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CROP ECOLOGY, CULTIVATION AND USES OF CACTUS PEAR

Final Version

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Origin and taxonomy of *Opuntia ficus-indica*

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02 Origin and taxonomy of *Opuntia ficus-indica*

INTRODUCTION

Opuntia ficus-indica is the cactus species of greatest agronomic importance, due to its delicious fruits, but also to its stems, which are used as fodder for livestock or as a vegetable for human consumption (Alkämper, 1984; Kiesling, 1999a; Casas and Barbera, 2002). The use and cultivation of opuntias dates back to prehistoric times, long before the Spaniards arrived in the Americas. The Indian chroniclers were the first to record these plants and its fruits, which were carried to Spain and initially used as ornamental plants (Casas and Barbera, 2002). It is probable that opuntias were brought back after the first or second visit of Columbus to the Caribbean, although the first definitive record is from Mexico in 1515 (in the chronicle of Fernández de Oviedo, reproduced by López Piñeiro *et al.*, 1992). The long history of the use, cultivation and domestication of *O. ficus-indica* and related species resulted in taxonomical and nomenclatural problems, summarized in this chapter.

ORIGIN AND TAXONOMY OF *OPUNTIA FICUS-INDICA*

The spineless form of *O. ficus-indica* – common in agriculture today – is the result of a long selection process in cultivation and it is absent in wild stocks. According to Bravo Hollis and Sánchez Mejorada (1991), its domestication began about 8 000 years ago. Reyes Agüero *et al.* (2005) maintain that domestication took place in the south of the meridional Mexican highlands. Archaeological references indicate that the opuntias used 8 000 years ago cannot be associated directly with *O. ficus-indica*. Callen (1965) studied the food habits of pre-Columbian Mexican Indians and found epidermis remnants of *Opuntia* in coprolites on the floor of caves, indicating that the consumption of *Opuntia* dated back thousands of years to at least 5200 BCE. According to Casas and Barbera (2002), archaeological remains of opuntias were found in caves of the Ajuereado phase (14000-8000 BCE).

Several taxa are mentioned as putative ancestors of *O. ficus-indica*, in particular *O. megacantha* and *O. streptacantha*. These and several other taxa and names are often confused due to ambiguous descriptions and a lack of types (Leuenberger, 1988).

Griffiths (1914) considered *O. megacantha* to be the wild thorny form of cultivated *O. ficus-indica* (in the narrow sense, or *O. ficus-indica f. ficus-indica*); this was later corroborated by molecular studies (Griffith, 2004). However, the most likely explanation is that they have a common ancestor. Both arose from natural hybridization and multiple sporadic interbreeding. Benson (1982) considers *O. megacantha* as a cultivated taxon and a synonym of *O. ficus-indica* in the "spiny form", and discards the category of variety or form. Other authors (e.g. Gibson and Nobel, 1986; Brutsch and Zimmermann, 1993) follow this reasoning. According to Kiesling (1999a), *O. megacantha* is a reversion to spined plants from escaped, spineless *O. ficus-indica* (see below).

One of the few authors mentioning *O. ficus-indica* solely in the spineless form is Bravo Hollis (1978), who uses only morphological characters for the delimitation; however, she contradicts herself more than once (1978). In the same book she lists six *variedades hortícolas* (which correspond to the concept of cultivar) based solely on the fruit characters. Scheinvar (1995) accepts three separate species: *O. ficus-indica*, *O. streptacantha* and *O. amyclaea*, but also considers *O. ficus-indica* as a cultivated form

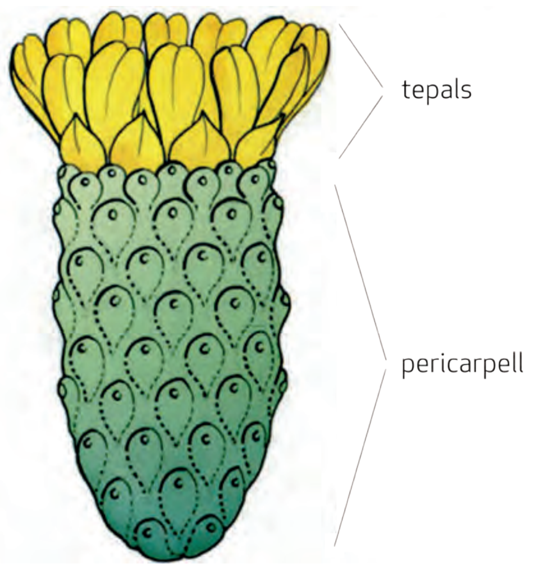


Figure 1
A typical characteristic of the Opuntia ficus-indica *flower is the long pericarpell, which is usually twice the size of the length of the tepals.*

originating from *O. streptacantha* and keeps it separate at a specific rank for practical reasons (L. Scheinvar, personal communication).

