

# Great Canadian Lagerstätten 5. Crawford Lake – A Canadian Holocene Lacustrine Konservat-Lagerstätte with Two-Century-Old Viable Dinoflagellate Cysts

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Résumé de l'article

En plus des microfossiles couramment conservés comme le pollen et les diatomées, les sédiments varvés du lac Crawford en Ontario, contiennent les restes fossilisés de microfossiles très rares. Le caractère anoxique des eaux de fond s'explique par la physiographie de ce petit lac profond et par une augmentation de la demande biochimique en oxygène (DBO) durant deux phases distinctes de peuplement humain : phase préhistorique iroquoise (environ 1268 à 1486 CE) et une phase historique euro-canadienne (depuis 1822 CE). La préservation exceptionnelle de délicats microfossiles à membranes organiques comme rotifère lorica et les thèques cellulodiques de dinoflagellés, ouvre une fenêtre inédite sur l'écosystème d'un lac d'eau douce Holocène et permet aux composants biologiques et taphonomiques de l'assemblage de fossiles d'être préservés isolément. L'anoxie des eaux de fond peut également avoir augmenté la longévité du contenu des cellules: kystes dormants de *Parvodinium* [*Peridinium*] *inconspicuum* (Lemmermann) Carty et de *Peridinium volzii* Lemmermann. Ces derniers ont été activés à partir de varves déposés il y a près de deux siècles, ce qui allonge la durée connue de la viabilité des dinoflagellés.

# SERIES



## Great Canadian Lagerstätten 5. Crawford Lake – A Canadian Holocene Lacustrine Konservat-Lagerstätte with Two- Century-Old Viable Dinoflagellate Cysts

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### SUMMARY

In addition to commonly preserved microfossils like pollen and diatoms, the varved sediments of Crawford Lake, Ontario, contain the fossilized remains of otherwise rare microfossils. Bottom water anoxia resulted from the physiography of this small, deep lake and enhanced biochemical oxygen demand (BOD) during two distinct phases of human settlement: prehistoric Iroquoians (approximately 1268–1486 CE) and historic Euro-Canadians (since 1822 CE). The exceptional preservation of delicate organic-walled microfossils like rotifer loricae and cellulosic dinoflagellate thecae provides unparalleled insights into a Holocene freshwater lake ecosystem and allows the biological and taphonomic components of the fossil assemblage to be isolated. Bottom water anoxia may also have increased the longevity of cell contents: resting cysts of *Parvodinium* [*Peridinium*] *inconspicuum* (Lemmermann) Carty and

*Peridinium volzii* Lemmermann. These were germinated from varves deposited nearly two centuries ago, extending the known span of viability of dinoflagellates.

### RÉSUMÉ

En plus des microfossiles couramment conservés comme le pollen et les diatomées, les sédiments varvés du lac Crawford en Ontario, contiennent les restes fossilisés de microfossiles très rares. Le caractère anoxique des eaux de fond s'explique par la physiographie de ce petit lac profond et par une augmentation de la demande biochimique en oxygène (DBO) durant deux phases distinctes de peuplement humain : phase préhistorique iroquoise (environ 1268 à 1486 CE) et une phase historique euro-canadienne (depuis 1822 CE). La préservation exceptionnelle de délicats microfossiles à membranes organiques comme rotifère lorica et les thèques cellulosiques de dinoflagellés, ouvre une fenêtre inédite sur l'écosystème d'un lac d'eau douce Holocène et permet aux composants biologiques et taphonomiques de l'assemblage de fossiles d'être préservés isolément. L'anoxie des eaux de fond peut également avoir augmenté la longévité du contenu des cellules: kystes dormants de *Parvodinium* [*Peridinium*] *inconspicuum* (Lemmermann) Carty et de *Peridinium volzii* Lemmermann. Ces derniers ont été activés à partir de varves déposés il y a près de deux siècles, ce qui allonge la durée connue de la viabilité des dinoflagellés.

Traduit par le Traducteur

### INTRODUCTION

The concept of *Konservat-Lagerstätten* is virtually absent from the Holocene literature (Allison and Briggs 1993), despite the fact that exceptionally preserved deposits would serve as an important quantifiable bridge between biological and paleontological records. Several examples of exceptionally preserved large mammals, like mammoths and bison, have been reported from permafrost, prehistoric human remains have been found in glaciers (e.g. Ötzi from the Eastern Alps and Kwäday Dän Ts'inch from the British Columbia Rockies) and peat bogs (*Moorleiche* like Tollund Man and Lindow Man; Painter 1991 and Oeggl et al. 2007), and concentrations of desiccated remains of plants and animals (*Konzentrat-Lagerstätten*) are known from cave deposits of various ages, including the Holocene. Examples of *Lagerstätten* representing a large fraction of the biocoenosis in modern lakes are rare, however, despite their relative abundance and the critical importance of freshwater resources.

Lakes tend to be characterized by continuous and relatively rapid sedimentation conducive to excellent paleontologic resolution (Schindel 1980) and lacustrine *Lagerstätten* such as the Eocene Green River Shale (Bradley 1931; Grande 1980; Buchheim and Surdham 1981), the Oligocene Enspel 'oilshale' (Köhler and Clausing 2000; Poschmann et al. 2010), and the Miocene Clarkia Beds (Smiley and Rember 1981, 1985; Batten et al. 1999) provide exceptional insights into ancient continental environments. Long-term (pre-instrumental) environmental trends can be assessed through paleolimnology, but it is difficult to apply the abundant phycological and zoological literature to micropaleontological samples without understanding the impact of taphonomy on modern lake sediment. The optimal use of paleolimnological data to inform ecological management (e.g. Cabecinha et al. 2009; Smol 2010) depends on an accurate assessment of the biological community (biocoenosis), relative to the fossil assemblages (thanatocoenosis), requiring a thorough understanding of the impact of transport into and out of the lake, differential preservation of the various components of the ecosystem, and time-averaging of the record (Kidwell and Flessa 1996).

