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# NUMERICAL CLASSIFICATION OF *STICTOSTROMA* PARKS FROM THE DEVONIAN OF SOUTHERN ONTARIO, CANADA

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*Abstract.* Recently developed methods of numerical taxonomy were applied to 28 specimens of the stromatoporoid genus *Stictostroma* Parks collected from the Hungry Hollow and Onondaga Formations of Ontario. Twenty-one morphologic features were encoded numerically on nominal, ordinal and interval-ratio scales. The degree of similarity between all possible pairs of specimens was computed by applying Goodall's (1964) measure of similarity. This similarity index closely approaches the intuitive procedures of classical taxonomic methods; in that it allows the use of data measured on different scales, weights each characteristic according to its commonness or rareness and defines similarity in the context of only those specimens under analysis. To find groups of highly related specimens, the matrix of similarity coefficients was treated by the method of principal components. This procedure, although theoretically not justified, outlined the major groups. These initial groupings were refined by an *ad hoc* method proposed by Goodall (1966), whereby the initial set of specimens was broken down into smaller and smaller subsets, each subset being defined at a given probability level. The groups achieved by this method corresponded to a high degree with those determined visually. They also allowed an assessment of inter-group similarity not often possible where groups have been defined visually. Further, the numerically derived groups have important stratigraphic significance.

## INTRODUCTION

Numerical classification is a rapidly expanding field that has had a great deal of stimulus from the development of high-speed electronic computers. The literature of paleontology describes numerous attempts to use quantitative methods, among which those of Pearson (1926), Burma (1948), Imbrie (1956), Olson and Miller (1958) and Olson (1964) — to name only a few—have shown that such method can be used to advantage in the study of fossils.

Since numerical taxonomic methods can be applied to a variety of disciplines, it is not surprising that techniques developed for one area may be used in others entirely different. Sokal and Sneath (1963) outlined not only the philosophy but a detailed procedure of numerical methods in taxonomy. Recently, Goodall (1964, 1966*a*, *b*) has presented a new application of the principle, in studies of bacteria. The application of Goodall's methods to some fossil material is the subject of the present paper.

The extinct Order of coelenterates, the Stromatoporoidea, is a particularly difficult group of organisms to classify. Their complex microstructure is subject to diagenetic alteration, so that observation of their morphological features becomes highly interpretive. It is not surprising, then, that there is a great deal of controversy about their classification: the grouping of genera into Families is a matter of considerable disagreement (Galloway & St. Jean, 1957; Lecompte, 1952; Yavorsky, 1962) and the criteria used to erect species, genera and families have been seriously questioned by Stearn (1966) and Klovan (1966).

The present paper attacks the problem of stromatoporoid classification at the lowest level; that is, it seeks to group specimens of one genus into taxonomically distinct units.

This study is an outgrowth of work done in collaboration with Dr J. St. Jean, Jr, who collected 28 specimens of *Stictostroma* from Middle Devonian strata in southern Ontario (Fig. 1). The stratigraphic positions of the formations sampled are indicated in Fig. 2. (The terminology used here follows Cooper *et al.* (1942) and is not generally used in Canada).

St. Jean visually classified the specimens into seven species, for some of which he has published descriptions (St. Jean, 1962). An example of a

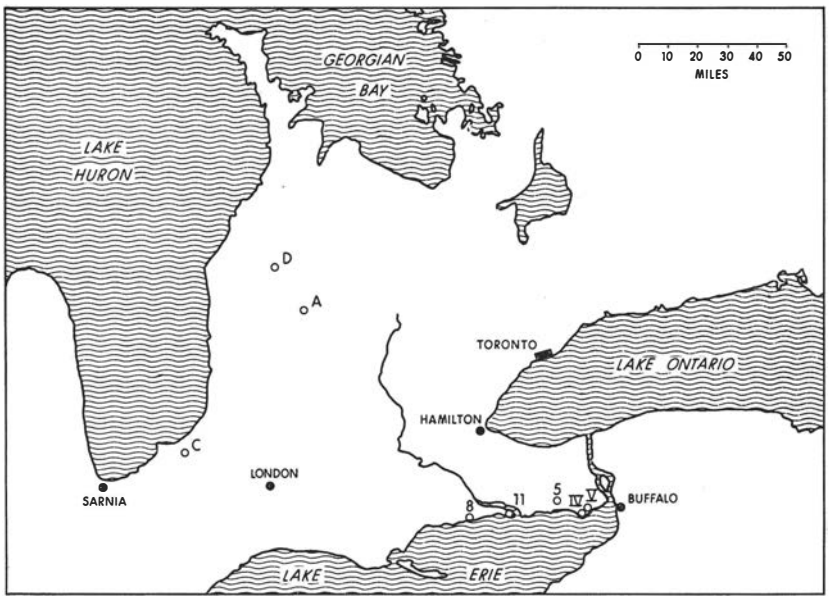


*Fig. 1.* Index map showing the locations of stromatoporoid collecting sites.

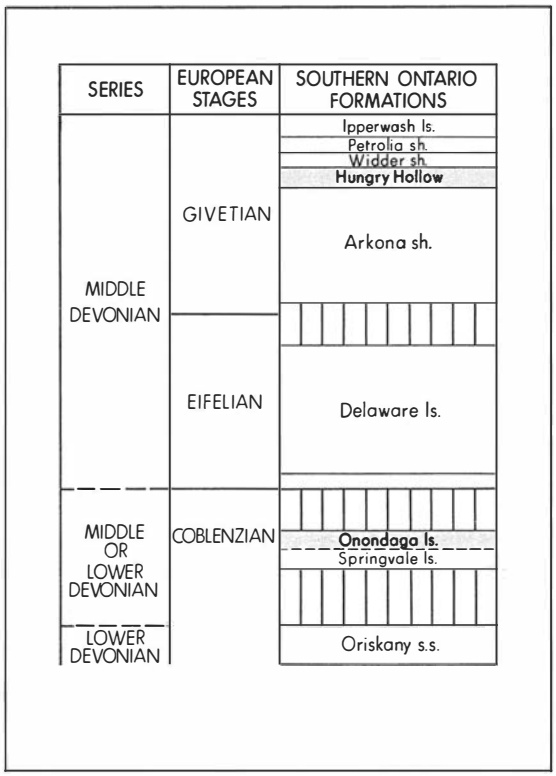


*Fig. 2.* Middle Devonian stratigraphic section, Southern Ontario. The Hungry Hollow and Onondaga Formations contain the stromatoporoid specimens under study.

Table I. *Typical description of a stromatoporoid specimen before encoding*

Genus and species: Stictostroma mamilliferum

*Coenosteum*

| | |
|---|---|
| Form: Laminar | Height: 1.2 cm. Diameter: 3.7 cm. |
| Surface: | |
| Mamelons: | Diameter: 3.7. Height: 1.5. Spacing: 8.7. |
| Papillae: | Form: obscure |
| Astrorhizae: | Form: none Spacing: |
| Latilaminae: | Thickness: 4 No. per 10 mm: 3 |

*Vertical section*

| | |
|---|---|
| Tissue: | Transversely tubulose and flocculent |
| Peritheca: | Form: none |
| Laminae: | Form: simple Thickness: .028 No. per 10 mm: 24 |
| Galleries: | Form: rectangular |
| Pillars: | Form: flocculent spools Width: .072 No. per 10 mm: 12 |
| Cyst plates: | Form: slightly curved, thin Abundance: moderate |

*Tangential section:*

| | |
|---|---|
| Tissue: | Flocculent, pseudomaculate |
| Pillars: | Form: rare round rings Diameter: .090 Spacing: .22 |
| Mamelon tubes: | Form: none Size: |
| % Tissue: 30 | |
| Astrorhizae: | Form: none Diameter: Tube diameter |

Code: OA–1. Horizon: Middle Devonian, Onondaga l.s. Locality: Gorrie, Ontario.

