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Application of fermentation for the valorization of residues from Cactaceae family

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ABSTRACT

Cactaceae family is well-known for their adaptations to drought and arid environments. This family, formed by four subfamilies (Cactoideae, Opuntioideae, Pereskioideae, and Maihuenioideae) are known for being leafless stem succulent plants with numerous spines, and their commercial fruits, distinguished by their bright colors and their skin covered with bracts. Some of these species have been traditionally used in the food industry (*e.g.,* pitaya, cactus, or prickly pear) or as pharmaceuticals to treat specific diseases due to their active properties. The processing of these fruits leads to different residues, namely pomace, skin, spines, and residues from cladodes; besides from others such as fruits, roots, flowers, mucilage, and seeds. In general, Cactaceae species produce large amounts of mucilage and fiber, although they can be also considered as a source of phenolic compounds (phenolic acids, flavonols and their glycosides), alkaloids (phenethylamines derived betalains), and triterpenoids. Therefore, considering their high content in fiber and fermentable carbohydrates, together with other target bioactive compounds, fermentation is a potential valorization strategy for certain applications such as enzymes and bioactive compounds production or aroma enhancement. This review will comprise the latest information about Cactaceae family, its potential residues, and its potential as a substrate for fermentation to obtain active molecules with application in the food industry.

1. Cactaceae family

1.1. Main genera, target species and current use

Cactaceae Juss. constitutes a wide plant family containing 1,922 species distributed into 130 genera (Ana Novoa et al., 2015). Due to the taxonomic heterogeneity of this plant family, no generic consensus on its phylogenetic classification has been achieved, but it is collectively assumed that Cactaceae species can be classified into 4 major subfamilies, namely: Cactoideae, Opuntioideae, Pereskioideae, and Maihuenioideae (Bárcenas et al., 2011). These species are considered xerophytic, presenting several common characteristics, such as high resistance to drought and heat as a consequence of their adaptation to the arid conditions found in their natural habitat (Nuzhyna et al., 2018), located in the American continent, specially Mexico, and other South American countries in a lesser extent, such as Brazil, Argentina, and Chile, among others (Bravo-Avilez et al., 2019; Ortega-Baes & Godínez-Alvarez, 2006). Among the adaptative anatomical and physiological traits attributed to Cactaceae species, the performance of crassulacean acid metabolism together with a spinous succulent body and extended root systems are some of the major characteristics devoted to the improvement of their water management systems (Santos-Díaz &

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Camarena-Rangel, 2019). Moreover, most species also contain edible fruits with sweet pulp, low acidity, and different attracting colors, ranging from yellow to red–purple (Bakar et al., 2020).

Concerning the human exploitation of Cactaceae, multiple applications have been largely established with different industrial purposes, including horticultural, food and livestock feed, and medicinal uses (Ana Novoa et al., 2015), being *Opuntia ficus-indica*, *Hylocereus undatus* and *Hylocereus polyrhizus* the most commercially employed species, commonly known as prickly pear, white pitahaya, and red pitahaya, respectively, whereas other species are still poorly underexploited, as it is the case of *Pilosocereus gounellei*, also named as xiquexique, and *Cereus jamacaru*, commonly known as mandacaru (de Araújo et al., 2021). With respect to industrial applications, cacti have been classically exploited in the food industry for the development and production of a wide range of products. Thus, *P. gounellei* flour has been satisfactorily used for cake and bread production, obtaining dough formulations with higher consumer acceptability and better color and flavor than those derived from wheat (Da Silva et al., 2018). The pulp from *C. jamacaru* was used to develop functional ice creams with enhanced physicochemical attributes for their industrialization, showing a greater sensory acceptance (de Fidelis, 2015). In parallel, the jelly from *C. jamacaru* pulp was incorporated to goat yogurt, promoting a longer storage with improved acidity, and lactose content profiles (Nobrega et al., 2020). Furthermore, *O. ficus-indica* fruits were also used for the elaboration of juice, retaining a high content of bioactive compounds after clarification (Cassano et al., 2010), whereas its red–purple betalains were shown to enhance the color stability of gummy candies (Otálora et al., 2019). In addition, several authors have reported the production of different active packaging systems for food purposes based on film structures derived from *O. ficus-indica* (Aparicio-Fernández et al., 2018) and *H. polyrhizus* (Qin et al., 2020).

More recently, besides their food applications, Cactaceae species have been exploited in other industrial sectors, including technological, pharmaceutical, and chemical applications (Fig. 1). For instance, cacti have been used for the production of nanomaterials, including gold, lithium, and zinc oxide nanoparticles with improved therapeutical performance (Alvarez-Bayona et al., 2019; Vishnupriya et al., 2020), cosmetic nanoemulsions with moisturizing properties (De Azevedo Ribeiro et al., 2015), cellulose nanowhiskers (Nepomuceno et al., 2017) and nitrogen-doped carbon dots (Arul et al., 2017). In the field of livestock feeding, different cladodes from Cactaceae species have been use for such purpose, showing no negative effects on meat quality with the exception of *O. ficus- indica*, which prompted an increase in polyunsaturated fatty acids on lamb and goat meats (Mahouachi et al., 2012). Another chemical application of cacti derived products has awaken much interest in the field of water treatment, since solid cactus materials from *O. ficus-indica* provoked the removal of turbid artifacts in water, thanks to their flocculating properties due to starch and quercetin (Bouaouine et al., 2019). In addition, the production of natural dyes has also enabled the exploitation of cacti in the chemical and cosmetic industry, mainly due to the isolation of pigments from *O. ficus-indica* (Guesmi et al., 2013) and *H. polyrhizus* pulp (Utpott et al., 2020). Finally, the pharmaceutical applications related to Cactaceae are a consequence of the biosynthesis of secondary metabolites with health-promoting properties, in response to the climatic and biological threats to which these species are subjected in their natural habitat (P García-Pérez et al., 2020).

1.2. Residues from Cactaceae family

1.2.1. Invasive species: A source of potential residues

Cactaceae family is native from American continent, from Southern Argentina to Northern Canada, except from *Rhipsalis baccifera* naturally distributed in Africa. However, in the last years, these species have been spread by seed companies and botanical gardens worldwide (A. Novoa et al., 2016). The easiness of this family for spreading has been linked to their rapid vegetative propagation and adaptation to arid conditions (Podda et al., 2017). This is the case of *Opuntia* spp., which has been frequently categorized as a highly invasive alien species specially in the Mediterranean Basin and South Africa (Erre et al., 2009; Podda et al., 2017). Different studies have researched the main factors that influence *O. stricta* distribution and proposed strategies to control these

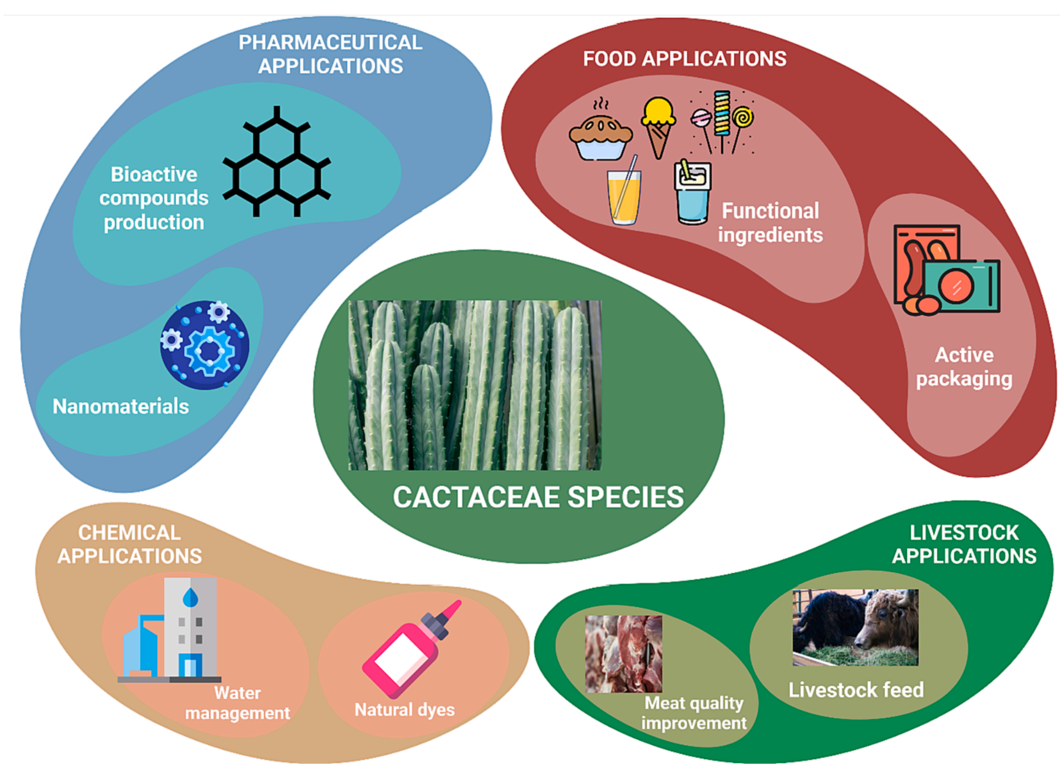

Fig. 1. Industrial applications of Cactaceae and derived by-products.

populations and protect natural biodiversity (Foxcroft et al., 2007; Rule & Hoffmann, 2018). From this perspective and to avoid the perturbation of ecosystems, some approaches have been considered, *i.e.*, phytoremediation, bioenergy production or development of added-value products with industrial applications (Kumar Rai & Singh, 2020). Removing these species from invaded ecosystems is a potential valorization strategy to use this underutilized discarded biomass to produce bioactive compounds or as a substrate for fermentation while taking advantage of the rapid growth of these species (Ahmed et al., 2020). However, even though it is critical to managing the spread of Cactaceae species, it should be considered that valorization strategies could have a counter-productive effect and promote the growth of these species so risks assessment should be deemed.

