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FRAXINUS BILTMOREANA AND *FRAXINUS SMALLII* (OLEACEAE), FOREST TREES OF THE EASTERN UNITED STATES

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ABSTRACT

Fraxinus biltmoreana Beadle and *Fraxinus smallii* Britton are recognized as species distinct from *F. americana* L., the white ash, closely following an earlier and informal delineation (Santamour 1962). Trees of *F. americana* sensu stricto are diploid, while those of *F. smallii* are tetraploid and those of *F. biltmoreana* are hexaploid. They differ by features of the fruits, leaf and twig vestiture, and shape and thickness of the petiole base; triploid and pentaploid hybrids apparently occur but are uncommon and probably sterile. *Fraxinus americana* (diploid) is more widely distributed to the west and north than the two polyploids, but the latter occur in 20 states of the eastern USA. *Fraxinus smallii* occurs from eastern Texas to Florida, north to Missouri, Ohio, and Pennsylvania; the range of *F. biltmoreana* is similar but it is rare in Arkansas, Louisiana, and Missouri and does not reach Texas. Differences in habitat appear to neglible or non-existent and two or all three of the species sometimes are encountered in close proximity. The distributions of *F. americana*, *F. smallii*, and *F. biltmoreana* are mapped at county level, and synonymy and typifications are provided for all three species. Other maps show the locations from which chromosome counts and estimates have been made. *Fraxinus albicans* Buckley, the Texas ash, and *F. pauciflora* Nutt., the swamp white ash, are similar in leaf morphology to the *F. americana* group and probably all are closely related among themselves.

KEY WORDS: *Fraxinus americana*, *Fraxinus biltmoreana*, *Fraxinus smallii*, *Fraxinus albicans*, *Fraxinus pauciflora*, Oleaceae, white ash

The taxonomic status of *Fraxinus biltmoreana* Beadle has been unsettled almost since its description in 1898, both with respect to its taxonomic rank and its biological reality. It has been treated as a synonym of *F. americana* L., as a variety of it (as *F. americana* var. *biltmoreana* (Beadle) J. Wright ex Fernald), or as a distinct species. Recent study suggests that both it and a closely related, mostly unrecognized entity should be treated at specific rank apart from *F. americana*.

Small (1933) treated *Fraxinus biltmoreana* as a separate species, as did Miller (1955, p. 41–42) in the most recent study of North American ash, who noted that “The presence of a papillose condition on the lower epidermis of the leaflets, coupled with “typical” red ash twigs characterized by acute terminal buds, reniform lateral buds, and truncate leaf scars, serves to distinguish *F. biltmoreana*. The heavy, terete bodies with strictly terminal wings differentiate the samaras from those of any other eastern North American ash, although they resemble most closely the samaras of *F. americana*.” Fernald (1950) recognized var. *biltmoreana*, noting the difference in vestiture and also the larger samaras, and var. *biltmoreana* was mapped separately from *F. americana* sensu stricto by Radford, Ahles, and Bell (1968) and Cooperrider (1995).

Wallander (2008) included an arboretum-grown sample of *Fraxinus biltmoreana* in her molecular-phylogenetic study and found that it did not cluster with *F. americana* sensu stricto. She implied that the phyletic disparity might reflect an origin of *F. biltmoreana* as a hybrid between tetraploid *F. americana* and diploid *F. pennsylvanica* Marsh., as earlier hypothesized by Miller (1955). At the end of the description of *F. americana*, Gleason and Cronquist (1991) referred to *F.*

biltmoreana as "a ± pubescent, chiefly southern form, perhaps reflecting hybridization with [*F. pennsylvanica*]."

In contrast, Little (1952) and Hardin and Beckmann (1982) did not recognize *Fraxinus biltmoreana* as formally distinct from *F. americana*. Hardin (1974) treated *F. americana* as a polymorphic species (including *F. biltmoreana*) without segregate species or infraspecific taxa. Schlesinger (1990) observed that white ash is a polyploid species and included *F. biltmoreana* simply as a synonym of *F. americana*; he did not mention the tetraploids with regard to any aspect of variability within the species. Wilson and Wood (1959) noted that "The status of *F. biltmoreana* Beadle is in need of further investigation."

Remarkably, the variation pattern within *Fraxinus americana* sensu lato was accurately described almost 50 years ago by Santamour (1962), built upon earlier discoveries by Wright (1945, 1957) that diploids, tetraploids, and hexaploids were widely distributed through the geographical range of white ash. Santamour found each ploidy level to be distinct in a combination of bud morphology, petiole morphology, and stem and leaf vestiture. He restricted the concept of *F. americana* to the diploids, recognizing the hexaploids and tetraploids together as *F. biltmoreana*. Confirmed here is the observation that the hexaploids and tetraploids, while more similar to each other than is either to *F. americana* sensu stricto (the diploids), are distinct from each other. The concept of *F. biltmoreana* is restricted to the hexaploids and the tetraploids are recognized as *Fraxinus smallii* Britton.

Rationale for recognition of *Fraxinus biltmoreana* and *Fraxinus smallii*.

Most collections of *Fraxinus americana* sensu lato can be identified by morphological features as one of the three ploidal taxa. The geographic range of the diploids (*F. americana* sensu stricto) completely encompasses that of hexaploids as well as the tetraploids and all three occur sympatrically in a large area of east-central USA. (Figs. 1, 2, 3 and 4, 5, 6). Intermediacy is uncommon or rare and thus it appears that the ploidal differences provide effective isolating mechanisms. Hexaploid/tetraploid crosses and tetraploid/diploid crosses would produce pentaploid and triploid offspring, respectively, which presumably would be infertile. It is possible that the tetraploids arose through a cross between *F. biltmoreana* (6x) and *F. americana* (2x), but the present evolutionary independence of the tetraploid entity is indicated by its wider westward geographical distribution (Figs. 2, 3), beyond that of the hexaploid. Further, the tetraploids are characterized by a flavonoid profile that is more than a simple combination of those from *F. americana* and *F. biltmoreana* (see comments below).

Morphological distinction and evolutionary independence (reproductive isolation) are generally regarded as criteria for the recognition of distinct species. Treatment of the sympatric diploids, tetraploids, and hexaploids of white ash at infraspecific rank within a single species does not recognize their apparent genetic isolation, as indicated by their sympatric distribution and non-intergrading morphology. Each of *Fraxinus americana*, *F. biltmoreana*, and *F. smallii* is morphologically distinct and apparently reproductively isolated, and each is treated here as a separate species. *Fraxinus biltmoreana* and *F. smallii* are more similar to each other in morphology and flavonoid profile than is either to *F. americana*. Morphological and molecular differences are discussed in detail below.

Hybrid origin of *Fraxinus biltmoreana* and *Fraxinus smallii*.

The hypothesized evolutionary origin of *Fraxinus biltmoreana* is analogous to that of *F. profunda* (Bush) Bush, also of the eastern USA — both are hexaploids and both are speculated to have originated through hybridization between *F. americana* and *F. pennsylvanica* (Miller 1955; Wright 1965). *Fraxinus profunda* is generally accepted as a distinct species (e.g., Nesom 2010a), although Miller (1955, p. 47) noted that "it is not clearly differentiated from the red ash [*F. pennsylvanica*] by a group of correlated morphological characteristics, but only by a series of 'gigas' characteristics." Samaras of *F. profunda* are similar to those of *F. smallii* and *F. biltmoreana* — all of large size and with bodies that tend to be dark orange at maturity.

Support in molecular evidence for the hypothesis of hybrid origin of both the hexaploid (*Fraxinus biltmoreana*) and tetraploid (*F. smallii*) white ashes, as well as the distinction of both, was provided in a study of leaf flavonoids by Black-Schaefer and Beckmann (1989). They found that each of the diploid, tetraploid, and hexaploid expressions of *F. americana* sensu lato is distinct in flavonoid profile. The hexaploids and tetraploids produce four compounds present in *F. pennsylvanica* but not in *F. americana* (diploid); on the other hand, three compounds in diploid *F. americana* do not appear in either of the polyploids, and two compounds in the tetraploids and one in the hexaploids do not appear in either *F. americana* or *F. pennsylvanica*. The samples in their study were from "trees in natural populations in central North Carolina;" no vouchers were cited, but these samples apparently were from the same locality as an earlier study (Black & Beckmann 1983), north of Raleigh in Granville County (R.L. Beckmann, pers. comm. 2009).

Morphological evidence for intermediacy of *Fraxinus biltmoreana* between *F. americana* and *F. pennsylvanica* was presented in tabular form by Miller (1955, Table 14). *Fraxinus smallii* is similar to *F. biltmoreana* in intermediacy of the same features. Both of the polyploid white ashes have papillose abaxial epidermal surfaces (Hardin & Beckmann 1982; Williams & Nesom 2010) and terete samara bodies like those of typical *F. americana*; in contrast they have mostly reniform lateral buds and shield-shaped leaf scars with truncate to slightly concave upper margins like *F. pennsylvanica* (compare Fig. 15). In the phylogenetic study by Jeandroz et al. (1997), *F. biltmoreana* is positioned as sister to the western *F. latifolia*.

Why the late recognition of *Fraxinus smallii*?

Prior attention to variation in *Fraxinus americana* has been focused mainly on *F. biltmoreana*, which is conspicuously distinguished by the characteristic vestiture of the twigs and leaves. Except in the comments of Santamour (1962), the tetraploids have been overlooked as an evolutionarily distinct variant, even when *F. biltmoreana* has been recognized as distinct from *F. americana*. The abbreviated form of Santamour's report, without maps, illustrations, or other critical documentation, perhaps led to its limited consideration in subsequent studies and floristic summaries. East of the Mississippi River, where all three of the ploidal expressions occur, observation of the tetraploid has simply been missed, even though it has morphological features of *F. biltmoreana*, except for vestiture, when contrasted with *F. americana*. Descriptions of deeply concave leaf scars in *F. americana* have discounted or ignored the significant variation introduced when the concept of the latter included tetraploids. Avowals that the three ploidy levels are morphologically indistinguishable (e.g., Armstrong 1982; Black & Beckmann 1983) either ignored Santamour's observations or were meant implicitly to take issue with it.

Early studies by Wright perhaps discouraged closer investigation of *F. americana*. He noted (1944a, p. 495) that "the Biltmore ash (*F. biltmoreana*) and the white ash (*F. americana*), now recognized as distinct species differing only in pubescence, need not be separated, either in taxonomy or in silviculture." This reflected his reliance on pubescence as the primary feature for the distinction of Biltmore ash and his observation that various glabrous parental individuals in his study produced pubescent progeny and that from one individual he identified as *F. biltmoreana*, more than half of the progeny were glabrous. "There was a high incidence of pubescence in the progenies of both glabrous and pubescent parents of the southern and intermediate ecotypes." As noted by Miller (1955), however, the progeny evaluated by Wright were only 2 years old, scored for "pubescence of the petiole and lower surface of the leaf." Santamour (1962) observed that "these seedlings at 2 years probably had not yet developed all their normal morphological traits."

