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Review

The genus *Datura* L. (Solanaceae) in Mexico and Spain – Ethnobotanical perspective at the interface of medical and illicit uses

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ABSTRACT

Ethnopharmacological relevance: The different species of the genus *Datura* have been used traditionally by some pre-Columbian civilizations, as well as in medieval rituals linked to magic and witchcraft in both Mexico and Europe. It is also noteworthy the use of different alkaloids obtained from the plants for medicinal purposes in the treatment of various groups of diseases, especially of the respiratory and muscularskeletal systems.
Aim of the study: A review of the ethnobotanical uses of the genus *Datura* in Mexico and Spain has been conducted. We focus on the medicinal and ritualistic uses included in modern ethnobotanical studies, emphasizing the historical knowledge from post-colonial American Codices and medieval European texts. *Datura's* current social emergency as a drug of recreation and leisure, as well as its link to crimes of sexual abuse is also considered. The work is completed with some notes about the distribution and ecology of the different species and a phytochemical and pharmacological review of *Datura* alkaloids, necessary to understand their arrival in Europe and the ethnobotanical uses made since then
Materials and methods: A literature review and compilation of information on traditional medicinal uses of the genus has been carried out from the main electronic databases. Traditional volumes (codices) have also been consulted in libraries of different institutions. Consultations have been made with the National Toxicological Services of Spain and Mexico for toxicological data.
Results: A total of 118 traditional uses were collected in both territories, 111 medicinal ones to be applied in 76 conditions or symptoms included in 13 pathological groups. Although there are particular medicinal uses in the two countries, we found up to 15 similar uses, of which 80% were previously mentioned in post-Colonial American codices. Applications in the treatment of asthma and rheumatism are also highlighted. Apart from medicinal uses, it is worth noting their cultural and social uses, in the case of Mexico relating to diseases such as being scared, astonishment or falling in love, and in the case of Spain, as a recreational drug and lately, for criminal purposes.
Conclusions: This review highlights the variety of uses traditionally given to the different species in both territories. The fact that most of the coincident or similar uses in both countries also appear in the classical codices can be found an example of the flow, not only of the plants from America to Europe, but also of their associated information. It is also relevant that particular uses have derived in both countries, reflecting the difference in the cultural factors and traditions linked to rituals and cultural practices. Finally, the significant growth of *Datura* consumption in recent years as a drug of leisure and recreation, as well as in crimes of sexual submission, should be considered as research of maximum relevance in the field of forensic botany and toxicology.

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1. Introduction

The Solanaceae family taxonomic classification has varied depending on which genera are included (about 90 in D'Arcy, 1979) and the subfamilies and tribes divisions (Wettstein, 1895; Bentham, 1876; Baehni, 1946; D'Arcy, 1975).

In recent years the genus *Datura* L. has been considered, with *Brugmansia* Pers. and *Iochroma* Benth., to form the *Datureae* Tribe of the Solanaceae family (Olmstead et al., 2008; Mace et al., 1999).

So the genus consists of 14 species and several hybrids, distributed in three sections: *Dutra* Section (*D. discolor* Bernh*., D. innoxia* Mill. (see TROPICOS, 2017 for the nomenclature conflict with the illegitimated *D. inoxia* Mill.)*, D. kymatocarpa* A.S. Barclay*, D. lanosa* Barclay ex Bye*, D.metel* L.*, D. pruinosa* Greenm.*, D. reburra* A.S. Barclay*, D. wrightii* Regel, all native to Mexico, *D. leichhardtii* F. Muell. ex Benth. endemic to Australia and *D. velutinosa* V.R. Fuentes, endemic to Cuba); *Datura* Section, with three species (*D. ferox* L.*, D. quercifolia* Kunth and *D. stramonium* L.) and the *Ceratocaulis* Section with only the species *D. ceratocaula* Ortega (Avery, 1959, Luna-Cavazos et al., 2009). However, recent studies on molecular phylogeny reconsider this taxonomy and identify two subgroups in the *Datureae* subtribe: one with two species of *Brugmansia* Pers., and the other with 13 species of *Datura* (Bye y Sosa, 2013). The genus *Datura* is, in turn, composed of two groups: the first with section *Ceratocaulis* with only the species *D. ceratocaula*; and the second comprising a conglomerate of the other species distributed into two sections: the section *Datura*: *D. arenicola* Gentry ex Bye & Luna-Cavazos*, D. discolor, D. ferox, D. kymatocarpa, D. leichhardtii. D. quercifolia* and *D. stramonium*, and the polyphyletic section *Dutra*, with *D. innoxia, D. lanosa, D. metel, D. reburra* and *D. wrightii* (Bye and Sosa, 2013). In this way, the three classical sections are validated, but the species they include vary between the *Datura* and *Dutra* sections. In addition, *D. pruinosa* (accepting *D. leichhardtii* subsp. pruinosa (Greenm.) A.S. Barclay ex K. Hammer) and *D. velutinosa* (synonymous of *D. innoxia*) taxa are reorganized. On the other hand, the consistency of the newly validated taxon *Datura arenicola* Gentry ex Bye & Luna-Cavazos (the accepted name of the taxon, not the invalidated *D. arenicola* Gentry ex D.R.A. Watson, Watson, 2013, cf. TROPICOS, 2017) is recognized at molecular level. It is this taxonomic treatment (Bye and Sosa, 2013) that is followed in this article.

The origin and naturalness of *Datura* species is also currently controversial. Some studies have mentioned the presence of *Datura* in Asia and Europe in the pre-Columbian periods (particularly *D. metel*; Rätsch, 1998, Geeta and Gharaibeh, 2007, Rivera and Obón, 1991, but also *D. ferox*, Haegi, 1976). Based on classical Arabic (9th to 14th centuries CE) and Indian (3rd C BCE to 4th C CE) texts and on the analysis of some sculptures from India, Geeta and Gharaibeh (2007) concluded that some *Datura* species originated in the Old World. The presence of these plants (particularly *D.* metel and *D. stramonium*) in the Old World in ancient times has even been pointed out as an evidence for transoceanic contacts between America and the Old World before Columbus (Soreson, 2005). Significantly perhaps the genus name *Datura* has a Sanskrit origin from the word *dhattūra* (or *dhatura*) found in several classical texts (applied for *D. metel*; Rätsch, 1998, Geeta and Gharaibeh, 2007; Gallego, 2012). Nevertheless, this name was first used by Linnaeus (1737a) to replace the genus name *Stramonium*, previously used by Tournefort (1694), and was explained in the *Hortus Cliffortianus* (Linnaeus, 1737b) “as the future participle of the verb to give” (Gallego, 2012), in which an Indian origin is also stated (“*crescit in india Occidentali; at naturalisata nunc ubbique per Europam*” Sic!). However, studies on molecular phylogeny of the species have confirmed their American origin. Mexico and the south-west United States were established as the main center of origin and evolution of the genus, and therefore, the center of diversity (e.g. Symon and Haegi, 1991, Daunay et al., 2007, Dupin, 2013), including *D. metel* (Luna-Cavazos et al., 2009). Accepting this phylogenetic theory, many authors claim that some of the species, such as *D. stramonium*, *D. metel* and *D. innoxia,* were transported to Asia and Europe after post-European contact (f.i., Gallego, 2012; Symon and Haegi, 1991; Flora of China, 2017). For this reason, species from the *Datura* genus are considered today as cosmopolitan and naturalized in many regions with tropical and temperate climate conditions.

At the botanical level, the genus is formed of annual herbs and perennial shrubs, generally unarmed (with the exception of the fruit), and pubescent or glabrescent. The stems are erect and branched, with terminal branches welded to the petiole of the leaf. Basal leaves are usually simple or scattered, while those of the terminal branches are usually opposite or subopposed, petiolate. The actinomorphic flowers, hermaphrodite, without bracts and short-pedicellated, form an inflorescence reduced to a single flower, axillary. The corolla may be tubular or infundibuliform, white or more or less stained with violet, with longitudinal folds and acuminate lobes. The androceus, inserted in the tube of the corolla, can have all 5 stamens of equal length or 2 (3) slightly longer. Some species, such as *Datura stramonium*, produce flowers with a variation in the anther-stigme distance that has been shown to influence the outcrossing ratio, which may affect the number of fruits, seeds per fruit and seeds per plants (Bello-Bedoy and Núñez-Farfán, 2010). The ovary is covered with lanceolate or triangular-lanceolate epidermal extensions that become spinescent in fructification (aculeolate). The fruit is a bilocular capsule, or rarely tetralocular, dehiscent, containing reniform seeds, foveolate (Gallego, 2012).

From an ecological perspective, the genus *Datura* typically grows in nitrogen-rich soils and disturbed habitats, although one species, *Datura ceratocaula*, is semiaquatic (Kariñho-Betancourt et al., 2014). As a colonizer of open sites, the species can mainly be found in unstable habitats in areas perturbed by human activity, such as near roads, constructions, dwellings and domestic animal corrals (Bye et al., 1991). The distribution of species is relatively well known, particularly the distribution of Central American and South American species (see distribution maps for species of the *Dutra* section in Luna-Cavazos et al., 2009). Since most species of *Datura* are native to Mexico, they are well adapted to xeric conditions. In Mexico, the Balsas River Basin is one of the biogeographic regions with the highest species richness in the world, and it is considered to be the center of diversity for the *Datura* genus (Bye and Sosa, 2013).

All *Datura* species contain tropane alkaloids: organic nitrogenated bicyclic compounds which derive from the secondary metabolism of some plants. This group of alkaloids is shared with other genera of the Solanaceae family such as *Brugmansia, Atropa, Mandragora, Physallis, Withania*, etc. (Bruneton, 2001a). In addition to in Solanaceae, they are also present in some genera of families such as Erythroxylaceae, Brassicaceae, Convolvulaceae, Olacaceae, Proteaceae and Rhizophoraceae (Grynkiewicz and Gadzikowska, 2008; Dräger, 2004; Griffin and Lin, 2000; Bruneton, 2001a; Evans, 2008). Hyoscyamine and hyoscine (also known as scopolamine) stand out among the major tropane alkaloids of the genus (Berkov et al., 2006; Dugan et al., 1989; Friedman, 2004).

The alkaloid content of the genus is the reason why the different species have had and still continue to have an important medicinal use in some countries (Grynkiewicz and Gadzikowska, 2008; Gaire, 2008; Gaire and Subedi, 2013; Figueroa-Morales, 2008). Species of *Datura* are used in many ways: as an antiparkinsonian (Poewe and Granata, 1997), antiepileptic (Peredery and Persinger, 2004), antispasmodic (Prabhakar and Nanda Kumar, 2006), antitussive (Dafni and Yaniv, 1994), medicine against facial neuralgia, head and ear pain (Ortíz de Montellano, 1980; Gorsi and Shanzad, 2002; Hussain et al., 2006; Ayyanar and Ignacimuthu, 2011), antiasthmatic (Pretorius and Marx, 2006), antirheumatic (Miraldi et al., 2001a), antimicrobial (Eftekhar et al., 2005), antifungal (Mdee et al., 2009) anti-inflammatory (Sonika et al., 2010), anthelmintic (Rajbhandari, 2001), and as an antidote in cases of cholinesterase poisoning (Bye et al., 1991). In addition, some in vitro studies point to the antibacterial activity of extracts of *D. innoxia* and *D. stramonium* against some Gram + bacteria (Eftekhar et al., 2005), *Klebsiella pneumoniae* and *Staphylococcus aureus* (Shagal et al., 2012), and some strains of *Vibrio cholera* and *V. parahaemolyticus* (Sharma et al., 2009). The anticancer effects of *D. metel* against human epidermal carcinoma have also been reported (Balachandran and Rajgopal, 2005), whereas the withanolides present in the seeds of *Datura metel* have been shown to have antiproliferative activity against human gastric adenocarcinoma and potential immunosuppressive effects (Yang et al., 2014). *Datura lanosa* extracts have cytotoxic activity in carcinomas of colon, breast and lung (Gutiérrez-Lugo et al., 1996).

