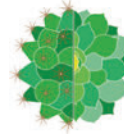


CactusWorld Special Issue

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# South American Cacti

Giovanna Anceschi and Alberto Magli



## Introduction

As an Editor, it is good to receive longer articles at times – something the more serious reader can get their teeth into. However, when the first article from these authors was designed and laid out, and it came to 24 pages, something had to be done.

Of course 24 pages would have filled almost half the Journal and so the idea of a Special Issue was considered. The same authors were able to write a second article on a similar theme – South America cacti – and so the Special Issue was born.

*CactusWorld* has always been a place for the publication of novel taxa (always after serious consideration and care not to publish names willy-nilly and at all cost), but has also provided a platform for new and alternate ideas of classification. This is the case in the Special Issue that you hold in your hands. Many will not

agree with the authors' proposals or their taxonomic suggestions, yet their ideas deserve to be heard.

They have hiked the hillsides and travelled the miles, and have spent many, many months in total in the field in South America, photographing, observing, studying and measuring the cacti in habitat. Back home, they have ploughed through the historic as well as the contemporary literature before coming to their conclusions. They have published their work in *Bradleya*, *Cactaceae Systematics Initiatives* and elsewhere, and it is an honour to publish their articles in this supplement.

And dear reader, if you find this all heavy going, at least you can enjoy the photos. Also be sure to check out their website:

<http://cactusinhabitat.org>

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All photographs by the authors.

Layout by Alice Vanden Bon

Cover design and layout by Sheila Cude

# Dominant species in *Parodia* Spegazzini s.l. Cactaceae

## Introduction

The idea for this article came from the Editor, who asked us to expand on our approach to classification (based primarily on the study of taxa in their natural habitats rather than in cultivation, especially in greenhouses), in relation to the genus *Parodia* Spegazzini, one of the genera we have studied the most within the Cactaceae. Actually, we did not intend to add any more data in such a short time to the contents of our extensive synopsis on the genus (Anceschi & Magli, 2018), where in terms of the history and taxonomy of the genus, we consider our current understanding of the matter exhaustive. The argument that made us think of a possible addition to the synopsis began from the possibility of being able to

broaden and describe our understanding of the definition of the relationships between species in their habitats: relationships that form the basis of our taxonomic system. In particular we wanted to discuss the concept of the dominant species, in the Darwinian evolutionary sense (Darwin, 1859). This concept plays such a fundamental role for us, that it can change the essence of our understanding of individual taxa. It can also change the scientific descriptions circumscribing them based on data relating to the morphology of the species collected in habitat.

We have been studying cacti for 15 years, and almost a third of that time has been spent working in their habitats (Anceschi & Magli, 2018: 75). It became clear to us that the populations that constitute a natural



Fig. 1 *Parodia nivoso* (*penicillata* populations). Argentina, Salta, Cafayate, Quebrada del Rio Chuscha, 2007-04-25, A&M 197

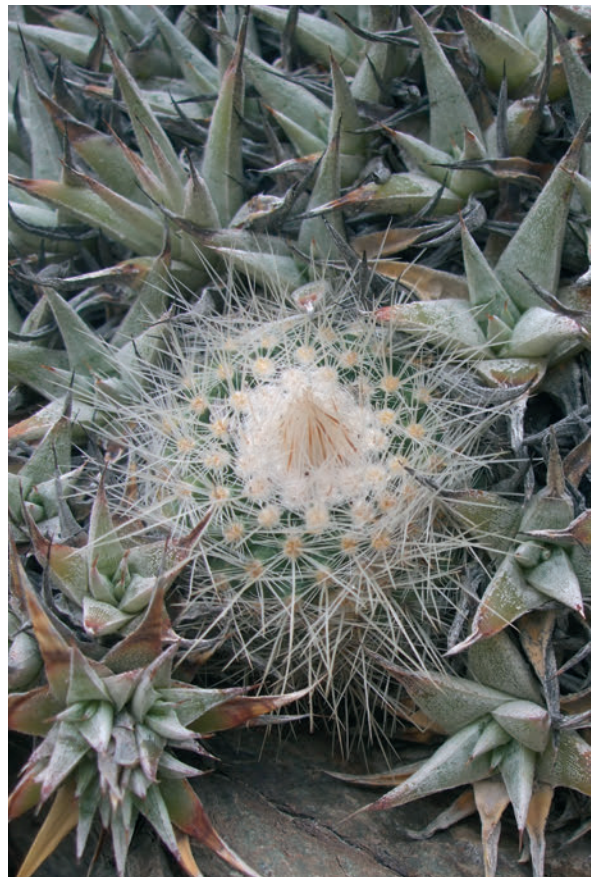


Fig. 2 *Parodia nivoso*. Argentina, Salta, Quebrada del Toro, 2007-03-14, A&M 157



Fig. 3 *Parodia maassii*. Argentina, Jujuy, south of Iturbe, 3,430m, 2015-12-29, A&M 1278

are often artificially fragmented, and have given rise to unnecessary distinctions. This numerical and spatial progression in addition to the variability of the natural populations connected to each other, led us to rediscover one of the fundamental ideas of the work of Charles Darwin (1859), that of the dominant species.

## Darwin's dominant species

We said "to rediscover" because quite likely the consequences of the disastrous outcomes of the ideologies of the Second World War had made us forget that the subtitle

species show a variability, which in nature is linked by a progression within a spatial continuum, compared to the plants in cultivation, which lack the transitional areas between the distinct populational semaphoronts,

of *On the Origin of Species by Means of Natural Selection* is the *Preservation of Favoured Races in the Struggle for Life*. It is evident (at least to us) that Darwin's 'favoured races' equates to 'dominant



Fig. 4 *Parodia microsperma*. Argentina, Catamarca, El Rodeo, Sierra de Ambato, Christo Redentor, 2013-11-15, A&M 864

Fig. 5 *Parodia erinacea*.  
Uruguay, Rio Negro, Nuevo  
Berlín, south of Nuevo  
Berlín, 2014-01-31, A&M 971



species', and that the concept of dominant species is at the basis of both Darwin's evolutionary theory and his concept of fitness. In his main work Darwin introduces his theory on the dominant species in this way, "...my tables further show that, in any limited country, the species which are most common, that is about most in individuals, and the

species which are most widely diffused within their own country..., often give rise to varieties sufficiently well-marked to have been recorded in botanical works. Hence it is the most flourishing, or, as they may be

called, the dominant species" (Darwin, 1859: 53). He continues, "We have, also, seen that it is the most flourishing and dominant species of the larger genera which on an average vary most;...The larger genera



Fig. 6 *Parodia mammulosa* (*mammulosa* populations). Uruguay, Rivera, Tranqueras, Valle del Lunarejo, Mario Padern property, 2006-11-21, A&M 72



