetic analysis. These assumptions must be recognized explicitly and thus rendered susceptible to independent analysis which would result in their rejection, conditional acceptance, or even modification to a form which allows them to be falsified. The major question for the present is this: Are relationships inferred by the paleontological argument assumptions or hypotheses? That is, are many paleontologists and some cladists justified in recognizing ancestral-descendant relationships or the plesiomorphic condition of a character on the basis of stratigraphic data of fossils? This is not an easy question to answer. Nelson (1978, p. 331) believes that relationships inferred by the paleontological argument are assumptions, incapable of unambiguous falsification in the manner of cladogenetic relationships. Two different but related questions are at issue here: the inference of an ancestral-descendant relationship and the inference of the ancestral condition of a character on the basis of its earlier appearance in the geologic record. The two inferences must be considered separately, because some biosystematists allow one but not the other. On the other hand, they are related because they both depend on our perception of the completeness of the fossil record. Nelson makes the excellent point that any potential falsifiers of an inferred phylogenetic relationship are "rendered impotent as falsifiers by the ad hoc alternative that the fossil record was not as complete as previously believed." That is, any potential falsifier can be dismissed simply by appealing to the inadequacy of the fossil record. For example, if a treasured phylogenetic hypothesis concerning the ancestral state of a character were falsified by the discovery of a different and more ancient character state, which thus
allows formulation of a new hypothesis, one could retain the original hypothesis by claiming that further search will reveal the preferred ancestral state in even older specimens. Clearly, the original phylogenetic hypothesis was not and therefore cannot be unambiguously falsified, for the discovery of additional fossil data falsifies "not only a previous evolutionary interpretation, but a previous application of the paleontologic argument (the application that led to the previous evolutionary interpretation)" (Nelson, 1978, p. 331). This being the case, we are no better off than we were before, since the resulting new evolutionary interpretation (hypothesis of phylogenetic relationship) is as "falsifiable" (e.g. unfalsifiable) as the first, by virtue of its very existence being due to the falsification of the paleontologic argument which created both it and its predecessor.

Nelson's criticism of the paleontologic argument is unanswerable without delving into the philosophy of science and scientific method, and I am not prepared to do this at present. Nevertheless, if we ignore the theoretical problem of constructing phylogenies with extrinsic stratigraphic data, we can justify such activity by its pragmatic benefits. Phylogenetic analysis is important in many aspects of paleobiosystematics for the reasons discussed earlier, that involve the study of macroevolutionary patterns and processes using fossil material. An appeal to pragmatism is not without value; I frankly wonder what paleontologists would do if they were prevented from constructing phylogenies by theoretical criticism from cladists. Certainly a major key to this impasse is the completeness of our knowledge of the fossil record. Remember that phylogenies are not cladogenies or genealogies, and that unlike these two, phylogenies
require stratigraphic historic data in addition to cladogenetic historic data, because anagentic data is plotted against an interval scale of equal known time increments (the zero point of a ratio scale, in which case absolute time would be known, is useful but not strictly necessary). Therefore, the best phylogenies could be constructed in light of the best and most completely known fossil records. These fossil records are so good that I strongly believe that a case could be made for the inference of semi-falsifiable phylogenetic relationships, although here I will justify such inference for pragmatic reasons only, and simply assume their potential falsifiability. I am speaking, of course, of the oceanic fossil records of Cenozoic formainifera, radiolarians, and nannofossils, whose records are so thoroughly known and tested in hundreds of cores of pelagic sediment that the completeness of the record can be assumed. The fossil records of these planktonic microfossils serve as the basis for marine biostratigraphy, and the fossil data is of such quality that phylogenetic inferences in these groups (despite the problem that these are protozoans) should be the best obtainable. The rest of this paper concerns itself with the problems involved in recognizing ancestral-descendant relationships and examining anagenetic change among taxa of radiolarians, and the implications these have for biostratigraphy.
Review of Examples in the Recent Literature

We are now in a position to study five well-known examples which can be discussed together with concepts derived from the previous analysis. The first example is the study of Ozawa (1975) which contains the only example of phyletic gradualism unequivocally accepted by Gould and Eldredge (1977). Has no one seriously questioned how samples from Japan, Malaya, Cambodia, and New Zealand, separated by thousands of miles and contained in different formations, can be so precisely ordered and correlated that the result is gap-free time scale with evenly-spaced sample intervals against which the morphometric data is plotted? Note that the time axis consists of a relative time stratigraphic column, although the equal sample spacing certainly suggests absolute time. How were the samples correlated? Hayami and Ozawa (1975, p. 10) state that 34 samples were studied, and of these, four were from the Sisophon Limestone in Cambodia, which has the "most complete" stratigraphic succession, while the other thirty (!) samples were "chronologically allocated to this sequence by means of faunal composition." Does this mean that accurate taxon-range-zones were used, or were notoriously unreliable assemblage-zones or acme-zones used? What biostratigraphically-useful organisms were used for the correlation? How does one manage to correlate samples over a large part of the western Pacific and order them into an evenly-spaced gap-free sequence using a "faunal composition" biozonation that cannot possibly be more accurate and reliable than that provided by fusulinids, such as the species under study? Perhaps only a biostratigrapher would be interested in these "details," and the diagram illustrating phyletic
gradualism of prolocular diameter of *Lepidolina multiseptata* should be taken at face values. Such diagrams, however, have been accepted on faith too often. I am sorry to report that by consulting Ozawa (1975) we learn that (1) fusulinids were used to correlate the samples, (2) many of the fusulinid zones are defined by the species *Lepidolina multiseptata* or its synonyms, (3) the sample horizons were first plotted on a stratigraphic correlation chart (Ozawa, 1975, Figure 2) which shows many of the samples at the same horizon and which is not possibly detailed enough to allow the fine ordering of the phylograms, (4) the correlation chart was constructed on fusulinid data and the unexplained work of numerous other authors, (5) no details about sample stratigraphic ordering were given, and (6) nothing in the paper suggests anything other than relative age was considered in constructing the phylograms, and certainly no absolute ages were used. Ozawa even states that only groups of his samples are actually in known stratigraphic order, and each group is slightly separated from each other group by an almost imperceptible gap which and easily escape one's notice. From these considerations, one can easily see that large intervals of elapsed time are undoubtedly hidden on the famous Ozawa diagram and that if these occur between groups of samples which show no significant change, then the diagram provides more evidence for a punctuated speciation model than a gradual one. More could be said about this example, but I will conclude by saying that this example of phyletic gradualism has been accepted uncritically by numerous workers, including Gould and Eldredge, who are not uncritical elsewhere.

The second example we will examine is equally illuminating: the phylograms constructed by the stratophenetic method of Gingerich
(1976a). The phylograms were discussed and criticized by Gould and Eldredge (1977), who argue that the data are inadequate to separate phyletic gradualism from geographic variation due to migration, that the trends do not really illustrate unidirectional change, and that the depicted rates of divergence are too slow to account for adaptive radiation. It is fair to say that these critical arguments are as controversial as the original interpretations reached by Gingerich from his Hyopsodus and Pelycodus data, and that current informed opinion is divided about the validity of both the interpretations and the criticisms against them. Since this discussion is not relevant to this paper, we will leave it and consider the problem from another direction.

First, we recognize that the diagrams in question, called stratophenograms by Gingerich, are phylograms which purport to contain anagenetic, cladogenetic, and ancestral-descendent data. It must be pointed out that the second and third types of data are inferred strictly by Gingerich's personal judgement and involve arbitrary decisions and hidden assumptions at every level. That is, a formal cladogenetic analysis followed by a formal genealogical analysis (in the sequence of biosystematic analysis previously elucidated) was not performed prior to the phylogenetic analysis which added anagenetic data to the family tree. Instead, as explained by Gingerich (1976b, 1979), the stratophenetic method simply requires that the character statistics be placed at their proper stratigraphic level on the diagram, i.e., anagenetic data is plotted first, and then the statistics are phenetically linked by the criterion of phenetic resemblance. The linked sample statistics are then arbitrarily divided to produce "species." Gingerich (1979, p. 48) explicitly defines species as "an
arbitrarily divided segment of an evolving lineage that differs morphologically from other such species in the same or different lineages" (italics in original). Arbitrariness, ad hoc decisions, and hidden assumptions are thus pervasive in this stratophenetic system, and even are explicitly acknowledged as such. They occur whenever a subjective decision is made to recognize phenetic resemblance or dissimilarity, to recognize ancestral-descendant relationships, to indicate splitting events on the basis of one character whose relative plesiomorphy or apomorphy has not been analyzed, and to subdivide evolving lineages on criteria such as fortuitous occurrence of a stratigraphic gap or some degree of morphologic change. Gingerich claims that the hypothetical results of the stratophenetic method can be tested, but I sincerely doubt that any test exists to rigorously decide among alternatives, since there are no real alternatives unless new data becomes available. If no new data is forthcoming to "test" the evolutionary hypotheses inferred by stratophenetics, then these hypotheses must remain as the only acceptable ones.

We need to examine the stratophenetic method further, however, because its concept is such an important part of paleontology that in some ways it is not possible to do without it. What are these ways? First, if we plot anagenetic statistical data on a time scale, we are not invoking hidden assumptions and making ad hoc decisions if we refuse to subdivide the resulting lineage into different "species" and refuse to recognize ancestors, descendents, and splitting events. This "portion of a phylogeny" that I discussed earlier is a valid representation of an evolutionary pattern that is necessary to test the amount of evolutionary change that occurs by anagenesis and see how this
compares to evolutionary change by cladogenesis. If the splitting events can be independently inferred by a cladogenetic analysis, then they may also be recognized on the phylogram. As for subdivision of the lineage and what this implies, more will be said later.

Remember that a valid phylogeny must be plotted on an absolute time scale which contains equal intervals of known duration. Although a paleomagnetic time scale, when available, is the best means to do this and may be the only assumption-free method, it is still possible to assume (1) that the sedimentation rate was uniform throughout the stratigraphic interval of interest, and (2) that it is possible to achieve a good estimate of the time duration in years for any part of the interval. These assumptions may or may not be legitimate when used, depending on circumstances. Gingerich, of course, invokes both assumptions, although they remain hidden in all of his diagrams and text. All of his phylogenies are plotted against a stratigraphic column with the samples vertically located on it by their lithostratigraphic level in feet. The equal intervals on the stratigraphic axis are thus rock thickness, not time. Gingerich's Figure 2 (1976a, p. 8) gives the impression that the Willwood Formation lithology is shale with a few discontinuous beds or lenses of sand and lignite. However, he states in the text (1976a, p. 5) that the rocks are "fluvial in origin" and "consist of an alternating series of sandstones and mudstones, with occasional beds of lignite and freshwater limestones." Here we must seriously consider that equal intervals of rock thickness do not represent equal intervals of time. Fluvial sandstones were deposited in much briefer time intervals than the alluvial mudstones, lignites, and lacustrine limestones; and the amount of time duration between levels on
the measured section, and thus between groups of fossils, depends strongly on the ratio of sandstone to mudstone contained in the stratigraphic interval between these levels. Since such an analysis was never made, Gingerich's phylogenies are based on relative time and thus are not rigorously valid. Gingerich (1976a, p. 6) acknowledges that the "sediments accumulated continuously (though not at an absolutely uniform rate)." He then makes the point that the samples in the measured section are well ordered by superposition. I agree, but equal time intervals, not just superposition, are required for a valid phylogeny reconstruction. Gingerich maintains (1976a, p. 9) that the "stratigraphic position of each locality is unlikely to be in error by more than 15 m (50 ft.), due to depositional...imprecision, which would not affect the general results appreciably." He is perhaps correct, but this problem nevertheless deserves additional investigation.

Gingerich's vertebrate phylogenies illustrate another important concept: that of correlation of samples. As previously discussed, Gingerich is well aware that the stratigraphic framework must be set up completely independently of the fossils of interest, and that it is not permissible to draw evolutionary conclusions from phylograms containing samples interpolated by criteria directly involving the fossils of interest. However, it is permissible to interpolate samples by lithostratigraphic criteria (Gingerich, 1979, p. 50). Presumably, Gingerich did this for his simple Hyopsodus phylogeny (Gingerich, 1976a, Fig. 4), since he states (1976a, p. 11) that the samples for this plot were taken directly from two measured sections which must have been geographically separated to some extent (we can't be sure because Gingerich's 1976a paper contains no map) and therefore had to be
correlated by lithostratigraphic tracing. Gingerich (1976a, p. 6) states that his fossil localities are "concentrated in a band across an area of some 1000 square km," yet he admits (p. 5) that the "sedimentary beds are discontinuous; while some can be traced for a kilometer or more, most probably cannot." Something is seriously wrong here, or at least some vital information is not readily apparent. Discontinuous beds are characteristic of fluvial depositional environments, and thus permit very limited lithostratigraphic tracing. How far apart were the two measured sections in a region of approximately 1000 sq km, and how were they correlated by discontinuous beds, few of which can be traced a kilometer or more?

The construction of the complete or "refined" Hyopsodus phylogeny (Gingerich, 1976a, Fig. 5) required additional sample interpolation within the section "based both on the geographic relationship of the locality in question to those already in the section and on the average size of each species sample from the locality." (1976a, p. 11). This "refined" phylogeny is worthless for all practical purposes, since geographic correlation is quite imprecise compared to lithostratigraphic correlation (in fact, I've never previously come across geographic correlation in the literature) and interpolating isolated samples into a trend showing anagenetic change by using the anagenetic change clearly begs the question. Gingerich provides a perfect example of the type of biosystematic practice which cladists decry: basing inferred evolutionary hypotheses and conclusions on preconceptions about the evolutionary process. By his actions in constructing the "refined" Hyopsodus phylogeny, Gingerich says, in effect, that since evolution proceeds by phyletic gradualism and the anagenetic change of phenetic
characters through time, then he is perfectly correct in placing
stratigraphically isolated samples into the statistical data set of the
stratigraphic sample which has the closest morphologic resemblance; the
resulting "refined" phylogram will unquestionably confirm his apriori
beliefs, and why shouldn't it, since it was constructed upon those
beliefs.

We will treat examples three, four, and five together, since they
are similar for a number of reasons. First, they represent the best
that has been done so far in constructing phylogenies to test the
occurrence of phyletic evolution. They use the paleomagnetic time scale
to provide absolute time for the stratigraphic axis of the phylogram.
And they use radiolarians and planktonic foraminifera, organisms which I
have long believed offer the best means to test macroevolutionary
hypotheses because of their great diversity, great abundance in
hiatus-free piston and DSDP cores, rapid evolution, easy preparation,
numerous morphometric characters, worldwide geographic range, and long
and interesting evolutionary history. These three examples are the work
of Davida Kellogg (1975a, 1975b, 1980, Kellogg and Hays, 1975), the work
of Lazarus, Hays and Prothero (1979, 1982 and the work of Malmgren and
Kennett (1980, 1981). These examples claim to provide documentation for
the existence of phyletic evolution (anagenesis) and also for phyletic
gradualism (the hypothesis that the bulk of evolutionary change is the
result of anagenesis rather than cladogenesis and thus evolutionary
patterns in geologic time are gradual rather than punctuated). Again,
these are controversial claims that require more detailed examination
than I can give them here, but what I wish to discuss right now concerns
not the validity of the conclusions, but whether these examples utilize
the optimum means to construct portions of phylogeny and therefore largely, if not entirely, avoid the pitfalls which unfortunately characterize the first two examples.

All three groups of authors rely on paleomagnetically zoned cores for the source of their samples. Sample statistics are therefore plotted against an absolute time scale provided by the paleomagnetic time scale which has been carefully built up over the past decade. All of the studies utilize samples from the Neogene. However, there is something more important here. Lazarus and others. state that their deep sea piston cores from all over the world ocean were "dated by independent paleomagnetic and biostratigraphic analyses...." Elsewhere I have criticized the supposed "independence" of biostratigraphic zonations based on evolutionary criteria, but here I wish to point out that biostratigraphers without an evolutionary basis can be constructed and tied to the paleomagnetic time scale, and these can provide a valid independent means of absolute age assignment and correlation when the paleomagnetic record is lacking in a core. A satisfactory paleomagnetic record is not found in every piston core, and of course cannot be determined in a typical DSDP core; furthermore, piston cores cannot penetrate thick sections to obtain a good paleomagnetic and biostratigraphic record in the same core to cover the Neogene. However, these problems are overcome by the fact that the entire Tertiary can be cored by a series of piston cores taken from the sea floor outcrops of Tertiary pelagic sediments exposed because of the nondeposition, erosion, or dissolution of the overlying younger sediments, and by hydraulic DSDP cores. The biostratigraphic record can be easily correlated with the paleomagnetic record in these cores, and thus other
cores which have no paleomagnetic record can be provided with an absolute time scale as if they did have such a record. This process is so well-known that today for the Neogene (and presumably soon for the Paleogene), it is common practice to simply plot zonation boundaries and biostratigraphically-determined events on an absolute time scale as if paleomagnetism were known. Such absolutely-dated cores provide the best means for phylogeny construction and allow precise correlation for analyzing geographic variation in the study of anagenesis, but it is imperative that the biozonation, which serve as the extensions from paleomagnetically-dated cores to cores without a paleomagnetic record, be free of the hidden evolutionary assumptions and apriori evolutionary criteria which unfortunately characterize many biostratigraphic zonalational systems. To do otherwise is to lose the potential that deep sea cores offer to test evolutionary hypotheses.

This last point will become important when we later analyze the tropical radiolarian biozonation, the system which is least free of hidden evolutionary assumptions and thus the least theoretically valid of the common microfossil zonations. The system works, of course, but only because of numerous ad hoc assumptions, idiosyncratically defined terms, and arbitrary typological species determinations. One of the purposes of this paper will be to redefine the various elements in this and similar zonations to improve their theoretical (and practical) basis, and thus bring biostratigraphy into the realm of science. The goal will be to preserve the pragmatic advantages of current biostratigraphic practice while correcting many common myths and errors within biostratigraphic theory. To return to the radiolarian examples, the studies can be faulted only if theoretically invalid
biostratigraphic system (such as the tropical radiolarian zonation) was used to correlate samples from different cores to study evolutionary patterns and test evolutionary hypotheses; such a method results in a subtle form of circular reasoning, because the biostratigraphic system presupposes the truth of the very hypothesis the study wishes to test. This statement will become clearer in later sections, but it can be pointed out now that the methods and conclusions of Kellogg (1975, etc.) who studied single cores or used only superposition and paleomagnetism for correlation, are probably more reliable than the methods and conclusions of other authors who explicitly use a number of cores and rely on the tropical microfossil zonations to correlate some of them.

Perhaps the most interesting feature of the studies of the three groups of authors working with planktonic microfossils is that all fail to adequately justify their conclusion of phyletic gradualism. They fail to document phyletic gradualism in radiolarians and planktonic foraminifera for one main reason: the stratophenograms each author or authors present to illustrate phyletic gradualism can be interpreted with at least equal and sometimes better justification to illustrate punctuation and stasis (punctuated equilibria). This is true for a number of reasons. Kellogg (1975a, Figure 4; 1980, Figures 5-8) plots her data against depth in core, thereby concealing periods of slow sedimentation which can hide punctuation events, thus resulting in a pattern of "phyletic gradualism." The sampling interval must be very fine to detect true phyletic gradualism, because punctuation and stasis can appear to be gradual in a stratigraphic sequence of variable sedimentation rate that is coarsely sampled. Furthermore, her Figure 4
(1975a) is actually better interpreted as punctuated equilibria, as Gould and Eldredge (1977) point out. Many of Kellogg's (1980) artiscin lineage stratophenograms, which she claims are of "chronospecies" on an "evolutionary continuum," also are best interpreted as exhibiting punctuation and stasis. Finally, and most importantly, Kellogg's 95% confidence intervals on Figures 5-8 (1980) do not show significant phyletic change when interpreted correctly according to the criteria specified by Simpson and others (1960, p. 353). That is, when the length of the longest 95% confidence interval is assigned to all the others in the stratophenetic "trend," they all overlap, and thus do not permit a conclusion of true gradual phyletic change. Therefore, Kellogg's claim that she has documented "microevolutionary mechanisms, which by their successive cumulative action result in macroevolutionary change" (1980, p. 204), is not justified. In fact, as documented in the present study, the artiscin lineages and species are differentiated by unique derived characters produced by cladogenesis.

The conclusion of phyletic gradualism in radiolarian lineages by Lazarus, Hays, and Prothero (1982) suffers from two of the same problems as Kellogg. Although the authors' Pterocanium stratophenetic data is correctly plotted against a ratio time scale provided by paleomagnetic dating, most of their 95% confidence intervals overlap, and all overlap if the length of the longest is assigned to the others. Also, their stratophenograms appear to document stasis with random or ecophenotypic change in no particular direction through time. I don't think their conclusion of phyletic gradualism is justified, except in the sense that what change does occur may occur gradually. Furthermore, Lazarus and others certainly haven't falsified the occurrence of any punctuation
events on the basis of their coarse sampling and their measurement of only a single character. Other characters on Pterocanium may exhibit punctuation.

Malmgren and Kennett's five stratophenograms (1981, p. 234–235, Figure 2) of a planktonic foraminifer lineage are plotted against depth in core, thereby greatly lessening their value. Furthermore, although the authors conclude that "gradual evolution (phyletic gradualism) clearly occurs in all but one measured parameter" in their lineage, their stratophenograms can all be interpreted to document stasis and punctuation. Their data show periods of stasis with random variation (95% confidence intervals overlap) with brief periods of rapid and significant change. Furthermore, I must point out that their significant punctuation events occur at stage boundaries, thus representing either a change in physical, biological, or climatic conditions or a change in rate of sedimentation. Paleobiosystematists should not ignore the stratigraphic record their fossil record is found in when making inferences about evolutionary history.

The main conclusions we can draw from these five examples are: (1) anagenetic evolution (anagenesis or phyletic evolution) undoubtedly occurs; (2) its frequency of occurrence, rate of progress, and degree to which it accounts for evolutionary change are in doubt; (3) biosystematists realize that it is important to recognize and measure anagenetic evolution and that this can be accomplished by constructing phylogenies or portions of phylogenies; (4) phylogenetic inference and phylogeny construction are not unproblematic tasks, but contain numerous traps for the unwary; and (5) a proper understanding of the role of
biostratigraphy and biosystematic analysis in phylogeny construction will result in fewer errors in the future.
RESULTS AND INTERPRETATION OF THE BIOSYSTEMATIC ANALYSIS OF THE MIOCENE ARTISCINAЕ

Biosystematic Analysis

Stratophenograms and Alternative Interpretations

The radiolarian subfamily Artiscinae is an excellent taxon with which to investigate problems of fossil evolution. It has a relatively large number of species with well-defined morphological features that undergo much evolutionary change through several million years. The morphological change can be measured and plotted against stratigraphic time. Such a plot, known as a stratophenogram (after Gingerich, 1976b), is a relatively unambiguous representation of phenetic evolutionary change that can ideally be compared to similar charts of other characters and other species.

A cladistic analysis usually begins with taxon discrimination and character identification by listing the characters (phenetic data) and separating plesiomorphies from apomorphies. This procedure works well with typical neontological and paleontological data, for such samples are taken at noncontinuous, randomly-spaced intervals on any time or space continuum. Since this is the case, it would be possible, perhaps probable, to identify and distinguish two different characters in two samples separated by some stratigraphic or geographic distance which are, in fact, actually a single character that exhibits anagenesis in time or continuous geographic variation in space. Such a character gradient is known as a chronocline in a stratigraphic sequence and a geocline in an areal continuum. If we consider only the former case, it
is clear that a chronoclone of a single character is the result of anagenesis. It is extremely difficult to recognize a chronoclone in the fossil record unless multiple samples are taken along a continuous stratigraphic sequence, yet this is rarely done for many reasons. Unless this sampling is undertaken, a paleobiosystematist may mistakenly identify as an apomorphy a character which is really a plesiomorphy undergoing anagenetic change. Although such sampling may not always be necessary, it is necessary whenever fossils suspected of exhibiting anagenesis are examined. Such is the case, of course, with radiolarians and other planktonic microfossils (and presumably Tertiary mammals!).

It is therefore sometimes necessary to construct stratophenograms of numerous characters of the taxa of interest before the traditional cladistic analysis is performed for taxonomic purposes. The stratophenograms thus serve two vital purposes: first, they allow one to identify gradually changing plesiomorphic characters and distinguish them from apomorphic punctuated continuous characters and newly-derived discrete characters, thus permitting one to avoid the use of the first type of character in taxonomy while permitting the use of the latter two types; second, they allow one to construct phylogenies by providing the necessary anagenetic data to combine with genealogies derived from the cladogram and stratigraphic ranges. For the first purpose alone, any fossil taxon with an excellent stratigraphic record needs to be examined stratophenetically before the cladistic analysis is performed. This conclusion is counter to the prevailing thought among cladists. On the other hand, eliminating the use of gradually-changing continuous characters for taxonomic purposes because they are plesiomorphic is
counter to the prevailing thought among microfossil taxonomists and biostratigraphers. But the reasons for this were explained and justified earlier.

