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# Ecology, morphology and distribution of *Anisota finlaysoni* Riotte (Lepidoptera, Saturniidae)

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## Abstract

Identifying the conservation needs of the short-horned oakworm, *Anisota finlaysoni* Riotte, has been hampered by incomplete resolution of species boundaries and geographic ranges of the *Anisota senatoria* species-group. Here, the life history, morphology, occurrence, and DNA barcode variation of *A. finlaysoni* and *A. senatoria* are compared across a transect of three key geographic regions in Ontario, Canada. Contrary to recent range depictions, our results show that *A. finlaysoni* is currently confirmed to occur only in the region of eastern Lake Ontario's north shore. Previous information on morphological characters used to distinguish *A. finlaysoni* is incomplete or erroneous. Lake Erie populations most recently assigned to *A. finlaysoni* exhibit some *finlaysoni*-like larval traits, but adult phenotype of all examined material is indistinguishable from *A. senatoria* of the Lake Huron region, and unlike topotypical *A. finlaysoni*. Although the cryptic occurrence of *A. finlaysoni* in the Lake Erie region cannot be ruled out, current data indicate that this species has a much smaller global range than previously believed, and is separated by a geographic gap of about 200 km from the nearest *A. senatoria* populations. Re-assignment of the Lake Erie populations from *A. finlaysoni* to *A. senatoria*, and the recognition of some peripheral occurrence records as historical errors, results in a significantly smaller global range for *A. finlaysoni*. DNA barcode data for the genus *Anisota* are at odds with current taxonomy, limiting the utility of barcodes in discriminating species of the *senatoria*-group. Because *A. finlaysoni* is distinct morphologically as adults and larvae from geographically nearby populations of *A. senatoria*, it should continue to be treated as a distinct species pending convincing evidence to the contrary.

**Key words:** Alvar, *Anisota senatoria,* Great Lakes, Napanee Limestone Plain, Short-horned oakworm

## Introduction

Historically considered to be a minor pest of oak, the short-horned oakworm (*Anisota finlaysoni* Riotte) is now a species of conservation concern with a very small global range that is limited to southern Ontario, Canada (COSEWIC 2023). It is the only species of wild silk moth (and indeed of superfamily Bombycoidea) endemic to Canada, and is currently ranked as "Special Concern" (COSEWIC 2023). However, uncertainty in the geographic range and taxonomic status of *A. finlaysoni* have hindered accurate conservation assessments. The diagnostic adult and larva traits used to distinguish *A. finlaysoni* from the closely-related *A. senatoria* (J. E. Smith) vary depending on taxonomic authority, but the conspicuous difference in the ornamentation of mature larvae is unequivocally considered to be the hallmark of *A. finlaysoni* (Riotte 1969; Ferguson 1971; Riotte & Peigler 1981). Yet, larva specimens from critical geographic areas were not studied previously. At issue is a key region between the western range terminus of *A. finlaysoni* and the northeastern edge of *A. senatoria*, comprising the region between the southeastern shore of Lake Huron to the Lake Erie region of southern Ontario, Canada (Fig. 1). Numerous *senatoria*-group specimens from southern Ontario were available to Riotte (1969) when he first described *A. finlaysoni*, but diagnostic comparison was complicated by the fact that identity of the voucher material from southern Ontario populations was largely based on adult specimens without assessment of larval morphology.

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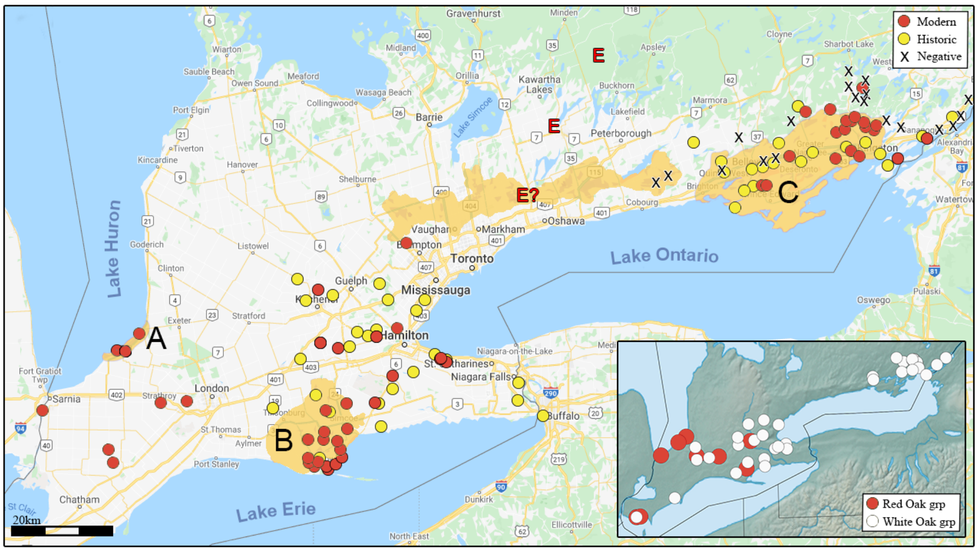


**FIGURE 1.** Map of geographic regions, place names, and *Anisota* occurrences in southern Ontario, Canada. Study regions include Huron, Lambton Co. (A); Erie, Norfolk Co. (B); Napanee, Frontenac Co. and Hastings Co. (C). Shaded orange areas (from west to east) correspond to the Lake Huron Dunes, Norfolk Sand Plain, Oak Ridges Moraine, and Napanee Limestone Plain (modified from Chapman and Putnam 1984). Modern *Anisota* occurrences (2000 or later) indicated by red circles, historic occurrences (pre-2000) by yellow circles. "E" indicates erroneous historic literature records discussed in the text, from north to south: Otter Lake, Lindsay/Victoria Co., and Durham—Ontario Co's. "X" indicates sites that yielded negative results in the 2024 pheromone survey. **Inset:** Overview of larval host plants recorded by the Forest Insect and Disease Survey, and during this study. Records are grouped by oak subgenus, where "Red Oak Grp" comprises black oak (subgenus *Erythrobalanus*) records, and "White Oak Grp" comprises white oak and bur oak (subgenus *Leucobalanus*) records.

A suite of adult phenotypic differences separate the two. Compared to *A. senatoria*, *A. finlaysoni* is slightly larger, with the ground color of both fore- and hindwing a duller, yellowish brown (versus maroon brown), the thoracic and abdominal vestiture also duskier yellowish brown (versus yellowish), and both sexes with less dark-scaled forewing speckling that is often absent altogether (Riotte, 1969; Ferguson, 1971; Riotte & Peigler 1981; Tuskes *et al.* 1996; Lemaire, 1988). Considering internal morphology, Riotte (1969) relied on two male genitalic characters for diagnostic comparison of *A. finlaysoni* to *A. senatoria*: the shape of the gnathos (rounded with a tapered, attenuated apex in *finlaysoni* vs. triangular and shield-like in *senatoria*), and the two vesica cornuti (large and with a serrate ventral edge in *finlaysoni* vs. smaller with a few thorn-like ventral serrations in *senatoria*). Subsequently Ferguson (1971) indicated that the gnathos shape was highly variable and that some *A. finlaysoni* were identical to *senatoria* in this respect, but concluded that the vesica cornuti were on average larger in *finlaysoni*, even though the extremes of variation overlapped.

