HYMENOZONOTRILETES LEPIDOPHYTUS KEDO, ITS DISTRIBU AND SIGNIFICANCE IN RELATION TO THE DEVONIAN—CA IFEROUS BOUNDARY

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SUMMARY

Miospore assemblages of Upper Devonian (Upper Famennian and Str age from Western Australia, North Africa, Belgium, Germany, Canada a U.S.S.R. are examined. Populations of *Hymenozonotriletes lepidophytus* scribed and the synonymous relationships between this and morpholo similar species are established. The stratigraphic distribution and the possi of utilising zones based on biometrically defined differences within the popul of *H. lepidophytus* for local correlation purposes are discussed. The g composition of Upper Devonian and Lower Tournaisian microfloras is reviewed.

INTRODUCTION

Recent investigations into the composition of Upper Devonian– Carboniferous miospore assemblages in various parts of the world by KEDO 1962, 1963), BALME and HASSELL (1962), WINSLOW (1962), WRAY (1964) and (1966) have drawn attention to the significance of a morphologically d complex of spores, assigned by the various authors to a number of di genera, which appear to be of considerable value in the determination Devonian–Carboniferous boundary.

Representatives of the complex were first described by KEDO (1957) the name *Hymenozonotriletes lepidophytus*, from the middle part of the Da Lebedyan horizon (Upper Famennian) of the Byelorussian S.S.R. A comparable, if not identical, form was described by BALME and HASSELL

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from the Fairfield Beds (Upper Famennian) of the Canning Basin, Western Australia as *Leiozonotriletes naumovae*. Although *L. naumovae* was recorded throughout the Upper Devonian succession examined by Balme and Hassell it never constituted the dominant form in any assemblage. In North America, WINSLOW (1962) has described the species *Endosporites lacunosus* which is at least in part identical to both *H. lepidophytus* and *L. naumovae*, from the upper part of the Ohio Shale (Upper Devonian) and the Bedford Shale and Berea Sandstone (Lower Mississippian) of Ohio. WRAY (1964), in a review of Palaeozoic palynomorphs in Libya, has commented on the value of a species of *Leiozonotriletes* with a coarsely reticulate sac for the determination of the Devonian–Carboniferous boundary. The most detailed account of the distribution of this complex is that of STREEL (1966) who, working on the Upper Famennian and Lower Tournaisian (Fm2b–Tn2a) deposits of the Dinant Basin, Belgium, has recorded *H. lepidophytus* in deposits of Tn1a and lower Tn1b age and by applying biometric methods has proposed a series of zones based on the size and frequency distribution of the representatives of the *H. lepidophytus* complex. This zonal scheme has been proved to be of considerable value in the elucidation of local correlation problems. Similar detailed investigations must, however, be carried out in other regions before the principle of this method of correlation can be applied on a wider regional basis.

In order to avoid confusion, representatives of this miospore complex are here referred to as *H. lepidophytus* in preference to *L. naumovae* and *E. lacunosus*, which are here regarded as junior synonyms. It must be pointed out, however, that the generic assignment of the representatives of this complex to any of the three genera mentioned above cannot be considered entirely satisfactory on structural or morphological grounds. The taxonomic position of the complex will be dealt with in a later publication. The synonymy of the various species assigned to this complex has been established by the examination of additional material from Western Australia, North Africa, Canada and the U.S.S.R.

## PLATE I

Hymenozonotriletes lepidophytus KEDO, × 500.

Figured specimens bearing the index letters MPK are stored in the collections of the Institute of Geological Sciences (Geological Survey), Leeds, (Great Britain); those with the index letters G.S.C. are housed in the paleobotanical type collection of the Geological Survey of Canada, Ottawa (Canada).

A. Fairfield Beds (Upper Devonian), Canning Basin, Western Australia. MPK 1.
B. Fairfield Beds (Upper Devonian), Canning Basin, Western Australia. MPK 2.
C. Fairfield Beds (Upper Devonian), Canning Basin, Western Australia. MPK 3.
D. Port Lambton Formation (Upper Devonian), southwest Ontario, Canada. G.S.C. 15486.
E. Fairfield Beds (Upper Devonian), Canning Basin, Western Australia. MPK 4.
F. Imperial Formation (Upper Devonian), Northwest Territories, Canada. G.S.C. 15487.
G. Imperial Formation (Upper Devonian), Northwest Territories, Canada. G.S.C. 15488.