Wright (1944a) concluded that polyploids had developed within *Fraxinus americana* sensu lato only after the differentiation of southern, intermediate, and northern ecotypes, since he found "no evident correlation between the degree of polyploidy and any gross morphological or physiological characters." In contrast, Clausen et al. (1981) were not able to recognize regional ecotypes in *F. americana*, but they did find that "ploidy variation accounted for most of the difference in fruit length, seed width, seedling height, and date of leaf fall."

Chromosome numbers/ploidy levels.

Wright (1944a) solicited seeds of *Fraxinus americana* sensu lato from various localities (each "locality" = "one limited geographical area," characterized in his report only by state and county) and grew progenies of 155 parental trees from 28 localities in 9 states of the eastern USA and Canada. From among these, he made chromosome counts from root tips of seedlings from 24 of the parents; for 39 other parents he estimated the chromosome number from measurements of mean guard cell length. In summarizing the geographic distribution for these 63 reports, he did not distinguish between actual chromosome counts and estimations. To this total of 63, he later added root tip chromosome counts from 9 others (6 diploids, 3 tetraploids) from other localities (Wright 1957). Wright's counts and estimations and their localities are summarized here (Appendix 1a).

Santamour (1962) sampled from one of the several test plantations of white ash earlier established by Wright (1944a) — in the Morris Arboretum in Philadelphia, Pennsylvania — which included "161 trees from 60 mother trees in 12 states throughout the range of *F. americana*." He made root tip chromosome counts that included 8 diploid and 9 tetraploid individuals from among 17 sets of progenies (of the original 60); estimates of ploidy levels, from measurements of guard cell length, of other individuals of each the same progenies agreed with the actual counts. From elsewhere on the Morris Arboretum grounds, Santamour's study of morphology also included trees previously determined by Wright as hexaploid and that "fitted the description of *F. biltmoreana* in all characters, including pubescence."

Schaefer and Miksche (1977) and Leser (1978) studied progeny of trees from 18 states and found diploids, tetraploids, and hexaploids (Appendices 1b, 1c), based primarily on estimates of ploidy level from photometrically determined nuclear DNA content from root tip cells of germinating embryos. Three embryos per tree were combined on a single slide. The estimate from one tree from Clark Co., Indiana, was pentaploid (Schaefer & Miksche 1977) and Leser (1978) also made similar "subhexaploid" estimates from individuals from Indiana, Louisiana, South Carolina, and Tennessee – – the alternative hypothesis that these were dysploid in chromosome number needs to be tested. In a study by Clausen et al. (1981, p. 94, 95), the authors noted that "Seeds were collected from up to 10 native parent trees in each of 59 locations [in five regions of the United States]. … Ploidy levels of 98 parent trees were determined cytophoto-metrically on the basis of DNA content by Schaefer and Miksche (1977) and Leser (1978)." Clausen et al. apparently made no new counts or estimates, apparently basing their study on the combined data of Schaefer and Miksche and Leser.

In connection with a study of wood characteristics of white ash, Armstrong and Funk (1980) made estimates of ploidy from trees from 7 general localities (by county) in 7 states. For the photometric determinations, they used tissue from the bark (phellogen, phelloderm, and cortical cells) of 2-year old seedlings from which they also made wood sections and macerations (see comments below). They found putative diploids, tetraploids, and hexaploids as well as possible triploids and pentaploids (Appendix 1d). Confirmatory chromosome counts were not made.

Black and Beckmann (1983) studied 25 white ash trees from east-central North Carolina (Granville Co.) and found pistillate and staminate individuals of diploids, tetraploids, and hexaploids "within immediate proximity of one another." One tree (no. 15) was estimated to be pentaploid, based on its intermediacy in nuclear DNA value; if this were confirmed, it apparently is the only putative pentaploid mature tree identified in studies that have provided chromosome counts or estimates of ploidy — other pentaploid estimates have come from germinating samaras. Among progeny from one diploid, pistillate, open-pollinated tree was one embryo (of total 30) estimated to be triploid, and among progeny from one open-pollinated tetraploid tree were nine embryos (of total 30) estimated to be pentaploid. Putative triploid and pentaploid seedlings also were grown by Armstrong and Funk (1980). Ploidy levels were estimated in the Black and Beckmann study from photometrically determined nuclear DNA content of leaf tissue, confirmed by chromosome counts from representative individuals (diploid, tetraploid, hexaploid).

Guard cell size was used by Wright (1944a, p. 494) in distinguishing diploids, tetraploids, and hexaploids, after "Preliminary work had shown sufficient correlation between degree of polyploidy and stomata size to make this approximation possible." He did not give cell measurements. Santamour confirmed the stomatal distinction between diploids (guard cell length averaged 16.8 ±1.1 microns) and tetraploids (guard cell length averaged 22.6 ±0.9 microns). Seemingly in contrast to his contemporary paper, Wright (1944b) noted that guard cell size variation in field-grown trees made estimates of ploidy unreliable. Hardin and Beckmann (1982, p. 136) commented that "Stomatal sizes are variable, and although the largest are in the polyploids, there is too much overlap in size to use this as a reliable characteristic for identification of ploidy in natural stands."

Chromosome counts and estimates of ploidy level are summarized in the maps of Figs. 4, 5, and 6, which show the localities (counties) where populations were sampled.

Wood characteristics.

Armstrong and Funk (1980) studied wood of 2-year-old white ash seedlings grown from seeds from various states and found that diploids from the southernmost seed source (Arkansas) produced slightly longer vessel elements and fibers than diploid trees from northern sources. Polyploid individuals produced the longest vessels and fibers.

In a more detailed follow-up, Armstrong (1982) studied wood variation in white ash from southern Illinois from 10 trees, including diploids, tetraploids, and hexaploids, as determined by cytophotometric methods. There were no differences in relative density but both the vessel elements and fibers of the tetraploid and hexaploid trees were longer than those of the diploids. The tetraploid and hexaploid vessel elements were 27% and 43% longer, respectively, and the tetraploid and hexaploid fibers were 18% and 41% longer.

Other differences.

Clausen et al. (1981) found that ca. 2-year-old nursery-grown tetraploids retained their leaves longer and were significantly taller than nursery-grown diploids and hexaploids. Pentaploids and hexaploids had the slowest growth in the nursery.

In a study of seedlings grown in the experimental nursery of the Harvard Forest in Massachusetts, Wright (1944) identified three ecotypes in *Fraxinus americana*, as distinguished by features of winter hardiness, root system morphology, and leaf vestiture and pigmentation: (1) the northern ecotype, from Michigan to central Pennsylvania and New England and northward; (2) the intermediate ecotype, in a narrow belt through southern Pennsylvania, northern West Virginia, and Ohio; and (3) the southern ecotype, all of the eastern USA south of the "intermediate belt." He found that "there were no apparent differences in growth rate, winter hardiness, or morphological characters which could be associated with the differences in chromosome number." Because the pattern of ecotypic variation seemed to Wright to be developed independently of the ploidal variation, he saw the polyploidy as "of rather recent origin, having arisen since the ecotype differentiation." Wright's conclusions regarding the ecotypical differentiation were not confirmed by Clausen et al. (1981), who noted stronger indication of clinal variation and the effects of ploidy.

Schlesinger (1990) noted other elements of variation: "White ash contains several phenotypic variants of leaf form that appear to be genetically controlled even though they are randomly distributed throughout the natural range. Chief among these are 9-leaflet, narrow-leaflet, blunt-leaflet, ascidiate leaflet, partially pubescent, purple-keyed, and crinkle-leaf forms. A purple leaf variant is vegetatively propagated and grown as an ornamental."

Large-fruited variants in the northeastern USA.

Scattered through New England, westward from Pennsylvania to Indiana, and south along the Appalachian backbone in North Carolina and Tennessee (Fig. 1) are trees of *Fraxinus americana* with glabrous twigs and leaves and the petiole morphology of diploids but with samaras of the same size class as polyploids. These have been mapped as diploids in the present study, weighting the petiole feature, but the biological nature of these individuals is unknown.

Only diploids are known from New England, but too few chromosome counts and estimates have been made to rule out the possibility that these large-fruited trees might be polyploid (distinct in origin from *Fraxinus smallii*?), especially if they are uncommon variants in areas where diploids of typical morphology are common.

Fraxinus albicans and *F. pauciflora* share diagnostic features of the *F. americana* group.

Fraxinus albicans Buckley (synonym = *F. texensis* (A. Gray) Sarg., the Texas ash) is similar to *F. americana* in its papillose abaxial leaf surfaces and samaras with terete bodies and the two have sometimes been treated as conspecific. The taxonomy and distribution of *F. albicans*, as distinct from *F. americana*, are discussed in detail in Nesom (2010b) but variation in samara morphology and leaf scar morphology are shown here (Figs. 7, 13) to contrast with others of the *F. americana* group. A chromosome number has not been reported for *F. albicans* but the relatively small fruits and leaves suggest that it is diploid.

Wallander (2008) found that her two samples of *Fraxinus albicans* (identified as *F. texensis*) grouped with the red ash (*F. pennsylvanica*) complex rather than with any of the *F. americana* samples and thus observed that "presence or absence of epidermal papillae appears not to be phylogenetically informative in [sect. *Melioides*]." The highly distinctive leaf morphology, however, strongly suggests that *F. americana* and its North American relatives comprise a monophyletic group within sect. *Melioides*, and the identy of Wallander's molecular vouchers needs to be confirmed. A morphological survey of the whole genus, including Old World species, at MO indicates that only one other species of *Fraxinus* produces the distinctive features of the abaxial leaf surface.

Fraxinus pauciflora Nutt. of Florida and Georgia also has papillose abaxial leaf surfaces like those of *F. americana* (Nesom 2010c). Two other wetland species of Florida and the southeastern USA, the water ashes *F. caroliniana* Mill. and *F. cubensis* Griseb., appear to be closely related to *F. pauciflora* and the latter is hypothesized to be of hybrid origin, incorporating a white ash genome. The abaxial leaf surfaces of *F. caroliniana* and *F. cubensis* are similar to those of *F. pennsylvanica*, which lack a cuticular overlay.

Description of a papillose abaxial leaf surface in *Fraxinus papillosa* Lingelsh. was based on a different micromorphology than that of *F. americana*. *Fraxinus papillosa* is very closely related to *F. velutina* Torrey (Williams & Nesom 2010), and perhaps not even specifically distinct.

Relationship of *Fraxinus uhdei*.

