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A QUANTITATIVE STUDY OF GENERIC DELIMITATION IN THE ADIANTOID FERNS

by
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A dissertation submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy in the
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PREFACE

Problems of generic delimitation in adiantoid ferns and their allies have been recognized for decades. Several outstanding pteridologists of this century, including Christensen (1924, p. 85), Weatherby (1941, p. 253 and 1943, p. 69) and Copeland (1947, pp. 66, 81, 82), have noted the confusion, but have not--using the knowledge and methods of their times--been able to place the many species into satisfactory genera.

My interest in this problem was aroused by Professor Warren H. Wagner, Jr., who suggested that the study would make a fine doctoral thesis. Dr. Rolla M. Tryon, Jr. recommended a study of about a dozen species of Cheilanthes, Notholaena, and Pellaea, which could be expected to result in a clarification of the limits among these genera. But an examination of this material demonstrated mostly the clear delimitation of species and the obscure or arbitrary boundaries of the "genera" into which they were currently assigned.

The natural thing to do, therefore, was to broaden the study to include specific examples of all the genera and sub-genera related to the three central genera. I was reminded, however, that the most noted pteridologists of a century had not bested this problem of generic delimitation; nor could I hope to--using their methods.

The adiantoid ferns share two characteristics with many other difficult taxonomic groups: the taxa are numerous and their variation patterns are complex. According to Christensen in Verdoorn (1938, pp. 537, 538), approximately 715 species in about twenty-six genera are directly involved. Not only do some of the so-called generic characters appear to be repeated in several genera, but, in my opinion, some of the genera seem badly delimited by arbitrary characters, probably because they were founded on the insufficient material available to the 18th and 19th century botanists. In such a group, the taxonomist finds his mental storage and correlative abilities insufficient.

Contrary to the claims of a few recent authors, such as Sokal and Sneath (1963, pp. 5-11) for example, our usual taxonomic procedures are, in the main, correct; they are useful, stable, and repeatable. A large body of satisfactory taxonomic work attests to this. The "ordinary" taxonomic method is really the usual way men reduce the phenomena of the world to the abstractions which constitute memory, thought, and language.

To discover a more natural grouping of these genera and subgenera, therefore, it seemed that an extension of the sound work of my predecessors was called for. I have tried to produce a data processing system that is roughly analogous to the taxonomist's mental processes, but one that does not easily run out of storage space or correlative capacity. Specifically, I have aimed for: an improved systematic philosophy, more data taken in an unbiased way, greater capability in

analyzing the data, and a more sophisticated taxonomic methodology, which, when it failed to resolve the data into probable groups, would give notice as to the likely causes of the failure.

I am grateful for the guidance, criticism, and encouragement of Professors T. H. Hubbell, W. S. Benninghoff, E. E. Steiner, C. A. Arnold, and, especially, W. H. Wagner, Jr., whose own work forms an extensive basis for this study. Thanks are also due C. V. Morton, for his counsel on matters both nomenclatural and taxonomic, and J. T. Parsons, for his programming skills which translated my verbal instructions into the language of the computer. Generous aid from the H. H. Rackham School of Graduate Studies in The University of Michigan, the H. H. Bartlett Travel Fund, and the National Science Foundation is hereby acknowledged. For their kindness in lending specimens, I wish to thank the Curators of the Herbaria of the Chicago Museum of Natural History, the University of California (Berkeley), the Gray Herbarium of Harvard University, The University of Michigan, and the Smithsonian Institution.

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CHAPTER I

REVIEW OF PRINCIPAL QUANTITATIVE TAXONOMIC METHODS

Introduction

Milestones in the progress of taxonomy are marked with the names of botanists who were sufficiently concerned with the principles of their craft to leave its practice long enough to describe the methodology which they employed. Linnaeus (1751, pp. 97-101), Adanson (1763), De Candolle (1813, particularly pp. xxxiv-lxij), Bessey (1915, pp. 112-117), Danser (1950, especially pp. 152-167), Sporne (1948, 1954, 1959), and Sneath (1957a, 1958) are some who come immediately to mind. An examination of these works reveals a trend toward increasingly sophisticated graphical and mathematical methods, with the biological assumptions necessary to each perceptively and sometimes even prophetically stated.

Recent writings of Gilmour (1961), Michener and Sokal (1957), Rao (1948), Sneath (1961), Sneath and Sokal (1962), Sokal (1958), Sokal and Sneath (1963), and Williams and Lambert (1961) summarize the quickening interest in objective methods of classifying living things. Published works concerning quantitative methods have increased greatly in the past few years. It is perhaps the physical scientists who have hastened the transformation of the taxonomic art into a more nearly exact science. Nor is this new science yet definitely named. Rogers (1963) points out five current appellations: quantitative

taxonomy, numerical taxonomy, taxonometrics, taxometrics, and taximetrics, all the while stressing that "taximetrics [is not even really] new; it merely reflects a growing concern for some aspects of the art or science. The new element is the . . . computer. . . . This device can be used, or misused, in the same way that other devices and concepts are used or misused."

The taxonomist working with biological material is faced with a situation that is at once both comforting and disquieting. Unlike the data of non-organismal material, the biologist's data are unique in being patterned in this particular way: they reflect the processes of organic evolution. The fact that the material shows specific kinds of non-random patterns sets the potential methods which might be used to classify biological data apart from methods used on other materials and in other disciplines. On the other hand, the discovery and characterization of the organismal patterns is far more difficult than the description of, for example, the periodic table of inorganic elements.

In Linnaeus' day the genus was considered the most real of hierarchical categories. Today, most herbarium taxonomists consider the species as their fundamental category. This taxon is, at best, a "kind"--discrete, homogeneous, and discontinuous from other species. But the study of population dynamics within species such as Drosophila melanogaster has shown that panmictic populations are the real building blocks of sexually breeding species, being the fundamental evolving units. When populations undergo the processes of mutation, introgression, migration, isolation, and so on, evolution is happening.

Sometimes these processes result in morphological or behavioral changes so profound that the systematist considers the population a distinct taxon. It is clear that which taxonomic level is regarded as fundamental is a function of the taxonomist's understanding of the group. Linnaeus often knew only a very small percentage of the extant species of his genera, just as modern taxonomists are acquainted with only a few of the expressed genotypes of every species. His genera were more nearly monothetic, with even unrelated species sharing the few characters he used. On the other hand, our species are often monotypic, in the sense that they are morphologically homogeneous for more than just the defining characters we employ.

The classification-producing taxonomist must interpret the available data so as to develop the kind of classification desired by induction from the evidence, using a suitable methodology. He must be aware of both the existing evidence and the intervening gaps in the data. Taxonomists of our time find themselves charged with the task of increasing the logicality and probability of their methods and classifications. Every taxonomist, therefore, should think out very carefully these fundamental questions:

(1) What are the purposes of the classification?

(2) Therefore, what kind of a classification is needed?

Once answers to these questions have been found, it becomes possible to ask:

(3) What are the data to be used?

(4) How should the data be used?

The concept of "correct" classification is necessarily a human judgement which ought to be applied in the light of the purposes which a classification is to serve. Thus an evolutionary classification could be well-suited and thus "correct" for its purpose of summarizing evolutionary knowledge, and yet be unsuited and therefore "incorrect" for some special, non-evolutionary purpose.

The ideal evolutionary classification would be the one which most accurately reflected the evolutionary history of the group in question. But the studies of evolution and speciation necessary to such a classification, particularly in the tropical floras and faunas, is more than an enormous task. Drosophila has been studied for fifty years. A few genera of plants have been examined over the same length of time, though scarcely in sufficient detail. Obviously, a world-wide working taxonomy would never be developed if it were approached in this ideal way.

The ideal, assortive, purely taxiometric classification would contain the greatest amount of information about the plants (but not necessarily about their evolution), and, at the same time, could be prepared with the greatest efficiency, using the fewest number of most meaningful and effective characters possible. Rogers and Tanimoto (1960) and Rogers and Fleming (1964), for instance, emphasize Shannon's information theories in analyzing data distributed in semimetric space. Gilmour (1937) asserts that natural classifications in the phylogenetic sense would have to have a phylogenetic basis. Data could be gleaned from two sources: genetic observations or experiments and phenetic characteristics. But the use of phenetic evidence would require the

assumption that similarity is a valid measure of evolutionary distance, convergence and parallelisms notwithstanding. In most cases, the former kind of evidence is virtually unobtainable, and the latter is not completely reliable. Under these circumstances, Gilmour thinks it best to restrict "natural classifications" to a slightly different meaning. He suggests that the natural classification should be "that arrangement of living things which enables the greatest number of inductive statements to be made regarding its constituent groups . . ." (Gilmour, 1937, p. 1042). This idea, too, reflects an interest in information content as a criterion of ideal assortive classifications.

Two other factors are employed in the evaluation of classifications, regardless of their basic methodology. These are the usability of the classification and the classificatory tradition. A certain degree of usability is demanded, even at the expense of some taxonomic truth. For instance, the division of large genera such as Polypodium into segregate genera is often defended on the basis of an increase in utility, although some of these "genera" must be defined in part on arbitrary and variable characters. Tradition, too, plays its role; Fragaria can scarcely be upheld on any other grounds (see Ellis, 1962, pp. 101, 102). It may be that no matter how quantitative and rigorously scientific our classifications become, the last criterion to be applied will remain usability. "The proof of the pudding is in the eating."

There is considerable debate as to what the purpose of classification should be. Some say that an easily repeatable similarity classification, which is a very generalized classification that serves

no specialized purpose, is the kind that should be adopted because of the objectivity, repeatability, and adaptability of the method for use by non-professional aides and computing machines. Others feel that any classification of organisms should attempt to be natural in the phylogenetic sense, that is, should reflect the most probable evolution of the organisms.

The recent literature, particularly certain writings of Davis and Heywood (1963, pp. 43, 44, 66-71) and Sokal and Sneath (1963, pp. 20-30) have clarified the distinctions between evolution and phylogeny. In the past, the two terms were often used as synonyms for one another; but now it should be understood that evolution refers to change in phenetic (or other character) distance, while phylogeny deals with the lineages of organisms through time. Figure 1 shows

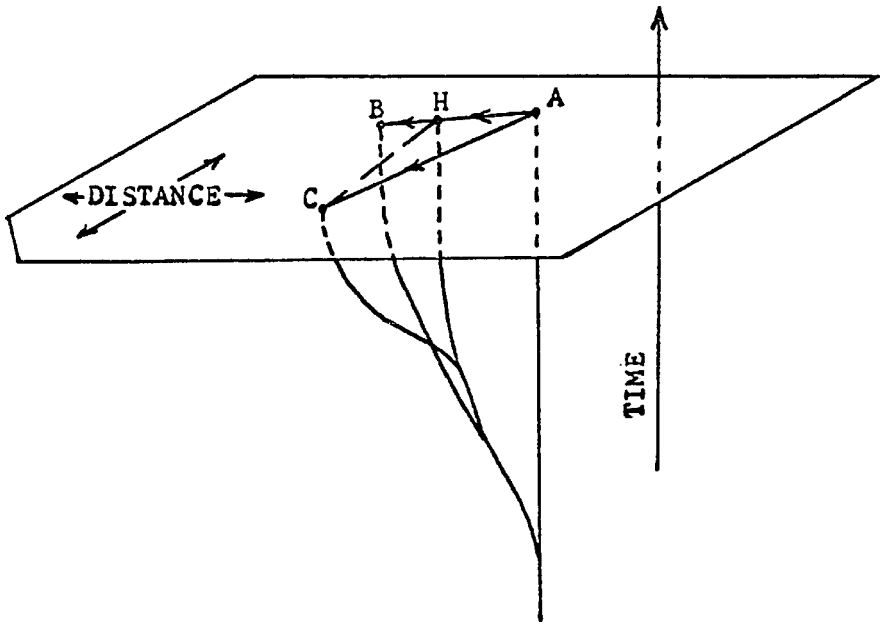


Fig. 1.--Evolution versus phylogeny

a phenetic diagram on the present time plane, with the phylogeny which it depicts displayed below. A pure phenetic taxiometric method would claim that taxon A is more distant from taxon C than it is from taxon B, and would also state the distance between B and C. If there is sufficient evidence, including some from adjacent taxonomic groups, a technique like Wagner's visual ground plan diagram can discover that taxon A is ancestral, and has the derivatives B and C at certain phenetic distances. It can also show that C has its closest affinity with point H, a non-extant taxon, rather than directly with point A. On the other hand, a phylogenetic classification would take into account not only these relationships, but also the relationships of points A, B, C, and H backwards in time. Therefore it would yield information not only concerning similarity of present taxa, but also about the speed of evolution which produced them from their points of inception in the past. These relationships are shown below the present time plane.

Outline and Comparison of Some Quantitative Methods

Present day quantitative taxonomic methods fall on a line between two opposing positions. In the postselective methods, a large series of characters is used, all usually with equal weight. No attempt is made to ascertain the significance of a character on an evolutionary, distributional, correlative, or functional basis. (Of course, character organization avoids logical dependencies and other situations which degrade information content.) Therefore no assumptions need be made regarding the origin or significance of characters. Analysis is

made of the resulting correlation matrix. The information about evolutionary patterns contributed by the correlated characters can be extracted from the "noise" of the uncorrelated, non-significant characters if the analysis technique is well designed. The postselection is of information ("messages") carried, usually as phenetic distances, but not as attributes of characters.

In the preselective methods certain tests are made of characters and attributes which are thought to carry information, usually to prove them of evolutionary or correlative significance. Other characters are excluded, so the correlation matrix which results is of high significance in describing well correlated groups or even evolutionary pathways. The method of analysis can be simpler or less precise because fewer meaningless characters, which could obscure patterns, are used in calculating the matrix. But preselection may have screened out usable, significant characters because the tests were too stringent or because the model of evolutionary mechanisms that was used in developing the tests was incorrect.

Postselective Methods.--Probably the least complex postselective method, both in its concepts and its execution, is that of Sneath (1957a, 1957b). His system rests on the premise that all available characters should be used with equal weight in constructing a taxonomy, because (1957a, p. 185) "unless we prove that any particular feature should carry greater weight than another we must either give equal weight to every feature or else give weight on unproven . . . grounds . . ." This is part of the prescient dicta of Adanson, fitted by Dr. Sneath to the capabilities of electronic data-processing

systems, and is also the basis for the work of Michener and Sokal. Sneath's papers and that of Sokal and Sneath (1963, pp. 16-18) contain the clearest modern discussion of the Adansonian philosophy.

Sneath evaluates each pair of taxa with an index of similarity, S:

$$S = n_s/(n_s + n_d)$$

where n_s is the number of positive features displayed by both taxa and n_d is the number of positive features displayed by either, but not both members of the pair. His index of similarity is particularly well suited to the + or - physiological tests with which he and other bacteriologists work.

The values of S for each taxon pair are arranged in a triangular half matrix, and are grouped into six ranges for visual comparison. Coherent groups can be discovered, and the matrix rearranged to demonstrate them, as shown in Figure 2.

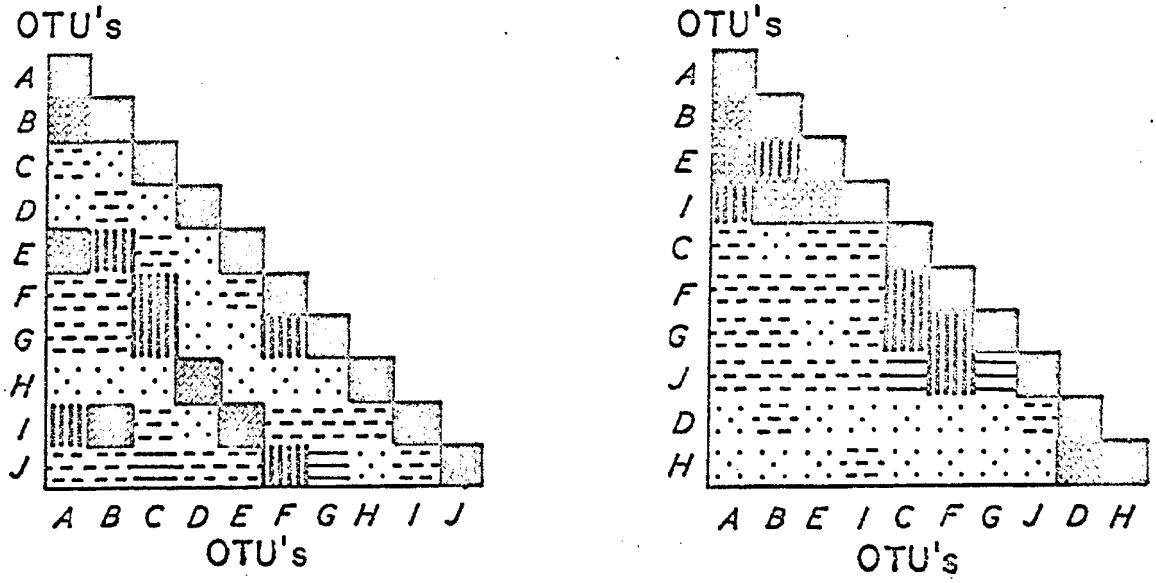


Fig. 2.--Unarranged and ordered shaded similarity matrices

Sneath has accomplished rearrangement by visual inspection of the rows and columns of the original half matrix. An objective method has been developed by Benninghoff and Southworth (1964), who have prepared computer programs which order matrices used in the comparison of phytosociological vegetation analysis plots. The S value ranges are analogous to plot presence data, and could be quickly arranged with Benninghoff and Southworth's technique. While clumping techniques for the two kinds of data may be parallel, there is a sharp difference in the data themselves: only the taxonomic data are organismal.

The quantitative methods used by Michener and Sokal, like those of Sneath, are postselective. In their pioneering study of non-social bees they used 122 characters, each given equal weight--certainly far more than could be used non-quantitatively with any degree of precision. Similarly to others using quantitative methods, Michener and Sokal (1957, p. 141) avoid false correlations based on the manner in which data are organized. "In all cases characters were reorganized or omitted to exclude correlations resulting from situations, where a certain state of one character requires a particular state of another."

The rather complicated Pearson's product-moment correlation coefficient, $r_{x \cdot y}$, serves as a measure of association between operational taxonomic units (OTU's), which are usually taxa, but may be characters. This allows a single character to have two or more character states, and is more flexible than Sneath's S, which permits only two. On the other hand, S is not burdened with the statistical assumption behind $r_{x \cdot y}$: that both variates be distributed with

reasonable normality. When dealing with few character states or with few OTU's this is an assumption that is unlikely to be met. Unless the absolute probability value of $r_{x \cdot y}$ is desired, however, one can hope that all the values are equally biased and that the distortion of the resulting dendrogram will not be severe.

Sokal and Michener (1958, pp. 1430-1436) utilize a clustering technique of their own design called the "weighted variable group analysis" to reduce the $\underline{i} \times \underline{i}$ matrix to a meaningful dendrogram which indicates similarities between OTU's and OTU groups. The correlation coefficient level at which each OTU and OTU group joins a cluster is determined using pre-set criteria for averaging group coefficients and for admitting new OTU's or groups to the cluster. Eventually, correlation coefficient values at various levels join together all the OTU's. Sokal and Michener (1958, p. 1422ff.) discuss the weighted variable group and other factor analytic methods. They conclude that the application of methods other than the weighted variable group method are generally not so satisfactory, except for solving certain special problems of species relationships, where they may excel other methods.

The correlation coefficient matrix yields a similarity classification. The values of the matrix can be formed into a likely looking family tree, yet this kind of a classification is based only on similarities of the various characters of the taxa, and may not accurately reflect evolutionary changes which have taken place. Therefore, Michener and Sokal refine their correlation coefficient diagrams by examining some of the taxa they have grouped in relation to

their descent (the pregroup-exgroup problem). They emphasize that the original similarity matrices and dendrograms are non-historical, and that it is this additional manipulation via other mathematical procedures that makes their final diagram evolutionarily meaningful (Michener and Sokal, 1957, pp. 148, 155 and Sokal, 1958, p. 410).

A third system, one that is more preselective than the systems of Sneath or Michener and Sokal, has been published by Rogers and Tanimoto (1960). In the 1960 work on Manihot and in a recent publication on Halimeda by Rogers and Fleming (1964), they chose relatively few characters (15 and 50) and attributes (86 and 286), but ones that seemed to be taxonomically important.

Characteristics like "color of stem" or "leaf shape" are divided into mutually exclusive, binary attributes, like "gray, brown, yellow, red" or "linear, obovoid, pandurate" (Rogers and Tanimoto, 1960, p. 1116). Presence is scored 1, absence 0, and no comparison -1. A measure of association more like Sneath's S relates the OTU's into a similarity matrix. This is the similarity value or similarity ratio, s_{ij}, which is computed from the binary data table by finding the sum of binary attributes shared by both species (matches) divided by the sum of the binary attributes present in either one or both of the OTU's (number of presences):

$$s_{ij} = \frac{\sum M_{ij}}{\sum N_{ij}}$$

These are then converted to distance functions, d_{ij}'s:

$$d_{ij} = -\log_2 s_{ij}.$$

The purpose of converting from similarity ratios to distance functions is that all the OTU's can be related to one another in semimetric space (hyperspace) using the distance functions. The closer two points are together, the greater the degree of similarity between the OTU's, or the less the phenetic distance.

The points, which can be imagined as a cloud of points in hyperspace, are then subjected to cluster analysis. First, Rogers and Fleming determine the centroid of the cluster, which is defined as the most generalized point or the point that has the maximum typicality. It is analogous to the population center of a country; both are the points which can be connected to all the other points by the least distance. A rough measure of typicality for the OTU's is the number of other OTU's with which an OTU shares at least one attribute in common. A more refined measure, and the one used to rank typicality in Rogers and Fleming's study, was to sum the distance from each OTU to all the others, then to divide by the number of OTU's with which each OTU shared at least one attribute in common.

Another constant is used to determine whether the distance between two OTU's is sufficient to consider them as representing two taxa, rather than one, at the lowest hierarchical level under study.

The determination of disorder and its relationship to relative and maximum entropy are important in segregating the OTU's into homogeneous groups. Clusters are made to be homogeneous (within certain pre-set limits) in the attributes which they share, and tend not to share attributes with other OTU's or OTU groups. The cluster analysis works by determining the jump in inhomogeneity as OTU's are

added or withdrawn from a provisional cluster. Parameters are set for the value of this jump in inhomogeneity. After adding and withdrawing OTU's from the cluster following the programmed set of instructions, the cluster satisfies the requirement for homogeneity, and contains all the OTU's that lie within its limits of homogeneity, but none which are sufficiently unlike to cause the inhomogeneity to rise above its pre-set level. The process is repeated with the remaining unclustered OTU's until all of them stand either in clusters or remain alone. Of particular interest is the enlarging and collapsing of provisional spheres representing the inclusive and exclusive phases of the search for OTU's which makes the most inclusive and homogeneous clusters.

Preselective Methods.--These methods have their roots in Aristotelian thought, were criticized with much validity in the 18th century by Adanson (1763), appear in the thinking of A. P. de Candolle (1827, p. 241), and have their fullest and most modern exposition by Danser (1950).

Basic is the notion that certain characters are useful to classification. A hundred years' study of evolution has shown this to be true; some characters are "good," as utilized in identification and classification, and some are not. The justifiable criticism by Adanson was that these characters had to be discovered for each taxonomic group, and were not necessarily those suggested by ancient authors or those transferred from one group to another. The process of discovery was slow before Darwin, since "naturalness" was a product of the unknown intent and design of special creation and because

specimens for study were less representative of the world's flora than they were by the end of the 19th century.

Typology, or idealistic morphology, is a system of thought which is also traceable to the time of Aristotle and which forms a workable basis for postselective methods. It flourished in Germany in the 19th century as an attempt to create groups of plants with "logical," hypothetical archetypes (Urpflanzen) which shared the generalized characters of the group. Unfortunately, the imaginations of some typologists were carried away. The concept fell into disrepute because of the weird conglomerations of plant parts which they gathered together on an intuitive basis and figured, sometimes to represent the archetype of an unnatural or highly heterogeneous group (see Danser, 1950, pp. 153-157).

The quantitative aspect of Sporne's (1954) advancement index method lies in his use of Chi-square to test the non-randomness in distribution of selected and presumably evolutionarily significant characters.

In listing advancement indices of dicotyledonous families, Sporne analyzes characters considered important by other systematists: woody habit, sympetaly, and zygomorphy, for example. As much as possible he pairs a vegetative and a floral character to avoid biasing the Chi-square test via structural or functional correlation. The occurrence together of a pair of characters significantly more often than would be expected on a random basis under the Chi-square distribution indicates that the pair are either both primitive or both advanced. On the other hand, if the two occur together significantly

less often than would be expected, one of the pair is advanced and the other is primitive. A modest amount of pairing and re-pairing (the calculations can be done on a desk calculator easily) will reveal which characters are primitive, which are advanced, and with what certainty either of these statements can be made.

While it is likely that pairs of primitive characters will be highly correlated, since they have descended together from a common ancestor, I cannot agree entirely with Sporne's argument about the high correlations of pairs of advanced characters. Advancement or divergence implies specializations in different directions in various derivative organs and organisms. There is no a priori reason why pairs of advanced characters will be found together, unless they are structurally or functionally (e.g., genetically) dependent, in which case they are not really different characters in the sense which Sporne uses the word. Although Sporne has avoided the structural pitfall by pairing characters of different organs, genetic correlation cannot be easily tested, and its effect on his Chi-square tests is therefore unknown.

In the case of dicot families, correlation with those families found in the fossil record is deemed of special importance, since Sporne [often erroneously] tends to consider the fossil-represented families primitive. He supplies some good data against equating primitiveness with antiquity, however (see p. 26).

The number of advanced characters of a taxon divided by the total number of advanced characters evaluated constitutes the taxon's advancement index. This is expressed as a percentage, with primitive

taxa having an advancement index of a few percent and advanced taxa reaching up to 100%. Sporne arranges the taxa on a chart of concentric rings, each ring inward for one less advanced character, down to the center, which is totally primitive (advancement index = 0%). Sporne (1948, pp. 46-47) then shifts the taxa radially, ". . . according to their local affinities (determined for the most part by characters other than those used in calculating the advancement index), so that related families are placed near each other or on the same radius."

The visual ground plan method, developed by Wagner, is largely preselective. The analytic technique (Wagner, 1961) which is used to reduce the data matrix to a visual ground plan diagram is not particularly powerful for separating the patterned from the non-patterned characters, should the latter comprise more than a small percentage of the characters. It is therefore necessary for the tests leading to the selection of characters to be quite rigorous and for the tests to be appropriate for the particular taxonomic level and taxon under study.

The basic assumption concerning evolution of attributes within the taxa of a natural group is that any one which is primitive in the group is likely to have been derived from a common ancestor, and, at least in the initial stage of evolution of the group, to be of frequent and general occurrence among the various subgroups. On the other hand, divergent or advanced attributes generally have evolved in just a few members of the group, either in parallel or not. Character selection tests operate under the foregoing assumption; they must be adequate to separate patterned characters that definitely exhibit a primitive

character state from all those which are unpatterned or have no detectable primitive character state.

Because the method deals with the radiation of specializations into groups and subgroups from a common ancestor, correlation or presence of characteristics in OTU's is considered across the diversity of taxonomic groups, rather than as a percentage or proportion of presence in the total number of taxa without reference to the subgroups to which those taxa belong. For instance, if a certain characteristic of a genus is found about two-thirds of the time in all the OTU's of all the subgenera, it is more likely to be primitive than one found with perfect constancy in the OTU's of most of the subgenera but not at all in the OTU's of the remaining subgenera.

Once patterned characters are found and their primitive states deduced, the visual ground plan is constructed with these characters. The OTU which has the fewest advanced character states is attached to the ground plan OTU, which by definition shows only primitive attributes and no advanced states. Additional OTU's are added to the diagram until all the OTU's have been attached in a branching, dendritic fashion. Each addition is made so as to keep the number of gains and losses (particularly the parallel gains of divergent attributes) at a minimum by arranging OTU's within and between the branches.

Methods of Comparing Taxiometric Results

Generally the comparison of various methods of classification has been empirical, by mentally evaluating dendrograms representing identical data prepared by various methods. Most comparisons have

been made in terms of similarity of results. Sokal and Rohlf (1962) have developed an objective technique for comparing dendrograms prepared by different techniques, so long as the dendrograms conform to the format of correlation coefficients, similarity values, or distance values on the ordinate. That such values will differ because of computation with different measures of association must be recognized, and such dendrogram comparisons must be evaluated cautiously.

Sokal (1964) has devised sets of carefully drawn, imaginary "beasties," as he calls them, which display taxonomically meaningful, patterned phylogenies. These serve as model sets of data for taxiometric analysis and subsequent comparison with the phylogenies which were originally drawn. Because all the steps in these phylogenies are known, the artificial data allow a better controlled test of taxiometric methods than do biological data of unknown or presumed phylogeny. But only if the phylogenies depicted by the "beasties" are good models of biological phylogenies is success in classifying "beasties" likely to be duplicated with biological material.

The ultimate comparison of taxiometric methods will come when every assumption and every manipulation of the data can be given a probability value, thus establishing the overall probability of the method and of the resulting classification. This would be a true evaluation of results without reference to any other method, and would not be a comparison of methods. It could take into account how well the method met the special demands of the classifier, and would be free from the danger of comparing diverse and fundamentally non-comparable methods with some standard technique.

Comparison of Ground Plan and Correlation Methods

A comparison of Figure 3 with Figure 4 shows that the visual ground plan and Michener and Sokal's correlation coefficient methods do not produce identical results when applied to a selected portion of Blasdell's (1963, pp. 32, 33, 80) data on Cystopteris, even when the data are identical. The visual ground plan diagram was prepared according to the instructions of Prof. W. H. Wagner, Jr. (pers. comm.), while the dendrogram followed the L method of Sokal and Michener (1958).

The phenetic relationships between Cystopteris douglasii Hooker, C. fragilis (L.) Bernh., and C. protrusa (Weatherby) Blasdell, for instance, are seen in the phenetic dendrogram. While these relationships can also be observed in the visual ground plan diagram, the most probable evolution of the three species (based on the data used) is also shown. Cystopteris montana (Lam.) Bernh., C. pellucida (Franch.) Ching ex C. Chr., and C. sudetica A. Braun & Milde exhibit a similar difference between the two diagrams. The cause of the different placement of Cystopteris diaphana (Bory) Blasdell on the two diagrams is at present inexplicable.

The disparity between the results obtained with the preselective visual ground plan diagram method versus the postselective weighted variable group analysis can be explained by (1) including too few characters in using the weighted variable group technique, (2) not employing additional statistical refinements to discover more about the relationships of descent among the species, and (3) including (on purpose) two sporadically occurring, non-correlated characters among

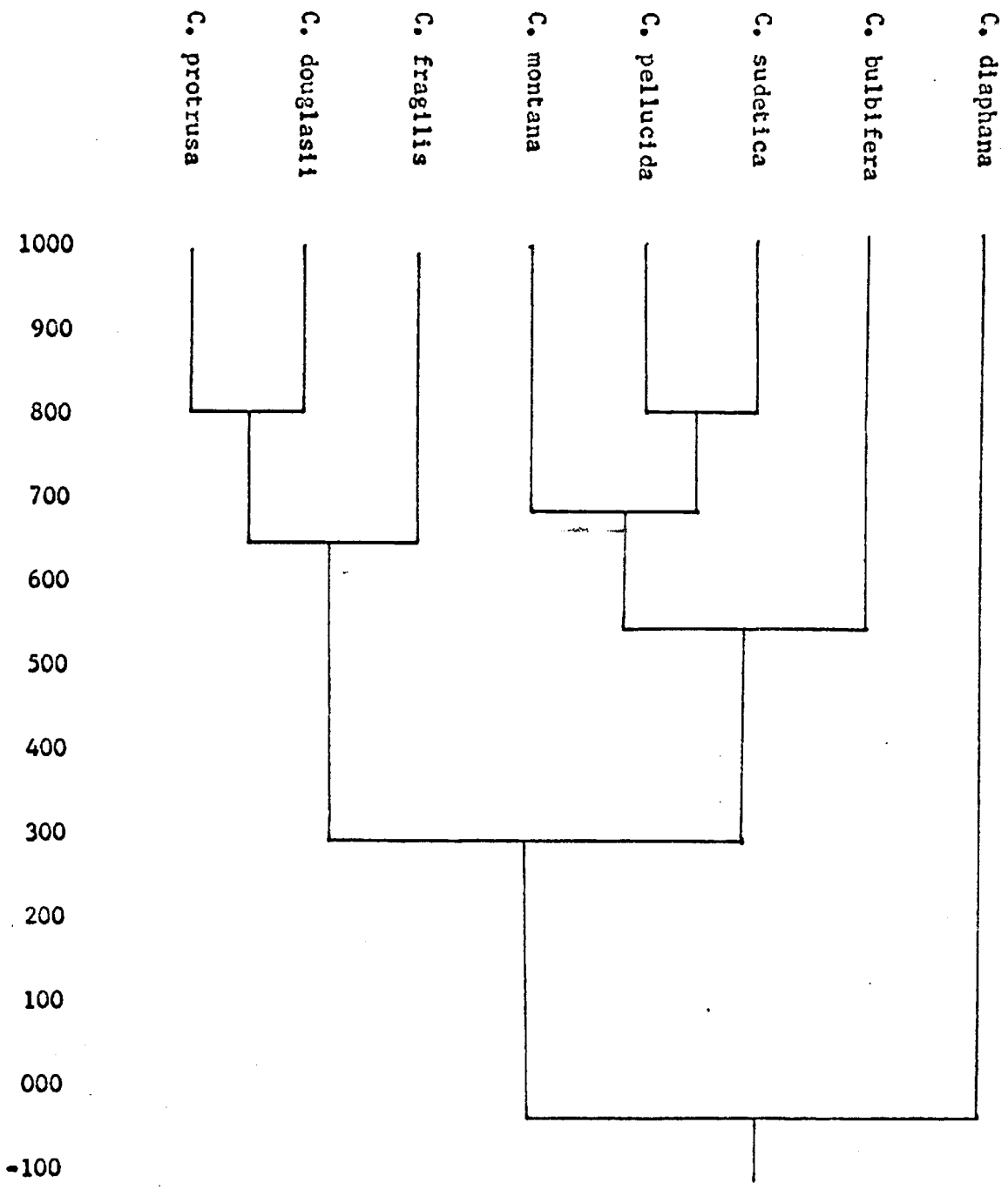


Fig. 3.--Phenetic dendrogram of selected Cystopteris data

the ten used. In this case the constitution of the group is not in question; the genus is well isolated morphologically; there are no reports of hybrids with other genera of the Aspidiaceae. The fact that 20% non-correlated characters caused apparent distortion in results of the weighted variable group analysis, however, tends to cast doubt on the effectiveness of that method when some of the data on which it operates are not preselected for being indicators of patterns, groups, or evolution. To ascertain the extent of the distortion would require a test of these species utilizing more data, perhaps over 100 characters.

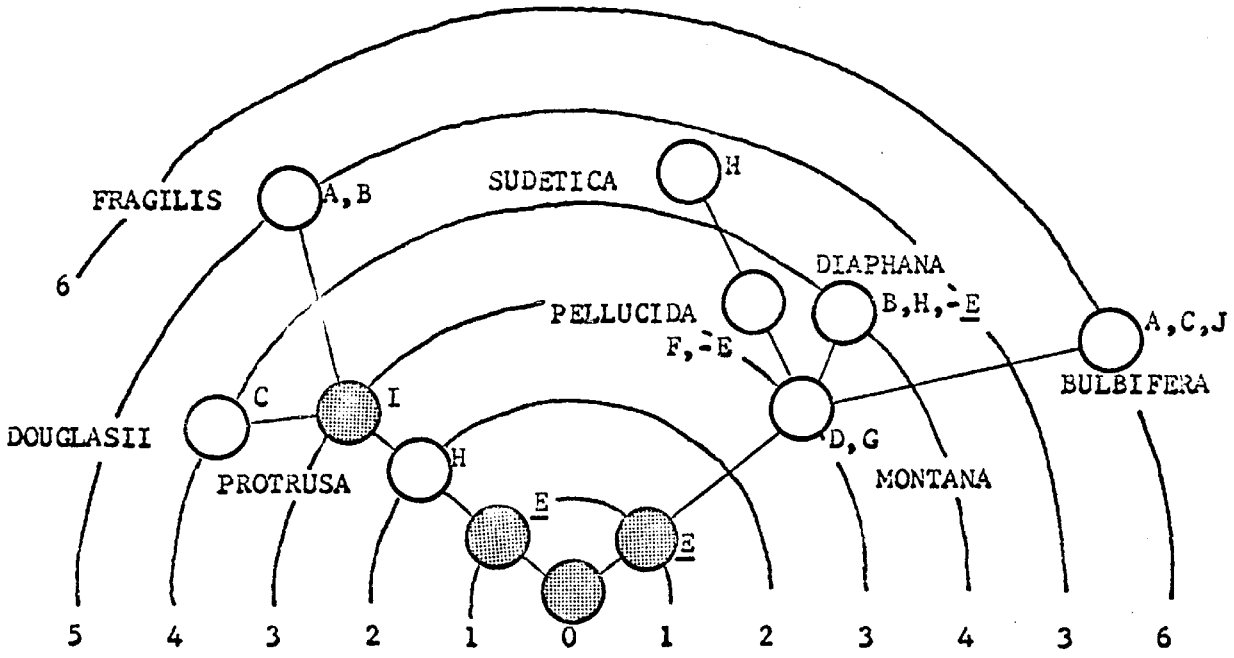


Fig. 4.--Visual ground plan diagram of selected Cystopteris data

Comparison of Taxiometric and Traditional Methods

The postselectionists have suggested that the traditional taxonomic methods should be abandoned because there is an inherent circularity in the reasoning between phylogenetic systems and classifications (groupings) (see Sokal and Sneath, 1963, pp. 6-11 and 21-23). They say that the traditional taxonomist makes his supposedly natural groups and OTU's a priori. He then searches for "good," well correlated characters, which means "homologous characters"--those which have a common descent throughout the group. And, as they say, the criterion of "homology" is dependent upon the constitution of the group. So that once the taxonomist uses these like characters to establish evolutionary patterns, he then proceeds to erect a phylogenetic classification, the outcome of which was to a large extent predetermined by the correctness of the a priori group he had originally chosen. This interdependency tends to promote the selection of characters which will group unlike, poorly chosen OTU's, if those are the ones which have indeed been chosen. Here the post-selectionists have an excellent argument. If the preselective tests depend on the members or limits of the group to be classified, then false limits or non-members will affect the result. Postselective methods, on the other hand, usually place unrelated OTU's in isolated positions, correlated at low levels with the true members of the group which is being classified. Waterman (1962, pp. 549-551) reasons through the problem of circularity in its most general setting--the scientific method. He claims that circularity is inevitable, and is not to be disavowed as unscientific.

Sokal and Sneath (1963, pp. 56-57) claim that the methods of assortive, numerical taxonomy can be free from circular reasoning. But I think the postselectionists' argument can be turned against them. They, too, must delimit OTU's and overall limits of the group to be classified. As I understand them, they first choose OTU's and then choose characters and attributes to describe OTU's, but without specifically evaluating the characters in terms of biological significance or attribute distribution in the OTU's. They try to describe as many variables of the material as they can, of course avoiding obvious structural and logical correlations in the design of characters. On this basis they make a similarity matrix from which a factor analysis extracts the taxonomically important information, which is displayed as a dendrogram. Now, if such a postselective method were to include rather unrelated organisms showing high degrees of parallel or convergent evolution, the usual factor analyses might not be powerful enough to detect and set apart these OTU's. I know of no quantitative data or studies directed to this point. Sets of Sokal's "beasties" could be designed with various amounts of parallelism for testing taxiometric methods. Whatever factor analytic method is used, character selection and codification will markedly affect the final result.

Character and attribute selection can be restricted by the choice of OTU's. Michener and Sokal (1957), for instance, have treated species in closely related genera, and a uniform set of characters and attributes easily described the entire group.

Of course, the predominant attributes might be one set within the group and other sets in any incorrectly included OTU's. But if the taxonomic level of the group were high enough and members of another taxon still were incorrectly included, surely the choice of characters would be restricted to a compromise between the characters of the group under study and the misincluded OTU's. This shows, I believe, that the postselectionists' methods actually do contain the inherent circular reasoning of the sort Waterman has discussed.

There is also a subsidiary argument to consider, one which includes the taxonomist's aim in making a classification. The preselectionists claim that postselection techniques are nothing more than assortive. They claim that the value of characters can be either intuitively or quantitatively discovered. They feel that assortive techniques, which fail to do this, may be repeatable and stable, but are non-evolutionary, and lead to classifications which are non-natural to the extent that the data they contain do not mirror evolutionary trends. But preselectionists tend to underestimate the power of a well designed factor analysis to separate the phenetic and evolutionary "message" contributed by correlated characters from the "noise" made by uncorrelated characters.

Choice of Method for this Study

If, and only if, the ultimate purpose of systematics is to construct a natural classification, then the ultimate aim of the systematist is to discover the entire phylogeny of plants. This goal unfortunately cannot be reached; the course of time has run too long.

Too much has not been preserved in the rocks, and too much that was preserved has subsequently been destroyed. For want of data the study of phylogeny has, on occasion, been driven to speculation, with unsatisfactory results.

Phylogenetic systems by definition include data from past geological times. These systems assume that data from the fossil record have a special significance, that antiquity generally equals primitiveness. This is not necessarily so; in fact, this can be a dangerous and misleading assumption. For instance, Sporne (1948, 1954), in my opinion, jeopardizes the validity of his conclusions because he tends to assume that fossil taxa are primitive. Early Cretaceous angiosperm fossils mentioned by Arnold (1947, pp. 337-338) include Sapindaceae, Populus (Salicaceae), and Sassafras and other Lauraceae. Sporne rates these families 25%, 36%, and 46% advanced, which hardly makes them primitive, although they are among the earliest known angiosperm fossils. Primitive Jurassic angiosperms doubtless existed, but our knowledge of them is still meager. Recent examination (see Arnold, 1947, pp. 335-337) has shown that most "Jurassic angiosperms" belong to other groups. Thus truly primitive angiosperms remain largely undiscovered.

Sporne has contended that phylogeny can be known (he means, I think, "known with certainty") only from the actual record of fossils. While this is true, the statement rests on knowing not only the fossils themselves, but also what relationships they bear to each other and to modern plants. Usually a reasonably complete series of fossil forms is necessary to discover this. Such data are seldom

available, and Sporne's dictum, while correct, is only infrequently applicable.

Because of the difficulty of reconciling paleontological and neontological data, some taxonomists have given up the idea that phylogeny or evolution can play a significant role in the design of classifications; they think the logical, safe, unspeculative end step of systematics should be an assortive classification.

Yet, there is a middle course between phylogenetic speculation and mere assorting of recent taxa. This is the method of typology, broadened and extended (some would say without justification or basis) to have an evolutionary meaning. Considering the incomplete state of the fossil record, at this late date we can do little but think in terms of characters which may be ancestral within certain groups. By placing the doctrines and methodology of typology on the quantitative basis of applying probability to the distribution of attributes among taxa according to a preconceived model of the mechanism of evolution, it is possible indeed to discover which attributes of taxa are likely to be primitive, and, by extension, which taxa are likely to be primitive. This method could aptly be called "probabilistic typology." But the visual ground plan ancestor should not be equated with Simpson's (1961, p. 185) "hypodigm," nor should the visual ground plan method be confused with Davis and Heywood's (1963, pp. 11-12) "neotypological concept." These are general, non-quantitative ways of describing the taxonomist's typologically derived mental concept of a taxon at or near the species level.

Davis and Heywood (1963, p. 11) remark that the population concept is of practical reality at and below the specific level, but that typological methods are necessary above the specific level. The problem, then, is not an objective one of whether to use typology at the generic-subgeneric level, but a subjective one of how to apply it most correctly. In general, information content (or coverage) and correctness are antithetical properties of typological statements. For instance, ground plans of genera are more likely to be correct than the ground plan of a family based on those generic ground plans. The data become more abstract and less attached to species as the hierarchical level increases. The greatest usefulness of typological methods for determining probable evolution lies in achieving a balance between information content and probability of correctness, i.e., between the high probability and restricted results of few or no typological conclusions based on the most rigorously chosen data and the low probability of many, broad conclusions drawn from poorly selected data.

According to Arber (1950, pp. 61-62) and Danser (1950, p. 158), the hypothetical archetype in the mind of the taxonomist should not become the ancestral plant; the two concepts should remain separate. Despite the criticism against transferring from the archetype to the ancestral plant, it seems to me that if the archetype is truly most probable (its characters have been chosen on a probabilistic basis using an adequate model of the evolutionary process), then it may really be the ancestral plant, but only with whatever probability can be established from the data.

One of the differences between the old phylogenetic systems and the evolutionary typological ones is that the geological time scale is replaced by an evolutionary scale of characteristic changes (changes in attributes). The two scales bear no constant relationship to one another; the number of changes in characteristics is not a function of geological time. This is in distinct contrast to the old phylogenetic systems, in which fossil forms were considered ancestral to recent forms for purposes of classification. It remains, of course, more probable that a fossil form is ancestral to a recent one than vice-versa, but this relationship is not axiomatic.

The question of whether to abandon the traditional taxonomic philosophy in favor of a strictly numerical or assortive approach is really a question of the adoption of one of two conflicting sets of principles. Either set may be best suited to the needs of some particular problem. There is scant reason, I think, to abandon either of the opposing methods.

Taxonomic "intuition," the non-verbalized assessment of similarities and differences, has been strongly criticized because it is not rigorously deductive and repeatable (see Sokal and Sneath, 1963, pp. 6-11). Yet in higher plants the classic modes of taxonomic operation have proven generally satisfactory for deducing likely, workable classifications and "phylogenies," except for difficult groups of confusing variation pattern and some "non-evolutionary" groups like apomicts. Indeed, the structure of thought itself represents similar modes of operation. Everyone knows hundreds of people by name on sight, and can usually tell them apart without

the slightest hesitation. But verbalizing their differences--making a dichotomous key to them, for instance--would be painfully difficult. And so it is with most of us who work in plant taxonomy. Few have so powerful an intuition as Paul Standley, who, at the height of his career, was able to make taxonomic decisions and to write 300 manuscript pages of a flora in less than six months (see Morton, 1963, p. 14). Intuition tends to fail only when characteristics of the taxa at hand are thoroughly scrambled and appear seemingly at random or when the group to be classified is so large that all of the details and patterns cannot be intuitively grasped at a single time.

The advantages of quantitative methods are their greater precision and their statement of procedure, which allows these methods and their results to be checked accurately by other workers. But in routine taxonomic problems, these advantages are more than outweighed by the time that is consumed in using taxiometric methods.

I make no plea for the use of quantitative analyses on all occasions. In making a decision concerning methodology, it is necessary to weigh the greater efficiency of intuitive methods against the greater repeatability of quantitative systems. The advantages of quantitative methods should be considered when intuition yields uncertain results, or is dwarfed by the magnitude of the task, or needs double-checking.

Improvements in the taxonomic process can be expected to arise from extensions of the familiar methods as well as from the newer, strictly meristic methods. My choice of method is to try to combine the best, proven features of classical taxonomic (intuitive) procedures

with quantification, which will help to extend the classical method into areas where it has formerly failed. Because I am convinced that the routine, intuitive methods are correct--although their results sometimes are not satisfactory--I think this combination offers considerable hope in solving many difficult taxonomic problems. While recognizing the constructive, well thought out, purely numerical approaches to grouping, I am not yet convinced that these methods make the best use of biological data when they follow a postselective rather than a preselective course. It seems to me that to ignore at the outset the inherent patterns of biological evolution that are present in some, but not all of the characters, is likely to be a mistake. Data on the probability of accuracy of the various methods would be most welcome.

CHAPTER II

THE THEORY AND PRACTICE OF THE VISUAL GROUND PLAN METHOD

Basic Premises

Inductive reasoning is the normal mode of taxonomic thought because deductive reasoning is too restrictive. Few premises of science, other than many of those of mathematics, can be put absolutely, which is usually necessary in framing deductive arguments. Statistical reasoning is a useful quantification of inductive reasoning. Because statistics deals with probabilities rather than certainties, it is an extremely useful tool for analyzing data. The scientific method of testing multiple hypotheses by matching observations against predictions of the hypotheses is a logical extension of the inductive method. The scientific method is argued against by some scientists, who claim that it causes an investigator to find what he seeks, that it biases his view (and his perception?) of data and that it prejudices his results. But against this must be weighed the considerable advantage of stating hypotheses, by which focus and direction are given to research.

The principle of Occam's Razor, which chooses the concept that offers the greatest economy of assumptions, arose in the Middle Ages. Perhaps a simple set of premises or statements explaining a hypothesis is more likely to be true than a complex set, but the principle is fallibile. Above all, the simplicity of assumptions should never be

considered a final measure of their truth; nor should simplicity necessarily be a major factor in choosing a set of assumptions.

Traditionally, taxonomists have made syntheses of data involving many hypotheses and assumptions. Some numerical taxonomists, however, have departed from this approach. Their greatest successes, in my opinion, have been in the taxonomy of the bacteria, a group in which it is difficult to state many taxonomic assumptions.

According to some people, evolution is itself the "grand assumption," and questionable. Evolution is occurring, this opinion notwithstanding, and what it has produced seems to be an accomplished fact. It should be unnecessary to defend the existence of evolution; the proofs of it are manifold. But, of course, models describing how evolution occurred, how it worked, and what it produced may be true or false in varying degrees.

There are a few points important to taxonomy which can be deduced from what we know about evolution. First, evolutionary distance can usually be inferred from morphological difference. Convergent or parallel evolution is the biggest exception to the general rule that things which look alike are probably closely related.

Second, it becomes increasingly difficult to find single, constantly valuable, definitive characteristics as one advances upward in the taxonomic hierarchy. Blockages of gene systems may be responsible for the "loss" of some characteristics. I believe that norms of characteristics among taxa may be more useful to evolutionary classification than the morphology of single exemplar taxa; classifications at the higher taxonomic levels in particular may have

to be based to some extent on potentialities, norms of characteristics, or ground plans, and not on actual characteristics of specific taxa. Ground plan characters and trends of specialization radiating from them are often useful because they illustrate what potentialities certain groups have, even when misleading absences of characteristics, which could be caused by blockages of gene systems, occur.

Lastly, and with special reference to the present study, five concepts regarding the diversity of nature have proved useful to me in making a model of evolution as a basis for classifying the genera and subgenera of the Adiantoideae.

1) Evolution is a more or less orderly changing of characteristics within sequences of organisms, in which both the characteristics and the organisms fall into patterns. Evolution is patterned rather than random because of the barriers to random assortment and expression of genetic material, which include spatial, genetic, and ecological isolating and differentiating mechanisms.

2) Most of these character gradients are divergent, which is to say, most evolution is divergent. Once isolating mechanisms come into play, differential selection pressures, however slight, cause once-similar stocks to diverge, as with Darwin's Galapagos finches. Of course, parallelisms, convergences, and even simple atavisms must sometimes occur. Indeed, it is these phenomena which constitute the principal barrier to successful intuitive interpretation of morphologically-based relationships.

3) Only natural groups, which are by definition monophyletic, have at their origin a common evolutionary ancestor. Natural groups

may be homogeneous in terms of their attributes, but homogeneity and naturalness are not necessarily coincidental. The former term does not imply the latter. The common ancestor may not exist today, but sometimes it can be inferred from the data of extant taxa.

4) Because of the divergent gradients of characteristics from original to derivative taxa, it is possible to infer the most probable characteristics of the common ancestor by interpolation and centripetal extrapolation, using the characteristics which, judging by their patterns in extant taxa, form the most highly patterned gradients.

5) Geological time is not an important dimension in describing evolutionary patterns, since rates of character change differ among characters and organisms. Because of this, organisms show different degrees of advancement. Some are highly specialized, having many advanced characteristics, while others are "living fossils" of ancient and primitive organisms.

The possibility of a natural system of classification of organisms is a notion which intrigued the ancients and remained a (mostly undiscoverable) certainty to Linnaeus. From the time of Aristotle, people had been sure that plants had an "essential" reality (see Cain, 1958, pp. 154-156). But it was Darwin's (1859) Origin of Species which allowed elaboration of the concept of "essence" within a sound framework of reality. Plants and animals were shown to be what they were and to be related the way they were because of their evolution (see Sokal and Sneath, 1963, pp. 12, 20). Hence it is only over the past hundred years that the search for a natural classification has been able to proceed on a basis of scientific concepts.

Although many classifications have been natural in part, the best natural system is the classification which would best mirror the evolution of organisms; it would be the one used if everything were known about all organisms and their evolution since they first existed on the earth. Classifications that attempt to be "natural" in this sense have this special purpose (cf. page 5), and the methods used to construct them are somewhat different from assortive, purely phenetic methods.

Nature is not a conscientious herbarium keeper. Although there is a diverse living flora, relatively little is known about the kinds of plants which preceded this flora. And the paleontological data are sometimes interpreted only with difficulty (see pages 26 and 27).

Any set of data which can be quantified and summarized in a model can be analyzed by operations which are based on the model or on its constituent hypotheses. Hypotheses about the nature of the data concern us first; until we have a concept of the data, we cannot make a set of methodological operations for dealing with the data. Among the hypotheses concerning variation in the data, one might assume that variation is random, hence there would be no evolutionary pattern. Here the resultant operational principle might be: "I quit!" On the other hand, the variation may be non-random. This is generally true of most biological data, which do show patterns, and any hypothesis or model ought to take this fact into account.

With horse phylogeny, Cuvier would perhaps have suggested that the model be linear advancement. In the evolution of the families and orders of dicotyledonous plants, the model might be always-

divergent evolution. In the Appalachian Aspleniums, Wagner (1954, 1963, pp. 145-146) has found a large series of interspecific hybrids all stemming from three basic diploids. The model would be one of always-reticulate evolution. To a taxonomist concerned with evolution within a genus of ferns or flowering plants in which some species were suspected hybrids, the model used to describe the data should allow for taxa produced either by divergent or by reticulate evolution. The point is that a suitable model must be used to account for the structure of the data, and an adequate methodology must be used to analyze the data.

The system probably will evaluate characters in some way; it will make assumptions about the mechanisms and products of evolution, and will relate the taxa in a graphical way. Compared with strictly assortive methods, the evolution-based technique is bound to be complex and to suffer from shortcomings. Sometimes it will fail to work at all; at other times it will be wrong, and its users may be hard put to learn this, or to discover what in the data, model, or operations has caused the error.

Definition of Terms

Wagner (1961) has long advocated the use of a visual ground plan analysis in determining the evolutionary relationships among related groups (usually species or genera) of plants. His method, also briefly discussed by Benson (1962, pp. 273-277 and 415-417), attempts to uncover the threads of consistent (patterned) character evolution from among the multitude of available characters. The next

few paragraphs will define the technical vocabulary of the ground plan method.

A ground plan is the sum of primitive characteristics held by a group of taxa which have diverged along evolutionary pathways from a common (i.e., ground plan) ancestor. The ground plan method seeks to construct this totally primitive ancestor by inference, from a correlative examination of the characteristics of the organisms descended from it. The ground plan ancestor may exist as a living plant or a fossil, or it may at present be hypothetical and presumably extinct.

Of the two fundamental processes involved in the ground plan method, the first is determining characters useful to the analysis. Characters are defined here as features--any features--which can be described by two or more mutually exclusive character states and subsequently designated by numbers (character state codes). Character states are the set of attributes under any character. For example, under the character "leaf size" might be the states " <1 cm., 1--3 cm., and >3 cm." Most characters exist in two or more states, one of which is primitive in the group at hand, while the other(s) are divergent character states. For example, in the subgenus Coptophyllum of the fern genus Anemia the character state "horizontal" is primitive and the character state "oblique or erect" is the advanced state of the character "rhizome habit" (see Mickel, 1962, p. 456). A few characters are found in only a single character state in a group. "Plant body constructed of many cells" is such a null character in the group of higher plants. Fluctuating characters, which in their divergent

(advanced) character state(s) are scattered and not patterned throughout the group under study, cannot be included in a visual ground plan analysis because they do not indicate evolutionary patterns. Taxonomists often call fluctuating characters "trivial." "Lamina glandular" is a fluctuating character in the Adiantoideae, although it may be a patterned or a null character in certain genera of the subfamily. Non-fluctuating characters are called patterned characters. They are useful to the analysis, since they indicate evolutionary pathways, but only after their primitive versus divergent character state(s) have been determined. The distribution of character states in the operational taxonomic units (OTU's) and in adjacent groups determines whether a character can be considered patterned and whether one character state can be called primitive. Operational taxonomic units are the coded items, usually taxa, although they may be characters and attributes.

