

Fungal spores record Iroquoian and Canadian agriculture in 2nd millennium A.D. sediment of Crawford Lake, Ontario, Canada

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Abstract Pollen analysis identified domestic *Zea mays* (corn, maize), *Phaseolus vulgaris* (kidney bean), *Helianthus annuus* (sunflower) and *Cucurbita pepo* (squash) accompanied by spores of fungi, many of which cause crop diseases, such as *Ustilago maydis* (= *U. zae*, corn smut), *Puccinia sorghi* (corn rust), *Uromyces appendiculatus* (bean rust) and *Puccinia graminis* (wheat rust). Spores were most abundant in two intervals, ca. A.D. 1300 to ca. 1500 when prehistoric Iroquoian agriculture flourished near the lake and since 1830, when historic *Triticum aestivum* (wheat) agriculture began. In addition to dispersal by wind, *Branta canadensis* (Canada goose) also transported fungal spores to the lake via their dung. Spores of fungi that parasitize crop plants may be more abundant than pollen of their host plants and therefore spores may more readily indicate ancient agriculture.

Keywords Fossil fungal spores · Crawford Lake · Crop plants · Iroquoian · *Branta canadensis* · Canada goose

Introduction

Crawford Lake sediment of the 2nd millennium A.D. has superb microfossil preservation including pollen grains of plants cultivated by prehistoric Iroquoians and historic Canadians (Fig. 1; Byrne and McAndrews 1975; McAndrews and Boyko-Diakonow 1989; Byrne and Finlayson 1998; Ekdahl et al. 2004; Turton and McAndrews 2006). In the Iroquoian Pollen Zone spanning ca. A.D. 1286–1500, pollen of cultivated *Zea mays* (corn, maize), *Phaseolus vulgaris* (kidney bean), *Cucurbita pepo* (squash) and *Helianthus annuus* (sunflower) were mostly delivered to the lake in dung pellets that DNA analysis sourced to *Branta canadensis* (Canada goose) (McAndrews and Turton 2007). Also abundant were fossil spores of the fungus *Ustilago maydis* (= *U. zae*, corn smut); we here document spores of this fungus and those of other fungi, many of which parasitize crop plants.

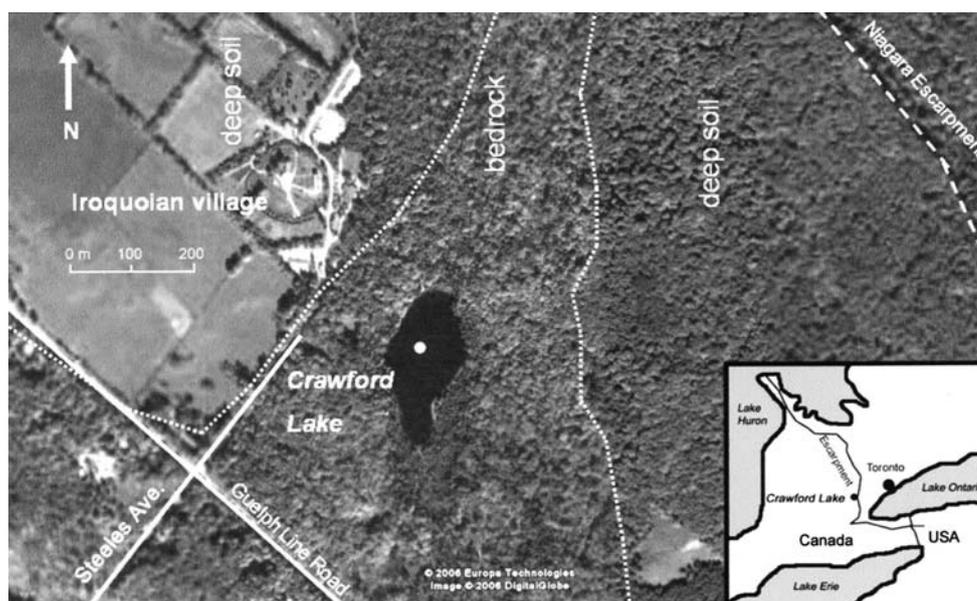
Fungi may be parasites such as *Ustilago maydis* on corn, or saprophytes that decompose cellulose of dead plant material such as the wood-rotters *Ustilina* spp. (carbon cushion) and *Geoglossum* spp. (earth-tongue). These aerobic fungi thrive on dry upland sites rather than in lakes. Tree ringing and forest clearance preceding cultivation provides habitat for wood-rotting fungi. Compared with pollen grains, fungal spores are usually rare or unreported in lake sediment, although mammals, such as *Equus caballus* (horse), may carry them from the upland to lake margins and deposit them via their dung (Davis et al. 1977). Fossil spores may be abundant in sediment eroded from the upland, for example in deltaic sediment (Muller 1959), in floodplain sediment (Jarzen and Elsik 1986) and in raised bog peat (Van Geel 1978). This paper describes, quantifies and interprets fossil fungal spores from Crawford Lake, emphasizing parasites of crop plants (Agrios 2005) transported to the lake by *Branta*.