Fraxinus uhdei (Wenzig) Lingelsh., native to Belize and Guatemala and northward in temperate Mexico to Veracruz, Puebla, and Querétaro, was originally described as a variety of *F. americana* (Wenzig 1883), apparently based on similarities in samara morphology. The abaxial leaf surfaces of *F. uhdei*, however, lack the papillose cuticular structure characteristic of *F. americana* and its presumed closest relatives in eastern North America. In Wallander's phylogenetic reconstruction, *F. uhdei* is a member of sect. *Melioides* and is sister to the red ash complex. Sect. *Melioides*, which is a clearly defined monophyletic group, comprises the white ash and red ash complexes, all taxa of which are native to North America.

Key to the species of the *Fraxinus americana* group.

Morphology of samaras and petiole bases/leaf scars is shown in Figs. 7–9 and 10–13.

1. Trees of swamp habitats; samara wings arising from near base of body .... **Fraxinus pauciflora**
1. Trees of upland habitats; samara wings arising from distal portion of body.

  2. Leaflet blades mostly 3–6(–8) cm, suborbicular-ovate to obovate, oblong-ovate, or elliptic, apex abruptly acute to rounded, base rounded; rachis (1–)2–6(–7) cm; leaf scars 2.5–3(–4) mm wide .... **Fraxinus albicans**
  2. Leaflet blades mostly 5.5–12(–15) cm, ovate to ovate-lanceolate or elliptic-lanceolate, apex acute-acuminate or less commonly obtuse, base cuneate to rounded; rachis 4–12 cm; leaf scars 3–4 mm wide.

    3. Petiole bases and leaf scars V- to U- or crescent-shaped with a deeply concave or notched apex; samaras (19–)25–32(–38) mm, wings 3–5(–6) mm wide, bodies (5–)6–11 x 1.5–2.5 mm; twigs, petioles, petiolules, and rachises glabrous .... **Fraxinus americana**
    3. Petiole bases and leaf scars oblong-obovate to widely obovate with a nearly truncate apex; samaras (32–)33–54 mm, wings (4.5–)5–8 mm wide, bodies (7–)10–15 x 2–4 mm; twigs, petioles, petiolules, and rachises glabrous or hirtellous to hirtellous-puberulent to tomentulose.

      4. Twigs, petioles, petiolules, and rachises glabrous; samaras (32–)36–44 mm, wings (4.5–)5–7 mm wide, bodies (9–)10–13 x 2–3.5 mm .... **Fraxinus smallii**
      4. Twigs, petioles, petiolules, and rachises sparsely to densely hirtellous to hirtellous-puberulent or tomentulose; samaras 33–54 mm, wings 6–8 mm wide, bodies (7–)11–15 x 2–4 mm .... **Fraxinus biltmoreana**

Comments on identification.

The most easily observable diagnostic feature among the upland taxa is the vestiture of *Fraxinus biltmoreana*, where the twigs, petioles, and leaf rachises are densely puberulent-tomentose (Fig. 12). Those of *F. americana* and *F. smallii* are glabrous to glabrate (Figs. 10, 11). In my observations, the correlation has been perfect between puberulent vestiture and the characteristic petiole base and samara size of the polyploids, apparently confirming the observations of Small, Fernald, Miller, Santamour, and others as noted above.

Wright (1944), however, made apparently contradictory observations regarding vestiture and concluded that *Fraxinus biltmoreana* could not justifiably be recognized as a distinct species. In observations of petioles and abaxial leaf surfaces of 2-year-old seedlings, he found that more than half of the seedlings among progeny of a pubescent parent from Indiana were glabrous. Similarly, he encountered pubescent progeny among seedlings from glabrous parents. Miller (1955) and Santamour (1962) reckoned that this unexpected variation (compared to the pattern predicted in mature trees) was associated with the juvenile nature of the seedlings studied by Wright.

The petiole bases and leaf scars in *Fraxinus americana* are V- to U- or distinctly crescent-shaped, with the lateral buds situated in the deep notch of the petiole base (Fig. 10). In *F. smallii* and *F. biltmoreana* the petiole bases and leaf scars are oblong-obovate to widely obovate with a nearly truncate apex, with the lateral buds at the top of the nearly truncate petiole base (Figs. 11, 12). This feature is particularly useful as it appears to consistently separate the glabrous diploids (*F. americana*) and tetraploids (*F. smallii*), especially when fruits are not available.

Bud morphology has been used in some discussions as a feature diagnostic among these species (e.g., especially Miller 1955). Terminal buds of *Fraxinus americana* are said to be "obtuse, ovoid" — vs. apiculate in *F. biltmoreana*, lateral buds of *F. americana* triangular and apically acute –– vs. rounded to reniform in *F. biltmoreana*. These distinctions, however, appear to be subtle and apparently not consistent enough for diagnostic use.

Contrasts in samara morphology between *Fraxinus americana* and *F. smallii* in Texas, Louisiana, and Arkansas are shown in Fig. 8. Samaras of *F. americana* from east of the Mississippi River appear to be slightly more variable in size; those from the northeastern USA perhaps are of two size classes (see comments above). Collections unambiguously identified as *F. biltmoreana* show samaras (Fig. 9) similar to those of *F. smallii*. In samaras of the tetraploids and hexaploids, wings are longer and wider and the bodies thicker compared to typical (diploid) *F. americana*.

Leser (1978) found that the average weight of hexaploid samaras was distinctly greater than that of the diploids, reflecting the evident difference in size. Average weight of the tetraploid samaras was intermediate between the diploid and hexaploid but, perhaps because of the low sample size for tetraploids in Leser's study, the differences were not statistically significant.

Taxonomy.

FRAXINUS SMALLII Britton, N. Amer. Trees, 805, f. 735. 1908. **TYPE**: USA. Georgia. Gwinnett Co.: Yellow River near McGuire's Mill, 750 feet, 2 Aug 1895, *J.K. Small s.n.* (holotype: NY! digital image!; isotype: GH!). Annotated as "*Fraxinus americana* L." by G.N. Miller, 25 May 1951.

Fraxinus americana var. *subcoriacea* Sargent, Bot. Gaz. 67: 241. 1919. **SYNTYPES**: USA. Massachussetts. Suffolk Co.: Boston, cultivated at the Arnold Arboretum in Jamaica Plain, 10 Oct 1905, collector not specified (AA 283679!, AA 73800!).

The protologue: "What may be considered the type of the variety has been growing in the Arnold Arboretum since 1874, where it was raised from seed sent by W.C. Hampton from Mount Victory, Harding County, Ohio, as 'Fraxinus C'."

In reference to var. *subcoriacea*, Sargent noted in the protologue that "The trees of this variety have grown more rapidly and are handsomer than any of the other American ashes in the collection. … These trees are so distinct in appearance and in their more rapid vigorous growth that it seems desirable to give them a varietal designation. … Individual trees of *F. americana* occur with thick, oblong-ovate, acuminate, entire or slightly serrate leaflets dark green and lustrous above, silvery white below, glabrous or slightly villous along the midribs, and 7.5–13 cm long."

Sargent (1922, p. 842) apparently mistakenly referred in text to this taxon as "var. crassifolia," citing the same type and paratypes as for var. *subcoriacea*.

Trees 7–20 m; twigs terete, glabrous; bark light to dark gray, evenly furrowed with smooth ridges and evenly reticulate; winter buds brown. **Leaves** deciduous, pinnate, 20–35 cm; leaflets 7–9, subcoriaceous, petioles, rachis, and petiolules glabrous, abaxially whitish to pale greenish, papillose, not scaly-punctate, blade 7–12 x 2.5–7 cm, ovate-lanceolate to narrowly ovate-lanceolate, elliptic-ovate, or oblong-ovate, apex acute to long-acuminate, base rounded to obtuse or abruptly attenuate, margins entire or usually subentire to very shallowly crenate, lateral petiolules 3–20 mm, not winged; rachis 7–12 cm, not winged; petiole bases not raised; leaf scars oblong-obovate to widely obovate, apex, shallowly concave to nearly truncate. **Flowers** unisexual (species dioecious), appearing with or just before leaves, wind pollinated; pistillate calyx present, persisting at base of samaras; petals absent. **Samaras** (32–)36–44 mm, body cylindric to subcylindric, wings 2, arising from distal 1/3–1/4 of body, (4.5–)5–7 mm wide. **2*n*** = 92.

Flowering Feb–Apr(–May). Bottomland forests, alluvial woods, creek terraces, flood plains, sandy swales, slopes, ridges, river bluffs, loess hills, beech-maple, upland hardwoods, oak-pine; 100–400(–1200, in Rabun County, Ga.) m; Ala., Ark., Fla., Ga., Ill., Ind., Ky., La., Md., Miss., Mo., N.J.?, N.C., Ohio, Okla.?, Pa., S.C., Tenn., Tex., Va.

Collections examined from **Texas**. **Bowie Co.**: near Texarkana, 3000 ft, 3 Sep 1898, *Heller 4206* (GH-2 sheets, NY); Texarkana, sandy bog near Texarkana, 16 Apr 1926, *Palmer 29666* (GH). **Newton Co.**: 23 Jul 1952, *Tharp & Gimbrede 52-627* (OKLA, TEX). **Polk Co.**: Livingston, sandy woods, 10 Apr 1914, *Palmer 5166* (GH). In the protologue of *Fraxinus americana* var. *subcoriacea*, Sargent noted "*Fraxinus americana* no. 4206, A. and E.G. Heller, Texarkana, Texas, September 1898, with entire and equally thick leaflets but not so pale below, is probably the same form."

FRAXINUS BILTMOREANA Beadle, Bot. Gaz. 25: 358. 1898. *Calycomelia biltmoreana* (Beadle) Nieuwland, Amer. Midl. Naturalist 3: 186. 1914. *Fraxinus americana* var. *biltmoreana* (Beadle) J. Wright ex Fernald, Rhodora 49: 159. 1947. *Fraxinus americana* subsp. *biltmoreana* (Beadle) A.E. Murray, Kalmia 13: 6. 1983. **TYPE**: USA. North Carolina. [Buncombe Co.:] Biltmore, Oct 1895, [*C.D. Beadle*] *No. 4049* (probable holotype: US-digital image!). The protologue says only "Biltmore herbarium, no. 4049, Biltmore, N.C. type locality." A collector is not specifically noted on the label, but "No. 4049" and "Type" are handwritten on a label with printed "Biltmore Herbarium" as heading. A separate annotation reads "Presented in 1917 by Mrs. George W. Vanderbilt." Sheets at GH and NY, with the collector and number specified as C.D. Beadle, No. 4049 (4049^a, 4049^b, 4049^c), were collected in 1897 and can be regarded as topotypes. A sheet labeled as *4049^a* (NY) was collected 2 Oct 1897.

