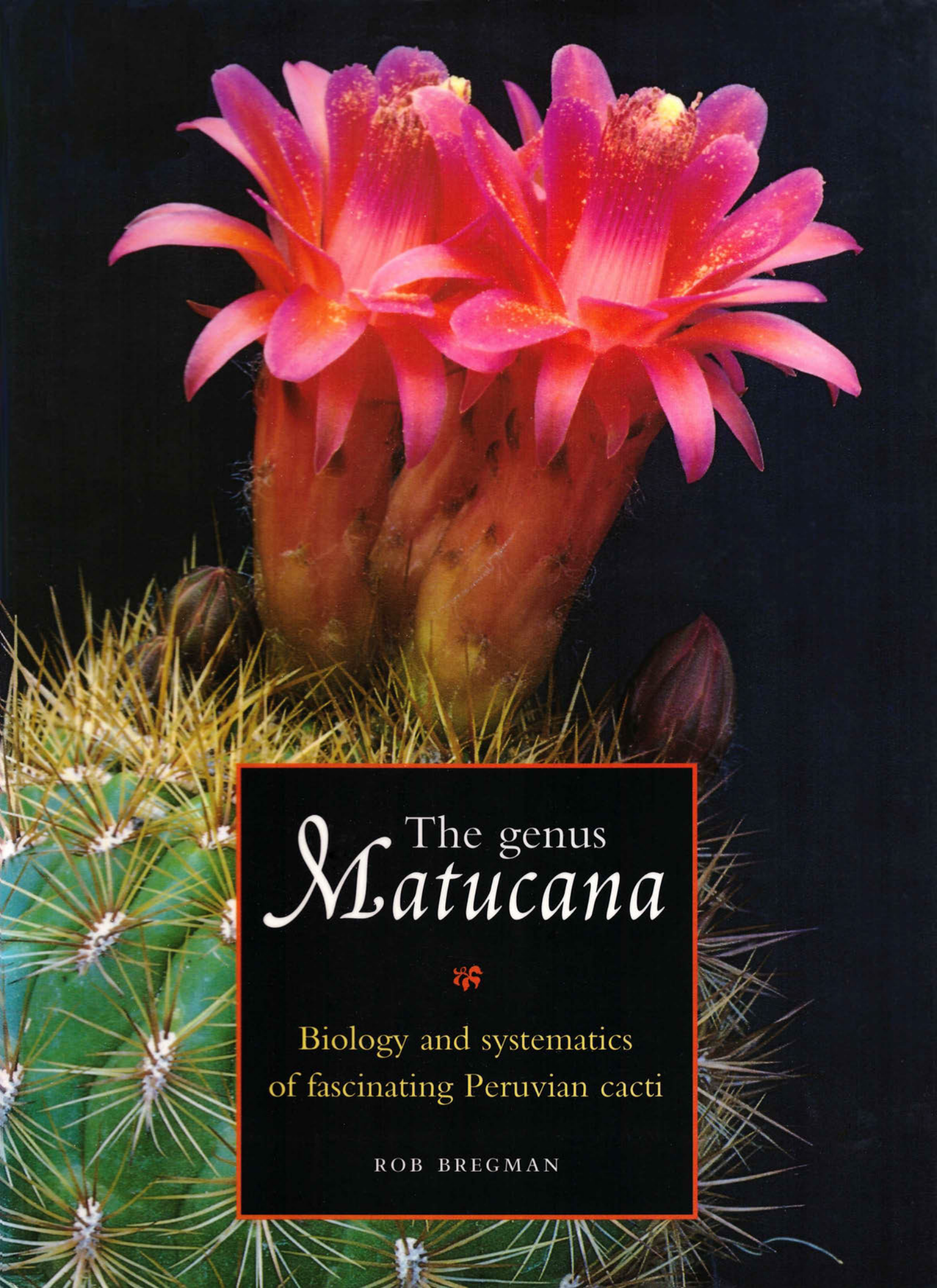

The genus *Matucana*

Biology and systematics of fascinating Peruvian cacti

ROB BREGMAN

As a result of the thorough search for cacti during the last decades, the number of genera, species and varieties has increased considerably, creating a need for specialised literature.
Few books specialising on South American cacti are available. The Peruvian genus *Matucana* (including the former genera *Submatucana* and *Eomatucana*) represents a popular group of plants, of which collections are widespread, but over which little information exists.
In contrast to most monographs, this book contains more than merely descriptions of a collection of species, but in addition provides information on morphology, ecology, pollination, seed development and seed dispersal.
The section on systematics emphasises seed morphology because of its great systematic and phylogenetic significance. Since there is still confusion as to which species should be recognised, much attention has been paid to the taxonomy of *Matucana*. The genus is proposed to consist of 19 species. All are described and depicted by colour plates, drawings of the flower and SEM micrographs of the seed.

