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CANADIAN AND AUSTRALIAN DEVONIAN SPORES: ZONATION AND CORRELATION

D.C. McGregor, G. Playford

1992

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PREFACE

Correlation of rock units over long distances is particularly important in Canada, a country with a land area of more than 85° of longitude and comprising several geological regions. Land derived palynomorphs are very useful for interregional correlation, especially of strata deposited in nonmarine and neritic environments, in which they may occur in prodigious numbers.

This report details the discovery, in Middle and Upper Devonian sedimentary rocks of Australia, of certain species of terrestrial palynomorphs (spores) that are previously known from Canada. The results establish correlation links between Canada and Australia, and provide additional defining species for existing northern hemisphere spore zones. This increases the capability of, and confidence in, spores used for interbasinal correlation of Devonian rocks in Canada. Such studies extend our understanding of the Paleozoic geology of Canada, and provide basic data important in the ongoing search for fossil fuels and minerals.

Elkanah A. Babcock
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PRÉFACE

La corrélation des unités lithologiques sur de grandes distances est particulièrement importante au Canada, un pays qui s'étend sur plus de 85° de longitude et qui comporte plusieurs régions géologiques. Les palynomorphes d'origine terrestre sont très utiles aux fins de corrélation interrégionale, notamment lorsque présents dans des couches déposées dans des milieux non marins et néritiques, où leur nombre peut être prodigieux.

Le présent rapport décrit dans le détail la découverte, dans des roches sédimentaires du Dévonien moyen à supérieur de l'Australie, de certaines espèces de palynomorphes terrestres (spores) déjà connues au Canada. Les résultats établissent des liens de corrélation entre le Canada et l'Australie, mais aussi ajoutent des espèces servant à définir les zones de spores qui existent dans l'hémisphère nord. Cela augmente la pertinence et la fiabilité d'utiliser les spores pour établir des corrélations interbassinales dans le cas des roches dévoniennes au Canada. Les études de cet ordre permettent d'élargir nos connaissances de la géologie du Paléozoïque au Canada et fournissent des données de base importantes pour poursuivre la quête de combustibles fossiles et de minéraux.

Elkanah A. Babcock
Sous-ministre adjoint
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CANADIAN AND AUSTRALIAN DEVONIAN SPORES: ZONATION AND CORRELATION

Abstract

Microscopic observations, in conjunction with a literature review of all available Australian Middle and Upper Devonian spore floras, and comparisons of these with coeval, palynostratigraphically zoned Canadian assemblages, reveal clear intercontinental similarities. Resemblances are evident in shared taxa (form, genera and species), morphons, and sequential introductions of particular morphological spore features. They are of sufficient scope to permit preliminary recognition in Australia of some of the palynozones established in 1986 for the Devonian in Canada and elsewhere in Euramerica, despite the present sporadic and incomplete knowledge of the Australian Devonian spore succession.

Key elements of the following Canadian palynozones occur within certain Australian sedimentary basins: *velata-langii* (Adavale Basin); *devonicus-naumovae* (Canning and Adavale basins); *lemurata-magnificus* (Canning and Drummond basins); *optivus-triangulatus* (Carnarvon, Canning, Adavale, and Tasmania basins); *ovalis-bulliferus* (Carnarvon, Canning, and Amadeus basins); *torquata-gracilis* (Carnarvon and Amadeus basins); and *pusillites-lepidophyta/lepidophyta-nitidus* (Canning and Bonaparte basins). Collectively, these zones span the lower Eifelian through uppermost Famennian. Australian palynological data, dependent almost entirely on the availability of subsurface materials, are most abundant for the upper Givetian-lower Frasnian (i.e., from rocks coeval with the Canadian *optivus-triangulatus* Zone). No Australian palynofloras are known from the Lower Devonian; and, apart from the uppermost Famennian, there is scant coverage of that stage. The Devonian-Carboniferous boundary in both Canada and Australia (and globally elsewhere) is conspicuously and reliably marked by the exit of the distinctive species *Retispora lepidophyta*.

The degree of palynological parallelism implies a commonality in the Devonian land vegetation between Canada and Australia, and supports suggestions of geographic proximity between Euramerica and eastern Gondwana during Middle through Late Devonian time. The present work also focuses on the incidence of certain endemic spore taxa, confined to either Canada or Australia, that signify, not unexpectedly, some floristic provincialism or phytogeographic segregation.

Consequential to this study are several important additions to the list of key species used in the recognition of most of the Middle and Upper Devonian palynozones. These provide further refinement to the zonal definitions, and enhance their correlative value within and beyond Canadian sequences. Overall, it is clear that Middle and Upper Devonian spore assemblages presently known from Australia are much more in unison with coeval Canadian assemblages than has hitherto been thought.

Résumé

L'observation au microscope et l'étude documentaire de toutes les flores de spores du Dévonien moyen à supérieur de l'Australie, afin de les comparer aux assemblages comtemporains à zonation palynostratigraphique du Canada, révèlent de nettes similitudes intercontinentales. Les ressemblances sont évidentes dans les taxons (formes, genres et espèces) et morphons communs, ainsi que dans les introductions séquentielles de traits morphologiques particuliers des spores. En première analyse, l'information est suffisante pour reconnaître, en Australie, certaines des palynozones établies en 1986 pour le Dévonien au Canada et ailleurs en Euramérique, malgré une connaissance erratique et incomplète de la succession des spores du Dévonien en Australie.

Les éléments clés des palynozones canadiennes suivantes se retrouvent dans certains bassins sédimentaires australiens : *velata-langii* (bassin d'Adavale); *devonicus-naumovae* (bassins de Canning et d'Adavale); *lemurata-magnificus* (bassins de Canning et de Drummond); *optivus-triangulatus* (bassins de Carnarvon, de Canning, d'Adavale et de Tasmanie); *ovalis-bulliferus* (bassins de Carnarvon, de Canning et d'Amadeus); *torquata-gracilis* (bassins de Carnarvon et d'Amadeus); et *pusillites-lepidophyta/lepidophyta-nitidus* (bassins de Canning et de Bonaparte). Collectivement, ces zones s'étendent de l'Eifélien inférieur au Famennien sommital. Les données palynologiques australiennes, qui dépendent presque entièrement de la disponibilité des matériaux en subsurface, sont particulièrement abondantes dans le cas des lithologies du Givétien supérieur–Frasnien inférieur (c.-à-d. qu'elles décrivent des roches contemporaines de la zone à *optivus-triangulatus* du Canada). On ne connaît aucune palynoflore australienne du Dévonien inférieur et, à l'exception du Famennien sommital, la couverture de cet étage est faible. La limite entre le Dévonien et le Carbonifère, autant au Canada qu'en Australie (et partout ailleurs dans le monde), est déterminée avec facilité et avec certitude par la disparition de l'espèce distinctive *Retispora lepidophyta*.

Le degré de parallélisme palynologique suppose des traits communs entre la végétation terrestre dévonienne du Canada et celle de l'Australie; il corrobore les suppositions de proximité géographique entre l'Euramérique et le Gondwana oriental à l'époque du Dévonien moyen à tardif. Le présent travail traite aussi de l'incidence de certains taxons de spores endémiques, confinés au Canada ou à l'Australie, qui dénotent, comme il fallait s'y attendre, d'un certain provincialisme floristique ou d'une certaine ségrégation phytogéographique.

Il découle de cette étude plusieurs additions importantes à la liste des espèces déterminantes pour la reconnaissance de la plupart des palynozones du Dévonien moyen à supérieur. Cela permet de raffiner les définitions zonales et d'en améliorer la valeur corrélative à l'intérieur et au-delà des séquences canadiennes. Globalement, il est clair que les assemblages de spores du Dévonien moyen à supérieur actuellement connus en Australie correspondent davantage aux assemblages canadiens contemporains que l'on avait d'abord cru.

Summary

In Canada, there are two main phytogeographic regions of Middle and Upper Devonian age, which can be recognized by their different spore assemblages: the northwestern mainland and Arctic Islands region, and southeastern Canada. Spores in the former region resemble those of the European U.S.S.R., whereas those in the latter are similar to those of northeastern U.S.A. and Western Europe. Certain taxa are common to all of these regions, and the Euramerican zonal scheme of Richardson and McGregor (1986) recognizes these similarities. However, much less is known about comparison of Canadian spore assemblages of this age with those of the southern hemisphere, including Australia. Previous studies showed that some northern and southern hemisphere spore assemblages do have distinctive taxa and morphological features in common. It appears, therefore, that an almost global, spore-based zonation may be possible.

Direct microscopic comparisons, in conjunction with review of the most definitive literature, now indicate that at least 44 Canadian/Euramerican spore genera and 80 species also occur in Australia. In addition, gradationally coherent morphological groups (morphons) centred around the following species are present in both regions: *Acinosporites lindlarensis, Ancyrospora simplex, A. longispinosa, Grandispora magnifica, Hystricosporites porrectus, Archaeozonotriletes variabilis, Cristatisporites triangulatus, Dibolisporites farraginis, Verrucosisporites scurrus, Emphanisporites rotatus, Geminospora lemurata*, and *Rhabdosporites langii.*

All but one of the Middle and Upper Devonian (Eifelian to Famennian) spore assemblage zones established in Canada are discernible, with various degrees of confidence, in Australia. In ascending stratigraphic order, the following zones can be recognized, with some qualifications, in one or more Australian sedimentary basins: the lower Eifelian *Grandispora velata-Rhabdosporites langii* Zone (Adavale Basin); the lower Eifelian-lower Givetian *Densosporites devonicus-Grandispora naumovae* Zone (Canning and Adavale basins); the lower to upper Givetian *Geminospora lemurata-Cymbosporites magnificus* Zone (Canning and Drummond basins); the upper Givetian to lowermost Frasnian *Contagisporites optivus* var. *optivus-Cristatisporites triangulatus* Zone (Adavale, Canning, Carnarvon,

and Tasmania basins); the lower to upper Frasnian *Archaeoperisaccus ovalis-Verrucosisporites bulliferus* Zone (Canning, Carnarvon, and Amadeus basins); the uppermost Frasnian to lower Famennian *Teichertospora torquata-Grandispora gracilis* Zone (Carnarvon and Amadeus basins); and the upper Famennian *Vallatisporites pusillites-Retispora lepidophyta* Zone and *Retispora lepidophyta-Verrucosisporites nitidus* Subzone (Canning and Bonaparte basins). The Devonian-Carboniferous boundary is well defined palynologically in both Canada and northwestern Australia (and elsewhere globally) by the disappearance of *Retispora lepidophyta*.

Enough similarities exist between Euramerican and Australian Middle and Upper Devonian spore assemblages to sustain long-distance biostratigraphic correlation using modifications of the assemblage palynozones of Richardson and McGregor (1986). Ten taxa shared by Canada and Australia are added to the characterizing taxon inventories of the Euramerican spore zones. At least 16 others may be added once their morphology, taxonomy, and stratigraphic ranges have been documented. The first appearance of key morphons and form features may also be useful for intercontinental correlation, complementary to the species-level comparisons. The resulting enhanced potential for global palynostratigraphic correlation also improves the capability for interregional correlation of Devonian rocks in Canada.

On the other hand, some described and undescribed Australian spore taxa and morphons appear, on the basis of present knowledge, to be absent from Euramerica; conversely, several hundred Canadian/Euramerican taxa have not been observed in Australian palynofloras. *Ambagisporites, Archaeoperisaccus indistinctus* (structurally different from true *Archaeoperisaccus*), *Medusaspora*, and a distinctive group resembling *Camptozonotriletes* and *Costazonotriletes* have not been recorded in Euramerica, whereas true *Archaeoperisaccus, Biornatispora, Contagisporites, Cornispora, Cyrtospora, Diducites, Lagenicula, Laiphospora, Lanatisporis, Ocksisporites, Periplecotriletes, Rugospora, Sinuosisporis*, and *Triangulatisporites* appear to be absent from the Australian Devonian. No unequivocal examples of cingulizonate spores (*Densosporites* spp. *sensu* Richardson, 1960)—common in the Euramerican Middle Devonian—have been found in Australia.

These qualitative palynofloral dissimilarities doubtless reflect phytogeographic differences related to climate, physiography, and continental plate configurations in Middle and Late Devonian time. However, the many similarities between Australian and Canadian spores do suggest significant floral cosmopolitanism in Devonian time, and sufficiently close proximity of Gondwana and the Old Red Sandstone Continent to allow considerable floristic interchange.

Sommaire

Au Canada, il existe deux grandes régions phytogéographiques du Dévonien moyen à tardif; elles se reconnaissent à leurs assemblages de spores différents et sont les suivantes : la région de la partie nord-ouest du continent et des îles de l'Arctique ainsi que celle de la partie sud-est du Canada. Les spores de la première région ressemblent à ceux de l'Union soviétique européenne, tandis que les spores de l'autre région s'apparentent à ceux de la partie nord-est des États-Unis et de l'Europe occidentale. Certains taxons sont communs à toutes ces régions et le plan zonal euraméricain de Richardson et McGregor (1986) relève ces ressemblances. Toutefois, la comparaison entre les assemblages de spores canadiens et ceux de l'hémisphère sud, dont l'Australie, est beaucoup moins documentée. Des études antérieures révèlent que certains assemblages de spores des hémisphères nord et sud ont en commun des taxons précis et des caractéristiques morphologiques distinctives. Il semble donc qu'il serait possible d'établir une zonation selon les spores à l'échelle de presque tout le globe.

Des comparaisons microscopiques directes combinées à un examen de la documentation la plus définitive indiquent qu'au moins 44 genres et 80 espèces de spores du Canada et de l'Euramérique se retrouvent aussi en Australie. En outre, les deux régions renferment des groupes morphologiques présentant une gradation dans les caractéristiques (morphons), centrés sur les espèces suivantes : *Acinosporites lindlarensis*, *Ancyrospora simplex*, *A. longispinosa*, *Grandispora magnifica*, *Hystricosporites porrectus*, *Archaeozonotriletes variabilis*, *Cristatisporites triangulatus*, *Dibolisporites farraginis*, *Verrucosisporites scurrus*, *Emphanisporites rotatus*, *Geminospora lemurata* et *Rhabdosporites langii*.

Sauf une exception, toutes les zones d'assemblages de spores du Dévonien moyen à supérieur (Eifélien au Famennien) établies au Canada se retrouvent en Australie, avec des degrés de confiance variables. Dans l'ordre stratigraphique ascendant, les zones suivantes sont reconnaissables, avec plus ou moins de certitude, dans un ou plusieurs bassins sédimentaires australiens : la zone à *Grandispora velata-Rhabdosporites langii* de l'Eifélien précoce (bassin d'Adavale); la zone à *Densosporites devonicus-Grandispora naumovae* de l'Eifélien inférieur-Givétien inférieur (bassins de Canning et d'Adavale); la zone à *Geminospora lemurata-Cymbosporites magnificus* du Givétien inférieur à supérieur (bassins de Canning et de Drummond); la zone à *Contagisporites optivus* var. *optivus-Cristatisporites triangulatus* du Givétien supérieur au Frasnien basal (bassins d'Adavale, de Canning, de Carnarvon et de Tasmanie); la zone à *Archaeoperisaccus ovalis-Verrucosisporites bulliferus* du Frasnien inférieur à supérieur (bassins de Canning, de Carnarvon et d'Amadeus); la zone à *Teichertospora torquata-Grandispora gracilis* du Frasnien sommital au Famennien inférieur (bassins de Carnarvon et d'Amadeus); ainsi que la zone à *Vallatisporites pusillites-Retispora lepidophyta* du Famennien supérieur et la sous-zone à *Retispora lepidophyta-Verrucosisporites nitidus* (bassins de Canning et de Bonaparte). La limite entre le Dévonien et le Carbonifère est bien définie palynologiquement, autant au Canada que dans le nord-ouest de l'Australie (et partout ailleurs dans le monde), par la disparition de *Retispora lepidophyta*.

Il existe assez de points similaires entre les assemblages de spores euraméricains et australiens du Dévonien moyen à supérieur pour établir une corrélation biostratigraphique sur de longues distances en modifiant les palynozones d'assemblage de Richardson et McGregor (1986). Dix taxons partagés par le Canada et l'Australie sont ajoutés aux répertoires de taxons permettant de caractériser les zones de spores euraméricaines. Au moins 16 autres pourraient s'ajouter lorsque leur morphologie, leur taxonomie et leur répartition stratigraphique auront été documentées. La première apparition de morphons clés et de caractéristiques morphologiques importantes pourrait aussi être utile aux fins de corrélation intercontinentale et compléteraient les comparaisons au niveau de l'espèce. Une telle augmentation des possibilités de corrélation palynostratigraphique à l'échelle de la planète, permet aussi d'améliorer les possibilités de corrélation interrégionale des roches dévoniennes au Canada.

Par ailleurs, certains taxons et morphons de spores, tant décrits que non décrits, semblent, dans l'état actuel de nos connaissances, ne pas se retrouver en Euramérique; plusieurs centaines de taxons canadiens/euraméricains n'ont pas encore été relevés dans les palynoflores australiennes. *Ambagisporites*, *Archaeoperisaccus indistinctus* (structuralement différents du vrai *Archaeoperisaccus*), *Medusaspora* et un groupe distinct ressemblant à *Camptozonotriletes* et à *Costazonotriletes* n'ont pas été observés en Euramérique; et il semble que les vrais *Archaeoperisaccus*, *Biornatispora*, *Contagisporites*, *Cornispora*, *Cyrtospora*, *Diducites*, *Lagenicula*, *Laiphospora*, *Lanatisporis*, *Ocksisporites*, *Periplecotriletes*, *Rugospora*, *Sinuosisporis* et *Triangulatisporites* soient absents du Dévonien australien. Aucun exemple non équivoque de spores cingulizonés (*Densosporites* spp. *sensu* Richardson, 1960), communs dans le Dévonien moyen de l'Euramérique, n'a été trouvé en Australie.

Ces différences palynoflorales qualitatives reflètent sans aucun doute les différences phytogéographiques liées au climat, à la physiographie et aux configurations des plaques continentales à l'époque du Dévonien moyen à tardif. Toutefois, les nombreuses ressemblances entre les spores australiens et canadiens indiquent l'existence d'une flore très cosmopolite au Dévonien de même qu'une proximité assez grande entre le Gondwana et le continent des Vieux-grès-rouges pour permettre un échange floristique considérable.

INTRODUCTION

In 1986, Richardson and McGregor defined 19 interregional spore assemblage zones embracing the Lower Silurian through Upper Devonian stratigraphic interval, and documented their distribution within, and marginal to, the Old Red Sandstone Continent. They referred to possible future recognition of some of the zones in certain regions of the southern hemisphere, including Australia. Some species characterizing these zones are already known to be cosmopolitan, whereas others apparently are more localized within continental areas that may have been contiguous in Devonian time (McGregor, 1979a, 1981; Streel, 1986).

In Canada, two main Middle and Upper Devonian phytogeographic regions can be recognized, as reflected by the geographic distribution of spore assemblages: the northwestern mainland and Arctic Islands region, which shares endemic taxa with European U.S.S.R. (McGregor and Camfield, 1982; Arkhangelskaya et al., 1990); and southeastern Canada, which has distinctive floral links with northeastern U.S.A. and southwestern Europe (McGregor and McCutcheon, 1988). Middle and Upper Devonian spore assemblages from these two regions are conspicuously different, yet have many taxa in common.

Assemblages from both of these palynogeographic regions have taxonomic affinities, not well understood, with assemblages from South America (Loboziak et al., 1988), Africa (Paris et al., 1985; Loboziak and Streel, 1989), and China (Lu, 1980, 1988). Balme (1988a), Grey (1991, 1992), and Playford (1976) have shown that Canadian and Australian Middle and Upper Devonian spore assemblages share several geographically widespread taxa. Although the studies referred to above have touched on certain aspects of Canadian/Euramerican-Gondwanic comparisons, no comparative overview of spore floras of these regions (see Fig. 1) has previously been undertaken.

The efficacy of spores for Devonian long-distance, temporal correlation, obviously important in Canada, would be improved by increased understanding of these global phytogeographic patterns, and how they relate to spore assemblage distribution in Canada. This comparative study of Canadian and Australian spore floras was undertaken to increase understanding of these matters. Streel et al. (1990) addressed some of these questions in a paper on the phytogeography of Euramerica and western Gondwana. We present here the results of our comparison of eastern Gondwanan (Australian) spore assemblages, within the lower Eifelian to upper Famennian interval, with approximately coeval assemblages from Canada and other parts of Devonian Euramerica and Gondwana.

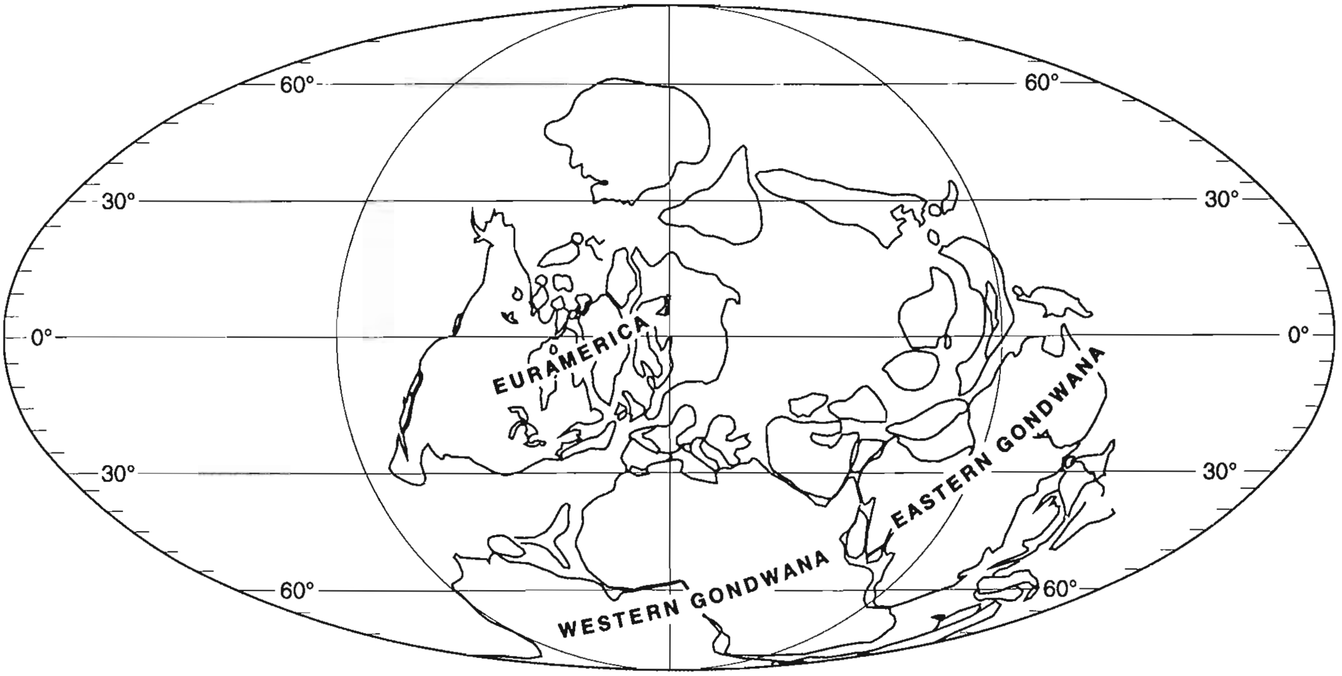

Figure 1. Givetian paleogeography after Scotese and McKerrow (1990), showing the relative positions of Euramerica, eastern and western Gondwana.

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SPORES AND STRATIGRAPHIC CORRELATION

Historical development

Spores of probable terrestrial origin have been found in rocks as old as Lower Ordovician (Gray et al., 1982). By the Late Silurian–Early Devonian they had increased significantly in abundance and morphological complexity as plant life progressively diversified on land. They were dispersed into a range of terrestrial and nearshore marine sedimentary environments, often in prodigious quantities. By their abundance, diversity, and interfacial distribution, dispersed spores represent a unique record of the evolution of terrestrial plant life. They are the most diverse and abundant fossils in the continental magnafacies, and provide an effective means of direct chronostratigraphic correlation between marine and nonmarine sedimentary sequences. Moreover, they are easily retrieved and concentrated from a wide range of host sediments.

Studies of Devonian spores for stratigraphic purposes began in Europe and North America (Naumova, 1953; Kedo, 1955; Hoffmeister et al., 1955; McGregor, 1957). With certain exceptions, this Euramerican focus has persisted until recently.

In North America, the first Devonian spore zonal schemes were developed to facilitate hydrocarbon exploration, and were mostly proprietary. In Europe, Devonian spore-based zonations were initiated in the Soviet Union and resulted in publication, and general acceptance there, of a system of 19 sequential "spore complexes" subdividing Devonian strata of the Russian Platform (Naumova, 1953). Since then, various independently developed regional sporological zonations have been devised for parts of the Devonian of Euramerica (e.g., Pykhova, 1960; Streel, 1966 et seq.; Arkhangelskaya, 1972 et seq.; McGregor and Camfield, 1976; Turnau, 1978; Loboziak and Streel, 1988).

Long-distance correlation

By the 1960s, it was evident that some taxa and distinctive morphological features of Devonian spores were geographically widespread. For example, several workers (e.g., Balme and Hassell, 1962; Kerr et al., 1965) had perceived similarities between Middle and Upper Devonian spores from various parts of the world and those from the U.S.S.R. described and stylistically figured by Naumova (1953) and Kedo (1955). McGregor (1967, 1969) pointed out the pronounced resemblance of assemblages from the Canadian Arctic and the Russian Platform.

Richardson (1974) produced a generalized stratigraphic overview of the ranges of taxa and form features of Devonian spores in the northern hemisphere. His preliminary synthesis, developed further and incorporating elements of local palynozonations, resulted in the more comprehensive interregional Euramerican zonal scheme proposed by Richardson and McGregor (1986). Key elements of this zonation have broad geographic distribution, as do representatives of some marine faunal groups, e.g., conodonts and ammonoids. The Euramerican zonation was not intended to supplant regional zonations such as those of Loboziak and Streel (1988). Regional zones, like regional chronostratigraphic units, can remain useful for local, more detailed stratigraphic subdivision.

Characterizing species of some of the Euramerican zones have been recognized in Poland (Turnau, 1986), the U.S.S.R. (Arkhangelskaya et al., 1990), North Africa (Streel et al., 1988), Australia (Balme, 1988a; Grey, 1991, 1992), Bolivia (Vavrdová et al., in press), and Brazil (Loboziak et al., 1988).

Some information has thus already accrued about patterns of interregional distribution and differentiation of Devonian spore assemblages (also see Streel, 1986). However, fewer data are available on which to assess their potential for global correlation. Effective long-distance distribution of plants (and their spores) was undoubtedly subject to a variety of intrinsic and extrinsic influences in the Paleozoic, as it is today. Such distribution may not necessarily have been geologically instantaneous (Dettmann, 1986; Laveine et al., 1989). Little information exists on the ecological and distributional attributes of particular kinds of Devonian plants (and spores), but we do know that the mobility of plant taxa today is extremely varied (Tryon, 1971, 1985). Such knowledge, when available for Devonian time, will supplement information of the kind presented in this report, providing additional measures for determining which taxa and morphons are most useful for long distance biogeochronology (see McGregor and Playford, 1990).

OUTLINE OF STRATIGRAPHY AND PREVIOUS SPORE STUDIES

Given below is a summary-review of Canadian and Australian stratal sequences from which miospores have been examined by us or have been described or recorded in previous reports. Figures 2 and 3 show generalized locations of the palyniferous lithostratigraphic units, which are tabulated chronostratigraphically in Figures 4 and 5.

Canada

Devonian continental to nearshore marine strata are widespread in Canada, and in some regions attain thicknesses of several thousand metres (e.g., on the northwestern mainland, in the Arctic Archipelago, and in the Gaspé region of the Atlantic coast). Spores can be obtained from surface exposures in most regions where facies are suitable for their occurrence. This contrasts with the rarity of spores in Australian outcrops, which tend to be strongly weathered and essentially devoid of palynomorphs.

For convenience of reference, the ensuing review of Canadian Devonian palyniferous strata follows the numbered sequence of geographic locations shown in Figure 2. Data relating to the lithostratigraphic units of the Arctic Islands clastic wedge are presented in Appendix Table 1.

Alberta and Prophet troughs

Upper Middle and Upper Devonian rocks in the Rocky Mountains of east-central British Columbia are represented by the predominantly shallow marine Fairholme Group (Figs. 2 and 4, loc. 1). They comprise, in ascending stratigraphic order, carbonate platform deposits (Flume Formation), a thick shallow marine shaly unit (Perdrix Formation), a thin bedded nodular limestone deposit (Mount Hawk Formation), and a silty carbonaceous sequence (Ronde Formation). The Flume, Perdrix, and Mount Hawk formations contain both miospores and invertebrate fossils indicating late Givetian to early Frasnian, early to late Frasnian, and late Frasnian ages respectively; and siltstone of the Calmar Formation, correlative with the lower Ronde Formation, contains late Frasnian spores (Geldsetzer, 1987; McGregor, unpublished data). McGregor et al. (1985) concluded that the Middle/Upper Devonian boundary is high in the Flume Formation.

Black shales of the Besa River Formation (Bamber et al., 1968; Richards, 1990, Fig. 9.29a, column 4, and Fig. 9.44, section 13) north of location 1 contain uppermost Devonian and Lower Carboniferous miospores (McGregor, unpublished; J. Utting, pers. comm. to DCM, 1990). They are thus in part coeval with the Exshaw-Banff sequence to the east and south. The Besa River Formation farther north (Morrow and Geldsetzer, 1989) grades into the Imperial Formation of the Mackenzie Basin (see below).

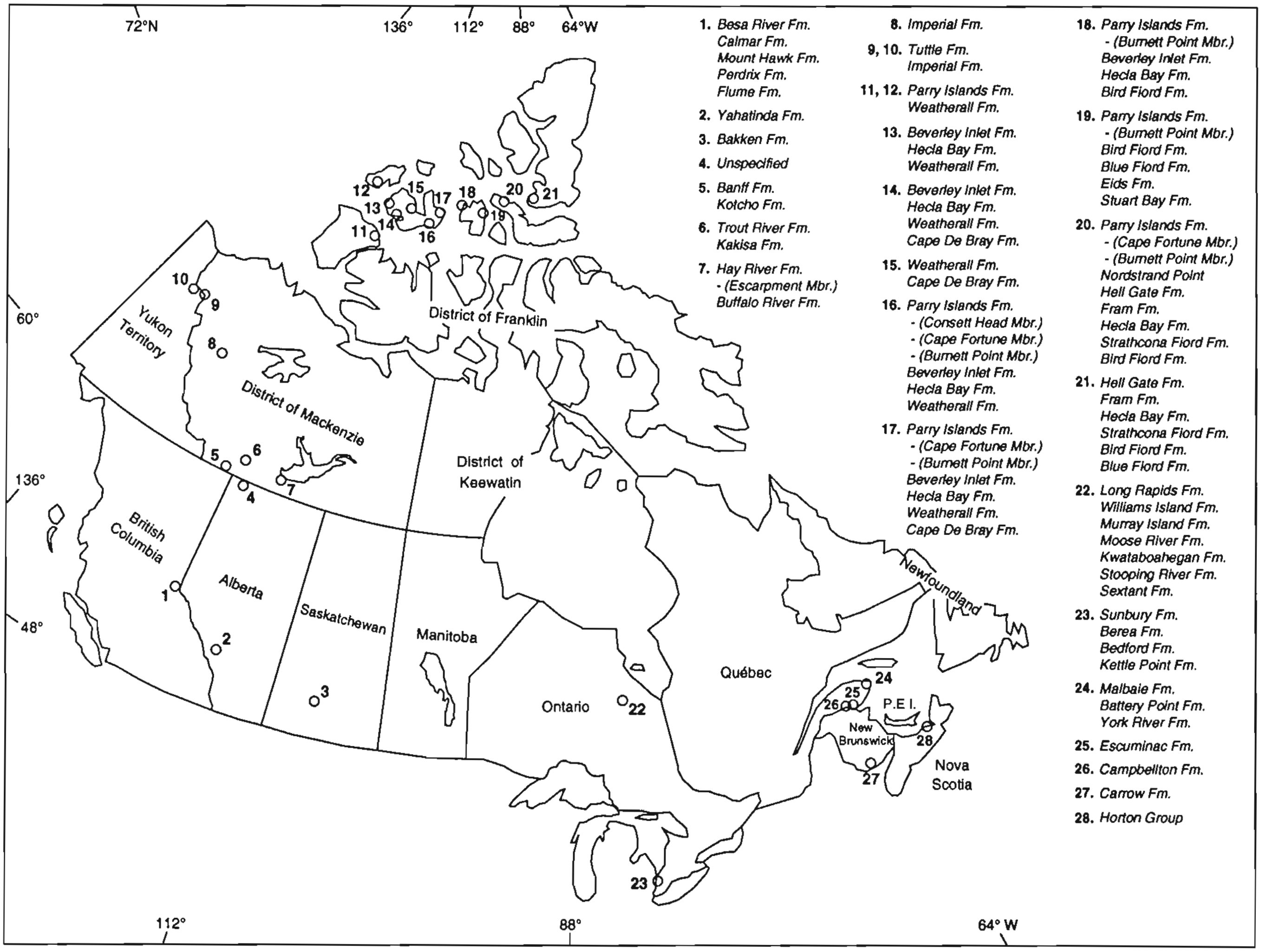

Figure 2. *Geographic locations (1–28) of Canadian upper Lower to uppermost Upper Devonian lithostratigraphic units from which spores were examined, or from which descriptions or illustrations of specimens are available. See Appendix Table 3 for detailed description of localities, and Figure 4 for chronostratigraphic correlation.*

To the south, in the Front Ranges of the Rocky Mountains near Calgary (loc. 2), vascular plant fragments and a small variety of carbonized miospores occur in the Yahatinda (formerly Ghost River) Formation (Greggs et al., 1962; McGregor, 1963, 1964; Scheckler, 1978). The dolomite and dolomitic shale of the Yahatinda are interpreted as channel fill deposits. On the basis of their mega- and palynofloral content, and their intergradational relationship with the overlying fossiliferous Fairholme Group, they are believed to be upper Givetian.

Williston Basin

The Bakken Formation of southern Saskatchewan (loc. 3) is part of the geographically extensive black shale sequence including, among others, the Exshaw Formation to the west. This sequence covered much of the North American craton in Late Devonian–Early Carboniferous time. Upper Famennian spores and microphytoplankton occur in the lower shale and middle sandstone members of the Bakken in Saskatchewan, as well as in the upper shale member where they may be reworked (Coquel et al., 1976; Playford and McGregor, in press). Holland et al. (1987) reported Lower *expansa* Zone (late Famennian) conodonts (see Fig. 6) in the lower shale, and Lower *crenulata* Zone (Kinderhookian) conodonts in the upper shale of the Bakken in adjacent North Dakota. In Saskatchewan, Uyeno (pers. comm. to DCM, 1990) found conodonts attributable to the *expansa* Zone in the lower member, and of early Tournaisian age (but not younger than the *crenulata* Zone) in the upper member.

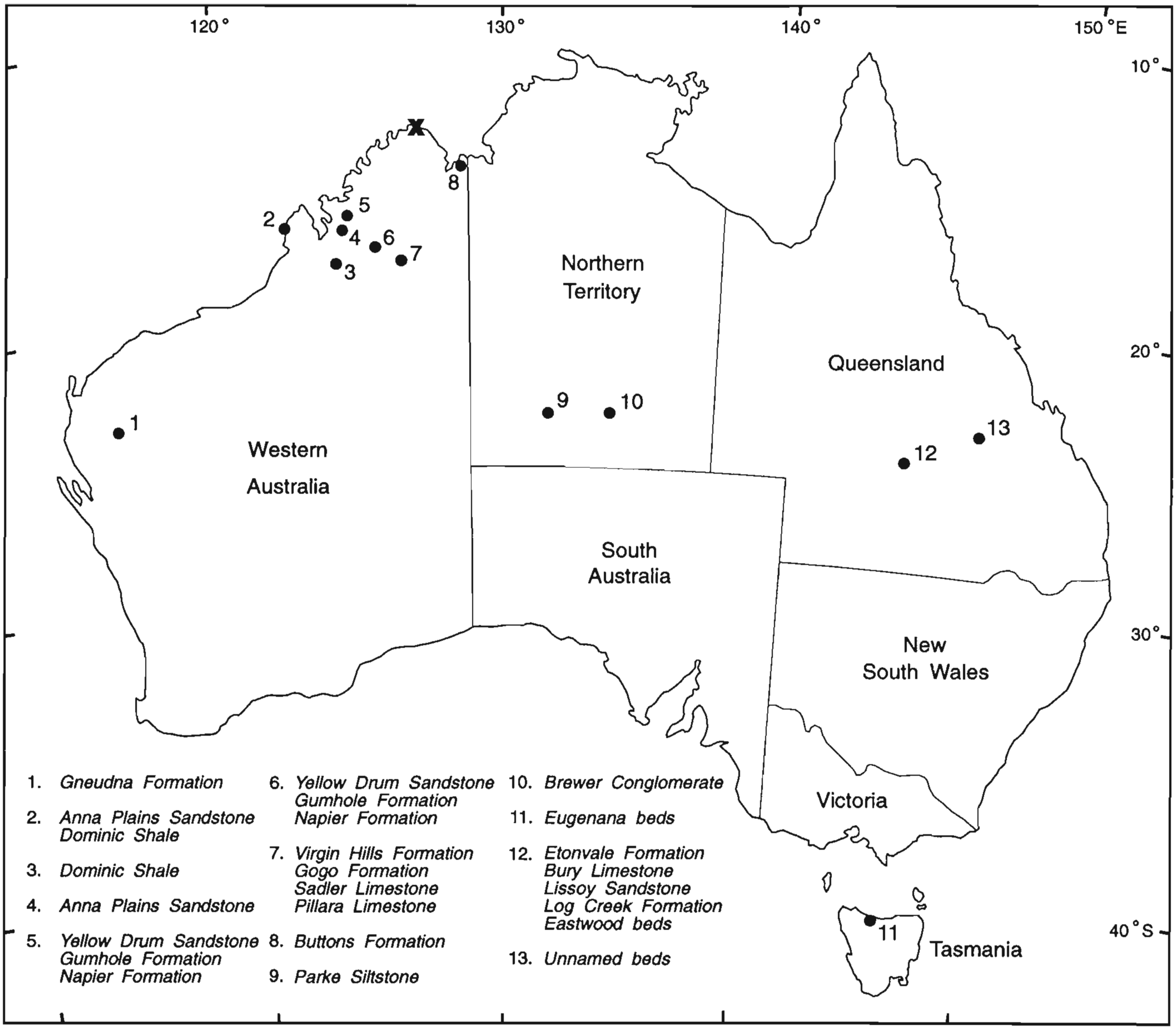

Figure 3. Geographic locations (1–13) of Australian Middle and Upper Devonian lithostratigraphic units from which spores were examined, or from which descriptions or illustrations of specimens are available. See Appendix Table 3 for detailed description of localities, and Figure 5 for chronostratigraphic correlation. x, *Amax Ellendale well.*

Interior Platform

In Western Canada, nearly horizontal Paleozoic cratonic sediments extend northward into the western District of Mackenzie. South and west of Great Slave Lake, Middle and Upper Devonian strata are sporadically palyniferous and commonly are associated with age-diagnostic marine fossils. Audretsch (1968) illustrated a selection of upper Givetian miospores, acritarchs, and chitinozoans from green calcareous shale of the Buffalo River Formation (see Kyle, 1981) in the subsurface near the western end of Great Slave Lake (loc. 7). Uyeno (unpublished data) recovered conodonts of late Givetian or early Frasnian age (*disparilis* to Lower *asymmetrica* zones) from a subsurface sample of the Buffalo River Formation in the same region.

A thick sequence of marine shale and intercalated thin, bioclastic, and silty limestone, the Hay River Formation, also occurs in this region. It contains abundant Frasnian corals and brachiopods (Belyea and

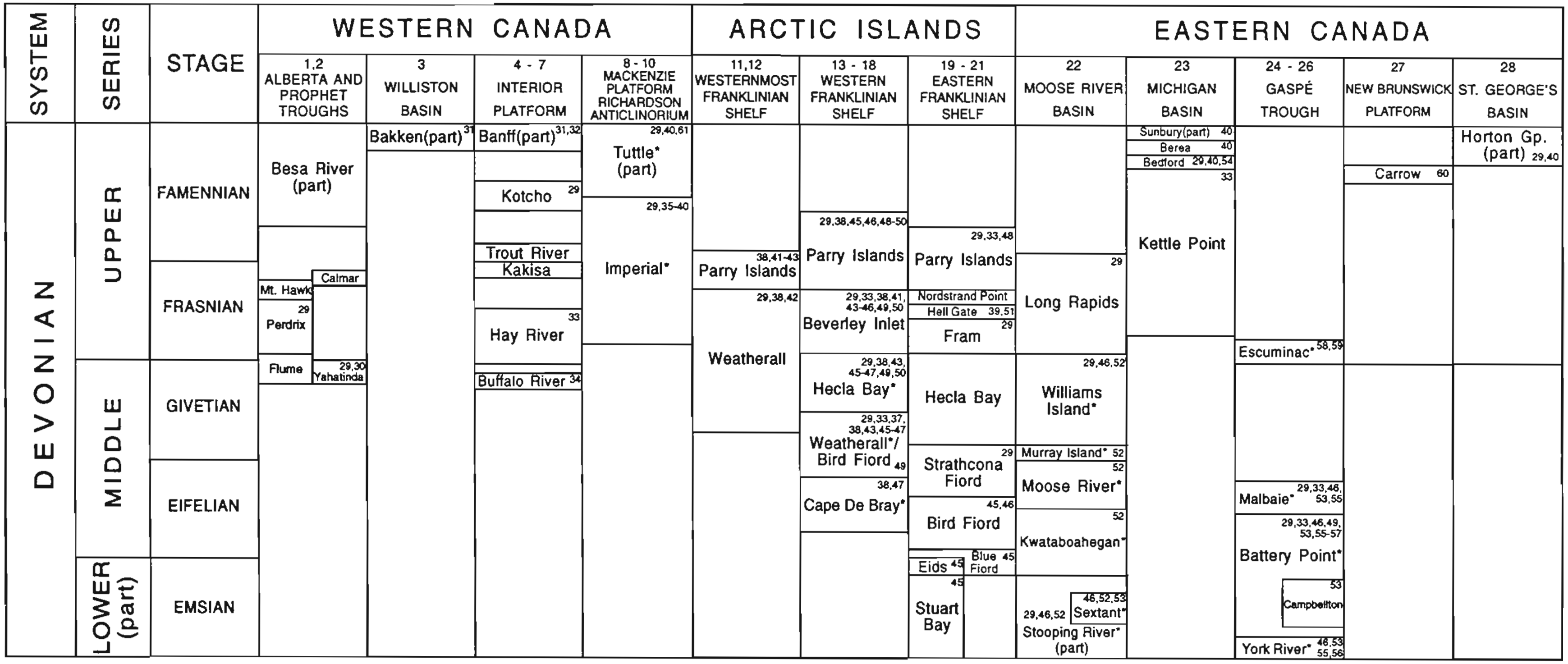

Figure 4. Approximate correlation of selected Canadian Devonian spore-bearing lithostratigraphic units. Unit thicknesses not to scale, and diachronous boundaries not shown. Empty spaces in columns do not necessarily signify absence of strata. Correlations are based on published biostratigraphic information (see nos. 29 to 61) in conjunction with unpublished palynological data. Asterisks indicate that formal descriptions of spores have been published.

