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Kurt D. Spearing

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by

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ABSTRACT

PHYLOGENETIC ANALYSIS OF THE RHABDOMESINE BRYOZOANS

By

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The Bryozoan suborder Rhabdomesina is a diverse group of Paleozoic invertebrates that have a well understood morphology, and are well represented in most stratigraphic divisions from the Arenigan to the Dzulfian. There have been several prior attempts to uncover the evolutionary history of the group, but none have been conclusive.

This phylogenetic study used groupings of rhabdomesine genera from several sources as a basis for the list of taxa, and the character lists were adapted mostly from the Treatise on Invertebrate Paleontology volume G (revised). This information was used to create a data matrix which then was entered into the PAUP and MacClade phylogenetic software packages. There were several runs of the data, differing by various removal of characters or taxa in attempts to lessen the effect of missing data. The data was also examined both with and without use of a stratigraphic character.

This study found that there are several groups of genera that cluster together consistently, but there are still many areas of uncertainly. There is a general two clade grouping that separates most arthrostylids from most other rhabdomesines. This is consistent with previous studies that divided the group into a rhabdomesine clade and put the arthrostylids into another clade grouped with the fenestrates, and shows a possible polyphyletic origin for the suborder.

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INTRODUCTION

The rhabdomesine suborder of bryozoans is a diverse group of generally slender, cylindrical, dendroid bryozoans that are found in Paleozoic marine sediments worldwide. Their morphology is well understood, and the size of the suborder (approximately 67 genera) made them a workable choice for phylogenetic analysis. They range in age from the Tremadocian (early Ordovician) to the Dzulfian (late Permian). This long time interval makes possible the inclusion of a large number of stratigraphic divisions for data entry in a cladistic study. Stratigraphic data have not been utilized in other cladistic studies specifically directed at rhabdomesines, and only one cladistic study (Blake and Snyder, 1987) has tried to deal with the rhabdomesine suborder on the generic level. Previous attempts to resolve the phylogeny of the rhabdomesines have not been conclusive. Blake and Snyder (1987) could not resolve the evolutionary history of the rhabdomesines using cladistic methods, although they claimed some success with phenetic techniques. They only were able to get satisfactory cladistic resolution when they ran the data in small blocks (14-21 genera). When the whole suborder was included in the analysis they claimed some broad consistencies between the many trees generated, but the overall results were inconclusive, with many equally parsimonious trees generated. Based upon analysis of family level taxa, the suborder Rhabdomesina was found by Anstey and Pachut (1995) to be either (1) a paraphyletic sister group to the fenestrates (their fig. 8.2), or (2) a partly monophyletic (four families) and partly polyphyletic group (5 families belonging to the fenestrates) (their figs. 8.2, 8.8). The

Order Cryptostomata, which conventionally includes the rhabdomesines, fenestrates, and ptilodictyines (Blake, 1983b), has been questioned as a clade; earlier results indicate that it might be monophyletic (Anstey and Pachut, 1995, fig. 8.2 and 8.8), polyphyletic (Anstey and Pachut, 1995, fig. 8.3), or paraphyletic (Anstey 1990). Systematists have recognized the affinities of the suborder in diverse ways: some hypotheses have considered the rhabdomesines to be a sister group to the ptilodictyines (Cuffey, 1973; Cuffey and Blake, 1991), whereas Anstey and Pachut (1995) found them to be, in part, a sister group to the fenestrates, and in part a member of that group. There are morphological convergences between some rhabdomesines and some trepostomes (Blake, 1980; Schulga-Nesterenko et. al., 1972), particularly with the trepostome Suborder Amplexoporina, and Dzik (1992; 1994) even claimed that the rhabdomesines may be trepostomes. Other cladistic results indicate the possible transfer of the families Arthrostylidae and Hyphasmoporidae from the rhabdomesines to the fenestrates (Anstey and Pachut, 1995). Anstey and Pachut (1995) also showed that when the rhabdomesine families Rhabdomesidae and Bactroporidae were added into an analysis where they had previously been absent, the cryptostome clade was "destroyed" due to the shifting of convergent character states from terminal to basal branches, the net result being the disjunction of the rhabdomesines and the ptilodictyines. The rhabdomesines are a diverse suborder in need of further phylogenetic analysis to address a variety of hypotheses concerning their interrelationships and evolutionary history.

Other than paleontologists, few systematists have considered stratigraphic data useful in evaluating phylogeny (Fisher, 1994). The rhabdomesines should benefit from the inclusion of geochronological data in a cladistic analysis, which would be an important ordering tool in comparing alternative phylogenies, and could provide an independent test of the branching order within cladograms (Huelsenbeck, 1994; Fisher, 1994). A cladistic study has the potential to resolve issues concerning the systematics, patterns of descent, rates of evolution, and macroevolutionary patterns displayed by this group. Some of these issues include: the validity of the current familial structure (taxonomy of the group) (Blake, 1983a); questions concerning ancestry and descent, and the effects of mass extinction, radiation, convergence, parallelism, evolutionary reversals, and heterochrony. Answers to many of these questions may present themselves, but the main purpose here will be on a refined tree definition and taxonomic conclusions based on the best supported trees that are generated. This choice was made because once clearer resolution is achieved, the tree structure of the group will be the major key in answering other questions.

METHODS

To examine the phylogeny of the rhabdomesines two primary computer software packages were used. The Phylogenetic Analysis Using Parsimony (PAUP) version 3.1.1 (Swofford, 1993) computer software was the main tool in this study, along with MacCLADE 3.0 (Maddison, and Maddison, 1992), another cladistics program, which is very useful for close examination and study of the trees that PAUP generates.

In this study I have used published descriptions and photographs to determine a list of characters displaying derived states in my operational taxonomic units (OTU's); these states are either nominal (0,1) or ordinal (0,1,2,3, etc.) in nature, based upon qualitative differences or multistate morphoclines. Character states were then polarized [evolutionary direction of a character transformation series from ancestral to derived (Mayr 1991)] by stratigraphic position. Primitive states, polarized by the oldest occurring state, were coded as 0 in the characters that can be clearly polarized and ordered; in cases lacking clear-cut criteria I simply left the characters in an unpolarized and unordered state (see Appendix 1). The main factor in the decisions concerning polarization and ordering was a consensus based upon the character states of the genera of the first two stages of the Ordovician (Tremadocian and Arenigian). Characters that did not seem to have clearly defined transitions between the older and younger taxa were treated as unordered characters, which means their states were coded arbitrarily and the software allowed for any state to change to any other state (example 1-2, 2-3, 3-1), as opposed to ordered states where the changes had to occur in a specific order (example 1-2-3). The geochronological character that I used was listed as an irreversible character, which is not only an ordered character, but one in which changes can only happen in one direction (for example 1-2, 2-3, but not 2-1, 3-2). This was done because that was the only way to introduce geological time in PAUP 3.1.1. The MacClade program has a stratigraphic character, but since most of the processing was done in PAUP, the irreversible method was more practical. To determine the base of the tree I decided to root it by either using the oldest known genus that is recognized as part of the suborder, namely *Arthroclema*, or by using all of the taxa that are in the two oldest stratigraphic units (up to seven genera are known from the Tremadocian and Arenigian), the final analyses used the second method, stratigraphic ranges of the genera in this study are listed on Table 1.

The OTU's in my study are the genera of the suborder. To decide which genera to include in the rhabdomesines I used lists of genera from several sources including: the Suborder Rhabdomesina in the Treatise on Invertebrate Paleontology (vol. G revised) (Blake, 1983), the group as defined by Dzik (1992, 1994), and the genera listed on the stratigraphic charts in Ross (1996). Where possible, I used the type species description and photographs to determine character states; however some genera had only partial descriptions so other sources had to be used. Some genera also were left out of some of the final studies due to problems in obtaining complete character state data; the most common reason for exclusion was that only silicified remains were known, which usually resulted in the preservation of only external character states (see results). From the various lists I included as many genera as possible from all sources, ending up with as many as 67 OTU's, which is a much higher number than used by any previous author (between 39 and 58 depending upon taxonomic treatment). Once the characters were coded (see Table 2 and Appendix 1), the PAUP and MacClade programs were executed.

Final runs of the PAUP 3.1.1 program included several variations based upon the exclusion of characters and taxa with respect to the missing data (see Table 3). These include: the full matrix (Table 2), the matrix minus the characters with missing data, the matrix minus the taxa with missing data, and the matrix minus the taxa with more than

TABLE 1: STRATIGRAPHIC RANGES OF THE GENERA IN THIS STUDY

Arthrostylus			2	3	4	5	6								
Arthroclema	0	1	2	3	4										
Arthrostyloecia		1	2	3	4										
Cuneatopora			2	3		5	6								
Glauconomella				3	4	5	6								
Heloclema											10				
Helopora			2	3	4	5	6	7	8	9					
Heminematopora		1	2	3	4										
Hemiulrichostylus			2	3											
Hexites											10				
Moyerella						5									
Nematopora			2	3	4	5	6	7	8	9	10	11	12		
Osburnostylus			2	3											
Pseudonematopora											10				
Sceptropora			2	3	4	5	6								
Tropidopora									8						
Ulrichostylus			2	3	4										
Rhabdomeson									8	9	10	11	12	13	14
Ascopora										9					
Mediopora										9	10				
Nemataxis								7	8						
Nickelsopora										9	10			13	14
Orthopora						5	6	7	8	9					
Trematella								7	8						
Rhombopora										9	10				
Klaucena											10		12	13	14
Megacanthopora										9	10	11	12	13	
Pamirella											10				
Primorella												11		13	14
Saffordotaxis											10	11		13	14
Bactropora				3					8		10				
Nikiforovella									8	9	10	11	12	13	
Acanthoclema								7	8						
Pinegopora															14
Streblotrypella								7		9	10	11			14
Hyphasmopora											10			13	14
Ogbinopora											10			13	14
Streblotrypa											10	11	12	13	14
Petaloporella									8						
Streblascopora											10	11		13	14
Maychella														13	14
Callocladia											10			13	14
Streblocladia														13	
Euthyrombopora											10				
Coelotubulipora											10				
Taeniodictya						5	6				10				
Heliotrypa											10				
Goldfussitrypa		1	2	3											
Nematotrypa			2	3	4										
Ottoseetaxis			2												
Mongoclema									8	9					
Linotaxis										9					
Clausotrypa													12	13	14
Nematoporella					4										
Arthrotrypa					4										
Europora											10				
Hyalotoechus										9					
Spira											10				
Kielcepora			2												
Ralfinella			2												
Ojlepora		1													
Kielanopora				3											
Enallopora			2												
Parachasmatopora			2												
Alwynopora		1													
Pseudohornera		1													
Pesnastylus							6								
	Tremadocian	Arenigian	Llanvernian	Caradocian	Ashgillian	L Silurian	U Silurian	L Devonian	M Devonian	U Devonian	L Carboniferous	M Carboniferous	U Carboniferous	L Permian	U Permian
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14

TABLE 2: DATA MATRIX

TAXON	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39
Arthrostylus	0	0	1	0	0	0	0	1	0	0	0	0	0	2	0	0	0	1	0	0	0	1	5	1	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Arthroclema	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Arthrostyloecia	0	0	0	0	0	0	0	0	0	0	?	0	0	1	0	0	0	1	0	0	0	0	5	1	?	0	0	0	0	0	0	0	?	?	?	?	?	?	?
Cuneatopora	1	1	0	1	0	0	0	0	1	0	0	1	0	2	0	1	1	0	0	0	1	1	2	1	6	0	0	0	0	1	0	0	0	0	0	0	0	1	0
Glauconomella	0	0	0	0	0	0	0	0	0	1	0	0	0	3	0	0	0	0	1	0	1	0	5	1	5	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Heloclema	0	0	1	1	0	0	0	0	0	1	0	1	3	A	0	0	0	1	0	0	1	1	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Helopora	1	1	0	1	0	0	0	0	1	0	1	1	0	2	0	1	1	0	0	0	1	1	0	0	4	0	1	0	0	0	0	0	0	0	0	1	0	0	0
Heminematopora	0	0	0	0	0	0	0	0	0	1	?	0	0	1	0	0	0	1	0	0	0	0	5	1	?	0	0	0	0	0	0	0	?	?	?	?	?	?	?
Hemiulrichostylus	0	0	0	0	0	0	0	0	0	1	?	0	0	2	0	0	0	0	0	0	0	0	5	1	?	0	0	0	0	0	0	0	?	?	?	?	?	?	?
Hexites	0	0	0	0	0	0	0	0	0	1	2	1	3	A	0	0	0	1	0	0	0	0	6	1	4	0	0	0	0	0	0	1	0	0	0	1	0	0	0
Moyerella	1	2	1	1	0	0	0	0	0	0	0	1	1	5	0	1	1	0	0	0	0	1	1	1	6	0	0	1	0	0	0	0	0	0	0	0	0	1	0
Nematopora	0	0	1	0	0	0	0	1	0	0	0	1	0	2	0	0	0	1	0	0	0	1	1	1	5	0	0	1	0	0	0	0	0	0	0	0	1	0	0
Osburnostylus	0	0	0	1	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0	1	1	2	1	5	0	0	0	0	1	0	0	0	0	0	0	1	0	0
Pseudonematopora	0	0	0	0	0	0	0	0	1	1	0	1	3	A	0	0	0	1	0	0	0	0	10	1	3	0	1	1	0	0	0	0	0	0	1	0	0	0	0
Sceptopora	0	1	1	0	0	0	0	0	0	0	0	1	0	2	0	0	0	1	0	0	1	1	0	1	3	0	1	0	0	0	0	0	0	0	1	0	0	0	0
Tropidopora	2	0	1	0	0	0	0	0	0	1	1	1	2	8	1	1	0	1	0	0	1	1	1	1	2	0	0	1	0	0	0	0	0	1	0	0	0	0	0
Ulrichostylus	0	0	1	0	0	0	0	1	0	0	2	1	0	2	0	0	0	1	0	0	1	1	2	1	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0
Rhabdomeson	1	0	1	1	0	0	0	0	1	1	12	1	2	8	0	1	1	1	0	3	1	1	4	1	34	1	0	0	0	0	0	0	0	0	0	1	0	0	0
Ascopora	1	0	1	1	0	0	1	0	1	1	1	1	3	9	0	1	1	1	0	3	1	1	3	1	4	0	0	0	1	0	0	0	0	0	0	1	0	0	0
Mediapora	2	1	0	1	0	0	0	0	1	1	1	1	2	9	1	1	0	1	0	0	1	1	3	1	4	0	0	0	1	0	0	0	0	0	0	1	0	0	0
Nemataxis	1	0	0	1	0	0	0	0	1	1	1	1	2	7	0	1	1	1	0	3	1	1	3	1	2	0	0	0	1	0	0	0	0	1	0	0	0	0	0
Nickelsopora	2	0	1	0	0	0	0	0	1	1	2	1	2	9	1	1	0	1	0	3	1	1	3	1	4	0	0	0	1	0	0	0	0	0	0	1	0	0	0
Orthopora	1	0	1	1	0	0	0	0	1	1	0	1	1	5	0	1	1	1	0	3	1	1	8	1	2	0	0	0	0	0	1	0	0	1	0	0	0	0	0
Trematella	2	1	1	1	0	0	0	0	1	1	1	1	2	7	1	1	0	1	0	2	1	1	8	1	2	0	0	0	0	0	1	0	0	1	0	0	0	0	0
Rhombopora	2	1	0	1	1	0	0	0	1	0	0	1	2	9	1	1	0	1	0	0	1	1	8	1	3	0	0	0	0	0	1	0	0	0	1	0	0	0	0
Klaucena	1	0	0	1	1	0	0	0	1	1	2	1	3	A	1	1	0	1	0	0	1	1	1	1	3	0	0	1	0	0	0	0	0	0	1	0	0	0	0
Megacanthopora	2	2	0	1	1	0	0	0	1	1	0	1	3	9	1	1	0	1	0	0	1	1	1	1	3	0	0	1	0	0	0	0	0	0	1	0	0	0	0
Pamirella	1	0	0	1	0	0	0	0	1	1	1	1	3	A	0	1	1	1	0	0	1	1	8	1	4	0	0	0	0	0	1	0	0	0	0	1	0	0	0
Primorella	2	0	0	0	1	0	0	0	1	1	1	1	3	B	1	1	0	1	0	0	1	1	1	1	3	0	0	1	0	0	0	0	0	0	1	0	0	0	0
Saffordotaxis	1	0	0	0	1	0	0	0	1	1	1	1	3	A	0	1	1	1	0	0	1	1	1	1	3	0	0	1	0	0	0	0	0	0	1	0	0	0	0
Bactropora	1	0	0	0	0	1	0	0	1	0	1	1	0	3	0	1	1	0	0	2	1	1	1	1	3	0	0	1	0	0	0	0	0	0	1	0	0	0	0
Nikiforovella	1	2	1	1	0	0	0	0	1	1	1	1	2	8	0	1	1	1	0	0	1	1	0	1	3	0	1	0	0	0	0	0	0	0	1	0	0	0	0
Acanthoclema	1	2	1	1	0	0	0	0	1	1	0	1	2	7	0	1	1	1	0	0	1	1	8	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
Pinegopora	1	2	0	1	0	0	0	0	0	1	1	1	4	E	0	1	1	1	0	0	1	1	8	1	3	0	0	0	0	0	1	0	0	0	1	0	0	0	0

