

D. Additional Notes

1. Species excluded from the New World Siricidae

Sirex juvenicus Linnaeus, 1758 has been commonly accepted as an established species in North America (Benson 1943, 1945 and 1963; Smith 1979). However, the species is not established though it has been intercepted at many sea ports in the United States and Canada. The species is a well known traveler; it also was often intercepted in New Zealand (FRNZ, NZAC and PANZ), Australia, and the Philippines. The range of *S. juvenicus* in the Old World is said to extend from Europe to Asia, but we have seen specimens only from Europe. The few specimens seen by us and labeled with this name in Asia are not *S. juvenicus*. In the New World, this species is clearly segregated on ovipositor pits size (pits size similar to those seen at middle of lancet in *S. nitidus*, but pits only slightly smaller on basal annuli) and flagellum color pattern. The main hosts of *S. juvenicus* are various species of *Picea*. These hosts do not occur around most ports in eastern North America where the species has been intercepted.

A specimen from one interception in the United States was even described as a new species, *S. hirsutus* Kirby, 1882. Surprisingly, the male type (BMNH) is typical in all details with those of the European *S. juvenicus*. Though this type specimen did not have a locality label, Kirby (1882: 380) believed that it was probably from "Georgia". If so, there was no host for *S. juvenicus* on the coast that it could have reproduced on so it could not have become established. *Sirex hirsutus* is a NEW SYNONYM of the European *S. juvenicus*.

Xeris spectrum has been commonly accepted as an established species in North America (Maa 1949, Ries 1951, Smith 1979, Schiff *et al.* 2006). However, it is not established, though it has been intercepted several times at various sea ports in the United States and New Zealand (specimens studied by us (FRNZ and USNM)). The range of *X. spectrum* extends from the Atlantic to the Pacific coasts in at least boreal regions of Eurasia (Maa 1949). The Nearctic species consists of two species, *X. caudatus* and *X. melancholicus*, and adults are distinguished from those of the *X. spectrum* complex by color pattern in both sexes and pit development on the ovipositor.

2. A name for the European "S. cyaneus"

The name *S. cyaneus* has long been used in Europe (Benson 1943) for a species presumed to be introduced from North America. The species does not match the North American *S. cyaneus* (see "Taxonomic notes" under *Sirex cyaneus* Fabricius). Based on ovipositor character states, the species is close to *S. nitidus* and *S.*

atricornis (see "Taxonomic notes" under *S. nitidus*) but does not match them or other Central European species of *Sirex*. Because the species is well represented in Central Europe and has been often intercepted at sea ports of North America and New Zealand, it is important to have a name for it. We studied about 40 specimens from SDEI, FRNZ, PANZ and USNM. We tried to find a described species within the range of *S. juvenicus* and *S. noctilio* that matches the species (which is, in fact, European, not North American) and found three: *S. torvus* M. Harris, 1779: 96 + plate 28 (figure 1 under *Sirex*), *S. duplex* Shuckard, 1837: 631, and *S. leseleuci* Tournier, 1890: 200. *Sirex torvus* is the oldest name for the European "*S. cyaneus*".

For reasons mentioned above ("taxonomic notes under *S. cyaneus* and *S. nitidus*) and the probable loss of the syntypes from the collection containing *S. torvus* (Evenhuis 1997) [ICZN 75(d) (4)], a neotype for *S. torvus* is required [ICZN 75(a), 75(d) (3)]. Even though the original illustration (Fig. D2.1) and description of the female are sufficiently diagnostic to distinguish the species from other species in Central Europe, *S. torvus* is extremely similar to the subarctic European *S. atricornis* and the North American *S. nitidus*. The neotype female, here designated, is deposited in SDEI [ICZN 75(d) (6)]. It is labeled as follows:

[White and black outline] Schwäbische Alp Plettenberg bei Dottenhausen 7.VIII, 1976 Lauterbach leg.

[White label and black outline] Paururus ♀ noctilio F. 6.79 P. Westrich det. [White and black outline] *Sirex cyaneus* Fabr. E.Jansen det.' 93

[Red] NEOTYPE ♀ *Sirex torvus* M. Harris Des. H. Goulet, 2011

[ICZN article 75(d) (2)]. The neotype is perfect except for the broken off right flagellum. Its type locality is from Germany as entered above [ICZN 75(f)]. Because *S. torvus* females and males may be confused with two other Central European species of *Sirex* (*S. juvenicus* and *S. noctilio*), they are distinguished from these briefly here to satisfy ICZN 75(b) (3). Females of *S. torvus* (Fig. D2.2, neotype) are distinguished from *S. juvenicus* by their black antenna and long ovipositor sheath (M. Harris 1779), and from *S. noctilio* by their very long ovipositor sheath (length of sheath portion beyond apex of cornus as long as combined length of terga 9 and 10) (Chrystal 1928) [ICZN article 75(d) (1)].

The synonymy is as follows:

Sirex torvus M. Harris, [1779]: 96, plate 28 [for publication year see Evenhuis 1997, and Blank *et al.* 2009].

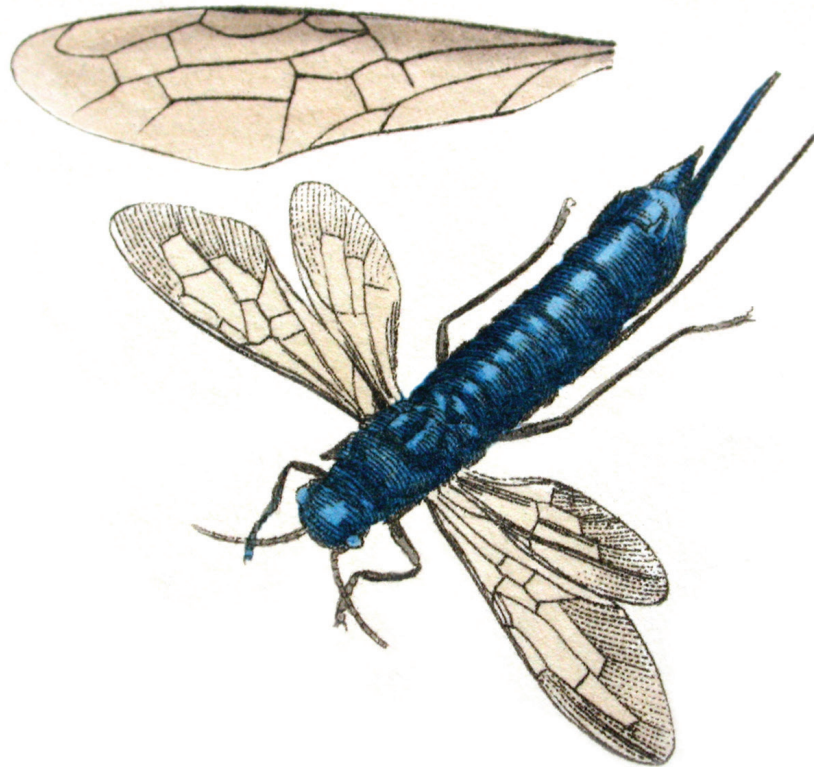
Sirex duplex Shuckard, 1837: 631. Syntypes: 43 males

and females (reared from *Pinus nigra* [now known as *Picea mariana* – information from P. Catling and G. Mitrow]), not seen. Shuckard's collection was auctioned off by T. Desvignes and J. C. Stevens in London in 1868 soon after Schuckard's death (Horn *et al.*, 1990: 364). Syntype depository unknown and specimens assumed lost. NEW SYNONYM. Type

locality: "Cambridgeshire".

Sirex Leseleuci Tournier, 1890: 200. Syntypes presumed lost, not seen. NEW SYNONYM. Type locality: "Douarnenez, France".

Sirex cyaneus; Benson, 1943: 38 (not Fabricius, 1781: 419).



D2.1: *S. torvus* ♀



D2.2: *S. torvus* ♀

E. Mitochondrial DNA results

1. Introduction

Although a large part of this work is a classical morphological revision of the New World Siricidae, DNA barcoding analysis was used to identify potential new species and develop a method to identify siricid larvae.

DNA barcoding as used here was originally proposed by Hebert et al (2003) as “a new approach to taxon identification.” They postulated that if we wished to identify extant biodiversity we needed a faster, easier system than classical morphological methods and proposed that animal species could be uniquely identified by an approximately 600 base pair DNA sequence (barcode) of the mitochondrial Cytochrome Oxidase 1 gene. The advantages of barcode analysis included that it was fast, inexpensive, the characters are relatively uniform and unbiased, the analysis is quantitative, it can be used on all life stages, and it requires no specialized taxonomic experience or knowledge.

Since the proposal of Hebert *et al.* in 2003, barcodes have been used to identify animals including birds, fish and arthropods, discover cryptic species and associate life stages (Hajibabaei *et al.* 2006, Hebert *et al.* 2004, Hebert *et al.* 2004A, Hogg and Hebert 2004, Ball and Armstrong 2006, Smith *et al.* 2006, Ward 2005). However, as more studies were published, theoretical and practical difficulties were used to challenge the use of DNA barcodes alone for new species identification and classification (summarized in Rubinoff *et al.* 2006). These issues included heteroplasmy, where more than one mitochondrial haplotype is present in an individual (Frey and Frey 2004); numts (Lopez *et al.* 1994) where a nuclear pseudogene of mitochondrial origin was sequenced instead of the mitochondrial gene itself (Song *et al.* 2008, Pamilo *et al.* 2007, Koutroumpa *et al.* 2009); hybridization or indirect selection resulting from organisms like *Wohlbachia* mediating mitochondrial introgression in closely related species (Whitworth *et al.* 2007, Linnen and Farrell 2007, 2008); effects related to the biology of mitochondria such as reduced population size, maternal inheritance and limited recombination; and, finally, how much genetic distance should be used to delimit species (see Rubinoff *et al.* 2006 and the references therein). These limitations made it very difficult to use DNA barcoding as an easy alternative to classical or more sophisticated molecular methods for identifying new species. However, DeSalle (2006) in a rebuttal to Rubinoff *et al.* (2006) made a distinction between “species discovery” and “species identification.” He argued that using barcodes alone for species discovery was indeed rife with difficulties, but that once a set of barcodes was established for a group of

species, unidentified specimens could be identified with the caveat that some specimens might not be resolvable. He suggested that a novel barcode sequence should be viewed as only a new species hypothesis to be tested and verified with more established methods. Although this resolution does not solve the challenge of how to recognize the vast number of undescribed species in the world, with our combined morphological and barcoding approach, it should allow us a means to identify adults and thus immature stages of New World Siricidae.

As with many groups of Hymenoptera, there are no morphological keys to immature stages of Siricidae, for several mostly practical reasons. First, until recently, there has been no pressing need for morphological keys to siricid larvae. *Sirex noctilio*, the most significant siricid pest, has only been an economic pest in conifer plantations in the Southern Hemisphere where there were no native woodwasps to confuse it with (Hoebeker *et al.* 2005). Second, rearing larvae from trees is costly and time consuming. Locating, harvesting and storing infested trees is labor intensive and because many species of woodwasps take up to several years to attain maturity it is quite time consuming and thus expensive. Third, until this manuscript, most woodwasps were not considered to be particularly host specific and because many species can attack the same host it was not easy to associate specific larvae with reared adults.

The primary reasons to identify larvae are to recognize an infestation of a pest species and to prevent further introductions of exotic species. As the larval stage is present for 11 months and adults are only present for a few weeks it would be advantageous to be able to identify larvae immediately using molecular methods (hours or days) rather than wait as much as a year or more until identifiable adults can be reared. Because DNA is the same for all life stages, a molecular technique that identifies adults will also identify immature life stages.

