

The prickly problem of interwoven lineages: hybridization processes in CactaceaeXochitl Granados-Aguilar^{1, 2*}, Ulises Rosas², Antonio González-Rodríguez³, and Salvador Arias²¹Posgrado en Ciencias Biológicas, Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City, Mexico.²Jardín Botánico, Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City, Mexico.³Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México, Morelia, Michoacán, Mexico.

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Table S1. Reports of natural hybrids in Cactaceae based on classic monographs and scientific articles following the taxonomic classification reported by Hunt *et al.* (2006). Information about ploidy level was consulted in The Chromosome Counts Database (CCDB).

Subfamily	Tribe	Genus	Hybridization Interspecific=a Intergeneric=b	Naturally- occurring hybrids	Reported ploidy	Evidence analyzed	Reference
Cactoideae	Echinocereae	<i>Pachycereus</i>	b (<i>Pachycereus</i> × <i>Stenocereus</i>)	<i>P. pringlei</i> × <i>S. thurberi</i>	2n	Morphological description / Molecular markers	(Hunt <i>et al.</i> 2006, Copetti <i>et al.</i> 2017)
		<i>Cephalocereus</i>	a	<i>C. tetetzo</i> × <i>C. columna-trajani</i> , <i>C. fulviceps</i>	-	Morphometric analysis / Molecular markers	(Vite <i>et al.</i> , 1996, Tapia <i>et al.</i> 2017)
		<i>Echinocereus</i>	a	<i>E. coccineus</i> × <i>E. dasyacanthus</i>	2n, 3n, 4n	Experimental crosses and chromosome counting	(Hunt <i>et al.</i> 2006, Powell <i>et al.</i> 1991)
		<i>Stenocereus</i>	a	<i>S. pruinosus</i> × <i>S. stellatus</i>	2n	Molecular markers	(Yáñez-López <i>et al.</i> 2016)
		<i>Bergerocactus</i>	b (<i>Bergerocactus</i> × <i>Pachycereus</i> , <i>Bergerocactus</i> × <i>Myrtillocactus</i>)	<i>B. emoryi</i> × <i>P. pringlei</i> , <i>B. emoryi</i> × <i>M. cochal</i>	4n	Morphological description	(Hunt <i>et al.</i> 2006)

		<i>Myrtillocactus</i>	b (<i>Myrtillocactus</i> × <i>Stenocereus</i>)	<i>M. geometrizans</i> × <i>S. dumortieri</i>	2n	Morphological description	(Hunt <i>et al.</i> 2006)
		<i>Escontria</i>	b (<i>Escontria</i> × <i>Polaskia</i>)	<i>E. chiotilla</i> × <i>P. chichipe</i>	-	Morphometric analysis, molecular markers and experimental crosses	(Cruz-Zamora <i>et al.</i> 2017)
	Hylocereeae	<i>Disocactus</i>	a	<i>D. phyllanthoides</i> × <i>D. speciosus</i> , <i>D. ackermannii</i> × <i>D. speciosus</i>	2n	Morphological description	(Anderson 2001)
		<i>Selenicereus</i>	a	<i>S. costaricensis</i> × <i>S. monacanthus</i> , <i>S. monacanthus</i> × <i>S. undatus</i> , <i>S. megalanthus</i> × <i>S. undatus</i> , <i>S. monacanthus</i> × <i>S. megalanthus</i>	2n, 4n	Experimental crosses and cytogenetic analyses	(Tel-Zur <i>et al.</i> 2004)
	Cereeae	<i>Arrojadoa</i>	a	<i>A. dinae</i> × <i>A. rhodantha</i>	2n	Morphological description	(Anderson 2001, Hunt <i>et al.</i> 2006)
		<i>Cereus</i>	b (<i>Cereus</i> × <i>Harrisia</i>)	<i>C. stenogonus</i> × <i>H. bonplandii</i>	2n	Morphological description	(Hunt <i>et al.</i> 2006)
		<i>Coleocephalocereus</i>	b (<i>Coleocephalocereus</i> × <i>Pilosocereus</i>)	<i>C. decumbens</i> × <i>P. magnificus</i>	-	Morphological description	(Hunt <i>et al.</i> 2006)