In Europe, the strength and anticholinergic properties of tropane and its pharmaceutical derivatives have led to the use of atropine sulfate in injectable solutions (European Pharmacopoeia, 2016). These solutions have been used in many remedies: in promoting auriculoventricular or atrioventricular block, in preventing and treating myocardial infarction, in pre-anesthesia for the symptomatic treatment of acute pain and functional disorders of the digestive and biliary tracts, as an antidote to acute anticholinesterase poisonings, as parasympathomimetic drugs, and for treatment of Parkinson (Giugni and Rodriguez-Cruz, 2016). In addition, atropine sulfate eye drops are used for treating inflammation of the uvea and to promote cyclopegia in cases of accommodative strabismus. Furthermore, scopolamine hydrobromide has been used to treat Parkinson's and painful spasms. However, it is most commonly used to prevent motion sickness. It is not the aim of this synthesis to detail these activities or to specify the contraindications. For this information, the reader should seek out specialized literature (European Pharmacopoeia, 2016; U.S. Pharm. http://www.usp.org/).

Nevertheless, the possible side effects of the plants and plant extracts are well known (Jäger, 2015; Evans, 2008). The presence of alkaloids is also responsible for the use of these plants in rituals of shamanism and witchcraft in many places around the world (Carod-Artal, 2015; Gaire and Subedi, 2013). At the same time, their use has also led to some tragic events (Ertekin et al., 2005; Jiménez-Mejías et al., 1991; Oberdorfer et al., 2002). A small difference between doses of tolerance and highly toxic doses has been the cause of overdose poisoning (Arnett, 1995). This has led to fatal consequences, sometimes by accidental consumption (Gaire and Subedi, 2013), and in other cases by consumption as a recreational drug (Iglesias-Lepine et al., 2012).

The above information highlights the medicinal potential and importance of different *Datura* species, their particular phytochemistry and powerful biological activity on organisms. In part, the medicinal applications come from the traditional use of different species by the Mesoamerican pre-Columbian cultures, the center of origin for most of the species; while other new uses are the result of social habits and customs in Western cultures. In this work we make a historical review of the medicinal and ritualistic uses of the different species of *Datura* in Mexico and Spain, with emphasis on the traditional uses referenced in both the post-colonial Codices and the medieval European texts, as well as those included in modern ethnobotanical studies. *Datura* emergence as a drug for recreation and leisure use is a social emergency, and its link to crimes of sexual abuse is also considered. Our work finishes with some notes about the distribution and ecology of the different species and a phytochemical and pharmacological review of *Datura* alkaloids, necessary to understand their arrival in Europe and the ethnobotanical uses made since then.

2. Species ecology and distribution in Mexico and Spain

The most widely-distributed species in Mexico are *D. discolor* and *D. stramonium*, whereas the most restricted are *D. kymatocarpa* and *D. reburra*. Species *D. innoxia*, *D. lanosa*, *D. metel*, *D. pruinosa*, *D. wrightii*, *D. quercifolia* and *D. ceratocaula* are also native to Mexico (Luna-Cavazos et al., 2009; Luna-Cavazos and Bye, 2011). There is a trend in species distribution depending on a latitudinal and humidity gradient, from northwest to southeast. Along the north-south latitudinal gradient, the primary distribution is in the north (e.g. *D. quercifolia*, *D. lanosa*, *D. reburra* and *D. wrightii*), followed by taxa typical of central Mexico (i.e. *D. stramonium*, *D. pruinosa* and *D. ceratocaula*) and taxa found in the south-southeast (i.e. *D. kymatocarpa* and *D. metel*). Taxa differentiation is also detected from the northwest to southeast, starting with the driest and lowest conditions found in the Sonora, Baja California and the northern Pacific coast, and continuing to the east, south, and southeastern parts of the country, which are characterized by higher altitude and more humid conditions (Luna-Cavazos and Bye, 2011). Furthermore, *D. discolor* is found in the south-west of the USA and in northern Mexico (Baja California, Sonora, Tamaulipas to Colima and Yucatán), from sea level to 200 m above sea level. In these regions, this species grows together with coastal dune communities, behaving like a ruderal plant species (Shreve and Wiggins, 1964; Wiggins, 1980).

In some states of Mexico, the genus is well represented: six species are found in Oaxaca (*D. ceratocaula*, *D. discolor*, *D. innoxia*, *D. pruinosa*, *D. metel*, *D. stramonium*), and in Queretaro (*D. discolor, D.innoxia, D. metel, D. quercifolia, D. stramonium*). Five species are found in Sonora, Durango, Sinaloa and Nayarit (i.e. the northwest region; Rodriguez, 2004). There are also five species recognized in New Mexico, USA (*D. ceratocaula, D. innoxia, D. wrightii, D. quercifolia, D. stramonium*; Allred, 2004). In addition, several authors have documented the widespread distribution of *D. stramonium* and *D. innoxia* in Central America following human migrations and environmental changes (i.e. Nee, 1986, Espinosa and Sarukhán, 1997; Azcárraga, 2001; Calderón and Rzedowski, 2004, Hinton and Hinton, 1995, Medina and Rodriguez, 1993).

In Spain it is generally recognized that some species of *Datura* were introduced in the 16th century, by post-colonial explorers and conquerors (Sanz-Elorza, 2004), for ornamental and pharmacological purposes, or as botanical curiosities. Today these species are widely distributed throughout Spain (Sanz-Elorza et al., 2001; Sobrino et al., 2002), and they are considered to be invasive species in natural and cultivated areas (Sobrino et al., 2002; Cavero et al., 1999).

Gallego (2012) recognized four species of *Datura* in Spain. Three of these species, *D. ferox*, *D. innoxia* and *D. stramonium,* have been classified as naturalized in several European countries (Moore, 1972) and are widely distributed. In Europe all three exhibit the same ruderal and nitrophilous character, and are frequently present in tailings, ditches, gravel, fallows, margins of rivers and streams, on sandy and clay substrates (Gallego, 2012), and other land subjected to some degree of anthropic influence (Sanz-Elorza et al., 2001). These three species are traditionally included within several regional floras (Sanz-Elorza et al., 2008, 2009, 2011; Valdés, 1987; Negrillo, 2009). However, Gallego (2012) also included *D. wrightii*, which has recently been cited as an introduced species in several Iberian localities (Verloove, 2008), although it may have a more widespread distribution because of its ruderal character. All four species are often cited as invasive species in Protected Natural Areas such as Cabañeros, Doñana and the Atlantic islands of Galicia (Heredia, 2010), the Natural Parks of Aragonese Pyrenean (Villar et al., 2001), Cardeña and Montoro (Quero Fernández de Molina, 2007), Cazorla, Segura and Alcaraz (Pajarón and Escudero, 1993), and the Sierra of Baza (Navarro et al., 2007). According to Sanz-Elorza et al. (2004), *Datura stramonium* presents an expansive demographic trend, while *D. innoxia* has not yet reached its full potential distribution, and is possibly still in its expansion phase, a question worthy of further investigating by ecologists.

3. Phytochemistry and pharmacology of *Datura*

Variations in the composition of alkaloids within the genus *Datura* may be qualitative (relative proportions of alkaloids or quantitative (total alkaloid content) (Bruneton, 2001b). In fact, the concentration and type of tropane alkaloids have been used as a taxonomic criterion in chemotaxonomy studies (Doncheva et al., 2006; Teteny, 1987; Griffin and Lin, 2000). For instance, up to 66 different alkaloids have been isolated from some varieties of *D. stramonium* (Lousnasmaa and Tamminem, 1993; El Bazaoui et al., 2011), whereas up to 30 alkaloids have been extracted in *D. innoxia* (Bye et al., 1991). As previously mentioned, hyoscyamine (and

Table 1
Alkaloid concentration on different organs of *Datura* species. TA: Total alkaloids; n.d.: no data; J.S.: Juvenil stage; R.S.: Reproductive stage. If the organ is not indicated quantities are referred to the whole plant. References: a. Parr et al., 1990; b. Evans and Somanabandhu 1974; c. Evans and Wellendorf 1959; d. Ionkova et al. 1989; e. Lindequist 1992; f. Vitale et al. 1995; g. Evans and Treagust 1973; h. Berkov et al., 2006; i. Bye et al., 1991; j: Kariñho-Betancourt et al., 2014; k: El Bazaoui et al., 2011; z Rätsch, 1998.