2. Results of DNA analysis

The 622 specimens of woodwasps sequenced were resolved into 31 taxa including 28 taxa of Siricidae (603 sequences) and one taxon each of Xiphydriidae (*Xiphydria mellipes*, 3 sequences), Syntexidae (*Syntexis libocedrii*, 12 sequences) and Orussidae (*Orussus thoracicus*, 4 sequences) (Fig. E2.1). Complete consensus sequences, 658 base pairs, were obtained for 29 of the 31 taxa ultimately resolved. The consensus sequences for *Sirex obesus* and *Sirex* near *californicus* were only 613 and 615 base pairs, respectively. Of the 622 specimens sequenced, 476 (76.5 %) were complete sequences; of the rest, 88 specimens were greater in length than 600 base pairs, 48 were longer than 500bp, 6 were longer than 400bp and 4 were longer than 300bp. Length of sequence

for individual specimens is recorded under each species description. All species except *Sirex obesus* and *Sirex* near *californicus* had at least one specimen with a full length sequence.

Although all 622 specimens were unambiguously assigned to the correct family, genus and species taxon according to the siricid family revision proposed here, when this work was started, under the former classification (summarized in Smith 1979, Smith and Schiff 2002, Schiff *et al.* 2006), barcoding results generated several new species level hypotheses. In two cases, one in *Xeris* and one in *Sirex*, pairs of what were considered to be good species or subspecies were found to share identical barcodes. What were formerly classified as *Sirex nigricornis* and *S. edwardsii* are now listed as *S. nigricornis* and what were formerly listed as *Xeris spectrum townesi* and *X. morrisoni indecisus* are now listed as *X. indecisus*. Further, two pairs of subspecies, *X. morrisoni morrisoni* and *X. morrisoni indecisus*, and *Urocerus gigas gigas* and *U. gigas flavicornis* were easily separated using barcodes and are now elevated to species as *Xeris indecisus*, *X. morrisoni*, *Urocerus gigas* and *U. flavicornis*, respectively. DNA barcodes also hypothesized or supported several new taxa. *Sirex abietinus* was a single novel sequence until the species was characterized morphologically and more specimens were obtained and sequenced. *Xeris melancholicus* was initially recognized by its unique barcode and then characterized morphologically. *Sirex obesus* was identified morphologically and then, when fresh

specimens were obtained and sequenced, supported by barcodes. Two other taxa, *Sirex* near *nitidus* and especially *Sirex* near *californicus* are recognized by barcodes but have not been assigned species names because we have been unable to find supporting morphological characters with so few specimens.

The neighbor-joining tree of consensus sequences of each taxon (Fig. E2.1) showed well-delimited taxa. Separate neighbor-joining trees (Figs. E2.2 to E2.5) for individual specimens of small groups of species showed low intra-specific and high inter-specific divergence with no overlap between species. Percent identity and divergence for consensus sequences of all taxa are presented in Table E2.6. The greatest divergences were between families of woodwasps (30–40%). Anaxyelidae was most divergent from the others (34.1%–45.5%) followed by Orussidae (30.5%–42.6%) and Xiphydriidae (30.5%–40.3%). Within the Siricidae, the genera were well defined with percent divergences in the 20s–30s and within genera as low as 1.7% to the 20s. Divergences for the closest pairs of taxa were 1.7% for *Sirex nitidus* and *S. near nitidus*, 2.2% for *Xeris indecisus* and *X. morrisoni*, 2.8% for *Urocerus gigas* and *U. flavicornis*, 3.3% for *Xeris caudatus* and *X. melancholicus*, 4.6% for *Sirex abietinus* and *S. varipes*, 5.1% for *Sirex californicus* and *S. near californicus* and approximately 3.7% for *Sirex cyaneus* and *S. nitidus* or *S. near nitidus*. Of these least divergent pairs the smallest and largest divergences were for pairs that lacked morphological support.

TAXA		Percent Identity																														
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
1	<i>Eri. formosus</i>	60.2	73.3	71.6	73.6	73.9	73.1	71.6	70.7	72.8	71.4	72.6	72.3	70.3	72.5	70.2	62.3	75.8	76.1	71.9	70.8	70.7	71.3	71.1	68.5	66.7	68.5	68.7	69.0	63.1	72.0	
2	<i>Oru. thoracicus</i>	42.6	63.1	66.6	63.1	66.3	65.3	65.4	65.0	65.6	64.6	66.6	62.8	64.7	65.6	65.2	64.7	59.7	64.9	64.6	64.9	66.0	65.5	64.4	62.7	63.5	63.5	63.5	68.7	62.6		
3	<i>Sir. abietinus</i>	27.5	37.7	84.3	84.7	88.9	89.7	82.4	90.4	89.2	87.7	89.8	90.1	88.6	95.4	85.6	64.7	74.5	71.6	77.7	77.7	76.7	77.7	77.1	74.9	76.6	76.7	76.0	76.1	67.5	76.3	
4	<i>Sir. areolatus</i>	29.4	34.5	15.5	85.9	83.7	85.3	87.8	84.7	87.4	85.4	86.6	85.9	82.7	85.1	84.2	64.7	73.4	68.8	80.2	78.3	79.5	79.6	79.9	77.7	77.1	78.0	75.5	74.8	66.6	76.3	
5	<i>Sir. behrensii</i>	26.8	37.7	15.7	14.2	83.6	83.4	86.9	83.4	83.9	85.0	84.3	85.7	84.3	84.8	85.3	63.7	72.8	71.3	78.6	78.3	76.3	78.4	78.9	74.8	76.6	77.1	75.1	74.3	67.3	78.3	
6	<i>Sir. californicus</i>	26.4	35.7	11.0	16.5	89.1	82.7	95.0	87.8	85.1	88.1	88.8	89.4	90.0	86.5	65.3	73.4	69.1	77.1	78.3	76.4	78.0	77.2	76.3	75.8	76.4	75.8	75.8	65.2	78.1		
7	<i>Sir. cyanus</i>	27.0	36.7	10.3	14.9	16.7	11.0	82.7	90.1	96.4	88.0	96.4	89.5	87.4	89.1	88.3	64.7	72.9	68.8	78.0	75.8	76.9	77.5	76.9	74.6	76.0	75.7	76.6	76.4	64.0	76.9	
8	<i>Sir. longicauda</i>	29.6	35.7	17.4	11.9	13.3	18.2	17.4	83.1	83.0	83.7	82.7	82.1	82.7	82.2	82.7	65.3	73.6	70.1	76.9	75.7	75.4	77.2	77.5	75.8	74.2	75.1	72.6	72.2	68.1	78.1	
9	<i>Sir. near californicus</i>	29.8	36.0	9.4	15.3	17.4	5.1	10.1	17.8	89.4	87.5	89.3	89.6	91.2	90.7	87.2	64.9	73.2	69.4	77.4	77.1	76.3	78.5	77.6	75.4	77.2	77.4	75.9	76.1	65.0	77.1	
10	<i>Sir. near nitidus</i>	27.5	37.2	10.6	12.7	16.3	12.3	3.8	17.2	10.7	88.6	98.3	90.0	87.1	88.6	88.3	64.4	72.9	70.1	78.6	76.9	78.4	78.7	78.1	75.4	76.3	76.1	75.4	76.3	64.6	76.9	
11	<i>Sir. nigricornis</i>	28.7	34.2	12.4	14.5	14.9	15.2	12.0	16.6	12.6	11.3	89.2	88.0	85.5	88.1	90.4	65.7	74.5	70.5	78.4	79.0	78.0	78.9	78.7	76.4	76.7	76.7	74.2	74.6	67.6	75.4	
12	<i>Sir. nitidus</i>	27.5	37.0	10.1	13.6	15.7	11.9	3.7	17.6	10.9	1.7	10.8	90.9	86.8	89.4	88.6	65.0	73.4	70.1	78.1	76.7	78.0	77.4	75.4	76.6	77.1	75.8	76.4	64.9	77.1		
13	<i>Sir. noctilio</i>	27.9	34.2	9.7	14.2	14.0	11.5	10.3	18.0	10.7	9.9	11.1	8.9	86.8	90.1	88.0	65.0	76.6	72.0	78.9	78.7	78.0	79.9	79.9	77.4	75.4	75.8	73.9	74.5	66.1	78.9	
14	<i>Sir. obesus</i>	29.4	37.9	10.8	16.9	15.3	10.4	11.9	16.9	8.0	12.3	14.1	12.7	12.5	88.3	85.0	63.8	73.1	68.7	77.2	78.1	76.3	78.1	77.5	75.7	76.2	76.0	75.0	75.7	64.6	75.2	
15	<i>Sir. varipes</i>	28.3	36.4	4.6	14.9	15.7	10.1	10.6	18.0	9.2	11.0	11.8	10.3	9.7	11.4	87.5	65.0	74.6	72.2	77.5	78.4	77.1	78.1	78.0	75.4	78.3	78.1	77.5	78.1	67.9	77.1	
16	<i>Sir. xerophilus</i>	29.7	35.5	14.6	15.5	14.7	13.5	12.0	17.8	13.0	11.9	9.8	11.7	11.7	14.7	12.6	63.8	72.9	69.9	77.1	76.6	75.2	76.7	75.8	74.9	75.8	76.1	73.7	73.7	66.0	75.8	
17	<i>Syn. libocedrii</i>	41.0	36.7	38.2	37.7	39.0	38.2	38.7	37.2	39.0	38.5	36.5	37.5	37.5	39.5	38.5	39.0	62.9	58.8	65.7	64.9	63.4	64.9	64.6	63.4	62.0	62.9	64.1	64.7	68.8	61.7	
18	<i>Tre. columba</i>	24.8	37.0	25.7	27.8	27.2	27.2	27.2	27.4	27.4	26.7	24.4	26.3	22.5	26.3	25.2	27.0	39.7	76.1	68.5	69.8	67.6	69.6	69.9	67.6	71.7	72.3	67.6	68.5	64.4	72.0	
19	<i>Tre. fusicornis</i>	25.2	42.1	29.2	32.2	29.4	31.8	31.3	30.5	31.3	29.9	29.4	29.2	27.9	30.9	28.3	30.1	45.5	24.4	69.3	67.3	67.6	67.3	68.1	65.0	70.1	70.7	67.5	67.9	61.7	71.6	
20	<i>Uro. albicornis</i>	27.8	36.7	21.9	19.9	21.1	22.6	20.9	22.8	22.4	20.3	21.3	20.7	20.3	21.6	22.3	22.5	36.5	31.2	30.3	91.2	91.8	93.0	92.9	90.3	76.0	76.3	74.9	75.1	69.0	76.6	
21	<i>Uro. californicus</i>	29.7	36.7	22.5	22.1	21.3	21.7	23.6	24.2	23.1	22.5	20.3	22.5	20.7	20.7	21.5	22.7	37.0	29.8	32.9	9.1	92.6	93.9	92.7	90.3	75.2	75.4	75.4	67.5	76.6		
22	<i>Uro. cressoni</i>	28.5	36.5	23.0	21.1	23.0	23.5	22.6	24.6	23.8	20.5	21.5	20.9	21.3	22.3	22.9	24.4	38.8	31.8	32.7	8.6	7.7	92.9	93.3	89.5	74.8	74.9	75.7	75.8	65.2	75.2	
23	<i>Uro. flavicornis</i>	28.8	35.7	22.8	20.9	21.3	22.2	22.2	23.2	21.5	20.7	20.9	21.5	19.7	20.9	22.3	22.7	37.5	29.6	32.5	7.2	6.4	7.6	97.3	91.5	75.4	75.4	74.8	75.5	68.7	77.5	
24	<i>Uro. gigas</i>	28.5	36.5	22.5	19.9	20.5	22.6	22.4	22.5	22.2	20.7	21.1	21.5	19.3	21.4	22.1	23.4	37.5	29.6	31.7	7.4	7.4	7.1	2.8	91.5	76.3	76.6	74.6	75.4	68.4	77.2	
25	<i>Uro. taxodii</i>	31.5	38.0	24.4	22.8	25.3	23.8	25.3	24.2	24.7	24.2	24.4	22.6	23.6	24.6	24.8	39.0	32.9	35.1	10.1	10.3	11.4	8.9	8.9	8.9	74.2	74.9	73.4	73.6	63.2	74.8	
26	<i>Xer. melancholichus</i>	34.6	39.2	23.4	23.1	23.8	24.8	24.2	26.6	23.3	23.4	23.4	22.8	24.3	23.9	22.1	24.6	41.3	29.7	30.6	22.9	24.4	24.6	24.2	22.9	25.7	96.8	88.1	88.0	64.1	73.7	
27	<i>Xer. caudatus</i>	31.9	38.2	23.6	22.5	23.3	24.3	25.1	25.9	23.3	24.0	23.8	23.0	24.7	24.5	22.5	24.8	40.3	29.5	29.5	23.2	24.4	24.6	24.4	22.7	24.8	3.3	88.0	88.4	64.7	74.8	
28	<i>Xer. indecisus</i>	31.2	38.5	23.8	25.3	25.3	25.0	23.6	24.7	24.7	26.8	26.2	25.5	24.8	22.7	27.4	38.2	34.0	34.0	25.5	25.1	24.6	25.9	25.9	27.5	11.9	12.5	97.9	63.1	74.0		
29	<i>Xer. morrisoni</i>	30.8	38.5	23.6	26.3	26.5	25.5	23.6	29.0	24.7	23.6	26.1	23.0	24.9	24.1	22.3	27.5	37.7	32.6	33.2	25.3	25.1	24.4	24.8	24.8	27.3	12.1	11.9	2.2	63.2	73.9	
30	<i>Xip. mellipes</i>	39.7	30.5	33.8	35.6	34.3	36.5	36.7	33.1	36.6	36.5	32.9	36.0	34.0	36.8	32.9	35.0	34.1	36.8	40.3	32.6	34.3	37.2	33.3	33.1	39.0	38.0	37.5	40.3	39.7	65.5	
31	<i>Xoa. matsumurae</i>	29.1	40.3	24.0	24.6	23.2	23.0	23.2	23.0	23.7	23.2	24.2	23.2	21.2	24.7	23.6	24.6	41.9	27.9	29.3	23.2	22.8	24.4	22.8	23.2	25.5	27.4	26.8	26.8	27.0	35.2	