Fig. 7 *Parodia ottonis*. Brazil, Rio Grande do Sul, Encruzilhada do Sul, south-west of Encruzilhada do Sul, 2016-02-17, A&M 1345

thus tend to become larger; and throughout nature the forms of life which are now dominant tend to become still more dominant by leaving many modified and dominant descendants” (Darwin, 1859: 59). Continuing, “We have seen that it is the common, the widely-diffused, and widely-ranging species, belonging to the larger genera, which vary most; and these will tend to transmit to their modified offspring that superiority which now makes them dominant in their own countries.” (Darwin, 1859: 128). Also, “As the modified descendants of dominant species, belonging to the larger genera, tend to inherit the advantages, which made the groups to which they belong large and their parents dominant, they are almost sure to spread widely, and to seize on more and more places in the economy of nature. The larger and more dominant groups thus tend to go on increasing in size; and they

Fig. 8 *Parodia aureicentra*. Argentina, Salta, Cachi Adentro, 2011-05-11, A&M 496



consequently supplant many smaller and feebler groups. Thus we can account for the fact that all organisms, recent and extinct, are included under a few great orders, under still fewer classes, and all in one great natural system.” (Darwin, 1859: 428–429).

At this point we could not fail to report this famous passage, which we believe is fundamental to the topic, “As natural selection acts solely by accumulating slight, successive, favourable variations, it can produce no great or sudden modification; it can act only by very short and slow steps. Hence the canon of ‘Natura non facit saltum’, which every fresh addition to our knowledge tends to make more strictly correct, is on this theory simply intelligible. We can plainly see why nature is prodigal in variety, though niggard in innovation.” (Darwin, 1859: 471). Finally we include the following quotation, “We can so far take a prophetic glance into futurity as to foretell that it will be the common and widely-spread species, belonging to the larger and dominant groups, which will ultimately prevail and procreate new and dominant species.... And as natural selection works solely by and for the good of each being, all corporeal and mental endowments will tend to progress towards perfection.” (Darwin, 1859: 489).

Regarding the statement, “mental endowments will tend to progress towards perfection”, it would be anachronistic to attribute to Darwin the lack of knowledge of the technological power that the dominant species *Homo sapiens* Linnaeus would have reached in our age, and the destructive use made of it. In this regard, we have repeatedly seen evidence that

many taxa whose previous dominance can be inferred on the basis of the current distribution, now show highly fragmented populations due to massive anthropogenic intervention. It is curious that these populations belonging to the same natural species, which are no longer connected to each other because of human intervention, are sometimes considered as separate taxa, with relative distinct assessments on their conservation status, as in the case of *Gymnocalycium schroederianum* Osten, which we will deal with in full in our next booklet (Anceschi & Magli, 2021, unpubl. data). In reality, we should not only make an effort to protect living things solely because of their IUCN conservation status, but we should respect the habitats of all taxa. Today's dominant species may be tomorrow's endangered species. We all know that declaring that a taxon is rare can lead to its extinction. In the genus *Parodia*, a case in point is that of *Parodia penicillata* Fechsler & Steeg, which we assimilated into *Parodia nivosa* Frič ex Backeberg in our synopsis (Anceschi & Magli, 2018: 125–127), in agreement with Kiesling & Ferrari (1990), as the populations of the two taxa are practically indistinguishable in habitat

(Figs. 1 & 2). Unfortunately populations of the first taxon have been decimated by the indiscriminate collections made by the cactus nursery in Cafayate (Salta, Argentina), which has annihilated the populations growing near the town, in order to sell “a rare plant that lives only in Cafayate”.

Other references to the concept of dominant species in Darwin's work available at: <http://darwin-online.org.uk/content/frameset?itemID=F373&viewtype=text&pageseq=1> can be found on the following pages: 54, 325, 326, 327, 343, 344, 350, 377, 380, 408, 411, 412, 433, 470, 475.

## Dominant species in *Parodia*

Summarising Darwin's premises and on the basis of what has been found in natural habitats, we have come to understand that the dominant species means, “the species more opportunistic and therefore better at adapting to different habitats [conditions], resulting in a greater numerical progression of individuals and populations, and higher variability” (Anceschi & Magli, 2012a: 27). Having defined the basic unit of our

Fig. 9 *Parodia commutans*. Bolivia, Tarija, Quebrada de Paicho Sur, 2011-06-29, A&M 560





**Fig. 10 *Parodia otaviana*. Bolivia, Chuquisaca, Tacaquira, Loc. El Puron, 2011-07-01, A&M 591**

despite the morphological and territorial proximity, a potential genetic flow is not evident, or it is not assumed (Anceschi & Magli, 2014: 67). Apart from the alleged potential of crossing (or not), if molecular tests are missing or insufficient, to investigate such low levels of genetic relationships, a useful operational concept to distinguish between all the populations of a dominant species, an internal vicariant from an external one, is comparative holomorphy between semaphoronts (Hennig, 1966: 66–67). The method can be used

taxonomic system, we now proceed with the definitions of the related elements that complete it. As already reported in ‘Comment guidelines’ in our synopsis of *Parodia* s.l. (Anceschi & Magli, 2018: 76), a dominant species may show:

a) Strong or weak internal vicariants (geographical races, subspecies, demes), depending on the degree of extinction risks afflicting its components. For internal vicariants we intend, in agreement with Hennig in his definition of species, “a complex of spatially distributed reproductive communities, or if we call this relationship in space ‘vicariance’, a complex of vicarying communities of reproduction.” (Hennig, 1966: 47). Substantially, defining one or more taxa as internal vicariants of a species recognises that at least potentially (Mayr, 1942: 120) all these components might cross each other as part of the same biological unit. Being the same biological unit, the internal vicariants of a species do not require a taxonomic rank.

b) Strong or weak external vicariants (or close relatives). For external vicariants we mean “the taxa probably belonging to the same ancestral line with which,

recognise genetic relationships that are to be presented in the taxonomic system. In the case of internal vicariance, the semaphoronts which are identifiers of the group in question, are actually found even among the populations of the type species. In the case of external vicariance, increased genetic autonomy is inferred by the fact that some semaphoronts which are identifiers of the taxonomic group are not found in the type species (for a case study in *Parodia*, see Anceschi & Magli, 2014: 60-73).



