# UPPER DEVONIAN PLANT MICROFOSSILS
# AND PALAEOECOLOGY

# UPPER DEVONIAN PLANT MICROFOSSILS FROM EASTERN AND ARCTIC CANADA: THEIR TAXONOMY AND PALAEOECOLOGICAL SIGNIFICANCE

by

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SCOPE AND CONTENTS:

Plant microfossils are extracted from strata of Upper Devonian age occurring at two previously uninvestigated localities in Eastern Canada and in the Canadian Arctic. The extraction procedure includes a new permanent palynological mounting technique using corn syrup and Permount, a synthetic resin. In addition, a method of eliminating by-product in residues after hydrofluoric acid, is also described.

A number of miospore and acritarch form species are described and figured; nine new form species of miospores are proposed. The miospore species recovered from both localities indicate a geological age of early Upper Devonian (Frasnian) for the enclosing strata.

A new way of assessing qualitative, regional palaeofloristic changes is provided by tabulation of morphological characteristics of individual miospores. The use of miospore species in defining Upper Devonian microfloral provinces and Upper Devonian-Lower Carboniferous migration of parent forms is demonstrated.

# PREFACE

Authors of earlier theses in the field of palynology have customarily included somewhat detailed résumés of the general history of palynology. As well, they have outlined the characteristics of plant microfossils. Since the general treatments of these subjects are adequately set out elsewhere (McGregor, 1957; Wilkinson, 1959), the author thinks that remarks on these topics may be confined to subject matter related more directly to the present research. In view of this, historical observations will be limited to Devonian palynology and discussion of plant microfossils will be concerned with certain areas of definition of terms and nomenclature. The discussion of these facets of plant microfossils will have some bearing on the remarks of a historical nature, and therefore, the former will be the subject of this preface while the latter will be outlined in a later chapter.

The concern of this preface is to make clear the meaning of several terms which have become vague or now have a different usage. 'Plant microfossil', 'microspore', 'miospore', and 'hystrichosphere' are among these terms.

In this thesis, 'plant microfossil' will include generally microscopic, acid-resistant forms commonly referred to as pollen grains, spores, dispersed fragments of cuticle, sporangia, and vascular elements of plants, as well as organic microplankton. It will not include siliceous remains with plant characteristics or remains of calcareous algae.

All spores described in this thesis are dispersed in a rock matrix and unattached to a parent plant. Under these conditions, botanical affinities of the spores are not likely to be deduced conclusively.

To follow the common practice of dividing dispersed spores into megaspores and microspores (the former equal to or greater than 200μ and the latter less than 200μ in size) would be somewhat misleading. The word 'isospore' used in this context would also be misleading, because true isospores (male and female spores of equal or nearly equal size) fall within the size range of microspores. It would also suggest that the state of homospory was known to exist in the parent plant.

To avoid these difficulties, the author will follow the practice of Guennel (1958) and refer to all spores and spore-like bodies under 200μ (including small megaspores, isospores, true microspores, pre-pollens, and pollen grains) as miospores. The arbitrary lower size limit for megaspores (200μ) will be retained for convenience.

Organic microplankton include the dinoflagellates, the hystrichospheres, and the acritarchs. Undoubted dinoflagellates have not been found in rocks older than the Triassic (Jansonius, 1962) and will not be discussed further. The terms, 'hystrichosphere' and 'acritarch' require further consideration.

The term 'hystrichosphere' originally encompassed a wide variety of forms, including many of uncertain affinities. Evitt (1961) pointed out that the group was heterogenous, containing forms definitely related to the dinoflagellates and forms of uncertain or unknown affinities. Evitt (1963) then proposed that 'hystrichosphere' be restricted to those forms showing an affinity to the dinoflagellates and placed the remaining organic microplankton of uncertain affinities in a new group, the Acritarcha. Downie, Evitt, and Sarjeant (1963) expanded this classification and regrouped genera to conform to this system. Since this seems to be the most satisfactory solution yet proposed to this problem, the author accepts this system and will classify appropriate forms in accordance with it.

The question of which nomenclatural code should be followed for taxonomy involving acritarchs is not so easily resolved. Some workers (as in Eisenack, 1963) follow the International Code of Zoological Nomenclature when dealing with these forms, while others (Downie, Evitt, and Sarjeant, 1963) treat them as plants and use the International Code of Botanical Nomenclature. The author chooses to follow the latter practice in view of the reasonable arguments advanced by Downie, et al. (1963) and the fact that the author's definition of plant microfossils includes forms usually assigned to the Acritarcha.

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# INTRODUCTION

## DEVONIAN PALYNOLOGY

Plant microfossils have been recognized in coals and clastic rocks for over a century (fide: Wilkinson, 1959). The use of miospores in correlation of coal seams and their potential use in correlation of other lithologies was realized three decades ago (Raistrick, 1934). The palaeobotanical significance of miospores has been recognized for almost as long (Knox, 1938; 1939).

Prior to 1953, however, relatively little work had been published on miospores extracted from rocks of Devonian age. The probable reasons for this were several. Coal seams and coaly rocks are relatively rare in the Devonian and much of the incentive for study of Palaeozoic spores derived from the use of miospores for the correlation of coal seams. Also, suitable techniques had been evolved for the maceration of coals, but comparatively few efficient methods had been developed for the treatment of clastic sedimentary rocks. Perhaps, as well, the relatively sparse occurrence of macrofloras comparable in scope to those commonly found in Carboniferous rocks, suggested a sparse microflora to early workers. Palaeobotanical papers, therefore, most often dealt with miospores of the Devonian in a secondary manner, while the description of macrofossils constituted the main part of the work. Such treatments may be found in papers by

Kidston and Lang (1917), Arnold (1936), Høeg (1942), and many others.

During the early 1930's, the great development of Carboniferous palynology, especially in the fields of taxonomy and correlation of coal seams led to an interest in Devonian miospores. Attention was turned for the first time to the study of the miospores in Devonian rocks, but compared with Carboniferous palynology, progress was slow. Elovskaya (1936) was perhaps the first to publish a paper devoted to a study of miospores of Devonian age. Baschnagel (1942) described some dinoflagellates (more likely acritarchs) from the Devonian of New York State, and Thomson (1940; 1952) in Europe and Hsü (1953) in China published accounts of Devonian miospores. These five papers constituted virtually all the literature of Devonian palynology in early 1953.

Since that time, a great deal of work has been done, particularly by Russian and North American workers, and by palynologists in the United Kingdom, Australia, and France. Numerous papers have appeared by Russian authors, that of Naumova's (1953) being the most outstanding despite the author's failure to designate types for many of her genera. Unfortunately, the majority of recent Russian papers consist only of lists of miospore assemblages and are poorly illustrated (if at all), making them nearly worthless taxonomically.

North American workers have also been extremely active. Radforth and McGregor (1954) have reported the finding of abundant miospores in Lower and Middle Devonian rocks of the Gaspé Peninsula. Hoffmeister, Staplin and Malloy (1955) have illustrated some Upper Devonian miospores from Western Canada and outlined the known range of many Palaeozoic miospore genera. McGregor (1960; 1961) published results of a study of material collected from various horizons of the Canadian Devonian. Other papers, by Radforth and Wilkinson (1959) on the Lower Devonian York River Formation, by Scott and Rouse (1961) on Lower Devonian Gaspé material, and by Griggs, et al. (1963), McGregor (1963; 1964) on the late Middle to Early Upper Devonian Ghost River Formation, and Owens (1965, in press) on the Upper Devonian Heckla and Griper Bay Formations (Canadian Arctic), have also appeared. Winslow (1962) has included some descriptions of Upper Devonian material from Ohio, although her publication deals mainly with Carboniferous plant microfossils.

A few lists of assemblages have been published by North American authors in conjunction with large scale reconnaisance mapping of the Canadian Arctic. Fry (1959) and McGregor (in: Fortier, et al., 1963; Tozer and Thorsteinsson, 1964) have listed miospore assemblages of Devonian age from Prince Patrick, Ellesmere, and Melville Islands.

In the United Kingdom, Richardson (1960; 1962; 1965), Chaloner (1959), Chaloner and Pettit (1964) and Pettit (in press) have published papers dealing with Devonian material, collected in the latter three cases in Canada. Sen (1958), of India, has redescribed megaspores of Upper Devonian age from Bear Island, collected by Nathorst. In Australia, Balme (1960) and Balme and Hassell (1962) have described Upper Devonian miospores from several locations. In France, Taugourdeau-Lantz (1960) and Caro-Moniez (1962) have reported on Middle and Upper Devonian miospores assemblages. Finally, Long (1963) has reported the presence, but not described, miospores that are believed to be of Lower Devonian age from the Horlick Mountains in Antarctica.

## THE CONTRIBUTIONS OF EARLIER WORK

The recent expansion of Devonian palynology has led to a better understanding of several aspects of Devonian miospores. Firstly, the morphology of Devonian miospores has proven to be complex and varied (Richardson, 1965). Both ornamentation and structure show wide variation ranging from organization usually considered simple (smooth, round trilete miospores) to those with massive cingulate structure (see Appendix I for explanation of terms) and complex ornamentation. Miospores with sacs or bladders enclosing an inner body have also been found, a mode of organization generally accepted as advanced because of the association of such forms with parent plants allied to heterosporous lycopsids and pteridosperms (Potonié, 1962). A number of morphographic trends have also been delineated, including the confining of miospores with proximal radial ribs to the Lower and Middle Devonian (McGregor, 1961) and the occurrence of miospores with bifurcate processes in Middle and Upper Devonian rocks (McGregor, 1960; Richardson, 1960; 1965).

Secondly, the distribution of Devonian miospores has been tentatively established. Geographically, miospores are known to occur in abundance at various localities in Canada and Russia, and in England, France, Germany, the Baltic region, China, Australia, the Antarctic and the United States. Stratigraphically, miospores have been found in rocks of various Devonian ages and have been used to make broad correlations between sections in various parts of the world (Richardson, 1965). Especially important is the fact that these miospores are often the only abundantly occurring fossils in rocks of non-marine origin.

Palaeobotanically, the discovery of certain morphological trends (Radforth and McGregor, 1956) and the occurrence of certain miospores in abundance at various localities has suggested the presence of macrofossil forms as yet undescribed (McGregor, 1961) or represented in the fossil record only by their spores.

The emphasis of previous research in Devonian palynology has varied from the almost completely stratigraphic papers of Russian authors (Ozolinya, 1960) to the palaeoecological papers of workers such as Radforth and Wilkinson (1959). The main emphasis, however, has been stratigraphical and taxonomical. At least one hundred miospore genera have been described. Papers dealing with the palaeoecological aspects of Devonian miospores have been few. Naumova (1953) has discussed the botanical affinites of miospores from the Russian Platform and outlined a number of trends having possible palaeoecological significance. Among these are a tendency for miospores having a particular ornamentation to occur in certain sedimentary facies and a possible relation of thin-walled forms to parent plants of aquatic habitat. Radforth and Wilkinson (1959) have suggested that the range of variation from simple miospores (for example: smooth, round, trilete) to more complex forms encountered within an assemblage, may be a measure of specialization within that assemblage. A recent trend has been the combining of taxonomic treatment with some evaluation of the palaeoecology of the miospores (McGregor, 1964; Richardson, 1965).

## THE OBJECTIVES OF THE PRESENT RESEARCH

Although much has been learned about Devonian miospores in the past decade, many of the results are only suggestive and require expansion.

The course of future research may be divided into three main categories: the examination of previously unexplored Devonian sections for miospores; the detailed studies of sections known to be fossiliferous, with regard to miospore taxonomy and stratigraphic division; and the assessment of palaeobotanical and palaeoecological data provided by miospores.

The main objectives of the present work will be to contribute new knowledge to the first of these avenues of research and for the last of these to formulate new ideas and new techniques.

Assuming that the Upper Devonian lithologies selected yield sufficiently abundant and well-preserved microfossils, the first step in carrying out these objectives will be to work out the taxonomy of the miospores and acritarchs in order to allow comparison with known assemblages and facilitate palaeoecological evaluation. The second step will be to collect data on the frequency of occurrence and the diversity of morphological characteristics of the miospores, the types of wood elements and other associated plant microfossils.

The final step in this program will be the synthesis of these data in order to give some palaeoecological evaluation of the miospores and extend the knowledge of the distribution of Upper Devonian miospores and their relation to older and younger microfloras.

# DEVONIAN PLANT PALAEOECOLOGY:
# CONCEPTS AND SOURCES OF INFORMATION

## INTRODUCTION

Plant microfossils, because of their abundance and variety of form, might be logically considered as excellent sources of palaeoecological data. Yet very little has been written on the question of palaeoecological assessment of Devonian plant microfossils. Consequently, there is a scarcity of theoretical groundwork on which to base an investigation of this type. Before the second of the two main objectives of the present work can be attempted, it will be necessary to consider the question of Devonian plant palaeoecology from several viewpoints.

Certain existing topics that are general in scope should be examined: the relation of ecology and palaeoecology; the limitations of palaeoecology; and the nature of Devonian plant palaeoecology. A discussion of these topics may prove to be useful in establishing broad guides to research and the interpretation of results.

Two main questions arise concerning data from microfossils. Firstly, what characteristics of plant microfossils can be interpreted to obtain palaeoecological data? Secondly, what reasons are there for considering the data meaningful? A discussion of these two aspects will form part of the subject material of this chapter.

## ECOLOGY AND PALAEOECOLOGY

Both modern ecology and palaeoecology deal in some manner with the interrelationships of plant organisms. When relationships are recognized, then certain patterns of organization become evident. Such patterns may be recognized in studies of either the spatial distribution of organisms or of the sequences of organisms in time at a particular site. Both types of patterns may be assumed to be functions of competition, migration, and displacement of groups of organisms by other groups or by the interaction of the environment and the organisms.

There are basic differences, however, in the way that ecology and palaeoecology approach these similarities. One important difference is that modern ecology deals with living organisms in their habitat while palaeoecology deals with fossils that are found in various states of preservation, in varying numbers, in varying lithological settings, and often outside their original habitat. Another very important difference is the time scale involved. Modern ecology works within a time scale that may extend a few hundreds of years while palaeoecology involves time spans of thousands to millions of years. Another feature is the relative disposition of geological time units usually available in palaeoecological studies, compared with the absolute span of modern ecology. These two basic differences lead to other secondary considerations and these will be discussed below.

## PALAEOECOLOGY AND FOSSILIZATION

Fossilization and the length of geological time give rise to a number of controls or limitations of a geological and biological nature. Geological limitations, in given cases, may include: random and discontinuous distribution of outcrop; poor or incomplete preservation of fossilized organisms; selective fossilization of organisms, depending on the distance of transport to a sedimentary basin; removal of strata by faulting or erosion; preservation of only certain biotic elements in the sedimentary record; and the most usual condition of fossils preserved in an environment other than their life environment. This last factor has particular significance for most fossil plants, since they must usually be transported away from their terrestrial habitat to lacustrine or near-shore marine environments in order to be preserved. The palaeoecologist therefore must interpret an incomplete record of organisms and habitats.

Considerations more biological in context must also be taken into account. There is no guarantee that organisms may not have changed their habits and habitats with time. In biological matters, the present cannot always be accepted as the key to the past (the Principle of the Uniformity of Nature). The organisms are dead and there is no direct way to study their physiology or their association in a natural community. Because of this, the functions of certain morphological features must be ascertained by interpretative techniques and the vegetal cover reconstructed on piecemeal evidence.

When these circumstances are considered, it appears that the bases and aims of modern ecology and palaeoecology are fundamentally different. While the two are connected historically (palaeoecology following the development of ecology), they are distinct disciplines. Palaeoecological approach parallels modern ecology as much as possible, but it cannot be regarded merely as palaeo-contemporary ecology.

Allusion has been made (p. 9) to the Principle of the Uniformity of Nature, or Uniformitarianism (the present is the key to the past). Many of the interpretations offered by palaeoecologists are based on this general statement.

There are at least two ways of applying this Principle. One way is to assume that Palaeozoic plants reacted to their environment in the same manner as do contemporary plants with similar habit. This outlook also involves the assumption that morphological features of Palaeozoic plants similar to those of modern forms may indicate the same taxonomic position. A second way is to admit the possibility of non-uniform ecological response with time and to be cautious in drawing conclusions from morphological similarities.

For example, Knox (1950) has shown that spores of the modern Selaginellaceae have spinose, tuberculate, or rod-like (setulate) ornamentation of the exine, and a rounded, tetrahedral shape. According to the first interpretation of Uniformitarianism, it might be concluded that Palaeozoic miospores showing a similar ornamentation to those of the modern Selaginellaceae belonged to parent plants of that family. Furthermore, there would be an implication that the parent plants of these Palaeozoic miospores occupied an ecological niche similar to that of the contemporary Selaginellaceae. The second interpretation would admit the possibility that other groups could show such miospore ornamentation in the Palaeozoic (not necessarily including the Selaginellaceae). In this view, there would be no evidence to support the contention that the parent plants occupied a habitat similar to that of the modern Selaginellaceae, although the possibility would not be denied.

Scott (1962, p. 524) has pointed out that these two interpretations are often used indiscriminately. He characterizes the first (strict uniformity) as uniformitarian and the second as empirical. The concept of uniformitarianism underlying this thesis is (*sensu* Scott) more empirical than uniformitarian. While comparisons of Devonian miospore morphology may be made with geologically younger and with modern forms, it cannot be concluded that similarities in miospore morphology indicate similar parent plants or ecological niches. The outlook of the author is similar to that of Glaessner (1955, p. 5) who states:

> "Although we use the present as a key to the past, we should not forget that hidden in the past record are further keys which may be quite different from those supplied by the present fauna."

Glaessner was speaking of foraminifera, but the principle stated applies to plant microfossils in view of the discussion.

## THE CONCEPT FOR DEVONIAN PLANT PALAEOECOLOGY

The fossil plant record, from sedimentary rocks increasingly older than the Tertiary, is characterized by an increasingly smaller proportion of modern forms, an increasing number of extinct forms (with respect to both micro- and macrofossil forms), and by an essential difference in geological time scales (Andrews, 1961; Delevoryas, 1962; Traverse, 1955). For these reasons, it will be convenient and useful to analyse in relation to Tertiary-Quaternary plant palaeoecology and pre-Tertiary palaeoecology, although the choosing of the base of the Tertiary is arbitrary.

It is generally accepted that as progressively younger rocks are investigated in Tertiary and Quaternary studies, macrofloras and microfloras contain an increasingly greater proportion of forms similar to modern taxa. The similarity of the fossils to living forms allows deduction by analogy with modern forms on a much sounder basis, a practice which becomes more unreliable as progressively older assemblages are studied. In contrast to this, fossil micro- and macrofloras do not contain forms resembling modern plants on a generic level, until the latter part of the Cretaceous (Andrews, 1961; Delevoryas, 1962).

As increasingly older assemblages are studied, the decrease and then disappearance of living taxa means an ever diminishing knowledge of the "instantaneous ecology" of these forms. The increase in proportion of extinct plant types eventually leads to microfloras and macrofloras composed entirely of extinct forms. Where living genera are not present, there is no basis on which to deduce by analogy. There is necessarily a change from the strict uniformitarian approach that the present is the key to the past to the empirical approach that the sediments and fossil forms must provide the data on which to base palaeoecological interpretations. In studying Devonian floras, for example, parallels to modern plants exist only in relation to life form (<u>Psilophyton</u> and <u>Psilotum</u>; lepidodendroids and arborescent modern forms).

Having considered the relation of modern ecology and palaeoecology and the controls arising from fossilization existing in palaeoecology, it is now appropriate to consider what is meant by the phrase 'Devonian plant palaeoecology'.

Firstly, Devonian plant palaeoecology should be considered in an empirical sense. That is, the fossils should provide most of the data, although the palaeoecological significance of the data may be better appreciated in the light of contemporary observations (Ager, 1963). Secondly, the plant fossils can serve only as an indication of the kinds of ecological associations present in Devonian times. Thirdly, the concept of Devonian plant palaeoecology must encompass the geological and biological limitations common to all palaeoecological investigations.

Devonian plant palaeoecology, then, emerges primarily as a palaeoecology of life-forms, of reconstruction of extinct floras and floral provinces, and of the chronicling of migration of extinct floras (phytogeography). As such, it is distinct from other palaeobotanical investigations of anatomy, morphology and phylogenetic appraisal, but is closely related to stratigraphical studies of plant micro- and macrofossils.

## PLANT MICROFOSSILS AND PALAEOECOLOGICAL DATA

All plant microfossil types have some palaeoecological significance in the sense that Devonian plant palaeoecology has been outlined here. That is, information may be gained about the plant life-forms that will in turn enable the investigator to reconstruct extinct floras and floral provinces.

Plant microfossils may be present in both marine and non-marine sedimentary environments of deposition. Of the plant microfossil types to be discussed, only the organic microplankton are usually indicative of a marine depositional environment, while miospores and other types are generally deposited in non-marine or near-shore environments. It will be convenient to discuss the marine and non-marine forms separately, beginning with the latter types.

Miospores are the most abundantly occurring plant microfossils found in non-marine sedimentary rocks and will be considered first. Since there is little information about the parent plants of these miospores (Potonié and Kremp, 1956b; Potonié, 1962), they must be appraised in a somewhat arbitrary manner. Only their morphological characteristics, which may be grouped into general categories of size, shape, ornamentation, and structure, can be used. Thus, miospores have been grouped into form genera and species on the basis of their morphology (Potonié and Kremp, 1954; 1955; and later papers). This procedure provides a convenient way of classifying the wide variety of forms encountered, but is also subjective. Different workers often "lump" or "split" forms according to their personal preferences.

Another method of organizing the information concerning morphological characteristics might prove useful. A second method, here proposed, is to tabulate the morphological characteristics of individual miospores rather than to sort them into form species. Such a method may allow variations of morphology, incorporated into species, to be expressed. Miospore specimens which occur rarely and which do not occur in sufficient abundance to set up species may also add to the total morphological character of the assemblage when expressed by this second method.

Miospores may also be examined on the basis of their total morphological characters for individual beds or sequences of beds. The sequence of miospore species can be correlated with the sequence of tabulated miospore characteristics for the same geological units.

The combined use of form species and the total morphological characteristics of individual miospores, independent of form species, provide two methods for classifying the palaeoecological data provided by miospores. Both methods are based on arbitrary criteria or groupings. The parental affinities of these miospores are not known. It would seem, therefore, that these methods might have no relation to natural systems of plant taxa and to ecological associations.

There is, however, evidence that spores have some taxonomic significance in the defining of modern taxa. For example, Knox (1950) has shown that for modern lycopod groups, spores of natural taxa have certain morphological similarities. If these spores are found dispersed, some estimation of their natural affinities can be attempted. Harris (1955), Erdtman (1957), and many others, have also demonstrated this in other pteridophytic and bryophytic groups. While it seems too much to assume (as do many Russian authors, *e.g.*: Naumova, 1953) that Palaeozoic spores with morphology similar to modern spores belong to the same natural groups, it is probable that Palaeozoic spores are related in some manner to natural groups living in that period of time. Thus, the grouping of miospores into form species may indicate the occurrence of natural groups and have palaeofloristic implications.

Concerning tabulations of morphological characteristics of miospores, there are no previous studies to provide working hypotheses, although several authors have considered the question of the significance of the morphological characters independently of miospores species. Radforth and McGregor (1956) summarized the knowledge then known about first and last appearances of a number of morphological characteristics, but were not concerned with the tabulations of data for individual assemblages. Radforth and Wilkinson (1959, p. 33) stated: "The microfossils of Tar Point (Lower Devonian)..., evidently show differences in pattern which arise from differences in biological trend". They did not, however, extend this to whole assemblages. In the absence of any previous hypotheses, therefore, several are proposed here, to provide working hypotheses.

A fluctuation or change in the diversity of morphological characteristics may have some palaeoecological significance; it may reflect, in some cases, response of parent plants. Differences in the type of ornamentation, the shape, the structure, and perhaps the size of miospores within an assemblage, may confirm a significant change in the parent flora, even when there is no apparent change in the assemblage as characterized by the species concept. This latter hypothesis perhaps especially applies to microfloral assemblages dominated by a few form species. Such assemblages are generally considered as indicating miospore deposition very close to the growing site of the parent flora. The use of the morphological tabulation method will be investigated in this thesis in relation to Devonian plant palaeoecology.

The other plant microfossil types generally found in non-marine depositional environments also contribute information about the palaeoecology of Devonian plants, but occur sparsely. Cuticular fragments may give some evidence of the nature of the epidermis (presence of stomata, size and shape of epidermal cells) of fossil forms not otherwise represented in the strata. Sporangia, whole or fragmented, may be identified on the basis of their organization, as belonging to a representative of some natural group. More rarely, they contain spores conspecific with a miospore species (Chaloner, 1953; Pettit, in press; Richardson, 1965), thus indicating something of the botanical affinities of the miospore. Vascular elements of plants also occur sparsely, compared to miospores. The occurrence of vascular elements may indicate the presence of certain groups of vascular plants in the provenance of the enclosing strata.

In marine sedimentary depositional environments, terrestrial plant microfossils may occur, but in general, organic microplankton are abundant. These plant microfossils offer no direct information about the palaeoecology of terrestrial or freshwater aquatic plants, unless some Devonian microplankton taxa are freshwater forms like some younger taxa (Krutszch, 1962; Churchill and Sarjeant, 1963). The ratio of miospores to organic microplankton, however, has been shown to indicate the proximity of the shoreline to the site of deposition (Sarmiento, 1957). The ratio of miospores to microplankton decreases as the distance from shoreline increases until the abundance of the microplankton markedly decreases as deeper water is reached. Thus, the main value of microplankton in this study is the information provided about the environment of deposition. The natural affinities of most Devonian microplankton taxa are not known.

# GEOLOGICAL AND GEOGRAPHICAL INFORMATION

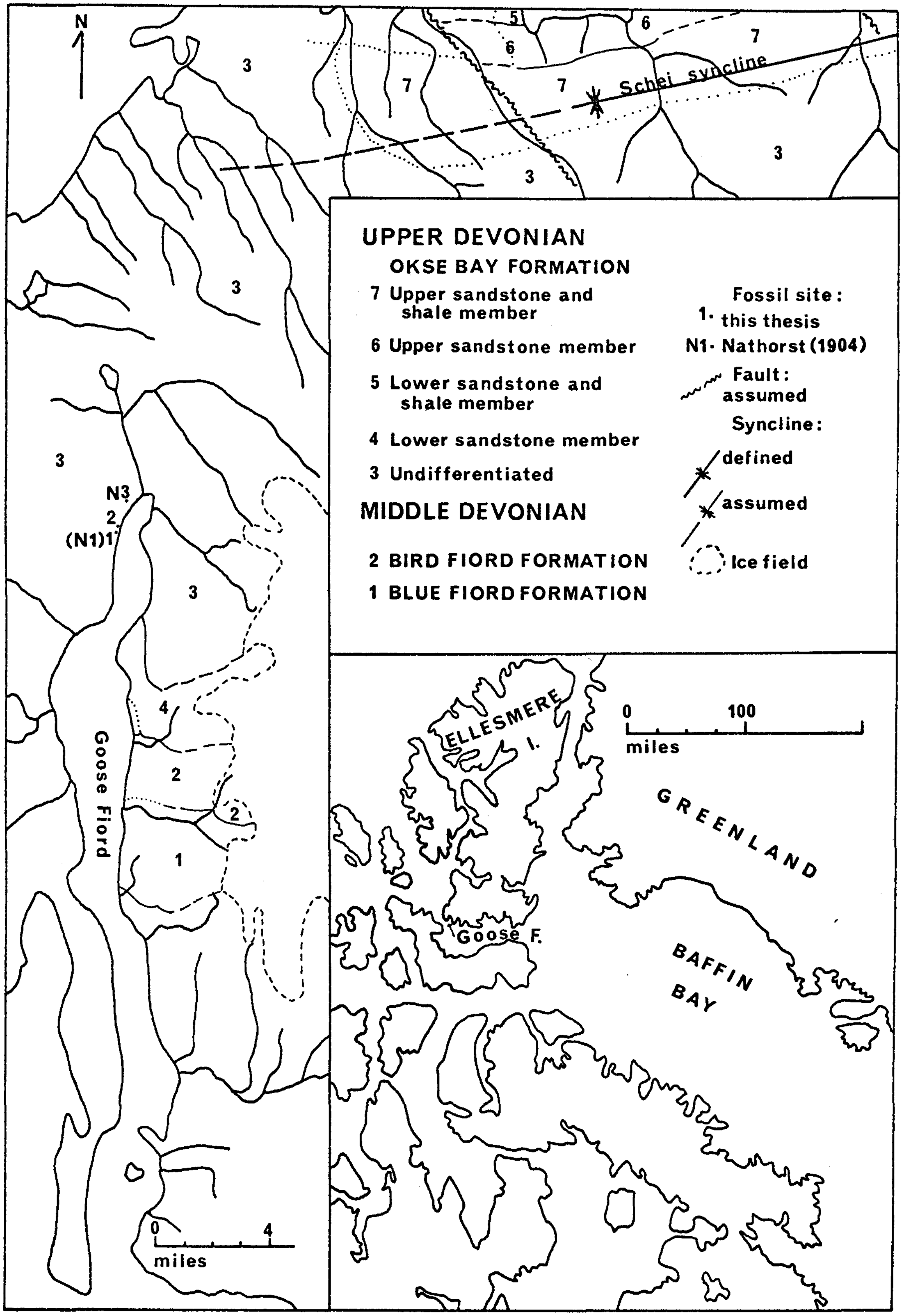
## INTRODUCTION

The material was collected from two widely separated localities, the one situated in the Canadian Arctic on Ellesmere Island, and the other located in the Gaspé Peninsula region in the vicinity of Escuminac Bay, Quebec. The samples from Ellesmere Island were collected from beds at the head of Goose Fiord, southwestern Ellesmere Island. The material from Escuminac Bay was collected from beds belonging to the Escuminac Formation. The geological age of the strata at both localities is considered to be Upper Devonian (Alcock, 1935; Fortier, et al., 1963).

The lithologies and stratigraphical relations of the two formations, as well as the lithologies of the samples and the locations of the fossil sites will be described below.

## STRATIGRAPHY OF THE OKSE BAY FORMATION

The name, Okse Bay Formation, has been given (Fortier, et al., 1963) to a largely non-marine series of quartzose sandstones, sandy mudstones and shales, and occasional thin coal seams outcropping in the southwestern part of Ellesmere Island. The strata outcrop around Okse Bay, the southern arm of Bird Fiord and the eastern and western arms of inner Goose Fiord (Text-fig. 1). The strata follow the course



Text-fig. 1. General geology and location of fossil sites, Upper Goose Fiord. Index map (inset) of the Ellesmere Island region. (Geology after Fortier, et al., 1963).

of the axis of the Schei syncline which extends in a northeasterly-southwesterly direction south of Okse Bay and Bird Fiord.

North of the synclinal axis, the beds have a maximum thickness of at least 10,100 feet, while south of the axis the thickness has been measured as about 2,500 feet. The total thickness of the formation is unknown because the top of the formation has been eroded.

The type section of the Okse Bay Formation was described from beds outcropping about Okse Bay and the south arm of Bird Fiord. The formation there is divisible into four members:

4. Upper sandstone and shale member
3. Upper sandstone member
2. Lower sandstone and shale member
1. Lower sandstone member

The Okse Bay Formation includes the Series E of Schei (<u>in</u>: Nathorst, 1904) and beds stratigraphically higher than Series E north of Goose Fiord. The Middle Devonian Bird Fiord Formation (Text-fig. 2) underlies the Okse Bay Formation and grades into it without sharp break. The top of the Okse Bay Formation is an erosional surface and is unconformable with overlying strata.