Species	Organ and TA	Hyoscyamine (1)	Hyoscine (Scopolamine) (2)	Other alkaloids
Section *Datura*				
D stramonium L.	Roots 0.18-0.22% z	1053 µg/g fr. Wt root culture a (0.11%)	0 µg/g fr. Wt root culture a	Apoatropine (4) [(8-methyl-8-azabicyclo[3.2.1]octan-3-yl) 2-phenylprop-2-enoate], tropine (5) [(1*S*,5*R*)-8-methyl-8-azabicyclo[3.2.1]octan-3-ol],
	Leaves J.S. 0.041% j Leaves R.S. 0.14% j Leaves 0.25-0.36% z Flowers up to 0.61% z Seeds up to 0.66%. z Dried leaves and seeds 0.1-0.6% z	J.S. 0.84 µg/g wt j R.S. 5.30 µg/g wt j	J.S. 161 µg/g wt j R.S. 634 µg/g wt j	belladonnine (6) [bis(8-methyl-8-azabicyclo[3.2.1]octan-3-yl) (1*S*,4*S*)-4-phenyl-2,3-dihydro-1H-naphthalene-1,4-dicarboxylate], hyoscyamine-N-oxide, solanine (7) [(3β)-Solanid-5-en-3-yl 6-deoxy-β-L-mannopyranosyl-(1- > 2)-[β-D-glucopyranosyl-(1- > 3)]-β-D-galactopyranoside], 3α,6β-ditigloyloxy-7β-hydroxytropane, 3α-tigloyoxytropane (8) (= tigloyltropeine) [(3-endo)-8-Methyl-8-azabicyclo[3.2.1]oct-3-yl (2E)-2-methyl-2-butenoate], 3,7-dihydroxy-6-propionyloxytropane, 6,7-dehydro-3-tigloyloxytropane, 3-tigloyloxy-6,7-epoxytropane, and many more different ones h,j,k,z
D. quercifolia Kunth	Roots	419 µg/g fr. Wt root culture a (0.042%)	Traces root culture a	Tropine, atropine (3) [[(1*R*,5*S*)-8-methyl-8-azabicyclo[3.2.1]octan-3-yl] 3-hydroxy-2-phenylpropanoate], solanine j
	Leaves J.S. 0.0038% j Leaves R.S. 0.01% j	J.S. 0.7 µg/g wt j R.S. 11.14 µg/g wt j	J.S. 30.89 µg/g wt j R.S. 71.42 µg/g wt j	
D. ferox L	Roots	849 µg/g fr. Wt root culture a (0.085%)	43 µg/g fr. Wt root culture a (0.004%)	3α- tigloyloxytropane, 3-phenylacetoxy-6β,7β-epoxytropane (= 3-phenylacetoxyscopine),
	Leaves J.S. 0.02% j Leaves R.S. 0.12% j	J.S. 17.83 µg/g wt j R.S. 125 µg/g wt j	J.S. 164.59 µg/g wt j R.S. 1014.8 µg/g wt j	apohyoscine (9) (=aposcopolamine) [(1*R*,2*R*,4*S*,5*S*,7*s*)-9-Methyl-3-oxa-9-azatricyclo[3.3.1.02,4]non-7-yl atropate], 7β-hydroxy-6β-propenyloxy-3α-tropoyloxytropane, traces of 7β-hydroxy-6β-isovaleroyloxy-3α-tigloyoxytropane, hygrine (10) [1-[(2*R*)-1-methylpyrrolidin-2-yl]propan-2-one], 3-phenylacetoxy-6β,7β-epoxytropane (= 3-phenylacetoxyscopine) f
Section *Dutra*				
D. discolor Bernh.	Entire plant 0.13 - 0.49% b	Ratio H/S: 1/1 b	Ratio H/S: 1/1 b	ND
	Dried herbage 0.17% b	Present b	0.08% dry weight b	Apohyoscine, norhyoscine (11) [(7(*S*)-(1alpha,.2beta,4beta,5alpha,7beta))-3-Oxa-9-azatricyclo(3.3.1.02,4) non-7-yl (hydroxymethyl)phenylacetate], meteloidine (12) [[(6*R*,7*S*)-6,7-dihydroxy-8-methyl-8-azabicyclo[3.2.1]octan-3-yl] (E)-2-methylbut-2-enoate], tropine (in dried herbage) b
	Dried roots 0.31% b	Present b	Mayor compound b	Norhyoscine, littorine (13) [[(1*S*,5*R*)-8-methyl-8-azabicyclo[3.2.1]octan-3-yl] (2*R*)-2-hydroxy-3-phenylpropanoate], meteloidine, 3α,6β-ditigloyloxytropane, 3α,6β-ditigloyloxytropane-7β-ol, cuscohygrine (14) [1,3-bis(1-methylpyrrolidin-2-yl)propan-2-one], tropine, and c-tropine b
	Leaves J.S. 0.019 % j Leaves R.S. 0.18 % j	J.S. 1.13 µg/g wt j R.S. 13.58 µg/g wt j	J.S. 183.76 µg/g wt j R.S. 1758 µg/g wt j	Atropine, tropine, solanine j
D. innoxia Mill.	Roots	486 µg/g fr. Wt root culture a (0.049%)	110 µg/g fr. Wt root culture a (0.001%)	Aboveground parts: Mainly hyoscine, with hyoscyamine f
	Seeds 0.3% c	0.21% c	0.09% c	Flowers with tyramine [4-(2-aminoethyl)phenol] f Stems with meteloidine f Roots with hyoscyamine, scopolamine, cuscohygrine, 3-tigloyloxytropane, 3-hydroxy-6-tigloyloxytropane, 6-hydroxyhyoscyamine, 6-tigloyloxyhyoscyamine [[3-[(2*S*)-3-hydroxy-2-phenylpropanoyl]oxy-8-methyl-8-azabicyclo[3.2.1]octan-6-yl] (E)-2-methylbut-2-enoate], and tropine d
	Leaves J.S. 0.022 % j Leaves R.S. 0.24 % j	J.S. 1.43 µg/g wt j R.S. 78.19 µg/g wt j	J.S. 186.34 µg/g wt j R.S. 2266 µg/g wt j	Atropine, tropine, solanine j
D. kymatocarpa A.S. Barclay	Leaves J.S. 0.049 % j Leaves R.S. 0.35 % j	J.S. 0.56 µg/g wt j R.S. 3.22 µg/g wt j	J.S. 264.02 µg/g wt j R.S. 2490 µg/g wt j	Atropine, tropine, solanine j
D. pruinosa Greenm.	Dried herbage 0.16% g	Present g	Present g	Apoatropine, noratropine (15) [8-azabicyclo[3.2.1]octan-3-yl 3-hydroxy-2-phenylpropanoate], norhyoscine, apohyoscine, littorine, tigloidine (= 3α-Tigloyloxytropane) [(8-methyl-8-azabicyclo[3.2.1]octan-3-yl) (E)-2-methylbut-2-enoate], meteloidine, tropine g
	Leaves J.S. 0.017 % j Leaves R.S. 0.028 % j	J.S. 1.83 µg/g wt j R.S. 5.88 µg/g wt j	J.S. 59.05 µg/g wt j R.S. 85.25 µg/g wt j	Atropine, tropine, solanine j
D. reburra A.S. Barclay	Leaves J.S. 0.022 % j Leaves R.S. 0.058 % j	J.S. 2.86 µg/g wt j R.S. 19.1 µg/g wt j	J.S. 197.47 µg/g wt j R.S. 499.47 µg/g wt j	Atropine, tropine, solanine j

(*continued on next page*)

Table 1 (*continued*)

Species	Organ and TA	Hyoscyamine (1)	Hyoscine (Scopolamine) (2)	Other alkaloids
D. wrightii Regel	Roots	820 µg/g fr. Wt root culture a (0.08%)	15 µg/g fr. Wt root culture a (0.002%)	Atropine, tropine, solanine j
	Leaves J.S. 0.013 % j	J.S. 32.43 µg/g wt j	J.S. 99 µg/g wt j	
	Leaves R.S. 0.191 % j	R.S. 427.15 µg/g wt j	R.S. 1130 µg/g wt j	
D. leichhardtii F. Muell. ex Benth.	n.d.	n.d.	n.d.	n.d.
D. velutinosa V.R. Fuentes	n.d.	n.d.	n.d.	n.d.
D. lanosa Bye	Dried vegetative parts 0.52% or 0.41 to 0.69% i	1.25 Total 0.39% leaves 0.25% stems 0.22% fruits & immature seeds 0.39% Roots (as atropine, i)	1.32 Total 0.41% leaves 0.26% stems 0.23% fruits & immature seeds 0.41% Roots i	Apoatropine, apohyoscine, atropine, cuscohygrine, 3α,6β-ditigloyloxytropane, meteloidine, tropine, solanine i,j
	Leaves J.S. 0.03 % j	J.S. 8.67 µg/g wt j	J.S. 291.58 µg/g wt j	
	Leaves R.S. 0.173 % j	R.S. 13.81µg/g wt j	R.S. 1607 µg/g wt j	
D.metel L.	Roots 0.1-0.2 % e	561 µg/g fr. Wt root culture a (0.057%)	9 µg/g fr. Wt root culture a (0.001%)	Whole plant: meteloidine, norhyoscine, norhyoscyamine [8-azabicyclo[3.2.1]octan-3-yl (2*S*)-3-hydroxy-2-phenylpropanoate], 6-hydroxy-hyoscyamine (=anisodamine) [[(3*S*,6*S*)-6-hydroxy-8-methyl-8-azabicyclo[3.2.1]octan-3-yl] (2*S*)-3-hydroxy-2-phenylpropanoate], datumetine [8-Methyl-8-azabicyclo[3.2.1]oct-3-yl 4-methoxybenzoate], solanine e,j
	Leaves 0.5% e			
	Leaves J.S. 0.03 % j	J.S. 0.98 µg/g wt j	J.S. 186.28 µg/g wt j	
	Leaves R.S. 0.297 % j	R.S. 37.41 µg/g wt j	R.S. 2502 µg/g wt j	
	Flowers 0.1-0.8% e			
	Fruits 0.12% e			
	Seeds 0.2-0.5% e			
Section *Ceratocaulis*				
D. ceratocaula Ortega	Root	160 µg/g fr. wt h (0.016%)	70 µg/g fr. wt h (0.007%)	Atropine, tropine, solanine j
	Stem	420 µg/g fr. wt h (0.042%)	200 µg/g fr. wt h (0.02%)	Up to 34 more alkaloids and related compounds (see h)
	Leaves	470 µg/g fr. wt h (0.047%)	290 µg/g fr. wt h (0.03%)	
	Leaves J.S. 0.022 % j	J.S. 0.76 µg/g wt j	J.S. 187.61 µg/g wt j	
	Leaves R.S. 0.045 % j	R.S. 1.58 µg/g wt j	R.S. 219.05 µg/g wt j	
	Flowers	410 µg/g fr. wt h (0.041%)	340 µg/g fr. wt h (0.034%)	
	Seeds	250 µg/g fr. wt h (0.025%)	70 µg/g fr. wt h (0.007%)	

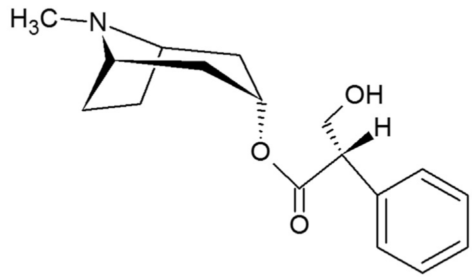
its racemic atropine) and hyoscine are the most interesting alkaloids from a pharmacological point of view. Hyoscyamine ($C_{17}H_{23}NO_3$; IUPAC name [(1*S*,5*R*)-8-methyl-8-azabicyclo[3.2.1]octan-3-yl] (2*S*)-3-hydroxy-2-phenylpropanoate) is an ester of the tropic acid, with a molecular weight of 289.3694 g/mol. Naturally in a levorotatory form, L- hyoscyamine is transformed when manipulated or when the plant is dried into a racemic mixture: DL-hyoscyamine [(+) and (−) isomers, sometimes denoted (±); Heinrich et al. (2012)], better known as atropine. Hyoscine (scopolamine; $C_{17}H_{21}NO_4$; molecular weight 303.353 g/mol and IUPAC name for (-)-Hyoscine: (1*R*,2*R,4S,*5*S*,7*s*)-9-Methyl-3-oxa-9-azatricyclo [3.3.1.02,4] non-7-yl (2*S*)-3-hydroxy-2-phenylpropanoate) is also an ester of the tropic acid but based on scopine. They both are competitive antagonists of choline esters or parasympathomimetic substances. Therefore, they inhibit the muscarinic receptors located at the peripheral level in organs innervated by parasympathetic postganglionic fibers, and also at the level of the central nervous system, producing an anticholinergic symptomatology.

Regarding the total alkaloids content in plants, it is known that concentrations are highly variable in certain species such as *D. stramonium* or *D. innoxia* (Rätchs, 1998), which causes considerable difficulty in establishing plant doses for traditional uses. Some studies have shown that atropine content in the seeds of *D. stramonium* can vary between 0.17 and 2.71 mg/g, while hyoscine content can vary between 0.12 and 0.69 mg/g (Friedman, 2004; Steenkamp al. et al., 2004). Variations in the composition and concentration of alkaloids can also exist between varieties of the same plant species, as well as between different parts of the plant. Thus, in *D. stramonium* var. *stramonium* and var. *tatula* up to 25 different alkaloids have been isolated, with the majority being 3α,6β-ditigloyloxy-7β-hydroxytropane, while in var. *godronii* it is hyoscyamine (Berkov et al., 2006; Doncheva et al., 2006). Changes have also been observed in tropane alkaloids concentration between inbred and outcrossed *D. stramonium* plants (Bello-Bedoy and Núñez-Farfán, 2010), and variations in the concentration of atropine in leaves that are eaten by specialized herbivores (Castillo et al., 2014). The location of the alkaloids also differs: in var. *stramonium* hyoscyamine is accumulated mainly in the leaves, as the atropine formed by racemization during the chemical extraction process, which includes the manipulation and desiccation of parts of the plants; in var. *godronii* it is more abundant in seeds (Miraldi et al., 2001a). Moreover, it has been found that the atropine and hyoscine content in *D. stramonium* depends on both the plant part and its developmental stage, with the highest concentrations of atropine found in the middle leaves of the stem and higher concentrations of hyoscine found in the apical leaves of young plants (Miraldi et al., 2001a). Stems of young plants may also concentrate higher amounts of tropane alkaloids than seeds (Miraldi et al., 2001b). The ontogenetic expression of the main tropane alkaloids has been studied, showing an increase in general alkaloid concentration in plants in the reproductive state in relation to those in the juvenile state, with ranges depending on the species (Kariñho-Betancourt et al., 2014). In that study, hyoscine and hyoscyamine (plus atropine) were found to exhibit the largest increases across the genus, and were dominant in leaf tissues. In general, for *Datura* and the related genera, alkaloid diversity is greater in the roots, since it is where biosynthesis occurs (Doncheva et al., 2006; Witte et al., 1987). Also several other studies have shown that the seeds contain higher amounts of alkaloids than the leaves (Gaire and Subedi, 2013; Gaire, 2008).