Several names of the series *Streptacanthae* and *Ficus-indicae* (Britton and Rose, 1919) correspond to minor morphological variations of *O. megacantha*. A description by Britton and Rose (1919) of the series *Ficus-indicae*, which includes the more or less spineless forms of the group discussed here, stated: "None of the species is definitively known in the wild state, but all doubtless originated from tropical ancestors, and they may all represent spineless races of plants here included in our series *Streptacanthae*."

On the other hand, others maintain that there are enough differences to keep the series *Streptacanthae* and *Ficus-indicae* separate. Colunga Garcia *et al.* (1986) wrote: "Thus, these two groups can be differentiated based on cladode size and areole length, fruit and seed length, as well as the length and weight of pulp of the fruit (the edible portion of the fruit). In our opinion, the cladode size, the weight of fruit pulp, as well the areole form may differ caused by the selection process that aims to improve the quality for use as animal fodder or for human consumption."

The spines – presence and size – represent another very variable character. Although the development of spineless forms was encouraged during the domestication process, the opposite – from spineless to spination – is also possible. Such reversions, where some branches of spineless forms produce spines after drought stress or other sorts of stress, are mentioned by several authors (Griffiths, 1912, 1914; Le Houérou, 1996a; Kiesling, 1999a). Moreover, when seeds of the spineless form are sowed, a small percentage of the seedlings develop spines; and vice versa, sowing of seeds from spiny plants results in a small proportion of spineless plants (Berger, 1905; M. Ochoa, personal communication; I. Chessa, personal communication; authors' experience). The reversion of spineless cultivars to spiny plants was also observed in South Africa and Sicily (Zimmermann, 2011; Leuenberger and Arroyo Leuenberger, 2014). The presence of spines is not a valuable character in *Opuntia* taxonomy, because the formation of spines is not independent of environmental factors (Labra *et al.*, 2003).

CHROMOSOME NUMBERS

Determination of chromosome number and ploidy level is a useful tool in plant taxonomy. The basic chromosome number in the cactus family is $n = 11$, and the number in somatic cells is mostly $2n = 22$. In the subfamily Opuntioideae, 64.3% of the taxa are polyploid (Pinkava *et al.*, 1985). Several karyotypic studies show tetra-, hexa- or octoploids in the putative relationship of *O. ficus-indica* (spiny form as *O. megacantha*) $n = 44$ (Pinkava *et al.*, 1973); *O. streptacantha* $n = 44$ (Pinkava and Parfitt, 1982); *O. streptacantha* $2n = 88$ (Palomino and Heras, 2001); *O. amyclaea* and *O. megacantha* $2n = 88$ (Sosa and Acosta, 1966); *O. polyacantha* $2n = 44$, 66 (Stockwell, 1935). Octoploids ($2n = 88$) are also reported for other taxa of the series *Streptacanthae* (including ser. *Ficus-indicae*) (Segura *et al.*, 2007; Majure *et al.*, 2012a). Polyploidy is favoured by hybridization. Natural, interspecific hybridization in the genus *Opuntia* has been proved by several studies (e.g. Benson and Walkington, 1965; Grant and Grant, 1982; Griffith, 2003; McLeod, 1975) and hybridization in cultivation is common too. The occurrence of higher ploidy levels of cultivars in comparison with wild relatives is obviously true for cultivated *O. ficus-indica* (Mondragón Jacobo and Bordelon, 1996). For *O. ficus-indica* alone, many chromosome counts show that both the spiny and the spineless forms are octoploid (Pinkava *et al.*, 1973, 1992). Cultivated plants of *O. ficus-indica* in Italy were found to be octoploid (Barbera and Inglese, 1993). However, this species is also reported as hepta-, penta-, hexa- and diploid, so there exists a variation of chromosome numbers, depending on the provenance (Spencer, 1955; Weedin and Powell, 1978; Pinkava, 2002; Majure *et al.*, 2012a) – unless the different numbers are the result of misidentified study material or anomalies in the meiosis. McLeod (1975) indicates the presence of hybrid specimens with $2n = 77$, in between *O. ficus-indica megacantha* (octoploid: $2n = 88$) and *O. phaeacantha* var. *major* Engelm. (hexaploid: $2n = 66$). Carpio (1952) mentions also $n = 44$ for *O. ficus-indica*. He suggests that the anomalous meiosis and the existence of tetravalentes show that *O. ficus-indica* is either an allopolyploid originating from two species with $2n = 44$ or an autopolyploid. Allopolyploidy of *O. ficus-indica* is confirmed by Griffith (2004).

