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Article abstract

Devonian strata of the present-day Arctic contain abundant and diverse assemblages of terrestrial palynomorphs, particularly from Middle and Upper Devonian sections; few intervals of Lower Devonian and Silurian strata have been palynologically studied, and these demonstrate strong palynofloral similarities across the region. Based on published records, we present a compilation of six last occurrence events (LOs), 44 first occurrence events (FOs) and one acme event that have proven of value in correlation in the present-day Arctic. Although their chronostratigraphic resolution is relatively low, and a scarcity of independent age control hampers precise age assignments, palynology is the only biostratigraphic discipline available for confident chronostratigraphic correlation of most Arctic Devonian strata.

Devonian palynoevents in the circum-Arctic region

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ABSTRACT

Devonian strata of the present-day Arctic contain abundant and diverse assemblages of terrestrial palynomorphs, particularly from Middle and Upper Devonian sections; few intervals of Lower Devonian and Silurian strata have been palynologically studied, and these demonstrate strong palynofloral similarities across the region. Based on published records, we present a compilation of six last occurrence events (LOs), 44 first occurrence events (FOs) and one acme event that have proven of value in correlation in the present-day Arctic. Although their chronostratigraphic resolution is relatively low, and a scarcity of independent age control hampers precise age assignments, palynology is the only biostratigraphic discipline available for confident chronostratigraphic correlation of most Arctic Devonian strata.

RÉSUMÉ

Les strates dévoniennes de l'Arctique d'aujourd'hui abritent des assemblages abondants et diversifiés de palynomorphes, terrestres, en particulier des sections du Dévonien moyen et supérieur. Quelques intervalles de strates du Dévonien inférieur et du Silurien ont fait l'objet d'études palynologiques et celles-ci ont révélé des similarités palynoflorales marquées à l'échelle de la région. Nous basant sur des documents publiés, nous présentons une compilation des six dernières occurrences (DO), des 44 premières occurrences (PO) et d'un phénomène d'abondance s'étant avérés utiles pour la corrélation dans l'Arctique d'aujourd'hui. Même si leur résolution chronostratigraphique est relativement faible et que la rareté des contrôles indépendants de la datation gêne l'attribution d'âges précis, la palynologie est la seule discipline biostratigraphique dont nous disposons pour l'établissement d'une corrélation chronostratigraphique sûre de la majorité des strates dévoniennes arctiques.

[*Traduit par la redaction*]

INTRODUCTION

This article is a contribution to the Circum-Arctic Palynological Events (CAPE) project, providing a scheme of selected events for the Devonian in the present-day Arctic. The Devonian Period, extending from 419 to 359.3 Ma (Becker *et al.* 2020), is a particularly interesting time in Earth history: it saw the establishment of the terrestrial carbon cycle with the origin and spread of the first forests; their deeply rooting plants had many implications for the Earth System. In addition, it witnessed the world's largest-known and most geographically widespread reefs, together with two first order mass extinctions, the later episode terminating the Devonian Period (Becker *et al.* 2020). The Devonian is divided into three series and seven stages: the Lower Devonian comprises the Lochkovian, Pragian and Emsian stages; the Middle Devonian includes the Eifelian and Givetian stages; and the Upper Devonian is composed of the Frasnian and Famennian stages. The Devonian, like the Silurian, had its stages defined early in the development of the modern geological time scale, the last-designated Global Boundary Stratotype Section and Point (GSSP) being for the base of the Emsian (Yolkin *et al.* 1998). Two of these stages are abnormally long: the Emsian and Famennian are 16.21 and 11.8 myr respectively.

The fossils most commonly used for stratigraphic correlation in the Devonian are conodonts and, following their earliest occurrence in the lower Emsian, ammonoids. Spores have also been widely employed in the Devonian, particularly in terrestrial and nearshore marine facies. Only two spore zonal schemes cover the entire Devonian. That by Richardson and McGregor (1986), which is based on assemblages and marker taxa, is particularly relevant here as it incorporates many sections from Arctic Canada. That of

Streel *et al.* (1987) is of higher resolution but is based on the classic European sections. In addition, that by Avkhimovitch *et al.* (1993) covers the late Emsian to late Famennian interval and includes many near-Arctic sections. Devonian palynological assemblages also include acritarchs, prasinophytes and chitinozoans, and these have proved very useful in stratigraphy. This is evident from the single comprehensive study of Devonian acritarchs by Playford (1977) from the sub-Arctic, which was done in parallel to that of McGregor and Camfield (1976) from the same samples.

The present Devonian compilation will complement those for other periods in the CAPE series. When all papers in the series are complete, the data will be provided as a "CAPE datapack" in Time Scale Creator (TSC; https://timescalecreator.org/index/index.php) and thus can be used with other data in TSC to make plots like that shown in Figure 1 (Bujak *et al.* 2021). Figure 1 includes the age calibration in millions of years (Ma) according to the 2020 version of TSC and Gradstein *et al.* (2020).

The events compiled herein include last occurrences (LOs), first occurrences (FOs), and an abundance event. Where possible, each event is correlated with the base of a chronostratigraphic unit, for example an ammonoid zone or a stage. If the event is not equivalent to the base of such a unit, then an estimation is given as a percentage above the base of the chronostratigraphic unit relative to the entire unit. Details of how a biostratigraphic datapack is constructed in TSC from such information are given in Bringué *et al.* (in press). Localities used for the present compilation are shown in Figure 2. Figure 1 gives a summary of zonation schemes discussed in the following section and referenced in the Palynoevents section.

PALYNOSTRATIGRAPHY

Devonian spore assemblages from the Arctic represent equatorial paleolatitude assemblages and differ from those from higher paleolatitudes where most of the calibration with marine invertebrate faunas (conodonts and ammonoids) has been based. Apart from parts of northern Russia, invertebrate zonations with zone index range bases tied to concurrent palynological zones have not been developed, and available information is generally restricted to single samples. In addition, conodont faunas are limited due to a lack of the favourable facies. This is not from lack of effort, as McGregor (1979), Streel *et al.* (1987) and others have emphasized the importance of independent age control.

A problem is a lack of studied sections from the Silurian and Early Devonian from the Arctic. Such sections exist — for example, the Silurian marine margin basin in North Greenland (Christiansen 1989). Reconnaissance studies by Nøhr-Hansen and Koppelhus (1988) and Nøhr-Hansen (1989) show that this basin contains Late Ordovician and Silurian spores, acritarchs and chitinozoans, but detailed studies are lacking. Early Devonian sections in Arctic Canada with spores have been studied (McGregor 1974; McGregor

and Narbonne 1978). Also, thick Early Devonian sections exist in Svalbard, but early workers (Allen 1967) struggled to get good palynological recovery from them. This situation is now being rectified, with good spore recovery from the Lochkovian and clear potential for the establishment of a local zonation scheme (Wellman *et al.* 2022). Early Devonian sections are unknown in East Greenland and the Timan (Komi Republic) in Russia as the sedimentary basins from these regions only developed to any extent in the Middle Devonian (Larsen *et al.* 2008; O'Leary *et al.* 2004), primarily following upper Middle Devonian tectonic extension.

Devonian spores of Arctic Canada

In the Canadian Arctic Islands palynological research began with the separation of megaspores (Chaloner 1959) and spores (McGregor 1960) from single coal samples held in the archives of the Geological Survey of Canada, leading to the description of several important new taxa. Papers describing Canadian Arctic assemblages (McGregor and Owens 1966; McGregor 1967) include several early stratigraphical applications (Kerr *et al.* 1965), and they illustrated the microfloras before their formal taxonomic documentation was established. In addition, McGregor (1969) provided a significant contribution on the important and related microspore and megaspore genera *Archaeoperisaccus* and *Nikitinsporites*. The first substantive monograph (Owens 1971) was based on 20 samples Eifelian to Frasnian samples, describing new stratigraphically important genera and species. These taxa included the distinctive grapnel-tipped spore *Ancyrospora*, subsequently reviewed by Owens *et al.* (2022) in a pan-Arctic study incorporating specimens of related Russian species unavailable for the original monograph.

Significant work was also done on sections on Melville Island, with parallel studies on conodonts (McGregor and Uyeno 1972); the palynological work appeared as partial range charts (McGregor 1981), a monograph (McGregor and Camfield 1982), and a stratigraphic summary in McGregor (1994), with additional information in Richardson and McGregor (1986). Although not found in a continuous section, the *Elenisporis biformis* Subzone was recognized from Ellesmere Island (Arkhangelskaya *et al.* 1990). The latter zone, dated as early Eifelian, was originally defined from western Russia and Belarus (Arkhangelskaya 1985). A contribution by Whiteley (1980) was based on cuttings samples from the Key Point well on the Parry Islands. Of the two assemblages identified, the upper assemblage containing *Archaeoperisaccus* spp. and bifurcate tipped spores was broadly assigned a Frasnian age, and the lower assemblage, dominated by the larger zonate and camerate spores such as *Grandispora* spp., assigned a late Givetian age.

