A Multi-proxy Paleoecological Study of Anderson Fen, Central Vancouver Island, British Columbia, Canada

by

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B.Sc., University of Lagos, 2014

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ABSTRACT

A paleoecological study was carried out on a 4.7 m peat core from Anderson Fen on central Vancouver Island, using a multi-proxy approach. Pollen, non-pollen palynomorphs, and physicochemical analyses were used to document past vegetation, peatland developmental history, and carbon and nitrogen accumulation rates over the last 14,000 years. Lake sediment and aquatic plant remains at the base of the core indicate a shallow pond was present at the site after deglaciation. By ~11,700 calendar years before present (cal yr BP), the shallow pond became a herb-dominated wetland (marsh) through terrestrialization. Bog formation started around 10,500 cal yr BP with decreasing water levels, as indicated by high C:N, *Sphagnum* and fungal remains, and testate amoebae such as *Archerella flavum* and *Heleopera*. A fen developed by ~9400 cal yr BP with fluctuating water levels through the rest of Holocene. Carbon accumulation rates were highest towards the surface and during the early Holocene warm period, with an overall mean rate of 12.9 g/m^2/cal yr, which is low compared to continental and northern peatlands. Pollen analysis reveals that non-arboreal communities dominated by *Salix* prevailed soon after deglaciation before the expansion of *Pinus* forests 13,200 cal yr BP. *Pseudotsuga menziesii* dominated forests between ~10,700 and 8400 cal yr BP under warm and dry conditions. *Tsuga heterophylla* rainforest was established by ~7000 cal yr BP under increasingly cool and wet conditions. Overall, Anderson fen and the surrounding area experienced major and rapid changes in environmental conditions and vegetation in response to climate change during the late glacial and early Holocene, while mid- to late Holocene changes have been more subtle and relatively gradual.

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Dedication

This research is dedicated to the glory of God and to my other half, Abimbola Agidi, for her patience, support, prayers, and undying love despite the million miles between us during the course of this research.

INTRODUCTION

Peatland Distribution and Importance

Peatlands are intermediate ecosystems between aquatic and terrestrial environments that support accumulation of plant materials over long periods of time, from centuries to millennia (e.g., Martini et al., 2006; Wieder and Vitt, 2006; Rydin and Jeglum, 2013). The accumulation of plant materials in peatlands is fostered by low oxygen and high water tables, which slow down decomposition (e.g., Martini et al., 2006; Rydin and Jeglum, 2013). For a wetland to be called a peatland, the accumulated peat must reach a certain depth, but this depth differs among countries (Joosten and Clarke, 2002). In Canada and Russia, the depth benchmark is at least 30 - 40 cm due to the variability in peat accumulation rate and formation process in different areas (National Wetlands Working Group, 1997; Martini et al., 2006).

Peatlands cover about 3% of the total global land area with most of this area in Eurasia and North America (Joosten and Clarke, 2002; Martini et al., 2006); however, the largest peatland area in the world is found in Siberia (e.g., Smith et al., 2004). Topography, temperature, water table depth, and oxygen levels are the major drivers of peatland distribution, and variability in these factors result in the formation of peatlands in different geographical areas, ranging from tropical to high latitudes. Peatlands are common in areas where water supply is greater than water loss and where accumulation of organic matter exceeds decomposition (Martini et al., 2006; Wieder and Vitt, 2006; Rydin and Jeglum, 2013). Peatlands hold about 30% of the total global carbon contained in the pedosphere, and northern peatlands contain most of this carbon (Roulet, 2000; Joosten and Clark, 2002; Martini et al., 2006). In addition to the role of peatlands as a carbon sink, peatlands also play an important role in the terrestrial hydrological cycle by improving water quality and serving as reservoirs. Peatlands also house a myriad of invertebrate species and unique plant species, contributing to global biodiversity (Rydin and Jeglum, 2013).

Types of Peatlands

Peatlands are classified based on their sources of water, nutrient contents, water movement (lentic or lotic), dominant plant community, water table depth, and pH. Based on these characteristics, peatlands are classified into bogs, fens, swamps, and marshes (National Wetlands Working Group, 1988; Martini et al., 2006; Rydin and Jeglum, 2013). Bogs and fens tend to accumulate more peat of greater depths than other types of wetlands.

Compared to fens, low water tables and lack of mineral nutrients typify bogs. They have low pH and high carbon-nitrogen ratios. Water or moisture in bogs is directly sourced from the atmosphere through rain, snow, and fog (ombrotrophic). Bogs occasionally support trees, but they are primarily characterized by *Sphagnum* mosses and ericads, and in some cases lichens (National Wetlands Working Group, 1988, 1997; Martini et al., 2006; Rydin and Jeglum, 2013). *Sphagnum* plays an important role in contributing to low pH in bogs due to its high cation exchange capacity (Weider and Vitt, 2006; Rydin and Jeglum, 2013). The upper layer of bogs (acrotelm) is separated from the deeper layer (catotelm) by the water table; however, some bogs can have higher water tables close to the surface (National Wetlands Working Group, 1997; Rydin and Jeglum, 2013). Generally, a bog's surface can be raised, flat or sloped (e.g., Turunen and Turunen, 2003; Huntley et al., 2013; Lacourse and Davies, 2015).

Fens are characterized by high water tables, near or above the surface, in addition to extremely low oxygen, and alkaline to slightly acidic mineral-rich water. The sources of water include surrounding lotic waters, channels, and periodic inundation by streams. Nitrogen is a major nutrient in fens and mainly sourced via fixation by algae and bacteria, but also from run-off and directly from the atmosphere (Martini et al., 2006; Rydin and Jeglum, 2013). Phosphorus and sulfur are also present in fens due to influx from surrounding water bodies (Wieder and Vitt, 2006). Water table and physicochemical contents mostly determine the plant community found in fens (Martini et al., 2006; Rydin and Jeglum, 2013). Cyperaceae, brown mosses, and other bryophytes typically occupy rich fens with high water tables, and when the water table drops, shrubs can become dominant. In typical poor fens, which have lower mineral nutrients, *Sphagnum* mosses and ericaceous shrubs dominate. Fens can develop on flat topographies or steep slopes (National Wetlands Working Group, 1997; Weider and Vitt, 2006; Rydin and Jeglum, 2013).

Swamps are usually characterized by trees but can also house floating plant communities. Water in swamps can be lentic or lotic and mineral-rich, and the pH ranges from acidic to above neutral. Swamps are usually inundated and mostly composed of ligneous peat (National Wetlands Working Group, 1988, 1997; Weider and Vitt, 2006; Rydin and Jeglum, 2013).

Marshes accumulate less peat due to high productivity and decomposition, in addition to unstable water tables caused by daily-seasonal-annual fluctuations. The water in marshes is lentic to semi-lotic, ranging from fresh, brackish to salt, which determines the plant community type. Found in marshes are Poaceae, Cyperaceae, bryophytes, macro-algae and macrophytes (National Wetlands Working Group, 1997; Weider and Vitt, 2006; Rydin and Jeglum, 2013).

Development of Peatlands

Peatland development can take different forms including terrestrialization, paludification, and primary peat formation. Terrestrialization involves the conversion of an already existing water body to peatland via infilling. Paludification is the establishment of peatland on moist to dry grounds, such as scrub, forest (Turunen and Turunen, 2003; Rydin and Jeglum, 2013) and tundra (Rydin and Jeglum, 2013; Ruppel et al., 2013) following an increase in the water table. Primary peat formation occurs on exposed wet sites without prior dryness, such as exposed sites after sea regression or ice retreat (Ruppel et al., 2013). However, these developmental pathways also overlap (Rydin and Jeglum, 2013; Ruppel et al., 2013). Peatland development is accompanied by steady modifications in plant communities over time as well as the elements that drive peat formation. These elements can be allogenic or autogenic, coming into play at different phases of peatland development (Wieder and Vitt, 2006). Peatland succession leads to greater acidity over time, which results in an ombrotrophic condition (Rydin and Jeglum, 2013). One especially important plant taxa in peatland development is *Sphagnum*. Its ability to resist decay and modify its environment, and its high cation exchange capacity contribute significantly to peat formation (Wieder and Vitt, 2006).

Peatland succession and development can be progressive or retrogressive, depending on autogenic factors such as inundation and allogenic factors related to climate (e.g., Shiller et al., 2006; Rydin and Jeglum, 2013; Lacourse and Davies, 2015). Many peatlands especially fens eventually transition into bogs. For example, a marshy site can turn into a rich fen, followed by a poor fen phase and then a bog. This is referred to as the common hydrosere succession (National Wetlands Working Group, 1988; Wieder and Vitt, 2006; Shiller et al., 2014). In this process, peat accumulation occurs beneath the water table, separating the surface from the impact of groundwater over time. This promotes the lowering of pH and organic buildup, usually resulting in a *Sphagnum*-dominated peatland. When the peatland has less water drainage, peat accumulation can also commence in the uppermost portion of the water table over time, especially in maritime environments (e.g., Martini et al., 2006; Rydin and Jeglum, 2013).

Peatland Paleoecology

Peatlands archive several types of information on past environmental conditions (Rydin and Jeglum, 2013). Evidence drawn from peats is used in reconstructing peatland development, carbon sequestration, and vegetation and fire history (e.g., Turunen and Turunen, 2003; Turetsky et al., 2004; Squeo et al., 2006; Gorham et al., 2007; Shiller et al., 2014; Lacourse and Davies, 2015). Evidence drawn from peatlands can also help in restoration by providing information regarding peatland succession history (Lavoie et al., 2001). Major proxies analyzed in peats for paleoecological studies include pollen and spores, plant macrofossils, carbon and nitrogen, testate amoebae, and charcoal. Accurate reconstruction of site history can be achieved when more than two proxies are combined simultaneously and treated independently, as shown in the studies of Huntley et al. (2013) and Lacourse and Davies (2015).

Plant macrofossils are very useful in understanding the history and development of peatlands (Loisel and Garneau, 2010), and particularly used for ^{14}C dating (Birks, 2007). They can be used to support hydrological proxies by providing information regarding past peatland nutrient status, and to support paleoclimate evidence (e.g., Blaauw et al., 2004; Loisel and Garneau, 2010). Plant macrofossil analysis is usually used to complement other paleoecological evidence, especially when the information provided by pollen analysis is unclear (Birks, 2003, 2007).

Pollen and spore analysis is useful in reconstructing vegetation history, as well as determining past environmental conditions at both regional and local scales, including peatland succession history (e.g., Faegri and Iversen, 1975; Turunen and Turunen, 2003; Lacourse and Davies, 2015). Pollen analysis can also be used to determine disturbance and to support peatland hydrological proxies (e.g., Williams et al., 2004; Lacourse and Davies, 2015).

Information regarding peatland hydrological history is mostly obtained from testate amoebae analysis (e.g., Lamentowicz and Mitchell, 2005; Payne et al., 2006; Loisel and Garneau, 2010; Swindles et al., 2015) due to their short generation time and high preservation potential (Loisel and Garneau, 2010). Inferences drawn from testate amoebae can be made quantitative with the application of transfer functions, which make use of the modern abundance of testate amoebae taxa in relation to their environments (e.g., Lamentowicz and Mitchell, 2005; Swindles et al., 2015; Taylor et al., 2019).

Charcoal occurs in peat as a result of partial burning of plants at about 280-500º C (Whitlock and Larsen, 2001). Analysis of charcoal remains are mainly used to investigate fire history and the influence of fire on peatlands and vegetation, which can be related to paleoclimate or human activities (e.g., Brown and Hebda, 2002; Shiller et al., 2014). Charcoal analysis involves macroscopic and microscopic charcoal remains, which offer local and regional fire information, respectively (Whitlock and Larsen, 2001).

Paleoecology of Peatlands in British Columbia

Peatlands in British Columbia occupy about 1% of the total land area and the majority are situated in isolated sites with progressive peat accumulation (Maynard, 1988). The major peatland areas in the province include the central north, coastal areas, the inland plateau with more concentration in the northeastern part of BC, and they include bogs, fens, swamps, and marshes (Maynard, 1988; National Wetlands Working Group, 1988; Warner and Asada, 2006).

However, bogs are the most common peatland type in British Columbia (National Wetlands Working Group, 1988). Some of these peatlands are being disturbed by agricultural activities (Maynard, 1988). Based on land use inventory data, about 79% and 76% of wetlands have been lost in and around Vancouver and Victoria, respectively, as of 1981 (National Wetlands Working Group, 1988). These wetlands can be better conserved and restored by understanding their developmental history with respect to climate and anthropogenic factors, but unfortunately, not many studies have been carried out on British Columbia peatlands.

Hansen (1940) studied two bogs in the southern part of British Columbia in order to reconstruct the paleoecology and paleoclimate of this area. This study recorded major flooding events in this environment, as well as changes in vegetation composition after deglaciation. However, this study only made use of fossil pollen evidence of trees, and peat cores lacked radiocarbon dating. Hansen (1950) conducted another palynology study of three bogs on Vancouver Island. The study established the history of only a few plant taxa in this environment with few inferences regarding paleoclimate, and also lacked radiocarbon dating.

Hebda (1977, PhD Thesis) reconstructed past changes in plant communities, paleoclimate, and developmental history of Burns Bog in the Fraser Valley. This study made use of different pollen analyses, including surface pollen rain analysis, pollen productivity, and pollen tetrad diameter analysis, and also examined the effect of fire and human activity on the bog development. Hebda (1983) studied another bog on northeastern Vancouver Island to reconstruct post-glacial vegetation history and paleoclimate. This study successfully documented post-glacial changes in plant communities in this area.

Warner et al. (1984) in their paleoecological study of an excavated peatland on Haida Gwaii used vegetation history to infer changes in precipitation during the mid-Wisconsin. This study also revealed glacial movements during this period and when *Abies* became extirpated from Haida Gwaii.

Brown and Hebda (2002) carried out a paleoecological study on southern Vancouver Island that included peat formation and plant community, paleoclimate, and fire history since deglaciation. The ratio of indicator tree species such as *Pseudotsuga menziesii* and *Tsuga heterophylla* was used as a precipitation index, which was integrated with peat formation, vegetation and fire history in order to make inferences regarding the paleoclimate of southern Vancouver Island.

Turunen and Turunen (2003) conducted a paleoecological study at a slope bog along the north coast of British Columbia to determine the history of formation and carbon accumulation. According to the authors, carbon accumulation in the bog was low compared to continental peatlands due to slow forest paludification triggered by climatic and local factors. Banner et al. (2005) also carried out a brief investigation in the same environment to understand the ecology of bogs in this area.

Sanborn and Jull (2008) determined the initiation timing of peat accumulation in four neighboring bogs in the east central area of British Columbia, showing that there was variability in depth and buildup of these bogs despite their close proximities. However, this work did not include the use of proxies such as pollen and spores, macrofossils, and charcoal amongst others as supporting evidence or to infer paleoecology.

Huntley et al. (2013) carried out a detailed study on a 90 cm peat core from Haida Gwaii and reported evidence of some key paleoclimatic events such as the Little Ice Age and post-Little Ice Age warming. Anthropogenic influence on the bog was also revealed with respect to peat development. This study clearly reconstructed the history of the bog over the last 1800 years and also made use of non-pollen palynomorphs to support their interpretations.

Lacourse and Davies (2015) carried out the most recently published paleoecological study on a British Columbia bog, on northern Vancouver Island, and made use of various lines of evidence including palynomorphs and non-palynomorphs as well as physicochemical measurements. This study was able to determine the bog formation history over the last 10,400 years with respect to hydrological dynamics, carbon sequestration and vegetation history, and paleoclimate in the Holocene.

Research Objectives

In general, there are very few comprehensive paleoecological studies in British Columbia peatlands. The main goal of this study is to use a multi-proxy approach to analyze peat cores from Anderson Fen on central Vancouver Island to reconstruct the paleoenvironment of this area since deglaciation. This multi-proxy approach includes the use of pollen, non-pollen palynomorphs, and carbon and nitrogen analyses, as well as peat composition analysis carried out by Stewart (2018, BSc Thesis). The paleoenvironmental reconstruction includes:

i. Long-term changes in regional and local vegetation;
ii. Developmental history of the peatland and local conditions such as hydrology; and,
iii. Changes in carbon and nitrogen accumulation rates through time.

The results from the aforementioned objectives will be discussed in the context of long-term changes in climate. This will help us understand the links between changes in vegetation, peatland developmental history and local conditions, as well as carbon accumulation with respect to paleoclimate.

ENVIRONMENT OF THE STUDY AREA AND SITE DESCRIPTION

Glacial History of Vancouver Island

Much of Vancouver Island was submerged under the Late Wisconsinan Cordilleran ice sheet that covered most of British Columbia until around ~18,000 – 17,000 cal yr BP and had an ice thickness of up to 3000 m (Blaise et al. 1990; Clague and James, 2002; Clague, 2017). The melting ice sheet was responsible for isostatic changes near Vancouver Island and in other parts of south-west British Columbia (Clague and James, 2002). This resulted in a sharp drop in relative sea level on the east side of central Vancouver Island from a high of about 150 m asl about 14,000 cal yr BP to a low of about −15 m asl by 11,500 cal yr BP (Clague and James, 2002; Hutchinson et al., 2004). Modern relative sea level was reached in the early to mid-Holocene (Hutchinson et al., 2004). In general, ice on Vancouver Island starting retreating to higher elevations after 15,600 yr BP (Blaise et al., 1990).

Vegetation History

Previous studies have reported open *Pinus* woodland vegetation on Vancouver Island between ~16,500 and 13,000 cal yr BP (Hansen, 1950; Hebda and Haggarty, 1997; Hebda, 1983; Lacourse, 2005). However, it has also been reported that non-arboreal communities were present before the arrival of *Pinus* (Hebda, 1983). Matthews and Clague (1982) and Lacourse et al. (2005, 2012) have recorded non-arboreal communities on the Queen Charlotte Islands (Haida Gwaii) before the arrival of *Pinus*.

A period of cooler and perhaps wetter conditions characterized by increases in *Tsuga mertensiana* between ~13,400 and 11,500 cal yr BP followed the development of *Pinus* forests (Hebda, 1983; Lacourse, 2005). *Tsuga mertensiana* has also been recorded at high elevations on central Vancouver Island (Mazzucchi, 2010 – PhD Thesis) and has been suggested to indicate a brief return to cool conditions that occurred at about the same time as the Younger Dryas cooling event (Mathewes, 1993; Lacourse, 2005). *Alnus* spp. have also been recorded to be an important component of the vegetation on northern Vancouver Island during the late glacial and early Holocene period (Lacourse, 2005). *Alnus crispa* (*Alnus viridis*-type; May and Lacourse, 2012) was abundant on central Vancouver Island during the late glacial period, and the vegetation was reported to be open at this time (Mazzucchi, 2010 – PhD Thesis).

