LAKEHEAD UNIVERSITY
DEPARTMENT OF GEOGRAPHY AND THE ENVIRONMENT

The influence of water table fluctuation on hydrarch succession in two subarctic peatlands in Eastern James Bay, Québec

BY

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Submitted in partial fulfillment of the degree of
MASTERS OF ENVIRONMENTAL STUDIES
NORTHERN ENVIRONMENTS AND CULTURES

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Abstract

Northern peatlands contain close to one-third of the world's soil carbon and changes to their ecology and hydrology play a major role in the fate of these carbon stocks and the direction of their climate feedbacks. Recent research has largely focused on modern controls on peatland development and only few studies have explored the long-term (millennial scale) synergies between peatland hydrology and ecological succession. In this study, I use two peat cores from eastern James Bay (Québec) to investigate the interaction between peatland ecology (hydrarch succession) and hydrology while considering both allogenic and autogenic drivers of peatland development. The James Bay region provides an ideal location for this study as the postglacial retreat of the vast Laurentide Ice Sheet has resulted in a unique land uplift phenomenon. This process is called glacio-isostatic rebound and has been ongoing for the last ~7000 years. One of the main consequences of glacio-isotatic uplift is rapid marine regression and the creation of a landscape gradient of increasing age (chronosequence), from the coastline to the interior, that features varying stages of peatland development. In my investigation, I use a suite of palaeoecological proxies (testate-amoeba, C/N ratios, and AMS carbon-14 chronostratigraphy) to reconstruct changes in peatland water table depth through time. This hydrological reconstruction was then compared to the reconstruction of wetland community change to determine how hydrology affects wetland successional changes (hydroseres) through time. My results indicate a nuanced role of hydrology in hydrarch succession ranging from substantial, at one site (OFL) to marginal, at the other (W55). My results further suggest that local factors (topography, drainage patterns, and local base levels) largely control peatland development in this region although large-scale drivers, such as climate and isostasy, have also played a role.

Keywords: northern peatlands, hydrology, Water Table Depth, testate amoeba, transfer function, hydrarch succession, disturbance, James Bay.

Acknowledgements

I would first and foremost like to thank my supervisor, Dr. Florin Pendea, for all of the encouragement, support, and faith he has shown throughout my study. I am grateful for being offered the opportunity to conduct this research study on sediment cores collected from James Bay by Dr. Pendea. This study could not have been completed without his prior knowledge of this area and the study sites. This experience has been an incredibly long road with many academic and personal struggles along the way, which at times brought me to the verge of giving up. Through the low times and the high, the laughter, and many tears, Dr. Pendea did not waver in his support. Though I am sure many times there was thought that finishing this thesis would be impossible, Dr. Pendea did not give up on me and I truly thank him for that. I do not know that anyone else would have continued this long journey with me after so very many setbacks. I cannot be more grateful.

Thank you to Dr. Rosario Turvey and Dr. Adam Cornwell my internal committee advisors, and Dr. Alwynne Beaudoin my external examiner; I appreciate the time you have taken from your busy lives to read and provide constructive criticism, insight, and guidance to this thesis. Your contribution is greatly appreciated.

An extended thank you to Dr. Robert K. Booth who transformed my raw data using his transfer functions for testate amoebae in peatlands of North America. This provided me with the very valuable Water-Table-Depth (WTD) levels used in this thesis for hydrological reconstructions of the two peat cores. This thesis could not have been written in nearly as full context without the data analysis provided by Dr. Booth. Thank you for devoting some of your valuable time and expertise to assist me in my research.

I would also very much like to thank Dr. Victoria TeBrugge, who I consider a great friend and mentor. Vicki was always around to help problem solve with research equipment, materials, space (we all know the feeling of tight spaces in Orillia), any general laboratory issues, and to always offer a kind word or two of encouragement. Though never obliged, Vicki always showed great interest and excitement about my work and wished me good luck during many months of long hours spent at the microscope. I will not forget all of your support and encouragement.

To my many fellow grad students at the Orillia campus including Kristen Tilotta, Amanda Grant, Kayla Snyder, and others unnamed here; thank you for the motivation, study breaks, brain storming, organizational skills, and hard work ethic I gained from spending time with all of you. To Kristen Tilotta in particular, thank you for those long shared lab sessions learning to identify testate amoebae, and general long discussions on our research. I certainly appreciated your companionship.

Last, but not least, I would like to thank my loving family. Their encouragement and support motivated me to forage on in those dark moments when quitting seemed the best and only option.

I gave this thesis a large part of myself, but it also took a lot from all of you I have mentioned and others I may have forgotten here. So I would like to say a very large thank you to all of you, I am forever grateful. Whatever role you played, large or small; I could not have completed this without you.

Contents

Chapter 1) Introduction

1.1 Background

The James Bay region consists of a vast boreal forest ecosystem, within which, peatlands cover 25-90% of the landscape (Glaser et al., 2004; Turetsky et al., 2007; Pendea, 2011). These peatland ecosystems sequester carbon in the form of peat under cool temperatures and excess moisture (Gorham, 1991; Halsey et al., 2000; Mitsch & Gosselink, 2007). In the Hudson-James Bay Lowlands, peat accumulation started soon after the last glacial retreat ~ 7000 cal yr BP and has resulted in the formation of one of the largest peat basins in the world (Gorham, 1991; Glaser et al., 2004; Pendea, 2011).

The ability peatlands have to sequester carbon through photosynthesis means that they play a major role in the removal and moderation of atmospheric carbon dioxide concentrations – a powerful greenhouse gas (Holden, 2005). On a global scale, northern peatlands contain close to one-third of the total soil carbon. The controls on carbon release and storage in soils of northern peatlands are still not well understood (Moore & Knowles, 1989; Gorham, 1991; Yu, 2006; Holmquist & MacDonald, 2014). Authors such as Moore & Knowles (1989), Blodau (2002), Holden (2005), Yu (2006), and Hargan et al. (2015) agree that local factors (ecology, hydrology, ad geochemical make-up) affecting peatland development must be well understood in order to predict future changes and feedbacks to climate change. Changes to these local factors have the potential to disrupt the existing carbon stocks and further induce feedbacks to the climate system. In particular, fluctuations in peatland water table levels, or hydrology is directly connected to gas diffusion redox rates, nutrient availability, and species composition. The hydrologic conditions are also important in the ecological succession and carbon sequestration and release processes within the northern peatlands (Holden, 2005; Yu, 2006).

Recent research has largely focused on modern controls on peatland development and carbon cycle, few studies have explored the possible synergies between peatland hydrology and ecological succession. In this study, I investigate how changes in peatland hydrology affected the development of two James Bay peatlands the last ~7000 years. The effect of changing hydrologic conditions is fundamental to understanding peatland development and decay (Moore & Knowles, 1989; Holden, 2005; Yu, 2006; Holmquist & MacDonald, 2014). How hydrology in particular affects the successional ecology of northern peatlands on a local level is essential to understanding how these ecosystems will respond to environmental changes and provide feedback to the global climate system (Holden, 2005; Yu, 2006).

The James Bay region is an ideal area for this research, the postglacial retreat of the Laurentide Ice Sheet has resulted in a dramatic glacio-isostatic rebound process ongoing for the past ~7000 years (Glaser et al., 2004; Pendea et al., 2010). This process has continuously modified the regional hydrology and vegetation development. For instance, glacio-isostatic rebound has created a landscape gradient of increasing age (chronosequence) from the coastline to the interior across which peatlands exist in various stages of development (Glaser et al., 2004; Pendea, 2011). My research uses two sediment cores sampled near the town of Wemindji in eastern James Bay, Québec, to track peatland hydrology changes through time and relate these to ecological reconstructions of wetland community change.

1.2 Research Questions

This study investigates the role of hydrology in northern peatland development. I specifically aim to answer the following questions:

1) Do changes in hydrology coincide with major shifts in peatland development?

2) Do changes in hydrology drive hydrarch succession in these peatlands?

3) What are the potential causes behind changes to peatland water table levels?

1.3 Aim and Objectives

To answer the research questions my study looks at two subarctic peatlands of similar age but different in their developmental history and seeks to determine whether major shifts in peatland development were influenced by changes to the hydrology. To investigate the dynamic of this relationship, I have three main objectives:

1) To develop an age-depth model for each peatland based on AMS carbon-14 chronology,

2) To reconstruct peatland Water-Table-Depth (WTD) variations at millennial scale through a testate amoeba-based transfer function, and

3) To compare the timing and nature of major palaeohydrological changes to the timing and nature of local hydroseral succession reconstructed by Pendea (2011) based on palynomorphs and carbon/nitrogen ratios.

The following chapter (2) will provide an overview of the existing literature regarding northern peatland development and hydrology, as well as the relevant literature related to carbon sequestration and landscape disturbance. Chapter 3 provides detail on the study region. Chapter 4 identifies the applied methods and data analyses. Results are presented in Chapter 5, followed by the discussion in chapter 6. The final Chapter includes the conclusion of the study, suggestions for future research, and limitations of the study.

Note: The original research in this thesis comprises the testate amoebae records from two cores, and the inferred wetland hydrology. These records are compared with pollen records from the same cores. The pollen work and associated statistical analysis was done by Pendea (2011). Permission has been granted to summarize this pollen work herein to enable the reader to directly compare the two data sets derived from different proxy indicators.

Chapter 2) Literature Review

2.1 Northern Peatlands at a glance

Wetlands, mires and peatlands are the three main terms used in current literature to describe the transitional habitats that exist between uplands and water where organic matter tends to accumulate in poorly-drained waterlogged conditions (Rydin et al., 2006). There is considerable overlap between the terms, though they are defined somewhat differently. The broadest concept is that of wetlands which includes shore, marsh, swamp, fen, and bog ecosystems that are characterized by a water table near the ground surface, poorly aerated substrate, and inundation that lasts for such a large part of the year that the dominant vegetation and organisms are those which exist in wet conditions (Rydin et al., 2006). The term mire is used to describe wet terrain dominated by living peat-forming plants. Peat is defined by Rydin et al. (2006) as the remains of plant and animal constituents accumulating under more or less water-saturated conditions due to incomplete decomposition. Peat is the organic material that has formed in place as a result of anoxic conditions, low decomposability of the plant material, and other complex causes (Rydin et al., 2006). Peatland is the term used to encompass peat-covered terrain and usually a minimum peat depth is required for a site to be classified as a peatland, in many countries and in the peatland statistics of the International Mire Conservation Group it is 30 cm (Joosten & Clarke, 2002). The bog and fen classifications are the most frequent types of wetlands found in the northern hemisphere and are collectively referred to as the northern peatlands (Mitsch & Gosselink, 2000).

The terms peatland and mire are considered narrower concepts than wetland because not all wetlands have conditions that allow peat to accumulate (Rydin et al., 2006). The term peatland is often used in forestry and land management which uses the peat depth limit for classification, this term is also more commonly used in North America. Mire is a term most commonly used in botanical and ecological investigations of the vegetation types or the process of peat formation. The term mire is more commonly used in Scandinavia but the term is problematic as the definition of the term uses the concept ‘peat-forming plants’ which is ambiguous. Even if some plants more commonly give rise to peat than others, peat formation is a process that can befall most plant materials (Rydin et al., 2006). For the purposes of this study, the terms wetland, peatland, and northern peatland will be used.

The mass accumulation of peat and formation of peatlands occurs geographically in cold temperate climates with high humidity. These conditions are achieved mostly in the north-boreal areas of North America and Eurasia, where precipitation exceeds evapotranspiration and moisture accumulates in soils resulting in the formation of what are known as the northern peatlands. These northern peatlands can be classified into three general types based on chemical and hydrologic conditions. These are the minerotrophic fens, transition or poor-fens, and ombrotrophic bogs (Mitsch & Gosselink, 2007).

Minerotrophic fens rely on the groundwater supply for nutrients and are typically nutrient rich with high microbial activity, a moderate pH level, and fast decomposition rates. These ecosystems experience low deposition in the form of peat. Minerotrophic fens are open wetland systems that receive some drainage from the surrounding mineral soils; these types of peatlands often support graminoid communities composed of grasses, sedges, or reeds (Mitsch & Gosselink, 2007).

In contrast to minerotrophic fens, ombrotrophic bogs are highly dependent on precipitation for nutrients and water which results in a low nutrient environment. The separation of this ecosystem from the mineral bearing groundwater results in lower pH and mineral concentration which supports the growth of acidophilic *Sphagnum* and other moss species (Mitsch & Gosselink, 2007). The nutrient poor, acidic environment provides little support for microbial activity and the result is the deposition of partially decomposed organic material in the form of peat (Holden, 2005).

The poor fen type of peatland is a transition ecosystem between the two previous types, which is considered to be neither nutrient poor nor nutrient rich but a balance between the two with a pH that tends to be lower than that of a true fen and higher than that of an ombrotrophic bog (Mitsch & Gosselink, 2007). Poor-fen ecosystems may receive their nutrients and moisture through a combination of precipitation and a connection to the groundwater supply which allows for the development of this transitional situation that is neither a true fen or bog but a stage somewhere in between both (Mitsch & Gosselink, 2007).

For the purposes of this study there is a fourth type of wetland ecosystem discussed called salt marsh or tidal marsh. This wetland type is discussed here because the study region was submerged by the Tyrrell Sea and the peatland development was initiated by a tidal marsh phase during marine regression. Studies by both Glaser et al. (2004) and Pendea et al. (2010) investigated the relationship between landscape changes and uplift in James Bay. Glaser et al. (2004) found that the combination of land uplift and marine regression resulted in the replacement of tidal marshes by a swamp forest (fen), followed by a forested bog, and finally a non-forested bog in all three of the selected sampling sites.

2.2 Peatland coverage and extent – Northern environments and the globe

The wetlands distributed in the cold temperate climates of high humidity in the northern hemisphere across Canada, Alaska, Europe, and Russia collectively are referred to as northern peatlands (Mitsch & Gosselink, 2000). Major areas of peatland coverage in this region include the Hudson Bay lowlands in Canada, the Fennoscandian Shield in northern Europe, and the western Siberian lowlands. The Hudson and James Bay lowlands comprise an extensive peatland area covering parts of northern Ontario, eastern Quebec, Manitoba, and the eastern part of the Northwest Territories, which is part of the vast subarctic wetland region of Canada. Canada has approximately 1.1 – 1.3 million hectares of peatlands, which collectively represent one of the largest peat resources in the world (Mitsch & Gosselink, 2000; Dobson & Frid, 2009).

Most of the world's wetlands are found in both the boreal and tropical regions with the least amount being found in temperate zones (Mitsch & Gosselink, 2007). It is estimated that half of all natural freshwater wetlands are in an almost continuous expanse across Canada, Alaska, and Russia (Dobson & Frid, 2009). Wetlands existing as subtropical, tropical, or southern peatlands have patterns and processes which differ to some degree from that of northern peatlands. Regardless, wetlands do not form a distinct biome therefore their extent cannot be determined based on any climatic region or type (Dobson & Frid, 2009).

According to Dobson & Frid (2009), calculation of the world's extent of wetland coverage is difficult because wetlands are scattered in various climatic regions and classification varies from author to author and country to country. Rydin et al. (2006) have also stated that the accuracy of the land or soil survey information from many countries of the world is highly variable but global estimates on peatland coverage have been increasing steadily over the last century as more and better inventory results have been made available (especially in the tropics). The Global Peatland Database of the International Mire Conservation Group (IMCG) has made one of the best attempts to compile data on peatland surface estimates. The database definition of a peatland refers to areas with a minimum of 30cm of peat thickness which means many artic and alpine wetland areas with shallower peat layers have been excluded from the total estimate by the IMCG. According to the data from the IMCG the total peatland area estimated was 4.16 million km^2 or approximately 3% of the earth's total land surface (Rydin et al., 2006). A more recent estimate was given by Dobson & Frid (2009) which estimated the global wetland coverage at approximately 8.5 million km^2 or about 6% of the world's land surface. The large varying estimates of wetland coverage show the lack of accurate evidence and difficulty of compiling data with varying definitions. The Dobson & Frid (2009) estimate is more recent however; it does not specify a minimum thickness of peat for classifying a peatland and instead estimates total global wetland surface areas. It is therefore possible the Dobson & Frid (2009) estimate is high due to the inclusion of areas with shallower peat layers and many other areas that fit the broader classification of 'wetland' that were excluded from Rydin et al. (2006). It is also possible that more recent and accurate data sets on wetland coverage have been created and used for the estimate from Dobson & Frid (2009). Whatever the case, exact estimates on total wetland surface area (or northern peatland coverage) are currently unavailable as the current methods used for defining wetlands and peatlands are ambiguous and allow for various interpretations which results in major variations of total surface area estimates.

2.3 Peatland development, productivity, and nutrient status

There are two main requirements for the development of peatlands. The first requirement is for excess moisture conditions, often in the form where precipitation exceeds evapotranspiration leading to conditions of moisture accumulation (Mitsch & Gosselink, 2007). The origin of moisture accumulation is an important factor controlling the composition of peatland vegetation (Sjörs, 1959). All peatlands receive a portion of their water in the form of precipitation; for some peatlands such as the ombrotrophic bogs, this is the only form of moisture

(Sjörs, 1959). In the absence of excess precipitation wetlands may develop in areas with a lack of subterraneous drainage, an influx of groundwater, or runoff. The second requirement for peat formation is biomass accumulation due to low decomposition under conditions of cold temperatures and slow rates of microbial activity (Mitsch & Gosselink, 2007). Primary productivity is generally low in northern peatlands compared to other ecosystems due to the cold environment, low pH, low nutrients, and low minerals. The result is reduced decomposition and the formation of peat (Mitsch & Gosselink, 2007).

The way in which a peatland receives its moisture is an important factor which controls the composition of peatland vegetation as well as productivity (Sjörs, 1959; Mitsch & Gosselink, 2007). Ombrotrophic bogs receive their moisture from precipitation only, which leads to strong acidic reactions of both water and peat. This acidification process occurs mainly due to the lack of nutrients and mineral salts from precipitation (Mitsch & Gosselink, 2007). Acidic conditions allow for development of highly specialized vegetation that is acidophilous, has few species of plants, and lower levels of productivity. The ombrotrophic bog vegetation consists mainly of mosses and some species of ericaceous shrubs (Mitsch & Gosselink, 2007). The other types of peatlands - the minerotrophic fen and the transition (poor) fen receive varying quantities of water from mineral soils (groundwater) as well as precipitation (Sjörs, 1959; Mitsch & Gosselink, 2007). These wetlands are considered open systems and are usually early stages in the hydrarch succession. The access to mineral soils leads fen ecosystems to higher nutrient availability, less acidification, higher productivity, and more diverse vegetation. Depending on the extent of minerotrophic influence, fens are classified as either rich or poor (transitional) (Mitsch & Gosselink, 2007).

Aquatic marginal (tidal marshes) and seasonally dry wetlands (fens) can be nutrient-rich, where as permanently waterlogged wetlands (ombrotrophic bogs) with little input of flowing water can be very nutrient-poor (Dobson & Frid, 2009). Nitrogen is an important limiting factor on plant growth and the availability of nitrogen in a peatland can affect microbial activity and determine the overall nutrient status. The ombrotrophic bogs are subject to anaerobic denitrification due to the presence of nitrifying bacteria which can convert ammonium to nitrate, which can then be broken down and released as gaseous nitrogen by denitrifying bacteria. The presence of aerobic and anaerobic conditions in very close proximity over a large surface area enhances this process which results in a nitrogen limited environment. In nutrient-poor conditions, wetland communities typically support plant species capable of exploiting alternative sources of nitrogen. Examples include vegetation such as *Alnus* (alder) and *Myrica* (bog myrtle) in Europe and North America, which maintain a symbiotic relationship with nitrogen fixing bacteria within their root nodules as well as *Drosera* (sundew), which obtains nitrogen compounds from trapped and digested insects (Dobson & Frid, 2009).

Carbon turnover and mineralization rate per cubic centimeter of peatland soils varies due to community type and aeration status (Bridgham et al., 1998). Bridgham et al. (1998) found that differences in carbon mineralization per cubic centimeter among community types were large and showed a general increase from ombrotrophic to minerotrophic conditions but differences in total carbon turnover among community types were relatively small. Results also indicated that there was a substantial increase in nitrogen availability in minerotrophic sites. Bridgham et al. (1998) also found that soils with a high turnover rate but low total nutrient content and low bulk density have low mineralization rate per unit of volume, while soils with a lower turnover rate, lower nutrients and high bulk density will have high rates of mineralization.

Ratios of carbon to nitrogen (C/N) reflect the composition of the dominant source of organic matter (Wilson et al., 2005). Carbon/nitrogen ratios have been used by several researchers such as Bridgham, et al. (1998), Bedford et al. (1999), Wilson et al. (2005), and Pendea (2011) as a proxy to indicate palaeoenvironmental changes. Carbon/nitrogen ratio values provide information about the source and amount of organic matter entering the ecosystem and therefore vegetation changes through time (Wilson, 2005). Pendea (2011) used carbon/nitrogen ratios to confirm transitions from tidal marsh to fen to bog as suggested by the pollen stratigraphy in the study. Higher carbon/nitrogen ratio values indicate nutrient-poor conditions whereas lower values indicate a more nutrient-rich minerotrophic status (Pendea, 2011).

2.4 Structures within Northern Peatlands

Clymo (1984) described peat forming-systems as existing in two layers. The acrotelm, or upper layer, is aerobic, generally ranges from 10 to 50 cm-deep, and experiences high hydraulic conductivity and a relatively high rate of decay. The catotelm is the lower layer, usually thicker and anaerobic with low conductivity and generally a low rate of decay. At the base of the acrotelm, plant structure collapses as a consequence of aerobic decay and hydraulic conductivity decreases. As the material is engulfed at the water table level, peat becomes anaerobic consequently marking the beginning of the catotelm layer. The rate of peat formation is determined by the rate at which material is input into the catotelm. The rate at which material is input into the catotelm layer is analogous to the rate of vegetation primary productivity in the acrotelm layer (Clymo, 1984). Peat layers are formed through time as each year’s cohort of litter undergoes aerobic decay and is buried under the weight of younger material until eventually the main plant structure collapses. The decrease in the size of pore spaces reduces the hydraulic conductivity of the peat. This leads to the dispersion of precipitation through the thinner acrotelm layer while lateral seepage through the denser catotelm layer is impeded (Belyea & Clymo, 2001).

Belyea & Clymo (2001) describe peat formation as occurring at the small-scale of individual hummock or hollow micromorphology through production, decomposition, and compression of organic matter derived from *Sphagnum* and vascular plants. Distinct microforms such as hummocks and hollows are formed in dry mound areas (hummock) or wet depressions areas such as pools (hollow) and are common features of northern peatlands. Belyea & Baird (2006) describe peatland microforms (hummocks and hollows) as fudamental component parts of peatland ecosystems. There are four distinctive features or "complex adaptive systems" that result in the formation of these microforms. These "complex adaptive systems" are: spatial heterogeneity, localized flows, self-organizing structure, and non-linearity. These complex adaptive systems result in the formation of microforms that differ in functional properties and create unequal flows of water and nutrients between adjacent microforms and peat layers. The persistence of these unequal flows is what favors the expansion of some microforms and the contraction of others (Belyea & Baird, 2006).

2.5 Hydrarch successional theories

Hydrarch, or wetland successional theory, explains how the orderly sequence of development occurs within peatland or 'wetland' communities. In the first half of the 20th century two main theories arose to describe the transition of plant communities (Mitsch & Gosselink, 2007). In early studies theorists struggled to describe long term changes due to difficulties involved in tracking vegetation development over long timescales (Hughes & Dumayne-Peaty, 2002). The first theory was defined by Clements in 1916 and applied by W. H. Persall in 1920 (Mitsch & Gosselink, 2007). This theory (also known as Clementsian theory) was founded on the principle that a variation in space could be substituted for changes through time (Hughes & Dumayne-Peaty, 2002). This theory was termed autogenic successional theory and can be described as ‘self-driven’ based on the following three main concepts. First, vegetation occurs in recognizable and characteristic communities. Second, community changes through time are brought about by the community members and changes are therefore ‘self’ or autogenically driven. Third, all changes are directed toward a ‘climax’ stable ecosystem (Mitsch & Gosselink, 2007). This theory was very influential during the first half of the 20th century.

The second contrasting theory proposed to describe hydrarch succession was termed the allogenic successional theory (also known as Gleasonian theory) (Mitsch & Gosselink, 2007). This theory excludes the idea of a ‘climax’ stage of succession and considers all stages to be part of the sequential replacement of different vegetation communities (Hughes & Dumayne-Peaty, 2002). This theory is based on several main concepts. The first, that succession is abiotically driven and the distribution of a species is governed by its environment. The second, states that each species adapts differently and no two species occupy the same exact niche. The third concept states that the vegetation replacement sequence is influenced by the chance occurrence of propagules at a site. This results in the existence of a continuum of overlapping set of species, which each respond subtly different to varying environmental cues (Mitsch & Gosselink, 2007). Lastly, allogenic successional theory claims that abiotic environmental factors often overwhelm biotic forces in wetlands and therefore the ecosystems change but without direction toward any particular stable state or ‘climax’ (Mitsch & Gosselink, 2007).

Modern palaeoecological techniques have enabled researchers to re-evaluate theories relating to long-term vegetation change using detailed archives of past biodiversity deposited in wetland ecosystems (Hughes & Dumayne-Peaty, 2002). In 1970, Walker used field stratigraphy and palynological evidence and demonstrated that peatland succession could experience reversals and skipped stages, an ombrotrophic bog was the most common end point in most sequences described (Walker, 1970). Studies from Klinger & Short (1996), Hughes & Dumayne-Peaty (2002) and Pendea (2011) have demonstrated that reversals in succession can occur and have suggested that the idea of the 'climax' ombrotrophic bog be reconsidered. Hughes & Dumayne-Peaty (2002) provide evidence demonstrating two contrasting pathways resulting in ombrotrophy; they also showed evidence of succession reversals and suggested that both allogenic and autogenic factors are important in determining successional direction. Mitsch & Gosselink (2007) question whether the idea of regional climax is appropriate. Beaulieu-Audy et al. (2009) conducted a palaeoecological reconstruction of Canadian boreal peatlands and found evidence of succession from salt marsh to fen to bog. The study suggests that the transitions occurred mainly due to autogenic processes, but factors such as isostatic uplift, local topography, and climatic conditions may have influenced the speed of succession (Beaulieu-Audy et al., 2009). Sjörs (1980) asserts that all biological systems must be open and unstable, life is a process and nothing would happen if living systems were closed and stable. All natural systems especially ones referred to as 'climaxes' are not self-stabilizing, they undergo short-term disturbances and there is no evidence they return to their former exact composition. Often categories of allogenic and autogenic succession are difficult to separate but under adverse conditions (such as those existing in higher alpine belts or the arctic) succession is predominantly environmentally conditioned or allogenically driven (Sjörs, 1980).

Hughes & Dumayne-Peaty (2002) consider it unwise to use the term succession to imply any particular process or mechanism, especially in the context of millennial-scale change. The term succession can be used instead as a descriptive term simply meaning the sequential replacement of vegetation communities. Loisel & Garneau (2010) found that ombrotrophy was established under both dry conditions as well as wet providing evidence supporting the development of ombrotrophy through different hydrology conditions. Results from Loisel & Garneau (2010) suggest the strong influence of local allogenic forces drove the hydroseral changes in this study.

The evidence provided lends to the conclusion that both autogenic and allogenic factors act to change wetland vegetation from one type of peatland to another and each stage is only semi-permanent; bogs may reverse to fens and alternative successional pathways to a linear autogenic model exist.

2.6 The climate context – a postglacial climate history of the James Bay region

Evidence provided by numerous marine and terrestrial archives across the northern hemisphere (e.g., Webb et al., 1987; Koç et al., 1993; Kerwin et al., 1999; Kerwin et al., 2004; Kaufman et al., 2004) indicate that the Holocene was characterized by several climate oscillations. Most evidence supports the existence of two major climate oscillations: the Mid Holocene Warm Period (MHWP), between 7000 and 4000 cal yr BP, and the late Holocene cooling Neoglaciation, between 4000 cal yr BP and present (*sensu* Kerwin et al., 2004, Denton & Porter, 1970). Some studies have also provided evidence for two more recent and shorter duration climate oscillations known as the Medieval Warm Period (MWP) and the Little Ice Age (LIA). The Medieval Warm Period was characterized as a period of slightly warmer temperatures occurring between 500 and 1000 cal yr BP (Keigwin, 1996; Viau et al., 2002). This atmospheric warming event was followed by the Little Ice Age, a colder period occurring between 300 – 400 cal yr BP (Keigwin, 1996; Viau et al., 2002). Most palaeoclimate reconstructions have a millennial-scale resolution and therefore, are unable to reconstruct short climate events such as MWP and LIA, however some palaeoenvironmental studies (Loisel & Garneau 2010; Booth et al., 2012; Lamarre et al., 2012; Hargan et al, 2015) provide reconstruction evidence supporting the occurrence of these climate events. Mann et al. (2007) review of climate over the past millennia points out that the short duration MWP and LIA climate events are more likely local regional events and should not be viewed as global scale climate events.

In the James/Hudson Bay region, there is some evidence for the mid Holocene warming and subsequent Neoglacial cooling (Gajewski et al., 1993), these changes were minor and considerably delayed in this region in comparison to recorded global trends (Lavoie & Arseneault 2001, Kerwin et al. 2004, Lavoie & Payette 1996). In particular, Kerwin et al. (2004) found that the warming was minimal in comparison with the rest of northeastern North America and that, in the region east of the James Bay coast, the warming was even less pronounced, if it occurred at all. De Vernal & Hillaire-Marcel (2006) suggest that there is no clear early or Mid-Holocene Warm Period (or thermal optimum) recorded along the eastern Canadian margin, but rather a series of minor cooling and warming stages. With respect to the late Holocene cooling, Kerwin et al. (2004) found that in eastern James Bay cooling was delayed until 1000 cal yr BP (as opposed to 4000 – 2000 cal yr BP in other regions), short in duration (lasting only 500 years) and was minimal (-0.5°C). Early palaeoecological studies in the Hudson Bay region (McAndrews et al, 1982; Yu & McAndrews, 1994) suggest a warming period occurred between 6500 – 3000 cal yr BP, followed by a Neoglacial cooling, which occurred after 2500 cal yr BP. Klinger & Short (1996) also concluded cooling occurred at approximately 2500 cal yr BP as suggested by pollen evidence.

O’Reilly (2011) investigated palaeoecological and carbon accumulation dynamics of the Victor fen in the Hudson Bay lowlands. The climate reconstruction from this study found predominantly low precipitation values between 6775 – 3000 cal yr BP and low temperature values beginning between 3500 – 2800 cal yr BP.

Bunbury et al. (2012) investigating Holocene hydro-climatic change in the Attawapiskat River watershed in the Hudson Bay Lowlands found no evidence of major changes to temperature. The data suggest a possibility of maximum Holocene temperatures, between 6500 – 3000 cal yr BP, and a Neoglacial cooling after 2000 cal yr BP. Specifically their data supports the possibility of warmer temperatures at 3400 cal yr BP as indicated by low water table positions (Bunbury et al., 2012).

Similar to McAndrews et al. (1982) and Bunbury et al. (2012), O’Reilly et al. (2014) reconstructed climate in the James Bay region and found indications of an increase in precipitation after 2400 cal yr BP. There were no major changes to the temperature recorded at that time (O’Reilly et al., 2014).

Holmquist & MacDonald (2014) reconstructed peatland water table depths from areas in central and northern Ontario and compared this to the regional evidence for the Holocene Thermal Maximum (HTM) and the Mid Holocene Warm Period (MHWP). The study results support the occurrence of the HTM at 4600 cal yr BP, where a shift to dry conditions occurred followed by a return to more wet conditions after 2550 cal yr BP.

The evidence provided from various studies in the Hudson and James Bay area suggests that the Mid Holocene Warm Period took place in the region from 6500 – 3000 cal yr BP and was characterized by evidence of slightly warmer temperatures and low precipitation values.

Studies from McAndrews et al. (1982), Yu & McAndrews (1994), and Bunbury et al. (2012) provided evidence to suggest the occurrence of warming between 6500 – 3000 cal yr BP with Bunbury et al. (2012) suggesting the warmest period or Holocene Thermal Maximum (HTM) occurred around 3400 cal yr BP. A separate study from Holmquist & Macdonald (2014) provided evidence to suggest that the HTM occurred in the region around 4600 cal yr BP. Precipitation data from a study by O'Reilly (2011) coincided with this evidence showing low precipitation values also occurred between 6775 – 3000 cal yr BP.

The occurrence of the Neoglacial cooling period beginning between 2550 – 2000 cal yr BP was also supported by various studies in the Hudson and James Bay area. The Neoglaciation period was characterized by evidence of slightly cooler temperatures and increased precipitation values. Studies from McAndrews et al. (1982) and Yu & McAndrews (1994) suggest cool temperatures occurred after 2500 cal yr BP. The study by Klinger & Short (1996) found evidence to support cooler temperatures beginning around 2500 cal yr BP and results from the Bunbury et al. (2012) study suggest cool temperatures occurred at 2000 cal yr BP. Additional evidence from the study by Holmquist & MacDonald (2014) supports a return to wet conditions after 2550 cal yr BP. The precipitation data from the O'Reilly et al. (2014) study indicates an increase to precipitation levels after 2400 cal yr BP supporting the occurrence of the Neoglaciation cooling period beginning between 2550 – 2000 cal yr BP.

2.7 The role of climate in peatland development

The role of climate as a driver to peatland succession is still largely unclear. Authors are in disagreement with the level of importance and impact of climate controls on peatlands. Some researchers argue if climate was a pressing factor then peatland area would be determined based on climatic region or type, but because peatlands do not form a discrete biome they cannot be quantified based on climate regions (Mitsch & Gosselink, 2007). In particular, Klinger & Short (1996) state that the vegetation communities along a longer, more extreme, latitudinal climate gradient show considerably less variation than along a longitudinal chronosequence of land emergence, suggesting climate has little influence on peatland type formation.

In contrast to Klinger & Short (1996) and Mitsch & Gosselink (2007), authors such as Booth & Jackson (2003), Glaser et al. (2004), Beaulieu-Audy at al. (2009), Loisel & Garneau (2010), Pendea (2011), Booth et al. (2012), Bunbury et al. (2012), Lamarre et al. (2012), Holmquist & MacDonald (2014), and Hargan et al. (2015) suggest that climate is a significant driving force during late successional stages of peatland development, whereas isostatic rebound and sea level fall are important during early succession. Compared to other processes, climate variability is often slow and progressive and, therefore, qualifies as long-term allogenic disturbance usually driving slow rate-of-change in peatland communities (Pendea, 2011). The isostatic rebound and sea retreat, on the other hand, which drove the initial development of the peatland, was a short-term, allogenic disturbance producing a high rate-of-change in peatland communities. Although isostatic uplift is still ongoing, its rate has diminished considerably since the mid Holocene and thus its effects, if any, are not visible in the palaeorecords (Pendea et al., 2010).

Booth & Jackson (2003) used testate amoebae, peat humification, pollen, stomata, and plant macrofossils to reconstruct late-Holocene surface-moisture and vegetation history of a raised bog in Michigan. Results showed good correspondence to the regional water history of Lake Michigan, indicating bog hydrology and Lake Michigan water levels have been driven by changes in large scale atmospheric circulation patterns for at least the past 3500 years (Booth & Jackson, 2003).

Beaulieu-Audy et al. (2009) found that local vegetation succession and peat accumulation create a coherent regional portrait that is in agreement with climatic inferences from other palaeoenvironmental studies in northern Québec.

Loisel & Garneau (2010) carried out a palaeoecological reconstruction study based on four peat sequences collected from two peat bogs in the James Bay lowlands, Québec. The study found evidence of autogenic, site-specific influences as well as allogenic, climate influences on peatland development. Specifically, the study found two synchronous hydroclimatic changes between two different peatland study sites. These hydroclimatic changes occur at intervals that correspond with the Medieval Climate Anomaly (MCA) at 1000 cal yr BP, and the Little Ice Age (LIA) at 250 cal yr BP. The dry event corresponding to LIA was not recorded at one of the sites suggesting that this peatland site had overall wetter local conditions than the other peatland sites studied (Loisel & Garneau, 2010).

Booth et al. (2012) used proxy records of vegetation, fire, and hydrology from a forest setting to investigate the hydroclimatic variations during the Medieval Climate Anomaly during 1050 – 600 cal yr BP. They found spatial patterns of drought and forest changes to be coherent suggesting that the climate variations and vegetation responses were spatially structured. Vegetation changes were more strongly expressed in areas of pronounced drought variability. Dramatic drought-induced forest changes that occurred in the Great Lakes region during the MCA indicate that this humid region is vulnerable to persistent droughts of sufficient severity to disrupt ecosystems at a regional scale (Booth et al., 2012).

Lamarre et al. (2012) provides additional evidence for hydroclimatic variations throughout the Holocene. The study used testate amoebae to reconstruct past hydrological conditions and found observed hydroclimatic variations correspond to previous studies from northern Québec. These findings confirm the variable sensitivity of subarctic ecosystems to climate change (Lamarre et al, 2012).

Hargan at al. (2015) studied peat cores spaning 2000 – 600 cal yr BP from peatlands in the Hudson Bay Lowlands and detected a correlation between their records and the Little Ice Age. This data demonstrates the effect of climate cooling in the late Holocene.

Various studies including: Booth & Jackson, 2003; Glaser et al., 2004; Beaulieu-Audy et al., 2009; Loisel & Garneau, 2010; Pendea, 2011; Booth et al., 2012; Bunbury et al., 2012; Lamarre et al., 2012; Holmquist & MacDonald, 2014; and Hargan et al., 2015 have provided evidence of synchronous changes ocurring at the regional scale, indicating the effect of regional climate change rather than local factors. In this region, characterized by time-transgressive land surfaces, synchronous changes in peatland ecology across the region are unlikely to be autogenic. Climate variability as an allogenic driver is more likely to be responsible for these synchronous changes.

