An Extinct Domesticated Subspecies of Erect Knotweed in Eastern North America: *Polygonum erectum* subsp. *watsoniae* (Polygonaceae)

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An Extinct Domesticated Subspecies of Erect Knotweed in Eastern North America: *Polygonum erectum* subsp. *watsoniae* (Polygonaceae)

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Abstract. This paper provides a description of an extinct domesticated subspecies of erect knotweed (*Polygonum erectum* L.). Masses of erect knotweed achenes are often recovered from archaeological sites in eastern North America dating to ca. 3000–600 BP. Several paleoethnobotanical assemblages from the later part of this era (ca. 1000–600 BP) contain achenes that are outside the range of natural variation for erect knotweed. The most well preserved of these archaeological assemblages, a desiccated cache of achenes from the Whitney Bluff site, Arkansas (ca. 900 BP), is compared to four closely related species and subspecies of *Polygonum* L. The Whitney Bluff achenes are most similar to those of *P. erectum*, but differ from modern fruits of this species in three respects: (1) fruits are larger, (2) average pericarp thickness is reduced, and (3) fruit dimorphism is greatly reduced. These differences are typical of domestication syndrome in annual seed crops. The Whitney Bluff assemblage is described as the type specimen of a domesticated subspecies, *P. erectum* subsp. *watsoniae* N. G. Muell.

Key words: Domestication, Eastern Agricultural Complex, fruit morphology, paleoethnobotany, *Polygonum*.

From ca. 3900–600 BP, a suite of native seed crops known as the Eastern Agricultural Complex (EAC) was cultivated in eastern North America (Smith & Yarnell, 2009). Previous studies have documented changes in seed shape and size to demonstrate that two of these crops were domesticated: *Iva annua* L. var. *macrocarpa* (S. F. Blake) R. C. Jacks. and *Chenopodium berlandieri* Moq. subsp. *jonesianum* Bruce Smith (Blake, 1939; Smith & Funk, 1985). The domestication of little barley (*Hordeum pusillum* Nutt.) has also been suggested based on differences in seed morphology between archaeological specimens and modern plants (Hunter, 1992; Adams, 2014). Erect knotweed (*Polygonum erectum* L.) was cultivated alongside these lost domesticates for hundreds of years. It has been found in hearths, storage pits, and human feces at archaeological sites across the Midwest dating from ca. 3000 to 600 BP (Asch & Asch, 1985b; Faulkner, 1991; Powell, 2000; Gremillion, 2004; Simon & Parker, 2006; Mueller, 2017b).

Polygonum erectum and many species within *Polygonum* L. sect. *Polygonum* exhibit seasonal achene dimorphism. Native or naturalized North American species that exhibit seasonal achene dimorphism include: *P. achoreum* S. F. Blake, *P. aviculare* L. complex (sensu Costea & Tardif, 2004), *P. glaucum* Nutt., *P. erectum*, *P. marinense* T. R. Mert. & P. H. Raven, *P. patulum* M. Bieb., *P. plebeium* R. Br., *P. ramosissimum* Michx., and *P. striatulum* B. L. Rob. These species produce two different fruit morphs, referred to by pericarp texture. Tubercled morphs have lower aspect ratios (i.e., a shorter length compared to width) and thicker pericarps with a variety of textures that are diagnostic of different species (Costea et al., 2005). Smooth morphs have a higher aspect ratio (i.e., a longer length compared to width) and thinner pericarps (Fig. 1). Tubercled morphs have layers of cuticle and wax in their pericarps that slow the penetration of moisture and pathogens, allowing seeds to remain viable for several seasons (Yurtseva, 2001). Smooth morphs germinate much more readily the spring after they are produced (Mueller, 2017a). Plants produce tubercled morphs throughout the growing season and begin to produce smooth morphs in mid-September.

Beginning in the 1980s, the achenes found in abundance at archaeological sites were identified by paleoethnobotanists as *Polygonum erectum* on the basis of their surface texture (striate-tubercled) and the distinctive shape of their tubercled achenes (Martin, 1954). Smooth achenes also occurred in most archaeological samples, and were assumed to also come from *P. erectum* plants, although their morphology has not been considered diagnostic to species by botanists or paleoethnobotanists (Asch & Asch, 1985a; Costea et al., 2005).

Speculation about a domesticated subspecies of erect knotweed began in the mid-1980s, when two strange assemblages were reported. At the Late

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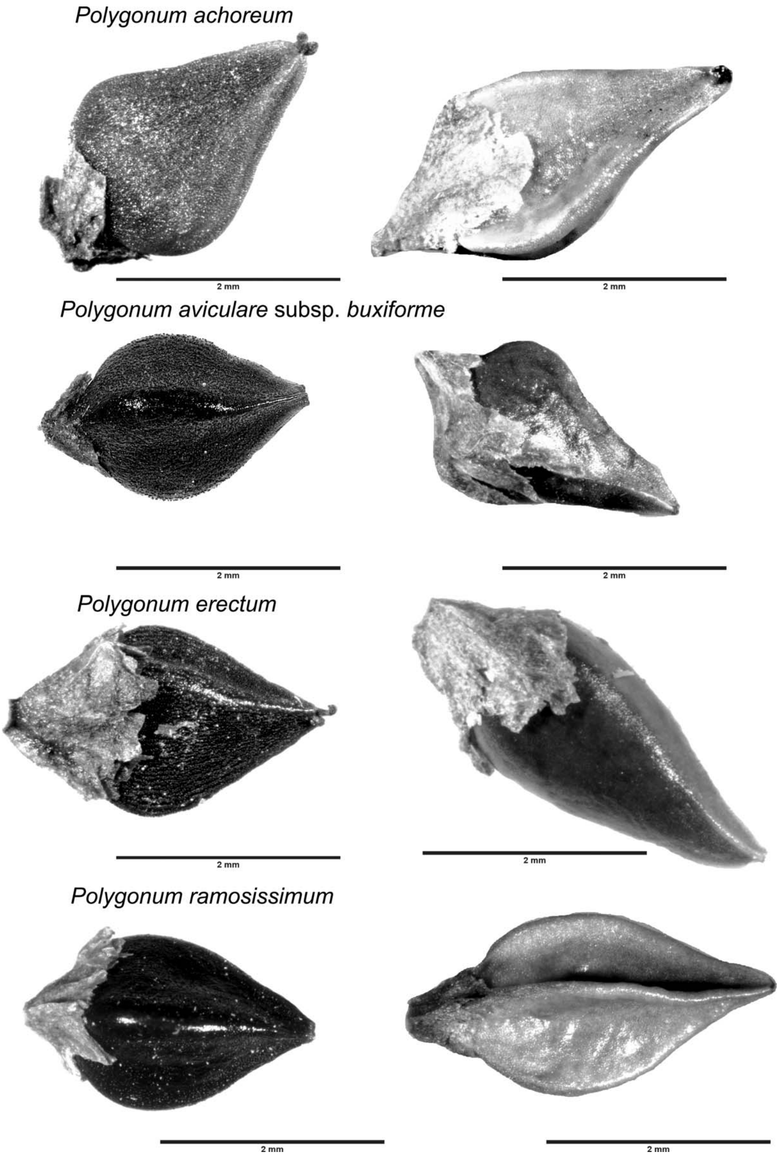
Polygonum achoreum