The Okse Bay Formation lies within the Central Ellesmere Fold Belt, in the unstable Innuitian region, and was deposited in a miogeosyncline. The non-marine character of the formation represents a trend towards non-marine deposition, compared to the predominantly marine Lower and Middle Devonian deposits of the same region. Concerning

| | | | | | |
|---|---|---|---|---|---|
| POST DEVONIAN | | CARBONIFEROUS: Bonaventure Fm. | JURASSIC | --------- | PENNSYLVANIAN |
| UPPER | FAMENNIAN | | ? ? | Erosion Surface<br>Okse Bay Fm. | Unconformity<br>Okse Bay Fm. |
| DEVONIAN | FRASNIAN | Unconformity<br>Escuminac Fm.<br>Fleurant Fm.<br>Pirate Cove Fm. | -Stevens Head Coal-<br>Melville | -Goose Fiord- | |
| MIDDLE | GIVETIAN | Malbaie Fm. | Island Fm.<br>? ? | Bird Fiord Fm. | Bird Fiord Fm. |
| DEVONIAN | EIFELIAN | ? ?<br>Gaspé | | Blue Fiord Fm. | Blue Fiord Fm. |
| LOWER | COBLENZIAN | Sandstone Group<br>? ?<br>Gaspé Limestone | | | Eids Fiord Fm. |
| DEVONIAN | GEDINNIAN | ? ? | | | |
| SERIES | STAGE<br>SITE | GASPE PENINSULA | MELVILLE ISLAND | ELLESMERE ISLAND: GOOSE FIORD | ELLESMERE ISL.: EIDS FIORD TO OSKE BAY |

Text-fig. 2. Selected stratigraphic columns of Devonian age for Eastern and Arctic Canada. (Derived from various publications of the Geological Survey of Canada.)

this formation, Fortier (in: Fortier, et al., 1963, p. 65) says:

> "The Okse Bay Formation is commonly crossbedded and in most areas contains abundant carbonaceous matter with more rarely, coal seams. It is believed to have been laid down under deltaic, largely freshwater conditions. Cyclical units of sandstone and shale, with or without coal, are common in the softer parts of the succession and suggest typical 'coal measure' type of deposition. ...The formation appears to pass into marine sandstones westward from Bathurst Island."

The age of the Okse Bay Formation has been considered Upper Devonian on the basis of plant remains collected and described by Nathorst (1904), and fish remains, collected and described by Kaier (1915). The plant collections by Nathorst were made on the inner western arm of Goose Fiord in the area from which the samples of the present study were collected (See text-fig. 1). Nathorst identified species of *Lyginodendron*, *Archaeopteris*, and cf. *Sphenopteridium*. Kaier (1915) described species of the fossil fish genera *Psammosteus*, *Bothriolepis*, *Holoptychius*, *Glyptolepis*, and *Osteolepis*. Both workers considered that the fossil evidence indicated an Upper Devonian age.

More recently, (Andrews, Radforth, and Phillips, 1963; Dr. N. W. Radforth, pers. comm., 1964) new plant fossil collections from Nathorst's localities and from new localities in the vicinity, support the Upper Devonian age assigned to the formation.

## STRATIGRAPHY OF THE ESCUMINAC FORMATION

The name, Escuminac Formation, was given by Alcock (1935, p. 88) to a sequence of grey, thin-bedded sandstones, shaly sandstones, and sandy shales outcroping along the north shore of the Baie de Chaleur from the vicinity of Maguasha Landing westward to Escuminac Point

(Text-fig. 3). The beds at the type section are folded into a shallow syncline west of Maguasha Landing and a shallow anticline just east of the Landing.

No definite measurements are available for the thickness of the Escuminac Formation, but measurements of a diagram by Alcock (_in_: Stockwell, ed., 1957, fig. 43, p. 162) suggest the thickness is approximately 170 feet. The maximum thickness is not known, because the top of the formation shows an erosional break.

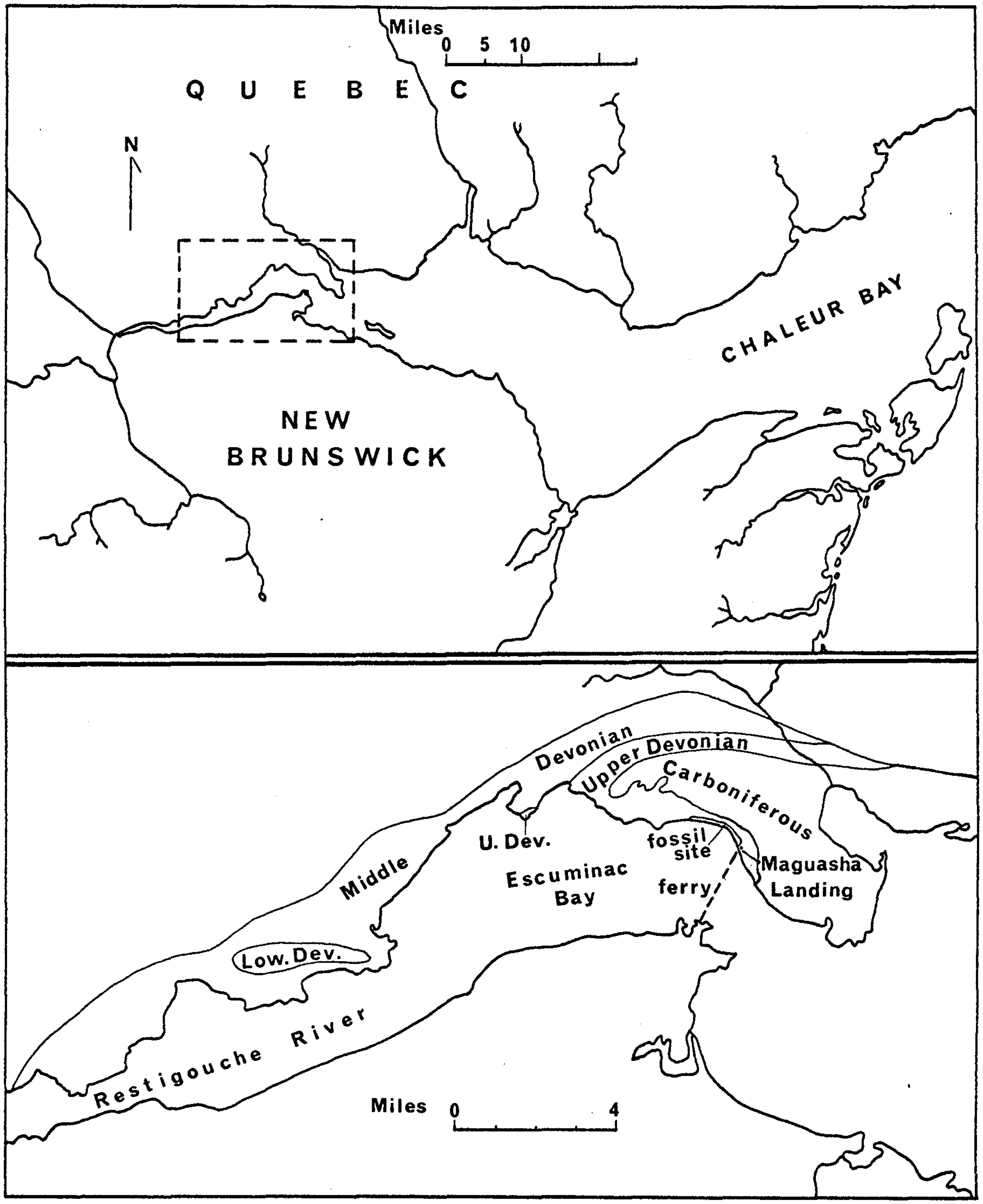
The Escuminac Formation is underlain by conglomerate of the Fleurant Formation; the boundary is marked lithologically by a gradation from conglomerate to grey shales of the basal Escuminac beds. The top of the Escuminac Formation is marked by an erosional disconformity. Basal red beds of the overlying Bonaventure Formation (Carboniferous) lie disconformably on the Escuminac strata (Text-fig. 2).

## STRATIGRAPHIC POSITION, LITHOLOGY, AND GEOGRAPHICAL LOCATION OF THE SAMPLE SITES

### Goose Fiord, Ellesmere Island

The strata exposed on the western arm of Goose Fiord and just northwest of the head of the Fiord have been considered equivalent to lower members of the Okse Bay Formation.

Examination of columnar sections numbered 28 and 32 (_in_: Fortier, _et al_., Sheet 4) shows that abundant plant remains occur at the 5,900' level in section 32 (Okse Bay region) and by the 5,400' level in section 28 (Central Goose Fiord region). The lithology of these stratigraphic levels corresponds to that at the collection



Text-fig. 3. Index map (top) and general geology (bottom) of the Escuminac Bay region, Gaspé Peninsula, Quebec. (Geology after Alcock, 1935).

sites; thin layers of silty shale or very-fine-grained sandstone alternate with more massive beds of medium-grained sandstone. This lithology is similar to that of the lower sandstone and shale member at the 5,900' level of the Okse Bay type section.

The lithologies of the samples are similar at both collecting sites: dark grey, very fine-grained, indurated carbonaceous sandstones or silty shales. This lithology appears to correspond to the "slates" of Schei (in: Nathorst, 1904, pp. 4-9).

The locations of the collection sites are indicated on the map (Text-fig. 1) as 1. and 2. Site Two is about one-third of a mile north of Site One; both sites are on the west side of Goose Fiord, about two miles from the head of the fiord. The strata at Site Two are approximately 150' stratigraphically above those at Site One (Radforth, N. W., field notes, 1962). (a) Site 1 appears to be located at or very near Site 1 (N1) of Nathorst (1904). (b) The two sites are stratigraphically below Site 3 of Nathorst (1904), indicated in Text-fig. 1 as N3; the beds in this region dip 5° northeast and are not faulted.

Sample numbers AEI-4367 to AEI-4375 were collected at Site One. The following sample numbers were collected at Site Two: AEI-1; AEI-7; AEI-13-46; L46-L63; L46-L67; and L45-L65. Each of these samples represents a separate lithological unit. The samples were collected in the summer of 1962 by Radforth, N. W., Andrews, H. N., and Phillips, T., while on a palaeobotanical expedition to re-examine the fossil sites of Nathorst (1904).

### Escuminac Bay, Quebec

The samples collected at this locality come from beds stratigraphically near the middle of the Escuminac Formation. The lithology bears a general resemblance to that at Goose Fiord. Massive sandstone beds alternate with thin shale and fine-grained sandstone partings.

The lithologies of the samples used in the study are of two main types. One type (*e.g.*: Sample AG-3) consists of light grey, fine-grained, relatively indurated, sandstone, with relatively minor amounts of carbonaceous material. The second type (*e.g.*: Sample AG-7) consists of medium dark grey, fine-grained, indurated, carbonaceous sandstone.

The samples were collected from outcrops along the shore of Escuminac Bay, about one-half mile west of Maguasha Landing. They are numbered AG-1 to AG-25, but are not in any stratigraphic order. The material was collected by Radforth, N. W. in 1959.

# DESCRIPTION AND DISCUSSION
# OF LABORATORY TECHNIQUES

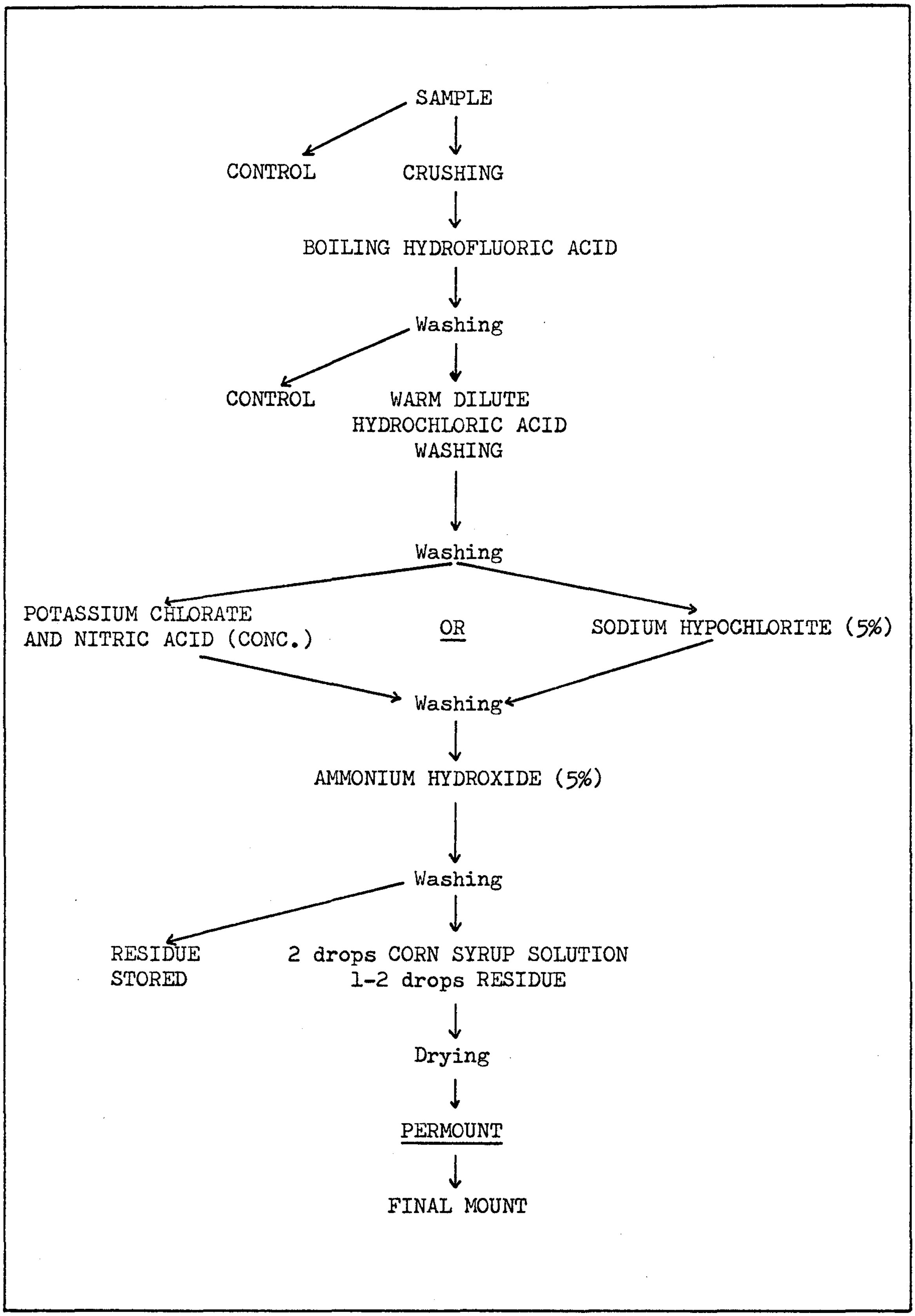
## EXTRACTION OF THE PLANT MICROFOSSILS

### Introduction

In this chapter, the extraction procedure will be described and discussed. Particular attention will be directed to two new steps. These are: the removal of flocculated by-product; and a new permanent mounting method. Part of the discussion will be concerned with the chemistry of the procedure, although a detailed discussion of this is beyond the scope of the thesis. Except for the two new steps, standard maceration techniques (Brown, 1960; Hoffmeister, 1960; and others) were used to extract the plant microfossils from the enclosing matrix. A flow chart of the procedure is presented in Text-fig. 4.

### Extraction Procedure: Description and Discussion

Crushing - About 5 cc. of the original sample were broken off and placed on a piece of newspaper on an iron slab or some other suitable surface. This material was crushed into particles of 1 mm. in diameter or less by grinding the rock against the iron slab with an ordinary geological hammer. After each sample was crushed, the newspaper was discarded and the hammer and plate were cleaned in hot, soapy water using a stiff wire brush.



Text-fig. 4. Flow chart of the extraction procedure described in the text.

Acid Treatment - The crushed sample was placed in a 200 ml. copper beaker and wetted with distilled water to minimize the original vigorous reaction with hydrofluoric acid. About 100 cc. of commercial grade hydrofluoric acid were then added slowly to the sample. All procedure was performed under a fume hood and precautions were taken against acid burns.

The acid-sample mixture was heated for about an hour with occasional gentle agitation to prevent clumping of the sample in the bottom of the beaker. Often near the end of the acid treatment, distilled water had to be added to prevent the mixture from boiling dry. Dehydration of the mixture resulted in complete destruction of usable microfossil material.

After treatment with hydrofluoric acid was completed, the residue was washed from the beakers into 50 cc. polyethylene test tubes. Several washes with distilled water, followed by centrifuging, were needed to remove the residual hydrofluoric acid.

The hydrofluoric acid reacts with the enclosing matrix and dissolves silica minerals and siliceous cement.

By-product Removal - During the reaction of the rock material with hydrofluoric acid, a by-product resulted that in some cases formed 70% of the residue. This by-product, present as a white to greyish or pinkish, gelatinous fraction, both in a layer and disseminated throughout the residue, was removed by a procedure new to this university, but used elsewhere (Dr. G. Norris, pers. comm., 1964).

The residue was gently mixed with 30% hydrochloric acid (diluted 1:3 with distilled water) and heated in a water bath (60° C.)

until a faint yellow to brownish-yellow colour appeared in a the supernatant liquid. The sample was centrifuged for about a minute and the supernatant liquid was decanted. If the residue retained a visible gelatinous layer, or, if on agitation part of the residue remained coagulated in the bottom of the tube, washing with hydrochloric acid was repeated. This was continued until the residue could be freely dispersed in water by a few agitations of the test tube.

Under a microscope, the by-product is visible as a finely divided, crystalline to cryptocrystalline, grey to brownish-grey mass, which obscures almost all but the larger plant microfossils. Samples, apparently barren, have proven to be highly fossiliferous on removal of by-product. The by-product apparently also coagulates about the microfossils, thus preventing effective use of the reagents in succeeding steps of the procedure.

Literature on the chemical nature of the by-product is sparse. Norem (1953) reports that it is made up of insoluble flakes of aluminium fluosilicates and that X-ray analyses also show the presence of double fluorides of Calcium, Magnesium, Sodium and Potassium. Forsman and Hunt (1959) in treating black shales of the Wilcox Formation (Eocene), encountered an insoluble gelatinous residue after hydrofluoric acid treatment. X-ray diffraction analysis indicated the residue consisted of potassium fluosilicate and minor amounts of aluminium oxyfluoride.

Forsman and Hunt (1959) removed by-product either by repeated washings in hot water (for shales) until iso-propyl alcohol gave no precipitate or by the addition of excess sodium carbonate (for calcareous rocks) until carbon dioxide gas ceased to be evolved.

The method used in this project, that of washing in dilute, warm, hydrochloric acid, is quite satisfactory. Certain samples required as many as seventeen washings; in general, however, only from two to eight were needed.

It is believed that the warm hydrochloric acid acts as a deflocculating agent, dispersing the gelatinous material into a sol and dissolving the crystalline material. The dispersed and dissolved material is then removed by centrifuging. The resulting residue is quite "loose" in texture and the microfossils are exposed for effective treatment with succeeding reagents.

Oxidation - Oxidation of the microfossils was necessary in all cases, although the amount required varied. The residue, washed of hydrochloric acid, was mixed with an equal portion of potassium chlorate and just enough distilled water to keep the mixture slightly moist. Then, 10 to 15 cc. of concentrated nitric acid were slowly added to the mixture. The sample was agitated occasionally during the treatment period (usually lasting one-half to one hour), and when effervescence ceased, the reaction was judged to be completed.

Occasionally, as in the case of several samples from Goose Fiord, further oxidation was necessary. These samples required more powerful oxidation; the substitution of 5% sodium hypochlorite solution proved effective.

Excess oxidation resulted in partial to complete destruction of miospores. In anticipation of this, the residue was examined several times during the process and destruction was prevented.

The nitric acid-potassium chlorate method is a variation of Raistrick's "dry" method as reported in Staplin, et al., (1960) and differs only in the substitution of a predominantly inorganic residue for coal. The use of sodium hypochlorite was first described by Hoffmeister (1960).

When miospores and other plant microfossils are released from the enclosing matrix, they are most often coloured a dark brown and are not transparent. The colour is attributed to humic material (Kosanke, 1950) which may be similar to the humic material in peats (Erdtman, 1952). Oxidation of this humic material results in the probable formation of oxides of carbon compounds, water, soluble acids and humic acids (Kosanke, 1950). Since oxidation may also affect the exine of the spore, it must be controlled to prevent destruction of the exine and differential damage to the ornamentation of the exine.

Much difficulty was experienced in the oxidation of miospores from Goose Fiord samples. The microfossils were extremely dark and required much oxidation in order to render them suitable for microscopic examination by transmitted light. The problem was complicated by the presence of exine corrosion by natural action.

Alkali Treatment - Ammonium hydroxide (5%) was used where microfossils required alkali treatment. About 10 cc. were added to the residue, and on appearance of a brownish colour (usually after 15 to 30 seconds), the residue was washed repeatedly with distilled water until the supernatant liquid remained clear.

The ammonium hydroxide reacts with the oxidized humic material colouring the organic matter. It dissolves soluble salts of compounds thought to be similar to the humic acids of peat samples

(Kosanke, 1950; Erdtman, 1952). This reaction gives the supernatant liquid a characteristic dark brown colour. The removal of this humic material renders the plant microfossils semi-transparent and suitable for examination under a microscope by transmitted light.

Mounting - A new permanent mounting process was developed during the preparation of the samples. It consists of mounting the plant microfossils in corn syrup (Radforth, 1938) and then making a permanent mount by covering the dried corn syrup surface with Permount and applying a coverslip. The procedure is described and discussed below.

The microfossils and residue were washed several times to remove traces of earlier reagents; excess water was decanted carefully leaving only a wet residue. One to two drops of this residue were pipetted onto a clean glass slide and mixed with two drops of pure, diluted corn syrup to which a few drops of phenol solution had been added as described by Radforth (1938).

This mixture was spread thinly and evenly over the slide and allowed to harden (protected from dust and air-borne particles) until the surface was firm. Then, several drops of Permount (60% synthetic resin) were applied and a coverslip was added. The Permount was allowed to set for a day and then the slide was ready for microscopic examination.

The use of the water soluable medium, corn syrup, allows preparation of numerous temporary slides and eliminates the need for special techniques prior to mounting. Slides prepared with corn syrup alone, however, have no degree of permanence, since they may be spoiled by water and excessive heat. Relocation of specimens at recorded co-ordinates cannot be relied on with any certainty.

The sealing of the mount with Permount saves much time and gives permanent mounts. Permount does not react with corn syrup and protects the mount from water damage and running due to excessive heat. No clouding has been observed due to the escape of water vapour and no bubbles have been noted in the preparations. Slides in existence for over a year and a half have retained their excellent optical properties and show no signs of deterioration.

Two precautions must be taken when using this method. Firstly, the corn syrup should be allowed to harden only enough to produce a firm surface. If the film is allowed to dry too much, wrinkles and cracks may appear. Secondly, care must be taken to use only sufficient corn syrup and Permount as are necessary, so that the total thickness of the mount does not exceed the working distance of the oil immersion objective.

It appears then that the corn syrup-Permount method constitutes a cheap, readily available, and efficient way of making permanent palynological mounts. It allows the elimination of several time-consuming steps and preserves the advantages of working with a water soluable medium.

## OTHER LABORATORY PROCEDURES

### Photography

Photographs of the microfossils were taken with a 35 mm. Leica camera mounted on a monocular tube of a Leitz Ortholux microscope.

The microfossils were photographed using a 12.5X ocular in combination with 25X, 40X, and 100X (oil) objectives and subsequently enlarged in printing to give actual magnifications of 250X, 500X, and 1000X.

Kodak 35 mm. Panatomic-X film and Kodak Microdol-X developer were used throughout photography. This combination provided the best balance of detail and contrast that could be obtained for the material to be photographed. All original prints were made on AGFA BN1 Normal paper. All photographs are unretouched.

### Marking of Slides

All slides suitable for study were marked with the sample number, maceration number of the sample, and slide number of the maceration in that order. For example, the first slide made from maceration three of sample AEI-4367 would be labelled: AEI-4367.3(i). Labelling was done with a diamond pencil.

# OBSERVATIONS ON
# THE DISCLOSED PLANT MICROFOSSILS
# AND TAXONOMY OF
# THE MIOSPORES AND ACRITARCHS

## GENERAL RESULTS

Plant microfossils were recovered from all samples collected at Goose Fiord and from eight out of ten samples collected at Escuminac Bay, Quebec. Of the fifteen samples macerated from Goose Fiord, thirteen contained abundant miospores (more than 200 per slide) and all yielded wood elements of vascular plants, occasional fragments of cuticle and microfossil forms referable to the Acritarcha.

Ten samples from Escuminac Bay were macerated. Of these, eight samples contained miospores, but only three yielded abundant miospores. Four samples contained microfossils referable to the Acritarcha. Wood elements and fragments of cuticle were only rarely encountered.

## Goose Fiord Samples

Miospores extracted from samples collected at Goose Fiord were darkly stained and often highly corroded, showing small pits and occasional degraded portions. Thinner walled miospores tended to be less affected by corrosion.

Wood elements of vascular plants were, in general, the best preserved plant microfossils in these samples. They included tracheids with simple pits, bordered pits, alternate pits, and ellipsoidal, alternate pit pairs (Pl. VIII, figs. 5-8). Tracheids with annular, spiral, and scalariform thickenings were also found. These elements occurred quite sparsely and rarely numbered more than 10 to 15 per slide. Little information could be gained from them.

Cuticle fragments were also found in small numbers. The fragments were generally highly degraded, and only in a few instances could cellular outlines be distinguished.

Forms referable to the Acritarcha occurred sparsely and were darkened and corroded. Preservation was so poor that it was thought unwise to attempt to assign these to form taxa.

## Escuminac Bay Samples

Eight of ten samples collected at Escuminac Bay yielded miospores; only three of these samples contained miospores in abundance. Most miospores were well preserved; details of ornamentation were excellent and the exine was uncorroded. One sample, however, contained relatively poorly preserved miospores.

Only a few wood elements were found in slides of Escuminac material, although the same techniques were used in preparing slides as for those from Goose Fiord. Absence of wood elements, therefore, is not accountable to laboratory technique.

Cuticular fragments were present in only two samples. One of these samples contained miospores in rare quantities (less than 50 per slide), but had relatively abundant cuticle fragments. The other sample contained abundant miospores but only a few cuticle fragments. The cuticle fragments rarely showed cellular outlines and were generally quite degraded in contrast to the preservation of the miospores.

Microfossil forms referable to the Acritarcha were also found in slides from four samples. These were well preserved, but occurred only rarely.

## RESULTS OF THE MORPHOLOGICAL CHARACTER STUDY

### Quantitative Results

For each sample yielding suitable material, 150 miospores, showing characteristics of size, shape, ornamentation, and structure (the items of these subsections are listed in Appendix II) were counted and their morphological characteristics recorded. Miospores not showing this minimum set of characters were not included in the count. Size was measured as the diameter along the radii, or taken as the length of the longest diameter if no radial symmetry was evident.

Slides were scanned transversely, beginning consistently at one side, and moving along the length until 150 suitable miospores had been counted. If more than one slide was needed, a second slide from the sample was traversed in the same manner until the total of 150 was reached.

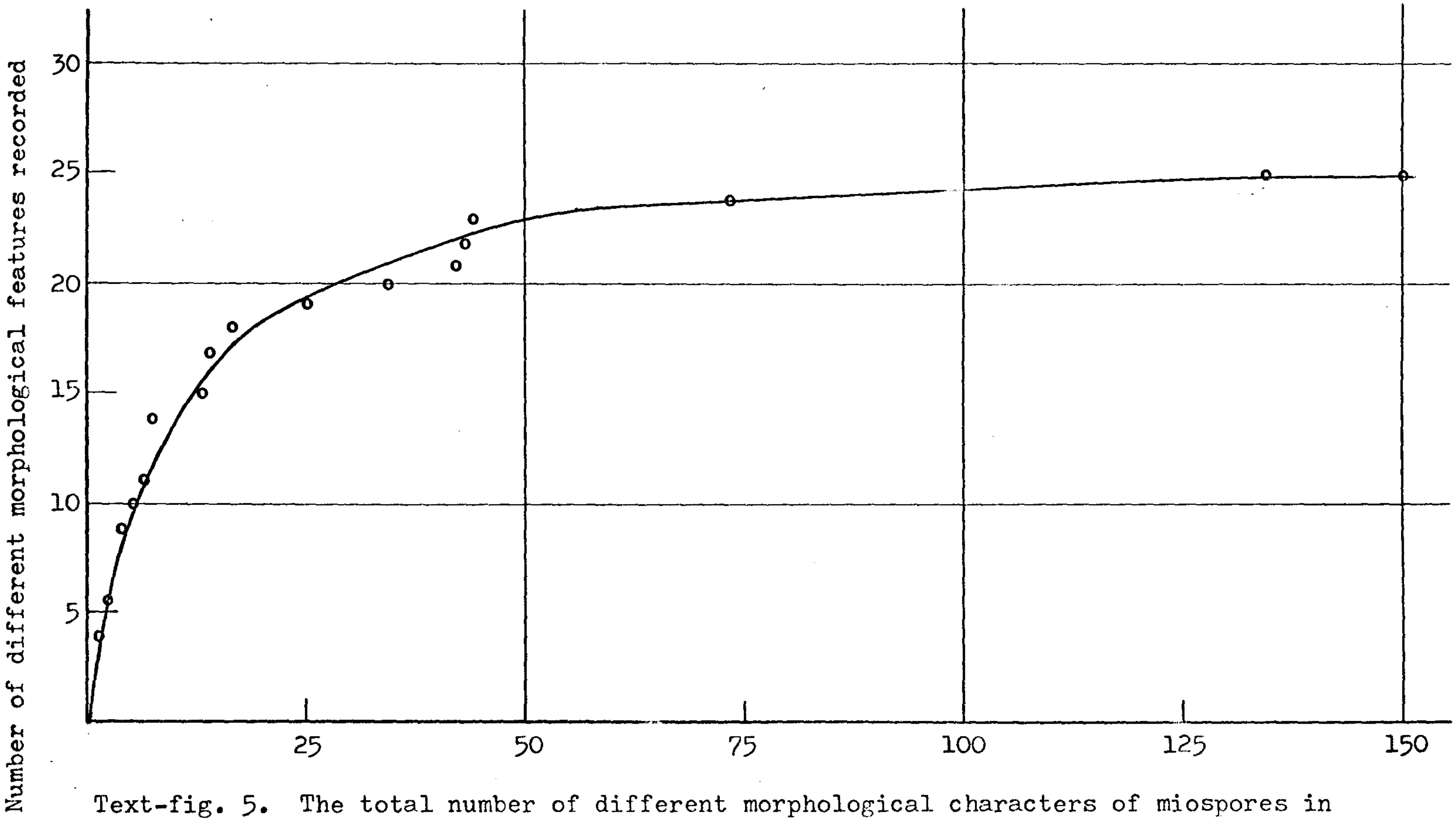
The number of 150 miospores was decided upon after a preliminary count (Sample AEI-4367) indicated that new morphological characters entered only rarely after 100 miospores and not at all after 135 miospores. The data from this count are present in Text-fig. 5.

The quantitative results of these counts are tabled in Text-fig. 6 and Text-fig. 7. Text-fig. 6 (in part) shows the totals of counts for twelve samples from Goose Fiord and four from Escuminac Bay, as well as the counts for each of the two sites at Goose Fiord. Text-fig. 7 shows the counts for each of the eight samples from Site One of Goose Fiord. The ornamentation of miospores from Sample AEI-4371 (Site One, Goose Fiord), was poorly preserved and specimens from that sample are not included in the counts.