1.2.2. *Industrial waste derived from food and beverage production*

Generally, Cactaceae species are formed by leaves or spines, areoles (unique structure of cacti), stems, fine roots, fruits, and flowers. Among them, stems and fruits are the parts that have been mostly used for food applications. Their fruits are also known as prickly or cactus pear (*Opuntia* spp.) or pitahaya or dragon fruit (*Hylocereus* spp.) and are composed of a thick peel with small thorns or bracts that protects a juicy pulp with a lot of seeds (the edible part) (Jiménez-Aguilar et al., 2015). The fruit is usually consumed as fresh fruit, juice, or jam. In turn, the stems, also called cladode or '*nopal*', are leafless and succulent covered with spines and multicellular hairs and are frequently used for animal feed or discarded (Marin-Bustamante et al., 2018). Likewise, some cultures have included cladodes in diverse food preparations, such as salads, jam, chutney, or pickles and candied *nopales* (Ginestra et al., 2009).

Processing Cactaceae plants for food and non-food applications leads to different residues, namely pomace, skin, spines, and residues from cladodes. Several industries can profit of such by-products for the development of sustainable products, including food and beverages (*e.g.*, functional foods, alcoholic and non-alcoholic beverages), livestock feed products (*e.g.*, supplements, feed from cladodes and waste from fruit processing, including skin and seeds), nutraceuticals (*e.g.*, fiber and flours from cladodes), pharmaceuticals (*e.g.*, gastric mucosal protectants from mucilage extracts, tablets and capsules of cladode powder and flower extracts), binding compounds for the construction industry (*e.g.*, binding compounds from mucilage/cladodes), biogas for the energy sector (*e.g.*, biogas from digestion of cladodes and factory waste streams), and agricultural inputs (*e.g.*, soils, organic materials, and improved drainage from the use of cactus pear plant products). However, not all the valorization strategies have the same importance; namely, those by-products recycled into new food products are the best option for managing residues in the context of the circular economy. On the contrary, those residues considered as "unfitted for human consumption" consist of degraded products that will be used for other purposes, such as animal feed or fuel production (Lavelli, 2021). In this context, this article will focus on the recovery strategies of active compounds for residues from the Cactaceae family for food applications.

Cactaceae family is cultivated around the world. According to their human exploitation, since *Opuntia* and *Hylocereus* are the most commercially employed species in the food industry, and their residues have been the most studied. *Opuntia* spp. is grown in more than 20 countries and up to 2.6 million ha are dedicated to this crop, mainly used for forage. In terms of production, more than 600,000 tons are produced annually and 96 % of the world's production is represented by 3 countries, namely Mexico (80 %), Italy (12,2%) and South Africa (3.7 %). Yields per country also vary between 6.5 t/ha in Mexico to 26 t/ha in US and Israel (FAO and ICARDA, 2017). *O. ficus-indica* is the most economically important species worldwide, being Mexico the main producer (*ca.* 44 % of the world production), followed by Italy, which is the main world exporter. However, during fruit processing (peeling, squeezing, clarification, etc.) waste and by-products are generated from the prickly pear (skin, seeds, and part of the pulp, depending on processing) and the cladodes (spines, glochids and the outer edible coating). These by-products account for 45 % of the whole fruit and are mainly peels (30 %) and endocarp with seeds (Melgar et al., 2017; Morales et al., 2015). *O. ficus-indica* by-products are valuable sources of beneficial nutrients, such as minerals and fatty acids and fiber (M. A. Silva et al., 2021). *Hylocereus* species are also cultivated worldwide in tropical or sub-tropical areas. The last data indicate a total production of *Hylocereus* spp. of more than 1 million tons. Vietnam is the top producer and exporter with more than 60 % of the production followed by China (20 %) and Indonesia, Taiwan, Malaysia, and Nicaragua. Yields per country vary between 4 and 6 t/ha in Mexico to 40–45 t/ha in Vietnam (Mercado-Silva, 2018). Fruit processing also generates by-products such as peels, seeds, and pulp. Around 50 % of *Hylocereus* spp. is the pericarp, majorly formed by peel by-products (30–35 %) (Montoya-Arroyo et al., 2014; Roriz et al., 2022). These by-products contain natural antioxidants like tocopherols, sterols or phenols that can be used in the food industry (Lim et al., 2010). For example, their seed oil displays fatty acid and phenolic compositions compared to canola, flaxseed, and grape seed oils.

A deeper insight into these bioactive compounds, mainly phenolic compounds, alkaloids, betalains, and terpenes, and their associated bioactivities are reported later in this review. Moreover, the high fiber and fermentable carbohydrates content of Cactaceae species and their potential as substrates for fermentation purposes and their applications in the food industry will be addressed.

2. Target bioactive compounds of Cactaceae residues

Cactaceae species should cope with harsh environmental conditions in their natural habitats, including intense heat, drought, radiation, and poor nutrient availability from the soil, together with biotic stresses, caused by insect and herbivore attacks. Consequently, to deal with this paradigm, cacti synthesize a wide range of secondary metabolites with bioactive properties, as part of their chemical defensive system, *i.e.*: phenolic compounds, alkaloids, and terpenoids, among others (Harlev et al., 2013). In addition to the environmental dependence, the phytochemical composition of cacti is also influenced by other factors, such as the cultivar, geographical distribution, and the plant tissue to be analyzed. Among the different species belonging to this family, those from the genus *Opuntia* have been largely defined in terms of bioactive compounds production, in particular the species *O. ficus-indica*, including both edible parts and derived by-products, like cladodes and fruits peels and seeds (Aruwa et al., 2018). Other cacti genera poorly characterized by means of bioactive compounds are *Hylocereus*, *Pereskia*, *Mamillaria*, and *Coryphantha* (Das et al., 2021). In this section, a detailed description of the phytochemicals present in Cactaceae by-products is provided in Table 1 and summarized in Fig. 2.

2.1. *Phenolic compounds*

Phenolic compounds (PC) constitute the largest family of secondary metabolites, with more than 10,000 individual compounds identified to date, being ubiquitously found in the plant kingdom (García-Pérez et al., 2021a), including cacti. Considering by-products, much attention has been paid to the phenolic composition of fruit peels, mainly, together with seeds, cladodes, and flowers (Table 1). Due to their role as antioxidant compounds, and UV-radiation scavengers, is it assumed that such compounds should be accumulated in the aerial parts of cacti, which are the tissues presenting a higher exposure to environmental threats (García-Pérez et al., 2019). PC have been identified in Cactaceae, ranging from simple phenolics, such as phenolic acids, including hydroxycinnamic and hydroxybenzoic acids, to more complex polyphenols, as it is the case of flavonoid glycosides, mostly represented by flavonol and flavone glycosides, tannins, coumarins, anthocyanins, and stilbenes.

A wide variety of common phenolic acids has been reported to cacti

Table 1
Relevant bioactive compounds found on Cactaceae species by-products.