Two lineages of artiscins have been identified in the relevant literature (e.g. refer to Figure 1 in this study from Kling, 1978, p. 237). These are known as the *Ommatartus tetrathalamus* lineage and the *O. hughesi* lineage, named after their terminal species (Kellogg, 1980). Individual specimens of the *tetrathalamus* lineage are illustrated in Figures 11-13 in this study, while specimens of the *hughesi* lineage are illustrated in Figures 14-15. One question that immediately arises is whether each artiscin lineage is a single lineage or an extended lineage; the answer appears to be the latter, since each lineage is composed of two or more species. However, segments of the extended *tetrathalamus* lineage that some authors claim consists of a number of successional species (paleospecies) may in fact be single lineages that were arbitrarily delimited by subdividing a gradually-changing character which underwent anagenesis. Kellogg (1980, p. 199) explicitly states that the named species are "stages" that do not represent "true biologic species" and should be more properly called "chronospecies or paleontological species." This characterization, however, was made without benefit of a complete biosystematic analysis, so its correctness remains to be tested. Also, Kellogg uses the language and methodology of evolutionary taxonomy as exemplified by Bock (1979). Her evolutionary taxonomic approach can be contrasted with the typological taxonomy of Riedel and Sanfilippo (1971), who initially placed all Artiscinae lacking polar caps in the genus *Cannartus* and all possessing polar caps in the genus *Ommatartus*. This typological taxonomic approach
Photomicrographs of *Ommatartus penultimus* from DSDP Core 9-77B, including forms previously known as *Cannartus laticonus*.

A. 17/1/24-26, W42/2, 2  
B. 17/1/24-26, M27, 2  
C. 17/2/68-70, D52  
D. 17/3/125-127, R43/1  
E. 17/5/125-127, F52, 2  
F. 18/1/20-22, E41, 2  
G. 18/2/73-75, M26, 2  
H. 18/2/73-75, F49/1, 2  
I. 18/2/125-127, W34  
J. 18/3/125-127, S46  
K. 18/5/125-127, F35/2, 2  
L. 19/1/25-27, D58, 2  
M. 19/3/125-127, J28  
N. 19/5/125-127, F58/2  
O. 20/1/25-27, N52, 2  
P. 20/2/78-80, S27/3  
Q. 20/5/25-27, U39/2, 2  
R. 21/1/23-25, ?, 2

Scale bar at lower right is 100 micrometers (0.1 mm) in length. Each radiolarian is identified by sample designation, England Finder coordinates, and slide number if no. 2.
FIGURE 12

Plutomicrographs of *Ommatartus penultimus* from DSDP Core 9-77B, including forms previously known as *O. antepenultimus*.

A. 14/5/125-127, N57/1, 2  
B. 14/5/125-127, B46, 2  
C. 15/1/25-27, T33  
D. 15/1/25-27, C47/4, 2  
E. 15/2/73-75, M34/1  
F. 15/2/73-75, B37/3  
G. 15/3/125-127, K48/3  
H. 15/3/125-127, K40/3  
I. 15/5/125-127, G48/2, 2  
J. 15/5/125-127, J52/3, 2  
K. 16/1/25-27, W47/2  
L. 16/2/73-75, M47/4, 2  
M. 16/2/73-75, B37, 2  
N. 16/2/73-75, N37  
O. 16/3/125-127, M48/3  
P. 16/3/125-127, J27  
Q. 16/5/125-127, D26, 2  
R. 16/5/125-127, G26, 2

Scale bar at lower right is 100 micrometers (0.1 mm) in length. Each radiolarian is identified by sample designation, England Finder coordinates, and slide number if no. 2.
Photomicrographs of *Ommatartus penultimus* and *O. tetrathalamus*.

A. 7/1/25-27, ?, 2
B. 7/1/25-27, ?, 2
C. 10/1/25-27, Q50/1, 2
D. 10/1/25-27, 049
E. 10/1/25-27, L47/3, 2
F. 11/1/148-150, N49/1, 2
G. 11/1/148-150, J49/1, 2
H. 11/1/148-150, J49/1, 2
I. 12/1/25-27, G59, 4, 2
J. 12/1/25-27, H60/4, 2
K. 12/2/77-79, T47/1, 2
L. 12/2/77-79, P52/2, 2
M. 14/1/25-27, R31/3, 2
N. 14/2/73-75, Q47/3
O. 14/2/73-75, J49/2
P. 14/3/125-127, H44
Q. 14/3/125-127, E46/2
R. 14/3/125-127, T38

Scale bar at lower right is 100 micrometers (0.1 mm) in length. Each radiolarian is identified by sample designation, England Finder coordinates, and slide number if no. 2.
Photomicrographs of *Ommatartus petterssoni* from DSDP Core 9-77B.

<table>
<thead>
<tr>
<th>Letter</th>
<th>Date/Depth</th>
<th>Sample Ref</th>
<th>Counts</th>
</tr>
</thead>
<tbody>
<tr>
<td>A.</td>
<td>17/5/125-127</td>
<td>N57</td>
<td></td>
</tr>
<tr>
<td>B.</td>
<td>17/5/125-127</td>
<td>R46/2</td>
<td></td>
</tr>
<tr>
<td>C.</td>
<td>17/5/125-127</td>
<td>J29/4, 2</td>
<td></td>
</tr>
<tr>
<td>D.</td>
<td>17/5/125-127</td>
<td>F52, 2</td>
<td></td>
</tr>
<tr>
<td>E.</td>
<td>18/1/20-22</td>
<td>T31/2, 2</td>
<td></td>
</tr>
<tr>
<td>F.</td>
<td>18/1/20-22</td>
<td>P56/4, 2</td>
<td></td>
</tr>
<tr>
<td>G.</td>
<td>18/3/125-127</td>
<td>W41/2</td>
<td></td>
</tr>
<tr>
<td>H.</td>
<td>18/5/125-127</td>
<td>S33, 2</td>
<td></td>
</tr>
<tr>
<td>I.</td>
<td>19/1/25-27</td>
<td>J34/4, 2</td>
<td></td>
</tr>
<tr>
<td>J.</td>
<td>19/1/25-27</td>
<td>K52/1</td>
<td></td>
</tr>
<tr>
<td>K.</td>
<td>19/3/125-127</td>
<td>Q28</td>
<td></td>
</tr>
<tr>
<td>L.</td>
<td>19/3/125-127</td>
<td>H28/2</td>
<td></td>
</tr>
<tr>
<td>M.</td>
<td>19/5/125-127</td>
<td>N53/1</td>
<td></td>
</tr>
<tr>
<td>N.</td>
<td>19/5/125-127</td>
<td>H45</td>
<td></td>
</tr>
<tr>
<td>O.</td>
<td>20/1/25-27</td>
<td>K32, 2</td>
<td></td>
</tr>
<tr>
<td>P.</td>
<td>20/3/125-127</td>
<td>J47/4, 2</td>
<td></td>
</tr>
<tr>
<td>Q.</td>
<td>20/3/125-127</td>
<td>Q26/3, 2</td>
<td></td>
</tr>
<tr>
<td>R.</td>
<td>20/5/25-27</td>
<td>E49/4</td>
<td></td>
</tr>
</tbody>
</table>

Scale bar at lower right is 100 micrometers (0.1 mm) in length. Each radiolarian is identified by sample designation, England Finder coordinates, and slide number if no. 2.
Photomicrographs of *Ommatartus petterssoni* and *O. hughesi* from DSDP Core 9-77B.

<p>| | | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>A.</td>
<td>15/1/25-27, D54</td>
<td></td>
</tr>
<tr>
<td>B.</td>
<td>15/2/73-75, T41/4</td>
<td></td>
</tr>
<tr>
<td>C.</td>
<td>15/3/125-127, F36</td>
<td></td>
</tr>
<tr>
<td>D.</td>
<td>15/5/125-127, P47/1, 2</td>
<td></td>
</tr>
<tr>
<td>E.</td>
<td>16/1/25-27, V42/4</td>
<td></td>
</tr>
<tr>
<td>F.</td>
<td>16/1/25-27, V28/2</td>
<td></td>
</tr>
<tr>
<td>G.</td>
<td>16/2/73-75, V41, 2</td>
<td></td>
</tr>
<tr>
<td>H.</td>
<td>16/3/125-127, F31/4</td>
<td></td>
</tr>
<tr>
<td>I.</td>
<td>16/5/125-127, K32, 2</td>
<td></td>
</tr>
<tr>
<td>J.</td>
<td>17/1/24-26, M35/3, 2</td>
<td></td>
</tr>
<tr>
<td>K.</td>
<td>17/1/24-26, K35/2, 2</td>
<td></td>
</tr>
<tr>
<td>L.</td>
<td>17/2/68-70, E50/3</td>
<td></td>
</tr>
<tr>
<td>M.</td>
<td>17/2/68-70, U41/1</td>
<td></td>
</tr>
<tr>
<td>N.</td>
<td>17/3/125-127, R58/1</td>
<td></td>
</tr>
<tr>
<td>O.</td>
<td>17/3/125-127, V50/2</td>
<td></td>
</tr>
<tr>
<td>P.</td>
<td>17/3/125-127, Q57/3</td>
<td></td>
</tr>
<tr>
<td>Q.</td>
<td>17/3/125-127, C40/3</td>
<td></td>
</tr>
<tr>
<td>R.</td>
<td>17/3/125-127, V43/1</td>
<td></td>
</tr>
</tbody>
</table>

Scale bar at lower right is 100 micrometers (0.1 mm) in length. Each radiolarian is identified by sample designation, England Finder coordinates, and slide number if no. 2.
guaranteed the creation of unnatural polyphyletic taxa, as was quickly found to be the case. Kellogg (1980, p. 197) successfully corrected Riedel and Sanfilippo’s polyphyletic taxa by including all artiscins under the genus *Ommatartus*, the solution followed in this study, but she persisted in retaining the typological artiscin paleospecies. Sanfilippo and Riedel’s (1980) subsequent attempt to correct their polyphyletic artiscin taxonomy by renaming all the species under two new genera is inadequate, too late, and probably nomenclaturally incorrect, since this is the second pair of genera in which these species have been classified. The present study attempts to evaluate the artiscin lineages from a third taxonomic approach, that of cladistic taxonomy.

Figures 11–13 reveal the plastic morphology of the *tetrathalamus* lineage. The extent of the lineage studied in this report in detail contains artiscins identified in the literature as *Ommatartus* (or *Cannartus*) *laticonus*, *O. antepenultimus*, and *O. penultimus*. As noted above, this lineage has been interpreted as an excellent example of the type of evolution which micropaleontologists believe is pervasive in the fossil record, phyletic gradualism. As shown in Figure 1 and discussed in detail later in this study, Riedel and Sanfilippo (1971a, 1971b, and 1978) believe that one species slowly and gradually evolves into another. They believe that every artiscin species evolves in this fashion (except the *laticonus to petterssoni* transition). Kling (1978, p. 231) states that “on the range chart, approximate known age ranges are indicated by the height of the illustration or by a vertical line either extending from or beside the illustration.” He does not explain that the ranges he illustrates are not the ranges of the morphological species but the ranges of “evolutionary” species that are identified by
a typological species concept which arbitrarily restricts species variability. Typology is necessitated in this method because a single continuous character is authoritatively chosen by the taxonomist to identify the different species in a long lineage which is assumed to gradually change through time.

The identification of a gradually changing character is not in itself undesirable; the tempo and mode of change could provide valuable data for understanding evolution. The problems arise when: (1) the single character alone is used to subdivide species, requiring (2) the typological subdivision of the character, thus (3) insuring that apomorphic characters are ignored; (4) since now the gradually changing character subsumes all species change within itself, (5) a new species appears when the character has changed enough to suit the requirements of the taxonomist. Thus, (6) the species are identified and placed in a genealogical diagram by their phenetic resemblance and sequence in the stratigraphic record, and (7) their classification is made consistent with the inferred genealogy. Although it is often emphasized that scientific interpretations must be made from data, I have clearly shown in the above example, which is by no means uncommon in micropaleontology, that here the barest use is made of data, and even this data is subjectively chosen and interpreted to suit the evolutionary presuppositions of the investigator. In this case the investigator ignores species variability by using a typological species concept, disregards many other characters, including important apomorphic characters which signal cladogenetic change, assumes the universality of gradualism to the exclusion of other forms of evolutionary change, and utilizes phenetic resemblance and stratigraphic level as the sole data
to infer phylogenetic relationship and to classify the species. Although this procedure certainly may be interpretation from data, the present study and many others have shown that it is not the best interpretation, because it endorses ad hoc explanations, uncorroborated assumptions, authoritative pronouncements, and untestable hypotheses. This situation arises because underlying theory is ignored and data alone is assumed to be supreme; that is, that biosystematics is something which one does, not something which one thinks about.

Many cladists assume that only discrete apomorphic characters are important in taxonomy, historical biogeography, phylogeny construction, any other types of biosystematic analysis. I disagree, since I have previously demonstrated the theoretical importance of punctuated continuous apomorphic characters in all levels of biosystematic analysis and of continuous and discrete plesiomorphic characters at higher levels. Particularly for fossils with excellent fossil records, it is vital not to ignore any continuous change which might involve an apomorphic character. To begin with, it is perfectly appropriate to measure the anagenetic change visible in some fossil lineages to determine if discontinuities are present. A sharp change from one character state to another in a gradually changing character would indicate the appearance of an autapomorphy. No discontinuity means that the character will remain a plesiomorphy and thus be useless for cladistic analysis. Of course, all discrete characters should be analyzed for their relative plesiomorphic and apomorphic relationship. Note that although theory requires that stratigraphic level not be used to initially determine this relationship, stratigraphic information can nevertheless be used to examine character continuity. Of course,
stratigraphic position can later be used to test the identification of apomorphies and to construct type 2 genealogies.

Species or taxon identification must precede cladistic analysis and classification, the first level in biosystematic analysis. For this purpose, continuous characters, discrete characters, and ratios are useful. Concerning ratios, Simpson and others (1960, p. 14-16) state: "Ratios of two continuous variates are in proper and widespread use in zoology, and they express characters that are of fundamental importance....Ratios may also be usefully based on discontinuous [discrete] variates....A ratio is useful only insofar as it makes apparent some biological characteristic not apparent in the original measurement." The characters originally chosen for species demarcation are often a matter of subjective decision on the part of the taxonomist; this is unavoidable, since any taxon theoretically has hundreds of characters. However, an effort should be made to search for apomorphies -- they should not be deliberately ignored. In this study, all of the commonly used and many formerly ignored continuous characters and ratios were measured in the artiscin lineage formerly identified as the Cannartus laticornus - Ommatartus antepenultimus - O. penultimus lineage and identified here as the O. tetrathalamus lineage, although the measurements of O. tetrathalamus are not reported here. The continuous character and ratio measurements are plotted on stratophenograms illustrated in Figures 16-29.

Examination of the stratophenetic data reveals stasis, some gradual phyletic trends, and perhaps some discontinuities or punctuated continuous character trends. Utilizing the statistical morphometric criteria discussed earlier for 95% confidence intervals, it is clear
FIGURE 16

Stratophenogram of Artiscin Total Length

Each sample is represented by the mean (black triangle), 95% confidence interval (thin rectangle), and standard deviation (horizontal line). For the number of specimens measured per sample, refer to Table 1.
FIGURE 17

Stratophenogram of Artiscin Cortical Shell Length

Each sample is represented by the mean (black triangle), 95% confidence interval (thin rectangle), and standard deviation (horizontal line). For the number of specimens measured per sample, refer to Table 1.
FIGURE 18

Stratophenogram of Artiscin Cortical Shell Width

Each sample is represented by the mean (black triangle), 95% confidence interval (thin rectangle), and standard deviation (horizontal line). For the number of specimens measured per sample, refer to Table 1.
FIGURE 19

Stratophenogram of Artiscin Spongy Column Length

Each sample is represented by the mean (black triangle), 95% confidence interval (thin rectangle), and standard deviation (horizontal line). For the number of specimens measured per sample, refer to Table 1.
FIGURE 20

Stratophenogram of Artiscin Spongy Column Width

Each sample is represented by the mean (black triangle), 95% confidence interval (thin rectangle), and standard deviation (horizontal line). For the number of specimens measured per sample, refer to Table 1.
FIGURE 21

Stratophenogram of Artisc in Polar Cap Length

Each sample is represented by the mean (black triangle), 95% confidence interval (thin rectangle), and standard deviation (horizontal line). For the number of specimens measured per sample, refer to Table 1.
Each sample is represented by the mean (black triangle), 95% confidence interval (thin rectangle), and standard deviation (horizontal line). For the number of specimens measured per sample, refer to Table 1.
FIGURE 23

Stratophenogram of Artiscin Polar Cap Length and Spongy Column Length

Each sample is represented by the mean (black triangle), 95% confidence interval (thin rectangle), and standard deviation (horizontal line). For the number of specimens measured per sample, refer to Table 1.
FIGURE 24

Stratophenogram of the Ratio of
Artiscin Spongy Column Length to Total Length

Each sample is represented by the mean (black triangle), 95% confidence interval (thin rectangle), and standard deviation (horizontal line). For the number of specimens measured per sample, refer to Table 1.
FIGURE 25

Stratophenogram of the Ratio of
Artiscin Cortical Shell Length to Total Length

Each sample is represented by the mean (black triangle),
95% confidence interval (thin rectangle), and standard
deviation (horizontal line). For the number of specimens
measured per sample, refer to Table 1.
FIGURE 26

Stratophenogram of the Ratio of Artiscin
Polar Cap Width to Cortical Shell Width

Each sample is represented by the mean (black triangle), 95% confidence interval (thin rectangle), and standard deviation (horizontal line). For the number of specimens measured per sample, refer to Table 1.
FIGURE 27

Stratophenogram of the Ratio of Artiscin

Polar Cap Length to Cortical Shell Length

Each sample is represented by the mean (black triangle), 95% confidence interval (thin rectangle), and standard deviation (horizontal line). For the number of specimens measured per sample, refer to Table 1.
FIGURE 28

Stratophenogram of the Ratio of Artiscin
Spongy Column Width to Polar Cap Width

Each sample is represented by the mean (black triangle), 95% confidence interval (thin rectangle), and standard deviation (horizontal line). For the number of specimens measured per sample, refer to Table 1.
FIGURE 29

Stratophenogram of the Ratio of Artiscin
Spongy Column Width to Cortical Shell Width

Each sample is represented by the mean (black triangle), 95% confidence interval (thin rectangle), and standard deviation (horizontal line). For the number of specimens measured per sample, refer to Table 1.
that Figures 16-19 and 22-25 exhibit stasis for each continuous character or ratio. This is because the 95% confidence interval for each sample overlaps with the intervals of all the other samples. Nonoverlap of the 95% confidence interval must occur (more exactly, nonoverlap of any two intervals compared while imagining the shorter to be equal to the longer) to conclude that significant evolutionary change has occurred to identify an evolutionary trend. Such a conclusion can be reached for Figures 20-21 and 26-29. The continuous characters of spongy column width (Figure 20) and polar cap length (Figure 21) shows excellent apparent gradual evolutionary trends through almost the entire stratigraphic interval of seven million years. Also, the ratios of these two characters plotted against static continuous characters (Figures 27-29) also show excellent gradual trends as would be expected. In these latter cases, therefore, plotting ratios did not make apparent some biological characteristic not apparent in the original measurements. Figure 26 is unusual, because it shows the gradually trending plot of a ratio of two continuous characters (polar cap width and cortical shell width) neither of which, by themselves, exhibited gradual change. Therefore, the ratio plotted in Figure 26 is valuable new information not apparent in the original measurements. However, the gradual evolutionary trend of Figure 26 is not as good as the trends in Figures 20-21 and 27-29, because it contains a quite long period of stasis and the final stage of the trend reverses back to the earliest values. Thus, its interpretation is ambiguous.

The five good gradual evolutionary trends plotted in stratophenogram Figures 20-21 and 27-29 are highly significant, because they provide excellent evidence for the occurrence of anagentic evolution. Since the
characters of spongy column width and polar cap length change continuously and gradually through time, these characters, and ratios in which they are included, remain plesiomorphic and therefore should not be used as characters to classify the artiscins. However, spongy column width and the ratio of polar cap length to cortical shell length are in fact the very two characters which have been used by previous workers to distinguish the species in this artiscin lineage. In particular, Riedel has subdivided the lineage into three species by the arbitrary and typological criterion of polar cap length to cortical shell length ratio, with 0.20 marking the boundary between C. laticonus and O. antepenultimus and 0.25 marking the boundary between O. antepenultimus and O. penultimus (Westberg and Riedel, 1978, and references therein). This typological practice, and the reasons for it, are discussed in detail in a later section of this study. However now we can understand why subdividing a gradually-changing continuous character is not only typological, but is also poor taxonomy. Because such a character is plesiomorphic, the classification following such a character discrimination is bound to result in paraphyletic and polyphyletic taxa, since a plesiomorphic character does not allow the identification of monophyletic taxa. If we eliminate the anagenetic plesiomorphic characters from our biosystematic analysis, we must attempt to recognize any apomorphic characters, there being two kinds: new discrete characters and punctuated continuous characters. Since we fail to find any, one must conclude that the entire artiscin lineage studied here, formerly identified as consisting of three species, is actually an evolving single lineage and therefore a single evolutionary species. Its name would be Ommatartus penultimus, the senior synonym. Thus, our
proper biosystematic analysis has identified and eliminated the anagenetic plesiomorphic characters formerly used to subdivide the single lineage into three unnatural species. Since all identified characters exhibit either stasis or gradual continuous change, there are no apomorphic characters with which to nonarbitrarily subdivide the lineage. Therefore, it must remain a single evolutionary species characterized by two obvious phyletic (not phylogenetic) trends.

The five gradually-trending stratophenograms can be given alternative interpretations. Instead of continuous, gradual change with minor fluctuations they can be interpreted to show stasis plus punctuation. Such alternative interpretations are illustrated in Figures 30-34. As with other authors' "gradual phyletic trends," degree of gradualism is in the eye of the beholder, and other workers may see stasis and punctuation where the author may see phyletic gradualism. However, most other phyletic trend studies were plotted on ordinal time scales which clearly do not allow unambiguous interpretations because of uncertain time intervals. Such plots are frankly impossible to interpret with confidence, so a claim of either phyletic gradualism or punctuated equilibria is open to question. The stratophenograms in the present study are plotted on an interval time scale, so interpretation is slightly easier and more convincing. While the stratophenograms in Figures 20-21 and 27-29 contain obvious periods of stasis, the possible punctuation events are not clear, because the "events" appear to take millions of years to occur. Thus, even these stratophenograms are ambiguous and don't allow precise interpretation, but I think that the recognition of good phyletic gradualism is satisfactory and relatively unobjectionable. I still claim that there are no unambiguous punctuated
FIGURE 30

Alternative Interpretations of the
Artiscin Spongy Column Width Stratophenogram

Figure 30A shows an interpretation of phyletic graduation,
while Figure 30B shows the same stratophenetic data
interpreted as punctuated equilibria.
FIGURE 31

Alternative Interpretations of the
Artiscin Polar Cap Length Stratophenogram

Figure 31A shows an interpretation of phyletic graduation,
while Figure 31B shows the same stratophenetic data
interpreted as punctuated equilibria.
FIGURE 32

Alternative Interpretations of the Ratio of the
Artiscin Polar Cap Length to
Cortical Shell Length Stratophenogram

Figure 32A shows an interpretation of phyletic graduation,
while Figure 32B shows the same stratophenetic data
interpreted as punctuated equilibria.
FIGURE 33

Alternative Interpretations of the Ratio of the
Artiscin Spongy Column Width to
Polar Cap Width Stratophenogram

Figure 33A shows an interpretation of phyletic graduation,
while Figure 33B shows the same stratophenetic data
interpreted as punctuated equilibria.
FIGURE 34

Alternative Interpretations of the Ratio of the
Artiscin Spongy Column Width to
Cortical Shell Width Stratophenogram

Figure 34A shows an interpretation of phyletic graduation,
while Figure 34B shows the same stratophenetic data
interpreted as punctuated equilibria.
continuous characters, despite the alternative interpretations shown in Figures 30–34. Therefore, there is still no unequivocal and nonarbitrary means to subdivide the O. penultimus single lineage as described here, and therefore it shouldn't be subdivided.

It might be argued that a discontinuity or punctuation in Figure 27 can be inferred from the data of his ratio between 8.8 and 8.4 m.y. involving a change in the ratio of approximately 0.23 to 0.27, thus suggesting that 0.25 might very well be an appropriate ratio to place a nonarbitrary limit between two gradually evolving species, as Westberg and Riedel (1978) maintain. There are many reasons to not do this, however. First, the transition between the two seemingly segregated groups of means in Figure 27 is itself gradual, running from approximately 0.21 to 0.30 m.y. Placing the actual demarcation limit at 0.25, for example, would then itself be arbitrary. Second, Figure 32 illustrates two equally valid alternative interpretations of the identical statistical data. One interpretation shows only continous gradual change through time. It is important to understand that either of these two interpretations is somewhat subjective and that the subjectivity is unavoidable, so both interpretations are legitimate. Because there is no nonarbitrary way to subdivide a continuous character which changes gradually, either rapidly or slowly, we cannot accept such a character as an apomorphy. The change must be discontinuous to signal the appearance of a uniquely derived character and the occurrence of a cladogenetic speciation event. The essential subjectiveness and arbitrariness of utilizing phenetic resemblance as a measure of genealogical relationship, such as the examination and subdivision of
continuous characters, is the reason why the phenetic method has been rejected as a scientific taxonomic tool by cladists.