Chi-square values were calculated for the following pairs of data: Site One, Goose Fiord and Site Two, Goose Fiord; and for the counts of Goose Fiord samples and the Escuminac Bay samples. Each morphological subsection of ornamentation, shape, structure and size was treated separately when determining chi-square values. Text-fig. 6 shows the calculated chi-square values for each individual cell (laevigate, scabrate, etc.) in the last two columns. Size is shown as a frequency distribution; arithmetic means and standard deviations were calculated for this subsection. These results are given in Text-fig. 6.

In using the non-parametric statistical method of chi-square, certain conditions must be observed. One of these is that no cell may contain less than five members. Thus, certain cells had to be combined. Similar or related ornamentation types were grouped together where possible.

The null hypothesis is proposed that there is in fact no significant difference in the pairs of data with respect to each of the subsections of shape, ornamentation, or structure at a probability



Text-fig. 5. The total number of different morphological characters of miospores in relation to the number of miospores counted. Preliminary count for Sample AEI-4367. (Goose Fiord: Site One).

| LOCATION | GOOSE FIORD | | | ESCUMINAC BAY | CHI-SQUARE VALUES FOR DATA PAIRS | |
|---|---|---|---|---|---|---|
| SUBSECTION | SITE ONE | SITE TWO | SITE ONE AND SITE TWO | | GOOSE FIORD SITES ONE AND TWO | GOOSE FIORD AND ESCUMINAC BAY TOTALS |
| **ORNAMENTATION** | | | | | | |
| Laevigate | 10 | 4 | 14 | 36 | 0.203 | 59.8 |
| Scabrate | 55 | 13 | 68 | 44 | 5.483 | 11.3 |
| Striate | 2 | 2 | 4 | 3 | ----- | ---- |
| Punctate | 44 | 24 | 68 | 68 | 0.015 | 40.1 |
| Vermiculate | 3 | 1 | 4 | 2 | ----- | ---- |
| Spinae | 12 | 12 | 24 | 3 | 2.675 | 3.1 |
| Coni | 13 | 33 | 46 | 16 | 29.366 | 0.01 |
| Echini | 927 | 476 | 1403 | 389 | 0.000 | 288.7 |
| Setulae | 1 | 2 | 3 | 3 | ----- | ----- |
| Granulose or Granulate | 63 | 3 | 66 | 17 | 25.434 | 1.3 |
| Verrucate | 23 | 15 | 38 | 9 | 3.593 | 1.1 |
| Rugulate | 23 | 12 | 35 | 2 | 1.516 | 5.0 |
| Obvermiculate | 3 | 4 | 7 | 2 | ----- | ----- |
| Cristate | 1 | 4 | 5 | 2 | ----- | ----- |
| Reticulate | 28 | 6 | 34 | 0 | 4.103 | 11.9 |
| Processes | 21 | 3 | 24 | 44 | 5.009 | 52.9 |
| TOTALS | 1229 | 614 | 1843 | 640 | 77.397 | 475.21 |
| **SHAPE** | | | | | | |
| Triangular convex | 109 | 91 | 200 | 21 | 14.133 | 28.3 |
| Triangular concave | 7 | 2 | 9 | 1 | 0.500 | 1.2 |
| Rounded | 1046 | 476 | 1522 | 568 | 2.009 | 5.3 |
| Ovoid | 38 | 31 | 69 | 10 | 4.174 | 6.4 |
| TOTALS | 1200 | 600 | 1800 | 600 | 20.816 | 41.2 |
| **STRUCTURE** | | | | | | |
| Cingulum or zona | 27 | 13 | 40 | 9 | 0.152 | 0.09 |
| Monosaccate | 4 | 1 | 5 | 34 | 1.200 | 106.66 |
| Dark contact area | 0 | 0 | 0 | 16 | ----- | 64.00 |
| Curvaturae | 851 | 498 | 1349 | 4 | 9.348 | 328.31 |
| Wall less than 3$\mu$ thick | 836 | 341 | 1177 | 505 | 8.634 | 105.63 |
| Wall 3$\mu$ or more thick | 364 | 259 | 623 | 95 | 20.701 | 29.88 |
| Perine | 4 | 6 | 10 | 6 | ----- | 3.06 |
| Laesurae simple | 429 | 124 | 553 | 239 | 27.989 | 52.17 |
| Laesurae compound | 371 | 208 | 579 | 144 | 2.231 | 0.003 |
| TOTALS | 2886 | 1450 | 4336 | 1052 | 70.255 | 689.803 |
| **SIZE (IN $\mu$)** | | | | | | |
| 21-40 | 62 | 37 | 99 | 168 | | |
| 41-60 | 368 | 312 | 680 | 282 | | |
| 61-80 | 548 | 218 | 766 | 57 | | |
| 81-100 | 185 | 24 | 209 | 35 | | |
| 101-120 | 16 | 3 | 19 | 23 | | |
| 121-200" | 15 | 6 | 21 | 32 | | |
| 200 or over | (6) | | (6) | (3) | | |
| Arithmetic mean diameter | 66.6 | 59.2 | 64.2 | 55.7 | | |
| Standard deviation | 17.7 | 15.5 | 16.2 | 26.4 | | |

NOTE: IN CALCULATING CHI-SQUARE VALUES THE FOLLOWING UNITS WERE COMBINED:

FOR BOTH DATA PAIRS:

STRIATE WITH SCABRATE

VERMICULATE WITH PUNCTATE

OBVERMICULATE AND CRISTATE WITH RUGULATE

FOR THE GOOSE FIORD SITES:

PERINE WITH MONOSACCATE

Text-fig. 6. Counts of morphological features of miospores from two sites at Goose Fiord and one site at Escuminac Bay. The counts for Goose Fiord, Site One (8 samples) and Site Two (4 samples) are shown. The calculated chi-square values used in tests of homogeneity are given in the last two columns for the individual cells.

| SAMPLE NUMBERS<br>GOOSE FIORD SITE ONE | AEI-4367 | AEI-4368 | AEI-4369 | AEI-4370 | AEI-4372 | AEI-4373 | AEI-4374 | AEI-4375 |
|---|---|---|---|---|---|---|---|---|
| **ORNAMENTATION** | | | | | | | | |
| Laevigate | 2 | 1 | 0 | 0 | 4 | 0 | 1 | 2 |
| Scabrate | 6 | 4 | 5 | 8 | 6 | 6 | 10 | 11 |
| Striate | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 |
| Punctate | 12 | 5 | 8 | 8 | 7 | 2 | 1 | 1 |
| Vermiculate | 0 | 0 | 1 | 0 | 2 | 0 | 0 | 0 |
| Spinae | 0 | 0 | 1 | 5 | 0 | 6 | 0 | 0 |
| Coni | 0 | 0 | 5 | 0 | 2 | 3 | 2 | 1 |
| Echini | 115 | 116 | 109 | 108 | 110 | 123 | 131 | 115 |
| Setulae | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| Granulose or Granulate | 16 | 20 | 10 | 2 | 3 | 3 | 4 | 5 |
| Verrucate | 0 | 2 | 2 | 3 | 4 | 2 | 1 | 9 |
| Rugulate (Includes Obvermiculate) | 1 | 3 | 3 | 1 | 6 | 4 | 5 | 3 |
| Cristate | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| Reticulate | 0 | 0 | 3 | 12 | 9 | 0 | 0 | 0 |
| Processes | 0 | 0 | 3 | 3 | 6 | 5 | 0 | 4 |
| **SHAPE** | | | | | | | | |
| Triangular convex | 20 | 9 | 22 | 12 | 18 | 11 | 18 | 19 |
| Triangular concave | 3 | 1 | 0 | 0 | 1 | 4 | 1 | 0 |
| Rounded | 113 | 134 | 109 | 123 | 124 | 132 | 128 | 123 |
| Ovoid | 14 | 9 | 19 | 15 | 7 | 3 | 3 | 8 |
| **STRUCTURE** | | | | | | | | |
| Cingulum or zona | 0 | 3 | 8 | 2 | 10 | 1 | 0 | 3 |
| Monosaccate | 0 | 0 | 3 | 1 | 0 | 0 | 0 | 0 |
| Curvaturae | 133 | 134 | 108 | 103 | 108 | 136 | 145 | 117 |
| Wall less than 3μ thick | 141 | 124 | 97 | 101 | 83 | 74 | 73 | 75 |
| Wall 3μ or more thick | 9 | 26 | 53 | 49 | 67 | 76 | 77 | 75 |
| Perine | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 |
| Laesurae simple | 101 | 93 | 57 | 39 | 43 | 24 | 35 | 37 |
| Laesurae compound | 26 | 32 | 43 | 29 | 43 | 68 | 84 | 46 |
| **SIZE ( IN μ)** | | | | | | | | |
| 21-40 | 14 | 4 | 3 | 9 | 11 | 13 | 4 | 2 |
| 41-60 | 19 | 27 | 51 | 72 | 69 | 74 | 30 | 25 |
| 61-80 | 66 | 81 | 73 | 57 | 51 | 53 | 81 | 85 |
| 81-100 | 48 | 38 | 14 | 8 | 12 | 7 | 34 | 24 |
| 101-120 | 3 | 0 | 1 | 4 | 1 | 0 | 0 | 6 |
| 121-200" | 0 | 0 | 3 | 0 | 4 | 2 | 0 | 6 |
| 200 or over | 0 | 0 | 0 | 0 | 2 | 1 | 1 | 2 |
| Number of different morphological characters | 21 | 22 | 29 | 27 | 32 | 27 | 24 | 28 |

Text-fig. 7. Counts of morphological features of miospores from eight samples at Site One, Goose Fiord. 150 miospores were counted for each sample. Sample AEI-4371 not included.

level of 0.05 (5%). If the calculated value of chi-square does exceed the value of chi-square at the 0.05 (5%) probability level, it would mean that the null hypothesis would have to be rejected. There would be in fact a significant difference in one or more of the subsections (shape, ornamentation, and structure). These statistical results would support the contention that factors other than mere chance were involved. It would suggest that perhaps other factors are operative, specifically, microfloral and palaeoecological factors suggested in Chapter Two (pp. 13-16).

The total of the chi-square values for the data pairs of the subsections, the number of degrees of freedom in each operation, and the value of the chi-square figure for the given degree of freedom at the 5% probability level is given in TABLE 1. The chi-square tests, as applied here, are essentially tests of homogeneity (Mills, 1955, p. 529).

TABLE 1. - Chi-square values for the subsections of Ornamentation. Shape, and Structure of the data pairs from Goose Fiord and Escuminac Bay.

| Data pairs | Subsection | Degrees of freedom | Chi-square values | |
|---|---|---|---|---|
| | | | From data | 5% level |
| Goose Fiord:<br>Sites 1 and 2<br>(Subtotals) | Ornamentation | 10 | 77.397 | 18.307 |
| | Shape | 3 | 20.816 | 7.815 |
| | Structure | 6 | 70.255 | 12.592 |
| Goose Fiord and<br>Escuminac Bay<br>(Totals) | Ornamentation | 10 | 198.77 | 18.307 |
| | Shape | 3 | 41.20 | 7.815 |
| | Structure | 8 | 689.80 | 15.507 |

The size of the miospores may be treated parametrically. Thus, under the subsection of size in Text-fig. 6, the mean and standard deviation of the size classes is given. In dealing with this subsection it is appropriate to test for significance of difference in the arithmetic mean and standard deviation of two sets of data. A significant difference in arithmetic mean size of the miospores, if not attributable to chance alone, might have an explanation in palaeoecological or palaeofloristic terms.

The null hypothesis is proposed that there is in fact no significant difference between the means of the data pairs (the sets of frequency distributions of miospore diameters). The data pairs are the same as those used in the chi-square tests (TABLE 1).

The test is an application of the T-test as outlined in Mills (1955, pp. 217-220). T is the discrepancy between the observed difference in the means and the null hypothesis value of zero, expressed in units of the standard error of the observed discrepancy. The critical probability for these tests is set at 0.05 (5%). The calculated and significant values for T for each of the pairs of data is given in TABLE 2.

TABLE 2. - Values of T calculated from arithmetic means of miospore size distributions of the data pairs from Goose Fiord and Escuminac Bay, compared to the values of T of the normal curve at the 5% level of probability.

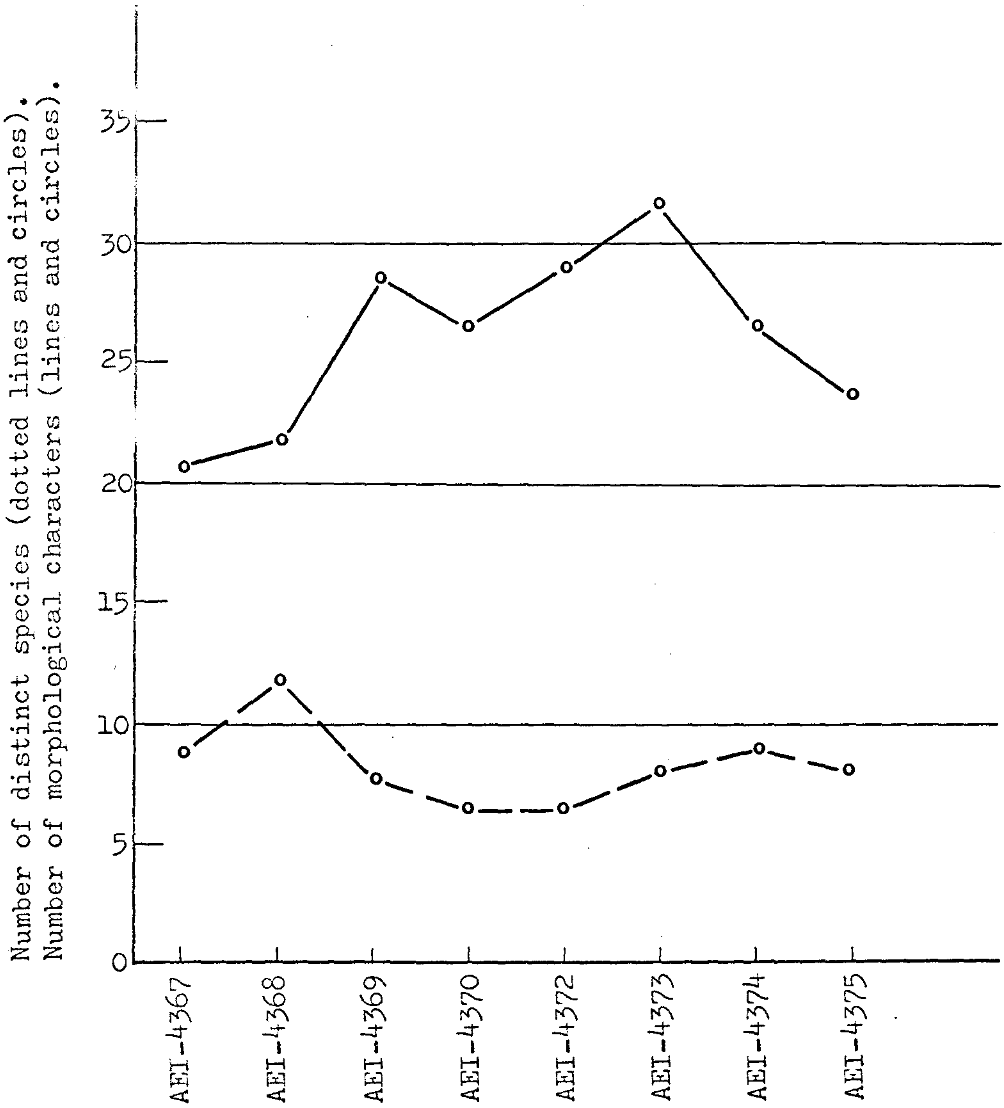
| Data Pairs | Calculated value of T | Value of T: 5% probability level |
|---|---|---|
| Goose Fiord: Sites 1 and 2 (Subtotals) | 9.09 | 1.950 |
| Goose Fiord and Escuminac Bay (Totals) | 7.44 | 1.950 |

The significance of the results of these tests will be considered in a later section.

## RESULTS OF OTHER QUANTITATIVE STUDIES

The number of different morphological characters occurring in each sample was recorded. As well, the number of form species in each sample (not including grouped units such as cingulate forms and monosaccate forms) was recorded. The results for the samples from Goose Fiord are plotted against the sample number in Text-fig. 8. This was done to provide some means of assessing the diversity as shown by morphological characters in comparison with the diversity as shown by the species concept.

To give some idea of the frequency of occurrence of miospore form species and unidentified miospores of form generic rank or higher



Text-fig. 8. The number of different morphological characteristics shown by individual miospores, compared with the number of distinct miospore species present in the same geological unit. Samples taken from Goose Fiord, Site One. Sample AEI-4371 is not included.

grouping, 150 miospores were counted for each sample from Goose Fiord and Escuminac Bay yielding suitable material. The counts for each sample are given in Text-fig. 9.

## TAXONOMY OF THE MIOSPORES AND ACRITARCHS

### Method of Classification

In the past three decades, a number of methods for classifying Palaeozoic miospores and other similar plant microfossils have been proposed. These have ranged from attempts to group miospores in relation to higher taxonomic units (Winslow, 1962), which in effect makes them organ genera and species (Potonié, 1958a), to the completely artificial classification of Potonié and Kremp (1954, 1955, 1956a, 1956b) and Potonié (1956, 1958b, 1960). This latter system is based strictly on the morphological characteristics of the miospores and therefore the genera and species are form genera and species. No attempt is made to fit these form taxa into a classification scheme involving higher natural taxa.

The naming of miospore genera and species has varied considerably as well. Raistrick (1934), Thomson (1940), and Radforth and McGregor (1954), as well as many others, use the system of designates. Schopf, Wilson, and Bentall (1944) and many others, have given binomial epithets to miospore species. This latter practice has become the most commonly used approach in the last few years.

The practice of designating a type species for each new form genus and a holotype for each new form species has not been followed consistently in the past. Often, as well, the rules of the International

Text-fig. 9. Numerical occurrence of miospore and acritarch species, species designates and morphological groupings (underlined) in samples from Goose Fiord and Escuminac Bay. A dash (-) indicates absence in the sample. An "X" indicates presence in the sample but not in the actual count. The incidental occurrence of megaspores and acritarchs during the counting of 150 miospores per sample is also given.

| SAMPLE NUMBER | GOOSE FIORD: SOUTHERN ELLESMERE ISLAND | | | | | | | | | | | | | ESCUMINAC BAY, QUEBEC | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | AKI-4367 | AKI-4368 | AKI-4369 | AKI-4370 | AKI-4371 | AKI-4372 | AKI-4373 | AKI-4374 | AKI-4375 | LA6-L63 | LA6-L67 | AKI-1 | AKI-13-46 | AG-3 | AG-11 | AG-13 | AG-23 | AG-24 |
| Leiotriletes sp A. | 2 | X | - | - | - | - | 1 | - | - | 1 | - | - | X | - | - | - | - | - |
| Leiotriletes sp B. | - | - | - | - | - | - | - | 1 | - | 1 | - | - | - | - | - | - | 1 | - |
| Leiotriletes spp. | - | - | 2 | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - |
| Punctatisporites tenuis | 5 | 2 | - | - | 2 | - | 1 | 1 | 1 | X | X | X | 2 | - | - | - | - | - |
| Punctatisporites lunaris | 3 | 1 | - | - | - | X | - | X | X | - | X | 2 | 2 | - | - | - | - | - |
| Punctatisporites glaber | - | - | - | - | - | - | - | - | - | - | - | - | - | 9 | X | - | - | 2 |
| Punctatisporites pseudobesus | - | - | - | - | - | - | - | - | - | - | - | - | - | 6 | - | - | X | - |
| Punctatisporites sp A. | - | 1 | 2 | - | - | X | - | - | - | - | X | 2 | 2 | - | - | - | - | - |
| Punctatisporites spp. | 3 | 5 | 4 | - | 5 | 4 | 1 | - | 1 | - | 3 | - | - | 7 | 2 | 2 | 6 | 4 |
| Punctatasporites? sp A. | - | - | - | - | - | - | - | - | - | - | X | 1 | - | - | - | - | - | - |
| Calamospora? similis | - | - | - | - | - | - | - | - | - | - | - | - | - | 2 | 3 | - | 4 | - |
| Calamospora atava | - | - | - | - | - | - | - | - | - | - | - | - | - | 3 | X | 1 | 2 | X |
| Calamospora spp. | - | 1 | - | - | - | - | - | - | - | - | - | - | - | 8 | 4 | - | 2 | 1 |
| Retusotriletes greggsi | 102 | 79 | 94 | 114 | 109 | 101 | 124 | 115 | 99 | 120 | 101 | 110 | 123 | - | - | - | - | - |
| Retusotriletes semizonalis | 33 | 52 | 26 | 22 | 16 | 31 | 19 | 31 | 28 | 20 | 34 | 22 | 14 | - | - | - | - | - |
| Retusotriletes spp. | - | 2 | - | - | - | - | - | 1 | - | - | - | - | - | 1 | - | 2 | 1 | - |
| Verrucosisporites certus | - | 1 | 2 | X | - | 1 | 1 | - | 4 | - | X | 3 | - | - | - | - | - | - |
| Verrucosisporites spp. | - | - | - | - | 1 | - | - | - | - | - | 2 | - | X | - | - | - | 1 | - |
| Granulatisporites sp A. | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Granulatisporites spp. | - | - | - | - | - | - | 1 | 1 | 2 | - | - | - | X | - | - | 1 | - | - |
| Cyclogranisporites spp. | 1 | 1 | - | - | - | 3 | - | - | - | - | X | 1 | - | - | - | - | - | - |
| Planisporites aculeatus | - | - | - | - | - | - | - | - | - | - | - | - | - | 55 | 111 | 115 | 105 | 118 |
| Planisporites spp. | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 2 | X | 8 | X |
| Apiculatasporites dilucidus | - | - | - | - | - | - | - | - | - | - | - | - | - | X | - | 1 | - | X |
| Apiculatisporis sp A. | X | - | 1 | X | - | - | X | - | 1 | 1 | - | - | 2 | - | - | - | - | - |
| Apiculatisporis sp B. | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 2 | - | 1 |
| Apiculatisporis spp. | - | - | - | - | 1 | - | - | - | - | - | - | - | - | 6 | 1 | 5 | 5 | 4 |
| Dictyotriletes trigonalis | - | - | - | 6 | 4 | - | - | - | - | 1 | 7 | 1 | - | - | - | - | - | - |
| Convolutispora tuberculata | - | 1 | - | - | 1 | X | 1 | - | 1 | - | - | 1 | - | - | - | - | - | - |
| Convolutispora spp. | X | X | X | 1 | - | 1 | - | - | 1 | - | - | X | X | - | 2 | - | - | - |
| Murornati spp. | - | - | - | - | 2 | - | X | X | - | - | - | - | - | - | - | - | - | - |
| Perotrilites spp. | - | - | - | - | - | 1 | - | - | - | 2 | 1 | - | X | X | - | X | - | - |
| Cingulati spp. | - | X | - | - | 1 | 3 | - | - | X | X | - | - | X | - | X | - | 1 | - |
| Stenozonotriletes clarus | - | - | - | - | - | - | - | - | - | - | - | - | - | 7 | 3 | X | - | 2 |
| Stenozonotriletes sp A. | - | X | X | - | - | - | X | X | - | - | - | - | - | - | - | - | - | - |
| Stenozonotriletes spp. | - | - | 2 | - | - | - | - | - | - | - | - | - | - | 2 | - | - | - | - |
| Lophozonotriletes crassirugulatus | - | - | 2 | - | X | - | X | X | 1 | - | X | - | X | - | - | - | - | - |
| Lophozonotriletes rarituberculatus | - | X | X | 4 | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Lophozonotriletes sp A. | - | - | - | - | - | - | - | - | - | - | - | - | - | 2 | - | - | - | 3 |
| Lophozonotriletes spp. | X | X | - | - | 2 | 2 | - | 1 | 3 | 2 | - | 7 | - | - | - | 1 | - | - |
| Zonati spp. | - | - | - | - | - | - | - | - | 2 | 1 | - | - | 1 | - | - | - | - | - |
| Cingulizonates boreus | - | 1 | - | 2 | X | 2 | - | - | 1 | 1 | X | 1 | 2 | - | - | - | - | - |
| Emphanisporites sp. | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | 1 | - | - |
| Ancyrospora ancyrea var. ancyrea | - | - | - | - | - | - | - | - | - | - | - | - | - | 28 | 5 | 3 | 5 | 7 |
| Ancyrospora ancyrea var. brevispinosa | - | - | - | - | - | - | - | - | - | - | - | - | - | 2 | - | - | - | - |
| Ancyrospora spp. | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - |
| Sporites spp. | - | - | - | - | 1 | 1 | 1 | - | 1 | - | X | - | - | 2 | - | - | 1 | - |
| Endosporites? granisaccatus | - | - | - | - | - | - | - | - | - | - | - | - | - | 2 | 4 | 3 | 2 | 2 |
| Endosporites sp A. | - | - | - | - | - | - | - | - | - | - | - | - | - | X | 2 | X | 1 | - |
| Rhabdosporites langi | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | 1 | X |
| Monosaccites spp. | - | - | 4 | 1 | 2 | - | - | - | 2 | - | - | 1 | - | 5 | 3 | 8 | 5 | 3 |
| Megaspore spp. | - | - | X | 2 | - | 1 | - | - | 2 | 1 | 1 | - | X | 1 | 1 | - | - | - |
| Acritarcha | | | | | | | | | | | | | | | | | | |
| Leiosphaeridia orbiculata | - | - | - | - | - | - | - | - | - | - | - | - | - | 6 | 3 | 1 | 1 | - |
| Leiosphaeridia microgranulifera | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 2 | 3 | - |
| Leiosphaeridia spp. | 4 | 1 | 6 | 3 | 4 | 3 | 2 | 2 | 3 | 1 | 3 | 2 | 4 | - | - | - | - | - |

Code of Botanical Nomenclature have been followed inconsistently, causing much confusion in the status of certain taxonomic entities. These last two points apply especially to many Russian authors.

In this thesis, the classification of Potonie and Kremp (1954) and later emendations (Potonié and Kremp, 1956; Potonié, 1956; 1958; 1960) will be followed. The order of genera in the systemics is also after Potonié and Kremp, 1955; 1956. Although shortcomings in this classification have been pointed out (Dettmann, 1963), it still remains, in the opinion of the author, the most comprehensive and ordered classification yet applied to miospores of uncertain botanical affinities.

To allow comparison with other taxonomic studies, spore species will be given binomial epithets, and the rules governing taxonomy, as set out in the International Code of Botanical Nomenclature (Lanjouw (ed.), 1956), will be followed. Holotypes will be designated for each new species proposed and the special provisions concerning fossil material will be observed (Lanjouw (ed.), 1956, pp. 55-57).

The author, in accordance with Article 29 of the International Code of Botanical Nomenclature, does not consider the duplication of this thesis to constitute effective publication. Confirmation of the new species proposed herein, as valid taxa, must await publication in a recognized journal in accordance with Article 33(2) of the Botanical Code.

## Criteria for New Species

To ensure that a reasonable range of variation has been encompassed, no new species have been proposed unless at least ten suitable specimens have been found on which to base a description. Species which could not be placed in existing taxa, but for which less than ten specimens were found, have been termed species designates, for example, *Calamospora sp.A.*, *Calamospora sp.B.*, and so on. Distinguishing features of a new species have been placed in a diagnosis and secondary features have been put in a subsidiary heading where the morphological characteristics may be so divided. Secondary features in a description may also, on occasion, be placed under the subsidiary heading of 'Other Features'.

## Relocation of Specimens

Co-ordinates of holotypes of new species are included in the description of the species. As well, co-ordinates of specimens illustrated have been given in the plate legends if a specimen other than the holotype is used.

Co-ordinates refer to those on the stage of the McMaster University, Department of Biology Microscope D-18 (a *Wild M-20* model with serial number 13035). A specimen occurring at (996 - 427) can be found approximately in the centre of the field at 125X power at stage co-ordinates 99.6 on the horizontal scale and 42.7 on the vertical scale. Slides were oriented on the stage with the slide label at the "western" edge of the stage. The addition of approximately 559 to the horizontal co-ordinate will give the vertical traverse line reading on the *Leitz Ortholux* Microscope (serial number 567124) in the Department of Biology, McMaster University.

## Explanation of Descriptive Terms and Headings

A complete glossary of descriptive terms is given in Appendix I at the end of the thesis. Where appropriate, reference will be made to usage of other authors and to publications which may have some bearing on the definition of a term.

Size ranges and mean sizes for the specimens of each miospore species are contained under the heading 'Dimensions' in the systematics section. Where dimensions of miospore species are recorded, the number of specimens will be given, followed by the size range and the arithmetic mean of the range in brackets. For example (11 specimens): 38μ(48μ)63μ, indicates that the observed specimens of the species had a size range of 38μ to 63μ and a mean diameter of 48μ.

## SYSTEMATICS

| | |
|---|---|
| Anteturma | SPORITES H. Potonié 1893 |
| Turma | TRILETES (Reinsch 1881) Pot. & Kr. 1954 |
| Subturma | AZONOTRILETES Luber 1935 |
| Infraturma | LAEVIGATI (Benn. & Kidst. 1886) Potonié 1956 |

Genus LEIOTRILETES (Naumova 1937) Pot. & Kr. 1954

*Type species*: *L. sphaerotriangulus* (Loose) Pot. & Kr.

### *Leiotriletes sp.A.*

Plate I, figs. 1, 2.

*Description*: Amb triangular to roundly triangular. Trilete;

laesurae extending 2/3 to 3/4 of radius; lips simple but occasionally folded about the commissure. Wall thin, occasionally folded. Ornamentation scabrate to faintly granulose.

Dimensions: (7 specimens): 25μ(35μ)41μ.

Distribution: Okse Bay Formation, sites 1 and 2.

Remarks: Laevigate, triangular forms, with simple construction are common in the Upper Devonian and Lower Carboniferous. The lack of specimens of *Leiotriletes* sp.A. makes comparison with these simple forms difficult. *Leiotriletes* sp.A. of Richardson, 1965, pp. 560-561; pl. 88, fig. 1, is similar but larger but may be synonomous. Richardson's species designate is of Middle Devonian age.

### *Leiotriletes* sp.B.

Plate I, fig. 3.

Description: Amb roundly triangular to triangular. Trilete; laesurae extend to equator; lips ridge-like and about $1\frac{1}{2}\mu$ wide. Wall thin. Ornamentation scabrate.

Dimensions: (5 specimens): 30μ(32μ)38μ.

Comparison: Wall thicker, and lips ridge-like compared to thin wall and simple commissures of *Leiotriletes* sp.A.

Distribution: Okse Bay Formation; Escuminac Formation.

Remarks: One specimen was found in sample AG-13 of the Escuminac material that agreed in all respects with the description of the species as found in the Okse Bay Formation. Since contamination may have occurred, the occurrence is questioned until further evidence is offered.

## Genus PUNCTATISPORITES (Ibrahim 1933) Pot. & Kr. 1954

Type species: *P. punctatus* Ibrahim 1933.

### *Punctatisporites tenuis* sp. nov.

Plate I, fig. 9.

Description: Amb round. Trilete; laesurae simple, extending 2/3 of the radius. Wall thin, occasionally folded near the equator. Ornamentation laevigate to scabrate.

Dimensions: (17 specimens): 28μ(43μ)54μ.