2.8 The role of hydrology in peatland development

Hydrology is the science that deals with water, its occurrence, circulation, and distribution, its physical and chemical properties; and its interrelationships with the environment including living organisms (Rydin et al., 2006). Hydrology is considered to be the most important condition influencing peatland ecology, development, functions, and processes (Sjörs, 1980; Moore & Knowles, 1989; Hughes, 2000; Holden, 2005; Rydin et al., 2006; Mitsch & Gosselink, 2007). According to Holden (2005), peatland hydrology influences gas diffusion rates, redox status, nutrient availability and cycling, and species composition and diversity. Hydrologic conditions also drive carbon sequestration and release processes and are important for water resource management, flooding, and stream water quality (Talbot at al., 2010). A study by Loisel & Garneau (2010) concluded that local-scale topographic differences may induce different sensitivity to hydroclimatic changes within a peatland and uneven peat thickness may be sufficient to induce different hydrological conditions (Loisel & Garneau, 2010).

Dobson & Frid (2009) state the abiotic environment of wetlands is dominated by the position of the water table relative to the substratum and depends on whether flooding or water-logging is a permanent or seasonal feature. The water-table determines the oxygen concentration within peat because decomposition of organic matter by microbial action depletes oxygen. Therefore rates of decomposition are significantly reduced in permanently waterlogged soil and the formation and deposition of peat begins to occur as a result (Dobson & Frid, 2009). The water table depth (WTD) is considered to be one of the most important measures relating to vegetational physiognomy, plant occurrence, and growth in northern peatlands (Rydin et al., 2006). There is a general trend of positive height relationships of vegetation forms with nutrient regime for the same water level and with different temperature regimes (Rydin et al., 2006).

Sjörs (1980) suggested that as latitude increases, patterns of northern peatlands become increasingly dependent on two external factors: hydrology and frost action. Hargan et al. (2015) suggested that freezing in peat can support the ombrotrophication of peatlands through water table drawdown.

Talbot et al. (2010) studied vegetation succession after drainage in a peat bog as an analogue for water table draw down due to climate change. The study conclusions cite water table drawdown as a possible consequence of climate warming in the northern peatlands and due to the peatlands’ strong control on carbon cycling it is important to understand how persistent water table draw down may affect vegetation communities, and the implications these changes may have on the global carbon cycle (Talbot et al., 2010).

Hughes & Dumayne-Peaty (2002) argue that it is difficult to disentangle successional changes by allogenic factors from changes by autogenic factors. They propose that wetland succession is a continuum of change subject to forcing from both factors. Hydrology and water table levels may be affected by either autogenic or allogenic factors but Hughes (2000) suggests it may be an overall change to the water table levels that drives and controls the direction of successional change in peatlands. All that is required to create ombrotrophic conditions is a separation of the growing surface from the groundwater supply and this can be accelerated by a drop in water table levels (Hughes, 2000).

The current studies available on long-term water table depth (WTD) fluctuations in peatlands are scarce but such studies are necessary to understand long-term trends in vegetation change, especially in relation to impacts of drainage and climate change (Rydin et al., 2006).

2.9 The role of isostasy in the development of peatland ecosystems from James/Hudson Bay region

In the James Bay region, isostatic rebound due to post-glacial uplift is one of the most important factors affecting watershed hydrology (Pendea, 2011). Early studies such as: McAndrews et al. (1982) and Yu & McAndrews (1994) were conducted on lake basins in the Hudson Bay lowlands and have provided reconstructions of shoreline emergence based on pollen. This has allowed for the determination of timing of land emergence in the area. Further studies, such as Lajeunesse & Allard (2003), Pendea et al. (2010), and Simon et al. (2014) have investigated timing of emergence as well as provided estimates for rates of land emergence in the Hudson Bay area. Mitsch & Gosselink (2000) report that isostatic rebound has resulted in the emergence of land from the sea at a rate of approximately 1.2 meters per century for the last

1000 years, the greatest rate of glacial rebound in the world. Lajeunesse & Allard (2003) reconstructed initial uplift rates of 7 meters per century for the interval 8300 – 6000 cal yr BP, followed by decreasing rates of 4 meters per century from 6000 – 5000 cal yr BP, 1.7 meters per century from 5000 – 1000 cal yr BP, and 1.6 meters per century for the last 1000 years. Pendea et al. (2010) developed a new shoreline displacement model and postglacial sea-level curve for eastern James Bay. They found that shoreline emergence was initially rapid at a rate of 6.5 meters per century between 6850 – 6400 cal yr BP, then slowed down to a rate between 1.4 – 2 meters per century during the late Holocene (Pendea et al., 2010). For the last 250 years, however, Pendea et al. (2010) estimate an increase in the rate of shoreline emergence to 2 meters per century. Simon et al. (2014) give an estimate for current ongoing uplift rates at Arivat, Nunavut located on the west coast of Hudson Bay. The study, based on measurement of present-day vertical land motion obtained by repeat Global Positioning System readings, suggests present day uplift rates of 1.38 – 1.5 meters per century (Simon et al., 2014).

Based on the evidence suggesting the occurrence of isostatic rebound in the Hudson/James Bay region, studies have been conducted to determine what effect this has had to peatland development. A study by Glaser at al. (2004) was carried out to determine rates and pathways of peatland development in the Albany River region in the Hudson Bay lowlands of Canada. The study found that each site had the same stratigraphic sequence, however, development was more rapid at the younger sites. The study suggests that the principal driver of peatland development was the differential rates of isostatic uplift across the region. Glaser et al. (2004) claim that the faster rate of uplift on the lower reaches of the drainage basin continually altered the hydrologic setting. The fast rates of uplift impede drainage, shift river channels and result in continuous alteration to the hydrology. It is therefore geological factors, rather than climate, which determine rates and directions of peatland succession. Differential patterns of uplift reduce the regional gradient at the same time the peatlands are continually adjusting to changes in rapidly evolving river systems which control the water table topography and interfluvial divides (Glaser et al., 2004). The study suggests that even in regions with more stable landscapes (i.e., no isostatic uplift) peatland development is constrained by local hydrologeological settings, and development of patterned peatlands may be predictable by coupling groundwater and ecosystem models (Glaser et al., 2004).

Klinger & Short (1996) used palaeoecological chronosequence reconstructions to investigate succession in the Hudson Bay lowlands. The study was based on the concept that isostatic uplift and autogenic processes are the main drivers of peatland development to a climax ‘bog’ stage. The Hudson Bay lowlands are largely a bog-dominated landscape and they suggest that mechanisms included in driving this development are a combination of isostatic uplift, succession, hydrology, topography, and climate (Klinger & Short, 1996).

Beaulieu-Audy et al. (2009) performed palaeoecological chronosequence reconstructions on three peatlands in the lower La Grande Rivière watershed in northern Québec. Their results suggest that the retreat of the Tyrrell Sea and subsequent isostatic uplift were critical in driving the initial peatland development. Beaulieu-Audy et al. (2009) note that Holocene climatic events also greatly influenced the peatland development.

Bunbury et al. (2012) studied Holocene hydro-climatic change effects on carbon accumulation in a peat bog in the Attawapiskat River watershed in the Hudson Bay lowlands. They determined that the effect of isostatic rebound on hydrology is an important consideration in this region. They suggest the influence of glacial isostasy in the middle Holocene in the Hudson Bay lowlands was a major driver of drainage pattern establishment, water table position, and peatland development, although they provide little specific evidence of the link between isostatic rebound and peatland hydrology (Bunbury et al., 2012).

2.10 The role of landscape disturbance in peatland development

Peat deposits in boreal regions are substantial stores of carbon in the form of dead and live organic matter (Mitsch & Gosselink, 2007). In order to assess the contribution of peatlands to the global carbon budget, the total coverage and rate at which carbon is accumulating now as well as in the past must be known. Though this stored soil carbon has been recognized as an important component of global carbon budgets and future climate change scenarios, little work has been done to consider the role peatland disturbance plays in carbon sequestration (Mitsch & Gosselink, 2007). If these peat deposits are disturbed, they could contribute significantly to increasing worldwide atmospheric carbon dioxide levels. The level of contribution depends on the balance between draining and oxidation of the peat deposits and their formation in active wetland areas. If the climate continues to warm and accelerate the decomposition of peatlands, then these peatlands could become an additional major source of carbon. This would result from the aerobic respiration of peat and the possibility of fires releasing stored carbon as CO_2 to the atmosphere (Mitsch & Gosselink, 2007).

According to Yu et al. (2014) the past two decades of research have shown an increase in peat-core analysis to provide long-term perspectives on Holocene peatland carbon dynamics. These analyses have been used to refine carbon stock estimates at local, regional, and global scales. Recently, studies have used the combination of basal peat ages with peat-core carbon accumulation records to estimate the peat carbon pool over time. This has been used as an alternative to the approach used by Gorham (1991), which was based on peat depth and volume estimates (Yu et al., 2014). Most authors (e.g., Gorham, 1991; Bridgham et al., 1998; Yu, 2006;

Mitsch & Gosselink, 2007; Ward et al., 2007; Sulman et al., 2012; Garneau et al., 2014; Waddington et al., 2014; Yu et al., 2014) are in agreement that northern peatlands comprise a globally important carbon pool, covering a massive area in the circumpolar region and containing approximately one third of global soil carbon. However, the northern peatlands face an increase in the severity, extent, and frequency of climate-mediated (wildfire and drought) and land use change (drainage, flooding, and mining) disturbances. Authors agree that anticipating how ecosystem structure and function will respond to current and future changes is a critical challenge for ecologists (Gorham, 1991;Yu, 2006; Mitsch & Gosselink, 2007; Ward et al., 2007; Bridgham et al., 2008; Sulman et al., 2012; Garneau et al., 2014; Waddington et al., 2014; Yu et al., 2014). Waddington et al. (2014) suggest that in order to understand the resistance, resilience, and vulnerability of northern peatlands to climate change, the role hydrological feedbacks play in regulating changes in precipitation and temperature must be determined.

Ward et al. (2007) used a 50-year-old field experiment to investigate the effects of long-term land management practices of repeated burning and grazing on peatland vegetation and carbon dynamics. The study found that both burning and grazing reduced carbon levels in the above ground stocks and surface peat. Results also found soil microbial properties showed minor responses to burning, such that the carbon/nitrogen (C:N) ratio of the microbial biomass increased. Ward et al. (2007) found that both controlled burning and grazing influenced carbon stocks. Moreover, burning had more impact on carbon stocks and fluxes than seasonal climatic conditions.

Talbot et al. (2010) studied the effects on vegetation succession after drainage in a peat bog. Their results showed post-drainage increase in tree cover, decrease in *Sphagnum* cover, and shifts in species composition of dominant shrubs. The multivariate analysis of vegetation communities showed that they were closely correlated with water table depth and variability.

Sulman et al. (2012) used the LANDIS-II forest landscape succession model coupled with a model of plant community and soil carbon responses to water table changes in order to explore the possible impacts of declining water table levels on regional carbon pools in a peatland. The simulated results showed an increase in both biomass accumulation and soil decomposition as a consequence of drying. Sulman et al. (2012) conclude that declining water table levels can increase carbon over timescales of a few hundred years but the longer term effect is overall potential loss of carbon as the biomass accumulation will plateau and soil carbon loss will continue constant.

Ireland & Booth (2012) tested the hypothesis that European settlement of eastern North America resulted in dramatic changes to a floating kettle peatland in north-western Pennsylvania, USA. They hypothesized that land clearance probably exposed soils to increased wind erosion impacting downwind ecosystems through enhanced dust deposition. This suggests that peatlands in agricultural landscapes may be vulnerable to nutrient enrichment through non-point source dust deposition resulting in considerable community-to-ecosystem level consequences. Dust deposition was found to be associated with reduced peat accumulation rates, nutrient enrichment, shifts from *Sphagnum* moss to vascular plant communities, and shifts in testate amoebae assemblages (Ireland & Booth, 2012).

Failkiewicz-Koziel et al. (2014) investigated long-term carbon accumulation rates in two poor-fens subjected to anthropogenic drainage in southern Poland. Their results indicated poor-fens are capable of sequestering carbon very efficiently and drained poor-fens are also effective at carbon sequestration post drainage events if the water regime is able to return to balance. They also detected minor climatic signals in the records, although anthropogenic disturbance predominates. Failkiewicz-Koziel et al. (2014) conclude peatlands exhibit higher rates of carbon accumulation compared to other boreal ecosystems and that low-temperate peatlands may be very important carbon sinks.

2.11 Palaeoecological records of change and the multi-proxy approach to peatland research

Northern peatlands are an important archive of evidence about past climate and environmental change (Clymo et al., 1998). Peat bogs display high preservation capacities of biological proxies as well as small inorganic particles (Chambers et al., 2011). The accumulation of carbon-rich peat deposits can yield continuous records of peat growth and sometimes archive climatic changes with a high temporal resolution, often decadal scale. These records can be used to infer changes in carbon sequestration rates, atmospheric temperature and surface moisture balance over the Holocene (Hargan et al., 2015). It is now widely acknowledged that multi-proxy approaches to reconstructing Quaternary environments result in a more complete picture of the past (Charman, 2001). Peatland stratigraphy, particularly the stratigraphy of bogs, has been used as a source of palaeoclimate data for over a century (Booth, 2002). Early palaeoclimate work was focused on documenting times of high-magnitude hydrological change at millennial timescales. More recently there has been a growing body of evidence to document high-frequency, low-magnitude climatic changes from bog stratigraphy (Booth, 2002).

Over the past two decades, various authors have conducted research using the multi-proxy approach in order to reconstruct northern peatland development and carbon sequestration though time. Authors such as: Klinger & Short (1996), Magyari et al. (2001), Hughes & Dumayne-Peaty (2002), Booth (2002), Glaser (2004), Lamentowicz & Mitchell (2005), Booth

(2007), Booth & Sullivan (2007), Beaulieu-Audy et al. (2009), Loisel & Garneau (2010), Pendea et al. (2010), Pendea (2011), Chambers et al. (2011), Booth et al. (2012), Lamarre et al. (2012, 2013), Holmquist & MacDonald (2014), and Hargan et al. (2015) used a combination of proxies to develop reconstructions of ecological changes over time in the northern peatlands.

Studies by Booth (2002, 2007), Booth & Sullivan (2007), and Booth et al. (2012) investigated hydrology patterns in northern peatlands and provided evidence for the use of testate amoebae as a proxy to reconstruct Water-Table-Depth (WTD) variations through time. These studies found that WTD levels could be reproduced from testate amoebae assemblages with a mean error of 6-8 cm.

Loisel & Garneau (2010) reconstructed past hydroclimatic conditions of peat accumulation and associated carbon dynamics during the Holocene in four peat sequences collected in two peat bogs in the Eastmain River watershed of the James Bay lowlands, Québec. The study included analyses of macrofossils, testate amoebae, peat humification, C/N ratios, and bulk density each performed at high-resolution along each peat core. Authors conclude that multi-proxy and multi-core studies provide a more realistic understanding of the complexity of peatland ecosystems by offering a more complete picture of environmental change than those obtained from the analysis of a single proxy and/or a single peat core. However, Loisel & Garneau (2010) caution such datasets may present challenges, since the sensitivity level of each proxy method and each coring site differs leading to local records of changes that cannot always be generalized.

Chambers et al. (2011) provided a review of developments in proxy-climate reconstructions from peatlands, chronicling the use of a range of pelaeo-proxies such as peat stratigraphy, plant macrofossils, peat humification, testate amoebae, and non-pollen palynomorphs. Chambers et al. (2011) concluded that the combination of inorganic geochemical proxies together with mineralogical and biological proxies are the key to better understanding the causes and consequences of short-term climatic events in the Holocene.

Lamarre et al. (2012) used testate amoebae to reconstruct Holocene hydroclimatic variations and carbon accumulation in the discontinuous permafrost zone near Kuujjuarapik, subarctic Québec. Their results showed the effectiveness of using testate amoebae in a permafrost peatland to reconstruct past hydrological conditions. They recommend a multi-proxy approach including testate amoebae-based water table depth reconstructions because surface hydrology dynamics are not well known in permafrost peatlands (Lamarre et al., 2012).

Holmquist & MacDonald (2014) conducted a study using radiocarbon dates, plant macrofossil analysis, and soil carbon estimates from an eight-core transect of the James Bay lowlands and surrounding regions to reconstruct the timings and patterns of fen to bog transitions as well as ranges and patterns of long-term apparent rate of carbon accumulation. The study found peatland initiation lagged land surface availability by several thousand years, fen to bog transitions also occurring thousands of years after initiation. Fen to bog transitions were variable in timing but generally followed a pattern of longer fen stages occurring in southern sites, and shorter stages occurring in more northern sites. Holmquist & MacDonald (2014) note that additional and detailed proxy records of temperature and surface moisture, estimates of below ground lost carbon over time, and a greater number of well-dated records in the area are needed to fully understand the relationship between carbon accumulation and climatic variation over the Holocene in the James Bay, Hudson Bay, and boreal shield regions of eastern Canada.

Hargan et al. (2015) analyzed diatom assemblages in three peat cores retrieved from ombrotrophic bogs across the Hudson Bay lowlands and compared them to testate amoebae and macrofossil data previously analyzed from the same cores, as well as regional pollen records from surrounding peatlands. Results suggested that combined use of diatoms and testate amoebae to track peatland changes are complementary. Testate amoebae are directly sensitive to hydrological changes while diatoms closely track the chemical conditions of a peatland which may also be influenced by changes to the hydrology. Hargan et al. (2015) suggest slight differences in the responses of these proxies to environmental change may be linked to different ecological tolerances.

Chapter 3) Site Description

3.1 The James Bay wetlands

In the James Bay region of Canada wetland ecosystems are a dominant feature of the coastal landscape. Together with the Hudson Bay lowlands, the James Bay coastal region is part of a vast subarctic wetland region of Canada, which stretches from the Hudson Bay toward the northwest corner of Canada into Alaska and covers ≈ 760 000 km^2. The James Bay lowlands are dominated by extensive areas of mud flats, intertidal marshes, and supertidal meadow marshes, which grade into peatlands, interspersed with small lakes, thicket swamps, forested bogs and fens, open bogs, fens, and marshes away from the shorelines (Mitsch & Gosselink, 2000). The high subarctic wetland region along the northern shore of the bay is dominated by sedges (*Carex* spp.), cotton grasses (*Eriophorum* spp.), and clumps of birches (*Betula* spp.). The more southerly low subarctic wetland region is made up of open bogs, sedge-shrub fens, moist sedge-covered depressions, open pools, and small lakes separated by ridges of peat, lichen-peat-capped hummocks, raised bogs, and beach ridges. Low-energy coasts with wide coastal marshes occur in the southern James Bay. Isostatic rebound following glacial retreat has resulted in the emergence of land from the bay at a rate of 1.2 meters per century for the last 1000 years, the greatest rate of glacial rebound in North America (Pendea et al., 2010).

Early studies on hydrarch (wetland) succession theory showed strong support for a linear progression toward a ‘climax bog’ and were based on studies that assumed variation in space could be substituted for changes through time (Hughes & Dumayne-Peaty, 2002). On the James Bay coast, there is an ongoing process of isostatic rebound resulting from the last glacial retreat which provides a modern field laboratory to test models of wetland succession through time (Pendea, 2011). Specifically, isostatic uplift provides a continuous landscape gradient of increasing age (chronosequence) from the present day coastline to the interior. The result of this process is the continuous plant colonization of new shorelines, which will develop into the various freshwater peatland types as the influence of the sea diminishes and more land becomes exposed (Pendea, 2011). This continuous pattern of uplift and successional development during the past ~7000 years makes James Bay an ideal location for conducting research that seeks to reconstruct peatland succession through time (Hughes & Dumayne-Peaty, 2002; Booth, 2007; Pendea, 2011).

3.2 Study area overview

The location of the study region is in the high boreal zone of eastern James Bay in northwestern Québec. The region was covered by the last remnants of the Laurentide ice sheet until the early Holocene, after which marine waters from the Tyrrell Sea began to flood the newly deglaciated surface (Dyke, 2004). The marine stage was short, followed by shoreline regression under the influence of glacio-isostatic rebound. A progressive landscape emergence from east to west began ~7000 years ago in the study region and is currently still underway (Pendea at al., 2010).

The James Bay Eco-region climate is continental subarctic and is part of the Perhumid High Boreal Eco-climatic Region. The mean January temperature is -23°C, mean July temperature is 14°C, and the annual precipitation ranges between 528 – 833 mm (Crins et al., 2009). The regional vegetation consists of open boreal taiga, which is dominated by stands of stunted *Picea mariana* with *Pinus banksiana*, *Alnus* spp., *Larix laricina*, and *Betula glandulosa* as secondary constituents, and is interspersed with open fens and bogs (Crins et al., 2009).

3.3 Sample site descriptions

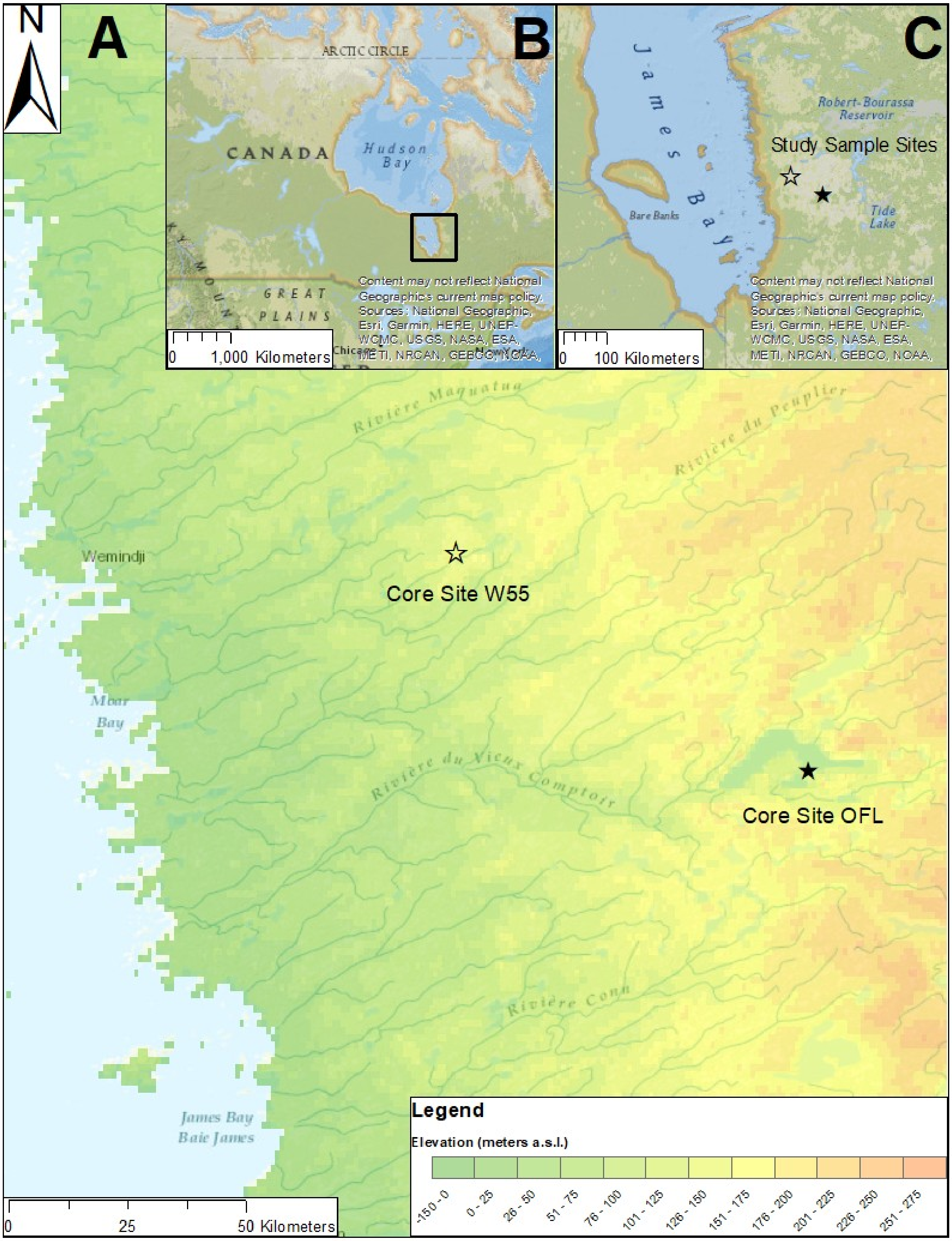
This study is based on two sampling sites from the Old Factory River watershed in eastern James Bay (Fig. 3.1).

Site W55 (53°1’ N, 78°10’ W) is a bog situated about 55 km east of the town of Wemindji (Québec). The site has an elevation of 130 m a.s.l. and is margined by relatively steep slopes towards the south. An intermittent brook on the northern margin partially drains the site, but the overall drainage is poor due to the underlying marine clays. The peatland developed in a former cove on the northwest side of a newly emerged island after 6400 cal yr BP (Pendea, 2011). The vegetation at the W55 site is dominated by *Sphagnum* mosses and ericaceous shrubs with patches of sedges and lichens. Stunted trees (*Picea mariana*) border the margins of the bog.

Peatland site OFL (52°47’ N, 77°31’ W) is a poor fen/bog complex situated on the southern shores of Old Factory Lake, approximately 110 km southeast from the town of Wemindji (Québec). The peatland has an elevation of 103 m a.s.l and is characterized by flat topography with no surface drainage. The surface vegetation is dominated by *Sphagnum* and ericaceous shrubs along with stunted *Picea mariana* trees found isolated throughout the bog (Pendea, 2011). The peatland developed on a former tidal flat, which at the time of emergence was a large protected bay (Pendea, 2011). When the sea finally retreated the former bay was replaced by the Old Factory Lake (Fig. 3.1). The local base level created by the Old Factory Lake is the primary control for the local water table level at this site. The subterraneous drainage is impeded due to the thick marine clay layer at its base.

Figure 3.1

Study site map



Chapter 4) Methodology & Materials

4.1 Methodology

My research looks at two subarctic peatlands of similar age but different in their developmental history and seeks to determine whether major shifts in peatland development are affected by changes to the local hydrology. To investigate the dynamic of this relationship, I ask whether changes in peatland hydrology (i.e., water-table-depths) coincide with major shifts in peatland development (hydroseres). I address this first question using a comparison of my hydrology reconstructions for each peat core overlain with the ecology reconstructions for each respective peat core (Pendea, 2011). I use these combined reconstructions to determine whether the recorded hydrology fluctuations align with shifts to the ecology. I also ask whether changes in peatland hydrology drive hydrarch succession in these peatlands. I look more specifically at the hydrology patterns (i.e., wet to dry, dry to wet, and long standing seemingly stable conditions) to determine if similar hydrology changes or patterns occur around successional shifts from marsh to fen, fen to bog, and bog to fen. Finally, I ask what underlying causes may be responsible for the recorded changes to hydrology in these two peatlands. To address this last question I investigate the records of isostasy and climate change in the James/Hudson Bay region to determine if the timing of any major event correlates with findings of major hydrology changes in the study. I also discuss how the local site conditions specific to each peatland may have affected the hydrology conditions at each peatland site over time. I reconstruct peatland hydrology as Water-Table-Depth (WTD) based on a transfer function using fossil testate amoebae retrieved from peat cores. I use AMS carbon-14 dating to produce an age-depth model that provides the chronological context. Peatland development was reconstructed by Pendea (2011) using palynomorphs and C/N ratios through a modern analogue approach (Pendea and Chmura, 2012).

4. 2 Field sampling and materials

All field work and field sampling was conducted by Dr. Pendea and his research team (Pendea, 2011). Five-cm diameter cores were extracted from the deepest part of each peatland with a 2 m-long Eikelkamp® piston corer (Pendea, 2011). The top 0.5m of the cores, containing *Sphagnum* peat with tough ericaceous root systems was cut with a knife. Cores were transported in PVC pipes and stored in a cold room at 4^{o}C until sub-sampled in the laboratory. Cores were then sliced into 0.5 or 1 cm-thick sections and from the center of each section a subsample was removed using a 1.5 cm-diameter metal cylinder. Thinner sections were cut above and below the marine/terrestrial interface. Mean sampling resolution within the cores was 6±3 cm (180 ±166 yrs) for the W55 core, 6 cm ±2 cm (133 ±90 yrs) for OFL core. Laboratory sub-sampling and processing was conducted by myself.

4.3 Dating and age-depth modelling

Accelerated Mass Spectrometry (AMS) radiocarbon measurements were obtained exclusively on macrofossils including seeds, twigs, leaves, and *Sphagnum* stems and leaves. AMS radiocarbon analysis was performed by Beta Analytic Inc. Quoted errors represent one relative standard deviation statistics (68% probability) and counting errors are based on the combined measurements of the sample, background, and modern reference standards. Radiocarbon ages were corrected for isotopic fractionation and were calibrated using the INTCal13 curve (Reimer et al., 2013) and the calculations were performed using the cubic spline fit (Talma and Vogel, 1993). Calibrated ranges are reported as two standard deviations (tables 5.1 and 5.2). Age-depth models for cores OFL and W55 (Fig 5.1. and 5.2) were derived using the Bayesian Bchron model as incorporated in the free Bchron R software package (Haslett and Parnell, 2008; Parnell et al., 2008). This model outperforms other age-depth models, as shown by a large-scale experiment conducted on Holocene lake sediments (Parnell et al., 2011).

4.4 Testate amoebae analysis

In this study, I use testate amoeba analysis to reconstruct the long term hydrological variability for the OFL and W55 peatlands, measured as water-table-depth (WTD). Testate amoebae are protozoans that inhabit distinct ecological niches related to moisture conditions and produce morphologically distinct shells that can be used as pelaeoecological indicators of hydrologic changes as they respond rapidly to changes in the hydrology (Mitchell et al., 2007). These proxy indicators are particularly abundant in *Sphagnum* dominated peatlands. The distinct siliceous shells of testate amoebae preserve well in peat deposits making them complementary indicators to other long-established indicators such as pollen, spores and macrofossils (Mitchell et al., 2007). Authors such as Woodland et al. (1998), Booth (2002), Booth and Zygmunt (2005), Booth (2007), Booth and Sullivan (2007), Booth et al. (2010), Amesbury et al. (2013), Lamarre et al. (2013), and van Bellen et al. (2014) have studied the ecology of testate amoebae and developed transfer functions from modern analogue data sets which relate community species assemblages to mean annual water table depths. The transfer functions were then used in various peatland studies to infer past and current hydrology conditions.

4.4.1 Sample preparation

The peat cores were sub-sampled every 5 to 10 cm, depending on the sediment accumulation rate and the depth of important transition in pollen and C/N stratigraphy (Pendea, 2011). Approximately 1.5 cm^3 of peat material from the center of each 1-cm thick slice was put in test tubes where a *Lycopodium* tablet of known spore number was added for calculation of test concentrations. The samples were then boiled in distilled water for 10 minutes followed by a two-part sieving process. The samples were passed through a 300 μm sieve and retained on a 15 μm sieve after thorough washing. Samples were then centrifuged to remove excess water and mounted on slides for identification. All samples were counted to 150 specimens, indicated by Booth & Sullivan (2007) to be a statistically significant sample size. The taxonomic framework and nomenclature follows Charman (2001) as modified by Booth (2007). Taxa identification was conducted using a key published by Booth and Sullivan (2007). The remainder of all testate amoebae subsamples will be stored indefinitely on location at Lakehead University in a locked fridge at 4°C.

4.4.2 Zonation

All taxa were used to subdivide the testate amoebae assemblage diagrams into local testate assemblage zones (LTAZ) using constrained cluster analysis by sum-of-squares (CONISS) as implemented in the Psimpoll 4.27 program (Bennett, 2007). Seven zones representing significant clusters were identified in each respective core and these are presented in detail in the Results section. These zones represent significant clusters according to the broken stick model (Bennett, 2007).

4.4.3 Water-Table-Depth (WTD) transfer function

Raw fossil test abundance data were transformed to percent relative abundance for each core. A transfer function was developed with the assistance of Dr. Robert K. Booth from Lehigh University using the weighted average partial least square (WA-PLS) model (Booth, 2007). The WA-PLS model returns the smallest WTD errors although the general performance is similar to that of other commonly used models, such as weighted averaging (WA), weighted averaging with tolerance downweighting (WA-Tol), and weighted modern analogue technique (WMAT). The modern analogue dataset (n=650) is based on testate amoebae species-environment relationships from 369 sites across North America (Booth, 2007). The transfer function model was applied to my fossil dataset using the C2 software (Juggins, 2003; Booth, 2007) and mean water-table-depth was inferred with a mean error of 6-8 cm (Booth, 2007). All water-table-depth values are representative for the fossil peat surface which at the time of the reconstruction had a different thickness than the one of today. The fossilization process is accompanied by decomposition and compression which renders the total peat thickness of today less than the one in the past.

4.5 Carbon/Nitrogen analysis

Sediment sub-samples were analyzed for organic carbon and nitrogen. Prior to analysis bulk samples were dried at 50^{o}C and ground into a fine powder. The samples were then collected onto glass fiber filters and were HCl-fumed in a desiccator for 48 hours to remove all inorganic carbon. The acid fumed filters were dried in an oven at 50^{o}C overnight before being processed into small pellets wrapped in aluminum foil. An autosampler was used to introduce 15-20 mg samples into a Carlo Erba Na-1500 CNS Elemental Analyzer which were then combusted at 1000^{o}C along with a stream of oxygen to form a mixture of CO_2, NO_x, and H_2O. Standards with known amounts of C and N were analyzed along with the samples in order to produce a standard curve which allows the conversion of the instrument units to micrograms of C and N. Replicate analysis of well-mixed samples indicated a precision of <0.2. C/N calculations are based on the molar weight. Higher values indicate nutrient-poor conditions, while lower values are indicative of a minerotrophic nutrient status. The cut-off values for minerotrophic and ombrotrophic conditions were determined based on modern C/N values from present day ecosystems in the research area (Pendea and Chmura, 2012). C/N results were plotted using the Psimpoll 4.27 program (Bennett, 2007).

4.6 Pollen analysis

Pendea (2011) conducted a palynomorph analysis (e.g., pollen, spores, dinoflagellate cysts) of a series of cores from eastern James Bay including the two cores (OFL and W55) used in this study. Using a suite of modern analogues from present-day ecosystems (Pendea and Chmura, 2012) reconstructed the successional development of these peatlands since their inception (Pendea et al., 2010; Pendea, 2011). To investigate the relationship between hydrology and peatland development, the palynomorph-based hydrarch succession analysis is reproduced with permission in the results section in order to compare it with the reconstructed palaeohydrology obtained in this thesis.

Chapter 5) Results

5.1 Peatland core lithostratigraphy

The OFL peatland (106 m a.s.l) was cored to 250 cm (Pendea et al., 2010). Basal sediments are marine grey-blue clayey silts overlain by tidal marsh, fen, and bog peats (Figure 5.6). At 237 cm, there is an abrupt shift to tidal marsh peat. The peat profile comprises eight successive subunits starting with tidal marsh, carr, sedge-*Sphagnum*, and then alternations of *Sphagnum* and Ericaceous-*Sphagnum* peat.

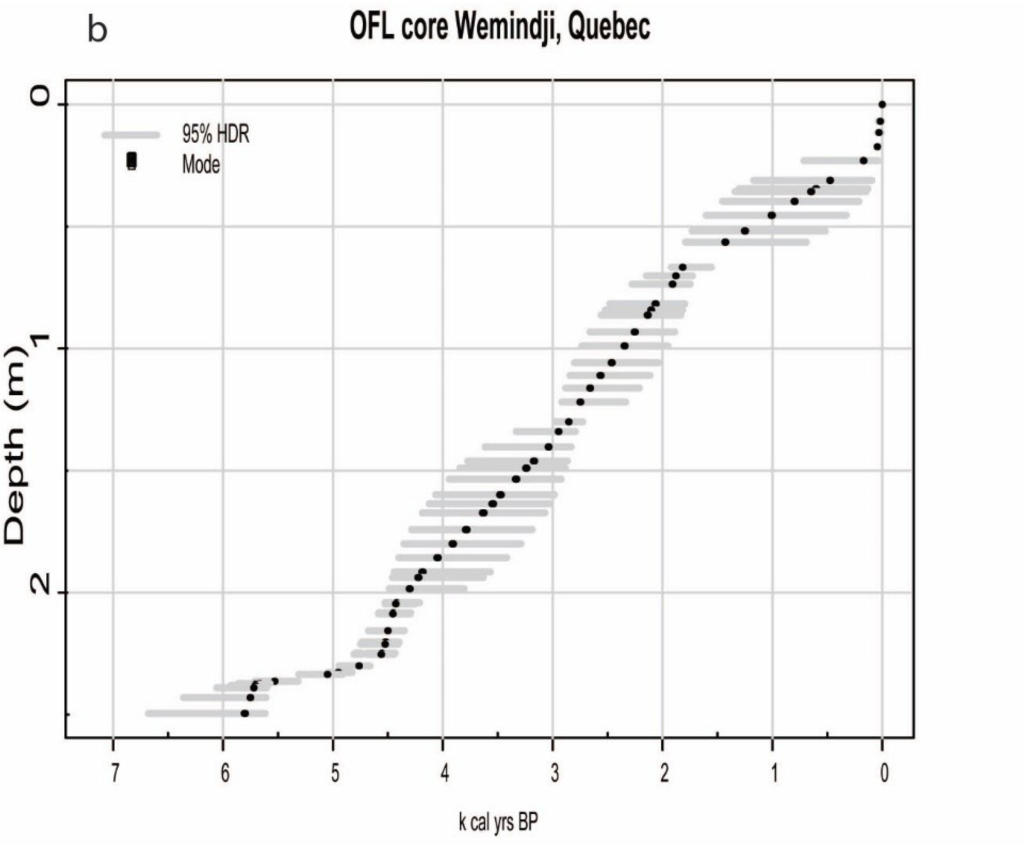
Site W55 (130 m a.s.l) was cored to 264 cm (Pendea et al., 2010). The basal sediments consist of marine silty sands overlain by tidal marsh, fen, and bog peats (Figure 5.7). The upper portion of this sand deposit is heavily oxidized and has an abrupt boundary with the overlying peat. The W55 peat profile consists of eight successive subunits beginning with tidal marsh, sedge-carr peat (humified), sedge-*Sphagnum*, sedge-brown moss, and then alternations of sedge-*Sphagnum* and *Sphagnum* peat. The tidal marsh peat, 2.5 cm thick, contains visible quartz and sand grains throughout. Above 140 cm the peat becomes rich in wood and twig remains and is heavily decomposed.