The global range limits of *A. finlaysoni* have been in dispute since its description as a new species in 1969. In the years following its discovery, Riotte (1969) and Ferguson (1971) considered *A. finlaysoni* to occur only in the Kingston to Belleville region of Lake Ontario's north shore (region C, Fig. 1), and also at five distant sites in Wisconsin and Minnesota; both authors considered that the populations in the intervening region of Lake Erie were *A. senatoria*, not *A. finlaysoni*. Subsequently, Riotte & Peigler (1981) revised the genus *Anisota* Hübner and re-identified some Lake Erie *A. senatoria* specimens as *A. finlaysoni*, but portrayed the two species as parapatric, with a dividing line just west of the Niagara Peninsula. Lemaire (1988) presented a third hypothesis, classifying all Ontario populations as *A. finlaysoni*. The most recent taxonomic treatise of *Anisota* reverted to classifying all Lake Erie populations as *A. senatoria*, whereas *A. finlaysoni* was considered to be disjunct and endemic to the Lake Ontario northeast shore (Tuskes *et al.* 1996). Tuskes *et al.* also re-identified Riotte's (1969) records of *A. finlaysoni* from Wisconsin and Minnesota as *A. senatoria*. Although larval morphology and biology is critical to determining the disputed taxonomic affinity of Lake Erie populations, biological information of these remains fragmentary.

Starting in 2018, populations of the *Anisota senatoria*-group increased to high densities in the areas of northern Lake Erie, eastern Lake Huron, and in 2023–2024 northeastern Lake Ontario. Based on the unique morphology of last-instar larvae (Riotte 1969; Riotte & Peigler 1981), Erie region *Anisota* were initially identified as *A. finlaysoni*, while larvae from the Lake Huron region were unambiguously identified as *A. senatoria*. Lake Ontario north shore populations have invariably been assigned to *A. finlaysoni* since its recognition as a distinct species; the type locality near Belleville is in the west-central part of the area (Fig. 1). The increased population densities between 2018 and 2023 in Ontario provided the opportunity to compare the biology, morphology and mtDNA barcode variation of *A. finlaysoni* and *A. senatoria* across the three regions (Fig. 1).

## Methods & Materials

This study focused on *Anisota* populations from three regions of southern Ontario (Fig. 1): Lambton Co., on the southeast shore of Lake Huron; Norfolk Co. and Haldimand Co., in the north-central Lake Erie region; and the southern portions of Northumberland to Frontenac Counties in the eastern Lake Ontario region. For convenience, these regions will be referred to as A) Huron, B) Erie and C) Napanee, respectively (Fig. 1).

Surveys for larvae were conducted by visual searches of oaks (*Quercus* spp.) during August, when defoliation and mid- to late instars are most evident. Roadside oak trees were surveyed in the Erie region in 2019 and 2020, and in the Napanee region in 2017, 2020 and 2023. Larvae were reared in large aluminum-screened cages (12 x 12 x 24 inches), or on oak branches with mesh sleeves. Pupae were overwintered outdoors in the screened cages laid flat on the ground, with pupae placed on a bed of 1–2 inches of peat moss and loosely covered with oak leaves.

Newly emerged, reared adult females emitting sex pheromones were set out in the screen cages described above to attract males, a method commonly employed for saturniids (see for example, Tuskes *et al.* 1996). To avoid potential effects of captive rearing affecting morphological comparisons, adult specimens in morphological comparisons were limited to wild-collected males using this method. Assessment of female morphology was limited to reared specimens by necessity. Lastly, pheromone attraction was also employed to survey for *A. finlaysoni* populations across the Napanee region (Fig. 1). For comparison of adult phenotypes, between 30 and 50 males and 10 and 20 females were examined from each region. Wing measurements were taken with calipers precise to the nearest 0.1 mm.

Records of *A. senatoria* and *A. finlaysoni* were compiled from taxonomic literature (Riotte 1969, Ferguson 1971, Riotte & Peigler 1981), the historic summaries of the Forest Insect and Disease Survey (Raizenne 1952, McGugan 1958, Livesey 1969, Sajan 1983, Barnes 1976, McLeod *et al.* 1988, Czerwinski & Biggs 1992), and the Toronto Entomological Association (Michaels and Riotte 1970). Specimens were examined from the Canadian National Collection of Insects, Arachnids and Nematodes (CNC, Agriculture and Agri-food Canada, Ottawa, Ontario), Royal Ontario Museum (ROM, online at https://collections.rom.on.ca), The Great Lakes Forestry Centre, Sault St. Marie, Ontario, and photo observations on iNaturalist (iNaturalist.org). Voucher specimens collected during the course of study are deposited in the CNC. All records were mapped using SimpleMappr (https://www.simplemappr.net).

DNA extraction, PCR amplification, and sequencing of the COI barcode region was performed at the Canadian Centre for DNA Barcoding and followed standard protocols (Hebert *et al.* 2003; http://www.ccdb.ca/resources.php). Resulting data were managed and analyzed using BOLD (Barcode of Life Data Systems; Ratnasingham & Hebert 2007), available at http://v4.boldsystems.org/. Mitogenomic divergence was calculated based on Kimura 2-Parameter (K2P) distances. Sequence comparisons were generated on the BOLD website with the following parameters: Distance Summary Model: Kimura 2 Parameter; Deletion Method: Pairwise Deletion; Alignment: BOLD Aligner (Amino Acid based HMM). Nineteen barcode sequences were selected for phylogenetic analysis, representing all barcode haplotypes of publicly available *Anisota* data in BOLD. The final dataset comprised 654 nucleotide positions with representative samples for 15 of the 16 known species, and all known haplotypes for the *senatoria*-complex (*A. senatoria*, *A. finlaysoni* Riotte and *A. peigleri* Riotte). Phylogenetic analysis was conducted using Maximum Likelihood methods with initial trees obtained through Neighbor-Join and BioNJ algorithms as implemented in T-REX (Boc *et al.* 2012).