Holotype: AEI-4367.2a(i); 1014 - 278; (51μ).

Locus typicus: Okse Bay Formation, sites 1 and 2.

Comparison: *Punctatisporites tenuis* is similar to several species of *Punctatisporites* described by McGregor (1960, pp. 28-29). It differs, however, in being either smaller in size or having a thinner wall, and in having less pronounced ornamentation.

### *Punctatisporites lunaris* sp. nov.

Plate I, fig. 6.

Description: Amb round. Trilete; laesurae simple, extending 2/3 to 3/4 of the radius. Wall thin, occasionally folded. Ornamentation punctate, but occasionally scabrate.

Dimensions: (14 specimens): 57μ(73μ)96μ.

Holotype: AEI-4367.2a(ii); 820 - 325; (83μ).

Locus typicus: Okse Bay Formation, sites 1 and 2.

Comparison: *Punctatisporites lunaris* is larger than species of *Punctatisporites* described by McGregor (1960, pp. 28-29), although some overlap in size exists with all three species. *P. lunaris* is distinguished from P. arcticus McGregor 1960, p. 28; pl. 11, fig. 5, and P. scabratus McGregor 1960, p. 29; Pl. 11, fig. 6 by its generally larger size and punctate ornamentation. P. lunaris sp. nov. has a thinner wall than P. putaminis McGregor, 1960, p. 29; Pl. 11, fig. 7 and is punctate.

P. lunaris sp. nov. differs from P. tenuis, this paper, by its larger size and punctate ornamentation.

### Punctatisporites glaber (Naumova) Playford 1962

Plate I, figs. 4, 5.

1938 Azonotriletes glaber (Naumova) Waltz in Luber and Waltz, p. 8; pl. 1, fig. 2 and pl. A, fig. 3.

1952 Leiotriletes glaber (Waltz) Ishchenko, pp. 13-14; pl. 2, figs. 15, 16. (fide: Playford, 1962, p. 576)

1955 Calamospora glabra (Naumova) Pot. & Kr., p. 47.

1955 Punctatisporites nitidus Hoffmeister, Staplin, and Malloy, pp. 393-394; pl. 36, fig. 4.

1955 Punctatisporites? callosus Hoffmeister, Staplin, and Malloy, p. 392; pl. 39, fig. 7.

1956 Leiotriletes glaber Naumova; Ischenko, pp. 18-19; pl. 1, figs. 7, 8.

1957 Punctatisporites nitidus Hoffmeister, Staplin, and Malloy, in Hacque and Barss, p. 13, pl. II, fig. 3.

1958 Punctatisporites cf. nitidus Hoffmeister, Staplin, and Malloy; Butterworth and Williams, p. 361; pl. 1, figs. 7, 8.

1960 Punctatisporites curviradiatus Staplin, p. 7; pl. 1, figs. 17-20.

1962 Punctatisporites glaber (Naumova) Playford, pp. 576-577; pl. 78, figs. 15, 16.

Description: Amb round. Trilete; laesurae simple or faintly raised, extending 2/3 to occasionally 3/4 of the radius. Wall 2-2½μ thick in optical section, rarely folded. Ornamentation laevigate to faintly scabrate or granulose.

Dimensions: (24 specimens): 26μ(37μ)55μ.

Distribution: Escuminac Formation.

Remarks: The author agrees with Playford's assessment of "...the multitudinous nomenclature prevailing among...simple, trilete, circular, laevigate spores...." (Playford, 1962b, p. 577). While the specimens of this study have perhaps slightly longer trilete rays and a slightly thicker wall, there are no real distinguishing features between these and Playford's specimens. The specimens of this paper are thus considered within the circumscription of Playford's material.

Punctatisporites platirugosus (Waltz) Sullivan, 1964, p. 358; pl. 57, figs. 7-9 may also be conspecific with P. glaber. Sullivan's description offers no diagnostic features to distinguish P. platirugosus from P. glaber and in fact he states (1964, p. 358): "Occasional specimens without folds...resemble Punctatisporites glaber (Naumova) Playford 1962".

Previous Records: Many localities in the Carboniferous (fide: Playford, 1962b).

### Punctatisporites pseudobesus Playford 1962

Plate I, fig. 8.

1962 Punctatisporites pseudobesus Playford, p. 578; pl. 78, figs. 17, 18.

Description: Amb round. Trilete; laesurae simple, occasionally with raised exine about the commissures, or widely gaping; laesurae extend about 3/4 of the spore radius. Wall thick (3 to 6μ, average 4μ) in optical section. Ornamentation scabrate.

Marked contact area occasionally present; contact area triangular in shape and extending most of the length of the laesurae. Spore wall dark brown.

Dimensions: (9 specimens): 80μ(114μ)147μ.

Comparison: Certain features (occasional presence of a contact area and laesurae longer than 3/4 of the spore radius) are not present in Playford's specimens. These differences, however, are not considered to be sufficient reasons to propose a new species.

Distribution: Escuminac Formation.

Previous Records: Triungen, Spitzbergen: Lower Carboniferous (Playford, 1962, p. 578).

### Punctatisporites sp.A.

Plate I, fig. 7.

Description: Amb round. Trilete; laesurae simple or slightly folded about the commissure; laesurae extend 3/4 of radius. Wall relatively thick (?3μ). Ornamentation scabrate to punctate.

Dimensions: (7 specimens): 34μ(42u)51μ.

Comparison: Distinguished from P. glaber (Naumova) Playford 1962b, pp. 576-577; pl. 78, figs. 15, 16 by a thicker wall and the scabrate to punctate ornamentation.

Distribution: Okse Bay Formation, sites 1 and 2.

Genus PUNCTATASPORITES Ibrahim 1933

Type species: P. sabulosus Ibrahim 1933.

Punctatasporites? sp.A.

Plate I, fig. 10.

Description: Amb round. Alete. Wall thin and often folded. Ornamentation punctate.

Dimensions: (4 specimens): 38μ, 42μ, 48μ, 50μ.

Distribution: Okse Bay Formation, site 2.

Remarks: The genus Punctatasporites is presently considered to be confined to the Carboniferous. The occurrence of Upper Devonian specimens falling within the circumscription of this form would be noteworthy. Although the specimens of this paper are referred to Punctatasporites, the small number does not permit positive identification and thus a qualification is made.

Genus CALAMOSPORA Schopf, Wilson, and Bentall 1944

Type species: C. hartungiana Schopf in Schopf, Wilson, and Bentall 1944.

Calamospora? similis sp. nov.

Plate I, fig. 11.

Description: Amb round. Wall thin (about 1μ) and highly folded. Ornamentation laevigate.

Other Features: Amb often irregular due to folding. Trilete mark not observed. Contact area not present.

Dimensions: (11 specimens): 58μ(72μ)90μ.

Holotype: AG-3.3(ii) 1032 - 362; (70μ).

Locus typicus: Escuminac Formation.

Remarks: The specimens are assigned only provisionally to the genus *Calamospora* because of the absence of a trilete mark and contact area. The thin, highly folded wall and laevigate ornamentation, however, correspond to the diagnosis of the genus.

No comparable forms were noted in assemblages described from other Upper Devonian localities, although many Carboniferous forms have a general resemblance to the specimens of this paper.

### *Calamospora atava* (Naumova) McGregor 1964

Plate I, figs. 12, 13, 14, 15.

1925 "Spore type D", Lang, p. 256; pl. 1, fig. 8.

1953 *Leiotriletes atavus* Naumova, p. 23 and p. 103; pl. 1, fig. 8 and pl. 16, fig. 3.

1955 *Leiotriletes atavus* Naumova *in* Kedo, p. 19; pl. 1, fig. 5.

1964 *Calamospora atava* (Naumova) McGregor, pp. 6-7; pl. 1, fig. 17.

Description: Amb round. Trilete; laesurae simple, extending a little more than ½ the spore radius. Wall 1 to 2μ thick and often folded. Ornamentation laevigate to scabrate.

Other Features: Prominent contact area on all forms, either with straight or concave boundaries, extending the length of the laesurae. Folds generally concentric.

Dimensions: (13 specimens): 51μ(69μ)84μ.

Comparisons: Lang's "spore type D" (1925, p. 256; pl. 1, fig. 8) appears identical to the specimens of *Calamospora atava* from Escuminac Bay, although the size range of the latter is greater (51 to 84μ) than that of Lang's form (60-75μ).

Naumova's illustration (1953, pl. 1, fig. 8) consists only of a drawing, but the simple nature of the spore permits a useful comparison. The specimens of this paper appear to agree in all respects with the form illustrated by Naumova except that her listed size range (60 to 70μ) is smaller than the range of the specimens of this paper.

The "thickened margin" of Kedo (1955, p. 19; pl. 1, fig. 5) may only be a thick wall, as in the Escuminac specimens, and her specimens are considered synonomous with those of this paper.

Calamospora atava (Naumova) McGregor, 1964, pp. 6-7; pl. 1, fig. 17 is probably synonomous, although the two specimens described, judging from his illustration, were probably poorly preserved. McGregor's illustrated form appears less similar to the form illustrated by Lang (1925, p. 256; pl. 1, fig. 8) then do the forms from Escuminac Bay. The contact area is not as marked and the exine shows variable thickening.

Distribution: Escuminac Formation.

Previous Records: Lang (1925) from the Middle Devonian of Cromarty (Miller's Bay, Navity); Naumova (1953) from the Middle and Upper Devonian of the Russian Platform; Kedo (1955) from the Middle Devonian of Belorussia; and McGregor (1964) from the late Middle to early Upper Devonian of the Ghost River Formation of Western Alberta, Canada.

## Genus RETUSOTRILETES Naumova 1953

Type species: Retusotriletes simplex Naumova 1953 (designated by by Potonié, 1958, p. 13)

Discussion: Richardson (1965, pp. 563-564) has emended this genus to include only laevigate spores. He has not, however, suggested a revised taxonomic position for other forms in the genus having ornamentation of coni, granuli, etc. His argument, that curvaturae perfecti are found consistently only on laevigate spores of this genus, is not borne out by species described in this thesis. Richardson, himself, qualifies his statement by adding the phrase, "in the assemblage studied" in speaking of curvaturae perfecti. Until further evidence is forthcoming and until the taxonomic position of apiculate-ornamented miospores with curvaturae perfecti is settled, the author will continue to follow a broad definition of the genus Retusotriletes.

### Retusotriletes greggsi McGregor 1964

Plate I, fig. 16; Plate II, figs. 1, 3, 4.

1964 Retusotriletes greggsi McGregor, pp. 8-10; pl. I, figs. 1-12.

Revised Diagnosis: Amb roundly triangular to round. Trilete; laesurae simple or with margins up to 2µ in width, extending about 4/5 spore radius. Curvaturae join the laesurae extremities and are proximal. Ornamentation variable: from minute echini visible only under oil immersion to elements 1-2µ in height (spinae).

Other Features: Curvaturae generally dark and up to 14µ wide, but usually between 4 to 8µ; occasionally not well marked because of overmaceration. Wall relatively thick (2µ or more in optical section) and only rarely folded. Curvaturae may be thickened at the extremities of the laesurae. Ornamentation may be reduced occasionally in the contact areas.

Dimensions: (94 specimens): 45µ(70µ)96µ.

Comparison: The comparison of R. greggsi with the similar form R. semizonalis is considered following the description of specimens referred to R. semizonalis.

Distribution: Okse Bay Formation, sites 1 and 2.

Remarks: Retusotriletes greggsi occurs abundantly at the Goose Fiord localities. Its occurrence at other Upper Devonian localities, occasionally in abundance, suggests it may be a useful palaeoecological indicator in the delineating of Upper Devonian microfloral provinces.

Previous Records: Late Middle to early Upper Devonian: Ghost River Formation, type section, Western Alberta, Canada; 35 miles north of type section in beds equivalent to the Ghost River Formation; Onteora Formation, Western New York State. All from McGregor (1964, p. 24).

### Retusotriletes semizonalis McGregor 1964

Plate II, fig. 2.

1964 Retusotriletes semizonalis McGregor, pp. 10-11; pl. II, figs. 1-5 and 7, 8.

Revised Diagnosis: Amb round to occasionally roundly triangular. Trilete; laesurae simple, but occasionally with margins about 1µ wide; laesurae extend more or less to the equatorial region. Wall generally thin (1 to 2µ in optical section) and only rarely folded. Equatorial curvaturae, generally well-defined, and occasionally slightly raised, join the extremities of the laesurae. Ornamentation minutely echinate, occasionally scabrate, only rarely granulose.

Other Features: Curvaturae variable in width and only occasionally slightly proximal; curvaturae generally thicker at ray extremities. Ornamentation often distinguishable only under oil immersion.

Dimensions: (48 specimens): 36μ(70μ)96μ.

Distribution: Okse Bay Formation, sites 1 and 2.

Remarks: See discussion following this description.

Previous Records: Late Middle to early Upper Devonian: Ghost River Formation, type section, McGregor (1964).

Discussion: Considerable difficulty was experience in separating *Retusotriletes greggsi* and *Retusotriletes semizonalis* on the bases of the original descriptions of McGregor (1964, pp. 8-11). A comparison of the two descriptions (which McGregor did not include) indicated that *R. semizonalis* could be distinguished from *R. greggsi* by the following criteria: slightly longer rays; narrow curvaturae that are not invaginated; uniform ornamentation inside and outside the area bounded by the curvaturae; the presence of consistently extremely minute ornamentation; and equatorial position of the curvaturae.

Except for the consistent presence of extremely minute ornamentation and equatorial position of the curvaturae, the other characters showed gradation and overlap with those of *Retusotriletes greggsi* in specimens from Goose Fiord.

Curvaturae varied in width and showed no relation to coarse or fine ornamentation. Reduced ornamentation in areas bounded by the curvaturae was observed on only a few specimens. The curvaturae showed thickenings at the ray extremities and invagination on both finely and coarsely ornamented specimens.

Using the two diagnostic features as a basis for distinguishing the two species, revised diagnoses were constructed for the forms, and secondary features, tending to be associated more with one species than the other, were set out in a second heading. To confirm these diagnostic features, the type of ornamentation present on 142 specimens belonging either to *R. greggsi* or *R. semizonalis* was correlated with the presence of proximal or equatorial curvaturae. The results are given below in TABLE 3.

TABLE 3. - Occurrence of ornamentation in relation to position of curvaturae on 142 specimens of miospores belonging to the species *Retusotriletes greggsi* and *R. semizonalis* from Goose Fiord, Ellesmere Island.

| Curvaturae position | Proximal | Equatorial |
|---|---|---|
| Type of Ornament | % of Specimens N = 94 | % of Specimens N = 48 |
| Minute echini ($\leq \frac{1}{2}\mu$) | 37 | 94 |
| Echini | 38 | 0 |
| Granulose-Granulate | 15 | 2 |
| Coni | 5 | 0 |
| Scabrate | 5 | 4 |

McGregor (in litt., November 12, 1964) confirms this: "...in the Ghost River assemblage *R. semizonalis* is quite clearly distinguishable from *R. greggsi* by its extremely minute ornament,.... Other features consistently associated with this feature in *R. semizonalis* are...more consistently equatorial curvaturae...". McGregor, however, did not state this clearly in his original description.

The results in TABLE 3 show quite clearly that the two diagnostic features of ornamentation and curvaturae are distinctly related. Specimens having procimal curvaturae and wide range of ornamentation belong to Retusotriletes greggsi, while specimens having equatorial curvaturae and minute ornamentation in 98% of the cases, belong to Retusotriletes semizonalis.

### Retusotriletes simplex? Naumova 1953

Plate II, fig. 5.

Description: Amb round. Trilete; laesurae simple, extending 2/3 of spore radius. Wall thin and unfolded. Curvaturae, about 1µ wide join the extremities of the laesurae; curvaturae slightly proximal and invaginating at the extremities of the laesurae. Ornamentation laevigate.

Dimensions: (1 specimen): 39µ.

Distribution: Escuminac Formation.

Remarks: The form described here also appears similar to Retusotriletes communis Naumova 1953, p. 97; pl. 15, figs. 15-17 and pl. 16, fig. 42 and pl. 17, figs. 20, 21. The curvaturae of the latter species, however, are decidedly proximal.

Since only one specimen was found, identification is not considered positive. The specimen most resembles R. simplex Naumova 1953, p. 29; pl. 2, fig. 9.

Previous Records: Middle and Upper Devonian of the Russian Platform (Naumova, 1953). Lower Devonian: Reported by McGregor, 1957, p. 72, unpub. from the Sextant Formation of Northern Ontario, Canada.

Infraturma APICULATI (Benn. & Kidst. 1886) Potonié 1956

Genus GRANULATISPORITES (Ibrahim) Pot. & Kr. 1954

*Type species*: *G. granulatus* Ibrahim 1933.

*Granulatisporites sp.A.*

Plate II, figs. 6, 7.

*Description*: Amb convexly triangular. Trilete; laesurae simple, extending more or less to the equator. Wall thin (1μ), occasionally folded. Ornamentation of small granules (less than 1μ wide and high); about 60 visible along the equator.

*Dimensions*: (6 specimens): 28μ(35μ)41μ.

*Distribution*: Okse Bay Formation, sites 1 and 2.

*Remarks*: *Granulatisporites sp.A.* resembles several Carboniferous forms, but too few specimens are available for a valid comparison.

Genus VERRUCOSISPORITES (Ibrahim 1933) Pot. & Kr. 1954

Type species: *V. verrucosus* Ibrahim 1933.

*Verrucosisporites certus* sp. nov.

Plate II, fig. 8.

*Diagnosis*: Amb round. Trilete; laesurae faint, ridge-like, extending 3/4 of spore radius. Wall about 1½μ thick and occasionally folded. Ornamentation verrucate; the verrucae 2 to 5μ in diameter, 1 to 2μ in height, isodiametric to faintly vermiform, never anastomosing.

*Other Features*: Laesurae may be obscured by ornamentation. Verrucae close set, approaching at times a negative reticulum. A few specimens show a fold or thickening near the equator.

Dimensions: (13 specimens): 40μ(53μ)67μ.

Holotype: AEI-4375d.1(i); 1231 - 297; 53μ.

Comparison: *Verrucosisporites papulosus* Hacquebard 1957, p. 311; pl. 2, figs. 4, 5, resembles *V. certus* sp. nov. but does not show a negative reticulum and has more elongate verrucae.

Locus typicus: Okse Bay Formation, sites 1 and 2.

### Genus PLANISPORITES (Knox 1950) Pot. & Kr. 1954

Type species: *P. granifer* (Ibrahim) Knox.

### *Planisporites aculeatus* sp. nov.

Plate II, figs. 9, 10, 11; Plate III, fig. 1.

Diagnosis: Amb round. Trilete; laesurae simple or with raised margins about 1μ wide, extending 3/4 of spore radius. Wall thin. Ornamentation of minute echini, closely set, slightly elongate rather than cone-like.

Other Features: Wall may be folded occasionally. Echini alike, ranging from 1/4 up to 1μ in height; height of echini slightly greater than width of base. Forms with margins about commissures generally occur in tetrads, rarely singly.

Dimensions: (75 specimens): 32μ(43μ)59μ.

Holotype: AG-3.3(i); 764 - 376; 35μ.

Locus typicus: Escuminac Formation.

Comparison: *Planisporites minimus* McGregor 1964, pp. 29-30; pl. 11, fig. 9, resembles *P. aculeatus* sp. nov. closely in size and shape. McGregor's species has, however, a smaller size range, shorter laesurae which are simple, and ornamentation distinctly cone-like in comparison to the relatively elongate and smaller echini of

*P. aculeatus*.

*Remarks*: The occurrence of forms with simple laesurae as single grains and forms with compound laesurae in tetrads suggests that mature and immature specimens are being encountered. An alternative explanation is that perhaps compression in the tetrad has caused the exine to fold about the commissures. In either case there is no good reason to separate these two forms into two form species or varieties of species in view of their otherwise pronounced similarities. Further support for this view is found in the fact that forms with compound laesurae rarely occur singly and that both types have been noted in close association in spore masses.

### Genus APICULATASPORITES Ibrahim 1933 (*sensu* Potonié 1960)

*Type species*: *A. spinulistratis* (Loose) Ibrahim 1933.

### *Apiculatasporites dilucidus* (McGregor 1960) McGregor 1964

Plate III, fig. 4.

Partial synonomy:

1960 *Planisporites dilucidus* McGregor, p. 30; pl. 11, fig. 10.

1964 *Apiculatasporites dilucidus* (McGregor 1960) McGregor, p. 13; pl. II, figs. 12-14.

*Description*: Amb round. Trilete; laesurae simple, extending 2/3 radius of spore; occasionally indistinct. Wall thin (1µ) and unfolded. Ornamentation echinate (height of echini 3/4 to 1µ).

*Dimensions*: (7 specimens): 50µ(53µ)57µ.

*Distribution*: Escuminac Formation.

*Remarks*: McGregor (1964, pp. 14-15) discusses similar forms at some length, none of which are placed in undoubted synonomy. Since only a few specimens are available for comparison with other forms, no attempt is made here to discuss probable synonomy.

*Previous Records*: Upper Devonian: Melville Island (McGregor, 1960); Ghost River Formation, type section (McGregor, 1964).

### Genus APICULATISPORIS Potonié and Kremp 1956

*Type species*: *A.* (*al Apiculatisporites*) *aculaetus* (Ibrahim, 1933, *non* Benn. & Kidst.) Pot. & Kr.

### *Apiculatisporis sp.A.*

Plate III, figs. 2, 3.

*Description*: Amb round. Trilete; laesurae simple commissures and extending almost to the equator. Wall 2 to 4μ thick and occasionally folded. Ornamentation of sharply tapering echini (1 to 1½μ in length, basal width 1μ), distinctly separated.

*Dimensions*: (9 specimens): 56μ(69μ)86μ.

*Comparison*: *Apiculatisporis elegans* McGregor 1960, p. 30; pl. 11, fig. 12, has a similar size range and similar ornamentation, but the apiculations have broader bases and the wall is thinner. As well, the apiculations are more closely packed than those on *Apiculatisporis sp.A.* of this paper.

*Lophotriletes magnus* Naumova 1953, p. 58; pl. 7, fig. 20, also is similar, but has a thin wall and closely spaced ornamentation. A detailed comparison, however, is not possible from her drawing.

*Distribution*: Okse Bay Formation, sites 1 and 2.

### *Apiculatisporis* *sp.B.*

Plate III, fig. 5.

*Description*: Amb round. Trilete; laesurae very faint, simple, extending about 2/3 spore radius. Wall thin. Ornamentation consists of rod-like setae about 2 to 3μ in length and less than 1μ in width. Setae widely spaced.

*Dimensions*: (3 specimens): 57, 57, 58μ.

*Distribution*: Okse Bay Formation, sites 1 and 2.

*Remarks*: The setulate ornamentation of this form makes it readily recognizable, but only a few specimens were found. The form resembles Carboniferous species but not enough material is available to make a detailed comparison.

## Infraturma MURORNATI Potonié and Kremp 1954 (*sensu* Sullivan 1964)

## Genus DICTYOTRILETES (Naumova 1937) Pot. & Kr.

*Type* *species*: *D.* *bireticulatus* (Ibrahim 1933) Pot. & Kr.

### *Dictyotriletes* *trigonalis* sp. nov.

Plate III, figs. 6, 7.

*Diagnosis*: Amb round. Trilete mark not observed. Wall about 3μ thick. Sculpture reticulate; muri low and from 2 to 4μ wide; lumina polygonal with a tendency to a trianguloid outline; lumina 6-12μ in longest diameter.

*Other* *Features*: Trianguloid lumina generally developed on only one face (distal?); often approach a triangular shape, but with the apices blunted.

Dimensions: (12 specimens): 48μ(65μ)94μ.

Holotype: AEI-4370.2a(i); 709 - 319; 57μ.

Locus typicus: Okse Bay Formation, sites 1 and 2.

Remarks: The trianguloid lumina make this species quite distinctive and easily recognizable. The possibility that the lumina have been formed by the infringements of mineral crystals during compaction in lithification exists. This seems unlikely, however, since such an occurrence would be noted in other species. No such features have been observed in examination of over 5,000 other specimens during this project.

Sullivan (1964, pp. 366-367) notes that Neves (in press) has amended the genus *Reticulatisporites* (Ibrahim 1933) Potonié and Kremp to include only those forms with a differentiated cingulum and a reticulum confined mainly to the distal hemisphere. The author, in placing *Dictyotriletes trigonalis* sp. nov. in the genus *Dictyotriletes*, has thus chosen to accept a broad definition of that genus, until such time as the 'Commission Internationale de Microflore Paleozoique' decides on the status of zonate and azonate reticulate species.

### Genus CONVOLUTISPORA Hoffmeister, Staplin and Malloy 1955

Type species: *C. florida* Hoff., Stap., and Malloy 1955.

### *Convolutispora tuberculata* (Waltz) Hoff., Stap., and Malloy

Plate III, fig. 8.

1938 *Azonotriletes tuberculatus* Waltz *in* Luber and Waltz, p. 12; pl. 1, fig. 12 and pl. 5, fig. 68, and pl. A, fig. 6.

1955 *Verrucosisporites tuberculatus* (Waltz) Pot. & Kr., p. 66.

1955 *Filicitriletes tuberculatus* (Waltz) Luber, p. 54; pl. 2, figs. 45, 46 (*fide*: Playford, 1962b, p. 592).

1955 Convolutispora tuberculata (Waltz) Hoffmeister, Staplin, and Malloy, p. 384.

1956 Lophotriletes tuberculatus (Waltz) Ishchenko, p. 40; pl. 6, figs. 75, 76.

1962 Convolutispora tuberculata Hoffmeister, Staplin, and Malloy in Playford, p. 592; pl. 81, figs. 4, 5.

Description: Amb round. Trilete; laesurae simple, extending 2/3 of spore radius, often obscured by sculpture. Wall relatively thick. Sculpture of low, irregular, anastomosing rugulae, which are rounded and closely packed so as to form small, irregular lacumae. The lacunae appear almost as coarse punctae. Rugulae about 2-4μ in width and 2μ in height, giving the margin of the spore an indulating appearance.

Dimensions: (4 specimens): 64,64,67,80μ.

Comparison: Convolutispora punctatimura Staplin, 1960, p. 12; pl. 2, figs. 12, 20. 21, appears similar in all respects to Convolutispora tuberculata, except for the variable sizes of the lacunae (larger on the distal surface), and is probably conspecific. The author, however, has not examined Staplin's holotype and for this reason synonomy is not listed.

Distribution: Okse Bay Formation, site 1.

Previous Records: Playford (1962b, p. 592) lists occurrences from Upper Devonian-Namurian rocks of the Dnieper-Donetz basin and the Lower Carboniferous of Spitzbergen.

Remarks: This work presents the first definite North American occurrence of this species and the first undoubted Upper Devonian occurrence.

### *Convolutispora sp.A.*

Plate III, fig. 9.

*Description*: Amb roundly subtriangular. Laesurae simple; commissures gaping, and extending 4/5 spore radius. Wall 2μ thick. Sculpture of irregular, anastomosing rugulae (3-5μ in height; 4-8μ wide), with rounded tops, and forming an open reticulum.

*Dimensions*: (1 specimen): 67μ.

*Distribution*: Okse Bay Formation, site 1.

### *Convolutispora sp.B.*

Plate III, fig. 10.

*Description*: Amb roundly triangular. Trilete; the laesurae simple commissures, extending 3/4 of spore radius. Wall 3μ thick, not including sculpture. Sculpture of irregularly shaped verrucae and anastomosing irregular rugulae (both about 3-6μ in height and 5-10μ wide) with rounded tops. The verrucae occasionally appear connected by a low ridge.

*Dimensions*: (1 specimen): 64μ.

*Distribution*: Okse Bay Formation, site 1.

### *Convolutispora sp.C.*

Plate III, fig. 11.

*Description*: (Specimen incomplete): Amb ovoid? or rounded. Trilete mark not visible. Wall about 3μ thick. Sculpture or rugulae bearing broadly rounded verrucae. Rugulae 2-4μ in width and 2-4μ in height (including the verrucae) and arranged to form a reticulate pattern simulating 'orthostichies' of rugulae. Lucunae so defined are irregular to ovoid in shape.

Dimensions: (1 specimen): 90μ; specimen incomplete, measurement made along longest diameter.

Distribution: Okse Bay Formation, site 1.

Remarks: The very distinctive sculpture of this form would make it a well defined and easily recognizable species; unfortunately, only one specimen was found, and that one was incomplete.

### Infraturma PERINOTRILITES Erdtman 1947

### Genus PEROTRILITES Erdtman ex Couper 1953

Type species: *P. granulatus* Couper 1953.

### *Perotrilites* sp.A.

Plate III, fig. 16.

Description: Amb round. Trilete; laesurae simple, extending 4/5 radius of spore. Wall dark and relatively thick. Perinate; the perine thin and laevigate. Ornamentation of spore wall laevigate.

Dimensions: (2 specimens): 38, 46μ (including perine).

Distribution: Okse Bay Formation, site 1.

Remarks: A number of forms apparently having a perispore were noted in samples from Goose Fiord. *Perotrilites* sp.A., however, is the only type described and illustrated; it possessed a distinct form and its structure could be interpreted from the few specimens available. The other forms are relatively poorly preserved and occur singly, making their description and interpretation difficult. These latter forms are referred to in the species counts as *Perotrilites spp*.

Turma ZONALES (Bennie and Kidston 1886) Potonié 1958

Subturma ZONOTRILETES Waltz 1935

Infraturma CINGULATI Potonié and Klaus 1955

Genus LYCOSPORA (S. W. & B. 1944) Pot. & Kr. 1954

*Type species*: *L. micropapillata* (Wilson and Coe 1940) S. W. & B. 1944.

### *Lycospora sp.A*.

Plate III, fig. 12.

*Description*: Amb roundly triangular. Trilete; laesurae simple, extending almost to the cingulum. Wall thick, 3μ in optical section. Cingulate; the cingulum 2-3μ wide. Ornamentation of granules on spore body and cingulum.

*Dimensions*: (1 specimen): 69μ.

*Distribution*: Escuminac Formation.

Genus MUROSPORA Somers 1952

*Type species*: *M. kosankei* Somers 1952.

### *Murospora*? *sp.A*.

Plate III, fig. 13.

*Description*: Amb roundly triangular and slightly convex interradially. Trilete; laesurae simple, extending almost to the cingulum. Wall 3μ in optical section. Cingulate; the cingulum more or less uniform, about 6μ in width. Ornamentation on spore body and cingulum of minute punctae, relatively widely spaced. These may be partly due to corrosion.

Dimensions: (1 specimen): 80μ.

Distribution: Escuminac Formation.

Remarks: Only one specimen was found and more material is needed to confirm the identification of *Murospora*. Many occurrences of this genus have been reported from the Lower Carboniferous (Playford, 1962b) and it seems quite possible that the range of this genus might extend back into the Upper Devonian.

### Genus STENOZONOTRILETES (Naumova 1937) Potonié 1958

Type species: *S. conformis* Naumova 1953.

### *Stenozonotriletes clarus* Ischenko 1958

Plate III, figs. 17, 18.

Description: Amb round to slightly rounded triangular. Trilete; laesurae simple, extending almost to the cingulum. Wall about 1½μ in optical section. Cingulate; the cingulum of uniform width (2-4μ). Spore body laevigate to scabrate; cingulum laevigate. Corrosion may give both a mottled appearance.

Dimensions: (22 specimens): 38μ(51μ)59μ.