Table II. *Basic data on specimens*

Each specimen is given an arbitrary number code; specimen numbers identify the collecting site and specimen number; species refer to the species to which the specimen was assigned by J. St. Jean, Jr by visual means.

| Code | Specimen no. | Species | Locality | Formation |
|---|---|---|---|---|
| 1 | 0A– 1 | mamilliferum | Gorrie | Onondaga |
| 2 | 0A– 4 | | | |
| 3 | 0A– 8 | | | |
| 4 | 0A– 9 | | | |
| 5 | 0D– 1 | | Formosa | |
| 6 | 0C– 3 | elevatum | Thedford | Hungry Hollow |
| 7 | 0C–11 | | | |
| 8 | 0C–16 | | | |
| 9 | 0C–17 | | | |
| 10 | 0C–50 | | | |
| 11 | 0C–22 | kayi | | |
| 12 | 0C–27 | | | |
| 13 | 0C–32 | | | |
| 14 | 0C–36 | | | |
| 15 | 0C–45 | | | |
| 16 | 0C–53 | | | |
| 17 | 0C–69 | | | |
| 18 | 0C–71 | | | |
| 19 | 05– 1 | problematicum* | Port Colburn | Onondaga |
| 20 | 05– 2 | | | |
| 21 | 05– 4 | | | |
| 22 | 011–30 | tubulomamilatum* | Port Maitland | |
| 23 | 011–49 | | | |
| 24 | 011–53 | | | |
| 25 | 0IV– 3 | | | |
| 26 | 0IV– 6 | lophiostromoides* excellens | Empire Beach | |
| 27 | 0IV– 8 | | | |
| 28 | 0V–11 | | | |

* informal names

specimen as he has described it is shown in Table I. The assignment of the individual specimens to the seven species, plus other information, is set out in Table II.

## NUMERICAL CLASSIFICATION METHODS

Sokal & Sneath (1963, p. 121) define the Operational Taxonomic Unit (OTU) as "... the hierarchic level of the taxonomic unit employed..." For this study the OTU is a stromatoporoid coenostial specimen, since stromatoporoid specimens are the objects to be classified.

In attempting to group these specimens into taxa which may represent species, it is well to expound briefly on the species concept to be adopted.

With a poorly understood group of extinct organisms, the most practical approach to species appears to be a phenetic one. The morphology of an individual colony is deemed to be the result of both genetic and environmental effects. It should therefore reflect the species, which (it is postulated) is also defined by genetic and enviromental controls. The hypothesis, then, is that an adequate description of the morphology of the individual colonies should allow a phenetically sound classification into species.

If the morphology of the organisms to be classified is relatively simple; that is, with few variable characters, and if the function of these characters is known, it is often possible to establish an effective morphological basis of classification by visual means or by simple plots of character versus character. But when, as with the organisms studied here, many characters vary from individual to individual, and their function is unknown, there are a great many potential combinations of characters, any one of which may best discriminate between the species.

The contention that the species themselves are not known *a priori* greatly compounds the problem.

To start with, it is suggested that in erecting species as many characters should be used as possible. Clearly, this cannot well be done visually, and a mathematical algorithm becomes necessary.

The process of optimum classification is viewed here as one of simultaneous comparison of similarities and differences within a suite of specimens. The problem then is not so much statistical as relativistic. The paleontologist trying to classify his fossils is concerned primarily with the collection before him, plus a large but finite number of previously described specimens, generally holotypes of species. The population of individuals to be assigned to species is therefore not excessively large, and generally at hand.

Numeric methods of classification involve three separate but interrelated steps: (1) the numeric description of morphological characters; (2) the definition of a mathematical index of similarity; (3) clustering methods.

The choice of similarity index largely predetermines the form of coding that can be used; conversely, a predetermined method of numerical description will largely preclude the use of certain similarity indices.

### *Numeric description*

In this paper three types of numeric scales, following Goodall (1964) and Siegel (1956), are recognized:

1. The nominal scale can be used for numerical coding of essentially qualitative data. Two types are available:

(a) The dichotomous nominal scale is used to code characters which can be described as being in either of two states; for example, either present or absent. The number 0 can represent absent, while 1 can represent present.

(b) The multistate nominal scale can be used to code qualitative characters that can be in any of several states. The states, however, are not in a logical numeric order. For example, the color of an object may take the states red, blue, green or brown. The numbers 1, 2, 3 & 4 may be used to represent these color states. It is important to recognize that the numbers serve merely as tags and do not imply any order, degree or magnitude.

2. The ordinal scale is convenient for coding characters whose states can be placed in an ordered sequence but whose absolute magnitudes cannot be determined. Thus, the surface of an object might be described as smooth, rough, very rough. This series of states might be coded 1, 2, 3 respectively, and here the numbers will refer to an ordered sequence. That is, 2 is in some way "greater" than 1, and 3 is greater than 2. However, the degree of roughness, in this example, between state 1 and 2 may be greater or less than that between states 2 and 3. In other words, the ordinal scale is used to rank the states of a character in a relative but not an absolute way.

3. Characters that can be measured metrically are expressed on the interval and ratio scales. Thus, length as stated in millimeters, or weight in grams, will be coded on the ratio scale. Here the interval between successive numbers is constant; for example, the interval between 2 and 3 millimeters is the same as that between 3 and 4 millimeters.

A variant of the interval-ratio scales is the so-called grouped interval-ratio scale. The range of values taken by a character may be divided into a number of classes, and the midpoint of each class may be used to denote any values falling within the class. The grouped interval-ratio scale is particularly useful for characters whose actual or estimated measurements are subject to rather large errors.

By selecting the scale appropriate to it, any morphologic feature can be described numerically. A far greater problem is the selection of characters to be used to describe the specimens. Here the matter is entirely subjective and few guidelines can be drawn. However, the method to be outlined here places no restriction on the number of characters used.

The approach adopted has been to use all the characters noted by St. Jean, even though some may have little value as discriminators between species. Table III lists the characters used in the present study, the scale on which they were coded, and what the various state-codes mean. Table IV contains all the coded information on the 28 specimens.

Some of the problems encountered in coding characters are as follows:

Table III. *Coding scheme for attributes*
The twenty-one attributes are enumerated, along with the type of scale used and the meaning of the various codes.

| Character | Code type | Codes |
|---|---|---|
| Astrorhizae | Nominal | 0 = Absent; 1 = Present |
| Peritheca | Nominal | 0 = Absent; 1 = Present |
| Gallery form | Nominal | 1 = Rectangular; 2 = Mixed<br>3 = Rectangular to Square<br>4 = Rectangular to Round<br>5 = Rectangular to Oval<br>6 = Round to Oval |
| Pillar form | Nominal | 1 = Spools; 2 = Cylinders<br>3 = Spools and Cylinders |
| Tissue type | Nominal | 1 = No Pores; 2 = Porous<br>3 = Tubulate; 4 = Pseudo-maculate; 5 = Fibrous |
| Peritheca | Nominal | 1 = Irregular; 2 = Regular |
| Pillar form | Nominal | 1 = Solid; 2 = Rings |
| Laminae form | Ordinal | 1 = Straight; 2 = Undulose;<br>3 = Irregular; 4 = Very Irregular |
| Cyst plate form | Ordinal | 1 = Straight; 2 = Slightly curved<br>3 = Curved; 4 = Sharply curved |
| Papillar form | Ordinal | 1 = None; 2 = Small<br>3 = Medium |
| Cyst plate abundance | Ordinal | 1 = None; 2 = Rare;<br>3 = Moderate<br>4 = Common; 5 = Very Common |
| | *Interval* | |
| Average Mamelon Diameter | | |
| Average Mamelon Height | | |
| Average Mamelon Separation | | |
| Average Laminar Thickness | | |
| Laminae per 4 mm | | |
| Average Pillar Width | | |
| Pillars per 4 mm | | |
| Average Pillar Diameter | | |
| Average Pillar Separation | | |
| Percent Tissue | | |