## Results

### Larval morphology

Huron region larvae exhibit orange lines and full-length mesothoracic scoli in all instars (e.g. iNaturalist 2020a, 2021a,b,c, 2022a), and adults are unequivocally identified as *A. senatoria* (Riotte & Peigler 1981; Tuskes *et al.* 1996). Erie region larvae vary from yellow to orange-yellow longitudinal lines and the length of the mesothoracic scoli is variable, as discussed below (Figs. 2–5). The transition between the variable Erie larvae and Huron *A. senatoria* larvae occurs east of the London region (Middlesex Co.), as larvae from this area are also more orangish with long scoli (e.g. iNaturalist 2022b), like those of the Huron region. *Anisota finlaysoni* from the Napanee region consistently displayed yellow lines and very short scoli in all instars (Figs. 6–10). Width of the longitudinal stripes varied slightly. Scolus length of Erie populations varied between and often within instars, even within a colony of siblings (Figs. 2, 4). This variation was most pronounced in early- to mid-instars; fifth instars typically had short scoli similar to those of Napanee *A. finlaysoni*, but fourth instars had short, moderate or long scoli (Fig. 4).

**FIGURES 2–5.** *Anisota senatoria* larvae, Norfolk Co., Ontario. First instars, depicting variable thoracic scoli length (2; photograph by Mike King, used with permission); second instars (3); fourth instars (4); fifth (final) instars.

### Host plants and habitat

In the Huron region, *A. senatoria* larvae occur almost exclusively on black oak (*Quercus velutina* Lam.), but also rarely on white-oak group (subgenus *Leucobalanus*) species (e.g. iNaturalist 2018). In the Erie region, all wild larvae observed in this study and those currently available on iNaturalist occurred on black oak. However, there are also historical larval collections from white oak (*Quercus alba* L.) and bur oak (*Quercus macrocarpa* Michx.) (Fig. 1, inset; Table S1). We observed moderate to heavy defoliation of black oak, with a preference for open-grown trees less than about 5 m tall. No larvae were found on mature trees along forest edges. *Ex ova* Erie larvae initially reared on white oak seemed to perform poorly (slow growth and reduced feeding), but improved upon being switched to black oak (J. Troubridge, pers. comm.). The only other Lepidopteran causing significant defoliation at Erie sites was *Lymantria dispar* L., but defoliation of the two species are characteristically different. *Lymantria dispar* larvae consume the entire leaf, whereas *Anisota* do not consume the leaf mid-vein. Also, the conspicuous defoliation by *Anisota* occurs later in the season as larvae reach maturity, after *L. dispar* has pupated and oak leaves have flushed out again.

**TABLE 1.** Comparison of diagnostic traits for three *Anisota senatoria*-group populations in southern Ontario in this study.

| | Trait | *A. finlaysoni* | Norfolk Co., Erie region | *A. senatoria* (Huron region) |
|---|---|---|---|---|
| **larva** | 5th instar mesothoracic scoli | very short | short | long |
| | 4th instar scoli | very short | short to long | long |
| | 5th instar ground colour | yellow | yellow to orange | yellow to orange |
| | | | | |
| **adult** | male forewing ground color | sepia brown | maroon brown | maroon brown |
| | female forewing ground color | pale yellowish | pinkish yellow | pinkish yellow |
| | thorax and abdomen color | duller yellowish brown | brighter saffron yellow | brighter saffron yellow |
| | male forewing spotting | absent | rarely absent | rarely absent |
| | female forewing spotting | rarely present | present | present |
| | male forewing length (n=25) | 18.5 mm | 17.9 mm | 18.0 mm |
| | cornuti size | large | small | small |
| | | | | |
| **ecology** | most common larval host | white oak, bur oak (subgenus *Leucobalanus*) | black oak (subgenus *Erythrobalanus*) | black oak (subgenus *Erythrobalanus*) |
| | habitat preference / substrate | open woodland / loam | open woodland / sand | open woodland / sand |
| | larval microhabitat | ground to high canopy of small to mature trees | small trees, near ground | small trees, near ground |
| | male attraction to light | no | yes | yes |
| | mtDNA haplotype group (Table 2) | A | A | A, B |

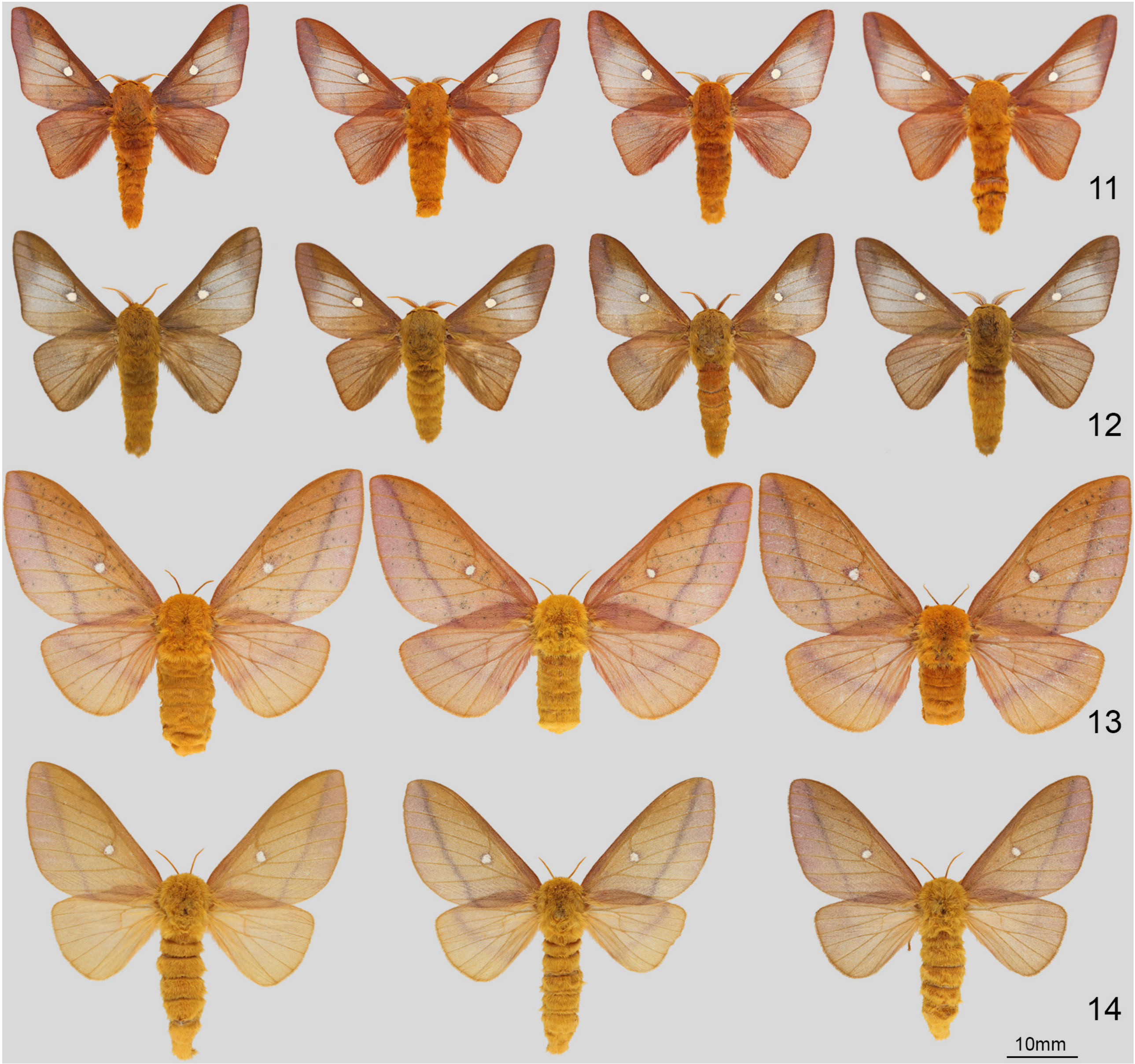
In contrast to the Erie and Huron regions, larvae in the Napanee region were invariably found on white or bur oak (most commonly the latter). Larvae were frequently observed with binoculars high in the canopy of large oaks (>8 m height), where the distinctive larvae defoliate terminal twigs. Even after larvae mature and disperse, the distinctive cast larval skins persist on defoliated outer twigs. A few colonies were found on white oak, but none on northern red oak (*Quercus rubra* L.), which seems generally to be avoided in all regions. The only other oaks in the Napanee region are swamp white oak (*Quercus bicolor* Willd.) and chinquapin oak (*Quercus muehlenbergii* Engelm.), both occurring too infrequently to have significant roles as larval hosts. Black oak is absent in the Napanee region, although it is locally common in the Oak Ridges Moraine immediately to the west. Larval searches on black oak there (Centreton, Northumberland Co.) were negative, as were pheromone attraction surveys (see below).