If we examine the other characters in the *O. penultimus* lineage, to see if any discontinuities are present, we find none. The species *C. laticonus* has a wide spongy column compared to *O. penultimus*, but examination of Figure 20 reveals that this character changes gradually. The apparent discontinuities within the characters of spongy column length (Figure 19), cortical shell width (Figure 18), and polar cap width (Figure 22) are again simply faster gradual changes on a generally stasigenetic lineage. No nonarbitrary division at any point is possible. Furthermore, none of these apparent discontinuities occur at the same time with each other. If all did occur at the same point in geological time, we would be strongly persuaded that a speciation event did occur. Finally, each of the interpretations of apparent discontinuity have an equally valid but more parsimonious explanation as status or trend. We would correctly choose the more parsimonious explanation if there was ever any ambiguity. As explained previously, it is almost impossible to eliminate ambiguity from any subjective interpretation of phenetic data, so although we must examine this data to demarcate species, we will use only a specific subset of the phenetic data, the apomorphies, for cladistic analysis.

The conclusion we may draw from the previous discussion is that there is no real discontinuity in the *O. penultimus* lineage data to justify a nonarbitrary division of the lineage into species; therefore, the lineage is a single lineage and thus is one species. We will henceforth refer to the *O. penultimus* lineage as the single species *O. penultimus*, the senior synonym of *O. antepenultimus* and *C. laticonus*. 
This conclusions directly follows from the evolutionary species definition discussed earlier and the present statistical morphometric data. It is important to realize that whenever the data reveal a continuous gradual change of any rate, no matter how fine the sampling interval or the time interval, we cannot impose our personal wishes upon nature and arbitrarily subdivide the single lineage. Thus, the apparent discontinuities contained in the data are not real discontinuities, but changes in rate of change for an interval of time. These changes are interesting for investigating tempo and mode in evolution, but not for species identification and classification.

The stratophenograms must be interpreted, at our current level of understanding, by simply noting the occurrence of either a gradual trend or non-change of the character in question. It is not possible to test the statistical significance of differences in means, but because of our inability to eliminate local environmental variation on single sample statistics, such a practice would not yield significant results. Obviously, the difference between any two samples could be caused by either or both evolutionary factors and environmental factors. To study only one factor, we first must eliminate the other. By ignoring minor pertubations or variation among statistical data points, we can assume than any trend we observe through time is evolution and not local environmental effect. There are other reasons to believe that what we observe is genetically-based evolutionary change and not ecophenotypic variation or phenotypic plasticity brought about by gradual environmental change through time. Primarily, our time scale is too long to seriously consider these short time scale biological changes. This is also the major argument against an interpretation of character
displacement which Kellogg (1975b, 1980) claimed for her radiolarian data.

**Cladistic Analysis**

I have identified one species, *Ommatartus penultimus*, and can choose five more species to construct a cladogram (Figure 36). The additional species are well demarcated by established and newly discovered apomorphic characters. Figure 35 illustrates five of the species on this cladogram. Additional species beyond the six could be used for the cladogram, but this one is purposely kept simple to aid instruction and analysis. The cladogram (Figure 36) was constructed according to the principles discussed in the references listed in an earlier section. While a cladogram is a nested set of synapomorphies, both plesiomorphies and autapomorphies are purposely kept in the cladogram for instruction value and further evaluation and comparison. The cladogram permits the segregation of the six species into four monophyletic clades: (1) *O. prismaticus* (2) *O. violina*, (3) *O. penultimus* and *O. tetrathalamus*, and (4) *O. petterssoni* and *O. hughesi*. For the purposes of classification, each clade could be given genus rank and four genera could be named. Alternatively, the clade of six species (any monophyletic group is a clade) could be considered a single genus, as is done here. The expression of clades within our hierarchal Linnean system of nomenclature is a methodological problem which still has not been solved, although a number of papers have been written which discuss the problem (Wiley, 1980). Therefore, while the identification of the clades is nonarbitrary, and their classification into successively more
FIGURE 35
A Cladogeny of Five Species of the Artiscinae

This cladogram represents the inferred cladogenetic relationships of five artiscin species. From left to right the species are: the stem artiscin species represented by *Ommatartus violina*, *O. tetrathalamus*, *O. penultimus*, *O. petterssoni*, and *O. hughesi*. The apomorphic characters whose analysis led to the construction of this cladogram are illustrated in Figure 36.
FIGURE 36

The Artiscin Cladogram Showing Apomorphies and Plesiomorphies

This cladogram depicts the inferred cladogeny of six species of artiscins. The species are grouped in five clades, two of two each, on the basis the apomorphic characters (open bars). Some plesiomorphic characters (solid bars) are also indicated. These characters are identified below.

A  bilateral symmetry
B  elliptical cortical shell
B' cortical shell with equatorial constriction
C  single medullary shell
C' double medullary shell
D  plicae (protuberances) on distal cortical shell
E  narrow spongy column
E' wide spongy column
F  no polar cap or clear area
F' polar cap or clear area
G  reduced cortical shell
cortical shell cylindrical with slight equatorial bulge
polar caps extend from cortical shell
polar cap, when extended along polar axis, has no pillars
polar cap supported by pillars
spongy column always present
no or greatly reduced spongy column
sometimes has multiple spongy columnar caps
multiple porous columnar caps
spongy column rounded and thickened distally
plicae rare or absent
inclusive monophyletic groups is nonarbitrary, the nomenclatural
categorical level (genus, family, etc.) assigned to these higher groups
is still arbitrary.

The characters chosen to construct the cladogram are presented in
Figure 36. For the most part, these are discrete characters, but some
apomorphic characters are continuous as well. A number of these
characters have not been used before in the classification of the
Artiscinae, but most have. Other characters could be used which would
corroborate or refute the cladogram, but the characters presented here
are sufficient to ensure a rigorous cladogenetic analysis. The major
apomorphic characters appeared during speciation events which were not
gradual. No or very few (typically one or two specimens in the hundreds
examined) possessed an intermediate form in regard to the characters.
This phenomenon contrasts considerably with that of the
gradually-changing continuous characters discussed above, which possess
immense variability. The point here is that the discrete, discontinuous
characters, especially uniquely derived characters, were searched for
and utilized in the cladogenetic analysis, not by purposely ignoring and
excluding continuous characters, but by first examining and measuring
all potentially continuous characters to discover whether they were in
fact continuous or discontinuous. Only after this analysis is it
possible to exclude truly continuous characters, since such characters
can only be plesiomorphic, no matter how much they continuously change.
This method differs considerably from the method practiced by other
radiolarian taxonomists, who purposely choose a single continuous
character to arbitrarily subdivide single lineages, and ignore many
obvious discrete characters, including some apomorphies.
The following characters are considered to be discrete and discontinuous apomorphic characters:

1. presence of polar caps or clear zones between the cortical shell and the polar column
2. pillars at the base of the polar cap
3. decrease in size of the cortical shell
4. rounded and thickened distal end of the spongy column
5. polar column changing from spongy to porous
6. cortical shell becoming cylindrical
7. equatorial constriction

These characters are sufficient to perform a cladistic analysis. The evidence for the discrete characters is contained in the photographs of Figures 11-15 and 35; the evidence for the discontinuity of the potentially continuous characters is contained in the stratophenograms. For example, *O. petterssoni* was thought to gradually evolve into *O. hughesi* by slowly adding polar caps within the spongy column. It was therefore difficult to differentiate a *O. petterssoni* with lots of caps from a *O. hughesi* by this criterion. However, more detailed study reveals that while *O. petterssoni* does indeed exhibit a phyletic trend of increasing numbers of caps, the application of an apomorphic criterion removes all ambiguity. The species *O. hughesi* has a porous polar column. This fact has been overlooked because it was formerly believed that *O. hughesi* had porous polar caps. But these caps are not homologous to the caps of other artiscins which grow out of or next to the cortical shell. The *O. hughesi* caps are formed from within a polar column which is spongy in the case of *O. petterssoni*, but porous in the case of *O. hughesi*. Therefore, because of the mistaken identification
of polar cap homology, the *O. hughesi* porous column was not correctly
differentiated from the *O. petterssoni* spongy column. While *O.
petterssoni* exhibits great variability in the degree of cap-formation
within the polar column, and *O. hughesi* exhibits great variability in
number of polar caps, in all of the hundreds of these species I have
examined, I found only one individual (Figure 15F) whose polar column
was partly porous and partly spongy. The transition from *O. petterssoni*
to *O. hughesi*, based on the degree of cap-formation, is another of
Riedel and Santilippo's "evolutionary" transitions which is necessarily
typological and arbitrary, because it is based on artifically
subdividing a continuous character (length of area which shows polar
caps). As in the case of the *O. penultimus* lineage, the present
analysis nullifies this method and removes the problem.

**Genealogical Analysis**

Figure 37 is a type 1 genealogy derived from the cladogram in Figure
35 by making certain assumptions. As previously discussed, it is
necessary to make these assumptions if one desires to proceed past the
cladogram in a biosystematic analysis. The assumptions include that the
known fossil record of the group is complete and that there are no
unknown artiscin species that may occur as intermediates. Strictly
speaking, the type 1 genealogy in Figure 37 is wrong, since there are
other artiscin species, such as *O. tubarius* and *O. mammiferus*, that are
not included in the genealogy. However, this genealogy is derived from
the cladogeny depicted in Figure 35 and is therefore only an
illustrative example.
FIGURE 37. A type 1 genealogy of five species of the Artiscinae. This genealogy is derived from the cladogram illustrated in Figure 35. The species are as follows: (A) stem artiscin species, such as *Ommatartus mammiferus*, (B) *O. tetrathalamus*, (C) *O. penultimus*, (D) *O. petteressoni*, (E) *O. hughesi*. 
Figure 38 is a type 2 genealogy derived from the type 1 genealogy plus additional stratigraphic information derived from the geologic and fossil records. In this example, the ancestral-descendant relationships of the species shown in Figure 37 remain the same, but now the stratigraphic ranges of the species are plotted and the time of splitting for each species is indicated. This genealogy or family tree shows some interesting relationships. First, two lineages, the *avitus-tetrathalamus* lineage and the *petterssoni-hughesi* lineage, split from the *penultimus* lineage at different times. The significance of this is that because the *penultimus* lineage changed gradually through time by anagenetic evolution, the characteristics of the two daughter lineages, which split by cladogenetic evolution from the parent lineage at the times of speciation, are heavily influenced by the point at which they split from the parent. That is, the *petterssoni-hughesi* lineage split from the *penultimus* lineage when 0. *penultimus* had short polar caps and thick polar columns, but the *avitus-tetrathalamus* lineage split when 0. *penultimus* had tall (long) polar caps and very narrow and short polar columns. Therefore, each daughter lineage at its first appearance was a combination of its cladogenetically-derived unique characters plus the continuous characters inherited unchanged from the parent lineage; since the parent lineage itself had changed considerably during the time between the first splitting event and the second, the characters which each daughter lineage inherited were quite different. Furthermore, the differences these inherited characters exhibited were due entirely to anagenetic evolution. Therefore, each daughter lineage is phenetically composed of both anagenetic and cladogenetic evolutionary components. Although only the cladogenetic components identify it as a new species,
FIGURE 38. A type 2 genealogy of five species of the Artiscinae.
it is differentiated from the other daughter species as much by anagenetic differences as by cladogenetic differences. Only the cladogenetic differences are apomorphic, and only these are necessary for cladistic analysis and classification, but for phylogeny construction and testing evolutionary hypotheses, it is clear that both the cladogenetic and anagenetic evolutionary components must be specified.

The artiscin lineages thus illustrate quite well the possibility that the morphologic characteristics of fossil taxa may benefit as much or more from the anagenetic evolution, which occurred prior and subsequent to the cladogenetic speciation event, as from the cladogenetic evolution which created the fossil taxa. The documented occurrence of this possibility by this study has great significance for testing among proposed models of evolution, especially between punctuation and gradualism.

**Phylogenetic Analysis**

Many different phylograms can be constructed from the data presented to this point in the study. The vertical interval time axis for any phylogram will be identical to the time axis of the type 2 genealogy in Figure 38, but the horizontal morphologic axis for a phylogem could be any of the horizontal axes of the fourteen stratophenograms presented in Figures 16-29. As discussed in a previous section, a proper rigorous phylogeny is a combination of a type 2 genealogy and a stratophenogram which attempts to represent anagenetic, cladogenetic, and ancestral-descendant relationships on a single diagram. Since
stratophenetic data for the O. petterssoni-O. hughesi lineage was not presented in this study, a phylogeny derived from the type 2 genealogy of Figure 38 cannot be constructed for any specific character and so is not presented here, but an idealized phylogeny for a character such as polar cap height, which increases in time for the O. penultimate lineage, can be recognized in the phylogeny of Figure 7.
Evolutionary Change Within the Artiscin Lineages

This investigation has demonstrated that both anagenetic and cladogenetic evolution are necessary to explain the totality of phenetic change of new species, that phylogenies (which illustrate both types of evolutionary change) are the proper level for analysis of the history of life, and that microevolution does influence, if not control, macroevolution, since the phenetic characters of higher taxa sometimes owe their origin to anagenetic change, a microevolutionary process. This is probably the most important conclusion of this study.

Species form by cladogenesis, not by anagenesis, yet it seems clear that for the artiscins, anagenesis does account for some of the evolutionary change which new species exhibit. The question is how much? Is cladogenetic change more important or less important than anagenetic change in determining the phenetic characters of new species and, by analogy, of higher taxa? The answer to this question would corroborate either the punctuated or gradualistic model of evolution as the correct hypothesis. My artiscin data, correctly interpreted within modern scientific bio sistematic theory and avoiding typological practices and evolutionary assumptions of all kinds, clearly indicate that, within the artiscins at least, evolution is both gradual and punctuational. Speciation is cladogenetic and occurs relatively rapidly, almost instantaneously in geological time, although of course gradually in ecological time. However, a great deal of evolutionary change also takes place by anagenesis within (not between) species.
Therefore, it does not appear that the punctuational evolutionary hypothesis should be preferred over the gradualistic hypothesis, since a large amount of evolutionary change (in artiscins, at least, but perhaps for other planktonic microfossils and even other organisms as well) does not take place at speciation events. Rather, my data indicate that evolutionary change is spread approximately evenly both within and between species. Anagenesis appears to be as important as cladogenesis in producing evolutionary change when examined at sufficiently fine intervals in a continuous and complete fossil record. Furthermore, my data show that in some cases microevolutionary processes can definitely influence, if not wholly account for, macroevolutionary effects. On the other hand, differential survival of species (species selection), a theoretical macroevolutionary process, can be invoked to explain the character of the phylogeny through time, since the individual single lineages do appear to exhibit new features and evolve in new directions on a seemingly random basis without respect for previous trends. Furthermore, some lineages, such as O. petterssoni and O. hughesi, become extinct (orthoextinct in the case of O. petterssoni and holoextinct in the case of O. hughesi) for some unknown reason which may be caused by species selection. But I see no way at present to test this hypothesis. Many more trends within a much larger clade, such as the whole of the Radiolaria, need to be studied before the macroevolutionary hypotheses of differential species survival and species selection can be used to explain visible macroevolutionary trends. Even at this level, however, some way must be formulated to test the macroevolutionary hypotheses.
Punctuation versus Gradualism

Three types of evolution are visible in the artiscin data: (1) stasis (Figures 16–19 and 22–25), (2) anagenesis (Figures 20–21 and 27–29), and (3) cladogenesis (Figure 36 and 38). The prevalence of stasis plus cladogenesis over anagenesis (as in the deep-dwelling plectopyramins, for example) would corroborate the punctuational model, while the prevalence of anagenesis over stasis and cladogenesis would corroborate the gradualistic model. Since neither mode of evolution is dominant, we cannot choose between the two models. Perhaps a third model which combines both modes is the best hypothesis; a number of authors have suggested precisely this approach (e.g. Sylvester-Bradley, 1977). However, a few points need to be borne in mind. The artiscins were chosen for this investigation because, in addition to other considerations, they were known or expected to exhibit good phyletic evolution. Apparently, the great majority of radiolarians as seen in the same excellent fossil record do not illustrate phyletic evolution at all. As stated in Schafersman (1978, 1980), most radiolarian species possess no unambiguous ancestors or descendants, most appear suddenly and disappear suddenly, and most apparently exhibit only stasis during their lifetimes. The data for this conclusion comes from personal examination of many samples from the complete pelagic sequence of core 9-77B, and agrees with the same personal observations of other biostratigraphers. This conclusion has never been tested except by personal nonquantitative observation; it could be easily tested by choosing twenty species at random from the middle and upper Miocene section of DSDP core 9-77B which provided the artiscin data, measuring a
sample of individuals of each species from each sediment sample, and statistically reducing the results to Hubbs and Hubbs diagrams in the same manner as performed here. This enormous undertaking would either corroborate the hypothesis of punctuational evolution by demonstrating the evolutionary stasis in all characters measured in all twenty species, or it would refute the punctuational model and corroborate the gradualistic model by revealing a significant amount of phyletic change. I strongly believe this project, if carried through to completion, would support the punctuational model. But this is only my personal belief. I must state that the artiscin data reported in this study do not support the punctuational model more strongly than the gradualistic model.
IMPLICATIONS FOR BIOSTRATIGRAPHY

The Use of Evolutionary Theory in Biostratigraphy

Biostratigraphy is the most interesting and most important branch of stratigraphy. The age assignment of strata by the use of fossils is second only to the use of superposition for determining the relative age of sedimentary rock layers. Some stratigraphers consider the ordering and correlation functions of stratigraphy to be all of stratigraphy, and thus do not recognize the description and classification functions of lithostratigraphy. Others do not recognize chronostratigraphy as a branch of stratigraphy different from biostratigraphy, but consider biostratigraphy by itself to possess all chronostratigraphic attributes. Although I and the majority of stratigraphers do not agree with the minority of stratigraphers who hold such views, their existence nevertheless underscores the great relevance of biostratigraphy to stratigraphy and thus to geology and paleontology.

Most of biostratigraphy seems quite straightforward, consisting as it does of simply noting the occurrence and change of fossils through rock layers and using these occurrences and changes elsewhere to assign the same relative age. What is simple in conception is quite complex and problematic in theory and practice, however. As an example, Temple (1978) points out that biostratigraphic units are dependent on the identification of fossil species, something that, in Temple's words,
are "currently indefinable." Turner's comment is a valid concern, and this study may shed some light on the problem. Temple further states that the definition of a fossil species "depends on knowledge of its spatial and temporal variation, and this knowledge cannot be obtained unless the time relations of the species occurrences are independently known: in other words, unless you can already correlate strata, you can't define or identify species on which you hope to base the correlation." Temple adds that this is the "fundamental logical difficulty in biostratigraphical correlation." According to Temple, therefore, we must know the strata fossil species' range of variation before we can use them in biostratigraphy to correlate, but we must be able to correlate strata before we can learn the temporal and spatial variation of the species. Can one correlate strata without using fossils? Yes, by lithostratigraphic tracing of beds and by paleomagnetic stratigraphy. The first is extremely unreliable because formations and beds are never isochronous over their total geographic extent; stratigraphers do not even call lithostratigraphic tracing "correlation." The second method is reliable for those few cores which preserve a good paleomagnetic record. A study of a single core has no correlation problems, since superposition is completely unambiguous. However, we cannot assume by the study of a single core that we know the entire range or even a good estimate of a species temporal and spatial variation. But how many cores do we need to study to obtain such information? Five, a dozen, or every deep sea core in the world's oceans? We shall see that Temple was somewhat wrong in his analysis of the "fundamental logical difficulty in biostratigraphical correlation," for the problem does not lie with our inability to correlate strata
independently of species definition and identification, but with the fact that our traditional methods of species definition and identification require that we know or have a good estimate of a species' temporal and spatial variation. This is due, of course, to the legacy of evolutionary taxonomy, phyletic gradualism, and the biological species concept, a legacy whose scientific usefulness is now in question. A single core may be sufficient for a scientifically valid study of species identification and evolution, and this may be combined with paleomagnetic data from that core to allow valid correlations with cores which lack such paleomagnetic data. We will see that while it may not be possible to produce a biozonation which is completely independent of species definition, it is nevertheless possible to produce one that avoids the pitfalls contained in our present biostratigraphic system which relies heavily on evolutionary assumptions.

Let us examine one reason why the traditional method of biostratigraphic correlation is unworkable. In a single continuous undisturbed deep-sea core, we know the time relations of a species' first and last appearance datums, independently of any biological attribute of the species, by using simple superposition (Schafersman, 1983). In the traditional method, we define and identify these species by reference to evolutionary theory as we understand it. As advocated by Simpson (1961) and Mayr (1969), this would be a biological or evolutionary species definition as interpreted through the Synthetic Theory of Evolution (Simpson, 1953; Mayr, 1963). (I wish to point out that this traditional method is an example of the best traditional method, for there is another typological traditional method utilized by many micropaleontologists which is even more invalid, as will be
discussed later. The present argument, however, requires that the strongest traditional example be used.) When we wish to correlate our cored sequence with others for purposes of extending the study, however, we find that we usually must use fossil species to do this.

The example I wish to present is the case in which we are studying the evolutionary changes which one or more species of interest undergo during geologic time as inferred from material in the core. We know that we cannot use the species of interest (e.g., radiolarians) to correlate with other cores, since the species identification and in some cases zonal boundaries depend explicitly on the very evolutionary criteria we wish to study. To do this would be circular reasoning. It is therefore commonly believed that we can use other fossil species (e.g. planktonic foraminifera or calcareous nannofossils) to "independently" correlate the cores. The point I which to make is that we cannot do this if the other species are also identified and their zonal boundaries determined, by precisely the same evolutionary theoretical criteria we wish to examine. What is forbidden with one group of organisms is not thereby permitted with another group simply because of a degree of taxonomic difference; at a higher taxonomic level (e.g. Protista) they are the same group. Thus, to use these other species to provide an "independent" correlation is also circular reasoning. In effect, this practice presumes the correctness or validity of the very theory we wish to examine by our study. The crucial factor to note here, since this is the essence of this paper, is that the explicit or implicit use of evolutionary theory in the necessary biosystematical aspects of biostratigraphy makes the biostratigraphical system untenable. This is not because evolutionary
theory is invalid, of course, but simply because it is a theory which must itself be tested. We may conclude, therefore, that we can use only a single core to investigate evolutionary processes and patterns in species without presuming we already know such processes and patterns in other species by using an "independent correlation."

Perhaps an example will make my argument clearer. In his well-known study of *Hyopsodus*, Gingerich (1976a) presents two stratophenetic diagrams illustrating morphometric change in the first molar of the species of *Hyopsodus*. The purpose of his study is to test the hypothesis of phyletic gradualism. The first diagram contains samples stratigraphically ordered by superposition (actually the samples were ordered by interpolation of all sample localities into a complete measured section by lithostratigraphic tracing, but with a presumed good sedimentary record in a restricted area; this amounts to the same as superposition, since Gingerich assumed that facies time transgression did not adversely modify the isochronality of individual beds). The second diagram contains many additional samples stratigraphically interpolated by assuming a gradual progressive change in molar size. Both Gingerich (1976a, p. 10-11) and Gould and Eldredge (1977, p. 129) make the point that the second diagram with the samples interpolated by molar size is invalid, since the stratigraphic framework must be set up completely independently of the fossils of interest. But consider a hypothetical case in which all samples containing *Hyopsodus* teeth also contain *Pelycodus* teeth (as many samples apparently do), and that the *Pelycodus* first molar also shows a gradual progressive morphologic change (which it does). Now let us assume that someone interpolates the additional *Hyopsodus* samples which cannot be ordered by stratigraphic
superposition into the second diagram on the basis of not _Hyopsodus_ molar size, but by _Pelycodus_ molar size in the same samples. Immediately, we would object that this is not any more an "independent correlation" than using _Hyopsodus_ molars alone, and that such an interpolation is equally as improper, not because _Pelycodus_ is not an independent group, for at the genus level it is, but because the validity of an evolutionary ordering method we question or wish to examine with one taxon is equally in question with another taxon, for at a higher taxonomic level they become the same taxon and any "independence" is a faulty assumption.

The example above is clear because the absurdity of the practice it represents is obvious. In this case an evolutionary model—that morphologic change procedes in a gradual progressive fashion—is assumed so that we may test the very same mode as an hypothesis; this is an invalid argument because of circular reasoning. Note that the truth or falsity of phyletic gradualism is not in question here, only that it cannot be used to test itself.

The argument I wish to make is much more subtle and may be difficult to see. For precisely the reason given above, i.e. circular reasoning, the use of traditional evolutionary theory to define, identify, and classify species and to define and delineate phyletic-biohorizons and lineage-zones in biostratigraphy causes the biostratigraphic system to be invalid. The strong overlay of evolutionary theory in biostratigraphy by species systematics and biozone definition, however, makes biostratigraphy internally inconsistent and makes it impossible (in a theoretical sense) to use in studies which test evolutionary theory. We therefore have a major problem, since in many cases biostratigraphy is...
the essential tool for testing evolutionary hypotheses about the fossil record.