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THE GENUS *MATUCANA*

Biology and systematics of fascinating Peruvian cacti

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Dust jacket:
Matucana aurantiaca, raised from seed collected near Cajamarca.

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Preface

All over the world many people enjoy growing cacti for their beautiful flowers and their peculiar appearance. With the increase in the number of genera of cacti, species and varieties that were described as the result of thorough exploration activities since the 1920s, the need for specialized literature has increased steadily. Many hobbyists, who have started with a collection of plants that belong to various genera, tend to specialize after some time in one genus or a group of genera in which they are particularly interested. For those the general handbooks provide insufficient information. Monographs (publications that deal with only one genus) may add valuable data, because they generally contain all current information about the genus in question.

For South American cacti few monographs have appeared so far. Plants that belong to the Peruvian genus *Matucana* are wide-spread in collections; almost any grower of cacti possesses one or more specimens. Therefore, I hope, there is a need for a specialized work on this genus, in which all species and varieties are described and depicted.

Emphasis has been laid on seed morphology because of its great systematic and phylogenetic significance. In contrast to most systematic treatments, I have deliberately tried to make this work not merely a collection of species descriptions, but have also included additional information covering various biological matters. This has been done to give some explanations for what we see: why a Matucana has such a long red flower, why the seeds are shaped the way they are; these and many more such questions are answered. One chapter is devoted to ecological factors like climate, vegetation and soil. Another chapter deals profoundly with the reproductive process; in addition seed development and seed dispersal is amply discussed. Phylogenetic relationships inside *Matucana* are detailed as well.

Several parts of this work were previously published in *Succulenta*, the journal of the Dutch/Belgian Cactus and Succulent Society, between 1986 and 1990. That was when the taxonomic treatment of the genus *Matucana*, viz. the recognition of 19 species, was first published. That taxonomy is adopted here as well, but it must be taken as a provisional concept since much field data is still lacking.

It is my hope that this book will enhance the popularity of these beautiful plants.

Amsterdam, October 7, 1994

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Acknowledgements of colour pictures

W. Alsemgeest: Plates 3, 21, 22, 27, 46, 53, 62, 80.
K. van Boxtel: Plate 4.
E. Gödde (F. Ritter): Plate 40.
B. Hensel: Plate 13.
A. Lau: Plate 49.
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P. Melis: Plates 1, 14, 15, 16, 17, 20, 25, 26, 31, 35, 36, 38, 51, 52, 68, 72, 78.
A.B. Pullen: Plates 5, 7, 48.

All other colour pictures, scanning electron micrographs, schemes and drawings were made by the author.

CHAPTER 1

Taxonomy and systematics

1.1 CLASSIFICATION

The name *Matucana* was introduced in 1922 for a new genus of cacti by the Americans N. Britton and J. Rose in their standard work *The Cactaceae*. This new genus was named after a small Peruvian town approximately 80 km east of Lima, where the type species had been found. This species, *Matucana haynei* (Plate 1), had already been known as *Echinocactus haynii* for quite some time; the plant was first described by Otto in 1849. (The epithet 'haynii' later turned out to be a misspelling of 'haynei'). At the time *Echinocactus* was a genus composed of all kinds of globular cacti. Britton and Rose took *E. haynii* out of this heterogeneous mixture of species for its typical long red zygomorphic flower, which differentiated it from the other *Echinocactus* species, in combination with the densely spinated plant body. No other species was included in the new genus, so for the time being *Matucana* was a monotypic genus.

However, 9 years before the erection of the genus *Matucana*, three other plants that we know today as *Matucana* species, had already been described (also in *Echinocactus*) by Vaupel in 1913. These are *E. weberbaueri*, *E. myriacanthus* and *E. aurantiacus*. Britton and Rose did not recognise these plants as Matucanas; *Echinocactus weberbaueri* Vaupel was reported to be insufficiently known but (quote) 'it much resembles *Matucana haynei*'. *Echinocactus myriacanthus* Vaupel was placed in the genus *Arequipa*, another newly described genus by Britton and Rose. *Echinocactus aurantiacus* Vaupel was eventually maintained in *Echinocactus* but was also transferred to *Arequipa* in 1930 by Werdermann. Nowadays it seems obvious that the comparatively little attention to fruit morphology in those days ('fruit not known') is responsible for the fact that Britton and Rose did not recognise these three species as close relatives of *Matucana haynei*, thus as true Matucanas.