MOLECULAR STUDIES

Given that morphological studies resulted in different taxonomic hypotheses, greater insight was expected from molecular studies (mainly of DNA) concerning variability, relationship and origin of the *Opuntia* species and *O. ficus-indica* in particular. Although several studies focus mainly on the genetic diversity of cultivars (e.g. Bendhifi *et al.*, 2013; El Finti *et al.*, 2013; Ganopoulos *et al.*, 2015), some give insight into the differentiation of *O. ficus-indica*. Wang *et al.* (1999) studied five cactus fruit cultivars from Mexico and Chile, two ornamental Texas accessions, and one vegetable accession from Mexico. The DNA analysis revealed significant differences between the market accessions, but only slight differences between the fruit cultivars (including spined and spineless forms). The genetic diversity of cultivated cacti seems to be low in general, probably because they originate from a narrow germplasm base (Boyle and Anderson, 2002).

In the study by Labra *et al.* (2003), molecular data revealed a high genetic similarity between *O. ficus-indica* and *O. megacantha*. The only (morphological) difference between the units is the presence of spines. The authors conclude that *O. ficus-indica* should be considered a domesticated form of *O. megacantha*.

Griffith (2004), when studying the origin of *O. ficus-indica* using molecular data, found a well-supported clade including *O. ficus-indica*, *O. streptacantha*, *O. tomentosa, O. leucotricha* and *O. hyptiacantha*, all from southern and central Mexico (diversity centres of *Opuntia* – Barthlott *et al.*, 2015). The analysis supports the hypothesis that the centre of domestication was central Mexico and *O. ficus-indica* may be polyphyletic, i.e. descended from different lineages. This could be due to hybridization (in nature or during cultivation), derivation of multiple unique clones from various parental stock, or lineage sorting of multiple internal transcribed spacer (ITS) copies in an ancestral population from which *O. ficus-indica* and closely related species may have descended (Griffith, 2004). Caruso *et al.* (2010) studied the genetic diversity of *O. ficus-indica* cultivated genotypes. Their analysis supports the hypothesis that *O. ficus-indica* consists of a group of multiple unrelated clones, derived from different parental species and selected for different agronomical features.

Majure *et al.* (2012b) concluded that *O. ficus-indica* is one of several species originating from allopolyploidization events caused by the hybridization of species belonging to different clades. The *O. ficus-indica* samples studied by Caruso *et al.* (2010) did not cluster separately from other species (*O. amyclaea, O. megacantha, O. streptacantha, O. fusicaulis* and *O. albicarpa*), indicating that the current taxonomical position and the genetic patterns do not fit very well. Lyra *et al.* (2013a) studied characteristics of cultivars of four species (*O. ficus-indica*, *O. albicarpa, O. streptacantha* and *O. robusta*), but with the used marker (ITS) it was not possible to assign the samples of these species to separate clades. This difficulty may arise from the fact that the samples are of hybrid origin or have a common ancestry. Valadez Moctezuma *et al.* (2015) advanced this latter assumption when *O. ficus-indica*, *O. albicarpa* and *O. megacantha* proved impossible to separate in different clades. Similarly, Samah *et al.* (2015) could not detect clear boundaries between *O. ficus-indica*, *O. albicarpa, O. megacantha, O. streptacantha, O. lasiacantha* and *O. hyptiacantha*. Astello Garcia *et al.* (2015), in a study on the molecular composition of five *Opuntia* species, could not verify a proposed domestication gradient for *O. ficus-indica*, when different cultivars of this species clustered within different groups. While the study failed to identify the ancestor, *O. hyptiacantha* could be related with the majority of the *O. ficus-indica* samples studied. Srikanth and Whang (2015) compared three taxa of *Opuntia* cultivated in Korea and found that the Korean *O. ficus-indica* is closely related to *O. engelmannii* and *O. ellisiana*, but not to the *O. ficus-indica* samples taken from the GenBank database. Molecular studies reveal the faultiness of the current taxonomy for the species and cultivar complex of *O. ficus-indica*, and question whether these problems are caused by hybridization, adaptive genetic responses, phenotypic plasticity, epigenetic bases or other factors (Valadez Moctezuma *et al.*, 2014).

