OLD-GROWTH FOREST SURVEY OF LONGBOOT LAKE, ALGONQUIN PARK

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SUMMARY

A tract of hemlock forest north of Longboot Lake, within the forest management zone of Algonquin Park, was identified as potential old-growth forest in 2021 by recreational users of the park. It is part of a 270 hectare area of maple and hemlock dominated forest that has no record of logging. We inventoried several stands as part of the Algonquin Park Old-growth Forest Project, and our results show that the hemlock forest north of Longboot Lake has ages, tree basal area, and coarse woody debris volume that are all indicative of high quality old-growth forest.

The mean age from tree cores sampled on a grid is 211 years, and the maximum age is 338 years. These ages are higher than most old-growth forests in eastern North America, but comparable to old-growth hemlock forests in Adirondack State Park and Algonquin Park.

The average live tree basal area from all plots was 30 m²/ha, which is consistent with old-growth forest in eastern North America. The average volume of logs from all transects was 137 m³/ha. This volume is very high for eastern North American forests, but consistent with the high stand age at Longboot Lake since studies have shown a strong positive correlation between volume of coarse woody debris and forest age.

Hemlock accounts for 62.7% of the basal area in our plots, and also makes up 50-60% of the Forest Resource Inventory stands where the plots are located. Although Algonquin Park makes up only 1.8% of the productive forest area of the Ontario, it contains 60% of the hemlock working group over the age of 140 in the province. Land use change and logging have led to a nearly 75% decline in hemlock abundance on the landscape adjacent to and west of the Park and have virtually eliminated hemlock in many parts of southern Ontario where it was once common.

Highly decayed conifer stumps were found in many parts of the forest. These are likely remnants from logging of white pine or hemlock that occurred 70-100 years ago. They were tallied at an estimated density of 19 stumps/ha. Given our other results this relatively light historic human disturbance in the old hemlock stands should not disqualify them as old-growth forest; however it does raise questions about old-growth forest definitions and how to apply them in Algonquin Park.

Ages obtained in the field confirm that older 1987 Forest Resource Inventory (FRI) data more accurately describes oldgrowth forest in Algonquin Park than updated FRI data, which significantly underestimates ages in many stands. This is important for ongoing old-growth surveys in the park.

Logging of old-growth forest in Algonquin Park clearly undermines the ecological integrity of the park. A strategy for properly identifying and protecting remaining old-growth forest and roadless areas in the park should be included in the next review of the Algonquin Park Management Plan.

INTRODUCTION

Significant tracts of old-growth forest remain unprotected in Algonquin Park, including large tracts of pristine oldgrowth forest with trees 300 to 400 years old that are available for logging (M. Henry & Quinby, 2006; M Henry et al., 2018; M Henry & Quinby, 2007, 2018). Given the rarity of such forests, this should be troubling for both forest managers and conservationists, however the province has made no effort to identify the remaining old-growth forests for either interim or permanent protection.

Repeated calls for a complete and detailed assessment of old-growth forests throughout the entirety of Algonquin Park (M. Henry & Quinby, 2006; M Henry et al., 2018; M Henry & Quinby, 2018) have gone unheeded. The Algonquin old-growth forest project was launched in 2022 to identify remaining old-growth forests in the recreation/utilization zone for protection from logging. Areas that are far from access roads and rail lines and/or are isolated by steep terrain or water bodies are less likely to have historical logging of hemlock and hardwood trees, since they could not be floated to mills. In some cases hemlock forests remain relatively intact even in managed landscapes due to the relatively low commercial value of the species. These are priority areas for old-growth surveys.

A large (270 ha) pocket of forest north and west of Longboot Lake shows up on maps as free of modern logging and containing significant old-growth forest according to forest resource inventory and harvest maps (Figure 1). However the area is surrounded by a dense network of forest access roads, diminishing the likelihood that it is entirely pristine. Our surveys would likely have skipped over Longboot Lake if not for information from local recreational users of the park who felt the area contained old-growth hemlock forest. The primary focus of this survey was two hemlock dominated stands totalling 51 hectares on FRI maps, while extensive (somewhat younger) old-growth sugar maple dominated forest to the west was not surveyed.