In 1941 W.T. Marshall and T.M. Bock published their work *Cactaceae*. These authors placed the genus *Matucana* in the tribe Cereae, subtribe Echinocactinae grouped with *Arequipa* and *Oroya*. *Matucana* remained monotypic: only *M. haynei* (Otto) Br. & R. was included. *Arequipa myriacantha* was considered to be

conspecific with *Arequipa leucotricha*, hence the future *Matucana myriacantha* remained an *Arequipa* species.

C. Backeberg demonstrated that on the basis of floral characteristics the genus *Matucana* could not be maintained in the subtribe Echinocactinae. During the period 1958-1962 he completed his 6-volume monumental work *Die Cactaceae* from which two memorable facts should be discussed. Firstly, *Matucana* was placed in the subtribe Austrocereinae, 'Sippe' Loxanthocerei, 'Untersippe' Brachyloxanthocerei (Table 1). By bringing together *Matucana* with *Denmoza* and *Arequipa*, Backeberg demonstrated his recognition of the close relationship between these genera. Strangely enough, Backeberg placed the genus *Oroya* in an entirely different group, namely in the 'Sippe' Austroechinocacti, together with, among others, *Parodia* and *Gymnocalycium*. A second important fact was the introduction of the genus *Submatucana*. The most significant difference with *Matucana* was the presence of hairs in the scale axils of the flower. This characteristic, shown by most species from northern Peru, was in contrast to the original description of *Matucana* by Britton and Rose, where the floral tube was described as being naked. Rather than revising the original description of *Matucana*, Backeberg prefered to introduce a new genus, *Submatucana*. *Echinocactus aurantiacus* Vaupel was designated as the type, now to be named *Submatucana aurantiaca* (Vaupel) Backeberg.

During the 1950s several new *Matucana* taxa were discovered by W. Rauh, which he described in 1956 in co-authorship with Backeberg. In 1958 he published the results of his extensive study of the Peruvian cactus flora.

In 1959 F. Buxbaum published a new classification of the Cactaceae. Here the introduction of the subtribe Borzicactinae was prefered as an alternative to Backeberg's approach. The genera originally included in subtribe Borzicactinae are shown in Table 2. In addition, Buxbaum expanded upon the original diagnosis of

Table 1. The genera of the 'Sippe Loxanthocerei' according to Backeberg (1958-1962) (*Winterocereus* Backeberg is a synonym of *Hildewintera* Ritter).

Euloxanthocerei		Brachyloxanthocerei	
Akersia	*Loxanthocereus*	*Arequipa*	*Matucana*
Bolivicereus	*Morawetzia*	*Denmoza*	*Submatucana*
Borzicactus	*Oreocereus*		
Cephalocleistocactus	*Seticereus*		
Cleistocactus	*Seticleistocactus*		
Clistanthocereus	*Winterocereus*		

Table 2. Composition of the subtribe Borzicactinae (tribe Trichocereae) when introduced by Buxbaum (1959).

Borzicactinae		
Arequipa	*Denmoza*	*Morawetzia*
Borzicatus (including *Bolivicereus* and *Clistanthocereus*	*Loxanthocereus* (including *Maritimocereus*)	*Oreocereus*
Cleistocactus	*Matucana*	*Oroya*
		Seticereus

Table 3. Classification of *Matucana* according to Hunt (1967).

Subtribe Cereinae, group C		
Arthrocereus	*Echinopsis*	*Oroya*
Borzicactus (including *Matucana*)	*Espostoa*	*Rebutia*
	Leocereus	*Trichocereus*
Cleistocactus	*Lobivia*	*Zehntnerella*
Denmoza	*Mila*	

Matucana formulated by Britton and Rose because a more complete description became necessary.

The classification of Backeberg with over 200 genera of Cactaceae, being an example of extreme taxonomic splitting, met considerable opposition. A reaction, representing the opposite concept of conservative taxonomic lumping, came from M. Kimnach in 1960. All species formerly published under the generic names of *Arequipa*, *Arequipiopsis*, *Bolivicereus*, *Clistanthocereus*, *Loxanthocereus*, *Maritimocereus*, *Matucana*, *Morawetzia*, *Oreocereus*, *Seticereus* and *Submatucana* were united into one large genus *Borzicactus* sensu lato (in broad sense). In Britain and the United States Kimnach's opinion met general approval but on the European continent this classification was rejected by most people. A taxonomic approach similar to Kimnach was adopted by D. Hunt. In 1967 he classified *Borzicactus* sensu Kimnach in group C of subtribe Cereinae (see Table 3). Accordingly, no separate genus *Matucana* was recognized.

