Figure 7-4. Bayesian analysis for 12 species of Cucurbita. Taxa in bold print are domesticated species. Values above the branches represent branch lengths. Values below the branches represent posterior probabilities (2,000,000 generations).
Table 7-2. List of Samples Analyzed

<table>
<thead>
<tr>
<th>Individual No.</th>
<th>Species</th>
<th>Origin</th>
</tr>
</thead>
<tbody>
<tr>
<td>1–3</td>
<td><em>C. maxima</em> Duchesne ssp. <em>andreana</em></td>
<td>Argentina (1) and Bolivia (2, 3)</td>
</tr>
<tr>
<td>4–10</td>
<td><em>C. maxima</em></td>
<td>Ecuador (4–8) and U.S. (9, 10)</td>
</tr>
<tr>
<td>11–16</td>
<td><em>C. ecuadorensis</em></td>
<td>Ecuador</td>
</tr>
<tr>
<td>17–22</td>
<td><em>C. argyrosperma</em> ssp. <em>sororia</em></td>
<td>Panama (17) and Mexico (18–22)</td>
</tr>
<tr>
<td>23–24</td>
<td><em>C. argyrosperma</em></td>
<td>Mexico</td>
</tr>
<tr>
<td>25–41</td>
<td><em>C. moschata</em></td>
<td>Puerto Rico (25), Panama (26, 31–32), Mexico (27), Colombia (28–29), Venezuela (30), Ecuador (33–36), Bolivia (37–41)</td>
</tr>
<tr>
<td>42–46</td>
<td><em>C. pepo</em> ssp. <em>pepo</em></td>
<td>Ecuador (42), Italy (43), U.S. (44), Hungary (45), Panama (46)</td>
</tr>
<tr>
<td>47</td>
<td><em>Miniature Ball</em>&lt;sup&gt;a&lt;/sup&gt;</td>
<td>U.S.</td>
</tr>
<tr>
<td>48–50</td>
<td><em>C. pepo</em> ssp. <em>fratema</em> (L. H. Bailey) Andres</td>
<td>Tamaulipas, Mexico</td>
</tr>
<tr>
<td>51–53</td>
<td><em>C. pepo</em> ssp. <em>ovifera</em> var. <em>ovifera</em></td>
<td>U.S. (acorn squash, striped pear gourd, bicolor gourd)</td>
</tr>
<tr>
<td>54</td>
<td><em>C. pepo</em> ssp. <em>ovifera</em> var. <em>ozarkana</em></td>
<td>U.S.</td>
</tr>
<tr>
<td>55–59</td>
<td><em>C. pepo</em> ssp. <em>ovifera</em> (L.) var. <em>texana</em> (Scheele) Decker</td>
<td>U.S.</td>
</tr>
<tr>
<td>60–61</td>
<td><em>C. martinezii</em> L. H. Bailey</td>
<td>Mexico</td>
</tr>
<tr>
<td>62–63</td>
<td><em>C. foetidissima</em> HBK</td>
<td>Mexico</td>
</tr>
<tr>
<td>64–66</td>
<td><em>C. ficifolia</em></td>
<td>U.S. (64), Mexico (65), Ecuador (66)</td>
</tr>
<tr>
<td></td>
<td><em>Citrullus lanatus</em> (Thunb.) Matsum. &amp; Nakai</td>
<td>Peru</td>
</tr>
<tr>
<td></td>
<td><em>Sechium edule</em> (Jacq.) Sw.</td>
<td>Panama</td>
</tr>
</tbody>
</table>

Note: Numbers in parentheses after countries of origin are individual numbers. Domesticated species are in boldface type.