Meromictic lakes (lakes with layers of water that do not intermix, resulting in bottom water anoxia) have long been known to promote excellent preservation, allowing the biological component of variance between samples to be isolated from the taphonomic component (Bell et al. 1987). Additionally, the virtual absence of bioturbation allows for very high resolution in commonly annually laminated sediment (varves), although these are typically not very long records, since lakes tend to fill in (Schindel 1980). Annual chronological resolution in the late Holocene varved record of Crawford Lake, Ontario, allowed comparison with archaeological and historical records that document two distinct phases of human settlement and associated cultural eutrophication (Boyko 1973; Byrne and McAndrews 1975; McAndrews and Boyko-Diakonow 1989; Ekdahl et al. 2004, 2007; McAndrews and Turton 2010). As a result, in addition to commonly-preserved microfossils like pollen (Boyko 1973; Byrne and McAndrews 1975; McAndrews and Boyko-Diakonow 1989) and diatoms (Ekdahl et al. 2004, 2007) the varves deposited below the chemocline in the deep basin of Crawford Lake since the 13<sup>th</sup> century CE contain the fossilized remains of otherwise rare microfossils. These provide exceptional insights into the lake ecosystem, compared with the vast majority of lacustrine records that have been more taphonomically altered.

## GEOLOGIC SETTING

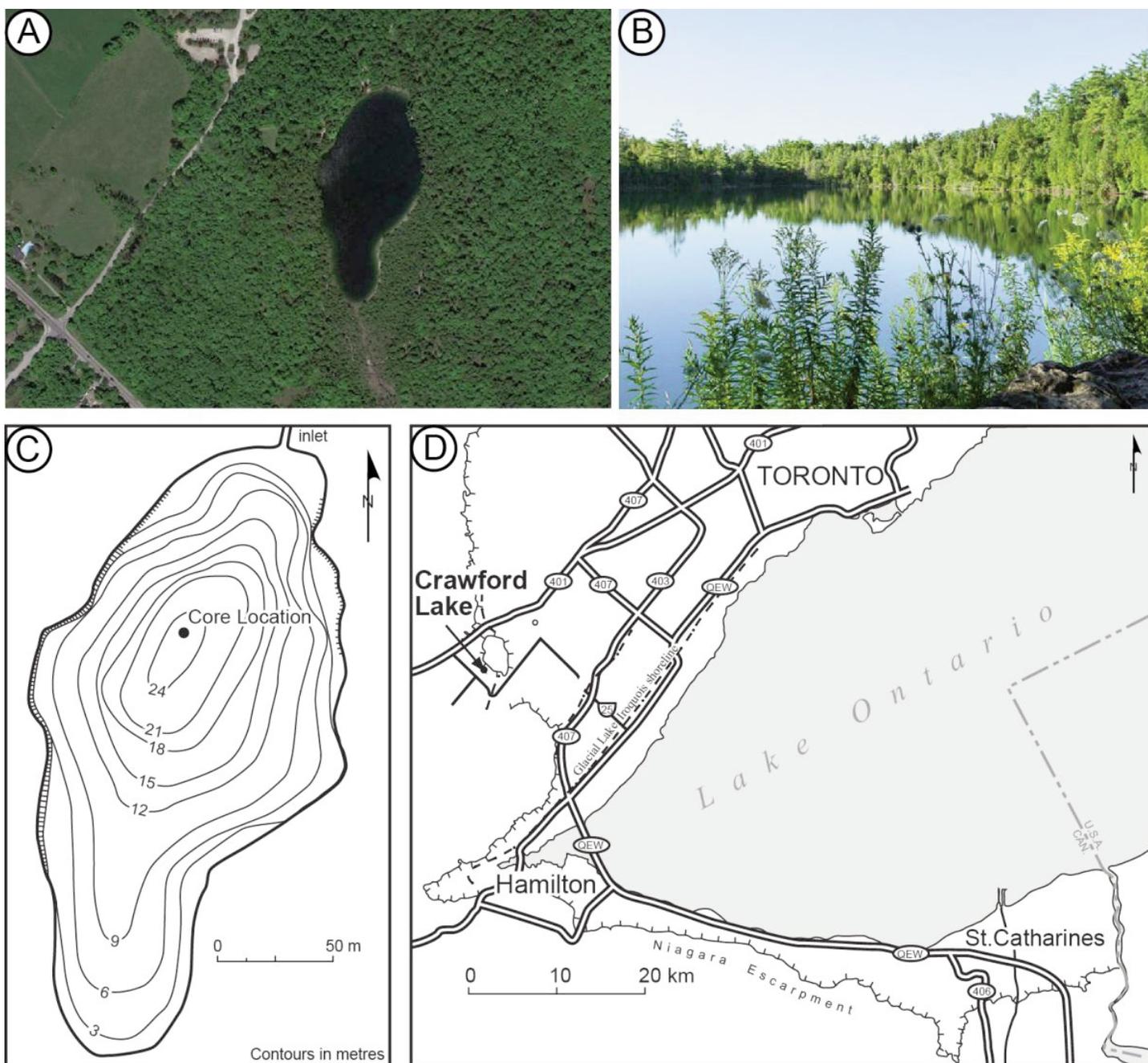
Crawford Lake occupies a small, deep dolostone basin adjacent to the edge of the Niagara Escarpment World Biosphere Reserve near Toronto (Fig. 1). The Crawford Lake Conservation Area has been designated as an Area of Natural and Scientific Interest (ANSI) by the Government of Ontario (Niagara Escarpment Plan 2005) due to its geological, ecological, and archaeological attractions – the latter including the 'Iroquoian Village' reconstructed in 1972 by the Halton Region Conservation Authority (Conservation Halton) following an archaeological survey (Finlayson 1998). This survey was initiated by the discovery of the remains of cultivars such as corn (*Zea*), and sunflower (*Helianthus*) pollen spores in varved sediment from around the middle of the last millennium (Fig. 2)

(Boyko 1973; Finlayson et al. 1973; Byrne and McAndrews 1975; McAndrews and Boyko-Diakonow 1989). This site, approximately 150 m from the lake, was intermittently occupied by between 200 and 300 people in the 13<sup>th</sup> to 16<sup>th</sup> centuries (Finlayson 1998; Byrne and Finlayson 1998) and was subsequently unoccupied until the Crawford homestead was established in ca. 1822 CE (McAndrews and Boyko-Diakonow 1989). The peak abundance of ragweed (*Ambrosia*) and other non-arboreal pollen in the late 19<sup>th</sup> century (Fig. 2) marks the most intensive Euro-Canadian impact in the watershed, when a sawmill operated on the southern shore of the small lake (Crawford Lake Conservation Area 2011).