Following this brief cool period, temperatures rose within ~1000 years, leading to the early Holocene warm period. Mixed coniferous forests dominated in the early Holocene with the expansion of *Picea* and *Tsuga heterophylla* as early as ~13,500 cal yr BP in northern areas of Vancouver Island (Hebda, 1983; Lacourse, 2005). Early Holocene forests have been described as closed and the increase in temperature allowed the expansion of *Pseudotsuga menziesii* towards its northern limit between ~10,000 and 8000 cal yr BP (Hebda, 1983; Lacourse, 2005; Lacourse and Davies, 2015). *Abies* spp. were an important component of forests on northwestern Vancouver Island at this time (Hebda and Haggarty, 1997) and in central areas especially at higher elevations, where *Abies lasiocarpa* still persists (Mazzucchi, 2010 – PhD Thesis).

Tsuga heterophylla has dominated forests on central and northern Vancouver Island since the middle Holocene (~8000 cal yr BP – present), as the climate became cooler and wetter (Hebda, 1983; Lacourse, 2005; Lacourse and Davies, 2015) and *T. mertensiana* has persisted at middle to high elevations in central areas (Mazzucchi, 2010 – PhD Thesis). At low elevations, the presence of other shade tolerant taxa such as *Abies* and *Thuja plicata* indicate the vegetation has remained closed during this period (Lacourse, 2005; Lacourse and Davies, 2015). *Thuja* *plicata and Chamaecyparis nootkatensis* have also dominated forests alongside *T. heterophylla* since ~2500 cal yr BP on northwestern Vancouver Island (Hebda and Haggarty, 1997).

The vegetation history of southern Vancouver Island shares some similarity with changes in forest composition on central and northern Vancouver Island. Brown and Hebda (2002, 2003) and Heusser (1983) recorded that open *Pinus* woodland also prevailed on southern Vancouver Island in the late-glacial period. Mixed coniferous forest then replaced *Pinus* forests between ~14,000 and 10,000 cal yr BP. The mixed forest was closed and composed of more shade-tolerant taxa such as *T. heterophylla, T. mertensiana* (at high elevations) and *Picea sitchensis*, under cool, moist conditions (Heusser, 1983; Brown and Hebda, 2002, 2003). A similar increase in *T. mertensiana* from ~14,000-13,000 cal yr BP likely reflects a period of colder or wetter conditions (Brown and Hebda, 2003).

In the early Holocene, *Pseudotsuga menziesii*-dominated forest prevailed on southern Vancouver Island as temperatures rose, although mixed coniferous forests were still present in moist areas during this time (Brown and Hebda, 2002, 2003; Lucas and Lacourse, 2013). In the mid-Holocene, there was an expansion of *T. heterophylla* and *Thuja plicata* alongside *P. menziesii*, *Picea* and *Abies* on southeastern Vancouver Island, which indicates an increase in wetness during this period (Brown and Hebda, 2002). *Quercus garryana* also became an important component of forests on southern Vancouver Island by about 7500 cal yr BP (Heusser, 1983; Allen, 1995 – MSc Thesis; Lucas and Lacourse, 2013). Closed forests dominated by *T. heterophylla*, *P. menziesii* and Cupressaceae have prevailed on southern Vancouver Island for the last several thousand years, although open forests are also present in some areas (Heusser, 1983; Brown and Hebda, 2002, 2003; Lucas and Lacourse, 2013).

Modern Climate and Vegetation

Generally, a mild, moist climate prevails on Vancouver Island and this allows temperate coniferous forests to dominate. In general, areas with abundant precipitation support *Tsuga heterophylla*-dominated forests, while areas on the east side of the island in the rainshadow of the Vancouver Island Ranges support *Pseudotsuga menziesii*-dominated forests. Higher elevation areas have *Tsuga mertensiana* forest and alpine tundra.

The Coastal Western Hemlock zone dominates most of the coast of British Columbia at low to mid-elevations, as well as north and south along the Alaska and Washington coasts (Meidinger and Pojar, 1991). The elevation of this zone ranges from 0 - 1050 m in the south and middle coast, and from 0 - 300 m towards the north (Meidinger and Pojar, 1991). This zone has one of the wettest climates in Canada with mean annual temperature and rainfall of 8ºC and 2230 mm, respectively (Meidinger and Pojar, 1991). Temperate coniferous rainforest is the dominant vegetation type. Aside from the dominant *T. heterophylla*, *Picea sitchensis* is abundant on coastlines, *Abies* spp. are present mostly at higher elevations, and *P. menziesii* occupies dry parts or areas after fires.

At higher elevations above the Coastal Western Hemlock zone is the Mountain Hemlock zone, which is mainly characterized by a subalpine climate. Cool summers, prolonged cold winters and short growing seasons prevail in this zone. The elevation ranges from 900 to 1800 m towards the south and 400 to 1000 m towards the north. Most precipitation falls as snow. The dominant species are *Tsuga mertensiana*, *Abies amabilis* and *Chamaecyparis nootkatensis*. Alpine tundra dominated by dwarf shrubs is present at higher elevations. Summer temperature is less than 10 ºC, mean annual precipitation ranges from 700-3000 mm, and frost is present almost year-round (Meidinger and Pojar, 1991).

The Coastal Douglas-fir zone is mainly dominated by *Pseudotsuga menziesii* and is present across the lowlands of southeastern Vancouver Island, generally below 150 m, with the prevalence of warm, relatively dry summers, and moderately wet, cool winters. The mean annual temperature and precipitation ranges from 9.2 to 10ºC and 650 to 1300 mm, respectively (Meidinger and Pojar, 1991).

Study Site: Anderson Fen

Anderson Fen (49° 44.1’ N, 125° 11.6’ W; 554 m asl) is a poor fen (pH 4.6) located along Strathcona Parkway to Mt. Washington, approximately 15 km northwest of Courtenay on central Vancouver Island, British Columbia (Figure 1). The fen sits in the Leeward Island Mountain Ecosection at a higher elevation to the west of the Nanaimo Lowlands, in the Georgia Depression. Anderson Fen is located within the moist maritime subzone of the Coastal Western Hemlock biogeoclimatic zone (Meidinger and Pojar, 1991) but forests surrounding the fen also contain species such as *Tsuga mertensiana* and *Chamaecyparis nootkatensis* that are more typical of the Mountain Hemlock biogeoclimatic zone, which occurs at higher elevations. The closest climate station (Black Creek), which is 13 km to the northeast at an elevation of 46 m, has a mean annual temperature of 9.2°C and a mean annual precipitation of 1645 mm (Environment Canada, 2018).

Anderson Fen is approximately 950 m long and 100 m wide at its widest point, with a surface area of 5.5 ha (Figures 2 and 3). The fen is part of the Courtenay River watershed and is connected to Anderson Lake and other surrounding wetlands at its western and eastern edges. Surface vegetation at Anderson Fen is dominated by *Sphagnum* mosses (*Sphagnum angustifolium, S. papillosum*), sedges (*Eriophorum angustifolium, Rhynchospora alba*), and ericaceous shrubs such as *Vaccinium oxycoccos* and *Kalmia microphylla* var. *occidentalis* (Figures 4, 5 and 6; Golinski, 2004 – PhD Thesis). Other common taxa include *Sphagnum fuscum*, *S. pacificum*, *Carex pauciflora*, *Rubus chamaemorus* (Figure 6), *Menyanthes trifoliata*, *Drosera anglica*, *D. rotundifolia* (Figure 4), *Rhododendron groenlandicum* (Figure 6), and *Vaccinium uliginosum* (Figure 6). At the time of sampling (August 2016), the water table was 20 cm below the surface at the coring location, although standing pools of water were present in some areas (Figure 7).

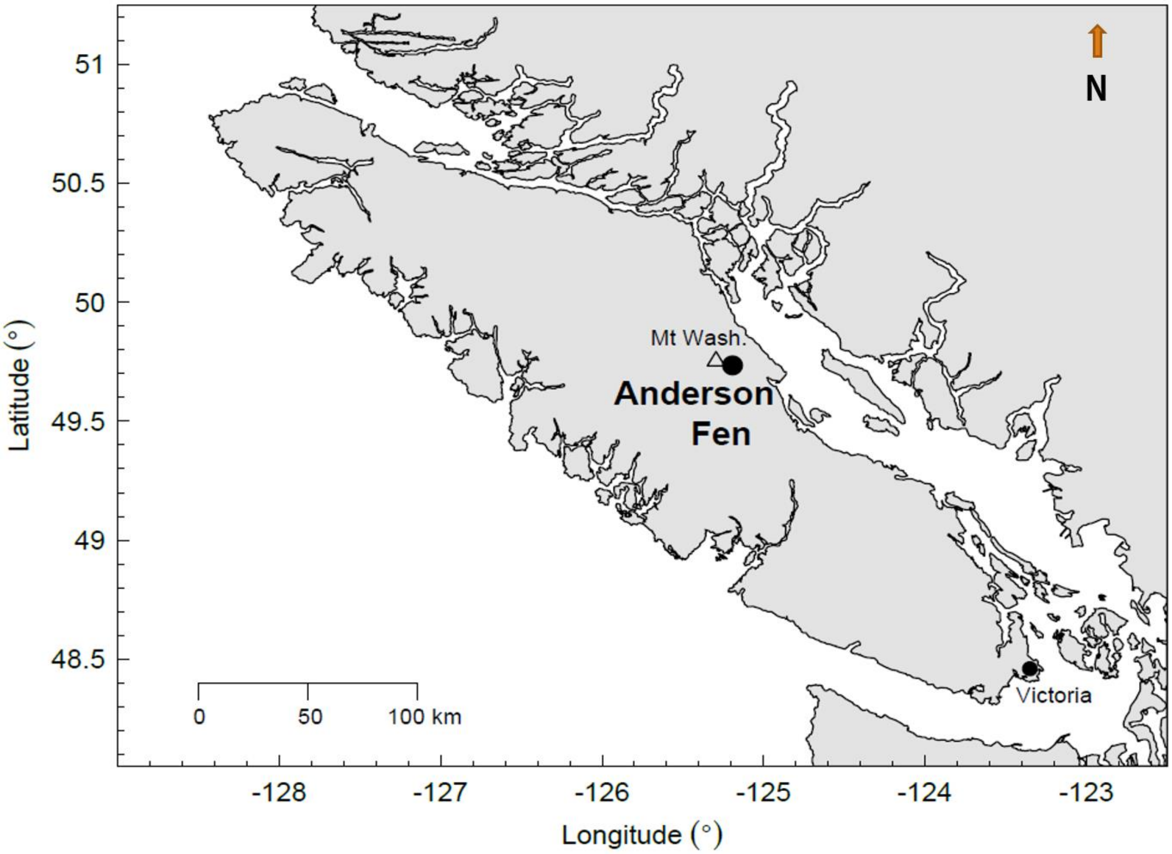

Figure 1: Location of Anderson Fen on central Vancouver Island, British Columbia, Canada.

Figure 2: Aerial view of Anderson Fen and surroundings on central Vancouver Island, BC. Star shows the coring location.

Figure 3: Landscape view of Anderson Fen looking northwest with Mount Washington in the background. (Photo by T. Lacourse)

Figure 4: Plants growing on the surface of Anderson Fen: *Sphagnum* spp., *Vaccinium oxycoccos*, *Kalmia microphylla, Drosera rotundifolia*. July 2016. (Photo by T. Lacourse)

Figure 5: Plants growing on the surface of Anderson Fen: *Eriophorum angustifolium.* July 2016. (Photo by T. Lacourse)

Figure 6: Plants growing on the surface of Anderson Fen: *Vaccinium uliginosum*, *Rubus chamaemorus*, *Rhododendron groenlandicum.* July 2016. (Photo by T. Lacourse)

Figure 7: Standing water on the surface of Anderson Fen. July 2016. (Photo by T. Lacourse)

MATERIALS AND METHODS

Field Methods

In August 2016, a complete peat and sediment sequence was obtained from Anderson Fen using a 50-cm long Russian peat sampler. Two adjacent holes were cored and samples were collected 50 cm at a time, alternating between the two holes with 10 cm overlap. The uppermost 30 cm of peat was collected as a large block using a keyhole saw and shovel. Samples were packaged tightly in plastic wrap and aluminum foil for storage and ex-situ analysis. Samples were then brought to the University of Victoria and stored at 4°C. The pH of the fen's standing water was measured using a YSI multimeter.

Radiocarbon Dating and Chronology

AMS radiocarbon ages (^{14}C yr BP) were obtained from Beta Analytic Inc. (Miami, Florida) on peat and plant macrofossils from eight depths in the core and were calibrated to calendar years (cal yr) using the IntCal13 calibration data set (Reimer et al., 2013). A smooth spline function with a 0.25 smoothing parameter and 10,000 iterations was used by T. Lacourse to create an age-depth model to predict unknown ages, using the 'clam' package (Blaauw, 2010) in R (R Core Team 2017). The model made use of an age of –66 cal yr BP for 0 cm, based on the year of collection (2016), and calendar ages for specific depths were estimated based on the weighted averages of all age-depth curves.

Loss-on-Ignition and Bulk Density Analysis

Loss-on-ignition followed the method outlined in Dean (1974) and Heiri et al. (2001). A total of 230 samples (1–3 cm^3) were taken along the core at 2 cm intervals, except for the last two samples at the base of the core, which were taken at 3 and 4 cm intervals. Samples were weighed on an analytical balance (Metter Toledo-XSE105) in ceramic crucibles of known weights, and then dried in a HERAtherm OGH60-S oven at 105ºC for 20 h. After determining dry weight, samples were ignited in a Vulcan 3-550 muffle furnace at 550ºC for 4 h and then weighed again. Samples were transferred into a desiccator for 30 min to cool to room temperature after every heat treatment and before weighing. Weight loss measurements (wet, dry and ignition weights) and initial wet volume (cm^3) were used to determine water content (%), organic content (%) and ash-free bulk density (g/cm^3).

Carbon and Nitrogen Analysis

A total of 88 samples of 1-3 cm^3 each were taken along the core at 100-200 cal yr intervals and dried at 50ºC for 48 h. Samples were then homogenized by reducing each to fine powder using a steel ball mill. C and N content were determined on 3-5 mg of dried homogenized peat, which was packaged in 5 × 8 mm tin capsules for analysis. In addition, replicate analyses were performed on 15% of samples. Analysis was done at the Pacific Center for Isotopic and Geochemical Research (PCIGR) at the University of British Columbia, using an Elementar Americas vario MICRO cube elemental analyzer. PCIGR provided %C and %N. Carbon and nitrogen accumulation rates (g/m^2/cal yr) were calculated using %C, %N, ash-free bulk density (g/cm^3) and estimated deposition time (cal yr/cm).

Pollen and Non-pollen Palynomorph Analyses

For this analysis, 116 samples of 1 – 2 cm^3 were taken along the core at 4 cm intervals except the last two depths of pure clay, which were sampled at 3 cm intervals. Samples were treated with warm 10% KOH for 8 min to remove humic materials. Samples were then sieved with a 150-µm mesh to separate materials >150 µm for peat composition analysis by Stewart (2018, BSc Thesis) and the <150 µm fraction for pollen and non-pollen palynomorph analyses. Samples were further treated with warm acetolysis solution (sulphuric acid and acetic anhydride at 1:9) for 2.5 min to remove pollenkitt and cellulosic materials for clear observation. Prior to chemical treatment, one *Lycopodium* tablet (Batch No. 177745 with 18,584 ± 829 spores) was added to each subsample in order to estimate microfossil concentrations. Finally, subsamples were dehydrated with 95% ETOH and stored in 2000 cs silicone oil. Five samples from below 455 cm that consisted of clay were also treated with hydrofluoric acid to break down silica in the samples and sieved with a 10-µm mesh to remove any remaining small particles.

A minimum of 400 terrestrial pollen and spores were identified in each subsample at a magnification of 400× using Zeiss Axio Lab.A1 and AxioImager.A2 compound microscopes. A minimum sum of only 100 was used in the four basal samples in the clay portion of the core due to extremely low pollen concentrations. Pollen and spores were identified to the lowest possible taxonomic level using dichotomous keys, photographs and other texts (Helmich, 1963; Richard, 1970; McAndrews et al., 1973; Bassett et al., 1978; Hebda, 1985; Moore et al., 1991; Kapp et al. 2000) and a modern reference collection in the Paleoecology Lab in the Department of Biology at the University of Victoria. *Pinus* pollen were typed to *Pinus contorta*, *Pinus monticola* or *Pinus* undifferentiated based on the presence or absence of visible verrucae on the distal surface. *Alnus* pollen were typed into *Alnus rubra*, *Alnus viridis* and *Alnus* undifferentiated based on arci thickness, wall thickness, distance of arci from the wall, and general size and shape, following the criteria outlined by May and Lacourse (2012).

Pollen percentages were calculated using a base sum of all terrestrial pollen and spores (trees, shrubs, herbs and ferns), excluding *Sphagnum* spores and aquatic pollen, which include *Nuphar*, *Isoëtes*, *Typha* and *Potamogeton*. *Sphagnum* and aquatic group percentages were calculated by adding the base sum to each group's sum. Pollen and spore concentrations were calculated using *Lycopodium* marker spores, which were counted along with fossil pollen and spores. Pollen diagrams were created using Tilia 2.0.41 and pollen assemblage zones were determined based on taxa with a minimum occurrence of 2% using CONISS cluster analysis after square root transformation (Grimm, 1987).

Non-pollen palynomorphs (NPPs) were counted and identified along with fossil pollen and spores. These include testate amoebae, aquatic plant microfossils, fungal spores, copepod and algal remains. Testate amoebae were identified using the key and diagrams in Charman et al. (2000) and Payne et al. (2012). Fungal spores and other NPP types were identified using van Geel (1978), van Geel et al. (1981), Round et al. (1990), Kuhry (1997), Chmura et al. (2006), and Montoya et al. (2010). NPP concentrations were determined using the *Lycopodium* counts as in the case of pollen, and the concentration diagram was created using Tilia 2.0.41. NPP zones were also determined using the cluster analysis method stated above, but based on the concentrations of all NPPs in this case. Samples at the base of the core that were treated with hydrofluoric acid were excluded from NPP analysis, as most NPPs are destroyed by this treatment.

RESULTS

Peat Chronology and Stratigraphy

A total of 470 cm of peat and sediment was collected at Anderson Fen, and eight AMS radiocarbon ages were obtained on peat and plant macrofossils from the core (Table 1). The resulting calibrated ages and an age of −66 cal yr BP for the surface were used (by T. Lacourse) to create an age-depth model based on a smooth spline function (Figure 8). The age-depth model predicted a basal age of 13,938 cal yr BP (13,473 – 14,117 cal yr BP). The estimated accumulation rates and deposition times range from 0.02 to 0.41 cm/yr and 2 to 52 yr/cm, respectively. The highest peat accumulation rates and lowest deposition times were recorded in the uppermost samples (0–45 cm) and between about 365 and 325 cm (~10,700 – 10,400 cal yr BP).

The basal portion of the Anderson Fen core is composed of clay with sand and gravel (470-454 cm), followed by lake sediment (454-411 cm) that gradually transitions to limnic peat (Figures 9 and 10). Peat composition analysis by Stewart (2018, BSc Thesis) indicates that the limnic peat is composed primarily of herbaceous plant remains with abundant *Nuphar* sclereids. This herbaceous peat (411-334 cm) is replaced by *Sphagnum*-dominated peat (334-286 cm) and then mixed peat (286-162 cm) with *Sphagnum*, herbaceous and woody remains in similar proportions. The top of the core (162-0 cm) is *Sphagnum*-dominated peat (Figures 11 and 12). In addition, seeds of *Nuphar polysepala*, *Menyanthes trifoliata*, and *Potamogeton* were recovered in the lower part of the core (Figure A4).

