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FOSSIL ZYGOSPORES OF DEBARYA GLYPTOSPERMA (DE BARY) WITTR. (ZYGNEMATACEAE) IN HOLOCENE SANDY SOILS

A. C. ELLIS née ADAM and B. VAN GEEL

Hugo de Vries Laboratorium, Universiteit van Amsterdam

SUMMARY

After the recognition of fossil zygospores of Holocene age as those of *Debarya glyptosperma* (De Bary) Wittr., a representative of a family of filamentous algae, the Zygnemataceae, the ecological amplitude of this manifestly rare species could be assessed indirectly by means of a paleoecological approach.

1. INTRODUCTION

During the years 1971–1974 excavations of a mediaeval settlement near Kootwijk (the Netherlands) were carried out under the direction of H. H. van Regteren Altena and H. A. Heidinga of the Albert Egges van Giffen Instituut (Dept. of Pre- and Protohistory of the University of Amsterdam). A palynological study of samples from that excavation was carried out by the second author (in prep.).

During that study of samples from the mediaeval arable soils and the undisturbed subsoils containing older, presettlement microfossils, pollen and all other distinctive microfossils were analysed. The mediaeval spectra of one of the diagrams (*Diagr. 1*) were interpreted by PALS & VAN GEEL (1978). In the undisturbed subsoil below the mediaeval cultivation layer, zygospores of *Debarya glyptosperma* and some other zygnemataceous spore types were present. Zygospores of *D. glyptosperma* were also observed in palynological samples of Atlantic age from the Wietmarscher Moor (Western Germany).

From earlier work (VAN GEEL 1976, 1978; VAN GEEL & VAN DER HAMMEN 1978) we knew that algae of the family Zygnemataceae produce spores that may become fossilized. By means of published descriptions and keys (CZURDA 1932; KOLKWITZ & KRIEGER 1941–1944; RANDHAWA 1959; TRANSEAU 1951) spores of Zygnemataceae can be identified to the species, genus or family level.

2. RECENT DISTRIBUTION AND ECOLOGY

TRANSEAU (1951) has pointed out that all *Debarya* species are exceedingly rare. On the other hand their geographical distribution is world-wide. It has in fact been encountered in the living state on all the continents except Australia (KOLKWITZ & KRIEGER 1941–1944). It has also been found on the North Island of New Zealand

(NORDSTEDT 1888 – this paper is incorrectly cited in a few frequently used handbooks as to the name of the journal). The gap is filled by fossil finds from Australia, dating back to the Permian (VAN GEEL & VAN DER HAMMEN 1978). Such a distribution is usually interpreted as being brought about by the opportunity an organism must have had to spread over Pangea before the latter broke up.

Data on environmental factors controlling the occurrence of Zygnemataceae are almost non-existent, as will be pointed out by Van Geel (in press). The rarity of the recorded species (*D. glyptosperma*) causes an extra impediment, because finds of this taxon are comparatively scarce. Since a number of records date from a time when the importance of more detailed descriptions of the collecting sites was not recognised, information of this kind is missing. The same holds for the indications of the localities: they are not exact enough to permit an ecological evaluation fo the collecting sites either. A notable exception is the description of the collecting sites, including a list of vascular plants, in a paper by ALLORGE &ALLORGE (1931). From this description we can form a picture of natural or artificial bodies of water of a moderate to large size (sometimes covering several square miles), which share the characteristics of being shallow and situated on siliciferous soil. The vegetation points to mesotrophic conditions with some slight pollution. In Normandy (department Manche) the same conditions prevail, judging by the desmid flora (P. F. M. Coesel, *pers. comm.*) recorded by FRÉMY & MESLIN (1927) together with *Debarya glyptosperma*, and by the vascular plants *Senecio erucifolius* L. and *Catabrosa aquatica* P.B. mentioned by those authors as forming the stands of vegetation bordering the nearly dried up ditch from which they collected their sample. (The authors stated erroneously that this find was the first record of this *Debarya* for France; it apparently escaped their attention that DE BARY'S (1858) description of the species is based on material from an adjacent department in Normandy.) SKUJA (1956) found *Debarya* in Swedish lakes but could not identify them to the species level because of the lack of zygospores.

