SUBFOSSIL OOSPORES OF CHARACEAE FROM TWO SITES IN THE INGLEBOROUGH REGION OF WEST YORKSHIRE

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Subfossil oospores of Characeae from two Late-glacial sites, Sniddle Moss and Thieves' Moss, in the Ingleborough Region of West Yorkshire, were examined under light and scanning electron microscopes. An attempt was made to identify tentatively the characean species based principally on features of the oospore wall. Doubt attaches to one of the two species of *Nitella* recognized (*N. flexilis, N. opaca*?), one *Chara* species was attributed to the *C. vulgaris* complex, and other oospores belonging to the latter genus were placed in groupings based on oospore characters.

Keywords. Algae, *Chara, Nitella*, subfossil oospores, West Yorkshire.

INTRODUCTION

The Ingleborough Region forms the western margin of the Craven District of Yorkshire. It is a particularly interesting area because of its diverse geology, topography, vegetation and archaeology and it has attracted many researchers. Large areas are covered by various types of peat deposits, and the Flandrian vegetational and archaeological history of the region has been investigated intensively (e.g. Gosden, 1965; Swales, 1987). In a recent work (Oybak, 1993), attention was focused on the Late-glacial vegetational development of the region, and two Late-glacial sites, Sniddle Moss (NGR SD 707695), a typical valley bog near Clapham, and Thieves' Moss (NGR SD 771736), an eroded raised bog on the Ingleborough Massif, were examined in order to give an insight into this interesting period (c.13,000–10,000 BP). During the macrofossil analysis, *Nitella* and *Chara* oospores were recovered from organic and inorganic sediments of both sites.

Earlier work on the fructifications of Characeae has shown that the oospores provide a valuable aid to the determination of species (e.g. Groves & Bullock-Webster, 1920, 1924). The surface pattern of the oospore wall in the fossa region as seen under the light microscope (LM) has long been used for diagnostic purposes in the family. Groves & Bullock-Webster (1920) produced a key to 32 British and Irish species based mainly on oospore characteristics. Horn af Rantzien (1956, 1959) used a number of characters of the oospore, including the outer wall structure, for distinguishing species of Characeae. Identification of subfossil oospores under the binocular microscope has been attempted by several workers (Krause, 1986; Haas, 1994). However, difficulties in interpretation of the ornamentation on the oospore

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wall have arisen and the nature of the oospore wall has frequently been misinterpreted. Recently, scanning electron microscope (SEM) studies have enabled the correct interpretation of oospore wall characters to be made, leading to a better understanding of the nature of the outer wall of oospores of modern and fossil representatives of the group (Caceres, 1975; Frame, 1977; Leitch, 1986; John & Moore, 1987; John et al., 1990; Leitch et al., 1990).

Oospores of the family Characeae are frequently found in Quaternary deposits. There are many records of *Nitella* and *Chara* oospores from Late-glacial and early Flandrian deposits of Britain and Ireland but few are named to species. In the present research an attempt has been made to make specific identifications of *Nitella* and *Chara* oospores recovered from Sniddle Moss and Thieves' Moss by using stereoscopic and light microscopes and the SEM.

MATERIALS AND METHODS

Peat samples for analyses were collected by a 'Russian' type peat borer.

(1) For the examination of macroscopic plant remains (including Characeae oospores) subsamples from the Sniddle Moss site were firstly treated with 10% nitric acid overnight and then strained through two sieves with meshes 425µm and 250µm respectively. The washed sample retained in the sieves was placed on a petri dish in small amounts of water to separate macrofossils. For the Thieves' Moss site, only the small amounts of sediment left after the treatment with HCl (5%) for pollen analysis were strained and examined.

(2) The oospores recovered were divided into types on the basis of some important characteristics such as shape, size and number of spiral convolutions. These types, identified with the help of stereoscopic and light microscopes, are A, B1 and B2 from Sniddle Moss and C and D from Thieves' Moss, and they have been compared with modern oospores of British species from G. R. Bullock-Webster's specimens in the Herbarium of the University of Leeds (LDS).