(Note: −1 used for missing data)

Table IV. *Numerically encoded data on 28 specimens of Stictostroma*

| SPECIMEN NO. | CODE | NOMINAL | | | | | | | ORDINAL | | | | INTERVAL - RATIO | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | ASTRORHIZAE | PERITHECA | GALLERY FORM | PILLAR FORM | TISSUE TYPE | PERITHECA | PILLAR FORM | LAMINA FORM | CYST-PLATE FORM | PAPILLAR FORM | CYST-PLATE ABUND. | AVERAGE MAMELON DIAMETER | AVERAGE MAMELON HEIGHT | AVERAGE MAMELON SEPARATION | AVERAGE LAMINAR THICKNESS | LAMINAE PER 4 mm | AVERAGE PILLAR WIDTH | PILLARS PER 4 mm | AVERAGE PILLAR DIAMETER | AVERAGE PILLAR SEPARATION | PERCENT TISSUE |
| A-1 | 1 | 0 | 0 | 1 | 1 | 4 | -1 | 2 | 1 | 2 | 2 | 3 | 37 | 15 | 87 | 28 | 24 | 72 | 12 | 90 | 22 | 30 |
| A-4 | 2 | 1 | 1 | 1 | 1 | 3 | 1 | 2 | 1 | 2 | 1 | 3 | 30 | 15 | 60 | 41 | 25 | 77 | 13 | 97 | 26 | 30 |
| A-8 | 3 | 1 | 1 | 3 | 3 | 1 | 2 | 1 | 1 | 1 | 1 | -1 | -1 | -1 | -1 | 35 | 26 | 57 | 13 | 84 | 20 | 55 |
| A-9 | 4 | 0 | 1 | 1 | 1 | 2 | -1 | 2 | 1 | 3 | 2 | 3 | 58 | 17 | 103 | 34 | 24 | 72 | 10 | 74 | 29 | 35 |
| D-1 | 5 | 0 | 1 | 1 | 2 | 2 | 2 | 2 | 1 | 4 | -1 | 5 | 00 | -1 | -1 | 54 | 22 | 80 | 14 | 88 | 20 | 50 |
| C-3 | 6 | 0 | 0 | 2 | 1 | -1 | -1 | 2 | 3 | 2 | 3 | 2 | 18 | 7 | 35 | 59 | 16 | 91 | 9 | 134 | 24 | 75 |
| C-11 | 7 | 0 | 0 | 5 | 2 | 1 | -1 | 1 | 3 | 2 | 3 | 3 | 21 | 10 | 47 | 72 | 12 | 122 | 8 | 91 | 27 | 60 |
| C-16 | 8 | 0 | 0 | 2 | 1 | 2 | -1 | 1 | 2 | -1 | 2 | 2 | 22 | 8 | 31 | 65 | 17 | 139 | 10 | 146 | 25 | 50 |
| C-17 | 9 | 0 | 0 | 5 | 3 | 1 | 1 | -1 | 3 | 2 | 1 | 2 | 13 | 3 | 25 | 59 | 15 | 91 | 11 | 159 | 34 | 50 |
| C-50 | 10 | 0 | 0 | 4 | 2 | 2 | 1 | -1 | 4 | 2 | 2 | 4 | -1 | -1 | -1 | 80 | 15 | 112 | 9 | 109 | 20 | 75 |
| C-22 | 11 | 0 | 0 | 2 | 1 | 2 | -1 | 1 | 3 | -1 | 2 | 1 | 8 | 6 | 14 | 63 | 20 | 116 | 12 | 107 | 21 | 55 |
| C-27 | 12 | 1 | 0 | 6 | 2 | 2 | -1 | 1 | 3 | 1 | 2 | 2 | 9 | 3 | 13 | 57 | 17 | 127 | 10 | 125 | 27 | 70 |
| C-32 | 13 | 0 | 0 | 4 | 2 | 2 | -1 | 1 | 3 | 2 | 2 | 2 | -1 | -1 | -1 | 62 | 18 | 80 | 13 | 99 | 21 | 70 |
| C-36 | 14 | 0 | 0 | 4 | 3 | 2 | -1 | 1 | 3 | 1 | 2 | 2 | -1 | -1 | -1 | 55 | 21 | 108 | 14 | 123 | 20 | 75 |
| C-45 | 15 | 0 | 0 | 6 | 3 | 2 | -1 | 1 | 3 | 1 | 2 | 2 | -1 | -1 | -1 | 99 | 19 | 169 | 14 | 105 | 24 | 75 |
| C-53 | 16 | 1 | 0 | 4 | 2 | 2 | -1 | 1 | 3 | -1 | 2 | 2 | 14 | 7 | 30 | 61 | 19 | 136 | 12 | 150 | 23 | 80 |
| C-69 | 17 | 1 | 1 | 4 | 2 | 2 | -1 | 1 | 3 | -1 | 2 | 2 | 10 | 3 | 22 | 65 | 23 | 105 | 16 | 82 | 17 | 80 |
| C-71 | 18 | 0 | 1 | 4 | 3 | 2 | 1 | 1 | 3 | 2 | 1 | 4 | 6 | 3 | 12 | 63 | 19 | 103 | 14 | 97 | 28 | 50 |
| 5-1 | 19 | 0 | 1 | 2 | 2 | 2 | -1 | 1 | 2 | 3 | -1 | 4 | -1 | -1 | -1 | 54 | 15 | 74 | 10 | 183 | 39 | 30 |
| 5-2 | 20 | 0 | 0 | 3 | 2 | 5 | -1 | 1 | 2 | 3 | 2 | 4 | 00 | -1 | -1 | 55 | 11 | 65 | 8 | 74 | 52 | 30 |
| 5-4 | 21 | 0 | 0 | 3 | 2 | 2 | -1 | 1 | 1 | 3 | 2 | 4 | 30 | 11 | 76 | 63 | 14 | 61 | 7 | 44 | 34 | 30 |
| II-30 | 22 | 0 | 0 | 3 | 3 | 2 | -1 | 1 | 1 | 4 | 1 | 5 | 31 | 10 | 75 | 51 | 14 | 96 | 10 | 93 | 35 | 35 |
| II-49 | 23 | 0 | 0 | 6 | 3 | 2 | -1 | 1 | 1 | 4 | 2 | 5 | 30 | 9 | 90 | 62 | 13 | 89 | 8 | 120 | 40 | 35 |
| II-52 | 24 | 0 | 1 | 6 | 3 | 2 | -1 | 1 | 1 | 4 | 1 | 5 | 38 | 10 | 64 | 68 | 15 | 111 | 9 | 124 | 36 | 40 |
| IV-3 | 25 | 0 | 1 | 1 | 2 | 3 | -1 | 1 | 1 | 3 | 1 | 3 | 8 | 1 | 13 | 80 | 10 | 135 | 2 | 76 | 78 | 30 |
| IV-6 | 26 | 0 | 1 | 1 | 2 | 3 | 1 | 1 | 3 | 4 | 1 | 3 | 40 | -1 | -1 | 58 | 12 | 85 | 4 | 70 | 43 | 35 |
| IV-8 | 27 | 0 | 1 | 1 | 2 | 3 | 1 | 1 | 1 | -1 | 1 | 3 | 10 | 1 | 13 | 54 | 9 | 53 | 3 | 101 | 53 | 30 |
| V-11 | 28 | 0 | 0 | 1 | 3 | 2 | -1 | 1 | 1 | 3 | 1 | 5 | 21 | 9 | -1 | 74 | 14 | 96 | 5 | 95 | 39 | 40 |

(1) Often a character has not been or cannot be described or measured in a particular specimen. This presents no real problem as, in the method used, a missing character can be ignored. The code –1 indicates that the character has not been observed in the specimen. (This, it should be emphasized, is not the same as a character not being present.)