Comparison: *Stenozonotriletes deltoides* Hacquebard 1957, p. 314; pl. 2, figs. 17-18, is larger and has raised lips. *S. extensus* var *major* Naumova 1953, *in* Hacquebard 1957, p. 314, pl. 2, figs. 19-20, is larger (although within the total reported range of *S. clarus*: *fide* Playford, 1962b, p. 607), has occasional thickenings about the lips, and infragranulate ornamentation. *S. conformis* Naumova 1953, pp. 33, 70, 130; pl. 3, fig. 15, pl. 10, figs. 11, 12, and pl. 19, figs. 12-14, is smaller than *S. clarus* and has laesurae of variable length according to the illustrations of Naumova.

*Distribution*: Escuminac Formation.

*Remarks*: The specimens described in this paper and assigned to *Stenozonotriletes clarus* have a narrower cingulum but are otherwise identical to the species of Ischenko. This work of this thesis thus confirms the extension of the range of the species back into the Upper Devonian.

*Previous Records*: Ischenko (1958) from Upper Devonian to Viséan strata of the Dnieper-Donetz basin; Playford (1962a) from the Lower Carboniferous of Spitzbergen.

### *Stenozonotriletes sp.A.*

Plate III, fig. 14.

*Description*: Amb rounded. Trilete; laesurae simple, extending to the cingulum. Wall thick (3μ). Cingulate; the cingulum uniform in width (8-10μ). Ornamentation of the spore body and cingulum punctate (partly corrosion pits?).

*Dimensions*: (5 specimens): 47μ(58μ)75μ.

*Comparison*: *S. facilis* var. *prae-crassus* Ischenko 1956, p. 72; pl. 14, fig. 161, resembles the specimens of *Stenozonotriletes sp.A.* (this paper) in size and cingulum width but has a markedly shorter trilete mark extending only half the spore radius.

*Distribution*: Okse Bay Formation, site 1.

### *Stenozonotriletes* *sp.B.*

Plate III, fig. 15.

*Description*: Amb roundly triangular. Trilete; laesurae with slightly thickened margins, extending to the cingulum. Wall about 3/4μ thick in optical section. Cingulum 4μ wide and uniform. Ornamentation of the spore body and cingulum consists of minute echini (less than 1μ).

*Dimensions*: (1 specimen): 48μ.

*Distribution*: Escuminac Formation.

## Genus LOPHOZONOTRILETES (Naumova) Potonié 1958

*Type species*: *L. lebedianensis* Naumova 1953.

### *Lophozonotriletes crassirugulatus* sp. nov.

Plate IV, fig. 1.

*Diagnosis*: Amb round. Trilete; laesurae simple and extending almost to the cingulum. Wall 1-2μ thick. Cingulum uniform to slightly irregular in width (6-10μ). Distal ornamentation on spore body of irregular rugulae, 10-30μ in length and 5-10μ in width, with rounded tops. Proximal face and cingulum scabrate.

*Other Features*: Occasionally the distal sculpture may consist partly of verrucae.

*Dimensions*: (15 specimens): 35μ(49μ)64μ.

*Holotype*: AEI-4369.2a(i); *974 - 435*; 57μ.

*Locus typicus*: Okse Bay Formation, sites 1 and 2.

*Comparison*: *L. crassatus* Naumova 1953, p. 76; pl. 11, fig. 14, appears to have similar ornamentation, but it is not clear from her illustration or her description whether this ornamentation is proximal or distal. The size of Naumova's species is also quite restricted (60-64μ) corresponding to the upper limit of L. crassirugulatus sp. nov.

Remarks: A number of closely related species of Lophozonotriletes have been described from rocks of Middle Devonian to Carboniferous age. All have some differences with respect to each other in size, type, and distribution of ornamentation, but all tend to have distal verrucae (e.g.: L. rarituberculatus (Luber) Kedo; L. grumosus Naumova; and others). L. crassirugulatus sp. nov. represents another tendency, that to distal rugulae, although verrucae are occasionally present. There appears to be a morphological series embracing these related species and perhaps their apparent difference is only one of degree.

### Lophozonotriletes rarituberculatus (Luber) Kedo 1957

Plate IV, fig. 2.

1941 Zonotriletes rarituberculatus Luber in Luber and Waltz, pp. 10, 30; pl. 1, fig. 5 and pl. 5, fig. 76.

(non) Lophozonotriletes rarituberculatus Naumova 1953, p. 76; pl. 11, fig. 11.

1956 Euryzonotriletes rarituberculatus (Luber) Ischenko var. triangulatus Ischenko, p. 51; pl. 8, fig. 104.

1957 Lophozonotriletes rarituberculatus (Luber) Kedo, p. 1166.

1961 Lophozonotriletes triangulatus Hughes and Playford, pp. 35-36; pl. 3, figs. 3-7.

1963 Lophozonotriletes rarituberculatus (Luber) Kedo in Playford, Part Two, pp. 638-639; pl. 91, figs. 8, 9.

Description: Amb round to roundly triangular. Trilete; laesurae simple, extending to the cingulum. Wall relatively thick. Cingulate;

the cingulum uniform except for corrosion pits; width from 1/3 to 2/5 total spore radius. Cingulum and proximal spore body scabrate; distal spore body ornamented with more or less isodiametric tubercules (verrucae); from six to twelve in number; verrucae 4-10µ in longest diameter.

*Dimensions*: (6 specimens): 45µ(53µ)61µ.

*Distribution*: Okse Bay Formation, site 1.

*Remarks*: The specimens assigned to *Lophozonotriletes rarituberculatus* are poorly preserved and often corroded.

*Previous Records*: From the Upper Devonian and Lower Carboniferous (*fide*: Playford, 1963a, Part Two, p. 689).

### *Lophozonotriletes sp.A.*

Plate IV, figs. 3, 4.

*Description*: Amb rounded. Trilete; laesurae simple and extending 3/4 radius of the spore body. Wall thin. Cingulate; the cingulum regular in outline (width 4-7µ). Ornamentation of verrucae present on both proximal and distal faces. Proximal verrucae scattered on spore body; distal verrucae more numerous and closely set. The presence of verrucae near and on the cingulum on both proximal and distal sides gives it an irregular lobed appearance. Verrucae 3-5µ in long diameter and up to 3µ in height.

*Dimensions*: (9 specimens): 53µ(61µ)68µ.

*Comparison*: *Lophozonotriletes macrogrumosus* Kedo 1957, p. 33; pl. IV, figs. 21-22, appears similar to this form. A translation of Kedo's description reads:

> "Spores triangular-round. ...perispore thickened... covered with close, uneven, tubercules with flat tops. Fringe...narrow and undulatory. Trilete rays simple".

Kedo gives a size range of 60-105μ, which includes the higher range of the specimens of this work.

L. grumosus var. grumosus Naumova 1953, p. 75; pl. 75; pl. 11, fig. 10, and L. lebedianensis Naumova 1953, pp. 119, 132; pl. 17, fig. 42, and pl. 19, figs. 32-34, are also similar in ornamentation and structure. It is difficult, unfortunately, to make valid comparisons from Naumova's illustrations and descriptions.

Distribution: Escuminac Formation.

Remarks: Miospores similar to Lophozonotriletes sp.A. appear to be common in the late Devonian of Russia and Canada. They have been reported from the Pripyat Depression, White Russia (Kedo, 1955) and from rocks of Frasnian and Famennian age of the Russian Platform (Naumova, 1953).

### Lophozonotriletes spp.

Plate IV, fig. 8.

Description: Amb generally rounded. Trilete; laesurae may be obscured by ornamentation, simple, extending 2/3 to 3/4 of spore radius. Wall relatively thin. Cingulate. Ornamentation of rounded verrucae variously arranged, generally more numerous on the distal face.

Distribution: Okse Bay Formation, sites 1 and 2.

Remarks: A number of specimens with this general morphology occur in samples from Goose Fiord. They are, however, too poorly preserved and too few in number to warrant separation into species. One of the better preserved forms is illustrated.

### Infraturma ZONATI Potonié and Kremp 1954

### Genus CIRRATRIRADITES Wilson and Coe 1940

Type species: *C. saturni* (Ibrahim) S. W. & B. 1944.

### *Cirratriradites*? *sp.A*.

Plate IV, fig. 7.

Description: Amb triangular with slightly rounded apices. Trilete; laesurae ridge-like and extending to the equatorial zona. Wall of varying thickness. Zonate; the zona about 1/4 of the spore radius.

Other Features: Distal ornamentation of small wart-like processes with setose tips, relatively widely spaced. Processes becoming joined by thin cristae as the zona is approached, with the zona being ornamented in this manner. Wall relatively thin for central spore body but becoming thicker at zona-spore body juncture.

Dimensions: (1 specimen): 98µ.

Distribution: Okse Bay Formation, site 2.

Remarks: Only one specimen of this form was found and consequently the morphology is difficult to interpret. The ornamentation appears cristate near the periphery but the processes are separate on the spore body. The darkened spore body-zona juncture may be the limit of an intexine or it may simply be an optical phenomenon.

Staplin and Jansonius (1962) figure a number of spores similar in general organization to this form. Miospores of this type are difficult to interpret without sectioning and without viewing specimens in a number of orientations.

### *Cirratriradiates* *sp.B.*

Plate IV, fig. 11.

Description: Amb broadly triangular. Trilete; laesurae present as distinct ridges extending almost to the edge of the zona. Spore body wall relatively thin but slightly thickened at the juncture with the zona. Zonate; the zona comprising about 1/5 the spore radius; zona thin with a few, widely spaced, radial thickenings; scabrate to punctate. Spore body punctate, although corrosion pits are also present.

Dimensions: (1 specimen): 160µ; zona about 25µ (radial width).

Distribution: Okse Bay Formation, site 2.

Remarks: Zonate forms of the genus *Cirratriradites* are only rarely represented in samples from both Goose Fiord and Escuminac Bay. Most of these specimens are highly corroded and poorly preserved.

## Genus CINGULIZONATES (Dybová and Jachowicz) Butterworth, *et al.*

(*in*: Staplin and Jansonius, 1964)

Type species: *C. tuberosus* Dybová and Jachowicz 1957.

### *Cingulizonates* *boreus* sp. nov.

Plate IV, figs. 5, 6.

Diagnosis: Amb rounded to roundly triangular. Trilete; tetrad mark visible as a prominent ridge extending to the spore periphery. Central body wall relatively thin. Zonate; the zona appearing bizonate; width of zona from 1/3 to 2/5 of total spore radius. Central body ornamentation punctate proximally and distally, and with occasional distal granules. Zona punctate? to granulose.

Other Features: Trilete ridge 2-4µ wide. Inner portion of zona about 2/5 of total zona width, appearing as a darkened region parallelling the amb of the spore. Specimens often corroded so that ornamentation of proximal area and of zona is difficult to determine. The outer margin of the zona may have small echinate extensions (less than 1µ) or be slightly irregular in outline.

Dimensions: (12 specimens): 72µ(90µ)113µ.

Radial width of zona: 7µ(11µ)14µ.

Holotype: AEI-4372.2a(i); 665 - 259; 74µ; zona, 17µ.

Locus typicus: Okse Bay Formation, sites 1 and 2.

Comparisons: *Cingulizonates boreus* sp. nov. is distinguished from *Cirratriradites*? *sp.A*. (this paper) by its rounded amb and lack of cristate ornamentation and distal ornamentation.

Remarks: Staplin and Jansonius (1962) emended *Cingulizonates* Dybová and Jachowicz on the grounds of "...exclusion of species with radially costate zonae and the placing of the emphasis on the cuesta" (Staplin and Jansonius, 1962, p. 105). The author, while agreeing with much of their diagnosis does not think that interpretations of the darkened portion of the zona as a "cuesta" (*vide*: Appendix I) or ridge, and the statement of the presence of an intexine are founded on definite evidence. Although Staplin and Jansonius advocate the use of thin sections and other means of working out the internal structure of "densospores" and related forms, no such evidence is utilized.

The reconstruction of elaborate forms, appearing under a light microscope to have thickenings and an intexine layer has proven to be incorrect in several past cases. Hughes, *et al*. (1962) and Dettmann and Playford (1963) illustrate sections of miospores which, in certain cases, contradict or prove wrong, interpretations made with light microscopes. Richardson's emendation of the genus *Ancyrospora* (Richardson, 1962) is another example.

A more conservative diagnosis of *Cingulizonates* might be in order until further conclusive evidence of the nature of the seemingly bizonate structure is offered, and until sections show the presence of an intexine.

## SPORITES

### *INCERTAE SEDIS*

### Genus EMPHANISPORITES McGregor 1961

*Type species*: *E. rotatus* McGregor 1961.

### *Emphanisporites sp.A*.

Plate IV, fig. 9.

*Description*: Amb roundly triangular. Trilete; laesurae simple, extending almost to the equator. Wall 1μ thick in optical section. Sculpture of proximal, radially disposed thickenings, extending from the proximal pole almost to the equator. Six to eight ribs are present in the interradial area.

*Dimensions*: (2 specimens): 22μ, 24μ.

Comparison: The two specimens found in this study resemble rather closely the species *E. rotatus* McGregor 1961, p. 3; pl. I, figs. 1-4 in ornamentation, number of ribs, and general structure, but are below the size range given by McGregor (33-60µ). More specimens are necessary before a definite assignment can be made to that species.

Distribution: Escuminac Formation.

Remarks: The presence of miospores belonging to the genus *Emphanisporites* has hitherto been unreported in Upper Devonian rocks in Canada. It appears that the morphological characteristic of proximal radial ribs is not confined to the Lower and Middle Devonian (McGregor 1961).

### Genus ANCYROSPORA (Richardson 1960) Richardson 1962

Type species: *A. grandispinosa* Richardson 1960.

### *Ancyrospora ancyrea* (Eisenack) Richardson 1962
### var. *ancyrea* Richardson 1962

Plate V, fig. 1, 2.

1925 Type G2 Lang, p. 257; pl. 1, figs. 16, 17.

1944 *Triletes ancyreus* Eisenack, p. 110 (pars); pl. 2, fig. 2 and pl. 1, figs. 7, 8 (*fide*: Richardson, 1965, pp. 177-178).

Description: *fide*: Richardson 1962, pp. 177-179.

Dimensions: (25 specimens): Spore body 100-165µ; excluding spines.
Inner body 64-145µ.
Spines; 10-50µ.

Distribution: Escuminac Formation.

Remarks: The specimens found at Escuminac Bay conform in all respects to the description of Richardson (1962, pp. 177-179).

*Previous Records*: Old Red Sandstone, Northern Scotland: Lang (1925); Richardson (1962); Eifelian to Givetian. The range of the variety is thus extended by this study into the Upper Devonian.

### *Ancyrospora ancyrea* (Eisenack) Richardson 1962
### var. *brevispinosa* Richardson 1962

Plate IV, fig. 10.

*Description*: *fide*: Richardson 1962, pp. 179-180.

*Dimensions*: (2 specimens): Spore body; 80, 123μ; excluding spines.
Inner body; 67, 109μ.
Spines; 5-15μ.

*Distribution*: Escuminac Formation.

*Remarks*: The ratio of the diameter of the intexine (inner body) to the total spore diameter falls within the range given by Richardson (1962, p. 179). The size of the spines slightly exceeds the limit of 13μ (Richardson, *ibid*.). The specimens are otherwise identical to those described by Richardson.

*Previous Records*: Richardson (1962): Old Red Sandstone, Northern Scotland (Eifelian to Givetian).

### *Ancyrospora ancyrea*? (Eisenack) Richardson 1962

Plate V, figs. 3, 4.

*Description*: Amb rounded. Trilete; laesurae distinct, ridge-like, extending almost to the periphery of the spore. Wall relatively thin. Exoexine(?) variably prolonged into a pseudoflange; intexine of central body(?) circular. Distal ornamentation of grapnel-tipped spines with broad bases, narrowing halfway along their length.

Dimensions: (1 specimen): Spore body 134μ; excluding spines.
Inner body 66μ.
Spines 10-25μ; bases 8-14μ.

Comparison: The specimen agrees in all respects with the diagnosis of *A. ancyrea* (Eisenack) Richardson 1962, pp. 176-177, except that the central body (intexine?) is distinctly circular rather than subtriangular or triangular. It conforms most closely in spine length and ratio of central body to the total spore diameter to the form *A. ancyrea* var. *ancyrea*.

Distribution: Escuminac Formation.

Remarks: Richardson (1962, p. 183, text-fig. 9) has outlined a number of morphological variations within the species *Ancyrospora ancyrea*. These include a change in the inner body (intexine)/ total spore diameter ratio and in the length of spines. The specimen here described may represent another variation, that of a circular intexine layer as opposed to the usual subtriangular shape shown by Richardson's specimens.

### Spore Type A

Plate VI, fig. 5.

Description: Amb triangular. Trilete; laesurae, ridge-like, extending to the spore periphery. Wall of inner region moderately thick, and markedly thickened at junction of spore body and zona. Zona thin and variable in width (about 1/3 spore radius) with eight grapnel-tipped projections at the periphery. Projections wide at the base (16μ) narrowing steadily to 3μ below the tips. Ornamentation of inner region scabrate; zona scabrate to vermiculate(?).

Dimensions: (1 specimen): Spore body 180μ.
Projections 16-22μ.

Distribution: Okse Bay Formation, site 1.

Remarks: This specimen resembles the genus Cirratriradites in having a wide, thin zona and triangular shape. No species of this genus, however, have been reported as having projections of the zona.

### Spore Type B

Plate VI, fig. 6.

Description: Amb rounded. Trilete mark not visible. Wall thick. Structure of spore body obscured. Periphery of spore with closely spaced processes. Each process with a rounded, sub-conical base from which a relatively thin, grapnel-tipped process extends. Often the processes are broken off, leaving only the conical base. Total length of processes up to 85μ; conical bases about 1/4 of total length. Base of the cone very broad, narrowing to half the basal width where the slender process arises. One specimen shows a flange-like structure developed on one side which extends 55μ and has four or five rod-like thickenings.

Dimensions: (2 specimens): Spore body 192μ, 198μ; excluding spines.

Distribution: Escuminac Formation.

Remarks: Unfortunately the specimens available do not reveal the structure of the spore body or the nature of the flange-like structure. The specimens bear some resemblance to species of Archaeotriletes figured by Naumova (1953) but are much larger. The flange-like structure is somewhat similar to that of Hystricosporites corystus Richardson 1962, pp. 173-174; pl. 25, figs. 1-2.

### Spore Type C

Plate VI, fig. 1.

Description: Amb round. Trilete; laesurae simple, extending 3/4 of spore radius and partly obscured by the ornamentation. Wall about 3μ thick in optical section. Ornamentation of thin processes, relatively uniform in height (5-7μ) and connected by thin cristae, apparently in pairs. The cristae appear as webbings between the processes and are generally one-half their height. The processes are parallel-sided and have rounded tips. Pairs of processes are spaced irregularly over the proximal face and are visible on the equator.

Dimensions: (1 specimen): 48μ; excluding processes.

Distribution: Okse Bay Formation, site 1.

### Spore Type D

Plate VI, fig. 2.

Description: Amb elongate, rounded, elliptical. Apparently monolete; laesure simple, extending the length of spore body. Wall relatively thick. Ornamentation scabrate. Spore appears cingulate; the cingulum thick and uniform in width (about 8µ) and scabrate.

Distribution: Okse Bay Formation, site 1.

Dimensions: (1 specimen): 66 x 50µ.

Remarks: Only one specimen was found of this type. It may represent an aberrant monolete form of one of the species of *Lophozonotriletes* described in this paper. Playford (1962b) has described such monolete aberrant forms for the miospore species *Murospora aurita*.

### Spore Type E

Plate VI, fig. 4.

Description: Amb roundly triangular. Trilete mark not visible. Wall thin. Ornamentation of long, thin, untapering processes with rounded apices (10-15µ long; 1-2µ wide).

Dimensions: (1 specimen): 96µ.

Distribution: Escuminac Formation.

Remarks: The specimen described here is similar to the genus *Acanthotriletes* except that the processes are bluntly rounded rather than sharply tapering.

### Spore Type F

Plate VI, fig. 3.

Description: Amb round. Trilete mark not visible. Wall folded and relatively thick. Ornamentation of long, bluntly rounded processes (10-15µ long and broadening to a basal width of 3-6µ).

Dimensions: (1 specimen): 87µ; excluding processes.

Comparison: This specimen is similar to 'Spore Type D' of Hoffmeister, Staplin, and Malloy, 1955b, p. 398; pl. 39, figs. 13, 16, in ornamentation and size.

Distribution: Escuminac Formation.

### Spore Type G

Plate VI, fig. 7.

Description: Amb ovoid. Tetrad mark not observed. Wall thin. Surface of body granulate. Widely spaced processes, with base slightly wider than tip. Tip of process curved almost at right angles and tapering to a sharp point. Length of processes 10 to 30µ.

Dimensions: (1 specimen): 62µ; not including processes.

Distribution: Okse Bay Formation, site 2.

Remarks: The placing of this specimen in Sporites is arbitrary.

### Anteturma POLLENITES R. Potonié 1931

### Turma SACCITES Erdtman 1947

### Subturma MONOSACCITES (Chitaley 1951) Pot. & Kr. 1954

### Infraturma TRILETESACCITI Leschik 1955

### Subinfraturma INTRORNATI Butterworth and Williams 1958

### Genus ENDOSPORITES Wilson and Coe 1940

Type species: *E. ornatus* Wilson and Coe 1940.

### *Endosporites? granisaccatus sp. nov.*

Plate VII, figs. 1, 2.

Diagnosis: Amb round. Trilete; laesurae simple, but often slightly folded about commissures; extending to the edge of the central spore body. Wall thin. Monosaccate; the saccus thin-walled, extending 3-8µ beyond the central body. Ornamentation of central body scabrate; saccus granulose to occasionally minutely echinate.

*Other Features*: Spore outline often irregular due to folding. Laesurae may appear thickened due to folding about the commissure. Ornamentation of saccus uniformly spaced and densely packed.

*Dimensions*: (13 specimens): Central body: 42μ(48μ)57μ.
Total diameter; 48μ(58μ)70μ.

*Holotype*: AG-3.3(i) *1048 - 352*; 48μ/56μ.

Description as in diagnosis, except ornamentation of saccus finely granulose.

*Paratype*: AG-3.3(ii) *764 - 404*; 57μ/70μ.

Description as in diagnosis, except ornamentation of saccus with granules.

*Locus typicus*: Escuminac Formation.

*Comparison*: *Endosporites*? *granisaccatus* sp. nov. is distinct from *E. micromanifestus* (*sensu* Hacquebard 1957, p. 317; pl. 3, fig. 16) in having definite external ornamentation on the saccus and a larger spore body/saccus ratio. It is distinct from *E. micromanifestus* (*sensu* Playford 1963a, p. 652; pl. 93, figs. 17, 18) in the much larger spore body/saccus ratio and the more pronounced external saccus ornamentation.

*Remarks*: *Endosporites*? *granisaccatus* sp. nov. is tentatively included in the genus *Endosporites*, although that genus is characterized as having infra-ornamentation on the bladder or saccus. It appears that the term infra-ornamentation has been used differently by various authors. Playford (1963a) figures specimens classified as *E. micromanifestus* which have small but distinct ornaments on the outer surface of the saccus. Infra-ornamentation in this sense would then mean very small ornamentation. Hacquebard (1957) also figures *E. micromanifestus*, and from his photographs, the saccus appears almost laevigate or with an infra-ornamentation in the sense of being on the inner surface of the saccus.

Butterworth and Williams (1958, pp. 384, 388) instituted the subinfraturmae Intrornati and Extrornati, defining the Intrornati to include monosaccate spores without "extra-ornamentation" on the saccus and the Extrornati to have miospores with "external ornamentation in part without recognizable infra-ornamentation" on the saccus. These subinfraturmae are mutually exclusive categories if the terms infra- and extra-ornamentation are understood in the sense of Hacquebard (1957). As well, Butterworth and Williams have restricted the genus *Endosporites* to include only those spores with lack of external bladder ornamentation, by implication. Thus, *E. micromanifestus* (*sensu* Playford 1963a) and *E*? *granisaccatus* would have to be referred to another genus and be placed in the Extrornati. Hughes and Playford (1961, p. 42) note this in connection with *E. macromanifestus*, Hacquebard 1957 but do not extend this view to *E. micromanifestus*, although the original description of this species by Hacquebard (1957, p. 317) states that it is, "identical to *E. macromanifestus* but smaller".

The original description of the type species *E. ornatus* by Wilson and Coe (1940, p. 184) mentions that the outer wall (of the saccus) is "granulose". If this refers to external ornamentation, then *Endosporites* would have to be relocated in the Extrornati as defined by Butterworth and Williams and would include, by implication, only those types with minor external ornamentation, A new genus would then have to be proposed to include species such as E. micromanifestus (sensu Hacquebard).

Further comment would have to await the examination of relevant type specimens and clarifications of terms used by various authors. The author, however, wishes to point out the existence of the discrepancy in terminology.

### Endosporites sp.A.

Plate VII, fig. 3.

Description: Amb round. Trilete; laesurae apparently compounded or perhaps folded; margin 2-3µ wide; laesurae extend just beyond the central body. Central body wall thin. Monosaccate; the saccus very thin, laevigate, and appearing microrugulate because of numerous small, irregular folds. Central body ornamentation indistinct.

Dimensions: (8 specimens): Total spore diameter: 38µ(44µ)49µ.

Saccus extends 1-3µ beyond the central body.

Comparison: Radialetes Playford 1962 is alete, and has definite thickenings rather than folds.

Distribution: Escuminac Formation.

Remarks: The interpretation of Endosporites sp.A. is difficult because the saccus is closely appressed to the central spore body. The folds at first appear to be radially disposed but are actually irregular. These folds also obscure the central body structure.

## Monosaccites Type A

Plate VII, fig. 5.

Description: Amb rounded, occasionally ovoid. Trilete; laesurae indistinct, visible on one specimen; simple, extending 2/3 radius of the inner spore body. Inner body wall, 1-2µ in optical section. Monosaccate; saccus of variable extent, generally 1/5 but as much as 2/5 of total spore radius. Saccus ornamented with punctae or infragranuli(?) (*sensu* Hacquebard, 1957). Inner body ornamentation obscured by saccus ornament.

Dimensions: (5 specimens): Total diameter; 54µ(56µ)58µ.

Comparisons: The specimens are similar to *E.*? *granisaccatus* (this paper), but lack a distinct trilete mark and external granulose bladder ornamentation.

Distribution: Escuminac Formation.

## Monosaccites Type B

Plate VII, fig. 6.

Description: Amb distinctly triangular, but inner body circular. Trilete mark not visible. Wall of inner body apparently thickened about the periphery to 5µ, otherwise thin. Monosaccate; saccus triangular in outline and laevigate; thrown into irregular, small folds giving the surface a pseudo-reticulate appearance.

Dimensions: (1 specimen): Inner body 38µ.
Outer body (total diameter) 49µ.

Distribution: Escuminac Formation.

### Monosaccites Type C

Plate VII, fig. 7.

Description: Amb ovoid. Tetrad mark not visible. Central body wall 1µ thick. Saccus variably extended from central body; ornamented with broad, low, irregularly anastomosing ridges, often enclosing small lacunae similar in appearance to those of *Convolutispora tuberculata* Hoff., Stap., and Malloy.

Dimensions: (1 specimen); total diameter: 61µ.

Distribution: Okse Bay Formation, site 1.

## Subinfraturma EXTRORNATI Butterworth and Williams 1958

### Genus RHABDOSPORITES Richardson 1960

Type species: *R. langi* (Eisenack) Richardson 1960.

### *Rhabdosporites langi* (Eisenack) Richardson 1960

Plate VII, fig. 4.

1925 Type B Lang, p. 256; pl. 1, figs. 3-6.

1944 *Triletes langi* Eisenack, p. 112; pl. 2, fig. 4.

1960 *Rhabdosporites langi* (Eisenack) Richardson, p. 54; pl. 14, figs. 8-9 and text-figs. 4, 6B.

Description: Amb ovoid to rounded. Trilete; laesurae simple, extending to the periphery of the spore body; apparently compound, but more probably, parallel folds in the saccus give this appearance. Central body wall thin, but thickened(?) about the periphery of the central body. Monosaccate; saccus completely encloses the central body; saccus ornamented with densely packed pila or setulae about 3µ in height and 1µ wide. Occasionally the rods are more conical in outline. Saccus thin-walled and folded.

Dimensions: (3 specimens): Total diameter: 162μ,163μ,170μ.
Inner spore body: 110μ,108μ,130μ.

Comparison: Rhabdosporites langi compares favourably with specimens of R. langi (Eisenack) Richardson 1960, except that one specimen of this study has ornamentation more cone-like than rod-like. The three specimens also show a thickening of the central body unlike the specimens described by Richardson.

Distribution: Escuminac Formation.

### Monosaccites Type D

Plate VIII, fig. 1.

Description: Monosaccate, the saccus trianguloid; central body roundly subtriangular. Trilete; laesurae compound, the margin about 4μ wide; laesurae extend almost to the periphery of the central body and are obscured somewhat by folds in the saccus. Central body and saccus thin-walled. Saccus ornamented with densely packed echini, sharply pointed, and of uniform height (about 1μ).

Dimensions: (1 specimen): Total diameter; 148μ.
Central body; 93μ.

Distribution: Escuminac Formation.

### Monosaccites Type E

Plate VII, fig. 8.

Description: Amb circular. Trilete; laesurae simple but appearing compound because of folds about the commissures; laesurae extend almost to the periphery of the saccus. Central body wall thin, apparently laevigate. Saccus thin-walled and ornamented with densely packed granuli (½ to 1μ in diameter and about 1μ in height).

Dimensions: (1 specimen): Total diameter; 183μ.
Central body; 122μ.

Comparison: This specimen conforms in all respects to the description of *Endosporites macromanifestus* Hacquebard 1957, p. 317; pl. 3, figs. 14-15 except that it is larger in size and has distinct extra-ornamentation (*sensu* Butterworth and Williams 1958) of granuli on the saccus.

Distribution: Escuminac Formation.

## INCERTAE SEDIS

### Group ACRITARCHA Evitt 1963

Diagnosis: Unicellular or apparently unicellular microfossils consisting of a test composed of organic substances and enclosing a central cavity. Shape of the test spherical, ellipsoidal, discoidal, elongate or polygonal; test surface smooth, granular, punctate or perforate. Spines or other processes, raised ridges (crests), flanges, wings or other outgrowths present or absent; where present, distributed regularly or irregularly. Inner capsule present or absent; where present, connected to test by varied means or lacking such a connection. Shell opens by rupture, splitting, or formation of a simple circular pylome. Rarely, a number of tests loosely associated in a chain.

### Subgroup SPHAEROMORPHITAE Downie, Evitt and Sarjeant 1963

Diagnosis: Acritarchs having a spherical to ellipsoidal shell lacking an inner body. Surface granular, smooth, punctate or perforate, but not otherwise ornamented. Without observed opening, with a simple circular pylome, or opening by splitting.

Genus LEIOSPHAERIDIA (Eisenack 1958) Downie and Sarjeant 1963

Type species: *L. baltica* Eisenack 1958.

Diagnosis: Spherical to ellipsoidal bodies without processes, often collapsed or folded, with or without pylomes. Wall granular, punctate or unornamented; thin. Without division into fields and without transverse or longitudinal furrows or girdles.

*Leiosphaeridia orbiculata* (Staplin) Downie and Sarjeant 1963

Plate VIII, figs. 2, 3.

1961 *Protoleiosphaeridium orbiculatum* Staplin, p. 405; pl. 48, fig. 12.

1963 *Leiosphaeridia orbiculata* (Staplin) Downie and Sarjeant, p. 95.

Description: Amb rounded to slightly ovoid. Wall up to 1μ thick in optical section and folded to unfolded. Wall laevigate. No pylome evident.