For the most part, primitive (unspecialized or ancestral) character states are present both in the majority of taxa of the group under study and also in adjoining groups of the next highest hierarchical level, such as adjacent genera in the study of the species of a single genus. Divergent (specialized or advanced) character states usually exist in few of the taxa under study and are not likely to exist frequently, if at all, in nearby groups (see Figure 5A). A rather different case occurs when a character state is found in most of the group under study, but is usually absent from the adjacent groups (Figure 5B). Within group a it is highly likely that this is a primitive character state of a patterned character, although the

distribution of this state in groups b-e is vastly different from the previous case. Both of these examples of patterned characters blend gradually into the more nearly random distribution of states that marks the non-usable fluctuating characters (Figure 5C).

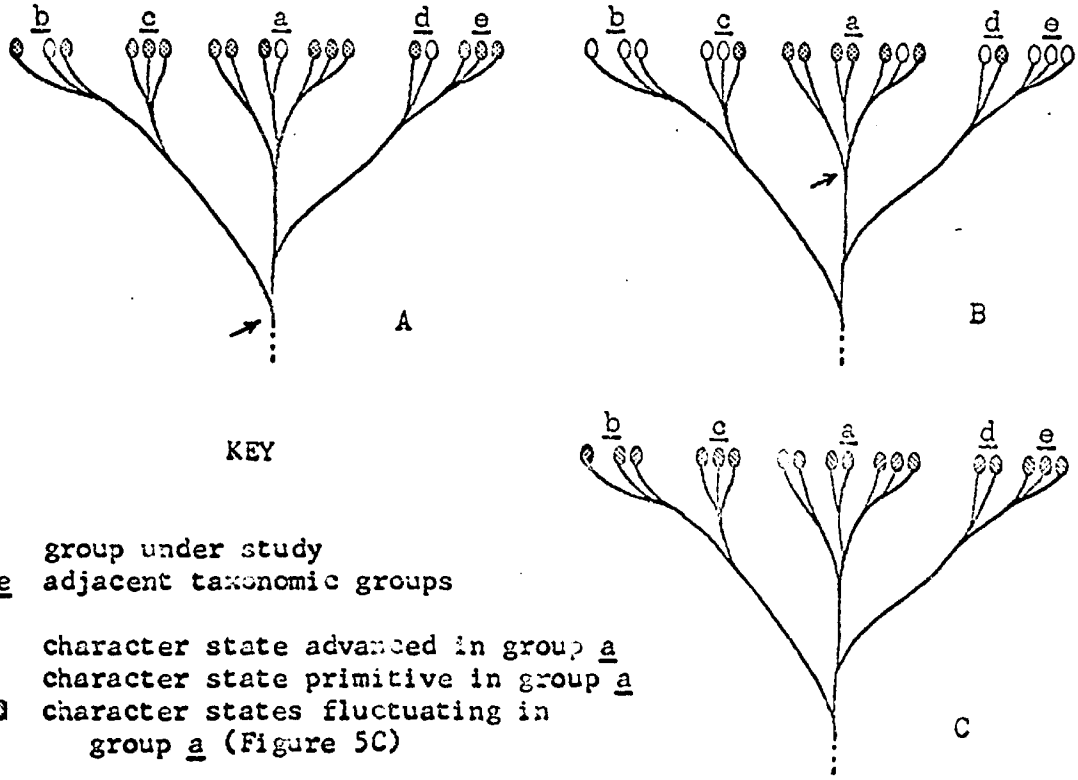


Fig. 5.--Models of character state distribution

Evolution has distributed character states into taxa, but whether we call a certain state primitive or advanced is determined by the limits of the group. In Figure 5B, the character state which is primitive in group a belongs to a patterned character. But in the group a-e neither character state has a clear majority, and the character is fluctuating.

A taxon x character table (i x m) is the way data from the OTU's are stored. Each taxon is examined for every character, and the body of the table is filled with the character states pertaining to every taxon and character. The characters of the raw data, which may have two or more character states under them, are for some purposes converted to binary characters, and the data arrayed in a binary taxon x character table. A taxon x taxon matrix (i x i) serves to associate or relate the similarity of every taxon with every other taxon. This is done by means of a measure of association, which mathematically assesses similarity (but not necessarily relationship) by means of evaluating the quantified characteristics of the two taxa at hand. Rogers' index of similarity (similarity ratio), s_{ij}, and Pearson's product-moment correlation coefficient, $r_{x.y}$, are examples. A character x character matrix (m x m), which is the inverse of a taxon x taxon matrix, is constructed by assessing the similarity of pairs of taxa until every character has been compared with every other character.

Outline of the Method

The first step of the ground plan method is to collect the data into a taxon x character (i x m) table. In the case of a small study not intended for computer analysis, this can be a mimeographed data recording sheet listing the characters as rows and the taxa as columns. In a larger study the data can be transferred to IBM cards, punching in the required format with a printing punch. This allows a visual check of the punches against the i x m table. Or IBM cards which are

to be punched out directly with a stylus as data are accumulated can be used (see page 58). The collection of the data into an $\underline{i} \times \underline{m}$ table, either on paper or cards, is analogous to mentally enumerating the various plants' characteristics.

It is best to be rather unselective of characters at this beginning stage. In fact, if the group is large, it may be useful to write short descriptions of the various OTU's, collate these, and select and codify the characters that are present. This decreases the likelihood of mistakenly overlooking some characters and, at the same time, including others which are correlated due to improper codification. In the body of the $\underline{i} \times \underline{m}$ table the character states for each character and taxon are shown as character state codes.

All of the data exist as characteristics of the various OTU's which have been entered into the $\underline{i} \times \underline{m}$ table. The task of the investigator or the computer is to evaluate the significance of each character as an indicator of evolutionary pattern. Only some, and perhaps just a few, of the characters are reliable or patterned; these characters belong to character complexes describing evolutionary patterns. For that reason they are usable in constructing a system of classification based upon those evolutionary patterns.

The non-null characters must be evaluated, and those which have a single primitive character state (versus one or more divergent states) selected. The model used to describe and explain the evolution of the primitive versus advanced states was discussed in the definitions on pages 39-40. Between the extremes of distribution patterns there is a range of patterns in which advancedness or primitiveness

cannot be decided upon surely. Ideally, the development of measures of probability for these intermediate patterns might permit the use of these characters. Sporne's use of the Chi-square distribution in this regard is not satisfactory, but it does point to the possibility of assigning probability values to characters as indicators of evolutionary trends. However, until satisfactory methods are developed, judging which characters to use depends (for reliability's sake) upon selecting only those characters which approach the extreme distribution patterns shown in Figures 5A and 5B. There is little doubt that much information is thereby lost, particularly in highly polythetic groups, where the defining set or "key characters" are not usually found all at once in an OTU, but a slightly varying subset is found in each of the various OTU's (see Sneath, 1962, p. 291). When doing a small ground plan analysis, within a genus, for example, the primitive states of the characters can often be discovered by inspection at the specific and generic level. In most small studies only one or two advanced states accompany the primitive state in each character. But if the project is large and machine computation needs to be used, then it is likely that an investigator will not have sufficient insight into the distribution of character states to permit a significant analysis of primitiveness or usefulness of characters as indicators of evolutionary patterns.

In this study three series of tests are used to distinguish patterned characters having a single primitive state. It is assumed that the most frequent states are the primitive ones, and it is the frequency distribution of these states which is tested.

A frequency test is performed to find what proportion of the total frequency lies in the most frequent state of each character. Pass lists are printed out for $f_1 \geq 0.5N$, 0.6N, 0.7N, 0.8N, and 0.9N (see Figure 6 and Appendix E). Examination of the frequency values in Appendix D yielded data for $f_1 \geq 0.3N$ and 0.4N. This test increases in selectivity rapidly as N's coefficient rises, as shown in Table 1. It excludes character state distributions where the most frequent state passes the proportion test, but the states are otherwise quite frequent and perhaps evenly divided in a long series, as shown in Figure 6A. Null characters, which automatically pass the distribution

Table 1.--Numbers and percentages of characters passing the frequency distribution test at five values of N

N	Tribe 1	Tribe 2	Tribe 3	Tribe 4	Tribe 5	Tribe 6
0.50	82 76%	67 62%	71 66%	58 54%	67 62%	82 76%
0.60	67 62%	58 54%	54 50%	50 46%	48 44%	82 76%
0.70	56 52%	40 37%	38 35%	39 36%	44 41%	58 54%
0.80	45 42%	26 24%	29 27%	33 31%	38 35%	58 54%
0.90	29 27%	15 14%	14 13%	28 26%	27 25%	27 25%

tests, but are of no value to the construction of the ground plans, account for, respectively, 29, 11, 7, 14, 23, and 27 characters in the six tribes (see the Introduction to Chapter IV) within the subfamily. Percentages are calculated by dividing the number of characters passing the tests by 108, the total number of characters used in the study.

$$N = \sum_{1}^{n} f_i$$

$f_2 \leq Xf_1$

X = a constant (see text)

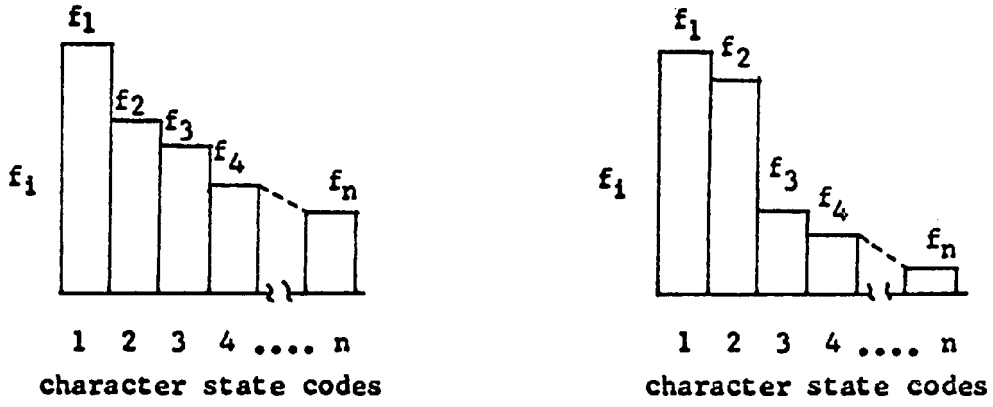


Fig. 6.--Character state frequency distribution histograms

The character state proportion test measures the relative frequency of the most frequent and second most frequent character states. Pass lists are printed out for $f_2 \leq 0.60f_1$, $0.65f_1$, $0.70f_1$, $0.75f_1$, and $0.80f_1$ (see Figure 6B and Appendix E). This test excludes characters which have (at least) two character states of high and fairly equal frequency, which is illustrated in Figure 6B. By definition there can be only a single primitive state, and if there seem to be more than one on the basis of character state distribution, then the character must be rejected. The number of characters passed in the six tribes is shown in Table 2. Increasing the proportion causes a less stringent selection, since the frequency of the second most frequent state can more closely approach that of the most frequent state. The number of null characters in the tribes is as was stated previously.

Table 2.--Numbers and percentages of characters passing the character state proportion test at five values of X

Prop.	Tribe 1	Tribe 2	Tribe 3	Tribe 4	Tribe 5	Tribe 6
0.60	81 75%	77 71%	69 64%	61 56%	75 69%	75 69%
0.65	84 78%	80 74%	76 70%	66 61%	79 73%	75 69%
0.70	93 86%	86 80%	81 75%	72 67%	83 77%	91 84%
0.75	99 92%	91 84%	88 81%	81 75%	89 82%	91 84%
0.80	99 92%	91 84%	88 81%	81 75%	89 82%	91 84%

The distribution of some character states is inconsistent across the diversity of taxa within the group under study; imagine a situation midway between the cases illustrated in Figures 5A and 5C. Here the adjacent group test helps to determine whether the most frequent character state is indeed primitive. If, as has been hypothesized, primitive character states are descended from a common ancestor, then the adjacent, coordinate groups of equal taxonomic rank are likely to show the same primitive character states. OTU's selected from the diversity of the adjacent taxa are used for this comparison. If highest frequency of a character state also occurs in the 75% or 80% majority of adjacent group OTU's, then that state is deemed primitive within the group under study (see Appendix E).

To allow for passing characters with the character state distribution hypothesized in Figure 5B, a frequency test result of $f_1 \geq 0.9N$ is taken as sufficient proof of common descent within the group, and the adjacent group test is not used. Greater risk in this bypassing of the adjacent group test would attend lower values of the

passing frequency and smaller groups, where statistical uncertainty is greater.

Once reliable information in the form of usable characters has been winnowed from the unsorted mass of data, these data are used to determine the most probable evolutionary patterns. These patterns are made by the association of complexes of characters which tend to be present as groups of divergent (advanced) attributes along the pathways of descent. The ground plan method seeks to determine the most probable pathways from among those that could be hypothesized within the limits of the data.

It seems reasonable to recognize economy of change as a guiding principle. It is less likely that the differences of each character between two taxa are the result of a long series of changes flip-flopping back and forth between advanced and primitive character states (Figure 7A1) than that the observed differences are the result of single changes (Figure 7A2). By rejecting the unpatterned characters, this conclusion is usually insured.

Similarly, the arrangement of taxa which requires the fewest number of changes--gains and losses--of characteristics to accomplish the patterns is sought (Figure 7B). The selection of patterned characters and careful ground plan analysis yields the result depicted in Figure 7B2, rather than that in Figure 7B1.

Of particular note are the so-called "losses" of characteristics. Sometimes after the data are fitted into a generally economical pattern, certain peripheral taxa lack advanced characteristics which were present in their progenitors. If a presumably derivative taxon has many of

these "losses," one suspects that the pattern that was worked out is not the most probable one (Figure 7C1) and that rearrangements are needed (Figure 7C2). If rearrangements of even the entire pattern make little improvement, or there is contravening biological evidence, such a lack of an advanced characteristic may be an extreme specialization, like the loss of chlorophyll in certain **Cuscutaceae**. Figure 7C1 illustrates this in character a.

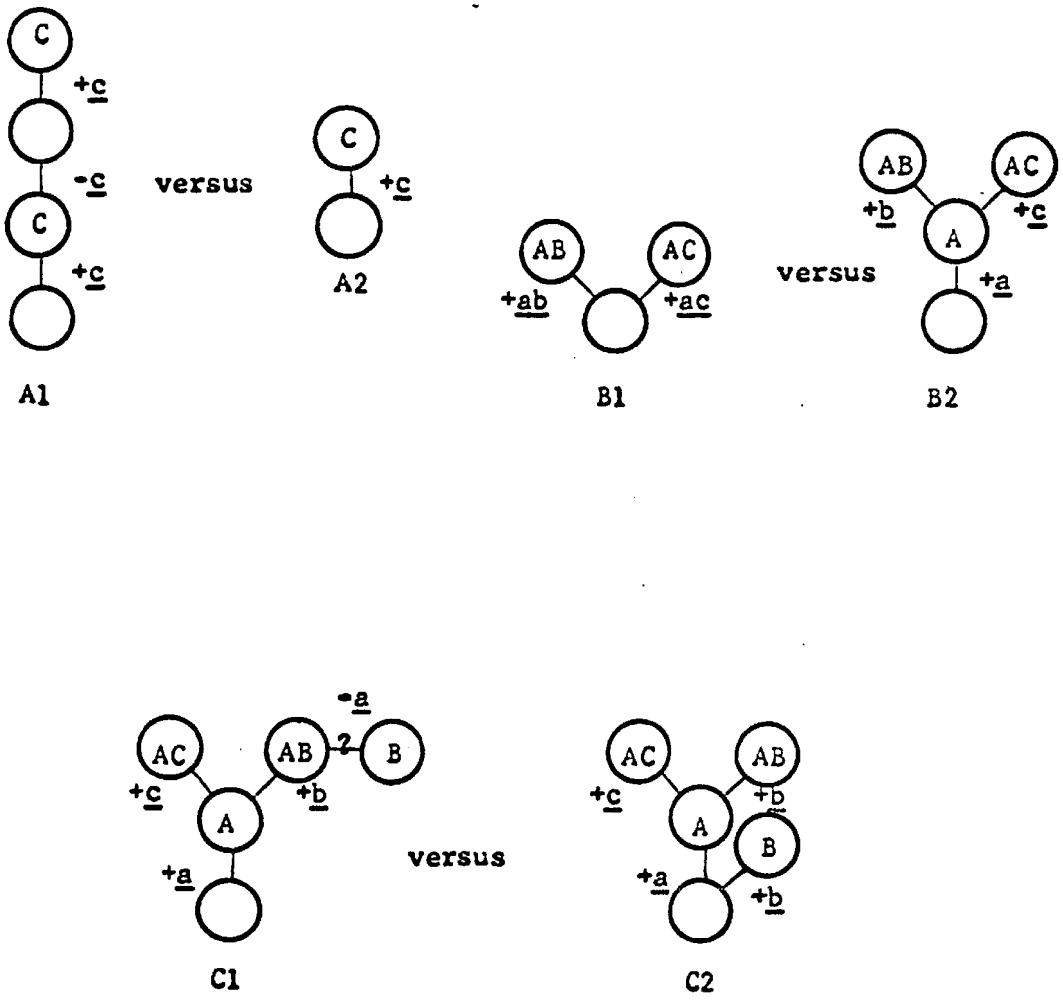


Fig. 7.--Construction of probable evolutionary pathways

Once a set of constant characters, each having a single character state that is primitive with high probability, has been found, these characters are used to generate a taxon x taxon ($\underline{i}$ x $\underline{i}$) matrix from the relevant rows of the $\underline{i}$ x $\underline{m}$ table. Such a process is in part the analogue of an intuitive assessment of relationship.

Pearson's product-moment correlation coefficient serves this purpose in studies of many multi-state characters in many taxa. Rogers' similarity ratio is perhaps even better suited, and it or Sneath's index of similarity can also be used with binary characters. The full data set of chosen characters should be used to calculate the $\underline{i}$ x $\underline{i}$ matrix, whatever measure of association is employed.

The next step is to prepare a visual ground plan diagram, which is based on a series of concentric rings. The radial distances indicate divergence from the ground plan ancestor, which lies at the center of the rings. The problem is to place the taxa on the diagram so that their connections, which are functions of similarity of character changes, trace the most probable evolutionary pathways. The finished diagram should illustrate the probable course of evolution of the taxa, and may resemble a family tree such as a classical taxonomist might develop from his unverbalized knowledge of taxon relationships.

In making a small scale visual ground plan diagram, the taxon with the lowest divergence index is first placed on the diagram. Then the remaining unplaced taxa are searched to see which of these is most like the taxon already placed. This process is repeated, each time trying to add and to rearrange the taxa so that there are the fewest

gains and losses of characters. Occasionally a hypothetical taxon will be added in an evolutionary line between two real taxa where a third taxon or evolutionary line branches off. After the ground plan diagram is complete, the fluctuating characters are assessed. They are either eliminated from a re-analysis and revised diagram or the taxa are rearranged to reduce or eliminate the fluctuations on the original diagram.

When the computer is used to process data for a ground plan diagram, the primitive character state, coded (0), is used against all the divergent states--no matter how many--which are lumped together and coded (1). This has the advantage that programming the computer is far simpler than with many states. But more important, the evolutionary relationships of the various advanced states is usually uncertain in large studies. Lumping has the disadvantage of losing some information and, especially, equating different advanced states on the diagrams. While the loss of information by no means precludes satisfactory results, the lumping becomes increasingly questionable at the higher taxonomic levels, and may reduce the effectiveness of evolutionary ground plan methods at those levels.

In most of the computer studies, the character selection tests have been stringent enough so that fluctuating characters which did pass the tests have not overpowered the patterned characters. The computer has produced a largely satisfactory result. But in almost all of these studies, one or two of the taxa seem to be out of place. Here, fluctuating characters isolate a highly advanced OTU from its nearest attachment to the remainder of the ground plan diagram by a

long series of character losses. The taxonomic importance of the fluctuations has been difficult to evaluate, since the studies have been at the generic and tribal level. In the computer technique, which will be described in greater detail in Chapter III, the computer makes the $\underline{i} \times \underline{m}$ and $\underline{i} \times \underline{i}$ tables. Divergence index relates taxa on the ground plan diagram at the beginning of an evolutionary line from a ground plan ancestor. Pearson's $r_{x \cdot y}$ is used to associate taxa in other positions on the diagram. Hypothetical intermediate taxa are calculated for every character change (at what would be each ring of the visual ground plan diagram, so to speak) on the basis of the characters' frequencies among the real taxa. The results are printed out by the computer as sequences leading from the point of attachment of the evolutionary line through the intermediates to the taxon to be added. The lists of taxa and their characters appear in such a way that a standard visual ground plan diagram can be readily produced from the computer output.

CHAPTER III

COLLECTION, EVALUATION, AND SYSTEMATIZATION OF THE DATA

The Nature of Characters

Any taxon can be considered as a set of characteristics. In most taxa these are morphological, but chemical and (in animals) behavioral characteristics are among the kinds useful to classification in some groups of organisms. The kind of characters available to the classifier will determine the taxa and, thereby, the kind of classification that can be made. Physiological characters will yield a "physiological classification" of organisms, for example. Conversely, data of a particular kind can be gathered if one wishes to produce a certain kind of classification.

A character is any feature of an organism which can be described by--and, for the purposes of computer work, quantified or reduced into--one of two or more mutually exclusive attribute classes (character states). These attributes describe a specimen, OTU, or taxon, but do not necessarily differentiate it from other specimens, OTU's, or taxa. In the past, "characters" of taxa have often been synonymous with "distinguishing characteristics." In taxiometrics the word is used primarily without reference to taxonomic groups, so it is unnecessary to use a circular definition for "characteristic" or "taxonomic character"--one which hinges on presence in certain predefined taxa and absence in others (see Sokal and Sneath, 1963, pp. 61-63).

The characteristics of an individual are known in a special way; statistically speaking, the population is the sample ($s = \sigma = 0$). In contrast, the attributes of taxonomic groups (above the level of single individuals) do not share this kind of reality, but are merely censuses, samples, or rarely averages or modes of the attributes of the constituent taxa or organisms ($s \neq \sigma \neq 0$). Similarly, the taxa above the level of single individuals lack "fundamental reality,[1]" for, unlike individuals, they, too, are compounded of the values of attributes of the characters of their constituent subgroups. The reason a species or genus seems to be "fundamentally real" to the human mind is that the censuses, samples, averages, or modes of attributes of the subgroups are nearly constant within that species or genus.

It could be suggested that the ultimate kind of classification will reflect the information of the gene pools of organisms and groups of organisms. But there is a certain unreality in gene pool classifications because multiple factors and mutations which cause blockages can interfere with the correspondence between the genes and their phenotypic expressions. Ehrlich (1964, pp. 114-118) has reasoned against genome-based classifications; he believes them to be no more heuristic or of greater general applicability than those classifications based on the more traditional approach of morphological characters. I agree; in addition, phenetic or, in certain groups of

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[1]Contrast the term "fundamental reality" with "synthetic reality." In phytosociology, the former would be a relevé of a sample plot and the latter an association table from which generalizations (abstractions) about several sample plots are drawn.

animals, behavioral expressions of taxa, and not their underlying gene pools, are the more "practical" reality. Of course, the more fundamental area should be investigated, too, since it often makes clear the evolutionary mechanisms which have produced certain morphological expressions. In terms of evolutionary classifications, the attributes which are passed from generation to generation over long spans of evolutionary time are most significant. In this framework, characters which are not selected for (have no positive selection value) are not of importance, since they will tend to perish along with the organisms which bear them. One could even value characters in terms of their tendency to be selected and passed on to succeeding generations with a "survival coefficient," but pleiotropy would make such analyses difficult. These lines of reasoning are more speculative than practical for any present technique or need. They illustrate, however, that the aims of the classifier are the basis on which the search for characters must proceed.

There is good evidence for a direct relationship between genes or their subunits and the action of enzymes, which, through auxins and other chemicals, largely controls morphology (see Wardlaw, 1952, pp. 138-141). Complexity of phenotypic expression, therefore, is probably proportional to the number of genes contributing to a given character. It is difficult to conceive how the multitude of features of a leaf, for example, could be controlled by only a few genes.

Characters which are controlled by single genes often seem to be of little taxonomic use, while characters determined by many genes may be of great taxonomic use. Within wide limits, character

reliability seems proportional to the complexity of the genic system which controls the character. There is a problem, however, in that well-adapted multi-gene systems can sometimes be blocked by single gene changes. These systems, which when expressed often yield characters that are reliable for taxonomic purposes, cannot be easily taken into account when their action is blocked.

Genetic complexity and resultant character reliability produces a statistical advantage. Averages of measurements of characters which are formed by the sum or interactions of many all-or-nothing processes will tend to follow the binomial distribution, which rapidly approaches the normal curve of variation as the number of factors increases. Such characters may thus be amenable to parametric statistical treatment.

In contrast to multi-gene systems which can be blocked are those genes or gene groups which yield so-called "fundamental" characters. They are just that because the operation of their genes is indispensable to the operation of the plant, although the characters of taxonomic value which they produce may or may not be important to the life of the organism. According to Muller (1939), the longer the time genes are established in genotypes, the greater their chance of acquiring multiple functions. And their damage or change is then likely to be lethal. On the other hand, such genes may become "buffered" or incorporated into blocs of interacting genes, and may become part of a homeostatically adjusted gene system in which simple changes in small parts of the system do not destroy its control.

Although any feature of the higher plants which can be studied may be a potential character, in most taxonomic practice this is reduced to characters visible on herbarium sheets. Almost any other type of character, at least in the tracheophytes, takes more time to find and analyze than it is worth in the alpha- or beta-taxonomic phase of classification. Considering facility of observation, total external morphology is best able to provide the data needed to make evolutionary classifications. Particularly if the assumption is made that all characters are of equal value (until proved otherwise), efficiency of information gathering dictates that "technical" characters largely be ignored. In detailed monographic studies, however, non-morphological data as well should be used, and conclusions based on morphology alone should be modified and corrected as additional data permit.

Developmental characters are a class intermediate between those of the mature plant, which are usually represented on herbarium sheets, and those of the gene pool. Developmental characters are all too often not available on the alpha- or beta-taxonmic level. In many cases, parallelisms and convergences of, for example, mature trichome types or leaf shapes could be understood by an examination of living plants over a period of time. Many problems of herbarium taxonomy have thus escaped solution.

In identification and key construction, knowledge of the limits of variability of characteristics is of prime importance in placing specimens into taxa. To be taxonomically useful, characteristics cannot much overlap in taxa which they are to distinguish. In the

evolutionary ground plan diagram method, on the contrary, overlap of single characters between OTU's is not of great importance; it is the correlation of characters and character complexes that is significant.

A large series of specimens must be studied when making keys in order to be sure of stating the range of variation of the few key characters correctly. For example, if the character state of some particular height is found in only 10% of a group of presumably conspecific specimens, a minimum of 100 specimens must be examined to be reasonably certain that such a specimen will be found at least once. On the other hand, a sample of only five specimens will normally serve to reveal a characteristic found 80% of the time within a population (see Mayr, Linsley, and Usinger, 1953, p. 128). Obviously, a person using the evolutionary ground plan diagram method, which deals largely with central tendencies and different values of many correlated characters, can succeed with far smaller samples than can the botanist who judges relationships of plants largely on the basis of correlations of a few key characters.

Data Collection and Organization

In the present study herbarium specimens were examined with a binocular microscope fitted with an ocular micrometer for making standardized measurements. Trichomes were mounted in Hoyer's solution, and pinnae or pinnules were cleared in sodium hydroxide, stained with celestine blue and safranin (see Gray and Pickle, 1956), and mounted in diaphane. Either dry or water-wetted material can be mounted directly in Hoyer's solution. Aqueous safranin was added directly to the Hoyer's solution. Cleared mounts were useful in determining

the nature of soriation and venation in species with laminae too thick to permit observations to be made directly from the herbarium specimens. Most of the genera were represented by herbarium mounts of entire, usually fertile plants. Complete data were obtained for all but four rare species (see Appendix A-1).

For rapid examination of characters present on the underside of loosely mounted specimens, a small mirror, thinner than a dentist's instrument, was made of a quarter inch square of chromium plated steel with a small tab for mounting at the end of a piece of dowel. Plant parts were lifted with a dissecting needle, and the underside view reflected up to the binocular microscope. The mirror and other dissecting and measuring tools were kept immediately at hand in a small, compartmented, open-topped tray mounted on the binocular microscope.

To eliminate errors during the transcription of handwritten data to IBM cards, Rogers and Fleming (1963) recorded the data in one step on special IBM cards with partially pre-punched holes, which were knocked out with a stylus. Such cards are held in a shallow tray which supports the card during the punching operation. Cards for manual punching have only forty columns. Three such cards would have been required for each taxon in my study. Instead, my data were collected on mimeographed sheets (see Appendix B-2), and were key-punched directly on eighty-column cards, followed by a visual check to insure that no errors had been introduced.

To avoid errors caused by recording wrong data from an adjoining column of figures, a cardboard slit with the character numbers on

either side was used, permitting only the column being coded to be seen.

The first step in the application of quantitative methods to a taxonomic problem is to observe what potential characters are found in the OTU's to be classified. The method I used was to write a brief description of the OTU's (species) chosen to represent the genera and subgenera under study. In order to make each description as complete as possible, a survey sheet of possible characters was compiled. This was prepared from one used by Dr. W. R. Maxon and one of my own design, and included the suggestions and criticisms of Mr. C. V. Morton and Prof. W. H. Wagner, Jr. After half a dozen descriptions had been prepared using this survey sheet, an improved one was designed and used throughout the work, until every species had been described (see Appendix B-1). The descriptions were collated, one descriptive category at a time, listing the various phrases used to describe that organ or constituent part. By this means the probable range of characters and attributes of each plant part over the whole group of OTU's was learned. In fact, reexamination of all of the material during the main data-taking process resulted in almost no additions to the initial list of characters and attributes.

In all taxiometric methods each character must be resolved into mutually exclusive attributes. The difficulty of changing the descriptive phrases into characters and attributes was inversely proportional to character complexity. All-or-nothing responses were of course the easiest to recognize, verbalize, and codify. Characters like frond shape were more difficult to treat, and variation within

an OTU and between OTU's meant that the limits of attributes were sometimes quite arbitrary. Transforming the verbal data of the improved description survey sheets yielded 124 characters, each having from two to nine states. Absence of any attribute was coded (0); (1) through (8) were the other attributes (although all eight states were rarely used), and (9) indicated missing data.

Six specimens were coded using the 124 characters, and then all the characters were evaluated, which led to a revision of characters and attributes (see pages 63-66). Sixteen characters were eliminated because they were either not amenable to coding and their attributes had no meaning or because they were logically interdependent with other characters, and would have introduced false correlations into the results. The revised character and state list was then used throughout the work (see Appendix A-2).

Character and Attribute Selection and Organization

Meristic Characters.--In selecting and codifying characters and attributes, the meristic characters pose a problem. Not all kinds of measurements are of equal value in taxonomic description or discrimination. The chosen measurement should be a good estimate of central tendency; or, if it is not that, it should be uniformly biased in all the taxa. It should also be a characteristic that is mostly under genic and not environmental control. An easily obtainable measurement is preferred over a difficult one, if their information content is the same. Regression analysis may indicate, for instance, whether measurements of some character of external morphology can substitute for measurements of some internal, anatomical character.

The surface area of a stele might be correlated with the diameter of the stem which bears it.

In routine taxonomic work, measurements are ideally recorded as means, normal range, and deviant extremes, in such a form as: (0.6)1--2--3.5(4.5). Often either the deviant extremes, the mean, or both are not stated. Observed range is stressed because non-overlapping ranges serve as distinguishing characteristics between taxa.

Figure 8 illustrates the effects of including juvenile, immature, and depauperate specimens on range value and means. The solid curves outline the expected frequency values for the size classes of random observations taken from (hypothetical) fronds of a single species in all conditions; the dashed lines delimit the normal curve that could be expected if juvenile, immature, and depauperate specimens were eliminated from the observations, leaving only the mature specimens, the size of which is, hopefully, genotypically controlled.

The important things to note are: (1) the solid curves are skewed to the left, indicating that in a random sample of observations, juvenile, immature, and depauperate specimens change the mean from that of mature-only specimens, (2) correspondingly, the variation of both frequency and size of observations in the skewed portion of the curve is likely to be greater than in the non-skewed portion (the solid curves are farther apart than the dashed ones), (3) the mean of the random specimens may therefore be expected to shift more than the mean of mature-only specimens, and (4) the maximum value usually

observed is less sensitive to the foregoing shift than either of the mean values.

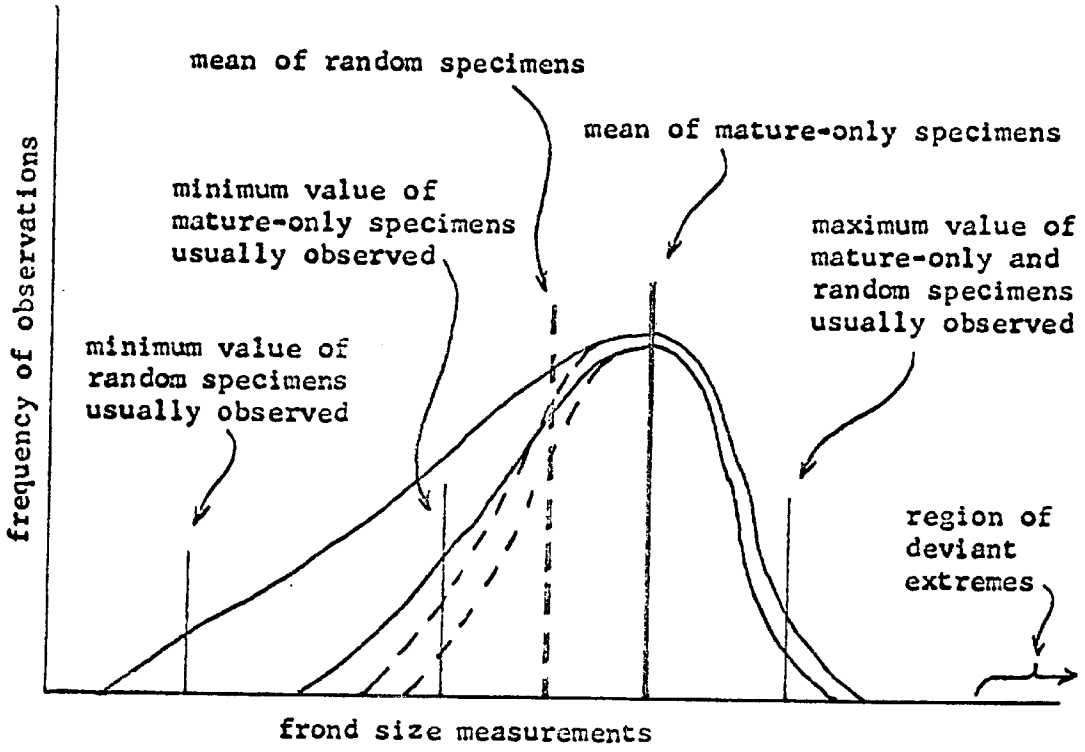


Fig. 8.--Hypothetical relationship of frond size and frequency in samples of mixed-age and mature material of a single species.

What value, then, will best characterize the taxon? Minimum size makes a poor character because of the interference of immature specimens. Although the mode might be suitable, it requires more measurements to achieve a satisfactory degree of precision than does the calculation of a mean. And, if the curve is flat-topped, it may be difficult to locate the mode. The mean of random observations may be close to the mean of the mature-only specimens, or because of phenotypic or genetic factors, it may be quite distant. Similarly, it may be close or distant from the mean of the population which

it is designed to characterize. The mean of the mature-only specimens will not bear a much more constant relationship to the mean of the population than will the mean of random specimens; it, too, will vary. But the maximum value usually observed, since it is more likely to be under genotypic control than the other measures, will vary even less than the mean of the mature-only specimens.

The maximum value usually observed does not always characterize the population, however, since sometimes deviant extremes are observed. Statisticians have a difficult time analyzing deviant extremes because they fall outside the normal curve of variation. In this study I have ignored observations more than two size classes larger or smaller than the body of observations, for such extremes must lie well outside the normal curve of variation.

Often a ratio relating to size of plant parts was recorded, rather than size itself. When size was taken into account, measurements were grouped into size class attributes which were usually equal divisions of the observed variation, except for the largest and smallest size classes (see Appendix A-2, character 44).

Arrangement of Characters and Character States.--If characters are improperly organized, the data will show false correlations. Character states which logically determine one another must be avoided. The character "wax presence" is logically dependent on the character "wax color," since the presence of wax of any color correlates with the positive state of "wax presence." This character should be made a state of the color character: "wax absent, white, yellow, etc." In addition, there is the problem of functional correlation.

Michener and Sokal (1957, p. 141) state: "In all cases characters were reorganized or omitted to exclude correlations resulting from such situations, where a certain state of one character requires a particular state of another."

In an attempt to minimize these correlations I divided the characters into groups which were likely to show a logical or structural relationship. Naturally, dependence due to manifold effects of single genes or gene blocs, particularly when acting in separated parts of the plants, could not be observed, and remained an unknown in setting up the characters and states. The characters of rhizome morphology are one of the groups I investigated. First the degree of dependence of every character upon every other was estimated by comparing the perfect matches between character states in a dozen OTU's. A correlation of 0-25% perfect matches was set equal to 0., 25-75% equal to 0.5, and 75-100% equal to 1.0. The values for every pair of characters were arrayed in a half matrix, and the sum for each character calculated as an "index of dependence" (see Figure 9). The seven original characters of the rhizome morphology group ranged from 0.583 to 0.000 in their indices, with an average of 0.334.

I was able to reject three of the original seven characters, but retained the pertinent information of two of these three by adding character states to the remaining characters. Using the same criteria for "index of dependence," I constructed a second half matrix with the perfect match data of the four remaining characters. The new range of dependence was 0.333-0.000, and the average 0.166.

RAW DATA

	1	2	3	4	5	6	7	Sum	Average
1:	-	0.0	1.0	1.0	1.0	0.5	0.0	3.5	0.583
2:		-	0.0	0.0	0.0	0.5	0.0	0.5	0.083
3:			-	0.5	0.5	0.5	0.0	2.5	0.418
4:				-	0.5	0.5	0.0	2.5	0.418
5:					-	0.5	0.0	2.5	0.418
6:						-	0.0	2.5	0.418
7:							-	0.0	0.000

REVISED DATA

	1	2	4	7	Sum	Average
1:	-	0.0	1.0	0.0	1.0	0.333
2:		-	0.0	0.0	0.0	0.000
4:			-	0.0	1.0	0.333
7:				-	0.0	0.000

Fig. 9.--Raw and revised rhizome morphology character group matrices (The character numbers do not refer to those listed in Appendix A-2)

To have as perfect a system as possible would require further distillation of characters and character states until all of the characters were logically and functionally independent. But the information lost might be excessive. In this case, only one of the remaining four characters shows undesirable correlations. If the character were eliminated, the system for differentiating between types of creeping rhizomes would be lost. Because the character has been retained, some error has been introduced, which may degrade the

resulting classification slightly. Throughout the study it was necessary to compromise between character independence and information retention. But in each group of characters, I tried to bring the "index of dependence" down to or below 0.200.

The Choice of Taxa and Operational Taxonomic Units

Eighty taxa were chosen to represent the various genera and subgenera from among the 700 to 750 species of Adiantoideae. Monotypic genera were represented by their single species. Larger genera were studied in the herbarium and through the literature, and then an attempt was made to choose an OTU for each genus or for the subgenera or sections of genera which had been so divided or whose range of variation seemed to warrant such treatment.

Most of the data are not measurements of the plants, but are state codes representing non-meristic qualities. Therefore, it was not meaningful to average state code values of many specimens to arrive at a particular value for a character. For instance, what would the state code average between green and black stipes be? A choice, then, had to be made between the specimens examined to decide which one would be used as the OTU. In the first place, specimens were chosen from the herbarium that were mature, complete, and representative of the material available for study of the species. From the start, I tried to eliminate aberrant, juvenile, immature, and teratological material. Then one specimen was coded for each OTU. After an interval of time (to preclude biasing by my remembering the states of the first specimen), a second specimen was coded. Pearson's product-moment correlation coefficient, $r_{x \cdot y}$, was calculated to estimate the

similarity between the two. If the value of the coefficient was greater than or equal to 0.900, the second, later-coded specimen was chosen to be the OTU, since I felt my ability to assign correct state codes increased as more specimens were coded. If the correlation coefficient between the two was less than 0.900, a third specimen was coded after another lapse of time. Additional coefficients were calculated between the first two specimens and the third. The specimen with the highest average correlation coefficient was chosen as the OTU. In terms of the coded characters it was the most representative of the three. The computations were recorded on the correlation coefficient worksheet (see Appendix B-3).

Character Patterns and Tabulation

Experience has shown that some characters are more taxonomically useful than others. The taxonomic value of characters depends upon their degree of association with other characters. Traditionally, these fundamental (key, constant, "good") characters have been chosen by "intuitive," largely non-verbalized mental correlation. When a taxon is defined by a group of characters which are highly correlated, the absence of a single one of the characters does not upset the inclusion of, for example, an aberrant species within its logical genus--even if the absent character is a key character. It is the totality of correlations which indicates affinity. By eliminating the useless and confusing, non-correlated characters, it is possible to increase the ratio of information-bearing characters to meaningless ones, hence to increase the accuracy and heuristic value of the classifications.

The "true being" or "essence" of a taxon is its catalogue of actual and potential, well-correlated character states. But the potential character states of taxa at the upper hierarchical levels can only be understood after considerable study (see pages 33-34). The beginning of such a study must be confined to the actual, expressed character states alone. These can be listed as multi-state characters of the OTU's. Inspection of such a multi-state $\underline{i} \times \underline{m}$ table involves not only position (in columns and rows), but also value of the character state code. It is easier to evaluate a character state list converted to binary characters, one for each attribute. For example, if a character has six states, it is divided into six binary characters, as in Figure 10. The binary characters for a group of OTU's are printed out one OTU per column and one binary character number (BCNR) per row. This is termed a binary $\underline{i} \times \underline{m}$ table (Appendix C).

	Taxa			
	1	2	3	4
CHAR 1 STATE:	1	6	4	3

	Taxa			
	1	2	3	4
BCNR 11:	1	0	0	0
12:	0	0	0	0
13:	0	0	0	1
14:	0	0	1	0
15:	0	0	0	0
16:	0	1	0	0

Fig. 10.--Conversion of a multi-state $\underline{i} \times \underline{m}$ table to a binary $\underline{i} \times \underline{m}$ table

Ordering the columns of such a table to form coherent presences of patterned binary characters across groups of columns is very difficult to do by inspection unless there is a preconceived order

to the columns. If, however, the subgroups are reasonably well known, the OTU's can be arranged into tentative groups of columns. The resulting table will tend to confirm or to deny the composition of subgroups, and the subgroups can be revised by inspection to improve the consistent presence of patterned characters within subgroups and the mutual exclusiveness of patterned characters between subgroups. Rogers' similarity ratio can be used to find the similarity between pairs of OTU's, although scanning the binary i x m table is difficult if the table is long.

By arranging and rearranging columns (OTU's) of the binary i x m table (Appendix C) I have been able to exclude Doryopteris, Ormopteris, Pellaea, and Saffordia from the relatively distinct cheilanthoid ferns sensu stricto, namely, Cheilanthes, Adiantopsis, Aleuritopteris, Notholaena, etc. So long as the former genera remained a part of the group of cheilanthoids s.s., the ground plan technique was completely unsuccessful in making a reasonable ground plan diagram. The pellaeoid genera were an aberrant element, and formed a relatively coherent group themselves. But no visual inspection of the specimens revealed this because of the variability and overlapping distribution of obvious characters in these intensely polythetic groups.

The entire subfamily was similarly divided up into six tribes:

#1, Onychioids: Actiniopteris, Afropteris, Anopteris, Cryptogramma, Llavea, Neurosoria, Ochropteris, and Onychium;

#2, Cheilanthoids: Adiantopsis, Aleuritopteris, "Argyrochosma," Aspidotis, Cheilanthes, Cheilanthopsis, Cheiloplecton, Mildella, Negripteris, and Notholaena;

#3, Pellaeoids: Doryopteris, Ormopteris, Pellaea, and Saffordia;

#4, Gymnopteroids: Anogramma, Bommeria, Gymnopteris, Hemionitis, Paraceterach, Pityrogramma (including Trismeria), Pleurosoriopsis, and Trachypteris;

#5, Eriosorioids: Aspleniopsis, Cerosora, Coniogramme, Eriosorus, Jamesonia, "Nephopteris," Platyzoma, Pterozonium, Rheopteris, Syngramma (including Craspedodictyum), Syngrammatopsis, Taenitis, and Toxopteris;

#6, Adiantoids: Adiantum.

Character Ordering and Evaluation

State Code Ordering Program.--Incomplete specimens with missing data were neither coded nor included in the computer analysis. Cards for the remainder of the taxa were operated upon by the state code ordering program, tribe-by-tribe (see Figure 11). States (0) through (8) were sorted into descending order of frequency within each character, and, as printed out in Appendix D, were assigned ordered state codes from (1) through (9), where (1) was most frequent, (2) second, and so on. Because the data of the tribes were operated upon separately, the state codes assigned by the program to the attributes of each character were not necessarily identical between tribes. An ordered deck of $i \times m$ (taxon) cards with the new state codes was punched out both for the taxa of the tribe and for the five adjacent group taxa, although these latter five OTU's were not censused in determining character state frequencies for the tribe.

Because the character numbers, the original state codes arranged in new order, and the frequencies of each state (displayed below the original state codes) were printed out, it was possible to return

to Appendix D and to the characters and character states of Appendix A-2 to determine which character state of every character used in the analysis had been considered the primitive one.

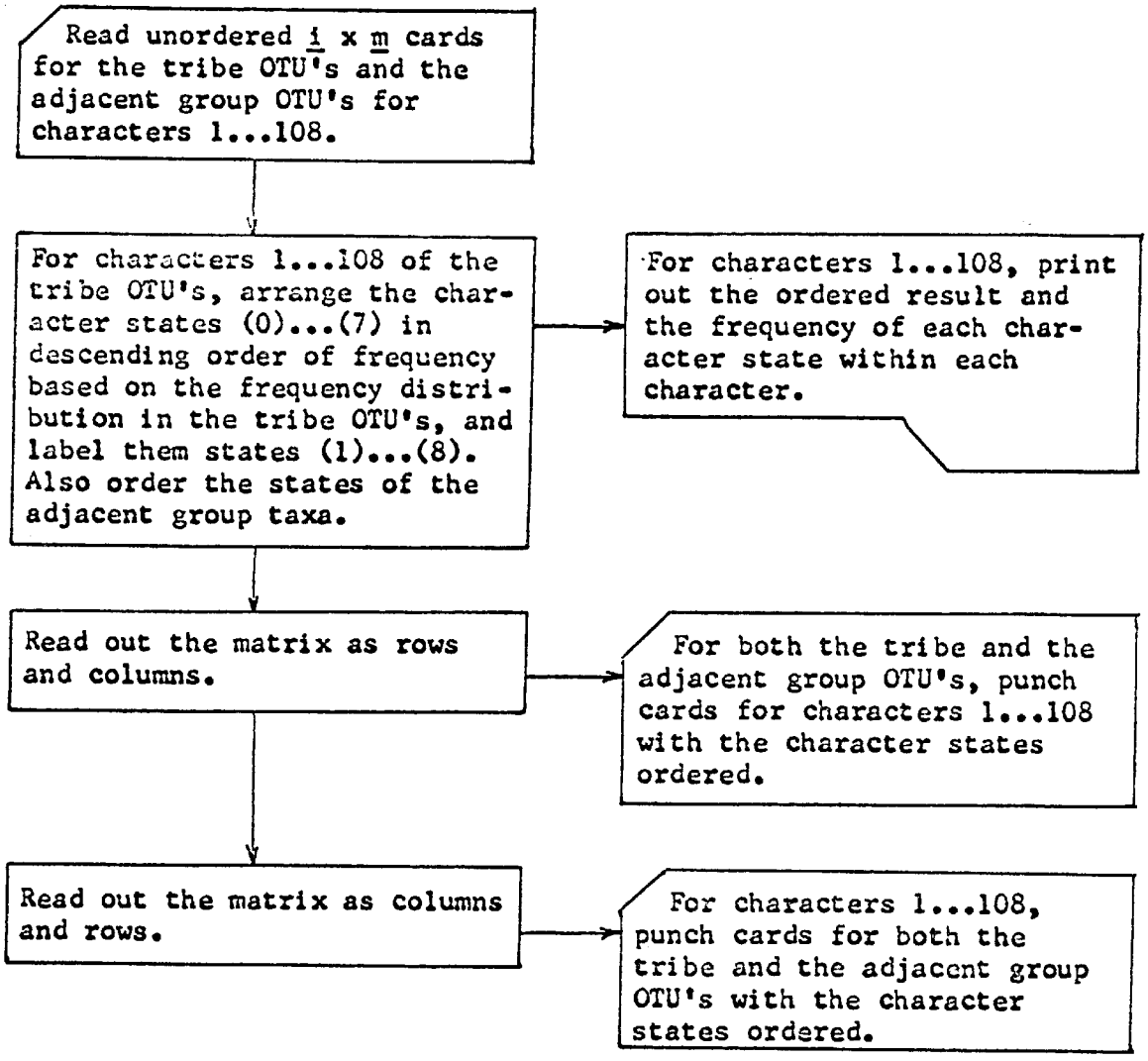


Fig. 11.--Flowchart of the state code ordering program

Along with the ordered i x m cards, a set of ordered m x i (character) cards was punched out at the same time, one card to each character, by punching out the i x m table as columns times rows, rather than rows times columns. These character cards were identified

by a three digit character number preceded by the letter C in columns 77-80. The taxon data was arranged in columns, working to the right from column 2, in taxon (OTU) code number order.

Character Distribution Selection Program.--The three tests used to eliminate fluctuating characters and to determine primitiveness of character states in the OTU's of the tribes were made independently so that the effect of each could be evaluated singly (see Figure 12 and Appendices E and F). The overall pass lists of characters were formed by combining characters passing the individual tests operating at whatever parameters were chosen (see pages 43-47).

The proportion, X, between the most frequent and the second most frequent character states of a character was measured for each character by recalculating in part the values printed out for the state code ordering program (see Figures 6 and 11). Pass lists were printed out for proportions of $X \geqslant 0.6$ to $X \geqslant 0.8$ in steps of 0.05. More characters passed when the proportion between the two states was less (i.e., when the value of X was increased). The probability of state (1) being primitive increases as the difference in frequency between it and state (2) increases.

Since I accept as valid the hypothesis of wide distribution of primitive character states, the most frequent character states were also screened. Pass lists were printed out for $f_1 \geqslant 0.5N$ through $f_1 \geqslant 0.9N$, in steps of 0.1 (see Figure 6A), and were read from Appendix D for $f_1 \geqslant 0.3N$ and $f_1 \geqslant 0.4N$. Primitiveness of the most frequent state of each character in a tribe was confirmed if it was found in three or four of the OTU's representing the other five

tribes. Although the adjacent group OTU's were coded along with the OTU's of each tribe, they were not used in computing state frequencies, divergence indices, or divergence sums. Nor were they carried through the analysis and placed on the visual ground plan diagram. Since the adjacent group OTU's were ordered along with the OTU's of the tribes, their presumably primitive states were also coded (1), and were called A through E in the program. The character number was passed whenever

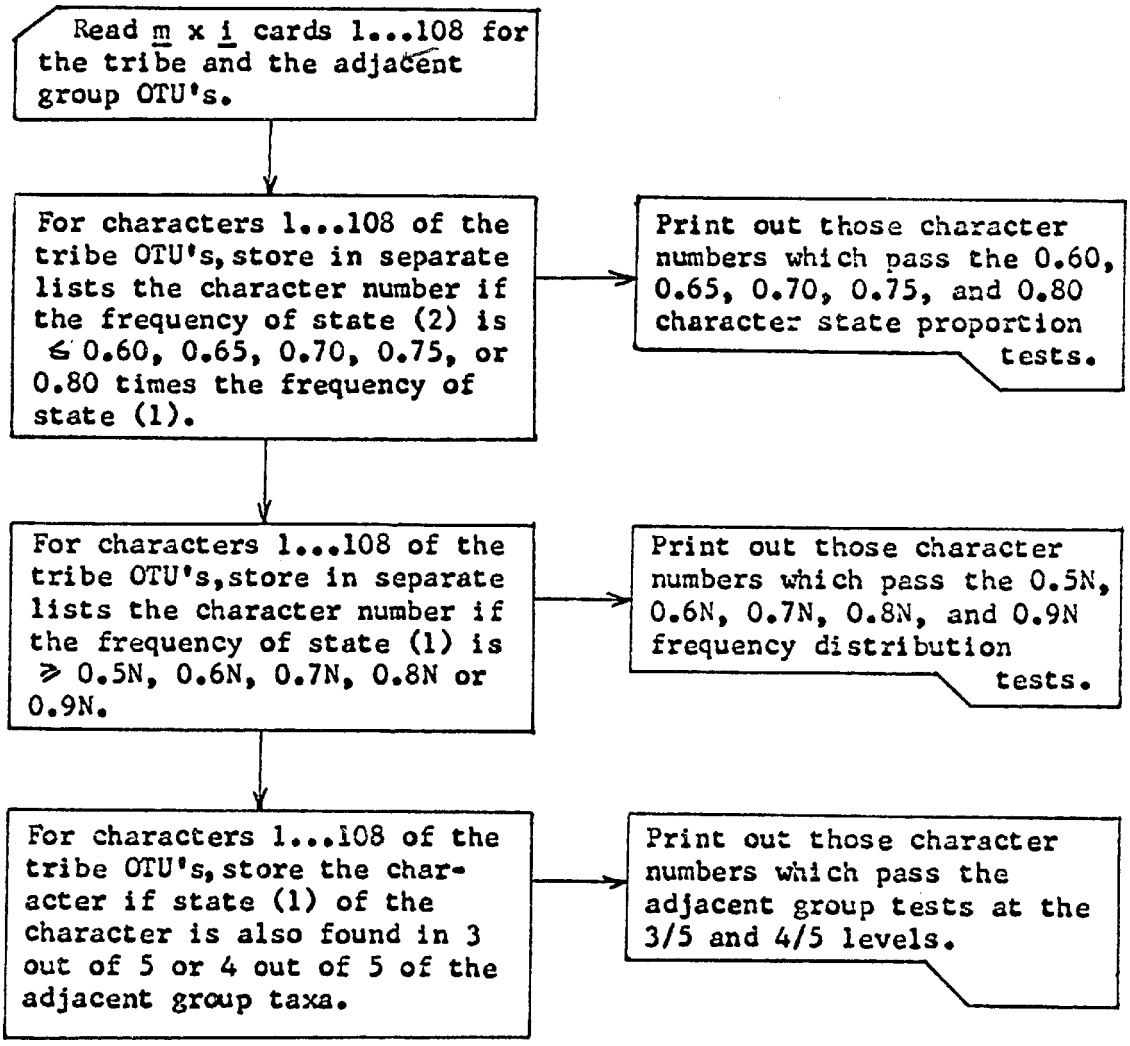


Fig. 12.--Flowchart of the character distribution selection program

(A x B x C x D x E) - (A + B + C + D + E) = -4. Routines which test each case against an exhaustive set of pass conditions are less efficient than this numerical approach.

Character Correlation Selection Program.--Another approach to character selection is to evaluate the contribution of information that each character makes to the analysis. This has nothing to do with determining primitiveness or character suitability from an evolutionary point of view. Consistent high correlations of one character with others describing the same structure indicate the others are contributing little information to the analysis. For example, if all stipe scales are 2--3 mm. long and are brown with a black central stipe, then if the scales are present, their colors and size are known. The latter two characters are redundant with the character "scales present," and may be eliminated.