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Fig. 1 Location map of Crawford Lake showing the Crawford Iroquoian village site located on deep soil suitable for farming. The sediment cores were lifted near the centre of the lake at latitude 43.468545 N, longitude -79.949027 W, where the water was 22.5 m deep. Modified from Google Earth and modified with permission from McAndrews and Turton (2007)



Environmental setting

Crawford Lake lies 50 km southwest of Toronto along the edge of the Niagara Escarpment (Fig. 1). Its basin was eroded in dolostone during the retreat of the Wisconsin glacier about 15,000 calendar years ago (Yu 2003). In the deepest part of the 2.4 ha lake, 22.5 m of water overlies 4.5 m of postglacial sediment. Owing to its great depth and small surface area, the lake is meromictic (with layers of water that do not intermix): the hypolimnion below 15 m lacks oxygen and has a constant temperature of 6°C (Ekdahl et al. 2004). In the upper 70 cm of sediment, carbonate-organic varves (Dickman 1979) deposited since at least 1,000 years (Boyko-Diakonow 1979) only became well preserved, episodically at first, since 1360 when the onset of meromixis excluded sediment-disturbing detritivores such as ostracods. This shift to meromixis and varve preservation parallels deposition of *Branta* dung, which supplied nutrients and gave rise to eutrophication, anoxia and permanent stratification (McAndrews and Turton 2007). Fossil *Branta* dung pellets are confined to the Iroquoian Zone (ca. 1286–1500); they are absent in the varved sediment of the overlying Post-Iroquoian Zone when there were no nearby *Zea* fields. Dung pellets have not been seen in the Canadian Zone (since ca. 1830) when *Branta* probably avoided the lake because of intense hunting with firearms. Since near extinction in the early 20th century, the bird has become abundant; in the past decade a few *Branta* roosted and a pair nested on the lake. Once established in the Iroquoian Zone, meromixis persisted to the present. An alternative view to eutrophication by *Branta* (guanotrophy) holds that eutrophication proceeded directly from human-generated nutrients (Ekdahl et al. 2007)

through overland flow of nutrient-rich runoff from the local Iroquoian village (John P. Smol, oral communication).

Zea appeared on pre-Iroquoian sites in southern Ontario in the second half of the 1st millennium; AMS dates on *Zea* kernels span A.D. 590 to 1030 (Crawford et al. 1997). It was several centuries later in the first half of the second millennium that people identified as Iroquoian (ancestors of historic Iroquois) built *Zea*-based agricultural villages. On their ancient village sites, charred food plant remains are mostly those of domestic plants, especially of *Zea* but also including *Phaseolus*, *Cucurbita* and *Helianthus*. Edible nuts of *Juglans cinerea* (butternut) and *Carya ovata* (shagbark hickory) are occasionally present; nuts of *Fagus grandifolia* (American beech) and *Quercus* spp. (oak) are very rare although they could have been famine food when the *Zea* crop failed. Village middens commonly yield bone of *Odocoileus virginianus* (white-tailed deer), *Canis lupus familiaris* (dog, the only domestic animal), *Ursus americanus* (black bear), *Castor canadensis* (beaver), *Ectopistes migratorius* (passenger pigeon) and *Branta canadensis*.