Some may object at this point and say that biostratigraphy has worked very well for geologists and that it doesn't need changing. I would agree to a point. I am objecting to biostratigraphy's theoretical framework, not to its total practice. As I will show later, most micropaleontologists and biostratigraphers give only lip service to evolutionary theory—they largely ignore it in practice. This has had both good and bad results. The good results are that biostratigraphy has proceeded as if evolution didn't exist, despite every biostratigrapher's claim to believe the contrary, and the biostratigraphical framework of our planet is largely very satisfactory because it is based on empirical morphologic data, not evolutionary theory. The bad results are that when evolutionary criteria are explicitly or implicitly invoked in biostratigraphy, correlation and age assignment have been mistaken and confusing. It is no accident that phenetic taxonomy often has species identified and classified in a way similar or identical to evolutionary taxonomy (this was even considered evidence for phenetic taxonomy's correctness). Cladistic taxonomy and evolutionary taxonomy can also lead to similar species identification and classifications. The theory underlying these three taxonomic systems, however, is quite dissimilar, and als scientists we should be concerned with the theory as much as the empirical results. The modifications I would suggest in biostratigraphy are of major theoretical importance, but will have minor practical effect on the system except for the Tertiary tropical radiolarian biozonation and a few other biozonations lineage-zones.
There may be difficulty in seeing exactly where evolutionary theory enters a biostratigraphic system. It enters in two ways: (1) whenever an evolutionary biosystematic analysis of a taxon (usually a species) is involved, and (2) whenever a biozone or biohorizon is explicitly defined by evolutionary criteria. The second category will be discussed in a later section of this paper, where I show that it is here that most biostratigraphical problems arise which are caused by poor biosystematical concepts. The first category, discussed now, pertains (1) whenever a species is defined by the biological species concept or this concept is acknowledged as the basis for a morphological, paleontological, or evolutionary species concept; (2) whenever species are recognized by subscription to the phenetic concept that the total species spatial and temporal variation, or a good estimate of it, must be known for proper taxonomic identification; (3) whenever evolutionary taxonomy is made the basis of species ordering and classification as advocated by Simpson (1961) and Mayr (1969); and (4) whenever species are discriminated by ancestor-descendant relationships, geographical relationships, and temporal (stratigraphic) relationships. All of these taxonomic practices have been extensively discussed and analyzed in the recent literature; references may be found in Cracraft and Eldredge (1979). All of these practices to a greater or lesser extent enter into the modern taxonomy of biostratigraphically-important fossil species. All of these practices are fundamentally based on modern evolutionary theory and enter the biostratigraphic system at different levels, with different degrees of intensity, and for different purposes. And most important, as has been recently shown, all of these practices are for one reason or another subjective, arbitrary, and often untestable.
My argument is that the mistaken biosystematical practices discussed above pervade biostratigraphy at many levels, and this fact precludes the independence of biostratigraphy from an evolutionary theory which biostratigraphy is being increasingly called upon to test (due to the new interest in fossil patterns of evolution). It is my wish to demonstrate that this argument is legitimate, that the biostratigraphical system is theoretically invalid whenever evolutionary concepts are implicitly or explicitly invoked, and that the system can be corrected very easily by a change in the erroneous practices which are currently authorized and even encouraged by the International Stratigraphic Guide.

Although these arguments are contained elsewhere in the recent biosystematical literature, let me briefly review the reasons why the four taxonomic practices in which biostratigraphers engage are antithetical to an optimum independent biostratigraphy. These practices have been criticized by workers who wish to improve biosystematic theory and practice; I agree with these criticisms, and the original contribution I make here is to show that the criticisms are also relevant to biostratigraphy and that a new and better theoretical understanding is imperative if biostratigraphy is to continue as a scientific practice. Indeed, I add to some of the criticisms by utilizing biostratigraphic data and reviewing a number of biostratigraphic examples which demonstrate the problems involved.

As has been noted by a number of biosystematic workers (scientist and philosophers), the biological species concept is neither useful nor valid, despite the claims of evolutionary systematists who justify this definition as the way which nature works (Hull, 1955, 1964; Ruse, 1969, 1973; Suppe, 1974). This is recognized by the evolutionary systematists
themselves, who have proposed a variety of morphological and taxonomic species definitions, sometimes based on a biological species definition or on other equally faulty criteria, and thus equally invalid and useless. Of course, the biological species concept was initially developed to replace the many "subjective" morphologic and taxonomic species definitions with an "objective" one; unfortunately, it was discovered that the morphologic and taxonomic definitions could not be dispensed with, so these definitions were retained and "based" on the biological species definition (a good example of this is Simpson, 1943). All of these definitions rely on obtaining knowledge of the complete spatial and temporal phenotypic character variation in a species either without recognizing that some characters may be more useful than others or, when characters are selected and weighted, without an analysis of plesiomorphy and apomorphy — that is, without the recognition that some ancaestral characters which are conservative and often used in a traditional species definitions should in fact be avoided. Paraphyletic groups, such as the taxon Reptilia, necessitate plesiomorphic characters for their justifications, but since plesiomorphies are irrelevant for indicating group membership, paraphyletic taxa are not meaningful biological entities (Bonde, 1975; Wiley, 1979, 1981). The most serious shortcoming of the biological species concept is its well known incompatibility with the fossil record. Again, many paleontological species definitions have been proposed which are explicitly based on biological, taxonomic, or morphological species definitions and which are compatible with the unique temporal and morphological demands of fossil organisms. These have lacked universal acceptance because they are by nature ad hoc
definitions with restricted usefulness. Obviously, a species definition should be useful and valid for both neontological and paleontological species. The only valuable species definition proposed to be such was the evolutionary species definition of Simpson (1961). However, as will be shown later, even this is flawed by its reliance on a phenetic concept of morphological resemblance and its necessarily arbitrary and untestable nature in practice. We may conclude that biosystematics needs a new species definition that is useful for all fossil and living organisms, that is based on criteria independent of any evolutionary theory, and that is nonarbitrary and testable. Biostratigraphers who have in the past advocated and used a biological, paleontological, evolutionary, or, as unfortunately is still common, typological species definition or concept, may perhaps find that they will have to adopt a new one.

Traditional taxonomic practice advocates knowing or estimating the complete spatial and temporal variation of a taxon for proper recognition of its limits and thus its place in a lineage and phylogeny. This is a phenetic concept which reaches its extreme form in phenetic taxonomy (Sneath and Sokal, 1973), but which is also explicitly advocated by evolutionary taxonomists such as Simpson (1961) and Mayr (1969). Clustering by complete phenetic data has been shown to be less natural (sensu Gilmour, 1961) and less stable than clustering by cladistic data (Farris, 1977; Mickevitch, 1978). Evolutionary taxonomic systems which also utilize phenetic concepts are equally suspect (Farris, 1977). In contrast, cladistic taxonomy relies on taxon identification, ordering, and ranking by apomorphic (derived) characters, not all of which need be known for taxonomic purposes. For
example, Platnick (1979, p. 248) recounts that three different students of arthropod taxonomy used three different types of data (head development, eye structure, and intersegmental tendons) to reach highly similar conclusions of arthropod phylogeny by cladistic methods. Of course, it is valuable to recognize and use all apomorphic characters available, and the absence of a sufficient number of such characters is often problem with fossil taxa, but these are methodological concerns. Cladistic theory does not require that the complete spatial and temporal variation be known or estimated. Because of this, cladistic taxonomy, unlike evolutionary taxonomy, does not rely on any specific evolutionary theory, but rather relies on only the fact of evolution. (The great theoretical difficulty of phenetic taxonomy which results in its poor comparison with cladistic taxonomy is that it relies on neither the fact nor the theory of evolution; the distinction between these will be discussed later.)

Many authors (e.g. Sokal and Sneath, 1963; Hemmig, 1965, 1966; Crowson, 1970; Nelson, 1972; Cracraft, 1974, 1979; Bonde, 1977; Gaffney, 1979) have pointed out that evolutionary taxonomy is often arbitrary, subjective, selective, and untestable. Evolutionary taxonomists state that a number of valid classifications can result from a single inferred phylogeny, that constructing a classification is an "art," that a number of taxonomic decisions, such as differentiating closely related species in a lineage, must be arbitrary, and that phenetic and cladistic taxonomic elements are combined in their classifications in subjective and therefore untestable combinations. The fact that by evolutionary taxonomy a taxonomist can construct a new classification from the same material and phenotypic characters as had been previously used by an
earlier taxonomist, justified by new "insight" rather than by new material, and then defend his new classification by virtue of his later authority, is, I believe, sufficient reason to abandon evolutionary taxonomy as it has been practiced. Cladistics offers a testable, nonarbitrary, and nonauthoritarian method to construct a classification.

Traditional taxonomy has commonly used both extrinsic data (geographical and temporal information about organisms) and intrinsic data (phenetic data: morphological, physiological, behavioral, etc., information about organisms) for taxonomic character analysis. This has especially been true in paleontology for two reasons: (1) the common paucity of intrinsic fossil data, and (2) the abundance and obviousness of extrinsic data. It is common practice to differentiate two morphologically similar taxa that would be conspecific if found sympatrically, because they occur at different geological times or in different continents or sedimentary basins. It is even more common to differentiate taxa which have been typologically defined; this was done even if the "taxa" occurred in the same formation and basin. Of course, the best evolutionary taxonomists did this rarely or never, and the very best (e.g. Simpson, 1940, 1961) spoke out against this practice. Because of our new awareness of continental drift, paleontological taxonomists are more careful today, but this hardly constitutes the right reason. All of the above only documents the arbitrariness of the situation. Cladistic biosystematics has stressed the necessity of using only intrinsic information for character analysis, primarily for the reason that the cladistic method requires only this type of data. Since cladograms have no inherent temporal content, stratigraphic data are irrelevant. I would add the following reason: the use of fossil taxa
in biostratigraphy does not permit stratigraphic and geographic data to be used to differentiate and classify such taxa, since these same taxa are often used to coarrelate strata in different regions. Again, we must avoid circular reasoning, and again, the argument that we can use evolutionary information obtained from one fossil group (for biostratigraphy) to aid in independently differentiating another fossil group (for taxonomy) is not valid, since the common underlying theory for all fossil groups is what is important here, and the separateness or independence of the two practices is an illusion.

Some sort of prior comparative analysis underlies all attempts to reconstruct phylogeny with the aid of stratigraphic criteria. Such a comparative analysis integrates, in some fashion, the temporal and spatial morphological variability of the fossil organisms, i.e. it provides a method for using morphologic, geographic, and stratigraphic data for phylogenetic inference. Since phylogenetic inference is itself the acknowledged basis for classification under the best taxonomic systems, the prior analysis which led to the phylogenetic reconstruction should be explicitly recognized whenever fossils are classified. Such prior analyses are never explicitly recognized, however, because they are merely the thought processes of the individual investigator and are not repeatable methods in any sense. In the presence of dense stratigraphic fossil records which have been richly sampled, such as those studied by Gingerich (1976a, 1976b, 1979), a method may be articulated, such as the "stratophenetic method" of Gingerich. But these methods are only useful with the extremely rare complete stratigraphic sequences containing numerous fossils, and are useless for the vast majority of cases. Gingerich's stratophenetic method, for example, is useful for
investigating evolutionary patterns or processes, and for eliminating plesiomorphicanagenetic characters, but it cannot be used for any taxonomic function by itself. We must have some consistent or universal method for comparative analysis leading to a phylogeny reconstruction that can be used in all cases; since densestratigraphic and geographic comparative data are rarely available, this method need dispense with such data.

There are other reasons to avoid using extrinsic data for fossil phylogeny reconstruction and fossil classification. Schaeffer, Hecht, and Eldredge (1972) stated that "it is dangerous to assume at the outset that a chronocline is a pure reflection of an ancestral-descendent sequence, no matter how complete the record may seem to be." Important taxa may be missing because of small population size, peripheral population location, and nonpreservation due to less-than-optimum conditions needed for fossilization. Even if one believes the fossil and stratigraphic record to be as excellent and complete as possible, as Harper (1978) apparently believes is often the case, it is important to recognize that the boundaries of all stratigraphic units are arbitrarily defined; this includes formations, stages and biozones. Although this fact is not relevant for a single stratigraphic section, it becomes important whenever correlations are made between sections which are geographically separated. Stratigraphic and geographic data among fossil taxa can rarely be used without constantly referring to basic yet arbitrarily-defined stratigraphic units; only in a few instance can we discuss such data with reference to non-arbitrary units, such as absolute time. Thus we rarely have extrinsic data for use in a phylogenetic inference using a rigorous methodology.
Another trap paleontologists have fallen into is believing that samples of contemporaneous fossils can be collected for determining geographic variation at a single stratigraphic level. This problem was explicitly recognized by Young (1960, p. 352), who stated the following:

The assumption that one can obtain samples so that geographic variation can be computed against time variation is extremely dangerous to biostratigraphic concepts and to evolutionary concepts because the data obtained by making the assumption are then immediately used to prove the assumption.

Young thus underscores the circular reasoning inherent in many biostrataligraphic practices which use fossil taxa differentiated and classified in part by extrinsic stratigraphic and geographic data.

The final case involves the narrow typological differentiation of species which would be conspecific if they occurred sympatrically. The distinction between such taxa in paleontology lies in their geographic or stratigraphic disjunction rather than their intrinsic character. My favorite example involves Gayle Scott's attempt to demonstrate that the American Midway and the Danish Danian are the same age (Scott, 1934). The fossil data were ambiguous except for the presence in each group of an almost identical species of nautiloid, Hercoglossa danica. This species was named H. ulrichi in the Midway on the basis of an extremely narrow interpretation. Scott called into question this procedure; he did not "believe it is based on sound biology." He stated:

A species in fossil forms depends more upon the concept of the student creating the species; consequently, the matter of species distinctions in fossils must always be, to a certain extent, a matter of opinion.

If fossil species are to be distinguished on the basis of their occurrence at widely separated localities, what distance shall be named as sufficient for determining a new species? (Scott, 1934, p. 1147)
In recognizing and decrying the arbitrariness of this particular practice in paleontology, Scott was years ahead of his time. Neontologists recognize phenotypic variation as a matter of fact and take it into account when differentiating living species. Paleontologist must likewise take both geographic and stratigraphic phenotypic variation into account when differentiating fossil species. The recognition of this was the basis for Young's paper. Young recognized that the new species concept of modern biology would jeopardize biostratigraphic practice which has always relied on narrowly defined (often typologically defined) species, since species which vary in both time and space cannot be used for the smaller biostratigraphic units which must be the goal of all biostratigraphers. As Young puts it, these species "are not sufficiently refined to meet the need for detail in modern and future stratigraphy" (Young, 1960, p. 347). The need for increased resolution and the means used to attain this end are particularly troublesome problems in biostratigraphy and are a major concern of this study. Young's solution to this problem, to deny the reality and objectivity of species and thus permit narrow and typological species definitions (Young, 1960, p. 356), is not acceptable. Young (1960), Shaw (1969), and many other biostratigraphers (by their practice) have advocated this solution. This solution is predicated by the widely accepted but, I believe, mistaken view that continued refinement of the biostratigraphic system must rely solely on more precise or detailed documentation of species' geographic and stratigraphic ranges. In this view, the easiest way to accomplish this is to narrowly or typologically define taxa so that precise range limits
are efficiently attained. This procedure may be good biostratigraphy, but it is poor biosystematics. As will be explained later, better methods are available to attain the desired biozonational precision without sacrificing paleobiological information.

The last use of evolutionary theory in biostratigraphic practice for taxon identification and differentiation is the practice of recognizing ancestor-descendant relationships. Although this practice is widely used in traditionally taxonomy for dividing lineages and discriminating species, and thus is relevant to the present discussion of the nature of defining species used in biostratigraphic zonations and the subtle theoretical errors thereby allowed, it is far more important in certain explicit biostratigraphical practices which will be discussed in the next section, and therefore will be fully considered at that time. Suffice it to say that the practice of recognizing ancestral-descendant relationships is equally as arbitrary and untestable as the practice previously discussed, and thus has only a desultory effect on biostratigraphy.

We may conclude this section on the use evolutionary theory in biostratigraphy by stating that, under current practice, theoretical evolutionary concepts are implicitly and subtly interwoven into some parts of the biostratigraphic framework, and that this is not a desirable feature. Such theoretical attributes are irreconcilable to the need for an independent biostratigraphy whose methods are often used to provide a time framework in which to examine and test hypotheses of evolutionary tempo and mode. The necessity to avoid circular reasoning makes it imperative to halt the use of evolutionary taxonomy, which is
based on evolutionary theory as explained by Simpson (1961, 1975), Mayr (1969), and Bock (1977), and instead adopt a cladistic taxonomy which does not possess this defect. Only then will we have biostratigraphical system in which we can have confidence.
Lineage-Zones and Phyletic-Biohorizons

in Biostratigraphy

Introduction

Erle Kauffman (1970, p. 612), in a detailed critique of biostratigraphic theory and practice in the country, noted the following:

The vitality of any scientific discipline is marked by a history of frequent challenge and innovation of its working concepts, and a continuous search for the interpretive potential of its data base. Measured against this, the field of biostratigraphy is virtually stagnant in the United States. Considering the large number of active biostratigraphers, the scope of available data, and the importance of the discipline to the solution of a broad spectrum of biological and geological problems, this complacency cannot be justified.

I heartily agree with Kauffman's criticism, even though many of my conclusions differ from his. I wish the present paper to be as much a challenge to the discipline of biostratigraphy as was his. Since Kauffman's essay was written, there have been a number of other papers published concerning the relationship between biostratigraphy and evolution, and I have already discussed some of these. Most of these papers have sought to "improve" biostratigraphy, as did Kauffman's, but many of the authors have reached incompatible conclusions. The reason for this may be illuminating, for I have detected a serious conceptual problem in current biostratigraphic theory and practice. The problem involves the almost universally accepted belief that lineage-zones and phyletic-biohorizons are superior to other types of biozones and
biohorizons, and that specific evolutionary models should be used in the practice of biostratigraphy. Conflict occurs when opinions differ among biostratigraphers about which evolutionary model or which evolutionary criteria are best used for defining lineage-zones. Despite problems, biostratigraphers have not hesitated to advocate lineage-zones and use them in biozonations, although they have thereby created theoretically syncretic and untenable systems which have inevitably led to taxonomic confusion, nomenclatural abuse, difficulty in zonal boundary interpretation, and concomitant loss of biostratigraphic usefulness and precision. I hope that this study demonstrates that biostratigraphy should logically and optimally avoid evolutionary theory in either theory or practice, because insurmountable problems and conflicts will inevitably accompany the use of such theory for biostratigraphic purposes.

In this section we will encounter specific examples of the often unfortunate effect the misuse of evolutionary criteria and misunderstanding of evolutionary concepts has had on the practice of biostratigraphy. Here we will investigate how the uncritical use of both popular and idiosyncratic evolutionary models and methods of phylogenetic inference have led to the creation of biozones and even complete biozonations which are theoretically untenable and in practice unacceptable. We will first describe the general characteristics of lineage-zones and phyletic-biohorizons and review the assumptions and theoretical problems which accompany their use, consider some examples of their use in micropaleontologic biostratigraphy, and finally conclude with a summary of the reasons why they should not be used.
Critique of Lineage-Zones and Phyletic-Biohorizons

We are fortunate that, largely by the encouragement of one man, the international stratigraphic community has produced an International Stratigraphic Guide (Hedberg, 1976) that serves to gather in one book an international consensus on stratigraphic classification, terminology, and practice. We can turn to this book to examine one aspect (phylozones) of one branch (biostratigraphy) of stratigraphy, confident that the view we wish to examine and criticize is in fact the accepted view, recognized as valid or (at least) acceptable by individuals and stratigraphic commissions the world over. The Guide has not escaped criticism before, especially in regard to the concepts concerning chronostratigraphy it promulgates, but the present study is the first detailed criticism of lineage-zones.

According to the Guide, a biozone is a body of rock strata unified, characterized, or identified by its fossil content. A biozone is present only within the limits of observed occurrence of the particular paleontologic feature on which it is based, i.e. the fossils must be in the rock before a biozone can be recognized. Note two things: First, a biozone is a body of rock, not a collection of fossils. Second, unless "the diagnostic paleontologic elements of a biostratigraphic unit are present, mere similarity of strata in age, or lithology, or environment of deposition to a given biostratigraphic unit does not justify inclusion in that unit" (Hedberg, 1976, p. 46). A number of biostratigraphers insist that biozones should be defined as a body of rock strata unified by being the rocks formed during a specific interval of geologic time and recognized by the contained fossils. They thus
maintain that biozones are chronozones as defined in the Guide, or, more exactly, that chronozones are redundant since their function has historically been and should continue to be filled by biozones. This belief is one of the two main criticisms which have previously been leveled at the Guide (the other is that lithostratigraphic units have no place in stratigraphy because stratigraphy is concerned exclusively with time relationships among rocks). Although I do not wish to exhaustively examine this topic, let me say that I completely agree with the chronozone concept as espoused by the Guide, because to credit biozones with the time significance of chronozones is something which must be demonstrated, not assumed. I believe it is a mistake to assume the isochronicity of any biozone, no matter how many biostratigraphers may support the idea. The reason for this is not because many biozones have been shown to be non-isochronous, but because presumed isochronicity of biozones invariably involves an interpretation of an evolutionary process such as synchronous speciation, extinction, or phyletic evolution involving the entire species populations, and this in turn requires numerous hidden and often specious assumptions. As an example of this, Van Hinte (1967, p. 270) defended his concept of the biozone as the "zone (which) encompasses all rocks deposited during the total known time of existence of the taxon." A biozone consists of those rocks "formed during the time of maximal known occurrence of the particular taxon that characterizes the zone" (p. 271). According to Van Hinte, the best biozone is the phyllozone, because "The total life time of a taxon can be recognized when the direct ancestor and the phylogenetic offspring are known" (p. 271). Van Hinte thus makes the point that the ability to recognize the total time range of a taxon is
biostratigraphically preferable to a partial time range, which is what we usually see when we use first and last occurrences rather than speciation and orthoextinction events. But Van Hinte never questions, only assumes, the notion that the "direct ancestor" and the "phylogenetic offspring" can be "known." The possibility of attaining this knowledge is never questioned because biostratigraphers view the paleontological world from under a cloven hoofprint of theory, where ancestors are recognized because they possess ancestral characters and occur in time before the descendant, where phylogentic offspring are recognized because they are modified from the ancestor and occur later in time, and where the constant repetition of these patterns in the fossil record leads, by the inexorable logic of inductive reasoning, to an absolute certainty of our knowledge and the unshakable conviction of its usefulness to biostratigraphy. This conceit is annihilated (as pointed out by Nietzsche in a similar context) by Pilate's question "What is truth?" (John 18:38). If we examine the phylogenetic "knowledge" which biostratigraphers claim to possess, its "truthfulness" is dependent on (unexamined and implicitly assumed) models of evolution, speciation, and extinction, methods of phylogentic inference, and the superiority of inductive logic. As we have seen, and will see, these models and methods of evolution and logic are not so immune from criticism as most biostratigraphers would believe. The claim that one is basing one's biostratigraphic interpretations on evolutionary hypotheses, which is what theory-based science is all about, can be countered by inquiring whether these hypotheses, which are the very basis of our empirically structured biostratigraphic system, are in fact corroborated hypotheses. Are they capable of being tested by the
potential falsification of predictions? Despite rigorous testing, have they escaped such falsification? And finally, is "knowing" the phylogenetic history of certain fossils really useful for biostratigraphy? All of these questions have escaped critical examination, because when everyone accepts authoritarian pronouncements, ad hoc explanations, hidden assumptions, and untestable uncorroborated hypotheses as the path to truthful knowledge, there is no need to examine them.

There are many types of biozones: assemblage-zones, acme-zones, range-zones, and interval-zones (Hedberg, 1976, p. 50). The last two types are important because they use biohorizons as the fundamental structural element; furthermore, these two zones are by far the most widely used in biostratigraphy, because it is widely recognized that, for various reasons, assemblage-zones and acme-zones have limited value in the detailed, cosmopolitan, environment-independent, and repeatable biozonations we have today. Since biohorizons are the primary feature of range-zones and interval-zones, we must define this term. A biohorizon is any "surface of biostratigraphic change or of distinctive biostratigraphic character" according to the Guide (p. 49). Biohorizons are often called datums, datum planes, datum levels, surfaces, boundaries, limits, etc. It is any taxon-specific biological event that is found throughout the geographic range of the taxon, is believed to have occurred at approximately one moment of time, and thus is believed to have biostratigraphic significance. The two most common and important biohorizons are taxon first occurrence (appearance) and taxon last occurrence (disappearance), which are generally equated with taxon origination and taxon extinction. There are many other types of
biohorizons, such as change in coiling, appearance and disappearance of structure, change in the number or size of a structure, etc. Often these changes are equated with changes in evolution. It is vitally important to recognize this practice of equating empirical occurrence with biological cause, for when this is done, the biostratigrapher must make some evolutionary theoretical interpretation which then becomes part of the biozonation. For example, a first-occurrence may be interpreted as a cladogenetic speciation or as phyletic transition (anagenetic "speciation"); in the latter case, the extinction of an ancestor marks the moment of first occurrence. A last occurrence may be interpreted as orthoextinction or holoextinction; in the former case, the origination of a descendant may mark the moment of last occurrence. Thus, an evolutionary model is chosen, ancestors and descendants are recognized, and a phylogeny is constructed. If a change in a structure marks the biohorizon, the change may be interpreted as gradual or punctuational; to be within a single lineage changing gradually by phyletic evolution or to be at a limit of a single lineage; to be of intraspecific significance or to mark the boundary of a new evolutionary species. Many interpretations are possible, but the investigator may choose to work within a single model of evolution and phylogenetic inference, and thereby interpret all or most visible changes in the fossil data as manifestations of this single model. When this is the case, the resulting biozonational system that relies upon the evolutionary biohorizons is hopelessly dependent upon the scientific acceptability of the single chosen evolutionary model. If this model should prove scientifically unacceptable, the entire biozonation would be in jeopardy. One last point: the Guide has no term for a biohorizon
which is defined by evolutionary criteria, i.e. a biohorizon which is recognized only when some phyletic or phylogenetic inference is made. Since I wish to distinguish this type of biohorizon from the ones which are recognized without such inference or evolutionary identification, a specific term is desirable. I first called such biohorizons phyletic-biohorizons (Schaferman, 1978), and I will continue to use this term.