Species	Residue	Extraction	Analysis	Compounds	Quantification*	Ref.
Opuntia joconostle	Fruit peel	SLE, 80 % MeOH and 50 % acetone	HPLC-PDA-EI/MS	Phenolic acids: protocatechuic, 4-hydroxybenzoic, caffeic, vanillic and syringic acids / Flavonoids: rutin, and quercetin, anthocyanins / Alkaloids: betacyanins	PA: 259.9 μg/g	(Osorio-Esquivel et al., 2011)
Opuntia spp.	Cladodes	SLE, 75:25 60 % MeOH: 6 M HCl	HPLC-DAD	Phenolic acids: caffeic, chlorogenic, *p*-coumaric, ferulic, gallic, *p*-hydroxybenzoic, syringic, and vanillic acids / Flavonoids: apigenin, isorhamnetin, quercetin, rutin, and luteolin glycosides	PA: 99.6 μg/g F: 31.2 μg/g	(López-Palacios & Peña-Valdivia, 2020)
		SLE, hexane	HPLC-UV/Vis	Terpenoids: β-amyrin, oleanolic acid, and peniocerol	67.2 μg/g	
	Fruit peel Ground seeds	SLE, 70 % EtOH SLE, 99:1 MeOH:HCl	Spectro-photometry	Total phenolic compounds, total flavonoids, total tannins	3,760 μg GAE/g 4,600 μg GAE/g	(Cardador-Martínez et al., 2011)
Opuntia ficus-indica	Cladodes	SLE, 99.9:0.1 80 % MeOH:HCOOH	UPLC-ESI-QTOF/MS	Phenolic compounds: hydroxycinnamic and hydroxybenzoic acids, lignans, tyrosols, anthocyanin, flavone, and flavonol glycosides	PA: 1453.8 mg FAE/kg	(Rocchetti et al., 2018)
		Extrusion and precipitation, EtOH	n.d.	Mucilage	n.d.	(Otálora et al., 2019)
	Seeds	Soxhlet, hexane	GC	Fatty acids: palmitic, stearic, oleic, vaccenic, and linoleic acids	9.3 % oil rate	(Chougui et al., 2013)
		SLE, 80 % MeOH	HPLC-DAD-LTQ/MS	Phenolic acids: ferulic acid and sinapic acid derivatives	890 μg GAE g	
		SLE, hexane	HPLC-refractometer detector	Tocopherols: α-, β-, γ-, δ-tocopherols	117.6 mg/kg	(El Kharrassi et al., 2018)
		SLE, 1:2 MeOH: $CHCl_3$ saponification	HRGC-FID	Fatty acids: myristic, palmitic, stearic, palmitoleic, oleic, linoleic, and linolenic acids / Phytosterols: ergosterol, campesterol, stigmasterol, lanosterol, β-sitosterol, and avenasterol	FA: 98.8 g/kg P: 9.3 g/kg	(Ramadan & Mörsel, 2003)
	Fruit peel	SLE, 80 % EtOH	HPLC-DAD-ESI/MS	Betalains: indicaxanthin, betanidin / Flavonoids: isorhamnetin, quercetin, and kaempferol glycosides	B: 3.9 mg/g F: 3.7 mg/g	(Melgar et al., 2017)
		SLE, MeOH	HPLC-PDA-MS/MS	Phenolic acids: quinic, malic, ferulic, syringic, *p*-coumaric, and sinapic acids and glycosides / Flavonoids: quercetin, kaempferol, rhamnetin, isorhamnetin glycosides / Fatty acids: eicosanoic acid, behenic acid	TPC: 165.2 mg GAE/g	(El-Hawary et al., 2020)
		SLE, THF, saponification with 30:70 MeOH:KOH	HPLC-PDA-APCI/MS	Xhantophylls: violaxanthin, neoxanthin, anteraxanthin, lutein, zeaxanthin, cryptoxanthin / Carotenes: α- and β-carotenes, and lycopene	TC: 1,693 μg/100 g	(Cano et al., 2017)
	Flowers	Maceration, 99:1 80 % acetone:HCl	HPLC-MS-ESI/MS	Phenolic acids: ferulic acid, chlorogenic acid, syringic acid, coumaric acid, caffeic acid / Flavonoids: isorhamnetin and quercetin glycosides	PA: 3.2 mg GAE/g F: 1.6 mg CAE/g	(Benayad et al., 2014)
Hylocereus polyrhizus and *Hylocereus undatus*	Fruit peel	SLE, 99:1 80 % MeOH: HCOOH, acid, and alkaline hydrolisis	UPLC-TOF/MS	Phenolic acids: gallic, syringic, sinapic, chlorogenic, *p*-hydroxycinnamic, caffeic, *p*-coumaric, ferulic, quinic, and isoferulic acids / Flavonoids: epicatechin, rutin, isoquercetin, kaempferol, isorhamnetin, quercetin, diosmetin, baicalein, tectorigenin	0.05–131.67 mg/kg	(Tang et al., 2021)
		Precipitation with acetone	n.d.	Mucilage	n.d.	(Le et al., 2020)
	Seeds	Soxhlet, pethroleum ether	GC	Fatty acids: myristic, palmitic, stearic, arachidic, palmitoleic, oleic, linoleic, linolenic acids	28.37 % oil rate	(Lim et al., 2010)
			HPLC-UV	Tocopherols: α- and γ-tocopherols	43.5 mg/100 g	
		SLE, 50:50 MeOH: hexane	HPLC-PDA	Phenolic acids: gallic, protocatechuic, *p*-hydroxybenzoic, vanillic, caffeic, syringic, and *p*-coumaric acids	4.26 mg/100 g	
		Saponification, 94:6 EtOH:KOH	GC-FID	Phytosterols: campesterol, stigmasterol, β-sitosterol	1,040 mg/100 g	
Hylocereus megalanthus	Fruit peel and seed mixture	Fungal fermentation & maceration, 50 % EtOH	HPLC-UV/Vis	Phenolic acids: gallic, *p*-hydroxybenzoic, vanillic, syringic, *p*-coumaric, and cinnamic acids / Flavonoids: catechin, epicatechin, quercetin / Stilbenes: resveratrol	102.32 mg/100 g	(Zambrano et al., 2018)
Hylocereus spp.	Fruit peel and flowers	SPE and SLE, 95:5 MeOH:TFA	HPLC-ESI-MS/MS	Betalains: betanidin, betaxanthin, indicaxanthin, betanin, isobetanin, phyllocactin, hylocerenin, isophyllocactin, and isohylocerenin glycosides	n.d.	(Wybraniec et al., 2007)
Pereskia aculeata	Leaves	SLE, 70 % EtOH	HPLC-DAD-ESI/MS	Phenolic acids: caftaric acid, caffeic acid derivatives / Flavonoids: quercetin, isorhamnetin, and kaempferol glycosides	PA: 12.32 mg/g F: 11.4 mg/g	(Garcia et al., 2019)
	Fruit peel	SLE, acetone	HPLC-DAD	Carotenoids: α- and β-carotenes	76.2 μg/g	(Agostini-Costa et al., 2014)

(*continued on next page*)

Table 1 (*continued*)

Species	Residue	Extraction	Analysis	Compounds	Quantification*	Ref.
Pereskia spp.	Leaves	SLE, acetone	HPLC-DAD	Carotenoids: α- and β-carotenes, zeaxanthin	210 μg/g	(Agostini-Costa et al., 2014)
Mammillaria herrerae	Callus	SLE, 80 % MeOH	UPLC-MS/MS	Citric acid, tyramine, sinapic, ferulic, and *p*-coumaric acids, quercetine, flavone, rutin, kaempferol, and isoflavone glycosides, bruguierol A	TPC: 15.22 mg GAE/g	(Song et al., 2020)
Mammillaria spp.	Stem	UAE, MeOH	HPLC-DAD	Phenolic acids: protocatechuic, gentisic, chlorogenic, *p*-hydroxybenzoic, caffeic, and sinapic acids	74.3 mg/100 g	(Elansary et al., 2020)
Coryphantha macromeris	Callus	UAE, MeOH	UHPLC-PDA-HESI-Orbitrap-MS/MS	Phenolic acids: protocatechuic, caffeic, syringic, ferulic, piscidic, benzoic, and sinapic acid glycosides / Chalcones: aspalathin / Flavonoids: glycitin, scutellarein, apigenin, and isoflavone glycosides	n.d.	(Cabañas-García et al., 2021)
Coryphantha spp.	Stems and roots	SLE, 80 % EtOH	Qualitative determination	Alkaloids, sterols, flavonoids, saponins	n.d.	(Sánchez-Herrera et al., 2011)

Abbreviations: APCI, atmospheric-pressure chemical ionization; DAD, diode-array detector; EI, electron-impact ionization; ESI, electrospray ionization; EtOH, ethanol; FID, flame ionization detector; GC, gas chromatography; HCl, hydrochloric acid; HCOOH, formic acid; HESI, heat-assisted electrospray ionization; HPLC, high performance liquid chromatography; HRGC, high-resolution gas chromatography; KOH: potassium hydroxide; LTQ, linear trap quadrupole; MeOH, methanol; MS, mass spectrometry; MS/MS, tandem mass spectrometry; n.d., not defined; PDA, photodiode array detector; QTOF, quadrupole coupled to time-of-flight; SLE, solid–liquid extraction; SPE, solid phase-assisted extraction; TFA: trifluoroacetic acid; THF, tetrahydrofuran; TOF, time-of-flight; UAE, ultrasound-assisted extraction; UPLC: ultra-high performance liquid chromatography; UV/Vis, ultraviolet/visible spectrophotometric detector; CE: cyanidin equivalents, GAE: gallic acid equivalents, FAE: ferulic acid equivalents; CAE: catechin equivalents. TC: Total carotenoids; TPC: total phenolic content. * Quantitative data correspond to the maximum total values obtained in each study.