		<i>Melocactus</i>	a	<i>M. ernestii</i> × <i>M. glaucescens</i> , <i>M. curvispinus</i> × <i>M. stramineus</i> , <i>M. ernestii</i> × <i>M. zehntneri</i> , <i>M. concinnus</i> × <i>M. glaucescens</i> , <i>M. concinnus</i> × <i>M. ernestii</i> , <i>M. concinnus</i> × <i>M. zehntneri</i> , <i>M. concinnus</i> × <i>M. paucispinus</i> (Khan et al. 2020)	2n, 4n	Molecular markers and morphometric analysis / Molecular markers	(Hunt et al. 2006, Lambert et al., 2006a, 2006b, Khan et al. 2020)
		<i>Micranthocereus</i>	b (<i>Micranthocereus</i> × <i>Pilosocereus</i>)	<i>M. purpureus</i> × <i>P. pentaedrophorus</i>	2n	Morphological description	(Hunt et al. 2006)
		<i>Pilosocereus</i>	a, b	<i>P. floccosus</i> × <i>P. magnificus</i> , <i>P. densiareolatus</i> × <i>P. pachycladus</i>	2n, 4n	Morphological description	(Anderson 2001, Hunt et al. 2006)
	Trichocereae	<i>Arthrocereus</i>	b (<i>Trichocereus</i> × <i>Denmoza</i>)	<i>T. atacamensis</i> × <i>D. rhodacantha</i>	-	Morphological description	(Font & Picca 2001)
		<i>Cleistocactus</i>	a, b (<i>Cleistocactus</i> × <i>Matucana</i> ,	<i>C. icosagonus</i> × <i>C. serpens</i> ,	2n	Morphological description	(Anderson 2001, Hunt et al. 2006)

			<i>Cleistocactus</i> × <i>Yungasocereus</i> , <i>Cleistocactus</i> × <i>Espostoa</i>)	<i>C. fieldianus</i> × <i>M. supertexta</i> , <i>C. laniceps</i> × <i>Y. inquisivensis</i> , <i>C. icosagonus</i> × <i>E. lanata</i>			
		<i>Denmoza</i>	b (<i>Denmoza</i> × <i>Echinopsis</i>)	<i>D. rhodacantha</i> × <i>E. atacamensis</i>	-	Morphological description	(Font & Picca 2001, Hunt <i>et al.</i> 2006)
		<i>Echinopsis</i>	a, b (<i>Echinopsis</i> × <i>Matucana</i>)	<i>E. strigosa</i> × <i>E. terscheckii</i> <i>E. senilis</i> × <i>M. comacephala</i>	2n	Morphological description / Morphological description	(Hunt <i>et al.</i> 2006, Eggli & Giorgetta 2018)
		<i>Espostoa</i>	b (<i>Espostoa</i> × <i>Haageocereus</i> , <i>Espostoa</i> × <i>Weberbauerocereus</i>)	<i>E. melanostele</i> × <i>H. pseudomelanostele</i> , <i>E. ruficeps</i> × <i>W. albus</i>	2n	Morphological description	(Hunt <i>et al.</i> 2006)
		<i>Gymnocalycium</i>	a	<i>G. esperanzae</i>	2n 4n	Molecular markers	(Řepka & Mráček 2012)
		<i>Harrisia</i>	b (<i>Cereus</i> × <i>Harrisia</i>)	<i>C. stenogonus</i> × <i>H. bonplandii</i>	2n	Morphological description	(Hunt <i>et al.</i> 2006)
		<i>Matucana</i>	b (<i>Matucana</i> × <i>Oroya</i> , <i>Matucana</i> × <i>Oreocereus</i>)	<i>M. yanganucensis</i> × <i>Oroya borchersii</i>	2n	Morphological description	(Hunt <i>et al.</i> 2006)
		<i>Oreocereus</i>	b (<i>Oreocereus</i> × <i>Echinopsis</i>)	<i>O. celsianus</i> × <i>E. tarijensis</i>	-	Morphological description	(Hunt <i>et al.</i> 2006)