Table 1: AMS radiocarbon and calendar ages from Anderson Fen, British Columbia

Depth (cm)	**Material**	**Lab Number**	**$\delta^{13}C$ (per mil)**	**Radiocarbon Age (^{14}C yr BP, 1σ error)**	**Calendar Age Range* (cal yr BP, 2σ)**
53-54	*Sphagnum* peat	Beta-466163	–25.4	130 ± 30	60-270
101-102	Mixed peat	Beta-472225	–27.8	1440 ± 30	1300-1380
149-150	*Sphagnum* peat	Beta-466164	–25.6	3010 ± 30	3080-3330
199-200	Mixed peat	Beta-472226	–25.3	4770 ± 30	5470-5590
241-242	Mixed peat	Beta-475649	–28.1	6190 ± 30	6990-7170
295.0-295.5	*Sphagnum* peat	Beta-463066	–24.8	8980± 30	9940-10,230
375-376	Herbaceous peat	Beta-472227	–25.0	9330 ± 30	10,430-10,650
448.5-449.0	Macrofossils from bulk lake sediment	Beta-463067	–24.8	11,360 ± 50	13,100-13,300

*Calendar age ranges are rounded to the nearest 10 yr

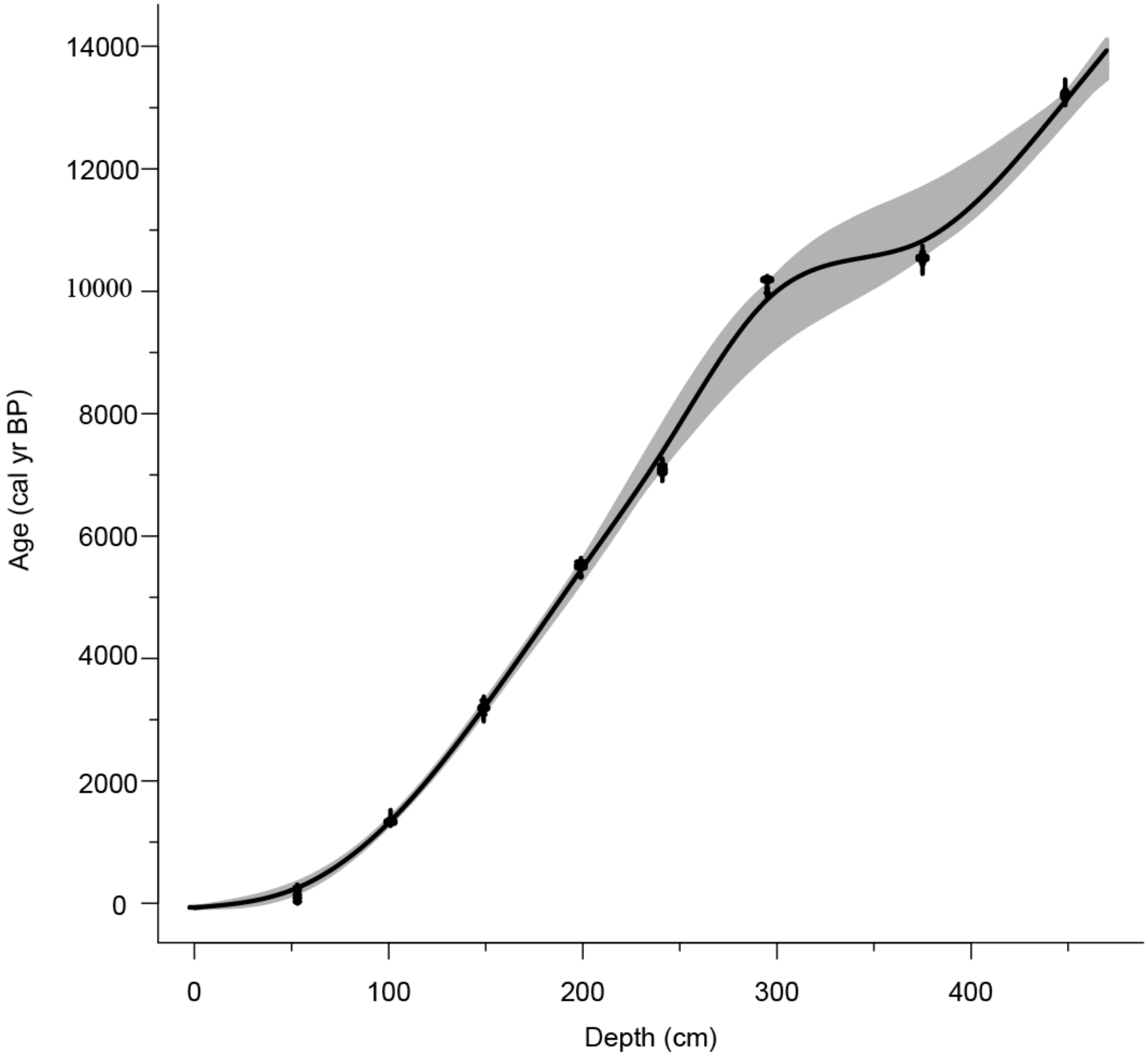

Figure 8: Age-depth model and calibrated radiocarbon ages for the Anderson Fen core. Model was built by T. Lacourse using a smooth spline in the 'clam' package (Blaauw, 2010) in R. Grey areas show 95% confidence intervals based on 10,000 iterations of the model.

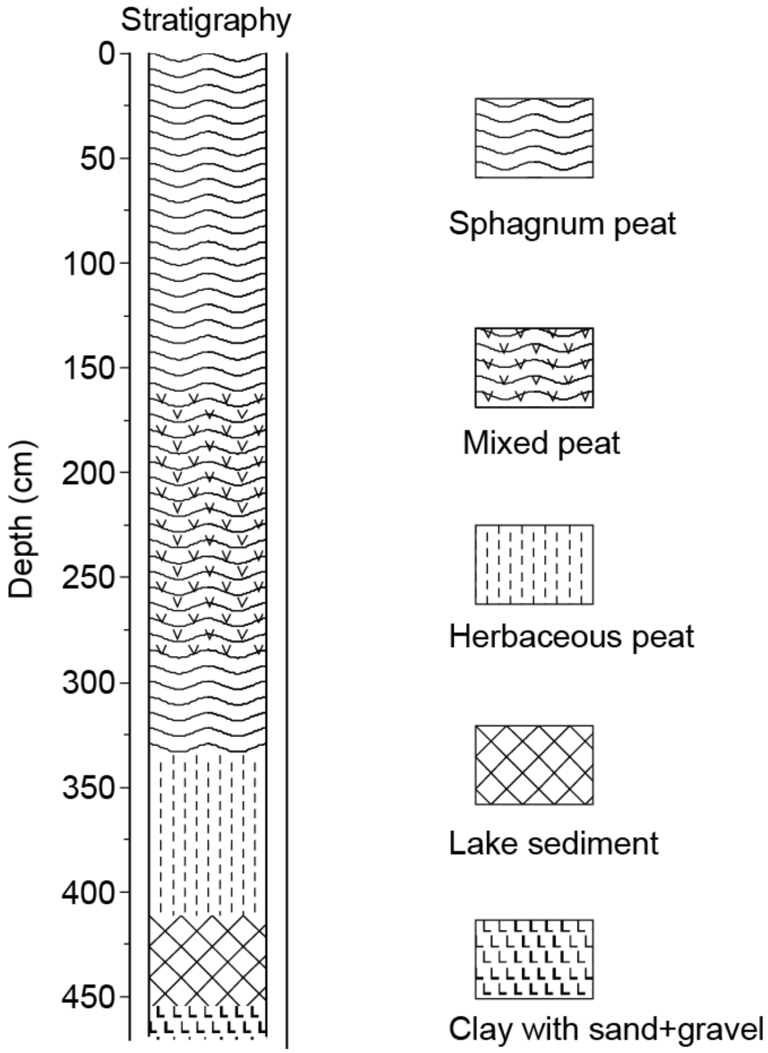

Figure 9: Generalized stratigraphy of the Anderson Fen core, based in part on peat composition analysis by Stewart (2018, BSc Thesis). Mixed peat consists of varying amounts of moss, herbaceous and woody remains.

Figure 10: The basal 50 cm of the core (420-470 cm) collected from Anderson Fen showing the transition from freshwater lake sediment to clay. (Photo by T. Lacourse)

Figure 11: One of the 50-cm peat sections (70-120 cm) collected from Anderson Fen. (Photo by T. Lacourse)

Figure 12: Uppermost peat (0-40 cm) collected from Anderson Fen showing a gradual increase in decomposition with depth. (Photo by T. Lacourse)

Loss-on-Ignition and Bulk Density Analysis

The mean water content, organic content and ash-free bulk density (AFBD) of the peat are 89.4%, 95.8% LOI and 0.09 g/cm^3, respectively. The water and organic content of the peat are fairly constant; however, both are low at the base of the core (470 – 455 cm), which corresponds to the inorganic portion of the core (Figure 13). AFBD ranges from 0.07 – 0.10 g/cm^3 in most parts of the core but is slightly lower at the very top and bottom of the core.

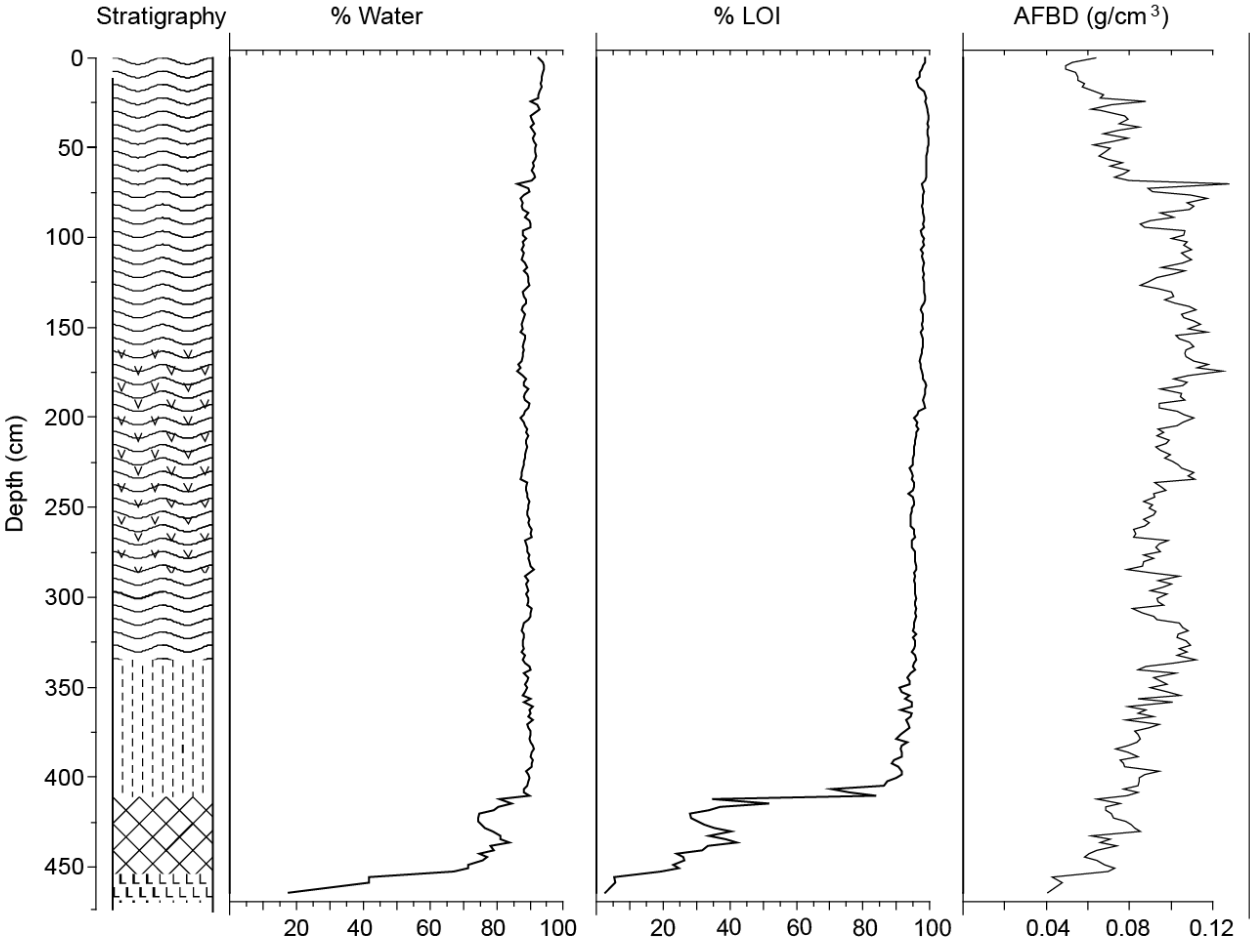

Figure 13: Physicochemical records from Anderson Fen (LOI= Loss-on-ignition; AFBD=Ash-free bulk density). See Figure 9 for stratigraphy legend.

Carbon and Nitrogen Analysis

Carbon and organic content (% LOI) follow similar patterns in the Anderson Fen core with the lowest %C in the inorganic portion of the core at the base (Figure 14). Carbon content is high and relatively stable from about 11,250 cal yr BP to the present, ranging from 46 – 54%. Nitrogen content is generally low with an overall mean of 1.5% (Figure 14). N content is lowest at the base of the core, between ~10,200 and 9600 cal yr BP and in the uppermost 67 cm, with values ranging from 0.8 to 1.0%. Conversely, C:N is highest between ~10,300 and 9600 cal yr BP, and towards the uppermost portion of the core. C:N exceeds 80 during accumulation of *Sphagnum* peat at the top of the core, at about 2000 cal yr BP and around ~10,000 cal yr BP (Figure 14). C:N is at or below 20 at depths below 400 cm.

Overall, carbon accumulation rates (CAR) in the Anderson Fen core mostly range between about 10 – 22 g/m^2/cal yr (Figure 15) with a time-weighted mean of 12.9 g/m^2/cal yr. The highest CAR is recorded in the upper 50 cm (~200 cal yr) and early Holocene (~11,500 – 9600 cal yr BP), reaching 116 g/m^2/cal yr and 80 g/m^2/cal yr, respectively. Also, CAR are very low below 408 cm (~11,500 cal yr BP), which is the least organic portion of the core. Similarly, nitrogen accumulation rates (NAR) follow the same trend reported for CAR with a time-weighted mean of 0.39 g/m^2/cal yr. The highest NAR (3 g/m^2/cal yr) is recorded at 10,500 cal yr BP (Figure 15).

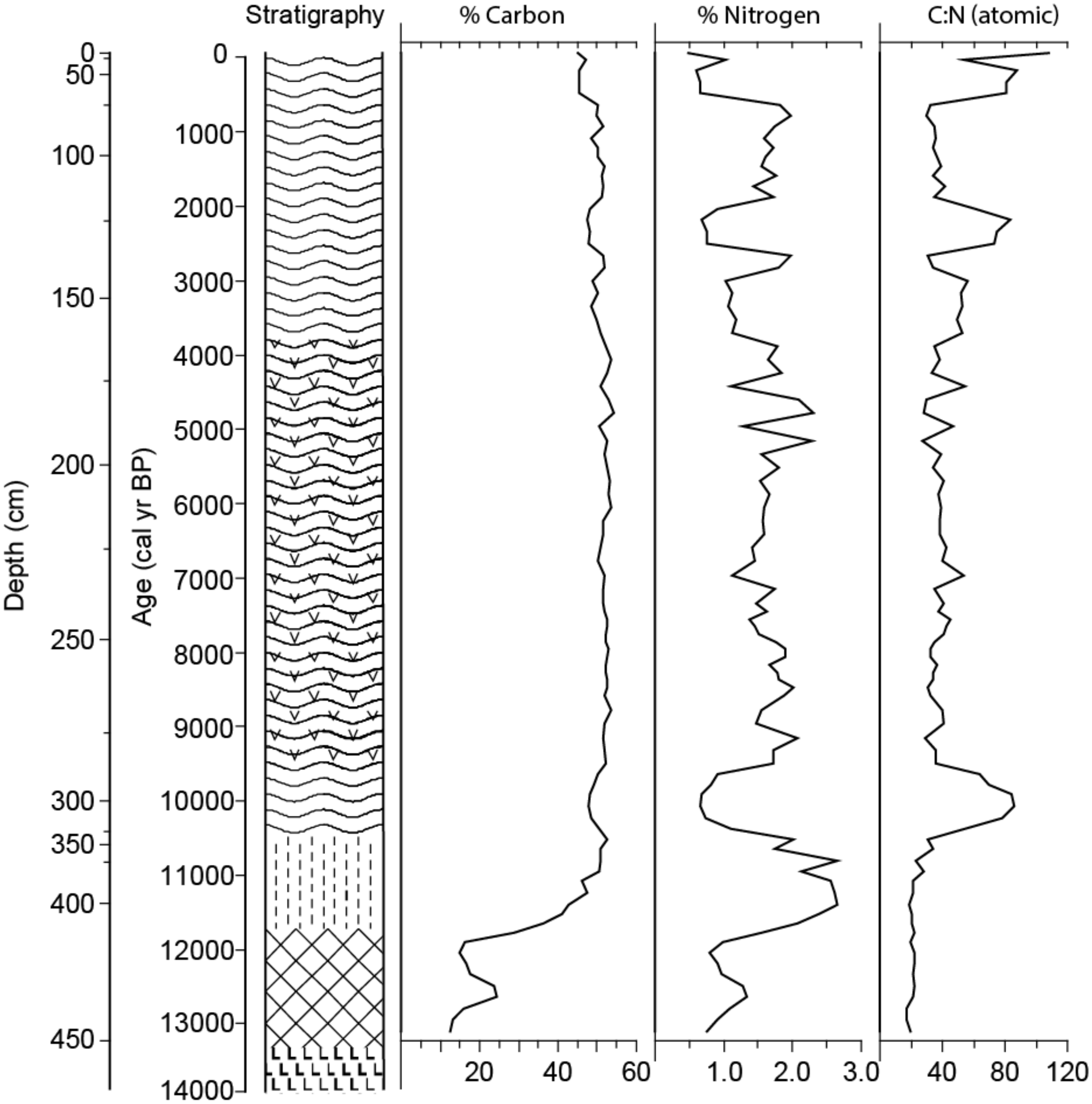

Figure 14: Stratigraphy, carbon (%), nitrogen (%) and C:N at Anderson Fen. See Figure 9 for stratigraphy legend.