The Crawford Lake basin is thought to have been excavated in relatively soft and soluble dolomite of the underlying Silurian Lockport Formation during the late Wisconsinan, when glacial meltwater flowed southward between two ablating ice lobes (McAndrews and Boyko-Diakonow 1989). Underground caves in this karstic region could have further facilitated this process. The lake does not fully overturn due to its relatively small surface area (about 250 x 150 m) and great depth (up to 22.5 m of water overlies approximately 4.5 m of postglacial sediment in the deepest part of the basin). Crawford Lake has a high affinity for meromixis (i.e.  $Z_r > 2$  using the equation of Hutchinson (1957),

$$Z_r = \frac{(50 \times Z_m \times \sqrt{\pi})}{(\sqrt{A})}$$

with  $Z_r = 10.25$  (where  $Z_r$  = relative depth,  $Z_m$  = maximum depth,  $A$  = surface area). Seepage from a catchment of about 80 km<sup>2</sup> is the main inflow into this small (about 2.4 ha) lake, minimizing disturbance of the water column, and the mature eastern white cedar (*Thuja occidentalis*) forest on the slopes surrounding the lake acts as a wind-break, further reducing mixing of the water column (Yu et al. 1997). Water below the thermocline at around 15 m thus has a constant temperature of 5–6°C (McAndrews and Turton 2010) and over the last millennium bioturbation has been largely suppressed by bottom water anoxia. Since the 13<sup>th</sup> century CE, when the Iroquoian village was established and BOD (biochemical oxygen demand) increased due to cultural eutrophication (Ekdahl et al. 2004, 2007; Turton and McAndrews 2006), annual sediment couplets – varves – consisting of a white calcite-rich layer and a dark organic-rich layer (Figs. 3, 4) have accumulated because the anoxic bottom waters were unable to support benthic animals and protists (Dickman 1979). It has been proposed that episodic reduction in benthic anoxia at times of reduced productivity and BOD between the two phases of human settlement in the catchment (Chan, C., personal communication 2011, unpublished benthic ostracode data) may have interrupted varve formation, explaining the observation that about 10% of the varves are missing in the Post-Iroquoian Zone when compared to Accelerated Mass Spectrometry–C<sup>14</sup> dating (Ekdahl et al. 2004, 2007). Nonetheless, varve counting together with carbon dating provides a very precise chronology, allowing the microfossil record to be compared with historic and archaeological data (Fig. 4). Freeze cores allow varves to be recovered, as the sediment freeze onto the hollow aluminum wedge filled with an ethanol and dry ice slurry; the wedge



**Figure 1.** Aerial view (A) and shore view (B) photos of Crawford Lake, Milton, Ontario (Google images 2015). Bathymetry of the small, deep, meromictic Crawford Lake (C) near the edge of the Niagara Escarpment World Biosphere Reserve, about 50 km west of Toronto (D).

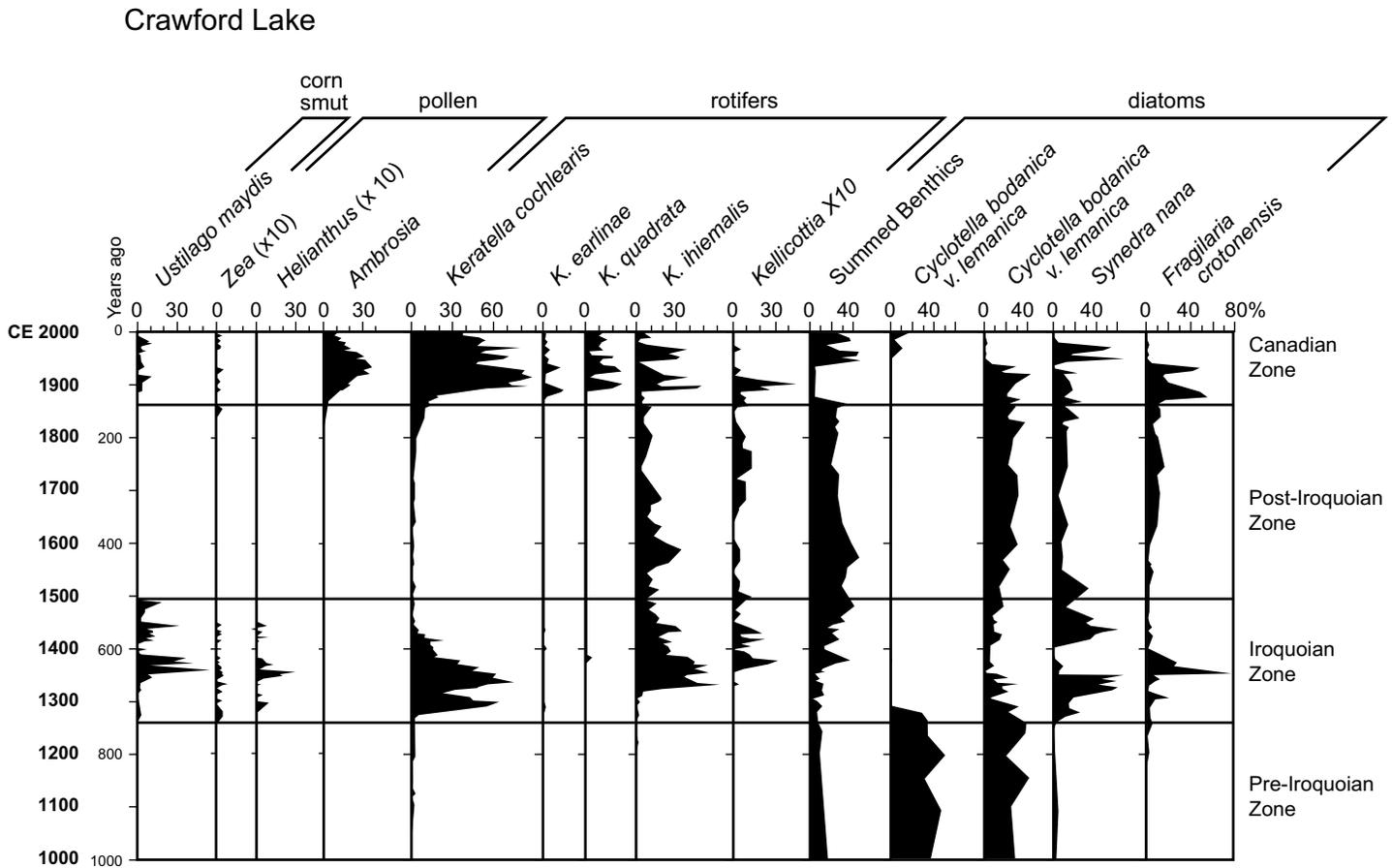
shape of the ‘frigid finger’ sampler allows for easy penetration into the sediments.