Another different view on the systematics of *Matucana* and related genera was shown by H. Krainz. In 1963, he transferred the genera *Matucana* and *Submatucana* in the sense of Backeberg to *Arequipa*. A consequence of this action was that all *Matucana* species known at the time including the type species *M. haynei*, were recombined to *Arequipa*.

In 1965 F. Ritter, who had been searching for cacti ever since the late 1920s, published some remarkable new species. For one of those the new genus *Eomatucana* was erected with *E. oreodoxa* as the type. This genus differed from *Matucana* in having an open nectar chamber instead of a nectary closed by a diaphragm. Another Ritter discovery was *Matucana aureiflora*, for which the new subgenus *Incaica* was set up. This plant has a funnel-shaped flower instead of the tubular one normally encountered in *Matucana*. In 1981 he changed the spelling of this taxon into 'Incaia'.

Buxbaum disagreed with the lumping of genera by Kimnach and Hunt. He supported the maintenance of *Matucana* as a separate genus. In 1974 he transferred a couple of *Matucana* species with long and slender flowers to the genus *Loxanthocereus*. Furthermore, he proposed the moving of all species of *Seticereus*, a cereoid genus from the Peru-Ecuadorian borderzone, to *Matucana*.

During 1970-1971 J. Donald wrote a series of commentaries on the subtribe Borzicactinae. He largely followed the classification by Kimnach and Hunt. He attempted to diagnose *Matucana* again, this time as a subgenus of *Borzicactus*.

In 1981 volume 4 of Ritter's work on the South American cacti appeared. He stuck to his previously introduced genus *Eomatucana* which contained the type

species *E. oreodoxa* as well as *E. madisoniorum*. The latter species was moved to *Eomatucana* because the flower has an open nectary. Backeberg's genus *Submatucana* was rejected; all species previously described in *Submatucana* were transferred to *Matucana*. According to Ritter the genus *Matucana* consisted of two subgenera: *Matucana* and *Incaia*.

Since 1986 the International Organization for Succulent Plant Study (IOS) has been trying to achieve consensus for a new system of classification. At first (Hunt & Taylor 1986, Barthlott 1988), *Matucana* was considered to be encompassed within *Oreocereus*. In the latest version of the consensus discussions (Hunt 1992), this idea has fortunately been dropped in order to bring back an earlier situation where *Matucana* (including *Submatucana* and *Eomatucana*) is treated as a genus.

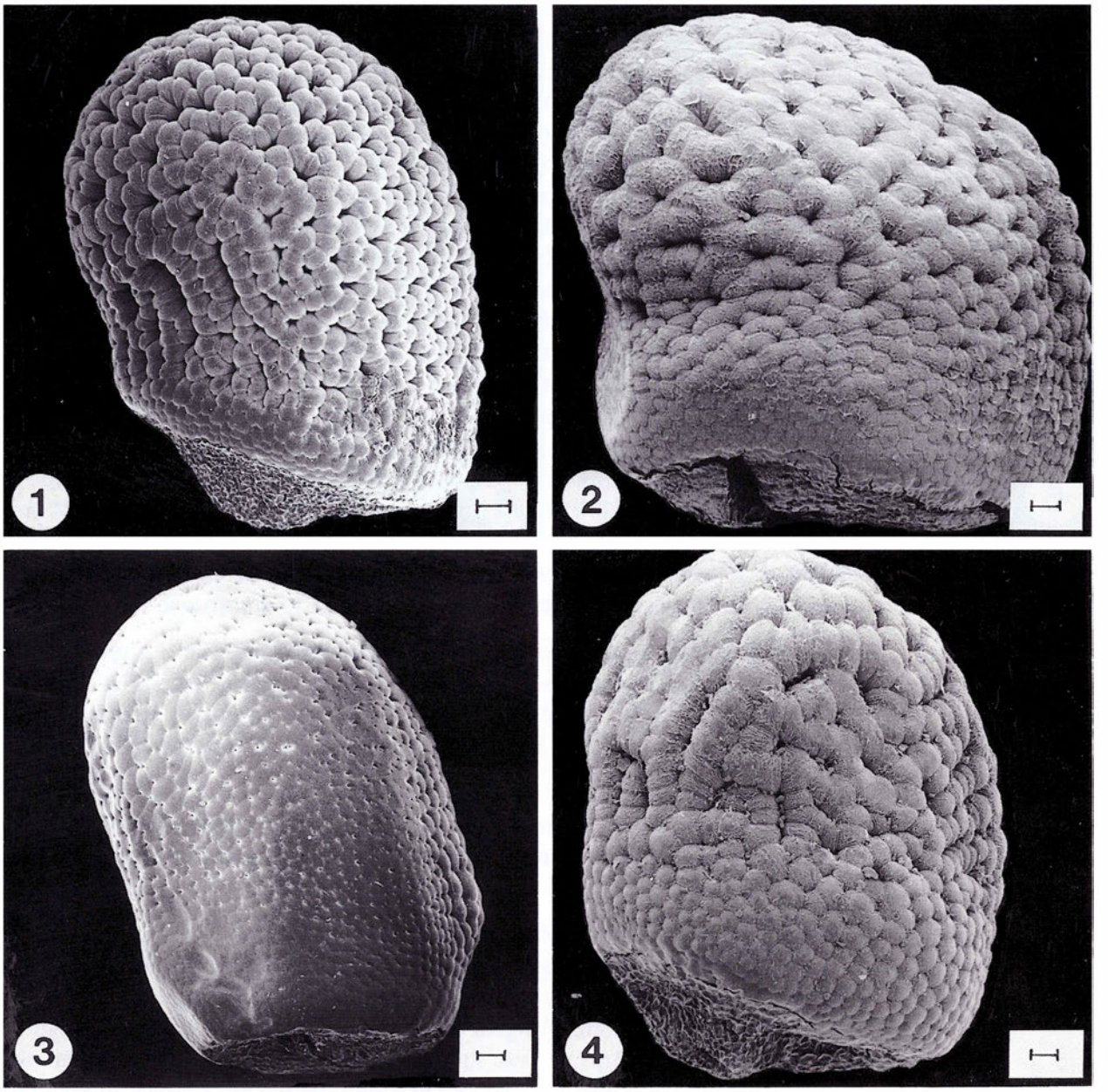
Even harder than the question as to whether *Matucana* is a distinct genus is the species problem in *Matucana*. The main reason is that so little field data is available; the distribution and natural variation of many *Matucana* species are poorly known. Beside this lack of information, the differences of opinion in this matter among 'cactus authorities' play an important role. Ritter (1981) recognized 26 species (probably 27 if he had known of *M. polzii*), the *CITES Cactaceae Checklist* (Hunt 1992) listed 10 good species and 11 preliminary ones. In this book 19 species have been identified. This taxonomic approach should be considered provisional. When additional field data becomes available, this number is likely to be altered.