<sup>a</sup>Miniature Ball has been placed in both ssp. *pepo* and ssp. *ovifera* by different molecular techniques. Our mtDNA data place it within ssp. *ovifera*.

rated by three base pairs from those of ssp. *pepo*. No wild taxon shared its molecular sequence with ssp. *pepo*. The cultivated varieties of *C. pepo* ssp. *ovifera*, however, share identical molecular sequences with the free-living gourds classified as *C. pepo* ssp. *fratema*, *C. pepo* ssp. *ovifera* var. *ozarkana*, and *C. pepo* ssp. *ovifera* var. *ozarkana* in Decker-Walters and colleagues (1993). Mitochondrial DNA data strongly suggest, therefore, that all of these shared the same maternal ancestor and belong to the ssp. *ovifera* lineage and that the Decker-Walters and colleagues (1993) classification delineating them as three separate varieties should be revised. Nor does there seem to be much support at the present for the ideas (Decker-Walters et al. 2002; Decker-Walters et al. 1993) that these wild gourds diverged long before domestication occurred in ssp. *ovifera* and that all cultivars of ssp. *ovifera* were derived from gourds belonging to var. *ozarkana* (see also Paris et al. [2003] and our discussion above).
Additionally, we have included Miniature Ball Gourd in our analyses. Previous molecular studies have placed this gourd in either the ssp. *ovifera* or the ssp. *pepo* group of taxa (e.g., Decker-Walters et al. 2002; Paris et al. 2003). Our mtDNA data suggest that Miniature Ball Gourd is more closely allied to the ssp. *ovifera* than the ssp. *pepo* group, as its molecular sequence is identical to those of the other ssp. *ovifera* taxa.

In summary, our mtDNA data agree with Wilson’s (1990; Wilson et al. 1992) isozyme and chloroplast DNA results and with the AFLP data of Paris and colleagues (2003) in indicating that free-living populations of *C. pepo* ssp. *ovifera* currently found over a wide geographic area extending from northeastern Mexico into the Gulf coast of the United States and northward into the midcontinental region of eastern North America have genetic profiles that make them possible ancestors for cultivars in the ssp. *ovifera* lineage of *C. pepo.* These and other issues concerning the relationships of the free-living taxa within the ssp. *ovifera* lineage of *C. pepo* to the cultivars require additional molecular work. More collections of the Mexican wild member of ssp. *ovifera*, *C. fraterna,* are also sorely needed.

The presently available archaeological evidence on the subject may constrain the possible zone of domestication more so than does the present molecular information. Seeds identified as domesticated ssp. *ovifera* on the basis of their size are present at the site of Phillips Spring in western Missouri, which is located within the range of var. *o. azarkana,* by 4440 B.P. (a direct AMS date on a domesticated seed; King 1985; Smith 1995, 2000; see Table 7-1). This finding, together with the close genetic relationship of wild eastern North American gourds to cultivated ssp. *ovifera,* supports an independent domestication of ssp. *ovifera* in eastern North America (e.g., Smith 1995). Archaeological sites in the state of Tamaulipas, northeastern Mexico, located less than 80 km from extant populations of *C. fraterna,* have produced domesticated-type seeds and peduncles from *C. pepo* ssp. *pepo* and from unclassified subspecies of *C. pepo* dated to between 4500 and 5500 B.P. (Smith 1997b). Identification of archaeological specimens of *C. pepo* from Missouri, other areas of the eastern United States, and northeastern Mexico should be pursued with mtDNA and other genetic analyses to investigate further to which subspecies of *C. pepo* they belong. Because no archaeological data from outside of the midcontinental region of eastern North America documenting a developmental sequence from wild to domesticated ssp. *ovifera* exist at present, populations of wild ssp. *ovifera* from the midcontinental zone appear to be the leading candidates for the wild ancestor of the domesticated variety of ssp. *ovifera* present in Missouri by 4400 B.P. The possibility that different cultivars of ssp. *ovifera* originated from different populations of wild ssp. *ovifera* (e.g., those formerly classified as *texana, fraterna, azarkana*) cannot be ruled out.