Polygonum aviculare subsp. *buxiforme*

Polygonum erectum

Polygonum ramosissimum

Figure 1. Examples of the dimorphic achenes of the four taxa considered in this analysis. Perianths have been removed. Left: Tubercled morphs with typical surface textures, shape, and size for each species. *Polygonum achoreum* S. F. Blake achenes are usually uniformly tubercled, *P. aviculare* L. subsp. *buxiforme* (Small) Costea & Tardif achenes are coarsely tubercled, *P. erectum* L. achenes are striate-tubercled; compare to those from Whitney Bluff. The *P. ramosissimum* Michx. achene pictured here is roughened, but surface texture varies within this species. Right: Smooth morphs of typical shape and size for each species. *Polygonum erectum* and *P. aviculare* subsp. *buxiforme* achenes pictured here have convex faces, which gives them a plump appearance. This is a rare morphology for *P. aviculare* subsp. *buxiforme* and a very common one for *P. erectum* (see Table 3). *Polygonum ramosissimum* and *P. achoreum* smooth morph achenes have concave faces and a deflated appearance. This *P. achoreum* smooth morph is an example where the central ridge has slumped over so one face is completely obscured, whereas the *P. ramosissimum* smooth morph has a sunken central ridge.

Mississippian (ca. 700 BP) Hill Creek site in Illinois, thousands of carbonized, smooth morph achenes were recovered from a large storage pit—no tubercled morphs were present (Asch & Asch, 1985a). The Hill Creek achenes were also larger than the erect knotweed smooth morphs in available reference collections. To ascertain whether or not erect knotweed was capable of producing such a harvest, Asch and Asch gathered achenes from *Polygonum erectum* populations in Kansas, Missouri, and Illinois during three different growing seasons (Asch & Asch, 1985a). This survey suggested that erect knotweed does not produce monomorphic harvests: tubercled morphs were always present. Asch and Asch (1985a: 144–145) concluded: "If assessments of variability in wild-type *P. erectum* are accurate, then two alternative explanations can be advanced to account for the peculiarities of the Hill Creek knotweed: (1) They are a domesticated form of erect knotweed... or; (2) The Hill Creek achenes are not erect knotweed, but some other species in the knotweed section of *Polygonum*...." In particular, Asch and Asch (1985b) suggested *P. ramosissimum*, which was known to produce many smooth, late season achenes (Mertens & Raven, 1965). Fritz (1986) reported a similar near-monomorphic assemblage of large, smooth morph achenes from the Mississippian Whitney Bluff site in Arkansas. These were desiccated in a dry rock shelter and were remarkably well preserved. But without a clearer sense of variability in seasonal achene production within and among species of *Polygonum*, erect knotweed domestication remained an open question.

The Whitney Bluff site was one of 80 Ozarks rock shelters excavated during the 1920s and 1930s by the University of Arkansas Museum. The results of these excavations were never published but are documented in field notes and photographs on file at the University of Arkansas Museum. The well-preserved plant remains from the rock shelters were first examined by Melvin Gilmore and Volney Jones (Gilmore, 1931). Since then, many scholars have examined parts of these important collections (see Fritz, 1986). The crop plant remains from 19 rock shelters, including Whitney Bluff, were analyzed and reported by Gayle Fritz (1986), who also synthesized field and laboratory notes for those 19 sites to reconstruct as much of the archaeological context as possible. The exact location of the Whitney Bluff site is one important piece of information missing from the original field reports, but excavation notes indicate that it is located in Benton County, Arkansas, on the banks of the White River. Materials recovered from Whitney Bluff include a woven bag, baskets, string, mussel shell, stone tools, one potsherd, cane tools, turkey bones, a smashed gourd bowl, and plant foods (Fritz, 1986).

Two large samples of *Polygonum* achenes were recovered from this site (University of Arkansas Museum accession numbers 32-57-3a and 32-57-5c). Both came from a "cache" that also contained a broken gourd bowl and a drawstring bag. It is unknown whether they were two distinct samples each from their own container, or mixed in a single context (Fritz, 1986: 107; 1986: 92). Domesticated *Chenopodium berlandieri* subsp. *jonesianum* was also recovered from this context (Fritz, 1986). A fragment of the gourd from the cache was dated to 785 ± 75 BP (AD 1042–1386; Fritz, 1986). The *Polygonum* itself yielded a date of 885 ± 20 BP (AD 1046–1217; NOSAMS sample number 123466). These two samples are comprised of 1307 achenes. Fritz (1986) measured the length and width of 200 achenes and noted that they were larger than available reference collections of *P. erectum*, and were all smooth morphs.

This study was designed to compare the Hill Creek and Whitney Bluff assemblages (among the 40 other archaeological assemblages that I analyzed in the course of a larger study) to erect knotweed and several other species from which they could possibly be derived. Two possibilities are considered here: (1) all archaeological assemblages, including those from Hill Creek and Whitney Bluff, fall within the range of natural variability for some species native to the study area; or (2) the archaeological assemblages from Hill Creek and Whitney Bluff exhibit domestication syndrome as a result of hundreds of years of cultivation. In either case, the first step is to determine which species is represented at these sites. All but one of the available archaeological assemblages have been distorted by carbonization, and require careful correction before they can be compared to uncarbonized fruits. The Whitney Bluff assemblage, on the other hand, was not subject to distortion because it was preserved via desiccation.

POLYGONACEAE SYSTEMATICS AND POTENTIAL PROGENITOR TAXA

Species were considered as possible progenitors of the Whitney Bluff assemblage if (1) they had similar fruit and perianth morphology; (2) they were native to pre-Columbian North America; and (3) they occur in the region where ancient knotweed cultivation is documented (parts of modern-day Arkansas, Illinois, Indiana, Iowa, Kentucky, Missouri, Ohio, and Tennessee). The relationships among species of *Polygonum* and between it and related genera have been debated and revised repeatedly for decades, so it was necessary to carefully review the bases for current taxonomies to make sure there were not species in other clades that should be considered, and to double-check the identifications of all specimens sampled for this study.

