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Résumé de l'article

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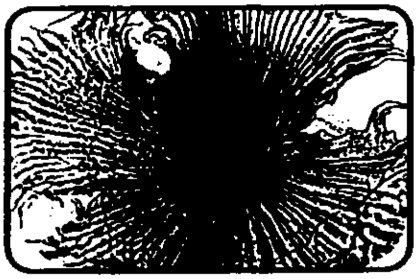

Methods in Quaternary Ecology #10. Other Fossils

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Summary

There are several plant and animal fossil types that are commonly encountered during routine analysis of other more conventional fossil groups. These less familiar or diagnostic remains can be important paleoecological indicators, often complementing paleoenvironmental reconstructions based on other more widely used fossil groups. The composition of the fossil sediment or peat itself contains important paleoecological information, in addition to the fossils contained within its matrix. Analysis of peat components can refine species identifications and, in general, yield useful information on peat-forming plant communities.

Introduction

As surprising as it may seem, the vast majority of terrestrial and freshwater plants and animals leave remains that may become fossilized in Quaternary deposits. Almost all non-vascular and vascular plant species produce some part that may be fossilized. In the case of animals, the fossils can be egg capsules, protective shells of resting bodies, fragments of larvae or early instars, or some part of the adult animal. It is probably not an exaggeration to state that almost any organism, given the right set of circumstances, may become fossilized. Some of the rarest fossils have been found entombed in calcareous concretions, amber, permafrost, tar seeps, and deep peat deposits. The problems, however, lie in recovering these fossils from the enclosing matrix, and the ability of a Quaternary paleontologist to identify these less familiar or diagnostic remains. The lack of suitable taxonomic aids, and inadequate information for interpreting the paleoecological significance further hamper routine use of these less conventional fossil types in paleoecological reconstructions.

Although the authors of the papers in this series have attempted to provide an overview of the most widely used groups in Quaternary ecology, this paper discusses the status and paleoecological significance of a number of additional plant and animal remains that rarely are reported in most publications. I do not intend this to be a complete list or detailed account of all fossil types reported here, but it is especially important to mention those only recently discovered in North American deposits or those types having the best potential in paleoecological studies given further work. The following papers provide additional information on the Quaternary record of the fossil groups considered in this paper: Frey (1964), Grosse-Brauckmann (1986), and Gray (1988), and the papers by Van Geel and co-workers (*i.e.*, Van Geel, 1978; Van Geel *et al.*, 1980, 1982; Pals *et al.*, 1980).

Numerous workers have noted that the next phase in Quaternary ecological research will involve multi-component studies of single cores or sites in an attempt to reconstruct whole ecosystems as completely as possible (West, 1985). Great strides have been made in recent years to improve processing techniques and data presentation, and hence the detail and accuracy of paleoenvironmental interpretations. The next most important contributions to Quaternary ecology should involve development of new fossil groups into useful paleoecological indicators. I echo some of Frey's (1964; p. 4-5) introductory comments made 25 years ago; the situation has not changed much in the intervening period: "the time is propitous for coordinated research by geologists, palynologists, paleobotanists, paleolimnologists, and zoologists on strategic sections... to attain that maturity of insight and understanding necessary for a realistic comprehension of the Quaternary and its biological consequences...". Furthermore, "Sometimes even these approximate identifications [to at least genus] are very useful in interpreting past ecological conditions... ".

Laboratory Procedures

Collection of field samples is the same as for any routine paleontological study. Extraction of many of the fossils encountered in Quaternary deposits, and of those included in this paper, need not involve specialized laboratory procedures. Procedures used for pollen analysis, extraction of macroscopic remains, or the observation of fossil remains in wet mounts of fresh sediment are probably sufficient for the identification and tabulation of most fossils, and any detailed analysis should probably employ all three treatments. Stains such as safranin-O or gentian violet may accentuate certain fossils in temporary slide mounts or permanent preparations of processed concentrate. As more is learned about the nature and occurrence of each fossil group, it might be expected that more specialized laboratory procedures might be developed for efficient, accurate, and quantitative analysis. For the time being, it seems appropriate to analyze all microfossil types composed of chitin and other inert polymers in pollen preparations, siliceous types in the residue used for diatom analysis, and other more fragile microfossils in water mounts.

Plants

Polypodiaceae

Spore-cases, or sporangia, are tiny stalked capsules containing the spores on the fronds of ferns. Sporangia are encircled by a jointed ring of cells which shrinks upon ripening and drying, splitting the sides of the sporangium to release the spores into the air. The ripened empty sporangia may be released from the frond either before or after death only to be incorporated into the underlying limnic or peat sediments (Figure 1).

There is not much morphological variation within sporangia of the Polypodiaceae to permit confident identification beyond the family level. The sporangia are not likely to be transported far beyond the plant, thereby providing evidence for local spore sources and presence of the plant. Sporangia are most likely recovered from peat or peaty gyttja where such wetland species as *Dryopteris thelypteris* or *Onoclea sensibilis* ferns may have lived. Sporangia have been found in abundance in interglacial deposits in Idaho (Bright, 1982). They were interpreted to represent a marsh where *Cystopteris fragilis* was abundant locally.

Gramineae

Among the suite of mineralized biological structures encountered in fossil deposits, cytoliths constitute one group of cellular structures or mineralized cells that may include phytoliths (Bombin, 1984). Phytoliths are opaline silica or biosilica bodies of diverse shapes that are produced by a variety of vascular plants. They occur in the epidermis (including hair cells, hair bases, and stomata), mesophyll, sclerenchyma, and vascular tissue (Figure 2). Despite their occurrence throughout both monocotyledons and dicotyledons, phytoliths have been studied mostly from grasses, sedges, and the palms. Grass phytoliths, perhaps, are the best known, largely as a result of a short-sighted belief among early workers that their phytoliths were the most abundant and diagnostic (Piperno, 1985). Phytoliths are abundant and well preserved in geological and archaeological deposits, and are morphologically diagnostic (Rovner, 1971; Carbone, 1977; Bombin, 1984; Piperno, 1985, 1988; Powers and Gilbertson, 1987). The concentration of phytoliths in some fossil deposits may reach up to 1.5-2.3 mg/cm^3.

Piperno (1985) provides the following comments on fossil phytolith classification. Phytoliths of silicified hair cells are tapering

