“*Opuntia dillenii*” – An Interesting and Promising Cactaceae Taxon♦

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ABSTRACT

The origin, distribution, and taxonomy of *Opuntia dillenii* are reported and the various investigations are reviewed, which have been carried out with this cactus during the last 25 years. Biological and chemical characterization revealed properties typical of succulent plants and betalains as most noticeable constituents accompanied by flavonoids, other phenolics, ascorbic acid, and certain minerals as significant compounds. Although practically not cultivated, *O. dillenii* has been used in several directions despite its stout spines on old cladodes. The fruits are consumed or provide colouring. Generative and vegetative parts of the cactus have had a lasting position in folk medicine and their effects could partly be proved in scientific experiments. In face of its valuable characteristics, *O. dillenii* is recommended as a promising candidate of programmes directed to the development of *Opuntia* species into crop plants.

1. INTRODUCTION

Members of the Cactaceae, a family from the Americas, are well known as ornamental plants in all temperate zones of the earth (Haage 1961, Brickell 2006). Many species also show features of practical interest. They have been used in several directions, especially by the inhabitants of their areas of origin for thousands of years (Alkämper 1984, Nobel 2002). Among the useful cacti the genus *Opuntia* Mill. (Howard and Touw 1981) plays an important role and *Opuntia ficus-indica* (L.) Mill. is its most prominent species (Russell and Felker 1987, Mohamed-Yassen et al. 1996). Nevertheless, also other taxa deserve individual attention, for instance *Opuntia dillenii*. The following chapters describe investigations performed with these plants during the last about 25 years and consider also certain publications on *Opuntia stricta* (Haw.) Haw. since 2003 (see 2.1.).

2. OCCURRENCE

When did *O. dillenii* appear in the taxonomic literature and what is its present position? Where is the habitat of this distinct *Opuntia* taxon and what distribution exists today?

2.1. Nomenclature

In 1732, Johann Jacob Dillen, named Dillenius (1684-1747), published the description of a characteristic cactus (Fig.1) cultivated in the famous garden of Eltham, which was ignored by Carl von Linné (1707-1778) (Schmidt 1965). Instead, John Bellenden Ker-Gawler (1764-1842) established in 1817 the species *Cactus Dillenii* on the basis of these data and further observations. Adrian Hardy Haworth (1768-1833) assigned the taxon to the genus *Opuntia* in 1819. The correct name of this species was *Opuntia dillenii* (Ker Gawl.) Haw. since then during one and a half centuries. Due to an obviously high similarity of *O. dillenii* to *Opuntia stricta* (Haw.) Haw. (Haworth 1812), Benson (1969)

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recommended to consider the former species as a variety of the latter one, named *Opuntia stricta* (Haw.) Haw. var. *dillenii* (Ker Gawl.) L.D. Benson. The "Flora of North America" accepts only the species *O. stricta* (Haw.) Haw. without subspecies (Pinkava 2003), although specialists think a subdivision reasonable in face of natural diversity (e.g., Scheinvar 2002). According to this handbook, *O. stricta* also comprises *Opuntia inermis* (DC.) DC. (de Candolle 1828) as a synonym indicating near relationship to *O. dillenii* (Pinkava 2003).

This review generally applies the term *O. dillenii* for its object in favour of taxonomic independence (Benson 1982, Scheinvar 2002) irrespective of the systematic rank.

2.2. Habitat and distribution

Opuntia dillenii originates from southeastern parts of North America, the east coast of Mexico, the Bermudas, the West Indies and from the north of South America (Britton and Rose 1963). Wild populations are nowadays reported in the same areas (Backeberg 1970, Benson 1982, Schultze-Motel1986, Scheinvar 2002, Anderson 2005) and additionally at the Gulf Coast of Texas (Benson 1982), the southeastern coastal margin of Brazil (Scheinvar 1984), and in Ecuador (Anderson 2005). The native locations of *O. dillenii* are mostly at an altitude near sea level in sand dunes, at edges of maritime forests, or associated with tropical plants (Benson 1982, Pinkava 2003).

Remarkably, *O. dillenii* was introduced into many parts of the earth. It is found around the Mediterranean (Schultze-Motel 1986, Gentile 1991), on the Canary Islands (Perfumi and Tacconi 1996, Loro et al. 1999, Anderson 2005, Díaz Medina et al. 2007), in the west and east of Africa (Schultze-Motel 1986), on Madagascar and Mauritius (Schultze-Motel 1986, Ellenberg 1989), in North Yemen (Ellenberg 1989), in India (Backeberg 1970, Badami and Thakkar 1984, Gupta et al. 2002), in the southeast of Asia (Schultze-Motel 1986, Jiang et al. 2006), and in Australia (Backeberg 1970, Schultze-Motel 1986, Ellenberg 1989). *Opuntia dillenii*, the coastal *Opuntia*, becomes naturalized under conditions different from those in its original areas and can even rapidly spread out (Ellenberg 1989). It was involved in dangerous infestations with several *Opuntia* species (Burdon and Marshall 1981), notably *O. stricta* (pest pear) in eastern Australia (Freeman 1992).

3. BOTANY

3.1. Morphology

Plants of *O. dillenii* (Fig. 2) sprawl out or erectly grow and reach a height of about 50 to 200 cm. They consist of flattened, elliptic and obovate stem segments, the cladodes, named also joints or pads, and are impressive for many stout spines. The joints are dull green or bluish-green in colour, 10 to 40 cm long, 5 to 15 cm broad, 1 to 2 cm thick, and irregularly trimmed with relatively few areoles. These pimple-shaped structures are some millimeters in height and in diameter and bear small scale-like leaves on young joints, later on 1 to 10 spines each. The spines are very variable in colour (yellow to brown) and length (1.5 to 6 cm) and can sometimes be lacking. They spread in all directions and are accompanied by glochids, short barbed bristles which form striking tufts (Backeberg 1970, Benson 1982, Ellenberg 1989, Anderson 2005). Cactus roots are generally less specialized in morphology than the above-ground vegetative parts of cacti. They show a shallow distribution, which enables them to exploit limited rainfall, and are rich in root hairs. Associations with fungi and bacteria can improve the capture of mineral nutrients. (Dubrovsky and North 2002, Land Protection 2006).

