

THE ORIGINS OF AN IMPORTANT CACTUS CROP, *OPUNTIA FICUS-INDICA* (CACTACEAE): NEW MOLECULAR EVIDENCE¹

M. PATRICK GRIFFITH²

Rancho Santa Ana Botanic Garden, Claremont, California 91711 USA

Opuntia ficus-indica is a long-domesticated cactus crop that is important in agricultural economies throughout arid and semiarid parts of the world. The biogeographic and evolutionary origins of this species have been obscured through ancient and widespread cultivation and naturalization. The origin of *O. ficus-indica* is investigated through the use of Bayesian phylogenetic analyses of nrITS DNA sequences. These analyses support the following hypotheses: that *O. ficus-indica* is a close relative of a group of arborescent, fleshy-fruited prickly pears from central and southern Mexico; that the center of domestication for this species is in central Mexico; and that the taxonomic concept of *O. ficus-indica* may include clones derived from multiple lineages and therefore be polyphyletic.

Key words: archaethnobotany; Bayesian analysis; crop origins; *Opuntia*; *Opuntia ficus-indica*.

Opuntia ficus-indica (L.) Mill. is a crop species (Fig. 1) that figures prominently in the modern folklore of ethnobotany. The narrative of Luther Burbank's development and promotion of certain clones of *O. ficus-indica* in the early 20th century is vividly chronicled (with sharp wit) by Benson (1982). Opuntoid cacti are recognized as ideal crops for arid regimes (Felger, 1979; Russell and Felger, 1987) because *Opuntia ficus-indica* is extremely efficient at converting water into biomass (Kluge and Ting, 1978). *Opuntia ficus-indica*, one of several long-domesticated cactus species (Casas et al., 1997; Casas and Barbera, 2002), is the most widespread and economically important of these cactus crops (Nobel, 2002; Nobel et al., 2002), as important as corn and tequila agave in the agricultural economy of modern Mexico (Barrientos, 1966). The facile introgression of *Opuntia* is very well documented; this genus is among the most interspecifically promiscuous plants, perhaps rivaled only by *Quercus* L. in this regard (Benson and Walkington, 1965; Grant and Grant, 1971b, 1979; Felger, 1979; Baker and Pinkava, 1987, 1999; Griffith, 2001a, b, 2003; Pinkava, 2002; among others). The relative ease of vegetative propagation of *Opuntia* is demonstrated by its occasional clonal dominance of certain areas (Grant and Grant, 1971a; Mandujano et al., 1996). This aspect of *Opuntia* marks it as a noxious weed in some places (Dodd, 1936; Nobel, 1994). This ease of clonal propagation was probably not lost on the very early human population of the New World. Evidence exists for the use of *Opuntia* as human food at least 9000 yr before the present (Kiesling, 1998) or even as early as 12000 yr ago (Callen, 1967), probably before cultivation (Ostolaza, 1994).

Opuntia ficus-indica is used in numerous ways. In modern times, first and foremost, *O. ficus-indica* is grown for the large,

sweet fruits (often called "tunas"), which are available in local and commercial markets worldwide (Basile, 2001; Inglese et al., 2002). Important tuna-growing regions include Mexico, Sicily, Algeria, Chile, Brazil, and northern Africa (Barbera et al., 1992; Inglese et al., 2002). In addition, the young cladodes (stem segments) of *O. ficus-indica* are harvested as a vegetable crop (often called nopalitos). Although this crop is less valuable worldwide than the fruit crop, vegetable products of *O. ficus-indica* are available in many local and commercial markets (Sáenz-Hernandez et al., 2002). Various other uses have been reported for *O. ficus-indica*, including as a binding and waterproofing agent in adobe (Cárdenas et al., 1998). Medicinal properties of *O. ficus-indica* have been documented as early as 1552 (Emmart, 1940). *Opuntia ficus-indica* (along with other *Opuntia* and *Nopalea* species) has been grown from pre-Columbian times as a host plant for cochineal insects (*Dactylopius coccus*) for the production of valuable, vivid red and purple dyes (Donkin, 1977; Nobel, 1994). See Anderson (2001) for a near-exhaustive review of the various other uses of *O. ficus-indica*.