It is easy to critize each system of classification. As long as biological classification exists, objections will be heard. These are especially numerous in plant groups of great horticultural importance such as orchids and cacti, where amateurs traditionally have been playing an important role in classification. Unfortunately, it is just these two popular plant families that are most notorious for their taxonomic problems and complexity. It should be borne in mind that classifying living organisms on the basis of human standards is purely artificial and depends upon the views of the taxonomist. For example, no rules can be given as to where to draw the boundaries between genera. The rank of species, which is the basal rank in taxonomy, is the only rank for which definitions have been formulated; different definitions by various authors, though, but with some common background. Consequently, no clear circumscription can be given for what exactly a species is, so the species problem will endure. Classification equates to drawing sharp boundaries between groups of organisms which are in most cases not sharply separated morphologically. It is of course the extreme complexity of nature itself that is responsible for our taxonomic problems. Let us just accept that.

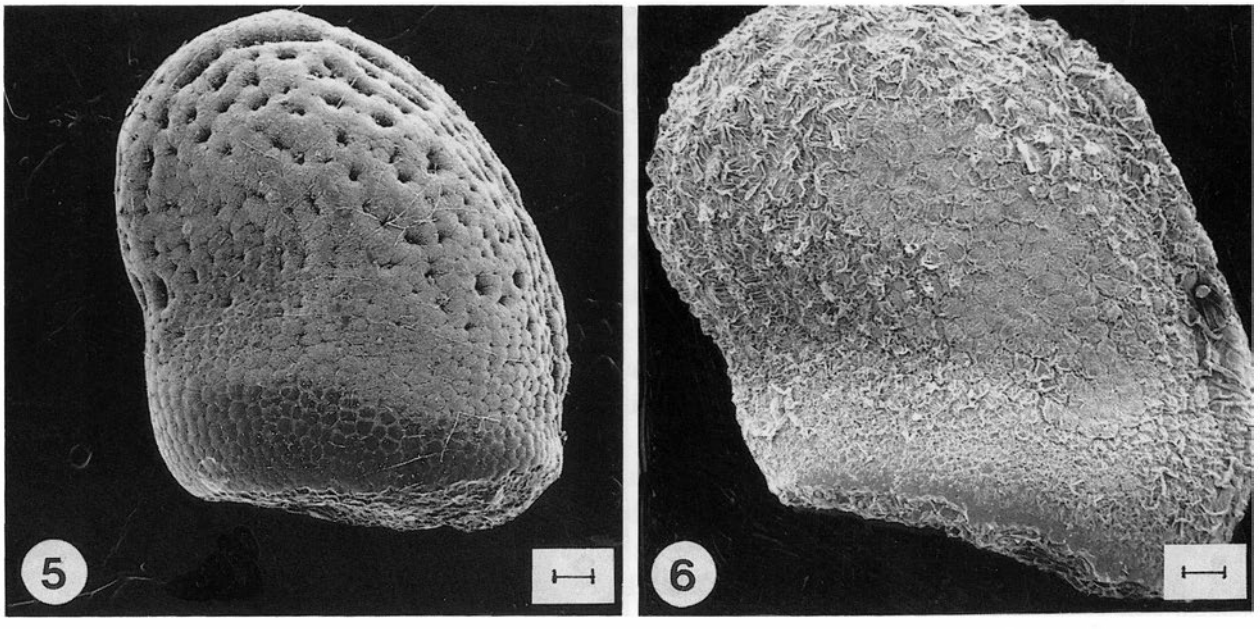
1.2 WHAT IS *MATUCANA*? DELIMITATION OF THE GENUS