Therefore, the total range of alkaloids and their concentration in the species of the *Datureae* tribe is not clearly defined. Thus, while some authors consider that the species with the highest concentration of alkaloids are *D. stramonium*, *D. innoxia* and *D. ceratocaula* (Mace et al., 1999), others consider that the species from the sections *Datura* and *Ceratocaulis* have smaller alkaloid content (Lounasmaa and Tamminem, 1993). Since many of the phytochemical studies did not include information about the ontogenetic state of the studied plants, more in depth studies are needed to clearly determine the alkaloid concentration in different organs for different states of development in each Datura species. In an attempt to contribute to this matter, Table 1 shows the concentration of total alkaloids, as well as hyoscyamine and hyoscine, for the different species of *Datura*. Fig. 1 includes some of the main alkaloids of the genus.

The alkaloids are well-absorbed orally, this being their main route of administration used for different purposes, but other routes include intravenously, by inhaling and by the mucous membranes through liniments. Atropine and hyoscyamine have a similar activity, although hyoscyamine is more active. Both can penetrate the blood-brain barrier and cause disturbance of the central nervous system, although hyoscine does so more easily because of its oxygen bridge between carbon atoms 6 and 7. The competitive and reversible inhibition of acetylcholine binding to its receptors causes apparently sympathomimetic effects in the corresponding organs: at the cardiac level, increase of heart rate after a temporary bradycardia; vasodilatation occurs at the vascular level (especially in overdose); at the level of smooth fibers, relaxation and motor inhibition, decreased tone and intestinal peristalsis, paralysis of the urethra, etc. At the level of secretions, decrease of salivary, sweat, gastric, pancreatic, bronchial and lacrimal functioning occurs. At the ocular level, the inhibition of acetylcholine binding generates a mydriasis characteristic of paralysis of the iris contracting muscles, in addition to cyclopegia and an increase of intraocular pressure. It also has central effects since it interacts with the muscarinic receptors of this system. This causes excitement, agitation, disorientation, increased reflexes, hallucinations, delirium, confusion, and insomnia, especially at high doses (Bruneton, 2001a). Hyoscine also has parasympatholytic activity, although less marked especially at the level of the myocardium. However, it has clear activity at the CNS level with sedative, depressive, hypnotic, and amnesia-inducing properties, so it is commonly called "incapacitating". That is why hyoscine is used as an agent of "chemical submission" for criminal purposes.

The onset of the symptoms usually begins 30–60 min after ingestion and in severe cases of overdose an anticholinergic syndrome occurs, which manifests itself with symptoms such as extreme dry mouth, sweating, mydriasis, hypertension, hallucinations, tachycardia, urinary retention and, in the most severe cases, coma and (sometimes) death (Peris and Stübbing, 2006; Oberdorfer et al., 2002; Jiménez-Mejías et al., 1991). In some cases it is difficult to differentiate between these symptoms and those experienced after consumption of other psychedelic drugs which also cause similar symptoms. The difference is that *Datura* consumers do not have the feeling of being under the influence of a toxic substance, but instead perceive they are in a real scenario (Diker et al., 2007). We can add that in some studies, an extract from *D. ferox* has been found to have high affinity to the serotonin transporter (Jäger, 2015). Other symptoms have also been described, such as muscle weakness, drowsiness and loss of sensation, which is aggravated by the exposure to other uncontrollable risks such as performance of activities dangerous to physical integrity (Ertekin et al., 2005). Some authors propose the following mnemonic rule to remember the symptoms produced by poisoning by *Datura*: "blind as a bat, mad as a hatter, red as a beet, hot as a hare, dry as a bone, bowel and bladder lose their tone, and the heart runs alone" (Diker et al., 2007; Arnett, 1995). In case the intoxicated person can still receive treatment, gastric lavage and the administration of activated charcoal are recommended, these must be administered within 24 h after ingestion, since gastrointestinal peristalsis is reduced after this period (Diker et al., 2007; Domínguez-Fuentes et al., 2008). If sedation is present benzodiazepines are recommended (Peris and Stübbing, 2006) and, in the most severe cases, physostigmine (a cholinergic agonist) is used to alleviate the ancholinergic effects (Salen et al., 2003; Rumack, 1973). The half-life of oral hyoscine is short at 4.5 +/- 1.7 h (Putcha et al., 1989). Accurate data on its pharmacokinetics can be found in Renner et al. (2005) and Tian et al. (2015). On the other hand, atropine has a longer half-life at 6.7 h (Tian et al., 2015).



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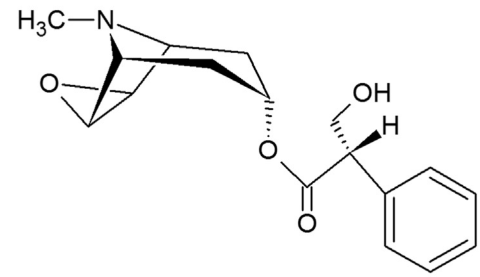

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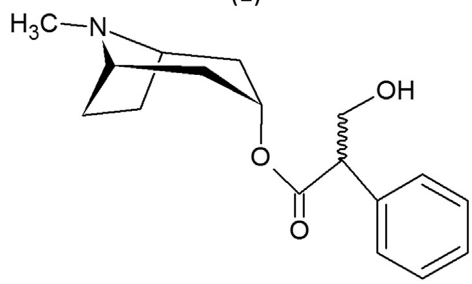

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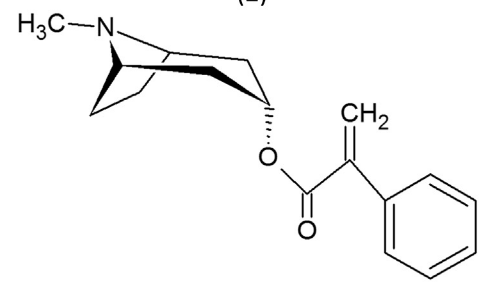

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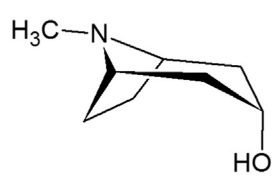

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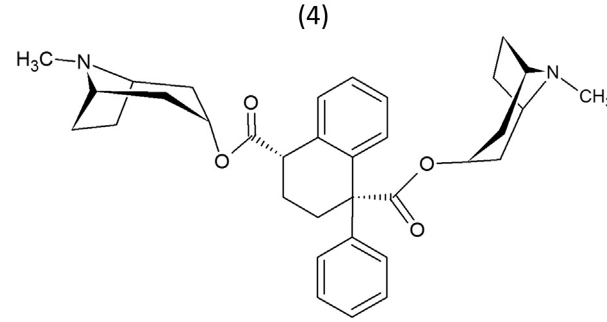

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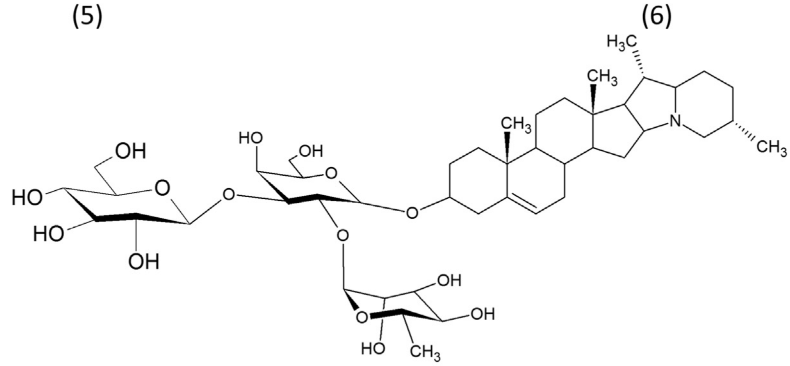

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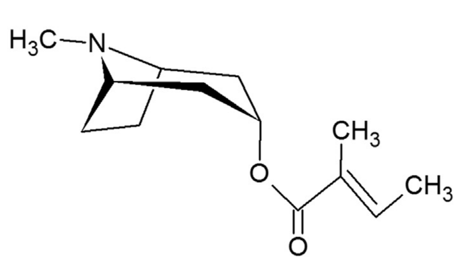

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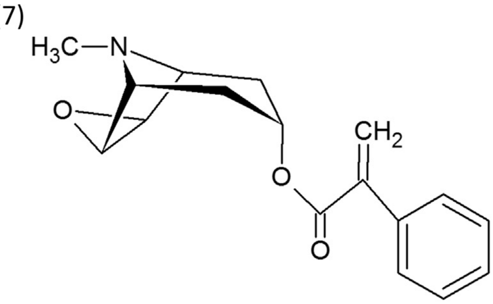

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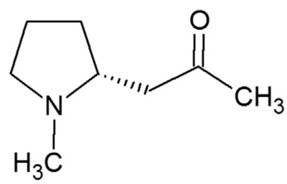
Fig. 1. Main alkaloids from *Datura* Species. Numbers are according to Table 1: hyoscyamine (1), hyoscine (scopolamine) (2), atropine (3), apoatropine (4), tropine (5), belladonnine (6), solanine (7), 3α- tigloyloxytropane (8), apohyoscine (9), hygrine (10), norhyoscine (11), meteloidine (12), littorine (13), cuscohygrine (14), noratropine (15).



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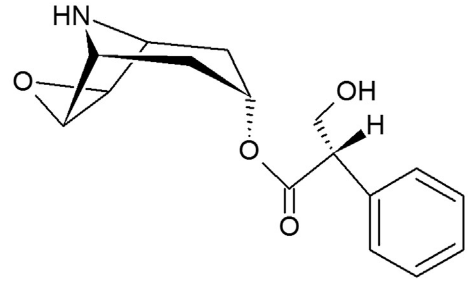

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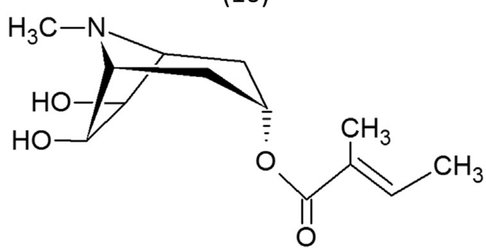

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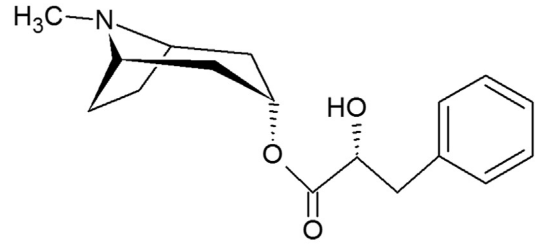

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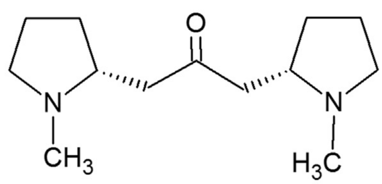

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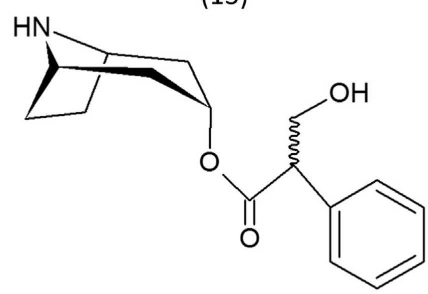

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Fig. 1. (*continued*)

4. Ethnobotanical review

4.1. Vernacular names

The extensive vernacular and nomenclature used to refer to different *Datura* species in Mexico reflects the widespread knowledge and use of these plants by different Mexican indigenous groups. *Toloache*, from the Nahuatl *toloatzin* ("to bow the head by the effect of sleep"), that is the main name known for *Datura innoxia* and used secondarily for *D. stramonium*, although it may also be applicable to other species (Figueroa-Morales, 2008; Aguilar et al., 1994). It is also known as *tlapatl* or *kiéry twyári*, meaning "wind tree" for Huicholes (Baytelman, 1980), *tapate*, *nacazul*, *dragon verde*, and *ericillo tapat* (León Jiménez, 2005). Other synonyms of *toloache* used in different Mexican territories are: *belladonna*, *ericillo* (Puebla); *chamico* (Tabasco); *chanico*, *chayotillo blanco* (Veracruz); *flor de muerto* (death flower), *gedionda* (Tlaxcala); *mata-noa* (kill it), *hierba hedionda* (stinking grass), *mehem-x-ton-kú*, *xtochu* (Yucatan); *tapat* (Hidalgo); *tapate*, *teloloachtl* (Morelos); *toloache chaparro*, *toloachil*, *cholo* (Oaxaca); *torescua* (Michoacán); *tornaloca*, *tuluache* and *vichu eskua* (Martínez, 1979; Hernández-Sánchez, 1989; Aguilar et al., 1994).