*Anisota finlaysoni* larvae at the Napanee sites were most often found in isolated clusters of mid-sized to large oaks along roadsides and field margins, surrounded by agricultural fields and remote from intact or continuous natural habitat. It appears that *A. finlaysoni* prefers the savannah-like (albeit artificial) habitat structure of open agricultural landscape with isolated groups of trees, since we consistently failed to locate larval colonies in undisturbed natural habitats such as wetlands, edges of closed-canopy forest, limestone alvars, and rock barrens woodland. The limited distribution of *A. finlaysoni* within the Napanee limestone plain could be linked to ground substrate requirements for pupation. With little or no soil and impermeable bedrock, both alvars and barrens can be either excessively dry or seasonally inundated, conditions that are unsuitable for pupal survival. At most of the Napanee sites where *A. finlaysoni* was detected, the soil type is Bondhead Loam and Guerin Loam, characterized as calcareous stony loam till that is imperfectly to well-drained (Gillespie *et al.* 1966). Larval searches and female pheromone trials were negative (Fig. 1) in nearby sites with continuous natural woodland in the granite bedrock region (Frontenac Arch) to the north and east of the Napanee Limestone Plain (with the exception of one isolated population near Glendower in an area of local sand and gravel deposits, marking the northeastern range limit). Unlike the Erie populations, defoliation by *A. finlaysoni* in the Napanee region was less evident because colonies often occurred in the canopies of large oaks. Most incidental observations of larvae occurred during the last week of August, when fully grown larvae begin to disperse away from the host trees in search of pupation sites. The host preference findings in the Napanee region are consistent with those reported in the early literature, as summarized by Riotte (1969).

**FIGURES 6–10.** *Anisota finlaysoni* larvae, Frontenac Co., Ontario. Fifth (final) instar, lateral view (6) and oblique dorsal view (7); molting and freshly molted second instars (yellow and grey-black), with smaller, tan-colored exuviae of first instars (8); mature second instars (9); third instars (10). Note freshly molted individuals appear yellow, the characteristic black pigmentation gradually increasing after time since molt.

## Adult morphology

Comparison of adult phenotype between Napanee *A. finlaysoni* and other populations reveal wing shape differences and marked differences in color pattern (Figs 11–14). Huron and Erie *Anisota* males have brighter maroon-pink wing coloration, usually with dark indistinct speckles (Fig. 11), compared to the dull sepia-brown wings that lack speckling in *A. finlaysoni* (Fig. 12). The transition from the translucent area of the forewing often appears more



**FIGURES 11–14.** Adults of *Anisota senatoria* and *A. finlaysoni* from Ontario, Canada. *A. senatoria* (male), Lambton Shores, Lambton Co., voucher # CNCLEP00345807 (11a); *A. senatoria* (male), Lambton Shores, Lambton Co., voucher # CNCLEP00345808 (11b); *A. senatoria* (male), Rowan Mills, Norfolk Co., voucher # CNCLEP00345814 (11c); *A. senatoria* (male), Rowan Mills, Norfolk Co., voucher # CNCLEP00347032 (11d); *A. finlaysoni* (male), Frontenac Co., CNCLEP00345818 (12a); *A. finlaysoni* (male), Frontenac Co., CNCLEP00345817 (12b); *A. finlaysoni* (male), Frontenac Co., CNCLEP00345815 (12c); *A. finlaysoni* (male), Frontenac Co., CNCLEP00345816 (12d); *A. senatoria* (female), Lambton Shores, Lambton Co., voucher # CNCLEP00345819 (13a); *A. senatoria* (female), Rowan Mills, Norfolk Co., voucher # CNCLEP00345822 (13b); *A. senatoria* (female), Rowan Mills, Norfolk Co., voucher # CNCLEP00345823 (13c); *A. finlaysoni* (female), Frontenac Co., CNCLEP00345826 (14a); *A. finlaysoni* (female), Frontenac Co., CNCLEP00345824 (14b); *A. finlaysoni* (female), Frontenac Co., CNCLEP00345825 (14c). All males are wild-collected adults, all females are reared ex larva. Complete collecting data is provided in Table S1.

diffuse in *A. finlaysoni*. The thoracic and abdominal vestiture in Erie and Huron *Anisota* is rusty orange-yellow (Fig. 11), whereas that of *A. finlaysoni* is a duller orange-sepia (Fig. 12). Similarly, females of Huron and Erie *Anisota* have a distinct pinkish cast with fine, indistinct forewing speckling (Fig. 13), whereas *A. finlaysoni* females are duller overall and sepia brown with a brownish-maroon outer margin, and no speckling (Fig. 14). Color differences were also noted by Tuskes *et al.* (1996), who distinguished *A. finlaysoni* based on "brownish earth tones." We confirmed the slightly larger size of *A. finlaysoni* males mentioned by Riotte (1969) and Ferguson (1971), with a forewing length of 18.5 mm compared to 18.0 mm for the Huron population and 17.9 mm for Erie (n = 25 for each group, wild-caught adults). *Anisota finlaysoni* females (Fig. 14) may average smaller than those of *A. senatoria* (Fig 13), but the validity of this difference is difficult to ascertain since nearly all female specimens are from larvae reared under different environmental conditions. Lastly, both the fore- and hindwing of male *A. finlaysoni* differ slightly in shape as indicated by Ferguson (1971): the forewing is less narrow/acute, and the hindwing has a more convex outer margin and more widely rounded anal angle (Fig. 12) compared to Huron and Erie specimens (Fig 11).