**EXCEPTIONALLY PRESERVED DINOFLAGELLATES**

In addition to commonly preserved pollen (Boyko 1973; Byrne and McAndrews 1975; McAndrews and Boyko-Diakonow 1989; Byrne and Finlayson 1998), fungal spores like corn smut (*Ustilago maydis*; McAndrews and Turton 2010), and diatoms (Ekdahl et al. 2004, 2007), rarely preserved microfossils are also found in varves deposited in the deep basin of Crawford Lake over the last 800 years. Turton and McAndrews (2006), for instance, reported common rotifer loricae that show a clear response to the increase in nutrients and abundance of algae

during the Iroquoian and Euro-Canadian zone (Fig. 2). Fossil remains of these pseudocoelomate microscopic aquatic ‘wheel animals’ of the Phylum Rotifera are rare except for their resting eggs (van Geel 2001), but other body parts can accumulate under exceptional circumstances that inhibit oxygen, such as preservation in amber (Waggoner and Poinar 1993), in rapidly accumulating early Holocene sediment (Swadling et al. 2001), and a rare example of a complete rotifer in Permian sediment from India (Jha et al. 2011).

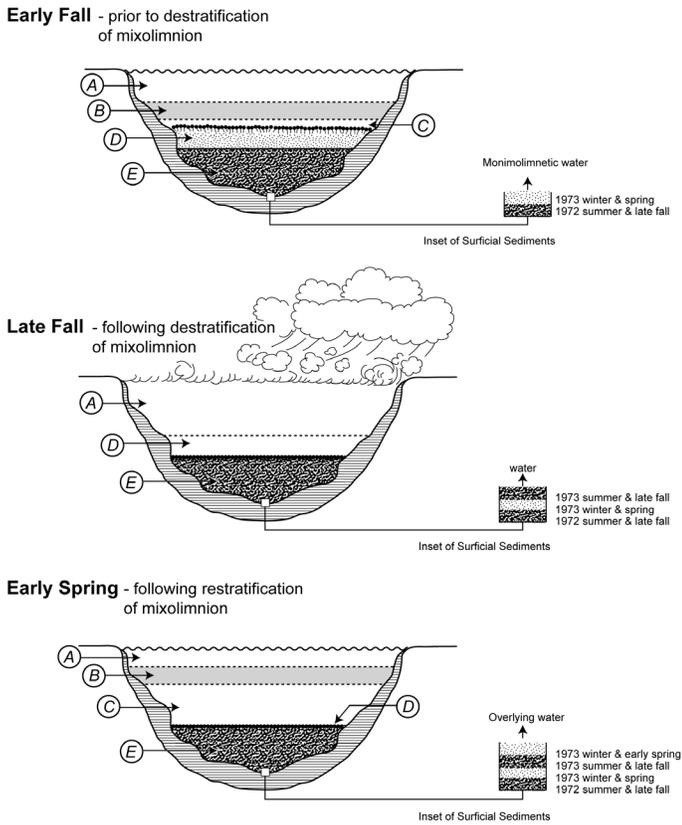
Rarely preserved cellulosic thecae of the dinoflagellate *Parvodinium* [*Peridinium*] *inconspicuum* (Lemmermann) Carty (Fig. 5A–C) were found together with abundant resting cysts in palynological preparations from varves deposited during the



**Figure 2.** Summary of microfossil occurrence in varved sediments from Crawford Lake showing two separate phases of human settlement in the catchment indicated by peaks in abundance of spores of *Ustilago maydis*, a pathogenic fungus that attacks corn ('corn smut') and pollen associated with agriculture and land disturbance, e.g. corn (*Zea*), sunflower (*Helianthus*), and ragweed (*Ambrosia*) (McAndrews and Turton 2007, 2010). Eutrophication of the lake is illustrated by peaks in rotifer loricae (Turton and McAndrews 2006) and diatoms (Ekdahl et al. 2004, 2007). Although there is microfossil evidence of improved water quality since the site was taken over by the Halton Region Conservation Authority (Conservation Halton) in 1972, the lake has not returned to pre-disturbance conditions.

early Iroquoian period (13<sup>th</sup> century CE) and from the Euro-Canadian Period (Fig. 6). Dinoflagellates are common components of the phytoplankton in lakes, with approximately 350 species of the Phylum Dinoflagellata Bütschli inhabiting freshwater environments (Popovsky and Pfister 1990; Mertens et al. 2012; Carty 2014). They have large, unusual dinokaryotic nuclei in which the chromosomes have unmasked DNA fibrils and are more or less continuously condensed (Fensome et al. 1993). The large nuclei contain the red pigment responsible for 'red tides'; they are bright red just prior to mitosis (McCarthy et al. 2011) and thus impart a red colour to the water during algal blooms. The life history of most dinoflagellates consists of a motile (vegetative) stage in which armored thecae composed of several cellulose plates whirl through the water column using their two flagellae – one transverse, along the cingulum (belt), and one longitudinal along the sulcus (groove) – and at least one nonflagellated benthic stage (cyst) (Bravo and Figueroa 2014). Fossilizable (long-term) resting cysts are composed of dinosporin, a complex biomacromolecular substance composed of phenolic, alcoholic and/or carboxylic hydroxides, fatty acids with tocopherols, and sterols (Kokinos et al. 1998; Versteegh et al. 2012). These are produced by some, but not all, species, and to date are known for only about 20% of fresh water species (Mertens et al. 2012), a percentage comparable to marine taxa (Head 1996).