The International Stratigraphic Guide (Hedberg, 1976, p. 53-59) recognizes four types of range-zones. A range-zone is simply a body of strata representing the total horizontal and vertical range of occurrence of any selected element of the fossil taxa in a stratigraphic sequence (p. 53). Although the Guide does not make this distinction, the primary difference between range-zones (and interval-zones) and other biozones is that definite biohorizons are much more important in the former. Acme-zones and assemblage-zones, by their very nature, are often hazy or imprecise at the vertical limits, and for this reason are not the most desirable. The superiority of range-zones and interval-zones is the supposed objectivity and sharp boundaries provided by distinct biohorizons. For this reason Oppel-zones (one type of range-zone recognized by the Guide) should be put in a separate category. An Oppel-zone is really a combination range-zone and assemblage-zone, and was really only included for historical reasons, since no one today (except for some California foraminifera specialists) would want to construct Oppel-zones when he or she could construct range-zones. For the same reason (the strict reliance upon biohorizons), interval-zones should not be separated from taxon-range-zones and concurrent-range-zones (the two main types of
range-zones). All three are zones whose boundaries are biohorizons. The difference among the three is that the biohorizons of a taxon-range-zone mark the first and last occurrence of a single taxon whose range constitutes the zone, the biohorizons of a concurrent-range-zone mark the first occurrence of one taxon and the last occurrence of a second taxon whose overlapping ranges constitute the zone, and the biohorizons of an interval-zone mark first or last occurrences of two taxa whose ranges do not overlap, the zone being defined simply as the stratigraphic interval between the biohorizons. The fact that range-zones are more desirable than interval-zones, because a single sample suffices to assign an age for the former while a series of samples is necessary for the latter, does not really justify their separation in the Guide's classification scheme. Planktonic microfossil zonations mix range-zones and interval-zones indiscriminately, but studiously avoid acme-zones and assemblage-zones.

I therefore disagree with the Guide's classification of biozones, believing that Oppel-zones should be removed from range-zones and that interval-zones should be listed with range-zones as biohorizon-dependent zones. But I object most strongly to the Guide's narrow definition of lineage-zone, which it classifies as the fourth type of range-zone. A lineage-zone (phylozone) is quite a bit different from other range-zones because it necessitates the recognition of its limiting biohorizons by evolutionary criteria, i.e. it formally and explicitly equates empirical occurrence with biological cause by a phyletic or phylogenetic inference. The Guide (p.58) defines a lineage-zone as "a type of range-zone consisting of the body of strata containing specimens representing a segment of an evolutionary or developmental line or
trend, defined above and below by changes in features of the line or trend." This is a good definition except for two things: first (which I will soon discuss in detail), the "changes in features of the evolutionary line or trend" are necessarily identified or equated with some evolutionary process or event; second, lineage-zones are unfairly restricted to range-zones. The criteria used to recognize a lineage-zone are that the top and bottom biohorizons must represent evolutionary changes in an inferred lineage, a segment of which must be contained in the strata which the zone represents. Figure 39 shows quite clearly that one type of interval-zone can be a perfectly good lineage-zone which meets all the criteria, since branching points can always determine the extent of lineage "segments." This second criticism of the lineage-zone definition is really a criticism of the Guide, which simply overlooked the fact that interval-zones could be lineage-zones under certain circumstances; it is easily corrected by changing "range-zone" to "biozone" in the definition. The first criticism, however, is a substantive criticism of the whole concept of lineage-zones, and one I wish to take to its limit to demostrate the nonvalidity of lineage-zones. The main point of this paragraph is that lineage-zones are not a type of range-zone: they are rather a type of biozone distinct from both range-zones and interval-zones.

To understand the biozone relationships more clearly, refer again to Figure 39 which illustrates the three main types of biozones used in micropaleontologic biostratigraphy today. Two are range-zones, but the single characteristic which necessitates their grouping together with interval-zones is that all three types of zones require unique and sharply-defined biohorizons for their existence. As mentioned before,
FIGURE 39. The four major types of biozones, illustrating how three different types of zones may become lineage-zones when their boundaries become phyletic-biohorizons.
this is not the case for assemblage-zones, acme-zones, or Oppel-zones, for which biohorizons are not important; this is not necessarily bad, but because this fact of such zones' nature results in fuzzy or imprecise zonal boundaries, detailed zonations prefer to avoid them. Thus the three types of biozones illustrated in Figure 39 possess a unique attribute in common — sharp biohorizons — which makes them the most useful in modern micropaleontologic biozonations born from the complete and continuous pelagic stratigraphic sequences that permit fine sampling and detailed zonations. If we examine all of the biozonations of marine planktonic microfossils, we indeed find that such zonations invariably are made up of long sequences of biohorizons grouped into taxon-range-zones, concurrent-range-zones, and interval-zones. To judge from the writings of many micropaleontologists, the biohorizons (or datums) are more important than the zones themselves; this is perfectly true, because the isochroneity, reliability, and distinctiveness of the biohorizons are what actually make the biozones succeed in practice.

Returning again to Figure 39, it is apparent that with the inference of an ancestral-descendant relationship between species and the recognition that each biohorizon is a phyletic-biohorizon, each biozone becomes a lineage-zone (phylozone). In each case, for the interval-zone as well as the range-zones, a simple first or last occurrence is interpreted to represent an evolutionary transition such that both biozone boundary biohorizons represent evolutionary change of a lineage, and a segment of the lineage lies within the biozone. But even more importantly, for this is a central thesis of this paper, the biozones would not become lineage-zones without explicit recognition of evolutionary transitions between taxa, usually species. If such
evolutionary transitions were not recognized, the objective first and last occurrences of the taxa would remain the same, the stratigraphic ranges would in no way be altered, and the empirical boundaries of the biozones would not change their position. This being the case, why do biostratigraphers wish to recognize evolutionary transitions and turn perfectly good range-zones and interval-zones into lineage-zones? The answer is because many biostratigraphers strongly believe that biozones based on evolutionary criteria are the most reliable and isochronous zones we can devise, because knowledge of evolutionary transitions between species supposedly insures that we would then know the true tops and bottoms of the species' stratigraphic ranges. I name this belief the "evolutionary biostratigraphic argument."

Despite the problems which biostratigraphers and micropaleontologists have had with modern evolutionary taxonomy, despite their relative ignorance of the relationship between evolutionary theory and modern biosystematic practice, and despite their singular lack of interest in investigating aspects of modern evolutionary theory resolvable at the level of the fossil and stratigraphic records, they are nevertheless very interested in identifying evolutionary lineages and trends that can be used in a biostratigraphic framework. Biostratigraphers strongly believe that a good understanding of the evolutionary relationships among fossil taxa will enable the construction of the best zonations. Let us examine why:

In theory, a system of overlapping zones based on several lineages offers one of the best assurances of reliable time-correlation on a biostratigraphic basis. (Hedberg, 1976, p. 59)
[There are] advantages of evolutionary studies as a basis for refined and consistent biostratigraphic zonation, as opposed to other methods of systematics. A biostratigraphic system has become one of the most refined and successful because its biological units are mainly derived from evolutionary studies of evolving lineages. (Kauffman, 1970, p. 629)

[A] zonation based on evolutionary steps tends to be better integrated and more reliable than the schemes...based on ranges of unrelated marker species. (Stainforth and others, 1975, p. 46)

[Zones] whose nominate taxa are connected to each other by a well-defined evolutionary relationship...are more likely to be isochronous over widely separated geographical areas. (Björck, 1970, p. 260)

If a system of zonation is to bear a time-stratigraphic significance it should be based as much as possible upon phylogenetic lineages in rapidly evolving fossil populations. Such a system of phylozonation provides the most reliable tool in correlation and age determination. (Berggren, 1971, p. 41)

A succession of phylozones is the most reliable tool in correlation and age determination, because it directly reflects the irreversible evolution of life on earth providing maximum exclusion of the environmental factor. In principle, each known phylogenetic line can be used for succession of phylozones. (Van Hinte, 1969, p. 272)

Biostratigraphers thus believe that biozones explicitly based on known fossil lineages and phylogenetic relationships are unquestionably the most accurate, isochronous, refined, successful, and reliable. I am probably the only scientist who believes otherwise. Before I discuss my objections, we need to be clear about exactly what I am criticizing. We have already examined the biological necessity of classifying taxa by the cladogenetic or branching aspects of evolution inferred by a
cladistic analysis. Although the biostratigraphers quoted above would no doubt prefer to classify taxa be either the traditional typological methods or by classical evolutionary taxonomy, my criticisms of this have already been stated. Although many of the same criticisms are relevant in the present context, the grouping, ordering, and ranking of taxa is not the issue here, for taxon classification is a necessity for all branches of biology and paleontology, including biostratigraphy. What is the issue is whether knowledge of evolutionary relationships among taxa automatically results in the best biozonations and whether this knowledge is in fact obtainable with the certainty and objectivity necessary to reasonably expect that by explicitly basing biozones on such knowledge, the zones will thereby be the most refined, isochronous, and reliable. I strongly believe that, contrary to the vast majority of biostratigraphers, knowledge of evolutionary relationships is irrelevant to biostratigraphy. The reasons for this belief are quite simple: (1) isochroneity of biohorizons and biozones is something that must be demonstrated and tested in every case—-it can never be assumed by any apriori criteria; (2) despite their common belief to the contrary, biostratigraphers can never "know" phylogeny with the certainty and objectivity necessary to legitimately construct phylogenetically-based biozones which presumably are to possess the very qualities of certainty and objectivity; (3) the reason for this is that phylogeny is something inferred, not observed, and while methods for phyletic inference certainly exist, they do not provide the objectivity, unambiguity, preciseness, refinement, and reliability which they seemingly promise and which biostratigraphers expect: (4) methods of phyletic and phylogenetic inference are in fact heavily theory-laden and depend for
their usefulness on numerous ad hoc, hidden, and untestable assumptions about the evolutionary process, completeness of the stratigraphic record, time-relationships and correlatability of samples, and so forth; (5) while the assumptions about the evolutionary process are bad enough; (e.g. irreversability of evolution, nature of speciation, ancestral-descendant relationships, evolutionary significance of any observed anagenetic change), the assumptions about the stratigraphic record, which are absolutely necessary to construct phylogenies, are even worse, for here an insidious element of circular reasoning enters, since quite a bit of our knowledge of the completeness and correlation of the stratigraphic record derives from biostratigraphic analysis; and finally, (6) the easily demonstrated fact that, theoretically, evolution is completely unnecessary and irrelevant for any biostratigraphic activity (see, for example, Schafersman, 1983).

The belief in the evolutionary biostratigraphic argument is unnecessary, because range-zones and interval-zones successfully serve as effective, reliable biozones without the needless step of transforming them into lineage-zones by the inference of evolutionary transitions between species. Evolutionary theory is irrelevant to biostratigraphy, and far from improving biozonations by its application, the more common result is the creation of confusing and subjective biozones defined by typological taxa. I claim that a non-evolutionary biostratigraphy will possess greater clarity, precision, and reliability than the present system which allows evolutionary inference to define biozones. Phylogeny construction and the inference of ancestral-descendant relationships, two practices which must precede the recognition and definition of all lineage-zones and phyletic-biohorizons, may have a number of valuable uses in science, but
biostratigraphy is not one of them. The additional information supposedly provided by these two phylogenetic practices actually adds nothing to the quality of the biozone. As previously discussed, the empirical material attributes of the biozone, the stratigraphic ranges of the taxa which actually make the zone work, are unchanged. All that is added is a deceptive presumption of the biozone's increased reliability and isochronity.

The belief in the evolutionary biostratigraphic argument is unwarranted, because it assumes that the knowledge of evolutionary transitions between species can, in fact, be known, whereas such knowledge is only (at present) an untestable hypothesis produced by any one of many unprincipled methods which use authority and specious arguments as the criteria of acceptability. Phylogenetic inference is not an unproblematic process. Phylogenetic inference requires an acceptable species definition, a model of the evolutionary process, a method for determining ancestral-descendant relationships, and a method for determining the amount of anagenesis in a lineage. All of these devices must be combined into a syncretistic system to produce the basic evolutionary insights from which lineage-zones are constructed. Most biosystematists are now aware that such a system simply does not exist in any acceptable scientific form. It is an act of authoritarianism to use a single evolutionary model (such as the most commonly used gradualistic model; refer to Figure 40) and a single biosystematic method (such as the most commonly used method of phylogenetic inference by simply "seeing evolution" of taxa through successive samples in a section), and then using such "results" to construct lineage-zones which other biostratigraphers are expected to use. Different authors of
FIGURE 40. The model of gradual planktonic foraminifer evolution espoused by most micropaleontologists. The caption to this figure from Stainforth and others (1975, p. 43) states that "characteristics of species tend to change gradually and progressively through time so that a purely objective definition of a species may be extremely difficult." The figure shows how a mean form, connected by a line, and its range of variation, indicated by an oval, changes gradually through successive times T1, T2, and so forth. Thus, "early forms...differ completely from late forms."
evolutionary-based biozones use different criteria for determining the evolutionary relationships in such zones, and each author necessarily assumes the truth of his evolutionary model and method of phylogenetic inference. This being the case, can such biozonational systems which result have any scientific value, since their evolutionary framework cannot be tested by any scientific method? Analysis by a method rather than authority by consensus must be the arbiter of scientific matters, but in biostratigraphy it is authority which tolerates lineage-zones. It is inadvisable to promote any specific model of evolutionary change or descent for inferring phylogenetic relationships of any kind, for if the model is later found to be inadequate, then the lineage-zones it spawned will also be inadequate. Without question, micropaleontologists and biostratigraphers have adopted the model of phyletic gradualism and have implicitly or explicitly incorporated its tenets into the lineage-zones used in the modern standard microfossil biozonations. Consequently, it becomes absurd to infer cladogenetic evolutionary change against a biostratigraphic time scale which interprets evolution as gradualistic. The scale should be free of any evolutionary implications, and it can be—without the loss of any biostratigraphic utility.

The belief in the evolutionary biostratigraphic argument is mistaken, because even if we did "know" the true ancestral-descendant and anagenetic relationships of some index fossil species, we should not thereby believe that biozones constructed on such information are therefore more reliable, isochronous, and otherwise superior to the typical range-zones and interval-zones. This assumption, like the
assumption of reliability and isochroneity we give any newly proposed biozone, deserves to be examined and tested by systematic comparisons with other biozones and physical horizons in geologic sections over the region of the zone's usefulness. Note that the criteria for testing all biozones are the utility, reliability, repeatability, clarity and apparent lack of diachroneity of the zone whenever it is used in new stratigraphic sections or applied to new biostratigraphic problems by subsequent workers. Note that the testing does not utilize any evolutionary criteria, such as ancestral-descendant relationships, except when necessary to recognize a lineage-zone. But can such evolutionary criteria be tested in fact? As explained in an earlier chapter, no. As also mentioned earlier, if lineage-zones automatically provide superior isochroneity and consistency, why are such zones quite uncommon in most biozonations? Simply because such desirable characteristics must be demonstrated, and lineage-zones under repeated testing have not fulfilled the promise they hold in most biostratigrapher's minds. It appears to be mistaken to assume that phyletic transitions between species are automatically isochronous.

The belief in the evolutionary biostratigraphic argument is counterproductive, because the effort spent searching out and recognizing lineages and other revolutionary relations for lineage-zone construction could be better spent in testing biozones with new sample material from other localities. Furthermore, the creation of a biozonational scheme heavily dependent on a subjective or poorly conceived species concept, evolutionary model, and method of phylogenetic inference will require extensive revision if (when!) the concept, model, and method are discovered to be inadequate or in error.
Finally, new data may sometimes change the interpretation of the lines of descent in the single lineage or phylogeny upon which the lineage-zone was based, again necessitating revision.

The belief in the evolutionary biostratigraphic argument is circular when a biozonation constructed under its tenets is used to assist in the inference of evolutionary relationships of similar taxa to examine, for example, interesting evolutionary patterns or processes. Obviously, when this occurs, the truth of some particular evolutionary process or pattern has already been assumed to enable construction of the zonation; therefore, it is absurd to then "investigate" the truth of some other evolutionary relationships by the use of the zonation for correlation purposes. Logically, the biozonation should be constructed by simple stratigraphic relationships, without any evolutionary inferences, to prevent the change of circularity when the evolutionary relationships of other taxa are studied. Biostratigraphy, a science in itself, serves as a tool for biosystematics and evolutionary paleontology, and therefore must be free of any evolutionary presuppositions when fossil evolutionary studies are conducted.

Finally, the belief in the evolutionary biostratigraphic argument invariably creates more problems than it solves, since it often leads to evolutionary contradictions, typological species interpretations, and invalid idiosyncratic taxonomic practices. This statement may seem remarkable, but I fully intend to demonstrate that it is perfectly true. Under the influence of this belief, biostratigraphers have named and delimited fossil species and lineages solely for their stratigraphic value, rather than for any acceptable taxonomic reasons. The biosystematic method used for the recognition and classification of
species also commonly serves biostratigraphic utility rather than taxonomy. Often, for example, some biostratigraphically-useful aspect of anagenetic change in an evolving species will be used to subdivide that species in such a way that a particularly-needed biohorizon will be created; other important morphological aspects such as significant newly-derived and shared-derived characters, are often ignored. Heavy reliance is often placed on continuous vertical variation or gradual anagenetic change to describe new species, since these factors are assumed to represent "true" evolution and thus result in the best biohorizons. Almost always, single lineages and extended lineages are superficially described in such a way that will be most useful for a zonation, not in any way consistent with a recognized method of taxonomy. Subdivision of lineages for biostratigraphic purposes often necessitates recognition of typological species, since phyletic gradualism is assumed, anagenetic change is searched for, and single lineages are subdivided when such change is found. I will argue later that such arbitrary subdivision of single lineages is permissible for biostratigraphy, but not for biosystematics, and since the later always accompanies the former, especially with lineage-zones, both become suspect. One common problem is that lineage-zones created by one worker with his own understanding of speciation and phylogeny are frequently misunderstood by other workers with differing views. For example, subsequent workers have sometimes had difficulty recognizing exactly at what point one species changes into another, and the result has been inconsistent determinations of stratigraphic levels of biozone boundaries and other biohorizons. Unless a biostratigrapher explicitly adopts the specific evolutionary model, species concept, and
biosystematics of the original author of the lineage-zone or phyletic-biohorizon, the zone or horizon cannot be precisely located. To adopt these may appear to be a straightforward, unobjectionable task; however, it frequently is difficult to define exactly what biosystematic method and species concept is required, and even when this is known, the application of such knowledge for correlation is usually not accomplished without considerable misgiving. The truth of this will be apparent when we shortly examine some popular evolutionary models and methods of phylogenetic inference currently used for such purposes.

It is well known that different worker's differing species concept will affect their identification of index species and result in ambiguity of zonal boundary placement with concomitant loss of reliability; thus, taxonomic stability is very desirable. The analogous problem is even more pronounced for different worker's differing understanding of evolution and phylogenetic inference when lineage-zone are utilized; but there is not yet, and doesn't appear to soon be, stability in our understanding of evolution and the correct method of recognizing ancestral-descendant relationships and constructing phylogenies. There is no question that lineage-zones and phyletic-biohorizons based on evolutionary criteria allow excellent correlation when the criteria are rigidly interpreted, according to the subjectively-supplied requirements. I object to such criteria in biostratigraphy because such rigid subjective interpretation is both absolutely necessary to make the zone work and scientifically mistaken when done, because such interpretation invariably is typological, untestable, circular—in short, scientifically insupportable. This being the case, I can only state that biostratigraphy should be divorced
from any specific evolutionary theory in the same way that taxonomy should be; the goals of biostratigraphy must never be allowed to stand in the way of good biosystematics.

**Lineage-Zones and Planktonic Foraminifera**

Many examples exist to substantiate the criticisms I have made above. It will be extremely illuminating to examine the case of *Globorotalia foehsi* and the lineage-zones constructed from its inferred evolutionary history. Although many biohorizons in the standard tropical planktonic foraminiferal zonations of the Tertiary are derived from evolutionary sequences, the example of *G. foehsi* is especially appropriate because (1) it has been responsible for inferring a number of widely accepted phyletic-biohorizons that are adjacent, so that actual lineage-zones are present, and (2) the interpretation of the taxa of this lineage has been controversial, so that a number of authors have been led to explicitly state their understanding of both evolutionary taxonomy and the application of evolutionary criteria to biostratigraphy, whereas usually these beliefs are unstated and implicit.

*Globorotalia foehsi* Cushman and Ellisor, 1939, was recognized by Cushman and Stainforth (1945) as a valuable biostratigraphic index fossil. Bolli (1950) later realized that *G. foehsi* comprised an evolving series of forms which could be used to subdivide the *G. foehsi* Zone of Cushman and Stainforth (1945). Bolli divided the evolving species into four subspecies based on the gradual changes observed in a number of characters. The rounded to subrounded periphery of the test "was found to develop gradually in the course of geologic time into an acute
periphery and, still later, to acquire a peripheral keel, at first visible only on the final chambers, but later becoming circumperipheral." Another progressively changing character was the "increasing lobation of the peripheral outline, culminating in a form with a distinctly cockscomb-shaped" margin. Finally, both size and robustness of the test gradually increased, so that the "final stage of the sequence was found in a compact, robust form, quite strongly keeled...which gradually developed..." into the largest form (all quotations from Bolli, 1967, p. 502). Figure 41 from Bolli (1967, p. 505) shows the six subspecies now recognized in stratigraphic sequence of first occurrence. As explained by Bolli (1967):

The *Colborotalia foehsi* lineage is one of the most clearly demonstrated evolutionary sequences of flowing morphological changes, not only in planktonic foraminifera but in the foraminifera as a whole. To show the close relationship between the distinguishable taxa of the lineage, Bolli (1950) proposed a subspecific rank for them. (p. 507)

It was thought logical to stress the close relationship of these four stratigraphically overlapping but consecutive forms—one developing from the other with every intermediate morphological state—including them in a single species and expressing their gradually changing features as subspecies. (p. 502)

The treatment of *G. foehsi* by Bolli (1950, 1967) has been accepted by almost all other biostratigraphers who work with planktonic foraminifera. For example, Stainforth and others (1975) state the following:
All figures × 66

1 *Globorotalia fohsi peripheroronda* Blow and Banner. Line drawing made from holotype, figure 1a, plate 1, of Blow and Banner, 1966.
2 *Globorotalia fohsi peripheroacuta* Blow and Banner. Line drawing made from holotype, figure 2a, plate 1, of Blow and Banner, 1966.
3 *Globorotalia fohsi praefohsi* Blow and Banner. Line drawing made from paratype, figure 3a, plate 1, of Blow and Banner, 1966.
4 *Globorotalia fohsi foehsi* Cushman and Ellisor. Line drawing made from holotype, figure 5a, plate 1, of Blow and Banner, 1966.
5 *Globorotalia fohsi lobata* Bermúdez. Line drawing made from hypotype, figure 13a, plate 28, of Bolli, 1957.
6 *Globorotalia fohsi robusta* Bolli. Line drawing made from holotype, figure 3a, plate 15, of Bolli, 1950.

