THE DISTRIBUTION OF DENSOSPORES

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ABSTRACT

Densospores include species of the miospore genera *Cingulizonates* (Dybova & Jachowicz), *Cristatisporites* (Potonié & Kremp), *Densosporites* (Berry) and *Radiizonates* Staplin & Jansonius from the literature of Europe and North America, and *Euryzonotriletes* Naumova, *Hymenozonotriletes* Naumova and *Trematozonotriletes* Naumova from the Russian literature. An account is given of the taxonomic position of densospores and of their morphographic variation in different parts of the column.

Densospores have been recorded in large numbers, mainly from coal seams, from the Devonian to the Permian of the northern hemisphere. The geographical distribution of these occurrences forms the subject matter of the present paper. In general densospores first occur in abundance in more northerly regions and are displaced gradually southwards during the Carboniferous. They are most common and have the longest ranges, in areas of slow subsidence.

INTRODUCTION

THE densospores are a group of miospores characterized by a thick cingulum or equatorial girdle which may be massive or variously differentiated into thinner and thicker parts. These spores are distinguished from more simple cingulate forms by the two-layered nature of the exine, the intexine forming the inner body and the exoexine being expanded equatorially to form the cingulum (BHARADWAJ, 1958; SMITH, 1960; HUGHES, DETTMANN & PLAYFORD, 1962). The group is essentially Carboniferous in age but has also been recorded from the Devonian and the Permian; it is restricted in occurrence to the northern hemisphere.

The botanical affinities of the densospore group are still somewhat obscure, (the relevant findings are summarized in BUTTERWORTH *et al.*, 1964a), but Chaloner (1958, 1962) and Bharadwaj (1958) have isolated various species from the cones of herbaceous lycopsids.

Very many species of densospores have been described and they have been subdivided at the generic level in various ways. Their taxonomic position as applied in Europe and North America is summarized by Butterworth *et al.* (1964a), and by Staplin & Jansonius (1964). These workers divide the group into four genera: *Densosporites* (Berry) Butterworth, Jansonius, Smith & Staplin, in which the cingulum is massive and the exine without prominent ornament; *Cristatisporites* (Potonié & Kremp) Butterworth, Jansonius, Smith & Staplin, in which the cingulum and whole of the distal surface are covered with rows or cristae of verrucae or spines; *Cingulizonates* (Dybova & Jachowicz) Butterworth, Jansonius, Smith & Staplin, in which the cingulum is prominently divided into an inner thick and an outer thin part; and *Radiizonates* Staplin & Jansonius in which the division of the cingulum into thicker and thinner parts is accompanied by radial striations. These four genera are included by Smith & Butterworth (in press) in a new infraturma — Cingulicavati, described to include trilete cavate spores with simple or ridged laesurae and a comprehensive equatorial thickening (cingulum) or extension (zona) of the outer exine layer. *Densosporites* and *Cristatisporites* were previcusly assigned to the infraturma Cingulati Potonié & Klaus along with cingulate genera in which the exine is not two-layered, whilst *Cingulizonates* and *Radiizonates* were assigned to the infraturma Cingulizonati Dybova & Jachowicz; both infraturma were designated for acavate, zonate spores.

In the U.S.S.R. the species of the group are variously assigned among the following genera: *Euryzonotriletes* Naumova, 1937, with a massive cingulum; *Hymenozonotriletes* Naumova, 1937, with a differentiated cingulum; and *Trematozonotriletes* Naumova, 1937 with an alveolate or punctate cingulum. Luber & Waltz (1941) include all spores of the group in the comprehensive genus *Zonotriletes* Waltz, 1935 which Potonié & Kremp (1954) use at subturma level. Ishchenko (1956, 1958) assigns species with a massive cingulum to *Euryzonotriletes* and others, including forms elsewhere assigned to *Cristatisporites* and *Cingulizonates*, to *Hymenozonotriletes*; one species only is

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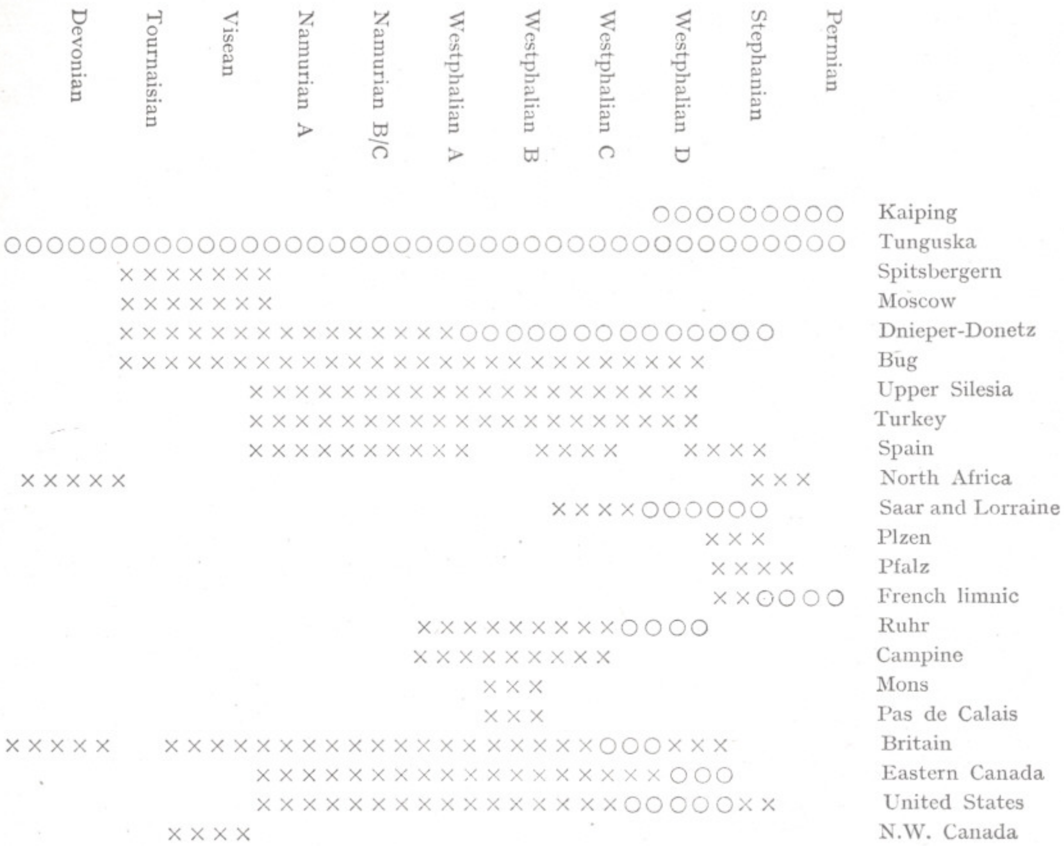
assigned to *Trematozonotriletes* — *T. variabilis* (Waltz) Ishchenko, with a markedly alveolate cingulum.