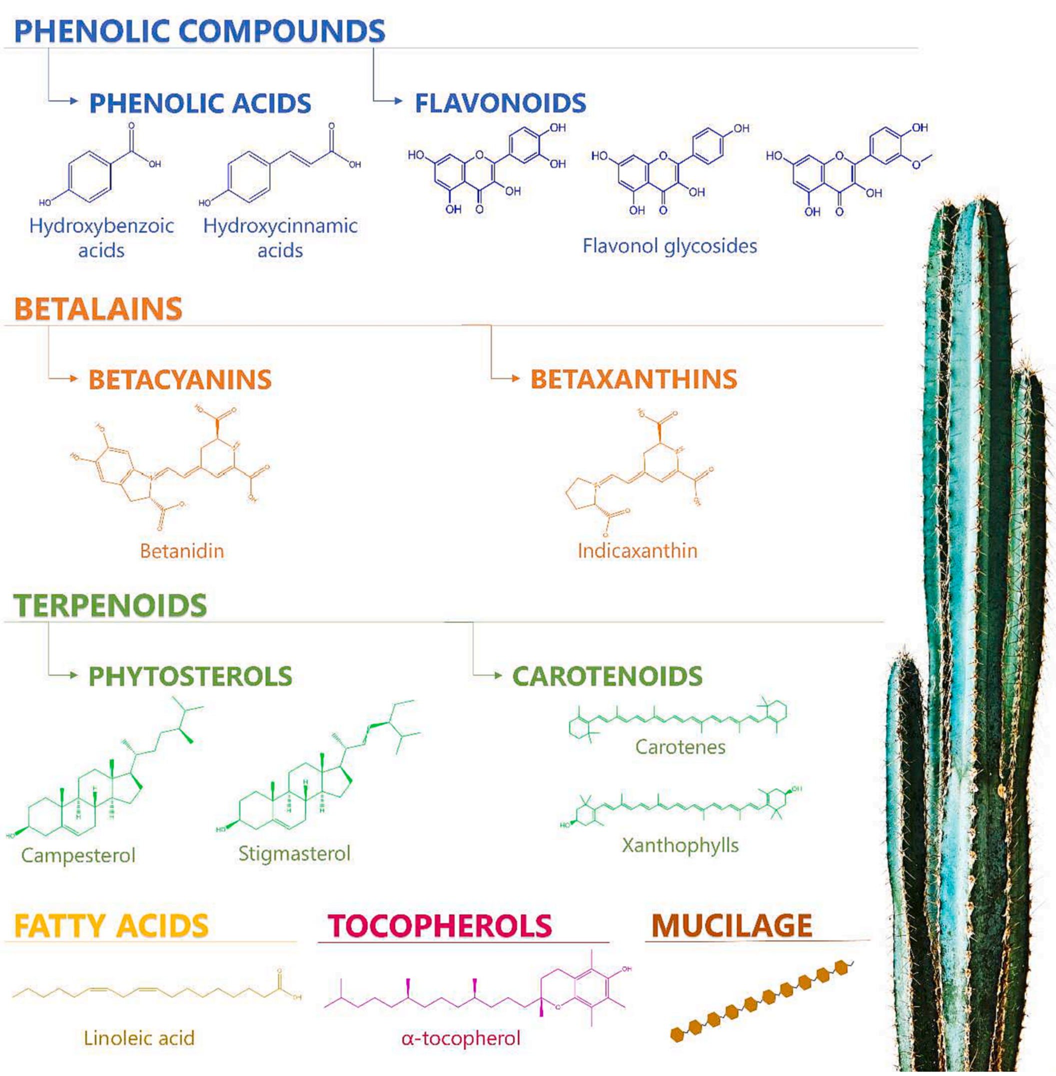

Fig. 2. Representative bioactive compounds from Cactaceae species and by-products.

by-products, whereas the flavonoid family was essentially formed by quercetin, kaempferol, and isorhamnetin glycosides (Cardador-Martínez et al., 2011; López-Palacios & Peña-Valdivia, 2020; Osorio-Esquivel et al., 2011). On the other hand, other subfamilies of PC were more restricted to some species, as it the case of anthocyanins in the cladodes of *O. ficus-indica,* with contents up to 1,444 mg/kg cyanidin equivalents (Rocchetti et al., 2018), or catechins (368.8 mg/kg) and resveratrol (28.2 mg/kg) in the mixture of fruit peels and seeds from *Hylocereus magalanthus* (Zambrano et al., 2018). Thus, *Opuntia* by-products have been revealed as promising sources of PC, especially, cladodes, seeds, fruit peels, and flowers (Benayad et al., 2014; Chougui et al., 2013; El-Hawary et al., 2020; Melgar et al., 2017; Rocchetti et al., 2018). Similar phytochemical composition has been reported to *Hylocereus* by-products, particularly those derived from *H. polyrhizus* and *H. undatus*, whose fruit peels, flowers and seeds have been thoroughly characterized in terms of phenolic profiling (phenolic acids concentration between 0.05 and 131.67 mg/kg) (Le et al., 2020; Lim et al., 2010; Tang et al., 2021). In a lesser extent, several species belonging to *Pereskia*, *Mammillaria*, and *Coryphantha* have been also subjected to the phytochemical analysis of their by-products, including leaves, calli, stems, and roots, showing not only the widely distributed phenolic acids and flavonol glycosides, but also more specialized compounds, such as caftaric acid, bruguierol A or aspalathin, probably due to existence of endangered species on these genera (Cabañas-García et al., 2021; Elansary et al., 2020; Song et al., 2020). Regarding the total phenolic content (TPC), it ranges between 15 and 165 mg GAE/g depending on the species (El-Hawary et al., 2020; Song et al., 2020).

2.2. Alkaloids

Alkaloids constitute a heterogeneous family of plant secondary metabolites characterized by the presence of nitrogen-containing heterocycles within their basic structure (García-Pérez et al., 2021b). Owing to biosynthetic properties, two major alkaloid classes are reported in Cactaceae: isoquinoline and phenethylamine derivatives, accounting for up to 50 and 80 individual compounds, respectively, in the whole family (Das et al., 2021). Between them, phenethylamines have focused the research on cacti alkaloids since many decades, firstly reported in the genus *Opuntia* (Meyer et al., 1980), although isoquinoline alkaloids, like tryptamine, have been also detected in the callus cultures of *Mammillaria* spp., and mescaline and pellotine in *Lophophora williamsii* and *Lophophora diffusa*, both with hallucinogenic effects (Santos-Díaz & Camarena-Rangel, 2019).

The most important phenetylamine derivatives found in cactus species and their by-products are betalains, considered as the major pigments of these species (Rahimi et al., 2019). Depending on the substitution degree of the basic betalain structure, known as betalamic acid, two different groups are described: red-violet betacyanins and yellow-orange betaxanthins (Slimen et al., 2017). Because of their pigment nature, betalains have been mostly reported as phytoconstituents of cacti fruits peels, causing their coloration (Table 1). Thus, betacyanins were reported in the peels of *Opuntia* fruits, like *Opuntia joconostle*, with maximum concentrations of 230.3 mg betanin/kg in the pericarp (Osorio-Esquivel et al., 2011) and *O. ficus-indica*, mostly represented by betanidin and its glycosides, isobetanin and gomphrenin I, with total betacyanin compounds up to 3.97 mg/g of extract (Melgar et al., 2017). These compounds are also found in the fruit peels of some *Hylocereus* species (pitahayas) in the form of apiosyl, feruloyl and sinapoyl esters, together with other specific compounds, such as phyllocactin and hylocerenin and their isomers and esterified derivatives (Herbach et al., 2006; Wybraniec et al., 2007). On the hand, betaxanthins have been reported in a lesser extent, being essentially reported in the fruit peels of *O. ficus-indica*, where up to 25 different compounds were isolated, including indicaxanthin as the most prevalent compound followed by vulgaxanthin I-IV, dopaxanthin, portulacaxanthin II-III and miraxanthin III (Kugler et al., 2007; Melgar et al., 2017).

2.2.1. Terpenoids

Terpenoids also make part of the secondary metabolites found on cacti, deriving from the condensation of different isoprene subunits, giving rise to different subfamilies depending on the condensation degree (García-Pérez et al., 2021b). In the case of Cactaceae family, highly condensed terpenoids are predominantly found, represented by triterpenoids and triterpenoid acids, phytosterols, and carotenoids. Due to the lipophilic nature of these compounds, they are mainly found as constituents of seed oils, although they can be secondarily isolated from other tissues, such as fruit peels and cladodes, where they constitute another source of pigmentation together with betalains (Table 1).

Thus, López-Palacios et al. isolated some triterpenoids from the cladodes of *Opuntia* spp., such as β-amyrin (1.33–4.39 μg/g), oleanolic acid (13.92–63.26 ng/g), and the phytosterol peniocerol (0.73–0.83 μg/g) (López-Palacios & Peña-Valdivia, 2020). Considering *O. ficus-indica*, both the seeds and derived oil are rich in a wide range of phytosterols, *i.e.*, ergosterol, cholesterol, campesterol, stigmasterol, lanosterol, avenasterol, and β-sitosterol (Ramadan & Mörsel, 2003), whereas the fruit peels contains relevant amount of carotenoids (total 16.93 mg/kg), including xanthophylls, such as violaxanthin, neoxanthin, anteroxanthin, lutein, zeaxanthin, and cryptoxanthin, as well as carotenoids: α- and β-carotenes, and lycopene (Cano et al., 2017). Accordingly to *Opuntia* seeds, those from *Hylocereus* species were also reported to contain different phytosterols (up to 10.4 mg/kg), like cholesterol, campesterol, stigmasterol, and β-sitosterol (Lim et al., 2010). Moreover, the leaves and fruit peels of different *Pereskia* species were shown to present α- and β-carotenes, together with zeaxanthin, only in the case of leaves (210 μg/g) (Agostini-Costa et al., 2014). Finally, other authors demonstrated the presence of sterols in the stems and roots of *Coryphantha* spp. (Sánchez-Herrera et al., 2011).