Early European botanists (often referring to Pliny or Theophrastus) called this cactus *Ficus indica* (Donkin, 1977), although some found this to be an unsuitable name, as the plant did not resemble the Indian fig (possibly *Ficus benghalensis* L.) already known (Anderson, 2001). Linnaeus published *Cactus opuntia* and *C. ficus-indica* in *Species Plantarum*. Miller combined these into *Opuntia ficus-indica* in 1768. In the recorded history of the Old World, *O. ficus-indica* was certainly known at the beginning of the 16th century (Donkin, 1977; Casas and Barbera, 2002), and it is believed that this species accompanied Columbus in his first return to Lisbon in 1493 (Russell and Felger, 1987; Anderson, 2001), placing *O. ficus-indica* in the Caribbean by at least the late 1400s, although whether it is native there is unknown. The plants are also recorded in cultivation in Tlaxcala, Mexico, in 1519 (Diaz del Castillo, 1632 in Idell, 1957). *Opuntia ficus-indica* fruits and shoots were also reportedly consumed by the Maya of southeastern Mexico (Coe, 1994). There is also some evidence for the use of *O. ficus-indica* by the Nazca of Peru, placing these plants in South America at a very early date (Sejuro, 1990). Other workers maintain that this taxon was unknown in pre-Columbian South America (Towle, 1961; Baker, 2002). The

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² E-mail: michael.patrick.griffith@cgu.edu.



Fig. 1. *Opuntia ficus-indica*, a domesticated species of cactus cultivated primarily for its fruits.

succulent, ever-fresh cladodes were certainly a novelty to late 15th century and later Europeans (Donkin, 1977) and were widely included in ships' stores as insurance against scurvy (Kiesling, 1998). This practice is thought to have contributed greatly to the present naturalized range of *Opuntia ficus-indica* throughout arid and semiarid habitats of the world (Anderson, 2001; Casas and Barbera, 2002; Sáenz-Hernandez et al., 2002). This widespread propagation (intended and unintended) throughout the Mediterranean obscured the geographic origins of this species; many early European botanists regarded this cactus to be native (Donkin, 1977; Barbera et al., 1992), as reflected in *Cactus opuntia* L. (i.e., spiny plant from near

Opus, Greece; Anderson, 2001). This Mediterranean naturalization may now be conceived as complete, as the Israelis of the mid-20th century often adopted the (believed-indigenous) *sabras* as a symbol of their struggle (and humanity) in adverse desert conditions (Uris, 1959).

Although most recent authors concede that this species is not native to the Old World, the geographic and evolutionary origins of *Opuntia ficus-indica* remain clouded in obscurity (Britton and Rose, 1919; Bravo-Hollis, 1978; Benson, 1982; Anderson, 2001). This mystery arises partly from the widespread cultivated distribution of the plants, both within and away from the New World (Anderson, 2001), but also from