**Fig. 11 *Parodia subterranea*. Bolivia, Chuquisaca, Pass between Culpina and Incahuasi, 2011-06-30, A&M 588 (BLMT 68.05)**





Fig. 12 *Parodia tuberculata*. Bolivia, Chuquisaca, west of Tarabuco, Khochi, 2,923m, 2014-03-15, A&M 1073

Given the importance of the two vicariant definitions above, we would like to clarify that the concept of vicariance originates from one of the basic processes on which modern biogeography is based. In its classic interpretation, vicariance tends to identify one of the modes of allopatric speciation (the other is peripatric speciation), ie when an ancestral species is geographically subdivided by a physical or climatic barrier, with subsequent speciation (Wiley & Liebermann, 2011: 42–44). In classical terms the relationship of vicariance is always ‘external’ to the species from which it comes. As reported above, the concept of internal vicariance derives from Hennig’s concept of species and in this case the vicariance process is assumed as ‘internal’ to the species. These are the ways we use the two concepts, but the novelty consists in the fact that we use both simultaneously, for a better definition of a clade (or of a natural species). Science always advances through new contributions elaborated on the basis of previously known theories. The important thing is to be fully aware of the theory you are using and in particular, highlight when you are modifying it. In our opinion, the static system of



Fig. 13 *Parodia horrida*. Argentina, Salta, Angastaco, RN40, 2007-03-09, A&M 154



Fig. 14 *Parodia erinacea*. Argentina, Buenos Aires, Olavarría, Sierra Chica, 160m, 2014-01-10, A&M 954

species-subspecies (according to Darwin, “Certainly no clear line of demarcation has as yet been drawn between species and sub-species – that is, the forms which in the opinion of some naturalists come very near to, but do not quite arrive at the rank of species; or, again, between sub-species and well-marked varieties, or between lesser varieties and individual differences. These differences blend into each other in an insensible series...” (Darwin, 1859: 51)), is replaced with a dynamic system, constituting at the starting point from dominant species in a Darwinian evolutionary sense, divided in their internal vicariants (in the Hennigian sense) and related to their external vicariants (in a classical sense as in Wiley & Liebermann’s treatment), strong or weak depending on their presence and continuity in the colonised territory. Finally, the other elements that complete our reference system for defining the relationships between taxa in their habitats are: 2) Relatively dominant species in a restricted area; 3) Ex-dominant species, now with fragmented distribution 4) Non-dominant species (or endangered species, at different degrees) (see Anceschi & Magli, 2018: 76).

After the reasons why we still believe the fundamental element on which a genealogical classification of living beings must operate, which is the dominant species in the Darwinian sense, as also underlined by Mayr’s biological species concept (Mayr, 1942: 120) in its first broader formulation and extension, used by us as an operational concept in our synopsis (Anceschi & Magli, 2018: 75), we now move on to discuss



Fig. 15 *Parodia erinacea*. Uruguay, Maldonado, Piriapolis, Cerro del Toro, 2007-01-02, A&M 54

the dominant species and their vicariants within *Parodia* s.l.

Of the 62 natural species accepted in our synopsis, five are identified as dominant: two in the Andean area (on the eastern slopes of the Andes in north-western Argentina and south-western Bolivia), ie *Parodia maassii* (Heese) A.Berger (Fig. 3) and *Parodia microsperma* (F.A.C.Weber) Spegazzini (Fig. 4), and three in the Pampas area (in the lowland pampas regions of north-eastern Argentina, southern Brazil, eastern Paraguay, and Uruguay), ie *Parodia erinacea* (Haworth) N.P.Taylor (Fig. 5), *Parodia mammulosa* (Lemaire) N.P.Taylor (Fig. 6), and *Parodia ottonis* (Lehmann) N.P.Taylor (Fig. 7). In turn, the five complexes constituted by the dominants involve a further 17 additional species as external vicariants, in addition to three internal vicariants, the latter all part of *P. mammulosa*.

The following are the five groups based on the dominant-vicariant relationship (for data relating to the extension of occurrence of taxa per group on the maps, we refer to Anceschi & Magli, (2018: 76-77)).



Fig. 16 *Parodia mammulosa* (*turecekiana* populations). Uruguay, Río Negro, Nuevo Berlin, 24m asl., 2014-01-27, A&M 966



Fig. 17 *Parodia mammulosa* (*submammulosa* populations). Argentina, San Luis, Inti Huasi, 1,478m, 2013-12-23, A&M 934

- 1) ***P. maassii* complex:** *P. maassii*, *P. aureicentra*, *P. commutans*, *P. otaviana*, *P. subterranea*, *P. tuberculata*
- 2) ***P. microsperma* complex:** *P. microsperma*, *P. horrida*
- 3) ***P. erinacea***
- 4) ***P. mammulosa* complex:** *P. mammulosa* (*mammulosa*, *submammulosa* and *turecekiana* populations), *P. curvispina*, *P. maldonadensis*, *P. mueller-melchersii*
- 5) ***P. ottonis* complex:** *P. ottonis*, *P. carambeiensis*, *P. gaucha*, *P. ibicuiensis*, *P. linkii*, *P. muricata*, *P. oxycostata*, *P. stockingeri*, *P. tenuicylindrica*

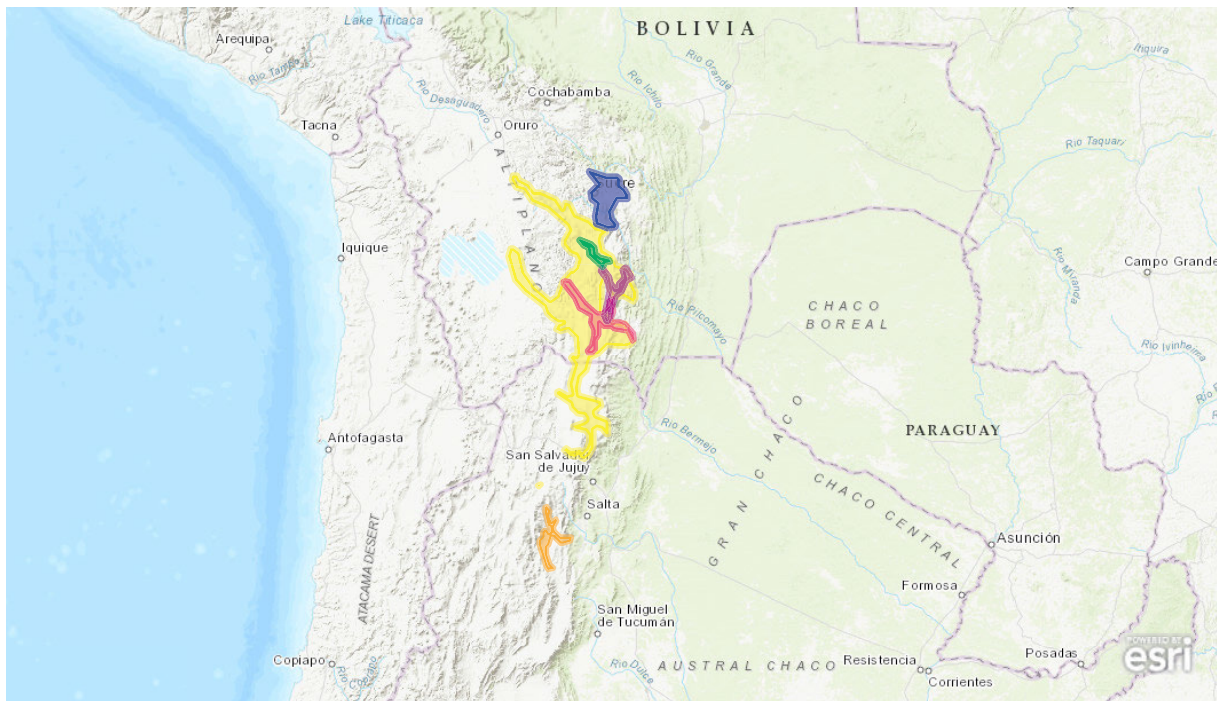
To emphasise the taxonomic and phytogeographic importance occupied by the dominant species within the ecosystems of reference, in tune with Darwin (1859: 53), and as already reported in our previous work (Anceschi & Magli, 2018: 71-72), we emphasise that a correspondence between the first taxa published within a genus and the dominant species in the genus itself appears evident. As evidence of this, look at the dates of publication for the following: *Cactus erinaceus* Haworth (1819), *Cactus ottonis* Lehmann (1827), *Echinocactus mammulosus* Lemaire (1838), *Echinocactus microspermus*