THE OCCURRENCE OF DENSOSPORES

The association of certain densospores with dull coal was first noted by Thiessen (1930) and was confirmed by other workers. Smith (1957, 1962, 1964) has shown that in the Upper Westphalian A and Westphalian B, *Densosporites sphaerotriangularis* Kosanke, characterising his Densospore Phase, occurs almost exclusively in bands of crassidurain, towards the middle and top of coal seams. Smith (1962) suggested that the peat forming crassidurain was deposited under at least partly aerobic conditions, and that it could have been formed wherever enough peat had accumulated above the general ground water level. This theory was borne out by Butterworth (1964) who showed that *D. sphaerotriangularis*, and hence crassidurain, is particularly abundant in the thick seams which occur towards the stable margins of basins of coal deposition. The prevalence of lycospores in the more expanded part of the sequence occurring nearer to the centres of basins of deposition was demonstrated by this author in the coalfields of Central England and by Hacquebard & Donaldson (1964) in the Sydney Coalfield of Nova Scotia.

The stratigraphical occurrences of spores of the densospore group, which are detailed in the following sections,* are summarized in Text-fig. 1.



TEXT-FIG. 1 — The distribution of densospores in coal basins from which miospore assemblages have been described. (Crosses denote miospore assemblages in which densospores are present, noughts miospore assemblages in which densospores have not been recorded.)

1. Devonian

Richardson (1960, 1965) has described several densospore species from the Middle Old Red Sandstone of north-east Scotland; although the differentiation of the exine into two layers has not been demonstrated in these species, they appear to have the same internal organisation as their Carboniferous equivalents; they differ from Carboniferous species in their much greater size (87 to 159 microns, compared with 25 to 110 microns in the Carboniferous). Two of the species, *Densosporites devonicus* Richardson and *D. orcadensis* Richardson, which have the characteristic bizonate cingulum of *Cingulizonates*, are ornamented with small bifurcating spines such as occur on many Devonian spores. The three species of *Cristatisporites* described differ from younger species only in their greater size. Similar forms have been described by Luber & Waltz (1941) from the Timan Peninsular and the Kuznetsk Basin, and by Naumova (1953) from the Upper Givetian of the Russian Platform.

McGregor (1960) has described a densospore, *D. crassus*, with a massive cingulum and of large size, from a coal of Givetian age in the Canadian Arctic. Since only three specimens of the spore were found this occurrence is perhaps not important; more significant is the record in this seam of 33 per cent of *Tholisporites* Butterworth & Williams, a genus differing from those of the densospore group only in the extension of the equatorial thickening over the distal polar area, and described originally from the Namurian A.

In Richardson *et al.* (1964, TEXT-FIG. 1) *Densosporites* is recorded by Taugourdeau-Lantz from the Frasnian of France and by Peniguel from the Givetian of North Africa. No details of abundance or speciation are given in this paper.

2. Tournaisian and Visean

The largest amount of data on Lower Carboniferous spore assemblage is that from the U.S.S.R. Luber & Waltz (1941, pp. 7, 8 of the Humble Oil and Refining Company's typescript of the Canadian Geological Survey's translation) state that in their Westphalian Floral Area, that is in areas adjoining the Urals, 72 per cent to 75 per cent of the total spores encountered in the Lower Carboniferous are zonate, and of these 60 per cent to 70 per cent are thickly fringed, that is have a cingulum. Of the seven predominant spores listed *Zonotriletes crassipterus* Waltz (*l.c.*, PL. 5, FIG. 64) is a typical *Densosporites* form with a massive cingulum, *Zonotriletes dentatus* Waltz (*l. c.*, PL. 7, FIG. 103) has a cingulum modified by the presence of small cones and *Z. variablilis* (*l. c.*, PL. 5, FIGS. 65, 66) has a punctate cingulum. In the Tunguska Floral Area, to the south and east, spores with ' thick massive fringes ' are stated to be completely lacking.