In the blossom, *O. dillenii* plants show 6 to 8 cm wide flowers that are finally lemon yellow in colour, but can be slightly reddish in early stages of development. The purple-skinned fruits are pear-shaped beers (Fig. 3), measure 4 to 7 cm in length and about 3 cm in diameter. They normally show no spines and their glochids mostly fall off from the few areoles during maturity. Nevertheless, *O. dillenii* is counted among the loosely defined group “prickly pear” including species of *Opuntia* and *Nopalea.* The juicy flesh of fruits is throughout purple in colour (Fig. 4) and contains many rounded seeds which are – obviously with an arillus-like envelop - about 4 mm in diameter and tan coloured (Backeberg 1970, Benson 1982, Ellenberg 1989, Anderson 2005, Land Protection 2006).

Morphological details of the hybrids *O. dillenii* x *Opuntia stricta* var. *stricta* (Haw.) L. D. Benson and *O. dillenii* x *Opuntia humifusa* var. *humifusa* (Rafinesque) Rafinesque reflect characteristic properties of both respective parents (Benson 1982). *Opuntia dillenii* can also hybridize with *Opuntia engelmannii* Salm-Dyck (probably var. lindheimeri) (Pinkava 2003).
These hybridizations may correspond with the assumption that *O. dillenii* – as other *Opuntia* species – is hybrid in nature (P. Felker, pers. comm.). Normally, hybrids from true species are sterile, but this is not the case for *O. dillenii*, and allopolyploidy could be the reason. It is probably difficult to evaluate the situation, because the basic number of chromosomes is x = 11 in all *Opuntia* species (Pinkava 2003). An analysis of characters, especially morphological ones, in the progenies from self-pollination of *O. dillenii* and potential parent species should bring further insights in this direction.

3.2. Physiology

From the wild locations of *O. dillenii* (see 2.2.) one can deduce the suitable conditions for growth and development of these plants. The soil should be rather sandy than too heavy or even wet. It shows generally pH 5 or a somewhat higher value. *Opuntia dillenii* plants are relatively sensitive to frost. At an annual mean temperature of 20°C to 30°C they need at least 150 to 250 mm precipitation per annum, but accept also lower temperatures (on average 10°C to 20°C) combined with much rain (about 1000 mm per annum). While the cactus populations feel well in the shade of scattered trees, dense shadow leads to their degeneration beginning with the loss of flowering and fruiting (Benson 1982, Ellenberg 1989, Díaz Medina et al. 2007).

The composition of plant tissues was investigated with peeled fruits of *O. dillenii* grown in the southern part of the isle of Tenerife. Some of the results are the following: moisture 81.68 and ash 0.44 per cent of fresh weight; °Brix 10.35, pH 3.34; protein 0.52, fat 0.71, total fiber 9.49 per cent of dry matter; ascorbic acid 29.7, and total phenolics 117.0 mg per 100 g fresh weight (Días Medina et al. 2007). The latter two positions are reported for different parts of *O. dillenii* fruits from the Penghu Islands as follows: 1.2, 15.1, 0.0 mg ascorbic acid and 133.4, 91.5, 212.8 mg total phenolics per 100 g fresh peel, pulp and seed, respectively (Chang et al. 2008). Among the minerals, K, Ca, Mg, Na, and Mn predominate by their weight proportions (Díaz Medina et al. 2007). The spiny cladodes (joints) of *O. dillenii* have been apparently not analysed in a respective manner. Cladodes of *O. inermis* had the following average composition when harvested 13 to 20 cm in length between 7.30 and 8.30 a.m.: moisture 91.7 per cent of fresh weight; protein 12.2, lipids 2.3, carbohydrates 55.5, crude fiber 13.8, and ash 16.8 per cent of dry matter; ascorbic acid 17.9 and carotenoids 38.4 mg per 100 g fresh material (Rodriguez-Felix and Cantwell 1988).

As a succulent plant *O. dillenii* shows two physiological peculiarities. Especially the cladodes produce mucilage, heterogenic polysaccharides with complex structures and a great capacity to absorb water (Goycoolea and Cárdenas 2003). And these green organs assimilate carbon in the way of the Crassulacean acid metabolism (CAM) characterized by nocturnal CO_2 fixation leading to malic acid. Decarboxylation of this substance releases CO_2 which is involved in photosynthetic processes during the day. Therefore, CAM plants are in the position to close their stomata when the temperature is high and have a very efficient water balance (Russell and Felker 1987). Another consequence is a diurnal fluctuation of the acid content of cladodes showing an increase of organic acids until morning and decreased sourness later on (Osmond et al. 1979, Rodriguez-Felix and Cantwell 1988).

Most families of the order Caryophyllales, including the Cactaceae, have a special phenylpropanoid metabolism in so far as no anthocyanins are formed. Instead, the biosynthesis of betalains (Mabry 1980), red-violet and yellow, nitrogen-containing pigments, takes place. This holds true also for *O. dillenii* whose fruit colouration, for instance, is caused by betacyanins (see 4.1.).

3.3. Propagation and cultivation

Although the flowers of *Opuntia* species are hermaphroditic, cross pollination by bees is the rule. After fertilization seeds develop which are eaten with the pulp by men and animals or released from overripe fruits. All these possibilities can be connected with a wide dispersal of seeds. It was observed that seeds of *O. dillenii* germinate best after intestinal passage (Reyes-Agüero et al. 2005, Land Protection 2006, Ellenberg 1989).