Numbers 1 to 28 refer to geographic locations in Figure 2. Numbers 29 to 61 refer to the following references: ***29***. *Richardson and McGregor (1986);* ***30***. *McGregor (1964);* ***31***. *Coquel et al. (1976);* ***32***. *Staplin and Jansonius (1964);* ***33***. *McGregor and Owens (1966);* ***34***. *Audretsch (1968);* ***35***. *Braman and Hills (1985);* ***36***. *Chi and Hills (1974);* ***37***. *Chi and Hills (1976a);* ***38***. *Chi and Hills (1976b);* ***39***. *McGregor (1969);* ***40***. *McGregor (1970);* ***41***. *Hills et al. (1975);* ***42***. *Hills et al. (1971);* ***43***. *Owens (1971);* ***44***. *McGregor (1960);* ***45***. *McGregor and Uyeno (1972);* ***46***. *McGregor (1979b);* ***47***. *McGregor and Camfield (1982);* ***48***. *Kerr et al. (1965);* ***49***. *McGregor (1967);* ***50***. *Whiteley (1980);* ***51***. *Chaloner (1959);* ***52***. *McGregor and Camfield (1976);* ***53***. *McGregor (1961);* ***54***. *Wood (1984);* ***55***. *McGregor (1973);* ***56***. *McGregor (1977);* ***57***. *Scott and Rouse (1961);* ***58***. *Arnold (1936);* ***59***. *Brideaux and Radforth (1970);* ***60***. *McGregor and McCutcheon (1988);* ***61***. *Hills, Hyslop, Braman and Lloyd (1984). For other Canadian Devonian lithostratigraphic units in which spores have been found, see McGregor (1979a) and McGregor and Camfield (1982).*

McLaren, 1962), benthic ostracodes (Braun, 1968), and *Polygnathus* biofacies conodonts (Klapper and Lane, 1985). McGregor and Owens (1966, Pl. 22–25) figured well preserved miospores from beds high in the Escarpment Member of the Hay River Formation. From Klapper and Lane's (1985) data, these beds appear to be correlative with the conodont *A. triangularis* Zone or Lower *gigas* Zone.

The uppermost Frasnian Kakisa Formation, about 1500 m higher in the sequence to the west of Great Slave Lake (loc. 6), consists of silty limestone, in part reefal, with a rich marine fauna of the conodont Upper *gigas* Zone (Belyea and McLaren, 1962; Braun and Lethiers, 1982; Klapper and Lane, 1985). The upper few metres of the Kakisa contain a diverse upper Frasnian spore flora (McGregor, unpublished data).

Calcareous sandstone of the Trout River Formation overlies the Kakisa Formation with a sharp lithological and faunal break. Excellently preserved spores are present in the lower few metres of the Trout River Formation (McGregor, unpublished data), a few metres below conodonts of the Lower or Middle *crepida* Zone (Klapper and Lane, 1985).

Famennian spores have been extracted from grey calcareous shale in a limestone–shale section about five

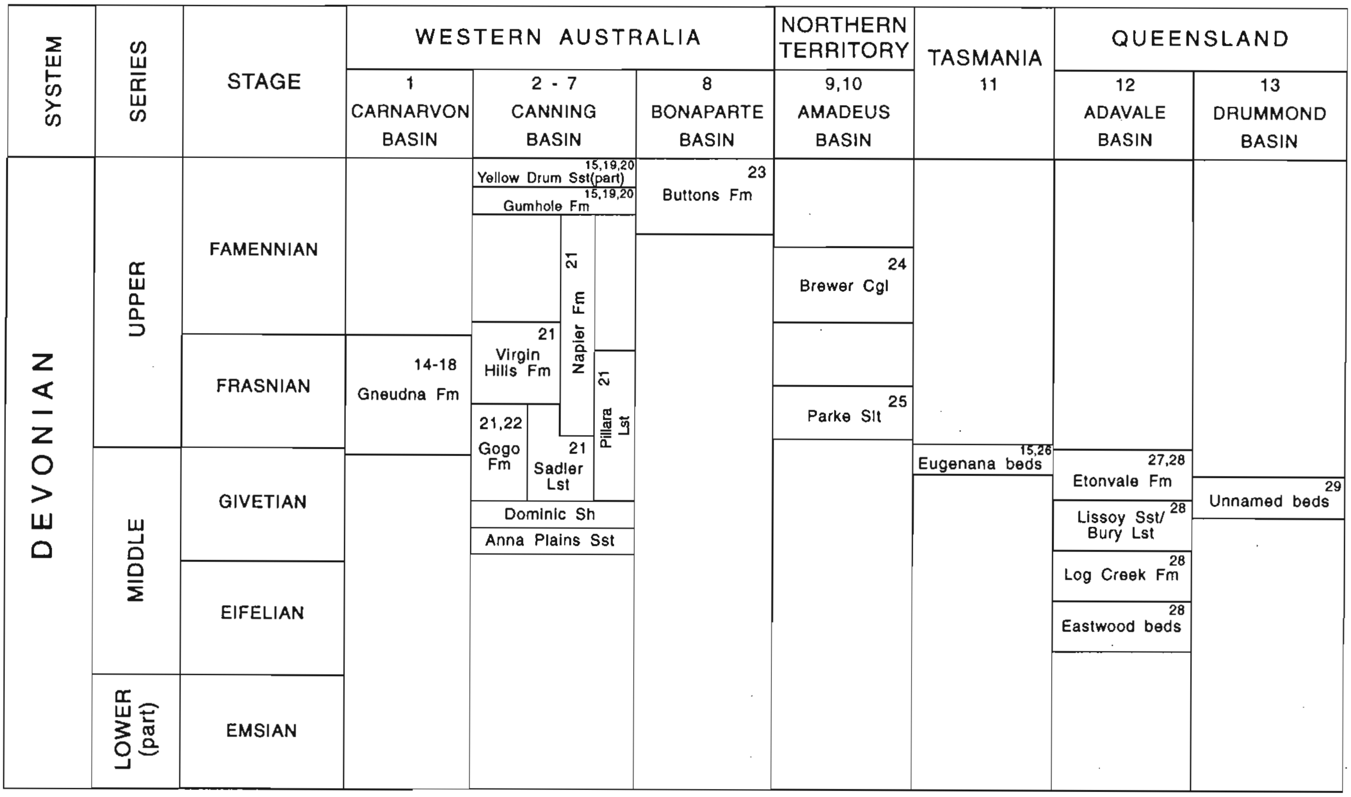

Figure 5. *Approximate correlation of Australian Devonian spore-bearing lithostratigraphic units. Unit thicknesses not to scale. Empty spaces in columns do not necessarily signify absence of strata. Correlations are based on published biostratigraphic information (see nos. 14 to 29) in conjunction with the present authors' examination of spore assemblages from all units except the Napier Formation and the Parke Siltstone.*

Numbers 1 to 13 refer to geographic locations in Figure 3. Numbers 14 to 29 refer to the following references: ***14.*** *Balme (1962);* ***15.*** *Balme (1964);* ***16.*** *Balme (1988a);* ***17.*** *Balme (1988b);* ***18.*** *Playford (1983);* ***19.*** *Balme and Hassell (1962);* ***20.*** *Playford (1976), see Druce and Radke (1979) for revision of stratigraphic nomenclature;* ***21.*** *Grey (1992);* ***22.*** *Grey (1974);* ***23.*** *Playford (1982);* ***24.*** *Playford et al. (1976);* ***25.*** *Hodgson (1968);* ***26.*** *Banks and Burns (1962);* ***27.*** *de Jersey (1966);* ***28.*** *Price (1980);* ***29.*** *Playford in D'Arcy (1987). For other Australian Devonian lithostratigraphic units in which spores have been found, see Balme (l988a, Fig. 10).*

SERIES	STAGE	STANDARD CONODONT ZONE (PELAGIC BIOFACIES)	
LOWER CARBONIFEROUS	TOURNAISIAN (part)	*crenulata*	Upper
			Lower
		sandbergi	
		duplicata	Upper
			Lower
		sulcata	
UPPER DEVONIAN	FAMENNIAN	*praesulcata*	Upper
			Middle
			Lower
		expansa	Upper
			Middle
			Lower
		postera	Upper
			Lower
		trachytera	Upper
			Lower
		marginifera	U'most
			Upper
			Lower
		rhomboidea	Upper
			Lower
		crepida	Upper
			Middle
			Lower
		P. triangularis	Upper
			Middle
			Lower
	FRASNIAN	*gigas*	U'most
			Upper
			Lower
		A. triangularis	
		asymmetrica	Upper
			Middle
			Lower
MIDDLE DEV.	GIVETIAN (part)		L'most
		disparilis	

Figure 6. Upper Givetian to lower Tournaisian standard conodont zones of pelagic facies (Sandberg et al., 1978; Ziegler and Sandberg, 1984). The conodont-based ages quoted in the text refer to this zonation rather than to the revision by Ziegler and Sandberg (1990).

metres below the top of the Kotcho Formation on the northern Interior Platform (loc. 5; Walton and Mason, 1967; McGregor, *in* Richards, 1989).

In southern Alberta, Upper Devonian and Lower Carboniferous black shale of the Exshaw Formation, coeval with the lower Bakken (see "Williston Basin", above), is overlain by the Lower Carboniferous Banff Formation. Farther north the diachronous Exshaw is entirely Devonian, and the basal Banff correlates with the lower Bakken Formation. At location 5, the lower Banff contains uppermost Devonian spores (Coquel et al., 1976; McGregor, *in* Richards, 1989, p. 130, 131). Givetian spores were reported from an unspecified stratigraphic unit in the Imperial Bistcho Lake No. 1 well at location 4 (Staplin and Jansonius, 1964).

Mackenzie Platform and Richardson Anticlinorium

Marine and nonmarine clastic sediments, up to about 3100 m thick and comprising the Imperial and succeeding Tuttle formations, are present over broad areas of the western District of Mackenzie and southern Yukon Territory. The Imperial Formation is lithologically variable: fine clastics and minor interbedded carbonate, largely of turbidite origin, occur to the east and southeast, whereas relatively coarse grained sandstone and flysch-like siltstone and shale are developed on the west side of the Richardson Anticlinorium (loc. 10; see Norris, 1985). In northeastern Yukon Territory, the Imperial is overlain by the coarse to fine grained clastic rocks of the Tuttle Formation (Pugh, 1983). Embry and Klovan (1976) suggested that the Imperial and Tuttle represent the southwestern extension of the clastic wedge of the Franklinian Shelf (see below).

Spores identified by Chi and Hills (1974, 1976b), Braman (1981), Hills, Hyslop, and Braman (1984), McGregor (*in* Norris, 1985), and Braman and Hills (1985), sporadic marine faunas (Norris, 1985), and regional stratigraphic relationships signify an early Frasnian to about mid-Famennian age for the Imperial Formation (locs. 8–10), encompassing the upper *optivus–triangulatus* to lower *pusillites–lepidophyta* assemblage zones of Richardson and McGregor (1986).

Spores are the only age-definitive fossils found in the Tuttle Formation (locs. 9 and 10). They indicate that its lower part is early to mid-Famennian (Hills, Hyslop, Braman, and Lloyd, 1984) and that its uppermost beds may be as young as mid-Tournaisian (see Norris, 1985). Strata containing the Strunian (=upper Famennian) spores figured by McGregor

(1970), formerly the Upper member of the Imperial Formation, are now included in the Tuttle Formation (Pugh, 1983).

Franklinian Shelf

The principal locus of Devonian sedimentation in the Canadian Arctic Archipelago was the Franklinian Shelf, the Lower and lowermost Middle Devonian strata of which are predominantly carbonates. Clastic deposition began in the northeast in the Eifelian, and had advanced over most of the shelf by the end of the Middle Devonian. By early late Famennian time (the age of the youngest Devonian rocks known in the region), more than 4000 m of clastic sediments had accumulated on the Franklinian Shelf.

Spores occur profusely throughout most of the formations of the clastic wedge, and less abundantly in the underlying carbonates (locs. 11-21, see Appendix Table 1). Marine fossils are common in the carbonates, and sporadic in the clastics (McGregor, in press, a). References to their provenance and age, and to other geological information concerning the palyniferous strata of the Franklinian clastic wedge, are given in Appendix Table 1. Much of the geological data is taken from Embry and Klovan's (1976) comprehensive stratigraphic and sedimentological account.

Moose River Basin

The Moose River Basin is the southernmost, and best known, of two intracratonic basins on the Hudson Platform in which sediments accumulated in Devonian (Gedinnian to Frasnian) time (Sanford and Norris, 1975). Devonian outcrops are scattered mainly along various rivers of the region. Several exploratory wells have penetrated Devonian rocks. About 130 m of Emsian and lower Eifelian carbonate of the upper Stooping River and lower Kwataboahegan formations were intersected in the Jaab Lake No. 1 well near the centre of the basin (loc. 22). Here, conodonts and other marine fossils are associated with spores and acritarchs (Sanford and Norris, 1975; McGregor and Camfield, 1976; Playford, 1977). Along the southern edge of the basin, a rich and varied spore assemblage occurs in the Sextant Formation, which is a thin wedge of continental clastics correlative with the upper Stooping River Formation (McGregor and Camfield, 1976).

Palynomorphs are sparse in the upper Kwataboahegan Formation and the Moose River and Murray Island formations, but are more abundant in the calcareous shale of the Givetian to lowermost Frasnian Williams Island Formation (McGregor and Camfield, 1976; Norris et al., 1992). The youngest Devonian unit in the Moose River Basin, the Long Rapids Formation of Frasnian age, consists mainly of dark, bituminous shale with abundant *Tasmanites* and rare, corroded spores (McGregor, unpublished data).

Michigan Basin

Upper Devonian strata at the eastern edge of the Michigan Basin extend into westernmost southern Ontario (loc. 23). The Frasnian-Famennian Kettle Point Formation rarely outcrops in this region, and the overlying uppermost Devonian Bedford, Berea, and lower Sunbury formations are known only in the subsurface. The Kettle Point Formation is an extension of the widespread black shale sequence of eastern North America that also includes the Long Rapids Formation of the Moose River Basin.

Conodonts in the Kettle Point range from early Frasnian to late Famennian in age (Uyeno et al., 1982), and corroded spores of latest Famennian (Strunian) age are present high in the formation (McGregor and Owens, 1966). The Bedford and Berea formations, collectively less than 100 m thick in southern Ontario, are Strunian as indicated by their palynomorph content (McGregor, 1970; Molyneux et al., 1984; Wood, 1984). The Sunbury Formation contains spores that, if not reworked, indicate a Strunian age for its lower part (McGregor, 1970, p. 322).

Gaspé Trough

About 3200 m of predominantly fluvial deposits, the York River, Battery Point, and Malbaie formations, outcrop on the shores of Gaspé Bay, Québec (loc. 24). The Battery Point Formation, constituting about two thirds of this sequence, contains one of the most diverse and best preserved Emsian and Eifelian terrestrial floras known (Dawson, 1871; McGregor, 1959). Spores occur in the finer grained beds virtually throughout the sequence (McGregor, 1973, 1977). They are accompanied by shelly fossils in marine interbeds of the York River Formation (Boucot and Johnson, 1967) and by infrequent vertebrates in the Battery Point Formation (Pageau, 1969). Spores are less abundant in the Malbaie Formation, where they occur in finer grained units in the predominantly conglomeratic sequence. Comparisons with spores from the Emsian-Eifelian boundary stratotype

(McGregor, unpublished data) show that this boundary lies within the upper Battery Point Formation.

A thinner succession of Emsian fluvial deposits is exposed on the lower reaches of the Restigouche River. On the New Brunswick side of the river (loc. 26) the Campbellton Formation outcrops sporadically; it probably has a total thickness of about 100 m (Williams et al., 1985). Like the lower Battery Point Formation with which it is coeval, it contains well preserved land plants and spores (Gensel et al., 1975; McGregor, unpublished data).

About 120 m of carbonate rich, coastal marine or fluviolacustrine mudstone and sandstone, the Escuminac Formation, occur on the north side of the estuary of the Restigouche River near Miguasha (loc. 25; Dineley and Williams, 1968; Schultze and Arsenault, 1985). They contain a remarkable assemblage of fish (Carroll et al., 1972), a megaflora consisting almost entirely of *Archaeopteris* (Arnold, 1936; Gensel and Lawrence, in press), and a diverse and abundant spore flora (McGregor, in press, b).

New Brunswick Platform

McGregor and McCutcheon (1988) illustrated an assemblage of carbonized, but otherwise moderately well preserved, upper Famennian spores from the Carrow Formation of southwestern New Brunswick (loc. 27). The Carrow is an alluvial fan deposit less than 250 m thick within the caldera complex of the Piskahegan Group. The formation is limited to a few square kilometres in known geographic extent, and apparently contains no other fossils.

St. George's Basin

Upper Devonian to Lower Carboniferous fluviolacustrine deposits of the Horton Group can be traced from southeastern New Brunswick, across northern Nova Scotia, to Cape Breton Island. The group has been subdivided on the basis of regional lithological variation (Williams et al., 1985), but remains undifferentiated in some places. One small exposure on the west side of St. George's Bay, northern Nova Scotia (loc. 28), contains spores discussed in this report (see also McGregor, 1970).

Australia

Palynological studies of Australian Devonian strata depend essentially on the availability of material from the subsurface, because the strongly weathered Australian terrain allows little palynomorph preservation in the often intensely oxidized surface exposures (Balme and Hassell, 1962, p. 2; Playford, 1985, p. 248-249). The most rewarding studies are from western marginal basins (viz., Canning, Carnarvon, and Bonaparte basins; see Fig. 5, locs. 1-8) for the following reasons: exploratory drilling for petroleum and other minerals, and for artesian water, has provided an appreciable amount of subsurface material, much of it cored; and the Devonian and other Paleozoic sedimentary contents of the basins are essentially undeformed and of low thermal maturity, thus often endowing an almost pristine preservational quality to the palynomorphs.

The geographic locations and approximate correlation of the Australian lithostratigraphic units investigated are given in Figures 3 and 5.

Carnarvon Basin

The upper Middle (Givetian) to Upper Devonian (Frasnian-Famennian) sequence of the Carnarvon Basin includes the richly fossiliferous, silty calcareous Gneudna Formation (Figs. 3 and 5, loc. 1). This unit has yielded generally profuse spore and acritarch floras (Balme, 1962, 1988a; Playford and Dring, 1981; Playford, 1981) together with diverse marine invertebrate and conodont faunas indicative of early Late Devonian (early Frasnian) age. However, possible downward extension into the late Givetian cannot be discounted, and the upper part of the formation could be as young as late Frasnian (McGregor and Playford, 1990). Cockbain and Playford (1989) envisaged an "epeiric ramp" depositional setting for the Gneudna Formation: entirely shallow water, nearshore marine, but incorporating some intertidal deposits along its eastern onlap with the Precambrian shield. Balme's (1988a) comprehensive systematic account of spores was based on the lower part of the Gneudna Formation, as intersected and cored in several boreholes along the eastern margin of the Carnarvon Basin. He reported 45 species comprising a well preserved and reasonably diverse miospore association (cf. Balme, 1962) dominated by the trilete cavate species *Geminospora lemurata* Balme, 1962 (see also Playford, 1983). The presence of this species, in conjunction with *Cristatisporites triangulatus* (Allen) McGregor and Camfield, 1982, led Balme to suggest palynostratigraphic correlation of the Gneudna with the *Contagisporites optivus* var. *optivus*-*Cristatisporites triangulatus* Assemblage Zone of Euramerica (Richardson and McGregor, 1986).

Canning Basin

As summarized by Cockbain and Playford (1989), the Devonian succession of the Canning Basin (locs. 2–7) is dominantly marine and probably has an aggregate thickness of 2000 m or more. The nature and extent of Devonian strata in the various depositional/structural entities of the basin are known or inferred mainly from subsurface data. Outcrops are limited to the northern margin (Lennard Shelf), where upper Middle to Upper Devonian reef complexes are exposed as a series of spectacular limestone ranges and eminences, collectively likened to an exhumed "Great Barrier Reef" (Playford, 1980). Palynological studies have focused almost entirely on suitable strata encountered by boreholes in the northern onshore sector of the basin (Fitzroy Trough and Lennard Shelf). The palyniferous rocks, discussed below, are representative of facies within upper Givetian–Frasnian reef complexes; of uppermost Devonian post-reef units; and, to a minor extent, of pre-reef complex strata (upper Middle Devonian).

Two relatively thin, wholly subsurface units—the coarse, fluviodeltaic Anna Plains Sandstone, and the more persistent, shelf/subtidal Dominic Shale (Lehmann, 1984, 1986)—are commonly regarded as Givetian and underlie the reef developments on the Lennard Shelf (locs. 2–4).

The complex reefal and associated facies have been categorized lithostratigraphically by Playford (1984) and Cockbain and Playford (1989); locations 5, 6, and particularly 7. Many of the component argillaceous and arenaceous beds have proven palyniferous, often profusely so (Grey, 1974, 1991, 1992; Colbath, 1990); viz., within the shaly/silty Gogo Formation (basin facies), the calcarenitic Virgin Hills and Napier formations (marginal slope and basin facies), the calcarenitic Sadler Limestone (marginal slope facies), and the biohermal-biostromal Pillara Limestone (platform facies). These and other units of the reef complexes contain rich marine faunas including age-diagnostic groups, notably conodonts and ammonoids, that facilitate precise dating within the standard late Middle–Late Devonian interval. From a palynostratigraphic standpoint, Grey (1991, 1992) has indicated possible correlations with Middle–Late Devonian miospore zones established by Richardson and McGregor (1986) from their comprehensive northern hemisphere studies.

The lower and middle units of the Fairfield Group (Gumhole Formation and part of the succeeding Yellow Drum Sandstone: Druce and Radke, 1979; locs. 5 and 6) embody interbedded limestone, dolostone, and calcareous arenaceous strata of shallow marine origin, containing invertebrate and conodont faunas that signify a latest Devonian age. These post-reef complex sediments pass upward into the earliest Carboniferous Laurel Formation (constituting the top of the Fairfield Group). The well preserved palynoflora of the Gumhole–Yellow Drum, as described by Balme and Hassell (1962) and Playford (1976), includes miospores and acritarchs; the former characterize the clearly differentiated *Retispora lepidophyta* Assemblage and confirm the faunally based dating of the host strata (see also Jones, 1987, for ostracode evidence).

Bonaparte Basin

The onshore Bonaparte Basin sequence includes a unit of mainly sandy and silty limestone that constitutes the Buttons Formation (loc. 8), a product of latest Devonian shallow marine to lagoonal deposition on the landward flanks of the Ningbing reef complex. Miospores reported by Playford (1982) from the type section belong to the *Retispora lepidophyta* Assemblage (Playford, 1976), signifying a late Famennian (Strunian) age. This chronology was later supported by ostracode data from the same exposures (Jones, 1985), and by further palynological evidence from the subsurface (Playford, unpublished data).

Amadeus Basin

Palynological microfossils have been retrieved from samples of two of the three formations that comprise the 4725 m thick, continental clastic Pertnjara Group, which is otherwise very scantily fossiliferous and hence difficult to date. These formations (locs. 9 and 10) are the Parke Siltstone, the basal Pertnjara unit, and the Brewer Conglomerate, constituting the topmost unit. From a single sample of the Parke Siltstone (loc. 9), Hodgson (1968) described a poorly diversified assemblage of trilete miospores, including *Geminospora lemurata* and several ancyrate forms. Both Hodgson (1968) and Balme (1988a, p. 158) likened the Parke assemblage to that of the Gneudna Formation (Carnarvon Basin), and accordingly favoured either an early Frasnian or possibly a late Givetian age.

The Brewer Conglomerate drillhole samples (loc. 10) studied by Playford et al. (1976) were from the Undandita Member, near the top of the formation (and hence of the group). The palynoflora proved more varied than, and qualitatively distinct from, the Parke assemblage, although it does contain *Geminospora lemurata*. Associated species include a few known from the *Retispora lepidophyta* Assemblage; however, *R. lepidophyta* (Kedo) Playford, 1976 itself is notably absent. The precise age of the Brewer assemblage remains equivocal (Balme, 1988a, p. 158), but almost certainly lies within the post-early Frasnian to pre-late Famennian interval, as concluded by Playford et al. (1976).

Tasmania

The Eugenana beds are bedded, terrestrial, lithologically heterogeneous cavern fillings (stratigraphic leaks) in Ordovician limestone of the Gordon Subgroup at Hallett's Quarry, near Eugenana in the Devonport area, north coastal Tasmania (loc. 11). Spore analysis of carbonaceous siltstone from the quarry (Balme, unpublished data, University of Western Australia; see Banks and Burns, 1962, p. 185) clearly indicated a Devonian age (Balme favoured late Middle Devonian, as we do) for these spelean deposits, which were originally thought to be Permian (Burns, 1964, p. 81).

Adavale Basin

This basin is known from drilling operations and geophysical surveys that have penetrated appreciably below Permian and/or Mesozoic strata, of the Galilee and Eromanga basins respectively, in southwest Queensland. The Adavale sequence (loc. 12)—judged to be largely, if not entirely, of Devonian age—comprises marine and continental deposits and (in the basal portion) volcanic rocks (Auchincloss, 1976; Paten, 1977; Jell, 1989, p. 764–766). Lithostratigraphic units known to be palyniferous (de Jersey, 1966; Price, 1980) are, in ascending stratigraphic order: the Eastwood beds (interbedded carbonaceous shale and sandstone; fluviatile and lacustrine); Log Creek Formation (sandstone, dolostone, limestone, siltstone; marginal marine to marine); Bury Limestone (shallow marine, with abundant shelly invertebrates) and its partly lateral equivalent Lissoy Sandstone (continental to marginal marine); and Etonvale Formation (siltstone, shale, sandstone, dolostone, anhydrite, salt; continental to shallow marine). A detailed palynotaxonomic study of the Etonvale Formation was done by de Jersey (1966). He reported 39 species in a miospore flora considered by him to be Middle Devonian, probably largely Givetian, in general agreement with previously accrued faunal evidence. Price (1980) studied palynofloras from samples of the Etonvale and the underlying formations listed above. In his unpublished report, Price recognized five successive palynostratigraphic "units", which he regarded as collectively spanning an interval from late Early Devonian (Eastwood beds) to Middle or even early Late Devonian (Etonvale Formation).

Drummond Basin

Three fully cored coal exploration boreholes drilled by the Queensland Department of Resource Industries in the Airlie district (loc. 13), near Emerald, east-central Queensland, penetrated a heterogeneous, nonmarine suite of what were termed "Undifferentiated Devonian-Carboniferous sediments" (D'Arcy, 1987). Selected core samples yielded miospores judged by Playford (*in* D'Arcy, 1987) to be of Middle Devonian age.

PROCEDURES AND LIMITATIONS

Age assessments

In this investigation, we are concerned mainly with identifying spore taxa and form features that are common to Euramerica and Australia. Independent age control is ultimately desirable (and available for some assemblages, see below), but it is not essential for fulfilment of this objective. Similarly, consideration of the precise stratigraphic ranges of the fossils (see Fig. 7) or the floristic and ecological implications of the results, although obviously important, are not our main objectives.

Some of our samples are from continental sequences that contain few stratigraphically useful fossils other than spores. Others are from marine sections, in which spores co-occur or interdigitate with invertebrate faunas, so that nonmarine and marine zones may be correlated.

Some faunal control exists for palyniferous strata in the Cape De Bray, Bird Fiord, Strathcona Fiord, Weatherall, Beverley Inlet, and Parry Islands formations (McGregor, 1981 and in press, a; McGregor and Camfield, 1982; Goodbody et al., 1988; Goodbody, 1989b), the Flume and Perdrix formations (McGregor et al., 1985); the Hay River Formation (McGregor and Owens, 1966; Klapper and Lane, 1985), and the Stooping River and Kwataboahegan formations (McGregor and Camfield, 1976; Sanford

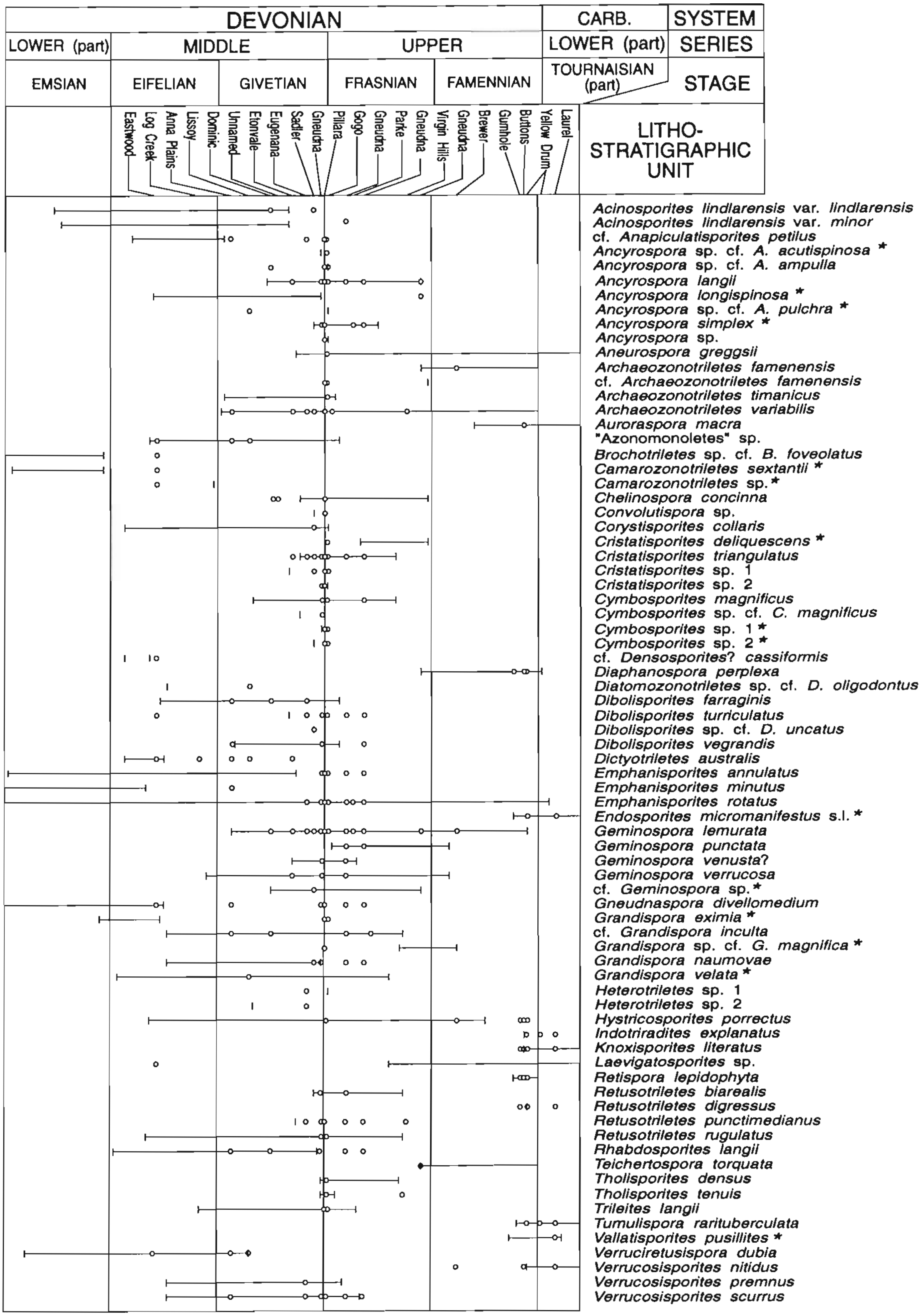

Figure 7. Taxa that occur in both the Canadian and the Australian Devonian, showing their Euramerican stratigraphic ranges (bars) and their approximate levels of occurrence in Australia (circles). Asterisks indicate uncertain taxonomic attribution of Australian specimens.

and Norris, 1975; Uyeno and Bultynck, in press) in Canada; the Gneudna (Balme, 1988a), Gogo, Sadler, and Pillara formations (Grey, 1991, 1992) in Australia; the Blacourt, Beaulieu, and Ferques formations of the Boulonnais, France (Loboziak and Streel, 1988); and Middle and Late Devonian strata of European U.S.S.R. (Arkhangelskaya and Ovnatanova, 1986; Arkhangelskaya et al., 1987).

Where spore and faunal ages have been determined in the same stratal sections, the results are in general agreement (see, for example, Jones, 1985, 1987; Arkhangelskaya et al., 1987; Balme, 1988a; McGregor, in press, a). Moreover, where both palynological and faunal dates exist for Australian sections, particularly in the late Givetian–early Frasnian and late Famennian intervals (Balme, 1988a; Jones, 1987), the sporological changes in these sections are broadly synchronous with corresponding faunally dated Euramerican spore events described by Richardson and McGregor (1986).

The Australian stratigraphic ranges of "Euramerican" species and morphons, where present, are as yet undetermined, mainly because continuous palyniferous sequences are scarce in Australia. Consequently, we have only broadly compared age ranges of spores in the two regions (see Fig. 7).

Identifications, interpretations, and comparisons

Our conclusions as to the identity of species in Euramerica and Australia are based largely on direct examination of specimens in whole assemblages from Canada and Australia. Publications by others on Australian Devonian spores, and those concerning spores from other parts of Euramerica, have proven useful if they contain adequate photographic illustrations and descriptions of fossils (e.g., Balme, 1988a, b; Allen, 1965; Arkhangelskaya, 1985). We regard unillustrated taxonomic listings and photographs of fossils without accompanying descriptions as inadequate for our purposes. For this reason, we have disregarded, or viewed cautiously, some published records.

Data from even the most detailed written accounts may be of limited value for comparisons of whole assemblages. For example, authors may not describe or illustrate all of the kinds of spores in an assemblage, preferring to omit rare or interpretationally difficult forms. Or, a newly discovered variant or intergrading form, if not disregarded, may be forced into an existing taxon, causing "ballooning" of the taxon and a misrepresentation of the taxonomic variation in the assemblage (see Hughes, 1970; Thomas, 1987). There may be a general "psychopalynological" tendency to overemphasize similarities between new forms and taxa previously described (cf. Chaloner and Lacey, 1973, p. 275). These potential taxonomic hazards may be minimized if specimens of whole assemblages are compared directly by the same people. This is the approach we have followed in the present investigation.

Direct comparison was essential for those assemblages that had not been formally described. This treatment was necessary for all of the Australian assemblages, except those from the Gneudna and Gumhole formations, and Yellow Drum Sandstone, described by Balme (1962; 1988a, b), Balme and Hassell (1962), and Playford (1976), and for the Canadian assemblages, except those from formations indicated by an asterisk in Figure 4.

As for most spore assemblages, the Canadian and Australian spores we studied consisted of both simple specimens and those of more complex morphology. The relatively simple unsculptured spores such as *Calamospora* Schopf, Wilson, and Bentall, 1944, *Punctatisporites* Ibrahim emend. Potonié and Kremp, 1954, and *Retusotriletes* Naumova emend. Streel, 1964, and the commonly abundant finely sculptured forms such as *Apiculatisporis* Potonié and Kremp, 1956, *Apiculatasporites* Potonié and Kremp, 1956, *Apiculiretusispora* Streel emend. Streel, 1967, and *Cyclogranisporites* Potonié and Kremp, 1954, can be morphologically matched in Canada–Australia comparisons throughout the Middle and Upper Devonian. Spores with uncomplicated structure and sculpture have been found in situ (i.e., in sporangia) in almost every Devonian plant group (Gensel, 1980), and may recur by homoplasy repeatedly through time. Intercontinental comparisons of these kinds of spores are unlikely to provide indications as to the commonality of floras between the regions. Therefore, with few exceptions, we have ignored them in our comparisons.

It seems reasonable to conclude that the more complicated the sculpture and structure of spores, the more likely they are to represent genetically closely related plants, even if found in geographically disparate regions. This assumption has not been tested empirically for most groups. Nevertheless, we assume it to be true for such spore species as *Acinosporites lindlarensis* Riegel, 1968 var. *lindlarensis* (the herbaceous lycopodiopsid *Leclercqia* spp.: Richardson et al., in press); *Geminospora lemurata* Balme, 1962 (the progymnospermous *Archaeopteris/Svalbardia* complex: Vigran, 1964; Med'yanik, 1982; but note tripapillate but otherwise *G. lemurata*-like spores in sporangia of the arborescent lycopodiopsid *Bisporangiostrobus harrisii* Chitaley and McGregor, 1988); and *Rhabdosporites langii* (Eisenack) Richardson, 1960 (known in situ from the progymnosperms *Tetraxylopteris* and *Rellimia*: Leclercq and Bonamo, 1971).

Some intricately constructed Devonian spores have yet to be found in situ, but their distinctive attributes seem less likely to be replicated homoplastically than do the features of simply constructed spores, and they may have been produced by the same groups of plants wherever they occur. *Emphanisporites* McGregor, 1961 and *Hystricosporites* McGregor, 1960, *Teichertospora torquata* (Balme) McGregor and Playford, 1990, and the *Cristatisporites triangulatus* Morphon are examples. Discovery of matching species and morphological series (partial or complete morphons) in geographically disparate regions may well signify close phyletic relationships.

Because of the morphological variability encompassed by some spore form genera (e.g., *Acinosporites* Richardson, 1965) and the relative simplicity of others (e.g., *Aneurospora* Streel, 1964), comparisons of genera may as a rule be less instructive for assessing phyletic relationships (and therefore zonal utility) than those at lower taxonomic levels. In other words, geographically disjunct records of species are more likely to signify botanical continuity, and relevance for temporal correlation (synchroneity), than such occurrences at the generic level.

Quantitative comparisons are not pertinent to the objectives of this study. One good specimen of a well characterized taxon is enough to establish its presence. Nonrecovery, or predominance, on the other hand, may depend on a combination of environmental, sedimentological, and botanical factors, as well as on laboratory extractive procedures and the experience of the observer. In terms of our objectives, the main advantage of having many specimens is that identifications may be considered more reliable, especially if the material is not well preserved.

BASES FOR COMPARISONS

Form taxa (genera and species)

Australian contributions by Balme (1962, 1988a), Balme and Hassell (1962), de Jersey (1966), Hodgson (1968), Playford (1976, 1982), Playford et al. (1976), Price (1980), and Grey (1991, 1992) demonstrate that there are many differences in the taxonomic composition of Euramerican and Australian Devonian spore assemblages. Conversely, the same body of literature has revealed some remarkable similarities in species content that link Australian spore floras with those of Euramerica. These resemblances are sufficient to suggest that some of the northern hemisphere zones of Richardson and McGregor (1986) may be recognizable in the Australian Devonian. Our first medium of comparison, therefore, is taxonomic.

Morphons

Comparison of spore assemblages is possible on a second level, using the morphon, defined as ". . . a group of species united by continuous variation of morphological characters" (van der Zwan, 1979, p. 11). Much variation exists in certain morpho-characters of Devonian spores. This phenomenon certainly is not uniquely Devonian, but it does seem to be particularly prevalent in Devonian spores. Comparable interspecific gradational morphological characteristics may be present in Australian and Canadian assemblages, particularly amongst ancyrate, verrucate, and zonate species.

Form features

Prior work also suggests that, taxonomy aside, there are approximately synchronous "fashions" of spore morphology in successive Devonian assemblages from the two regions. For the Canadian Devonian, Radforth and McGregor (1956) and Richardson and McGregor (1986) have perceived that these gross morphological attributes may have biostratigraphic value. Certain sculptural and structural features seem to be geographically widespread and characteristically (if not uniquely) Devonian. Grapnel tipped processes, proximal radial ribs, prominent equatorial/distal exinal thickenings and/or sculptural development, curvaturae, biform sculpture, sloughing sculptured layers, bizonate cingula (cingulizonae), and monolete zonate/cavate structure are particularly noticeable features of spores in parts of the Euramerican Devonian stratigraphic sequence. Some of these characters have already been recognized in the Australian Devonian (see Balme, 1988a).

COMPARISONS

Endemic genera

Several genera are restricted to either Euramerica (or parts thereof) or Australia. Euramerican Middle and Upper Devonian genera not found in Australia are: *Archaeoperisaccus* Naumova, 1953; *Biornatispora* Lele and Streel, 1969; *Contagisporites* Owens, 1971; *Cornispora* Staplin and Jansonius, 1961; *Cyrtospora* Winslow, 1962; *Diducites* van Veen, 1981; *Lagenicula* Bennie and Kidston ex Zerndt, 1934; *Laiphospora* Playford, Wicander, and Wood, 1983; *Lanatisporis* Arkhangelskaya, 1985; *Ocksisporites* Chaloner, 1959; *Periplecotriletes* Naumova ex Ishchenko, 1952; *Rugospora* Neves and Owens, 1966; *Sinuosisporis* Arkhangelskaya, 1985; and *Triangulatisporites* Potonié and Kremp, 1954.

Rare specimens from the Canning Basin, Western Australia, have been attributed by Grey (1991, 1992) to four other Euramerican genera, viz. *Biharisporites* Potonié, 1956; *Clivosispora* Staplin and Jansonius, 1964; *Densosporites* Berry, 1937, sensu Richardson, 1960; and *Nikitinsporites* Chaloner, 1959; but we regard their identification as unsubstantiated.

The only supposedly endemic Australian genera of Devonian spores so far described are *Ambagisporites* Balme, 1988 and *Medusaspora* Balme, 1988, from the Gneudna Formation. *Medusaspora* (Pl. 20, figs. 5, 10) also occurs in the Gogo, Pillara, and Sadler formations; and similar spores, not yet conclusively identifiable as *Medusaspora*, have been reported in the latest Devonian of eastern North America (see "Shared form features", below). Some forms present in Australia but not in Euramerica may represent undefined genus level groups. One is the monolete saccate (or pseudosaccate) form *Archaeoperisaccus indistinctus* Lu, 1988, found commonly in the Gogo and Lissoy formations (Pl. 17, fig. 4). The exoexine of this species is thin and commonly is folded across, and independently of, the intexine. Such characteristic folding, unreported in any Euramerican species of *Archaeoperisaccus*, suggests a relationship between the exinal layers fundamentally different than that which exists in bona fide *Archaeoperisaccus*. This suggestion is supported by Meier and Raskatova's (1984) observation that topotypic specimens of *Archaeoperisaccus* from Petino, U.S.S.R., are acavate, with an alveolar exoexinal extension equatorially (also see Meier-Melikyan and Tel'nova, 1989). *Archaeoperisaccus indistinctus* occurs in both China and Australia, where Euramerican-type *Archaeoperisaccus* has not been found.

Two other groups of spores not recorded in Euramerica may represent undescribed endemic Australian genera. Components of one (Pl. 18, figs. 6–10) have been referred tentatively to *Camptozonotriletes* Staplin, 1960. Members of this complex have been recovered from the Gneudna, Gogo, Pillara, Sadler, and Virgin Hills formations, and the Eugenana beds, as well as from unnamed strata in the Drummond Basin (Airlie area). Some members of this group resemble (perhaps superficially) figured specimens of *Costazonotriletes* Lu, 1988 from Yunnan, China. The other group (Pl. 19, figs. 6, 8) comprises curvaturate, cavate forms with a scabrate and sparsely conate or microspinose exoexine. Specimens of this group, dubitably referred herein to *Grandispora* Hoffmeister, Staplin, and Malloy, 1955, are abundant in the Gogo Formation, and sparse in the Pillara Formation.

Shared genera

The following genera are present in both regions, but with no species so far found (or confirmed) in common: *Camarozonotriletes* Naumova ex Ishchenko, 1952; *Cirratriradites* Wilson and Coe, 1940; *Crassispora* Bhardwaj, 1957; *Kraeuselisporites* Leschik, 1956; *Leiozonotriletes* Hacquebard, 1957; *Lophozonotriletes* Naumova emend. van der Zwan, 1980; *Reticulatisporites* Ibrahim emend. Potonié and Kremp, 1954; *Schopfites* Kosanke, 1950; and *Stenozonotriletes* Naumova ex Ishchenko, 1952.

It should be noted that identification of *Camarozonotriletes, Lophozonotriletes*, and *Stenozonotriletes* may depend on subjective interpretation of the thickness of the exine equatorially. These genera intergrade structurally with *Granulatisporites* Ibrahim emend. Potonié and Kremp, 1954, *Verrucosisporites* Ibrahim emend. Smith and Butterworth, 1967, *Tumulispora* Staplin and Jansonius, 1964, and *Punctatisporites* Ibrahim, 1933 respectively. For example, it may be difficult to differentiate between a genuine *Tumulispora* (cingulate) and a thick walled, similarly sculptured, but acingulate *Lophozonotriletes* or *Verrucosisporites*. Comparisons of specimens potentially assignable to these genera should therefore be made cautiously. Perhaps less weight should be accorded to apparent similarities and differences than with more clearly demarcated genera, because of these interpretational difficulties.