FIGURE 1 LOCATION OF LONGBOOT LAKE AND KNOWN LOGGING IN THE ALGONQUIN PARK PANHANDLE



METHODS

We use rapid survey techniques to collect useful data as quickly and cheaply as possible. Sampling is conducted along pre-planned transects and in plots, which are located on a grid pattern oriented to fit within old-growth forest stands (in this case FRI stands with high stand ages). Hemlock forest is also prioritized in transect placement as it is a species of particular concern. Variable radius plots (prism sweeps) are located at the end points of each 150 m transect, where

tree and snag basal area is recorded by species and diameter class. One or more trees are selected for coring at each point based on age characteristics.

All movement within old-growth stands is treated as an informal transect: presence of stumps is noted, and additional data collection including tree coring may take place along these routes.

A more detailed description of the methods and data sheets can be found in the first report in this series (Henry, 2023a).

TRANSECTS: GENERAL HABITAT DESCRIPTION AND STUMP SURVEY FOR HISTORICAL LOGGING

Transects are divided into 150 m sections and along each section the following data are recorded:

- stumps within line of sight of the transect are counted and grouped by decay class categories (1-3 and 4-5), decay class is used to provide an estimated time since logging. photos may be taken.
- Trees with old-age characteristics along transects may be selected for aging by tree core. Cores are collected in paper or plastic straws and counted after field work is completed.
- Qualitative observations of old-growth characteristics are recorded.
- Qualitative observations of stand age class distribution and regeneration are recorded.
- invasive species, disease resistant trees, and other conservation features are noted, locations may be saved and reported to iNaturalist projects (https://www.inaturalist.org/projects/invasivespecies-in-ontario, https://www.inaturalist.org/projects/beech-bark-disease-resistance, etc.)

TREES, SNAGS, AND LOGS

Trees and snags over 10 cm were measured at the end points of each 150 m transect, using a BAF2 wedge prism and DBH of trees that were "in." Logs were measured using line intersect along 30m transects beginning at each plot center, and following the transect bearing. Log diameter was recorded at the intersect point (Van Wagner, 1982) and also at large end to allow the logs to be analyzed more accurately by size classes (Bate et al., 2009). The formula to calculate volume (from Van Wagner 1982), is:

$V = (k/L) * Sum(D^2)$

Where V is volume in m3/ha, k is a constant (1.234), L is the transect length (m), D is diameter at intersect point (cm).

When the transect crosses over highly decayed stumps they typically have very large diameter but are low to the ground. Including these significantly skewed the data, so they were omitted from the total volume calculation.

RESULTS AND DISCUSSION

TREE AGES

Twelve trees were cored at Longboot Lake; 10 were within the prism sweeps on the predetermined grid, two others were visible from transects or scouting routes and were selected based on age characteristics (Table 1; Figure 2). Plot 4 is located within an intensively logged area just outside the boundary of the old growth, if it is excluded the mean stand age is 220 years. This is an underestimate since three of the cores were incomplete due to heart rot and one had a small section of lost core. A more conservative stand age, using only the cores obtained from plots on the grid (but excluding plot 4) is 211 years.

While some studies use the average of tree cores to define stand age (e.g. Hale et al., 1999; Keeton et al., 2007), stand age in old growth forests is also commonly defined by the oldest trees, which represent the minimum period since a stand replacing disturbance (e.g. Tyrrell & Crow, 1994; Ziegler, 2000, 2011). Using this approach the stand age would be 338 years - the forest is likely even older since it's improbable that 12 tree cores, mostly collected at predetermined points, captured the oldest trees in the forest.

Plot	Tree species	DBH (cm)	Ring count	Adjustment	Age	Notes
1	hemlock	79	255	24	279	
2	hemlock	55.5	138	24	162	heart rot, incomplete core
	hemlock	87	224	24	248	heart rot, incomplete core
3	white spruce	63	130	15	145	
3	hemlock	54	292	24	316	lost ~ 1.5 cm of core in field
4	red maple	45	82	15	97	in heavily logged area
5	white pine	70	99	15	114	
6	hemlock	68	222	24	246	
7	hemlock	82	153	24	177	
8	hemlock	62	127	24	151	
9	hemlock	70	157	24	181	
10	hemlock	75.5	314	24	338	
	hemlock	76.6	264	24	288	heart rot, incomplete core

TABLE 1 AGES OF TREES FROM CORES COLLECTED AT LONGBOOT LAKE

Both the mean and max ages obtained at Longboot Lake are exceptional compared to most old-growth forest types in eastern North America, but are comparable to other old-growth hemlock forests (Table 2). A literature review by Thom et al. (2019) found that "less than 0.2% of the investigated sites are currently occupied by forests older than 200 years [...] This suggests a large potential to improve joint ESB [ecosystem services and biodiversity] outcomes in temperate and boreal forests of eastern North America by enhancing the representation of late-successional and older forest stand structures."