(2) Alternative methods of coding character states are often possible. The most serious decision revolves about the handling of some characters which may not be present in all specimens and, when they are, assume several states. Here there are two courses possible:

(a) Describe two characters—one, presence or absence; the other, the states when present.

(b) Use one nominally coded character with several states, one of which refers to absence.

As an example of the problem consider the feature "peritheca". It may be present or absent and, when present, it may be regular or irregular. With alternative (a), the coding scheme would be to set up a single nominally coded character describ-

ing presence or absence (0 = absent, 1 = present) and a second nominally coded character describing the type of peritheca when present (1 = irregular, 2 = regular); and when peritheca is not present, code this second character −1, thus ignoring it in that instance. With alternative (b), one character, coded 1 = absent, 2 = irregular, 3 = regular, would be used.

Arguments may be raised for both alternatives and probably each has its place, depending on the type of feature being described. Alternative (a) was used in two cases, one dealing with "peritheca", the other with "cyst-plates".

## SIMILARITY INDEX

Goodall (1964), (1966 *b*) described the technical details of the probabilistic similarity index used in the present study. These details will not be given here; rather, a more generalized, intuitive description will be presented.

Similarity is considered as a relation between pairs of individuals within a *specified* population. This means that the similarities to be computed are based on the individuals currently under study —the specimens on hand constitute the population. Thus, the degree of similarity between two specimens is expressed in the context only of the other items studied.

The similarity index allows nominal, ordinal and interval type characters to be used simultaneously. Thus, in the computation of degree of similarity, any feature of the specimen that can be coded numerically will be taken into account.

The index of similarity is computed as follows: "For each pair of individuals (specimens) in a sample or population, the exact probability is computed for each character in turn that a random sample of two will resemble one another not less closely than the two under test." (Goodall, 1964.) The probabilities for all the attributes are then appropriately combined, and the complement of this probability is used as the index of similarity.

Although the concept behind this index may not be as immediately apparent as for other types of indices, it does have many advantages which are not difficult to appreciate. Aside from the facts that the results depend solely on the specimens at hand, and that all types of characters may be used in the analysis, the similarity index has a built-in weighting function. The rationale behind the weighting is as follows: if two specimens both possess a character state that does not occur commonly in the population, then these two specimens will be considered more similar than two which both possess a commonly occurring character state. In the computation of similarity, then, a character state that is present in all members of the population would be completely ignored. This procedure is very like the action of the taxonomist who "visually" estimates the degree of resemblance between specimens, and is a nice compromise between those taxonomists who argue for the weighting of certain characters (generally a subjective determination) and those who argue for equal weighting of all attributes (claiming that this insures an objective determination).

When similarity indices have been computed for all possible pairs of specimens, they may be conveniently arranged in a similarity matrix (Table V).

### *Clustering methods*

Several methods have been devised to extract groups of similar specimens from a similarity matrix. This procedure, generally known as cluster analysis, has been reviewed extensively by Sokal & Sneath (1963). Recent papers on the subject by Parks (1966) and Bonham-Carter (1967) are also pertinent.

The majority of these techniques attempt to delineate clusters of similar items on a sequential basis. The similarity matrix is scanned to find those pairs of specimens that have the highest mutual similarities. Each such pair is then combined (by various alternative methods), and similarities between the combinations and the remaining specimens are computed. This grouping process is repeated until the groups have been reduced to two.

The objection to this type of approach is that, like any other process that involves averaging, it introduces a considerable amount of distortion. Further, it reduces the problem of classification to a simple two-dimensional situation, whereas actually the true relationships may be multidimensional.

Two alternative methods of clustering have recently been proposed by Goodall (1966 *a*) and Rubin (1965). Both were used in the present study with essentially similar results. Since Goodall's

Table V. *Matrix of similarity coefficients between 28 specimens of Stictostroma*

The matrix has been reordered so that the clustering of specimens is more evident.

