

ASPECTS OF LATE DEVONIAN AND EARLY CARBONIFEROUS PALYNOLOGY OF SOUTHERN IRELAND. I. THE *CYRTOSPORA* *CRISTIFER* MORPHON

C. J. VAN DER ZWAN

Laboratory of Palaeobotany and Palynology, State University, Utrecht (The Netherlands)

(Received September 4, 1978)

ABSTRACT

Van der Zwan, C. J., 1979. Aspects of Late Devonian and Early Carboniferous palynology of southern Ireland. I. The *Cyrtospora cristifer* morphon. Rev. Palaeobot. Palynol., 28: 1–20.

In the Tournaisian deposits of southern Ireland, *Cyrtospora cristifer* (Luber) nov. comb. et emend. Van der Zwan, *Ceratospirites* sp.A (present paper) and *Mooreisporites* sp.A (present paper) are regular components. These species show continuous variation. In order to emphasize such a variation, the morphon concept is here established. This concept is intermediate between the typological classification and the interpretative palynodeme concept.

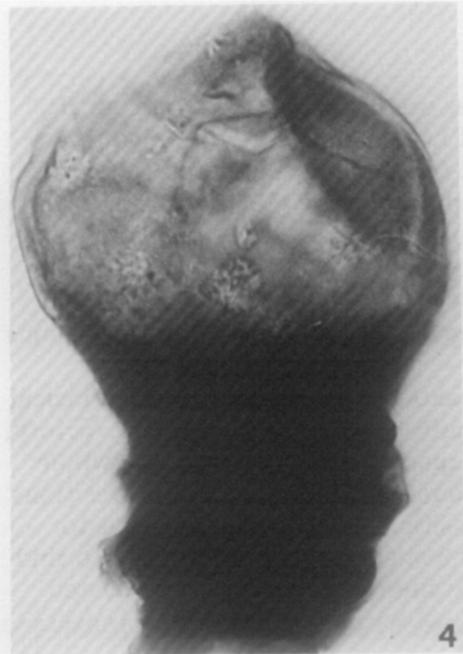
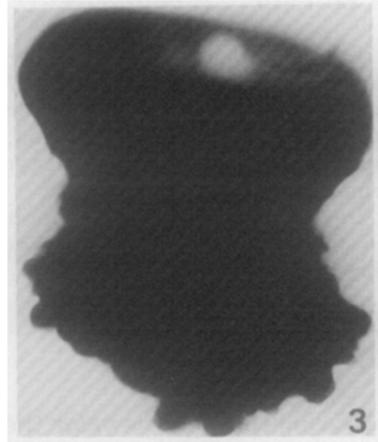
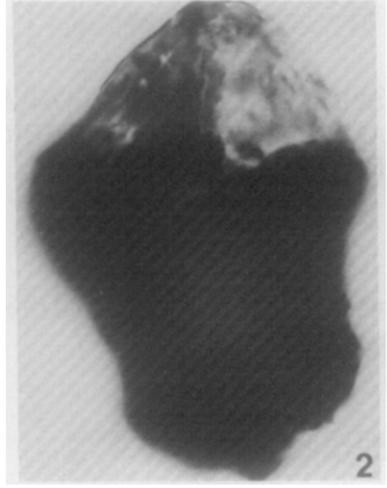
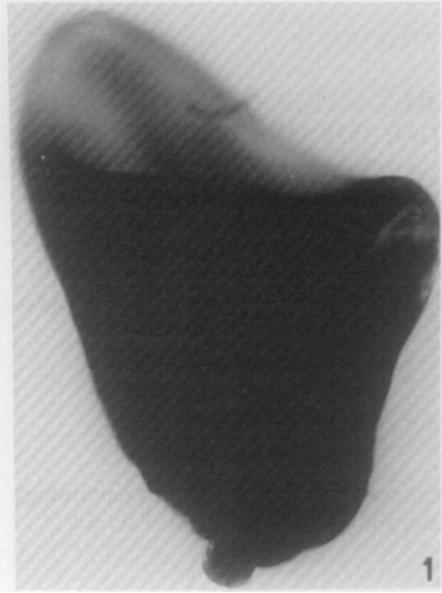
In the present paper the taxonomy of the individual species united into the *C. cristifer* morphon, and the application of the *C. cristifer* morphon in biostratigraphy and phytogeography are discussed.

INTRODUCTION

During the last few years the author has been engaged in palynological investigations of the Upper Devonian and Lower Carboniferous of southern Ireland. These investigations resulted in a first publication emphasizing the relationship between palaeogeography and palynology (Van der Zwan and Van Veen, 1978) and will, in due time, culminate in a synthesis of the palynology, palynostratigraphy and palaeogeography of this area.

In the present paper the author discusses one of his views on the taxonomy and on the stratigraphically and geographically determined relationships of palynomorphs.

During this research the conventional taxonomic concepts of a typological approach to the identification of palynomorphs proved rather unsatisfactory, as this approach emphasizes one selected specimen as typical for the whole species. In the material under consideration, however, all kinds of transitions from one species to another and even transitions from one form genus to another were considered. This assessment instigated research in order to find other concepts emphasizing the variability among morphologically related



palynomorphs. As a result of this research, the morphon is here introduced. This concept is complementary to the typological approach and may find practical application in stratigraphically and geographically restricted palynological studies.

In the present paper the concept is illustrated on the basis of a discussion of the taxonomy, morphological variation, biostratigraphical and geographical distribution of *Cyrtospora cristifer* (Luber, 1941) nov. comb. et emend. Van der Zwan (present paper), *Ceratosporites* sp.A (present paper) and *Mooreisporites* sp.A (present paper), which are united into the *C. cristifer* morphon.

DESCRIPTIVE PALYNOLOGY

Form genus: *Cyrtospora* Winslow 1962.

Type species: *Cyrtospora clavigera* Winslow 1962.

nom. illeg. (correct name *Cyrtospora cristifer* (Luber, 1941) nov. comb. Van der Zwan).

Remarks: The monotypic form genus *Cyrtospora* was established by Winslow (1962). Previously, however, a palynological species showing the morphological characteristics of *Cyrtospora* was already formally described by Luber and Waltz (1941) as *Azonotriletes cristifer*. This species has subsequently been included in *Lophozonotriletes*, *Anisozonotriletes* and in *Tholisporites*. An identical form has been described as *Torispora? tiara* by Staplin (1961).

Species: *Cyrtospora cristifer* (Luber, 1941) nov. comb. et emend. Van der Zwan.

Basionym: *Azonotriletes cristifer* Luber, 1941, in Luber and Waltz (1941), Soviet Union Geol. Inst. Trans. (VSEGEI), Fascicle 139, p.12.

1957: *Lophozonotriletes cristifer* (Luber) Kedo

1961: *Torispora? tiara* Staplin

1962: *Cyrtospora clavigera* Winslow

1966: *Tholispora cristifer* (Luber) Luber

1971: *Anisozonotriletes cristifer* (Luber) Byvsheva

Holotype: *Azonotriletes cristifer* Luber, 1941, pl.I, fig.10.