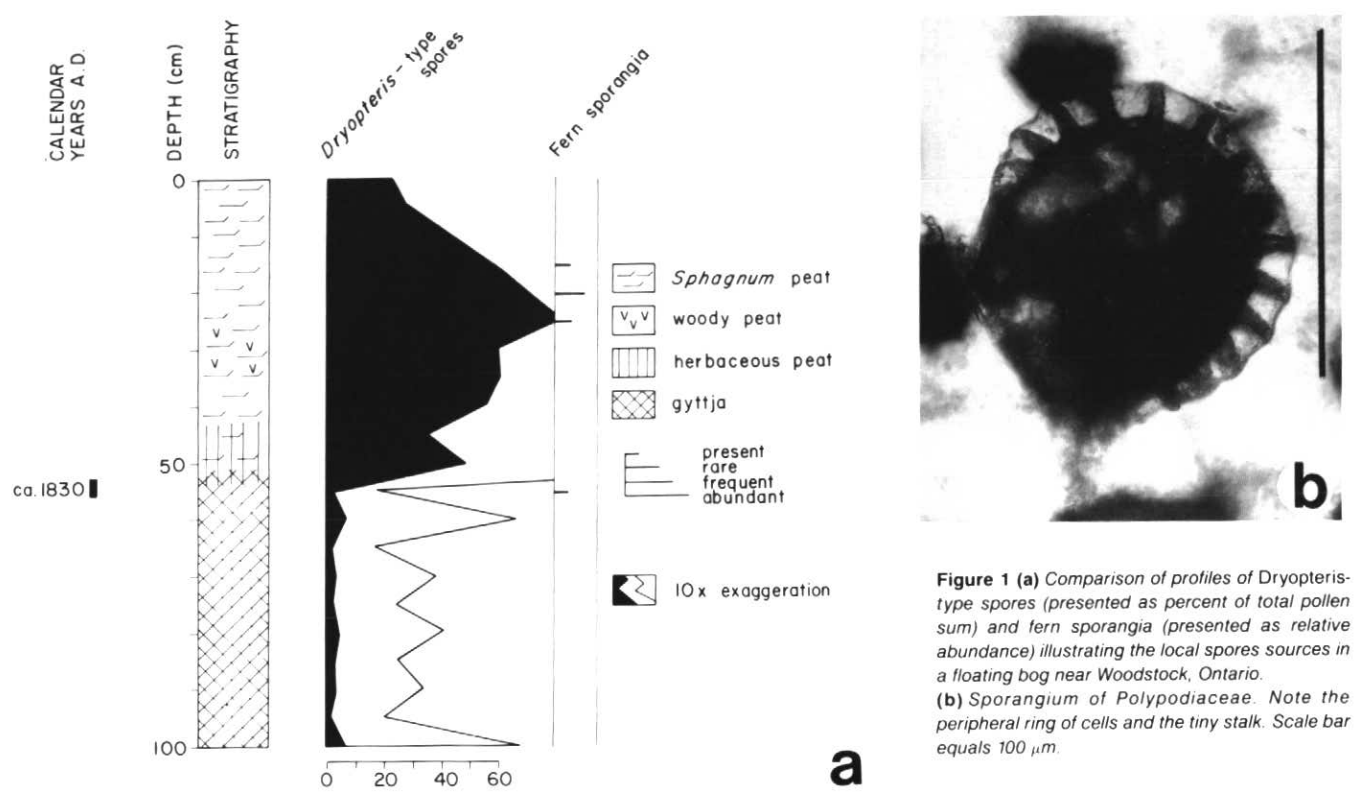


Figure 1 (a) *Comparison of profiles of* Dryopteris-*type spores (presented as percent of total pollen sum) and fern sporangia (presented as relative abundance) illustrating the local spores sources in a floating bog near Woodstock, Ontario.*
(b) *Sporangium of Polypodiaceae. Note the peripheral ring of cells and the tiny stalk. Scale bar equals 100 μm.*

and triangular along the shaft, the base of which is flat, spheroidal or ellipsoidal. The hair cells may be segmented or non-segmented. Both the hair cells and hair bases can be characterized further by shapes, sizes, and unique surface patterns. Phytoliths within epidermal cells occur in a variety of shapes, from conical and spherical to non-spherical shapes. Sclereids (situated within the thick and lignified sclerenchyma tissue) and tracheids (occurring within the vascular tissue of xylem) may be silicified also. Good introductions to phytolith classification and analysis are Bombin (1984) and Piperno (1985; 1988).

As phytoliths are an important component in atmospheric dust, their use in paleoecology is much under-used. Phytolith analysis is potentially as important as pollen or diatom analysis in terms of abundance in and ease of recovery from sediments, and in importance as a source of paleoecological information (Bombin, 1984).

In a detailed study of phytoliths from Alaska and the Yukon, Bombin (1984) found that phytoliths were abundant and widespread in non-fluvial deposits, including dung deposits from Beringia, and their stratigraphic changes correlated well with changes in other more conventional fossil indicators such as pollen and diatoms.

In addition to phytoliths, grasses possess distinctive leaf cuticular epidermal features (hairs, papillae, cell shapes, and stomata). Both fossil grass phytoliths and cuticle have been most widely used in tropical and other arid regions where grasses are diverse and a major component of the vegetation (Palmer, 1976). Warner *et al.* (1987) found fossil leaves of wild rice *(Zizania palustris)*, in mid-Holocene deposits in north-central Ontario which confirmed the natural range of the plant, disproving beliefs that the plant was a

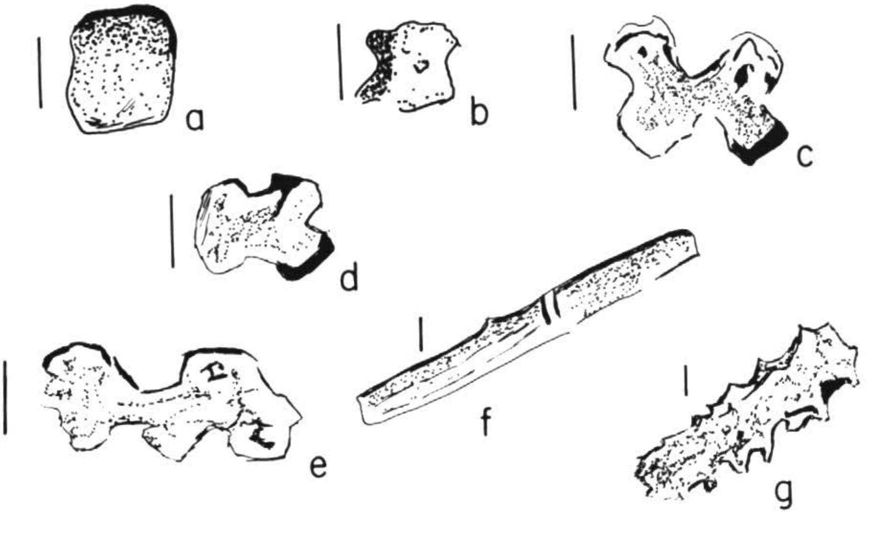


Figure 2 *Representative types of phytoliths. Scale bars equal 50 μm.*

recent anthropogenic introduction to the local region.

Ceratophyllaceae

Ceratophyllum is a perennial, free-floating, submerged aquatic plant lacking roots. Two species are known in Canada, *C. demersum* and *C. echinatum*; the former is the most widespread (Les, 1986). The principal leaves are in forked segments with distinct serrations and marginal leaf spines (Figure 3a). The marginal teeth are readily preserved in limnic sediments and can be encountered in pollen preparations.

The leaf spines vary from 190 to 220 μm in length (Figure 3b). They are straight, tapering to a sharp point, and thick walled. The base comes to a pyramidal point that fits into the main leaf segment of the plant. The leaf spines are probably siliceous in composition, in which case they might be regarded as a type of phytolith.

Ceratophyllum leaf spines are useful fossil indicators in Quaternary ecology because they are preserved better and produced in greater abundance than are the pollen or seeds, particularly in instances where only vegetative plants may have been present. Leaf spines of *Ceratophyllum* are known from a few localities in Canada (Figure 4); four localities lie beyond or near the modern distributional range limit. The paleoecological significance and possible reasons for these distributional shifts are probably interdependant and complex. *C. demersum* grows in habitats with high pH and alkalinities, and in waters where dissolved free CO_2 is limited or totally depleted (Table 1). The capacity of *C. demersum* to take up low amounts of CO_2 or to utilize bicarbonate ions in photosynthesis probably contributed to its

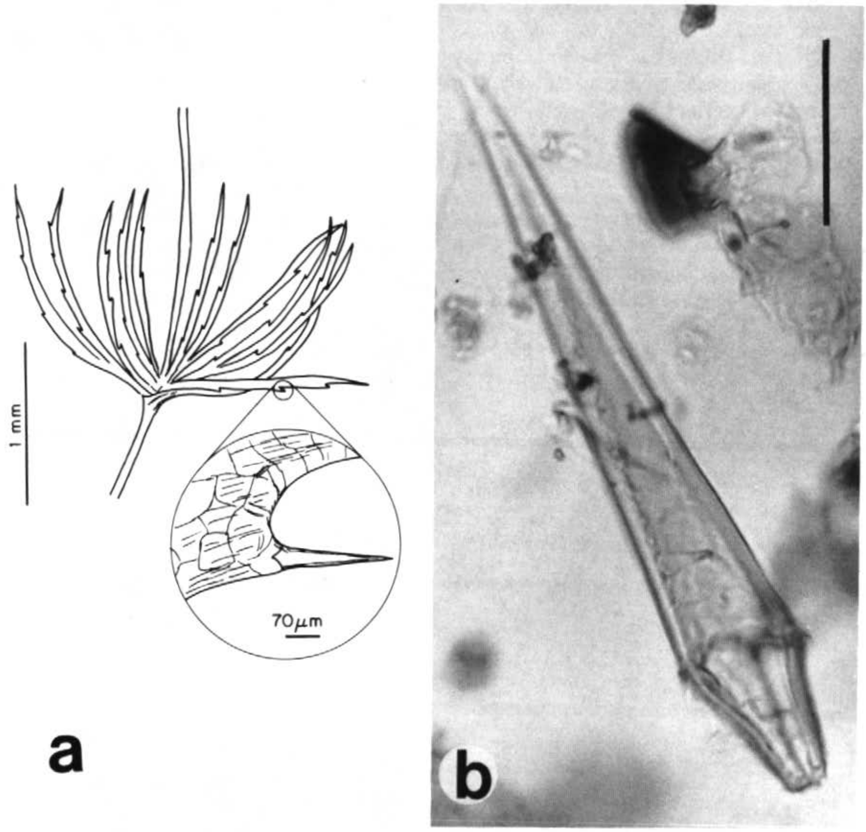


Figure 3 (a) *Sketch of forked segments of* Ceratophyllum demersum *showing the position of marginal leaf spines.* **(b)** *Fossil leaf spine from a Holocene marl deposit in northern Ontario. Scale bar equals 50 μm.*

Table 1 Summary of water chemistry values for *Ceratophyllum demersum* in North America.