				<i>O. celsianus</i> × <i>E. ferox</i>			
		<i>Rauhocereus</i>	b (<i>Rauhocereus</i> × <i>Espostoa</i>)	<i>R. riosaniensis</i> × <i>E. superba</i>	-	Morphological description	(Hunt <i>et al.</i> 2006)
	Cacteae	<i>Escobaria</i>	a	<i>E. guadalupensis</i> × <i>E. sneedii</i>	2n	Morphometric analysis	(Baker & Johnson 2000)
		<i>Ferocactus</i>	b (<i>Ferocactus</i> × <i>Leuchtenbergia</i>)	<i>Ferocactus</i> × <i>L. principis</i>	2n	Morphological description	(Anderson 2001)
		<i>Geohintonia</i>	b (<i>Geohintonia</i> × <i>Aztekium</i>)	<i>G. mexicana</i> × <i>A. hintonii</i>	-	Morphological description	(Anderson 2001, Hunt <i>et al.</i> 2006)
		<i>Sclerocactus</i>	a	<i>S. wetlandicus</i> × <i>S. brevispinus</i> , <i>S. glaucus</i> × <i>S. parviflorus</i>	2n	Experimental crosses / Molecular markers	(Tepedino <i>et al.</i> 2010, Schwabe <i>et al.</i> 2015)
		<i>Turbinicarpus</i>	a	<i>T. laui</i> × <i>T. pseudopectinatus</i>	2n	Morphological description	(Anderson 2001, Hunt <i>et al.</i> 2006)
	Notocacteae	-	-	-	-	-	-
	Rhipsalideae	-	-	-	-	-	-
Opuntioideae	Cylindropuntieae	<i>Cylindropuntia</i>	a	<i>C. acanthocarpa</i> × <i>C. whipplei</i> , <i>C. arbuscula</i> × <i>C. spinosior</i> , <i>C. echinocarpa</i> × <i>C. whipplei</i> , <i>C. acanthocarpa</i> × <i>C. leptocaulis</i> , <i>C.</i>	2n, 3n, 4n, 8n	Morphometric, chromosome counting and pollen viability	(Baker & Pinkava 1987, Hunt <i>et al.</i> 2006)

				<i>imbricata</i> × <i>C.</i> <i>whipplei</i> , <i>C.</i> <i>arbuscula</i> × <i>C.</i> <i>versicolor</i> , <i>C.</i> <i>acanthocarpa</i> × <i>C.</i> <i>echinocarpa</i> , <i>C.</i> <i>fulgida</i> × <i>C.</i> <i>spinosior</i> , <i>C.</i> <i>acanthocarpa</i> × <i>C.</i> <i>bigelovii</i> , <i>C.</i> <i>bigelovii</i> × <i>C.</i> <i>echinocarpa</i> , <i>C.</i> <i>spinosior</i> × <i>C.</i> <i>versicolor</i>			
	Opuntieae	<i>Opuntia</i>	a	<i>O. littoralis</i> × <i>O.</i> <i>phaeacantha</i> , <i>O.</i> <i>fragilis</i> × <i>O.</i> <i>polyacantha</i> , <i>O.</i> <i>engelmannii</i> × <i>O.</i> <i>macrorrhiza</i> , <i>O.</i> <i>chlorotica</i> × <i>O.</i> <i>phaeacantha</i> , <i>O.</i> <i>aureispina</i> × <i>O.</i> <i>phaeacantha</i> , <i>O.</i> <i>littoralis</i> × <i>O.</i> <i>engelmannii</i> × (<i>O.</i>	2n, 3n, 4n, 5n, 6n, 8n, 9n	Chromosome counting / Molecular markers	(Pinkava 2002, Hunt <i>et al.</i> , 2006, Majure <i>et al.</i> 2012b, 2014, 2017)

				<i>phaeacantha</i>), <i>O. aureispina</i> × <i>O. macrocentra</i> , <i>O. engelmannii</i> × <i>O. microdasys</i> 20 taxa of hybrid origin (Majure <i>et al.</i> 2012a) <i>O. dillenii</i> × <i>O. abjecta</i> , (Majure <i>et al.</i> 2014) <i>O. cespitosa</i> , <i>O. humifusa</i> , <i>O. nemoralis</i> (Majure <i>et al.</i> 2017)			
		<i>Tacinga</i>	a	<i>T. inamoena</i> × <i>T. palmadora</i>	2n, 4n	Morphological description	(Anderson 2001, Hunt <i>et al.</i> 2006)
		<i>Consolea</i>	b (<i>Consolea</i> × <i>Opuntia</i>)	<i>C. rubescens</i> × <i>O. dillenii</i> , <i>C. nashii</i> × <i>O. dillenii</i> , <i>O. acaulis</i> <i>O. bahamana</i> <i>O. lucayana</i>	2n, 6n, 8n, 12n	Chromosome counting	(Negrón-Ortiz 2007, Majure <i>et al.</i> 2012b)
Pereskioideae	-	-	-				-
Maihuenioideae	-	-	-				-