Since each areole has the ability to produce roots or shoots, asexual reproduction essentially contributes to the propagation of *O. dillenii* in nature. Broken parts of plants can be transported in animal coats or running water over long distances and grow out under suitable conditions after location on the ground. The effective propagation strategies of *O. dillenii* both by seeds and vegetative parts is one of the features that enable this taxon to compete and become pest (Land Protection 2006, Ellenberg 1989).

Several experiments directed to *in vitro* propagation of “Milpa Alta edible cactus (*Opuntia dillenii*)” were reported and the following protocol is recommended: Young cladodes are harvested and kept for 3 to 5 days. Explantation of their top segments on MB medium containing 1.0 mg 6-benzyladenine (6-BA) and 0.2 mg naphthaleneacetic acid (NAA) per litre results in optimum bud formation. Half-strength Murashige-Skoog (MS) medium with 0.3 mg NAA/L induces especially growing roots. Optimum multiplication of plantlets takes place under the influence of MB medium supplemented with 0.5 mg 6-BA and 0.1 mg NAA per litre. Transplantation in sand results in 90.1 per cent survival (Liu et al. 2005). In similar experiments with the same material only MS medium was applied and 2,4-dichlorophenoxyacetic acid, indole-3-acetic acid or indolebutyric acid administered as additional auxin (Zhao et al. 2003).

Directed propagation is a prerequisite for the economical cultivation of crop plants. In case of *O. dillenii*, this stage has been obviously not reached so far. It is not cultivated in Mexico (Pimienta-Barrios 1994, Scheinvar 1995 and pers. comm.), the greatest producer of edible cactus parts worldwide (Inglese et al. 2002), and in Texas (Felker, pers. comm.). Cultivars of several *Opuntia* species exist in South Africa (Oelofse et al. 2006, Potgieter and Smith 2006), but there is no indication of *O. dillenii*. Remarkable research activities with *O. dillenii* even directed to industrial utilization (see 5.1., 5.3.) point out at least restricted cultivation of this cactus in China.

4. CHEMICAL CHARACTERIZATION

4.1. Secondary metabolites

There is no doubt that betalains are the most characteristic substances of *O. dillenii*. Their biosynthesis depends on the ability of plants to form betalamic acid (Fig. 5a) which condenses preferentially with *cyclo*-DOPA or amino acids in nonenzymatic reactions (Hempel and Böhm 1997, Böhm and Mäck 2004, Schliemann et al. 1999), leading to red-violet betacyanins (e.g., betanidin, Fig. 5b) or yellow betaxanthins (e.g., indicaxanthin, Fig. 5c). While the latter compounds contain no glycosidic groups, betacyanins are mostly glycosides (Strack et al. 2003).

Corresponding results confirmed the finding (Sciuto et al.1972) that betanin (Fig. 6a) and isobetanin, 5-*O*-glucosyl derivates of betanidin differing in their stereochemistry at C15, are the main betacyanins of *O. dillenii* fruits (Zhang and Liu 1992, Lin et al. 2001, Schliemann and Böhm 2004, Chang et al. 2008). In ripe fruits collected at the western coast of the isle La Palma, neobetanin, i.e., 14,15-dehydrobetanin, as well as the C15 stereoisomers gomphrenin I (Fig. 6b) and isogomphrenin I were minor components (Schliemann and Böhm 2004). Neobetanin was considered an artifact (Wyler 1986), but could be isolated as genuine component from *O. ficus-indica* fruits (Strack et al. 1987) and may be formed from betanin during ripening. The presence of betacyanins glucosylated in the *O*-6 position indicates the activity of the corresponding enzyme, UDP-glucose:betanidin 6-*O*-glucosyltransferase (Heuer et al. 1996). Since gomphrenin I was also found in *Opuntia robusta* Wendl. and some *O. ficus-indica* clones (Stintzing et al. 2005), one can assume that the genus *Opuntia* belongs to the rare plant groups (Strack et al. 2003) showing *O*-6 substitution of betanidin. Traces of betaxanthins were not identified in the ripe *O. dillenii* fruits from La Palma. The content of betacyanins of these organs amounted 445 µg (betanin equivalents) per 1 g fresh material (Schliemann and Böhm 2004). Parts of other *O. dillenii* fruits contained 349 µg (peel) and 373 µg (seedless pulp) betanin/isobetanin per 1 g fresh weight (Chang et al. 2008). These concentrations are lower than that reported for *O. stricta* fruits (800 µg/g fresh weight), but remarkably higher than those in red-violet coloured fruits of *Opuntia undulata* Griff. and *O. ficus-indica* (200 µg and 150 µg/g fresh weight, respectively) (Castellar et al. 2003) and comparable with the betacyanin content in dark purple fruits of *O. robusta* (Stintzing et al. 2005).

The yellow colour of *O. dillenii* flowers is certainly caused to a high degree by betaxanthins which, however, have been apparently not investigated. Furthermore, flavonols contribute to this pigmentation. From earlier and recent findings quercetin 3-*O*-glucoside (isoquercitrin; Nair and Subramanian 1964), kaempferol 3-*O*-arabinoside, isorhamnetin 3-*O*-glucoside and isorhamnetin 3-*O*-rutinoside (Ahmed et al. 2005) are known in petals. The identification of their aglycones (Fig. 7a) and further derivatives in cladodes (Qiu et al. 2000, 2002, 2003) and the additional isolation of the flavanols catechin and epicatechin (Fig. 7b) from fruits (Chang et al. 2008) led to a total of 16 flavonoids of *O. dillenii* described up to now (Table 1). Obviously, fruits contain only quercetin and its glycosides as flavonols (Kuti 2004, Chang et al. 2008).

Low molecular phenolics derived from benzoic acid (gallic acid, vanillic acid, 3,4-dihydroxy- benzoic acid, ethyl 3,4-dihydroxybenzoate) and from cinnamic acid (sinapic acid, ferulic acid, p-coumaric acid) were found in fruits (Chang et al. 2008) and cladodes (Qiu et al. 2003) of *O. dillenii.* Some of them are known as precursors in the biosynthesis of more complex secondary metabolites (Luckner 1990).