Location and Reference	pH	Alkalinity ($mg \cdot L^{-1} CaCO_3$)	Conductivity ($\mu mhos \cdot cm^{-1}$@25°C)
North Carolina (Beals, 1977)	6.3 - 8.3	-	-
NE USA (Hellquist and Crow, 1980)	5.7 - 7.8	5.5 - 151.0	-
Central North America (Pip, 1988)	-	40.0 - 558.0	-
Alberta (Doherty and LaRoi, 1973)	5.7 - 10.5	70.0 - 260.0	-
Minnesota (Moyle, 1945)	6.3 - 9.0	23.0 - 376.0	-
Minnesota and North Dakota (Birks, 1973)	-	-	180.0 - 300.0
Southern Ontario (Wile and McCombie, 1972)	7.8 - 8.4	172.0 - 204.0	-
Southern Ontario (Crowder *et al.*, 1977)	-	-	124.0 - 316.0
Alaska/NWT (Holmquist, 1971)	7.7 - 9.2	77.0 - 142.0	-
Central British Columbia (Reynolds and Reynolds, 1975)	7.8 - 9.7	-	600.0 - 830.0

Figure 4 *Modern distribution of* Ceratophyllum demersum *(after Riley and MacKay, 1980; and simplified after Les, 1986). Occurrences of fossil leaf spines are shown with squares (Terasmae and Craig, 1958; Warner, 1984b, and unpublished data).*

success and more widespread distribution in postglacial waterbodies that probably had low amounts of free CO_2. Some workers have suggested that distribution beyond its northern range limit may be due to more favourable climatic conditions (Terasmae and Craig, 1958; Petersen *et al.*, 1983). It is possible that its more widespread distribution was controlled by its photosynthesizing capacity, the hydrochemical and physical characteristics of the site, and dispersibility of diaspores, rather than past climatic conditions (Warner, 1984a). Furthermore, its establishment and survival can be temporary, and the apparent range expansions in the past may really be of little paleoenvironmental significance.

Nymphaeaceae

Sclerenchyma tissue in the petiole and peduncle of *Nuphar* and *Nymphaea* contain specialized stellate cells referred to as stone-cells, or sclereids (Ogden, 1974). They are thick walled, consisting of lignin and hardened cellulose, and are present singly or in clusters (Figures 5a and b). The sclereids are microscopic, ranging in size from 100 to 400 μm. The complex polymers comprising the lignin and cellulose make the sclereids much more resistant to decay than the enclosing sclerenchyma. The sclereids survive acid treatments in pollen analysis, and often can be viewed in the slide preparations.

Nuphar and *Nymphaea* have cells at the base of leaf hairs composed of suberin. The fatty acids of the suberin are derived from respiratory processes and presumably aid in maintaining buoyancy of the large, floating leaves of the plant. The cells are thin walled, clear, and circular in cross-section, varying from 35 to 42 μm in width (Figure 7b). They may be composed of many individual round, stacked cells. The suberized basal cells are readily incorporated and fossilized in the sediment following the death of the plant. The suberin resists acid treatments, and can be viewed in pollen slide preparations.

Both sclereids and the suberized basal cells of the Nymphaeaceae leaf hairs are most common in gyttja and peaty gyttja sediments, although they may be found in deposits of aquatic environments that may have supported Nymphaeaceae.

A good example of Nymphaeaceae sclereids and leaf hair cells is from a lake on Graham Island, British Columbia (Warner, 1984b). Fossil pollen analysis shows that the

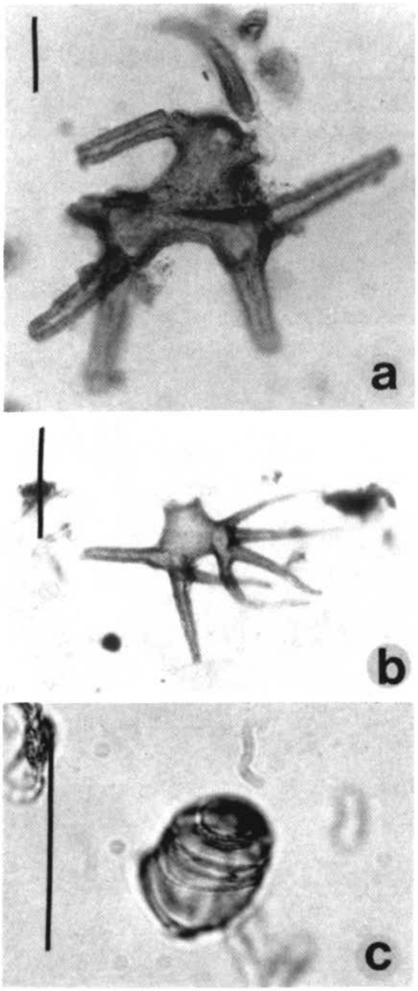


Figure 5 (a,b) *Fossil Nymphaeaceae sclerids.* **(c)** *Fossil leaf hair basal cells of Nymphaeaceae. Scale bars equal 100 μm for a, b, and 50 μm for c.*

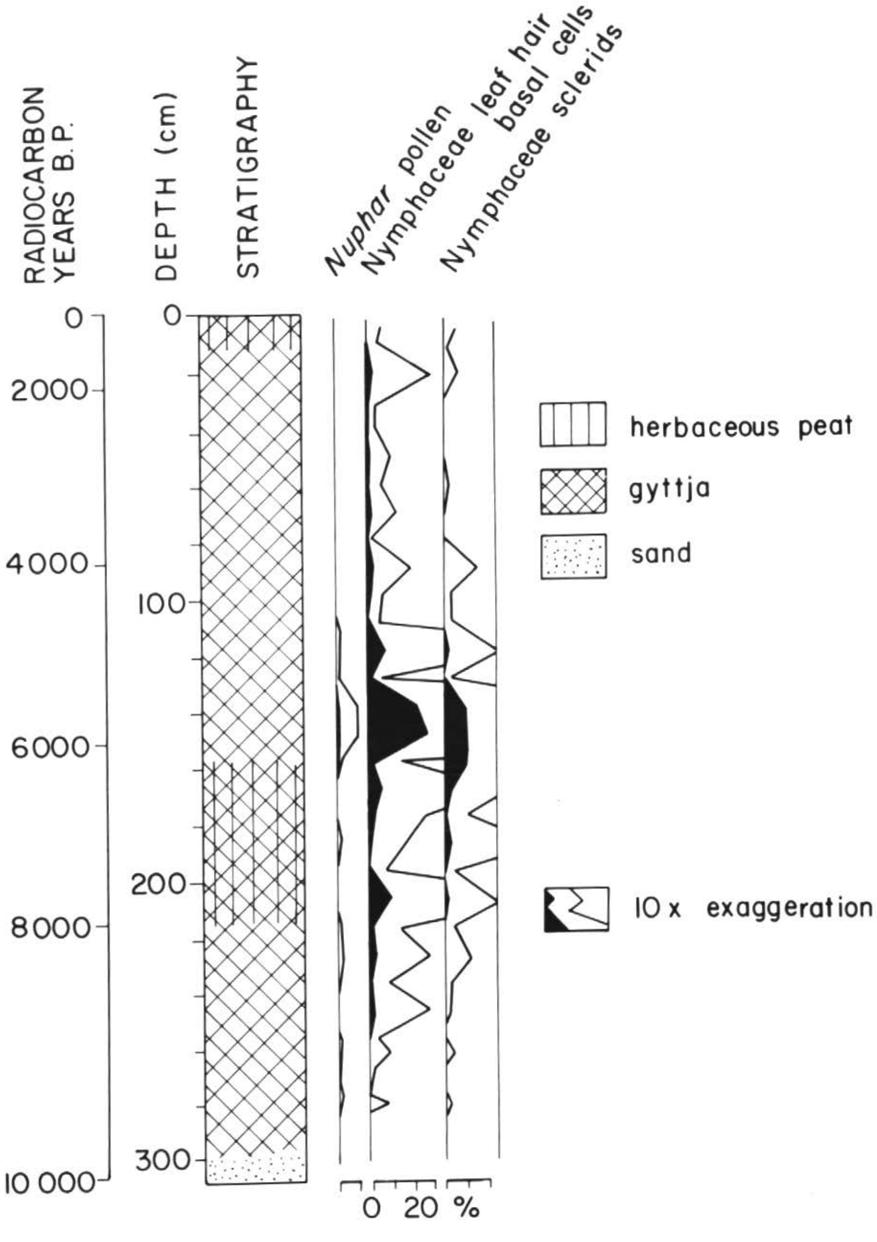


Figure 6 *Profile of fossil Nymphaeaceae pollen, leaf hair basal cells, and sclerids from Boulton Lake, Graham Island, British Columbia (Warner, 1984b). Pollen is presented as percentage of total pollen including aquatic taxa, and the basal cells and sclerids are presented as percentage of total pollen and total of basal cells and sclerids. Note the peak of all fossil types at about 140 cm depth.*

sclereids and leaf hair cells are from *Nuphar lutea* ssp. *polysepala* (Figure 6). It is interesting to note that in samples where no pollen was found, sclereids and leaf hair cells were abundant, contributing to a much more complete paleoenvironmental representation of the plant.