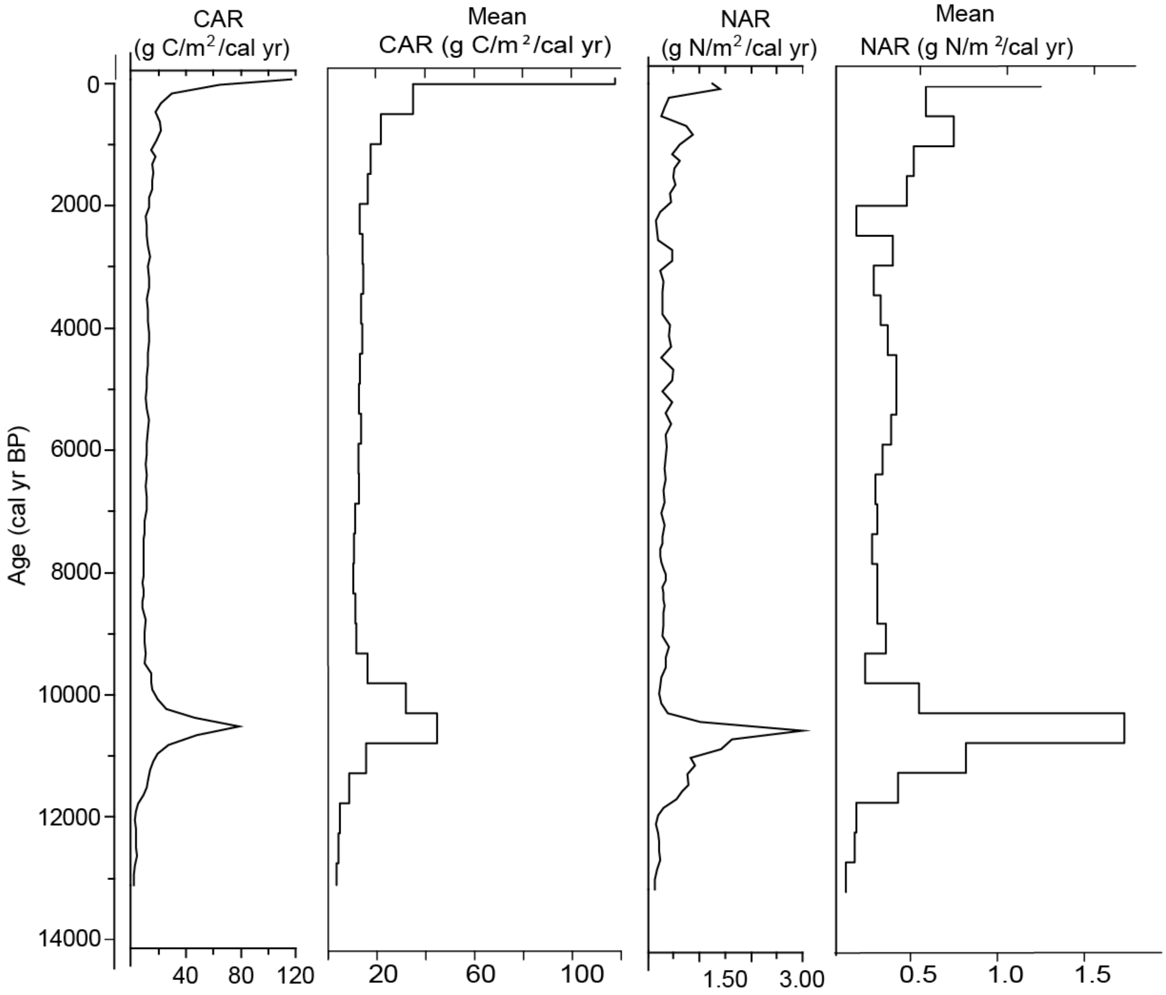

Figure 15: Anderson Fen C and N accumulation rates and mean rates of C and N accumulation in 500 cal yr bins.

Non-pollen Palynomorphs (NPP)

In total, 57 different NPPs were identified in the Anderson Fen record and they include testate amoebae and fungal, algal, aquatic plant and invertebrate remains (Figures 16, 17, A1, A2, and A3). NPP assemblages are divided into three major zones based on cluster analysis, which are described below.

NPP Zone 1: 453 – 330.5 cm (~13,280 – 10,500 cal yr BP)

This zone corresponds with the lake sediment and limnic peat in the deepest part of the core and is primarily characterized by freshwater diatoms, Nymphaeaceae leaf hair basal cells and chironomid remains (Figure 17). Other NPPs present in this zone are *Pediastrum* algae and *Dactylobiotus*-type remains. Diatoms and *Pediastrum* algae decrease in abundance through subzone 1a (at the base of the core) and are more or less absent from the rest of the record. The recorded diatoms include *Pinnularia*, *Navicula* and *Eunotia*. Nymphaeaceae leaf hair basal cells increase through the zone from about 10,000 to >100,000 cells/cm^3. Subzone 1b is marked by increases in fungal groups including *Gelasinospora* (Figures 17, A2, and A3) and minor occurrences of testate amoebae including *Archerella flavum* and *Assulina muscorum* (Figure 16), which do not occur in subzone 1a.

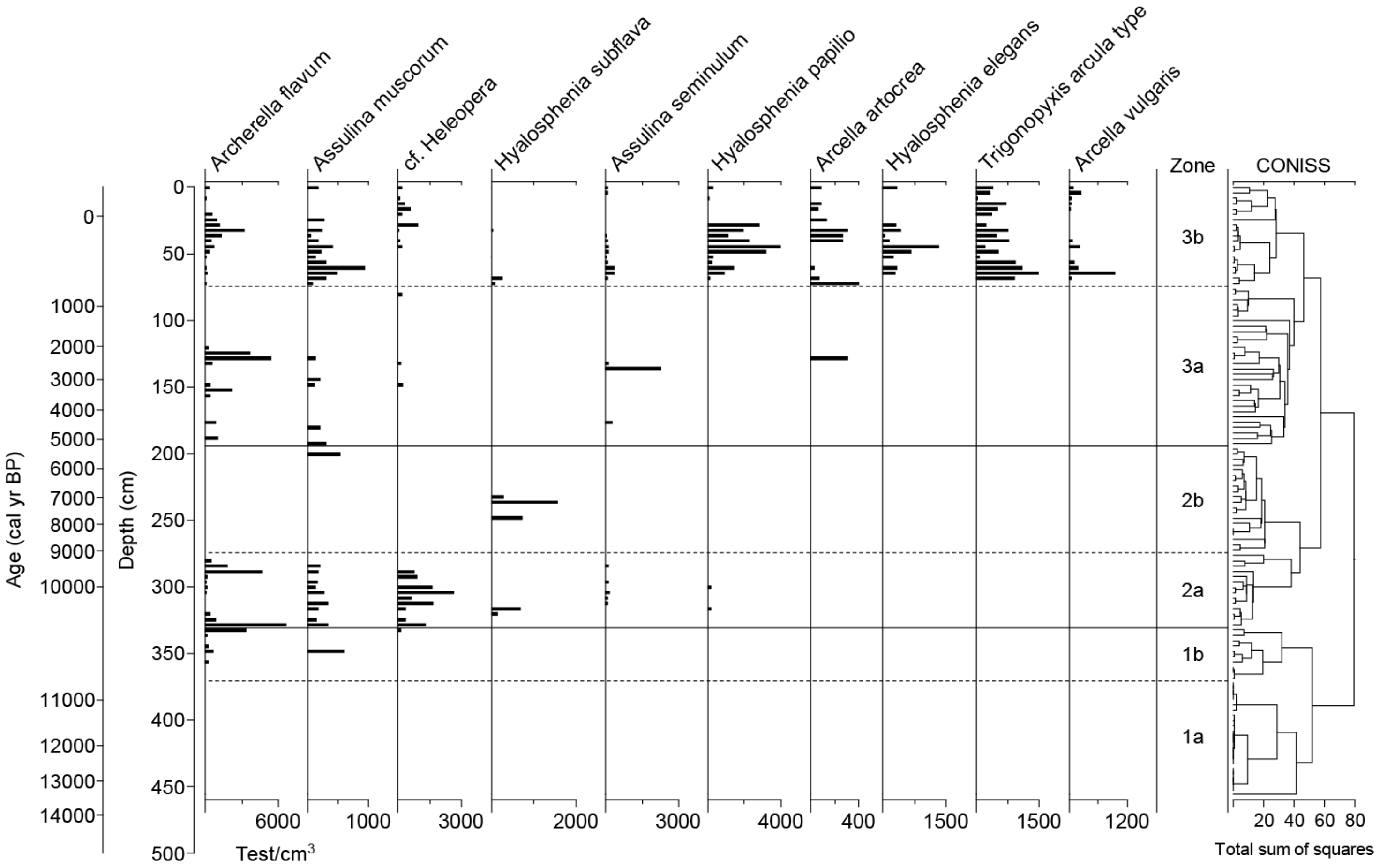

Figure: 16: Concentrations of testate amoebae in the Anderson Fen core. Note changes in scale on the x-axes.

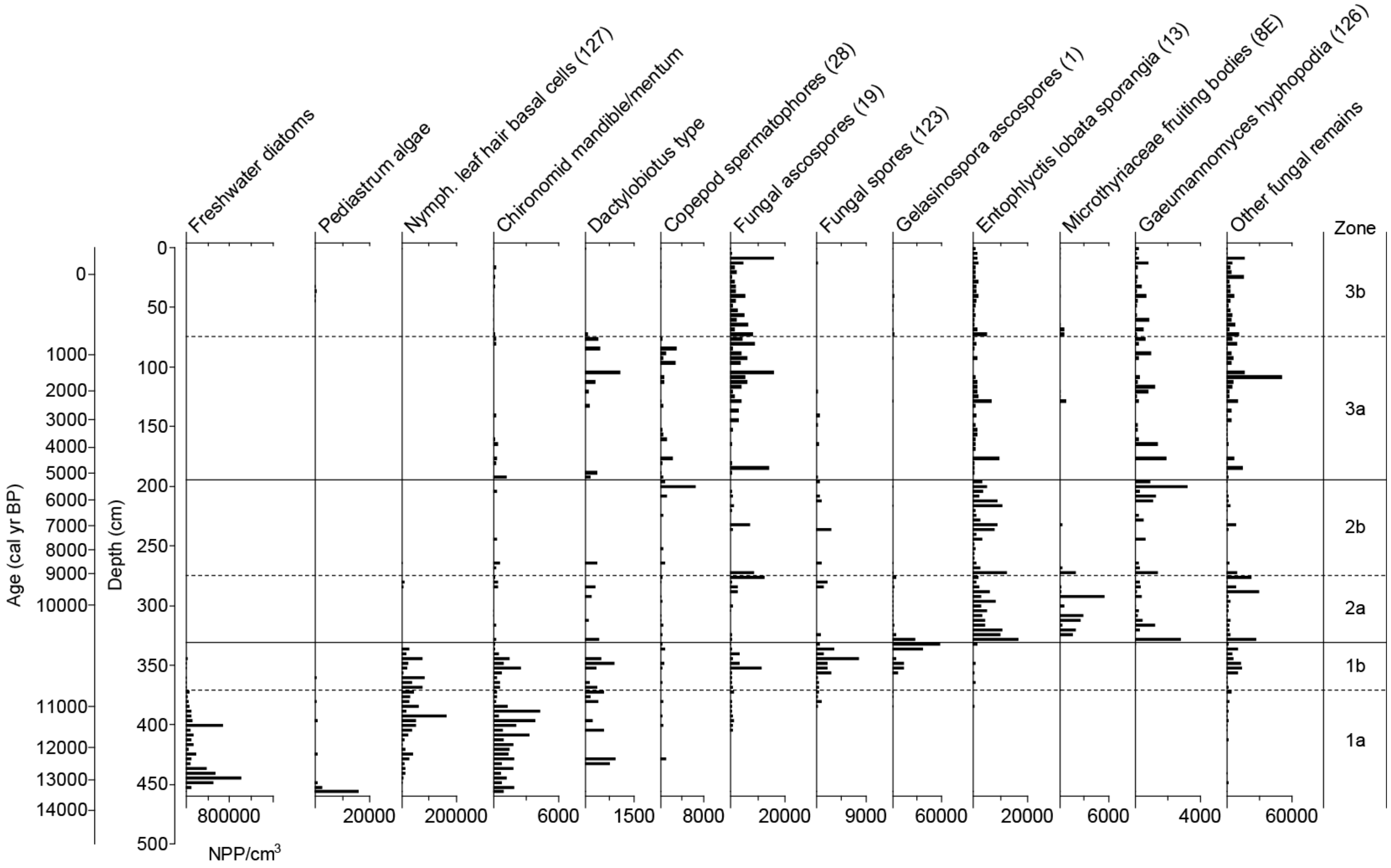

Figure: 17: Concentrations of fungal, algal and other remains in the Anderson Fen core. Numbers in brackets refer to NPP types (van Geel, 1978; van Geel et al., 1981). Note changes in scale on the x-axes.

NPP Zone 2: 330.5 – 194.5 cm (~10,500 – 5100 cal yr BP)

Fungal remains, especially *Entophlyctis lobata* generally dominate this zone with an average of over 3900 cells/cm^3 (Figure 17). Other fungal remains (e.g., *Gaeumannomyces* hyphopodia) are generally less abundant. Microthyriaceae fruiting bodies are mostly restricted to subzone 2a. Testate amoebae are also abundant in subzone 2a. *Archerella flavum* and cf. *Heleopera* are most abundant, reaching over 6000 and 2000 tests/cm^3 respectively. *Assulina muscorum, A. seminulum* and *Hyalosphenia papilio* are also present. Testate amoebae are mostly absent in subzone 2b although *A. muscorum* and *H. subflava* occur in a few samples.

NPP Zone 3: 194.5 – 0 cm (~5100 cal. yr BP – Present)

This uppermost zone is characterized by an abundance of both testate amoebae and fungal remains. Compared to zone 2, *E. lobata* is less abundant and fungal ascospores (type 19) are more abundant (Figure 17). *Archerella flavum* and *Assulina muscorum* reappear in subzone 3a. Other testate amoebae including cf. *Heleopera* and *Arcela artocrea* are also present in a few samples in subzone 3a. Copepod spermatophores and *Dactylobiotus*-type tardigrade eggs also increase in subzone 3a but are absent from subzone 3b. In subzone 3b (~600 cal yr BP – present), several other testate amoebae appear in addition to *Archerella flavum* and *Assulina muscorum* including species of *Arcella* and *Hyalosphenia* as well as *Trigonopyxis arcula* type and cf. *Heleopera*. *Archerella flavum* and *Hyalosphenia* spp. dominate subzone 3b with concentration peaks of over 3000 tests/cm^3 (Figure 16).

Pollen and Spore Assemblages

In total, 58 pollen and spore taxa were identified in the Anderson Fen record, including angiosperms, gymnosperms, ferns and fern allies, and bryophytes (Figures 18, 19, A1 and A4). Overall, gymnosperm pollen dominate the record except at the base where pollen from *Salix* shrubs are abundant (Figure 18). The pollen percentage data are divided into five major zones, which are described below.

Pollen Zone 1: 470 – 450.5 cm (~14,000 – 13,200 cal yr BP)

The basal portion of the pollen record is dominated by *Salix* and *Pinus contorta*. *Salix* accounts for between 30-50% of the sum and then decreases abruptly at the transition to zone 2, whereas *P. contorta* increases from 27% to 48% (Figure 18). The pollen concentrations of both taxa increase over the course of the zone, with *P. contorta* increasing from <2000 to over 32,000 pollen/cm^3 and *Salix* increasing from <2000 to 17,000 pollen/cm^3 (Figure 20). *Alnus viridis* is also present in this zone, accounting for about 10% with a concentration of about 6900 pollen/cm^3. Trace amounts (<3%) of pollen from other conifers such as *Abies* and *Picea* (Figure 18) and *Shepherdia canadensis* (Figure 19) are also present. Cyperaceae is also present in this zone, reaching up to 8% and then decreasing to <5% (Figure 19). Other non-arboreal taxa such as *Artemisia*, *Isoëtes, Athyrium filix-femina* and *Cryptogramma* were also recorded in small amounts (<6%). This zone, which corresponds with the clay portion of the core, has the lowest total pollen and spore concentration with a mean of 16,695 pollen/cm^3.

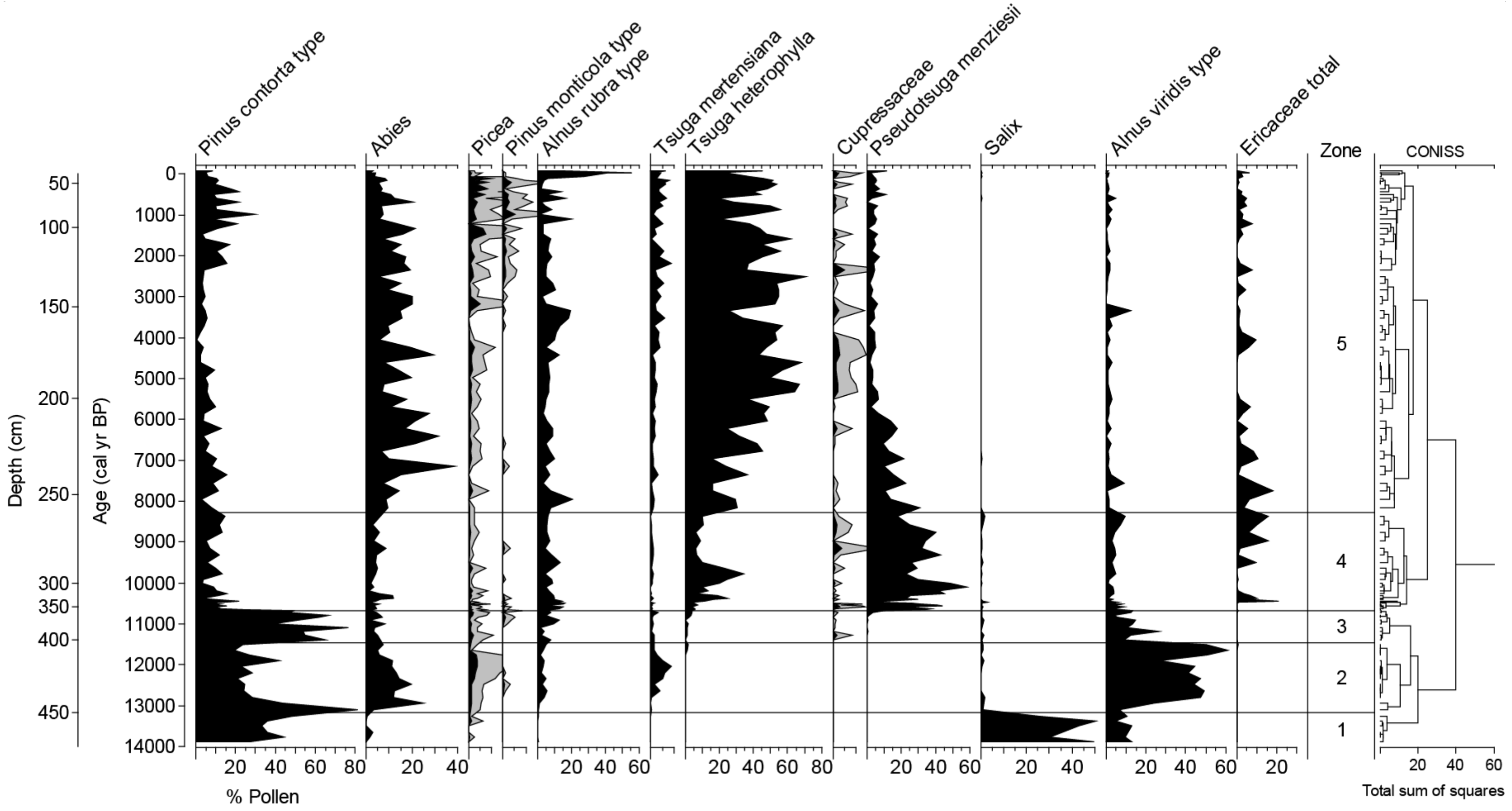

Figure 18: Pollen and spore percentages for Anderson Fen, showing major trees and shrubs and 5× exaggeration (light grey) for taxa with low percentages. Ericaceae total includes *Vaccinium*-type, *Ledum*-type and undifferentiated Ericaceae pollen.