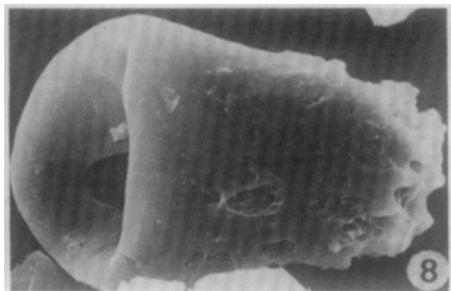
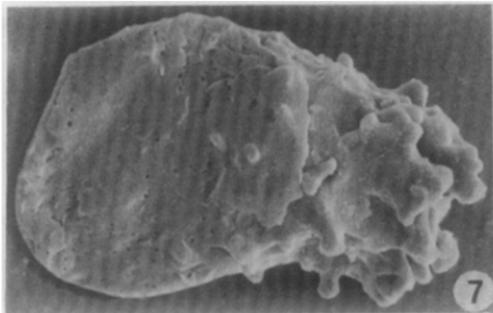
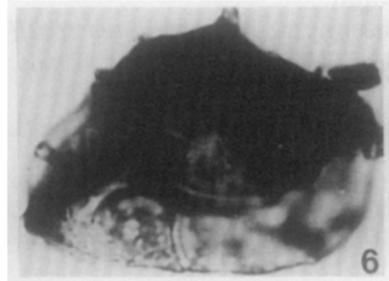
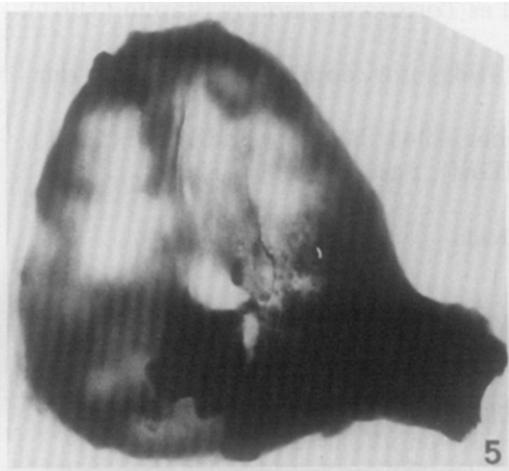
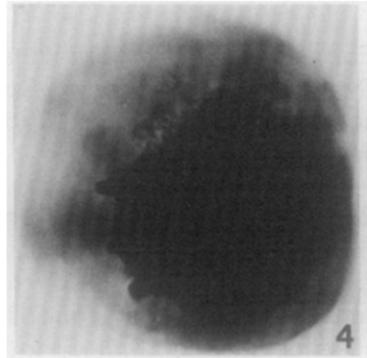
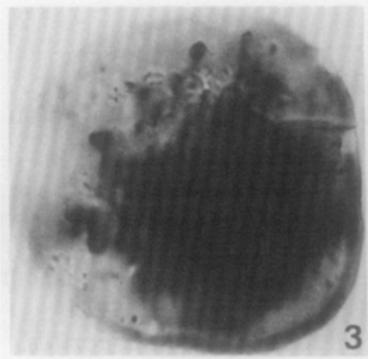
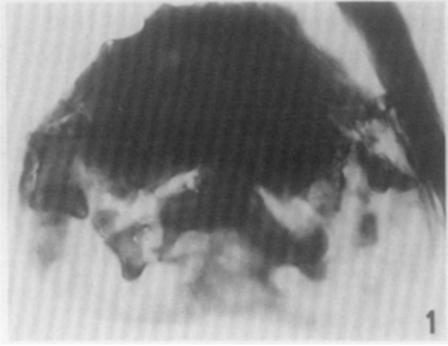
Figured specimens: Plates I, II, III, 1–3, Plate V, 1–5.

Emended diagnosis: Trilete miospores. Overall outline in polar view, subtriangular with convex sides to subcircular, in equatorial view distally extended. Exine proximally thin (1–3 μm) smooth or with scattered puncta. Trilete

PLATE I (approx. \times 1250)

Cyrtospora cristifer (Luber) nov. comb. et emend. Van der Zwan.

1–5. Variant A, specimens in characteristic longitudinal compression. (1: specimen showing folded proximal hemisphere; 5: corroded specimen).



rays distinct, simple or labrate, length $2/3-1/1$ spore radius. Distal exine thickened to a well-developed crassitude with its greatest thickness at the distal pole. Distal crassitude highly variable in shape and size: long and narrow, short and wide, converging or diverging to the distal pole, or reduced and rosette-shaped. Distal ornamentation mainly consisting of bacula of variable shape and size and to a minor degree coni and verrucae (height $1-8\ \mu\text{m}$, width $1-7\ \mu\text{m}$). The bases of the elements are sometimes fused to ridges. Density of ornaments variable, the larger, more closely spaced elements are situated around the distal pole, the smaller more scattered elements are found at or near the equator.

Observed dimensions: Length polar axis: $28-75\ \mu\text{m}$, length without crassitude: $8-35\ \mu\text{m}$; equatorial diameter: $28-40\ \mu\text{m}$.

Variants: Within the observed range of variability of *Cyrtospora cristifer* the following variants are informally recognized. Variant A (Plates I, II, 7, 8, Plate V, 1-3) characterized by the presence of a well-developed distal crassitude, which is distally strongly elongated giving the spore a preferred longitudinal compression. Variant B (Plate II, 1-6, Plate III, 1-3, Plate V, 4, 5) characterized by the presence of a reduced distal crassitude, rosette-shaped. The spore has a preferred excentrically polar compression.

Remarks: The species is here incorporated in *Cyrtospora* on the basis of a baculate distal crassitude, such in contrast with *Archaeozonotriletes* Naumova, 1953 emend. Allen, 1965; *Tholisporites* Butterworth et Williams, 1958, and *Anisozonotriletes* Naumova, 1939 (nomen nudum). *Torispora* Balme, 1952, is monolete, though occasionally trilete specimens may occur; the form genus possesses a distal crassitude, which seems less bound to a position around the distal pole. Variant A is comparable with specimens described in the literature as *Lophozonotriletes cristifer* (Luber) Kedo, 1957. Variant B is comparable with the holotype of *Cyrtospora clavigera* Winslow, 1962, pl.22, fig.19. The drawing of the holotype of *Azonotriletes cristifer* Luber, 1941, shows a specimen intermediate in structure between the two variants. *Cyrtospora cristifer* is distinguished from forms described in the present paper as *Ceratosporites* sp.A and *Mooreisporites* sp.A in having a distal crassitude.

Form genus: *Ceratosporites* Cookson et Dettmann 1958.

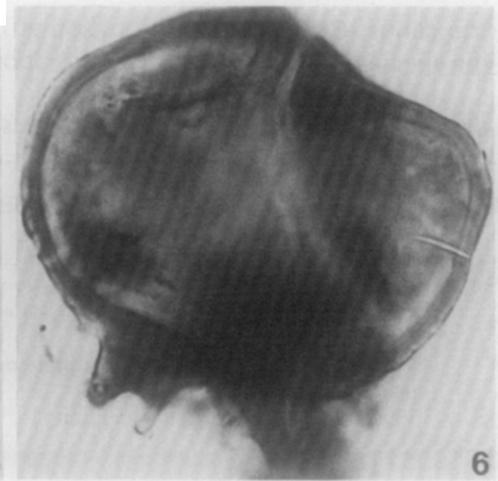
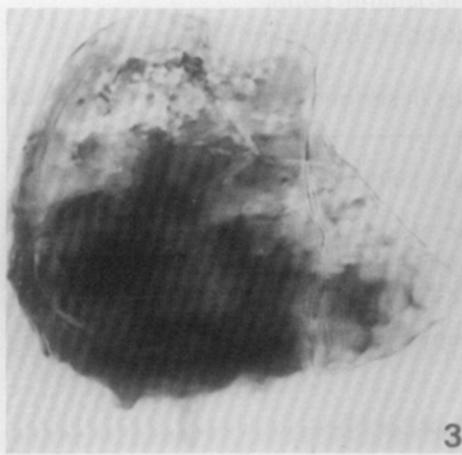
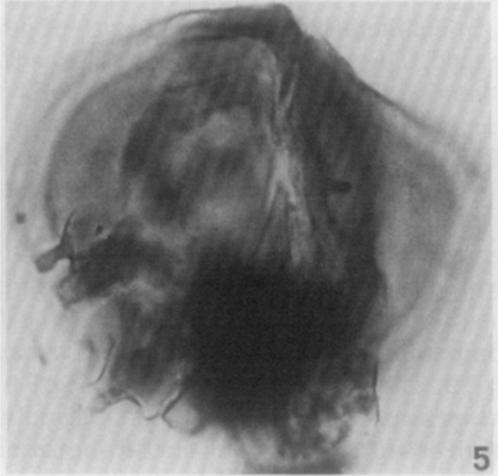
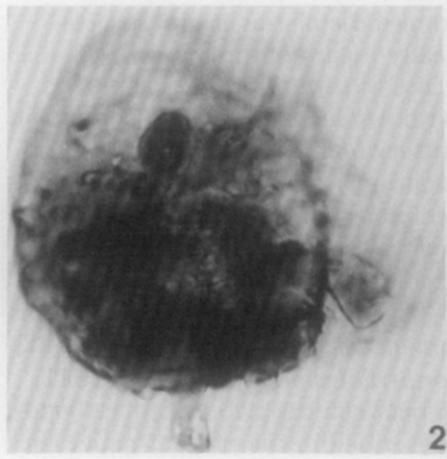
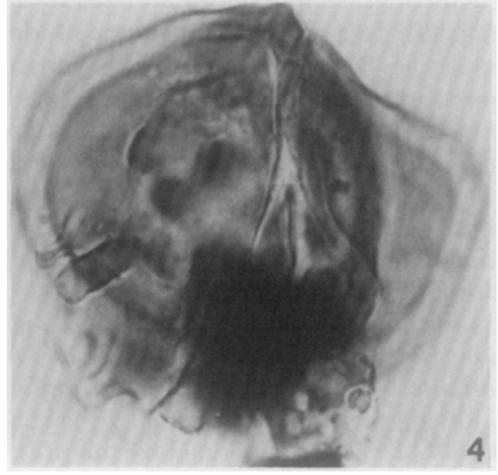
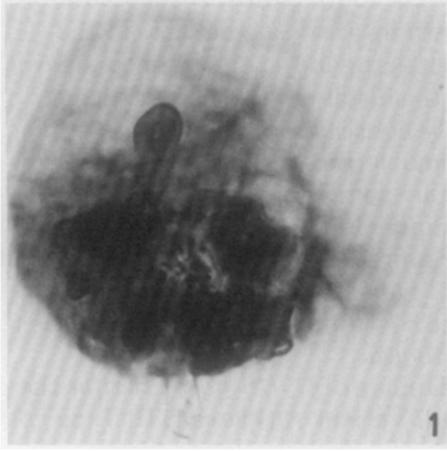
Type species: *Ceratosporites equalis* Cookson et Dettmann 1958.