The question 'what is Matucana' can simply be answered by saying: Matucana is a collection of mutually related plants that have a number of features in common, which are described in the genus description. So the only thing to do is to make a clear description of the genus.

Unfortunately it's not as simple as that. The difficulty is that plant features can be qualified in different ways. In addition, living organisms possess all kinds of



Photograph 1. Scanning electron micrographs (SEM) of seeds of *Matucana* and its related genera in lateral view. Ventral side left, dorsal side right. Scale bar is 0.1 mm. 1. *Oreocereus* (*Arequipa erectocylindrica*), 2. *Oreocereus* (*O. celsianus*), 3. *Oreocereus* (*Morawetzia doelziana*), 4. *Denmoza* (*D. rhodacantha*).



Photograph 1 (continued). 5. *Oroya* (*O. peruviana* var. *brevispina*), 6. *Matucana* (*M. haynei*).

features, not only clearly visible ones but also not outwardly visible properties such as chemical and physiological characteristics. One taxonomic rule says that all species of the same genus must be more related to themselves than to species from other genera. Given the assumption that related plants have more features in common than non-related plants (which is not always the case), taxonomists have always searched for similarities between taxa as a tool for determining the mode of relationship. For practical reasons floral characteristics were mostly used in the past, because they are clearly visible and comparatively uniform within populations. That is why many authorities (Backeberg, Buxbaum, Kimnach, Donald, etc.) stressed floral features of cacti for the classification of genera. If only stem and flower characteristics were available, it would be very difficult to separate many genera of the Borzicactinae, for example *Matucana* and *Arequipa*, because of their more or less similar plant body and flower structure. But when we also take the fruit and the seed into account, then it is much easier to draw borderlines between genera.

The first description of the genus *Matucana* by Britton and Rose was insufficient. Many characteristics which we now feel should not be ignored in diagnoses of plant genera were absent. Today it would not be acceptable to describe a plant genus or species without saying anything about the fruit and the seed, as was the case in the first description of *Matucana*. Their description was as follows:

Usually simple, small and globular, rarely elongated; ribs numerous, broad, low, somewhat tubercled; areoles approximate, very woolly when young, with numerous acicular or bristly spines; flower slender, tubular, scarlet, with a narrow limb; scales on the ovary and flower-tube scattered, naked in their axils; fruit not known.

Backeberg (1958) separated the genus into two genera: *Matucana* and *Submatucana*. His additional description of *Matucana* (translated from the original German text) is:

Body flat-globose to cylindrical, often changing habit form in later life, simple or weakly offsetting to developing large clumps; receptacle rather slender, axils of scales naked, throat oblique, perianth segments more or less straight to more or less bent; style, stigma and filaments mostly brightly coloured, stigma and sometimes the stamens protruding; flower length very variable, 3-8 cm long; fruit mostly small, about 1 cm across, dehiscing by vertical slits.

Backeberg's description of *Submatucana* was (also translated):

Body simple or offsetting, globose; ribs tuberculate, tubercles mostly more or less hexagonal with a more or less clear short groove to the base of the tubercle above; flower with robust receptacle; throat more or less oblique; perianth segments more or less bent; stamens erect and bunched around the style; receptacle with scales acute at the top, axils strongly or weakly pubescent; in the base of the receptacle a ring of hairs (like in Loxanthocereus) or absent; fruit round, drying, dehiscing vertically.

Ritter (1981) included *Submatucana* in *Matucana*, but of course maintained his 1965 genus *Eomatucana* as a separate genus. The principal differences between

Eomatucana and *Matucana/Submatucana* are found in the flower. In *Eomatucana* the flower is actinomorphic and has a long and slender tube, the diaphragm is absent and there is no ring of primary stamens in the base of the floral tube.