2.3. Other compounds

Together with the most relevant bioactive compounds found on cacti and their by-products, additional compounds with associated biological properties are present in a lesser extent (Table 1). For instance, fatty acids constitute the major constituents of cacti seeds and oil. Depending on the cacti species, different oil rates have been obtained ranging from 9.3 % to 28.37 % (Chougui et al., 2013; Lim et al., 2010) Thus, they present a combination of saturated, monounsaturated, and polyunsaturated fatty acids (SFA, MUFA, and PUFA, respectively). Cacti SFAs are mostly represented by palmitic, stearic, myristic acids, found in the seeds of *O. ficus-indica* (Chougui et al., 2013), *H. polyrhizus*, and *H. undatus* (Lim et al., 2010), whereas behenic acid has been also isolated in the fruit peels of *Opuntia* species (El-Hawary et al., 2020). In the case of unsaturated fatty acids, they were found in lower proportions in the seeds of the same species, containing oleic and palmitoleic acids as the principal MUFAs, whereas both omega-3 and omega-6 PUFAs have been also reported, namely linoleic and linolenic acids, respectively (Chougui et al., 2013; Lim et al., 2010). In addition to fatty acids, tocopherols were also reported in the seeds of cactus species, representing bioactive antioxidants of lipophilic nature. In this sense, Lim et al. identified α- and γ-tocopherol in the seeds of *Hylocereus* spp. (435 mg/kg) (Lim et al., 2010). More recently, other authors spotted the presence of multiple tocopherol isoforms, including α-, β-, γ, and δ- isomers in both oil seed and cladode essential oils of *Opuntia megacantha* (117.6 mg/kg) (El Kharrassi et al., 2018).

On the other hand, concerning polysaccharides, mucilage is considered a functional biopolymer, mostly isolated from cactus cladodes, and largely used with industrial purposes in both food sector, as a gelling, stabilizing and encapsulating agent, and in pharmacy, due to its antioxidant and other bioactivities, together with its properties as an efficient natural drug delivery system (Gheribi & Khwaldia, 2019; Messina et al., 2021). As previously observed for other bioactive compounds, the cladodes of *O. ficus-indica* represents an important source of cactus mucilage (Otálora et al., 2019), although it can also be isolated from the fruit peels of *Hylocereus* spp., being incorporated in different food-related applications (Le et al., 2020).

3. Fibers and fermentable carbohydrates of Cactaceae residues

Cactaceae species have gained attention not only because of its attractive nutritional composition but also for being a rich source of bioactive compounds with promising health-related benefits (M. A. Silva et al., 2021). Among the different species belonging to this family, those from the genus *Opuntia* is the most extensively explored and distributed genus within the Cactaceae family and includes nearly 1,500 species (Chahdoura et al., 2015). Therefore, waste and by-products are mostly generated from the prickly pear and cladodes processing. It has been estimated that about 20 % of cladodes and 45 % of fruits fresh weight are discarded, and such by-products have a higher content of dietary fiber than their corresponding commercial edible parts (Bensadón et al., 2010). Therefore, the valorization of *Opuntia* wastes and by-products by recovering their bioactive compounds and dietary fiber is a potential strategy to sustainably manage these residues. In this context, the composition of dietary fiber present in *Opuntia* spp. by-products is described in this section. The physicochemical characteristics, as well as their health-related properties, are also presented.

3.1. Composition and types of fiber

Opuntia spp. waste and by-products are rich sources of dietary fiber. The insoluble fiber is composed of structural polysaccharides, such as cellulose, and hemicellulose and acts as protecting barrier against pathogenic microorganisms. On the other hand, the soluble fiber is composed of pectin, mucilage, and loosely bound hemicelluloses whose main function in plants is to avoid tissue dehydration by forming complexes with water (Ventura-Aguilar et al., 2017). The content of dietary fiber strongly depends on the part of the plant, cultivar, geographical location, maturity stage, etc. Table 2 depicts the dietary fiber composition of the by-products of *Opuntia* spp. cultivated in different geographical regions.

Regarding prickly pears by-products, El Kossori et al., 1998 found that *O. ficus-indica* sp. cultivated in Morocco had the highest total fiber content in the seeds (54.2 % w/w DW, dry matter), followed by the skin (40.8 % w/w DW) and the pulp (20.5 % w/w DW) (El Kossori et al., 1998). These authors observed that seed's fiber was mostly composed of cellulose (83.2 % of total fiber), while skin's fiber was rich in hemicellulose and cellulose and the pulp had the highest pectin content (70.3 % of total fiber). None of these by-products showed a significant content of lignin in their composition (El Kossori et al., 1998). Similar results were found by Jiménez-Aguilar et al., 2015 who reported a higher content of total fiber in the seeds (81.5–93.8 % w/w, DM) of four varieties of *O. ficus-indica* from Mexico, followed by skin (43.2–58.1 % w/w DM) and pulp (14–16.6 % w/w DM) (Jiménez-Aguilar et al., 2015). These authors also reported that seeds were mainly composed of insoluble fiber (98 % of total fiber), whereas a higher content of soluble fiber was found in skin (22–38 % of total fiber). In addition, the highest content of soluble fiber was reported in pulp (50–70 % of total fiber). On the other hand, in a recent study, it was reported that the total fiber content in the skin and pulp of *O. ficus-indica* cultivated in Egypt (El-Beltagi et al., 2019) was significantly lower than that previously reported (El Kossori et al., 1998), obtaining values of 5.83 and 4.65 % w/w DW, respectively. Similarly, Medina et al., 2007 found that the total fiber content in green and orange pulp of *O. ficus-indica* from the Canary Islands was 5.65 and 4.86 % w/w DW, respectively (Medina et al., 2007). Thus, these differences can be attributed to geographical variation, harvesting time, growth conditions, cultivar, etc. In a deep study, it was determined the composition of total dietary fiber of sweet and acid fruits of *Opuntia* spp. (Peña-Valdivia et al., 2012). These authors observed that the total fiber content of the whole sweet fruits was in the range of 6.17–10.07 % w/w DW, being the soluble fiber the predominant fraction (59–75 % of total fiber). The soluble fiber of sweet fruits of *Opuntia* spp. was composed of mucilage (0.79–1.03 %), pectin (1.45–2.14 %), and loosely bound hemicelluloses (1.58–2.11 %). These authors highlighted that the content of these three soluble non-starch polysaccharides was significantly lower than that found in the acid cultivar which in turn, was similar to those values found in cladodes (Peña-Valdivia et al., 2012).

Concerning cladodes' by-products, Ramírez-Moreno et al., 2013 found that the total fiber content in cladodes of *O. ficus-indica* ranged

Table 2
Dietary fiber of the *Opuntia ficus-indica* by-products cultivated in different geographical regions.

PRICKLY PEAR			CLADODE		Reference
Pulp	**Seed**	**Skin**	**Spine**	**Whole cladode**	
Total dietary fiber (% w/w DM)					
20.5	54.2	40.8	–	–	(El Kossori et al., 1998)
14–16.6	81.5–93.8	43.2–58.1	–	–	(Jiménez-Aguilar et al., 2015)
4.65	–	5.83	–	–	(El-Beltagi et al., 2019)
4.86–5.65	–	–	–	–	(Medina et al., 2007)
–	–	–	46.12	–	(Marin-Bustamante et al., 2018)
–	–	–	–	30.93	(Ayadi et al., 2009)
–	–	–	–	62.05–64.25	(Bensadón et al., 2010)
–	–	–	–	23–45	(Peña-Valdivia et al., 2012)
–	–	–	–	20.86–29.43	(López-Palacios et al., 2012)
–	–	–	–	47.48–51.14	(Ramírez-Moreno et al., 2013)
Soluble fiber (% w/w DM)					
14.41	3.74	3.14	–	–	(El Kossori et al., 1998)
7.6–12.4	2.2–2.9	9.8–19.3	–	–	(Jiménez-Aguilar et al., 2015)
–	–	–	–	13.38–21.19	(López-Palacios et al., 2012)
–	–	–	–	16–30	(Peña-Valdivia et al., 2012)
–	–	–	–	7.83	(Ayadi et al., 2009)
–	–	–	–	5.68–7.07	(Ramírez-Moreno et al., 2013)
–	–	–	–	8.92–9.8	(Bensadón et al., 2010)
Insoluble fiber (% w/w DM)					
6.08	50.48	37.62			(El Kossori et al., 1998)
4.2–7.6	78.6–91.3	28.2–40.9			(Jiménez-Aguilar et al., 2015)
–	–	–	–	6.62–8.47	(López-Palacios et al., 2012)
–	–	–	–	7.8–16.2	(Peña-Valdivia et al., 2012)
–	–	–	–	20.87	(Ayadi et al., 2009)
–	–	–	–	41.80–44.07	(Ramírez-Moreno et al., 2013)
–	–	–	–	53.13–54.45	(Bensadón et al., 2010)

Abbreviations: DM, dry matter.

47–51 % w/w DM, being the insoluble fiber the predominant fraction (41.80–44.07 % of total fiber) (Ramírez-Moreno et al., 2013). Similarly, (Bensadón et al., 2010) reported that the insoluble fraction in the cladodes' by-products (*O. ficus-indica*) ranged between 53.13 and 54.45 % w/w DW whereas the soluble one was within 8.92 and 9.8 % w/w DW. These authors highlighted that the by-products' composition was comparable to that observed in the edible parts of cladodes, suggesting that by-products of cladodes are an underexploited source of health-promoting compounds. Regarding the composition of dietary fiber, López-Palacios et al. (2012) found that *nopalitos* (edible young cladodes) were a rich source of soluble fiber mainly composed of mucilage (11.72 % w/w DM), followed by loosely bound hemicellulose (4.59 % w/w DM) and pectin (1.83 % w/w DM) with the lowest content (López-Palacios et al., 2012). In contrast, the insoluble fraction of *nopalitos* was composed of cellulose (5.49 % w/w DM) and tightly bound hemicellulose (2.30 % w/w DM). In this line, it was found that *nopalitos* of *O. ficus-indica* were composed of pectins (6.1–14.2 % w/w DM), mucilages (3.8–8.6 % w/w DM) and loosely bound hemicelluloses (4.9–10.7 % w/w DM), representing the soluble fiber (Peña-Valdivia et al., 2012). These authors agreed that mucilages and pectins can protect *Opuntia* spp. from drought through a hydrating mechanism allowing them suitably grow in the arid or semiarid areas. Regarding the insoluble structural polysaccharides, Peña-Valdivia et al. (2012) reported that low content of tightly bound hemicellulose (2.2–4.6 % w/w DM) were found in *nopalitos* while the cellulose content ranged 5–15 % w/w DM, representing the most abundant structural polysaccharide (Peña-Valdivia et al., 2012). These authors also reported the absence of lignin in *nopalitos* of *Opuntia* cultivars. On the other hand, spines represent 3.7 % of the total waste from *O. ficus-indica* processing in Mexico per year. In addition, other authors found that spines were mostly composed of cellulose (39.7 % w/w DM), hemicellulose (32.8 % w/w DM) and lignin (24.6 % w/w DM) (Marin-Bustamante et al., 2018). In this regard, the insoluble structural polysaccharides profile makes spines a cheap and underexploited lignocellulosic biomass to produce bioethanol (de Souza Filho et al., 2016).