F.A.C.Weber in Bois (1896), and *Echinocactus maassii* Heese (1907), all taxa between the first to be published among those considered part of the current concept of *Parodia* s.l. This is because they have populations that are more common and/or numerous and therefore more evident in the habitats.

In addition to the above mentioned comparative holomorphy between semaphoronts, (Hennig, 1966: 32-33, 66-67), based on the comparison of characters



Fig. 18 *Parodia curvispina*. Brazil, Rio Grande do Sul, Lavras do Sul, RS 630, 2011-11-05, A&M 803



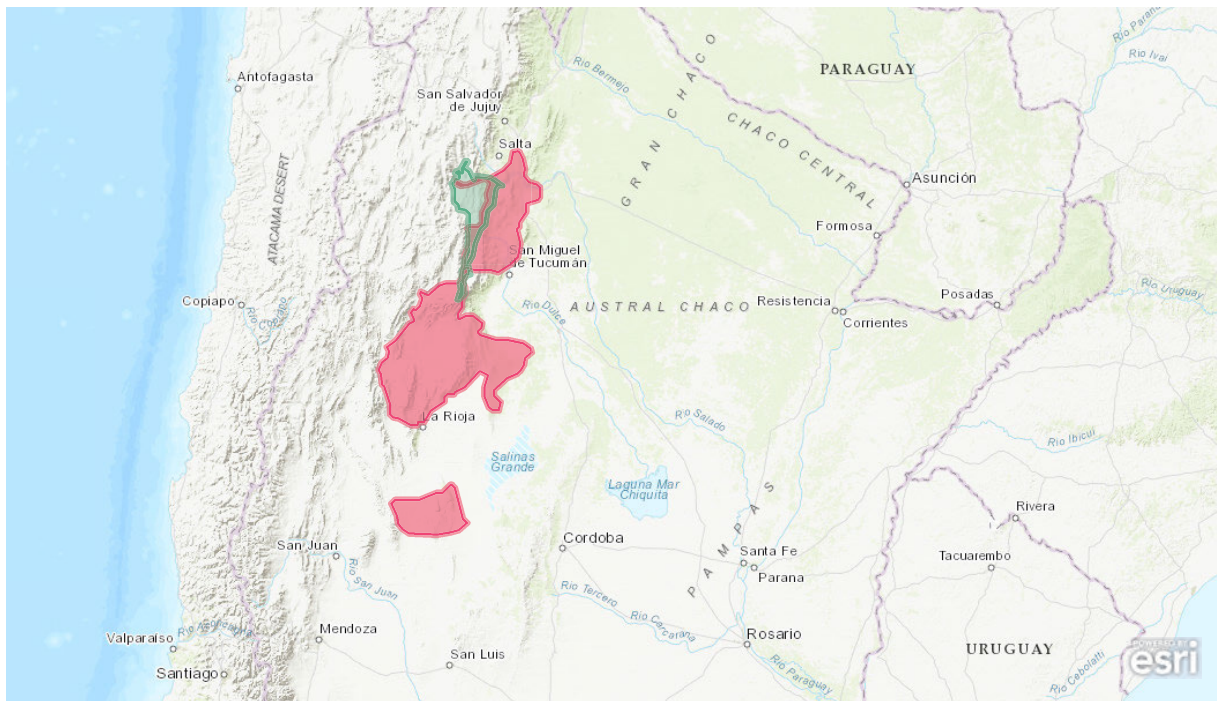
**Map 1** *P. maassii* complex. Extent of occurrence of: *P. maassii* (yellow), *P. aureicentra* (orange), *P. commutans* (fuchsia), *P. otaviana* (green), *P. subterranea* (violet), *P. tuberculata* (blue)

constant enough to be considered discrete (distinct growth phases or semaphoronts), in the ontogenetic processes of the analysed taxa (see also Anceschi & Magli, 2013: 31–32), useful for distinguishing between the internal and external vicariant of a species (when present), let us move on to indicate some filter operations, in turn useful for a better definition of the characters of a dominant species and the relationships between its external vicariants. As already mentioned in our first booklet (Anceschi & Magli 2010, 14), in the filter for choosing the identifying characters of the populations or/and internal vicariants that make up a dominant natural species, we must use a coarse-grained sieve (ie use as many characters as possible shared by populations for the constitution of the figure of the dominant). Using instead a fine-grained one to define, with the greatest possible precision, the transitional species (where present) between one external vicariant and another (ie using

the least possible number of characters to identify the passage). The latter operation outlines those transitional species useful to stabilise the taxonomic complex, which we identify as ‘technical species’, in this regard see below the cases of *P. ibicuiensis* and *P. oxycostata*, both relating to a greater definition of



**Fig. 19** *Parodia maldonadensis*. Uruguay, Rocha, P. N. Santa Teresa, 2006-12-19, A&M 97



Map 2 *P. microsperma* complex. Extent of occurrence of: *P. microsperma* (fuchsia), *P. horrida* (green)

the relationships between the external vicariants in the *P. ottonis* complex.

We look at some examples of the operational criteria outlined above for these five groups.

***P. maassii* complex:** the habitats colonised by the *P. maassii* complex include pre-Puna rocky slopes, Puna rocky outcrops, and arid inter-Andean rocky valleys, 2000–4200m (Map 1). This case shows no internal vicariants (all populations of *P. maassii* are morphologically homogeneous), and highlights a group of five external vicariants, namely: *Parodia aureicentra* Backeberg (Fig. 8), *Parodia commutans* F.Ritter (Fig. 9), *Parodia otaviana* Cárdenas (Fig. 10), *Parodia subterranea* F.Ritter (Fig. 11), and *Parodia tuberculata* Cárdenas (Fig. 12), all considered strong, considering that all components are constituted by numerous populations, in turn composed of numerous individuals. The only exception is *P. aureicentra*; this vicariant is relatively strong, because despite

the small extent of occurrence, ie 2,000km<sup>2</sup> (Ortega-Baes & Kiesling, 2017), the populations are not fragmented, and constituted by a large number of individuals. The morphological range of the external vicariants of *P. maassii* is clearly characterised, except for *P. otaviana* which being holomorphologically very close to the dominant (distinguishable only by the



Fig. 20 *Parodia mueller-melchersii*. Uruguay, Tacuarembó, old road between Valle Eden and Tambores, 2008-11-22, A&M 280



Fig. 21 *Parodia mueller-melchersii*. Uruguay, Rivera, Tranqueras, Valle del Lunarejo, Mario Padern property, 2006-11-21, A&M 73



Fig. 22 *Parodia mammulosa* (*mammulosa* populations). Uruguay, Rivera, Tranqueras, Valle del Lunarejo, 2006-11-23, A&M 76

white spines of its populations) can also be interpreted as an internal vicariant of the main taxon.

