

# *The Cactician*



A MISCELLANY OF TOPICS ON  
THE SUBJECT OF SUCCULENT  
PLANTS AUTHORED AND  
EDITED BY ROY MOTTRAM

Taxonomy  
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&c.

## Allotaxa of the Cactaceae

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### Summary

In contradistinction to a Darwinian theory of evolution which proposes a linear pattern of decent with new species arising through branching divergence from ancestral stock, polyploidy and especially allopolyploidy involves a reticulate pattern of evolution through plant to plant interactions creating new lineages. This paper is an introduction to a method of recording plant taxa that have been identified as actual or putative botanical or cultivar taxa of allopolyploid origin, with an alphabetic checklist of examples randomly taken from the *Cactaceae*. Some of these have been suggested before elsewhere, while others are proposed here for the first time.

### New taxa proposed in this paper:

*Anhaloniopsis* (Buxb.) Mottram comb. nov. (p.11)

*Anhaloniopsis madisoniorum* (Hutchison) Mottram comb. nov. (p.11)

*Austrocephalocereus streckeri* (van Heek & van Crieke) Mottram comb. nov. (p.15)

*Aztekonía* Mottram nothogen. nov. (p.15)

*Aztekonía hintonii* (Glass & FitzMaurice) Mottram comb. nov. (p.15)

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## Allotaxa of the *Cactaceae*

“The most curious feature about the crossing of the giant opuntias with the small species, in particular with the little cactus known as *Opuntia vulgaris*, was that the hybrid was intermediate between the parents in every character but one. In size, stem, manner of growth and form of pads, it made a complete blend of the traits of the two totally dissimilar parents. But its blossom was a relatively enormous flower, much larger than that of either parent. This intermediate type, strikingly dissimilar to either parent, yet obviously blending the characteristics of both, bred true to form, showing nothing of that tendency to racial variation in the second generation that marks hybrids in general and the hybrids of the other cactuses very conspicuously.” (Luther Burbank, *His methods & discoveries* 8: 179-181. 1914)

**“Not only does this new mode hold true under cultivation but species are also summarily produced in a wild state by natural crossing.”** (Luther Burbank, Presentation to the American Breeders Association, Jan 1909).



Fig. 1 Luther Burbank portrait, inset on the cover of his 1914 autobiography.

The two quotations above, uttered by Luther Burbank (1849-1926) more than 100 years ago, describe how he generated the first artificially created cactus allopolyploid, and by logically predicting that this phenomenon also occurs in nature he had stumbled across the most important of all the factors that contribute to species diversity. Despite his fame as a plant breeder, this hugely important contribution to evolutionary biology went barely recorded and largely ignored, even to this day. (Fig. 1-3)





**Mr. Burbank Selecting Cactus Seedlings**

Remember that most of these little fellows are covered with spicules. Mr. Burbank's hands are also covered with spicules; and his clothes are full of them. He asserts that the task of dealing with these tiny citizens, in the effort to educate them into spinelessness, was the most painful one in his experience.

Fig. 2 Burbank's opuntia trial grounds. Glass plate photo, from John Cox archive.

Fig. 3 Burbank selecting opuntia seedlings, from Burbank, *Luther Burbank, his methods & discoveries and their practical application* 8: 185. 1914.

New species and other taxa in nature can be created by conventional hybridisation, followed by a protracted process of selection and in-breeding, or they may be produced more or less instantaneously by allopolyploidy, which is a summation of the genetic material of two distinct taxa.

Allopolyploids are true-breeding taxa, whose nomenclature is today treated the same as conventional botanical taxa in accordance with the *International Code of Nomenclature*, without the need of hybridity signs. Normal hybrids are identifiable because from the second generation onwards their progeny exhibit a full spectrum of variation between the parent taxa and they are not the equivalent of new species.

In order to distinguish allopolyploids from species and hybrids, it is here proposed to use the mathematical summation sign  $\Sigma$ , the Greek capital letter sigma, as a shorthand notation.

The new species, genera and other taxonomic ranks thus created are here called **allotaxa**, from the Greek ἄλλος, other, and they are equivalent to the nothotaxa of conventional hybrids that are signified with the multiplication sign  $\times$ . Both normal hybrids and allopolyploids can arise from the cross-pollination of two dissimilar parents, but allopolyploids are not hybrids, although they have often been treated as such, while in other instances they can go unnoticed because they behave like true species.

Traditionally allospecies and allosubspecies have their epithets written without the hybrid sign. This is because they behave as though they are conventional taxa and are not easily distinguishable from them, so the assumption that has been built into all editions of the *International Code of Botanical Nomenclature* to date is that they should be treated the same as species.



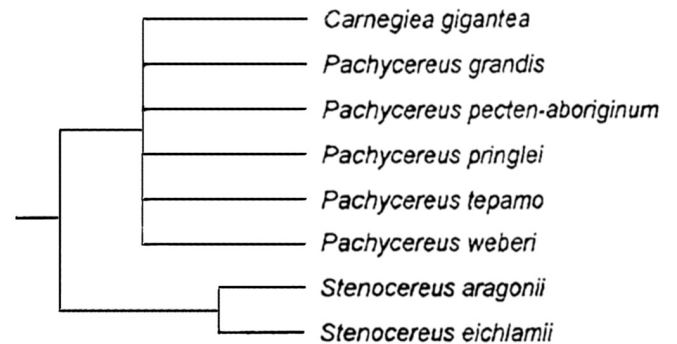
## Intergeneric allotaxa

When an allopolyploid arises from taxa belonging to different genera, they are plants which do not belong to the genus of either parent. On the other hand they are not nothogenera either. The formulaic nature of nothogeneric names could theoretically be applied to them, but that would be confusing, and as it involves the creation of many more names than exist at present it is predictable that we could soon run out of possible recombinations of name parts. There is also a certain degree of conflict with the separate system for the naming of graft-chimera genera that is a special case of the system for the naming of hybrids.

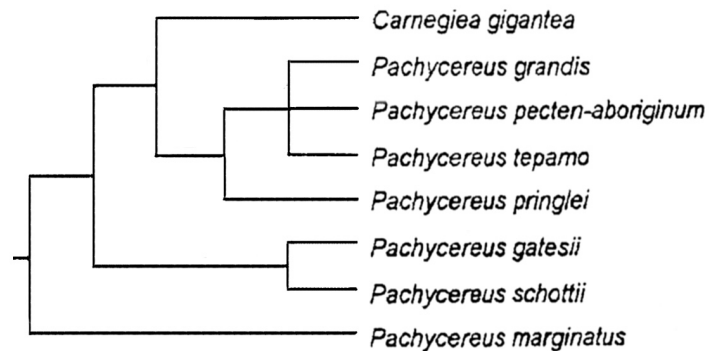
By way of a compromise, names have been adopted in this paper that either already exist as genera or nothogenera or may be newly formed from any source whatsoever.

Fig. 4 Comparison of nuclear and plastid DNA data (adapted from Arias & al., 2003) & corrected phylogenetic scheme for the *Pachycereinae*.

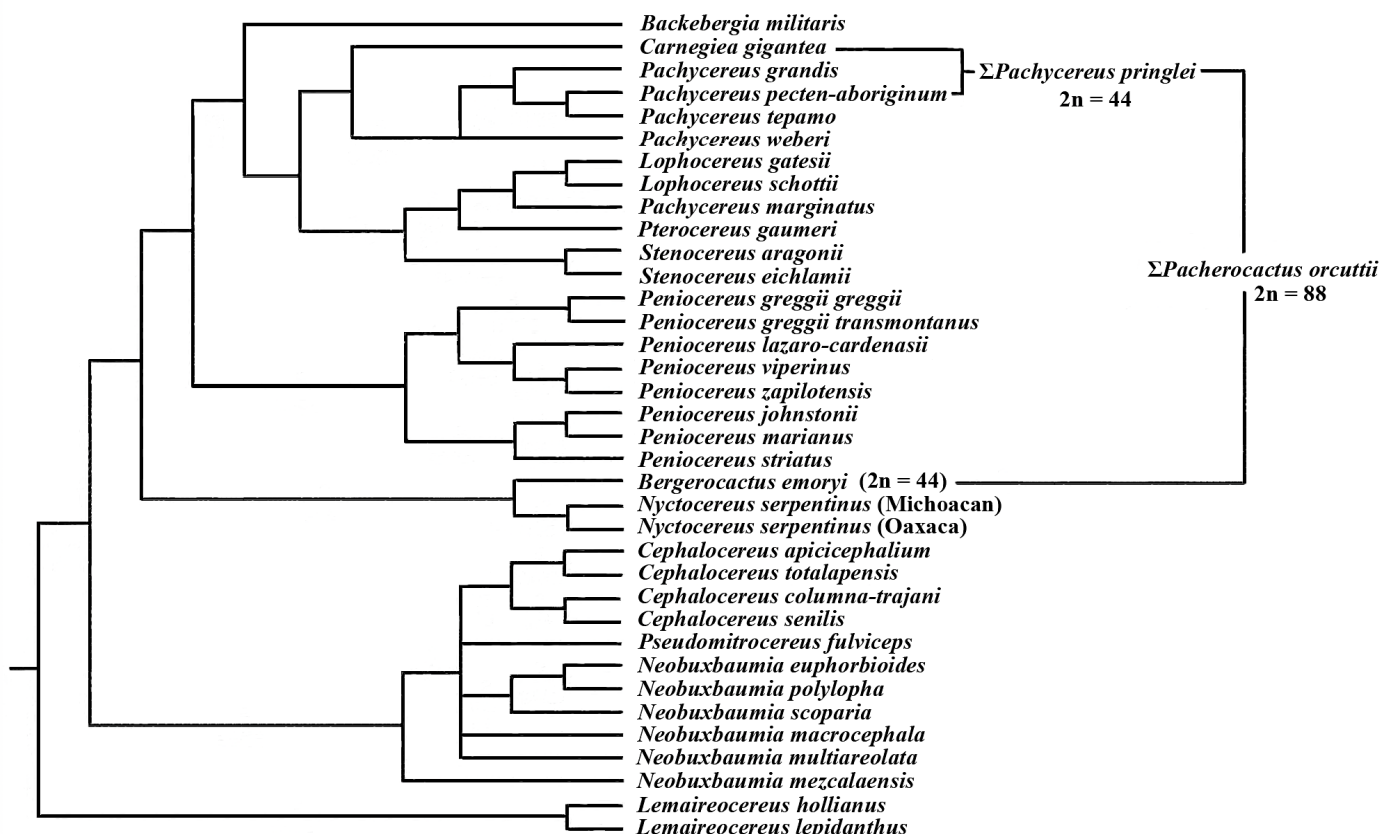
It follows logically that phylogenetic trees drawn without recognition of the allopolyploids are always going to be wrong or misleading. In fact phylogenies are not branched trees at all, but a network of branches built on a cascade of allopolyploid



Pachycereinae and outgroup taxa based on nuclear ITS1, 5.8S, and ITS2 sequences (ITS).