Polygonum belongs to the family Polygonaceae, a monophyletic group (Cuénoud et al., 2002) characterized by several synapomorphies, including ocrea (sheathing stipules), orthotropous ovules, and quincuncial aestivation. Many members have trigonous achenes, while others have lenticular biconvex or discoid fruits. Older taxonomic treatments recognized three or four distinct subfamilies, but more recently specialists have mainly dealt with two subfamilies separated on the basis of molecular and morphological characters: Eriogonoideae and Polygonoideae (Sanchez & Kron, 2008; Burke & Sanchez, 2011). As currently circumscribed, monophyletic Polygonoideae remain a fairly distinctive clade. Members are herbs, shrubs, or lianas with ocrea, swollen nodes, flowers subtended by bracteoles, lenticular or trigonous achenes, and lobed or entire endosperm (Sanchez et al., 2011).

Within Polygonoideae, three tribes contain species native to eastern North America: Persicarieae (smartweeds), Polygoneae (knotweeds), and Rumiceae (docks). Within Rumiceae, only species in *Rumex* L. are native to the study area (*R. altissimus* Alph. Wood, *R. hastatulus* Baldwin, *R. maritimus* L., *R. salicifolius* Weinm., and *R. verticillatus* L.) Their achenes are trigonous but are easily distinguished from the archaeological specimens by their more acute angles in cross-sectional view, and their symmetrical, ovoid shape in plan-view (i.e., when viewed from above, see illustrations in Martin, 1954: 514). Their tepals, which give the flowers a winged appearance (or in the case of *R. maritimus*, toothed, bristle-like tepals), are very different from the perianths preserved on many desiccated archaeological specimens from Whitney Bluff (see Fig. 2), so a native species of *Rumex* can be positively ruled out.

Several of the smartweeds (*Persicaria* Mill.) that are native to the study area produce biconvex or discoid achenes and can easily be eliminated (*P. amphibia* (L.) Gray, *P. arifolia* (L.) Haraldson, *P. careyi* (Olney) Greene, *P. glabra* (Willd.) M. Gómez, and *P. pensylvanica* (L.) M. Gómez). Three others, *P. bicornis* (Raf.) Nieuwl., *P. hydropiper* (L.) Spach, and *P. lapathifolia* (L.) Delarbre, produce mostly biconvex or discoid achenes and rarely produce trigonous achenes, so archaeological assemblages that are composed entirely of trigonous achenes cannot come from these species. Five other smartweeds native to the study area produce only or primarily trigonous achenes somewhat similar to those found archaeologically (*P. hydropiperoides* (Michx.) Small, *P. punctata* (Elliott) Small, *P. sagittata* (L.) H. Gross, *P. setacea* (Baldwin) Small, *P. virginiana* (L.) Gaertn.). These were also examined but were found to be easily distinguishable from archaeological specimens. The achenes I observed at the Missouri Botanical Garden herbarium conform to the illustrations of Martin (1954) for several of these species (at the time, they were all considered to be members of *Polygonum*). In plan-view, in comparison to the Whitney Bluff achenes, the achenes of these species are variously (1) more symmetrical and ovoid (*P. punctata*); (2) more ovoid, with a sharper point at the apex (*P. hydropiperoides*), or; (3) lack clear faces and are only vaguely trigonous (*P. virginiana*). *Persicaria sagittata* and *P. setacea* have achenes that somewhat resemble the tubercled morphs recovered from archaeological sites in shape, but they have a smooth pericarp texture (the latter species also has much smaller achenes than any recovered archaeologically). Even more obviously (with the exception of *P. virginiana*), the adhering campanulate perianths of these species do not resemble those of the Whitney Bluff specimens (Fig. 2). In addition, within these species of *Persicaria*, the perianth almost always completely encloses the mature achene, whereas the Whitney Bluff achenes are partially exserted.

Polygoneae has recently gone through a major revision based on molecular data. As currently circumscribed, Polygoneae are monophyletic and include *Atraphaxis* L., *Duma* T. M. Schust., *Fallopia* Adans., *Knorringia* (Czukav.) Tzvelev, *Muehlenbeckia* Meisn. (including *Homalocladium* (F. Muell.) L. H. Bailey), *Polygonum* (including *Polygonella* Michx.), and *Reynoutria* Houtt. (Schuster et al., 2011). Besides the members of *Polygonum* in the strict sense sampled for this study (discussed below), there are only two species native to the study area in these genera: *F. cilinodis* (Michx.) Holub, and *F. scandens* (L.) Holub. These can be distinguished from archaeological specimens based on the shape of their achenes (ovoid in plan-view) and, in the case of *F. scandens*, by its distinctive winged tepals.

Within *Polygonum* in the strict sense, Schuster and colleagues (2011) found molecular support for three sections corresponding to the treatment of Ronse De Craene et al. (2004).

1. Species in *Polygonum* sect. *Pseudomollia* Boiss. are mostly restricted to Central Asia and the Middle East, and do not occur in North America at all (Schuster et al., 2011: 1661).
2. *Polygonum* sect. *Duravia* S. Watson is composed of two geographically distinct North American clades, subsection *Duravia* (S. Watson) Ronse Decr. & S. P. Hong of western North America, and subsection *Polygonella* (Michx.) Ronse Decr. & S. P. Hong of southeastern North America. The same close relationship between these two subgroups had previously been recovered using cladistic analyses of morphological characters (Ronse De Craene et al., 2000) and is further supported by the fact that *Polygonum* sect. *Duravia* (including *Polygonella*) does not share the pollen morphology common to all other members of *Polygonum* (Hong et al., 2005), but *Polygonella* is still treated as a distinct genus in the *Flora of North America* (Freeman, 2005). All but one member of subsection *Duravia* occur