The rather more detailed assemblages given by Ishchenko (1958, FIGS. 1-11) for sequences in the Dnieper-Donetz Basin show that whereas *Hymenozonotriletes bialatus* (Waltz) Ishchenko, a spore with a bizonate cingulum, and *Trematozonotriletes variablilis* (Waltz) Ishchenko are both common at some horizons in the Tournaisian they are more dominant in the Visean, where in addition *H. commutatus* (Waltz) Ishchenko, with a bizonate cingulum, and *Euryzonotriletes crassipterus* (Waltz) Ishchenko are also common.

Jackowicz (1964, PL. 2) records low numbers of *Densosporites* from the Tournaisian of the Bug Basin of Eastern Poland; this genus is more common in the Visean where species of *Cingulizonates* are also present.

Several of the coals and shales examined by Playford (1962, 1963a) from the Lower Carboniferous of Spitsbergen contain high numbers of densospores. In this author's Tournaisian material (PLAYFORD, 1963a, TABLE 1, p. 661) the coal sample G1091 contains 36 per cent *Densosporites dentatus* (Waltz) Potonié & Kremp and smaller percentages of *D. spitsbergensis* Playford [*D. regalis* (Bharadwaj & Venkatachala) Smith & Butterworth] and *D. diatretus* Playford, forms with verrucose and spinose ornament of the cingulum, and *D. variomarginatus* Playford, which has an irregularly thickened cingulum and a characteristic undulating equatorial outline. Several of the assemblages from other sediments contain over 20 per cent of densospores, the most commonly occurring forms being *D. dentatus*, *D. diatretus* and *D. variomarginatus*. The Visean material examined also contained a coal rich in densospores (*l.c.*, TABLE 2, p. 662, sample G1092) in which the dominant species are *D. variabilis* and

D. regalis; these species, along with *D. bialatus* and *D. dentatus* are sometimes also abundant in the associated sediments. Bharadwaj & Venkatachala (1961, p. 40) record 2·4 per cent of *Densosporites* and 60·8 per cent of *Cristatisporites* in a Lower Carboniferous shale from Spitsbergen; their interpretation of *Cristatisporites* is somewhat broader than that used here and includes species which the present author would assign to *Densosporites*.

Sullivan (1964a & b) has described Tournaisian and Viséan assemblages from the Forest of Dean in Britain; no densospores occurred in the former, but in the latter *Densosporites* (*Anulatisporites*) *anulatus* (Loose) Schopf, Wilson & Bentall, *Densosporites covensis* Berry, forms with a massive cingulum, and species of the related genus *Vallatisporites* Hacquebard are represented. None of these species was common.

Spores very similar to *Densospores regalis* have been found in Visean coals from the north of Engaland (Smith & Butterworth, in press) along with forms with a bizonate cingulum referable to *Cingulizonates bialatus* (Waltz) Smith & Butterworth. Slightly higher in the sequence *D. triangularis* Kosanke, with a massive cingulum, and *Tholisporites scoticus* Butterworth & Williams may be abundant; *Cingulizonates* cf. *capistratus* (Hoffmeister, Staplin & Malloy) Staplin & Jansonius, with a coarsely alveolate cingulum, appears in the uppermost Viséan.

Hacquebard's (1957) and Playford's (1963b) descriptions of spores from the Horton Group of Nova Scotia contain few references to spores of the densospore group; *Vallatisporites*, not dissimilar to *Radiizonates*, however is a related form morphologically and is abundant in four of Playford's samples (*l.c.*, Table 1, p. 38) and *Cristatisporites* is present but rarely common. Staplin (1960, p. 3, Fig. 2a) obtained almost 20 per cent of densospores from the underclay of a coal in the Golata Formation of Alberta (Visean); these were mainly spores with a massive cingulum but included a markedly bizonate species, *Cingulizonates landesii* (Staplin) Staplin & Jansonius, and *Densosporites spinifer* Hoffmeister, Staplin & Malloy, with apiculate ornament of the cingulum. A Visean coal from the South Nahanni River area of Canada (Hacquebard & Barss, 1957) contained 23 per cent of *Densosporites*, most of which were forms with a bizonate cingulum and some evidence of radial plications (*l. c.*, Pl. 4, Figs. 11-14). A similar assemblage, in which *Cingulizonates bialatus* was the second most abundant spore encountered, has been described by Playford & Barss (1963) from Axel Heiberg Island in the Canadian Arctic. These authors state (*l.c.*, p. 4) that a comparable assemblage occurred in a sample examined from Ellesmere Island, also in the Canadian Arctic.

3. Namurian

Records of densospores in rocks of Middle and Upper Carboniferous age in the U.S.S.R. are scant. Luber & Waltz (1941) state that in the Middle Carboniferous of the Donetz Basin there is an almost complete lack of spores with thickened fringes. Ishchenko (1958) however records certain densospore species as characteristic spores at seven of the eight Namurian localities examined from the Dnieper-Donetz Basin; *Hymenozonotriletes bialatus* is the most recurrent species, but *H. commutatus*, *Euryzonotriletes crassipterus*, *H. intermedius* (Waltz) Ishchenko with verrucose ornament, and *Trematozonotriletes variabilis* are also mentioned. Only *H. bialatus* and *H. commutatus* are recorded from the Bashkirian.

Densosporites formosus Artüz, with a massive cingulum, similar to *D. triangularis* Kosanke, is stated by Artüz (1957, p. 259) to be the only densospores species characteristic of the Namurian Alimolla Seam of the Zonguldak area of Turkey. Agrali (1964) records the occurrence of densospores having massive, cristate and bizonate cinguli throughout the Namurian of the Amasra Basin; they attain their greatest frequency in the middle of the Namurian where they constitute from five to ten per cent of the assemblages of the two lower seams examined, and from 25 to 50 per cent of the assemblages of the highest seam (*l.c.*, Fig. 1). The dominant species present is *Densosporites marginatus* Artüz (cf. *Cingulizonates bialatus*).