Pachycereinae and outgroup taxa based on plastid *trnL* intron



events throughout history, interspersed with periods of natural selection. It will never be possible to trace the complete ancestry of any lineage, but approximate trees should improve with the addition of new data.

Up to now the majority of trees drawn from molecular data have used only plastid DNA markers. These follow the maternal lines of descent only. Where an allopolyploid event has taken place it will misleadingly appear in the female lineage, not at the beginning of a completely new and independent lineage based on a combination of dissimilar taxa.

It is necessary to identify allopolyploid events in the phylogeny by measuring markers of both plastid (and/or mitochondrial) and nuclear origin, and to make careful comparisons between them. Where they differ is usually an indication of where an allopolyploid event has taken place. (Fig. 4)

Allotaxa, as with hybrids, occur randomly in nature and rely only the presence of two species being sympatric. Since they share genes that may have been handed down from differing lineages, failure to recognise them results in taxa being considered as conventional but paraphyletic taxa, whereas they are in fact resulting from random gene sharing. The resulting classification and its nomenclature will be flawed, unless the allopolyploids have been identified and new randomly created lineages put in place to accommodate them.

The long process of identifying allotaxa has barely begun. However, it will be necessary to gain a fairly broad idea of their presence in order to take them out of the equation and correctly classify in Darwinian evolutionary terms what remains of each lineage. The current debates about monophyly versus paraphyly thus seems premature, and the problem may be completely resolved once

the allotaxonomy of a group has become sufficiently well documented.

Allopolyploidy is an extremely powerful evolutionary force, because the progeny have more vigour than their parents and are better able to survive extreme conditions. For this reason, many examples of allotaxa are hard to identify because one or both parents, being weaker, have died out. For this same reason many species that are basal to most lineages can be expected to have had allopolyploidy as their origin, the weaker parents having long since died out, mainly because of climate change and especially during ice ages. Some of those with the oldest origins whose parents are extinct may never be successfully resolved, because the evidence has disappeared along with the parents. Most importantly of all, allopolyploidy creates new taxa instantaneously and is not a product of Darwinian natural selection or random mutation.

The vigour induced by higher ploidy levels is essential for the survival of taxa that are subjected to stresses that may eliminate their parents. Hence ploidy levels beyond the basic diploids are mainly found in new habitats that are too harsh to sustain the parent taxa, usually on the margins of their geographical distribution. In less severe habitats, and where the conditions become more amenable again after a stressful interlude, the ploidy levels always tend to reduce again. Meiosis of polyploids can be irregular, with a result that overall fertility is lower than in diploids. So in geographical areas that can sustain plants with lower ploidy levels, normality will be resumed by natural selection, with diploids again outnumbering and/or replacing tetraploids for example. Diploids will always predominate wherever environmental conditions will allow their survival.



## Properties and the recognition of allopolyploids

Allopolyploids are the progeny of cross-pollinations between parents of different taxa where all the genetic material from both parents is handed down. The chromosomes do not divide and therefore do not recombine in compatible pairings. For this reason there are no theoretical compatibility barriers to allopolyploids and they may therefore take place between very distantly related plants.

An allopolyploid is exactly intermediate between its two parents when their chromosomes are equal in number and there is little or no variation. Where one parent has a higher chromosome number, the intermediate nature of the progeny will demonstrate a bias towards that parent which has the higher chromosome number. In cases where one parent is a very high polyploid, the progeny will look very similar to that parent, but they are never exact replicas.

Because polyploids have greater amounts of DNA than their parents, this gives them larger cells in all their parts, which in turn provides extra vigour for survival. This gives them an advantage in stressful environments, so they can occupy a greater geographical range than their parents. So you often find that the higher ploidy numbers are at the margins of the geographical distribution.

Allopolyploids are almost fully fertile and reproduce correctly and constantly from seed, unlike hybrids which produce a spectrum of variation between the original parents and can only be stabilised by the iterative process of gradual selection for the desired characters. Any cross-pollination that results in true-breeding progeny is not a hybrid but an allopolyploid, and this is one of the easiest means of distinguishing them.

Traditionally, botanists have referred to polyploids as a doubling or multiplication of the number of chromosomes. This is wrong. The process is one of addition, not multiplication, and polyploids are only a special subset in which the parents happen to belong to the same species. Dividing autopolyploids and allopolyploids as though somehow different is a somewhat artificial distinction. Whether they occur internally within a species or externally between species is really immaterial. One term could cover all, and ploid is probably the most obvious choice of terminology.

## Chromosome reduction

Meiotic division may sometimes result in a reduction in the number of chromosomes, and this also applies to allopolyploids. In all plant populations there is a mixture of chromosome levels, but given the environmental conditions that can sustain them, the basic level of  $2n = 22$  will usually predominate in cacti, but there will still always be a few  $2n = 44$  or higher among these, and sometimes also  $2n = 11$ . However, the polyploids have a lowered fertility and the odd numbered species will be sterile. Thus, the basic level of  $2n = 22$  will predominate in most populations by the process of natural selection. (Fig. 5-7)

If, on the other hand, environmental conditions deteriorate, normal diploids will tend to die out while the polyploids are able to survive because of the greater vigour endowed on them by the extra DNA and larger cells. For example, it can be inferred that *Opuntia phaeacantha* needs to have  $2n = 66$ , the only number so far found in all its populations, for it to continue to survive.

Newly created allopolyploids will always have  $2n = 44$  or higher, but in time chromosome reduction can take place again

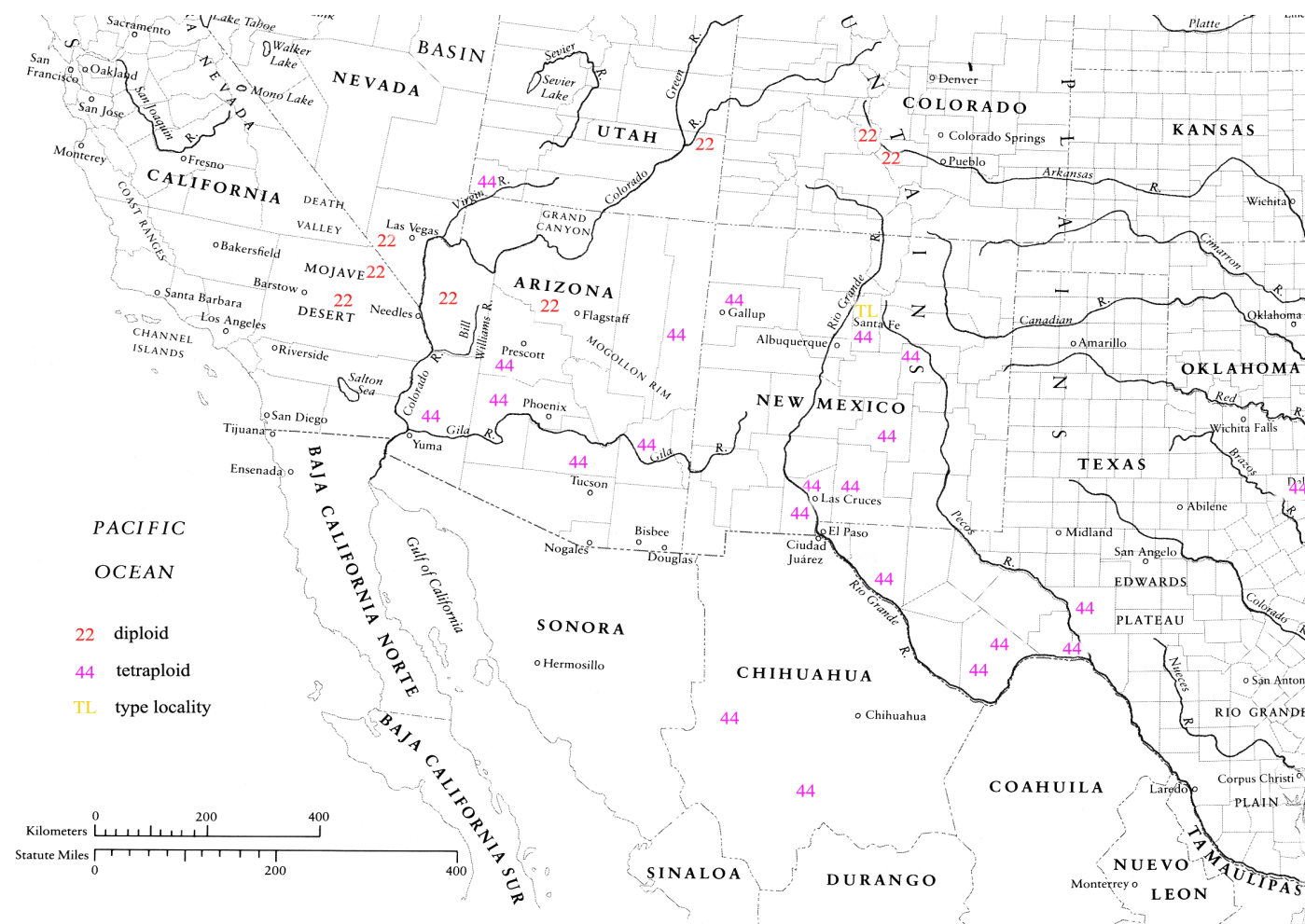


Fig. 5 *Echinocereus triglochidiatus* (sensu Benson) distribution map. An example of a species that has two ploidy levels. The distribution here suggests that the higher number allows the species to invade areas of the USA to the east that are wetter, where the diploids would not survive without rotting or being out-competed by denser vegetation.

Fig. 6 *Echinocereus triglochidiatus* ssp. *mojavensis* (USA, California, Inyo County, c.10km NE of Big Pine, c.2000m) Roy Thackeray photo.  $2n = 22$ .

Fig. 7 *Echinocereus triglochidiatus* SB236 (New Mexico, Otero Co., Jarilla Mtns.) Pink flowered form not far from the type locality.  $2n = 44$ .





if environmental conditions allow. Therefore, a putative allopolyploid does not necessarily have higher ploidy levels today, which makes their detection somewhat harder, but the other clues such as an intermediate morphology with little or no variation will still be present.

