Marshelder (*Iva annua* L.) Seed Morphology and Patterns of Domestication in Eastern North America

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Abstract

Domestication of the extinct eastern North American crop, marshelder (*Iva annua* L. var. *macrocarpa* Jackson) is investigated through quantitative analysis of samples from archaeological sites. Change in marshelder achene (fruit) size over time sheds light on patterns of regional and subregional domestication processes and patterns of diffusion. The hypothesis that marshelder was introduced into the Cumberland Plateau of eastern Kentucky rather than domesticated *in situ* is evaluated through spatial and temporal statistical tests from measurements of achene size collected by researchers throughout eastern North America. Statistical analyses show that although there is some evidence for increased achene size under domestication, this pattern does not indicate a smooth and gradual trend. Patterns of variability in achene size, in contrast, seem to reflect geographical location rather than temporal placement. These data support an introduction of marshelder to eastern Kentucky from the Illinois River Valley, where the first domesticates are found.
Dedication

For Sam and Lena
Acknowledgments

I would like to thank the faculty, staff, and graduate students of The Ohio State University Anthropology Department for their indefatigable support, especially my advisor, Kristen J. Gremillion. I would also like to thank George Crothers (University of Kentucky) and Charles Faulkner for their generous contribution of hard-earned data.
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# Table of Contents

Abstract ............................................................................................................................... ii

Dedication .......................................................................................................................... iii

Acknowledgments.............................................................................................................. iv

Vita ...................................................................................................................................... v

Fields of Study .................................................................................................................... v

Major Field: Anthropology ................................................................................................. v

Table of Contents ............................................................................................................... vi

List of Tables ................................................................................................................... viii

List of Figures .................................................................................................................... ix

Chapter 1: Introduction ...................................................................................................... 1

Chapter 2: Background ..................................................................................................... 14

Chapter 3. Data Analysis ................................................................................................. 19

Chapter 4: Discussion ....................................................................................................... 34
Chapter 5: Conclusion....................................................................................................... 40

References......................................................................................................................... 42

Appendix A.: Sites by time period with mean length, mean width, and U.S. state (54 archeological sites, 11 modern wild collection sites) ................................................................. 49

Appendix B.: Coefficient of variation (CV) confidence intervals (L_1, L_2).................... 52

Appendix C. Histograms.................................................................................................. 55

Appendix D: Boxplots ...................................................................................................... 62
List of Tables

Table 1: Twelve Archaeological sites for which radiocarbon dates were available (n=994). Hooton Hollow, Thor’s Hammer and Collins excluded from tests using CV due to low n. ........................................................................................................................................ 23
List of Figures

Figure 1: Map of significant sites discussed (adapted from Smith 1992) ......................... 10

Figure 2: Achene (right) and kernel (left) of modern wild marshelder (Photo: Kristen J.
Gremillion) ...................................................................................................................................... 16

Figure 3: Linear regressions of site mean achene measurements vs. years calibrated BP,
and individual achene measurements vs. years calibrated BP .............................................. 26

(a) Linear regression with 95% confidence intervals for mean achene length vs. years
calibrated BP (n=16, t=11.15, p<0.0001, r²=0.4315) ........................................................................ 26

(b) Linear regression with 95% confidence intervals for mean achene width vs. years
calibrated BP (n=16, t=11.78, P<0.0001, r²=0.3996) ............................................................ 26

(c) Linear regression with 95% confidence intervals for individual achene lengths from
11 sites vs. years calibrated BP (n=994, t=-10.71, p<0.0001, r²=0.1037) .................. 26

(d) Linear regression with 95% confidence intervals for individual achene widths from 11
sites vs. years calibrated BP (n=994, t=-10.26, p<0.0001, r²=0.09) ................................. 26

Figure 4: Mean site achene length by period and region (n=52) ............................................ 27

Figure 5: Coefficient of variation (CV) for length of marshelder achenes with 95%
confidence intervals. Horizontal lines indicate CV; vertical lines represent the range
between upper and lower 95% confidence intervals of CV. AP=Appalachian
(Cumberland Plateau) sites, WT=Western Tennessee sites, OZ=Ozark sites, IL=Illinois sites, MW=modern wild samples. Sites are listed from left to right in order of appearance in the archaeological record.

Figure 6: Simple linear regressions of achene measurements from Cumberland Plateau sites only.

(a) Linear regression with 95% confidence intervals for individual achene lengths of eight Cumberland Plateau sites vs. years calibrated BP (n=461, t=-3.49, p=0.0005, r²=0.0259).

(b) Linear regression with 95% confidence intervals for individual achene widths of eight Cumberland Escarpment vs. years calibrated BP (n=461, t=-2.72, p<0.0001, r²=0.0159).

Figure 7: Waller Duncan K-ratio t-test for length grouped visually in Venn diagram.

AB=Alred Bluff, RH=Rogers/Haystack, CR=Courthouse Rock, TH=Thor’s Hammer, NK=Newt Kash Hollow, HH=Hooton Hollow, CS=Cloudsplitter, SCM=Salts Cave Middle, BB=Big Bone Cave, SCU=Salts Cave Upper, CN=Collins, CA=Cahokia-ICT.

Figure 8: Thor's Hammer achene length (mm), n=16
Figure 9: Thor's Hammer achene width (mm), n=16
Figure 10: Salts Cave Upper achene length (mm), n=239
Figure 11: Salts Cave Upper achene width (mm), n=239
Figure 12: Salts Cave Middle achene length (mm), n=235
Figure 13: Salts Cave Middle achene width (mm), n=235
Figure 14: Rogers, Haystack achene length (mm), n=92 ................................................. 56
Figure 15: Rogers, Haystack achene width (mm), n=92 .................................................. 56
Figure 16: Newt Kash achene length (mm), n=100........................................................... 57
Figure 17: Newt Kash achene width (mm), n=100........................................................... 57
Figure 18: Hooton Hollow achene length (mm), n=11..................................................... 57
Figure 19: Hooton Hollow achene width (mm), n=11..................................................... 57
Figure 20: Courthouse Rock achene length (mm), n=98.................................................. 58
Figure 21: Courthouse Rock achene width (mm), n=98.................................................. 58
Figure 22: Collins achene length (mm), n=19 ................................................................. 58
Figure 23: Collins achene width, n=19 ............................................................................. 58
Figure 24: Cold Oak (Early Woodland) achene length (mm), n=21 ................................. 59
Figure 25: Cold Oak (Early Woodland) achene width (mm), n=21 .................................. 59
Figure 26: Cloudsplitter achene length (mm), n=143 ....................................................... 59
Figure 27: Cloudsplitter achene width (mm), n=143 ....................................................... 59
Figure 28: Cahokia ICT achene length (mm), n=65 ......................................................... 60
Figure 29: Cahokia ICT achene width (mm), n=65 .......................................................... 60
Figure 30: Big Bone Cave achene length (mm), n=-206 .................................................. 60
Figure 31: Big Bone Cave achene width (mm), n=206 ..................................................... 60
Figure 32: Alred Bluff achene length (mm), n=103 ......................................................... 61
Figure 33: Alred Bluff achene width (mm), n=103 .......................................................... 61
Figure 35: Boxplot of width by region; AP=Cumberland Plateau, IL=Illinois, OZ=Ozarks, WT=Western Tennessee/Kentucky .......................................................... 63
Figure 36: Boxplot of length by period; 2=Terminal Archaic, 3=Early Woodland, 4=Middle Woodland, 5=Early Late Woodland, 6=Late Woodland, 7=Late Prehistoric.. 64