***P. microsperma* complex:** the habitats colonised by the complex are represented by arid ‘Precordillera’ valleys and ‘quebradas’, 500–3,000m (Map 2). Also this case does not highlight internal vicariants, being the taxon populations (despite the 62 synonyms), poorly differentiated, and only one external vicariant, which is *Parodia horrida* F.Brandt (Fig. 13), which can be defined as strong, being composed of numerous populations, with many individuals. In our synopsis (Anceschi & Magli, 2018: 103–105) we considered that the fierce and strong spination that identifies the semaphoront that distinguishes these populations from those of the dominant, and the generally north-western habitat (the two species overlap in the area of Cafayate, Salta (AR), are sufficiently distinct elements to recognise *P. horrida* as external vicariant. We have made various study trips to Cafayate, and we are knowledgeable about the area and the cactus populations growing there, having lived in the town for two months in 2007. We would like to stress that whereas *P. nivosa* and *P. penicillata*, as already shown, are the same in habitat, there is always a constant difference in spination between the populations of *P. microsperma* and *P. horrida*.

***P. erinacea*:** its distribution range consists essentially of Pampa grasslands with rocky outcrops in Argentina, Uruguay and southern Brazil, up to 30m, and



Fig. 23 *Parodia maldonadensis*. Uruguay, Maldonado, Piriapolis, Cerro del Toro, 2011-12-18, A&M 832



Map 3 *P. erinacea*. Extent of occurrence (orange)

'Blanqueales' with allomorphic soils, in the wooded savanna of the Rio Uruguay, in Uruguay (Map 3). This case does not highlight any internal vicariants. All populations within the species are poorly differentiated between them, and only at the intra-population level (within the same population) two distinct semaphoronts are recognisable. In the first phase of the ontogenesis process, the taxon assumes a discoid-globular aspect (the semaphoront known as *P. erinacea* / *P. turbinata*) (Fig. 14), then moves to a second phase indicated by a typical elongated shape (the semaphoront known as *P. sellowii*) (Fig. 15) (Anceschi & Magli, 2013: 32). Also with regard to the relations of external vicariance, the taxon does not show particular relations with other species of the genus, apart from the apical woolliness that is characteristic to all the ex-wigginsias.

***P. mammulosa* complex:** the habitats colonised by the *P. mammulosa* complex include Pampa grasslands with rocky

outcrops in Argentina, Uruguay and southern Brazil, the Monte Desert in Argentina, and the wooded savanna of the Rio Uruguay in Argentina and Uruguay, up to 1,500m (Map 4). The taxon is characterised by two internal vicariants, the *submammulosa* and *turecekiana* populations of *P. mammulosa* (Lemaire) N.P.Taylor. While *Parodia*



Fig. 24 *Parodia linkii*. Brazil, Rio Grande do Sul, Cambará do Sul, east of Cambará do Sul, 2011-11-23, A&M 827



**Map 4** *P. mammulosa* complex. Extent of occurrence of: *P. mammulosa* (*mammulosa* populations (orange), *submammulosa* populations (yellow) and *turecekiana* populations (fuchsia), *P. curvispina* (violet), *P. maldonadensis* (sky-blue), *P. mueller-melchersii* (green)

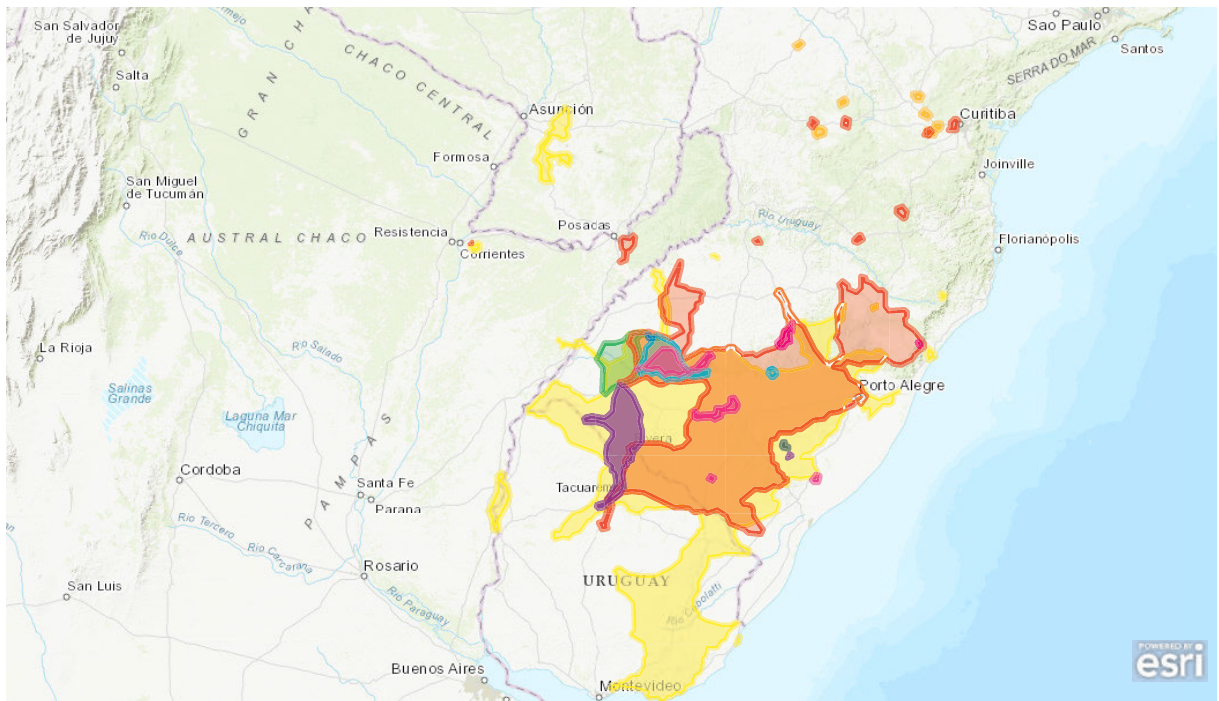
*submammulosa* (Lem.) R.Kiesling appears to be a strong internal vicariant, since populations like those of *P. mammulosa* are widespread and not subject to any risks of extinction, *Parodia turecekiana* R.Kiesling proves to be a rather weak link, with severely fragmented populations located in rather specific areas (ie the 'Blanqueales' with allomorphic soils, in the