TABLE 2: CONTINUED

TAXON	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39
Streblotrypella	1	2	0	1	1	0	0	0	0	1	1	1	2	7	0	1	1	1	0	0	1	1	1	1	2	0	0	1	0	0	0	0	0	1	0	0	0	0	0
Hyphasmopora	1	2	0	0	0	0	0	0	0	1	2	1	3	A	0	1	1	1	0	1	1	0	0	1	4	0	1	0	0	0	0	0	0	0	0	1	0	0	0
Ogbinopora	1	2	0	0	0	0	1	0	0	1	2	1	3	A	0	1	1	1	0	3	1	0	0	1	4	0	1	0	0	0	0	0	0	0	0	1	0	0	0
Streblotrypa	1	2	1	1	0	0	1	0	0	1	2	1	3	A	0	1	1	1	0	1	1	1	3	1	4	0	0	0	1	0	0	0	0	0	0	1	0	0	0
Petaloporella	1	2	0	0	0	0	0	0	1	1	1	1	2	8	0	1	1	1	0	0	1	0	0	1	3	0	1	0	0	0	0	0	0	0	1	0	0	0	0
Streblascopora	0	2	1	1	0	0	1	0	1	1	0	1	3	A	0	0	0	1	0	2	1	1	3	1	4	0	0	0	1	0	0	0	0	0	0	1	0	0	0
Maychella	2	2	0	0	0	0	0	0	1	?	1	1	4	D	1	1	0	?	0	0	1	0	3	1	4	0	0	0	1	0	0	0	0	0	0	1	0	0	0
Callocladia	2	1	0	1	0	0	0	1	1	1	1	1	3	A	1	1	0	?	0	0	0	1	4	1	5	1	0	0	0	0	0	0	0	0	0	0	1	0	0
Streblocladia	2	0	0	0	0	0	0	0	1	1	?	0	4	D	1	1	0	1	0	0	0	0	5	1	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Euthyrombopora	2	0	1	1	0	0	0	0	1	?	2	1	3	A	1	1	0	1	0	1	0	1	3	1	4	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Coelotublipora	2	1	0	0	0	0	0	0	1	?	1	1	3	A	1	1	0	1	0	?	1	0	4	1	3	1	0	0	0	0	0	0	0	0	1	0	0	0	0
Taeniodictya	0	1	0	0	0	0	0	0	1	0	0	1	2	5	0	0	0	1	0	3	0	0	?	1	5	0	?	?	?	?	?	?	0	0	0	0	1	0	0
Heliotrypa	2	1	0	0	1	0	0	0	1	0	1	1	3	A	1	1	0	?	0	1	0	1	1	1	5	0	0	1	0	0	0	0	0	0	0	0	1	0	0
Goldfussitrypa	2	2	0	0	0	1	0	0	1	1	1	1	0	1	1	1	0	?	0	0	1	1	1	1	2	0	0	1	0	0	0	0	0	1	0	0	0	0	0
Nematotrypa	2	0	0	1	0	0	1	0	1	?	1	1	0	2	1	1	0	?	0	?	1	1	2	1	3	0	0	0	0	1	0	0	0	0	1	0	0	0	0
Ottoseetaxis	1	0	0	0	0	1	0	0	1	1	0	1	0	2	0	1	1	1	0	0	1	1	1	1	2	0	0	1	0	0	0	0	0	1	0	0	0	0	0
Mongloclema	2	2	0	0	0	0	0	0	1	?	1	1	2	8	1	1	0	?	0	0	1	0	1	1	4	0	0	1	0	0	0	0	0	0	0	1	0	0	0
Linotaxis	1	2	0	0	0	0	0	0	1	1	2	1	2	9	0	1	1	1	0	0	0	0	8	1	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0
Clausotrypa	2	1	0	1	0	0	0	0	0	1	0	1	3	C	1	1	0	1	0	0	0	1	1	1	3	0	0	1	0	0	0	0	0	0	1	0	0	0	0
Nematoporella	0	0	0	0	0	0	0	1	0	1	1	1	0	4	0	0	0	0	0	0	0	0	6	1	5	0	0	0	0	0	0	1	0	0	0	0	1	0	0
Arthrotrypa	0	0	0	0	0	0	0	1	0	0	1	1	0	4	0	0	0	1	0	0	0	0	6	1	5	0	0	0	0	0	0	1	0	0	0	0	1	0	0
Europora	1	0	0	1	0	0	0	0	1	?	2	1	3	A	0	1	1	1	0	2	1	1	3	1	4	0	0	0	1	0	0	0	0	0	0	1	0	0	0
Hyalotaechus	1	0	0	1	0	0	0	1	1	1	1	1	2	9	0	1	1	1	0	0	0	1	8	1	2	0	0	0	0	0	1	0	0	1	0	0	0	0	0
Spira	1	1	0	1	1	0	0	0	1	1	2	1	3	A	0	1	1	1	0	0	1	1	0	1	4	0	1	0	0	0	0	0	0	0	0	1	0	0	0
Kielcepora	0	0	0	1	0	0	0	0	0	1	?	0	0	2	0	0	0	1	0	?	0	1	5	1	?	0	0	0	0	0	0	0	?	?	?	?	?	?	?
Ralfinella	0	1	0	0	0	0	0	0	0	1	1	0	0	2	0	0	0	1	0	0	0	0	5	1	?	0	0	0	0	0	0	0	?	?	?	?	?	?	?
Ojlepora	0	0	0	0	0	0	0	0	0	1	?	0	0	1	0	0	0	1	0	?	0	0	5	1	?	0	0	0	0	0	0	0	?	?	?	?	?	?	?
Kielanopora	0	0	0	0	0	0	0	0	1	1	?	0	0	3	0	0	0	1	0	?	0	0	5	1	?	0	0	0	0	0	0	0	?	?	?	?	?	?	?
Enallopora	2	0	0	1	0	0	0	0	0	1	?	0	0	2	1	1	0	1	0	?	0	1	5	1	3	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Parachasmatopora	2	0	0	0	0	0	0	0	0	1	?	0	0	2	1	1	0	1	0	?	0	0	5	1	?	0	0	0	0	0	0	0	?	?	?	?	?	?	?
Alwynopora	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	0	0	1	0	0	0	0	5	1	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Pseudohornera	0	0	0	0	1	0	0	0	0	1	1	0	0	1	0	0	0	1	0	0	1	1	5	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Pesnastylus	0	0	0	0	0	0	0	0	0	1	0	0	1	6	0	0	0	0	1	0	1	0	5	1	3	0	0	0	0	0	0	0	0	0	1	0	0	0	0

TABLE 3: TAXA OR CHARACTERS REMOVED DURING DIFFERENT EXECUTIONS OF THE SOFTWARE

TAXA								CHARACTERS						
Arthrostylus								1						
Arthroclema								2						
Arthrostyloecia	x	x						3						
Cuneatopora								4						
Glauconomella								5						
Heloclema								6						
Helopora								7						
Heminematopora	x	x						8						
Hemiulrichostylus	x	x						9						
Hexites								10			x			
Moyerella								11			x			
Nematopora								12						
Osburnostylus								13						
Pseudonematopora								14						
Sceptropora								15						
Tropidopora								16						
Ulrichostylus								17						
Rhabdomeson								18			x			
Ascopora								19						
Mediopora								20			x			
Nemataxis								21						
Nickelsopora								22						
Orthopora								23			x			
Trematella								24						
Rhombopora								25			x			
Klaucena								26						
Megacanthopora								27			x			
Pamirella								28			x			
Primorella								29			x			
Saffordotaxis								30			x			
Bactropora								31			x			
Nikiforovella								32			x			
Acanthoclema								33			x			
Pinegopora								34			x			
Streblotrypella								35			x			
Hyphasmopora								36			x			
Ogbinopora								37			x			
Streblotrypa								38			x			
Petaloporella								39			x			
Streblascopora														
Maychella		x												
Callocladia		x												
Streblocladia		x												
Euthyrombopora		x												
Coelotubulipora		x												
Taeniodictya	x	x												
Heliotrypa		x												
Goldfussitrypa		x												
Nematotrypa	x	x												
Ottoseetaxis														
Mongloclema		x												
Linotaxis														
Clausotrypa														
Nematoporella														
Arthrotrypa														
Europora		x												
Hyalotoechus														
Spira														
Kielcepora	x	x												
Ralfinella		x												
Ojlepora	x	x												
Kielanopora	x	x												
Enallopora		x												
Parachasmatopora	x	x												
Alwynopora														
Pseudohornera														
Pesnastylus														
	tree1,2	tree 3,4	tree5,6	tree7,8	tree9,10	tree11,12			tree1,2	tree3,4	tree5,6	tree7,8	tree9,10	tree11,12

two missing characters; also some characters were left out of all of the computer runs as discussed in Appendix 1. Each version of the matrix was run both with and without the geochronological character. Then (due to limited computer access) I limited each execution of the PAUP software to a run of approximately 3 hours. This amount of time was chosen because previous runs had shown that very few changes in tree length occurred after 3 hours. Also, due to memory limitations of the computer, the maximum number of trees that the computer would save of any given length was limited to 1000.

RESULTS

The geochronological character appears to be instrumental in the ordering of the phylogenetic trees; when this character was left out (trees 2,4,6,8,10,12), there was no definable tree structure at all in the strict consensus. The entire consensus tree was reduced to a single basal polytomy [branching point giving rise to more than two branches (Mayr, 1991)]. The morphological characters (mostly taken or modified from the type descriptions in the treatise) were less definitive. If there is a single trait or combination of traits that unquestionably shows the phylogeny of this group, it cannot be resolved in this study.

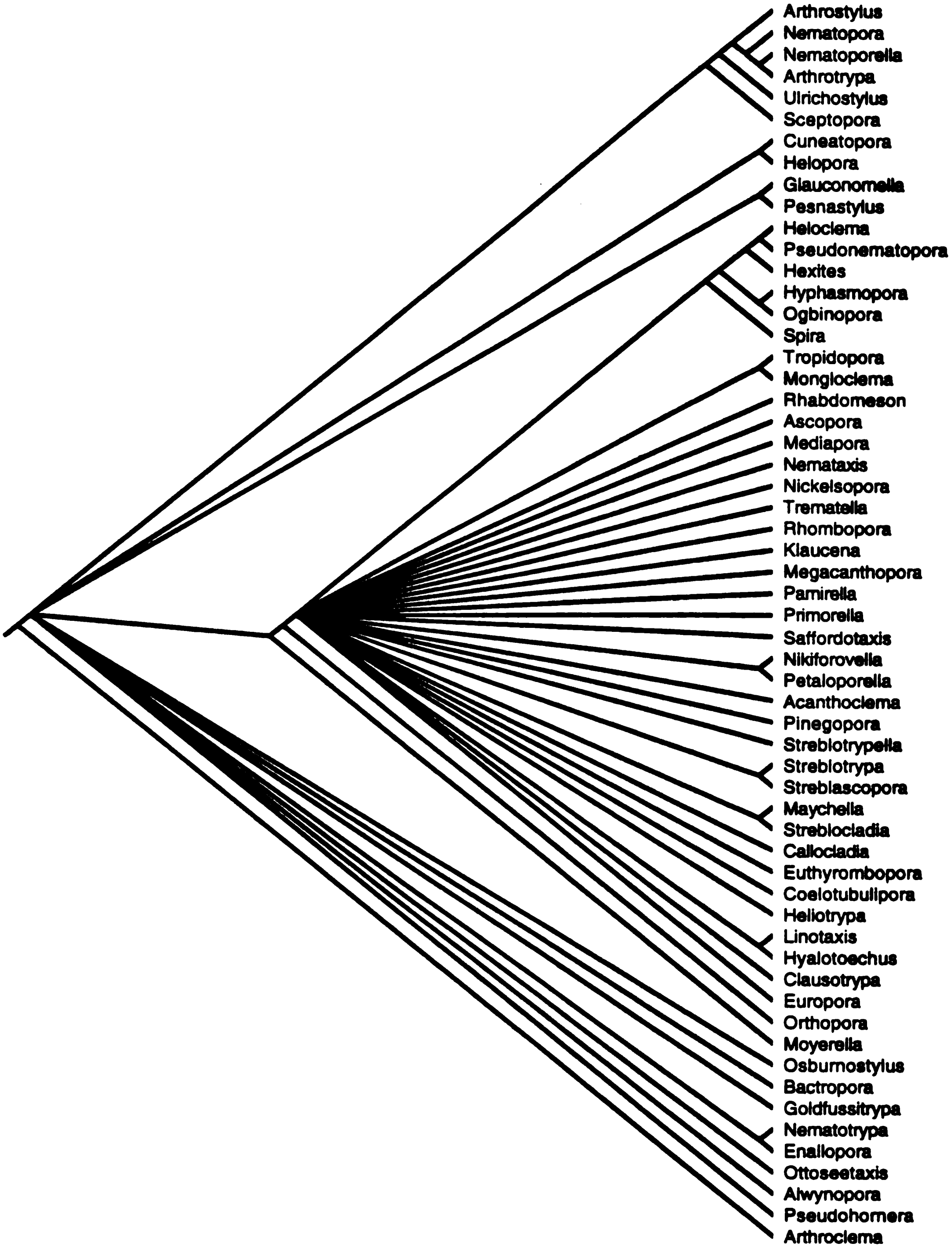
I have presented the twelve consensus trees that were produced by the PAUP software, and I also have included the 50% majority consensus trees. A consensus tree is an artificial tree that can be thought of as an average of all of the trees in a given run of the PAUP software; in such trees only the branching patterns that are present in all or nearly all of the trees are shown, and the areas of indecision are collapsed into polytomies. The 50% majority trees are also consensus trees, but any branching that occurs on 50% or more of the trees is included. The percentages that appear on the majority rule trees (figures 1b-12b) show the percent of the trees that support a given node. Table 4 shows the treelength, consistency index, retention index, and the number of trees found for each run of the PAUP software. All of the odd numbered trees (figures 1,3,5,7,9,11,) were run with the geochronological character, and all of the even numbered trees (figures 2,4,6,8,10,12) were run without it.

Trees one and two were run with full character sets, but all taxa with more than two pieces of missing data were removed. Tree one (figure 1a) has a large polytomy one node up from the base of the tree, which shows some uncertainty as to how the Arthrostylidae should be arranged around the base. There is a second large polytomy at one of the internal nodes that shows almost no clear definition in a group of 32 genera (nearly half of the suborder). Several of the areas of defined structure in the tree are, however, very consistent with other runs of the data. The majority rule tree (figure 1b) for this run of the software shows tree structure that has some similarities with other trees in the study, but the overall strength of the tree is in question due to the number of basal nodes with frequencies of less than 80%.

Tree two (figure 2a) demonstrates how important the geochronological character is, since its absence is the only change from tree one, and, without it, all structure in the strict consensus tree has been lost. The majority rule frequencies near the base of the second tree (figure 2b) are even lower than in tree one, resulting in a basal polytomy.

TABLE 4: TREE STATISTICS

Tree Number	Tree Length	Consistency Index	Retention Index	Number of Trees Saved
consensus tree 1	258	0.205	0.727	107
consensus tree 2	196	0.199	0.56	1000
consensus tree 3	209	0.254	0.738	141
consensus tree 4	165	0.236	0.568	1000
consensus tree 5	144	0.222	0.831	617
consensus tree 6	80	0.225	0.753	1000
consensus tree 7	273	0.194	0.731	870
consensus tree 8	202	0.193	0.6	1000
consensus tree 9	280	0.189	0.728	447
consensus tree 10	210	0.186	0.595	1000
consensus tree 11	274	0.193	0.729	575
consensus tree 12	205	0.19	0.59	1000



Arthrostylus
Nematopora
Nematoporella
Arthrotrypa
Ulrichostylus
Sceptopora
Cuneatopora
Helopora
Glauconomella
Pesnastylus
Heloclema
Pseudonematopora
Hexites
Hyphasmopora
Ogbinopora
Spira
Tropidopora
Mongloclema
Rhabdomeson
Ascopora
Mediapora
Nemataxis
Nickelsopora
Trematella
Rhombopora
Klaucena
Megacanthopora
Pamirella
Primorella
Saffordotaxis
Nikiforovella
Petaloporella
Acanthoclema
Pinegopora
Streblotrypella
Streblotrypa
Streblascopora
Maychella
Streblocladia
Callocladia
Euthyrombopora
Coelotubulipora
Heliotrypa
Linotaxis
Hyalotoechus
Clausotrypa
Europora
Orthopora
Moyerella
Osburnostylus
Bactropora
Goldfussitrypa
Nematotrypa
Enallopora
Ottoseetaxis
Alwynopora
Pseudohornera
Arthroclema

Figure 1a

```
                                                /------ Arthrostylus(1)
                                             /100 /---- Nematopora(9)
                                             |  100 /-- Nematoporella(50)
                                           100    100-- Arthrotrypa(51)
    /------------------------------------100 \--------- Ulrichostylus(14)
    |                                      \----------- Sceptopora(12)
    |                                               /-- Cuneatopora(3)
    |        /------------------------------------100-- Helopora(6)
    |        |                                      /-- Heloclema(5)
    |        |                                    100-- Pseudonematopora(11)
    |        |                                  100---- Hexites(7)
    |        |                               /100   /-- Hyphasmopora(33)
    |        |                             100  \-100-- Ogbinopora(34)
    |        |                           /96 \--------- Spira(54)
    |        |                         /96 \----------- Europora(52)
    |        |                         | \------------- Pamirella(25)
    |        |                       /93          /---- Pinegopora(31)
    |        |                       | \---------96 /-- Maychella(38)
    |        |                  /---93            100-- Streblocladia(40)
    |        |                  |    |              /-- Linotaxis(48)
    |        |                  |    \------------100-- Hyalotoechus(53)
    |        |                  |                   /-- Tropidopora(13)
    |        |                  |  /--------------100-- Mongloclema(47)
    |        |                  |  | /----------------- Mediapora(17)
    |        |                  |  | |   /------------- Rhombopora(22)
    |        |                  +-96 |   |        /---- Klaucena(23)
    |        |                /96  | |   |      /85 /-- Primorella(26)
  100      /92                | |  \96 /81   /-74 \93-- Saffordotaxis(27)
  | |      | |                | |    | | | /93  \------ Heliotrypa(43)
  | |      | |                | |    | | \78 \--------- Clausotrypa(49)
  | |      | |                | |    \93   \----------- Megacanthopora(24)
  | |      | |              /92 |      |            /-- Callocladia(39)
  | |      | |              | | |      \-----------85-- Coelotubulipora(42)
  | |      | |              | | |                   /-- Nikiforovella(29)
  | |      | |            /88 | \-----------------100-- Petaloporella(36)
  | |      | |            | | \------------------------ Streblotrypella(32)
  | |      | |            | \-------------------------- Acanthoclema(30)
  | |      | |          /63                /----------- Rhabdomeson(15)
  | |    /89 |          | |                | /--------- Ascopora(16)
  | |    | | |          | \---------------96 |  /------ Nickelsopora(19)
  | |    | | |        /60                  \96  |   /-- Streblotrypa(35)
  | |    | | |        | |                    \-96 100-- Streblascopora(37)
--+ |    | | |     /100 |                       \96---- Euthyrombopora(41)
  | |    | | |     |  | \------------------------------ Nemataxis(18)
  | | /-66 | |   100  \-------------------------------- Trematella(21)
  | | |  | | | 100 \----------------------------------- Orthopora(20)
  | | |  | | \92 \------------------------------------- Moyerella(8)
  | | |  | |   \--------------------------------------- Bactropora(28)
  | | |  | |                                        /-- Nematotrypa(45)
  | \72  | \--------------------------------------100-- Enallopora(55)
  |   |  \--------------------------------------------- Osburnostylus(10)
  |   |                                             /-- Glauconomella(4)
  |   |                                      /----100-- Pesnastylus(58)
  |   |                                      |      /-- Goldfussitrypa(44)
  |   \-------------------------------------66    /97-- Ottoseetaxis(46)
  |                                          |  /72---- Alwynopora(56)
  |                                          \-66------ Pseudohornera(57)
  \---------------------------------------------------- Arthroclema(2)
```

Figure 1b

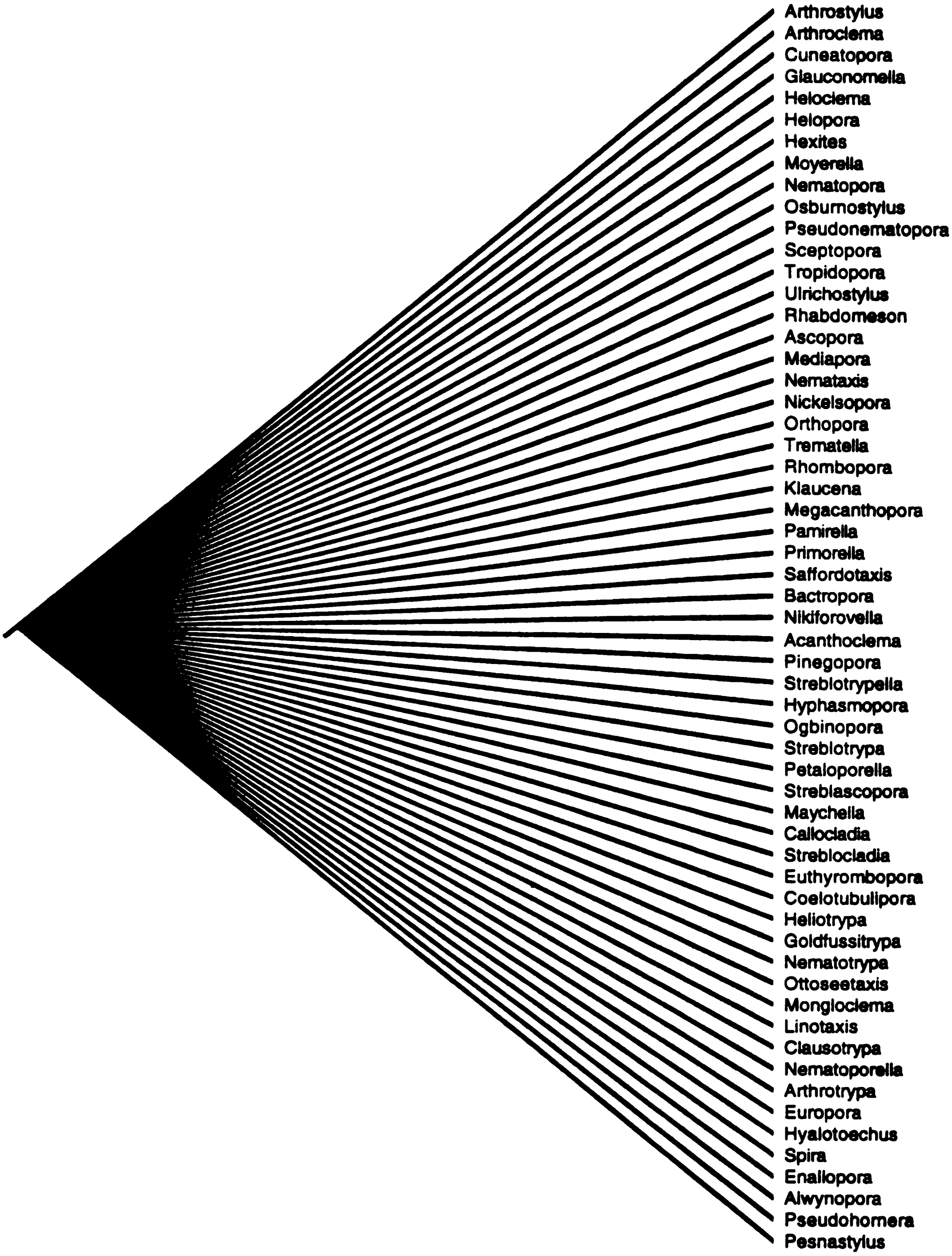

Arthrostylus
Arthroclema
Cuneatopora
Glauconomella
Helociema
Helopora
Hexites
Moyerella
Nematopora
Osburnostylus
Pseudonematopora
Sceptopora
Tropidopora
Ulrichostylus
Rhabdomeson
Ascopora
Mediapora
Nemataxis
Nickelsopora
Orthopora
Trematella
Rhombopora
Klaucena
Megacanthopora
Pamirella
Primorella
Saffordotaxis
Bactropora
Nikiforovella
Acanthoclema
Pinegopora
Streblotrypella
Hyphasmopora
Ogbinopora
Streblotrypa
Petaloporella
Streblascopora
Maychella
Callocladia
Streblocladia
Euthyrombopora
Coelotubulipora
Heliotrypa
Goldfussitrypa
Nematotrypa
Ottoseetaxis
Mongloclema
Linotaxis
Clausotrypa
Nematoporella
Arthrotrypa
Europora
Hyalotoechus
Spira
Enallopora
Alwynopora
Pseudohomera
Pesnastylus