**Cucurbita pepo ssp. pepo in Southern Mexico**

With regard to the other domesticated lineage of *C. pepo,* ssp. *pepo,* our mtDNA data agree with other molecular results in indicating that a wild ancestor has yet to be discovered. Differences at three adjacent base pairs (GAC) separate ssp. *pepo* from the ssp. *ovifera* group of taxa (TTA). A predomestication
divergence of the wild ancestor of ssp. *pepo* from that of ssp. *ovifera* is suggested by the fact that GAC is a derived character also present in the *C. sororia* and *C. moschata* group of taxa. Therefore, it was probably present in the progenitor of ssp. *pepo*. In light of the existing archaeological record, which documents domestication of ssp. *pepo* by 9000 B.P. (about 10,000 calendar years ago) in the southern highlands of Mexico (Flannery 1986; Smith 1997a), this region can be considered as its most probable area of origin. Searches for *C. fraterna*-like populations in southern Mexico that possibly are genetically divergent from those extant in the northeastern parts of the country as a result of geographic isolation may further inform this problem.

**C. sororia/C. argyrosperma in Tropical Southwestern Mexico**

Previous isozyme, crossing, and ecological studies have indicated that *C. sororia*, a wild taxon native to warm and low-elevation habitats from Mexico to Panama, is the wild ancestor of the domesticated species *C. argyrosperma* (Merrick 1990, 1995; Nee 1990). Our mtDNA data strongly support these conclusions and show that *C. sororia* is a highly variable species. We found four different haplotypes of *C. sororia* within the six individuals sequenced from six different regions of Central America ranging from Mexico to Panama. Two populations of Mexican *C. sororia* from the central Balsas River valley of the state of Michoacán (No. 20 in Figure 7-1) and the state of Jalisco (No. 18 in Figure 7-1) share identical mitochondrial sequences with *C. argyrosperma*, suggesting that the domestication of *C. argyrosperma* probably occurred in one of these two regions. Molecular studies carried out by John Doebley and colleagues (e.g., Doebley 1990) have suggested that teosinte populations centered in the central Balsas Valley, including Michoacán, gave rise to maize. Thus, molecular data suggest that the history of two important crop plants, maize and *C. argyrosperma*, may profitably be sought in this little-studied region of tropical Mexico.

The earliest archaeological evidence for *C. argyrosperma*, dated to 4450 14C years B.P. (about 5,100 calendar years ago), presently comes from outside its area of origin in the mountains of Tamaulipas, Mexico (Smith 1997b). This situation highlights the paucity of archaeological research that has been carried out in the Balsas River valley and other tropical regions of Mexico.

**C. moschata in Tropical Northern South America**

*Cucurbita moschata* is adapted to high temperatures and high humidity, is the least cold tolerant of the domesticated *Cucurbita*, and was probably brought under domestication somewhere in the humid tropical lowlands. At European contact, it was an important food source throughout tropical America (Sauer 1950), and it is still the most common squash grown in the Central and South American lowlands and Antilles. Previous isozyme and crossing studies have indicated that *C. moschata* is more closely related to *C. argyrosperma* and *C. sororia* than to other taxa of *Cucurbita*. *Cucurbita moschata* and the *sororia* group taxa share some isozyme bands, but the banding pattern is sufficiently distinct to recognize two different species. *Cucurbita moschata* and *C. argyrosperma* can
hybridize with each other, but only if *C. argyrosperma* is the female parent (Merrick 1990, 1995; Wessel-Beaver 2000a). Indeed, farmers in Mexico today sometimes cross *C. argyrosperma* with *C. moschata* to achieve the dual benefits of large seed size from the former and high seed number from the latter (Merrick 1990).

Macromorphology also suggests a close relationship. *Cucurbita argyrosperma* and *C. moschata* can sometimes be difficult to distinguish on the basis of plant, fruit, and seed morphology alone, for example. Despite these similarities, no known wild gourd in the *sororia* group of taxa appears to be a suitable wild ancestor for *C. moschata*, and other wild species currently recognized from Central America can similarly be ruled out as wild progenitors on the basis of isozyme incongruities and fertility barriers (Merrick 1990, 1995).

The mtDNA data also indicate that *C. moschata* has a close evolutionary relationship to the *sororia* group taxa, as they formed a group in the mtDNA tree (Figure 7-4). There is no specimen of *C. sororia* with a haplotype closely aligned to *C. moschata*, however, further indicating that a wild progenitor for this crop plant is unknown.