An R-matrix redundancy test was used to screen characters arrayed in an $\underline{m} \times \underline{m}$ matrix (see Figure 13). Perfect correlations usually occurred between characters describing single structures by means of

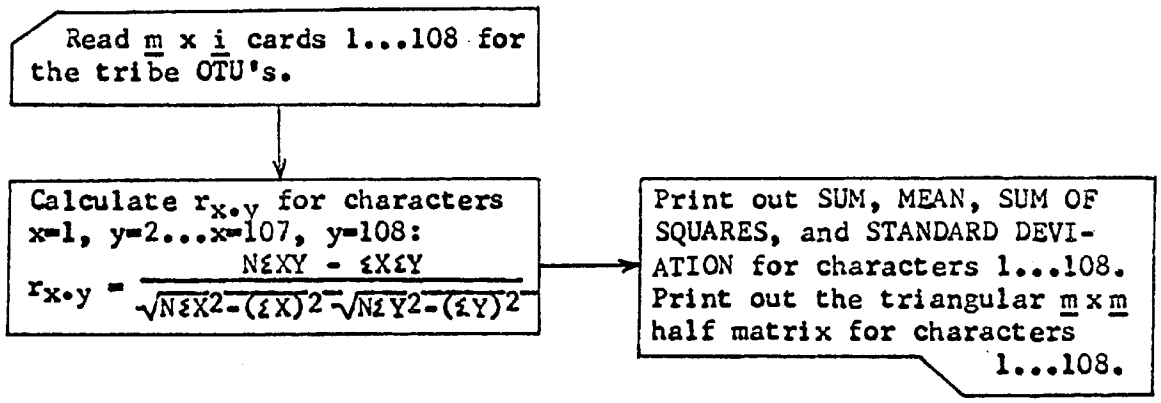


Fig. 13.--Flowchart of the character correlation selection program

a long series of characters. The redundancies of these various characters may be artifacts of character organization which were not recognized when the characters were selected and coded, and may not be a reflection of the distribution of valid characters among the specimens. On the other hand, they may be independent and correlated "reinforcing characters," hence valuable to the analysis. Their nature may be difficult to ascertain; this is a problem of biology, not mathematics.

The $\underline{m}$ x $\underline{m}$ tables for the tribes were inspected visually to detect those character pairs showing correlations from 0.900 to 0.999 and those with $r_{x \cdot y} = 1.000$ (see Appendix F). Another approach would have been to do the correlation computations, saving for pass lists those character number pairs exceeding certain preset correlation values.

Combined Pass Lists.--In making evolutionary ground plan diagrams of each of the tribes, several combinations of pass lists were used. In general, only when there was agreement of the supposed primitiveness of character states from within (by the frequency and proportion tests) and from without (by the adjacent group test) were the characters included for use in constructing evolutionary ground plan diagrams. R-matrix (character correlation) screening for $r_{x \cdot y} \geqslant 0.900$ was used in Tribe 3, and some additional characters which had proved to be non-patterned in previous trials were also eliminated in Tribes 1 and 3. The values of the coefficients of the proportion test and the frequency distribution test in the tribes are: Tribe 1--0.7, 0.5, Tribe 2--no tests, Tribe 3--0.7, 0.5, Tribe 4--0.7, 0.4, Tribe 5--0.65, 0.4, and

Tribe 6--0.7, 0.4. The adjacent group tests used were more stringent: 4 out of 5 for Tribes 1 and 3 and the 3 out of 5 for Tribes 4--6. All of these values refer to Figures 17 through 25, and not for unsuccessful trial diagrams not figured in this study.

Comparisons Among Data

Most comparisons of classifications have analyzed the visual end products of taxiometric research, the dendrograms (see pages 18 and 19). Besides this possibility of comparing different taxiometric methods, it is useful to compare different sets of data from the same OTU's, without introducing as a variable the factor analysis or OTU-grouping process itself. This I have done by comparing $\underline{i} \times \underline{i}$ matrices upon which the evolutionary ground plan diagrams are based. Figure 14 is a flowsheet of the matrix comparison program.

Spearman's (nonparametric) rank correlation coefficient, r_s, is used to evaluate matrix pair similarity. Because of the mathematics peculiar to and the easy development of this program, it was written in FORTRAN rather than MAD.[2] Data for each matrix to be compared are read from the $\underline{m} \times \underline{i}$ cards into an $\underline{i} \times \underline{m}$ matrix. Because the $\underline{m} \times \underline{i}$ cards are used, the characters to be used to represent the OTU's in calculating the $\underline{i} \times \underline{i}$ matrices can be selected by hand before submitting them and the program cards to the computer.

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[2]In developing computer programs, two factors regarding computer costs must be considered: compilation time (from source language like MAD to binary machine language) and execution time. During development, program changes are many. MAD, which compiles faster than FORTRAN, saves money because each time a change is made a new compilation from the source to the machine language must be made. After programs are operative, converting from MAD to a binary machine language equivalent of FORTRAN saves money because FORTRAN executes faster than MAD.

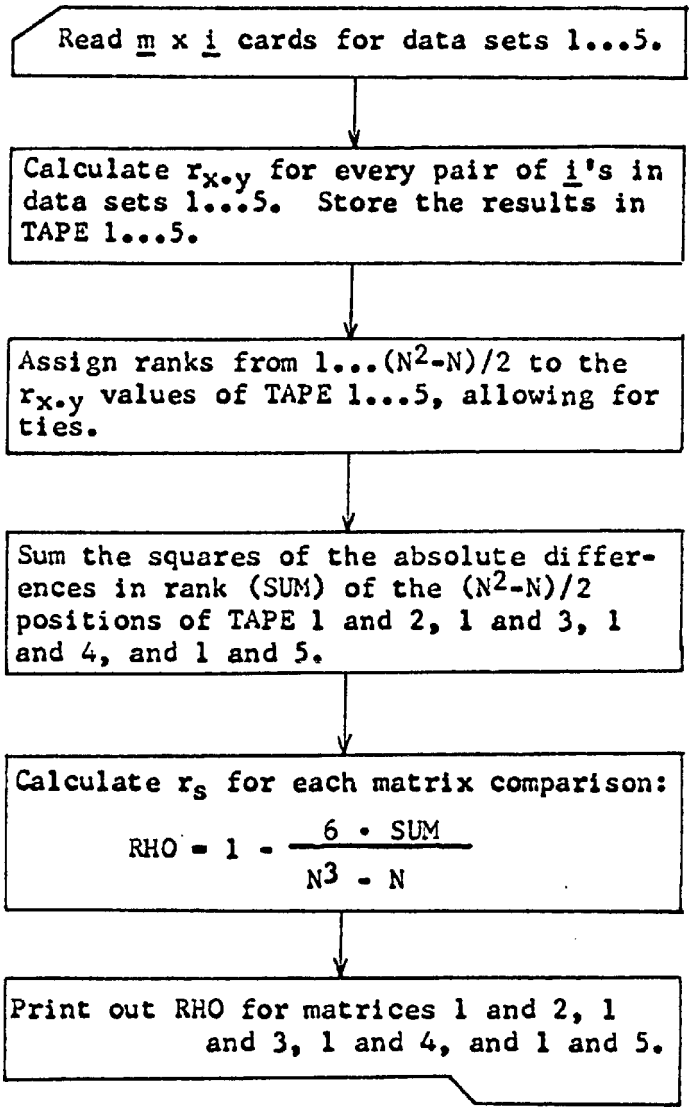


Fig. 14.--Flowchart of the matrix comparison program

From the i x m data for each matrix the computer calculates and stores an i x i matrix, using Pearson's correlation coefficient to assess the degree of similarity of pairs of OTU's identically to its use in the evolutionary ground plan diagram program. The principal constraint of the present program is that the number of taxa, i, must be identical in all matrices to be compared. But m, the number of characters used to form each i x i matrix, can vary. The i x i matrices

are the same size, and are read row-by-row onto storage tapes so that similar portions of the different matrices are on analogous parts of the tapes. The similarity values on the tapes are replaced by ranks, with the lowest similarity value ranked 1 and the highest $(N^2-N)/2$ for each matrix; N is the number of entries in the matrix. Ties are averaged; for instance, if the third and fourth lowest similarity values were identical, the rank for each would be 3.5.

Because storage space in the computer was limited, the primary matrix can be compared with any of up to five secondary matrices, but the secondary matrices cannot be compared with one another. Spearman's rank correlation coefficient, r_s, but called RHO in the program, is used to assess similarity of the ranked matrix pairs:

$$r_s = 1 - \frac{6 \sum_{i}^{N} d_i^2}{N(N^2 - 1)}$$

where d_i is the absolute difference between two coordinate ranks, Σd_i^2 is SUM in the program, and N is the number of variables (taxa). While r_s is not equal to Pearson's $r_{x \cdot y}$ for the same data, it does enable a comparison of various pairs of matrices to be made. Values of significance and high significance can be determined from published tables.

The similarity of matrices made with decreasing numbers of characters and identical sets of OTU's was studied. Similarity matrices were prepared using Pearson's $r_{x \cdot y}$ and seventy-four OTU's of the Adiantoideae. The principal matrix had N = 108. Secondary matrices were made by dropping every other character and recomputing the $\underline{i} \times \underline{i}$

matrix, until the smallest matrix used only seven characters. The results are shown in Figure 15. Using $\log_{10} r_s$ straightens out the lower end of the curve somewhat, but does not produce a linear relationship between the two variables. Matrices with $N < 28$ are quite unlike the full matrix, although even the $N = 7$ matrix is significantly correlated with the $N = 108$ matrix.

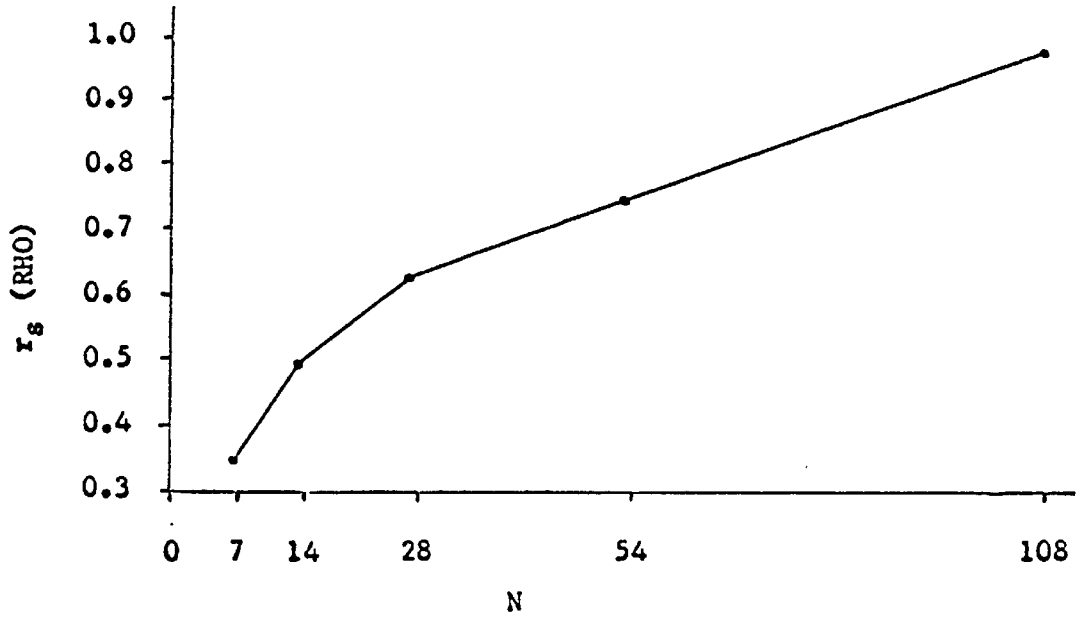


Fig. 15.--The relationship of character number and similarity between matrices of 108 and fewer characters

A preliminary series of matrices was run to learn which organs would produce a matrix most like the full matrix of 108 characters. In all cases, the entire group of seventy-four adiantoid fern OTU's was used. The m x i cards were divided into rhizome, root, stipe and rhachis, and lamina. The i x i matrices calculated with $r_{x \cdot y}$ were compared with the principal matrix of all 108 characters, using r_s. The values obtained are listed in Table 3. The significance value

for r_s is 0.194 ($p = 0.05$); some of the values are not statistically significant. The stipe and rhachis character matrix resembled the full matrix more closely than did any other secondary matrix. The low root character comparison seems reasonable enough, but the lamina comparison is surprisingly low. Several groups of lamina characters and a large block of stipe and rhachis characters are devoted to indument, but the two are often poorly correlated. Holttum (1960b) has stressed the use of stipe and rhachis architecture in distinguishing the genera of dryopteroid ferns; but such characters do not seem to be particularly important in the Adiantoideae.

Table 3.--Comparison of organ matrices with the full matrix for seventy-two OTU's of the Adiantoideae

Secondary Organ Matrix	N	r_s
Rhizome	17	0.242
Root	7	0.015
Stipe & Rhachis	39	0.440
Lamina	44	0.152

The similarity of a matrix made with characters selected on the basis of their distribution in seventy-four adiantoid OTU's versus a full, 108-character matrix for the same OTU's was calculated. A frequency distribution test ($f_1 \geq 0.5$), a proportion test ($f_2 \leq 0.7f_1$), and an adjacent group test (similarity in three of four adjacent groups) were used. Thirty-seven characters passed these tests. The r_s with the full matrix was 0.504. Apparently many characters contribute little or no useful information to the full matrix.

An m x m matrix was used to estimate the correlation between all the pairs of the 108 characters of the same seventy-four OTU's of the Adiantoideae. Four characters showed perfect correlation. A matrix made with the characters passed by the character distribution selection mentioned in the paragraph above was compared against a matrix made with those characters less the four fully redundant ones. The similarity of the two matrices was 0.999. Almost no information was lost by dropping the four redundant characters.

Systematization Through the Evolutionary Ground Plan Method

At the heart of any taxiometric system is the method which is used to convert the similarity matrix data into a dendrogram, evolutionary ground plan diagram, or other visual representation of the data. It is this procedure which in the evolutionary ground plan method, but not in other current taxiometric methods, is closely associated with a model of evolution.

Because the evolutionary ground plan diagram method utilizes a model of divergent evolution, the diagrams it produces consist of dichotomizing (or rarely trichotomizing) pathways extending along divergent gradients of advanced characteristics from the ground plan ancestor to OTU's which stand for taxa included in the study. Some real OTU's lie along the pathways or at branching points, as well as at the termini of all branches of the diagram.

The data, consisting (for real taxa) of character states which are most likely to be primitive and to show evolutionary patterns, are converted into an i x i matrix and are stored in an i x m table (M),

one taxon to a column. From this the divergence sums (CSUM) and the divergence indices (PSUM) are totalled as the sum of primitive character states across each row and P (the number of characters) minus the sum of the primitive character states down each column, respectively.

As with other taxiometric methods, OTU's are associated with one another in terms of the similarity of characteristics which they share. In constructing ground plan diagrams of the tribes, the similarity of multi-state characteristics is assessed with Pearson's product-moment correlation coefficient, $r_{x.y}$. Rogers' similarity ratio, s_{ij}, is used with the binary characters of the subfamily ground plan diagram. Either measure of association can range from +1. (100% positive correlation) through 0 (no correlation) to -1. (100% negative correlation), but for the most part, correlations between taxa range upward from -0.2.

To save computer time, the standard deviations (STD) used in the character correlation selection program are included as data. An internal function calculates the indices of similarity from STD, N, P, and PSUM. The number of correlation coefficients which must be calculated for an $\underline{i} \times \underline{i}$ matrix of both real and hypothetical intermediate OTU's seems to be controlled by: (1) the number of real OTU's, (2) the number of characters, (3) the distances, in terms of the number of character differences, between the OTU's, and (4) the degree of pattern shown by the characteristics. The details of the evolutionary ground plan diagram program follow in the paragraphs below, and are summarized in Figure 16.

The ground plan ancestor, which is defined as that real or hypothetical OTU with all primitive characteristics, is generated by filling P spaces with character state (1). Code number 501 is assigned, and the data for this OTU are stored in TAPE. Code numbers 502 through 999 remain available for the hypothetical OTU's yet to be generated by the computer; in the figures these are labelled upwards from 1, rather than 501.

The real OTU most similar to the ground plan ancestor is the one with the fewest advanced character states, which in this program are coded (0). This OTU has the lowest divergence index (highest PSUM), and is thus chosen by the computer from the list PSUM.

A comparison is made between the two OTU's, the one "previously placed" and the other to be "added." Characters which are advanced in the added OTU but are primitive in the previously placed OTU are put in temporary list ADV. Those which are advanced in the previously placed OTU but are primitive in the added one go in temporary list LOSS.

Whether there are one or several differences in advanced characteristics between the previously placed and the added OTU's, the code numbers of the previously placed, the hypothetical intermediate(s) (if any), and the added OTU's are printed out in order, along with their sets of characters, whether in the primitive or advanced state (coded (1) and (0), respectively, in the output). In addition, for all but the previously placed OTU, the one character which has changed in each OTU is also printed out. Thus the evolutionary ground plan diagram is built up OTU-by-OTU and character

change-by-character change, like beads on strings (see Appendix G and Figures 17 through 25).

When there is more than one character difference between the previously placed OTU and the OTU to be added, the CSUM values are used to sort these differences in decreasing order of their frequency in the real OTU's of the group being diagrammed. They are attached outward in this decreasing frequency of advanced state order, both to the hypothetical intermediate OTU's which will be intercalated between the previously placed OTU and the OTU to be added. The census of character states of a hypothetical OTU is the sum of advanced and primitive character states of other OTU's leading up to it from the ground plan ancestor plus the one change that it has in a character state that its proximal, neighboring OTU does not have. For example, in going from a previously placed OTU with advanced character b to an OTU to be added with advanced characters bcde, if d had the highest divergence sum (highest CSUM) and e the lowest of characters c, d, and e, then d would be the first to be added and e the last. The sequence of advanced character state gains would be b-bd-bcd-bcde. The first and last character state groups belong to real OTU's. The middle two have been constituted for hypothetical OTU's, and code numbers are assigned from the top of a list called HTNUM.

Just storing the full i x i matrix for the N real OTU's takes $(N^2-N)/2$ spaces. To generate and store in addition the indices of similarity of all the hypothetical OTU's times the real OTU's is beyond the capabilities of most computers. Therefore, only the one highest correlation coefficient for each unplaced OTU and its real or

hypothetical mate is stored in HCOL. The code numbers of the OTU pairs are stored in HRN.

Assuming that there are more real OTU's to place in the ground plan diagram list (list UNPL is scanned to determine this), the OTU to be added is chosen on the basis that it is the highest one in HCOL. Parallel list HRN indicates the code numbers of the previously placed OTU and the OTU to be added.

If the correlation between the previously placed OTU and the one to be added is not statistically significant (the value, called RHO is assigned as a constant on a control card) for a test of $\rho = 0$ at the level of $p \leq 0.05$, then the OTU in list UNPL with the highest PSUM is chosen to be put on the output list next, starting a new line from the ground plan ancestor. The added OTU's code number is removed from list UNPL.

But if RHO is exceeded, and the correlation is statistically significant, then the code number of the OTU to be added is removed from UNPL, the data of the added and previously placed OTU's are compared, with temporary lists ADV and LOSS used as before, and the added OTU is placed on an evolutionary line stemming from some real or hypothetical OTU more advanced than the ground plan ancestor.

When all the data of real OTU's have been processed, the list UNPL is empty, and the program terminates.

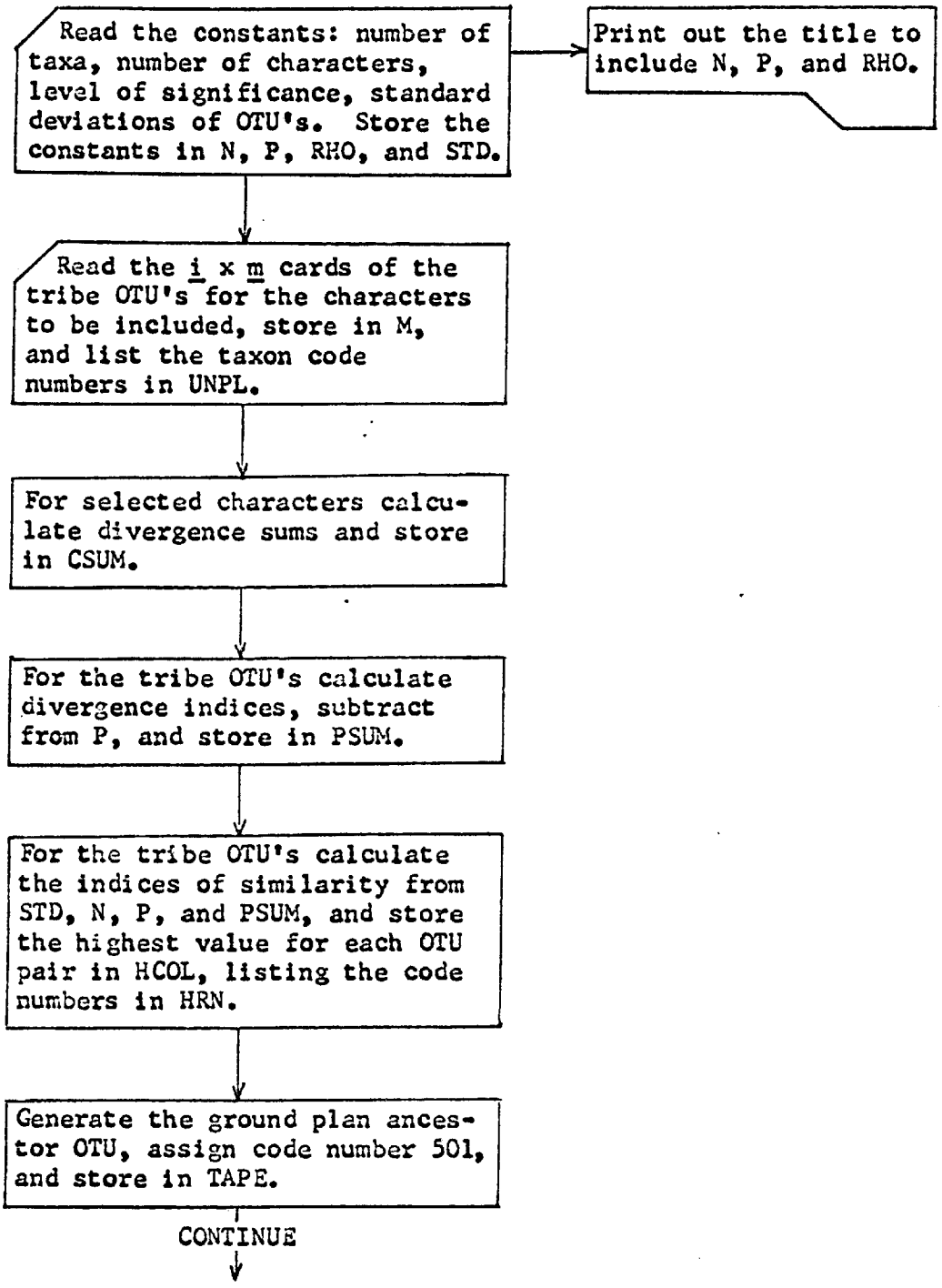


Fig. 16.--Flowchart of the state code ordering program, begun

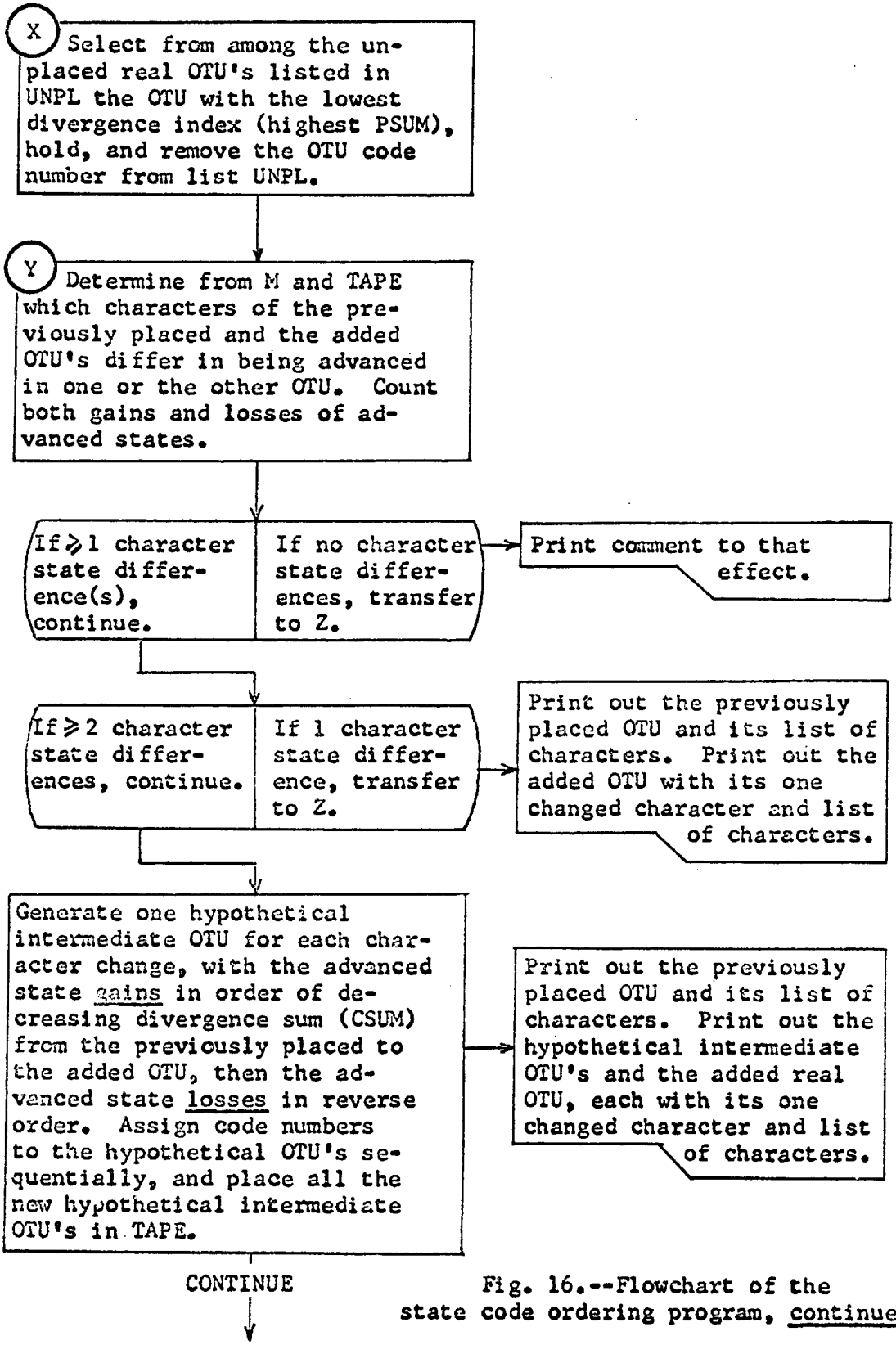


Fig. 16.--Flowchart of the state code ordering program, continued

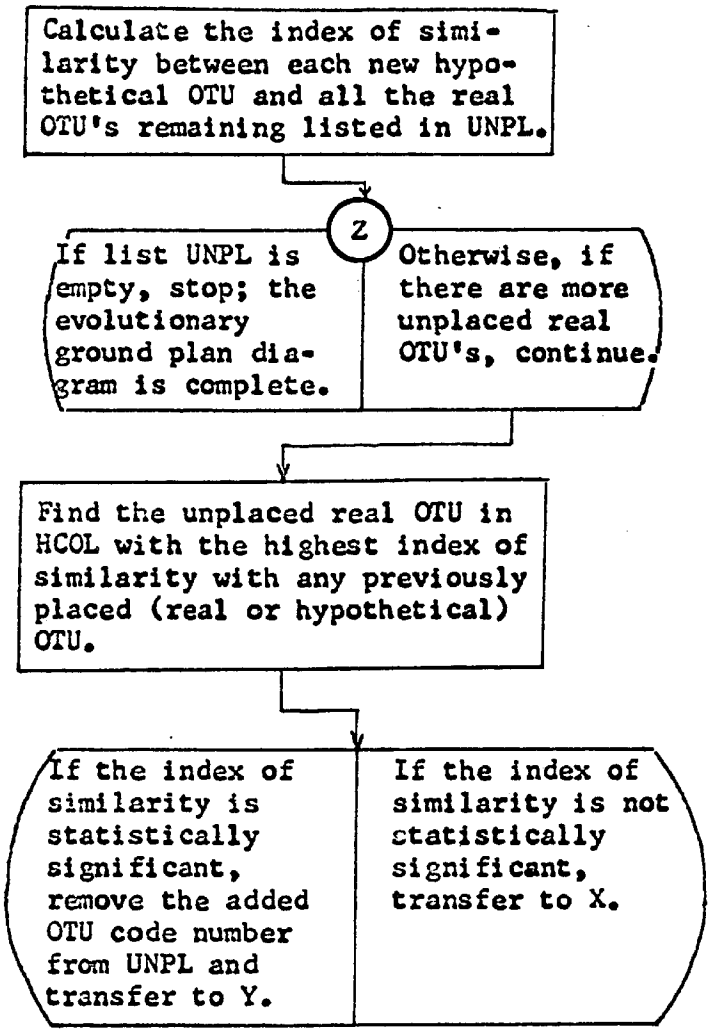


Fig. 16.--Flowchart of the state code ordering program, concluded

CHAPTER IV

SYSTEMATICS OF THE ADIANTOIDEAE AND ITS TRIBES

Introduction

The Adiantaceae Ching is comprised of two subfamilies, the Vittarioideae sensu C. Chr. and the Adiantoideae, which is the correct name for the Gymnogrammoideae sensu Holtt. Compared with most other families or subfamilies of ferns, the Adiantoideae is rather heterogeneous. It is difficult to form a mental image of a typical fern of this subfamily, compared to, say, a typical member of the Aspleniaceae or Polypodiaceae sensu stricto. In terms of its constituent genera, the Adiantoideae can be thought of as a residuum of Copeland's (1947, pp. xii, xiii) Pteridaceae after the dicksonioid, dennstaedtioid, lindsaeoid, and pteroid elements have been removed.

Because of its heterogeneity, the Adiantoideae can better be comprehended as a group of six tribes, each one of which is far more homogeneous than the subfamily as a whole. A list of genera divided by tribes is given on page 69, and the coded OTU's are grouped in Appendix C. The construction of this appendix is mentioned on pages 68 and 69.

Although the tribes were delimited before satisfactory evolutionary ground plan diagrams were prepared for each tribe, in this chapter the tribes are discussed first, and their relationship

to one another follows, since data for the latter came from a study of the tribal ground plan characters and not directly from the raw data.

Tribe 1.--Onychieae

Onychieae Ching ex Pic.-Serm., Webbia 17: 306. 1963. Type genus: Onychium Kaulf. The same name was proposed by Ching (1940, p. 225) under Sinopteridaceae, but invalidly so because no Latin description was provided.

This tribe is a rather diverse group of about twenty-three species in eight genera showing four evolutionary lines, two of which are monotypic and less typical of the tribe as a whole. The Onychieae is characterized by glabrous, greatly dissected (except Actiniopteris and Neurosoria) fronds (BCNR 810 and 704-706). The ultimate segments are usually elongate and are never beadlike (BCNR 761, 763, and 764). In contrast to the other tribes of the Adiantoideae, the stipes (BCNR 295-297) and rhachises (BCNR 463) show little development of a dark, sclerenchymatous outer cortex (except Neurosoria and Afropteris). These two genera and Onychium § Chrysonychium share greatly elongate, laterally inrolled fertile segments. The remaining genera tend to have thin, elongate, plane, apically toothed segments, with obviously indusiate[3], marginal sori and

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[3]The term "indusiate" has been used throughout this study to define modified frond margins or outgrowths of margins which fold over, protect, and (in the Adianteae) even bear the sori. The lack of these modifications is termed "exindusiate." These are not true indusia like those found in the Aspidiaceae. Morphologically speaking, the terms "pseudoindusiate" or "indusioid" could be adopted, but "expseudoindusiate" is rather difficult to pronounce, and "indusioid" ferns are not those plants which resemble indusia.

sporangia which are borne on a commissural vein in Anopteris and Ochropteris.

1. Onychium Kaulf., Berl. Jahrb. Pharm. 20: 45. (1819) 1820; Enum. Fil. 144. 1824. Type: Trichomanes japonicum Thunb. The typification of this genus has been incorrect in the past. Although the first species mentioned by Kaulfuss in his Enumeratio Filicum was his own O. auratum [=O. siliculosum (Desv.) C. Chr.], which commonly has been accepted as the type of the genus, he had in fact published the genus previously in his 1820 paper, with a brief but clearly identifiable German description. There he cited no species or specimens, but commented, "Nur Eine Art vom Vorgebirge der guten Hoffnung." He can only have been referring to the second of the two species listed in the Enumeratio, O. capense Kaulf. [=O. japonicum (Thunb.) Kunze]. This species, then, must be considered the type of the genus, as Pichi-Sermolli (1963, p. 309) has pointed out.

Cryptogramme § Onychium (Kaulf.) Diels in Engler & Prantl, Nat. Pflanz. 1(4): 279. 1899. Based on Onychium Kaulf.

In my opinion, the division of Onychium into two subgenera by Kümmerle (1930) and Ching (1934) is justifiable on the basis of correlated differences in glandularity, rhizome habit, and segment architecture. I do not think, however, that there is any commanding practical reason to maintain two sections in this small genus. But since the recent change in typification of the genus upsets Kümmerle's and Ching's nomenclature, the following synonymy is presented.

1a. Onychium § Onychium. Type: same as the genus.

Onychium § Cryptogrammopsis Kümm., Am. Fern J. 20(4): 131. 1930. Type: not stated; included are O. melanolepis (Dcne.) Kunze [=O. divaricatum (Poir.) Alst.] and O. japonicum (Thunb.) Kunze.

Leptostegia Don, Prodr. Fl. Nepal. 14. 1825. Type: L. lucida Don [=O. japonicum var. lucidum (Don) Christ].

Onychium § Leptostegia (Don) Ching, Lingnan Sci. J. 13(3): 495. 1934. Based on Leptostegia Don.

Cryptogramme § Onychium (Kaulf.) Diels in Engler & Prantl, Nat. Pflanz. 1(4): 279. 1899. Based on Onychium Kaulf.

1b. Onychium § Chrysonychium Pic.-Serm., Webbia 17: 311. 1963. Type: Pteris siliculosa Desv.

OBS. The genus contains six species in Asia and one in Africa. Ching's (1934) paper is a useful treatment of the genus. O. siliculosum (Desv.) C. Chr. seems to be the most derived element.

2. Ochropteris J. Smith, Hook. J. Bot. 4(27): 158. (1841) 1842. Type: Adiantum pallens Swartz.

Cryptogramme § Ochropteris (J. Smith) Prantl, Bot. Jahrb. Engler 3: 414. 1882. Based on Ochropteris J. Smith. I have indicated Prantl's combination as a section, but his exact intention is uncertain. He greatly broadened the circumscription of Cryptogramma, and then divided it into five parts: "Die Gattung Cryptogramme gliedert sich folgendermassen: . . . V. ? Ochropteris (J. Sm.)." There follows a short Latin description.

OBS. A single species from Réunion (Bourbon), Mauritius, and Mahé, Seychelles (according to a specimen in the U. S. National

Herbarium). Perhaps to be expected on other islands in the Seychelles. Both this genus and the next are rather local derivatives, but hardly seem to stem directly from Onychium.

3. Afropteris Alst., Bol. Soc. Broteriana 2ª, 30: 5. 1956a. Type: not stated; Pteris repens C. Chr. was chosen by Tardieu-Blot (1964, p. 172). Pichi-Sermolli (1963, p. 305) points out that "Aropteris" is a typographical error for Afropteris, which is the name Alston intended to use. Although Alston did not designate a type species, publication of the genus is valid, since it occurred before 1958.

OBS. One species in western tropical Africa and one in the Seychelles. The evolutionary ground plan diagram indicates the affinity of Afropteris to Ochropteris. Indeed, A. barklyae (Baker) Alst. has been considered to belong to the latter genus.

4. Cryptogramma R. Br. in Richardson in Franklin, Narr. of a Journey. 767. 1823. Type: C. acrostichoides R. Br. If the genus Allosorus Bernhardi (1805, pp. 5, 36) were typified, as Ching (1940, p. 225) has done, by "A. crispus (L.) Bernh.," it would be desirable to conserve Cryptogramma. But Ching's choice is long antedated by the inferential choice of a lectotype by Swartz (1806), who maintained the species Pteris crispa (L.) Allione. See further discussion of the typification of Allosorus under Cheilanthes (pages 100-101).

Phorobolus Desv., Prodr. Fam. Foug. 291. 1827. Type: not stated; Osmunda crispa L. was chosen by Copeland (1947, p. 72).

Allosorus § Homopteris Rupr., Distr. Crypt. Vasc. Imp. Ross. Type: Pteris stelleri Gmel., according to Christensen (1905, p. 187 and 1906, p. XLII). Reference not seen.

Cryptogramma § Homopteris (Rupr.) C. Chr., Ind. Fil. XLII. 1906. Based on Allosorus § Homopteris Rupr.

OBS. Four or five species in temperate and cool regions of the northern hemisphere and one species in southern South America.

5. Llavea Lagasca, Gen. Sp. Pl. 16. 1816. Type and sole species: L. cordifolia Lagasca.

Ceratodactylis J. Smith ex Hooker, Gen. Fil. t.36. 1840. Type and sole species: C. osmundioides J. Smith ex Hooker [=L. cordifolia Lagasca].

Botryogramme Fée, Gen. Fil. 166. (1850-52) 1852. Type and sole species: Allosorus karwinskii Kunze [=L. cordifolia Lagasca].

Cryptogramme § Llavea (Lagasca) Prantl, Bot. Jahrb. Engler 3: 414. 1882. Based on Llavea Lagasca. See comment under Ochropteris on page 92.

OBS. One species in Mexico and Guatemala. The genus is presumably related to Cryptogramma, with which (in Figure 17) it shares the characters of smooth-edged rhizome scales and the principle segment vein flush with the lower surface of the segment.

6. Anopteris (Prantl) Diels in Engler & Prantl, Nat. Pflanz. 1(4): 288. 1899. Based on Cryptogramma § Anopteris Prantl.

Cryptogramma § Anopteris Prantl, Bot. Jahrb. Engler 3: 414. 1882. Type: Adiantum hexagonum Prantl.

OBS. One species in the West Indies and Bermuda. This genus, containing three subspecies, is thoroughly treated in a revision by Morton (1957). Along with Cryptogramma and Llavea, these genera are the New World representatives of the tribe. References to Onychium

in the New World generally prove to be this genus.

7. Neurosoria Mett. ex Kuhn, Bot. Zeitg. 27(27): 437. 1869. Type: Acrostichum pteroides R. Br.

OBS. One species in northern Australia. The ground plan characters of this genus are so unlike those of the other genera of the tribe, that Neurosoria is attached directly to the ground plan ancestor. An analysis of the data of Appendix C indicates that the affinities of the genus are with the Onychieae to a somewhat greater extent than they are with the Cheilantheae or with any of the other tribes of the Adiantoideae.

8. Actiniopteris Link, Fil. Sp. Hort. Reg. Bot. Berol. Cultae. 73, 79, 80. 1841. Type: Asplenium radiatum Swartz.

Asplenium § Actiniopteris J. Smith, Hist. Fil. 231. 1875. Based on Actiniopteris Link.

OBS. Five species variously distributed from Africa to India, Nepal, and perhaps Thailand. This genus has been monographed by Pichi-Sermolli (1962), who describes three new species and considers the genus to belong to the monotypic family Actiniopteridaceae Pic.-Serm. The genus is certainly distinct enough to be maintained on a separate evolutionary line from the other genera of this tribe.

Tribe 2.--Cheilantheae

Cheilantheae Horvat, Acta Bot. Inst. Bot. Univ. Zagreb. 2: 109. 1927. Type genus: Cheilanthes Swartz. Circumscription of the tribe is virtually identical with that of Diels' subtribe Cheilanthinae. Horvat indicated this taxon as a tribe in several places in the text.

Cheilanthinae Diels in Engler & Prantl, Nat. Pflanz. 1(4): 255. 1899. The German language description is sufficient for valid publication at that date. Type genus: Cheilanthes Swartz.

The Cheilantheae number about 238 to 270 species in eleven genera, and share a pair of characteristics: sori round or oval (BCNR 1001) and sori terminal on vein endings (BCNR 1021), which will serve to distinguish them from the other tribes, except for a few Pellaeas, insofar as the data of this study go. Members of the tribe, except for Adiantopsis and Cheilanthopsis, have 2--4-pinnate fronds with small to bead-like segments (Cheilanthes, Aspidotis, and "Argyrochosma"), have small pinnatifid to pinnate-pinnatifid pinnae (Mildella, Negripteris, Notholaena, Sinopteris, and some Aleuritopteris), or have mostly pinnatifid, often quadrangular or pentagonal blades (some Cheiloplecton and most Aleuritopteris). The rhizome indument is of scales, but that of the fronds may be of hairs, scales, glands, or some mixture of these.

The evolutionary ground plan diagram presented in Figures 18--21 utilizes all 108 characters. Several combinations of character selection test parameters all produced diagrams which grouped apparently anomalous elements at more points than did this one, which seemed to seriously misplace only Cheilanthes regularis Mett. and C. lendigera (Cav.) Swartz. The groupings stress the characters of indument. For example, Aleuritopteris and "Argyrochosma" are waxy, while Notholaena and Cheilanthes lendigera (Cav.) Swartz are scaly and hairy.

Because all of the OTU's are related to the ground plan ancestor through a single stem, one can conclude that they are more closely correlated than are the OTU's of the Onychieae.

1. Aleuritopteris Fée, Gen. Fil. 153. t.12B. f.1-2. (1850-52) 1852. Type: not stated; Pteris farinosa Forsk. was chosen by Christensen (1906, p. XLII).

Cheilanthes § Aleuritopteris (Fée) Hooker in Hooker & Baker, Syn. Fil. 41. (1868) 1866. Based on Aleuritopteris Fée.

OBS. About twenty species in China and the adjoining Himalayas, with one of these more widespread in southeast Asia and A. farinosa (Forsk.) Fée nearly pantropic. Two more species occur in Africa. The genus has been studied in detail by Ching (1941), although it is possible that additional problems of cytology exist, particularly in those species from the Himalayas. Ching proposed three sections invalidly; they lack Latin diagnoses. These sections seem natural to me, but not having studied the species closely, I do not propose that they be validated.

2. Adiantopsis Fée, Gen. Fil. 145. (1850-52) 1852. Type: not stated; Adiantum radiatum L. was chosen by Christensen (1906, p. XLI).

Cheilanthes § Actinopteris J. Smith, Curtis's Bot. Mag. 72 [=III, 2]: Comp. 20. 1846. Type: Adiantum radiatum L.

Adiantopsis § Adiantastrum Fée, Mém. Foug. 8: 115. 1857, nomen nudum, was published in synonymy.

OBS. Five or six species in South America, Central America, and the West Indies. Adiantopsis can only be maintained as a genus, in my opinion, for the species closely related to the type, i.e.,

those which share the stiff, bicolorous rhizome scales, thin, brown rhachis wings, bipinnate fronds, obscure venation of the ultimate segments, and discrete sori. Copeland (1947, p. 66) provisionally agreed, saying, ". . . It is possible to typify it [Adiantopsis] by A. radiata, and then to recognize it as a small genus."

The character of the sori is shared with several species that properly belong in Cheilanthes, e.g. C. capensis (Thunb.) Swartz and C. regularis Mett. Judging by the totality of their characters, these species belong to Cheilanthes and must have acquired their discrete Adiantopsis-like sori independently. I further base this decision on intergrades between discrete and continuous sori found, for example, in C. angustifolia H.B.K., which even exhibit a tendency toward end-to-end fusion of flaring fertile vein tips, and also on the extreme parallelisms which occur between some so-called Adiantopsises and other species which are traditionally placed in Cheilanthes. Two such pairs, illustrated in Plates I--IV, are "Adiantopsis capensis (Thunb.) Fée"--Cheilanthes yunnanensis Brause and "Adiantopsis rupicola Maxon"--Cheilanthes microphylla Swartz.

3. Aspidotis Nutt. ex Copel., Gen. Fil. 68. 1947. Type: Hypolepis californica Hooker.

Hypolepis § Aspidotis Nutt. ex Baker in Hooker & Baker, Syn. Fil. 131. (1868) 1867. Type: Hypolepis californica Hooker.

Hypolepis subg. Aspidotis (Nutt. ex Baker in Hooker & Baker) C. Chr., Ind. Fil. XLII. 1906. Based on Hypolepis § Aspidotis Nutt. ex Baker in Hooker & Baker.

OBS. Two species in California, one in Mexico, and one in eastern Africa. Although superficially like some members of the Onychieae, Aspidotis has more character states in common with the Cheilantheae, as shown in Appendix C. Maxon (1918) and Wagner & Gilbert (1957) seem correct in placing Cheilanthes siliquosa Maxon with Aspidotis californica (Hooker) Nutt. ex Copel., but both should be in Aspidotis, to which the former species has not yet been transferred, and where it must bear the earlier epithet, densa.

4. Argyrochosma (J. Smith), nomen ineditum. Type: To be based on Notholaena § Argyrochosma J. Smith.

Cincinalis Desv., Ges. Naturf. Freunde Berl. Mag. 5: 311. 1811, non Gleditsch. Type: not stated; inferentially typified by Baker in Hooker & Baker (1868, p. 373) who included in his transfer of the name to sectional rank under Notholaena only the two waxy species of all the Notholaenas which Desvaux had called Cincinalis. On this basis I place Cincinalis under "Argyrochosma," rather than under Notholaena.

Notholaena § Argyrochosma J. Smith, Hook. J. Bot. 4(25): 50. (1842) 1841. Type: Pteris nivea Poir.

Notholaena § Cincinalis (Desv.) Baker in Hooker & Baker, Syn. Fil. 373. 1868. Based on Cincinalis Desv.

Pellaea § Cincinalis (Desv.) Prantl, Bot. Jahrb. Engler 3: 417. 1882. Based on Cincinalis Desv.

Notholaena § Chrysochosma J. Smith, Hist. Fil. 279. 1875. Type: Pteris sulphurea Cav.

Pellaea § Argyrochosma (J. Smith) C. Chr., Ind. Fil. XL. 1906. Based on Notholaena § Argyrochosma J. Smith.

Chrysochosma (J. Smith) Kümmerle, Magyar Bot. Lapok 13: 39. 1914. Based on Notholaena § Chrysochosma J. Smith.

OBS. About 38 species in the western hemisphere, mostly in Central and South America. The species of this genus all have waxy laminae, and many have hairs or scales on the laminae also. R. M. Tryon (1956) has published an excellent revision of these plants, along with Notholaena sensu stricto, all considered under the generic name Notholaena.

5. Cheilanthes Swartz, Syn. Fil. 5, 126. 1806, nomen conservandum. Type: not stated; C. micropteris Swartz, lectotypus conservandus, rather than the first lectotype, Trichomanes tenuifolium Burm., which was chosen by J. Smith (1875, p. 282). Typification of the genus has been discussed in detail by Weatherby (1943). He was working before the present rules for typification had been promulgated, and his confirmation of C. micropteris Swartz as the type, which had originally been chosen by Maxon in Britton & Brown (1913, p. 25), was neither necessary nor correct. In this he was followed by the Committee for Pteridophyta at the Eighth International Botanical Congress.

Allosorus Bernh., Neues J. Bot. Schrader 1(2): 5, 36. t.2. f.6. (1806) 1805, nomen rejiciendum. Type: not stated; Adiantum pusillum Willd. ex Bernh. [=Cheilanthes fragrans (L. fil.) Swartz], lectotypus conservandus. The genus is a mixture, containing several genera of Adiantoideae, most notably Pellaea, Cheilanthes, Cryptogramma, and Doryopteris, plus Paesia and many synonyms of Pteridium

aquilinum (L.) Kuhn and its varieties. The inferential elimination of Osmunda crispa L. as a lectotype was made by Swartz (1806, p. 425), who said, "Allosorus Bernh. -- est Cheilanthes." Swartz maintained Pteris crispa (L.) Allione (see Swartz, 1806, p. 101). The arguments for typification of Allosorus and its rejection in favor of Cheilanthes are presented by Pichi-Sermolli (1953, pp. 393-395) and in unpublished notes by C. V. Morton submitted to the Committee for Pteridophyta at the Eighth International Botanical Congress, Paris, 1954.

5a. Cheilanthes § Cheilanthes. Type: same as the genus.

Adiantopsis § Cheilanthastrum Fée, Mém. Foug. 8: 115. 1857. Type: not stated: Adiantum capense Thunb. was chosen by Christensen (1906, p. XLI).

Cheilanthes § Pteridopsis J. Smith, Hist. Fil. 283. 1875. Type: not stated; included in the variety of mostly Cheilanthes species are C. tenuifolia (Burm.) Swartz and C. micropteris Swartz.

Cheilosoria Trev., Atti Ist. Veneto V, 3: 579. 1877. Type: not stated; Trichomanes tenuifolium Burm. was chosen by Christensen (1906, p. XLII). He also typified subg. Cheilanthes by Polypodium pteroides Reichenb. [=Cheilanthes fragrans (L. fil.) Swartz]. Either this typification or the present choice of C. micropteris Swartz as the type of the genus and, hence, of the typical section permits Cheilosoria to stand as a valid genus or section, should this prove taxonomically desirable.

Cheilanthes § Cheilosoria (Trev.) C. Chr., Ind. Fil. XLII. 1906. Based on Cheilosoria Trev.

Cheilanthes § Hypolepidopsis Hieron., Hedwigia 62: 28. 1920a. Type: C. bergiana Schlecht.; the other species included in the section is C. capensis (L.) Swartz.

5b. Cheilanthes § Othonoloma Link ex C. Chr., Ind. Fil. XLII. 1906. Type: C. marginata H.B.K. Link (1833, p. 41) did not validly publish the generic name Othonoloma; Moore (1857, p. cxxxvi) considered it a nomen provisium, synonymous with at least a portion of Cheilanthes.

Cheilanthes § Parallosorus Keys., Polypodiac. Cyatheac. Herb. Bung. 5. 1873. Type: not stated; included are C. marginata H.B.K., C. pulchella Bory ex Willd., and C. quadripinnata (Forsk.) Kuhn [=Pellaea quadripinnata (Forsk.) Prantl].

Pellaea § Hymenoloma Davenp., Bot. Gaz. 21: 262. pl.XVIII. f.5-6. 1896. Type: P. membranacea Davenp.

5c. Cheilanthes § Physapteris Presl, Tent. Pterid. 160. 1836. Type: not stated; C. lendigera (Cav.) Swartz was chosen by Christensen (1906, p. XLII). Also included are C. myriophylla Desv. and C. scariosa (Swartz) Presl.

Cheilanthes § Phaeanthes Link, Hort. Reg. Bot. Berol. Descr. 2: 41. 1833. Type: not stated; included are C. odora Swartz [=C. fragrans (L. fil.) Swartz], C. hirta Swartz, C. lendigera (Cav.) Swartz, C. tomentosa Link, and C. viscosa Link [=C. kaulfussii Kunze].

Myriopteris Fée, Gen. Fil. 148. (1850-52) 1852. Type: M. marsupianthes Fée [=C. lendigera (Cav.) Swartz].

Myriopteris § Cheilanthastrum Fée, Gen. Fil. 149. (1850-52) 1852. Type: Acrostichum scariosum Swartz. All of the species included are currently considered to be Cheilanthes.

Oeosporangium Visiani, Atti Ist. Veneto III, 12: 656. 1867. Type: Notholaena persica Bory in Belanger. Reference not seen; quoted from Christensen (1906, pp. XLII and 466).

Cheilanthes § Cheilanthastrum (Fée) C. Chr., Ind. Fil. XLII. 1906. Based on Myriopteris § Cheilanthastrum Fée.

Cheilanthes § Oeosporangium (Visiani) C. Chr., Ind. Fil. XLII. 1906. Based on Oeosporangium Visiani.

Cheilanthes subg. Physapteris (Presl) C. Chr., Ind. Fil. XLII. 1906. Based on Cheilanthes § Physapteris Presl.

Pomataphytum M. E. Jones, Contr. Western Bot. 16: 12. 1930. Type: P. pocillatum M. E. Jones [=C. lendigera (Cav.) Swartz].

OBS. At least 120 species, and perhaps as many as 150. The typical section contains the most species, and is the most widespread, occurring on all continents. It is more heterogeneous an assemblage of species than most of the genera and sections in this study, and could be subdivided into several subsections. Section Othonoloma comprises the species allied to C. marginata H.B.K. Cheiloplecton, which I have maintained as distinct, has its affinities with these plants. The group of C. angustifolia H.B.K. seems possibly allied to section Othonoloma. Section Physapteris contains the highly divided, beaded-segmented species, which are mostly scaly and hairy, although a few bear only hairs. These are western hemisphere plants exclusively.

The only comprehensive monograph of the genus (Mettenius, 1858) remains usable despite its age, but a revision would be welcomed.

6. Notholaena R. Br., Prodr. Fl. Nov. Holl. 145. 1810. Type: Acrostichum marantae L. Nothochlaena is an inadmissible change of name.

The type species was transferred to the genus by Desvaux, not by R. Brown.

Notholaena § Eriochosma J. Smith, Hook. J. Bot. 4(25): 50. (1842) 1841. Type: not stated; N. rufa Presl [=N. aurea (Desv.) Weatherby] was chosen by Christensen (1906, p. XLI).

Notholaena § Lepichosma J. Smith, Hook. J. Bot. 4(25): 50. (1842) 1841. Type: not stated; Acrostichum marantae L. was chosen by Christensen (1906, p. XLI).

Notholaena § Alloesthes Moore, Ind. Fil. Syn. lxx. 1857. Type: not stated; included are species of Notholaena.

Cosentinia Todaro, Giorn. Sci. Nat. Econ., Palermo 1(3,4): 219. [=Enum. Pl. Sic. 13.] 1866. Type: not stated; Acrostichum velleum Ait. [=Notholaena lanuginosa (Desv.) Poir. in Lam.] was chosen by Christensen (1906, p. XLI).

Notholaena subsect. Cosentinia (Todaro) C. Chr., Ind. Fil. XLI. 1906. Based on Cosentinia Todaro.

Notholaena subsect. Eriochosma (J. Smith) C. Chr., Ind. Fil. XLI. 1906. Based on Notholaena § Eriochosma J. Smith.

OBS. Twenty-four species in the western hemisphere, plus about a dozen in the Old World. Unlike "Argyrochosma," these plants are never waxy, but have an indument of scales or hairs. Some seem to approach Pellaea, and look quite like the African species allied to P. doniana (J. Smith) Hooker. But on the basis of all of the characters used in this study, their affinities are with the Cheilantheae.

7. Negripteris Pic.-Serm., Nuovo Giorn. Bot. Ital, NS 53(1,2): 129-169. t.XIV-XVI. 1946. Type species: Mohria scioana Chiov.

OBS. Two species in Africa. Pichi-Sermolli (1946) considers these species to be distinct enough to warrant family status. His decision is based on the non-polypodioid annuli (see also Pichi-Sermolli, 1950), which have even the outer cell walls indurated and none of the cells of the annulus elevated much above the general surface of the sporangium, which itself lacks a stomium. Weatherby (1948) points out, however, that other characteristics of Negripteris mentioned by Pichi-Sermolli, like oligosporangiate sori and short-stalked sporangia, are found in other genera of the Cheilantheae. The single fact of annulus construction does not, in my mind, sufficiently differentiate these ferns to remove them from the Cheilantheae. The characteristics which they share with the other genera of that tribe are too many.

8. Mildella Trevisan, Rendic. Ist. Lombardo, Milano II, 9: 810. 1876. Type: Pteris inframarginalis Kaulf. ex Link.

OBS. One species in Central America, one in the West Indies, and at least four in Asia. The genus is distinctive because of the short, cylindrical to slightly clavate, few-celled hairs which line the adaxial groove and raised edges of the stipes and rhachises.

9. Cheiloplecton Fée, Mém. Foug. 7: 33. 1854. (as "Cheilopecton"). Type: Pteris rigida Swartz.

OBS. Two species in Central America and two or three species in South America. This genus is characterized by its broad, plane segments, bipinnate to tripinnate fronds, and continuous, somewhat inflated, crenellated indusia.

10. Sinopteris C. Chr. & Ching, Bull. Fan. Mem. Inst. Biol. 4: 359. 1933. Type: Cheilanthes grevilleoides Christ in Lecomte.

OBS. Three species in China. This little-known genus, and one for which herbarium specimens were not available to me, seems rather doubtfully distinct from Aleuritopteris, to which Ching allied it. The specializations pointed out by Christensen and Ching (1933, pp. 356-359) are logical end points of trends within Aleuritopteris: monangial sori, short-stalked sporangia, and sporangia with broad annuli.

11. Cheilanthopsis Hieron., Notizbl. Bot. Gart. Berl.-Dahlem 7: 406-409. 1920b. Type: Woodsia indusiosa Christ.

OBS. One species in Yunnan, China, allied to Cheilanthes and compared with C. fragilis Hooker by Ching (1932, p. 156). No complete specimens were available to me for this study. An isotype in the U. S. National Herbarium, consisting of most or all of a single blade, is pinnate-pinnatifid, thin, linear-lanceolate, about 35 cm. long, and bears upwards of seventy pinnae. The rhachis is stramineous. The pinnae are equilateral with more or less truncate bases and rounded apices; they are thin and sparsely covered with lax, multicellular hairs. Each segment of the pinnae has a principal vein with branches running toward the apices of the shallow lobes. Nearly scarious, reflexed, marginal indusia protect the submarginal sori.