Elaeagnaceae

The shrubs, *Shepherdia canadensis* and *S. argentea*, possess deciduous leaves, with rusty-coloured scales, and silvery down on the underside. These rusty-coloured scales are umbrella shaped, peltate trichomes that preserve and can be recovered with the pollen. The trichomes may be up to 0.5 mm in diameter, with a radiating pattern of linear cells (Figure 7).

The trichomes are usually found with notable proportions of *S. canadensis* pollen (Mathewes, 1973; Warner, unpublished), particularly from late-glacial sites where this shrub was especially important in the local vegetation. Perhaps careful attention to fossil trichomes in the prairie region of Canada where *Shepherdia* attains its greatest representation in the vegetation will reveal a long and more complete fossil record for the shrubs.

Animals

Flatworms

Flatworms of the Order Neorhabdocoela (Class Turbellaria, Phylum Platyhelminthes) produce egg capsules that are incorporated and preserved in fossil freshwater deposits. The neorhabdocoeles reproduce sexually, and lay single eggs, some of which are encapsulated in a stalked coccoon for attachment to some substrate. Two types of eggs are laid: thin-shelled "summer" eggs which hatch promptly, and thick-shelled eggs which may lie dormant for long periods (Pennak, 1978). The latter types are those that are most likely to be recovered as fossils. The egg capsules vary from 80 to 600 μm in size. They are elliptical to spherical in shape, consisting of the main body and an operculum. The operculum is usually missing in the fossils (Harmsworth, 1968). There are three main types of capsules. The first type is the *Gyratrix*-type which is stalked, shaped like a wine glass, dark coloured, and may or may not be striated (Figure 8a). The second type, referred to as the *Microdalyellia*-type, is U-shaped and dark in colour (Figure 8b). The third type is a spherical-shaped capsule, much lighter in colour than the other two types (Figure 8c).

It is difficult to assess the paleoecological significance of the fossils as little is known about both the modern ecology and paleoecology of neorhabdocoeles. However, it would seem that neorhabdocoel egg capsules hold much promise largely because the animals are cosmopolitan in distribution, and different species occupy entire lake basins in a variety of microhabitats. The capsules can be abundant and well preserved, they are readily recovered from the sediment, and can even be observed in fossil pollen preparations (Harmsworth, 1968; Pennak, 1978). In one of the few systematic

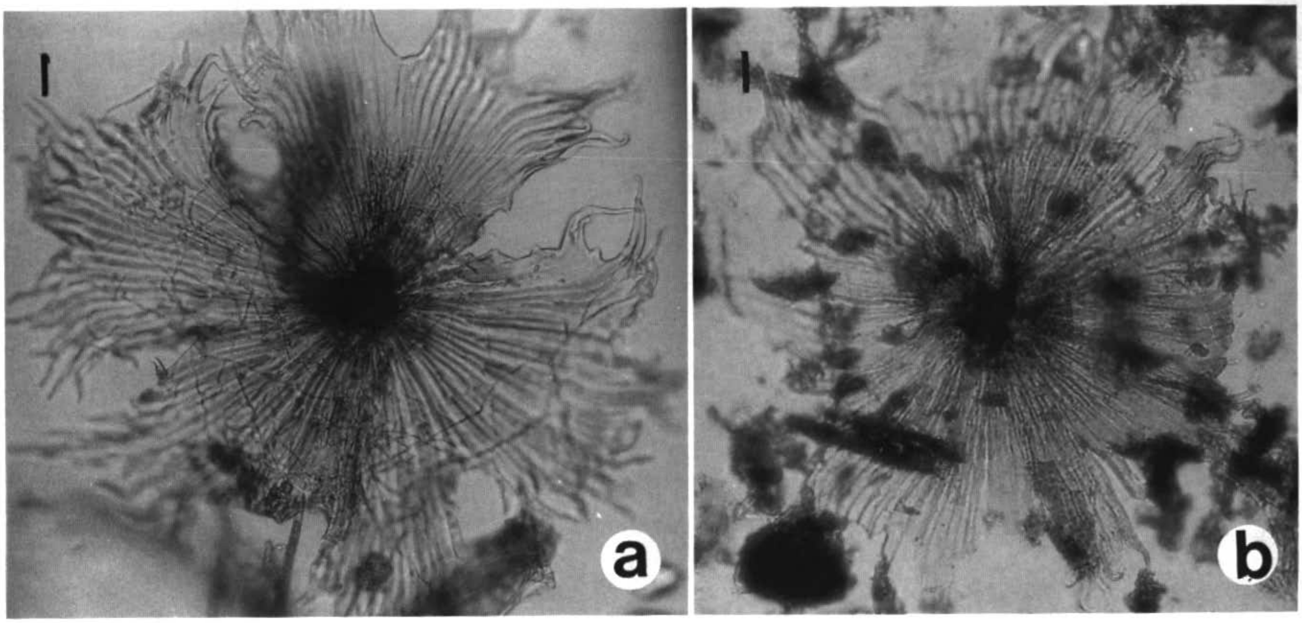


Figure 7 **(a)** *Modern and* **(b)** *fossil peltate trichomes of* Shepherdia canadensis. *Most fossils occur as fragments of the complete trichome. Scale bars equal 100 μm.*

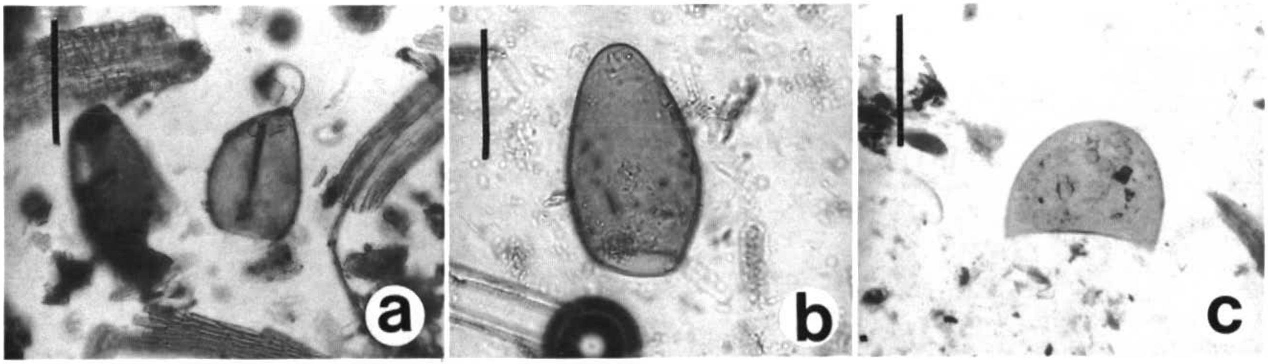


Figure 8 *Neorhabdocoel egg capsules.* **(a)** Gyratrix-*type;* **(b)** Microdalyellia-*type;* **(c)** *spherical-shaped capsule. Scale bars equal 50 μm.*

studies of fossil capsules, Sreenivasa (1973) found them to exceed 1500 per gram (ash weight) of lake sediment at a site in southern Ontario. Their peak abundances corresponded to eutrophic phases in the lake, but whether neorhabodocoel capsules can be used as eutrophic indicators remains to be established by comparison with modern faunal surveys.

Rotifers

Rotifers, classified in the Phylum Rotifera, are common within zooplankton communities. They are cosmopolitan in distribution, living in a variety of aquatic and semi-aquatic habitats in lakes, puddles, damp soil, and wet mosses.