5.2 AMS Chronostratigraphy

Table 5.1 and 5.2 show the radiocarbon age measurements obtained on the macrofossil fragments (Pendea, 2011) from discrete levels in each core. The radiocarbon ages were used to produce age-depth models for both the OFL and W55 core (Fig. 5.1 and 5.2).

Figure 5.1

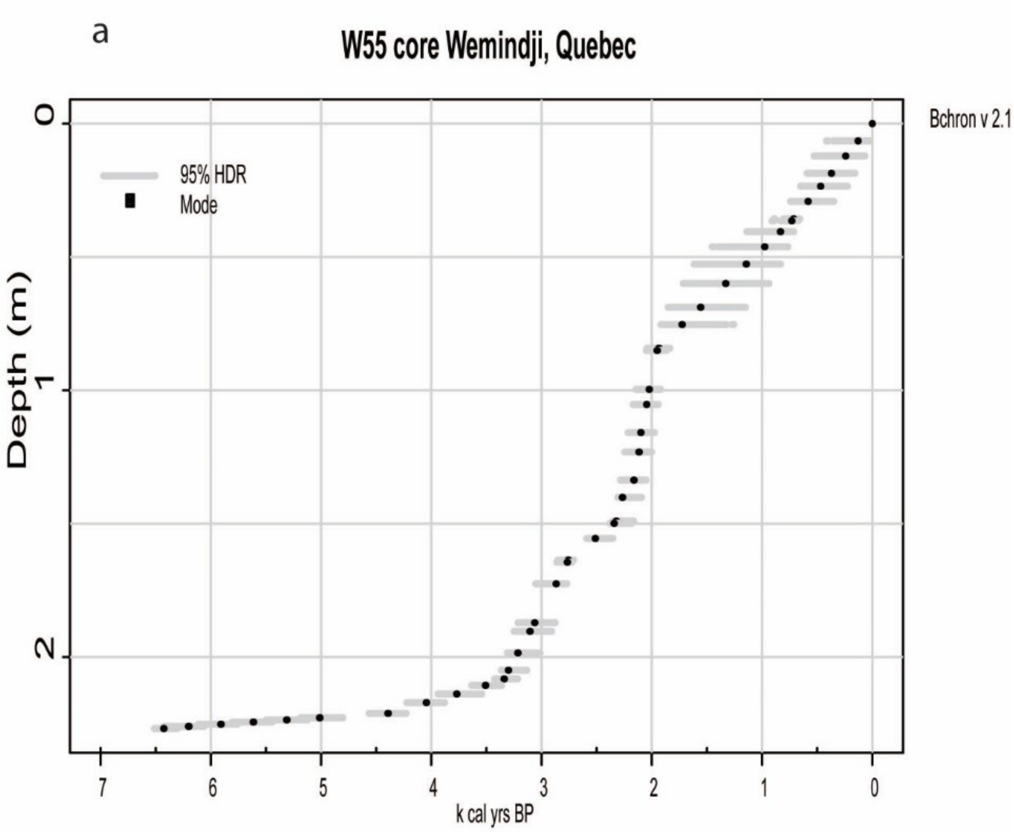
The age-depth model for core OFL based on radiocarbon dates as constructed by the Bchron software (Haslett and Parnell, 2008; Parnell et al., 2008).



*Grey bars represent the 95% confidence interval of calendar ages.

Figure 5.2

The age-depth model for core W55 based on radiocarbon dates as constructed by the Bchron software (Haslett and Parnell, 2008; Parnell et al., 2008).



*Grey bars represent the 95% confidence interval of calendar ages.

The earliest part of the OFL peatland development (5700 – 4900 cal yr BP) was characterized by low rate of sediment accumulation. The model shows near constant accumulation rates between 4900 and 2000 cal yr BP. From 2000 cal yr BP to present, the model shows a decrease in peat accumulation rates. The top-most 19 cm of peat represent well-preserved, partly living and uncompressed *Sphagnum* material that accumulated after AD 1950 as indicated by a radiocarbon measurement at 19 cm (123.9 ± 0.5 pMC; Beta -263331). The age-depth model shows very high accumulation rates above the 19 cm depth, due in part to the non-humified and uncompressed nature of the acrotelm.

Results for the W55 peatland core shows a rather smooth age-depth model with the exception of the bottom section (6400 to 4000 cal yr BP) characterized by very low accumulation rates. The fastest peat accumulation rate was between 4000 and 2000 cal yr BP, followed by a decrease by almost 50% between 2000 cal yr BP and present.

Table 5.1

Radiocarbon measurements and associated calendar ages based on macrofossils from OFL peat core James Bay, Québec (Pendea, 2011).

Sample Depth (cm)	Dated material	Beta code	Radiocarbon age (yr BP)	2σ probability CAL age (yr BP)		
				1st	2nd	Midpoint
19	*Sphagnum* stems and leaves	263331	123.9±0.5 pMC	Modern		0*
67	Charred twig, *Betula* bark	251803	1880 ±40	1720-1900		1810
130	*Sphagnum* stems and leaves	257587	2770 ±40	2770-2960		2865
204	*Sphagnum* stems and leaves	251801	3980 ±40	4400-4530		4465
225	*Alnus* twig	251802	4040 ±40	4770-4790	4420-4620	4780
233	*Alnus* bark and twig	251800	4320 ±40	4970-4840		4905
237	Charred material (seeds, wood, and *Picea* needle)	257586	4970 ±40	5830-5860	5600-5750	5675

(* We assume this to be close to AD 1950 given its subfossil depth.)

Table 5.2

Radiocarbon measurements and associated calendar ages based on macrofossils from W55 peat core James Bay, Québec (Pendea, 2011).

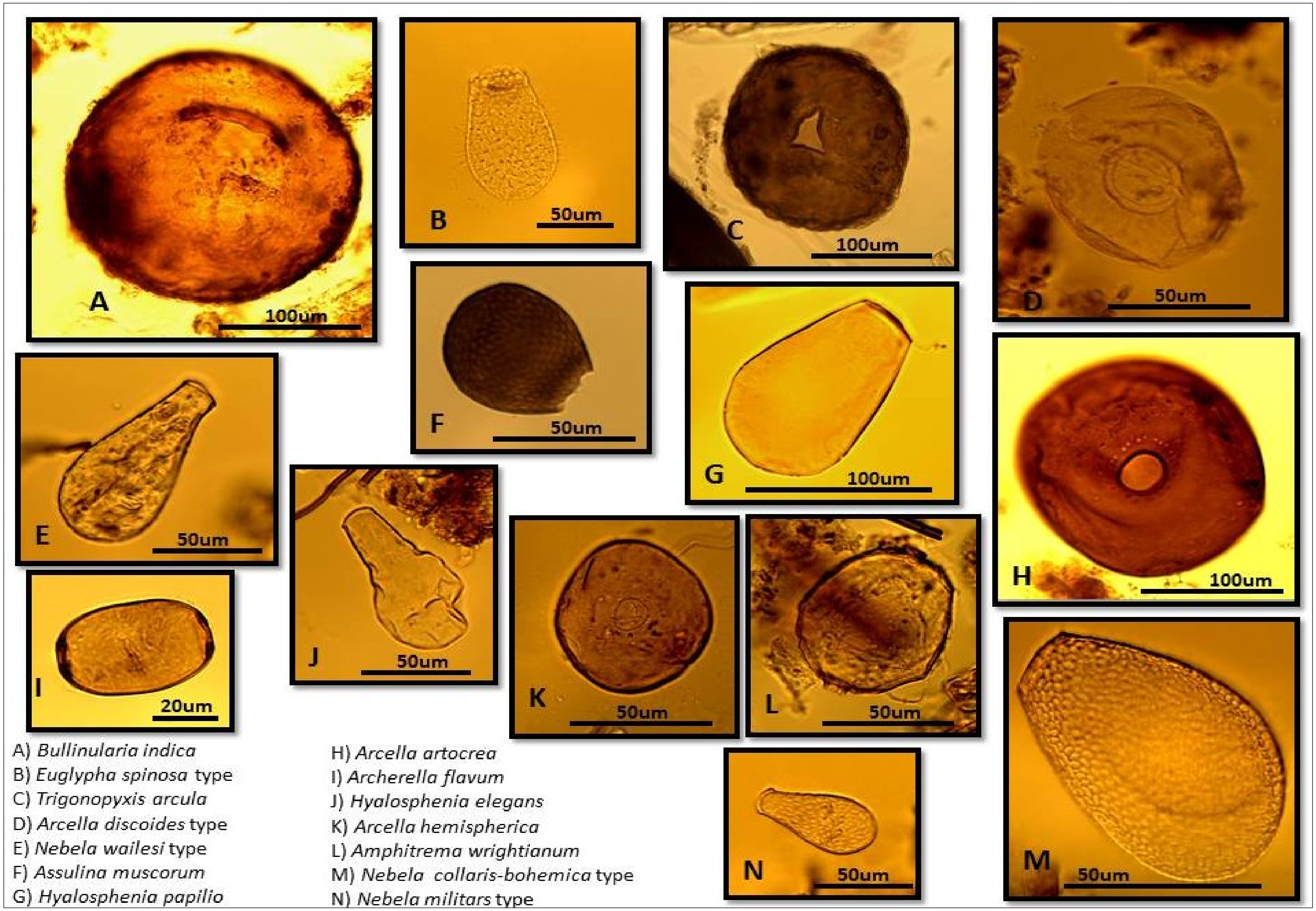
Depth (cm)	Dated material	Beta code	Radiocarbon age (yr BP)	2σ probability CAL age (yr BP)		
				1st	2nd	Midpoint
36	Twig	251810	800 ±40	670-780		725
84	*Sphagnum* stems and leaves	257588	2010 ±40	1880-2050		1965
149	*Sphagnum* stems and leaves	251809	2240 ±40	2150-2340		2245
164	*Larix laricina* spurs	251808	2640 ±40	2730-2790		2760
208	*Alnus* twig	251807	3090 ±40	3220-3390		3305
221	*Alnus* twig, *Betula* leaf	251806	3930 ±40	4510-4480	4440-4250	4345
226	*Alnus* twig	251805	5630 ±40	6490-6310		6400

5.3 Testate amoeba assemblages

I analysed 74 samples from the OFL core and 77 samples from the W55 core. Testate amoeba were identified to the lowest taxonomic level possible, resulting in 46 different taxa identified throughout the OFL peat core and 42 different taxa for the W55 peat core. A photo collection of some of the commonly observed testate amoebae taxa from both peat cores is presented in Figure 5.3. Percent relative abundance of testate amoebae was plotted against depth (cm) and age (cal yr BP) (Fig. 5.4 and 5.5). C/N ratio data was presented alongside the test abundance data. The testate amoeba assemblages were subdivided into local assemblage zones using constrained cluster analysis by sum-of-squares (CONISS) as implemented in the Psimpoll 4.27 program (Bennett, 2007).

Figure 5.3

Photo collection of commonly observed testate amoebae for OFL and W55 peat cores, James Bay, Québec.



A) *Bullinularia indica*
B) *Euglypha spinosa* type
C) *Trigonopyxis arcula*
D) *Arcella discoides* type
E) *Nebela wailesi* type
F) *Assulina muscorum*
G) *Hyalosphenia papilio*
H) *Arcella artocrea*
I) *Archerella flavum*
J) *Hyalosphenia elegans*
K) *Arcella hemispherica*
L) *Amphitrema wrightianum*
M) *Nebela collaris-bohemica* type
N) *Nebela militars* type

5.3.1 OFL peat core

Zone O-1 (5900 – 4900 cal yr BP)

The O-1 zone consists mainly of *Difflugia pulex*, which ranges from 40-65% abundance in this zone. Other important taxa are *Trigonopyxis minuta* (3-20%), *Difflugia oblonga* (8-16%), *Difflugia lucida* (2-10%), and *Heleopera sphagni* (0-10%). Several other taxa, including *Arcella artocrea*, *Centropyxis aculeata*, *Heleopera sylvatica*, *Bullinularia indica*, *Assulina muscorum*, *Trigonopyxis arcula*, *Cyclopyxis arcelloides*, *Arcella hemispherica*, *Amphitrema wrightianum*, *Difflugia leidyi*, *Heleopera petricola*, and *Archerella flavum* are present in an abundance of 5% or less. The C/N ratio ranges from 15 – 30 for this zone.

Zone O-2 (4900 – 3900 cal yr BP)

Zone O-2 is characterized by a fluctuating abundance of *Difflugia pulex*, with values ranging between 5-35%. Other important taxa are *Arcella catinus* (5-20% abundance), *Arcella hemispherica* (5-30%), *Heleopera sylvatica* (0-25%), *Difflugia lucida* (5-25%), *Arcella discoides* (0-20%) and *Trigonopyxis arcula* (0-20%). Taxa that are somewhat more irregular in frequency are *Archerella flavum* (1 and 20%), *Trigonopyxis minuta* (5-15%), *Amphitrema wrightianum* (8-10%), *Phryganella acropodia* (2-10%), and *Difflugia oblonga* (2-10%). There are several minor taxa that display an abundance of 5% or less including *Bullinularia indica*, *Assulina muscorum*, *Difflugia globulosa, Arcella artocrea*, *Difflugia leidyi, Heleopera petricola*, and *Hyalosphenia papilio*. The C/N ratio ranges from 82 – 110 for the O-2 zone.

Zone O-3 (3900 - 2800 cal yr BP)

In Zone O-3, *Difflugia pulex* displays a higher overall abundance (35-78%) than in Zone O-2, with minimum values occurring at 3400 cal yr BP. *Arcella catinus* shows a relatively stable abundance around 5%, with two peaks of 12-13%. There is only one spike of *Heleopera* *sylvatica* species present in this zone occurring at 3350 cal yr BP with 15% abundance. Other important taxa are *Arcella hemispherica* (5-15%), *Diffligia oblonga* (4-15%), *Trigonopyxis minuta* (5% to 16%), *Arcella discoides* (4-20%), *Phyrganella acropodia* (4-15 %). Taxa which have minor and/or irregular appearance are: *Archerella flavum* (maximum 7%), *Trigonopyxis arcula* (<5%), *Difflugia lucida* (<5%), and *Difflugia globulosa* (<5%). The C/N ratio for this zone ranges from 85 – 150.

Zone O-4 (2800 - 1600 cal yr BP)

The abundance of *Difflugia pulex* increases further in Zone O-4 with a frequency ranging from 40 to 90%. Other important taxa are *Difflugia oblonga* (5-35%), *Archerella flavum* (5-22%), *Heleopera sylvatica* (5-7%), *Difflugia lucida* (5-10%), *Phryganella acropodia* (5-12%), *Hyalospenia subflava* (5-10%), and *Trinema lineare* (0-15%) although most of these appear infrequently. Minor taxa (<5%) are *Arcella catinus*, *Trinema/Corythion* type, *Assulina muscorum*, *Trigonopyxis arcula*, *Hyalosphenia minuta*, *Arcella hemispherica*, *Difflugia globulosa*, *Amphitrema wrightianum*, *Arcella discoides*, *Nebela vitraeae*, and *Nebela collaris-bohemica.* Notable is the absence of *Trigonopyxis minuta* – a taxon that was well represented in Zones O-1 to O-3. The C/N ratio ranges from 55 – 135 for the O-4 zone.

Zone O-5 (1600 - 1300 cal yr BP)

Zone O-5 spans a short time interval of only 300 years. This zone is characterized by a substantial decline in abundance of *Difflugia pulex* compared to previous zones, with a maximum occurrence of 22%. The role of dominant taxon is now assumed by *Archerella flavum* which reaches 60% abundance at 1400 cal yr BP. *Hyalosphenia subflava* averages around 10% abundance for the zone. Minor taxa (<5%) characterizing Zone O-5 are *Spenoderia lenta*, *Tracheuglypha dentata*, *Arcella catinus*, *Euglypha rotunda*, *Heleopera sylvatica*, *Trinema* *lineare*, *Trigonopyxis minuta*, *Arcella hemispherica*, *Difflugia lucida*, *Difflugia globulosa*, *Arcella discoides*, and *Heleopera sphagni*. The C/N ratio ranges from 70 – 78 for the O-5 zone.

Zone O-6 (1300 - 200 cal yr BP)

The beginning of Zone O-6 features an increase in the abundance of *Difflugia pulex* population, which assumes dominance once again (32-65%). Other important taxa are *Difflugia oblonga* (10-30%), *Difflugia lucida* (0-10%), *Heleopera sylvatica* (≈6%), *Assulina muscorum* (≈7%), and *Difflugia bacillifera* (≈7%), the latter appearing for the first time in the pelaeoecological record of the OFL site. Other taxa that appear for the first time at this site are *Nebela militaris* and *Euglypha strigosa*. Minor taxa (<5%) that characterize Zone O-6 are *Archerella flavum*, *Arcella catinus*, *Trinema lineare*, *Trigonopyxis minuta*, *Amphitrema wrightianum*, *Arcella discoides*, *Phrygaella acropodia*, and *Nebela collaris-bohemica*. The C/N ratio ranges from 40 – 78 for the O-6 zone.

Zone O-7 (200 cal yr BP - present day)

The most recent testate amoeba assemblage zone (O-7) is characterized by the emergence *Hyalosphenia elegans,* which appears now for the first time in the OFL pelaeoecological record with a maximum abundance of 30%. The population abundance of *Diffligia pulex* shows a significant decline from previous zones, reaching <10% in the O-7 zone. Other important taxa are *Archerella flavum* (maximum 30%), *Hyalosphenia papilio* (10-25%), *Euglypha strigosa* (maximum 10%), *Heleopera sylvatica* and *Assulina muscorum*, the latter two species present below 8% abundance. Minor taxa (<5% abundance) are *Nebela militaris*, *Nebela wailesi*, *Tracheuglypha dentata*, *Arcella catinus*, *Euglypha rotunda*, *Hyalosphenia subflava*, *Trinema lineare*, *Hyalosphenia minuta*, *Trigonopyxis minuta*, *Difflugia oblonga*, *Arcella hemispherica*, *Arcella discoides*, *Euglypha strigosa*, *Heleopera petricola*, *Nebela griseola*, and *Nebela collaris-bohemica*. The C/N ratio ranges 60 – 80 for the O-7 zone.

5.3.2 W55 peat core

Zone W-1 (6500 – 5000 cal yr BP)

The earliest zone of the W55 peat core is characterized by the dominance of *Difflugia pulex*, which reaches 20-50% abundance. Other significant taxa are *Difflugia oblonga* (5-37%), *Archerella flavum* (5-35%), *Phryganella acropodia* (5-15%), *Heleopera sylvatica* (maximum 10%) and *Difflugia globulosa* (maximum 10%). Minor taxa with abundance ranging below 5% are *Arcella catinus*, *Trinema corythion* type, *Hyalosphenia subflava*, *Trigonopyxis minuta*, *Arcella hemispherica*, *Difflugia globulosa*, *Heleopera sphagni*, and *Nebela vitraeae*. The C/N ratio ranges from 20 – 75 for the W-1 zone.

Zone W-2 (5000 - 4200 cal yr BP)

Zone W-2 is dominated by *Archerella flavum* with an abundance ranging from 48 to 65%. *Difflugia pulex* decreases in abundance from 50% in Zone W-1 to 4% in W-2. Other important taxa are *Amphitrema wrightianum* (8-15% abundance), *Heleopera sylvatica* (0-10%), *Assulina muscorum* (3-10%), and *Difflugia oblonga* (2-12%). Taxa that are minor (<5%) and/or infrequent are *Arcella artocrea*, *Arcella catinus*, *Trigonopyxis arcula*, *Trigonopyxis minuta*, *Arcella hemispherica*, *Difflugia lucida*, *Arcella discoides*, *Phryganella acropodia*, *Nebela vitraeae*, *Heleopera petricola*, and *Nebela griseola*. The C/N ratio ranges from 42 – 65 for the W-2 zone.

Zone W-3 (4200 – 3150 cal yr BP)

Tests of *Difflugia pulex* display a higher abundance in zone W-3 compared to W-2, ranging between 20 – 52% and become co-dominant together with *Archerella flavum* (15-50%). Other notable taxa are *Heleopera sylvatica* (5-14%), *Assulina muscorum* (0-12%), *Difflugia lucida* (3-12%), and *Phryganella acropodia* (3-6%). Minor (<5%) and/or infrequent taxa are *Arcella artocrea*, *Arcella catinus*, *Trinema corythion* type, *Bullinularia indica*, *Hyalosphenia subflava*, *Hyalosphenia subflava*, *Trigonopyxis arcula*, *Arcella hemispherica*, *Difflugia globulosa*, *Apmhitrema wrightianum*, *Arcella discoides*, *Heleopera sphagni*, and *Nebela griseola*. The C/N ratio ranges from 34 – 45 for the W-3 zone.

Zone W-4 (3150 – 2800 cal yr BP)

Zone W-4 is characterized by a slight decline in the abundance of tests of *Difflugia pulex* (22-40%) and an increase in *Heleopera sylvatica,* which now reaches its highest abundance in the W55 record and co-dominant status (11-45%). Other important taxa are *Archerella flavum* (2-20%), *Difflugia lucida* (6-12%), *Trigonopyxis minuta* (0-9%), *Phryganella acropodia* (3-8%), *Trigonopyxis arcula* (2-7%), and *Hyalosphenia subflava* (0-7%). Minor taxa (<5%) are *Nebella collaris-bohemica*, *Hyalosphenia elegans*, *Arcella artocrea*, *Trinema corythion* type, *Difflugia oblonga*, *Arcella hemispherica*, *Heleopera sphagni*, *Nebela vitraeae*, and *Nebela griseola*. The C/N ratio ranges from 38 – 45 for the W-5 zone.

Zone W-5 (2800- 1650 cal yr BP)

The W-5 zone features a notable increase in the abundance of *Difflugia pulex* tests compared to the previous zone, the taxon now ranges between 48 – 74%. Other notable occurrences are *Phryganella acropodia* (2-27%), *Archerella flavum* (0-18%), *Difflugia oblonga*

(5-15%), *Trigonopyxis minuta* (2-15%), *Difflugia lucida* (1-12%), and *Hyalosphenia subflava* (5-7%). *Nebela griseola* tests shows one significant peak of abundance (15%) at 2180 cal yr BP, the highest recorded for this species in the W55 core. Minor taxa (<5%) recorded in this zone are *Difflugia pristis*, *Arcella catinus*, *Trinema/corythion* type, *Trigonopyxis arcula*, *Arcella hemispherica*, *Difflugia globulosa*, *Amphitrema wrightianum*, *Heleopera sphagni*, and *Nebela vitraea*. The C/N ratio ranges from 50 – 95 for the W-5 zone.

Zone W-6 (1650 - 650 cal yr BP)

The W-6 zone is characterized by the decline of *Difflugia pulex,* which ranges between 10 – 55% in abundance, and large fluctuations in the abundance of *Trinema lineare* (0-35%). *Phryganella acropodia* is present at low abundance values (<5%) until 850 cal yr BP, when it increases dramatically to 44%. Other notable occurrences are *Archerella flavum* (1-32%), *Trinema/Corythion*-type (2-14%), and *Hyalosphenia subflava* (3-12%). *Difflugia globulosa* is not present until 950 cal yr BP, when it increases in abundance into the W-7 zone, ending the W-6 zone at 8%. Similarly, *Nebela griseola* makes a brief appearance at 1150 cal yr BP (6%), but is otherwise absent from zone W-6. Minor and/or infrequent taxa characterizing zone W-6 are *Hyalosphenia elegans*, *Sphenoderia lenta*, *Tracheuglypha dentata*, *Nebela militars*, *Euglypha rotunda*, *Heleopera sylvatica*, *Assulina muscorum*, *Trigonopyxis arcula*, *Hyalosphenia minuta*, *Trigonopyxis minuta, Difflugia* undiff., *Difflugia oblonga*, *Arcella hemispherica*, *Arcella discoides*, *Heleopera sphagni*, *Nebela vitraeae*, and unknown 1. The C/N ratio ranges from 32 – 51 for the W-6 zone.

Zone W-7 (650 cal yr BP – present day)

Phryganella acropodia, which reaches 72% abundance at 600 cal yr BP, the highest value recorded at this site. It dominates the most recent testate amoeba assemblage zone at the

W55 site. *Trinema lineare* features fluctuating but significant proportions (0-40%), while *Difflugia pulex* (the most frequently ocurring species in the W55 record) remains below 22% abundance. Other important taxa are *Hyalosphenia subflava* (0-14%), *Difflugia globulosa* (3-12%), and *Archerella flavum* (2-12%). A notable first time occurrence is *Placocista spinosa,* which reaches maximum abundance (7%) at 150 cal yr BP. Minor (≤5%) and/or infrequent taxa are *Nebela collaris-bohemica*, *Heleopera rosea*, *Hyalosphenia elegans*, *Difflugia bacillifera*, *Arcella artocrea*, *Nebela flabellum*, *Nebela militaris*, *Euglypha tuberculata*, *Centropyxis arculeata*, *Euglypha rotunda*¸*Heleopera sylvatica*, *Cetropyxis ecornis*, *Assulina muscorum*, *Trigonopyxis arcula*, *Cyclopyxis arcelloides*, *Hyalosphenia minuta*, *Trigonopyxis minuta*, *Nebela barbata*, unknown 1, *Arcella hemispherica*, *Difflugia lucida*, *Difflugia acuminata*, *Amphitrema writghtianum*, *Arcella discoides*, *Difflugia leidyi*, *Nebela marginata*, *Euglypha strigosa*, *Nebela vitraeae*, *Heleopera petricola*, *Nebela griseola*, and *Hyalosphenia papilio*. A notable absence from zone W-7 is *Difflugia oblonga*, which was commonly present in all other zones. The C/N ratio ranges from 30 – 48 for the W-7 zone.

Figure 5.4 (a)

Testate amoebae assemblage and Carbon/Nitrogen diagram for peat core OFL, James Bay (Québec).

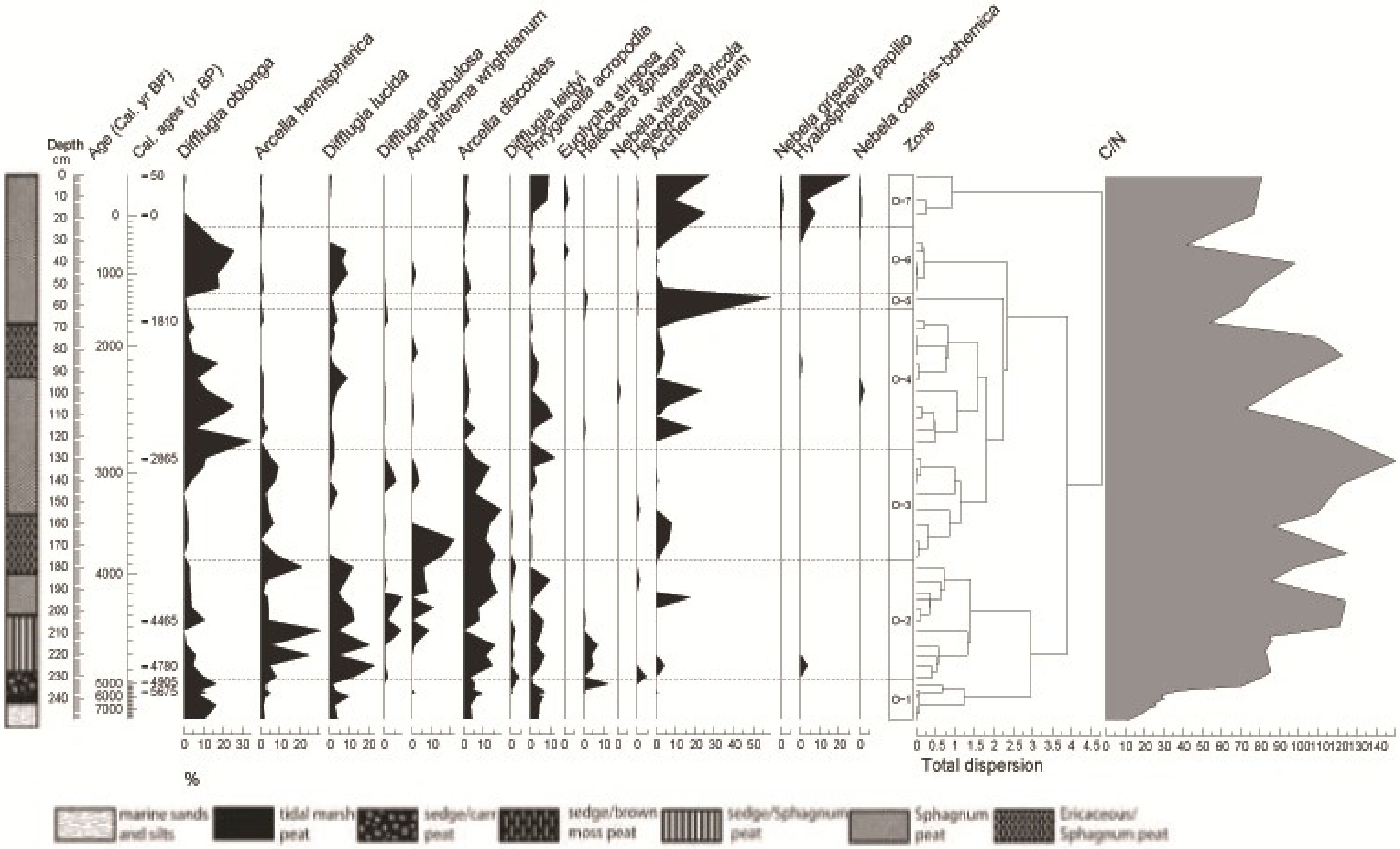


Figure 5.4 (b)

Testate amoebae assemblage and Carbon/Nitrogen diagram for peat core OFL, James Bay (Québec).

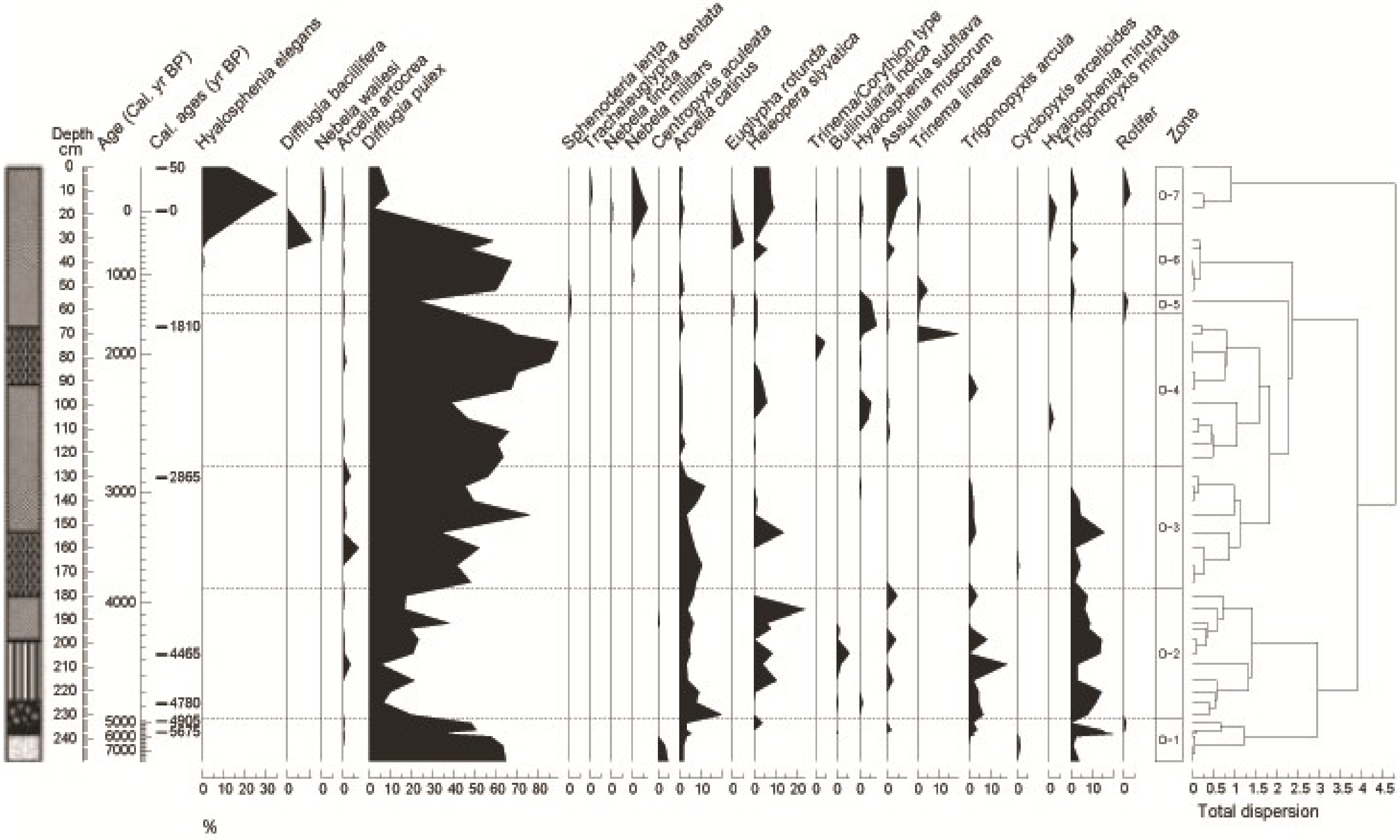


Figure 5.5 (a)

Testate amoebae assemblage and Carbon/Nitrogen diagram for peat core W55, James Bay (Québec).