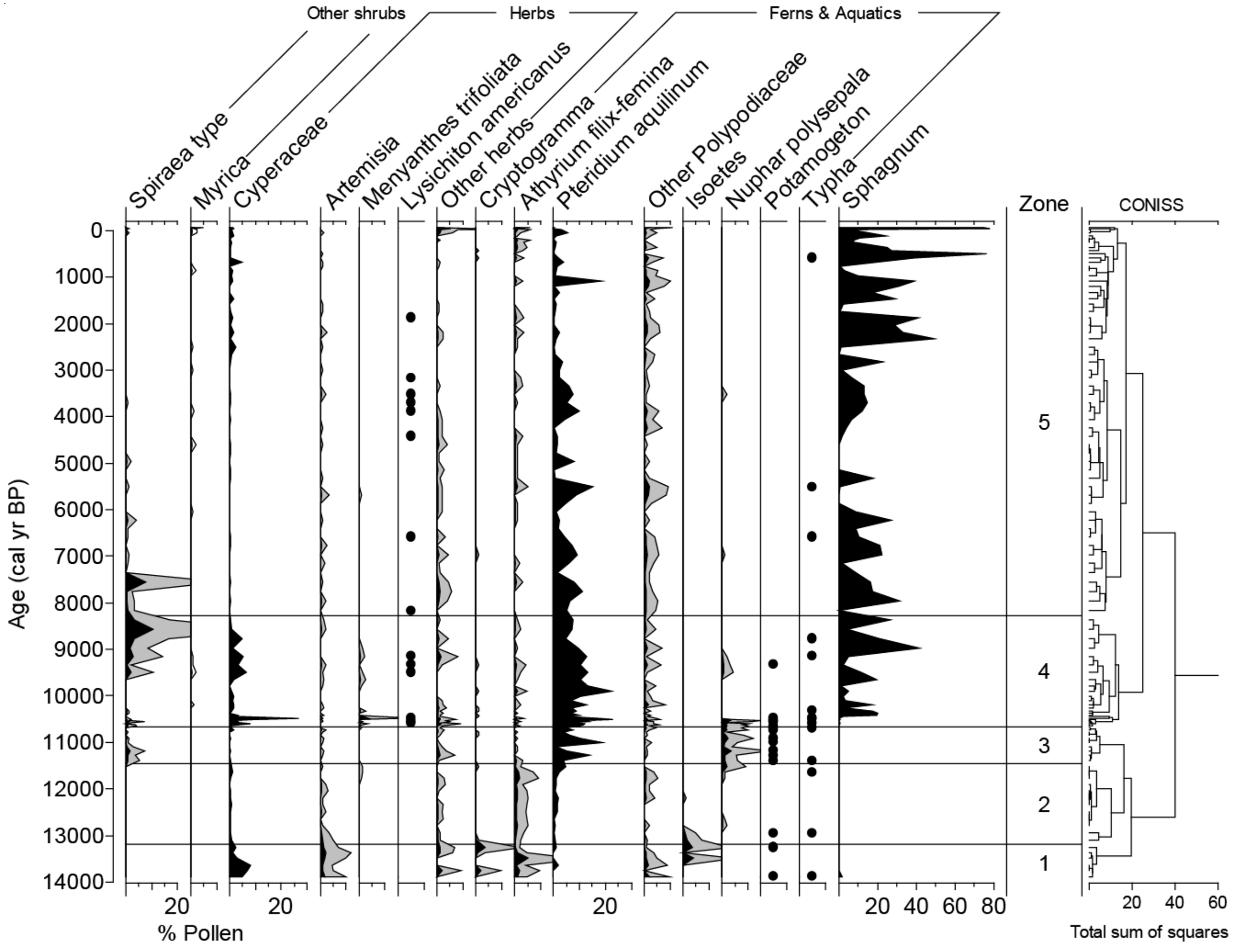

Figure 19: Pollen and spore percentages for Anderson Fen, showing herbs, ferns, aquatic taxa, and other shrubs with 5× exaggeration (light grey) for taxa with low percentages. Circles indicate presence of taxa with <5 pollen grains in an individual sample.

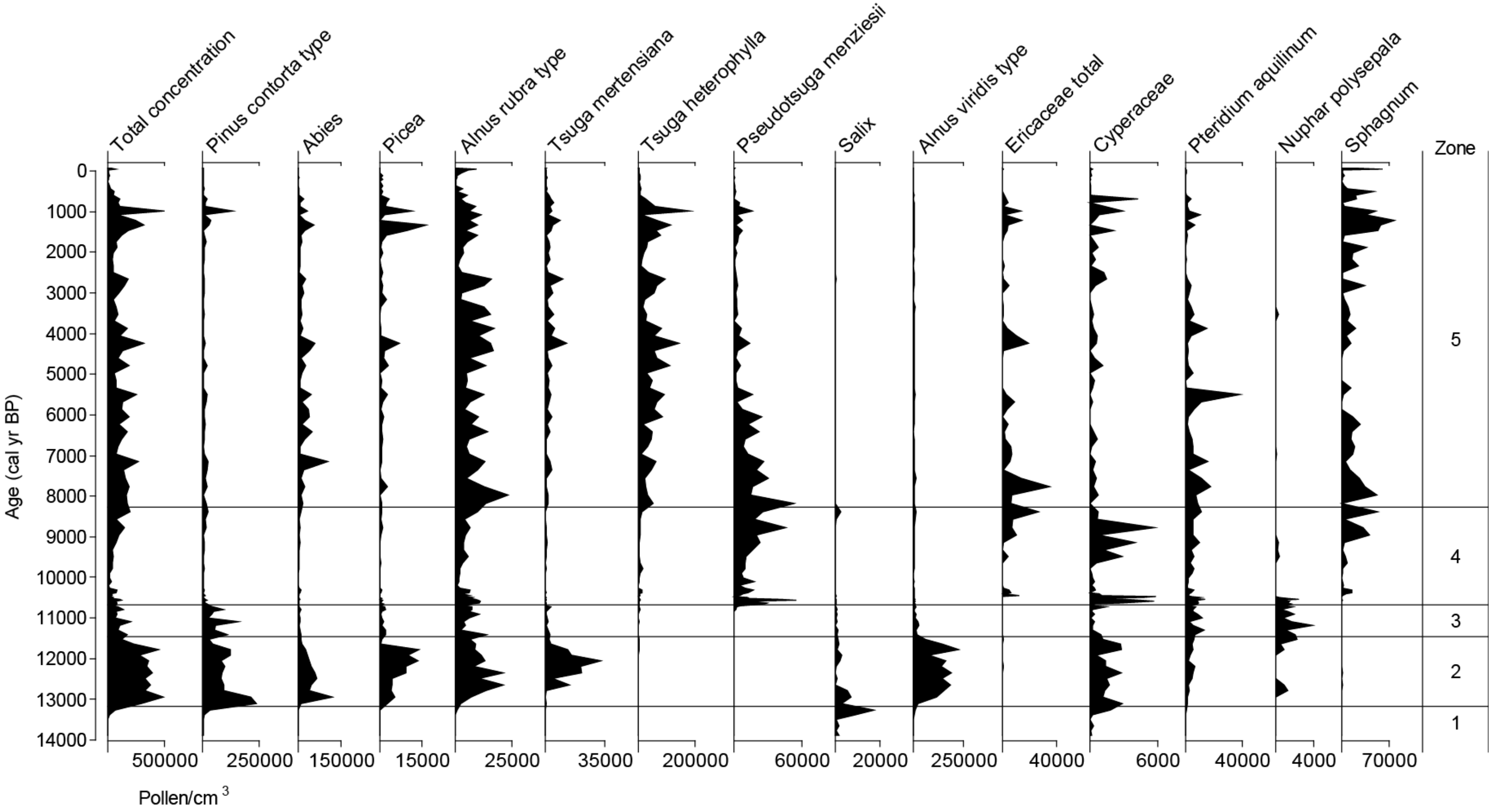

Figure: 20: Pollen and spore concentrations from Anderson Fen, showing major taxa only. Note changes in scale on the x-axes. Total concentration does not include aquatics and *Sphagnum*.

Pollen Zone 2: 450.5 – 402.5 cm (~13,200 – 11,500 cal yr BP)

Pinus contorta pollen percentages increase dramatically at the beginning of this zone to 81% and then decrease to about 30% for the remainder of the zone (Figure 18). *Pinus* concentrations follow a similar pattern (Figure 20). In general, *A. viridis* is the dominant pollen type in this zone, accounting for about 40 - 60% with a concentration peak of over 228,000 pollen/cm^3 (Figures 18 and 20). *Abies* and *Tsuga mertensiana* also increase in this zone, reaching up to 25% and 9%, respectively with corresponding increases in concentrations. *Picea* and *Pteridium aquilinum* were recorded in this zone at <5% and *Alnus rubra* remains more or less constant at 6%. In addition, *Tsuga heterophylla* appears for the first time towards the end of this zone. Total pollen and spore concentration increase in this zone to a mean of 305,244 pollen/cm^3, which is the highest concentration for the entire record.

Pollen Zone 3: 402.5 – 362.5 cm (~11,500 – 10,700 cal yr BP)

Pinus contorta increases to 60 – 80% in this zone for about 800 years; however, *Pinus* concentrations remain more or less the same as in zone 2 (Figures 18 and 20). *Alnus viridis* decreases to <30% and <20,000 pollen/cm^3. Pollen from other conifers such as *T. mertensiana*, *Picea* and *Abies* decrease through this zone as well. Cupressaceae pollen is present, although it remains below 3%. *Pseudotsuga menziesii* appears towards the end of the zone. *Pteridium aquilinum* increases from about 5% to almost 20%, and *Nuphar polysepala* pollen was also recorded at about 5%. The mean total pollen and spore concentration decreases in this zone to about 108,000 pollen/cm^3.

Pollen Zone 4: 362.5 – 258.5 cm (~10,700 – 8400 cal yr BP)

Pseudotsuga menziesii increases abruptly in this zone (59%) until about 10,000 cal yr BP, and then decreases gradually over the course of the rest of the zone (Figure 18). *Tsuga heterophylla* increases more gradually, accounting for up to 34% and then dropping to <15%. *Pinus contorta* drops sharply to 10-15% and remains at or below this level for most of the remainder of the record. *Abies*, *Picea*, *Tsuga mertensiana* and Cupressaceae are present at levels similar to the previous zone, while *Alnus rubra* increases to about 15%. *Pteridium aquilinum* is also abundant, accounting for 10 – 22%. Cyperaceae pollen accounts for about 5%, although an isolated peak of 26% was recorded at ~10,500 cal yr BP. Ericaceae becomes consistently present by ~10,400 cal yr BP and accounts for up to 27%. *Sphagnum* is well represented by the same time, reaching up to about 40% in this zone (Figure 19). Mean total pollen and spore concentrations decrease further in this zone to about 61,500 pollen/cm^3.

Pollen Zone 5: 258.5 – 0 cm (~8400 cal yr BP – Present)

This is the uppermost and largest zone, which accounts for more than half of the entire pollen record. *Tsuga heterophylla* dominates this zone, increasing from about 30% to 70%, with *Abies* an important secondary component (10-40%). *Pseudotsuga menziesii* decreases compared to the previous zone to <10% by ~5000 cal yr BP. Pollen from other trees are similar to the previous zone, although there are slight increases in *Pinus contorta*, *Pinus monticola*, *Picea* and *T. mertensiana* over the last 3000 - 2000 cal yr (Figures 18 and 20). *Alnus rubra* increases to 56% in the uppermost samples; however, this increase is not reflected in the concentration data. *Sphagnum* also varies greatly from trace levels to almost 80%, while Ericaceae and *P. aquilinum* decrease somewhat over the last 7000 cal yr. The mean total pollen and spore concentration of this zone is about 118,000 pollen/cm^3; however, concentrations decrease in the uppermost samples.

DISCUSSION

Developmental History of Anderson Fen

The Anderson Fen record spans ~14,000 cal yr BP to the present. The basal portion of the record begins with the deposition of clay until about 13,300 cal yr BP and then organic lake sediments until ~11,700 cal yr BP. The presence of *Nuphar polysepala* and chironomid larval remains, as well as 1-2% N, suggest a shallow pond was present at the site (Figure 21). *Pediastrum* algae and the eggs of *Dactylobiotus*, a freshwater tardigrade, were also recorded, which further indicate the presence of a water body during this period (Kaczmarek et al., 2008; Montoya et al., 2010). *Nuphar polysepala* suggests the pond was not only shallow but also lentic (Pojar and MacKinnon, 1994). *Potamogeton* is also present in the record, starting from ~13,900 cal yr BP, which also indicates an aquatic environment prevailed at this site after deglaciation.

Limnic peat, dominated by herbaceous remains (Stewart, 2018 – BSc Thesis), accumulated at the site between ~11,700 and 10,500 cal yr BP. Herbaceous plants especially Cyperaceae have been used to infer the presence of shallow water during peat initiation in fens (Foster and King, 1984). This period also has the highest nitrogen content, which suggests a relatively high water level at this time compared to the rest of the peat record. It is most likely that peat formation began with the advancement and formation of herbaceous mats on the surface of the shallow pond during this period. The presence of aquatic plants such as *Nuphar polysepala* and *Potamogeton* as well as algal remains likely explains the increase in nitrogen content at this time (Pichrtova et al., 2016).

Between ~ 10,500 and 9400 cal yr BP, *Sphagnum* peat with high C:N and low %N characterized Anderson Fen, which suggests a bog was formed during this interval (Figure 21). Increases in *Entophlyctis lobata* sporangia and Microthyriaceae fruiting remains reflect nutrient-

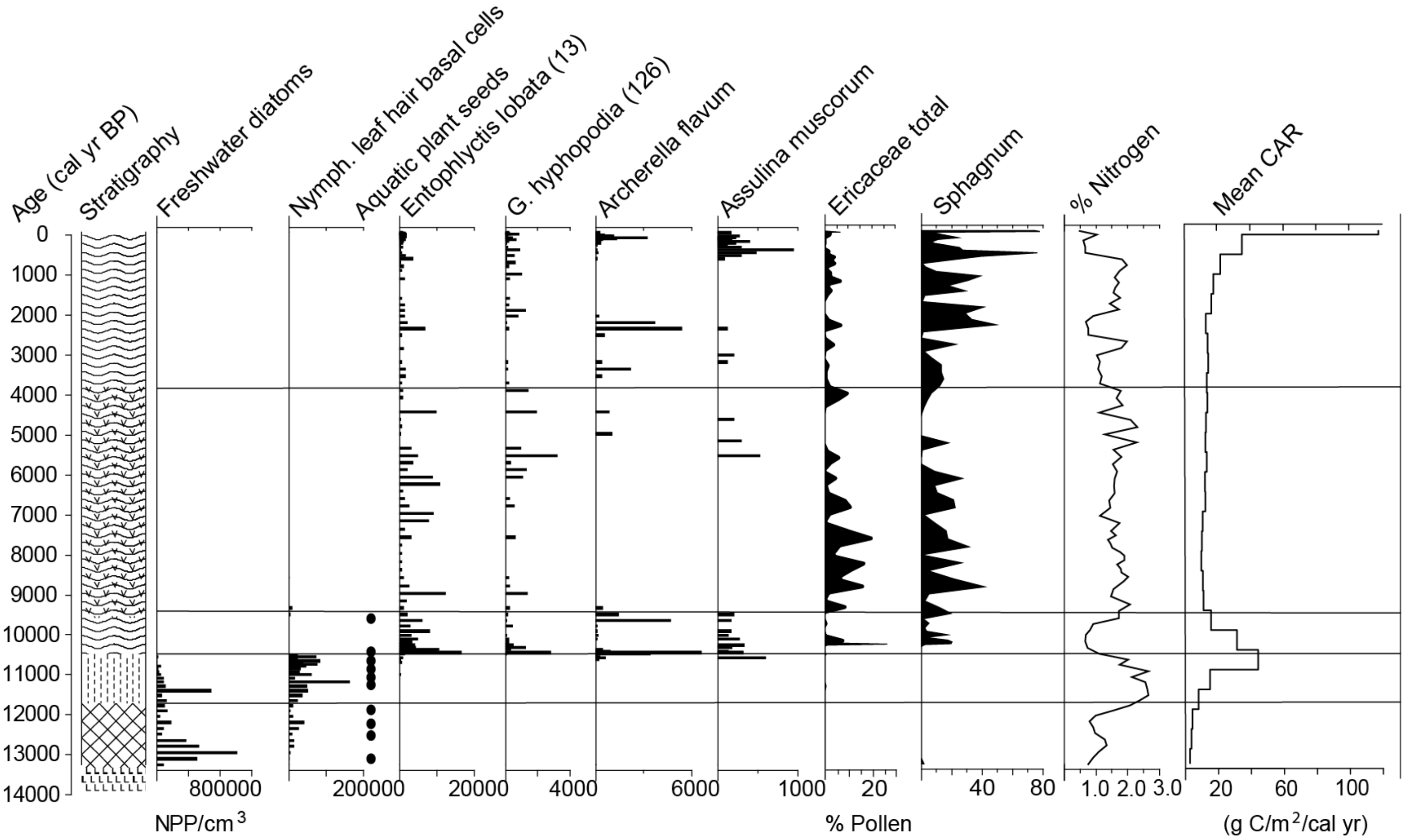

Figure 21: Summary of Anderson Fen peat development and carbon accumulation history, showing the concentrations of important non-pollen palynomorphs, percent Ericaceae pollen and *Sphagnum* spores, percent nitrogen, and mean carbon accumulation rates in 500 cal yr bins. The presence of aquatic plant seeds (*Nuphar polysepala* and *Potamogeton*) is shown with circles. See Figure 9 for stratigraphy legend.

poor *Sphagnum* peat formation and also suggest a low water table during this period (van Geel, 1981; Kuhry, 1997; Yeloff et al., 2007). *Gelasinospora* ascospores also suggest relatively dry conditions prevailed (van Geel, 1981). The presence of *Archerella flavum*, *Heleopera*, and *Assulina muscorum* during this period reflect the ombrotrophic condition that prevailed with low water level at this time (Tolonen et al., 1992; Charman and Warner, 1997; Charman et al., 2000; Lamentowicz and Mitchell, 2005; Booth and Zygmunt, 2005; Qin and Xie, 2011; Payne et al., 2016; Glime, 2017; Taylor et al., 2019). Cyperaceae and Ericaceae shrubs were present locally in addition to *Sphagnum*, which dominated the site. The recovery of *Menyanthes* seeds and pollen confirms it was also growing locally at the site. An isolated peak in Cyperaceae pollen is recorded during this period. It likely includes *Dulichium arundinaceum*, which inhabits wetlands and shallow areas in aquatic environments, as Stewart (2018, BSc Thesis) recorded the seeds of this plant around this period in her analysis of the Anderson Fen core. Peat formation during this time is likely via terrestrialization (Weider and Vitt, 2006; Rydin and Jeglum, 2013) driven, in part, by early Holocene temperature increases. The formation of a *Sphagnum* bog in the early Holocene warm period has been recorded on northern Vancouver Island as well, with associated decreases in the water table (Lacourse and Davies, 2015).