Members of the Order Bdelloidea occupy submerged, emergent, and mossy habitats that may be occasionally wet. The bdelloids are colourless, transparent animals possessing highly contractile bodies, some of which are protected in a shell. The dark, proteinaceous shells of one member of the Bdelloidea, *Habrotrocha angusticollis*, are particularly common in fossil peat and gyttja deposits (Figure 9a; Warner and Chengalath, 1988).

The fossil shells may be pale, to yellow-brown, to dark brown in transmitted light. They are flask-shaped and elongate, with a long neck and obovate body. The width across the body measures 100 μm, and around 56 μm at the base of the body. *H. angusticollis* shells are diagnostic because they are smooth, and do not contain extraneous material such as fungal hyphae, plant detritus, or mineral particles. They are striated, and have an obvious thickened lip around the anterior end (Figure 9a). The fossil shells resist destruction by acids used in fossil pollen preparations, and may be observed in wet mounts of untreated peat samples also.

The distribution and ecology of *H. angusticollis* in North America are not well known. This makes it difficult to assess its paleoecological significance. The bdelloids as a group are most characteristic of *Sphagnum* and other mossy habitats. They are associated with mosses in *Sphagnum* bogs, marshes, and with floating mats and other emergent vegetation along the shores of lakes and ponds. Shells of *H. angusticollis* have been found in *Sphagnum* bogs in Ontario throughout a range of soil moisture regimes from 82 to 98% (Warner and Chengalath, 1988).

Warner and Chengalath (1988) examined fossil *H. angusticollis* in two *Sphagnum* bogs in northern Ontario, and concluded that *H. angusticollis* flourished at a time when there was probably more open water with wet mosses and emergent vegetation than exists at the sites today.

Resting eggs of rotifers may become fossilized, but their morphology is not sufficiently diagnostic to confidently differentiate them from resting eggs of some other freshwater invertebrate groups.

Bryozoans

Freshwater bryozoans are colonial, sessile animals forming large, encrusting masses on submerged stones, logs, twigs or any other solid substrate in shaded areas of permanent water bodies. Phylum Bryozoa contains mainly marine representatives, but there are at least 20 species confined to freshwater habitats in Canada and the United States (Pennak, 1978).

Individual bryozoans resemble some coelenterate polyps by being organized in cylindrical zooids with thin body walls. A mouth is situated on a large lophophore with ciliated tentacles on the anterior end of the animal. The lophophore, tentacles, and the base of the lophophore form a polypide, which comprises the living part of an individual bryozoan. The coelom is continuous from one zooid to another and interconnects the individuals into highly branched colonies.

Members of the Class Phylactolaemata produce asexual statoblasts. Statoblasts are internal buds which protect internal organelles in two tightly fitted convex sclerotized valves. The statoblasts are released by the animal and can be carried by water currents, wind, in mud on bird feet, or attached to animal bodies to establish new colonies. Statoblasts can be produced in such abundance as to form windrows along the shore of some waterbodies (Pennak, 1978). These factors make statoblasts conducive to preservation in limnic sediments.

There are three main types of statoblasts differentiated by their mode of production. All genera, except *Fredericella*, produce floatoblasts. Generally, they are released from the living zooid. Floatoblasts are equipped with an annulus of thin air cells or spines and hooked processes around the central thickened capsule (Figure 9b). Sessoblasts are produced by *Fredericella, Hyalinella, Plumatella* and *Stolella*. Usually they lack an annulus, and possess a peripheral girdle which attaches the sessoblast to the zooecium wall by cement. Lastly, only *Fredericella* produces somewhat more special-

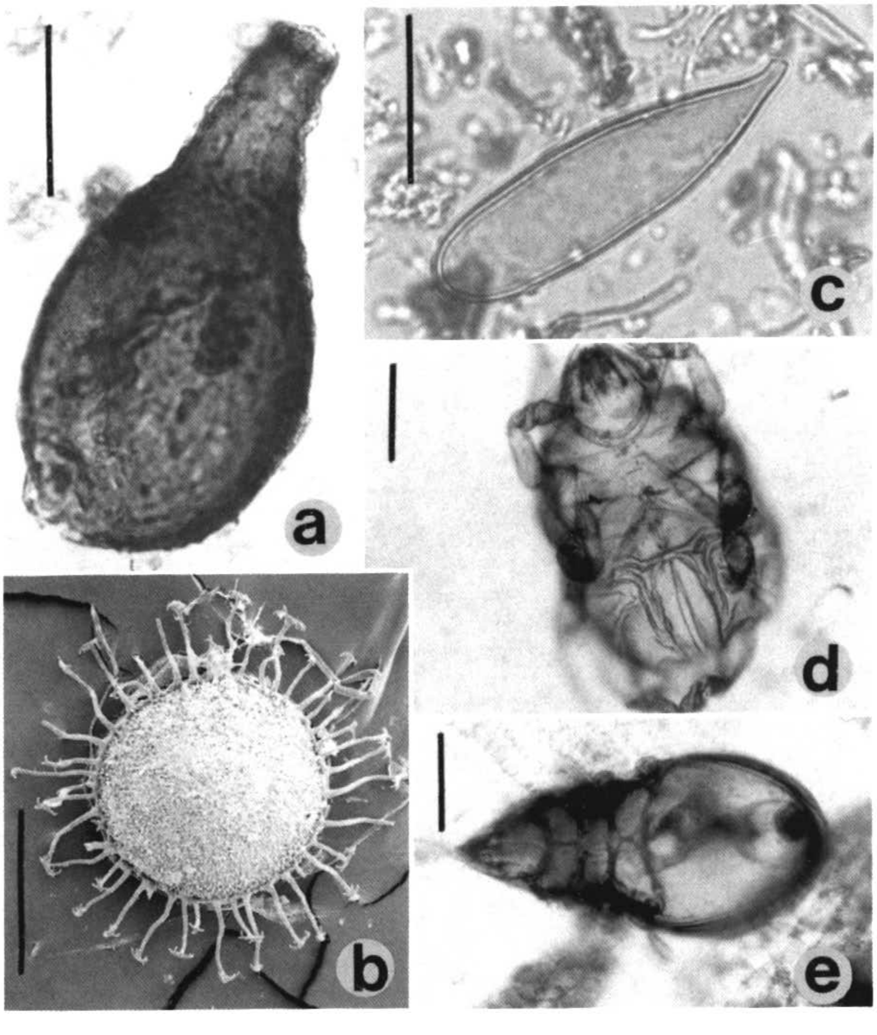


Figure 9 (a) *Fossil* Habrotrocha angusticollis *(Bdelloidea: Rotifera) capsule,* **(b)** *fossil* Cristatella mucedo *statoblast;* **(c)** *fossil copepod spermatophore;* **(d,e)** *representative examples of fossil oribatid mites. Scale bars equal 50μm for a,b; 25μm for c; and 100 μm for d,e.*

ized statoblasts, called piptoblasts, which are neither cemented to the surface of the zooecium nor capable of floating. Usually piptoblasts sink to the bottom when the animal dies and the body decays.

Kuc (1973) recovered well-preserved *Cristatella mucedo* statoblasts in abundance from Early Pleistocene interglacial and interstadial deposits in the Arctic. These fossils are far north of the modern known distributional northern limit for the animal. He surmised that interglacial limnological conditions in the Arctic were much more oligotrophic than modern conditions in the region today.

In a detailed study of surficial sediments in 30 Florida lakes, Crisman *et al.* (1986) concluded that statoblasts are most abundant in lakes with an extensive littoral zone and a low phytoplankton biomass. This study emphasizes the potential for developing bryozoan statoblasts further as a new paleoecological tool, but problems exist such as the patchiness in space and time of modern faunas and the interpretation of their fossil counterparts. Of interest is Sreenivasa's (1973) interpretation of fossil statoblasts at Sunfish Lake. *Plumatella* statoblasts were found to be most abundant at a time when the littoral zone became larger compared to the open pelagic area. *Plumatella* seems to have taken advantage then of a larger area of submerged aquatic macrophytes, and an increase in water transparency and substrates for colonization.

Some other reports of fossil statoblasts in Canada include: Schofield and Robinson (1960), Matthews (1980), Klassen *et al.* (1983), Warner *et al.* (1984, 1987), and Garneau (1987). The oldest Quaternary records are from western Alaska (Matthews, 1974), the western Arctic (Kuc, 1973), and Toronto (Kerr-Lawson, 1985).