Figure 2a

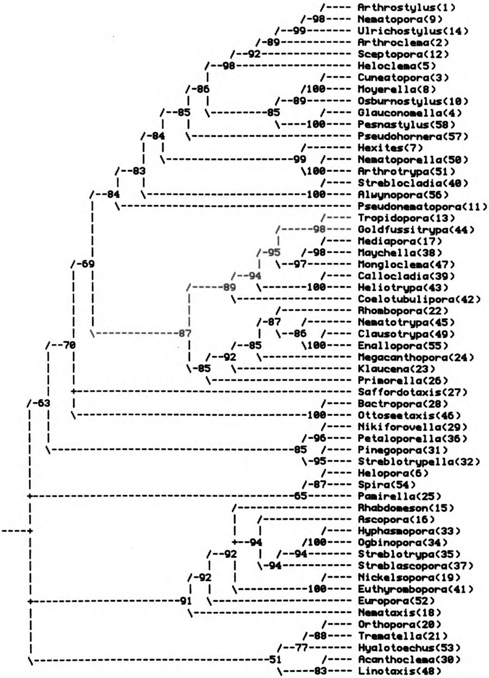

98
Arthrostylus(1)
Nematopora(9)
99
Ulrichostylus(14)
89
Arthroclema(2)
92
Sceptopora(12)
98
Heloclema(5)
Cuneatopora(3)
86
100
Moyerella(8)
89
Osburnostylus(10)
85
85
Glauconomella(4)
100
Pesnastylus(58)
84
Pseudohornera(57)
Hexites(7)
99
Nematoporella(50)
83
100
Arthrotrypa(51)
Streblocladia(40)
84
100
Alwynopora(56)
Pseudonematopora(11)
Tropidopora(13)
98
Goldfussitrypa(44)
Mediapora(17)
95
98
Maychella(38)
69
97
Mongloclema(47)
94
Callocladia(39)
89
100
Heliotrypa(43)
Coelotubulipora(42)
Rhombopora(22)
87
Nematotrypa(45)
87
86
Clausotrypa(49)
70
85
100
Enallopora(55)
92
Megacanthopora(24)
85
Klaucena(23)
Primorella(26)
Saffordotaxis(27)
63
Bactropora(28)
100
Ottoseetaxis(46)
Nikiforovella(29)
96
Petaloporella(36)
85
Pinegopora(31)
95
Streblotrypella(32)
Helopora(6)
87
Spira(54)
65
Pamirella(25)
Rhabdomeson(15)
Ascopora(16)
Hyphasmopora(33)
94
100
Ogbinopora(34)
92
94
Streblotrypa(35)
94
Streblascopora(37)
92
Nickelsopora(19)
100
Euthyrombopora(41)
91
Europora(52)
Nemataxis(18)
Orthopora(20)
88
Trematella(21)
77
Hyalotoechus(53)
51
Acanthoclema(30)
83
Linotaxis(48)

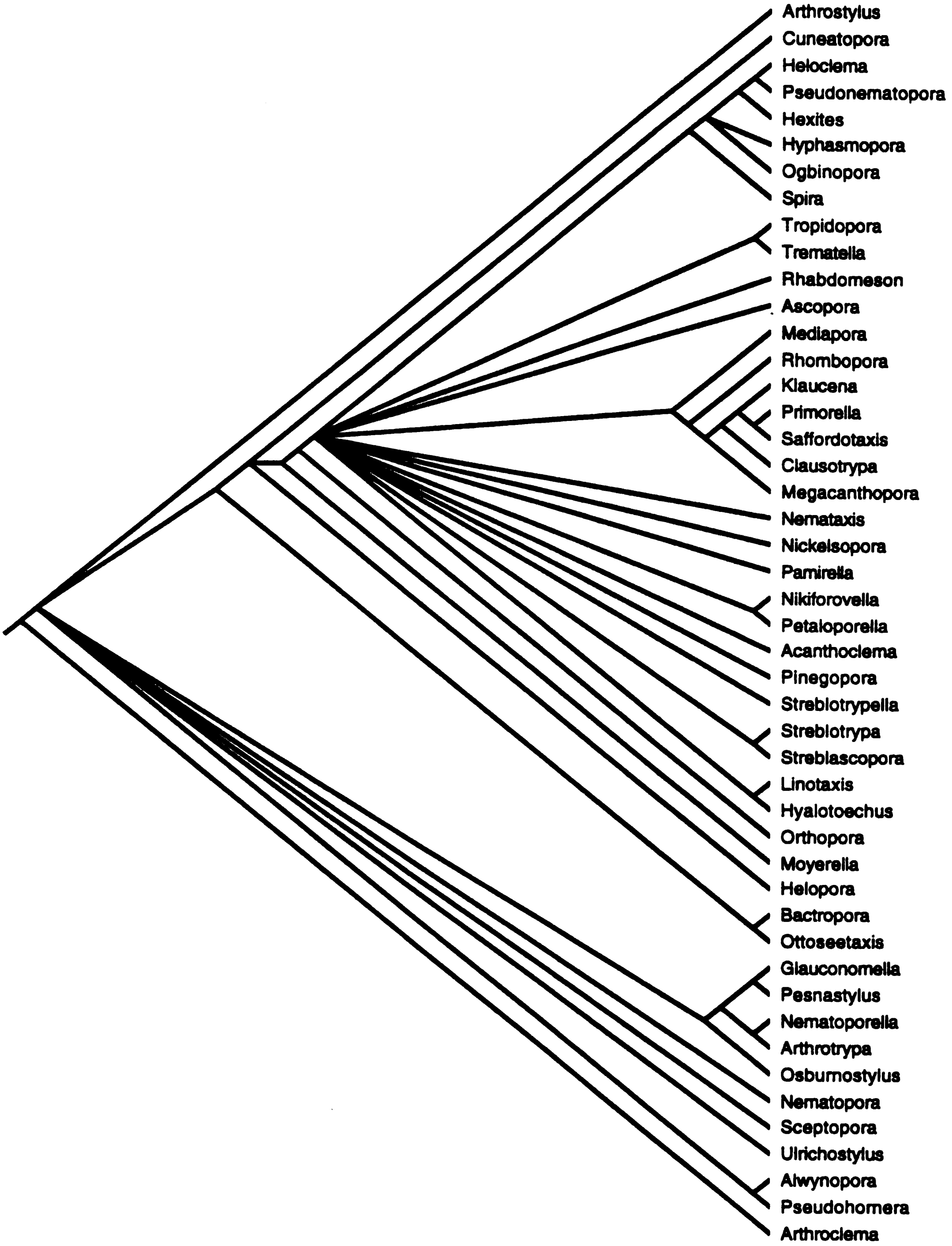
Figure 2b

There are other polytomies which indicate areas that cannot be resolved. There are also very few nodes that are supported in more than 95% of the trees.

Trees three and four were run with the full character set, but eleven genera with missing data were removed (see Table 3). Tree three also has the near basal polytomy one node up from the base; however it is reduced to 7 branches instead of the 11 that were found in figure 1a, and still shows uncertainty about the monophyly of the Arthrostylidae as a basal family. There is again another polytomy of 14 branches at one of the internal nodes; however it is not nearly as extreme as the 27 branches in figure 1a. The tree overall shows much more definition, and familial groupings are much more easily deduced (see conclusions). Tree three's majority rule data (figure 3b) shows the overall strength of the tree, but also indicates why there are some polytomies in the strict consensus. There are two regions in the tree where the nodes have very low percentages; these correspond with the two large polytomies in the consensus tree.

Tree four (figure 4a) has the same problem as all of the trees with no geochronological character, i.e. no structure is visible in the strict consensus tree. In addition very few of the nodes in the majority rule tree (figure 4b) have the high percentages that were present in tree 3, and the basal branches have percentages below 80%.

Trees five and six were run with full sets of taxa, but all nineteen characters with missing data were removed (see Table 3). In tree five (figure 5a) the basal polytomy that has occurred in all of the geochronological trees is present once again, but it now includes 20 branches. In this tree the internal polytomy of 33 branches is the dominant


Arthrostylus
Cuneatopora
Helociema
Pseudonematopora
Hexites
Hyphasmopora
Ogbinopora
Spira
Tropidopora
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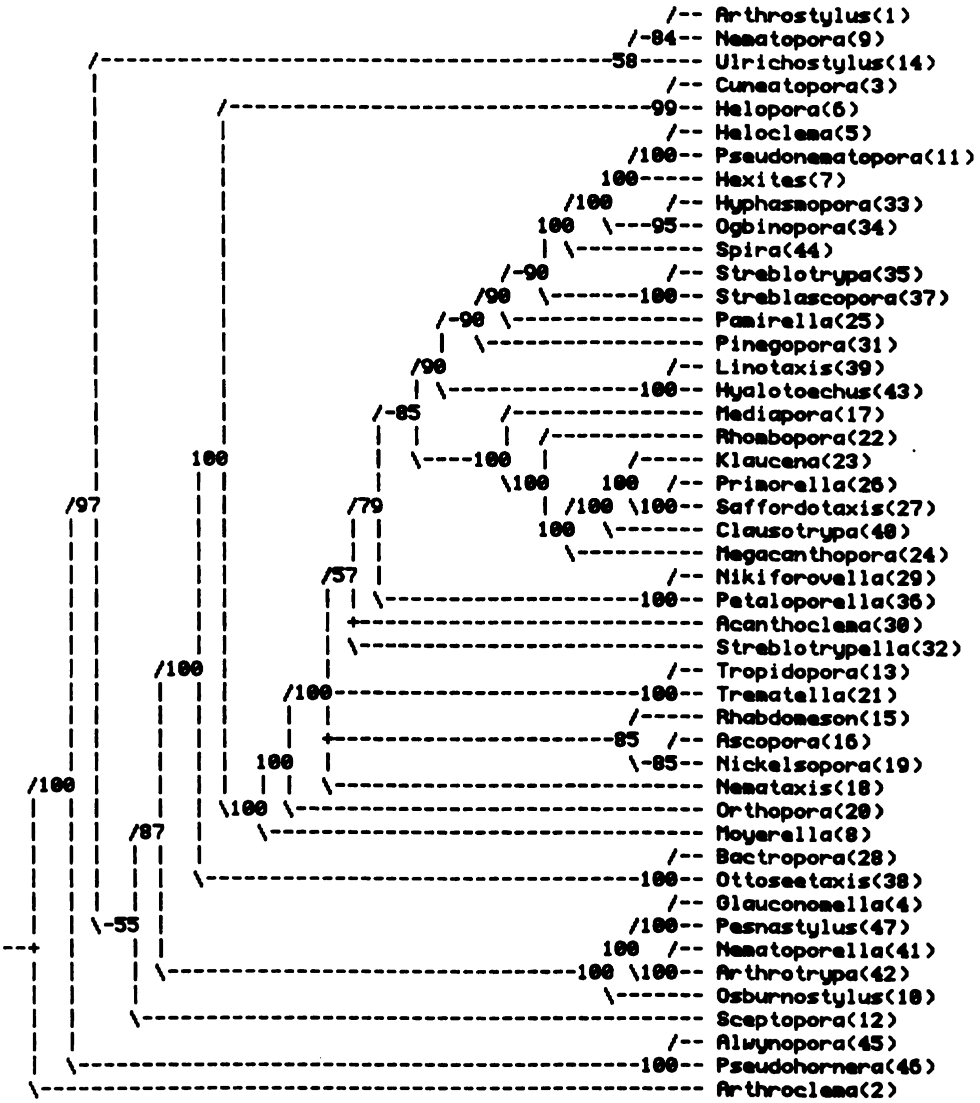
Rhabdomeson
Ascopora
Mediapora
Rhombopora
Klaucena
Primorella
Saffordotaxis
Clausotrypa
Megacanthopora
Nemataxis
Nickelsopora
Pamirella
Nikiforovella
Petaloporella
Acanthoclema
Pinegopora
Streblotrypella
Streblotrypa
Streblascopora
Linotaxis
Hyalotoechus
Orthopora
Moyerella
Helopora
Bactropora
Ottoseetaxis
Glauconomella
Pesnastylus
Nematoporella
Arthrotrypa
Osburnostylus
Nematopora
Sceptopora
Ulrichostylus
Alwynopora
Pseudohornera
Arthroclema

Figure 3a


Arthrostylus(1)
Nematopora(9)
Ulrichostylus(14)
Cuneatopora(3)
Helopora(6)
Heloclema(5)
Pseudonematopora(11)
Hexites(7)
Hyphasmopora(33)
Ogbinopora(34)
Spira(44)
Streblotrypa(35)
Streblascopora(37)
Pamirella(25)
Pinegopora(31)
Linotaxis(39)
Hyalotoechus(43)
Mediapora(17)
Rhombopora(22)
Klaucena(23)
Primorella(26)
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Clausotrypa(40)
Megacanthopora(24)
Nikiforovella(29)
Petaloporella(36)
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Tropidopora(13)
Trematella(21)
Rhabdomeson(15)
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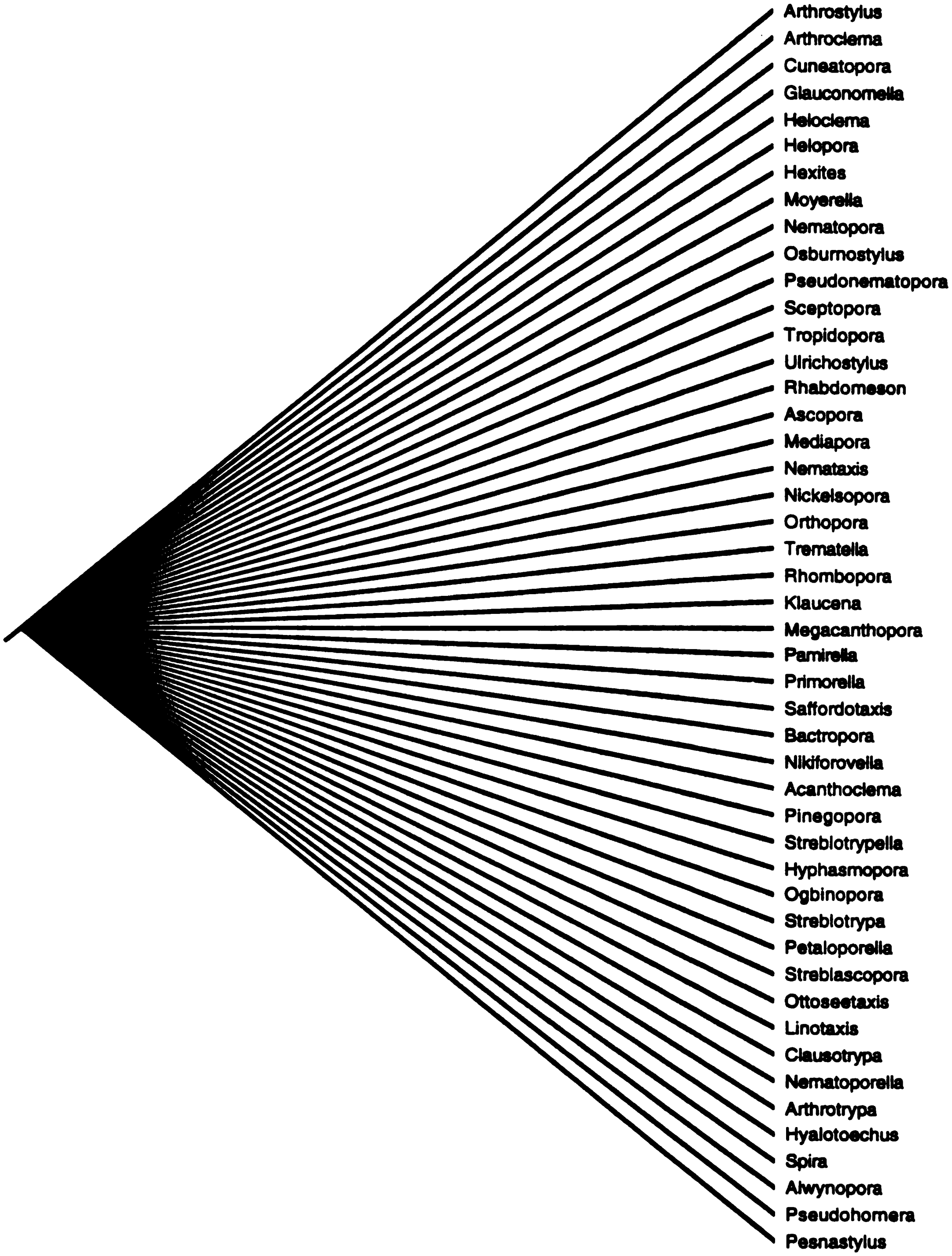
Nemataxis(18)
Orthopora(20)
Moyerella(8)
Bactropora(28)
Ottoseetaxis(38)
Glauconomella(4)
Pesnastylus(47)
Nematoporella(41)
Arthrotrypa(42)
Osburnostylus(10)
Sceptopora(12)
Alwynopora(45)
Pseudohornera(46)
Arthroclema(2)