1.2.1 *Matucana, Submatucana and Eomatucana: One genus?*

Eomatucana Ritter contains two species. One of them, *E. madisoniorum*, does not belong there, as will be explained elsewhere in this book (Chapter 11). The other species, *E. oreodoxa*, is indeed a plant with a flower that differs from all other Matucanas and Submatucanas. Its fruits and seeds, on the other hand, are typical *Matucana*. Therefore, *Eomatucana* has been included in *Matucana*.

The morphological boundary between *Matucana* and *Submatucana* sensu Backeberg is vague. When neatly grouped in the greenhouse, the poorly spinated species from the Rio Maranon area (the most typical group of *Submatucana*) look entirely different from the densely spinated *M. haynei* and its affinities. These two groups are the extremes but in between them there are many species with intermediate features. Three examples are given:

– *M. aurantiaca* has the stem of *Submatucana* but the seed of *Matucana*. Its flower may be either naked or hairy, so in that respect it is both *Matucana* and *Submatucana*!

– *M. myriacantha* has the stem of *Matucana*. Its flower has a narrow and naked tube (*Submatucana* and *Matucana* respectively).

– *M. weberbaueri* has the spination and flower (in different colour) of *Matucana*. The seeds are similar to those of *M. aurantiaca* which is the type species of *Submatucana*!

These examples indicate that it is impossible to circumscribe *Matucana* and *Submatucana* separately without considerable overlap. Thus, the only possible solution is to put them together in one genus. When doing so, the typical seed and fruit characteristics can be utilised as generic features. Combining *Matucana* s.s., *Submatucana* and *Eomatucana*, all species have a very similar type of fruit. As to the seeds, only *M. madisoniorum* has a different seed type. In flower appearance only two species deviate: *M. oreodoxa* and *M. aureiflora*. So there are three *Matucana* species with deviating features. That is not unusual for a genus of 19 species. Besides, these deviating species inside *Matucana* make them easy to identify when using a key.

To summarize, *Matucana* Britton & Rose, *Submatucana* Backeberg and *Eomatucana* Ritter are treated here as one genus *Matucana*, which is described as follows:

Plant globose to short cylindrical, sometimes cereoid.

Flowers borne from the young areoles, more or less zygomorphic, coloured, 4-10 cm long. Nectar chamber short, mostly with a diaphragm which tapers into a bunch of filaments. Receptacle mostly more or less tube-shaped, with few scales. Stamens inserted in 3 sections: 1. Many in a ring above the nectar chamber (primary stamens), which are absent in two species only; 2. Few in the inner floral tube wall (secondary stamens); 3. Many in a ring at the edge of the receptacle (secondary stamens). Filaments hugging the style, most of them reaching beyond the flower margin, coloured, seldom white all over; anthers cream, sometimes

violet. Stigma mostly stretching beyond the anthers, greenish, sometimes yellow, seldom red. Perianth coloured (mostly scarlet, sometimes yellow, orange, pink or purple), often multi-coloured, the upper segments more straight, the lower ones mostly spread, seldomly all perianth segments equally spread.

Fruit very characteristic: globose to oval, usually about 1 cm across, green, often red to brown basally, mostly ribbed longitudinally, dehiscing by three vertical slits which stretch upwardly to half or 2/3 of the fruit length.

Seed dull yellowish brown to black, short bag-shaped and relatively broad, mostly appr. 1 mm long and wide, mostly with a partly detached paper-like outer cuticular layer; testa cells irregularly arranged with mostly folded cuticle; hilum as large as the entire seed width, including the small micropyle. Embryo oval with weakly curved short cotyledons. Perisperm absent.

The morphological properties of Matucanas are described in detail and illustrated in Chapter 2.

1.2.2 *Differences between Matucana and related genera*

The genera which have the closest affinity to *Matucana* are *Oreocereus* (including the former genera *Arequipa* and *Morawetzia*), *Oroya* and probably *Denmoza*, although some specialists are not quite sure about the position of the latter genus. This group of four genera constitutes a part of the subtribe Borzicactinae Buxbaum which has adapted to Andean conditions at elevations above 2000 m. (Some exceptions, e.g. the occurrence of some species at lower altitudes are taken to be of secondary origin.) Within the Borzicactinae the genera mentioned are believed to descend from one common ancestor sharing the combination of two important features, viz. dry dehiscent fruits (although less clear in *Denmoza*) and large verrucose seeds with a broad hilum.