Since the identification of the species requires the availability of zygospores, the period in which the latter are formed could be gathered from the recorded sampling dates (which are equally scarce, however). SKUJA (1928) is the most explicit and stated that conjugation takes place in the month of May and that the zygospores mature in June (in Latvia). FRÉMY & MESLIN (1927) made their collecting trip on July 12th (in Normandy). ALLORGE & ALLORGE (1931) give only the total period in which all the samples involved in the study were collected, which ranged from May till July (in N.W. Spain). The same holds for the samples from New Zealand surveyed by NORDSTEDT (1888), having been collected in January and February. As the climate is roughly similar to that of Western Europe this period may be considered to be comparable with our midsummer, the temperature attaining its maximum and the rainfall its minimum. This fits in with the general idea that zygospore formation in this group of algae is induced by rising temperatures when the habitat is in an advanced state of desiccation.

3. PALEO-ECOLOGICAL INFORMATION CONCERNING DEBARYA GLYPTOSPERMA

Pollen diagrams of sandy soils mostly reflect local vegetational successions (cf. HAVINGA 1962). Although sample 199 of the pollen diagram (diagram 1) already contains some *Secale*, washed down from the overlying arable soil, there is no

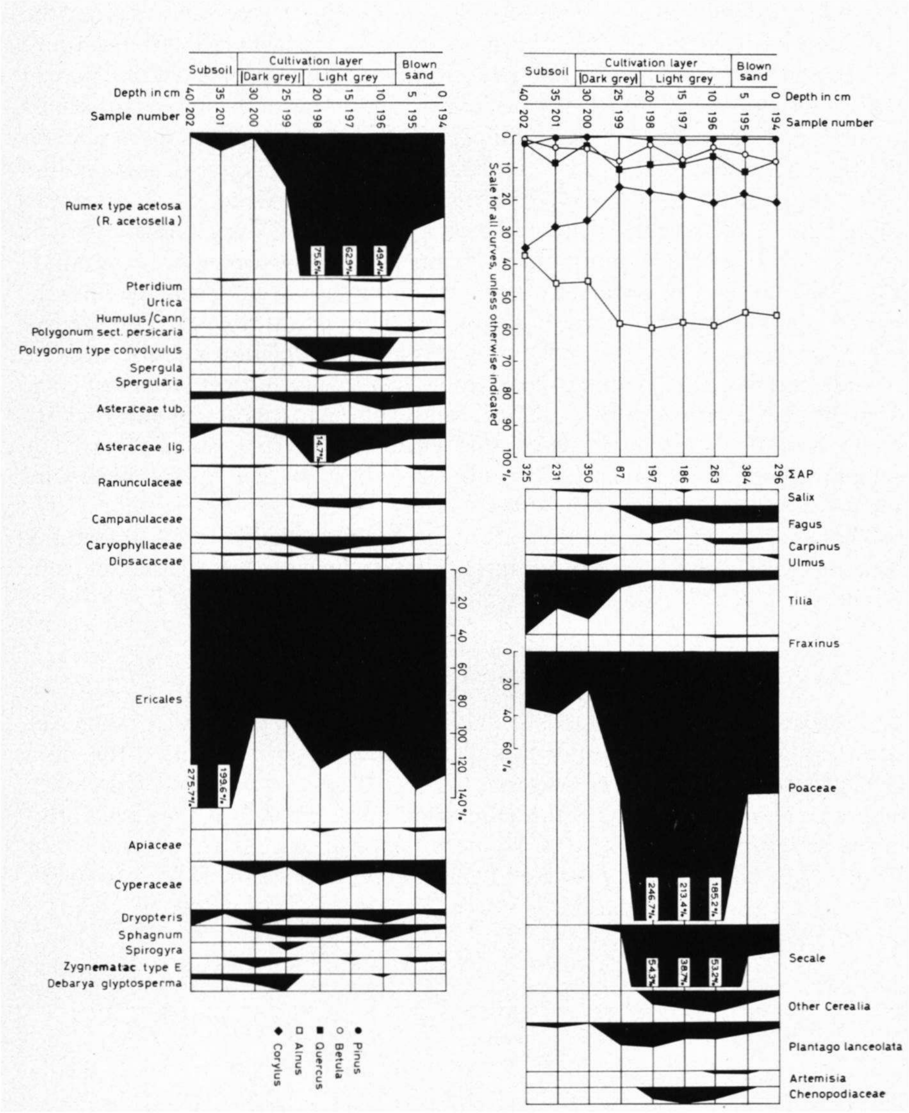


Diagram 1. Pollen diagram (drawing B. Donker, I. P. P.) from a sandy soil near Kootwijk, showing spectra of a mediaeval cultivation layer and underlying undisturbed subsoil containing zygospores of *Debarya glyptosperma*.

doubt that the lower four samples represent such a local vegetational succession. The dark grey layer (samples 200 and 199) was interpreted during the excavation as the lower part of the cultivation layer; the pollen spectra show that this interpretation was erroneous. The following explanation seems to be more probable. The relatively high *Tilia* percentage in the lowest three spectra indicate that originally (during the Atlantic period, maybe still during the early Subboreal) a mull was present. The dominant trees were *Tilia* and *Corylus*. During the Subboreal and the Subatlantic a leaching of the soil took place owing to a climatic deterioration, possibly in combination with human influence, and finally resulted in a podzol and the development of a mor. Because of the degradation of the soil. *Tilia* declined to disappear altogether as it seems (the *Tilia* values of about 3% in the arable soil probably represent re-worked presettlement pollen). The high Ericaceae pollen percentages in the lowest samples originated from local stands of Ericaceae (*Calluna*, *Erica*) in a heath of presettlement age on podzol. Since drainage of such soils is often hampered, inundated places must have occurred and we expect that *Debarya glyptosperma* occurred in such wet places drying up during the summer season. Zygospores of *Debarya glyptosperma* (at that time not yet recognized as such) were also observed in palynological samples (diagram unpublished) of Atlantic age from the Wietmarscher Moor. *Debarya glyptosperma* was of local occurrence at the transition from a poor sandy subsoil to a mesotrophic peat bog. From the pollen diagram it may be concluded that *D. glyptosperma* occurred in temporarily inundated places in a heath rich in *Lycopodium* (unfortunately no records of macrofosills are available).

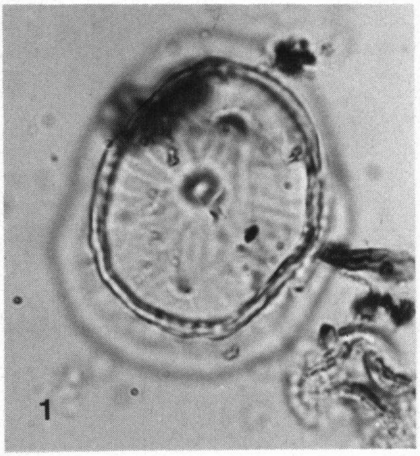
The paleo-ecological indications are in accordance with the data of ALLORGE & ALLORGE (1931) and of FRÉMY & MESLIN (1927) who collected this species from wet heaths in N.W. Spain and in Normandy, respectively.

4. THE ZYGOSPORES OF DEBARYA GLYPTOSPERMA

The zygospores are so characteristic that identification of this species, when met with, is absolutely reliable. For this reason there never was a need for more elaborate descriptions and critical comparisons of collected material with earlier descriptions and treatments of the taxon in question. Therefore, De Bary's original description (of 1858) is still the most complete one. As the species is not abundant, it has not been possible to gain a good impression of the variability within and between populations.

Figs. 1–3. *Debarya glyptosperma*, fossil zygospores (halves), from sandy soils near Kootwijk (× 1000).