Figure 3b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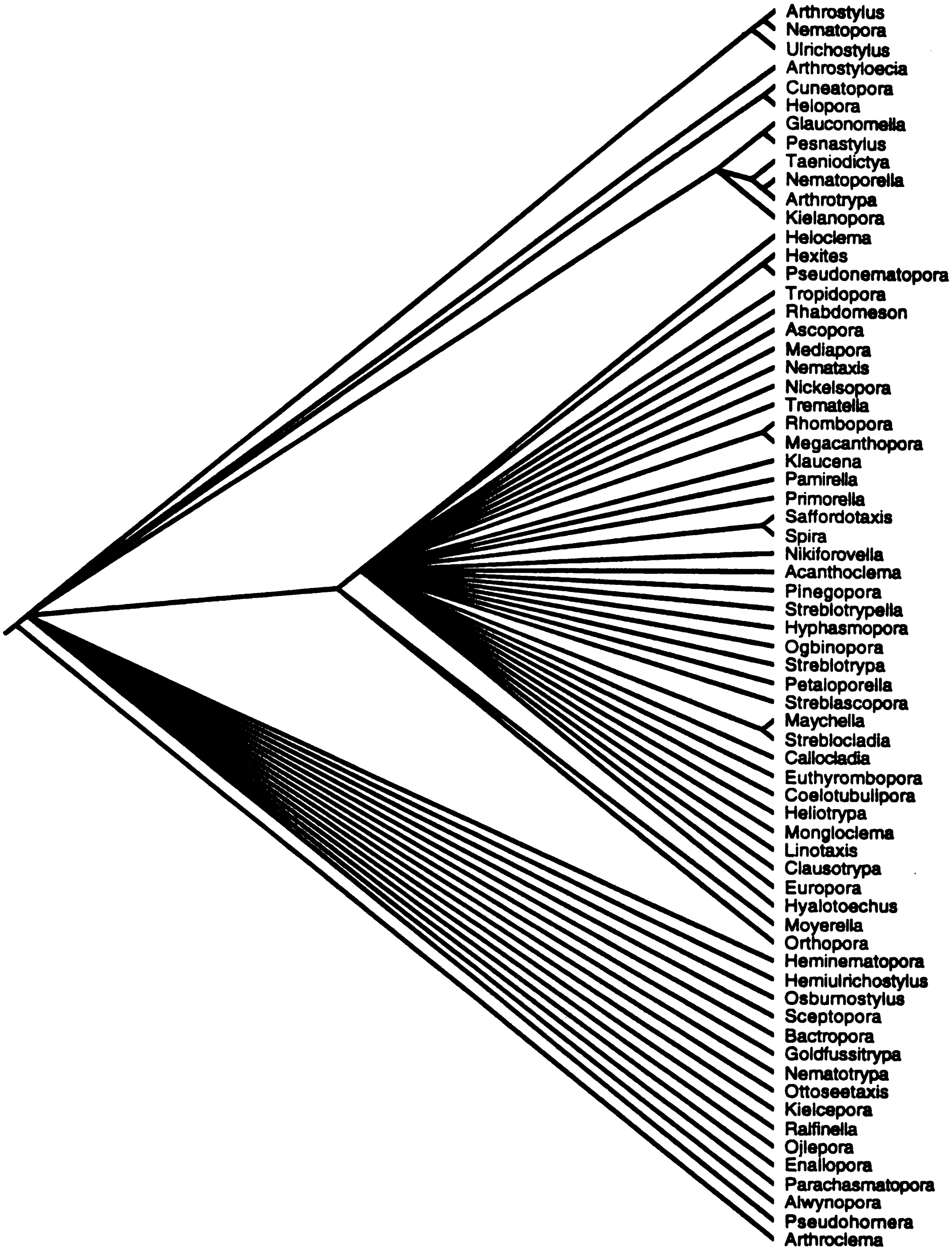
Arthroclema
Cuneatopora
Glauconomella
Helociema
Helopora
Hexites
Moyerella
Nematopora
Osburnostylus
Pseudonematopora
Sceptopora
Tropidopora
Ulrichostylus
Rhabdomeson
Ascopora
Mediapora
Nemataxis
Nickelsopora
Orthopora
Trematella
Rhombopora
Klaucena
Megacanthopora
Pamirella
Primorella
Saffordotaxis
Bactropora
Nikiforovella
Acanthoclema
Pinegopora
Streblotrypella
Hyphasmopora
Ogbinopora
Streblotrypa
Petaloporella
Streblascopora
Ottoseetaxis
Linotaxis
Clausotrypa
Nematoporella
Arthrotrypa
Hyalotoechus
Spira
Alwynopora
Pseudohomera
Pesnastylus

Figure 4a

```
                                                   /--- Arthrostylus(1)
                                                 /89--- Nematopora(9)
     /------------------------------------------78----- Ulrichostylus(14)
     |  /---------------------------------------------- Arthroclema(2)
     |  |                                          /--- Cuneatopora(3)
     |  |       /--------------------------------100--- Moyerella(8)
     |  |       |                                  /--- Helopora(6)
     |  |       |                                /98--- Spira(44)
     |  |       |                             /-52----- Pamirella(25)
     |  |       |                          /-62-------- Mediapora(17)
   /51  |       |                     /---50----------- Nemataxis(18)
   | |  |       |                     |    /----------- Ascopora(16)
   | |  |       |                     |    |       /--- Hyphasmopora(33)
   | |  |       |                  /-52 /-95     100--- Ogbinopora(34)
   | |  |       |                  |  | |  |  /-98----- Streblotrypa(35)
   | |  |       |               /-66  \94  \-97-------- Streblascopora(37)
   | |  |       |               |  |    \-------------- Nickelsopora(19)
   | |  |       |             /67  \------------------- Rhabdomeson(15)
   | \-86       |             | |                  /--- Orthopora(20)
   |    |    /-94          /-56 \----------------100--- Trematella(21)
   |    |    |  |          |  \------------------------ Acanthoclema(30)
   |    |    |  |       /-66                       /--- Linotaxis(39)
   |    |    |  |       |  \----------------------95--- Hyalotoechus(43)
   |    |    |  |       |                          /--- Rhombopora(22)
   |    |    |  |       |                        /99--- Clausotrypa(40)
   |    |    |  |       |                     /-99----- Megacanthopora(24)
   |    |    |  |     /84                  /-99-------- Klaucena(23)
   |    |  /94  |     | |               /-99----------- Primorella(26)
---+    |  | |  |     | |             /99-------------- Saffordotaxis(27)
   |    |  | |  |     | |          /-99            /--- Bactropora(28)
   |    |  | |  |  /-87 |          |  \----------100--- Ottoseetaxis(38)
   |    |  | |  |  |  | \---------86               /--- Nikiforovella(29)
   |    \-89 |  \-94  |            \--------------89--- Petaloporella(36)
   |       | |     |  \-------------------------------- Pinegopora(31)
   |       | |     \----------------------------------- Streblotrypella(32)
   |       | \----------------------------------------- Osburnostylus(10)
   |       |                                       /--- Glauconomella(4)
   |       \-------------------------------------100--- Pesnastylus(47)
   |                                               /--- Heloclema(5)
   +----------------------------------------------93--- Sceptopora(12)
   |                                             /----- Hexites(7)
   |                                          /100 /--- Nematoporella(41)
   |                                          |  100--- Arthrotrypa(42)
   |                                       /-88    /--- Pseudonematopora(11)
   |                                    /-73  \---89--- Alwynopora(45)
   \-----------------------------------63  \----------- Pseudohornera(46)
                                        \-------------- Tropidopora(13)
```

Figure 4b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Ulrichostylus
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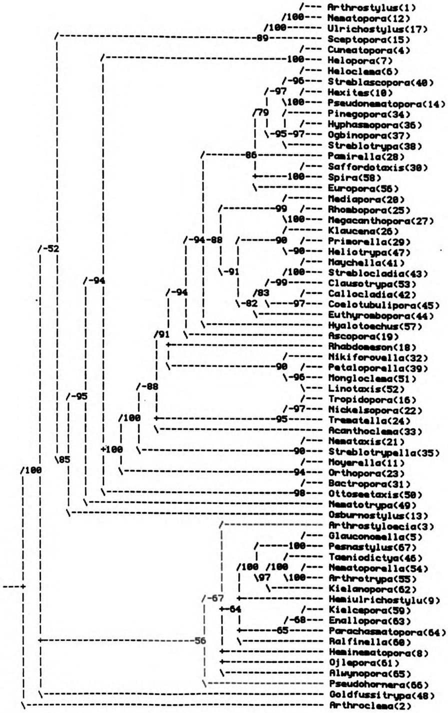
Cuneatopora
Helopora
Glauconomella
Pesnastylus
Taeniodictya
Nematoporella
Arthrotrypa
Kielanopora
Helocilema
Hexites
Pseudonematopora
Tropidopora
Rhabdomeson
Ascopora
Mediapora
Nemataxis
Nickelsopora
Trematella
Rhombopora
Megacanthopora
Klaucena
Pamirella
Primorella
Saffordotaxis
Spira
Nikiforovella
Acanthoclema
Pinegopora
Streblotrypella
Hyphasmopora
Ogbinopora
Streblotrypa
Petaloporella
Streblascopora
Maychella
Streblocladia
Callocladia
Euthyrombopora
Coelotubulipora
Heliotrypa
Mongloclema
Linotaxis
Clausotrypa
Europora
Hyalotoechus
Moyerella
Orthopora
Heminematopora
Hemiulrichostylus
Osburnostylus
Sceptopora
Bactropora
Goldfussitrypa
Nematotrypa
Ottoseetaxis
Kielcepora
Ralfinella
Ojilepora
Enallopora
Parachasmatopora
Alwynopora
Pseudohornera
Arthroclema

Figure 5a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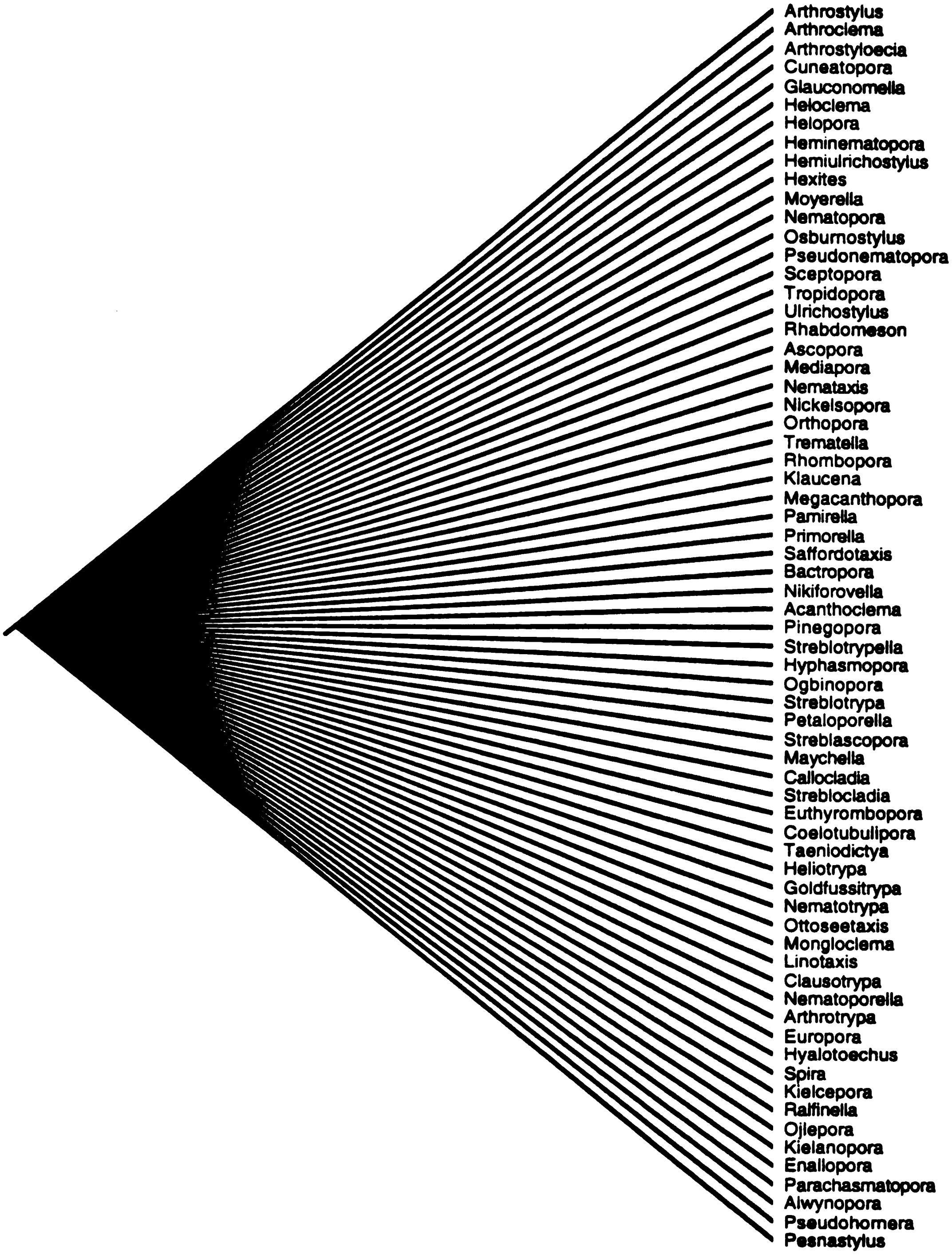
Ulrichostylus(17)
Sceptopora(15)
Cuneatopora(4)
Helopora(7)
Heloclema(6)
Streblascopora(40)
Hexites(10)
Pseudonematopora(14)
Pinegopora(34)
Hyphasmopora(36)
Ogbinopora(37)
Streblotrypa(38)
Pamirella(28)
Saffordotaxis(30)
Spira(58)
Europora(56)
Mediapora(20)
Rhombopora(25)
Megacanthopora(27)
Klaucena(26)
Primorella(29)
Heliotrypa(47)
Maychella(41)
Streblocladia(43)
Clausotrypa(53)
Callocladia(42)
Coelotubulipora(45)
Euthyrombopora(44)
Hyalotoechus(57)
Ascopora(19)
Rhabdomeson(18)
Nikiforovella(32)
Petaloporella(39)
Mongloclema(51)
Linotaxis(52)
Tropidopora(16)
Nickelsopora(22)
Trematella(24)
Acanthoclema(33)
Nemataxis(21)
Streblotrypella(35)
Moyerella(11)
Orthopora(23)
Bactropora(31)
Ottoseetaxis(50)
Nematotrypa(49)
Osburnostylus(13)
Arthrostyloecia(3)
Glauconomella(5)
Pesnastylus(67)
Taeniodictya(46)
Nematoporella(54)
Arthrotrypa(55)
Kielanopora(62)
Hemiulrichostylu(9)
Kielcepora(59)
Enallopora(63)
Parachasmatopora(64)
Ralfinella(60)
Heminematopora(8)
Ojlepora(61)
Alwynopora(65)
Pseudohornera(66)
Goldfussitrypa(48)
Arthroclema(2)

Figure 5b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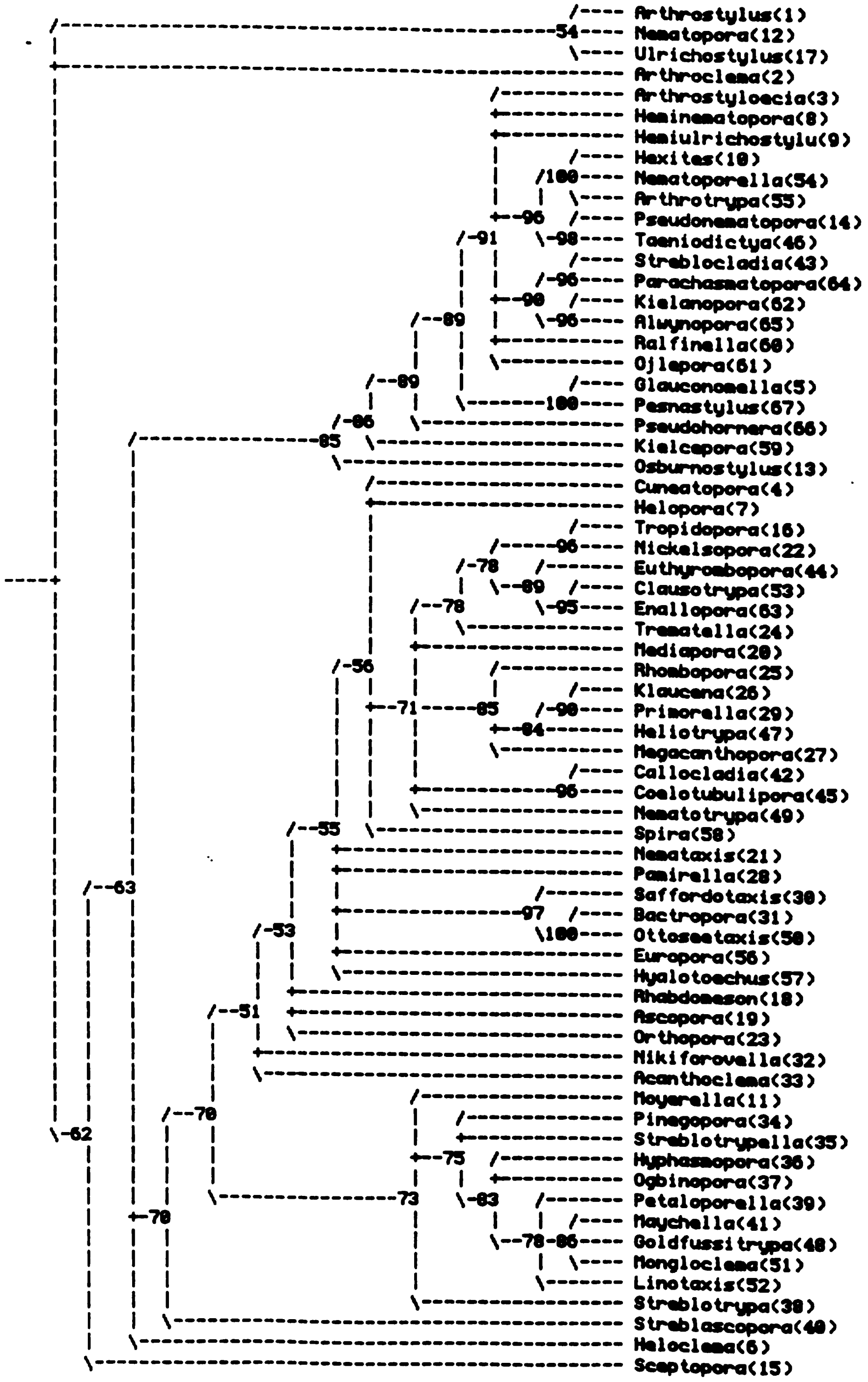
Arthrostyloecia
Cuneatopora
Glauconomella
Heloclema
Helopora
Heminematopora
Hemiulrichostylus
Hexites
Moyerella
Nematopora
Osburnostylus
Pseudonematopora
Sceptopora
Tropidopora
Ulrichostylus
Rhabdomeson
Ascopora
Mediapora
Nemataxis
Nickelsopora
Orthopora
Trematella
Rhombopora
Klaucena
Megacanthopora
Pamirella
Primorella
Saffordotaxis
Bactropora
Nikiforovella
Acanthoclema
Pinegopora
Streblotrypella
Hyphasmopora
Ogbinopora
Streblotrypa
Petaloporella
Streblascopora
Maychella
Callocladia
Streblocladia
Euthyrombopora
Coelotubulipora
Taeniodictya
Heliotrypa
Goldfussitrypa
Nematotrypa
Ottoseetaxis
Mongloclema
Linotaxis
Clausotrypa
Nematoporella
Arthrotrypa
Europora
Hyalotoechus
Spira
Kielcepora
Ralfinella
Ojlepora
Kielanopora
Enallopora
Parachasmatopora
Alwynopora
Pseudohornera
Pesnastylus