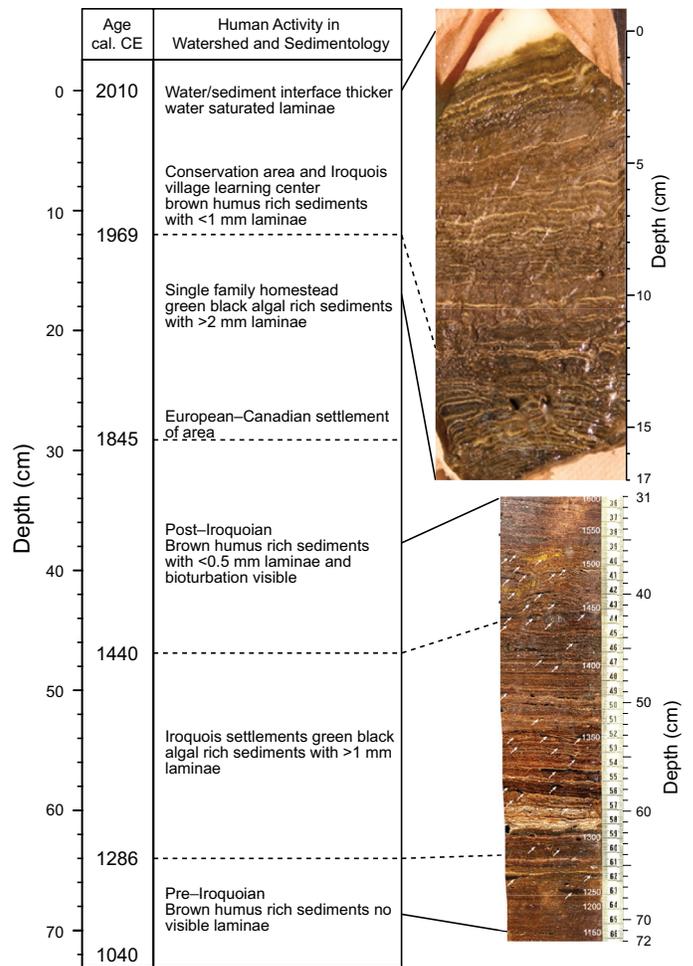
Unlike marine taxa, however, cyst-theca relationships are known for very few freshwater dinoflagellate taxa (Wall and Dale 1968; McCarthy et al. 2011; Mertens et al. 2012; Drljepan et al. 2014). Even in studies where both phycological and palynological approaches are combined (e.g. Chu et al. 2008), it has proven difficult to definitively relate thecae in the water column with dinoflagellate cysts preserved in sediment on the lakebed (Popovský 1983; McCarthy and Krueger 2013). As a result, few detailed paleolimnological studies have been published using dinocysts since Traverse (1955) recorded the first known fossil freshwater dinoflagellates (*Peridinium hansonianum*) from Oligocene lignite. Most of these are monospecific or very low diversity assemblages from sites exhibiting exceptional preservation, such as varved lacustrine deposits of the Miocene Clarkia lake succession in northern Idaho (Batten et al. 1999), the Upper Oligocene Enspel *Lagerstätte* in the Westerwald area of Germany (Köhler and Clausen 2000), rapidly deposited Holocene sediment from the alpine Lake Nero di Cornisello, Italy (Tardio et al. 2006), and Holocene microlaminated sediments from Lake Xiaolongwan in northeastern China (Chu et al. 2008). Drljepan et al. (2014) reported a relatively high diversity Holocene record from the deep basin of a meromictic lake in Massachusetts, particularly at times of natural and cultural eutrophication during the dry mid-Holocene 'hemlock minimum' when low lake levels are recorded



**Figure 3.** Mechanism of varve formation in Crawford Lake (modified from Dickman 1979). Wind mixing of the mixolimnion, surface waters, during fall turnover introduces oxygen into the chemocline and resulting mass mortality of photosynthetic anaerobic bacteria produces a dark organic-rich lamina; when water temperatures rise in spring, calcite starts to precipitate, forming a white calcium-rich lamina. (A) Upper mixolimnion; (B) thermocline; (C) lower mixolimnion (partially aerated zone); (D) lower mixolimnion (anaerobic zone); (E) monimolimnion. Sediment oxygen demand (SOD) produces bottom water anoxia, inhibiting bioturbation and promoting preservation of rare microfossils such as cellulosic thecae of dinoflagellates.

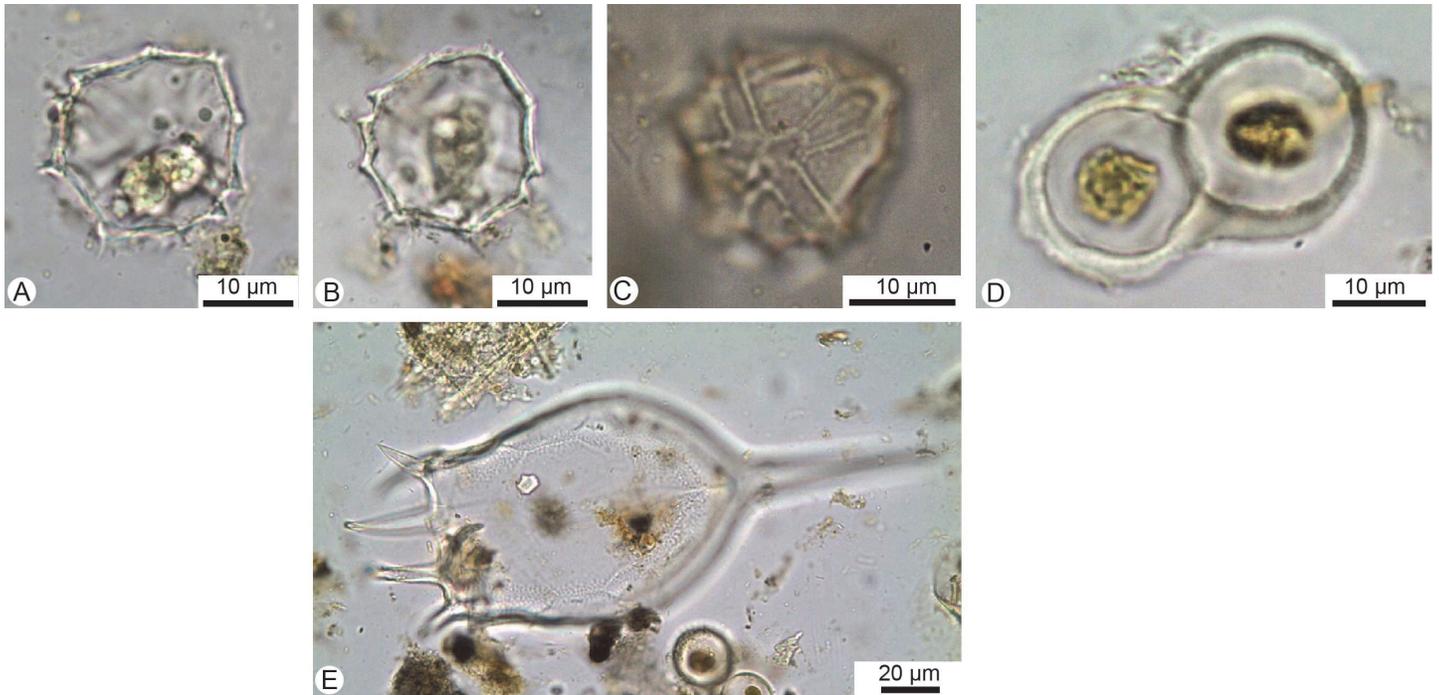
throughout New England, and over the last four centuries in response to anthropogenic impact.