Fraxinus catawbiensis Ashe, Bot. Gaz. 33: 230. 1902. **TYPE**: USA. North Carolina. [Granville Co.:] Eclipse P.O., bank of Catawba River at farm of Mr. Bird, 7 Aug 1901, *W.W. Ashe s.n.* (holotype: NCU!). In the protologue, Ashe noted that "It is closely related to the white ash, from which it is separated by the darker foliage, glaucous white beneath, the soft pubescence of the twigs and petiole, and the darker winter-buds; while from *Fraxinus biltmoreana* and *F. profunda*, which it closely resembles in foliage and pubescence, it is separated by the shorter and smaller fruit and smaller calyx."

Trees, 8–35 m. **Stems**: twigs terete, sparsely to densely hirtellous to hirtellous-puberulent or tomentulose; bark light to dark gray, evenly furrowed with smooth ridges and evenly reticulate. **Winter buds** brown. **Leaves** deciduous, pinnate, 20–35 cm; leaflets 7–9, abaxially whitish to pale greenish, subcoriaceous, papillose, not scaly-punctate, petioles, rachis, and petiolules sparsely to densely hirtellous to hirtellous-puberulent or tomentulose; blade ovate to ovate-lanceolate, elliptic-ovate, or elliptic-oblong, (6–)8–11(–15) x (2.5–)3.5–6(–7.5) cm, base rounded to truncate or obtuse, margins entire or usually subentire to very shallowly crenate, apex acute to acute-acuminate, lateral petiolules 3–15 mm, not winged; rachis 4–12 cm, not winged; petiole bases not raised; leaf scars oblong-obovate to widely obovate, apex shallowly concave to nearly truncate. **Flowers** unisexual (species dioecious), appearing with or just before leaves, wind pollinated; pistillate calyx present, persisting at base of samaras; petals absent. **Samaras** 33–54 mm, body cylindric to subcylindric, wings 2, arising from distal 1/3–1/4 of body, 6–8 mm wide. **2*n*** = 138.

Flowering Apr–May. Bluffs, rocky slopes, mesic woods, river and creek banks and terraces, woods margins, rocky woods, maple-post oak slopes, pastures; 50–1100 m; Ala., Ark., Ga., Ill., Ind., Ky., Md., Miss., Mo., N.J., N.C., Ohio, Pa., S.C., Tenn., Va., W.Va.

Fraxinus biltmoreana is rare west of the Mississippi River (Fig. 3). There is an enclave of the species in southeastern counties of Missouri, at the apparent western edge of the range of the species. Records in Arkansas and Louisiana appear to be rare and disjunct from the main geographic range, but the occurrence of hexaploids in both states is confirmed in Arkansas by a chromosome count from Pope County (Wright 1957) and a ploidy estimate from Boone County (Armstrong & Funk 1980) and in Louisiana by a estimate from East Baton Rouge Parish (Leser 1978).

Specimen examined from **Arkansas**. **Clark Co.**: Little Missouri River bottoms, 220 ft, Gurdon P.O., 6 Jun 1973, *Demaree 66612* (SMU). This individual is characterized by features typical of *Fraxinus biltmoreana*: large fruits, shallowly concave leaf scars, and puberulent stems, petioles, rachises, and petiolules.

FRAXINUS AMERICANA L., Sp. Pl. 2: 1057. 1753. *Calycomelia americana* (L.) Kosteletzky, Allg. Med.-Pharm. Fl. 3: 1004. 1834. **LECTOTYPE** (Fernald 1946, p. 391, plate 3): [*Clayton 742*,] Herb. Linn. No. 1230.3 (LINN digital image!, photo-NY!; isolectotype: BM digital image!). The Catesby plate cited by Linnaeus depicts *Fraxinus caroliniana* Miller; in order to maintain the traditional association of the epithet, Fernald selected as lectotype a specimen in the Linnaean herbarium that is an incomplete leaf — the petiole base is not included, and of the 4 pairs of large leaflets, 3 of them are missing the opposite leaflet. The associated label reads "Fraxinus femina foliis utrinque acuminatis seminibus alatis pendulis vid. Catesb. N. Hist. tab. 8a Clayton n. 742." The BM specimen also is a single leaf, missing several leaflets but showing a U-shaped petiole base and confirming the identity as *F. americana* sensu stricto (diploid). The LINN sheet has no collection information; the BM is more complete and includes an indication of "Clayton 742."

Fraxinus curtissii Vasey, Cat. Forest Trees U.S., 20. 1876. *Fraxinus americana* var. *curtissii* (Vasey) Sudw., U.S. Div. Forest. Bull. 14: 327. 1897. **TYPE**: USA. Alabama. [Barbour Co.:] Eufaula, [Chattahoochi R., Aug 1875,] *A.H. Curtiss s.n.* (holotype: US digital image!; isotype: GH!). The protologue: "Southern States. Mr. Curtiss found at Eufala, Ala., a large ash with remarkably small fruit. This species is provisionally called *F. curtissii*. It requires further investigation." *Fraxinus curtissii* apparently is homotypic with *F. americana* var. *microcarpa*. The type specimen has a handwritten annotation by Asa Gray as "*F. americana* var. *microcarpa*" — see below.

Fraxinus americana var. *microcarpa* A. Gray, Syn. Fl. N. Amer. 2(1): 75. 1878. **TYPE**: USA. Alabama. [Barbour Co.:] Eufala, Chattahoochi R., Aug 1875, *A.H. Curtiss s.n.* (holotype: GH!; isotype: US digital image!). The protologue cites *F. albicans* and *F. curtissii* in synonymy: "*F. albicans,* Buckley in Proc. Acad. Philad. 1862, partly. *F. curtissii*, Vasey, Cat. Trees U.S. 20." See comments regarding the name *Fraxinus albicans* in Nesom (2010b).

Fraxinus americana forma *iodocarpa* Fernald, Rhodora 14: 192. 1912. *Fraxinus americana* var. *iodocarpa* (Fernald) Fernald ex Rehder, in L.H. Bailey, Stand. Cycl. Hort., 1275. 1915. **SYNTYPES**: USA. Massachusetts. Middlesex Co.: Winchester, bank of Mystic Lake, 17 Jun

1911, *F.F. Forbes and M.L. Fernald s.n.* (GH 00219144!, GH 00219143!). Maine. [Kennebec Co.:] Gardiner, 13 Jun 1911, *J.M.H. Morrell s.n.* (GH!).

Trees, (5–)15–30(–40) m. **Stems**: twigs terete, glabrous; bark light to dark gray, evenly furrowed with smooth ridges and evenly reticulate. **Winter buds** brown. **Leaves** deciduous, pinnate, 15–30(–35) cm; leaflets 5–9, abaxially whitish to pale greenish, dark green adaxially, subcoriaceous, papillose, not scaly-punctate, glabrous or short-villous abaxially when young, especially along midrib and laterals; blade ovate to ovate-lanceolate, elliptic-lanceolate, or oblong-elliptic, 5.5–12(–15) x (2–)2.5–6(–7.5) cm, base cuneate to rounded, margins usually entire to shallowly crenate serrate on distal 3/4, apex acute to acute-acuminate or less commonly obtuse, lateral petiolules 4–13(–15) mm, not winged; rachis 5–10 cm, not winged; petiole bases not raised; leaf scars V- to U- or crescent-shaped, apex deeply concave or notched. **Flowers** unisexual (species dioecious), appearing with or just before leaves, wind pollinated; pistillate calyx present, persisting at base of samaras; petals absent. **Samaras** (19–)25–32(–38) mm, body cylindric to subcylindric, wings 2, arising from distal 1/3–1/4 of body, 3–5(–6) mm wide. **2*n*** = 46.

Flowering Feb–Apr(–May). Creek sides and alluvial terraces, flood plains, hammocks, low woods, mesic woods, coves, dry hills; 50–1200(–1500) m; N.B., N.S., Ont., P.E.I., Que.; Ala., Ark., Colo., Conn., Del., D.C., Fla., Ga., Ill., Ind., Iowa, Kans., Ky., La., Maine, Md., Mass., Mich., Minn., Miss., Mo., Nebr., N.H., N.J., N.Y., N.C., Ohio, Okla., Pa., R.I., S.C., Tenn., Tex., Vt., Va., W.Va., Wis.; introduced in Europe (England, Hungary), Africa, Pacific Islands (Hawaii), Australia.

Postscript.

The current report is primarily a review and synthesis of previous research on the *Fraxinus americana* group. It also provides documentation for the briefer taxonomic treatment of the genus in a forthcoming volume of the Flora of North America. Perhaps most significantly, and hopefully, this presentation may serve as a stimulus toward further research. Among significant taxonomic questions to be answered regarding white ash taxonomy are these.

* Are the tetraploid and hexaploid taxa hybrid in origin, and if so what are the parents? Did the tetraploid and hexaploids each have a single and independent origin?

* Putatively triploid and pentaploid individuals have been encountered as embryos, but are triploid and pentaploid trees common or rare in nature?

* What is the biological nature of these trees with large, polyploid-sized fruits but with diploid petiole morphology (as mapped in Fig. 1)? Are they ecotypic variants, or are they a lineage distinct from the sympatric diploid trees with typical-sized fruits? Diploid or polyploid?

* What is the relationship of *Fraxinus albicans*, the Texas ash, to *F. americana*?

* What is the relationship of *Fraxinus pauciflora*, the swamp white ash, to the upland forest trees of the white ash group? Is it of hybrid origin, and if so what are its parents?

Typifications of various names potentially allied with the white ash group (and also the green ash group) remain to be formally clarified. A manuscript on this is in preparation, to be published separately.

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Appendix 1. Chromosome number counts and estimations by Wright (1944a, 1957), Schaefer & Miksche (1977), Leser (1978), and Black & Beckmann (1983). States and counties/parishes.

1a. Chromosome number counts and estimations by Wright (1944a, 1957).

<u>2n = 46</u>
Indiana: Decatur (NEG-788), Marion (NEG-789, NEG-797), Ripley (NEG-799)
Maryland: Washington
Massachusetts: Berkshire (NEG-400)
Ohio: Hocking, Muskingum, Wayne
Pennsylvania: Berks, Lancaster, Montgomery (NEG-393), Schuylkill, Westmoreland, York
Tennessee: Anderson (NEG-811)
West Virginia: Marshall, Pocahontas

<u>2n = 92</u>
Alabama: Chilton, Marion
Arkansas: Pope (NEG-773)
Indiana: Decatur (NEG-785), Greene
Maryland: Washington
Ohio: Wayne
Pennsylvania: Lancaster, Montgomery (NEG-391, NEG-392), Westmoreland

<u>2n = 136</u>
Alabama: Chilton
Arkansas: Pope
Indiana: Greene, Owen
Maryland: Washington
Pennsylvania: Lancaster
West Va.: Marshall

1b. Chromosome number counts and estimations by Schaefer & Miksche (1977). Localities are deduced from the latitude/longitude coordinates provided by the authors.