the phenotypic variability and artificial selection of the plants (Benson, 1982). The specific epithet (from P. Miller, 1768) may reflect the 16th-century European opinion that the plants are native to the West Indies (Barbera et al., 1992; Casas and Barbera, 2002). The name “tuna” is Caribbean in origin (Bravo-Hollis, 1978; Kiesling, 1998). Other early work proposed that *O. ficus-indica* was a spineless cultivar derived from *O. megacantha*, a species of central Mexico (Griffiths, 1914). A recent, important paper explored this relationship with amplified fragment length polymorphism (AFLP) data and reported that *O. ficus-indica* had the closest affinity with *O. megacantha* (Labra et al., 2003), corroborating the Griffiths (1914) hypothesis. Other authors, however, consider *O. megacantha* also to be a cultivated taxon (Benson, 1982) or a name applied to multiple ruderal reversioners to spininess from escaped, cultivated *O. ficus-indica* (Kiesling, 1998) and treat *O. megacantha* as a later synonym (Benson, 1982; Kiesling, 1998). Uphof (1968) and Zeven and Zhukovsky (1975, p. 164) place the origin of this cactus within “Mexico” or the “Central American and Mexican centre” of domestication, but without reference to a specific region. Some recent cytological work proposes that octoploid, cultivated *O. ficus-indica* is derived from a diploid Mexican (but unnamed) progenitor (Kiesling, 1998). Benson (1982) states that *O. ficus-indica* is native to mild tropical upland habitat (not deserts), but does not state where. Given the conflicting, sometimes confusing, and often unclear hypotheses as to the origins of this cactus crop, a wide molecular phylogenetic analysis has potential to elucidate the biogeography of this species. The current study addresses the biogeographic and evolutionary origins of *O. ficus-indica* through modern molecular means. To this end, I have gathered and analyzed DNA sequence data from a number of accessions of *O. ficus-indica* representing plantings throughout the world.

METHODS AND MATERIALS

Live material was obtained from plantings at Desert Botanical Garden, Phoenix, Arizona, USA; Sul Ross State University Cactus Garden, Alpine, Texas, USA; Rancho Santa Ana Botanic Garden, Claremont, California, USA; and Texas A & M University (Kingsville), Kingsville, Texas, USA; or from specimens field collected by the author in 1999–2003. The sampling structure attempted to represent all major geographic lineages (via the infrageneric series of Britton and Rose, 1919) and include a broad sample of *O. ficus-indica* accessions. A list of specimens used in this study is found in Appendix 1 (see Supplemental Data accompanying the online version of this article). Total DNA was extracted from fresh tissue using a protocol for mucilaginous tissues (Griffith and Porter, 2003). Amplification of the internal transcribed spacer (nrITS) region of the nuclear ribosomal DNA follows Columbus et al. (1998). Fluorescent sequencing used Big Dye (Applied Biosystems, Foster City, California, USA) chemistry, according to the manufacturer’s specifications. All DNA sequence data was gathered using an Applied Biosystems 3100 Genetic Analyzer. Chromatograms derived from sequencing were edited and consensus sequences obtained using Sequencher version 4.1 (Gene Codes, Ann Arbor, Michigan, USA). Consensus sequences were aligned manually via Se-AL version 2.0a7.2 (Rambaut, 1996); sequence alignment was unambiguous. A Bayesian analysis of the data was performed with MrBayes version 2.01 (Huelsenbeck and Ronquist, 2001). For each analysis, a site-specific gamma model was employed. A random starting tree was used, and four Markov chain Monte Carlo (MCMC; Metropolis et al., 1953) replicates were run for 250 000 generations, sampling every 50. Metropolis-coupled MCMC analyses were performed using the Metropolis-Hastings-Green algorithm (Huelsenbeck and Ronquist, 2001), as implemented by Mr. Bayes. The log likelihood (lnL) for all sampled trees was viewed and graphed in Microsoft Excel (Microsoft, Seattle, Washington, USA). Trees from the burn-in period (Huelsenbeck and Ronquist, 2001) were discarded, and a majority rule consensus tree was ob-