Comparison of male genitalic structured showed that gnathos shape and cornutus size is highly variable, even within populations. Since no consistent differences could be found between the three populations, genitalic morphology seems not to offer any species diagnostic traits between these two closely-related *Anisota*.

We attempted two pheromone cross-attraction trials between the Erie and Napanee regions. Females sourced from the Erie population (Norfolk Co.) failed to attract males in Northumberland County west of the Napanee region (Fig. 1); however, this may reflect a true absence of *Anisota* there, despite the local abundance of black oak. *Anisota finlaysoni* females from the Napanee region were not available prior to 2024, and the only trial of Napanee females in Norfolk County yielded inconclusive results, since the female did not initiate calling behaviour. Lastly, there appear to be differences in adult attraction to artificial light, since both sexes have been light-caught in Norfolk County, while Lambton County catches are strictly females (J. Troubridge, pers. comm.). Light trapping has not been conducted in the Napanee region for *A. finlaysoni*, but no light-trapped adult specimens from that region have ever been recorded (Ward *et al.* 1974; Riotte and Peigler 1981).

## Geographic distribution

Historic literature records indicate that periodically abundant populations of *A. senatoria* group taxa occurred in most regions of southern Ontario, from northwestern Lake Ontario west to the Trent River; and from the Hamilton region south to the Niagara Peninsula, Lake Erie north shore, and west to southeastern Lake Huron (Fig. 1). Local outbreaks were noted in the Niagara Peninsula, Norfolk County and Lake Huron regions. Bowser and Jansons (1974) noted that "*High larval populations … continued in the southeastern part of the Cambridge District and in the northern part of the Niagara District for the third consecutive year* [1973]." The historical Cambridge District is west of Toronto in the Kitchener-Hamilton region and marks the eastern terminus of the Erie region *Anisota* populations. Occurrences from the area between the Erie and Napanee regions are particularly relevant given that it's situated between the two morphologically different *Anisota* populations. This area spans a minimum gap of 180 km between verified occurrences, along the northwestern shore of Lake Ontario and centered on the Oak Ridges Moraine (Fig. 1). The only *Anisota* records from this region trace to Raizenne (1952), repeated in McGugan (1958) and Riotte & Peigler (1981). Raizenne gave regional summaries from Forest Insect & Disease Surveys (FIDS) carried out in Ontario between 1937 and 1948, which he grouped by county: light infestations of "*Anisota senatoria*" on oak in Durham Co. and Ontario Co., (present-day Durham to Oshawa region), and Victoria Co. (present-day Kawartha Lakes District). A FIDS record from "Lindsay" is also cited in Riotte & Peigler (1981) and mapped in McGugan (1958). The town of Lindsay is in the historical county of Victoria, so Raizenne's "Victoria Co." and Riotte and Peigler's "Lindsay" probably represent the same original record. No voucher specimens could be traced for any of these three counties in FIDS records (GLFC), nor for anywhere else in the region. However, several voucher specimens with the original FIDS sampling forms include the handwritten location "Lindsay", but this is in reference to the "Forest District:" rather than the town. The expansive Lindsay Forest District included known *A. finlaysoni* sites such as Campbellford, specific localities included on the same FIDS form. The Lindsay / Victoria County references are therefore most likely a data transcription error for collections from the Lindsay Forest District. No voucher *Anisota senatoria*-group larvae were documented anywhere near the town of Lindsay in the subsequent 50 years of FIDS surveys. Similarly, no specific FIDS records could be traced for Raizenne's "Durham Co." and "Ontario Co." reference, nor were any *A. senatoria*-group collections recorded there subsequently. In the absence of accurate data and verifiable vouchers, Raizenne's (1952) Durham County and Ontario County records must also be considered dubious, especially given their geographic isolation from verified sites. Lastly, a record for "Otter Lake" cited by Riotte & Peigler (1981) is mapped in COSEWIC (2023) at approximately 44.72°N, 77.76°W in central Hastings County. This historical record is detailed by Ward *et al.* (1974), and given as "Otter Lake, Frontenac Co.", which is located at 44.508°N, 76.565°W, about 100 km ESE of that depicted in the COSEWIC (2923) map. Presence of *Anisota finlaysoni* was confirmed at a nearby site in 2024 (Bedford Hall, ~10km NNW of North Otter Lake). In summary, verifiable occurrences of *A. finlaysoni* from the Napanee region are limited to the area between the Trent River and Rockport (Fig 1). The minimum area polygon based on verified historic and modern occurrences here is about 5500 km$^2$.

Surveys for *Anisota finlaysoni* populations using pheromone-emitting females were conducted as females emerged from pupal diapause, between June 20 and 29th in 2024. Efforts to locate extant populations of *A. finlaysoni* at the eastern and western limits of historical occurrences were unsuccessful, although numerous new occurrences were documented within the core range (Fig. 1). When *A. finlaysoni* was present, males responded almost immediately to calling females, arriving within the first 3–4 minutes of the trial. Female calling behaviour commenced around 1200h, and males were responsive under sunny and warm (20–25°C) conditions until at least 1630h, when trials were stopped. Sites with negative results were surveyed on the same day under similar weather conditions for a minimum of 10 minutes, so the probability of false negatives is considered to be very low. The pheromone surveys in the Napanee region suggest that the modern range of *A. finlaysoni* has either contracted compared to the maximum historical extent, or peripheral populations occur only temporarily during population peaks. Why some range-edge historical sites are not occupied is not clear; for example, the western-most historical occurrences were along the Trent River (Campbellford, Frankford, and Glen Miller), but pheromone survey results there in 2024 were negative. Some relatively large tracts of oak-hickory woodland remain intact in the region (Catling 2008), and are seemingly ideal habitat. The reason for the absence of *A. finlaysoni* there is not obvious.