2n = 46

Arkansas:	Marion
Connecticut:	New Haven
Illinois:	Effingham, Gallatin, Jackson
Kentucky:	Scott
Maine:	Hancock
Michigan:	Washtenaw
Mississippi:	Greene, Oktibbeha
New York:	Cayuga, Essex
North Carolina:	Henderson
Ohio:	Warren, Wayne
Tennessee:	Franklin
West Virginia:	Tucker
Wisconsin:	Langlade

2n = 92

Louisiana:	East Baton Rouge
Mississippi:	Oktibbeha
Texas:	Hardin

2n = 136

Ohio:	Warren
Kentucky:	Scott
Illinois:	Gallatin, Jackson
Indiana:	Clark
North Carolina:	Henderson, Wake

pentaploid?

Indiana:	Clark

1c. Chromosome number counts and estimations by Leser (1978).

2n = 46

Alabama:	Madison
Illinois:	Gallatin, Jackson, Union, Williamson
Kentucky:	Lyon, Trigg
Mississippi:	Oktibbeha
North Carolina:	Chatham, Orange
Ohio:	Warren
Tennessee:	Franklin, Fentress, McMinn, Overton

2n = 92

Louisiana:	East Baton Rouge
Texas:	Hardin

2n = 136

Illinois:	Jackson, Saline, Union
Indiana:	Crawford, Jackson, Washington
Louisiana:	East Baton Rouge
South Carolina:	Pickens
Tennessee:	Smith

pentaploid?

Indiana:	Crawford-Jackson-Washington (6795)
Louisiana:	East Baton Rouge (6738)

South Carolina: Pickens (6784)
Tennessee: Overton-Fentress-Smith (6864)

1d. Chromosome number estimations by Armstrong and Funk (1980).

2n = 46
New Brunswick: Northumberland
Vermont: Addison
New York: Onondaga
Ohio: Warren

2n = 92
Illinois: Jackson-Union-Williamson (mapped as Jackson)
Indiana: Harrison-Washington-Jackson (mapped as Washington)

2n = 136
Arkansas: Marion-Boone (mapped as Boone Co.)

triploid?
Indiana: Harrison-Washington-Jackson (not mapped)

pentaploid?
Indiana: Harrison-Washington-Jackson (not mapped)

1e. Chromosome number counts and estimations by Black & Beckmann (1983).

2n = 46
North Carolina: Granville

2n = 92
North Carolina: Granville

2n = 136
North Carolina: Granville

triploid?
North Carolina: Granville

pentaploid?
North Carolina: Granville

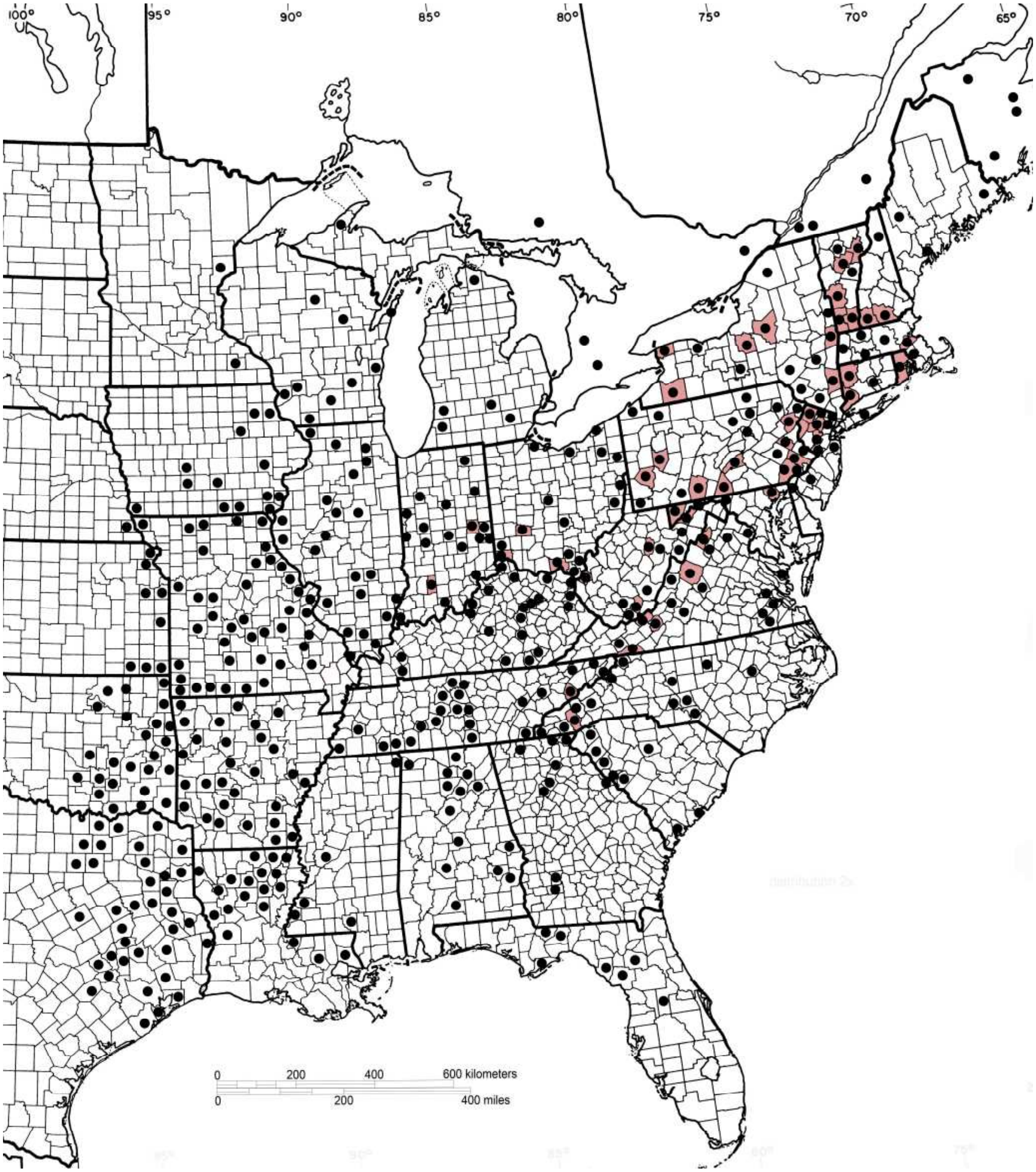

Figure 1. Geographic distribution of *Fraxinus americana* sensu stricto. Shaded counties are those from which large-fruited but "diploid-petioled" collections (see text) have been seen. In Canada, white ash also occurs in Nova Scotia and on Prince Edward Island (not mapped).

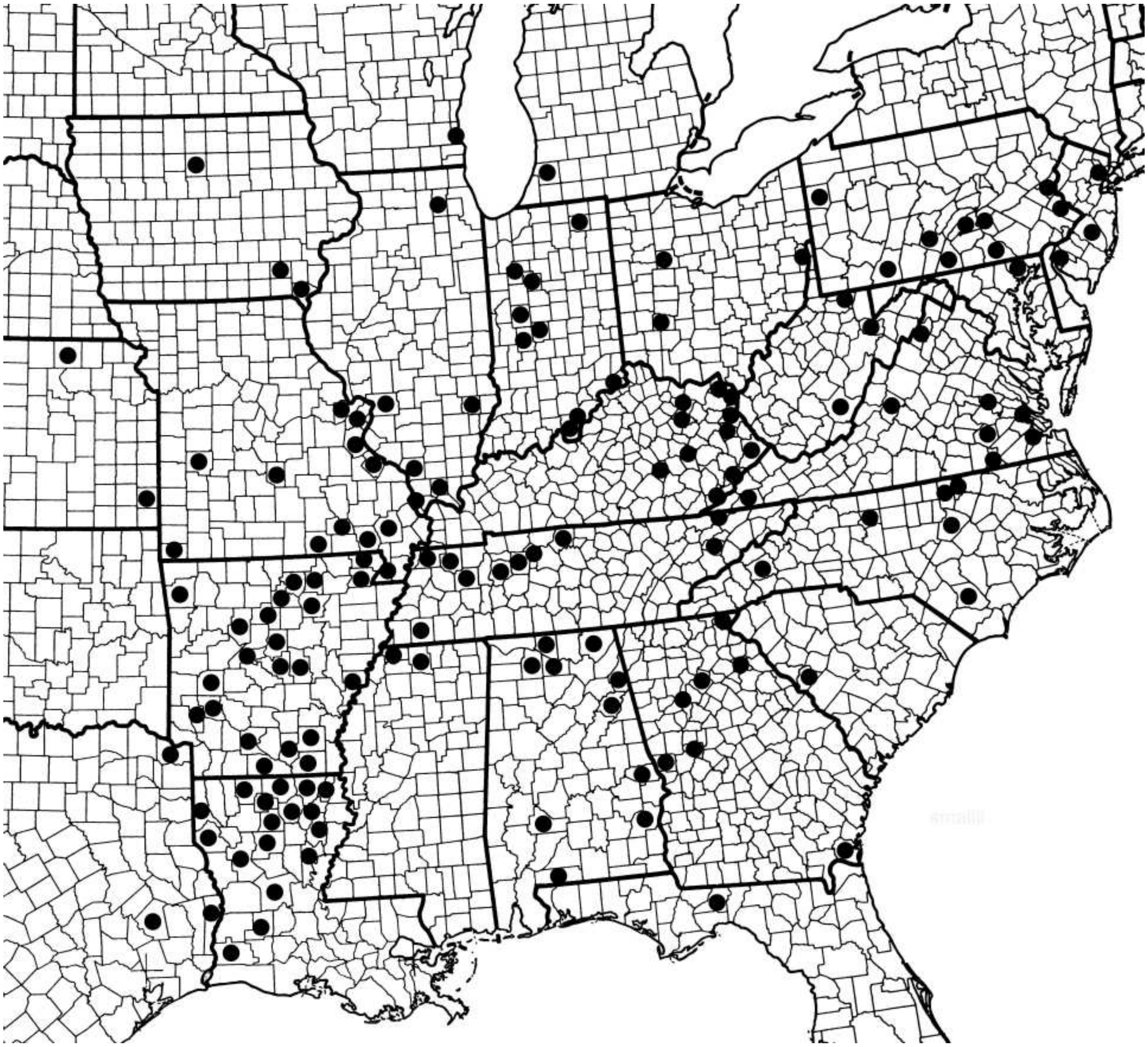

Figure 2. Geographic distribution of *Fraxinus smallii*.