(3) The scanning electron microscope was also employed in order to understand the nature of the wall of the subfossil samples and to make an attempt at further determinations. The SEM technique applied is as follows: after washing in distilled water, selected subfossil oospores were mounted on aluminium stubs with double-sided tape and coated with a gold layer of 50nm using a POLARON sputter coater. Photographs were taken using a CAM SCAN SERIES 3 scanning electron microscope.

A survey of the characteristics of the subfossil types is given in Table 1.

Terminology relating to general morphology of oospores revealed by the light microscope follows Horn af Rantzien (1956). Descriptive terms for details of the oospore wall used by Frame (1977) and John et al. (1990) have been adopted.

TABLE 1. Characters of the subfossil oospore types from Sniddle Moss and Thieves' Moss where doubt attaches to their identity, especially to species.

	Sniddle Moss						Thieves' Moss			
	Nitella (type A)		*Chara* (type B1)		*Chara* (type B2)		*Nitella* (type C)		*Chara* (type D)	
Characters	LM	SEM	LM	SEM	LM	SEM	LM	SEM	LM	SEM
LPA (length of the polar axis)	520 640μm	620μm	664 840μm	633μm*	620 700μm	770μm**	420μm	302μm	630 740μm*	567μm
LED (largest equatorial diameter)	450 520μm		430 550μm		320 390μm		360μm*	258μm	370 550μm	367μm
Shape	Subprolate		Perprolate		Prolate		Subprolate		Prolate	
AND (anisopolar distance: distance from the apical pole to the largest equatorial diameter)	300μm		300 400μm	333μm	300 360μm		200μm		300 400μm	300 400μm
ANI (anisopolar index: AND/LPA × 100)	53 (ellipsoidal)		44 (ellipsoidal)		50 (ellipsoidal)		48 (ellipsoidal)		48 (ellipsoidal)	
Maximum width of the basal pore	80 140μm		100 160μm		100 120μm				70μm	
No. of convolutions of the fossules	6 7		12 13		12 14		6		11 14	
No. of convolutions of the spirals	6 7		12 14		13		7		11 14	
Height of the basal claw			40 100μm		20 50μm				50 70μm	
Ornamentation on the fossa wall		spongy with mesh size c.1.2μm		roughened (pits and pores)		low pustular elevations with pores		roughened (very small granules and pits)		granules/papillae
Surface of the ribbon				low, fused nodular elements						low, fused nodular elements
Width of the ribbon				c.30μm						

*excluding basal cage
**including basal claws

NOTES ON CHARACEAE OOSPORES RECOVERED

Nitella

Type A (Fig. 1a–c)
Nitella flexilis (L.) C. Agardh

The oospores of type A compared well with the modern oospores of herbarium specimens of *Nitella flexilis* on the basis of general appearance. Frame (1977), who worked on the fine surface ornamentation in the tribe Nitelleae with the SEM, points out that in various forms of *Nitella flexilis* there are highly variable surface patterns, either smooth, pitted, finely spongy or scabrous. The comparison between his study (see Frame, 1977: 47, pl. III, figs 19 & 20) and the SEM photographs of the oospore wall of *Nitella* showing a spongy pattern (Fig. 1b–c) from Sniddle Moss allowed for intraspecific determination and suggested that it is *Nitella flexilis* var. *flexilis* f. *flexilis*.