| | 24 | 23 | 28 | 22 | 19 | 21 | 20 | 25 | 27 | 26 | 2 | 1 | 4 | 3 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 24 | 1.0000 | | | | | | | | | | | | | |
| 23 | 0.9929 | 1.0000 | | | | | | | | | | | | |
| 28 | 0.9864 | 0.9864 | 1.0000 | | | | | | | | | | | |
| 22 | 0.9979 | 0.9930 | 0.9997 | 1.0000 | | | | | | | | | | |
| 19 | 0.8850 | 0.7660 | 0.8761 | 0.9017 | 1.0000 | | | | | | | | | |
| 21 | 0.6183 | 0.9355 | 0.8167 | 0.9594 | 0.9745 | 1.0000 | | | | | | | | |
| 20 | 0.1094 | 0.6847 | 0.3493 | 0.5971 | 0.9984 | 0.9905 | 1.0000 | | | | | | | |
| 25 | 0.0808 | 0.0037 | 0.5196 | 0.0482 | 0.5583 | 0.1316 | 0.8304 | 1.0000 | | | | | | |
| 27 | 0.0342 | 0.0055 | 0.3477 | 0.1191 | 0.8025 | 0.0990 | 0.8565 | 0.9981 | 1.0000 | | | | | |
| 26 | 0.6859 | 0.8254 | 0.6637 | 0.7927 | 0.6249 | 0.3093 | 0.5834 | 0.9510 | 0.9939 | 1.0000 | | | | |
| 2 | 0.1097 | 0.0539 | 0.3229 | 0.3483 | 0.5115 | 0.1941 | 0.0593 | 0.5179 | 0.9334 | 0.9398 | 1.0000 | | | |
| 1 | 0.0099 | 0.0775 | 0.0787 | 0.2101 | 0.5116 | 0.2896 | 0.2925 | 0.0268 | 0.0642 | 0.1889 | 0.9972 | 1.0000 | | |
| 4 | 0.0588 | 0.1371 | 0.1125 | 0.3040 | 0.9106 | 0.2157 | 0.8174 | 0.2783 | 0.0442 | 0.6599 | 0.9641 | 0.9985 | 1.0000 | |
| 3 | 0.2841 | 0.0185 | 0.2545 | 0.6251 | 0.0267 | 0.1782 | 0.1596 | 0.1149 | 0.4610 | 0.1131 | 0.9846 | 0.6236 | 0.5958 | 1.0000 |
| 5 | 0.5841 | 0.5672 | 0.5254 | 0.8026 | 0.7552 | 0.0861 | 0.6193 | 0.2156 | 0.7357 | 0.6186 | 0.8882 | 0.8389 | 0.8028 | 0.9923 |
| 11 | 0.0845 | 0.0992 | 0.0806 | 0.0293 | 0.2502 | 0.0765 | 0.0631 | 0.0769 | 0.0168 | 0.0047 | 0.0513 | 0.3676 | 0.0272 | 0.4617 |
| 13 | 0.0720 | 0.5916 | 0.2012 | 0.2313 | 0.3071 | 0.4163 | 0.2104 | 0.0134 | 0.1487 | 0.1578 | 0.7424 | 0.6690 | 0.1495 | 0.4544 |
| 16 | 0.0105 | 0.0446 | 0.0211 | 0.0064 | 0.1454 | 0.0278 | 0.0402 | 0.0807 | 0.0007 | 0.0089 | 0.0253 | 0.0471 | 0.0001 | 0.2218 |
| 14 | 0.7293 | 0.4701 | 0.1314 | 0.2792 | 0.1377 | 0.0363 | 0.2545 | 0.0013 | 0.0209 | 0.0111 | 0.0484 | 0.2052 | 0.0498 | 0.8549 |
| 15 | 0.2452 | 0.3409 | 0.1164 | 0.1244 | 0.0089 | 0.0207 | 0.0100 | 0.0025 | 0.0035 | 0.0002 | 0.0784 | 0.1659 | 0.0306 | 0.5621 |
| 12 | 0.5412 | 0.2194 | 0.0215 | 0.1076 | 0.5954 | 0.0179 | 0.2302 | 0.2100 | 0.1410 | 0.0614 | 0.0220 | 0.0002 | 0.0144 | 0.1105 |
| 10 | 0.9212 | 0.3411 | 0.3624 | 0.3682 | 0.7236 | 0.5588 | 0.4180 | 0.2637 | 0.2045 | 0.2666 | 0.2139 | 0.1472 | 0.0449 | 0.1460 |
| 8 | 0.2579 | 0.2403 | 0.2412 | 0.2348 | 0.9543 | 0.1665 | 0.3740 | 0.0161 | 0.0001 | 0.0044 | 0.0756 | 0.0954 | 0.2159 | 0.0178 |
| 18 | 0.4276 | 0.1105 | 0.6818 | 0.4198 | 0.4726 | 0.1801 | 0.1705 | 0.2047 | 0.6652 | 0.5850 | 0.8653 | 0.0061 | 0.0142 | 0.7077 |
| 17 | 0.0262 | 0.0022 | 0.0238 | 0.0034 | 0.0830 | 0.0047 | 0.0694 | 0.1776 | 0.1223 | 0.0659 | 0.1013 | 0.0091 | 0.0153 | 0.8009 |
| 6 | 0.2096 | 0.3534 | 0.1695 | 0.1039 | 0.5579 | 0.0273 | 0.0887 | 0.0000 | 0.0004 | 0.1490 | 0.3590 | 0.4442 | 0.2532 | 0.0070 |
| 7 | 0.2683 | 0.3559 | 0.7274 | 0.3753 | 0.1605 | 0.2698 | 0.5604 | 0.1020 | 0.0210 | 0.3928 | 0.1184 | 0.2532 | 0.0181 | 0.4100 |
| 9 | 0.4346 | 0.3388 | 0.5453 | 0.5885 | 0.6501 | 0.1783 | 0.0344 | 0.0175 | 0.3974 | 0.7082 | 0.1474 | 0.0018 | 0.0004 | 0.7602 |

| 5 | 11 | 13 | 16 | 14 | 15 | 12 | 10 | 8 | 18 | 17 | 6 | 7 | 9 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1.0000 | | | | | | | | | | | | | |
| 0.4054 | 1.0000 | | | | | | | | | | | | |
| 0.8964 | 0.9825 | 1.0000 | | | | | | | | | | | |
| 0.0738 | 0.9100 | 0.9777 | 1.0000 | | | | | | | | | | |
| 0.8887 | 0.9264 | 0.9526 | 0.9082 | 1.0000 | | | | | | | | | |
| 0.1979 | 0.8700 | 0.8976 | 0.9192 | 0.9952 | 1.0000 | | | | | | | | |
| 0.0801 | 0.7658 | 0.9182 | 0.9360 | 0.9231 | 0.8472 | 1.0000 | | | | | | | |
| 0.4115 | 0.8549 | 0.8553 | 0.6376 | 0.9560 | 0.6189 | 0.6821 | 1.0000 | | | | | | |
| 0.0927 | 0.9300 | 0.7290 | 0.9439 | 0.4815 | 0.6126 | 0.9021 | 0.3379 | 1.0000 | | | | | |
| 0.8782 | 0.8612 | 0.9423 | 0.5600 | 0.8948 | 0.8635 | 0.5672 | 0.9349 | 0.2477 | 1.0000 | | | | |
| 0.5595 | 0.6802 | 0.8911 | 0.9571 | 0.9510 | 0.4821 | 0.8623 | 0.6494 | 0.3807 | 0.9213 | 1.0000 | | | |
| 0.2552 | 0.8401 | 0.8430 | 0.8789 | 0.8337 | 0.8347 | 0.7942 | 0.9046 | 0.9791 | 0.0921 | 0.2344 | 1.0000 | | |
| 0.0797 | 0.2782 | 0.5775 | 0.2541 | 0.2440 | 0.2745 | 0.6596 | 0.7353 | 0.5070 | 0.1807 | 0.1147 | 0.9117 | 1.0000 | |
| 0.1394 | 0.3782 | 0.5473 | 0.5384 | 0.4844 | 0.2189 | 0.6764 | 0.7347 | 0.5798 | 0.9643 | 0.2295 | 0.9667 | 0.8801 | 1.0000 |

technique makes use of the probabilistic nature of his index, it has been used here.

As opposed to the usual methods of building up a hierarchy from nuclear pairs, Goodall's approach breaks down the initial set of individuals into smaller and smaller subsets, each subset being defined at a given level of probability. The similarity matrix is scanned to find groups of items whose mutual similarity is greater than can be expected by chance at the 0.05 probability level.

In cases like the present study, which involves 392 coefficients, this scanning process is laborious. To shorten the procedure, the principal components of the similarity matrix were extracted. Because the matrix is not Grammian, negative eigenvalues emerged during the diagonalization process,

Table VI. *Principal components matrix showing loadings of specimens on the first four principal axes*

| Specimen | Factor 1 | Factor 2 | Factor 3 | Factor 4 |
|---|---|---|---|---|
| 1 | 0.4389 | −0.2210 | 0.5550 | 0.2903 |
| 4 | 0.4233 | −0.4935 | 0.4976 | 0.4319 |
| 2 | 0.5878 | −0.4453 | 0.7843 | 0.0419 |
| 3 | 0.6320 | −0.0392 | 0.6094 | −0.4634 |
| 5 | 0.7980 | −0.3575 | 0.5269 | −0.2954 |
| 19 | 0.8270 | −0.5732 | −0.2474 | 0.4074 |
| 20 | 0.5595 | −0.5761 | −0.0781 | 0.4592 |
| 21 | 0.5082 | −0.5237 | −0.4799 | 0.0169 |
| 22 | 0.6659 | −0.5944 | −0.3718 | −0.3514 |
| 23 | 0.6245 | −0.4323 | −0.5935 | −0.1872 |
| 24 | 0.6503 | −0.3330 | −0.5582 | −0.4440 |
| 28 | 0.6360 | −0.5557 | −0.4440 | −0.2678 |
| 25 | 0.3468 | −0.4503 | 0.2274 | 0.3319 |
| 26 | 0.6092 | −0.7009 | 0.0799 | 0.0199 |
| 27 | 0.4635 | −0.5119 | 0.4429 | 0.1341 |
| 11 | 0.7176 | 0.6352 | 0.0941 | 0.0924 |
| 13 | 0.9161 | 0.4460 | 0.2078 | 0.0246 |
| 14 | 0.8460 | 0.5462 | 0.0621 | −0.3493 |
| 15 | 0.6587 | 0.6122 | 0.0274 | −0.0911 |
| 16 | 0.6495 | 0.7348 | −0.0090 | 0.1904 |
| 17 | 0.6072 | 0.5268 | 0.3044 | −0.2714 |
| 6 | 0.7389 | 0.4713 | −0.1902 | 0.4944 |
| 8 | 0.6560 | 0.3938 | −0.2780 | 0.5607 |
| 12 | 0.7377 | 0.5695 | −0.2007 | 0.2269 |
| 7 | 0.5856 | 0.0672 | −0.3402 | 0.2283 |
| 9 | 0.7413 | 0.1045 | −0.2325 | −0.0573 |
| 10 | 0.8629 | 0.2435 | −0.2561 | −0.0540 |
| 18 | 0.8682 | 0.1509 | 0.2966 | −0.4902 |

so that theoretically this step is not sound. However, the first few positive principal components reveal a structure that does aid in the initial clustering.