Source	Maximum age	Mean age	Location
This Study	338	211	Longboot Lake, south Algonquin Park, ON
Henry et al. 2018	408	294	Cayuga Lake, NW Algonquin Park, ON (preliminary results)
Henry & Quinby 2006	433	287	6 old-growth sites in Algonquin Park, ON
Henry & Quinby 2018	295	232	Hurdman Creek, N Algonquin Park, ON (preliminary results)
Keeton et al. 2007		205-410	10 old-growth forests in western Adirondack Park, NY
Hale et al. 1999		124-172	11 maple-basswood forests > 120 years old in Minnesota
Hale et al. 1999		128-164	7 oak forests >120 years old in Minnesota
Vasiliauskas 1995	454	154	1,576 hemlock tree cores in Algonquin Park, ON
Ziegler 2011	253-390		12 OG hemlock forests in Adirondack Park, NY

TABLE 2 TREE AGES FROM OLD-GROWTH FORESTS IN EASTERN CANADA AND ADJACENT USA

FIGURE 2 LOCATION AND AGES OF INCREMENT BORES



ACCURACY OF FOREST RESOURCE INVENTORY (FRI) AGES

There are large discrepancies between the most recent FRI stand ages (2008 imagery) and those from the 1987 data, particularly among the oldest age classes; it appears that old-growth ages have consistently decreased across the park in the new inventory data. Ideally newer data should have greater accuracy, but in this case the 1987 stand ages (updated to 2022) are remarkably similar to the mean age from all tree cores at Longboot Lake. The 1987 adjusted stand ages where our plots were located are 226 years (plots 1-6, 10), and 221 years (plots 7-9). The 2021 FRI data shows a stand age of 143 years, significantly below our mean stand age of 211, and far below the maximum age of 338.

The divergence was even greater in preliminary surveys of Hurdman Creek and Cayuga Lake old-growth forests (Henry et al., 2018; Henry & Quinby, 2018) - the 2021 FRI ages for the sampled stands in these areas is less than half the mean age from 18 tree cores of various species in several different forest stands (see table 3). In the preliminary surveys tree coring wasn't on a pre-set grid (as in Longboot) which may result in somewhat higher mean ages. Nevertheless the older FRI data is clearly more dependable for locating and describing old-growth forest in Algonquin Park, and likely in other parts of Ontario.

Source	Max age	Mean age	FRI 1987 +35 yrs (% from mean)	FRI 2021 (% from mean)
This Study	338	211	224 (+6%)	143 (-32%)
Henry et al. 2018	408	294	224 (-24%)	112 <mark>(-62%)</mark>
Henry & Quinby 2018	295	232	210 (-9%)	110 <mark>(-53%)</mark>

TABLE 3 COMPARISON OF AGES OBTAINED FROM INCREMENT BORE TO FOREST RESOURCE INVENTORY STAND AGE

TREE BASAL AREA AND SIZE CLASS DISTRIBUTION

The average tree basal area from all plots was 30 m²/ha. This compares favourably with other studies and literature reviews (see table 4). Keddy and Drummond reviewed 10 studies in old growth forests from 1958-1991, and proposed basal area over 29 m²/ha as being the normal condition of primary old growth forest (although they recognize that site conditions can have a large influence on basal area). At 30 m²/ha the Longboot Lake survey area fits this criterion for old growth forest.