Figure 37: Boxplot of width by period; 2=Terminal Archaic, 3=Early Woodland, 4=Middle Woodland, 5=Early Late Woodland, 6=Late Woodland, 7=Late Prehistoric.. 65

Figure 38: Boxplot of width by years calibrated BP ........................................................ 66

Figure 39: Boxplot of length by years calibrated BP...................................................... 67
Chapter 1: Introduction

Seed morphology can provide domestication researchers with much-needed information about the rates, patterns, and diffusion of domesticates (Fuller, et al. 2012; Gremillion 1993; Harlan, et al. 1973; Smith 1985; Yarnell 1981). Genetic change observed in domestication is a biophysical imprint resulting from the selective environment created by a long-term human adaptive strategy. Tracking the domestication process through the morphological changes of a domesticated plant can provide one of the few windows through which archaeologists can view the selective pressures created by prehistoric interactions with plants. Eastern North America is one region which researchers have described in great detail morphological evidence for plant domestication in the set of native crop plants known as the Eastern Agricultural Complex (EAC) (Linton 1924). Less is known, however, about the cultural practices and large-scale populational patterns that influenced the selective environments in which EAC crops underwent morphological changes.

One of the major domesticates of the EAC is the weedy annual marshelder or sumpweed (*Iva annua* L. var. *macrocarpa* Jackson). Research on this plant for over 50 years has demonstrated that selection for larger seeds and fruits (achenes) took place under human influence between 3620 and 600 years cal. BP. The domesticated form of
marshelder became extinct in the Late Prehistoric around 600 BP, probably due to disuse and introgression with the wild morph. Wild marshelder, previously to its domestication—as today—had an average achene length of around 3 mm, never surpassing 4.5 mm, whereas domesticated marshelder often reached 9 mm, frequently documented with a mean length of 6 mm in archaeological samples. Smith (1992) has demarcated the minimum measurement to consider marshelder domesticated at 4.0-4.2 mm long.

This thesis expands upon the work of the past 50 years by more closely examining temporal trends in average achene size, and by adding consideration of the amount and patterning of variation in this trait. The data used to accomplish this task are published and archived measurements of both archaeological and modern marshelder achenes from the Illinois River Valley, the Ozarks, western Tennessee, and the Cumberland Plateau. I analyze temporal and spatial patterns of variation in achene size in order to shed light on culturally influenced selective pressures arising from the management and transmission of this crop plant.

Selective Pressures on Seed Morphology

The selective environment can be easily changed by anthropogenic activities. Seed size, like many highly conserved reproductive traits, is one the least plastic traits in a plant, yet will still respond to selective extremes. The selective pressures of a seedbed, for instance, are distinct from those of non-human landscapes (Harlan et al. 1973). In
wild scenarios of high interspecies competition, higher amounts of smaller seeds (r-selected) are a preferable adaptation to smaller amounts of larger seeds (K-selected). However, in a seedbed of the same or similar species, where tilling or digging sticks are involved, seeds are often planted deeper, making larger seeds more advantageous (Harper, et al. 1970) because each needs more endosperm to provide the duration of energy required to crest the soil horizon.

When only the large seeds are harvested to be consumed or to store for planting next season, disruptive selection may occur, in which it is to the advantage of some early-maturing, small seeds to “escape” (Harlan, et al. 1973), before the larger ones are selected. When stands of plants are thinned, there is a tendency to for seeds to become larger during the life cycle of individual plants. When lower branches are cut, more energy is focused on fewer flowers and seeds. This growth pattern can be maintained by careful tending to garden plots (Harlan, et al. 1973).

Seed size can also be affected by human harvesting, in which selective pressure eventually results in what is known as the “sunflower effect”, or “terminalization” (Harlan, et al. 1973). This growth pattern is caused by a simultaneous intentional selection for larger seeds, and time of year a plant is harvested, which can cause an inadvertent selection for uniform maturation of seeds. When a plant’s flowering takes place throughout the season, the later infilling of fruit is spread out temporally, resulting in different seed sizes at differing stages of maturity existing simultaneously on a plant at
any given harvest time. When a plant’s primary means of dispersal is human sowing from previously harvested seed, there is a selective tendency for a plant to invest less energy into branching, and “terminalize” its flowers and seed to be more effectively collected, as seen in wild vs. domesticated sunflower. This could be generally characterized as a uniformity of maturation due to the plant’s life cycle being more controlled than in the wild, but researchers have disputed the exact outcome. “Great variation in seed size may, therefore, be expected in cultivated cereals, but they are usually (not always) larger than seeds of the wild races” (Harlan, et al. 1973). Smith (1985) contradicts the effect of maturation over a narrower range of time, stating that it would result in a narrower range in fruit size. Baker (1971:34) states that “rapid and uniform germination has been selected for even when the seeds are not the edible part of the plant…”.

Marshelder and the EAC

Of the plants associated with the EAC, marshelder is one of five species with prehistoric morphological evidence for domestication, along with chenopod (Chenopodium berlandieri), pepo squash (Curcubita pepo), bottle gourd (Lagenaria spp.), and sunflower (Helianthus annuus). Other plants often included in the EAC, with extensive archaeological evidence for intensive utilization and likely intentional cultivation show no morphological signs of domestication (i.e., larger seeds/fruit, non-shattering seed heads, thinner seed coats). These include amaranth (Amaranthus spp.),
maygrass (*Phalaris caroliniana*), giant ragweed (*Ambrosia trifida*), erect knotweed (*Polygonum erectum*), and little barley (*Hordeum pusillum*). All of these domesticated and cultivated plants are found in various combinations throughout eastern North America, beginning around 3800 cal. BP (Smith and Yarnell 2009). Melvin Gilmore spurred research into the EAC upon discovery of many of these plants in association in Ozark “Bluff-Dweller” rock shelters (Gilmore 1931). Research increased in depth and breadth when botanical flotation methods began to be utilized in the 1970s. Now, with a series of radiocarbon dates from hundreds of archaeological sites, the EAC is one of the most well-documented primary centers of domestication in the world, along with the Near East and Mesoamerica (Smith 2011).