## DNA barcodes

DNA barcode variation showed some unexpected patterns that are not consistent with the current taxonomic understanding of the genus *Anisota*. Ontario populations exhibit two widely divergent haplotype groups with a minimum difference of about 2.5% (Fig. 15). The first group (haplotypes A1 and A5) is present in all three study regions. Haplotype A5 was present in Erie, Huron, and Napanee (Table 2); haplotype A1 was from a single Huron region specimen. Other A-group haplotypes represent North American *A. senatoria* populations outside of Ontario (Table 2). The second group (haplotypes B1 and B2) includes specimens from Huron, Essex Co. in southwestern-most Ontario, and Michigan / Wisconsin (Fig. 15; Table 2). Thus, only one haplotype (A5) is known for *A. finlaysoni*, which is present also in the Huron and Erie *Anisota* populations, but so far not detected outside of Ontario. The Huron *A. senatoria* population contains haplotypes from the two widely divergent groups (Table 2).

**TABLE 2.** Sampling locations and BIN numbers for barcode haplotypes of the *A. senatoria* species group.

| haplotype | BIN | species | *n* | Prov/State | Study region |
|---|---|---|---|---|---|
| A-1 | BOLD:AAB8796 | *A. senatoria* | 1 | ON | Huron |
| A-2 | BOLD:AAB8796 | *A. peigleri* | 3 | SC, GA | - |
| A-3 | BOLD:AAB8796 | *A. peigleri* | 2 | TX | - |
| A-4 | BOLD:AAB8796 | *A. senatoria* | 98 | ON | Huron, Erie |
| A-4 | BOLD:AAB8796 | *A. finlaysoni* | 5 | ON | Napanee |
| A-5 | BOLD:AAB8796 | *A. senatoria* | 3 | MA, CT | - |
| B-1 | BOLD:AFA1678 | *A. senatoria* | 19 | ON, MI | Huron |
| B-2 | BOLD:AFA1678 | *A. senatoria* | 4 | ON | Essex Co. |

The Barcode Index Number (BIN) is a unique identifier designed to closely approximate a single species, based on mtDNA barcode sequence variation (Ratnasingham & Hebert 2013). Within the context of the entire genus and *senatoria*-group samples outside of the study area, BINs correspond poorly to current *Anisota* species taxonomy (Fig. 15). Sequence data were available for 15 of the 16 known species of *Anisota*; only seven species are assigned to unique BINs (Table 2). Two BINs are a mix of related and unrelated species, and members of the *senatoria*-complex are split between both BINs. This accounts for the large divergence observed between Ontario populations discussed above. *Anisota senatoria*-group haplotypes A1 to A5 are assigned to BIN BOLD:AAB8796, which also

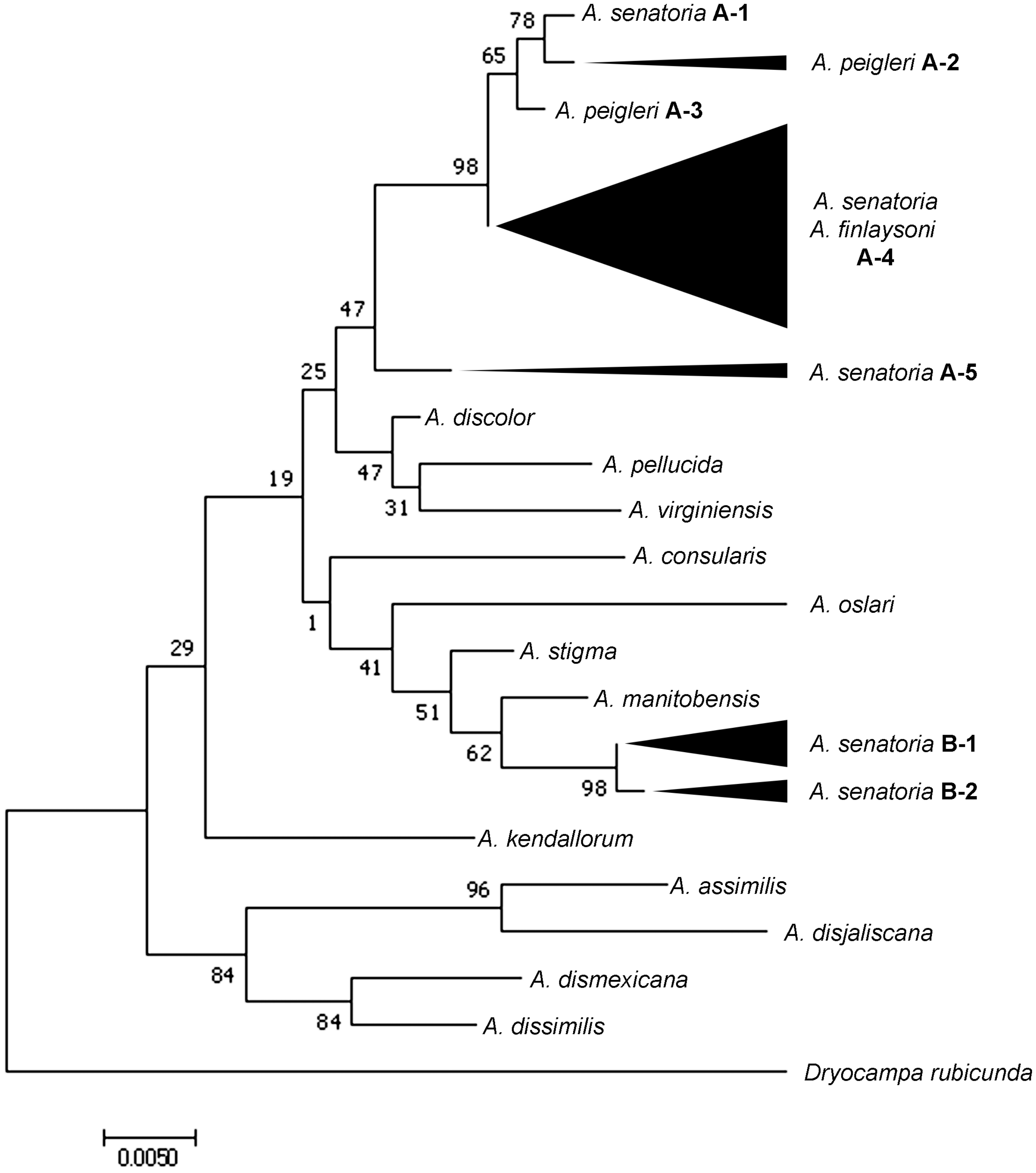


**FIGURE 15.** Maximum likelihood tree based on COI barcode sequence for *Anisota*. All haplotypes of the *A. senatoria*-group are included and placed among a representative haplotype for each of 12 other *Anisota* species. Terminals for *A. senatoria*-group haplotypes are labelled alpha-numerically, with number of replicate specimens proportional to expanded triangles. Additional corresponding sample data is given in Table 2. Tree topology is inferred using the ML method and based on the K2P model, with the depicted tree based on the highest log likelihood (-1847.22). Numbers on internal branches indicate the percentage of trees in which the associated taxa clustered together.

includes *A. virginiensis*, *A. pellucida* and *A. discolor*, whereas *senatoria*-group haplotypes B1 and B2 are assigned to BIN BOLD:AFA1678 that also includes *A. manitobensis* and *A. stigma*. Although divergences between species within a BIN vary, the *virginiensis*-group (*virginiensis*-*pellucida*-*discolor*) and the *stigma*-group (*stigma*-*manitobensis*) are not considered to be closely related to the *senatoria*-group (Riotte & Peigler 1981; Tuskes *et al.* 1996). There are several possible causes for this discordance (Funk & Omland 2003), but resolving this requires nuclear and genomic data which is beyond the scope of the current work. It is clear that mtDNA barcode variation alone is insufficient as a molecular marker to resolve *Anisota* taxonomy.