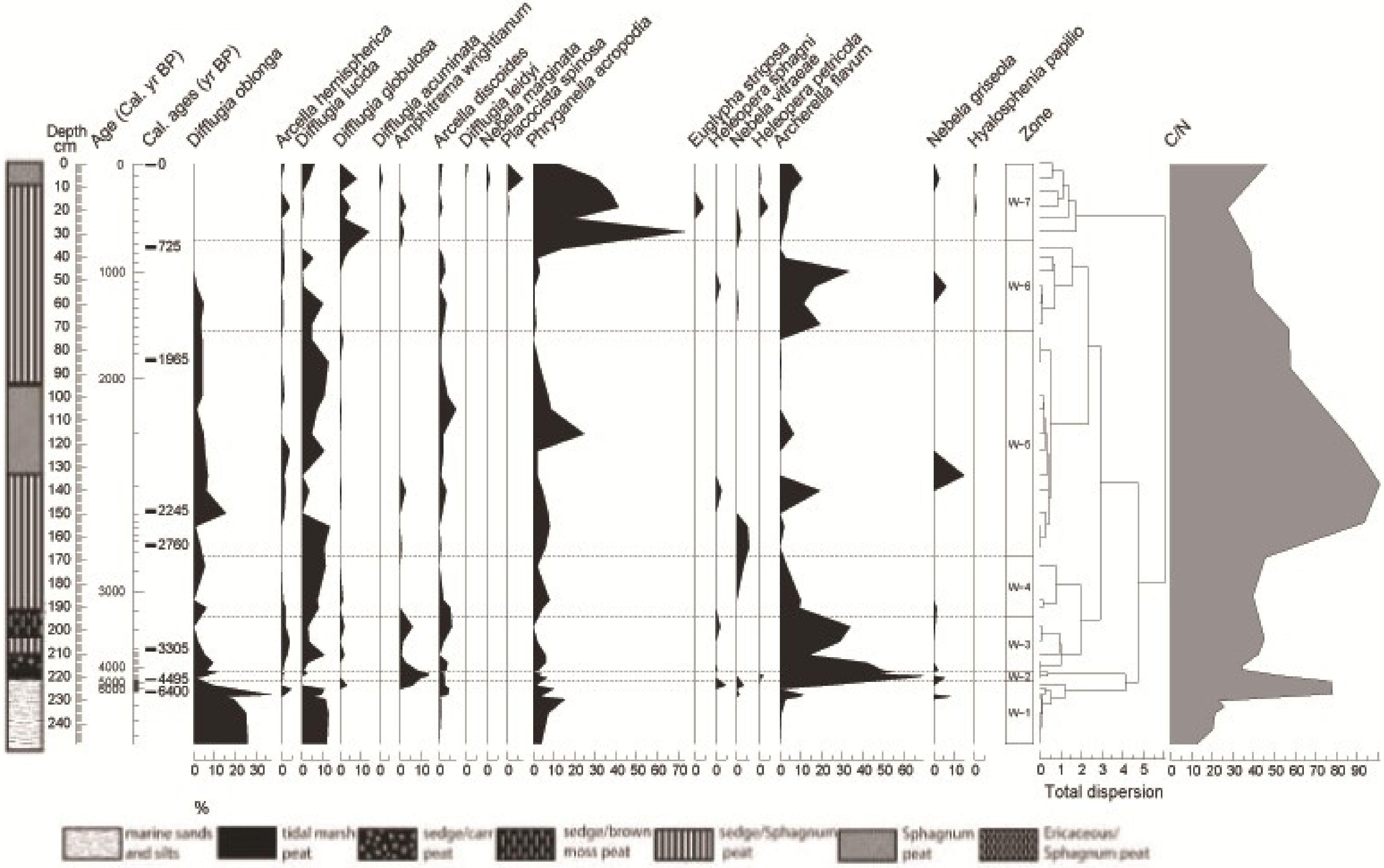
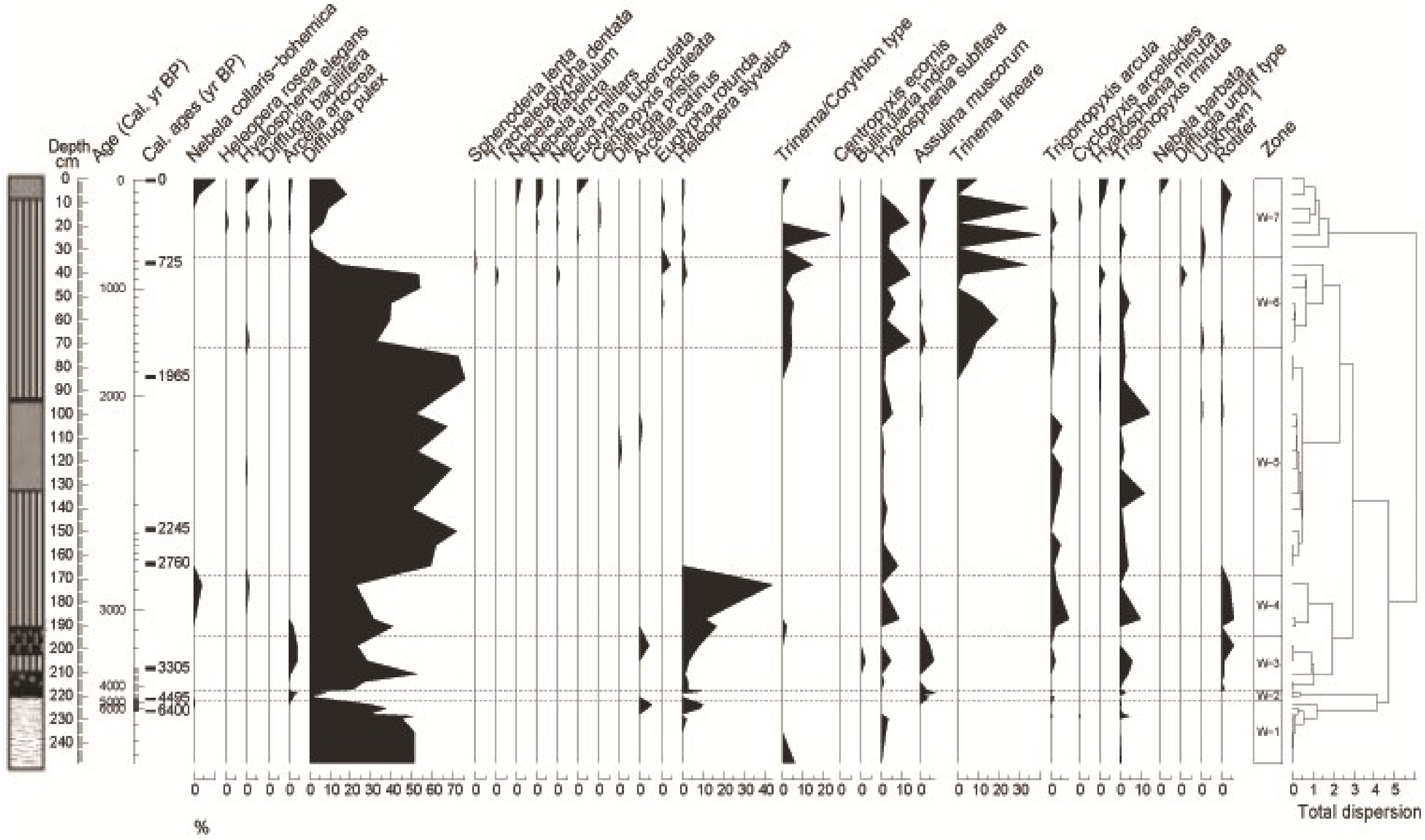


Figure 5.5 (b)

Testate amoebae assemblage and Carbon/Nitrogen diagram for peat core W55, James Bay (Québec).



5.4 C/N Analysis

In this thesis, I use C/N ratios of peatland sediments as a proxy of changes in palaeonutrient status, an important parameter in wetland succession (Pendea and Chmura, 2012). In a previous study, Pendea and Chmura (2012) surveyed 44 different modern wetlands in the James Bay region and determined the specific C/N ratio of present day low tidal marsh, high tidal marsh, fen and bog ecosystems. C/N ratios were most distinct for low marsh and bog. The average C/N were lowest for low marsh (10.2 ± 2.6) and slightly higher for high marsh (14.1 ± 1.7) and fen (14.1 ± 6.5). Bog C/N values were distinctly higher (61.3 ± 17.8) and, within the standard deviation, the bog C/N range did not overlap with any other sample group. In this thesis, I use these values as modern analogues for palaeo-C/N ratios in both OFL and W55 cores. The C/N ratio values are presented alongside the testate amoeba assemblages (Fig. 5.4 a and b; Fig. 5.5 a and b) and the palynomorph stratigraphy from Pendea (2011) (Fig. 5.6 and 5.7).

5.5 Palynomorph analysis and hydrarch succession

Fossil palynomorph data (pollen, spores, and dinoflagellate cysts) from each core were compared to modern analogues from 44 sites across eastern James Bay using squared chord distance and Discriminant Analysis (Pendea, 2011). The Discriminant Analysis identified nine palynomorph taxa in modern samples as strong indicators of various wetland types (Pendea, 2011, Pendea and Chmura, 2012). Dinoflagellate cysts, *Plantago,* and the ratio between whole and broken grains of saccate pollen were strong indicators of low marshes. Cyperaceae, Poaceae, and *Potamogeton-Triglochin*- type were important to the classification of high marshes. Bryidae spores and *Myrica gale* are indicative of fen and *Sphagnum* spores are a strong indicator of bog. For each reconstructed palaeo-wetland stage, the Discriminant Analysis derived a probability of a modern analogue (p) and, for samples with a mixed group (ecosystem) membership, the probability of group membership (P).

W55 site

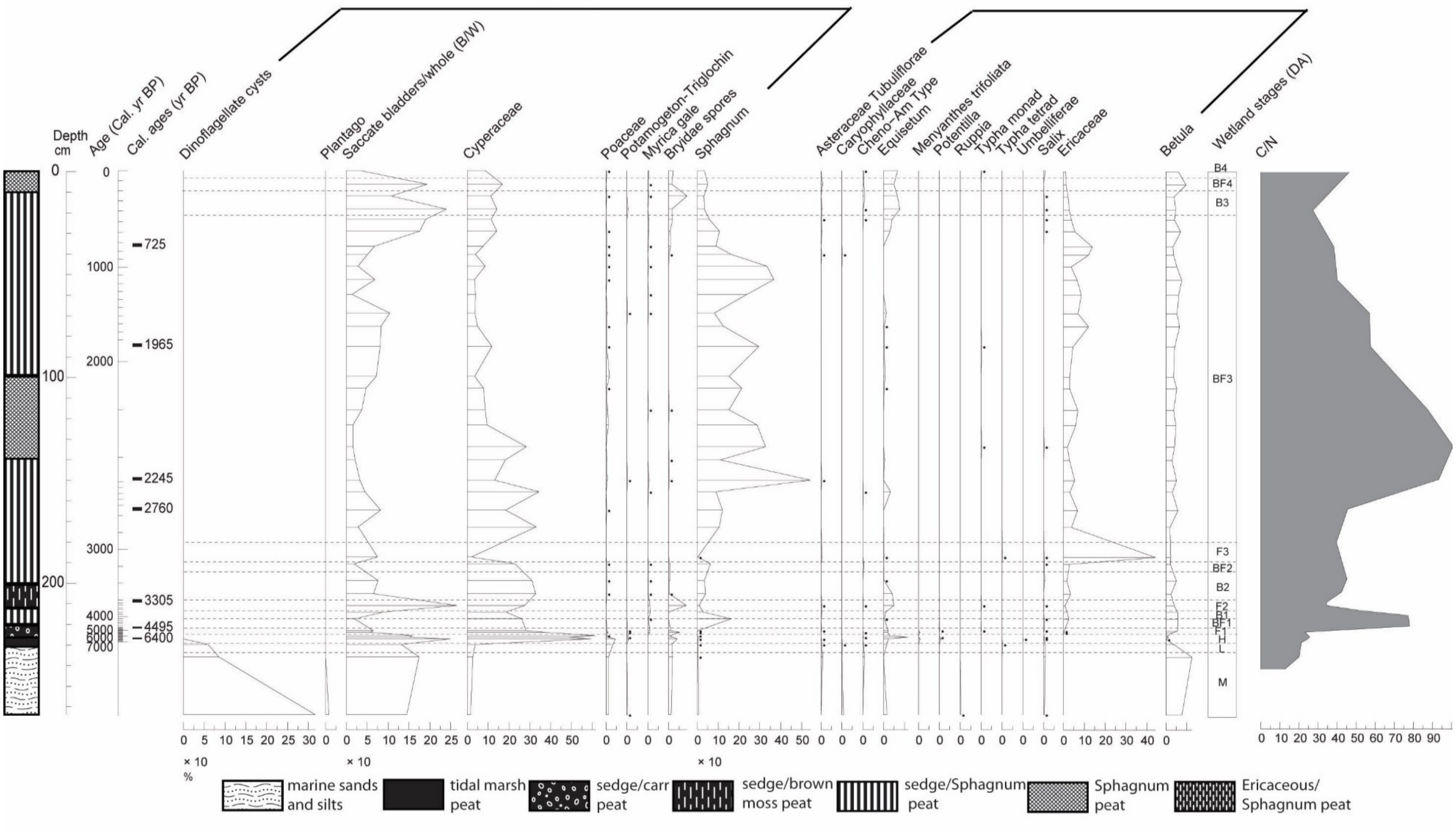
In core W55 (Fig. 5.6), the Discriminant Analysis identified 14 successive stages (Pendea, 2011). A summary of his analysis follows. The low marsh is characterized by the presence of dinoflagellate cysts and increasing proportions of Cyperaceae. The low marsh developed around 6450 cal yr BP but its duration is difficult to estimate because of the lack of age control before this time. The high marsh replaced the low marsh at 6450 cal yr BP and is defined by poor analogues and mixed group membership of Poaceae, Cyperaceae, and *Potamogeton-Triglochin* type, which attained the highest values during this phase. Around 5500 cal yr BP the high marsh is replaced by fen. The shift from high marsh to fen is characterized by the appearance of *Myrica gale* and a spike in Bryidae spores. The end of the first fen stage around 4600 cal yr BP, is indicated by a sharp rise in *Sphagnum* and a drop in broken saccate pollen and a shift from sedge-carr to sedge- *Sphagnum* peat. The following stage 4600-4000 cal yr BP is a bog/fen non-analogue. This first bog/fen is followed by a short bog stage at 4000 cal yr BP. Fen conditions then return around 3700 cal yr BP indicated with a drop in *Sphagnum* and an increase in Bryidae spores and broken saccate pollen. This corresponds to stratigraphic shift from sedge- *Sphagnum* to sedge-brown moss peat. After 3400 cal yr BP development is characterized by several oscillations between bog and bog/fen non-analogue. There is an exception at 3050 to 2950 cal yr BP where fen conditions briefly returned and Ericaceae pollen attained maximum abundance. The pollen assemblage is characterized by the dominance of *Sphagnum* varying proportions of Cyperaceae, and broken saccate pollen.

The OFL site

For the OFL site (Fig. 5.7), ten successive developmental stages were identified by Discriminant Analysis (Pendea, 2011). A summary of his analysis follows. Peat inception began in a low marsh ecosystem at ~5900 cal yr BP and persisted until 5600 cal yr BP. The low marsh phase was defined by poor analogues, but had the second highest predicted ecosystem membership as either high marsh or fen. The basal non-analogue (M) and low marsh (L) stages (Fig. 5. 7) are characterized by high values of dinoflagellate cysts and high values of broken saccate pollen. The disappearance of dinoflagellate cysts at 5600 cal yr BP and the increase of *Sphagnum* spores at 4950 cal yr BP bracket the appearance of a fen. After 4950 cal yr BP the peatland development is characterized by several bog/fen non-analogue and bog stages. The bog/fen non-analogue stage has a group membership that is primarily closest to that of bog and second closest to fen. For convenience, this non-analogue stage type has been termed "bog/fen". The pollen assemblage for this period is identified by large variations in *Sphagnum* abundance and low values for broken saccate pollen and Cyperaceae. During the last bog stage the presence of Cyperaceae species increases considerably. Stratigraphically, the bog/fen non-analogue stages are generally characterized by alternations of sedge- *Sphagnum*, Ericaceaous- *Sphagnum*, and *Sphagnum* peat, whereas during bog stages only pure *Sphagnum* peat is deposited (Pendea, 2011).

Figure 5.6

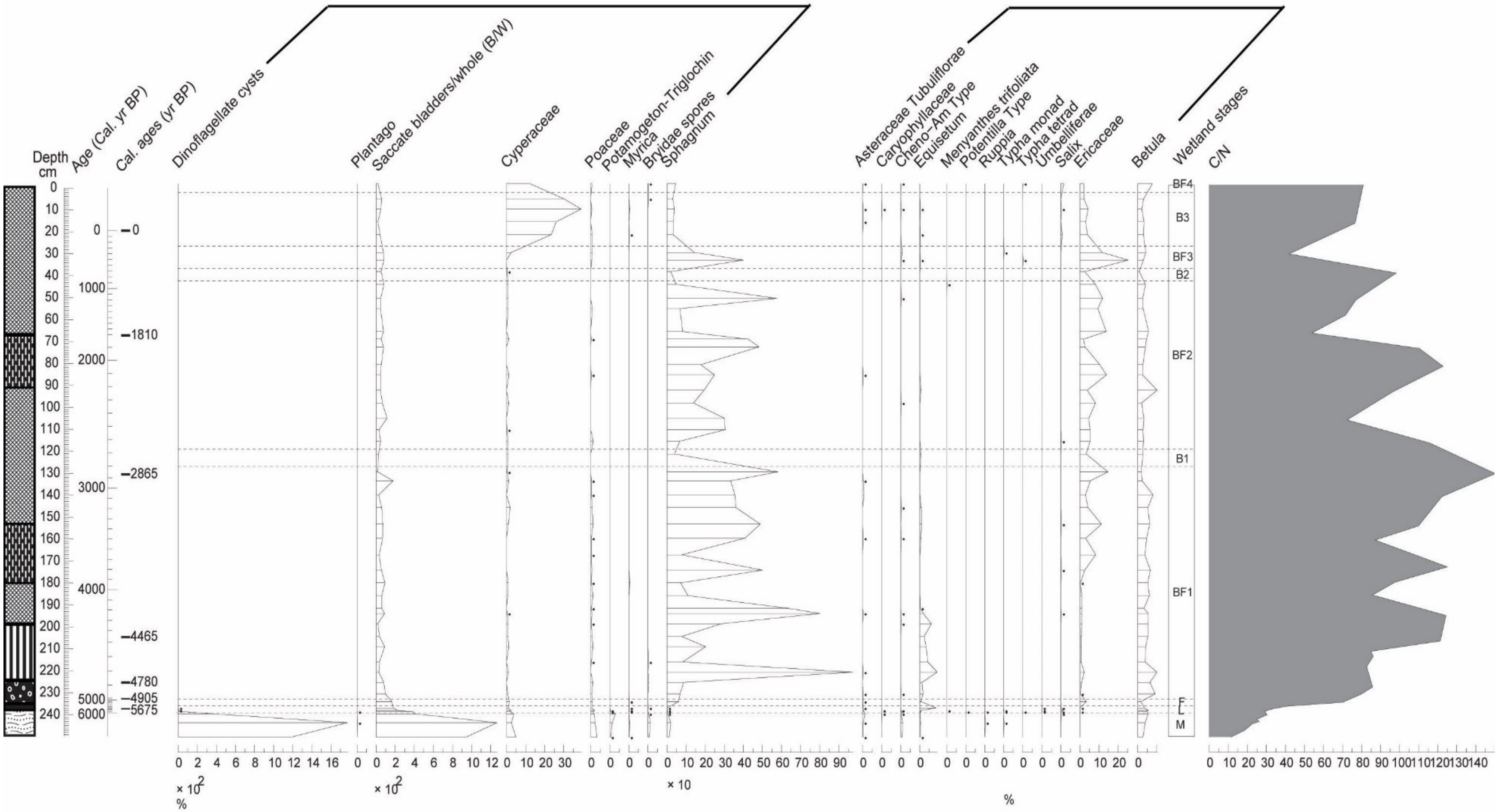
Pollen assemblage diagram displayed alongside C/N data and stratigraphy for W55 peat core James Bay, Québec (Pendea, 2011). Pollen data was plotted against depth and age (cal yr BP).



(*Note: Wetland stages: M = marine, L = low marsh, H = high marsh, F = fen, BF = bog/fen, B = bog)

Figure 5.7

Pollen assemblage diagram displayed alongside C/N data and stratigraphy for OFL peat core James Bay, Québec (Pendea, 2011). Pollen data was plotted against depth and age (cal yr BP).



(*Note: Wetland stages: M = marine, L = low marsh, H = high marsh, F = fen, BF = bog/fen, B = bog)

(*The legend for stratigraphy is the same as Figure 5.6)

5.6 Testate amoeba-inferred Water-Table-Depth (WTD)

WTD results for the OFL core

The palaeohydrological reconstruction of the OFL peatland shows an average WTD that is somewhat less variable than that of the W55 core. The average WTD for the OFL core was 11.05 cm with an average standard error of ± 10.6 cm.

Between 5800 and 5600 cal yr BP the WTD was relatively large (up to 20 cm) followed by a considerable decrease (≈ 5 cm) at 5000 cal yr BP. There is also a significant increase in the WTD (≈ 15 cm) between 3500 – 3400 cal yr BP where the WTD reaches 27 cm. The WTD shows a decrease (≈ 24 cm) after this drying event, resulting in a WTD level of just 2 cm at 2700 cal yr BP. The remainder of the core shows a fluctuating WTD pattern with slight drying at 1400 cal yr BP, followed by wetting at 900 cal yr BP. During the last millennium, WTD at the OFL site shows a general decrease (drying) with the exception of a wetter phase during the last few decades.

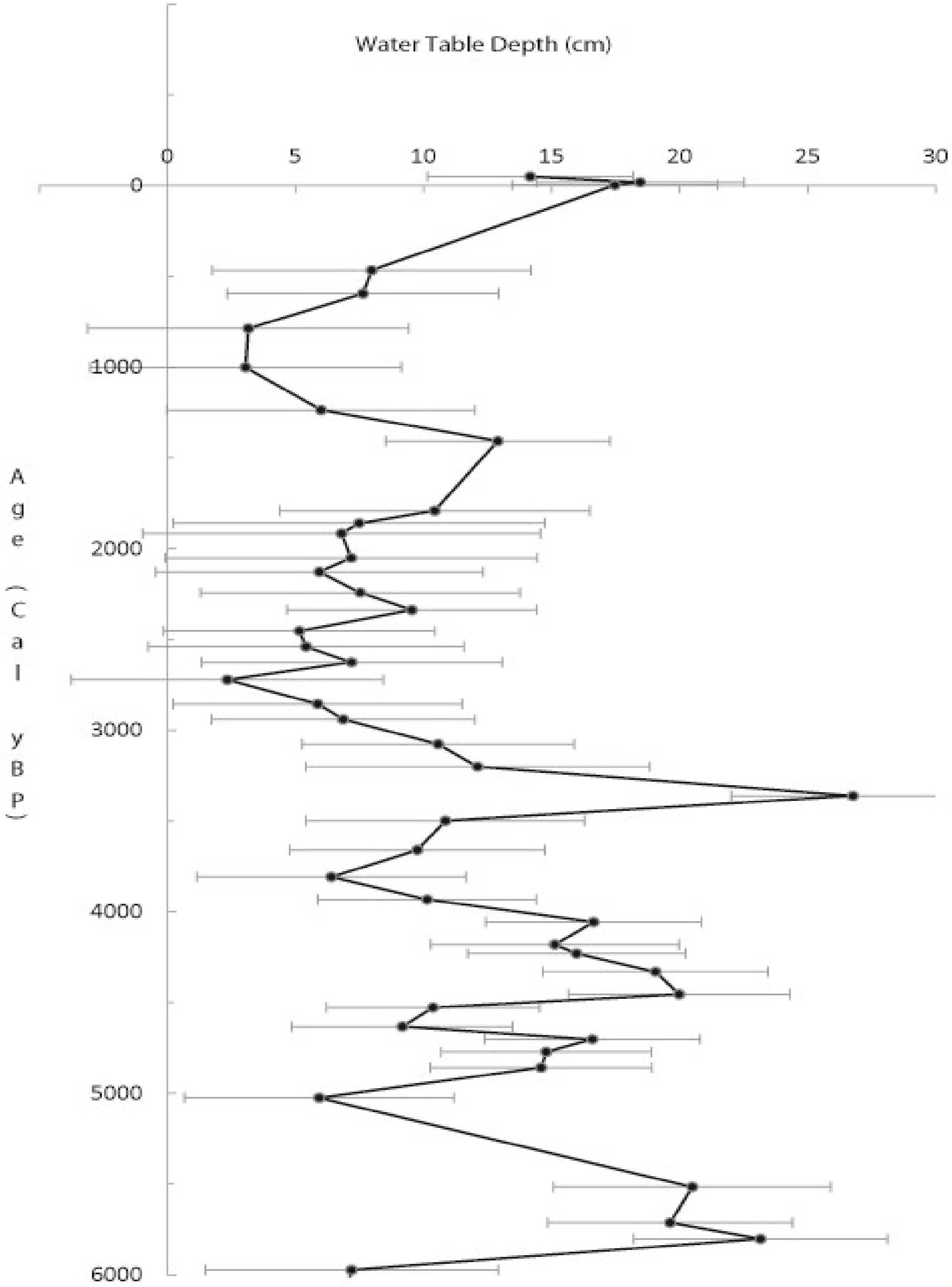
The WTD results for the W55 core

The palaeohydrological reconstruction of the W55 peatland shows a highly fluctuating WTD. The average WTD for the W55 core was 10.56 cm with the average standard error of ±9.96 cm.

Between 6450 – 5500 cal yr BP the WTD shows an increase from 2 to 8 cm. There is a significant drying event that begins at 3550 cal yr BP, which shows a WTD increase of ≈ 10 cm, followed by a quick decline (≈ 7 cm) and then further increase (≈ 15 cm), when the W55 WTD level reaches the maximum value. This drying phase is followed by a decrease in the WTD of ≈ 15 cm and further by an extended period (2 millennia) of drastic fluctuation in the WTD. During the last 500 years, the W55 WTD values shows a steep decrease to their wettest level in the site's history, although this trend seems to reverse during the last 60 years.

Figure 5.8

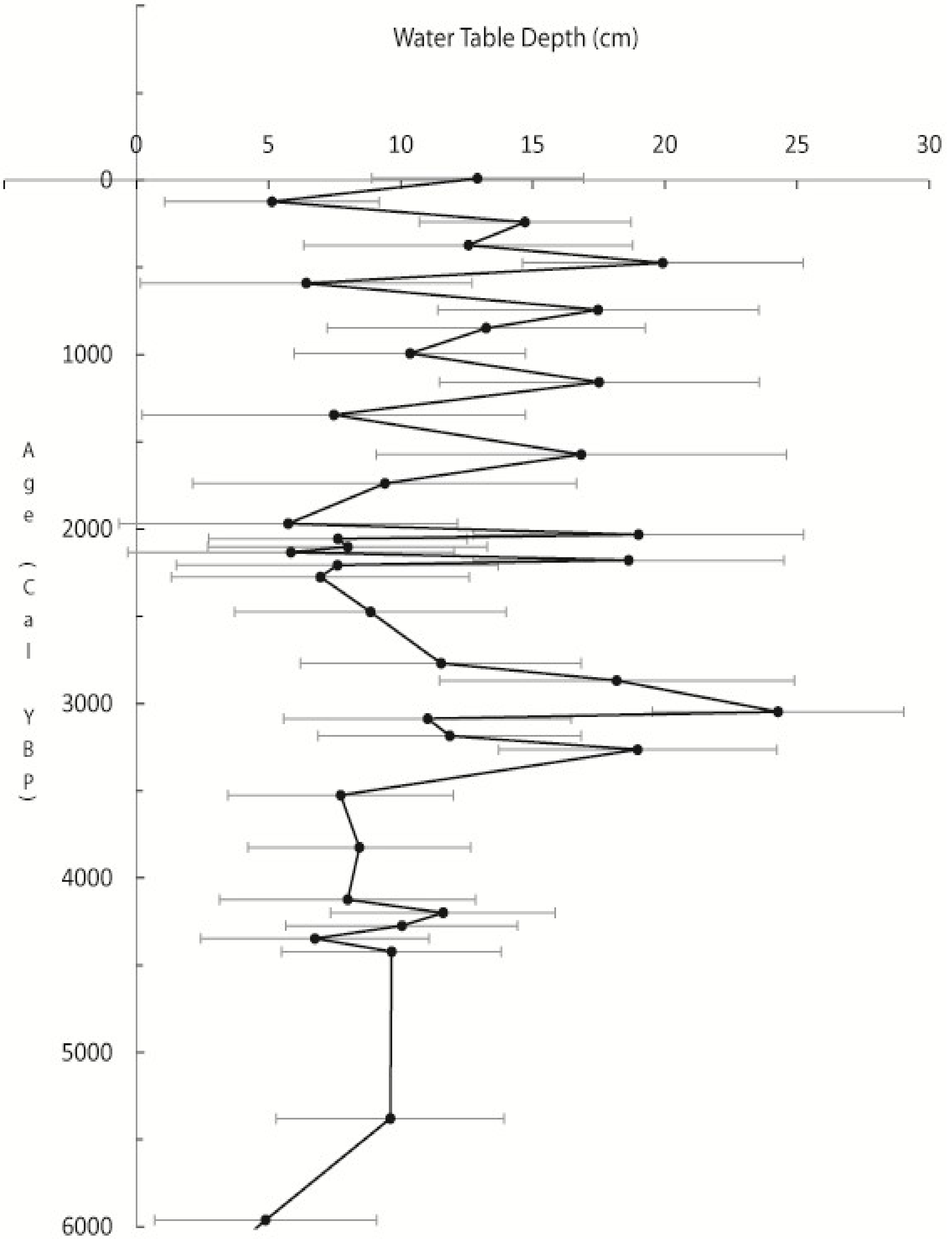
Water-Table-Depth/Age diagram for OFL peat core James Bay, Québec.



Raw testate data plotted using the WA-PLS model (Booth, 2007) applied using C2 software (Juggins, 2003).

Figure 5.9

Water-Table-Depth/Age diagram for W55 peat core James Bay, Québec.



Raw testate data plotted using the WA-PLS model (Booth, 2007) applied using C2 software (Juggins, 2003).

5.7 Water-Table-Depth and palynomorph-inferred hydrarch succession overlay

In order to investigate whether the changes to the water table levels coincide with major shifts to peatland development and to determine whether these changes have a causal relationship, the testate amoebae-inferred hydrology (WTD) results were compared to the hydrarch succession inferred through palynomorphs by Pendea (2011). The results for the OFL core are presented in Figure 5.10 and for the W55 core in Figure 5.11.

The following sections will present the analysis of the hydroseral transitions in relation to the recorded changes to hydrology throughout the two peat cores. The hydroseral nomenclature is statistical as given by Pendea (2011). However, the ecological status of the bog-fen non-analogue is similar to that of poor fen ecosystems (Pendea, 2011).

5.7.1 The OFL peat core

Stage 1: Marine (Before 5900 cal yr BP)

The first stage from 8000 – 5900 cal yr BP was classified as marine and therefore has no relevance to my research question.

Stage 2: Low Marsh (5900 – 5600 cal yr BP)

The second stage marks the beginning of peat inception at the site and was classified as low marsh. The retreat of the marine waters and the beginning of the tidal influence is marked by a dramatic drying of the peat surface (increase in WTD to 24 cm), followed by slight fluctuations thereafter.

Stage 3: Fen (5600 – 4950 cal yr BP)

This early fen phase is characterized by a major swing to wetter conditions as indicated by the decrease in WTD to 6 cm.

Stage 4: Bog-Fen (4950 – 2800 cal yr BP)

The first bog-fen (poor fen) stage appears at 4950 cal yr BP and this time period shows varying hydrologic conditions with a WTD range between 8 and 27 cm. The driest peat surface is attained at ~3400 cal yr BP, followed by a substantial wetting (WTD of 6 cm) towards the end of this stage.

Stage 5: Bog (2800 – 2650 cal yr BP)

The first bog stage begins at 2800 cal yr BP and lasts only a couple of hundred years. The palaeohydrology of this phase indicates the wettest conditions in the site's history, when water above the peat surface may have been possible.

Stage 6: Bog-Fen (2650 – 900 cal yr BP)

The second bog-fen zone follows a similar pattern to the first bog-fen zone with varying WTD levels. The WTD fluctuates between 5 and 13 cm, with the driest phase at 1400 cal yr BP.

Stage 7: Bog (900 – 650 cal yr BP)

The second bog stage at the OFL was short, lasting only 250 years. Similar to the previous bog stage, the hydrological conditions at the peat surface were clearly wet as indicated by a WTD of ≈4 cm.

Stage 8: Bog-Fen (650 – 300 cal yr BP)

The third bog-fen stage is shorter in duration than the previous two. The WTD shows a general increase from 4 – 9.5 cm.

Stage 9: Bog (300-50 cal yr BP)

The lack of sufficient sample resolution (data points) for the last bog stage makes an analysis of the relationship between hydroseral succession and hydrology difficult. However, the end of this zone is marked by an increase in the WTD which suggest drying of the peat surface towards the next developmental stage.

Zone 10: Bog-Fen (50 cal yr BP -present day)

The final bog-fen stage is characterized by relatively low water table, oscillating between 14 and 18 cm. The vegetation survey conducted by Pendea in 2007 confirms the presence of a poor fen ecosystem at this site although some areas of the OFL peatland feature domed ombrotrophic communities typical of bogs.

5.7.2 The W55 peat core

Stage 1: Marine (Before 6500 cal yr BP)

The marine silty-sands deposited before 6500 were reconstructed as a submerged marine ecosystem and therefore has no relevance to my research question.

Stage 2: Low Marsh (6500 – 6450 cal yr BP)

The low marsh developed after ~6500 cal yr BP, however, due to poor age control in this interval it is difficult to precisely estimate the length of this stage. The WTD during this stage is variable (2-10 cm) but generally indicative of a wet peat surface.

Stage 3: High Marsh (6450 – 5500 cal yr BP)

The high marsh stage begins ~6450 cal yr BP with a water table close to the surface (2 cm), increasing to 8 cm towards the end of this stage.

Stage 4: Fen (5500 – 4600 cal yr BP)

The first appearance of fen conditions at the W55 site occurs at ~5500 cal yr BP. Unfortunately, the peat layer deposited during this stage was thin and compacted, which resulted in a low sampling resolution (few data points) during this period. The WTD values for this stage are similar to those of the high marsh.

Stage 5: Bog-Fen (4600 – 4000 cal yr BP)

The first poor fen stage at the W55 site shows a relatively stable WTD with minor fluctuations between 7 and 12 cm.

Stage 6: Bog (4000 - 3700 cal yr BP)

The first bog stage is short and is characterized by a WTD similar to that of the previous stage.

Stage 7: Fen (3700 – 3400 cal yr BP)

The second fen stage at the W55 site is shorter than the first and is characterized by an increasing WTD, reaching 15 cm towards the end of this stage.

Stage 8: Bog (3400 – 3150 cal yr BP)

The second bog zone is slightly shorter than the first and features relatively dry peat surface conditions (WTD 9-20 cm).

Stage 9: Bog-Fen (3150 – 3050 cal yr BP)

The second poor fen stage is one of the shortest hydroseres at the W55 site (100 years). The WTD in this zone begins at 8 cm and then increases for the rest of the zone into the following fen zone.

Stage 10: Fen (3050 – 2950 cal yr BP)

The third fen stage is short (100 years) and is characterized a marked drying of the peat surface with the WTD reaching 25 cm.

Stage 11: Bog-Fen (2950 – 400 cal yr BP)

The third poor fen stage is the longest hydrosere at the W55 site. The stage is characterized by a highly variable water table (6-21 cm), with a generally wetter sub-stage between 2950 – 2000 cal yr BP and a somewhat drier sub-stage thereafter.

Stage 12: Bog (400 – 200 cal yr BP)

The third bog stage is shorter than the previous two lasting only about 200 years. The WTD is relatively stable with values between 11 and 13 cm.

Stage 13: Bog-Fen (200 – 100 cal yr BP)

The last poor fen stage is short (100 years) and is characterized by slightly wetter conditions than that of the previous stage 12.

Stage 14: Bog (100 cal yr BP –present day)

The last bog stage represents the modern ecosystem at the W55 site. The palynomorph-inferred reconstruction is confirmed by the modern vegetation survey conducted by Pendea in 2007, which identified a raised ombrotrophic bog at the site. The reconstructed WTD is ≈ 13 cm.

Figure 5.10

Biplot illustrating the relationship between hydrology (WTD) and hydrarch succession for the OFL peat core, James Bay, Québec.

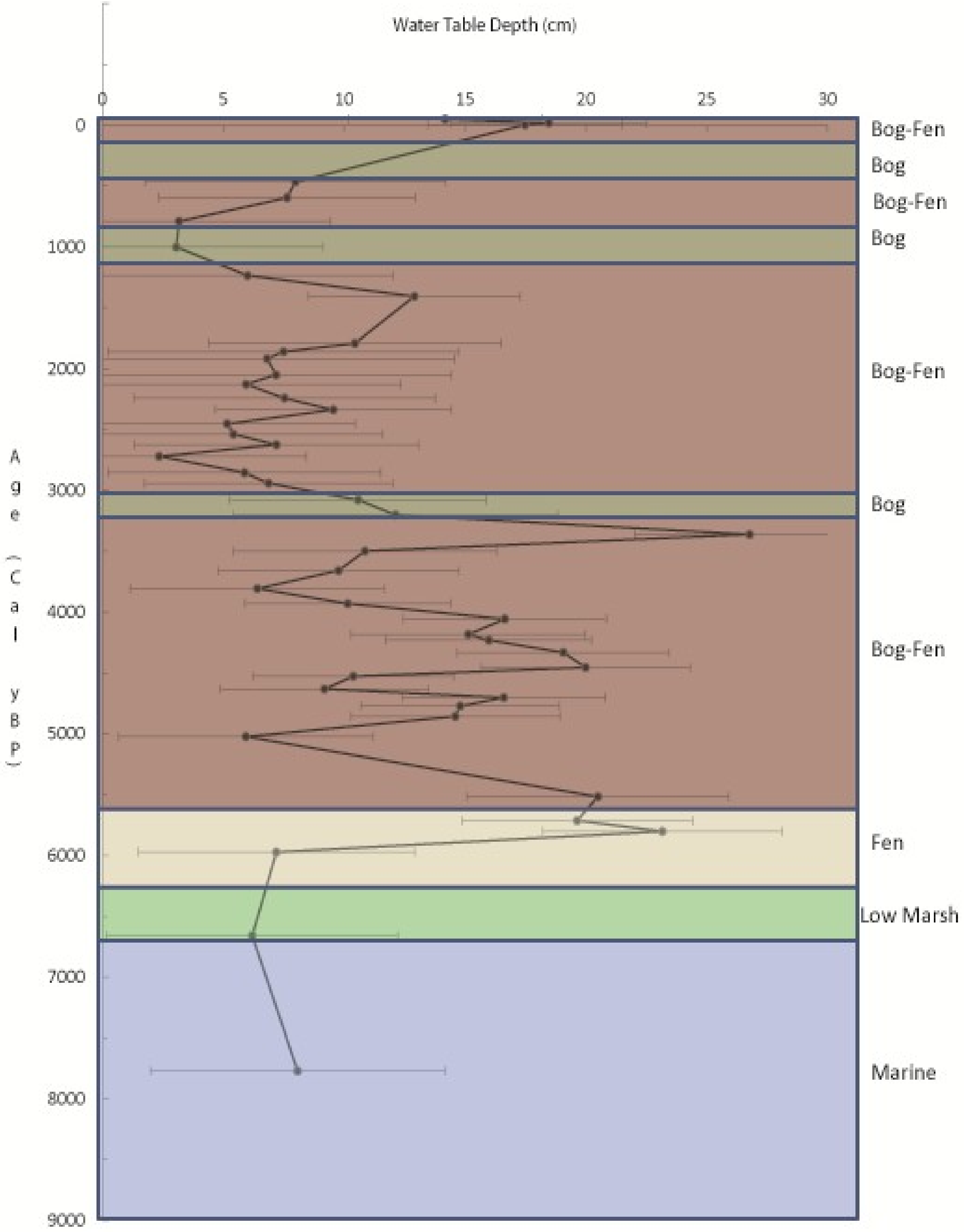
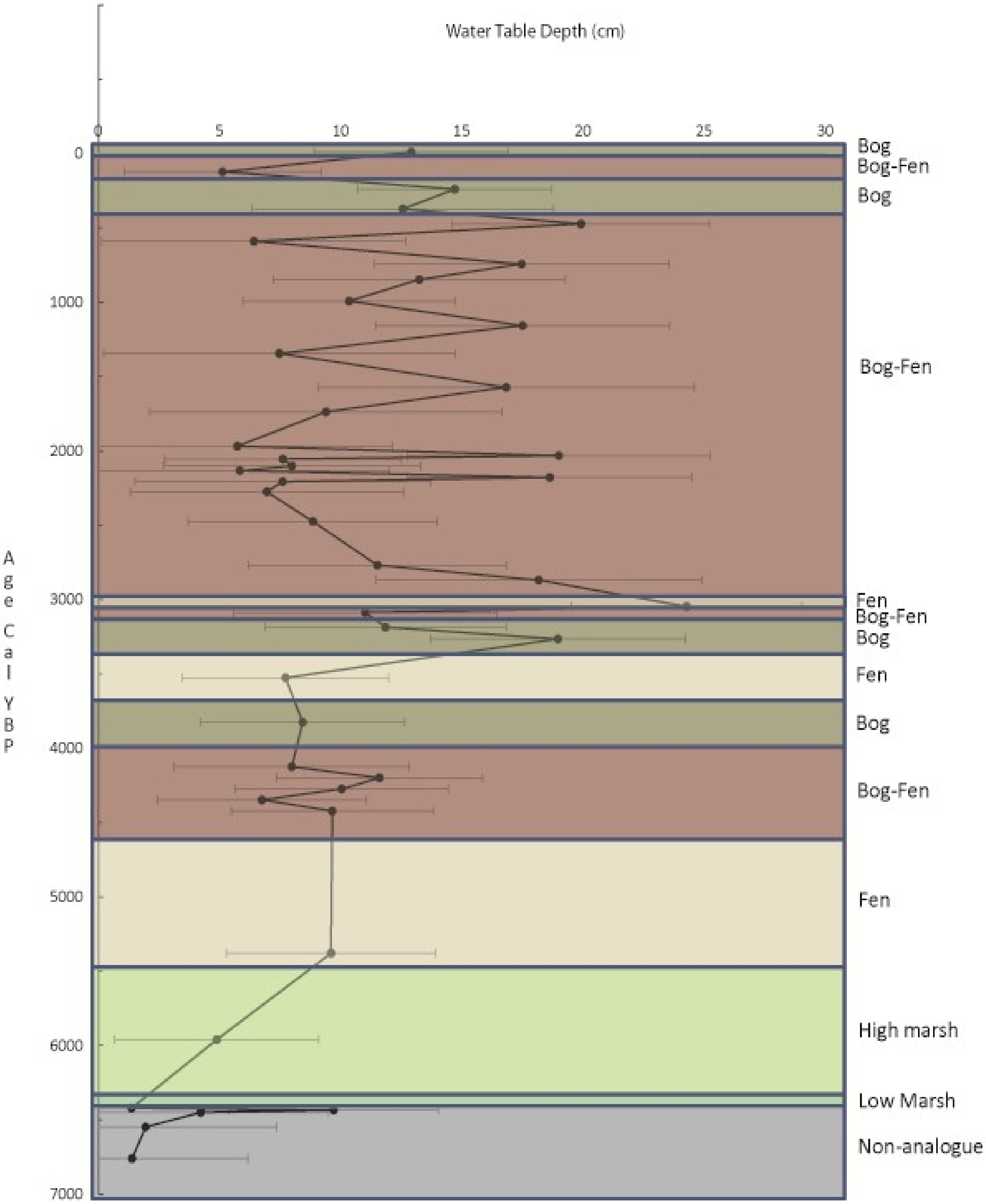


Figure 5.11

Biplot illustrating the relationship between hydrology (WTD) and hydrarch succession for the W55 peat core, James Bay, Québec.