Remarks: The form genus *Ceratosporites* is described from the Cretaceous of

PLATE II (approx. $\times 250$; scanning micrographs $\times 1000$)

Cyrtospora cristifer (Luber) nov. comb. et emend. Van der Zwan.

- 1-4, 6. Variant B, specimens in characteristic polar compression. (1, 2: distal and proximal view of the same specimen; 3, 4: equatorial and distal view of the same specimen; 6: distal view).
 5. Variant B, specimen in longitudinal compression, having a distal crassitude composed of a single huge baculum.
 7, 8. Variant A. (8: corroded specimen).



Australia, it is here used for the first time to accommodate Palaeozoic, trilete miospores, characterized by the combination of a laevigate proximal, and a baculate distal hemisphere.

Species: *Ceratosporites* sp.A.

Figured specimens: Plate IV, 6–8, Plate V, 7, 8.

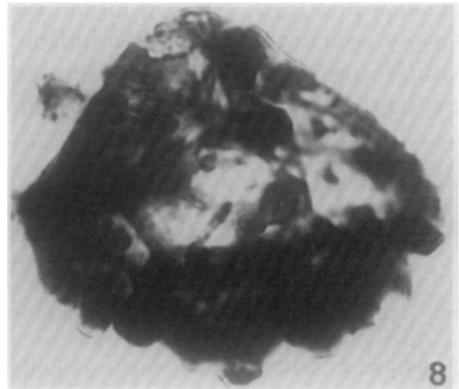
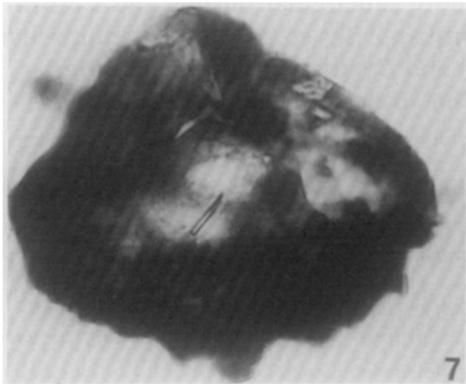
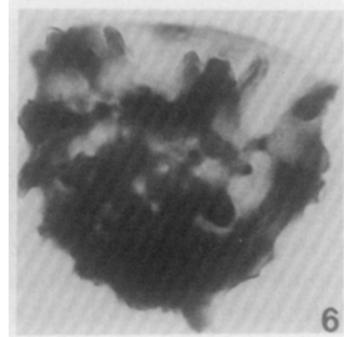
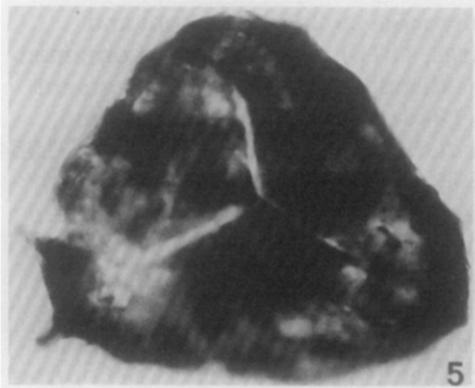
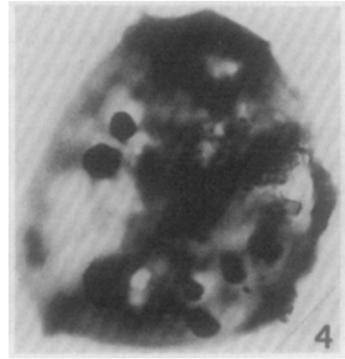
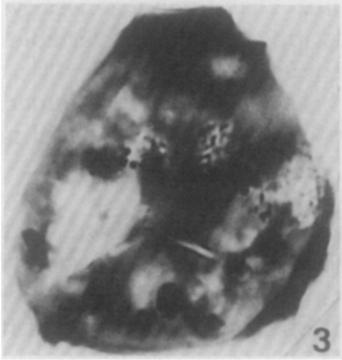
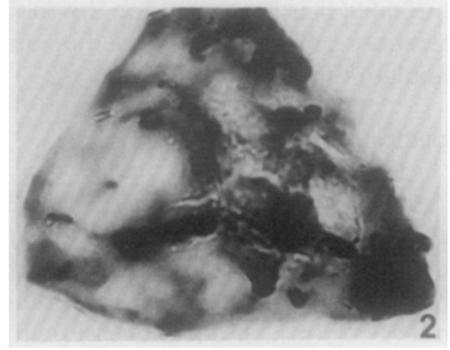
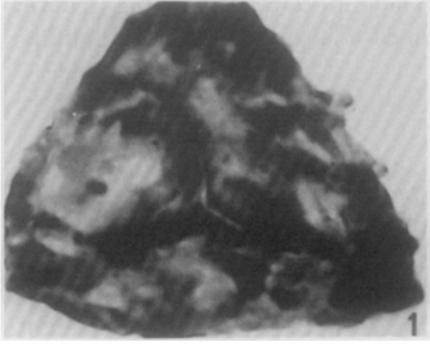
Identifying characters: Trilete miospores, overall outline subtriangular with convex sides to subcircular. The profile of the distal hemisphere is strongly arched, giving the spore a preferred eccentric orientation. Exine proximally thin (1–2 μm), smooth, occasionally punctate. Trilete rays distinct, straight, simple, occasionally labrate, 2/3–1/1 spore radius. Distal exine generally thicker (2–3 μm); ornamentation mainly consisting of bacula of variable shape and size and to a minor degree of blunt conical and verrucae (1–10 μm high, 1–10 μm in width); elements sometimes basally connected. Elements randomly distributed, but frequently concentrated at or near the distal pole, around which larger elements occur.

Observed diameter: 33–50 μm .