Dimensions: (14 specimens): 21μ(29μ)41μ.

Comparison: The specimens of this paper agree in all respects with those called *Protoleiosphaeridium orbiculatum* (Staplin, 1961, p. 405).

Distribution: Escuminac Formation.

Discussion: Downie and Sarjeant (1959, p. 88) point out that *Protoleiosphaeridium* (cf. Staplin, 1960) may be retained as a valid subgenus of *Leiosphaeridia* to include thin-walled forms having a diameter of less than 50μ. Staplin's view (1960, pp. 403-404) that forms with a pylome should be excluded from the genus *Leiosphaeridia*, according to the original diagnosis of Eisenack (1958), is based on a misinterpretation of the diagnosis. This is made clear by Downie and Sarjeant (1963, p. 88).

The author thinks that arbitrary subdivision of a form genus by size, despite a lack of morphological difference, and especially when no marked size classes exist, is unnecessary. Thus, the taxonomic practice of Downie and Sarjeant (1963) and of Norris and Sarjeant (in press) has been followed.

### *Leiosphaeridia microgranulifera* (Staplin) Downie and Sarjeant 1963

Plate VIII, fig. 4.

1961 *P. microgranifer* Staplin, p. 405; pl. 48, fig. 4.

1963 *L. microgranulifera* (Staplin) Downie and Sarjeant, p. 95.

*Description*: Amb round to irregularly ovoid due to folding. Wall thin and often highly folded. Ornamentation granulose.

*Dimensions*: (5 specimens): 34µ(35µ)37µ.

*Comparison*: The specimens of this paper are identical to those described by Staplin as *Protoleiosphaeridium microgranifer*, except for the smaller size range exhibited.

*Distribution*: Escuminac Formation.

*Previous Records*: Upper Devonian: Woodbend Fm., Duvernay mem., Edmonton, Alberta.

# DISCUSSION

## MORPHOLOGICAL CHARACTERISTICS AND MIOSPORE ASSEMBLAGES

### Valuation of Hypotheses

A number of hypotheses have been proposed earlier (vide: pp. 14-17) in relation to the method of tabulation of morphological features of individual miospores. It is now possible to discuss these with respect to the data provided by several miospore assemblages.

In discussing the hypotheses, use will be made occasionally of evidence provided by the statistical tests of chi-square and significance of the difference of arithmetic means (the T-test). While the statistical evidence may support the hypotheses, it cannot be used to substantiate interpretations of the hypotheses. The statistical evidence may be said not to be in conflict with the hypotheses.

Several types of assemblages are available for discussion. Miospore assemblages from Goose Fiord and Escuminac Bay may be considered as complete assemblages; in addition, the sites from Goose Fiord provide two sub-assemblages. Variations within a relatively small vertical stratigraphic section containing a similar assemblage, therefore, may be considered.

Several of the hypotheses concern the relation of miospore species and tabulation of morphological characteristics independent of species. Acceptance of these hypotheses would constitute a rational basis for continuing the use of the tabulation method in conjunction with the miospore species method. Because of this, it is appropriate to consider such hypotheses first.

It has been proposed that variations within miospore species are obscured by the necessity of grouping morphological characteristics in defining form species. A tabulation of these morphological characteristics independent of the species concept might allow such variations to be expressed.

Morphological variation within miospore species is evident in assemblages from Goose Fiord. *Retusotriletes greggsi*, the dominant miospore species at both sites, is characterized by a wide variation in ornamentation. The variety of ornamentation occurs along with the constant feature of proximal curvaturae (TABLE 3); the ornamentation bears no relation to size or wall thickness. It does not seem advisable, therefore, to divide this species into several taxa with ornamentation as the only criteria. These variations, however, may be tabulated in absolute abundance by the morphological tabulation method (Text-fig. 6). *Lophozonotriletes crassirugulatus* sp. nov. may be taken as another example. In this species, both rugulae and verrucae may occur on the distal face. Although the rugulae predominate, the occasional occurrence of verrucae are recorded by the tabulation method. In samples from Escuminac Bay, specimens of *Punctatisporites pseudobesus* occasionally possess a contact area; this feature is not considered sufficient to exclude these specimens from the species as defined by Playford (1962b). The occasional occurrence of this feature is, however, recorded in the tabulation counts and contributes to the character of the whole assemblage. Other examples could be cited.

These examples suggest acceptance of the hypothesis. The tabulation method does allow expression of variation within species. In addition, it allows this variation to be expressed in proportion to its frequency of occurrence.

Miospore specimens occurring rarely, and those specimens that cannot be assigned more accurately than the generic, or higher, level (e.g.: turma or infraturma level) have been suggested as contributing to the total morphological character of the assemblage. The implication is present in this hypothesis that such forms would necessarily be ignored in assessing an assemblage on the basis of distinct miospore species.

Text-fig. 9 shows the results of a count of 150 miospores for each sample and gives values for the occurrence of distinct species, representatives of genera unassigned to species, and forms assigned to turmae or infraturmae. The presence of a miospore in a sample, though not in the actual count, is denoted by an "X". The two sites at Goose Fiord may be used as an example. For these two sites, a total of 1930 miospores have been counted. Of these, 98 specimens, or 5% of the total, are unassigned to a species. This fraction would not be included in a standard survey of distinct species. Some examples of this neglected fraction may be mentioned. It includes miospores with a perine layer. These constitute about 0.5% of the assemblage. Miospores with triangular shape and concave interradii constitute another 0.5% of the total count (Text-fig. 6). Other examples may be noted: monosaccate specimens in the Goose Fiord assemblage; and specimens with curvaturae in Escuminac Bay samples.

Tabulation of the morphological characteristics of these miospores thus ensures a more complete survey of the morphological variation present in an assemblage and in proportion to its occurrence.

Correlation of miospore species with morphological characteristics of the assemblage in the same geological unit depends on a consideration of the hypothesis discussed above. To the extent that unassigned specimens comprise the assemblage, then to a corresponding degree, morphological characteristics will not correlate with the miospore species assemblage in the same geological unit. The variation from bed to bed at Site One, Goose Fiord, (Text-fig. 7) in number of miospores with punctate, scabrate, and rugulate ornamentation, not only can be correlated partly with variation within species of Retusotriletes, but also with fluctuating numbers of unassigned forms of Punctatisporites, Lophozonotriletes, and other forms.

On the basis of the preceding discussion, the three hypotheses relating miospore species and morphological characteristics of assemblages may be accepted. There is a rational basis for continuing the tabulation method independently of the miospore species method.

The preceding conclusions dealing on relation of miospore species and the tabulation method were first suggested as working hypotheses. A further conclusion of this type is suggested by examination of the data. Reference to Text-fig. 7 shows that in all individual samples, certain features of ornamentation, shape, and structure are prominent and certain other features are accessory. Sample AEI-4367 contains miospores which are dominantly echinate in ornamentation, with accessory ornamentation of granuli or punctae. The miospores are generally round, radial, with curvaturae, simple lips and relatively thin-walled. In sample AEI-4370, miospores are also predominantly ornamented with echini, but show accessory ornamentation of a reticulate, scabrate, or punctate type. The structure and shape remain essentially unchanged. Other examples could be demonstrated in other individual beds.

This suggests that individual units within a sequence may be characterized by the morphological characteristics of the contained assemblage of miospores. This is not to say that such characteristics may be used to correlate units stratigraphically. The use of this method in correlation would depend on how far such assemblage characters extended laterally. This problem has not yet been investigated.

If individual beds may be characterized in this manner, then it seems reasonable to extend this to complete assemblages. Miospores from Goose Fiord sites are rounded, occasionally triangular, radial, and generally thin-walled with curvaturae and simple laesurae. Ornamentation is predominantly echinate with accessory ornamentation of a granulate, punctate, or scabrate type. Miospores from Escuminac Bay, in contrast, are only rarely triangular in shape and rarely possess curvaturae. Reticulate forms are absent and laevigate forms assume more importance. The percentage of rugulate forms is considerably reduced. Like miospores from Goose Fiord, however, specimens from Escuminac Bay are generally round, radial, thin-walled forms with simple laesurae and predominantly echinate.

Thus, the tabulation of morphological characteristics of individual miospores in assemblages permits a detailed and precise qualitative summation of the similarities and differences in morphological characteristics between assemblages, and the dominant characters within an assemblage.

Two hypotheses remain to be discussed. The first concerns fluctuation in the total number of morphological characteristics within geological units containing a similar miospore assemblage. The second concerns changes in the morphological character of two assemblages in relation to changes and similarities in the occurrence of miospore species.

Fluctuation in number of different morphological features within an assemblage may be examined by reference to counts of miospore characteristics for different beds within the stratigraphic interval of the assemblage. The data obtained from the miospore assemblages of individual beds at Site One, Goose Fiord, (Text-figs. 7, 8) provide examples. Reference to these text-figures shows that from 21 to 32 out of a possible 36 characteristics have been recorded from samples within the sequence of beds containing the assemblage. Thus a numerical basis for the hypothesis exists. There appears to be no correlation between the number of distinct miospore species and the number of different characteristics present in the same geological unit (Text-fig. 8). The possible palaeoecological significance of this variation will be discussed in a later section.

The remaining hypothesis proposed earlier (vide: p. 16) suggested that some palaeoecological significance might be attached to changes in total morphological character in relation to changes in the occurrence and type of miospore species.

Two alternatives, each with two possibilities, are contained in this hypothesis. Firstly, there may be a significant difference (statistically) in ornamentation, size, shape, and structure for two assemblages. Such a change may or may not be reflected in a change in the total numerical occurrence of miospore species. Secondly, there may be no significant change in the morphological characteristics of two assemblages, while there may or may not be a significant change in the occurrence of miospore species.

The number of variables involved in this hypothesis has made the use of a non-parametric statistical test desirable. The statistical methods used in connection with this hypothesis have been described earlier (pp. 40, 44, 45). Reference to TABLE 1 (p. 44) shows that chi-square values obtained from comparison of the subsections of miospore morphology from both pairs of assemblages (Goose Fiord and Escuminac Bay; Goose Fiord, Sites One and Two) are highly significant. The deviations between the calculated and theoretical values of chi-square would be expected much less than once in a thousand (Fisher and Yates, 1953, p. 41). The null hypothesis of no significant difference must be rejected. There is in fact a highly significant statistical difference between the two pairs of assemblages with respect to the subsections of ornamentation, shape and structure.

Arithmetic mean diameters of miospores from the two pairs of assemblages were also tested for significant difference using the T-test (pp. 45, 46). The results of this test (TABLE 2) indicate that the differences between the arithmetic means of the diameters of miospores from the two pairs of assemblages are highly significant. Such a difference, if the two means were considered as coming from the same population of miospores, could be expected much less than once in a thousand (Fisher and Yates, 1953). The null hypothesis must be rejected. The samples of miospores from which the respective pairs of arithmetic means were drawn could not have come from the same population of miospores with respect to size (long diameter).

Statistical considerations thus indicate that the size, shape, ornamentation, and structure of miospores from Goose Fiord and Escuminac Bay and from the two sites at Goose Fiord, are significantly different.

Examination of Text-fig. 10 shows that only one specimen of one species exists in common between the Goose Fiord and Escuminac Bay assemblages. The significant difference in morphological characteristics is thus to be expected in this case. If the morphological characteristics had shown no significant difference, the result would have been unexpected.

Where miospore species are similar in number and type, the morphological characteristics of the assemblages might be expected to be similar. The sites at Goose Fiord show a similar species assemblage, but have a significantly different set of morphological characteristics. If the numerical occurrence of the distinct miospore species and species designates can be shown to differ significantly, then the result may be explained on this basis. If this is not the case, then this is in fact an instance of the second possibility of the first alternative of the hypothesis.

A chi-square test for significant difference of the numerical occurrence of miospore species at the two sites is appropriate. Chi-square as used here is essentially a test of homogeneity with respect to the numerical occurrence of miospores species in two sub-assemblages. The null hypothesis is proposed that there is in fact no significant difference in the numerical occurrence of miospore species at the two sites. A probability level of 0.05 (5%) is appropriate for this test. Certain species (_Leiotriletes_ _sp.A_. and _L_. _sp.B_.) will have to be grouped in order to keep the numerical content of individual cells greater than five (Mills, 1957).

The occurrence of each species at the sites, the chi-square values for each cell, and the calculated and theoretical values of chi-square are included in TABLE 4.

The results indicate that there is no significant difference in the abundance of miospore species at the two sites. The null hypothesis must in fact be accepted. Such a calculated value of chi-square (at 11 degrees of freedom) could occur as a result of chance alone as much as 10% of the time (Fisher and Yates, 1953, p. 41).

For the two sites at Goose Fiord, the second possibility of the first alternative of the hypothesis holds. There is a significant difference in ornamentation, shape, structure and size (*vide*: p. 110) of the miospores at Site One compared with those at Site Two, but there is no significant difference in the occurrence of miospores and species designates in the two sub-assemblages.

TABLE 4. Numerical occurrence of distinct miospore species and species designates at Goose Fiord, Sites One and Two. The chi-square values (calculated) are shown for each individual cell. Some species are combined for the test.

| Miospore Species | Number of Specimens | | Chi-square values (calculated) |
|---|---|---|---|
| | Site One | Site Two | |
| *Leiotriletes sp.A.* | 4 | 2 | 0.007 |
| *Leiotriletes sp.B.* | - | - | ----- |
| *Punctatisporites tenuis* | 12 | 2 | 1.775 |
| *Punctatisporites lunaris* | 4 | 4 | 0.145 |
| *Punctatisporites sp.A.* | 3 | 2 | 0.417 |
| *Retusotriletes greggsi* | 937 | 454 | 1.747 |
| *R. semizonalis* | 258 | 90 | 4.303 |
| *Verrucosisporites certus* | 9 | 3 | 0.191 |
| *Apiculatisporis sp.A.* | 2 | 3 | 2.143 |
| *Dictyotriletes trigonalis* | 10 | 9 | 2.363 |
| *Convolutispora tuberculata* | 4 | 1 | 0.417 |
| *Lophozonotriletes crassirugulatus* | 9 | 0 | 2.800 |
| *L. raritiberculatus* | - | - | ----- |
| *Cingulizonates boreus* | 6 | 4 | 0.476 |
| TOTALS | 1258 | 574 | 17.691 |

Number of degrees of freedom: 11

Chi-square value for 11 degrees of freedom at 5%: 19.675

Note: *Leiotriletes sp.A.* and *L. sp.B.* combined.
*Lophozonotriletes crassirugulatus* and *L. rarituberculatus* combined.

## Morphological Tabulation and Devonian Plant Palaeoecology

The conclusions presented in the preceding section are practical ones, based solely on numerical data. They suggest certain theoretical interpretations and implications of a palaeo-ecological nature.

The morphological tabulation method allows expression of the type and frequency of variation within distinct species. These variations, as in Retusotriletes greggsi, may not be marked enough, or consistent enough, to warrant the separation of a species into several new form species. Perhaps, however, these variations represent the presence of more than one natural species, or of two or more closely related species. While the presence of such forms would not be suggested by the species method, it would be emphasized by the tabulation method. The variations may represent the influx or emigration of parent plant forms in the vicinity of the depositional site.

Rare and unassigned specimens have been shown to contribute to the overall character of the morphology of a miospore assemblage. This conclusion suggests certain palaeoecological interpretations. These rare forms perhaps represent miospores of plants not growing in the immediate vicinity. For example, (Text-fig. 6) the cingulate, zonate, and saccate forms which are present in the Goose Fiord assemblage are not characteristic of the miospore assemblage. They contrast with the less structurally complex forms like Punctatisporites and Leiotriletes. Because the miospore assemblage at Goose Fiord is dominated by two closely related species, it is suggested that most of the miospores in the assemblage were transported relatively short distances. Thus, these rare forms might be interpreted as being the miospores of plants growing some distance from the site of deposition, representatives of parent forms inhabiting upland regions (Chaloner, 1958a). Two other interpretations of these rare miospore specimens are possible. Such miospores may represent parent forms whose dispersal mechanism was relatively inefficient, or whose spores were not so easily transported by wind. Finally, they may also represent, of course, miospores of parent plants that produced relatively few spores compared to the plants that produced Retusotriletes greggsi. There is not enough information available to suggest which of these interpretations is the most probable.

Tabulation of morphological characteristics of individual miospores allows a detailed and precise summation of similarities and differences in morphological characteristics between assemblages and of dominant characteristics within an assemblage. The tabulation method thus provides a way, independent of species, of assessing morphological trends within related sub-assemblages and between assemblages. These morphological trends may have their origin in palaeofloristic changes in the parent flora. The implication is especially important with regard to individual geological units within a section. Changes in the dominant characteristics within these units as the stratigraphic interval is traversed may reflect fluctuations of parent floras in the region.

Fluctuation in the total number of different morphological features, in units of a stratigraphic interval containing the same miospore species, has been demonstrated at two sites at Goose Fiord. Assessment of this variation in relation to Devonian plant palaeoecology is difficult. Radforth and Wilkinson (1959, p. 33) suggest, that for miospores (of Tar Point, Quebec), differences in pattern arise from differences in biological trend. If this is so, then the variation in total number of characteristics at Goose Fiord sites may mean a variation in complexity of the parent plant assemblage as reflected in the elaboration of their spores. Relatively simple, punctate miospores are common in sample AEI-4367, while more elaborate, cingulate miospores are present in sample AEI-4369. The variation may arise from elaboration of the parent flora at the site, but may also be introduced by miospores occurring rarely and suggested as being representatives of forms not growing near the deposition site. Such elements, for example, are introduced in sample AEI-4369 by the presence of monosaccate forms.

It has already been shown that the number of distinct miospore species in a geological unit at a site does not correspond to the number of different morphological features (Text-fig. 8). This would tend to support the view that complexity in the miospore rather than variation in species numbers is the determining factor in the fluctuation. Confirmation of these interpretations, however, must await more positive evidence. Because an abstract principle is involved, and not a direct comparison, a study of the relation of the complexity in a region, of modern plants, to that of their spore morphology might be useful in the solution of this question.

The relationship of miospore species and morphological characteristics between two assemblages has been shown to have two aspects (vide: pp. 108, 109). Palaeoecological interpretations of these aspects may now be explored.

If the morphology and species show significant change in two widely separated assemblages (such as those at Goose Fiord and Escuminac Bay, Quebec), then it is likely that this indicates a definite floristic difference in the parent flora. The reasons for this difference may be several and complex, probably palaeogeographic and palaeoclimatic. If this should occur within an assemblage (a condition not represented in assemblages discussed in this work), it may reflect an incursion of new parent forms into the vicinity of the depositional site, replacing the old forms and occupying a similar or changing ecological niche.

If the species are similar in numerical occurrence and the morphological characteristics are significantly different, other interpretations are suggested. Such an occurrence has been demonstrated at Sites One and Two of Goose Fiord. At these sites, there may have been a change in the parent flora not reflected by the species concept. If so, this represents a more refined palaeoecological indicator of palaeofloristic changes. The gradual incursion of new forms into a region would be visible first in morphological tabulation counts and then become evident in form species.

Other possibilities are not represented in assemblages described in this study, but their palaeoecological significance may be profitably discussed. Assemblages may occur having similar species and similar morphology or with similar morphology but different species. In the first instance, which might be the one expected where species are similar, parent floras are probably very much alike. The second case offers more possibilities. If a microflora is composed of a number of species of Punctatisporites, for example, there is little lattitude for variation in morphological characteristics (round, scabrate, punctate). If the contention of Radforth and Wilkinson (1959) is supported, then this may indicate little specialization in the parent floras. This lack of specialization might be reflected in few different parent genera and species or in a number of closely related genera and species occupying the same ecological niche. These possiblities as well as the two represented in the assemblages are synopsized in TABLE 5.

TABLE 5. Synopsis of the relation between morphological features of individual miospores and miospore species in different miospore assemblages.

| SPECIES | MORPHOLOGY | |
|---|---|---|
| | SIMILAR | DIFFERENT |
| SIMILAR | Parent floras probably quite similar. | Impending changes in parent floras not suggested by the species concept. |
| DIFFERENT | Little change in specialization of parent flora. Forms may be different in the two assemblages. | Floras probably totally different. Reasons varied and complex (Climatic, geographical). |

## Objections to Palaeoecological Interpretations

Certain objections, some fundamental, others secondary, may be made to the interpretations of palaeoecological significance. One of the fundamental objections arises from the relation of the miospore to parent forms. It has been emphasized previously that the botanical affinities of the miospores are not known. This also means that nothing is known about the habits and taxonomic positions of the parent plants. Further, nothing is known about the habitat of the parent flora. In view of this, may the use of miospores as palaeoecological indicators be considered valid?

No conclusion is drawn or interpretation made about the habit, habitat, or taxonomic position of the parent floras on miospore evidence alone. The miospores have been considered consistently as abstract indicators of palaeofloristic changes; this view is in perfect accord with the concept of palaeoecology presented throughout the thesis. In the sense, therefore, that Devonian plant palaeoecology has been outlined, the attempt is valid.

A second fundamental objection concerns the interpretations of differences in frequency of occurrence of morphological characteristics. Because the parent plants are unknown, there is no way of being certain of the numbers of miospores produced by these plants. The varying frequencies of occurrence of miospore species, therefore, may be a result of both different numbers of spores being produced by parent plants and the numbers of these plants in the vicinity of the depositional basin. The frequency of morphological characteristics depends to some extent on the numbers of the various miospore species present. Thus the tabulation method presents a misleading picture. To formulate hypotheses on this basis and suggest palaeoecological interpretations is therefore an invalid practice.

This objection would be a serious one if statements were made about numerical occurrence of parent floras. It would also be valid if numerical results of morphological counts were used to suggest changes of a quantitative nature in floras represented by their miospores. In this thesis no such statements are made; a few speculations are offered, but these are not presented as conclusions, only as alternatives and in relation to other considerations.

The morphological tabulation method is concerned only with presenting aspects of microfloral assemblages not emphasized by the species method. When numerical frequencies of morphological characteristics are compared, the process is done in relation to the numerical frequencies of the miospore species or in terms of dominance of certain characteristics. Such a comparison is consistent, in the first case, because the same miospores are being regarded from different aspects. Thus such a hypothesis as was proposed concerning the frequency of miospore species and the frequency of morphological characteristics (*e.g.*: if the species are similar in type and number, the morphology of the assemblages will be similar) embraces nothing outside of this system. If differences are detected that are inconsistent with the hypothesis, then it is reasonable to propose that other factors may be active. In this thesis, palaeoecological factors are suggested. The explanations are independent of the numerical results.

In the second case, nothing is being concluded on the basis of absolute numerical abundance of morphological characters. Only the relative dominance of certain characteristics is pointed out. Palaeoecological interpretation of this hypothesis may not be rejected on the basis of the objection put forward above.

The secondary objections are concerned with specific conclusions. It may be contended that variation of morphology within miospore species, supposedly of palaeoecological significance, may arise from improper speciation. An example may be the dominant species of the Goose Fiord assemblages, Retusotriletes greggsi. It has been pointed out that taxonomically, no sound basis exists for splitting this species into a number of species. In any case, if the species was split (for example into forma), such action would not alter the expression of variation afford by the tabulation method. Further splitting would also emphasize the possibility of palaeoecological interpretation of these variations.

Rare specimens and those unassigned to distinct species have been suggested as having palaeoecological significance. Such an interpretation may be criticized on the basis that this significance is only apparent. If enough of these forms could be found, they could be incorporated into distinct species. It may be pointed out that over 5000 miospores from Goose Fiord and at least 1000 from Escuminac Bay were examined. The rare specimens still did not occur enough to provide material for speciation. Their palaeoecological significance, in any case, would not be lost because they occurred in sufficient numbers to be classified as distinct species.

Finally, there is the contention that the variations from sample to sample may be artifacts arising from techniques. Lee (1964) has presented results which show the pronounced differences in generic assemblages from the same sample processed by different methods. In this study, however, preparation methods were kept as similar as possible throughout. The substitution of sodium hypochlorite as the oxidizing agent in the case of certain samples from Goose Fiord was the only departure from the usual procedure. Oxidation with this reagent was carefully controlled, however, so that the degree of oxidation remained comparable to that obtained by the dry Schulze method. Any effect of the preparation method, therefore, was constant.

### The Morphological Tabulation Method:

### General Conclusions

The preceding discussion of the morphological tabulation method has been concerned with individual hypotheses. These have been valuated and shown to have foundation in the data. Palaeoecological interpretations of the individual hypotheses have been advanced and objections to the interpretations have been considered. It is appropriate now to consider the method in its entirety and to indicate its application and its scope in general terms.

The method of tabulation of morphological characteristics of individual miospores provides much useful information not supplied by the species method. While no quantitative conclusions may be reached about the palaeoecology of parent floras, using this information, certain qualitative interpretations may be advanced.

The palaeoecological interpretations are palaeofloristic in scope, in accordance with the definition of Devonian plant palaeoecology offered earlier. Moreover, these palaeofloristic interpretations seem suited (for the most part) to investigations of assemblages of relatively small geographical extent. The method thus provides a complementary technique to that supplied by the use of the species concept (*e.g.*: Playford, 1963b; Hacquebard and Barss, 1957) which has a much wider geographical scope.

The results of the investigation of this method, therefore, are positive in nature and suggest that the individual hypotheses and the interpretations suggested by them may be further profitably investigated.

## MIOSPORE SPECIES AND DEVONIAN PALAEOFLORAS

### Microfloras and Parent Floras

Miospore species, although based on arbitrary groupings of spores with similar morphological characteristics, probably represent natural groups at the genus or species level (Knox, 1950; and others). Miospore species assemblages, therefore, may be considered as corresponding broadly to particular parent floras. Even though the parent plants are not known, the miospore species may be used as indicators of palaeofloral changes.

Morphological circumscriptions of miospore genera are usually much too broad in scope and tend to suggest similarity between assemblages which may be somewhat misleading. When miospores are used for this purpose, therefore, it is best to work at the species level.

On the background of these considerations, the miospore species assemblages of Goose Fiord and Escuminac Bay may be compared with each other and with miospore species assemblages of Middle Devonian to Lower Carboniferous age reported by other workers.

## Comparison of Microfloral Assemblages

Goose Fiord Assemblage - Six species in this assemblage do not occur elsewhere: *Punctatisporites tenuis*, *P. lunaris*, *Verrucosisporites certus*, *Dictyotriletes trigonalis*, *Lophozonotriletes crassirugulatus*, and *Cingulizonates boreus*, all new species. In addition, several forms of *Leiotriletes*, *Punctatisporites*, *Granulatisporites*, *Apiculatisporites*, and *Stenozonotriletes*, not assigned a specific epithet, occur only at Goose Fiord (Text-fig. 10).

A number of species are common to this and other assemblages. *Retusotriletes greggsi* and *R. semizonalis* occur in the Ghost River Formation, (McGregor, 1964) of late Middle or early Upper Devonian age, in Alberta. *R. greggsi* has also been reported in the Onteora Formation of New York State (McGregor, 1964) of Upper Devonian age.

*Convolutispora tuberculata* has been reported from the Upper Devonian in southern Russia (Dnieper-Donetz Basin, Ischenko, 1956) and from the lower Carboniferous in western and southern Russia (Luber and Waltz, 1938; Ischenko, 1956), Spitzbergen (Playford, 1962b), and Axel Heiberg Island, in the Canadian Arctic (Playford and Barss, 1963).

*Lophozonotriletes rarituberculatus* has been reported from the

Text-fig. 10. The geographical distribution of miospore and acritarch species and species designates occurring at Goose Fiord and Escuminac Bay. A single unbroken line indicates occurrence in rocks of Middle to Upper Devonian age, a double unbroken line Middle Devonian to Lower Carboniferous age, and a paired broken and unbroken line, Lower Carboniferous age. Arctic Canada includes the Goose Fiord locality. Information derived from various sources.

| LOCATION<br>SPECIES | GOOSE FIORD | ESCUMINAC BAY | ARCTIC CANADA | WESTERN CANADA | EASTERN UNITED STATES | CENTRAL RUSSIA RUSSIAN PLATFORM | SOUTHERN RUSSIA DNIEPER-DONETZ BASIN | WESTERN RUSSIA AND LATVIA | SPITZBERGEN | SCOTLAND |
|---|---|---|---|---|---|---|---|---|---|---|
| Leiotriletes sp A. | — |  | — |  |  |  |  |  |  |  |
| Leiotriletes sp B. | — | — | — |  |  |  |  |  |  |  |
| Punctatisporites tenuis | — |  | — |  |  |  |  |  |  |  |
| P. lunaris | — |  | — |  |  |  |  |  |  |  |
| P. sp A. | — |  | — |  |  |  |  |  |  |  |
| Retusotriletes greggsi | — |  | — | — | — |  |  |  |  |  |
| R. semizonalis | — |  | — | — |  |  |  |  |  |  |
| Granulatisporites sp A. | — |  | — |  |  |  |  |  |  |  |
| Verrucosisporites certus | — |  | — |  |  |  |  |  |  |  |
| Apiculatisporis sp A. | — |  | — |  |  |  |  |  |  |  |
| Dictyotriletes trigonalis | — |  | — |  |  |  |  |  |  |  |
| Convolutispora tuberculata | — |  | ═ |  |  |  | ═ |  | —<br>- - |  |
| Stenozonotriletes sp A. | — |  | — |  |  |  |  |  |  |  |
| Lophozonotriletes crassirugulatus | — |  | — |  |  |  |  |  |  |  |
| L. rarituberculatus | — |  | ═ |  |  |  | ═ | —<br>- - | —<br>- - |  |
| Cingulizonates boreus | — |  | — |  |  |  |  |  |  |  |
| Punctatisporites glaber |  | — | —<br>- - | —<br>- - | —<br>- - |  | ═ |  | —<br>- - |  |
| P. pseudobesus |  | — |  |  |  |  |  |  | —<br>- - |  |
| Calamospora? similis |  | — |  |  |  |  |  |  |  |  |
| C. atava |  | — |  | — |  | — |  | — |  | — |
| Retusotriletes simplex? |  | — |  |  |  | — |  |  |  |  |
| Planisporites aculeatus |  | — |  |  |  |  |  |  |  |  |
| Apiculatasporites dilucidus |  | — | — | — |  |  |  |  |  |  |
| Stenozonotriletes clarus |  | — |  |  |  |  | ═ |  | —<br>- - |  |
| Lophozonotriletes sp A. |  | — |  |  |  |  |  |  |  |  |
| Emphanisporites sp. |  | — |  |  |  |  |  |  |  |  |
| Ancyrospora ancyrea var. ancyrea |  | — |  |  |  |  |  |  |  | — |
| A. ancyrea var. brevispinosa |  | — |  |  |  |  |  |  |  | — |
| Endosporites? granisaccatus |  | — |  |  |  |  |  |  |  |  |
| Endosporites sp. A. |  | — |  |  |  |  |  |  |  |  |
| Rhabdosporites langi |  | — |  |  |  |  |  |  |  | — |
| **Acritarcha** |  |  |  |  |  |  |  |  |  |  |
| Leiosphaeridia orbiculata |  | — |  | — |  |  |  |  |  |  |
| L. microgranulifera |  | — |  | — |  |  |  |  |  |  |

Latvian SSR and White Russia (Kedo, 1955; 1957), as well as from localities listed for *Convolutispora tuberculata*.