Recently, Andres and Piperno (1995) found populations of a wild gourd in central Pacific Panama that on a morphological basis (e.g., fruits with a light green to white longitudinal mottle-striped pattern and tan seeds) were identifiable as *C. sororia*. These specimens represented the first reported occurrence of a wild gourd in Panama and suggested that *C. sororia* or a wild gourd closely related to it had a natural distribution that extended into southern Central America. Bitter-fruited *Cucurbita* with pale orange flesh (in contrast to the deep orange flesh of cultivated *C. moschata*) were also found growing spontaneously between populations of *C. sororia* and *C. moschata* that appeared to be natural hybrids between the two. That these two species can naturally hybridize has been subsequently borne out by recent crossing studies (Wessel-Beaver 2000b). Because of this finding and the growing evidence that *C. moschata*, while closely related to *C. argyrosperma*, was probably independently domesticated in southern Central America or northern South America, Andres and Piperno (1995; see also Piperno and Pearsall 1998:142–144) suggested that the Panamanian wild gourds might represent the wild ancestor of *C. moschata*.

Our mitochondrial data, however, do not support this hypothesis. Instead, the gourds appear to be natural populations of the highly variable taxon *C. sororia* at or near the southern limit of its distribution (Figure 7-1). Moreover, a fairly extensive archaeological record spanning the past 11,000 years from the region of Panama where *C. sororia* is most abundant today contains phytolith (plant silica body) evidence for a domesticated species of squash, probably *C. moschata*, during the preceramic period (ca. 5000 to 8000 B.P.) but no sign of an earlier exploitation of a wild gourd (Piperno 2004a; Piperno et al. 2000; Piperno and Pearsall 1998). Wild populations of *C. sororia* in Panama are not likely to be escapes from cultivation because *C. argyrosperma* was not grown there during the pre-Columbian period and no reliable evidence for its cultivation in Panama has been demonstrated since then. The recent discovery of *C. sororia* in Panama, despite this region's being the focus of collection efforts for years, underscores the constant need for more botanical exploration to delimit the geographical distribution of possible crop-plant ancestors. With pesticides being increasingly
used and human development destroying its natural habitats, C. sororia appears to be struggling to maintain a foothold in the modern Panamanian flora.

We sampled 16 different landraces of C. moschata distributed from Mexico to Bolivia and found little haplotypic variation among the specimens from this broad geographic range. The small amount of genetic variation in C. moschata may be a result of landrace divergence from a common ancestor, although more population-level work is needed on this question. The most parsimonious interpretation of the mtDNA tree is that C. moschata was domesticated once, from an undiscovered wild progenitor that is closely related to C. sororia. Existing macrofossil (seed and fruit) evidence is sparse, fairly late, and from outside its area of origin (Table 7-1). We believe, however, that phytolith studies will be important in elucidating the early history of this plant (Piperno 2004b; Piperno et al. 2000; Piperno et al. 2002). Northern South America, in particular Colombia, has been identified as an area of high diversity for C. moschata, where landraces exhibiting primitive characteristics (e.g., very small and dark seeds; highly lignified and warty rinds) are common (Nee 1990; Wessel-Beaver 2000b). An origin for this domesticated squash near the southern limit of C. sororia would also make sense because this is the wild species most closely related to C. moschata.