FIGURE 41. Illustrations of the *Globorotalia fohsi* subspecies. The subspecies are drawn in spiral view and are arranged from left to right in order of first stratigraphic appearance. It can be seen from the figures that although a number of gradual phylogenetic trends are apparent, the subspecies and species are nevertheless quite distinct and recognizable entities. Figure from Bolli (1967, p. 505).
The concept of evolutionary lineages is firmly accepted as a significant factor in investigation of planktonic foraminifers ...(p. 38)

The concept of evolutionary lineages is easy to comprehend, for it simply postulates an ancestral form succeeded by divergent progeny which changed gradually in one or more of their physical attributes.... The stages of development of a given lineage from primitive to advanced provide clues to their stratigraphic levels.... By efficient edification and nomenclature of successive development phases of a lineage, its evolution can be utilized for definition of a precise zonal scheme. (p. 38-39)

A pioneer case was Bolli's recognition (1950) that four seemingly distinct species of Globorotalia occur both in stratigraphic order and in a consistent morphologically intergraded sequence of forms which logically could be treated as subspecies of Globorotalia fohsi. (p. 39)

I document these authors to emphasize a single, extremely important point. Despite the fact that the subspecific forms in the *G. fohsi* single lineage are changing in a "gradually" and "flowing" way, with "every intermediate morphological stage" present, the separate subspecies are nevertheless "distinguishable," "overlapping," and could even be called "seemingly distinct species of Globorotalia." This state of affairs is clarified by referring to Figure 42 which shows the overlapping stratigraphic ranges of the *G. fohsi* subspecies and their sharply delimited levels of first occurrence. Now, I can easily accept the concept of separate, related taxa with overlapping ranges, each produced cladogenetically, and I can well understand the concept of arbitrarily subdividing a gradually evolving lineage into successive, consecutive taxa. But I frankly find the case of *G. fohsi* difficult to understand, because it seemingly involves both concepts at the same
FIGURE 42. Chart of the *Globorotalia fohsi* lineage-zones. Despite the *G. fohsi* lineage being "one of the most clearly demonstrated evolutionary sequences of flowing morphological changes" (Bolli, 1967, p. 507), the chart reveals that the subspecies are distinct entities that have rather definite and recognizable stratigraphic range boundaries. Figure from Bolli (1967, p. 506).
time. Biostratigraphers constantly refer to this example as the best case of "gradual, flowing morphological change," yet the entities within it have obviously undergone cladogenetic splitting because (1) the G. fohsi subspecies are easily distinguishable and even could be called species, (2) the first occurrence of the subspecies is relatively well defined and unambiguous (although Bolli [1967, p. 502] notes that "The gradual morphological changes between the subspecies made a distinction of boundaries somewhat arbitrary, though always within tolerable limits."), and (3) the different subspecies have overlapping ranges after their origination. These facts seem to contradict the claim that the subspecies "flow" into each other. Let me ask: What happens to the ancestral subspecies at the time when it flows into a new subspecies? Does the gradual morphologic change it has exhibited up to this point cease, and does it then remain stable for the remainder of its existence? It can not "become" the descendant subspecies by the flowing change, since it would cease to exist if this happened. Or perhaps the ancestral subspecies is morphologically stable from its first occurrence, but at the same time the descendant subspecies appears, some part of the ancestral species population (some part, since another part must exist unchanged for the ancestral subspecies to continue) begins to gradually change and flow into the new subspecies. These are the best two explanations I can think of to understand the G. fohsi lineage as it is so often pictured. I emphasize that in either case, the subspecies exhibit morphological stasis, not change, over most of their ranges, and that each descendant subspecies appears rather suddenly at the time of first occurrence. Furthermore, I can't understand if the biozonation is to remain stable and useful, how G. fohsi subspecies could be gradually
changing in a flowing manner at any time in their stratigraphic range, except possibly for a brief moment when a subpopulation is cladogenetically changing into a new descendant subspecies. In fact, I predict that when the *G. fohsi* lineage is studied in the detail it deserves, the subspecies will be discovered to have been created by cladogenesis, they will be shown to remain morphologically stable throughout their ranges, and the concept of one taxon changing into another by "flowing morphological change," except possibly in finely sampled intervals at the point of splitting, will be found to be a chimera created in the minds of planktonic foraminiferal biostratigraphers working under the cloven hoofpoint of phyletic gradualism.

The *Globorotalia fohsi* case would be a good story even if I ended here, but fortunately I don't have to. In 1966, Blow and Banner (1966) extensively revised the *G. fohsi* lineage, and later Blow (1970) used this example and others to evaluate the validity of biostratigraphic correlations based on the Globigerinacea, especially for biohorizons and biozones constructed by evolutionary criteria. These two papers and Bolli's (1967) answer to the first constitute perhaps the best example of the nonvalidity of lineage-zones, although both Blow and Bolli strongly support the concept.

Blow and Banner (1966) proposed a number of revisions necessitated by inadequate and incorrect early descriptions, re-examination of types, and nomenclatural problems. These corrections are nonproblematical and were accepted by Bolli (1967) and subsequent workers. At the same time, however, Blow and Banner (1966, p. 286) propose the "use of different biocharacters in the differential diagnoses of the various 'subspecies'"
and note that this "effectual revision of them" will affect "their biostratigraphical application." This situation unfortunately occurs in biostratigraphy which, after all, relies on described taxa for its use. I only wish to suggest that it would be an improvement if such revisions could be the result of a relatively unambiguous scientific analysis, such as cladistic taxonomy, rather than the result of differing opinions. The present example belongs to the latter case, as witnessed by the fact that none of Blow and Banner's "effectual revisions" have won acceptance in the opinion of subsequent workers. For example, Stainforth and others (1975, p. 82) state: "We prefer to follow mainly Bolli (1950, ...1967) in applying subspecies of G. foehsi to zonation, rather than Blow and Banner (1966), whose proposed revision offers little practical improvement over the existing scheme." This statement reveals a great deal about the problem I wish to examine, for not only can we see the authoritarianism present by the ability to "prefer" a certain classification, but also we have the explicit statement that the criterion of acceptance is whether a certain classification offers "practical improvement over the existing scheme." That is, whether the classification will allow more precise or reliable practical biostratigraphic application, rather than any taxonomic improvement for a more natural or stable classification. This remarkable justification for a classification's acceptance is unfortunately not an isolated occurrence, but represents the common view in biostratigraphy.

Blow and Banner (1966, p. 287) apply their "biostratigraphical subdivision in terms of the progressive development of an imperforate keel, without regard to the degree of lobulation exhibited by the last few chambers of the larger specimens." They further propose precise
distinctions between the carina (imperforate peripheral "keel"), pseudo-carina (perforate "keel" or marginal thickening), and true keel to the taxonomy of the G. fohsi lineage. On the basis of the states of this single character (the progressive development of the keel), Blow and Banner created two subgenera, four species, and two formae out of the single species G. fohsi which Bolli had previously divided into four subspecies on the basis of five characters (development of keel, degree of peripheral rounding or acuity, degree of lobation of the peripheral outline, size and robustness). I certainly do not object to creating species out of subspecies if the situation warrants; in fact, if the G. fohsi subspecies are the result of cladogenesis, as I believe, then I would indeed promote them to species. What I object to here is that Blow and Banner, solely for the purpose of "biostratigraphic subdivision," created two new subgenera and three new species on the basis of the inferred evolution of a single character. Because the "application of precise distinction" (p. 287) had to be applied to the developing keel to permit sharp demarcation between the species, the taxa are typological. Bolli is equally critical. He states (1967, p. 507):

[T]he gradual development of peripheral keels, like other forms of ornamentation, should not be used as a supraspecific criterion. The present example clearly demonstrates how unnatural it is to divide and subdivide such a short-lived, rapidly developing lineage into two different subgenera and six different species, based only on a gradually developing peripheral keel.

Blow and Banner's 1966 paper contains all that is wrong with taxonomy as it is practiced by biostratigraphers: subjective classification of taxa
into artificial and unnatural units purely for biostratigraphic utility rather than by objective taxonomic analysis, typology, arbitrary subdivision of gradually changing characters, and ignoring uniquely derived characters in preference to inferred slowly evolving ones. Bolli (1967) documents a number of other peculiarities in Blow and Banner's paper which don't concern us here.

Bolli himself is not immune from criticism, however. He makes the following concluding remark (1967, p. 511):

The division of any continuum has to be arbitrary. In the case of *Globorotalia fohsi* s.l., the present writer...proposed a division into subspecies and a zonation on their range. The scheme has proved itself practicable, as is shown in the publications of numerous other authors. Certainly, other schemes might be applied, but the only reasonable justification for a change would be either a less arbitrary basis or a more practical application, such as more uniform thicknesses of the zones.

(emphasis added)

Here we see that Bolli is perfectly willing to accept a taxonomic revision if the result increases biostratigraphic utility. He also accepts the criterion of popularity among other authors as a measure of his classification's value, but every taxonomist before cladistic taxonomy was invented did this. Proposing a new classification or revising an existing one for improved biozonational application is peculiar to the biostratigrapher, however. For example, Sylvester-Bradley (1959, p. 51) was able to claim that

the practice of giving different specific names to morphological variants which grade into each other within an assemblage drawn from a single horizon and a single geographical province...obscures genetic reality, is a disservice to the stratigrapher, and seriously confuses the evolutionary picture to which the
Thus, while criticizing horizontal typology by splitting similar taxa that lived at one time, Sylvester-Bradley is quite willing to encourage vertical typology by splitting similar taxa from different horizons to enable "finer zonal classifications." The intolerance of normal species variability is a "disservice" in one case, but "is to be commended" in the other. Surely this state of affairs can not continue to remain unchallenged.

Blow (1970) makes a last effort to promote his brand of biosystematics in biostratigraphy. He believes that observations on the evolution of some "orthogenetic" branches or lineages "seem to indicate that once a trend is initiated it goes rapidly to completion...." (p. 258). He believes that "phylogenesis...accompanied by a strongly modified autecology" may be responsible for the restricted geographic occurrences of two *G. fohsi* taxa; the ecological factors (not surprisingly!) "appear to leave much of the associated planktonic foraminiferal fauna unaffected" (p. 258). Because of the "phylogenesis" and the "modified autecology" associated with it, Blow (1970, p. 258-259) concludes that:

From this it will be seen that the end-ranges of some highly specialized, last descendant forms are highly variable in the time sense from one area to another, and that zonal boundaries based on "extinctions" of such forms are strongly suspect as to their degree of diachroneity when used for correlative purposes. It was for these
reasons that the writer rejected the "extinction horizon" of \( G. (G.) fohsi robusta \) (of Bolli, 1957a) as delimiting a zonal boundary. Thus, especially in forms which have a strongly specialized morphologic development per se and which are the end forms of progressively specialized evolutionary plexi, . . . . it is unwise to place any over-reliance on the local "extinction" horizons of such forms for correlation. . . .

Blow, for his own evolutionary reasons, is opposed to the use of extinctions as biohorizons, although he ignores the fact that the example given above has proven to be a reliable and useful biohorizon that is widely accepted after years of testing. If Blow assumes the inferiority of extinction horizons for evolutionary reasons, what zones for what reasons does he consider superior. You guessed it.

[Zones] whose nominate taxa are connected to each other by a well-defined evolutionary relationship (as expressed by a recognizable morphogenesis is through a given time interval) are more likely to be isochronous over widely separated geographical areas than zones based on local (facies controlled) exclusions which are considered as "extinction horizons." (Blow, 1970, p. 260-261)

Again, Blow assumes the quality of biozones for evolutionary reasons before they are tested by workers in the field. In actual practice, of course, any new proposed zone is assumed to be valid until demonstrated otherwise by repeated testing against other zones, in new stratigraphic sections, in new geographical regions, etc.; this practice is the only way to corroborate a zone's value and build a refined, isochronous zonation—evolutionary implications or inferences are irrelevant. Another example: Blow (1970, p. 262) harshly criticized Berggren (1969)
for mixing extinction biohorizons with origination biohorizons in a Tertiary biozonation. Of the twelve extinction horizons, Blow claimed apriori that, "in the writer's view, they should not necessarily be considered as forming isochronous surfaces for world-wide correlation...," while for the eight supraspecific first occurrence biohorizons, Blow state that "It would seem that only these eight datum planes have any reasonable degree of biostratigraphic validity; even then, care must be taken to ensure the recognition, in a stratigraphic sequence of sediments, of both the evolutionary antecedents and the descendants of the form marking the supraspecific morphological change." Such apriori assumptions are common in biostratigraphy where the evolutionary biostratigraphic argument holds sway, and is not a belief peculiar to Blow. Many of the extinction biohorizons Berggren proposed are now known to be reliable and are widely accepted today, while the opposite is true of some of the origination biohorizons. Fortunately, most of biostratigraphy is characterized by the pragmatic use of any possible and useful biohorizon without reference to assumed evolutionary appropriateness; such biohorizons are then tested against the material rock record in subsequent years by other workers. The work of Berggren with planktonic foraminifera is a prime example of this empirical school of biostratigraphy, in contrast to the example of the radiolarian biozonation we will soon examine. Although Berggren agrees with Blow about the theoretical superiority of phyletic-biohorizons and lineage-zones, he does not allow this belief to stand in the way of the construction of a pragmatic and material biozonational scheme free of apriorisms. Common sense and necessity have always led biostratigraphers to use anything that works.
Blow certainly recognizes what is perhaps the major problem in biostratigraphy: the "difficulties due to the subjective recognition of taxa" (1970, p. 261) and the effect this has on the recognition of biohorizons. He states (p. 261):

It must be apparent that one worker may have different opinions concerning the taxonomic and nomenclatorial recognition of morphologic entities as compared to other workers in the same field of specialized endeavour. To some extent, these difficulties may be reduced by clear description and illustration of the taxa involved and by a rigid adherence to the specified morphologic limits of the taxa throughout the stratigraphic record of forms. However, what is important in the application of a worker's zonal scheme by another is that other workers should be prepared to base their correlative results on the criteria used by the original author of the zonal scheme. (emphasis added)

In other words, for biostratigraphy to work with any degree of precision and accuracy, subsequent workers must be willing to adopt the typological taxa, evolutionary model, and biosystematic method of the biozonation's original author, no matter how objectionable this is in terms of ad hoc assumptions, subjectivity, and typology. I consider this situation to be deplorable and in drastic need of change. Is there a method for the non-subjective recognition and classification of taxa? Yes—cladistic taxonomy. Do taxa need to be typological in biostratigraphy? No—not if species criteria and relationships are analyzed by a testable scientific method, such as cladistic taxonomy using the evolutionary species concept. Are specific evolutionary models and methods of phylogenetic inference necessary for either the classification of taxa or the construction of biozones? No—but only
if one renounces both phylogenetically-based taxonomic systems and phylogenetically-based biozonation systems, that is, classical evolutionary taxonomy and lineage-zones (Table 5). The assumptions about evolution which necessarily accompany either system are often not testable, are uncorroborated, and are completely unnecessary for the successful scientific practice of either taxonomy or biostratigraphy.

Fortunately for us, Blow (1970, p. 264) described in detail the reasoning for his belief in the evolutionary biostratigraphic argument. Despite the fact that almost every biostratigrapher strongly believes in this argument (as documented earlier), Blow’s account is the only complete and candid description we have; the others merely state their belief and assume it is noncontroversial. Blow states:

[It] is necessary to be reasonably sure that [phylectic-biohorizons are] sensibly isochronous. In the ultimate reasoning there is no way of being able to prove the isochronity of such an evolutionary event except for absolute dating on a scale and with degree of precision which, at the present time, is not likely. It is therefore a matter of fundamental postulation that such evolutionary events are to be regarded as sensibly isochronous.

From general considerations of the palaeontological record, it can be observed that the less specialized forms are the least influenced by ecological factors. If given a reasonable degree of constancy of the environment in time, it is more likely that, over the immediate change from one palaeontologically defined taxon to another, we are dealing with a single biological entity which is completely interbreeding. In other words, although we are recognizing two palaeontological morphological taxa we are in fact dealing with a single, interbreeding, genetically plastic, biological entity. Under these conditions, and over the shore segment of the evolutionary series involved, the ecologic
factors may be considered not to act differentially on the two morphotypes. Thus, if it is possible to recognize an approximate degree of constancy in the gross environment, the short segment of the evolutionary series is very likely to be impervious to the more subtle environmental changes which affect specialized end-forms with a rigidly fixed gene pattern. It will be seen that this assumption is quite acceptable even if the morphological changes of the evolutionary series are environmentally induced, so long as the change in environment is unidirectional and not oscillatory or fluctuational.

It is suggested that once the new morphotype is established and expressed genetically by the viability and taxonomic isolation of the new form, it will quickly spread throughout the whole of the available habitat by means of population gene-flow and geographic dispersal. From this it would appear that there are sufficient theoretical grounds for assuming that many, quickly developing, non-repetitive, evolutionary first appearances are sensibly isochronous within observational limits.

I present the above quotation without editing to illustrate all of the \textit{ad hoc} assumptions and \textit{a priori} arguments necessitated to propose a single phyletic-biohorizon. Let me list them:

1. Assumes that the less specialized taxa are the least influenced by ecological factors, and that it is possible to recognize which taxa these are.

2. Assumes the constancy of the environment and that it is possible to recognize when this is the case, or failing this, that the environmental change is unidirectional and that this is determinable.

3. Assume the species population is a single biological entity which is completely interbreeding.
4. Assumes that the segment of the evolutionary series which is undergoing change is short.

5. Assumes that the ecologic factors will not act differently on the ancestral and descendant taxa.

6. Assumes that the short evolutionary segment is very likely to be impervious to environmental changes (and thus its isochroneity is not affected by environmental influences).

7. Assumes that specialized taxa at the end of lineages have rigidly fixed gene patterns (and thus their isochroneity is affected by environmental influences).

8. Assumes that the descendant taxon will quickly spread throughout the whole of the available range by gene-flow and geographic dispersal, and thus its first occurrence in the stratigraphic record is extremely isochronous.

Not only are all of these apriori assumptions uncorroborated, many are untestable, idiosyncratic, and just plain absurd. For example, in No. 5, if environmental factors were not operating differently on the ancestor and descendant taxa, why did they split in the first place? Was there some inner, vitalistic force which cause the differentiation, totally independent of the environment? In No. 7, is it possible for any taxon to have a "rigidly fixed gene pattern?" Of course not! But the most important point I can make about these eight theoretical evolutionary assumptions is that all are topics which need to be investigated, not assumed apriori to justify phyletic-biohorizons and lineage-zones. All of these ecological and evolutionary assumptions are simply unnecessary and irrelevant to biostratigraphy, for any biohorizon or biozone can be proposed without any ad hoc evolutionary theoretical
baggage, simply by defining the zonal criteria in materialistic terms without evolutionary overtones. These range-zones or interval-zones are then tested and either are successful or are discarded. Because of the untestable, aprioristic, and unwarranted theoretical evolutionary assumptions which necessarily accompany their use, lineage-zones and phyletic-biohorizons are theoretically invalid.

As a final, illuminating example, Blow (1970, p. 261) advocates the "Globigerinoides datum" as the base of the Miocene (as do most other biostratigraphers) because the "datum-plane is in fact based on the development of Globigerinoides quadrilobatus primordius from its ancestral Globigerina praebulloides occlusa..." Neglecting the fact that Blow has no difficulty in inferring the descent of one subspecies from another in a different genus, the denouement appears in an excellent paper by Lamb and Stainforth (1976), who demonstrate the unreliability of the Globigerinoides datum because it is undoubtedly diachronous. Their remarkable conclusions follows (p. 1567-1568):

For pragmatic purposes this outcome is a disappointment, depriving stratigraphers of a seemingly simple criterion for separating Neogene from Paleogene. Perhaps more deeply significant than the pragmatic aspects is demonstration of diachronity of a simply evolutionary event. Biostratigraphers in general regard the steps in evolving lineages as direct keys to chronostratigraphic correlation. Many of the datum levels used in planktonic foraminiferal zonation of the Tertiary are derived from evolutionary sequences. It is salutary to observe that exceptions may arise.

Indeed it is salutary. Science has often been defined as common sense rigorously applied, and it is heartening to note that common sense prevailed in this case. Hopefully, this definition of science will
spread throughout the biostratigraphic and micropaleontologic communities, and we will see the end of lineage-zones and phyletic-biohorizons.
Lineage-Zones and Radiolaria

The previous section documented and criticized the frequent use of evolutionary theory in the construction of planktonic foraminiferal biohorizons and biozones. This practice was found to be invalid because (1) it inevitably requires the choice of a specific evolutionary model, and invariably phyletic gradualism is chosen, (2) it always requires a typological species concept to ensure precise species distinctions for biostratigraphic utility, and (3) it necessitates choice of a method of phylogenetic inference which must be primarily authoritarian in nature, since there is at present no scientific method available. I earlier documented the pervasive acceptance of phyletic gradualism among biostratigraphers and micropaleontologists, while pointing out that this evolutionary model may be wrong and definitely remains to be tested and corroborated. I do not need to give the arguments against typology, since these are presumably so well known, but I did document its admittedly frequent occurrence in micropaleontologic biostratigraphy. Biostratigraphers have never been inhibited about inferring ancestral-descendant relationships, identifying extended lineages, and constructing phylogenies, but the method they have chosen to do this relies upon "seeing evolution in the rocks" and makes use primarily of stratigraphic data to link morphologically-similar taxa into plausible schemes. The acceptance of anyone's plausible scheme in the scientific community invariably rests on the authority of the author and frequently upon its biostratigraphic appropriateness. A rigorous biosystematic analysis, with proper regard for hidden assumptions and the limits of
the empirical data, is usually never undertaken. Character states and their transformations, which cannot be analyzed apart from evolutionary theory, are frequently taken and inserted arbitrarily into lineage-zones.

The above criticisms are fairly leveled at all paleontological taxonomists, of course, not just biostratigraphers. The situation in biostratigraphy is particularly unfortunate, however, because it need never have arose: phyletic-biohorizons and lineage-zones are simply unnecessary for practical and optimum performance of biozonational systems. The entire biostratigraphic system of our planet could be constructed solely with empirically-defined range-zones and interval-zones free of all theoretical evolutionary implications and assumptions. This being the case, why do biostratigraphers persist in indentifying fossil lineages and using them to define phyletic-biohorizons and lineage-zones? Because of their universal and explicit belief in the evolutionary biostratigraphic argument which I have characterized as being invalid because of its hidden assumptions and erroneous arbitrary apriorisms.

This study has presented the argument for adopting an evolutionary species definition, for using cladistic analysis as the method of biosystematic inference, and for eschewing all models of evolution (even a punctuational model) as inapppropriate from a scientific methodic viewpoint and unnecessary from a practical standpoint. Finally, the case for abandoning the practice of lineage-zone and phyletic-biohorizon construction has been expressed repeatedly. Lest any reader remain unconvinced about the validity of my arguments, we will examine a last example in detail which, I hope, will serve to seal forever the bottle
containing the insidious imp of non-science in micropaleontology and biostratigraphy. We will examine an important planktonic microfossil biozonation whose authors have deliberately searched for evolutionary transitions between taxa and wherever possible used these to define phyletic-biohorizons and lineage-zones. They explicitly adopt a typological species definition, an evolutionary model of phyletic gradualism, and the use of stratigraphic data to justify the final lineage interpretation and biological classification. The phyletic-biohorizons in the zonation are explicitly defined in terms of the gradual evolution of one species into another. Here we surely will realize, beyond any doubt, that "validity of such a zonation depends entirely on an author's subjective interpretation of evolutionary processes" (Stainforth and others, 1975, p. 46), for this zonation works, in practice, only by adopting the extreme views of the zonation's authors; any subsequent worker who has different and more acceptable views about species variability and the evolutionary process will have difficulty reproducing the zonal boundary levels in different sections or even in the type sections. This difficulty has, in fact, occurred with resultant misunderstanding and confusion, and the proposed ad hoc "solutions" to this problem have only made it worse. For these reasons, such a biozonation made up of phyletic-biohorizons and lineage-zones is invalid form practical biostratigraphic standpoint as well as a thecretical evolutionary standpoint.

The standard tropical Cenozoic radiolarian zonation is one of the three most important planktonic microfossil biozonations, the other two being those for tropical planktonic foraminifera and calcareous
nannofossils. All three make use of the excellent complete and continuous pelagic sedimentary sequences available in DSDP cores and piston cores. The radiolarian zonation was first proposed and subsequently refined primarily by two people, W. R. Riedel and A. Sanfilippo, in papers published between 1970 and 1978, although other workers have contributed to its revision in minor ways. The theory and practice of this zonation will provide the primary example and evidence supporting the arguments in this study.

In 1959, Riedel (1959, p. 289) figured a "suggested phyletic sequence" of a group of raiolarians known today as the artiscins (sub-family Artiscinae). As inferred from the text of the paper, Riedel used both mophologic and stratigraphic data to diagram "a possible evolutionary sequence of these related forms" (p. 292). In Riedel's paper, he suggested that the sequence implies a gradual change in a number of features, but that each species is nevertheless distinct. In 1970, with some of the first DSDP samples, Riedel and Sanfilippo (1970, p. 536-537) recognized a number of evolutionary lineages. They state that the "recognition of such phylogenetic series" permits the construction of a taxonomic system which "more closely reflects natural relationships" and provides "a more reliable basis for the zonation and correlation of radiolarian sequences than would be provided by cryptogenetic species." Thus we have the first indication of the authors' belief in the evolutionary biostratigraphic argument. By 1971, the DSDP had provided enough long sequences of radiolarian sediments from the Atlantic and Pacific Oceans for Riedel and Sanfilippo (1971a) to state the following:
It is not particularly difficult to correlate Cenozoic sediment columns from widely separated localities, because the sequence of changes in the radiolarian assemblages show few differences from one region to another.

A number of evolutionary lineages have been established, by tracing morphologic changes through time. Generally, ancestor-descendant relationships are unambiguous, because there are no unrelated forms with confusingly similar morphology co-occurring. Evolutionary change in the radiolarians evidently occurred as a continuum, not step-wise. The course of morphologic change in an evolutionary succession is often linear, i.e. it can be described in a few simple terms such as "decrease in size of the spongy columns, with concomitant growth of the polar caps" (in the Cannartus-Ommatartus lineage), or "increase in size of abdomen and its pores relative to the thorax" (in the subgenus Lampterum), etc. The highest degree of biostratigraphic resolution can be attained by describing these continua of morphologic change, rather than by dividing the lineages arbitrarily into species. Many extinct lineages terminated in "bizarre" forms, with morphologic charaters unusual for radiolarians.