Figs. 4–6. *D. glyptosperma*, recent zygospores (× 1000), from Massachusetts, U.S.A. (Phycotheca Boreali-Americana no. 1419); figs. 5 and 6: high and low focus images of the same spore.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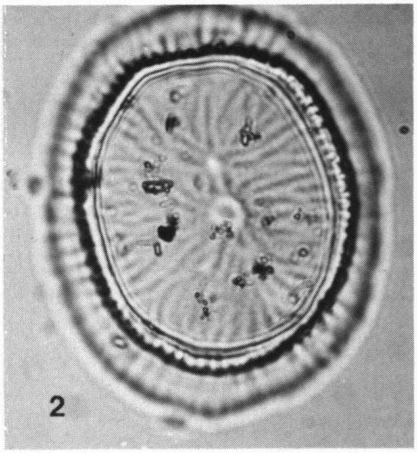
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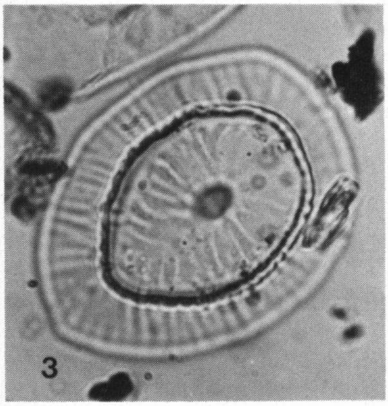
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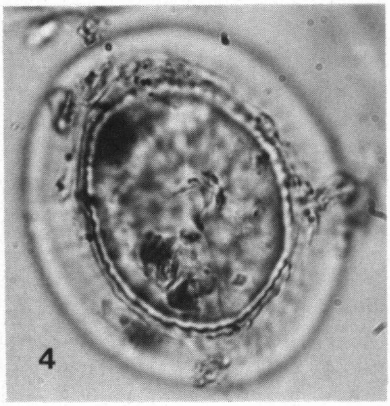
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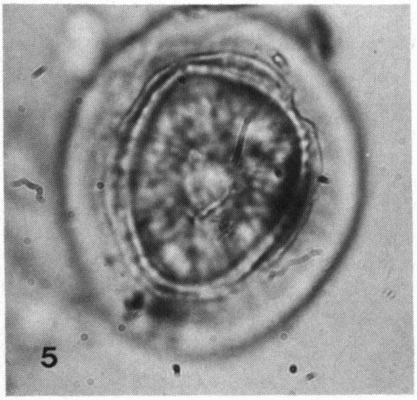
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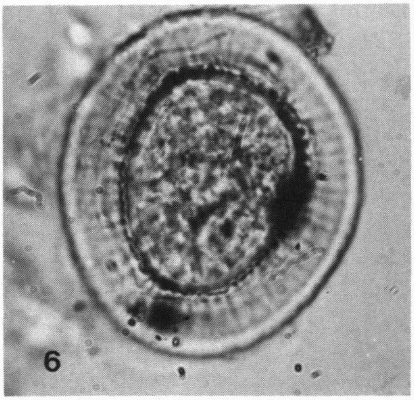
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The concave slope between the median and lateral keels of the spore is corrugated radially by regularly alternating ribs and furrows. All published figures seen by the present authors agree in this respect (*e.g.*, DE BARY 1858; WOLLE 1887; FRÉMY & MESLIN 1927; SECKT 1929; ALLORGE & ALLORGE 1931; BOURRELLY 1966). The pattern is not always exactly radial in all our fossil specimens (see *fig. 3*), although it still gives the impression of a great regularity (cf. TRANSEAU 1925, t.1, f.4).

In some of our fossil specimens the ribs and furrows are of equal width, but in most of them the ribs are broader than the furrows. De Bary's fig. 25 shows the reverse, while NORDTSTEDT (1888) assumed them to be narrower, and even fewer in number, in his specimens from New Zealand. In a few cases we observed a bifurcating rib, or two ribs confluent to form a single one.

As recent material we had at our disposal a sample from Winchester (Massachusets, U.S.A.), *Phycotheca Boreali-Americana* No 1419 from the Rijksherbarium, Leiden); these specimens in this sample display the regular alternation of broader and darker, and narrower and lighter striae (*fig. 6*) on the slope.

In addition, we could study material of the samples No. 750 of Wittrock & Nordtstedt's *Algae exsiccatae ... &c.* (in which *D. glyptosperma* is intermingled) kindly sent by Botaniska Museet (Uppsala) and the British Museum (Nat. Hist.). Although this material is rich in zygospores we did not succeed in procuring specimens from it which showed the striation described above.