DISTRIBUTION AND NATURALIZATION

While its ancestors originate in central Mexico (Griffith, 2004), *O. ficus-indica* has been taken by humans to other areas of the world with warm climates. Following the introduction of *O. ficus-indica* in Spain around 1500, the species (and others of the same genus) spread and naturalized throughout the Mediterranean area, soon becoming a characteristic element of the landscape. It was already widespread in Europe in 1550 (Mottram, 2013). Therefore, it is not surprising that one species, *O. amyclaea*, was described in 1826 as coming from Italy, where it had been found near the town of Amyclæ (today Monticelli). It corresponds to the spiny form of *O. ficus-indica*. *O. amyclaea* was considered a form of *O. ficus-indica* by Schelle (1907); for this reason, in the taxonomic rank of form its previous name was *O. ficus-indica f. amyclaea*. Berger (1905, 1912b) also assumed that this *Opuntia* established in Italy must be the original form of *O. ficus-indica*, i.e. an ancestral form. A form of *O. ficus-indica* from Argentina was also described as a new species (*O. cordobensis*), and similarly a form from Bolivia (*O. arcei*) (Kiesling, 2013). At the beginning of the twentieth century, the American botanist and agronomist David Griffiths studied and cultivated opuntias in Texas for taxonomic and agronomic evaluation (Benson and Walkington, 1965; Walkington, 1968). He described several species from cultivated specimens, and some of these species – better treated as cultivars – are considered synonyms or hybrids of *O. ficus-indica* today (e.g. *O. fusicaulis*, 1908; Kiesling *et al.*, 2008). In the eighteenth century, *O. ficus-indica* was introduced to other continents by navigators who – given its vitamin C content and low perishability – used it as a vegetable to prevent scurvy (Diguet, 1928). They also transported it to:

- meet the demand for carmine dye from cochineal, which feeds on *Opuntia*;
- use as fodder;
- incorporate in the human diet; and

- make living fences.

Adapted to harsh and dry conditions, opuntias could easily escape and naturalize in arid areas of Africa, Asia and Australia. *O. ficus-indica* had already been introduced to South America by the Spanish conquerors, for example, in Bolivia (Hoffmann, 1955). Opuntias spread rapidly in many regions, sometimes becoming invasive: a threat to native biodiversity and to agricultural land use (Brutsch and Zimmermann, 1993; Barbera and Inglese, 1993: 11). Today *O. ficus-indica* is naturalized in 26 countries outside its native range (Novoa *et al.*, 2014).

In all tropical arid countries where it is cultivated or naturalized, *O. ficus-indica* has undergone genetic alterations and phenetic modifications, resulting in new forms that have been distinguished and formally named. Sometimes they are classified as species or varieties, even when a classification and naming as cultivars of the two forms (*O. ficus-indica* f. *amyclaea* and *O. ficus-indica* f. *ficus-indica*) would be more appropriate (cf. Brickell *et al.*, eds, 2009).

While there are numerous recordings of the introduction of the spineless *O. ficus-indica* f. *ficus-indica* to different countries, it should be noted that there are almost no references concerning the introduction of the spiny form.

VERNACULAR NAMES

Given the importance of *O. ficus-indica* and its numerous benefits, it has been given many names in its native range and in the regions where it has been introduced (Reyes Aguero *et al.*, 2005). Some of these names are a good illustration of the origin of introduction and distribution.

The name "tuna" is of Caribbean origin (Bravo Hollis and Sánchez Mejorada, 1991) and was used by the first Spaniards arriving in the Americas. To be precise, it is a Tain name (Moringo, 1966). It usually refers to the fruits, but is also used for the vegetative parts of the *Opuntia* species. The name is currently in use in a very extensive area, which suggests that it was the first name known by the Spaniards, even before the Mexican names (since they reached the Caribbean islands before the mainland).