Some other genera are represented in both Canada and Australia by a single common species. For some of these genera, additional (unshared) species also occur in either Canada (C) or Australia (A): *Acinosporites* Richardson, 1965 (C); *Anapiculatisporites* Potonié and Kremp, 1954 (C, A); *Aneurospora* Streel, 1964 (C); *Brochotriletes* Naumova ex Ishchenko, 1952 (C, A); *Chelinospora* Allen, 1965 (C, A); *Convolutispora* Hoffmeister, Staplin and Malloy, 1955 (C, A);

Corystisporites Richardson, 1965 (C, A); *Diaphanospora* Balme and Hassell, 1962 (C, A); *Diatomozonotriletes* Naumova ex Playford, 1963 (C); *Dictyotriletes* Naumova ex Ishchenko, 1952 (C, A); *Endosporites* Wilson and Coe, 1940 (C); *Gneudnaspora* Balme, 1988 (A); *Hystricosporites* McGregor, 1960 (C, A); *Indotriradites* Tiwari, 1964; *Knoxisporites* Potonié and Kremp, 1964 (C); *Laevigatosporites* Ibrahim, 1933; *Retispora* Staplin, 1960 (C); *Rhabdosporites* Richardson, 1960 (C); *Teichertospora* Balme, 1988; *Trileites* Erdtman ex Potonié, 1956; *Tumulispora* Staplin and Jansonius, 1964 (C); *Vallatisporites* Hacquebard, 1957 (C); and *Verruciretusispora* Owens, 1971 (C).

Finally, certain genera are represented by two or more shared species, and in some cases by some apparently endemic (unshared, C or A) species as well. These include *Ancyrospora* Richardson, 1962 (C, A); *Archaeozonotriletes* Naumova, 1953 (C); *Auroraspora* Hoffmeister, Staplin and Malloy, 1955 (C); *Cristatisporites* Potonié and Kremp, 1954 (C, A); *Cymbosporites* Allen, 1965 (C, A); *Dibolisporites* Richardson, 1965 (C, A); *Emphanisporites* McGregor, 1960 (C); *Geminospora* Balme, 1962 (C); *Grandispora* Hoffmeister, Staplin, and Malloy, 1955 (C, A); *Heterotriletes* de Jersey, 1966 (C, A); *Retusotriletes* Naumova emend. Streel, 1964 (C, A); and *Verrucosisporites* Ibrahim emend. Smith and Butterworth, 1967 (C, A).

In summary, 44 genera of Devonian spores occur in both Euramerica and Australia. Thirty-five of these genera contain one or more species in common. Seventeen Euramerican genera have not been found in Australia, and two Australian genera have not been reported from Euramerica. At least three other possibly endemic Australian genera have not yet been formally defined.

Endemic species

Several hundred formally described Middle and Upper Devonian Euramerican species have not yet been recognized in Australia. Our survey has also revealed about 150 Australian species that apparently are unrepresented in Euramerican assemblages (including many undescribed). Listing them here would probably not serve any useful purpose, because the numbers will undoubtedly change significantly as new assemblages are discovered and additional species are described from both regions. Some of the geographically restricted species are illustrated in Plates 14–16 (Euramerican) and 17–20 (Australian).

Shared species

Those species, described and undescribed, that we have found to occur in both Euramerica (mainly Canada) and Australia (Fig. 7) are illustrated in approximate alphabetical order in Plates 1–13. Also included are some specimens similar to, if not identical with, named species; the taxonomic uncertainty is either because we have too few specimens or because those at hand are inadequately preserved for accurate identification.

Confidently identified shared species are:

Acinosporites lindlarensis Riegel, 1968 var. *lindlarensis*
A. lindlarensis Riegel, 1968 var. *minor* McGregor and Camfield, 1976
cf. *Anapiculatisporites petilus* Richardson, 1965
Ancyrospora sp. cf. *A. ampulla* Owens, 1971
A. langii (Taugourdeau-Lantz) Allen, 1965
A. sp. cf. *A. simplex* Guennel, 1963
Ancyrospora sp.
Aneurospora greggsii (McGregor) Streel, 1974
Archaeozonotriletes famenensis Naumova, 1953
cf. *A. famenensis*
A. timanicus Naumova, 1953
A. variabilis Naumova, 1953 emend. Allen, 1965
Auroraspora macra Sullivan, 1968
"Azonomonoletes" sp.
Brochotriletes sp. cf. *B. foveolatus* Naumova, 1953
Chelinospora concinna Allen, 1965
Convolutispora sp.
Corystisporites collaris Tiwari and Schaarschmidt, 1975
Cristatisporites triangulatus (Allen) McGregor and Camfield, 1982
C. sp. 1
C. sp. 2
Cymbosporites magnificus (McGregor) McGregor and Camfield, 1982
C. sp. cf. *C. magnificus*
cf. *Densosporites*? *cassiformis* (Chibrikova) Arkhangelskaya, 1985
Diaphanospora perplexa Balme and Hassell, 1962
Diatomozonotriletes sp. cf. *D. oligodontus* Chibrikova, 1962
Dibolisporites farraginis McGregor and Camfield, 1982
D. turriculatus Balme, 1988
D. sp. cf. *D. uncatus* (Naumova) McGregor and Camfield, 1982
D. vegrandis McGregor and Camfield, 1982
Dictyotriletes australis de Jersey, 1966
D. australis?

Emphanisporites annulatus McGregor, 1961
E. minutus Allen, 1965
E. rotatus McGregor, 1961 emend. McGregor, 1973
Geminospora lemurata Balme, 1962 emend. Playford, 1983
G. punctata Owens, 1971
G. venusta? (Naumova) McGregor and Camfield, 1982
G. verrucosa Owens, 1971
Gneudnaspora divellomedium (Chibrikova) Balme, 1988
Grandispora cf. *inculta* Allen, 1965
G. naumovae (Kedo) McGregor, 1973
Heterotriletes sp. 1
H. sp. 2
Hystricosporites porrectus (Balme and Hassell) Allen, 1965
Indotriradites explanatus (Luber) Playford, 1991
Knoxisporites literatus (Waltz) Playford, 1963
Laevigatosporites sp.
Retispora lepidophyta (Kedo) Playford, 1976
Retusotriletes biarealis McGregor, 1964
R. digressus Playford, 1976
R. punctimedianus Balme, 1988
R. rugulatus Riegel, 1973
Rhabdosporites langii (Eisenack) Richardson, 1960
Teichertospora torquata (Higgs) McGregor and Playford, 1990
Tholisporites densus McGregor, 1960
T. tenuis McGregor, 1960
Trileites langii Eisenack, 1944
Tumulispora rarituberculata (Luber) Playford, 1991
Verruciretusispora dubia (Eisenack) Richardson and Rasul, 1978
Verrucosisporites nitidus Playford, 1964
V. premnus Richardson, 1965
V. scurrus (Naumova) McGregor and Camfield, 1982

Two additional shared species may be added to this list, based on published taxonomic records from Australia:

Gorgonispora convoluta (Butterworth and Spinner) Playford, 1976 (Playford, 1976; Grey, 1992)
Grandispora senticosa (Ishchenko) Byvsheva, 1985 (Playford, 1976, as *G. uncata*; Playford, 1991)

Certain other Canadian/Australian pairs, although possibly not identical, are close to one another in general morphology. The following described Euramerican species are similar to the Australian member of the pair:

Ancyrospora longispinosa Richardson, 1962
Camarozonotriletes sextantii McGregor and Camfield, 1976
Cristatisporites deliquescens (Naumova) Arkhangelskaya, 1987
Endosporites micromanifestus Hacquebard, 1957 sensu lato
Grandispora eximia (Allen) McGregor and Camfield, 1982
G. velata (Eisenack) Playford, 1971
Vallatisporites pusillites (Kedo) Dolby and Neves, 1970

In addition, the following Australian forms are similar to Euramerican forms, as yet undescribed:

Ancyrospora sp. cf. *A. acutispinosa* Chi and Hills, 1976
A. sp. cf. *A. pulchra* Owens, 1971
Camarozonotriletes sp.
Cymbosporites sp. 1
C. sp. 2
cf. *Geminospora* sp.
Grandispora sp. cf. *G. magnifica* (Owens) Chi and Hills, 1976

Species of *Camarozonotriletes* recovered from the Eastwood beds (Adavale Basin) resemble the Russian species *C. elegans* L.G. Raskatova, 1969 and *C. rarus* L.G. Raskatova, 1969 (see Pl. 18, figs. 1 and 5, respectively), to the extent that they can be compared using the drawings and brief descriptions in Raskatova (1969, Pl. 11).

Figure 7 shows the stratigraphic distribution in Australia of species identical with or comparable to those found in Euramerica, their stratigraphic ranges in Euramerica, and the estimated ages of the strata in which they have been found in Australia.

Endemic morphons

Appendix Table 4 is a summary of the morphological features that characterize the morphons (those introduced herein and those defined by others) that are referred to in this report. Morphons are regarded as informal groupings of taxa; their circumscribing morphocharacters and the lists of their constituent species are subject to emendation as work continues on these and other morphologically gradational forms.

One of the most conspicuous features of the Australian assemblages is the lack of unequivocal examples of zonate, annularly thickened spores (*Densosporites* sensu Richardson, 1960), exemplified by *D. devonicus* Richardson, 1960. *Densosporites* spp. (Pl. 14, figs. 14, 15; Pl. 15, fig. 1) predominate in some Euramerican mid-Eifelian to Givetian assemblages, in both Europe and Canada. In all of the Australian material examined, we found only three poorly preserved specimens that, doubtfully, might be assignable to the *D. devonicus* Morphon (here named). All were from the Gogo Formation. Grey (1992, p. 40), in her study of Middle and Upper Devonian spores from the Canning Basin, found in the Gogo Formation and correlative strata a few specimens that she referred, with caution, to *Densosporites* ". . . because they show some darkening of the inner margin of the zona. The sculpture, however, is sometimes more typical of *Ancyrospora* in having biform tips and a deeply scalloped margin. Additional specimens are required to resolve the problem of generic assignment."

Another group of Euramerican species that displays continuous morphological variation is the *Dibolisporites echinaceus* Morphon (here designated; Pl. 14, fig. 5; Pl. 15, fig. 5). Its main characteristics are approximately circular amb, relatively thin wall, biform sculptural elements, and narrow, simple labra of about even width. Besides *D. echinaceus* Richardson, 1965, the morphon includes *D. pseudoreticulatus* Tiwari and Schaarschmidt, 1975; *D. radiatus* Tiwari and Schaarschmidt, 1975; *D. triangulatus* Tiwari and Schaarschmidt, 1975; *D. varius* Tiwari and Schaarschmidt, 1975; *Apiculatasporites microconus* (Richardson) McGregor and Camfield, 1982; and *Bullatisporites bullatus* Allen, 1965. It intergrades with the *Apiculiretusispora arenorugosa* Morphon (see below) and with simple, minutely ornamented forms such as *Apiculiretusispora brandtii* Streel, 1964, and *A. densiconata* Tiwari and Schaarschmidt, 1975. No unequivocal occurrences of this morphon are known from Australia. Specimens identified as *Dibolisporites* sp. cf. *D. echinaceus* by Grey (1991, Pl. 1, fig. 9; 1992, Pl. 14, figs. 1 and 2) may be *Acinosporites lindlarensis* var. *lindlarensis*, as they have separated wall layers and crowded, galeate, polygonal-based ornaments characteristic of that taxon.

The *Apiculiretusispora arenorugosa* Morphon (here named) comprises *A. arenorugosa* McGregor, 1973; *A. brandtii* Streel, 1964, sensu McGregor (1973); *A.* sp. cf. *A. brandtii* sensu Riegel (1973); and *A. plicata* (Allen) Streel, 1967. Its most important unifying feature is the tendency of the outer, relatively fragile, finely sculptured wall layer to slough off completely or in patches. There are no confirmed records of spores of this morphon in Australia. However, it should be noted that in Euramerica this morphon is largely confined to the Lower and lower Middle Devonian, an interval in which virtually no palynological studies have been conducted in Australia. The oldest Australian strata that we have examined, the Eastwood beds, do not contain any representatives of this morphon with a visibly separated sculpture-bearing layer, but they do include minutely sculptured spores with intact walls, similar to the curvaturate specimens of *A. plicata* described by Allen (1965).

The *Cyrtospora cristifera* Morphon (van der Zwan, 1979; van der Zwan and Walton, 1981) is also apparently absent from Australia. Devonian species of this morphon [*C. cristifera* (Luber) van der Zwan, 1979, and *Cornispora* spp.; Pl. 14, figs. 11, 12] are common components of Famennian assemblages from the northern fringes of the Old Red Sandstone Continent, and of upper Famennian and lower Tournaisian assemblages in virtually all of Euramerica.

The *Archaeoperisaccus ovalis* Morphon (here named) consists of monolete forms with a rather rigid, laevigate to finely ornamented exoexine, viz. *A. artus* Braman and Hills, 1985; *A. echinatus* L.G. Raskatova, 1975; *A. elongatus, A. completus, A. concinnus, A. menneri, A. mirus*, and *A. ovalis*, all described by Naumova (1953); *A. regalis* Braman and Hills, 1985; *A. scabratus* Owens, 1971 (Pl. 14, fig. 7); and possibly *A. oviformis* Lu, 1980 and *A. xichongensis* Lu, 1980. None of these species has been identified in Australia.

The *Archaeoperisaccus verrucosus* Morphon (here named) includes *A. timanicus* Pashkevich, 1964 and *A. verrucosus* Pashkevich, 1964 (both ascribed to the new genus *Archaeomonoletes* by Med'yanik, 1980); *A. oblongus* Owens, 1971; and *A. signus* Braman and Hills, 1985. These intergrading taxa (e.g., Pl. 14, figs. 8, 9) bear relatively coarse conate, verrucate, to rugulate ornamentation. Like the *Archaeoperisaccus ovalis* Morphon, the *A. verrucosus* Morphon is confined in Euramerica to the northern regions of the Old Red Sandstone Continent (McGregor, 1979a) and has not been discovered in Australia.

In the Soviet Union and in Canada, elements of the *A. verrucosus* Morphon intergrade with members of the *Cristatisporites triangulatus* Morphon. Perhaps surprisingly, the latter is present in Australia (our observations, see below; Balme, 1988a; Grey, 1991, 1992), whereas the former is not.

Recent work on Middle Devonian assemblages in Canada and the U.S.S.R. (Arkhangelskaya et al., 1990) suggests the presence there of a group of intergrading species with sinuous proximal folds and a narrow zona, that is here termed the *Sinuosisporis sinuosus* Morphon. It includes *S. sinuosus* (V. Umnova) Arkhangelskaya, 1985 (Pl. 16, fig. 7); other species of this genus described by Arkhangelskaya (1985); and *Kraeuselisporites ollii*? (Chibrikova) McGregor and Camfield, 1982. No trace of this morphon has been found in any Australian spore assemblage.

Another endemic Euramerican complex of species that may constitute a morphon includes *Laiphospora membrana* (Sanders) Playford, Wicander, and Wood, 1983, *Membrabaculisporis comans* (Filimonova) Arkhangelskaya, 1985, and possibly *M. radiatus* (Naumova) Arkhangelskaya, 1985. *Lanatisporis* spp. of Arkhangelskaya (1985), including *Geminospora*? *bislimbata* (Chibrikova) McGregor and Camfield, 1982 [Pl. 15, fig. 13; = *Lanatisporis bislimbatus* (Chibrikova) Arkhangelskaya, 1985], may be end members of this complex, possibly collectively constituting a morphon. This group may be united by possession of a complex outer layer with more or less radially oriented tendril-like rods. We prefer not to designate it as a morphon until the structure and intergradational patterns of the constituents are better understood. None of these species has been found in Australia.

In Euramerica, *Acinosporites acanthomammillatus* Richardson, 1965 (Pl. 14, fig. 1) intergrades with *A. hirsutus* (Brideaux and Radforth) McGregor and Camfield, 1982; with *Cristatisporites albus*? (Arkhangelskaya) McGregor and Camfield, 1982 and certain other (undescribed) zonate spores assignable to *Cristatisporites*; with *C. hesperus* (Allen) McGregor and Camfield, 1982; and with *C. dasydentatus* (Chibrikova) Arkhangelskaya, 1985 (see McGregor and Camfield, 1982, p. 11, 31). This group of spores is referred to herein as the *Acinosporites acanthomammillatus* Morphon. Its salient features are prominent, fold-like labra; commonly biform sculptural elements that are fused basally to form anastomosing ridges; and the tendency for fusion of sculpture to form an incipient subequatorial zona. Components of the morphon intergrade through intermediaries with extreme forms of *Cymbosporites magnificus* (op. cit., p. 11). *Cymbosporites magnificus* and morphologically related spores are present in Australia, but neither the *A. acanthomammillatus* Morphon nor *Cristatisporites albus*? have been found there (see below).

Certain spores recovered from the Gogo, Pillara, and Sadler formations and the Eugenana beds, the "*Cristatisporites* sp. morphon" (Pl. 18, figs. 11-15), superficially resemble *Cristatisporites albus*?, but lack the latter's internal, concentric thickening at the inner limit of the zona. The phyletic relationship of the Australian spores to *C. albus*? from Canada, and to *C. albus* from the Soviet Union, is unknown. As their structure seems rather different from Euramerican forms, once formally described they may be sustainable as an endemic Australian morphon.

The *Diducites mucronatus* Morphon (van Veen, 1981), common in Euramerica in the southern regions of the Old Red Sandstone Continent, has not been recognized in Australia.

One of the common Australian endemic groups, possibly comprising several species of a morphon, is the group herein referred to as *Camptozonotriletes* spp. (Pl. 18, figs. 6-10; see "Endemic genera", above). Nothing closely similar to it has been reported from Euramerica, although the morphologically related *Cristatisporites triangulatus* Morphon occurs in both regions (see below).

Shared morphons

Several distinctively Devonian morphons occur in both Euramerica and Australia. Some are named here for the first time, although the intergradational character of the constituent taxa of most of them has been recognized previously.

The *Acinosporites lindlarensis* Morphon (Richardson et al., in press) at present includes only the eponym's two varieties, *minor* McGregor and Camfield, 1976 and *lindlarensis* which, taken together, embody a considerable range of sculptural variation. The morphon is characterized by varied, mainly biform, distal sculpturing elements that are basally fused to form interconnected muri. Curvaturae are delimited by longer spinose to galeate elements. Spores of this group are cavate to paracavate (Balme, 1988a): wall separation, if detectable, commonly is slight. Both *A. lindlarensis* var. *lindlarensis* (Pl. 1, figs. 1, 2) and *A. lindlarensis* var. *minor* (Pl. 1, figs. 9, 10) have been found in Australia. A specimen illustrated by Grey (1991, Pl. 1, fig. 9) may be var. *lindlarensis*.

One of the most characteristic of Devonian spore types, found virtually worldwide in Middle and Upper Devonian rocks, is the complex encompassed by the genus *Ancyrospora* Richardson, 1960. Members of this relatively diverse taxon share the common characteristics of zonate structure and grapnel-tipped (bifurcate or multifurcate) exoexinal processes. We have found it convenient to divide it into two informal groups based on the nature of the equatorial exoexinal extension. Group one, which includes the type species, *A. grandispinosa* Richardson, 1960, comprises spores having an entire, equator-encircling, slightly or strongly scalloped zona bearing discrete processes. Group two, exemplified by *A. longispinosa* Richardson, 1962, features tapered processes with broad, contiguous bases arising from the equatorial and distal regions of the exine. In polar view, the spores of the second group appear zonate, owing to the equatorial concentration of variably confluent process bases. Both groups are present in Euramerica and Australia.

The *Ancyrospora simplex* Morphon is part of group one and includes, among others, *A. simplex* (? = *A. melvillensis* Owens, 1971), *A. ampulla*, and some specimens that have been ascribed to *A. langii* (e.g., by Allen, 1965, Pl. 106, fig. 5; Richardson and McGregor, 1986, Pl. 16, figs. 2, 3). Spores of this morphon are illustrated in Plate 2, figures 5, 6 and Plate 3, figures 1-6 (herein), and in Balme (1988a) and Grey (1991, 1992).

The *Ancyrospora longispinosa* Morphon of group two (see Pl. 1, figs. 11, 12; Pl. 2, figs. 1-4 and 7, 8) comprises, among others, *A. longispinosa, A. pulchra, A. furcula* Owens, 1971, *A. involucra* Owens, 1971, *A. ancyrea* Richardson, 1962, some spores attributed to *A. langii* (e.g., Taugourdeau-Lantz, 1971, Pl. 15, fig. 10; Loboziak and Streel, 1981, Pl. 4, fig. 2), and possibly *A. acutispinosa* Chi and Hills, 1976. Most of the multifurcate-spined taxa so far described are in group two.

Collectively, the spores identified as *Ancyrospora langii* in the literature include members of both the *A. simplex* and *A. longispinosa* morphons, as well as morphologically transitional forms (see Balme, 1988a, Pl. 11, figs. 7, 9; Taugourdeau-Lantz, 1971, Pl. 15, figs. 9-11, 13, 14; Becker et al., 1974, Pl. 22, figs. 11-16). The holotype itself is intermediate, perhaps more allied to group one (Taugourdeau-Lantz, 1960, Pl. 3, fig. 33).

Another ancyrate group present in Euramerica and Australia is the cavate complex here designated the *Grandispora magnifica* Morphon, after *G. magnifica* (Owens) Chi and Hills, 1976. It also includes *G. cassidea* (Owens) Chi and Hills, 1976. The spores illustrated in Plate 9, figures 8 and 11 probably represent different (and new) species, but their overall structural organization seems to be the same, i.e., a wide, unscalloped equatorial extension, and discrete spinae, bacula, and/or ancyrate processes. *Ancyrospora douglastownense* McGregor, 1973, is structurally similar to, but not included in, the morphon as it is of late Emsian-early Eifelian age, much older than the Frasnian-Famennian taxa cited above.

The other major taxon of ancyrate spores, *Hystricosporites* McGregor, 1960, is represented in Euramerica and Australia by the *H. porrectus* Morphon, herein designated. *Hystricosporites porrectus* (Balme and Hassell) Allen, 1965 is the only species of the group that has been reported from both regions (Pl. 10, figs. 3, 4; Balme and Hassell, 1962; Playford, 1976). Other components of the morphon are: in Australia, *H. richardsonii* de Jersey, 1966 and an undescribed form (*H.* sp. cf. *H. reflexus*) found in the Sadler and Gogo formations; in Euramerica (Spitsbergen), *H. mitratus* Allen, 1965. All have an apical prominence and numerous relatively small, slender, ancyrate processes. Some Euramerican species of generally similar morphology, e.g., *H. costatus* Vigran, 1964, *H. delectabilis* McGregor, 1960, *H. furcatus* Owens, 1971, and *H. reflexus* Owens, 1971, are excluded from this morphon because of their radially costate contact areas. The latter feature is not known to occur in any Australian specimens of *Hystricosporites*.

Taxa of the *Archaeozonotriletes variabilis* Morphon (here named), i.e., *A. variabilis* var. *variabilis, A. timanicus,* and possibly *Geminospora punctata*, occur in both regions (Pl. 4, figs. 3a, 3b, 4a, 4b; Pl. 8, figs. 13, 14). *Archaeozonotriletes variabilis* var. *insignis* Sennova, 1971 has not been found in Australia. The morphon is characterized by a variably developed, entire or variously dissected patina that is thickest distally.

Euramerican and Australian spore assemblages both contain spores that intergrade morphologically with *Cristatisporites triangulatus* sensu Allen, 1965. Allen (1982) has included some of the eastern European forms in his concept of this species (e.g., *Hymenozonotriletes duplex* Pychova ex Shishova, 1971), but has excluded at least one form "of similar construction" but with a small apiculate ornament. Balme (1988a, p. 137, Pl. 7, figs. 8-11) appears to accept a broader range of sculptural and zonal variation in the species, using the circular intexinal body centred in polar aspect in the triangular exoexine as the main unifying feature. If Balme's (1988a) view is adopted, the "core" of the *C. triangulatus* Morphon (here named) may have about the same scope as the species (Pl. 6, figs. 1-8), and is similar in Euramerica and Australia.

However, in Canada the *Cristatisporites triangulatus* Morphon includes *C. inusitatus* (Allen) McGregor and Camfield, 1982 (but see Allen, 1982, p. 159), and is morphologically gradational (McGregor, unpublished data) with the contemporaneous *Archaeoperisaccus verrucosus* Morphon. Neither *C. inusitatus* nor *Archaeoperisaccus* spp. has been found in Australia. In Australia, the *C. triangulatus* Morphon intergrades with the *Camptozonotriletes* spp. complex, which has not been detected in Euramerica.

Examination of assemblages from Arctic Canada containing *Cymbosporites* (McGregor, unpublished data) has shown that several undescribed patinate forms with discrete or interconnected sculptural elements intergrade with *C. magnificus* to constitute the *C. magnificus* Morphon (here named). Similar variations of the basic *C. magnificus* structural plan have been found in Australia (Pl. 5, figs. 3-6; Pl. 6, figs. 11, 12, 17, 18).

In Canada, the group of simply constructed, variably sculptured spores that intergrades with *Dibolisporites farraginis* (the *D. farraginis* Morphon, herein designated) includes *D. vegrandis, D. uncatus,* and the species we have referred to as *Heterotriletes* sp. 1. All of these have also been recovered from Australian strata (Pl. 7, figs. 3, 4, 7-10; Pl. 10, figs. 5, 6).

Morphological intermediates occur between the *Dibolisporites farraginis* Morphon and the *Verrucosisporites scurrus* Morphon (here named). In Canada the *V. scurrus* Morphon is most common in the Franklinian shelf deposits (Fig. 4), where it includes *V. premnus, V. tumulentus* Clayton and Graham, 1974, *Geminospora verrucosa, Convolutispora crassata*? (Naumova) McGregor and Camfield, 1982, and *C. tegula* Allen, 1965. The *V. scurrus* Morphon is represented in Australia by the eponym, as well as *V. premnus* and *Geminospora verrucosa* (Pl. 9, figs. 3, 4; Pl. 13, figs. 1, 2, 5, 6). *Heterotriletes* sp. 2, present in both regions (Pl. 10, figs. 7, 8), may be part of the morphon.

In Euramerica, the *Emphanisporites rotatus* Morphon (here named) comprises the following laevigate, proximally radially ribbed species of the genus, in addition to the eponym: *E. annulatus, E. densus* Tiwari and Schaarschmidt, 1975, *E. macgregorii* Cramer, 1967, *E. minutus, E. multicostatus* Rodriguez, 1978, *E. neglectus* Vigran, 1964, *E. obscurus* McGregor, 1961, *E. pantagiatus* Allen, 1965, *E. partitus* Lanninger, 1968, *E. perfilum* Rodriguez, 1983, and *E. tener* Kedo, 1976. It also includes *Retusotriletes actinomorphus* Chibrikova, 1962 and *Zonomonoletes actinobolus* Chibrikova, 1962. In some assemblages this complex intergrades with forms, at present excluded from the morphon, in which the ribs radiate from foci in the contact areas [*E. erraticus* (Eisenack) McGregor, 1961 and *E. schultzii* McGregor, 1973]. *Emphanisporites rotatus* (virtually the whole range of its Euramerican variation; see McGregor, 1973), *E. annulatus*, and *E. minutus* have been found in Australia (Pl. 6, figs. 15, 16; Pl. 7, figs. 11, 12, 21, 22). *Emphanisporites rotatus* is especially common in the predominantly Frasnian Gneudna Formation. In Canada, *E. rotatus* attains its acme in the Lower Devonian, and is rare in younger Devonian rocks.

Geminospora lemurata in Australia includes distally and equatorially thickened, pseudosaccate, trilete spores with a range of combinations and variations of wall separation, exoexinal thickness, and size and distribution of small sculptural elements (Playford, 1983). Few Australian specimens of the genus fall outside the limits now ascribed to this species; *G. venusta*? (Naumova) McGregor and Camfield, 1982 (Pl. 8, figs. 7, 8) may be one example. In Canada, essentially the complete Australian range of variation of *G. lemurata* is present (Pl. 8, figs. 1-6, 9-12), as well as species with coarser sculpture, i.e., *G. venusta, G. spinosa* Allen, 1965, *G. tuberculata* (Kedo) Allen, 1965, and several Soviet species of *Archaeozonotriletes*: viz., *A. comptus* Naumova, 1953; *A. meonacanthus* Naumova ex Chibrikova, 1959 and its varieties (Chibrikova, 1962; Pykhova, 1960). *Rhabdosporites minutus* Tiwari and Schaarschmidt, 1975 and *Geminospora svalbardiae* (Vigran) Allen, 1965 are also included in this group. This range of forms is here categorized as the *Geminospora lemurata* Morphon (Pl. 8, figs. 1-12). The eponym intergrades with *Archaeozonotriletes basilaris* Naumova, 1953 and *Aneurospora greggsii* (McGregor) Streel, 1974.

In Euramerica, the pseudosaccate trilete species *Rhabdosporites langii* constitutes a morphon with other finely sculptured species of the genus, viz. *R. parvulus* Richardson, 1965, *R. scamnus* Allen, 1965, and *R.*(?) *vermiculatus* Sanders, 1968 (*R. cymatilus* Allen, 1965 being excluded). Richardson (1965) accommodated a wide range of specimen sizes in *R. langii*, and McGregor and Camfield (1982) and Marshall and Allen (1982) broadened the concept of the genus to include limbate as well as nonlimbate specimens, as well as those with grana, coni, and minute spinae in addition to bacula. *Archaeozonotriletes macromanifestus* Naumova, 1953 is tentatively included within the *Rhabdosporites langii* Morphon (here named). *Geminospora micropaxilla* (Owens) McGregor and Camfield, 1982 is considered part of the morphon, although, with its thickened, rigid exoexine, it is intergradational with the *Geminospora lemurata* Morphon. *Dibrochosporites nodosus* Urban, 1968 may also belong to this group. Australian specimens from the Poulton and Gneudna formations (e.g., Pl. 11, fig. 6) conform with *Rhabdosporites langii* as expanded by McGregor and Camfield (1982, p. 59). In Australia, some specimens of *Leiozonotriletes laurelensis* Balme and Hassell, 1962 (e.g., their Pl. 4, fig. 15; this paper, Pl. 19, fig. 12) may be appropriately contained within the *R. langii* Morphon.

Shared form features

All of the morphological characters we have observed in Australian spore assemblages are replicated in the Euramerican Middle and Upper Devonian assemblages. Even elongate fibrilliform processes, like those of *Medusaspora*, are present, e.g., in "Filiformispora" from the latest Devonian of Ohio and New York (Eames, 1974; pers. comm. to DCM) and *Archaeotriletes capillatus* Raskatova, 1969, from Givetian strata of the Voronezh district of the U.S.S.R.

One of the features most typical of Euramerican Middle and Upper Devonian spore assemblages is ancyrate (bifurcate or multifurcate) exoexinal processes. These may be borne by spores that are otherwise structurally distinct, e.g., zonate (*Ancyrospora*), "cingulizonate" (=pseudobizonate; *Densosporites*), pseudosaccate (*Grandispora*), azonate acavate (*Hystricosporites*), and gulate (*Nikitinsporites*), and on megaspores as well as miospores. Bifurcate processed spores are present in all of the Australian assemblages examined, except those from the Eastwood beds and the Virgin Hills Formation. Multifurcate processes occur in the Gogo and Pillara formations.

Proximal, radially oriented costae on trilete (and rarely on monolete) spores are found throughout the Devonian. In Euramerica this feature is prevalent in many Early Devonian assemblages, rare in those of Middle and Late Devonian age, and in some regions common again close to the Devonian–Carboniferous boundary. In Australia, radially costate spores have been observed sporadically in the Anna Plains, Gneudna, Gogo, and Pillara formations, and in the Brewer Conglomerate and Eugenana beds. Radially disposed thickenings of the exoexine are present in the contact areas of some Euramerican species of *Hystricosporites*, but were not observed on any Australian ancyrate spores.

Another common feature of Devonian spores in both Euramerica and Australia is a prominent equatorial/distal thickening or patina. This character is present in many miospores to some degree, but among some Devonian spores it is strongly developed, either as a fairly even exinal thickening (e.g., *Geminospora lemurata* and *Tholisporites densus*), or as a callus-like concentration of sculpture (e.g., *Archaeozonotriletes timanicus* and *Chelinospora concinna*). Pronounced equatorial and/or distal development of the exine into horn-like protuberances, as in *Cyrtospora* and *Cornispora*, has not been observed in Australian spores.

Curvaturate thickenings or discontinuities of sculpture are also typical of Devonian spores, although not confined to spores of that age. They are most obvious in the Lower Devonian where spore exinal sculpture is minor or absent, so the boundaries of the contact areas are not obscured or elaborated by coarse ornamentation and cingulizonate structures. In the Middle and Upper Devonian, spores tend to be more ornate and proximal curvaturae less conspicuous, except in relatively uncomplicated spores, such as those of the the *Dibolisporites echinaceus* Morphon. Curvaturae may thus to some extent be a function of intricacy of exinal ornamentation. Also, curvaturae may be transformed into quasi-equatorial elaborations by haptotypic development. Whatever the reason, curvaturae are less obvious among Middle and Upper Devonian assemblages than in those from the Lower Devonian. Nevertheless, curvaturate spores are evident in Australian Middle and Upper Devonian spore assemblages, just as they are in those from Euramerica.

Biform sculpture (sensu Playford, 1976, p. 14) is a common feature of Devonian spores in Euramerica. The *Dibolisporites echinaceus* Morphon, which has this feature, has not been recognized in Australia, but several taxa with biform ornaments do occur there in Upper Devonian/Lower Carboniferous rocks: *Dibolisporites distinctus* (Clayton) Playford, 1976; *D. montuosus* Playford, 1976; *D. capitulosus* Balme, 1988; *D. turriculatus* Balme, 1988; *D.* sp. of de Jersey (1966, p. 11); and *Acinosporites lindlarensis* (this paper; also see Grey, 1991 and, 1992, *D.* sp. cf. *D. echinaceus*).

Cingulizonate structure is perhaps more common in Carboniferous spores, but it occurs in the Devonian as well. In Euramerica, cingulizonate spores are particularly evident in Eifelian and Givetian assemblages (*Densosporites* spp; less prominently developed in *Cristatisporites albus*? of McGregor and Camfield, 1982). In Australia no undoubtedly cingulizonate Devonian spores have been found; some ancyrate spores (Pl. 3, figs. 2, 4, 6) may have an inner darkened annular zone, but none possesses a well developed bizonate cingulum.

Monolete sutures occur in Euramerican and Australian spores at certain stratigraphic levels, e.g., "Azonomonoletes" sp. in the Weatherall and Hecla Bay formations in Canada, the Calceola Horizon in the U.S.S.R. (Chibrikova, 1962), and the Lissoy Formation, Anna Plains Sandstone, and Eastwood beds in Australia; *Archaeoperisaccus* in the upper Givetian and Frasnian of Canada and the U.S.S.R.; and "*Archaeoperisaccus*" (*A. distinctus* Lu, 1988) in the Gogo and Lissoy formations. Some Devonian monolete spores may be teratological, such as occasional monolete versions of *Geminospora lemurata* seen during this investigation (see also Playford, 1983, fig. 4), and rare Canadian and Australian specimens judged to be aberrant *Emphanisporites rotatus* (cf. *Zonotriletes actinobolos* Chibrikova, 1962, Pl. 16, fig. 17).

DISCUSSION

Comparison of floras

An understanding of fossil spore-plant associations is advantageous to biostratigraphy. A spore zonation that is linked to biological relationships will be more soundly based than a purely form-taxonomic one. Therefore, it seems appropriate to give some attention to the possible botanical relationships of the spores constituting the Canadian and Australian assemblages.

Cutinized spores, as elements of the life cycle of terrestrial plants, obviously bear some phyletic relationship to the plants that produced them. Also, as part of the whole plant, they represent part of the ecological spectrum of the time and place in which they grew. The kinds of spores produced by present-day plants can be readily determined. In contrast, relatively little is known about the relationships of Middle and Upper Devonian spore taxa or their morphological features to their parent plants. Some Middle and Upper Devonian spores have been linked to form taxa of plants as a result of their discovery in situ, i.e., in sporangia borne by identifiable plants (Allen, 1980; Gensel, 1980). However, in proportion to the number of Devonian spore species known, such associations are rare, and the botanical affiliations of most species consequently have yet to be established. Even the affinities of some morphons, and other groups of spores united by shared (not necessarily intergrading) morphological features, have not been determined by their discovery in situ or from other evidence.

Also, different species of a given spore form genus, or spores sharing particular form features (such as biform sculpture), may have been allied with various kinds of parent plants (see below). On the other hand, some genera, based primarily on one or a few distinctive features, e.g., *Ancyrospora*, and *Emphanisporites*, could well represent coherent phyletic groups. But this cannot be ascertained unless their parental sources are determined. Also helpful would be an understanding of the environmental pressures that may have led to the development of their most distinctive features (in the above examples, ancyrate processes and proximal radial ribs, respectively). In fact, little is known of the ecological preferences of most Devonian plants (and their spores), although we may assume that the fossil record is skewed in favour of plants that either grew near water, or produced large numbers of readily wind-borne spores.

From the foregoing, it is clear that inferences about Devonian vegetational composition (both qualitative and quantitative) based on current information from palynological studies, are largely speculative. The distribution of form genera of dispersed spores may be a tenuous basis for deductions regarding the degree of similarity of floras in various regions. Of necessity, these genera are conceived and diagnosed without any requisite reference to the natural affinities of the spores (although knowledge of spore morphology in certain plant groups may serve as a guide to appropriate limits in the scope of genera). Devonian spore genera may approach taxonomic or phyletic entities of plants to various degrees, but more commonly may include forms that originated from a range of plants that were not necessarily closely related.

Nonetheless, some Middle and Upper Devonian plants have been found with attached sporangia that contain well preserved spores (see Gensel, 1980). They constitute vital reference points from which an understanding of the plant-spore relationships of that time and gross floristic composition can be inferred. Furthermore, recent studies (e.g., Streel and Scheckler, 1990) show qualitative and quantitative relationships between dispersed spore assemblages (and related plants) and inferred depositional environments and climates.

In referring to suprageneric plant groups in the ensuing discussion, we have followed the classification of Meyen (1987).

Genera

The following spore genera, apparently restricted to Euramerica, have been linked to particular kinds of plants: in situ *Nikitinsporites* megaspores to lycopodiopsids (Nikitin, 1934); in situ *Archaeoperisaccus* microspores, to the same lycopodiopsid plant (Nikitin, 1934; McGregor, 1969), and dispersed specimens of the genus, by their sporoderm structure, to conifers (Meier and Raskatova, 1984) and archaeopterids (Meier-Melikyan and Tel'nova, 1989); in situ *Biharisporites* to the progymnosperm *Archaeopteris* (Pettitt, 1965; Med'yanik, 1982); in situ *Contagisporites* (as "*Biharisporites*") to progymnosperms (Krassilov, Raskatova, and Ishchenko, 1987); in situ *Lagenicula* to lycopodiopsids (Chaloner, 1968); and probable in situ *Chelinospora* to bryophytes (Krassilov, Ishchenko, and Raskatova, 1987). *Densosporites* microspores were produced by four lycopodiopsid species, i.e., *Porostrobus zeilleri* (Nathorst) Nathorst, 1914, of Early Carboniferous age (Bharadwaj, 1959); and *Selaginellites canonbiensis* Chaloner, 1958, *Sporangiostrobus kansanensis* Leisman, 1970, and *S. puertollanensis* Remy and Remy, 1975, all of Late Carboniferous age. Of these, *Selaginellites canonbiensis* and *Sporangiostrobus kansanensis* have cingulizonate spores that in this respect resemble Devonian specimens of *Densosporites* sensu Richardson (1960). Cingulizonate densospores have not, however, been found directly associated with any Devonian plants.

On the other hand, the parent plants of *Biornatispora, Clivosispora, Cornispora, Cyrtospora, Laiphospora, Lanatisporis, Ocksisporites, Periplecotriletes, Rugospora, Sinuosisporis,* and *Triangulatisporites* — genera not so far encountered in the Australian Devonian — are unknown.

Similarly, there is still no conclusive evidence as to the botanical affinities of the Australian genera *Ambagisporites* and *Medusaspora*, or of the plants represented by *Archaeoperisaccus indistinctus* and *Camptozonotriletes*? spp. Balme (1988a) noted that *Ariadnaesporites* Potonié, 1956 and *Caudaspora* Elsik, 1966, both of Late Cretaceous age, have extremely long thread-like processes similar to those of *Medusaspora*. He concluded that these enations were independently developed in the Cretaceous in a plant group possibly related to the Marsileaceae.

From consideration of apparently endemic spore genera, some tentative conclusions may be drawn about the *differences* between Canadian and Australian floras of the Middle and Late Devonian epochs. First, none of the seemingly endemic Australian genera or putative genera have been recognized among the hundreds of thousands of Canadian Devonian spores examined by the first author, and none have been reported from elsewhere in Euramerica. Therefore, it seems reasonable to conclude that the plants producing them did not inhabit Euramerica.

Conversely, *Contagisporites, Laiphospora, Ocksisporites, Triangulatisporites,* and true *Archaeoperisaccus* are all upper Givetian to lower Frasnian genera found in Canada. Palynologically this is the best known Devonian stratigraphic interval in Australia (Fig. 7), no specimens of these genera have been found there. This implies that the corresponding spore-producing plants of late Middle to early Late Devonian time did not occur in Australia.

Failure to find certain other "Euramerican" spore genera in the Middle and Upper Devonian of Australia may, on the other hand, be less compelling evidence for their absence. *Lanatisporis, Periplecotriletes,* and *Sinuosisporis* (all Eifelian), *Densosporites* (Eifelian to lower Givetian), and *Cornispora* and *Cyrtospora* (both Famennian) occur in Canada in parts of the Devonian that have been little studied palynologically in Australia. It would clearly be premature to suggest that they, and the corresponding parental vegetation, were absent from Australia in the Devonian.

In summary, the evidence of some palynological exclusiveness between Canada/Euramerica and Australia implies concomitant floristic differences in Middle to Late Devonian time. However, there is little evidence of the botanical nature of these differences. The affinities of the *Nikitinsporites/Archaeoperisaccus* complex (lycopodiopsid?) remain ambiguous. *Contagisporites* suggests a Euramerican progymnosperm component that may not have been present in Australia. On the other hand, the progymnosperm *Archaeopteris*, which is widespread in Euramerica, also occurs in Australia (Chapman, 1921; F.M. Hueber, pers. comm. to DCM, 1990), as do the possibly related *Geminospora* spores. *Biharisporites*, the suggested Euramerican megaspore of *Archaeopteris* (see above), has not been identified with certainty in Australia.

Of the shared genera, *Knoxisporites* and *Verrucosisporites* range into the Carboniferous, where they have been found in organic connection with plants of that age. Spores identified as *Knoxisporites* were discovered in an isolated, unidentified, but possibly polypodiopsid, sporangium of late Tournaisian age (Scott et al., 1985). *Verrucosisporites* spores occur in situ in the Stephanian ferns *Zygopteris* sp. (Bougneres and Remy, 1957) and *Senftenbergia pennaeformis* (Brongniart) Stur, 1877 (Remy and Remy, 1955). Some spores of the latter species may be assigned to *Convolutispora* (Laveine, 1969). It is interesting to note that some Devonian species of *Verrucosisporites* intergrade morphologically with *Convolutispora* (McGregor and Camfield, 1982). Spores of these genera have never been seen in Devonian sporangia, but the evidence cited above regarding the affinities of Carboniferous representatives perhaps provides tenuous clues to the botanical relationships of Devonian species.

Dibolisporites has been linked to the Eifelian cladoxylalean ferns by the discovery of *Dibolisporites echinaceus* [*D.* sp. cf. *D. gibberosus* (Naumova) Richardson var. *major* (Kedo) Richardson, 1965] in sporangia of *Calamophyton bicephalum* Leclercq and Andrews, 1960 (Bonamo and Banks, 1966). However, although several species of *Dibolisporites* occur in Australian strata, unquestionable specimens of *D. echinaceus* have not been found.

Diaphanospora spores have been recovered from two species of *Rhacophyton*, a possible progymnosperm precursor (Andrews and Phillips, 1968; Ishchenko and Sorokina, 1968).

Shared genera of spores, found in attached sporangia, thus suggest similar polypodiopsid elements in the Euramerican and Australian floras, and perhaps forms ancestral to the progymnosperms. This is of course speculative, as there is no conclusive evidence to indicate that spores of the genera cited were confined to these plant groups.

Certain genera that are common to Euramerica and Australia, but have not yet been found in situ, may have originated from the same unspecified but phyletically related groups of plants in both regions. Among them may be those that encompass the more complexly constructed spores, which are perhaps less likely to have been duplicated by homoplasy (*Ancyrospora, Chelinospora, Emphanisporites, Gneudnaspora, Hystricosporites,* and *Teichertospora*). These genera are virtually restricted to, and highly characteristic of, Devonian strata (*Emphanisporites* and *Hystricosporites* may occur, rarely, in basal Carboniferous strata in some regions). They thus represent essentially Devonian plant groups that evidently were able to maintain their phyletic integrity during long-distance dispersal. All are temporally long ranging, some through several chronostratigraphic series or stages. Clearly, the plant groups that produced them would have had correspondingly broad geographic and stratigraphic distribution.