The first stratigraphic study of megaspores was by Hills *et al.* (1971) from northeastern Banks Island, now in Nunavut. This theme was further developed in a major taxonomic study of megaspores (Chi and Hills 1976a, b) from multiple sections on Banks, Melville and Prince Patrick islands, partly from the same intervals covered by McGregor and
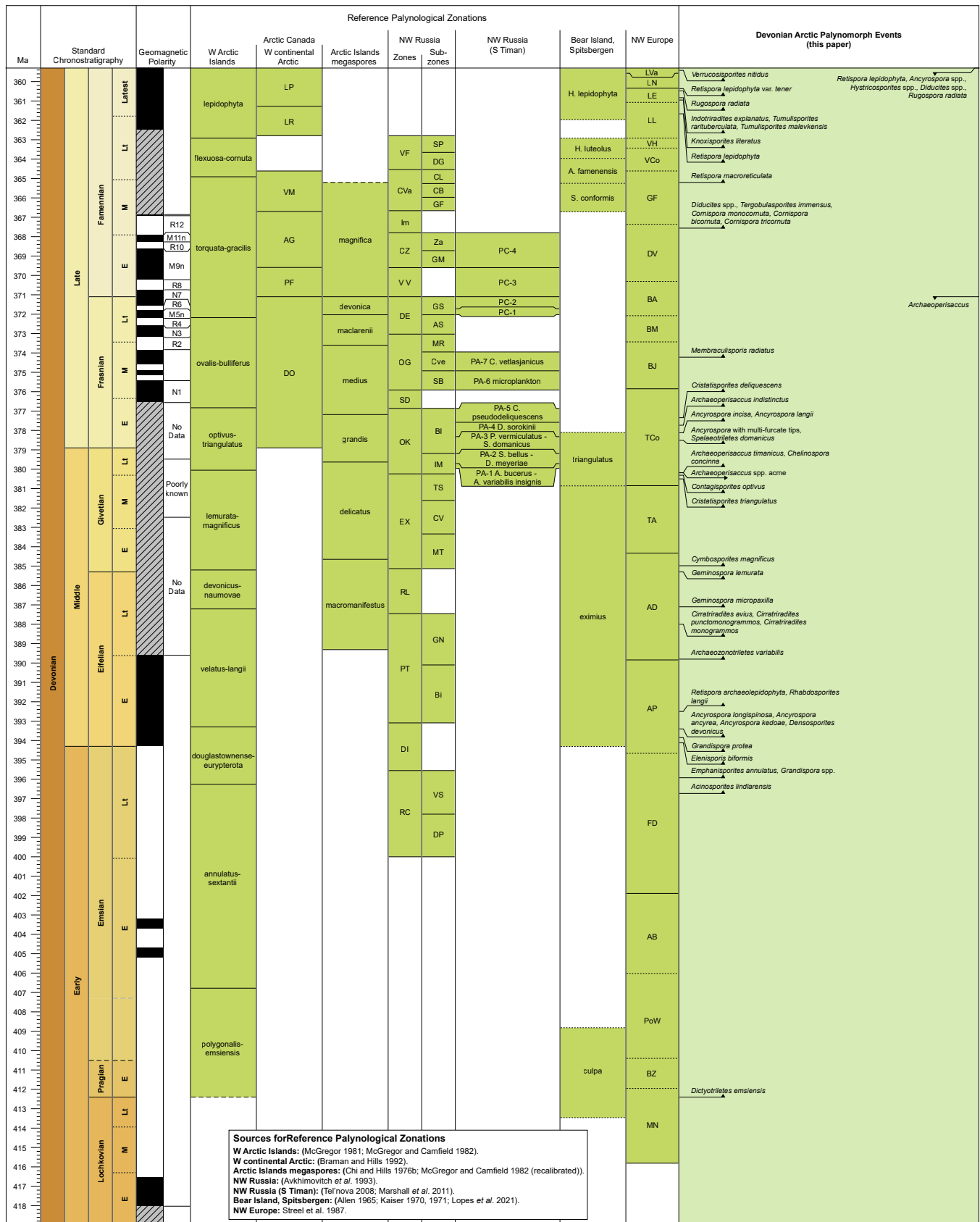
Figure 1. Chronostratigraphic plot generated using TSC showing stratigraphically significant Devonian palynological events together with Arctic and a northeastern European palynological zonation. Columns to the left of the "Reference Palynological Zonations" column are from TSC: broken lines suggest degrees of uncertainty (dashed = probable and dotted = possible). W = western; NW = northwestern; S = southern.
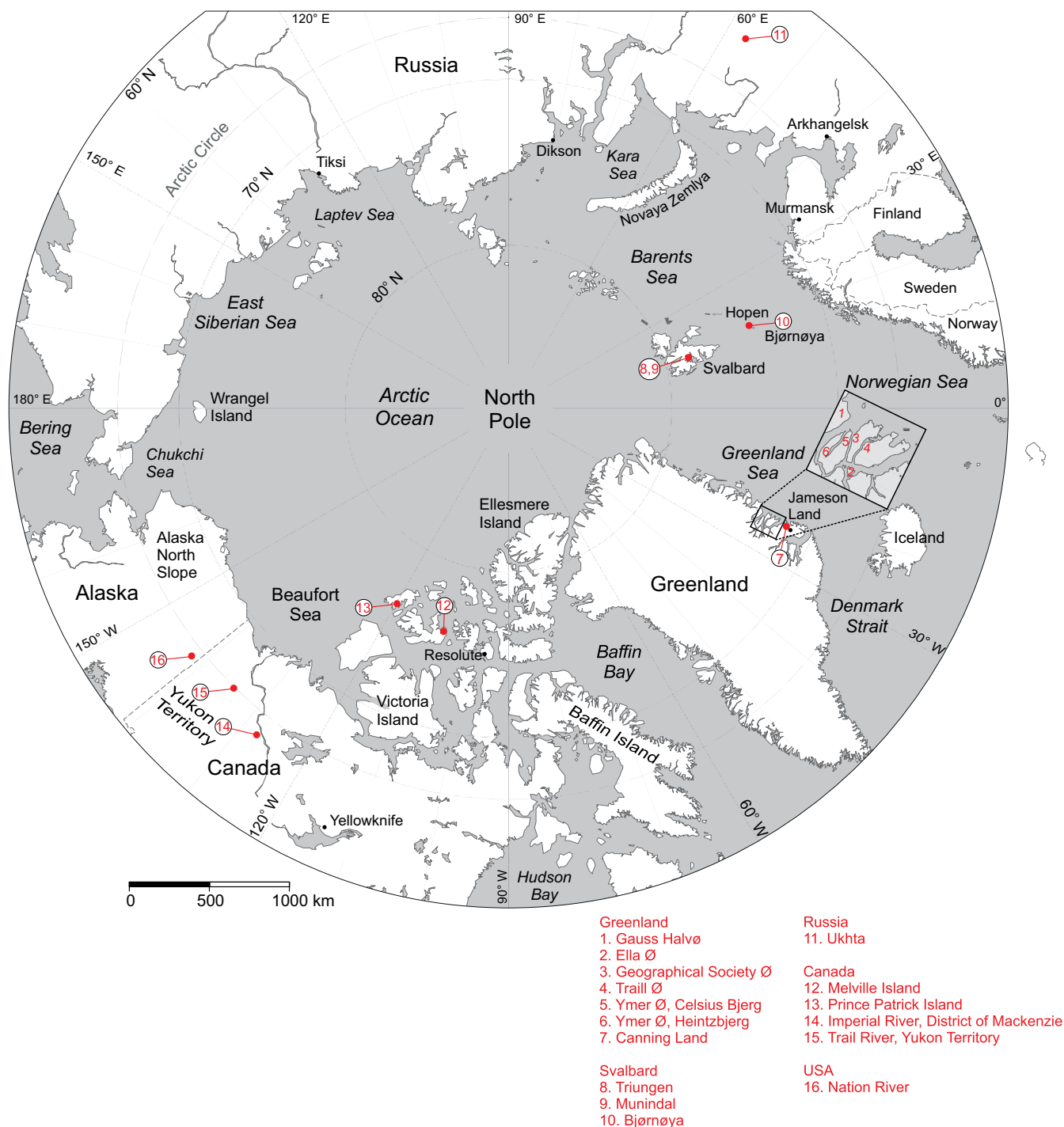
Greenland
1. Gauss Halvø
2. Ella Ø
3. Geographical Society Ø
4. Traill Ø
5. Ymer Ø, Celsius Bjerg
6. Ymer Ø, Heintzbjerg
7. Canning Land

Svalbard
8. Triungen
9. Munindal
10. Bjørnøya

Russia
11. Ukhta

Canada
12. Melville Island
13. Prince Patrick Island
14. Imperial River, District of Mackenzie
15. Trail River, Yukon Territory

USA
16. Nation River

Figure 2. Circumpolar projection map showing the main Devonian localities discussed herein.