By about 9400 cal yr BP, C:N dropped, *Sphagnum* decreased in abundance and herbaceous macro-remains increased, reflecting the formation of a fen with the accumulation of mixed peat. The formation of a fen may be driven by an increase in precipitation towards the end of the early Holocene. In addition, *Spiraea* pollen recorded in the early to mid-Holocene may reflect fluctuating water levels or periodic inundation of the fen (Golinski, 2004 – PhD Thesis).

Around 6000 cal yr BP, herbaceous plants dominated Anderson Fen although *Sphagnum* and Ericaceae shrubs were still present. *Archerella flavum* and *Assulina muscorum* are intermittently present in the mid- to late Holocene and may suggest a moderate to fluctuating water table (Payne et al., 2012). This is also suggested by high variability in the nitrogen content of the peat during this period. The increase in copepod spermatophores from about ~5000 to 1000 cal yr BP compared to the rest of the record may reflect the presence of standing water at some times, as precipitation increased through the mid- to late Holocene (Huntley et al., 2013; Lacourse and Davies, 2015). *Drosera anglica* type pollen recorded during this period also suggests relatively wet, nutrient-poor conditions in the fen (Klinka et al., 1989).

From ~3800 cal yr BP to the present, the site was characterized by *Sphagnum*-dominated peat, accumulating in a poor fen with fluctuating C:N, which is likely due to variable water table (Rydin and Jeglum, 2013). The slight increase in *Pinus* pollen percentages and concentrations over the last ~2000 years may reflect a gradual increase in the acidity of this peatland. Lacourse and Davies (2015) also reported the colonization of an acidic bog by *Pinus* around 3500 cal yr BP on northern Vancouver Island. Over the last ~500 cal yr, various testate amoebae including *Assulina* spp., *Trigonopyxis arcula*, *Arcella* spp., *Hyalosphenia* spp., and *A. flavum* increase. Because these taxa have different moisture requirements, the increases may reflect hydrological and nutrient variability in the peatland, such that some areas had standing water, while other areas remained dry, as is the case now at Anderson Fen (Charman et al., 2000; Booth, 2002; Payne et. al. 2006; Taylor et al., 2019). However, the dominance of *A. flavum* and *Hyalosphenia papilio* likely reflects the fen's nutrient poor condition during this period (Taylor et al., 2019). Generally, hydrological instability driven by climate has been reported to play a major role in fen development in the Holocene (Thompson and Bettis III, 1994).

Carbon and Nitrogen Accumulation at Anderson Fen

The overall long-term carbon accumulation rate (CAR) at Anderson Fen (12.9 g/m^2/cal yr) is low compared to the mean for northern peatlands (22.9 g/m^2/cal yr) estimated by Loisel et al. (2014) and that recorded at Port McNeill Bog on northern Vancouver Island (Lacourse and Davies, 2015), which is estimated to be 16.1 g/m^2/cal yr. It is also low compared to the accumulation rate (32.5 g/m^2/cal yr) in some continental fens in western Canada (Yu et al., 2014). However, CAR at Anderson Fen is higher than that recorded by Turunen and Turunen (2003) at a slope bog on the north coast of British Columbia (8.6 g/m^2/cal yr).

CAR is highest at the surface (116 g/m^2/cal yr) of Anderson Fen and between ~11,000 and 10,000 cal yr BP with a peak of about 80 g/m^2/cal yr. This early Holocene peak in CAR has also been recorded in other northern and continental peatlands (Loisel et al., 2014; Smith et al., 2004; Yu et al., 2010; Jones and Yu, 2010; Yu et al., 2014; Lacourse and Davies, 2015). This period falls within the early Holocene Thermal Maximum, which promoted peat accumulation due to warm summers that increased productivity, while respiration loss of carbon was low due to cold winters (Loisel et al., 2014; Yu et al., 2014; Lacourse and Davies, 2015). Loisel et al. (2014) suggested that peat type, growing season length, and other environmental factors contributed to high CAR in the early Holocene aside from the increased summer temperatures during this period.

Following the early Holocene peak, CAR decrease to a mean of 11.5 g/m^2/cal yr for most of the rest of the Holocene (Figure 21). This decrease has also been recorded in northern and continental peatlands, and has been suggested to be as a result of the onset of cool, moist conditions with increasing precipitation in the mid- to late Holocene (Loisel et al., 2004; Yu et al., 2010; Yu et al., 2014; Lacourse and Davies, 2015). Over the last ~200 cal yr, CAR increase towards the surface, reaching about 116 g/m^2/cal yr, due to the presence of undecomposed plant matter in the acrotelm, which has not yet been transferred to the catotelm (Loisel and Yu, 2013).

Nitrogen accumulation rates (NAR) follow a pattern similar to CAR. NAR was highest in the early Holocene warm period between ~11,000 and 10,000 cal yr BP with a mean accumulation of 1.3 g/m^2/cal yr and a maximum of 3 g/m^2/cal yr. However, the overall long-term NAR in Anderson Fen record is low (0.39 g/m^2/cal yr), which is typical of peatlands. The low NAR at this mid-elevation site reflects a more or less terrestrial condition with a low water table for most of the Holocene. In general, peat development at Anderson Fen follows a herbaceous to *Sphagnum* peat direction, as documented in most peatlands (Hughes, 2000), with higher CAR and NAR during accumulation of herbaceous peat than *Sphagnum* peat.

Postglacial Vegetation History of Central Vancouver Island

Late-glacial period

The pollen record from Anderson Fen begins at ~14,000 cal yr BP with *Pinus contorta* and *Salix* recorded as the dominant species until ~13,200 cal yr BP. *Salix* likely formed dense thickets near the site, which could have inhibited regeneration of *Pinus* and other conifers (Klinka et al., 1989; Forest Practices Branch, Ministry of Forests, 1997). The presence of non-arboreal communities before the arrival of *Pinus* has been recorded on northern and southern Vancouver Island (Hebda, 1983; Brown and Hebda, 2002; Lacourse, 2005; Lacourse et al., 2005). Late Pleistocene – Holocene records from Haida Gwaii have also revealed that non-arboreal communities with *Salix* characterized the late-glacial environment before the establishment of *Pinus* woodland (Mathewes and Clague, 1982; Lacourse et al., 2005, 2012). *Salix* species are known to be early seral species that inhabit disturbed sites and floodplains, and grow best in moderately nitrogen-rich soils (Klinka et al., 1989). *Alnus viridis* and *Shepherdia canadensis,* two nitrogen-fixing shrub species, were also present in these late-glacial plant communities. The low amount of *Abies* and *Picea* pollen in the record at this time suggests that these conifers occurred as scattered individuals or that the pollen was transported from larger populations elsewhere.

This late glacial early seral phase coincides with deposition of inorganic sediments at Anderson Fen with low pollen concentrations, which suggests sparse vegetation and low productivity (Cwynar, 1987; Brown and Hebda, 2003; Lacourse, 2005). *Artemisia*, Cyperaceae and other herbs also suggest the vegetation was open. *Cryptogramma* and *Athyrium filix-femina* were also present, suggesting it was relatively moist at this time as well, at least locally (Klinka et al., 1989; Pojar and Mackinnon, 1994). *Isoëtes*, *Potamogeton* and *Typha* were also growing locally.

Pinus contorta populations expanded between ~13,400 and 12,800 cal yr BP, forming *Pinus* forest as temperatures began to increase. Between ~12,900 to 11,500 cal yr BP, other conifers (*Abies*, *Picea*, *Tsuga mertensiana*) and *Alnus rubra* became part of the *Pinus* forest, suggesting an increase in forest density and canopy cover. The *Abies* species recorded throughout the late-glacial record likely include *Abies lasiocarpa*, as suggested by Heinrichs et al. (2002) in their study of *A. lasiocarpa* in the late-glacial period in British Columbia. Mazzucchi (2010, PhD Thesis) also recorded needles of *Abies lasiocarpa* at high elevations on central Vancouver Island in the early Holocene. However, the most striking change during this time is the massive increase in *Alnus viridis* that appears to be accompanied by a decrease in *Pinus contorta*. The abundance of *Alnus viridis* around this period has also been recorded at high elevation sites on central and northern Vancouver Island by Mazzucchi (2010, PhD Thesis). This period also has the highest overall pollen concentration for the entire Anderson Fen record, which is likely due in part to the lacustrine nature of the site at this time, which would have effectively trapped deposited pollen. The late glacial increase in *T. mertensiana* has been reported in other studies on Vancouver Island and nearby sites as evidence of Younger Dryas-aged cooling (12,900-11,750 cal yr BP), which is now recognized as a near global event (Hebda, 1983; Brown and Hebda, 2003; Lacourse, 2005; Leopold et al., 2016). The decrease in air temperature during the Younger Dryas was estimated to be 2-3°C in a recent paleo-temperature study on southern Vancouver Island by Lemmen and Lacourse (2018). Generally, *T. mertensiana* is underrepresented in pollen assemblages compared to its extent on the landscape, which suggests its recovery at Anderson Fen means its presence in the local environment (Hebda, 1983; Allen et al., 1999). It is mostly found in sub-alpine and mountainous terrains, and in fossil pollen records, it suggests a maritime climate of cool and moist conditions with substantial snowpacks (Heusser, 1977; Klinka et al., 1989; Pojar and Mackinnon, 1994). *Alnus* has also been used to infer solifluction disturbance during the Younger Dryas cooling event on southern and northern Vancouver Island (Brown and Hebda, 2002).

Early Holocene

Following the Younger Dryas cool period, by ~11,400 cal yr BP, *Alnus viridis*, *Abies*, *T. mertensiana*, and *Picea* decreased, and *Pteridium aquilinum* and *A. rubra* increased. The major increase in *Pinus contorta* pollen percentages at this time is not accompanied by an increase in *P. contorta* concentration. This suggests that the abundance of *P. contorta* remained more or less the same during this period. By ~10,700 cal yr BP, a *Pseudotsuga menziesii*-dominated forest took over this mid-elevation environment as temperatures increased. The high percentage of *P. menziesii* in the early Holocene shows it was an important component of forests surrounding this site, considering its underrepresentation in fossil pollen records (Hebda and Allen, 1993; Allen et al., 1999). *Pteridium aquilinum* was also abundant at this time, and likely growing in the forest gaps. *Tsuga heterophylla* and Cupressaceae (*Chamaecyparis nootkatensis*, *Thuja plicata*, or both) were probably present locally at this time as well. Small amounts of *Acer macrophyllum* pollen between ~11,200 and 10,400 cal BP suggest its local presence in association with *P. menziesii*. *Pseudotsuga menziesii* forests have also been reported to dominate southern Vancouver Island landscapes in the early Holocene (Brown and Hebda, 2002; Lucas and Lacourse, 2013). The expansion of *P. menziesii* on Vancouver Island and at nearby sites in Washington in the early Holocene reflects a warm and dry period (Barnosky, 1983; Brown and Hebda, 2002; Lacourse, 2005; Leopold et al., 2016). This also agrees with the paleo-temperature study from Saltspring Island, which shows temperature was 2-3º C warmer during this period than today (Lemmen and Lacourse, 2018). As temperature decreased into the mid-Holocene, *P. menziesii* decreased in abundance throughout much of the region, as recorded at Anderson Fen.

Mid- to late Holocene

The establishment of forest dominated by *Tsuga heterophylla* started around 8400 cal yr BP. The expansion of *T. heterophylla,* a shade-tolerant and late seral species suggests closed coniferous forests on acidic, nutrient poor soil under cool and wet conditions (Fowells, 1965; Klinka et al. 1989). *Abies* was an important secondary component of this *Tsuga heterophylla* forest. The abundant *Abies* pollen in the mid-to late Holocene portion of the Anderson Fen record is likely mostly from *Abies amabilis*. *Tsuga mertensiana* and Cupressaceae were also present, although in higher abundance over the last 5000 cal yr. *Pseudotsuga menziesii* decreased in abundance in the mid-Holocene but continued to be present locally. The presence of *Pteridium* in low percentages suggests it continued to be present as well, likely in association with *P. menziesii*.

Over the last ~2500 years, the abundance of other conifers including *Picea* increased, leading to forest with an increasingly mixed composition as is the case today near Anderson Fen. The increase in *P. contorta* has been observed at a number of paleoecological sites in the region and has been linked to an expansion of peatlands in the mid- to late Holocene (Heusser, 1960; Hebda, 1983; Cwynar, 1987; Lacourse, 2005; Lacourse and Davies, 2015). The increase in *Pinus monticola*, a shade-intolerant species that regenerates after disturbance at high elevations and sometimes at lower elevations (Klinka et al., 1989; Pojar and Mackinnon, 1994; Harvey et al., 2008), may reflect cooler climate or disturbance, or both during this period.

The large increase in *Alnus rubra* pollen percentages over the last 100 years likely reflects disturbance in the region (Klinka et al., 1989; Huntley et al., 2013). Intensive logging activities occurred on central Vancouver Island between 1910 and 1945 (Mackie, 2000). This increase in *A. rubra* pollen has also been recorded on northern Vancouver Island, where it was associated with logging activities that commenced in the 1930s (Lacourse and Davies, 2015).

In general, non-arboreal communities dominated the landscape near Anderson Fen by 14,000 cal yr BP, before the establishment of *Pinus* woodland ~13,200 cal yr BP and extensive *Alnus viridis* populations between ~13,000 and 11,500 cal yr BP. The early Holocene (~10,700 – 8400 cal yr BP) was characterized by forest dominated by *Pseudotsuga menziesii* under warm and dry conditions. The modern forest was established in the mid-Holocene, and is composed of mixed coniferous rainforest under cool, wet conditions, primarily dominated by *T. heterophylla*.

CONCLUSIONS

Summary

The Anderson Fen record spans the late and post-glacial period (~14,000 cal yr BP – present). A shallow pond was present at the site before terrestrialization/infilling began about 11,700 cal yr BP, leading to the formation of a herb-dominated marsh and then at about 10,500 cal yr BP a *Sphagnum* bog. A poor fen developed about 9400 cal yr BP and continues at the site today. Carbon accumulation at Anderson Fen is low compared to continental and northern peatlands, and N content is low in the record as well. The overall low CAR at this middle elevation site may be as a result of slow accumulation and low productivity due to relatively cool, dry summers.

The vegetation history from Anderson Fen is similar to other records from central and northern Vancouver Island. *Salix*-dominated non-arboreal communities prevailed before the establishment of *Pinus* woodland around 13,200 cal yr BP. *Alnus viridis* then became abundant in the local environment until about 11,500 cal yr BP. The early Holocene was dominated by *P. menziesii* forests under warm, dry conditions. The development of *P. menziesii*-dominated forest shows that *P. menziesii* not only expanded its range towards the north during the early Holocene warm period but also to higher elevations. *Tsuga heterophylla*-dominated forest was established by 7000 cal yr BP under increasingly cool, wet conditions and has been relatively stable in composition since then. This stability reflects a relatively stable climate over this period. Overall, the late glacial and early Holocene was characterized by rapid and substantial changes in climate and vegetation, while the mid- to late Holocene changes in climate and vegetation have been relatively gradual.

Significance of the study and Future Research

This study is the first mid-elevation, paleoecological peatland study in coastal British Columbia, adding to the very few paleoecological studies on peatlands in British Columbia as a whole. This peatland study will help in future conservation and restoration plans in British Columbia by providing baseline data for future investigation of peatland carbon budgets and restoration. This study also provides more insight into the existing knowledge of late glacial vegetation history and *Pseudotsuga* expansion during the early Holocene.

Comparing the peatland record from a lower elevation on Vancouver Island (Lacourse and Davies, 2015) to the Anderson Fen record suggests that peatlands at low elevations tend to have higher CAR than peatlands at middle to high elevations. Lacourse and Davies (2015) in their study of Port McNeill Bog recorded higher CAR at their lower elevation site compared to what is recorded at Anderson Fen. In order to better understand this difference, there is a need for more peatland paleoecological studies at middle to high elevations on Vancouver Island to investigate if cooler climates consistently result in lower carbon accumulation in coastal BC peatlands.

Future studies should also make efforts to separate *Sphagnum* spore types into different morphological types and if possible identified to species level, in order to better understand the role of different *Sphagnum* species in peatland ecology and formation through time. In addition, future studies on British Columbia peatlands should also focus more on non-pollen palynomorphs, as there are some non-pollen palynomorphs in Anderson Fen peat that have not been explored previously in Vancouver Island peatlands. For example, tardigrade eggs are common in peat samples but have not been given attention in Vancouver Island peatlands and British Columbia generally.

REFERENCES

Allen, G. B. (1995). Vegetation and climate history of southeast Vancouver Island, British Columbia. M.Sc. Thesis. School of Earth and Ocean Sciences, University of Victoria, Victoria, British Columbia.

Allen, G. B., Brown, K. J. and Hebda, R. J. (1999). Surface pollen spectra from southern Vancouver Island, British Columbia, Canada. Canadian Journal of Botany 77: 786–799.

Banner, A., Le Page, P., Morun, J. and de Groot, A. (eds.). (2005). The Hyp^3 project: Pattern, process, and productivity in hypermaritime forests of coastal British Columbia-A synthesis of 7-year results. Ministry of Forest Research, Victoria, British Columbia 2(2): 142p.

Barnosky, C. W. (1983). Late Pleistocene and early Holocene environmental history of southwestern Washington State, U.S.A. Canadian Journal of Earth Sciences 21: 619 – 629.

Bassett, I. J., Crompton, C. W. and Parmelee, J. A. (1978). An Atlas of Airborne Pollen Grains and Common Fungus Spores of Canada. Research Branch, Agriculture Canada. Monograph No. 18. 321p.

Birks, H. H. (2003). The importance of plant macrofossils in the reconstruction of Lateglacial vegetation and climate: examples from Scotland, western Norway, and Minnesota, USA. Quaternary Science Reviews 22(5–7): 453-473.

Birks, H. H. (2007). Plant macrofossil introduction. In: Elias, S. A. (ed.), Encyclopedia of Quaternary Science, Vol. 3. Elsevier, Amsterdam. pp. 2266-2288.

Blaauw, M. (2010). Methods and code for 'classical' age-modelling of radiocarbon sequences. Quaternary Geochronology 5: 512-518.

Blaauw, M., van der Plicht, J. and van Geel, B. (2004). Radiocarbon dating of bulk peat samples from raised bogs: Nonexistence of a previously reported ‘reservoir effect’? Quaternary Science Reviews 23: 1537-1542.