Horst (1955) records very high numbers of an indeterminate densospore (?*Densosporites intermedius* Butterworth & Williams) in the upper part of the Namurian A of Western Upper Silesia, especially in the Andreas Seam (*l.c.*, p. 185), and also in the Sattelflöz Group (Namurian B) of the Mahrisch-Ostrau region, which contains a single thick coal seam. Dybova & Jachowicz (1957) give detailed tables of spore frequencies in Upper Silesia which include data for the genera *Anulatisporites* (interpretated by these authors as spores with an alveolate or pitted cingulum), *Densosporites*, including *Cristatisporites*, and *Cingulizonates*, including *Radiizonates*. *Densosporites*, mainly *D. granulatus* Dybova & Jachowicz, comparable to *D. triangulatus* Kosanke, and *D. verrucosus* Dybova & Jachowicz, approaching the genus *Cristatisporites* in its density of ornament, reach peaks of a little less than 30 per cent in the Namurian A and of more than 70 per cent in the Namurian B/C. *Anulatisporites*, mainly *Densosporites* (*Anulatisporites*) *anulatus* (Loose) Schopf, Wilson & Bentall (1944), *A. baccatus* Dubova & Jachowicz and *A. coronatus* Dybova & Jachowicz, both alveolate, reach peaks of 60 per cent in the lower part of the Namurian A and at the junction of the Namurian A with the Namurian B/C. Moderate numbers of *Cingulizonates* [*C. tuberosus* Dybova & Jachowicz and *C. radiatus* Dybova & Jachowicz, comparable to *C. bialatus* and *Radiizonates striatus* (Knox) Staplin & Jansonius respectively] occur in the Namurian A and are more common (about 15 per cent) in the Namurian B/C where they occur along with *C. asteroides* Dybova & Jachowicz and *C. karczewskii* Dybova & Jachowicz, analogous to *Radiizonates aligerens* (Knox) Staplin & Jansonius and *R. rotatus* (Kosanke) Staplin & Jansonius respectively. In the Bug Basin *Densosporites* and *Cingulizonates* both reach maximum percentages in the higher part of the Namurian (JACHOWICZ, 1964, PL. 2, and p. 1203) and *Radiizonates* (*Cingulizonates*) *asteroides* Dybova & Jachowicz first appears at these horizons.

Neves (1964) records abundant *Densosporites anulatus*, *D. spinosus* Dybova & Jachowicz, *D. triangularis* and *Radiizonates striatus* from lower Namurian coals in Northern Spain. Higher in the sequence these species occur along with *Densosporites crassigranifer* Artüz, *D. microanatolicus* Artüz (forms with ornament intermediate between those of *Cristatisporites* and *Cingulizonates*) and *D. sphaerotriangularis* Kosanke.

British Namurian A coals with assemblages containing the genera *Rotaspora* and *Tripartites* have been described by Butterworth & Williams (1958) from Scotland. In these coals *Cingulizonates* cf. *capistratus* (Hoffmeister, Staplin & Malloy) Staplin & Jansonius are abundant and *Densosporites intermedius* Butterworth & Williams, *D. pseudoannulatus* Butterworth & Williams and *D. triangularis* (with which *D. spongeosus* Butterworth & Williams is synonomous) are common. At slightly higher horizons in the Namurian of the South Pennines Neves (1961) found *Densosporites spinosus* Dybova & Jachowicz (approaching *Cristatisporites* in form) to be common in some coals and marine shales.

Hacquebard, Barss & Donaldson (1960) record *Densosporites* from the Canso Group (?Namurian A) of Nova Scotia, but give no frequencies.

The genus *Densosporites* was first described by Berry (1937) from the Pennington Coal of Tennessee, of Mississippian age; the assemblage contained several spores with a massive cingulum, including the type species of the genus — *D. covensis* Berry. Hoffmeister, Staplin & Malloy (1956b, P. 378) state that *Densosporites* is a characteristic genus of Upper Mississippian and Lower Pennsylvanian rocks generally. In the Hardinsburg Formation of Kentucky and Illinois (Lower Namurian or Upper Visean in age, containing the genera *Rotaspora* and *Tripartes*) they record from one to sixteen per cent of *Densosporites* at all horizons examined (*l.c.*, p. 377, TABLE 1). *Densosporites intermedius*, with which *D. tenuis* Hoffmeister, Staplin & Malloy is synonomous, is the only abundant species noted. Schemel (1950) recorded 92 per cent of densospores from a coal of similar age from Daggett County, Utah; they were referred to *Densosporites dominatoris* Schemel and are not unlike *D. intermedius*.

4. Westphalian

Ishchenko (1958) lists no densospores among the characteristic species present in Moscovian coals of the Dnieper-Donetz Basin but includes *Hymenozonotriletes bialatus* and *H. commutatus* in the lists for the two Bashkirian sequences examined. According to his frequency table (*l.c.*, TABLE 3) these species do not persist above the Bashkirian and are the only two densospores to survive the Namurian A.