Table 2.6. Percent identity between species of sequenced Siricidae and one taxon in three related families (Orussidae, Syntexidae and Xiphytriidae).

3. Discussion

The most important question when deciding to use a new technique to identify species is: does the technique unambiguously identify specimens of each species correctly 100% of the time? In the case of using DNA barcodes to identify New World Siricidae the answer is yes but it was difficult to get to this answer because the Siricidae was in need of revision when the project was started. Our simultaneous morphological and barcoding analyses are in almost complete agreement. Unique barcodes exist for all morphologically distinct species for which we could obtain sequences. However, two of the morphologically distinct species, *Sirex californicus* and *S. nitidus*, each appear to harbor a cryptic taxon that is only recognizable by DNA barcode. The question remains: are these cryptic taxa good species? It is possible they could be artifacts of barcoding such as heteroplasmy or numts or it may be they are very good cryptic species and we have been unable as yet to discover morphological or behavioral support for them. To reduce the risk of heteroplasmy we directly sequenced double stranded PCR products. If there were rare haplotypes they would be masked by the most common haplotype. If there were two or more common haplotypes there would have been double peaks and the sequences would have been difficult to read. To reduce the possibility of having amplified numts we isolated samples from mitochondrial rich tissue and we inspected translated sequences to look for artifacts common in numts such as stop codons, insertions and deletions. There were no stop codons, insertions or deletions in any of the samples except for *Orussus thoracicus* which was missing one codon, in frame. We do not believe this is indicative of a nuclear mitochondrial pseudogene however, as the same codon is absent in three other *Orussus* species (data not presented). Either, all four *Orussus* species have the same pseudogene which is amplified preferentially over the mitochondrial gene, which seems unlikely, or the missing codon reflects a genuine difference between *Orussus* and all the other woodwasps. Although we believe the cryptic taxa are probably valid species, until we can examine more specimens and do further analyses we have chosen to leave the cryptic taxa unnamed. Despite the utility of barcodes for identifying Siricidae we still believe new species require a morphological description.

One of the reasons barcoding was so useful in revising the North American Siricidae is because it is color blind. Prior to this study, abdomen and leg color were often used as simple diagnostic characters for siricid species (Middlekauf 1960, Smith and Schiff 2002, Schiff *et al.* 2006). However, identical DNA barcodes supported by morphological characters suggested that pairs or groups of what were considered to be good species based on abdomen color were really single species. In

this study there were three examples, *Sirex nigricornis*, *Xeris indecisus* and *Tremex columba*. In the first two examples, each species has two female color morphs with either red (the former *Sirex nigricornis* and the former *Xeris morrisoni indecisus*) or black (the former *Sirex edwardsii* and the former *Xeris spectrum townesi*) abdomens. In the third example, females of *T. columba* have one of three color morphs associated with wing color differences. These color morphs were recognized as separate species until Bradley (1913) lumped them together, a position supported by the current barcode results. Whereas it is easy to understand why such dramatic characters would be considered diagnostic for species, this study demonstrates that abdomen color can be misleading. Interestingly, in the original description Brullé suggested that the only difference he saw between *Sirex edwardsii* and *Sirex nigricornis* was that the abdomen was blue and he even suggested that it might just be a variety of *Sirex nigricornis*. Genetic control of abdomen color must be fairly loose in Symphyta because there are several examples of different color morphs in at least four different families. Species with both red and black abdominal color morphs have been recorded in the Xiphydriidae (*Xiphydria tibialis* Say, in Smith 1976), Xyelidae (*Macroxyela ferruginea* (Say), in Smith and Schiff 1998), Tenthredinidae (*Lagium atroviolaceum* (Norton), in Smith 1986) and, Siricidae (present study). Barcodes were also useful in resolving leg color morphs. *Sirex californicus*, *S. nitidus* and *S. noctilio* each have pale and dark leg color morphs. At least for *Sirex californicus* and *S. nitidus* both color forms have the same barcode. We have no sequences for the dark color morph of *Sirex noctilio*. Ironically, abdomen and leg color are still useful characters for identifying woodwasps (e.g., *Sirex varipes*) but this work shows that they should not be used as sole diagnostic characters. Instead, they should be combined with other characters, as we do here, to lead to a diagnosis.

To identify any stages of woodwasps using barcodes, a novel sequence should be aligned with the 31 consensus sequences reported here (See appendix 3) using Clustal V and then visualized in a neighbor-joining tree using appropriate software. The novel sequence should align very closely with the branch of its congener. The range of intra-specific variation is represented in the species trees (Figs. E2.2 –E2.5) and it should be easy to recognize if a species falls outside its expected range. Determining a species threshold limit for barcode data of unknown taxa is quite controversial (Rubinoff *et al.* 2006). Hebert *et al.* (2003) originally proposed that a 2–3% difference would be sufficient to separate animal species. At that level, we might not be able to separate *Sirex nitidus* from the cryptic taxon *S. near nitidus*, or two pairs of closely related but morphologically distinct species, *Urocerus flavicornus*

from *U. gigas* and *Xeris morrisoni* from *X. indecisus*. Later, Hebert *et al.* (2004A) proposed a threshold that was 10 times the mean intraspecific variation for the group under study. This new threshold addresses the diagnostic value of the relationship of interspecific to intraspecific variation but still presupposes a level of species uniformity. Both of these thresholds could be problematic if we were trying to separate species from a sea of unknowns; fortunately, we are trying to identify unknowns by comparison to a relatively well sampled database of recognized species. Unknown sequences will either match one of the known species or become a new hypothesis to be evaluated with morphological or other methods. Although all the species represented here are well delimited, it is possible that barcodes for newly recognized, closely related species could overlap and this database would not be able to resolve them.

We believe the consensus tree (Fig. E2.1) is robust because of the species sampling that went into it. We obtained representatives of each species from as much of the geographic and temporal ranges as possible, as can be seen in the specimens for molecular studies section under each species description. Although sampling can never be complete, multiple samples across the range are a more cogent representation of the species variation than a single specimen from one location in its range.

4. Conclusion

The combination of classical morphological and DNA barcoding methods have allowed us to revise New

World Siricidae and develop a DNA database that will enable identification of most New World siricid larvae. Each morphological species has a corresponding well-delimited barcode. Two species appear to have a cryptic taxon which we have chosen to keep unnamed because they lack morphological support. Our work demonstrates that barcodes are a useful addition to other taxonomic methods, especially for tasks such as associating life stages.

Outgroups studied and illustrated in consensus tree (Fig. E2.1):

Orussus thoracicus

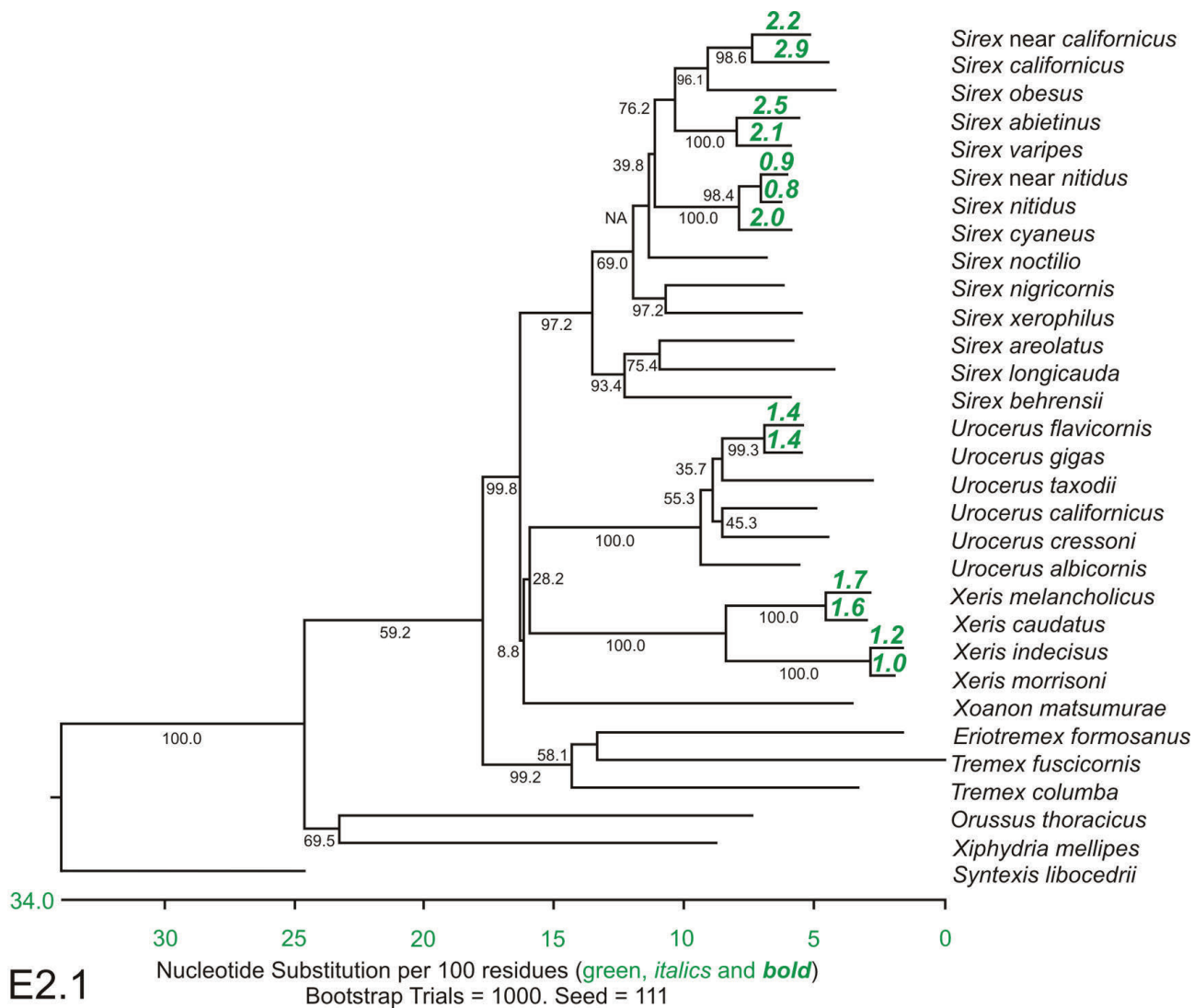
USA. California: 2005, *CBHR* 35, 655; 2005, *CBHR* 306, 655; 2005, *CBHR* 307, 655; 2005, *CBHR* 308, 655.