wooded savanna of the Rio Uruguay, in Uruguay and the 'La Mesopotamia' in Argentina). The inclusion of the latter among the synonyms for *P. mammulosa* in our synopsis is because of the distinctive semaphoront of the taxon, ie the two longer and flattened central spines, is evident in *P. turecekiana* especially in the juvenile phase and early adulthood, whilst older plants look like *P. submammulosa* (Figs. 16–17). Moreover, the phases where the evidence of central spines is more relevant can also be found in semaphoronts of *P. submammulosa* (Anceschi & Magli, 2014: 64). In our understanding, there appear to be three external vicariants of *P. mammulosa*: *Parodia curvispina* (F.Ritter) D.R.Hunt (Fig. 18), *Parodia maldonadensis* (Herter) Hofacker (Fig. 19), and *Parodia mueller-melchersii* (Frič ex Backeberg) N.P.Taylor (Fig. 20). All three external vicariants are considered



**Fig. 25** *Parodia carambeiensis*. Brazil, Paraná, Ponta Grossa, P. E. Vila Velha, 2008-10-13, A&M 253





**Map 5** *P. ottonis* complex. Extent of occurrence of: *P. ottonis* (yellow), *P. carambeiensis* (ochre-yellow), *P. gaucha* (dark-green), *P. ibicuiensis* (grass green), *P. linkii* (red), *P. muricata* (sky-blue), *P. oxycostata* (fuchsia), *P. stockingeri* (blue), *P. tenuicylindrica* (violet)

weak, and this weakness is due to the extreme localisation and fragmentation of the three taxa. This is the situation of many taxa in Rio Grande do Sul (Anceschi & Magli, 2018), due to anthropic intervention. Eucalyptus and pine plantations, cattle ranching, a general decline of habitat quality resulting from various human activities near the small rocky outcrops where the species lives and illegal collection. These are problems that in the last 15 years we have seen worsen, year after year, and we try to highlight it every time we write on the topic. The three external vicariants are morphologically well differentiated from the dominant, in this regard as already highlighted (Anceschi & Magli, 2014: 60–73), for *P. mueller-melchersii* and *P. maldonadensis*, increased genetic autonomy is inferred by the fact that some semaphoronts which are identifiers of the taxa are not found in *P. mammulosa*

(ie the *winkleri* and *veeniana* forms of *P. mueller-melchersii* (Fig. 21), and the woolly crown of *P. maldonadensis*). Regarding the inclusion of an *exwigginsia* in the group of *P. mammulosa*, we would like to highlight the existence of molecular evidence showing that *Notocactus* and *Wigginsia* are closely related within *Parodia* s.l. (Eggl & Nyffeler, 2010).



**Fig. 26** *Parodia gaucha*. Brazil, Rio Grande do Sul, Encruzilhada do Sul, south-west of Encruzilhada do Sul, 105m, 2016-02-17, A&M 1343

Confirming the above, we would like to point out that in Anderson & Eggl (2011: 495) the genus *Parodia* s.l. is divided into the following sub-generic groups:

- 1) *Parodia* subgroup [this subgroup is divided into]:
  - 1a) *Parodia* s.s. group
  - 1b) *Notocactus* group (= *Notocactus* s.s. + *Wigginsia*)
- 2) *Eriocactus* subgroup
- 3) *Brasilicactus* subgroup

In summary, given the close phylogenetic relationship highlighted by the results of the molecular analysis between *Notocactus* and *Wigginsia*, so no embarrassment for our definition of *P. maldonadensis* as “a *mammulosa* s.l. with a very woolly stem apex.” (Figs. 22–23), (Anceschi & Magli, 2014: 70).

***P. ottonis* complex:** the distribution range colonised by the complex consists essentially of Pampa grasslands with rocky outcrops in Argentina, Uruguay, and southern Brazil, 50–1,000m, Pampa grasslands with rocky outcrops at the border with the Araucaria moist forest ecoregion in southern Brazil, 900–1,000m,

and the ex-Mata Atlantica area in south-east Paraguay (Map 5). The *P. ottonis* group represents the most interesting and complex case among those outlined by the dominants in *Parodia* s.l. Despite the variability and the extent of the distribution range of the dominant taxon, there are no evident internal vicariants, as all populational variants enjoy a morphological autonomy where it is more apt to define them as external vicariants rather than internal populations of the species. This in some cases is made possible also through the recognition of some ‘technical species’ that we will better define. *P. ottonis* has in fact eight external vicariants of which one, *P. linkii* (Fig. 24), represents a species with a large extent of occurrence, numerous populations with numerous individuals within them, and a genetic potential that appears second only to that of the dominant. The other seven vicariants are all weak, namely: *P. carambeiensis* (Fig. 25), *P. gaucha* (Fig. 26), *P. ibicuiensis* (Fig. 27), *P. muricata* (Fig. 28), *P. oxycostata* (Fig. 29), *P. stockingeri* (Fig. 30) and *P. tenuicylindrica* (Fig. 31). This extended group of external vicariants is considered weak, since more or



Fig. 27 *Parodia ibicuiensis*. Brazil, Rio Grande do Sul, Unistalda, west of Unistalda, 2011-10-14, A&M 765

less all members have limited areas both of extension and occupancy, consisting of scarce and fragmented populations, mostly composed of a low number of individuals. As already stated in the synopsis, “a possible hypothesis to justify the considerable number of the *P. ottonis*’ external vicariants, and the precariousness almost all of them show, would lead us to consider the idea of an occurred “radiation” in Hennig’s sense (1966: 216–217), ie an accumulation of dichotomous cleavage in a relatively short period of time, with not always successful evolutionary results, as in the cases of *P. ottonis* and *P. linkii*.” (Anceschi & Magli, 2018: 130). Having the dominant taxon a certain variability, it can in fact show 6–15 (or more) indifferently rounded or acute ribs (Figs. 32–33), and sharing the semaphoront with acute rib with



Fig. 28 *Parodia muricata*. Brazil, Rio Grande do Sul, Nova Esperança do Sul, 2011-10-16, A&M 770



Fig. 29 *Parodia oxycostata*. Brazil, Rio Grande do Sul, Santiago, between Santiago and Nova Esperança do Sul, 2011-10-16, A&M 768