Important enzymes involved in the transformation of phenolic substances are polyphenol oxidases (PPO; Mayer 2006). Since a PPO from *O. dillenii* cladodes shows pH optima at 4.0, 7.0 and 10.0, it should consist of three isoenzymes the activity of which was reduced by several acids in the following order: ethylene diamine tetraacetic acid < ascorbic acid < citric acid. These inhibitors act through chelating Cu^{2+} ions as enzymatic cofactors and/or lowering the pH level of the reaction (Qin et al. 2004).

Further characteristic secondary metabolites of *O. dillenii* isolated from cladodes are α-pyrones, e.g., opuntiol and some derivatives (Qiu et al. 2002, 2003, 2007), and several steroids, among them the C_{29}-5β-sterol opuntisterol and its glucoside, opuntisteroside (Jiang et al. 2006).

4.2. Other substances

Air-dried seeds of *O. dillenii* consist of oil at 7.5 per cent of their weight. Among the fatty acids revealed by hydrolysis linoleic acid predominates. It is followed by palmitic and oleic acid in about identical quantities, while stearic, arachidic, and myristic acid are minor components (Badami and Thakkar 1984).

Taurine, an aliphatic aminosulfonic acid derived from L-cysteine, first isolated from ox bile, is ubiquitous in mammals and many sea organisms, but was only found in low concentrations in some higher plants. Since it has essential functions in men (Schuller-Levis and Park 2003) which may be influenced by dietary taurine (Eppler and Dawson 2001, Yu et al. 2007), the report on 300 to nearly 600 mg/L taurine in fruit flesh from *O. ficus-indica* cultivars grown in Mexico and South Africa (Stintzing et al. 1999) has been interesting. This level, however, could not be confirmed. In Silician *O. ficus-indica* cultivars, taurine was detectable in a maximum concentration of 117 mg/kg pulp (Tesoriere et al. 2005) or completely absent (Kugler et al. 2006). Nevertheless, *O. ficus-indica* seems to be a new source of taurine in higher plants. Probably, *O. dillenii* belonging to the same genus also contains taurine, but this remains to be clarified.

5. USE

According to literature, cacti and especially members of the genus *Opuntia* are manifold used (Hammer 1978, Alkämper 1984, Russell and Felker 1987, Mohamed-Yasseen et al.1996, Nobel 2002, Stintzing and Carle 2005, Moßhammer et al. 2006, Feugang et al.2006). What is true of *O. dillenii*?

5.1. Use as food plant

The fruits of *O. dillenii* have as foodstuffs a number of advantageous properties: Their tight skin is spineless and attractively coloured (Fig. 3). The juicy and purple flesh (Fig. 4) encloses edible seeds, and both constituents contain besides fibre also low molecular health-promoting substances in relatively high amounts when compared with fruits of *O. ficus-indica* (Díaz Medina et al. 2007). The taste is refreshing. Indeed, *O. dillenii* fruits are of repute even outside their natural occurrence not only by individuals (e.g. H. Manitz and J. Reckin, pers. comm.; H. Böhm) who had the opportunity to enjoy them but also in scientific publications. A leading German food encyclopedia (Ternes et al. 2005) writes (translated) under the headword Kaktusfeige: "*Opuntia dillenii* (Ker-Gawl.) Haw. and *Opuntia megacantha* Salm-Dyck cultivated in Mexico provide the best fruits" and Rudolf Mansfeld's well known compendium of crop plants (Schultze-Motel 1986) stated (translated) "*Opuntia dillenii* (Ker-Gawler) Haw. is one of the most important fruit-producing *Opuntia* species". However, neither the cultivation of *O. dillenii* nor the export of its fruits are compatible with the situation noticed above (see 3.3.), and one could comment these citations with Shakespeare: "Thy wish was father, Harry, to that thought" (King Henry IV, Part 2).

But the lack of cultivation does not exclude the utilization of plants by men. Ellenberg (1989) described women and children harvesting fruits of wild *O. dillenii* with wooden poles having each a nail at the tip. This may illustrate that the formidable spines of cladodes are a handicap to the utilization of the cactus. Another report points to the problem that *O. dillenii* fruits are avoided due to their relatively sour taste. The edible parts show an acidity corresponding to 1.23 g citric acid per 100 g fresh weight, whereas the respective mean value is 0.08 g/100 g for *O. ficus-indica* the fruits of which are preferred to those of *O. dillenii* by the Canary population (Díaz Medina et al. 2007). *Opuntia dillenii* fruits are mostly eaten fresh, but also boiled or dried in the sun. The traditional preparation of jam, syrup, and similar products is usual (Hammer 1978a, Ellenberg 1989, Díaz Medina et al. 2007). Juice can be squeezed from fresh cactus fruits and is of industrial interest besides its preparation at home (Saenz and Sepulveda 2001). According to the available knowledge in this field (Moßhammer et al. 2006), fruits of *O. dillenii* should be a suitable raw material for technological processes because they are relatively small, sour and stably coloured.