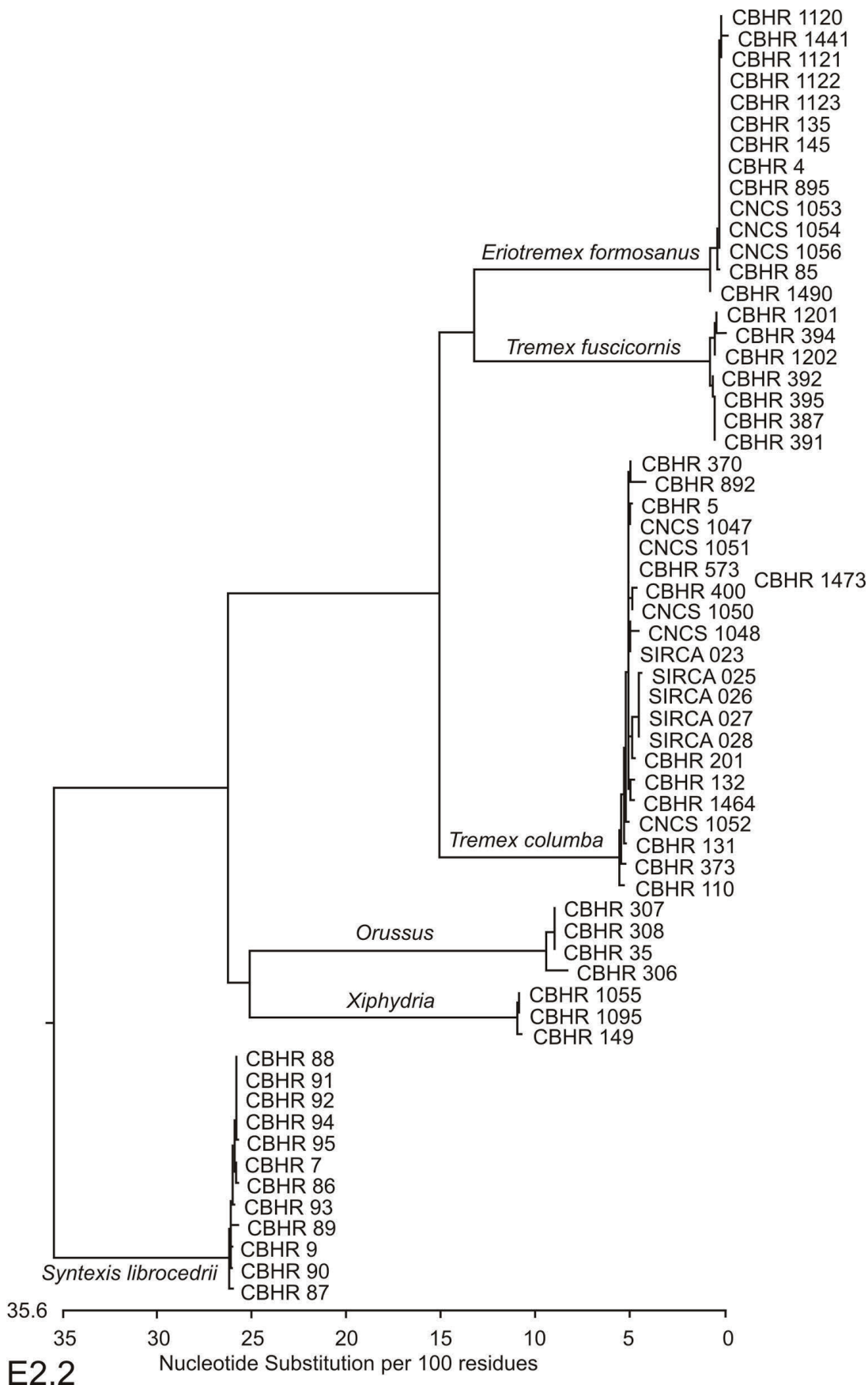
Syntexis libocedrii:

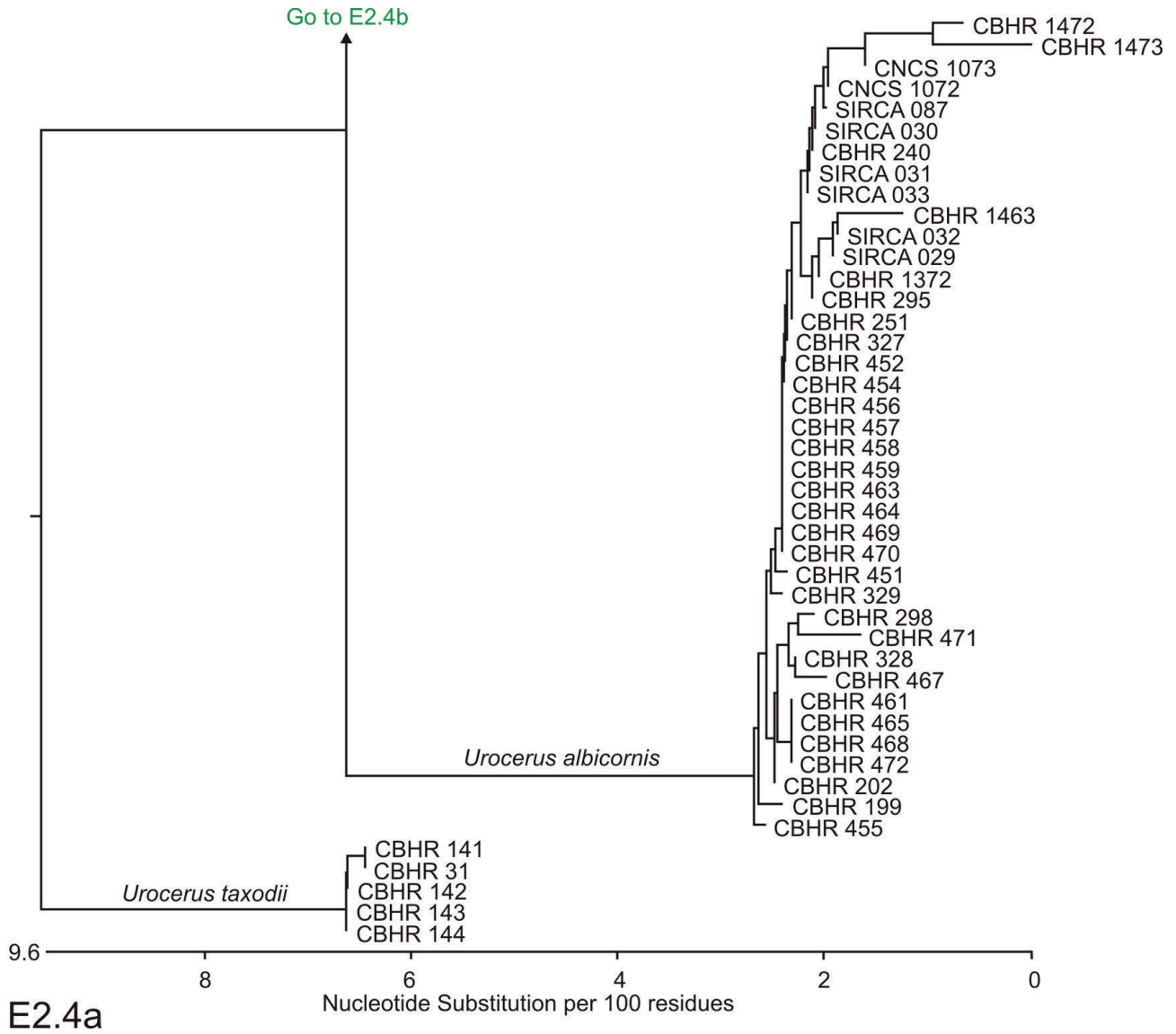
USA. California: 2005, *CBHR* 86, 658; 2005, *CBHR* 87, 658; 2005, *CBHR* 88, 658; 2005, *CBHR* 89, 658; 2005, *CBHR* 90, 658; 2005, *CBHR* 91, 658; 2005, *CBHR* 92, 658; 2005, *CBHR* 93, 658; 2005, *CBHR* 94, 658; 2005, *CBHR* 95, 658. **Oregon:** 2003, *CBHR* 7, 658; 2003, *CBHR* 9, 658.