3.2. Physicochemical properties

The functional properties of *Opuntia* spp. by-products, such as water retention capacity, swelling capacity, glucose retention index, fat adsorption capacity and rheological properties should be considered when dietary fiber is used as a functional ingredient during the development of novel foods. In this regard, purple cactus pear waste showed similar functional properties (water retention capacity, swelling capacity and emulsion capacity) than those observed in commercial fiber (Monter-Arciniega et al., 2019). These authors highlighted that cactus waste exhibited the highest fat adsorption capacity, suggesting that dietary fiber from cactus waste could be used for delaying lipid digestion and thus controlling cholesterol levels (Monter-Arciniega et al., 2019). In addition, dietary fiber obtained from cactus pear waste showed a non-Newtonian pseudoplastic behavior and high viscosity at a concentration of 5 %, which was comparable with xanthan gum at the same concentration (Monter-Arciniega et al., 2019). Such properties may support the use of cactus pear waste as sustainable food ingredients according to the circular economy concepts. In this way, Ramírez-Moreno et al., 2013 observed that water retention and swelling capacity of raw cladodes (*O. ficus-indica*) were unaltered after boiling (as it is commonly processing), suggesting that the high content of insoluble fiber and mucilage with high molecular weight could form a complex network with water capable of producing an increase in viscosity of the liquid phase (Ramírez-Moreno et al., 2013). However, boiled cladodes also reported a thixotropic behavior with an irreversible structural breakdown of the gel. This fact was attributed to the hydrolysis of mucilage's structure by cooking, leading to the release of soluble fiber components into the boiling water, thus reducing the gel's consistency and viscosity (Ramírez-Moreno et al., 2013). These changes in rheological properties of boiled cladodes negatively affected their glucose retention capacity into the food matrix (57–75 % lower than untreated cladodes) and thus reducing the physiological benefits of cladodes on the control of post-prandial glucose levels.

Likewise, Ayadi et al., 2009 found that cladodes from *O. ficus-indica* obtained similar values of swelling capacity than other vegetable sources (wheat and carrot). In addition, the dietary fiber of cladodes showed high water retention capacity, demonstrating their ability to interact with water. In turn, their fat adsorption capacity was comparable with that found in other vegetable sources, suggesting their technological potential. These authors also enriched wheat flour with cladode powder at different concentrations (5, 10, 15 and 20 %) obtaining significant effects on dough properties. In fact, they observed that increasing the cladode proportion in the flour led to an increase in dough's tenacity, energy, adhesion, stickiness, and hardness. However, sensory quality limited the amount of dietary fiber from cladodes that could be added to wheat flour since incorporating more than 5 % of cladodes led to unacceptable scores of overall qualities (Ayadi et al., 2009).

3.3. Associated health benefits

Opuntia spp. by-products have shown health-related properties associated to dietary fiber, such as antioxidant and antimicrobial activities *in vitro* (Sánchez et al., 2014) and anti-inflammatory, and anti-diabetic properties *in vivo* (Fernandez et al., 1994). Controlling the postprandial serum glucose level (Frati et al., 1990) and reducing the blood cholesterol levels (Fernandez et al., 1994), as well as retarding gastric emptying have been attributed to soluble fiber. In turn, the increase in fecal bulk, reduction of constipation's symptoms and the stimulation of colonic fermentation (resulting in the production of short chain fatty acids) have been ascribed to the insoluble fraction (Sáenz et al., 2004). These physiological effects were associated with previously mentioned functional properties (water retention capacity, fat adsorption capacity, emulsion activity, and swelling). In this regard, several diseases (*e.g.*, cardiovascular, type II diabetes mellitus and obesity) could be prevented by daily consuming fiber-enriched foods (recommended dietary fiber intake 25–30 g/day) (Abirami et al., 2014).

Bensadón et al., 2010 found that cladodes and fruits' by-products of *O. ficus-indica* cultivars have high total antioxidant activity measured through ABTS (52.37–66.33 μmol trolox equivalents/g DM) and FRAP (40.39–65.33 μmol trolox equivalents/g DM) assays, and these values were comparable to those of other foods (*e.g.*, nuts and fruits) (Bensadón et al., 2010). This was attributed to their high content of phenolic (1.54–3.71 GAE/100 g DM) and carotenoid (15.16–22.84 mg β-carotene equivalents/g DM) compounds. These authors reported that polyphenols and some carotenoids could be bound to insoluble dietary fiber and the resulting complex may resist the gastrointestinal digestion and reach the gut almost intact. Therefore, by-products obtained from cladodes and fruits may combine the beneficial effect of both dietary fiber and antioxidant compounds in a single source, providing a product with multiple properties suitable as dietary supplement or food ingredient. However, considering the high content of dietary fiber in *Opuntia* spp. by-products (53.13–54.45 % w/w DW), comprehensive knowledge about the bioavailability of these bioactive compounds to ensure their physiological role is needed. Similarly, Melgar et al., 2017 identified twelve PC in the *Opuntia* spp. skin, which showed high correlation with all antioxidant activity assays (DPPH radical scavenging activity, reducing power and β-carotene bleaching), indicating that these bioactive compounds contributed to the total antioxidant activity (Melgar et al., 2017). As it can be observed from Table 2, *Opuntia* spp. skin is also a good source of dietary fiber, and thus the insoluble fraction could bind to the PC affecting their release during the passage through the gastrointestinal tract.

Sánchez et al., 2014 studied the antibacterial activity of cladodes from eight cultivars of cactus pear against *Campylobacter jejuni, Vibrio cholera, and Clostridium perfringens* (Sánchez et al., 2014). The minimum bactericidal concentrations (MBC) of cladodes were in the range of 1.1–1.25 mg/mL (*C. jejuni*), 4.4–30 mg/mL (*V. cholera*), and 0.8–16 mg/mL (*C. perfringens*). These authors also reported that total phenolic content (TPC) in cladodes ranged 1.49–3.80 mg GAE/100 g DM and the total flavonoids content in cactus cultivars were within 15.4 and 36.6 mg QE/g DW. From these results, (Sánchez et al., 2014) hypothesized that PC in cladodes composition with demonstrated antimicrobial activity were responsible for such effect. Likewise, the antibacterial and antifungal activity of *Opuntia* spp. skin was studied against eight pathogenic strains. It was found that *Opuntia* extracts showed a higher inhibition capacity against the pathogenic microorganisms in comparison to ampicillin and ketoconazole or bifonazole drugs. This was also attributed to the phenolic composition of *Opuntia* spp. by-products whose antimicrobial effect could be explained by their ability to be adsorbed to cell membranes, interact with enzymes, or deprive of substrate and metal ions (Melgar et al., 2017).

4. Fermentation of residues as a valorization strategy

Cactaceae species have been processed for food and non-food applications, including diverse fields such as construction, energy, or agriculture. Such potential opens several possibilities for innovation, in which fermentation might play a key role because of both the occurrence of a variety of fermentable carbohydrates and derivatives in the by-products derived from these plants (*e.g.*, poly and oligosaccharides, mucilage) and the diversity of microorganisms able to use them as carbon sources (*e.g.*, lactic acid bacteria (LAB), fungus, yeasts). Among the different species belonging to this family, *Opuntia* has been the most studied genus for fermentation applications due to its high content in dietary fiber although some examples in other species can be found.

4.1. Microorganisms used in fermentation and fermentation design

Opuntia fruit seeds, skin, and spines are the most common residues arising from the use of pulps to prepare juices and other food products. Skin and spines are rich in mucilages, hydrocolloids that can be employed as thickeners and be fermented by microorganisms. In addition, the fragility and ease deterioration of *Opuntia* fruits (*e.g.*, almost neutral pH and high availability of carbon sources) may limit the large-scale marketing. Therefore, their fermentation with appropriate microorganisms appears as an appropriate strategy to add them value. Besides contributing to environmental sustainability, fermentation of *Opuntia* residues enables the release of many nutritionally relevant compounds, making them more bioaccessible and thus, bioavailable. In this regard, different species of lactobacilli and bifidobacteria can release polyphenols. Likewise, dehydrated skin from *Opuntia* has been used as substrate of fermentation, leading to products employed in animal feed. Tripodo et al., 2002 used skin and juices as substrates to produce food grade yeasts (*Saccharomyces cerevisiae*) and animal feed. Using *Geotrichum candidum* on these substrates allowed increasing the protein content of the feedstuffs up to 8.1 %. In addition, the digestibility of skin also increased as result of yeasts' fermentation (Tripodo et al., 2002). Skin and spines enable the production of the feeding of ruminants, stable for up to 21 days and with high content of fiber and non-fiber carbohydrates, soluble sugars, able to be fermented by LAB (cocci and bacilli) (T. C. do Santos et al., 2015; Todaro et al., 2020).