"Nopal" is a Mexican name derived from the Nahuatl *Nopalli* (Bravo Hollis and Sánchez Mejorada, 1991; Moringo, 1966), and is used for several species. *Tenochtli* is the original name used in large parts of Mexico.

The first Spanish name is *higo de las Indias*, a reference to its origin, the New Indies; it gave rise to the first scientific name: *Cactus ficus-indica* Linné. The epithet, *ficus-indica*, was used as a "diagnostic phrase" long before Linné, to designate several more or less similar species. In other languages, similar vernacular names are used: *figo da India* (Portuguese); Indian fig (English); *figuier d'Inde* (French); *Indianische Feige* (German); *fico d'India* (Italian) (Reynolds and Arias, 2001).

Another widely known name is *tuna de Castilla* (or *nopal de Castilla*), obviously derived from the name of the former Spanish kingdom of Castilla, from where Opuntia was distributed to other countries. Le Houérou (1996a) mentions Andalusia as the first propagation centre in that continent – the region Christopher Columbus returned to after his voyages. Following the dissemination of *Opuntia* in Spain, it was introduced to North Africa, where it was called *higo de los cristianos*. The spiny form is currently widespread in Morocco, where it is called *tapia* (from the Spanish word for fence), a reference to its use as a hedge (A. Prina, personal communication). The name "sabra" – a word used to refer both to the native people and to the prickly pear plant – illustrates the extent of its distribution in the Mediterranean area. Indeed, the species is frequently used to illustrate postage stamps in several countries around the Mediterranean Sea.

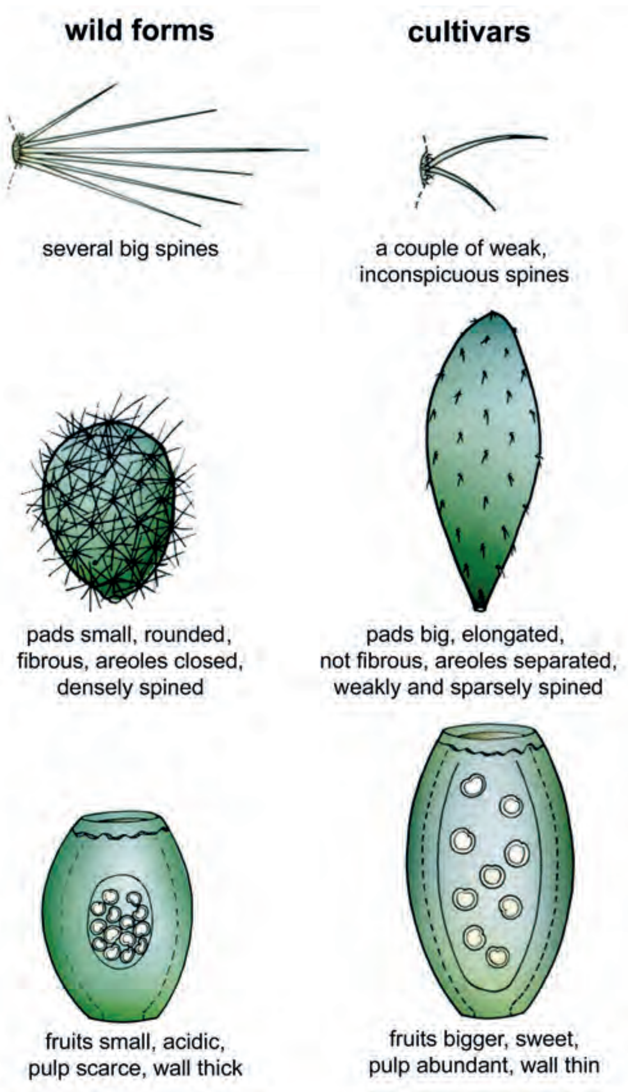
In 1769, the Franciscan missionaries took the cultivated form from Mexico to California, where it is called "mission cactus" (Benson and Walkington, 1965; Walkington, 1968). However, it is not certain whether the natives already cultivated this species before the arrival of the Franciscans. Walkington (1968) used the name *O. ficus-indica* in a wide sense.

The species is very important for the economy of northeast Brazil, where it is mainly used as forage throughout the year and is called *palma forrageira*. It is not known when it was introduced to that country (Domingues, 1963). *Palma-de-gado* is another common name for *O. ficus-indica* in northeast Brazil. Several other vernacular names beginning with "palma" are applied to the species in regions of the Brazilian state Bahia, where the pads are used as forage and the fruits, mucilage and roots have several uses in human nutrition and medicine (Andrade, 2008).