Earthworms

Most everyone is familiar with earthworms found in terrestrial soils, but there are aquatic and amphibious species too, found in lakes, ponds, or marshes and in the wet soils at the edges of these water bodies. Although the soft-bodies of the adults are not conducive to preservation in fossil deposits, their chitinous-like coccoons are resistent to decay. The coccoons are smooth, spheroidal or ellipsoidal, with a spike, tube or tuft at opposite ends of the main structure. The size may reach 3 mm along the longest axis.

The first report in North America of fossil earthworm coccoons was found in a Holocene marl sequence in southern Ontario (Schwert, 1979). Subsequently, Warner *et al.* (1984) found them in Holocene peats on Manitoulin Island. Most terrestrial earthworms are circumpolar or cosmopolitan in distribution. The occurrence of coccoons 7000 years old or older in Ontario dispels the long-held belief among zoologists that terrestrial earthworms in North America are European introductions (Schwert, 1979). More finds of fossil earthworm coccoons will illuminate the zoogeographic problems of distribution and dispersal of earthworms throughout the northern hemisphere.

Copepods

Along with the cladocerans, ostracods, and rotifers, copepods are universally distributed in the planktonic, benthic, and littoral regions of freshwater bodies. Free-living forms include the suborders Calanoida, Cyclopoida, and Harpacticoida; they are not as morphologically modified and specialized as their parasitic relatives. The free-living copepods are the best known and most frequently collected. A single cyclopoid species commonly characterizes the limnetic plankton, occasionally with subordinate presence of a calanoid. Littoral communities, especially in aquatic vegetation, contain a variety of cyclopid and calanoid species but in lower densities.

Harpacticoids are confined to the benthos within lakes. In Europe, they have been found in unusual habitats such as in interstitial waters of sandy lake beaches, in springs, in caves, and in damp forest mosses (Pennak, 1978).

Breeding habits within the free-living copepods are similar. The male clasps the female with antennae and sometimes with a modified fifth leg to pair up the genital pores which are located on the genital (or last thoracic) segment. The male transfers the sperm to the female in small, pocket-like spermatophores, usually with the aid of the legs during clasping. The female then stores the sperm in a special ventral area of her genital segment, into which she will eventually release eggs for fertilization. It is the male spermatophore that is preserved and fossilized in Quaternary limnic deposits.

The fossil spermatophores are usually translucent to pale yellow. They are teardrop shaped with a short, coiled, tail-like appendage. The spermatophore is up to 50 μm in length. The entire tail segment is often broken off in fossil specimens (Figure 9c).

Copepods are soft-bodied individuals and undergo complete decomposition following death. Apart from resting eggs, which are not particularly diagnostic, spermatophores provide the best fossil record of copepods.

Mites

Soil or moss mites, also referred to as oribatids, are a small group of arthropods living in terrestrial soils, peatlands, and fresh waters. Classified in Class Arachnida and Suborder Oribatida, the Subclass Acari are particularly abundant as fossils in lacustrine and peat deposits. Some fossil oribatids have been found in Mexican amber. Fossil numbers can reach 23 per gram of marl (Erickson, 1988).

The animals are small (usually less than 500 μm) and possess a coriaceous, sclerotized body that is readily preserved almost intact; such exceptional preservation provides all details of mouthparts and genital and anal areas necessary for identification (Frey, 1964; Erickson, 1988). Oribatids have a characteristic "tear-drop" shaped body, with fused cephalothorax and abdomen, six pairs of appendages, and are dark-coloured (Figures 9d and e). Ecologically, oribatids are most common in forest and peatland soils, litter, and mosses, and are less frequent in aquatic habitats (Pennak, 1978; Erickson, 1988). Aquatic species are most abundant in littoral submerged and emergent plant beds, and are less common on wave-washed lake shores, and in the deeper parts of lake bodies. Oribatid mites may be valuable indicators of change in peatlands due to drainage (Markkula, 1986).

Frey (1964), Krivolutsky and Druk (1986), Erickson (1988) and Schelvis and van Geel (1989) have reviewed the Quaternary record of oribatids; the latter paper is one of the most detailed studies in North America.

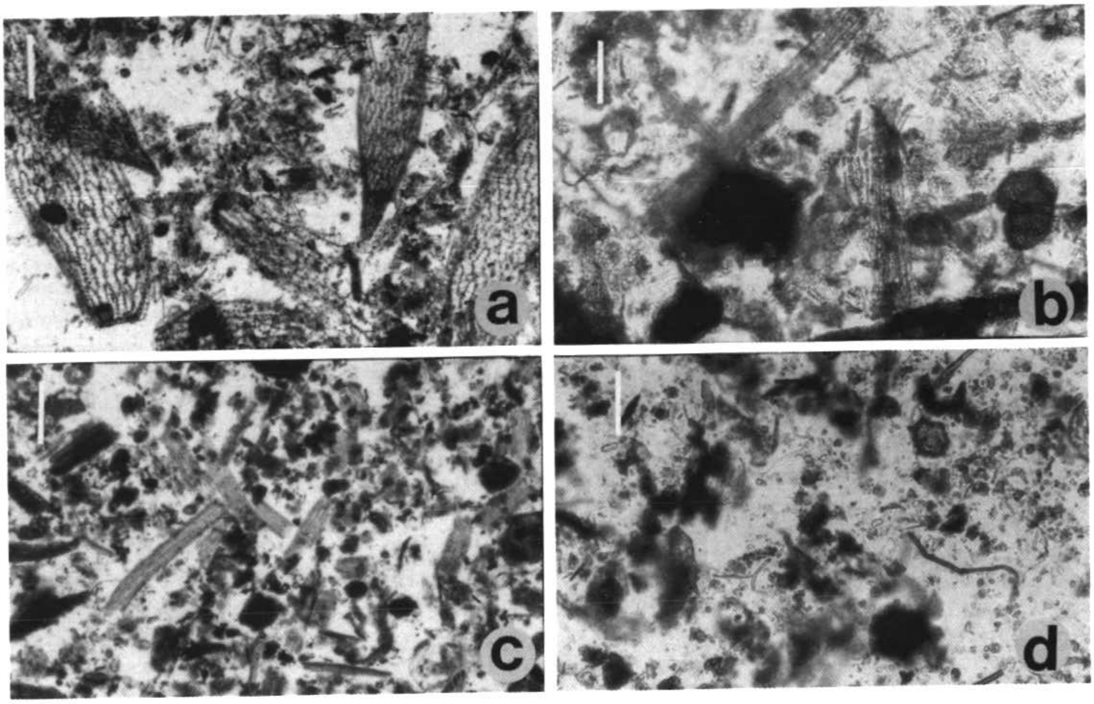
Peat and Sediment Composition

The scientific definition of peat is partially decayed organic matter mainly of plant origin. Almost any plant community can form peat, however, only a few plants can grow in the wet conditions and saturated soils of peatlands. Peatlands store the plants that grew in them in the form of wood, stems, leaves, roots, rhizomes, fruits, seeds, and pollen.

Lakes, like peatlands, contain in their sediments fossil representatives of the plankton communites from both the littoral and pelagic parts of the basin that sink to the bottom sediments when they die. One main difference between lakes and peatlands is that the fossils in lake sediments may have moved from their original site of deposition either by within-basin processes or by external processes such as surface feeder streams or runoff. Such preferential sorting, long-distance transport, and reworking processes are negligible or minimized in peatlands.

Other contributions in this series, and the first part of this paper, have described some of the fossils in peatlands and their use in paleoecology. Not only are the fossils contained within them of importance, but the nature and composition of the sediments themselves contain a wealth of paleoecological information.