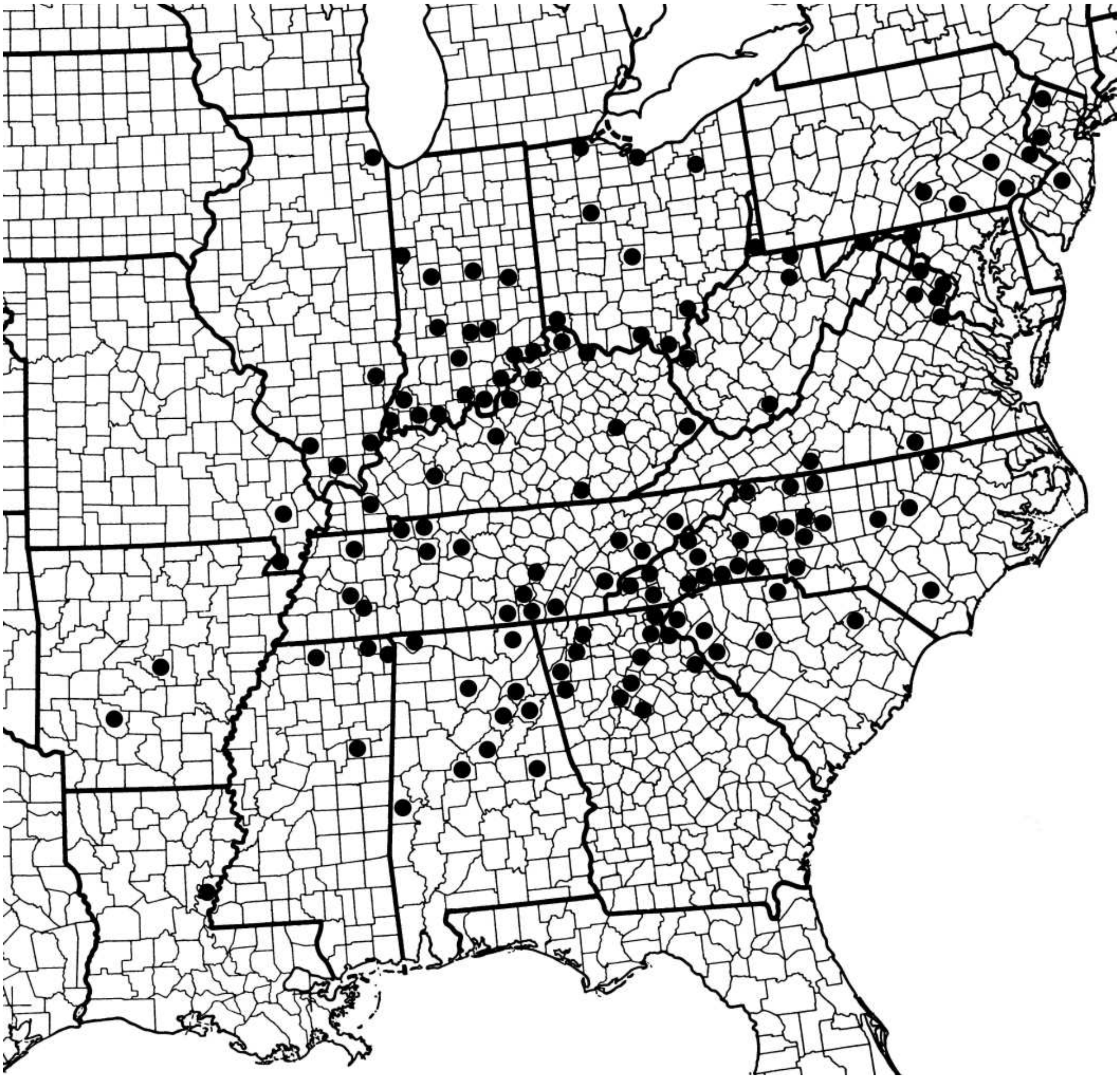

Figure 3. Geographic distribution of *Fraxinus biltmoreana*. Map points have been added from the online atlas for the "NCU Flora of the Southeastern United States," based on specimens at NCU (http://www.herbarium.unc.edu/seflora). Chromosome counts and ploidy estimates from cytophotometry corroborate the presence of *F. biltmoreana* in Arkansas and Louisiana.

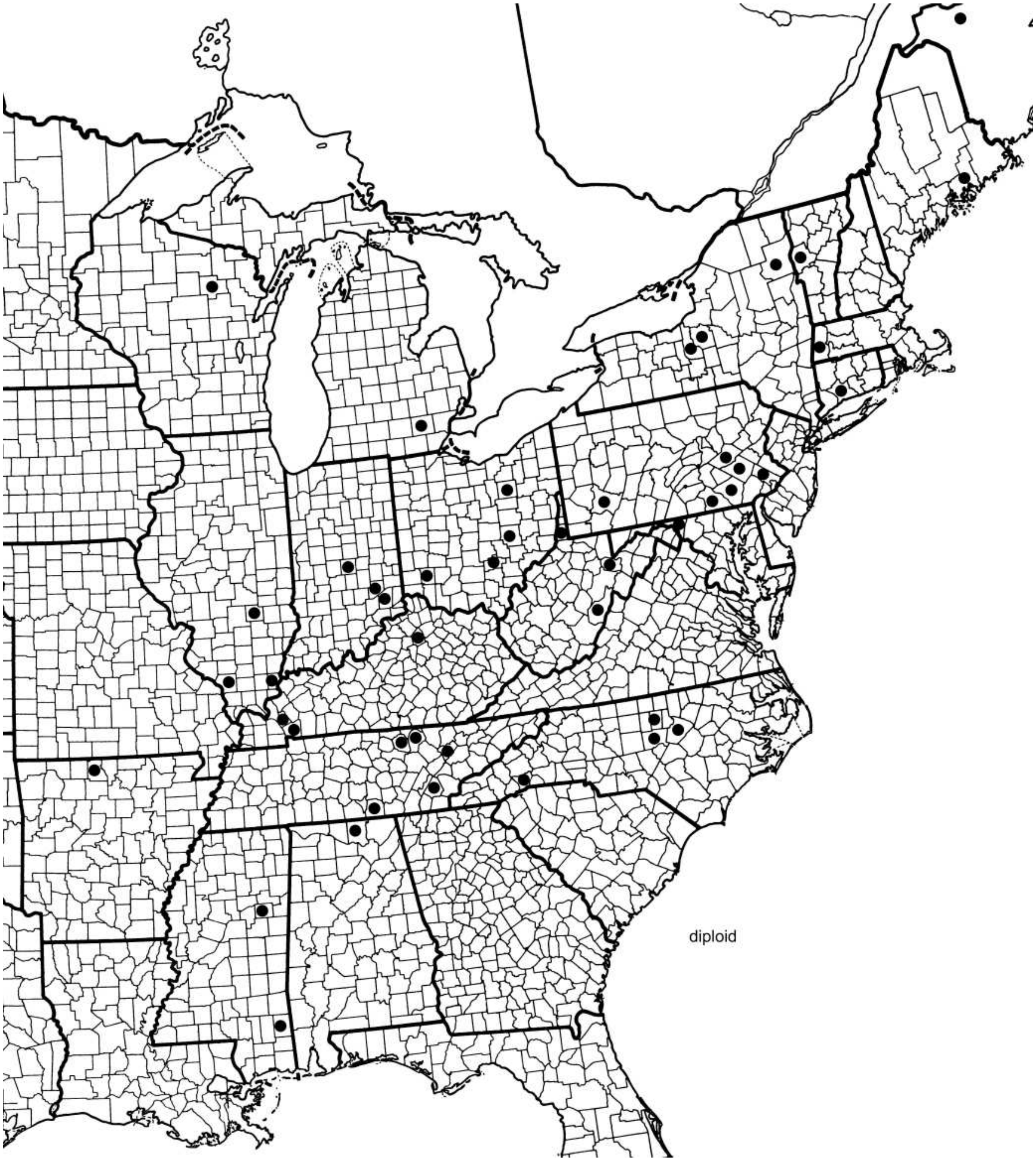

Figure 4. *Fraxinus americana* sensu stricto, diploid — localities for reported chromosome counts and estimations. See Appendix 1 for documentation.

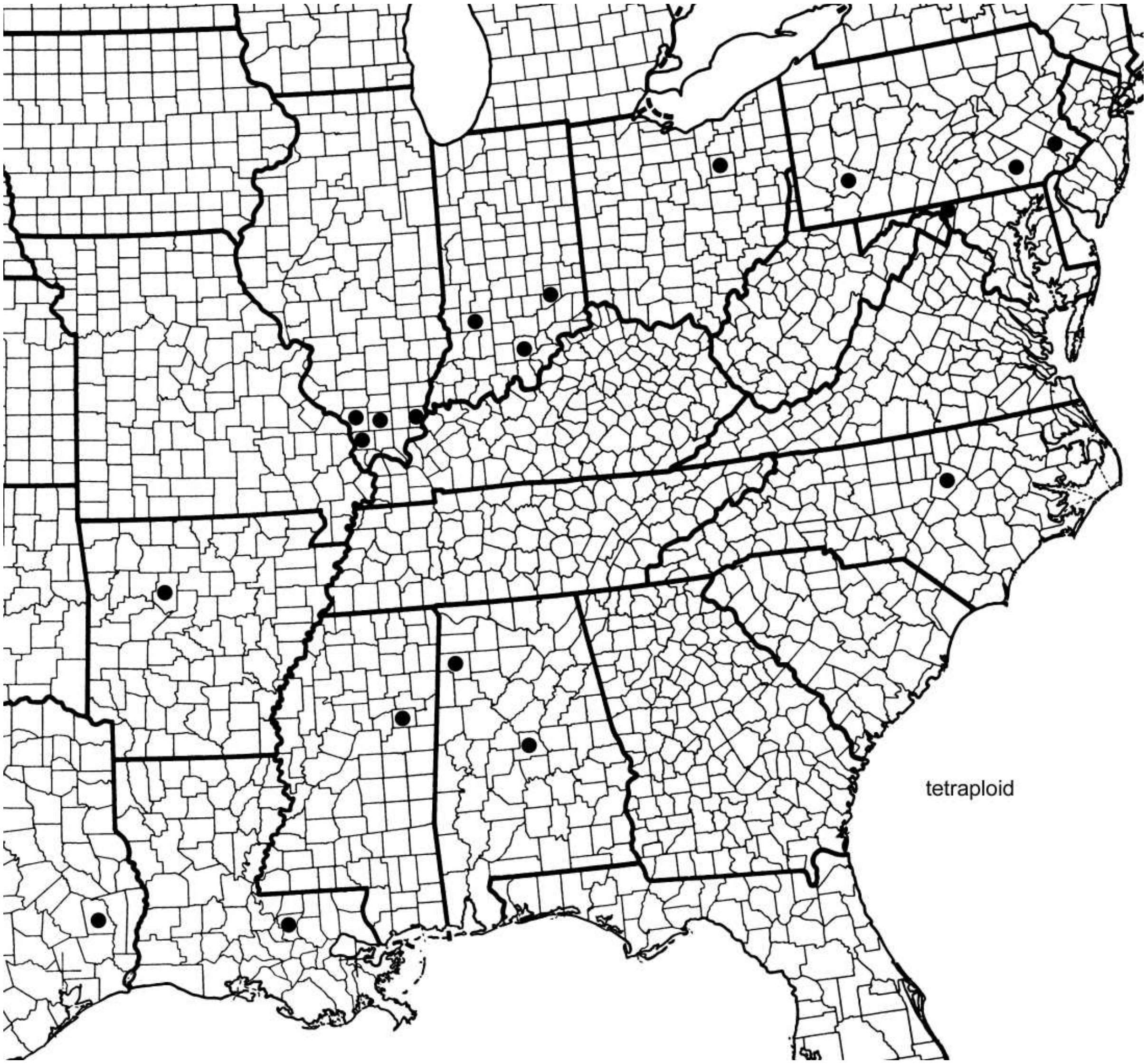

Figure 5. *Fraxinus smallii*, tetraploid — localities for reported chromosome counts and estimations. See Appendix 1 for documentation.