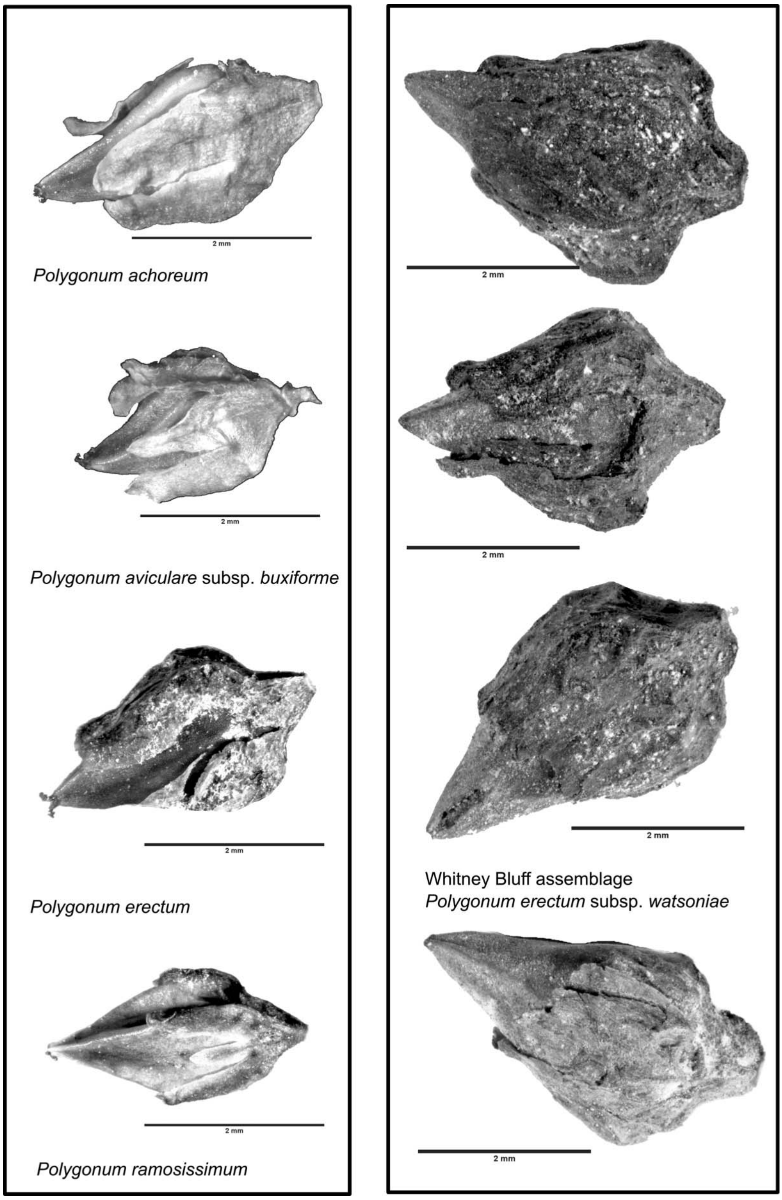

Figure 2. Left: Examples of the smooth morph achenes for each of the four taxa with perianth adhering. *Polygonum ramosissimum* Michx. is significantly more exserted from its perianth than the other three species. Right: Examples of Whitney Bluff achenes, to scale with those from modern species. Convex faces are almost universal within this assemblage, as within *P. erectum* L. (see Fig. 1, Table 3).

only in the western United States. One is very common in the Midwest (*Polygonum tenue* Michx.), but is easily ruled out by its elliptic to oblong fruits. Two species of subsection *Polygonella* occur in the study area (most are restricted to the Gulf Coast states). One of these is a perennial shrub (*Polygonum americanum* (Fisch. & C. A. Mey.) T. M. Schust. & Reveal), and the other is an annual herb (*Polygonum articulatum* L.) that grows on sand dunes and lakeshores. Both have flowers that do not resemble those preserved on archaeological specimens (having distinct rather than connate tepals) and fruits that in cross section have acute angles like those of *Rumex* species.

3. By process of elimination, only species within *Polygonum* sect. *Polygonum* remain for consideration.

Unfortunately, within *Polygonum* sect. *Polygonum* there are some unresolved taxonomic issues at the specific level. This is especially true of the common species *P. aviculare* s. str. and its closely related taxa, which are now treated as the *P. aviculare* complex by

Table 1. Achenes for the photo sample were taken from the loose materials packets of the herbarium specimens listed in Appendix 1. If many fruits were in the packet, a sample of 20 was photographed. Otherwise, all loose fruits were photographed. The measurements and observations reported in Table 3 are drawn from this photo sample.

Herbarium photo sample summary		
Species	# of plants sampled	# of achenes
Polygonum erectum	21	153
P. achoreum	10	60
P. ramosissimum	11	100
P. aviculare subsp. *buxiforme*	10	92
Total	52	405

	# of achenes: total (tubercled /smooth /indeterminate)			
Collection season	*P. erectum*	*P. achoreum*	*P. ramosissimum*	*P. aviculare* subsp. *buxiforme*
June 1–August 31	16 (14/0/2)	23 (21/1/1)	34 (34/0/0)	30 (25/5/0)
September	70 (66/4/0)	24 (24/0/0)	14 (0/14/0)	34 (31/3/0)
October 1–November 24	67 (51/16/0)	13 (6/7/0)	52 (25/27/0)	28 (6/20/2)

the *Flora of North America* (Costea & Tardif, 2004; Costea et al., 2005). Members of this complex are found all over the world as cosmopolitan weeds. The *P. aviculare* complex encompasses numerous taxa that were treated as separate species in overlapping and conflicting taxonomies for centuries (*P. aviculare* L. s. str.; *P. depressum* A. Cunn. ex Meisn. [= *P. arenastrum* Boreau]; *P. neglectum* Besser; and *P. buxiforme* Small). Costea and Tardif (2004) merged what had previously been five species into one because the previously recognized species could not be separated by chromosome number or be reliably differentiated morphologically. They also considered it likely that hybridization is frequent within the *P. aviculare* complex. Of the recognized subspecies, only *P. aviculare* subsp. *buxiforme* (Small) Costea & Tardif is native to North America (Costea & Tardif, 2004).

Specimens of *Polygonum aviculare* subsp. *buxiforme* recently reexamined by Costea et al. (2005) for the *Flora of North America*, or by Yatskievych (2013) for the *Flora of Missouri*, were included in this study. Three other native species within *Polygonum* subsect. *Polygonum* occur in the study area: *P. erectum*, *P. ramosissimum*, and *P. achoreum*. All of the other species of *Polygonum* that occur in the study area are introduced from the Eastern Hemisphere.

Achene Morphology and Dimorphism

There is a long history of attempts to distinguish species of *Polygonum* based on achene morphology (e.g., Martin, 1954; Mertens & Raven, 1965; Wolf & McNeill, 1986). Surface texture, relative width of the three faces, convexivity of the faces and edges, and color of tubercled achenes have all been used in taxonomies to distinguish species, yet these treatments frequently contradict one another. For example, while tubercled morph surface texture is sometimes diagnostic of species, it can also vary within species. In *Flora of North America* (Costea et al., 2005), *P. erectum* tubercled morphs are described as "striate-tubercled," i.e., the tubercles are arranged in rows. The specimens I examined confirm this, and most treatments agree. But other species are not so consistent. *Polygonum ramosissimum* tubercled achenes are described in *Flora of North America* as "smooth to roughened, sometimes uniformly or obscurely tubercled." Uniformly tubercled achenes have dense tubercles with no rows discernible, while obscurely tubercled achenes have tubercles that are inconspicuous or restricted to certain areas of the achene. Wolf and McNeill (1986: 478) describe *P. ramosissimum* achenes as "smooth (rarely roughened)," not recognizing any tubercled achenes for this species. Of the 59 *P. ramosissimum* tubercled achenes in my photo sample, all four of these textures are present in addition to seven achenes that are distinctly striate-tubercled, a texture not mentioned by either treatment and considered by paleoethnobotanists to be diagnostic of *P. erectum*. *Polygonum achoreum* achenes are described as uniformly tubercled in most treatments. The majority do fit that description, but 10 out of 51 tubercled achenes in the photo sample are striate-tubercled. *Polygonum aviculare* subsp. *buxiforme* achenes are described in *Flora of North America* as "coarsely striate-tubercled to obscurely tubercled"—about a quarter of those in my photo sample are coarsely striate-tubercled (Costea et al., 2005; Fig. 1). In other words, all four taxa produce the striate-tubercled achenes that most paleoethnobotanists consider diagnostic of *P. erectum*, but at different frequencies (Table 3). Martin

Table 2. Gives the formulas used to generate the morphometric measures reported in Table 3. All image analysis was completed using ImageJ open source image analysis software.