Artüz (1957) records a varied suite of densospores from the Westphalian A Sulu and Büyük Seam of the Zonguldak area of Turkey; this includes *Densosporites micro-*

silvanus Artüz, a granulate form with a massive cingulum, *D. adornatus* Artüz and *D. marginatus* Artüz, forms with a bizonate cingulum referable to *Cingulizonates, Densosporites flavus* Artüz, and the rather unusual *D. microponticus* Artüz and *D. microanatolicus* Artüz, cristate forms which also exhibit an inner thickening of the cingulum. *D. microanatolicus* and an unnamed species of *Densosporites* were also abundant (10 to 30 per cent) in the Westphalian C Kalin and Ara Seams of the Amasra-Tarlaagzi Basins (ARTÜZ, 1963). Agrali (1964) records extremely varied and abundant densospore assemblages from the Westphalian of the Amasra Basin. These spores are present in all of the seams examined, constituting over 50 per cent of the assemblages of several seams in the Westphalian A and B and the lower part of the Westphalian C, and ranging from five to 25 per cent in the upper part of the Westphalian D (*l.c.*, FIG. 1). The ranges given for the 22 species considered are long and very much at variance with their ranges elsewhere; no photographs or descriptions are given to support the identifications made. Forms with a massive cingulum and cristate and bizonate forms range from the Westphalian A to the Westphalian D; *Densosporites lobatus* Kosanke, with a massive cingulum, is one of the most abundant species throughout the Westphalian B and C. Radiizonate forms extend from the middle of the Westphalian A to the top of the Westphalian D and *Radiizonates* (*Densisporites*) *faunus* (Ibrahim) Butterworth & Smith is one of the dominant species of the Westphalian C.

Neves (1964) records *Densosporites microanatolicus* from the Westphalian A of Northern Spain, where it occurs in association with *Densosporites crassigranifer* Artüz, a bizonate species with radially arranged verrucae, *Densosporites anulatus, D. sphaerotriangularis* and *Radiizonates* (*Densosporites*) *striatus*.

Dybova & Jachowicz (1957) record copious densospores from the Westphalian of Upper Silesia. As a genus *Densosporites* (*l.c.*, TABLE 168) reaches peaks of almost 30 per cent in the Westphalian A and B and peaks of more than 70 per cent in the Westphalian C. In the Westphalian D it tends to decline. The most prominent species throughout is *D. granulatus* Dybova & Jachowicz; this is accompanied by the *Cristatisporites*-like *D. verrucosus* Dybova & Jachowicz and *D. spinosus* Dybova & Jachowicz in the Westphalian A, and by *D. decorus* Dybova & Jachowicz [equated by these authors, p. 163, with *Cristatisporites indignabundus* (Loose) Potonié & Kremp] at higher horizons. *Anulatisporites* persists throughout at lower levels of frequency but may reach 20 or 30 per cent in the lower part of the Westphalian B. *Cingulizonates* reaches a peak of 30 per cent in the middle part of the Westphalian A and is not recorded from above the Westphalian B. The main species in the Westphalian A is *C. tuberosus* Dybova & Jachowicz, analogous to *C. bialatus*, and the *Radiizonates*-like species *C. asteroides* Dybova & Jachowicz and *C. karczewskii* Dybova & Jachowicz also occur; these latter persist into the Westphalian B as important species.

In the Bug Basin of Poland (JACHOWICZ, 1964, PL. 2) *Densosporites* is common throughout the Westphalian, decreasing slightly towards the top of the sequence, and *Cingulizonates* is common at the base of the Westphalian A, but thereafter becomes less frequent and disappears in the lower part of the Westphalian C. *Cristatisporites* (JACHOWICZ, in Discussion of BUTTERWORTH *et al.*, 1964a, p. 1055) is confined to the Westphalian.

Grebe (1962) has listed the frequencies of *Densosporites* (including *Cristatisporites*) and *Anulatisporites* in the Westphalian B and C coals of the Ruhr. She shows (*l.c.*, TABLE 1) that *Anulatisporites*, mainly *Densosporites* (*Anulatisporites*) *anulatus*, is most prevalent in the Westphalian B and only occasionally reaches frequencies greater than 20 per cent. *Densosporites* seldom exceeds a frequency of 50 per cent but may be greater than 60 per cent in the lower part of the Westphalian C where it reaches a maximum. *D. sphaerotriangularis* Kosanke may be prominent in the Westphalian B but the most common species, particularly in the Westphalian C, is *Radiizonates* (*Densosporites*) *faunus* (Ibrahim) Smith & Butterworth. Other species, including those which would be assigned to *Cingulizonates*, are rare. *Cristatisporites indignabundus* (Loose) Potonié & Kremp and *C. connexus* Potonié & Kremp, spinose and verrucose forms respectively, seldom exceed 10 per cent.

These results compare with those of Kremp (in BHARADWAJ & KREMP, 1955,

TABLE 3, p. 57) in which the presence is also noted of *Densosporites sphaerotriangularis* in the Westphalian A coals of the Ruhr. Bharadwaj & Kremp (*l.c.*, TABLE 5, & BHARADWAJ, 1957b) found no densospores in the Velener Beds which lie above the Dorstener Beds, the highest horizons examined by Grebe; the Velener Beds are said to lie at the base of the Westphalian D.

Piérart (1962) records abundant *Densosporites* (*Anulatisporites*) *anulatus* from the Westphalian B of the Mons area of Belgium. Other species of *Densosporites*, including those which would be assigned to the genus *Cingulizonates*, are not common and *Cristatisporites* is recorded from only two horizons (*l.c.*, TABLE 2). *Densosporites* is also sometimes abundant in the Westphalian A and B of the Belgian Campine (NOEL, in BUTTERWORTH *et al.*, 1964b); in the upper Westphalian C Piérart (1958) records *Radiizonates* (*Densosporites*) *faunus* and *Densosporites sphaerotriagnularis* throughout, and a species of *Anulatisporites* from several horizons.