O. ficus-indica skin and spines were successfully used as carbohydrate feedstock to improve the production of baker's yeasts (Diboune et al., 2019). (Diaz-Vela et al., 2013) reported that skins from *O. indica* were suitable sources of carbon for fermentation using probiotic strains (*Pediococcus pentosaceus*, *Aerococcus viridans, Lacticaseibacillus rhamnosus*) that led to the increase of total fiber, which is an appropriate carbon source for LAB, also having prebiotic properties. Fermenting *Opuntia* spp. cladodes with strains of *Lactiplantibacillus plantarum* (CIL6, POM1 and 1MR20), *Levilactobacillus brevis* (POM2 and POM4), *Lactobacillus rossiae* 2LC8 and *Pediococcus pentosaceus* CILSWE5 enhanced the production of γ-amino butyric acid, the antioxidant, and immunomodulatory properties, also retaining the levels of ascorbic acid and carotenoids (Filannino et al., 2016).

On the other hand, the richness of cladodes in lignocellulosic residues and proteins convert them in substrates of great potential for the fermentation by aspergilli fungi without supplementation with nitrogen, minerals, and vitamins. Growing *Aspergillus niger* in cladodes led to an increase in the protein content and a reduction of cellulose, hemicellulose, and lignin, which facilitated their degradability and the production of bioethanol (de Souza Filho et al., 2016). Growing *Lactobacillus diolivorans* in cladode hydrolysates (inoculum 5 %) was comparable with that obtained in MRS at industrial level and using cladode hydrolysates as the only sugar source showed a 1,3-propanediol production close to that of a medium having only glucose as the sugar source. This supports using cladode hydrolysates to produce 1,3 propanediol in a sustainable and cost-effective manner (J. S. de Santana et al., 2021). In turn, growing *Candida utilis* in cladodes' hydrolysates from *O. ficus-indica* also improved the total protein content of the biomass product as result of the addition of yeasts proteins to cladodes (Akanni et al., 2015).

Moreover, fermentation has been also used as a valorization strategy in other Cactaceae species. Growing *L. acidophilus* LA-05 or *Bifidobacterium animalis* ssp. *lactis* BB-12 in red pitaya pulp increased the content and bioaccessibility and antioxidant activity of phenolics and flavonoids (*e.g.*, catechin, epigallocatechin gallate, procyanidin B2) as well as that of organic acids resulting from bacterial metabolism (Mora-Cura et al., 2017; Morais et al., 2019). In addition, supernatants of red pitaya pulps fermented with *L. plantarum, P. pentosaceus and L. pentosus* strains demonstrated strong antifungal properties against *A. niger* and *Cladosporium sphaerospermum*. These properties were ascribed to a higher content of PC, released in supernatants after fermentation (Omedi et al., 2019). Similarly, red pitaya pulps fermented with *L. plantarum* FBS05 showed inhibitory effect on *Escherichia coli, Salmonella Typhimurium, Pseudomonas aeruginosa* and *Staphylococcus aureus* (Muhialdin et al., 2020).

4.2. Application of fermentation

4.2.1. Production of enzymes

Enzymes are mostly produced when Cactaceae species are fermented with different genera and species of fungi. Solid-state fermentation of *O. ficus-indica* with *A. niger* potentiated the release of industrially relevant and stable xylanases, β-glucosidases (Tamires Carvalho dos Santos et al., 2018), amyloglucosidases (R. S. M. de Santana et al., 2012) and cellulases (Oliveira et al., 2001) in a cost-effective manner. In turn, the growth of *Acremonium* sp. from Antarctica in *O. ficus-indica* led to the production of extracellular proteases with promising biotechnological applications (Nascimento et al., 2015).

4.2.2. Aroma enhancement

Aroma compounds mostly result from the fermentation of *Opuntia* spp. with LAB and yeasts, especially when producing alcoholic beverages. The composition of volatiles is strongly determined by the species within the genus *Opuntia* employed and from the color, size, seed content, sugars, proteins, fats, pectins and non-volatile organic acid present in the fruits, which change during ripening. Such composition is different from that of other fruits because of the higher content of nonen-1-ols, which produce a melon-like flavor (Arrizon et al., 2006). Fermentation of *O. humifusa* with LAB led to an increase in the content of isorhamnetin, quercetin, total polyphenols, and total flavonoids. In addition, fermented extracts of *O. humifusa* increased the α-glucosidase inhibition activity, increased the overall sensory acceptability, the DPPH radical scavenging activity and the glucose tolerance (Park et al., 2021). Solid-state fermentation of *O. ficus-indica* with *Klyuveromyces marxianus* produced nine fruity aroma compounds, including alcohols, esters and aldehydes, ethyl acetate (responsible for the fruity aroma), ethanol and acetaldehyde being the major compounds produced (Medeiros et al., 2000).

Alcoholic fermentation of prickly pear juice from *O. hemifusa* with *Pichia fermentans* and *S. cerevisiae*, followed by malolactic fermentation with *Oenococcus oeni* led to the production of many aroma compounds, including ethyl acetate (etherial, fruity, sweet, grape), 2-methylpropan-1-ol (bitter), 3-methylbutyl acetate (fruity, particularly banana), ethyl hexanoate (fruity, strawberry, anise), isopentanol 3-methylbutan-1-ol (alcoholic, pungent, etherial, cognac, fruity, banana and molasse), ethyl octanoate (fruity, floral, green leafy, menthol, anise), 3,4-dimethylpentan-1-ol, ethyl decanoate (grape, fruity, particularly apple), ethyl dec-9-enoate (fruity, sweet), 2-phenylethyl acetate (sweet, honey, floral rosy, cocoa, and balsamic nuance) ethyl dodecanoate (fatty and fruity), 2-phenylethanol (sweet, honey-like, yeast-like, floral, spicy), octanoic acid and decanoic acid (Navarrete-Bolaños et al., 2013; Rodríguez-Lerma et al., 2011). Other authors fermented *O. hemifusa* with *Citrus junos* and *Psidium guajava* L, observing changes in the content of isoharmnetin, quercetin and total polyphenols and flavonoids, and a decrease in the concentration of hesperidin and naringin (Park et al., 2021).

4.2.3. Bioactive compounds production

The most studied bioactive properties of fermented *Opuntia* wastes (pulp, skin, cladodes, spines) are those associated with antioxidant and immunomodulatory properties through modulation of cytokine secretion, which opens several perspectives for innovation in the development of diverse products with health benefits (Barba et al., 2020). Lactic acid fermentation can increase the content of bioactive peptides, short chain fatty acids or polysaccharides, whereas the contents of sugar or antinutritional compound can decrease. During lactic acid fermentation, PC are converted into substances with increased biological value, and the fermented products are also sources of pre and probiotics, with well-known beneficial effects (Barba et al., 2020).

Fermentation of cladodes with *Lactiplantibacillus plantarum* and *Bacillus subtilis* was reported to enhance the production of nitric oxide, cytokines secretion, nuclear factor-κB (NF-κB) activity, and mitogen-activated protein kinase (MAPK) phosphorylation in RAW 264.7 cells, thus supporting a promising use as immunostimulatory therapeutics (Filannino et al., 2016; Hwang & Lim, 2017). In the same line, fermentation with *Leuconosctoc mesenteroides* markedly inhibited the inflammatory status of Caco-2/TC7 cells, maintaining the integrity of tight junctions and showed antioxidant properties (Di Cagno et al., 2016). Administration of *O. ficus-indica* fermented with *L. plantarum* to obese mice decreased the body weight gain, improved the insulin resistance, and reduced the hyperglycemia and hyperlipemia associated to obesity (Verón et al., 2019).

5. Trends and applications of Cactaceae family residues in the food industry

In recent years, technological applications of some species of cacti have been noted, as they constitute a good source of healthy food and natural food ingredients. As mentioned before, and due to its diversity and economic importance, one of the most studied genera of the Cactaceae family is *O. ficus-indica* which is abundant in dietary fiber and natural antioxidants. Their by-products, such as cladodes and fruits, may be suitable for inclusion in functional foods (Bensadón et al., 2010; El Kossori et al., 1998; Jiménez-Aguilar et al., 2015). Seeds of the *O. ficus-indica* varieties contained a significant amount of oil and unsaturated fatty acids (Chougui et al., 2013). Their peels can be incorporated into food products such as beverages, capsules, and colorants (Jiménez-Aguilar et al., 2015). However, by-porducts from other species of belonging to Cactaceae family have been tested for industrial applications in the food industry. Among them, *H. polyrhizus, H, undatus, Cereus jamacar* and *Pilosocereus gounellei* can be highlighted (Table 3).

Bakery is one of the food industries where cacti by-products have been used. Fortifying wheat flour with cladodes powder from *O. ficus-*

Table 3
Applications of Cactaceae family residues in the food industry.