Camfield 1982). Chi and Hills (1976) erected seven mega-spore zones for the Middle and early Late Devonian. These are shown in Figure 1, which also includes the important chronostratigraphic recalibration of these zones by McGregor and Camfield (1982). Subsequently, a series of taxonomic and stratigraphic papers from northern Canada (from locations now in Nunavut and the Northwest Territories sensu stricto — the latter formerly District of Mackenzie) by Chi and Hills (1974), Hyslop and Hills (1982) and Hills *et al.* (1984)

used the same zonation. A major monograph (Braman and Hills 1992) included multiple sections from the Frasnian to Tournaisian in the Northwest Territories (sensu stricto) and Yukon. Braman and Hills proposed six Devonian spore zones, albeit with a middle to late Famennian stratigraphic gap. They recognized the significance of a middle Famennian zone (VM) with *Cornispora* spp. that puts in context the earlier contribution of Van der Zwan and Walton (1981). In addition Braman and Hills (1985) produced a largely

taxonomic paper on the zonally important and distinctive monolete spore *Archaeoperisaccus*, which is generally restricted to the Frasnian Stage and the present-day Arctic. No Devonian/Carboniferous boundary sections are preserved in the Canadian Arctic Islands, there being a general stratigraphic gap from about the middle Famennian up into the Visean (Utting *et al.* 1989). The Yukon sections of Braman and Hills (1992) do have a Devonian/Carboniferous boundary section but with a late Famennian stratigraphic gap between their VM and LR spore zones, consequently involving a delayed range base to *Retispora lepidophyta*.

Devonian spores of Alaska

A single data point from Alaska (Scott and Doher 1967), Frasnian in age, includes such distinctive spores as *Archaeoperisaccus* cf. *timanicus*, *Cristatisporites triangulatus*, *Contagisporites optivus* and possibly *Cymbosporites*.

Devonian spores of Greenland

Initial palynological studies from East Greenland by K.C. Allen were included in a review in Friend *et al.* (1983). Other publications focused on megaspores, including seed-megaspores and their paleobiological significance (Allen 1972). This seed-megaspore work was continued by Marshall and Hemsley (2003) who described an important early seed-mega-spore from the Givetian of Ella Ø (Ø means island), and the accompanying spore assemblage. Marshall and Astin (1996) gave a brief account of Eifelian and Givetian spores from Canning Land, including recognition of the first occurrence of the base-Givetian marker *Geminospora lemurata*. Vigran *et al.* (1999) published a palynostratigraphic scheme for the Carboniferous of East Greenland that included two zones (the *Retispora lepidophyta* Abundance Zone and the *Spelaeotriletes* spp. – *Lophozonotriletes malevkensis* Concurrent Range Assemblage) within the latest Devonian. Marshall *et al.* (1999) reported on additional palynological assemblages from the late Famennian that resolved a dating controversy involving East Greenland early tetrapods. The Devonian/Carboniferous boundary was picked within the Obrutschew Formation and further defined by Streel and Marshall (2006) and Marshall (2021). A much more detailed account was provided in the Supplementary Material (SM) of Marshall *et al.* (2020); their discussion of the Devonian/Carboniferous boundary terrestrial mass extinction was accompanied by a range chart and spore illustrations for the latest Famennian inter-val, including recognition of the spore LL, LE, LN* and VI zones.

Devonian spores of Svalbard

The first Devonian palynological work, spanning the period, was from Spitsbergen, Svalbard (Høeg 1942). This study was unusual for its time in that spores were described both from within sporangia and dispersed in the enclosing sedimentary rocks. The first specifically palynological paper was by Vigran (1964), who described spore assemblages from five late-Middle Devonian samples from the Mimerdalen area of Dickson Land, including a number of important new species (e.g., *Lycospora svalbardiae* — now *Geminospora svalbardiae*). These species have tended to be overlooked in synonymies, but their publication predates both Richardson (1965) and Allen (1965). Allen (1965, 1967, 1973) made a significant contribution in a study of both Early and Middle Devonian spores from Dickson Land (including Mimerdalen) in central Vestspitsbergen. In addition, Allen (1967) sampled numerous localities in Andrée Land, but found only rare, poorly preserved spores.

The Mimerdal sections were later investigated via a series of boreholes (Pčelina *et al.* 1986) from which several palynological assemblages were documented. Results from this work were later incorporated into Piepjohn and Dallman (2014).

Additional spores, including the first assemblages from Andreé Land, were illustrated in Schweitzer's (1999) review of the Spitsbergen Devonian flora. These later contributions concluded that the Mimerdal sequence was as young as latest Famennian based on the occurrence of *Retispora lepidophyta*. This conclusion was challenged by Berry and Marshall (2015) based on detailed resampling through the Planteryggen and Plantekløfte formations. These authors noted that the specimen of *Retispora lepidophyta* (now lost, but illustrated in Schweitzer 1999, Plate 6, fig. 10, Plate 7, fig. 1) was much larger than typical specimens, and that it had square fovea that were in fact pits caused by pyrite cubes in a specimen of *Grandispora*. Berry and Marshall (2015) also demonstrated that, from their detailed palynological and palaeobotanical analyses of the Mimerdal successions, robust correlations could be drawn to established conodont-controlled sections in Poland (Turnau and Racki 1999), as well as to the PA-3 Zone from the Timan, Russia (Tel'nova 2008) (Fig. 1). Berry and Marshall also noted that the black mudstone unit 6 of Vogt (1941), now at the base of the Fiskekløfte Member of Piepjohn and Dallman (2014), was equivalent to the late Givetian Taghanic Onlap.

The age of the Hørbyebreen Formation has been difficult to establish, estimates ranging from Famennian to Visean (Dallmann *et al.* 1999). However a key section, rediscovered during a search for early tetrapods on Triungen is a thin (~45 m) succession unconformably overlying the Emsian Wood Bay Group, and was found to contain a diversity of *Cornispora* spp. that correlate with CB Subzone of the CVa Zone (Avkhimovitch *et al.* 1993) of middle Famennian age (Marshall *et al.* 2015). This key section is unconformably succeeded by a Visean section (Lopes *et al.* 2019). A single sample from a similarly thin sequence was reported from Lomfjorden by Scheibner *et al.* (2012), and this again contained the middle Famennian *Cornispora*/*Cyrtospora* assemblage.

Palynological work on the Devonian of Bjørnøya began with descriptions of megaspores by Nathorst (1902), updated and refigured by Sen (1958). The Bjørnøya sequence has always attracted interest as it includes the then-earliest-

known commercially mined coals, which were well documented in a monograph by Horn and Orvin (1928). Spores from Bjørnøya were initially studied by Playford (1962), and were subsequently monographed by Kaiser (1970, 1971) and integrated with the paleobotanical studies of Schweitzer (1967, 1969). The spores are at a high level of thermal maturity and are not well preserved, having mineral damage. The important Bjørnøya section was resampled and restudied by Lopes *et al.* (2021), who reinterpreted the palynological assemblages with the advantage of decades of palynological studies on Devonian/Carboniferous boundary sections. These authors were able to identify and revalidate Kaiser's (1970, 1971) zonation, and also recognized the parallel zonation developed within both eastern and western Europe. Lopes *et al.* found that the *Cornispora* assemblage was present and thus permitted recognition of the Cva Zone (Avkhimovitch *et al.* 1993), together with the overlying VF Zone. Above this zone level, correlations are with western Europe, and the section includes the first occurrence of *Retispora lepidophyta* and forms allowing recognition of the upper LL to LN zones. The latter zonal attribution is based on the presence of *Indotriradites explanatus* in some sections, together with *Retispora lepidophyta* var. *minor*, which is characteristic of the *tener* event (Prestianni *et al.* 2016). Some differences in the Bjørnøya section are apparent, with *Tumulispora malevkensis* having an apparent earlier first occurrence than in western Europe. It remains unclear whether this difference is related to the more humid conditions in this paleoequatorial location.

Devonian spores of Russia

Spore assemblages from Russia occupy a special place in the study of Devonian palynology, particularly with respect to the Arctic. The systematic study of Devonian spores, motivated by the need to improve understanding of Devonian hydrocarbon reservoirs, started in Russia. A series of significant monographs, starting with that by Naumova (1953), has resulted in a unified zonation scheme (Avkhmovitch *et al.* 1993) for the Russian Platform. The scheme incorporates the same paleoequatorial palynological assemblages as found in Arctic Canada, Greenland and Svalbard. Moreover, these sections include prolific faunas of ammonoids (Becker *et al.* 2000; House *et al.* 2000) and conodonts (Ovnatanova and Kononova 2008); these two key Devonian fossil groups are central to Devonian biostratigraphy and have been continually revised and updated (Ovnatanova *et al.* 2017). The zonation in the Timan region (Sennova 1972; Durkina 1984; Avkhimovitch *et al.* 1993) extends from the late Middle Devonian to the early Famennian. In addition to regional schemes, higher resolution palynological zonations have been developed within the Timan region (Fig. 1) includ-ing seven zones (PA-1 to PA-7) through the late Givetian to middle Frasnian interval (Tel'nova 2008), and a further four zones (PC-1 to PC-4) spanning the Frasnian/Famennian boundary (Marshall *et al.* 2011).

ARCTIC DEVONIAN PALYNOEVENTS

All taxon names with authorship are listed in Appendix A and a summary of the following Devonian palynoevents is provided as Appendix B.

FO of *Dictyotriletes emsiensis*

Dictyotriletes emsiensis was originally described from short stratigraphic sections from Vestspitsbergen, Svalbard, and regarded as Emsian, but without independent age evidence apart from fossil fish. The only section from northern higher latitudes where it occurs in a long section is that from the Moose River Basin in Ontario, Canada (McGregor and Camfield 1976), where it defines the base of the *caperatus-emsiensis* Zone of late Pragian age; this section has been independently dated using conodonts (Uyeno and Bultynck 1993). The age of *Dictyotriletes emsiensis* was confirmed with a similarly faunal-controlled first occurrence in northwestern Europe. This taxon is an important spore inception, commonly used to define a zone across a wide area, including Gondwana (Melo and Loboziak 2003; Breuer and Steemans 2013), northern Europe (Streel *et al.* 1987) and Canada (McGregor 1977).