Alpern (1959, p. III of complément) records about 5 per cent of *Densosporites* from the Westphalian B of the Pas de Calais Coalfield.

In Britain densospores have been found at all Westphalian horizons with the exception of the higher part of the Westphalian C where there is a notable hiatus (Smith & Butterworth, in press). Lower Westphalian A horizons are characterized by *Densosporites anulatus* and *Radiizonates striatus*. *Densosporites sphaerotriangularis* and species of *Cristatisporites* appear at about the middle of the Westphalian A and remain abundant almost to the top of the Westphalian B where they tend to be replaced by *Cingulizonates loricatus* (Loose) Butterworth & Smith and *Cristatisporites solaris* (Balme) Butterworth & Smith in the lower part of the Westphalian C. *Radiizonates aligerens* (Knox) Staplin & Jansonius and *R. striatus* characterize the higher part of the Westphalian A, *Radiizonates tenuis* (Loose) Butterworth & Smith the Westphalian B, and *R. faunus* the lower part of the Westphalian C. Higher in the Westphalian C smaller species of *Cristatisporites* such as *C. saarensis* Bharadwaj may occur. In the southern part of the country spores indistinguishable from *Densosporites sphaerotriangularis*, except for their smaller size, have been found in Westphalian D coals.

Turning to the limnic coal basins of Europe, Bharadwaj (1955, 1957a) has described a suite of densospores from the upper part of the Westphalian C of the Saar; this includes *D. sphaerotriangularis*, *D. lori* Bharadwaj, a bizonate species, *Cristatisporites elegans* Bharadwaj and *C. saarensis* Bharadwaj, which are notable for their small size — all, excepting the first, are less than 50 microns in diameter.

The distribution of Westphalian densospores in the French coal basin of Lorraine is summarized by Alpern (1963b, p. 2) who divided the group into *Cingulizonates* and *Cristatisporites*, forms with a massive cingulum being either not present or not considered. The specimens photographed are not so small as those described by Bharadwaj from the Westphalian C of the Saar. *Critatisporites* is fairly common in the Westphalian B, reaches a maximum of 65 per cent in the Westphalian C, ranges from 8 to 30 per cent in the lower part of the Westphalian D, and then disappears. *Cingulizonates* is confined to the Westphalian B and C where it maintains a frequency of about 25 per cent. Venkatachala & Bharadwaj (1962, p. 195) record less than one per cent of *Cristatisporites* in one of the 13 coals examined by them from the Westphalian D of Faulquemont Colliery, Lorraine.

In Spain Wagner (in Discussion of WAGNER, 1962, p. 762) has indicated that *Densosporites* occurred in a sample examined from the Westphalian C of Lieres (Asturias); examination of Wagner's material and unpublished photographs has indicated that these are forms with a massive cingulum, or radiizonate forms not unlike *R. faunus*.

In the Maritime Provinces of Canada, Hacquebard, Barss & Donaldson (1960, FIG. 2) record *Densosporites* and *Cristatisporites* in the lower part of the Westphalian A (Howley Beds of Newfoundland), the latter genus only in the upper part of the Westphalian A (Riversdale Group), *Cristatisporites* and rare *Densosporites* in the Westphalian B (Cumberland Group) and *Critatisporites* in the *Lonchopteris* Zone of the Westphalian C. *Densosporites* is recorded from one seam only in the lower part of the Westphalian D.

The most comprehensive description of Westphalian densospores in North America is that given by Kosanke (1950) for the Pennsylvanian of Illinois. He found *Densosporites* (*l.c.*, PL. 17) to be restricted entirely to the Tradewater and Caseyville Groups. This range corresponds to the Westphalian A-C (Kosanke, in Butterworth *et al.*, 1964b, TABLE 1). Densospores are abundant only in the Reynoldsburg Coal towards the base of the sequence in which *D. reynoldsburgensis* Kosanke (*D. anulatus*) is the chief species present (KOSANKE, 1950, p. 31). Elsewhere in the sequence Kosanke (personal communication) has indicated that *Densosporites lobatus* Kosanke is the most representative species and that forms attributable to the genera *Cristatisporites* and *Cingulizonates* are much less prominent than at equivalent horizons in Europe. *Radiizonates difformis* (Kosanke) Staplin & Jansonius and *R. rotatus* (Kosanke) Staplin & Jansonius are restricted to a few coals towards the base of the Tradewater Group.

Cross (1947) in a preliminary study of miospore distribution in the lower part of the Pennsylvanian in the Appakctian region, noted the presence of *Densosporites*, particularly in the Alma Seam where it is the dominant spore (*l.c.*, p. 305). This work was expanded by Cross & Schemel (1952) who compared the ranges of the genus *Densosporites* in the Western Interior Basin (Schemel's work), the Easter Interior Basin (Kosanke's work) and the Appalachian region (CROSS & SCHEMEL, 1952, FIG. 4). They found that the upper limit of the genus occurred at almost equivalent horizons in all three regions, viz. near to the base of the Carbondale Formation.

Hoffmeister, Staplin & Malloy (1955a) compared the known ranges of all miospore genera in North America with their ranges elsewhere in the world. They state that the genus *Densosporites* reaches its maximum frequencies in the upper part of the Mississippian and the lower part of the Pennsylvanian; they quote the range given above and also note the occurrence of densospores in the uppermost Pennsylvanian of West Texas.