### **Nomenclatural treatment**

The ICN has no rules specifically designed for use with allopolyploids. The only examples of allopolyploids in the Code appear under Art. H.3.3 Note 1, although not referred to by that term, but instead called “true-breeding tetraploid”, “stabilised hybrid” or “genome comprising several wild species”. There it suggests that they be treated as species, without the hybridity sign. No examples of intergeneric allopolyploids are quoted.

The rules of nomenclature applied in this paper assume the following new aphorisms:

1. The rank of an allotaxon should be the same as that of its parents, i.e. an intergeneric allotaxon has the rank of genus, interspecific allotaxon the rank of species, and so on.
2. A new allogeneric name may not repeat the name of an existing genus or nothogenus, and the same at other ranks.
3. The name of a new allotaxon may be from any source whatsoever, and does not necessarily have to be a condensed formula, but an existing nothotaxon name can be adopted or a new nothotaxon created, with the same rules for nothotaxon formation.
4. A new name that is not a nothotaxon must have a new description or refer to one. A nothotaxonic name may be applied to either a hybrid or an allopolyploid taxon.

5. An allotaxon requires a statement of parentage, and at least one parent must be known or postulated. This is necessary and sufficient for the name of a nothotaxon.

6. Allogenera are to be typified by the name of an included species, and other ranks by an element included in the protologue, and may be of wild or cultivated origin. It is recommended that the rules applying to botanical taxa from the ICN or to plants of cultivated origin from the ICNCP be followed as far as possible.

7. Use of the summation symbol  $\Sigma$  is optional. Lack of, or usage of the wrong symbol, may be treated as correctable.

8. Parentage formulae are arranged in alphabetic order. The female parent is to be indicated with the symbol ♀, where known. The direction of a hybrid or allopolyploid interaction is important, because the plastid and mitochondrial DNA will always be identical with that of the female parent only.

### **Checklist of putative or known allotaxa for the *Cactaceae*.**

The taxa shown here are all believed to have an allopolyploid origin. The list is by no means exhaustive, and its purpose is mainly to exemplify a method of recording them.

Accepted names and basionyms are underlined for clarity. Details of synonymy and type are annotated for completeness of the data.

**Key to abbreviations & glossary of terms:**

**allogen. nov.** (allogenus novus) Name of a genus based on intergeneric allopolyploid origins.

**allopolyploid** Any polyploid created from two separate species. cf. autopolyploid.

**allotaxon** The name of a species or other rank which has arisen as the result of allopolyploidy. Indicated using the summation symbol  $\Sigma$ .

**Art.** Article (rule) of the *ICN* (Botanical Code).

**autopolyploid** Any polyploid that occurs within a species. cf. allopolyploid.

**autotype.** A type generated by application of the rules, rather than cited by the author or otherwise designated.

**Bas.** Basionym.

**Chr.** Chromosome number.

**Cult.Art.** Article (rule) of the *ICNCP* (Cultivar Code).

**ET.** A representative specimen or illustration to clarify the application of the name of a taxon when the holotype is not readily identifiable.

**Etym.** Etymology. The source of the formation of a name or word and its meaning.

**gen.** Genus.

**HT.** Holotype.

**hybrid** A taxon, usually very variable, which has arisen as the result of cross-pollination of two different taxa. Indicated using the multiplication symbol  $\times$ . Cross-pollinations between disjunct populations of the same species are also technically hybrids because they are genetically different and would not normally occur in nature.

**ICN** International code of nomenclature for algae, fungi, and plants. (Melbourne Code, 2012), currently in its 13th. edition: *Regnum Vegetabile* 154. (Dec 2012).

**ICNCP** International code of nomenclature for cultivated plants. The Cultivar Code, currently in its 8th. edition: *Scripta Horticulturae* 10. (Oct 2009).

**infragen.** (infragenus) Unspecified rank.

**LT.** A replacement type selected from elements cited in the protologue.

**nom. nov.** (nomen novum) Replacement name for one that cannot be used, usually one that was illegitimate.

**nom. nud.** (nomen nudum) Name published without, or with inadequate, description for validation.

**nothogen.** (nothogenus) Name of hybrid origin.

**NT.** Replacement type selected when no original material is extant.

**Obs.** (observatio) An observation.

**OM** Other material.

**Par.** (parentes) Parentage, either putative or known.

**ploid** A collective term for any chromosome level, whether within a species (autopolyploid) or external (allopolyploid).

**ploidy level** The number of basic sets of chromosomes in a given ploid. 1-ploid = monoploid, 2-ploid = diploid, etc.

**polyploid** Having more than two sets of chromosomes, i.e. > 2-ploid.

**pro** As.

**Ref.** A conservative, broadly circumscribed genus to which the taxon is referred.

**Rep. Syn.** Replaced synonym. An illegitimate or otherwise unusable name on which a new name has been based. Not the same as the basionym of new combination.

**sensu** In the sense of.

**Syn.** A homotypic synonym (sharing the same type).

**T.** (typus) Data for the specimen or illustration on which the taxon is based.

**unest.** (unestablished) A cultivar name that is not established. The cultivar equivalent of being invalid.

Generic and nothogeneric names accepted here are underlined. All scientific names and book & journal titles are shown in italics in accordance with international convention.

Author abbreviations are the internationally accepted standard forms given in Brummitt & Powell, *Authors of plant names* (1992).



The rules of nomenclature and the Articles cited in this document are those contained in: McNeill, J., Barrie, F. R., Buck, W. R., Demoulin, V., Greuter, W., Hawksworth, D. L., Herendeen, P. S., Knapp, S., Marhold, K., Prado, J., Prud'homme van Reine, W. F., Smith, G. F., Wiersema, J. H., & Turland, N.

J. (ed.) **International code of nomenclature for algae, fungi, and plants (Melbourne Code) adopted by the Eighteenth International Botanical Congress Melbourne, Australia, July 2011.** *Regnum Vegetabile* **154**. Koeltz Scientific Books, Königstein, for the International Association for Plant Taxonomy, Bratislava, 2012.

**ΣAnhaloniopsis** (Buxb.) Mottram **allogen. et comb. nov.** [Bas: *Loxanthocereus* subgen. *Anhaloniopsis* Buxb., Gattung *Loxanthocereus*, in Krainz (ed.) *Die Kakteen* (58): [8]. (1 Jul 1974).].

*Par. Matucana* Britton & Rose Σ *Thrixanthocereus* Backeb.

*Etym*: From the substantive *Anhalonium*, and the Latin *-opsis*, -like.

*T*: *Borzicactus madisoniorum* Hutchison = Σ*Anhaloniopsis madisoniorum* (Hutchison) Mottram.

**Anhaloniopsis Σmadisoniorum** (Hutchison) Mottram **allospec. et comb. nov.** [Bas: *Borzicactus madisoniorum* Hutchison, *Cact. Succ. J. (US)* **35**(6): 167(descr.),170(typ.). (Nov-Dec) 1963. (Fig. 8-11)].

*Par: Matucana paucicostata* F.Ritter Σ *Thrixanthocereus blossfeldiorum* (Werderm.) Backeb. (2n = 22).

*Chr*: Not known.

Taxonomic history:

*Borzicactus madisoniorum* Hutchison, *Icones plantarum succulentarum* 22. *Borzicactus madisoniorum*, sp. nov., *Cactus and Succulent Journal of the Cactus and Succulent Society of America* **35**(6): 167-170-172. (Nov-Dec) 1963.

*Submatucana madisoniorum* (Hutchison) Backeb., *Kakteenlexikon*: 412. 1966.

*Matucana madisoniorum* (Hutchison) G.D.Rowley, *Repertorium plantarum succulentarum* **22**: 10. 1973.

*Loxanthocereus madisoniorum* (Hutchison) Buxb., Gattung *Loxanthocereus*, in Krainz (ed.) *Die Kakteen* (58): [8]. (1 Jul) 1974.

*Eomatucana madisoniorum* (Hutchison) F.Ritter, *Kakteen in Südamerika* **4**: 1487. 1981.

*Etym*: Named for Marshall P. & Elena Eyre MADISON, of San Francisco and Atherton, California, donors to the Cactus and Succulent Research Fund, University of California, via their own Madison Fund, San Francisco.

*T*: Peru, Dept. Amazonas, Prov. Bagua, Rio Marañon valley several km. below its junction with the Rio Utcubamba, between km.243 (Rentema) and km.247 (Campomiento Santa Rosa) E of Olmos on the Mesones-Muro highway, on steep cliff and hill faces E of the river just above the road, c.400m; *Paul C. HUTCHISON 1521*.

*HT*: UC 1188467.

*IT*: F. NY. UC (boxed). US. USM.

*OM*: 19 collected plants and a number of seedlings in cultivation at the University of California Botanic Garden. Plate by May Blos and several photos accompany the protologue.





Fig. 8 *Anhaloniopsis*  $\Sigma$ madisoniorum. The stem will elongate with age reaching up to 30cm. in height. The diameter here is around 9cm., but it does not expand much more with age.

Fig. 9 *Anhaloniopsis*  $\Sigma$ madisoniorum. A white flowered form.