The FO of *Dictyotriletes emsiensis* is taken here as the base of the Pragian based on correlations in the Ardenne–Rhenish region (Streel *et al.* 1987).

FO of *Acinosporites lindlarensis*

Acinosporites lindlarensis has a possible first occurrence at the base of the section on Melville Island and assigned an early Eifelian age. It is the in situ spore of the lycopod *Leclercqia*, which has a late Emsian first occurrence (Richardson *et al.* 1993). Note that this spore has a densely sculptured outer wall layer that spalls off from an inner body such that it can resemble *Geminospora*, and some occurrences were initially placed in this genus — e.g., *Geminospora treverica* of Riegel (1973). In the Jaab Lake No. 1 well, the base of *Acinosporites lindlarensis* appears immediately below that of the inception of *Emphanisporites annulatus* (McGregor and Camfield 1976).

The FO of *Acinosporites lindlarensis* is taken here as 85% up from the base of the Emsian.

FO of *Emphanisporites annulatus*

Emphanisporites annulatus is a very distinctive, biostratigraphically significant spore. It has very few published occurrences in the Arctic, with only a single unequivocal specimen from Melville Island (McGregor and Camfield 1982); this record is from within the Eifelian and above its range base as defined elsewhere. However, the range base occurs in the Moose River Basin (McGregor and Camfield 1976), where conodonts indicate an upper Emsian inception above the incomplete range of the conodont *serotinus* Zone (Uyeno and Bultynck 1993).

The FO of *Emphanisporites annulatus* is taken here as 90% up from the base of the Emsian.

FO of *Grandispora* spp.

This event marks the first occurrences of the wider group of camerate spores that are zonate — i.e., have an equatorial extension. They all have well-spaced sculpture that varies from small coni to long spines, normally bearing simple tips. They have no documented first occurrences in the Arctic, but occur in the latest Emsian in the Moose River Basin (McGregor and Camfield 1976). Sporadic earlier occurrences occur in Gondwana (Melo and Lobziak 2003).

The FO of *Grandispora* spp. is taken here as 90% up from the base of the Emsian.

FO of *Elenisporis biformis*

This event is defined on the inception of *Elenisporis biformis* a spore characterized by prominent ribs on the proximal contact face. It has been widely recognized across western Russia and Belarus, where it has been incorporated into regional spore zonations (Arkhangelskaya 1985). Subsequently it has been recognized at a single level from Ellesmere Island (Arkhangelskaya *et al.* 1990). Its associated palynological assemblage and a conodont assemblage higher in a correlative section places it in the early Eifelian.

The FO of *Elenisporis biformis* is taken here as 2% up from the base of the Eifelian stage.

FO of *Grandispora protea*

On Melville Island (McGregor and Camfield 1976) *Grandispora protea* has a first occurrence in the earliest Eifelian, above that of *Rhabdosporites langii*; but in western Europe *Grandispora protea* appears earlier.

The FO of *Grandispora protea* occurs in the early Eifelian and is taken here as 5% above the base of the Eifelian.

FOs of *Ancyrospora longispinosa*, *Ancyrospora ancyrea*, *Ancyrospora kedoae* and *Densosporites devonicus*

Important from the latest Early Devonian to the Devonian-Carboniferous boundary are a group of spores with processes that have bifurcate tips. Those with an extended zona are placed in *Ancyrospora*. *Ancyrospora longispinosa* has long bifurcate tipped processes and an early Eifelian first occurrence on Melville Island (McGregor and Camfield 1976), more or less synchronous with the first occurrence of the much smaller (in size and spine length) *Ancyrospora ancyrea*. However, *Ancyrospora ancyrea* has a longer range, and both species are more typical of the Eifelian.

Ancyrospora kedoae is representative of a distinctive group of species within *Ancyrospora* that have relatively small bifurcate tipped spines on an otherwise relatively large spore. Others within the group are *Ancyrospora eurypterota*, *Ancyrospora loganii* and *Ancyrospora nettersheimensis*. On

Melville Island (McGregor and Camfield 1976) all species in this group have early Eifelian first occurrences at the base of the studied section. In the Ardenne–Rhenish region of northwestern Europe they have earlier first occurrences, in the latest Emsian, and form a distinctive assemblage (Riegel 1982).

Densosporites devonicus has a distinctive annular thickening within a thinner equatorial cingulum. Although it is assigned to *Densosporites*, it is quite dissimilar to the diverse group of Carboniferous densospores (Staplin and Jansonius 1964)

The FOs of *Ancyrospora longispinosa*, *Ancyrospora ancyrea*, *Ancyrospora kedoae* and *Densosporites devonicus* occur in the early Eifelian and are taken here as 10% above the base of the Eifelian.

FO of *Retispora archaeolepidophyta*

This species consists of camerate spores with an exoexine that forms a reticulate mesh. Although placed appropriately within *Retispora*, it appears unrelated to *Retispora lepidophyta*, and a considerable range gap occurs between their occurrences. The exoexine of *Retispora archaeolepidophyta* is more like to a mesh, whereas in *Retispora lepidophyta* it has the form of an outer wall perforated by foveae. On Melville Island *Retispora archaeolepidophyta* is persistent through the Eifelian and early Givetian (McGregor and Camfield 1976). Although rarely reported, the species does occur in the Eifelian of both Shetland (at 60°N; Marshall 1988) and Caithness (personal observations) in northern Scotland. The species was originally described from Belarus (Kedo 1955), and Plax *et al.* (2016) included more recent late Eifelian records that are independently dated with conodonts.

The FO of *Retispora archaeolepidophyta* occurs in the early Eifelian and is taken here as 20% above the base of the Eifelian.

FO of *Rhabdosporites langii*

This spore is known in situ from the aneurophytalean progymnosperms and is particularly abundant in the late Eifelian and early Givetian. It is distinctively camerate and covered by closely packed coni. Its first occurrence in Melville Island is below the base of the studied section (McGregor and Camfield 1982). In the Moose River Basin (Jaab Lake No. 1 well) it has a delayed first occurrence (McGregor and Camfield 1976) above an interval with poor spore recovery.

The FO of *Rhabdosporites langii* is taken here as 60% above the base of the conodont *costatus* Zone based on its first occurrence in the Ardenne–Rhenish area (Riegel 1982). This equates with 20% above the base of the Eifelian.

FO of *Archaeozonotriletes variabilis*

Archaeozonotriletes variabilis is a somewhat unusual spore in having a distinctive distal thickening or patina. It is widely distributed paleogeographically and is present in

many Arctic sections. It has a middle Eifelian first occurrence on Melville Island (McGregor and Camfield 1982) that is partially age-controlled by conodont assemblages (McGregor 1981).

The FO of *Archaeozonotriletes variabilis* is taken here as 50% above the base of the Eifelian.

FO *Cirratriradites avius, Cirratriradites punctomonogrammos* and *Cirratriradites monogrammos*

Cirratriradites avius was described by Allen (1965) from Svalbard but may be a heterotypic junior synonym of *Cirratriradites punctomonogrammos. Cirratriradites avius* is a distinctive flattened zonate spore with a prominent triangular shape. *Cirratriradites monogrammos* is identical but has a distal sculpture in the form of a flattened reticulum. All forms are widely distributed paleogeographically (Xu *et al.* 2014).

In Svalbard *Cirratriradites avius* has a Givetian age but, as it occurs in a short stratigraphic section, its true range remains unknown. However, data from Lithuania, Russia and Belarus (the RL Zone of Avkhimovitch *et al.* 1993; Plax *et al.* 2016), all south of the Arctic, indicate a late Eifelian first occurrence. The range of *Cirratriradites avius* and related species includes the conodont *kockelianus* and *ensis* zones, which are late Eifelian.

The FOs of *Cirratriradites avius, Cirratriradites punctomonogrammos* and *Cirratriradites monogrammos* occur in the late Eifelian and are taken here as 70% above the base of the Eifelian.

FO of *Geminospora micropaxilla*

Geminospora is a genus of small camerate spores, often with a subtle separation between a thin walled intexine and a patinate or thickened exoexine. It contains a number of related forms sometimes separated into distinct species, but the variation can be circumscribed broadly under the name *Geminospora lemurata* (McGregor and Camfield 1982). The surface beyond the contact face is covered with closely packed coni. The species is the in situ microspore of archaeopteridalean progymnosperms, an important group of plants with a Givetian first occurrence that formed the first deeply rooted forests (Stein *et al.* 2019). Some authors (e.g., Tel'nova 2007) recognize several species of *Geminospora* based on both specimens found in situ from fertile *Archaeopteris* fronds and dispersed spores. On Melville Island (McGregor and Camfield 1982) the earliest species of *Geminospora* to occur is *Geminospora micropaxilla* (originally *Rhabdosporites micropaxillus*); compared to other species in the genus, this species is larger in diameter and has a wider separation between intexine and exoexine. It is thus closer in morphology to the *Rhabdosporites* spores of the aneurophytalean progymnosperms, the group into which this species was originally assigned. Other species of *Geminospora* appear higher in the section on Melville Island, above the range of *Cymbosporites magnificus*.