Marshelder achene size increased over time in eastern North America (Jackson 1960; Smith, et al. 1992; Yarnell 1972; Yarnell 1981), quickly surpassing maximum wild dimensions (4.5 mm) in the Late Archaic period (ca 5000 to 3000 BP) and increasing gradually thereafter. As Yarnell (1981) notes, there are some exceptions to this trend in mean achene size. Rather than being considered problematic, these anomalies can be used to better understand the large-scale cultural behavior that led to this selection. Regional patterns, timescale data, and measurements of achene size mean and variation per archaeological site can contribute to our understanding of the types of human behavior that led to the domestication of marshelder in eastern North America.
Protracted Transition

Findings in archaeology have influenced domestication research, moving the paradigm from a “rapid transition” to a “protracted transition” (Allaby 2010). Archaeological theory over the past few decades has also moved from a dualistic description of foraging and farming to attempts to describe the “middle ground” societies that do not fit into either subsistence mode.

As archaeological records get more detailed in the Near East, Mesoamerica, and eastern North America, it has become apparent that societies exist for thousands of years in this state of “transition”, using subsistence strategies that must have been more than sufficiently adapted to have operated economically for such a duration. These were societies of people living rich lives, making subsistence choices based on rich cultural and ecological histories, not simply hunting-gathering societies in transition from scarcity of resource depression to the abundance of agriculture’s cornucopia. Smith (2001) has argued that in models attempting to describe these “middle ground” societies, domestication should be removed from both the boundary between hunting-gathering and the “middle ground” and likewise removed from the boundary between the “middle ground” and intensive agriculture. Domestication, according to Smith, is a major occurrence in a cultural history, but not indicative of the type of subsistence economy. This distinction liberates the process of domestication from being linked intrinsically to any one type of society, which is particularly useful concerning EAC crop use in North
America. The artifacts and cultural associations with EAC crops, especially marshelder, range from semi-nomadic societies organized at the band level, to sedentary Mississippian societies incorporating EAC crops in with their plots of Mesoamerican imports, maize, squash, and beans. Most of the societies in eastern North America utilizing the EAC engaged in what Smith (2001) would call “low-level food production”. This indicates the fact that many of these societies incorporated domesticates into a lower proportion of a larger subsistence strategy of hunting and collecting, but not necessarily the level of selective pressure that human populations had on these crops. Marshelder certainly could not have changed so drastically in size had there not been some sort of force of evolution acting upon it, most likely artificial selection.

If the theoretical framework of protracted transition is adopted, there are a number of expectations that should be applied to domesticates that are distinct from the expectations of the rapid transition model. Most of these expectations are outlined by Allaby (2010) to be applied to genetic studies, however they can be applied to this study of one phenotypic trait. The following are some expectations of the protracted transition model to be considered during investigation of seed size evolution, and the assumed origin of marshelder in the Illinois River Valley.

1. Protracted transition occurs because selection is weak or the net effect of selection is weak, or in a case where selection is weak for a long time, then strong.
2. Traits are selected separately, rather than simultaneously, as the rapid transition suggests. For this reason, length and width are considered separately in this thesis.

3. If selectively neutral mutants meet from two different regions, they can have a selectively neutral effect (Allaby 2010:939) that may make useful analysis of phenotype impossible.

4. It may be impossible to distinguish between multiple origins and introgression from wild populations (Allaby 2010:941).

5. Domestication may not be possible without translocation of the plant out of its biogeographical range (Allaby 2010:938)

_Rockshelter vs. the Floodplain Weed Theory_

Marshelder and its EAC associates are especially prevalent in the rockshelters of eastern Kentucky, in an area known as the Cumberland Plateau. One such site, the Newt Kash Hollow rockshelter, was one of the first places excavated outside of Gilmore’s Ozark bluffs to uncover EAC crops (Jones 1936). Many of the most well preserved caches of EAC crops exist at these sites in the Cumberland Plateau. However, whether these crops were domesticated from local wild populations of the Cumberland Plateau or were imported from elsewhere in the region is as yet unknown. The local domestication
scenario envisions a process similar to Smith’s (1992) “floodplain weed theory”, in which seeds of marshelder and other weedy crops that grow most easily in disturbed soils are carried by water along riverine areas, and extended into the terraces by floods. Humans throughout these riverine networks, taking advantage of these ruderal weeds, began to domesticate them either through “automatic selection” (unintentional selection through intensive harvesting; Harlan, et al. 1973), or intentionally, by cultivating them with digging sticks and weeding. Other researchers (Gremillion 2005; Ison 1991; Windingstad, et al. 2008) have suggested possible upland cultivation of EAC crops, using central place foraging theory and soil composition to demonstrate why farmers would have grown EAC crops closer to the rockshelter dwellings in which archaeologists find remains of these plants. Although the upland cultivation hypothesis is a viable alternative to Smith’s floodplain cultivation model, it is not an alternative to the floodplain weed theory’s explanation of initial domestication. The floodplain weed theory of cultivation is useful to describe the domestication process in the drainage system where marshelder originated, but most likely does not account for the distribution of domesticated marshelder throughout the rest of eastern North America.
Figure 1: Map of significant sites discussed (adapted from Smith 1992)
**Hypothesis**

The first evidence of wild-size marshelder in an archaeological context occurs in the Late Archaic (6055 cal BP) at the Koster Site (Horizon 6), and the first evidence of domesticated marshelder in the Terminal Archaic (3620 cal BP) at Riverton (Smith and Yarnell 2009). Both of these sites are in the Illinois River Valley. Domesticated marshelder at Riverton precedes the first marshelder in the Terminal Archaic Cumberland Plateau (Hooton Hollow 3315 cal BP), already in its domesticated form. This paucity of wild progenitors, along with the non-existence of modern, wild marshelder in most of Kentucky (Black 1963), indicates that human intervention was most likely behind the introduction of domesticated marshelder to the Cumberland Plateau. This study uses marshelder phenotypic variation and distribution over time throughout eastern North America to evaluate the hypothesis that marshelder in the Cumberland Plateau was introduced by diffusion or migration from the west, where it had earlier been domesticated from its wild state as a floodplain weed.