Source	Tree BA (m²/ha)	Snag BA (m ² /ha)	Location
This Study	30	3.2	Longboot Lake, southern Algonquin Park, Ontario
Spetich et al. 1999	28	3	12 old-growth sites in IN, IL, MO, and IA
Larson et al. 1999	36		35 heritage (OG) woodlands in southern Ontario
Hale et al., 1999	31		11 OG maple-basswood forests >120 years in MN
Hale et al., 1999	32		10 oak forests >120 years old in MN
Keddy & Drummond 1996	29		Average from 10 studies in eastern North America
Keeton et al., 2007	33	8	10 old-growth forests in Adirondack Park, NY

TABLE 4 BASAL AREA OF OLD-GROWTH FORESTS IN EASTERN NORTH AMERICA

FIGURE 3 SIZE CLASS DISTRIBUTION



TABLE 5 BASAL AREA OF PRIMARY FOREST STANDS, FROM KEDDY AND DRUMMOND 1996

Basal area (m²/ha)*	Study site†	Forest type	Source
Old-growth stands			
28	Michigan	Fagus-Acer	Schmelz and Lindsey (1965)
32	Pennsylvania	Tsuga–Fagus	Hough (1936)
40	Ohio	Acer-Fagus	Boerner and Cho (1987)
29	Indiana	Fagus-Acer-Quercus	Lindsey et al. (1958)
28	Indiana	Acer-Fagus	Abrell and Jackson (1977)
26	Indiana	Fagus-Acer	Schmelz and Lindsey (1965)
26	Indiana	Acer	Schmelz and Lindsey (1965)
23	Indiana	Fagus–Acer	Schmelz and Lindsey (1965)
32	Ohio	Acer–Quercus	McCarthy et al. (1987)
30	Kentucky	Deciduous	Bougher and Winstead (1974)
$(\bar{X} = 29, \text{ sd} = 4)$			
Altered sites			
24	New Hampshire	Fagus-Acer-Betula	Whittaker et al. (1974) Logged 57 yr before study
21	Tennessee	Acer saccharum	Onega and Eickmeier (1991) Nonclimax site
19	Indiana	Upland deciduous	Schmelz and Lindsey (1965) Recently altered forest
$(\bar{X} = 21, \text{ sd} = 3)$			2

* Altered sites' basal areas based on a minimum stem diameter of 10.2 cm, except Boerner and Cho (1987) and McCarthy et al. (1987) used 2.5 cm and Hough (1936) used 9.1 cm. Values have been rounded up to the even number. † Study sites are listed in the order of ascending latitude.

TREE SPECIES COMPOSITION

Hemlock accounts for 62.7% of the basal area in our plots, and also makes up 50-60% of the Forest Resource Inventory stands where the plots are located. Eastern white cedar and red maple account for another 18%, and a variety of species make up the remainder (see figure 4). The eastern hemlock forests may have been left unlogged to date because of the low commercial value of the wood.

Old-growth eastern hemlock forests have high ecological value, and Algonquin Park bears a disproportionate responsibility for



FIGURE 4 TREE SPECIES COMPOSITION (% OF BASAL AREA) IN PLOTS

their conservation in Ontario and globally. Although Algonquin Park makes up only 1.8% of the productive forest area of Ontario, it contains 60% of the hemlock working group over the age of 140 in the province (Henry & Quinby 2006).

COARSE WOODY DEBRIS

The average volume of logs from all transects was 137 m³/ha. This volume is high for eastern North American forests (Table 6), but not unexpected given the high stand age derived from tree cores. Many studies have shown a strong positive correlation between volume of coarse woody debris and age of the forest (Spetich et al., 1999; Tyrrell & Crow, 1994; Susy Svatek Ziegler, 2000). Spetich et al (1999) found an average volume of 60.4 m³/ha across 12 old growth sites in middle America but found wood volume increased with age after around 70 years. Their oldest site was 200-250 years old with a volume of 111 m³/ha. Ziegler found the average volume of logs in old-growth hemlock plots in the Adirondacks was 126 m³/ha, whereas the average volume of logs in younger stands was 63 m3/ha. In 25 old-growth hemlock-hardwood forests in WI and MN, Tyrrell and Crow found that forests over 200 years old had upwards of 150-200 m³/ha of coarse woody debris. Plots of CWD volume vs age do a good job at predicting the volume found at Longboot Lake (Fig 5-7).