Figure 6a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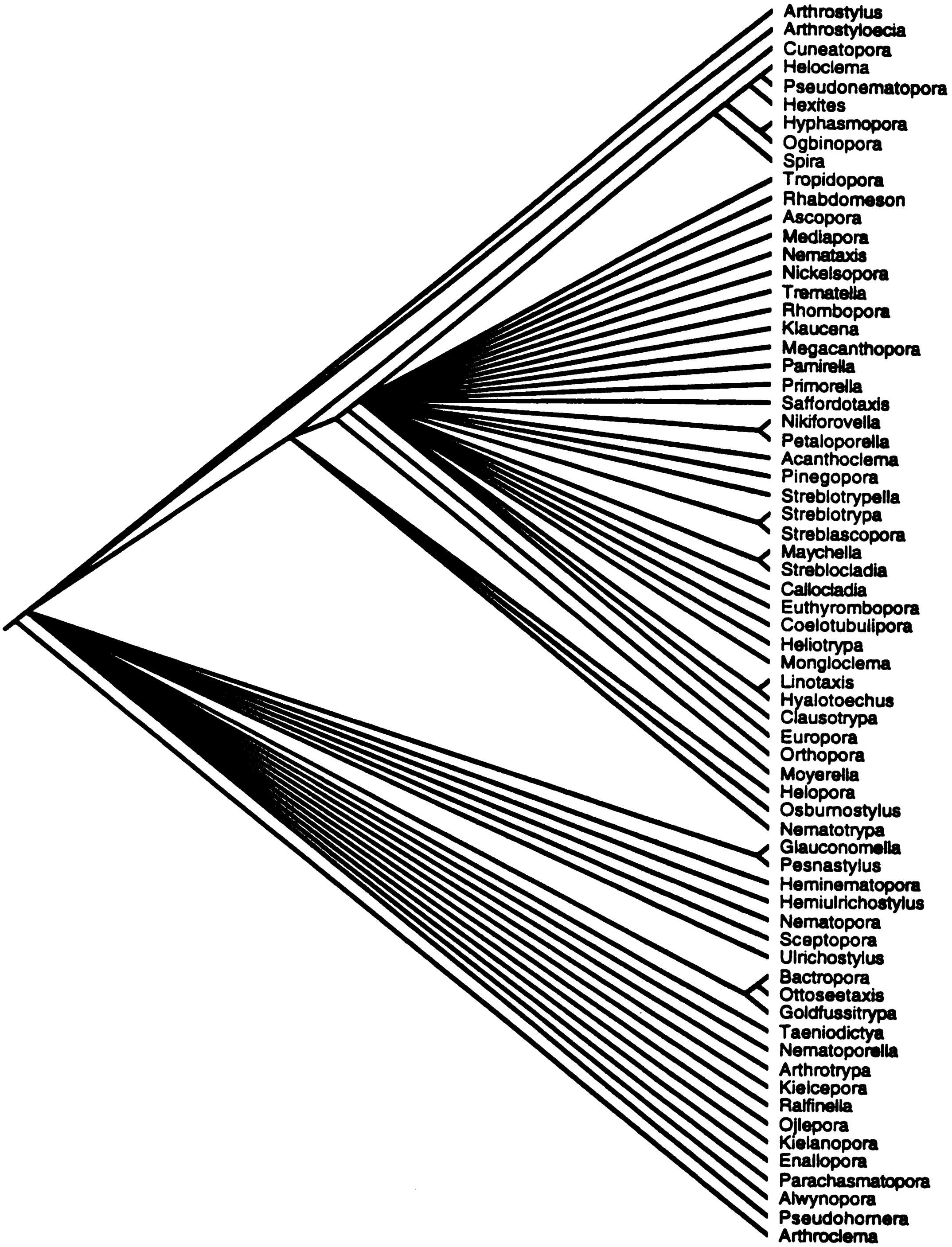
Arthroclema(2)
Arthrostyloecia(3)
Heminematopora(8)
Hemiulrichostylu(9)
Hexites(10)
Nematoporella(54)
Arthrotrypa(55)
Pseudonematopora(14)
Taeniodictya(46)
Streblocladia(43)
Parachasmatopora(64)
Kielanopora(62)
Alwynopora(65)
Ralfinella(60)
Ojlepora(61)
Glauconomella(5)
Pesnastylus(67)
Pseudohornera(66)
Kielcepora(59)
Osburnostylus(13)
Cuneatopora(4)
Helopora(7)
Tropidopora(16)
Nickelsopora(22)
Euthyrombopora(44)
Clausotrypa(53)
Enallopora(63)
Trematella(24)
Mediapora(20)
Rhombopora(25)
Klaucena(26)
Primorella(29)
Heliotrypa(47)
Megacanthopora(27)
Callocladia(42)
Coelotubulipora(45)
Nematotrypa(49)
Spira(58)
Nemataxis(21)
Pamirella(28)
Saffordotaxis(30)
Bactropora(31)
Ottoseetaxis(50)
Europora(56)
Hyalotoechus(57)
Rhabdomeson(18)
Ascopora(19)
Orthopora(23)
Nikiforovella(32)
Acanthoclema(33)
Moyerella(11)
Pinegopora(34)
Streblotrypella(35)
Hyphasmopora(36)
Ogbinopora(37)
Petaloporella(39)
Maychella(41)
Goldfussitrypa(48)
Mongloclema(51)
Linotaxis(52)
Streblotrypa(38)
Streblascopora(40)
Heloclema(6)
Sceptopora(15)
54
100
96
98
91
96
90
96
89
100
89
86
85
96
78
89
78
95
56
71
85
90
84
96
55
97
100
53
63
51
70
75
73
83
78
86
70
62

Figure 6b

feature, causing very little structure to be seen in this consensus, and only a few of the branching patterns that are common in the other trees are present. The majority rule tree for this data (figure 5b) also shows the effect of losing information by eliminating characters. Even in this tree there are ten polytomies. To have multiple polytomies in a tree of this type indicates extreme uncertainty in the tree structure.

Tree six (figure 6a) has the same dominant polytomy that occurs in all of the consensus trees that lack the geochronological character. The majority rule tree (figure 6b) for this run of the data shows even more polytomies (16) than the tree with the temporal character (figure 5b), and also shows some very low percentages on several nodes.

Trees seven and eight were run using the full data matrix as shown in Table 2 (with the exceptions noted in the appendix). I made all of the previous runs because I had achieved less than satisfactory results with the complete data set, and I had wanted to see if the exclusion of characters or taxa with missing data would improve the definition of the suborder. The same near basal polytomy exists in tree seven (figure 7a), which leaves the Arthrostylidae in this area of indecision at the base of the tree, along with the Bactroporidae, which has brought two new genera in to a small grouping with it. The internal polytomy in this tree is also very similar to the ones seen in other runs of the data, and is somewhat severe (28 branches). This polytomy includes most of the members of the other families mentioned in Blake 1983b (see also Table 5). The majority rule tree for data set seven is fairly strong, with high percentages at most nodes,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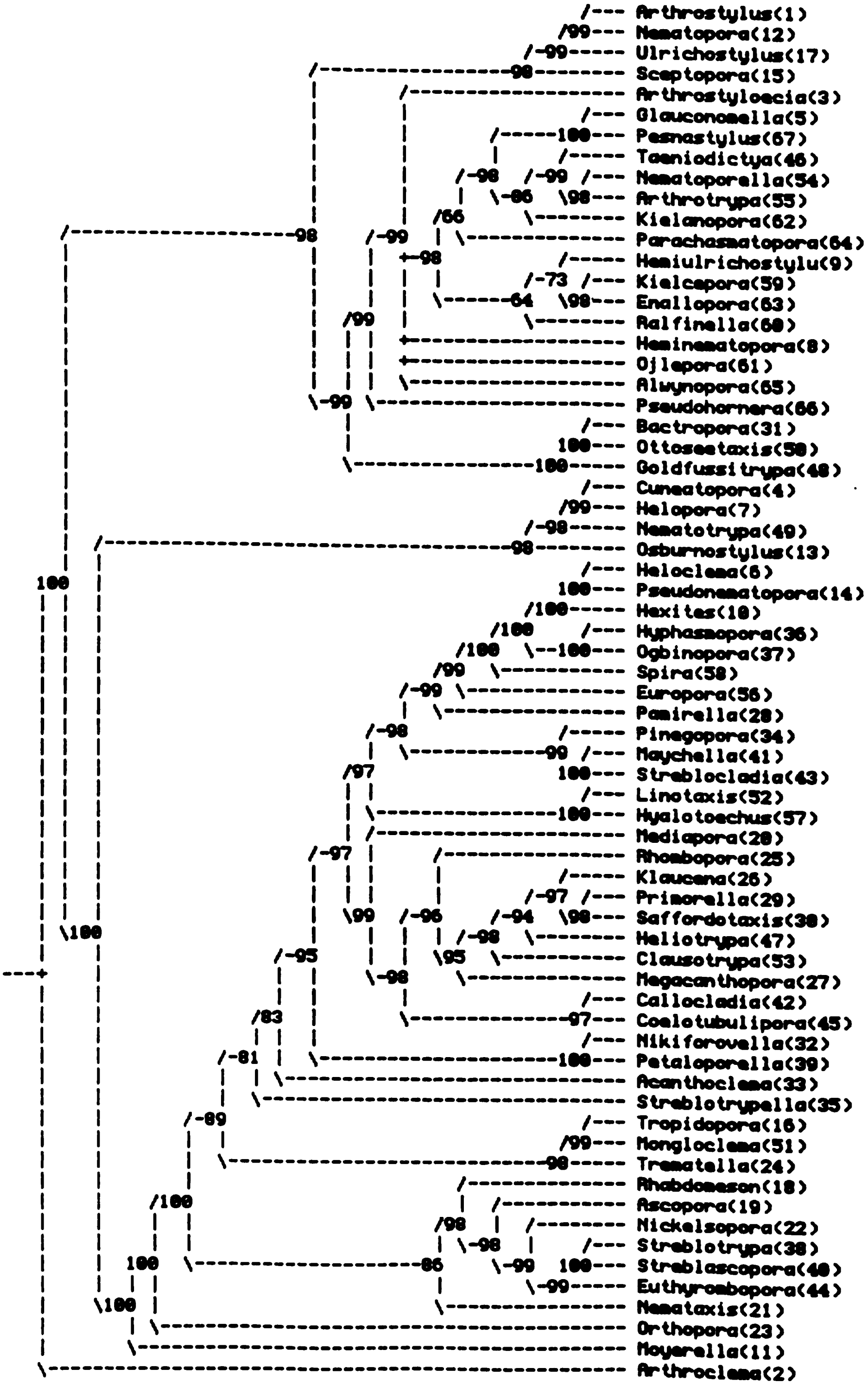
Arthrostyloecia
Cuneatopora
Helociema
Pseudonematopora
Hexites
Hyphasmopora
Ogbinopora
Spira
Tropidopora
Rhabdomeson
Ascopora
Mediapora
Nemataxis
Nickelsopora
Trematella
Rhombopora
Klaucena
Megacanthopora
Pamirella
Primorella
Saffordotaxis
Nikiforovella
Petaloporella
Acanthoclema
Pinegopora
Streblotrypella
Streblotrypa
Streblascopora
Maychella
Streblocladia
Callocladia
Euthyrombopora
Coelotubulipora
Heliotrypa
Mongloclema
Linotaxis
Hyalotoechus
Clausotrypa
Europora
Orthopora
Moyerella
Helopora
Osburnostylus
Nematotrypa
Glauconomella
Pesnastylus
Heminematopora
Hemiulrichostylus
Nematopora
Sceptopora
Ulrichostylus
Bactropora
Ottoseetaxis
Goldfussitrypa
Taeniodictya
Nematoporella
Arthrotrypa
Kielcepora
Ralfinella
Ojlepora
Kielanopora
Enallopora
Parachasmatopora
Alwynopora
Pseudohornera
Arthroclema

Figure 7a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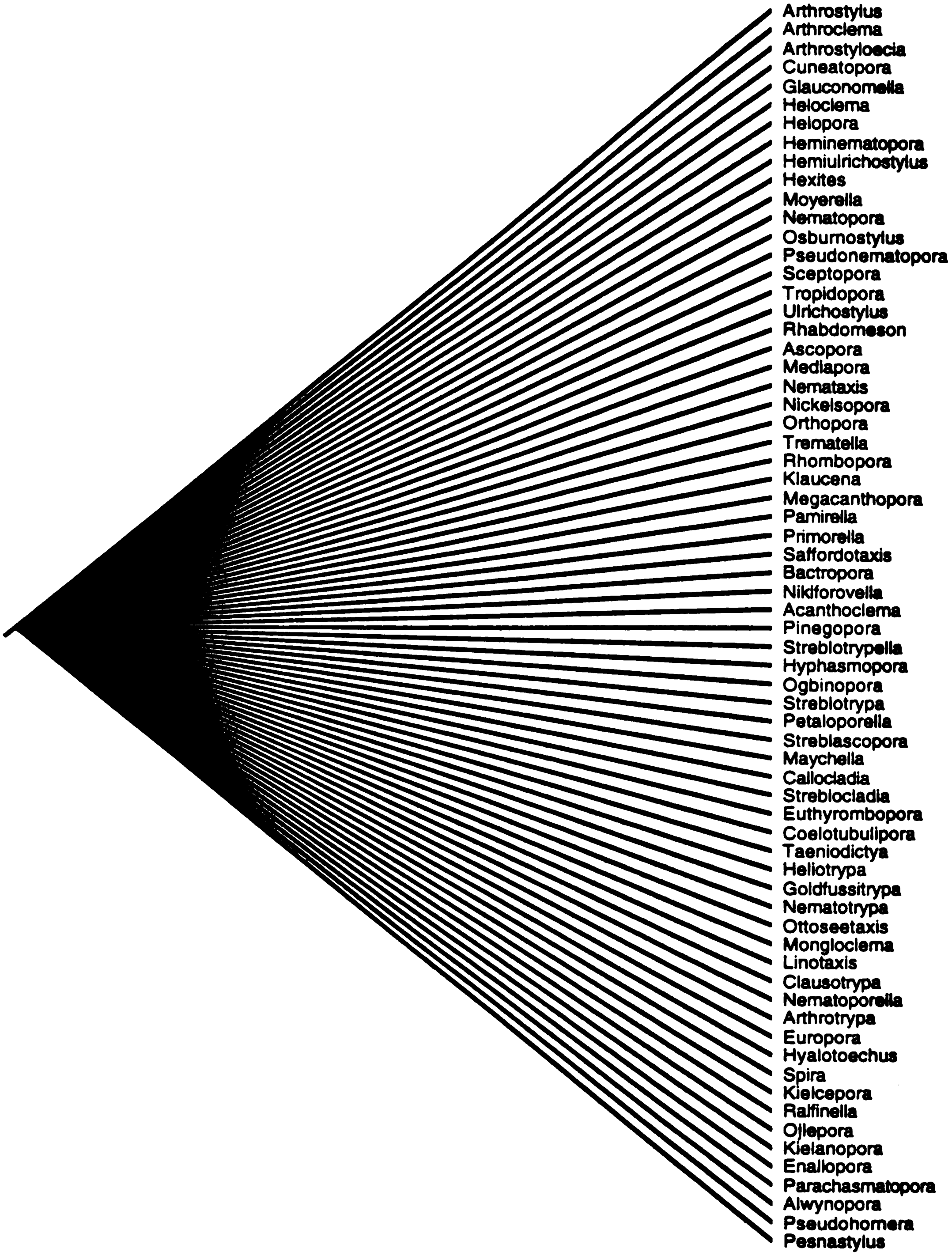
98 Sceptopora(15)
Arthrostyloecia(3)
Glauconomella(5)
100 Pesnastylus(67)
Taeniodictya(46)
98 99 Nematoporella(54)
86 98 Arthrotrypa(55)
66 Kielanopora(62)
98 99 Parachasmatopora(64)
98 Hemiulrichostylu(9)
73 Kielcepora(59)
64 98 Enallopora(63)
99 Ralfinella(60)
Heminematopora(8)
Ojlepora(61)
Alwynopora(65)
99 Pseudohornera(66)
Bactropora(31)
100 Ottoseetaxis(50)
100 Goldfussitrypa(48)
Cuneatopora(4)
99 Helopora(7)
98 Nematotrypa(49)
98 Osburnostylus(13)
Heloclema(6)
100 100 Pseudonematopora(14)
100 Hexites(10)
100 Hyphasmopora(36)
100 100 Ogbinopora(37)
99 Spira(58)
99 Europora(56)
Pamirella(28)
98 Pinegopora(34)
99 Maychella(41)
97 100 Streblocladia(43)
Linotaxis(52)
100 Hyalotoechus(57)
Mediapora(20)
97 Rhombopora(25)
Klaucena(26)
97 Primorella(29)
99 96 94 98 Saffordotaxis(30)
100 98 Heliotrypa(47)
95 95 Clausotrypa(53)
98 Megacanthopora(27)
Callocladia(42)
83 97 Coelotubulipora(45)
Nikiforovella(32)
81 100 Petaloporella(39)
Acanthoclema(33)
Streblotrypella(35)
89 Tropidopora(16)
99 Mongloclema(51)
98 Trematella(24)
Rhabdomeson(18)
100 Ascopora(19)
98 Nickelsopora(22)
98 Streblotrypa(38)
100 86 99 100 Streblascopora(40)
99 Euthyrombopora(44)
100 Nemataxis(21)
Orthopora(23)
Moyerella(11)
Arthroclema(2)

Figure 7b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Arthrostyloecia
Cuneatopora
Glauconomella
Helociema
Helopora
Heminematopora
Hemiulrichostylus
Hexites
Moyerella
Nematopora
Osburnostylus
Pseudonematopora
Sceptopora
Tropidopora
Ulrichostylus
Rhabdomeson
Ascopora
Mediapora
Nemataxis
Nickelsopora
Orthopora
Trematella
Rhombopora
Klaucena
Megacanthopora
Pamirella
Primorella
Saffordotaxis
Bactropora
Nikiforovella
Acanthoclema
Pinegopora
Streblotrypella
Hyphasmopora
Ogbinopora
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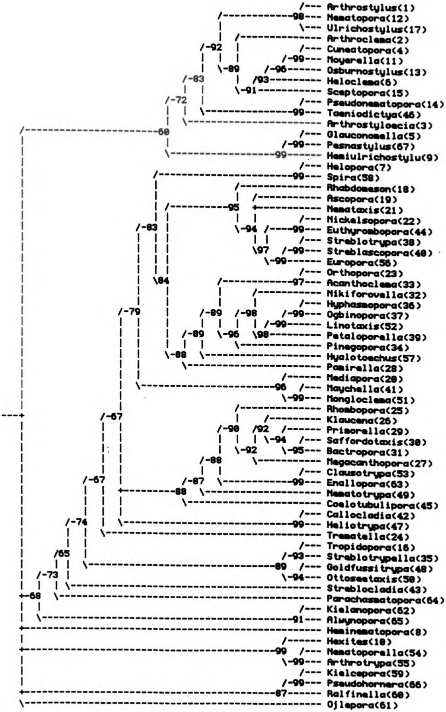
Petaloporella
Streblascopora
Maychella
Callocladia
Streblocladia
Euthyrombopora
Coelotubulipora
Taeniodictya
Heliotrypa
Goldfussitrypa
Nematotrypa
Ottoseetaxis
Mongloclema
Linotaxis
Clausotrypa
Nematoporella
Arthrotrypa
Europora
Hyalotoechus
Spira
Kielcepora
Ralfinella
Ojlepora
Kielanopora
Enallopora
Parachasmatopora
Alwynopora
Pseudohornera
Pesnastylus

Figure 8a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Arthroclema(2)
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Moyerella(11)
Osburnostylus(13)
Heloclema(6)
Sceptopora(15)
Pseudonematopora(14)
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Arthrostyloecia(3)
Glauconomella(5)
Pesnastylus(67)
Hemiulrichostylu(9)
Helopora(7)
Spira(58)
Rhabdomeson(18)
Ascopora(19)
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Nickelsopora(22)
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Maychella(41)
Mongloclema(51)
Rhombopora(25)
Klaucena(26)
Primorella(29)
Saffordotaxis(30)
Bactropora(31)
Megacanthopora(27)
Clausotrypa(53)
Enallopora(63)
Nematotrypa(49)
Coelotubulipora(45)
Callocladia(42)
Heliotrypa(47)
Trematella(24)
Tropidopora(16)
Streblotrypella(35)
Goldfussitrypa(48)
Ottoseetaxis(50)
Streblocladia(43)
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Kielanopora(62)
Alwynopora(65)
Heminematopora(8)
Hexites(10)
Nematoporella(54)
Arthrotrypa(55)
Kielcepora(59)
Pseudohornera(66)
Ralfinella(60)
Ojlepora(61)

Figure 8b

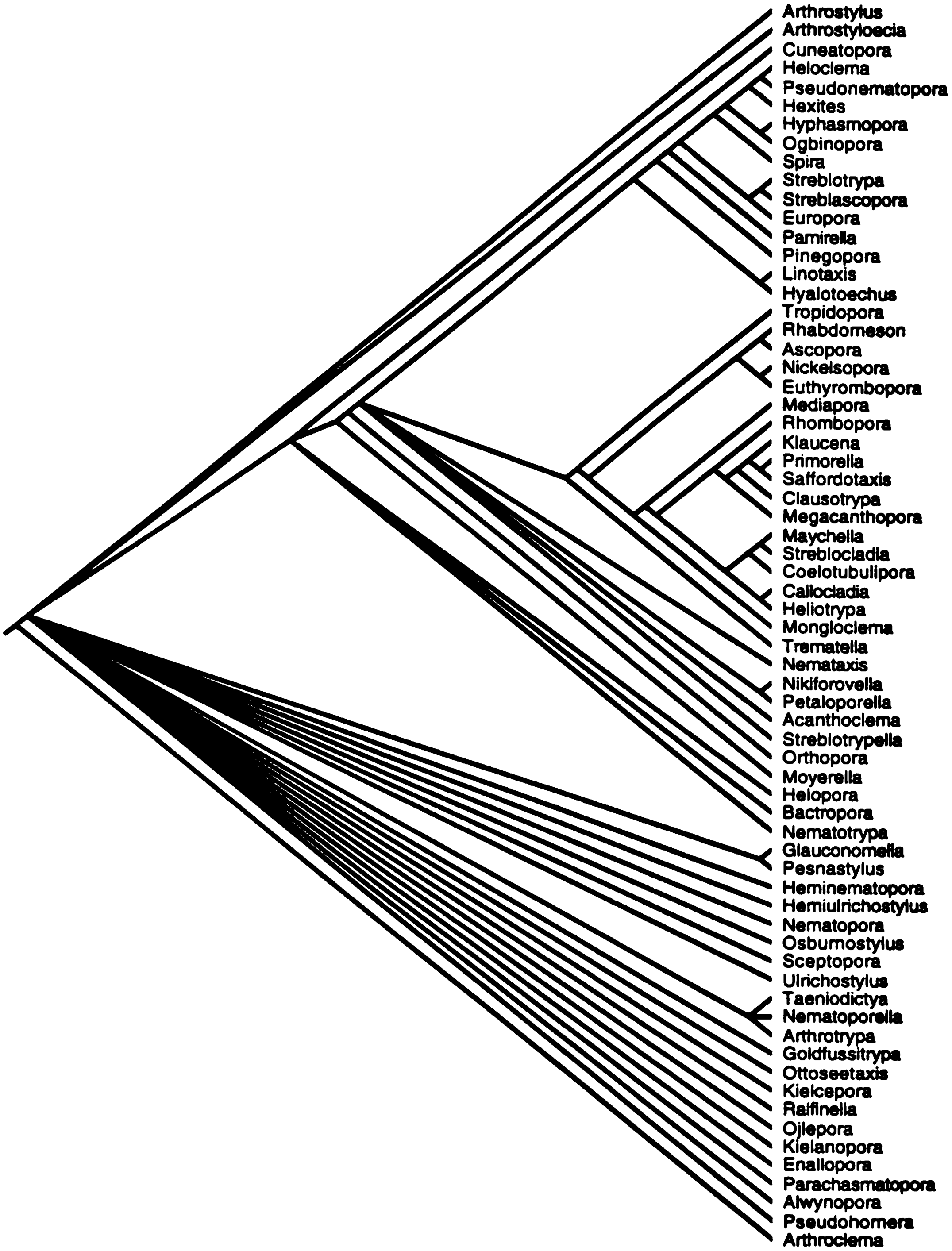
the exceptions being at some of the internal areas where the groupings are consistent, but the internal arrangement of the given group is in question.