Tribe 3.--Pellaeae

Pellaeae, nomen ineditum. Type genus: To be based on Pellaea Link. No name available through transfer exists for this tribe.

Formerly the genera included here were placed with the Cheilantheae, to which they seem to bear their closest relationship. I have separated them because as two tribes the homogeneity of each is much greater than when the two were combined. Before separation of the Pellaeae from the Cheilantheae, I was unable to make a satisfactory evolutionary ground plan diagram with characters chosen by several different sets of parameters. In every case OTU's of different genera were grouped together in obviously anomalous ways.

The characters of sori restricted to the segment margins (BCNR 1011), which is present in most of the Pellaeae included in the study, and indusia as marginal outgrowths from the laminae (BCNR 1032) distinguishes the Pellaeae from the Gymnopterideae and Eriosoreae. Long, narrow, flattened rhizome scales (BCNR 84) distinguishes them from the Onychieae. Fluted roots (BCNR 204) and flattened root hairs (BCNR 223) separates them from the Cheilantheae and Adianteae in most instances.

The constitution of the three lines leading from the ground plan ancestor might well be altered by the addition of a wider range of material than was included in this study. For instance, Pellaea ambigua (Fée) Baker, which Fée called Synochlamys, seems close to Ormopteris gleichenioides (Gardn. ex Hooker) J. Smith. And although it would seem that the highly compound Pellaeas, like Pellaea quadripinnata (Forsk.) Prantl, should be generically separated from the less divided members of the genus, I hesitate to do so because members of some of the groups of Pellaea (which are mentioned under the discussion of that genus) were not included in this study. Pellaea

bridgesii Hooker seems misplaced in Figure 22. It doubtless belongs closer to the stem containing P. atropurpurea (L.) Link, P. doniana (J. Smith) Hooker, and P. falcata (R. Br.) Fée. Indeed, W. H. Wagner, Jr. (unpubl. ms. in the U. S. Nat. Herb.) has studied hybrids between P. bridgesii Hooker and P. mucronata (Eaton) Eaton. For all of these reasons, more evidence is needed before a taxonomic segregation of the genus is attempted.

1. Pellaea Link, Fil. Sp. Hort. Reg. Bot. Berol. Cultae. 59. 1841, nomen conservandum. Type: Pteris atropurpurea L.

Platyloma J. Smith, Hook. J. Bot. 4(27): 160. (1842) 1841, nomen rejiciendum. Type: P. brownii J. Smith [=Pellaea paradoxa (R. Br.) Hooker]. Smith's article appeared in August, 1841, about a month before Link's book.

Allosorus § Monomorphi Presl, Tent. Pterid. 152. 1836, pro parte. Type: not stated; included are species of Cheilanthes, Cheiloplecton, Jamesonia, Mildella, and, mostly, Pellaea. Presl's other section, Eutypici, contains species of Cheilanthes, Mildella, and Onychium.

Synochlamys Fée, Mém. Foug. 7: 35. t.XX. f.4. (1854-57) 1854. Type: S. ambigua Fée.

Pellaea § Holochlaena Baker in Hooker & Baker, Syn. Fil. 153. (1868) 1867. Type: not stated; the two species included are P. burkeana (Hooker) Baker [=P. dura (Willd.) Baker] and P. articulata (Kaulf. ex Spreng.) Baker [=P. angulosa (Bory) Baker].

Pellaeopsis J. Smith, Hist. Fil. 289. 1875. Type: Pteris articulata Kaulf. ex Spreng.

Choristosoria Mett. ex Kuhn in v. d. Decken, Reisen in Ost-Afrika 3(3): 13. 1879. Type: Adiantum pteroides L.

Pteridella Mett. ex Kuhn in v. d. Decken, Reisen in Ost-Afrika 3(3): 13. 1879. Type: not stated; with the exception of Pellaea quadripinnata (Forsk.) Prantl, the other species are all of the Pellaea doniana (J. Smith) Hooker--Pellaea viridis (Forsk.) Prantl type.

Pellaea § Pteridellastrum Prantl, Bot. Jahrb. Engler 3: 419. 1882. Type: not stated; the species included are mostly those of Pteridella Mett. ex Kuhn in v. d. Decken, with the addition of what are now called Cheilanthes regnelliana Mett. and C. dichotoma Swartz.

OBS. About forty-five to sixty species, mostly in the African region and in the Americas. Like Cheilanthes, this genus is more heterogeneous than most included in the present study. Further researches may indicate possible subgeneric or sectional divisions. Pellaea § Pellaea, for instance, has already been treated by A. F. Tryon (1957). Other potential sections include those species with mostly once-pinnate fronds and linear segments, called Pteridella, the Pellaea quadripinnata (Forsk.) Prantl--P. striata (Desv.) C. Chr. group, which has basiscopically developed, 3--4-pinnate fronds, the P. falcata (R. Br.) Fée--P. paradoxa (R. Br.) Hooker group, which has long-creeping rhizomes but otherwise superficially resembles the Pteridella group, and the group centering around Synochlamys, which contains once-pinnate species with strongly inrolled pinnae.

2. Doryopteris J. Smith, Hook. J. Bot. 4(27): 162. (1842) 1841. Type: not stated. Morton (1944, p. 26) points out that Smith's (1875, p. 275) choice of D. pedata (L.) J. Smith for the type cannot be

maintained, since it was not one of the taxa included in the genus at the time of its establishment. He suggests that Pteris palmata Willd. [=Doryopteris pedata var. palmata (Willd.) Hicken] is the logical choice for a type.

Doryopteris J. Smith, Hook. J. Bot. 3: 404. 1841a, nomen nudum.

2a. Doryopteris subg. Doryopteris. Type: same as the genus.

Litobrochia § Doryopteris (J. Smith) Moore, Ind. Fil. Syn. xliv. 1857. Based on Doryopteris J. Smith.

Pteris § Doryopteris (J. Smith) Baker in Hooker & Baker, Syn. Fil. 166. (1868) 1867. Based on Doryopteris J. Smith.

Pellaea § Doryopteris (J. Smith) Prantl, Bot. Jahrb. Engler 3: 419. 1882. Based on Doryopteris J. Smith.

Heteropteris Fée, Crypt. Vasc. Brésil 1: 123. 1869. Type: H. doryopteris Fée [=Doryopteris lonchophora (Römer ex Mett.) J. Smith], which could possibly be excluded from the subgenus or even from the genus Doryopteris, according to R. M. Tryon (1942, p. 71).

2b. Doryopteris subg. Lytoneuron Klotzsch, Linnaea 20: 343. 1847. Type: not stated; species included are D. geraniifolia (Raddi) Klotzsch [=D. concolor (Langsd. & Fisch.) Kuhn var. concolor] and D. lomariacea Klotzsch.

Pellaea § Doryopteridastrum Fée ex Prantl, Bot. Jahrb. Engler 3: 418. 1882. Type: not stated, nor did R. M. Tryon (1942, pp. 15-16) choose a lectotype.

OBS. About thirty-three species, twenty-three in the New World, nine in the Old World, and one pan-tropical. R. M. Tryon (1942, pp. 3-4) indicates some doubt about the naturalness of the genus,

particularly the disposition of the miscellaneous species which lie in neither of the subgenera. In the years since the publication of Tryon's revision, some of the more problematical of these species have been removed from Doryopteris. According to the data on which Figure 22 is based, the subgenera are allied, and the genus is probably natural.

3. Ormopteris J. Smith, Hist. Fil. 281. 1875. Type: Cassebeera gleichenioides Gardn. ex Hooker.

Cassebeera Kaulf., Enum. Fil. 216. 1824, non Cassebeeria Dennstaedt, according to R. M. Tryon (1942, p. 11). Type: not stated; included are C. triphylla (Lam.) Kaulf. and C. pinnata Kaulf.

Bakeriopteris Kuntze, Rev. Gen. Pl. 2: 807. 1891. Type: not stated; included are B. gleichenioides (Gardn. ex Hooker) Kuntze, B. pinnata (Kaulf.) Kuntze, B. triphylla (Lam.) Kuntze, and B. "? petiolata (Fée)" Kuntze [=B. pinnata (Kaulf.) Kuntze].

OBS. Three species in South America. These plants resemble in some respects the Synochlamys group of Pellaea, but differ in their reddish, tawny, concolorous scales and in the thick-margined sinuses which divide the pinnae into lobes. R. M. Tryon (1942, pp. 66-69) briefly discusses members of the genus.

4. Saffordia Maxon, Smiths. Misc. Coll. 61(4): 1-5. 1913a. Type and sole species: S. induta Maxon.

OBS. This single Peruvian species seems rather distantly related to the bulk of Pellaea. Its association with two of the several times pinnate species of that genus (in Figure 22) may be caused more by convergence of characters than by any real relationship.

Maxon (1913a, pp. 3-5) suggests that this genus stands between Doryopteris and Trachypteris, but judging by the character associations listed in Appendix C, its affinities are with the former genus, and not the latter. Saffordia superficially resembles Doryopteris, except that it has a dense covering of scales on the undersurfaces of the blades, and its stipes and rhizomes tend to be more densely scaly than those of Doryopteris. Saffordia's scales are thin and broadly lanceolate, and all except those of the rhizome are ciliate.

Tribe 4.--Gymnopterideae

Gymnopterideae Ching, Sunyatsenia 5(4): 228. 1940, nomen nudum. No Latin description is provided. Type genus: To be based on Gymnopteris Bernh.

The Gymnopterideae contain about forty-five species in eight genera. In this study they are distinguished from the Eriosoreae by their tan root hairs (BCNR 243) and from the Onychieae, Cheilantheae, Pellaeae, and Adianteae by their sori, which are scattered on the backs of the fertile segments (BCNR 1014).

Three groups of genera can be discerned in Figure 23: (1) Pityrogramma and its reduced derivatives, Anogramma and Pleurosoriopsis, (2) Hemionitis, Bommeria, Gymnopteris, and Paraceterach, and (3) Trachypteris.

1. Pityrogramma Link & Otto, Handb. Gewächse 3: 19. 1833. Type: not stated; Acrostichum chrysophyllum Swartz was chosen by Maxon (1913b, p. 173).

Ceropteris Link, Fil. Sp. Hort. Reg. Bot. Berol. Cultae. 141. 1841. Type: same as Pityrogramma. Ceropteris is therefore a superfluous generic name.

Gymnogramme § Cerogramme Diels in Engler & Prantl, Nat. Pflanz. 1(4): 260. 1899. Type: none stated; included are Gymnogramme sulphurea Desv., G. argentea Mett., and G. argentea var. aurea Mett.

Gymnogramma § Calomelanos Presl, Tent. Pterid. 218. 1836. Type: not stated; the bulk of the species belong to Pityrogramma, and among them is Gymnogramma chrysophylla (Swartz) Kaulf.

Trismeria Fée, Gen. Fil. 164. t.14. f.1-2. (1850-52) 1852. Type: not stated; T. aurea Fée [=Acrostichum trifoliatum L.] was chosen by Maxon (1926, p. 436).

Pityrogramma § Ceropteris (Link) Domin, Publ. Fac. Sci. Univ. Charles 88: 4. 1928. Based on Ceropteris Link.

Pityrogramma § Trichophylla Domin, Publ. Fac. Sci. Univ. Charles 88: 8. 1928. Type: not stated; Gymnogramme ferruginea Kunze was chosen by Christensen (1934, p. 10).

Pityrogramma § Oligolepis Domin, Publ. Fac. Sci. Univ. Charles 88: 8. 1928. Type: not stated; Acrostichum sulphureum Swartz was chosen by Christensen (1934, p. 10).

OBS. Thirteen species, eleven variously distributed in South, Middle, and adjacent North America and two species in central and southern Africa, Madagascar, and the Mascarene Islands. Two of the New World species apparently have been introduced into the Old World. The genus has been treated recently by R. M. Tryon (1962). I concur with his transfer of Trismeria trifoliata (L.) Diels in Engler & Prantl to Pityrogramma.

2. Anogramma Link, Fil. Sp. Hort. Reg. Bot. Berol. Cultae. 137. 1841. Type: Polypodium leptophyllum L.

Dicranodium Newman, Hist. Brit. Ferns, ed. 3. 13. 1854. Type: same as Anogramma. Dicranodium is therefore a superfluous generic name.

Pityrogramma § Anogramma (Link) Domin, Publ. Fac. Sci. Univ. Charles 88: 9. 1928. Based on Anogramma Link.

Pityrogramma § Monosorus Domin, Publ. Fac. Sci. Univ. Charles 88: 10. 1928. Type: Gymnogramme microphylla Hooker.

OBS. Seven species, including four in the New World, one in Asia, one in Africa, and one distributed from Mexico and South America through Europe and Africa to India; it also occurs in New Zealand.

Rogers' similarity coefficients calculated for all characters of Appendix C are not statistically significantly higher between Anogramma microphylla (Hooker) Diels in Engler & Prantl and Pityrogramma schizophylla (Baker) Maxon or Anogramma leptophylla (L.) Link, its nearest neighbors on the ground plan diagram, than they are with either Taenitis, Syngramma, or Toxopteris, the other genera with which an alliance has been suggested. Perhaps the true affinities of A. microphylla (Hooker) Diels in Engler & Prantl are obscured because the reduced and simple plant has lost characters indicative of its ancestry.

3. Pleurosoriopsis Fomin, Bull. Jard. Bot. Kieff. No. XI. 8-9. 1930. Type: Gymnogramme makinoi Maxim in Makino.

OBS. A single species in eastern Asia, including Japan. It is likely that the species is misplaced in Figure 23. It could better stem from hypothetical taxon 6 or 13 or real taxon 67, any of which would show fewer losses of advanced attributes. The genus is presumably

a simplified, reduced analogue of Anogramma; it is most likely that it arose from the typical Pityrogrammas or from their ancestors.

4. Hemionitis L., Sp. Pl. 2: 1077. 1753. Type: not stated; H. palmata L. was chosen by Maxon (1913b, p. 171). Linnaeus' other species is actually Antrophyum lanceolatum (L.) Kaulf.

Hemionitis § Cardinitis J. Smith, Hist. Fil. 151. 1875. Type: H. cordata Roxb. [=H. arifolia (Burm.) Moore].

Hemionitis subsect. Cardinitis (J. Smith) C. Chr., Ind. Fil. XXXVIII. 1906. Based on Hemionitis § Cardinitis J. Smith.

OBS. Five species in Central America, one in Jamaica, and one is Asia. Hemionitis has slightly dimorphic, pedate, simple-bladed fronds. The fertile fronds slightly to greatly exceed the sterile ones. The dimorphism is sometimes incomplete; specimens can be found in which the shorter fronds are partially fertile. The naked sporangia are inserted dorsally on the veins of the blades.

5. Bommeria Fournier in Baillon, Dict. de Bot. 1: 448. 1876. Type: Hemionitis pedata Swartz.

Schizogramma Link, Fil. Sp. Hort. Reg. Bot. Berol. Cultae. 136. 1841. Type: Hemionitis pedata Swartz. Link (1841, pp. 136, 140) erred in substituting the epithet palmata for pedata, which he had cited correctly earlier (Link, 1833, p. 49). Christensen (1906, p. XXXVIII) did not detect Link's error, and transferred Schizogramma to subsectional rank under Hemionitis, while maintaining the same type for Gymnopteris § Bommeria.

Gymnogramme § Stegnogramme Klotzsch, Linnaea 20: 411. 1847. Type and sole species: G. ehrenbergiana Klotzsch.

Stegnogramme (Klotzsch) Fournier, Mex. Pl. 1: 71. 1872, non Blume. Based on Gymnogramme § Stegnogramme Klotzsch.

Gymnogramme § Bommeria (Fournier in Baillon) Christ, Farnkr. 67. 1897. Based on Bommeria Fournier in Baillon.

Gymnopteris subg. Bommeria (Fournier in Baillon) C. Chr., Ind. Fil. XXXIX. 1906. Based on Bommeria Fournier in Baillon.

OBS. Five species in Mexico, with one of these extending into Guatemala and another into the United States. Maxon (1913b, pp. 168-171 and 1942, pp. 59-61) has treated the species of this genus. Bommeria is monomorphic, with pedate fronds bearing sporangia restricted to a broad marginal band. The fronds are more dissected than those of Hemionitis, but the two genera are closely related, both phenetically and geographically.

6. Gymnopteris Bernh., J. Bot. Schrader 1(2): 297. 1799. Type: Acrostichum rufum (L.) L. R. M. Tryon (1964, p. 82) points out that the genus is not based on Pteris ruffa L. [which was not mentioned at all by Bernhardi], nor is the combination Gymnopteris rufa attributable to Bernhardi, but was apparently first made by Underwood (1902, p. 627). Confusion over the type has occurred because, of the references given by Linnaeus (1753, p. 1074) under Pteris ruffa L., part of those in his Hortus Cliffortianus do not refer to the plant now called Gymnopteris. But in making the name Acrostichum rufum (L.) L., Linnaeus (1759, p. 1320) cited the Sloane plate alone, thus typifying the name on the Gymnopteris element and excluding other references and species.

Gymnogramma Desv., Ges. Naturf. Freunde Berl. Mag. 5: 304. 1811. Type: not stated. Among the species now placed in several genera is Gymnogramma rufa (L.) Desv., the type of Bernhardi's earlier-published Gymnopteris. Thus Gymnogramma is a superfluous generic name.

Neurogramma Link, Fil. Sp. Hort. Reg. Bot. Berol. Cultae. 138. 1841. Type: not stated; Acrostichum rufum (L.) L. was chosen by Christensen (1906, p. XXXIX). Included are N. rufa (L.) Link, N. tomentosa (Lam.) Link, and N. pedata (Swartz) Link.

Gymnopteris subg. Neurogramma (Link) C. Chr., Ind. Fil. XXXIX. 1906. Based on Neurogramma Link.

OBS. Three species in Middle and South America, plus another three in China and one in India. The gain of advanced characteristics of characters 12 and 36 for a second time (in hypothetical 15, 16, 30, 38, 39, and real taxon 37 of Figure 23) casts doubt on the correctness of Gymnopteris's placement. It might better be attached to hypothetical taxon 29, which would leave Bommeria and Hemionitis on one stem and Gymnopteris on another, to be joined, provisionally, by Paraceterach. Gymnopteris has pinnate fronds arising from a compact rhizome. The sporangia follow the secondary veins of the lanceolate to elliptical pinnae from near the costae to near the margins of the pinnae. The fronds bear acicular to fairly lax, multicellular hairs.

7. Paraceterach (Mueller) Copel., Gen. Fil. 75. 1947. Based on Grammitis § Paraceterach Mueller.

Grammitis § Paraceterach Mueller, Fragmenta 5: 138. (1865) 1866. Type: Gymnogramme muelleri Hooker.

Gymnopteris subg. Paraceterach (Mueller) C. Chr., Ind. Fil. XXXIX. 1906.

OBS. One or perhaps two species in Australia. The systematic position of this little-known genus is somewhat uncertain. I have had access only to fragmentary and incomplete specimens, so complete coding and machine evaluation has not been possible. In habit, frond form, and venation Paraceterach resembles Gymnopteris more closely than Saffordia, Bommeria, or Hemionitis. On the other hand, the scales of its blades are more like those of Bommeria than Hemionitis. Of course, they are quite unlike the hairs of Gymnopteris. Because of the contrary evidence, I associate Paraceterach only provisionally with Gymnopteris.

8. Trachypteris André ex Christ, Denkschr. Schweiz. Naturf. Ges. 36(1): [=Monogr. Elaph.] 150-151. 1899. Type: Acrostichum aureo-nitens Hooker [=T. pinnata (Hooker fil.) C. Chr.]. Christ's reference to André's publication in Revue Horticole is false; there is no such article.

Elaphoglossum § Heteroglossum Diels in Engler & Prantl, Nat. Pflanz. 1(4): 334. 1899. Type: Acrostichum aureo-nitens Hooker.

OBS. One to three species in South America and another in Madagascar. Among the characters used in this study that were common to Hemionitis, Bommeria, and Gymnopteris, Trachypteris lacks so many that it was placed as a separate line attached to the ground plan ancestor. Trachypteris is more sharply dimorphic than Bommeria. It has a basal rosette of oblanceolate, sterile fronds and a few, erect, long stipitate, pinnate fertile fronds bearing up to about ten pinnae,

which are less divided than those of Bommeria. The sporangia are borne in a marginal band reminiscent of Bommeria.

Tribe 5.--Eriosoreae

Eriosoreae, nomen ineditum. Type genus: To be based on Eriosorus Fée.

Gymnogrammeae Diels in Engler & Prantl, Nat. Pflanz. 1(4): 254. 1899. Type genus: Gymnogramme auctt., non Desv. [=Eriosorus Fée].

Gymnogrammeae Horvat, Acta Bot. Inst. Bot. Univ. Zagreb. 2: 109. 1927. Type genus: Gymnogramme auctt., non Desv.

The Eriosoreae includes upwards of 110 species in thirteen genera. The members of the tribe in this study are distinguished from all but the Gymnopterideae, Notholaena, and Saffordia by being exindusiate (BCNR 1050). From the Gymnopterideae they can generally be distinguished by their brown, straight root hairs (BCNR 193, 231). Notholaena and Saffordia share rhizome scales with wavy or irregular margins (BCNR 122), which the Eriosoreae lack.

The evolutionary ground plan diagram of Figure 24 is by no means completely satisfactory. In general, there are too many losses of advanced character states. Some of these losses can be traced to reduction. For example, "Eriosorus lehmannii" [=Gymnogramme lehmannii Hieron.] has but a pinnatifid blade, and Pterozonium reniforme Fée has a simple one. On the other hand, "Craspedodictyum" [=Syngramma] is not a reduced plant, and it, too, shows many losses of advanced characters in the hypothetical taxa leading to it. "Craspedodictyum" is probably wrongly placed on the diagram. Several other diagrams of

this tribe were more poorly organized than Figure 24; but they all had this one feature in common: Eriosorus, Jamesonia, "Nephopteris," and Pterozonium were always grouped together away from the other genera of the tribe.

1. Syngramma J. Smith, Lond. J. Bot. 4: 168. 1845. Type: S. vittaeformis J. Smith. Copeland (1947, p. 56) points out that Christensen's (1906, pp. XXXVII and 628) choice of S. "alismifolia (Pr.) J. Sm." is incorrect.

Oxygonium Presl, Tent. Pterid. 117. 1836. Type: not stated; included are O. ovatum Wall. ex Presl and O. alismaefolium Presl. Both are species of Diplazium, and the latter is specifically excluded by Smith (1845, p. 168) from Syngramma alismaefolia J. Smith. The combination, S. alismaefolia (Presl) J. Smith, reported by Christensen (1906, p. 628) is thus in error.

Trichogramme Kuhn, Festschr. 50 Jahr Jub. K. Realschule Berl. 325. (Chaetopt. 5) 1882, pro parte. Type: not stated; a mixture of Syngramma and Toxopteris species.

Neurogramme § Trichogramme Christ, Farnkr. 63. 1897, pro parte. Type: not stated; a mixture of Syngramma, "Craspedodictyum," Syngrammatopsis, and Toxopteris species.

Austrogramme Fournier, Ann. Sci. Nat., Paris, Bot. V, 18: 278. 1873. Type: not stated; Gymnogramme marginata Mett. was chosen by Christensen (1906, p. XXXVII).

Callogramme Fée, Gen. Fil. 169. (1850-52) 1852. Type: C. caeciliae Fée [=Syngramma alismifolia J. Smith].

Syngramma subg. Austrogramme (Fournier) C. Chr., Ind. Fil. XXXVII. 1906. Based on Austrogramme Fournier.

Syngramma subg. Callogramme (Fée) C. Chr., Ind. Fil. XXXVII. 1906. Based on Callogramme Fée.

Craspedodictyum Copel., Phil. J. Sci., C, 6(2): 84. 1911. Type: not stated; C. grande Copel. was chosen by Copeland (1947, p. 57).

OBS. About fifteen species variously distributed in Malaya and adjacent India, Java, Sumatra, Borneo, New Guinea, New Caledonia, the Philippines, Fiji, and other micronesian islands. On the basis of frond architecture, venation, and paraphyses, I agree with Holttum (1954, p. 579) in not separating "Craspedodictyum" from Syngramma. On the other hand, the differences between Toxopteris and Syngramma are much greater than those between Syngramma and "Craspedodictyum." I do not think the computer's placement of "Craspedodictyum quinatum (Hooker) Copel." in Figure 24 reflects its most likely evolution because of the large number of losses of advanced character states. In character 47, for instance, the advanced state is gained and lost twice (at hypothetical taxa 4, 25, 71, and 78).

2. Syngrammatopsis Alston, Mutisia 7: 7. 1952. Type: Gymnogramme elaphoglossoides Baker.

OBS. Six species in the Guayana Highlands of Venezuela, Colombia, and British Guiana, with one of the species also known from Tafelberg, Surinam. The genus can be distinguished from Pterozonium by its elongate fronds and rhizome bristles.

3. Toxopteris Trevisan, Atti Ist. Veneto V, 3: 591. 1877. Type: not stated; Gymnogramme borneensis Hooker was chosen by Christensen

(1906, p. XXXVII). Also included in the genus are T. cartilagidens (Baker) Trevisan, T. lobbiana (Hooker) Trevisan, and "Tox. ?subtrifoliata Trevis." [=Stenochlaena subtrifoliata (Hooker) Copel., according to Copeland (1906, p. 152), who did not consider the name validly published by Hooker.].

Syngramma subg. Toxopteris (Trevisan) C. Chr., Ind. Fil. XXXVII. 1906. Based on Toxopteris Trevisan.

OBS. Seven species in Malesia. This genus differs from Syngramma in having short to obsolete rather than long stipes, attenuate rather than acute frond bases, and narrow, linear lanceolate rather than lanceolate or elliptic laminae.

4. Taenitis Willd. ex Spreng., Anleit. Kenntn. Gewächse 3: 374. t.10. f.106. 1804. Type: Pteris blechnoides Willd. Sprengel refers to Willdenow (1794, p. 13) for a description to validate his name.

Platytaenia Kuhn, Festschr. 50 Jahr Jub. K. Realschule Berl. 330. (Chaetopt. 10) 1882. Type: Acrostichum requinianum Gaud. in Freyc.

OBS. Five species in Malesia, with one of these reaching India and the Philippines, plus two on some of the smaller islands of the Pacific and in New Guinea. Copeland (1912) was the first person to suggest that Taenitis belonged to the eriosorioid ferns, and the morphological evidence for this is considerable. Taenitis is the only genus of the Adiantoideae, however, that is known to have other than a basic chromosome number of 29 or 30; in this genus it is 44. Unfortunately, chromosome data are lacking for several presumably related genera like Rheopteris and Cerosora. Holttum (1958, 1960a,

and in litt. to C. V. Morton on December 18, 1957) seems correct when he suggests that Taenitis and Syngramma make a rather isolated natural group, and that Schizoloma cordatum Gaud. and Syngramma pinnata J. Smith both belong to Taenitis.

5. Rheopteris Alston, Nova Guinea NS, 7(1): 2. 1956b. Type: R. cheesmaniae Alst.

OBS. Two species in New Guinea, both of which grow in stream beds in running water. I have not seen specimens or photographs of either. Holttum (1962, pp. 531-2) discusses the relationships of Rheopteris, and has concluded that the genus ". . . belongs to the subfamily Gymnogrammoideae of Christensen's scheme in Verdoorn's Manual of Pteridology (1938, p. 537)." In my opinion, which is based solely on Holttum's and Alston's discussions, Rheopteris probably lies between the bristly, thin-laminate Taenitis and the flat-scaled Eriosorus, perhaps branching off near hypothetical taxon 15 in Figure 24. Rheopteris has pinnate to tripinnate fronds with unequal to dimidiate ultimate segments or pinnae. The rhizomes are creeping and clothed with bristle-tipped, ciliate scales. The sori are round and terminal or elongate and dorsal on the free veins, and are multicellular paraphysate.

6. Cerosora (Baker) Domin, Acta Bot. Bohemica 8: 3. 1929. Based on Gymnogramma § Chrysosora Baker.

Gymnogramma § Chrysosora Baker, J. Linn. Soc. Lond. 24: 260. 1887. Type: Gymnogramma chrysosora Baker.

OBS. One species in Sarawak and one in Sumatra. I have seen no specimens of either, and accept Holttum's (1958, p. 450) opinion

in allying the genus with the bristly-rhizomed members of this tribe, Taenitis and Syngramma. A photograph of the type of C. chrysosora (Baker) Domin in the U. S. National Herbarium shows a plant with an erect, ascending rhizome, fronds about 15--20 cm. long, blades lanceolate with about 20 pinna pairs, each pinna ovate-lanceolate with about ten mostly oblanceolate pinnules obliquely inserted on the costa. The outline of the fronds is not unlike some specimens of West Indian Pityrogramma chrysophylla (Swartz) Link. Judging by Holttum's (1962, pp. 531-2) comments, there seems to be some resemblance to Rheopteris asplenioides Holtt.

7. Coniogramme Fée, Gen. Fil. 167. (1850-52) 1852, nomen conservandum. Type: Diplazium fraxineum Don [=Coniogramme javanica (Blume) Fée].

Dictyogramme Fée, Mém. Soc. Mus. d'Hist. Nat. Strasb. 4(1): 202. 1850, nomen rejiciendum. Type: Hemionitis japonica Thunb.

Notogramme Presl, Epim. Bot. 263. (1849) 1851, nomen rejiciendum. Type: Hemionitis japonica Thunb. "Notogramme" was written in hand by Presl in favor of the obliterated printed word "Dyctiogramme," which he subsequently used as a subgenus of Polypodium (see Hieronymus, 1916, p. 269).

X Coniodictyogramme Nakai, Bull. Nat. Sci. Mus. Tokyo 27: 22. 1949. Based on Coniogramme fraxinea (Don) Diels in Engler & Prantl X Dictyogramme japonica (Thunb.) Fée [=C. japonica (Thunb.) Diels in Engler & Prantl].

OBS. About fifteen to twenty species in Asia and the Pacific Islands, plus one each in Africa and Madagascar. The species commonly

known as Coniogramme americana (Eaton & Davenp.) Maxon seems to me to be a Gymnopteris. The species have been quite narrowly defined by Hieronymus (1916). A revision of this genus is needed to consider the collections which have accumulated since Hieronymus wrote.

8. Pterozonium Fée, Mém. Soc. Mus. d'Hist. Nat. Strasb. 4(1): 202. 1850; Gen. Fil. 178. t.16A. (1850-52) 1852. Type: Gymnogramme reniforme Martius.

OBS. Nine species confined to the Guayana Highlands of Venezuela, Colombia, British Guiana, and Tafelberg in Surinam, plus the type species, which ranges more widely into adjacent areas. All but the two pinnate species are simply bladed; and all have thick, coriaceous, reniform to oblanceolate blades or segments. Unlike Syngrammatopsis, Pterozonium has flattened, multiseriate scales.

9. "Nephopteris" Maxon, in ined. ms.

OBS. This unpublished, monotypic genus is known to me from two Colombian collections: Pennell 4258, Paramo de Chaquiro, Cordillera Occidental, February 23, 1918 (NY, US) and Grubb & Guymer P.68, Alto del Oso, Sierra Nevada de Cocuy, 18.8.1957 (US). The genus resembles Eriosorus in segment architecture. Its sterile fronds are short-stipitate and trifoliate; its fertile fronds are long-stipitate and pinnate. The frond dimorphism does not link this genus with Hemionitis or Trachypteris. Rather, it seems to be a specialized, derivative genus of this tribe, the Eriosoreae.

10. Eriosorus Fée, Gen. Fil. 152. t.13B. f.1. (1850-52) 1852. — Type: E. scandens Fée [=Gymnogramme aureo-nitens Hooker].

Gymnogramme auctt., non Desv.

Psilogramme § Eupsilogramme Kuhn, Festschr. 50 Jahr Jub. K. Realschule Berl. 335. (Chaetopt. 15) 1882. Type: not stated; Gymnogramme elongata Hook. & Grev. was chosen by Copeland (1947, p. 58). Kuhn also included the type of Eriosorus, which makes Psilogramme a superfluous name.

Gymnogramme § Isgnogramme Hieron., Bot. Jahrb. Engler 34(4): 474-475. 1904. Type and sole species: G. lehmannii Hieron.

Gymnogramma subg. Isgnogramme (Hieron.) C. Chr., Ind. Fil. XXXVIII. 1906. Based on Gymnogramme § Isgnogramme Hieron.

OBS. About thirty species in Central and South America. In contrast to Jamesonia, this genus is monophyletic, if the results displayed in Figure 24 are valid. R. M. Tryon (1962, p. 70) has transferred Gymnogramma lehmannii Hieron. to Pityrogramma on the basis of its spores, among other things. But this species shares many more of its character states with the Eriosoreae than with the Gymnopterideae.

11. Jamesonia Hook. & Grev., Icon. Fil. 2: t.178. (1831) 1829. Type: J. pulchra Hook. & Grev.

Gymnogramma § Jamesonia (Hook. & Grev.) Klotzsch, Linnaea 20: 407. 1847. Based on Jamesonia Hook. & Grev.

Psilogramme § Jamesonia (Hook. & Grev.) Kuhn, Festschr. 50 Jahr Jub. K. Realschule Berl. 332. (Chaetopt. 12) 1882. Based on Jamesonia Hook. & Grev.

OBS. The genus contains nineteen species, and is principally Andean, with extensions north to Mexico and east to southern Brazil. A. F. Tryon (1962) has prepared a comprehensive monograph of the genus.

The data plotted in Figure 24 bear out her (1962, pp. 114ff.) contention that Jamesonia is polyphyletic from Eriosorus. But Jamesonia imbricata var. glutinosa (Karst.) A. F. Tryon is probably misplaced. This may be due to the hybridity of the taxon (see A. F. Tryon, 1962, p. 114).

12. Platyzoma R. Br., Prodr. Fl. Nov. Holl. 160. 1810. Type: P. microphyllum R. Br.

OBS. One species in northern and western Australia. The systematic position of this genus has been the subject of considerable discussion by Holttum (1957) and by A. F. Tryon (1961, 1964). I agree with their conclusion that this genus does not belong in the Gleicheniaceae. A. F. Tryon (1964) removes Platyzoma from the Adiantoideae altogether. She concludes that Platyzoma is sufficiently distinct from the other genera of the Polypodiaceae sensu Christensen to merit subfamily status under that family, placed between his "Gymnogrammoideae" and "Pteridoideae." I have insufficient quantitative data on which to confirm her conclusion. If Platyzoma is to be maintained in the Adiantoideae, however, it must be placed as an isolated genus in the Eriosoreae.

13. Aspleniopsis Mett. ex Kuhn, Festschr. 50 Jahr Jub. K. Realschule Berl. 324. (Chaetopt. 4) 1882. Type: Gymnogramme decipiens Mett.

Gymnogramme § Aspleniopsis (Mett. ex Kuhn) Christ, Farnkr. 68. 1897. Based on Aspleniopsis Mett. ex Kuhn.

OBS. One species in New Caledonia, the New Hebrides, Fiji, and, according to Copeland (1947, p. 77), in New Ireland. Despite its many resemblances to Asplenium, Aspleniopsis is eriosorioid. W. H. Wagner,

Jr. (in litt. September 12, 1964) points out the tetrahedral spores, gymnogrammeoid sporangia, paraphyses, and chromosome number of n = ca. 58. But this strange genus cannot be placed with certainty in any one tribe of the Adiantoideae. Copeland (1947, p. 77) appended it ". . . to the hairy gymnogrammoid [sic] ferns." I find that of the ground plan characters of the various tribes, Aspleniopsis shares one with the Pellaeae, two with the Gymnopterideae, and three with the Eriosoreae. And so I place it, provisionally, as a separate evolutionary line from the ground plan ancestor of the Eriosoreae.

Tribe 6.--Adianteae

Adianteae. Type genus: same as the family, Adiantum L. The tribe is distinguished from the other tribes of the subfamily by its sori, which are restricted to the indusium (BCNR 1015). The tribe consists of the single genus Adiantum.

1. Adiantum L., Sp. Pl. 2: 1094. 1753. Type: not stated; Pichi-Sermolli (1957, p. 369) chose A. capillus-veneris L. on the grounds that it is a classical, European species with a long history in European botany. But the first person to divide the genus into subgeneric taxa seems to be Presl (1836, p. 157), who did not include A. capillus-veneris L. in his section Adiantum. Thus the proper lectotype may have to be chosen from those Linnaean species which Presl did cite.

The utter confusion and lack of typification of subgeneric names in Adiantum is complete. Christensen (1906, p. XLIII) avoided the question, as did Ching (1957), who followed the unfortunate

precedent, which apparently began with Keyserling (1875), of dividing the genus into nomenclatorially unrecognized "groups." For these reasons I find it necessary to omit the subgeneric nomenclature of Adiantum.

OBS. About 200 species in the warm and temperate regions of the world, divided nearly evenly between the eastern and western hemispheres. Kuhn (1881) provides a key and brief descriptions for 113 species. Keyserling (1875) enumerates only sixty-seven species. Among the recent work, Ching (1957) treats the Chinese species, although his new combinations and new subgeneric names are invalid because basionyms and Latin diagnoses are omitted. R. M. Tryon (1964, pp. 135-180) reviews the considerable number of Adiantums which grow in Peru.

While I do not think that "Hewardia" merits generic standing (to be consistent, all of the groups within the genus would have to be so raised), I agree with Ching (1957, p. 349) that if "Hewardia" is to be a natural group, several species with non-anastomosing veins would have to be included with the type of "Hewardia."

In Figure 25, "Hewardia," represented by A. olivaceum Baker, shares several characteristics with A. caudatum L., which is a member of the "caudatum group." A. capillus-veneris L. seems to be relatively primitive. A. flabellulatum L., a representative of the "pedatum group," is perhaps the most isolated of the species studied. Another ground plan diagram, utilizing only ten characters, seven of which were the same as in this diagram, yielded substantially the

same results. So the organization of the OTU's on the ground plan diagram is apparently real, and is not an artifact of the small number of characters used. But the present study is probably too superficial to warrant taxonomic changes. And all changes must be avoided until the problem of typification is settled.

The Subfamily Adiantoideae

Judging the relationships of the tribes or making an evolutionary ground plan diagram of the subfamily is a more difficult task than performing the same operations on the generic or tribal level. As the hierarchical rank increases, fewer characters are patterned, and more are present in parallel. With quantitative methods, statistical uncertainty increases as the number of characters decreases.

Species of the tribes within the Adiantoideae often grow in similar habitats, in contrast to the different habitats of the subfamilies Adiantoideae and Vittarioideae.(see page 132). Each tribe, however, has a few defining characteristics which are found in most, if not all, of the members of the tribe. Because of this unity of genera within each tribe, I suspect that the tribes have been separate for long enough a span of evolutionary history that the genera of the different tribes are not directly related to the genera of the other tribes, nor to the immediate common ancestors of other tribes. There is also a unity of the tribes, which is shown in the characters held in common by the six tribes.

Parallelisms observed in species are of two kinds: between species or genera of a single tribe and between species or genera of two or more tribes.

The dimorphic fronds of Cryptogramma and Llavea versus those of Neurosoria illustrates parallelism between genera of a single tribe, in this case the Onychieae. Trachypteris and Hemionitis, both of the Gymnopterideae, are a similar occurrence. In the Cheilantheae, Adiantopsis is marked by discrete sori. This condition is also found in some species of Cheilanthes and in Aspidotis, but in these two genera some species have a continuous indusium which protects a marginal "fusion sorus" or a series of discrete sori at the ends of veins. Intermediate conditions are found in both genera. The transitions between discrete and continuous sori in the latter genus may be of hybrid origin (see Wagner & Gilbert, 1957). In Adiantum, too, some species have discrete sori and indusia; others have a trend toward a continuous marginal indusium, with the fertile area continuous beneath. Apparently no commissural vein develops.

Even highly complex characters like frond form are developed in parallel within a single tribe. Cheilanthes regularis Mett., a species long placed incorrectly in Adiantopsis, does resemble in many respects the segment and pinna architecture of the non-radiate Adiantopsises (see Plates V and VI). Platyzoma and Jamesonia in the Eriosoreae share the character of many minute pinnae, creating a frond that is almost filament-like. A similar parallel reduction occurs from Polystichum to Papuapteris, which are both in the Aspidiaceae.

While the Gymnopterideae and the Eriosoreae presumably share the exindusiate characteristic in common, members of other tribes have become exindusiate independently. Notholaena, in the Cheilantheae,

and Saffordia, in the Pellaeae, are both exindusiate, but both have indusiate ancestors. Frond form is duplicated between tribes, too. Aleuritopteris duclouxii (Christ) Ching resembles Doryopteris collina (Raddi) J. Smith (see Plates VII and VIII). The former is in the Cheilantheae, and the latter is in the Pellaeae.

The validity of the adjacent group technique can be questioned when it is used on the subfamily level. For instance, the subfamily Adiantoideae is predominantly epipetric, while the subfamily Vittarioideae is mostly epiphytic. These diverse habits are probably correlated with the diverse habitats of the plants, and may explain in part their sharply different characteristics. While the adjacent group taxa for the tribes of the Adiantoideae tend to share many characteristics, the adjacent group taxa for the two subfamilies of the Adiantaceae show different characteristics. In using taxa of the Vittarioideae for adjacent group comparisons with the Adiantoideae, then, one is forced to exclude many data that were included in making evolutionary ground plan diagrams of the tribes of the Adiantoideae.

Another question relating to the use of the adjacent group test at the subfamily level concerns the relationship of the adjacent groups to the Adiantoideae. The tribes of this subfamily are all more closely related to one another than any one is to the adjacent groups with which the Adiantoideae has been thought to be related: the Vittarioideae, Pteris, and other "pteroids." One is left, however, with the question of weighting information gained from these adjacent groups, not to mention the problem of circular reasoning in their construction (see pages 23-25). The data used in this study

indicate only that the Vittarioideae share fewer characteristics with the Adiantoideae than do either the four members of the genus Pteris or the three members of the other "pteroids." And the characters which pass an adjacent group test on the basis of comparison with Pteris species are different from those which pass when comparing with species of the Vittarioideae.

For these reasons, I have abandoned the use of an adjacent group test, and instead use only characters which are present in four or five of the adjacent group taxa of the tribes (real taxa 5, 20, 31, 53, 63, and 74) as a basis for selecting characters on which to base an evolutionary ground plan diagram of the tribes of the Adiantoideae. Characters present in all six of the taxa are null, of course. Of the characters present in four or five of the OTU's representing the tribes, I chose those which had been shown to have classificatory value in this study, and in the works of others. Within the selected characters, all the character states are used. For instance, if character 19 is chosen because one of its states is present in four of the six OTU's representing the tribes (the distribution being, say, 2, 1, 3, 3, 3, 3), then BCNR 191, 192, and 193 are used in making the evolutionary ground plan diagram. Character 102 was also included because it sharply defines tribes.

The first trial using the chosen set of characters produced strong divergences among the tribes. Long series of hypothetical intermediate taxa separated the real OTU's. These were caused by redundant characters--19 versus 18 and 20, and 86 versus 87, for example. In the second trial, which is shown in Figure 26, the

redundancies were eliminated, and a more satisfactory result was obtained.

Because there were only six OTU's and twenty-four binary characters, machine computation was unnecessary. The hand operations were, insofar as possible, analogous to the machine procedure. Rogers' similarity ratio, s_{ij}, was used to calculate a matrix of similarity coefficients. The divergence index of each OTU was the same (each had one of the attributes of every character) because all of the states were treated as being advanced, with some OTU's having certain attributes and other OTU's having different ones. This is a departure from the usual ground plan method, justified, I believe, by its use with data which were useful in making evolutionary ground plans at a lower hierarchical level. Because of the identical divergence indices, real taxon 74 was arbitrarily chosen to begin the diagram, since the Eriosoreae seemed to be the most generalized tribe, in my opinion. Hypothetical intermediate taxa were assembled, recorded in the $i \times m$ table, and additional similarity indices calculated. Highest similarity ratios were used to place the real OTU's. The brief order of operations was: (1) Place real taxon 5, (2) Place real taxon 3 (s_{ij} = 0.800 with hypothetical taxon 509), (3) Place real taxon 1 (s_{ij} = 0.538 with hypothetical taxon 511), (4) Place real taxon 2 (s_{ij} = 0.500 with hypothetical taxon 512), (5) Place real taxon 4 (s_{ij} = 0.462 with hypothetical taxon 510), and (6) Place real taxon 6 (s_{ij} = 0.500 with hypothetical taxon 522).

The resulting diagram seems reasonable. The Cheilantheae and Pellaeae are grouped together, along with the Onychieae.

These equal the Sinopteridaceae Koidz. The Eriosoreae is centrally placed, and has the Gymnopterideae and the Adianteae attached. These are the "Gymnogrammaceae" of Ching and the Adiantaceae Ching.