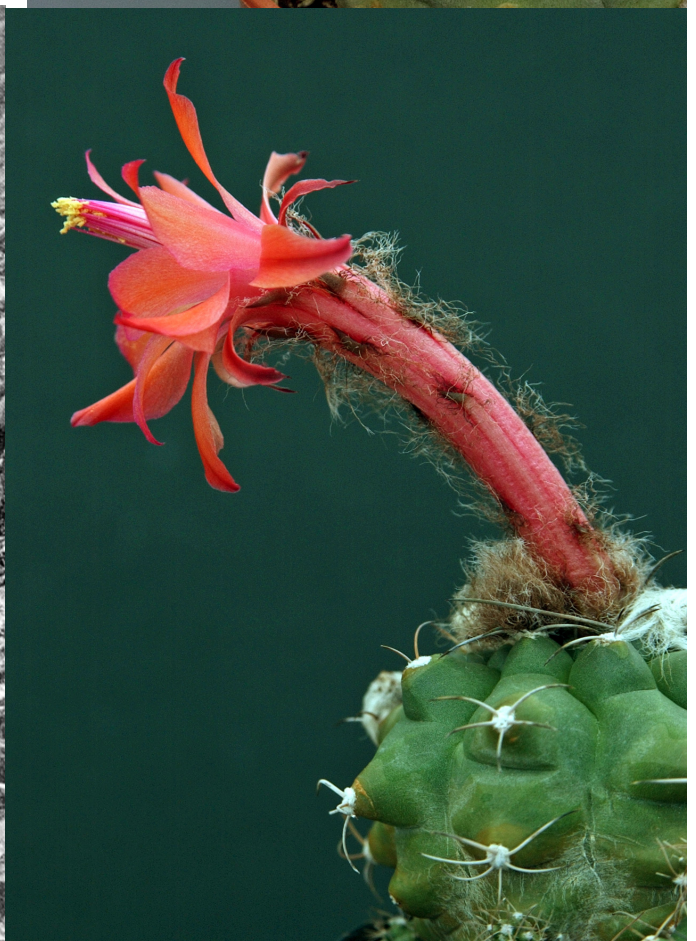
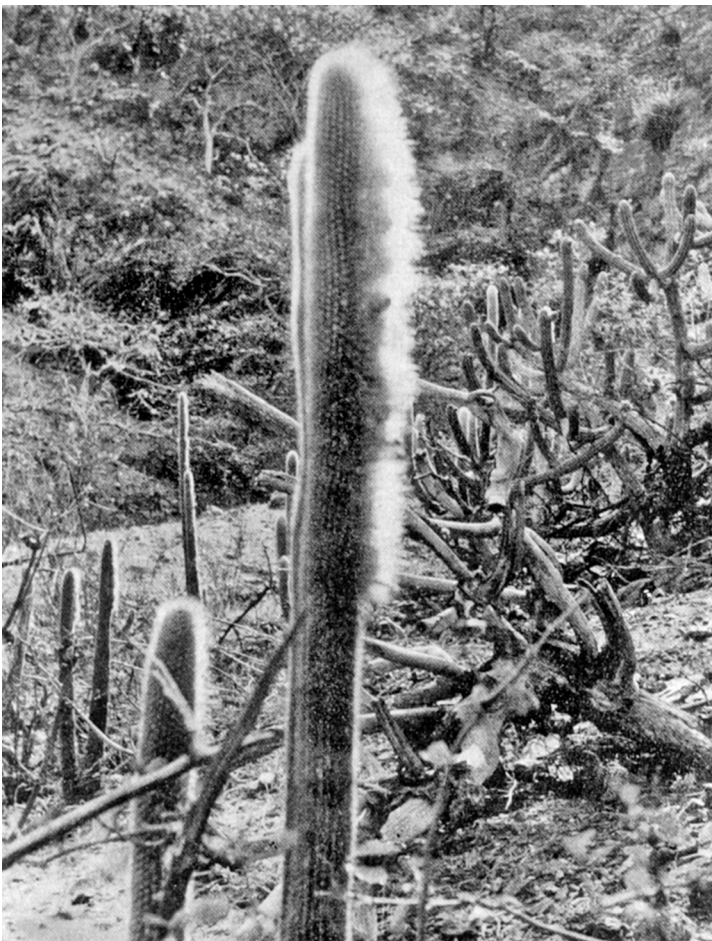


Fig. 10 *Thrixanthocereus* *blossfeldiorum* Backeberg photo 1937 in the Huancabamba valley near the type locality.

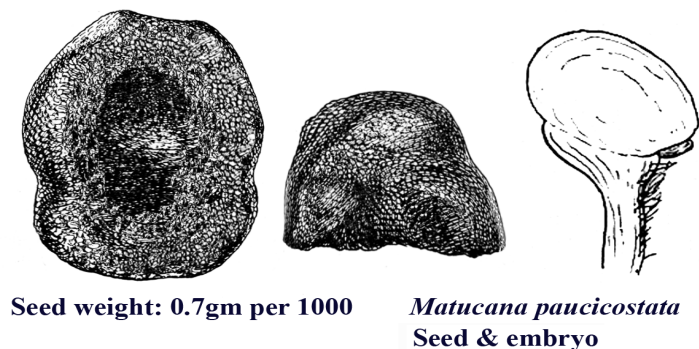
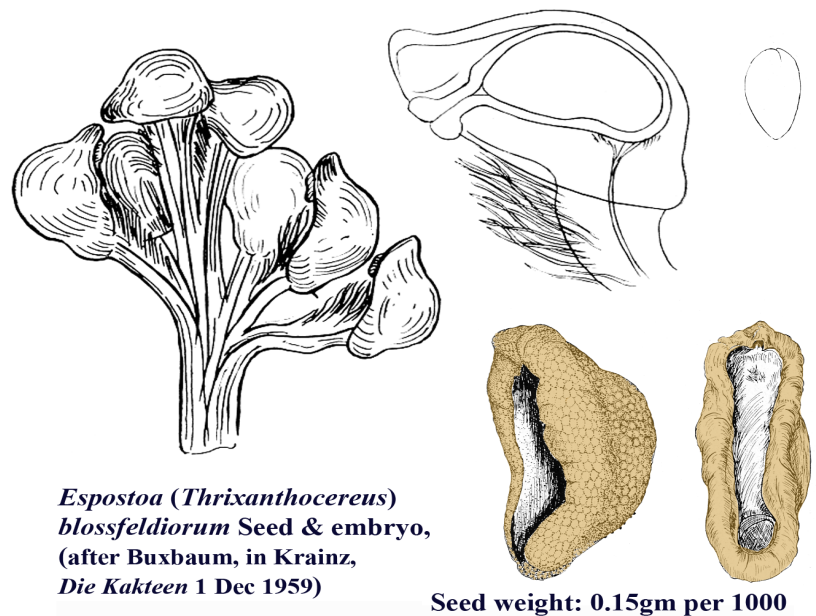
Fig. 11 *Matucana* *paucicostata*.



Fig. 12 Comparisons of ovules and seeds of *Thrixanthocereus blossfeldiorum* (top), *Anhaloniopsis Σmadisoniorum* (middle), and *Matucana paucicostata* (bottom).

Obs: *Thrixanthocereus blossfeldiorum* has an apomorphy of having one of the lowest weight seeds of any cactus, but an expanded testa to increase its volume, and thus adapted to wind dispersal. This is partially inherited by *Anhaloniopsis Σmadisoniorum*, whose seed weight is the sum of that of its putative parents. (Fig. 12)

*Matucana ×pujupatii* (Donald & A.B.Lau) Bregman appears to be a back-cross of *A. Σmadisoniorum* with *M. paucicostata* at the higher altitude of 1000-1500m., where the latter species still occurs but not *A. Σmadisoniorum*.



Plants of the type population appear to have been first generation hybrids that have never been found again. (Fig. 13) Strictly speaking, a new nothogenus to accommodate the hybrid *Anhaloniopsis Σmadisoniorum* × *M. paucicostata* is justified, but as *Matucana ×pujupatii* appears to have died out there seems little point in burdening the system with yet another new name.

Fig. 13 *Matucana ×pujupatii* Lau 107 (type collection). This clone has flowers with no diaphragm, like *Anhaloniopsis Σmadisoniorum*, but Donald reported that in his type plant, a diaphragm was present, demonstrating the variability of the hybrid population. Diaphragms are always present in *Matucana paucicostata*.





***Arrojadoa*** Britton & Rose  $\Sigma$  ***Austrocephalocereus*** Backeb.

*Par. Arrojadoa dinae* Buining & Brederoo  $\Sigma$  *Austrocephalocereus* [pro *Micranthocereus*] sp.

*Chr.* Not known.

Taxonomic history:

*Arrojadoa multiflora* ssp. *hofackeriana* P.J.Braun & Esteves, *Kakteen und andere Sukkukulenten* **53**(3): 75. 2002.

*Micranthocereus hofackerianus* (P.J.Braun & Esteves) M.Machado, *Kakteen und andere Sukkukulenten* **57**(10): 272. 2006.

*T:* Brazil, Bahia, nr. Piatã, c.1100m; *Ingo HORST* 1394.

*HT:* UFG 22429.

*IT:* ZSS.

*Obs:* A putative hybrid origin had been suggested by Machado (2008: 13-14), but it is a true-breeding taxon and therefore an allopolyploid. If confirmed this will require a new allogenus.

**$\Sigma$ Arrojadoopsis** Guiggi, *Cactology* **1**: 26. 2007 (pro gen.).

*Par. Austrocephalocereus* Backeb.  $\Sigma$  *Melocactus* (L.) Link & Otto.

*T:* *Arrojadoa marylanae* Soares Filho & M.Machado.

**$\Sigma$ Arrojadoopsis marylanae** (Soares Filho & M.Machado) Guiggi (Fig. 14)

*Par:* Probably *Cereus leucostele* Gürke  $\Sigma$  *Melocactus ernestii* Vaupel.

*Chr.* Not known.

*Etym.* From the substantive name *Arrojadoa*, and the Greek suffix *-opsis*, -like.



Taxonomic history:

*Arrojadoa marylanae* Soares Filho & M.Machado, *British Cactus & Succulent Journal* **21**(3): 114. 2003.

*Arrojadoopsis marylanae* (Soares Filho & M.Machado) Guiggi, *Cactology* **1**: 26. 2007.

*T:* Brazil, Bahia, Mun. Tanhaçu, Suçuarana, Serra Escura; 19 Apr 2003, *Marlon C. MACHADO* 28.

*HT:* HUEFS.

*Obs:* A putative hybrid origin was first suggested by Taylor & Zappi (2004: 302), without parentage, speculating that perhaps *Arrojadoa* and *Coleocephalocereus* may have been involved, but the stature and morphology seem to be more suggestive of the parentage suggested above.

Fig. 14 *Arrojadoopsis*  $\Sigma$  *marylanae* MACHADO 28 (Bahia, Mun. Tanhaçu, Suçuarana district, Serra Escura). Protologue photo of plant in fruit, from *British Cactus & Succulent Journal* **21**(3): 118, 119, 114. (Dec) 2003.



**Austrocephalocereus Streckeri** (van Heek & van Criekinge) Mottram.

*Micranthocereus polyanthus* (Werderm.) Backeb. ( $2n = 22$ )  $\Sigma$  *Micranthocereus purpureus* (Gürke) F.Ritter ( $2n = 22$ ).

*Chr.* Not known. Parentage suggests  $2n = 44$ , but it has probably undergone reduction to 22.

Taxonomic history:

*Micranthocereus Streckeri* van Heek & van Criekinge, *Kakteen und andere Sukkukulenten* **37**(5): 102-105. 1986 (pro sp.).