It is not a goal of our work to make an exhaustive analysis of the vernacular nomenclature, as has been done in other studies (Dafni et al., 2013; Waniakowa, 2007). More names can be seen in Bye et al. (1991) for *D. lanosa*, or in different languages in Rätsch (1998). However, we aim to comment on some significative names applied in Spain (mostly collected using the database Anthos (2017)), with regards to either its traditional uses or morphological features. The most well-known name for these plants is *estramonio*, which originally referred to *D. stramonium*, but is currently also applied to other *Datura* species in several Spanish regions. Some names derived from it, such as *estramonia loca* or *antimonio*, are also used for *D. stramonium*, while names such as *métel*, *métel de los Arabes* (métel from the Arabs), or derivatives such as *metela*, used in The Canary Islands (Salas and Cáceres, 2003) are applied to *D. metel*. These names, generally used specifically for these species, are clearly derived from their scientific binomial. Another group of names are those derived from the flower morphology, such as flor *de trompeta* (trumpet flower) or *trompetillas*, or from the fruit morphology, such as *nuez morada del diablo* (devil´s purple walnut), *nueza blanca* (white walnut), or *manzana espinosa* (maybe literally translated from its English name "thorn apple"). Other names refer to the bad smell of the plant: *hedionda/o* (stinking), *hierba hedionda* (stinking grass), *higuera hedionda* (stinking fig plant), *yerba hedionda* (hideous yerba) and derivates such as *jeyondera* and *malhuele* (bad-smelling). The characteristic bad smell and possibly its well-known toxicity, have led to the use of other names that reflect the use of these plants against some animals: *espantalobos* (scare wolves), *flor de topo* (mole´s blossom), *haba topera* (mole´s bean), *hierba de los topos* or *hierba topera* (moles' grass), *hierba hormiguera* (ant´s grass), *espantarratones* (scare mice), or *matatopos* (mole killer). Its wide use to avoid the presence of rodents and insects is clearly reflected in these vernacular names (Villar et al., 1987; Villar, 2003). The ecological preference of the plants for farmland habitats (as nitrophilous plants) is also reflected in names: *hierba de las coles* (cabbage grass). The similarity of leaves with those of a fig tree has also been used: *higuera hedionda*, *higuera del infierno*, *higuera loca* (hideous fig tree, hell fig tree, crazy fig tree). Finally, the well-known toxicity is also evident in many of the popular names: *berenjenas del diablo* (Devil´s aubergines), *nuez del Diablo* (Devil´s walnut), *mata del infierno* (hell shrub), *higuera del infierno* or, simply, *veneno* (poison).

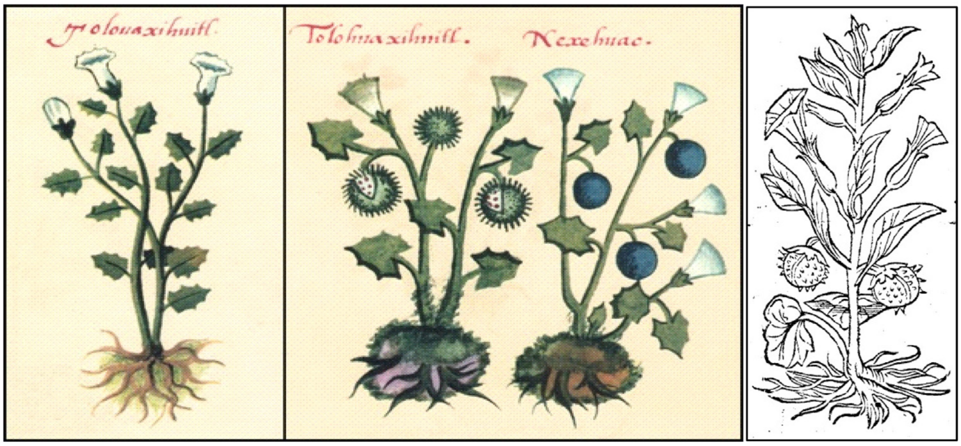

Fig. 2. Left: three different supposed types of *Datura* illustrated in the códice *Libellus de Medicinalibus Indorum Herbis* (De la Cruz and Badiano, 1964). Right: *stramonia*, one of the first illustrations in a European version of Dioscorides' Materia Medica; Laguna, 1555.

4.2. Historical uses and ancient codices

The *Datura* genus has a long cultural history in Mexico and in indigenous America in general and has been archaeologically dated as early as 5000 years ago (Boyd, 1998). Its use, aside from in ancient times, is still valid in both rural-indigenous and urban-mestizo sectors in contemporary Mexico. This is due to its medical and therapeutic uses, which depending on the cultural group where it is used, also influences the various contexts of the management (preparation, consumption, use) and mythical treatment with the plant (the worldview of *Datura*-Human social relationship) (Schultes and Hofmann, 2008; Litzinger, 1981).

Numerous studies document the cultural function, psychoactive effects and medicinal applications of *Datura* in pre-hispanic cultures, these are supported by archaeological evidence of: artistic works (sculpture, pottery and murals), codices and other colonial sources (Driver, 1965; De la Garza, 2012; Carod-Artal, 2015; Bye and Sosa, 2013). The use of *Datura* is documented along with other plants, such as peyote (*Lophophora williamsii* (Lem. ex Salm-Dyck) J.M.Coult) and ololiuhqui (*Ipomoea violacea* L.), for the preparation of ritual drinks (Furst, 1980; De la Garza, 2012; Rätsch, 1998), in addition to the consumption of psychoactive substances, practices of self-sacrifice, sexual abstinence, long fasting and states of ecstasy to achieve communication with deities or nonhuman entities, and to obtain knowledge for the divination of the causes of the diseases (De la Garza, 2012). The delirium provoked by its consumption, was interpreted by the Spaniards as dealing with the devil (Bye and Linares, 2013) and witchcraft (Aguirre-Beltrán, 1963). Nevertheless, the therapeutic value of *Datura* was recognized as important and it was used to alleviate diseases considered to be water-based and cold-formed, which according to the Nahua worldview were sent by Tlaloc (rain deity), such as gout, which they treated with *toloatzin* or *tlapatl* (De la Garza, 2012; Furst, 1980).

Focusing on Europe, some authors have concluded that there is no reason to think that Dioscorides (or other Greeks) knew anything about *Datura* (Geeta and Gharaibeh, 2007) and that the identification of *Datura* with Dioscorides' *Struchnon manicon* is a mistake. On the other hand, these authors suggest that a number of Arabic texts from 9th to 14th C CE include at least one *Datura* species (named Gawz mathil), with a detailed first description in Al-Ghafiqi (12th C CE), and later authors such as Ibn al-Baytar (13th C CE), supporting the theory of an Old World origin of some (or at least one) species. Special mention needs to be given to the marginal inclusion of *Datura* in the main annotated translations of Dioscorides´ De Materia Medica from the 16th century, i.e. Matthioli (1548, 1565) and Laguna (1555). Even though the plants were not mentioned in the first Latin translation of the Greek Codice by Jean Ruelle (Ruelle, 1516), both Matthioli and Laguna make short comments on *stramonia* in the CXLI chapter about nuts, after description of the toxic *nux metela*. But, in their comments on the several different types of *Solanum* they add a mention of *Solanorum genera duo* (Matthioli, 1565: 1075) or *Solano que engendra locura* (Laguna, 1555: 420). This last author stated “drunk with wine it represent vain images but very pleasing to the senses, and drunk in double quantity, it has the man beside himself for three days, and in fact it kills”. Despite the difficulties of identifying the plants in classical texts (a well-studied subject; Font-Quer, 1961; De Vos, 2010; El-Gharbaoui et al., 2017), both authors refers to the plant as “stramonia”.

Apart from the above, one of the earliest descriptions of the genus *Datura* in Europe comes from the Codex *Libellus of Medicinalibus Indorum Herbis* (also known as the *Badianus manuscript* or the *Codex Barberini*), written in the first half of the sixteenth century where at least three species of *Datura* were illustrated (Fig. 2) and described for medical purposes (De la Cruz and Badiano, 1964; originally from 1552; Gates, 1939). The plant was named *tlapatl* (medicine) and *tolohuaxihuitl* (head-tilting herb). Some authors proposed that such names correspond to *D. stramonium* and *D. innoxia* respectively (Ocegueda et al., 2005). From analyzing the illustrations Symon and Haegi (1991) and Walcott Emmart (1940) came to different opinions about the appearance of the species (see Daunay et al., 2007). Regarding its herbal use, Martín de la Cruz wrote that it served to alleviate pain and reduce swelling: "the ground leaves are smeared under the ears to treat discomforts in purulent ears, sponges or tumors, side pain and ointment for the cracks in the feet" (Bye and Linares, 2013).

In the *Florentine Codex* (*General History of the Things of New Spain*, by Fray Bernardino de Sahagún,1547), apart from several illustrations (Daunay et al., 2007), it was pointed out that *Datura* was used for gout, swollen body, infected wounds, eruptions on the back and for intermittent cold fevers. Likewise, he adds that *toloache* (*D. stramonium*) "make not want to eat to those who drink it, it makes them drunk and go crazy perpetually” (Sahagún, 2000, originally from 1547). Later, Hernández de Toledo (1651), in his work *Rerum medicarum Novae Hispaniae thesaurus*, described the plant with the name of *tlapatl* and described it as a hypnotic and poisonous plant. He wrote that the cataplasms of the crushed leaves applied to different parts of the body served to alleviate migraine, to reduce inflammation caused by the effect of *bad winds* and falls, and asthma, but used excessively, it could provoke disturbance of the mind. It was also used to cure fever, ear inflammation and deafness.

In Spain the largest number of citations related to the historical uses of *Datura* are found in the volumes and articles that collect the legends and traditions of Spanish magic and witchcraft, particularly in the Middle Ages (Gómez-Fernández, 1999). These plants were common in the recipes of medieval grimoires and rituals, such as the "Celtic ritual of the call" in which the presence of form was invoked (Lamberti, 2001). Its most notable use was in the well-known *witch ointments*. This mixture consisted, among other ingredients and according to the references, of boiled child-fat, poisonous snakes, lizards, toads, a blessed host, ground bones and a mixture of plants, among other Solanaceae, such as belladonna (*Atropa belladona* L.), mandrake (*Mandragora* spp.), henbane (*Hyoscyamus albus* L.; *H. niger* L.) and datura (*D. stramonium, D. innoxia*) (Porta, 1558; Balasch and Ruiz, 2001; Pérez, 2010). This mixture, with the appearance of ointment, was directly smeared on the genitals or on the stick of a broom causing, when directly absorbed through the skin and mucous membranes, strong hallucinations. The stories told directly by those involved or by others who were perplexed by attending the meetings were the origin of the legend of the flight of witches on brooms (Schultes and Hofmann, 2008; Summers, 2008). The different composition and concentration of tropanic alkaloids of the species used in the formula generated an even greater effect than that of the already potent substances in their individual forms. Of all of them, *stramonium* is considered to be the most dangerous, since after the first of consumption it produces agitation, soon followed by deep sleep and an awakening similar to the hangover of the drunkenness, and interpreted by some to be similar to the phases of possession by the devil and trance (Balasch and Ruiz, 2001).