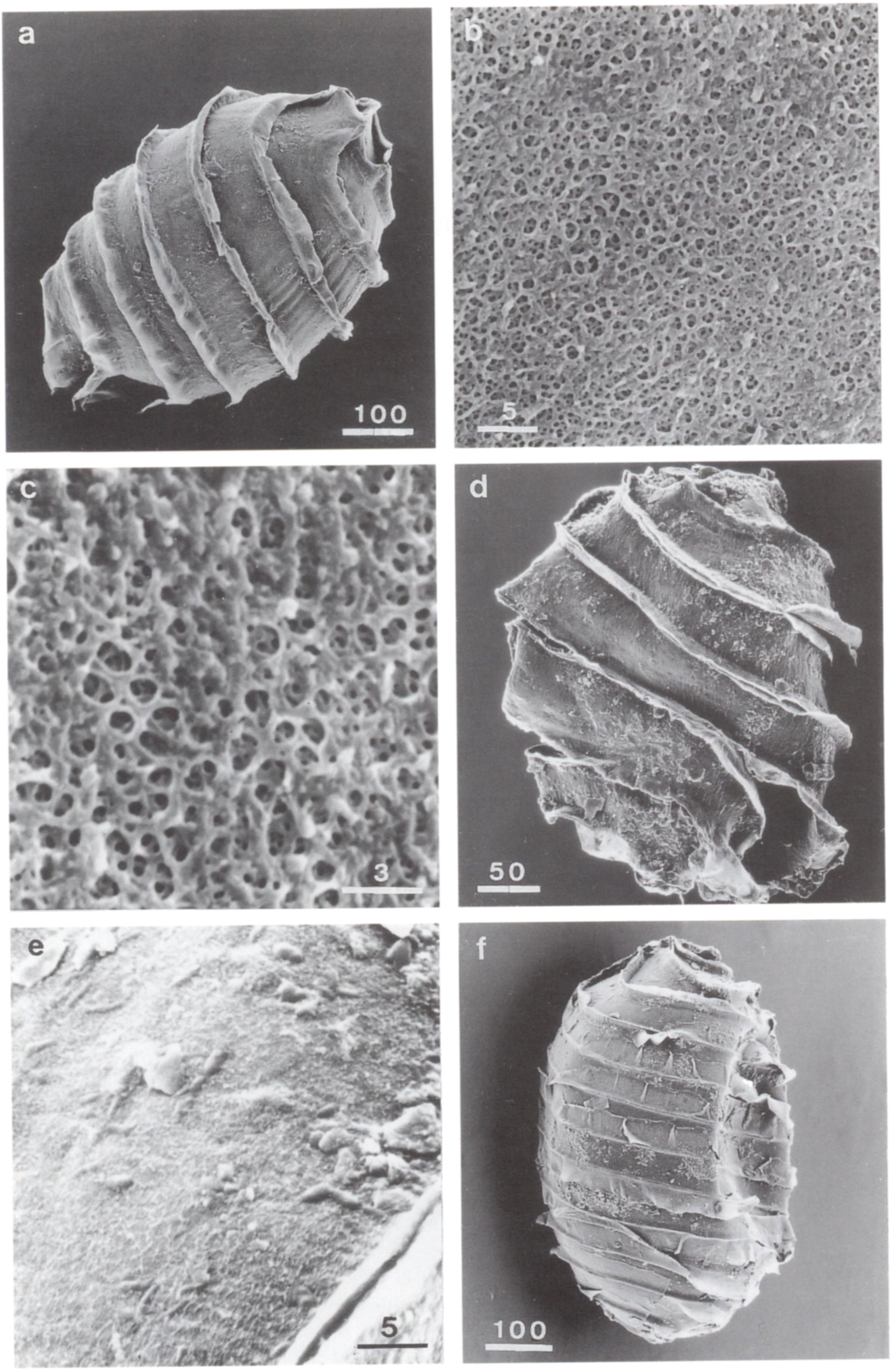
Type C (Fig. 1d–e)
Nitella opaca (Bruzelius) C. Agardh

The position of modern *Nitella opaca* is taxonomically problematical because this taxon and *N. flexilis* display a range of morphological characters that could fall within both taxa (Moore, 1986). Groves & Bullock-Webster (1920), however, separate *N. opaca* from *N. flexilis* on the basis of several characters including the oospore size: the oospore of *N. opaca* is smaller than that of *N. flexilis*. In this study, it was possible to distinguish *Nitella* oospores (type C) found at Thieves' Moss from those (type A) recovered from Sniddle Moss under the binocular microscope: type C is smaller and more compressed than type A (see Table 1). The oospore wall of type C (*Nitella opaca*) also shows a different feature under the SEM: there are very small granules and pits giving a roughened surface (Fig. 1e).