Wilson & Hoffmeister (1956) described *Cirratriradites intermedius* from the Westphalian D Croweburg Coal in Oklahoma. This spore (*l. c.*, PL. 2, FIG. 9) has the appearance of a densospore with a relatively narrow, massive cingulum. In the Croweburg Coal samples its greatest frequency was 5·5 per cent, average 1·3 per cent.

Guennel (1958) recorded abundant densospores at certain horizons in the lower Pennsylvanian of Indiana. He ascribed the spores to two species only — *Densosporites reynoldsburgensis* (equals *D. anulatus*) and *D. lobatus* Kosanke which includes forms with a massive or slightly differentiated cingulum. Peaks of abundance are shown (*l.c.*, FIG. 7) at a low horizon in the Mansfield Formation and at an horizon in the lower part of the Brazil Formation higher in the sequence.

Cropp (1960) found *Densosporites* to be continuously present throughout coals of Pottsville age (Westphalian A to C approximately) in the Warrior Basin of Mississippi and Alabama; they were abundant in three coals towards the middle of the sequence (*l.c.*, TEXT-FIG. 4). The same author (CROPP, 1963) described, at generic level, the spore contents of 15 coals from the Pennsylvanian of Tennessee and found *Densosporites* to be common in most of them and abundant in a few. By analogy with the word of Kosanke (1950) he concluded that the strata concided roughly with the Caseyville, Abbott and Spoon Formations (Westphalian A to C; Caseyville and Tradewater Groups of Kosanke, 1950).

5. Stephanian and Permian

Piérart (1956, PL. 5, FIG. 7) figures densospores with spinose ornament from the French limnic basins of Blanzy and Decazeville (Middle, and Middle and Upper Stephanian respectively), and Doubinger (1958) records high numbers of densospores with a massive cingulum, sometimes slightly ornamented, from the Decazeville Basin, but found them to be less common at Saint-Perdoux (IDEM, 1951).

Alpern (1959, p. III of complément; 1960, PL. 19) has indicated that densospores disappear in the Westphalian D of France and reappear in the Lower and Middle Stephanian; they diminish again and are extremely rare in the Upper Stephanian and Permian. Further details of the Stephanian coals of Lons in the Jura (ALPERN, 1959, pp. 231, 232) indicate that the densospores present are very similar to some of the Westphalian B species — *Densosporites lobatus* Kosanke, *D. sphaerotriangularis* Kosanke, *D duriti* Potonié & Kremp (a slightly more ornate form of *D. sphaerotriangularis*), *Cristatisporites indignabundus* (Loose) Potonié & Kremp and *C. solaris* (Balme) Butterworth & Smith. On the whole however they tend to be larger — *Densosporites major* Alpern, which is restricted to the Stephanian, has a diameter of from 100 to 160 microns. Alpern (1959, pp. 232, 246) has demonstrated that in the Lons area the densospores have a cyclic distribution which is of use in the correlation of the coals. *Densosporites* is rare in the Decize Basin (ALPERN, 1959. p. 284) and less than one per cent of *Cristatisporites* are recorded by Alpern (1963a, p. 2) from the coals in the upper part of the Stephanian and the base of the Autunian of St. Étienne. On the other hand no densospores were recorded by Alpern (1959) in the Stephanian coals of Lorraine (MORSBACH, *l. c.*, p. 266), the Loire Basin (TRIOLLIÈRE, *l. c.*, p. 275) or from the Permian coals of the Aumance Basin (*l.c.*, p. 296).

Bharadwaj & Venkatachala (1957, p. 9, TABLE 4) record less than 5 per cent of a species of *Densosporites* from an upper Stephanian C coal in the Pfalz Basin, and unassigned densospores are recorded by Kalibova (1962, PL. 4, FIG. 1) from the Stephanian Kounov Seam of the Kladno-Rakovnik Basin, and by the same author (1964) from a Lower Stephanian coal of the Plzen Basin; further details of each of these latter occurrences are to be published later. Bharadwaj (1955, 1957a) does not record any densospores from the Stephanian coals of the Saar.

In the limnic basins of Spain Wagner (in Discussion of WAGNER, 1962, p. 762) has indicated that *Densosporites* occurs in three samples investigated from the Stephanian B/C of Puertollano (Cuidad Real) and that in two of these they were particularly abundant; one of the seams was No. 3 Coal of Santa Maria Colliery and all were samples from which Dijkstra (1955) has published descriptions of megaspores. Examination of Wagner's material and unpublished photographs has indicated that the spores are highly ornamented, approaching *Cristatisporites* in form.

Zonate densospores with a crenulate flange and prominent laesurae extending to the equator have been isolated from sandy shales, of probable Permian age, from the Eastern Desert of Egypt (SCHÜRMANN, BURGER & DIJKSTRA, 1963, PL. 1, FIG. 2).

Densospores were not found in the Upper Carboniferous coals of the Donetz Basin described by Luber & Waltz (1941) or in the Stephanian and Permian assemblages described by Imgrund (1960) from the Kaiping Basin of China.

In North America Hoffmeister, Staplin & Malloy (1955a) note the occurrence of ?*Densosporites* and *Cristatisporites* in the Upper Cisco (Pennsylvanian) or Lower Wolfcamp (Permian) of North Texas (*l.c.*, p. 13). Peppers (1964) has recorded about one per cent of *Densosporites* from clastic sediments at several horizons in the McLeansboro Group at the top of the Pennsylvanian; he attributes these occurrences either to the reworking of older sediments or to the continued growth of the parent plants in areas outside those of coal formation (*l.c.*, p. 60).