The fruits of *Opuntia* species (prickly pears) rich in betanin and isobetanin are considered a better source of food colorants than the presently used red beets (*Beta vulgaris* L.) (Stintzing et al. 2001, Moreno et al. 2008) which transmit their earthy flavour, caused by geosmin (Lu et al. 2003), to the separated betacyanins. Therefore, isolation and stability have been investigated with the red pigments occurring in *O. dillenii* (Zhang and Liu 1992, Fu and Wu 1994) and *O. stricta* fruits (Castellar et al. 2003, 2006, Fernández-López et al. 2007). Among several solutions assayed for extraction, a 60 to 40 mixture (v/v) of ethanol and water led to a product high in betacyanin yield and low in viscosity. After 40-fold concentration the residue showing pH 3.4 and a water content of 571 g/kg should have the calculated half-life time of 236.6 days at 4°C (Castellar et al. 2006). Experiments with higher purified fruit pigments from both *Opuntia* species confirmed that the stability of betanin and isobetanin is negatively influenced by light, water activity, elevated temperatures, and pH levels different from that at about 5. The addition of ascorbic acid as an antioxidant can enhance the stability (Zhang and Liu 1992, Fu and Wu 1994, Castellar et al. 2003). Extracts with identical betacyanin concentrations were kept at 50°C and pH values of 3, 5, and 7 for 28 hours. Monitoring revealed a continuous colour loss up to 7.5 per cent of the initial intensity in the third variant, whereas under the influence of both pH 5 and pH 3 about 50 per cent of the starting quantities were detectable after 16 hours decreasing to final retentions of 20% and 30%, respectively, of the initial betacyanin concentrations. These findings may indicate the importance of pH values within the parameters relevant to the stability of isolated betacyanins. And there are also qualitative aspects: At the end of the reaction time (28 hours) the pigments mainly consisted of betanin and 15-descarboxy-betanin, a degradation product, on the pH 5 level. In contrast, the first compound was absent in the pH 3 variant and the second one under the influence of pH 7. While neobetanin was detectable only in the starting material at the pH 3 level, it was present also after 8 hours reaction time in the pH 5 and pH 7 variants (Fernández-López et al. 2007).

Besides the fruits of *Opuntia* species, frequently called tunas, vegetative parts of these cacti, the nopales or nopalitos, are also used as foodstuffs (Stintzing and Carle 2005). Although young joints are preferred and generally spineless, it is understandable that those of *O. dillenii* are avoided because of the many stout spines of elder plant parts. Additionally, their epidermis is relatively thick and stiff. However, joints of *O. dillenii* were reported to be squashed in getting a liquid mash as drink in case of severe drought (Ellenberg 1989).

Already the Aztecs used the fruit juice of *Opuntia* species to make an alcoholic beverage (Kiple and Ornelas 2000). Nowadays, there is more an interest to obtain ethanol by the fermentation of various cactus material (Retamal et al. 1987, Turker et al. 2001). But also a kind of beer prepared from *O. dillenii* juice was recently reported (Shi et al. 2004).

5.2. Use as fodder plant

Since the old joints of *Opuntia* species normally serve as alternative fodder for cows and sheep, it is not surprising that those of *O. dillenii* are only used under extreme conditions. Then, their many long spines together with the glochids must be removed by fire which also softens the epidermis (Ellenberg 1989). Another way to make old *O. dillenii* joints a useable cattle feed should be the preparation of silage from these plant parts (Hammer 1978b).

5.3. Use as medicinal plant

The cactus *O. dillenii* has had a lasting position in the folk medicine of many countries, for instance India, where it is called Kanthari or Nagphana in Hindi (Gupta et al. 2002), the Canary Islands (Perfumi and Tacconi 1996, Loro et al. 1999), Taiwan (Chang et al. 2008), and China (Qiu et al. 2002) where it has the name Xian Ren Zhang. In the last-mentioned country, *O. dillenii* is obviously very reputable as indicated by a compilation of literature on its pharmacological properties (Chen and Zhao 1998) and the preparation of several health drinks from this plant (Yi and Lin 2000, Weng and Wu 2000, Shi et al. 2004). Recent investigations resulted in the following data.

5.3.1. *Antioxidant activities*

It is generally assumed that free radicals, especially oxygen compounds (reactive oxygen species, ROS), can cause damage to desoxyribonucleic acid (DNA) and proteins, possibly leading to chronic or degenerative diseases in humans (Aruoma 1998). While ROS are normal metabolites in living organisms, their excess is dangerous. In the case of such an oxygen stress, mammals activate a range of native antioxidants, first of all enzymes (Sies 1993). Since antioxidants coming from outside could support the internal defence system and prevent human diseases (Halliwell 1997), there is a keen interest in substances of plant foodstuffs and drugs which are able to catch ROS (Boudet 2007). Their scavenging capacity is measured with various *in vitro* methods whose results sometimes differ from each other for the same substance (Huang et al. 2005).

Plant phenols are highly potent ROS scavengers and among them the flavonoids are most prominent (Rice-Evans 2001). As reported above (see 4.1., Table 1), several of these secondary metabolites occur in *O. dillenii* and they may contribute a great deal to the antioxidant activity of an aqueous ethanolic extract obtained from cladodes (Qiu et al. 2002). In a comparison of extracts from fruits of four *Opuntia* species, the antioxidant capacity followed the total flavonoid content. The lowest value was found for yellow coloured *O. stricta* fruits although they showed the highest carotenoid concentration besides a small amount of quercetin. Ascorbic acid content did not detectably influence the position of an extract from *Opuntia* fruits in the ranking list of antioxidant activities. Surprisingly, betalains were not considered in this investigation (Kuti 2004) of differently coloured fruits. Those with the highest antioxidant capacity contained not only the maximum flavonoid concentration, but were certainly also richest in betacyanins because of throughout purple in colour. However, the methanolic extract from betacyanin-free seeds of *O. dillenii* showed in three assay systems a higher antioxidant capacity than extracts from peel and pulp with betacyanins in nearly identical concentrations (Chang et al. 2008). This comparison confirms that the content of flavonoids and phenolic acids decisively influences the antioxidant ability of *Opuntia* fruits. Seeds contained no ascorbic acid and pulp about 12-fold more than peel. Nevertheless, extract from the latter portion had a higher antioxidant capacity than that from the former one, obviously because of a greater amount of total phenolics (133.4 versus 91.5 mg/100 g fresh weight) (Chang et al. 2008). The inhibition of lipid peroxidation as demonstrated in these experiments was shown already with aqueous extracts from *O. dillenii* (Chen and Meng 1997).