Although the last sentence of this passage won't become meaningful until later in our discussion, it is obvious that by 1971 the widespread sequences of changes in radiolarian lineages were being interpreted as phyletic gradualism, i.e. gradual evolutionary change from one species to the next in an extended lineage. Furthermore, because of the excellent stratigraphic record and the reoccurrence of the same pattern in dozens of deep-sea cores, "ancestor-descendant relationships are unambiguous." (The statement about losing biostratigraphic resolution by arbitrarily subdividing these morphologic "continua" into species is anomalous, since this is exactly what Riedel and Sanfilippo did.) The beliefs expressed in this 1971 abstract serve to guide radiolarian taxonomy and biostratigraphy to this day.
I have remarked on a number of previous occasions that the explicit use of phyletic-biohorizons and lineage-zones, while universally acknowledged among biostratigraphers as desirable, is relatively rare because unambiguous evolutionary transitions are not that common. In the case of radiolarians, however, the situation is different (for the explicit use of evolutionary-based biohorizons and biozones, because I shall show that evolutionary transitions in radiolarians are not as unambiguous as some individuals may believe). Riedel and Sanfilippo (1971b, p. 1530) made phyletic gradualism the explicit justification for one type of biohorizon in their biozonation. They defined the stratigraphic limits of species in "two fundamentally different ways," which they termed "morphotypic" and "evolutionary." "Morphotypic limits must be used when the evolutionary development of a species is not known, whereas when the phylogeny is known evolutionary limits may be applied." Now, one may suspect that in almost every case the two types of limits would coincide, especially when the stratigraphic record is so complete and continuous. Not so! Because they had explicitly adopted phyletic gradualism as their evolutionary model, Riedel and Sanfilippo state:

To explain the difference between these two types of limits, Figure 1 illustrates the situation faced by a paleontologist who wishes to divide a series of continuously evolving forms (A → B → C → D → E) into five species. In the tabulation of these successively younger forms in a series of successively younger assemblages, C indicates "common," F "few" and R "rare." The evolutionary change from A to E is clearly indicated by the drift of the C's across the tabulation from lower left to upper right. Morphological characters change continuously with time, and intraspecific variation is such
that the dominant form in any assemblage is accompanied by fewer specimens morphologically identical with its ancestor(s) and descendant(s). The ranges of the morphotypes are long, and overlap one another to considerable extent.

It would be possible to define the five morphotypes as separate species, but it seems more "biologically correct" to classify each population rather than each specimen, and to define the species in such a way that their ranges are contiguous but not overlapping. This requires a statistical definition of the range of variation of the morphological characters, and the resulting limits of the time-ranges of species are of the type here termed "evolutionary". In those cases in which we have plotted the upper or lower limit of a species as "evolutionary"..., we have used the level at which more than half of the individual in the population have the character(s) that distinguishes the species from its ancestor or descendant.

Their Figure 1 is reproduced here in Figure 43. Surely there can be no clearer representation of phyletic gradualism than this, whereby every successive species in an extended lineage evolves into the next by phyletic transition (anagenetic "speciation"). Their desire to make their taxonomic inference more "biologically correct" is salutary, but I question whether they have succeeded. Not only are they forcing evolving species it a gradualistic straightjacket, but they must arbitrarily limit the ancestor from the descendant by choosing the level at which the two morphotypes occur in equal numbers. Thus Riedel and Sanfilippo reject the more common criterion of subdividing a gradually changing lineage into successional species by choosing the level at which the morphological difference between them is as least as great as the sequential difference between related or similar contemporaneous
These two diagrams illustrate the "evolutionary limit" concept of Riedel and Sanfilippo. The upper chart, from Riedel and Sanfilippo (1971, p. 1531), shows how the "morphotype ranges" of fossil species are arbitrarily subdivided into "species" with "evolutionary ranges" on the basis of the morphotype abundance in samples. The authors note that "it would be possible to define the five morphotypes as separate species," but because "morphological characters change continuously with time," the authors claim that "it seems more 'biologically correct' to classify each population rather than each species, and to define the species in such a way that their ranges are contiguous but not overlapping." The authors' criterion for distinguishing each species is "the level at which more than half of the individuals in the population have the character(s) that distinguish the species from its ancestor or descendant" (Riedel and Sanfilippo, 1971, p. 1530). The lower diagram, from Sanfilippo and Riedel (1973, p. 479), illustrates the same concept. The rightmost trend shows how each lanceolate morphotype is arbitrarily subdivided into "species" at the point in geologic time when the descendant morphotype occurs in equal abundance to the ancestor morphotype. The dashed line designated "e" is an "evolutionary limit" according to this concept. "Morphotypic limits" are used only when there is a "lack of knowledge" about the evolutionary relationships of the taxa.
<table>
<thead>
<tr>
<th>Successively younger samples</th>
<th>Successively younger forms</th>
<th>Morphotype Ranges</th>
<th>Evolutionary Ranges</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spl. 11</td>
<td>A</td>
<td>B</td>
<td>C</td>
</tr>
<tr>
<td>Spl. 10</td>
<td>R</td>
<td>F</td>
<td>C</td>
</tr>
<tr>
<td>Spl. 9</td>
<td>R</td>
<td>C</td>
<td>F</td>
</tr>
<tr>
<td>Spl. 8</td>
<td>F</td>
<td>C</td>
<td>F</td>
</tr>
<tr>
<td>Spl. 7</td>
<td>R</td>
<td>F</td>
<td>C</td>
</tr>
<tr>
<td>Spl. 6</td>
<td>R</td>
<td>C</td>
<td>F</td>
</tr>
<tr>
<td>Spl. 5</td>
<td>R</td>
<td>C</td>
<td>F</td>
</tr>
<tr>
<td>Spl. 4</td>
<td>R</td>
<td>F</td>
<td>C</td>
</tr>
<tr>
<td>Spl. 3</td>
<td>R</td>
<td>C</td>
<td>F</td>
</tr>
<tr>
<td>Spl. 2</td>
<td>F</td>
<td>C</td>
<td>F</td>
</tr>
<tr>
<td>Spl. 1</td>
<td>C</td>
<td>F</td>
<td></td>
</tr>
</tbody>
</table>

The diagram on the right illustrates the relationship between time and morphological change.
These two diagrams reveal Riedel and Sanfilippo's belief in (1) the dominance of phyletic gradualism and the non-occurrence of punctuated speciation (2) the irrelevance of both cladogenesis and recognizing apomorphic characters (3) the desirability of choosing gradually-changing plesiomorphic characters for species designation (4) the desirability of arbitrarily and typologically dividing a continuous single lineage--on the basis of one anagenetic character--so as to create contiguous, non-overlapping "species" useful for biostratigraphic purposes and (5) the willingness to use morphotype abundance in a sample ("population size") as a criterion of actual evolutionary change in the population. Criticism of all of these beliefs is found in the text.
species. But note why they can do this: At the time of the inferred evolutionary transition (which they designate an "evolutionary limit" for biostratigraphic purposes), two morphotypes exist. One might suspect that the morphotypes should be called species, but Riedel and Sanfilippo believe it more "biologically correct" to recognize ancestors and descendants and draw the actual species boundary at the 50%-50% abundance level of each morphotype. This means that at any one time, each "species" consists of two or more morphotypes together in the species population.

By including what they considered to be natural intraspecific variation in each identified evolutionary species by this method, Riedel and Sanfilippo recognized dozens of "evolutionary limits" of index species in their biozonation. Suspicion may arise, however, when we contemplate the fact that the "morphologic ranges" have rather sharp upper and lower boundaries, in contrast to the "evolutionary ranges" whose boundaries extend over tens of thousands of years and must be arbitrarily determined, and that many more "morphotypic limits" were used in the biozonation than "evolutionary limits." Could it be, for example, that the morphotypes are species, relatively stable in geologic time in a manner similar to the stability species exhibit today, and that the gradual phyletic evolutionary transition between ancestor and descendant which Riedel and Sanfilippo believe they see actually consists of two similar separate species (perhaps ancestor and descendant or perhaps not) whose ranges overlap and whose relative numbers change through time as the "descendant" becomes more abundant than the "ancestor?" Could it be that the 50%-50% relative abundance
level has nothing to do with evolution, but quite a bit to do with population ecology or competitive exclusion? Could it be that the assumption of phyletic gradualism as the process of evolution and the need to recognize ancestors and descendants for biostratigraphic application has colored the authors' perception of reality? When we examined the criteria used for discriminating between the "evolving species," we find that usually one character—which sometimes exhibits phyletic evolution, but sometimes not—is used to determine the level of equal abundance of the morphotypes. Other characters, including many uniquely derived characters (autapomorphous characters), are ignored. In a desire to avoid ignoring intraspecific variation in their "evolving species" by an idiosyncratic model, Riedel and Sanfilippo typologically restrict the intraspecific variation in the morphotypic species by arbitrarily limiting its expression and ignoring autapomorphies. But the most important observation to make is that in their method all morphotypes are recognized as species when the ancestor and descendant are not known, but when genealogical relationships are inferred, the morphotypes are not species, but different and varying forms within "evolving species." I know of no other more arbitrary and less valid species distinction than this in the taxonomic literature.

In 1973, Sanfilippo and Riedel (1973, p. 477) revised their biohorizon concept by subdividing their "morphotypic limit":

A significant difference between the presentation of the radiolarian results here and for Leg 7 (Riedel and Sanfilippo, 1971) is in the recognition of a third type of stratigraphic limit of a radiolarian taxon. In the earlier report, we distinguished between morphotypic limits (m-for taxa whose ancestors and/or
descendants are not known, and for the lower limits of taxa known to have evolved from an ancestor that ranges upward for a considerable time beyond the origin of the descendant) and evolutionary limits (e-for extinctions at the terminations of evolutionary lineages, and points of arbitrary subdivision of continuous evolutionary lineages in which the ancestor does not long persist together with the descendant). It now seems desirable to separate as morphotypic-evolutionary (m-e) the second type of limit formerly included under the term morphotypic—namely, the lower limit of a taxon known to have evolved from an ancestor that ranges upward for a considerable time beyond the origin of the descendant. This morphotypic-evolutionary type of limit may be expected to have greater reliability for purposes of stratigraphic correlation than the cryptogenetic limits to which the term morphotypic is now restricted. Figure 4 illustrates the three types of limits distinguished in this chapter.

Application of the concept expressed by the new term morphotypic-evolutionary will not involve a change in the time-significance of such an event, which was formerly termed simply morphotypic. However, when a cryptogenetic event (formerly termed morphotypic) can as a result of later work be recognized as part of an evolutionary lineage with little overlap between ancestral and descendant morphotypes, and is thus replaced by an evolutionary limit, its time-significance...will in most cases be changed.

Their Figure 4 is reproduced here in Figure 43. By revising their biohorizon concept they admit that the time-significance of a number of inferred limits is changed. More important is the logic behind their changes. In 1973, they claim that what they wish to recognize as a "morphotypic-evolutionary" limit was in 1971 included under the "morphotypic limit," but they had never stated this in 1971. Apparently, they now wish to identify even more evolutionary
originations than they had in the past by creating them from previously recognized "morphotypic" first occurrences by recognizing ancestors. The unstated reason for this is, of course, the anticipated greater biostratigraphic reliability of such a phyletic-biohorizon. A second anomaly is their altered definition for the "evolutionary limit" in 1973, which they change without explanation. In 1971, they explicitly stated that the evolutionary limit marked a sharp, arbitrary level where the ancestral and descendant morphotypes shifted their relative abundance. The ranges of the morphotypes are long, and "overlap one another to a considerable extent" (1971). On the other hand, the actual "evolving species" had sharp, non-overlapping ranges by definition. Yet in 1973, the authors state that at the "points of arbitrary subdivision of continuous evolutionary lineages...the ancestor does not long persist together with the descendant." Now, whether they consider either the morphotypes or the "evolving species" in 1971 as the ancestor and descendant in 1973, the 1973 definition of "evolutionary limit" is contradictory and confusing. To make matters even more confusing, the upper limit of a taxon's range which begins with a morphotypic-evolutionary limit is defined in 1973 to be an evolutionary limit, despite the fact that this upper limit terminates with no descendants to continue the lineage. This limit, in my opinion, should be a morphotypic limit, since "no descendant is known." But because the lineage is an "evolutionary lineage," its upper limit must be an "evolutionary limit" and not a morphotypic limit. But Sanfilippo and Riedel never discuss why a lineage which has morphotypic limits is a non-evolutionary lineage. Simply because no ancestor or descendant is
known does not make the lineage non-evolutionary. Obviously, there must have been an ancestor, and there may have been one or more descendants that have not yet been discovered. In point of fact, every lineage is "evolutionary." A lineage is a single ancestral-descendant temporal sequence, regardless of whether any phenetic change has occurred, and regardless of whether the lineage terminated with or without descendants. Its limits may be defined as morphotypic if no ancestor or descendant is known (despite the fact that there must have been an ancestor) or as evolutionary if ancestors or descendants are known, but a limit cannot be defined as evolutionary because the lineage is an "evolutionary lineage," as Sanfilippo and Riedel have done.

They may have reasoned that because the lineage has an evolutionary lower limit (more precisely, a morphotypic-evolutionary lower limit), it must have an evolutionary upper limit (despite the fact no descendant is known). I cannot follow this line of reasoning, for it seems to me necessary to be consistent if one is to make arbitrary definitions of lineage limits, and being "evolutionary" is no excuse for a lineage to receive special treatment, for every lineage is "evolutionary."

It should be obvious by now that Riedel and Sanfilippo's biohorizon definitions are neither internally nor historically consistent. They are, in fact, arbitrary and *ad hoc* definitions designed to serve the purpose of their own radiolarian studies. This in itself is not critical, since Riedel and Sanfilippo always document their studies in excellent fashion by providing all of the empirical taxonomic, range, and abundance data from their DSDP samples. Other researchers are free to use this primary data for their own studies without having to adopt
the idiosyncratic terminology and evolutionary implications which accompanies them. Unfortunately, Riedel and Sanfilippo have built the standard tropical Tertiary radiolarian zonation from both this data and their remarkable inferences about the evolutionary process, so other students of microfossils must perforce adopt the same standards if they wish to use or understand the biozonation.

To perform the radiolarian biostratigraphy on DSDP Leg 30, Holdsworth (1975) adopted the biohorizon criteria of Riedel and Sanfilippo which are necessary to use their zonation. Holdsworth states (p. 511):

> Where morphologic affinities between two taxa are such as to suggest that an ancestor-descendant relationship exists, the level at which the apparent descendant first becomes more abundant than the ancestral morphotype is considered to [be] the level of "evolutionary transition" (Riedel and Sanfilippo, 1971) and is indicated by an arrow.

One of the important biohorizons in the radiolarian zonation is the evolutionary transition of *Ommatartus antepenultimus* to *O. penultimus* which occurs within the *O. penultimus* zone as now defined. Holdsworth could not find this transition at the stratigraphic level it should occur due to difficulty in species discrimination. He states (1975, p. 522)"

> Differentiation of this species morphotype from the later *O. antepenultimus* morphotype is virtually impossible, in the writer's experience, at levels where, according to earlier accounts, the evolutionary transition from *O. antepenultimus* to *O. penultimus* should
occur. The difficulty has probably led to rather widely differing interpretations of the O. penultimus Zone in previous reports. In this account the name "O. penultimus" has been restricted to specimens in which the caps are distinctly inflated and in which at least one cap is roughly as large or larger than half the cortical shell.

The two species exhibit a great deal of variability as O. antepenultimus supposedly changes slowly into O. penultimus. Here we have an excellent example of the situation where two similar but distinct morphotypes overlap each other's stratigraphic range to a considerable degree, so that the actual species boundary (and phyletic-biohorizon) must be drawn at the level where the two morphotypes occur in equal abundance. Westberg and Riedel take Holdsworth to task for his uncertainty and his willingness to make a subjective arbitrary distinction which differs from the original arbitrary distinction. They state (Westberg and Riedel, 1978, p. 8):

A...kind of taxonomic imprecision is illustrated by the upper evolutionary limit of Ommatartus antepenultimus. Riedel and Funnell (1964, p. 311) restricted the definition of O. penultimus to include only forms in which "the polar caps are at least as large, and as well separated from the cortical shell as those of the holotype" (Riedel, 1957, pl. 1, fig. 1). The proportion of the height of the polar caps to length of cortical shell in the holotype is 0.25. However, during the course of work on DSDF sequences, the concept of the limit between O. penultimus and O. antepenultimus drifted to the extent that specimens were not assigned to O. penultimus unless at least one polar cap was 0.5 the size of the cortical shell (Holdsworth, in Andrews et al., 1975, p. 522). In the present work, we have used as a limit between these two species a ratio of polar cap height to shell length of 0.25, which essentially conforms to the original definition.
The passage in Riedel and Funnell (1964, p. 311) states:

"[The species *Ommatartus penultimus*] is restricted to those forms in which the polar caps are at least as large, and as well separated from the cortical shell, as those of the holotype.

This is typology, pure and simple. Typology occurs whenever a species' range of variation in time or space is arbitrarily circumscribed or limited by subjective criteria for the purpose of taxonomic clarity or precision. As pointed out earlier, typology is implicit in much of biostratigraphy by the need for narrow taxonomic limits to preserve biostratigraphic utility. However, the emphasis on the holotype, as indulged in by Riedel in 1964 and 1978, is particularly notorious (Schopf, 1960, p. 1043). As Schopf emphasizes, the holotype is nothing more than a namebearer, and does not represent any "typical" form of the species. Simpson (1940, 1961) was especially forthright in criticizing this desultory practice. Schopf concludes:

Pre-Darwinian "typology" with implications harking back to fixity of species and special creation, is frequently involved with a "typical" concept of "type." Emphasis on description of the holotype, rather than on the concept of a species population, does not seem likely to improve our means of classifying organisms or in understanding other essential aspects of biologic problems.

It is well to point out that this example of typology is not an isolated occurrence. Westberg and Riedel (1978, p. 8) "more precisely" define the morphologic limits of *Artostroblum doliolum*, which originally was described as having a maximum width of 75-100 mm. This range of
variation was found to be "unsatisfactory in application" to distinguish this species from its "immediate ancestor," so they redefine it to have a minimum third stricture width of 65 mm. No doubt the "unsatisfactory application" involved difficulty in biostratigraphic interpretation. In fact, Westberg and Riedel (1978, p. 7) state that:

Radiolarian species described during...the early stages of the stratigraphic utilization of radiolarians...were not delimited with the precision now required. The limits of many stratigraphically important species have recently been redefined (Riedel and Sanfilippo, 1978) to satisfy present needs, but there will always be species requiring still more precise delimitation, as the needs of stratigraphy become more demanding.

In other words, species will be made increasingly more typological to improve their biostratigraphic utility. They believe that fossil species are only narrowly-defined biostratigraphic markers, not living organisms with an evolutionary history that must be interpreted by a testable, repeatable, and non-arbitrary scientific method before classification is pursued.

For a further example of the lengths to which some biostratigraphers will go to utilize their subjective understanding of the evolutionary process in biostratigraphic application, we may examine Westberg and Riedel's (1978, pl. 8-11, Table 8, Figures 4-8) exercise in the sub-division of an important evolutionary lineage. They state (p. 8):

In at least some evolutionary lineages of radiolarians, morphologic change appears to have occurred continuously, not step-wise, and consequently the dividing lines between species have been placed arbitrarily along the continuum. Theoretically, therefore, it should
be possible to subdivide these lineages into a greater number of smaller units, provided only that the gradual morphological changes would be described more precisely. The larger number of species resulting from this would permit finer subdivision of sediment sequences, and consequently increased biostratigraphic resolution.

The authors measure the gradual morphologic change in *Ommatartus antepenultimus*, specifically the ratio of polar cap height to cortical shell length. As with many other radiolarian species used in the standard zonation, the "upper and lower evolutionary limits of this species have been defined on the basis of a single character, in this case the height of the polar caps, which has increased through time" (Westerg and Riedel, 1978, p. 8-9). In the four cores for which they present data, there is not the slightest doubt that the ratio gradually changes through time at a constant rate, that the change is relatively consistent over a wide geographic region, and that measurement and calculation of this ratio can serve as an excellent biostratigraphic indicator for this brief period of geologic time. These results are straightforward and acceptable; my objections lie elsewhere.

The upper "evolutionary limit" of *O. antepenultimus* is at the cap height/shell length ratio of 0.25 (as described earlier), while the lower evolutionary limit is at 0.20. The inferred evolutionary transitions of *Camnartus laticornus* to *O. antepenultimus* and of *O. antepenultimus* to *O. penultimus* are two important phyletic-biohorizons in the radiolarian zonation, so sharp arbitrary subdivision of the phyletic trend of the single character of cap height is necessary for biostratigraphic utility. In fact, the authors are willing to go
further: "It seems clear from this data that *O. antepenultimus* could be divided into two stratigraphically useful species..., one with polar caps larger than 0.225 cortical shell length and the other with lower caps..." (p. 9). This explicit statement of the authors' idiosyncratic taxonomic philosophy is remarkable enough, but even more remarkable is the fact that in the data tables of radiolarian occurrences of the four sites from which the evolutionary ratio data were obtained, the species *O. antepenultimus* and *O. penultimus* overlap to a considerable degree. Furthermore, if we check the occurrence data tables in all the DSDP site reports, including those of Riedel and Sanfilippo, we find the same thing: the stratigraphic ranges of all the identified ancestral-descendant species pairs overlap one another to a significant degree, yet the "evolutionary limit" or boundary between them is placed approximately midway in the zone of overlap, so that this level marks the "true" boundary of each "species." This means that, in Riedel's practice, radiolarian species are identified by empirical morphological criteria and are listed as species in range charts for DSDP sites, yet are not considered to be species for the purpose of identifying evolutionary species for biostratigraphy. In biozones, the morphotypic species, which have relatively sharp upper and lower limits and which persist relatively unchanged throughout their range (although some species do exhibit anagenesis or phyletic evolution in certain characters), are considered by Riedel to be "morphotypes" and have "morphotype ranges," while the true, "biologically correct" species are those which are inferred and subdivided from "continuous evolutionary lineages" made up of the morphotypes, with arbitrary upper and lower
"evolutionary limits" placed in the middle of morphotype overlap, so that each true radiolarian "species" has a true "evolutionary range." Therefore, depending on the circumstances, a radiolarian biostratigrapher can call whatever he wants a "species," and know that in either case, morphotypic or evolutionary, he can justify it by a set of theoretical, "biologically correct" criteria. Can such equivocation be called "science?" The justification for these incredible evolutionary and taxonomic distortions is biostratigraphic utility, a justification which is totally unnecessary, since biostratigraphy doesn't need these distortions to work successfully.

Let's examine the *O. antepenultimus* example of Westberg and Riedel more closely. The means of the cap height/shell length ratio measurements are plotted against time. From this data, we can distinguish between two cases:

1. The gradual evolutionary change by phyletic evolution and phyletic transition of *Cannartus laticonus* to *O. antepenultimus* to *O. penultimus*, such that this continuously evolving lineage must be arbitrarily subdivided to introduce species limits.

2. The ecological replacement in time of successively appearing species with overlapping ranges, each species speciating by cladogenesis and continuing unchanged throughout its range, yet the population size of each and its representation in the community does change as the later or descendant species displaces the earlier or ancestral species.
Westberg and Riedel clearly support the first interpretation—this is the only one they give. But what does one make of their range charts, which clearly illustrate the overlapping ranges of all three of the species they measured? Which of the two different species boundaries do they wish us to believe: the typological evolutionary limits or the empirical morphological limits? In this paper and all his others, Riedel has accepted the typological evolutionary limits as the true limits, and he has made this a major feature of his biozonation. If Westberg and Riedel had provided information about the range and standard deviation of each of the samples, we could easily judge between the two interpretations. If the range extends far from the mean and the standard deviation is large, the second interpretation would be the better, and we could discover if Westberg and Riedel have let their expectation of phyletic gradualism distort their interpretation of nature. Also, we must not forget that Riedel's evolutionary interpretations in this case and many others is based on the evaluation of one anagenetically evolving character which he typologically chose to base his species determinations. Other characters, including apomorphies, are ignored.

It might be argued at this point that biostratigraphers are only interested in nomenclature—not taxonomy—and are only interested in evolutionary change—not biosystematics. Their goal is biostratigraphic application, not studying evolutionary processes and patterns or in discovering underlying regularities in evolution that could improve our understanding of biology and paleontology. All this might be true, but it provides no excuse for publishing one's evolutionary idiosyncracies
in the scientific literature and classifying species on that basis and for biostratigraphic utility. A number of petroleum companies proceed in a laudatory manner by classifying fossil genera by their own typological system in which the taxa are only used for company studies, and are never published in the open literature. Often in such a system, for example, a new species is identified to genus and then numbered. Since only a few individuals perform the work for any fossil group with a major company, questions about species limits are quickly resolved and there are never any problems in taxonomic identification. Of course, one result of this system is that much paleontologically-valuable information, often obtained at great expense and effort, is not made available to science; but the greater advantage remains that the immense amount of extra work involved to search the literature, research synonymies, and perfect one's taxonomic expertise is avoided, and taxonomy is saved from having to tolerate subjective or typological species determinations and classifications. Whenever fossil species are described and classified, whether they are useful for biostratigraphy or not, the taxonomist has the responsibility to use an acceptable method of biosystematic analysis and classification, and to avoid hidden assumptions and unwarranted beliefs which affect the scientific value of the work. Until a consensus is reached among biostratigraphers and paleontologists about the classification of fossils, the species used in biozonations will continue to be typological and contradictory. I encourage the abandonment of lineage-zones and phyletic-biohorizons as the first step to improve the situation. Surely this recommendation has merit. I further advocate the adoption of an evolutionary species
concept and a cladistic method of biosystematic analysis and classification, since these are the least subjective and most scientific of the available systems. Evolutionary theory is not yet understood well enough to permit constructing classifications on phylogeny or basing biostratigraphical concepts on it. Biostratigraphy is a science and a tool that we will use to investigate the evolutionary processes and patterns we see in the fossil record, and it is inadvisable to assume the correctness of any evolutionary process or pattern for biostratigraphic utility. The search for gradual anagenetic changes in the fossil record should be continued, but any occurrence of phyletic evolution should not immediately allow one to assume the truth of phyletic gradualism and construct entire biozonational systems upon this assumption. Other workers may not want to accept the evolutionary criteria which support such a system. Only in an orthodoxy are people obliged to accept the subjective interpretations of the authorities. Science is not an orthodoxy. We must seek to become scientists, not high priests.
Critique of Idiosyncratic Evolutionary Theory in Radiolarian Taxonomy and Biostratigraphy

Riedel and Sanfilippo (1978) present the standard tropical Cenozoic radiolarian zonation in revised and up-to-date summary form (Figure 44). Of the 26 zonal boundaries, twelve are phyletic-biohorizons and fourteen are first and last occurrence biohorizons (morphologic tops and bottoms). The zonation contains many other phyletic-biohorizons within biozones, some of which were once zonal boundaries, but now are not. Two of these in particular are revealing. The lower limit of the Ommatartus penultimus Zone used to be the evolutionary transition from O. antepenultimus to O. penultimus, but this has been changed because "the level of transition from one species to another is difficult to determine" (p. 63). For the Ommatartus antepenultimus Zone, "the use of the evolutionary transition from Cannartus laticonus to Ommatartus antepenultimus to define the lower limit of this zone was unsatisfactory because of the difficulty in determining whether a terminal cap was present and large enough" (p. 63). Thus, the upper and lower evolutionary limits of O. antepenultimus were removed from zonal boundary status because other workers were having a difficult time determining the stratigraphic level. This should tell us something about ad hoc evolutionary criteria used to define practical biohorizons.