THE ROLE OF COCHINEAL

The cochineals of the genus *Dactylopius* parasite on many cactus species, including those of the genus *Opuntia*. Cochineals have great species-specificity. *Dactylopius coccus*, also known as grana, has an absolute preference for *O. ficus-indica* and for taxa that are considered its synonyms or are closely related (e.g. *O. megacantha, O. streptacantha, O. cordobensis*). José de Acosta (1590, cited after Di Lullo, 1944) wrote about tunales domésticos in High and Low Peru (today, Bolivia and Peru), and his observations are in line with current knowledge of *O. ficus-indica*; it can therefore

Figure 2
Spination, pad morphology and fruit characteristics were altered by men during the long lasting selection process.



be deduced that this cactus was probably present in those areas in that early period. In Peru, the use of grana dates to the pre-Hispanic period, probably as far back as the time of Christ (Marín, 1991; Sáenz *et al.*, 2002a); however, it is not clear whether it was *D. coccus* or another cochineal species. Fester (1941) and Fester and Lexow (1943) mentioned a spectrometric analysis of the colours of pre-Hispanic tissues (Paracas, from Peru) and of tissues from northern Argentina, demonstrating that the red colorant probably originates not from *D. coccus* in Mexico and Central America, but from other species of *Dactylopius*.

The economic importance of cochineal production in the nineteenth and twentieth centuries led to the introduction of both host plant and parasite into several countries outside their native distribution area. According to Piña (1981), *D. coccus* was introduced to Peru in the nineteenth century, before the country began to export *grana* in 1830.

For Argentina, Lafone Quevedo (1927) described how *grana* was harvested from *quiscaloro* (vernacular name for the wild species *Opuntia sulphurea* and *O. anacantha*, among others). According to the Argentinean entomologists, Claps and de Haro (2001), five wild and red-dye-producing species of *Dactylopius* parasite on several cactus species native to Argentina. A sixth species is *D. coccus*, found on cultivated and naturalized *O. ficus-indica*. During the 1980s, the former President Menem introduced *D. coccus* to encourage the production of *grana* in Argentina. While this attempt at *grana* production was not successful, naturalized *D. coccus* was recorded for the first time in 1999 in La Rioja, Argentina (De Haro and Claps, 1999). Later, there were also recordings in Salta (Van Dam *et al.* 2015). Hence, it is plausible that the red colorant extracted in the past was obtained from other *Dactylopius* species. The same researchers state that while the native cochineal live on different Cactaceae species, they live neither on *O. ficus-indica* nor on *O. cordobensis* – a strong indication in favour of its species-specificity. According to Van Dam *et al.* (2015), *D. coccus* is a domesticated form, as is also assumed for the host plant *O. ficus-indica*.

From the known records it can be deduced that *D. coccus* was not present in Andean South America before the arrival of the Spanish conquerors.

TAXONOMICAL AND NOMENCLATURAL CONSPECTUS

The different entities considered and denominated under several scientific names as species correspond to a single biological entity. In the strictest sense, *O. ficus-indica* is not a natural species (Kiesling, 2013), rather a complex of cultivars and naturalized clones.

O. ficus-indica can be distinguished from other species by several characters. The receptacle of the flower and later the fruits have many areoles (≥ 38), with a very small number of cultivars having fewer (Pinkava *et al.*, 1992; Kiesling, 1999a); the areoles are situated mostly on very notable tubercles. Other *Opuntia* species have fewer areoles at the flowers and fruits, situated on less prominent tubercles.

The name *Opuntia ficus-indica* has priority over other names given to this species (Kiesling, 1999b). Nomenclatural types based on herbarium specimens, which determine the application of names, were not designated for *O. ficus-indica* until 1991, and for *O. streptacantha* and *O. megacantha* until 2010 (Leuenberger, 1991; Scheinvar *et al.*, 2010), although all three names were published in the eighteenth or nineteenth century and widely used afterwards. The specimen chosen as nomenclatural type (lectotype) of *O. ficus-indica* (Leuenberger, 1991) corresponds to a plant without (or with very small) spines. However, the presence/absence of spines is not a useful character for distinguishing *O. ficus-indica* from other species, and the spiny and spineless forms must be considered different phenotypes of one species. Nevertheless, this character is used here to separate the spiny and spineless plants of *O. ficus-indica* formally in the rank of form (the lowest level of the taxonomic categories), even if both forms can arise from each other.