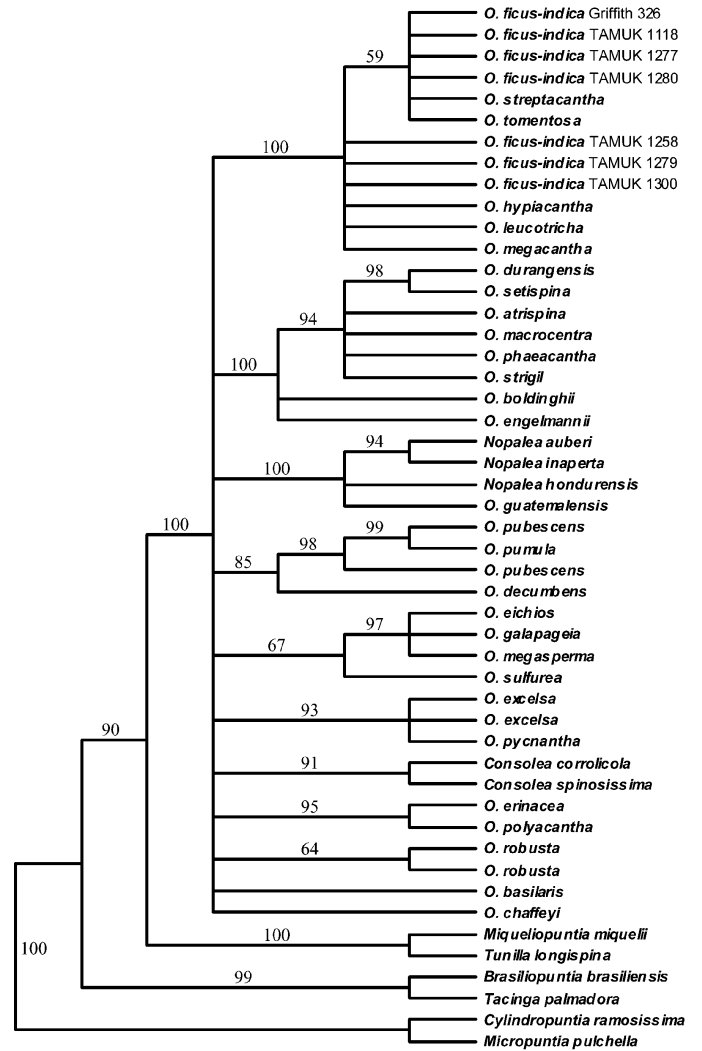


Fig. 2. Phylogenetic analysis of *Opuntia ficus-indica* and related taxa: Bayesian consensus of 130 000 high likelihood trees remaining after trees from the burn-in period were discarded. Numbers above branches represent the posterior probabilities of those clades existing given the data. Sampled *O. ficus-indica* specimens are included in a well-supported clade with other arborescent central Mexican *Opuntia* species.

tained with PAUP* version 4.10 β (Swofford, 1998) for the remaining trees sampled. This Bayesian analysis was performed 10 times, and the results from each run compared for consistency. Estimations of confidence in the clades obtained by the Bayesian analysis are the posterior probabilities of those clades occurring given the data (Miller et al., 2002), which are indicated by the percentage consensus values obtained by PAUP. These values are interpreted similarly to bootstrap percentage values on a maximum likelihood tree (Huelsenbeck and Ronquist, 2001).

RESULTS AND DISCUSSION

The aligned data matrix of all 49 specimens included in this study was 733 bases in length. Phylogenetic analyses of this data are presented in Figs. 2 and 3. All seven specimens of *O. ficus-indica* are included in a very well-supported (100% Bayesian posterior probability; Fig. 2) clade with *O. hypiacantha*, *O. leucotricha*, *O. megacantha*, *O. streptacantha*, and *O. tomentosa*, a group of arborescent, fleshy-fruited prickly pears from central Mexico (Britton and Rose, 1919; Bravo-