While any transformation from volume to weight using the limited dataset is bound to be an approximation, it is useful to be able to compare our data to CWD weights in the published literature. We use the green weight of hemlock for this conversion because it is a common component of the logs and it also has an intermediate specific gravity. (0.956 Mg/m³). Adams & Owens (2001) found that across 21 hardwood species, mean specific gravity decreased by nearly 50 percent from decay class 1 to 3 (the average decay class in our data was 3.75), so we use a conversion of 0.478 to transform volume to weight. This gives a very rough approximate weight of 65.5 Mg/ha in this forest, well over the 27 Mg/ha suggested as a minimum for old-growth forests by Keddy & Drummond (1996). One Megagram (Mg) is equivalent to a metric tonne, so there are some 65 tonnes of logs per hectare at the Longboot Lake site.

mean log diameter was 32.7 cm when using large end diameters (as per Bate et al. 2009), which is slightly higher than (Larson et al., 1999) who found a mean log diameter of 31.7 cm.

Source	Volume (m ³ /ha)	Mean Diameter (cm)	Location
This study	137	32.7	Southern Algonquin Park
Spetich et al. 1999	60.4		12 old-growth sites in IN, IL, MO, and IA
Larson et al. 1999		31.7	35 heritage (OG) woodlands in southern Ontario
Hale et al., 1999	55 (12-121)		11 OG maple-basswood forests >120 years in MN
Hale et al., 1999	48 (21-68)		10 oak forests >120 years old in MN
Ziegler, 2000	126		12 OG hemlock forests in Adirondack Park, NY
Keeton et al. 2007	163.6		10 old-growth forests in Adirondack Park, NY

TABLE 6 COARSE WOODY DEBRIS VOLUME AND DIAMETER IN OLD-GROWTH FORESTS OF EASTERN NORTH AMERICA





FIGURE 7 LOG VOLUME VS AGE IN 25 OLD GROWTH STANDS, FROM TYRRELL AND CROW 1994

STUMP SURVEYS AND HISTORICAL LOGGING

Stumps were noted as we travelled through the stands, and a formal stump count was conducted along the transects. Total transect length was 1200 m in this forest. Any stumps that were visible were tallied, and assuming that visibility was approximately 10 m to either side (depending on vegetation) the total surveyed area equates to roughly 2.4 ha.

46 stumps were counted, which was skewed upwards somewhat by higher stump counts near the boundaries, particularly near plot 4. This equates to an estimate of roughly 19 stumps/ha.

All the stumps were mid size or large conifers of decay class 4 or 5 (highly decayed). It seems that either some hemlock or more likely white pine was cut from the forest, probably 70 to 80 years ago or more. Stumps were seen in most parts of the forest. Logging several decades old was seen to the south and east of the forest, roughly matching forest depletion maps obtained from the Algonquin Forestry Authority.

It's worth noting that while some stumps occur in the old-growth forest, the more heavily managed forest surrounding the old-growth hemlock is markedly younger and could have undergone several harvests in the time since some cutting occurred in the old-growth forest (given that selection harvests occur at 25 year intervals in the Park).

The relatively light historic human disturbance in the old-growth hemlock stands, occurring some 80+ years ago, should not disqualify them as old-growth forest. However it does raise questions about old-growth forest definitions and how to apply them in Algonquin Park.



CONCLUDING THOUGHTS

Logging of old-growth forest and roadless areas in Algonquin Park clearly undermines the ecological integrity of the park. A strategy for protecting remaining old-growth forest and roadless areas in the park should be included in the next review of the Algonquin Park Management Plan. Adding the remaining unprotected roadless areas and intact old-growth forest to the protected zones of Algonquin Park would likely increase the protected area of the park by only five to six percent, from 35% to around 40%.

A review of the Algonquin Park Management Plan was scheduled for 2018 (ECO, 2014) but has not occurred. When this review occurs a strategy for properly identifying and protecting remaining old-growth forest and roadless areas in the park should be included. Protection of high-quality old growth and roadless areas such as are found at Longboot Lake should not be at the discretion of forest managers; this and other high value areas should be identified and incorporated into the protected zones of Algonquin Park.