Chapter 6) Discussion

6.1 Hydrological change and hydrarch succession – is there a causal relationship?

The palaeoenvironmental data presented in Chapter 5 allows me to explore the relationship between peatland hydrology and major shifts in peatland development that have occurred in two peatlands from northern Quebec over several millennia. I specifically ask whether changes in hydrology drive hydrarch succession in these peatlands and seek to identify the potential causes of hydrological changes. The combined testate amoeba and palynomorph data reveal that the OFL and W55 peatlands have evolved differently during the last 5500 years although there are some interesting commonalities, both taxonomic and temporal.

6.1.1 OFL site

The OFL site emerged from the sea after 5900 cal yr BP under the influence of isostatic rebound (Pendea, 2011). The establishment of a tidal wetland between 5900 and 5600 cal yr BP is marked by a lowering of the water table most probably due to the continuing decline of the sea level. At this stage, the causal relationship between the lowering of the water table and hydroseral succession is obvious. After the terrestrialisation of the site at 5600 cal yr BP, major water table fluctuations are consistently associated with shifts in hydroseral development. For instance, major episodes of wetting at 5000, 2700, and 900 cal yr BP are associated with shifts towards ombrotrophy, the first from fen to poor fen and the latter from poor fen to ombrotrophic bog. The consistent association between the rise of the water table and the initiation of bog communities at the OFL site raises an interesting question: did wetting of the peat surface drive the advent of bog communities? Although correlation doesn't necessarily imply causation, the palaeohydrological reconstruction suggest that in all three cases the rise in the water table started before the hydroseral change and thus hydrology could be viewed as a driver. The only exception is the last bog phase when ombrotrophy seems to be achieved through a downward movement of the water table. However, the interval between 600 cal yr BP and present is characterized by several short hydroseres dominated by poor fen conditions and therefore it is difficult to conclude on causality.

6.1.2 W55 site

The W55 site emerged from the sea after 6500 cal yr BP under the influence of rapid isostatic rebound (Pendea et al., 2010). The sharp decline in the water table level during the tidal wetland stages show the continued effect of isostatic rebound and subsequent sea retreat. As in the case of the OFL site, the lowering of the water table was clearly responsible for the appearance of tidal wetland conditions during this time. After the retreat of the tidal influence at 5500 cal yr BP, the W55 peatland undergoes several hydroseral shifts that seem to be associated, to some extent, with swings in water table levels. For instance, the W55 site undergoes a major drying phase at 3100 cal yr BP, which corresponds to a shift towards more minerotrophic conditions (lower C/N ratios; Fig. 5.6) and the appearance of a fen community at the site. The single large peak in Ericaceous pollen suggests a rather dramatic shift in the peatland community (Fig. 5.6). However, the relationship between drying and the appearance of fen conditions is not straight forward as hydroseral succession shows several contrasting shifts between the relatively long period of water table high stand (5500 – 3500 cal yr BP) and the extreme drying episode at 3100 cal yr BP. This situation suggests that rather than causing a unidirectional shift in the hydroseral development, the drying process destabilized the peatland community into contrasting shifts in opposite directions. The following section will focus more specifically on the possible underlying mechanisms behind these shifts. The same type of instability seems to be generated during a relative rise in the water table level between 500 cal yr BP and present. In this case, however, the higher water table position seems to favor the development of bogs, somewhat similar to the OFL site. The relationship between water table shifts and change in the wetland community is less obvious here. For instance, the relative rise in water tables between 500 cal yr BP and present seems to be associated with two short lived bog phases, although a causal relationship is difficult to establish, particularly since similar water table shifts (i.e., between 3000 and 2000 cal yr BP) have resulted in no such hydroseral development.

6.2 Inter-site comparison of long-term hydrological development

After the initial terrestrialisation and the retreat of tidal influence, the local hydrology patterns are largely different between the two sites with a notable exception between 3500 – 2900 cal yr BP (discussed in section 6.4). These differences suggest that hydrology was controlled, to a large extent, by local factors such as topography, drainage patterns and proximity to local base levels.

The OFL site developed on a tidal flat, which before land emergence was a large protected bay (Pendea, 2011). When the sea finally retreated, the former bay was replaced by a lake (Old Factory Lake), with almost the same spatial extent and general landscape configuration. The current elevation of the lake water level is at 103 m a.s.l. This local base level created by the Old Factory Lake represents the primary control for the local water table level at this site. The flat local topography, the lack of surface drainage, and poor subterraneous drainage due to the thick marine clay layer at its base, represent the other controls on wetland development.

The W55 site developed from a small cove on the northwest side of a newly emerged island (Pendea, 2011). Following rapid sea level fall, the site developed into a coastal meadow and ultimately a peatland surrounded by relatively steep slopes. The site currently has an elevation of 130 m a.s.l. and is partially drained by a brook on the northern margin. Consequently, the W55 peatland may have received substantial surface runoff and may have had its local water tables controlled, at least to some extent, by surface drainage. The subterraneous drainage, however, was largely similar to that of the OFL site because marine clays also form the basal sediments of the W55 peatland.

The hydrology pattern for the OFL peatland compared to that of W55 site reveals a much closer association with hydrarch succession, suggesting that hydrology may have been the predominant factor in directing successional development of peatland communities near Old Factory Lake. In contrast, the hydrarch succession of the W55 site is more variable and the presence of successional reversals points to an important allogenic control with drivers other than hydrology. Still, I suggest that the noisier hydrology signal from the W55 peatland, may have contributed to the successional instability of this site, although direct correlation between hydrologic shifts and discrete successional stages is largely lacking. The continuous pattern of water table fluctuation in the W55 peatland could have been driven, in part, by slope runoff patterns and fluvial processes. Runoff and fluvial activity may have also controlled nutrient loading in the peatland, which in turn would have affected the ecological succession of peatland communities.

One exception to the site-specific hydrological pattern characterizing the two peatlands is the period between 3500 – 2900 cal yr BP, when both sites experience a substantial lowering of the water table. This synchronous and syn-directional hydrological event for two peatlands that evolved in such different geomorphological conditions points to a regional controlling factor, possibly climate (full discussion in section 6.4).

6.3 Contrasting successional pathways: the role of water table depth

The millennial-scale variability of peatland water table depth at the two peatland sites in the context of local successional changes suggests that hydrarch succession, in particular the transition to ombrotrophic conditions, can be achieved through contrasting pathways. These contrasting pathways have also been identified by Hughes and Dumayne-Peaty (2002) who suggest the achievement of ombrotrophy can occur through both lowering and rising water table conditions. While most fen to poor fen and poor fen to bog transitions at the two sites investigated here were mediated by rising water tables and/or wetter peat surface (Fig. 5.10 and Fig. 5.11) in some instances, oligotrophic and/or ombrotrophic communities seem to be favored by falling and/or unstable water table levels. For instance, the OFL bog stage at 400 cal yr BP and W55 bog stage at 3300 cal yr BP occurred during relative dry episodes. While, similar contrasting pathways to ombrotrophy have been found elsewhere in the Hudson/James Bay region (Beaulieu-Audy et al., 2009; Lamarre et al., 2012; Bunbury et al., 2012; Hargan et al., 2015) and in other regions (Hughes, 2000; Hughes and Dumayne-Peaty, 2002), the underlying mechanisms behind this phenomenon are less than straightforward.

In their seminal paper, Hughes & Dumayne-Peaty (2002) found direct, palaeoecological evidence supporting contrasting pathways towards ombrotrophy. Their study found two contrasting fen to bog transitions, one initiated from dry-hummocky communities, and the other from wet-tussocky communities surrounded by shallow bog pools. The authors suggests that in the latter case, the transition occurred from the formation of the shallow bog pools combined with the leaching of nutrients from the tops of the tussocks and the cation absorption capacity of the tussock forming species *Eriophorum vaginatum*, which may have been the dominant processes causing acidification leading to ombrotrophic conditions. This process may have been aided by an increase in precipitation, which would cause the leaching of nutrients resulting in widespread establishment of *Sphagnum* (Hughes & Dumayne-Peaty, 2002).

In southeastern James Bay (Eastmain Basin), Loisel & Garneau (2010) found evidence that suggests ombrotrophy was achieved through dry conditions at one site and wetter hydroclimatic conditions at another. The authors suggest in the latter case, that ombrotrophic conditions were achieved through highly humified peat that isolated the growing surface from groundwater supplies.

Hughes (2000) found shifts in peatland development from fen to bog to be associated with high standing water levels. The authors suggest that the development of catotelmic peat during the initial minerotrophic stages allows for the creation of a doming or raised mound effect by either impeding drainage or the entrapment of methane. Authors suggest that environmental conditions that favor the production of highly humified, finely structured peats with low permeability may be expected to provide optimal foundations for the formation of a raised water mound. They suggested that the commonly found universal bed of highly degraded *Eriophorum/Calluna* peat lying above fen levels and below the upper fresher *Sphagnum* peat within raised bogs provides evidence to support the theory of water mound formation resulting as a consequence of the production of a relatively impermeable, finely continuous peat layer (Hughes, 2000)

In the case of this study, the OFL peatland showed a tendency toward formation of bog conditions under high standing water levels. It is possible that this transition occurred similarly to the process described by Hughes & Dumayne-Peaty (2002). The formation of shallow bog pools which become domed due to the development of catotelmic peat that impedes drainage combined with the leaching of nutrients from the tops of the vegetation causing acidification may have been the mechanism driving the change from fen to bog under high standing water levels. This process could also have been aided or advanced by increased precipitation levels because the OFL site is relatively flat, therefore an increase to the overall precipitation could result in raised water table levels.

The appearance of successional reversals in peatlands offers an opportunity to investigate further the role of hydrology. For instance, Holmquist & MacDonald (2014) found a peak in moisture to be associated with a reversal from *Sphagnum* to herbaceous dominated peat. They suggest this development would only occur in permafrost areas, under conditions of permafrost degradation due to warming. Although, for the W55 peatland the hydrology seems to have played a lesser role in hydrarch succession, there are some successional reversals where shifting water tables may have played a role. For instance, the hydrosere reversals such as bog to poor fen, took place under drying conditions (e.g., 3700 cal yr BP and 3050 cal yr BP) and low water table levels (Fig 5.11). The establishment of fen communities under drying conditions was also recorded by other researchers in the region (e.g., O'Reilly, 2011) and elsewhere (Hughes et al., 2007). In the case of O'Reilly (2011), the study found the persistence of a fen community under drying conditions that would generally favor bog development. The author suggests that the persistence of the fen-type ecosystem and lack of transition to ombrotrophy under drying conditions is the result of persisting minerotrophic influence (i.e., nutrient loading from connection to the minerotrophic waters of the local drainage network). This is due to the long term structural and compositional stability of the fen, which the author suggests should be considered the climax community for that particular site. Hughes et al. (2007) found that recent reversals from bog to fen-type ecosystems appear under conditions of nutrient loading (nitrogen and phosphorus). They suggest that this nutrient loading is a key driver of the establishment of minerotrophic conditions (Hughes et al., 2007).

Based on the combined results of the palaeoecological and hydrological conditions of the W55 site, it is likely that the geomorphological features of the site were capable of causing similar conditions to those identified by Hughes et al. (2007) and O'Reilly (2011) where continuous nutrient loading resulted in the persistence of (or reversal to) fen communities. Supporting evidence is provided by the C/N ratios for the W55 peatland which shows much lower C/N values than the OFL peatland. The low C/N values indicate higher levels of nitrogen and therefore more available nutrients in the W55 peatland. In contrast, the OFL peatland, which showed a greater tendency towards ombrotrophy shifts, had much lower overall C/N values, which indicate lower nutrient input into the OFL peatland.

6.4 Factors affecting hydrology in peatlands

The role of hydrology as an important allogenic factor in peatland development has been well established even as the exact mechanisms are, to some extent, still unclear. However, hydrology is mostly an intermediary factor in peatland development because the initial allogenic drivers are often climatic, geomorphologic, or anthropogenic. In this section, I will attempt to answer my third and last research question: What are the factors driving peatland hydrology changes in the study region?

6.4.1 Isostatic rebound

The influence of isostatic rebound on the James Bay coast is clearly reflected in the initial stages of the hydrological reconstruction for the OFL (Figure 5.10) and W55 (Figure 5.11) peatlands. In both cases, the hydroseral transitions from marine to tidal marsh stages are marked by lowering water table levels, which would be expected as falling sea levels would induce a lowering of the local water table levels. The drying recorded in these initial tidal marsh stages ends, in both cases, with the development of the freshwater fen, which marks a relative disconnect between the continuing isostatic rebound (Pendea et al., 2010) and water table fluctuations. The differences between the OFL and W55 long-term hydrological regimes, after the disappearance of tidal influence, provides further evidence that isostatic rebound was an early but short-lived driver of peatland hydrology. Similar finds were obtained throughout the Hudson/James Bay region by Klinger & Short (1996), Glaser et al. (2004), Beaulieu-Audy et al. (2009), Pendea et al. (2010), and Bunbury et al. (2012) who suggest that, after terrestrialisation, peatland development is largely constrained by local topography, hydrologeological settings, and climate.

Studies on shoreline displacement in the James/Hudson Bay region indicate that initial land emergence and shoreline displacement was much greater than today's levels, which range from 1.2 - 1.5 meters per century for the past 1000 years (Lajeunesse & Allard, 2003; Pendea et al., 2010; Simon et al., 2014). Initial rates of uplift have been estimated to be anywhere between 6.5 to 7 meters per century, for the period between 8300 – 6000 cal yr BP, and 3.4 to 4 meters per century for the time period between 6000 – 5000 cal yr BP (Lajeunesse & Allard, 2003, Pendea et al., 2010). The evidence of early high rates of isostatic uplift has been suggested as one of the most influential drivers of succession in peatland studies in the James/Hudson Bay region (McAndrews et al., 1982; Klinger & Short, 1996; Glaser et al., 2004; Pendea et al., 2010; O'Reilly et al., 2014; Bunbury et al., 2012). The decreasing rate of isostatic rebound after the terrestrialisation of the two sites (Pendea et al., 2010) seems to have had little, if any, effect on hydrarch succession. As a regional driver, the isostatic rebound would be expected to induce largely synchronous shifts in WTD for the two peatlands, which are relatively close to each other

(≈75 km). Yet, the WTD reconstruction for OFL and W55 peatlands shows strong local specificities that are probably caused by more local factors. Of course, isostatic rebound may still play a role in the restructuring of local drainage networks and, thus, its effects would be more nuanced, but based on the evidence in this study it is hard to argue for a strong, sustained impact of isostasy on peatland hydrology at the two sites.

6.4.2 Climate

In the study region, different geomorphological and environmental settings (see section 3.3) led to differences in millennial-scale peatland hydrology variations and local specificities with respect to allogenic and autogenic succession (Pendea, 2011). Yet, the period between 3500 – 2900 cal yr BP shows a quasi-synchronous decrease in water table levels in both the OFL and W55 peatlands, followed by an overall increase in the water table levels. There are two probable reasons behind such a development: tectonics and climate. The regional tectonic history, particularly as it relates to glacio-isostatic rebound shows no event that could be causing a particularly strong regional lowering of the water-table. On the contrary, the rate of isostatic rebound has diminished considerably over time (Hardy, 1977; McAndrews et al, 1982; Yu & McAndrews, 1994; Peltier, 1998; Mitrovica et al., 2000; Lajeunesse & Allard 2003; Pendea et al., 2010; Simon et al., 2014). It follows, therefore, that climate conditions around this time could be considered as a potential cause for this quasi-synchronous drying of the peat surface at the two locations. The regional Holocene climate history reveals that climate could have indeed driven this event.

The consensus from studies in the James Bay region is that the two major Holocene climate oscillations - the Mid Holocene Warm Period (MHWP) and the subsequent Neoglacial cooling – were much delayed here compared to elsewhere in the Northern Hemisphere (Webb et al., 1987; Koç et al., 1993; Kerwin et al., 1999; Kerwin et al., 2004; Kaufman et al., 2004). Several studies in the James/Hudson Bay region provide evidence to support a delayed timing and/or lower magnitude for both MHWP and the Neoglaciation (McAndrews et al., 1982; Yu & McAndrews, 1994; Klinger & Short, 1996; Kerwin et al., 2004; O'Reilly, 2011; Bunbury et al., 2012; O'Reilly et al., 2014; Holmquist & MacDonald, 2014). The consensus in these studies suggests that the MHWP took place in the region from 6500 – 3000 cal yr BP followed by a low magnitude Neoglaciation cooling between 2550 – 2000 cal yr BP (McAndrews et al, 1982; Yu & McAndrews, 1994; Klinger & Short, 1996; Kerwin et al., 2004; Bunbury et al., 2012; O'Reilly, 2011; O'Reilly et al., 2014; Holmquist & MacDonald, 2014). Elsewhere in the Northern Hemisphere, these two major climate shifts were stronger and occurred 2000 to 500 years earlier (Kerwin et al., 2004; Kaufman et al., 2004)

The quasi-synchronous decreases in Water Table Depth (WTD) (drying) between 3300 – 3100 cal yr BP for both the OFL and W55 peatlands could be related to the end of the MHWP in the James Bay region, such that warming may have caused increased evapotranspiration and thus drier peat surfaces. These water table drawdown conditions persist until a return to wetter peat surface 2900 cal yr BP, which could be a reflection of the Neoglacial cooling that increased the effective moisture due to lower evapotranspiration. This interpretation of WTD results is supported by the climate reconstructions of Yu & McAndrews (1994), O'Reilly (2011), and O'Reilly et al. (2014) conducted in the James/Hudson Bay region. Yu & McAndrews (1994) used radiocarbon chronology, carbon accumulation data, and pollen evidence from peat sediments and found low water table levels occurred during the MHWP caused by a warm and dry climate between 6000 and 4000 – 3000 cal yr BP. O'Reilly (2011) and O'Reilly et al. (2014) reconstruct warmer temperatures and lower total precipitation between 6775 and 3000 cal yr BP, followed by a decline in annual temperatures between 3500 – 2800 cal yr BP and a corresponding increase in precipitation after 3000 – 2800 cal yr BP.

The reconstruction of peatland hydrology in this study correlates well with the findings of Bunbury et al. (2012) in the Hudson Bay lowlands, who found dry conditions (low water table) at 3400 cal yr BP followed by a shift back to wet conditions with high standing water table levels at 2400 cal yr BP. Although more studies are needed to increase the certainty of my interpretation and to rule out the possibility of a coincidence for synchronous peatland hydrology events such as the one presented here, the existence of independent studies with similar finds, such as Bunbury et al (2012), suggests that climate may have been indeed an important player in peatland hydrology in the James/Hudson Bay region.

Chapter 7) Conclusions

7.1 Major points of interest

Most of the research undertaken on northern peatlands in the last few decades focused on modern and palaeoenvironmental investigation of wetland ecology and carbon balance. Although the role of hydrology has been noted in many of these studies, relatively few authors have focused on deciphering the concrete role that hydrology plays in peatland development from a long-term perspective. In this study, I used a suite of palaeoecological proxies (testate amoebae, C/N ratios) along with radiocarbon chronology to reconstruct the millennial scale water table variability in two peatlands from subarctic James Bay (Canada). I then compared these reconstructions with a previously reconstructed hydrarch succession during the same time frame. The study focused on determining whether major peatland ecosystem changes coincided with major hydrology fluctuations and if these hydrology changes acted as a possible driver to peatland succession. The study also sought to identify the potential causes behind the shifts in hydrology. My results point to a nuanced role of hydrology in the hydroseral development of peatlands and suggest that local conditions are, to some extent, more important than large-scale drivers.

The results of the study suggest that hydrology was a major factor in peatland succession at one site (OFL), but less so at the other (W55). While autogenic controls (i.e., peat growth rates, raised water table mounds formation in peat tussocks) may have been responsible, in part, for the observed differences in hydrological regimes, the results obtained in this study point to a strong influence of local conditions (topography, local base level, and surface drainage patterns).

In terms of specific successional pathways through which hydrology influenced hydrach succession, the OFL peatland showed a tendency to achieve ombrotrophy under wetting conditions similar to results from studies by Hughes (2000) and Hughes & Dumayne-Peaty (2002). The ombrotrophic regime may have been achieved and maintained through doming of bog pools caused by the development of catotelmic peat which impedes drainage. This process coincides with leaching of nutrients from the tops of the vegetation resulting in acidification of the site which drives ombrotrophic conditions under high water table levels. For the W55 peatland, water table depth was less influential in driving hydrarch succession, but the highly variable water table may have caused an overall higher successional instability (including successional reversals) than in the case of the OFL peatland.

While local conditions were probably the most important factor of peatland hydrology change, large-scale, regional factors were, at times, important as well. Both OFL and W55 peatland hydrological reconstructions captured an initial drying stage during the transition from marine to tidal marsh and subsequent fresh water marsh, which likely occurred under the influence of glacio-isostatic rebound. The hydrological reconstructions for both peatlands also recorded a quasi-synchronous decrease in water table levels during the period between 3500 and 2900 cal yr BP, followed by an overall increase in the water table levels and return to wet conditions after 2900 cal yr BP. A similar development was observed elsewhere in the region (Bunbury et al., 2012) and, as such, I suggest that these particular drying and wetting episodes were the result of the two discrete climate oscillations (Mid Holocene Warm Period and the Neoglacial cooling, respectively). Studies suggest that the Mid Holocene Warm Period (6500 – 3000 cal yr BP) was a drying episode marked by lower precipitation and warmer temperatures and was followed by the Neoglaciation cooling (2550 – 2000 cal yr BP), which was marked by cooler temperatures and increased precipitation (McAndrews et al, 1982; Yu & McAndrews, 1994; Klinger & Short, 1996; Kerwin et al., 2004; O'Reilly, 2011; Bunbury et al., 2012; O'Reilly et al., 2014; Holmquist & MacDonald, 2014).

This research study was undertaken in order to address the gap in knowledge on the relationship between hydrarch succession and hydrology. Hydrological reconstructions on a millennial timescale in northern peatlands are scarce particularly in the northern James Bay region. By contrasting the millennial-scale hydrological reconstructions in two different peatlands, I was able to separate the local controls on peatland development (base-level, topography, drainage) from those of a more regional nature (climate, tectonics). Results of the study provide evidence to support contrasting pathways in peatland development and underscore the overall complexity of peatland development. Hydrarch succession is subject to a combination of factors that drive peatland development with no one factor reigning supreme.

7.3 Limitations and suggestions for future research

Future work in these two peatlands could include a macrofossil investigation, which would better constrain the nature of hydrarch succession, particularly as it pertains to autogenic factors such as acidification and peatland micromorphology (tussocks and lawns). A macrofossil study would also provide information about local vegetation and differences between the two sites. A local palaeoclimate reconstruction would also be beneficial because previous reconstructions in the region are still some distance away from my sampling sites.

A specific limitation in this study was the low peat accumulation rate, particularly for parts of the W55 core, which forced a less-than-ideal sampling resolution in some sections.

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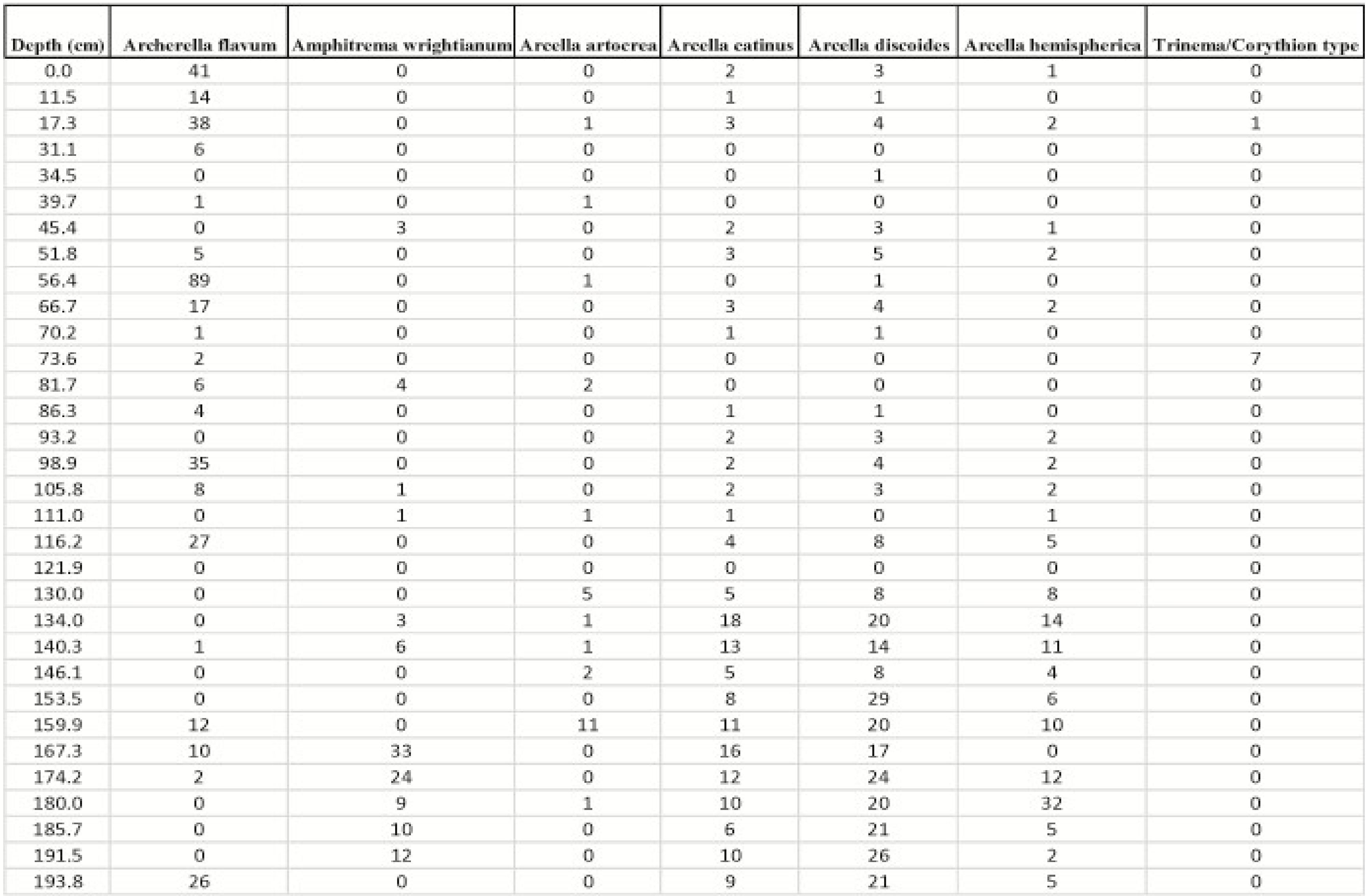
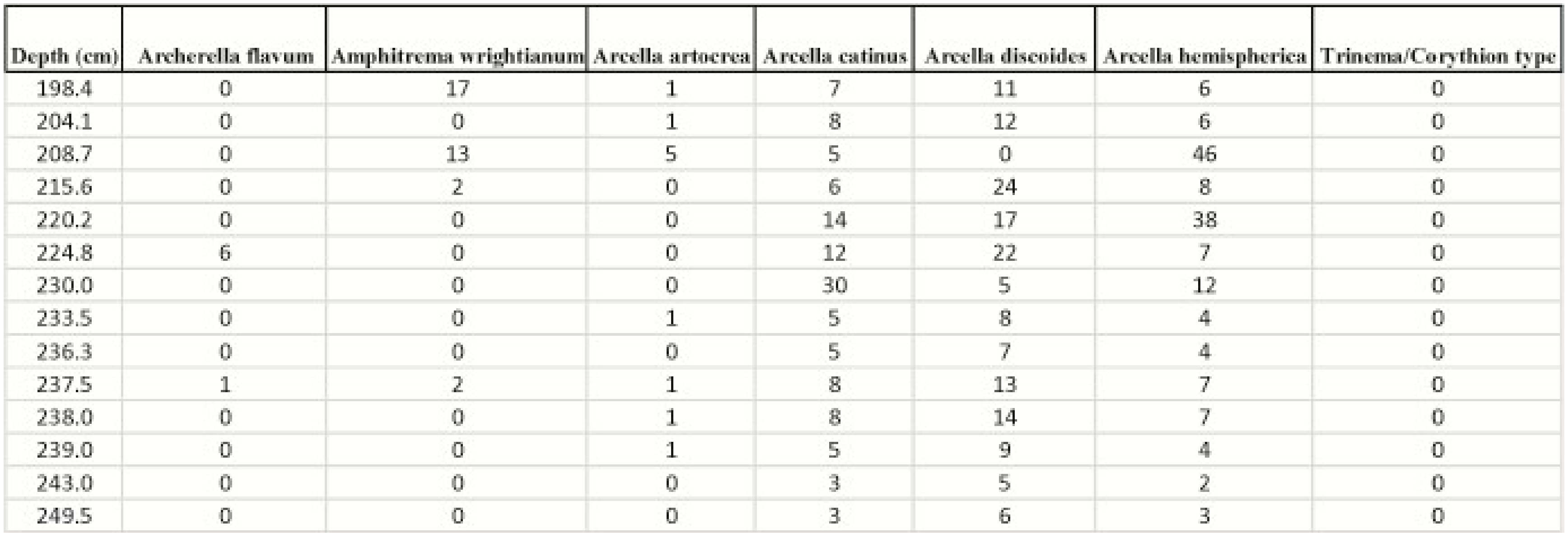
Appendices

Appendix 1) OFL core Testate Amoebae raw data: 1/14



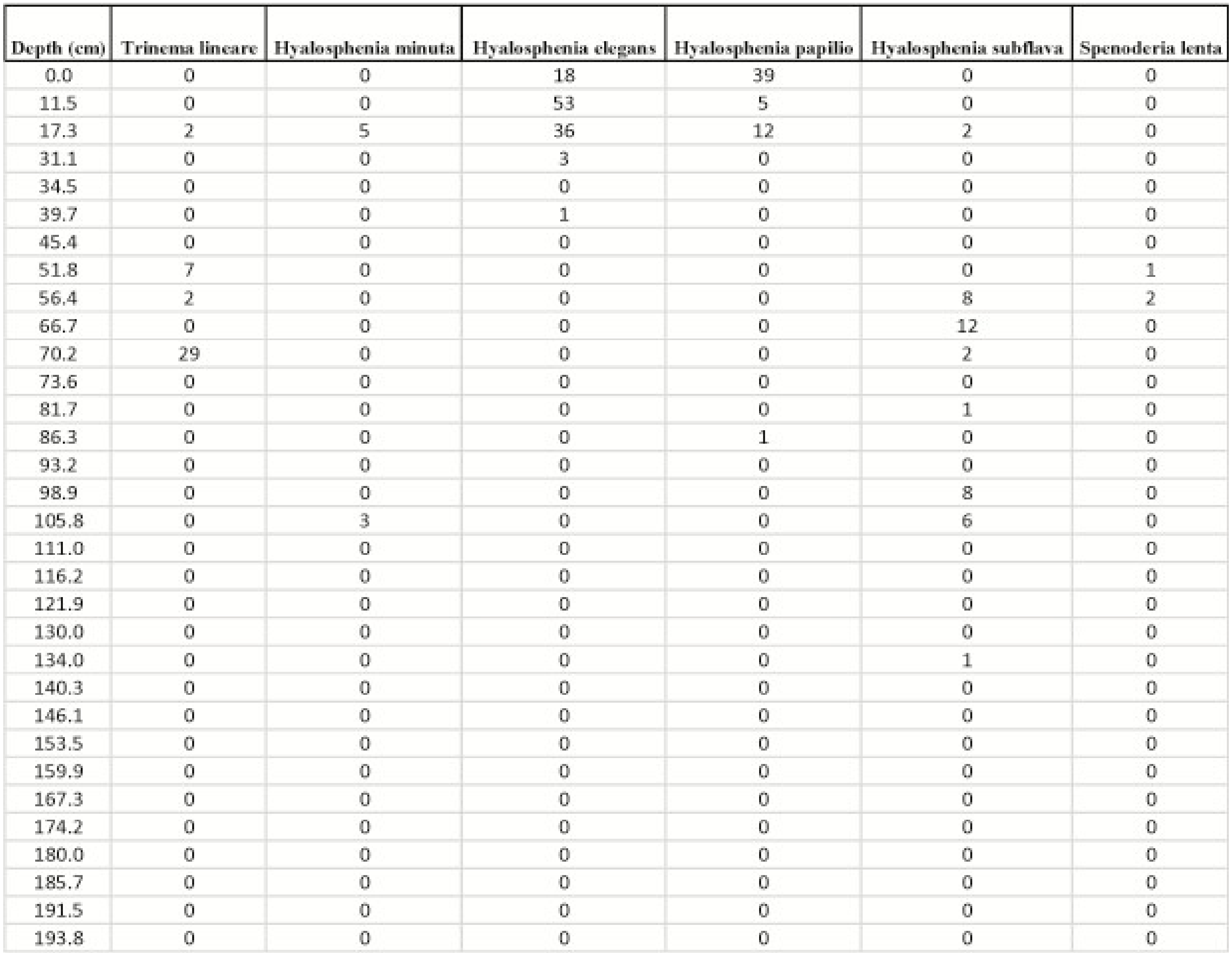
Depth (cm)	Archerella flavum	Amphitrema wrightianum	Arcella artocrea	Arcella catinus	Arcella discoides	Arcella hemispherica	Trinema/Corythion type
0.0	41	0	0	2	3	1	0
11.5	14	0	0	1	1	0	0
17.3	38	0	1	3	4	2	1
31.1	6	0	0	0	0	0	0
34.5	0	0	0	0	1	0	0
39.7	1	0	1	0	0	0	0
45.4	0	3	0	2	3	1	0
51.8	5	0	0	3	5	2	0
56.4	89	0	1	0	1	0	0
66.7	17	0	0	3	4	2	0
70.2	1	0	0	1	1	0	0
73.6	2	0	0	0	0	0	7
81.7	6	4	2	0	0	0	0
86.3	4	0	0	1	1	0	0
93.2	0	0	0	2	3	2	0
98.9	35	0	0	2	4	2	0
105.8	8	1	0	2	3	2	0
111.0	0	1	1	1	0	1	0
116.2	27	0	0	4	8	5	0
121.9	0	0	0	0	0	0	0
130.0	0	0	5	5	8	8	0
134.0	0	3	1	18	20	14	0
140.3	1	6	1	13	14	11	0
146.1	0	0	2	5	8	4	0
153.5	0	0	0	8	29	6	0
159.9	12	0	11	11	20	10	0
167.3	10	33	0	16	17	0	0
174.2	2	24	0	12	24	12	0
180.0	0	9	1	10	20	32	0
185.7	0	10	0	6	21	5	0
191.5	0	12	0	10	26	2	0
193.8	26	0	0	9	21	5	0