While no species in common with the Goose Fiord assemblage have been reported by Naumova (1953) in her work on the Middle and Upper Devonian of the Russian Platform (west-central Russia), certain similarities are evident in morphology and structure of species between the two assemblages. *Leiotriletes simplex* and *L. laevis* are similar to *Leiotriletes sp.A*. (this work). Naumova's species, *Lophozonotriletes torosus*, *L. tylophorus*, *L. rarituberculatus non* (Luber) Kedo , and *L. scurrus* resemble the Goose Fiord species, *Lophozonotriletes crassirugulatus* sp. nov. and *L. rarituberculatus* (Luber) Kedo, in shape, size range, structure of cingulum, and ornamentation. The species listed above, that are described by Naumova (1953), are among those listed as dominant forms in her spore complexes VII and VIII of Upper Frasnian age (Lower Upper Devonian).

Species described in this work from Goose Fiord, *Punctatisporites tenuis* sp. nov. and *P. lunaris* sp. nov., show close similarity in size range and ornamentation to *P. arcticus*, *P. scabratus*, and *P. putaminis* described by McGregor (1960) from coal of early Upper Devonian age on Melville Island in the Canadian Arctic. Other species of this assemblage, however, show little similarity to the assemblage described here from Goose Fiord, Ellesmere Island, despite the relative geographical proximity of the two sites. Because the former assemblage was preserved in a coal seam and the latter in clastic, probably deltaic rocks, the difference may be due to ecological preferences of the parent floras.

Escuminac Bay Assemblage - Three miospore species in the Escuminac Bay assemblage do not occur elsewhere. These are: Calamospora? similis sp. nov., Planisporites aculeatus sp. nov. and Endosporites? granisaccatus sp. nov. Several forms not given specific epithets and belonging to the genera Lophozonotriletes and Endosporites? have not been reported elsewhere.

Seven species are also found in other miospore assemblages (Text-fig. 10). Punctatisporites glaber has been reported from the Upper Devonian (Dnieper-Donetz Basin; Ischenko, 1958) and from the Lower Carboniferous of Spitzbergen (Playford, 1962b), the Dnieper-Donetz Basin (Ischenko, 1958), and the Viséan (Upper Mississippian) of Axel Heiberg Island, Canadian Arctic (Playford and Barss, 1963), the Eastern United States (Illinois and Kentucky) (Hoffmeister, et al., 1955b) and Alberta (Staplin, 1960). Punctatisporites pseudobesus, found at Escuminac Bay, has also been reported by Playford (1962b) from the Lower Carboniferous of Spitbergen.

Calamospora atava has been reported elsewhere from a wide variety of localities: the Middle Devonian of Scotland (Lang, 1925); Belorussia (Kedo, 1955); the Middle and Upper Devonian of the Russian Platform (Naumova, 1953); the late Middle or Early Upper Devonian of Alberta (McGregor, 1964); and the Upper Devonian of the Latvian SSR (Ozolinya, 1960).

Apiculatasporites dilucidus has been described from Alberta, (McGregor, 1964) and Melville Island, Canadian Arctic, (McGregor, 1960). Both these localities are probably late Middle or Early Upper Devonian in age.

*Stenozonotriletes clarus* occurs in the Dnieper-Donetz Basin (Ischenko, 1956; 1958), from the Upper Devonian to the Lower Carboniferous, and in the Lower Carboniferous of Spitzbergen (Playford, 1962b).

*Ancyrospora ancyrea* var. *ancyrea* and *A. ancyrea* var. *brevispinosa* occur in the Middle Devonian of Scotland. *Rhabdosporites langi*, which occurs at Escuminac, is a species occurring both in the Middle Devonian of Scotland and the Baltic region (Richardson, 1965).

Naumova (1953) has described species from the Russian Platform that are similar in construction and ornamentation to several occurring at Escuminac Bay. *Archaeozonotriletes polymorphous* Naum. and *Lophozonotriletes lebedianensis* Naum. are comparable to *Lophozonotriletes sp.A.* (this study). *Stenozonotriletes conformis* Naum., *S. extensus* Naum., and *S. simplex* Naum., are similar in construction and ornamentation to *S. clarus* from Escuminac Bay. Miospores similar to these species of *Stenozonotriletes* have also been reported from the Upper Devonian of France (Taugourdeau-Lantz, 1960).

### Miospore Species and Microfloral Provinces

Miospores are often distributed in distinct geographical patterns. Such patterns may originate in the distribution of parent plants. Alternatively, they may be artifacts, arising from an incomplete knowledge of the geographical occurrence of miospores. Many palynologists (*e.g.*: Hacquebard and Barss, 1957; Playford and Barss, 1963) have called such patterns microfloral provinces.

While microfloral provinces may be nothing more than patterns, they may have some relation to palaeofloristic associations existing in Upper Devonian-Lower Carboniferous times. It is useful, therefore, to investigate the geographical distribution of miospores reported from strata of this age.

The incomplete record of Middle and Upper Devonian microfloras, and differences in nomenclature used by various schools (Naumova, 1953; Potonié and Kremp, 1954), make it rather difficult to assess the question of late Devonian-early Lower Carboniferous microfloral provinces. Although a number of Upper Devonian miospore assemblages have been described, usually only a few species are common to two or more assemblages. An example of this is provided by the two miospore assemblages described in this work.

McGregor (1960) suggests that this apparently discrete distribution of late Devonian miospores results from an imperfect knowledge of Devonian miospore assemblages. To this may be added the observation that ecological control is probably also a significant factor in determining the species distribution.

It is possible, however, to point out several tentative microfloral provinces in the late Devonian. These suggestions will serve, at least, to direct attention to critical areas where microfossil evidence may resolve the problem.

A major Upper Devonian microfloral province appears to embrace southern Russia, the Russian Platform, and the northeastern part of the Canadian Arctic (Ellesmere Island) (Text-fig. 11). Convolutispora tuberculata and Lophozonotriletes rarituberculatus both occur in the Dnieper-Donetz Basin and at Goose Fiord. In addition, a number of similar species of *Lophozonotriletes* and *Leiotriletes* occur in the Russian Platform and at Goose Fiord (Text-fig. 10).

*Retusotriletes greggsi* and *R. semizonalis* occur at Goose Fiord and in Alberta in the Upper Devonian; *Apiculatasporites dilucidus* is found on Melville Island and in Alberta as well during this time. The occurrence of these three species suggest an overlapping sub-province embracing the Canadian Arctic and Western Canada in the Upper Devonian.

The Upper Devonian strata of Escuminac Bay and southern Russia contain several species in common (*Punctatisporites glaber* and *Stenozonotriletes clarus*). Species of *Stenozonotriletes* from the Russian Platform are also similar to *S. clarus*. This association suggests a second sub-province including southern Russia, the more westerly portion of the Russian Platform and Escuminac Bay (Eastern Canada). Information is not available on Upper Devonian miospore species present in Spitzbergen, but it appears from this distribution that similar forms would be found there.

There is an overlap of the two sub-provinces near the southern Russian region into one single province. Progression further along the arms of the inverted V of the distribution (Text-fig. 11) leads to occurrence of new elements (especially in Western Canada), until at the ends of the V, the general similarities only are evident (Escuminac Bay) or the forms have changed completely (Western Canada). There is a continuum along the arms of the inverted V, however, which is quite evident. It is interesting to note the occurrence of the seemingly cosmopolitan species *Apiculatasporites dilucidus*. If the

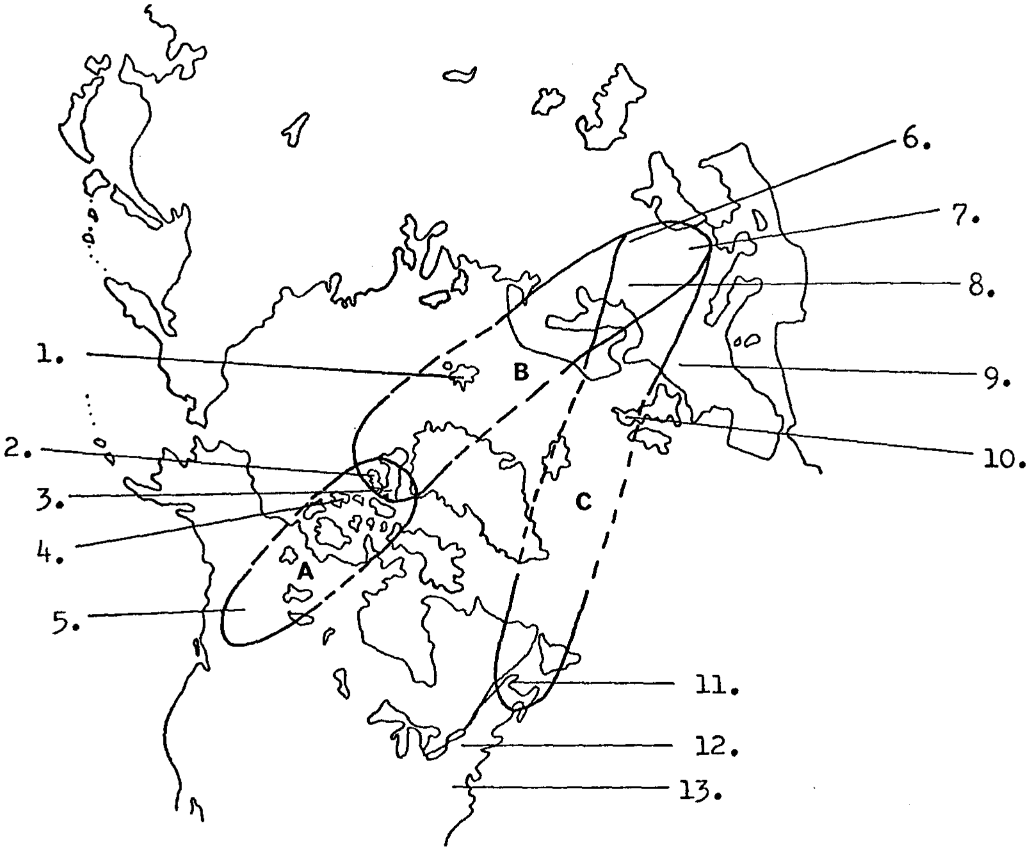
LEGEND

1. SPITZBERGEN
2. AXEL HEIBERG I.
3. ELLESMERE I.
4. MELVILLE I.
5. WESTERN CANADA (ALBERTA)
6. RUSSIAN PLATFORM
7. DNIEPER-DONETZ BASIN
8. LATVIAN SSR
9. FRANCE-BELGIUM
10. SCOTLAND
11. ESCUMINAC BAY
12. NEW YORK STATE
13. EASTERN UNITED STATES

A. WESTERN CANADIAN-ARCTIC PROVINCE

B. RUSSIAN-ARCTIC PROVINCE

C. RUSSIAN-EASTERN CANADIAN PROVINCE



Text-fig. 11. Part of the Northern Hemisphere in polar projection, showing location of geographical areas and proposed microfloral provinces referred to in the text. Where microfloral province boundaries are dotted, evidence is not available for the region enclosed.

continuum is postulated as being due to ecological factors, this miospore species may represent a parent form that was adaptable to a number of different environments.

The similarities at the species level of Lower Carboniferous assemblages in the Arctic, the Soviet Union, Spitzbergen, and Western Canada have led Playford and Barss (1963, p. 4) to suggest that an extensive microfloral province embraced these areas at this time. It appears from the species described in the present work, that such a province was in existence in the Upper Devonian and was actively expanding to the boundaries it held by Lower Carboniferous times (*vide*: Playford, 1962a).

## Miospore Species and Floral Migration

A number of miospore species occurring in the Middle Devonian of Scotland and the Baltic are found in the Upper Devonian of Escuminac Bay. Upper Devonian assemblages described from France (Taugourdeau-Lantz, 1960), Belgium (Caro-Moniez, 1962), Latvia (Ozolinya, 1960), Belorussia (Kedo, 1955), and the Russian Platform (Naumova, 1953), show no similarity at the species level with Middle Devonian forms from Scotland. This strongly suggests that parent forms of the species common to the Scotland Middle Devonian and Escuminac Bay Upper Devonian may have migrated westward over a period of about ten million years. It would be interesting to know whether or not these species occurred in the Upper Devonian of Scotland or in the Middle Devonian of Eastern Canada. McGregor (1962) has noted the occurrence of *Ancyrospora* in the late Lower Devonian to Early Middle Devonian

Gaspé Sandstone group, but does not mention species similarities.

Punctatisporites glaber offers another suggestion of microfloral migration. This species is found in Southern Russia and at Escuminac Bay in the Upper Devonian. By the late Lower Carboniferous (Viséan) it is reported in the Canadian Arctic, Western Canada and from the Eastern United States. It is possible that the parent form or forms producing this miospore may have migrated from Southern Russia across the Canadian Arctic and into Western Canada. Because this form is found in the Eastern United States by Viséan time, it is also a possibility that the parent form may have spread southwards from Escuminac Bay to this region. Punctatisporites glaber does not appear in the Upper Devonian and Mississippian assemblages described from Ohio (Winslow, 1962); this fact lends added support to the hypothesis proposed above.

Convolutispora tuberculata provides one further example of microfloral migration. It is present at Goose Fiord and in southern Russia in the Upper Devonian and appears in the Viséan of Axel Heiberg Island (Playford and Barss, 1963) as well as occurring in Russia and in the Lower Carboniferous of Spitzbergen (Playford, 1962b).

It is too early to establish conclusions as to the significance of these microfloral migrations. Bearing in mind, however, that these microfloral migrations probably mean migration of parent forms, there is a suggestion that southern Russia may have been a centre of dispersal during the Upper Devonian and Lower Carboniferous. There appears to be a definite expansion across the Arctic, during this period, of forms emanating from southern Russia.

### Miospore Species: General Observations

Both the morphological tabulation and the species concept methods provide palaeofloristic knowledge of Devonian floras. The species method, unlike the other one, is broad in scope, having world-wide application. The scope of this latter method has been well demonstrated by the preceding discussion.

## STRATIGRAPHIC POSITION OF THE ASSEMBLAGES

The geological age of the Escuminac Formation and the Okse Bay Formation is considered to be Upper Devonian (*vide*: Text-fig. 2, and p. 23). Richardson (1965, p. 601) gives the age of the Escuminac Formation as Lower Frasnian but does not give the source of this information.

The miospore assemblages obtained from these two formations contain species found in a number of localities in many parts of the world. It may be possible, from a consideration of this evidence, to give a more precise geological age determination for the two formations.

### Geological Age of the Lower Okse Bay Formation

It was indicated earlier that the miospores described from the Okse Bay Formation have, in all likelihood, been obtained from the lower sandstone and shale member of the formation. The age determination will thus be valid for the lower part of the formation.

*Lophozonotriletes rarituberculatus* and *Convolutispora tuberculata* have been found in the Famennian of European Russia and range into the Lower Carboniferous. *Retusotriletes greggsi* and *R. semizonalis* have been found previously in rocks no older than late

Givetian, and which are probably early Frasnian (McGregor, 1963; 1964). R. greggsi has also been found in the Upper Devonian Onteora Formation of New York State (McGregor, 1964). The general aspect of the Goose Fiord assemblage corresponds most closely to the spore complexes VII and VIII of Naumova (1953).

From this evidence, the lower part of the Okse Bay Formation is perhaps middle or late Frasnian, and is certainly Frasnian in age. The presence of several species previously ranging only as far back as the Famennian suggests the middle or late Frasnian age, but further information is needed to confirm this more precise age.

## Geological Age of the Escuminac Formation

Ancyrospora ancyrea and Rhabdosporites langi have been reported previously only from Middle Devonian rocks (Richardson, 1965). Calamospora atava has a reported range of Givetian to early Frasnian (numerous authors); Apiculatasporites dilucidus occurs in rocks of Upper Givetian to perhaps late Frasnian in age (McGregor, 1960; 1964). On the basis of this information, the age of the Escuminac Formation would appear to be Lower Frasnian.

The presence, however, of Punctatisporites glaber, P. pseudobesus, and Stenozonotriletes clarus, species previously reported (Ischenko, 1956; 1958; Playford, 1962b) from rocks of Famennian age or younger, suggests that the age of the Escuminac Formation may be as young as Upper Frasnian.

On the basis of the reported ranges of the species mentioned above, the probable age of the Escuminac Formation is middle to late

Frasnian. This age corresponds to the age of the lower members of the Okse Bay Formation, exposed at Goose Fiord, southern Ellesmere Island.

## Extension of Stratigraphic Ranges

From the work of this thesis, a number of extensions of stratigraphic ranges of miospore species can be made. These revised ranges are listed below, with the older limit retained in brackets:

Lophozonotriletes rarituberculatus: Frasnian (Famennian) to Viséan.
Convolutispora tuberculata: Frasnian (Famennian) to Viséan.
Retusotriletes greggsi: ?Upper Givetian to Frasnian (?Lower Frasnian).
Retusotriletes semizonalis: ?Upper Givetian to Frasnian (?Lower Frasnian).
Punctatisporites glaber: Frasnian (Famennian) to Viséan.
Punctatisporites pseudobesus: Frasnian to (Lower Carboniferous).
Stenozonotriletes clarus: Frasnian (Famennian) to Viséan.
Ancyrospora ancyrea: Eifelian to (Givetian) Frasnian.
Rhabdosporites langi: Eifelian to (Givetian) Frasnian.

## BOTANICAL AFFINITIES OF THE MIOSPORES

None of the miospores described in this thesis correspond to spores extracted from sporangia of parent plants. A few general remarks may be made about botanical affinites of the miospores.

Spores conformable with the form genus Leiotriletes have been found associated with the Bryopsida and the Marattiales (Potonié and Kremp, 1956b; Potonié, 1962, p. 94). Punctatisporites has been found in the sporangia of many forms, including the Psilopsia, Filicinae, and the Cycadofilicales (Potonié and Kremp, 1956b, p. 81). The genus *Calamospora* is associated with various orders of the Sphenopsida (Potonié and Kremp, 1954, p. 126; Brush and Barghoorn, 1964, p. 329). *Granulatisporites* has been found in sporangia of forms allied to the Filices (Potonié and Kremp, 1954, p. 126). *Verrucosisporites* has been found in the sporangia of the fern forms *Corynepteris* and *Zygopteris* (*fide*: Playford, 1962b, p. 586).

McGregor (1964) suggested that *Retusotriletes greggsi* belonged to the plant genus *Svalbardia*. Recently, however, the author has been able to examine photographs of the spores obtained from *Svalbardia polymorpha* Høeg (Høeg, 1942) (through the kind permission of Dr. D. C. McGregor). What appeared to be curvaturae on these specimens, were actually concentric folds near the equator of the spores. The similarity of the ornamentation and these folds gave the impression that the spores were conspecific with *Retusotriletes greggsi*. This suggestion must now be abandoned.

Spores similar to *Rhabdosporites parvulus* Richardson, have been found by Pettit (in press) in sporangia of *Archaeopteris* cf. *A. jacksoni* from Escuminac Bay, Quebec. There is a suggestion, then, that the genus *Rhabdosporites* may be associated with *Archaeopteris* or forms allied to this type. *Rhabdosporites langi* has been reported from Escuminac Bay (this work).

*Endosporites* has been reported from plant forms assigned to the Lycopsida (Chaloner, 1953; 1958a). *Densosporites* and *Lycospora* have been found in sporangia of herbaceous(?) and arborescent Lycopsida respectively (Potonié and Kremp, 1954; *fide*: Playford, 1963a).

Considering the sparse botanical evidence offered by the miospores, it appears that the parent plant assemblages were made up, in part at least, of pteridophytes (probably ferns) at both Escuminac Bay and Goose Fiord. Miospores with lycopsid affinities are notable for their absence at both localities. *Calamospora* is found in the Escuminac Bay region but rarely at Goose Fiord; there appears to be a lack of sphenopsid forms in the Goose Fiord assemblage.

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# APPENDIX I

## GLOSSARY OF DESCRIPTIVE TERMS

### ORNAMENTATION

| | |
|---|---|
| Laevigate: | Smooth. |
| Scabrate: | Roughened, with irregular pits or fine, short irregular ridges (Harris, 1955, p. 18). Chagrinate, like fine leather (Staplin and Jansonius, 1964, p. 98). |
| Striate: | With parallel thickenings or ridges (ribs). These may be curved or linear (*vide*: Pl. IV, fig. 9). In any case the ridges are only faintly raised above the surface of the exine. |
| Punctate: | Small pits in the exine, generally less than 2μ in diameter, and not forming a reticulum. Pits generally isodiametric (*vide*: Pl. I, fig. 6). This includes the foveolate of Harris (1955, p. 18) and Erdtman (1952, p. 416). |
| Vermiculate: | With grooves in the exine shaped like worm tracks (after Kosanke, 1950). |
| Echinate: | Small, tapering apiculations, less than 1½μ in height and basal width. Height generally greater than width of base. Blunt apiculations less than ½μ may also be included here (*vide*: coni). |

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| Spinae: | Width of base generally less than height. Apices pointed; spines tapering. Height or basal width greater than or equal to 1½μ. |
| Coni: | Base generally as broad or broader than height. Apices bluntly rounded; outline somewhat conical. Very small coni (½μ or less) may often not be distinguished from echini and are classed under this heading. |
| Setulate: | Ornamented with setulae; parallel-sided, rod-like projections ending bluntly and not tapering to the end. Tips may be occasionally expanded or swelled and are then termed <u>pila</u> (Potonié and Kremp, 1955). Diameter of the setulae less than 1½μ. |
| Apiculation: | A collective term used to refer to echini, spinae and coni. |
| Granulate: | With more or less isodiametric, rounded elements, 1 to 2μ in height, If individual granules are less than 1μ in width and height, the term granulose is used (in this thesis). In any case, the diameter does not exceed 1/20 of the equatorial diameter of the miospore if the diameter is equal to or less than 40μ. |
| Verrucate: | With elevations, irregular to regular (isodiametric) in outline; tops are rounded. Diameter greater than 2μ or greater than 1/20 the miospore diameter if the latter is equal to or less than 40μ. |

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| Rugulate: | With irregular, wrinkled, irregularly to regularly distributed elements. Distinctly raised above the surface of the exine (*vide*: Pl. IV, fig. 1). |
| Obvermiculate: | Elements similar to rugulae but only slightly raised from the surface of the exine. |
| Cristate: | Comb-like or crest-like ridges. Crests may be ornamented with apiculations, etc. Arrangement may be concentric or occasionally anastomosing. |
| Reticulate: | Network pattern of raised walls (muri) enclosing cavities (lacuna). Muri generally regular in height and with flattened or rounded tops. Lumina may be polygonal to rounded in outline. |
| Negative reticulum: | Ornamentation (especially verrucae or apiculations) may be so closely spaced as to give the impression of a negative reticulum, the depressions between the ornaments forming a network pattern. |
| Lacunae: | Irregularly shaped depressions enclosed by the anastomosing or rugulae, vermiculae or other raised ornamentation of a similar nature (*vide*: *Convolutispora tuberculata*, Pl. III, fig. 8). The use of this term is similar to Harris (1955, p. 26). |
| Processes: | Elongate, tapering projections, usually greater than $10\mu$ in height. Base may or may not broaden considerably. Tips blunt (*vide*: Pl. VI, figs. 3, 4) or bifurcated, ending in grapnel or anchor-shaped configurations (*vide*: Pl. V, figs. 1-4). |

## STRUCTURE

Structure, in this thesis, is used in the sense of construction of the miospore rather than the form and arrangement of the individual elements within the outer miospore wall layer (the exine) (cf. Faegri and Iverson, 1950, p. 18).

Distal pole: The pole opposite the proximal face.

Distal face: The part of the miospore directed outwards in its tetrad (Erdtman, 1952, p. 452).

Equator: The border line between the proximal and distal faces of the miospore (Erdtman, 1952, p. 467).

Interradial region: The region including the proximal face between the tetrad mark and the corresponding part of the distal face.

Proximal face: The part of the miospore directed inwards in its tetrad.

Radial region: The region including the proximal surface in the immediate area about the tetrad mark (and at the extremities of the rays) and the corresponding distal face.

Tetrad mark: The mark on that part of the proximal surface which was in contact with the other miospores of the tetrad. In trilete and monolete miospores, the tetrad mark corresponds in position to the laesurae.

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| Laesura: | The proximal aperture of trilete and monolete miospores. Trilete miospores possess three laesurae radiating from a proximal pole. Monolete miospores have one laesura with its centre at the proximal pole. |
| Commissure: | Where no margo is present, the laesura may be termed a commissure (Harris, 1955, p. 25). |
| Margo: | A transition zone between the commissure and the remainder of the exine. The exine may be thickened at this transition or the ornamentation may differ in degree or type from that of the rest of the proximal surface. |
| Exine: | The outer usually resistant layer of the miospore wall. The exine may be divided into several layers: an outer exoexine (often called the sexine), which bears the sculpture; and an inner intexine (nexine) which is without sculpture.<br>The intexine is rarely visible in fossil miospores, but may correspond to the central body of monosaccate types (<u>vide</u>: Pl. V, figs. 1-4). |
| Perine: | An outermost, extraexinal layer present in some miospores (<u>vide</u>: Pl. III, fig. 16). The layer is generally without ornamentation or with minor elements. The origin of the layer is not definitely known. The layer termed 'perine' in fossil spores may or may not be homologous with the perine layer of |

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| | contemporary spores and pollens. Erdtman (1952, p. 466) and Harris (1955, pp. 16-17) discuss the matter at some length. Miospores with a perine are termed perinate. |
| Cuesta: | The ridge marking an elevation of the surface of the zona above the surface of the central proximal area (Staplin and Jansonius, 1964, p. 98). |
| Cingulum: | A thickening of the equatorial portion of the exine. Transverse sections may show the cingulum to be tapering slightly or sharply. The cingulum is generally considered as being thicker and more narrow in width than a zona. |
| Zona: | An encircling equatorial widening or 'flange', generally much wider and thinner than a cingulum, and not wedge-shaped in cross-section. It is formed by the extension of the equatorial exine (exoexine). |
| Cavate: | Miospores without a saccus or bladder and in which the wall layers (exoexine and intexine) are almost completely or partially separated from each other by a cavity (Dettmann, 1963, p. 19). |
| Monosaccate: | Possessing a single air-sac or bladder, formed of the exoexine. The bladder is more or less radially symmetrical about the polar axis (a line connecting the poles of the miospore). In Palaeozoic miospores, the intexine (nexine) may not be present, or may be hard to detect when present. Thus the confusion which |

may arise in distinguishing between saccate and cavate miospores in Mesozoic forms is not likely to occur. Dettmann (1963, p. 19) distinguishes saccate forms from trilete, cavate miospores by the presence of small, baculoid (setulate) elements adhering to the inner surface of the saccus. Forms described in this thesis (e.g.: Endosporites? granisaccatus sp. nov.) without baculoid elements on the inner surface of the exoexine, but with structure otherwise similar to monosaccate forms, are considered as saccate rather than cavate.

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| Curvaturae: | Arcuate, fine markings, which may often be raised and darkened, outlining the limits of the contact area of the miospore. Curvaturae generally are parallel or sub-parallel to the equator. They may often invaginate at the extremities of the laesurae or they may not quite join the extremities. In such a case they are more properly termed curvaturae imperfecti. Curvaturae may be proximal to equatorial in position (vide: Pl. I, fig. 16 and Pl. II, figs. 1, 2 and 5). |
| Contact area: | The region of the proximal face that was in contact with the other spores of the tetrad. Often marked near the pole by a triangular darkened region (vide: Pl. I, figs. 14, 15). In this thesis, the term is most often used in reference to this darkened region, but it properly refers to the whole contact area. |

## SHAPE

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| Amb: | The outline of a miospore in proximal or polar view. |
| Profile: | The outline of a miospore in equatorial view. |

# APPENDIX II

## CHECK LIST OF MORPHOLOGICAL TERMS USED IN THE MORPHOLOGICAL TABULATION STUDY

### Subsection: Ornamentation

Laevigate
Scabrate
Striate
Punctate
Vermiculate
Spinae
Coni
Echini
Setulae
Granulose or granulate
Verrucate
Rugulate
Obvermiculate
Cristate
Reticulate
Processes

### Subsection: Shape

Triangular: convex in interradial region
Triangular: concave in interradial region
Rounded
Ovoid

### Subsection: Structure

Cingulum or zona
Monosaccate
Darkened contact area
Curvaturae
Wall less than 3μ thick
Wall 3μ thick or more
Perine
Laesurae simple (commissures)
Laesurae compound (with margo)

### Subsection: Size (in μ)

21 - 40
41 - 60
61 - 80
81 - 100
101 - 120
121 - 200 (*i.e.*: less than 200μ)
200 and over

Size was measured to the nearest 1μ. A miospore having a diameter of 40.4μ would be classed in the (21 - 40μ) class. A miospore with diameter 40.5μ would be classed in the (41 - 60μ) category.

## PLATE I

All figures (Plates I - VIII) are proximal views
at X500 unless otherwise noted.

Figure 1. *Leiotriletes sp.A.* AEI-4367.2a(i) 1017 - 380
2. *Leiotriletes sp.A.* AEI-4367.2a(ii) 907 - 257
3. *Leiotriletes sp.B.* AEI-4374.1(i) 1204 - 435
4. *Punctatisporites glaber* AG-3.3(i) 1192 - 308
5. *Punctatisporites glaber* AG-3.3(ii) 723 - 296
6. *Punctatisporites lunaris* sp. nov. Holotype.
7. *Punctatisporites sp.A.* AEI-4369.2a(i) 980 - 287
8. *Punctatisporites pseudobesus* AG-3.3(i) 787 - 338
9. *Punctatisporites tenuis* sp. nov. Holotype.
10. *Punctatisporites sp.A.* AEI-1.3(ii) 1203 - 339
11. *Calamospora? similis* sp. nov. Holotype.
12. *Calamospora atava* AG-24.1(i) 963 - 287
13. *Calamospora atava* AG-11.1(ii) 1026 - 443
14. *Calamospora atava* AG-3.3(ii) 703 - 394
15. *Calamospora atava* AG-3.3(ii) 966 - 330
16. *Retusotriletes greggsi* AEI-4368.1a(i) 697 - 303
Partially an equatorial view.

# PLATE I


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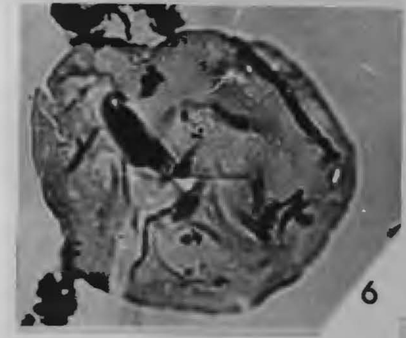
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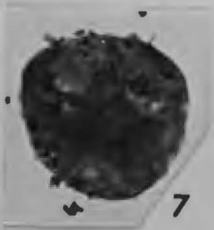
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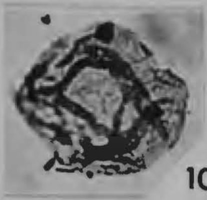
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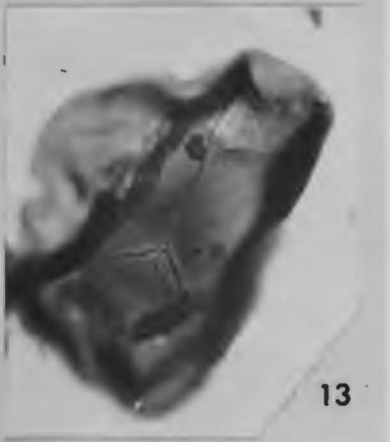
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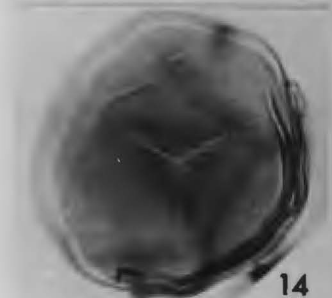
14


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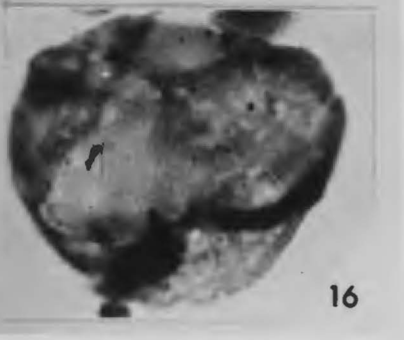

16

## PLATE II

Figure 1. Retusotriletes greggsi AEI-4368.1a(i) 750 - 339

Tetrad

2. Retusotriletes semizonalis AEI-4368.1a(i) 693 - 343
3. Retusotriletes greggsi AEI-4368.1a(ii) 934 - 405

X1250 (oil immersion) showing minute echini.