*Austrocephalocereus Streckeri* (van Heek & van Criekinge) Mottram **comb. nov.** [Bas: *Micranthocereus streckeri* van Heek & van Criekinge, *Kakt. and. Sukk.* **37**(5): 105. 1986].

*T.* Brazil, Bahia, W of Seabra; van Heek & al. 85/250.

*HT.* KOELN.

*Obs.* An allopolyploid origin was suggested by M.Machado, *Bradleya* **26**: 7-10. (18 Jul) 2008.

**Aylostera** Speg., Breves notas cactològicas, *An. Soc. Cient. Arg.* **96**: 75. 1923.

*Par.* *Echinopsis* Zucc.  $\Sigma$  *Rebutia* K.Schum.

*Etym.* From the Greek *aylos*, tube, and *stereos*, solid. A reference to the solid axis of the floral receptacle tube.

*T.* *Echinopsis pseudominuscula* Speg. Autotype (Art. 10.2). The only included species.

*Obs.* In the past usually mostly merged with *Rebutia* K.Schum., but molecular data and a preponderance of tetraploids suggests that this genus arose in the first instance by intergeneric allopolyploidy.

**Aztekonina** Mottram **nothogen. et allogen. nov.**

*Par.* *Aztekium* Boed.  $\Sigma$  *Geohintonia* Glass & FitzMaurice.

*Etym.* Condensed formula.

*T.* *Aztekium hintonii* Glass & FitzMaurice.

*Obs.* Proposed here under the rules for forming nothogenera. Its description is that of *Aztekium hintonii* Glass & FitzMaurice (*Cactus y Suculentas Mexicanas* **37**(1): 13-16. 1992).

**Aztekonina Shintonii** (Glass & FitzMaurice) Mottram **comb.nov.** [Bas: *Aztekium hintonii* Glass & FitzMaurice, *Cactus y Suculentas Mexicanas* **37**(1): 13-16. 1992]. (Fig. 15)

*Par.* *Aztekium ritteri* (Boed.) Boed.  $\Sigma$  *Geohintonia mexicana* Glass & FitzMaurice. (Fig. 16-17)

*Chr.* Not known. An exact intermediate between the parent morphologies, so the parents were probably both diploids.

Taxonomic history:

*Aztekium hintonii* Glass & FitzMaurice, *Cactus y Suculentas Mexicanas* **37**(1): 13-16. 1992.

*T.* Mexico, Nuevo León; *G. HINTON s.n.*

*HT.* CANTE, in IEBJ.

*Obs.* A putative hybrid origin was discussed in Machado (2008: 14-15). In this population, *Aztekium ritteri* is not present and has either died out or the allotaxon has invaded new territory.





Fig. 15 *Aztekonia Shintonii* (Glass & FitzMaurice) Mottram. Flowering plant in the collection of David Quail.



Fig. 16 *Aztekium ritteri* (Boed.) Boed.

Fig. 17 *Geohintonia mexicana* Glass & FitzMaurice.





Fig. 18 *Coryphantha* 'Trish' (*Coryphantha dasyacantha* Engelm.  $\Sigma$  *Coryphantha minima* Baird. The two protologue photos by its author.



***Coryphantha* 'Trish' (Fig. 18)**

*Par:* *Coryphantha dasyacantha* Engelm. ( $2n = 22$ )  $\Sigma$  *Coryphantha minima* Baird ( $2n = 22$ ).

*Chr:* Not known, but likely to be  $2n = 44$  from its parentage.

Taxonomic history:

*Escobaria* 'Trish' Horton, *CactusWorld* **25**(4): 233, 234. 2007.

*Obs:* Artificially created in cultivation. However, the same origin in nature would have been given the name of a botanical species, being fertile and reproducing correctly.



***ΣCylindropuntia chuckwallensis* M.A.Baker & Cloud-Hughes**

*Par.* *Opuntia multigeniculata* Clokey ( $2n = 44$ , a now extinct tetraploid of *O. echinocarpa*  $\Sigma$  *whipplei*)  $\Sigma$  *Opuntia acanthocarpa* Engelm. & J.M.Bigelow ( $2n = 22$ ).

*Chr.*  $2n = 66$  (4 populations).

Taxonomic history:

*Cylindropuntia chuckwallensis* M.A.Baker & Cloud-Hughes, *Cylindropuntia chuckwallensis* (Cactaceae), a new species from Riverside and Imperial Counties, California, *Madroño* **61**(2):231-243. (Apr) 2014.

*Etym:* Named for the Chuckwalla Mountains, Riverside County. Chuckwallan *Cylindropuntia*.



T: USA, California, Riverside County, Chuckwalla Mountains, along Corn Springs Wash, 2.5km WNW of Corn Springs, 33.6327°N 115.3527°W, alt. 550m.; 9 Apr 2012, Marc A.

BAKER 17534 & Michelle A. CLOUD-HUGHES.

HT: ASU.

IT: SD.

**Digitostigma** Velazco & Nevárez, Nuevo género de la familia *Cactaceae* en el Estado de Nuevo León, México, *Cactus y Suculentas Mexicanas* 47(4): 76-79-86. (Jan) 2003.

Par. *Astrophytum* Lem. ♀ Σ *Echinocereus* Engelm.

Etym. From the Latin *digitus*, finger, and *stigma*, mark or spot. A reference to the flecked epidermis but grammatically incorrect, meaning ‘fingered spot’ instead of the intended ‘spotted finger’.

Typ. *Digitostigma caput-medusae* Velasco & Nevárez.

Syn: *Digitostigma* Velazco & Nevarez (2002); *Astrophytum* subgen. *Stigmatodactylus* Hunt (2003).

Obs: Embryology and other characters suggest that this is an allopolyploid of a species of *Astrophytum* with a much older taxon. *Echinocereus poselgeri* is possibly the other parent, as it occurs at the same location and has the tuberous rootstock that is prominent feature of *Digitostigma*.

**Digitostigma caput-medusae** Velazco & Nevárez. (Fig. 19)

Par. *Astrophytum capricorne* (A.Dietr.)

Britton & Rose ♀ (2n = 22) Σ

*Echinocereus poselgeri* Lem.

Chr: Not known.

Taxonomic history:

*Digitostigma caput-medusae* Velazco & Nevárez, *Cactus y Suculentas Mexicanas* 47(4): 81-84. 2002.

*Astrophytum caput-medusae* (Velazco & Nevárez) D.R.Hunt, in Hunt & Taylor, *Notulae systematicae Lexicon Cactacearum spectantes III, Cactaceae Systematics Initiatives* (15): 6. (Apr) 2003.

T: Mexico, Nuevo León, 100-200m;

Manuel NEVÁREZ DE LOS REYES M. &

Carlos G. VELAZCO MACÍAS s.n.

HT: UNAL 023704.

Obs: Seedlings of this taxon often have three cotyledons, which is a useful morphological marker for allopolyploids.

Fig. 19 *Digitostigma* Σ*caput-medusae*  
Flower 7.2cm. long and broad.





***Echinocactus Σparryi*** Engelm., *Synopsis of the Cactaceae of the territory of the United States and adjacent regions*: 20. 1856 [Preprinted from *Proceedings of the American Academy of Arts and Sciences* **3**: 276. 1857]. (Fig. 20)

*Par*: *Astrophytum capricorne* (A.Dietr.) Britton & Rose ( $2n = 22$ ) Σ *Echinocactus polycephalus* Engelm. & J.M.Bigelow♀ ( $2n = 22$ ).

*Chr*: Not known. Parentage suggests  $2n = 44$ , but might have undergone reduction to 22.

Taxonomic history:

*Echinocactus parryi* Engelm., *Synopsis of the Cactaceae of the territory of the United States and adjacent regions*: 20. 1856.

*Echinocactus polycephalus* var. *parryi* (Engelm.) Borg, *Cacti* ed.2: 307. 1951.

*Emorycactus parryi* (Engelm.) Doweld, *De polyfylye van het geslacht Echinocactus, Succulenta* **75**(6): 270. 1996.

*T*: Mexico, Chihuahua, Lago Guzmán, W & SW of El Paso; *Charles Christopher PARRY s.n.*

*HT*: Not found.

*LT*: Engelmann, *Cactaceae of the Boundary*, in Emory, *Report on the United States and Mexican Boundary Survey* **2**(1): t.32, figs 6-7. 1859. Designated by Eggli, in Anderson, *Das Grosse Kakteen Lexikon*: 189. 2005.

*Obs*: The hypothesis that this was an allopolyploid was first suggested by Zlatko Janeba in *CactusWorld* **27**(1): 64-65. 2009. Molecular data places this taxon adjacent to *Echinocactus polycephalus*, so that is likely to have been the female parent. *Astrophytum* is very close to *Echinocactus* and regarded as synonymous by some authors. The possibility of a new generic name perhaps proving to be superfluous in the long run is the reason why this taxon is for now being kept within *Echinocactus*.



Fig. 20 *Echinocactus Σparryi* Flower 6.7cm. long, 6cm. diam.

**Gymnocalycium Esperanzae** Řepka & Kulhánek

*Gymnocalycium castellanosii* ssp. *armillatum* Piltz  $\Sigma$  *Gymnocalycium bodenbenderianum* (Hosseus) A.Berger.

*Chr*: Not known.

Taxonomic history:

*Gymnocalycium esperanzae* Řepka & Kulhánek, *Gymnocalycium esperanzae* Řepka et Kulhánek, a new species from La Rioja Province, Argentina, *Schütziana* **2**: 3-21. 2011.

*Gymnocalycium*  $\times$  *esperanzae* (Řepka & Kulhánek) Řepka & Mráček, *Haseltonia* **18**: 114. 2012.

*Etym*: Named for the village Esperanza, the closest village to the type locality.

*Gymnocalycium* of Esperanza.

*T*: Argentina, La Rioja, General San Martín Dept., W of Nueva Esperanza (Las Tres Marias), c.500m.; 21 Jan 2010, R. Řepka RER434 = TOM 09-436/1.

*HT*: CORD.

*Obs*: Described with a suggestion of it being of a stabilised hybrid origin on p.20 of the protologue.

**Gymnocalycium ‘Jan Suba’** (Fig. 21)

*Gymnocalycium baldianum* (Speg.) Speg. ( $2n = 22$ )  $\Sigma$  *Gymnocalycium denudatum* (Link & Otto) Mittler ( $2n = 22$ ). (Fig. 22-23)

*Chr*: Not known, but likely to be  $2n = 44$  based on the parentage.

Taxonomic history:

*Gymnocalycium denudatum* ‘Jan Suba’ Pazout, *Friciana* **1**(7): 5. 1962.