Cellulosic dinoflagellate thecae are typically reported to be non-fossilizable, but rare examples of preservation have been reported from amber collected from a Late Albian/lowermost Cenomanian black paralac deposit in southwestern France (Masure et al. 2013) and from anoxic Recent sediment from another meromictic eastern North American lake (Drljepan 2014; Drljepan et al. 2014). The exceptional preservation of thecae of *Parvodinium inconspicuum* in several samples from Crawford Lake allowed Krueger (2012) to infer the affinity of the abundant tiny (about 16–20 µm in diameter), spherical, unornamented cysts with visible cell contents (illustrated in Fig. 5E with a rotifer lorica) in the same palynological preparations from varved sediments from a freeze core collected in February, 2011. The affinity of these tiny, spherical, unornamented cysts to *Parvodinium inconspicuum* was also confirmed by comparison with illustrations of the characteristic ‘peanut-shaped’ cell during reproduction in Pfister et al. (1984), when five samples dating from about 1920 to 1845–1860 CE (20 cm to 29 cm) germinated during an unplanned hiatus in palynological processing (McCarthy and Krueger 2013). A 72 cm-long freeze core was recovered on January 25, 2011, from the

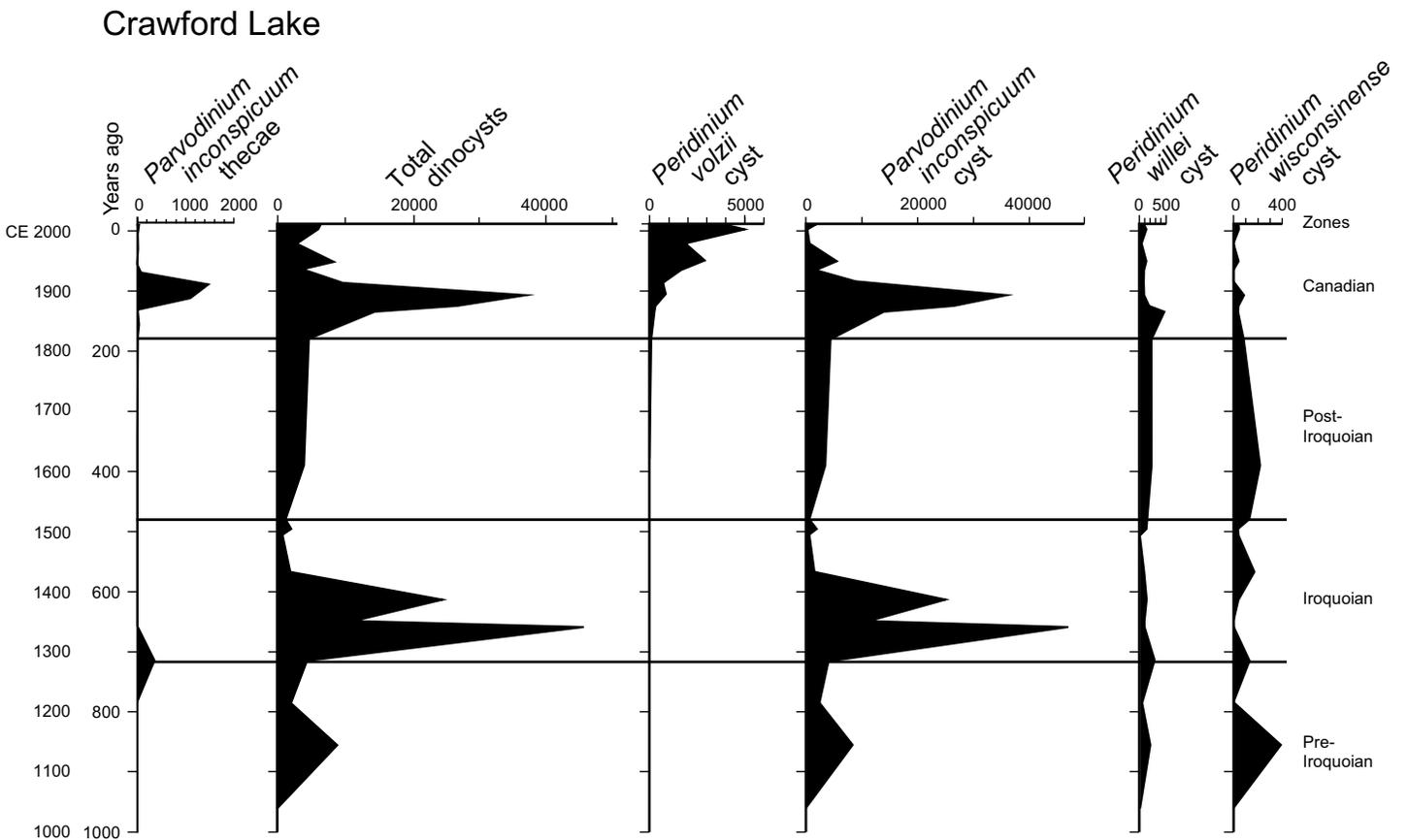


**Figure 4.** Varve counting provides a very precise chronology, allowing the microfossil record to be compared with historic and archaeological data. Both phases of human settlement, by the Iroquois (between 1268–1486 CE) and historic Euro-Canadians (since around 1820 CE), are associated with a change in colour and increase in the thickness and continuity of laminae (from Krueger 2012).