To test this hypothesis in the framework of protracted transition, this study applies rigorous quantitative methods to morphometric and time scale data collected from publications and notes from previous research, along with new data from a Terminal Archaic feature at Courthouse Rock, KY (3284 cal. BP). In the framework of the protracted transition, four hypotheses are tested statistically with these data that would
corroborate expectations for human introduction of domesticated marshelder into the Cumberland Plateau.

**H1:** *If the protracted transition model of domestication is appropriate for marshelder in eastern North America, there should not be a rapid linear rise in achene size in eastern North America as a whole.* The actual transition from wild to the domesticate morph (>4.0-4.2 mm long) of marshelder achenes is limited to a small number of samples from archaeological sites in the Illinois River Valley exhibiting wild sized marshelder dated before the first domesticate-sized samples. Based on the archaeological data we have, this initial domestication process was relatively rapid (approximately 1655 years). After the initial domestication of marshelder, achene size continued to increase over time.

**H2:** *If marshelder was introduced by humans into the Cumberland Plateau,* intrapopulational variation of achene size in domesticated archaeological marshelder *should be evident in a decrease in site sample variation over time in that region.* A decrease in variation would occur either because of the founder effect of genetic drift in a region geographically isolated from wild populations, or because of intensive directional selection for larger seeds.

**H3:** *If marshelder was introduced by humans into the Cumberland Plateau already domesticated, as the archaeological record and modern plant distributions indicate,* there should not be a rapid or drastic change in achene size within the region over time. Very few wild-sized (<4.0-4.2 mm long) achenes should be expected. If marshelder was
not domesticated \textit{in situ}, then we should expect few smaller-sized achenes, and a steady human selective pressure for increased seed size, maintaining the domesticate status, with no decline in seed size over time.

\textbf{H4:} \textit{If marshelder was domesticated in one region, and then disseminated to other regions in its domesticated form, each regional population should have its own typical achene size distribution, forming a cline with domesticated marshelder in adjacent regions.} This would occur due to geographic isolation from wild populations, and gene flow between adjacent populations of domesticated marshelder.
Chapter 2: Background

Marshelder

*Iva annua* L. var. *macrocarpa* Jackson, known by the common names of “marshelder” and “sumpweed”, belongs to the Asteraceae family, sub-tribe Ambrosiinae of the tribe Helianthae, which is the sunflower tribe. Indeed, Yarnell (1972) suggests a prehistoric co-development of marshelder with sunflower (*Helianthus annuus*). Jackson (1960) is responsible for marshelder’s most up-to-date taxonomic classification.

This variety has been found only in the bluff dwelling sites in Arkansas, Kentucky, and Missouri and probably represents a cultigen derived in a manner similar to *Helianthus annuus* var *macrocarpus* (DC.) Ckll. The achenes are usually larger than any existing races of *I. annua*. The presence of achenes of var. *macrocarpa* in the remains of various bluff dwellings and in the feces of their inhabitants indicate its use as a food and/or medicinal plant (Blake, 1939).

(Jackson 1960:814)

Marshelder has been extracted from the contents of many paleofecal samples throughout eastern North America, including Salts Cave, KY, Newt Kash, KY, and Hooton Hollow, KY. Its use in diet is well-supported, and it is thought to have been used in soups for its high oil content. Asch and Asch (1978), through harvesting
experiments and nutritional assays, demonstrated that the high nutritive value of marshelder could allow an adult harvesting for one hour his or her nutrients for one day. To better understand the process behind this, Gremillion (2004:225) conducted experiments with Iva that showed mastication had little impact and pounding with a pestle or grinding with sandstone resulted in high rates of breakage. Gremillion concludes “the sumpweed consumed in eastern Kentucky 3,000 years ago probably was processed by winnowing followed by grinding or milling.” (Gremillion 2004:225)

Marshelder, as the name indicates, prefers bottomlands, but has very little tolerance for tree cover. Therefore, it could be expected in treeless bottomland with no explicit preference for soil type (Yarnell 1972). Yarnell suggests that neither soil fertility, nor intensive gathering can account for larger achenes because no modern achenes living in a range of conditions have ever surpassed 4.5 mm in length. Furthermore, he suggests that anthropogenically nitrogen-rich environments, in combination with harvesting selection could account for the larger archaeological achene size (Yarnell 1972:339).

Since the 1970s (Yarnell 1972), marshelder achene and kernel size have been used to distinguish domesticated marshelder from wild. Therefore, it has been standard practice for archaeobotanists to measure marshelder achenes to document human selection and food production. Although the record is still is patchy in some areas, samples have been measured from a sufficient number of sites to allow a quantitative analysis providing a picture of the patterns of human-marshelder interactions.
Variation

Variation is basic to natural selection as proposed by Charles Darwin in explaining speciation. It is a general assumption that genetic and phenotypic variation extant in wild populations is narrowed with the bottlenecking events usually associated with domestication. Loss of genes through the bottlenecking events necessary in the domestication process should be expected in the phenotype as well.

[genes that influence desirable phenotypes experienced a more drastic loss of diversity because plants carrying favored alleles contributed the most progeny to each subsequent generation and other alleles were eliminated from the population (Doebley, et al. 2006).]
Gremillion (1993) demonstrated loss of variation in domesticates with chenopods 
(*Chenopodium* spp.) by plotting coefficient of variation (CV; standard deviation divided 
by mean) over time. She successfully showed that the CV for seed diameter per sample 
decreased with radiocarbon years BP (n=17, r=0.53, p=0.03), although a similar test for 
seed testa thickness did not approach significance. Contrastingly, in a sophisticated 
genetic study of rice cultivars, Takano-Kai et al. (2009) did not observe a difference in 
seed size between wild and cultivated rice, yet CVs of the cultivated *Oryza sativa* were 
significantly greater in seed width, seed length/width ratio, and seed weight than the wild 
progenitor, *Oryza rufipogon*. Takano-Kai et al. argue that this greater variation was the 
adaptive strategy of domesticated rice, which has resulted in the wide varieties of 
cultivated rice we have today. These represent two alternative trends and sets of 
expectations with CV in populations of plants at different stages of evolution.

Smith (1985) discusses the difficulty of using variation as a measure of 
domestication when discussing North American chenopod domestication, saying that the 
variation in fruit size in wild chenopod populations is too poorly documented—that the 
few comparative studies carried out do not show a significantly lower standard deviation 
value for domesticated chenopods. Lastly, he points out that 

it would be difficult to demonstrate that a relatively narrow range of size variation 
and few immature fruits in an archaeobotanical assemblage of a domesticated 
population, rather than a nonrepresentative sample of a wild or weedy population
resulting either from a nonrandom harvesting method or differential preservation (Smith 1985:57).