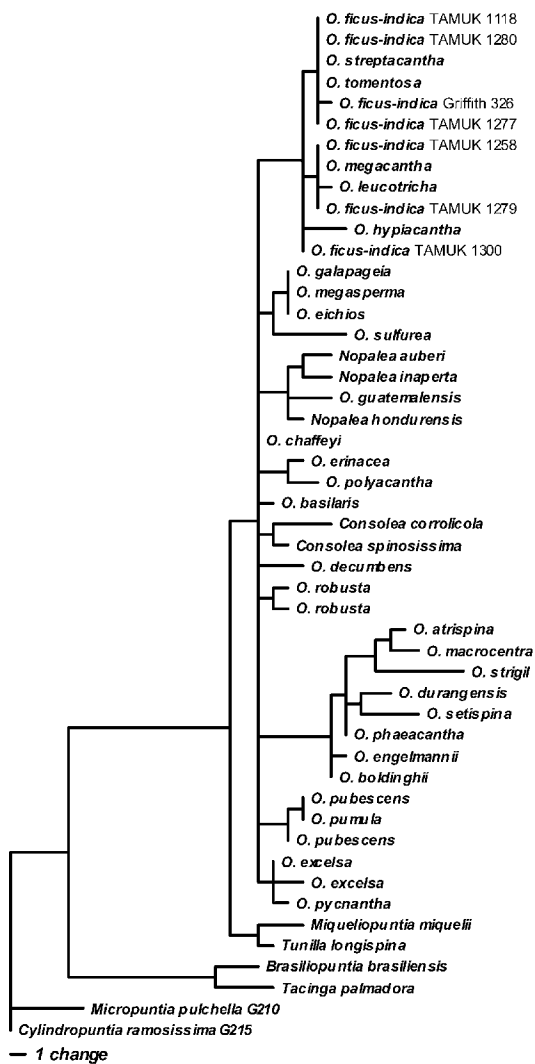


Fig. 3. The highest likelihood tree recovered from the Bayesian analyses. With uninformative characters excluded, length = 109; lnL = -1653.265; consistency index = 0.7424; retention index = 0.7444. Of the seven *Opuntia ficus-indica* specimens sequenced, four sequence variants for the ITS region were recovered.

Hollis, 1978; Anderson, 2001). This clade excludes arborescent plants from the Caribbean (*Consolea* spp. and *O. boldinghii*) and from South America and the Galapagos (*O. eichios*, *O. galapageia*, *O. megasperma*, and *O. sulfurea*) included in this study. Also notably excluded from the *O. ficus-indica* clade are *O. durangensis* and *O. robusta*, two large, polyploid, fleshy-fruited taxa from central and northern Mexico. *Opuntia durangensis* can often be very large and treelike (to 5 m; personal observation) and is found in the central and southern Chihuahuan Desert region (Anderson, 2001; personal observation); *Opuntia robusta* (nopal tapon) is cultivated throughout Mexico for its large edible fruits (Anderson, 2001) or for ornamental purposes (personal observation).

The inferences gained here support the hypothesis that *O. ficus-indica* is a crop domesticated from ancestral stock of arborescent, fleshy-fruited plants growing in central Mexico. From this center of origin, *O. ficus-indica* cultivation likely spread through trade amongst the peoples of Mesoamerica.

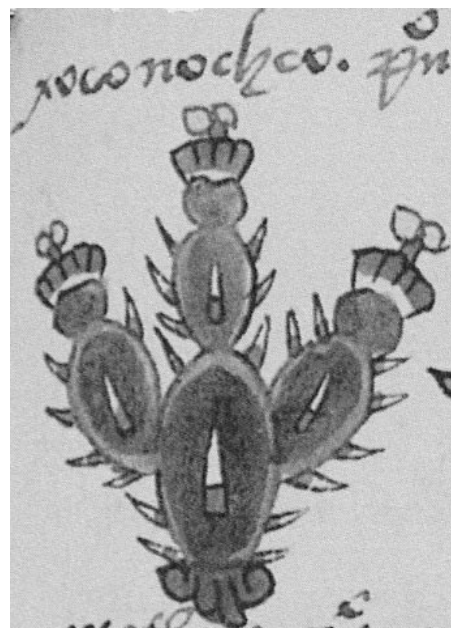


Fig. 4. Early colonial period (ca. 1550) Mesoamerican depiction of *Opuntia ficus-indica* as a possible tribute item (detail from Codex Mendoza, folio 47r, Bodleian Library, Oxford University, Oxford, UK). Trade of *Opuntia* produce in ancient times greatly expanded the range of the plants.