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REFERENCES

Adams, M. B., & Owens, D. R. (2001). Specific Gravity of Coarse Woody Debris For Some Central Appalachian Hardwood

Forest Species The Authors. http://www.fs.fed.us/ne

- Bate, L. J., Torgersen, T. R., Wisdom, M. J., & Garton, E. O. (2009). Biased estimation of forest log characteristics using intersect diameters. *Forest Ecology and Management*, *258*(5), 635–640. https://doi.org/10.1016/j.foreco.2009.04.042
- Environmental Commissioner of Ontario. (2014). MANAGING NEW CHALLENGES: ANNUAL REPORT 2013/2014. http://docs.assets.eco.on.ca/reports/environmental-protection/2013-2014/2013-14-AR.pdf
- Hale, C. M., Pastor, J., & Rusterholz, K. A. (1999). Comparison of structural and compositional characteristics in oldgrowth and mature, managed hardwood forests of Minnesota, USA. *Canadian Journal of Forest Research*, 29(10), 1479–1489. https://doi.org/10.1139/x99-076
- Henry, M., & Quinby, P. (2006). A Preliminary Survey of Old-Growth Forest Landscapes on the West Side of Algonquin Provincial Park, Ontario. *Ancient Forest Exploration & Research*, *32*, 1–28. http://www.ancientforest.org/wpcontent/uploads/rr32.pdf
- Henry, M, & Quinby, P. (2007). *Mapping Threatened Old-Growth Forests of Algonquin Park: The First Step. 27.* http://www.ancientforest.org/wp-content/uploads/flb27.pdf
- Henry, M, & Quinby, P. A. (2018). The Hurdman Creek Old-Growth Forest. *Preliminary Results Bulletin*, 2. www.ancientforest.org
- Henry, M, Torenvliet, N., & Quinby, P. A. (2018). The Cayuga Lake Old-Growth Forest Landscape: An Unprotected Endangered Ecosystem in Algonquin Provincial Park, Ontario. *Preliminary Results Bulletin*, 6. www.ancientforest.org
- Henry, M. (2023). Old-growth forest survey methods. Algonquin Old-Growth Forest Project, 1.
- Keddy, P. A., & Drummond, C. G. (1996). Ecological properties for the evaluation, management, and restoration of temperate deciduous forest ecosystems. *Ecological Applications*, 6(3), 748–762. https://doi.org/10.2307/2269480
- Keeton, W. S., Kraft, C. E., & Warren, D. R. (2007). Mature and old-growth riparian forests: Structure, dynamics, and effects on adirondack stream habitats. *Ecological Applications*, *17*(3), 852–868. https://doi.org/10.1890/06-1172
- Larson, B. M., Riley, J. L., Snell, E. A., & Godschalk, H. G. (1999). *The Woodland Heritage of Southern Ontario: A Study of Ecological Change, Distribution and Significance.* Federation of Ontario Naturalists. https://books.google.ca/books?id=YA4JAQAAMAAJ
- Spetich, M. A., Shifley, S. R., & Parker, G. R. (1999). Regional Distribution and Dynamics of Coarse Woody Debris in Midwestern Old-Growth Forests. *Forest Science*, *45*(2).
- Thom, D., Golivets, M., Edling, L., Meigs, G. W., Gourevitch, J. D., Sonter, L. J., Galford, G. L., & Keeton, W. S. (2019). The climate sensitivity of carbon, timber, and species richness covaries with forest age in boreal-temperate North America. *Global Change Biology*, *25*(7), 2446–2458. https://doi.org/10.1111/gcb.14656
- Tyrrell, L. E., & Crow, T. R. (1994). Structural Characteristics of Old-Growth Hemlock-Hardwood Forests in Relation to Age. *Ecology*, 75(2), 370–386. https://doi.org/10.2307/1939541
- Van Wagner, C. E. (1982). Practical aspects of the line intersect method. In Information Report PI-X-12.
- Vasiliauskas, S. A. (1995). Interpretation of age-structure gaps in hemlock (Tsuga canadensis) populations of Algonquin Park [Queen's University]. http://www.algonquin-eco-watch.com/reference-material/Vasiliauskas Study.pdf
- Ziegler, Susy S. (2011). Global Ecology and Biogeography. *Global Ecology and Biogeography*, 20(6), 931–932. https://doi.org/10.1111/j.1466-8238.2011.00723.x
- Ziegler, Susy Svatek. (2000). A comparison of structural characteristics between old-growth and postfire secondgrowth hemlock-hardwood forests in Adirondack Park, New York, U.S.A. *Global Ecology and Biogeography*, *9*(5), 373–389. https://doi.org/10.1046/j.1365-2699.2000.00191.x