The FO of *Geminospora micropaxilla* occurs in the latest Eifelian and is taken here as 80% above the base of the Eifelian.

FO of *Geminospora lemurata*

A stratigraphically higher group of *Geminospora* includes *Geminospora tuberculata* and *Geminospora micromanifesta.* The latter is probably a heterotypic junior synonym of *Geminospora svalbardiae* (D.C. McGregor, pers. comm.), first described by Vigran (1964) from Svalbard or more generally within *Geminospora lemurata. Geminospora svalbardiae* is abundant within the Mimerdalen Subgroup but no clear range base was determined from the limited sections available to Allen (1965, 1967). However, the range base of *Geminospora lemurata* is present within the Nathorst Fjord Group in Canning Land, East Greenland (Marshall and Astin 1996) although not constrained by any independent faunal evidence apart from some rather ambiguously dated fish.

On Melville Island (McGregor and Camfield 1982) the situation is more problematic as five species and varieties of *Geminospora* were identified, all of which could probably be placed within *Geminospora lemurata*. Their appearance may mark the base of the Givetian stage, but there is insufficient conodont data to be more specific.

The FO of *Geminospora lemurata* occurs at the base of the Givetian based on conodont correlations in Germany (Loboziak *et al.* 1991).

FO of *Cymbosporites magnificus*

Cymbosporites magnificus is a spore distinguished by a patinate or thickened exoexine covered with closely packed verrucae. It probably derives from the arborescent lycopod *Protolepidodendropsis* and is abundant in Givetian and early Frasnian sections in the Arctic (Berry and Marshall 2015). It has long been known to occur in Arctic coals (McGregor 1960) where its dominance demonstrates that its parent plant formed paleoequatorial wetland forests at that time (Marshall *et al.* 2019). The first occurrence of *Cymbosporites magnificus* on Melville Island postdates that of *Geminospora micropaxilla*. It occurs widely across the Arctic — in Svalbard, the sub-polar Urals, and as far south as the Volga River area, where it has been called *Archaeozonotriletes vorobjensis* and *Archaeozonotriletes tamilii* (V.N. Mantsurova, pers. comm. 2014). The parent plant is heterosporous and has a much larger, but morphologically similar, megaspore referred to *Verrucisporites submamillarius*. This megaspore is widely known from Arctic Canada (Chi and Hills 1976a). However, it does not occur across the entirety of the Arctic, being absent from sections in East Greenland that are either too distant from the paleoequator or too arid, being deep within the Old Red Sandstone Continent (Torsvik and Cocks 2017). It is also absent from both western Europe (including Shetland at 60°N) and southern North America.

The FO of *Cymbosporites magnificus* occurs in the early Givetian and is taken here as 5% above the base of the Givetian.

FO of *Cristatisporites triangulatus*

Cristatisporites triangulatus is a distinctive species that has some biostratigraphic significance and has been used to define a zone base in several schemes. Allen (1982) revised the species description using additional material, including further Arctic occurrences. The species consists of small lightly sculptured spores with a circular inner body and a distinctly triangular equatorial cingulum that is extended along the trilete rays but thins to almost nothing in the interradial areas. In Arctic Canada McGregor (1981) assigned it a late Givetian first occurrence, whereas in western Europe it has an early Givetian conodont-controlled first occurrence (Loboziak *et al.* 1991); however, the identity of these much earlier specimens is the subject of discussion (Turnau and Narkiewicz 2011).

The FO of *Cristatisporites triangulatus* on Melville Island is placed high in the Givetian based on its co-occurrence with *Archaeoperisaccus timanicus*, and beneath the occurrence of the influx of *Archaeoperisaccus* spp. In terms of conodont stratigraphy this event occurs in the middle of the conodont *triangularis* Zone (McGregor 1981, 1994). This placement is supported by the appearance of *Cristatisporites triangulatus* in the late Givetian of Russia in or slightly below the TS Subzone (Avkhimovitch *et al.* 1993).

The FO of *Cristatisporites triangulatus* is taken here as 75% above the base of the Givetian.

FO of *Contagisporites optivus*

Contagisporites optivus is the megaspore pairing with the microspore *Geminospora lemurata*. It occurs widely across the Arctic, in Arctic Canada, Alaska, East Greenland, Svalbard and the Timan. Regarding its range base, the best study was by Chi and Hills (1976a), which was exclusively on mega spores. Importantly these authors studied the identical section on Melville Island as that examined by McGregor and Camfield (1982).

Contagisporites optivus is rare at its range base. It usually only becomes abundant in the latest Givetian, above the Taghanic Event and coincident with the Geneseo Taghanic Onlap. Spore extinctions occur at the Taghanic Event, and both *Geminospora* and *Contagisporites* become more dominant at and above this level; hence the latter's appearance in zonal schemes at this horizon (e.g., the OK Zone of Avkhimovitch *et al.* 1993 with the O referring to *optivus*). Before the definition of the base Frasnian GSSP, the stage base was considered coincident with the latest Givetian Geneseo Onlap, and this was a much more obvious level at which to place the boundary. This history explains why older zonations give *Contagisporites optivus* a Frasnian range base. On Melville Island the first occurrence of *Contagisporites optivus* is not coincident with that of either *Geminospora micropaxilla* or *Geminospora tuberculata/micromanifestus*, but 200 m higher and above a sample gap. But it should be noted that earlier occurrences of *Contagisporites optivus* can be somewhat morphologically different from typical specimens of the species (Marshall 1996). No range base for *Contagisporites optivus* is known in other Arctic sections, although the species occurs in Canning Land. The sections in the Timan probably start just above its range base (Tel'nova 2008).

The FO of *Contagisporites optivus* occurs at the base of the late Givetian at the Geneseo Onlap and coincident with the base of the conodont *Schmidtognathus hermanii* Zone. It is taken here as the base of the late Givetian.

FO of *Chelinospora concinna*

A prominent group of Givetian small spores with a thick distal patina centre around *Archaeozonotrileties variabilis*. In northwestern Europe this group is given an early Givetian first occurrence, but has been recorded as having a somewhat earlier late Eifelian first occurrence from the Melville Island section (McGregor and Camfield 1982). *Archaeozonorileties variabilis* is widely distributed across the Arctic and is well known from Spitsbergen and northern Russia (Allen 1965, 1967; Avkhimovitch *et al.* 1993). *Chelinospora concinna* is similar to *Archaeozonotrileties variabilis* in having a much reduced distal patina dissected to a reticulum. Together with related species, *Chelinospora concinna* occurs in profusion (Allen 1965, 1967) in the Givetian of Spitsbergen.

The FO of *Chelinospora concinna* is placed 80% above the base of the Givetian.

FO *Archaeoperisaccus timanicus* and the acme of *Archaeoperisaccus* spp.

This group of sculptured monolete spores characterize the Frasnian of the Arctic regions; they have been recorded in Canada, Alaska, northern Russia, Greenland and Spitsbergen, but have not been found farther south than the northern North Sea, the Baltic area (Latvia) and Siberia (Marshall *et al.* 1996). Spores in this group have first occurrences in the latest-Givetian BI Subzone of Avkhimovitch *et al.* (1993), with *Archaeoperisaccus timanicus* being a typical and common species. These first occurrences were often placed in the early Frasnian because the latest Givetian OK Zone was assigned to the early Frasnian prior to definition of the base-Frasnian GSSP. A significant number of *Archaeoperisaccus* species have been described and an attempt was made to discriminate between them by Braman and Hills (1985). They reach an acme in the OG Zone of Avkhimovitch *et al.* (1993), then declining and becoming extinct in the very latest Frasnian, at the Frasnian/Famennian mass extinction. *Archaeoperisaccus* species have range bases on Melville Island (McGregor 1981) that were also placed in the latest Givetian and broadly coincident with that of *Chelinospora concinna*, but in a widely spaced set of samples and without independent age control.

The FO of *Archaeoperisaccus timanicus* is taken here as 80% above the base of the Givetian. The acme is in the middle Frasnian, 50% above the base of the stage.

FO of *Ancyrospora* with multifurcate tips

Most species of *Ancyrospora* and *Hystricosporites* have spines with bifurcate or grapnel tips. But in the Frasnian, including in the Arctic (McGregor and Owens 1966; Owens 1971) the trend is for more species to have multifurcate tips, the grapnels having been reduced to a number of spines. These species with multifurcate tips have a conodont-controlled earliest-Frasnian first occurrence (Turnau and Narkiewicz 2011); they all became extinct at the Devonian/Carboniferous boundary.

The FO of *Ancyrospora* with multi-furcate tips is taken here as 5% above the base of the Frasnian.