Morphometric measurements		
Measurements	Description	Procedure/Formula
Area	# of pixels within the margins of object	select image of achene, area measured in mm^2
Length	# of pixels along major axis of selected object	draw line to measure length in mm
Width	# of pixels along minor axis of selected object	draw line to measure length in mm
Shape factors		
Aspect ratio	degree of elongation; major axis divided by (mean of) minor axis (axes). Axes derived from an ellipse fitted around the selected object.	[major axis]/[minor axis]
Roundness	roughly inverse of aspect ratio, a measure of elongation of the major axis with respect to the object's area. Axis derived from an ellipse fitted around the selected object.	$4 \times ([area]/(\pi \times [major axis]$
Circularity	relationship between perimeter and area; degree of departure from a circle. 1.0 is a perfect circle, 0.0 is a straight line.	$4\pi \times [area]/[perimeter]^2$

(1954) recognized that the identification of *Polygonum* seeds to species required consideration of multiple characters including shape, size, and surface characteristics. Even taking into account all of these, Martin (1954: 514) conceded: "the process is not always easy and sure," citing variability within a species and even between the fruits on a single plant.

All of this variability is exhibited by the ostensibly *diagnostic* tubercled achenes—the smooth, late-season achenes have not previously been considered systematically. As noted above, knotweeds exhibit seasonal achene dimorphism: they produce two distinct fruit types in ratios that vary over the course of the growing season. In the past, taxonomists have considered smooth morphs to be undiagnostic. For example, in *Flora of North America* smooth achenes in *Polygonum* sect. *Polygonum* are summarized thus: "Late-season [smooth] achenes in all species are hypertrophied, olivaceous, lanceolate, exserted, and smooth. They have little taxonomic significance" (Costea et al., 2005). Wolf and McNeill (1986) and Mertens and Raven (1965) deal with late-season achenes only to note that they are more common on

Table 3. Formulas for shape descriptors are given in Table 2. Deflation refers to subequal faces that are markedly concave, resulting in a flattened achene, with the central ridge sunken or sometimes slumped over to one side (see Figs. 1 and 2).

Summary statistics by species compared to Whitney Bluff					
	Polygonum achoreum	*P. buxiforme*	*P. erectum*	*P. ramosissimum*	Whitney Bluff
Smooth morphs					
Area	3.38 ± 0.257*	2.28 ± 0.349*	3.22 ± 0.780*	4.21 ± 1.338*	5.66 ± 0.683
Length	3.20 ± 0.222*	2.69 ± 0.270*	3.23 ± 0.329*	3.64 ± 0.609*	4.16 ± 0.243
Width	1.70 ± 0.095*	1.35 ± 0.163*	1.63 ± 0.190*	1.78 ± 0.366*	2.30 ± 0.257
Circularity	0.54 ± 0.137*	0.52 ± 0.154*	0.44 ± 0.126	0.49 ± 0.091	0.46 ± 0.073
Aspect ratio	1.89 ± 0.126	2.00 ± 0.434*	1.95 ± 0.279*	2.03 ± 0.283*	1.76 ± 0.227
Roundness	0.53 ± 0.034	0.52 ± 0.108*	0.52 ± 0.072*	0.50 ± 0.07*	0.58 ± 0.069
Deflated/total	9/9	12/15	41/41	1/20	3/200
Tubercled morphs					
Area	3.34 ± 0.651	2.37 ± 0.354	3.49 ± 0.528	2.99 ± 0.761	4.15
Length	2.85 ± 0.309	2.40 ± 0.197	2.92 ± 0.202	2.79 ± 0.433	3.40
Width	1.88 ± 0.222	1.55 ± 0.171	1.88 ± 0.208	1.63 ± 0.181	2.23
Circularity	0.64 ± 0.199	0.65 ± 0.515	0.56 ± 0.104	0.56 ± 0.086	0.55
Aspect Ratio	1.47 ± 0.125	1.52 ± 0.156	1.51 ± 0.147	1.65 ± 0.192	1.51
Roundness	0.69 ± 0.058	0.66 ± 0.063	0.67 ± 0.065	0.61 ± 0.067	0.66
Striate-tubercled/total	10/51	14/62	131/131	7/59	1/1

* Indicates a significant difference from the Whitney Bluff assemblages according to Tukey's honest significant difference test, $P < 0.05$.

some species than others, and to point out that plants bearing such fruits have been mistaken for separate species in the past. This study by necessity asks whether or not the morphology of smooth achenes is diagnostic of particular species, since the goal here is to identify archaeological assemblages composed mostly, or occasionally exclusively, of smooth achenes.

Materials and Methods

I concur with Fritz's (1986) observation that the two samples of *Polygonum* from Whitney Bluff are very similar and probably came from the same context. They are treated as a single sample in this analysis. The morphometric analysis of achenes was performed using digital images of a photo sample. The Whitney Bluff assemblage is only one of 40 archaeological assemblages that I analyzed as part of a larger study of pre-Columbian agricultural practice. Per sampling protocol for the larger study, the size of the photo sample was determined by the weight of the entire assemblage. I photographed one achene per 0.01 g. I chose to subsample by weight rather than by count in order not to bias the sample against poorly preserved carbonized assemblages, where fewer measurable achenes were present as a percentage of the total identifiable knotweed. Although the Whitney Bluff *Polygonum* was not carbonized, I adhered to this sampling strategy for the sake of consistency. I randomly selected a photosample of 80 achenes from 32-57-3a and 120 from 32-57-5c. Many of the Whitney Bluff achenes retain some or all of their perianth parts. The presence of the perianth or parts of the perianth may somewhat inflate area and width measurements, but the perianths of the Whitney Bluff achenes generally tightly conform to the shape of the underlying fruit (Fig. 2). Of the 1307 achenes in the two samples, all but two were smooth morphs. The two tubercled morphs were also photographed and measured and are described below (Fig. 3). Measurements of length and width reported here are very similar to those reported by Fritz (1986) on two different subsamples of 100 achenes.