PLATE I
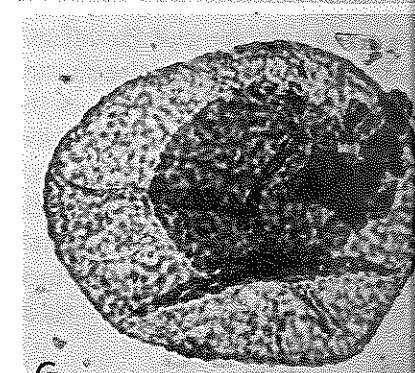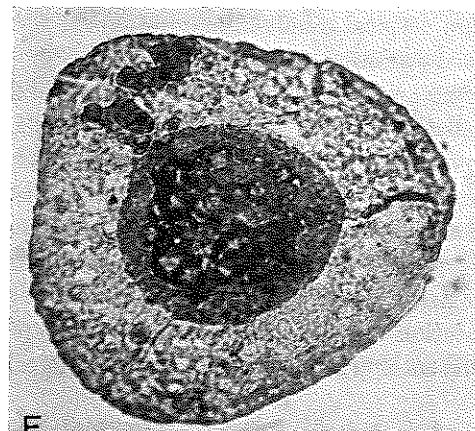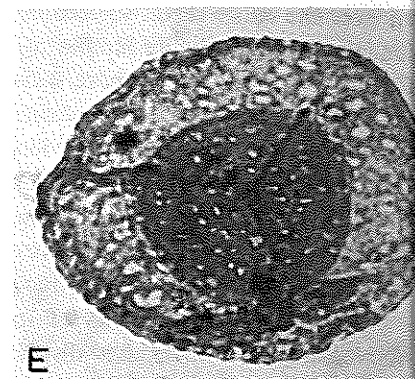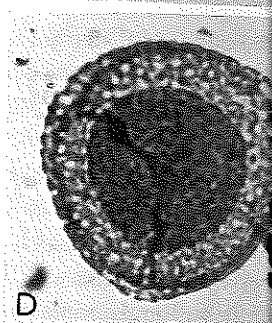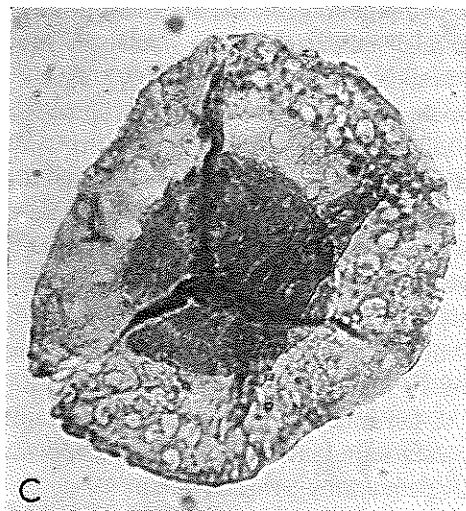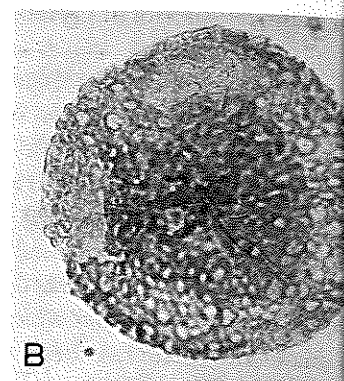
Spores radial, trilete, camerate. Amb broadly rounded triangular, subcircular or circular. Exine composed of two layers, the intexine which forms a subcircular or rounded triangular inner body and the exoexine which is attached to the intexine only on its proximal surface, being separated in the equatorial region and over the entire distal surface (see Plate I). Trilete mark distinct, laesurae normally indistinct, probably extending to the equatorial margin of the intexine, commonly obscured by thin, elevated, flexuous folds of exoexine which are up to 5μ high at the proximal pole but which decrease in height towards the equatorial margin. Ends of the trilete rays are connected by ill-defined curvaturae which are clearly invaginated in the radial positions but which are more or less coincident with the equatorial margin of the spore for the remainder of their length. Curvaturae defined by a minor change in exoexine thickness. Intexine thin (up to 2μ thick), surface laevigate or minutely roughened, distal surface commonly bears independent, randomly orientated, taper-point compression folds. Exoexine minutely and densely punctate, contact areas smooth, distal surface bears numerous subcircular, polygonal or irregularly shaped lumina, separated by narrow ridges of normal exoexine which may bear an ornament of small, scattered cones, spines or verrucae. Lumina which normally are $2-10\mu$ in diameter, are variable in form and distribution. In some specimens the lumina may be more or less uniformly distributed over the entire distal surface of the exoexine, whilst in others there may be a tendency for the smaller lumina to be more widely spaced in the polar region and for the larger ones to be more densely distributed in the more equatorial regions. Equatorial margin of the exoexine slightly undulate and may possess a narrow limbate structure up to 2.5μ wide. Maximum equatorial diameter of the spore $43-119\mu$, maximum equatorial diameter of the inner body $26-72\mu$ (measurements based on 315 specimens). The diameter of the inner body normally constitutes $50-80\%$ of the total spore diameter. Smaller representatives of *H. lepidophytus* (minimum diameter 24μ) were recorded in Belgium by STREEL (1966).