Tree eight (figure 8a) is another polytomy, the same problem inherent to the other atemporal strict consensus trees. The majority rule tree (figure 8b) has a basal polytomy, and has the added problem of low percentages on many basal branches.

Trees nine and ten both use the entire data matrix but characters 2 (number of metapores) and 11 (development of the zooecial bend) were changed from an unordered state to an ordered state. This was done because progressions from none to few to many, and strong to weak to negligible seemed to have a logical basis, even though some of the earlier runs did not support a clear order in these characters (see Appendix 1 for more details). Tree nine (figure 9a) has a large polytomy one step up from the tree base, just as many of the other trees did, showing no clear relationship among the arthrostylids and other early genera. The upper part of the tree has a moderately well developed structure and has only two small polytomies. The majority rule tree (figure 9b) for this data set is strong with percentages dropping below 90% only in the arrangement of the arthrostylids.

Tree ten (figure 10a), like all of the other trees that lack the geochronological character, consists only of a universal polytomy. The majority rule tree (figure 10b), however, shows a very strikingly different structure than the other trees in this study, but the supporting percentages on the basal branches are very low.

Trees eleven and twelve used the full data matrix, but the coding had been altered so that the oldest genus *Arthroclema* is a true ancestral genus. What this means is that all of the characters were recoded so that the *Arthroclema* had all zeroes for its character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Streblascopora
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Pamirella
Pinegopora
Linotaxis
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Tropidopora
Rhabdomeson
Ascopora
Nickelsopora
Euthyrombopora
Mediapora
Rhombopora
Klaucena
Primorella
Saffordotaxis
Clausotrypa
Megacanthopora
Maychella
Streblocladia
Coelotubulipora
Callocladia
Heliotrypa
Mongloclema
Trematella
Nemataxis
Nikiforovella
Petaloporella
Acanthoclema
Streblotrypella
Orthopora
Moyerella
Helopora
Bactropora
Nematotrypa
Glauconomella
Pesnastylus
Heminematopora
Hemiulrichostylus
Nematopora
Osburnostylus
Sceptopora
Ulrichostylus
Taeniodictya
Nematoporella
Arthrotrypa
Goldfussitrypa
Ottoseetaxis
Kielcepora
Ralfinella
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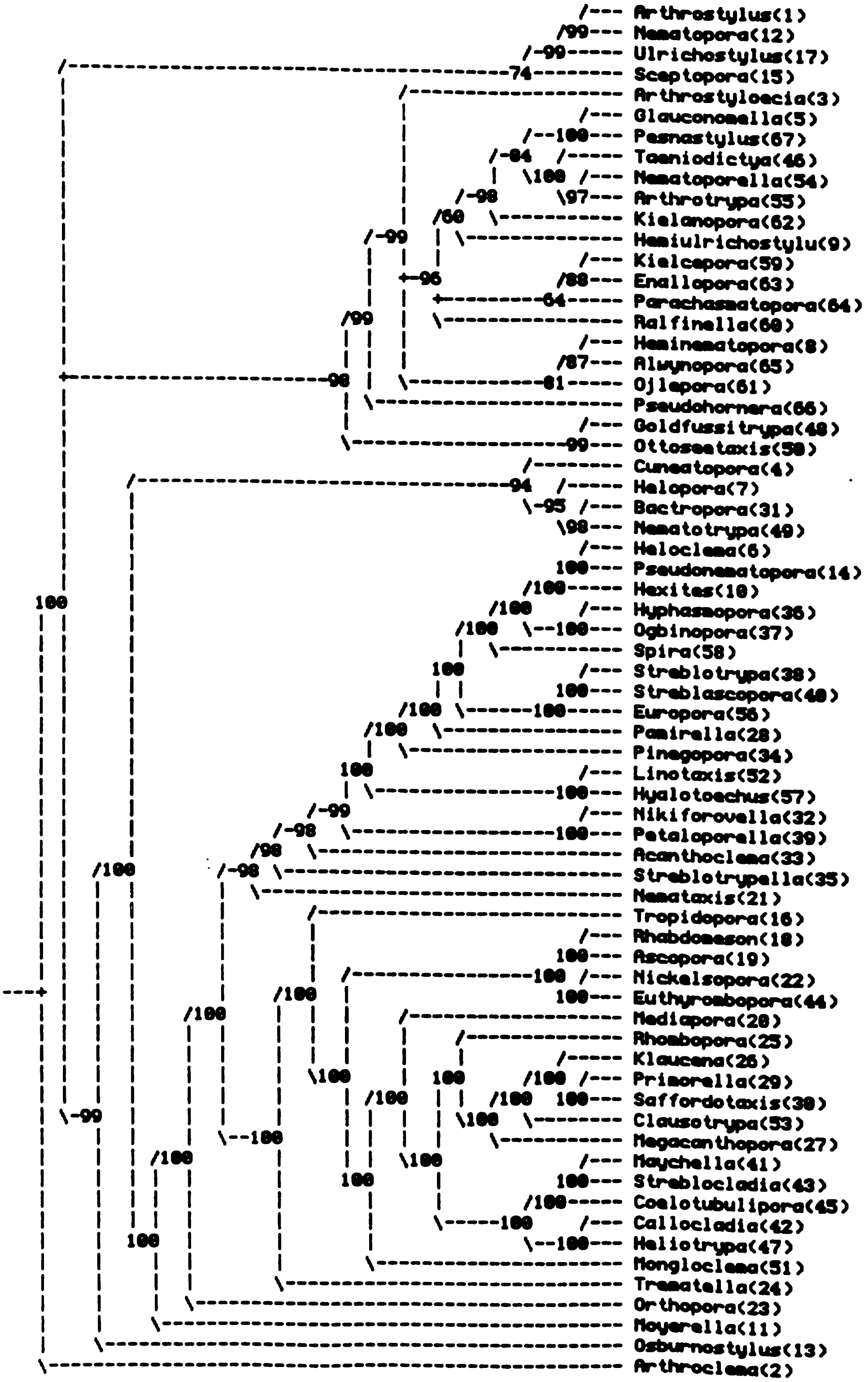
Kielanopora
Enallopora
Parachasmatopora
Alwynopora
Pseudohornera
Arthroclema

Figure 9a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Kielcepora(59)
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Ralfinella(60)
Heminematopora(8)
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Ojlepora(61)
Pseudohornera(66)
Goldfussitrypa(48)
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Helopora(7)
Bactropora(31)
Nematotrypa(49)
Heloclema(6)
Pseudonematopora(14)
Hexites(10)
Hyphasmopora(36)
Ogbinopora(37)
Spira(58)
Streblotrypa(38)
Streblascopora(40)
Europora(56)
Pamirella(28)
Pinegopora(34)
Linotaxis(52)
Hyalotoechus(57)
Nikiforovella(32)
Petaloporella(39)
Acanthoclema(33)
Streblotrypella(35)
Nemataxis(21)
Tropidopora(16)
Rhabdomeson(18)
Ascopora(19)
Nickelsopora(22)
Euthyrombopora(44)
Mediapora(20)
Rhombopora(25)
Klaucena(26)
Primorella(29)
Saffordotaxis(30)
Clausotrypa(53)
Megacanthopora(27)
Maychella(41)
Streblocladia(43)
Coelotubulipora(45)
Callocladia(42)
Heliotrypa(47)
Mongloclema(51)
Trematella(24)
Orthopora(23)
Moyerella(11)
Osburnostylus(13)
Arthroclema(2)

Figure 9b

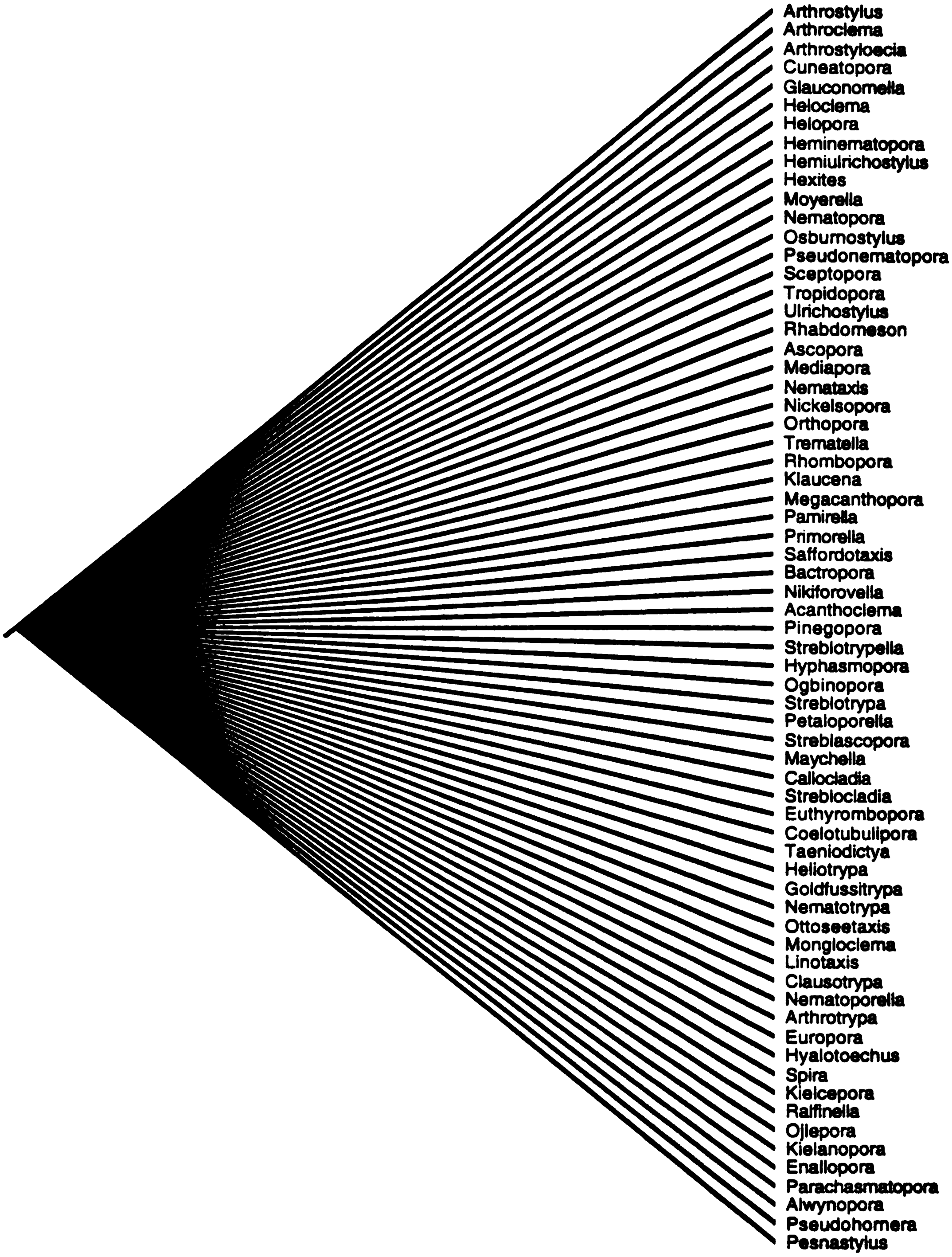
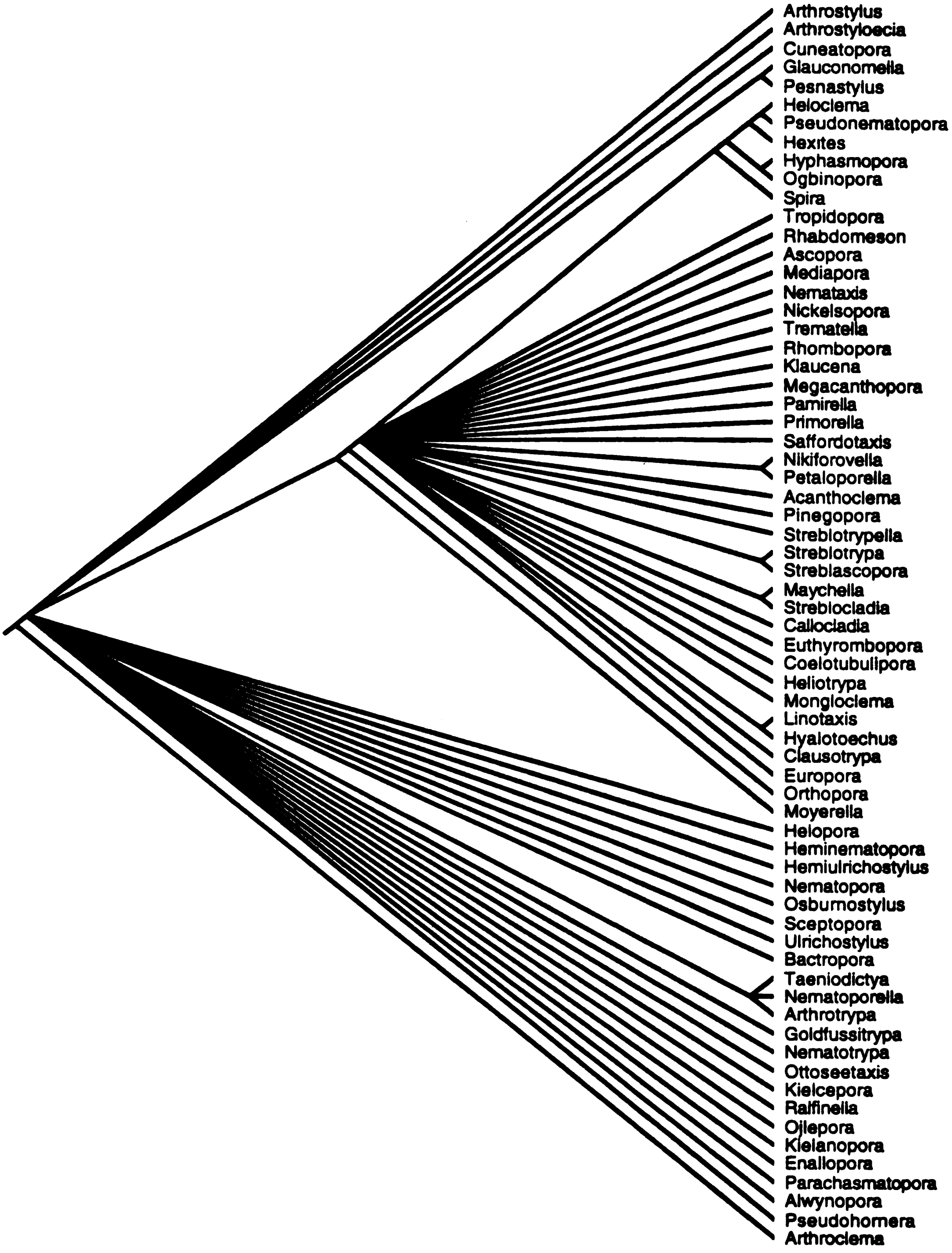

Arthrostylus
Arthroclema
Arthrostyloecia
Cuneatopora
Glauconomella
Heloclema
Helopora
Heminematopora
Hemiulrichostylus
Hexites
Moyerella
Nematopora
Osburnostylus
Pseudonematopora
Sceptopora
Tropidopora
Ulrichostylus
Rhabdomeson
Ascopora
Mediapora
Nemataxis
Nickelsopora
Orthopora
Trematella
Rhombopora
Klaucena
Megacanthopora
Pamirella
Primorella
Saffordotaxis
Bactropora
Nikiforovella
Acanthoclema
Pinegopora
Streblotrypella
Hyphasmopora
Ogbinopora
Streblotrypa
Petaloporella
Streblascopora
Maychella
Callocladia
Streblocladia
Euthyrombopora
Coelotubulipora
Taeniodictya
Heliotrypa
Goldfussitrypa
Nematotrypa
Ottoseetaxis
Mongloclema
Linotaxis
Clausotrypa
Nematoporella
Arthrotrypa
Europora
Hyalotoechus
Spira
Kielcepora
Ralfinella
Ojlepora
Kielanopora
Enallopora
Parachasmatopora
Alwynopora
Pseudohornera
Pesnastylus

Figure 10a

```
                                                 /----- Arthrostylus(1)
                                       /--------95 /--- Nematopora(12)
                                       |         \94--- Ulrichostylus(17)
                                       | /------------- Arthroclema(2)
                                    /-92 |         /--- Cuneatopora(4)
                                    |  | |       /99--- Moyerella(11)
                                    |  \92    /-95----- Osburnostylus(13)
                                 /-91    |  /91-------- Heloclema(6)
                                 |  |    \-90---------- Sceptopora(15)
                                 |  \------------------ Arthrostyloecia(3)
                               /86                 /--- Glauconomella(5)
                               | |               100--- Pesnastylus(67)
                            /-72 \-------------100----- Hemiulrichostylu(9)
                          /65  \----------------------- Heminematopora(8)
                          | \-------------------------- Ojlepora(61)
                       /-71                        /--- Kielcepora(59)
                       |  |                      100--- Pseudohornera(66)
                     /71  \---------------------88----- Ralfinella(60)
                     | |                         /----- Hexites(10)
                     | \-----------------------100 /--- Nematoporella(54)
                     |                           100--- Arthrotrypa(55)
                  /-89                             /--- Streblocladia(43)
                  |  |                           100--- Parachasmatopora(64)
                  |  |                        /-91----- Alwynopora(65)
               /-89  \-----------------------94-------- Kielanopora(62)
               |  |                                /--- Pseudonematopora(14)
             /86  \-------------------------------99--- Taeniodictya(46)
             | |                                   /--- Bactropora(31)
          /-86 \----------------------------------99--- Ottoseetaxis(50)
          |  |                                     /--- Tropidopora(16)
        /86  \------------------------------------99--- Goldfussitrypa(48)
        | \-------------------------------------------- Heliotrypa(47)
     /-71---------------------------------------------- Primorella(29)
   /55  \---------------------------------------------- Saffordotaxis(30)
   | \------------------------------------------------- Klaucena(26)
   |                                               /--- Helopora(7)
   |                           /------------------98--- Spira(58)
   |                           |                 /----- Rhabdomeson(18)
   |                           |         /------94 /--- Nickelsopora(22)
   |                           |         |       100--- Euthyrombopora(44)
   |                           |       /91  /---------- Ascopora(19)
   |                           |       | |  |      /--- Hyphasmopora(36)
   |                           |       | \-97    100--- Ogbinopora(37)
   |                        /-89       |    | /-98----- Streblotrypa(38)
   |                        |  |    /-83    \98-------- Streblascopora(40)
   |                        |  |    |  |      /-------- Nemataxis(21)
   |                        |  |    |  |      |    /--- Orthopora(23)
   |                        |  | /-92  \-----96  /98--- Trematella(24)
   |                        |  | |  |         \-97----- Hyalotoechus(57)
---+                      /88  \94  \------------------ Europora(56)
   |                      | |    \--------------------- Pamirella(28)
   |                      | |                      /--- Nikiforovella(32)
   |                      | |                    /99--- Petaloporella(39)
   |                      | |                 /-98 /--- Pinegopora(34)
   |                   /-86 |                 |  \95--- Streblotrypella(35)
   |                   |  | \----------------93     /--- Acanthoclema(33)
   |                   |  |                   \---97--- Linotaxis(52)
   |                   |  |                      /----- Mediapora(20)
   |                 /85  \---------------------95 /--- Maychella(41)
   |                 | |                         100--- Mongloclema(51)
   |                 | |                           /--- Callocladia(42)
   |              /-70 \--------------------------96--- Coelotubulipora(45)
   |              |  |                             /--- Rhombopora(25)
   |              |  |                           /99--- Megacanthopora(27)
   \-------------54  \--------------------------82 /--- Clausotrypa(53)
                  |                              100--- Enallopora(63)
                  \------------------------------------ Nematotrypa(49)
```