*Gymnocalycium*  $\times$  *pazoutianum* Halda, *Acta Musei Richnoviensis* **5**: 161-194. 1998.

*Obs*: Artificially created in cultivation.



Fig. 21 *Gymnocalycium* ‘Jan Suba’ (*Gymnocalycium baldianum* (Speg.) Speg.  $\Sigma$  *Gymnocalycium denudatum* (Link & Otto) Mittler.





Above:

Fig. 22 *Gymnocalycium baldianum* (Speg.) Speg.

Right:

Fig. 23 *Gymnocalycium denudatum* (Link & Otto) Mittler.  
LB811 (Uruguay) Flower 5.4cm. long, 7.3cm. diam.

**ΣKroenleinia** J.Lodé, *Kroenleinia* gen. nov. J.Lodé 2014: A new genus for a well-known cactus: *Echinocactus grusonii*, *Cactus-Aventures International* (102): 25-26-29. (Apr) 2014.

*Par:* *Echinocactus* Link & Otto Σ *Echinofossulocactus* Lawr.

*Etym:* Named for the Monegasque Marcel KROENLEIN (1928-1994), Director of the Jardin Exotique from 1969 to 1993.

*T:* *Echinocactus grusonii* Hildm. Autotype (Art. 10.2). The only included species.

*Obs:* A putative allopolyploid with chromosome reduction.

**Kroenleinia Σgrusonii** (Hildm.) J.Lodé (Fig. 24)

*Par:* *Echinocactus platyacanthus* Link & Otto (2n = 22) Σ *Echinofossulocactus* (*Ferocactus*) *glaucescens* DC.

*Chr:* Not known.

Taxonomic history:

*Echinocactus grusonii* Hildm., *Echinocactus Grusonii* Hildm., *Deutsche Gartenzeitung* 1(3): 27-28. (20 Jan) 1886 ("Grusoni").

*Kroenleinia grusonii* (Hildm.) J.Lodé, *Kroenleinia* gen. nov. J.Lodé 2014: A new genus for a well-known cactus: *Echinocactus grusonii*, *Cactus-Aventures International* (102): 25, 27. (Apr) 2014.

*Etym:* Named for Herman GRUSON (1821-1895), a German businessman and owner of a succulent plant collection in Magdeburg.

*T:* Mexico. Imported by H. DROEGE in autumn 1885.

*HT:* Engraved illustration (fig. 6) of a young plant by Behrend, in *Deut. Gartenz.* 1(3): 28. 1886. Autotype (Art. 9.1). The only included element.

*Obs.* Lodé cited the wrong basionym, treated here as an error to be corrected (Art. 41.8a). The new combination appeared on p.27 and the supposed basionym for it on p.25. The two disjunct populations are slightly different in character and may have arisen independently from the same parentage.



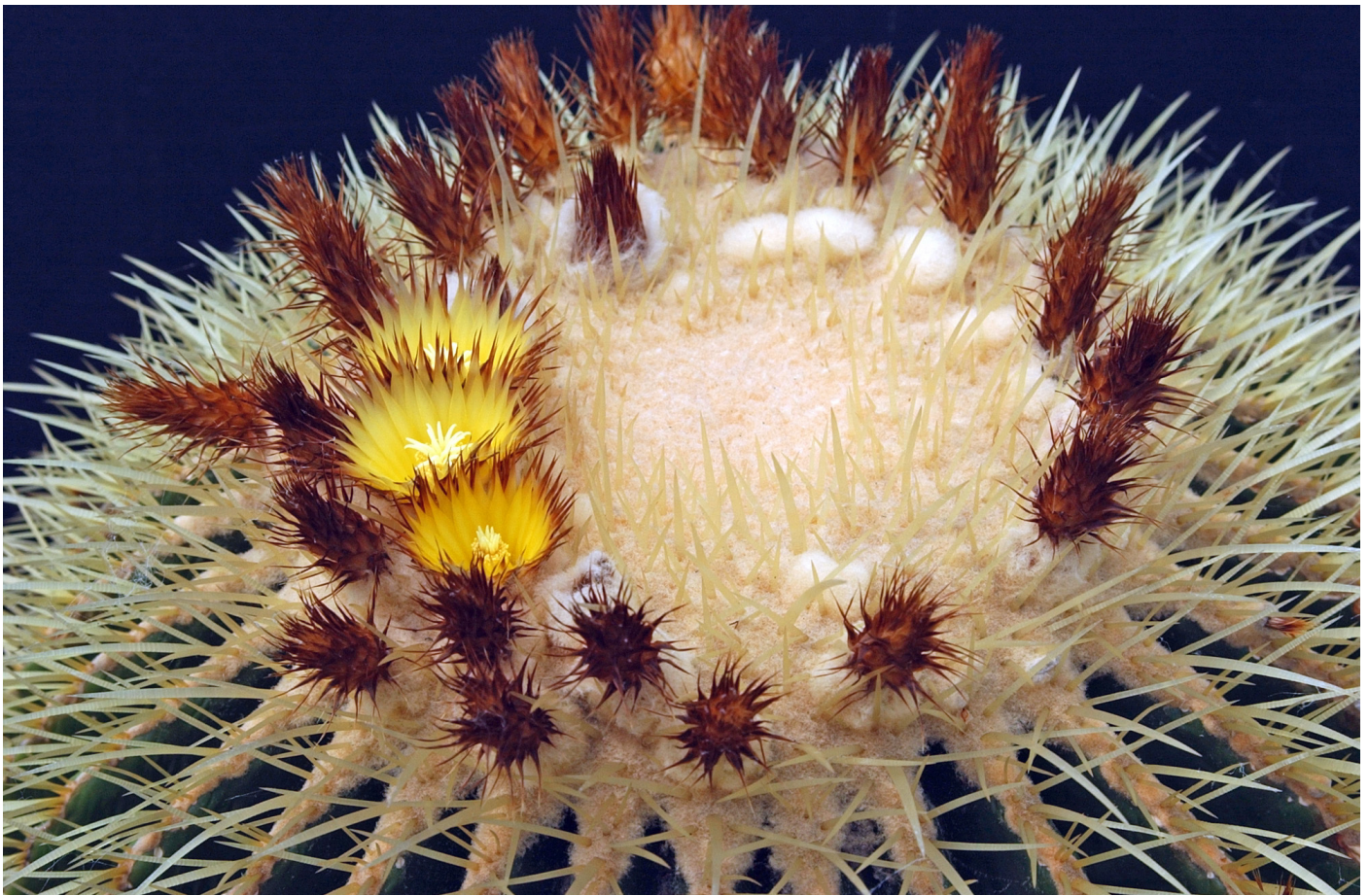


Fig.24 *Kroenleinia Sgrusonii* (Hildm.) J.Lodé. Plant 30cm. diam. Flowers up to 3.8cm. diam.

**Matucana Sclendinensis** F.Ritter. (Fig. 25)

*Par: Matucana aurantiaca* (Vaupel) Buxb.  $\Sigma$  *Matucana intertexta* F.Ritter. (Fig. 26-27)

*Chr:* Not known.

*Taxonomic history:*

*Matucana celendinensis* F.Ritter, Nieuwe vondsten van cactussen in Peru, *Succulenta* **45**(8): 118. (Aug) 1966.

*Borzicactus intertextus* var. *celendinensis* (F.Ritter) Donald, A commentary upon the subtribe *Borzicactinae* Buxbaum (Part 4), *National Cactus and Succulent Journal* **26**(1): 10. (Mar) 1971.

*Submatucana celendinensis* (F.Ritter) Knize, *Cactaceae index of field numbers of collected specimens in Central - South America 1967-1977 by Karel Knize*: 36. (30 Nov) 1977 nom. inval. (Art. 41.5).

*Matucana intertexta* var. *celendinensis* (F.Ritter) Bregman, Meerstadt, Melis & A.B.Pullen, Het geslacht *Matucana* Br. & R. (XVI), *Succulenta* **67**(5): 100. 1988.

*Etym:* Named for Celendín, a town in Cajamarca, Peru.

*T:* Peru, Cajamarca, between Celendín and Balsas; May 1957, *Friedrich RITTER* 692.

*HT:* U. A stem fragment.

*Obs:* More vigorous than either parent, with seeds weighing 2.2gm. per 1000 seeds compared with half that for each parent. Seed weight equal to the sum of that of the parents is often an excellent first clue to the presence of allopolyploidy.



Fig. 25 *Matucana Scelendinensis* F.Ritter. (Peru, Dept. Cajamarca, near the mouth of the Rio Crisnejas; *M. DE MUNTER s.n.*) Stem 11.5cm. diam. Flower 6.1cm. diam.



Fig. 26 *Matucana aurantiaca* (Vaupel) Buxb. LAU 115 (Cajamarca, W of Cajamarca, 2200-2500m) Stem 9.5cm. diam. Flower 7.5cm. long, c. 4.7cm. diam.



Fig. 27 *Matucana intertexta* LAU 108 (Cajamarca, Crisnejas, 500-800m) Heads 9.3-10.0cm. diam. Flowers 8.3cm. long, 6.1cm. diam., tube 1.0cm. thick.



**Melocactus Σalbicephalus** Buining & Brederoo

*Par: Melocactus ernestii* Vaupel (2n = 44) Σ *Melocactus glaucescens* Buining & Brederoo (2n = 44).

*Chr:* 2n = 44.

Taxonomic history:

*Melocactus Σalbicephalus* Buining & Brederoo, in Krainz, H (ed.), *Die Kakteen* (52): CVId, [1-3]. 1973 (pro sp.).

*T:* Brazil, Bahia, W Serra do Espinhaço, nr. Morro do Chapéu; *HU* 350.

*HT:* U.

*Obs:* A hybrid origin was first proposed for this taxon by N. P. Taylor, The genus *Melocactus* in Central and South America, *Bradleya* **9**: 52, 80. 1991. Allopolyploid origin was suggested by M. Machado, *Bradleya* **26**: 5. (18 Jul) 2008. This would have to include a chromosome reduction since its creation because its original parentage would have resulted in 2n = 88.

***Opuntia ficus-indica*** cv. (2n = 88) Σ ***Opuntia humifusa*** (2n = 22) Burbank, *His methods & discoveries* 8: 179-181. 1914 (without name).

*Chr:* Not known, but probably 2n = 110 from the parentage.

*Obs:* Artificially created in cultivation. Does not appear to have survived, perhaps because it did not meet Burbank's breeding criterion of spinelessness.