Chara

The SEM photographs of *Chara* oospores from the study sites were compared with those of modern *Chara* oospores in John et al. (1990). *Chara* oospores, in general, have fewer types of ornamentation, and surface features are taxonomically less significant than in *Nitella*. Unfortunately, this conservative nature of the oospore wall in *Chara* makes further determination difficult. In addition, general morphological

FIG. 1. Scanning electron micrographs of oospores of Characeae from Sniddle Moss and Thieves' Moss. a–c *Nitella flexilis* (type A) from Sniddle Moss: (a) oospore with its flanged striae; (b) spongy patterning on the fossa wall; (c) close view of the wall showing meshes. d–e *Nitella opaca* (type C) from Thieves' Moss: (d) oospore with some debris; (e) fossa wall (between the two ridges) roughened due to presence of very small granules and pits. (f) *Chara* sp. (*C.*? *aspera*) (type B1) from Sniddle Moss, oospore with some debris. Scale numbers are microns.


a
100
b
5
c
3
d
50
e
5
f
100

characters including size do not help very much. Consequently, the grouping of the outer fossa wall given by John et al. (1990) has been considered and subfossil *Chara* oospores have been placed in certain groups.

Type B1 (Fig. 1f, Fig. 2a)
Chara sp. (*Chara* ? *aspera* (Dethard.) Willd.)

This type has been placed in group (I)-B (John et al., 1990). The group includes *Chara aspera, C. baltica* Bruzelius, *C. capensis* E. Mey. ex Kutz. and *C. strigosa* A. Braun characterized by either relatively smooth or roughened (due to presence of numerous small pits, pores and depressions) oospore wall in the fossa region and low, fused, nodulated elements on the surface of the ribbon. A closer examination suggests that type B1 has some features more similar to *Chara aspera* than other species in the group, namely that the fossa wall has pores varying in size; larger ones range from 0.05–1μm in diameter (Fig. 2a).

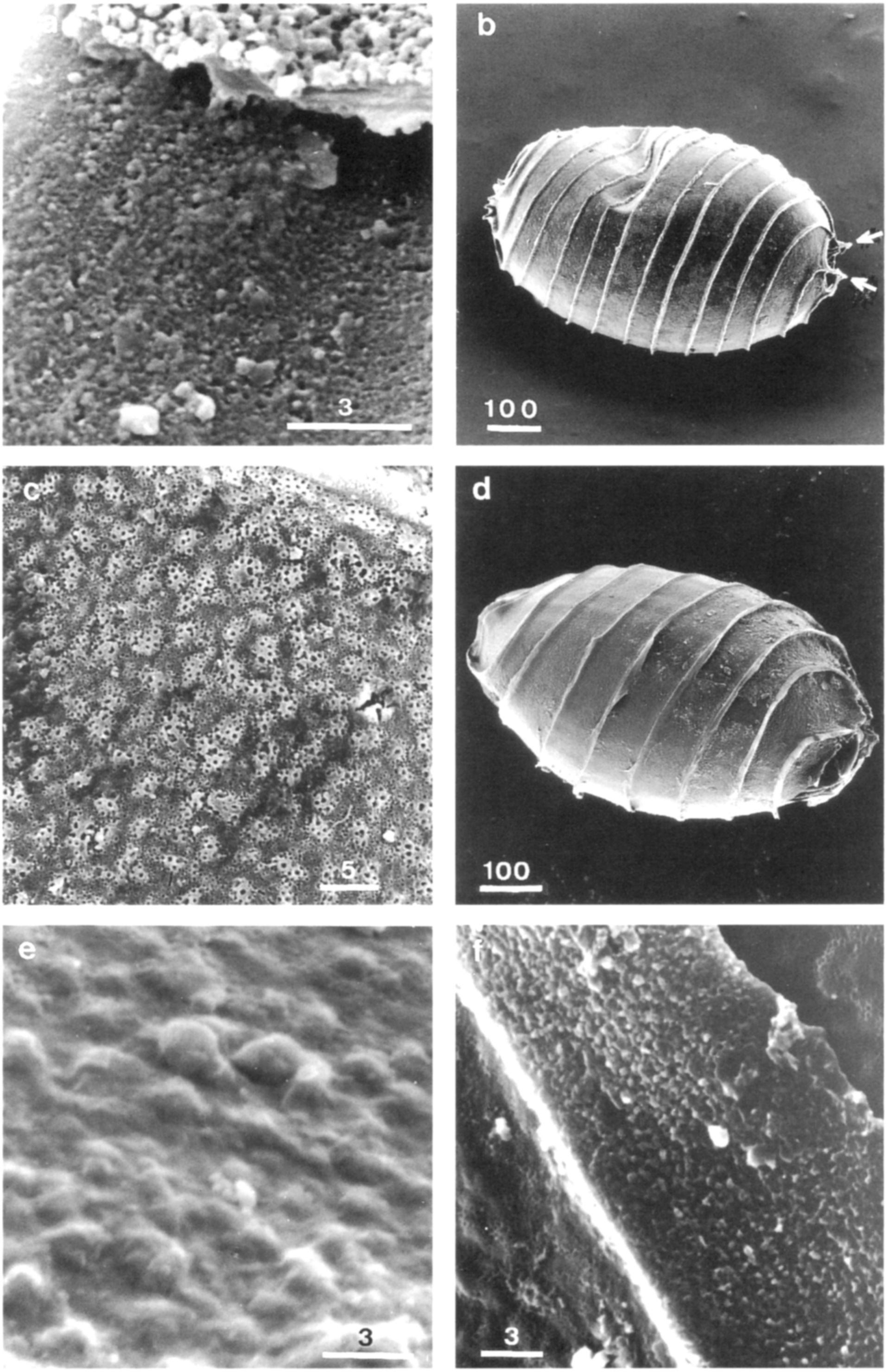
Type B2 (Fig. 2b–c)
Chara sp.