Within 3 km of Crawford Lake there were seven Middle Iroquoian villages, each occupied for up to 30 years, with estimated populations ranging from 200 to 3000 people (Finlayson 1998), dating to A.D. 1200–1500 (Dodd et al. 1990). The small (0.4 ha) Crawford Lake Village lying 150 m from the lake was intermittently occupied by ca. 200 people during the 1400s (Finlayson 1998; Byrne and Finlayson 1998). From ca. 1500 when Iroquoians moved away until the early 1800s, the area around the lake was unsettled. Beginning about 1830, Canadians cleared forest for farming and grew *Triticum aestivum* (bread wheat) in their early fields; *Puccinia graminis* (wheat stem rust) infected the *Triticum* (Jones 1946). In the past several decades, common

crops were *Triticum*, *Zea* and *Glycine max* (soybean) together with forage legumes such as *Medicago sativa* (alfalfa, lucern) and *Trifolium* spp. (clover).

On the higher land around the lake is mixed forest (Scott 1995) of *Pinus strobus* (white pine), *Thuja occidentalis* (eastern white cedar), *Tsuga canadensis* (hemlock), *Acer saccharum* (sugar maple), *Quercus rubra* (red oak), *Ulmus americana* (white elm), *Fagus grandifolia* (American beech), *Fraxinus americana* (white ash), *Betula papyrifera* (white birch), *Ostrya virginiana* (ironwood) and *Tilia americana* (basswood), all represented by fossil pollen grains. On the cliff around the lake grow ancient white cedar (Larson and Kelly 1991) infected by *Pestalotiopsis funerea* (cedar shoot blight). The regional climate is humid cool-temperate-continental with a mean yearly precipitation of 910 mm, mean July temperature of 20.3°C and mean January temperature of −6.0°C.

Methods

We collected sediment of the past 1,000 years with a freezing sampler (McAndrews and Turton 2007) and visually correlated it with the 2001 collection that was dated with 25 AMS dates and varve counts since 1867 (Ekdahl et al. 2004). We gently treated for ca. 1.5 min a sieved fraction (between 200 and 10 µm) with warm dilute KOH and cold dilute HCl, then stained with safranin and mounted in glycerin. To determine the robustness of fungal spores relative to pollen grains, a duplicate sample was also treated with harsh reagents—hot hydrofluoric acid and hot acetolysis mixture. A sum of 100 tree pollen was used to calculate microfossil

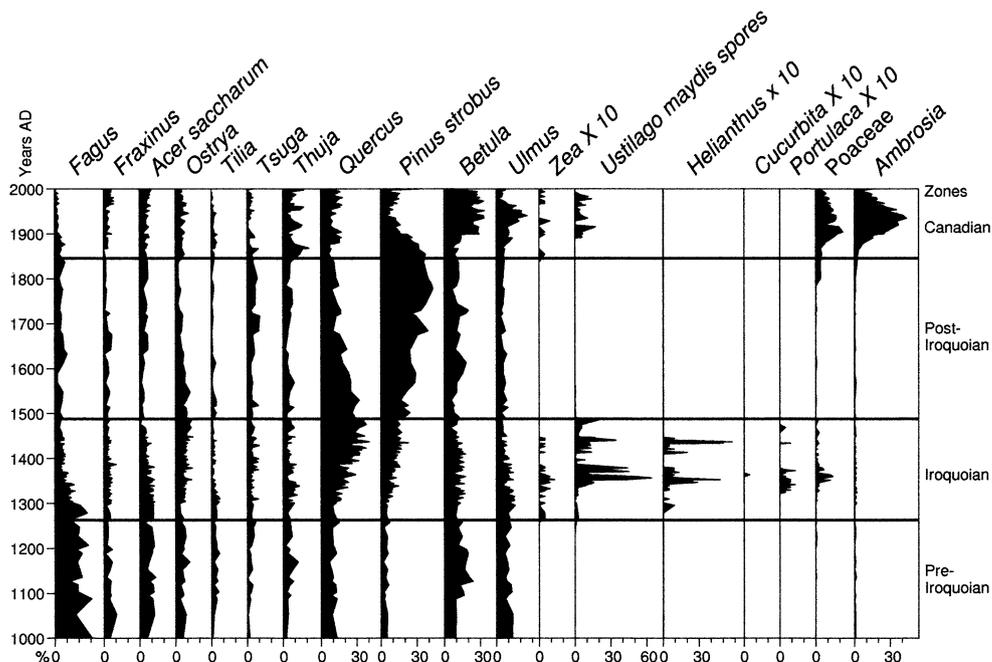
percentages. Our identifications follow McAndrews et al. (1973), Kapp et al. (2000), Van Geel (2001) and Lacey and West (2006). Fungal names for crop pathogens follow the American Phytopathological Society (2008).