Remarks: The species has not been formally named since the present material can not be kept in a permanently transparent condition. The species can be distinguished from *Ceratosporites equalis* Cookson et Dettmann, 1958, by the characteristic distribution pattern and variation in shape and size of its ornaments. Identical forms have been informally designated as *Raistrickia* sp. (Doubinger and Rauscher, 1966), *Raistrickia* sp.2928 (Lanzoni and Magloire, 1969) and *Schopfites* sp.A (Higgs, 1975). Since the main ornamentation consists of bacula, restricted to the distal hemisphere, an assignment to *Raistrickia* Schopf, Wilson et Bentall, 1944, emend. Potonié et Kremp, 1954, *Schopfites* Kosanke, 1950, *Anapiculatisporites* Potonié et Kremp, 1954, *Brevitriletes* Bharadwaj et Srivastava, 1969, *Horriditriletes* Bharadwaj et Salujha, 1964, or *Lophotriletes* Naumova, 1939, ex Ischenko, 1952, is here rejected. *Ceratosporites* sp.A can be distinguished from *Anapiculatisporites? retusus* Winslow, 1962, by its size and by its coarser, less dense ornamentation, though a close morphological relationship is suspected. *Lophotriletes primitivus* Ischenko, 1956, has a comparable morphology, but from the description it is not clear whether the proximal hemisphere is laevigate. *Schopfites augustus* Playford, 1963, is larger, has a more subcircular outline and a more densely concentrated ornamentation. *Ceratosporites* sp.A can be distinguished from *Mooreisporites* sp.A (present paper) and *Cyrtospora cristifer* (Luber) nov. comb. et emend. Van der Zwan by the absence of crassitides.

PLATE III (approx. $\times 1250$)

- 1–3. *Cyrtospora cristifer* (Luber) nov. comb. et emend. Van der Zwan variant B, specimen having very reduced distal crassitude. (1: most distally focussed view; 2: distal view; 3: proximal view).
- 4–6. Transitional form between *Cyrtospora cristifer* (Luber) nov. comb. et emend. Van der Zwan variant B and *Ceratosporites* sp.A (present paper). (4: most distally focused view; 5: distal view; 6: equatorial view).



Form genus: *Mooreisporites* Neves 1958.

Type species: *Mooreisporites fustis* Neves 1958.

Remarks: Forms assigned to *Mooreisporites* are important constituents of Late Carboniferous assemblages. The here described species is probably the earliest record of forms attributable to this genus.

Species: *Mooreisporites* sp.A.

Figured specimens: Plate IV, 1–5, Plate V, 9–11.

Identifying characters: Trilete miospores, overall outline subtriangular with straight to convex sides with pointed, rounded or truncated apices. Exine, 1–2 μm in thickness, proximally smooth, occasionally irregularly punctate or granulate, in the latter case only a few scattered elements are met with. Trilete rays distinct, straight, simple, occasionally accompanied by parallel internal thickenings of the exine, up to 2 μm in width. Rays $2/3$ – $1/1$ of spore radius. Distal hemisphere, as well as the radial extremities of the proximal hemisphere, mainly ornamented with bacula of variable shape and size and to a minor degree with blunt conical and verrucae (2–6 μm high, 1–5 μm in width), sometimes fused at the bases. Elements randomly distributed or in clusters, usually concentrated at or near the apices. In the latter case one may observe radial crassitudes, formed by the lateral fusion of the bases of the ornaments (thickness up to 5 μm). The largest elements are often found at the radial crassitudes. The occurrence of radial crassitudes is restricted to one or two apices. (In none of the specimens so far observed were all three apices bearing crassitudes).

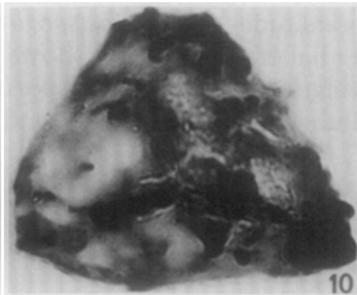
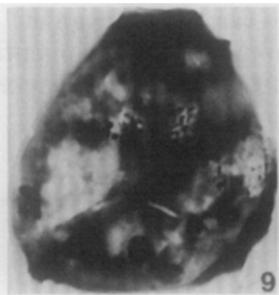
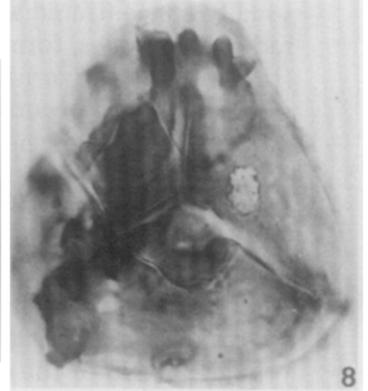
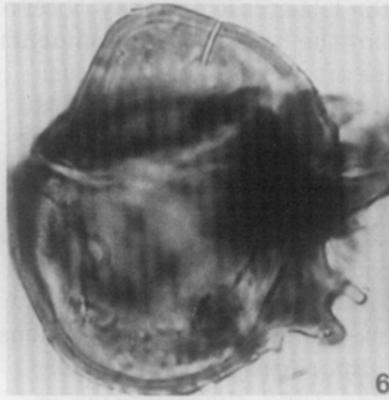
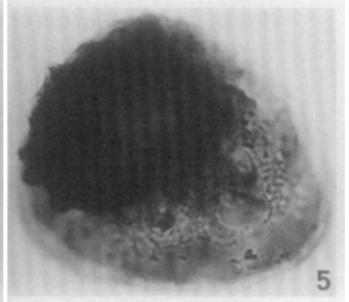
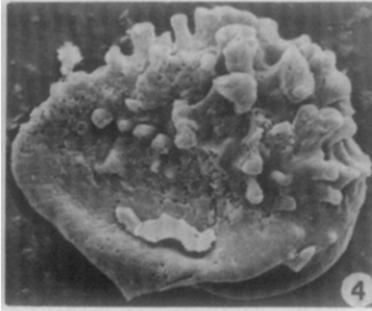
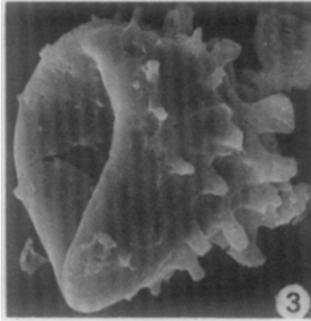
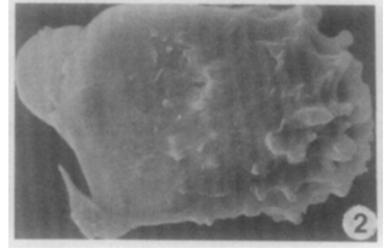
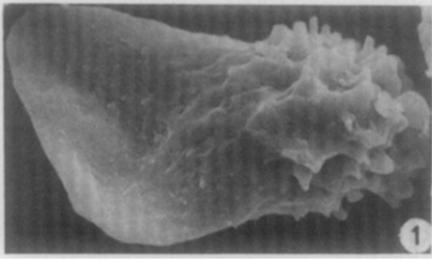
Observed diameter: 30–44 μm .

Remarks: The species has not been formally named since the present material cannot be kept in a permanently transparent condition. *Mooreisporites* sp.A can be distinguished from the other species of *Mooreisporites* by the presence of one or two radial crassitudes, rather than three, and by the relatively dense ornamentation of the distal hemisphere. *Mooreisporites* sp.A can be well compared with *Granulatisporites loganii* Winslow, 1962, the latter species, however, lacks the radial crassitudes. Also *Pilosporites verutus* Sullivan et Marshall, 1966, lacks the radial crassitudes and shows more pointed elements. *Mooreisporites* sp.A is distinguished from *Ceratosporites* sp.A (present paper) and *Cyrtospora cristifer* (Luber) nov. comb. et emend. Van der Zwan by having radial crassitudes.

PLATE IV (approx. $\times 1250$)

- 1–5. *Mooreisporites* sp.A (present paper). (1, 2: proximal and distal view of the same specimen; 3, 4: proximal and distal view of the same specimen; 5: equatorial view).
6–8. *Ceratosporites* sp.A (present paper), specimens in characteristic eccentric compression. (6: showing distal ornamentation; 7, 8: showing trilete rays and distal ornamentation of the same specimen).