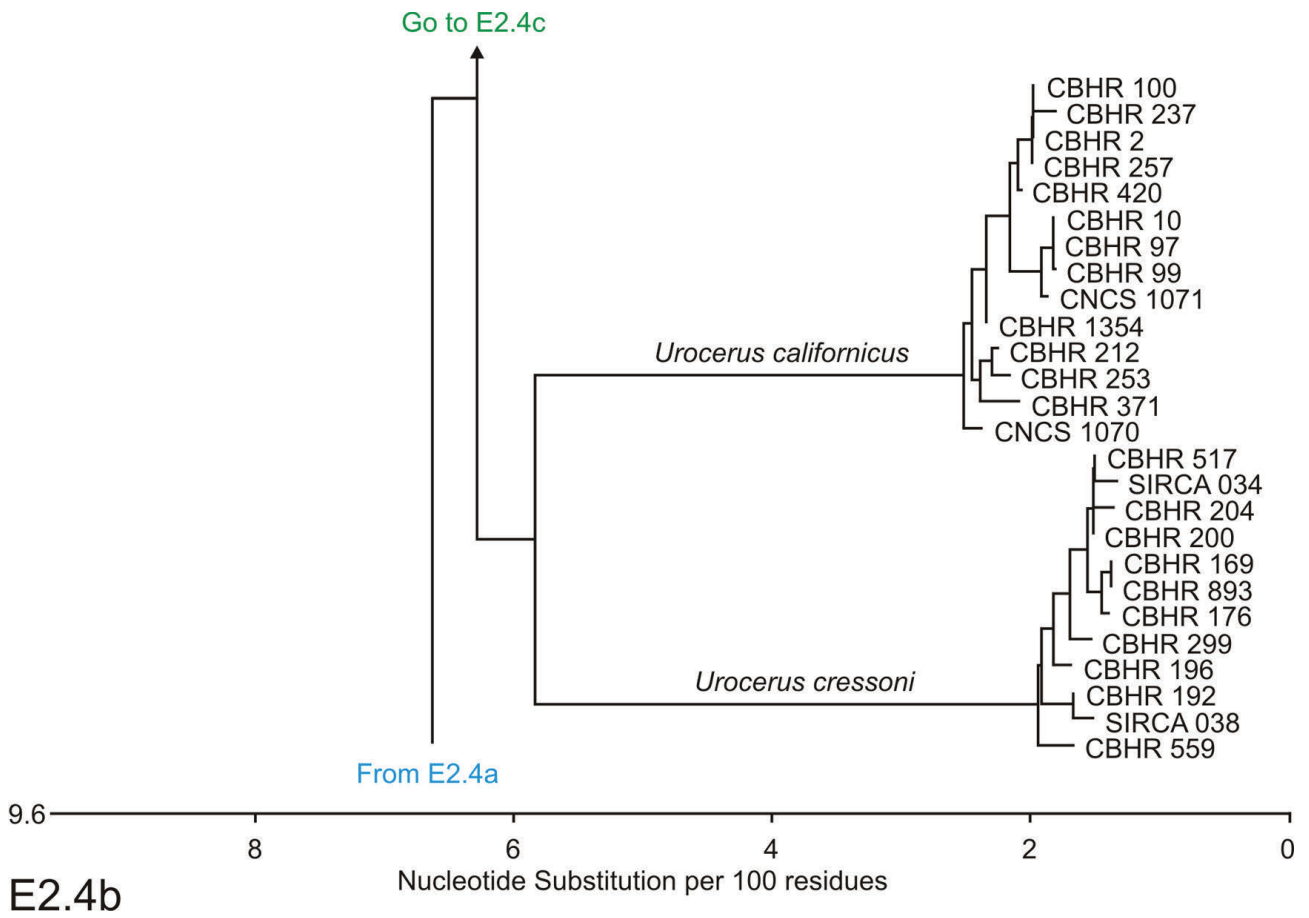
Xiphydria mellipes:

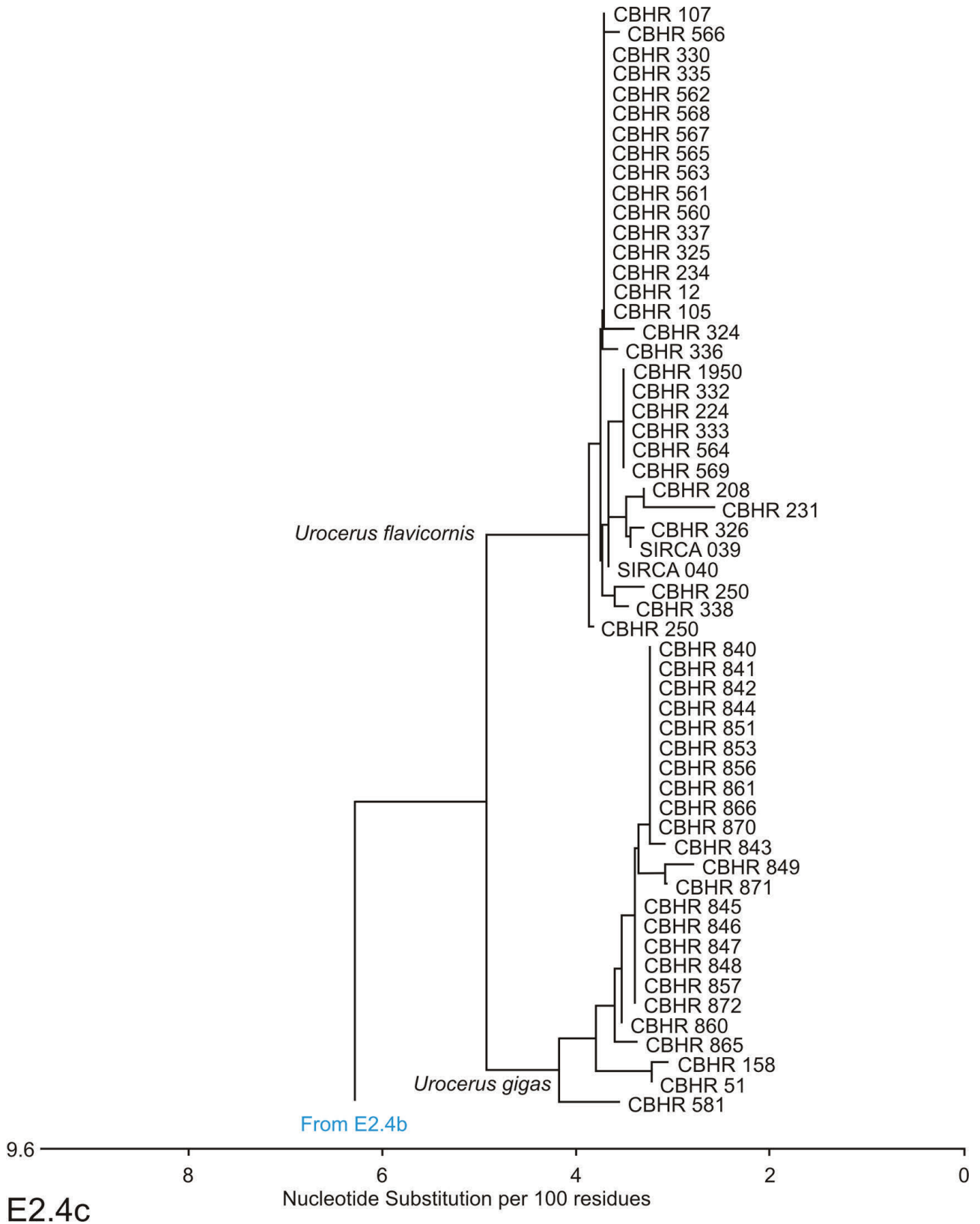
CANADA. Ontario: 2005, *CBHR* 1055, 658; 2005, *CBHR* 1095, 658. **USA. Wisconsin:** 2005, *CBHR* 149, 658.