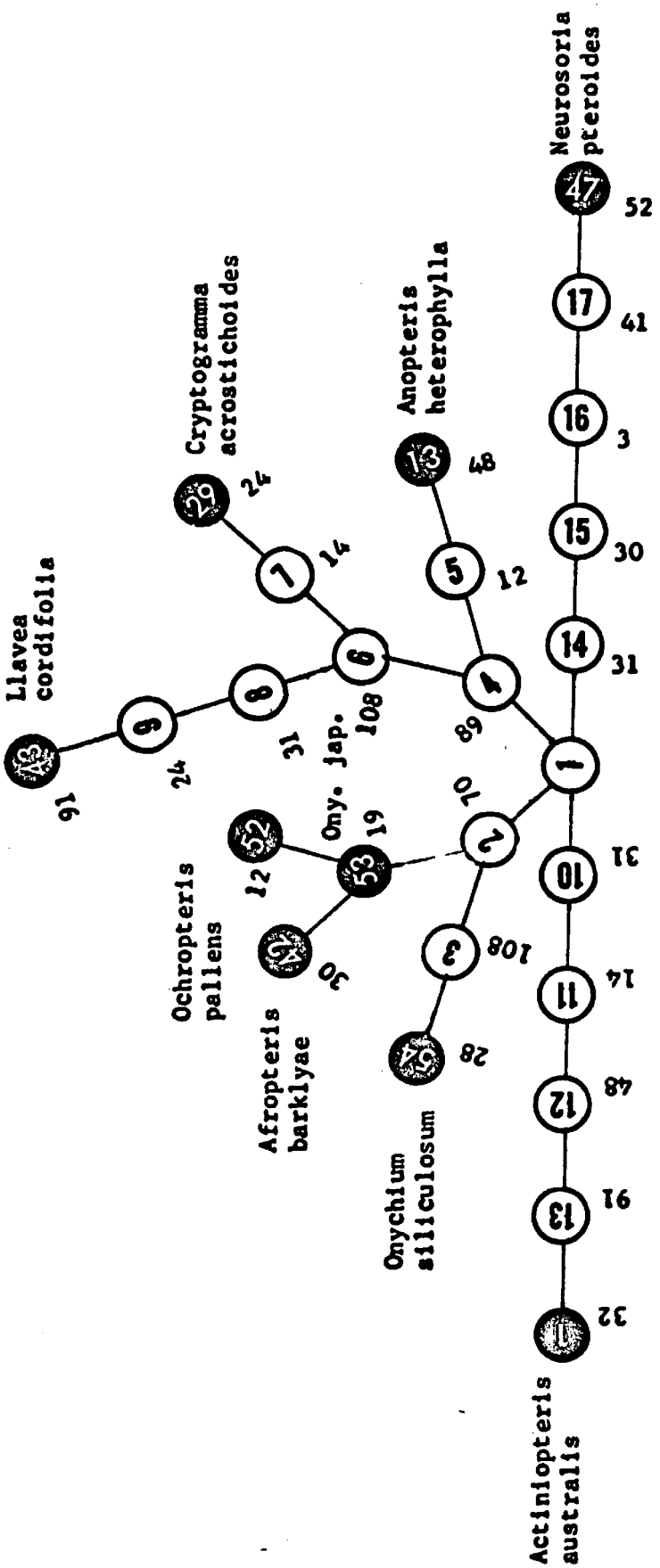


Fig. 17.--Evolutionary ground plan diagram of the Onychieae

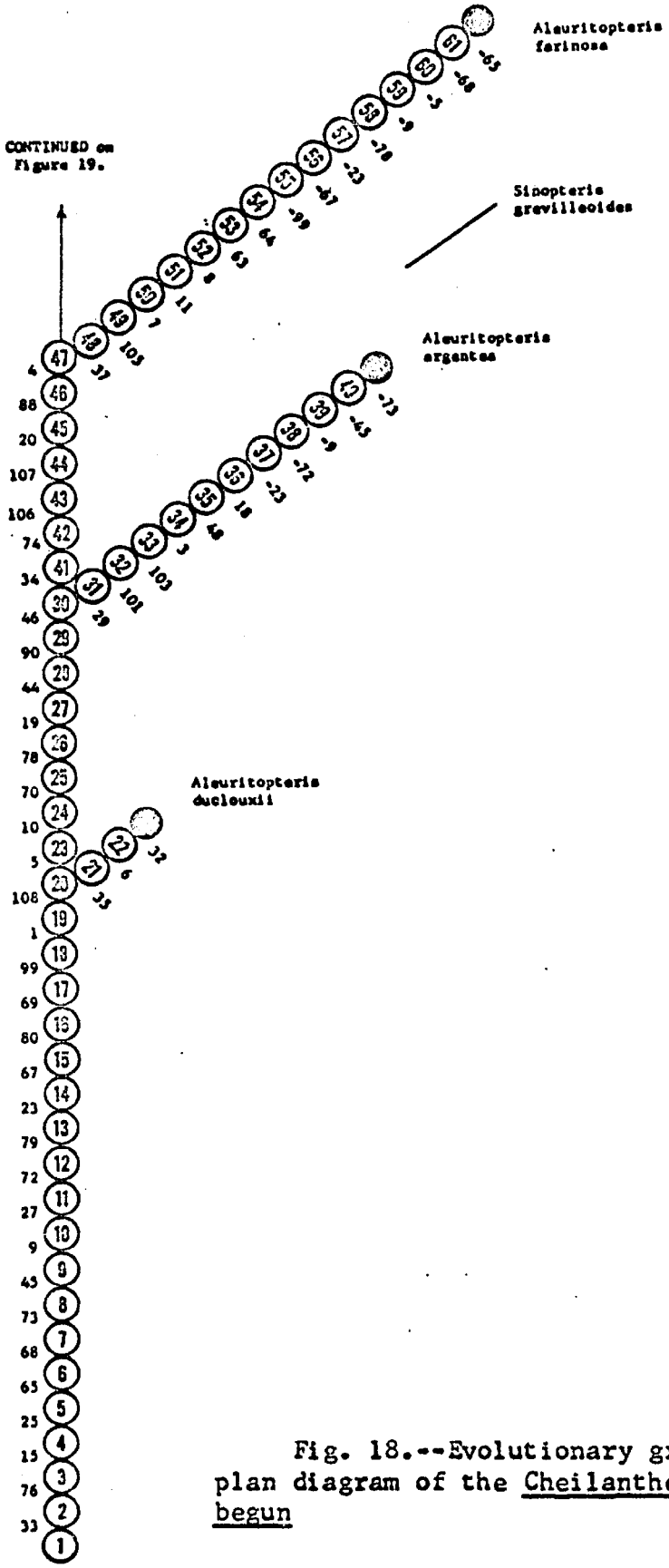


Fig. 18.--Evolutionary ground plan diagram of the Cheilantheae, begun

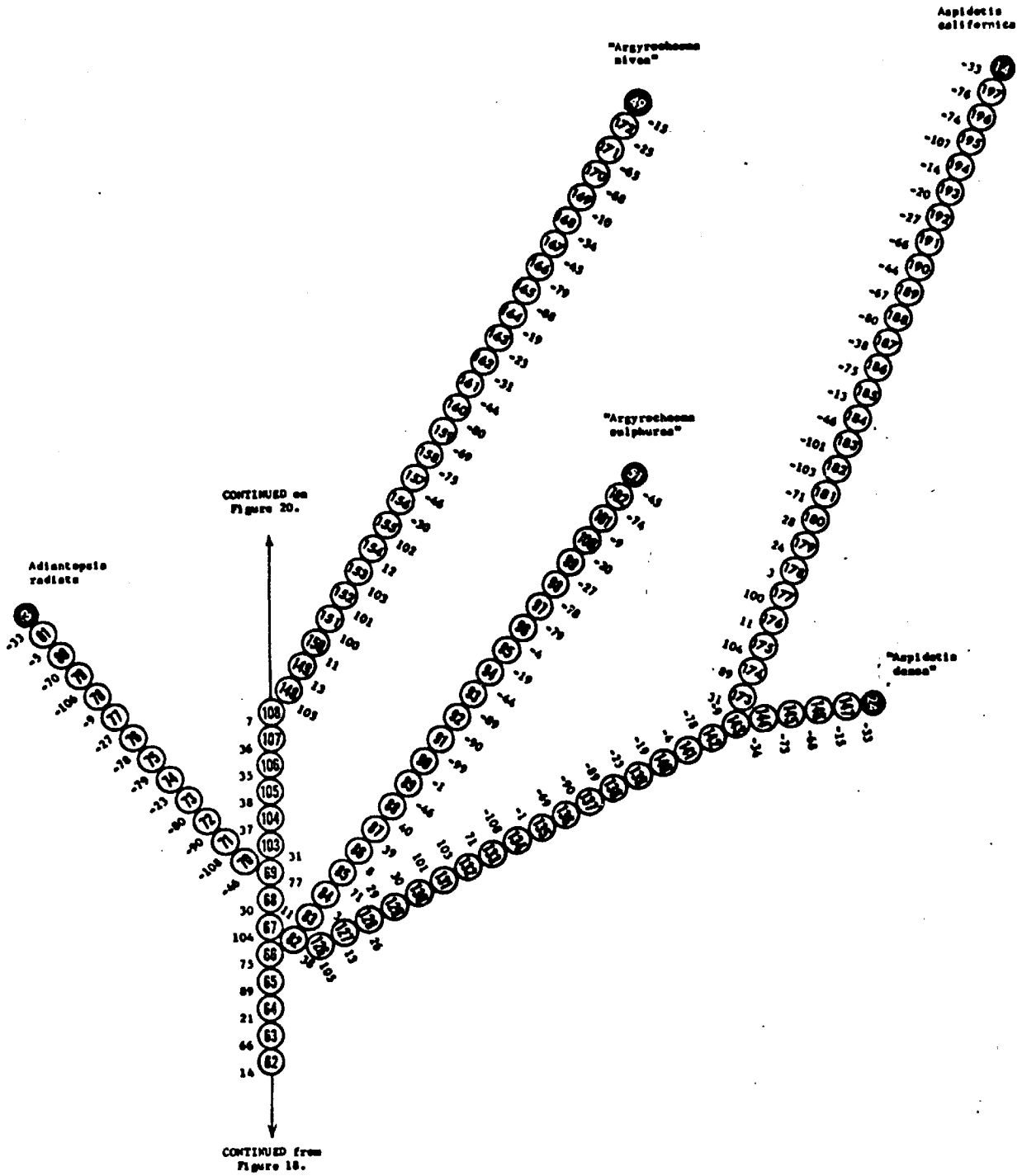


Fig. 19.--Evolutionary ground plan diagram of the Cheilantheae, continued

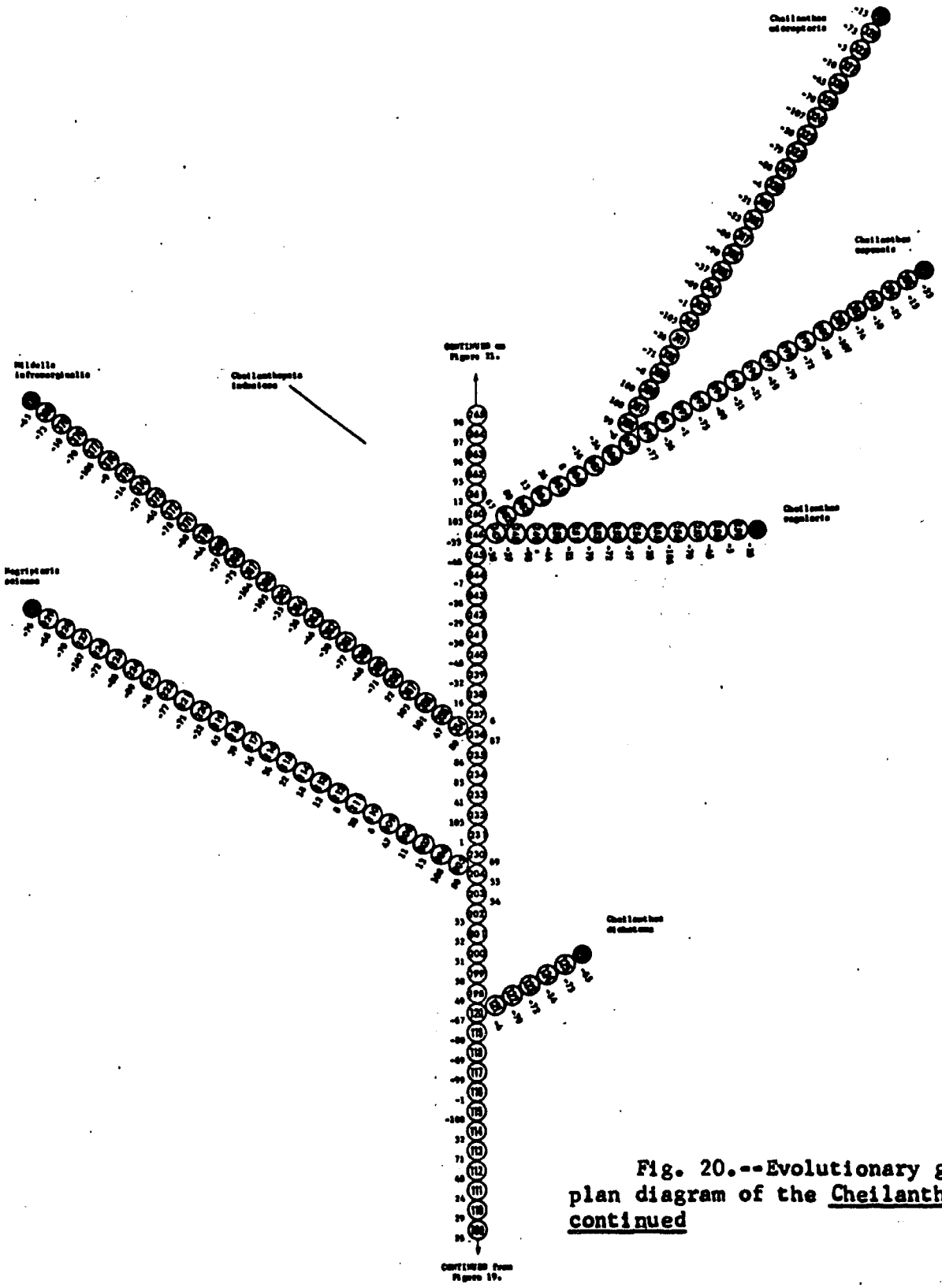


Fig. 20.--Evolutionary ground plan diagram of the Cheilantheae, continued

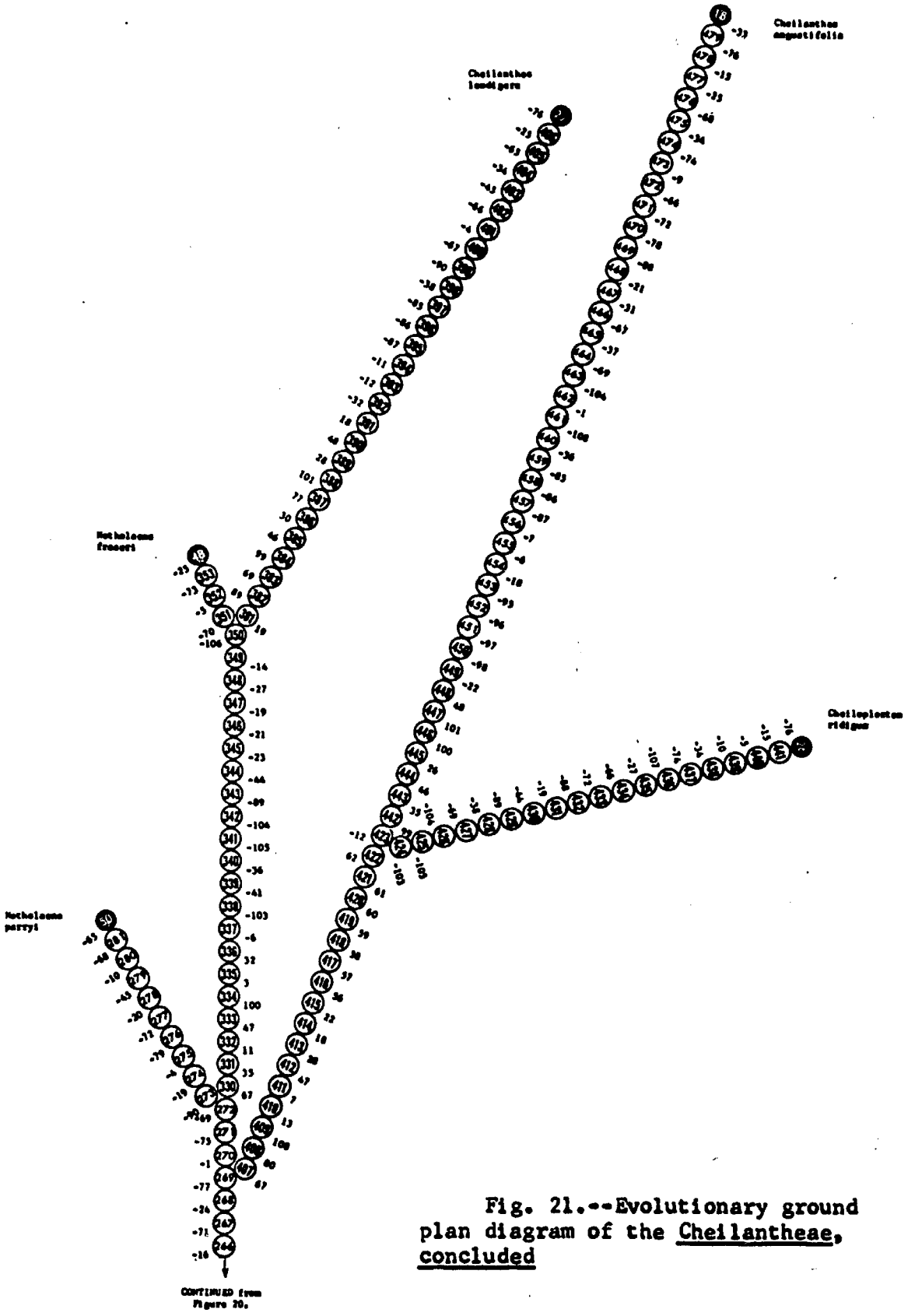


Fig. 21.--Evolutionary ground plan diagram of the Cheilantheae, concluded

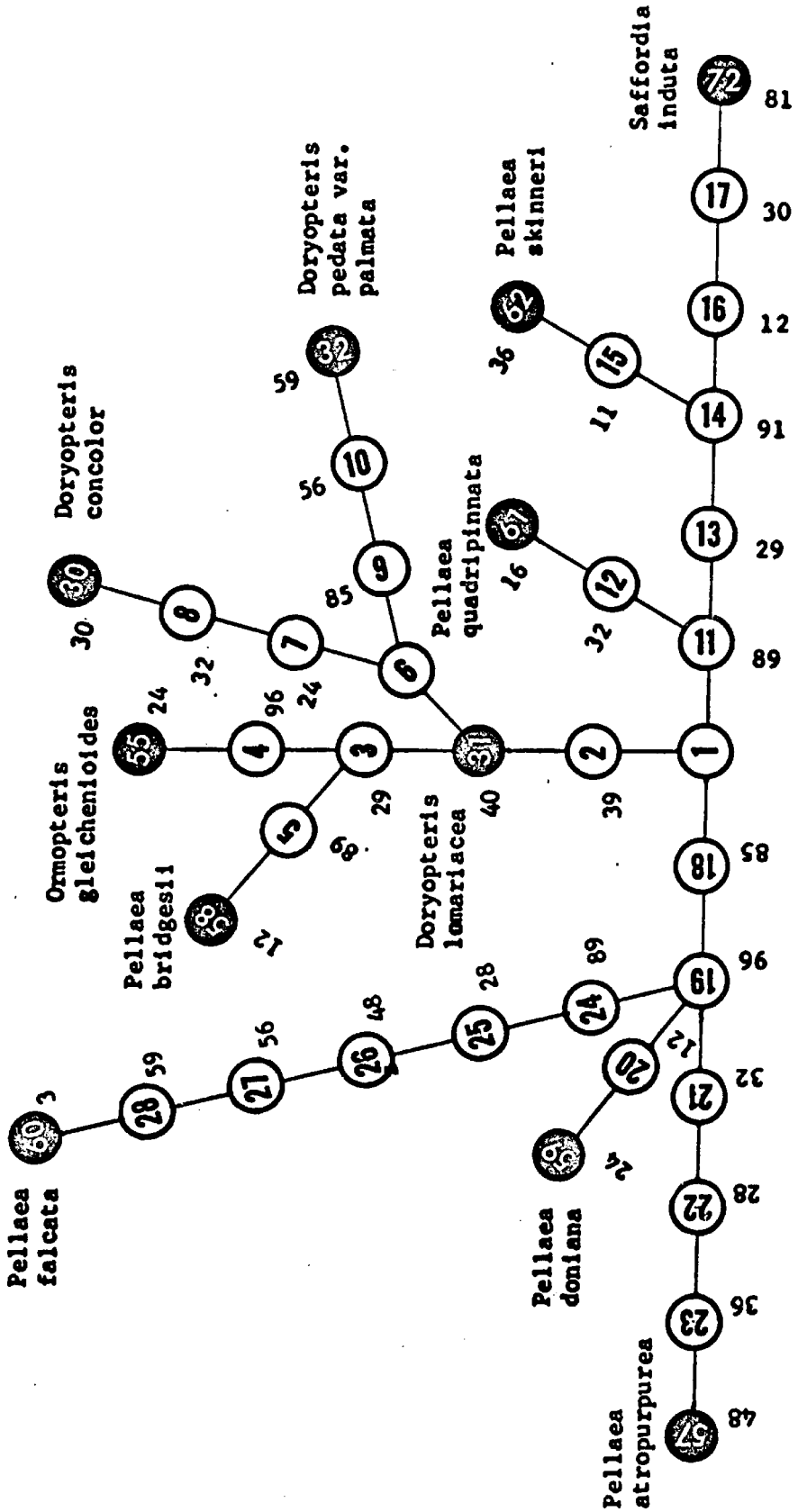


Fig. 22.--Evolutionary ground plan diagram of the Pellaeae

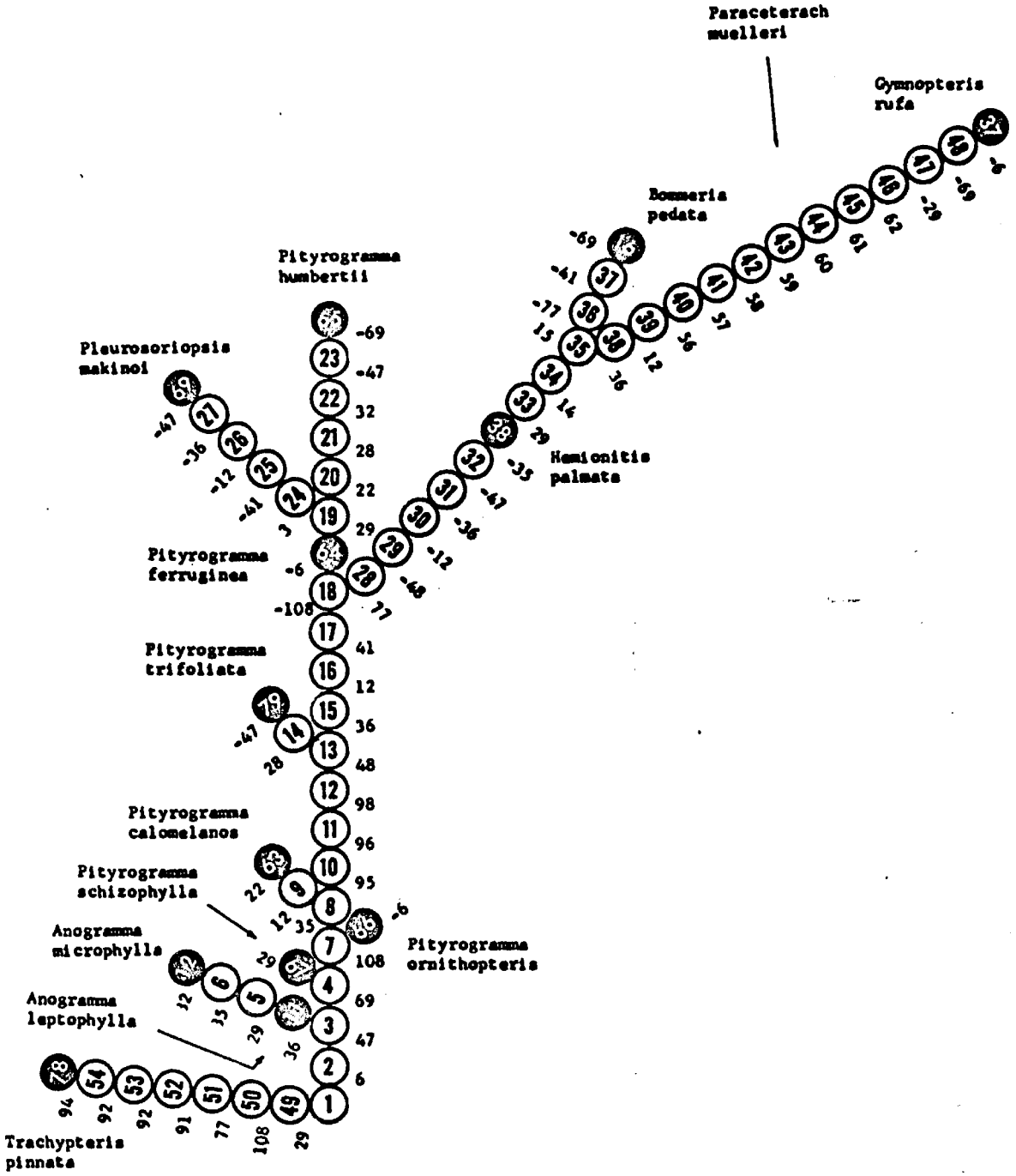


Fig. 23.--Evolutionary ground plan diagram of the Gymnopterideae

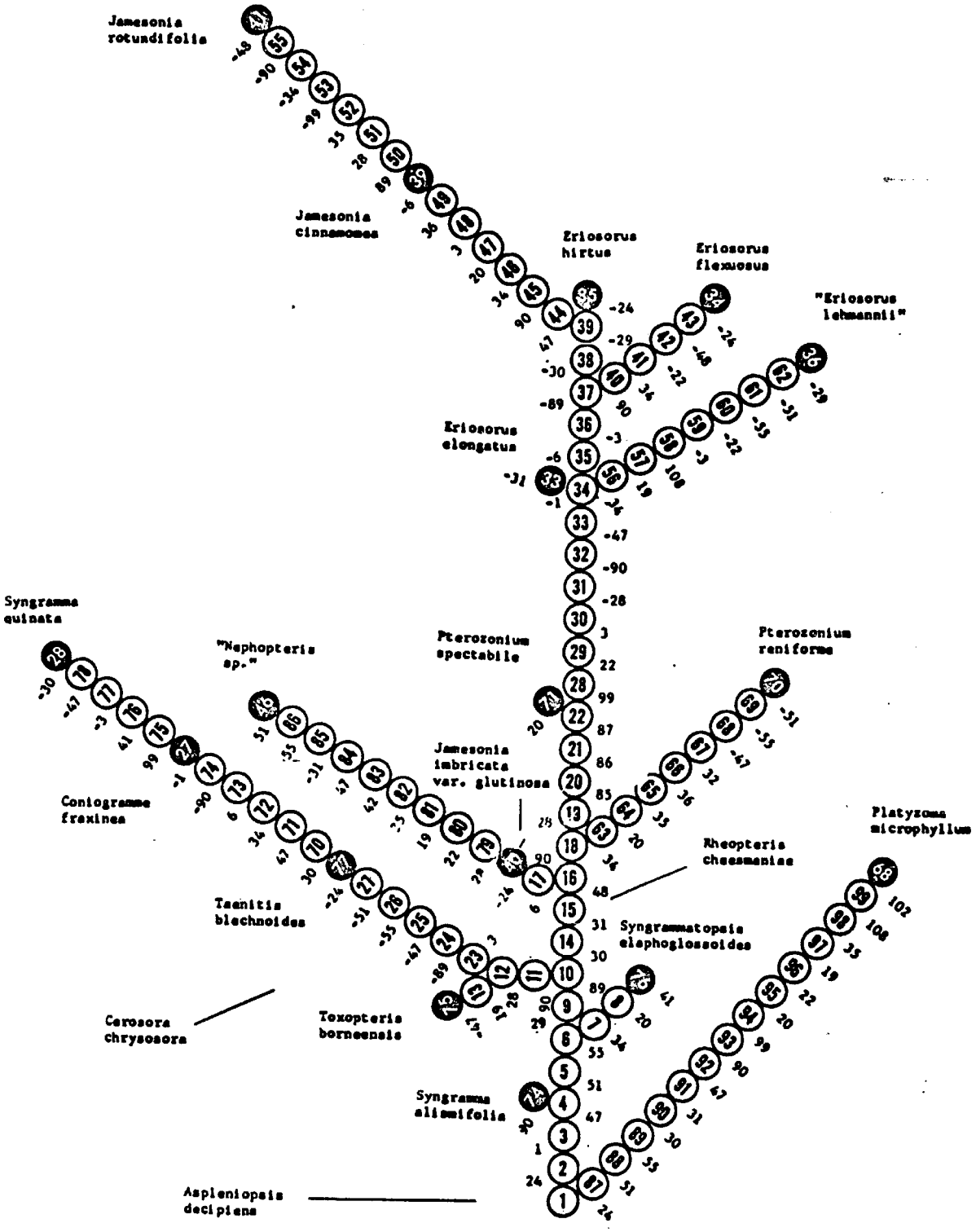


Fig. 24.--Evolutionary ground plan diagram of the Eriosoreae

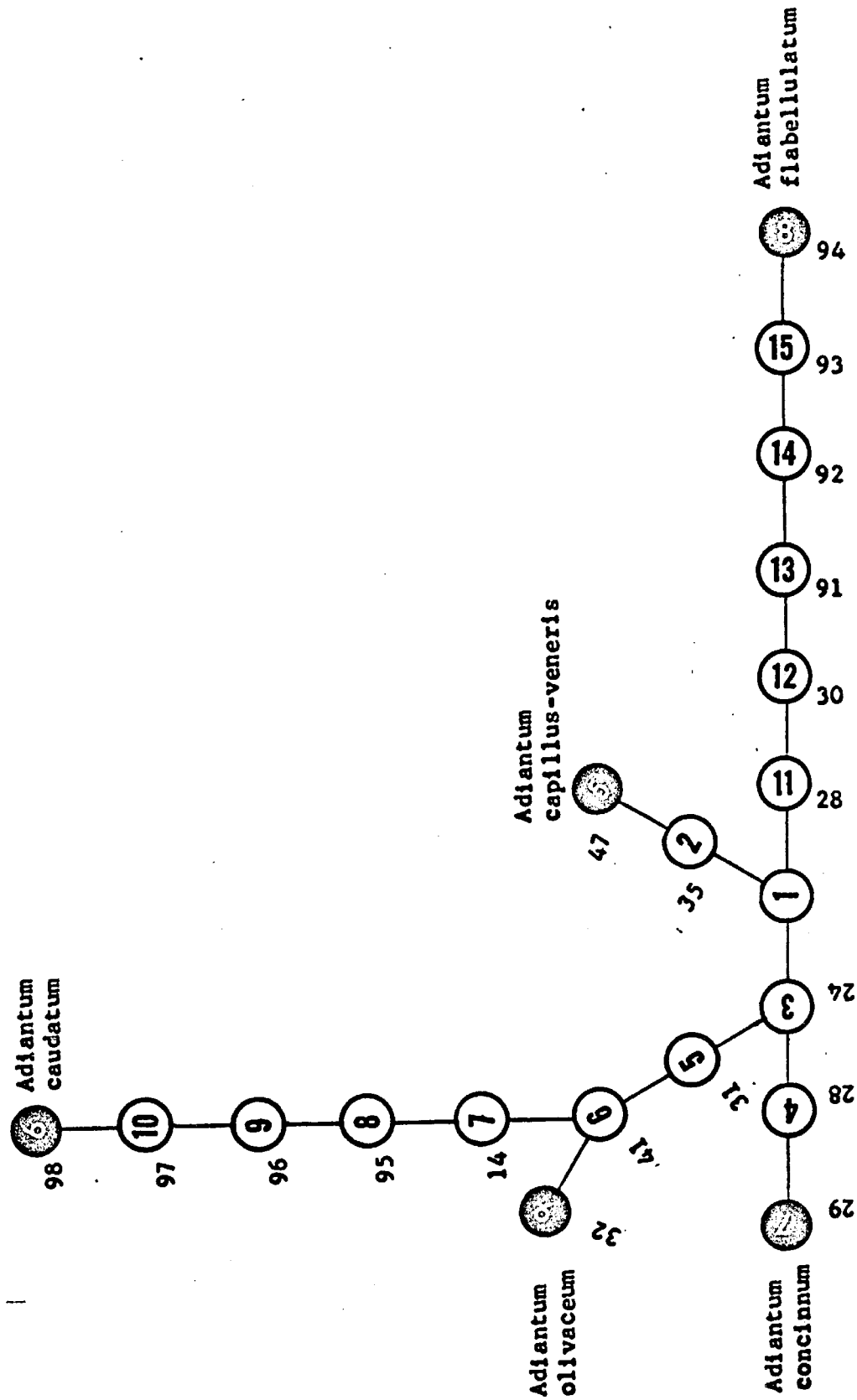


Fig. 25.--Evolutionary ground plan diagram of the Adianteae

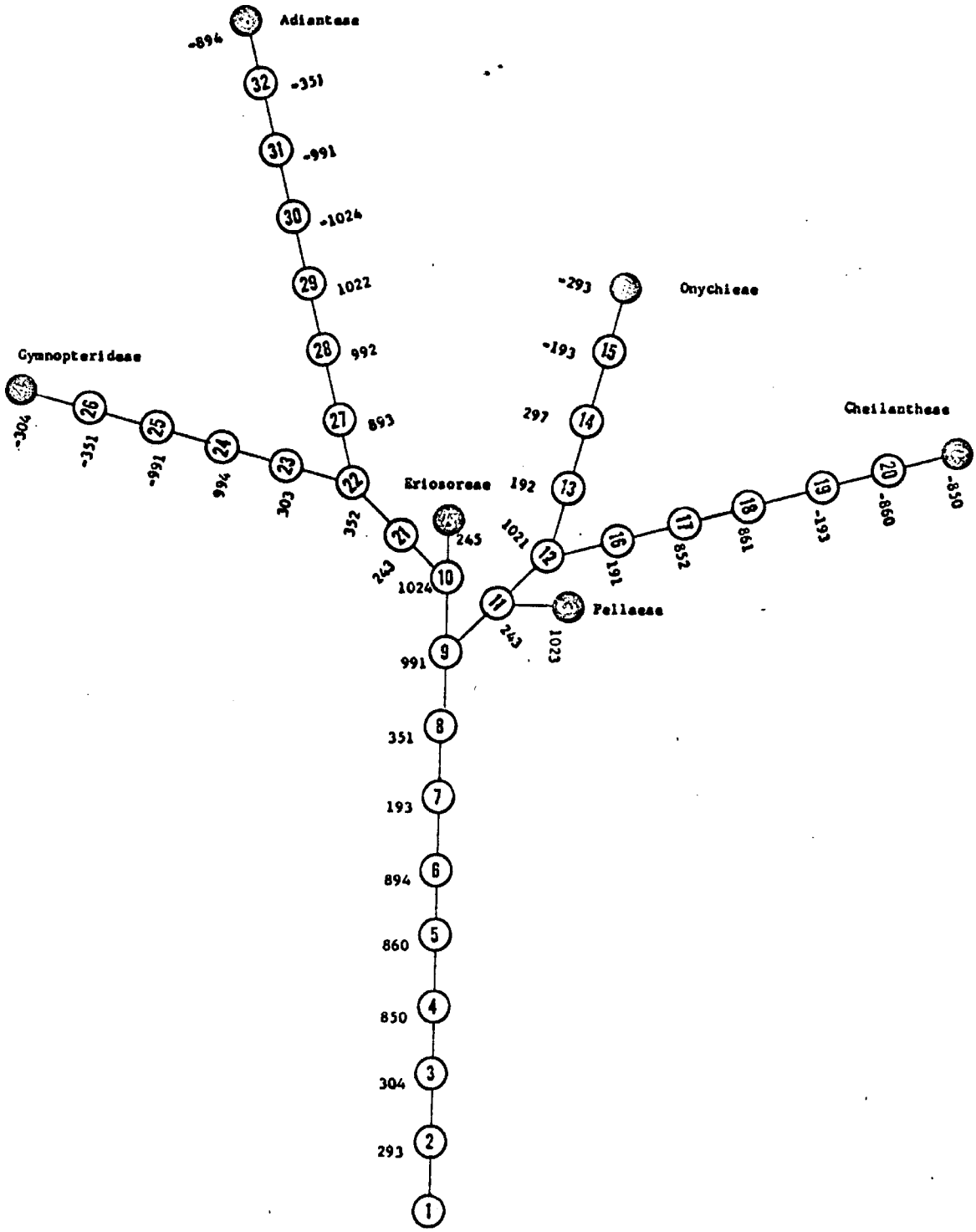


Fig. 26.--Evolutionary ground plan diagram of the Adiantoideae

CHAPTER V

CRITIQUE OF THE EVOLUTIONARY GROUND PLAN METHOD

Introduction

The use of the evolutionary ground plan method with the Adiantoideae or its tribes seems never to be an unqualified success. This would doubtless be true with any group of organisms. But it is possible to learn from even the failures of the method, by endeavoring to diagnose their causes. In this way the ground plan method can perhaps be improved and made more accurate.

Not all biological populations or sets of specimens are suited to the present method, for some taxa or groups of specimens do not show divergent evolutionary trends. In these circumstances the method either must be adapted to this different material or the material studied by some other taxiometric approach. At other times, when the material seems unsuited because the ground plan diagram results are incoherent, a change in the method of data taking which preserves more of the information about correlation of OTU's may yield valid results. A third category of difficulties stems from the use of a model which fits the data inaccurately orffrom data which are distorted or ignored by the mechanics of constructing the ground plan diagram. Improvements over the original concepts and operations have been made in all phases of the method during the present studies; many more improvements are needed if the evolutionary ground plan

method is to have its widest application and to bring forth its surest results.

Just as there is no one correct kind of classification which suits all purposes (see pages 4-6), also there is no absolute standard with which to judge the correctness of any classification. The time may come when the results of highly refined taxiometric techniques will be accepted as conclusive. Today, however, the taxonomist is only aided by the computer, and he renders the final judgement on both conventional taxonomic and taxiometric conclusions. The classification of the Adiantoideae presented in Chapter IV has been changed and refined (with considerable help from the computer) during the course of study. But when "correct" or "satisfactory" results are mentioned, the opinion is mine.

Diagnosis and Correction of Faulty Results

Sometimes all sets of character selection parameters yield unsatisfactory ground plan diagrams. Even after many tries, every diagram contains numerous fluctuating characters and sets of characters which are developed apparently in parallel in different lines. Since no character selection scheme works, presumably nothing can be done (assuming that the data-taking techniques were adequate). The material is just too disordered and has too few trend-bearing characters to enable the methods of data selection to extract enough information to make a ground plan diagram.

Well-correlated characters which show evolutionary trends range in taxa from groups in which these characters have a nearly pure

branching pattern (probably many birds and mammals) through groups in which parallel trends and reductions make the ground plan technique problematical (the Cheilantheae, for instance) to groups in which evolutionary trends cannot be defined with enough certainty to use the ground plan technique at all (most bacteria at the present state of our knowledge). Non-evolutionary, phenetic, numerical taxiometric methods offer a stable, repeatable way to classify these latter two groups. Graphic examples of these patterns and the methods which will discover their correlated characters are illustrated in Figure 27.

In cases where the ground plan failed in this study, there were two possibilities, if the ground plan method was not to be given up altogether. The first was use of all the characters in making the evolutionary ground plan diagram. It was necessary to do this in the Cheilantheae, where all the schemes for selecting characters produced disordered ground plan diagrams. This was a dangerous circumvention, however, since without preselecting evolutionarily important characters, the methods of association and dendrogram development in this technique were not stringent enough to assure highly parsimonious or valid results. The method was clearly being pushed to the borderline of its capacities.

The second was to reexamine specimens and data to see if any division of the OTU's into two or more separate groups would result in more homogeneous groups. This was done in splitting the Cheilantheae sensu Christensen in Verdoorn (1938, p. 538) into the Cheilantheae sensu stricto and the Pellaeae. Until this was done, the ground plan diagrams of the tribe were quite confused--more so than afterward.

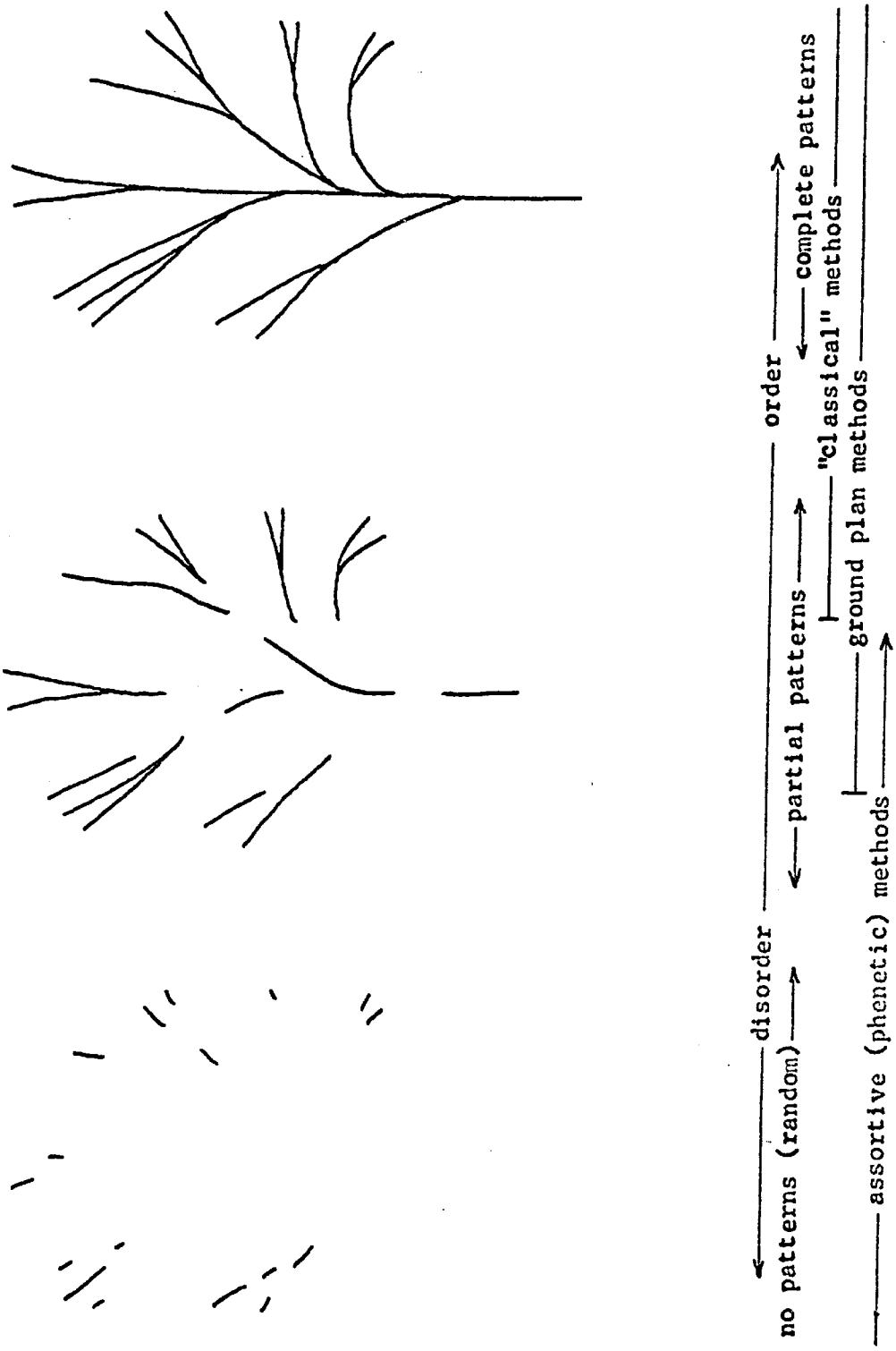


Fig. 27.--Diagrams of hypothetical character correlations

In working with the Adiantoideae and its tribes it became apparent, after trying several sets of character selection parameters, that no single set would produce satisfactory ground plan diagrams in all the tribes (see pages 75-76). Parameters which gave good results in the Onychieae failed in the Eriosoreae, for instance. The characters of different tribes varied in their classificatory usefulness and in their frequency distribution within the OTU's of the different tribes, and the ground plan diagrams reflected these differences.

In the majority of cases the ground plan method produced diagrams that seemed correct for the most part, but in which one or a few OTU's seemed misplaced. Of course, it was possible for me to be mistaken in my a priori assessment of relationship of these "misplaced" OTU's. But whatever the decision, one of the principal benefits of the method was that attention was focused on OTU's which were difficult to group correctly.

When a placement error seemed evident, and the number of advanced characteristics lost in lines leading to the OTU was few, the error was often attributable to the use of too few characters. To a certain extent this was true in the Pellaeae (Figure 22), where some highly compound Pellaeas and Saffordia were grouped together. A relatively small number of characters were used to make this ground plan diagram. Apparently Saffordia shared enough of them in parallel to group it with the Pellaea species.

If the number of OTU's which seemed misplaced was fairly large, the offending characters were eliminated, and a new ground plan diagram was made. In using the smaller number of characters, correlation

coefficients had to be recalculated, and a new set of characters became parallel because the recomputed correlation coefficients caused new and different groupings of OTU's. The results were often unsatisfactory, but if the process was repeated, the results were usually even worse.

In some ground plan diagrams a few of the OTU's were separated from their branching point by long strings of hypothetical OTU's, some of which differed by a series of characters which described a single part of the plant. For instance, characters 91-93 in Figure 25 described the scales (if any) found on the undersurface of the laminae. The long separation of the OTU's at the end of these lines from the OTU's on the remainder of the diagram was an artifact of data organization. The series characters generally had a high correlation coefficient value among themselves, as discovered with an R-matrix (see pages 74-75). In instances where distortion was severe, it was possible to retain a single character of such a series before computing an $\underline{i} \times \underline{i}$ matrix or making the evolutionary ground plan diagram. The experience gained in working with the subfamily permitted some such characters to be eliminated by inspection.

In the Cheilantheae (Figures 18-21) almost all of the real OTU's were separated by long strings of hypothetical OTU's, even though only some of them displayed series of adjacent characters. In general this was caused by too lax character selection. Of course, in this tribe there was (deliberately) no character selection because all the selections were unsatisfactory. In the other tribes when this occurred, one or more of the parameters of the tests was altered to exclude

additional characters. A knowledge of the sensitivity of the tests (see Tables 1 and 2) is helpful in judging how to alter test parameters.

In order for the computer program to function, it assumed that every OTU was different from every other OTU in at least one characteristic. If too few characters were used because the selection parameters had been too stringent, certain real OTU's, sometimes not even closely related ones, shared exactly the same character states in the few characters that were used. The computer considered them as a single OTU, and printed a note to that effect. If this happened often, a set of less selective parameters was tried.

One of the parameters of the evolutionary ground plan method was the significance value of the similarity coefficients below which an insignificant degree of biological relationship was assumed, despite some correlation between the OTU to be placed on the diagram and the point on the diagram with which it had its highest correlation. In these cases, the OTU was inserted on a separate evolutionary line directly from the ground plan ancestor. If the similarity value cutoff was too high, seemingly related OTU's were branched off from the ground plan ancestor on separate lines. If the cutoff value was too low, then OTU's which probably belonged on different evolutionary lines were all associated together on a single line stemming from the ground plan ancestor. In either case, the cutoff value was adjusted to provide a more reasonable result.

The ground plan diagrams of both the Gymnopterideae and the Eriosoreae showed some lines in which there were many losses of advanced characteristics. These losses were attributed to three things.

First, some of the OTU's undoubtedly represented reduced, simplified species modified from more complex and elaborate ancestors. This determination remained my responsibility; the presence of losses of advanced characteristics leading to a real OTU perhaps signaled reduction, but certainly did not prove it. Second, when there were double gains and losses, it was rather likely that there had been a misplacement, which may have been due to a convergence of characters, a poor choice of characters, or the operations of the evolutionary ground plan diagram program. It was sometimes possible to refer the origin of the OTU's line to a more proximal taxon. Third, the plants of the group being diagrammed were morphologically divergent, and perhaps divisible into two groups, as the hairy and scaly members of the Eriosoreae. Some characters of the hairy, antecedent plants seemed to have been lost in their scaly descendants. No alteration of the diagram was necessary in this case, although a more severe divergence between the groups would have led to an incoherent diagram.

On the ground plan diagram of the Adiantoideae (Figure 26) some identical characters were gained or lost in two lines of evolution that stemmed from a common point. Thus, more evolutionary steps were taken to diagram the probable evolution than were absolutely necessary; the ground plan diagram was not the most parsimonious or efficient possible. Because the OTU's were associated with one another using a measure of association like Pearson's correlation coefficient or Rogers' similarity ratio, these identical changes were taken into account in an additive way. In constructing a line to an added OTU from its point of attachment, the characters were assorted into the hypothetical OTU's

on the basis of their frequency in the real OTU's. The position of the identical characters was not considered by the computer, for the lines were made one at a time and without reference to one another. Identical characters were thus duplicated in various evolutionary lines.

It is possible to interpret the diagrams and to rework them by hand, bringing the identical characters to positions below the common point in order to eliminate them and to make the diagram more parsimonious. Although the ground plan diagrams were constructed with the fewest number of steps, or nearly so (see pages 47-48), one can question equating parsimony with correctness. If the methods of character selection were perfect, only true parallelisms would occur on the diagram. These, of course, should not be eliminated by rearranging character order. Because the correctness of character selection must at present be judged subjectively, the same kind of judgement must apply to eliminating identical characters in lines arising from a single point; therefore, the evolutionary ground plan diagrams presented in this study are the computer's unmodified output.

The OTU's were grouped on the basis of characters employed. If there was a bias in those characters, it was apparent in the results. One example was in the Cheilantheae (Figure 21), where C. lendigera (Cav.) Swartz, a densely scaly plant, was placed with the scaly Notholaenas; in this instance a large portion of the characters described indument. If this bias had been objectionable to my aims as a classifier, either some offending characters could have been eliminated or those characters could have been reorganized to reduce their number without sacrificing much information.

Potential Improvements

Judging by the flaws in the present method, improvements in the method should be sought in three areas: data taking, theoretical models, and evolutionary ground plan diagram construction.

The principal concern in data taking is to include as much information as possible about the organisms in coding and selecting characters and characteristics. Then this information must be analyzed with as little loss as possible in making a similarity matrix. The analysis, done with a measure of association, is rather fixed in its approach to the data. Pairs of OTU's are evaluated, one character (attribute pair) at a time. In the present technique, a total mismatch (no correlation) is scored unless the character states are identical. But surely some character states deserve a partial correlation, even though the two states of the pair are not identical. Blue flowers are more closely related to purple than either is to yellow, for instance. This is a problem which deserves more attention from numerical taxonomists. In the past, most of their effort has gone into methods of similarity matrix analysis.

While data taking was discussed in Chapter III, one recent advance could lead to considerable improvement in the ground plan technique. Rogers, who began with a simple, linear coding of characteristics within a character, has refined his methods to provide for grouping of characteristics within a character in order to retain information about partial matches. For instance, if flower color is considered as a single character, the attributes fall into two groups, the red--purple--blue anthocyanins and the orange--yellow carotenoids.

Two OTU's with identical states (orange flowers) have a correlation coefficient of 1. Between groups (blue versus yellow) the coefficient is 0, while within a group (red versus blue) the coefficient might be 0.5. More information is retained here than in a simple linear system in which either the coefficient is zero except for exact matches or drops off as the numberical distance between code numbers of attributes increases.

Rogers (pers. comm.) is preparing an even more flexible system for scoring partial matches between attributes. Each character is to have a triangular matrix for its attribute pairs, which will be filled in by the taxonomist with whatever similarity values from 0 to 1 he considers appropriate to characterize the relationship or correlation of each attribute pair. By assigning values to attribute pairs, the taxonomist is in a sense estimating the probability of their intra-character taxonomic importance as indicators of relationship. Then, by summing these values, the correlation coefficient or index of similarity for a pair of taxa becomes the estimated probability of their relationship.

The model representing evolution in the Adiantoideae, and under which the evolutionary ground plan method worked, seems to be adequate for the task to which it has been put. There are, however, many other situations in which the model obviously would not describe the evolution of the group. For instance, if one were working with the species of a genus, it would be well to alter the model and, consequently, the method of analysis to include detection of hybrid OTU's and discovery of their probable parentage. Presumably the intermediacy

of hybrids between two (or more?) putative parents would be the criterion for separation from non-hybrid taxa. With the present scheme, hybrid OTU's should be excluded before attempting evolutionary ground plan diagram analysis. A hybrid OTU, which shares characteristics of both parents, will be placed as a descendant of one of the parents or as an antecedent of one or both. A reticulation on the diagram is impossible, and the investigator is given no substantial clue that the OTU is a hybrid.

The present computer method for constructing dendrograms from the data arrayed in similarity matrices does not always yield the most parsimonious possible dendrogram. Camin and Sokal have developed an as yet unpublished "Method for Deducing Phylogenies," presented at the meetings of the Society of Systematic Zoology held at Knoxville, Tennessee in December, 1964. The one empirical test of the method known to me was performed by Prof. T. H. Hubbell (unpublished lecture notes, The University of Michigan); the most parsimonious dendrogram resulted. But this was an analysis of simple data, without losses of advanced characteristics in distal OTU's, hybrids, or other complicating factors. More complex groups might presumably be treated with equal satisfaction. But the Camin and Sokal method, which is based on a character-by-character analysis and comparison, has one virtually fatal flaw. Among the working assumptions, which Hubbell states are ". . . regarded as probably true for the majority of characters and taxa, but known to have exceptions," is that the direction of evolutionary trends among the states of each character must be known, or the character cannot be used. It may be possible to

determine this direction for many binary characters, in which characteristics need be compared only two at a time. (Compare Sporne's pairing of characters and use of Chi-square to test their correlation in order to infer their primitiveness or advancedness.) But to demand such a prerequisite in multistate characters is to condemn the method to disuse. In the evolutionary ground plan diagram method all the advanced character states are lumped, because I was unable to devise any way of ordering multi-state characters into evolutionary trends. In my opinion, Camin and Sokal's method needs either an emendation to eliminate the need for foreknowing the direction of evolutionary trend or a new method for determining this trend. In either case it is regrettable that the question of evolutionary trends in characters was begged, since it is, by all accounts, a far more crucial question that the analysis of similarity matrices themselves.

Uses and Misuses of the Method

The evolutionary ground plan method, as it currently stands, is useful with groups of sufficient homogeneity and those which have several to many characters which show evolutionary trends. The method is most useful on taxonomic levels from genera to subfamilies or families, providing the groups are not too inhomogeneous. It is certainly a most useful technique with genera containing many species, although one could expect some erroneous placements of OTU's because of hybrids unless a method of detecting and eliminating hybrids were available. I think the method has little applicability in the classification of the higher taxonomic categories, for too few patterned

characters can be adduced. Similarly, it probably has little to offer on the subspecific levels, particularly in the study of phenomena like introgression and population analysis. Since it is an evolutionary method, its application where evolutionary trends are not expected would be a misuse. If merely a factor analytic method is desired, many others are more powerful than this.

One of the limiting factors in the use of the evolutionary ground plan method, as in ordinary phenetic numerical taxonomy, is the laboriousness of character and character state design and data accumulation. For the most part, a competent taxonomist can satisfactorily organize the species of a genus or the genera of a family without the use of quantitative methods. It is mostly those problems mentioned in the Introduction which make worthwhile the hours spent in the onerous tasks necessary to quantitative methods.

Using the ground plan method, either in its machine form or by hand, is like being on a taxonomic team. The silent, analytical partner sometimes confirms and sometimes denies one's preconceived notions about evolutionary relationships. The method is important in helping the taxonomist visualize the relationships of taxa. It aids in defining taxonomic groups, both as to included taxa and common characters. Sometimes it points to misplaced taxa.

I have found that the principal goal of the typological method, which is to construct the most probable archetypical plant of a natural group (see Danser, 1950, p. 125), has not been its most significant contribution to my knowledge of the Adiantoideae. Rather, it has been the visual display of OTU's representing genera and subgenera which

confirmed or made me revise my ideas about the relationships of these taxa. And in this connection the inaccuracies which have attended the transfer from the pre-evolutionary typological to evolutionary and neo-typological thought and from the archetypical plant to the most probable ancestral plant (see page 28 and Danser, 1950, pp. 158 and 162) lose some of their importance, because neither the archetype nor the ancestral plant plays an important part in forming ideas about the relationships of the taxa within the group.

Taxonomists are generally visual creatures; their data are based on visual observations. They do not often think in mathematical formulae or verbal expressions, which generally are but pale abstractions of their visual data. The evolutionary ground plan method permits easy communication of concepts which are hard to verbalize. It aids in communicating to others the structure of taxonomic groups and their probable evolutionary patterns.

APPENDIX A-1

LIST OF SPECIES WITH CODE NUMBERS

Explanation

OTU's for which only a partial data set was obtainable are indicated by *. Those which are not members of the Adiantoideae are marked #. Those members of the Adiantoideae which were used as adjacent group taxa for comparison with other tribes of the Adiantoideae are preceded by §. Code numbers follow the names.

List

#Acrostichum aureum L. (201) Copel. Herb. 1979 (MICH)

Actiniopteris australis (L.) Link (1) Rodin 4407 (US)

Adiantopsis capensis (Thunb.) Fée see Cheilanthes capensis (Thunb.) Swartz
A. dichotoma (Swartz) Moore see Cheilanthes dichotoma Swartz
A. radiata (L.) Fée (3) Maxon 2954 (US)
A. regularis (Mett.) Moore see Cheilanthes regularis Mett.

§Adiantum capillus-veneris L. (5) Bartlett 10471 (MICH)
A. caudatum L. (6) Ream 453 (MICH)
A. concinnum Humb. & Bonpl. ex Willd. (7) Downing (MICH)
A. flabellulatum L. (8) Tsang 21724 (MICH)
A. olivaceum Baker (9) Linden 9 (GH)

Afropteris barklyae (Baker in Hooker & Baker) Alst. (42) Meriau (US)

Aleuritopteris argentea (Gmel.) Fée (19) Smith (US)
A. duclouxii (Christ) Ching (21) Hancock 31 (US)
A. farinosa (Forsk.) Fée (10) Elmer 5889 (MICH)

#Ananthacorus angustifolius (Swartz) Underw. & Maxon (101) Taylor 1258 (MICH)

Appendix A-1 (continued)

Anogramma leptophylla (L.) Link (11) Baenitz (US)
A. microphylla (Hooker) Diels (12) Ex Herb. Hort. Bot. Calcutt. (GH)

Anopteris heterophylla (L.) Prantl (13) Maxon 9370 (US)

#Antrophyum plantagineum (Cav.) Kaulf. (102) St. John 18048 (MICH)

Argyrochosma nivea (Poir.) comb. ined. (49) Stuckert 11714 (MICH)
A. sulphurea (Cav.) comb. ined. (51) Orcutt 1852 (US)

Aspidotis californica (Nutt. ex Hook.) Copel. (14) Miller (US)
A. densa (Brack.) comb. ined. (24) Suksdorf (MICH)

Aspleniopsis decipiens (Mett.) Kuhn (15) Herb. Blanchard (US)

Bommeria pedata (Swartz) Fournier (16) McVaugh 16424 (US)

*Cerosora chrysosora (Baker) Domin (17)

Cheilanthes angustifolia H.B.K. (18) Palmer 177 (US)
C. argentea (Gmel.) Kunze see Aleuritopteris argentea (Gmel.) Fée
C. californica (Nutt. ex Hooker) Mett. see Aspidotis californica (Nutt. ex Hooker) Copel.
§C. capensis (Thunb.) Swartz (20) Esterhuysen 26260 (US)
C. dichotoma Swartz (2) Pedersen 989 (US)
C. duclouxii (Christ) Ching in C. Chr. see Aleuritopteris duclouxii (Christ) Ching
C. farinosa (Forsk.) Kaulf. see Aleuritopteris farinosa (Forsk.) Fée
C. inframarginalis (Kaulf. ex Link) Hooker see Mildella inframarginalis (Kaulf. ex Link) Trev.
C. lendigera (Cav.) Swartz (22) Pringle 3368 (MICH)
C. micropteris Swartz (23) Herter 882a (US)
C. regularis Mett. (4) Leite 3423 (MICH)
C. siliquosa Maxon see Aspidotis densa (Brack.) comb. ined.
C. straminea Brause see Cheilanthopsis indusiosa (Christ) Ching

*Cheilanthopsis indusiosa (Christ) Ching (25) Maire 6487 (US)

Cheiloplecton rigidum (Swartz) Fée (26) Palmer 729 (US)

Coniogramme fraxinea (Don) Diels (27) Levine, et al. 6821 (US)

Craspedodictyum quinatum (Hooker) Copel. see Syngramma quinata (Hooker) Carr. in Seem.

Cryptogramma acrostichoides R. Br. (29) Bolander 6241 (US)

Appendix A-1 (continued)

Doryopteris concolor (Langsd. & Fisch.) Kuhn (30) Tsang 23790 (US)
D. duclouxii Christ see Cheilanthes duclouxii (Christ) Ching
§D. lomariacea Klotzsch (31) Hatschbach 6431 (US)
D. pedata (L.) Fée var. palmata (Willd.) Hicken (32) Pittier 9473 (US)

Eriosorus elongatus (Hook. & Grev.) Copel. (33) Wiggins 10819 (US)
E. flexuosus (Humb. & Bonpl.) Copel. (34) Pittier 6263 (US)
E. hirtus (H.B.K.) Copel. (35) Wiggins 10985 (US)
E. lehmannii (Hieron.) comb. ined. (36) Lehmann (US)

Gymnopteris rufa (L.) Underw. (37) Lehmann 6017 (US)

Hemionitis palmata L. (38) Papenfuss (US)

Jamesonia cinnamomea Kunze (39) Cuatrecasas 20223 (F)
J. imbricata (Swartz) Hook. & Grev. var. glutinosa (Karst.) A. F. Tryon (40) Steyermark 57403 (F)
J. rotundifolia Fée (41) Haught 5652 (F)

#Lindsaya virescens Swartz (203) Wagner (MICH)

Llavea cordifolia Lagasca (43) White & Chatters 152 (MICH)

Mildella inframarginalis (Kaulf. ex Link) Trevisan (44) Purpus 241 (US)

#Mohria cafforum (L.) Desv. (401) Brass 16162 (US)

Negripteris scioana (Chiov.) Pic.-Serm. (45) Doflers 600 (GH)

Nephopteris ined. (46) Grubb & Guymer P-68 (US)

Neurosoria pteroides (R.Br.) Mett. in Kuhn (47) Flecker (MICH)

Notholaena fraseri (Mett.) Baker (48) Herrera 3295 (US)
N. nivea (Poir.) Desv. see Argyrochosma nivea (Poir.) comb. ined.
N. parryi Eaton (50) Clover 4255A (MICH)
N. sulphurea (Cav.) J. Smith see Argyrochosma sulphurea (Cav.) comb. ined.

Ochropteris pallens (Swartz) J. Smith (52) Zenker (F)

§Onychium japonicum (Thunb.) Kunze (53) McFadden 96699 (US)
O. siliculosum (Desv.) C. Chr. (54) Hoogland 3291 (US)

Ormopteris gleichenioides (Gardn.) J. Smith (55) Williams & Assis (GH)

*Paraceterach muelleri (Hooker) Copel. (56) Bancroft (MICH)

Appendix A-1 (continued)

Pellaea atropurpurea (L.) Link (57) Moore & Steyermark 3580 (MICH)
P. bridgesii Hooker (58) Constance 2361 (MICH)
P. densa Hooker see Aspidotis densa (Brack.) comb. ined.
P. doniana J. Smith ex Hooker (59) Peter 21251 (US)
P. falcata (R. Br.) Fée (60) Constable P2076 (US)
P. gleichenioides (Gardn.) Christ see Ormopteris gleichenioides (Gardn.) J. Smith
P. quadripinnata (Forsk.) Prantl (61) Mogg 857 (US)
P. rigida (Swartz) Hooker see Cheiloplecton ridigum (Swartz) Fée
P. skinneri Hooker (62) Smith 1087 (MICH)

§Pityrogramma calomelanos (L.) Link (63) McVaugh 11936 (US)
P. ferruginea (Kunze) Maxon (64) Steyermark 35197 (US)
P. humbertii C. Chr. (65) Humbert 8862 (US)
P. lehmannii (Hieron.) Tryon see Eriosorus lehmannii (Hieron.) comb. ined.
P. ornithopteris (Klotzsch) Maxon ex Kunth (66) Ariste-Joseph (US)
P. schizophylla (Jenman) Maxon (67) Leonard 4774 (US)
P. trifoliata (L.) R. M. Tryon (79) Killip 110 (US)

Platyzoma microphyllum R. Br. (68) Hubbard & Winders 6856 (US)

Pleurosoriopsis makinoi (Maxim in Makino) Fomin (69) Togasi (GH)

#Polytaenium lineatum (Swartz) J. Smith (103) Holdridge 1967 (MICH)

#Pteridium aquilinum (L.) Kuhn (202) Sallet (MICH)

#Pteris cretica L. (301) Mexia 9067 (MICH)
#P. quadriaurita Retz. (302) Bartlett 17443 (MICH)
#P. tremula R. Br. (303) Clemens (MICH)
#P. vittata L. (304) Walker et al. 7077 (MICH)

Pterozonium reniforme Fée (70) Schultes & Cabrera 13359 (US)
P. spectabile Maxon & Smith (71) Cardona 239 (US)

*Rheopteris cheesmaniae Alst. (80)

Saffordia induta Maxon (72) Sagástegui A. (GH)

*Sinopteris grevilleoides (Christ) C. Chr. & Ching (73)

§Syngramma alismifolia J. Smith (74) Molesworth-Allen 1851 (US)
S. borneensis (Hook.) J. Smith see Toxopteris borneensis (Hook.) Trev.
S. elaphoglossoides (Baker) Diels see Syngrammatopsis elaphoglossoides (Baker) Alst.
S. quinata (Hooker) Carr. in Seem. (28) Grether & Wagner 4146 (US)

Syngrammatopsis elaphoglossoides (Baker) Alst. (76) Steyermark 58362 (US)

Appendix A-1 (continued)

Taenitis blechnoides (Willd.) Swartz (77) Toroes 1699 (US)

Toxopteris borneensis (Hooker) Trevisan (75) Molesworth-Allen 3030 (US)

Trachypteris pinnata (Hooker f.) C. Chr. (78) Taylor 1211 (US)

Trismeria trifoliata (L.) Diels see Pityrogramma trifoliata (L.) R. M. Tryon

#Vittaria lineata (L.) J.E. Smith (104) Pringle 5579 (MICH)

APPENDIX A-2

LIST OF CHARACTERS AND ATTRIBUTES

Summary

Rhizome:	General	1- to	5-
	Principal vestiture	6- to	15-
	Secondary vestiture	16-	
	Glands	17-	
Root:	General	18- to	24-
Frond:	General	25-	
Stipe:	General	26- to	30-
	Principal vestiture	31- to	40-
	Secondary vestiture	41-	
	Glands	42- to	43-
Rhachis:	General	44- to	48-
	Principal vestiture	49- to	55-
	Secondary vestiture	56- to	62-
	Glands	63- to	64-
Lamina:	General	65- to	71-
	Pinnae	72- to	78-
	Upper surface	79- to	87-
	Lower surface	88- to	98-
	Sori	99- to	102-
	Indusia	103- to	107-
	Glands	108-	

Explanation

Each character is listed as a group of binary characters. For example, Character 1 with seven states is binary character number (BCNR) 10 through 16; Character 108 with six states is BCNR 1080 through 1085.

Only fertile fronds of dimorphic species were coded.

Appendix A-2 (continued)

Observations were made with the unaided eye, a simple hand lens, or a dissecting microscope. Where particular magnifications are noted, the dissecting microscope was used. In addition, cellular detail of indument, for instance, was sometimes checked with a compound microscope.

Phrases modifying the character names or attribute names are in parentheses. Alternate terminology is in brackets.