Table VI shows the loadings of the 28 items on the first four principal components. These principal components may be thought of as representing orthogonal reference axes in four-dimensional space. A row of Table VI, then, represents the coordinates of that particular specimen in four-space. Fig. 3 illustrates some of the possible two-dimensional views of this four-space. Definite clusters of points are readily apparent.

The view in Fig. 3 (top left), normal to the first and second principal axes, shows the specimens forming two discrete clusters. Without exception, all the specimens with negative loadings on the second principal axis occur in the Hungry Hollow Formation; those with positive loadings in the Onondaga Formation. Thus the technique was able to separate the specimens into their correct stratigraphic positions strictly on the basis of their morphologies.

Fig. 3 (top right) shows the 2–3 plane. Here the Onondaga specimens are separated into two distinct clusters of points. There is also a tendency for the Hungry Hollow specimens to form two vague clusters. Fig. 3 (bottom left) shows the 2–4 plane with a further split in the Onondaga specimens.

The dashed lines enclosing clusters of points have been drawn after consideration of all six possible views of the four-space. Although in any one view clusters may appear to overlap, this is merely a function of that particular view. A separation between clusters in any view is real; overlap, on the other hand, may be only apparent.

On the basis of this preliminary sorting, and further visual inspection, the rows and columns of the original similarity matrix were reorganized as shown in Table V.

The final definition of clusters was achieved by an iterative procedure that isolated specimens with mutual similarities above a significant value. Similarity coefficients were then computed within each group and examined for additional clusters. If additional clusters could be identified, these too were isolated, in which case the similarity matrices had to be recalculated, because similarity as here used (following Goodall, 1964) can be defined only within the context of the specimens under consideration.

## RESULTS

Table V shows that within the Onondaga samples four clusters of specimens can be established. Group 1, consisting of specimens 24, 23, 28, 22, has mutual similarities all greater than 0.9864, and none of the similarities between these specimens and specimens outside this Group exceeds this value. The probability of 6 out of 392 coefficients with this value occurring by chance is exceedingly small. Group 2 consists of specimens 19, 21, 20; it too contains mutual similarities of a significantly high value which are not exceeded elsewhere, and the same can be said of Group 3 which includes specimens 25, 27, 26.

Group 4 is not as tightly knit as the other three: two of the ten coefficients are not significant at the 0.05 level. As both these values are associated with specimen 3, it might be considered as a separate group; for the present, however, it is included in Group 4.

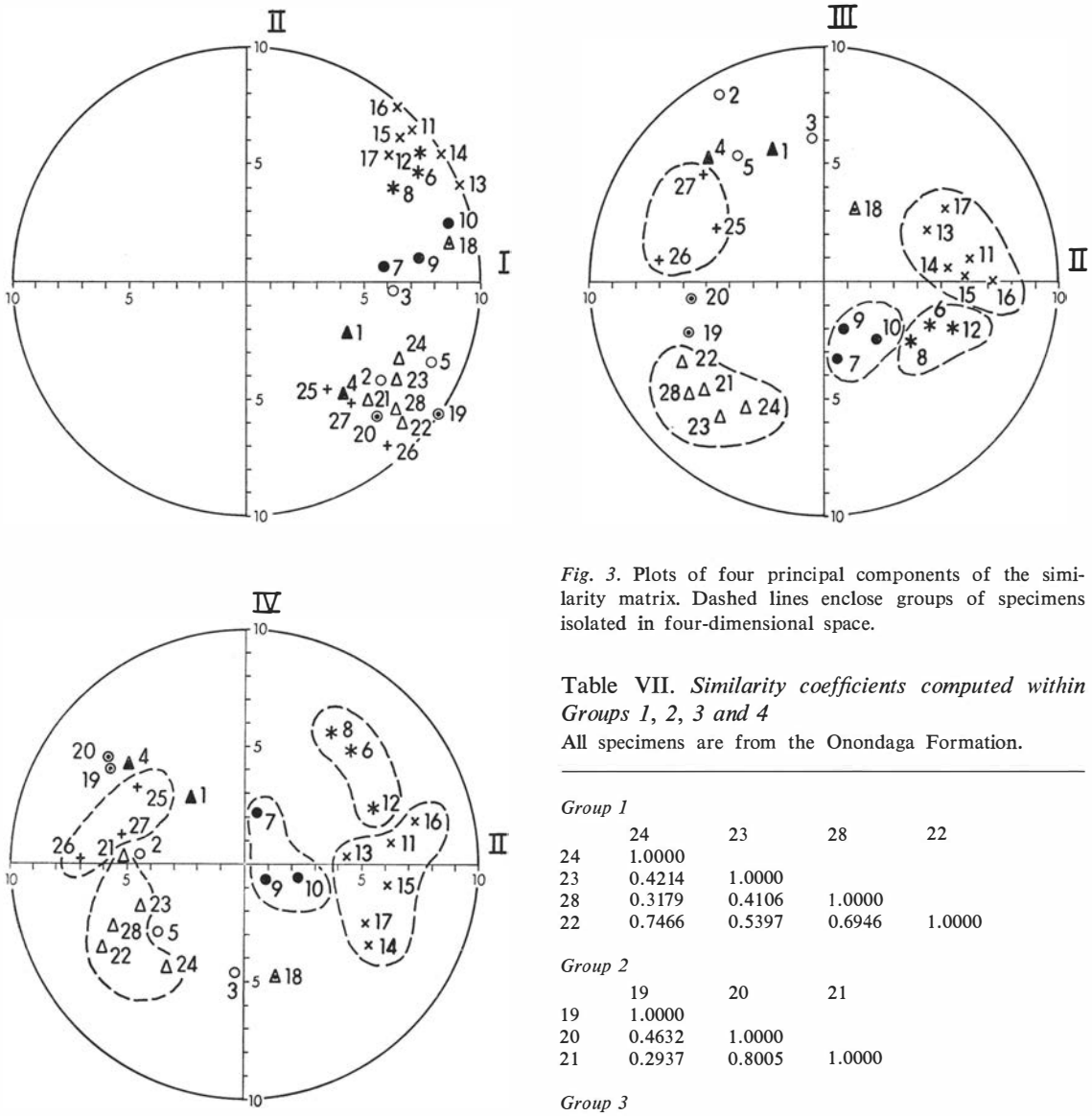


*Fig. 3.* Plots of four principal components of the similarity matrix. Dashed lines enclose groups of specimens isolated in four-dimensional space.

Table VII. *Similarity coefficients computed within Groups 1, 2, 3 and 4*

All specimens are from the Onondaga Formation.