One artifact that indicates the value of prickly pear as a trade item is the Codex Mendoza (ca. 1535–1550), which depicts Aztec tribute rolls (Berdan and Anwalt, 1992). This codex includes a representation of *Opuntia* cladodes amongst other items such as ocelot and jaguar skins (Fig. 4). This is the only early colonial period representation of *Opuntia* as a possible trade item, although the plant is often depicted in such codices outside of this context (Emmart, 1940; Robertson, 1959). This depiction may also represent a location (Xoconochco) as in the Codex Mendocino (Penafiel, 1885). Cochineal dye, for which *Opuntia* cultivation is required, is also depicted here as paid tribute to the Aztecs (Berdan and Anwalt, 1992; Fig. 5).

From Mesoamerica, these plants were introduced into Cuba, Hispaniola, and other Caribbean islands, where early European explorers first encountered the plants (Donkin, 1977; Russell and Felker, 1987). It seems conceivable that these plants were also brought to South America in pre-Columbian times, although their early presence in Peru is disputed (Towle, 1961; Sejuro, 1990); there is evidence that the pre-Columbian Incas certainly cultivated cochineal, however (Donkin, 1977). A summary of the biogeographic conclusions supported by the present study is presented in Fig. 6.

Sequences recovered for *O. ficus-indica* did not show polymorphism within accessions. The recovery of multiple (four) ITS sequence variants among the sampled *O. ficus-indica* specimens (Fig. 3) may result from one or more of several phenomena, discussed next.

Natural hybridization—Polyploidy and hybridization are well documented in the opuntoid cacti (Benson and Walkington, 1965; Grant and Grant, 1971b, 1979; Baker and Pinkava, 1987, 1999; Griffith, 2001a, b, 2003; Pinkava, 2002). *Opuntia ficus-indica* is octaploid (Pinkava, 2002), possibly through ancient allopolyploidy. Natural biological events may have led

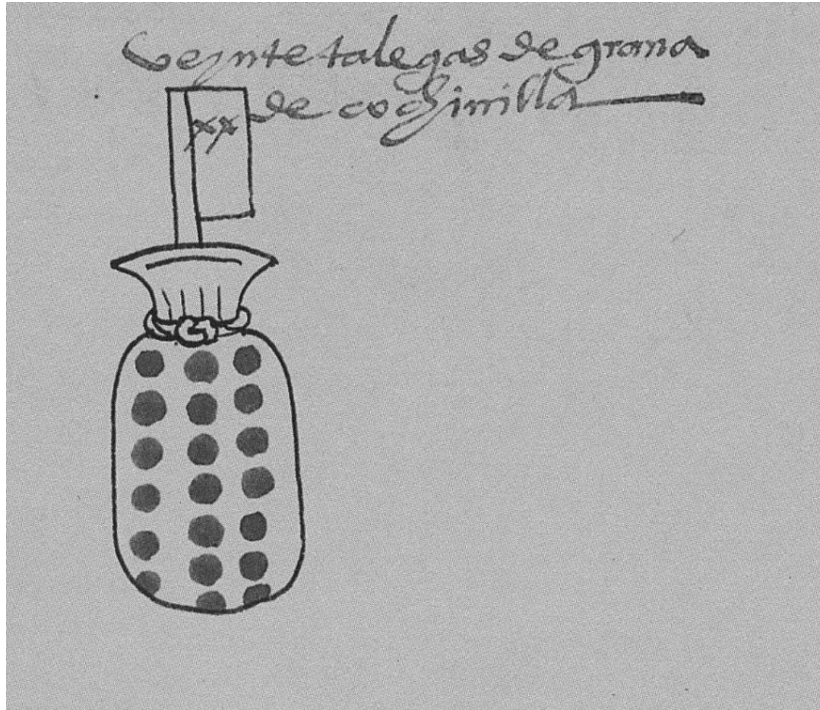


Fig. 5. Depiction of cochineal dye, a secondary *Opuntia* product, given as tribute to the Aztecs (detail from Codex Mendoza, folio 44r, Bodleian Library, Oxford University, Oxford, UK). This dye was extremely valuable to early 16th- through late 19th-century Europeans, and its demand strongly influenced the distribution of *O. ficus-indica* plantations in Sicily, the Canary Islands, and North Africa (Donkin, 1977; Nobel, 1994). If cochineal dye production was a strong economic motivator for Mediterranean cultivation, then it probably strongly influenced pre-Columbian distribution as well.

to the pattern of relationships in *O. ficus-indica* recovered for the ITS data set.