List

BCNR 1- RHIZOME: habit
10 absent
11 erect
12 clustered-erect [multicipital]
13 erect-ascending
14 short creeping--ascending
15 short creeping (≤5 times as long as wide)
16 long creeping (>5 times as long as wide)

BCNR 2- RHIZOME: secondary axes [primary axes with "spur branches"]
20 absent
21 present

BCNR 3- RHIZOME: branching of primary axes
30 absent
31 occasional (≤1 per 3 cm. of length) and equal forking
32 frequent (>1 per 3 cm. of length) and equal forking
33 occasional monopodial
34 frequent monopodial

BCNR 4- RHIZOME: diameter in mm.
40 absent
41 ≤1
42 >1 - ≤2
43 >2 - ≤3
44 >3 - ≤4
45 >4 - ≤6
46 >6 - ≤8
47 >8 - ≤10
48 >10

Appendix A-2 (continued)

BCNR 5- RHIZOME: coloration (13X)
50 absent
51 black
52 purple-black [atropurpureous]
53 dark brown
54 brown
55 tan
56 reddish brown
57 cream to ivory
58 light yellow

BCNR 6- RHIZOME: principal vestiture, abundance
60 absent
61 few trichomes scattered or locally abundant on the rhizome
62 many trichomes more or less covering the rhizome
63 abundant trichomes overlapping on the rhizome

BCNR 7- RHIZOME: principal vestiture, maximum length in mm.
70 absent
71 ≤2
72 >2 - ≤4
73 >4 - ≤6
74 >6

BCNR 8- RHIZOME: principal vestiture, shape
80 absent
81 filiform hairs [bristles]
82 linear uniseriate scales [flattened hairs]
83 alternately flattened uniseriate scales [catenate hairs]
84 attenuate, triangular scales, >6 times longer than wide
85 attenuate, triangular scales, >3 - ≤6 times longer than wide
86 attenuate, triangular scales, ≤3 times longer than wide
87 lanceolate scales, narrowed distinctly at base

BCNR 9- RHIZOME: principal vestiture, texture
90 absent
91 scarious to membranaceous (flexible)
92 thin (moderately stiff)
93 thick (stiff)
94 very thick (obviously 3-dimensional at low magnifications)

BCNR 10- RHIZOME: principal vestiture, reflectability (13X)
100 absent
101 dull (no spectral highlights)
102 rather shiny (scattered, patchy spectral highlights)
103 very shiny (more or less uniform spectral highlights)

Appendix A-2 (continued)

BCNR 11- RHIZOME: principal vestiture, most common cell shape
110 absent
111 rectangular, isodiametric, or round, side walls straight
112 elongate with perpendicular ends, side walls straight
113 elongate with oblique ends, side walls straight
114 elongate with spindle shaped ends, side walls straight
115 elongate with wavy side walls

BCNR 12- RHIZOME: principal vestiture, margins
120 absent
121 smooth
122 wavy or irregular
123 crisped
124 short ciliate

BCNR 13- RHIZOME: principal vestiture, concolorous color (13X by reflected light)
130 absent or vestiture bicolorous
131 black
132 dark brown
133 tan
134 reddish brown
135 purple-black [atropurpureous]
136 whitish
137 yellow-tan

BCNR 14- RHIZOME: principal vestiture, bicolorous marginal color (13X by reflected light)
140 absent or vestiture concolorous
141 black
142 brown
143 tan
144 reddish brown
145 purple-black [atropurpureous]
146 whitish
147 yellow-tan

BCNR 15- RHIZOME: principal vestiture, bicolorous central color (13X by reflected light)
150 absent or vestiture concolorous
151 black
152 dark brown
153 tan
154 reddish brown
155 purple-black [atropurpureous]
156 whitish
157 yellow-tan

BCNR 16- RHIZOME: secondary vestiture
160 absent
161 scales of morphology similar to hairs
162 scales of morphology different from hairs

Appendix A-2 (continued)

BCNR 17- RHIZOME: glands
170 absent
171 present

BCNR 18- ROOT: maximum diameter in mm. (13X or 30X)
180 absent
181 ≤0.30
182 >0.30 - ≤ 0.60
183 >0.60 - ≤ 0.90
184 >0.90

BCNR 19- ROOT: color (13X)
190 absent
191 black
192 dark brown
193 brown
194 golden brown
195 reddish brown
196 purple-black [atropurpureous]

BCNR 20- ROOT: surface sculpturing type (30X, with material at a right angle to the illuminating beam)
200 absent
201 smooth
202 minutely fluted (>3.5 corrugations per 0.1 mm.)
203 ---
204 fluted (>1 - ≤3.5 corrugations per 0.1 mm.)
205 coarsely fluted (>0.5 - ≤ 1 corrugation per 0.1 mm.)
206 ridged (≤0.5 corrugations per 0.1 mm.)
207 pitted [roughened]

BCNR 21- ROOT: surface sculpturing regularity (30X)
210 absent
211 regular
212 rather irregular
213 irregular

BCNR 22- ROOT: hair cross-section (30X)
220 absent
221 cylindrical or elliptical
222 ---
223 flattened or strongly flattened

BCNR 23- ROOT: hair morphology (30X)
230 absent
231 straight
232 wavy
233 crinkly
234 crisped
235 twisted

Appendix A-2 (continued)

BCNR 24- ROOT: hair color (30X by reflected light)
- 240 absent
- 241 brown
- 242 golden [golden bronze]
- 243 tan
- 244 reddish brown
- 245 yellow
- 246 translucent white

BCNR 25- FROND: stipe/rhachis length coefficient
- 250 absent
- 251 ≤0.5
- 252 >0.5 - ≤1
- 253 >1 - ≤1.5
- 254 >1.5 - ≤2
- 255 >2 - ≤3
- 256 >3 - ≤4
- 257 >4
- 258 indefinite because rhachis is indeterminate

BCNR 26- STIPE: cross-section midway between base and lamina
- 260 absent
- 261 round winged
- 262 round, elliptical, or square
- 263 round with flattened (or flattened-winged) side
- 264 round grooved
- 265 U-shaped or W-shaped
- 266 V-shaped or Y-shaped
- 267 square grooved
- 268 X-shaped or X-shaped

BCNR 27- STIPE: maximum width at midpoint in mm.
- 270 absent
- 271 ≤0.5
- 272 >0.5 - ≤1
- 273 >1 - ≤1.5
- 274 >1.5 - ≤2
- 275 >2 - ≤2.5
- 276 >2.5

BCNR 28- STIPE: surface sculpturing (30X, with material at a right angle to the illuminating beam)
- 280 absent
- 281 smooth (not necessarily shiny)
- 282 more or less tuberculate with vestiture bases
- 283 irregularly roughened
- 284 striate [minutely fluted]
- 285 fluted
- 286 ridged [grossly fluted]

Appendix A-2 (continued)

BCNR 29- STIPE: ground color (13X)
290 absent
291 reddish brown
292 brown
293 purple-black [atropurpureous]
294 black
295 straw-colored [stramineous]
296 greenish
297 straw-colored to reddish brown

BCNR 30- STIPE: striping (30X)
300 absent (stipe or rhachis absent)
301 scarcely or obscurely striped
302 minutely striped (≥3 stripes per 0.1 mm.)
303 obviously striped (<3 stripes per 0.1 mm.)
304 not striped

BCNR 31- STIPE: principal vestiture, longitudinal abundance and position (13X)
310 absent
311 few proximal and few distal
312 many proximal and few or none distal
313 many distal and few or none proximal
314 many proximal and many distal
315 few proximal and none distal

BCNR 32- STIPE: principal vestiture, radial position (13X or 30X)
320 absent
321 evenly distributed
322 rarely adaxial
323 mostly adaxial
324 entirely adaxial
325 entirely abaxial

BCNR 33- STIPE: principal vestiture, maximum length in mm.
330 absent
331 ≤0.5
332 >0.5 - ≤1
333 >1 - ≤1.5
334 >1.5 - ≤2
335 >2 - ≤3
336 >3 - ≤4
337 >4 - ≤6
338 >6

Appendix A-2 (continued)

BCNR 34- STIPE: principal vestiture, shape
340 absent
341 cylindrical, acicular, or flattened unicellular hairs
342 cylindrical, acicular, or flattened multicellular hairs
343 alternately-flattened uniseriate scales [catenate hairs]
344 linear uniseriate scales [flattened hairs]
345 attenuate, triangular scales, >6 times longer than wide
346 attenuate, triangular scales, >3 - ≤6 times longer than wide
347 attenuate, triangular scales, ≤3 times longer than wide
348 lanceolate scales, narrowed distinctly at base

BCNR 35- STIPE: principal vestiture, gross aspect
350 absent
351 straight or smooth
352 wavy (mostly in hairs) or twisted (mostly in scales)
353 crinkly

BCNR 36- STIPE: principal vestiture, cell wall thickening
360 absent
361 even all around
362 thickened at ends only
363 thickened at corners only
364 thickened along sides only

BCNR 37- STIPE: principal vestiture, texture
370 absent
371 membranaceous (flexible)
372 thin (moderately stiff)
373 thick (stiff)
374 very thick (obviously 3-dimensional at low magnifications)

BCNR 38- STIPE: principal vestiture, concolorous color
(13X by reflected light)
380 absent
381 black
382 brown
383 tan
384 yellow to tan
385 reddish brown
386 purple-black [atropurpureous]
387 whitish
388 clear

Appendix A-2 (continued)

BCNR 39- STIPE: principal vestiture, bicolorous central color (13X by reflected light)
- 390 absent
- 391 black
- 392 reddish brown
- 393 purple-black [atropurpureous]
- 394 brown
- 395 tan
- 396 yellow tan
- 397 whitish
- 398 clear

BCNR 40- STIPE: principal vestiture, bicolorous marginal color (13X by reflected light)
- 400 absent
- 401 brown
- 402 tan
- 403 yellow to tan

BCNR 41- STIPE: secondary vestiture type
- 400 absent
- 401 cylindrical, acicular, or flattened unicellular hairs
- 402 cylindrical, acicular, or flattened multicellular hairs
- 403 alternately-flattened uniseriate scales [catenate hairs]
- 404 linear uniseriate scales [flattened hairs]
- 405 attenuate, triangular scales, >6 times longer than wide
- 406 attenuate, triangular scales, >3 - ≤6 times longer than wide
- 407 attenuate, triangular scales, ≤3 times longer than wide
- 408 lanceolate scales, narrowed distinctly at base

BCNR 42- STIPE: glands, morphology
- 420 absent
- 421 unstalked [globular]
- 422 linear
- 423 linear to clavate
- 424 clavate
- 425 capitate

BCNR 43- STIPE: glands, wax color
- 430 absent
- 431 white
- 432 yellow

BCNR 44- RHACHIS: maximum width at midpoint in mm.
- 440 absent
- 441 ≤0.5
- 442 >0.5 - ≤1
- 443 >1 - ≤1.5
- 444 >1.5 - ≤2
- 445 >2

Appendix A-2 (continued)

BCNR 45- RHACHIS: cross-section at midpoint
- 450 absent
- 451 round or elliptical
- 452 round with flattened (or flattened-winged) side
- 453 round grooved
- 454 round winged
- 455 U-shaped or W-shaped (may be winged in plane of the blade)
- 456 X-shaped or X-shaped
- 457 Y-shaped
- 458 square or square grooved

BCNR 46- RHACHIS: surface, color (13X)
- 460 absent
- 461 reddish brown
- 462 brown
- 463 straw-colored [stramineous]
- 464 tan
- 465 purple-black [atropurpureous]
- 466 black
- 467 straw-colored to tan or brown
- 468 green

BCNR 47- RHACHIS: surface, striping (30X)
- 470 not striped
- 471 slightly or obscurely striped
- 472 minutely striped (>4 lines per 0.1 mm.)
- 473 obviously striped (≤4 lines per 0.1 mm.)
- 474 spindle-shaped striped
- 475 not striped because rhachis absent

BCNR 48- RHACHIS: surface, sculpturing
- 480 absent
- 481 smooth
- 482 smooth with scattered tubercles
- 483 irregularly roughened
- 484 fluted

BCNR 49- RHACHIS: principal vestiture, abundance and longitudinal distribution
- 490 absent
- 491 few proximal and few distal
- 492 many proximal and few or none distal
- 493 many distal and few or none proximal
- 494 many proximal and many distal
- 495 few proximal and none distal

BCNR 50- RHACHIS: principal vestiture, radial distribution
- 500 absent
- 501 evenly distributed
- 502 mostly adaxial
- 503 entirely adaxial
- 504 mostly abaxial
- 505 entirely abaxial

Appendix A-2 (continued)

BCNR 51- RHACHIS: principal vestiture, maximum length in mm.
510 absent
511 ≤0.5
512 >0.5 - ≤1
513 >1 - ≤1.5
514 >1.5 - ≤1
515 >2

BCNR 52- RHACHIS: principal vestiture shape
520 absent
521 cylindrical, acicular, or flattened unicellular hairs
522 cylindrical, acicular, or flattened multicellular hairs
523 alternately-flattened uniseriate scales [catenate hairs]
524 linear uniseriate scales [flattened hairs]
525 attenuate, partially or wholly multiseriate scales
526 lanceolate scales, narrowed distinctly at base

BCNR 53- RHACHIS: principal vestiture, gross aspect
530 absent
531 straight or smooth
532 curved
533 wavy or twisted
534 crinkly

BCNR 54- RHACHIS: principal vestiture, cell wall thickening (30X or higher)
540 absent
541 even all around
542 at ends only
543 along sides only
544 at corners only

BCNR 55- RHACHIS: principal vestiture, color (central stripe, if scale bicolorous; 30X by reflected light)
550 absent
551 black
552 brown
553 tan
554 yellow-tan
555 reddish brown
556 purple-black [atropurpureous]
557 whitish
558 clear

BCNR 56- RHACHIS: secondary vestiture, abundance and longitudinal position
560 absent
561 few proximal and few distal
562 many proximal and few or none distal
563 many distal and few or none proximal
564 many proximal and many distal
565 few proximal and none distal

Appendix A-2 (continued)

BCNR 57- RHACHIS: secondary vestiture, radial distribution
570 absent
571 evenly distributed
572 entirely abaxial
573 mostly abaxial
574 mostly adaxial
575 entirely adaxial

BCNR 58- RHACHIS: secondary vestiture, max. length in mm.
580 absent
581 ≤0.5
582 >0.5 - <1
583 >1 - <1.5
584 >1.5 - <2
585 >2

BCNR 59- RHACHIS: secondary vestiture, shape
590 absent
591 cylindrical, acicular, or flattened unicellular hairs
592 cylindrical, acicular, or flattened multicellular hairs
593 alternately-flattened uniseriate scales [catenate hairs]
594 linear uniseriate scales [flattened hairs]
595 attenuate, partially or wholly multiseriate scales
596 lanceolate scales, narrowed distinctly at base

BCNR 60- RHACHIS: secondary vestiture, gross aspect
600 absent
601 straight or smooth
602 curved
603 wavy or twisted
604 crinkly

BCNR 61- RHACHIS: secondary vestiture, cell wall thickening
610 absent
611 even all around
612 at ends only
613 along sides only
614 at corners only

BCNR 62- RHACHIS: secondary vestiture, color (central stripe, if scale bicolorous; 30X by reflected light)
620 absent
621 black
622 brown
623 tan
624 yellow-tan
625 reddish brown
626 purple-black [atropurpureous]
627 whitish or clear
628 tan or clear with brown or tan cell wall (ends only)

Appendix A-2 (continued)

BCNR 63- RHACHIS: glands, morphology
630 absent
631 unstalked [globular]
632 linear
633 linear to clavate
634 clavate
635 capitate

BCNR 64- RHACHIS: glands, wax color
640 absent
641 white
642 yellow
643 tan

BCNR 65- LAMINA: average length/width coefficient
650 absent
651 ≤1
652 >1 - ≤1.5
653 >1.5 - ≤2
654 >2 - ≤3
655 >3 - ≤4
656 >4 - ≤10
657 >10
658 indeterminate frond growth

BCNR 66- LAMINA: length from widest point to apex/length from widest point to base coefficient
660 absent
661 ≤0.25
662 >0.25 - ≤0.5
623 >0.5 - ≤1
624 >1 - ≤2
625 >2 - ≤4
626 >4 - ≤7
627 >7
628 indeterminate frond growth

BCNR 67- LAMINA: general outline type
670 absent
671 parallel-sided [linear, oblong]
672 long and pointed [long-attenuate, lanceolate]
673 rounded and vertically asymmetrical [ovate, long-ovate]
674 rounded and vertically symmetrical [elliptic, orbiculate]
675 rounded-triangular [deltoid-lanceolate, deltoid]
676 angular-pentagonal [subpentagonal, pentagonal]
677 angular non-pentagonal [triangular, obtriangular, quadrangular, hastate-quadrangular]

Appendix A-2 (continued)

BCNR 68- LAMINA: base outline type
680 absent
681 attenuate
682 cuneate
683 acute
684 obtuse
685 truncate
686 rounded
687 indented [cordate, hastate]

BCNR 69- LAMINA: apex outline type
690 absent
691 attenuate
692 acute
693 obtuse
694 rounded

BCNR 70- LAMINA: degree of dissection
700 absent
701 simple to pinnatisect
702 pinnatifid to 1-pinnate
703 1-pinnate-pinnatifid to 2-pinnate
704 2-pinnate-pinnatifid to 3-pinnate
705 3-pinnate-pinnatifid to 4-pinnate
706 4-pinnate-pinnatifid to 5-pinnate
707 >5-pinnate

BCNR 71- LAMINA: texture
710 absent
711 herbaceous
712 intermediate
713 coriaceous

BCNR 72- LAMINA: pinnae, average number
720 absent (frond less than pinnately divided)
721 >1 - ≤4
722 >4 - ≤8
723 >8 - ≤14
724 >14 - ≤22
725 >22 - ≤32
726 >32 - ≤44
727 >44
728 indeterminate frond growth

BCNR 73- LAMINA: pinnae, arrangement of fully developed "pairs"
730 absent (frond less than pinnately divided)
731 opposite
732 opposite to subopposite
733 opposite to alternate
734 alternate
735 digitate
736 alternate to subopposite
737 subopposite

Appendix A-2 (continued)

BCNR 74- LAMINA: pinnae, attachment to rhachis
740 absent (frond less than pinnately divided)
741 not decurrent and not winged
742 slightly decurrent and not winged
743 decurrent and not winged
744 decurrent and with basipetal wings
745 decurrent and with both basipetal and acropetal wings
746 decurrent and with acropetal wings

BCNR 75- LAMINA: pinnae, usual angle of attachment
750 absent (frond less than pinnately divided)
751 30°
752 30° - 45°
753 45°
754 45° - 60°
755 60°
756 45° - 90°
757 60° - 90° (sometimes in a double bend)
758 90°

BCNR 76- LAMINA: pinnae, typical supra-basal, shape
760 absent (frond less than pinnately divided)
761 lanceolate (rounded at base) [triangular to lanceolate, ovate-lanceolate, asymmetrical deltoid lanceolate]
762 triangular (truncate at base) [asymmetrical deltoid, hemitriangular, obtriangular]
763 parallel sided [attenuate distally]
764 ovate or elliptical
765 basally truncate ovate or elliptical
766 rounded or lobed, and always small
767 beadlike
768 rounded or lobed, and always large

BCNR 77- LAMINA: pinnules or ultimate segments, attachment
770 absent (frond less than pinnate-pinnatifidly divided)
771 short-stalked or long-stalked and neither winged nor decurrent
772 winged acropetally and/or basipetally, but not decurrent
773 not winged, but decurrent
774 winged basipetally and decurrent
775 winged acropetally and basipetally and decurrent
776 winged acropetally and decurrent

Appendix A-2 (continued)

BCNR 78- LAMINA: pinnules or ultimate segments, shape
780 absent (frond less than pinnate-pinnatifidly divided)
781 parallel-sided
782 more or less lanceolate
783 ovate or elliptical
784 triangular
785 obovate, oblanceolate, or obtriangular
786 variously rounded and lobed
787 beadlike
788 quadrangular

BCNR 79- LAMINA: upper surface sculpturing (30X)
790 absent
791 irregularly roughened
792 irregularly papillose
793 regularly papillose
794 ---
795 striate [elongate papillose]
796 minutely pitted

BCNR 80- LAMINA: upper surface, principal vein position
800 absent
801 immersed
802 impressed
803 impressed-channeled
804 flush
805 slightly superficial
806 superficial
807 superficial-channeled

BCNR 81- LAMINA: upper surface, scale shape
810 absent
811 attenuate, partially or wholly multiseriate
812 lanceolate
813 uniseriate scale (reduced scales only one cell wide)

BCNR 82- LAMINA: upper surface, scale color
820 absent
821 brown
822 tan
823 whitish or translucent

BCNR 83- LAMINA: upper surface, scale distribution
830 absent
831 on costae and/or costules
832 on both costae and/or costules and on laminae
833 on laminae

Appendix A-2 (continued)

BCNR 84- LAMINA: upper surface, scale abundance
840 absent
841 rare
842 occasional (on ≤25% of surface)
843 frequent (on >25% of surface)

BCNR 85- LAMINA: upper surface, hair shape
850 absent
851 unicellular
852 acicular or flattened multicellular
853 cylindrical multicellular
854 alternately flattened multicellular [catenate]

BCNR 86- LAMINA: upper surface, hair distribution
860 absent
861 on costae and/or costules
862 on laminae
863 on both costae and/or costules and on laminae

BCNR 87- LAMINA: upper surface, hair abundance
870 absent
871 few, scattered
872 frequent, the surface clearly showing through
873 many, more or less densely covering the surface

BCNR 88- LAMINA: lower surface, sculpturing (30X)
880 absent
881 irregularly roughened
882 irregularly papillose
883 regularly papillose
884 striate [elongate papillose]
885 minutely pitted
886 smooth

BCNR 89- LAMINA: lower surface, principal vein position
890 absent
891 immersed
892 flush
893 slightly superficial
894 superficial
895 subsurface visible

BCNR 90- LAMINA: lower surface, side vein position
900 absent
901 immersed
902 subsurface visible
903 flush
904 superficial
905 impressed

Appendix A-2 (continued)

BCNR 91- LAMINA: lower surface, scale shape
- 910 absent
- 911 attenuate, partially or wholly multiseriate
- 912 lanceolate
- 913 uniseriate scale (reduced scales only one cell wide)

BCNR 92- LAMINA: lower surface, scale color
- 920 absent
- 921 white
- 922 tan
- 923 purple-black [atropurpureous]

BCNR 93- LAMINA: lower surface, scale distribution
- 930 absent
- 931 on costae and/or costules
- 932 on laminae
- 933 on both costae and/or costules and on laminae
- 934 on receptacles
- 935 on sporangia

BCNR 94- LAMINA: lower surface, scale abundance
- 940 absent
- 941 few, scattered over the surface or locally abundant
- 942 many, covering the surface more than 25%

BCNR 95- LAMINA: lower surface, hair shape
- 950 absent
- 951 unicellular
- 952 flattened, multicellular
- 953 cylindrical multicellular
- 954 alternately flattened multicellular [catenate]

BCNR 96- LAMINA: lower surface, hair color
- 960 absent
- 961 clear
- 962 white
- 963 tan
- 964 white or clear with tan or brown cell wall (ends only)
- 965 black with white patches
- 966 reddish brown

BCNR 97- LAMINA: lower surface, hair distribution
- 970 absent
- 971 on costae and/or costules
- 972 on laminae
- 973 on both costae and/or costules and on laminae
- 974 on receptacles only or in fertile areas, if fronds acrostichoid
- 975 on sporangia

Appendix A-2 (continued)

BCNR 98- LAMINA: lower surface, hair abundance
- 980 absent
- 981 few, scattered over the surface or locally abundant
- 982 frequent, the surface clearly showing through
- 983 many, more or less densely covering the surface
- 984 abundant as paraphyses, in fertile areas only

BCNR 99- LAMINA: sori, abundance and distribution
- 990 absent
- 991 more or less entire fronds fertile
- 992 few pinnae of fronds fertile
- 993 fertile areas scattered
- 994 more or less entire plant fertile

BCNR 100- LAMINA: sori, shape
- 1000 absent
- 1001 round or oval (length:width 1:1 - 2:1)
- 1002 elongate (length:width 2:1 - 5:1)
- 1003 linear (length:width >5:1)
- 1004 linear appearing pseudoacrostichoid (length:width >5:1)
- 1005 shapeless because either pseudoacrostichoid or acrostichoid
- 1006 shapeless because more or less monangial

BCNR 101- LAMINA: sori, position with reference to margin
- 1010 absent
- 1011 marginal (sori restricted to the margin)
- 1012 inframarginal (sori restricted to a band behind the margin)
- 1013 submarginal (sori spreading backwards from the margin)
- 1014 supralaminar (sori on the lamina in general)
- 1015 indusial (sori restricted to the indusium)

BCNR 102- LAMINA: sori, position with reference to veins
- 1020 absent
- 1021 terminal
- 1022 subterminal
- 1023 commissural
- 1024 dorsal
- 1025 not restricted to veins

BCNR 103- LAMINA: indusia, origin
- 1030 absent
- 1031 marginal underrolling
- 1032 marginal outgrowth from the lamina
- 1033 submarginal outgrowth from the lamina

Appendix A-2 (continued)

BCNR 104- LAMINA: indusia, lateral extent
1040 absent
1041 continuous (each indusium covers many discrete sori)
1042 subcontinuous (each indusium covers 2--a few discrete sori)
1043 discrete (each indusium covers 1 discrete sorus)
1044 syndusium (each covers a synangium or fertile area composed of fused, discrete sori)

BCNR 105- LAMINA: indusia, margins
1050 absent
1051 smooth
1052 erose
1053 crenulate
1054 ciliate
1055 laciniate

BCNR 106- LAMINA: indusia, texture
1060 absent
1061 scarious to thin
1062 membranaceous
1063 membranaceous and glandular or pustulose
1064 thick

BCNR 107- LAMINA: indusia, color
1070 absent
1071 white or clear
1072 tan to white
1073 straw-colored [stramineous]
1074 tan
1075 tan to brown
1076 light green to white
1077 light green
1078 light green to tan

BCNR 108- glands, shape
1080 absent
1081 linear
1082 clavate
1083 capitate
1084 globular-based linear
1085 unstalked [globular]

APPENDIX B-1

DESCRIPTION SURVEY SHEET

Name:
Coll. & No.: Herb. & No.:
Locality: Habitat:
Type of: Reference:

I. RHIZOMES
  A. Habit
  B. Branching
  C. Length
  D. Diameter
  E. Coloration
  F. Scales
    1. Abundance
    2. Attachment
    3. Size
    4. Shape
    5. Texture & surface
    6. Margins
    7. Color
    8. Cell structure
  G. Hairs
  H. Glands
II. ROOTS
  A. Diameter
  B. Color
  C. Surface
  D. Hairs
III. FRONDS
  A. Number
  B. Attachment
  C. Length
IV. STIPES
  A. Length & width
  B. Cross-section
  C. Surface
  D. Scales
  E. Hairs
  F. Glands
V. MAIN RHACHISES
  A. Length & width
  B. Cross-section
  C. Surface
  D. Scales
  E. Hairs
  F. Glands

Appendix B-1 (continued)

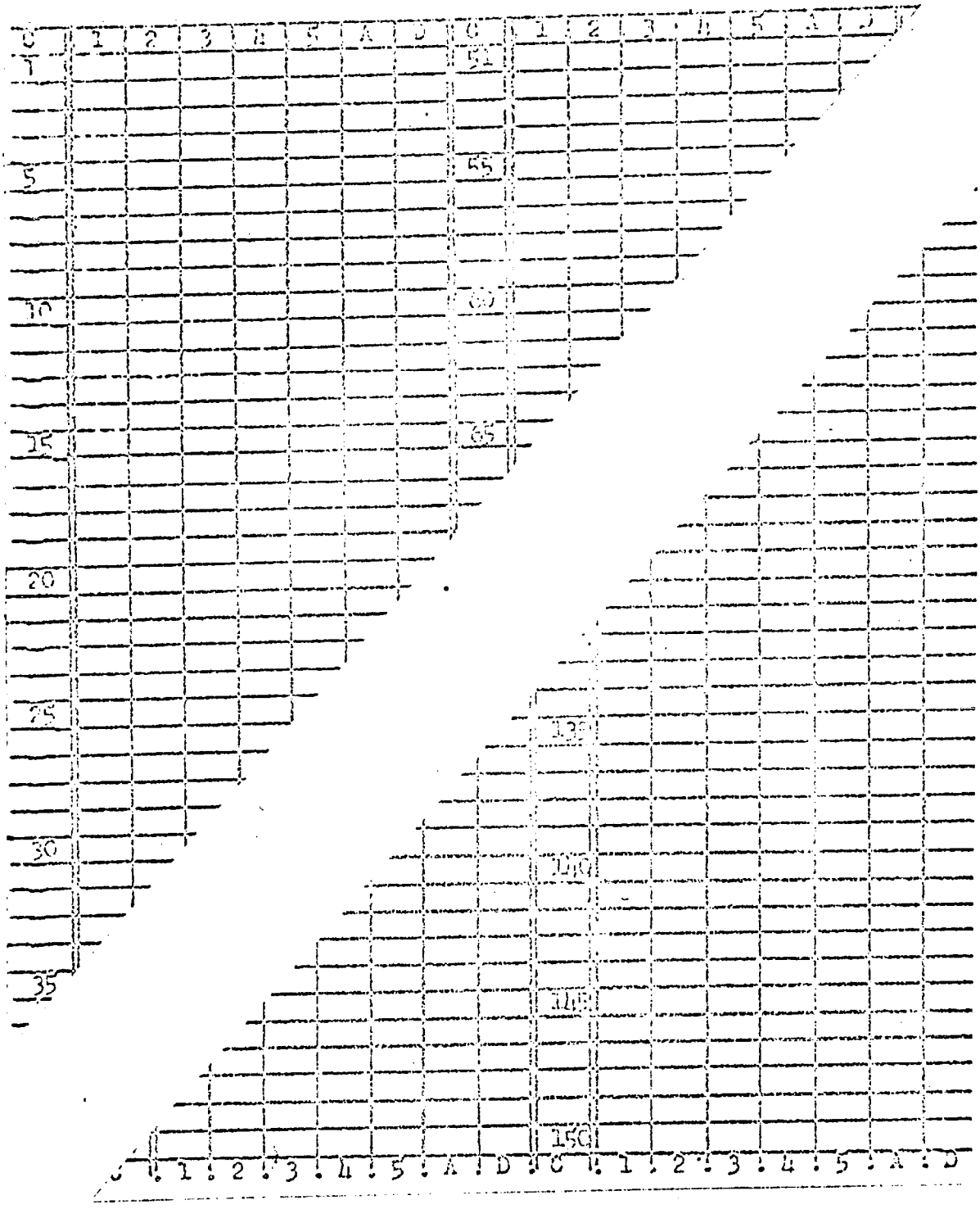
VI. LAMINAS
- A. Length & width
- B. Growth
- C. Outline
- D. Dissection
- E. Texture
- F. Pinnae
  - 1. Number
  - 2. Attachment
  - 3. Direction
  - 4. Dissection
  - 5. Shape
- G. Pinnules or ultimate segments
  - 1. Attachment
  - 2. Shape
  - 3. Upper surface
    - a. Scales
    - b. Hairs
  - 4. Lower surface
    - a. Scales
    - b. Hairs
- H. Sori
  - 1. Abundance
  - 2. Position
  - 3. Shape
  - 4. Size
- I. Indusia
  - 1. Origin
  - 2. Shape
  - 3. Color
  - 4. Texture
- J. Glands

APPENDIX B-2

CHARACTER STATE RECORDING SHEET

Taxon:
Representative of:

Sheet Number Of



APPENDIX B-3

CORRELATION COEFFICIENT WORKSHEET

Taxon: ID Number:

1 x 2 $\Sigma X =$ $N =$ $\Sigma Y =$
$\Sigma X^2 =$ $2\Sigma XY =$ $\Sigma Y^2 =$

$$\frac{\qquad\qquad}{\sqrt{\qquad\qquad}\sqrt{\qquad\qquad}} = \frac{\qquad\qquad}{\qquad\qquad} = \frac{\qquad\qquad}{\qquad\qquad} = 0.$$

1 x 3 $\Sigma X =$ $N =$ $\Sigma Y =$
$\Sigma X^2 =$ $2\Sigma XY =$ $\Sigma Y^2 =$

$$\frac{\qquad\qquad}{\sqrt{\qquad\qquad}\sqrt{\qquad\qquad}} = \frac{\qquad\qquad}{\qquad\qquad} = \frac{\qquad\qquad}{\qquad\qquad} = 0.$$

2 x 3 $\Sigma X =$ $N =$ $\Sigma Y =$
$\Sigma X^2 =$ $2\Sigma XY =$ $\Sigma Y^2 =$

$$\frac{\qquad\qquad}{\sqrt{\qquad\qquad}\sqrt{\qquad\qquad}} = \frac{\qquad\qquad}{\qquad\qquad} = \frac{\qquad\qquad}{\qquad\qquad} = 0.$$

APPENDIX C

BINARY I X M TABLE FOR THE ADIANTOIDEAE

APPENDIX C (continued)

```
BNCR  92   0 1010 001 0  1010 0000 1 000 0010  0011C CCC110  CC111CCCC 100 1  CC1101 11101110001  01010  1
BNCR  93   1 0000 010 1  0101 1111 0 111 1001  10000 C10000  C1000000C 010 0  01CC1C 00001000C  00101  0
BNCR  54   0 0000 000 0  0000 0001 0 000 0000  00000 C00000  C0000000C 000 0  CCCCCC CCCCCCCCC  00000  0
BNCR  100  0 0000 000 0  0000 0000 0 000 0000  00000 C00000  C0000000C 000 0  CCCCCC CCCCCCCCC  00000  0
BNCR  101  0 0011 001 1  0010 0101 1 000 0110  00101 110001  1CCCCCC011 110 1  CCCCCC CCCCCCCCC  00000  0
BNCR  102  1 0000 110 0  0100 0001 0 100 1001  11010 001111  1CCCCC0100 C01 0  CCCCC1 C1CC011CCC  11101  0
BNCR  103  0 1000 000 0  1100 0011 0 011 0000  11000 000000  C1111CCCC 000 0  011100 1111CCC111  00010  1
BNCR  110  0 1110 000 0  0000 0000 0 000 0000  00000 000000  C0000000C 000 0  CCCCCC CCCCCCCCC  00000  0
BNCR  111  0 0000 000 0  0000 0001 0 000 0000  00000 000000  C0000000C 000 0  CCCCCC CCCCCCCCC  00000  0
BNCR  112  0 1000 001 0  0100 0001 0 100 0001  10000 000001  1CCCCC0001 C01 1  CCCCC1 CCCCCCCCC  00001  0
BNCR  113  0 1000 100 1  0100 0001 0 100 0001  10000 000001  1CCCCC0001 C01 1  CCCCC1 CCCCCCCCC  00001  0
BNCR  114  1 0001 000 0  0000 0000 0 000 0000  00000 000000  C0000000C 000 0  CCCCCC CCCCCCCCC  00000  0
BNCR  115  0 0000 000 0  0000 0000 0 000 0000  00000 000000  C0000000C 000 0  CCCCCC CCCCCCCCC  00000  0
BNCR  120  0 0100 000 0  0000 0000 0 000 0000  00000 000000  C0000000C 000 0  CCCCCC CCCCCCCCC  00000  0
BNCR  121  1 1001 111 1  1111 1110 1 111 0001  11110 100111  1CCCCC0111 101 1  CCCCCC CCCCCCCCC  00000  0
BNCR  122  0 0010 000 0  0000 0000 0 000 0000  00000 000000  C0000000C 000 0  CCCCCC CCCCCCCCC  00000  0
BNCR  124  0 0000 000 0  0000 0000 0 000 0000  00000 000000  C0000000C 000 0  CCCCCC CCCCCCCCC  00000  0
BNCR  130  1 0100 100 0  1010 0001 0 100 1011  11101 111111  1CCCCC0111 111 1  CCCCCC CCCCCCCCC  00000  0
BNCR  131  0 0000 011 1  0000 0000 0 000 0000  00000 000000  C0000000C 000 0  CCCCCC CCCCCCCCC  00000  0
BNCR  132  0 0000 001 0  0000 0000 0 000 0000  00000 000000  C0000000C 000 0  CCCCCC CCCCCCCCC  00000  0
BNCR  133  0 0011 000 0  0000 0000 0 011 0000  00000 000000  C0000000C 000 0  CCCCCC CCCCCCCCC  00000  0
BNCR  134  0 0000 000 0  0000 0000 0 000 0100  00000 000000  C0000000C 000 0  CCCCCC CCCCCCCCC  00000  0
BNCR  135  0 0000 000 0  0000 0000 0 000 0000  00000 000000  C0000000C 000 0  CCCCCC CCCCCCCCC  00000  0
BNCR  136  0 0000 000 0  0000 0000 0 000 0000  00000 000000  C0000000C 000 0  CCCCCC CCCCCCCCC  00000  0
BNCR  137  0 0000 000 0  0000 0000 0 000 0000  00000 000000  C0000000C 000 0  CCCCCC CCCCCCCCC  00000  0
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BNCR  142  0 0000 000 0  0000 0000 0 000 0000  00000 000000  C0000000C 000 0  CCCCCC CCCCCCCCC  00000  0
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BNCR  215  0 0000 000 0  0000 0000 0 000 0000  00000 000000  C0000000C 000 0  CCCCCC CCCCCCCCC  00000  0
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APPENDIX C (continued)

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BNCR  245  0 0000 100 0  0x1C1C0 0001 0 100 0000  10000 C01C00  CCCCCCCCC CCC 0  0C1CC0 1C1110000C0  C0001  0
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BNCR  253  0 1000 001 0  0x0000 0011 1 000 1100  00000 C00011  1000C1CCC 0C0 0  011CC0 C0C0C1000C1  0C0C0  0
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BNCR  263  0 0000 000 0  0x0000 0010 1 000 1111  C1C01 111C00  CCCCCC1CC 110 0  CCCCC0 1C0C0C0C0C0  C0C00  0
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APPENDIX C (continued)

```
BNCR 331 0 0000 000 0 0111 0 000 0000 0000 0
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APPENDIX C (continued)

APPENDIX C (continued)

```
BNCR  555  0 0000 0000 0000
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APPENDIX C (continued)

APPENDIX C (continued)

```
BNCR  780  0 0000 0000 0  0000 0000 0000 
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APPENDIX C (continued)

APPENDIX C (continued)

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BNCR 1044  0 0020 000 0  0000000 0000 0 000 0000  00010 00000  0000000000 000 0  00000 00000  0
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BNCR 1072  0 0000 000 0  0011001 0010 0 010 1000  11010 00000  0000000000 000 0  00000 00100  0
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BNCR 1082  0 0000 000 0  0000000 0000 0 000 0000  00000 00000  0000000000 000 0  00000 00000  0
BNCR 1083  0 0000 010 0  0000001 0001 0 000 0101  00000 00000  0000000000 000 1  00000 00000  0
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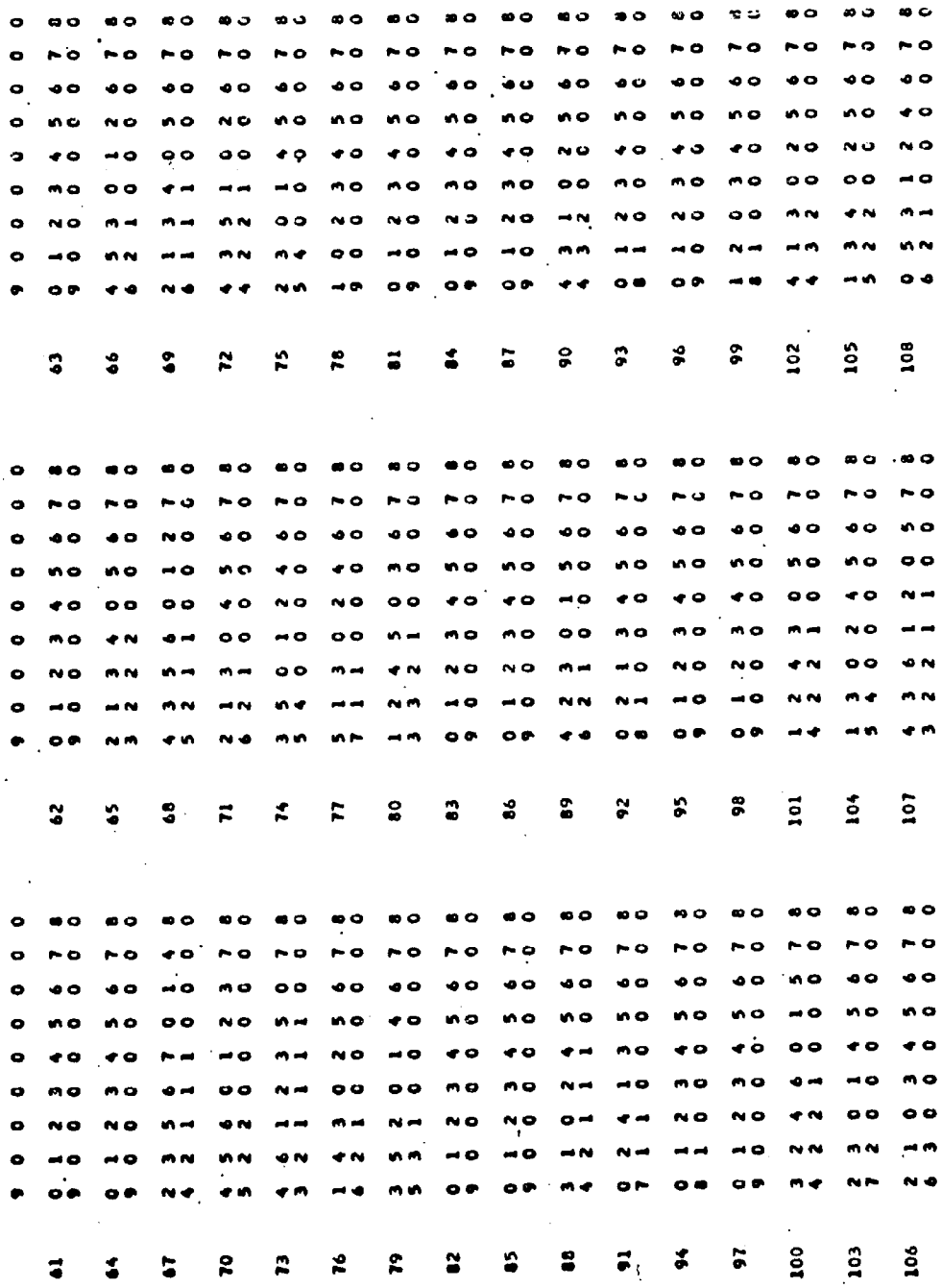
APPENDIX D

ORDERED RESULTS FOR THE TRIADS OF THE ADJECTIVAL Orychlass

CHAR. NO. **KEY TO ORDERED RESULTS**

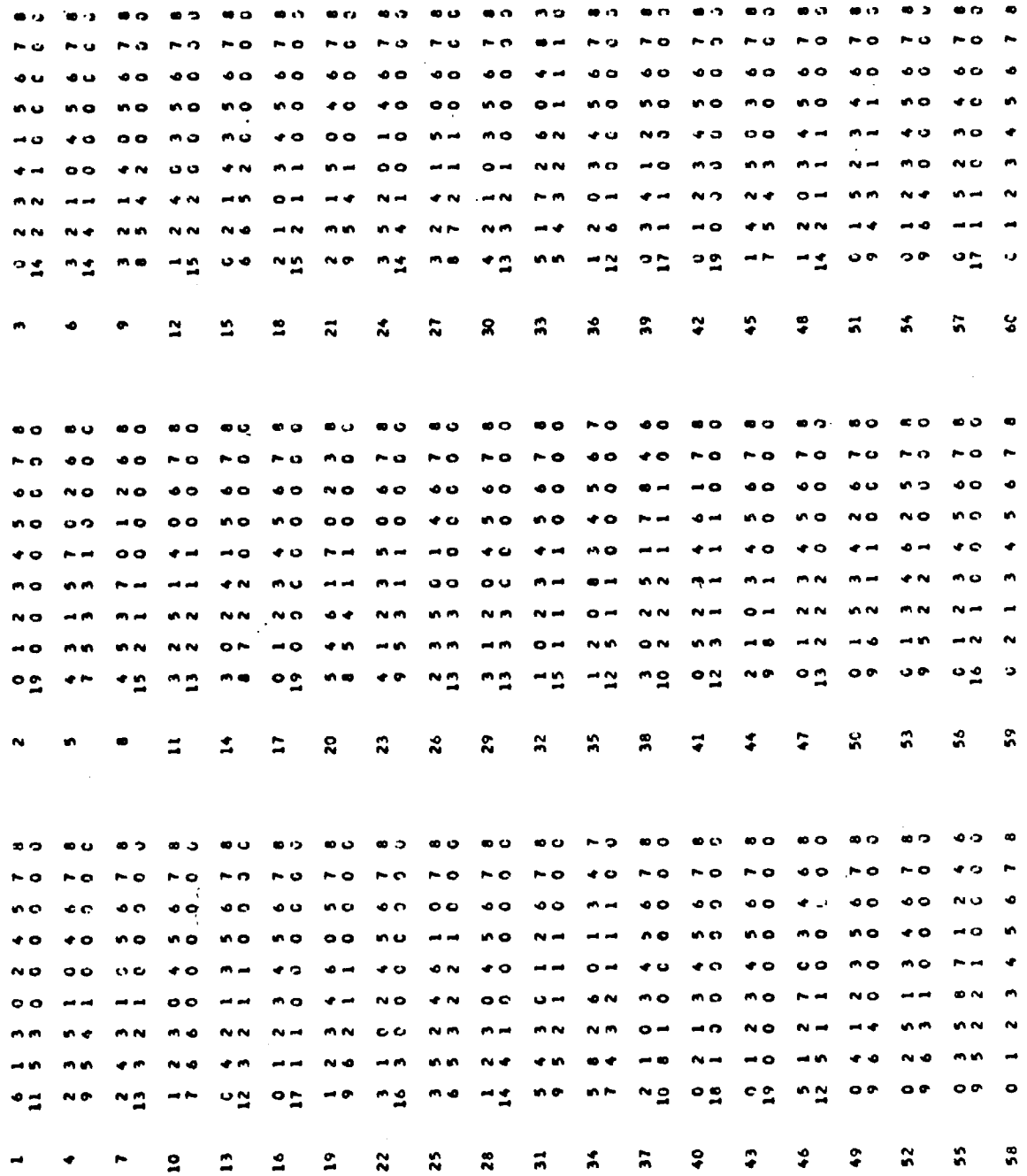
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2	0	1	2	3	4	5	6	7	8
	9	0	0	0	0	0	0	0	0
3	0	3	1	2	4	5	6	7	8
	8	1	0	0	0	0	0	0	0
4	3	2	5	8	0	1	4	6	7
	6	1	1	1	0	0	0	0	0
5	5	3	4	1	6	0	2	7	8
	3	2	2	1	1	0	0	0	0
6	2	3	1	0	4	5	6	7	8
	3	3	2	1	0	0	0	0	0
7	2	1	3	0	4	5	6	7	8
	3	2	2	1	1	0	0	0	0
8	5	7	0	4	6	1	2	3	8
	4	2	1	1	1	0	0	0	0
9	2	1	3	0	4	5	6	7	8
	3	2	2	1	1	0	0	0	0
10	1	2	0	3	4	5	6	7	8
	4	3	1	1	0	0	0	0	0
11	3	4	0	2	5	1	6	7	8
	4	2	1	1	1	0	0	0	0
12	1	0	2	3	4	5	6	7	8
	7	1	1	0	0	0	0	0	0
13	0	1	3	2	4	5	6	7	8
	3	2	2	1	1	0	0	0	0
14	0	3	1	2	4	5	6	7	8
	7	2	0	0	0	0	0	0	0
15	0	1	5	2	3	4	6	7	8
	7	1	1	0	0	0	0	0	0
16	0	1	2	3	4	5	6	7	8
	9	0	0	0	0	0	0	0	0
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	9	0	0	0	0	0	0	0	0
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	6	2	1	0	0	0	0	0	0
19	3	1	2	5	0	4	6	7	8
	6	1	1	1	0	0	0	0	0
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	7	1	1	0	0	0	0	0	0
21	1	2	3	0	4	5	6	7	8
	5	3	3	0	0	0	0	0	0
22	3	1	0	2	4	5	6	7	8
	5	4	0	0	0	0	0	0	0
23	1	4	2	0	3	5	6	7	8
	5	3	1	0	0	0	0	0	0
24	3	2	5	0	1	4	6	7	8
	7	1	1	0	0	0	0	0	0
25	2	3	4	5	0	1	6	7	8
	5	2	1	1	0	0	0	0	0
26	5	4	1	8	0	2	3	6	7
	4	3	1	1	0	0	0	0	0
27	4	2	3	6	0	1	5	7	8
	4	3	1	1	0	0	0	0	0
28	1	2	0	3	4	5	6	7	8
	8	1	0	0	0	0	0	0	0
29	5	7	1	3	6	0	2	4	8
	3	3	1	1	1	0	0	0	0
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	7	2	0	0	0	0	0	0	0
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	6	2	1	0	0	0	0	0	0
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	8	1	0	0	0	0	0	0	0
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	3	2	2	1	1	0	0	0	0
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	5	2	1	1	0	0	0	0	0
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	5	4	0	0	0	0	0	0	0
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	9	0	0	0	0	0	0	0	0
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	5	3	1	0	0	0	0	0	0
38	3	2	4	5	0	1	6	7	8
	5	2	1	1	0	0	0	0	0
39	0	1	2	3	4	5	6	7	8
	9	0	0	0	0	0	0	0	0
40	0	1	2	3	4	5	6	7	8
	9	0	0	0	0	0	0	0	0
41	0	3	1	2	4	5	6	7	8
	8	1	0	0	0	0	0	0	0
42	0	1	2	3	4	5	6	7	8
	9	0	0	0	0	0	0	0	0
43	0	1	2	3	4	5	6	7	8
	9	0	0	0	0	0	0	0	0
44	2	0	3	1	4	5	6	7	8
	7	1	1	0	0	0	0	0	0
45	3	5	0	4	6	8	1	2	7
	3	2	1	1	1	1	0	0	0
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	5	1	1	1	1	0	0	0	0
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	7	1	1	0	0	0	0	0	0
49	0	1	2	3	4	5	6	7	8
	8	1	0	0	0	0	0	0	0
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	8	1	0	0	0	0	0	0	0
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	8	1	0	0	0	0	0	0	0
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	8	1	0	0	0	0	0	0	0
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	8	1	0	0	0	0	0	0	0
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	8	1	0	0	0	0	0	0	0
55	0	3	1	2	4	5	6	7	8
	8	1	0	0	0	0	0	0	0
56	0	1	2	3	4	5	6	7	8
	9	0	0	0	0	0	0	0	0
57	0	1	2	3	4	5	6	7	8
	9	0	0	0	0	0	0	0	0
58	0	1	2	3	4	5	6	7	8
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60	0	1	2	3	4	5	6	7	8

APPENDIX D (continued)

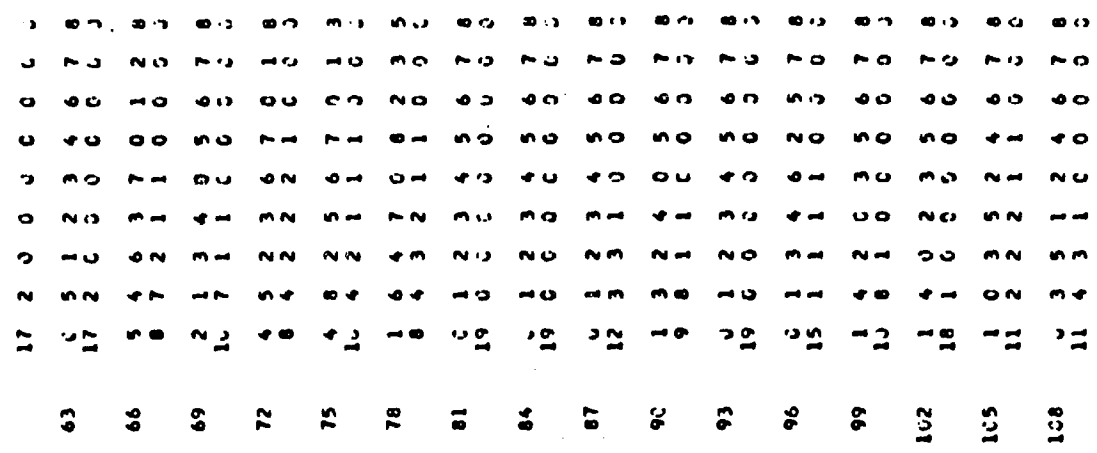


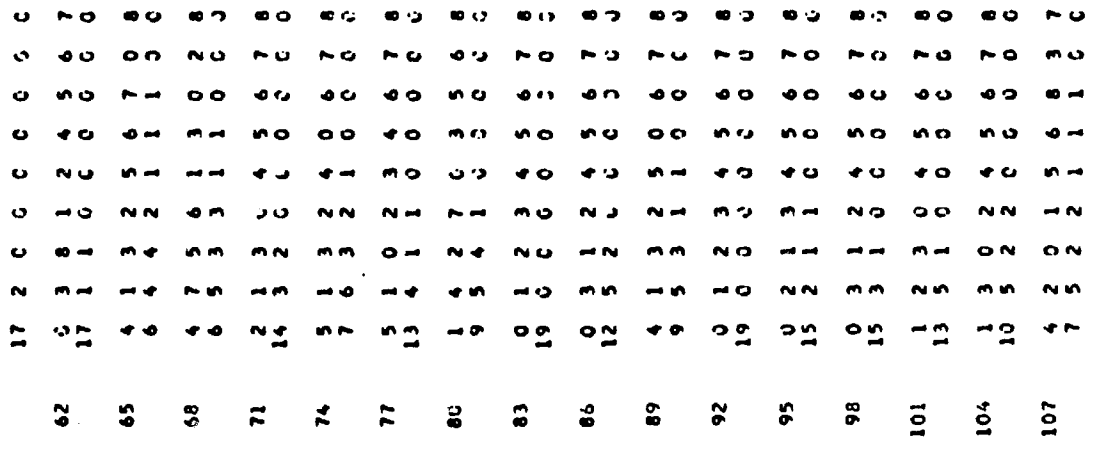
APPENDIX D (continued)

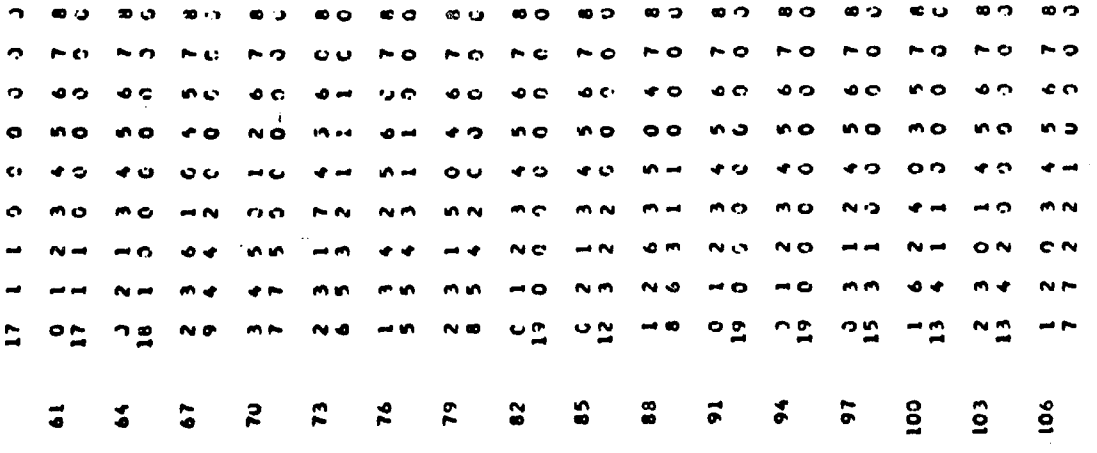
Cheilantheas



APPENDIX D (continued)