C. andreana/C. maxima in Southern South America

Cucurbita maxima comprises the turban, buttercup, and Hubbard squashes and the giant reddish-orange pumpkins sold at Halloween time in United States supermarkets. The species is, however, South American in origin. In our mtDNA analysis, C. maxima and C. andreana, a wild gourd native to southern South America (Figure 7-2), share identical haplotypes, strongly supporting the presumed ancestral position of C. andreana (Nee 1990). It has been thought that the direct ancestor of C. maxima will be found among those fairly well-described populations of C. andreana growing in warm, temperate areas of Argentina (Nee 1990). Free-living populations of C. andreana recently discovered by Michael Nee in the humid, lowland tropics of Bolivia also share their haplotypes with C. maxima, perhaps extending the zone of domestication into this region (Figure 7-2). Few historical data are available for the Bolivian gourds, however, and we are not certain at this time whether they represent truly wild populations or naturalized escapes from cultivation. Cucurbita maxima was grown on the Peruvian coast by about 4000 B.P. but never left its continent of origin during the pre-Columbian period (Sauer 1993). Earlier archaeological evidence from closer to its birthplace on the other side of the Andes is currently unavailable, but phytolith studies may considerably inform this question (Piperno et al. 2002).

Wild C. ecuadorensis/Domesticated C. ecuadorensis in Southwestern Ecuador

An interesting species of Cucurbita is C. ecuadorensis. This species is today endemic to Ecuador but it may have been distributed farther south along the northern Peruvian coast in the past. Cucurbita ecuadorensis is demonstrated by our mtDNA analysis to be closely related to the C. andreana/C. maxima
complex. Nee (1990) suggested that *C. ecuadorensis* represented a plant that was semidomesticated during the pre-Columbian era and then nearly lost from use, because some modern populations, though free-living, have nonbitter flesh and much larger fruits (around 11–13 cm) than are typical of wild gourds. Recent, more extensive, collections of *C. ecuadorensis* made by Andres in southwestern Ecuador support Nee’s suggestion and also indicate that modern populations of the species are represented by both wild and cultivated varieties (Andres et al. 2002; Andres and Robinson 2002).

Andres found fruits with a number of traits indicating domestication in house gardens, and humans were consuming them. The fruits were nonbitter and occurred in large sizes of up to 14 cm in length and 18 cm in breadth; fruit color and pattern varied and they had nonlignified rinds. Archaeological phytolith evidence from sites in southwestern Ecuador belonging to the preceramic Las Vegas culture demonstrates an ancient date for the exploitation and domestication of *C. ecuadorensis*. Phytolith data indicate that wild populations of *C. ecuadorensis* were collected during the terminal Pleistocene period (between ca. 10,000 and 11,000 B.P.) and then brought under cultivation and domesticated between 9300 and 10,000 B.P. (Piperno et al. 2000; Piperno and Pearsall 1998; Piperno and Stothert 2003).

There has been some question regarding the relationship of *C. ecuadorensis* to *C. andreana* and *C. maxima* (Wilson et al. 1992). Our mtDNA data suggest that *C. andreana* has a haplotype that is ancestral to *C. ecuadorensis*, raising the possibility that *C. maxima* and *C. ecuadorensis* are both derived from *C. andreana*. Nonetheless, current botanical and archaeological data favor an origin of the domesticated forms of the species in Ecuador from a wild *C. ecuadorensis*. For example, the distribution of *C. andreana*, even with the new collections from central Bolivia, is decidedly southern South American and east of the Andes (Figure 7-2), and although *C. maxima* is recorded archaeologically and ethnohistorically in intervening areas, *C. ecuadorensis* is not (Sauer 1993). Moreover, as mentioned above, archaeological phytolith data from southwestern Ecuador also indicate that *C. ecuadorensis* was a native component of the flora of northwestern South America since the Late Pleistocene and that it was taken under cultivation and domesticated by 9300 B.P. (Piperno and Stothert 2003). The wild-type *Cucurbita* phytoliths recovered from the terminal Pleistocene occupations of the Las Vegas culture sites bear close morphological and size similarities to modern wild *C. ecuadorensis* but are morphologically unlike those from modern fruits of *C. andreana* (Piperno et al. 2000; Piperno et al. 2002; Piperno and Stothert 2003).