Species

Because they are morphologically less variable, shared species of dispersed spores may be a more objective basis than shared genera for determining detailed floral similarities. Each of the species listed on p. 21, 22 herein may represent a floral component shared by the Devonian vegetation of Euramerica and Australia. This is speculative, as none of these species have been reported in sporangia of particular plants in both regions. However, some of them are known botanically in situ in Euramerica, thus offering some indication of the kinds of plants that may have been common to the two regions.

In eastern North America, *Acinosporites lindlarensis* var. *lindlarensis* has been extracted from sporangia of two species of the lycopodiopsid genus *Leclercqia* (Banks et al., 1972; Richardson et al., in press). Although spores have not been found in *Leclercqia* sporangia in Australia, *A. lindlarensis* occurs in the Canning Basin of Western Australia (this report), and *Leclercqia* is present in the Burdekin Basin of north Queensland (Fairon-Demaret, 1974).

Another shared species, *Aneurospora greggsii*, intergrades morphologically in Euramerica and Australia with *Geminospora lemurata*. Both taxa have been linked with the cosmopolitan progymnospermous plant *Archaeopteris* (Playford, 1983; Chitaley and McGregor, 1988).

In situ spores of two other progymnosperms, *Tetraxylopteris schmidtii* Beck, 1957 emend. Bonamo and Banks, 1967, and *Rellimia* (al. *Milleria*) *thomsonii* Leclercq and Bonamo, 1973, are identical with the Euramerican/Australian spore species *Rhabdosporites langii* (Leclercq and Bonamo, 1971).

Miospores similar to *Diaphanospora perplexa* were recovered in situ from *Rhacophyton ceratangium*, which Andrews and Phillips (1968, p. 37) suggested may be a progymnosperm precursor. Ishchenko and Sorokina (1968) obtained nearly identical spores, ascribed by them to *Hymenozonotriletes varius* var. *minor* Naumova, 1953, from sporangia of

Rhacophyton incertum (Dawson) Kräusel and Weyland, 1941.

Spores from within mature "clavae" of the probable anthocerotid bryophyte *Bitelaria* Ishchenko and Ishchenko, 1981, are comparable to *Chelinospora concinna* (Krassilov, Ishchenko, and Raskatova, 1987).

Some species of dispersed spores are so broadly constituted or interpreted that the forms included in them by various authors may well have been produced by phyletically disparate plants. One such species, common to Euramerica and Australia, is *Cristatisporites triangulatus* sensu lato. It is characterized primarily by a zona that is widest interradially. Various authors have included in it spores with diverse exoexinal sculpture, from conate to cristate to rugulate, and with or without development of the zona interradially (e.g., Lu, 1980; Arkhangelskaya, 1985; Loboziak and Streel, 1980, but see Streel and Loboziak, 1987). *Cristatisporites triangulatus* sensu stricto (see Allen, 1965), with discrete or interconnected (cristate) distal coni and barely perceptible zona development interradially, may represent a taxonomically more narrowly circumscribed plant group. On the other hand, virtually the entire range of variation observed in Euramerican specimens of *C. triangulatus* sensu lato is present in Australian strata of comparable age (late Givetian-early Frasnian; Pl. 6, figs. 1-8), suggesting a possible phytophyletic correlation between the two regions for the whole complex. No specimens of *C. triangulatus* have been recorded from sporangia in either region.

Another species of unknown botanical affinities that has received a morphologically extended range of forms in the literature is the patinate form *Cymbosporites magnificus*. An appreciation of the variability ascribed to this taxon may be obtained by comparing specimens described by McGregor (1960) as *Lycospora magnifica*; by Allen (1965), Tiwari and Schaarschmidt (1975), and Moreau-Benoit (1980), as *C. cyathus*; by Owens (1971) as *Verruciretusispora magnifica*; and by Lu (1988) as *C. cyathus* and *C. magnificus*. The full range of variation exhibited by this species is difficult to determine, as some of the proposed constituents have not been described: e.g., *Retusotriletes tamilii* Filimonova *nomen nudum* in Nazarenko (1965), and *R. vorobievensis* Naumova, 1953, *nomen nudum*, both of which were placed in synonymy with *C. magnificus* by Arkhangelskaya (1985, p. 51). In general, the range of morphological variation, including that of entities included in synonymies, approximates the range of variation present in Canada and Australia. One may speculate, cautiously, that this spectrum of spores was produced by a correlative, phyletically related (although botanically unknown) array of plants in both regions.

Morphons

Of the endemic Euramerican morphons of Middle and Late Devonian age, only two, the *Dibolisporites echinaceus* and *Archaeoperisaccus ovalis* morphons, have been linked to plant fossils by discovery in situ: *D. echinaceus* to the fern *Calamophyton bicephalum* (see above); and *A. concinnus*? to the questionable lycopodiopsid *Kryshtofovichia africani* Nikitin, 1934 (McGregor, 1969). The botanical affinities of the two suggested "Australian" morphons, *Camptozonotriletes* spp. and *Cristatisporites* spp., remain unknown.

The possible botanical affiliations of *Geminospora lemurata, Rhabdosporites langii* (progymnosperms), and *Verrucosisporites scurrus* (ferns?), are alluded to in the discussion of shared species (above). No components of the other shared morphons have been reported from fructifications or in consistent association with any particular plant group, either in Devonian rocks or those of another age.

Form features

Cingulizonate structure is particularly common in Middle Devonian spore assemblages of Euramerica. Spores with this feature have not been found in any Devonian sporangia. In the Carboniferous, cingulizonate spores were produced by some lycopodiopsids (see above).

Collectively, spores with ancyrate exinal processes range through the entire Middle and Upper Devonian, and virtually disappear near the Devonian-Carboniferous boundary. Ancyrate processes recur sporadically higher in the column, e.g., on Lower Carboniferous spores attributed to *Hamatisporites, Hystricosporites,* and *Trichodosporites* of unknown affinities (Candilier et al., 1982); on megaspores of the Carboniferous plant *Lycostrobus scottii* (Nathorst) Nathorst, 1908 (Potonié, 1967, Pl. 3, figs. 48-51 and ?55); on *Grapnelispora* megaspores of Cretaceous age (Stover and Partridge, 1984); on Recent microspores of *Selaginella* (Taugourdeau-Lantz, 1971); and on massulae surrounding the microspores (but not on the spores themselves) of some species of the Cretaceous to Recent "water fern" *Azolla* (see Collinson, 1980). Some of the records of post-Devonian ancyrate spores represent phyletically related plants inasmuch as they point to the lycopodiopsids. *Kryshtofovichia africani* and *Borysthenostrobus mirandus* Ishchenko and Semenova, 1982, the only Devonian plants so far known to have borne ancyrate spores, may be affiliated with this group (McGregor, 1969; Ishchenko and Semenova, 1982). However, the meagre evidence is insufficient to suggest that ancyrate exinal processes were restricted to the lycopodiopsids, either in the Devonian or later.

Spores bearing radially arranged costae on their proximal faces have not been linked reliably with any particular plant group. The putative occurrence of such spores (*Emphanisporites*) in sporangia of *Horneophyton lignieri* (Kidston and Lang) Barghoorn and Darrah, 1938, may have have been based on a misinterpretation (Allen, 1980, p. 256; Gensel, 1980, p. 104-107).

Distal crassitudes (patinas) are not restricted to Devonian spores. Laveine (1969) has reported unsculptured, patinate spores from several species of the Carboniferous fern *Pecopteris* (Brongniart) Sternberg, 1825. They resemble certain Devonian forms (e.g., *Archaeozonotriletes variabilis*), except that they are monolete. However, crassitudinous spores with variously sculptured and asymmetrically disposed patinas are particularly conspicuous in Middle and Upper Devonian dispersed spore assemblages. All are trilete, and none have been found in situ.

Spores with entirely proximal (i.e., not equatorial) curvaturae like those of rhyniopsids and zosterophyllopsids (Gensel, 1980) are common in Lower Devonian assemblages. In the Middle and Upper Devonian, they are less evident, but were also produced by various plants, e.g., *Barinophyton* White, 1905 (Barinophytopsida; Brauer, 1980); *Borysthenostrobus* Ishchenko and Semenova, 1982 (Lycopodiopsida); *Cyclostigma* Haughton, 1859 (Lycopodiopsida; Chaloner, 1968); *Protosalvinia* (Dawson) Clarke, 1885 (Phaeophyta?; Schopf, 1978; Gray and Boucot, 1979); and *Tanaitis* Krassilov, Raskatova, and Ischenko, 1987 (Progymnospermopsida).

Middle to Upper Devonian assemblages contain spores with various kinds of biform sculpture, including mammillae (e.g., *Verrucisporites* Chi and Hills, 1976), capitate structures (e.g., *Dibolisporites turriculatus*), and elongate elements of variable shape (e.g., *D. echinaceus*). We suspect, although without evidence, that such diverse sculptural projections may have been produced independently by a range of plant groups. The only Devonian plant known to have produced spores with biform ornaments is *Calamophyton bicephalum* (see above).

Monolete spores (*Archaeoperisaccus, Limbomonoletes, Laevigatosporites, Latosporites*) evidently represent structurally consistent (i.e., not teratological) elements of certain Middle and Upper Devonian plants. Their natural affinities are uncertain: *Archaeoperisaccus* may be lycopodiopsid (McGregor, 1969); *Laevigatosporites* and *Latosporites* have been found in equisetopsid and fern sporangia in the Carboniferous (Potonié, 1967), but exclusively as *sporae dispersae* in the Devonian.

Biostratigraphy

Botanical basis for long-distance correlation by spores

In this paper, we assume that the presence of a number of shared spore taxa and morphons, apparently representing a diversity of plant groups, indicates close phyletic affinities of some floral components between Canada/Euramerica and Australia in the Devonian. This signifies a sound botanical basis for constructing a long-distance zonation based on spores. Available information on Australian Middle to Upper Devonian megafloras, though limited, supports the palynological indications of some similarities in the vegetation of Australia and Euramerica. A Givetian-Frasnian flora from northern Queensland contains several northern hemisphere genera and, like Euramerican floras, is characterized by arborescent progymnosperms and a wide variety of fern-like plants, in addition to lycopsids which dominate most known southern hemisphere Devonian assemblages (Hueber, 1978).

The efficacy of biostratigraphic correlation obviously depends in part on how nearly isochronous the fossils are. Whether fossils (in this case dispersed spores) are inherently capable of wide geographic dispersal, and whether the resultant distribution is geologically "isochronous", obviously are functions of the rate of their effective dispersal, their capacity to cross physiographic and climatic barriers, and the ability of their biological support systems to move with them. Mere transport of disseminules across an ocean 1000 km wide, a feat not unusual for most modern fern spores, for example (Tryon, 1970), would not necessarily guarantee establishment (effective propagation) of the species on the other side, especially if the new region were already occupied by well established plant communities.

Plants vary greatly in the means, rates, and effectiveness with which they can spread extensively (Chaloner and Creber, 1988). The migration of some present day bryophytic and pteridophytic plants and plant communities is impeded by climatic differences and by physiographic barriers such as mountain ranges and wide bodies of water (see arguments in Streel et al., 1990, p. 293). It seems reasonable to conclude that the dispersal of some plants would have been similarly obstructed in the Devonian period. This could explain the apparent absence in Australia of the *Acinosporites acanthomammillatus*, *Archaeoperisaccus ovalis, A. verrucosus, Cyrtospora cristifera, Densosporites devonicus, Dibolisporites echinaceus, Diducites mucronatus*, and *Sinuosisporis sinuosus* morphons.

On the other hand, some extant free-sporing plants are remarkably proficient disseminators (Tryon, 1970; 1986, p. 141) as, apparently, were some Devonian plants: e.g., *Leclercqia* Banks, Bonamo, and Grierson, 1972 (Gensel and Andrews, 1984, p. 140); and *Uskiella* Shute and Edwards, 1989. In the Devonian, similar levels of dispersal capability may have been attained by the various parent plants of spores comprising the two *Ancyrospora* morphons and the *Archaeozonotriletes variabilis, Cristatisporites triangulatus, Cymbosporites magnificus, Dibolisporites farraginis, Emphanisporites rotatus*, *Hystricosporites porrectus*, and *Verrucosisporites scurrus* morphons. The progymnosperms probably were efficient long-distance colonizers, owing to the adaptive advantage conferred by their arborescent habit. This would be consistent with the wide geographical distribution attained by some elements of the *Geminospora lemurata* and *Rhabdosporites langii* morphons.

Canada-Australia correlation

Richardson and McGregor (1986) proposed nineteen spore assemblage zones encompassing the Silurian and Devonian of the Old Red Sandstone Continent region of Euramerica. Of these zones, ten cover the Middle through Upper Devonian interval that is the subject of this report.

For each assemblage zone, the authors proposed a list of "characterizing species" considered to have achieved sufficiently wide geographic spread to be useful for interbasinal correlation in that broad region. They also noted that some of the characterizing species occur in Devonian rocks located well beyond Euramerica (e.g., in Australia) and, accordingly, that such species offer scope for more extended, intercontinental, correlation.

Table 1 shows the zonal characterizing species proposed by Richardson and McGregor (1986), and those shared (characterizing and other) species that may allow recognition of equivalent time intervals in Australia. This table should be read in context with the range chart (Fig. 7). In particular, it is important to note that the stratigraphic ranges of some of the shared characterizing species extend into overlying zones in Euramerica (Richardson and McGregor, 1986, Fig. 3) and, evidently, in Australia. For example, *Verruciretusispora dubia*, a characterizing species of the upper Lower Devonian *annulatus-sextantii* Zone, first appears in that zone, but it also may be present in the overlying four lower zones of the Middle Devonian (Eifelian to lower Givetian). It occurs in the Eastwood beds of probable early Eifelian age (*velata-langii* Zone?), which are the oldest Devonian strata in Australia to have undergone palynological study. It seems reasonable to speculate that if late Emsian spore assemblages are found in Australia, they may include *V. dubia*.

Some Australian specimens resemble Euramerican zonal taxa i.e., *Camarozonotriletes sextantii, Cristatisporites deliquescens, Grandispora eximia, G. velata,* and *Vallatisporites pusillites*, but their taxonomic identifications need confirmation. The last species may be present in the Australian upper Famennian (as *V.* sp. cf. *V. pusillites* of Playford, 1976).

As can be seen from Table 1, certain species that co-occur in Australia and Euramerica are not among those chosen as characterizing species by Richardson and McGregor (1986). Some of these, such as *Dibolisporites turriculatus, Dictyotriletes australis, Retusotriletes digressus, R. punctimedianus, Tholisporites densus, Trileites langii,* and those in open nomenclature ("sp.") or qualified by the designation "cf.", are still not well circumscribed taxonomically and/or stratigraphically in one region or the other. Others, e.g., *Emphanisporites minutus, E. rotatus, Gneudnaspora divellomedium,* and *Hystricosporites porrectus*, are too long-ranging to be useful zonally unless, perhaps, at their level of stratigraphic first appearance (which, except for *H. porrectus*, occurred earlier than the age range with which we are concerned here). None of these taxa seems to be relevant, at the present state of knowledge, to narrowly focused Middle or Late Devonian age determinations or correlations. Nevertheless, their presence in Australia and Euramerica does suggest floral continuities, and so may enhance confidence in the botanical rationale for long-distance correlation using other taxa.

TABLE 1

Characterizing species of Euramerican spore assemblage zones (Richardson and McGregor, 1986), and approximate recorded zonal positions of those that have been found in Australia

Zone and age	Euramerican zonal characterizing species	Occurrence of characterizing species in Australia	Occurrence of other shared taxa in Australia
nitidus-verrucosus (*lepidophyta-nitidus* Subzone) late Famennian	***Verrucosisporites nitidus*** *Vallatisporites verrucosus* ***Retispora lepidophyta*** *Cyrtospora cristifera* ***Endosporites micromanifestus*** *Grandispora echinata* ***Indotriradites explanatus*** ***Knoxisporites literatus*** *Raistrickia corynoges* ***Tumulispora rarituberculata***	***Verrucosisporites nitidus*** ***Retispora lepidophyta*** ***Endosporites micromanifestus*** ***Indotriradites explanatus*** ***Knoxisporites literatus*** ***Tumulispora rarituberculata*** (?)*Vallatisporites pusillites*	*Diaphanospora perplexa* *Hystricosporites porrectus* *Retusotriletes digressus*
pusillites-lepidophyta late Famennian	*Vallatisporites pusillites* ***Retispora lepidophyta*** *Diducites poljessicus* *Diducites versabilis* ***Endosporites micromanifestus*** *Grandispora echinata* ***Knoxisporites literatus*** *Raistrickia variabilis* *Rugospora radiata* ***Tumulispora rarituberculata***	***Retispora lepidophyta*** ***Knoxisporites literatus*** ***Auroraspora macra***	*Diaphanospora perplexa* *Hystricosporites porrectus* *Retusotriletes digressus*
radiata-cornuta* early late Famennian	*Rugospora radiata* *Grandispora cornuta* *Auroraspora hyalina* ***Auroraspora macra*** ***Teichertospora torquata*** *Cornispora varicornata* *Cyrtospora cristifera* *Diducites poljessicus* *Diducites versabilis* *Grandispora gracilis* *Hystricosporites multifurcatus* *Lagenicula* sp. *Retispora cassicula* *Retusotriletes phillipsii*		
torquata-gracilis latest Frasnian and early Famennian	***Teichertospora torquata*** *Grandispora gracilis* ***Aneurospora greggsii*** ***Archaeozonotriletes famenensis*** *Auroraspora hyalina* ***Auroraspora macra*** *Auroraspora pseudocrista* *Cornispora varicornata* *Crassispora catenata* *Cyrtospora cristifera*	***Teichertospora torquata*** ***Archaeozonotriletes famenensis*** ***Ancyrospora langii*** ***Geminospora lemurata*** ***Verrucosisporites nitidus***	*Hystricosporites porrectus*

Zone and age	Euramerican zonal characterizing species	Occurrence of characterizing species in Australia	Occurrence of other shared taxa in Australia
	Diducites poljessicus *Diducites versabilis* (?)*Hymenozonotriletes denticulatus* *Hystricosporites multifurcatus* *Knoxisporites dedaleus* *Lophozonotriletes lebedianensis*		
ovalis–bulliferus Frasnian	*Archaeoperisaccus ovalis* *Verrucosisporites bulliferus* *Ancyrospora furcula* *Ancyrospora melvillensis* **Aneurospora greggsii** *Archaeoperisaccus opiparus* cf. *Archaeozonotriletes laetus* *Diaphanospora reticulata* **Geminospora lemurata** *Cristatisporites deliquescens* *Nikitinsporites canadensis*	**Geminospora lemurata** **Ancyrospora langii** **Archaeozonotriletes variabilis** **Cristatisporites triangulatus** **Cymbosporites magnificus** **Emphanisporites annulatus** **Grandispora naumovae** **Rhabdosporites langii** **Verrucosisporites scurrus**	*Acinosporites lindlarensis* var. *minor* *Ancyrospora simplex* *Dibolisporites turriculatus* *Dibolisporites vegrandis* *Emphanisporites rotatus* *Geminospora punctata* *Geminospora venusta?* *Geminospora verrucosa* *Gneudnaspora divellomedium* cf. *Grandispora inculta* *Retusotriletes biarealis* *Retusotriletes punctimedianus* *Tholisporites tenuis*
optivus–triangulatus late Givetian and early Frasnian	*Contagisporites optivus* var. *optivus* **Cristatisporites triangulatus** *Ancyrospora involucra* **Ancyrospora langii** *Ancyrospora melvillensis* *Aneurospora goensis* **Aneurospora greggsii** *Archaeoperisaccus timanicus* **Chelinospora concinna** *Chelinospora ligurata* **Geminospora lemurata** *Grandispora tomentosa*	**Cristatisporites triangulatus** **Ancyrospora langii** **Aneurospora greggsii** **Chelinospora concinna** **Geminospora lemurata** **Acinosporites lindlarensis** var. **lindlarensis** **Archaeozonotriletes timanicus** **Archaeozonotriletes variabilis** (?)*Cristatisporites deliquescens* **Cymbosporites magnificus** **Emphanisporites annulatus** (?)*Grandispora eximia* **Grandispora naumovae** **Retusotriletes rugulatus** **Rhabdosporites langii** **Verrucosisporites premnus** **Verrucosisporites scurrus**	cf. *Anapiculatisporites petilus* *Ancyrospora simplex* *Ancyrospora* sp. cf. *A. acutispinosa* *Ancyrospora* sp. cf. *A. ampulla* *Ancyrospora* sp. cf. *A. pulchra* *Ancyrospora* sp. cf. *Archaeozonotriletes famenensis* *Convolutispora* sp. *Corystisporites collaris* *Cristatisporites* sp. 1 and 2 *Cymbosporites* sp. cf. *C. magnificus* *Cymbosporites* sp. 1 and 2 *Dibolisporites farraginis* *Dibolisporites turriculatus* *Dibolisporites* sp. cf. *D. uncatus*? *Dibolisporites vegrandis* *Dictyotriletes australis* *Geminospora venusta*? *Geminospora verrucosa* cf. *Geminospora* sp.

Zone and age	Euramerican zonal characterizing species	Occurrence of characterizing species in Australia	Occurrence of other shared taxa in Australia
			Gneudnaspora divellomedium *Heterotriletes* sp. 1 and 2 *Hystricosporites porrectus* *Retusotriletes biarealis* *Retusotriletes punctimedianus* *Tholisporites densus* *Tholisporites tenuis* *Trileites langii*
lemurata–magnificus early and mid Givetian	***Geminospora lemurata*** ***Cymbosporites magnificus*** ***Ancyrospora langii*** *Aneurospora goensis* ***Aneurospora greggsii*** ***Archaeozonotriletes variabilis*** ***Archaeozonotriletes timanicus*** *Biharisporites parviornatus* *Corystisporites serratus* *Lanatisporis bislimbatus* *Grandispora tomentosa* *Hymenozonotriletes celeber* *Perotrilites conatus* *Perotrilites heclaensis*	***Geminospora lemurata*** ***Acinosporites lindlarensis*** var. ***lindlarensis*** ***Chelinospora concinna*** ***Rhabdosporites langii***	*Ancyrospora* sp. cf. *A. ampulla* *Dibolisporites farraginis* cf. *Grandispora inculta*
devonicus–naumovae early Eifelian to early Givetian	*Densosporites devonicus* ***Grandispora naumovae*** *Acinosporites acanthomammillatus* *Acinosporites macrospinosus* *Ancyrospora grandispinosa* *Cristatisporites orcadensis* *Densosporites inaequus* *Grandispora inculta* *Grandispora mammillata* *Hystricosporites gravis* *Hystricosporites reflexus* *Kraeuselisporites rugosus* *Lophotriletes devonicus* *Perotrilites conatus* *Retispora archaelepidophyta* *Retusotriletes distinctus* ***Retusotriletes rugulatus*** ***Rhabdosporites langii*** ***Verrucosisporites premnus*** ***Verrucosisporites scurrus***	***Rhabdosporites langii*** ***Verrucosisporites scurrus*** ***Archaeozonotriletes variabilis*** (?)*Grandispora velata* ***Verruciretusispora dubia*** ***Verrucosisporites scurrus***	cf. *Anapiculatisporites petilus* *Ancyrospora* sp. cf. *A. pulchra* *Anulatisporites* sp. "Azonomonoletes" sp. *Diatomozonotriletes* sp. cf. *D. oligodontus* *Dibolisporites farraginis* *Dibolisporites vegrandis* *Dictyotriletes australis* *Emphanisporites minutus* *Gneudnaspora divellomedium* cf. *Grandispora inculta*
velata–langii early Eifelian	*Grandispora velata* ***Rhabdosporites langii*** *Acinosporites acanthomammillatus*	***Rhabdosporites langii*** ***Retusotriletes rugulatus*** (?)*Camarozonotriletes sextantii*	*Anulatisporites* sp. "Azonomonoletes" sp. *Brochotriletes* sp. cf. *B. foveolatus*

Zone and age	Euramerican zonal characterizing species	Occurrence of characterizing species in Australia	Occurrence of other shared taxa in Australia
	Acinosporites macrospinosus *Anapiculatisporites petilus* *Ancyrospora ancyrea* var. *ancyrea* *Corystisporites multispinosus* *Densosporites concinnus* *Grandispora longa* *Kraeuselisporites acerosus* *Kraeuselisporites ollii*? *Periplecotriletes tortus* *Perotrilites bifurcatus* *Retusotriletes distinctus* ***Retusotriletes rugulatus***	***Verruciretusispora dubia***	*Camarozonotriletes* sp. *Dibolisporites turriculatus* *Dictyotriletes australis* *Gneudnaspora divellomedium* *Laevigatosporites* sp.
douglastownense-eurypterota late Emsian and early Eifelian	*Grandispora douglastownense* *Ancyrospora eurypterota* *Acinosporites apiculatus* *Ancyrospora kedoae* *Ancyrospora nettersheimensis* *Ancyrospora loganii* *Apiculiretusispora gaspiensis* *Calyptosporites* sp. Riegel *Dibolisporites echinaceus* *Grandispora eximia* *Hystricosporites* sp. cf. *H. corystus* *Hystricosporites microancyreus* *Spinozonotriletes arduinnae*		
annulatus-sextantii Emsian	***Emphanisporites annulatus*** *Camarozonotriletes sextantii* ***Acinosporites lindlarensis*** var. ***lindlarensis*** *Apiculatasporites microconus* *Apiculiretusispora brandtii* *Apiculiretusispora plicata* *Grandispora biornata* *Camptozonotriletes* sp. cf. *C. aliquantus* *Dibolisporites echinaceus* *Dibolisporites eifeliensis* *Dictyotriletes canadensis* *Dictyotriletes gorgoneus* *Emphanisporites schultzii* ***Verruciretusispora dubia***		

Shared zonal species are in bold type. Other shared species are listed, according to approximate age of their occurrence in Australia, in column four. (?), uncertain identification.

*See Avchimovitch et al. (1988)

The remainder of the co-occurring species comprise forms that ultimately may represent new zonal indices. Except for "Azonomonoletes" sp., they are established species, and none has been regarded previously as a zone-characterizing species. They occur in sufficient numbers in several regions, localities, and lithofacies of Euramerica and Australia to allow their known stratigraphic limits to be regarded as approximating their maximum temporal ranges. They are: *Ancyrospora simplex*, "Azonomonoletes" sp., *Corystisporites collaris, Diaphanospora perplexa, Dibolisporites farraginis, D. vegrandis, Geminospora verrucosa, G. punctata, Retusotriletes biarealis,* and *Tholisporites densus*.

In Canada, most of the shared Canadian/Australian Middle and Upper Devonian spore types occur in the east as well as in the west and Arctic, i.e., in regions representing both the southern and the northern parts of Euramerica. However, a few of them seem, on present evidence, to be regionally restricted within Canada: e.g., *Camarozonotriletes sextantii, Grandispora naumovae,* and *Teichertospora torquata* (southern Euramerica); and *Archaeozonotriletes famenensis*, "Azonomonoletes" sp., and *Tholisporites densus* (northern Euramerica). Thus, current data suggest that Australian Devonian spore assemblages do not have an exclusive or favoured affinity with either of the major Devonian floristic regions of Canada and Euramerica. In other words, assemblages of the two Canadian/Euramerican regions appear to offer comparable scope for palynostratigraphic correlation with Australia.

The estimated Australian stratigraphic ranges or recorded occurrences of most of the species listed above and other established Euramerican zonal taxa in late Givetian to Famennian strata of the Carnarvon, Canning, and Bonaparte basins approximate, or lie within, the ranges previously established for them in Euramerica (Fig. 7). In these basins, independent support for age determinations of some of the palyniferous strata is provided by associated marine faunas. There is thus reasonably good evidence that some taxa are approximately coeval in Euramerica and Australia. This suggests that the potential for palynostratigraphic correlation between the two regions may be improved by adding some or all of these species to the existing inventory of zone-characterizing taxa.

However, the Australian time ranges of most of these species are still not well defined. Few stratigraphically sequential Devonian palynological studies have been done in Australia, and, of these, few have been integrated with studied zonal faunas. The potential clearly exists for palynostratigraphic correlations between Australia and Euramerica because they share many spore taxa and morphologically intergrading spore complexes. The next step in the realization of an Australian/Euramerican zonation lies in the independent corroboration of the ages of the shared key taxa and morphons in Australia.

Insufficient data are available at present to determine whether the first occurrences of many of the key taxa were synchronous in Australia and Euramerica. However, this information may not be critical to the initial establishment of a workable zonation. Previous work has shown that first appearances of certain individual species of spores may, by themselves, be less reliable than co-occurrences of species and morphons (assemblage zones) as indices for time correlation (see McGregor, 1981; Richardson and McGregor, 1986).

Based on the results of our studies, we propose that enough similarities exist between Euramerican and Australian Middle and Upper Devonian spore assemblages to sustain long-distance biostratigraphic correlation (see Tables 1 and 2, and Fig. 8) using modifications of the assemblage palynozones of Richardson and McGregor (1986). The first occurrence of key morphons and form features may also be useful, complementary to this species taxonomic level of comparison. The soundest basis for correlation, therefore, may be a combination of co-occurring taxa, morphons, and spore form features.

Occurrence of the shared taxa, morphons, and form features in extra-Australian Gondwana

The records of endemic and shared spore taxa and morphons suggest that: 1) through Middle and Late Devonian time broadly similar successions of plant communities existed in Euramerica and Australia, and 2) a few plant groups of undetermined phyletic level were not able to establish themselves in both regions. Streel et al. (1990) found a generally similar distributional pattern and vegetational succession between southern Euramerica (mainly western Europe) and western Gondwana (North Africa and Brazil), although according to their interpretation the proportion of shared species of morphologically "elaborate miospores" was higher there than between Euramerica and Australia.

At least 32 of the 80 spore taxa that are, or possibly are, common to Euramerica and Australia have, in our

TABLE 2

Estimated correlation of Australian lithostratigraphic units (studied spore assemblages only) with Euramerican spore assemblage zones of Richardson and McGregor (1986), in ascending stratigraphic order

Euramerican spore assemblage zone	Australian lithostratigraphic unit
nitidus–verrucosus (lepidophyta–nitidus Subzone*)*	Buttons Formation Yellow Drum Sandstone
pusillites–lepidophyta	Buttons Formation Gumhole Formation
radiata–cornuta	
torquata–gracilis	Brewer Conglomerate Gneudna Formation
ovalis–bulliferus	Virgin Hills Formation Parke Siltstone Gneudna Formation
optivus–triangulatus	Gogo Formation Gneudna Formation Pillara Limestone Sadler Limestone Eugenana beds Etonvale Formation
lemurata–magnificus	Unnamed beds (Drummond Basin) Dominic Shale
devonicus–naumovae	Lissoy Sandstone Anna Plains Sandstone Log Creek Formation
velata–langii	Eastwood beds

STAGE	EURAMERICAN SPORE ASSEMBLAGE ZONE	AUSTRALIAN SEDIMENTARY BASINS						
		CARNARVON	CANNING	BONAPARTE	AMADEUS	TASMANIA	ADAVALE	DRUMMOND
FAMENNIAN	*lepidophyta-nitidus*		●	●				
	pusillites-lepidophyta		●	●				
	radiata-cornuta							
	torquata-gracilis	●			●			
FRASNIAN	*ovalis-bulliferus*	●	●		●			
GIVETIAN	*optivus-triangulatus*	●	●			●	●	
	lemurata-magnificus		●					●
EIFELIAN	*devonicus-naumovae*		●				●	
	velata-langii						●	

Figure 8. *Inferred occurrence of Euramerican Middle and Upper Devonian spore assemblage zones of Richardson and McGregor (1986) in Australian sedimentary basins.*

opinion, been reported convincingly from various other regions thought to have been part of Gondwana, i.e., Antarctica, South America, Africa, and the Middle East (Fig. 9). This conservative estimate of the extent of co-occurrence of Gondwanan-Euramerican taxa derives from scrutiny of published records that are supported by photographs or descriptions of the specimens. An additional 20 Euramerican species apparently occur in one or more of these Gondwanan regions (Fig. 10), but have not yet been recognized in Australia.

Although little is known about intergrading spore groups (morphons) in Gondwanan Devonian deposits outside Australia, some information may be gleaned from literature concerning Middle and Upper Devonian morphic variation in those strata. Two or more components of some of the shared Euramerican/Australian morphons are present in the Givetian–Frasnian of the Parana Basin, Brazil: members of the *Ancyrospora simplex* Morphon (Daemon et al., 1967, Pl. 3, figs. 42 and 43) and the *A. longispinosa* Morphon (op. cit., Pl. 3, figs. 41 and possibly 44); variants of the *Verrucosisporites scurrus* Morphon (Burjack et al., 1987, Pl. 1, figs. 8, 9, and possibly 13); some elements of the *Cristatisporites* *triangulatus* Morphon (op. cit., Pl. 3, figs. 5, 6 and possibly 7 and 8); and two elements of the *Rhabdosporites langii* Morphon (op. cit., Pl. 3, figs. 1 and 2).

A limited range of forms representing some Euramerican/Australian morphons has been reported from the Middle to Upper Devonian of North Africa: the *Cristatisporites triangulatus* Morphon (Loboziak

BRAZIL	BOLIVIA	ANTARCTICA	MOROCCO	ALGERIA TUNISIA LIBYA	GHANA	TURKEY	IRAN	SAUDI ARABIA	EGYPT	
22, 31	17			27						*Acinosporites lindlarensis* var. *lindlarensis*
22, 31				23, 27						*Ancyrospora langii*
	29									*Aneurospora greggsii*
	29									*Archaeozonotriletes timanicus*
22, 31				28, 32						*Archaeozonotriletes variabilis*
22, 31				26						*Auroraspora macra*
				27						*Camarozonotriletes sextantii*
22										*Chelinospora concinna*
22	29			18, 27						*Cristatisporites triangulatus*
22										*Cymbosporites magnificus*
				3, 18, 23						*Diatomozonotriletes* sp. cf. *D. oligodontus*
22										*Dibolisporites farraginis* (as *V.* sp. cf. *V. uncatus*)
			16	4,14,20,26			13			*Endosporites micromanifestus* s.l.
2	17			3, 12, 18 19, 23, 27	9		25			*Emphanisporites annulatus*
	17									*Emphanisporites minutus*
22, 31	17	5, 6		1,3,4,12,23		15	25	7	10, 21, 30	*Emphanisporites rotatus*
22, 31	29	5		23, 27	9		25	7		*Geminospora lemurata*
	29			12	9					*Geminospora verrucosa*
				12						*Gneudnaspora divellomedium*
22										*Grandispora eximia*
				27						*Grandispora naumovae*
22				27						*Grandispora velata*
						15				*Hystricosporites porrectus*
				14, 26						*Indotriradites explanatus*
							13			*Knoxisporites literatus*
8, 24, 34	11, 29		16, 33	1,4,12,14, 18,19,20,26		15	13			*Retispora lepidophyta*
				27						*Retusotriletes rugulatus*
22, 31				18		15				*Rhabdosporites langii*
24										*Tumulispora rarituberculata*
				18						*Vallatisporites pusillites*
									30	*Verrucosisporites nitidus*
22, 31	29			18, 27						*Verrucosisporites premnus*
22, 31				18, 27, 32						*Verrucosisporites scurrus*

Figure 9. *Canadian/Australian shared (and possibly shared) taxa that occur elsewhere in Gondwana. The list includes only those for which, in our opinion, the authenticity of the identifications is supported by illustrations or descriptions.*

Numbers refer to records in the following publications: ***1.*** *Wray (1964);* ***2.*** *Daemon et al. (1967);* ***3.*** *Jardiné and Yapaudjian (1968);* ***4.*** *Lanzoni and Magloire (1969);* ***5.*** *Helby and McElroy (1969);* ***6.*** *Kemp (1972);* ***7.*** *Hemer and Nygreen (1967);* ***8.*** *Daemon (1974);* ***9.*** *Bär and Riegel (1974);* ***10.*** *Kruchinina et al. (1974);* ***11.*** *Lobo Boneta (1975);* ***12.*** *Massa and Moreau-Benoit (1976);* ***13.*** *Coquel et al. (1977);* ***14.*** *Attar et al. (1980);* ***15.*** *Akyol (1981);* ***16.*** *Marhoumi (1984);* ***17.*** *McGregor (1984);* ***18.*** *Paris et al. (1985);* ***19.*** *Massa and Moreau-Benoit (1985);* ***20.*** *Coquel and Moreau-Benoit (1986);* ***21.*** *Schrank (1987);* ***22.*** *Loboziak et al. (1988);* ***23.*** *Boumendjel et al.(1988);* ***24.*** *Quadros (1988);* ***25.*** *Ghavidel-Syooki (1988);* ***26.*** *Coquel and Latreche (1989);* ***27.*** *Loboziak and Streel (1989);* ***28.*** *Moreau-Benoit (1989);* ***29.*** *McGregor (unpublished);* ***30.*** *El-Ghazaly and Ali (1985);* ***31.*** *Burjack et al. (1987);* ***32.*** *Moreau-Benoit (1988);* ***33.*** *Rahmani-Antari (1990);* ***34.*** *Loboziak et al. (1991).*

and Streel, 1989, Pl. 4, figs. 6–10); the *Emphanisporites rotatus* Morphon (Boumendjel ct al., 1988, Pl. 1, figs. 11–14; Massa and Moreau-Benoit, 1976, Pl. 1, figs. 4 and 10, Pl. 2, fig. 14); the *Rhabdosporites langii* Morphon (Loboziak and Streel, 1989, Pl. 3, figs. 4–6); the *Verrucosisporites scurrus* Morphon (op. cit., Pl. 1, figs. 7–9 and possibly 23).

Richardson and McGregor (1986, p. 4) proposed to define the Euramerican spore zones in part by the first appearance of spore form features ("events") that transgress conventional taxonomic divisions. Some of these morphological attributes, viz., ancyrate processes, proximal radial costae, patinate exoexines, biform sculpture, and foveoreticulate pseudosacci (Fig. 11), are typically (if not uniquely) Devonian, are shared by Euramerican and Australian assemblages, and are present in assemblages from virtually all other Gondwanan regions where palynological studies have been conducted. Other morphological features are less widespread in Gondwana, based on present records: filiform processes in North Africa (*Acanthotriletes longispinosus* Coquel and Moreau-Benoit, 1986); cingulizonate structure in Libya, Ghana, and Saudi Arabia and possibly in Brazil; and monolete sutures in Antarctica, Ghana, and Egypt. Many of the regions included in Figure 11 have received only cursory palynological investigation, and some stratigraphic intervals have not been studied at all. Considering the sparseness of the data base, it would be premature to do more than suggest that any of these form features were geographically localized. For example, present records do not show cingulizonate spores to be prominent components of spore assemblages anywhere or at any time in the Gondwanan Devonian, as they were through most of the Middle Devonian in Euramerica. Some of the spore form features that characterize Middle and Upper Devonian assemblages in Euramerica appear to have been distributed essentially globally, whereas others may have been regionally restricted.

Some morphological features or combinations of features originated in the Devonian, but were not confined to, or especially characteristic of, that period. Richardson and McGregor (1986, Fig. 2) attached zonal significance to their first occurrences. Irregular large verrucae, vacuolate zonas, and thick exoexined

BRAZIL	BOLIVIA	MOROCCO	ALGERIA TUNISIA LIBYA	TURKEY	IRAN	
22						*Acinosporites acanthomammillatus*
22			27			*Acinosporites apiculatus*
22						*Acinosporites macrospinosus*
			23, 27			*Ancyrospora nettersheimensis*
22, 31						*Auroraspora hyalina*
22						*Chelinospora ligurata*
22			27			*Corystisporites multispinosus*
			27			*Cymbosporites catillus*
		16	14, 18, 19, 20, 26		13	*Cyrtospora cristifera*
			27			*Densosporites devonicus*
			27			*Diatomozonotriletes franklinii*
			14, 26			*Dictyotriletes fimbriatus*
			27			*Grandispora douglastownense*
			27			*Grandispora inculta*
22, 31			3, 27			*Grandispora protea*
	17					*Lophotriletes devonicus*
22			27			*Lophozonotriletes media*
			26			*Raistrickia corynoges*
34	29		14, 18, 19, 23, 26	15	13	*Rugospora radiata*
22			12, 27			*Verrucosisporites bulliferus*

Figure 10. *Selected Canadian taxa not found in Australia that have, in our opinion, been reliably reported from other parts of the Gondwana Devonian. Numbers refer to bibliographic records cited in caption for Figure 9.*

BRAZIL	BOLIVIA	PARAGUAY	ANTARCTICA	MOROCCO	ALGERIA TUNISIA LIBYA	GHANA	TURKEY	IRAN	SAUDI ARABIA	EGYPT	
2,8,22	11, 35			33	1,4,12,14,18, 23,27,28,32, 39		15	13,25	7, 36		Ancyrate processes
2	29, 35		6	16	18,23,27, 28	9		25			Biform sculpture
22?					27	9			36		Cingulizona
					14,20						Filiform processes
8, 24, 34	11			16, 33	1,4,12,14, 18,19,20,26		15	13,25			Foveoreticulate pseudosaccus
			6			9				10	Monolete suture
2,22	29		5	16	14,18,20, 26,27,28,31	9		13	36		Patina
2,22	17, 35	38	5, 6, 37	16	1,3,4,12,14,18, 19,20,23,26,27, 28	9	15	13,25	7, 36	10, 21, 30	Proximal radial costae

Figure 11. Records of Canadian/Australian shared spore form features in other parts of the Gondwana Devonian.

Numbers refer to bibliographic records cited in caption for Figure 9, and to the following: 35. Cousminer (1964); 36. Hemer (1965); 37. Kyle (1977); 38. Menendez and Pöthe de Baldis (1967); 39. Candilier et al. (1982).

cavate structure began in the Middle or Late Devonian in both Gondwana and Euramerica. Other features, e.g., verrucate and biform sculpture, the zona, and large ("megaspore") size, originated before the Eifelian, so their first appearances are not relevant to this study.

Implications for interregional spore correlation in Canada

Because spores are present in terrigenous strata bridging Middle and Upper Devonian stage boundaries in several Canadian sedimentary basins (McGregor, in press, a; McGregor et al., 1985), refinement of the existing northern hemisphere spore zonation would improve the capability for interregional correlation of Devonian chronostratigraphic boundaries in Canada.

As a result of their discovery in Australia, we propose that ten taxa be added to the list of characterizing species of Euramerican spore zones (Fig. 12 and Table 3). These taxa extend geographically beyond the bounds of Euramerica, they are sufficiently distinctive to be easily identified, and they have relatively well defined Euramerican stratigraphic ranges. They would thus seem to represent useful additions to a possible worldwide, and interregional Canadian, spore zonation scheme for the Devonian.

An additional sixteen distinctive forms (Table 3) may be added to the assemblage zonation later, when they have been formally described and named and/or their Canadian/Euramerican stratigraphic ranges have been better defined. Other refinements to the definition of the Euramerican spore zones, beyond the scope of this report, are necessary as a result of recent discoveries by the first author and others (e.g., Richardson and Ahmed, 1989; Loboziak et al., 1990).

Paleogeography

Some spores that are stratigraphically useful in Canada have not been found outside the borders of Euramerica, either by us during this study (Table 1), or by other workers in regions believed to have been part of the Gondwana landmass: e.g., *Contagisporites optivus* (Chibrikova) Owens, 1971; *Cornispora varicornata* Staplin and Jansonius, 1961; *Kraeuselisporites rugosus* (Owens) McGregor and Camfield, 1982; *Periplecotriletes tortus* Egorova, 1974; and *Sinuosisporis sinuosus* (V. Umnova) Arkhangelskaya, 1985. They may prove to be reliable indicators of Devonian paleogeographic patterns and may, for example, indicate the existence and provenance of exotic terranes.