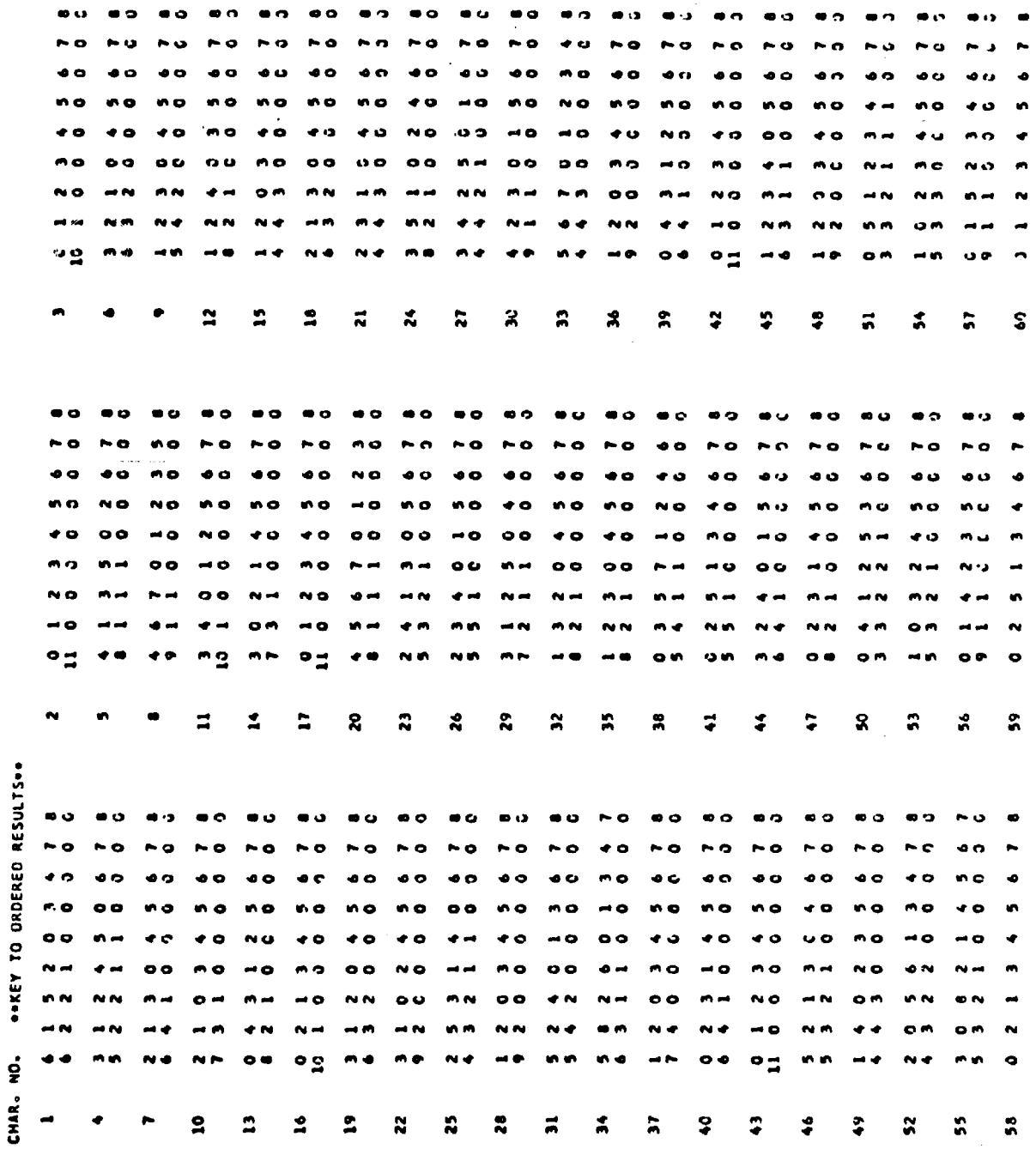




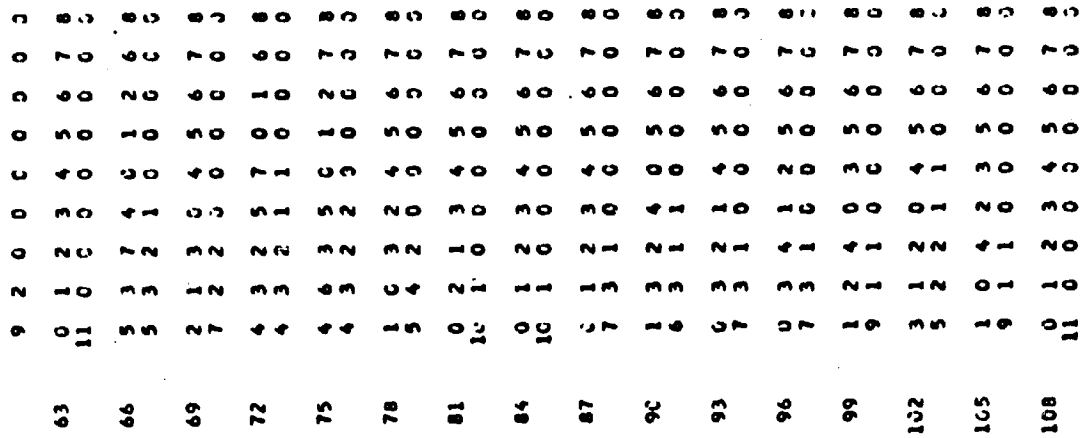


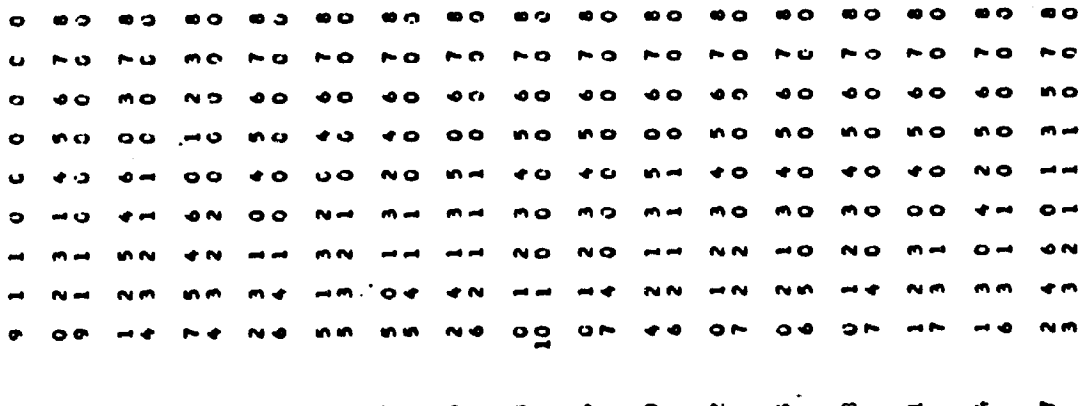
APPENDIX D (continued)

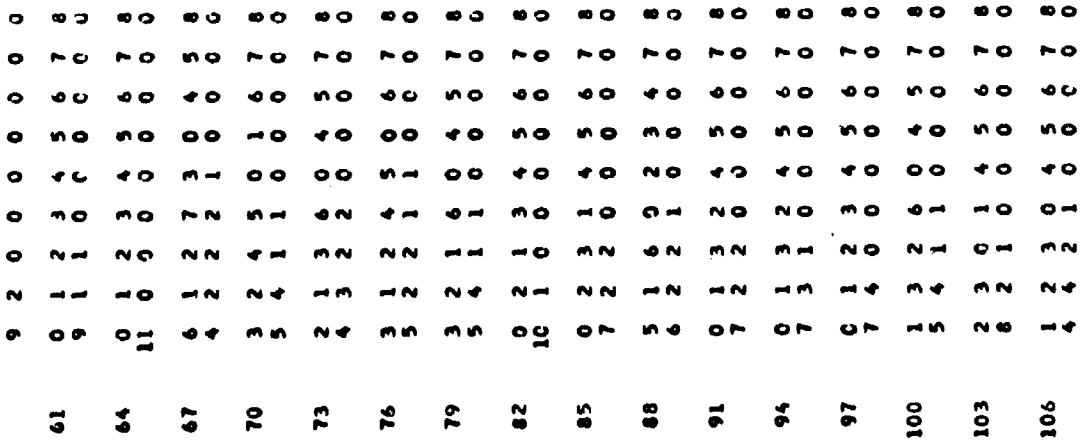
Pellaeae



APPENDIX D (continued)





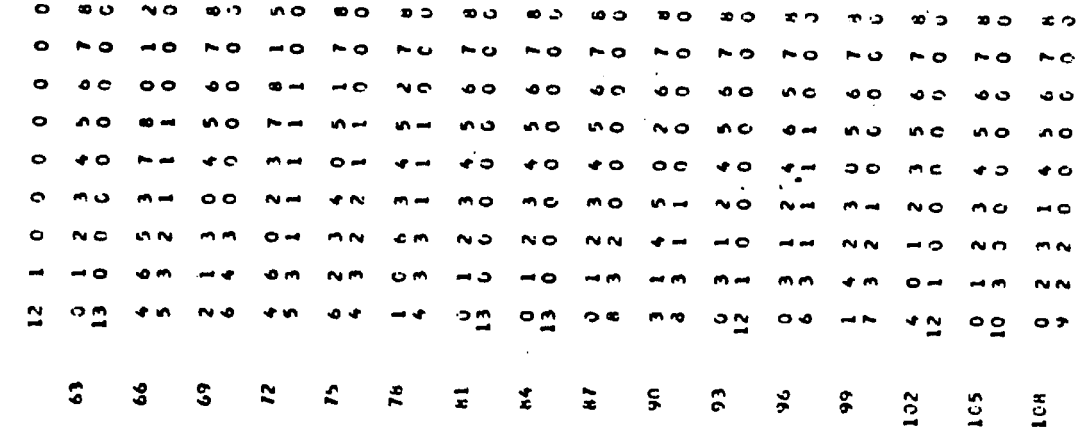


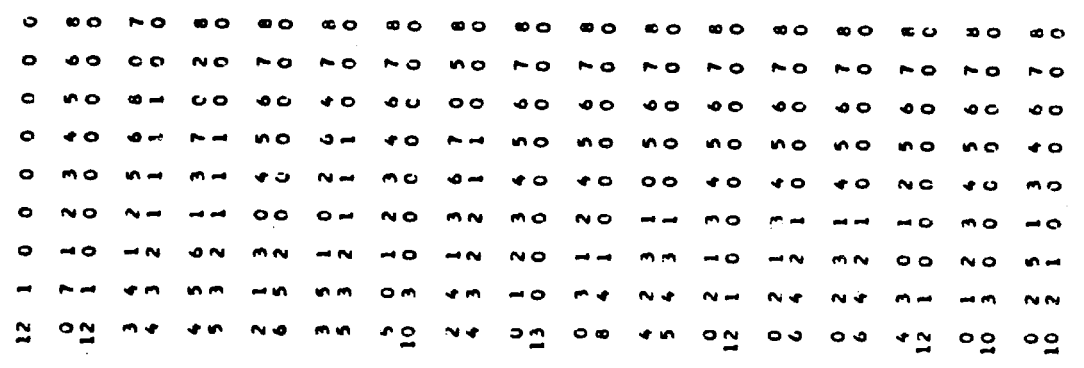
APPENDIX D (continued)

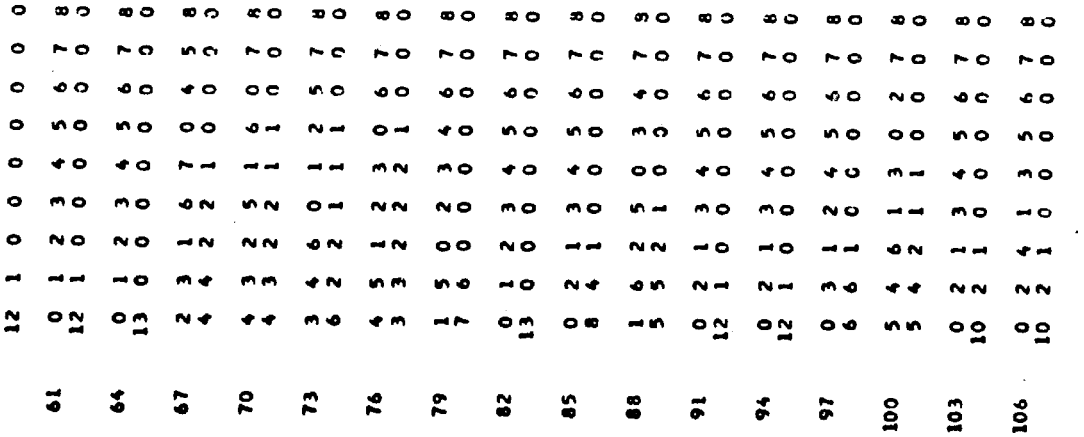
Osmundaceae

| CHAR. NO. | **KEY TO ORDERED RESULTS** | | |

APPENDIX D (continued)







APPENDIX D (continued)

Eriogonum

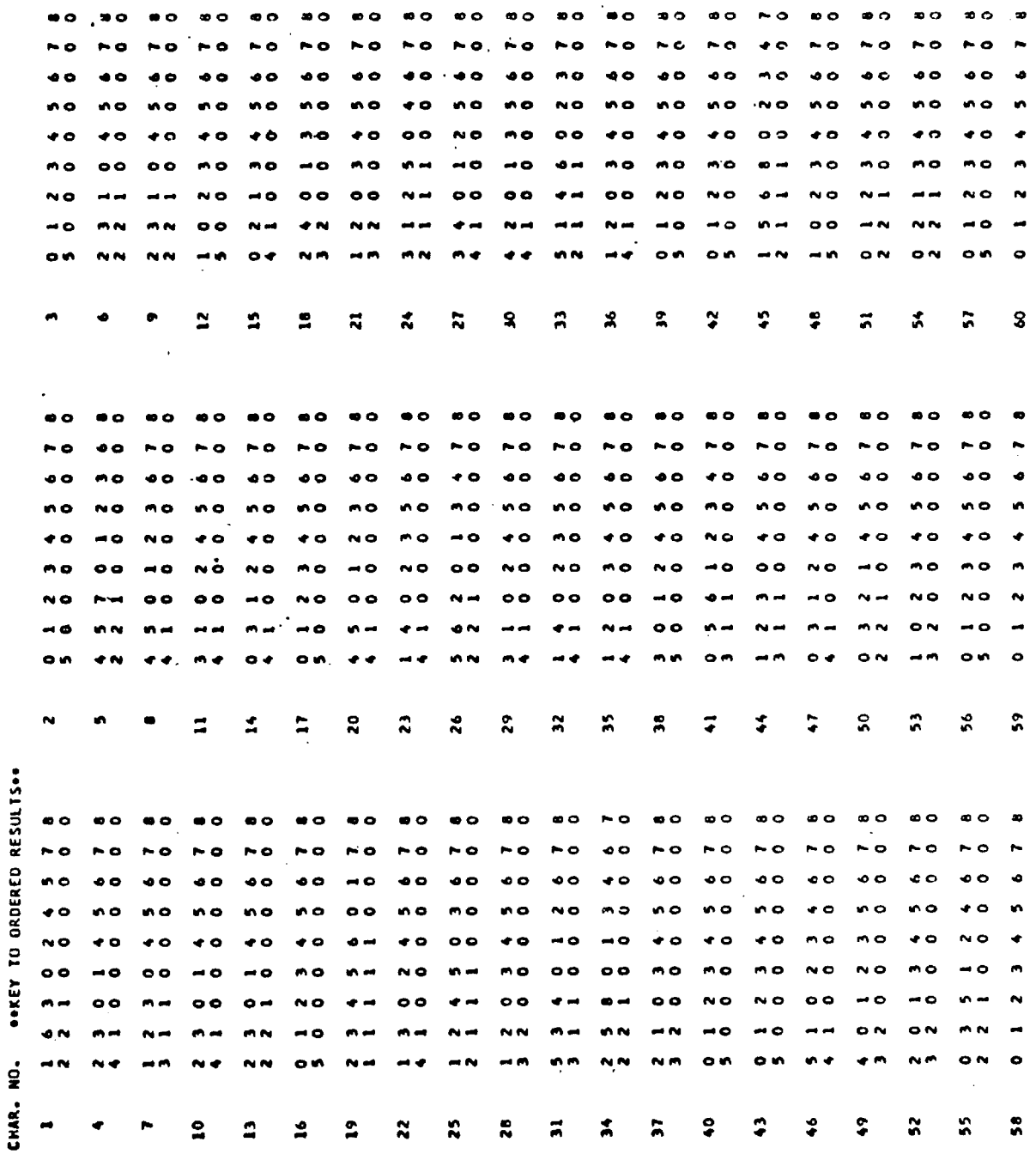
| CHAR. NO. | **KEY TO ORDERED RESULTS** | | |

APPENDIX D (continued)

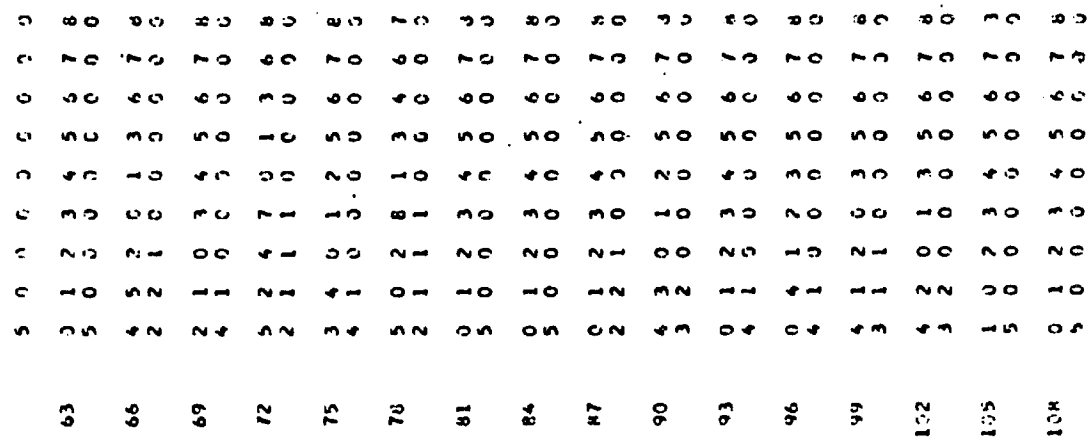
61	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
62	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
63	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
64	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
65	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
66	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
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67	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
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69	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
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71	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
72	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
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73	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
74	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
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75	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
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76	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
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91	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
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92	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
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93	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
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94	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
95	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
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96	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
97	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
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98	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
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99	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
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103	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
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104	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
105	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
106	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
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107	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
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108	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
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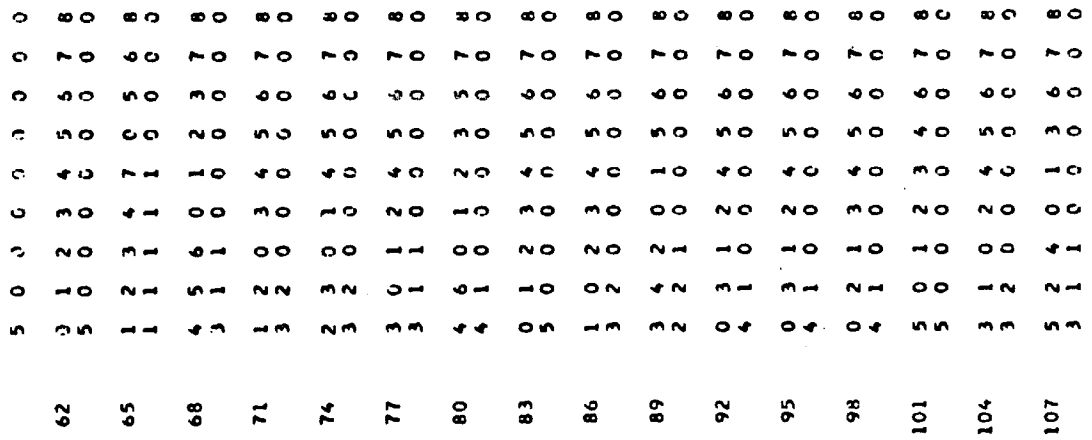
APPENDIX D (continued)

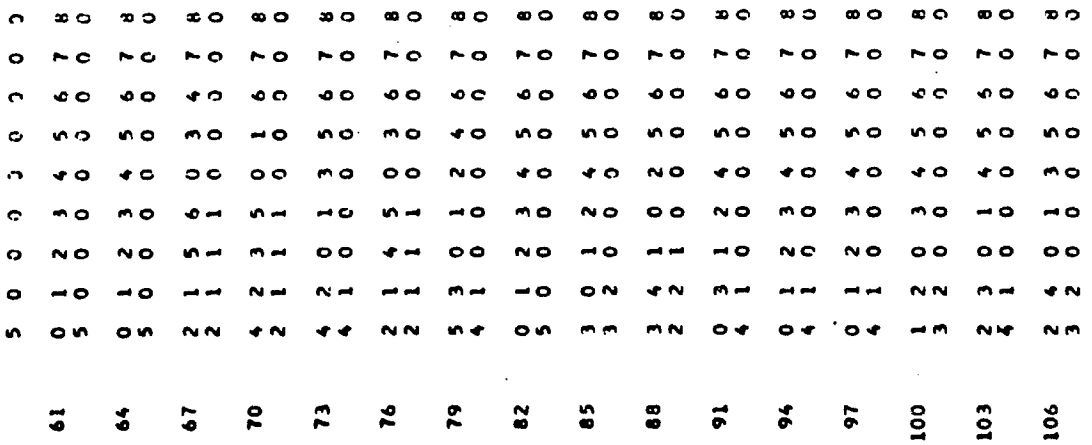
Adiantaceae



APPENDIX D (continued)







APPENDIX E

CHARACTER DISTRIBUTION SELECTION TEST RESULTS FOR THE TRIBES OF THE ADIANTOIDEAE

Onychieae

3/4 adjacent group test: 2, 3, 7, 12, 14-17, 19, 24, 28, 30-32, 35, 36, 39-43, 48-64, 70, 71, 77, 81-87, 89, 91-99, 108.

4/5 adjacent group test: 2, 3, 12, 14-17, 19, 24, 28, 30-32, 36, 39-43, 48-64, 70, 81-87, 89, 91-98, 108.

0.60 character state proportion test: 2-4, 8, 11, 12, 14-20, 24, 25, 28, 30-32, 34, 36, 38-44, 46-64, 66-72, 76-78, 81-89, 91-101, 103, 105, 106, 108.

0.65 character state proportion test: 2-4, 8, 11, 12, 14-20, 23-25, 28, 30-32, 34, 36-44, 46-64, 66-72, 76-79, 81-89, 91-101, 103, 105, 106, 108.

0.70 character state proportion test: 2-5, 7-9, 11-20, 23-25, 28, 30-34, 36-73, 76-79, 81-89, 91-101, 103, 105-108.

0.75 character state proportion test: 1-5, 7-20, 23-28, 30-34, 36-73 76-79, 81-103, 105-108.

0.80 character state proportion test: 1-5, 7-20, 23-28, 30-34, 36-73, 76-79, 81-103, 105-108.

0.30 frequency test: 1-108.

0.40 frequency test: 1-4, 8, 10-12, 14-20, 22-28, 30-32, 34-44, 46-64, 66-72, 74-79, 81-106, 108.

0.50 frequency test: 2-4, 12, 14-20, 22-25, 28, 30-32, 34-44, 46-64, 66, 68-71, 74-79, 81-87, 89, 91-99, 103-106, 108.

0.60 frequency test: 2-4, 12, 14-20, 24, 28, 30-32, 36, 39-44, 47-64, 66, 69, 71, 76-78, 81-87, 89, 91-99, 103, 106, 108.

0.70 frequency test: 2, 3, 12, 14-17, 20, 24, 28, 30, 32, 36, 39-44, 47-64, 77, 78, 81-87, 91-99, 103.

Appendix E (continued)

0.80 frequency test: 2, 3, 16, 17, 28, 32, 36, 39-43, 47, 49-64, 78, 81-87, 92-99.

0.90 frequency test: 2, 16, 17, 36, 39, 40, 42, 43, 56-64, 78, 81-87, 95-98.

Cheilantheae

3/4 adjacent group test: 2, 3, 6, 7, 12, 15-17, 24, 28-32, 35, 36, 39-43, 48-64, 67, 69, 71, 77, 78, 81-87, 89, 91-99, 108.

4/5 adjacent group test: 2, 3, 12, 15-17, 24, 28-32, 36, 39-43, 48-64, 67, 69, 71, 81-87, 89, 91-98, 108.

0.60 character state proportion test: 1-4, 6-8, 11-13, 16-18, 21-24, 26, 28-32, 34-36, 38-43, 46-48, 51, 53, 55-64, 67, 71, 72, 75, 77, 78, 80-87, 89, 91-98, 100-105, 108.

0.65 character state proportion test: 1-4, 6-9, 11-13, 16-18, 20-24, 28-32, 34-36, 38-43, 46-48, 51, 53, 55-64, 67, 71, 72, 75, 77-87, 89, 91-98, 100-105, 108.

0.70 character state proportion test: 1-4, 6-9, 11-13, 16-24, 26, 28-32, 34-36, 38-43, 46-65, 67, 71, 72, 75, 77-87, 89, 91-98, 100-105, 108.

0.75 character state proportion test: 1-9, 11-13, 16-24, 26, 28-32, 34-36, 38-43, 45-65, 67, 69, 71, 72, 75, 77-89, 91-98, 100-105, 107, 108.

0.80 character state proportion test: 1-9, 11-13, 16-24, 26, 28-32, 34-36, 38-43, 45-65, 67, 69, 71, 72, 75, 77-89, 91-98, 100-105, 107, 108.

0.30 frequency test: 1-32, 34-75, 77-108.

0.40 frequency test: 1-4, 6-9, 11-14, 16-24, 26-32, 35-44, 46-64, 66, 67, 69, 71, 72, 75, 77-105, 108.

0.50 frequency test: 1-3, 6-8, 11-13, 16-18, 22, 24, 26, 28-30, 32, 35-43, 46-48, 56-64, 69, 71, 75, 77, 81-87, 91-105, 108.

0.60 frequency test: 2, 3, 6-8, 11-13, 16-18, 22, 24, 26, 28-30, 32, 35, 36, 39-43, 46-48, 56-64, 71, 77, 81-87, 91-98, 100-103.

0.70 frequency test: 2, 3, 6, 8, 12, 16-18, 22, 24, 28, 32, 39, 40, 42, 43, 48, 56-64, 71, 81-84, 91-98, 102.

Appendix E (continued)

0.80 frequency test: 2, 16, 17, 22, 39, 40, 42, 43, 56-64, 81-84, 91-94, 102.

0.90 frequency test: 2, 17, 40, 42, 43, 64, 81-84, 91-94, 102.

Pellaeae

3/4 adjacent group test: 2, 3, 6, 7, 12, 16, 17, 24, 28-32, 35, 36, 39-43, 48, 50, 51, 56-64, 71, 77, 81-87, 89, 91-99, 108.

4/5 adjacent group test: 2, 3, 12, 16, 17, 24, 28-32, 36, 39-43, 48, 50, 51, 56-64, 81-87, 89, 91-98, 108.

0.60 character state proportion test: 1-6, 8, 10-14, 16-20, 22, 24, 28-30, 32, 34-37, 42, 43, 45, 47, 48, 56-64, 67, 69, 76, 80-94, 96-99, 101-105, 108.

0.65 character state proportion test: 1-6, 8, 10-14, 16-19, 20, 20, 22-24, 28-30, 32, 34-37, 42, 43, 45-48, 53-64, 66, 67, 69, 74, 76, 80-94, 96-99, 101-105, 108.

0.70 character state proportion test: 1-8, 10-14, 16-20, 22-24, 28-30, 32, 34-37, 39, 40, 42-48, 53-64, 66, 67, 69, 71, 74, 76, 80-94, 96-99, 101-105, 108.

0.75 character state proportion test: 1-8, 10-14, 16-20, 22-25, 28-30, 32, 34-37, 39, 40, 42-48, 52-69, 71-76, 80-94, 96-99, 101-105, 108.

0.80 character state proportion test: 1-8, 10-14, 16-20, 22-25, 28-30, 32, 34-37, 39, 40, 42-48, 52-69, 71-76, 80-94, 96-99, 101-105, 108.

0.30 frequency test: 1-49, 52-106, 108.

0.40 frequency test: 1-14, 16-20, 22-24, 26, 28-32, 34-48, 53-64, 66, 69-71, 74, 76-105, 108.

0.50 frequency test: 1-3, 5-8, 10-14, 16-20, 22, 24, 28-30, 32, 34-37, 39, 40, 42-45, 47, 48, 56-64, 69, 71, 80-99, 101, 103-105, 108.

0.60 frequency test: 2, 3, 5, 8, 10-14, 16, 17, 20, 22, 24, 28-30, 32, 35-37, 42, 43, 47, 48, 56-64, 69, 81-87, 91-94, 96-99, 101, 103, 105, 108.

0.70 frequency test: 2, 3, 5, 8, 11-13, 16, 17, 20, 22, 24, 28, 30, 32, 35, 36, 42, 43, 47, 48, 56-64, 81-84, 99, 103, 105, 108.

0.80 frequency test: 2, 3, 8, 11, 16, 17, 22, 28, 30, 36, 42, 43, 48, 56-64, 81-84, 99, 105, 108.

Appendix E (continued)

0.90 frequency test: 2, 3, 11, 16, 17, 42, 43, 63, 64, 81-84, 108.

Gymnopterideae

3/4 adjacent group test: 2, 3, 6, 7, 9, 12, 14-17, 20, 24, 28-30, 32, 35, 36, 39-43, 47, 48, 50-64, 69, 71, 77, 81-87, 89, 91-99, 108.

4/5 adjacent group test: 2, 3, 6, 9, 12, 14-17, 20, 24, 28-30, 32, 35, 36, 39-43, 48, 50-64, 69, 81-87, 89, 91-99, 108.

0.60 character state proportion test: 2, 3, 5, 7, 8, 11, 12, 14-17, 19, 22, 24, 28, 29, 32, 33, 35-37, 39-43, 47, 48, 56-64, 73, 77, 81-87, 90-94, 96, 99, 101-108.

0.65 character state proportion test: 2, 3, 5, 7, 8, 11, 12, 14-17, 19, 22, 24, 28, 29, 32, 33, 35-37, 39-43, 47, 48, 55-64, 66, 68, 72-74, 77, 81-87, 90-94, 96, 99, 101-108.

0.70 character state proportion test: 2, 3, 5-9, 11, 12, 14-17, 19, 21, 22, 24, 28, 29, 32, 33, 35-37, 39-43, 47, 48, 55-64, 66, 68, 69, 72-74, 77, 81-87, 90-96, 98, 99, 101-108.

0.75 character state proportion test: 2, 3, 5-9, 11-17, 19, 21, 22, 24-29, 32, 33, 35-37, 39-43, 47, 48, 55-66, 68-70, 72-75, 77, 78, 80-87, 90-96, 98, 99, 101-108.

0.80 character state proportion test: 2, 3, 5-9, 11-17, 19, 21, 22, 24-29, 32, 33, 35-37, 39-43, 47, 48, 55-66, 68-70, 72-75, 77, 78, 80-87, 90-96, 98, 99, 101-108.

0.30 frequency test: 1-75, 77-108.

0.40 frequency test: 1-3, 5-9, 11, 12, 14-17, 19-24, 28, 29, 32, 35-37, 39-43, 45-49, 56-64, 69, 71, 73, 77, 79, 81-87, 90-99, 101-108.

0.50 frequency test: 2, 3, 5, 7, 11, 12, 14-17, 19, 22, 24, 28, 29, 32, 35-37, 39-43, 47, 48, 56-64, 77, 79, 81-87, 90-94, 99, 101-108.

0.60 frequency test: 2, 3, 7, 12, 14-17, 22, 24, 28, 32, 36, 37, 39-43, 48, 56-64, 77, 81-87, 90-94, 101-108.

0.70 frequency test: 2, 3, 14-17, 22, 24, 28, 32, 39, 40, 42, 43, 56-64, 77, 81-84, 91-94, 101-107.

0.80 frequency test: 2, 3, 14-17, 22, 24, 28, 32, 39, 40, 42, 43, 56-64, 81-84, 91-94, 101, 102.

0.90 frequency test: 2, 3, 16, 17, 24, 39, 40, 42, 43, 56-64, 81-84, 91-94, 101, 102.

Appendix E (continued)

Eriosoreae

3/4 adjacent group test: 1-3, 6, 12, 14-17, 24, 28-32, 35, 36, 39-43, 47-64, 71, 81-87, 89, 91-94, 99, 108.

4/5 adjacent group test: 1-3, 12, 14-17, 24, 28-32, 36, 39-43, 48-64, 81-87, 89, 91-94, 108.

0.60 character state proportion test: 1-3, 6, 8-12, 14-17, 19-24, 26, 29-32, 34-36, 39-43, 45, 47, 48, 51, 55-64, 67, 70, 77, 78, 81-95, 99-108.

0.65 character state proportion test: 1-3, 6, 8-12, 14-24, 26, 28-32, 34-37, 39-43, 45, 47, 48, 51, 55-65, 67, 70, 77, 78, 81-95, 99-108.

0.70 character state proportion test: 1-3, 6, 8-12, 14-24, 26-32, 34-37, 39-43, 45, 47, 48, 51, 55-67, 70, 77, 78, 81-97, 99-108.

0.75 character state proportion test: 1-3, 5, 6, 8-12, 14-24, 26-37, 39-45, 47, 48, 51, 53-67, 70, 71, 77, 78, 81-97, 99-108.

0.80 character state proportion test: 1-3, 5, 6, 8-12, 14-24, 26-37, 39-45, 47, 48, 51, 53-67, 70, 71, 77, 78, 81-97, 99-108.

0.30 frequency test: 1-3, 5-24, 26-32, 34-37, 39-45, 47-64, 66, 67, 69-71, 75, 77-79, 81-97, 99-108.

0.40 frequency test: 1-3, 5, 6, 8-24, 26, 28-32, 34-37, 39-45, 47-64, 67, 70, 71, 77, 78, 81-95, 99-108.

0.50 frequency test: 1-3, 6, 9-12, 14-23, 26, 28, 32, 34-36, 39-43, 45, 47, 48, 56-64, 67, 77, 78, 81-94, 99, 101-108.

0.60 frequency test: 2, 3, 6, 12, 14-17, 19, 20, 22, 23, 32, 35, 36, 39-43, 56-64, 77, 78, 81-84, 91-94, 101-108.

0.70 frequency test: 2, 3, 12, 14-17, 19, 23, 32, 35, 36, 39-43, 56-64, 77, 78, 81-84, 91-94, 101-108.

0.80 frequency test: 2, 12, 14-17, 32, 36, 39-43, 56-64, 81-84, 91-94, 101-108.

0.90 frequency test: 2, 12, 14-17, 32, 39, 40, 42, 43, 56-62, 81-84, 91-94, 102.

Adianteae

3/4 adjacent group test: 2, 3, 12, 14-17, 20, 22, 24, 28-32, 35, 36, 39-43, 48, 50, 51, 54-64, 67, 69, 81-84, 87, 91-98, 108.

Appendix E (continued)

4/5 adjacent group test: 2, 3, 12, 14-17, 24, 28-32, 35, 36, 39-43, 48, 50, 51, 54-64, 81-84, 87, 91-98, 108.

0.60 character state proportion test: 2-4, 7, 8, 10-12, 14-17, 20, 22-25, 27, 29-33, 35, 36, 38-48, 56-64, 67-70, 72, 73, 75-84, 91-99, 101, 103, 105, 107, 108.

0.65 character state proportion test: 2-4, 7, 8, 10-12, 14-17, 20, 22-25, 27, 29-33, 35, 36, 38-48, 56-64, 67-70, 72, 73, 75-84, 91-99, 101, 103, 105, 107, 108.

0.70 character state proportion test: 2-4, 7, 8, 10-12, 14-18, 20-25, 27-33, 35-49, 52, 53, 56-64, 67-86, 90-108.

0.75 character state proportion test: 2-4, 7, 8, 10-12, 14-18, 20-25, 27-33, 35-49, 52, 53, 56-64, 67-86, 90-108.

0.80 character state proportion test: 2-4, 7, 8, 10-12, 14-18, 20-25, 27-33, 35-49, 52, 53, 56-64, 67-86, 90-108.

0.30 frequency test: 1-18, 20-64, 66-108.

0.40 frequency test: 1-18, 20-64, 66-108.

0.50 frequency test: 2-4, 7, 8, 10-12, 14-18, 20-23, 27-32, 35-44, 46-49, 52, 53, 56-64, 68, 69, 71, 73-75, 77, 79-86, 90-108.

0.60 frequency test: 2-4, 7, 8, 10-12, 14-18, 20-23, 27-32, 35-44, 46-49, 52, 53, 56-64, 68, 69, 71, 73-75, 77, 79-86, 90-108.

0.70 frequency test: 2-4, 8, 10-12, 14-17, 20, 22, 23, 27, 29, 30, 32, 35, 36, 38-40, 42, 43, 46-48, 56-64, 69, 73, 75, 79-84, 91-98, 101, 103, 105, 108.

0.80 frequency test: 2-4, 8, 10-12, 14-17, 20, 22, 23, 27, 29, 30, 32, 35, 36, 38-40, 42, 43, 46-48, 56-64, 69, 73, 75, 79-84, 91-98, 101, 103, 105, 108.

0.90 frequency test: 2, 3, 12, 16, 17, 38-40, 42, 43, 48, 56-64, 81-84, 101, 105, 108.

APPENDIX F

R-MATRIX VALUES EXCEEDING r = 0.900 AND OF r = 1.000
FOR THE TRIBES OF THE ADIANTOIDEAE

TRIBE	r ≥ 0.900	r = 1.000
Onychieae	4 x 44 4 x 91 20 x 65 23 x 72	3 x 41, 47, 49-55 32 x 50-55 41 x 47, 49-55 44 x 91 47 x 49-55 49 x 50-55 50 x 51-55 51 x 52-55 52 x 53-55 53 x 54-55 54 x 55 92 x 93-94 93 x 94
Cheilantheae and Pellaeae	57 x 58-60, 62 58 x 60-62 59 x 60 60 x 61 92 x 93, 99 95 x 97, 98	81 x 82-84 82 x 83-84 83 x 84 93 x 94 97 x 98
Gymnopterideae	50 x 51 85 x 87 97 x 98 103 x 104, 105 104 x 106, 107 105 x 106, 107	56 x 57-62 57 x 58-62 58 x 59-62 59 x 60-62 60 x 61-62 61 x 62 91 x 92-94 92 x 93-94 93 x 94 103 x 106, 107 104 x 105 106 x 107
Eriosoreae	49 x 50 63 x 64 71 x 87 103 x 104-107	42 x 43 63 x 108 104 x 106, 107 106 x 107

Appendix F (continued)

Adianteae

1 x 25
7 x 71
9 x 76
18 x 25, 67, 70, 78
21 x 68, 72, 77
25 x 100
26 x 33
33 x 52, 53, 85, 86
37 x 68, 72
49 x 76, 107
52 x 76, 99, 107
53 x 76, 99, 107
54 x 70
55 x 70, 78
67 x 100
70 x 100, 104, 106
72 x 102
76 x 85, 86, 99, 107
77 x 90, 102
78 x 100, 104, 106
85 x 99, 107
86 x 99, 107

4 x 35, 47, 79, 80
8 x 11, 22, 32, 103
10 x 30, 91-94
11 x 22, 23, 32, 103
14 x 15, 20, 36, 69, 73, 75, 80, 95-98
15 x 20, 36, 69, 73, 75, 80, 95-98
18 x 100, 104, 106
20 x 36, 69, 73, 75, 80, 95-98
21 x 37, 69, 90, 102
22 x 23, 32, 103
23 x 32, 103
27 x 29, 46, 49
29 x 46
30 x 91-94
32 x 103
35 x 47, 79
36 x 69, 73, 75, 80, 95-98
37 x 90, 102
47 x 79
49 x 52, 53, 85, 86, 99
50 x 51, 87
51 x 87
52 x 53, 85, 86
53 x 85, 86
54 x 55
68 x 77
69 x 73, 75, 80, 95-98
73 x 75, 80, 95-98
75 x 80, 95-98
78 x 80
80 x 95-98
85 x 86
90 x 102
91 x 92-94
92 x 93, 94
93 x 94
94 x 96-98
95 x 97, 98
96 x 98
98 x 107
99 x 104, 106
104 x 106

APPENDIX G

EVOLUTIONARY GROUND PLAN DIAGRAM DIRECTIONS
FOR THE TRIBES OF THE ADIANTOIDEAE

Onychieae

EVOLUTION OF 19 TAXA DETERMINED USING 108 CHARACTERS AND .224 AS THE LEVEL OF SIGNIFICANCE.

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501   ***  1111111111 1111111111 1111111111 1111111111 1111111111 1111111111 1111111111 1111111111 1111111111 1111111111 11111111
502    33  1111111111 1111111111 1111111111 1111111111 1111111111 1111111111 1111111111 1111111111 1111111111 1111111111 11111111
503    76  1111111111 1111111111 1111111111 1101111111 1111111111 1111111111 1111111111 1111111111 1111111111 1111111111 11111111
504    15  1111111111 1111011111 1111111111 1101111111 1111111111 1111111111 1111111111 1111111111 1111111111 1111111111 11111111
505    25  1111111111 1111011111 1111011111 1101111111 1111111111 1111111111 1111111111 1111111111 1111111111 1111111111 11111111
506    65  1111111111 1111011111 1111011111 1101111111 1111111111 1111111111 1111111111 1111111111 1111111111 1111111111 11111111
507    68  1111111111 1111011111 1111011111 1101111111 1111111111 1111111111 1111111111 1111111111 1111111111 1111111111 11111111
508    73  1111111111 1111011111 1111011111 1101111111 1111111111 1111111111 1111111111 1111111111 1111111111 1111111111 11111111
509    45  1111111111 1111011111 1111011111 1101111111 1111111111 1111111111 1111111111 1111111111 1111111111 1111111111 11111111
510     9  1111111111 1111011111 1111011111 1101111111 1111111111 1111111111 1111111111 1111111111 1111111111 1111111111 11111111
511    27  1111111111 1111011111 1111011111 1101111111 1111111111 1111111111 1111111111 1111111111 1111111111 1111111111 11111111
512    72  1111111111 1111011111 1111011111 1101111111 1111111111 1111111111 1111111111 1111111111 1111111111 1111111111 11111111
513    79  1111111111 1111011111 1111011111 1101111111 1111111111 1111111111 1111111111 1111111111 1111111111 1111111111 11111111
514    23  1111111111 1111011111 1111011111 1101111111 1111111111 1111111111 1111111111 1111111111 1111111111 1111111111 11111111
515    67  1111111111 1111011111 1111011111 1101111111 1111111111 1111111111 1111111111 1111111111 1111111111 1111111111 11111111
516    80  1111111111 1111011111 1111011111 1101111111 1111111111 1111111111 1111111111 1111111111 1111111111 1111111111 11111111
517    69  1111111111 1111011111 1111011111 1101111111 1111111111 1111111111 1111111111 1111111111 1111111111 1111111111 11111111
518    99  1111111111 1111011111 1111011111 1101111111 1111111111 1111111111 1111111111 1111111111 1111111111 1111111111 11111111
519     1  0111111111 1111011111 1111011111 1101111111 1111111111 1111111111 1111111111 1111111111 1111111111 1111111111 11111111
520   108  0111111111 1111011111 1111011111 1101111111 1111111111 1111111111 1111111111 1111111111 1111111111 1111111111 11111111
521    35  0111111111 1111011111 1111011111 1101111111 1111111111 1111111111 1111111111 1111111111 1111111111 1111111111 11111111
522     6  0111111111 1111011111 1111011111 1101111111 1111111111 1111111111 1111111111 1111111111 1111111111 1111111111 11111111
 21    32  0111111111 1111011111 1111011111 1101111111 1111111111 1111111111 1111111111 1111111111 1111111111 1111111111 11111111

520   ***  0111111111 1111011111 1101010111 1101111111 1111011111 1111111111 1111010001 1001101100 1111111111 1111111101 11111111
523     5  0111011101 1111011111 1101010111 1101111111 1111011111 1111111111 1111010001 1001101100 1111111111 1111111101 11111111
524    10  0111011111 1111011111 1101010111 1101111111 1111011111 1111111111 1111010001 1001101100 1111111111 1111111101 11111111
525    70  0111011101 1111011111 1101010111 1101111111 1111011111 1111111111 1111010001 1001101100 1111111111 1111111101 11111111
526    78  0111011111 1111011111 1101010111 1101111111 1111011111 1111111111 1111010001 1001101100 1111111111 1111111101 11111111
527    19  0111011111 1111011111 1101010111 1101111111 1111011111 1111111111 1111010001 1001101100 1111111111 1111111101 11111111
528    44  0111011111 1111011111 1101010111 1101111111 1111011111 1111111111 1111010001 1001101100 1111111111 1111111101 11111111
529    90  0111011111 1111011111 1101010111 1101111111 1111011111 1111111111 1111010001 1001101100 1111111111 1111111101 11111111
530    46  0111011111 1111011111 1101010111 1101111111 1111011111 1111111111 1111010001 1001101100 1111111111 1111111101 11111111
531    29  0111011111 1111011111 1101010101 1101111111 1111011111 1111111111 1111010001 1001101100 1111111111 1111111101 11111111
532   101  0111011111 1111011111 1101010101 1101111111 1111011111 1111111111 1111010001 1001101100 1111111111 1111111101 11111111
533   103  0111011111 1111011111 1101010101 1101111111 1111011111 1111111111 1111010001 1001101100 1111111111 1111111101 01111111
534     3  0101011111 1111011111 1101010101 1101111111 1111011111 1111111111 1111010001 1001101100 1111111111 1111111101 01011111
535    48  0101011111 1111011111 1101010101 1101111111 1111011111 1111111111 1111010001 1001101100 1111111111 1111111101 01011111
536    18  0101011111 1111011111 1101010101 1101111111 1111011111 1111111111 1111010001 1001101100 1111111111 1111111101 01011111
537   -23  0101011111 1111011111 1111010101 1101111111 1111011111 1111111111 1111010001 1001101100 1111111111 1111111101 01011111
538   -72  0101011111 1111011111 1111010101 1101111111 1111011111 1111111111 1111010001 1001101100 1111111111 1111111101 01011111
539    -9  0101011111 1111011111 1111010101 1101111111 1111011111 1111111111 1111010001 1001101100 1111111111 1111111101 01011111
540   -45  0101011111 1111011111 1111010101 1101111111 1111011111 1111111111 1111010001 1001101100 1111111111 1111111101 01011111
 19   -73  0101011111 1111011111 1111010101 1101111111 1111011111 1111111111 1111010001 1001101100 1111111111 1111111101 01011111

530   ***  0111011111 1111011111 1101010111 1101111111 1111011111 1111111111 1111010001 1001101100 1111111111 1111111101 11111111
541    34  0111011111 1111011111 1101010111 1101111111 1111011111 1111111111 1111010001 1001101100 1111111111 1111111101 11111111
542    74  0111011111 1111011111 1101010111 1101111111 1111011111 1111111111 1111010001 1001101100 1111111111 1111111101 11111111
543   106  0111011111 1111011111 1101010111 1101111111 1111011111 1111111111 1111010001 1001101100 1111111111 1111111101 11111111
544   107  0111011111 1111011111 1101010111 1101111111 1111011111 1111111111 1111010001 1001101100 1111111111 1111111101 11111111
545    20  0111011111 1111011111 1101010111 1101111111 1111011111 1111111111 1111010001 1001101100 1111111111 1111111101 11111111
546    88  0111011111 1111011111 1101010111 1101111111 1111011111 1111111111 1111010001 1001101100 1111111111 1111111101 11111111
547     4  0111011111 1111011111 1101010111 1101111111 1111011111 1111111111 1111010001 1001101100 1111111111 1111111101 11111111
548    37  0111011111 1111011111 1101010111 1101111111 1111011111 1111111111 1111010001 1001101100 1111111111 1111111101 11111111
549   105  0111011111 1111011111 1101010111 1101111111 1111011111 1111111111 1111010001 1001101100 1111111111 1111111101 11111111
```

590	7	0110010100	1111011100	1101010111	1100110111	1110001111	1111111111	1111010000	1000101000	1111111010	1111111101	1111000
591	11	0110010100	0111011100	1101010111	1100110111	1110001111	1111111111	1111010000	1000101000	1111111010	1111111101	1111000
592	8	0110010000	0111011100	1101010111	1100110111	1110001111	1111111111	1111010000	1000101000	1111111010	1111111101	1111000
593	63	0110010000	0111011100	1101010111	1100110111	1110001111	1111111111	1101010000	1000101000	1111111010	1111111101	1111000
594	64	0110010000	0111011100	1101010111	1100110111	1110001111	1111111111	1100010000	1000101000	1111111010	1111111101	1111000
595	-99	0110010000	0111011100	1101010111	1100110111	1110001111	1111111111	1100010000	1000101000	1111111010	1111111111	1111000
596	-67	0110010000	0111011100	1101010111	1100110111	1110001111	1111111111	1100011000	1000101000	1111111010	1111111111	1111000
597	-23	0110010000	0111011100	1111010111	1100110111	1110001111	1111111111	1100011000	1000101000	1111111010	1111111111	1111000
598	-78	0110010000	0111011100	1111010111	1100110111	1110001111	1111111111	1100011000	1000101000	1111111010	1111111111	1111000
599	-9	0110010010	0111011100	1111010111	1100110111	1110001111	1111111111	1100011000	1000101000	1111111010	1111111111	1111000
600	-5	0110110010	0111011100	1111010111	1100110111	1110001111	1111111111	1100011000	1000101000	1111111010	1111111111	1111000
601	-68	0110110010	0111011100	1111010111	1100110111	1110001111	1111111111	1100011000	1000101000	1111111010	1111111111	1111000
19	-65	0110110010	0111011100	1111010111	1100110111	1110001111	1111111111	1100011000	1000101000	1111111010	1111111111	1111000

547	***	0110011100	1111011100	1101010111	1100111111	1110001111	1111111111	1111010000	1000101000	1111111010	1111111101	1111000
562	14	0110011100	1110011100	1101010111	1100111111	1110001111	1111111111	1111010000	1000101000	1111111010	1111111101	1111000
563	66	0110011100	1110011100	1101010111	1100111111	1110001111	1111111111	1111000000	1000101000	1111111010	1111111101	1111000
564	21	0110011100	1110011100	0101010111	1100111111	1110001111	1111111111	1111000000	1000101000	1111111010	1111111101	1111000
565	89	0110011100	1110011100	0101010111	1100111111	1110001111	1111111111	1111000000	1000101000	1111111000	1111111101	1111000
566	75	0110011100	1110011100	0101010111	1100111111	1110001111	1111111111	1111000000	1000101000	1111111000	1111111101	1111000
567	104	0110011100	1110011100	0101010111	1100111111	1110001111	1111111111	1111000000	1000101000	1111111000	1111111101	1110100
568	30	0110011100	1110011100	0101010110	1100111111	1110001111	1111111111	1111000000	1000101000	1111111000	1111111101	1110100
569	77	0110011100	1110011100	0101010110	1100111111	1110001111	1111111111	1111000000	1000100000	1111111000	1111111101	1110100
570	-46	0110011100	1110011100	0101010110	1100111111	1110011111	1111111111	1111000000	1000100000	1111111000	1111111101	1110100
571	-108	0110011100	1110011100	0101010110	1100111111	1110011111	1111111111	1111000000	1000000000	1111111000	1111111101	1110100
572	-90	0110011100	1110011100	0101010110	1100111111	1110011111	1111111111	1111000000	1000000000	1111111001	1111111101	1110100
573	-80	0110011100	1110011100	0101010110	1100111111	1110011111	1111111111	1111000000	1000000001	1111111001	1111111101	1110100
574	-23	0110011100	1110011100	0111010110	1100111111	1110011111	1111111111	1111000000	1000000001	1111111001	1111111101	1110100
575	-79	0110011100	1110011100	0111010110	1100111111	1110011111	1111111111	1111000000	1000000011	1111111001	1111111101	1110100
576	-78	0110011100	1110011100	0111010110	1100111111	1110011111	1111111111	1111000000	1000000111	1111111001	1111111101	1110100
577	-27	0110011100	1110011100	0111011110	1100111111	1110011111	1111111111	1111000000	1000000111	1111111001	1111111101	1110100
578	-9	0110011110	1110011100	0111011110	1100111111	1110011111	1111111111	1111000000	1000000111	1111111001	1111111101	1110100
579	-106	0110011110	1110011100	0111011110	1100111111	1110011111	1111111111	1111000000	1000000111	1111111001	1111111101	1110110
580	-70	0110011110	1110011100	0111011110	1100111111	1110011111	1111111111	1111000001	1000000111	1111111001	1111111101	1110110
581	-5	0110111110	1110011100	0111011110	1100111111	1110011111	1111111111	1111000001	1000000111	1111111001	1111111101	1110110
3	-33	0110111110	1110011100	0111011110	1100111111	1110011111	1111111111	1111000001	1000000111	1111111001	1111111101	1110110

566	***	0110011100	1110011100	0101010111	1100111111	1110001111	1111111111	1111000000	1000010000	1111111000	1111111101	1111000
582	38	0110011100	1110011100	0101010111	1100111111	1110001111	1111111111	1111000000	1000001000	1111111000	1111111101	1111000
583	11	0110011100	0110011100	0101010111	1100111111	1110001111	1111111111	1111000000	1000001000	1111111000	1111111101	1111000
584	3	0100011100	0110011100	0101010111	1100111111	1110001111	1111111111	1111000000	1000001000	1111111000	1111111101	1111000
585	71	0100011100	0110011100	0101010111	1100111111	1110001111	1111111111	1111000000	0000001000	1111111000	1111111101	1111000
586	8	0100011000	0110011100	0101010111	1100111111	1110001111	1111111111	1111000000	0000001000	1111111000	1111111101	1111000
587	39	0100011000	0110011100	0101010111	1100111111	1110001111	1111111111	1111000000	0000001000	1111111000	1111111101	1111000
588	40	0100011000	0110011100	0101010111	1100111110	1110001111	1111111111	1111000000	0000001000	1111111000	1111111101	1111000
589	-46	0100011000	0110011100	0101010111	1100111000	1110001111	1111111111	1111000000	0000001000	1111111000	1111111101	1111000
590	-1	1100011000	0110011100	0101010111	1100111000	1110001111	1111111111	1111000000	0000001000	1111111000	1111111101	1111000
591	-99	1100011000	0110011100	0101010111	1100111000	1110001111	1111111111	1111000000	0000001000	1111111000	1111111111	1111000
592	-90	1100011000	0110011100	0101010111	1100111000	1110001111	1111111111	1111000000	0000001000	1111111001	1111111111	1111000
593	-89	1100011000	0110011100	0101010111	1100111000	1110011111	1111111111	1111000000	0000001000	1111111011	1111111111	1111000
594	-44	1100011000	0110011100	0101010111	1100111000	1110011111	1111111111	1111000000	0000001000	1111111011	1111111111	1111000
595	-19	1100011000	0110011110	0101010111	1100111000	1110011111	1111111111	1111000000	0000001000	1111111011	1111111111	1111000
596	-4	1101011000	0110011110	0101010111	1100111000	1110011111	1111111111	1111000000	0000001000	1111111011	1111111111	1111000
597	-79	1101011000	0110011110	0101010111	1100111000	1110011111	1111111111	1111000000	0000001010	1111111011	1111111111	1111000
598	-78	1101011000	0110011110	0101010111	1100111000	1110011111	1111111111	1111000000	0000001110	1111111011	1111111111	1111000
599	-27	1101011000	0110011110	0101011111	1100111000	1110011111	1111111111	1111000000	0000001110	1111111011	1111111111	1111000
600	-20	1101011000	0110011111	0101011111	1100111000	1110011111	1111111111	1111000000	0000001110	1111111011	1111111111	1111000
601	-9	1101011010	0110011111	0101011111	1100111000	1110011111	1111111111	1111000000	0000001110	1111111011	1111111111	1111000

APPENDIX G (continued)

APPENDIX G (continued)

APPENDIX G (continued)

```
758    -45   0110001100 1110001101 1100011111 0100101111 0111111100 0000011111 1111001001 0100000011 1111000001 1111111111 1110010
759     -5   0110101100 1110001101 1100011111 0100101111 0111111100 0000011111 1111001001 0100000011 1111000001 1111111111 1110010
  4    -25   0110101100 1110001101 1100111111 0100101111 0111111100 0000011111 1111001001 0100000011 1111000001 1111111111 1110010