PLATE V



THE MORPHON CONCEPT

In the above taxonomic approach it has been attempted to classify a group of morphologically related species within the typologically determined morphological classification system of dispersed spores. The individual taxa recognized (*Cyrtospora cristifer*, *Ceratospurites* sp.A and *Mooreisporites* sp.A) can be reasonably identified in palynological assemblages. Yet, by careful analysis, it is evident that the three species are linked by forms showing a morphology transitional between that of the separately diagnosed species (Plate III, 4–6, Plate V, 6, 8).

Similar continuous morphological variation, linking species of either one or more form genera, can be frequently observed when studying dispersed spores and pollen grains from stratigraphically and geographically restricted successions. The standard morphological procedures in palynological taxonomy are often unsuitable for the discussion and interpretation of continuous variation. Therefore, the term morphon is here introduced, to denote “a group of palynological species united by continuous variation of morphological characteristics”.

For discussion purposes, this morphon concept is thought to be complementary to the typological approach in palynological taxonomy in that:

- (1) The morphon emphasizes the continuity of the morphological characteristics rather than the discontinuity.
- (2) The morphon may reveal the connection between seemingly unrelated morphological features.
- (3) The morphon facilitates the recognition of morphological variation transgressing the often rigid delimitation of form genera.
- (4) The morphon may facilitate the recognition of time-proportionate and/or geographically and environmentally dependant morphological trends.
- (5) The morphon may facilitate subsequent interpretation of morphological variation in terms of natural variation.

A morphon may be informally named after one or more of its constituent

PLATE V (approx. $\times 900$; scanning micrographs $\times 750$)

C. cristifer morphon. The photomicrographs show the gradual reduction of the distal exine thickness and also the transitions between the species and variants.

1. *C. cristifer* variant A; specimen with long distal crassitide.
2. *C. cristifer* variant A; specimen with medium distal crassitide.
3. *C. cristifer* variant A; specimen with short distal crassitide.
- 4, 5. *C. cristifer* variant B; specimens with reduced rosette-shaped distal crassitide.
6. Transitional form between *C. cristifer* variant B and *Ceratospurites* sp.A; specimen lacking distal crassitide.
7. *Ceratospurites* sp.A; specimen showing thicker distal exine.
8. *Ceratospurites* sp.A; specimen comparable with *Mooreisporites* sp.A, but lacking radial crassitides.
9. *Mooreisporites* sp.A; specimen with small radial crassitides.
10. *Mooreisporites* sp.A; specimen with distinct radial crassitides.
11. *Mooreisporites* sp.A; specimen with distinctly baculate radial crassitides.

species. It can be diagnosed by enumerations of both the common and the variable morphological characteristics.

THE *CYRTOSPORA CRISTIFER* MORPHON

The *C. cristifer* morphon unites the species *Cyrtospora cristifer* (Luber) nov. comb. et emend. Van der Zwan, *Ceratosporites* sp.A (Van der Zwan, present paper) and *Mooreisporites* sp.A (Van der Zwan, present paper).

Common characteristics: (1) Equatorial outline — subtriangular with straight or convex sides, occasionally subcircular. (2) Trilete mark — simple, straight; laesurae 2/3 — 1/1 of spore radius. (3) Ornamentation — proximal hemisphere generally smooth; distal hemisphere ornamented with a great variety of processes, mainly bacula of variable shape and size, and to a minor degree, coni and verrucae.

Fig.1 shows the different types of elements: (a) Bacula, with straight, converging or diverging sides, with flat, blunt, bi- or trifurcating tops, or bearing small cone- or rodlike processes. (b) Coni with convex sides and blunt apices, or bearing a minute spine. (c) Verrucae with smoothly convex sides.

The basal outline of the elements can be circular, elliptical or beanshaped. Sometimes the elements are fused at their bases.

Variable characteristics (Plate V): (1) Variation in the ornamentation — continuous variation in the arrangement of ornaments from a concentrated position at or near the distal pole, via randomly distributed distal elements, to equatorial concentrations at the radial extremities; concentrations of elements frequently include larger elements. (2) Variation in the exine thickness — continuous variation in exine thickness from an elongated distal crassitude, via a distal exine slightly thicker than the proximal exine, to one or two radial crassitudes.

MOOREISPORITES SP.A		2-(3)-6µm high, 1-(2)-5µm wide, 0-10µm apart.
CERATOSPORITES SP.A		1-(5)-10µm high, 1-(3)-10µm wide, 0-10µm apart.
CYRTOSPORA CRISTIFER VARIANT B		1-(2)-8µm high, 1-6µm wide, 0-5µm apart.
CYRTOSPORA CRISTIFER VARIANT A		1-(3)-8µm high, 1-7µm wide, 0-5µm apart.

Fig.1. Comparison of ornamentation between the members of the *C. cristifer* morphon.

BIOSTRATIGRAPHICAL AND PALAEOGEOGRAPHICAL SIGNIFICANCE

The present concept of the *C. cristifer* morphon has been based on material derived from samples of Early Carboniferous deposits of the Bantry Bay section, southwest Ireland. When applying the scheme of compositional development of Late Devonian—Early Carboniferous palynological assemblages, reconstructed by Van der Zwan and Van Veen (1978), these deposits can be correlated with the LCr phase of the *Retispora lepidophyta* Assemblage Zone; the phases of the *Verrucosisporites nitidus* Assemblage Zone and the PV phase of the *Spelaeotriletes pretiosus* Assemblage Zone. The individual species have their first appearance at different intervals of this scheme;

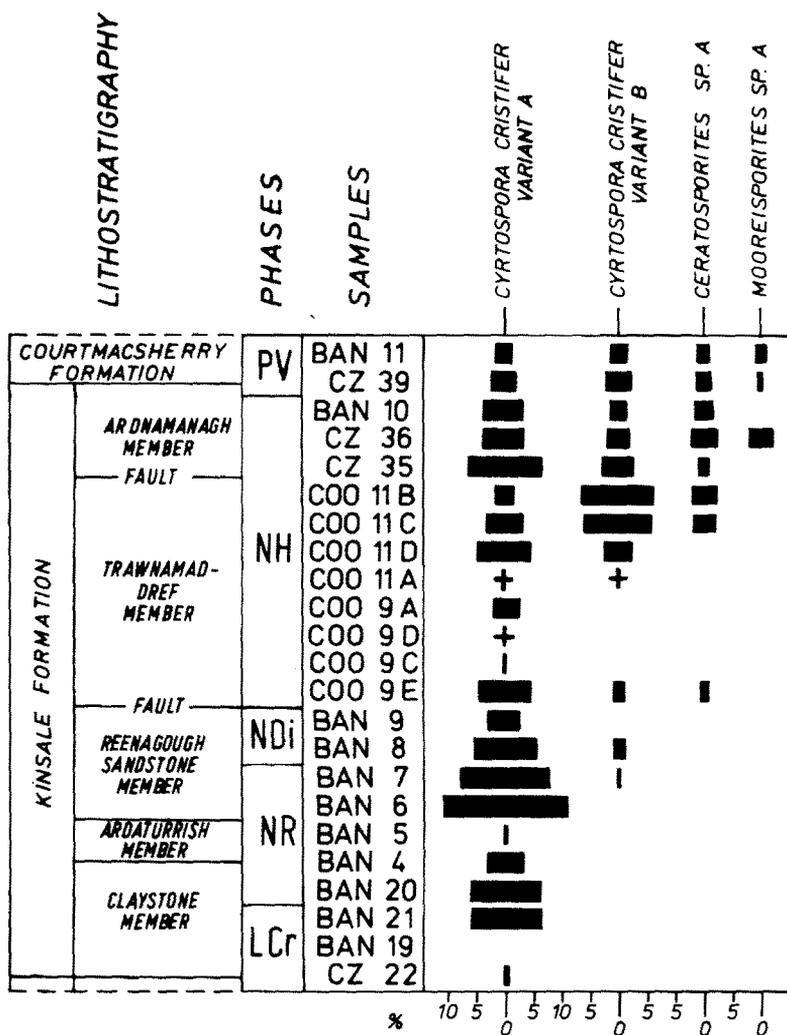


Fig.2. Quantitative distribution of the *C. cristifer* morphon in the Bantry Bay section, southwest Ireland (+, qualitative record).