The strong hallucinatory effects provoked by these mixtures were the cause of condemnation of many women who were assured "*to have gone to akelarres and to ride on beasts, even to cause damage to creatures under its effects*" (Weyer, 1563; Reguera, 2012). Knowing the exact composition of these ointments was one of the primary objectives of the Spanish Inquisition, which in some of its trials used the analyzes made by apothecaries and doctors as condemnatory evidence (Summers, 2008; Pérez, 2010).

4.3. Current ethnobotanical uses

In a synthesized way, the uses collected in ethnobotanical works in Mexico and Spain are presented in Table 2. For Spain, we have considered and updated a review on the ethnobotanical uses of *Datura stramonium* (D'Ambrosio et al., 2018). For Mexico, Biblioteca Digital de la Medicina Tradicional Mexicana (2009), which includes some important review works (as Argueta et al., 1994), and Aguilar et al. (1994) were noble starting points. Conditions or uses were included according to the emic categorization of the original ethnobotanical source. Traditional uses for species currently included in genus *Brugmansia* were not included (as, f.i., in Alcorn, 1984 or Aguilar et al., 1994), as well as those related for other American ethnicities that do not refer to Mexican territory (as, f.i., in Moerman, 2009).

A total of 118 traditional uses and 135 preparation forms were collected in both territories, including 7 non-medicinal uses (repellent for 3 animal types, tobacco substitute and toxic). Up to 111 medicinal uses were recorded, to be applied in 76 conditions or symptoms included in 13 pathological groups according to the ICPC-2 classification (followed after Staub et al., 2015), with a category of Magical-Religious diseases or symptoms. In Spain, 36 traditional uses were recorded in the review (29 medicinal ones) for 3 species: *D. stramonium*, *D. innoxia* and *D. ferox*. In Mexico, the list reaches 82 medicinal uses for 6 species: *D. stramonium*, *D. innoxia, D. meteloides, D. lanosa, D. quercifolia* and *D. metel*, although several authors pointed out the difficulty to verify the specific plant identifications on some historical and ethnobotanical documents (Bye et al., 1991).

At present, *Datura* continues to be frequently use by several indigenous cultures of North America and Mexico, among which the use of leaves, stems and roots as anesthetic is very widespread, as well as to produce visions and ecstatic dreams, "seeing" or to diagnose diseases, to visualize non-human beings, to have luck when hunting, to detect bewitching or to see lost or stolen objects (Driver, 1965¸ Dobkin de Rios, 1990). For the Tarahumaras or Raramuri these plants (*Datura* spp.) are called *rikuhuri*, but it actually means a possessed soul that appears and acts as a human (Bye et al., 1991). For them, because it is considered such a powerful medicine, only special shamans can employ it by using *peyote* or *jicuri* (*Lophophora williamsii*). Most Tarahumaras fear and avoid visual and physical contact with the plant, although it can be used to induce visions in the beverage known as *tesgüino* (Bye et al., 1991). In the Huichol region of Jalisco, *hikuli* (*jicuri*) and *kieri* (*Datura*, *Brugmansia* and *Solandra*) are recognized as brothers, sons of the sun and grandchildren of fire, where *kieri* constitutes a set of beings and phenomena associated with the underworld and predation (Aedo-Gajardo, 2008). Yaqui women and other ethnicities in northern Mexico use cooked *Datura* leaves to alleviate suffering during childbirth. On the other hand, Hopi medicine men chew their root to induce visionary states that allow them to diagnose diseases (Rätsch, 1998). Other ritual uses include the application to people suffering from high levels of libido and women who have been forced into prostitution (amongst others for the Navajo, from the USA; Brugge, 1982). These plants are also frequently used as antiasthmatic, or for rheumatic and neuralgic pains (Martínez, 1979). Among the current Maya, a tincture or crushed leaves are still used for rheumatism, neuralgia and headache, as well as hemorrhoids and ulcers (Echanove Trujillo, 1977; Roys, 1931). The use of *D. innoxia* in the so-called "affairs of love" has also been recorded. In this case, the colorless, odorless and tasteless character of some of the alkaloids it possesses are mixed with food, drink, as mescal of agave or tejuino of maize, to increase its intoxicating power (Díaz, 1977), or with chocolate, among the Indian women of Mérida to "stun" their husbands. Today, *D. innoxia* and *D. stramonium* are regularly sold in the markets of central Mexico for wounds and inflammations (Argueta et al., 1994; Bye and Sosa, 2013), and have been the basis of black magic in Mexico, as well as in other parts of the world (Yetman and Van Devender, 2002).

The catalog of traditional uses collected in current ethnobotanical sources is also relatively extensive in Spain. Its most frequent use in Spain is as an anti-asthmatic, where cigarettes are prepared with the leaves of *D. stramonium* sting. The use of poultices and plasters made with *Datura* leaves for anti-inflammatory and antirheumatic purposes is also frequently cited. However, there are also many references to hypnotic, narcotic or toxic plants (Fresquet et al., 2001; Benítez, 2009; Kunkel, 1987; Álvarez-Escobar, 2011; Fajardo et al., 2007). This draws attention to some of the uses mentioned in the literature. Thus, Font-Quer (1961) cites, among the advantages of *D. stramonium*, its use against nymphomania, and although no explanation is included about its mode of action, some previous studies had already demonstrated its calming and antispasmodic action on the sexual organs (De Groetz, 1847). On other occasions, *D. stramonium* seeds are known to have been used as a trick at treats and celebrations, when mixed with food, giving rise to a strong purgative effect (Fajardo et al., 2007).

Fig. 3 includes the traditional uses of *Datura* in Mexico, Spain, and both together, sorted by pathological group. It can be seen the high importance of medicinal uses in dermatologic conditions (as Frei et al., 1998 pointed up), respiratory, and the so-called “magical-religious” uses in Mexico, as some of the above mentioned.

4.4. Coincident uses

In spite of the disparity by way of referring to medicinal uses in both countries, as a result of differences in traditions, the emic interpretation of effects and the way of referring to them, up to 15 similar uses have been found, which are presented in Table 3. In some cases the uses are not the same, but are somehow related when taking into account the observed differences on the emic categorization and concept of disease. This can be seen in the case of *D. stramonium*, used in Mexico as purgative (probably with the aim to purge and eliminate the parasites), and in Spain against helminthiasis (i.e., use described in the ethnobotanical source in a more specific way). These coincident uses possibly reflect the flow, not only of the plants from America to Europe, but also of the information associated with them. Most of the uses (12 uses, 80% of the coincident ones) were described by some of the cited classical texts on

Table 2
Ethnobotanical uses for the *Datura* species in Mexico and Spain. Legend: Pathological groups according to ICPC-2. A: General and Unspecified; D: Digestive; H: Ear; K: Cardiovascular; L: Musculoskeletal; N: Neurological; P: Psychological; R: Respiratory; S: Skin; T: Endocrine/Metabolic and Nutritional; W: Pregnancy, Childbearing, Family Planning; X: Female genital tract. MR: Magical-Religious diseases. BDMTM, 2009: Biblioteca Digital de la Medicina Tradicional Mexicana (2009). N.a.: not available.

Species	Use/Condition	Pathological Group	Part used	Preparation form	References
Mexico					
D. discolor	Asthma	R	Indet.	Indet.	Aguilar et al. (1994)
	Toothache	D	Indet.	Indet.	Aguilar et al. (1994)
	Hemorrhoids	K	Indet.	Indet.	Aguilar et al. (1994)
	Wounds, ulcers	S	Indet.	Indet.	Aguilar et al. (1994)
	Ear (otitis?)	H	Indet.	Indet.	Aguilar et al. (1994)
D. innoxia	Asthma	R	Leaves	¿?	BDMTM, 2009
	Cough	R	Leaves	Cigarettes	García Rivas (1990)
	Stomachage	D	Indet.	Indet.	BDMTM, 2009
	Latido (palpitation in the pit of the stomach)	D	Leaves	Decoction	BDMTM, 2009
	Navel pain	D	Indet.	Indet.	BDMTM, 2009
	Inflammation	S	Leaves	Cataplasm	BDMTM, 2009
			Indet.	Boiled	Aguilar et al. (1994)
	Rheumatism	L	Leaves	Cataplasm	BDMTM, 2009
			Seeds, Leaves, Roots	Tincture, Maceration	García Rivas (1990)
	Muscle pains	L	Leaves	¿?	BDMTM, 2009
	Hits, strokes	L	Indet.	Indet.	BDMTM, 2009
	Diabetes	T	Fruits	Decoction	BDMTM, 2009
			Leaves	Cigarettes	García Rivas (1990)
	Hemorrhoids	K	Leaves	¿?	BDMTM, 2009
	Pain	A	Flowers	Spread	BDMTM, 2009
			Leaves	Heatened, boiled	Aguilar et al. (1994)
	Dengue treatment	A	Indet.	Indet.	BDMTM, 2009
	Fever ("calentura")	A	Indet.	Indet.	BDMTM, 2009
	Snakebite	S	Indet.	Indet.	BDMTM, 2009
	Hallucinogenic beverage enhancer	N	Indet.	Indet.	BDMTM, 2009
	Neurotoxic pains	N	Seeds, Leaves, Roots	Tincture, Maceration	García Rivas (1990)
	Headache	N	Flowers, Leaves	Decoction and chewed	Avilés and Jiménez, 1994
	Peyote ceremony: divination, prophecies, etc.	MR	Indet.	Indet.	BDMTM, 2009
	”lovesickness”	MR	Buds	Infusion	BDMTM, 2009
D. lanosa	Asthma	R	Leaves	Cigarettes	Bye et al. (1991)
	Giving bith pain	W	Leves	Brew	Bye et al. (1991)
	Headache	N	Leaves	Direct aplication	Bye et al. (1991)
	Skin ulcers	S	Leaves	Lotion	Bye et al. (1991)
	Sores	S	Leaves	Mixed with grease	Bye et al. (1991)
	Bruises, swellings, boils	S	Leaves	Crushed on the part of the body or heated with cooking oil	Bye et al. (1991)
	Pain in the left side	K	Leaves	Mixed with grease	Bye et al. (1991)
	Drunkness treatment	MR	Leaves	Infusion, cigarettes	Bye et al. (1991)
			Fruits	Chewed	Bye et al. (1991)
	Peyote ceremony: divination, prophecies, hunt, etc.	MR	Leaves	Indet.	Bye et al. (1991)
	To avoid the soul-possesing soul of "rikúhuri"	MR	Leaves	Indet.	Bye et al. (1991)
	Vissions inductor	MR	Seeds and leaves	Oinment smeared on the stomach	Bye et al. (1991)
	Drunkness treatment	MR	Leaves	Infusion, cigarettes	Bye et al. (1991)
D. metel	Pain in the lung	R	Flowers	Chopped and macerated in alcohol	Aguilar et al. (1994)
	Cough	R	Flowers	Chopped and macerated in alcohol	Aguilar et al. (1994)
	Angina	K	Flowers	Local application	Aguilar et al. (1994)
D. meteloides	Pimples, grains	S	Leaves	Cataplasm	BDMTM, 2009
	Wounds, ulcers	S	Leaves	Cataplasm	BDMTM, 2009
	Muscle pains	L	Seeds	Cataplasm	BDMTM, 2009
	Hemorrhoids	K	Roots	Cataplasm	BDMTM, 2009
	Otitis	H	Leaves	Applying smoking smoke	BDMTM, 2009
D. quercifolia	Lices	S	Leaves	Chooped	Aguilar et al. (1994)
	Inflammation / massage	S	Leaves	Chooped with butter	Aguilar et al. (1994)
	Hemorrhoids	K	Leaves	Chooped with butter	Aguilar et al. (1994)
D. stramonium	Cough	R	Indet.	Indet.	BDMTM, 2009
			Leaves	Infusion	Aguilar et al. (1994)
	Asthma	R	Indet., leaves, roots	Indet., cigarettes, decoction	BDMTM, 2009