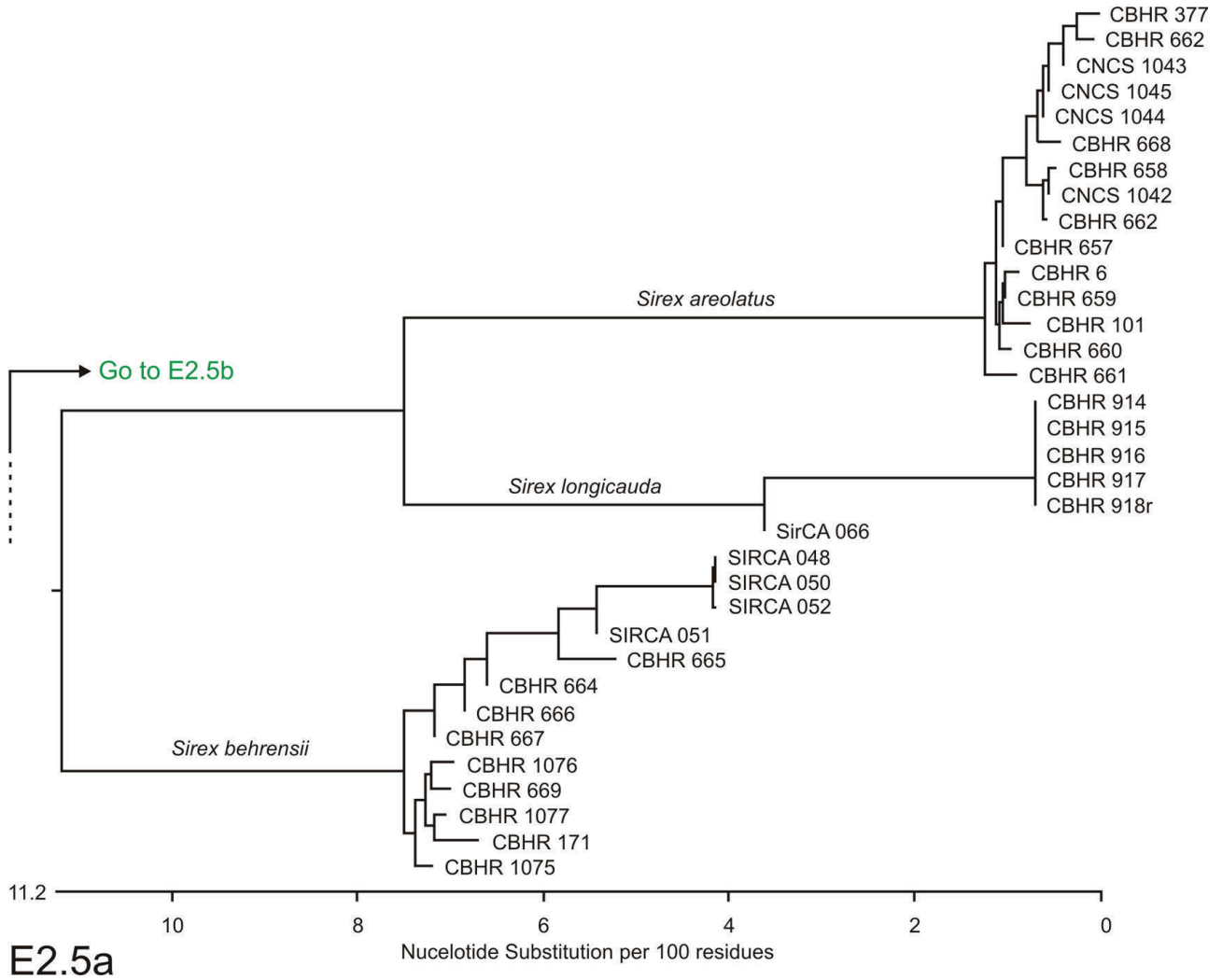


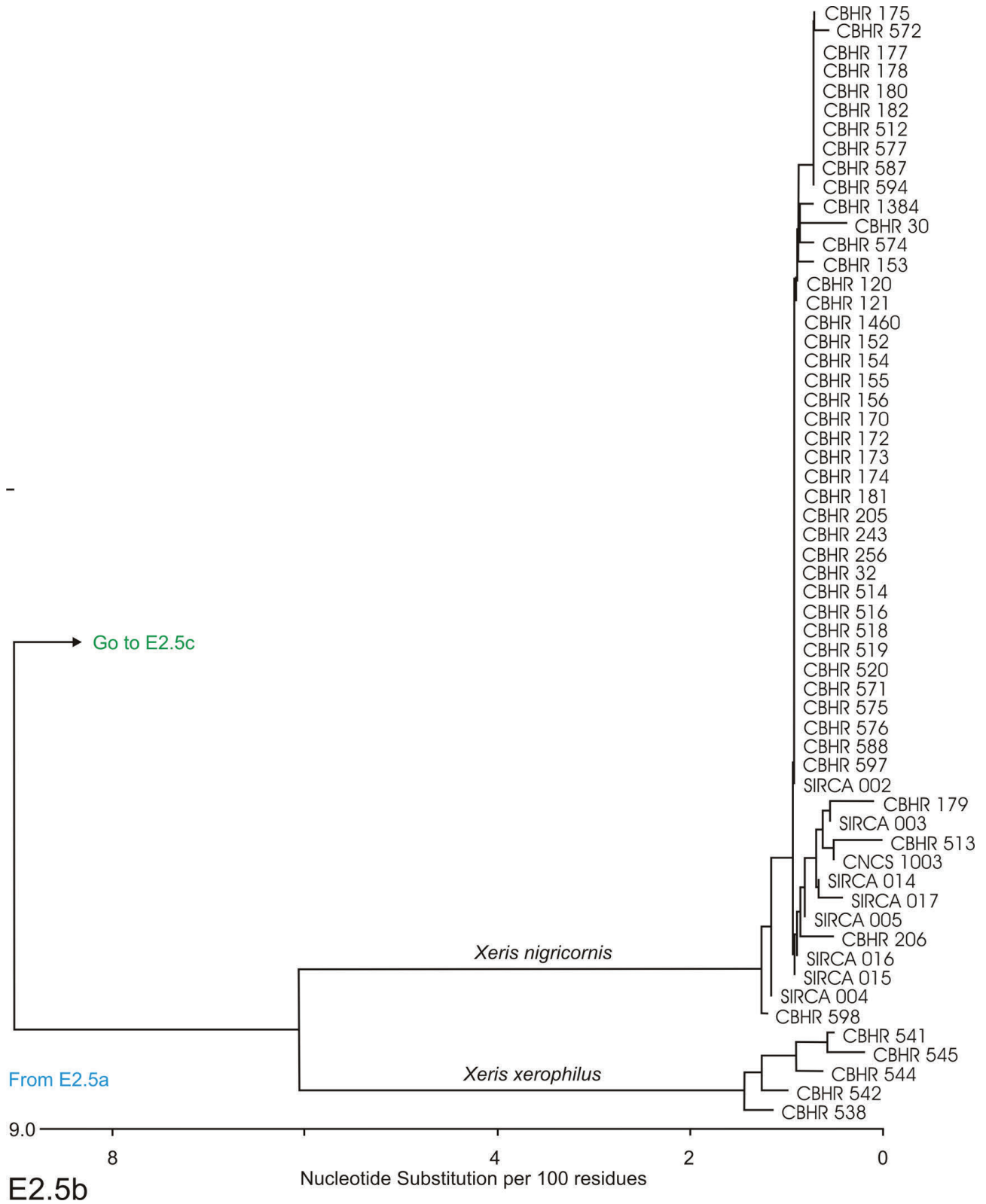


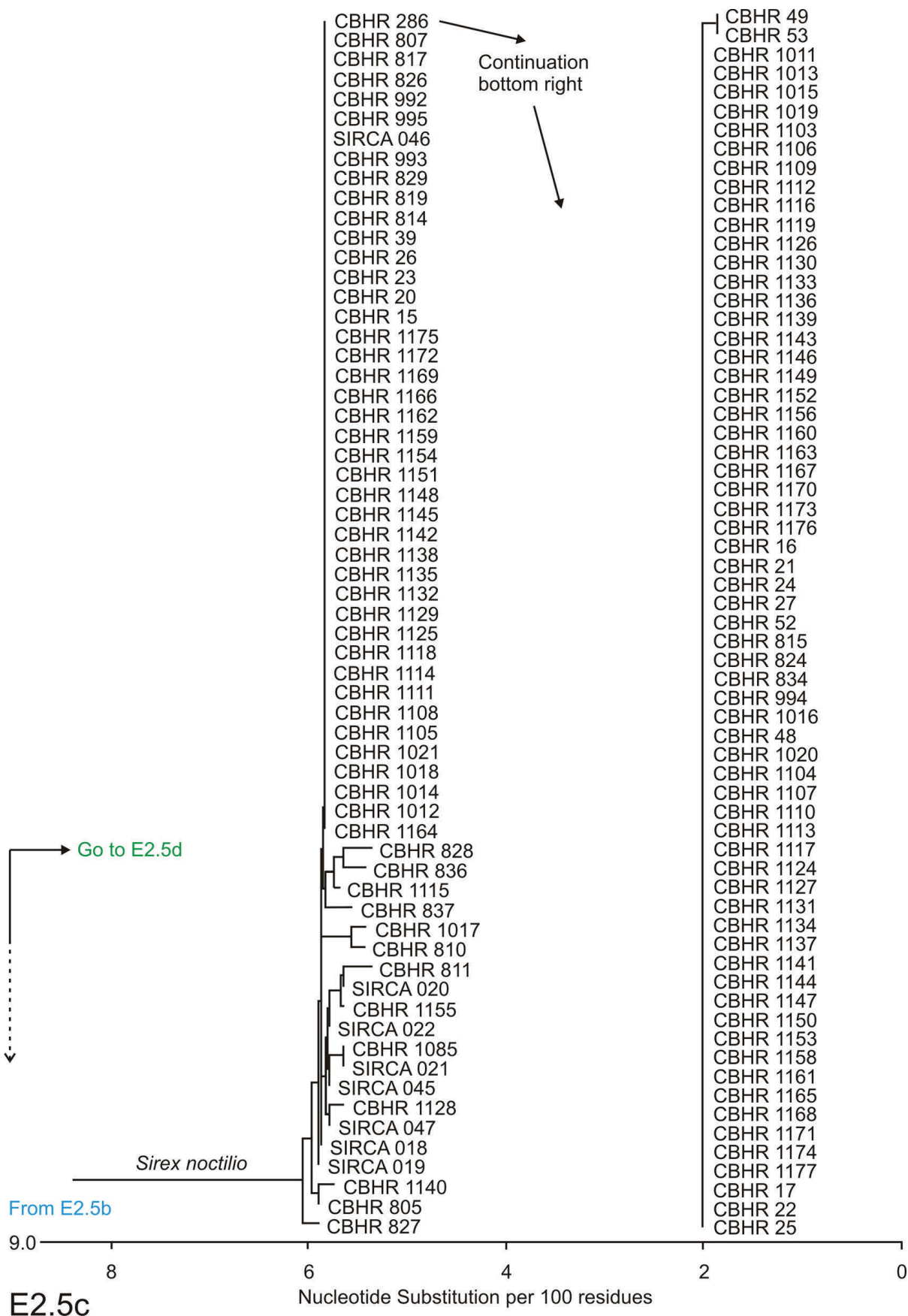


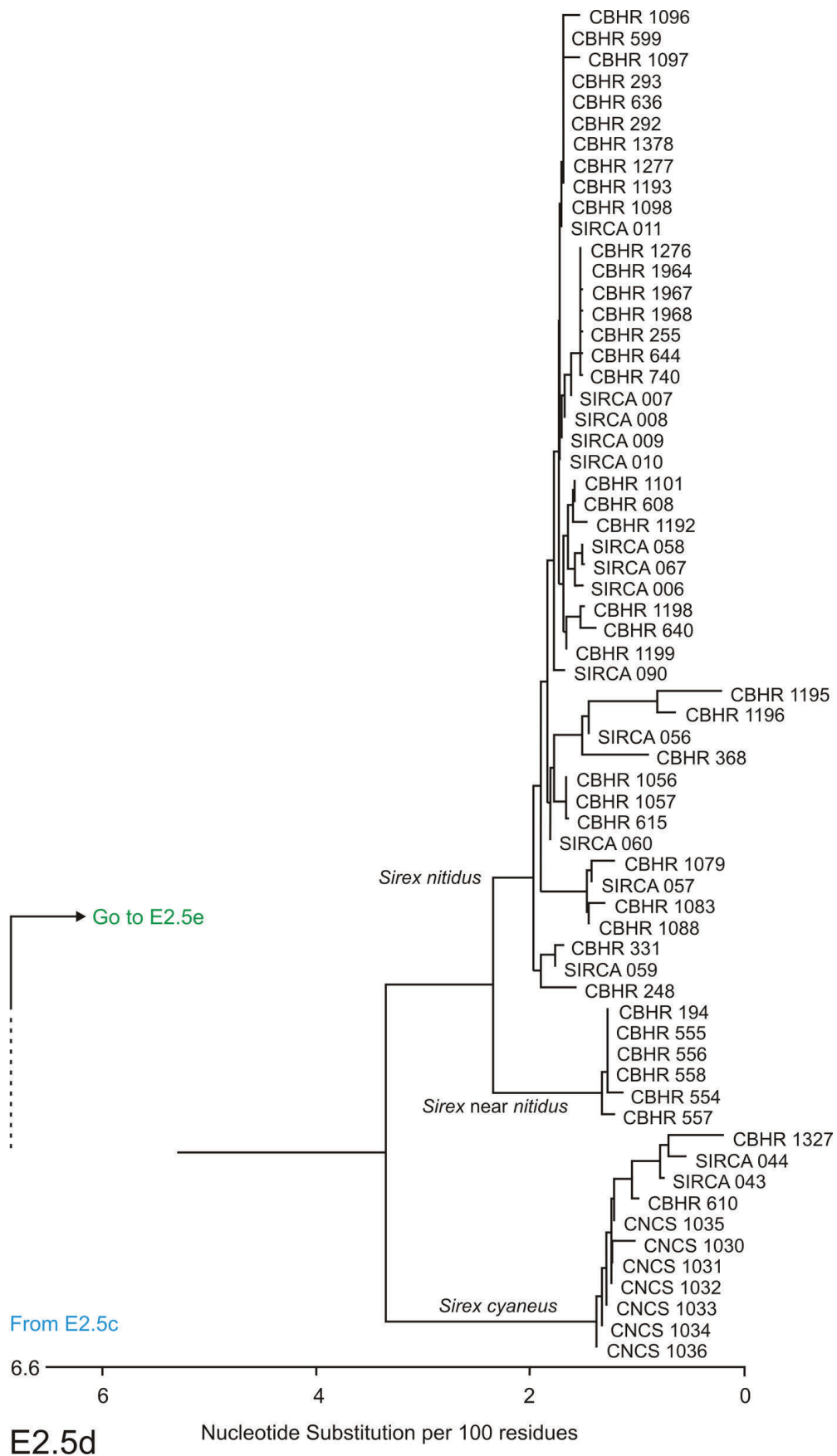


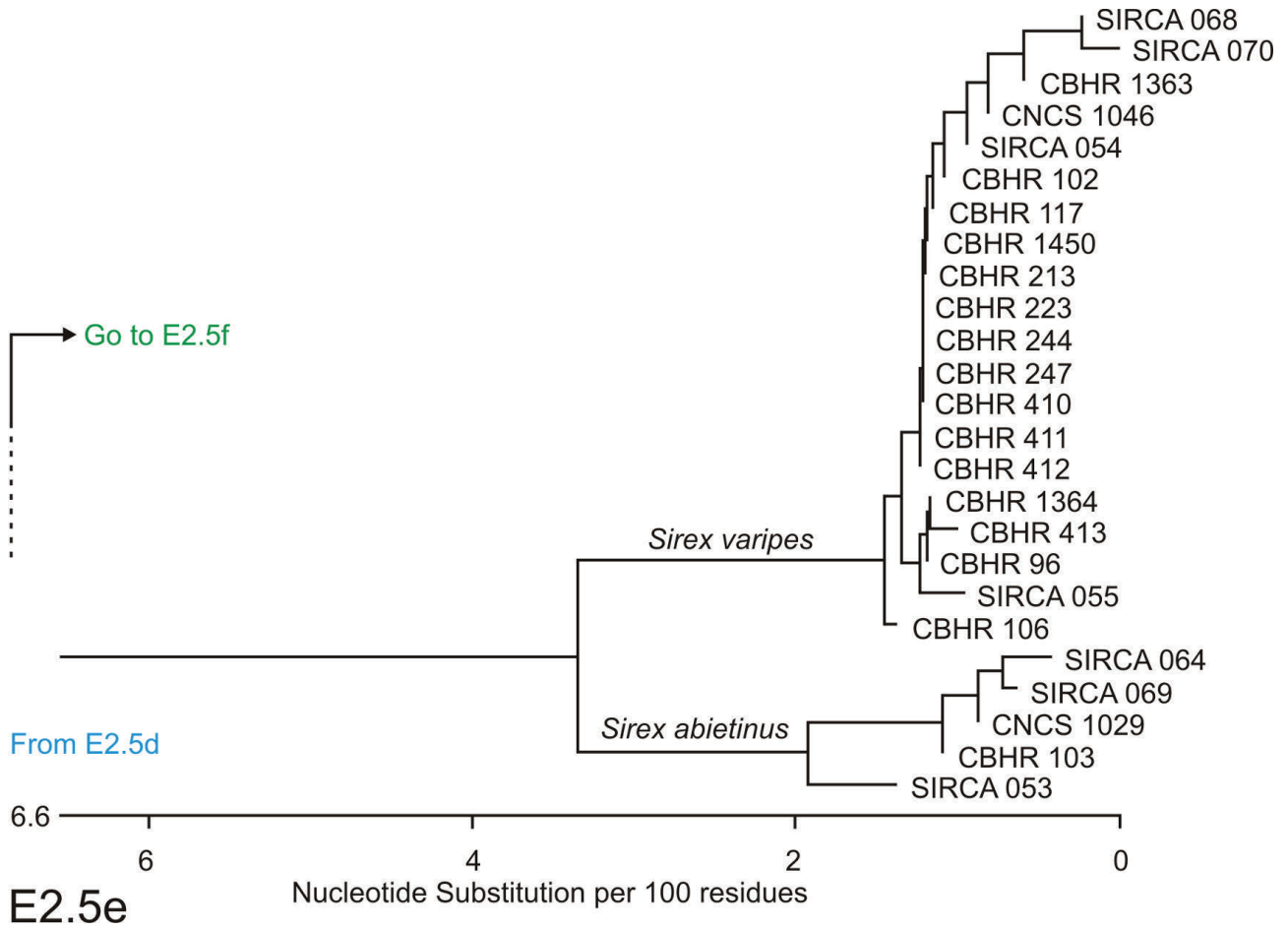


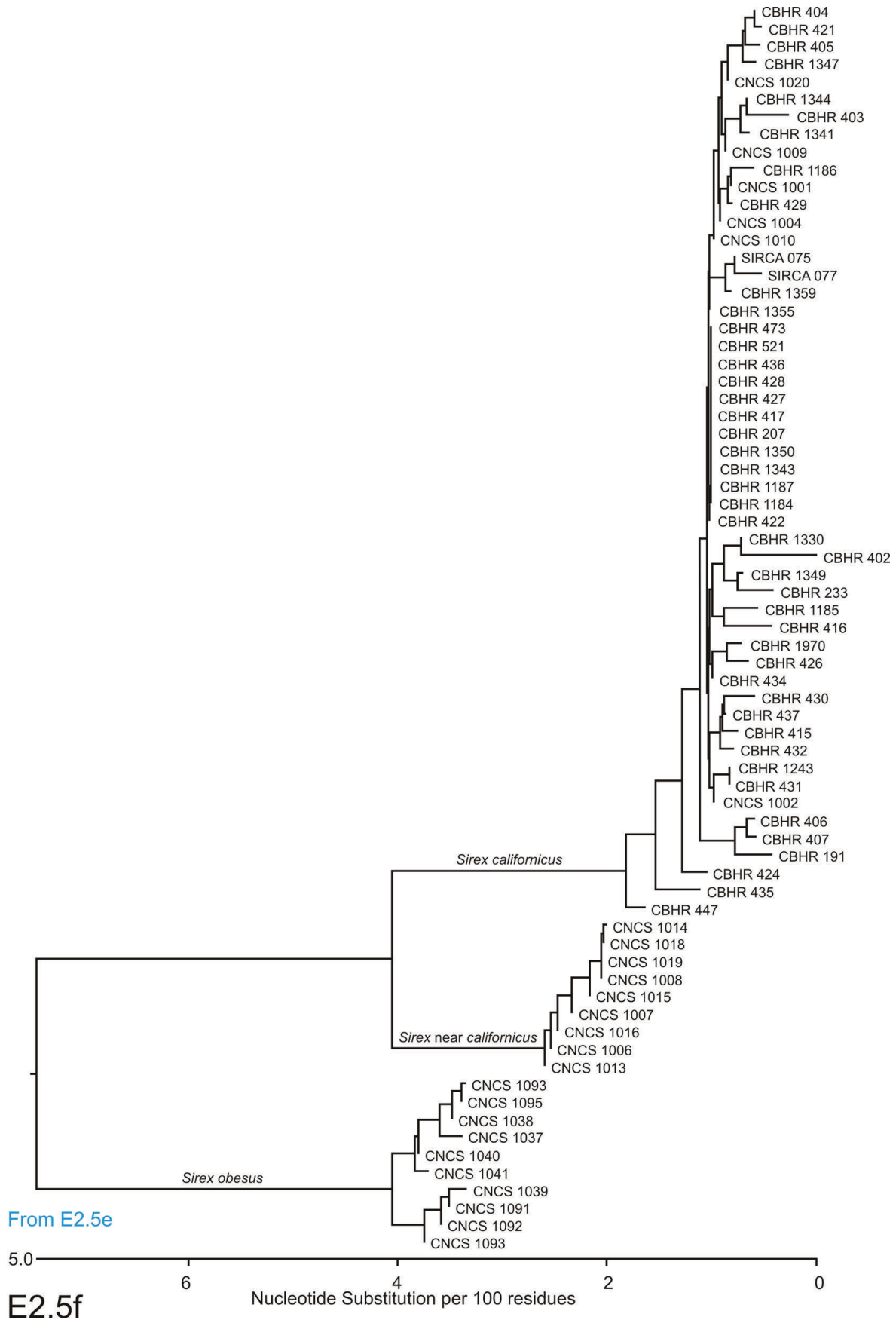












F. Acknowledgements

Many colleagues generously contributed various elements that helped us produce a comprehensive revision. We are most appreciative of and indebted for their support.

Systematic research is based on specimens stored in collections and looked after by conscientious colleagues. The quality of research is proportional to the number of specimens studied. We were fortunate to obtain a large number of them and are most thankful to the curators mentioned under “Materials and methods” that either facilitated our visit to their collection or sent us specimens on loan. With the establishment of *Sirex noctilio* in the Great Lake region, many surveys were carried out and long series of specimens were submitted to us for identification. We greatly appreciate the survey specimens of Siricidae generously given to us by H. Douglas (CFIA), D. Langor (NFRFC), the late P. de Groot, K. Nystrom and I. Ochoa (GLFC), L. Humble and J. Smith (PFRC), J. J. Jones (Alberta), J. Kruze (USFS–AK), D. Miller (USFS–GA), C. Piché (MNRQ), J. Sweeney and J. Price (FRLC), and K. Zylstra (USDA). These fresh and clean specimens permit us to study the DNA of significant specimens and enriched our collections.

We would like to thank A. Abel, A. Lancaster, C. Oberle, and C. Wilkins for assistance in the lab and with rearing specimens and the following who helped either with specimens or in the field: I. Aguayo, M. Allen, R. Bashford, L. Bezark, C. Brodel, M. Chain, K. Cote, D. Crook, E. Day, Y. DeMarino, P. Denke, D. Duerr, the Fish family, H. Hall, D. Haugen, S. Heydon, R. Hoebeke, B. Hofstrand, A. Horne, L. Humble, W. Johnson, V. Klasmer, R.L. Koch, B. Kondratief, J. Kruse, J. Labonte, P. Lago, E. Lisowski, V. Mastro, S. McElway, H. McLane, J. Meeker, D. Miller, A. and G. Mudge, D. Patterson, T. Price, J. Quine, L. Reid, V. Scott, C. Snyder, S. Spichiger, W. Tang, P. Tolesano, M. Ulyshen, M. Vardanega, G. Varkonyi, S. Vaughn, J. Vlach, and R. Westcott.

Traditionally, only morphological features were studied from specimens in collections. Lately, DNA sequencing of properly preserved specimens has opened a new set of characters previously unavailable. Many of the submitted specimens were freshly collected and offered us the opportunity to extract information from DNA barcodes (cytochrome *c* oxidase 1 – CO1). This new tool in conjunction with the classical morphological approach gave us much confidence in our conclusions. We greatly appreciate having access to specimens properly preserved for DNA sequencing provided by H. Douglas (CFIA), V. Grebennikov (CFIA), D. Langor (NFRFC), P. de Groot, K. Nystrom and I. Ochoa (GLFC), L. Humble and J. Smith (PFRC), and D. Miller (USFS–GA). We are also very grateful for support from the

Government of Canada through Genome Canada and the Ontario Genomics Institute in support of the International Barcode of Life Project. This funding allowed staff at the Biodiversity Institute of Ontario under the leadership of P. Hebert to sequence more than 300 specimens of Siricidae, and covered the costs in the preparation and digitization of specimen data by J. Fernandez–Triana. We also appreciate the time spent by A. Smith and J. Fernandez–Triana explaining details of the results to HG.