SUMMARY OF OCCURRENCES

Densospores are first recorded from the Devonian of Russia, Scotland, France and North Africa, and, in very low numbers, from the Canadian Arctic.

The earliest densospores with a more Carboniferous aspect, that is with a smaller size and without the grapnel-like ornament characteristic of Devonian spores in general, are described from the Lower Carboniferous of northern latitudes, with the greatest diversity occurring in Spitsbergen.

By Namurian times the plants producing densospores had passed their peak in European Russia but flourished in Canada, Britain, Silesia and, further south, in the United States, Northern Spain and Turkey. The greatest diversity in the assemblages occurred at the European localities.

The group declined in the upper part of the Namurian in European Russia and in the middle of the Westphalian in North America. The most varied Westphalian A assemblages occur where the underlying Namurian assemblages are also varied but in the Westphalian B and C the centres of diversity moved to the coalfields of northern Europe, and densospores occurred for the first time in the European limnic fields. There was a general decline in densospore-producing plants in the Westphalian D but they persisted, patchily, in the Stephanian and Permian of the limnic basins.

No densospores have been recorded from the Tunguska area (Angara) of Asiatic Russia or from the Kaiping Basin of China.

Comparisons among the frequencies of the various genera present at different localities must be treated with caution since not all of the assemblages have been described in the same detail. The forms described from North America are restricted in variety, having either a massive cingulum or one which is weakly bizonate or cristate; forms with a bizonate cingulum appear to dominate in European Russia. Bizonate and radiizonate forms are not generally found above the Westphalian C although they are recorded from the Westphalian D of Turkey and a related form occurs in the Permian of Egypt.

DISCUSSION

The foregoing data are fragmentary and future investigations will doubtless disclose the presence of further densospore-rich coal horizons. There is sufficient evidence however to demonstrate that the densospores, which have been used by various workers, including the present author, as time indices, have widely different stratigraphical ranges in different parts of the northern hemisphere. Although they are frequently present in Carboniferous coal seams there are extensive sequences of coals in which they do not occur. When present, their numbers and variety show considerable variation between localities. In general the diversity of densospores is greatest in Spitsbergen and other northern areas in the Lower Carboniferous, and in European localities in the Upper Carboniferous.

The longest ranges of densospores are found, as might be expected, in the paralic basins of the continental shelf areas (Britain, Poland and Upper Silesia) and other areas such as the Turkish Amasra Basin where because of the relative stability the formation of coal itself was most prolonged. Elsewhere, in the areas of the foredeeps, various parts of the sequence are represented by marine beds and coal formation was thus delayed or brought prematurely to an end. Even in the shelf area, in Britain for instance, coal formation was possible in Visean and Namurian times only in the northern part of the country; further south the Coal Measures-type rocks are replaced by limestone sequences. Coal formation generally, and the presence of the plants producing densospores in particular, were also impeded by the effects of earth movements. The coal swamps which became established after the various movements had died down were only occasionally of the type to yield densospores; in Britain the red beds, representing arid, uplifted areas, form the whole of the upper part of the Westphalian in the northern part of the country; further south, in the English Midlands, the red beds of the Westphalian C, the Etruria Marl, are succeeded by more coal-bearing rocks but in these the coals, which are generally thin and impersistent, do not contain densospores. It is only in the coalfields of the extreme south of the country that conditions in the Westphalian D were suitable for the growth in any numbers of the densospore-bearing plants.

In Europe there are few Carboniferous coal sequences in which densospores do not occur, and these sequences are not extensive. In Russia and North America on the other hand there are long sections of coal-bearing strata from which densospores have not been recorded. A particularly detailed account of one such section is available for the Illionis Basin (KOSANKE, SIMON, WANLESS & WILLMAN, 1960) from which Kosanke (1950) has described the miospore assemblages. The Pennsylvanian of Illinois is divided into three groups: the McCormick Group at the base consists of the Caseyville and Abbott Formations and is characterized by thick sandstones, thin discontinuous coals and rare limestones; the succeeding Kewanee Group, including the Spoon and Carbondale Formations, has more widespread coal development, fewer sandstones and widespread limestones of uniform thickness; and the McLeasnboro Group at the top of the sequence has thick, abundant limestones and thin coal seams. The densospores recorded by Kosanke (1950) are restricted to the coals of the McCormick Group and to the Spoon Formation of the Kewanee Group. They are prominent at only two horizons in this sequence and show relatively little variation in form. The Carbondale Formation contains coal seams from two to seven and occasionally fifteen feet thick; the absence of densospores from such an apparently congenial environment, and at horizons equivalent to those at which they were present elsewhere in the northern hemisphere, suggests that the prohibiting factor may have been climatic, most likely a decrease in humidity (*see* SMITH, 1964). It is conceivable that the climatic changes which led to the disappearance of densospores in the upper part of the Westphalian C in parts of Europe were also responsible for the decline of the densospores in Illinois; in Europe the climatic changes were closely followed by uplift of the land areas which precluded the formation of coal, whereas in Illinois coal formation continued but without the development of the type of swamps in which the plants producing densospores thrived.

CONCLUSIONS

Densospores cccur in coals deposited between the Middle Devonian and the Autunian in the Euranevican Province of the northern hemisphere. They first appear in the more northern latitudes and are displaced gradually southwards. The youngest densospores occur in the European limnic basins.

Densospores are most varied and abundant in Western Europe, especially in regions of slow subsidence such as continental shelf areas where they tend also to have the longest stratigraphical ranges, but their presence may be further controlled by considerations of climate.

It is concluded that densospores can be used as stratigraphic indices only when their ranges within a particular area are known.

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