Although the majority of forms conform closely to the description given above, some specimens may display certain atypical trends in morphological and structural variation. The most pronounced variation (trend A of STREEL, 1966) is seen in the form of the lumina. In some specimens the lumina on the distal surface are regular in shape and are separated by relatively wide ridges of exoexine, whilst in others the lumina may be separated by extremely narrow ridges. In other specimens the ridges of exoexine separating the lumina may become discontinuous and may ultimately be reduced to a series of irregular crests or verrucae. Streel has also noted that there is a tendency (trend B of STREEL, 1966) in specimens possessing a relatively narrow equatorial extension of the exoexine for the exoexine to be relatively thicker. The range of variation displayed by the form and distribution of the distal lumina does not at present appear to have any stratigraphical

significance; it is interesting to note, however, that certain of the trends do appear to have a restricted geographical occurrence.

Although considerable variation has been recorded in the size of specimens, it is noteworthy that the size range recorded in any one population is normally small. This has been observed in samples from North Africa, Canada and Western Australia, suggesting that it is probable that the concept of Streel's biometrically defined zones could be successfully applied in other regions.

KEDO (1963) has divided the representatives of the *H. lepidophytus* complex into two groups, *H. lepidophytus* sensu stricto and *H. lepidophytus* var. *tener* KEDO. The reason for this division was not clearly stated by Kedo, but examination of the specimen of *H. lepidophytus* var. *tener* illustrated by KEDO (1963, pl.5, fig.110) suggests that it was on the basis of its smaller size and considerably finer reticulate ornament. Kedo suggests that *H. molestus* ISHCHENKO (1958) which was described from the Devonian, Tournaisian and Visean deposits of the Dnieper-Donetz Basin is synonymous with *H. lepidophytus* var. *tener*, but the present authors consider both of these forms, together with *H. mentitus* ISHCHENKO, which was also described from the same Russian deposits, to be more closely comparable with *Retispora florida* STAPLIN which was described from the Golata Formation (Upper Mississippian) of Alberta, Canada. *H. molestus* appears to differ from *H. lepidophytus* by possessing a finer reticulate ornament in which the lumina are smaller, more densely packed and separated by narrower ridges of exoexine than those of *H. lepidophytus* and also by the apparent absence of clearly defined curvaturae. *Retispora florida* appears superficially similar to some members of the *H. lepidophytus* complex in structural organisation, but may be distinguished by possessing a considerably finer distal reticulate ornament, by lacking the development of clearly defined curvaturae and by occasionally possessing three variably defined apical papillae. It is of interest to note that although many of Winslow's specimens of *E. lacunosus* appear closely comparable to *H. lepidophytus*, some differ in possessing three well defined apical papillae.