We intended this work to be profusely illustrated. We had access to lots of dried adults, but we wanted to show how they looked when alive. Unless properly equipped, finding live specimens of Siricidae is often difficult. We therefore thank P. de Groot (GLFC), J. Sweeney and J. Price (FRLC), and K. E. Zylstra (USDA) for providing live specimens of some species of Siricidae or their parasitoids for live habitus images. We also appreciated movies of parasites and Siricidae provided by J. Read (CNC).

Adults of Siricidae are easily damaged so we were worried about borrowing type specimens. We tried to study types during our visit to various North American collections but we did not have the opportunity to visit European collections. To avoid having types sent by post, we studied the description and previous opinions about each type. Then, we decided if photos of a type would be enough to resolve its identity. Through the kindness of G. Hancock (HMUG), J. E. Hogan (OXUM), L. Vilhelmsen (ZMUC), we were able to get the necessary pictures taken.

Much information came from many colleagues. The following colleagues kindly spent time trying to find specimens of unusual species in their respective collections, providing information about types whereabouts, and hand carrying of such specimens. We are very grateful to C. P. D. T. Gillett (BMNH), H. Vardal (Swedish Museum of Natural History), Y. Bousquet (CNC), V. Grebennikov (CFIA), G. Hancock (HMUG), J. Karlson (Swedish Malaise Trap Project), J. Genaro (Toronto, Ontario), M. Sharkey (Kentucky), A. Shinohara (EIHU) for their efforts. Because of widespread surveys around the Great Lakes, we had access to records of numerous locations for each species. We greatly appreciate not only the data but the coordinates, allowing us to map rapidly the range of many species within the survey area. For this information we are indebted to R. Favrin and L. Dumouchel (CFIA), R. Hoebecke (CUIC), S. Long (CUIC), K. Nystrom (GLFC), and C. Piché (MNRQ). Preparing this paper for the internet involved new knowledge with new software programs. We are most grateful for the training provided by J. Read (CNC) to C. Boudreault (CNC), and her help in designing various templates. In addition we thank L. Bearss (CNC) for training C. Boudreault in the use of a mapping program.

When problems arise there is nothing better than your closest colleagues to discuss them. We are much indebted to S. M. Blank (SDEI), L. Masner (CNC), A. Hajek (CUIC), and J. T. Huber (CNC). Sometimes questions go beyond Siricidae and even insects. We greatly appreciate detailed information provided by our esteemed botanical colleagues P. Catling and G. Mitrow (National Collection of Vascular Plants, Department of Agriculture, Ottawa), about the nomenclatural history of the black spruce as used in Europe in the first half of the 19th century. Finally, we thank the late R. Roughley (EDUM), G. E. Ball and D. Shpeley (UASM) for courtesies extended during our visits to their respective institutions.