## Discussion

The taxonomic delimitation and geographic distribution of *A. finlaysoni* has been uncertain since its description as a new species 56 years ago. Previous authoritative works have relied on limited voucher specimens, incomplete knowledge of morphological variation, and geographically distant populations of *A. senatoria* for comparative study (Riotte 1969; Ferguson 1971; Riotte & Peigler 1981; Tuskes *et al.* 1996). The results reported here are the first to examine the two taxa in detail across southern Ontario by comparing topotypical *A. finlaysoni* across a transect to *A. senatoria* populations.

Morphology of fifth-instar larvae has invariably been considered as the most reliable diagnostic trait for *A. finlaysoni*. Based on this, *Anisota* populations from the Lake Erie region have been identified as *A. finlaysoni*, since fifth instars have short mesothoracic scoli. However, early and mid-instar larvae of Erie populations differ significantly from nominate *A. finlaysoni*, since scoli length can vary from short to long, even between siblings. Additionally, larval color differences can be subtle, varying from yellow to yellow-orange, rendering interpretation of differences somewhat subjective. Since color is also known to vary among other *A. senatoria* populations (Riotte & Peigler 1981), the diagnostic value of this trait is unreliable. No diagnostic differences could be found in genitalic structure, but adult phenotype readily distinguishes nominate *A. finlaysoni* from both Huron and Erie populations. Conversely, adults of Huron versus Erie populations cannot be reliably distinguished.

Although habitat preference across the three regions is dictated largely by biophysical conditions and what oaks species are available, ecological preferences are also apparent. In all regions isolated trees or groups of trees are preferred, and closed-canopy forest is seemingly avoided, even if host oaks are present. *Anisota finlaysoni* larvae feed on small to mature oaks, and were often observed in the canopy of large to very large oaks. In the Huron region, black oak (red-oak group) is by far the predominant host of *A. senatoria*. In the Erie region, *A. senatoria* larvae were observed almost exclusively on small or mid-sized black oaks. Broadly speaking, *senatoria*-group populations occur in two landscape types in Ontario, limestone-bedrock woodland with well- to imperfectly-drained soil, where bur oak and white oak are the larval hosts and black oak is absent; and woodland with sandy soil where black oak is the predominant host plant. The two habitat types transition in the Erie region: in the eastern portion thereof (Flamborough Limestone Plain—Niagara Peninsula), black oak is scarce or absent and larval records are from white and bur oak (Fig. 1, inset), and in the western portion (Norfolk Sand Plain) where black oak is present, that species is utilized and seemingly preferred (Fig. 1 inset). Regional adaptation to the oak species predominating in openly wooded landscapes therefore seems to account for differences in host preferences observed within the Erie region. Alternatively, the possibility remains that the historic populations recorded from white and bur oak in the eastern Erie region actually represent *A. finlaysoni*, and differ from the black-oak feeding Erie populations studied here. However, morphology of voucher specimens and photos studied to date do not provide evidence for this.

All specimens examined in this study indicate that *Anisota finlaysoni* is restricted essentially to the Napanee Limestone Plain of the northeastern Lake Ontario region. Historically, *A. finlaysoni* was probably linked to other *Anisota* populations to the west, as evidenced by a haplotype shared among (but globally unique to) all three study regions, and the presence of short larval scoli in intervening populations. The distribution gap along the northeast shore of Lake Ontario is relatively small, especially compared to the gap south of *A. finlaysoni* to next-nearest *senatoria* populations (Fig. 16). However, no verifiable specimens from the intervening region exist, and a minimum distance of 180 km separates the *A. finlaysoni* sites from those of the nearest *A. senatoria* populations in the Oakville region (Fig. 1). Although undetected populations may exist in this region centered on the Oak Ridges moraine, the expansive, heavily urbanized greater Toronto area separates the Napanee populations from the nearest extant populations in the Hamilton region, bounded by Lake Ontario to the south. The lack of records in the greater Toronto area despite an active, long-term entomological community and intensive recent coverage of observations via citizen science platforms is notable. Bowser & Jansons (1974) noted high larval populations in the Hamilton to Niagara region historically, with moderate to severe defoliation of open- and edge-grown white oaks in four townships (Trafalgar, Beverly, Binbrook and Grimsby) spanning from at least 1970 to 1973. Few subsequent records exist for this area (but see iNaturalist 2020b), none for the easternmost portion which has undergone extensive urbanization. Similarly, only historic records exist for the Niagara Peninsula (Fig. 1). Raizenne (1952) noted heavy defoliation of oak here, reported under "*Anisota senatoria*". The Niagara Peninsula has undergone intensive land use changes, since it is one of Canada's top wine-producing regions; the alvar habitats that once existed there have been largely destroyed (Catling & Brownell 1995). The current occurrence pattern of *A. senatoria* for the Erie-Niagara-Toronto region is consistent with range contractions due to extirpation of historic peripheral populations.

Although the black-oak feeding, Erie populations in this study are unequivocally not *A. finlaysoni*, it is necessary to consider the possibility that *A. finlaysoni* is also present there but remains undocumented, and/or that some unverifiable historic records represent this species. Riotte (1969) initially considered the Lake Erie populations to be *A. senatoria*, but subsequently revised his identification to *A. finlaysoni*, probably based on the discovery of larvae in Norfolk Co. (Michaels and Riotte 1970). As documented here, larvae of Erie populations can indeed be indistinguishable from *A. finlaysoni*. Based on host plant and habitat preferences, *A. senatoria* is associated with black oak of the Norfolk Sand Plain, whereas *A. finlaysoni* might be expected to occur in association with white and bur oak on the adjacent Flamborough Limestone Plain—Niagara Peninsula. Thus, study of *Anisota* from the latter area is of particular importance. Unfortunately, *Anisota* were last recorded on the Niagara Peninsula over 50 years ago (Table S1), and there are no modern records of white/bur-oak feeding larvae from here. The few modern records from the area north of there are consistent with *A. senatoria* in adult phenotype (e.g. iNaturalist 2020b) and host plant (e.g iNaturalist 2019). Tuskes *et al.* (1996) also pointed out that the adult phenotype of specimens from Kitchener were representative of *A. senatoria*, not *A. finlaysoni*. Addressing this knowledge gap will require discovery and study of white/bur oak associated populations, via larval searches and pheromone surveys.