This difficulty is fully recognized, and addressed below.
Chapter 3. Data Analysis

Methods

Attempting to establish a baseline expectation for coefficient of variation (CV) for domesticated marshelder, standard deviation, mean, and date were obtained from the supplemental materials provided by Fuller et al. (2012) in their worldwide study of the rate of evolution in domesticated plants. In a cursory statistical test, CVs (standard deviation/mean) were plotted in a simple linear regression over the years BC provided. None of the regressions approached significance, of the 8 species’ (Vigna radiata, Pennesitum glaucum, Oryza sativa, Triticum, Hordeum, Helianthus annuus, Cucurmis melo, and Pisum sativum) traits plotted, with the exception of melon (Cucurmis melo) seed length CV increase over time (n=7, t=4.12, p=0.0092, r²=0.5857). Archaeological domesticated marshelder, similarly to most world crops listed above did not show a significant change over time in a linear regression with length and width vs. calibrated years BP (length CV: n=13, t= -0.54, p=0.5996; width CV n=13, t=0.12, p=0.9172).

Although CV has been shown to be useful in some species as a measure of domestication, there is sufficient reason to question the universality of CV reduction with domestication. This paper uses CV in a similar way to investigate marshelder domestication, but it is not clear what sort of evolutionary trend higher and lower CV indicates.

Criteria necessary to test each hypothesis dictated the sites used. Data were obtained from published materials, notes from Professor Kristen J. Gremillion, and from
the generous contribution of spreadsheets from George Crothers and Charles Faulkner (Appendix A, Table 2). Crothers’ and Faulker’s data sets were compiled for an unpublished paper presented at the 1993 Southeastern Archaeological Conference (Crothers and Faulkner 1993).

To test H₁, linear regressions of were used for 16 site mean achene measurements and 994 individual measurements of achene length and width from 11 sites (Table 1). Both sets required calibrated radiocarbon dates and that n>20. H₁ is further demonstrated with mean achene length from 54 archaeological sites for which Eastern Woodland periods were published, but not calibrated years BP (Appendix A. Table 2). Regions are categorized as Appalachia, Western Tennessee, Illinois, and Ozarks. Appalachia mainly consists of eastern Kentucky Cumberland Plateau sites, but includes Warren Wilson, NC. Western Tennessee includes Salts Cave in central Kentucky, and other sites in central and western Tennessee. Illinois includes both sites from the Illinois River Valley, and the American Bottom. Ozarks includes both Arkansas and Missouri sites. To test H₂, in which CVs were determined, 10 archaeological samples and 12 modern wild collected samples were chosen for which either individual measurements or SD and mean of achene length and width were available. SD, mean, and n from each sample was entered into a Forestry Products Laboratory module (Verill 2013; Verrill and Johnson 2007) to obtain 95% confidence intervals for CV (Appendix B., Table 3). H₃ was tested using eight sites from the Cumberland Plateau (Cloudsplitter, Cold Oak, Courthouse Rock, Hooton Hollow, Newt Kash Hollow, Roger’s/Haystack, and Thor’s Hammer) in a linear regression of individual measurements vs. years calibrated BP. The one-way ANOVA in
$H_4$ required individual measurements from the 12 sites compared with length as the dependent variable. As expected, differences were significant ($p<0.0001$), so a Waller-Duncan K-ratio t-test was performed. Unlike the more commonly used Tukey’s test, Waller Duncan does not control for Type I error, but compares the Type I and Type II errors, based on Bayesian principles (Steel and Torrie 1980).

Although smaller sample sizes were useful for mean length and width, these became problematic when CV was obtained, sometimes exaggerating the coefficient to be much higher. Sample sizes were most useful for all tests used when they neared $100n$. Some sites that initially appeared useful had to be discarded. For instance, Cold Oak had a total of 27 achenes, but when divided between the Terminal Archaic component and the Early Woodland components, the numbers became too few to be used in statistical tests.

All dates are radiocarbon laboratory results calibrated in OxCal 4.2 Online (Bronker Ramsey 2010), using the median within the two-sigma range. The presentation of this median rather than the range is used for input into statistical programs, and retained throughout the text for coherence. One exception to these calibrated radiocarbon dates is Thor’s Hammer, as it has no radiocarbon date. Due to its cultural level associations with nearby sites, it has arbitrarily been assigned the Early Late Woodland date of 1350 B.P., so that it could be incorporated into the regressions below.

None of the published material reporting measurements described methods, as the process is quite simple, and authors are usually more concerned with determining domesticate or wild status of marshelder by obtaining a mean over 4.0-4.2 mm. In the Courthouse Rock, KY sample the author used a dissecting microscope with a reticule.
eyepiece at a magnification of 10x, which allowed for accuracy of measurement to 0.1 mm. Achenes were measured along the longest part along the center, from the ovary attachment to the end of the fruit. Width was measured at the widest section of these relatively flat fruits. Quantitative analysis was performed using SAS 9.3.
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Table 1: Twelve Archaeological sites for which radiocarbon dates were available (n=994). Hooton Hollow, Thor's Hammer and Collins excluded from tests using CV due to low n.
Results

The earliest evidence of marshelder in an archaeological context is in the Titterington Phase of the Koster Site, dating to 6055 cal. BP, in the Illinois River Valley. Mean length and width for these achenes fall well within the wild size range (2.3 x 1.9 mm, n=44). The earliest evidence for domesticated marshelder is from two achenes from Feature 29 of the Riverton Site, dated to 3620 cal BP (Smith and Yarnell 2009). These fall within the domesticated range, with a length above 4.5 mm (4.5 X 2.5 mm; 4.5 X 3.4 mm, respectively). A number of rockshelters in the Cumberland Plateau (Hooton Hollow, Courthouse Rock, Newt Kash) have significant caches of domesticate-morph marshelder by the Terminal Archaic (3500-3000 BP). Yet, rather than showing a steady increase in size over space and time, Illinois Terminal Archaic sites contain marshelder achenes with means well-below the domesticate cutoff of 4.0-4.2 mm. Cahokia Interpretive Center Tract (ICT) (Nassaney et al. 1982), and Titus Horizon 2 (Asch and Asch 1978) are two such examples.