Results

Figure 2 shows an abbreviated pollen diagram of the upper 70 cm of sediment. The Pre-Iroquoian Zone featuring mixed forest dominated by *Fagus* and *Acer saccharum* lacks cultigen and weed pollen. In the Iroquoian Zone A.D. 1286–1500, crop and weed pollen appear and forest succession is to *Quercus*, a response to warming in this period. The Post-Iroquoian succession to *Pinus strobus* reflects Little Ice Age Period cooling. In the Canadian Zone defined by peaks of Poaceae and *Ambrosia*, *Pinus* declines due to logging followed by forest succession to *Betula* and *Ulmus*. *Ulmus* declines due to disease ca. 1970.

Fungal spores were six times more abundant per hundred pollen grains in the gently treated samples than in those concentrated with harsh reagents (Table 1), indicating that spores are more fragile than pollen grains: *Alternaria* spp. (leaf spot) was especially prone to disappear. Figure 3 illustrates the more abundant fungal spores. *Pestalotiopsis funerea* spores (Fig. 3a) have three or four psilate cells arranged in a row. *Thuja* trees growing on cliffs around the lake provide a ready source of these fossil spores through air dispersal or included with branchlets falling into the lake. Plant macrofossils and fossil pollen indicate that cedar grew on the cliffs for the past 10,000 years (Yu 1997).

Fig. 2 Diagram of main pollen types from Crawford Lake that spans the second millennium A.D. The pollen sum is 200 tree pollen grains; to plot extreme values the herb pollen and *Ustilago maydis* spore counts were added to the sum before their values were calculated. Modified from McAndrews and Turton (2007)



The most abundant spore type among crop parasites (Fig. 3; Table 2) was *Ustilago maydis*; the tiny spores (Fig. 3b) are inaperturate spheroidal unicells 7–10 µm in

Table 1 Fungal spore counts after harsh (HF, acetolysis) and gentle (dilute HCl and dilute KOH) treatments of a *Branta canadensis* dung pellet at 43 cm depth dating ca. A.D. 1430

	Harsh	Gentle
<i>Alternaria</i> spp.	3	153
<i>Corynespora cassiicola</i>	0	2
<i>Epicoccum nigrum</i>	11	72
<i>Pestalotiopsis funerea</i>	0	3
<i>Puccinia sorghi</i>	0	4
<i>Sphacelotheca reiliana</i>	54	147
<i>Ustilago maydis</i>	8	76
Other	8	18
Total spores	70	475

In each sub-sample, 100 tree pollen grains were also counted

diameter with a scabrate surface sculpture. *Sphacelotheca reiliana* (corn head smut) (Fig. 3c) spores are similar but larger, 12–15 µm in diameter with verrucae on a relatively thick wall. *Puccinia sorghi* (common corn rust) has two kinds of spores, a psilate unicellular uredospore (Fig. 3d) with one to four pores and a two-celled teliospore (Fig. 3e) that is borne on a stalk. *Setosphaeria turcica* (northern leaf blight of corn) has spores (Fig. 3f) of four to six cells arranged linearly. *Corynespora cassiicola* (corynespora blight) spores are often fragmented conidiophores (Fig. 3g), which are multicellular, linear and psilate with an apical thickening. *Uromyces appendiculatus* (bean rust) has 30 µm long thick-walled subspheroidal teliospores (Fig. 3h) that are scabrate with one pore, whereas the less common uredospore (Fig. 3i) is psilate, 20 µm with three pores. *Puccinia graminis* uredospores (Fig. 3j) (teliospores were not seen) are subspheroidal (ca. 24 × 27 µm) and scabrate with three or four pores; it is confined to the Canadian Zone.