Fig. 30 *Parodia stockingeri*. Brazil, Rio Grande do Sul, Unistalda, west of Unistalda, 250 m, 2016-05-26, A&M 1363

another taxon of the group, namely *P. oxycostata* (Buining & Brederoo) Hofacker, we believe that the concept of *P. oxycostata* (having a distinctive meaning, within the *P. ottonis* complex, and at the same time being close to the description of *Notocactus oxycostatus* Buining & Brederoo), could at most include *Notocactus acutus* F.Ritter, the only taxon that seems to be really conspecific. The ribs of the latter are in fact acute at the apex and sharp, as shown in the photo of the taxon in Ritter (1979: 355, Fig. 235), and the number of ribs goes from 6–7, 3.5–4cm wide (in *P. oxycostata*), to 7–9, 3cm wide (in *N. acutus*) (Fig. 34). The broad view of the synonymy in *P. oxycostata* and its subspecies *gracilis*, as proposed by Hunt et al (2006: 310), including in addition to *Notocactus acutus* a group of taxa with rather heterogeneous characters such as *N. campestris*, *N. eurypleurus*, *N. glaucinus*,



Fig. 31 *Parodia tenuicylindrica*. Brazil, Rio Grande do Sul, Santana do Livramento, between BR 293 and Cerros verdes, 2011-11-11, A&M 816



Fig. 32 *Parodia ottonis*. Brazil, Rio Grande do Sul, Santana da Boa Vista, 2011-10-30, A&M 798

*N. gracilis*, *Parodia oxycostata* subsp. *gracilis*, *N. harmonianus*, *N. incomptus*, *N. miniatispinus*, *N. minusculus*, *Parodia nothominuscula*, *N. securituberculatus*, in addition to *N. ibicuiensis* (all taxa from

us now included in *P. ottonis*, excluding *P. ibicuiensis*), gave rise to a serious interference that no longer allowed to distinguish *P. oxycostata* from the populations of *P. ottonis*.



Fig. 33 *Parodia ottonis*. Brazil, Rio Grande do Sul, São Francisco de Assis, north of Esquina da Silva, 2011-10-20, A&M 782



Fig. 34 *Parodia oxycostata*. Brazil, Rio Grande do Sul, Santiago, between Santiago and Nova Esperança do Sul, 2011-10-16, A&M 768.



Fig. 35 *Parodia ottonis* (*glaucina* populations). Brazil, Rio Grande do Sul, west of Unistalda, 2011-10-14, A&M 764

Hence the need to use in this case a fine-grained sieve, ie using as few characters as possible to identify *P. oxycostata*. Another case of definition of an external vicariant within the *P. ottonis* group through the use of the fine-grained sieve, is constituted by *Parodia ibicuiensis* (Prestlé) Anceschi & Magli, a taxon we outlined to identify those transitional populations between *P. ottonis* (*glaucina* populations) (Fig. 35) and *Parodia stockingeri* (Prestlé) Hofacker & P.J.Braun (Fig. 36), through the recognition in *P. ibicuiensis*

of the distinctive semaphoront 'diamond-shaped' (Fig. 37). Indeed, morphologically, *P. ibicuiensis* differs from the two previous taxa because it is short cylindrical from a juvenile stage, while some individuals of *P. glaucina* can become like that only in adulthood. The question we can ask ourselves is: are *P. oxycostata* and *P. ibicuiensis*, which we call 'technical species', real species? Believing that through the use of theories and techniques that contemporary science makes available, our definition of something approximating the truth in nature can be related only to the internal coherence achieved in the system (taxonomic in this case) thus created, our answer is yes. The

difficulty highlighted above, ie the definition of external vicariants morphologically close to each other, through the identification of discrete populations in the transition between the taxa in question (populations defined by us as 'technical species'), is not the prerogative of plant communities alone. During our surveys in habitats, we have repeatedly found that similar difficulties also exist in defining the transitional areas where plants live. As example, for a better definition of what has already



Fig. 36 *Parodia stockingeri*. Brazil, Rio Grande do Sul, Unistalda, west of Unistalda, 250m, 2016-05-26, A&M 1363



Fig. 37 *Parodia ibicuiensis*. Brazil, Rio Grande do Sul, Alegrete, west of Alegrete, 138m, 2016-05-17, A&M 1355



Fig. 38 Habitat of *Parodia haselbergii* (*graessneri* populations). Brazil, Rio Grande do Sul, Cambará do Sul, P. N. da Serra Geral, Cânion da Fortaleza, 2011-11-24

been explained in the entries on *Parodia haselbergii* (Haage ex Rümpler) F.H.Brandt in the synopsis (Anceschi & Magli, 2018: 100–101), the Cânion da Fortaleza, in the P. N. da Serra Geral, RS (where the *graessneri* populations lives), is partly surrounded by Pampas reaching the edge of the canyon (Fig. 38). In a similar case the ‘two’ ecosystems are not disconnected, because just as we cannot disconnect the waterfall from the river, we cannot separate a rocky wall from the plateau that creates it. Another example is represented by the *graessneri* populations living in the area of Caxias do Sul, RS, where the Pampas enters the ‘Serra Gaucha’ creating habitats that can still be defined as “Pampa grassland with rocky outcrops”, with a few more metres higher (Fig. 39). This is why we prefer to report both ecosystems as habitat of the taxon in question, ie “Pampa grasslands with rocky outcrops, and canyons of the Serra Geral formation, surrounded by humid subtropical forest, in southern Brazil, 200–1500m”. Using a scientific (inductive) approach, things appear a little more complex, or preferring to use a philosophical (deductive) one, simpler, compared to the current viewpoint.

As highlighted in the introduction, the most evident result obtained from our approach to the understanding of the relationships between taxa in their natural habitats, based on the figure of the dominant species in the Darwinian evolutionary sense (Darwin, 1859), is related to the consequent transformation of the scientific descriptions of the species involved. This expanded vision of the species, implemented through the use of a coarse-grained sieve for the filtering operation of the characters capable of constituting the dominants, takes into account in the descriptions of taxa, all the additional data that this new understanding entails, on the basis of the data relating to the morphology of all the internal populations of the species collected in habitats. As indicated in the synopsis (Anceschi & Magli, 2018: 77) the description of the 62 accepted species, “are based on a mix that consider *The Cactus Family* (Anderson, 2001), *The New Cactus Lexicon* (Hunt et al, 2006), *Das Grosse Kakteen Lexicon* (Anderson & Eggli, 2011), expanded by our field data [in square brackets].” We point out that the part of the data collected in habitat, highlighted in the descriptions in square brackets,



Fig. 39 *Parodia haselbergii* (*graessneri* populations). Brazil, Rio Grande do Sul, Caxias do Sul, 2011-11-16, A&M 820

redesigned the species in question, transforming a taxonomy based on abstract types into one based on real populations, which considers in the description of the examined taxa, also the synonymies subsumed in them.