Although the betacyanins are obviously not successful in assays of the antioxidant capacity of extracts from *O. dillenii* fruits, betanin and isobetanin occurring in relatively high amounts in these organs (Schliemann and Böhm 2004, Chang et al. 2008) result in remarkable values when individually measured *in vitro* (Butera et al. 2002, Cai et al. 2003, Chang et al. 2008). Their structures even make them very strong ROS scavengers at certain pH levels (Gliszczynska-Świgło et al. 2006). They have, therefore, the potency to act health-protecting in the human body, and these processes are in detail under investigation (Livrea and Tesoriere 2006, Allegra et al. 2007).

5.3.2. *Disease-directed activities*

The effects shown by *O. dillenii* in disease models certainly arise from the various properties of cactus components.

Carrageenan-induced inflammation was inhibited by aqueous and alcoholic extracts from fruits (Loro et al. 1999) and cladodes, flowers and fruits (Ahmed et al. 2005), respectively, on paws of rodents. The extracts were lyophilized or evaporated to dryness, the residues dissolved and volumes corresponding to 50 to 400 mg/kg body weight were administered orally or by injection. A dose-related inhibition could be found (Loro et al. 1999), and at the level of 200 mg/kg b.w. the extract from flowers was more effective than those of other organs, probably due to the presence of certain flavonols (Ahmed et al. 2005). Both publications also report that the investigated extracts from *O. dillenii* exhibited analgesic activity against pain caused by heat, acid, and electrical current in rodents. Again, dose dependence was demonstrated (Loro et al. 1999), but in this direction the fruit had the highest potency (Ahmed et al. 2005).

In order to find out basic processes responsible for the position of *O. dillenii* as an antidiabetic drug in folk medicine, experiments with normoglycemic and alloxan-induced diabetic rabbits were performed (Perfumi and Tacconi 1996). In both groups, the application of juice from ripe fruits (5 ml/kg body weight) did not influence the plasma glucose concentrations, whereas it significantly lowered the glucose levels resulting from oral administration of glucose (1 g/kg b.w.). This effect was absent when normoglycemic rabbits were intravenously loaded with glucose. Fruit juice showed no influence on the glucose-induced plasma insulin levels. It is assumed that some compounds of the investigated part of *O. dillenii* reduce the intestinal absorption of glucose and others could have an insulin-like character (Perfumi and Tacconi 1996). In a clinical trial, 46 type 2 diabetes patients were treated with tablets consisting of *O. dillenii* crude drug (2.5 g) or starch (0.5 g) for four weeks. Four tablets each were daily taken 30 minutes prior to (drug) or after (starch) three meals. Measurement of several parameters allowed the following résumé: Tablets from *O. dillenii* can efficiently improve clinical symptoms and the glycometabolism of patients with diabetes mellitus type 2. Indeed, 33.33 per cent of the verum group were cured and the state of about the same number positively changed (Zhao et al. 2002).

Opuntia stricta (Haw.) Haw. subspec. *reitzii* (Scheinvar) Scheinvar and A. Rodr., previously described as *O. dillenii* (Ker-Gawl.) Haw. var. *reitzii* (Scheinvar 1984), is one object of a broad study devoted to the antitumor and trypanocidal activities as well as alkaloid profiles of Brazilian Cactaceae (Valente et al. 2007). An extract obtained with dichloromethane: methanol (1:1) from lyophilized cladode slices was applied to four cultured cancer cell lines. It inhibited cell proliferation in each case, mostly to 88 per cent. Since the extract of *O. stricta*, as that of all other examined objects, was inactive in an assay using Saccharomyces cerevisiae deficient in DNA repair or recombination, respective mechanisms should not be involved in the antitumor effect of the cactus extract (Valente et al. 2007).

Also a powerful activity against *Trypanosoma cruzi*, the pathogen of the Chagas disease, could be found for *O. stricta*. When incubated with the extract described before, trypomastigote forms of the parasite were completely killed within 24 hours (Valente et al. 2007).

5.3.3. *Antispermatogenic effect*

The residue of a methanolic extract from *O. dillenii* cladodes was fed to male rats (250 mg/kg body weight) for 60 days. After this time, the treated animals showed reduction of weight as well as structure of the genital organs and had totally lost their fertility. The effects could be attributable to the detected flavonoids (Gupta et al. 2002) among them, however, vitexin has been absent in *O. dillenii* cladodes of different origins (see Table 1).

5.4. Use in other directions

Two characteristic historic examples are the *O. dillenii* plantations of Seringapatam (India) and Hisn az Zahir (North Yemen). In the first case, the Ruler of Mysore, Tippu Sultan (1750-1799), reinforced the fortification around his residence with the cactus because of its formidable spines (Hammer 1978b). Secondly, in 1930 the Imam established the cactus near his castle in order to use the purple coloured fruit juice as ink (Ellenberg 1989).

Opuntia dillenii is still planted in fencings of farms and pasture land and on dunes with the aim to prevent sand movement (Schulze-Motel 1986, Ellenberg 1989). Fruit juice and even pulp are today used as colouring agents not only for certain foodstuffs, e.g., ice cream and drinks (Qiu et al. 2002, Anderson 2005, Chang et al. 2008) but also for drugs (Qiu et al. 2002).

The mucilage of *Opuntia* species, and also of *O. dillenii*, is considered to be more involved in biotechnological processes (Goycoolea and Cárdenas 2003, Sáenz et al. 2004). Its pectin-like parts are degraded with enzymes in technological processes (Moßhammer et al. 2005), but these methods are still unsuitable for the elucidation of the complex mucilage structure.

The sandwich configuration of copper, a 0.5 cm thick cladode slice from *O. dillenii* and zinc operated as an electrochemical cell and could, from the authors' point of view, open a new interdisciplinary field (Deshpande and Joshi 1994).