Present distribution records suggest that some of the shared Australian/Euramerican species are geographically restricted within the contemporary northern hemisphere. *Archaeozonotriletes famenensis, A. timanicus,* "Azonomonoletes" sp., *Cymbosporites magnificus, Dibolisporites farraginis, D. vegrandis, Dictyotriletes australis, Tholisporites densus,* and *T. tenuis* have so far been reported reliably only from

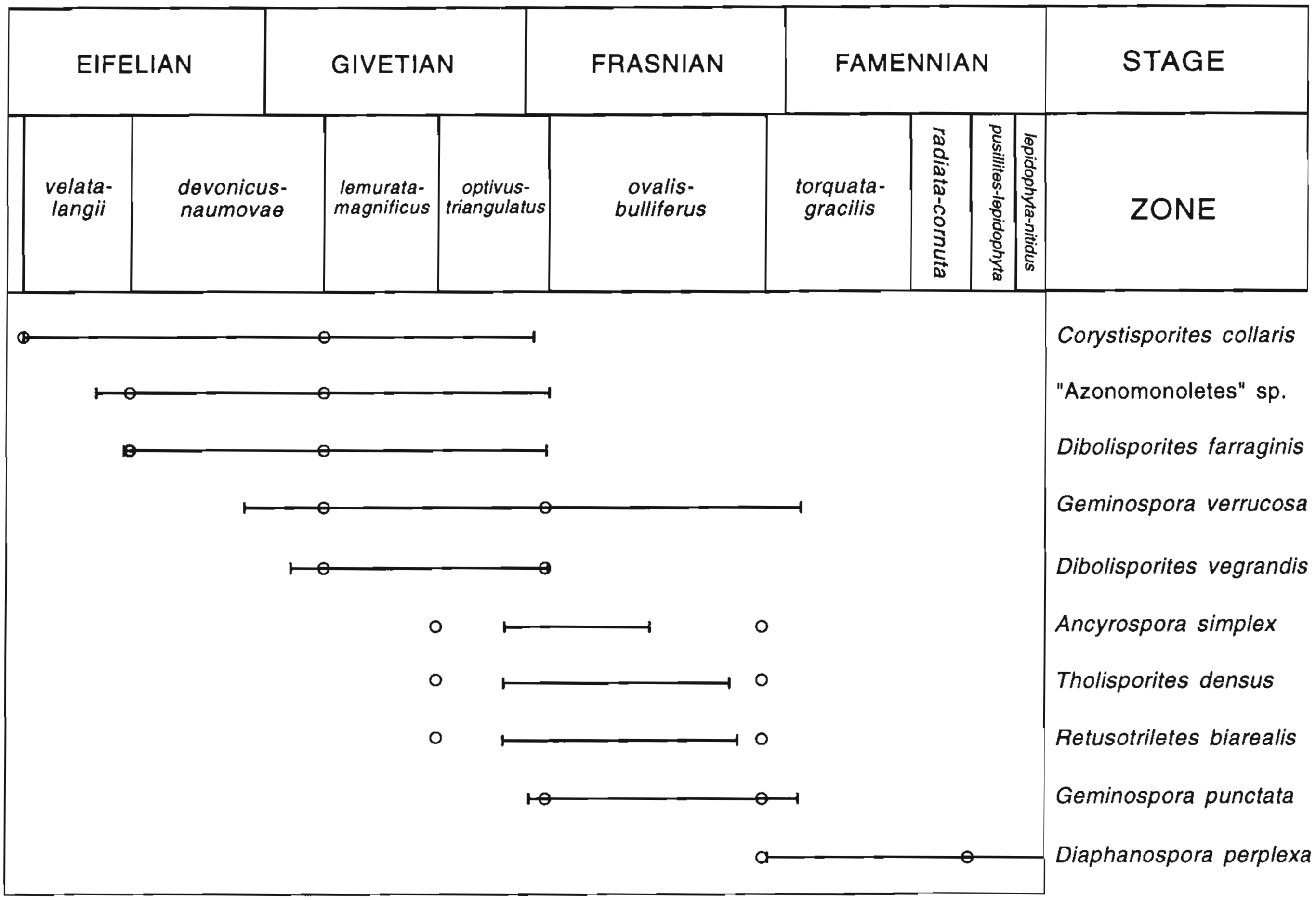

Figure 12. Euramerican stratigraphic ranges of proposed new characterizing taxa of spore assemblage zones of Richardson and McGregor (1986). Circles indicate upper and lower boundaries of zonal range chosen as "characterized" for each taxon.

northerly parts of Euramerica, i.e., from western North America through the Canadian Arctic to the Russian Platform. As mentioned earlier, *Cymbosporites magnificus* may occur in the European U.S.S.R. (as *Retusotriletes tamilii* and *R. vorobievensis*); it has not been recorded in eastern North America, and records of it in Western Europe (Higgs, 1975, Pl. 3, fig. 11; Tiwari and Schaarschmidt, 1975, Pl. 15, figs. 4 and 5; Higgs and Russell, 1981, unillustrated; Wohlfeil, 1984, Pl. 5, fig. 2; Marshall, 1988, fig. 3, no. 11) are not well substantiated, in our opinion.

The significance of these apparently provincial patterns of occurrence is not known. The Australia/Euramerica territorial limitation of these species contrasts with that of *Teichertospora torquata*, which has a southern Euramerican-Western Australian distribution (McGregor and Playford, 1990). The picture is not so simple, however, as *T. torquata* itself may be diachronous in southern Euramerica: in Western Europe it has not been recorded prior to the late Famennian, whereas in eastern North America (and apparently in Australia) it also occurs in the late Frasnian to early Famennian interval (McGregor and Playford, 1990, Fig. 1).

It therefore seems relevant to examine the paleobotanical evidence for the pattern of distribution of Devonian plants, and the methods and limits of dispersal of Recent Bryophyta and Pteridophyta in order to ascertain the limits to dispersal of Devonian plants, and what these limits may mean regarding the phytogeography of that time. It is also important to take into account what is known about the physiography, climate, and distribution of Devonian land masses. Comparison of spore assemblages produced by land plants from different paleocontinents

TABLE 3

Additions and possible future additions to lists of characterizing species of Euramerican spore assemblage zones (Richardson and McGregor, 1986)

Zone	New characterizing species	Possible new characterizing species*
nitidus–verrucosus		*Retusotriletes digressus*
pusillites–lepidophyta		*Retusotriletes digressus*
radiata–cornuta	*Diaphanospora perplexa*	
torquata–gracilis	*Diaphanospora perplexa*	
ovalis–bulliferus	*Ancyrospora simplex* *Geminospora punctata* *Retusotriletes biarealis* *Tholisporites densus*	
optivus–triangulatus	*Ancyrospora simplex* *Dibolisporites vegrandis* *Geminospora verrucosa* *Retusotriletes biarealis* *Tholisporites densus*	*Cristatisporites* sp. 1 *Cristatisporites* sp. 2 *Cymbosporites* sp. 1 *Cymbosporites* sp. 2 *Dibolisporites turriculatus* *Dibolisporites* sp. cf. *D. uncatus* *Geminospora venusta*? *Heterotriletes* sp. 1 *Heterotriletes* sp. 2
lemurata–magnificus	*Dibolisporites farraginis* *Dibolisporites vegrandis* *Geminospora verrucosa*	cf. *Grandispora inculta* *Heterotriletes* sp. 2 *Trileites langii*
devonicus–naumovae	"Azonomonoletes" sp. *Corystisporites collaris* *Dibolisporites farraginis*	cf. *Densosporites*? *cassiformis* *Diatomozonotriletes* sp. cf. *D. oligodontus* *Dictyotriletes australis* cf. *Grandispora inculta* *Hystricosporites porrectus* *Trileites langii*
velata–langii	*Corystisporites collaris*	*Dictyotriletes australis*

*pending definition of the taxon and/or its stratigraphic range in Euramerica.

may elicit evidence bearing on the timing of continental collisions or separations. To fully understand the distribution of Devonian vegetation, one must determine which, if any, plants of that age were obtained from exotic terranes. The paleogeographic distribution of vertebrates provides another important continentally based perspective, complementary to the paleobotanical/palynological evidence, for interpreting Middle and Upper Devonian paleogeography (Johnson, 1980, p. 45-47; Long, 1986, p. 16; Young, 1987). We are presently engaged in a study of these questions, and the results will be published separately.

CONCLUSIONS

This detailed comparative survey of Devonian spore floras from Canada and Australia, undertaken mainly from a stratigraphic perspective, allows the following conclusions to be drawn.

1. With one exception, all of the Middle to Late Devonian (Eifelian to Famennian) spore assemblage zones established in Canada are discernible, with various degrees of confidence, in approximately age-equivalent sequences examined in Australia. This affirms the long-distance stratigraphic-correlative potential of the Euramerican spore zonation scheme established by Richardson and McGregor (1986), and signals opportunities for further Devonian palynostratigraphic refinements in both countries.

2. The Canadian-Australian comparisons show unmistakable similarities in terms of stratigraphic distribution of certain shared form taxa (genera and species), morphons, and gross trends in spore morphology.

3. Forty-four Canadian/Euramerican spore genera, and 80 species, are now known to occur in Australia, though we emphasize that the palynological coverage in the latter is very uneven, and is much more detailed for the upper Givetian-lower Frasnian and the upper Famennian than for other parts of the Australian Devonian.

4. In ascending stratigraphic order, the following Canadian spore assemblage zones can be recognized, with some qualifications, in certain Australian sedimentary basins: lower Eifelian *Grandispora velata-Rhabdosporites langii* Zone (Adavale Basin); lower Eifelian-lower Givetian *Densosporites devonicus-Grandispora naumovae* Zone (Canning and Adavale basins); lower to upper Givetian *Geminospora lemurata-Cymbosporites magnificus* Zone (Canning and Drummond basins); upper Givetian-lower Frasnian *Contagisporites optivus* var. *optivus-Cristatisporites triangulatus* Zone (Canning, Carnarvon, Adavale, and Tasmania basins); Frasnian *Archaeoperisaccus ovalis-Verrucosisporites bulliferus* Zone (Carnarvon, Canning, and Amadeus basins); uppermost Frasnian-lower Famennian *Teichertospora torquata-Grandispora gracilis* Zone (Carnarvon and Amadeus basins); and upper Famennian *Vallatisporites pusillites-Retispora lepidophyta* Zone and *Retispora lepidophyta-Verrucosisporites nitidus* Subzone (Canning and Bonaparte basins). The Devonian-Carboniferous boundary is well defined palynologically in both Canada and northwestern Australia by the disappearance of the distinctive trilete, pseudosaccate, uppermost Famennian spore *Retispora lepidophyta*.

5. Spore assemblages indicative of the Canadian/Euramerican Lower Devonian (Gedinnian to Emsian) palynozones have not been found in Australia (where no palynological studies of the Lower Devonian have been conducted).

6. Ten taxa shared by Canada and Australia may now be added to the characterizing taxon inventories of the Euramerican spore zones. At least 16 further species are likely to be incorporated as stratigraphic indices once their morphology, taxonomy, and stratigraphic ranges have been documented fully. Such refinements will further enhance the importance and applicability of the palynozones in Canadian interbasinal correlations, and their recognition elsewhere.

7. Many described and undescribed taxa appear to be restricted to Australia. Conversely, several hundreds of known Canadian/Euramerican taxa have yet to be observed in Australian palynofloras. In other words, qualitative palynofloral dissimilarities certainly exist between Australian and Canadian Middle and Upper Devonian sequences, and doubtless reflect phytogeographic differences related to climate, physiography, and continental plate configurations.

8. Notwithstanding conclusion 7 (above), the distinct Australian-Canadian congruences assuredly lend support — more so than hitherto suggested — to previous megafloristically based indications of significant floral cosmopolitanism in Devonian time, and specifically to Loboziak and Streel's (1989, p. 195) view that Gondwana and the Old Red Sandstone Continent were in sufficiently close proximity to allow considerable floristic interchange.

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APPENDIX

TABLE 1

Geological information and literature concerning palyniferous strata of the Franklinian clastic wedge

	Formation/ member	Predominant lithology	Depositional environment	Maximum thickness	Age	SELECTED REFERENCES Palynological	SELECTED REFERENCES Other	Location (Fig. 2)
Parry Islands	Consett Head	White sandstone	Braided stream	150	Mid Famennian	McGregor (in press, a)	Embry & Klovan (1976)	16
	Cape Fortune	Shale, minor siltstone and sandstone	Deltaic marine, braided stream	250	Early Famennian	Chi & Hills (1976b); Goodbody et al. (1988); McGregor (in press, a)	Embry & Klovan (1976)	16, 17
	Burnett Point	Shale, siltstone, sandstone, coal	Braided and meandering stream	700	Late Frasnian and early Famennian	Kerr et al. (1965); McGregor (1967, in press, a); Owens (1971); McGregor & Uyeno (1972); Chi & Hills (1976b); Whiteley (1980)	Embry & Klovan (1976)	12, 16, 18, 20
Nordstrand Point		Shale, siltstone, sandstone	Meandering stream	674	Late Frasnian	Goodbody et al. (1988)	Embry & Klovan (1976)	20, 21
Hell Gate		White sandstone, minor shale, siltstone	Braided stream	637	Mid Frasnian	Chaloner (1959); McGregor (1969)	Embry & Klovan (1976)	20, 21
Fram		Shale, siltstone, sandstone	Meandering stream	1480	Early Frasnian	Goodbody et al. (1988); McGregor et al. (1985)	Embry & Klovan (1976)	20, 21
Beverley Inlet		Shale, siltstone, sandstone	Meandering stream	777	Early and late Frasnian	McGregor (1960, 1967, in press, a); Owens (1971); McGregor & Uyeno (1972); Chi & Hills (1976b); Whiteley (1980)	Embry & Klovan (1976); Goodbody (1989a)	13, 14, 17, 18

Hecla Bay	White sandstone, minor shale, siltstone	Deltaic marine, braided stream	1143	Early Givetian to early Frasnian	McGregor (1967, in press, a); Owens (1971); McGregor & Uyeno (1972); Chi & Hills (1976b); Whiteley (1980); McGregor & Camfield (1982); McGregor et al. (1985); Goodbody et al. (1988)	Tozer & Thorsteinsson (1964); Kerr (1974); Embry & Klovan (1976); Goodbody (1989a)	13, 14, 17, 18, 21
Weatherall	Shale, siltstone, sandstone	Deltaic marine	1445	Late Eifelian to late Frasnian	McGregor (1960, in press, a); Hills et al. (1971); Owens (1971); McGregor & Uyeno (1972); Chi & Hills (1976b); McGregor & Camfield (1982)	Tozer & Thorsteinsson (1964); Embry & Klovan (1976); Goodbody (1989a)	11, 12, 14, 16
Strathcona Fiord	Shale, siltstone, sandstone, minor limestone	Deltaic marine, meandering stream	1100	Early Eifelian to early Givetian	Goodbody et al. (1988); Arkhangelskaya et al. (1990)	Embry & Klovan (1976); Trettin (1978); Rice (1988); Uyeno (1989)	20, 21
Bird Fiord	Shale, siltstone, sandstone, limestone near base	Deltaic marine	900	Early and late Eifelian	McGregor (1967); McGregor & Uyeno (1972); Goodbody et al. (1988)	Kerr (1974); Embry & Klovan (1976); Uyeno & Klapper (1980); Brice (1982); Pedder & Goodbody (1983); Goodbody (1989b); Uyeno (1989)	18, 19, 21
Cape De Bray	Silty shale	Marine slope	1025	Early Eifelian to early Givetian	Chi & Hills (1976b); McGregor & Camfield (1982); McGregor (in press, a)	Tozer & Thorsteinsson (1964); Embry & Klovan (1976); Goodbody (1989a)	11, 12, 15, 17
Blue Fiord	Limestone and shale	Shallow marine, lagoonal, back reef	1375	Late Emsian and early Eifelian	McGregor & Uyeno (1972)	Kerr (1974); Trettin (1978); Mayr (1980); Uyeno & Klapper (1980); Brice (1982); Uyeno (1989)	19, 21

Eids	Calcareous and silty shale, calcareous siltstone, limestone	Outer shelf, marine slope	1150	Early and late Emsian	McGregor & Uyeno (1972)	Kerr (1974); Trettin (1978); Mayr (1980); Uyeno (1989)	19, 21
Stuart Bay	Calcareous mudstone, shale, sandstone, conglomerate, limestone	Marine shelf	2100	Early and late Emsian	McGregor & Uyeno (1972)	Hueber (1971); Kerr (1974); Mayr (1980)	19

TABLE 2

Register of illustrated specimens

Plate/figure	Locality or sample number	Slide number	England finder	Type number
1/1	GSC A-008057	A-008057/B	SM	GSC 41757
1/2	GSWA 72314	72314/10	H52/4	GSWA F485272
1/3	GSC O-102849	O-102849/2	U49/4	GSC 99189
1/4	UQ A966	H063/58	SM	GSWA F485273
1/5	GSC O-102853	O-102853/2	J54	GSC 99190
1/6	UQ A966	H063/37	SM	GSWA F485274
1/7	GSC C-084874	C-084874/1	P57/3	GSC 99191
1/8	UQ A1186	H371/26	SM	UQ F.6761
1/9	GSC A-008057	A-008057/A	SM	GSC 41758
1/10	UWA 6832	6832/20	N41/3	UWA 113288
1/11	GSC C-137914	C-137914/1	N44/1	GSC 99192
1/12	UQ A966	H063/6	SM	GSWA F485275
2/1	GSC A-008278	A-008278/B	SM	GSC 99193
2/2	UQ A2773	C003/1	D48/3	GSWA F485276
2/3	GSC C-091907	C-091907/1	M59/4	GSC 99194
2/4	UQ A3329	B1629/2	E43/1	UWA 113289
2/5	GSC O-097074A	O-097074/A10	M42/1	GSC 99195
2/6	UQ 7570	H382/8	SM	UQ Y.6762
2/7	GSC C-137840	C-137840/1	M60/3	GSC 99196
2/8	UQ A3317	B1598/3	W27	UQ Y.6763
3/1	GSC C-137840	C-137840/1	Q69/3	GSC 99197
3/2	UWA (C. Cuvier)	CC-20	B39/1	UWA 113290
3/3	GSC A-008278	A-008278/C	SM	GSC 99198
3/4	UQ A2773	C003/A	V24	GSWA F485277
3/5	GSC O-097074A	O-097074/A10	L52/2	GSC 99199
3/6	UQ A1263	D419A/1	L33/1	GSWA F485278
3/7	GSC A-008272	A-008272/40	L55/2	GSC 99200
3/8	UQ A2773	C003/16	SM	GSWA F485279
3/9	GSC A-008311	A-008311/30	U67/2	GSC 99201
3/10	UQ A3319	B1587/5	R31/4	UQ Y.6764
3/11	GSC C-027096	C-027096/11	J14/4	GSC 99202
3/12	UQ A1076	H258/3	R39/3	UQ Y.6765
4/1	GSC C-140667	C-140667/2	O63/1	GSC 99203
4/2	UQ A1263	D419A/1	P31	GSWA F485280
4/3a, b	GSC A-008333	A-008333/D	SM	GSC 66216
4/4a, b	UWA 6833	6833/20	R51/1	UWA 113291
4/5	GSC O-101178	O-101178/1	V63/1	GSC 99205
4/6	UQ A2765	B1512/1	F53/2	GSWA F485281
4/7	GSC C-082856K	P-17443/02	D42/0	GSC 73309
4/8	UQ A933	K451/1	S26	UQ Y.6766
4/9	GSC C-129371	C-129371/1	F39/4	GSC 99206
4/10	UQ A3318	B1586/1	O29	UQ Y.6767
4/11	GSC A-005571	A-005571/8	O58/2	GSC 15127
4/12	UQ A3319	B1587/5	T23	UQ Y.6768
4/13	GSC A-008101	A-8101/A	SM	GSC 41750
4/14	UQ A3321	B1589/1	L38/3	UQ Y.6769

Plate/figure	Locality or sample number	Slide number	England finder	Type number
4/15	GSC A-008267	A-008267/40	R52/1	GSC 99207
4/16	UQ A3279	B1539/1	U34/2	GSWA F485282
5/1a, b	GSC C-137814	C-137814/1	R38/4	GSC 99208
5/2a, b	Denison 180, 278.12 m	B855/1	M36/3	UQ Y.6770
5/3	GSC A-008256	A-008256/6	P62/2	GSC 99209
5/4	GSWA F8481	480-490′/1	Q41/2	GSWA F485283
5/5	GSC A-008266	A-008266/40	U68/1	GSC 99210
5/6	UWA 6809	6809/10	U40	UWA 113292
5/7	GSC A-008267	A-008267/40	J69/1	GSC 99211
5/8	UQ A1263	D419A/1	O22/1	GSWA F485284
5/9	GSC O-102857	O-102857/3	R68/3	GSC 99212
5/10	UQ A2773	C003/A	J50/3	GSWA F485285
5/11	GSC A-008058	A-008058/8	M41/2	GSC 99213
5/12	UQ A1272	D429/4	F22	GSWA F485286
5/13	GSC O-101178	O-101178/1	V38/3	GSC 99214
5/14	UQ A3258	B1523/1	U49/2	UQ Y.6771
6/1	GSC C-129494	C-129494/4	J63/1	GSC 99215
6/2	UQ A3258	B1523/8	SM	UQ Y.6772
6/3	GSC D-000136N	P-7418/01	S33/3	GSC 49842
6/4	UWA 6814	6814/10	U36	UWA 113293
6/5	GSC C-129492	C-129492/10	H50/1	GSC 99216
6/6	UWA A3329	B1629/2	L20	UWA 113294
6/7	GSC O-101178	O-101178/1	W54/1	GSC 99217
6/8	UQ A2773	C003/1	Specimen not relocated	
6/9	GSC A-008311	A-008311/30	E42/4	GSC 99218
6/10	UQ A3317	B1598/1	S35/1	UQ Y.6773
6/11	GSC C-129457	C-129457/2	P61/2	GSC 99219
6/12	UQ A966	H063/40	SM	GSWA F485287
6/13	GSC A-008311	A-008311/30	V62/2	GSC 99220
6/14	UQ A3319	B1587/1	U35/4	UQ Y.6774
6/15	GSC A-005384	A-005384/14	Y44/3	GSC 99221
6/16	GSWA 23405	23405/2	W45/1	GSWA F485288
6/17	GSC A-008267	A-008267/40	Q63/3	GSC 99222
6/18	UQ A1286	D441/2	R38/4	GSWA F485289
7/1	GSC O-059040	O-059040/3	U67/4	GSC 13601
7/2	UQ A992	H100/1	U16/2	UQ Y.2264
7/3	GSC C-129465	C-129465/8	Y52/1	GSC 99223
7/4	GSWA (Tappers I)	/10	N26	GSWA F485290
7/5	GSC A-008058	A-008058/8	U62/1	GSC 99224
7/6	UQ A3320	B1588/1	R30/4	UQ Y.6775
7/7	GSC A-008267	A-008267/41	N38/3	GSC 99225
7/8	UQ A1718	D447/3	J25/3	GSWA F485291
7/9	GSC A-008267	A-008267/41	J62	GSC 99226
7/10	UQ A1219	P5544/3	L32/4	GSWA F485292
7/11	GSC A-008791	A-008791/3	M49/1	GSC 99227
7/12	UWA (Balme, 1988a, Pl. 6, fig. 4)			UWA 101656
7/13	GSC A-008342	A-008342/30	S50/3	GSC 99228
7/14	GSWA 72314	72314/10	Q40/4	GSWA F485293
7/15	GSC A-008755	A-008755/8	M48/2	GSC 99229
7/16	UQ A3319	B1587/1	H31	UQ Y.6776

Plate/figure	Locality or sample number	Slide number	England finder	Type number
7/17	GSC A-008759	A-008759/8	Q66/1	GSC 99230
7/18	UQ A3317	B1598/1	W37/1	UQ Y.6777
7/19	GSC D-002527	P-25058/11	L36	GSC 86099
7/20	UQ A998	P4017/6	Q40/1	UQ Y.2269
7/21	GSC A-007126	A-007126/30	Y69/3	GSC 99231
7/22	UQ A1718	D447/11	SM	GSWA F485294
8/1	GSC O-101178	O-101178/1	Y49/2	GSC 99232
8/2	UQ A1718	D447/3	D41/1	GSWA F485295
8/3	GSC A-008266	A-008266/40	F50/3	GSC 99233
8/4	UQ A1182	H388/62	SM	UWA 94209
8/5	GSC A-008342	A-008342/3	F46/1	GSC 66303
8/6	UQ A1718	D447/3	Q35/2	GSWA F485296
8/7	GSC A-008266	A-008266/40	V60/1	GSC 99234
8/8	UQ A1718	D447/3	G24/1	GSWA F485297
8/9	GSC A-008266	A-008266/40	K58	GSC 99235
8/10	UQ A1182	5765/1	E30/4	UWA 94211
8/11	GSC A-008267	A-008267/40	R45/3	GSC 99236
8/12	UQ A1186	H371/6	B20/3	UWA 113295
8/13	GSC A-008266	A-008266/40	R66/4	GSC 99237
8/14	UQ A1186	H371/6	D21	UWA 113296
9/1	GSC A-007132	A-007132/40	Q41/1	GSC 99238
9/2	UWA 6809	6809/10	Q38	UWA 113297
9/3	GSC A-008266	A-008266/40	H56/2	GSC 99239
9/4	UWA 6809	6809/10	O53	UWA 113298
9/5	GSC O-102849	O-102849/2	J50/2	GSC 99240
9/6	UQ 7570	H382/24	K30	UQ Y.6778
9/7	GSC A-008288	A-008288/17	E59/1	GSC 99241
9/8	UQ A1263	D419A/1	L51	GSWA F485298
9/9	GSC C-084874	C-084874/11	V41/1	GSC 96777
9/10	UQ A1718	D447/37	SM	GSWA F485299
9/11	GSC A-008339	A-008339/7	F48/4	GSC 99242
9/12	UQ A1718	D447/3	N33	GSWA F485300
10/1	GSC D-001726	P14715/03	J41/0	GSC 73313
10/2	UQ A989	H099/3	U59	UQ Y.2261
10/3	GSC C-140667	C-140667/2	T59/1	GSC 99243
10/4	UQ A992	H107/11	P35	UQ Y.2242
10/5	GSC C-129465	C-129465/8	X69/4	GSC 99244
10/6	UQ A3257	B1522/1	M39/3	UQ Y.6779
10/7	GSC A-008259	A-008259/30	O55/2	GSC 99245
10/8	UQ A3258	B1523/1	L22	UQ Y.6780
10/9	GSC O-102876	O-102876/2	X40/3	GSC 99246
10/10	UQ A3320	B1588/1	T43/1	UQ Y.6781
10/11	GSC C-082856F	P-17439/02	M40/3	GSC 99247
10/12	UQ A1073	P4204/1	M45	UQ Y.2216
10/13	GSC C-084874	C-084874/24	O49/1	GSC 96781
10/14	UQ A3317	B1598/3	T37/2	UQ Y.6782
11/1	GSC D-001726	P-14715/03	J44/1	GSC 99248
11/2	UQ A926	K444/2	U44	UQ Y.2146
11/3	GSC A-008266	A-008266/40	H69/3	GSC 99249
11/4	UQ A3279	B1539/1	O48/2	GSWA F485301

Plate/figure	Locality or sample number	Slide number	England finder	Type number
11/5	GSC O-102850	O-102850/3	N59/4	GSC 99250
11/6	UQ A1718	D447/14	SM	GSWA F485302
11/7	GSC D-001239	P-16977/02	L27/4	GSC 99251
11/8	UQ A1075	P2454/3	Y34	UQ Y.2302
11/9	GSC C-094912	C-094912/1	L29/1	GSC 99252
11/10	UQ A1718	D447/50	SM	GSWA F485303
11/11	GSC O-102875	O-102875/3	G62/1	GSC 99253
11/12	UQ A966	H063/B	V51/4	GSWA F485304
12/1	GSC D-002527	P-25058/01	M42/2	GSC 95679
12/2	UWA (C. Cuvier)	CC-20	F49/4	UWA 108469
12/3	GSC D-002527	P-25058/01	F34/3	GSC 99255
12/4	UWA (C. Cuvier)	CC-20	D47/2	UWA 108468
12/5	GSC A-008241	A-008241/3	H57/1	GSC 99256
12/6	UQ A1286	D441/2	O40/2	GSWA F485305
12/7	GSC O-101217	O-101217/50	N58/4	GSC 99257
12/8	UQ A998	P4107/4	N42/2	UQ Y.2253
12/9	GSC A-008241	A-008241/3	J48/1	GSC 99258
12/10	UQ A3319	B1587/1	R39	UQ Y.6783
12/11	GSC C-082856F	P-17439/02	Y37	GSC 99259
12/12	UQ A998	P4017/17	S36	UQ Y.2225
12/13	GSC C-137826	C-137826/1	K50/4	GSC 99260
12/14	UQ A3279	B1539/1	Q52/4	GSWA 485306
13/1	GSC A-008058	A-008058/8	O51/3	GSC 99261
13/2a, b	UQ A1718	D447/54	SM	GSWA F485307
13/3	GSC A-008313	A-008313/2	Z52/2	GSC 66390
13/4	UQ A3319	B1587/5	P40	UQ Y.6784
13/5	GSC A-008266	A-008266/40	G38/1	GSC 99262
13/6	UQ A3257	B1522/1	O57/2	UQ Y.6785
13/7	GSC D-002450	P-21716/02	G30/3	GSC 99263
13/8	GSC O-097057	O-097057	J40/1	GSC 73314
13/9	GSC A-005116	A-005116/40	SM	GSC 13044
13/10	UQ A966	H063/54	SM	GSWA F485308
14/1	GSC A-008233	A-008233/1	K67/4	GSC 99264
14/2	GSC C-084874	C-084874/11	P40/2	GSC 99265
14/3	GSC C-091998	C-091998/7	Z51/1	GSC 99266
14/4	GSC A-008311	A-008311/30	Z43/1	GSC 99267
14/5	GSC A-008320	A-008320/M	SM	GSC 66215
14/6	GSC A-008272	A-008272/40	L42/1	GSC 99268
14/7	GSC A-008272	A-008272/40	N44/2	GSC 99269
14/8	GSC A-008272	A-008272/40	U62/3	GSC 99270
14/9	GSC A-008272	A-008272/40	W68/3	GSC 99271
14/10	GSC D-002527	P25058/11	P34/4	GSC 86117
14/11	GSC A-007254	A-007254/2	F49/3	GSC 99272
14/12	GSC A-008293	A-008293/1a	W50/4	GSC 99273
14/13	GSC O-102860	O-102860/3	D53/3	GSC 99274
14/14	GSC A-008233	A-008233/1	N36/4	GSC 29390
14/15	GSC A-008320	A-008320/05	SM	GSC 99275
15/1	GSC A-008320	A-008320/1	J46/4	GSC 99276
15/2	GSC O-079320	O-079320/1	O43/2	GSC 73303
15/3	GSC D-002527	P25058/11	Q36/4	GSC 86104

Plate/figure	Locality or sample number	Slide number	England finder	Type number
15/4	GSC D-002527	P25058/11	W44/1	GSC 86101
15/5	GSC A-007132	A-007132/40	Q51/4	GSC 99277
15/6	GSC C-084874	C-084874/24	R70/3	GSC 96771
15/7	GSC A-007094	A-007094/1	E32/3	GSC 15065
15/8a, b	GSC A-008266	A-008266/40	Q54/2	GSC 99278
15/9	GSC D-002136	P17610/01	H29/4	GSC 99279
15/10	GSC A-008057	A-008057/1	T34/2	GSC 41770
15/11	GSC A-008323	A-008323/5	L48/0	GSC 66356
15/12	GSC A-005310	A-005310/A	Q43/1	GSC 32034
15/13	GSC A-008339	A-008339/4	S34/1	GSC 66295
15/14	GSC A-007048	A-007048/4	L56/4	GSC 25496
16/1	GSC D-002136	P17610/02	Q46/1	GSC 73305
16/2	GSC C-120465	C-120465/2	G11/3	GSC 99280
16/3	GSC C-084874	C-084874/2	S65/2	GSC 99281
16/4	GSC D-002527	P25058/11	V46/1	GSC 86109
16/5	GSC A-008244	A-008244/7	E43/2	GSC 29387
16/6	GSC O-103058	O-103058/1	Q48/2	GSC 99282
16/7	GSC C-084874	C-084874/11	SM	GSC 99283
16/8	GSC A-007059	A-007059/1	T37/1	GSC 25445
16/9	GSC A-007059	A-007059/2	E24/3	GSC 25454
16/10	GSC A-008342	A-008342/4	V35/1	GSC 66372
16/11	GSC A-008335	A-008335/1	Q51/1	GSC 66362
16/12	GSC O-101178	O-101178/1	Y69/1	GSC 99284
16/13	GSC C-046837D	C-046837D/1	N36/3	GSC 99285
16/14	GSC C-028109	C-028109/35	J9/4	GSC 49845
17/1	UQ A2773	C003/A	P22	GSWA F485309
17/2	UQ A2773	C003/A	O21/2	GSWA F485310
17/3	UWA 6814	6814/10	E37/2	UWA 113299
17/4	UQ A2773	C003/8	SM	GSWA F485311
17/5	UQ A3319	B1587/1	V21	UQ Y.6786
17/6	UQ A992	H107/7	M34/3	UQ Y.2204
17/7	UQ A992	H100/1	N50/4	UQ Y.2206
17/8	UQ A1286	D441/2	N27/1	GSWA F485312
17/9	UWA 6813	6813/10	P47	UWA 113300
17/10	UQ A1187	H372/6	SM	UWA 113301
17/11	UWA 6809	6809/10	X41	UWA 113302
18/1	UQ A3321	B1589/1	M37	UQ Y.6787
18/2	UQ A3319	B1587/1	L44/2	UQ Y.6788
18/3	UQ A3319	B1587/1	V32	UQ Y.6789
18/4	UQ A3318	B1586/1	N28	UQ Y.6790
18/5	UQ A3319	B1587/1	J30/2	UQ Y.6791
18/6	UQ A1286	D441/2	W27	GSWA F485313
18/7	UQ A1718	D447/3	Q26	GSWA F485314
18/8	UQ A3279	B1539/1	T31/4	GSWA F485315
18/9	UQ A1186	H371/6	G31/1	UWA 113303
18/10	UQ A1186	H371/6	F25/2	UWA 113304
18/11	UQ A966	H063/25	SM	GSWA F485316
18/12	UQ A966	H063/7	SM	GSWA F485317
18/13	UQ A966	H063/41	SM	GSWA F485318
18/14	UQ A966	H063/4	SM	GSWA F485319
18/15	UQ A966	H063/29	SM	GSWA F485320

Plate/figure	Locality or sample number	Slide number	England finder	Type number
19/1	UQ A1075	P2454/8	SM	UQ Y.6792
19/2	UQ A992	H107/2	P34/4	UQ Y.2279
19/3	UQ A1075	P2454/3	W47	UQ Y.2249
19/4	UQ A1272	D429/4	G48/4	GSWA F485321
19/5	UQ A933	K451/2	N24/1	UQ Y.2286
19/6	UQ A1286	D441/2	T44/1	GSWA F485322
19/7	UQ A3258	B1523/8	SM	UQ Y.6793
19/8	UQ A3329	B1629/3	A39/4	UWA 113305
19/9	UQ A926	K444/48	O44	UQ Y.2159
19/10	UQ A3317	B1598/1	M34/4	UQ Y.6794
19/11	UQ A992	H100/3	S54/4	UQ Y.2256
19/12	UQ A992	H100/2	J20/4	UQ Y.2328
19/13	UQ A3319	B1587/1	O48/3	UQ Y.6795
19/14	UQ A3317	B1598/1	D50/2	UQ Y.6796
20/1	UQ A3317	B1598/1	C28/4	UQ Y.6797
20/2	UQ A1187	H372/3	E50/2	UWA 113306
20/3	UQ A1186	H371/36	SM	UWA 113307
20/4	UQ A1286	D441/2	Q36	GSWA F485323
20/5	UQ A1186	H371/6	R22	UWA 113308
20/6	UQ A3320	B1588/1	V52	UQ Y.6798
20/7	UQ A3329	B1629/3	T41/1	UWA 113309
20/8	UQ A3257	B1522/1	W41/4	UQ Y.6799
20/9	UQ A3317	B1598/1	W41/4	UQ Y.6800
20/10	UQ A1186	H371/34	SM	UWA 113310

GSC A–, GSC plant localities curated in Ottawa; GSC C-, GSC localities curated in Calgary; GSC D-, GSC localities curated at the Atlantic Geoscience Centre, Dartmouth; GSC O-, GSC localities curated in Ottawa.

SM, single specimen mount; GSC, Geological Survey of Canada; GSWA, Geological Survey of Western Australia, Perth; UQ, Department of Earth Sciences, The University of Queensland, Brisbane; UWA, Department of Geology, The University of Western Australia, Perth.

TABLE 3

Specimen localities

Sample/locality number	Locality	Rock unit	Spore(s) illustrated (yes/no)
GSC A-005116	West coast of Melville Island, 1.6 km north of Stevens Head; from stream talus	Beverley Inlet Fm.	yes
GSC A-005310	Eastern Quebec, north side of Southwest Arm of Gaspé Bay, halfway between Gaspé bridge and Cape O'Hara	Battery Point Fm.	yes
GSC A-005384	Eastern Quebec, south shore of Gaspé Bay, about 230 m north of mouth of Rivière de l'Anse à Brillant	Battery Point Fm.	yes
GSC A-005571	Eastern Quebec, Cap Gaspé, shore cliff below lighthouse, about 6 m stratigraphically below prominent bentonite band	Shiphead Fm.	yes
GSC A-007048	northeastern Yukon Territory, east flank of Richardson Mountains, Trail River between 66°24′30″N, 135°31′W and 66°27′30″N, 135°22′W; 328.3 m above base of formation	Tuttle Fm.	yes
GSC A007059	Southwestern Ontario, Lambton County, Imperial Courtright No. 6 well, lot 26, concession 25	Bedford Fm.	yes
GSC A-007094	Eastern Quebec, south shore of Gaspé Bay, about 1.4 km south of mouth of Rivière de l'Anse à Brillant	Battery Point Fm.	yes
GSC A-007126	Eastern Quebec, south shore of Gaspé Bay, 91 m southeast of most prominent point between Cap Rouge and Pointe Jaune	Battery Point Fm.	yes
GSC A-007132	Eastern Quebec, south shore of Gaspé Bay, 59.5 m southeast of conglomerate of Pointe Jaune	Malbaie Fm.	yes
GSC A-007254	northeastern Bathurst Island, 6.4 km north of largest river entering Reindeer Bay; 154 m above base of formation	Parry Islands Fm. Burnett Point Mbr.	yes
GSC A-007850	northern Ontario, Moose River Basin, Argor ETA No. 2 well, Kiasko River, 50°41′30″N, 80°48′00″W; 41.7 m	Sextant Fm.	no
GSC A-008057	northern Ontario, Moose River Basin, Ontario Department of Mines, Jaab Lake No. 1 well, 51°11′54″N, 82°56′00″W; 48.0–48.6 m	Williams Island Fm.	yes

Sample/locality number	Locality	Rock unit	Spore(s) illustrated (yes/no)
GSC A-008058	As above, but 51.7–52.3 m	Williams Island Fm.	yes
GSC A-008099	As above, but 188.1–188.7 m	Stooping River Fm.	no
GSC A-008101	As above, but 194.8–195.4 m	Stooping River Fm.	yes
GSC A-008233	Southeastern Melville Island, 75°10′45″N, 107°30′00″W, south flowing stream about 14.5 km northeast of head of Beverley Inlet; 402.3 m above base of formation	Weatherall Fm.	yes
GSC A-008241	As above, but 582.6 m above base of formation	Weatherall Fm.	yes
GSC A-008244	Southeastern Melville Island, 75°10′30″N, 107°31′00″W, south flowing stream about 14 km northeast of head of Beverley Inlet; 628 m above base of formation	Weatherall Fm.	yes
GSC A-008255	Southeastern Melville Island, 75°10′15″N, 107°33′00″W, south flowing stream about 13 km northeast of head of Beverley Inlet; 715 m above base of formation	Weatherall Fm.	no
GSC A-008256	As above, but 741 m above base of formation	Weatherall Fm.	yes
GSC A-008257	As above, but 769 m above base of formation	Weatherall Fm.	no
GSC A-008259	Southeastern Melville Island, 75°10′00″N, 107°33′00″W, south flowing stream about 12.5 km northeast of head of Beverley Inlet; 833 m above base of formation	Weatherall Fm.	yes
GSC A-008262	As above, but 42 m above base of formation	Hecla Bay Fm.	no
GSC A-008266	Southeastern Melville Island, 75°10′00″N, 107°35′00″W, south flowing stream about 12 km northeast of head of Beverley Inlet; 872 m above base of formation	Hecla Bay Fm.	yes
GSC A-008267	As above, but 1052 m above base of formation	Hecla Bay Fm.	yes
GSC A-008272	Southeastern Melville Island, 75°09′45″N, 107°37′00″W, south flowing stream about 11 km northeast of head of Beverley Inlet; 465 m above base of formation	Beverley Inlet Fm.	yes

Sample/locality number	Locality	Rock unit	Spore(s) illustrated (yes/no)
GSC A-008278	Southeastern Melville Island, 75°09′30″N, 107°38′00″W, south flowing stream about 10 km northeast of head of Beverley Inlet; 633 m above base of formation	Beverley Inlet Fm.	yes
GSC A-008288	Southeastern Melville Island, 75°09′15″N, 107°39′00″W, south flowing stream about 9.5 km northeast of head of Beverley Inlet; 1148 m above base of formation	Parry Islands Fm. Burnett Point Mbr.	yes
GSC A-008293	As above, but 1406 m above base of formation	Parry Islands Fm. Cape Fortune Mbr.	yes
GSC A-008311	Northeastern Melville Island, 75°49′45″N, 106°14′00″W, southerly flowing stream about 10 km east of inlet on east side of east arm of Weatherall Bay; 567 m above base of formation	Weatherall Fm.	yes
GSC A-008313	As above, but 647 m above base of formation	Weatherall Fm.	yes
GSC A-008320	Northeastern Melville Island, 75°48′45″N, 106°14′00″W, southerly flowing stream about 10 km east of inlet on east side of east arm of Weatherall Bay; 796 m above base of formation	Weatherall Fm.	yes
GSC A-008323	Northeastern Melville Island, 75°48′30″N, 106°15′00″W, southerly flowing stream about 10 km east of inlet on east side of east arm of Weatherall Bay; 916.5 m above base of formation	Weatherall Fm.	yes
GSC A-008333	Northeastern Melville Island, 75°47′30″N, 106°16′00″W, southerly flowing stream about 10 km east of inlet on east side of east arm of Weatherall Bay; 208 m above base of formation	Hecla Bay Fm.	yes
GSC A-008335	As above, but 290.5 m above base of formation	Hecla Bay Fm.	yes
GSC A-008339	Northeastern Melville Island, 75°46′45″N, 106°18′00″W, southerly flowing stream about 10 km east of inlet on east side of east arm of Weatherall Bay; 379.5 m above base of formation	Hecla Bay Fm.	yes
GSC A-008342	As above, but 474 m above base of formation	Hecla Bay Fm.	yes
GSC A-008754	West-central Ellesmere Island, about 78°30′00″N, 82°51′00″W, about 11.4 km southwest of head of Strathcona Fiord; 39.5 m above base of formation	Strathcona Fiord Fm.	no

Sample/locality number	Locality	Rock unit	Spore(s) illustrated (yes/no)
GSC A-008755	As above, but 107 m above base of formation	Strathcona Fiord Fm.	yes
GSC A-008759	As above, but 349 m above base of formation	Strathcona Fiord Fm.	yes
GSC A-008791	Northern Ontario, Moose River Basin, Argor ETA No. 2 well, Kiasko River, 50°41′30″N, 80°48′00″W; 49.3–49.4 m	Sextant Fm.	yes
GSC C-027096	Northwestern District of Mackenzie, Richardson Mountains, Stony Creek, 67°23′N, 135°00′W	Unknown	yes
GSC C-028109	Western District of Mackenzie, Oscar Creek H-71 well, 65°30′20″N, 127°31′26″W; 640–730 ft. (195.1–222.6 m)	Hare Indian Fm.	yes
GSC C-046837D	Banks Island, Elfex et al. Kusrhaak D-16 well, 73°25′N, 120°05′W; 700–750 ft. (213.4–228.7 m)	Unknown	yes
GSC C-082856F	District of Mackenzie, Imperial Island River No. 1 well, 60°09′N, 121°08′W; 837.7 m	Banff Fm.	yes
GSC C-082856K	As above, but 1062.2 m	Kotcho Fm.	yes
GSC C-084874	Southwestern Ellesmere Island, 9.5 km east of Bird Fiord, UTM Zone 16, 519550E, 856910N; 8 m above base of formation	Strathcona Fiord Fm.	yes
GSC C-091907	Southwestern Ellesmere Island, about 7.5 km southwest of head of Sor Fiord, 77°15′N, 84°34′W.	Fram Fm.	yes
GSC C-091998	Southwestern Ellesmere Island, along river about 23 km south southwest of Sor Fiord, 77°04′49″N, 84°34′17″W; 441.5 m above base of section	Helca Bay Fm.	yes
GSC C-094910	East central British Columbia, McBride area, UTM 68885E, 59731N; 2.5 m above base of formation	Flume Fm.	no
GSC C-094912	As above, but 12 m above base of formation	Flume Fm.	yes
GSC C-095223	Eastern Alberta, Percé Mountain, Ancient Wall, ridge just east of glacier remnant, 53°26′06″N, 118°49′39″W; 15 m above base of formation	Calmar Fm.	yes
GSC C-120465	Central Cornwallis Island, Taylor River graben, 75°07′N, 95°00′W	Parry Islands Fm.	yes