Figure 10b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Arthrostyloecia
Cuneatopora
Glauconomella
Pesnastylus
Heloclema
Pseudonematopora
Hexites
Hyphasmopora
Ogbinopora
Spira
Tropidopora
Rhabdomeson
Ascopora
Mediapora
Nemataxis
Nickelsopora
Trematella
Rhombopora
Klaucena
Megacanthopora
Pamirella
Primorella
Saffordotaxis
Nikiforovella
Petaloporella
Acanthoclema
Pinegopora
Streblotrypella
Streblotrypa
Streblascopora
Maychella
Streblocladia
Callocladia
Euthyrombopora
Coelotubulipora
Heliotrypa
Mongloclema
Linotaxis
Hyalotoechus
Clausotrypa
Europora
Orthopora
Moyerella
Helopora
Heminematopora
Hemiulrichostylus
Nematopora
Osburnostylus
Sceptopora
Ulrichostylus
Bactropora
Taeniodictya
Nematoporella
Arthrotrypa
Goldfussitrypa
Nematotrypa
Ottoseetaxis
Kielcepora
Ralfinella
Ojilepora
Kielanopora
Enallopora
Parachasmatopora
Alwynopora
Pseudohornera
Arthroclema

Figure 11a

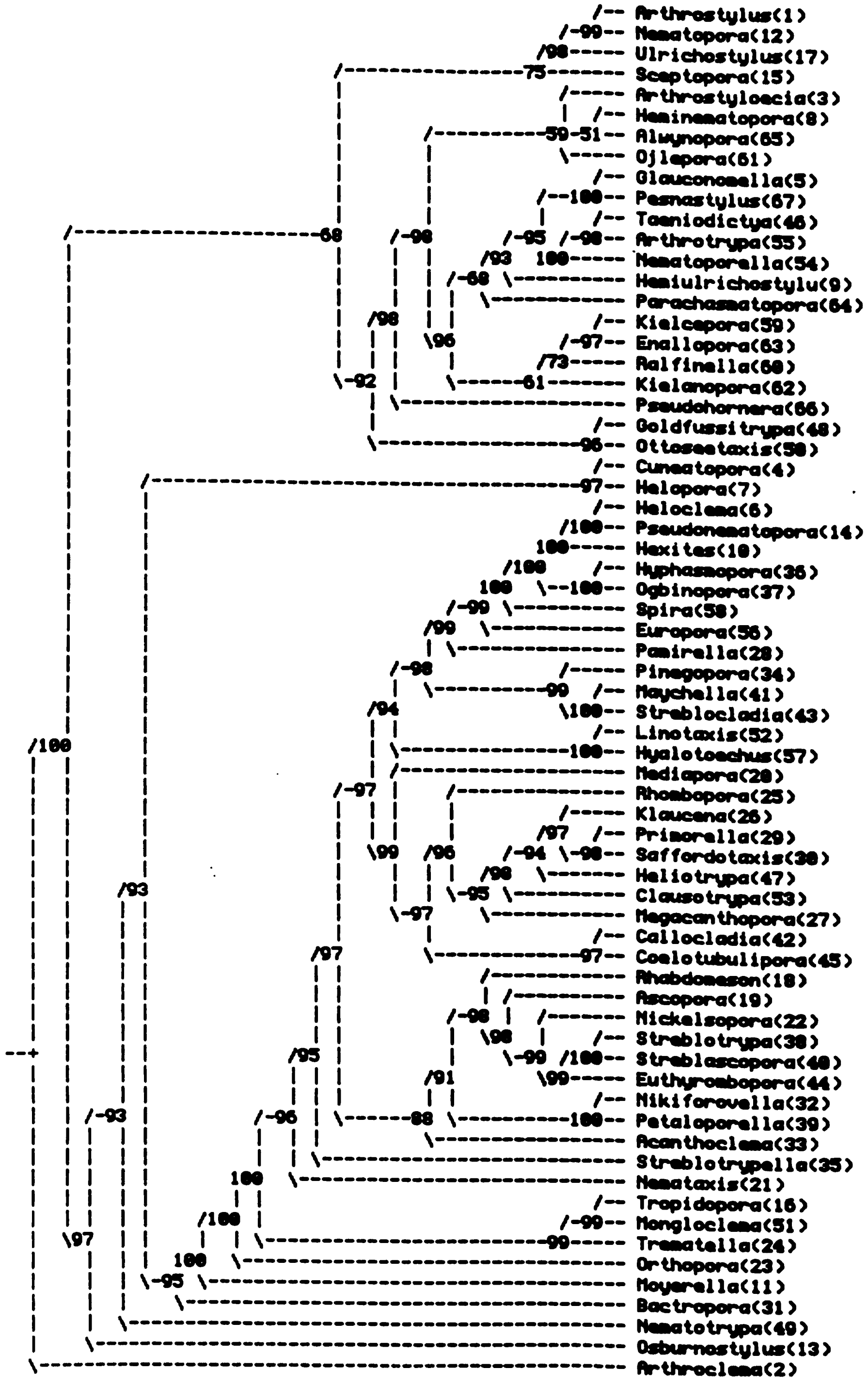
Arthrostylus(1)
Nematopora(12)
Ulrichostylus(17)
Sceptopora(15)
Arthrostyloecia(3)
Heminematopora(8)
Alwynopora(65)
Ojlepora(61)
Glauconomella(5)
Pesnastylus(67)
Taeniodictya(46)
Arthrotrypa(55)
Nematoporella(54)
Hemiulrichostylu(9)
Parachasmatopora(64)
Kielcepora(59)
Enallopora(63)
Ralfinella(60)
Kielanopora(62)
Pseudohornera(66)
Goldfussitrypa(48)
Ottoseetaxis(50)
Cuneatopora(4)
Helopora(7)
Heloclema(6)
Pseudonematopora(14)
Hexites(10)
Hyphasmopora(36)
Ogbinopora(37)
Spira(58)
Europora(56)
Pamirella(28)
Pinegopora(34)
Maychella(41)
Streblocladia(43)
Linotaxis(52)
Hyalotoechus(57)
Mediapora(20)
Rhombopora(25)
Klaucena(26)
Primorella(29)
Saffordotaxis(30)
Heliotrypa(47)
Clausotrypa(53)
Megacanthopora(27)
Callocladia(42)
Coelotubulipora(45)
Rhabdomeson(18)
Ascopora(19)
Nickelsopora(22)
Streblotrypa(38)
Streblascopora(40)
Euthyrombopora(44)
Nikiforovella(32)
Petaloporella(39)
Acanthoclema(33)
Streblotrypella(35)
Nemataxis(21)
Tropidopora(16)
Mongloclema(51)
Trematella(24)
Orthopora(23)
Moyerella(11)
Bactropora(31)
Nematotrypa(49)
Osburnostylus(13)
Arthroclema(2)

Figure 11b

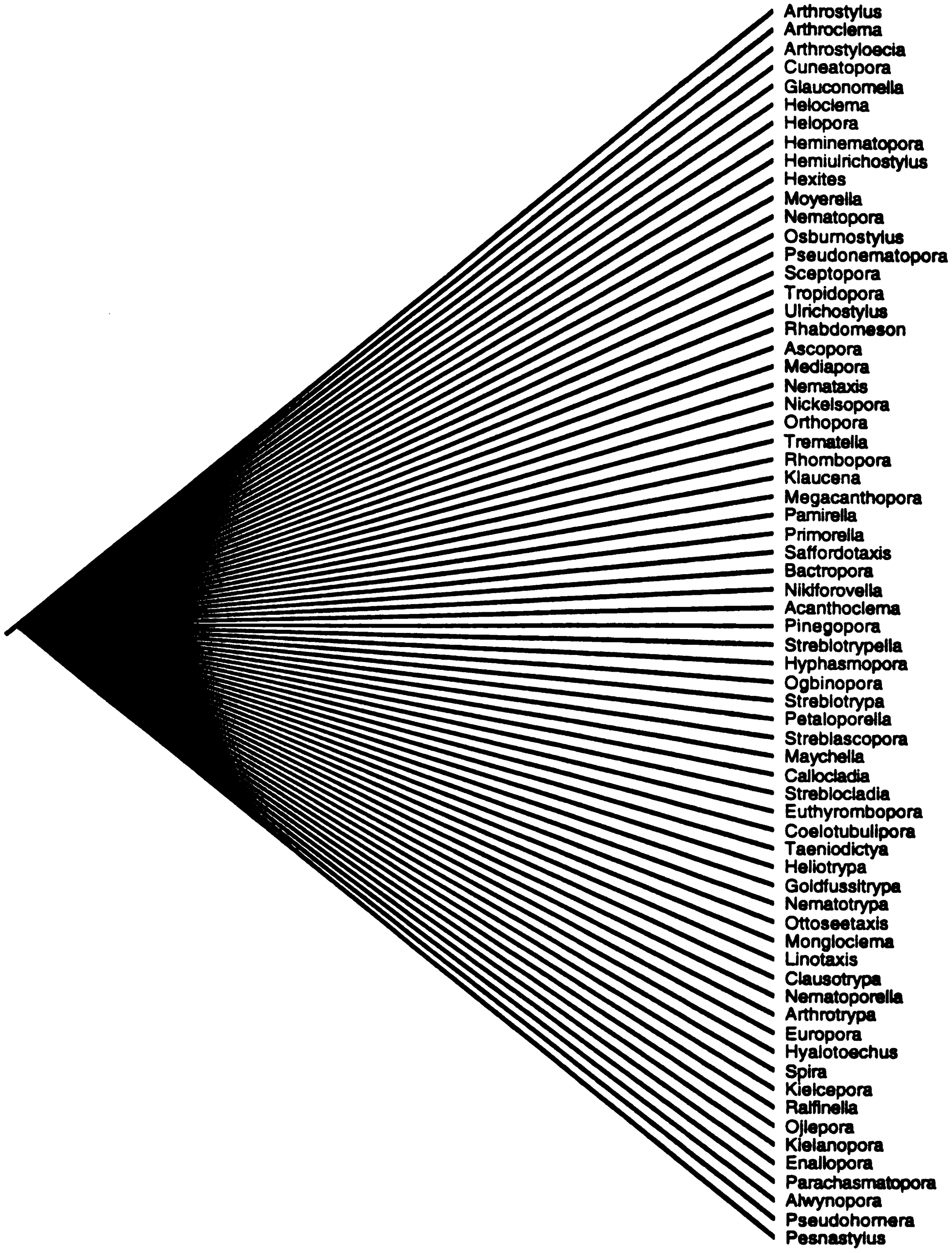
Arthrostylus
Arthroclema
Arthrostyloecia
Cuneatopora
Glauconomella
Helociema
Helopora
Heminematopora
Hemiulrichostylus
Hexites
Moyerella
Nematopora
Osbumostylus
Pseudonematopora
Sceptopora
Tropidopora
Ulrichostylus
Rhabdomeson
Ascopora
Mediapora
Nemataxis
Nickelsopora
Orthopora
Trematella
Rhombopora
Klaucena
Megacanthopora
Pamirella
Primorella
Saffordotaxis
Bactropora
Nikiforovella
Acanthoclema
Pinegopora
Streblotrypella
Hyphasmopora
Ogbinopora
Streblotrypa
Petaloporella
Streblascopora
Maychella
Callocladia
Streblocladia
Euthyrombopora
Coelotubulipora
Taeniodictya
Heliotrypa
Goldfussitrypa
Nematotrypa
Ottoseetaxis
Mongloclema
Linotaxis
Clausotrypa
Nematoporella
Arthrotrypa
Europora
Hyalotoechus
Spira
Kielcepora
Ralfinella
Ojlepora
Kielanopora
Enallopora
Parachasmatopora
Alwynopora
Pseudohomera
Pesnastylus

Figure 12a

```
                                                   /--- Arthrostylus(1)
                                           /------99--- Nematopora(12)
                                           |       \--- Ulrichostylus(17)
                                        /-98  /-------- Arthroclema(2)
                                        |  |  |    /--- Heloclema(6)
                                        |  \-95  /97--- Osburnostylus(13)
                                      /98     \-96----- Sceptopora(15)
                                      | |          /--- Pseudonematopora(14)
                                   /-98 \--------100--- Taeniodictya(46)
                                   |  \---------------- Arthrostyloecia(3)
                                /-93               /--- Glauconomella(5)
                                |  |             100--- Pesnastylus(67)
                              /83  \-----------100----- Hemiulrichostylu(9)
     /-----------------------78 \---------------------- Heminematopora(8)
     |                        \------------------------ Ojlepora(61)
     |                                             /--- Cuneatopora(4)
     |                                        /--100--- Moyerella(11)
     |                                        |    /--- Orthopora(23)
     |                                     /-90  /93--- Linotaxis(52)
     |                                     |  \-90----- Acanthoclema(33)
     |                                  /-90       /--- Nikiforovella(32)
     |                                  |  |     /99--- Petaloporella(39)
     |                                /82  \----82 /--- Pinegopora(34)
     |                                | |        \92--- Streblotrypella(35)
     |                          /----82 \-------------- Hyalotoechus(57)
     |                          |     \---------------- Pamirella(28)
     |                          |                /----- Rhabdomeson(18)
     |                          |       /-------99 /--- Nickelsopora(22)
     |                          |       |        100--- Euthyrombopora(44)
     |                        /85     /97  /----------- Ascopora(19)
     |                        | |     | |  |       /--- Hyphasmopora(36)
     |                        | |     | \-98     100--- Ogbinopora(37)
     |                        | |  /-97    |  /-98----- Streblotrypa(38)
     |                     /-91 |  |  |    \-90-------- Streblascopora(40)
     |                     |  | \-97  \---------------- Europora(56)
     |                     |  |    \------------------- Nemataxis(21)
     |                  /-85  |                    /--- Helopora(7)
     |                  |  |  \-------------------98--- Spira(58)
   /61                  |  |                     /----- Mediapora(20)
   | |                /80  \--------------------94 /--- Maychella(41)
   | |                | |                        100--- Mongloclema(51)
   | |                | |                          /--- Callocladia(42)
   | |                | \-------------------------97--- Coelotubulipora(45)
   | |             /-84                          /----- Rhombopora(25)
   | |             |  |                       /-95 /--- Klaucena(26)
   | |             |  |                       |  \96--- Megacanthopora(27)
   | |          /-78  |                    /-95    /--- Clausotrypa(53)
   | |          |  |  \-------------------94  \--100--- Enallopora(63)
   | |          |  |                       \----------- Nematotrypa(49)
   | |          |  \----------------------------------- Trematella(24)
   | |       /-91                       /-------------- Tropidopora(16)
   | |       |  |                       |     /-------- Primorella(29)
---+ |       |  |                       |  /-92  /----- Saffordotaxis(30)
   | |       |  \----------------------88  |  \-96 /--- Bactropora(31)
   | |     /91                          +-93     \98--- Ottoseetaxis(50)
   | |     | |                          |  \----------- Heliotrypa(47)
   | |     | |                          \-------------- Goldfussitrypa(48)
   | |  /-83 +----------------------------------------- Streblocladia(43)
   | |  |  | \----------------------------------------- Parachasmatopora(64)
   | +-88  \------------------------------------------- Alwynopora(65)
   | |  \---------------------------------------------- Kielanopora(62)
   | |                                             /--- Kielcepora(59)
   | |                                           100--- Pseudohornera(66)
   | \------------------------------------------88----- Ralfinella(60)
   |                                             /----- Hexites(10)
   \--------------------------------------------57 /--- Nematoporella(54)
                                                 \94--- Arthrotrypa(55)
```

Figure 12b

states in the data matrix. This was done because it is the oldest taxon in the study which, if the fossil record were complete, should be the ancestor; however it has more in common with some of the other younger taxa and varies on some points from the trends in the other older taxa. These are the reasons that it was not used as the sole basis for character polarization. Tree eleven (figure 11a) has a structure with a polytomy one step up from the base of the tree, as well as a large internal polytomy similar to trees 5 and 7. Figure 11b (the majority rule data) shows two large groupings as well as the ancestral genus, but the reasons for the polytomies in 11a are clear because the majority rule data shows mid to low range percentages in many locations.

Tree twelve (figure 12a) has the same universal polytomy that is present in all of the other trees that lack the geochronological character. The majority rule information (figure 12b) for the tree shows a fairly good structure, but the percentages around the base are often well below 90%.

DISCUSSION

As mentioned above, in this study the geochronological character was invaluable in the production of a definable tree structure in the Rhabdomesina, as shown strongly in the strict consensus trees. The 50% majority rule trees also showed structure, but the percentage of consistencies among the trees were often quite low in the non-geochronological trees, which shows their apparent weakness in comparison to the geochronological trees. For an analysis of the familial structure, unless otherwise stated,

TABLE 5: FAMILIAL GROUPINGS USED BY OTHER AUTHORS

Arthrostylus	a							a												u
Arthroclema	a							a												u
Arthrostyloecia	a							a												u
Cuneatopora	a							a												u
Glauconomella	a							a							k					
Heloclema	a								rha											u
Helopora	a							a												u
Heminematopora	a							a									r			
Hemiulrichostylus	a							a												u
Hexites	a							a												u
Moyerella	a							a												u
Nematopora	a							a											e	
Osburnostylus	a							a												u
Pseudonematopora	a							a												u
Sceptropora	a							a												u
Tropidopora	a							a							k					
Ulrichostylus	a							a												u
Rhabdomeson		rha							rha											u
Ascopora		rha							rha											u
Mediopora		rha							rha											u
Nemataxis		rha							rha											u
Nickelsopora		rha							rha											u
Orthopora		rha							rha											u
Trematella		rha							rha											u
Rhombopora			rho							rho										u
Klaucena			rho						rha											u
Megacanthopora			rho						rha											u
Pamirella			rho						rha											u
Primorella			rho						rha											u
Saffordotaxis			rho						rha											u
Bactropora				b							b					b				
Nikiforovella					n							n								u
Acanthoclema					n							n?	h?							u
Pinegopora					n							n								u
Streblotrypella					n							n?	h?							u
Hyphasmopora						h							h							u
Ogbinopora						h							h							u
Streblotrypa						h							h							u
Petaloporella							u							u						u
	Arthrostylidae	Rhabdomesidae	Rhomboporidae	Bactroporidae	Nikiforovelidae	Hyphasmoporidae	Not mentioned or Uncertain	Arthrostylidae	Rhabdomesidae	Rhomboporidae	Bactroporidae	Nikiforovellidae	Hyphasmoporidae	Not mentioned or Uncertain	Kielceporidae	Bactroporidae	Ralfinidae	Nematotrypidae	Enalloporidae	Not mentioned or Uncertain
				Blake							Ross						Dzik			

TABLE 5: CONTINUED

	Arthrostylidae	Rhabdomesidae	Rhomboporidae	Bactroporidae	Nikiforovelidae	Hyphasmoporidae	Not mentioned or Uncertain	Arthrostylidae	Rhabdomesidae	Rhomboporidae	Bactroporidae	Nikiforovellidae	Hyphasmoporidae	Not mentioned or Uncertain	Kielceporidae	Bactroporidae	Ralfinidae	Nematotrypidae	Enalloporidae	Not mentioned or Uncertain
Streblascopora						h							h							u
Maychella							u					n								u
Callocladia							u			rho										u
Streblocladia							u			rho										u
Euthyrombopora							u			rho										u
Coelotubulipora							u			rho										u
Taeniodictya							u							u						u
Heliotrypa							u							u						u
Goldfussitrypa							u	a												u
Nematotrypa							u	a										ne		
Ottoseetaxis							u	a												u
Mongloclema							u						h							u
Linotaxis							u			rho										u
Clausotrypa							u					n								u
Nematoporella							u							u						u
Arthrotrypa							u							u						u
Europora							u							u						u
Hyalotoechus							u							u						u
Spira			rho											u						u
Kielcepora							u							u	k					
Ralfinella							u							u			r			
Ojlepora							u							u	k					
Kielanopora							u							u					e	
Enallopora							u							u					e	
Parachasmatopora							u							u					e	
Alwynopora							u							u					e	
Pseudohomera							u							u						u
Pesnastylus							u							u						u
				Blake							Ross						Dzik			

I shall be referring to the families as defined by Blake (1983a), but I have included a table listing the groupings defined by other authors as well (see Table 5). I will use the majority rule trees from data sets seven, nine, and eleven; even though other trees were better in some statistical ways, I will use the trees based upon the whole data set for this discussion.