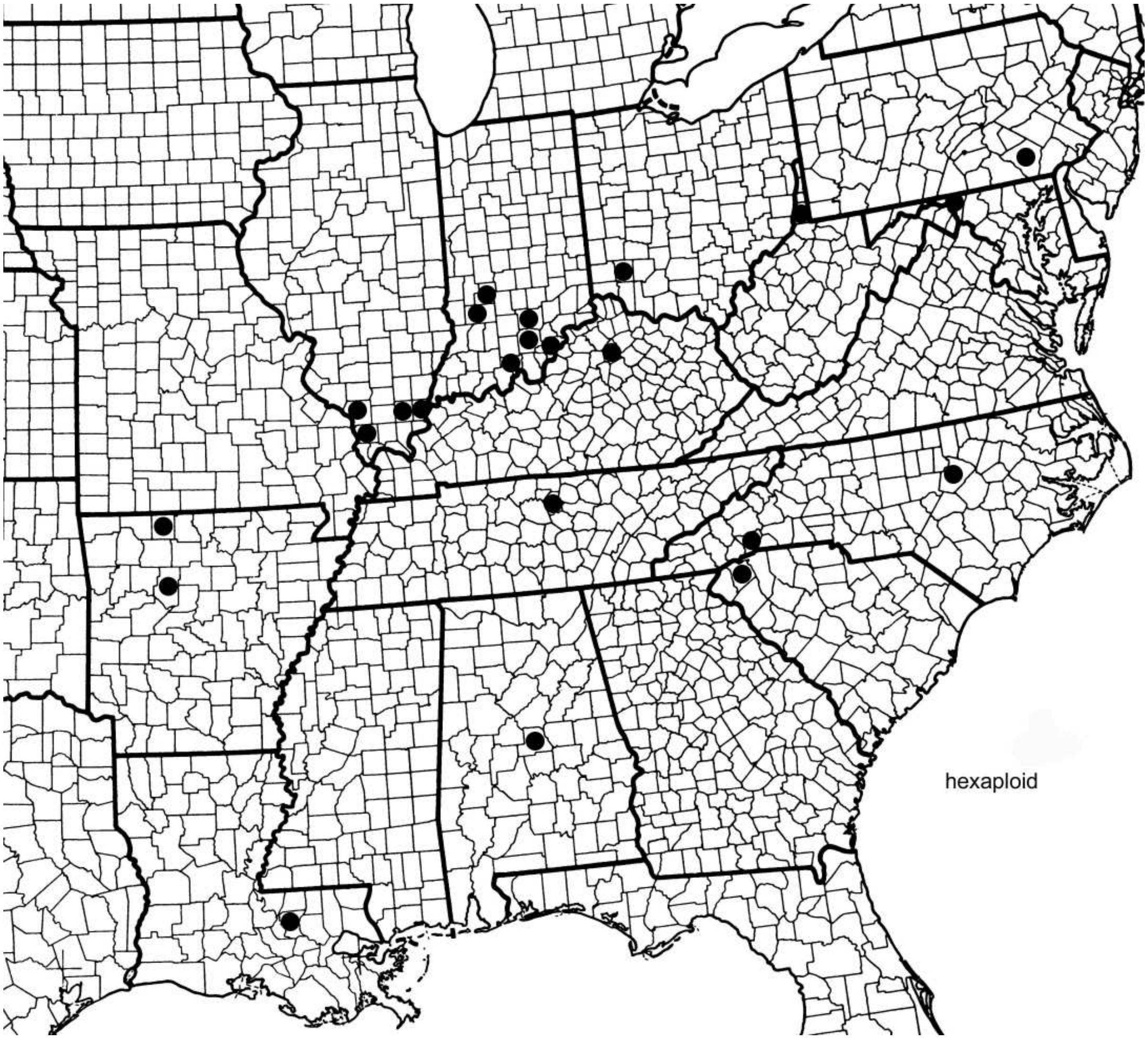

Figure 6. *Fraxinus biltmoreana*, hexaploid — localities for reported chromosome counts and estimations. See Appendix 1 for documentation.

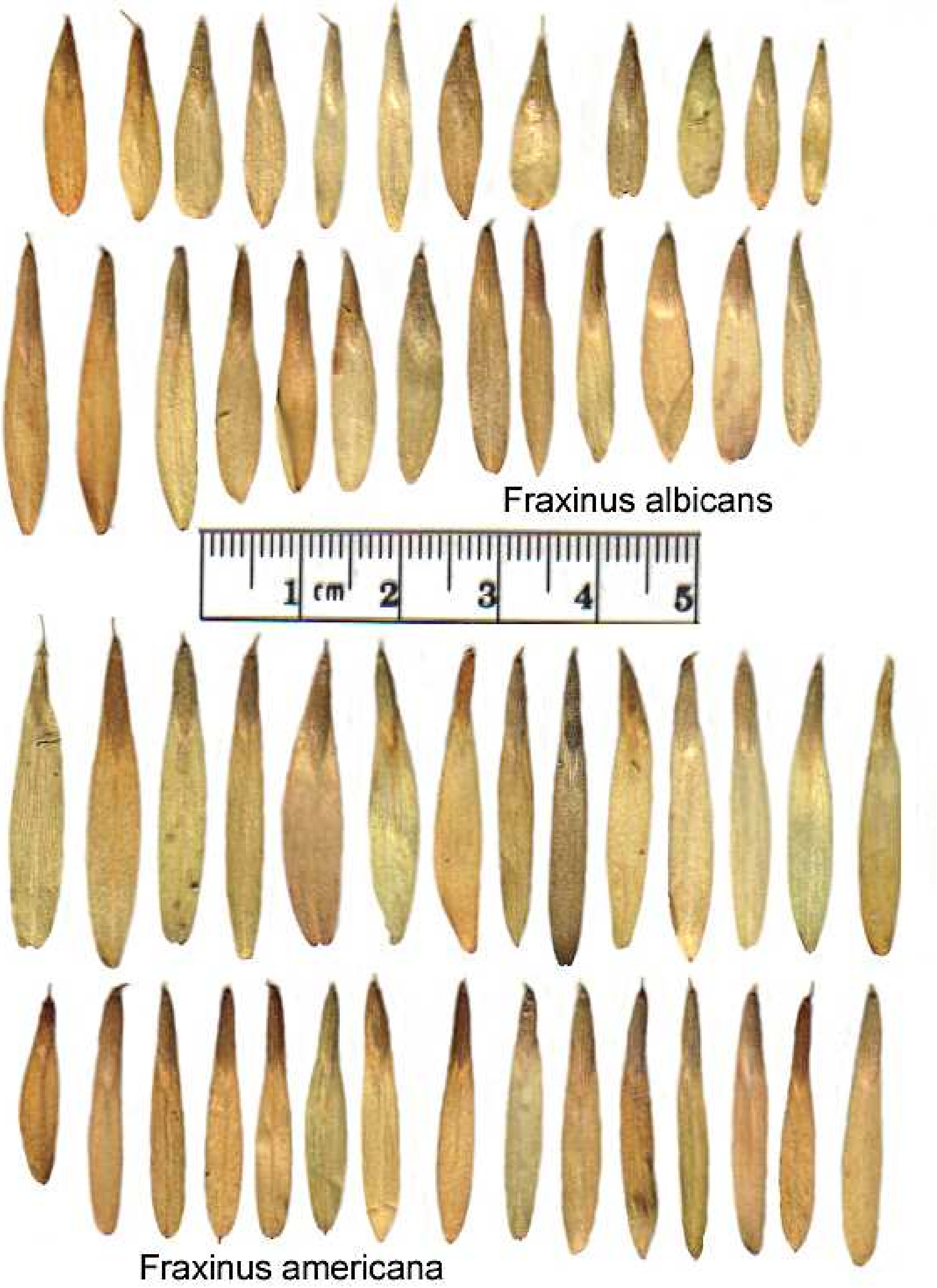

Figure 7. Samara variation in *Fraxinus albicans* and *F. americana*. Top two rows, Texas ash (*Fraxinus albicans*) in Texas and Oklahoma. Bottom two rows, typical diploid white ash (*Fraxinus americana*) in Texas, Oklahoma, and Louisiana.