FO of *Spelaeotriletes domanicus*

A plexus of robust species of *Spelaeotriletes* with well-spaced sculpture consists of *Spelaeotriletes krestovnikovii*, *Spelaeotriletes bellus* and *Spelaeotriletes domanicus*. *Spelaeotriletes krestovnikovii* has a range base at basement in the Timan, where it occurs with abundant *Contagisporites optivus* and *Ancyrospora incisa* (Tel'nova 2008). There then follow the successive appearances of *Spelaeotriletes bellus* and *Spelaeotriletes domanicus*. The most distinctive species is *Spelaeotriletes domanicus*, with a coarse net or reticulum on the surface of the exoexine, which has nodes at the bases of the spines. *Spelaeotriletes domanicus* was recorded as *Hymenozonotriletes domanicus* in the Frasnian of Arctic Canada (the DO Zone of Braman and Hills 1992), but again at the base of the studied section; so the first occurrence is not known. The species also occurs at 58.8°N in BP well 14/6-1 in the North Sea (Marshall *et al*. 1996). Avkhimovitch *et al*. (1993) noted the increasing abundance of the species in their IM Subzone.

The FO of *Spelaeotriletes domanicus* is taken here as 5% above the base of the Frasnian.

FOs of *Ancyrospora incisa* and *Ancyrospora langii*

Ancyrospora incisa is an important biostratigraphic indicator that marks the base of the *incisa-micromanifesta* Zone that has a conodont-controlled first occurrence in the latest Givetian (Turnau and Racki 1999). It has been recorded mostly from Russia and Poland. The closely related *Ancyrospora langii* was first described from France and then in the Arctic, in Spitsbergen and Canada (McGregor 1981; Braman and Hills 1992; Owens *et al*. 2022). Allen (1965) considered that *Ancyrospora langii* would be conspecific with *Ancyrospora incisa* if the latter was shown to have bifurcate tips although these were not evident from its original description and illustration. It is now known to possess bifurcate tips (Kedo and Obukhovskaya 1981; Avkhimovitch *et al*. 1993). *Ancyrospora langii* has a first occurrence in the late-Early Frasnian DO Zone in Yukon (Braman and Hills 1992) and occurs above *Archaeoperisaccus timanicus* in Melville Island (McGregor 1981).

The FOs of *Ancyrospora incisa* and *Ancyrospora langii* are

taken here as 10% above the base of the Frasnian.

FO of *Archaeoperisaccus indistinctus*

Archaeoperisaccus indistinctus has a somewhat surprising first occurrence within the Frasnian of East Greenland. It is a distinctive species of *Archaeoperisaccus*, first described from China and northern Australia as *Archaeoperisaccus indistinctus* or *Archaeoperisaccus rhacodes*. (Lu 1988; Hashemi and Playford 2005). It was earlier considered to be restricted to Australasia but appears in the early Frasnian in East Greenland (JEAM personal observations).

Its FO is uncertain, but it occurs with *Cristatisporites deliquescens* and *Membraculisporis radiatus*. It is taken as 15% above the base of the Frasnian.

FO of *Cristatisporites deliquescens*

Cristatisporites deliquescens is an important component of Frasnian spore assemblages, having a first occurrence in the early Frasnian SD Zone of Avkhimovitch *et al*. (1993) and an extinction at the Frasnian/Famennian boundary. Braman and Hills (1992) recorded its first occurrence at the base of the DO Zone and the base of their section. In the Timan (Tel'nova 2008) the first occurrence is in the PA-5 assemblage of the Ust'-Yarega Formation, which contains the goniatite *Hoeninghausia nalivkini* (Becker *et al*. 2000), equivalent to the conodont MN3 Zone of early Frasnian age.

The FO of *Cristatisporites deliquescens* is taken here as 20% above the base of the Frasnian.

FO of *Membraculisporis radiatus*

Membraculisporis radiatus is a very distinctive spore with three clearly distinguishable wall layers, the outer one being covered with radial folds. It is a typical species in the middle to late Frasnian in the Arctic, occurring in East Greenland, Yukon (Braman and Hills 1992), with a range base coincident with the middle DO Subzone. The species was first recognized in Russia, occurring in the Timan (Avkhimovitch *et al*. 1993), where it it has an inception and sporadic occurrence in the conodont CVe Zone (with lower *Palmatolepis gigas* Zone conodonts), but becomes more abundant upwards and defines the MR zone, where it is abundant; its abundance is a characteristic that continues into the overlying DE Zone.

The FO of *Membraculisporis radiatus* is taken here as 60% above the base of the Frasnian.

LO of *Archaeoperisaccus*

The mass extinction at the Frasnian/Famennian boundary includes spore disappearances, although this aspect is not particularly well understood because of a general absence of high-resolution studies. The mass extinction is, in fact, a pair of extinction events, each characterized by a black mudstone (the Lower and Upper Kellwasser; Becker *et al*. 2020)

within each of which multiple taxa become extinct among conodonts, ammonoids, trilobites and cnidarians. The only high-level clade to become extinct was the tentaculoids (Bond 2006), and this can be recognized palynologically (Marshall and Tel'nova 2017) through the disappearance of the internal linings of these otherwise calcareous microfossils. The current consensus, as evidenced by the mercury proxy (Racki *et al.* 2018) and geochronological dating (Ernst *et al.* 2020), is that the cause of the Frasnian–Famennian mass extinction was the the destabilization of the Earth System by two major phases of eruption from a large igneous province. The only detailed record through "Arctic" Frasnian–Famennian spore assemblages is that by Braman and Hills (1992). In their account, the boundary is placed on an older conodont definition (within the conodont *triangularis* Zone) rather than at the conodont *gigastriangularis* Zone boundary. Palynological assemblages across the boundary were reviewed by Streel *et al.* (2000), who replotted data, including those from Braman and Hills 1992) so as to show last occurrences. As for the invertebrates, the compilation by Streel *et al.* shows a series of spore extinctions somewhat below the level of the Frasnian/Famennian boundary and coincident with the PF/DO zonal boundary of Braman and Hills (1992). Notable extinctions include all species of *Archaeoperisaccus*, the only clade that appears to become extinct (but see Marshall 2021). Other notable extinctions are *Spelaeotriletes domanicus*, *Membraculisporis radiatus* and a several species of *Ancyrospora* and *Hystricosporites*. Braman and Hills (1992) defined the boundary as the replacement in a lineage of *Vallatisporites preanthoideus* by *Vallatisporites anthoideus* at their spore PF/AG Zone boundary.

Many of the Frasnian/Famennian boundary sections are in marginal marine sedimentary successions and include hiatuses above both of the Kellwasser black mudstones. This situation is present throughout much of the Timan (Obukhovskaya *et al.* 2000). However, a science borehole at Sosnogorsk was drilled through a more complete Frasnian/Famennian boundary section that enabled the recognition of four palynocomplexes (PC 1–4), with the disappearance of characteristic Frasnian taxa occurring in PC-2 (Marshall *et al.* 2011). In addition, the PC-2 assemblage was also characterized by the incoming of highly variable species, *Grandispora pseudodeliquescens* (Tel'nova and Marshall 2009).

The LO of *Archaeoperisaccus* is taken as the base of the Famennian.

FOs of *Tergobulasporites immensus* and *Diducites* spp.

The first occurrence of the megaspore *Tergobulasporites immensus*, formerly known as *Lagenoisporites immensus*, was used to define the base of the lm Zone of Avkhimovitch *et al.* (1993). This event coincides with the first occurrence of the distinctive group of Famennian species of *Diducites* (e.g., *Diducites poljessica* and *Diducites*

versabilis), characterized with an external diaphanous third wall layer of outer exoexine. These species appear in East Greenland, but above their range base (Marshall *et al.* 2020). The lm Zone is placed in the latest early Famennian.

The FOs of *Tergobulasporites immensus* and *Diducites* spp. are taken here as 30% above the base of the Famennian.

FOs of *Cornispora monocornuta, Cornispora bicornuta* and *Cornispora tricornuta*

This very distinctive plexus of spores are characterized by the variable development of one, two or three irregularly developed horns on an otherwise simple spore. They are characteristic of assemblages across the Arctic (Streel 1986) and have a middle Famennian first occurrence. However, they do not occur further south until the delayed latest Devonian first occurrence of the related *Cyrtospora cristifera*. In the Timan the three species are used to define two subzones of the CVa Zone, with a maximum proliferation and diversity of 1–3 horned forms defining the CB Subzone. In Canada, *Cornispora bicornuta* and *Cornispora tricornuta* are grouped as the *Cornispora varicornuta* morphon (Van der Zwan and Walton 1981) and used to define the VM Zone (Braman and Hills 1992). They are also present in both Vestspitsbergen (Scheibner *et al.* 2012) and Bjørnøya. Importantly, the Bjørnøya section (Kaiser 1971; Lopes *et al.* 2021) is continuous with overlying latest Famennian strata characterized by *Retispora lepidophyta*.

The FO of *Cornispora monocornuta* is coincident with that of *Tergobulasporites immensus* and *Diducites* spp., so the FOs of *Cornispora monocornuta, Cornispora bicornuta* and *Cornispora tricornuta* are taken here as 30% above the base of the Famennian, although in Russia they are reported as occurring in the sequential order of *Cornispora monocornuta, Cornispora bicornuta* and *Cornispora tricornuta* (Avkhimovitch *et al.* 1993; Sennova 1972).