OFL core Testate Amoebae raw data: 2/14



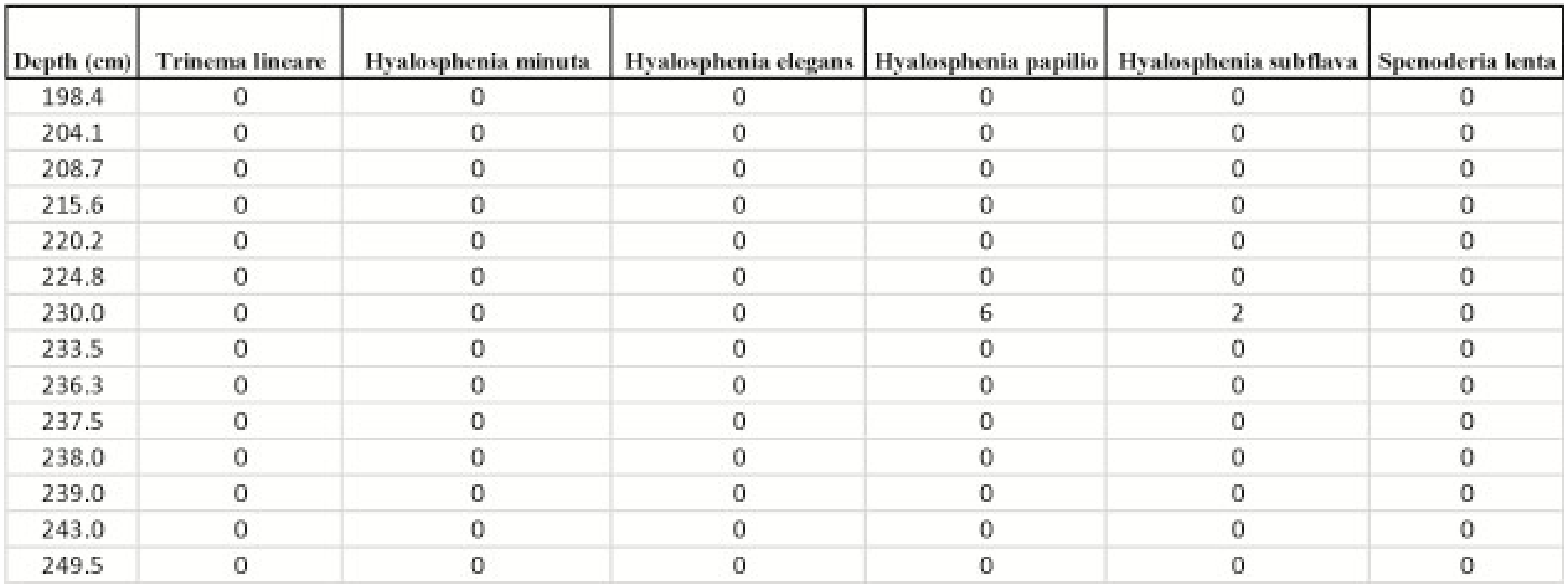
Depth (cm)	Archerella flavum	Amphitrema wrightianum	Arcella artocrea	Arcella catinus	Arcella discoides	Arcella hemispherica	Trinema/Corythion type
198.4	0	17	1	7	11	6	0
204.1	0	0	1	8	12	6	0
208.7	0	13	5	5	0	46	0
215.6	0	2	0	6	24	8	0
220.2	0	0	0	14	17	38	0
224.8	6	0	0	12	22	7	0
230.0	0	0	0	30	5	12	0
233.5	0	0	1	5	8	4	0
236.3	0	0	0	5	7	4	0
237.5	1	2	1	8	13	7	0
238.0	0	0	1	8	14	7	0
239.0	0	0	1	5	9	4	0
243.0	0	0	0	3	5	2	0
249.5	0	0	0	3	6	3	0

OFL core Testate Amoebae raw data: 3/14



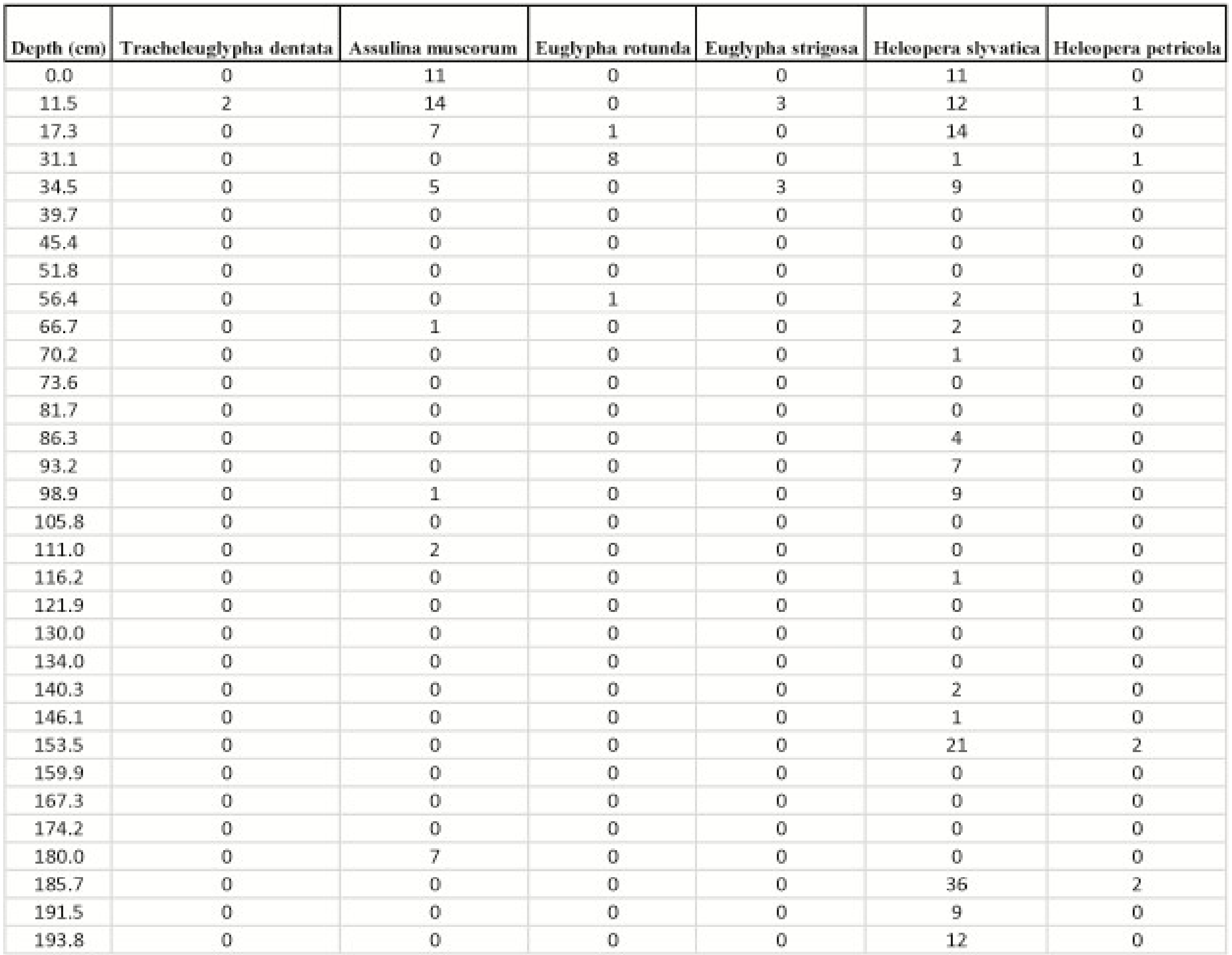
Depth (cm)	Trinema lineare	Hyalosphenia minuta	Hyalosphenia elegans	Hyalosphenia papilio	Hyalosphenia subflava	Spenoderia lenta
0.0	0	0	18	39	0	0
11.5	0	0	53	5	0	0
17.3	2	5	36	12	2	0
31.1	0	0	3	0	0	0
34.5	0	0	0	0	0	0
39.7	0	0	1	0	0	0
45.4	0	0	0	0	0	0
51.8	7	0	0	0	0	1
56.4	2	0	0	0	8	2
66.7	0	0	0	0	12	0
70.2	29	0	0	0	2	0
73.6	0	0	0	0	0	0
81.7	0	0	0	0	1	0
86.3	0	0	0	1	0	0
93.2	0	0	0	0	0	0
98.9	0	0	0	0	8	0
105.8	0	3	0	0	6	0
111.0	0	0	0	0	0	0
116.2	0	0	0	0	0	0
121.9	0	0	0	0	0	0
130.0	0	0	0	0	0	0
134.0	0	0	0	0	1	0
140.3	0	0	0	0	0	0
146.1	0	0	0	0	0	0
153.5	0	0	0	0	0	0
159.9	0	0	0	0	0	0
167.3	0	0	0	0	0	0
174.2	0	0	0	0	0	0
180.0	0	0	0	0	0	0
185.7	0	0	0	0	0	0
191.5	0	0	0	0	0	0
193.8	0	0	0	0	0	0

OFL core Testate Amoebae raw data: 4/14



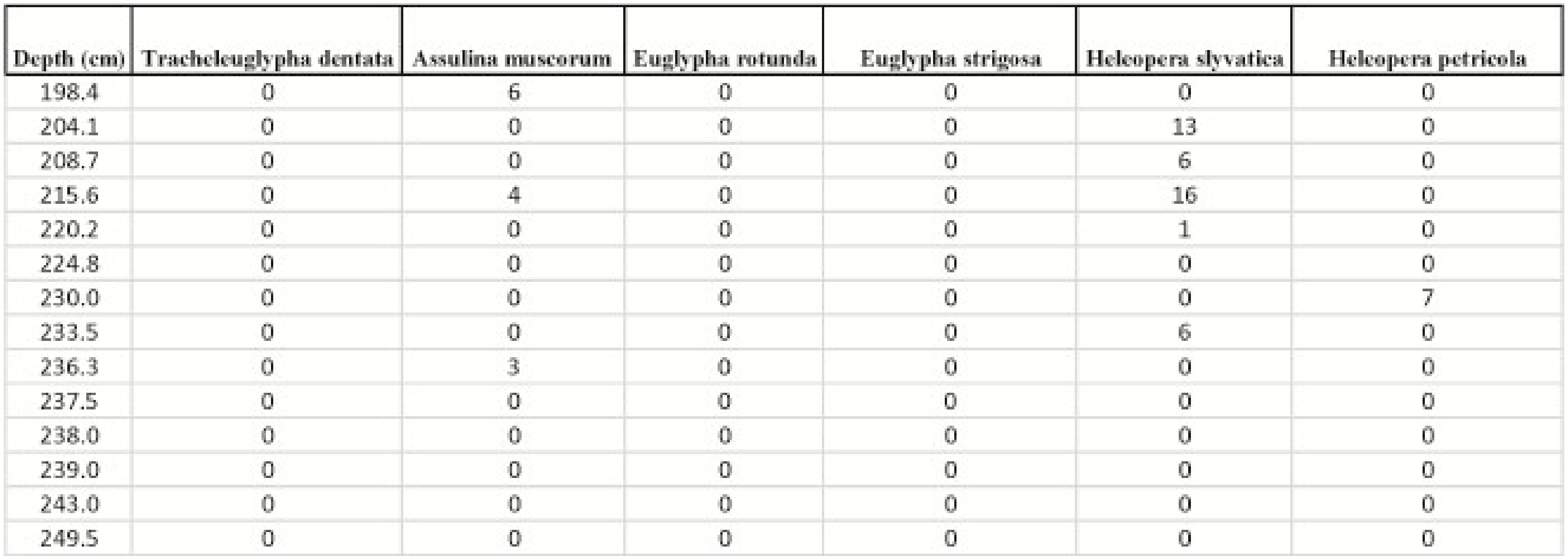
Depth (cm)	Trinema lineare	Hyalosphenia minuta	Hyalosphenia elegans	Hyalosphenia papilio	Hyalosphenia subflava	Spenoderia lenta
198.4	0	0	0	0	0	0
204.1	0	0	0	0	0	0
208.7	0	0	0	0	0	0
215.6	0	0	0	0	0	0
220.2	0	0	0	0	0	0
224.8	0	0	0	0	0	0
230.0	0	0	0	6	2	0
233.5	0	0	0	0	0	0
236.3	0	0	0	0	0	0
237.5	0	0	0	0	0	0
238.0	0	0	0	0	0	0
239.0	0	0	0	0	0	0
243.0	0	0	0	0	0	0
249.5	0	0	0	0	0	0

OFL core Testate Amoebae raw data: 5/14



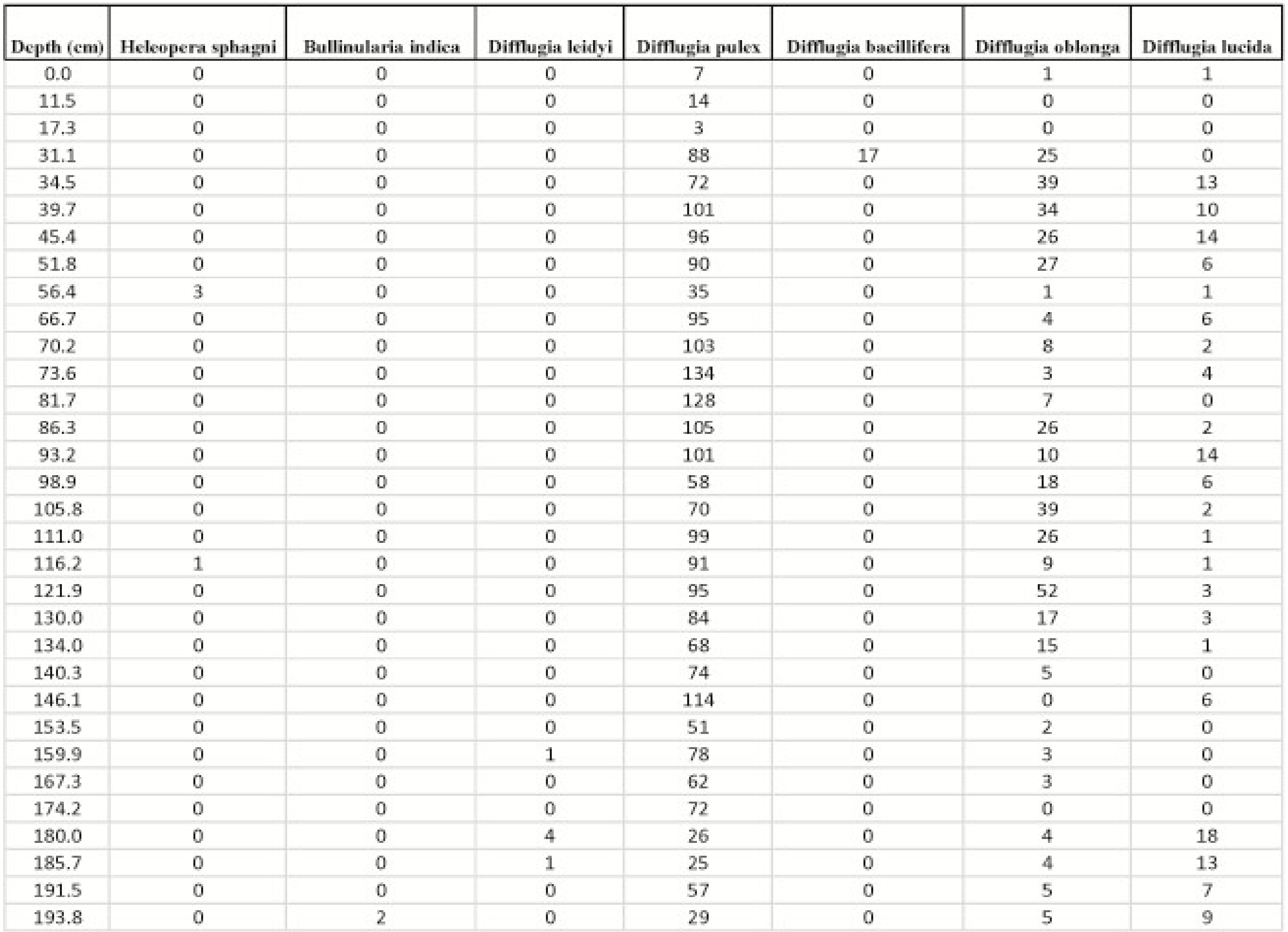
Depth (cm)	Tracheleuglypha dentata	Assulina muscorum	Euglypha rotunda	Euglypha strigosa	Heleopera slyvatica	Heleopera petricola
0.0	0	11	0	0	11	0
11.5	2	14	0	3	12	1
17.3	0	7	1	0	14	0
31.1	0	0	8	0	1	1
34.5	0	5	0	3	9	0
39.7	0	0	0	0	0	0
45.4	0	0	0	0	0	0
51.8	0	0	0	0	0	0
56.4	0	0	1	0	2	1
66.7	0	1	0	0	2	0
70.2	0	0	0	0	1	0
73.6	0	0	0	0	0	0
81.7	0	0	0	0	0	0
86.3	0	0	0	0	4	0
93.2	0	0	0	0	7	0
98.9	0	1	0	0	9	0
105.8	0	0	0	0	0	0
111.0	0	2	0	0	0	0
116.2	0	0	0	0	1	0
121.9	0	0	0	0	0	0
130.0	0	0	0	0	0	0
134.0	0	0	0	0	0	0
140.3	0	0	0	0	2	0
146.1	0	0	0	0	1	0
153.5	0	0	0	0	21	2
159.9	0	0	0	0	0	0
167.3	0	0	0	0	0	0
174.2	0	0	0	0	0	0
180.0	0	7	0	0	0	0
185.7	0	0	0	0	36	2
191.5	0	0	0	0	9	0
193.8	0	0	0	0	12	0

OFL core Testate Amoebae raw data: 6/14



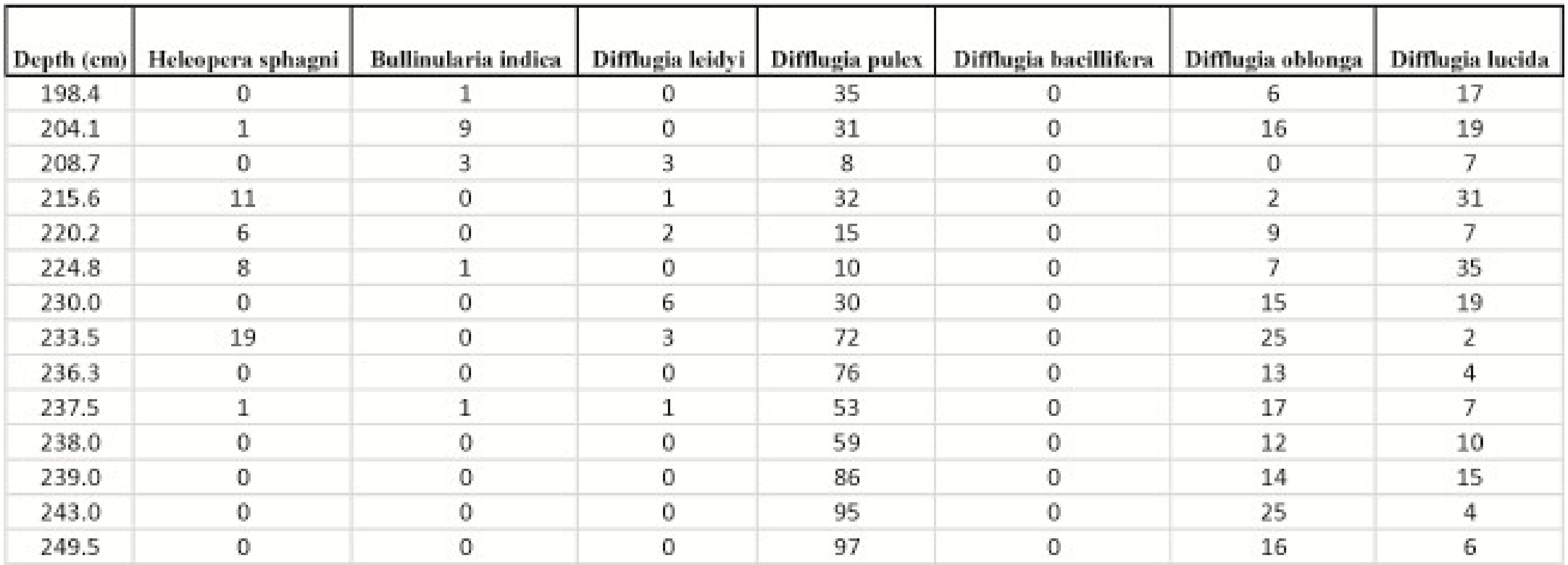
Depth (cm)	Tracheleuglypha dentata	Assulina muscorum	Euglypha rotunda	Euglypha strigosa	Heleopera slyvatica	Heleopera petricola
198.4	0	6	0	0	0	0
204.1	0	0	0	0	13	0
208.7	0	0	0	0	6	0
215.6	0	4	0	0	16	0
220.2	0	0	0	0	1	0
224.8	0	0	0	0	0	0
230.0	0	0	0	0	0	7
233.5	0	0	0	0	6	0
236.3	0	3	0	0	0	0
237.5	0	0	0	0	0	0
238.0	0	0	0	0	0	0
239.0	0	0	0	0	0	0
243.0	0	0	0	0	0	0
249.5	0	0	0	0	0	0

OFL core Testate Amoebae raw data: 7/14



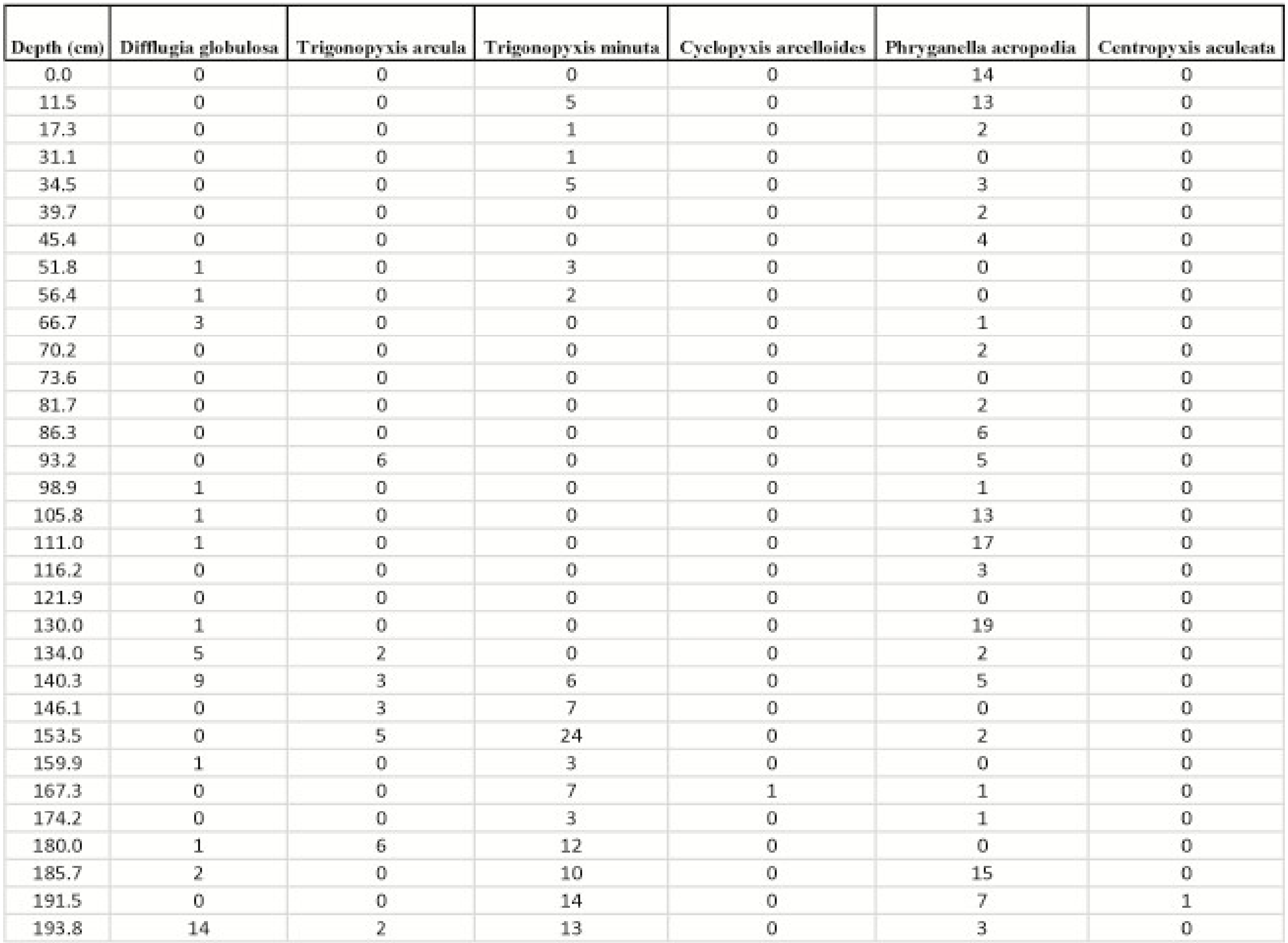
Depth (cm)	Heleopera sphagni	Bullinularia indica	Difflugia leidyi	Difflugia pulex	Difflugia bacillifera	Difflugia oblonga	Difflugia lucida
0.0	0	0	0	7	0	1	1
11.5	0	0	0	14	0	0	0
17.3	0	0	0	3	0	0	0
31.1	0	0	0	88	17	25	0
34.5	0	0	0	72	0	39	13
39.7	0	0	0	101	0	34	10
45.4	0	0	0	96	0	26	14
51.8	0	0	0	90	0	27	6
56.4	3	0	0	35	0	1	1
66.7	0	0	0	95	0	4	6
70.2	0	0	0	103	0	8	2
73.6	0	0	0	134	0	3	4
81.7	0	0	0	128	0	7	0
86.3	0	0	0	105	0	26	2
93.2	0	0	0	101	0	10	14
98.9	0	0	0	58	0	18	6
105.8	0	0	0	70	0	39	2
111.0	0	0	0	99	0	26	1
116.2	1	0	0	91	0	9	1
121.9	0	0	0	95	0	52	3
130.0	0	0	0	84	0	17	3
134.0	0	0	0	68	0	15	1
140.3	0	0	0	74	0	5	0
146.1	0	0	0	114	0	0	6
153.5	0	0	0	51	0	2	0
159.9	0	0	1	78	0	3	0
167.3	0	0	0	62	0	3	0
174.2	0	0	0	72	0	0	0
180.0	0	0	4	26	0	4	18
185.7	0	0	1	25	0	4	13
191.5	0	0	0	57	0	5	7
193.8	0	2	0	29	0	5	9

OFL core Testate Amoebae raw data: 8/14



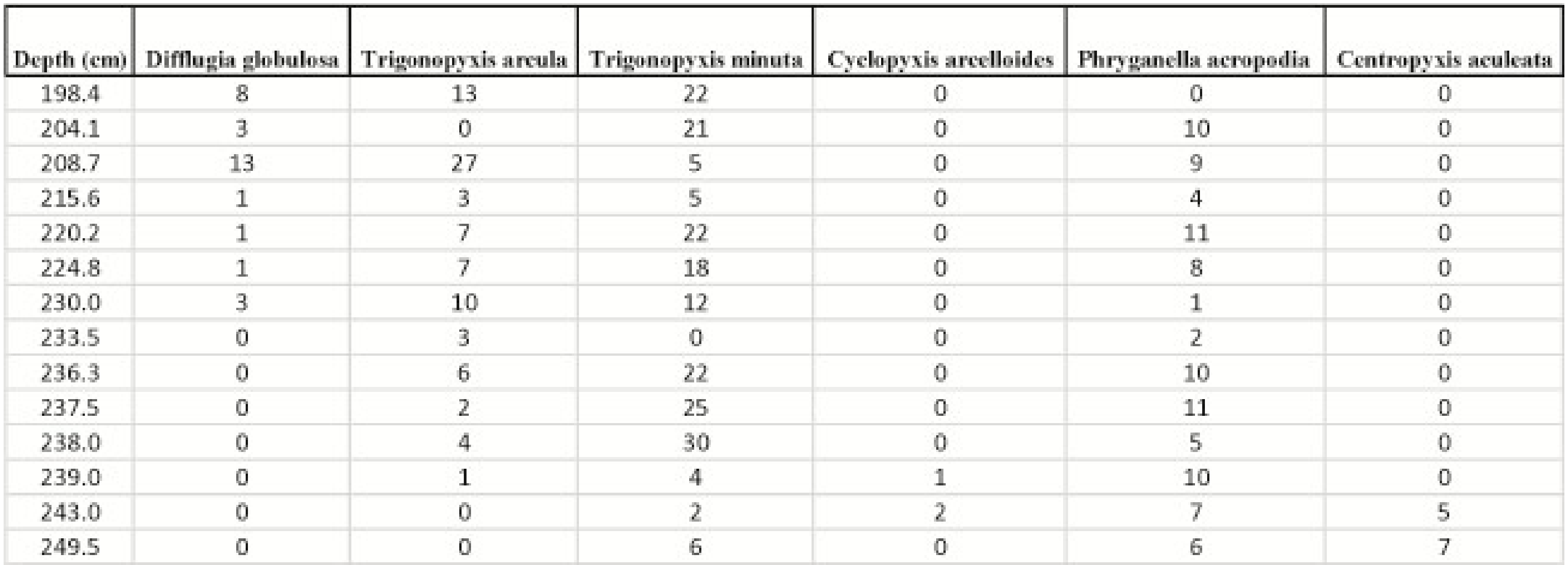
Depth (cm)	Heleopera sphagni	Bullinularia indica	Difflugia leidyi	Difflugia pulex	Difflugia bacillifera	Difflugia oblonga	Difflugia lucida
198.4	0	1	0	35	0	6	17
204.1	1	9	0	31	0	16	19
208.7	0	3	3	8	0	0	7
215.6	11	0	1	32	0	2	31
220.2	6	0	2	15	0	9	7
224.8	8	1	0	10	0	7	35
230.0	0	0	6	30	0	15	19
233.5	19	0	3	72	0	25	2
236.3	0	0	0	76	0	13	4
237.5	1	1	1	53	0	17	7
238.0	0	0	0	59	0	12	10
239.0	0	0	0	86	0	14	15
243.0	0	0	0	95	0	25	4
249.5	0	0	0	97	0	16	6

OFL core Testate Amoebae raw data: 9/14



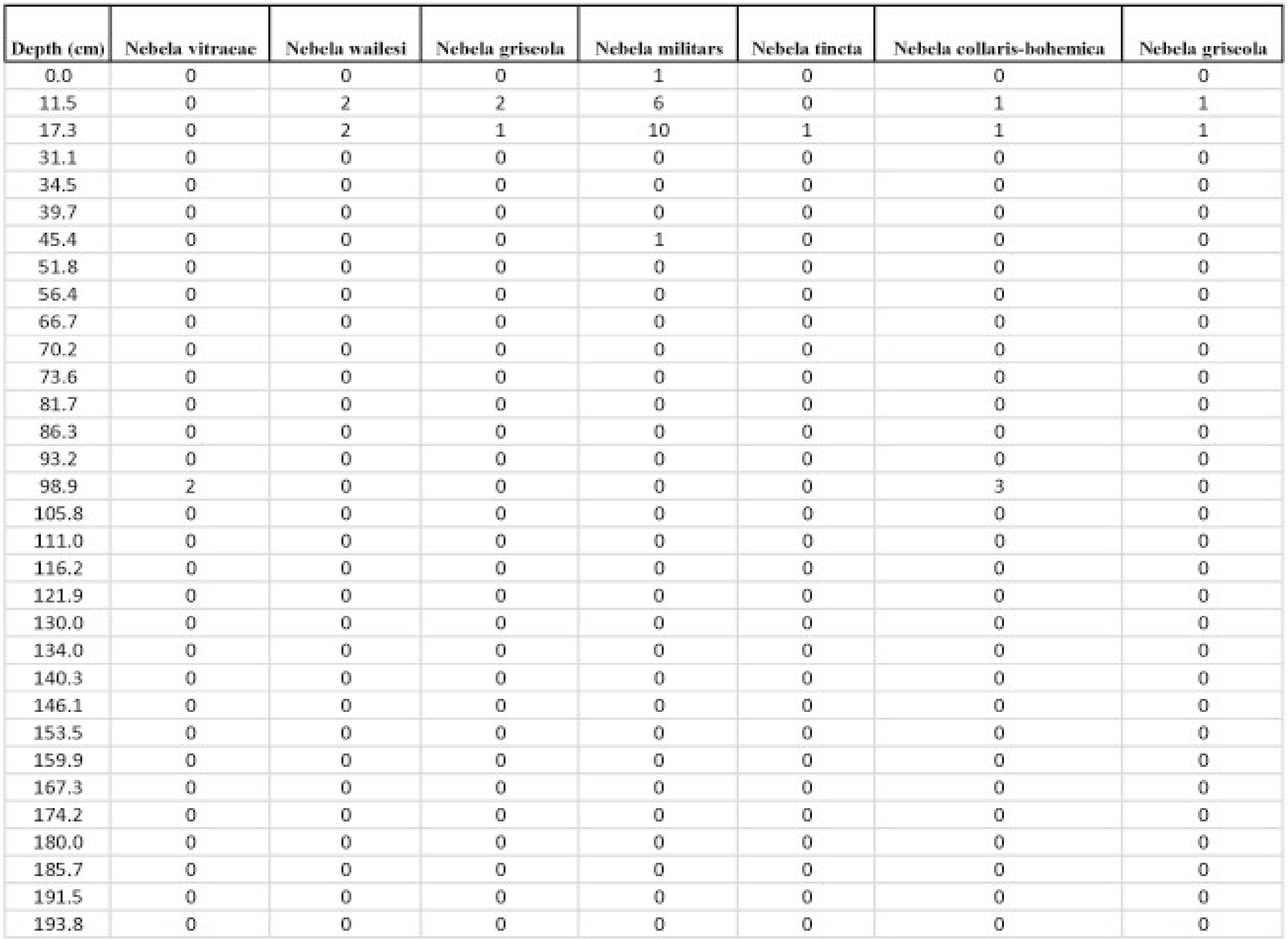
Depth (cm)	Difflugia globulosa	Trigonopyxis arcula	Trigonopyxis minuta	Cyclopyxis arcelloides	Phryganella acropodia	Centropyxis aculeata
0.0	0	0	0	0	14	0
11.5	0	0	5	0	13	0
17.3	0	0	1	0	2	0
31.1	0	0	1	0	0	0
34.5	0	0	5	0	3	0
39.7	0	0	0	0	2	0
45.4	0	0	0	0	4	0
51.8	1	0	3	0	0	0
56.4	1	0	2	0	0	0
66.7	3	0	0	0	1	0
70.2	0	0	0	0	2	0
73.6	0	0	0	0	0	0
81.7	0	0	0	0	2	0
86.3	0	0	0	0	6	0
93.2	0	6	0	0	5	0
98.9	1	0	0	0	1	0
105.8	1	0	0	0	13	0
111.0	1	0	0	0	17	0
116.2	0	0	0	0	3	0
121.9	0	0	0	0	0	0
130.0	1	0	0	0	19	0
134.0	5	2	0	0	2	0
140.3	9	3	6	0	5	0
146.1	0	3	7	0	0	0
153.5	0	5	24	0	2	0
159.9	1	0	3	0	0	0
167.3	0	0	7	1	1	0
174.2	0	0	3	0	1	0
180.0	1	6	12	0	0	0
185.7	2	0	10	0	15	0
191.5	0	0	14	0	7	1
193.8	14	2	13	0	3	0

OFL core Testate Amoebae raw data: 10/14



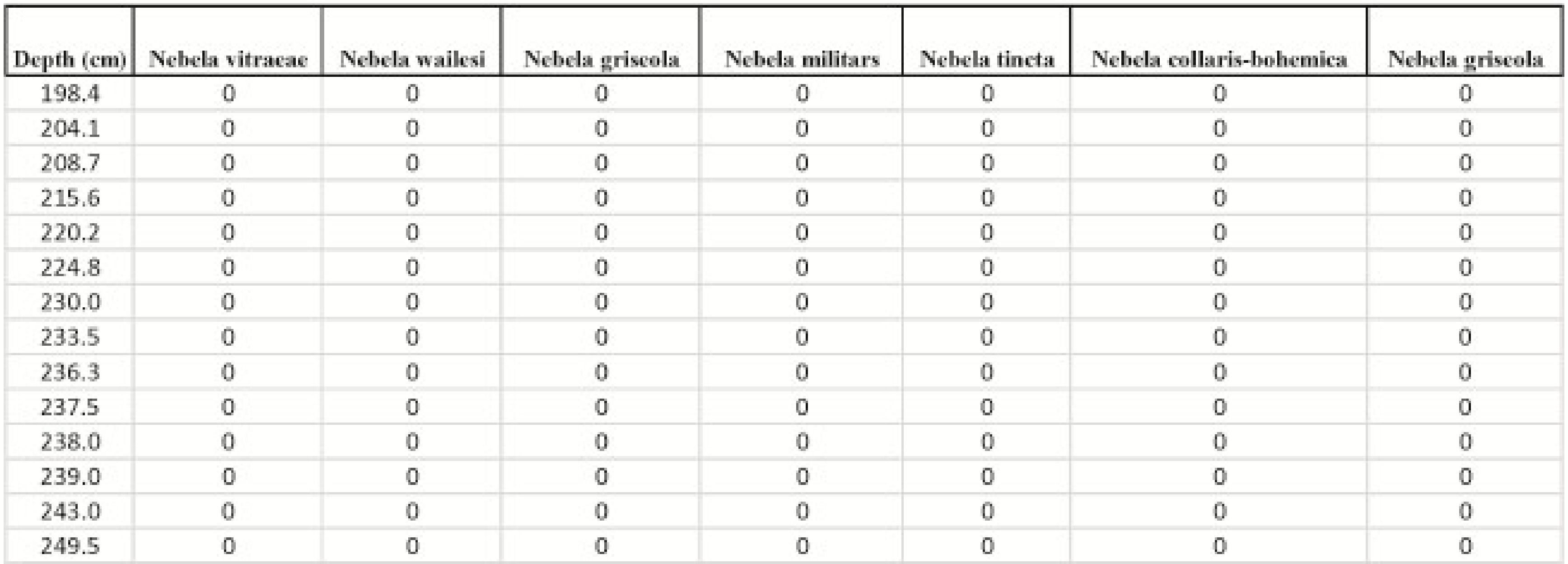
Depth (cm)	Difflugia globulosa	Trigonopyxis arcula	Trigonopyxis minuta	Cyclopyxis arcelloides	Phryganella acropodia	Centropyxis aculeata
198.4	8	13	22	0	0	0
204.1	3	0	21	0	10	0
208.7	13	27	5	0	9	0
215.6	1	3	5	0	4	0
220.2	1	7	22	0	11	0
224.8	1	7	18	0	8	0
230.0	3	10	12	0	1	0
233.5	0	3	0	0	2	0
236.3	0	6	22	0	10	0
237.5	0	2	25	0	11	0
238.0	0	4	30	0	5	0
239.0	0	1	4	1	10	0
243.0	0	0	2	2	7	5
249.5	0	0	6	0	6	7