A total of 73 herbarium specimens of *Polygonum achoreum*, *P. aviculare* subsp. *buxiforme*, *P. erectum*, and *P. ramosissimum* from the Missouri Botanical Garden and the National Herbarium were examined (Appendix 1). The photo sample used for morphometric analysis was taken from 51 of these (Table 1). These species were sampled because (1) they had fruit and perianth morphology similar enough to that of the Whitney Bluff assemblage to warrant comparison, (2) they were native to pre-Columbian North America and, (3) they occur in the region where ancient knotweed cultivation is documented. I considered *P. erectum* and *P. achoreum* as two different species (Mertens & Raven, 1965; Löve & Löve, 1982; Wolf & McNeill, 1986; Costea et al., 2005; Yatskievych, 2013). I did not consider specimens of *P. aviculare* other than *P. aviculare* subsp. *buxiforme*, although given the messy taxonomic history, many of these specimens may be native plants or hybridized with native plants. Only loose fruits were removed from the herbarium sheet packets on specimens collected since 1950, per the sampling regulations of the Missouri Botanical Garden and the National Herbarium. These loose fruits comprise the photo sample, whose morphology is described in detail below. Because taxonomy within *Polygonum* has varied greatly over the past century, whenever possible I only used samples that had been examined for the latest treatments in the *Flora of North America* and/or the *Flora of Missouri* (Costea et al., 2005; Yatskievych, 2013). Where I had to use specimens that were not examined for these treatments, I double-checked the identification myself using keys from those treatments.

I took grayscale photographs of each fruit selected for the photo sample in the same orientation with the widest of their three sides down (Figs. 1, 2) using a Zeiss SV11 microscope (Zeiss, Oberkochen, Germany) fitted with a manual stage, z-stepping motor, and an AxioCam MRC5 digital camera (Zeiss). I recorded the texture of each pericarp as "Smooth" or "Tubercled." Using ImageJ open source software, I measured several shape factors and area, length, and width. In order to take area and shape measurements, the object to be measured must be thresholded (differentiated from the background on the basis of color or shade). With solid objects such as seeds on a white or black background it is usually easy to select all non-white or non-black pixels, but it is sometimes necessary to manually trace the outline of fruits that are similar in color to the background. The shape factors collected for each achene are aspect ratio, roundness, and circularity. Formulas for each are given in Table 2. Length and width are the two longest perpendicular straight line distances across the image of the achene. All morphometric measurements were taken using ImageJ.

Results and Discussion

The Whitney Bluff assemblage is most obviously different from a normal harvest of erect knotweed achenes in that it is very nearly monomorphic: smooth morph achenes are overwhelmingly predominant. In the recent herbarium specimens examined for this study, the ratio of smooth to tubercled morphs

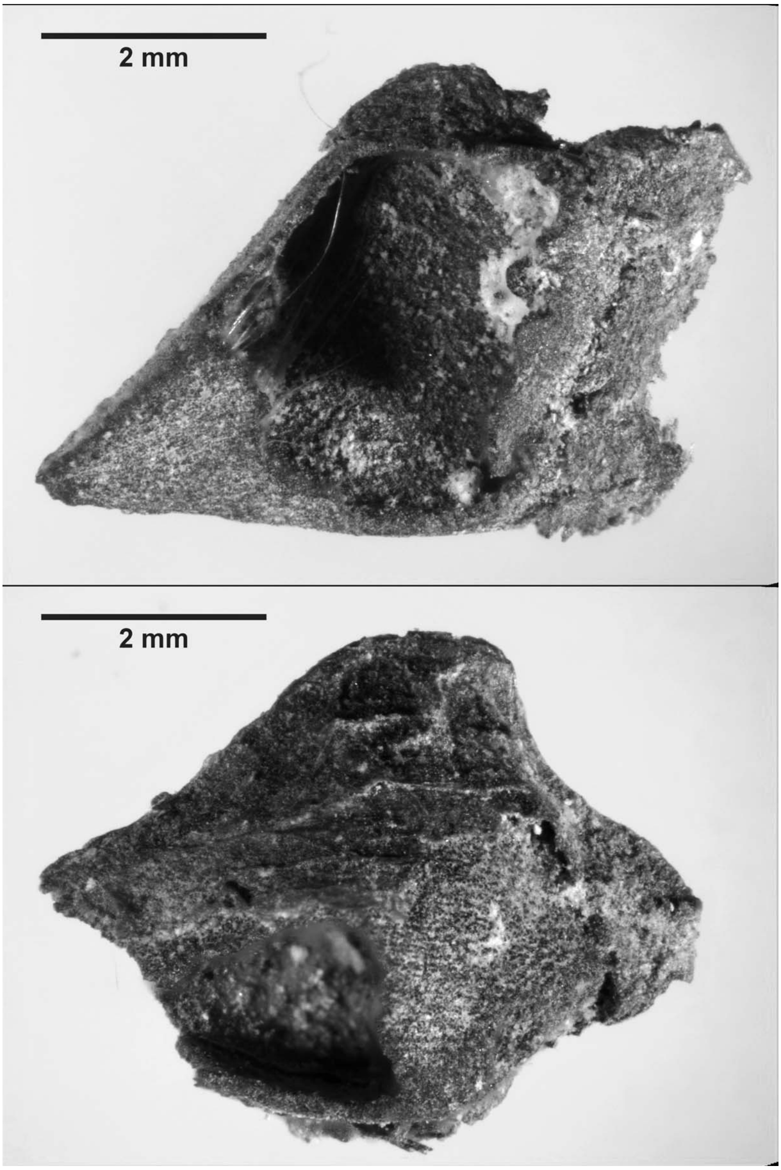

Figure 3. Whitney Bluff tubercled morphs, with striate-tubercled surface texture. Compare to tubercled morphs in Figure 1.

varies from species to species, among individuals of the same species, and according to the season (Table 1). Seasonality is certainly a factor for all four taxa: smooth achenes are rare before the middle of September. But even with only a small photo sample of five to 20 seeds from each plant, there were only two instances of uniformly smooth morph photo samples from any one plant. This indicates that smooth morphs rarely predominate in any of the four taxa: even late in the season, tubercled morphs are present even in a small random sample of fruits. The two exceptions were both *Polygonum ramosissimum* specimens, one collected on September 22 and the other on October 23. After analyzing the photo samples from these plants ($n = 12$ and $n = 14$, respectively), I checked whether the plants in question had really produced only smooth morphs. All of the hundreds of observable achenes on both specimens were smooth morphs. Thus *P. ramosissimum* does occasionally produce monomorphic assemblages of smooth morph achenes. Further study of this species is necessary to determine what conditions produce this effect. However, the Whitney Bluff achenes are easily distinguished from those of *P.*

ramosissimum. Smooth achenes of *P. ramosissimum* are almost completely exserted from their perianth. Indeed, plants with this fruit morphology were once thought to be a different species, *P. exsertum* Small, but are now considered a variant of *P. ramosissimum* (Mertens & Raven, 1965: 85). In contrast, Whitney Bluff smooth achenes are more enclosed in their perianths, similar to those of the other three species examined (Fig. 2).