Another peculiarity of the paper by Riedel and Sanfilippo (1978) is that the authors assert that their biozones are in fact chronozones. They define their zones "as the interval of time between two events..." (p. 61). This is truly a remarkable claim, not only because it violates
FIGURE 44. The tropical Cenozoic radiolarian biozonation of Riedel and Sanfilippo (1978). The arrows indicate phyletic-biohorizons recognized by "evolutionary transition."
the International Stratigraphic Guide (Hedberg, 1976) written by the International Subcommission on Stratigraphic Classification (ISSC), but also because Riedel and Sanfilippo justify their action by stating that they are following ISSC terminology! The authors state (p. 63):

The lack of a requirement that certain species must be present in an assemblage before it can be assigned to a zone means that none of the ISSC terminology for biostratigraphic zones is here applicable, and that chronostratigraphic terms are appropriate.

While it is true that the radiolarian biozones contain non-boundary biohorizons that permit their recognition in sequences where some of the zonal boundary species are absent, the zones are nevertheless defined as interval-zones and fit the Guide's requirements perfectly. I honestly cannot understand the reasoning behind the "lack of a requirement" invalidating the zones as biozones, and chronostratigraphic terms are far from "appropriate." Chronostratigraphic units are bodies of rock strata which are unified by being the rocks formed during a specific interval of geologic time (Hedberg, 1976, p. 67), and to use radiolarians to define chronozones, Riedel and Sanfilippo must assume that radiolarian biohorizons are isochronous and that radiolarians can be used in all Cenozoic rocks over the world, neither of which is true. The authors impart both an undemonstrated time significance and an impossible applicability to radiolarians by claiming that their zonation contains chronozones.

Riedel and Sanfilippo (1978, p. 61) state that: "In examining the stratigraphically useful species and their phyletic relationships, information has been gained on the course of radiolarian evolution." In
a wonderful little book, Flew (1976) documents the easy path from identifying a trend, to asserting a tendency, to finally establishing a law of development. We frequently do this unconsciously in all spheres of activity, including science. Close behind this process is something called the Naturalistic Fallacy—believing what is, ought to be. But the question of immediate concern is not this, but rather why we think we know what the laws of the evolutionary process are. If a paleontologist sees "trends" every working day of his life (a situation in which most paleontologists, fortunately or unfortunately, do not find themselves), is he not led to believe that such a phenomenon is actually an evolutionary "tendency?" And if this surely is an evolutionary tendency, then he must certainly have discovered a law of evolutionary development. I must admit that only radiolarian biostratigraphers see "trends" (valid or not) every day of their working careers, and they and their planktonic foraminiferal colleagues have never failed to assert the existency of an evolutionary tendency which manifests itself in the creation of continuous, gradually-changing single-lineages and extended-lineages among planktonic microfossils. This being the case, might we someday expect the revelation of a new evolutionary law or principal that explains the origin of the tendency and all the trends? The day has arrived, but unfortunately it is sixty years too late.

In their discussion of radiolarian evolution, Riedel and Sanfilippo (p. 84) state that "it seems possible to distinguish two different kinds of evolutionary change which need to be described in different terms."
The first is simple rectilinear morphologic change characterized by its undeviating trend, continuous (not step-wise) change, and constant rate. The second is an unusual type of morphologic change characterized by independent tendencies which appear and disappear in different combination at different times, as if the lineage contains a great deal of plasticity and variation which express themselves in no regular pattern. Although I will not dwell on this fact here, Riedel and Sanfilippo ignore a third type of evolutionary change which is by far the most common and most important in all the samples they examined: creation of new species by cladogenesis and persistence of the species as relatively stable entities through time.

Riedel and Sanfilippo (1978, p. 84-86) state:

It has been possible to recognize a number of natural genera or subgenera, each comprising an evolutionary lineage undergoing morphologic change proceeding along a simple direction for a long period of time, in which the morphologic change appears to have occurred continuously, not step-wise, and at a constant rate (or acceleration) as far as can at present be determined.... [M]any of the lineages which are extinct terminate in forms with very unusual ("bizarre") morphologies....

The characteristics outlined above of these monophyletic lineages suggest that their evolution may be "inertial," the tendency for a change being established within the organism, and not influenced (except perhaps at the initiation of the lineage, and certainly at its termination) by the forces of natural selection. This inertial evolution, postulated by Von Nageli (1884) and Doderlein (1887) and named "orthogenesis" by Haacke (1893), has long been anathema to Darwinists, although a few paleontologists continued to consider it a useful hypothesis (see Summary by Rensch, 1959, p. 204 et seq.) It seems to us quite possible that the orthogenesis is manifested by the radiolarians (simple organisms with practically
no power of directional movement, internal skeletons, presenting to the environment a subspherical surface with radiating pseudopods, and inhabiting the relatively unvarying environment of the upper few hundred meters of the tropical oceanic waters), whereas the process is likely to be obscured in larger, more complex organisms living in more complex and less stable environments, where the effects of natural selection are predominant. Whether or not it will prove correct that these lineages exhibit a kind of evolution different from (and supplementary to) that guided by natural selection, this hypothesis provides a practically satisfactory perspective from which to view and describe these long, simple continuous lineages.

Let me ask: How will it be possible to "prove correct" the existence of orthogenesis and non-effect of natural selection? Do the authors believe that cataloging presumed instances of phyletic trends in the fossil record will eventually "prove," by the force of inductive logic, that orthogenesis occurs? The authors illustrate one such example, the gradual increase in numbers of pores on circumference of the abdomen in the Podocystis (Lampterygium) lineage. Their figure shows the inferred gradual change of P. chalara to P. mitra to P. sinuosa by arbitrarily subdivided phyletic transition. This presumed orthogenetic trend contains one sample each of P. chalara and P. sinuosa at the beginning and end of the trend, while the five samples containing P. mitra exhibit phyletic evolution of this one character. P. chalara and P. sinuosa are quite different from P. mitra in a number of distinct characters, and it is a gross misrepresentation to imply that this lineage serves as an example of an orthogenetic trend in an extended lineage. Because the three species are different in a number of characters, a better explanation is that each was produced by cladogenesis, one character of
P. mitra anagenetically evolved, and the possibility of plotting the pore abundance on a single line is an unimportant coincidence. Certainly no orthogenesis, or even ancestral–descendant relationship, can be inferred from this example; Riedel and Sanfilippo do so only because they are working under a cloven hoofprint of theory which leads them to interpret any superficial lineage as phyletic gradualism or orthogenesis.

Riedel and Sanfilippo's concept of "bizarre" forms of radiolarians at the ends of lineages is another manifestation of the psychologism they wish to impose upon science. There is no such thing as a "bizarre" radiolarian in scientific terms. The concept of "bizarreness" is a subjective interpretation of presumed nonadaptation because the fossil appears odd to the investigator and because the fossil occurs at the end of an extended lineage the investigator knows will soon end in holoextinction. This is reasoning by hindsight: because the form became extinct, it must have lost adaption, and something must have caused its loss of adaption, the something being its odd or bizarre morphology produced by unidirectional evolutionary change carried to inadaptive lengths by evolutionary momentum or "inertia." Thus, "bizarreness" is inferred by (1) the location of the fossil species near the termination of a lineage and (2) the assumption of an orthogenetic evolutionary model, not by any objective or scientific method which examines the morphology of the fossil. The claim that the morphology alone leads to the recognition of bizarreness is scientifically invalid, since such a recognition, by itself, is nothing more than personal nontestable opinion.
Riedel and Sanfilippo believe in the process of hypertely, the notion that orthogenetic evolutionary change propels the taxon past the point of adaption so that extinction ensues. Both orthogenesis and hypertely are claimed to be caused by some unknown antichance and antiselection orienting factor that is inherent in the organism and predetermines its future. This idea is known as vitalism (or finalism), and its adoption is a prerequisite for any orthogenetic or hypertelic explanation. As Riedel and Sanfilippo understand quite well, vitalism and orthogenesis have a long history in science as an evolutionary explanation opposed to natural selection. However, they apparently don't understand why vitalism and orthogenesis have been discarded by scientists, and why all evolutionary explanations today are presented in the context of natural selection. Simpson (1949, 1953) and Rensch (1959) both adequately disposed of these unscientific concepts by their careful arguments. Riedel and Sanfilippo's reference of Rensch (1959, p. 204 et seq.) as a summary of the views of paleontologists who support the hypothesis of orthogenesis is ironic, because Rensch quotes them only to demonstrate the theoretical and empirical paucity of their views. Confusion may arise, however, in that Rensch uses the term "orthogenetic" to mean only unidirectional, as in an "orthogenetic trend," without the additional vitalistic sense of an inherent predetermined tendency or urge for evolution to continue in a given direction. Nevertheless, Rensch is quite clear about both his opposition to inertial inner-directed tendencies and his decided preference for natural selection as the correct hypothesis for explaining unidirectional trends.
As Simpson (1953, p. 275) points out, there is a reasonable explanation for the appearance of inadaptive characters in organisms: correlated change. It is possible that strong selection for one character leading to adaptive change may cause nonadaptive or inadaptive changes in an unselected correlated character (correlation of characters is by gene association, allometry, functional association, etc.). However, adaptiveness or its absence is not the problem here, since the "bizarre" radiolarians, which Riedel and Sanfilippo believe were so poorly adaptive to cause holoextinction of their lineage, nevertheless lived for millions of years. The problem is the explanation for the unidirectional phyletic and phylogenetic trends which do exist in radiolarians. Although not nearly as common as Riedel and Sanfilippo believe, phyletic evolution exhibited by radiolarians is a fact. Furthermore, it is possible to plot characters of inferred extended lineages to produce phylogenetic trends; how advisable this is, is another question. Riedel and Sanfilippo's implication of nonadaptation has no validity, but their hypothesis of orthogenesis as an explanation for simple straight-line evolution requires further examination.

Straightaway, we can state that biosystematics and evolutionary biology or paleontology have no adequate or conclusive explanation for the unidirectional phyletic and phylogenetic trends we see in the fossil record. These are phenomena which are currently under intense examination by myself and other paleobiologists; the theory which allows us to understand such trends simply is not yet available. Furthermore, the existence of an internal predetermining vitalistic tendency in organisms has never been disproven. Why, therefore, is not orthogenesis a legitimate explanation for the phenomena we observe. The fact that
something **could** exist does not justify the conclusion or belief that it **does** exist. While science must take many possibilities into account and cannot dogmatically reject anything possible, this does not mean that every possibility **must** be considered by science. Science restricts its possibilities to the material universe and investigates events, processes, and objects that are natural and susceptible to logical testing by empirical observation and mechanistic explanation. Specifically, science does not consider possibilities which deal with supernatural, idealistic, or vitalistic phenomena, since these concepts are not subject to empirical testing and material explanation. The belief or acceptance of these phenomena are certainly permitted in our world, but not in science. Orthogenesis as an evolutionary hypothesis falls into this category, since mysterious and unknown vitalistic phenomena **must** be invoked to make orthogenesis work. Thus, orthogenesis fails as an adequate explanation not because it is necessarily wrong, but because it isn’t scientific. Let me make clear the point that there **could** be a vitalistic inner urge or tendency within living organisms that affects their evolution. But the hypothesis of such a tendency, vitalistic or otherwise, within organisms will not be scientifically acceptable until it is expressed in natural and material terms that permit empirical observation and testing.

Riedel and Sanfilippo’s inability to provide a material and natural description of how the process of orthogenesis operates leads them to resort to some **ad hoc** arguments which they believe supports their hypothesis. They argue that unicellular organisms, being so much less complex than metazoans, will react in less complex ways to environmental and selection pressures, thus permitting orthogenesis to manifest itself
in radiolarians when it is so obviously absent or "obscured" in more complex organisms, which are more affected by natural selection. This wonderfully ad hoc argument is easily refuted when we consider that protozoans have increased in intracellular complexity to a far greater degree than metazoans. To call protozoans "simple organisms" is a misnomer. They relate to their environment by occupying niches in every way comparable in subtlety and complexity to extracellularly-complex metazoans. Certainly, the same environmental factors affect both protozoans and metazoans. Riedel and Sanfilippo further argue that the pelagic (planktonic) environment is uniform, simple, stable, etc., and that this contrasts to the benthonic or terrestrial environments which are more complex, variable, etc. This is not strictly true. The planktonic environment is certainly not very variable with regard to physical and chemical factors, but biologically it is quite complex, much more so that other environments where physical and chemical factors (temperature, altitude, salinity, etc.) are the limiting or controlling factors. Thus, the planktonic environment is the ideal place to study biological interactions, since other environmental factors are so limited, and biological factors would be obscured in more typical benthic and terrestrial environments. We know the pelagic environment is biologically complex because so many different species live there. The competitive exclusion principle, that no two species can occupy the same niche, applies to the plankton as well as to other organisms, and the "paradox of the plankton" (which is their relatively high species diversity in a seemingly uniform environment) has been largely dispelled by theoretical studies which demonstrate the complex biological interactions which affect plankton. Furthermore, plankton display a
distinct patchiness when detailed sampling studies are performed. The patchiness further suggests complex biological interactions in a complex environment.

It is clear that the hypothesis of orthogenesis, like the hypothesis of universal recapitulation (Gould, 1977) and many other formerly widely held scientific theories, was never disproven as such; rather, the hypothesis was quietly discarded by the last generation of scientists because of the growing realization that it conflicted with scientific method as well as scientific theory. However, in the same way that each generation of citizens must relearn the fact that freedom is not a right, but must be possessed by constant effort and diligence, each generation of scientists must relearn the structure of science and scientific method. In the case of evolution, the current generation is dangerously close to forgetting these things. Witness the acceptance of the pseudoscientific concept of "scientific creationism" among a small number of scientists. Even more to the point, what does one make of the following passage from Kling (1978, p. 224) in the excellent textbook Introduction to Marine Micropaleontology (Haq and Boersma, 1978):

[Many extinct lineages tend to end in very unusual ("bizarre") forms.... These traits suggested to Riedel and Sanfilippo an "inertial" kind of evolution, in which trends are "established within the organism, and not influenced (except perhaps at the initiation of the lineage, and certainly at its termination) by the forces of natural selection." This, they pointed out, is unlike Darwinian natural selection, but perhaps a reasonable hypothesis for these fairly simple organisms living in relatively stable tropical environments.]
Thus, Riedel's orthogenetic, hypertelic, vitalistic doctrine has now appeared in a student textbook. Another such example is an otherwise excellent review paper on oceanic micropaleontology, in which the authors Berger and Roth (1975, p. 584) state that radiolarian lineages often "end in 'bizarre' forms with very unusual morphologies, a sequence that is highly intriguing from an evolutionary standpoint." To support this statement they reference the papers of Riedel and Sanfilippo. I would not object to either of these two quoted passages if they were based on testable scientific theory and a reasonable interpretation of the empirical evidence. But they are not, and I believe that such uncritical citations in the secondary scientific literature are detrimental to the scientific endeavor.

To conclude this chapter, in which I had a number of adversely critical comments about the work of some of my micropaleontologist colleagues, let me state that I do not claim to possess answers to the questions about phyletic and phylogenetic evolution which their work originally raised. In the Forward to Rensch's 1959 book on the synthetic theory of evolution, Theodosius Dobzhansky pointed out that the theory of evolution is not now complete except for some emendation. He stated that "radical changes and major upsets are not only possible but almost certain to occur." Such changes in evolutionary theory are occurring today. For example, how do we explain phyletic and phylogenetic trends? The classic explanation has always been orthoselection, environmental selection continuing to operate in a given direction for a long time. Most modern evolution textbooks, such as Grant (1977), Dobzhansky and others (1977), and Stanley (1979), continue to accept this process as readily as did Simpson (1953). Orthoselection
is a microevolutionary process which directly explains phyletic trends, and assuming that microevolutionary processes can be directly extrapolated to explain macroevolutionary phenomena, orthoselection also explains phylogenetic trends. But today we no longer wish to make the unwarranted assumption that macroevolution is a simple extrapolation of microevolution; there may be uniquely macroevolutionary process, such as differential species survival (species selection), that will only be visible and testable in the fossil record in geologic time. For these reasons, Eldredge (1978, p. 132) considers orthoselection to be a "fantasy," at least as a macroevolutionary process. But further problems remain. The philosophical claim that natural selection is untestable has led to its defense by scientists who have demonstrated its testability on the genetic level. But are the concepts of orthoselection and species selection testable on the macroevolutionary levels with reference to the fossil record? Never before have paleontologists been faced with such major challenges as presented by our new ideas and understanding about the evolutionary process. I believe that the empirical work of Riedel and Sanfilippo, however much one may disagree with their interpretations, is extremely valuable and will provide significant data and insight for further evolutionary studies. This is true for all such micropaleontologic biostratigraphic data: The DSDP volumes and petroleum company files are waiting to be tapped.
SUMMARY OF MAJOR CONCLUSIONS

1. A cladistic analysis is the best method of investigating taxa, including fossil taxa, for classification purposes. However, if the occurrence of anagenesis (phyletic evolution) in the fossil taxa is suspected or known, a complete biosystematic analysis will have to begin with the construction of stratophenograms if the quality of the fossil and stratigraphic records permit. This will allow the investigator to recognize gradually-changing plesiomorphic characters and eliminate them from the cladistic analysis.

2. A complete biosystematic analysis proceeds from a cladogeny to a type 1 genealogy, type 2 genealogy, phylogeny, and scenario. Each step attempts to synthesize and present increasingly larger amounts of data about the taxa, but each step also requires greater assumptions about the reasonableness of the data. A cladogram makes no assumptions about any particular theory of evolution, the quality of the fossil record, or the identity of ancestors. Genealogic trees and phylograms typically require assumptions about these things. Stratophenograms and type 2 genealogic trees are combined to construct rigorous phylograms, but stratophenograms may also be used to help construct cladograms by helping to distinguish apomorphic and plesiomorphic characters.

3. Although a cladogenetic analysis is sufficient for taxonomy, it is frequently necessary to perform genealogic and phylogenetic analyses in addition to help test hypotheses about evolutionary processes, patterns, and products. These three analyses, plus a

324
stratophenetic analysis, constitute a complete biosystematic analysis. Cladistic taxonomists should not ignore the higher levels of biosystematic analysis because of perceived untestability or irrelevance, for the higher levels have their proper and necessary uses. In particular, it is vital that we investigate the assumptions and testability of the steps leading from a cladistic analysis to a type 1 genealogy, to a type 2 genealogy, and finally to a phylogeny. Such theoretical investigations are in the realm of a more advanced and refined biosystematic analysis.

4. A cladogram is not plotted on a time scale; a type 1 genealogy is plotted on an ordinal time scale; a type 2 genealogy is plotted on an ordinal or interval time scale; a phylogram is plotted on an interval or ratio time scale.

5. The evolutionary species concept is redefined to make explicit its identity as a single lineage and its origin as a result of a splitting (cladogenetic) event.

6. Three types of lineages (fractional, single, and extended) are defined and used in this study. Also, three types of extinction are defined (pseudoextinction, orthoextinction, and holoextinction). These new terms and their distinction are vital for a better scientific understanding of phyletic and phylogenetic evolutionary processes and patterns.

7. The evolutionary taxonomic practice of arbitrarily delimiting the vertical anagenetic change of an evolving single lineage to produce sharply-bounded paleospecies or chronospecies is just as typological as arbitrarily delimiting the horizontal geographic
variation of an evolving population to produce a sharply-bounded
taxonomic species.

8. A new species and its phenetic characteristics may be more heavily
indebted to the anagenesis which proceeded or succeeded its origin
than to the cladogenesis which created it.

9. Apomorphic characters include new discrete (discontinuous)
characters and punctuated continuous characters, while
plesiomorphic characters include anagenetic continuous characters
and stasisgenetic characters.

10. A biosystematic analysis reveals that the three artiscin species
Cannartus laticomus, Ommatartus antepenultimus, and O. penultimus
are really forms of a single evolving lineage, the evolutionary
species O. penultimus, O. tetrathalamus, O. petterssoni, O.
hughesi, O. violina, and O. prismaticus are also valid evolutionary
species (not paleospecies or chronospecies). All the species can
be distinguished by discrete, discontinuous apomorphic characters
that do not gradually change through time in an evolutionary trend.

11. Two continuous characters in the O. penultimus artiscin lineage
exhibit good phyletic evolutinary change through most of the 7 m.y.
study interval. These are the spongy column width and polar cap
length. In this lineage, anagenesis is the dominant evolutionary
process. Also, this microevolutionary change influences the
characteristics of the two cladese which split from the penultimus
clade; thus, microevolution can control macroevolution.

12. Although judging the relative amounts of anagenesis, cladogenesis
and stasigenesis in an evolving clade, lineage, or taxon is not
straightforward, it appears that the two artiscin lineages exhibit
all three types of evolutionary patterns in approximately equal amounts. Therefore, there is no reason to prefer a punctuated model over a gradualistic model for this subfamily. However, the Radiolaria as a whole definitely do exhibit more stasis and punctuation than anagenesis, so a model of punctuated equilibria is better supported than a model of phyletic gradualism for radiolarians.

13. The columnar caps of *O. petterssoni* and *O. hughesi* are not homologous with the polar caps of *O. penultimus* and *O. tetrathalamus*. The former grow out of the polar column and the latter out of the cortical shell. Also, *O. hughesi* is better recognized by the possession of a porous column, rather than by the possession of increasing numbers of columnar caps, since this latter character is a gradual plesiomorphic character caused by anagenetic evolution from the spongy column of *O. petterssoni*.

14. It is biosystematically improper to search for plesiomorphies to use to typologically subdivide gradually changing single lineages for biostratigraphic utility. By this method, apomorphies are ignored, polyphyletic and paraphyletic taxa are created, and species become notoriously typological and therefore unnatural.

15. It is well known that index fossils are often typological, since this increases their biostratigraphic utility. Allowing index species to exhibit a normal amount of both horizontal and vertical variation would reduce a biozonation's value. However, what is good for biostratigraphy is not necessarily good for biosystematics, especially if unnatural taxa are created.
16. Lineage-zones and phyletic-biohorizons are not theoretically valid because to be used they must invoke specific evolutionary models and methods of genealogic and phylogenetic inference. However, such models of evolution and biosystematic methods must not be assumed, since they themselves are subjects of scientific investigation. In fact, biostratigraphy is increasingly being called upon to help test such evolutionary and biosystematic hypotheses, and it would be circular reasoning to have any biozonational scheme used in such testing to be heavily indebted for its usefulness upon the very hypotheses it is testing.

17. Lineage-zones and phyletic-biohorizons, which are used extensively in the standard tropical Cenozoic radiolarian biozonation, should be revised to empirical morphologic or taxonomic zones without any invocation of evolutionary models or methods of phylogenetic inference, including ancestor/descendant recognition. This revision will greatly increase the biozonation's accuracy, precision, and usefulness.
REFERENCES


R. B. Masterson, W. Hodos, and H. Jerison, eds., Evolution, brain
Cambridge.
and mode of evolution reconsidered. Paleobiology, 3: 115-151.
418 p.
and A. Boersma, eds., Introduction to marine micropaleontology.
Elsevier, New York.
Haq, B. U., and A. Boersma, 1978. Introduction to marine
Lethaia, 8: 1-14.
1205 p.
97-116.


Kellogg, D. E., 1980. Character displacement and phyletic change in the
evolution of the radiolarian subfamily Artisciniae.

Kellogg, D. E., and J. D. Hays, 1975. Microevolutionary patterns in


A. Boersma, eds., Introduction to marine micropaleontology.
Elsevier, New York.

Lamb, J. L. and R. M. Stainforth, 1976. Unreliability of
1564-1569.

evolution: punctuated or gradual? Geol. Soc. Am. Abstracts with
programs, 11(7): 464.

Mamet and B. J. Copeland, eds., Third North American paleontological


Malmgren, B. A., and J. P. Kennett, 1980. Phyletic gradualism in a Late
Cenozoic planktonic foraminiferal bioseries: DSDP, southwest


Phylogenetic analysis and paleontology. Columbia Univ. Press, New 
York.

Wiley, E. O., 1980. Is the evolutionary species fiction? A 
consideration of classes, individuals, and historical entities. 

Wiley, E. O., 1981. Phylogenetics, the theory and practice of 