We have had more than one occasion to see assimilated in a species as synonyms, taxa which manifested distinct semaphoronts from the species in question, without anything changing in its scientific description. Here is an example: our taxonomic understanding of *P. mueller-melchersii*, matches that of the *New Cactus Lexicon*, that considers synonyms for the taxon to be *Notocactus winkleri* Vliet = *Parodia mueller-melchersii* subsp. *winkleri* (Vliet) Hofacker, and *Notocactus veenianus* Vliet = *Parodia rutilans* subsp. *veeniana* (Vliet) Hofacker. As already pointed out in a comment on the topic in our first booklet (Anceschi & Magli, 2010: 26–28), we consider the two taxa to be identifiers of different ontogenetic stages (semaphoronts) of *P. mueller-melchersii*. In this regard, we also noted how Backeberg's description

(1966) which is almost unchanged with respect to the sizes in Hunt et al (2006) and describes a taxon of about 8cm in height, 6cm in diameter, with a pale yellow central spine with dark edges, should be expanded to include the populations of the two above mentioned taxa, with specimens reaching 20cm and more in height, specimens with a completely red central spine, and other specimens showing both characters (Figs. 40–42) (see the description below):

*Parodia mueller-melchersii* (Frič ex Backeberg) N.P.Taylor

**Description:** Habit solitary, stem globose to short cylindrical, 8[–22]cm high × 6[–9]cm diameter. Ribs [17–]20–24, low, with small rounded tubercles. Central spines 1(–3), straight, awl shaped [or flattened, <2.3cm long, whitish] or pale yellow, darker [or dark red] at base and apex. Radial spines [10]–18, slender, <0.8cm long, whitish, [or whitish with dark red base and apex]. Flower 3cm high × 4.5–5cm diameter, pale golden-yellow, citron-yellow or reddish. Fruit





Fig. 40 *Parodia mueller-melchersii*. Uruguay, Tacuarembó, Tambores, 2008-11-22, A&M 284

elongating, 2(-3)cm high × [1.8]cm diameter, [dry, felted white, with reddish bristles], thin-walled, green (Anceschi & Magli, 2018: 120–121).

It can be seen that a good part of the scientific description has been redesigned [new data in red in square brackets] on the basis of the data collected on the individuals of the populations in the taxon



Fig. 41 *Parodia mueller-melchersii*. Uruguay, Tacuarembó, Tambores, 2008-11-22, A&M 284



Fig. 42 *Parodia mueller-melchersii*. Uruguay, Rivera, Tranqueras, Valle del Lunarejo, Mario Padern property, 2006-11-21, A&M 73

habitats. As indicated above, the characters relating to the semaphoronts of the taxa assimilated as synonyms were also considered in the description, deriving both from the descriptions in the cited lexicons and from the data of the surveys relating to them being collected in their habitats. This was done for all the 62 accepted taxa in the synopsis. We are convinced that this approach to classification has changed firstly in substance, and then in numerical data, the information that existed before for these species.

We have discussed the classification of the genus *Parodia* Spegazzini on the basis of the data relating to the holomorphology of taxa collected in habitats, in consideration of the operational concepts used. Regarding our theoretical approach to the results of molecular analysis, often in line with the results of our field data, we refer to ‘Molecular results and principle of monophyly. Some clarifications’ (Anceschi & Magli, 2018: 74–75).

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## GLOSSARY:

**‘Blanqueales’ with allomorphic soils** – Along Uruguay’s western coast, on the flood plains of the Río Uruguay, there are areas of wooded savanna [Fig.4] with allomorphic soil (Duran, 1985, quoted from Fagúndez, 2003: 5). The main characteristic of this kind of soil is the sodium interchangeably, that is sometimes higher than 15% (Dochafour, 1984, *ibid*). This soil composition causes the water absorption capacity to be very limited, with a high loss of organic matter and clay and a consequent loss of structure that favours surface erosion. The residual sand has the typical white colour that gives these strips of lands their name: *blaqueales*. The basic material has a sedimentary origin and it generally dates from the Middle Pleistocene to the Holocene (Duran, 1985, quoted from Fagúndez, 2003: 6).

The physicochemical properties of these soils induce the growth of a specific flora, consisting of species which are able to tolerate such a high salinity. Plants (halophytes) adapted in order to withstand the high salt concentration or to resist the toxic action of some of them (Ragonese & Covas, 1947, *ibid.*) (quoted from Anceschi & Magli, 2014: 62).

**Holomorphy or Holomorphology** – The holomorphology of an organism is the total spectrum of characters exhibited by that organism during its lifetime: its character’s properties. (Wiley & Liebermann, 2011: 15).

**Ontogeny** – The entire sequence of events involved in the development of an individual organism (Collins English Dictionary).

**Peripatric speciation** – peripatric speciation occurs when a small number of individuals become isolated from the central population and differentiate. Peripatric is another term for peripheral isolate speciation (Mayr, 1963), except that it represents the general case rather than referring only to situations where a small population colonises new ranges or becomes isolated around the periphery of the ancestral range (Wiley & Liebermann, 2011: 44).

**Semaphoront** – at the morphological level, or preferably holomorphological, the instrument made available by Hennig to define the lower taxa (species) is based on the concept of semaphoront (1966, 6-7, 32-33, 63, 65-67). The cornerstone at the basis of the biological system is neither the species nor the individual but: “... the individual at a particular point of time, or even better, during a certain, theoretically infinitely small, period of its life. We will call this element of all biological systematics... the character-bearing semaphoront” (*ibid.*, 6). The author specifies that a semaphoront is the individual during a certain, however brief, period of time, and “not at a point in time” (*ibid.*). Adding that there are no rules to define how long the semaphoront exists as a taxonomic entity, and that this depends on the rate at which the different characters change. In the maximum extreme it can take the entire life of the individual, but in many cases, especially in organisms that undergo metamorphic or cyclomorphotic processes, it would be notably shorter. In the summary of Taxonomic Tasks in the Area of the Lower Categories, Hennig summarises his idea: “The semaphoront (the character bearer) must be regarded as the element of systematics because, in a system in which the genetic relationships between different things that succeed one another in time are to be represented, we cannot work with elements that change with time. Accordingly the semaphoront corresponds to the individual in a certain, theoretically infinitely small, time span of its life, during which it can be considered unchangeable.” (*ibid.*, 65).

# Introduction to the authors

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Giovanna Anceschi (b. Milan, Italy, 1963) and Alberto Magli (b. Bologna, Italy, 1960) decided to dedicate their lives to cactus in 2004.

The couple, who are based in Bologna, Italy, have been travelling and researching nonstop ever since, with a focus on field-based taxonomy. Since 2010, they have managed the comprehensive online archive [cactusinhabitat.org](http://cactusinhabitat.org), together with the publication of the related booklets (2010, 2013), dedicated to the documentation and

classification of cactus populations in Argentina, Bolivia, Brazil, Chile, Paraguay, Peru, and Uruguay. Their extended trips have produced notes and photography on more than 350 species in the wild.

They have contributed taxonomical studies on *Echinopsis* s.l. to *Cactaceae Systematics Initiatives* (2013) and on *Parodia* s.l. to *Bradleya* (2018) and *The Cactus Explorer* (2013–2014).

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Giovanna Anceschi and Alberto Magli. Bolivia, Santa Cruz, Comarapa, north of Comarapa, 2,159m, 2016-01-30