**Pachycereus Σpringlei** (Fig. 28, 30)

*Par: Cereus giganteus* Engelm. (2n = 22) Σ *Cereus pecten-aboriginum* Engelm. ♀ (2n = 22). (Fig. 29, 31)

*Chr:* 2n = 44.

Taxonomic history:

*Cereus pringlei* S. Watson, *Proceedings of the American Academy* **20**: 368. 1885.

*Pilocereus pringlei* (S. Watson) F.A.C. Weber, *Pilocereus* in Bois, *Dictionnaire d'Horticulture* **2**(31): 966 (Aug) 1898.

*Pachycereus pringlei* (S. Watson) Britton & Rose, The genus *Cereus* and its allies in North America, *Contributions from the US National Herbarium* **12**(10): 422. (21 Jul) 1909.

*Etym.* Named for the plant collector Cyrus PRINGLE (1838-1911).

*Typ.* Mexico, Arizona, hills & mesas S of the Altar River, Aug 1884, *Cyrus Guernsey PRINGLE* 7841.

*HT:* Not cited.

*LT:* GH 61815.

*Obs.* A classic example of an allopolyploid, retaining the extra DNA that has helped it to occupy new areas of the Sonoran Desert and Baja California (Fig. 31). This is the type species of *Pachycereus* (A. Berger) Britton & Rose. In a narrow sense it would therefore retain that name, but in a broader sense, *Carnegiea* Britton & Rose and *Pachycereus* (A. Berger) Britton & Rose are both referable to *Cephalocereus* Pfeiff.

Because Σ*Pachycereus pringlei* shares an equal amount of DNA from each parent, its morphology is halfway between. It has 11-17 ribs (median 14) compared with 12-24 (median 18) for *Carnegiea* and 10-11 (median 10) for *P. pecten-aboriginum*. Spination is intermediate in both stems and flowering zones. *P. pecten-aboriginum* is notable for its exceptionally spiny fruits, while *Carnegiea* is more or less naked. *P. pringlei* fruits have short spination.





Fig. 28 *Pachycereus Σpringlei* Gorelick photo in the Desert Botanical Garden, Arizona.

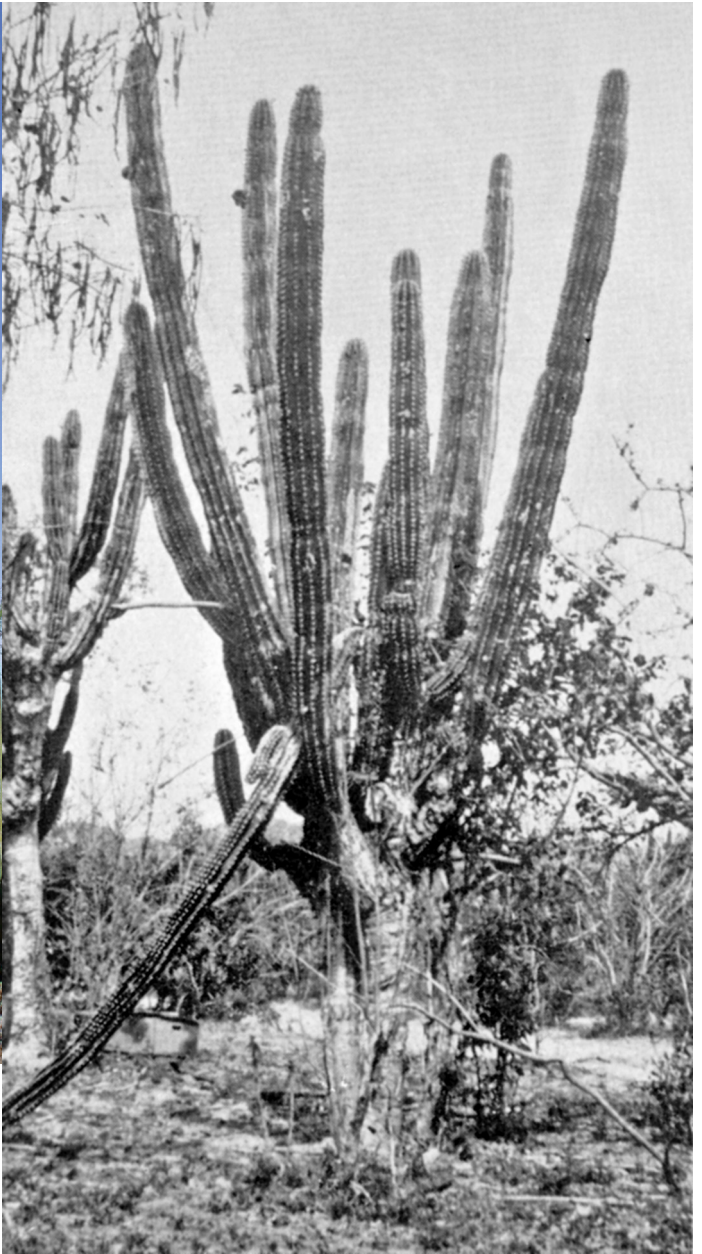
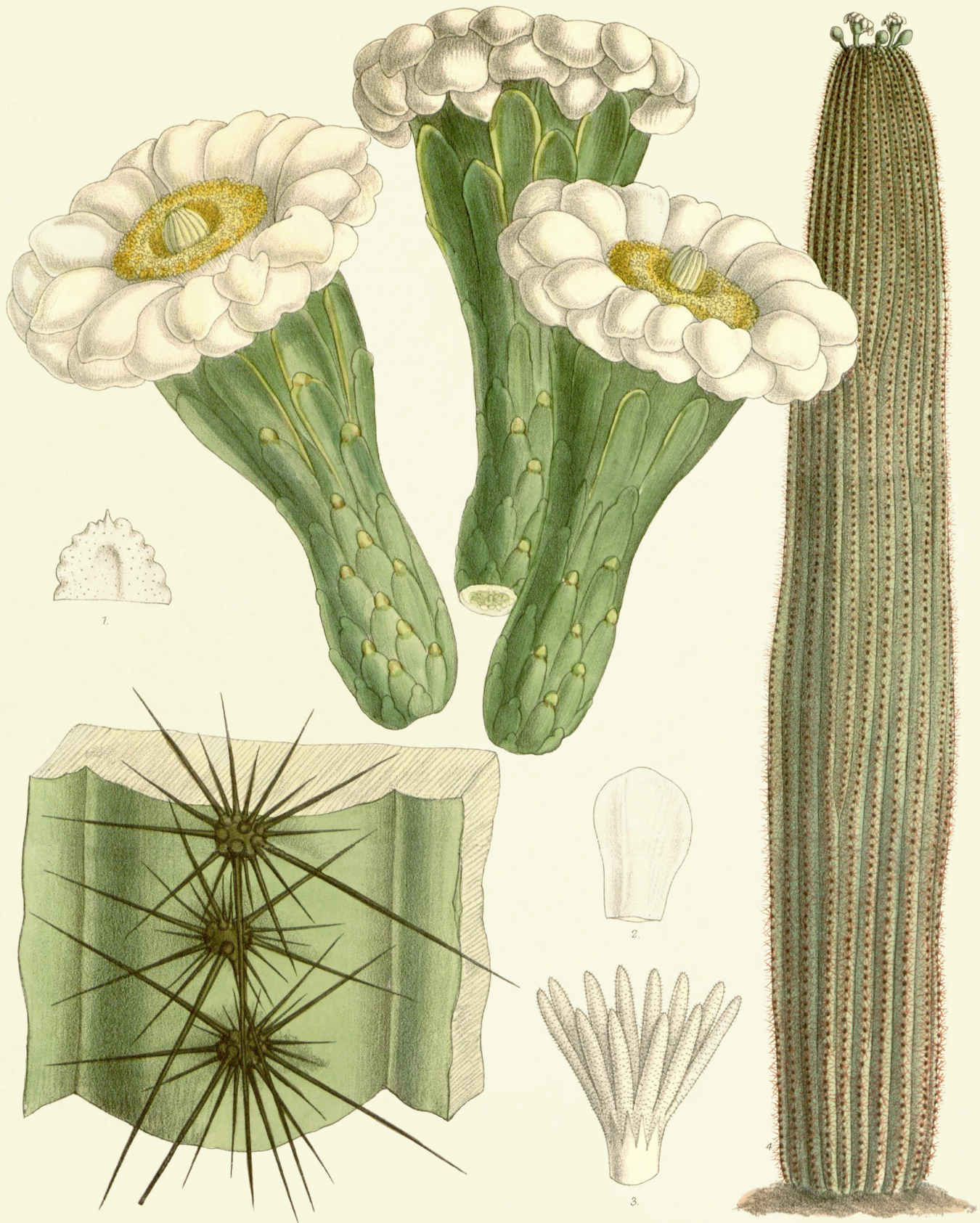


Fig. 29 *Pachycereus pecten-aboriginum* (Mexico, Baja California, nr. Todos Santos, foothills of the Sierra de la Laguna Mountains, on the Pacific coast side) Gates photo, from *The Cactus Journal* 3(4): 78. (Jun) 1935.



Fig. 30 *Pachycereus Σpringlei* Top of a plant in cultivation at Worfield Gardens nursery in 1970.





M.S. del, J.N. Fitch lith.

I. Reeve &amp; Co. London

Vincent Brooks Day &amp; Son Imp

Fig. 31 *Carnegiea gigantea* Fitch hand-coloured engraving, from Hooker, J.D., *Curtis's Botanical Magazine* **118**: t.7222. (Mar) 1892.