Type B2 has been placed in group (I)-A-iii (John et al., 1990) whose members (*Chara corallina* Klein ex Willd., *C. desmacantha* (H. & J. Groves) J. Groves & Bull.-Webst. and *C. rusbyana* M. Howe) have pusticular projections and low domes with or without an opening on the fossa wall. Unfortunately, direct comparison is now impossible as this type does show oospore wall characters – low pustular elevations perforated by more or less regular openings – not seen in modern specimens investigated so far.

Type D (Fig. 2d–f)
Chara vulgaris L. complex

The determination of this type is based on the comparison with the outer wall structure of *Chara vulgaris* specimens seen with the SEM (see John et al., 1990, figs 60–62) (in this study Fig. 2e–f): there are granules or papillae in the fossa region (there are five granules along a 10μm width across the fossa) and the surface of the ribbon is characterized by low, fused nodular elements. However, it should be stated that a large number of taxa are assembled in *Chara vulgaris*. Moore (1986) writes that *Chara vulgaris* and its related taxa display the greatest degree of morphological

FIG. 2. SEMs of *Chara* oospores from Sniddle Moss and Thieves' Moss. (a) *Chara* sp. (*C.*? *aspera*) (type B1) from Sniddle Moss, surface of the fossa wall covered by numerous pits, pores and depressions and of the broken ribbon shrouding the fossa wall. b–c *Chara* sp. (type B2) from Sniddle Moss: (b) oospore with basal claws (arrowed) in lateral view; (c) fossa wall showing low pustular elevations with perforations. d–f *Chara vulgaris* (complex) (type D) from Thieves' Moss: (d) oospore in lateral view; (e) fossa wall covered by projections; (f) surface of the ribbon and of the fossa wall. Scale numbers are microns.


a
3
b
100
c
5
d
100
e
3
f
3

variation. John et al. (1990) examined only a few taxa which were grouped as varieties and forms of *Chara vulgaris* by Wood & Imahori (1965). Their preliminary investigation revealed that, of the taxa studied, only *C. denudata* A. Braun (= *Chara vulgaris* L. var. *denudata* (A. Braun) R.D. Wood f. *denudata*) shows an oospore wall character similar to the specimens of *C. vulgaris*. In the light of these views the authors of this paper prefer to place type D in the *C. vulgaris* complex.

CONCLUSION

This study shows that, although there are considerable difficulties in the taxonomy and identification of members of the Characeae, particularly from subfossil oospores, the use of scanning electron microscopy can take identification considerably further than the use of light microscopy alone.

Unfortunately, detailed habitat preferences for many of the taxa of *Nitella* and *Chara* are not well known so that information about their distribution and former occurrence does not tell us much about former conditions.

In spite of its shortcomings, we hope that this study will form part of the record of the occurrence of Characeae in Quaternary deposits.

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