The following section discusses each of the hypotheses presented above and the degree to which metric data supports them. The first hypothesis is a prediction that should be supported if the protracted transition is an appropriate model for marshelder domestication in eastern North America. The three other hypotheses are predictions that should receive some support if domesticated marshelder was introduced to the Cumberland Plateau rather than domesticated from local wild populations.
Following the protracted transition model of domestication, there should not be a rapid linear rise in achene size in eastern North America as a whole. Yet, as Yarnell (1981) has shown, when mean alone is considered, length and width of archaeological marshelder achenes increase over time in a linear fashion. When plotted in a linear regression, the mean length and mean width increase dramatically over time, with time explaining around 40% of the variation in this increase (Fig. 3a, 3b). However, when individual measurements (and therefore intrasite variation) are considered, the increase is far less dramatic (Fig. 3c, 3d). Time still explains the increase in achene size, fitting a simple linear regression, but when all length and widths from each site are considered, time only explains around 10% of the variation.

When sites are divided regionally by period rather than by numerical date, some accuracy is lost of course, as Eastern Woodland periods cannot be plotted in a linear regression as can years calibrated BP. However, this allows the inclusion of sites for which radiocarbon data were not available. In all four regions (Appalachian, Western Tennessee, Illinois, and Ozarks) mean achene length per site increases in later periods (Fig. 4). It is evident that each region has its own trajectory of increase, along with some regions exhibiting contemporaneous sites with very different mean lengths (such as the Early Woodland Ozark sites Collins and Alred Bluff), or fairly indiscernible patterns (such as in the Western Tennessee sites).
(a) Linear regression with 95% confidence intervals for mean achene length vs. years calibrated BP (n=16, t=11.15, p<0.0001, r²=0.4315)

(b) Linear regression with 95% confidence intervals for mean achene width vs. years calibrated BP (n=16, t=11.78, P<0.0001, r²=0.3996)

(c) Linear regression with 95% confidence intervals for individual achene lengths from 11 sites vs. years calibrated BP (n=994, t=-10.71, p<0.0001, r²=0.1037)

(d) Linear regression with 95% confidence intervals for individual achene widths from 11 sites vs. years calibrated BP (n=994, t=-10.26, p<0.0001, r²=0.09)

Figure 3: Linear regressions of site mean achene measurements vs. years calibrated BP, and individual achene measurements vs. years calibrated BP
Figure 4: Mean site achene length by period and region (n=52)
If marshelder was introduced by humans into the Cumberland Plateau, and there was no wild marshelder already present, then founder effect would be expected in which variation would decrease. This should be evident in phenotypic variation of seed size as measured by the CV for achene length and width.

CV for marshelder achene length is slightly higher in most modern wild marshelder samples than those of Cumberland Plateau archaeological samples, but most are in the range of respective lower and upper 95% confidence intervals (Fig.5, See Appendix B., Table 1 for actual measurements). CVs of two modern wild samples of marshelder fall outside this range: a previously mowed stand at Apple Creek, IL, and Oceola, AR.

The drastic differences in CV are most apparent when archaeological samples from different regions are compared. All of the Western Tennessee sites (including those nearby in Kentucky) have similar CVs to those of the Cumberland Plateau. The CV of achene length from Koster, IL is comparable to both Cumberland Plateau sites Cloudsplitter and Rogers/Haystack. But, the American Bottom site, Cahokia-ICT, IL has a CV surpassing all other samples. The Ozark site, Alred Bluff, also has a high CV, only falling into the range of the mowed modern wild sample at Apple Creek, IL.
Figure 5: Coefficient of variation (CV) for length of marshelder achenes with 95% confidence intervals.

Horizontal lines indicate CV; vertical lines represent the range between upper and lower 95% confidence intervals of CV. AP=Appalachian (Cumberland Plateau) sites, WT=Western Tennessee sites, OZ=Ozark sites, IL=Illinois sites, MW=modern wild samples. Sites are listed from left to right in order of appearance in the archaeological record.
In a model of human introduction of marshelder into the Cumberland Escarpment, there should not be a rapid or drastic change in achene size within the region over time. Although wild-size (<4.0-4.2 mm) achenes are extant in the Cumberland Plateau, they are within populations that have a domesticate-size mean length hovering around 6.0 mm., yet widely range in size. There is no population exhibiting wild-size in earlier times, nor is there a drastic increase. Time only explains about 2% of the variation observed in samples from the Cumberland Plateau (Fig. 6a, 6b)
(a) Linear regression with 95% confidence intervals for individual achene lengths of eight Cumberland Plateau sites vs. years calibrated BP (n=461, t=-3.49, p=0.0005, \(r^2=0.0259\)).

(b) Linear regression with 95% confidence intervals for individual achene widths of eight Cumberland Escarpment vs. years calibrated BP (n=461, t=-2.72, p<0.0001, \(r^2=0.0159\)).

Figure 6: Simple linear regressions of achene measurements from Cumberland Plateau sites only
If marshelder was domesticated in one region, and then anthropogenically diffused to other regions in its domesticated form, each regional population should have its own typical achene size distribution, forming a cline with adjacent regions.

A monophyletic origin of domesticated marshelder, diffused to other regions anthropogenically, may be evident in each region having its own typical achene size distribution. Domesticated marshelder would then form a cline with domesticated marshelder in adjacent regions. This was tested by comparing the distributions of individual achene lengths in various samples. A Waller Duncan ANOVA post-hoc seems to group samples along regional lines (Fig. 7). Cumberland Escarpment sites cluster together, with the exceptions of Hooton Hollow and Cloudsplitter. Hooton Hollow overlaps with Newt Kash and Cloudsplitter overlaps with Hooton Hollow. Salts Cave Middle overlaps with Cloudsplitter’s distribution of lengths, Big Bone Cave overlaps with Salts Cave Middle, and Salts Cave Upper overlaps with Big Bone Cave. Altogether, these clusterings resemble a cline, with Cloudsplitter as the sample that links the Cumberland Plateau and Western Tennessee. Alred Bluff, AR, Collins, MO, and Cahokia-ICT, IL are all outliers to this apparent cline. Although the two Ozarks sites, Alred Bluff and Collins do not overlap, it is clear that at least in the Cumberland Plateau, intra-sample achene length distribution is similar within the region, regardless of existing at different time periods.
Figure 7: Waller Duncan K-ratio t-test for length grouped visually in Venn diagram. AB=Alred Bluff, RH=Rogers/Haystack, CR=Courthouse Rock, TH=Thor’s Hammer, NK=Newt Kash Hollow, HH=Hooton Hollow, CS=Cloudsplitter, SCM=Salts Cave Middle, BB=Big Bone Cave, SCU=Salts Cave Upper, CN=Collins, CA=Cahokia-ICT
Chapter 4: Discussion
Marshelder achene length and width increase gradually over time among all populations in Eastern North America between 3100 and 600 B.P. Yet, time only explains approximately 10% of variation when individual measurements are considered. Time, measured here in calibrated years BP, and set against change acts a stand-in for whatever evolutionary forces is at play. Regional, microclimatological, and seasonal effects such as average temperature, average rainfall, exposure to sunlight, and time of harvesting must account for the plastic effects on achene size. Although the archaeobotanical record is rich in eastern North America, even an infinitely detailed record could never account for all possible variation in achene size created by these factors, that could vary at any point in time, from valley to hillside.