(*continued on next page*)

Table 2 (*continued*)

Species	Use/Condition	Pathological Group	Part used	Preparation form	References
			Leaves	Cigarettes	Morton, 1981
			Root	Decoction	Morton, 1981
	Cold, catarrh	R	Indet.	Indet.	BDMTM, 2009
	Toothache	D	Seeds	Direct application	BDMTM, 2009
			Leaves	Cataplasm	BDMTM, 2009
	Mumps	D	Leaves	Decoction and externally applyed	BDMTM, 2009
	Helminthiasis	D	Indet.	Indet.	BDMTM, 2009
			Leaves	Decoction	Aguilar et al. (1994)
	Hemorrhoids	K	Indet.	Indet.	BDMTM, 2009
			Leaves	Decoction	Aguilar et al. (1994)
	Rheumatism	L	Roots, Leaves	Macerated in water or alcohol, Cataplasm,	BDMTM, 2009; Aguilar et al. (1994)
			Seeds	Tincture	Morton, 1981
	Joint pain	L	Leaves, Seeds	Decoction and added to a bath, or spread. Direct application	BDMTM, 2009
	Pimples, grains, "tlacotles"	S	Leaves	Decoction and externally applyed	BDMTM, 2009; Aguilar et al. (1994)
			Leaves	With oil	Aguilar et al. (1994)
	Superficial tumors	S	Indet., leaves	Indet.	BDMTM, 2009; Alcorn (1984)
	Wounds, ulcers	S	Indet.	Indet.	BDMTM, 2009
			Leaves	Decoction, bath	Aguilar et al. (1994); Alcorn (1984)
	Burns	S	Leaves	Direct application	Alcorn (1984)
	Erysipelas	S	Leaves	Direct application (externally)	BDMTM, 2009
	Parasites ("bichos")	S	Leaves	With butter	Aguilar et al. (1994)
	Inflammation	S	Leaves	Direct application, infusion	Aguilar et al. (1994)
	Indet. dermatological illnesses	S	Indet.	Indet.	Frei et al. (1998)
	Pertussis	A	Leaves	Decoction and added to a bath	BDMTM, 2009
	General "sick"	A	Indet.	Indet.	Alcorn (1984)
	Inflammation of the uterus	X	Leaves	Direct application (externally)	BDMTM, 2009
	Vaginal infections	X	Indet.	Indet.	BDMTM, 2009
	Menstrual blleding	X	Leaves	Indet.	Alcorn (1984)
	Labor pain	W	Indet., Seeds	Indet. Cataplasm. Decoction	BDMTM, 2009; Morton, 1981
	Headache	N	Flor	Decoction	BDMTM, 2009
			Leaves	Direct application	BDMTM, 2009
			Seeds	Tincture	Morton, 1981
	Neuritis	N	Indet.	Indet.	BDMTM, 2009
	Neuralgia	N	Seeds	Tincture	Morton, 1981
	Tranquilizer - Sedative CNS	P	Indet.	Indet.	BDMTM, 2009
	Gout	T	Indet.	Indet.	BDMTM, 2009
	Cultural diseases: "scare", "astonishment", "falling in love"	MR	Indet., leaves, flowers	Indet., decoction	BDMTM, 2009; Aguilar et al. (1994)
	To "do evil"	MR	Indet.	Indet.	BDMTM, 2009
	To "get in a trance"	MR	Indet.	Indet.	BDMTM, 2009
	Psychotrope; to "tell the truth"	MR	Seeds	Direct ingestion; in water	BDMTM, 2009; Aguilar et al. (1994); Alcorn (1984)
	Divination "with medicinal purpose"	MR	Leaves, Flowers, seeds	Direct application	BDMTM, 2009; Aguilar et al. (1994)
	"Ataques"	MR	Leaves	Indet.	Aguilar et al. (1994)
Spain					
D. ferox	Toxic to man / animals	Non-Medicinal	Whole plant	Not preparation	Verde (2002); Fajardo et al. (2007);
D. innoxia	Asthma	R	Flowers	Cigarettes	Álvarez-Escobar (2011); Perera (2005)
			Leaves	Cigarettes	Font-Quer, 1961 (as *D. metel*); Álvarez-Escobar (2011)
	Diarrhea	D	n.a.	n.a.	Kunkel (1987)
	Constipation / Laxative	D	Seeds	Added to the food	Mesa (1996)
	Rheumatism	L	Leaves	Cataplasms	Font-Quer, 1961 (as *D. metel*)
	Dermatitis	S	n.a.	n.a.	Kunkel (1987)
	Burns	S	Leaves	Cataplasm	Font-Quer, 1961 (as *D. metel*)
	Toxic to man / animals	Non-Medicinal	Whole plant	Not preparation	Álvarez-Escobar (2011);Perera (2005)
D. stramonium	Asthma	R	Leaves, Flowers	Cigarettes (Leaves infusion, one reference in Valencia)	Velasco (2009); Fresquet et al. (2001); Salas y Cáceres, 2003; Carrió and Vallés, 2012; Font-Quer (1961); Kunkel (1987); Garrido (2008), Parada (2008); Agelet (1999); Raja (1995); Moll (2005); Carrió (2013); Jaén-Otero (1984); Fuente (1999); Perera (2006)
	Cough	R	Leaves	Cigarettes	Velasco (2009); Kunkel (1987);
	Bronchitis	R	Flowers	Fumigated	Carrió (2013)
	Cold, catarrh	R	Leaves?	Cigarettes	Carrió (2013)
	Purgative	D	Seeds	Direct application	Fajardo et al., 2013

(continued on next page)

Table 2 (*continued*)

Species	Use/Condition	Pathological Group	Part used	Preparation form	References
	Vomiting inducer	D	Seeds	Infusion	Salas and Cáceres, 2003
	Digestive spasm	D	Leaves	Cigarettes	Garrido (2008)
	Hemorrhoids	K	Leaves		Salas and Cáceres, 2003
	Hinoptic, Narcotic, Psychotrope	N	Leaves	Cigarettes, Infusion	Fresquet et al. (2001); Benítez (2009); Kunkel (1987); Álvarez-Escobar (2011)
	Tranquilizer - Sedative CNS	P	Leaves	Cigarettes, Decoction	Garrido (2008); Raja (1995)
	Rheumatism	L	Leaves	Cataplasm	Velasco et al. (2010); Font-Quer (1961); Garrido (2008); Jaén-Otero (1984)
	Inflammation	L	Leaves	Cataplasm	Villar et al. (1987)
	Bones conditions	L	Aereal parts	Cataplasm	Akerreta et al. (2013)
	Tendonitis	L	Aereal parts	Cataplasm	Akerreta et al. (2013)
	Burns	S	Leaves	Cataplasm	Salas and Cáceres, 2003; Font-Quer (1961)
	Wounds, ulcers	S	Leaves	Direct application	Kunkel (1987); Perera (2006)
	Dermatitis	S	Leaves	n.a.	Kunkel (1987)
	Eczema	S	Aereal parts	Cataplasm	Akerreta et al. (2013)
	Calmative	S	Leaves	Infusion	Fresquet et al. (2001)
	Anesthetic	A	Leaves	Cataplasm	Velasco (2009)
	Sudorific	A	Seeds	Infusion	Salas y Cáceres, 2003
	Nymphomania	X	n.a.	n.a.	Font-Quer (1961)
	Avoid pregnancies	W	Flowers	Cataplasm	Moll (2005)
	Repellent: mice and rats	Non-Medicinal	Leaves, Whole plant	Grown in the orchard	Fajardo et al. (2007); Villar (, 2001, 2003); Bonet (1991); Verde et al. (1998)
	Repellent: moles	Non-Medicinal	Whole plant	Not preparation	Parada et al. (2002); Raja (1995); Agelet (1999); Molina (2001); Velasco et al. (2010)
	Repellent: aphids and flies	Non-Medicinal	Whole plant	Not preparation	Tejerina (2010)
	Tobacco substitute	Non-Medicinal	Leaves	Cigarettes	Velasco et al. (2010)
	Toxic to man / animals	Non-Medicinal	Whole plant	Not preparation	Benítez (2009) Carrió (2013) Fajardo et al. (2007); Tejerina (2010); Velasco et al. (2010); Verde et al. (1998); Pardo-de-Santayana (2008); Villar et al. (1987); Gómez-Cuadrado (2011);

the Aztec use of medicinal plants, i.e. in De la Cruz and Badiano (1964); Sahagún (2000); and Hernandez de Toledo (1651) (Table 3). Nevertheless, it is important to highlight that most of the total 93 traditional medicinal uses are not coincident, showing some cultural differences in the traditional use of the plants.

The use of *D. stramonium* and *D. innoxia* to treat asthma, as cigarettes of the leaves, and against rheumatism, by applying cataplasms externally on the affected part, coincide in both countries, this was mentioned in Hernández de Toledo (1651). *D. stramonium* is used, as well as an antiasthmatic, against coughs and colds in both countries, this is widely mentioned in the bibliography consulted. Treatments also coincide in the use of this species externally for wounds, although in Spain *D. innoxia* is also used for burns. The topical application of the plant for these conditions was also quoted in the three classic codices. It seems that one of the effects of external application is the anti-inflammatory, and as such it is used in both countries with certain nuances: in Mexico external use is specified for inflammation of the uterus; in Spain generally for inflammation or blows. Something similar should be detected with respect to dermatological conditions, referred to as erysipelas or eczema, but in fact, poultices are applied to skin conditions whether due to infectious causes or not. Curiously, the use of stramonium as a tranquillizer is known in both territories, although this use probably has many suitable differences regarding the form and the context of use. In other cases, such as muscle or bone pain or hemorrhoids, although the use is coincident, the species do not exactly match. In both cases in Mexico *D. innoxia* is used in addition to *D. meteloides*, which is not present in Spain, as we have observed. However, in Spain these uses are not associated with this species, but instead with the best known species, *D. stramonium*. This may indicate that information about uses may have come from the Americas but, since specific species are not found here, it has traditionally been used with the most widely dispersed and known congener, the stramonium. Both *D. stramonium* and *D. innoxia* are used as anesthetics, although in Mexico many more detailed uses have been recorded, referring to the part of the body where there is pain that can be treated with plants, for example whether a headache, labor pains, pain in the stomach or teeth.

As mentioned above, it is noteworthy that the existence of many differences in the medicinal uses related to so-called cultural diseases,

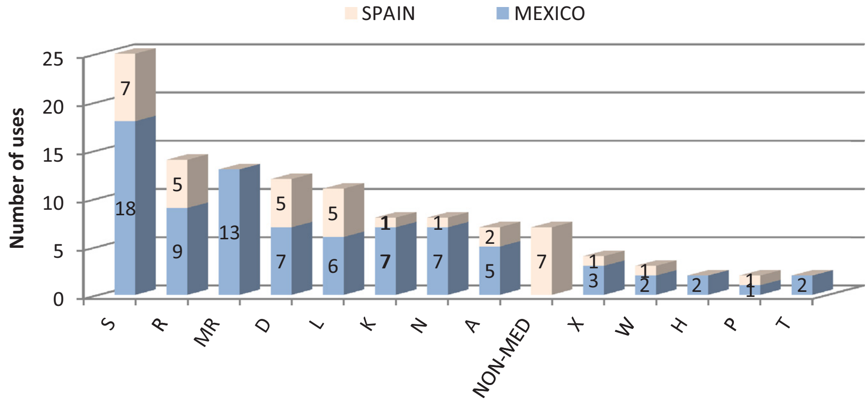

Fig. 3. Traditional uses of *Datura* species in Mexico, Spain, and total ones per pathological group. A: General and Unspecified; D: Digestive; H: Ear; K: Cardiovascular; L: Musculoskeletal; N: Neurological; P: Psychological; R: Respiratory; S: Skin; T: Endocrine/Metabolic and Nutritional; W: Pregnancy, Childbearing, Family Planning; X: Female genital tract. MR: Magical-Religious diseases.