Though there are many shifts in overall tree structure, several similarities in generic position occur in all three trees. First, the family Arthrostylidae has split up. There are two well-defined groups, and a number of genera that have scattered around the tree. An interesting development is that all of the unilaminate arthrostylids are grouped together with all of the unilaminates that were not included in Blake 1983b (see Table 3) in one clade, with just the unilaminate genera *Arthrostylus* and *Streblocladia* appearing elsewhere on the tree, however the internal arrangement of genera is variable. Another aspect of this group is that three radial genera appear consistently, *Arthrotrypa*, *Nematoporella*, and *Taeniodictya*. The other main stable arthrostylid group is much smaller, and unlike the unilaminate group its internal arrangement seems stable. This group consists of the genera *Arthrostylus*, *Nematopora*, *Ulrichostylus*, and *Sceptropora*. The radial arthrostylid *Arthroclema*, the oldest genus in the suborder, always appears alone at the base of the tree (as I have mentioned above). Eight other arthrostylids are in other places around the tree.

The family Rhabdomesidae has been scattered, but a small grouping has developed around the type genus. This small cluster consists of *Rhabdomeson*, *Ascopora*, *Nickelsopora*, and *Euthyrombopora*, and in two of the three trees *Streblotrypa* and *Streblascopora* are also present.

The Rhomboporidae stayed together fairly well, and also incorporated several of the uncertain genera, in a large consistent grouping. This group includes *Rhombopora Klaucena*, *Primorella*, *Saffordotaxis*, *Heliotrypa*, *Clausotrypa*, *Megacanthopora*, *Callocladia*, *Coelotublipora*, and *Mediapora*.

The Bactroporidae jumped around the tree, sometimes pairing with *Cuneatopora* and *Nematotrypa*, other times matching up with *Ottoseetaxis* and *Goldfussitrypa*, but it did not have a stable position among the three trees.

The Nikiforovelidae was dismantled as a family; genera placed in this family were often within the same larger clade, but not together in a cohesive unit.

In the Hyphasmoporidae the genera were split up with only two groups of two genera consistently together. *Streblotrypa* and *Streblascopora*, as well as *Hyphasmopora* and *Ogbinopora*, but the placement of these pairings was unstable.

There were also several pairings that were consistent in the three trees but their locations were variable. These were: *Cuneatopora* and *Helopora*, *Ottoseetaxis* and *Goldfussitrypa*, *Linotaxis*, and *Hyalotoechus*, and *Nikiforovella* and *Petaloporella*. Only one large consistent grouping was found that did not precisely match up with the current familial structure, including: *Heloclema*, *Pseudonematopora*, *Hexites*, *Hyphasmopora*, *Ogbinopora*, and *Spira*, and in two of the three trees *Europora* and *Pamirella* as well.

It does not seem that any large scale reworkings of rhabdomesine familial structure can be made from this study, due to a lot of ambiguity in the high numbers of trees; however it does seem that the unilaminate arthrostylids should be placed in their own family. One other finding of note is that all of the trees that showed structure divided the suborder into two general groups, one that included most of the arthrostylids, and one that included the majority of the remaining families. Both clades had somewhat variable members depending upon which tree was observed, but several members of each clade remained the same. This information correlates with some of the findings of Anstey and Pachut (1995). In their study of all Paleozoic bryozoan families, the Arthrostylidae were in a group with the fenestrates, and the Rhabdomesine families were in another group. This two clade structure is possibly the most important result of this study, as it shows a possible polyphyletic origin for the suborder, and when compared to prior studies it shows that the Arthrostylidae may have stronger affinities to the fenestrates than the rhabdomesines.

FUTURE WORK

Future work based upon this study should go in two directions: 1) Use this study as a starting point for a more thorough study of the original type specimens, 2) There are less than 450 genera of Paleozoic bryozoans known, and an analysis including all of them would provide a means of looking at the relationships of all of the genera without starting with predesigned orders to trap studies of the systematics. I believe that this more comprehensive generic level study of Paleozoic bryozoans as a whole could very well clarify the phylogeny of this group, and answer some of the questions that this study could not.

APPENDIX A

APPENDIX A

List of characters and their states along with their types and a brief explanation of each.

1. Apertural arrangement: 0 linear rows, 1 rhombic, 2 irregular [unordered]

This character describes the arrangement of the apertural openings in the colonial skeleton. The most primitive state is that where the openings are in a linear arrangement that runs down the length of the colony, usually two to four rows are encountered. The rhombic arrangement is most easily described as a situation where the openings are in diagonal rows, where the apertures (when taken in groups of four) form rough rhombuses. The irregular arrangement, as can be deduced by its name, are the colonies that do not seem to have any consistent pattern to their apertures. Originally I thought that there seemed to be a noticeable trend from linear to rhombic to irregular when the genera were looked at through time, however I later decided that, all I could be sure of was that the linear state was primitive, and the other two states were derived, but not necessarily from one to the other. In the final analyses this character was dropped in favor of characters 15, 16, and 17. These characters looked more specifically at the three aspects of character 1, whether or not the openings are rhombic, linear or organized.

2. Metapores: 0 none, 1 few or not in all species, 2 many [unordered]

Metapores are variably sized cavities in the surface of the zoarial wall, most likely used to space the zooecia in the colony. They are present in many genera, but not always in all species of the genus. Also there are varying numbers occurring on different genera, some have only a small number scattered around the zoaria, while others are covered almost solidly with them. The absence of this structure is clearly synapomorphic, but there never seemed to be a clear trend between state 0 and the other two states. I tried running this character as both an ordered and an unordered character, with few differences being shown, but the consistency index for this character was higher in the unordered state, so I left it that way for the most of the final analyses. The exceptions to this were trees nine and ten, which were run to see if their ordering had a significant impact.

3. Paurostyles: 0 no, 1 yes [ordered]

Characters 3-6 all deal with the presence or absence of various types of spine like protrusions from the external zoarial wall, approximately perpendicular to the zoarial surface and parallel to the zooecium. There are four different types of these stylets that exist within the suborder, which are all pictured and described in Blake (1983a pp. 537-541). The first that I have listed is the type known as paurostyles. These stylets are the smallest and most difficult to see, they have somewhat clear cores and appear as small deflections in the lamellae of the wall. I usually had to rely on written descriptions to account for this character, as these structures are very difficult to see in photographs. Their presence was apomorphic due to their inconsistent presence in the early genera of the suborder.

4. Acanthostyles: 0 no, 1 yes [ordered]

The second and most prominent type of stylets were the acanthostyles. These stylets are the largest type of stylet, which can be seen as large hollow cores that run perpendicular to the surface of the zoaria; these were seen in many genera. Their presence was also apomorphic due to inconsistent presence in the early genera. (See also character 3)

5. Aktinotostyles: 0 no, 1 yes [ordered]

The third type of style is the aktinotostyles; these are also quite large structures which can be differentiated from the acanthostyles by their dark cores. Their presence was apomorphic due to their rare occurrence, being in only a few genera. (See also character 3).

6. Heterostyles: 0 no, 1 yes [ordered]

The final type of stylet is the heterostyle; these small rare structures only occur in three genera, and for that reason their occurrence was considered an apomorphy. These structures were difficult to see and I had to rely on written descriptions to use them in the data matrix. (See also character 3).

7. Vertical axial zooecia: 0 no, 1 yes [ordered]

This character is somewhat rare and exists only in a few genera. It looks for the presence of a cluster of zooecia in the central region of the zoaria that are running parallel to the colony branch; its rare presence is an apomorphic state.

8. Branch cross-section: 0 subcircular, circular, round, 1 polygonal [ordered]

Character eight was looking at the overall shape of the zoarial branch in cross section. State zero was used for any degree of roundness that was observed in the taxa, while the apomorphic state was reserved for the younger occurrence of a rigid polygonal state.

9. Longitudinal ridges: 0 yes, 1 no [ordered]

This character was looking for ridge-like structures that ran the length of the zoarial branches. Since they were common in the older taxa I decide to make their presence the plesiomorphic state.

10. Zoarial jointing: 0 yes, 1 no [ordered]

This character dealt with the presence of segmented joints in the zoarial branches. As the character was common only in the older taxa I decided to make its absence the apomorphic state.

11. Zooecial bend: 0 strong, 1 weak, 2 negligible [unordered]

The zooecial bend is the curvature of the zooecial chamber as it runs from the zoarial surface to the center of the zoaria. As in many of my unordered characters, I could easily determine the plesiomorphic state, but had difficulty deciding an order for the other states. I experimented with it both ways and from the trees that were produced I decided that I could not justify a specific order for this character, however I did use this as an ordered character in the runs that created trees nine and ten, to see if there was an impact on the final analyses.

12. Zooecia on both sides: 0 no, 1 yes [ordered]

This character describes the unilaminate or radial form of the zoarial branches. The simplest description is the one I originally used in the character name, a state where zooecia exist on only one side. Almost all of the unilaminate genera are early in the history of the suborder, so that is why having zooecia on both sides is an apomorphy. (See character 23)

<u>13.</u> Time: 0 Ordovician, 1 Silurian, 2 Devonian, 3 Carboniferous, 4 Permian (not used in final study in favor of character 14) [irreversible up]

This coarse grained geochronological character is a carry over from when I did not have enough information to complete character 14.

<u>14.</u> Time: 0 Tremadocian, 1 Arenigian, 2 Llanvirnian, 3 Caradocian, 4 Ashgillian, 5 L Silurian, 6 U Silurian, 7 L Devonian, 8 M Devonian, 9 U Devonian, 10 L Carboniferous, 11 M Carboniferous, 12 U Carboniferous, 13 L Permian, 14 U Permian [irreversible up]

This geochronological character is one of the major focuses of my study. As I have previously mentioned not everyone sees the value in the use of time as a cladistic character, but in this study this character was the only saving one that was able to put conclusive order in the strict consensus trees. The irreversible up setting allows for the character to change as far as it needs to in the higher states, but cannot change backwards (as time cannot go backwards).

<u>15.</u> Ordered zooecial arrangement: 0 yes, 1 no [ordered]

This character looks for organization in the arrangement of the apertural openings, by looking at the older genera in the suborder I determined that order is plesiomorphic, and that the genera showing strong disorder were apomorphic. (See character 1 for further discussion).

16. Zooecia in rows: 0 yes, 1 no [ordered]

This character regards the linear arrangement of the apertures, usually in two to six rows along the zooecial branches. By looking at the oldest genera in the suborder I decided that linear arrangement was synapomorphic and non-linear arrangements were apomorphic. (see character 1 for further discussion).

17. Zooecia rhombicly arranged: 0 no, 1 yes [ordered]

Much like the two previous characters this one deals with the arrangement of the apertural openings. As the oldest genera were all arranged in a linear fashion, I used the absence of rhombic arrangement as the plesiomorphic state, and the presence of this arrangement as the apomorphic state. (See character 1 for further discussion).

18. Branched zoaria: 0 no, 1 yes [ordered]

This character is used to describe zooarial forms that have a branching pattern of some form, but not a pinnate one (see character 19). An extreme majority of the zoarial shapes displayed by this group are branched in some way, however a few of the earliest genera, including the oldest one, are single unbranched forms. Character 18 was used to show this difference, branching was considered an apomorphic state, while non branching forms were considered plesiomorphic.

19. Pinnate zoaria: 0 no, 1 yes [ordered]

This character was originally included when I thought that a clear connection to the fenestrate bryozoans (which often have pinnate or grid-like forms) was going to be more noticeable. However when I began to code characters I realized that almost none displayed this unusual branching form, and in the end only two taxa were apomorphic for this state, *Glauconomella* and *Pesnastylus*.

20. Hemisepta: 0 none, 1 upper wall, 2 lower wall, 3 both walls [unordered]

This character deals with protrusions from the walls of the zooecial chamber, and which walls they protrude from. Again, the plesiomorphic state was easily determined but the order in the apomorphic states was not clear. I tried running this character in an ordered state, but even then no clear patterns emerged, so I left the character in an unordered state.

21. Peristomal ridges: 0 yes, 1 no [ordered]

Peristomes are small ridges that form around the zooecial opening in the colony branches. These ridges are common in the older taxa of the suborder, and that is why I decided that their presence should be plesiomorphic and their absence apomorphic.

22. Stylets: 0 no, 1 yes [ordered]

This character was to reinforce situations when I knew that stylets were present but could not be completely certain of the type. In following with the other stylet characters I made their presence an apomorphy.

23. Zooecial pattern in cross-section: 0 radial, 1 bilaminate, 2 strongly radial, 3 close packed, 4 hollow central chamber, 5 unilaminate, 6 hexagonal, 7 NOT USED, 8 medial rows (not used in final study in favor of characters 12, 26-32) [unordered]

This character is a description of the arrangement of the zooecia and the other internal structures as viewed from a cross section of the zoarial branches. I tried for some time to find a way for this character to be put in an ordered state, but to no avail. The blank spot in state 7 is due to a state that I had thought was to be included, but only after the information had been entered into the computer did I realize that it was not needed. See the aforementioned characters for details of the states; all characters have the presence of the state as an apomorphy.

<u>24.</u> Large central style: 0 yes, 1 no [ordered]

This rare trait was seen in only a few genera, and since only one occurred outside of the Ordovician I decided to make the trait a plesiomorphy, and the lack of it an apomorphy.

<u>25.</u> Zooecial shape (as defined in Blake, 1983a, pg. 535.) 0 type 7, 1 type 1, 2 type 2, 3 type 3, 4 type 4, 5 type 5, 6 type 6 (not used in final study in favor of characters 33-39) [unordered]

The trait can only be best described by looking at the figure in Blake 1983a (reproduced as Figure 13). Each type is a different kind of zooecial chamber construction. The types range from a nearly perpendicular chamber in type 6, to a straight diagonal chamber like in type 1. Originally I tried to polarize this character, but had too many difficulties in deciding the order after the first, so I converted the character into seven smaller characters where each type was apomorphic for the presence of a given type. (See characters 33-39).

<u>26.</u> Hollow central x-section: 0 no, 1 yes

This describes the hollowness of the center of some zoarial branches, in some cases possibly due to a form of encrusting behavior. (See character 23).

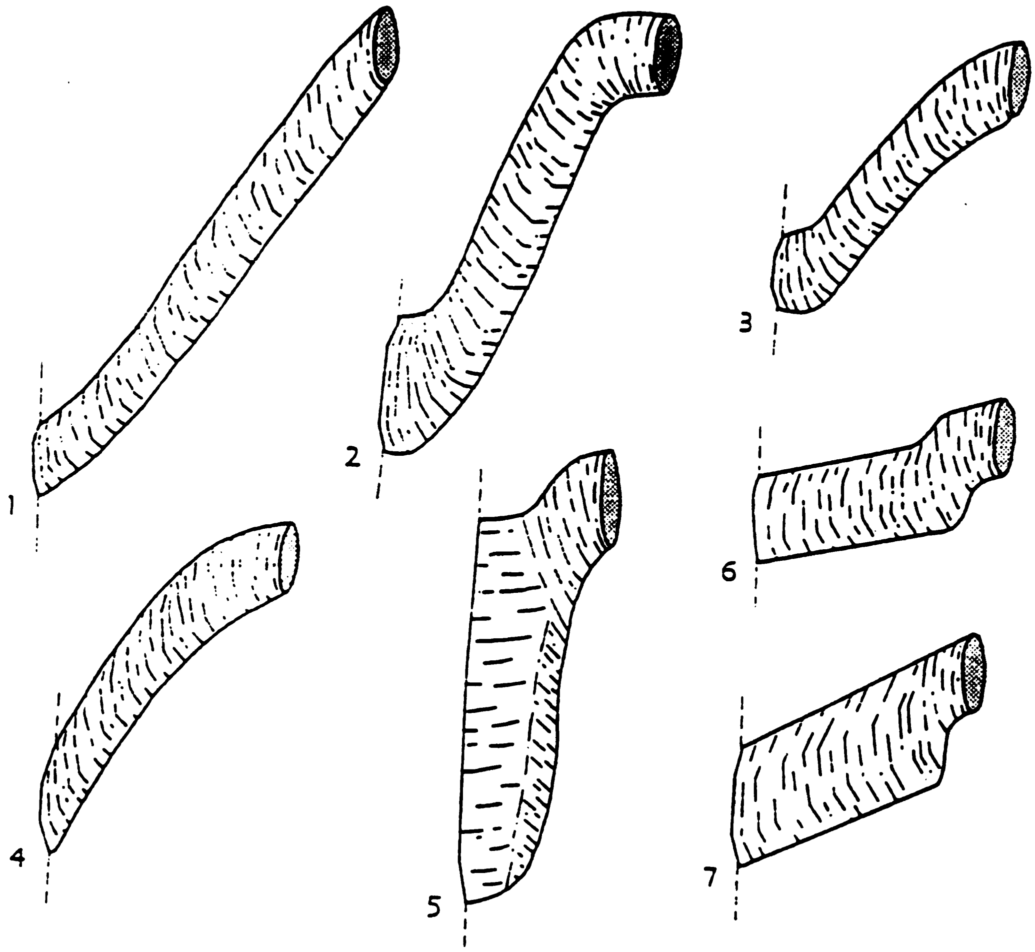

Figure 13
Taken From Blake 1983b, pp. 535

27. Radial central x-section: 0 no, 1 yes

A radial cross section appears to have the supporting walls of the zoaria radiating out from the center of the branch. (See character 23).

28. Bilaminate central x-section: 0 no, 1 yes

The zooecial chambers have a bilaminate pattern in this type of cross section. (See character 23).

29. Trepostome like central x-section: 0 no, 1 yes

This character has a cross section that is convergent with the kind that is seen in the order Trepostomata. All of the zooecial chambers are closely packed together in a tight bundle. (See character 23)

30. Strongly radial central x-section: 0 no, 1 yes

This type of cross section is similar to the radial type, but the radiating wall structures have a strong spoke like look to them. (See character 23).

31. Medial rows in central x-section: 0 no, 1 yes

The type of cross section that has medial rows will have one or two rows of zooecia that will seem to be parallel to the branch and will be the center for the lateral zooecia. (See character 23)

32. Hexagonal central x-section: 0 no, 1 yes

A hexagonal cross section has a radial appearance, but the spokes are so strong that the entire branch takes on a hexagonal shape. (See character 23)

33. Type 1: 0 no, 1 yes

(See character 25)

34. Type 2: 0 no, 1 yes

(See character 25)

35. Type 3: 0 no, 1 yes

(See character 25)

36. Type 4: 0 no, 1 yes

(See character 25)

37. Type 5: 0 no, 1 yes

(See character 25)

38. Type 6: 0 no, 1 yes

(See character 25)

39. Type 7: 0 no, 1 yes

(See character 25)

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