FO of *Retispora macroreticulata*

This species is similar to *Retispora lepidophyta* but with a much larger overall size (average 150 µm) and with larger foveae. It has a first occurrence before that of *Retispora lepidophyta* and the two species have a partial range overlap. The species and range overlap occur in East Greenland, but the range bases are not seen there (Marshall *et al.* 2020). In Avkhimovitch *et al.* (1993), *Retispora macroreticulata* has a first occurrence in the DG Zone, and co-occurs with foraminifera of the *Quasiendothyra communis* Zone.

The FO of *Retispora macroreticulata* is taken here as 50% above the base of the Famennian.

FO of *Retispora lepidophyta*

Retispora lepidophyta is the most significant latest Famennian spore; it appears to be globally distributed and has a short range and a distinctive morphology. Outside the Arctic it has a FO just below the base of the conodont upper *exp-*

ansa Zone (Streel 2009). It is a component of all latest Famennian zonations. Braman and Hills (1992) reported it above a stratigraphic gap in their LR and LP Zones in Yukon. It is also abundant in many localities in Bjørnøya but, as shown by Lopes *et al.* (2021), these represent short sections that are difficult to correlate. The sections probably start high in the LL Zone, so the range base of *Retispora lepidophyta* is not present.

In East Greenland the best section with *Retispora lepidophyta* is on Stensiö Bjerg on Gauss Halvø (Marshall *et al.* 2020). Here the first occurrence of *Retispora lepidophyta* occurs in the upper part of the Britta Dal Formation, above some 500 m of section barren of spores. This event accompanies a change in the paleoclimate from a long interval of sustained aridity to one of higher seasonality that included humid episodes. The first occurrence *Retispora lepidophyta* is some 100 m below the first occurrence of *Indotriradites explanatus*, so a significant fraction of its total range must be present. *Retispora lepidophyta* was also used by Vigran *et al.* (1999) to define the *Retispora lepidophyta* Abundance Zone and the *Spelaeotriletes* spp. – *Lophozonotriletes malevkensis* Assemblage Zone. The first occurrence of *Retispora lepidophyta* has been extensively studied (e.g., Streel 2009) although the event appears not to have been independently dated in the Arctic.

The FO of *Retispora lepidophyta* is taken here as 80% above the base of the Famennian.

FO of *Knoxisporites literatus*

In East Greenland (Marshall *et al.* 2020, Supplementary Material) *Knoxisporites literatus* has a FO in the uppermost LL Zone, immediately beneath that of *Indotriradites explanatus*. So its FO is taken here as 86% above the base of the Famennian.

FOs of *Indotriradites explanatus, Tumulispora rarituberculata* and *Tumulispora malevkensis*

Indotriradites explanatus is a widely distributed spore with a distinctive zona, including a thickened inner ring. It occurs in the latest Famennian of Bjørnøya (Lopes *et al.* 2021), which supports the general late LL to LE age given to the sections there. In East Greenland it occurs in both the Stensiö Bjerg and Nathorst Bjerg sections (Marshall *et al.* 2020), where its first occurrence is coincident with strata representing a stratified lake deposit that reflects a short interval of warmer, more humid climate.

Streel (2009) placed the base of *Indotriradites explanatus* at about the base of the conodont lower *presulcata* Zone, some 1.6 myr below the Devonian/Carboniferous boundary and 13% into the estimated duration of the Famennian; thus, the FO of *Indotriradites explanatus* is taken here as 87% above the base of the Famennian.

Tumulispora rarituberculata and *Tumulispora malevkensis* are distinctive spores that have been used in zonation schemes by, for example, Higgs *et al.* (1988), which specify a first occurrence at the base of the LN Zone. However, in Bjørnøya the two species have an earlier first occurrence (Lopes *et al.* 2021); and in East Greenland (Marshall *et al.* 2020), their first occurrences are coincident with the base of the LE Zone. So the presence of humid conditions was appears to have controlled the first occurrence of these spores.

The FOs of *Tumulispora rarituberculata* and *Tumulispora malevkensis* coincide with that of *Indotriradites explanatus* and are taken here as at 87% above the base of the Famennian.

FO of *Rugospora radiata*

Rugospora radiata has a first occurrence in East Greenland above that of *Indotriradites explanatus* (Marshall *et al.* 2020). It was not recorded in the Yukon sections of Braman and Hills (1992), or from Bjørnøya by Lopes *et al.* (2021). In terms of section thickness, it lies at 25% into the interval between the first occurrence of *Indotriradites explanatus* and the Devonian/Carboniferous boundary; so the FO of *Rugospora radiata* is taken here as is 90% above the base of the Famennian.

FO of *Retispora lepidophyta* var. *tener*

This first occurrence is the *tener* event of Prestianni *et al.* (2016), defined by the occurrence of a small variant of *Retispora lepidophyta*. The event was reported from Bjørnøya by Kaiser (1970, 1971) as the *Hymenozonotriletes lepidophytus* var. *minor* Zone and this identification as the *tener* event was corroborated by Lopes *et al.* (2021). In East Greenland small specimens of *Retispora lepidophyta* occur after the first occurrences of both *Indotriradites explanatus* and *Rugospora radiata* (JEAM, personal observations). In age, this event occurs one-third up in the section between the FO of *Indotriradites explanatus* and the Devonian/Carboniferous boundary: hence, the FO of *Retispora lepidophyta* var. *tener* is taken here as 91% above the base of the Famennian.

FO of *Verrucosisporites nitidus*

The first occurrence of *Verrucosisporites nitidus* defines the base of the LN Zone. Difficulties in its application have arisen because spores that are variably verrucate have been placed in the species. Turnau *et al.* (1994) gave a more tightly circumscribed definition, restricting the species to spores with a continuous cover of hemispherical verrucae. In addition, the first occurrence has also caused problems as it appears to be absent in some sections. Differences in the timing of inception have been variously attributed to ecological control or, by Prestianni *et al.* (2016), to differential spore transport to distal environments. The section from East Greenland clarified this situation, with Marshall (2021) finding a distinct increase in diversity, including *Verrucosisporites nitidus*, some 1.5 m below the Devonian/Carboniferous boundary, associated with the humidification that accompanied the flooding of the basin by the deep,

stratified and wide lake represented by the Obrutschew Formation. This change reflected the climatic amelioration that accompanied the collapse of the terminal latest Famennian glaciation. Hence, the first appearance of *Verrucosisporites nitidus* is controlled by climate — specifically relatively more humid conditions. This increase in spore diversity immediately beneath the VI zone has been recognized in other sections and referred to as the LN transitional zone (notation as LN*) of Higgs *et al.* (1993).

The FO of *Verrucosisporites nitidus* in East Greenland occurs within the Obrutschew lake cycle that is coincident with the Devonian/Carboniferous boundary (Marshall *et al.* 2020). This orbitally forced lacustrine cycle represents either precession or obliquity, i.e., a fraction of 20 or 40 kyr. With a Famennian duration conservatively estimated at some 12 myr (Becker *et al.* 2020), the lacustrine cycle represents less than 1% of that total duration. So the FO of *Verrucosisporites nitidus* is taken here as 99% above the base of the Famennian.

LOs of *Retispora lepidophyta*, *Ancyrospora* spp., *Hystricosporites* spp., *Diducites* spp. and *Rugospora radiata*

High resolution sampling across the Devonian/Carboniferous boundary from sections in East Greenland (Marshall *et al.* 2020; Marshall 2021) show that the distinctive, abundant and globally distributed spore species, *Retispora lepidophyta*, becomes extinct over a short time interval; the event is coincident with the disappearance of *Diducites*, all the grapnel tipped spores (*Ancyrospora* and *Hystricosporites*), and *Rugospora radiata*. The event marks the LN*/VI zonal boundary. This combined last appearance is seen in other Arctic sections, most notably at the LP/VB zonal boundary of Braman and Hills (1992). In Bjørnøya, no stratigraphic sections with continuous palynological recovery occur across the Devonian/Carboniferous boundary, but there is a clear extinction of *Retispora lepidophyta* and related forms (Kaiser 1970). The extinction of *Retispora lepidophyta* has also been recognized in a number of sections in the Timan (Sennova 1972; Durkina 1984).

We note here that *Vallatisporites pusillites* and *Vallatisporites verrucosus* are important first occurrences in latest Famennian zonations from lower latitudes (e.g., New York State, USA). However, these species are absent or rare in Arctic assemblages below the earliest Carboniferous VI spore assemblage (Mangerud *et al.* 2021).

The LOs of *Retispora lepidophyta*, *Ancyrospora* spp., *Hystricosporites* spp., *Diducites* spp. and *Rugospora radiata* are taken here as the base of the Tournaisian.

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Editorial responsibility: Robert A. Fensome

APPENDIX A: TAXON NAMES WITH AUTHORSHIP CITATIONS

Note: we acknowledge that combinations by Avkhimovitch *et al*. 1993 have not been validly published, but to validate them is beyond the scope of the present work.