The Whitney Bluff assemblage resembles *Polygonum erectum*, as opposed to any of the other three species, in having smooth morph achenes with convex rather than plane or concave faces. This criterion refers to the degree of fruit concavity as observed on the two subequal faces of the achene (see Figs. 1, 2). When these faces are markedly concave, the achene becomes flattened, with the central ridge sunken or sometimes slumped over to one side. Mertens and Raven (1965: 85) described the late-season achenes of *P. ramosissimum* as "flattened and wrinkled." This description is apt and also applies to most of the smooth morphs of *P. aviculare* subsp. *buxiforme* and *P. achoreum* observed for this study, but not to those of *P. erectum*. *Polygonum erectum* smooth achenes, like the Whitney Bluff achenes, almost always have convex faces when mature, giving them a plump appearance in comparison to the other species (Fig. 1, Table 3). *Polygonum erectum* is the only species that produces a majority of plump, smooth morphs, although a small minority of smooth *P. aviculare* subsp. *buxiforme* achenes was also relatively convex.

The Whitney Bluff smooth morphs are significantly different from all four modern taxa in terms of size, whether measured by area, length, or width, as expected of a domesticated plant (Table 3). Fruit circularity indicates that the Whitney Bluff assemblage, *Polygonum erectum*, and *P. ramosissimum* form a similar group in terms of shape, and that *P. aviculare* subsp. *buxiforme* and *P. achoreum* are significantly different (Table 3).

Of the 1307 achenes with observable pericarps in the Whitney Bluff assemblage, two were tubercled morphs. Both exhibit the striate-tubercled surface texture and shape typical of *Polygonum erectum* tubercled morphs (Fig. 3, compare with Fig. 1). All four taxa sometimes produce striate-tubercled achenes, but only *P. erectum* produces a majority of this type (Table 3). Only one is complete enough to be measured, and it is compared to the tubercled morphs from the herbarium samples in Table 3. Similar to the smooth morphs, the Whitney Bluff tubercled achene is also uncommonly large and groups by circularity with *P. erectum* and *P. ramosissimum*. The two tubercled achenes from Whitney Bluff are thus most parsimoniously identified as *P. erectum*.

This study suggests that the morphology of smooth morph (late-season) achenes within *Polygonum* sect. *Polygonum*, which has long been considered taxonomically useless, does vary systematically. Both the size and shape of smooth morphs differ among the four taxa considered here (Table 3), suggesting that further studies of smooth achene morphology may be taxonomically fruitful. These results also suggest that paleoethnobotanists should be more cautious when using pericarp surface texture to identify assemblages to species. Tubercled morph surface texture cannot be used to positively determine the species when only a few achenes are preserved (as often occurs with archaeological assemblages) because all four of the taxa examined here occasionally produce striate-tubercled achenes. As with smooth morphs, both area and circularity are useful for distinguishing between species. Mean area can be used to reliably distinguish *P. ramosissimum* and *P. aviculare* subsp. *buxiforme* from the other species, but *P. erectum* and *P. achoreum* have similarly sized tubercled achenes (Table 3). In terms of circularity, for both tubercled and smooth morphs, *P. ramosissimum* and *P. erectum* form one group, and *P. aviculare* subsp. *buxiforme* and *P. achoreum* form another (Table 3). Using a combination of metric and non-metric criteria, small assemblages of tubercled morphs or even single achenes can be more confidently assigned to species. For example, the Whitney Bluff tubercled achene groups with *P. erectum* and *P. ramosissimum* in terms of circularity and its surface texture indicates that it is more likely to belong to the former. Since it is much larger than normal for any of the species, area is not helpful in this case.

The Whitney Bluff achenes are identified as a subspecies of *Polygonum erectum*, rather than one of the other possible species, on the weight of several lines of evidence. Circumstantial evidence strongly supports the hypothesis that the Whitney Bluff achenes came from erect knotweed plants: *P. erectum* was cultivated for ca. 1500 years; it is documented in clear storage, cooking, and consumption contexts at hundreds of sites; and there is no evidence that any other species of knotweed was ever cultivated. But strong evidence is required to argue for an extinct domesticate, and other possible explanations must be ruled out. Of the four taxa of *Polygonum* native to the study area, only *P. ramosissimum* occasionally produces monomorphic harvests of smooth achenes. But the Whitney Bluff achenes are distinguishable from *P. ramosissimum* smooth morphs on the basis of two clear characters: they are not nearly as exserted from their perianths and they do not have concave faces. The latter character also differentiates the Whitney Bluff achenes from those of *P. achoreum* and *P. aviculare* subsp. *buxiforme*, which in any case are shaped quite differently, being much more circular in plan-view (Table 3). The two tubercled morphs from Whitney Bluff, with their striate-tubercled surface texture, also support the designation of the Whitney Bluff assemblage as a subspecies of *P. erectum*.

This conclusion could be further strengthened by extracting DNA from the Whitney Bluff achenes and comparing it to that of modern species. Ancient DNA (aDNA) could also help answer questions about how the process of domestication unfolded. It is probable that aDNA is preserved in the Whitney Bluff *Polygonum* achenes: two previous projects have successfully extracted DNA from *Chenopodium berlandieri* seeds (Kistler & Shapiro, 2011) and *Cucurbita* L. seeds (Kistler et al., 2015) from nearby rock shelters that are the same age or older than the *Polygonum* cache at Whitney Bluff. Although permission has been granted to attempt aDNA extraction from the Whitney Bluff *Polygonum*, this project is hampered by the fact that information about genetic variation within *Polygonum* is very low-resolution. An initial attempt to use plastid genome variation to characterize the four taxa analyzed here was a failure: plastid genome variability was found to be too low (Logan Kistler, pers. comm.). Assembly of a nuclear genome for *P. erectum* is the next step in this project and is currently underway.

Although the archaeological specimens described here are most similar to *Polygonum erectum*, they differ from modern *P. erectum* in three ways. Average size for the Whitney Bluff achenes is greater than that of any of the four modern taxa, whether measured by area (as determined from photographs), length, or width (Table 3). They are also distinguished by a great reduction in achene dimorphism. Of the 32 *P. erectum* herbarium specimens and hundreds of wild-growing plants I observed during the course of this study, none produced a monomorphic harvest. Even in late October and early November, *P. erectum* plants still usually produce a majority of tubercled morph fruits. Preliminary data indicate that a typical late October/early November harvest of a population of *P. erectum* plants will yield a proportion of smooth morphs between 30% and 70% (Mueller, 2017a). Both the Whitney Bluff assemblage and the Hill Creek assemblage are thus far outside the normal range of variation. Because the plant represented in these assemblages produces fewer tubercled morphs, which have thicker pericarps, than *P. erectum* subsp. *erectum*, average pericarp thickness would be greatly reduced for any given harvest from the former. Both the increase in fruit size and the reduction of germination inhibitors are classic indicators of domestication syndrome in annual seed crops. Considering the extensive contextual evidence for cultivation from archaeological sites, this material should be considered an extinct domesticate. It is therefore recognized herein as a new subspecies of *P. erectum*. The probable selective pressures that caused the evolution of the domesticated subspecies documented in this study have been explored experimentally (Mueller 2017a) and archaeologically (Mueller 2017b, 2017c).