Sample/locality number	Locality	Rock unit	Spore(s) illustrated (yes/no)
GSC C-129371	Southeastern Melville Island, northeast of Ross Point, 75°01′00″N, 106°53′00″W; 272 m above base of formation	Weatherall Fm.	yes
GSC C-129457	Western Melville Island, north of Murray Inlet, 75°29′50″N, 114°03′00″W; 81.7 m above base of formation	Hecla Bay Fm.	yes
GSC C-129465	As above, but 246.6 m above base of formation	Hecla Bay Fm.	yes
GSC C-129492	Western Mevlille Island, west of Murray Inlet, 75°21′30″N, 114°45′00″W; 63.0 m above base of formation	Hecla Bay Fm.	yes
GSC C-129494	As above, but 134.2 m above base of formation	Hecla Bay Fm.	yes
GSC C-129499	As above, but 206.4 m above base of formation	Hecla Bay Fm.	no
GSC C-137814	Southwestern Melville Island, on coast about 8 km east southeast of Cape Victoria, 75°01′30″N, 115°59′00″W; 129 m above base of section	Hecla Bay Fm.	yes
GSC C-137826	As above, but 230.5 m above base of section	Beverley Inlet Fm.	yes
GSC C-137840	As above, but 382.9 m above base of section	Beverley Inlet Fm.	yes
GSC C-137914	West coast of Melville Island, north of Comfort Cove, 75°22′30″N, 117°31′30″W; 3.6 m above base of section	Hecla Bay Fm.	yes
GSC C-140667	District of Mackenzie, west bank of Trout River, 100 m above Coral Falls, UTM 3473E, 6786N; 0.06 m below top of formation	Kakisa Fm.	yes
GSC D-000136N	Newfoundland, Grand Banks, Amoco Imperial Skelly Phalarope P-62 well, 45°11′49″N, 51°24′15″W; 9250–9280 ft. (2820.1–2829.3 m)	Unnamed	yes
GSC D-001239	Nova Scotia, Antigonish County, west side of St. George's Bay on McInnis Brook, 45°98.8′N, 61°56.25′W	Unnamed	yes
GSC D-001726	Nova Scotia, Antigonish County, west side of St. George's Bay, north of McIsaac Point, 45°44′24″N, 61°53′28″W	Unnamed	yes
GSC D-002136	Nova Scotia, Antigonish County, west side of St. George's Bay on Cape George Brook, 45°50′05″N, 61°57′00″W	(?)McAras Brook Fm.	yes

Sample/locality number	Locality	Rock unit	Spore(s) illustrated (yes/no)
GSC D-002450	Southern New Brunswick, southeast side of road about 335 m southwest of Carsonville intersection, 45°51′25″N, 65°21′25″W	?Albert Fm.	yes
GSC D-002527	Southwestern New Brunswick, Rio Tinto drillhole M-6, 45°34′47″N, 66°35′27″W; 72.85 m	Carrow Fm.	yes
GSC O-059040	Northeastern Bathurst Island, 3.2 km from shore in stream valley west of Sargeant Point, 76°11′10″N, 97°35′00″W; 396 m above base of formation	Parry Islands Fm.	yes
GSC O-079320	Northern Ontario, Moose River Basin, east bank of Abitibi River 1.2 km south of Williams Island, 50°23′20″N, 81°34′10″W	Long Rapids Fm.	yes
GSC O-096385	Northern New Brunswick, south shore of Restigouche River, 0.8 km west of Dalhousie Junction, about 0.6 m above high tide	Campbellton Fm.	no
GSC O-097057	Northernmost Western Australia, Amax Ellendale well; cuttings at 1750.5 m	Unknown	yes
GSC O-097074A	Southeastern Quebec, north side of Chaleur Bay west of Miguasha ferry, 48°04′N, 66°18′W	Escuminac Fm.	yes
GSC O-101178	As above, 12.43–14.51 m above base of formation	Escuminac Fm.	yes
GSC O-101217	Northwestern Pennsylvania, Erie County, Union City Dam on French Creek; 0.5 m above base of formation	Venango Fm.	yes
GSC O-102846	Devon Island, Grinnell Peninsula, Tucker River, base of section at 76°41′30″N, 93°43′20″W; about 42 m above base of formation	Hecla Bay Fm.	no
GSC O-102849	As above, but 6.0 m below top of formation	Strathcona Fiord Fm.	yes
GSC O-102850	As above, but 17 m below top of formation	Hecla Bay Fm.	yes
GSC O-102851	As above, but about 9 m below top of formation	Hecla Bay Fm.	no
GSC O-102853	Devon Island, Grinnell Peninsula, most easterly tributary of Tucker River, base of section at 76°41′54″N, 93°22′00″W; 0.5 m above base of section	Fram Fm.	yes

Sample/locality number	Locality	Rock unit	Spore(s) illustrated (yes/no)
GSC O-102857	As above, but 91.35 m above base of section	Fram Fm.	yes
GSC O-102858	As above, but 104.75 m above base of section	Fram Fm.	no
GSC O-102860	As above, but 155 m above base of section	Hell Gate Fm.	yes
GSC O-102866	As above, but 418.5 m above base of section	Nordstrand Pt. Fm.	no
GSC O-102875	As above, but 578.5 m above base of section	Nordstrand Pt. Fm.	yes
GSC O-102876	As above, but 588.35 m above base of section	Nordstrand Pt. Fm.	yes
GSC O-102883	As above, but 1013.8 m above base of section	Parry Islands Fm. Burnett Point Mbr.	no
GSC O-102894	Devon Island, Grinnell Peninsula, Cape Disraeli, base of section at 76°41′13″N, 93°13′30″W; 750 m above base of formation	Parry Islands Fm. Cape Fortune Mbr.	no
GSC O-103058	Northern nova Scotia, Antigonish County, on St. George's Bay between southern limit of Wilkie Brook Formation and mouth of Wilkie Brook; 192 m below unconformity at top of formation	Unnamed	yes
GSWA 72314	Western Australia, Canning Basin, Limestone Billy Hills (or Pillara Range?), BHP Minerals PD250 borehole; core at 179.25 m	Sadler Lst.	yes
GSWA F8481	Western Australia, Canning Basin, near Sadler Ridge and Longs Well Creek, 18°34′13″S, 125°58′16″E, BMR Noonkanbah No. 1 borehole; cuttings at 480–490 ft. (146.3-149.4 m)	Gogo Fm.	yes
GSWA 23405	Western Australia, Canning Basin, Wapet Blackstone No. 1 well, 17°35′14″S, 124°21′01″E; core 12, 6480-6510 ft. (1976-1985 m)	Anna Plains Ss.	yes
—	Western Australia, Canning Basin, Wapet Tappers Inlet No. 1 well, 16°51′38″S, 122°35′22″E; core 2, 6400-6450 ft. (1951.2-1966.5 m)	Dominic Sh.	yes
—	As above, but core 3, 6514-6529 ft. (1986-1991 m)	Anna Plains Ss.	yes
UQ 7570	Western Australia, Canning Basin, Wapet Barbwire No. 1 well, 19°10′38″S, 125°00′58″E; 790-800 ft. (240.9-243.9 m)	Pillara Lst.	yes

Sample/locality number	Locality	Rock unit	Spore(s) illustrated (yes/no)
UQ A926 UQ A937	Western Australia, Canning Basin, BMR Laurel Downs No. 2 well, 18°07′24″S, 125°19′58″E; core 3, 76.2–79.2 m	Fairfield Fm.	yes
UQ A933	Western Australia, Canning Basin, BMR Laurel Downs No. 2 well, 18°07′24″S, 125°19′58″E; core 10, 304.8–307.8 m	Laurel Fm.	yes
UQ A966	Western Australia, Canning Basin, near Sadler Ridge and Longs Well Creek, BMR Noonkanbah No. 1 borehole, 18°34′13″S, 125°58′16″E; core 5, 389.7 ft. (118.8 m)	Gogo Fm.	yes
UQ A989	Western Australia, Canning Basin, BMR Noonkanbah No. 4 well, 18°04′30″S, 125°25′00″E; core 11, 27.4 m	Yellow Drum Ss.	yes
UQ A992	As above, but core 25, 68.0 m	Yellow Drum Ss.	yes
UQ A998	Western Australia, Canning Basin, BMR Lennard River No. 2 well, 17°57′45″S, 125°16′30″E; core 20, 63.4 m	Laurel Fm.	yes
UQ A1073	Western Australia, Canning Basin, BMR Laurel Downs No. 2 well, 18°07′24″S, 125°19′58″E; core 18, 541.0–544.1 m	Gumhole Fm.	yes
UQ A1075	Western Australia, Canning Basin, Pickands Mather A.H. 2 well, 17°38′15″S, 125°56′20″E; cuttings at about 36 m	Fairfield Fm.	yes
UQ A1076	Central Australia, Amadeus Basin, Uranerz EW30 borehole, 23°56′18″S, 133°54′23″E; 78.74 m	Brewer Cgl.	yes
UQ A1077	Central Australia, Amadeus Basin, Uranerz EW34 borehole, 133°54′21″S, 23°56′44″E; 227.38 m	Brewer Cgl.	no
UQ A1182	Western Australia, Carnarvon Basin, about 17.5 km west of Lyndon Homestead, Aquitaine DDH1 borehole; core at 34.7 m	Gneudna Fm.	yes
UQ A1186	Western Australia, Carnarvon Basin, about 20 km southeast of Moogooree Homestead, Uranerz DDH4 borehole; core at 20.7 m	Gneudna Fm.	yes
UQ A1187	Western Australia, Carnarvon Basin, about 20 km southeast of Moogooree Homestead, Uranerz CDH1 borehole; core at 58.2 m	Gneudna Fm.	yes

Sample/locality number	Locality	Rock unit	Spore(s) illustrated (yes/no)
UQ A1218	Western Australia, Canning Basin, northern Limestone Billy Hills, BHP Minerals PD15 borehole; core at 15.5 m	Pillara Lst.	no
UQ A1219	Western Australia, Canning Basin, northern Limestone Billy Hills, BHP Minerals PD19 borehole; core at 220 m	Sadler Lst.	yes
UQ A1263	Western Australia, Canning Basin, northeast of Limestone Billy Hills, BHP Minerals PD37 borehole; core at 140.5 m	Pillara Lst.	yes
UQ A1272	Western Australia, Canning Basin, northeast of Limestone Billy Hills, BHP Minerals PD42 borehole; core at 115 m	Gogo Fm.	yes
UQ A1286	Western Australia, Canning Basin, northern Limestone Billy Hills, BHP Minerals PD71 borehole; core at 49.0 m	Gogo Fm.	yes
UQ A1718	Western Australia, Carnarvon Basin, about 16 km north of Carnarvon, Pelican Hill (Bibbawarra) well; core at 662.6–666.3 m	Gneudna Fm.	yes
UQ A2765	Western Australia, Canning Basin, northern Limestone Billy Hills, BHP Minerals PD124 borehole; core at 372.0 m	Pillara Lst.	yes
UQ A2773	Western Australia, Canning Basin, about 12 km southwest of Virgin Hills, BHP Minerals RD5 borehole; core at 33.8 m	Gogo Fm.	yes
UQ A3257 UQ A3258	Northern Tasmania, near Eugenana, Hallett's Quarry	Gordon Subgroup Eugenana beds	yes
UQ A3279	Western Australia, Canning Basin, northwestern Pillara Range, BHP Minerals PD153 borehole; core at 32.6 m	Virgin Hills Fm.	yes
UQ A3310	Queensland, Adavale Basin, Etonvale No. 1 well; core 23, 9609 ft. 5 in. (2929.8 m)	Log Creek Fm.	no
UQ A3315	Queensland, Adavale Basin, Boree No. 1 well; core 10, 4776 ft. 6 in. (1456.2 m)	Etonvale Fm.	no
UQ A3317	Queensland, Adavale Basin, Carlow No. 1 well, 24°50′27″S, 145°25′48″E; core 10, 6726 ft. 2 in. (2050.7 m)	Lissoy Ss.	yes
UQ A3318	As above, but core 11, 7067 ft. 11 in. (2154.9 m)	Eastwood beds	yes

Sample/locality number	Locality	Rock unit	Spore(s) illustrated (yes/no)
UQ A3319	As above, but core 12, 7400 ft. 1 in. (2256.4 m)	Eastwood beds	yes
UQ A3320	Queensland, Adavale Basin, Allandale No. 1 well, 25°25′00″S, 145°54′15″E; core at 7675 ft. 5 in. (2340.1 m)	Eastwood beds	yes
UQ A3321	Queensland, Adavale Basin, Carlow No. 1 well, 24°50′27″S, 145°25′48″E; core 12, 7396 ft. (2254.9 m)	Eastwood beds	yes
UQ A3324	Central Australia, Amadeus Basin, NT bore K3; core 11, 85.54–85.59 m	Unknown	no
UQ A3329	Western Australia, Carnarvon Basin, Wapet Cape Cuvier No. 1 well, 24°13′35″S, 113°23′13″E; core at 431.6 m	Gneudna Fm.	yes
—	Central Queensland, Drummond Basin, Airlie station, 24 km west southwest of Emerald, Denison 180 borehole; 53.35 m (Prep. B858)	Unnamed unit	yes
—	As above, but 278.12 m (Prep. B855)	Unnamed unit	no
UWA 6809	Western Australia, Carnarvon Basin, about 17.5 km west of Lyndon Homestead, Aquitaine DDH2 borehole; core at 141.8 m	Gneudna Fm.	yes
UWA 6813	As above, but core at 158.5 m	Gneudna Fm.	yes
UWA 6814	As above, but core at 176.8 m	Gneudna Fm.	yes
UWA 6832	Western Australia, Carnarvon Basin, about 17.5 km east of Moogooree Homestead, Uranerz CDH8 borehole; core at 91 m	Gneudna Fm.	yes
UWA 6833	As above, but core at 95.4 m	Gneudna Fm.	yes
C. Cuvier	Western Australia, Carnarvon Basin, Wapet Cape Cuvier No. 1 well, 24°13′35″S, 113°23′13″E, core at 430.0–431.6 m (Slide CC-20 provided by B.E. Balme)	Gneudna Fm.	yes
R. Purcell	Western Australia, Canning Basin, Matches Springs No. 1 well, 18°41′28″S, 124°03′11″E; core 11, 5611–5619 ft. (1710.7–1713.1 m)	Dominic Sh.	no

TABLE 4

Spore morphons and their characterizing features referred to in the text

Name	Proposed in	Some constituent taxa	Morpho-characters
Acinosporites acanthomammillatus	This paper, page 24	*Acinosporites acanthomammillatus* *Acinosporites hirsutus* *Cristatisporites albus*? *Cristatisporites dasydentatus* *Cristatisporites hesperus*	Verrucae and biform elements on anastomosing ridges; incipient subequatorial zona; prominent fold-like labra.
Acinosporites lindlarensis	Richardson et al., in press	*Acinosporites lindlarensis* var. *lindlarensis* *Acinosporites lindlarensis* var. *minor*	Varied, mainly biform elements on interconnected muri; elongate curvatural spinae; cavate with slightly separated walls.
Ancyrospora longispinosa	This paper, page 25	*Ancyrospora longispinosa* *Ancyrospora ancyrea* *Ancyrospora furcula* *Ancyrospora involucra* *Ancyrospora langii* (pars) *Ancyrospora pulchra* (*Ancyrospora acutispinosa*)	Processes apically furcate, evenly tapered, broad based, and basally variably confluent; pseudoflange; elevated trilete folds.
Ancyrospora simplex	This paper, page 25	*Ancyrospora simplex* *Ancyrospora ampulla* *Ancyrospora langii* (pars)	Processes apically furcate, evenly tapered, discrete; zona entire, with slightly or strongly scalloped margin.
Apiculiretusispora arenorugosa	This paper, page 23	*Apiculiretusispora arenorugosa* *Apiculiretusispora brandtii* *Apiculiretusispora* sp. cf. *A. brandtii* *Apiculiretusispora plicata*	Minute, closely spaced spinae/coni; fragile, closely adhering sculptured layer tends to tear away; curvaturae; thin wall.
Archaeoperisaccus ovalis	This paper, page 23	*Archaeoperisaccus ovalis* *Archaeoperisaccus artus* *Archaeoperisaccus completus* *Archaeoperisaccus concinnus* *Archaeoperisaccus echinatus* *Archaeoperisaccus elongatus* *Archaeoperisaccus menneri* *Archaeoperisaccus mirus* *Archaeoperisaccus regalis* *Archaeoperisaccus scabratus* (*Archaeoperisaccus oviformis*) (*Archaeoperisaccus xichongensis*)	Laevigate to minutely sculptured; monolete, radially elongate, cavate; equatorial extension of constant width or widest opposite ray ends.
Archaeoperisaccus verrucosus	This paper, page 23	*Archaeoperisaccus verrucosus* *Archaeoperisaccus oblongus* *Archaeoperisaccus signus* *Archaeoperisaccus timanicus*	Relatively coarse coni/verrucae/rugulae; monolete, radially elongate, cavate; equatorial extension widest opposite ray ends.
Archaeozonotriletes variabilis	This paper, page 25	*Archaeozonotriletes variabilis* *Archaeozonotriletes timanicus* (*Geminospora punctata*)	Patina commonly unequally thick equatorially, thickest distally, variably dissected or entire; laevigate.

Name	Proposed in	Some constituent taxa	Morpho-characters
Cristatisporites triangulatus	This paper, page 25	*Cristatisporites triangulatus* *Cristatisporites inusitatus* *Hymenozonotriletes duplex*	Discrete or fused coni/verrucae on distal central area; body subcircular; zona of constant width or widest radially, laevigate or sparsely sculptured.
Cymbosporites magnificus	This paper, page 26	*Cymbosporites magnificus* Undescribed spp.	Closely spaced or basally fused verrucae/mammillae distally and equatorially; patina thickest at equator.
Cyrtospora cristifera	van der Zwan, 1979, p. 12; van der Zwan and Walton, 1981, p. 144	*Cyrtospora cristifera* *Cornispora monocornata* *Cornispora varicornata* *Ceratosporites* sp. A, van der Zwan *Mooreisporites* sp. A, van der Zwan	Discrete or basally fused coni/verrucae/bacula on distally or laterally extended, one or multi "horned" crassitude; trilete or monoletoid.
Densosporites devonicus	This paper, page 23	*Densosporites devonicus* *Densosporites concinnus* *Densosporites inaequus* *Densosporites weatherallensis*	Discrete or basally fused coni/spinae/ancyrate elements on zona and distally; wall equatorially/distally thick; prominent fold-like labra.
Dibolisporites echinaceus	This paper, page 23	*Dibolisporites echinaceus* *Apiculatasporites microconus* *Bullatisporites bullatus* *Dibolisporites pseudoreticulatus* *Dibolisporites radiatus* *Dibolisporites triangulatus* *Dibolisporites varius*	Densely spaced biform sculpture; narrow, untapered labra; thin wall, subcircular amb.
Dibolisporites farraginis	This paper, page 26	*Dibolisporities farraginis* *Dibolisporites uncatus* *Dibolisporites vegrandis* *Heterotriletes* sp. 1	Mixture of mostly discrete grana/coni/spinae/biform elements of various sizes; simple laesurae; subcircular amb.
Diducites mucronatus	van Veen, 1981, p. 279	*Diducites mucronatus* *Diducites plicabilis* *Diducites poljessicus* *Diducites versabilis*	Cavate; outer wall smooth to wrinkled, two layered; laesurae not exceeding inner wall radius.
Emphanisporites rotatus	This paper, page 26	*Emphanisporites rotatus* *Emphanisporites annulatus* *Emphanisporites densus* *Emphanisporites macgregorii* *Emphanisporites minutus* *Emphanisporites multicostatus* *Emphanisporites neglectus* *Emphanisporites obscurus* *Emphanisporites pantagiatus*	Proximal costae radiate from pole; distally laevigate; curvaturae, if present, close to equator interradially.

Name	Proposed in	Some constituent taxa	Morpho-characters
		Emphanisporites partitus *Emphanisporites perfilum* *Emphanisporites tener* *Retusotriletes actinomorphus* *Zonomonoletes actinobolus*	
Geminospora lemurata	This paper, page 26	*Geminospora lemurata* *Archaeozonotriletes comptus* *Archaeozonotriletes meonacanthus* *Geminospora spinosa* *Geminospora svalbardiae* *Geminospora tuberculata* *Geminospora venusta* *Rhabdosporites minutus*	Small sculpturing elements (mostly less than $3\mu m$ high) distally/equatorially; pseudosaccate; contact areas large; exoexine thick, especially at equator.
Grandispora magnifica	This paper, page 25	*Grandispora magnifica* *Grandispora cassidea*	Discrete, small spinae/bacula/ancyrate elements; cavate; wide, rigid equatorial extension with unscalloped margin.
Hystricosporites porrectus	This paper, page 25	*Hystricosporites porrectus* *Hystricosporites mitratus* *Hystricosporites richardsonii*	Processes discrete, slender, relatively small, apically furcate; apical prominence; contact areas acostate.
Rhabdosporites langii	This paper, page 26	*Rhabdosporites langii* *Geminospora micropaxilla* *Leiozonotriletes laurelensis* (pars) *Rhabdosporites parvulus* *Rhabdosporites scamnus* *Rhabdosporites*(?) *vermiculatus* (*Archaeozonotriletes micromanifestus*) (*Dibrochosporites nodosus*)	Discrete, small, closely spaced bacula/grana/apiculae; pseudosaccate; exeoexine thin, commonly folded, may be pseudolimbate.
Sinuosisporis sinuosus	This paper, page 24	*Sinuosisporis sinuosus* *Kraeuselisporites ollii*? *Sinuosisporis aculeatus* *Sinuosisporis flavus* *Sinuosisporis kalugianus*	Discrete, small grana/apiculae; narrow zona of even or uneven width; sinuous proximal folds; prominent labra.
Verrucosisporites scurrus	This paper, page 26	*Verrucosisporites scurrus* *Convolutispora crassata*? *Convolutispora tegula* *Geminospora verrucosa* *Verrucosisporites tumulentus* *Verrucosisporites premnus* (*Heterotriletes* sp. 2)	Varied, closely spaced or fused, evenly or asymmetrically distributed, broad coni/bacula/verrucae; simple laesurae; subcircular amb.

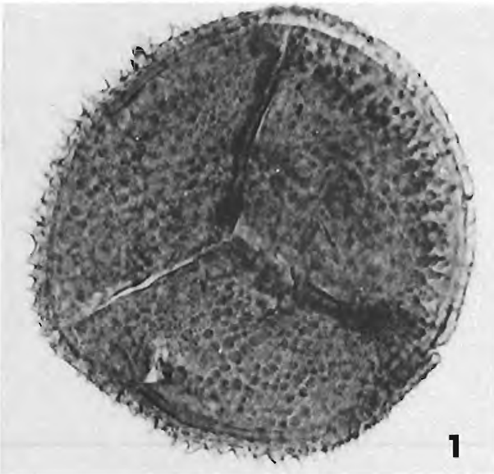
Names in parentheses indicate tentative inclusion in the morphon.

PLATES 1–20

Locality/sample numbers, slide numbers, England finder locations, type numbers, and specimen repositories are given in Appendix Table 2. Figure numbers in boldface on the plates indicate Canadian specimens, with the exception of Plate 12, figure 7 (specimen from Ohio, U.S.A.); all other figure numbers (normal typeface) refer to Australian specimens. Species that we have found in both Euramerica and Australia (Fig. 7) are illustrated in approximately alphabetical order in Plates 1–13. Selected unshared species are shown in Plates 14–16 (Euramerican) and 17–20 (Australian).

PLATE 1

Figures 1, 2.	*Acinosporites lindlarensis* Riegel, 1968 var. *lindlarensis*; x750.
Figures 3, 4, 7, 8.	cf. *Anapiculatisporites petilus* Richardson, 1965; 3, 7, x750; 4, x400; 8, x500.
Figures 5, 6.	*Ancyrospora* sp. cf. *A. ampulla* Owens, 1971; x500.
Figures 9, 10.	*Acinosporites lindlarensis* Riegel, 1968 var. *minor* McGregor and Camfield, 1976; x750.
Figures 11, 12.	*Ancyrospora* sp. cf. *A. acutispinosa* Chi and Hills, 1976; 11, x500; 12, x250.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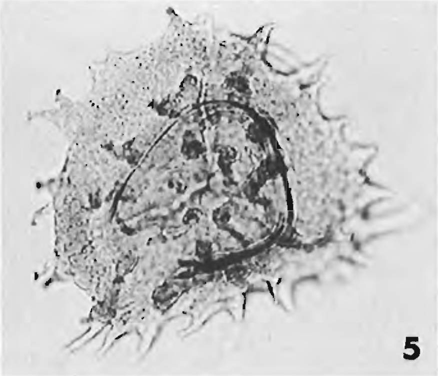
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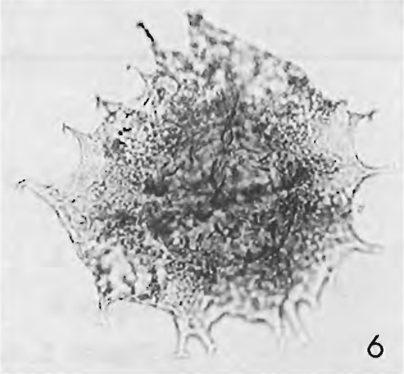
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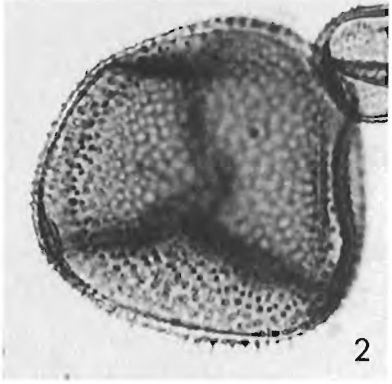
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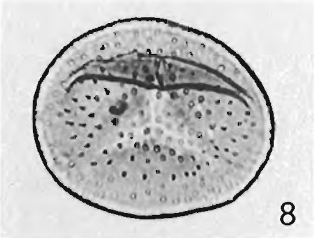
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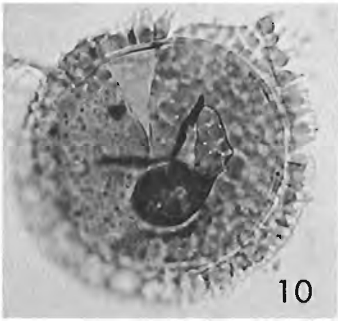
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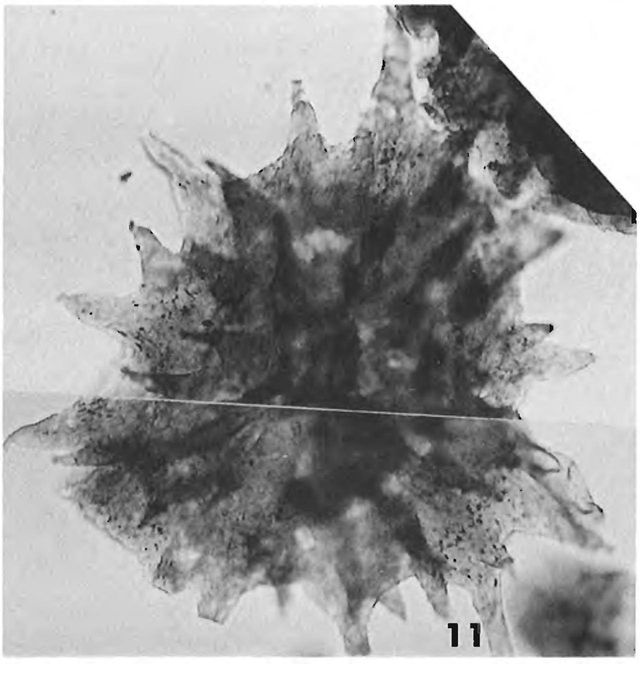
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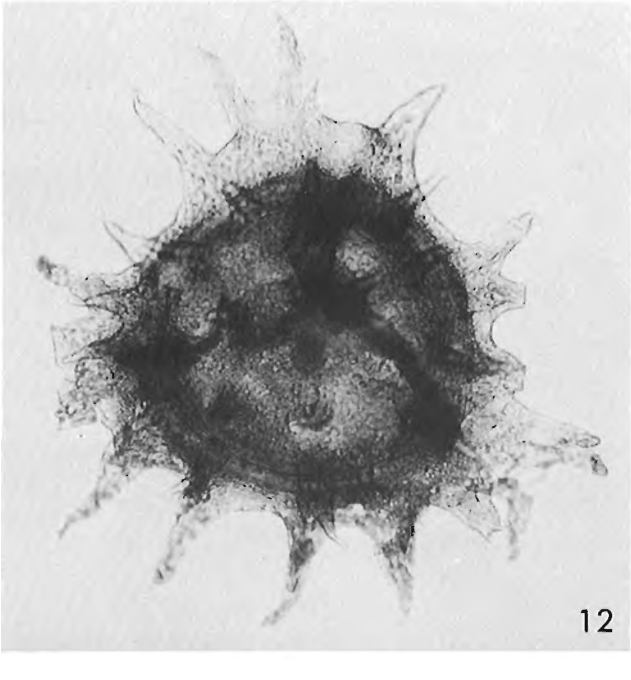
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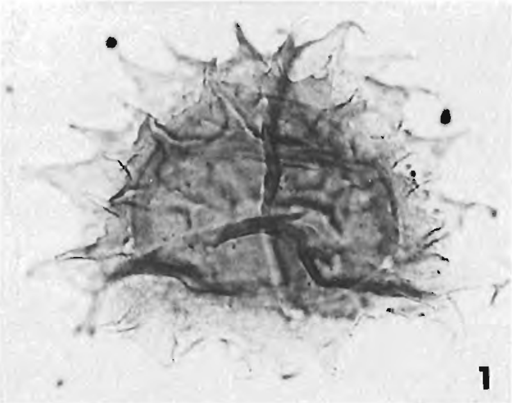
PLATE 2

Figures 1, 2.	*Ancyrospora langii* (Taugourdeau-Lantz) Allen, 1965; 1, x500; 2, x400.
Figure 3.	*Ancyrospora longispinosa* Richardson, 1962; x500.
Figure 4.	*Ancyrospora longispinosa*?; x500.
Figures 5, 6.	*Ancyrospora* sp. cf. *A. simplex* Guennel, 1963; x500.
Figures 7, 8.	*Ancyrospora* sp. cf. *A. pulchra* Owens, 1971; 7, x500; 8, x400.

PLATE 2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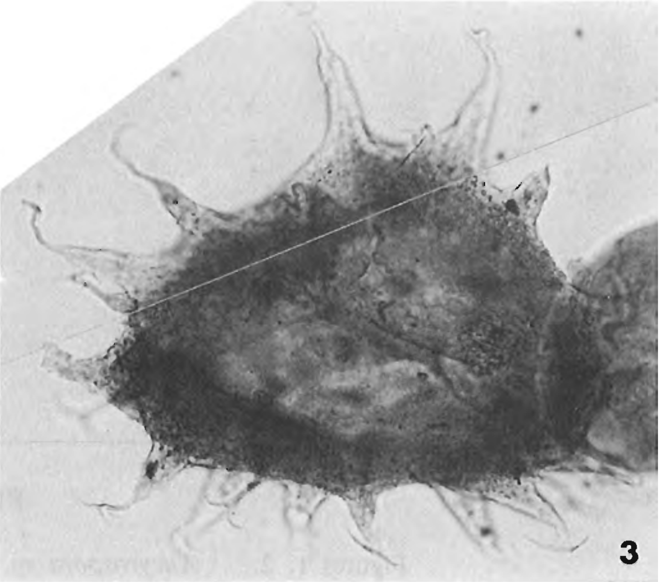
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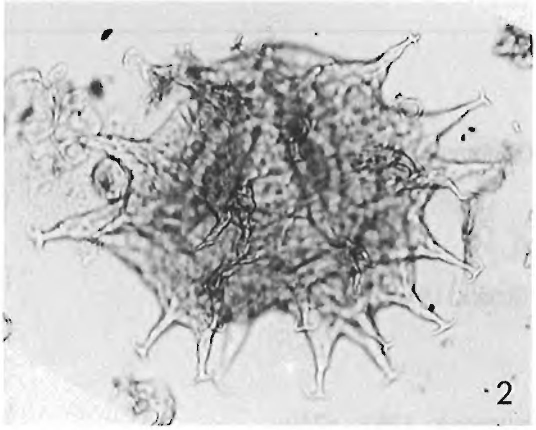
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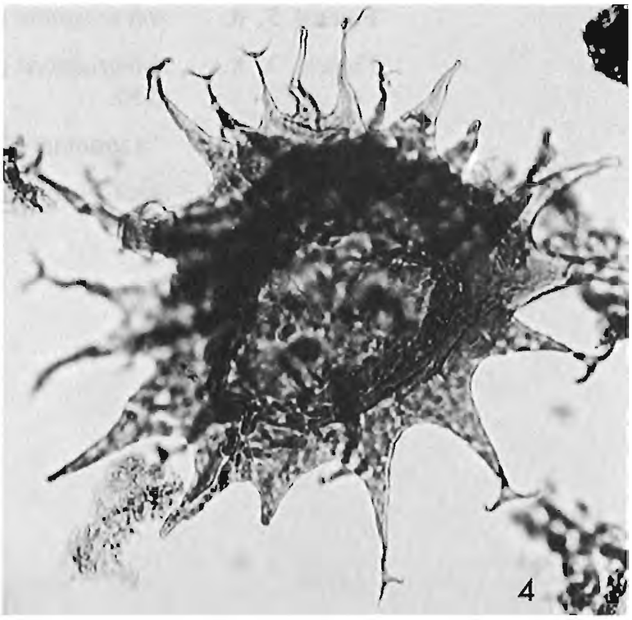
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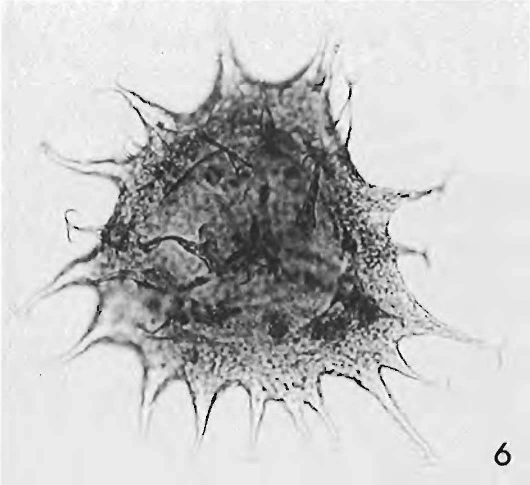
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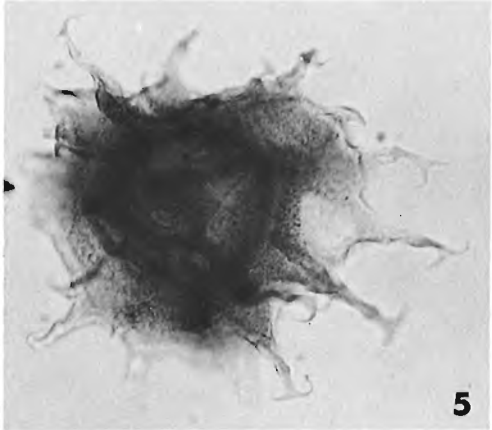
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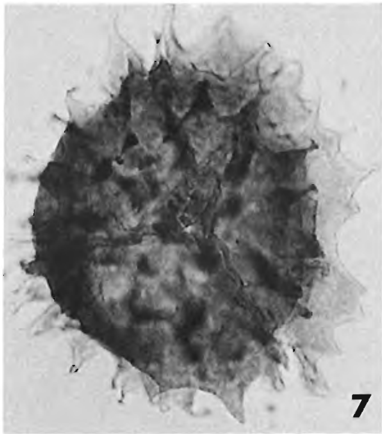
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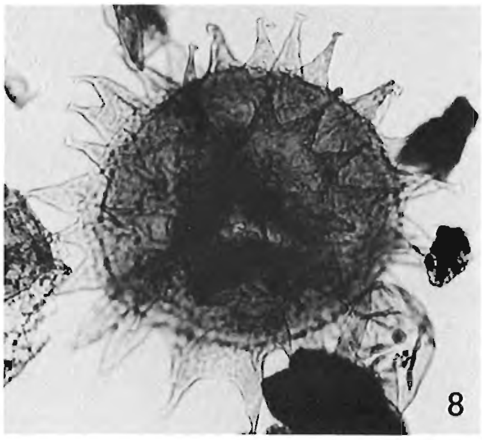
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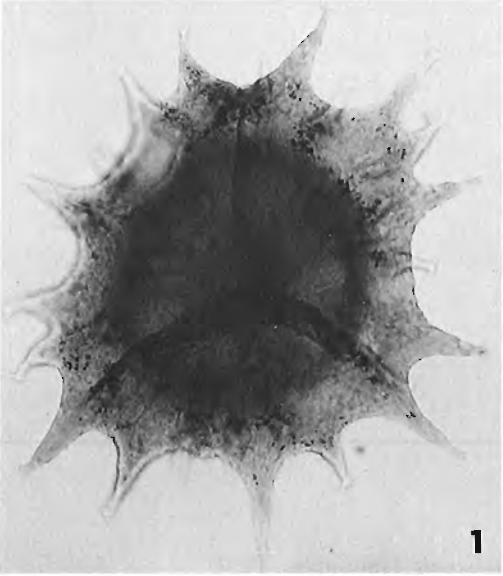
PLATE 3

Figures 1, 2.	*Ancyrospora* sp. cf. *A. simplex* Guennel, 1963; x500.
Figures 3, 4.	*Ancyrospora* sp.; x500.
Figures 5, 6.	*Ancyrospora* sp.; 5, x500; 6, x400.
Figures 7, 8.	*Aneurospora greggsii* (McGregor) Streel, 1974; 7, x500; 8, x750.
Figures 9, 10.	"Azonomonoletes" sp.; x1000.
Figures 11, 12.	*Archaeozonotriletes famenensis* Naumova, 1963; x750.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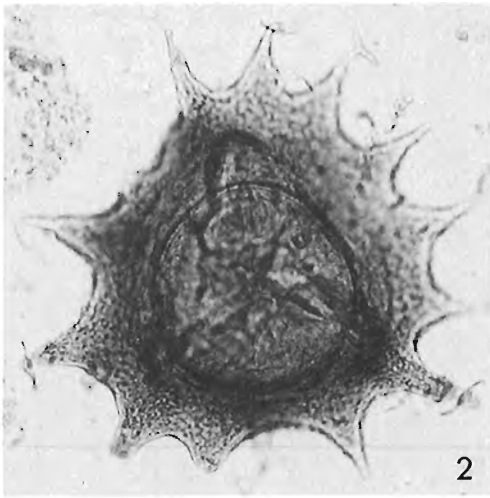
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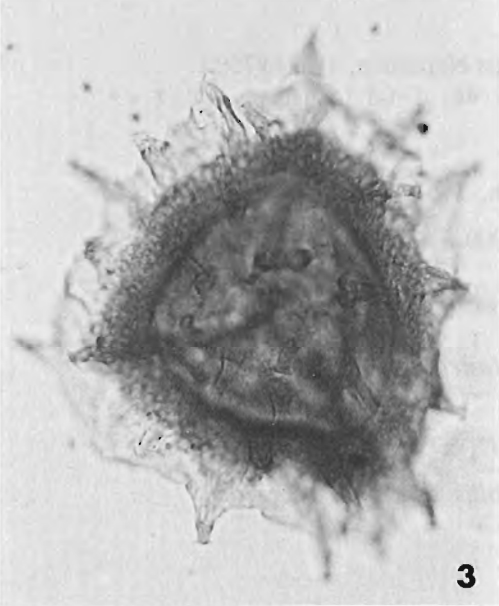
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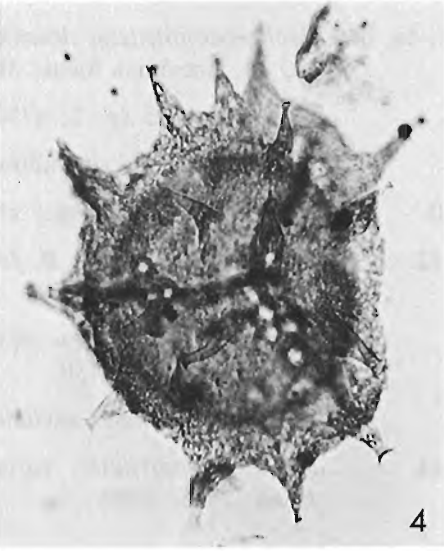
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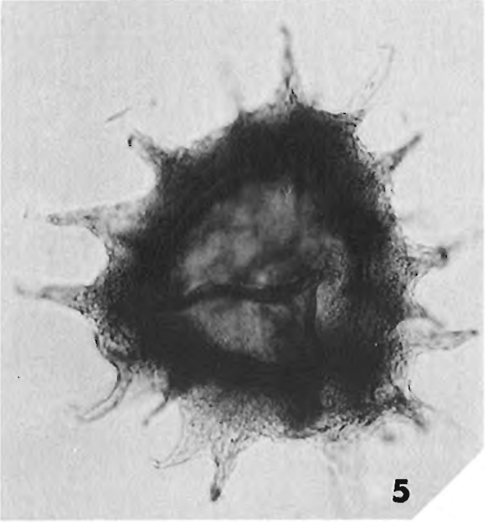
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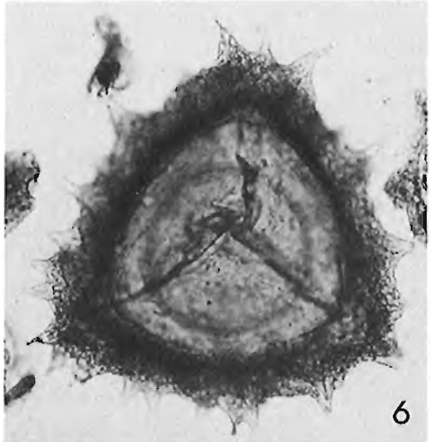
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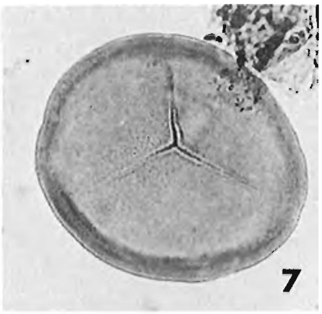
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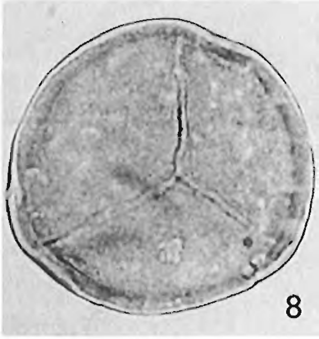
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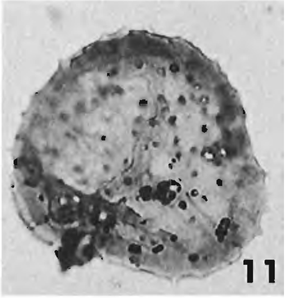
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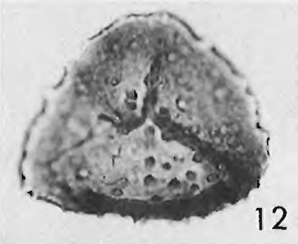
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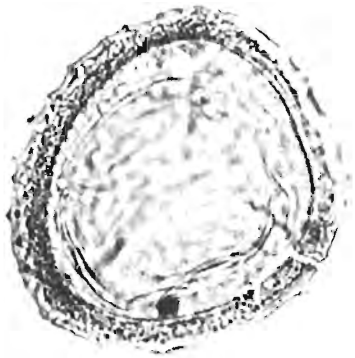
PLATE 4

Figures 1, 2.	cf. *Archaeozonotriletes famenensis* Naumova, 1953; x750.
Figures 3a, b, 4a, b.	*Archaeozonotriletes timanicus* Naumova, 1953; x750; 3a, 4a, proximal focus; 3b, 4b, distal focus.
Figures 5, 6.	*Cristatisporites* sp. 2; x750.
Figures 7, 8.	*Auroraspora macra* Sullivan, 1968; x750.
Figures 9, 10.	*Camarozonotriletes* sp.; x1000.
Figures 11, 12.	*Brochotriletes* sp. cf. *B. foveolatus* Naumova, 1953; x750.
Figure 13.	*Camarozonotriletes sextantii* McGregor and Camfield, 1976; x750.
Figure 14.	*Camarozonotriletes sextantii*?; x750.
Figures 15, 16.	*Archaeozonotriletes variabilis* Naumova emend. Allen, 1965; x500.