Cyrtospora cristifer variant A in the LCr phase, *Cyrtospora cristifer* variant B late in the NR phase, *Ceratosporites* sp.A early in the NH phase and *Mooreisporites* sp.A within the NH phase. Consequently, it is only in the later part of the NH phase and in the PV phase that all the individual members of the group are jointly represented.

After their first appearance, the four members show a gradual increase in quantitative importance. Thus one may recognize a biostratigraphically significant trend in the *C. cristifer* morphon, useful for local stratigraphy (Fig.2).

In order to assess the regional and interregional stratigraphical and/or evolutionary importance of this trend, the *C. cristifer* morphon is compared with similar situations elsewhere (Fig.3).

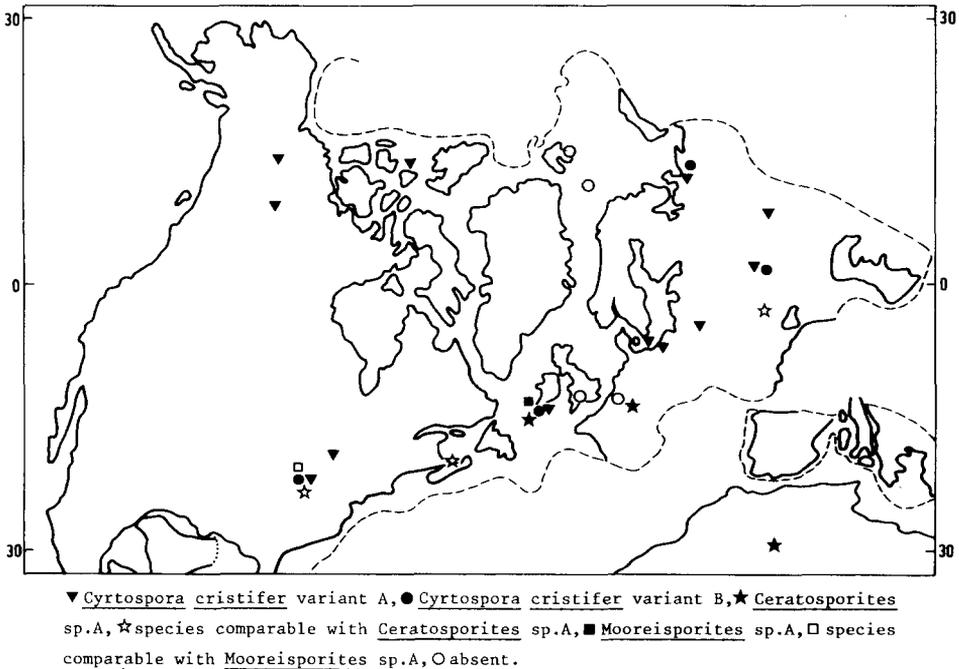


Fig.3. Geographical distribution of the *C. cristifer* morphon and comparable forms. Reassembly of continents after Smith et al. (1973).

Comparison with other data from Ireland

Keegan (1977) recorded from Galley Head—Leap Harbour, southwest Ireland, the occurrence of *Cyrtospora cristifer* in his zone VI (*Verrucosiporites nitidus* Assemblage Zone; NR—NH phases of Van der Zwan and Van Veen) and also the occurrence of *Ceratosporites* sp.A (*Schopfites* sp.A of Higgs, 1975) in the upper part of Zone VI. Any relationship between the two species was not mentioned. *Cyrtospora cristifer* was subsequently recorded from most sections in southern Ireland (Clayton et al, 1977). Its quantitative distribution and its relationship with the regional geography was incorporated in the discussion of the integration of palaeogeographical and palynological data by Van der Zwan and Van Veen (1978).

In spite of the scarcity of the information, the additional records from southern Ireland support the view that the local trend recognized in Bantry Bay could well have a regional significance.

Comparison with Ohio, U.S.A.

Winslow (1962) described a group of spores from Late Devonian—Early Carboniferous deposits of Ohio which show a comparable morphological variation to that found in the *C. cristifer* morphon. The species represented are: (1) *Cyrtospora cristifer* (*C. clavigera*) exhibiting the same variation as found

in Ireland; the specimen depicted in Winslow's plate 22, fig. 20 is identical with the present *C. cristifer* variant A and the specimen depicted in plate 22, fig. 19 is identical with the present *C. cristifer* variant B; (2) *Anapiculatisporites? retusus* (plate 22, fig. 12) showing a morphology comparable with *Ceratosporites* sp. A, though the ornamentation is generally of smaller dimensions; (3) *Granulatisporites loganii* (plate 22, fig. 10, 11) resembles *Mooreisporites* sp. A but lacks the radial crassitudes.

The presence of continuous variation between the species is, of course, impossible to assess. The stratigraphical range of the species does not fully correspond to the situation known in Ireland. The ranges of *Cyrtospora cristifer* and of *Granulatisporites loganii* in Ohio are more or less comparable with the ranges of *Cyrtospora cristifer* and *Mooreisporites* sp. A in Ireland, but *Anapiculatisporites? retusus* appears much earlier than *Ceratosporites* sp. A and matches continuously the range of *Cyrtospora cristifer*. Furthermore, no samples containing all species together have been found; this is probably due to very scarce information on the interval intermediate between the last occurrences of *Cyrtospora cristifer* and *Anapiculatisporites? retusus*, and the first appearance of *Granulatisporites loganii*.

From the information so far available it seems impossible to draw many conclusions, the variation together with the ranges of the species found in Ohio neither supports nor rejects the presence of a trend in continuous variation in the *C. cristifer* morphon.

Nevertheless, this information is the only record from outside Ireland that might show a more or less similar morphological variation to that found in the *C. cristifer* morphon.

Geographical distribution of individual taxa

Cyrtospora cristifer. Apart from the above-mentioned occurrence of a group of species in Ohio that might be compared with the *C. cristifer* morphon, *Cyrtospora cristifer* as an individual taxon is long since known from various parts of Europe and North America in strata of latest Frasnian—Middle Tournaisian age. The records are very scattered, and *C. cristifer* is strikingly absent in some well-documented localities: Spitsbergen (Playford, 1962, 1963), Bear Island (Kaiser, 1970), Belgium (Paproth and Streel, 1970), England (Dolby and Neves, 1970) and Nova Scotia (Playford, 1964; McGregor, 1970).

The species has been recorded from Ireland (Higgs, 1975; Keegan, 1977; Van der Zwan and Van Veen, 1978), the D.D.R. (Burmam, 1975), Poland (Turnau, 1978), the Pripyat Depression, U.S.S.R. (Kedo, 1957, 1963; Kedo and Golubtsov, 1971), the central Russian Platform, U.S.S.R. (Umnova, 1971), the eastern part of the Russian Platform, U.S.S.R. (Byvsheva, 1976), the Timan-Pechora province of the U.S.S.R. (Luber and Waltz, 1941), the Arctic Archipelago, Canada (Kerr et al., 1965), the North West Territories, Canada (Staplin, 1961), Yukon, Canada (Norris, 1968; McGregor, 1970), Ontario, Canada (McGregor, 1970) and Ohio, U.S.A. (Winslow, 1962). Out-

side Euramerica it occurs neither in northwestern Australia (Playford, 1976), nor in Algeria (Lanzoni and Magloire, 1969). The only record which might be from outside Euramerica is from Iran (Coquel et al., 1977). They compared the Visean part of their assemblages with assemblages known from Libya; the Tournaisian assemblages, however, are quite comparable with those from Euramerica. From the evidence known, it is not yet possible to conclude whether the assemblages represent either Gondwanan or Euramerican floras.