6. CONCLUSIONS

Both its history and its present appearance justify that *O. dillenii* keeps an independent taxonomic position like that recommended by Benson (1969). Its name should not be eliminated since it stands for some characteristics. There are, first of all, the fruits: spineless, palatable, attractively coloured, with edible seeds and many health-promoting components. They would certainly meet with a market, for instance in Europe, and offer a rich source of red food dye. Fruits and cladodes of *O. dillenii* have shown remarkable effects against several diseases which could partly be confirmed by recent investigations and may be of special interest with respect to the rapidly increasing prevalence of diabetes type 2 in many parts of the world (Wild et al 2004).

A prerequisite for the more intensive work with and the cultivation of the well-growing, adaptable *O. dillenii* plants is the reduction or even removal of the stout spines. They should be attainable through the propagation of respective mutants occurring in nature or in experiments with established *in vitro* methods. Then, the completely or nearly spineless *O. dillenii* plants can be bred in order to enlarge fruit size and to lower pulp sourness or to improve relevant properties. The absence of spines will also favour the use of cladodes as vegetable and for medicinal purposes.

Consequently, *O. dillenii* is a highly promising candidate of programmes directed to the development of *Opuntia* species into crop plants (Mohamed-Yasseen et al. 1996), and it is surprising that this cactus has been neglected in the areas of origin (Pimienta-Barrios 1994, Scheinvar 1995) whereas it has found attention in other parts of the world.

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Table 1. Occurrence (+) of flavonoids in *Opuntia dillenii* plant parts (Nair and Subramanian 1964, Qiu et al. 2000, 2002, 2003, Ahmed et al. 2005, Chang et al. 2008).

Substance	Cladodes	Flowers	Fruits
Kaempferol	+		
Kaempferide	+		
Quercetin	+		+
3-*O*-Methylquercetin	+		
Isorhamnetin	+		
3-*O*-Methylisorhamnetin	+		
Kaempferol 7-*O*-glucoside	+		
Kaempferol 7-*O*-glucosyl(1→ 4)-glucoside	+		
Kaempferol 3-*O*-arabinoside		+	
Quercetin 3-*O*-glucoside (Isoquercitrin)		+	
Quercetin 3-*O*-rutinoside (Rutin)	+		+
3-*O*-Methylquercetin 7-*O*-glucoside	+		
Isorhamnetin 3-*O*-glucoside		+	
Isorhamnetin 3-*O*-rutinoside		+	
Catechin			+
Epicatechin			+

Figure 1. The first description of *Opuntia dillenii* in Hortus Elthamensis, 1732 (from the library of Herbarium Haussknecht, Friedrich Schiller University, Jena, Germany; courtesy of Dr. H.-J. Zündorf).

Figure 2. Yellow flowers and unripe fruits on old cladodes with stout spines predominate in this general view of an *Opuntia dillenii* plant (from Anderson 2005).

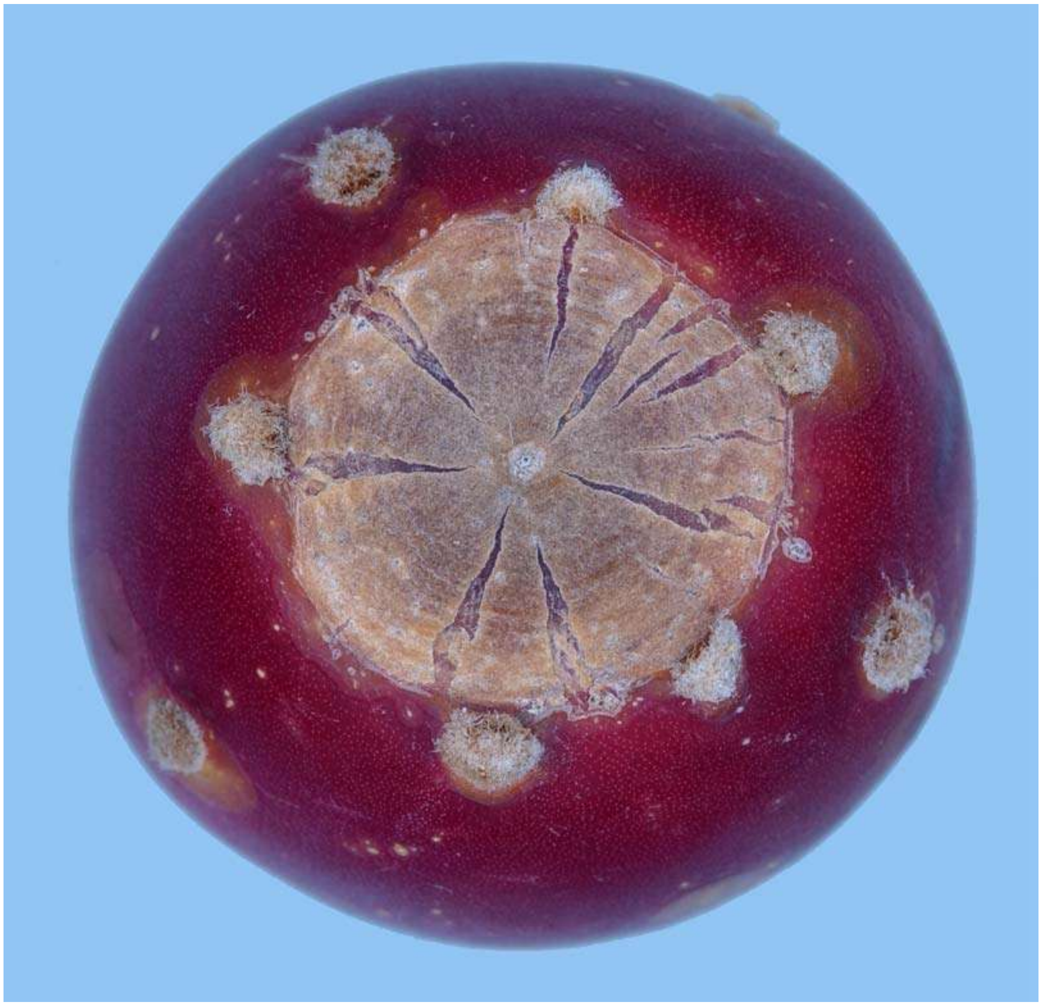

Figure 3. Ripe *Opuntia dillenii* fruits are not only spineless but also practically free from glochids. These examples measure 3.9 to 4.6 cm in length and 2.6 to 3.5 cm in diameter (photo by A. Kohlberg).