PLATE 4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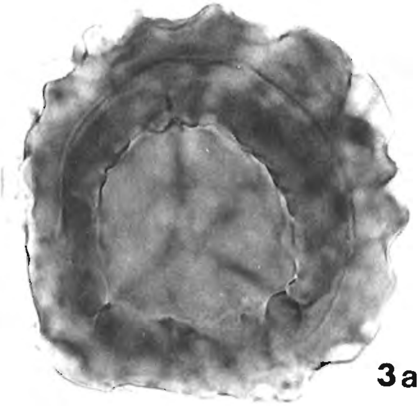
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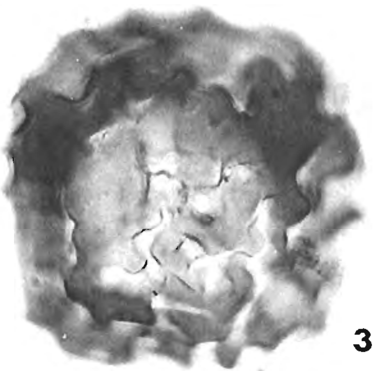
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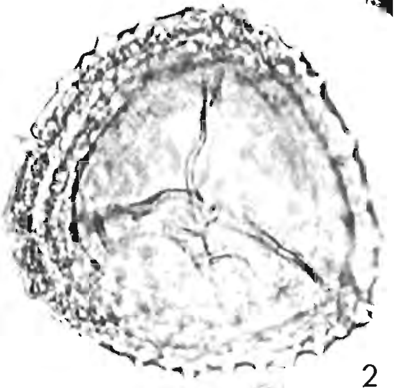
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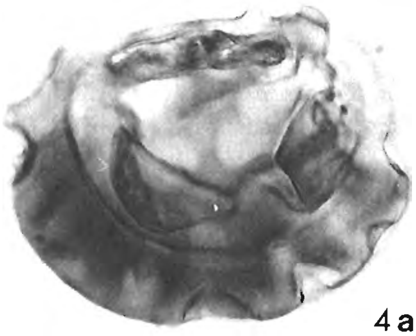
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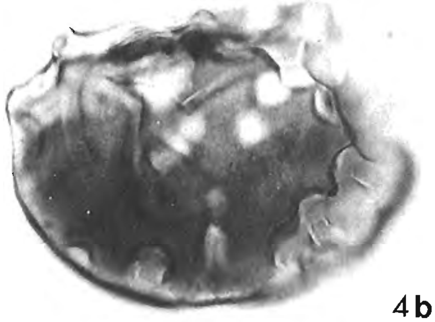
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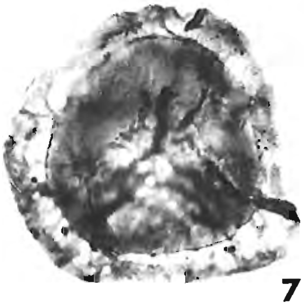
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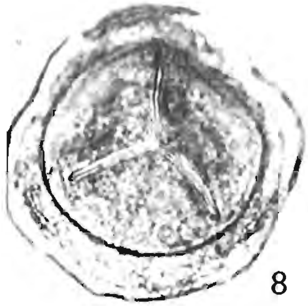
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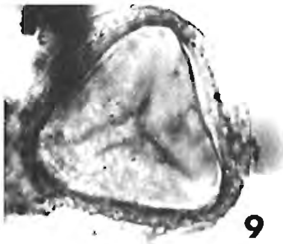
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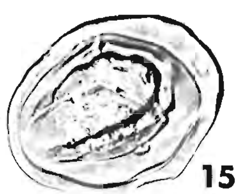
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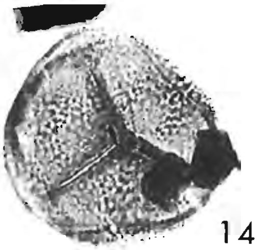
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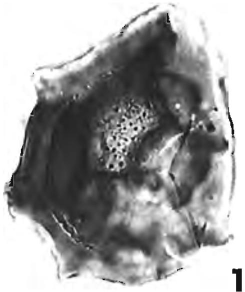
PLATE 5

Figures 1a, b, 2a, b.	*Chelinospora concinna* Allen, 1965; x750; 1a, 2a, proximal focus; 1b, 2b, distal focus.
Figures 3, 4.	*Cymbosporites magnificus* (McGregor) McGregor and Camfield, 1982; x750.
Figures 5, 6.	*Cymbosporites* sp. cf. *C. magnificus*; x750.
Figures 7, 8.	*Convolutispora* sp.; x750.
Figure 9.	*Cristatisporites deliquescens* (Naumova) Arkhangelskaya, 1987; x500.
Figure 10.	*Cristatisporites deliquescens*?; x500.
Figures 11, 12.	*Cristatisporites* sp. 1; x500.
Figures 13, 14.	*Corystisporites collaris* Tiwari and Schaarschmidt, 1975; x500.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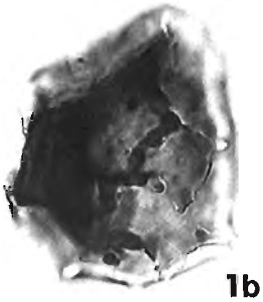
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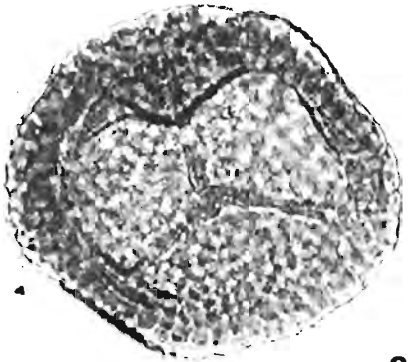
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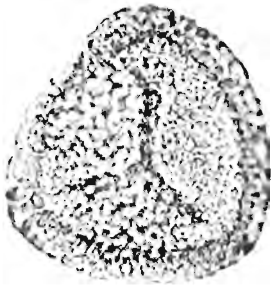
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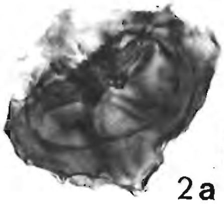
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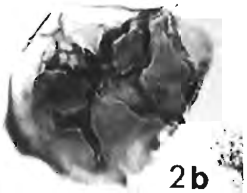
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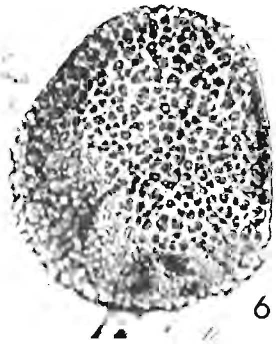
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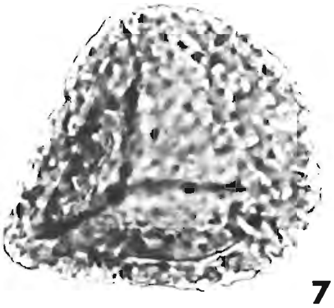
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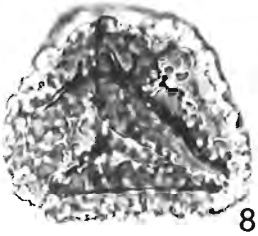
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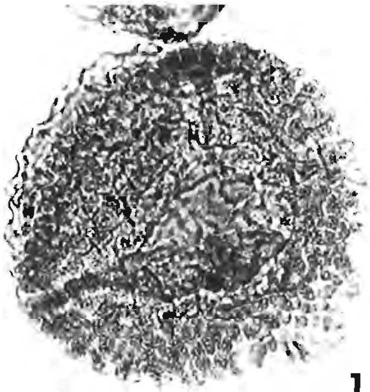
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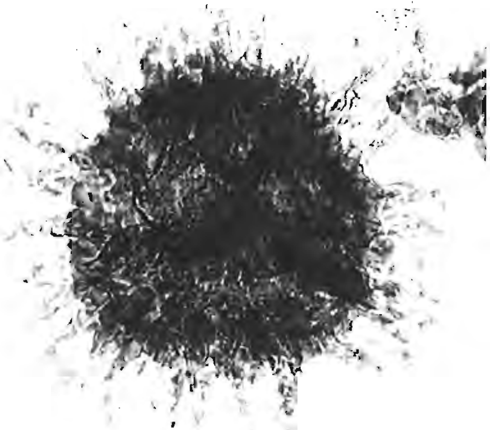
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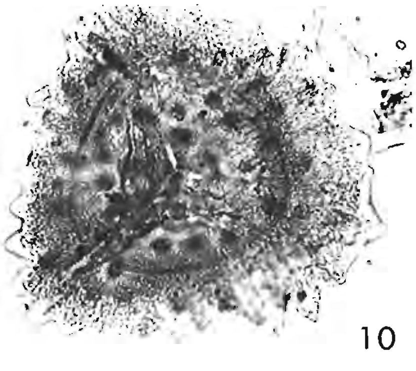
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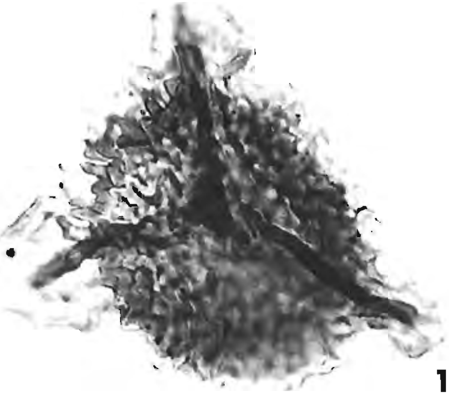
PLATE 6

Figures 1–8.	*Cristatisporites triangulatus* (Allen) McGregor and Camfield, 1982; x750.
Figures 9, 10.	*Diatomozonotriletes* sp. cf. *D. oligodontus* Chibrikova, 1962; x1000.
Figures 11, 12.	*Cymbosporites* sp. 1; x750.
Figures 13, 14.	cf. *Densosporites*? *cassiformis* (Chibrikova) Arkhangelskaya, 1985; x1000.
Figures 15, 16.	*Emphanisporites minutus* Allen, 1965; x1000.
Figures 17, 18.	*Cymbosporites* sp. 2; x750.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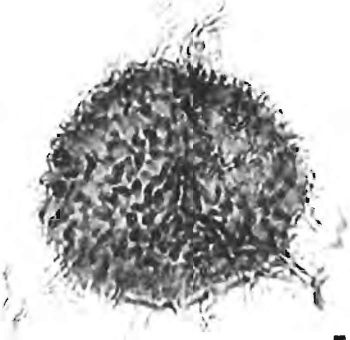
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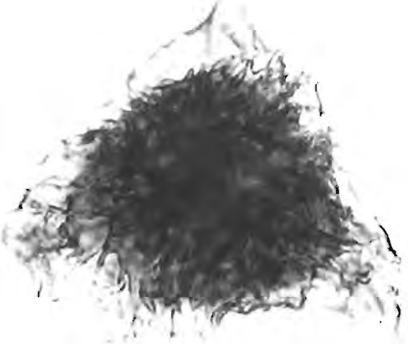
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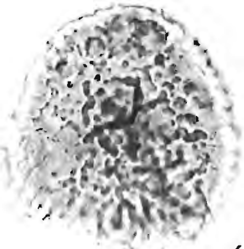
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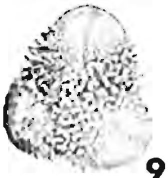
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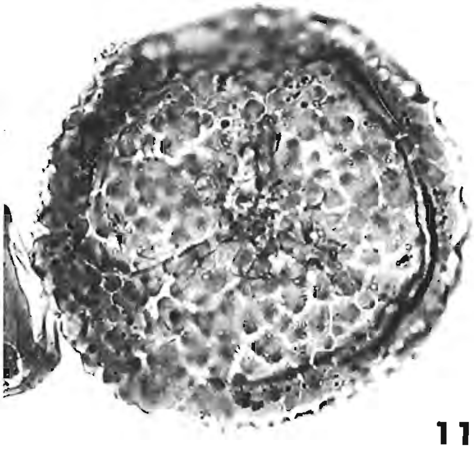
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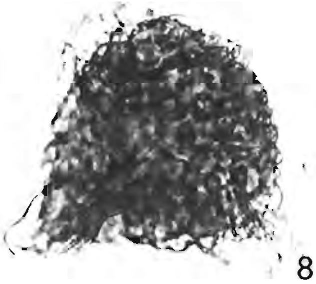
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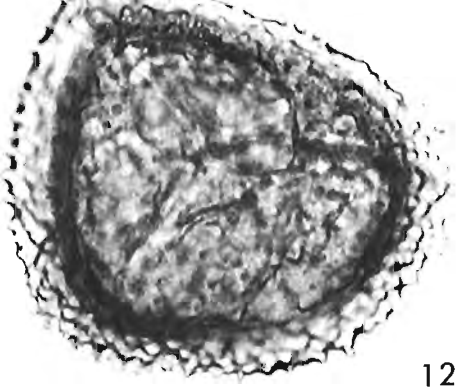
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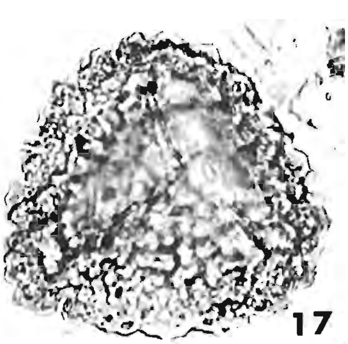
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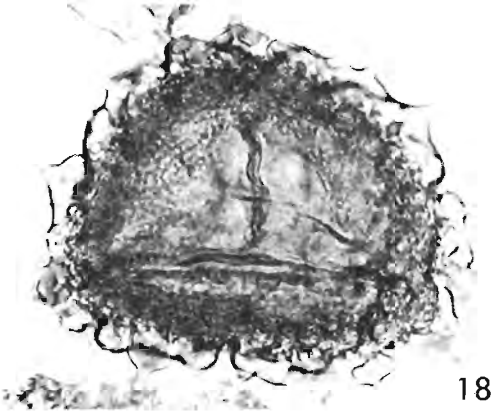
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PLATE 7

Figures 1, 2.	*Diaphanospora perplexa* Balme and Hassell, 1962; x750.
Figures 3, 4.	*Dibolisporites farraginis* McGregor and Camfield, 1982; x750.
Figures 5, 6.	*Dibolisporites turriculatus* Balme, 1988; 5, x750; 6, x500.
Figures 7, 8.	*Dibolisporites vegrandis* McGregor and Camfield, 1982; x750.
Figures 9, 10.	*Dibolisporites* sp. cf. *D. uncatus* (Naumova) McGregor and Camfield, 1982; x750.
Figures 11, 12.	*Emphanisporites annulatus* McGregor, 1961; 11, x750; 12, x600.
Figures 13, 14.	cf. *Geminospora* sp.; x750.
Figures 15, 16.	*Dictyotriletes australis*? de Jersey, 1966; x750.
Figures 17, 18.	*Dictyotriletes australis*; x750.
Figures 19, 20.	*Endosporites micromanifestus* Hacquebard, 1957 sensu lato; x500.
Figures 21, 22.	*Emphanisporites rotatus* McGregor, 1961; x750.


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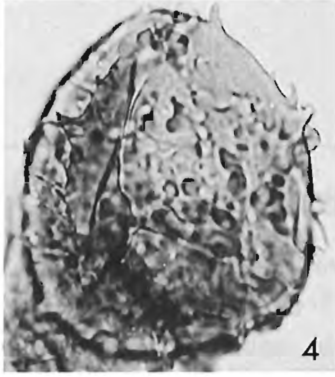
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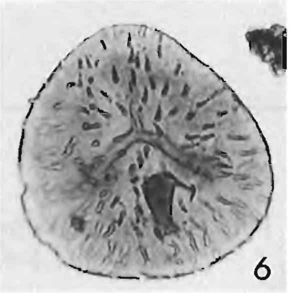
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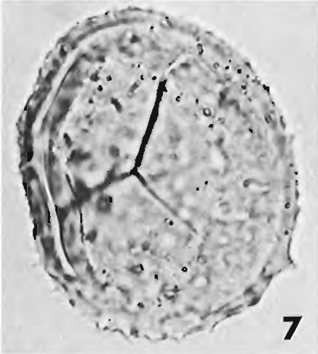
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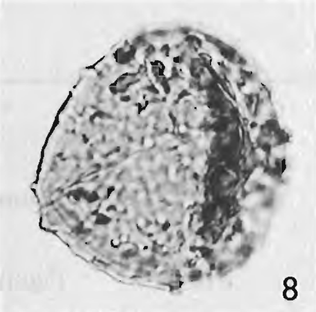
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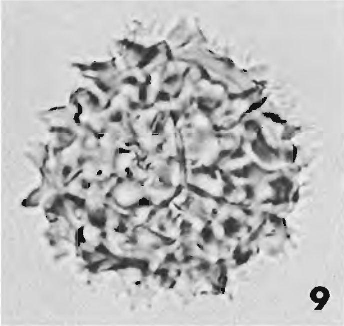
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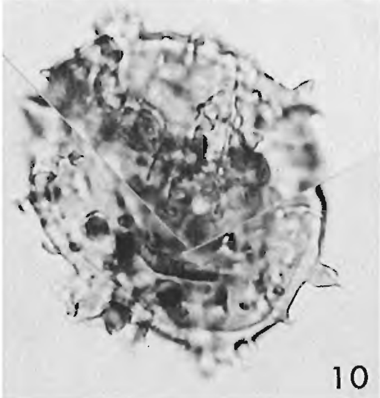
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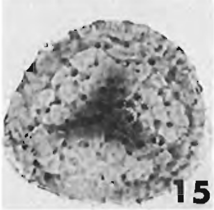
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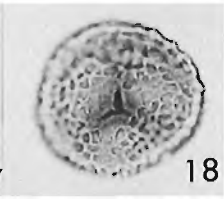
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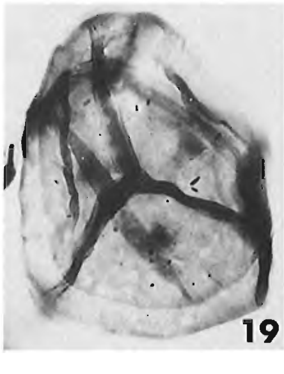
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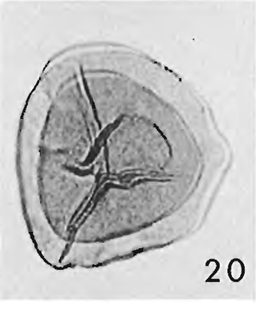
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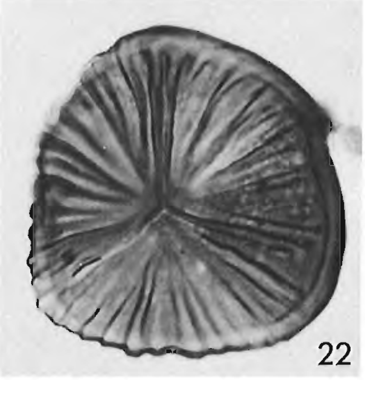
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PLATE 8

Figures 1–6, 9–12.	*Geminospora lemurata* Balme, 1962 emend. Playford, 1983; 1–4, 6, 9–12, x750; 5, x500.
Figures 7, 8.	*Geminospora venusta*? (Naumova) McGregor and Camfield, 1982; x750.
Figures 13, 14.	*Geminospora punctata* Owens, 1971; x750.


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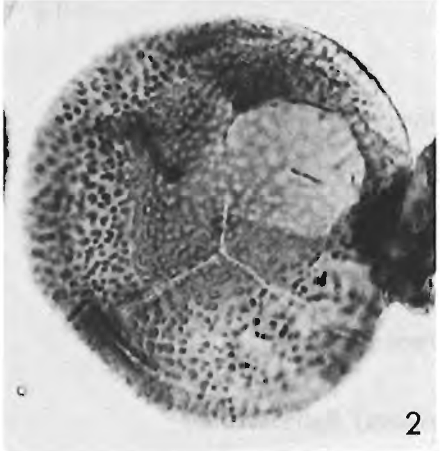
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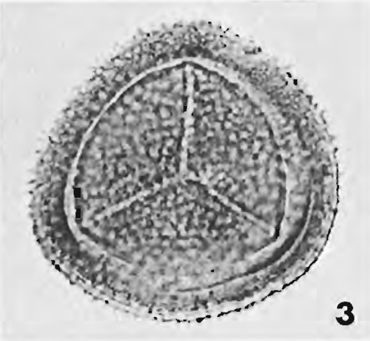
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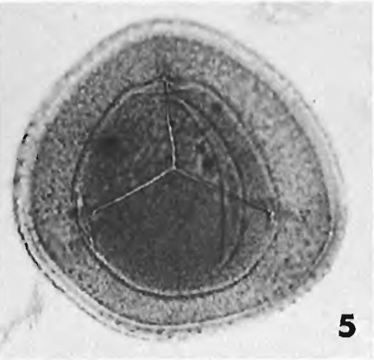
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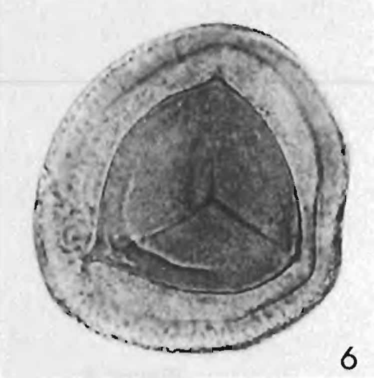
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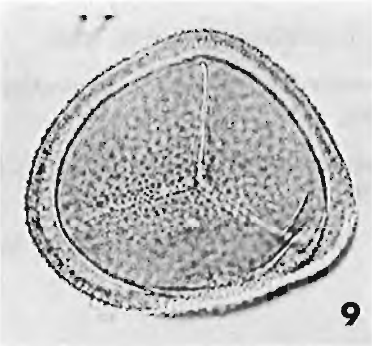
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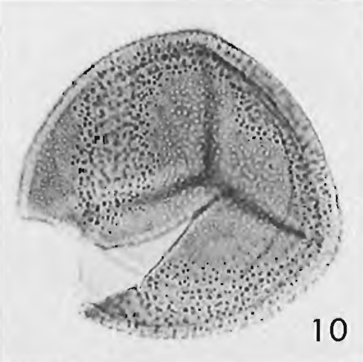
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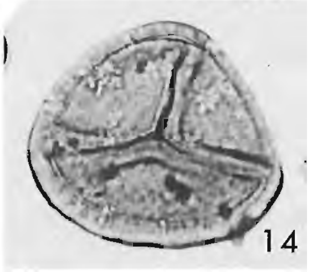
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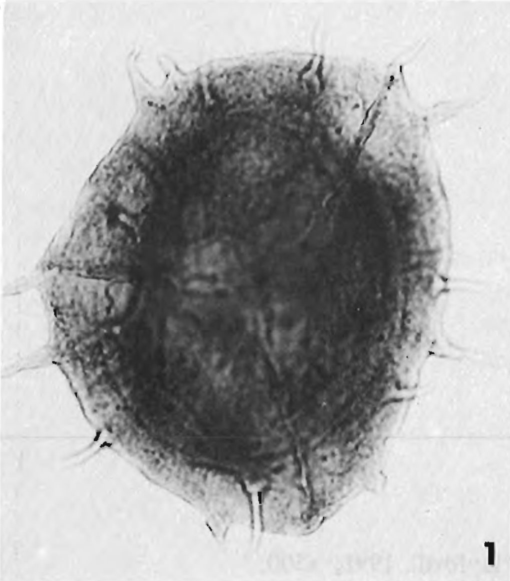
PLATE 9

Figures 1, 2.	*Grandispora naumovae* (Kedo) McGregor, 1973; x500.
Figures 3, 4.	*Geminospora verrucosa* Owens, 1971; x750.
Figure 5.	*Grandispora eximia* (Allen) McGregor and Camfield, 1982; x750.
Figure 6.	cf. *Grandispora eximia*; x500.
Figures 7, 8.	*Grandispora* sp. cf. *G. magnifica* (Owens) Chi and Hills, 1976; x750.
Figures 9, 10.	*Gneudnaspora divellomedium* (Chibrikova) Balme, 1988; x750.
Figures 11, 12.	cf. *Grandispora inculta* Allen, 1965; x750.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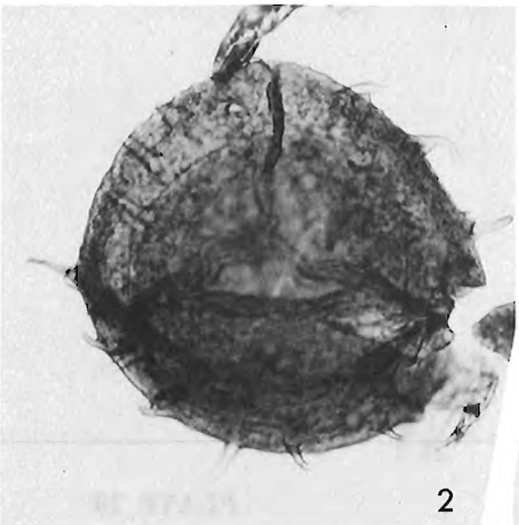
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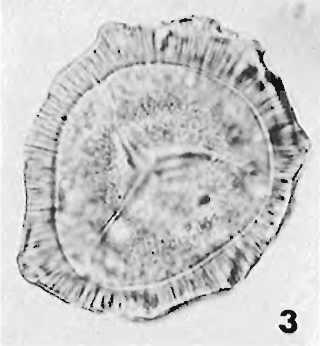
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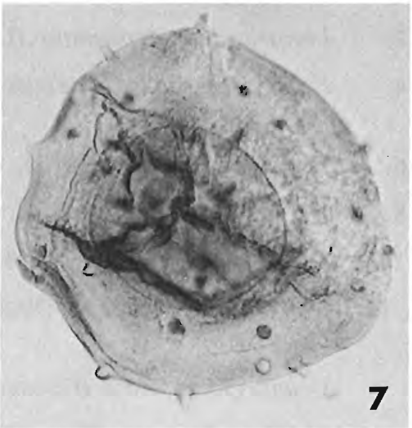
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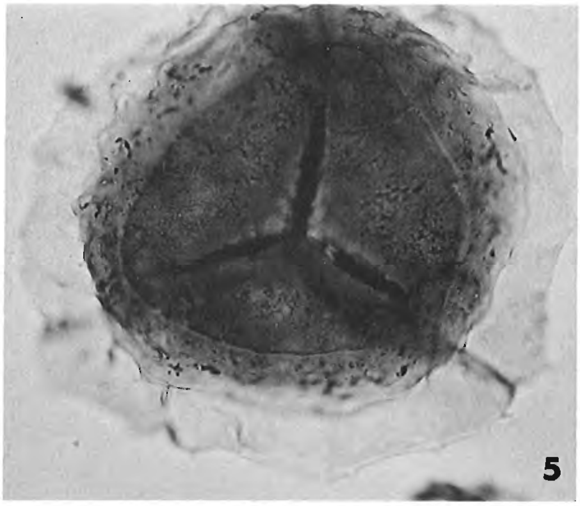
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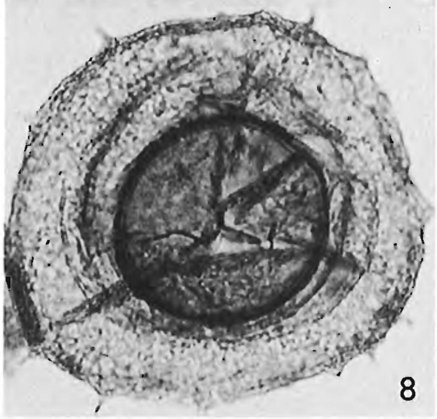
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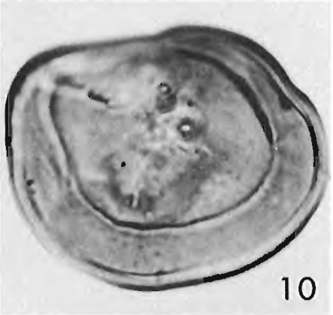
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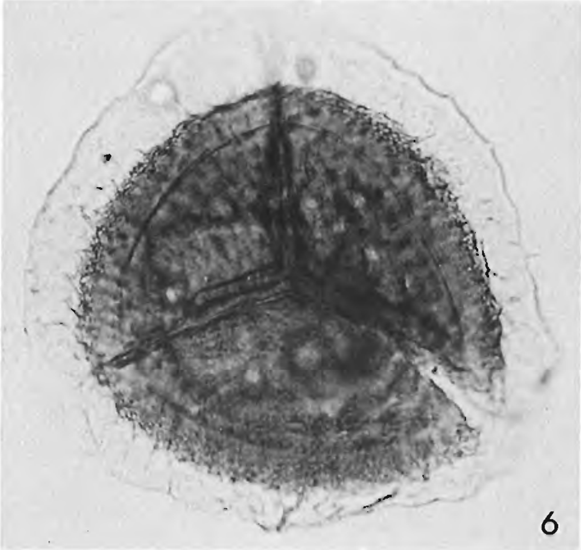
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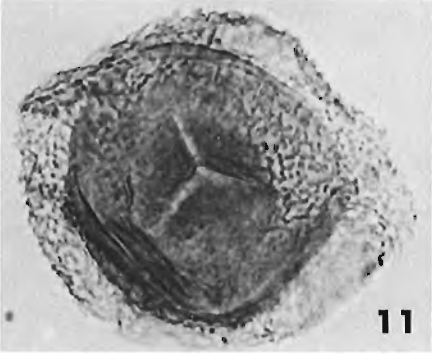
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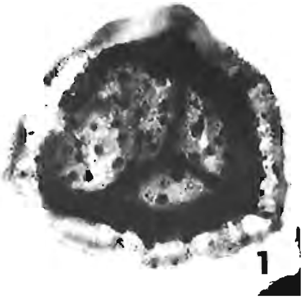
PLATE 10

Figures 1, 2.	*Indotriradites explanatus* (Luber) Playford, 1991; x500.
Figures 3, 4.	*Hystricosporites porrectus* (Balme and Hassell) Allen, 1965; x500.
Figures 5, 6.	*Heterotriletes* sp. 1; x750.
Figures 7, 8.	*Heterotriletes* sp. 2; x750.
Figures 9, 10.	*Laevigatosporites* sp.; x750.
Figures 11, 12.	*Knoxisporites literatus* (Waltz) Playford, 1963; 11, x750; 12, x500.
Figure 13.	*Grandispora velata* (Eisenack) Playford, 1971; x500.
Figure 14.	cf. *Grandispora velata*; x400.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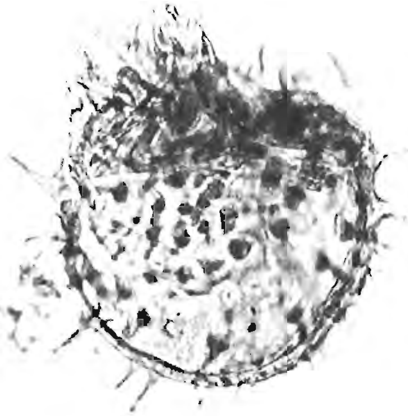
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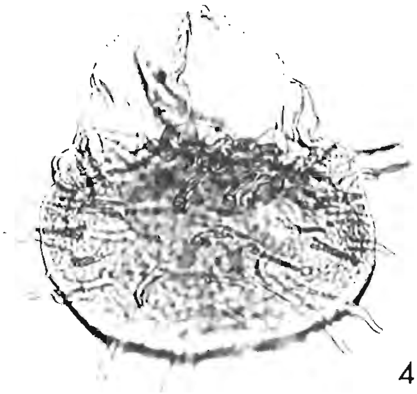
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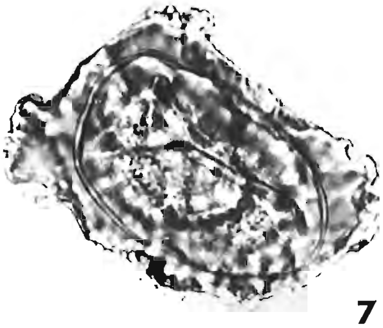
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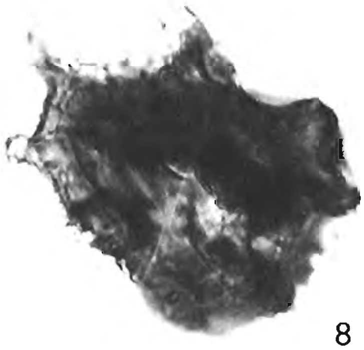
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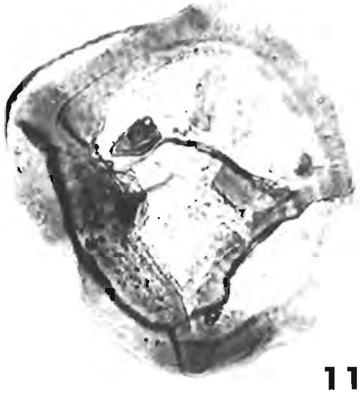
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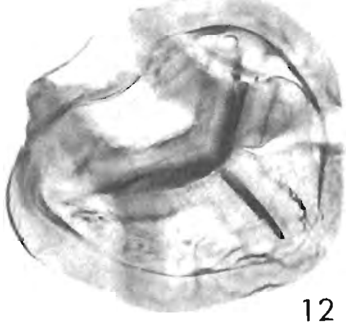
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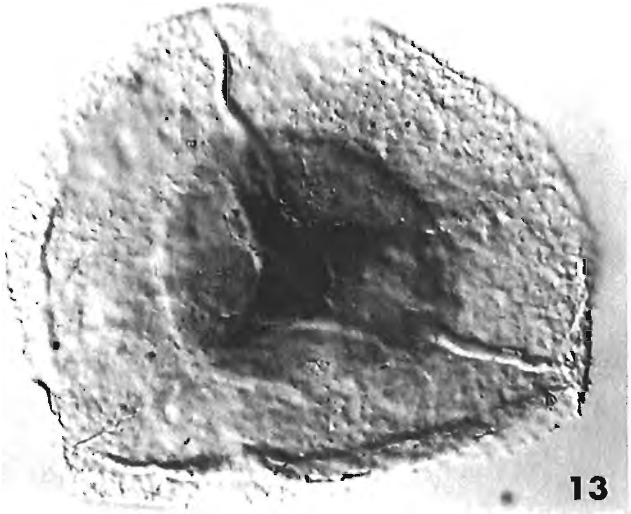
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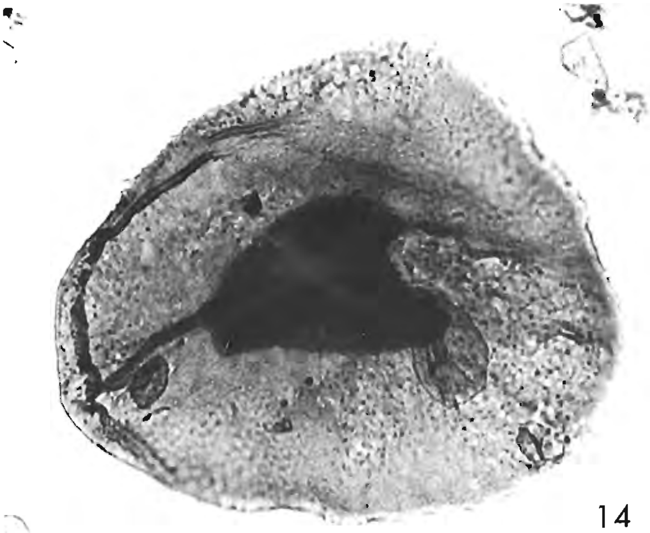
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PLATE 11

Figures 1, 2. *Retusotriletes digressus* Playford, 1976; 1, x750; 2, x500.

Figures 3, 4. *Retusotriletes punctimedianus* Balme, 1988; x750.

Figures 5, 6. *Rhabdosporites langii* (Eisenack) Richardson, 1960; x750.

Figures 7, 8. *Retispora lepidophyta* (Kedo) Playford, 1976; x750.

Figures 9, 10. *Retusotriletes biarealis* McGregor, 1964; x750.

Figures 11, 12. *Retusotriletes rugulatus* Riegel, 1973; x750.


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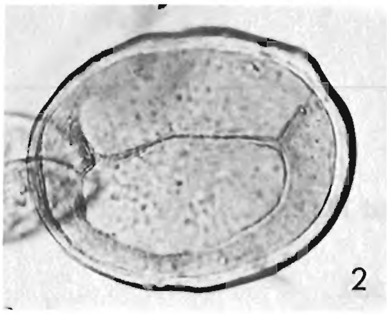
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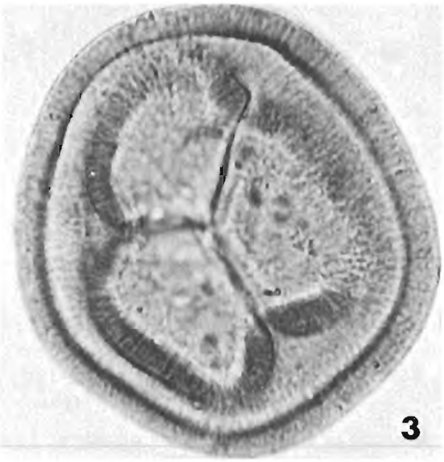
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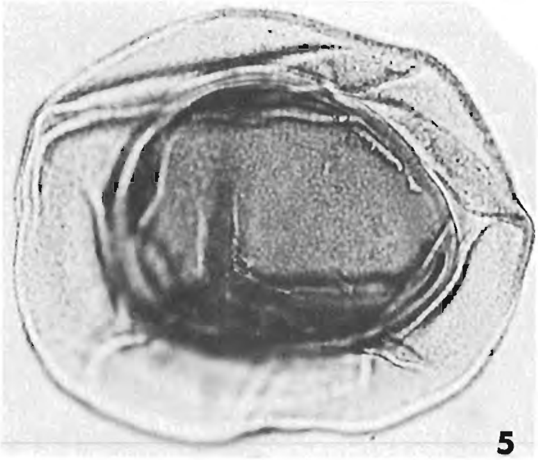
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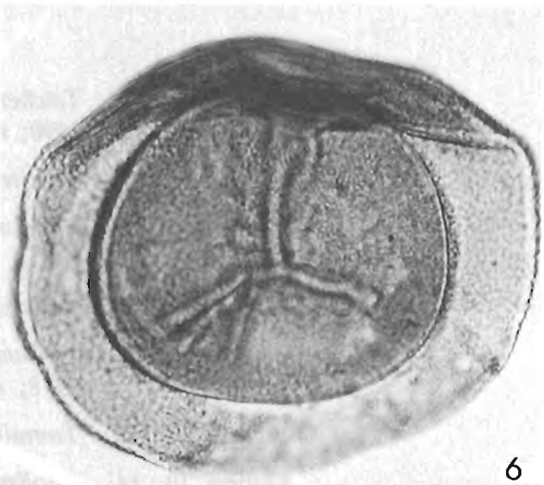
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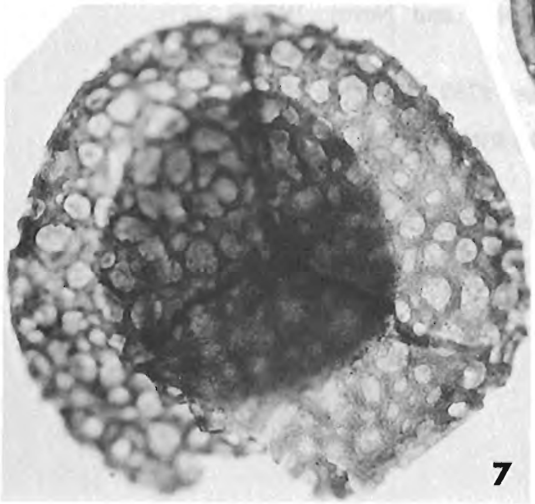
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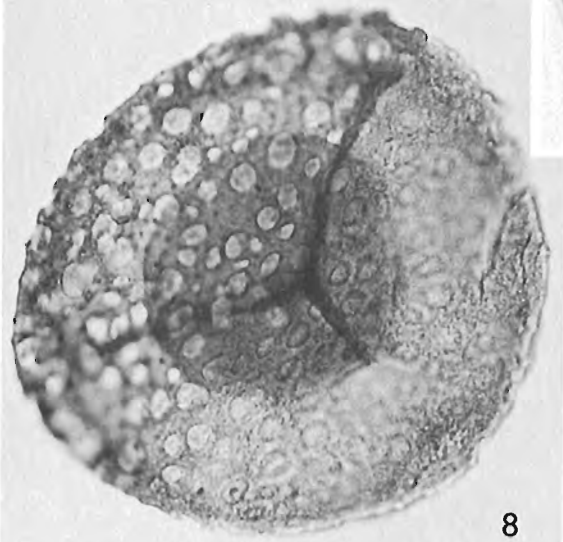
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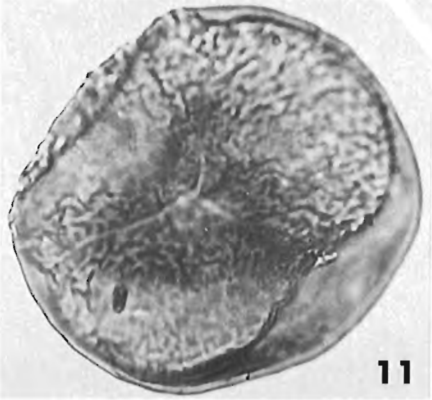
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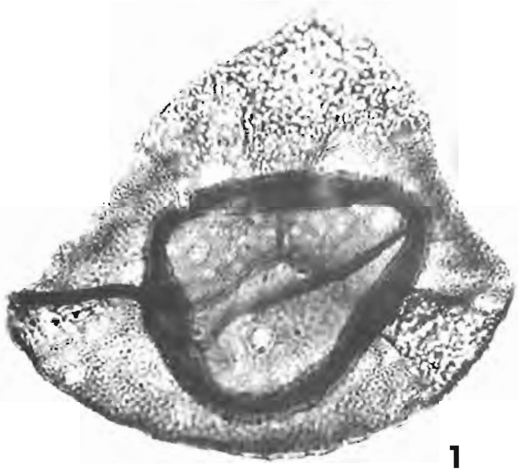
PLATE 12

Figures 1-4.	*Teichertospora torquata* (Higgs) McGregor and Playford, 1990; x500.
Figures 5, 6.	*Trileites langii* Eisenack, 1944; 5, x300; 6, x500.
Figure 7.	*Vallatisporites pusillites* (Kedo) Dolby and Neves, 1970; x750.
Figure 8.	*Vallatisporites* sp. cf. *V. pusillites*; x750.
Figures 9, 10.	*Verruciretusispora dubia* (Eisenack) Richardson and Rasul, 1978; x750.
Figures 11, 12.	*Tumulispora rarituberculata* (Luber) Playford, 1991; x750.
Figures 13, 14.	*Tholisporites tenuis* McGregor, 1960; x750.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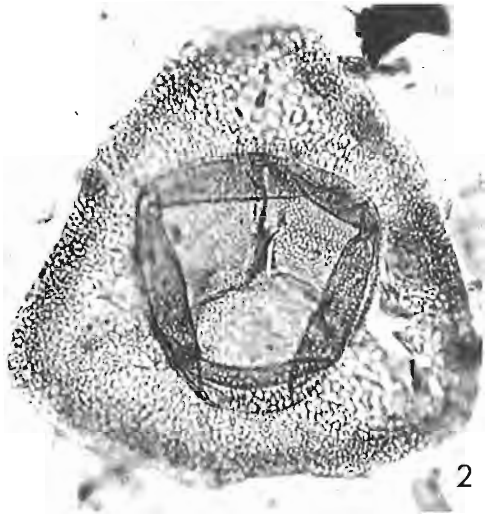
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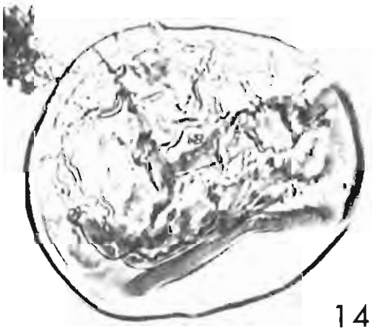
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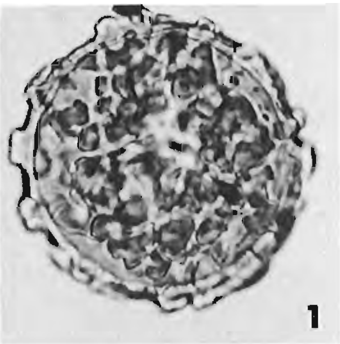
PLATE 13

Figures 1, 2a, b.	*Verrucosisporites scurrus* (Naumova) McGregor and Camfield, 1982; x750; 2a, proximal focus; 2b, distal focus.
Figures 3, 4.	*Verruciretusispora dubia* (Eisenack) Richardson and Rasul, 1978; 3, x500; 4, x750.
Figures 5, 6.	*Verrucosisporites premnus* Richardson, 1965; x750.
Figures 7, 8.	*Verrucosisporites nitidus* Playford, 1964; x750.
Figures 9, 10.	*Tholisporites densus* McGregor, 1960; x750.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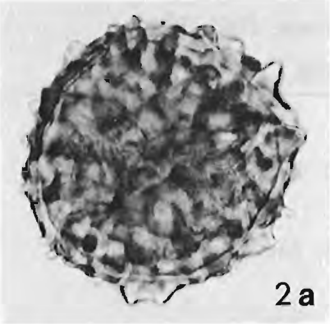
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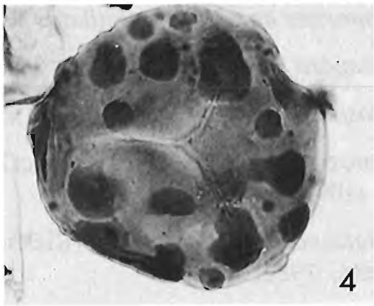
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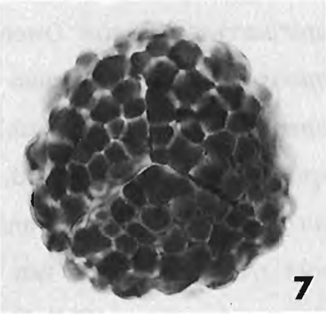
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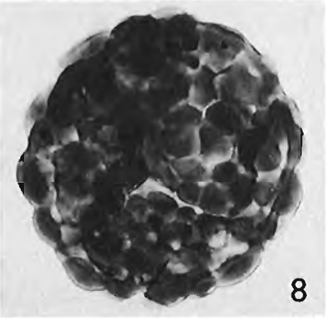
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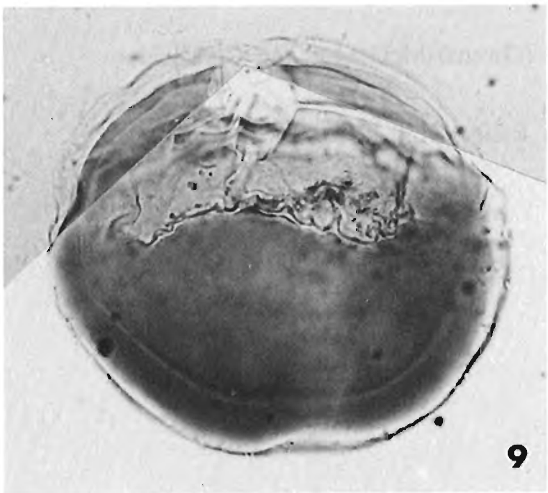
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PLATE 14

Figure 1. *Acinosporites acanthomammillatus* Richardson, 1965; x500.