Blaise, B., Clague, J. J. and Mathewes, R. W. (1990). Time of maximum late Wisconsin glaciation, west coast of Canada. Quaternary Research 34: 282-295.

Booth, R. K. (2002). Testate amoebae as paleoindicators of surface-moisture changes on Michigan peatlands: modern ecology and hydrological calibration. Journal of Paleolimnology 28: 329 – 348.

Booth, R. K. and Zygmunt, J. R. (2005). Biogeography and comparative ecology of testate amoebae inhabiting *Sphagnum*-dominated peatlands in the Great Lakes and Rocky Mountain regions of North America. Diversity and Distributions 11: 577 – 590.

Brown, K. J. and Hebda, R. J. (2002). Origin and development and dynamics of coastal temperate conifer rainforest of southern Vancouver Island, Canada. Canadian Journal of Forest Research 32: 353 – 372.

Brown, K. J. and Hebda, R. J. (2003). Coastal rainforest connections disclosed through a Late Quaternary vegetation, climate, and fire history investigation from the Mountain Hemlock Zone on southern Vancouver Island, British Colombia, Canada. Review of Palaeobotany and Palynology 123: 247 – 269.

Charman, D. J. and Warner, B. G. (1997). The ecology of testate amoebae (Protozoa: Rhizopoda) in oceanic peatlands in Newfoundland, Canada: modelling hydrological relationships for palaeoenvironmental reconstruction. Ecoscience 4 (4): 555 – 562.

Charman, D. J., Hendon, D. and Woodland, W. A. (2000). The Identification of Testate Amoeba (Protozoa: Rhizopoda) in Peats. Technical Guide No. 9. Quaternary Research Association, London. 147p.

Chmura, G. L., Stone, P. A. and Ross, M. S. (2006). Non-pollen microfossils in Everglades sediments. Review of Palaeobotany and Palynology 141: 103 – 119.

Clague, J. J. (1976). Quadra sand and its relation to the late Wisconsin glaciation of southwest British Columbia. Canadian Journal of Earth Sciences 13: 803-815.

Clague, J. J. (2017). Deglaciation of the Cordillera of western Canada at the end of the Pleistocene. Cuadernos de Investigación Geográfica 43: 449-466.

Clague, J. J. and James, T. S. (2002). History and isostatic effects of the last ice sheet in southern British Columbia. Quaternary Science Reviews 21: 71-87.

Cwynar, L. C. (1987). Fire and the forest history of the North Cascade Range. Ecology 68(4): 791-802.

Dean, W. E. Jr. (1974). Determination of carbonate and organic matter in calcareous sediments and sedimentary rocks by loss on ignition: comparison with other methods. Journal of Sedimentary Petrology 44: 242–248.

Environment Canada (2018). Climate Normals 1981-2010. Black Creek Station. Available at: http://climate.weather.gc.ca/climate_normals/results_1981_2010_e.html.

Faegri, K. and Iversen, J. (1975). Textbook of Pollen Analysis. Hafner Press, New York. 295p.

Forest Practices Branch, Ministry of Forests (1997). Operational summary for vegetation management: Willow complex. Province of British Columbia. 11p.

Foster, D. R. and King, G. A. (1984). Landscape features, vegetation and developmental history of a patterned fen in southeastern Labrador, Canada. Journal of Ecology 72(1): 115 – 143.

Fowells, H. A. 1965. Silvics of forest trees of the United States. United States Department of Agriculture Handbook 271.

Glime, J. M. (2017). Protozoa. In: Glime, J. M. (ed) Bryophyte Ecology: Bryological Interaction, vol. 2. Ebook sponsored by Michigan Technological University and the International Association of Bryologists. Available at: http://digitalcommons.mtu.edu/bryophyte-ecology2/2/

Golinski, G. K. (2004). Mires of Vancouver Island, British Columbia: vegetation classification and differences between disturbed and undisturbed mires. Ph.D. Thesis. Interdisciplinary Studies, University of Victoria, Victoria, British Columbia. 167p.

Gorham, E., Lehman, C., Dyke, A., Janssens, J. and Dyke, L. (2007). Temporal and spatial aspects of peatland initiation following deglaciation in North America. Quaternary Science Reviews 26: 300-311.

Grimm, E. C. (1987). CONISS: a FORTRAN 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. Computers & Geoscience 13: 13-35.

Hansen, H. P. (1940). Paleoecology of two peat bogs in southwestern British Columbia. American Journal of Botany 27(3): 144-149.

Hansen, H. P. (1950). Pollen analysis of three bogs on Vancouver Island, Canada. Journal of Ecology 38(2): 270 – 276.

Harvey, A. E., Byler, J. W., McDonald, G. I., Neuenschwander, L. F., and Tonn, J. R. (2008). Death of an ecosystem: perspectives on western white pine ecosystems of North America at the end of the twentieth century. United States Department of Agriculture, Forest

Service Rocky Mountain Research Station, General Technical Report RMRS-GTR-208. 10p.

Hebda, R. J. (1977). The paleoecology of a raised bog and associated deltaic sediments of the Fraser River delta. PhD Thesis. Department of Botany, University of British Columbia, Vancouver. 202p.

Hebda, R. J. (1983). Late-glacial and postglacial vegetation history at Bear Cove Bog, northeast Vancouver Island, British Columbia. Canadian Journal of Botany 61: 3172 – 3192.

Hebda, R. J. (1985). Pollen morphology of *Ligusticum* (Apiaceae) in Canada. Canadian Journal of Botany 63: 1880-1887.

Hebda, R. J. and Allen, G. B. (1993). Modern pollen spectra from west central British Columbia. Canadian Journal of Botany 71: 1486 – 1495.

Hebda, R. J. and Haggarty, J.C. (Eds.). (1997). Brooks Peninsula: an ice age refugium on Vancouver Island. British Columbia Ministry of Environment, Lands and Parks, Occasional Paper No. 5, Victoria, Canada.

Heinrichs, M. L., Antos, J. A., Hebda, R. J. and Allen, G. B. (2002). *Abies lasiocarpa* (Hook.) Nutt. in the late-glacial and early-Holocene vegetation of British Columbia, Canada, and adjacent regions in Washington, USA. Review of Palaeobotany and Palynology 120: 107 – 122.

Heiri, O., Lotter, A. F. and Lemcke, G. (2001). Loss on ignition as a method for estimating organic and carbonate content in sediments: reproducibility and comparability of results. Journal of Paleolimnology 25: 101-110.

Helmich, D. E. (1963). Pollen morphology in the maples (*Acer* L.). Papers of the Michigan Academy of Science, Arts and Letters 48: 151-164.

Heusser, C. J. (1960). Late-Pleistocene environments of North Pacific North America. American Geology Society Special Publication 35. 308p.

Heusser, C. J. (1977). Quaternary palynology of the Pacific slope of Washington. Quaternary Research 8: 282-306.

Heusser, L. E. (1983). Palynology and paleoecology of postglacial sediments in an anoxic basin, Saanich Inlet, British Columbia. Canadian Journal of Earth Sciences 20: 873-885.

Hughes, P. D. M. (2000). A reappraisal of the mechanisms leading to ombrotrophy in British raised mires. Ecology Letters 3: 7 – 9.

Huntley, M. J. W., Mathewes, R. W. and Shotyk, W. (2013). High-resolution palynology, climate change and human impact on a late Holocene peat bog on Haida Gwaii, British Columbia, Canada. The Holocene 23(11): 1572 – 1583.

Hutchinson, I., James, T. S., Clague, J. J., Barrie, J. V. and Conway, K. W. (2004). Reconstruction of late Quaternary sea-level change in southwestern British Columbia from sediments in isolation basins. Boreas 33: 183–194.

Jones, M. C. and Yu, Z. C. (2010), Rapid deglacial and early Holocene expansion of peatlands in Alaska. Proceedings of the National Academy of Sciences 107: 7347–7352.

Joosten, H. and Clarke, D. (2002). Wise use of mires and peatlands. International Mire Conservation Group and International Peat Society, Saarijarvi, Finland. 304p.

Kaczmarek, T., Michalczyk, T. and Eggermont, H. (2008). *Dactylobiotus lud*, a new freshwater tardigrade (Eutardigrada: Macrobiotidae) from the Rwenzori Mountains, Uganda. African Zoology 43(2): 150 – 155.

Kapp, R. O., Davies, O. K. and King, J. E. (2000). Pollen and Spores. Second edition. The American Association of Stratigraphic Palynologists Foundation, Dallas. 279p.

Klinka, K., Krajina, V. J., Ceska, A. and Scagel, A. M. (1989). Indicator Plants of Coastal British Columbia. University of British Columbia Press, Vancouver, Canada. 288p.

Kuhry, P. (1997). The palaeoecology of a treed bog in western boreal Canada: a study based on microfossils, macrofossils and physico-chemical properties. Review of Palaeobotany and Palynology 96: 183 – 224.

Lacourse, T. (2005). Late Quaternary dynamics of forest vegetation on northern Vancouver Island, British Columbia, Canada. Quaternary Science Reviews 24: 105 – 121.

Lacourse, T. and Davies, M. A. (2015). A multi-proxy peat study of Holocene vegetation history, bog development, and carbon accumulation on Northern Vancouver Island, Pacific coast of Canada. The Holocene 25(7): 1165 – 1178.

Lacourse, T., Mathewes, R. W. and Fedje, G. W. (2005). Late-glacial vegetation dynamics of the Queen Charlotte Islands and adjacent continental shelf, British Columbia, Canada. Palaeogeography, Palaeoclimatology, Palaeoecology 226: 36 – 57.

Lacourse, T., Delepine, J. M., Hoffman, E. H. and Mathewes, R. W. (2012). A 14,000 year vegetation history of a hypermaritime island on the outer Pacific coast of Canada based on fossil pollen, spores and conifer stomata. Quaternary Research 78: 572-582.

Lamentowicz, M. and Mitchell, E. A. D. (2005). The ecology of testate amoebae (Protists) in *Sphagnum* in North-western Poland in relation to peatland ecology. Microbial Ecology 50(1): 48-63.

Lavoie, C., Zimmerman, C. and Pellerin, S. (2001). Peatland restoration in southern Quebec, Canada: A paleoecological perspective. Écoscience 8(2): 247-258.

Lemmen, J. and Lacourse, T. (2018). Fossil chironomid assemblages and inferred summer temperatures for the past 14,000 years from a low-elevation lake in Pacific Canada. Journal of Paleolimnology 59: 427 – 442.

Loisel, J. and Garneau, M. (2010). Late Holocene paleoecohydrology and carbon accumulation estimates from two boreal peat bogs in eastern Canada: Potential and limit of multi-proxy archives. Palaeogeography, Palaeoclimatology, Palaeoecology 291: 493-533.

Loisel, J. and Yu, Z. (2013). Recent acceleration of carbon accumulation in a boreal peatland, south central Alaska. Journal of Geophysical Research: Biogeosciences 118: 41-53.

Loisel, J., Yu, Z., Beilman, D. W., Camill, P., Alm, J., Amesbury, M. J., Anderson, D., Andersson, S., Bochicchio, C., Barber, K., Belyea, L. R., Bunbury, J., Chambers, F. M., Charman, D. J., De Vleeschouwer, F., Fiałkiewicz-Kozieł, B., Finkelstein, S. A., Gałka, M., Garneau, M., Hammarlund, D., Hinchcliffe, W., Holmquist, J., Hughes, P., Jones, M. C., Klein, E. S., Kokfelt, U., Korhola, A., Kuhry, P., Lamarre, A., Lamentowicz, M., Large, D., Lavoie, M., MacDonald, G., Magnan, G., Mäkilä, M., Mallon, G., Mathijssen, P., Mauquoy, D., McCarroll, J., Moore, T. R., Nichols, J., O'Reilly, B., Oksanen, P., Packalen, M., Peteet, D., Richard, P. J. H., Robinson, S., Ronkainen, T., Rundgren, M., Sannel, A. B. K., Tarnocai, C., Thom, T., Tuittila, E., Turetsky, M., Väliranta, M., van der Linden, M., van Geel, B., van Bellen, S., Vitt, D., Zhao, Y. and Zhou, W. (2014) A database and synthesis of northern peatland soil properties and Holocene carbon and nitrogen accumulation. The Holocene 24(9): 1028–1042.

Lucas, J. D. and Lacourse, T. (2013). Holocene vegetation history and fire regimes of *Pseudotsuga menziesii* forests in the Gulf Islands National Park Reserve, southwestern British Columbia, Canada. Quaternary Research 79: 366-376.

Mackie, R. (2000). Island Timber: a social history of the Comox Logging Company, Vancouver Island. Sono Nis Press. 309p.

Martini, I. P., Cortizas, A. M. and Chesworth, W. (2006). Peatlands: evolution and records of environmental and climate changes. Developments in Earth Surface Processes, Vol. 9. Elsevier, Amsterdam/Oxford. 587p.

Mathewes, R. W. (1993). Evidence for Younger Dryas-age cooling on the north Pacific coast of America. Quaternary Science Reviews 12: 321-331.

Mathewes, R. W. and Clague, J. J. (1982). Stratigraphic relationships and paleoecology of a late-glacial peat bed from the Queen Charlotte Islands, British Columbia. Canadian Journal of Earth Sciences 19: 1185 – 1195.

May, L. and Lacourse, T. (2012). Morphological differentiation of *Alnus* (alder) pollen from western North America. Review of Palaeobotany and Palynology 180: 15-24.

Maynard, D. E. (1988). Peatland Inventory of British Columbia. Mineral Resources Division-Geological Survey Branch. 72p.

Mazzucchi, D. (2010). Postglacial vegetation history of mountainous landscapes on Vancouver Island, British Columbia, Canada. Ph.D. Thesis. School of Earth and Ocean Sciences, University of Victoria, Victoria, British Columbia. 199p.

McAndrews, J. H., Berti, A. A. and Norris, G. (1973). Key to the Quaternary Pollen and Spores of the Great Lakes Region. Royal Ontario Museum Life Sciences Miscellaneous Publication, Toronto. 64p.

Meidinger, D. and Pojar, J. (Eds). (1991). Ecosystems of British Columbia. BC Ministry of Forests Research Branch, Special Report Series 6, Victoria, British Columbia. 342p.

Montoya, E., Rull, V. and van Geel, B. (2010). Non-pollen palynomorphs from surface sediments along an altitudinal transect of the Venezuelan Andes. Palaeogeography, Palaeoclimatology, Palaeoecology 297: 169 – 183.

Moore, P. D., Webb, J. A. and Collinson, M. E. (1991). Pollen Analysis. Second edition. Blackwell Scientific Publication, Oxford. 216p.

National Wetlands Working Group (1988). Wetlands of Canada. Ecological Land Classification Series 24, Sustainable Development Branch, Environment Canada, Ottawa, Ontario, and Polyscience Publications Incorporation, Montreal, Quebec. 452p.

National Wetlands Working Group (1997). The Canadian Wetland Classification System. Warner, B. G. and Rubec, C. D. A. (eds.). Wetlands Research Centre, University of Waterloo, Waterloo. 68p.

Payne, R. J., Kishaba, K., Blackford, J. J. and Mitchell, E. A. D. (2006). The ecology of testate amoebae (Protista) in south-central Alaskan peatlands: building transfer-function models for palaeoenvironmental studies. The Holocene 16:403 – 414.

Payne, R. J., Lamentowicz, M., van der Knaap, W. O., van Leeuwen, J. F. N., Mitchell, E. A. D. and Mazei, Y. (2012). Testate amoebae in pollen slides. Review of Palaeobotany and Palynology 173: 68-79.

Payne, R. J., Malysheva, E., Tsyganov, A., Pampura, T., Novenko, E., Volkova, E., Babeshko, K. and Mazei, Y. (2016). A multi-proxy record of Holocene environmental change, peatland development and carbon accumulation from Staroselsky Moch peatland, Russia. The Holocene 26(2): 314 – 326.

Pichrtova, M., Arc, E., Stoggl, W., Kranner, I., Hajek, T., Hackl, H. and Holzinger, A. (2016). Formation of lipid bodies and changes in fatty acid composition upon pre-akinete formation in Arctic and Antarctic *Zygnema* (Zygnematophyceae, Streptophyta) strains. FEMS Microbiology Ecology 92(7): fiw096.

Pojar, J. and MacKinnon, A. (1994). Plants of Coastal British Columbia. B.C. Ministry of Forests and Lone Pine Publishing, Vancouver, British Columbia. 527p.

Qin, Y. and Xie, S. (2011). Moss-dwelling testate amoebae and their community in Dajiuhu peatland of Shennongjia Mountains, China. Journal of Freshwater Ecology 26(1): 3-9.

R Core Team (2017). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria (version 3.4.3.). Available at: http://www.R-project.org/.

Reimer, P. J., Bard, E., Bayliss, A., Beck, J. W., Blackwell, P. G., Ramsey, C. B., Buck, C. E., Cheng, H Edwards, R. L., Friedrich, M., Grootes, P. M., Guilderson, T. P., Haflidason, H., Hajdas, I., Hatté, C., Heaton, T. J., Hoffmann, D. L., Hogg, A. G., Hughen, K. A., Kaiser, K. F., Kromer, B., Manning, S. W., Niu, M., Reimer, R. W., Richards, D. A., Scott, E. M., Southon, J. R., Staff, R. A., Turney, C. S. M. and van der Plicht, J. (2013). Intcal13 and marine13 radiocarbon age calibration curves 0–50,000 years cal BP. Radiocarbon 55(4): 1869-1887.

Richard, P. (1970). Atlas pollinique des arbres et de quelques arbustes indigènes du Québec. Le Naturaliste Canadien 97: 241-306.

Roulet, N. T. (2000). Peatlands, carbon storage, greenhouse gases, and the Kyoto Protocol: Prospects and significance for Canada. Wetlands 20: 605-615.

Round, F. E., Crawford, R. M. and Mann, D. G. (1990). The Diatoms: Biology and Morphology of the Genera. Cambridge University Press, Cambridge. 747p.

Ruppel, M., Väliranta, M., Virtanen, T. and Korhola, A. (2013). Postglacial spatiotemporal peatland initiation and lateral expansion dynamics in North America and northern Europe. The Holocene 23(11): 1596 –1606.

Rydin, H. and Jeglum, J. K. (2013). The Biology of Peatlands. Second edition. Oxford University Press, New York. 432p.

Sanborn, P. and Jull, T. (2008). The timing of peatland initiation in east-central British Columbia: A first look. Natural Resources and Environmental Studies Institute Research Extension Note No. 2, University of Northern British Columbia, Prince George, Canada.

Shiller, J. A., Finkelstein, S. A. and Cowling, S. A. (2014). Relative importance of climatic and autogenic controls on Holocene carbon accumulation in a temperate bog in southern Ontario, Canada. The Holocene 24(9): 1105-1116.

Smith, L. C., MacDonald, G. M., Velichko, A. A., Beilman, D. W., Borisova, O. K., Frey, K. E., Kremenetski, K. V. and Sheng, Y. (2004). Siberian peatlands a net carbon sink and global methane source since the early Holocene. Science 303: 353 – 356.