*Group 1*

| | 24 | 23 | 28 | 22 |
|---|---|---|---|---|
| 24 | 1.0000 | | | |
| 23 | 0.4214 | 1.0000 | | |
| 28 | 0.3179 | 0.4106 | 1.0000 | |
| 22 | 0.7466 | 0.5397 | 0.6946 | 1.0000 |

*Group 2*

| | 19 | 20 | 21 |
|---|---|---|---|
| 19 | 1.0000 | | |
| 20 | 0.4632 | 1.0000 | |
| 21 | 0.2937 | 0.8005 | 1.0000 |

*Group 3*

| | 25 | 26 | 27 |
|---|---|---|---|
| 25 | 1.0000 | | |
| 26 | 0.1072 | 1.0000 | |
| 27 | 0.7393 | 0.7132 | 1.0000 |

*Group 4*

| | 2 | 1 | 4 | 3 | 5 |
|---|---|---|---|---|---|
| 2 | 1.0000 | | | | |
| 1 | 0.8340 | 1.0000 | | | |
| 4 | 0.2448 | 0.9437 | 1.0000 | | |
| 3 | 0.7275 | 0.1317 | 0.0741 | 1.0000 | |
| 5 | 0.1226 | 0.2836 | 0.2767 | 0.5338 | 1.0000 |

Examination of inter-group similarities shows that Groups 1 and 2 are closely related, although, two values are very low and two are borderline. Groups 2 and 3 are related to some degree. Group 4 shows weak relationships to Groups 2 and 3, but the coefficients that suggest this could have arisen by chance.

Thus, in the initial iteration, the Onondaga specimens can be subdivided into four Groups.

The Hungry Hollow specimens (6 to 18) show the difficulty of applying the present procedure: no clearly defined clusters are evident in Table V. While specimens 11, 13, 16, 14, 15, 6, and 8 all contain mutual similarities significant enough to form a cluster at the 0.05 level, there are nu-

Table VIII. *Similarity coefficients computed within Group 5*
All specimens are from the Hungry Hollow Formation.

| | 11 | 13 | 14 | 15 | 16 | 12 | 10 | 8 | 6 | 9 | 18 | 17 | 7 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 11 | 1.0000 | | | | | | | | | | | | |
| 13 | 0.9455 | 1.0000 | | | | | | | | | | | |
| 14 | 0.7831 | 0.7589 | 1.0000 | | | | | | | | | | |
| 15 | 0.7332 | 0.7275 | 0.9856 | 1.0000 | | | | | | | | | |
| 16 | 0.6504 | 0.9199 | 0.6766 | 0.7843 | 1.0000 | | | | | | | | |
| 12 | 0.4590 | 0.7682 | 0.8034 | 0.7148 | 0.7173 | 1.0000 | | | | | | | |
| 10 | 0.6830 | 0.5882 | 0.8240 | 0.2953 | 0.2072 | 0.3321 | 1.0000 | | | | | | |
| 8 | 0.6212 | 0.3807 | 0.1494 | 0.3104 | 0.7956 | 0.6134 | 0.0859 | 1.0000 | | | | | |
| 6 | 0.3587 | 0.4496 | 0.4565 | 0.5269 | 0.5249 | 0.3214 | 0.7232 | 0.8819 | 1.0000 | | | | |
| 9 | 0.0452 | 0.1406 | 0.1380 | 0.0291 | 0.1492 | 0.2058 | 0.4344 | 0.1857 | 0.8363 | 1.0000 | | | |
| 18 | 0.6834 | 0.8852 | 0.6967 | 0.7503 | 0.1053 | 0.2463 | 0.8754 | 0.0240 | 0.0005 | 0.9507 | 1.0000 | | |
| 17 | 0.3390 | 0.6556 | 0.8335 | 0.2477 | 0.7737 | 0.6205 | 0.2926 | 0.0626 | 0.0045 | 0.0250 | 0.8329 | 1.0000 | |
| 7 | 0.0197 | 0.2791 | 0.0182 | 0.0338 | 0.0131 | 0.1897 | 0.6480 | 0.1090 | 0.4761 | 0.2275 | 0.1137 | 0.0032 | 1.0000 |

merous coefficients outside the cluster that exceed this value. It was therefore decided to retain all the Hungry Hollow specimens as Group 5. Only 14 out of the 195 coefficients between members of Group 5 and of the other Groups exceed 0.70.

In an attempt to subdivide these Groups further, similarity coefficients were computed within each, with the results shown in Tables VII, VIII and IX.

No further breakdown of Groups 1 to 4 is possible (Table VII); they appear to be homogeneous although some of the coefficients in Groups 3 and 4 are disturbingly low.

In the similarity coefficients computed within the Hungry Hollow specimens (Table VIII) there is no obvious clustering, although specimens 11–16 do show a relatively high degree of mutual similarity. On rather tenuous grounds, these are designated Group 5 a; the remaining specimens are left in a residue group, 5 b. The similarities within these Groups are shown in Table IX, clearly no further subdivision is possible.

Table IX. *Similarity coefficients computed within Groups 5 A and 5 B*

*Group 5 B*

| | 6 | 7 | 8 | 9 | 10 | 17 | 18 |
|---|---|---|---|---|---|---|---|
| 6 | 1.0000 | | | | | | |
| 7 | 0.6103 | 1.0000 | | | | | |
| 8 | 0.9814 | 0.5392 | 1.0000 | | | | |
| 9 | 0.8469 | 0.2124 | 0.4531 | 1.0000 | | | |
| 10 | 0.7662 | 0.5868 | 0.2527 | 0.4176 | 1.0000 | | |
| 17 | 0.0690 | 0.0647 | 0.1941 | 0.3879 | 0.5030 | 1.0000 | |
| 18 | 0.0434 | 0.3789 | 0.1466 | 0.9195 | 0.7684 | 0.8918 | 1.0000 |

*Group 5 A*

| | 11 | 12 | 13 | 14 | 15 | 16 |
|---|---|---|---|---|---|---|
| 11 | 1.0000 | | | | | |
| 12 | 0.0015 | 1.0000 | | | | |
| 13 | 0.8165 | 0.5147 | 1.0000 | | | |
| 14 | 0.6715 | 0.5406 | 0.4743 | 1.0000 | | |
| 15 | 0.2821 | 0.2527 | 0.3840 | 0.8964 | 1.0000 | |
| 16 | 0.0511 | 0.0985 | 0.7310 | 0.2756 | 0.6455 | 1.0000 |

## DISCUSSION

Although the procedures advocated here are not as rigorous as some previously suggested methods of numerical taxonomy, they offer certain advantages. As has been noted, the probabilistic similarity index is extremely versatile in that it will accept attributes determined on various scales. Further, its intrinsic weighting function is very close to that used by classical taxonomists. The clustering process is strictly an *ad hoc* procedure, but should be amenable to a more objective treatment; the results of the present example demonstrate its merit.