Almost all occurrences of *C. cristifer* are from marine strata (mainly clastics, occasionally carbonates) or from continental strata with marine incursions, indicating their connection with coastal environments. Only one fully continental record is known to the author (viz. the extremely rare occurrence of the species at Hook Head, Ireland).

In the marine or coastal—continental deposits which contain *C. cristifer* and which have been investigated quantitatively, the species is an important constituent of the assemblages. Such in contrast with the continental record of Hook Head, where the rareness of *C. cristifer* seems to correspond with the absence of the species in the continental deposits of, e.g., Spitsbergen, Bear Island and Nova Scotia.

Evaluating the above given information, it is evident that the *C. cristifer* producing plant preferred a coastal environment. But this coastal environment should comply with certain demands, otherwise *C. cristifer* should also be represented in the assemblages from coastal—marine sediments from England and Belgium. Perhaps such a coastal environment should consist of a broad coastal plain, or, following the great lithological similarity between Ohio and Bantry Bay, there should be a coastal—deltaic environment.

Ceratosporites sp.A. This species has so far only been recorded from Middle Tournaisian and Visean strata from Ireland (Higgs, 1975; Keegan, 1977), France (Doubinger and Rauscher, 1966) and from Algeria (Lanzoni and Magloire, 1969). Since the species is only known from marine deposits, it may be concluded that the plant producing *Ceratosporites* sp.A might be restricted to a coastal environment.

The similar form *Anapiculatisporites? retusus* from the Upper Famennian—Lower Tournaisian of Ohio (Winslow, 1962) is known from deposits indicative of a coastal—deltaic environment. In contrast the morphologically comparable forms *Lophotriletes primitivus* (Visean of the Donetz Basin, Ischenko, 1956) and *Schopfites augustus* (Middle Tournaisian of Nova Scotia, Playford, 1964) originate from continental deposits.

Mooreisporites sp.A. This species has so far only been recorded from Middle Tournaisian marine deposits of Ireland (present paper). The comparable form *Granulatisporites loganii* from Ohio (Winslow, 1962) also originates from Middle Tournaisian marine deposits.

CONCLUSIONS

Summarizing the above given information, it is evident that the species of the *C. cristifer* morphon are united by continuous variation.

Furthermore, it has been demonstrated that in the *C. cristifer* morphon within Ireland a time-proportionate trend may be recognized, based on the first occurrences and increase in quantitative importance of the different members. This trend could not be traced outside Ireland. However, based on occurrences of individual species of the *C. cristifer* morphon the trend may find some support, as *C. cristifer* occurs generally in older strata (Upper Frasnian—Middle Tournaisian) than *Ceratosporites* sp.A (Middle Tournaisian—Viséan).

Finally the geographical dependence (coastal—marine) has been demonstrated for *C. cristifer*. Such a dependence could not be demonstrated with as much confidence for *Ceratosporites* sp.A and *Mooreisporites* sp.A since these species are only rarely recorded. Nevertheless, as the taxa have only been found in marine strata, it seems possible that all members of the *C. cristifer* morphon are restricted to the same environment. This could be translated into the *C. cristifer* morphon being the reflection of one or more plant taxa preferring a coastal environment. There is even some evidence that one may think of an exclusively coastal—deltaic environment for these plant taxa.

Additionally, some species have been noted outside Ireland which are morphologically comparable, though not identical, with *Ceratosporites* sp.A. These species do not necessarily prefer the same environment; some are recorded from continental strata. The combination of slight morphological differences and differences in environmental control strongly suggests that these spores originated from different plant taxa.

The present considerations have been concerned with palynological species, united into a morphon, and all the applications of this concept are based on observations. As a logical consequence, however, the thought arises as to whether we are dealing with the reflection of either one natural plant species, or a group of plant species.

Visscher (1971, 1972) introduced the term palynodeme to denote “any group of contemporaneously dispersed spores or pollen grains, which may be suspected to represent a palynological reflection of a known or hypothetical plant species”. There are many similarities as to the non-typological classification procedure within the morphon and the palynodeme. The palynodeme concept, however, was principally developed as an aid to evolutionary palynology.

If we would adhere to the view that the *C. cristifer* morphon reflects the natural variation of a hypothetical plant (chrono) species, in every assemblage the spores assignable to the *C. cristifer* morphon could be interpreted in terms of a palynodeme.

The differences in the composition of the succession of such palynodemes found in the Bantry Bay section (Fig.2) then might reflect a time-proportionate evolutionary change.

However, the quantitative information available cannot be clearly reconciled with an evolutionary model of a gradual shift in the relative proportions of the four species ("norms" in the terminology of Visscher, 1971). It would be premature, therefore, to recognize *C. cristifer* palynodemes.

From the above discussion it is not possible to decide whether or not we are dealing with palynodemes and whether or not we are dealing with one or more natural plant species.

Yet gradual morphological variation is to be observed in many pollen grains and spores. The morphon, as exemplified by the *C. cristifer* morphon, provides a practical unit for classifying variation. The morphon concept is complementary, not conflicting, with both the conventional concept of form taxa and the interpretative palynodeme concept: the recognition of variation transgressing the limits of form taxa can be expressed within a morphon; the interpretation of a morphon in terms of natural variation leads to the recognition of palynodemes.

ACKNOWLEDGEMENTS

The author wishes to thank Dr. H. Visscher, Utrecht, for his guidance. He is also indebted to Prof. Dr. F.P. Jonker, Utrecht, for his stimulating advice and to Dr. P.R.R. Gardiner, Dublin, for critically reading the manuscript. Thanks are also due to Drs. P.M. Van Veen for the stimulating discussions. Grateful acknowledgement is extended to Mr. H. Rijpkema and Mr. M. Groeneveld for drawing the diagrams and to Mr. H.A. Elsendoorn and Mr. Th.P.A. Molenaar for preparing the photomicrographs and for taking the scanning micrographs, respectively.

REFERENCES

- Allen, K.C., 1965. Lower and Middle Devonian spores of North and Central Vestspitsbergen. *Palaeontology*, 8(4): 687-748.
- Alpern, B., Doubinger, J. and Horst, U., 1965. Révision du genre *Torispora* Balme. *Pollen Spores*, 7(3): 565-572.
- Balme, B.E., 1952. On some specimens from British Upper Carboniferous coals. *Geol. Mag.*, 89: 175-184.
- Burmann, G., 1975. Sporen aus dem Tournai von Rügen. *Z. Geol. Wiss. Berlin*, 3(7): 875-905.
- Butterworth, M.A. and Williams, R.W., 1958. The small spore floras of coals in the Limestone Group of the Lower Carboniferous of Scotland. *Trans. R. Soc. Edinb.*, 63(2)17: 353-392.
- Byvsheva, T.V., 1976. Zonation of spore complexes from Devonian-Carboniferous boundary deposits from the eastern part of the Russian Platform. In: T.V. Byvsheva (Editor), *Results of Palynological Researches of the Precambrian, Paleozoic and Mesozoic of the U.S.S.R.* Trudy VNIGRI, 192: 67-93 (in Russian).
- Clayton, G., Coquel, R., Doubinger, J., Gueinn, K.J., Loboziak, S., Owens, B. and Streeel, M., 1977. Carboniferous miospores of western Europe; illustration and zonation. *Meded. Rijks Geol. Dienst*, 29: 1-71.
- Cookson, I.C. and Dettman, M.E., 1958. Some trilete spores from Upper Mesozoic deposits in the eastern Australian Region. *Proc. R. Soc. Vic., N.S.*, 70(2): 95-128.