Literature cited

- Anderson EF. 2001. *The Cactus family*. Portland, Oregon: Timber Press. ISBN: 9780881924985
- Baker MA, Johnson RA. 2000. Morphometric analysis of *Escobaria sneedii* var. *sneedii*, *E. sneedii* var. *leei*, and *E. guadalupensis* (Cactaceae). *Systematic Botany* **25**: 577-587. DOI: <https://doi.org/10.2307/2666722>
- Baker MA, Pinkava DJ 1987. A cytological and morphometric analysis of a triploid apomict, *Opuntia* × *kelvinensis* (subgenus *Cylindropuntia*, Cactaceae). *Brittonia* **39**: 387-401. DOI: <https://doi.org/10.2307/2807141>
- Copetti D, Búrquez A, Bustamante E, Charboneau JL, Childs K L, Eguiarte LE, Lee S, Liu TL, McMahon MM, Whiteman NK, Wing RA, Wojciechowski MF, Sanderson MJ. 2017. Extensive gene tree discordance and hemiplasy shaped the genomes of North American columnar cacti. *PNAS* **114**: 12003-12008. DOI: <https://doi.org/10.1073/pnas.1706367114>
- Cruz-Zamora Y, Cruz-García F, Orozco-Arroyo G, Reyes-Santiago J, Martínez-Castilla LP, Wegier A, Vázquez-Santana S. 2017. × *Polascontria* (Cactaceae), a nothogenus that represents the gene flow between *Escontria* and *Polaskia*. *Phytotaxa* **295**: 141-158. DOI: <https://doi.org/10.11646/phytotaxa.295.2.3>
- Eggl U, Giorgetta M. 2018. A putative intercladal *Echinopsis* s. l. (Cactaceae) hybrid from Andean Chile. *Haseltonia* **2018**:7-16. DOI: <https://doi.org/10.2985/026.024.0103>
- Font F, Picca P. 2001. Natural hybridization between *Trichocereus atacamensis* (Philippi) Marshall and *Denmoza rhodacantha* (Salm-Dyck) Britton & Rose (Cactaceae). *Bradleya* **19**: 59-66. DOI: <https://doi.org/10.25223/brad.n19.2001.a7>
- Hunt DR, Taylor NP, Charles G. 2006. *The new cactus lexicon: Text*. Inglaterra: DH books. ISBN: 9780953813452.

- Khan G, Franco FF, Silva GAR, Bombonato JR, Machado M, Alonso DP, Ribolla PEM, Albach DC, Moraes EM. 2020. Maintaining genetic integrity with high promiscuity: Frequent hybridization with low introgression in multiple hybrid zones of *Melocactus* (Cactaceae). *Molecular Phylogenetics and Evolution* **142**: 106642. DOI: <https://doi.org/10.1016/j.ympev.2019.106642>
- Lambert SM, Borba EL, Machado MC, Andrade DS. 2006a. Allozyme diversity and morphometrics of *Melocactus paucispinus* (Cactaceae) and evidence for hybridization with *M. concinnus* in the Chapada Diamantina, North-eastern Brazil. *Annals of Botany* **97**: 389-403. DOI: <https://doi.org/10.1093/aob/mcj052>
- Lambert SM, Borba EL, Machado MC. 2006b. Allozyme diversity and morphometrics of the endangered *Melocactus glaucescens* (Cactaceae), and investigation of the putative hybrid origin of *Melocactus* × *albicephalus* (*Melocactus ernestii* × *M. glaucescens*) in north-eastern Brazil. *Plant Species Biology* **21**: 93-108. DOI: <https://doi.org/10.1111/j.1442-1984.2006.00155.x>
- Majure LC, Judd WS, Soltis PS, Soltis DE. 2012a. Cyto geography of the Humifusa clade of *Opuntia* s.s. Mill. 1754 (Cactaceae, Opuntioideae, Opuntieae): correlations with Pleistocene refugia and morphological traits in a polyploid complex. *Comparative Cytogenetics* **6**: 53-77. DOI: <https://doi.org/10.3897/CompCytogen.v6i1.2523>
- Majure LC, Judd WS, Soltis PS, Soltis DE. 2017. Taxonomic revision of the *Opuntia humifusa* complex (Opuntieae: Cactaceae) of the eastern United States. *Phytotaxa* **290**: 1-65. DOI: <https://doi.org/10.11646/phytotaxa.290.1.1>
- Majure LC, Puente R, Griffith MP, Judd WS, Soltis PS, Soltis DE. 2012b. Phylogeny of *Opuntia* s.s. (Cactaceae): Clade delineation, geographic origins, and reticulate evolution. *American Journal of Botany* **99**: 847-864. DOI: <https://doi.org/10.3732/ajb.1100375>
- Majure LC, Soltis DE, Soltis PS, Judd WS. 2014. A case of mistaken identity, *Opuntia abjecta*, long-lost in synonymy under the Caribbean species, *O. triacantha*, and a