Although mean achene size is predicted by time, intrapopulational phenotypic variation of marshelder achene size is not predicted by time in archaeological samples, nor does it seem to predict wild vs. domesticated status. Yet, there is some amount of control in understanding what CV represents because we know the amount of variation expected to be present in modern wild samples. Each of these samples was gathered from a single wild stand, so that the CV for each does not represent many temporal and spatial possibilities, but only variation in achene size on one plant, or between plants in the same stand. Fluctuations in variation of achene size are either due to introgression
between wild and domesticated stands, archaeobotanical preservation, or problematic sampling. It is assumed that introgression in this case would result in the simultaneous existence of both the wild and domesticate morph. Archaeobotanical preservation is nearly impossible to control for. Problematic sampling and reporting is difficult to control for when using secondary data sets. The data available for Cahokia-ICT (Nassaney et al. 1983) is aggregated from various features from distinct temporal components. Feature 19 dated to the Terminal Archaic (3321 cal BP) has the most marshelder achenes, mostly wild-sized (<4.0-4.2 mm; see Appendix D, Figs. 28, 29), and is likely to represent most of the data set. However, other temporal periods are likely included in this data set. Less is known about the collection of the Alred Bluff sample (measured by Yarnell), but Fritz (1986) has noted the disturbed context of this and many other Ozark bluff sites.

Admittedly, determining what a sample represents is at the core of the difficulty in using CV as a measure of domestication patterns. Even in features where disturbance, sampling and radiocarbon dates are not problematic, this difficulty exists. Does a sample represent a single deposit from one plant at one collection site, or does it represent multiple deposits from one or two hundred years of collection from many stands located in many different microclimates? CV, therefore, may be measuring any one of these scenarios, and not providing information about introgression or isolation. If marshelder
measurements are assigned specific provenience with a calibrated radiocarbon date, then it is more likely to measure introgression.

If it is introgression causing the high CV in Alred Bluff, AR and Cahokia-ICT samples, then this provides more evidence for human introduction of marshelder into the Cumberland Plateau. The paucity of high CV in Cumberland Plateau samples may indicate a lack of introgression, meaning that there were no wild stands with which to cross-pollinate. If there were no wild stands in the Cumberland Plateau, and there is a sudden appearance of the domesticate-sized achenes (>4.0-4.2 mm), then it is likely marshelder was introduced either through migration or cultural diffusion into that region. Intentionality of domestication is always difficult to read into the archaeological record, however, the spread of marshelder outside of its natural range in an already domesticated form does not imply accidental introduction. If the archaeological record showed the wild form of marshelder spreading out of its natural range to new areas, an accidental introduction, or a slow, large, regional evolutionary pattern following the floodplain weed theory of domestication could be easily posited. However, evidence available points to the process described in the floodplain weed theory taking place elsewhere, not in the Cumberland Plateau—most likely the Illinois River Valley.

Marshelder achene length and width do not increase rapidly in the Cumberland Plateau between 3100 and 1300 BP, and achenes are persistently large (>4.0-4.2 mm) in size. Time, again as a stand-in for evolutionary forces, only explains around 2% of variation in the Cumberland Plateau. Again, rest of variation in achene size must be attributable to plasticity of the trait: on one plant, in one stand, between multiple stands,
between multiple years. Despite the residual variation, size increase does follow a linear model in the Cumberland Plateau, as shown in Figure 4.

Similarities in achene size frequency distribution and mean cluster according to region rather than time period. While larger achenes are a trend, circumstances leading to larger marshelder achenes are not the same across Eastern North America. The cline depicted in Figure 5 implies different trajectories of domesticated marshelder evolution. With the exception of Cahokia-ICT, it does not depict samples with mean achene length in the wild range (<4.0-4.2 mm). The overlap of western Tennessee (and western Kentucky) sites with Cumberland Plateau sites of eastern Kentucky does not include sites where introgression seems likely. Alred Bluff, AR and Collins, MO sites are outliers in the Ozarks, while Cahokia-ICT, IL is an outlier from the American Bottom. These three sites could have introgressed with wild stands in the natural range of wild marshelder, while the overlap between the Cumberland Plateau and western Tennessee represents a similarity between domesticated marshelder populations, perhaps cross-pollinating somewhere in central Kentucky, where the two domesticates came into contact, creating a cline of domesticated marshelder.

Marshelder is not native to the modern Cumberland Plateau. Modern distribution has been extrapolated to prehistory (Black 1963), implying a later introduction either by humans or flooding (Smith, et al. 1992). Marshelder introduction to the Cumberland Plateau can be explained by one of the three following scenarios: (1) domesticated marshelder from the west was imported through diffusion or migration, and maintained in their domesticate form; 2) wild marshelder from the west was imported through diffusion
or migration, and plants responded to the new environment with larger achene size; or 3) wild plants were dispersed from the west without human intervention, and plants responded to the new environment with larger achene size.

The first scenario seems most likely. The stability of achene size over time in this region with no dramatic increase in size supports the hypotheses of an introduction of an already domesticated marshelder. Similarly, the comparatively “normal” CV provides evidence for a relatively homogenous population. For, if there were no wild stands of marshelder in the Cumberland Plateau, gene flow and introgression would have been non-existent due to geographic isolation. The clustering of sites along regional rather than temporal categories supports a single origin hypothesis for marshelder domestication given the influence of latitude and temperature on plastic traits in plants.

Unless there was a rapid and expansive selection against the wild form of marshelder, the expectation for the second two scenarios would be that wild plants responding to the new environment would phenotypically exhibit both the wild and domesticate morph. Therefore, we would expect a very high CV, which we do not observe in the Cumberland Plateau.

Trends observed here support many of the expectations of the protracted transition (Allaby 2010). The scenario in which selection is weak for a long time, then becomes strong is evident in a steady achene size during many periods, suddenly larger in Mississippian sites (Fig. 4). Length and width follow a similar phenotypic track of change, but may have undergone selection separately rather than simultaneously (Fig 3c, 3d). The case for a monophyletic single origin of marshelder in the Illinois River Valley
may be difficult to make base on the fact that selectively neutral traits from polyphyletic origins may cancel each other out. Similarly, it may be impossible when marshelder is actually submitted to aDNA analysis, to determine the difference between multiple origins and introgression. Allaby’s (2010:938) observation that domestication may not be possible without translocation of the plant out of its biogeographical range is most interesting for this discussion.