- Coquel, R., Loboziak, S., Stampfli, G. and Stampfli-Vuille, B., 1977. Palynologie du Dévonien supérieur et du Carbonifère inférieur dans l'Elburz oriental (Iran nord-est). *Rev. Micropaléontol.*, 20(2): 59—71.
- Dolby, G. and Neves, R., 1970. Palynological evidence concerning the Devonian—Carboniferous boundary in the Mendips, England. *Congr. Int. Stratigr. Geol. Carboniferous*, 6th. Sheffield, 1967, C. R., 2: 631—646.
- Doubinger, J. and Rauscher, R., 1966. Spores du Viséen marin de Bourbach-le-Haut dans les Vosges du Sud. *Pollen Spores*, 8(2): 361—405.
- Gilmour, J.S.L., 1960. Deme terminology. *Rept. Scott. Plant Breeding Station*, 1960: 99—105.
- Higgs, K., 1975. Upper Devonian and Lower Carboniferous Miospore assemblages from Hook Head, Co. Wexford, Ireland. *Micropaleontology*, 21(4): 393—419.
- Ischenko, A.M., 1956. Spores and pollen of the Lower Coal Beds from the westerly extension of the Donetz Coal Basin and their stratigraphical significance. *Acad. Sci. Ukrainian S.S.R. Geol. Inst. Bull. Ser. Stratigr. Palaeontol.*, 2: 186 pp. (in Russian).
- Kaiser, H., 1970. Die Oberdevon-Flora der Bäreninsel. 3. Mikroflora des höheren Oberdevons und des Unterkarbons. *Palaeontographica*, B, 129(1—3): 71—124.
- Kedo, G.I., 1957. Spores from the supra-salt Devonian deposits of the Pripyat Depression and their stratigraphical significance. *Acad. Sci. Belorussian S.S.R., Inst. Geol., Paleontol. Stratigr.*, No.2: 3—43 (in Russian).
- Kedo, G.I., 1963. Spores of the Tournaisian Stage of the Pripyat Depression and their stratigraphical significance. *Acad. Sci. Belorussian S.S.R., Inst. Geol., N. Palaeontol. Stratigr.*, 4: 3—131 (in Russian).
- Kedo, G.I. and Golubtsov, W.K., 1971. Palynological means of distinguishing the Devonian—Carboniferous boundary in the Pripyat Depression. In: *Palynological Investigations in Belorussia and Other Regions of the U.S.S.R.* Izdatelstvo Nauka i Tekhnika, Moscow, pp.5—44 (in Russian).
- Keegan, J.B., 1977. Late Devonian and Early Carboniferous miospores from the Galley Head—Leap Harbour Region of southwest Ireland. *Pollen Spores*, 19(4): 545—573.
- Kerr, J.W., McGregor, D.C. and McLaren, D.J., 1965. An unconformity between Middle and Upper Devonian rocks of Bathurst Island, with comments on Upper Devonian faunas and microfloras of the Parry Islands. *Bull. Can. Pet. Geol.*, 13(3): 409—431.
- Kosanke, R.M., 1950. Pennsylvanian spores of Illinois and their use in correlation. *Ill. State Geol. Surv. Bull.*, 74: 128 pp.
- Lanzoni, E. and Magloire, L., 1969. Associations palynologiques et leurs applications stratigraphiques dans le Dévonien supérieur et Carbonifère inférieur du Grand Erg occidental (Sahara Algérien). *Inst. Fr. Pét. Rev.*, 24(4): 441—469.
- Luber, A.A. and Oshurkova, M.V., 1966. Carboniferous spore—pollen complexes of the U.S.S.R. In: M. Prokrovskaya (Editor), *Paleopalynology*. *Min. Geol. S.S.S.R., Tr. VSEGEI*, N.S., 141(2): 53—99 (in Russian).
- Luber, A.A. and Waltz, I.E., 1941. Atlas of Microspores and Pollen grains of the Paleozoic of U.S.S.R. *Sov. Union Geol. Inst. Trans. VSEGEI*, 139: 107 pp. (in Russian).
- McGregor, D.C., 1970. *Hymenozonotriletes lepidophytus* Kedo and associated spores from the Devonian of Canada. In: *Colloque sur la stratigraphie du Carbonifère*. *Congr. Coll. Univ. Liège*, 55: 315—326.
- McGregor, D.C. and Owens, B., 1966. Illustrations of Canadian fossils, Devonian spores of eastern and northern Canada. *Geol. Surv. Can. Pap.*, 66—30: 66 pp.
- Nalivkin, D.V., 1973. *Geology of the U.S.S.R.* Oliver and Boyd, Edinburgh, 855 pp.
- Naumova, S.N., 1939. Spores and pollen of the coals of the U.S.S.R. *Rep. Int. Geol. Congr. 17th Sess., Moscow, 1937*, 6: 353—364.
- Neves, R., 1958. Upper Carboniferous plant spore assemblages from the *Gastrioceras subcrenatum* Horizon, North Staffordshire. *Geol. Mag.*, 95(1): 1—19.
- Norris, A.W., 1968. Reconnaissance Devonian stratigraphy of northern Yukon Territory and northwestern District of MacKenzie. *Geol. Surv. Can. Pap.*, 67-53: 1—287.

- Paproth, E. and Streeel, M., 1970. Corrélations biostratigraphiques près de la limite Dévonien/Carbonifère entre les faciès littoraux ardennais et les faciès bathyaux rhénans. In: Colloque sur la stratigraphie du Carbonifère. Congr. Coll. Univ. Liège, 55: 365—398.
- Pepper, J.F., Wallace de Witt, J.R. and Demarest, D.F., 1954. Geology of the Bedford Shale and Berea Sandstone in the Appalachian Basin. Geol. Surv. Prof. Pap., 259: 111 pp.
- Playford, G., 1962. Lower Carboniferous microfloras of Spitsbergen. Part I. Palaeontology, 5(3): 550—618.
- Playford, G., 1963. Lower Carboniferous microfloras of Spitsbergen. Part II. Palaeontology, 5(4): 619—678.
- Playford, G., 1964. Miospores from the Mississippian Horton Group, Eastern Canada. Geol. Surv. Can. Bull., 107: 47 pp.
- Playford, G., 1976. Plant Microfossils from the Upper Devonian and Lower Carboniferous of the Canning Basin, western Australia. Palaeontographica, B, 158(1—4): 1—71.
- Smith, A.G., Briden, J.C. and Dewry, G.E., 1973. Phanerozoic world maps. In: N.F. Hughes (Editor), Organisms and continents through time. Spec. Pap. Palaeontol., 12: 1—42.
- Staplin, F.L., 1961. New plant spores similar to *Torispora* Balme. J. Paleontol., 35(6): 1227—1231.
- Sullivan, H.J. and Marshall, A.E., 1966. Visean spores from Scotland. Micropaleontology, 12(3): 265—285.
- Turnau, E., 1978. Spore zonation of uppermost Devonian and Lower Carboniferous deposits of western Pomerania (N. Poland). Meded. Rijks Geol. Dienst, 30(1): 1—35.
- Umnova, V.T., 1971. On the Devonian—Carboniferous boundary of the Central Area of the Russian Platform based on palynomorphs. Lett. Acad. Sci. S.S.S.R. Geol. Ser. Moscow, 1971, No.4: 109—122 (in Russian).
- Utting, J. and Neves, R., 1970. Palynology of the Lower Limestone Shale Group (basal Carboniferous Limestone Series) and Portishead Beds (Upper Old Red Sandstone) of the Avon Gorge, Bristol, England. In: Colloque sur la stratigraphie Carbonifère. Congr. Coll. Univ. Liège, 55: 411—422.
- Van der Zwan, C.J. and Van Veen, P.M., 1978. The Devonian—Carboniferous transition sequence in southern Ireland: Integration of Palaeogeography and Palynology. Palynologia, 1: 469—479.
- Visscher, H., 1971. The Permian and Triassic of the Kingscourt outlier, Ireland — a palynological investigation related to regional stratigraphical problems in the Permian and Triassic of western Europe. Geol. Surv. Ireland, Spec. Pap., 1: 114 pp.
- Visscher, H., 1972. The *Lueckisporites* palynodemes. Congr. Int. Stratigr. Geol. Carb. 7th. Krefeld 1971, C.R., 1: 354—358.
- Winslow, M.R., 1962. Plant spores and other microfossils from Upper Devonian and Lower Mississippian rocks of Ohio. Geol. Surv. Prof. Pap., 364: 93 pp.