The unifying characteristic of aquatic and peatland plants is that their bulk is composed of aerenchyma and parenchyma tissue. These plant tissues form an open network of living cells separated by air spaces which supply the plant with oxygen and give it buoyancy to keep it afloat. Specific plants have their own individual systems to perform these functions by possessing their own intricate cellular designs. The fossil tissue patterns and structures can be identified under the microscope to recognize plant species and reconstruct past plant communities. These analyses are another area of paleoecological research,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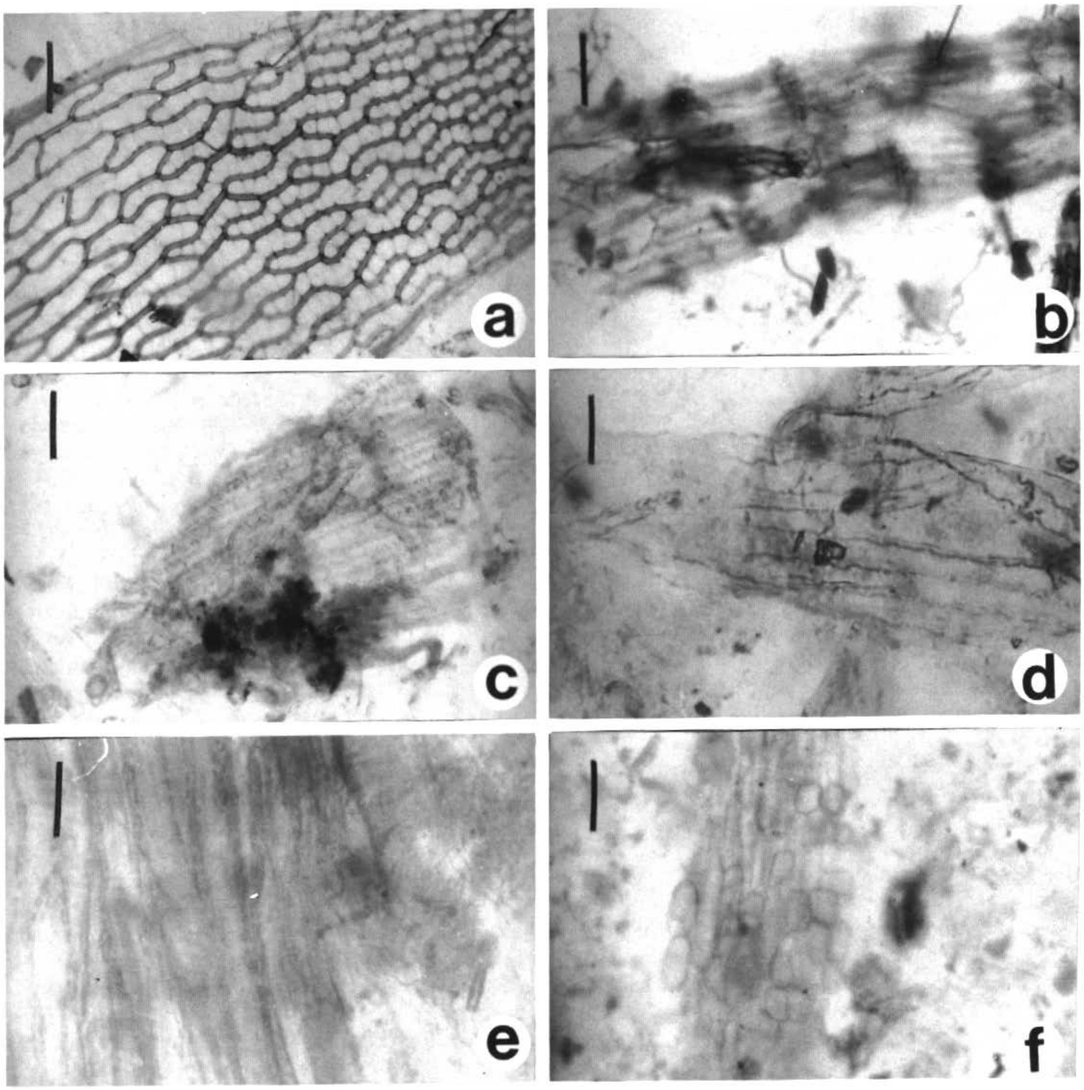
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which when performed in conjunction with analysis of pollen, plant macrofossils, testate amoebae, and some other important animal types, provides a fairly complete representation of past peat-forming or lacustrine communities.

The guide by Lévesque *et al.* (1988) is a useful introduction to analysis of Canadian peats. Other keys such as Stoddard (1965) and Riegert and Singh (1982) may serve to identify plant fragments in certain types of fossil deposits. The following papers discuss some aspects of peat analysis in more detail: Heikurainen and Huikari (1952), MacFarlane and Radforth (1968), Haihu and Etelämäki (1986), Svensson (1986), and Warner (1989).

Detailed examination of the character and composition of peat constituents can reveal information such as past hydrological and oxygenation conditions of the site by noting such features as the degree of humification and quality of preservation, or other details of the plant species acting as major peat-formers (Figures 10, 11, and 12). Mosses of the genus *Sphagnum*, commonly known as the "peat mosses", and mosses primarily of the family Amblystegiaceae, commonly known as "brown mosses", and vascular plants in the Cyperaceae are the main peat-formers in Canadian wetlands.

Although it is difficult to accurately quantify sedimentary and peat components, it is possible to estimate the relative proportion of the various identifiable remains. Profiles can be constructed in much the same manner as is done for other fossil groups, illustrating the various sedimentary components (Figures 13 and 14).

Clearly, much more work remains to be done on the lesser known fossil groups. Only with further information on the distribution and ecology of modern counterparts, will it be possible to improve the effectiveness of fossil representatives in the Quaternary fossil record.

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Figure 10 ***(opposite page: upper)*** *Fossil peat types.* **(a)** Sphagnum *peat;* **(b)** *cyperaceous peat, with* Eriophorum *fragments;* **(c)** *brown moss; and detrital peat;* **(d)** *limnic peat, with fungal hyphae (arrow) and fine detritus. Scale bars equal 100 µm.*

Figure 11 ***(opposite page: lower)*** *Common plant fragment types encountered in peat deposits.* **(a)** Sphagnum *leaf;* **(b)** Sphagnum *stem;* **(c)** Eriophorum *leaf;* **(d)** Carex *leaf;* **(e)** Scheuzeria palustris *leaf;* **(f)** Carex limosa-*type rootlet. Scale bars equal 100 µm.*

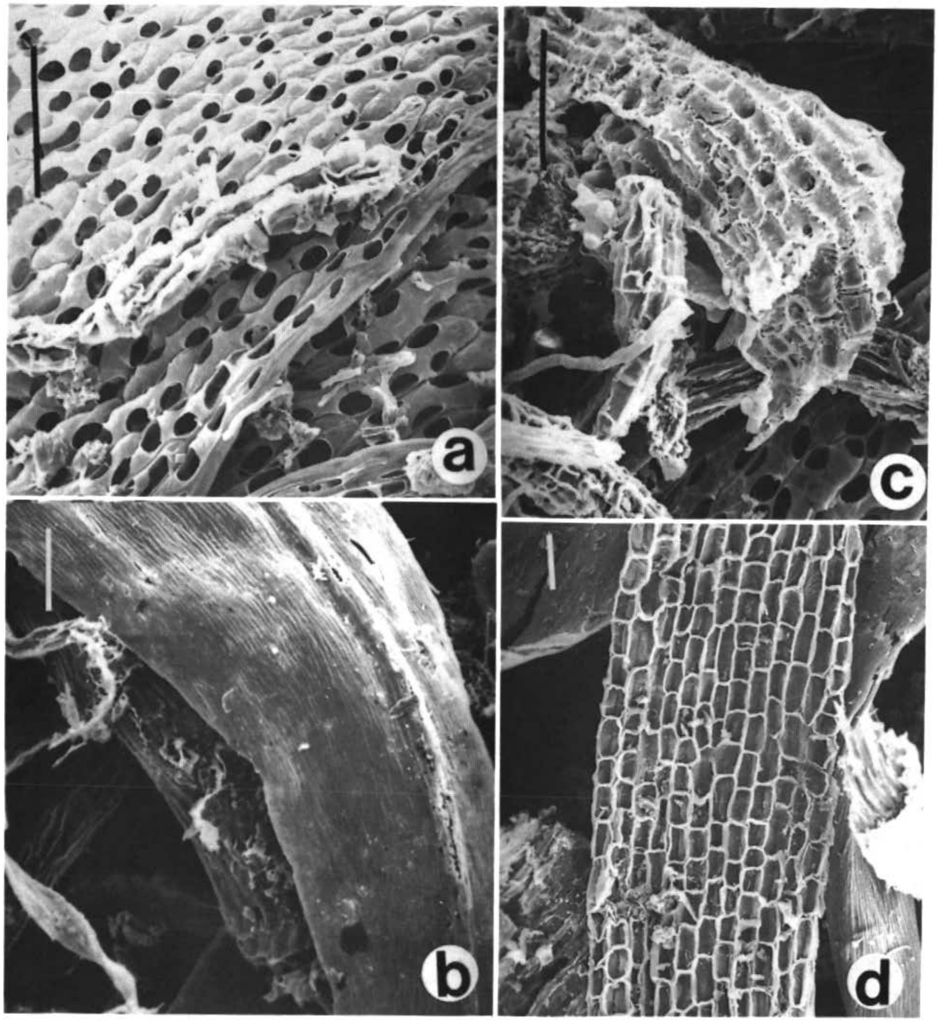

Figure 12 *Scanning electron micrographs of selected peat plant fragments types.* **(a)** Sphagnum *leaf;* **(b)** *brown moss leaf;* **(c)** *probably* Carex *leaf; and* **(d)** *Cyperaceae stem. Scale bars equal 100 µm.*