TAXONOMIC TREATMENT

Polygonum erectum L. subsp. **watsoniae** N. G. Muell., subsp. nov. TYPE: U.S.A. Arkansas: Benton Co., Whitney Bluff rock shelter (3BE20), 1932, *W. Henbest & C. Finger Jr. 32-57-5c* (holotype, UARK No. 20121!; isotype, Arkansas Museum!).

Diagnosis. *Polygonum erectum* L. subsp. *watsoniae* N. G. Muell. most closely resembles *P. erectum* subsp. *erectum*, but can be distinguished from it by greatly reduced achene dimorphism: almost all achenes have smooth pericarps, 30–70 μ thick, with very few achenes having striate-tubercled pericarps 120–150 μ thick; smooth achenes are larger than those of *P. erectum* subsp. *erectum*, averaging 4.2 × 2.3 mm, and are shaped differently, having a lower aspect ratio (mean 1.76); they also differ from smooth achenes of *P. ramosissimum* Michx. in having a plump appearance caused by convex subequal faces, unwrinkled pericarps, and retained perianths that cover > 50% of the length of the achene.

Discussion. Assemblages of *Polygonum erectum* subsp. *watsoniae* have been found in excavations of Native American sites in Arkansas and Illinois dating to ca. AD 1000–1400, along with the seeds and fruits of other plants cultivated by the ancestors of Native Americans. This domesticated subspecies is now believed to be extinct. Its name commemorates archaeologist Patty Jo Watson, whose pioneering research was instrumental to the recognition of the Eastern Agricultural Complex.

The holotype preserved at UARK is a subsample taken from one of the two large samples of Whitney Bluff achenes that are preserved at the Arkansas Museum; the remainder of that sample constitutes an isotype.

Paratype. U.S.A. **Arkansas:** Benton Co., Whitney Bluff rock shelter (3BE20), 1932, *W. Henbest & C. Finger Jr. 32-57-3a* (Arkansas Museum).

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Appendix 1. Herbarium specimens examined for this study.

HS ID	Herbarium	Number	Determined by	State	Collection month	Photo sample
Polygonum achoreum S. F. Blake						
11	US	1826799	Costea	MN	June	2
51	MO	2224128	Katz	NE	June	2
10	US	2876171	Costea	MT	July	5
50	MO	3667043	Rhode	ND	July	5
8	US	2329091	Costea	QC	Aug.	4
9	US	1826754	Costea	SD	Aug.	5
7	US	2004170	Costea	ND	Sep.	5
49	MO	4957772	Cusick	OH	Sep.	9
53	MO	5839142	Yurtseva	MO	Sep.	10
52	MO	5288218	Yurtseva	MO	Oct.	13
Subtotal						60
Polygonum aviculare L. subsp. *buxiforme* (Small) Costea & Tardif						
1	US	1465810	Costea	KY	June	3
2	US	1465809	Costea	KY	June	1
6	US	1436192	Costea	AK	June	5
4	US	2235643	Costea	IA	July	3
55	MO	2588081	Hinds	IL	July	
3	US	1113306	Costea	ME	Aug.	5
58	MO	4074038	Brant	MO	Aug.	13
5	US	1925995	Costea	RI	Sep.	5
54	MO	4641381	Brant	MO	Sep.	
56	MO	3671302	Hinds	AL	Sep.	8
57	MO	4005057	Hinds	TX	Sep.	20
70	MO	2158865	Brant	MO	Oct.	22
72	MO	5093323	Hudson	MO	Oct.	
71	MO	5093336	Hudson	MO	Oct.	7
Subtotal						92
Polygonum erectum L.						
16	US	2727807	F. R. Fosberg	VA	June	5
38	MO	5393684	Reed	KY	June	
39	MO	5393682	Reed	KY	June	
48	MO	5400840	Moe	IL	June	
17	US	2667449	Costea	OH	Aug.	2
34	MO	4292384	Brant	MO	Aug.	3
42	MO	3450151	Thomas	TN	Aug.	6
44	MO	4292383	Brant	MO	Aug.	
12	US	1925748	Costea	PA	Sep.	5
13	US	298208	Costea	PA	Sep.	4
15	US	3495558	L. B. Smith	PA	Sep.	3
18	US	228405	Costea	IN	Sep.	3
20	US	309488	Costea	IN	Sep.	4
21	US	797318	Costea	WV	Sep.	3
29	US	2746624	Kral	AL	Sep.	
30	US	2605290	Costea	NY	Sep.	

Appendix 1. Continued.

HS ID	Herbarium	Number	Determined by	State	Collection month	Photo sample
33	MO	4292359	Brant	MO	Sep.	
35	MO	5814504	Smith	PA	Sep.	11
36	MO	4074041	Brant	IL	Sep.	5
37	MO	6152618	Reid and Gentry	AR	Sep.	5
40	MO	5393680	Pretz	PA	Sep.	10
41	MO	3680707	Hill	MD	Sep.	
43	MO	3476886	Raven	MO	Sep.	
45	MO	3913996	Christ	MO	Sep.	
46	MO	3226768	Brant	MO	Sep.	17
47	MO	3493891	Brant	MO	Sep.	
65	MO	5151138	Brant	MO	Sep.	
14	US	298794	Costea	PA	Oct.	5
19	US	2664048	Costea	KY	Oct.	4
31	MO	1135807	Brant	MO	Oct.	10
32	MO	2158858	Brant	MO	Oct.	10
69	MO	5159294	Mueller	MO	Oct.	18
22	Washu Pbot	65	Blake	MO	Oct.	20
Subtotal						153
Polygonum ramosissimum Michaux						
23	US	2067911	Webster and Wilbur	TX	June	4
60	MO	5970916	Brant	MO	June	10
59	MO	4236452	Brant	MO	Aug.	10
64	MO	2005129	Katz	ND	Aug.	10
24	US	1125	Costea	TX	Sep.	
25	US	1888718	Costea	KY	Sep.	
73	MO	4J657068	Summers	MO	Sep.	14
28	US	2802647	Costea	KY	Sep.	
26	US	1885904	Costea	TX	Oct.	
27	US	329	Costea	MO	Oct.	
61	MO	6013115	Brant	MO	Oct.	10
62	MO	1757520	Brant	MO	Oct.	4
63	MO	5387653	Skykora	OK	Oct.	4
66	MO	4610390	Henderson	MO	Oct.	12
67	MO	4074031	Brant	MO	Oct.	12
68	MO	5074499	Jacobs	MO	Oct.	10
Subtotal						100
Total achenes analyzed						405