Archaeozonotriletes microreticulatus CARO-MONIEZ, *A. fenestratus* CARO-MONIEZ and *Hymenozonotriletes reticulatus* CARO-MONIEZ, which were described from Tournai, Belgium by CARO-MONIEZ (1962) from an horizon which was stated to be of Frasnian-Famennian age, all appear to be closely related to *H. lepidophytus*. Examination of the types of these species by one of the present authors (M. Streel) has shown that these species can be readily fitted into the variation pattern exhibited by the *H. lepidophytus* complex and are probably comparable to the form named but not formally described by KEDO (1962) as *H. lepidophytus* var. *minor* which was recorded from the upper part of the Dankov-Lebedyan horizon in the Byelorussian S.S.R. STREEL (1966, p.91) has commented that the size distribution exhibited by the Tournai populations would be sufficient justification to date the assemblages as being of lower Tn1b age rather than Frasnian-Famennian as suggested by Caro-Moniez.

Several authors have attached considerable stratigraphical significance to the distribution of the *H. lepidophytus* complex. KEDO (1957, 1962, 1963) noted that *H. lepidophytus* s.s. appeared in abundance and was restricted in occurrence to the middle part of the Dankov–Lebedyan horizon in the Byelorussian S.S.R. and also that the smaller form of the species, *H. lepidophytus* var. *minor*, replaced it in the upper part of the Dankov–Lebedyan horizon though it constituted a considerably smaller part of the total assemblage.

A more detailed assessment of the value of the *H. lepidophytus* complex for the elucidation of local correlation problems has been demonstrated by STREEL (1966). The examination and the application of biometric techniques to the populations of *H. lepidophytus* in the deposits of Tn1a and Tn1b age in the Dinant Basin of Belgium has enabled Streel to propose a series of 7 zones (zones A–G of STREEL, 1966), four of which are characterised by a distinctive population of *H. lepidophytus* and all of which can be accurately defined in terms of the standard subdivisions of the Belgian Tn1a–Tn1b succession as proposed by CONIL (1964) and MICHOT et al. (1967). Representatives of the complex appear first in small numbers in zone B which is equivalent to part of Tn1a α as defined by MICHOT et al. (1967). In zone C, which is equivalent to the remaining part of Tn1a α and all of Tn1a β, large representatives of *H. lepidophytus* (greater than 70μ) constitute the dominant element of the assemblages. Zone D, which is equivalent to the lower part of Tn1a γ, is characterised by assemblages containing a small number of large forms, whilst zone E which is equivalent to the upper part of Tn1a γ is characterised by the complete absence of large forms and the presence of atypical forms exhibiting the morphological features of trend A. The highest zone, zone F, which is equivalent to the upper part of Tn1a γ and, probably, the lower part of Tn1b α is characterised by assemblages containing large numbers of atypical forms exhibiting variation of both trend A and trend B types.

Because the base of the *Gattendorfia* zone which defines the base of the Carboniferous system (as adopted by the International Congress on the Stratigraphy and Geology of the Carboniferous, Heerlen, 1935) must be placed in the lower part of Tn1b in Belgium, the deposits containing the *H. lepidophytus* complex must be considered to be uppermost Devonian or Strunian. Close agreement, therefore, exists between the distribution of this species in Belgium and the Byelorussian S.S.R.

The only palynological investigation of comparable horizons in North America is that carried out by WINSLOW (1962) on the Upper Devonian and Lower Mississippian deposits of Ohio. Winslow has recorded representatives of the *H. lepidophytus* ($\equiv$ *E. lacunosus*) complex from sediments allegedly of both Upper Devonian and Lower Mississippian age. Representatives of the complex appear in considerable numbers at one locality in the Cleveland member of the Ohio Shale (Upper Devonian) but were first recorded in considerable numbers from other localities in the overlying Bedford Shale and Berea Sandstone which were considered by Winslow to be of Lower Mississippian age. The occurrence of this complex in both the Upper Devonian and Lower Mississippian rocks of Ohio is anomalous when compared with its restricted distribution in the Upper Famennian or Strunian in other parts of the world. The boundary between the Ohio Shale and the Bedford Shale (i.e., between the Devonian and Mississippian) appears to be defined principally by lithological criteria and may therefore be diachronous in character. This suggestion is to some extent substantiated by the unusual distribution of the *H. lepidophytus* complex. Elsewhere this complex appears in considerable numbers in the Upper Devonian and is unknown in Lower Carboniferous deposits, but in Ohio it occurs at some localities in the upper part of the Ohio Shale, whereas at adjacent localities it did not occur until the Bedford Shale. If the appearance of this species in considerable numbers was an event which took place more or less simultaneously, it seems probable that either the lower or the upper limit of the distribution of this complex would provide a more reliable datum plane than the present lithological boundary.