Human manipulation—If *O. ficus-indica* is of hybrid origin, it is conceivable that the hybridization was human facil-

itated. This may have occurred indirectly, by bringing allopatric ancestors into cultivated sympatry. One intriguing possibility is that hybridization of ancestral *O. ficus-indica* stock was instead performed directly by Mesoamerican agriculturalists. There is evidence for the intensive selective breeding of

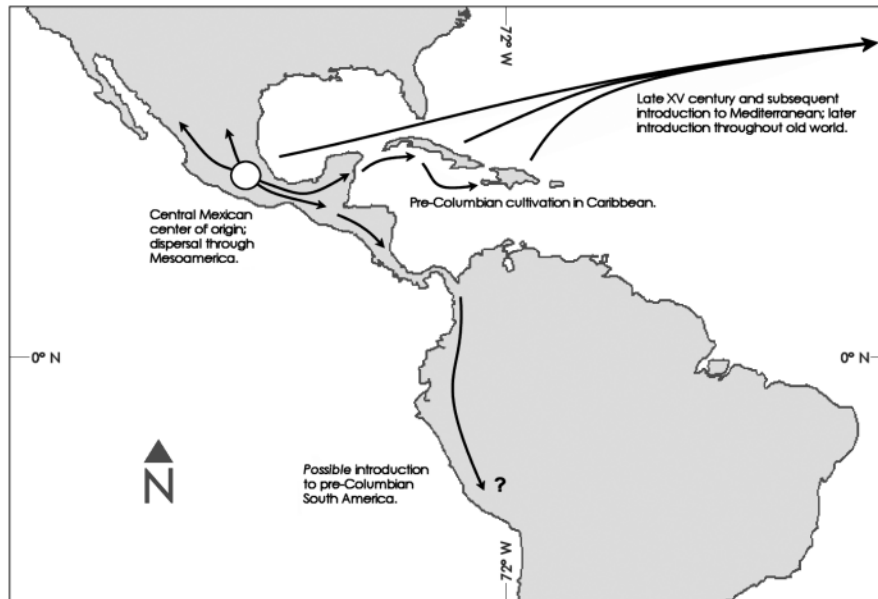


Fig. 6. A biogeographic model of dispersal of *Opuntia ficus-indica*. From central Mexico, the ancestors of *O. ficus-indica* were selected from arborescent, fleshy-fruited taxa (one or more species such as *O. leucotricha*, *O. hyptiacantha*, *O. megacantha*, and *O. streptacantha*). The cultivated plants then spread through trade throughout Mesoamerica and the Caribbean and possibly into South America. European travelers then spread these plants into Mediterranean Europe and North Africa and subsequently throughout arid and semiarid regions of the world.