**C. ficifolia in Andean South America**

Archaeologically and botanically, this black-seeded domesticated species is probably the least understood (Andres 1990). Aztec elite used the large and hard *C. ficifolia* fruits as containers from which they drank agave wine and cacao and toasted their gods (Coe 1995). For these reasons and the clear ecological preference of *C. ficifolia* to high elevations, the origins of this squash have often been attributed to highland Mesoamerica. Intensive searches for a wild progenitor in Mexico have not yielded evidence of any such populations, however (Andres 1990). The only reliable archaeological records come from the arid coast
of Peru, where the species has been recovered in sites dated to circa 5000 B.P. (Sauer 1993). These plants were probably grown in the montaña and brought down as trade items, because cultivating C. *ficifolia* on the Peruvian coast would have been difficult to impossible. There is no wild species in our mtDNA analysis with a haplotype closely aligned with that of C. *ficifolia*, which supports other information that it lacks a known wild ancestor (Andres 1990; Nee 1990). Andean South America is its most probable area of origin (Andres 1990).

**Summary and Conclusions**

Studying the geographic origins and history of domesticated plants requires data from a number of different disciplines and the use of multiple molecular markers. Information from molecular biology, while often extremely valuable, is not a silver bullet. The genus *Cucurbita* well illustrates the potentials and problems of using molecular tools to study crop-plant domestication. The exceptional number of domestications in *Cucurbita* achieved by Native Americans, which may be equal to or more than is presently recognized for any other genus of plant (Harlan 1992), has created the astonishing array of cultivars that delights modern investigators but then in turn demands greater precision from the data and care in their interpretation.

The following points underscore the complexities involved in interpreting current archaeobotanical and molecular records:

1. Domestication appears to have occurred twice in a single biological species of *Cucurbita*, *C. pepo*,
2. a suitable wild ancestor for one of the domesticated lineages, ssp. *pepo*, has not been collected,
3. extant free-living populations of *C. pepo* found in northeastern Mexico and eastern North America, whose histories and pre-Columbian ranges are not well understood, form suitable wild progenitor populations for the other domesticated lineage of *C. pepo* ssp. *ovifera*,
4. all of these widely ranging and highly polymorphic wild and domesticated varieties of *C. pepo* ssp. *ovifera* are completely interfertile, and complex and still poorly understood patterns of hybridization and creation of feral populations have with little doubt occurred that would introduce possible noise into the phylogenetic signal derived from molecular studies,
5. only four collections of *C. fraterna* exist and we do not know nearly enough about the geographic distribution and natural levels of genetic variability in this wild gourd presently known only from the northeastern part of Mexico, (6) natural, interspecific crop/weed hybridization between *C. fraterna* and *C. argyrosperma* and between *C. sororia* and *C. moschata* has been documented (Andres and Piperno 1995; Wilson et al. 1994), and (7) three domesticated species, *C. pepo*, *C. argyrosperma*, and *C. moschata*, the last two of which also hybridize naturally, overlapped considerably in their ranges in Mexico and North America during the pre-Columbian era, and *C. maxima*, *C. moschata*, and to a lesser extent *C. ecuadorensis* did the same in parts of South America; distinguishing among the seeds of these species in archaeological assemblages can sometimes be difficult (e.g., Fritz 1994) and thus caution should be exercised in archaeobotanical identification in areas where species overlap occurred.
At present, we are more informed about how many domestications occurred in *Cucurbita* than about where and when these events took place. For two species, *C. argyrosperma* and *C. maxima*, molecular, botanical, ecological, and archaeological data are concordant in identifying wild progenitors and circumscribing broad areas of origin (southern Mexico and southern South America, respectively). Archaeological research addressing their earliest history and spread is just beginning, however, and there is much to be learned. Two species, *C. ficifolia* and *C. moschata*, that were probably brought under cultivation and domesticated in highland and lowland South America, respectively, lack wild ancestors and are documented archaeologically only outside their areas of origin. Our views as to where they were originally domesticated are educated guesses based on the various lines of available data. There is good archaeological evidence that *C. ecuadorensis*, a wild species native to the low-lying regions of Ecuador and perhaps northwestern Peru, was brought under cultivation and domesticated during the early Holocene in southwestern Ecuador. It may be that only when we have a composite picture agreed on by archaeology, genetics, and botany will we be able to specify with more confidence where and when domestication in *Cucurbita* arose.

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