Species	Product	Purpose	Result	Reference
Opuntia ficus-indica	Bakery	Increase dietary fiber and increase water absorbency in flour	Dough showed better functional properties	(Ayadi et al., 2009)
	Rice- and corn-based snacks	To fortify extruded products	Increase in the content of flavanols	(Moussa-Ayoub et al., 2015)
	Wine	To obtain high-quality fermented beverages	Produce a fermented product with a unique flavor and taste	(Rodríguez-Lerma et al., 2011)
	Edible films	To produce carboxymethyl cellulose (CMC) edible films	High concentration of aqueous extract and peel powder in CMC films increased the bioactive compounds content, antioxidant capacity	(Aparicio-Fernández et al., 2018)
	Kiwifruit	Packaging	The use of mucilage coating improved the quality of products such as firmness, ascorbic acid, pectin contents and flavor	(Allegra et al., 2016)
Hylocereus polyrhizus	Bread	Use of flour as a fat replacer	The formulated bread showed acceptable physical characteristics and sensory response	(M Utpott et al., 2018)
	Ice cream	To enhance the antioxidant properties of ice cream	Increased in color acceptability and functional properties	(Gengatharan et al., 2021)
	Ice cream	Use as a fat replacer	Reduced the fat content of ice cream and improved acceptability and viscosity	(Utpott et al., 2020)
	Beer	Intelligent packaging by incorporating betalains	Monitored the freshness of beverage	(Qin et al., 2020)
Cereus jamacaru	Bread	Fruit skin flour for bread formulation	More favorable taste and color	(Nascimento et al., 2015)
Pilosocereus gounellei	Cake	Partial replacement of wheat flour	The cake observed that formulations containing 20, 40 and 60 % of the flour of this species had greater acceptability	(da Silva, 2019)
Cereus jamacaru and *Opuntia ficus-indica*	Ice cream and yogurt	Better physical properties and development of by-products	The formulation showed desirable physicochemical properties and high content of vitamin C	(de Fidelis, 2015)

(*continued on next page*)

Table 3 (*continued*)

Species	Product	Purpose	Result	Reference
Hylocereus undatus	Fruit juice	To produce lacto-fermented dragon fruit juice with high biological activity	Improved the functional properties, consumer acceptability and shelf life	(Muhialdin et al., 2020)

indica increased dietary fiber content, resulting in increased water absorbency in flour and altered properties of the dough. The cladodes powder increased dough and cake tenacity and considerably decreased their elasticity. According to the baking test, cladodes incorporation resulted in a significant change in cake quality and aspect and it also influenced the cake's crust color and tone (Ayadi et al., 2009). Cakes made with cladodes flour scored poorly on sensory evaluation compared to control cakes except when it was 5 % of total flour content (Ayadi et al., 2009; de Waal et al., 2015). The same results were obtained for bread using cladode flour mixed with whole wheat flour (Msaddak et al., 2017). In another study, 10 % flour from the *Cereus jamacaru* fruit skin was used for producing a bread product more appealing, flavorful, and with improved color (M. A. G. do Nascimento, 2014). The loaf bread flour from *Hylocereus polyrhizus* skin resulted in low specific volume and lightness value and high redness and yellowness values. It showed higher crumb and crust firmness, integrity, plasticity, and gumminess with excellent sensory response (M Utpott et al., 2018). Cookies and carrot cakes made with cladode flour replaced with respectively 10 % and 25 % of flour resulted in acceptable taste and texture (de Waal et al., 2015). Cake formulated with specific percentages of *Pilosocereus gounellei* powder showed high acceptance (C. E. da Silva, 2019).

Cacti have been also used in ice cream and yogurt production. Some studies have been conducted in line with this concept. Studying yogurt formulations based on adding the pulp or peel of *C. jamacaru* and *O. ficus-indica* showed the highest percentage of soluble solids, pH, total acidity, and content of vitamin C (de Fidelis, 2015). *O. ficus-indica* is an excellent alternative to produce ice cream due to its state of acidity, sugary taste, aspects of nutrition, and colors. Adding the pulp to ice cream produced a very suitable product, so it would be feasible to produce *O. ficus-indica* ice cream on a large industrial scale (El-Samahy et al., 2009). The ice creams made from *C. jamacaru* and *P. gounellei* pulp are technically suitable for manufacturing. Overall, all formulations demonstrated good sensory acceptability. Gengatharan et al., 2021 reported that betacyanins from *H. polyrhizus* act as a functional natural colorant that can be used in ice cream, increasing the color acceptability of the product (Gengatharan et al., 2021). Using *H. polyrhizus* skin flour in another study reduced the fat content of ice cream and improved acceptability and viscosity (Utpott et al., 2020). Juice concentrates from *O. ficus-indica* had the potential for using in ice cream or yogurt preparations as a proper coloring aliment (Moβhammer et al., 2006). *O. ficus-indica* juice is a convenient way to consume the fruit. However, because of its high pH value, juice requires a stabilization treatment to preserve its microbiological quality (Barba et al., 2017). A study has recently assessed clarifying effects on *O. ficus-indica* fruit juice composition. The results showed that the microfiltration (MF) and ultrafiltration (UF) processes did not impact soluble solids, pH, or acidity (Cassano et al., 2010). Fermentation of *H. undatus* juice with *Lactobacillus plantarum* showed high potential for being marketed as a functional drink. Its antibacterial activity was significantly improved by fermentation. Also, the antioxidant activity of fermented juice was higher than fresh juice. This study showed that consumers highly accepted fermented juice with fresh fruit and had a low microbial load while retained a steady shelf life (Muhialdin et al., 2020).

Sarkar et al., 2011 reported that the utilization of prickly pear fruit solids mixed with rice flour can improve the quality of extruded products (Sarkar et al., 2011). Incorporating *O. ficus-indica* peel acquired during processing with rice or maize flour could be used to produce cereal-based snacks high in flavanols (Moussa-Ayoub et al., 2015). It was found that the improved *O. ficus-indica* snacks had a more significant nutritional effects than either the rice-based snacks or the corn-based snacks. Moreover, the snacks obtained by this process were well received by consumers. There was also a significant increase in the amount of β-carotene, improving both polyphenolic content and antioxidant activity (Namir et al., 2017). Cacti also have the potential to use them in the wine and beer industry. A traditional method of fermenting *O. ficus-indica* juice provides low-alcohol beverages, which can be further processed into spirits and vinegar by a subsequent acetic fermentation (FAO, 2013). In a different study, a selected mixed culture *(P. fermentans and S. cerevisiae*) for the fruit of prickly pears fermentation produced a wine with distinct flavor and aroma characteristics. This study showed the existence of major volatile compounds essential for a delicate wine flavor (Rodríguez-Lerma et al., 2011). de Waal et al. (2015) reported that fermented beer made from maize or sorghum was produced to replace 25 % of the flour with cladode powder of *O. ficus-indica* (de Waal et al., 2015).

Food Packaging is one of the essential activities in food industry where cacti can play an important role. Novel food packaging films were manufactured by adding betacyanin-rich *H. polyrhizus* peel extract into starch/polyvinyl alcohol. These films are also used as intelligent packaging to monitor the freshness of protein-rich animal foods (Qin et al., 2020). Biodegradable food packaging materials combined with beneficial antioxidant combinations can be produced from *O. ficus-indica* peel. The addition of red prickly pear peel powder and its aqueous extracts significantly impacted the physical and antioxidant features of carboxymethyl cellulose (CMC) palatable films. The developed palatable films showed the existence of betalains and PC (Aparicio-Fernández et al., 2018). Mucilage from *O. ficus-indica* and *O. elatior* has been used for several industrial applications. Using this biopolymer as packaging to ensure food safety and quality will extend new opportunities and bring new trends to the food packaging market. Whether used as palatable film and coating, the use of cacti mucilage could also be economically profitable due to its low price, accessibility, and usefulness when used as primary packaging for food products and because of its advantageous effects could be used for packaging applications in the future (Gheribi & Khwaldia, 2019).

6. Conclusions

Cactaceae family comprises different genus of succulent plants adapted to cope with severe environmental conditions, including high temperatures, drought, and poor nutrient availability. Among its four subfamilies, Cactoideae and Opuntioideae are the most representative with *Hylocereus* and *Opuntia* as the most known genera. The residues from processing Cactaceae species can be considered as a source of bioactive compounds, namely phenolic compounds (hydroxycinnamic and hydroxybenzoic acids, flavonoid glycosides, tannins, coumarins, anthocyanins, and stilbenes), alkaloids (isoquinoline and phenethylamine derivatives), terpenoids (triterpenoids, phytosterols, and carotenoids) and other compounds such as fatty acids, tocopherols, or polysaccharides (mucilage). However, it has been estimated that this discarded biomass has a higher content of dietary fiber than their corresponding commercial edible parts so they can be considered as excellent substrate for fermentation. The content of dietary fiber depends on different factors such as the part of the plant, cultivar, geographical location, or maturity stage, but their health benefits have been associated to both soluble and insoluble dietary fiber. Different microorganisms can be used for fermentation of residues, but lactic acid bacteria should be highlighted. At last, Cactaceae residues have been exploited for the formulation of new products of the food industry mainly bakery and dairy products, but also fermented drinks and food packaging systems. Taking all together, Cactaceae species could be exploited for different industrial sectors including food, technological, pharmaceutical, and chemical applications because of their high content in fiber and active compounds. Nevertheless, studies are limited to few species and more research is still needed in terms of using fermentation as a valorization strategy.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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