Figure 4. The cross section of an *Opuntia dillenii* fruit reveals purple pigmentation throughout the juicy pulp (photo by A. Kohlberg).

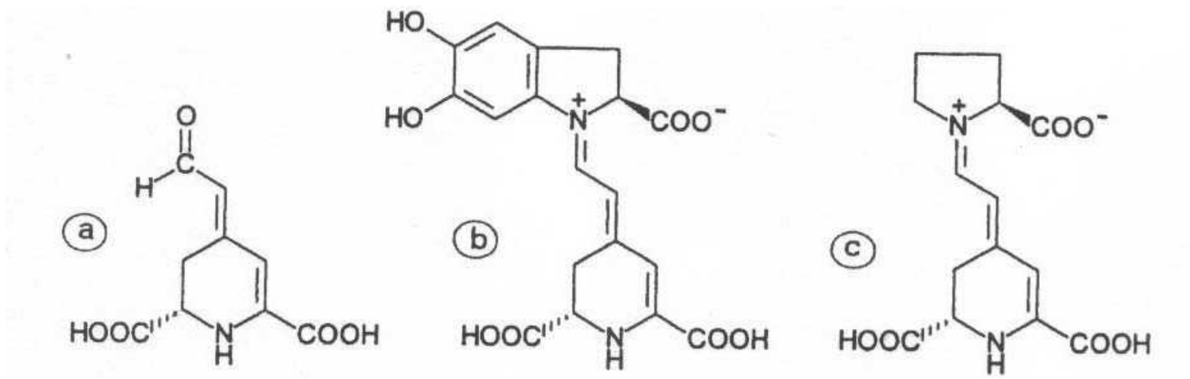

Figure 5. Betalamic acid (a) is the typical precursor of all betalains. Betanidin (b) from *Beta vulgaris* and Indicaxanthin (c) from *Opuntia ficus-indica* are the first betacyanin and betaxanthin, respectively, whose structures were elucidated (see Strack et al. 2003).

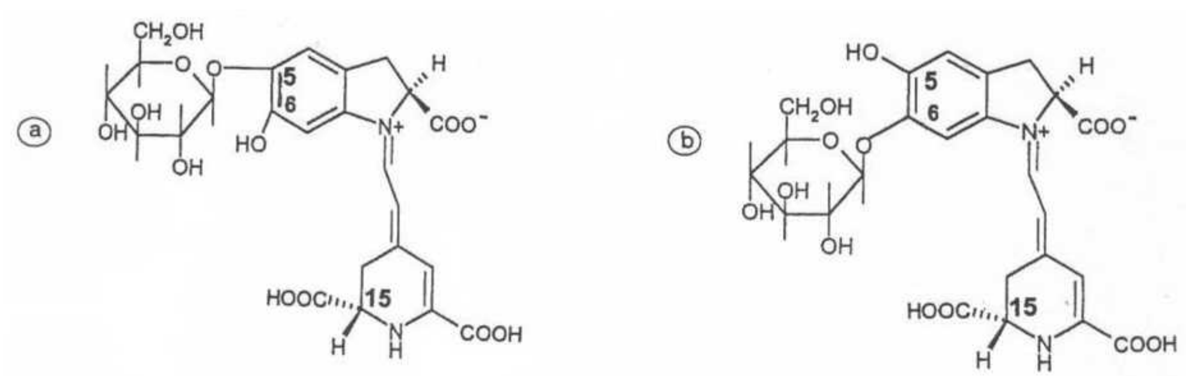

Figure 6. While betanin (a) is common in Caryophyllales, gomphrenin I (b) seems to be characteristic of the genus *Opuntia*.

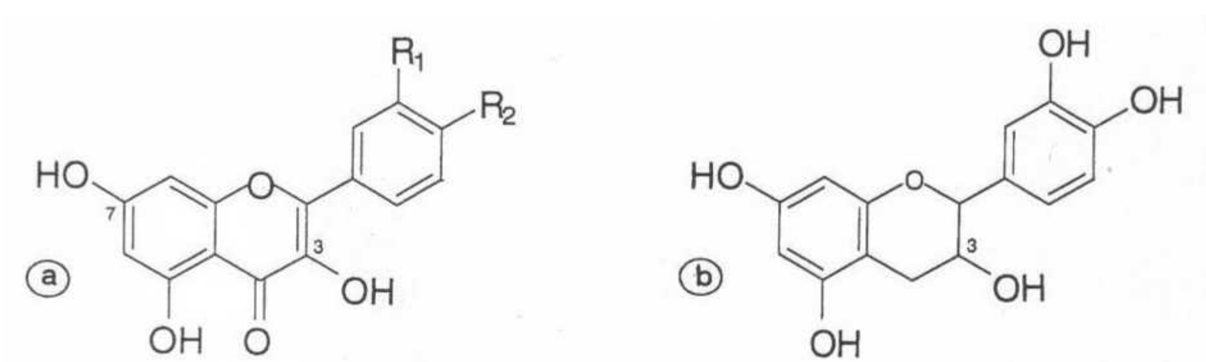

Figure 7. Structures of flavonoid aglycones from *Opuntia dillenii*. (a) Flavonols: kaempferol, R_1 = H, R_2 = OH; kaempferide, R_1 = H, R_2 = OCH_3; quercetin, R_1 = R_2 = OH; isorhamnetin, R_1 = OCH_3, R_2 = OH. (b) Flavanols: catechin and epicatechin that differ from each other in their stereochemistry at C3 in a given position of the free aromatic ring.