Acinosporites lindlarensis Riegel 1968

Ancyrospora Richardson 1960

Ancyrospora ancyrea (Eisenack 1944) Richardson 1962

Ancyrospora eurypterota Riegel 1973

Ancyrospora incisa (Naumova 1953) Raskatova and Obukovskaya in Avkhimovitch *et al*. 1993

Ancyrospora kedoae (Riegel 1973) Turnau 1974

Ancyrospora langii (Taugourdeau-Lantz 1960) Allen 1965

Ancyrospora loganii McGregor 1973

Ancyrospora longispinosa Richardson 1962

Ancyrospora nettersheimensis Riegel 1973

Archaeoperisaccus (Naumova 1953) McGregor 1969

Archaeoperisaccus indistinctus Lu 1988

Archaeoperisaccus rhacodes Hashemi and Playford 2005

Archaeoperisaccus timanicus Pashkevitch 1964

Archaeozonotriletes tamilii Filippova *et al*. 1958 (name not validly published — no description or illustration; synonym of *Cymbosporites magnificus* according to V.N. Mantsurova personal communication to JEAM 2014)

Archaeozonotriletes variabilis (Naumova 1953) Allen 1965

Archaeozonotriletes vorobjensis Naumova (name not validly published; synonym of *Cymbosporites magnificus* according to V.N. Mantsurova personal communication to JEAM 2014)

Chelinospora concinna Allen 1965

Cirratriradites avius Allen 1965

Cirratriradites monogrammos (Arkhangelskaya 1963) Arkhangelskaya 1985

Cirratriradites punctomonogrammos (Arkhangelskaya 1963) Arkhangelskaya 1985

Contagisporites Owens 1971

Contagisporites optivus (Chibrikova 1959) Owens 1971 (megaspore pairing to *Geminospora lemurata*)

Cornispora Staplin and Jansonius in Staplin 1961

Cornispora bicornata Nazarenko in Kedo *et al*. 1971

Cornispora monocornata Nazarenko in Kedo *et al*. 1971

Cornispora tricornata Nazarenko in Kedo *et al*. 1971

Cristatisporites deliquescens (Naumova 1953) Arkhangelskaya 1987

Cristatisporites triangulatus (Allen 1965) McGregor and Camfield 1982

Cymbosporites Allen 1965

Cymbosporites magnificus (McGregor 1960) McGregor and Camfield 1982

Cyrtospora Winslow 1962

Cyrtospora cristifera (Luber in Luber and Waltz 1941) Van der Zwan 1979

Densosporites Berry 1937

Densosporites devonicus Richardson 1960

Dictyotriletes emsiensis (Allen 1965) McGregor 1973

Diducites Van Veen 1981

Diducites poljessica (Kedo 1957) Van Veen 1981

Diducites versabilis (Kedo 1957) Van Veen 1981

Elenisporis biformis (Arkhangelskaya 1963) Arkhangelskaya 1985

Emphanisporites annulatus McGregor 1961

Geminospora Balme 1962

Geminospora lemurata (Balme 1962) Playford 1983

Geminospora micromanifesta (Naumova 1953) Arkhangelskaya 1985

Geminospora micropaxilla (Owens 1971) McGregor and Camfield 1982 (originally *Rhabdosporites micropaxillus*)

Geminospora svalbardiae (Vigran 1964) Allen 1965 (originally *Lycospora svalbardiae*)

Geminospora treverica Riegel 1973 (now *Acinosporites lindlarensis*)

APPENDIX A: continued.

Geminospora tuberculata (Kedo 1955) Allen 1965

Grandispora Hoffmeister *et al.* 1955

Grandispora protea (Naumova 1953) Moreau-Benoit 1980

Grandispora pseudodeliquescens Tel'nova and Marshall 2009.

Hymenozonotriletes domanicus Naumova 1953

Hymenozonotriletes lepidophytus var. *minor* Kedo 1963

Hystricosporites McGregor 1960

Indotriradites explanatus (Luber in Luber and Waltz 1941) Playford 1991

Knoxisporites literatus (Waltz in Luber and Waltz 1938) Playford 1963

Lagenoisporites immensus Nazarenko and Nekriata in Kedo *et al.* 1971

Lophozonotriletes malevkensis Naumova in Kedo 1963

Lycospora svalbardiae Vigran 1964 (now *Geminospora svalbardiae*)

Membraculisporis radiatus (Naumova 1953) Arkhangelskaya 1985

Nikitinsporites Chaloner 1959

Retispora Staplin 1960

Retispora archaeolepidophyta (Kedo 1955) McGregor and Camfield 1982

Retispora lepidophyta (Kedo 1957) Playford 1976

Retispora lepidophyta var. *minor* Kedo 1971

Retispora lepidophyta var. *tener* Prestianni *et al.* (2016)

Retispora macroreticulata (Kedo 1974) Byvsheva 1985

Rhabdosporites Richardson 1960

Rhabdosporites langii (Eisenack 1944) Richardson 1960

Rhabdosporites micropaxillus Owens 1971 (now *Geminospora micropaxilla*)

Rugospora radiata (Yushko 1960) Byvsheva 1985

Spelaeotriletes Neves and Owens 1966

Spelaeotriletes bellus (Naumova 1953) Obukhovskaya in Avkhimovitch *et al* . 1993

Spelaeotriletes domanicus (Naumova 1953) Obukhovskaya in Avkhimovitch *et al.* 1993

Spelaeotriletes krestovnikovii (Naumova 1953) Obukhovskaya in Avkhimovitch *et al.* 1993

Tergobulasporites immensus (Nazarenko and Nekriata in Nazarenko *et al.* 1971) Turnau 2002
   (previously *Lagenoisporites immensus*)

Tumulispora malevkensis (Kedo 1957) Turnau 1978

Tumulispora rarituberculata (Luber in Luber and Waltz 1941) Playford 1991

Vallatisporites Hacquebard 1957

Vallatisporites anthoideus (Sennova in Nazarenk*et al.* 1971 Braman and Hills 1992

Vallatisporites preanthoideus Braman andHills 1992

Vallatisporites pusillites (Kedo 1957) Dolby and Neves 1970

Vallatisporites verrucosus Hacquebard 1957

Verrucisporites submamillarius (McGregor 1960) Chi and Hills 1976a

Verrucosisporites nitidus (Naumova 1953) Playford 1964

APPENDIX B: SPREADSHEET SUMMARIZING PALYNOEVENTS

Event	Calibration
FO of *Dictyotriletes emsiensis*	Base of the Pragian
FO of *Acinosporites lindlarensis*	85% up the Emsian
FO of *Emphanisporites annulatus*	90% up the Emsian
FO of *Grandispora* spp.	90% up the Emsian
FO of *Elenisporis biformis*	2% up the Eifelian
FO of *Grandispora protea*	5% up the Eifelian
FO of *Ancyrospora ancyrea*	10% up the Eifelian
FO of *Ancyrospora k* edoae	10% up the Eifelian
FO of *Ancyrospora longispinosa*	10% up the Eifelian
FO of *Densosporites devonicus*	10% up the Eifelian
FO of *Retispora archaeolepidophyta*	20% up the Eifelian
FO of *Rhabdosporites langii*	20% up the Eifelian
FO of *Archaeozonotriletes variabilis*	50% up the Eifelian
FO of *Cirratriradites avius*	70% up the Eifelian
FO of *Cirratriradites monogrammos*	70% up the Eifelian
FO of *Cirratriradites punctomonogrammos*	70% up the Eifelian
FO of *Geminospora micropaxilla*	80% up the Eifelian
FO of *Geminospora lemurata*	Base of the Givetian
FO of *Cymbosporites magnificus*	5% up the Givetian
FO of *Cristatisporites triangulatus*	75% up the Givetian
FO of *Contagisporites optivus*	Base of the late Givetian
Acme of *Archaeoperisaccus* spp.	80% up the Givetian
FO of *Archaeoperisaccus timanicus*	80% up the Givetian
FO of *Chelinospora concinna*	80% up the Givetian
FO of *Ancyrospora* with multi-furcate tips	5% up the Frasnian
FO of *Spelaeotriletes domanicus*	5% up the Frasnian
FO of *Ancyrospora incisa*	10% up the Frasnian
FO of *Ancyrospora langii*	10% up the Frasnian
FO of *Archaeoperisaccus indistinctus*	15% up the Frasnian
FO of *Cristatisporites deliquescens*	20% up the Frasnian
FO of *Membraculisporis radiatus*	60% up the Frasnian
LO of *Archaeoperisaccus*	Base of the Famennian
FO of *Diducites* spp.	30% up the Famennian
FO of *Tergobulasporites immensus*	30% up the Famennian
FO of *Cornispora bicornuta*	30% up the Famennian
FO of *Cornispora monocornuta*	30% up the Famennian
FO of *Cornispora tricornuta*	30% up the Famennian
FO of *Retispora macroreticulata*	50% up the Famennian
FO of *Retispora lepidophyta*	80% up the Famennian
FO of *Knoxisporites literatus*	86% up the Famennian
FO of *Indotriradites explanatus*	87% up the Famennian
FO of *Tumulisporites malevkensis*	87% up the Famennian
FO of *Tumulisporites rarituberculata*	87% up the Famennian
FO of *Rugospora radiata*	90% up the Famennian
FO of *Retispora lepidophyta* var. *tener*	91% up the Famennian
FO of *Verrucosisporites nitidus*	99% up the Famennian
LO of *Ancyrospora* spp.	Base of the Tournaisian
LO of *Diducites* spp.	Base of the Tournaisian
LO of *Hystricosporites* spp.	Base of the Tournaisian
LO of *Retispora lepidophyta*	Base of the Tournaisian
LO of *Rugospora radiata*	Base of the Tournaisian