Table 3
Correlation between uses in Mexico and Spain: probable use coincidences. In classical texts DC: De la Cruz and Badiano (1964); SA: Sahagún (2000); HT: Hernández de Toledo (1651).

Pathological Group	Species used in Mexico	Use/Condition Mexico	Species used in Spain	Use/Condition Spain	Classical texts
D	***D. stramonium***	Purgative	***D. stramonium***	Helminthiasis	
K	***D. stramonium, D. innoxia, D. meteloides***	Hemorrhoids	***D. stramonium***	Hemorrhoids	Inflammations / wounds SA HT
L	***D. innoxia***	Hits, strokes	***D. stramonium***	Inflammation	Inflammations / wounds / strikes SA HT
L	***D. stramonium, D. innoxia***	Rheumatism	***D. stramonium, D. innoxia***	Rheumatism	Side pain / pain / swelling DC SA HT
N	***D. innoxia***	Hallucinogenic beverage enhancer	***D. stramonium***	Hinoptic, Narcotic, Psychotrope	Get drunk / hipnotic SA
P	***D. stramonium***	Tranquilizer - Sedative CNS	***D. stramonium***	Tranquilizer - Sedative CNS	
R	***D. stramonium, D. innoxia, D. lanosa***	Asthma	***D. innoxia***	Asthma	Asthma HT
R	***D. stramonium***	Cold, catarrh	***D. stramonium***	Cold, catarrh	Cold fever SA
R	***D. stramonium***	Cough	***D. stramonium***	Cough	
S	***D. stramonium, D. meteloides***	Wounds, ulcers	***D. stramonium***	Wounds, ulcers	Tumors / wounds / falls DC SA HT
S	***D. stramonium, D. lanosa***	Burns, skin ulcers, sores	***D. stramonium, D. innoxia***	Burns	Wounds SA
S	***D. innoxia***	Inflammation	***D. stramonium, D. innoxia***	Dermatitis	Sponges? / eruptions DC? SA
S	***D. stramonium***	Erysipelas	***D. stramonium, D. innoxia***	Dermatitis	Sponges? / eruptions DC? SA
S	***D. stramonium, D. meteloides***	Pimples, grains	***D. stramonium, D. innoxia***	Dermatitis	Eruptions SA
S	***D. stramonium, D. meteloides***	Pimples, grains	***D. stramonium***	Eczema	Eruptions SA

are clearly present in current Mexican culture, such as in lovemaking, "medicinal fortune telling", "drunkenness" or " telling the truth", or cultural illnesses such as "fright ","astonishment" and "falling in love" or "heartbeat" (palpitation in the pit of the stomach). Also, its use as an active ingredient in hallucinogenic drinks, or to "get into trance" or "do evil" has not been referred to as hallucinatory in Spain, which is a well-known use found in the literature, which derives from the toxicological problems that will be discussed in the following section.

5. Poisoning, clinical reports and recreational use

The potent psychodysleptic effects of tropane and its derivatives have likely associated it with recreational drug use, which is a far cry from its ancestral shamanic and ritual use in its countries of origin, as described in numerous anthropological works and by many ethnobotanists (e.g., Applegate, 1975, or in the famous and controversial work Castaneda, 1968, 1971). On several occasions consumptions of these plants have had fatal consequences (Iglesias-Lepine et al., 2012; Domínguez-Fuentes et al., 2008; Oberdorfer et al., 2002).

As mentioned previously, the concentration and composition of alkaloids varies between species, parts of the same plant (Doncheva et al., 2006; Miraldi et al., 2001b) and ontogenetic stages (Kariñho-Betancourt et al., 2014). This is very important to highlight and should be clearly known by those looking to use it as a recreational drug. Thus, regarding the plant, organ and state of development, there can be a small difference between hallucinogenic doses and lethal ones. In the case of *D. stramonium*, the concentration of hyoscyamine is slightly higher in the leaves than in the seeds for all the varieties except var. *godronii*; however, the seeds have a higher concentration of hyoscine (Berkov et al., 2006; Doncheva et al., 2006), which means that fewer of these have higher neurotoxic effects than leaves are used. Other studies have showed that hyoscine concentration can vary notably between leaves of non-flowered plants and the flowered ones: 161–634 μg/g wt (Kariñho-Betancourt et al., 2014). While the overdose of hyoscyamine can cause "atropine delirium," the consumption of barely 30 g of seeds, along with enhancers such as alcohol, can have fatal consequences (Oberdorfer et al., 2002). We must add that, although there may be species that are easily recognizable at the level of genus by any botanist, the differentiation between species is not always so easy, leading in many cases to the observation, and obtaining information about concentrations of alkaloids or possible drug doses, assumed to be of only the best known, *D. stramonium*, even though it could be a different species.

In reviewing the poisoning cases attributed to *Datura* plants or alkaloids, there are also some differences between cases registered in Mexico and Spain. While in Mexico the cases registered in the Emergency Medical Services are usually due to voluntary consumption (Pérez-Belmont et al., 2012; Cox, 1994; Müller, 2008), in Spain cases of intoxication because of criminal activity are increasing (Xifró et al., 2014). Thus, in Mexico news about poisoning by toloache is frequent, since a potion is still used for love, which allows the tying up of the loved one. Even the term "*entoloachamiento*" is used to for the state of "automaton without will" of users (Monsalve-Maestro and Nogué-Xarau, 2006). The use of *Datura* as a folkloric substance in traditional shamanic medicine is also a cause of intoxication in both adults and children (Pérez-Belmont et al., 2012; De Pardo Guetti et al., 2009). In a study that reviewed the epidemiological panorama of intoxications in Mexico, *Datura* is cited as one of the main causes of accidental intoxication in children and voluntarily intoxication in the young and adults (Rodríguez-Pimentel et al., 2005). However, in recent years the Toxicological Information and Assistance Center of Mexico have had no notice of intoxications or even consultations about *Datura* (Viquez Guerrero, J.E., pers. commun.).

In Spain, cases of *Datura* plants or alkaloids intoxication are related to activities as diverse as leisure and crime. There are numerous reports that point to *Datura stramonium* as an emerging drug in new forms of leisure, especially among young people (Martínez-Montseny et al., 2015), sometimes resulting in death (Soler Carracedo et al., 2013), as happened in August 2011 (Quesada, 2011). In an analysis of the consultations carried out to the National Toxicology Service, during the 2005–2015 period only 0.02% of total consultations (285 cases) were made to the following terms: "datura", "brugmansia", "burundanga", and "scopolamine ", so it can be interpreted that they were related to *Datura* poisoning (term "brugmansia" was added to the consult due to the mentioned taxonomical relation of both genus, and to the current adscription of some species in *Brugmansia*, f.i., *B. arborea* (L.) Steud. = *Datura arborea* L.). Some 44.9% of these consultations referred to "datura", and 27% to "scopolamine". Out of these, 4.6% were for toxic contact and 3.2% referred to drug abuse. The route of entry of the toxin was mostly oral (43.2%), although in 5.3% of cases it was inhalation and in 41% of the cases it was unknown. It is necessary to clarify that the consultations do not involve intoxication, they can simply be requests for information. It has also been noted that the number of consultations has increased in recent years, probably influenced by the publicity given to the plant and its compounds in the media (f.i, Robledo, 2011). Spanish Legislation (Ministerial Order SCO/190/2004, of January 28) by the Ministry of Health and Consumption of the Government of Spain, which establishes the list of plants whose sale to the public is prohibited or restricted due to its toxicity, recognized *D. stramonium* (including *D. tatula*), *D. innoxia* and *D. metel* as toxic, in particular, their leaves and seeds. However, it does not include the less frequent *D. ferox* and *D. wrightii*, which, as mentioned above, also grow naturally in Spain.

It is also common to be poisoned by accidental consumption of some parts of the plants or their seeds, both in the case of humans and animals (Peris and Stubbing, 2006; Calbo-Mayo et al., 2004; Cavero et al., 1999 Soler-Rodríguez et al., 2006, Bye and Sosa, 2013). There are references to accidental intoxication from ocular contact with hands after touching a species of this genus or *Brugmansia*, both from children playing in areas where they are cultivated (Firestone and Sloane, 2007), and from gardeners who cultivate these plants (Voltz et al., 1992). To a lesser extent, but also with serious consequences, there are cases of poisoning of animals by consumption of *Datura* mixed with the feed. It is interesting to note that although in the wild the animals tend to avoid the grasses due to their strong smell and unpleasant taste, these disappear over time and go unnoticed among the rest of the feed, causing colic and, sometimes, the death of the animal (Soler-Rodríguez et al., 2006; Bofill et al., 2007).

In the field in which *Datura* has probably had the greatest increase in use is in its use in crimes against sexual freedom (see, for example, Sau, 2016). The effects caused by the accidental consumption of hyoscine, either in a pure state or mixed with other compounds such as benzodiazepines, are usually similar to transient global amnesia, which causes the victim to be submissive and experience loss of will (Ardilla-Ardila et al., 2006). This has extended its use as a substance used in cases of chemical submission for sexual purposes (Xifró et al., 2014), the frequency of which has increased in Spain in recent years (Gomila-Muñiz et al., 2016). Currently, rapid hyoscine determination methods are being developed for these cases (Sáiz et al., 2013; Steenkamp et al., 2004). Unfortunately, the word "burundanga", which can be used to refer to either hyoscine or its mix with benzodiacepines or other chemical compounds, is becoming common in the media alluding to the use of chemicals to promote a transient global amnesia in order to perform sexual crimes. The word seems to have a Colombian origin meaning "soporific substance that is administered to a person to steal", it is also used in Colombia and the Antilles as "tangle, confusion" (R.A.E, 2017).

6. Conclusions

This review of the ethnobotany of the genus *Datura* in two different territories, and in turn with a shared common past, highlights the variety of uses of the different species in both sites, with up to 111 medicinal ones to be applied in 76 conditions. Out of these, 15 traditional uses coincide in both countries, so it seems that in addition to the early flow of these plants to Europe, there was also a very significant flow of information with respect to their traditional uses. Some 80% of uses were also mentioned in early texts on medicinal uses of American plants. This tradition has reached to modern days with clear differences between Mexico and Spain. In addition to many uses that are not coincident, there are differences in the popular consideration of the plant: although in Mexico *Datura* is still widely used as a medicinal plant by different local ethnicities, in Spain one can highlight the increasing use as a leisure and recreation drug, as well as in crimes of sexual submission. This last aspect should be considered as a frontier of toxicological research that needs further studies in the field of forensic medicine and botany that solves the knowledge gap on the possible used species and structures, their chemical composition, alkaloid concentration and toxic effects. The presence of tropanic compounds, characteristic of the family Solanaceae to which it belongs, also opens up a wide range of possibilities for medicinal use in the treatment of certain ailments. Due to numerous ethnobotanical references in both countries, the use for treatment of asthma should be subject to more scientific research, especially to avoid the serious consequences that non-scientific therapy may have. Finally, it should be noted that during the research for this work we have verified the widespread use of *Datura* in many cultures on all continents, so it would be advisable to review and update all the ethnobotanical and ethnopharmacological knowledge about these plants, which would allow an advance in the medical research and in the standardization of safer protocols and reduce severe cases of intoxication.

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Author's contribution

GB: extraction of results; drawing tables and figures; writing and review of the article.

MMS: compilation of information about uses in Spain; contribution to the writing of the article.

AVK: bibliographical review; contribution to the writing; compilation of information about uses in Mexico.

UCJ: review and compilation of information in classic codices.

JH: compilation of information about uses in Mexico.

NMO: compilation of information about uses in Spain.

JMO: compilation of information about uses in Spain.

PC: design of the article; extraction of results; writing and review of the article.

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