The Western Australian populations of *H. lepidophytus* ($\equiv$ *L. naumovae*) described by BALME and HASSELL (1962) which were obtained from well-documented Upper Famennian horizons, are closely comparable in composition to the Belgian populations.

Additional well-preserved populations of *H. lepidophytus* have also been obtained from material of Upper Devonian age from Western Australia, North Africa, Canada and the U.S.S.R., but as these populations are from isolated samples it is only possible at the present time to establish the close morphological and structural similarity between the representatives of these populations and those from the Belgian succession.

MIOSPORES ASSOCIATED WITH H. LEPIDOPHYTUS POPULATIONS

Although considerable uniformity is known to exist concerning the stratigraphic distribution of representatives of the *H. lepidophytus* complex in various parts of the world, the other components in the assemblages containing *H. lepidophytus* show considerable regional differences.

The assemblages recorded by KEDO (1962) from the middle part of the Dankov–Lebedyan horizon in the Byelorussian S.S.R., which were characterised by containing *H. lepidophytus* as the dominant form, contained the following distinctive association of accessory spores: *Lophotriletes rotundus* NAUMOVA, *Hymenozonotriletes ventosus* KEDO, *Archaeozonotriletes variabilis* NAUMOVA, *A. dedaleus* NAUMOVA, *Lophozonotriletes rarituberculatus* (LUBER) KEDO, and *L. macrogrumosus* KEDO. The upper portion of the Dankov–Lebedyan horizon, which may be distin-

guished by the complete absence of *H. lepidophytus*, contained the following association of accessory spores: *Leiotriletes minutissimus* NAUMOVA, *Trachytriletes solidus* NAUMOVA, *Lophotriletes rugosus* NAUMOVA, *Dictyotriletes crassipterus* NAUMOVA, *Hymenozonotriletes pallidus* NAUMOVA, *H. hyalinus* NAUMOVA, *Archaeozonotriletes parvibasilaris* NAUMOVA, *Lophozonotriletes malevkensis* (NAUMOVA) KEDO, and *L. cristifer* KEDO. In the assemblages from the lower portion of the overlying Malevka deposits which are of Lower Tournaisian age, KEDO (1957, 1962, 1963) has assigned considerable significance to the occurrence of *Hymenozonotriletes pusillites* KEDO which, although present in considerable numbers, is restricted stratigraphically to this horizon. This form, which is structurally analogous with many representatives of the genus *Vallatisporites* (HACQUEBARD) SULLIVAN, is considered by Kedo to be a reliable index species for the recognition of the base of the Tournaisian in the Byelorussian S.S.R.

Comparison of the overall composition of the assemblages described by STREEL (1966) from the Namur Basin to the Velberter Sattel (Rhineland) with those from the Byelorussian S.S.R. reveals only a few forms occurring in common to both regions. Forms superficially similar in structural organisation to *H. pusillites* were recorded by Streel from Tn1a deposits and representatives of *L. rarituberculatus* were recorded from the upper part of Tn1a and the lower part of Tn1b. The distribution of the latter species is closely comparable with its recorded occurrence in the Byelorussian S.S.R., but it would seem that the forms superficially similar in structure and organisation to *H. pusillites* appear in Belgium slightly earlier than in the Byelorussian S.S.R.