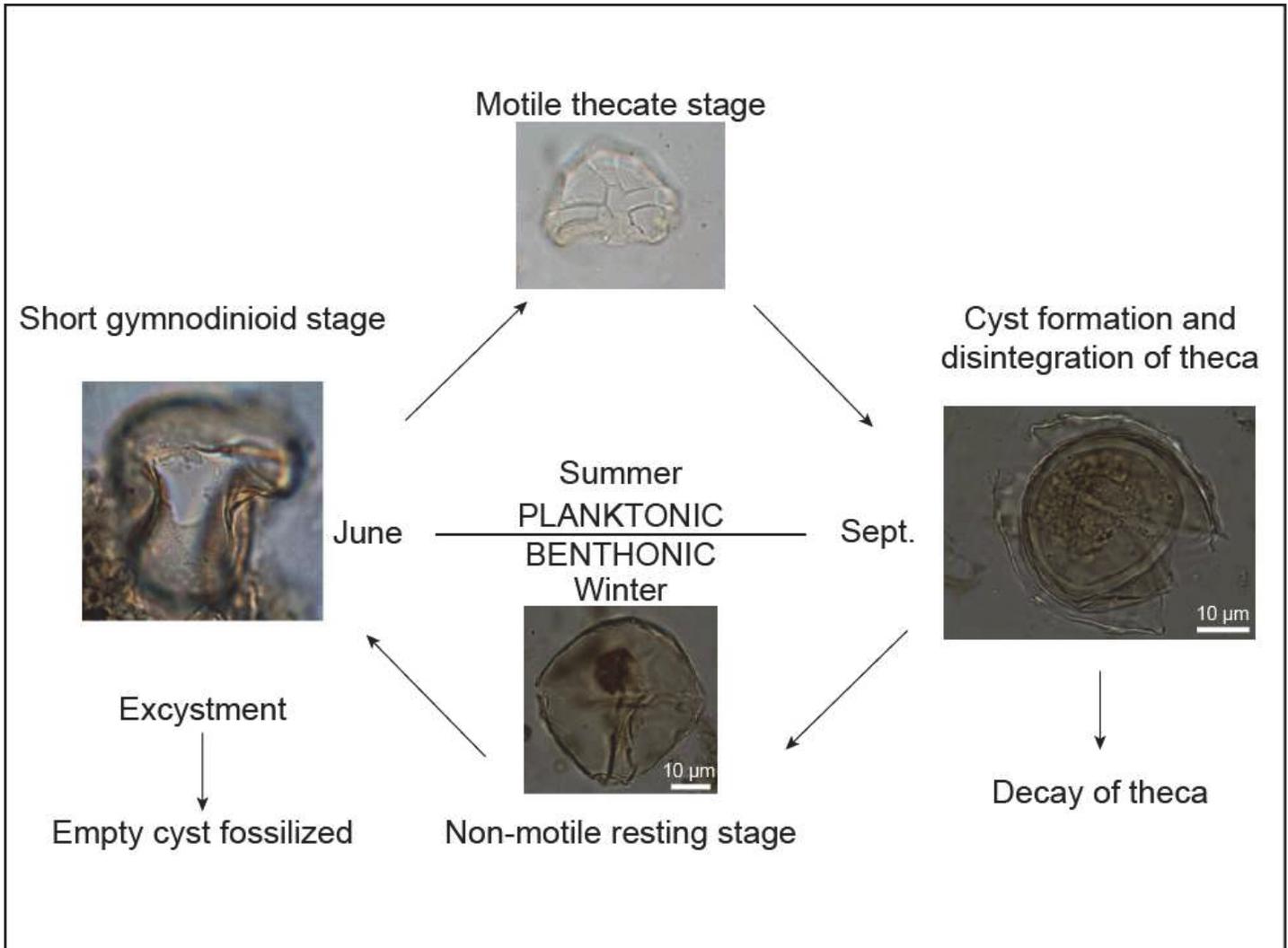
deepest point in Crawford Lake (up to 22.5 m) using a frigid fingernail sampler. The core was brought back to Brock University where it was kept in a freezer wrapped in dry ice awaiting further processing that occurred in late February 2011. Inadvertent culturing occurred when samples were left in test tubes for a week after processing with a weak HCl solution and rinsed with distilled water. The samples were kept at room temperature (about 22°C) under fluorescent lights. This allowed the various stages of the dinoflagellate life cycle to be observed in the resulting slides (Fig. 7), including meiosis and mitosis showing the characteristic lack of breakdown of the nuclear envelope during mitosis (Fig. 5D). Excystment allowed us to suggest that the cysts inferred by Chu et al. (2008) to be cysts of *Parvodinium inconspicuum* are actually cysts of *Parvodinium [Peridinium] umbonatum* (Stein) Carty (McCarthy and Krueger 2013), probably because the thecae in the water column were incorrectly identified. Both the thecae and cysts of *P. umbonatum* were identified in sediment from a meromictic lake in Massachusetts (Drljepan et al. 2014) and the cysts resemble those illustrated by Tardio et al. (2006). The abundance of cysts of *P. inconspicuum* in Crawford Lake at times of anthropogenic impact is consistent with the tolerance of this



**Figure 5.** Small, thick-walled cellulosic thecae of *Parvodinium* [*Peridinium*] *inconspicuum* (Lemmermann) Carty with visible nucleus (A, B) and plate tabulation (C), and a hypnozygote of this taxon undergoing meiosis (D) (from Krueger 2012). A rotifer lorica (genus *Keratella*) with tiny cysts assigned to *Parvodinium inconspicuum* (E); note the large dinokaryotic nuclei.



**Figure 6.** Cysts and rarely fossilized thecae of dinoflagellates (shown as absolute abundances per ml sediment measured by liquid displacement) in varved sediments from a freeze core collected in February 2011. Peak dinocyst abundances near the base of the Iroquoian zone suggest that the peak impact on the lake ecosystem was shortly after the village was settled and peak impact in the Euro-Canadian phase coincides with operation of the lumber mill. The presence of thecae in varves dated to the early 13<sup>th</sup> century and mid-19<sup>th</sup> to early 20<sup>th</sup> century suggests extreme anoxia at these times and a slightly earlier date for occupation of the Iroquoian village than previously published.