At completion of a large manuscript, it is very difficult to see one's own errors in the text. Despite our efforts we missed numerous punctuation, grammatical mistakes, overly long sentences, sentences with missing words, and duplication of part of sentences during copy and

paste work. We are most thankful to reviewers, G. A. P. Gibson, J. T. Huber, S. A. Marshall, S. Blank, A. Liston, A. Taeger, R. A. Ochoa and T. J. Henry. We are especially thankful to J. T. Huber who read the text very critically three times. He rounded up most errors and insured a uniformity of style.

We would also like to thank the managers and staff for use of the following natural areas; Yazoo National Wildlife Refuge, Dahomey National Wildlife Refuge, Delta National Forest, Crossett Experimental Forest, Delta Experimental Forest.

This project was supported by a Forest Health Protection, Special Technology Development Program Grant to N. M. Schiff and A. D. Wilson and a CANACOLL Collection improvement grant to work on Siricidae in the Canadian National Insect Collection, Ottawa, Canada to N. M. Schiff.

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Appendix 1: Statistical data

Species (source)	Number of specimens	Length of annulus 10 relative to diameter of ovipositor at annulus 10					
		Mean	St. Dev.	+2 S.D.	-2 S.D.	Min.	Max.
<i>Sirex nitidus</i> (QC)	32	1.54	0.13	1.81	1.29	1.27	1.85
<i>Sirex nitidus</i> (AK)	30	1.65	0.12	1.87	1.39	1.43	1.76
<i>Sirex cyaneus</i> (NB)	40	1.57	0.12	1.82	1.33	1.30	1.77
<i>Sirex abietinus</i> (BC)	26	2.06	0.15	2.37	1.75	1.85	2.05

Table 1. Mean, standard deviation (values for 1, +2 and -2) and range for the proportion of the length of annulus 10 between pits 9 and 10 relative to the diameter of the ovipositor at annulus 10.

Species	Number of specimens	Length of basal relative to apical sheath sections					
		Mean	St. Dev.	+2 S. D.	-2 S. D.	Min.	Max.
<i>Sirex longicauda</i>	17	0.51	0.05	0.61	0.41	0.41	0.57
<i>Sirex areolatus</i>	28	0.66	0.07	0.79	0.53	0.49	0.75
<i>Sirex behrensii</i>	25	1.05	0.06	1.18	0.93	0.87	1.20
<i>Sirex nigricornis</i>	30	1.26	0.09	1.45	1.07	1.07	1.44
<i>Sirex noctilio</i>	30	1.170	0.06	1.28	1.05	1.06	1.31
<i>Sirex californicus</i>	30	1.17	0.07	1.32	1.03	1.06	1.35
<i>Sirex varipes</i>	53	0.98	0.03	1.05	0.91	0.87	1.09
<i>Sirex nitidus</i>	30	1.04	0.06	1.17	0.91	0.89	1.21
<i>Sirex cyaneus</i>	30	1.00	0.06	1.12	0.87	0.83	1.10
<i>Sirex abietinus</i>	28	0.87	0.06	1.00	0.74	0.73	0.97

Table 2. Mean, standard deviation (values for 1, +2 and -2) and range for the proportion of the length of the basal sheath section relative to the apical sheath section.

Species	Number of specimens	Length of sheath relative to length of fore wing					
		Mean	St. Dev.	+2 S. D.	-2 S. D.	Min.	Max.
<i>Sirex longicauda</i>	17	1.10	0.08	1.41	1.25	1.16	1.39
<i>Sirex areolatus</i>	28	0.84	0.09	1.21	1.03	0.82	1.23
<i>Sirex behrensii</i>	25	0.68	0.04	0.82	0.75	0.69	0.855
<i>Sirex nigricornis</i>	30	0.57	0.03	0.69	0.63	0.592	0.73
<i>Sirex noctilio</i>	30	0.61	0.03	0.74	0.67	0.60	0.74
<i>Sirex californicus</i>	30	0.58	0.05	0.79	0.69	0.55	0.78
<i>Sirex varipes</i>	53	0.70	0.03	0.83	0.77	0.68	0.90
<i>Sirex nitidus</i>	30	0.66	0.03	0.80	0.73	0.64	0.78
<i>Sirex cyaneus</i>	30	0.71	0.04	0.86	0.79	0.71	0.88
<i>Sirex abietinus</i>	28	0.65	0.07	0.95	0.80	0.63	0.97

Table 3. Mean, standard deviation (values for 1, +2 and -2) and range for the proportion of the length of the sheath relative to the length of the fore wing.

Species (source)	Number of specimens	Length of apical relative to basal sheath sections					
		Mean	St. Dev.	+2 S.D.	-2 S. D.	Min.	Max.
<i>Urocerus gigas</i>	9	1.40	0.02	1.48	1.31	1.34	1.45
<i>Urocerus flavicornis</i>	20	1.32	0.10	1.51	1.12	1.16	1.46

Table 4. Mean, standard deviation (values for 1, +2 and -2) and range for the proportion of the length of apical section of the sheath relative to that of the basal section of the sheath.

Species (source)	Number of specimens	Length of metatarsomere 2 relative to maximum height of metatarsomere 2					
		Mean	St. Dev.	+2 S.D.	-2 S. D.	Min.	Max.
<i>Urocerus flavicornis</i>	30	6.80	0.60	8.00	5.54	5.58	8.25
<i>Urocerus albicornis</i>	30	4.61	0.30	5.21	4.00	4.00	5.11
<i>Urocerus gigas</i>	21	5.38	0.45	6.27	4.50	4.5	6.27

Table 5. Mean, standard deviation (values for 1, +2 and -2) and range for the proportion of the length of the metatarsomere 2 relative to the maximum height of the metatarsomere 2.

Appendix 2: Revision to Schiff *et al.* (2006)

Schiff *et al.* (2006) published a key to genera and species of the North American Siricidae. Their excellent illustrations should help anyone without a reference collection trying to identify a specimen. However, the revisions below should first be made in the text.

Page 7, Figure 3 at centre is a *Urocerus* and at right a *Xeris*.

Page 16, There are several problems with the key, and it should be avoided. For instance, in key couplet 7 the antennal color for *Sirex juvencus juvencus* does not work at all (this is *S. nitidus* or a European specimen of *S. juvencus*); in couplet 9, *Sirex juvencus californicus*, should be *S. californicus* (the pale legged form of the species is not considered in the key and would key to *S. cyaneus* in couplet 10), and *Sirex edwardsii* is the dark color form of *S. nigricornis*.

Page 17, Figure 5 (top) is either *S. cyaneus* or *S. nitidus*.

Page 27, Figure (left) the metatibia and metafemur are oddly colored (the species cannot be recognized); figure (right) is either a *S. nitidus* or *S. varipes* because of spot on the mesotibia and mesotarsomeres 1 and 2.

Page 28. The figure is either *S. cyaneus* or *S. nitidus*.

Page 29. The figure is *S. nitidus* (based on the visible portion of the ovipositor).

Page 31. *Sirex edwardsii* is the dark color form of *S. nigricornis*.

Page 35. *Sirex juvencus californicus* should be *S. californicus*. Females exist in two color forms. The dark form is as in figures on pp. 36 and 37. The pale form is not illustrated but it resembles *S. cyaneus* or *S. nitidus*.

Page 39. The top figure is *S. cyaneus*, the left figure may be *S. cyaneus*, but it is not clear, the right figure is probably *S. juvencus* based on its antennal color pattern (a pattern that is almost never seen in North America). *Sirex juvencus* is not found in North America though it has been intercepted many times.

Pages 40 and 41. The image is either *S. cyaneus* or *S. nitidus*.

Page 56. The key to species of *Urocerus* is good, but the species name of couplet 11 should be interchanged.

Page 57. Figure 8. The caption should be reversed. The top image is *Urocerus albicornis* and the bottom image is *U. flavicornis*.

Page 80. The key is not clear enough as it attempt to segregate only three species of *Xeris*. Two of the species, *X. morrisoni* and *X. spectrum*, are complexes of two and three species respectively. We now know of seven species of *Xeris* for the region. The figures are clear, however.

Page 83. *Xeris morrisoni indecisus* should be replaced by *X. indecisus*. This is the pale color form of the species.

Page 87. *Xeris morrisoni morrisoni* should be replaced by *Xeris morrisoni*.

Page 91. The illustration is a male of the black form of *Xeris indecisus*, not of *X. spectrum spectrum*.

Pages 92 and 93. *Xeris spectrum spectrum* is either *X. melancholicus* or *X. caudatus*.

Pages 95 and 96. The illustrations are females of the black form of *X. indecisus* (*X. spectrum townesi* is a synonym).

Appendix 3: Disposition of Sequences

FASTA Sequences representing each of the 31 species of this study are deposited in Genbank and at the Center for Bottomland Hardwoods Research Web Site.

A set of zipped files can be downloaded from the CBHR site at the following URL: http://www.srs.fs.usda.gov/cbhr/products/downloads/2012_nms_SiricidFASTA.zip

The Genbank and Canadian accession numbers are as follows:

Sequence ID	Species name	Specimen code	Genbank accession number	Canadian collection specimen code
Seq1	<i>Eriotremex formosana</i>	CBHR4	JQ619784	
Seq2	<i>Orussus thoracicus</i>	CBHR35	JQ619785	
Seq3	<i>Sirex abietinus</i>	CBHR103	JQ619786	
Seq4	<i>Sirex areolatus</i>	CBHR377	JQ619787	
Seq5	<i>Sirex behrensii</i>	CBHR669	JQ619788	
Seq6	<i>Sirex californicus</i>	CBHR1184	JQ619789	
Seq7	<i>Sirex cyaneus</i>	CBHR610	JQ619790	
Seq8	<i>Sirex longicauda</i>	CBHR914	JQ619791	
Seq9	<i>Sirex near californicus</i>	CNCS1018	JQ619792	SIR 018
Seq10	<i>Sirex near nitidus</i>	CBHR555	JQ619793	
Seq11	<i>Sirex nigricornis</i>	CBHR30	JQ619794	
Seq12	<i>Sirex nitidus</i>	CBHR615	JQ619795	
Seq13	<i>Sirex noctilio</i>	CBHR815	JQ619796	
Seq14	<i>Sirex obesus</i>	CNCS1039	JQ619797	SIR 039
Seq15	<i>Sirex varipes</i>	CBHR104	JQ619798	
Seq16	<i>Sirex xerophilus</i>	CBHR541	JQ619799	
Seq17	<i>Syntexis libocedrii</i>	CBHR9	JQ619800	
Seq18	<i>Tremex columba</i>	CBHR5	JQ619801	
Seq19	<i>Tremex fuscicornis</i>	CBHR392	JQ619802	
Seq20	<i>Urocerus albicornis</i>	CBHR199	JQ619803	
Seq21	<i>Urocerus californicus</i>	CBHR2	JQ619804	
Seq22	<i>Urocerus cressoni</i>	CBHR169	JQ619805	
Seq23	<i>Urocerus flavicornis</i>	CBHR12	JQ619806	
Seq24	<i>Urocerus gigas</i>	CBHR842	JQ619807	
Seq25	<i>Urocerus taxodii</i>	CBHR31	JQ619808	
Seq26	<i>Xeris caudatus</i>	CBHR229	JQ619809	
Seq27	<i>Xeris indecisus</i>	CBHR216	JQ619810	
Seq28	<i>Xeris melancholicus</i>	CBHR300	JQ619811	
Seq29	<i>Xeris morrisoni</i>	CBHR190	JQ619812	
Seq30	<i>Xiphydria mellipes</i>	CBHR1055	JQ619813	
Seq31	<i>Xoanon matsumurae</i>	SIRCA188	JQ619814	SIR 193