Fig. 3 Fossil fungal spores from Crawford Lake: *U* uredospore, *T* teliospore. **a** *Pestalotiopsis funerea*, **b** *Ustilago maydis*, **c** *Sphacelotheca reiliana*, **d** *Puccinia sorghi* (U), **e** *P. sorghi* (T), **f** *Setosphaeria turcica*, **g** *Corynespora cassiicola*, **h** *Uromyces appendiculatus* (T), **i** *U. appendiculatus* (U), **j** *Puccinia graminis* (U), **k** *Pseudoperonospora cubensis*, **l** *Alternaria alternata*, **m** *A. helianthi*, **n** *Epicoccum nigrum*, **o** *Ustilina* sp., **p** *Geoglossum* sp., **q** *Tilletia* cf. *caries* (T), **r** *Curvularia* sp., **s** *Pleospora herbarum*, **t** *Glomus* sp. with attached hypha

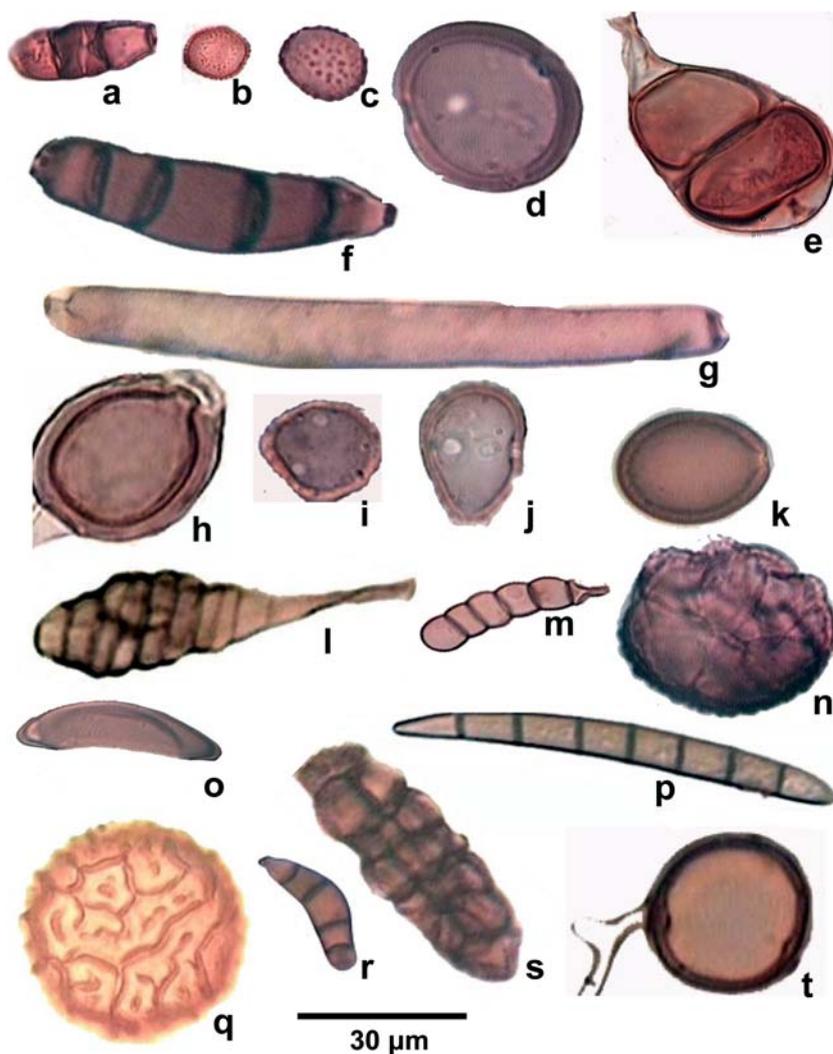


Table 2 Fungus names and hosts

Latin name	Common name	Host
<i>Alternaria alternata</i>	Alternaria leaf spot	<i>Cucurbita pepo</i> , <i>Zea mays</i> , <i>Phaseolus vulgaris</i>
<i>Alternaria cucumerina</i>	Alternaria leaf blight	<i>Cucurbita pepo</i>
<i>Alternaria helianthi</i> (rare)	Sunflower leaf spot	<i>Helianthus annuus</i>
<i>Corynespora cassiicola</i>	Corynespora blight	<i>Cucurbita pepo</i>
<i>Curvularia</i> sp.	Curvularia	Poaceae, etc.
<i>Epicoccum nigrum</i>	Minor leaf spot	<i>Zea mays</i>
<i>Geoglossum</i> sp. (rare)	Earth-tongue	Dead plant matter
<i>Glomus</i> sp. (rare)	Glomus	Live roots
<i>Pestalotiopsis funerea</i>	Cedar shoot blight	<i>Thuja occidentalis</i>
<i>Pleospora herbarum</i> (rare)	Pleospora	Poaceae, etc.
<i>Pseudoperonospora cubensis</i>	Downy mildew	<i>Cucurbita pepo</i> , etc.
<i>Puccinia graminis</i>	Wheat stem rust	<i>Triticum aestivum</i>
<i>Puccinia sorghi</i>	Common corn rust	<i>Zea mays</i>
<i>Setosphaeria turcica</i> (rare)	Northern leaf blight	<i>Zea mays</i>
<i>Sphacelotheca reiliana</i>	Corn head smut	<i>Zea mays</i>
<i>Sporormiella</i> spp. (absent)	Dung fungi	Mammal dung
<i>Tilletia</i> sp. (rare)	Bunt fungi, smut	Poaceae, etc.
<i>Ustilago maydis</i> (=U. <i>zeae</i>)	Corn smut	<i>Zea mays</i>
<i>Uromyces appendiculatus</i>	Bean rust	<i>Phaseolus vulgaris</i>
<i>Ustilina</i> sp. (rare)	Carbon cushion	Dead wood

Most fungi are not host-specific and attack both crops and wild plants. *Pseudoperonospora cubensis* (downy mildew) attacks many taxa including squash; its spores (Fig. 3k) are ca. 24 μm and psilate to scabrate with a single pore. *Alternaria* spp. produces spores (Fig. 3l) which are often poorly preserved, with two to 10 cells borne on a stalk, with a beaked apical cell; sculpturing is psilate to scabrate: *A. helianthi* (Fig. 3m), which infects *Helianthus*, has spore cells (Fig. 3m) arranged linearly. *Epicoccum nigrum* (minor leaf spot) has 35 μm spores (Fig. 3n) of five or more irregular cells covered with variable-sized verrucae. *Ustilina* spp. are wood-rotting fungi that are often found on decaying *Fagus* wood, which may be linked to Iroquoian woodland clearance; its spores (Fig. 3o) are elongate and psilate. *Geoglossum* spp., a saprophyte fungus, has a spore (Fig. 3p) that is linear, multicellular and psilate. *Tilletia* spp. (bunt fungi), which infect grasses, have thick-walled spores (Fig. 3q) with variable sculpturing (Castlebury and Farr 2008). *Curvularia* spp. infect plants and animals; its spore (Fig. 3r) is crescent-shaped, five-celled and psilate. *Pleospora herbarum* attacks herbaceous dicotyledons; its spores (Fig. 3s) are multicellular, with transverse and longitudinal cell walls. *Glomus* spp. (Fig. 3t) are mycorrhizal symbionts on roots and probably grew on herb roots eaten by *Branta*.

Fungal spores occur in all levels (Fig. 4a) but those taxa that infect crop plants, and thus indicate agriculture, predominate in the Iroquoian and Canadian Zones but are absent in the pre-Iroquoian Zone. Dispersal to the sediment

was through the atmosphere or via *Branta* dung; dispersal via runoff is less likely because of the permeable bedrock around the lake. Figure 4b shows that goose dung pellets contain many more spores of crop plant fungi, both in number and kind relative to the matrix samples (Fig. 4a), just as they contain more crop pollen grains. *Branta* grazing on Iroquoian fields followed by roosting and defecation on the lake would have been the main method of delivery to the sediment.

Discussion

In general, fungal spores are smaller than pollen grains and therefore more easily dispersed by wind. However, unlike tree pollen, spores of fungi growing on herbs are not dispersed from a height where distant wind dispersal is efficient. Both *Branta* and to a lesser extent atmospheric delivery were responsible for dispersal of spores in the Iroquoian Zone. Wind delivery seems to be responsible in the Canadian Zone (Fig. 4a) as there are no *Branta* dung pellets among the varves where we would expect dung pellets to be preserved. Domestic animals are a possibility despite treacherous topography, but we have seen no mammal dung spores, such as *Sporormiella* spp.

Crawford Lake is not unique in having well-preserved spores. Miller Lake, located 2.2 km to the south, has similar pollen (Turton and Byrne 1998) and fungal spore

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