**Figure 7.** Two samples germinated during an unplanned hiatus in palynological processing, allowing all stages of the life cycle to be observed, as illustrated by Krueger (2012) for *Peridinium volzii* Lemmermann. Counter-clockwise from bottom: a resting cyst showing viable cell contents, an empty cyst with an archeopyle from which the cell excysted, the epitheca of the motile stage made of cellulosic plates, and an encystment and sloughing of the theca to avoid adverse conditions.

species to eutrophic conditions (Koryak 1978; Moiseenko 2005), particularly when pH is above 6 (Perez et al. 1994), as it is in this dolomitic basin.

The oldest dinoflagellate to excyst was from varves deposited in Crawford Lake around AD 1820; just as the Crawford family began clearing land in the catchment to build their homestead according to McAndrews and Boyko-Diakonow (1989). The cysts of *P. inconspicuum* that germinated are nearly twice as old as the oldest cysts of *Pentapborsodinium dalei* Indelicato et Loeblich that Ribeiro et al. (2011) were able to germinate from sediment cores retrieved from a low-oxygen sill fjord, and much older than previous reports of cyst germination following decades of dormancy (Keafer et al. 1992; McQuoid et al. 2002; Mizushima and Matsuoka 2004). Anoxic conditions in the deep basin of Crawford Lake appear to have promoted the long-term viability of the resting cysts that may have contributed to the survival of these cyst-forming genera during times of ecological catastrophe like the K–T boundary event (Ribeiro et al. 2011).

The inadvertent excystment during processing also allowed small (approximately 30 × 40 µm) slightly ovate non-motile

dinospore resting cysts previously recorded as *Peridinium willei* (“small”) in sediments from Georgian Bay (McCarthy et al. 2011) to be assigned to *Peridinium volzii* Lemmermann (Krueger 2012). The restriction of cysts of *P. volzii* as well as the loricae of *Keratella earlinae* and *Keratella quadrata* to varves deposited since about 1880 CE (Figs. 2, 6) suggests that these organisms were incidentally introduced when the naturally fishless lake was stocked with fish (Turton, C., personal communication 2011; Krueger 2012), around the same time that a lumber mill was erected by the south end of the lake (Crawford Lake Conservation Area 2011).

**CULTURAL EUTROPHICATION, ENHANCED PRODUCTIVITY AND PRESERVATION**

An increase in absolute abundance of aquatic microfossils (biomass) and a transition from oligotrophic to eutrophic species assemblages is evident in the fossil record of phytoplankton (diatoms – Ekdahl et al. 2004, 2007, and dinoflagellates – Krueger 2012; McCarthy and Krueger 2013) as well as herbivores like rotifers (Turton and McAndrews 2006) that thrived in response to the increase in food supply during the

two separate human settlement phases (Fig. 2). The exceptional preservation of cellulosic thecae and the unparalleled longevity of cell contents is attributed to especially pronounced bottom water anoxia resulting from cultural eutrophication-induced sediment oxygen demand (SOD) (Hargrave 1972; Walker and Snodgrass 1986), evident in the suppression of benthic diatoms (Fig. 2) (Ekdahl 2004, 2007) and benthic ostracodes that was only episodically interrupted (Chan, C.C.H., unpublished data). Peak anoxia appears to coincide with 1) initial settlement and land clearing beginning in 1822 CE and lumbering on the shores of Crawford Lake during the 1880s (Krueger 2012) recorded by thick accumulations of woody debris near the base of the *Ambrosia* rise near the north shore of the lake (McCarthy et al. 2011), and 2) during the earliest phase of Iroquoian settlement, when the village was established and trees were cut to clear land for the village and corn fields and to provide building material for the longhouses. McAndrews and Turton (2007, 2010) suggested that increased nutrient input from the dung of Canada geese (*Branta canadensis*) that grazed on the cultivated fields and then roosted at Crawford Lake was the main cause of eutrophication during Iroquoian settlement. The peak concentrations of cellulosic thecae (around 1500 thecae per ml) in varves deposited coincident with the establishment of the lumber mill suggests that Euro-Canadian land clearing was the most intense contributor to BOD/ SOD.

It is clear from the increase in algal (diatom and dinoflagellate) and herbivore (rotifer) biomass and from the changes in assemblages to favour eutrophic plankton and nekton (Figs. 2, 6) that the Iroquoian village had a strong and irreversible impact on the lacustrine ecosystem. Although there was resurgence in oligotrophic algae (e.g. *Cyclotella bodanica* var. *lemanica* and *Peridinium wisconsinense*) during the post-Iroquoian interval, the lake did not return to pre-disturbance conditions.

## CONCLUSIONS

Preservation of rarely fossilized microscopic organisms in varved sediments from Crawford Lake, notably cellulosic thecae and cysts of dinoflagellates with viable cell contents deposited nearly 200 years ago, allowed reconciliation of the thanatocoenosis with the biocoenosis in this unusual group of organisms. Exceptional preservation of organisms rarely present in lacustrine sediment allows unparalleled insights into the response to perturbation of various trophic levels in a mid-latitude lacustrine ecosystem. The correspondence between the palynological record in the varves from Crawford Lake and the components of the ecosystem is closer than typically found in lacustrine sediment, allowing insights from the phycological and zoological literature into dinoflagellate cyst–theca relationships. Varve counting provides a precise chronology allowing correlation with archaeological and historic records, and the increase in nutrients that accompanied Iroquoian and later Euro-Canadian settlement of the uplands north of the small, deep lake promoted the bottom water anoxia that allowed exceptional preservation of dinoflagellate thecae and rotifer loricae. The existence of an interpretive centre managed by Conservation Halton in this Area of Natural and Scientific Interest (ANSI) on the edge of the Niagara Escarpment World Biosphere Reserve provides an opportunity to promote *Konservat-Lagerstätten* to the general public in a highly populat-

ed region. In addition, the insights into the various trophic levels in this temperate lake as extant primary producers and consumers twice responded to cultural eutrophication can assist in linking the fields of limnology and paleolimnology allowing for improved management of important fresh water resources.

## ACKNOWLEDGEMENTS

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