Is it possible that marshelder had to be imported into the geographic isolation of the Cumberland Plateau before it could be domesticated? Could it have its natural range in the Illinois River Valley, and other parts of the Mississippi River drainage, but achieve full domestication only after a bottleneck in a geographically isolated region? Domestication of plants necessitates some level geographic isolation, but rarely reproductive isolation to the point of speciation (Harlan, et al. 1973). There is no evidence that intensive harvesting of wild stands alone can have a genetic effect on populations of plants selected by humans (Harlan, et al. 1973; Yarnell 1972). Therefore, there must be some level of intentionality to the domestication process, either by: 1) moving a plant from its natural range; 2) changing the selective environment through land management; or 3) intentionally isolating domesticates from their wild brethren through garden plot location or harvesting practices.
Chapter 5: Conclusion

The origin of domesticated marshelder was most likely not in the Cumberland Plateau. Although not definitively demonstrated by this multi-region statistical evaluation, the hypotheses tested here corroborate a western origin for domesticated marshelder. The implications for human-plant interactions are two-fold: 1) the apparent lack of introgression in Cumberland Plateau samples suggests importation (possibly by humans); and 2) the apparent lack of introgression in Illinois populations (see Koster, IL in Figure 5) where wild stands are thought to have existed suggests an intentional segregation of domesticated garden plots from wild stands. Although the intensive harvesting suggested by Rindos (1984) and others may have been a precursor to the long standing middle ground of “low-level food production”, it cannot account for this intentional isolation of domesticate from wild marshelder. Furthermore, it may have been necessary for marshelder to be exported from its native area to places like the Cumberland Plateau for the plant to become fully domesticated. It is possible that the domesticated marshelder observed in Riverton (3800 cal. BP) is a re-introduction of a newly, fully domesticated marshelder. This is just speculation, but supported by what we know about geographic isolation. Another possibility is that domestication could have been much earlier than any archaeological records show, and early wild size achenes at the Koster site may be anomalous, like those found later at Titus, Napoleon Hollow, and Cahokia-ICT.
Domestication could have occurred anywhere in eastern North America, but our best archaeological evidence at this time points to domestication in the Illinois River Valley, or thereabouts.

Regardless of the origins of domesticated marshelder, the fact remains that it is prolific in archaeological deposits that span multiple cultures and multiple subsistence strategies from the Late Archaic through the Late Prehistoric. Marshelder is found in contexts of semi-nomadic peoples of eastern Kentucky to the great Cahokian civilization, and evidence suggests that it was used by both economies resembling classic conceptions of hunting-gathering societies and economies resembling classic conceptions of agriculturists. Most of the societies using domesticated marshelder, however, belong to the “middle ground” mixed subsistence strategies that make up a great deal of the prehistory of eastern North America, beginning in the Late Archaic (Smith 2001). This reliance upon some crops incorporated into a general hunting-gathering subsistence strategy is problematic for any attempt to replicate a unilineal model of food production. The archaeological record in general and seed morphology specifically contradicts this stage of mixed economy as transitional. However, the early domestication of marshelder by such groups and the level of intentionality implied by evidence for geographic isolation defy attempts to categorize this “middle ground” as transitional. Rather, evolution of marshelder achene size implies relatively large-scale manipulations of the landscape by people utilizing this crop.
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Takano-Kai, Noriko, Hui Jiang, Takahiko Kubo, Megan Sweeney, Takashi Matsumoto, Hiroyuki Kanamori, Badri Padhukasahasram, Carlos Bustamante, Atsushi Yoshimura, Kazuyuki Doi and Susan McCouch

Verill, Steve

2013  Exact confidence bounds for a normal distribution coefficient of variation.  
http://www1.fpl.fs.fed.us/covnorm.dcd.html  Forestry Service, Department of Agriculture.

Verrill, Steve and Richard A. Johnson


Windingstad, J. D., S. C. Sherwood, K. J. Gremillion and N. S. Eash


Yarnell, R. A.


Yarnell, Richard A.

Appendix A. Sites by time period with mean length, mean width, and U.S. state (54 archeological sites, 11 modern wild collection sites)

<table>
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Appendix B.: Coefficient of variation (CV) confidence intervals (L₁, L₂)

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Appendix C. Histograms

Figure 8: Thor's Hammer achene length (mm),
n=16

Figure 9: Thor's Hammer achene width (mm),
n=16

Figure 10: Salts Cave Upper achene length (mm),
n=239

Figure 11: Salts Cave Upper achene width (mm),
n=239
Figure 12: Salts Cave Middle achene length (mm),
n=235

Figure 13: Salts Cave Middle achene width (mm),
n=235

Figure 14: Rogers, Haystack achene length (mm),
n=92

Figure 15: Rogers, Haystack achene width (mm),
n=92
Figure 20: Courthouse Rock achene length (mm), n=98

Figure 21: Courthouse Rock achene width (mm), n=98

Figure 22: Collins achene length (mm), n=19

Figure 23: Collins achene width, n=19
Figure 24: Cold Oak (Early Woodland) achene length (mm), n=21

Figure 25: Cold Oak (Early Woodland) achene width (mm), n=21

Figure 26: Cloudsplitter achene length (mm), n=143

Figure 27: Cloudsplitter achene width (mm), n=143
Figure 28: Cahokia ICT achene length (mm), n=65

Figure 29: Cahokia ICT achene width (mm), n=65

Figure 30: Big Bone Cave achene length (mm), n=206

Figure 31: Big Bone Cave achene width (mm), n=206
Figure 32: Alred Bluff achene length (mm), n=103

Figure 33: Alred Bluff achene width (mm), n=103
Figure 34: Boxplot of length by region; AP=Cumberland Plateau, IL=Illinois, OZ=Ozarks, WT=Western Tennessee/Kentucky
Figure 35: Boxplot of width by region; AP=Cumberland Plateau, IL=Illinois, OZ=Ozarks, WT=Western Tennessee/Kentucky
Figure 36: Boxplot of length by period; 2=Terminal Archaic, 3=Early Woodland, 4=Middle Woodland, 5=Early Late Woodland, 6=Late Woodland, 7=Late Prehistoric.
Figure 37: Boxplot of width by period; 2=Terminal Archaic, 3=Early Woodland, 4=Middle Woodland, 5=Early Late Woodland, 6=Late Woodland, 7=Late Prehistoric
Figure 38: Boxplot of width by years calibrated BP
Figure 39: Boxplot of length by years calibrated BP