Among the other forms recorded by Streel from the Tn1a–Tn1b deposits of the Dinant Basin, it is interesting to note the occurrence of typical Devonian forms possessing an ornament of elements with bifurcate or multifurcate terminations which are closely comparable with *Dicrospora multifurcata* WINSLOW which was recorded from the Upper Devonian and Lower Mississippian deposits of Ohio by WINSLOW (1962). In addition, Streel recorded several species including *Punctatisporites irrasus* HACQUEBARD, *Retusotriletes incohatus* SULLIVAN, *Raistrickia* sp. *A* SULLIVAN, cf. *Crassispora balteata* (PLAYFORD) SULLIVAN, *Endosporites* cf. *minutus* HOFFMEISTER, STAPLIN et MALLOY, and *Spinozonotriletes* cf. *uncatus* HACQUEBARD, all of which were recorded by SULLIVAN (1964) from the Lower Limestone Shales (Tournaisian) of the Forest of Dean, England. Sullivan did not, however, record *Dicrospora multifurcata*, *Hymenozonotriletes lepidophytus* or *H. pusillites* in the Forest of Dean material.

The species associated with the *H. lepidophytus* populations in the Ohio Shale, Bedford Shale and Berea Sandstone of Ohio bear little comparison with either the Belgian or Byelorussian assemblages. *Dicrospora* spp., certain examples of which were recorded by Streel in the Belgian deposits, were recorded by Winslow from the Ohio Shale, Bedford Shale and Berea Sandstone, disappearing at approximately the same horizon as the representatives of the *H. lepidophytus* complex.

The Upper Devonian and Lower Mississippian horizons of Ohio also contain numerous representatives of *Reticulatisporites* (IBRAHIM) POTONIÉ et KREMP and *Canthospora* WINSLOW which appear broadly comparable with several forms of the *Knoxisporites* spp.—*Archaeozonotriletes literatus* (WALTZ) NAUMOVA complex which has been recorded as a characteristic component of Tournaisian assemblages by several workers in the U.S.S.R. and western Europe. Specimens recorded by Winslow from the Bedford Shale and Berea Sandstone (Lower Mississippian) as *Lycospora* sp. *A* appear to be similar in structure and morphology to *H. pusillites*.

An assemblage more closely comparable in composition to the microfloral assemblages from the Dankov–Lebedyan horizon of the Byelorussian S.S.R. has, however, been recognised by one of the present authors (B. Owens) from the Imperial Formation of the Richardson Mountains region, Northwest Territories, Canada. This assemblage, in addition to containing representatives of the *H. lepidophytus* complex, contained an association of spores including *Retispora florida*, *Lophozonotriletes malevkensis*, *L. rarituberculatus*, and *L. cristifer*.

CONCLUSIONS

From the evidence presented above it is apparent that although the *H. lepidophytus* complex has an extremely short stratigraphical range, it has been recorded in considerable numbers from many parts of the world. The species may therefore be regarded as a valuable index form for the recognition of Upper Famennian or Strunian deposits.

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PALEOZOIC SPORES AND TRIASSIC POLLEN GRAINS FROM SOME TUNISIAN WELL SAMPLES

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SUMMARY

Two different floristic assemblages are reported from some wells drilled by AGIP Direzione Mineraria in southern Tunisia. The first assemblage was found in Triassic beds, the second in the immediately underlaying Paleozoic beds.

INTRODUCTION

During the deep exploration of the Tunisian subsurface performed for oil searching by AGIP Direzione Mineraria since 1964, some wells were drilled in southern Tunisia.

The rock samples, both bottom cores and cuttings, were palynologically examined and provided a rich spore-pollen assemblage in the lower beds of the Mesozoic as well as in the Paleozoic section.

This work aims to illustrate the forms found in these beds and to point out the remarkable differences between the Mesozoic and the Paleozoic assemblages.

BRIEF STRATIGRAPHY OF THE WELLS

The section crossed by the examined wells (about ten) is nearly the same everywhere owing to the short distances between the wells. In this area there are out-crops of the Senonian formations, below which the wells crossed a succession of sediments, regularly stratified, down to the Triassic.

In Tunisia, Triassic sediments are known to have different lithological features, so that it is possible to establish three different formations. The Triassic section is the following, from top to bottom:

(*1*) Adjadj Formation (evaporitic Triassic): Anhydrite with frequent rock-salt and multicoloured shales interbedded, and rare, small levels of brown dolomite.