Figure 2. *Ancyrospora eurypterota* Riegel, 1973; x500.

Figure 3. *Aneurospora goensis* Streel, 1964; x750.

Figure 4. *Diatomozonotriletes franklinii* McGregor and Camfield, 1982; x1000.

Figure 5. *Apiculatasporites microconus* (Richardson) McGregor and Camfield, 1982; x500.

Figure 6. *Archaeoperisaccus opiparus* Owens, 1971; x500.

Figure 7. *Archaeoperisaccus scabratus* Owens, 1971; x500.

Figure 8. *Archaeoperisaccus signus* Braman and Hills, 1985; x750.

Figure 9. *Archaeoperisaccus timanicus* Pashkevich, 1964; x500.

Figure 10. *Auroraspora pseudocrista* Ahmed, 1980; x500.

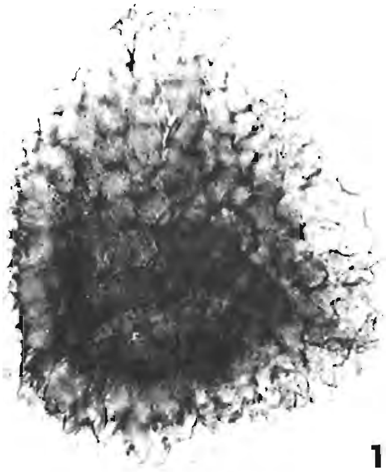
Figure 11. *Cornispora varicornata* Staplin and Jansonius, 1961; x750.

Figure 12. *Cyrtospora cristifera* (Luber) van der Zwan, 1979; x750.

Figure 13. *Contagisporites optivus* (Chibrikova) Owens, 1971 var. *optivus*; x750.

Figure 14. *Densosporites concinnus* (Owens) McGregor and Camfield, 1982; x500.

Figure 15. *Densosporites devonicus* Richardson, 1960; x500.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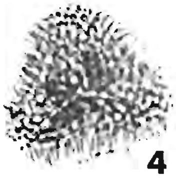
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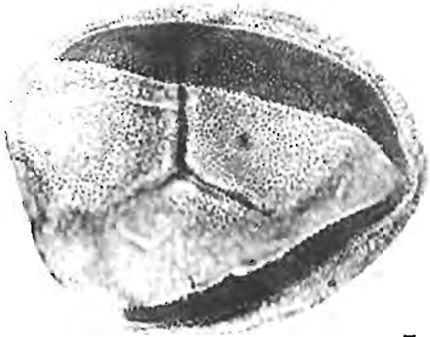
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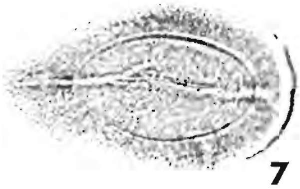
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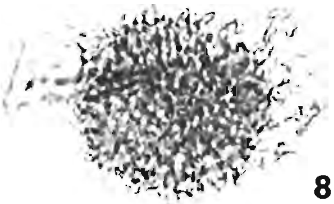
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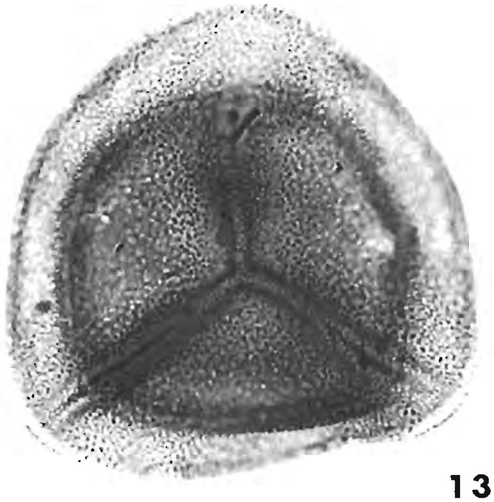
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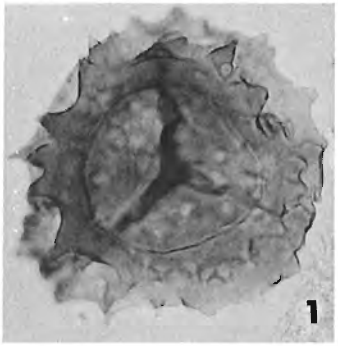
PLATE 15

Figure 1.	*Densosporites inaequus* (McGregor) McGregor and Camfield, 1982; x500.
Figure 2.	*Diaphanospora reticulata* Guennel, 1963; x750.
Figure 3.	*Diducites plicabilis* van Veen, 1981; x750.
Figure 4.	*Grandispora gracilis* (Kedo) Streel, 1974; x750.
Figure 5.	*Dibolisporites echinaceus* (Eisenack) Richardson, 1965; x500.
Figure 6.	*Elenisporis biformis* (Arkhangelskaya) Arkhangelskaya, 1985; x750.
Figure 7.	*Emphanisporites schultzii* McGregor, 1973; x1000.
Figure 8a, b.	*Geminospora* sp.; x500; 8a, proximal focus; 8b, distal focus.
Figure 9.	*Grandispora cornuta* Higgs, 1975; x750.
Figure 10.	*Grandispora tomentosa* Taugourdeau-Lantz, 1967; x500.
Figure 11.	*Lophotriletes devonicus* (Naumova ex Chibrikova) McGregor and Camfield, 1982; x1000.
Figure 12.	*Grandispora douglastownense* McGregor, 1973; x500.
Figure 13.	*Lanatisporis bislimbatus* (Chibrikova) Arkhangelskaya, 1985; x500.
Figure 14.	*Grandispora echinata* Hacquebard, 1957; x750.

PLATE 15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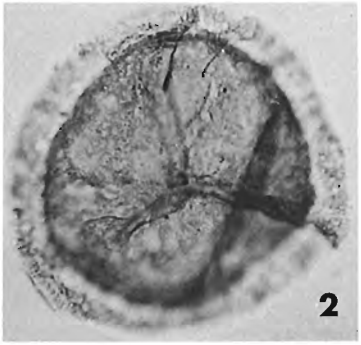
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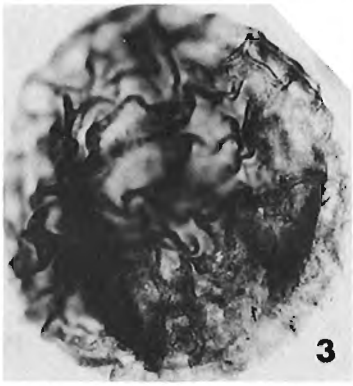
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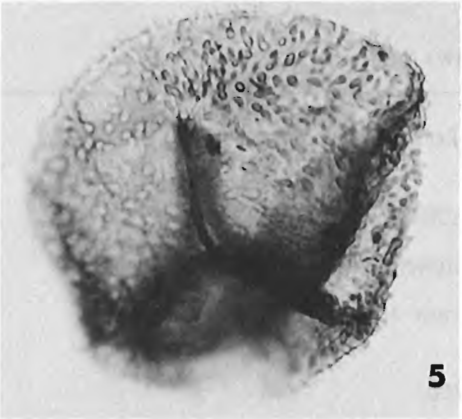
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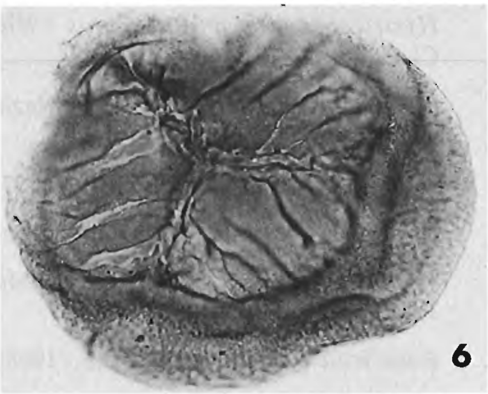
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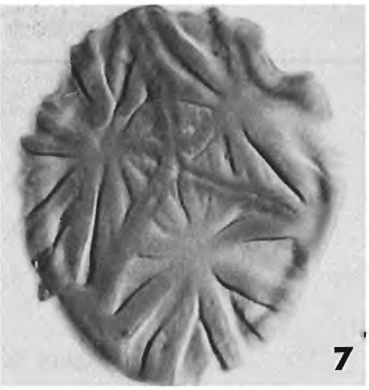
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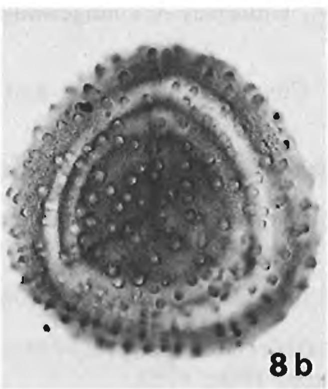
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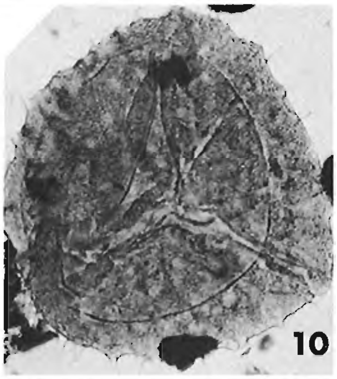
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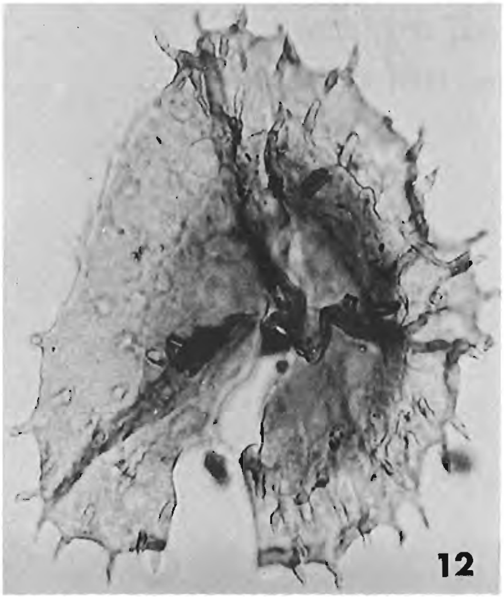
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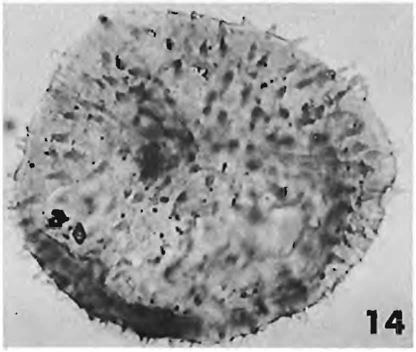
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PLATE 16

Figure 1.	*Hystricosporites multifurcatus* (Winslow) Mortimer and Chaloner, 1967; x500.
Figure 2.	*Hymenozonotriletes immensus* Nazarenko and Nekryata, 1971; x500.
Figure 3.	*Periplecotriletes tortus* Egorova, 1974; x500.
Figure 4.	*Retispora cassicula* (Higgs) Higgs and Russell, 1981; x750.
Figure 5.	*Kraeuselisporites rugosus* (Owens) McGregor and Camfield, 1982; x500.
Figure 6.	*Raistrickia corynoges* Sullivan, 1968; x750.
Figure 7.	*Sinuosisporis sinuosus* (V. Umnova) Arkhangelskaya, 1985; x500.
Figure 8.	*Retusotriletes phillipsii* Clendening, Eames, and Wood, 1980; x750.
Figure 9.	*Rugospora radiata* (Yushko) Byvsheva, 1988; x750.
Figure 10.	*Retispora archaelepidophyta* (Kedo) McGregor and Camfield, 1982; x500.
Figure 11.	*Perotrilites heclaensis* McGregor and Camfield, 1982; x750.
Figure 12.	*Verrucosisporites bulliferus* (Taugourdeau-Lantz) Richardson and McGregor, 1986; x750.
Figure 13.	*Hymenozonotriletes anthoideus* Sennova, 1971; x750.
Figure 14.	*Hymenozonotriletes celeber* Chibrikova, 1959; x500.

PLATE 16


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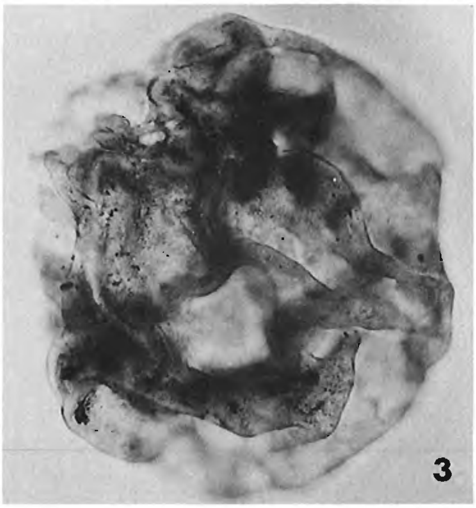
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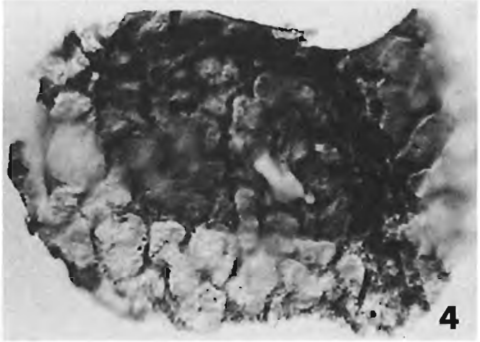
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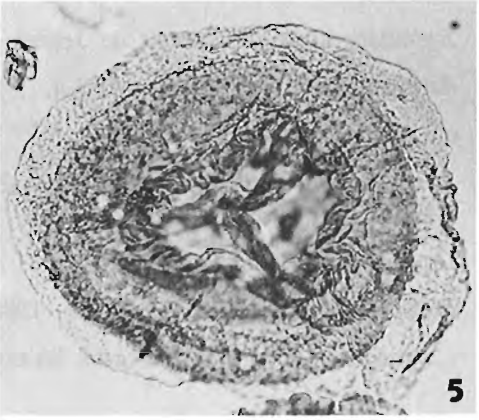
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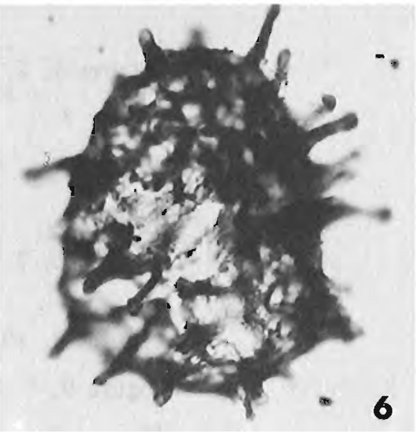
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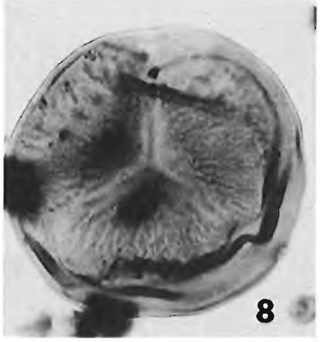
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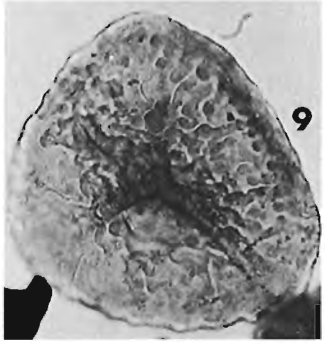
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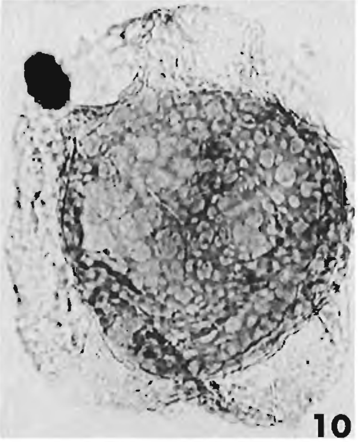
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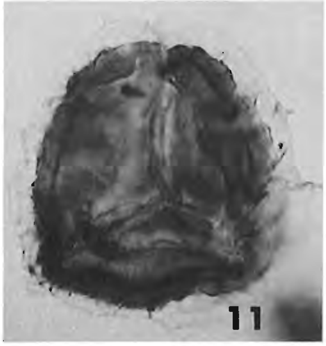
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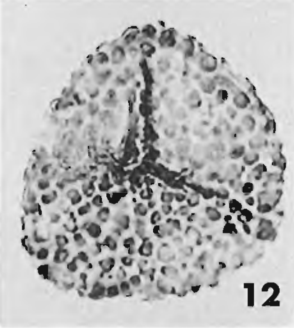
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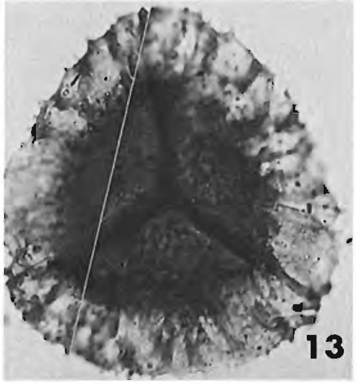
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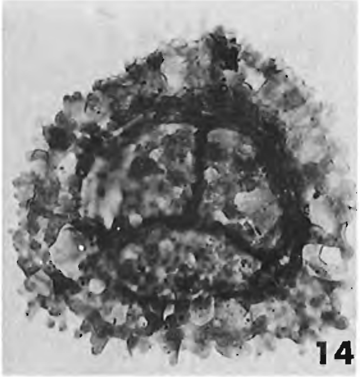
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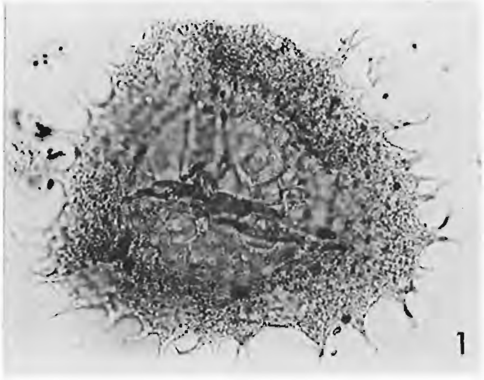
PLATE 17

Figures 1, 2.	*Ancyrospora* sp.; x500.
Figure 3.	*Apiculatisporis adavalensis* de Jersey, 1966; x500.
Figure 4.	*Archaeoperisaccus indistinctus* Lu, 1988; x500.
Figure 5.	cf. *Breconisporites* sp.; x750.
Figures 6, 7.	*Brochotriletes textilis* (Balme and Hassell) Playford, 1976; 6, x500; 7, x1000.
Figures 8, 10.	*Camptozonotriletes* spp.; x750.
Figure 9.	*Calyptosporites stolidotus* Balme, 1988; x500.
Figure 11.	*Calyptosporites proximocavatus* Balme, 1988; x500.

PLATE 17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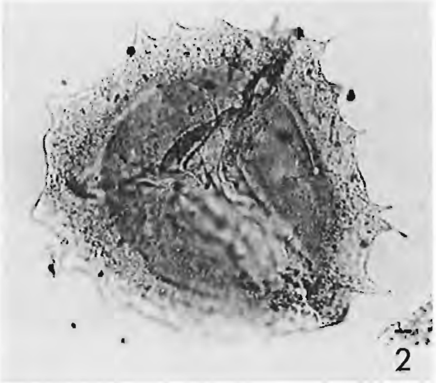
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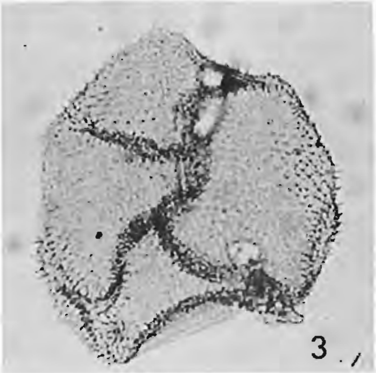
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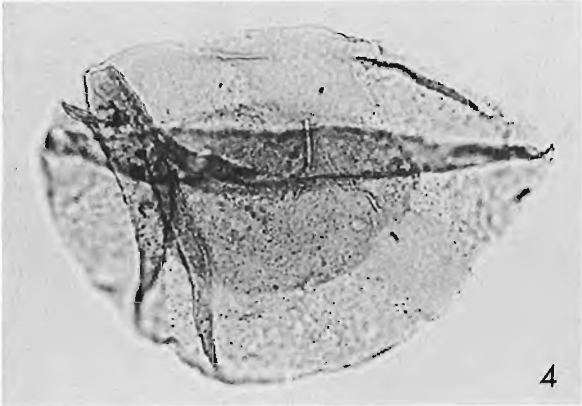
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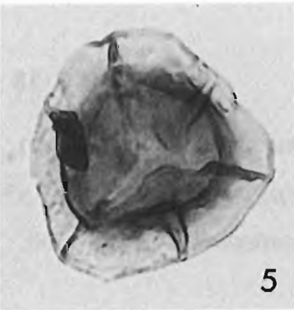
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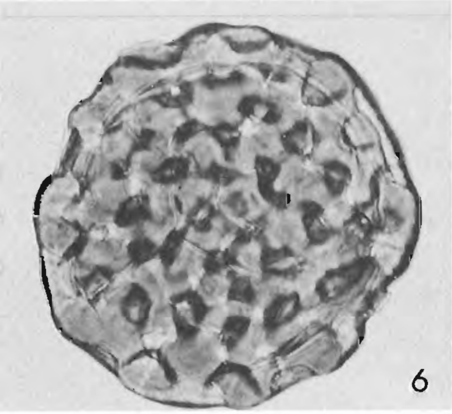
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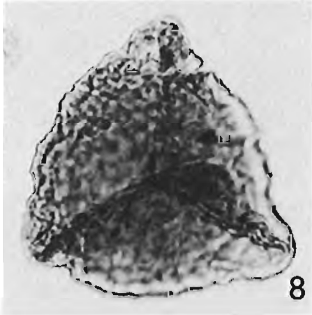
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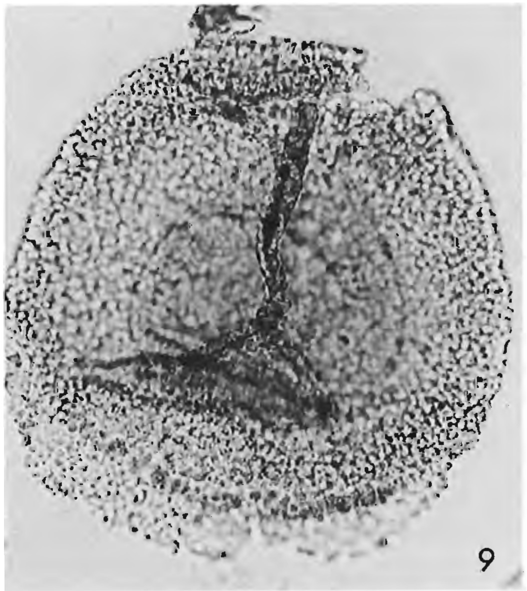
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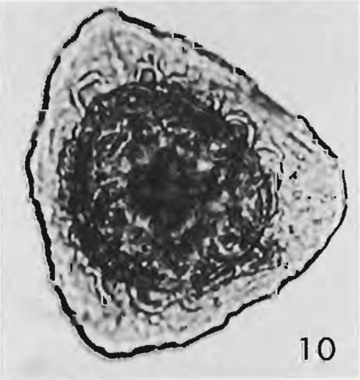
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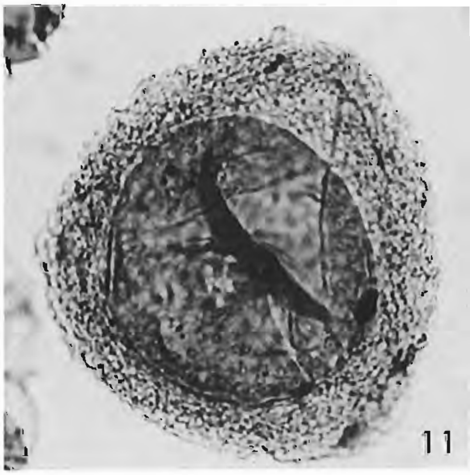
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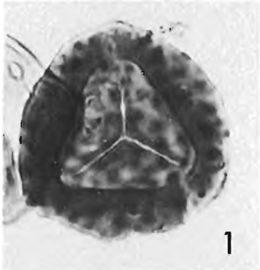
PLATE 18

Figures 1–5. *Camarozonotriletes* spp.; 1, 4, 5, x1000; 2, 3, x750.

Figures 6–10. *Camptozonotriletes* spp.; x750.

Figures 11–15. *Cristatisporites* spp.; x500.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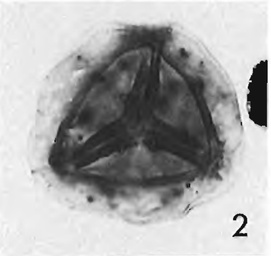
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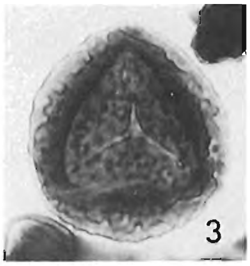
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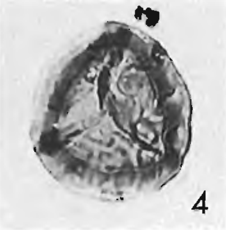
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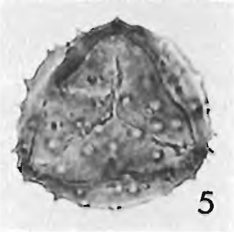
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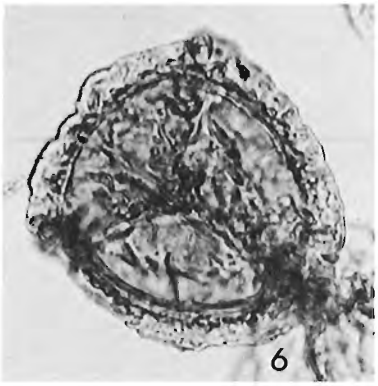
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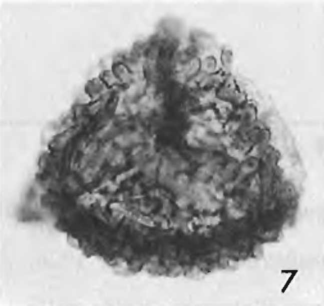
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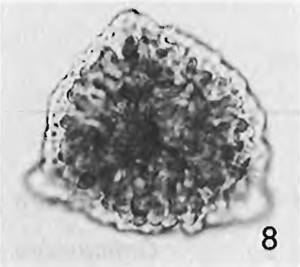
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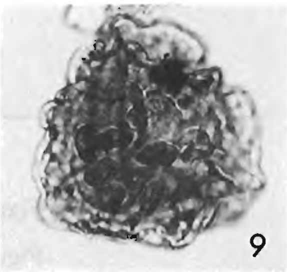
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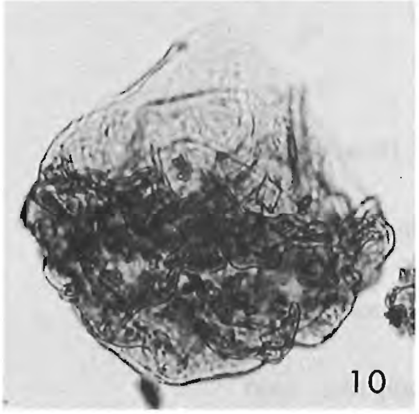
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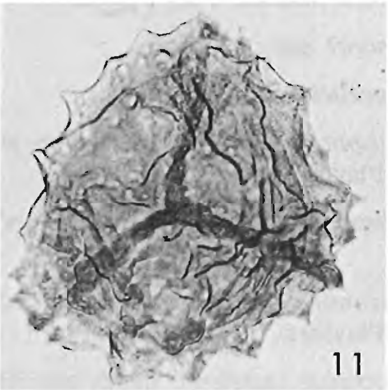
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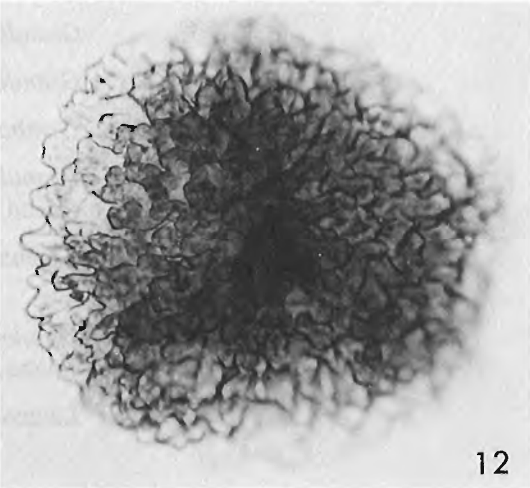
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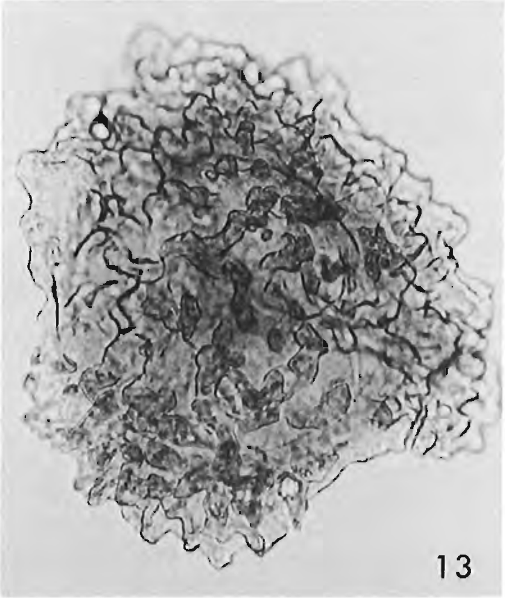
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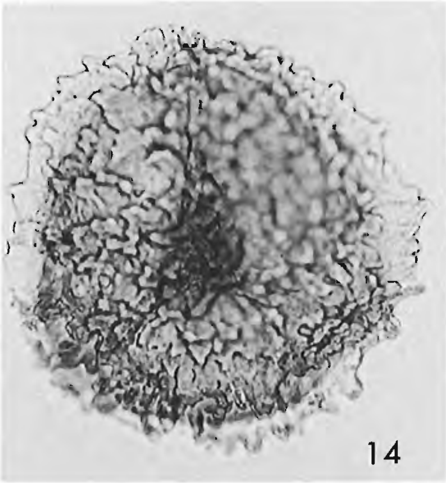
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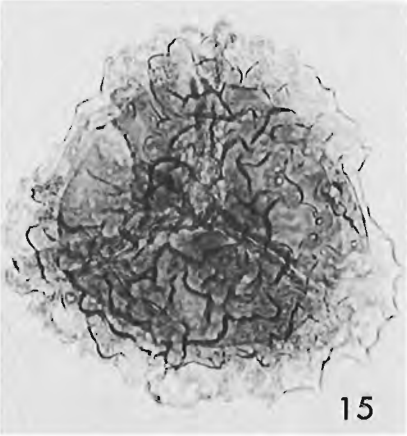
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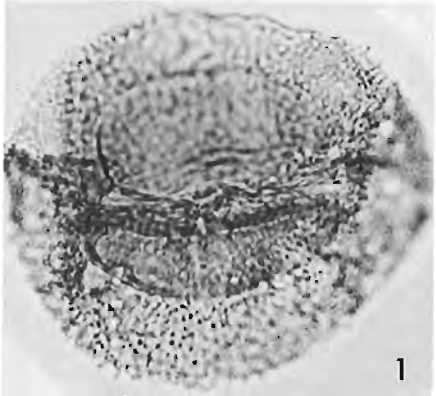
PLATE 19

Figure 1.	*Grandispora praecipua* Playford, 1976; x750.
Figure 2.	*Grandispora clandestina* Playford, 1976; x750.
Figure 3.	*Crassispora drucei* Playford, 1976; x500.
Figure 4.	*Grandispora* sp.; x750.
Figure 5.	*Grandispora notensis* Playford, 1971; x500.
Figures 6, 8.	*Grandispora*? spp.; x750.
Figure 7.	*Cymbosporites* sp.; x750.
Figure 9.	*Granulatisporites frustulentus* Balme and Hassell, 1962 emend. Playford, 1971; x750.
Figures 10, 13, 14.	*Kraeuselisporites* spp.; 10, x1000; 13, x750; 14, x500.
Figure 11.	*Hymenozonotriletes scorpius* Balme and Hassell, 1962 emend. Playford, 1976; x750.
Figure 12.	*Leiozonotriletes laurelensis* Balme and Hassell, 1962; x500.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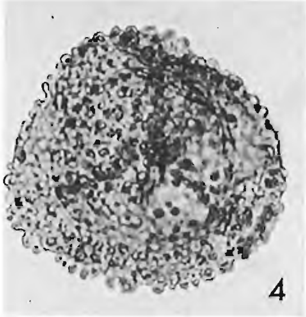
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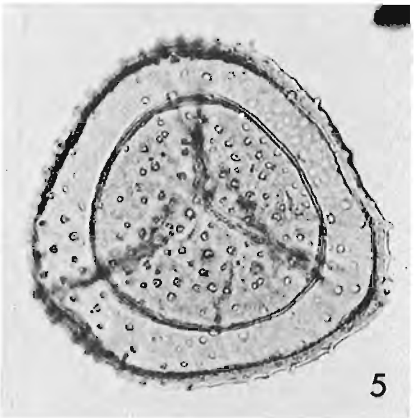
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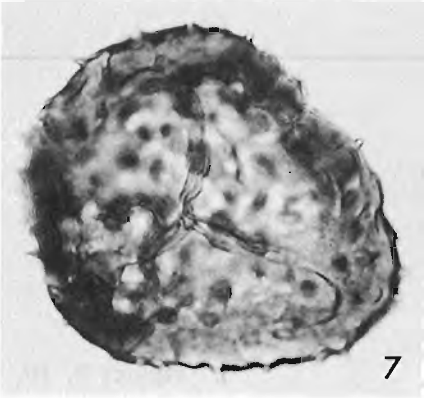
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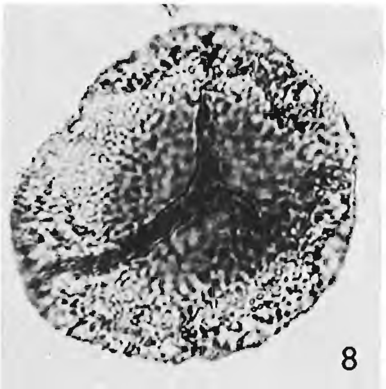
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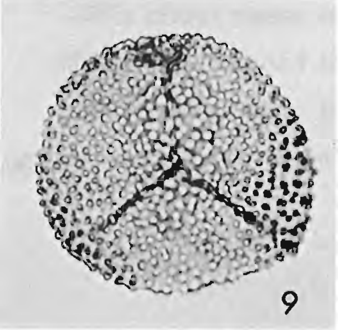
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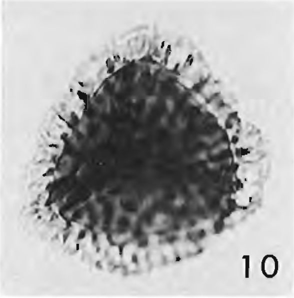
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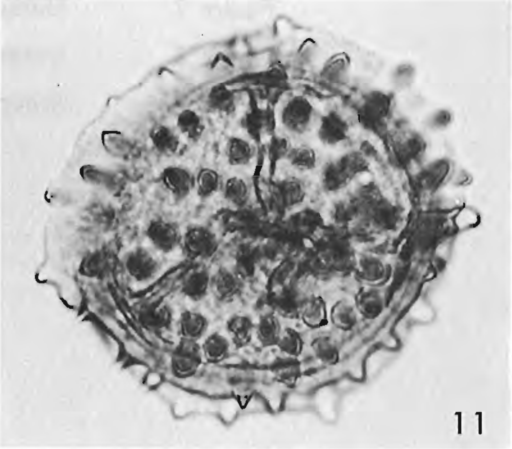
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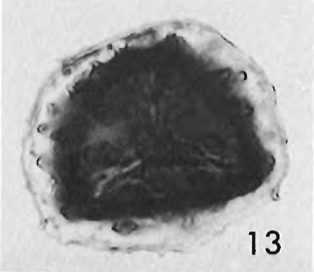
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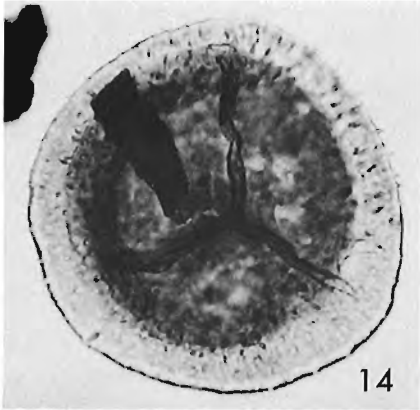
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PLATE 20

Figure 1.	*Retusotriletes* sp.; x500.
Figure 2.	*Rhabdosporites*? sp; x500.
Figure 3.	*Leiotriletes liebigensis* Hodgson, 1968; x750.
Figure 4.	Unidentified ?cavate spore; x750.
Figures 5, 10.	*Medusaspora dringii* Balme, 1988; x750.
Figure 6.	Unidentified zonate spore; x750.
Figure 7.	Unidentified baculate spore; x750.
Figure 8.	Unidentified cavate spore; x500.
Figure 9.	*Schopfites microverrucatus* de Jersey, 1966; x750.


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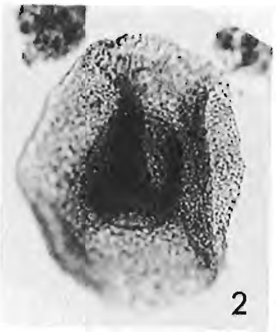
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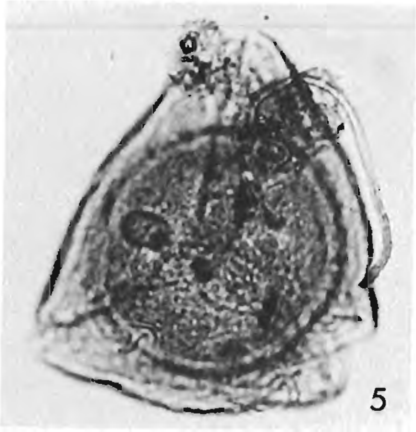
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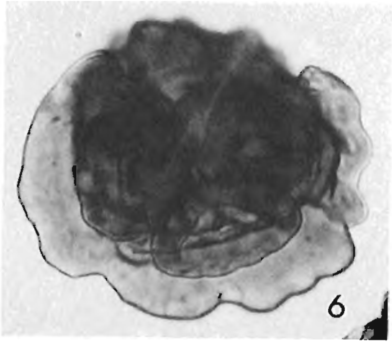
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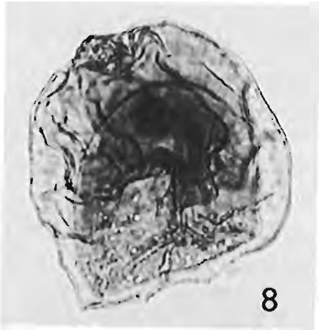
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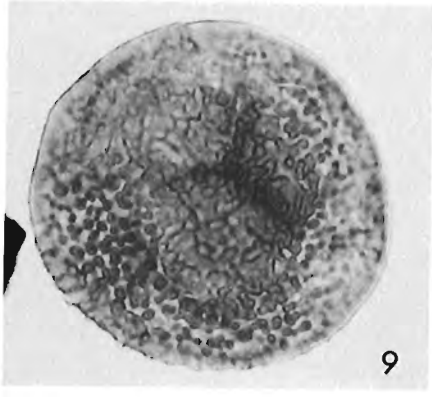
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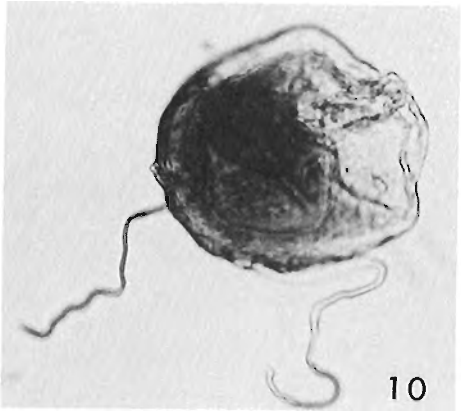
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