OFL core Testate Amoebae raw data: 11/14



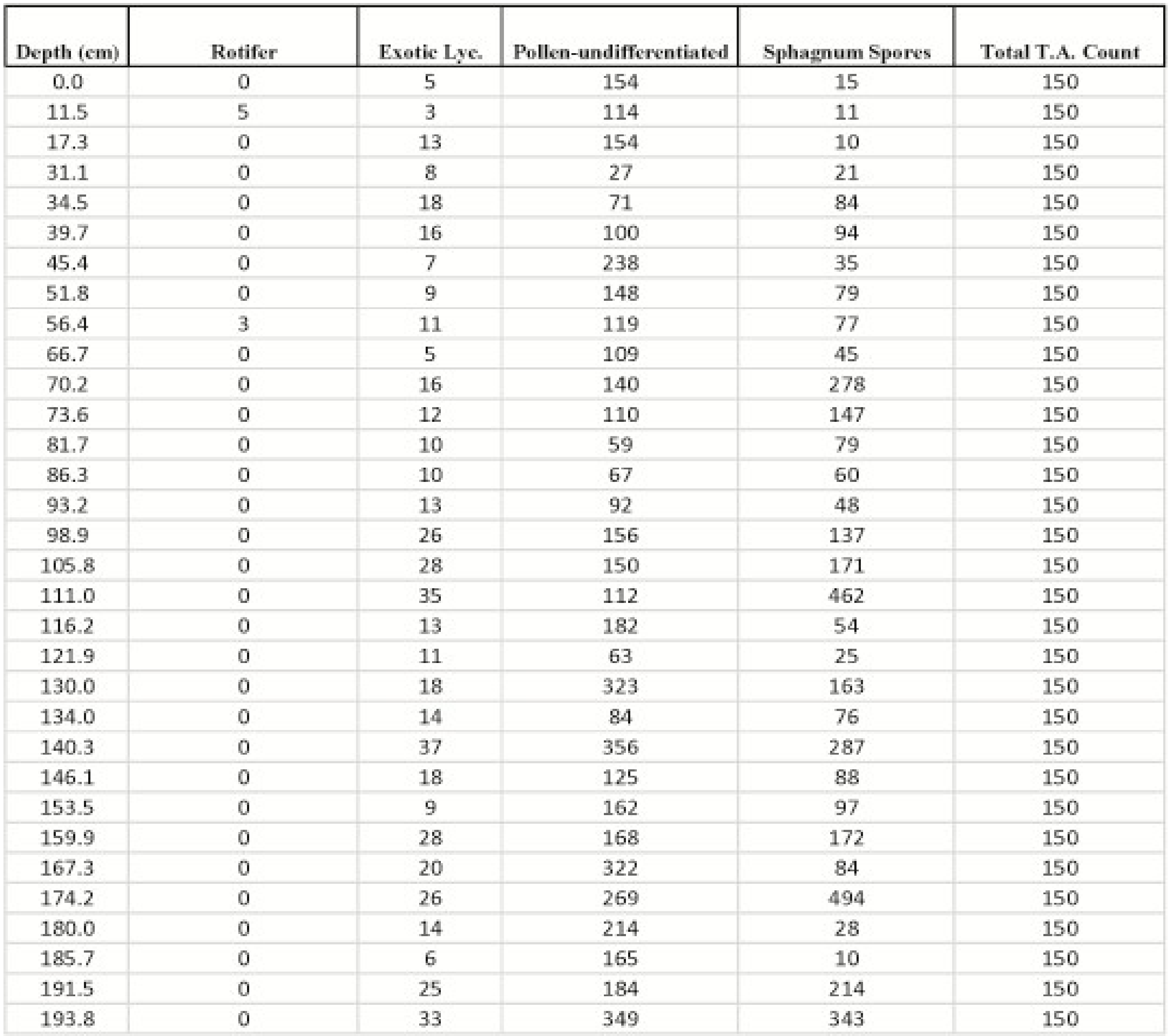
Depth (cm)	Nebela vitraeae	Nebela wailesi	Nebela griseola	Nebela militars	Nebela tincta	Nebela collaris-bohemica	Nebela griseola
0.0	0	0	0	1	0	0	0
11.5	0	2	2	6	0	1	1
17.3	0	2	1	10	1	1	1
31.1	0	0	0	0	0	0	0
34.5	0	0	0	0	0	0	0
39.7	0	0	0	0	0	0	0
45.4	0	0	0	1	0	0	0
51.8	0	0	0	0	0	0	0
56.4	0	0	0	0	0	0	0
66.7	0	0	0	0	0	0	0
70.2	0	0	0	0	0	0	0
73.6	0	0	0	0	0	0	0
81.7	0	0	0	0	0	0	0
86.3	0	0	0	0	0	0	0
93.2	0	0	0	0	0	0	0
98.9	2	0	0	0	0	3	0
105.8	0	0	0	0	0	0	0
111.0	0	0	0	0	0	0	0
116.2	0	0	0	0	0	0	0
121.9	0	0	0	0	0	0	0
130.0	0	0	0	0	0	0	0
134.0	0	0	0	0	0	0	0
140.3	0	0	0	0	0	0	0
146.1	0	0	0	0	0	0	0
153.5	0	0	0	0	0	0	0
159.9	0	0	0	0	0	0	0
167.3	0	0	0	0	0	0	0
174.2	0	0	0	0	0	0	0
180.0	0	0	0	0	0	0	0
185.7	0	0	0	0	0	0	0
191.5	0	0	0	0	0	0	0
193.8	0	0	0	0	0	0	0

OFL core Testate Amoebae raw data: 12/14



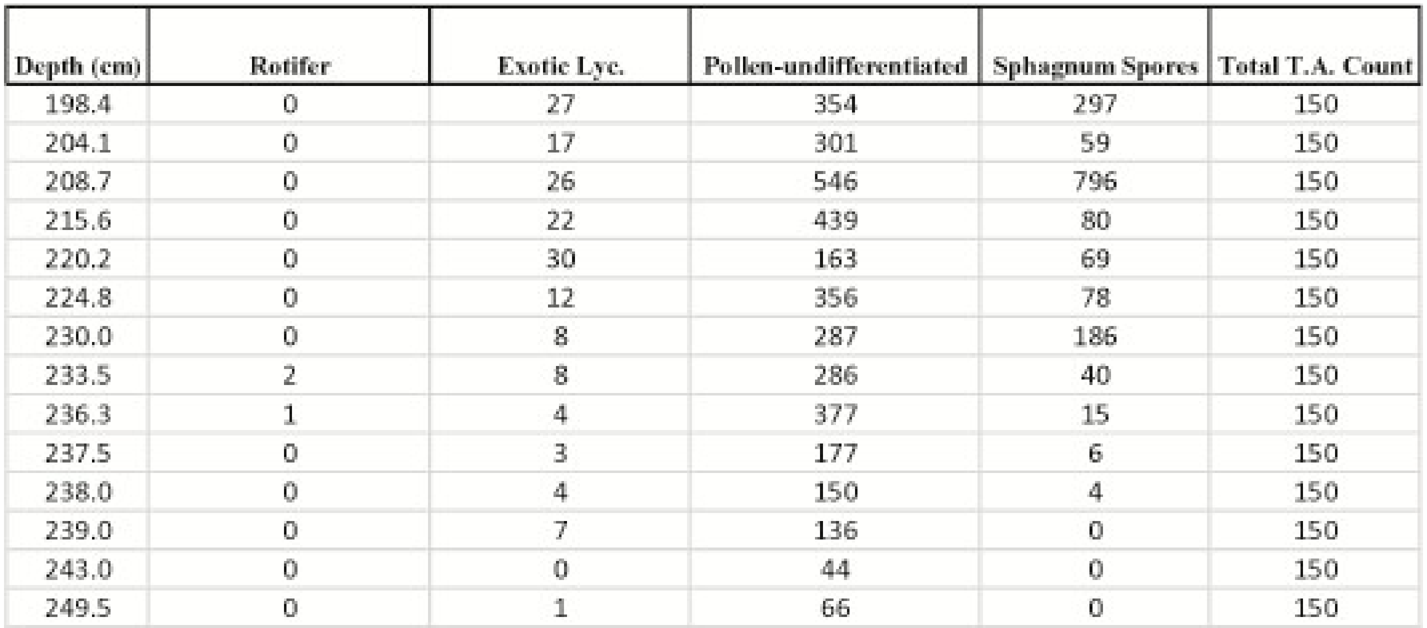
Depth (cm)	Nebela vitraeae	Nebela wailesi	Nebela griseola	Nebela militars	Nebela tincta	Nebela collaris-bohemica	Nebela griseola
198.4	0	0	0	0	0	0	0
204.1	0	0	0	0	0	0	0
208.7	0	0	0	0	0	0	0
215.6	0	0	0	0	0	0	0
220.2	0	0	0	0	0	0	0
224.8	0	0	0	0	0	0	0
230.0	0	0	0	0	0	0	0
233.5	0	0	0	0	0	0	0
236.3	0	0	0	0	0	0	0
237.5	0	0	0	0	0	0	0
238.0	0	0	0	0	0	0	0
239.0	0	0	0	0	0	0	0
243.0	0	0	0	0	0	0	0
249.5	0	0	0	0	0	0	0

OFL core Testate Amoebae raw data: 13/14



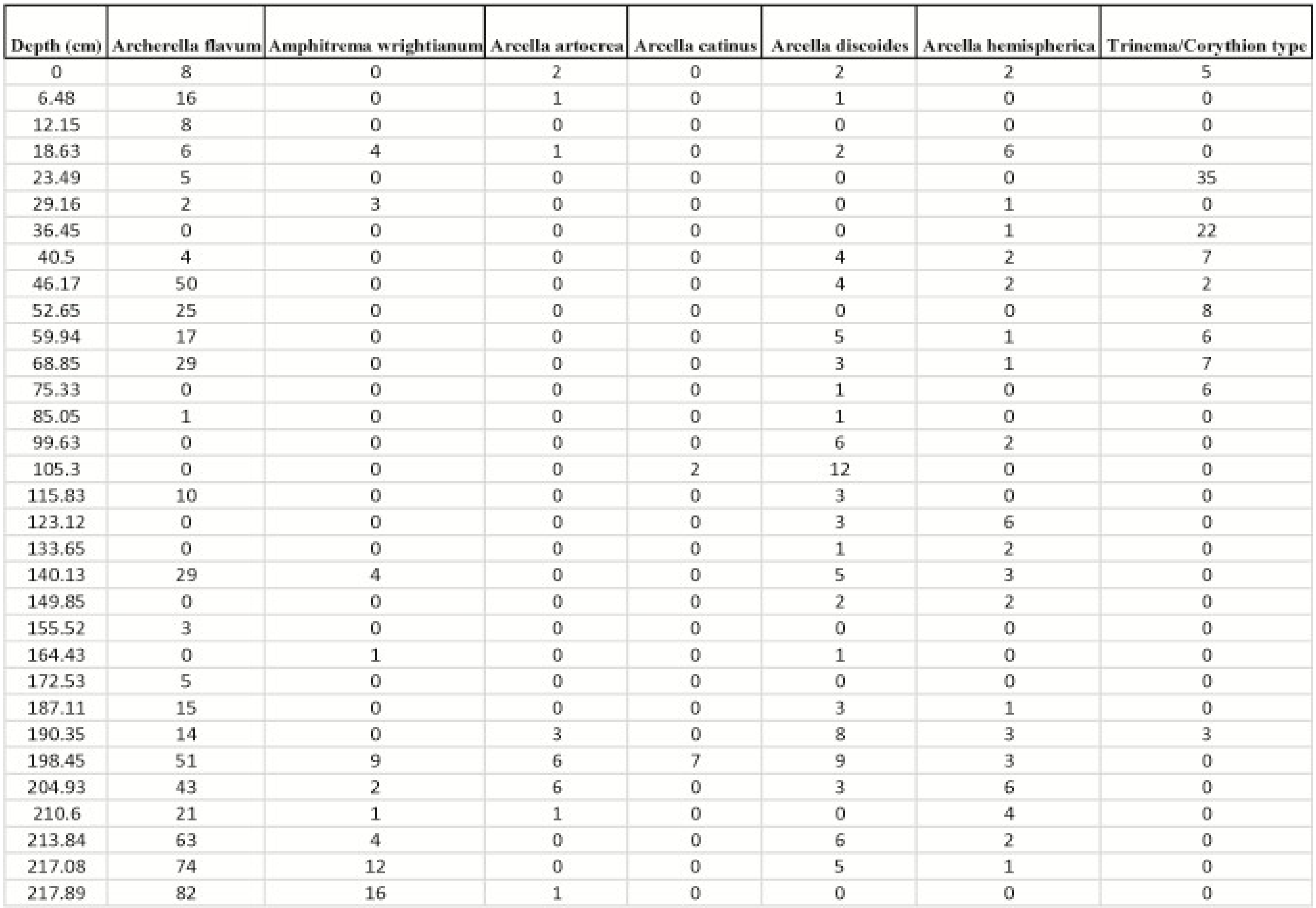
Depth (cm)	Rotifer	Exotic Lyc.	Pollen-undifferentiated	Sphagnum Spores	Total T.A. Count
0.0	0	5	154	15	150
11.5	5	3	114	11	150
17.3	0	13	154	10	150
31.1	0	8	27	21	150
34.5	0	18	71	84	150
39.7	0	16	100	94	150
45.4	0	7	238	35	150
51.8	0	9	148	79	150
56.4	3	11	119	77	150
66.7	0	5	109	45	150
70.2	0	16	140	278	150
73.6	0	12	110	147	150
81.7	0	10	59	79	150
86.3	0	10	67	60	150
93.2	0	13	92	48	150
98.9	0	26	156	137	150
105.8	0	28	150	171	150
111.0	0	35	112	462	150
116.2	0	13	182	54	150
121.9	0	11	63	25	150
130.0	0	18	323	163	150
134.0	0	14	84	76	150
140.3	0	37	356	287	150
146.1	0	18	125	88	150
153.5	0	9	162	97	150
159.9	0	28	168	172	150
167.3	0	20	322	84	150
174.2	0	26	269	494	150
180.0	0	14	214	28	150
185.7	0	6	165	10	150
191.5	0	25	184	214	150
193.8	0	33	349	343	150

OFL core Testate Amoebae raw data: 14/14



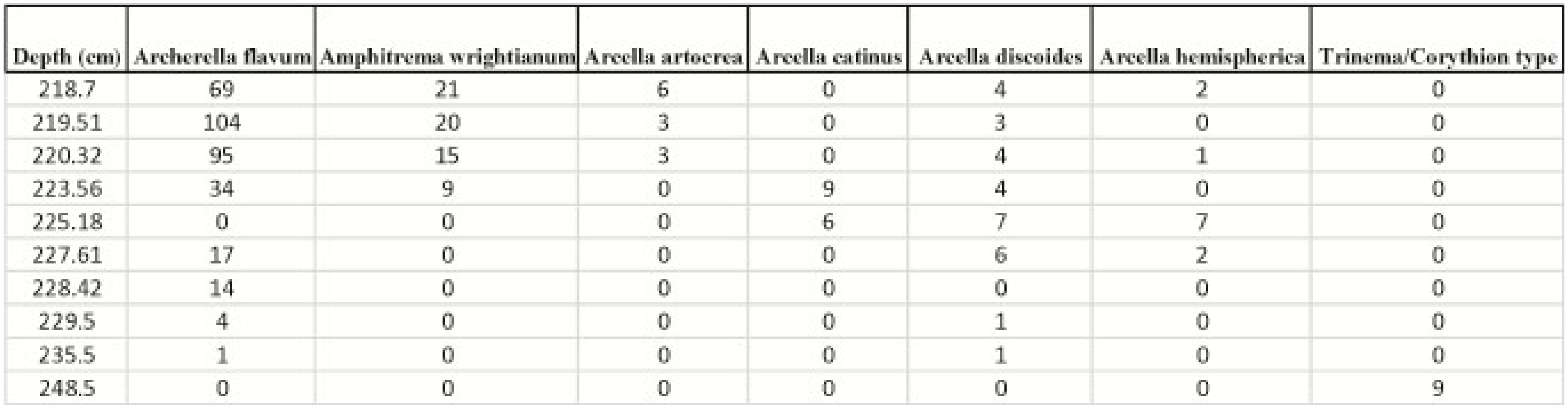
Depth (cm)	Rotifer	Exotic Lyc.	Pollen-undifferentiated	Sphagnum Spores	Total T.A. Count
198.4	0	27	354	297	150
204.1	0	17	301	59	150
208.7	0	26	546	796	150
215.6	0	22	439	80	150
220.2	0	30	163	69	150
224.8	0	12	356	78	150
230.0	0	8	287	186	150
233.5	2	8	286	40	150
236.3	1	4	377	15	150
237.5	0	3	177	6	150
238.0	0	4	150	4	150
239.0	0	7	136	0	150
243.0	0	0	44	0	150
249.5	0	1	66	0	150

Appendix 2) W55 core Testate Amoebae raw data: 1/16



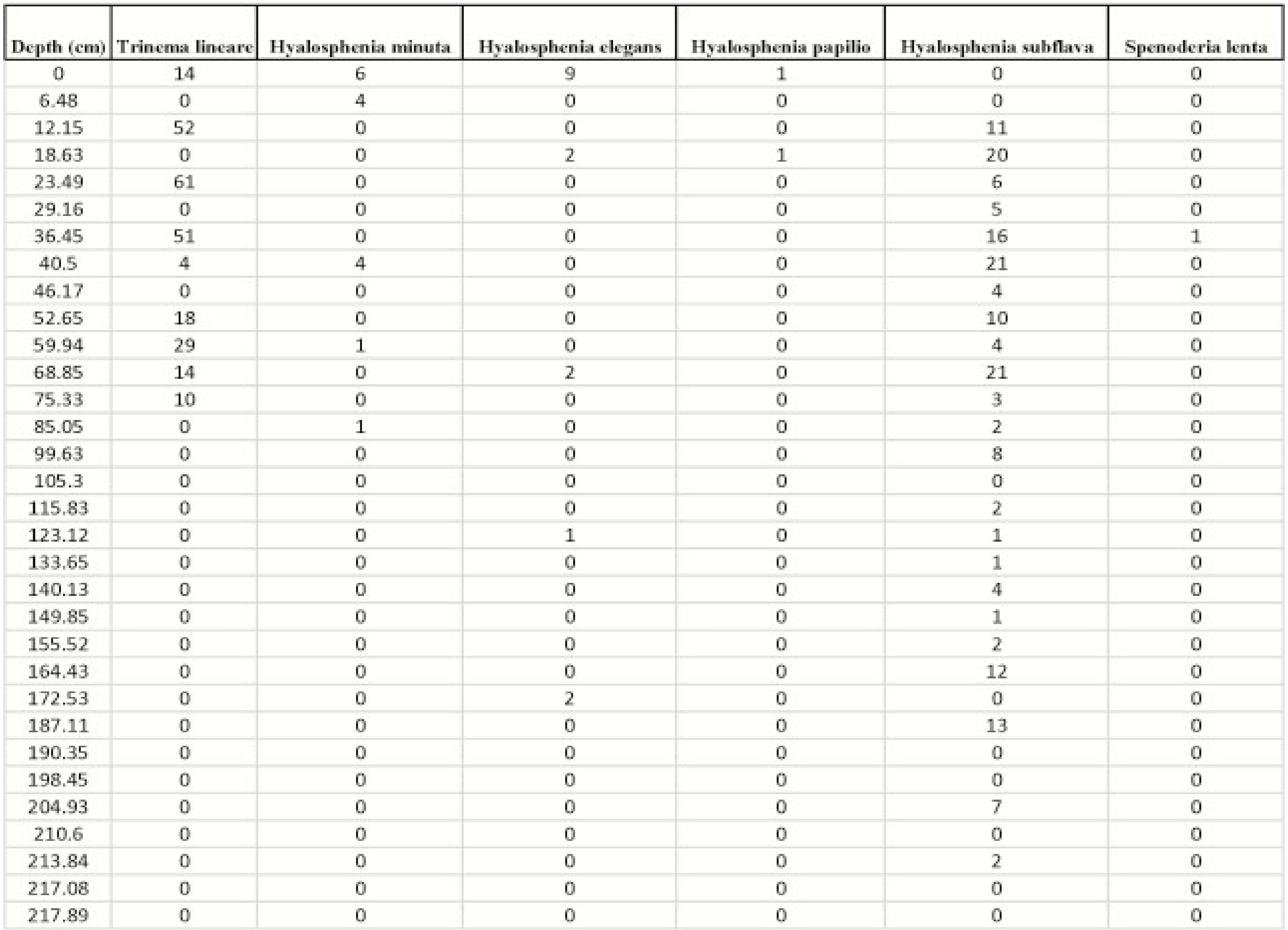
Depth (cm)	Archerella flavum	Amphitrema wrightianum	Arcella artocrea	Arcella catinus	Arcella discoides	Arcella hemispherica	Trinema/Corythion type
0	8	0	2	0	2	2	5
6.48	16	0	1	0	1	0	0
12.15	8	0	0	0	0	0	0
18.63	6	4	1	0	2	6	0
23.49	5	0	0	0	0	0	35
29.16	2	3	0	0	0	1	0
36.45	0	0	0	0	0	1	22
40.5	4	0	0	0	4	2	7
46.17	50	0	0	0	4	2	2
52.65	25	0	0	0	0	0	8
59.94	17	0	0	0	5	1	6
68.85	29	0	0	0	3	1	7
75.33	0	0	0	0	1	0	6
85.05	1	0	0	0	1	0	0
99.63	0	0	0	0	6	2	0
105.3	0	0	0	2	12	0	0
115.83	10	0	0	0	3	0	0
123.12	0	0	0	0	3	6	0
133.65	0	0	0	0	1	2	0
140.13	29	4	0	0	5	3	0
149.85	0	0	0	0	2	2	0
155.52	3	0	0	0	0	0	0
164.43	0	1	0	0	1	0	0
172.53	5	0	0	0	0	0	0
187.11	15	0	0	0	3	1	0
190.35	14	0	3	0	8	3	3
198.45	51	9	6	7	9	3	0
204.93	43	2	6	0	3	6	0
210.6	21	1	1	0	0	4	0
213.84	63	4	0	0	6	2	0
217.08	74	12	0	0	5	1	0
217.89	82	16	1	0	0	0	0

W55 core Testate Amoebae raw data: 2/16



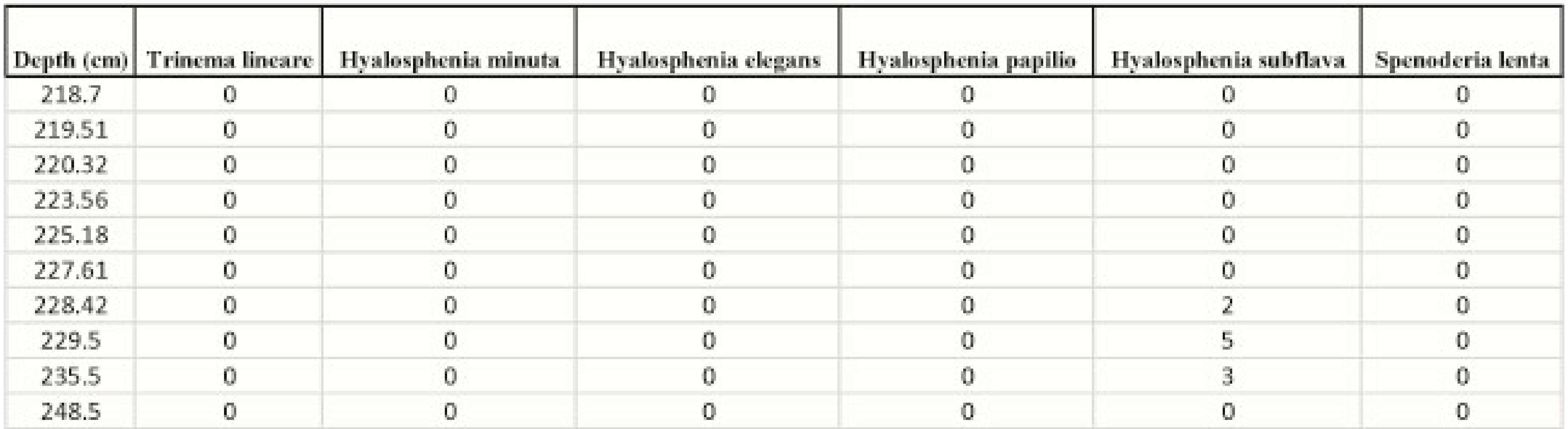
Depth (cm)	Archerella flavum	Amphitrema wrightianum	Arcella artocrea	Arcella catinus	Arcella discoides	Arcella hemispherica	Trinema/Corythion type
218.7	69	21	6	0	4	2	0
219.51	104	20	3	0	3	0	0
220.32	95	15	3	0	4	1	0
223.56	34	9	0	9	4	0	0
225.18	0	0	0	6	7	7	0
227.61	17	0	0	0	6	2	0
228.42	14	0	0	0	0	0	0
229.5	4	0	0	0	1	0	0
235.5	1	0	0	0	1	0	0
248.5	0	0	0	0	0	0	9

W55 core Testate Amoebae raw data: 3/16



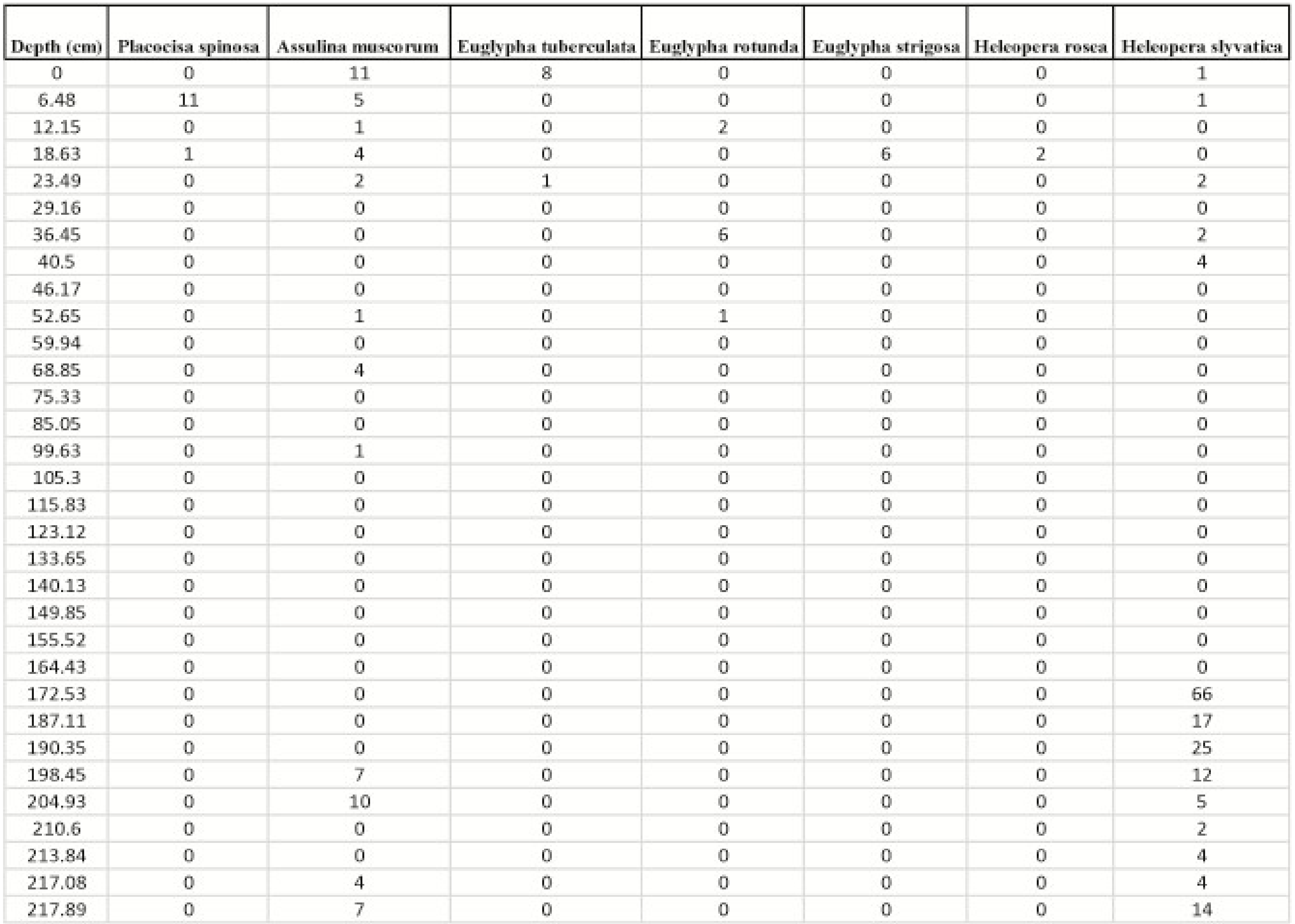
Depth (cm)	Trinema lineare	Hyalosphenia minuta	Hyalosphenia elegans	Hyalosphenia papilio	Hyalosphenia subflava	Spenoderia lenta
0	14	6	9	1	0	0
6.48	0	4	0	0	0	0
12.15	52	0	0	0	11	0
18.63	0	0	2	1	20	0
23.49	61	0	0	0	6	0
29.16	0	0	0	0	5	0
36.45	51	0	0	0	16	1
40.5	4	4	0	0	21	0
46.17	0	0	0	0	4	0
52.65	18	0	0	0	10	0
59.94	29	1	0	0	4	0
68.85	14	0	2	0	21	0
75.33	10	0	0	0	3	0
85.05	0	1	0	0	2	0
99.63	0	0	0	0	8	0
105.3	0	0	0	0	0	0
115.83	0	0	0	0	2	0
123.12	0	0	1	0	1	0
133.65	0	0	0	0	1	0
140.13	0	0	0	0	4	0
149.85	0	0	0	0	1	0
155.52	0	0	0	0	2	0
164.43	0	0	0	0	12	0
172.53	0	0	2	0	0	0
187.11	0	0	0	0	13	0
190.35	0	0	0	0	0	0
198.45	0	0	0	0	0	0
204.93	0	0	0	0	7	0
210.6	0	0	0	0	0	0
213.84	0	0	0	0	2	0
217.08	0	0	0	0	0	0
217.89	0	0	0	0	0	0

W55 core Testate Amoebae raw data: 4/16



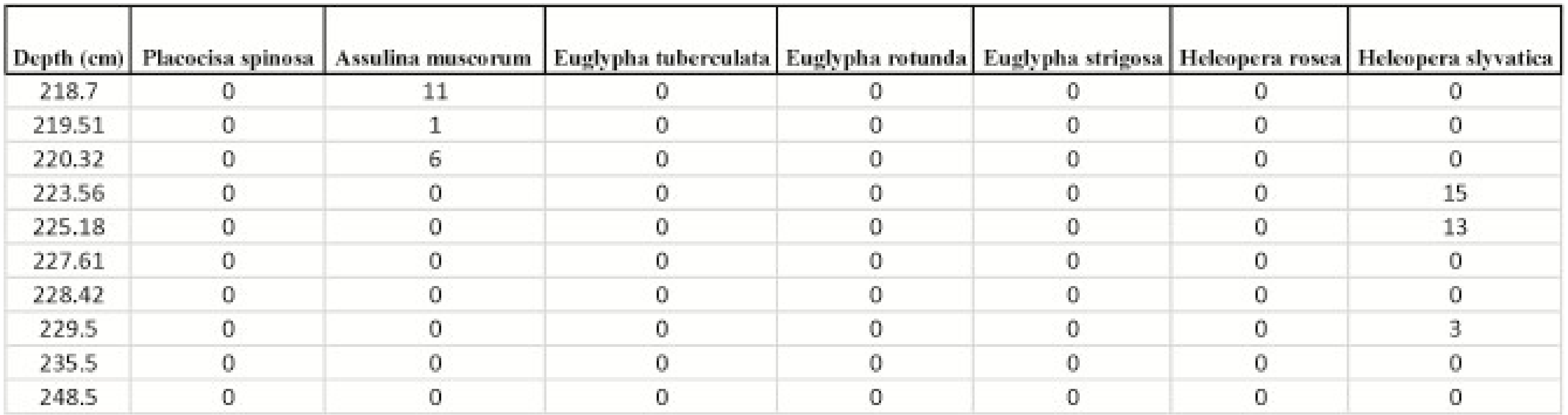
Depth (cm)	Trinema lineare	Hyalosphenia minuta	Hyalosphenia elegans	Hyalosphenia papilio	Hyalosphenia subflava	Spenoderia lenta
218.7	0	0	0	0	0	0
219.51	0	0	0	0	0	0
220.32	0	0	0	0	0	0
223.56	0	0	0	0	0	0
225.18	0	0	0	0	0	0
227.61	0	0	0	0	0	0
228.42	0	0	0	0	2	0
229.5	0	0	0	0	5	0
235.5	0	0	0	0	3	0
248.5	0	0	0	0	0	0

W55 core Testate Amoebae raw data: 5/16



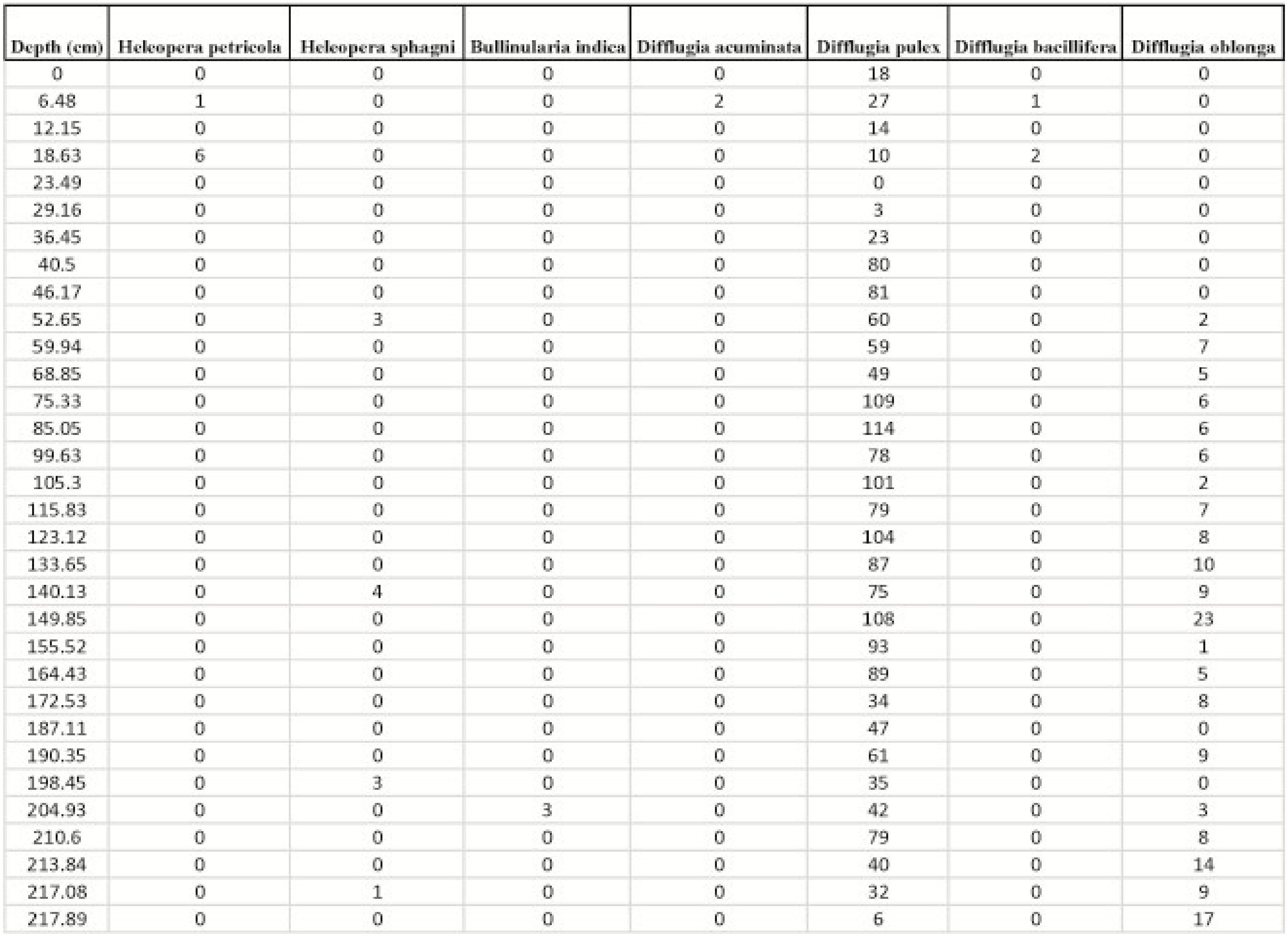
Depth (cm)	Placocisa spinosa	Assulina muscorum	Euglypha tuberculata	Euglypha rotunda	Euglypha strigosa	Heleopera rosea	Heleopera slyvatica
0	0	11	8	0	0	0	1
6.48	11	5	0	0	0	0	1
12.15	0	1	0	2	0	0	0
18.63	1	4	0	0	6	2	0
23.49	0	2	1	0	0	0	2
29.16	0	0	0	0	0	0	0
36.45	0	0	0	6	0	0	2
40.5	0	0	0	0	0	0	4
46.17	0	0	0	0	0	0	0
52.65	0	1	0	1	0	0	0
59.94	0	0	0	0	0	0	0
68.85	0	4	0	0	0	0	0
75.33	0	0	0	0	0	0	0
85.05	0	0	0	0	0	0	0
99.63	0	1	0	0	0	0	0
105.3	0	0	0	0	0	0	0
115.83	0	0	0	0	0	0	0
123.12	0	0	0	0	0	0	0
133.65	0	0	0	0	0	0	0
140.13	0	0	0	0	0	0	0
149.85	0	0	0	0	0	0	0
155.52	0	0	0	0	0	0	0
164.43	0	0	0	0	0	0	0
172.53	0	0	0	0	0	0	66
187.11	0	0	0	0	0	0	17
190.35	0	0	0	0	0	0	25
198.45	0	7	0	0	0	0	12
204.93	0	10	0	0	0	0	5
210.6	0	0	0	0	0	0	2
213.84	0	0	0	0	0	0	4
217.08	0	4	0	0	0	0	4
217.89	0	7	0	0	0	0	14