Table X. *Comparison of numerical taxonomy with "visual" taxonomy*
The correspondence between the two schemes is evident from the high values in the diagonal of the matrix.

| | Group | | | | | |
|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5*a* | 5*b* |
| S. tubulomamilatum | 3 | | 1 | | | |
| S. problematicum | | 3 | | | | |
| S. lophiostromoides | | | 2 | | | |
| S. mamilliferum | | | | 5 | | |
| S. excellens | 1 | | | | | |
| S. kayi | | | | | 6 | 2 |
| S. elevatum | | | | | 3 | 2 |

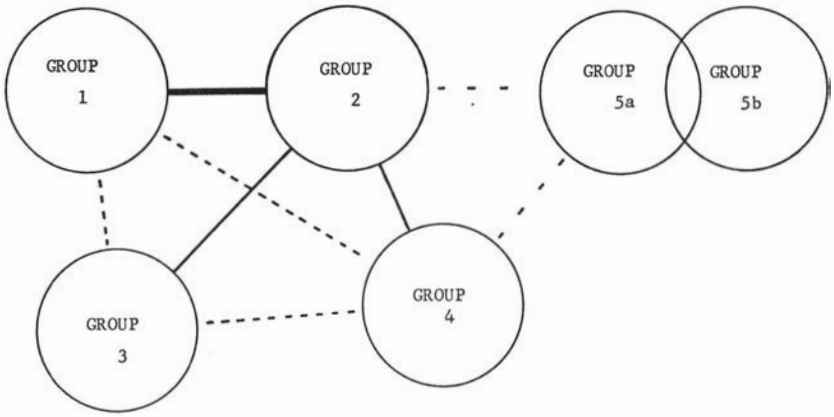


*Fig. 4.* Intergroup relationships subjectively defined by inspection of intergroup similarities of Table V.

The 28 specimens considered here were first placed into species by St. Jean. Table X compares his results with those of the present analysis. Reading down a column of this chart reveals the correspondence between St. Jean's Groups and the ones established here. Reading across a row gives the reverse picture. For example, Group 1 contains three specimens assigned by St. Jean to *S. tubulomamilatum,* as well as the one specimen of *S. excellens.* One of the original members of *S. tubulomamilatum* has been placed in Group 3, along with the two specimens of *S. lophiostromoides.* In general, the agreement in results from the two methods is very high. In the case of the Hungry Hollow specimens, it seems unlikely that we can distinguish *S. kayi* from *S. elevatum.* St. Jean (1962) pointed out that these two species are very close and are distinguished primarily by subtle differences in microstructure—features that were not taken into account in the present study.

Figure 4 portrays the intergroup relationships based on a rather subjective appraisal of Table V, from which it is evident that there is considerable intergradation between the Groups. This perhaps is what one should expect from evolutionary theory.

## CONCLUSIONS

Numerical taxonomic study of a limited number of specimens of *Stictostroma* has largely confirmed the original diagnosis based on conventional taxonomy. Considering the amount of disagreement among stromatoporoid experts on the basis of classification, this outcome is both gratifying and reassuring. The technique proposed, although not as rigorous as others previously described, is an effective method of numerical taxonomy that can be applied directly to many paleontological problems.

## ACKNOWLEDGMENTS

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*Sommaire.* Des traits morphologiques de 28 exemplaires du stromatoporoïde *Stictostroma* ont été rangés numériquement à l'aide d'échelles nominales, ordinales et d'intervalles. Ces données ont été soumises à une technique de taxonomie numérique récemment développée dans le but de réaliser une classification phénétique objective.

Les exemplaires avaient été rassemblés dans les formations du Devon central de Hungry Hollow et d'Onondaga, dans l'Ontario du Sud. Ils ont été décrits en un article précédent par St Jean. Une table des similitudes, proposée par Goodall (1964), a été employée pour déterminer le degré de ressemblance entre toutes les comparaisons possibles, faites par paires. Cette table, basée sur la probabilité, a des avantages sur celles publiées jusqu'ici. Ainsi, par example, elle accorde de l'importance aux signes distinctifs selon leur apparition rare ou répétée dans la série d'exemplaires à considérer et tend ainsi à imiter le jugement intuitif du classificateur. D'autres avantages sont qu'à l'aide de cette table on peut traiter en même temps des données nominales, ordinales et d'intervalles; les données manquantes sont admises, et les similitudes sont définies dans le contexte uniquement des exemplaires actuellement observés.

Plusieurs méthodes de trouver une structure parmi les coefficients de similitude ont toutes donné des résultats en somme identiques. Finalement, on a adopté une méthode modifiée des composantes principales.

Les résultats de cette méthode montrent que les exemplaires peuvent être divisés en deux groupes qui correspondent, sans exceptions, aux collections des deux formations différentes. Les deux groupes peuvent être encore partagés en petits groupes d'exemplaires qui se séparent en détails seulement d'espèces que l'on peut reconnaître visuellement.

Les relations entre les groupes et le diagnostic des signes distinctifs de chaque groupe sont faciles à déterminer par cette analyse.

## REFERENCES


Bonham-Carter, G. F. 1967. Fortram IV Program for Q-Mode Cluster Analysis of Nonquantitative Data Using IBM 7090/7094 Computers. *Computer Contribution* 17, State Geological Survey Univ. Kansas.

Burma, B. H. 1948. Studies in Quantitative Paleontology: I, Some Aspects of the Theory and Practice of Quantitative Invertebrate Paleontology. *J. Paleont.* 12, 725–61.

Cooper, G. A., Butts, C., Caster, K. E., Chadwick, G. H., Goldring, W., Kindle, E. M., Kirk, E., Merrian, C. W., Swartz, F. M., Warren, P. S., Warthin, A. S. & Willard, B. 1942. Correlation of the Devonian Sedimentary Formation of North America. *Bull. geol. Soc. Amer.* 53, 1729–1794.

Galloway, J. J. and St. Jean, J., Jr. 1957. Middle Devonian Stromatoporoids of Indiana, Kentucky and Ohio. *Bull. Amer. Paleont.* 37, 24–308.

Goodall, D. W. 1964. A Probabilistic Similarity Index. *Nature* 203, 1098.

— 1966 *a*. Numerical Taxonomy of Bacteria—Some Published Data Re-examined. *J. gen. Microbiol.* 42, 25–37.

— 1966. *b*. A New Similarity Index Based on Probability. *Biometrics* 22, 882–907.

Imbrie, J. 1956. Biometrical Methods in the Study of Invertebrate Fossils. *Bull. Amer. Mus. nat. Hist.* 108, 211–52.

Klovan, J. E. 1966. Upper Devonian Stromatoporoids from the Redwater Reef Complex, Alberta, Canada. *Bull. geol. Surv. Can.* 133, part I.

Lecompte, M. 1951–1952. Les Stromatoporoides du Devonien Moyen et Supérieur du Bassin de Dinant. *Mém. Inst. Sci. nat. Belg.* 116 (1951), 1–215; 117 (1952), 216–256.

Olson, E. C. 1964. Morphological Integration and the Meaning of Characters in Classification Systems. Systematics Association Publication No. 6, *Phenetic and Phylogenetic Classification,* 123–156.

Olson, E. C. & Miller, R. L. 1958. *Morphological Integration*. Univ. of Chicago Press.

Parks, M. J. 1966. Cluster Analysis Applied to Multivariate Geological Problems. *J. Geol.* 74, 703–715.

Pearson, K. 1926. On the Coefficient of Racial Likeness. *Biometrika* 18, 105–117.

Rubin, J. 1965. Optimal Taxonomy Program, (7090-IBM-0026). IBM, Program Information Dept., Hawthorne, New York.

Siegel, S. 1956. *Nonparametric Statistics for the Behavioral Sciences*. McGraw-Hill, New York.

Sokal, R. R. and Sneath, R. H. A. 1963. *Principles of Numerical Taxonomy*. W. H. Freeman Co., San Francisco.

Stearn, C. W. 1966. The Microstructure in the Stromatoporoids. *Palaeontology* 9, 74–124.

St. Jean, J., Jr. 1962. Micromorphology of the Stromatoporoid Genus *Stictostroma* Parks. *J. Paleont.* 36, 185–200.

Yavorski, V. I. 1962. Some Results of a Study of the Stromatoporoids of the U.S.S.R. *Paleont. J.* 1, 19–30. (Translations in the files of the Geological Survey of Canada.)