Opuntia ficus-indica (L.) Mill., Gard. Dict. ed. 8, Nr. 2; 1768

Basionym: *Cactus ficus-indica* L., Sp. pl.: 468. 1753.
Plants are shrubby or tree-like, up to 6 m high, usually with well-developed trunks. Stem segments are variable, broadly obovate or oblong to spatulate, flattened, 20-50 cm long, 20-30 cm wide, about 2 cm thick, matt green, covered by a very thin waxy layer, areoles 2-5 cm apart. Glochids falling away early, spines absent or 2 (-7) per areole, 0.5-1.0 cm long, weak whitish. Flowers yellow, rarely orange, 6-8 cm long and 5-10 cm in diameter during anthesis. Fruit with numerous (approx. 30-40) areoles, with glochids, rarely with spines, tuberculate, ovoid to oblong, 6 (-8) cm long, 3 (-5) cm in diameter, yellow, orange, pink–green or reddish.

Opuntia ficus-indica f. *ficus-indica*

Synonyms: *Opuntia ficus-indica* var. *gymnocarpa* (F.A.C. Weber) Speg., Anales Mus. Nac. Buenos Aires ser. 3, 4: 512. 1905. *Opuntia ficus-indica* var. *decumana* (Haw.) Speg., Anales Mus. Nac. Buenos Aires ser. 3, 4: 512. 1905. *Opuntia ficus-barbarica* A. Berger. Monatsschr. Kakteenk. 22: 181. 1912. *Opuntia tuna-blanca* Speg. An. Soc. Cient. Arg. 99: 107. 1925.
Areoles without spines or with only small and weak spines.

Opuntia ficus-indica f. *amyclaea* (Ten.) Schelle, Handb. Kakteenkultur: 51. 1907

Basionym: *Opuntia amyclaea* Ten., Fl. Neap. Prod. App.: 15. 1826.
Synonyms: *Opuntia ficus-indica* var. *amyclaea* (Ten.) A. Berger, Hort. Mortol: 411. 1912. *Opuntia megacantha* Salm-Dyck, Hort. Dyck.: 363. 1834. *Opuntia streptacantha* Lem., Cact. Gen. Sp. Nov. 62. 1839. *Opuntia cordobensis* Speg., Anales Mus. Nac. Buenos Aires ser. 3, 4: 513. 1905. *Opuntia arcei* Cárdenas, Cact. Succ. J. (Los Angeles) 28: 113. 1956.
Areoles with notable spines.

CONCLUSIONS

Based on the facts presented and biological knowledge, the following conclusions can be drawn:

- *O. ficus-indica* f. *ficus-indica* is the result of a long-lasting selection process during cultivation. A result of this process is the development of polyploid (up to octoploid) and more vigorous forms or cultivars, more convenient for human use than their wild relatives. The selection of less spiny plants has led to spine-free forms. Fruit size and quality also influenced the selection process, which had begun before the arrival of the Spaniards in Mexico. Intraspecific as well as interspecific hybridization suggests a polyphyletic origin.
- The cultivated, spineless form was introduced to Spain, probably a few years after the discovery of America (c. 1500), and initially used as an ornamental plant and a curiosity in the gardens of the nobility. From there it was taken to other countries in the Mediterranean as well as to South America, South Africa, India and Australia. Navigators increased its distribution by taking it as a fresh vegetable to guard against scurvy. The main reasons for the further dissemination of *O. ficus-indica* by humans were the production of fodder in arid areas, the use of the fruits or pads for human consumption, and cochineal production.
- In several countries with a suitable warm and arid climate, the species was introduced and cultivated, spreading by vegetative and generative reproduction until it became naturalized. This process happened independently and more than once in several places, in different countries, and on all continents, in the native as well as the new distribution areas. This resulted in new centres of infraspecific differentiation, with the emergence of cultivars and subsequently naturalized clones and hybrids. The naturalized forms developed slightly different morphological and physiological characters compared with the cultivated clones. Spiny forms emerged repeatedly from the spineless plants.
- *O. ficus-indica* is considered a species, or a group of multiple unrelated clones derived from different parental species. The native distribution area of the ancestral taxa is central Mexico.