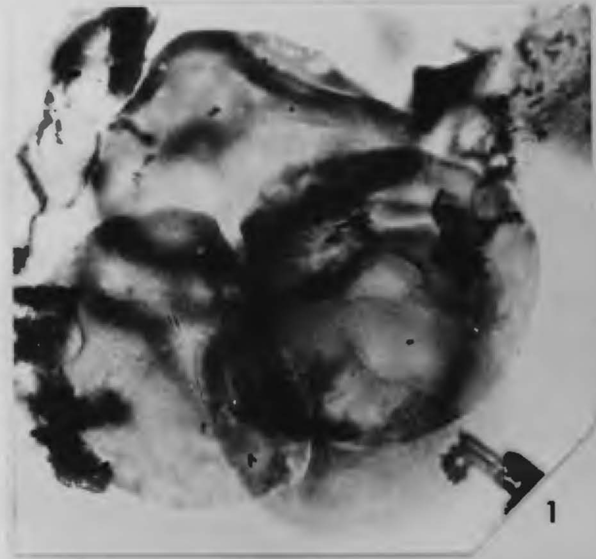
4. Retusotriletes greggsi AEI-4367.2a(1) 810 - 368

X1250 (oil immersion) showing small coni.

5. Retusotriletes simplex? AG-23.2(ii) 1083 - 402
6. Granulatisporites sp.A. AEI-4367.2a(ii) 796 - 409
7. Granulatisporites sp.A. AEI-13.46(iii) 783 - 267
8. Verrucosisporites certus sp. nov. Holotype.
9. Planisporites aculeatus sp. nov. Holotype. Distal view.
10. Planisporites aculeatus sp. nov. AG-23.2(ii) 1083 - 335
11. Planisporites aculeatus sp. nov. AG-3.3(i) 1101 - 435

Tetrad.

# PLATE II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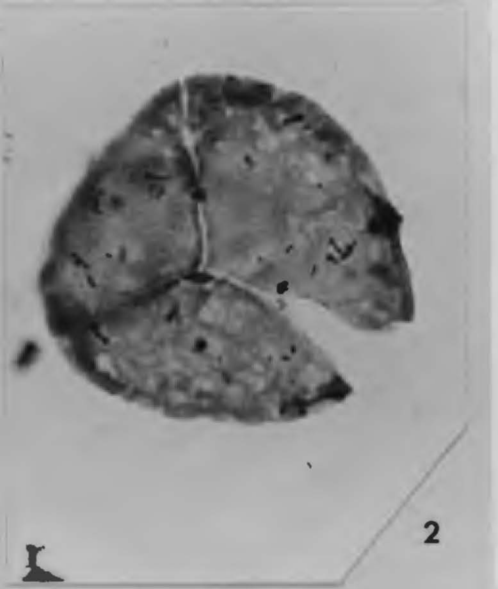
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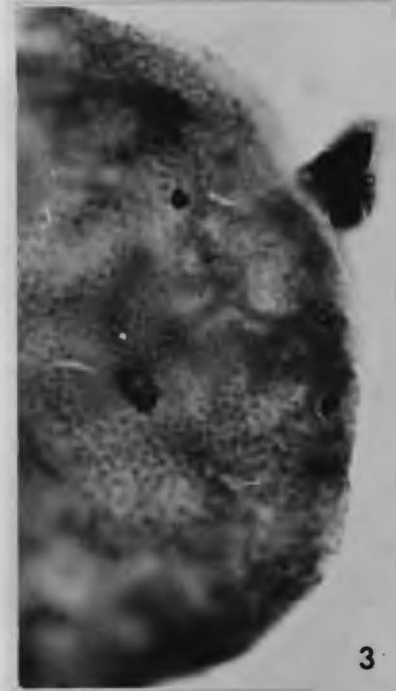
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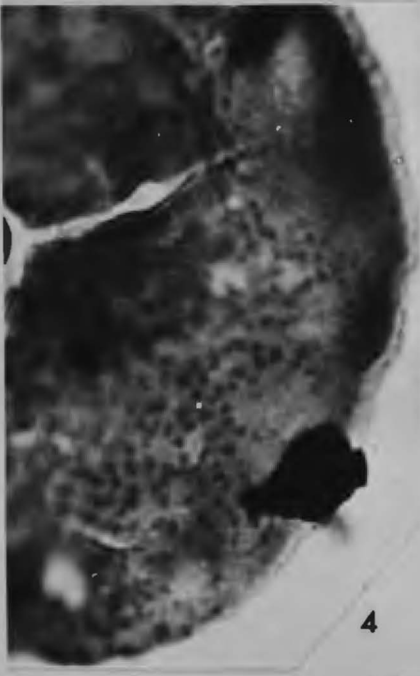
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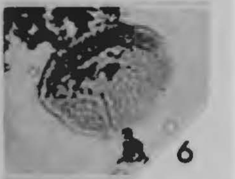
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# PLATE III

Figure 1. *Planisporites aculeatus* AG-3.3(i) *1013 - 374*

X1250 (oil immersion) showing minute echini.

2. *Apiculatisporis sp.A.* AEI-4369.2a(i) *1219 - 310*

3. *Apiculatisporis sp.A.* AEI-4373.3(i) *946 - 416*

4. *Apiculatasporites dilucidus* AG-3.3(ii) *1203 - 372*

5. *Apiculatisporis sp.B.* L46-L63.2(i) *1016 - 268*

6. *Dictyotriletes trigonalis* sp. nov. Holotype.

High focus showing trianguloid lumina.

7. *Dictyotriletes trigonalis* L46-163.2(iii) *1154 - 437*

Median focus showing distal? face.

8. *Convolutispora tuberculata* AEI-4368.1a(i) *629 - 328*

9. *Convolutispora sp.A.* AEI-4369.2a(i) *782 - 329*

10. *Convolutispora sp.B.* AEI-4368.1a(ii) *781 - 356*

11. *Convolutispora sp.C.* AEI-4375.1(i) *1165 - 358*

12. *Lycospora sp.A.* AG-13.1(ii) *826 - 459*

13. *Murospora sp.A.* AG-23.2(i) *943 - 412*

14. *Stenozonotriletes sp.A.* AEI-4369.2a(i) *1224 - 335*

15. *Stenozonotriletes sp.B.* AG-3.3(i) *1203 - 323*

16. *Perotrilites sp.A.* AEI-4372.2a(i) *1098 - 368*

17. *Stenozonotriletes clarus* AG-3.3(i) *1023 - 346*

Distal view.

18. *Stenozonotriletes clarus* AG-3.3(i) *703 - 363*

# PLATE III


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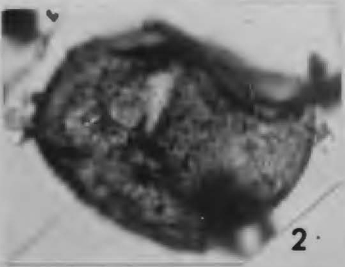
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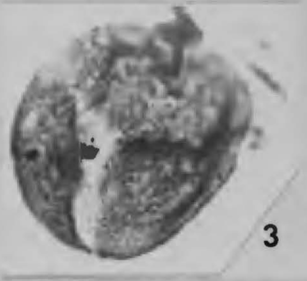
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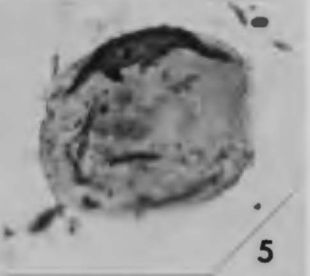
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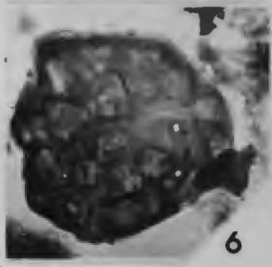
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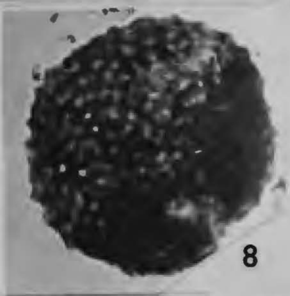
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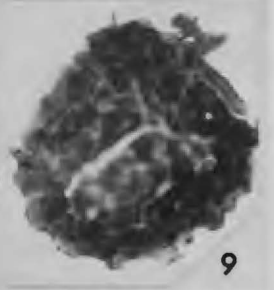
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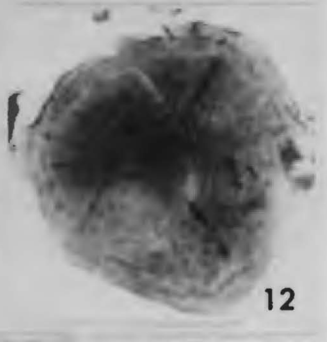
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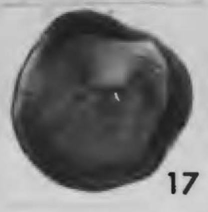
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## PLATE IV

Figure 1. *Lophozonotriletes crassirugulatus* sp. nov. Holotype.

2. *Lophozonotriletes raritutuberculatus* AEI-4369.2a(i) 974 - 435

3. *Lophozonotriletes sp.A.* AG-3.3(ii) 1048 - 389 Laesurae in focus.

4. *Lophozonotriletes sp.A.* Same specimen. Focus on verrucae.

5. *Cingulatizonates boreus* sp. nov. Holotype.

6. *Cingulatizonates boreus* sp. nov. AEI-4372.2a(i) 1128 - 368

7. *Cirratriradites? sp.A.* L46-L63.2(i) 996 - 254

8. *Lophozonotriletes sp.* AEI-4368.1a(ii) 942 - 289

9. *Emphanisporites sp.A.* AG-3.3(ii) 687 - 314 X1250 (oil immersion).

10. *Ancyrospora ancyrea* var. *brevispinosa* AG-3.3(ii) 1093 - 453

11. *Cirratriradiates sp.B.* AEI-13.46.2(iii) 1091 - 370

# PLATE IV


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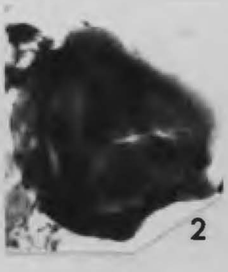
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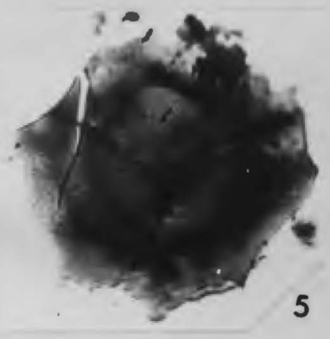
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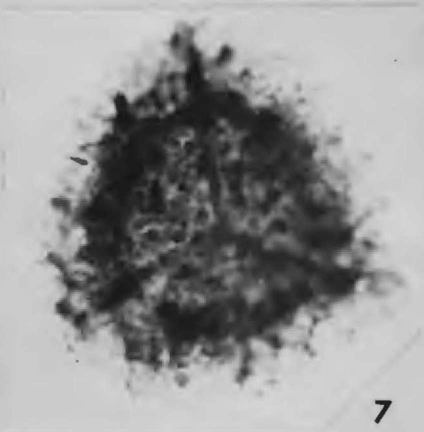
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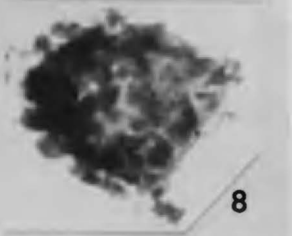
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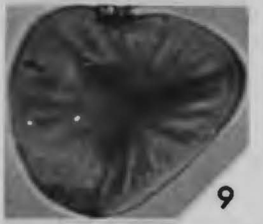
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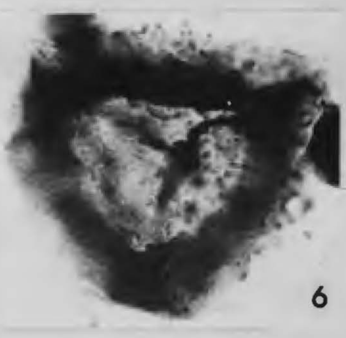
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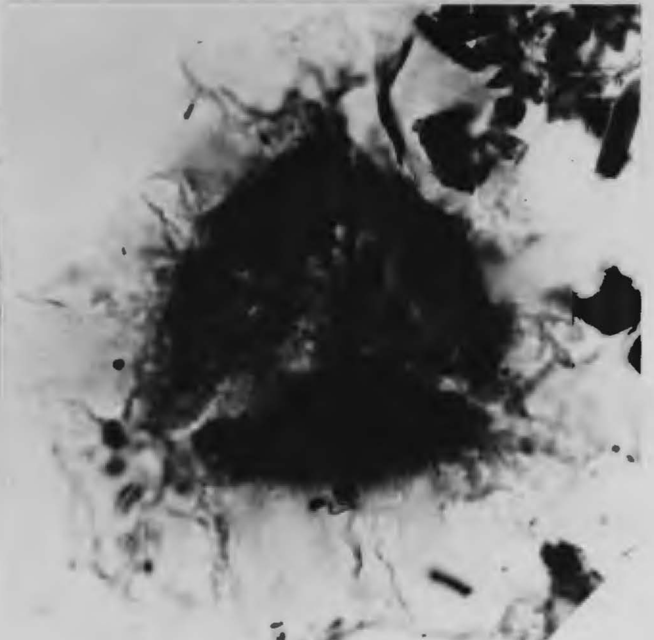
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## PLATE V

Figure 1. *Ancyrospora* *ancyrea* var. *ancyrea* AG-3.3(i) 932 - 300

Distal view.

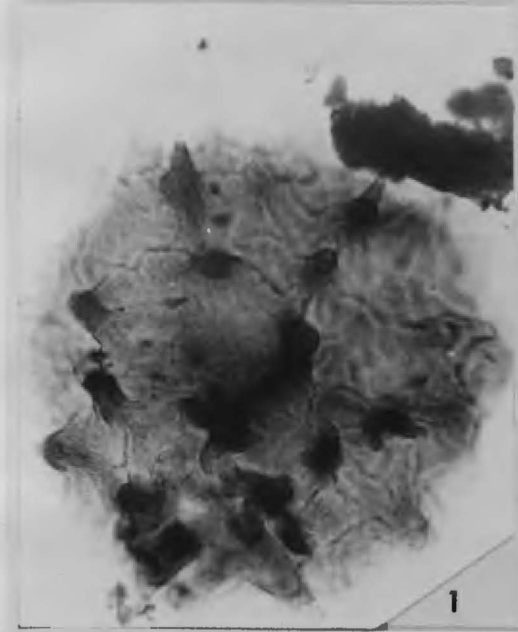
2. *Ancyrospora* *ancyrea* var. *ancyrea*. Same specimen.

3. *Ancyrospora* *ancyrea*? AG-3.3(ii) 1094 - 268

Distal view; distal face in focus.

4. *Ancyrospora* *ancyrea*? Same specimen. Distal view; laesurae on proximal face in focus.

# PLATE V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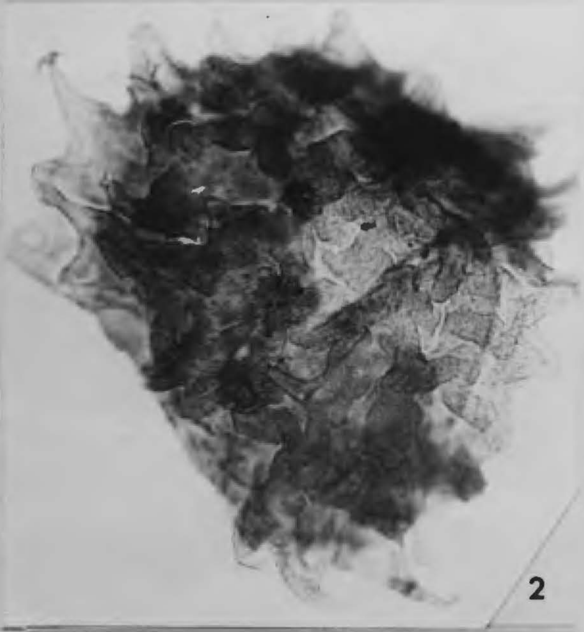
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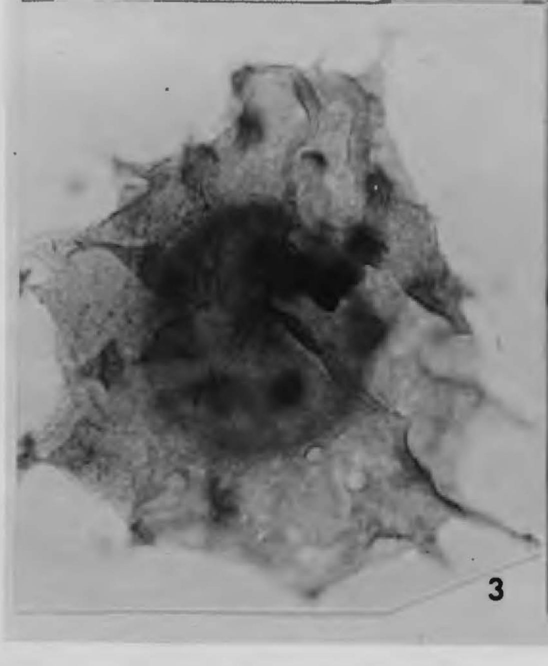
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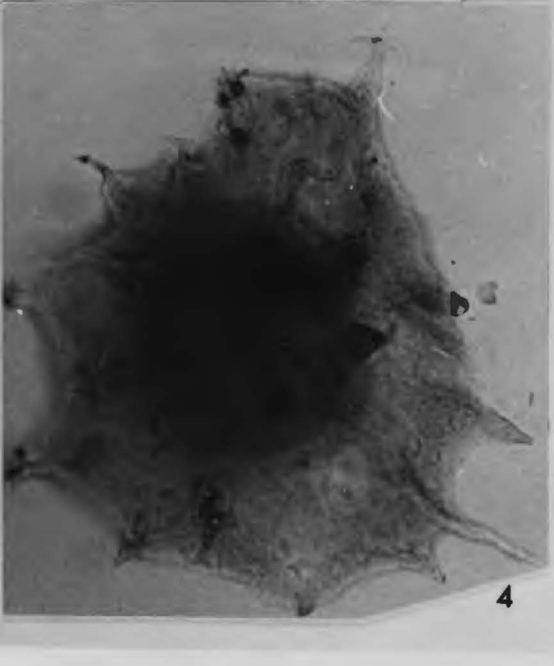
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# PLATE VI

Figure 1. <u>Spore Type C</u>. AEI-4368.1a(ii) <u>710 - 289</u>

2. <u>Spore Type D</u>. AEI-4369.2a(i) <u>947 - 418</u>

3. <u>Spore Type F</u>. AG-13.1(i) <u>898 - 425</u>

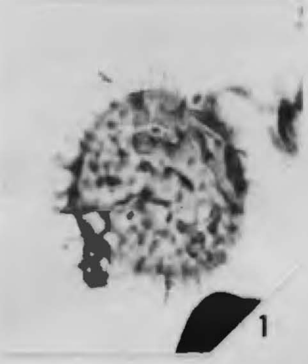
4. <u>Spore Type E</u>. AG-24.1(i) <u>1058 - 286</u>

5. <u>Spore Type A</u>. AEI-4375.1(i) <u>1080 - 399</u>

6. <u>Spore Type B</u>. AG-3.3(i) <u>915 - 277</u>. Distal? view.

7. <u>Spore? Type G</u>. AEI-13.46.2(iii) <u>1000 - 346</u>

# PLATE VI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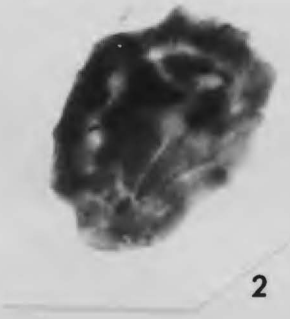
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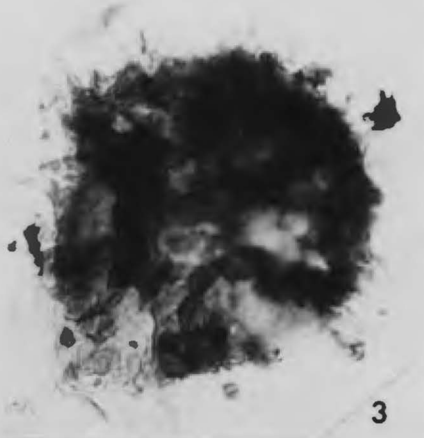
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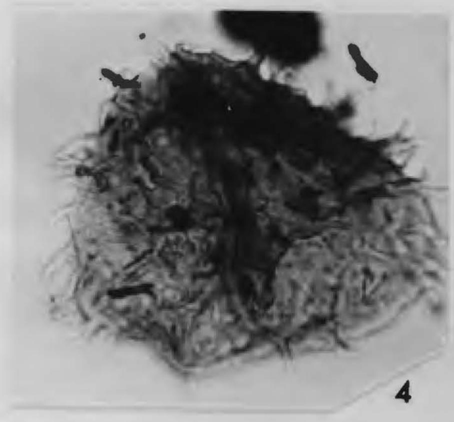
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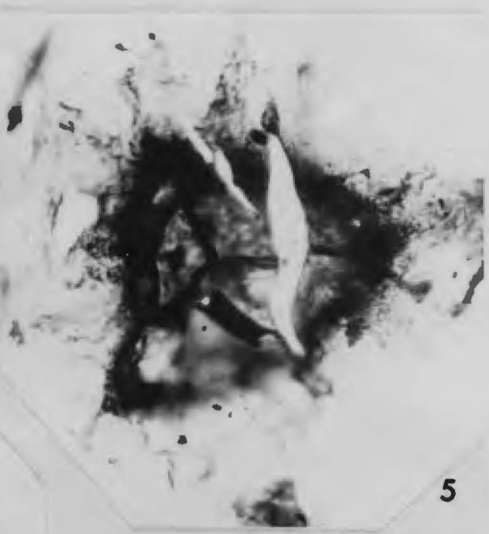
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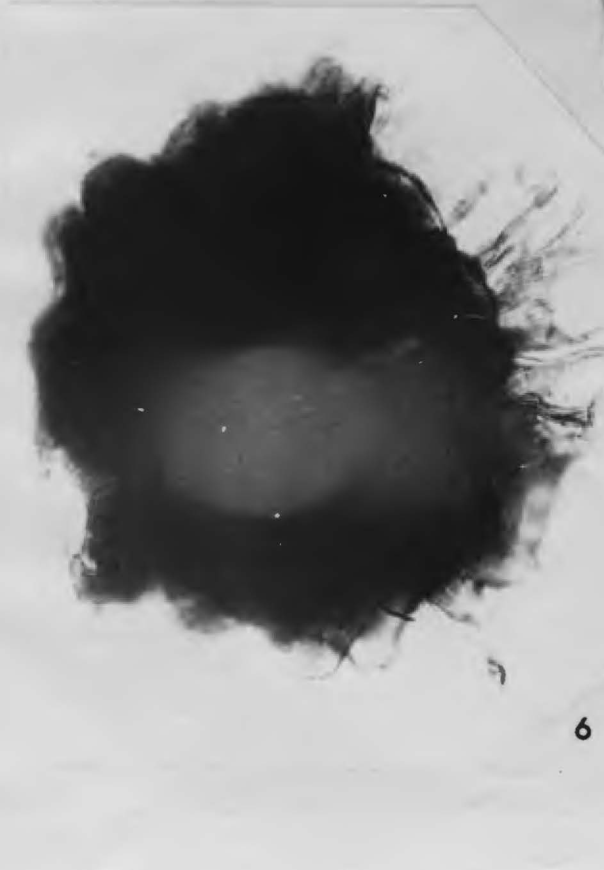
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## PLATE VII

Figure 1. *Endosporites*? *granisaccatus* sp. nov. Holotype.

2. *Endosporites*? *granisaccatus* sp. nov. Paratype.

3. *Endosporites* *sp.A*. AG-3.3(i) *763 - 320*
Laesurae in focus.

4. *Rhabdosporites* *langi* AG-3.3(i) *1144 - 277*

5. *Monosaccites* *Type A*. AG-3.3(i) *1105 - 449*

6. *Monosaccites* *Type B*. AG-3.3(ii) *918 - 287*

7. *Monosaccites* *Type C*. L46-L67.2(iii) *1167 - 293*

8. *Monosaccites* *Type E*. AG-3.3(i) *1035 - 443*

# PLATE VII


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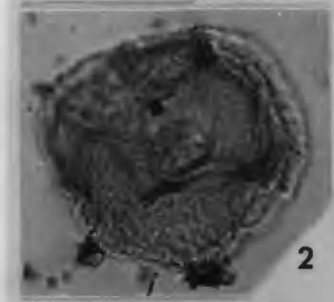
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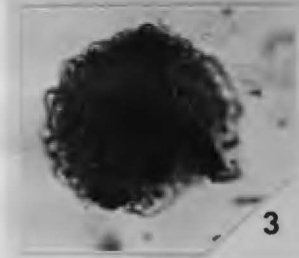
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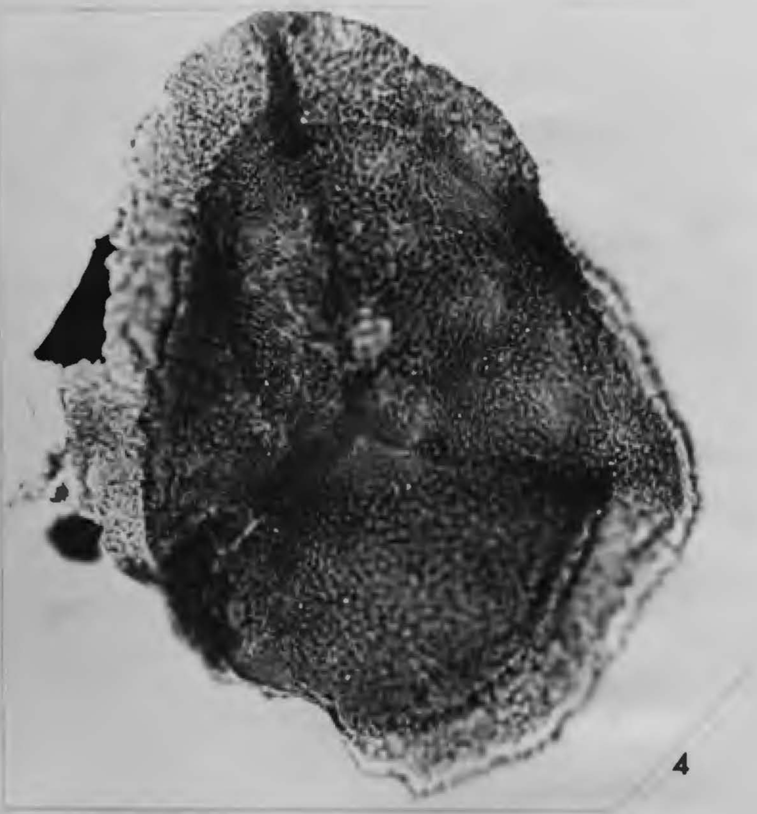
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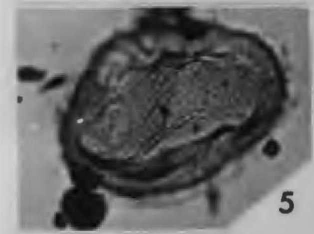
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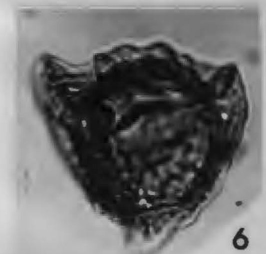
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# PLATE VIII

Figure 1. Monosaccites Type D. AG-3.3(i) 1164 - 294

2. Leiosphaeridia orbiculata AG-3.3(i) 1058 - 423

3. Leiosphaeridia microgranulifera AG013.i(ii) 1026 - 378

4. Leiosphaeridia microgranulifera AG-23.2(i) 1048 - 398

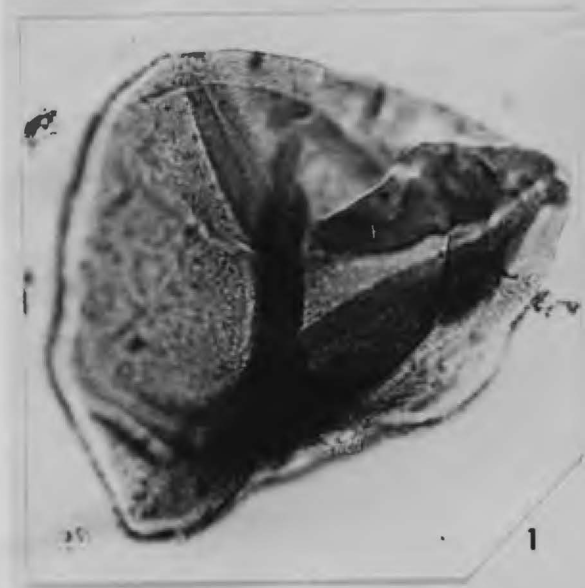
5. Simple ovoid pits in a tracheid fragment. Note hexagonal outlines (crassulae?) about pits.

6. Tracheid fragment with regular scalariform pitting.

7. Tracheid fragment with alternative, ovoid bordered pit pairs. Such xylem elements have been observed in the secondary wood of Callixylon (vide: Kräusel and Weyland, 1937, figs. 30-31).

8. Tracheid fragment with a single row of ovoid, bordered pit pairs.

# PLATE VIII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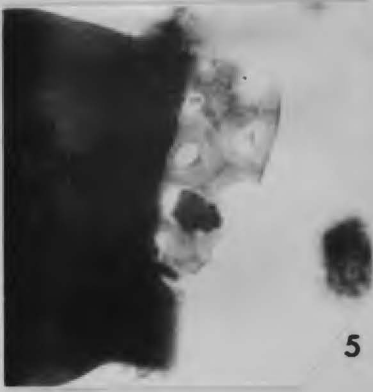
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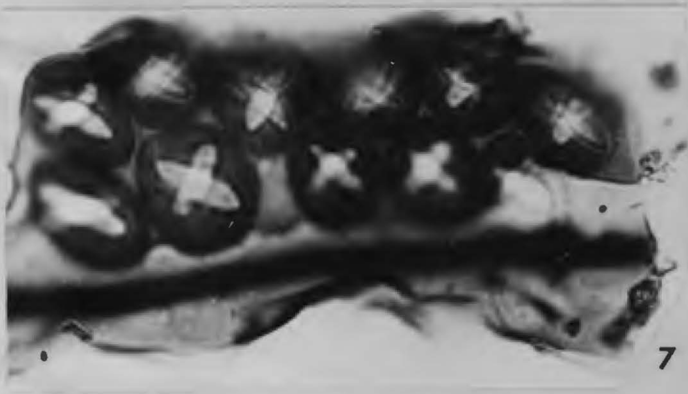
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