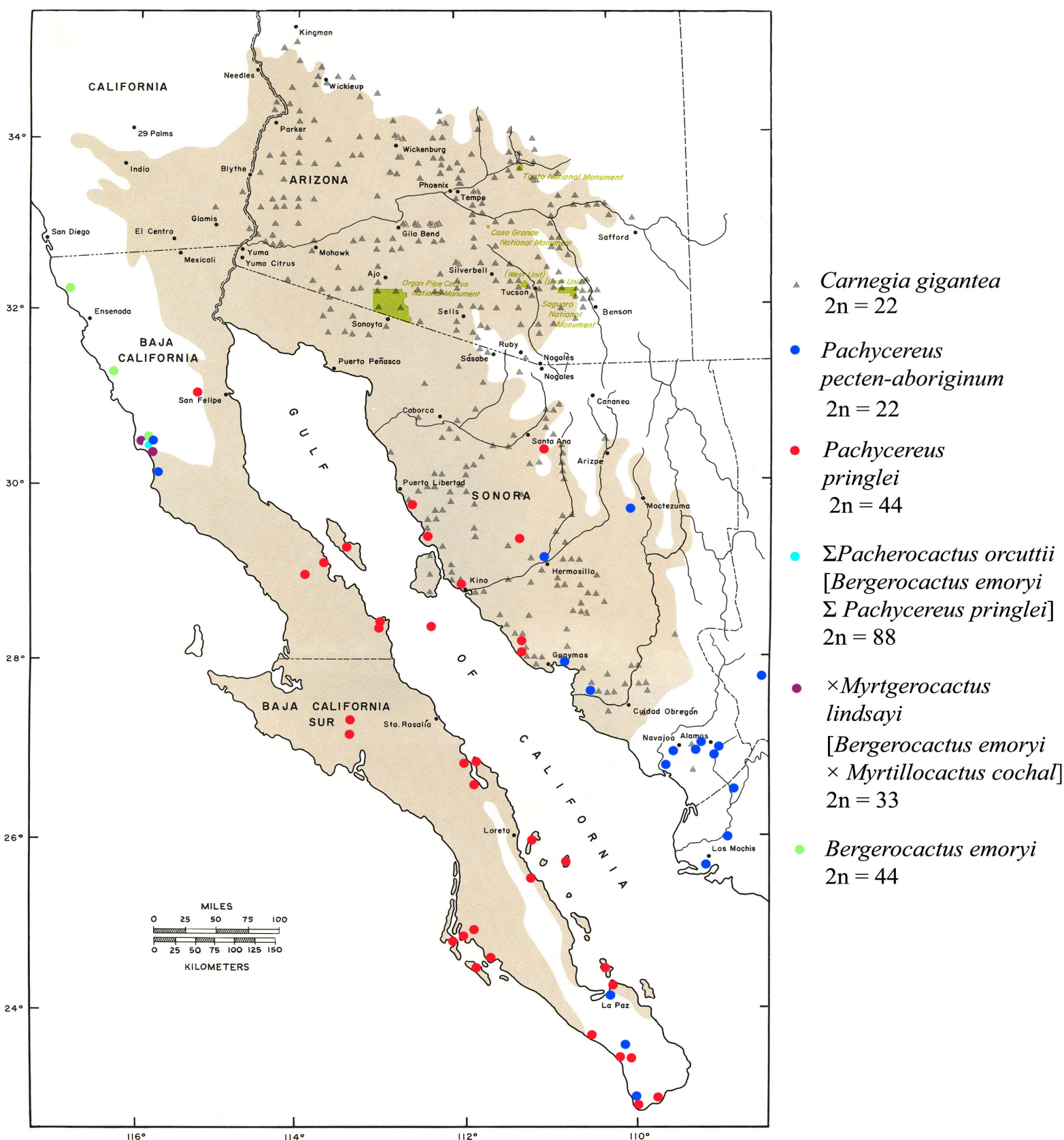


Fig. 32 Distribution of *Carnegiea gigantea*, *Pachycereus pecten-aboriginum*, *P. Σpringlei*, *Bergerocactus emoryi*,  $\Sigma$ *Pacherocactus orcuttii*,  $\times$ *Myrtgerocactus lindsayi*. Limits of the Sonoran Desert shown in brown. Map adapted from Steenberg & Lowe, *Ecology of the saguaro II* (1977). Shows how *Pachycereus Σpringlei* has been able to penetrate new habitats

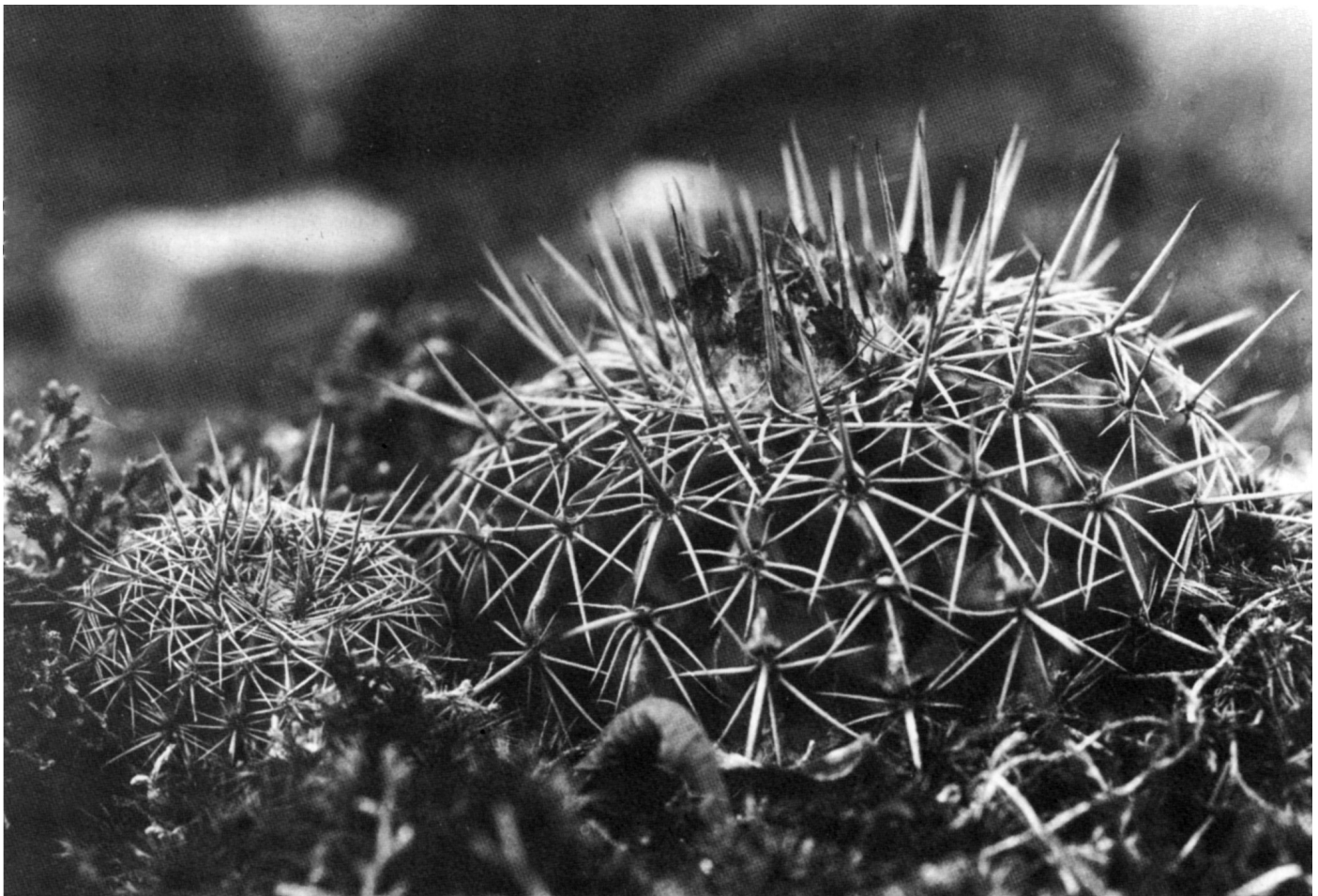


Fig. 33 *Parodia Sneoarechavaletae* (Uruguay, Maldonado, Piriapolis, Pan de Azúcar) Frič habitat photo of the type collection, second expedition 1903.

***Parodia Sneoarechavaletae*** (Havlicek) D.R.Hunt. (Fig. 32)

*Par*: *Parodia sellowii* (Link & Otto) D.R.Hunt  $\Sigma$  *Parodia submammulosa* (Lem.) R.Kiesling (2n = 44).

*Chr*: Not known.

Taxonomic history:

*Echinocactus acuatus* var. *arechavaletae* K.Schum. ex Speg., Cactacearum Platensium Tentamen, *Anales del Museo Nacional de Buenos Aires* **11**: 494. (19 Jan) 1905 (“arechavaletai”).

*Notocactus neoarechavaletae* Havlicek, *Kaktusz Vilag* **18**(4): 79. 1989 (“arechavaletai”).

*Parodia neoarechavaletae* (Havlicek) D.R.Hunt, New names and combinations in various genera, *Cactaceae Consensus Initiatives* (4): 6. (Oct) 1997.

*T*: Uruguay, Dept. Maldonado, Piriapolis, Pan de Azúcar; *Alberto V. Frič*.

*Obs*: The same allopolyploid appears to have arisen in two disjunct and quite distant locations independently. As well as the type locality, it was also found by Stuchlík (*Kaktusy* **41**(1): 22-24) in Rio Grande do Sul, near the town of Pedras Altas.

***Sclerocactus Snyensis*** Hochstätter (Fig. 33)

*Par*: *Sclerocactus polyancistrus* (Engelm. & J.M.Bigelow) Britton & Rose  $\Sigma$  *Sclerocactus pubispinus* (Engelm.) L.D.Benson.

*Chr*: Not known.



Taxonomic history:

*Sclerocactus nyensis* Hochstätter, *Succulenta* **71**(6): 253-255. 1992.

*Pediocactus nyensis* (Hochstätter) Halda, *Acta Musei Richnoviensis, Sect. Natur.* **5**(1): 15. 1998.

*T*: USA, Nevada, Western Nye County, 1500-1700m; 1988, *Fritz HOCHSTÄTTER* 105.

*HT*: HBG.

*Obs*: The hypothesis that this was an allopolyploid was first suggested by Zlatko Janeba in *CactusWorld* **27**(1): 63-64. 2009.



Fig. 34 *Sclerocactus Nyensis* Hochstätter (USA, Nevada, S of Tonopah) Janeba photo 2009.

#### Literature cited:

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**Horton, R.** (2007) My hybrids, *CactusWorld* **25**(4): 233-235. (13 Dec).

**Janeba, Z.** (2009) Hybridisation in the evolution of cacti. In Mottram, R. (ed.) CactusTalk, *CactusWorld* **27**(1): 63-65. (12 Mar).

**Machado, M. C.** (2008) What is the role of hybridization in the evolution of the *Cactaceae*?, *Bradleya* **26**: 1-18. (18 Jul).

**Mottram, R.** (2008) Hybridisation in nature. In Mottram, R. (ed.) CactusTalk, *CactusWorld* **26**(1): 48-49. (13 Mar).

**Taylor, N. P., & Zappi, D.** (2004) *Cacti of eastern Brazil*. Royal Botanic Gardens, Kew.