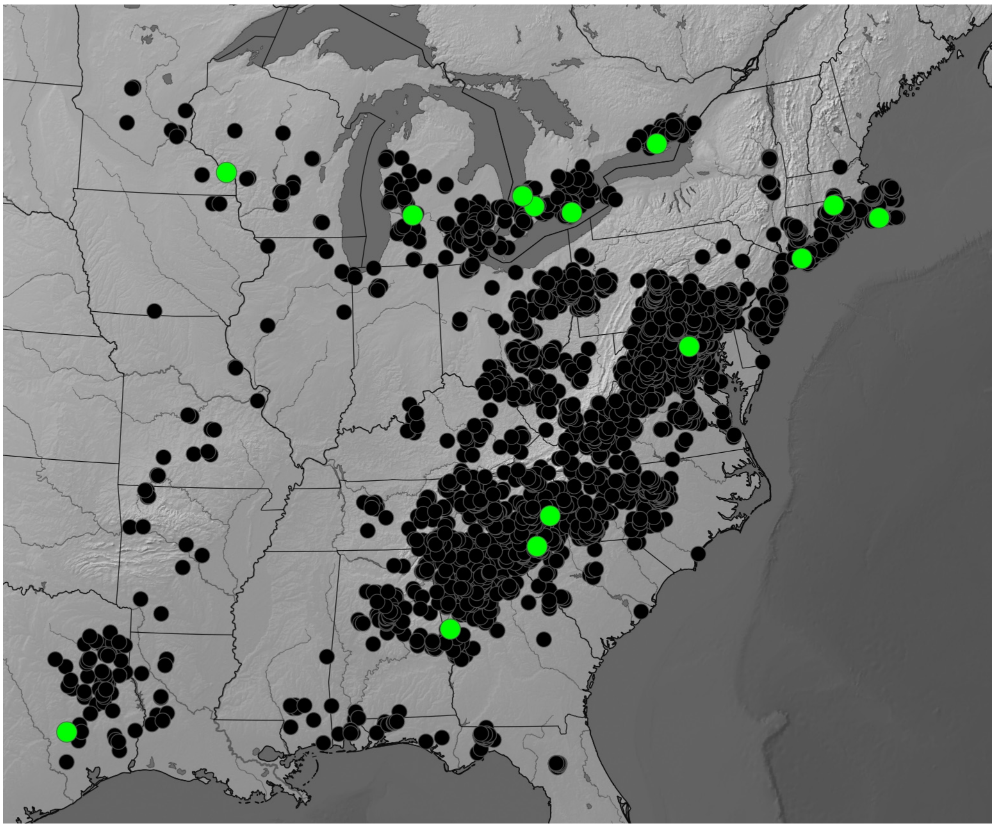


**FIGURE 16.** Distribution of the *Anisota senatoria* complex, comprising *A. senatoria*, *A. finlaysoni* and *A. peigleri*. Sourced from specimens examined herein, citations in primary taxonomic literature (Riotte & Peigler 1981, Ferguson 1971) and independently verified records on iNaturalist (Table S1). Green circles indicate DNA barcode vouchers of the *senatoria*-group (*A. senatoria*, *A. peigleri*, *A. finlaysoni*) shown in Fig. 15 and Table 2.

*Anisota finlaysoni* is not currently known in the USA, but its range may extend into New York state in the St. Lawrence River region at the east end of Lake Ontario (Fig. 1). It should be sought in the region of the Chaumont limestone barrens, which is similar in habitat and less than 30km from Ontario sites. Based on current and historic verifiable records, the global range of *A. finlaysoni* is approximately 5500 km$^2$, significantly less than another recent estimate (COSEWIC 2023). This decrease is a result of re-identification of Erie populations as *A. senatoria*, and the exclusion of erroneous and spurious historic literature records.

Lastly, the global distribution of *A. senatoria* warrants scrutiny since it may shed light on the unexpected geographic mtDNA divergence patterns discussed herein. Generalized range maps (Tuskes *et al.* 1996) depict *Anisota senatoria* as occurring continuously from the south-central US into southern Ontario, but the entire species-group is actually absent from most of New York state and the northern half of Pennsylvania. Furthermore, there are no historical or contemporary records from most of the Mississippi Valley (Fig. 16), although present in east Texas north into the Ozark Plateau and Missouri. A lack of historical and contemporary records forms a gap spanning from southwestern Iowa through southern Illinois and southern Indiana.

## Conclusions

Numerous differences are apparent among the *Anisota senatoria*-group populations across the three regions in this study. The most pronounced differences are between nominate *A. finlaysoni* compared to the Erie to Huron populations to the west. Although some of the traits previously deemed diagnostic for *A. finlaysoni* proved consistent with larger sample sizes, some traits are highly variable with little or no diagnostic value. Importantly, the evaluation of all character sets across the three populations indicate that the Erie and Huron populations studied to date should not be included within the concept of *A. finlaysoni*. This is consistent with the taxonomic concept of Tuskes *et al.* (1996), but not that used in the most recent conservation assessment of *A. finlaysoni* (COSEWIC 2023).

There is some indication of clinal variation or genetic admixture across the three study regions based on morphology of the mature larva, shared mtDNA haplotypes, and host plant preference. Yet, early- to mid-instar morphology and adult morphology is not clinal, with nominate *A. finlaysoni* both disjunct and morphologically distinct from the Erie and Huron populations. An alternative taxonomic arrangement with *finlaysoni* as a subspecies of *A. senatoria* would require assessment of population genetics and a better understanding of isolating mechanisms such as pheromone cross-attraction. Regardless of taxonomic rank, it is evident that *A. finlaysoni* is ecologically and morphologically distinct from populations of the Erie and Huron regions. With a disjunct global range that is restricted to eastern Lake Ontario, *A. finlaysoni* has an estimated maximum extent of about 5500 km$^2$, based on current verifiable historic and modern occurrences.

We hope the data presented here will serve as a starting point for additional research into the natural history and distribution of *Anisota* in Ontario, as many questions remain. Pheromone cross-attraction trials with *A. finlaysoni* would help shed light on the extent of reproductive isolation from adjacent populations, and should be used to seek *A. finlaysoni* in northernmost New York state near the eastern end of Lake Ontario, and elsewhere in southern Ontario. Finally, a better understanding of larval and pupal ecology is needed to effectively monitor and manage the habitat requirements of *A. finlaysoni*.

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**SUPPLEMENTARY MATERIALS.** The following supporting information can be downloaded at the DOI landing page of this paper.

**Supplementary Table S1.** Voucher specimens examined in this study.