As to the polar surface, the most distinct feature is what TRANSEAU (1925) has named the polar hub. It is apparently very variable in shape, having been depicted as an orbicular (TRANSEAU 1925; BOURRELLY 1966), as an oval (DE BARY 1858; SECKT 1929; BOURRELLY 1966) and as a slit-like (ALLORGE & ALLORGE 1931) structure. The polar hub is described as more or less raised above the level of the lateral keel, resembling a minute volcano with concave slopes. These slopes are also corrugated by radially arranged ribs and grooves of variable regularity. We found this pattern to be very faint in untreated American specimens, which was partly due to the presence of the protoplasmic remains and partly to the fact that the gametangial walls were still present. Judging from their figures, this complication was also met with by WOLLE (1887), WEST (1904), and FRÉMY & MESLIN (1927). In cleared specimens from the American sample, the corrugations turned out to be similar as those seen in some of the fossils, *i.e.*, they appear to be repeatedly and irregularly branched.

The material from the Wittrock and Nordstedt collection did not show this pattern; since BOURRELLY (1966, pl. 82, fig. 1–4) made his drawings, which show the radiating pattern quite clearly, after duplicate material of the same collection, we assume that our specimens were still immature.

In contrast to recent spores, the fossil ones exhibit the structure very clearly because only the mesosporium is left, although in some of them the pattern is not so distinct, which is probably due to the zygospore not yet having reached full maturity (WOLLE 1887). The ribs, appearing as dark markings broader than the thinner, lighter parts of the wall, are up to twice as broad. Their width is constant over their whole length and the regularity in the alternation of dark and light stripes is achieved by branching. This branching can be very regular, all the bifurcations being situated on an imaginary circle, but mostly some of the ribs bifurcate once or twice in an arbitrary point while others remain unbranched. Anastomosis may occur as well, sometimes even resulting in a reticulate pattern. In our material (of 22 specimens) the pattern can be said to show a continuous variation. Since cogent evidence whether or not this also holds for recent populations is lacking, we cannot extract any ecological pointers from them.

The polar hub (there may be two) is, like the ribs on the polar surface, also more distinct in the fossils and less so in the recent material where it is sometimes only indicated by wrinkles in the overlying gametangial walls.

The ribs of the polar surface and the lateral slope meet on the lateral keel, which, therefore, in optical section appears as a string of beads (*fig. 6*; DE BARY 1858, *fig. 25*). On this keel, perpendicular to the polar surface, a thin transparant vertical membrane is present, which is worn down in the fossils (*fig. 1, 3*), but rather high in recent material (*fig. 5*; DE BARY 1858, *fig. 24*).

Records of the spore dimensions are plentiful, however, although in some cases we had to calculate them from the indicated magnification of the figure (WOLLE 1887; FRÉMY & MESLIN 1927; BOURRELLY 1966), those of DE BARY (1858) were converted from Paris lignes into metric units (MOHR 1938).

The available ranges of the length and the width are 30–72 μm and 16–50 μm respectively. There is a considerable overlap between the individual records and the differences do not suggest a definite pattern of, *e.g.*, geographical variation. Although the existence of such a phenomenon may not be excluded, it is safer, for the time being, to attribute the differences to the unequal numbers of specimens from which the dimensions were taken. The measurements taken from those specimens (from Kootwijk) mounted in the slides in such a position as to yield reasonably accurate figures fit well into this range, the length varying between 39 and 55 μm (mean: 45; s:5; n:13) and the width between 25 and 53 μm (mean: 39; s:7; n:11).

VAN GEEL & VAN DER HAMMEN (1978) described and depicted fossil zygospores of *Debarya* with an irregular, additional structure in the centre of the polar surface, from Colombian lake deposits. Because of the difference with the "hub" of *Debarya glyptosperma*, as discussed and usually illustrated in literature, they suggested that their *Debarya* zygospores may belong to an as yet undescribed species, related to *D. glyptosperma*. However, the specimen depicted by ALLORGE & ALLORGE (1931, *pl. 32, fig. 6*), might be an indication that the Colombian material fits within the range of variation of the latter species.

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