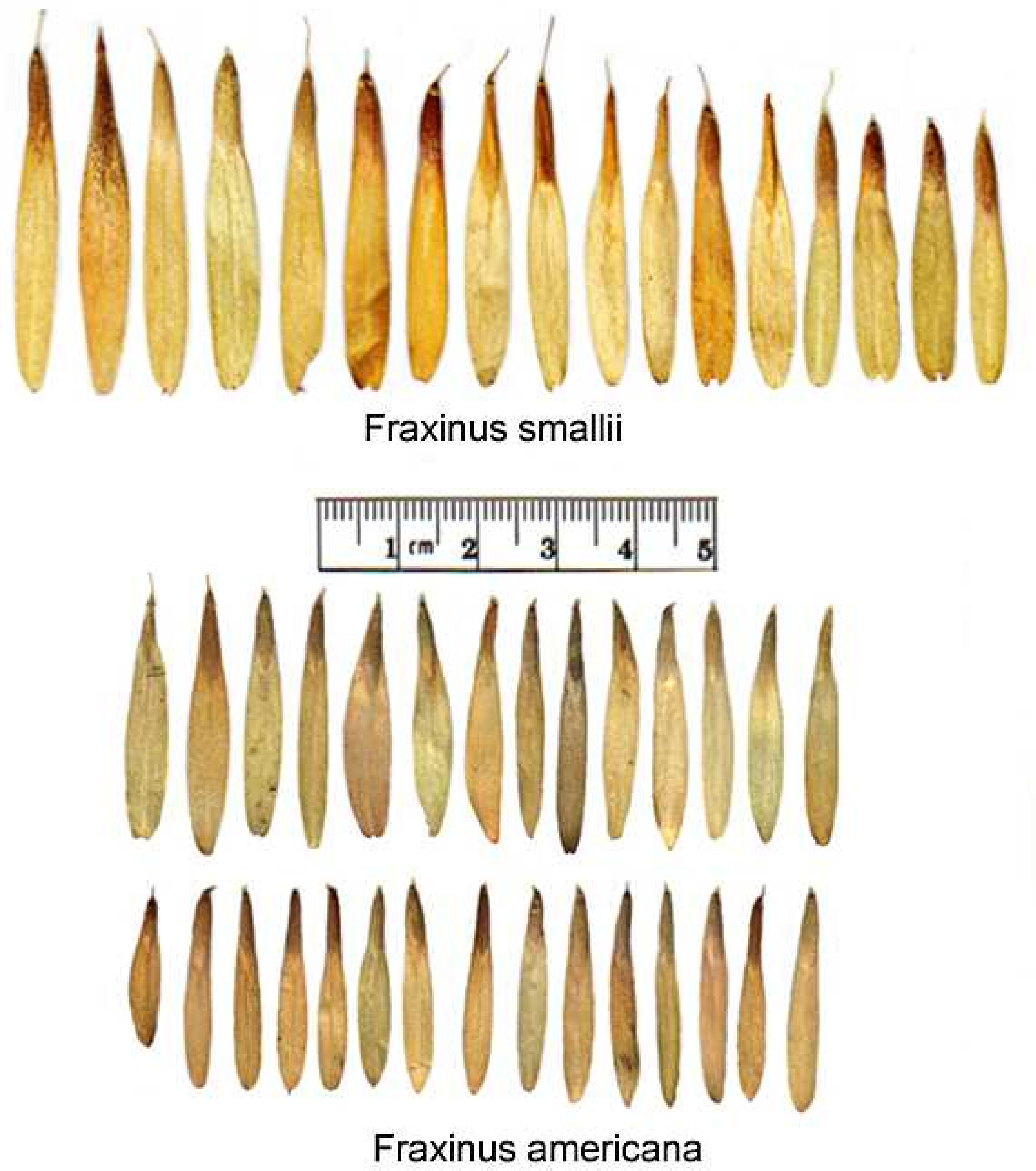

Figure 8. Samara variation in *Fraxinus smallii* and *F. americana*. Top row, *Fraxinus smallii* in Texas, Louisiana, and Arkansas. Size and shape are similar in other parts of the range. Bottom two rows, typical diploid white ash (*Fraxinus americana*) in Texas, Oklahoma, and Louisiana (same as from Fig. 7).

Fraxinus biltmoreana

Fraxinus americana

Figure 9. Samara variation in *Fraxinus biltmoreana* and *F. americana*. Top row, *Fraxinus biltmoreana* over its range. Bottom two rows, typical diploid white ash (*Fraxinus americana*) in Texas, Oklahoma, and Louisiana (same as from Fig. 7 and Fig. 8).

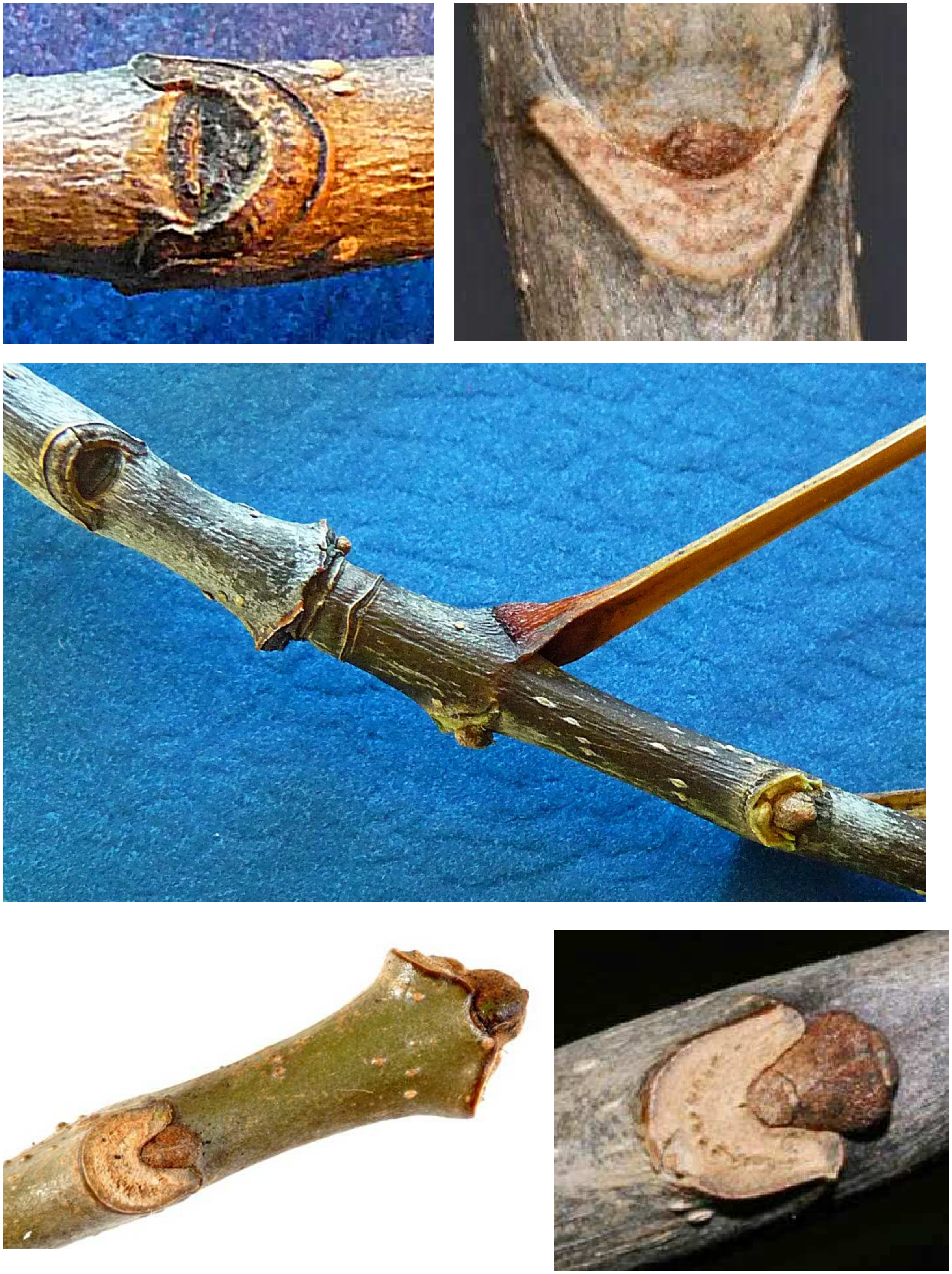

Figure 10. Leaf scar morphology: *Fraxinus americana*. Bottom left by B. Eugene Wofford, University of Tennessee Herbarium website, used with permission.

Figure 11. Leaf scar morphology: *Fraxinus smallii*.

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Figure 12. Leaf scar morphology: *Fraxinus biltmoreana*.

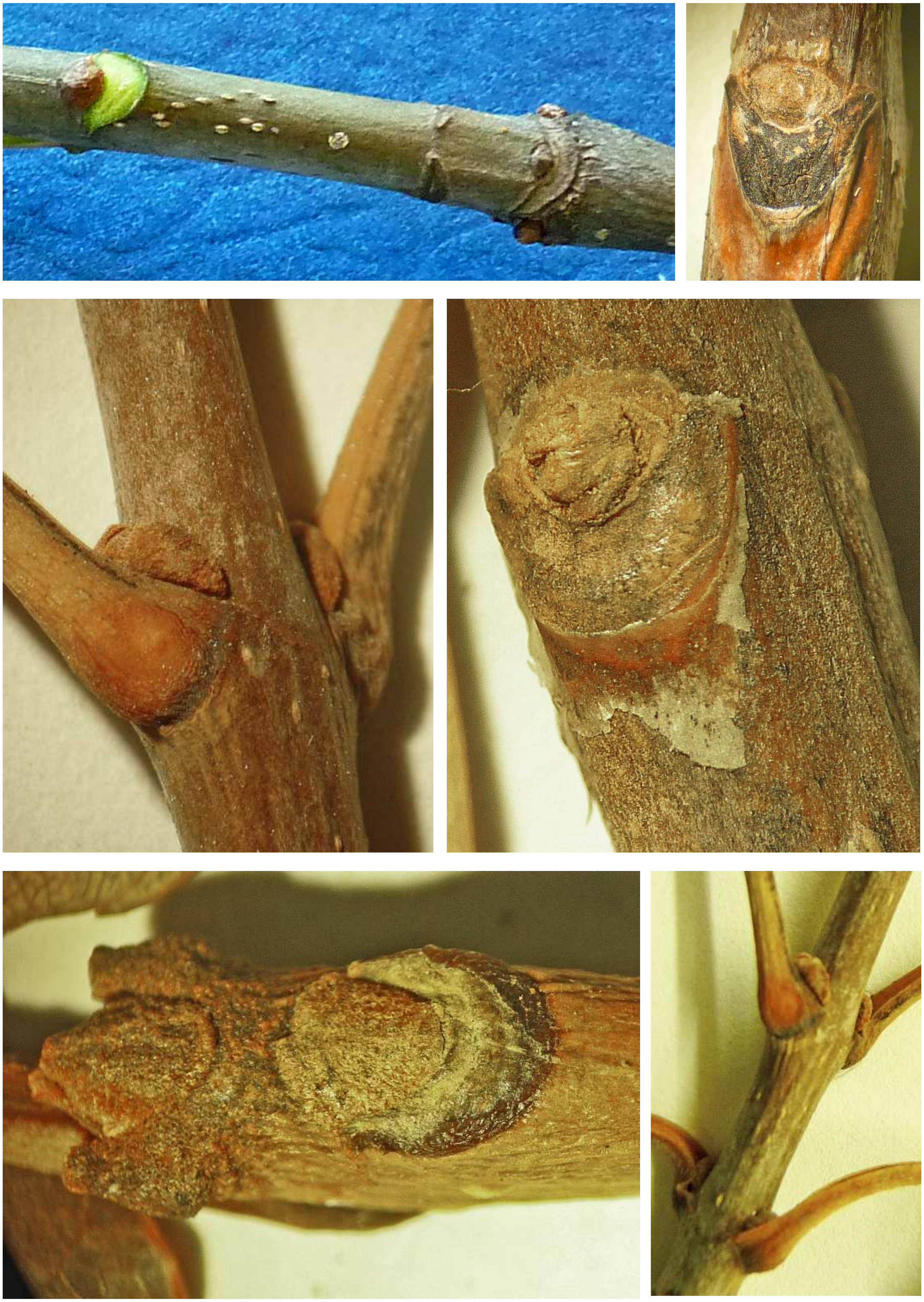

Figure 13. Leaf scar morphology: *Fraxinus albicans*.

Figure 14. Leaf scar morphology: *Fraxinus pauciflora*.

Figure 15. Leaf scar morphology: *Fraxinus pennsylvanica*.