Squeo, F. A., Warner, B. G., Aravena, R. and Espinoza, D. (2006). Bofedales: High altitude peatlands of the Central Andes. Revista Chilena De Historia Natural 79(2): 245-255.

Stewart, J. (2018). Developmental history of a mid-elevation fen on central Vancouver Island. B.Sc. Thesis. Department of Biology, University of Victoria. 30p.

Swindles, G. T., Amesbury, M. J., Turner, T. E., Carrivick, J. L., Woulds, C., Raby, C., Mullan, D., Roland, T. P., Galloway, J. M., Parry, L., Kokfelt, U., Garneau, M., Charman, D. J. and Holden, J. (2015). Evaluating the use of testate amoebae for palaeohydrological reconstruction in permafrost peatlands. Palaeogeography, Palaeoclimatology, Palaeoecology 424: 111-122.

Taylor, L. S., Swindles, G. T., Morris, P. J. and Gałka, M. (2019). Ecology of peatland testate amoebae in the Alaskan continuous permafrost zone. Ecological Indicators 96:153–162.

Thompson, C. A. and Bettis III, E. A. (1994). Age and developmental history of Iowa fens. The Journal of the Iowa Academy of Science 101(3-4): 73 – 77.

Tolonen, K., Warner, B. G. and Vasander, H. (1992). Ecology of testaceans (Protozoa: Rhizopoda) in mires in southern Finland: I. Autecology. Archiv für Protistenkunde 142 (3-4): 119-138.

Turetsky, M. R., Amiro, B. D., Bosch, E. and Bhatti, J. S. (2004). Historical burn area in western Canadian peatlands and its relationship to fire weather indices. Global Biogeochemical Cycles 18: GB4014.

Turunen, C. and Turunen, J. (2003). Development history and carbon accumulation of a slope bog in oceanic British Columbia, Canada. The Holocene 13(2): 225 – 238.

van Geel, B. (1978). A paleoecological study of Holocene peat bog sections in Germany and the Netherlands based on the analysis of pollen, spores and macro- and microscopic remains of fungi, algae, cormophytes and animals. Review of Palaeobotany and Palynology 25: 1-120.

van Geel, B., Bohncke, S. J. P. and Dee, H. (1981). A palaeoecological study of an upper Late Glacial and Holocene sequence from "De Borchert", The Netherlands. Review of Palaeobotany and Palynology 31: 367 – 448.

Warner, B. G. and Asada, T. (2006). Biological diversity of peatlands in Canada. Aquatic Science 68: 240-253.

Warner, B. G., Clague, J. J. and Mathewes, R. W. (1984). Geology and paleoecology of a mid-Wisconsin peat from the Queen Charlotte Islands, British Columbia, Canada. Quaternary Research 21: 337-350.

Whitlock, C. and Larsen, C. (2001). Charcoal as a fire proxy. In: Smol, J. P., Birks, H. J. B. and Last, W. M. (eds.), Tracking Environmental Changes Using Lake Sediments, vol. 3. Terrestrial, Algal and Siliceous Indicators. Kluwer Academic Publisher, Dordrecht, The Netherlands. pp. 75-97.

Wieder, R. K. and Vitt, D. H. (Eds.). (2006). Boreal Peatland Ecosystems. Ecological Studies, Vol. 188. Berlin, Heidelberg: Springer-Verlag. 435p.

Williams, J. W., Shuman, B. N., Webb, N., Bartlein, P. J. and Leduc, P. L. (2004). Late-Quaternary vegetation dynamics in North America: Scaling from taxa to biomes. Ecological Monographs 74(2): 309-334.

Yeloff, D., Charman, D., and van Geel, B. and Mauquoy, D. (2007). Reconstruction of hydrology, vegetation and past climate change in bogs using fungal microfossils. Review of Palaeobotany and Palynology 146: 102 – 145.

Yu, Z., Loisel, J., Brosseau, D. P., Beilman, D. W. and Hunt, S. J. (2010). Global peatland dynamics since the Last Glacial Maximum. Geophysical Research Letters 37: L13402.

Yu, Z., Vitt, D. H. and Wieder, R. K. (2014). Continental fens in western Canada as effective carbon sinks during the Holocene. The Holocene 24(9): 1090 – 1104.

APPENDIX

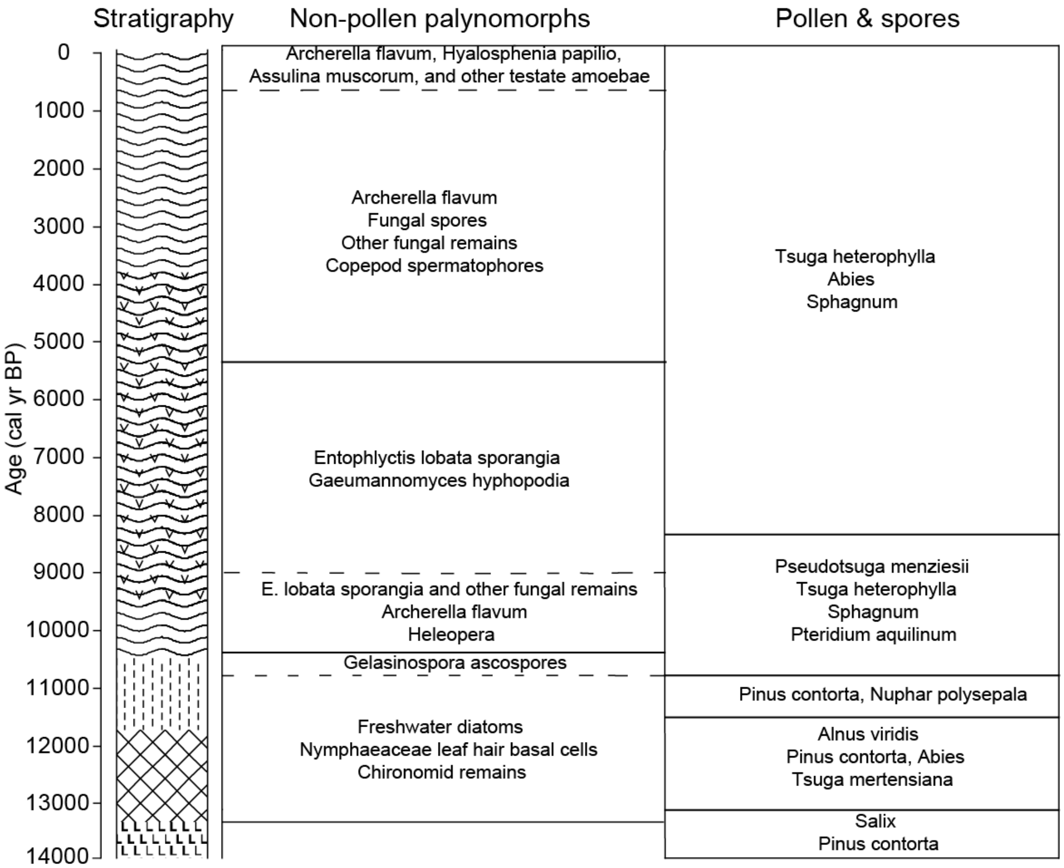

Figure A1: Summary diagram comparing stratigraphy, and non-pollen palynomorph and pollen and spore zones from Anderson Fen. See Figure 9 for stratigraphy legend.

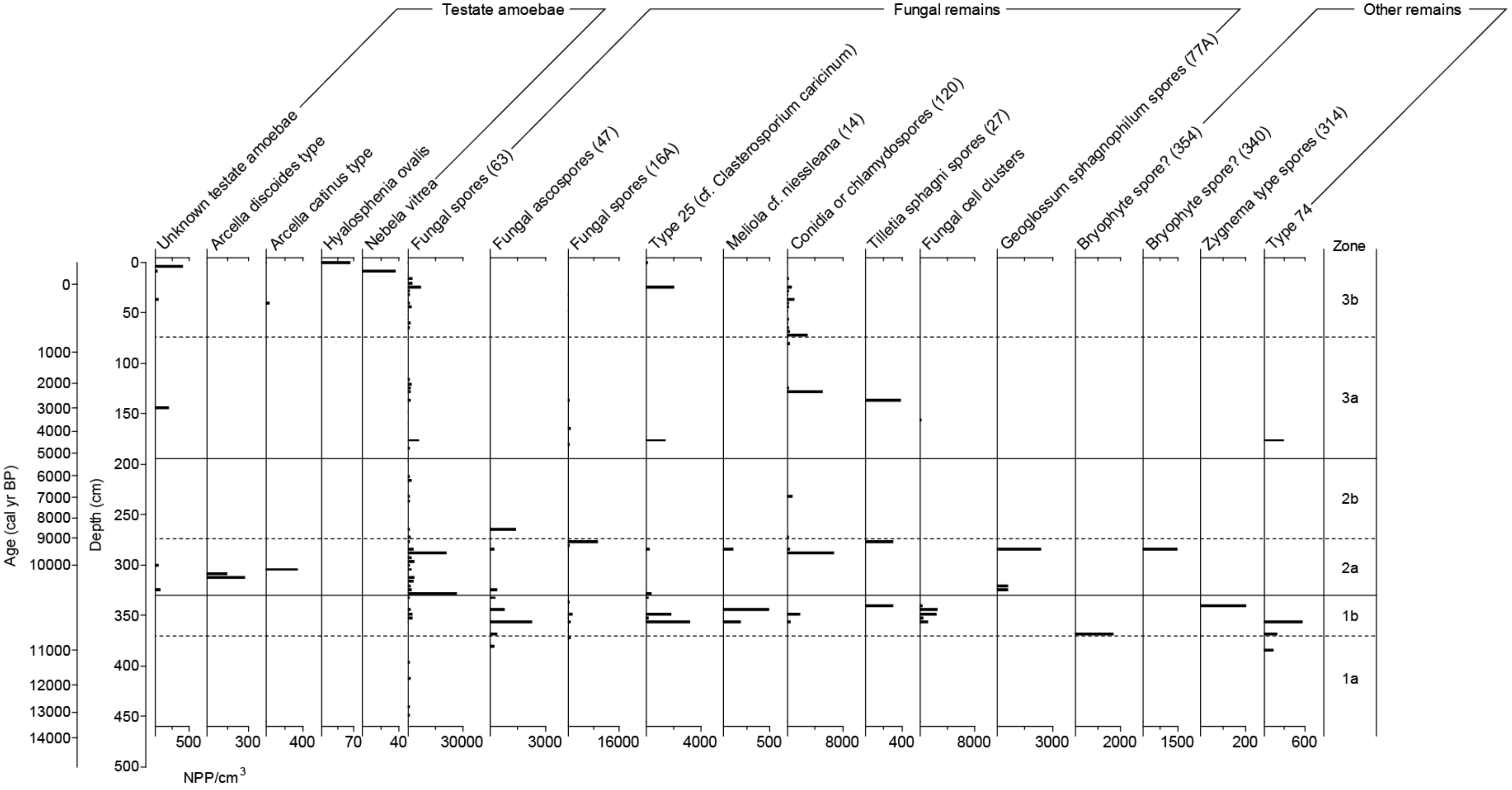

Figure A2: Concentrations of infrequent testate amoebae, fungal, and other non-pollen remains at Anderson Fen. Number in brackets refer to NPP types (van Geel, 1978; van Geel et al., 1981). Note changes on the x-axes scale.

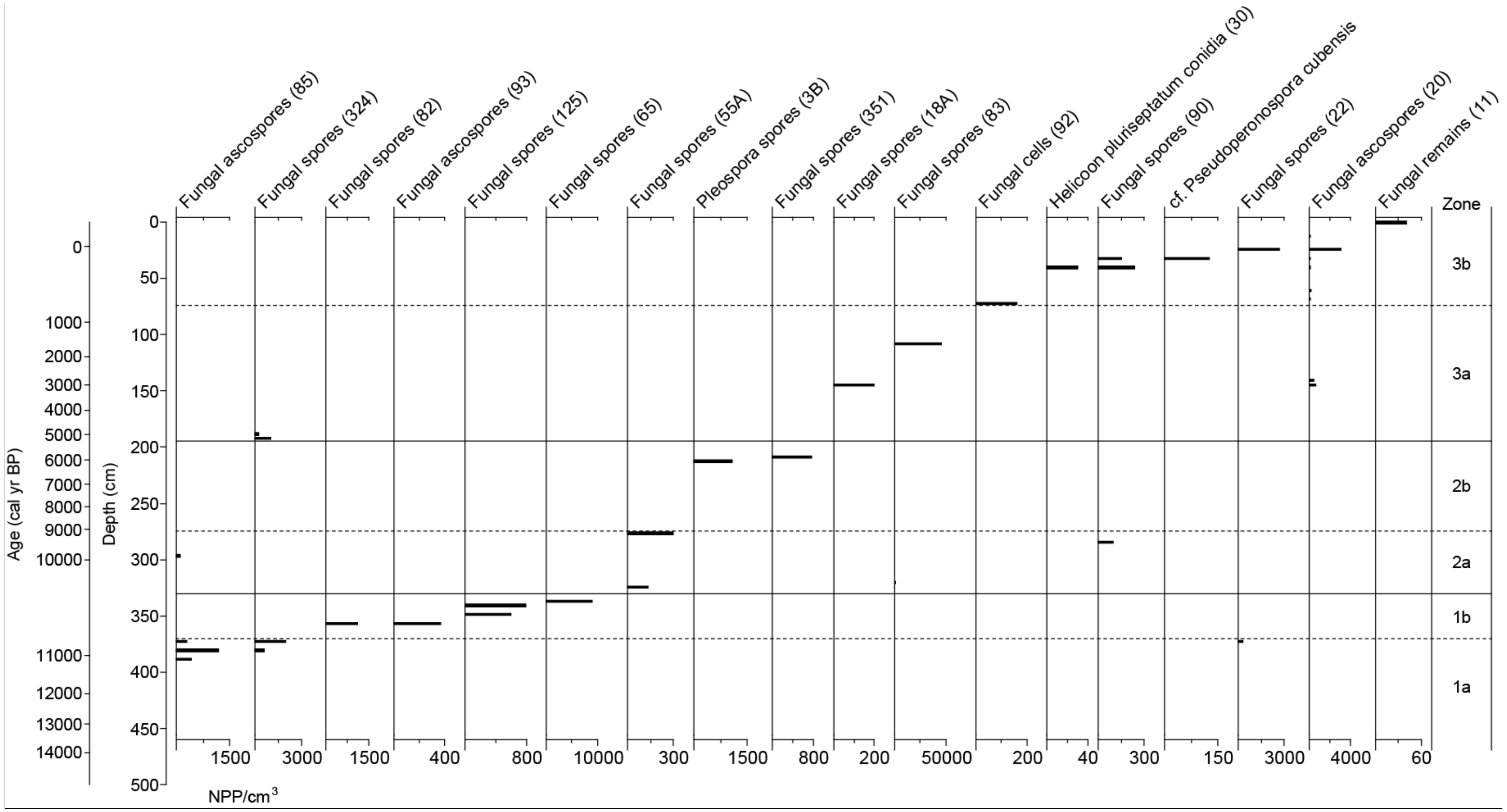

Figure A3: Concentrations of other infrequent fungal remains at Anderson Fen. Number in brackets refer to NPP types (van Geel, 1978; van Geel et al., 1981). Note changes on the x-axes scale.

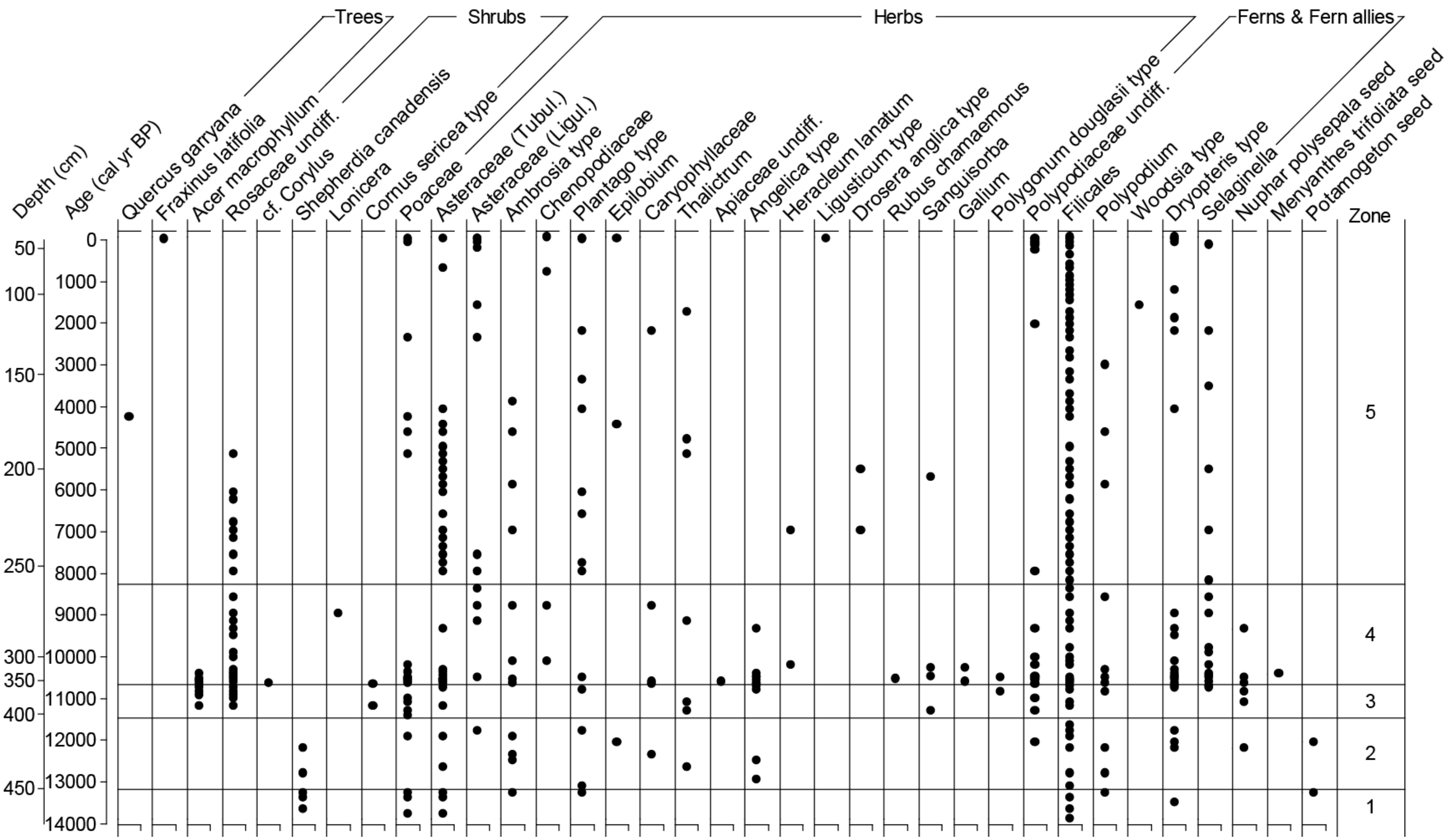

Figure A4: Infrequent pollen and spores at Anderson Fen. Also shown are seeds recovered by T. Lacourse. Circles indicate presence of each taxon.