- reassessment of the enigmatic *O. cubensis*. *Brittonia* **66**: 118-130. DOI: <https://doi.org/10.1007/s12228-013-9307-z>
- Negrón-Ortiz V. 2007. Chromosome numbers, nuclear DNA content, and polyploidy in *Consolea* (Cactaceae), an endemic cactus of the Caribbean Islands. *American Journal of Botany* **94**: 1360-1370. DOI: <https://doi.org/10.3732/ajb.94.8.1360>
- Pinkava DJ. 2002. On the evolution of the North American Opuntioideae. *Succulent Plant Research* **6**: 59-98.
- Powell AM, Zimmerman AD, Hilsenbeck RA. 1991. Experimental documentation of natural hybridization in Cactaceae: origin of Lloyd's Hedgehog Cactus, *Echinocereus* × *lloydii*. *Plant Systematics and Evolution* **178**: 107-122.
- Řepka R, Mráček, J. 2012. *Gymnocalycium esperanzae*: A nothospecies? *Haseltonia* **18**: 105-115. DOI: <https://doi.org/10.2985/026.018.0113>
- Schwabe AL, Neale J R, McGlaughlin ME. 2015. Examining the genetic integrity of a rare endemic Colorado cactus *Sclerocactus glaucus* in the face of hybridization threats from a close and widespread congener *Sclerocactus parviflorus*. *Conservation Genetics* **16**: 443-457. DOI: <https://doi.org/10.1007/s10592-014-0671-3>
- Tapia HJ, Bárcenas-Argüello ML, Terrazas T, Arias S. 2017. Phylogeny and circumscription of *Cephalocereus* (Cactaceae) based on molecular and morphological evidence. *Systematic Botany* **42**: 709-723. DOI: <https://doi.org/10.1600/036364417X696546>
- Tel-Zur N, Abbo S, Bar-Ziv D, Mizrahi Y. 2004. Genetic relationships among *Hylocereus* and *Selenicereus* vine cacti (Cactaceae): Evidence from hybridization and cytological studies. *Annals of Botany* **94**: 527-534. DOI: <https://doi.org/10.1093/aob/mch183>
- Tepedino VJ, Griswold TL, Bowlin WR. 2010. Reproductive biology, hybridization, and flower visitors of rare *Sclerocactus* taxa in Utah's Uintah Basin. *Western North American Naturalist* **70**: 377-386. DOI: <https://doi.org/10.3398/064.070.0310>

Vite F, Portilla E, Zavala-Hurtado JA, Valverde PL, Díaz-Solís A. 1996. A natural hybrid population between *Neobuxbaumia tetetzo* and *Cephalocereus columna-trajani* (Cactaceae). *Journal of Arid Environments* **32**: 395-405. DOI: <https://doi.org/10.1006/jare.1996.0033>

Yáñez-López ML, Barbosa-Martínez C, Serrato-Díaz A, Balderas-Morales A, Campos-Muñiz C, Fernández FJ, Armella-Villalpando MA. 2016. Genetic relationships between varieties of *Stenocereus pruinosus* (Cactaceae) in the states of Puebla and Oaxaca, Mexico, by means of AFLP markers. *Agrociencia* **50**: 595-601.