746    ***   0110001100 1110001100 0100010111 0100100011 0110011100 0000011111 1111001000 0000000001 1111000000 1111111111 1110000
769    103   0110001100 1110001100 0100010111 0100100011 0110011100 0000011111 1111001000 0000000001 1111000000 1111111111 1110000
761     12   0110001100 1010001100 0100010111 0100100011 0110011100 0000011111 1111001000 0000000001 1111000000 1111111111 1100000
762     95   0110001100 1010001100 0100010111 0100100011 0110011100 0000011111 1111001000 0000000001 1111000000 1111111111 1100000
763     96   0110001100 1010001100 0100010111 0100100011 0110011100 0000011111 1111001000 0000000001 1111000000 1111111111 1100000
764     97   0110001100 1010001100 0100010111 0100100011 0110011100 0000011111 1111001000 0000000001 1111000000 1111111111 1100000
765     98   0110001100 1010001100 0100010111 0100100011 0110011100 0000011111 1111001000 0000000001 1111000000 1111111111 1100000
766    -16   0110001100 1010001100 0100010111 0100100011 0110011100 0000011111 1111001000 0000000001 1111000000 1111111111 1100000
767    -71   0110001100 1010001100 0100010111 0100100011 0110011100 0000011111 1111001000 0000000001 1111000000 1111111111 1100000
768    -24   0110001100 1010001100 0100010111 0100100011 0110011100 0000011111 1111001000 0000000001 1111000000 1111111111 1100000
769    -77   0110001100 1010001100 0100010111 0100100011 0110011100 0000011111 1111001000 0000000001 1111000000 1111111111 1100000
770     -1   0110001100 1010001100 0100010111 0100100011 0110011100 0000011111 1111001000 0000000001 1111000000 1111111111 1100000
771    -75   0110001100 1010001100 0100010111 0100100011 0110011100 0000011111 1111001000 0000000001 1111000000 1111111111 1100000
772    -69   0110001100 1010001100 0100010111 0100100011 0110011100 0000011111 1111001000 0000000001 1111000000 1111111111 1100000
773    -90   0110001100 1010001100 0100010111 0100100011 0110011100 0000011111 1111001000 0000000001 1111000000 1111111111 1100000
774    -19   0110001100 1010001100 0100010111 0100100011 0110011100 0000011111 1111001000 0000000001 1111000000 1111111111 1100000
775     -4   0110001100 1010001100 0100010111 0100100011 0110011100 0000011111 1111001000 0000000001 1111000000 1111111111 1100000
776    -79   0110001100 1010001100 0100010111 0100100011 0110011100 0000011111 1111001000 0000000001 1111000000 1111111111 1100000
777    -72   0110001100 1010001100 0100010111 0100100011 0110011100 0000011111 1111001000 0000000001 1111000000 1111111111 1100000
778    -53   0110001100 1010001100 0100010111 0100100011 0110011100 0000011111 1111001000 0000000001 1111000000 1111111111 1100000
779    -45   0110001100 1010001100 0100010111 0100100011 0110011100 0000011111 1111001000 0000000001 1111000000 1111111111 1100000
780    -10   0110001100 1010001100 0100010111 0100100011 0110011100 0000011111 1111001000 0000000001 1111000000 1111111111 1100000
781    -68   0110001100 1010001100 0100010111 0100100011 0110011100 0000011111 1111001000 0000000001 1111000000 1111111111 1100000
 50    -65   0110001100 1010001100 0100010111 0100100011 0110011100 0000011111 1111001000 0000000001 1111000000 1111111111 1100000

747    ***   0110001100 1110001100 0100010111 0100100011 0110011100 0000011111 1111001000 0000000001 1111000000 1111111111 1100000
782     67   0110001100 1110001100 0100010111 0100100011 0110011100 0000011111 1111001000 0000000001 1111000000 1111111111 1100000
783     80   0110001100 1110001100 0100010111 0100100011 0110011100 0000011111 1111001000 0000000001 1111000000 1111111111 1100000
784     13   0110001100 1110001100 0100010111 0100100011 0110011100 0000011111 1111001000 0000000001 1111000000 1111111111 1100000
785     26   0110001100 1110001100 0100010111 0100100011 0110011100 0000011111 1111001000 0000000001 1111000000 1111111111 1100000
786      8   0110001000 1110001100 0100000111 0100100011 0110011100 0000011111 1111001000 0000000001 1111000000 1111111111 1100000
787    -16   0110001000 1110001100 0100000111 0100100011 0110011100 0000011111 1111001000 0000000001 1111000000 1111111111 1100000
788    -24   0110001000 1110001100 0100000111 0100100011 0110011100 0000011111 1111001000 0000000001 1111000000 1111111111 1100000
789     -6   0110001000 1110001100 0100000111 0100100011 0110011100 0000011111 1111001000 0000000001 1111000000 1111111111 1100000
790    -77   0110001000 1110001100 0100000111 0100100011 0110011100 0000011111 1111001000 0000000001 1111000000 1111111111 1100000
791    -36   0110001000 1110001100 0100000111 0100100011 0110011100 0000011111 1111001000 0000000001 1111000000 1111111111 1100000
792     -1   0110001000 1110001100 0100000111 0100100011 0110011100 0000011111 1111001000 0000000001 1111000000 1111111111 1100000
793    -75   0110001000 1110001100 0100000111 0100100011 0110011100 0000011111 1111001000 0000000001 1111000000 1111111111 1100000
794    -89   0110001000 1110001100 0100000111 0100100011 0110011100 0000011111 1111001000 0000000001 1111000000 1111111111 1100000
795    -31   0110001000 1110001100 0100000111 0100100011 0110011100 0000011111 1111001000 0000000001 1111000000 1111111111 1100000
796    -21   0110001000 1110001100 0100000111 0100100011 0110011100 0000011111 1111001000 0000000001 1111000000 1111111111 1100000
797    -19   0110001000 1110001100 0100000111 0100100011 0110011100 0000011111 1111001000 0000000001 1111000000 1111111111 1100000
798    -79   0110001000 1110001100 0100000111 0100100011 0110011100 0000011111 1111001000 0000000001 1111000000 1111111111 1100000
799    -72   0110001000 1110001100 0100000111 0100100011 0110011100 0000011111 1111001000 0000000001 1111000000 1111111111 1100000
800    -20   0110001000 1110001100 0100000111 0100100011 0110011100 0000011111 1111001000 0000000001 1111000000 1111111111 1100000
801   -107   0110001000 1110001100 0100000111 0100100011 0110011100 0000011111 1111001000 0000000001 1111000000 1111111111 1100000
802    -74   0110001000 1110001100 0100000111 0100100011 0110011100 0000011111 1111001000 0000000001 1111000000 1111111111 1100000
803    -10   0110001000 1110001100 0100000111 0100100011 0110011100 0000011111 1111001000 0000000001 1111000000 1111111111 1100000
804    -25   0110001000 1110001100 0100000111 0100100011 0110011100 0000011111 1111001000 0000000001 1111000000 1111111111 1100000
805    -15   0110001000 1110001100 0100000111 0100100011 0110011100 0000011111 1111001000 0000000001 1111000000 1111111111 1100000
 20    -33   0110001000 1110001100 0100000111 0100100011 0110011100 0000011111 1111001000 0000000001 1111000000 1111111111 1100000

789    ***   0110001000 1110001100 0100000111 0100100011 0110011100 0000011111 1111001000 0000000001 1111000000 1111111111 1100000
```

APPENDIX G (continued)

859	22	0110010100	1110011100	0000000100	0000000011	0110000000	0000011111	1111001000	0000000000	1111000000	1111111111	01000001
859	-71	0110010100	1110011100	0000000100	0000000011	0110000000	0000011111	1111001000	0000000000	1111000000	1111111111	01000001
859	-48	0110010100	1110011100	0000000100	0000000011	0110000000	0000011111	1111001000	0000000000	1111000000	1111111111	01000001
861	-77	0110010100	1110011100	0000000100	0000000011	0110000000	0000011111	1111001000	0000000000	1111000000	1111111111	01000001
862	-30	0110010100	1110011100	0000000100	0000000011	0110000000	0000011111	1111001000	0000000000	1111000000	1111111111	01000001
863	-46	0110010100	1110011100	0000000100	0000000011	0110000000	0000011111	1111001000	0000000000	1111000000	1111111111	01000001
864	-36	0110010100	1110011100	0000000100	0000000011	0110000000	0000011111	1111001000	0000000000	1111000000	1111111111	01000001
865	-35	0110010100	1110011100	0000000100	0000000011	0110000000	0000011111	1111001000	0000000000	1111000000	1111111111	01000001
866	-105	0110010100	1110011100	0000000100	0000000011	0110000000	0000011111	1111001000	0000000000	1111000000	1111111111	01000001
867	-104	0110010100	1110011100	0000000100	0000000011	0110000000	0000011111	1111001000	0000000000	1111000000	1111111111	01000001
868	-75	0110010100	1110011100	0000000100	0000000011	0110000000	0000011111	1111001000	0000000000	1111000000	1111111111	01000001
869	-37	0110010100	1110011100	0000000100	0000000011	0110000000	0000011111	1111001000	0000000000	1111000000	1111111111	01000001
870	-44	0110010100	1110011100	0000000100	0000000011	0110000000	0000011111	1111001000	0000000000	1111000000	1111111111	01000001
871	-88	0110010100	1110011100	0000000100	0000000011	0110000000	0000011111	1111001000	0000000000	1111000000	1111111111	01000001
872	-73	0110010100	1110011100	0000000100	0000000011	0110000000	0000011111	1111001000	0000000000	1111000000	1111111111	01000001
873	-66	0110010100	1110011100	0000000100	0000000011	0110000000	0000011111	1111001000	0000000000	1111000000	1111111111	01000001
874	-27	0110010100	1110011100	0000000100	0000000011	0110000000	0000011111	1111001000	0000000000	1111000000	1111111111	01000001
875	-14	0110010100	1110011100	0000000100	0000000011	0110000000	0000011111	1111001000	0000000000	1111000000	1111111111	01000001
876	-9	0110010100	1110011100	0000000100	0000000011	0110000000	0000011111	1111001000	0000000000	1111000000	1111111111	01000001
877	-106	0110010100	1110011100	0000000100	0000000011	0110000000	0000011111	1111001000	0000000000	1111000000	1111111111	01000001
878	-70	0110010100	1110011100	0000000100	0000000011	0110000000	0000011111	1111001000	0000000000	1111000000	1111111111	01000001
879	-19	0110010100	1110011100	0000000100	0000000011	0110000000	0000011111	1111001000	0000000000	1111000000	1111111111	01000001
880	-73	0110010100	1110011100	0000000100	0000000011	0110000000	0000011111	1111001000	0000000000	1111000000	1111111111	01000001
44	-65	0110010100	1110011100	0000000100	0000000011	0110000000	0000011111	1111001000	0000000000	1111000000	1111111111	01000001
850	-88	1100011100	0011011110	1111011111	0000010011	1111010100	0000011111	1111000010	1000101001	1111000010	1111000010	11111101
851	19	1100011100	0011011100	1111011111	0000010011	1111010100	0000011111	1111000010	1000101001	1111000010	1111000010	11111101
852	89	1100011100	0011011100	1111011111	0000010011	1111010100	0000011111	1111000010	1000101001	1111000000	1111000010	11111101
853	69	1100011100	0011011100	1111011111	0000010011	1111010100	0000011111	1111000000	1000101001	1111000000	1111000010	11111101
854	99	1100011100	0011011100	1111011111	0000010011	1111010100	0000011111	1111000000	1000101001	1111000000	1111000000	11111101
855	46	1100011100	0011011100	1111011111	0000010011	1111000100	0000011111	1111000000	1000101001	1111000000	1111000000	11111101
856	30	1100011100	0011011100	1111011110	0000010011	1111000100	0000011111	1111000000	1000101001	1111000000	1111000000	11111101
857	77	1100011100	0011011100	1111011110	0000010011	1111000100	0000011111	1111000000	1000100001	1111000000	1111000000	11111101
858	101	1100011100	0011011100	1111011110	0000010011	1111000100	0000011111	1111000000	1000100001	1111000000	1111000000	01111101
859	28	1100011100	0011011100	1111011010	0000010011	1111000000	0000011111	1111000000	1000100001	1111000000	1111000000	01111101
860	48	1100011100	0011011100	1111011010	0000010011	1111000000	0000011111	1111000000	1000100001	1111000000	1111000000	01111101
861	18	1100011100	0011011000	1111011010	0000010011	1111000000	0000011111	1111000000	1000100001	1111000000	1111000000	01111101
862	-32	1100011100	0011011000	1111011010	0100010011	1111000000	0000011111	1111000000	1000100001	1111000000	1111000000	01111101
863	-12	1100011100	0111011000	1111011010	0100010011	1111000000	0000011111	1111000000	1000100001	1111000000	1111000000	01111101
864	-11	1100011100	1111011000	1111011010	0100010011	1111000000	0000011111	1111000000	1000100001	1111000000	1111000000	01111101
865	-87	1100011100	1111011000	1111011010	0100010011	1111000000	0000011111	1111000000	1000100001	1111000000	1111000000	01111101
866	-86	1100011100	1111011000	1111011010	0100010011	1111000000	0000011111	1111000000	1000100001	1111000000	1111000000	01111101
867	-65	1100011100	1111011000	1111011010	0100010011	1111000000	0000011111	1111000000	1000100001	1111000000	1111000000	01111101
868	-38	1100011100	1111011000	1111011010	0100010111	1111000000	0000011111	1111000000	1000100001	1111000000	1111000000	01111101
869	-90	1100011100	1111011000	1111011010	0100010111	1111000000	0000011111	1111000000	1000100001	1111000000	1111000000	01111101
900	-67	1100011100	1111011000	1111011010	0100010111	1111000000	0000011111	1111000000	1000100001	1111000000	1111000000	01111101
901	-4	1101011100	1111011000	1111011010	0100010111	1111000000	0000011111	1111000000	1000100001	1111000000	1111000000	01111101
902	-66	1101011100	1111011000	1111011010	0100010111	1111000000	0000011111	1111000000	1000100001	1111000000	1111000000	01111101
903	-45	1101011100	1111011000	1111011010	0100010111	1111000000	0000011111	1111000000	1000100001	1111000000	1111000000	01111101
904	-34	1101011100	1111011000	1111011010	0101010111	1111000000	0000011111	1111000000	1000100001	1111000000	1111000000	01111101
905	-65	1101011100	1111011000	1111011010	0101010111	1111000000	0000011111	1111000000	1000100001	1111000000	1111000000	01111101
906	-25	1101011100	1111011000	1111011010	0101010111	1111000000	0000011111	1111000000	1000100001	1111000000	1111000000	01111101
22	-76	1101011100	1111011000	1111011010	0101010111	1111000000	0000011111	1111000000	1000100001	1111000000	1111000000	01111101
769	100	0110001100	1010011100	0101010111	0100100011	0110011100	0000011111	1111001000	1000001001	1111000000	1111000011	11000001
907	67	0110001100	1010011100	0101010111	0100100011	0110011100	0000011111	1111000000	1000001001	1111000000	1111000011	11000001
908	89	0110001100	1010011100	0101010111	0100100011	0110011100	0000011111	1111000000	1000001000	1111000000	1111000011	11000001
909	108	0110001100	1010011100	0101010111	0100100011	0110011100	0000011111	1111000000	1000001000	1111000000	1111000011	11000000

APPENDIX G (continued)

APPENDIX G (continued)

```
966   -67   1111011000 1101111100 0101001011 2102111011 2110000000 0110011100 1300001000 1111111000 0101010001
967   -31   1111011000 1101111000 0101010011 2102111011 2110000000 0110011100 1300001000 1111111000 0101010001
968   -21   1111011000 1101111000 0101010011 2102111011 2110000000 0110011100 1300001000 1111111000 0101010001
969   -98   1111011000 1101111000 0101010011 2102111011 2110000000 0110011100 1300001000 1111111000 0101010001
970   -78   1111011000 1101111000 0101010011 2102111011 2110000000 0110011100 1300001000 1111111000 0101010001
971   -72   1111011000 1101111000 0101010011 2102111011 2110000000 0110011100 1300001000 1111111000 0101010001
972   -66   1111011000 1101111000 0101010011 2102111011 2110000000 0110011100 1300001000 1111111000 0101010001
973    -9   1111011000 1101111000 0101010011 2102111011 2110000000 0110011100 1300001000 1111111000 0101010001
974   -74   1111011000 1101111000 0101010011 2102111011 2110000000 0110011100 1300001000 1111111000 0101010001
975   -34   1111011000 1101111000 0101010011 2102111011 2110000000 0110011100 1300001000 1111111000 0101010001
976   -68   1111011000 1101111000 0101010011 2102111011 2110000000 0110011100 1300001000 1111111000 0101010001
977   -25   1111011000 1101111000 0101010011 2102111011 2110000000 0110011100 1300001000 1111111000 0101010001
978   -15   1111011000 1101111000 0101010011 2102111011 2110000000 0110011100 1300001000 1111111000 0101010001
979   -76   1111011000 1101111000 0101010011 2102111011 2110000000 0110011100 1300001000 1111111000 0101010001
 18   -33   1111011000 1101111000 0101010011 2102111011 2110000000 0110011100 1300001000 1111111000 0101010001
```

EVOLUTION OF 11 TAXA DETERMINED USING 23 CHARACTERS AND .378 AS THE LEVEL OF SIGNIFICANCE.

```
501     ***   --1-------- 11---1---- ---1---111 -1---1--11 --------1-- -----1--1- ---------- ---------- 1---1---1- 1----1---- --------
502      39   --1-------- 11---1---- ---1---111 -1---1--01 --------1-- -----1--1- ---------- ---------- 1---1---1- 1----1---- --------
 31      40   --1-------- 11---1---- ---1---111 -1---1--00 --------1-- -----1--1- ---------- ---------- 1---1---1- 1----1---- --------

 31      ***  --1-------- 11---1---- ---1---111 -1---1--00 --------1-- -----1--1- ---------- ---------- 1---1---1- 1----1---- --------
503      29   --1-------- 11---1---- ---1---101 -1---1--00 --------1-- -----1--1- ---------- ---------- 1---1---1- 1----1---- --------
504      96   --1-------- 11---1---- ---1---101 -1---1--00 --------1-- -----1--1- ---------- ---------- 1---1---1- 1----0---- --------
 55      24   --1-------- 11---1---- ---0---101 -1---1--00 --------1-- -----1--1- ---------- ---------- 1---1---1- 1----0---- --------

503      ***  --1-------- 11---1---- ---1---101 -1---1--00 --------1-- -----1--1- ---------- ---------- 1---1---1- 1----1---- --------
505      89   --1-------- 11---1---- ---1---101 -1---1--00 --------1-- -----1--1- ---------- ---------- 1---1---0- 1----1---- --------
 58      12   --1-------- 10---1---- ---1---101 -1---1--00 --------1-- -----1--1- ---------- ---------- 1---1---0- 1----1---- --------

 31      ***  --1-------- 11---1---- ---1---111 -1---1--00 --------1-- -----1--1- ---------- ---------- 1---1---1- 1----1---- --------
506      91   --1-------- 11---1---- ---1---111 -1---1--00 --------1-- -----1--1- ---------- ---------- 1---1---1- 0----1---- --------
507      24   --1-------- 11---1---- ---0---111 -1---1--00 --------1-- -----1--1- ---------- ---------- 1---1---1- 0----1---- --------
508      32   --1-------- 11---1---- ---0---111 -0---1--00 --------1-- -----1--1- ---------- ---------- 1---1---1- 0----1---- --------
 30      30   --1-------- 11---1---- ---0---110 -0---1--00 --------1-- -----1--1- ---------- ---------- 1---1---1- 0----1---- --------

506      ***  --1-------- 11---1---- ---1---111 -1---1--00 --------1-- -----1--1- ---------- ---------- 1---1---1- 0----1---- --------
509      85   --1-------- 11---1---- ---1---111 -1---1--00 --------1-- -----1--1- ---------- ---------- 1---0---1- 0----1---- --------
510      56   --1-------- 11---1---- ---1---111 -1---1--00 --------1-- -----0--1- ---------- ---------- 1---0---1- 0----1---- --------
 32      59   --1-------- 11---1---- ---1---111 -1---1--00 --------1-- -----0--0- ---------- ---------- 1---0---1- 0----1---- --------

501      ***  --1-------- 11---1---- ---1---111 -1---1--11 --------1-- -----1--1- ---------- ---------- 1---1---1- 1----1---- --------
511      89   --1-------- 11---1---- ---1---111 -1---1--11 --------1-- -----1--1- ---------- ---------- 1---1---0- 1----1---- --------
512      32   --1-------- 11---1---- ---1---111 -0---1--11 --------1-- -----1--1- ---------- ---------- 1---1---0- 1----1---- --------
 61      16   --1-------- 11---0---- ---1---111 -0---1--11 --------1-- -----1--1- ---------- ---------- 1---1---0- 1----1---- --------

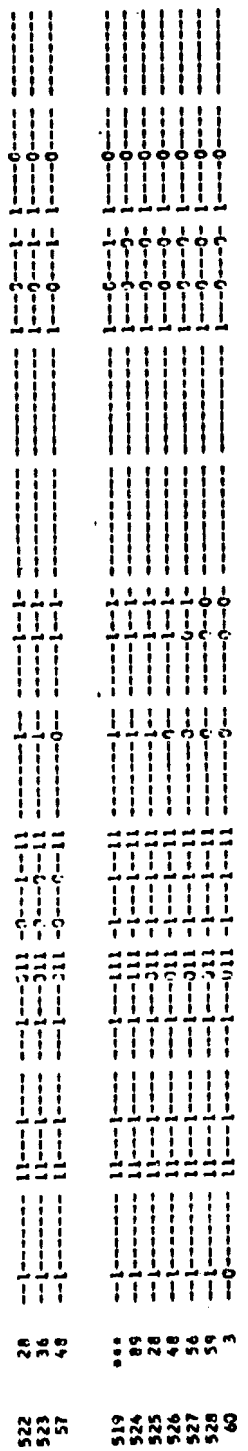
511      ***  --1-------- 11---1---- ---1---111 -1---1--11 --------1-- -----1--1- ---------- ---------- 1---1---0- 1----1---- --------
513      29   --1-------- 11---1---- ---1---101 -1---1--11 --------1-- -----1--1- ---------- ---------- 1---1---0- 1----1---- --------
514      91   --1-------- 11---1---- ---1---101 -1---1--11 --------1-- -----1--1- ---------- ---------- 1---1---0- 0----1---- --------
515      36   --1-------- 11---1---- ---1---101 -1---0--11 --------1-- -----1--1- ---------- ---------- 1---1---0- 0----1---- --------
 62      11   --1-------- 01---1---- ---1---101 -1---0--11 --------1-- -----1--1- ---------- ---------- 1---1---0- 0----1---- --------

514      ***  --1-------- 11---1---- ---1---101 -1---1--11 --------1-- -----1--1- ---------- ---------- 1---1---0- 0----1---- --------
516      12   --1-------- 10---1---- ---1---101 -1---1--11 --------1-- -----1--1- ---------- ---------- 1---1---0- 0----1---- --------
517      30   --1-------- 10---1---- ---1---100 -1---1--11 --------1-- -----1--1- ---------- ---------- 1---1---0- 0----1---- --------
 72      81   --1-------- 10---1---- ---1---100 -1---1--11 --------1-- -----1--1- ---------- ---------- 0---1---0- 0----1---- --------

501      ***  --1-------- 11---1---- ---1---111 -1---1--11 --------1-- -----1--1- ---------- ---------- 1---1---1- 1----1---- --------
519      85   --1-------- 11---1---- ---1---111 -1---1--11 --------1-- -----1--1- ---------- ---------- 1---0---1- 1----1---- --------
519      96   --1-------- 11---1---- ---1---111 -1---1--11 --------1-- -----1--1- ---------- ---------- 1---0---1- 1----0---- --------
520      12   --1-------- 10---1---- ---1---111 -1---1--11 --------1-- -----1--1- ---------- ---------- 1---0---1- 1----0---- --------
 59      24   --1-------- 10---1---- ---0---111 -1---1--11 --------1-- -----1--1- ---------- ---------- 1---0---1- 1----0---- --------

519      ***  --1-------- 11---1---- ---1---111 -1---1--11 --------1-- -----1--1- ---------- ---------- 1---0---1- 1----0---- --------
521      32   --1-------- 11---1---- ---1---111 -0---1--11 --------1-- -----1--1- ---------- ---------- 1---0---1- 1----0---- --------
```

APPENDIX G (continued)



EVOLUTION OF 13 TAXA DETERMINED USING 45 CHARACTERS AND .347 AS THE LEVEL OF SIGNIFICANCE.

```
501    ***  -11--1---- -1-1111--- -1-1---11- -1--11--11 111---11-- -----11111 1111----1- ------1--- 1111------ 111111-1-- -------1
502      6  -11--0---- -1-1111--- -1-1---11- -1--11--11 111---11-- -----11111 1111----1- ------1--- 1111------ 111111-1-- -------1
503     47  -11--0---- -1-1111--- -1-1---11- -1--11--11 111---01-- -----11111 1111----1- ------1--- 1111------ 111111-1-- -------1
11      36  -11--0---- -1-1111--- -1-1---11- -1--10--11 111---01-- -----11111 1111----1- ------1--- 1111------ 111111-1-- -------1

503    ***  -11--0---- -1-1111--- -1-1---11- -1--11--11 111---01-- -----11111 1111----1- ------1--- 1111------ 111111-1-- -------1
504     69  -11--0---- -1-1111--- -1-1---11- -1--11--11 111---01-- -----11111 1111----0- ------1--- 1111------ 111111-1-- -------1
67      29  -11--0---- -1-1111--- -1-1---10- -1--11--11 111---01-- -----11111 1111----0- ------1--- 1111------ 111111-1-- -------1

11     ***  -11--0---- -1-1111--- -1-1---11- -1--10--11 111---01-- -----11111 1111----1- ------1--- 1111------ 111111-1-- -------1
505     29  -11--0---- -1-1111--- -1-1---10- -1--10--11 111---01-- -----11111 1111----1- ------1--- 1111------ 111111-1-- -------1
506     35  -11--0---- -1-1111--- -1-1---10- -1--00--11 111---01-- -----11111 1111----1- ------1--- 1111------ 111111-1-- -------1
12      32  -11--0---- -1-1111--- -1-1---10- -0--00--11 111---01-- -----11111 1111----1- ------1--- 1111------ 111111-1-- -------1

504    ***  -11--0---- -1-1111--- -1-1---11- -1--11--11 111---01-- -----11111 1111----0- ------1--- 1111------ 111111-1-- -------1
507    108  -11--0---- -1-1111--- -1-1---11- -1--11--11 111---01-- -----11111 1111----0- ------1--- 1111------ 111111-1-- -------1
66      -6  -11--1---- -1-1111--- -1-1---11- -1--11--11 111---01-- -----11111 1111----0- ------1--- 1111------ 111111-1-- -------0

507    ***  -11--0---- -1-1111--- -1-1---11- -1--11--11 111---01-- -----11111 1111----0- ------1--- 1111------ 111111-1-- -------0
508     35  -11--0---- -1-1111--- -1-1---11- -1--01--11 111---01-- -----11111 1111----0- ------1--- 1111------ 111111-1-- -------0
509     12  -11--0---- -0-1111--- -1-1---11- -1--01--11 111---01-- -----11111 1111----0- ------1--- 1111------ 111111-1-- -------0
63      22  -11--0---- -0-1111--- -0-1---11- -1--01--11 111---01-- -----11111 1111----0- ------1--- 1111------ 111111-1-- -------0

508    ***  -11--0---- -1-1111--- -1-1---11- -1--01--11 111---01-- -----11111 1111----0- ------1--- 1111------ 111111-1-- -------0
510     95  -11--0---- -1-1111--- -1-1---11- -1--01--11 111---01-- -----11111 1111----0- ------1--- 1111------ 111101-1-- -------0
511     96  -11--0---- -1-1111--- -1-1---11- -1--01--11 111---01-- -----11111 1111----0- ------1--- 1111------ 111100-1-- -------0
512     98  -11--0---- -1-1111--- -1-1---11- -1--01--11 111---01-- -----11111 1111----0- ------1--- 1111------ 111100-0-- -------0
513     48  -11--0---- -1-1111--- -1-1---11- -1--01--11 111---00-- -----11111 1111----0- ------1--- 1111------ 111100-0-- -------0
514     28  -11--0---- -1-1111--- -1-1---01- -1--01--11 111---00-- -----11111 1111----0- ------1--- 1111------ 111100-0-- -------0
79     -47  -11--0---- -1-1111--- -1-1---01- -1--01--11 111---10-- -----11111 1111----0- ------1--- 1111------ 111100-0-- -------0

513    ***  -11--0---- -1-1111--- -1-1---11- -1--01--11 111---00-- -----11111 1111----0- ------1--- 1111------ 111100-0-- -------0
515     36  -11--0---- -1-1111--- -1-1---11- -1--00--11 111---00-- -----11111 1111----0- ------1--- 1111------ 111100-0-- -------0
516     12  -11--0---- -0-1111--- -1-1---11- -1--00--11 111---00-- -----11111 1111----0- ------1--- 1111------ 111100-0-- -------0
517     41  -11--0---- -0-1111--- -1-1---11- -1--00--11 011---00-- -----11111 1111----0- ------1--- 1111------ 111100-0-- -------0
518   -108  -11--0---- -0-1111--- -1-1---11- -1--00--11 011---00-- -----11111 1111----0- ------1--- 1111------ 111100-0-- -------0
64      -6  -11--1---- -0-1111--- -1-1---11- -1--00--11 011---00-- -----11111 1111----0- ------1--- 1111------ 111100-0-- -------1

64     ***  -11--1---- -0-1111--- -1-1---11- -1--00--11 011---00-- -----11111 1111----0- ------1--- 1111------ 111100-0-- -------1
519     29  -11--1---- -0-1111--- -1-1---10- -1--00--11 011---00-- -----11111 1111----0- ------1--- 1111------ 111100-0-- -------1
520     22  -11--1---- -0-1111--- -0-1---10- -1--00--11 011---00-- -----11111 1111----0- ------1--- 1111------ 111100-0-- -------1
521     28  -11--1---- -0-1111--- -0-1---00- -1--00--11 011---00-- -----11111 1111----0- ------1--- 1111------ 111100-0-- -------1
522     32  -11--1---- -0-1111--- -0-1---00- -0--00--11 011---00-- -----11111 1111----0- ------1--- 1111------ 111100-0-- -------1
523    -47  -11--1---- -0-1111--- -0-1---00- -0--00--11 011---10-- -----11111 1111----0- ------1--- 1111------ 111100-0-- -------1
65     -69  -11--1---- -0-1111--- -0-1---00- -0--00--11 011---10-- -----11111 1111----1- ------1--- 1111------ 111100-0-- -------1

519    ***  -11--1---- -0-1111--- -1-1---10- -1--00--11 011---00-- -----11111 1111----0- ------1--- 1111------ 111100-0-- -------1
524      3  -10--1---- -0-1111--- -1-1---10- -1--00--11 011---00-- -----11111 1111----0- ------1--- 1111------ 111100-0-- -------1
525    -41  -10--1---- -0-1111--- -1-1---10- -1--00--11 111---00-- -----11111 1111----0- ------1--- 1111------ 111100-0-- -------1
```

APPENDIX G (continued)

Histogram

EVOLUTION OF 17 TAXA DETERMINED USING 29 CHARACTERS AND .212 AS THE LEVEL OF SIGNIFICANCE.

```
501    ***   1-1--1----- --------11 -1-1---111 11-111---- 11----11-- 1---1----- ---------- ---------- ----111-11 --------1- -1-----1
502     24   1-1--1----- --------11 -1-0---111 11-111---- 11----11-- 1---1----- ---------- ---------- ----111-11 --------1- -1-----1
503      1   0-1--1----- --------11 -1-0---111 11-111---- 11----11-- 1---1----- ---------- ---------- ----111-11 --------1- -1-----1
504     47   0-1--1----- --------11 -1-0---111 11-111---- 11----C1-- 1---1----- ---------- ---------- ----111-11 --------1- -1-----1
 74     90   0-1--1----- --------11 -1-0---111 11-111---- 11----C1-- 1---1----- ---------- ---------- ----111-11 --------1- -1-----1
                                                                                                       ----111-10 --------1- -1-----1

504    ***   0-1--1----- --------11 -1-0---111 11-111---- 11----C1-- 1---1----- ---------- ---------- ----111-11 --------1- -1-----1
509     51   0-1--1----- --------11 -1-0---111 11-111---- 11----01-- C---1----- ---------- ---------- ----111-11 --------1- -1-----1
506     55   0-1--1----- --------11 -1-0---111 11-111---- 11----C1-- C---0----- ---------- ---------- ----111-11 --------1- -1-----1
507     34   0-1--1----- --------11 -1-0---111 11-011---- 11----C1-- 0---0----- ---------- ---------- ----111-11 --------1- -1-----1
508     20   0-1--1----- --------10 -1-0---111 11-011---- 11----C1-- 0---0----- ---------- ---------- ----111-11 --------1- -1-----1
 76     41   0-1--1----- --------10 -1-0---111 11-011---- C1----C1-- C---0----- ---------- ---------- ----111-11 --------1- -1-----1

506    ***   0-1--1----- --------11 -1-0---111 11-111---- 11----C1-- 0---0----- ---------- ---------- ----111-11 --------1- -1-----1
509     29   0-1--1----- --------11 -1-0---101 11-111---- 11----C1-- 0---0----- ---------- ---------- ----111-11 --------1- -1-----1
510     89   0-1--1----- --------11 -1-0---101 11-111---- 11----01-- 0---0----- ---------- ---------- ----111-01 --------1- -1-----1
511     90   0-1--1----- --------11 -1-0---101 11-111---- 11----C1-- C---0----- ---------- ---------- ----111-00 --------1- -1-----1
512     28   0-1--1----- --------11 -1-0---001 11-111---- 11----C1-- C---0----- ---------- ---------- ----111-00 --------1- -1-----1
513     19   0-1--1----- --------01 -1-0---001 11-111---- 11----C1-- 0---0----- ---------- ---------- ----111-00 --------1- -1-----1
 75    -47   0-1--1----- --------01 -1-0---001 11-111---- 11----11-- 0---0----- ---------- ---------- ----111-00 --------1- -1-----1

510    ***   0-1--1----- --------11 -1-0---101 11-111---- 11----01-- C---0----- ---------- ---------- ----111-01 --------1- -1-----1
514     30   0-1--1----- --------11 -1-0---100 11-111---- 11----01-- C---0----- ---------- ---------- ----111-01 --------1- -1-----1
515     31   0-1--1----- --------11 -1-0---100 01-111---- 11----C1-- 0---0----- ---------- ---------- ----111-01 --------1- -1-----1
516     48   0-1--1----- --------11 -1-0---1C0 01-111---- 11----00-- C---0----- ---------- ---------- ----111-01 --------1- -1-----1
517      6   0-1--0----- --------11 -1-0---1C0 01-111---- 11----C0-- C---0----- ---------- ---------- ----111-01 --------1- -1-----1
 40    -24   0-1--0----- --------11 -1-1---1C0 01-111---- 11----CC-- C---0----- ---------- ---------- ----111-01 --------1- -1-----1

516    ***   0-1--1----- --------11 -1-0---100 01-111---- 11----C0-- 0---0----- ---------- ---------- ----111-01 --------1- -1-----1
518     90   0-1--1----- --------11 -1-0---100 01-111---- 11----C0-- 0---0----- ---------- ---------- ----111-00 --------1- -1-----1
519     28   0-1--1----- --------11 -1-0---C00 01-111---- 11----C0-- C---0----- ---------- ---------- ----111-00 --------1- -1-----1
520     85   0-1--1----- --------11 -1-0---000 01-111---- 11----C0-- 0---0----- ---------- ---------- ----011-00 --------1- -1-----1
521     86   0-1--1----- --------11 -1-0---C00 01-111---- 11----C0-- 0---0----- ---------- ---------- ----001-00 --------1- -1-----1
522     87   0-1--1----- --------11 -1-0---0C0 01-111---- 11----C0-- 0---0----- ---------- ---------- ----000-00 --------1- -1-----1
 71     20   0-1--1----- --------10 -1-0---CCC 01-111---- 11----CC-- C---0----- ---------- ---------- ----000-00 --------1- -1-----1

512    ***   0-1--1----- --------11 -1-0---001 11-111---- 11----C1-- 0---0----- ---------- ---------- ----111-00 --------1- -1-----1
523      3   0-0--1----- --------11 -1-0---001 11-111---- 11----C1-- 0---0----- ---------- ---------- ----111-00 --------1- -1-----1
524    -89   0-0--1----- --------11 -1-0---001 11-111---- 11----01-- C---0----- ---------- ---------- ----111-10 --------1- -1-----1
529    -47   0-0--1----- --------11 -1-C---001 11-111---- 11----11-- C---0----- ---------- ---------- ----111-10 --------1- -1-----1
526    -55   0-0--1----- --------11 -1-0---001 11-111---- 11----11-- 0---1----- ---------- ---------- ----111-10 --------1- -1-----1
527    -51   0-0--1----- --------11 -1-0---C01 11-111---- 11----11-- 1---1----- ---------- ---------- ----111-10 --------1- -1-----1
 77    -24   0-0--1----- --------11 -1-1---C01 11-111---- 11----11-- 1---1----- ---------- ---------- ----111-10 --------1- -1-----1

522    ***   0-1--1----- --------11 -1-0---000 01-111---- 11----C0-- 0---0----- ---------- ---------- ----000-00 --------1- -1-----1
528     99   0-1--1----- --------11 -1-0---000 01-111---- 11----C0-- 0---0----- ---------- ---------- ----000-00 --------0- -1-----1
529     22   0-1--1----- --------11 -0-0---C00 01-111---- 11----C0-- 0---0----- ---------- ---------- ----000-00 --------0- -1-----1
530      3   0-0--1----- --------11 -0-0---C00 01-111---- 11----C0-- C---0----- ---------- ---------- ----000-00 --------0- -1-----1
531    -28   0-0--1----- --------11 -0-0---100 01-111---- 11----C0-- C---0----- ---------- ---------- ----000-00 --------0- -1-----1
532    -90   0-0--1----- --------11 -0-0---100 01-111---- 11----CC-- C---0----- ---------- ---------- ----000-01 --------0- -1-----1
533    -47   0-0--1----- --------11 -0-0---1C0 01-111---- 11----10-- C---0----- ---------- ---------- ----000-01 --------0- -1-----1
```

```
536     -1  1-0--1----  --------11  -0-0---1C0  01-111----  11----1C--  C---0-----  ----------  ----------  ----000-01  --------0-  -1-----1
 33    -31  1-0--1----  --------11  -0-0---100  11-111----  11----1C--  0---0-----  ----------  ----------  ----000-01  --------0-  -1-----1

534     ...  1-0--1----  --------11  -0-0---1C0  01-111----  11----1C--  C---0-----  ----------  ----------  ----000-01  --------0-  -1-----1
535       6  1-0--0----  --------11  -0-0---1C0  01-111----  11----1C--  C---C-----  ----------  ----------  ----000-01  --------0-  -1-----1
536      -3  1-1--0----  --------11  -0-0---1C0  01-111----  11----1C--  C---0-----  ----------  ----------  ----000-01  --------0-  -1-----1
537     -89  1-1--0----  --------11  -0-C---100  01-111----  11----10--  0---0-----  ----------  ----------  ----000-01  --------0-  -1-----1
538     -30  1-1--0----  --------11  -0-0---101  01-111----  11----10--  C---0-----  ----------  ----------  ----000-11  --------0-  -1-----1
539     -29  1-1--0----  --------11  -0-C---111  01-111----  11----10--  0---0-----  ----------  ----------  ----000-11  --------0-  -1-----1
 39     -24  1-1--0----  --------11  -0-1---111  01-111----  11----1C--  C---0-----  ----------  ----------  ----000-11  --------0-  -1-----1

537     ...  1-1--0----  --------11  -0-0---1C0  01-111----  11----10--  0---0-----  ----------  ----------  ----000-11  --------0-  -1-----1
540      90  1-1--0----  --------11  -0-0---1C0  01-111----  11----10--  0---C-----  ----------  ----------  ----000-10  --------0-  -1-----1
541      34  1-1--0----  --------11  -0-0---1C0  01-011----  11----10--  C---0-----  ----------  ----------  ----000-10  --------0-  -1-----1
542     -22  1-1--0----  --------11  -1-0---100  01-C11----  11----1C--  C---0-----  ----------  ----------  ----000-10  --------0-  -1-----1
543     -48  1-1--0----  --------11  -1-0---100  01-011----  11----11--  0---0-----  ----------  ----------  ----000-10  --------0-  -1-----1
 34     -24  1-1--0----  --------11  -1-1---1C0  01-011----  11----11--  0---0-----  ----------  ----------  ----000-10  --------0-  -1-----1

539     ...  1-1--0----  --------11  -0-0---111  01-111----  11----10--  C---0-----  ----------  ----------  ----000-11  --------0-  -1-----1
544      47  1-1--0----  --------11  -0-0---111  01-111----  11----C0--  C---0-----  ----------  ----------  ----000-11  --------0-  -1-----1
545      90  1-1--0----  --------11  -0-0---111  01-111----  11----C0--  0---0-----  ----------  ----------  ----000-10  --------0-  -1-----1
546      34  1-1--0----  --------11  -0-0---111  01-011----  11----C0--  C---0-----  ----------  ----------  ----000-10  --------0-  -1-----1
547      20  1-1--0----  --------1C  -0-0---111  01-C11----  11----C0--  C---0-----  ----------  ----------  ----000-10  --------0-  -1-----1
548       3  1-0--0----  --------10  -0-0---111  01-011----  11----C0--  C---0-----  ----------  ----------  ----000-10  --------0-  -1-----1
549      36  1-0--0----  --------10  -0-0---111  01-C1C----  11----CC--  0---0-----  ----------  ----------  ----000-10  --------0-  -1-----1
 39      -6  1-0--1----  --------10  -0-0---111  01-C1C----  11----C0--  C---0-----  ----------  ----------  ----000-10  --------0-  -1-----1

 39     ...  1-0--1----  --------10  -0-C---111  01-01C----  11----CC--  C---0-----  ----------  ----------  ----000-10  --------0-  -1-----1
550      69  1-0--1----  --------10  -0-0---111  01-01C----  11----CC--  C---0-----  ----------  ----------  ----000-10  --------0-  -1-----1
551      28  1-0--1----  --------10  -0-0---011  01-01C----  11----CC--  0---0-----  ----------  ----------  ----000-00  --------0-  -1-----1
552      35  1-0--1----  --------1C  -0-0---011  01-000----  11----C0--  C---0-----  ----------  ----------  ----000-00  --------0-  -1-----1
553     -59  1-0--1----  --------10  -0-0---011  01-000----  11----CC--  C---0-----  ----------  ----------  ----000-00  --------0-  -1-----1
554     -34  1-0--1----  --------10  -0-0---011  01-1C0----  11----CC--  C---0-----  ----------  ----------  ----000-00  --------1-  -1-----1
555     -90  1-0--1----  --------10  -0-0---011  01-1C0----  11----C0--  0---0-----  ----------  ----------  ----000-00  --------1-  -1-----1
 41     -48  1-0--1----  --------10  -0-0---C11  01-100----  11----01--  C---0-----  ----------  ----------  ----000-01  --------1-  -1-----1

534     ...  1-0--1----  --------11  -0-C---1C0  01-111----  11----1C--  C---0-----  ----------  ----------  ----000-01  --------0-  -1-----1
556      34  1-0--1----  --------11  -0-0---100  01-C11----  11----10--  0---0-----  ----------  ----------  ----000-01  --------0-  -1-----1
557      19  1-0--1----  --------01  -0-0---100  01-011----  11----1C--  0---0-----  ----------  ----------  ----000-01  --------0-  -1-----1
558     108  1-0--1----  --------01  -0-0---1C0  01-011----  11----10--  C---0-----  ----------  ----------  ----000-01  --------0-  -1-----1
559      -3  1-1--1----  --------01  -0-0---1C0  01-011----  11----1C--  C---0-----  ----------  ----------  ----000-01  --------0-  -1-----0
560     -22  1-1--1----  --------01  -1-0---1C0  01-C11----  11----10--  0---0-----  ----------  ----------  ----000-01  --------0-  -1-----0
561     -55  1-1--1----  --------01  -1-0---1C0  01-011----  11----10--  0---1-----  ----------  ----------  ----000-01  --------0-  -1-----0
562     -51  1-1--1----  --------01  -1-C---1C0  01-011----  11----1C--  1---1-----  ----------  ----------  ----000-01  --------0-  -1-----0
 36     -29  1-1--1----  --------01  -1-0---11C  01-011----  11----10--  1---1-----  ----------  ----------  ----000-01  --------0-  -1-----0

518     ...  0-1--1----  --------11  -1-C---1C0  01-111----  11----C0--  0---0-----  ----------  ----------  ----111-00  --------1-  -1-----1
563      34  0-1--1----  --------11  -1-0---1C0  01-011----  11----C0--  0---0-----  ----------  ----------  ----111-00  --------1-  -1-----1
564      20  0-1--1----  --------10  -1-0---1C0  01-011----  11----C0--  C---0-----  ----------  ----------  ----111-00  --------1-  -1-----1
565      35  0-1--1----  --------10  -1-0---1C0  01-C01----  11----C0--  C---0-----  ----------  ----------  ----111-00  --------1-  -1-----1
566      36  0-1--1----  --------10  -1-0---100  01-C00----  11----CC--  0---0-----  ----------  ----------  ----111-00  --------1-  -1-----1
567      32  0-1--1----  --------10  -1-0---1C0  CC-C00----  11----C0--  0---0-----  ----------  ----------  ----111-00  --------1-  -1-----1
568     -47  0-1--1----  --------10  -1-0---1C0  C0-C00----  11----10--  C---0-----  ----------  ----------  ----111-00  --------1-  -1-----1
569     -55  0-1--1----  --------1C  -1-0---1C0  00-CCC----  11----1C--  C---1-----  ----------  ----------  ----111-00  --------1-  -1-----1
```

```
70    -51   0-1--1---- --------10 -1-0---100 00-CCC---- 11----1C-- 1---1----- ---------- ---------- ----111-00 --------1- -1-----1

77    •••   C-0--1---- --------11 -1-1---001 11-111---- 11----11-- 1---1----- ---------- ---------- ----111-10 --------1- -1-----1
570   30    0-0--1---- --------11 -1-1---CC0 11-111---- 11----11-- 1---1----- ---------- ---------- ----111-10 --------1- -1-----1
571   47    0-0--1---- --------11 -1-1---0C0 11-111---- 11----C1-- 1---1----- ---------- ---------- ----111-10 --------1- -1-----1
572   34    0-0--1---- --------11 -1-1---000 11-011---- 11----C1-- 1---1----- ---------- ---------- ----111-10 --------1- -1-----1
573   6     C-0--0---- --------11 -1-1---CC0 11-011---- 11----C1-- 1---1----- ---------- ---------- ----111-10 --------1- -1-----1
574   -90   C-0--0---- --------11 -1-1---CC0 11-011---- 11----01-- 1---1----- ---------- ---------- ----111-10 --------1- -1-----1
27    -1    1-0--0---- --------11 -1-1---CC0 11-011---- 11----C1-- 1---1----- ---------- ---------- ----111-11 --------1- -1-----1
                                                                                                      ----111-11 --------1- -1-----1

27    •••   1-0--0---- --------11 -1-1---0C0 11-011---- 11----01-- 1---1----- ---------- ---------- ----111-11 --------1- -1-----1
575   99    1-0--0---- --------11 -1-1---CC0 11-011---- 11----01-- 1---1----- ---------- ---------- ----111-11 --------0- -1-----1
576   41    1-0--0---- --------11 -1-1---CC0 11-011---- C1----C1-- 1---1----- ---------- ---------- ----111-11 --------0- -1-----1
577   -3    1-1--0---- --------11 -1-1---CC0 11-C11---- C1----C1-- 1---1----- ---------- ---------- ----111-11 --------0- -1-----1
578   -47   1-1--0---- --------11 -1-1---CC0 11-011---- C1----11-- 1---1----- ---------- ---------- ----111-11 --------0- -1-----1
28    -30   1-1--0---- --------11 -1-1---CC1 11-011---- C1----11-- 1---1----- ---------- ---------- ----111-11 --------0- -1-----1

40    •••   0-1--0---- --------11 -1-1---1C0 01-111---- 11----CC-- C---0----- ---------- ---------- ----111-01 --------1- -1-----1
579   28    0-1--C---- --------11 -1-1---000 01-111---- 11----C0-- 0---0----- ---------- ---------- ----111-01 --------1- -1-----1
580   22    0-1--0---- --------11 -0-1---CC0 01-111---- 11----C0-- C---0----- ---------- ---------- ----111-01 --------1- -1-----1
581   19    0-1--0---- --------01 -0-1---CC0 01-111---- 11----C0-- C---C----- ---------- ---------- ----111-01 --------1- -1-----1
582   35    0-1--0---- --------01 -0-1---000 01-101---- 11----CC-- C---0----- ---------- ---------- ----111-01 --------1- -1-----1
583   42    0-1--C---- --------01 -0-1---0C0 01-101---- 10----CC-- 0---0----- ---------- ---------- ----111-01 --------1- -1-----1
584   -47   0-1--0---- --------01 -0-1---CC0 01-101---- 1C----CC-- 0---0----- ---------- ---------- ----111-01 --------1- -1-----1
585   -31   0-1--0---- --------01 -0-1---CC0 11-101---- 1C----10-- C---0----- ---------- ---------- ----111-01 --------1- -1-----1
586   -55   0-1--0---- --------01 -0-1---000 11-101---- 10----10-- 0---1----- ---------- ---------- ----111-01 --------1- -1-----1
46    -51   0-1--0---- --------01 -0-1---000 11-101---- 10----1C-- 1---1----- ---------- ---------- ----111-01 --------1- -1-----1

501   •••   1-1--1---- --------11 -1-1---111 11-111---- 11----11-- 1---1----- ---------- ---------- ----111-11 --------1- -1-----1
587   24    1-1--1---- --------11 -1-0---111 11-111---- 11----11-- 1---1----- ---------- ---------- ----111-11 --------1- -1-----1
588   51    1-1--1---- --------11 -1-0---111 11-111---- 11----11-- C---1----- ---------- ---------- ----111-11 --------1- -1-----1
589   55    1-1--1---- --------11 -1-0---111 11-111---- 11----11-- 0---0----- ---------- ---------- ----111-11 --------1- -1-----1
590   30    1-1--1---- --------11 -1-0---110 11-111---- 11----11-- C---0----- ---------- ---------- ----111-11 --------1- -1-----1
591   31    1-1--1---- --------11 -1-0---110 01-111---- 11----11-- C---0----- ---------- ---------- ----111-11 --------1- -1-----1
592   47    1-1--1---- --------11 -1-0---110 01-111---- 11----C1-- C---0----- ---------- ---------- ----111-11 --------1- -1-----1
593   90    1-1--1---- --------11 -1-0---110 01-111---- 11----C1-- C---0----- ---------- ---------- ----111-11 --------1- -1-----1
594   59    1-1--1---- --------11 -1-0---11C 01-111---- 11----C1-- 0---0----- ---------- ---------- ----111-10 --------1- -1-----1
595   20    1-1--1---- --------10 -1-0---110 01-111---- 11----C1-- C---0----- ---------- ---------- ----111-10 --------0- -1-----1
596   22    1-1--1---- --------10 -0-0---110 01-111---- 11----C1-- C---0----- ---------- ---------- ----111-10 --------0- -1-----1
597   19    1-1--1---- --------0C -0-0---110 01-111---- 11----C1-- C---0----- ---------- ---------- ----111-10 --------0- -1-----1
598   35    1-1--1---- --------00 -0-0---110 01-111---- 11----C1-- C---0----- ---------- ---------- ----111-10 --------0- -1-----1
599   108   1-1--1---- --------00 -0-0---11C 01-101---- 11----01-- C---0----- ---------- ---------- ----111-10 --------0- -1-----1
68    102   1-1--1---- --------00 -0-0---110 01-101---- 11----C1-- C---0----- ---------- ---------- ----111-10 --------0- -1-----0
                                                                                                      ----111-10 --------0- -0-----0
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EVOLUTION OF 5 TAXA DETERMINED USING 42 CHARACTERS AND .358 AS THE LEVEL OF SIGNIFICANCE.

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501    ***  -11------- -1-1-11--- ---1---111 11--1---11 111---11-- -----11111 1111------ ---------- 1111------ 11111111-- -------1
502     35  -11------- -1-1-11--- ---1---111 11--0---11 111---11-- -----11111 1111------ ---------- 1111------ 11111111-- -------1
  5     47  -11------- -1-1-11--- ---1---111 11--0---11 111---01-- -----11111 1111------ ---------- 1111------ 11111111-- -------1

501    ***  -11------- -1-1-11--- ---1---111 11--1---11 111---11-- -----11111 1111------ ---------- 1111------ 11111111-- -------1
503     24  -11------- -1-1-11--- ---0---111 11--1---11 111---11-- -----11111 1111------ ---------- 1111------ 11111111-- -------1
504     28  -11------- -1-1-11--- ---0---011 11--1---11 111---11-- -----11111 1111------ ---------- 1111------ 11111111-- -------1
  7     29  -11------- -1-1-11--- ---0---001 11--1---11 111---11-- -----11111 1111------ ---------- 1111------ 11111111-- -------1

503    ***  -11------- -1-1-11--- ---0---111 11--1---11 111---11-- -----11111 1111------ ---------- 1111------ 11111111-- -------1
505     31  -11------- -1-1-11--- ---0---111 01--1---11 111---11-- -----11111 1111------ ---------- 1111------ 11111111-- -------1
506     41  -11------- -1-1-11--- ---0---111 01--1---11 011---11-- -----11111 1111------ ---------- 1111------ 11111111-- -------1
  9     32  -11------- -1-1-11--- ---0---111 00--1---11 011---11-- -----11111 1111------ ---------- 1111------ 11111111-- -------1

506    ***  -11------- -1-1-11--- ---0---111 01--1---11 011---11-- -----11111 1111------ ---------- 1111------ 11111111-- -------1
507     14  -11------- -1-0-11--- ---0---111 01--1---11 011---11-- -----11111 1111------ ---------- 1111------ 11111111-- -------1
508     95  -11------- -1-0-11--- ---0---111 01--1---11 011---11-- -----11111 1111------ ---------- 1111------ 11110111-- -------1
509     96  -11------- -1-0-11--- ---0---111 01--1---11 011---11-- -----11111 1111------ ---------- 1111------ 11110011-- -------1
510     97  -11------- -1-0-11--- ---0---111 01--1---11 011---11-- -----11111 1111------ ---------- 1111------ 11110001-- -------1
  6     98  -11------- -1-0-11--- ---0---111 01--1---11 011---11-- -----11111 1111------ ---------- 1111------ 11110000-- -------1

501    ***  -11------- -1-1-11--- ---1---111 11--1---11 111---11-- -----11111 1111------ ---------- 1111------ 11111111-- -------1
511     28  -11------- -1-1-11--- ---1---011 11--1---11 111---11-- -----11111 1111------ ---------- 1111------ 11111111-- -------1
512     30  -11------- -1-1-11--- ---1---010 11--1---11 111---11-- -----11111 1111------ ---------- 1111------ 11111111-- -------1
513     91  -11------- -1-1-11--- ---1---010 11--1---11 111---11-- -----11111 1111------ ---------- 1111------ 01111111-- -------1
514     92  -11------- -1-1-11--- ---1---010 11--1---11 111---11-- -----11111 1111------ ---------- 1111------ 00111111-- -------1
515     93  -11------- -1-1-11--- ---1---010 11--1---11 111---11-- -----11111 1111------ ---------- 1111------ 00011111-- -------1
  8     94  -11------- -1-1-11--- ---1---010 11--1---11 111---11-- -----11111 1111------ ---------- 1111------ 00001111-- -------1
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PLATE I. "Adiantopsis capensis"

PLATE I. "Adiantopsis capensis (Thunb.) Fée"



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PLANTES DU YUNNAN (Chine)

G. BONATI, Pharmacien de 1re Classe, LURE (Haute Saône)

PLATE II. Cheilanthes yunnanensis

PLATE II. Cheilanthes yunnanensis Brause



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EXPLORATION OF CUBA
PROVINCE OF PINAR DEL RIO
BAÑOS SAN VICENTE
NO. 749
Adiantopsis rupicola Maxon
N. L. BRITTON, E. G. BRITTON, O. S. GAGER } COLLECTORS
SEPT. 12-16, 1910

PLATE III. "Adiantopsis rupicola"

PLATE III. "Adiantopsis rupicola Maxon"



PLATE IV. Cheilanthes microphylla

PLATE IV. Cheilanthes microphylla Swartz



PLATE V. Adiantopsis paupercula (Kunze) Fée



PLATE VI. Cheilanthes regularis

PLATE VI. Cheilanthes regularis Mett.



PLATE VII. Aleuritopteris duclouxii (Christ) Ching



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J. N. ROSE, Collector
P. G. RUSSELL, Assistant

PLATE VIII. Doryopteris collina

REVISION OF DORYOPTERIS

D. collina (Raddi) J.Sm.

R.M. TRYON, JR. 1941

PLATE VIII. Doryopteris collina (Raddi) J. Smith