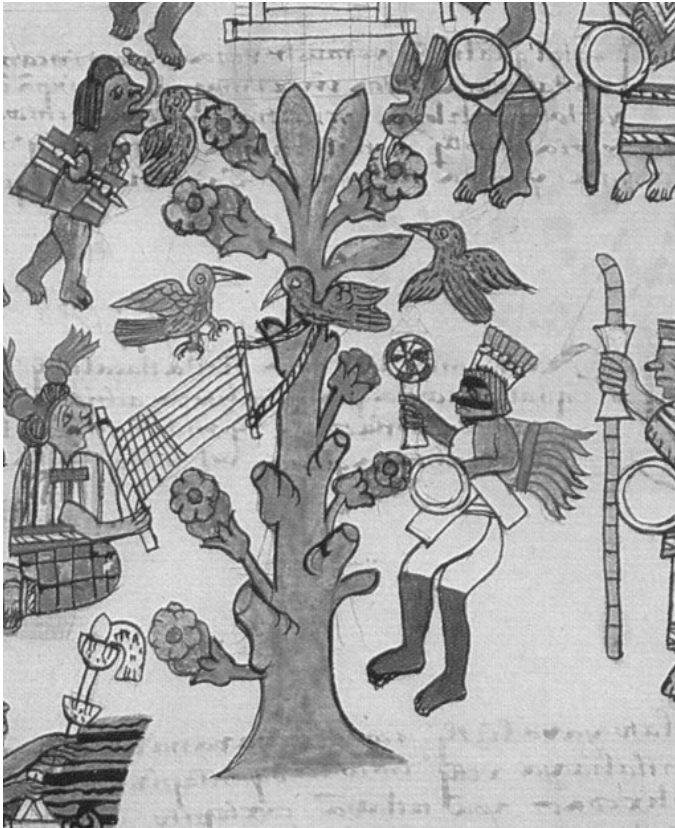


Fig. 7. Early colonial period (ca. 1558) Mesoamerican depiction of hummingbird pollination (detail from *Primeros Memoriales*, Cap. I, folio 254r, Biblioteca del Palacio Nacional, Madrid, Spain). The ancient Mesoamerican agriculturalists may have had knowledge of pollination biology, much like their contemporaries in Mesopotamia.

fruit crops by pre-Columbian peoples (Bergh, 1995); it is possible that Mesoamerican knowledge of plant reproduction included pollination technology. Descriptions and depictions of Mesopotamian date palm (*Phoenix* spp.) cultivation dating to 1750 BC or earlier are interpreted as the earliest documentation of human use of artificial pollination in fruit crop selection (Paley, 1976; Roth, 2000; Janick, 2005). Although there is no direct evidence of pollination for crop manipulation of *O. ficus-indica* in contemporary Mesoamerica, the early knowledge of its biological function is suggested by the depiction of hummingbird pollination in the *Primeros Memoriales* of Sahagún (ca. 1558; Fig. 7).

Multiple unrelated clones—Another likely explanation for the polyphyly of *O. ficus-indica* is that this species concept may consist of multiple unique clones derived from various parental stock, selected for reduced spination and desirable fruits, artificially converging further upon these traits, and propagated clonally to the present day. This scenario is supported by Janick (2005), who states that most fruit cultivation was likely achieved through maintenance of unique clones, in contrast to cereal cultivation. Therefore, it is possible that the taxonomic concept of *O. ficus-indica* may circumscribe a non-monophyletic group of convergent cultivars derived from different parental species.

Lineage sorting—Another possible explanation for this pattern of genetic relationships is lineage sorting (Pamilo and Nei, 1988) of multiple ITS copies in a widespread ancestral population of *Opuntia* that gave rise to *O. ficus-indica* and its close relatives.

These four hypotheses should be tested through other independent molecular investigations. Other DNA sequence-based phylogenetic estimations may be of use, but the low level of variation in the ITS region for the genus *Opuntia* may indicate that a genome-wide approach may yield more useful variation. Reticulate evolution in *Opuntia* has been investigated via random amplified polymorphic DNA (RAPD) data (Mayer et al., 2000; Griffith, 2003), and some modern clones of *O. ficus-indica* have been characterized via this method (Wang et al., 1998) as being either for fruit or vegetable production. Other data that may elucidate these relationships might include AFLP (as in Labra et al., 2003) and microsatellite data. This population genetic approach may elucidate potential differences in heterozygosity between *O. ficus-indica* populations from different localities within central Mexico and abroad, which could further pinpoint the location of the wild progenitors of this species. Ongoing investigations will involve these data types interpreted in a historical and archaeological context and may illuminate the ancient selection of these plants by the oldest inhabitants of Mexico.

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