W55 core Testate Amoebae raw data: 6/16



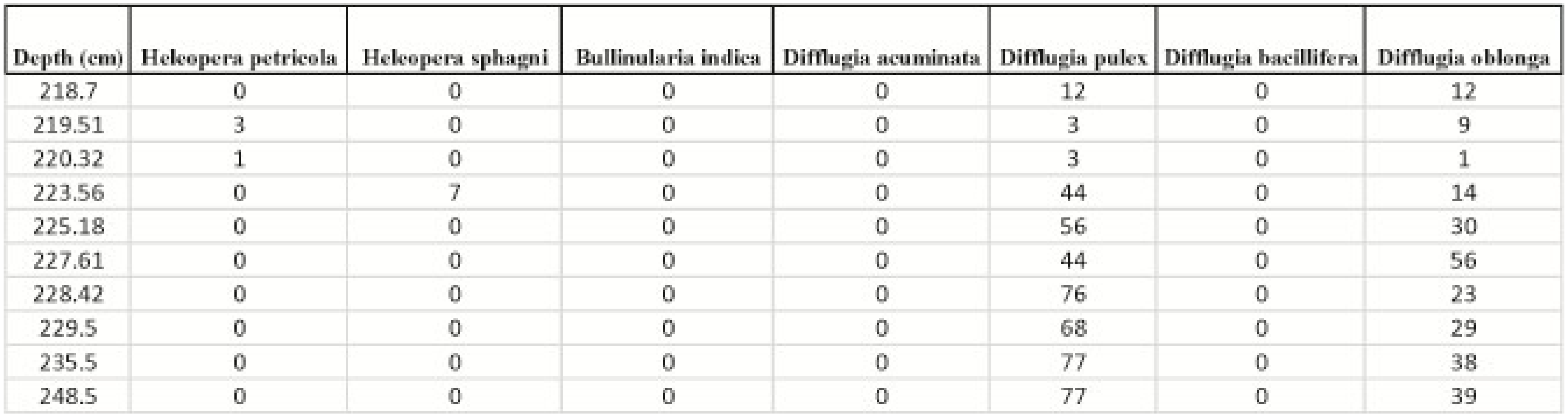
Depth (cm)	Placocisa spinosa	Assulina muscorum	Euglypha tuberculata	Euglypha rotunda	Euglypha strigosa	Heleopera rosea	Heleopera slyvatica
218.7	0	11	0	0	0	0	0
219.51	0	1	0	0	0	0	0
220.32	0	6	0	0	0	0	0
223.56	0	0	0	0	0	0	15
225.18	0	0	0	0	0	0	13
227.61	0	0	0	0	0	0	0
228.42	0	0	0	0	0	0	0
229.5	0	0	0	0	0	0	3
235.5	0	0	0	0	0	0	0
248.5	0	0	0	0	0	0	0

W55 core Testate Amoebae raw data: 7/16



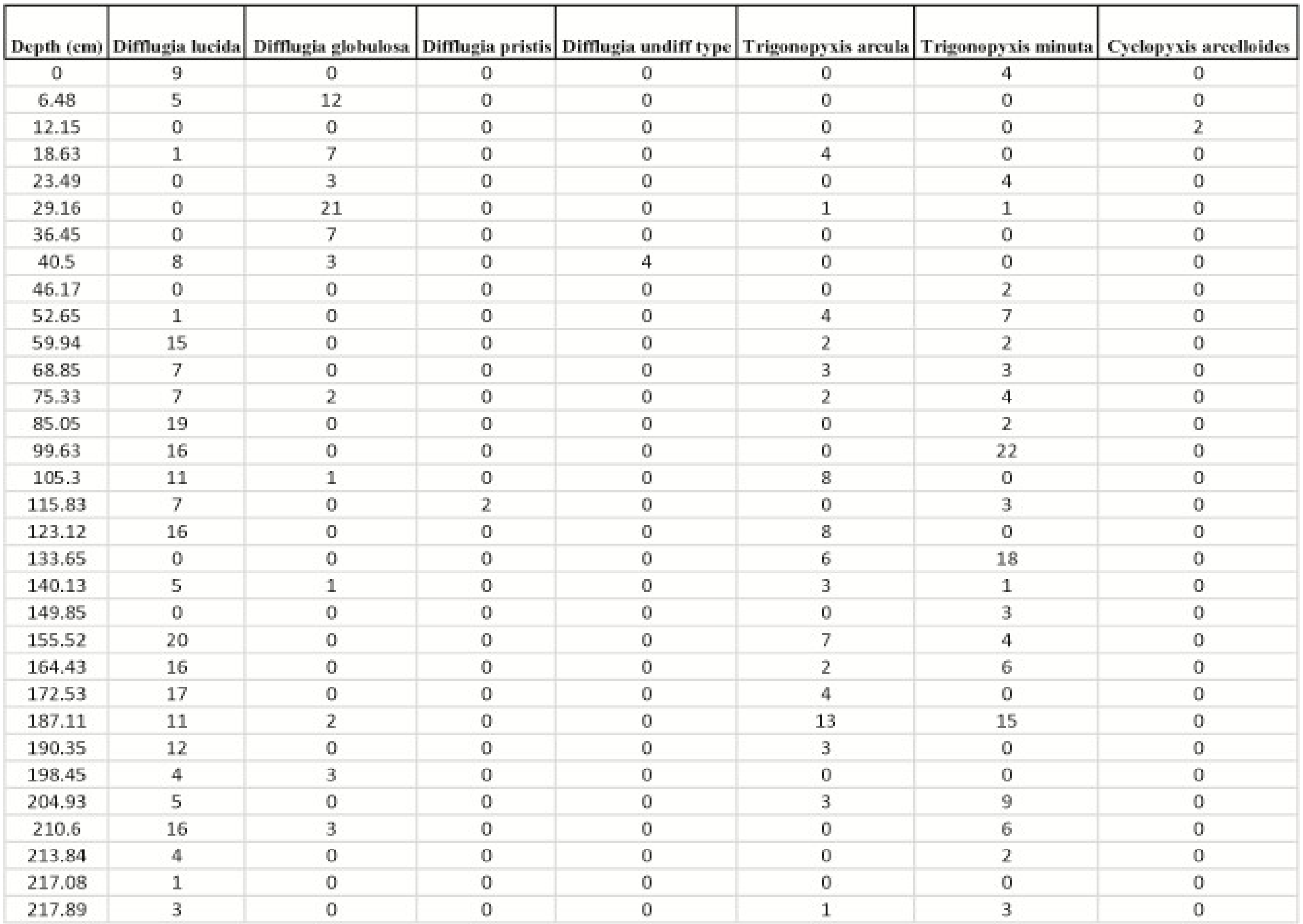
Depth (cm)	Heleopera petricola	Heleopera sphagni	Bullinularia indica	Difflugia acuminata	Difflugia pulex	Difflugia bacillifera	Difflugia oblonga
0	0	0	0	0	18	0	0
6.48	1	0	0	2	27	1	0
12.15	0	0	0	0	14	0	0
18.63	6	0	0	0	10	2	0
23.49	0	0	0	0	0	0	0
29.16	0	0	0	0	3	0	0
36.45	0	0	0	0	23	0	0
40.5	0	0	0	0	80	0	0
46.17	0	0	0	0	81	0	0
52.65	0	3	0	0	60	0	2
59.94	0	0	0	0	59	0	7
68.85	0	0	0	0	49	0	5
75.33	0	0	0	0	109	0	6
85.05	0	0	0	0	114	0	6
99.63	0	0	0	0	78	0	6
105.3	0	0	0	0	101	0	2
115.83	0	0	0	0	79	0	7
123.12	0	0	0	0	104	0	8
133.65	0	0	0	0	87	0	10
140.13	0	4	0	0	75	0	9
149.85	0	0	0	0	108	0	23
155.52	0	0	0	0	93	0	1
164.43	0	0	0	0	89	0	5
172.53	0	0	0	0	34	0	8
187.11	0	0	0	0	47	0	0
190.35	0	0	0	0	61	0	9
198.45	0	3	0	0	35	0	0
204.93	0	0	3	0	42	0	3
210.6	0	0	0	0	79	0	8
213.84	0	0	0	0	40	0	14
217.08	0	1	0	0	32	0	9
217.89	0	0	0	0	6	0	17

W55 core Testate Amoebae raw data: 8/16



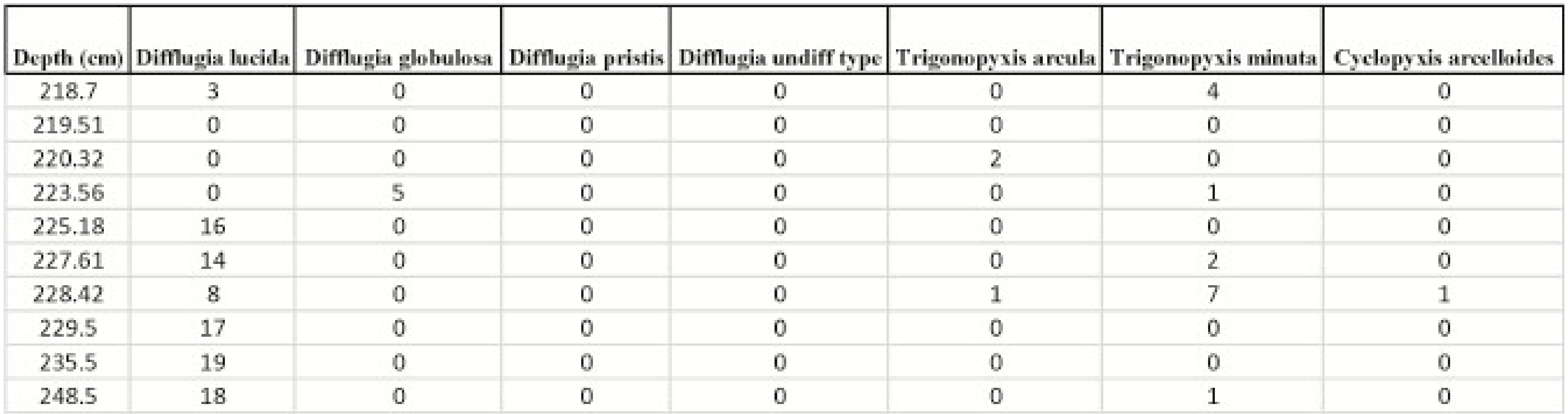
Depth (cm)	Heleopera petricola	Heleopera sphagni	Bullinularia indica	Difflugia acuminata	Difflugia pulex	Difflugia bacillifera	Difflugia oblonga
218.7	0	0	0	0	12	0	12
219.51	3	0	0	0	3	0	9
220.32	1	0	0	0	3	0	1
223.56	0	7	0	0	44	0	14
225.18	0	0	0	0	56	0	30
227.61	0	0	0	0	44	0	56
228.42	0	0	0	0	76	0	23
229.5	0	0	0	0	68	0	29
235.5	0	0	0	0	77	0	38
248.5	0	0	0	0	77	0	39

W55 core Testate Amoebae raw data: 9/16



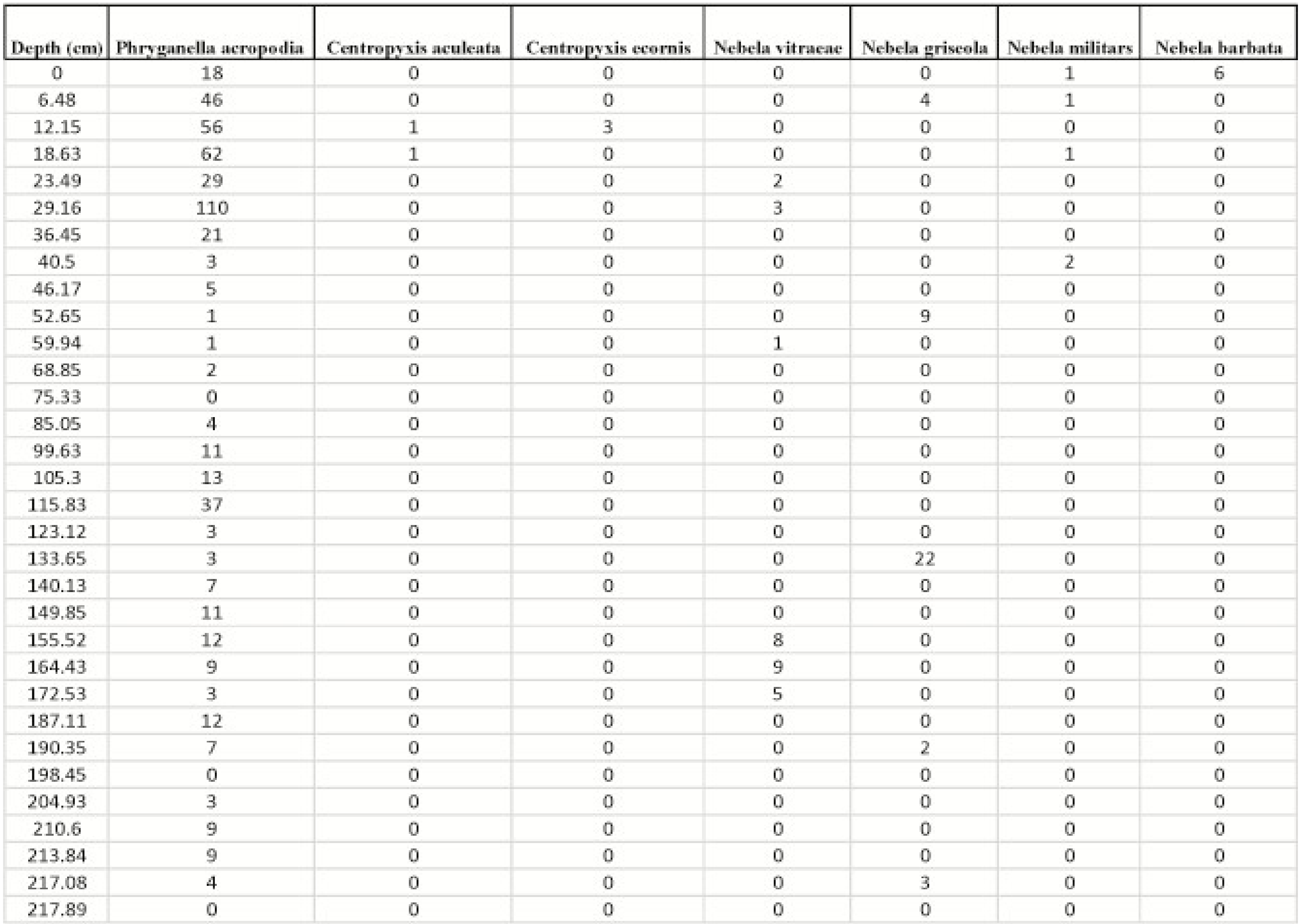
Depth (cm)	Difflugia lucida	Difflugia globulosa	Difflugia pristis	Difflugia undiff type	Trigonopyxis arcula	Trigonopyxis minuta	Cyclopyxis arcelloides
0	9	0	0	0	0	4	0
6.48	5	12	0	0	0	0	0
12.15	0	0	0	0	0	0	2
18.63	1	7	0	0	4	0	0
23.49	0	3	0	0	0	4	0
29.16	0	21	0	0	1	1	0
36.45	0	7	0	0	0	0	0
40.5	8	3	0	4	0	0	0
46.17	0	0	0	0	0	2	0
52.65	1	0	0	0	4	7	0
59.94	15	0	0	0	2	2	0
68.85	7	0	0	0	3	3	0
75.33	7	2	0	0	2	4	0
85.05	19	0	0	0	0	2	0
99.63	16	0	0	0	0	22	0
105.3	11	1	0	0	8	0	0
115.83	7	0	2	0	0	3	0
123.12	16	0	0	0	8	0	0
133.65	0	0	0	0	6	18	0
140.13	5	1	0	0	3	1	0
149.85	0	0	0	0	0	3	0
155.52	20	0	0	0	7	4	0
164.43	16	0	0	0	2	6	0
172.53	17	0	0	0	4	0	0
187.11	11	2	0	0	13	15	0
190.35	12	0	0	0	3	0	0
198.45	4	3	0	0	0	0	0
204.93	5	0	0	0	3	9	0
210.6	16	3	0	0	0	6	0
213.84	4	0	0	0	0	2	0
217.08	1	0	0	0	0	0	0
217.89	3	0	0	0	1	3	0

W55 core Testate Amoebae raw data: 10/16



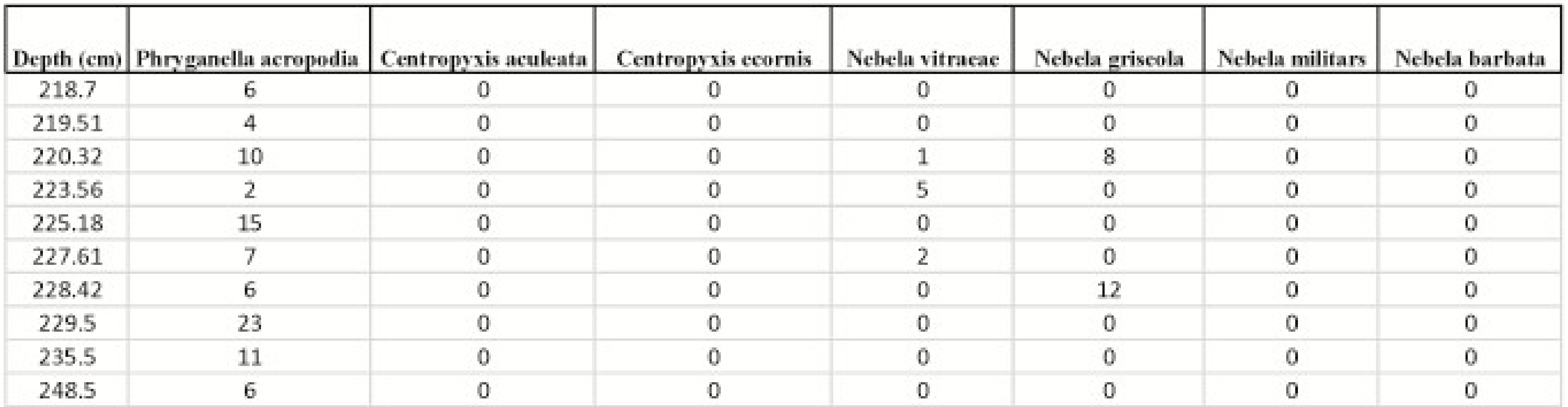
Depth (cm)	Difflugia lucida	Difflugia globulosa	Difflugia pristis	Difflugia undiff type	Trigonopyxis arcula	Trigonopyxis minuta	Cyclopyxis arcelloides
218.7	3	0	0	0	0	4	0
219.51	0	0	0	0	0	0	0
220.32	0	0	0	0	2	0	0
223.56	0	5	0	0	0	1	0
225.18	16	0	0	0	0	0	0
227.61	14	0	0	0	0	2	0
228.42	8	0	0	0	1	7	1
229.5	17	0	0	0	0	0	0
235.5	19	0	0	0	0	0	0
248.5	18	0	0	0	0	1	0

W55 core Testate Amoebae raw data: 11/16



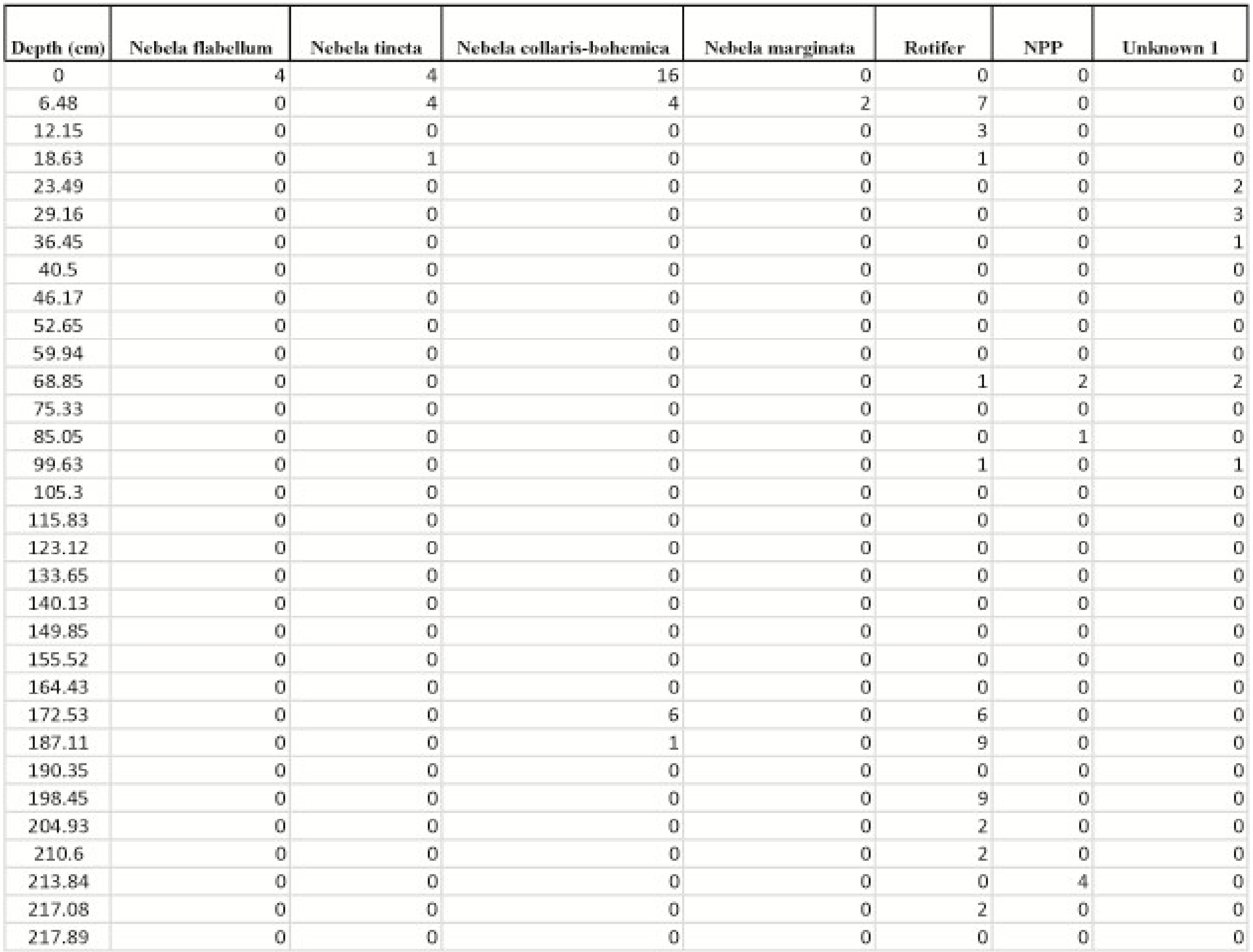
Depth (cm)	Phryganella acropodia	Centropyxis aculeata	Centropyxis ecornis	Nebela vitraeae	Nebela griseola	Nebela militars	Nebela barbata
0	18	0	0	0	0	1	6
6.48	46	0	0	0	4	1	0
12.15	56	1	3	0	0	0	0
18.63	62	1	0	0	0	1	0
23.49	29	0	0	2	0	0	0
29.16	110	0	0	3	0	0	0
36.45	21	0	0	0	0	0	0
40.5	3	0	0	0	0	2	0
46.17	5	0	0	0	0	0	0
52.65	1	0	0	0	9	0	0
59.94	1	0	0	1	0	0	0
68.85	2	0	0	0	0	0	0
75.33	0	0	0	0	0	0	0
85.05	4	0	0	0	0	0	0
99.63	11	0	0	0	0	0	0
105.3	13	0	0	0	0	0	0
115.83	37	0	0	0	0	0	0
123.12	3	0	0	0	0	0	0
133.65	3	0	0	0	22	0	0
140.13	7	0	0	0	0	0	0
149.85	11	0	0	0	0	0	0
155.52	12	0	0	8	0	0	0
164.43	9	0	0	9	0	0	0
172.53	3	0	0	5	0	0	0
187.11	12	0	0	0	0	0	0
190.35	7	0	0	0	2	0	0
198.45	0	0	0	0	0	0	0
204.93	3	0	0	0	0	0	0
210.6	9	0	0	0	0	0	0
213.84	9	0	0	0	0	0	0
217.08	4	0	0	0	3	0	0
217.89	0	0	0	0	0	0	0

W55 core Testate Amoebae raw data: 12/16



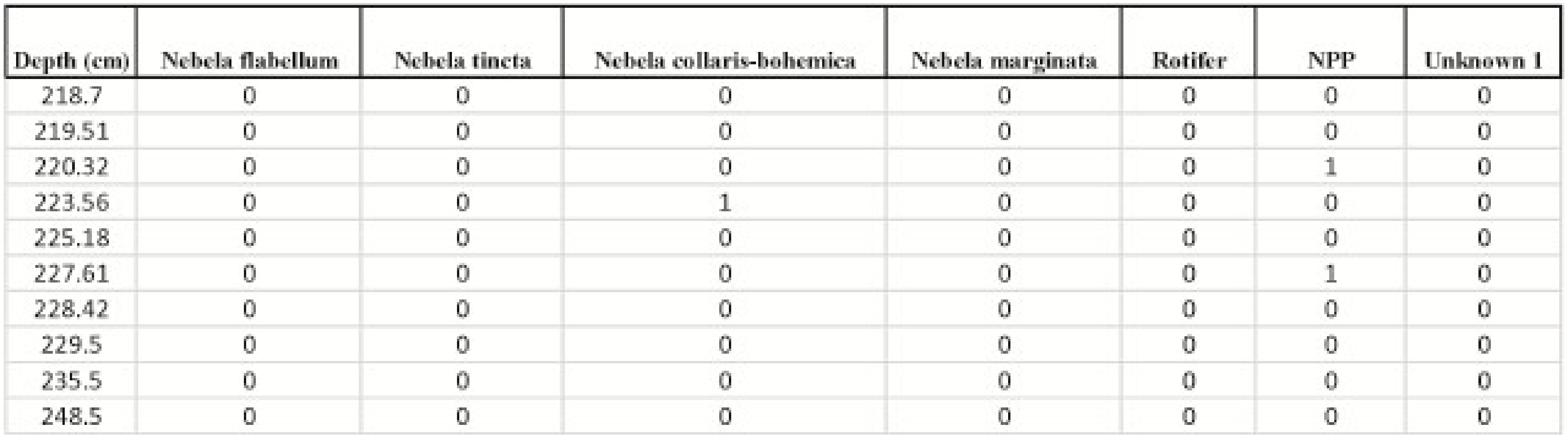
Depth (cm)	Phryganella acropodia	Centropyxis aculeata	Centropyxis ecornis	Nebela vitraeae	Nebela griseola	Nebela militars	Nebela barbata
218.7	6	0	0	0	0	0	0
219.51	4	0	0	0	0	0	0
220.32	10	0	0	1	8	0	0
223.56	2	0	0	5	0	0	0
225.18	15	0	0	0	0	0	0
227.61	7	0	0	2	0	0	0
228.42	6	0	0	0	12	0	0
229.5	23	0	0	0	0	0	0
235.5	11	0	0	0	0	0	0
248.5	6	0	0	0	0	0	0

W55 core Testate Amoebae raw data: 13/16



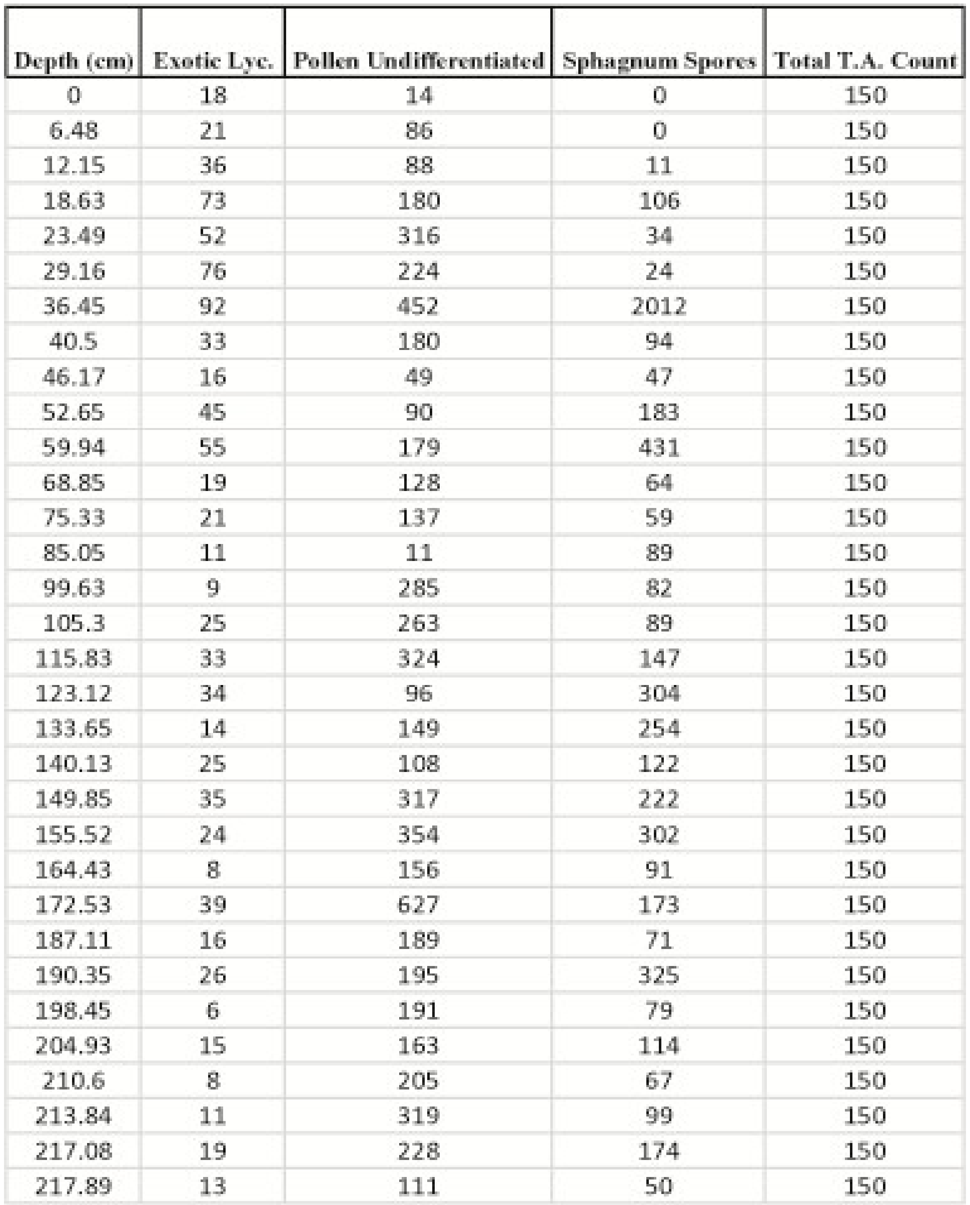
Depth (cm)	Nebela flabellum	Nebela tincta	Nebela collaris-bohemica	Nebela marginata	Rotifer	NPP	Unknown 1
0	4	4	16	0	0	0	0
6.48	0	4	4	2	7	0	0
12.15	0	0	0	0	3	0	0
18.63	0	1	0	0	1	0	0
23.49	0	0	0	0	0	0	2
29.16	0	0	0	0	0	0	3
36.45	0	0	0	0	0	0	1
40.5	0	0	0	0	0	0	0
46.17	0	0	0	0	0	0	0
52.65	0	0	0	0	0	0	0
59.94	0	0	0	0	0	0	0
68.85	0	0	0	0	1	2	2
75.33	0	0	0	0	0	0	0
85.05	0	0	0	0	0	1	0
99.63	0	0	0	0	1	0	1
105.3	0	0	0	0	0	0	0
115.83	0	0	0	0	0	0	0
123.12	0	0	0	0	0	0	0
133.65	0	0	0	0	0	0	0
140.13	0	0	0	0	0	0	0
149.85	0	0	0	0	0	0	0
155.52	0	0	0	0	0	0	0
164.43	0	0	0	0	0	0	0
172.53	0	0	6	0	6	0	0
187.11	0	0	1	0	9	0	0
190.35	0	0	0	0	0	0	0
198.45	0	0	0	0	9	0	0
204.93	0	0	0	0	2	0	0
210.6	0	0	0	0	2	0	0
213.84	0	0	0	0	0	4	0
217.08	0	0	0	0	2	0	0
217.89	0	0	0	0	0	0	0

W55 core Testate Amoebae raw data: 14/16



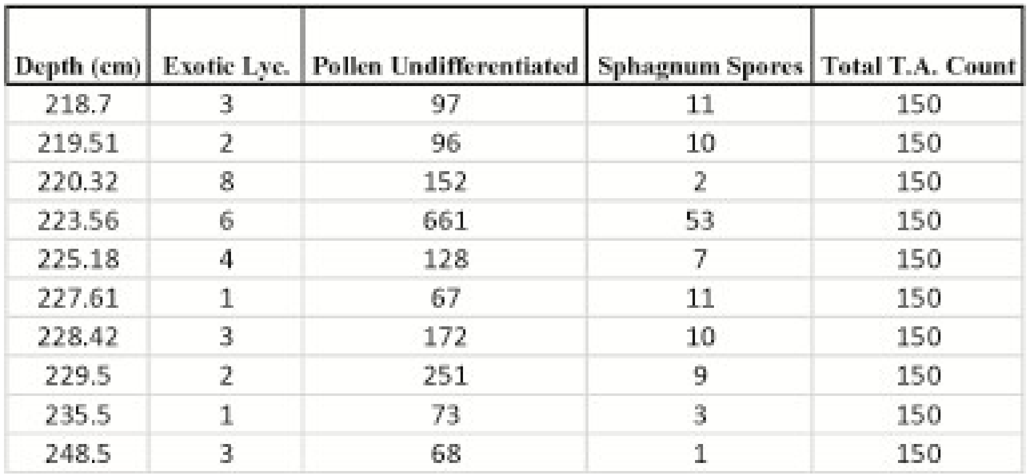
Depth (cm)	Nebela flabellum	Nebela tincta	Nebela collaris-bohemica	Nebela marginata	Rotifer	NPP	Unknown 1
218.7	0	0	0	0	0	0	0
219.51	0	0	0	0	0	0	0
220.32	0	0	0	0	0	1	0
223.56	0	0	1	0	0	0	0
225.18	0	0	0	0	0	0	0
227.61	0	0	0	0	0	1	0
228.42	0	0	0	0	0	0	0
229.5	0	0	0	0	0	0	0
235.5	0	0	0	0	0	0	0
248.5	0	0	0	0	0	0	0

W55 core Testate Amoebae raw data: 15/16



Depth (cm)	Exotic Lyc.	Pollen Undifferentiated	Sphagnum Spores	Total T.A. Count
0	18	14	0	150
6.48	21	86	0	150
12.15	36	88	11	150
18.63	73	180	106	150
23.49	52	316	34	150
29.16	76	224	24	150
36.45	92	452	2012	150
40.5	33	180	94	150
46.17	16	49	47	150
52.65	45	90	183	150
59.94	55	179	431	150
68.85	19	128	64	150
75.33	21	137	59	150
85.05	11	11	89	150
99.63	9	285	82	150
105.3	25	263	89	150
115.83	33	324	147	150
123.12	34	96	304	150
133.65	14	149	254	150
140.13	25	108	122	150
149.85	35	317	222	150
155.52	24	354	302	150
164.43	8	156	91	150
172.53	39	627	173	150
187.11	16	189	71	150
190.35	26	195	325	150
198.45	6	191	79	150
204.93	15	163	114	150
210.6	8	205	67	150
213.84	11	319	99	150
217.08	19	228	174	150
217.89	13	111	50	150

W55 core Testate Amoebae raw data: 16/16



Depth (cm)	Exotic Lyc.	Pollen Undifferentiated	Sphagnum Spores	Total T.A. Count
218.7	3	97	11	150
219.51	2	96	10	150
220.32	8	152	2	150
223.56	6	661	53	150
225.18	4	128	7	150
227.61	1	67	11	150
228.42	3	172	10	150
229.5	2	251	9	150
235.5	1	73	3	150
248.5	3	68	1	150