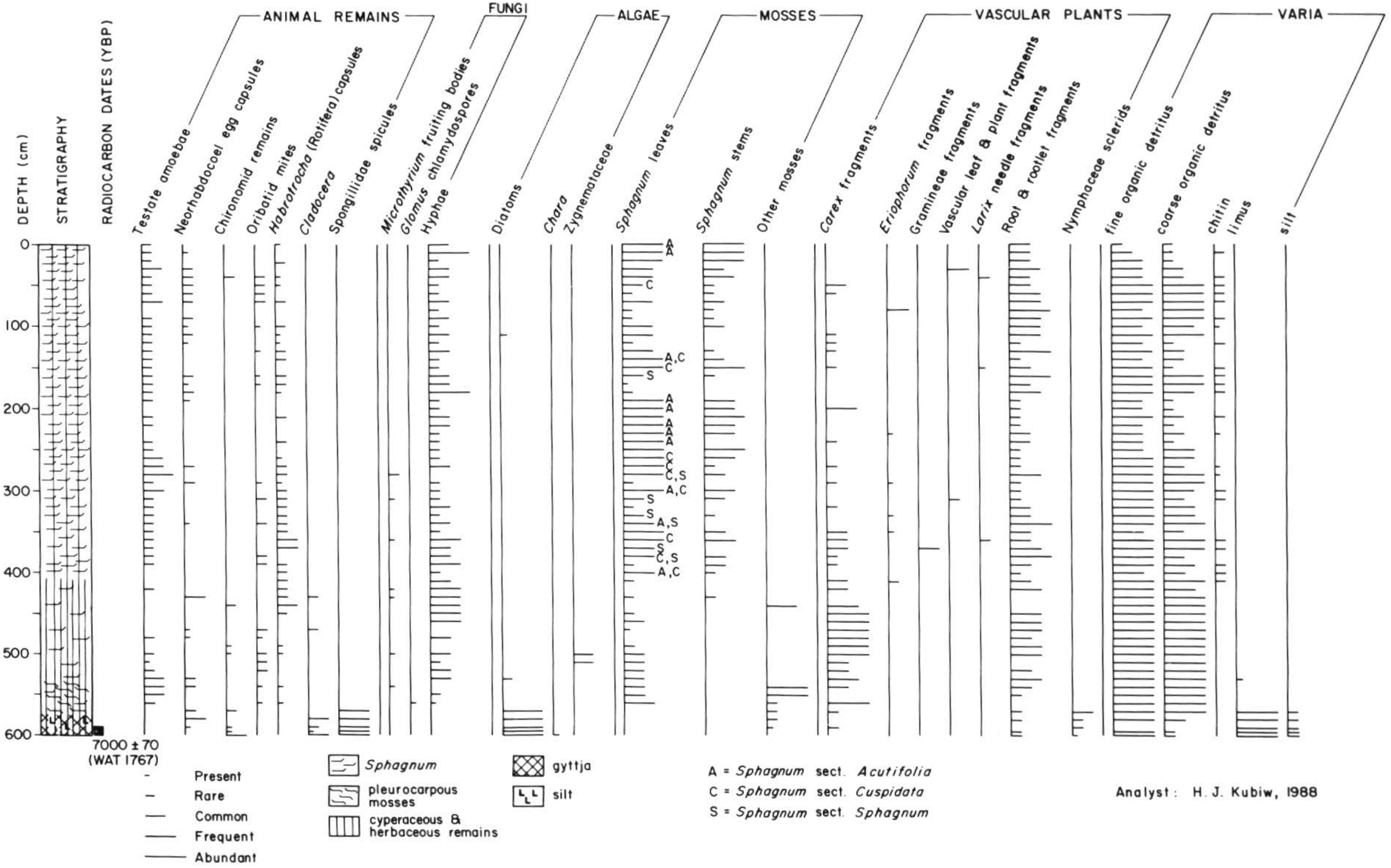

Figure 13 *A diagram of peat and sediment components from a* Sphagnum *bog near Thunder Bay, Ontario. (From Warner, 1989).*

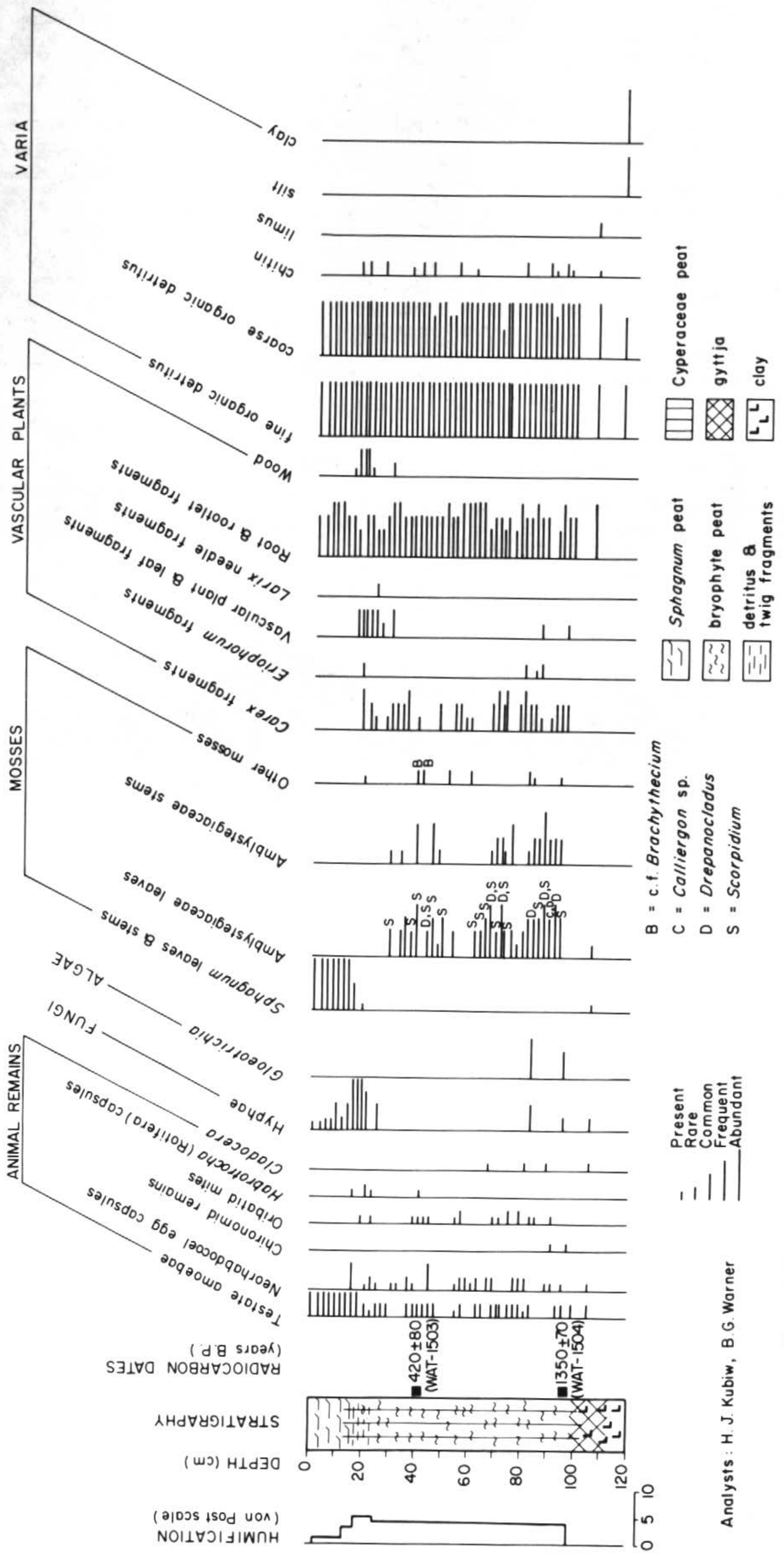

Figure 14 *Representative diagram of various peat and sediment components from a Sphagnum bog on the Albany River in northern Ontario. (From Warner, 1989).*

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