The major differences between *Matucana* and its three most related genera are to be found in the flowers, the fruits and the seeds. Only a few stem features can be used for identification. *Oreocereus* differs in this respect from *Matucana* in having areolar trichomes; moreover, a number of species have a very wooly floral zone provided with bristles and hairs. The large globular stems of *Denmoza* are also different from the stems of *Matucana*.

Table 4. Main differences in seed characteristics in *Oreocereus, Oroya, Denmoza* and *Matucana*.

Genus	Seed surface	Testa cells	Cuticle	Hilum
Oreocereus (including *Morawetzia* and *Arequipa*)	Verrucose or smooth, pitted	Convex	Not detached	Weakly depressed
Oroya	Weakly verrucose, pitted	Convex	Not detached	Weakly depressed
Denmoza	Verrucose, pitted	Strongly convex	Not detached	Strongly depressed
Matucana	Verrucose, not pitted	Weakly convex	Detached	Weakly to strongly depressed

In floral morphology two of the genera mentioned are different. *Denmoza* flowers have strongly reduced perianth segments causing the filaments and the style to protrude far beyond the perianth. *Oroya* has relatively small campanulate flowers.

The vertical splitting of *Matucana* fruits is not encountered in its related genera *Oreocereus*, *Oroya* and *Denmoza*. The first two mentioned genera produce globular to elliptical fruits without ribs and without the typical vertical dehiscense by three slits. Instead, these fruits dehisce by a basal pore. Moreover, they are mostly yellowish, whereas *Matucana* fruits are green or brown. In some *Oreocereus* species the fruits are even fleshy. *Denmoza* fruits usually dehisce by a lateral split caused by the pressure of the pulp and then dry out.

The seeds are different as well (Photograph 1). The main differences in seed features between *Matucana* and its related genera are given in Table 4.

CHAPTER 2

Morphology

In the previous chapter, the features which determine whether or not a given plant belongs to the genus *Matucana* have been described. These are the characteristics for the entire genus, so they are expected to be present in every species of *Matucana*. Let us now look more closely at these characteristics to see how they may vary.

2.1 STEM

An often-heard complaint of people who have just started collecting succulents is that a cactus without a flower is very hard to identify. Once the plant has produced a flower, it is usually a lot easier to find out to what genus the plant in question belongs. The genus *Matucana* is no exception to this; a Matucana without flowers may be taken by non-specialists for a Neoporteria, an Echinopsis, a Lobivia or other genus.

A wide range of stem variants can be found in *Matucana*. Tall plants or small plants, many ribs or few ribs, dense spination or no spination at all, all kinds of variants can be found, depending upon the species. Even within a single species these features, particularly the spination, are often highly variable, hence they are not very useful for the identification of a species. In the past there have been occurrences of plants from one population but with different spination being described as different species or varieties.

The southern species have mostly bodies that are globular when young but later become elongated. Some species are able to reach one meter in height (*M. comacephala*). These plants have many ribs with a dense spination (Plate 2).

Other species, mostly more northerly in distribution, have an entirely different plant body. They are usually globose in shape, with less ribs and less spines. The smallest *Matucana* species is *M. oreodoxa* with a body less than 5 cm across; the areoles bear only 5 or 6 spines. Completely spineless may be *M. madisoniorum* (a few spines are formed but they detach rather easily) which makes the plant (without flowers) look like a Lophophora or a Gymnocalycium (Plate 3). Also *M. polzii* is a small plant with a low number of spines on each areole. The many offsets on the lateral and basal areoles make this plant look like an Echinopsis

(Plate 4). On the other hand, there are populations of *M. aurantiaca* consisting of large globose specimens more than 20 cm across and tall, with a dense spination. Young specimens of *M. intertexta* are flat globose and densely spinated with short white spines, whereas the mature plant has a much more open spination.

The colour of the plant body may be either bright grass-green or grey-green. The species with a grey-green body are restricted to the Rio Maranon valley and are here designated as the paucicostata group. In *M. pujupatii* the colour of the body is even bluish grey-green, as though the plant has been powdered with chalk dust. Furthermore, these grey-green bodies are dull due to a papillate surface, whereas the remaining species have a more or less glossy epidermis.

Generally, very little is known about the micromorphology of the spines. The spines of most cacti look more or less the same under the microscope. Therefore, it is to be expected that among Matucanas there is not very much difference in spine morphology either. In this respect only *M. paucicostata* has been studied. The spines of young seedlings are provided with numerous tiny, radially spreading hairs, which make them look like feathers (Photographs 2.1 and 2.2). In older plants the spines are without these hairs and have a verrucose surface instead (Photographs 2.3 and 2.4). This is due to folding of the surface resulting in numerous tube-like cavities. These structures may be related to water uptake by the spines.

2.2 FLOWER

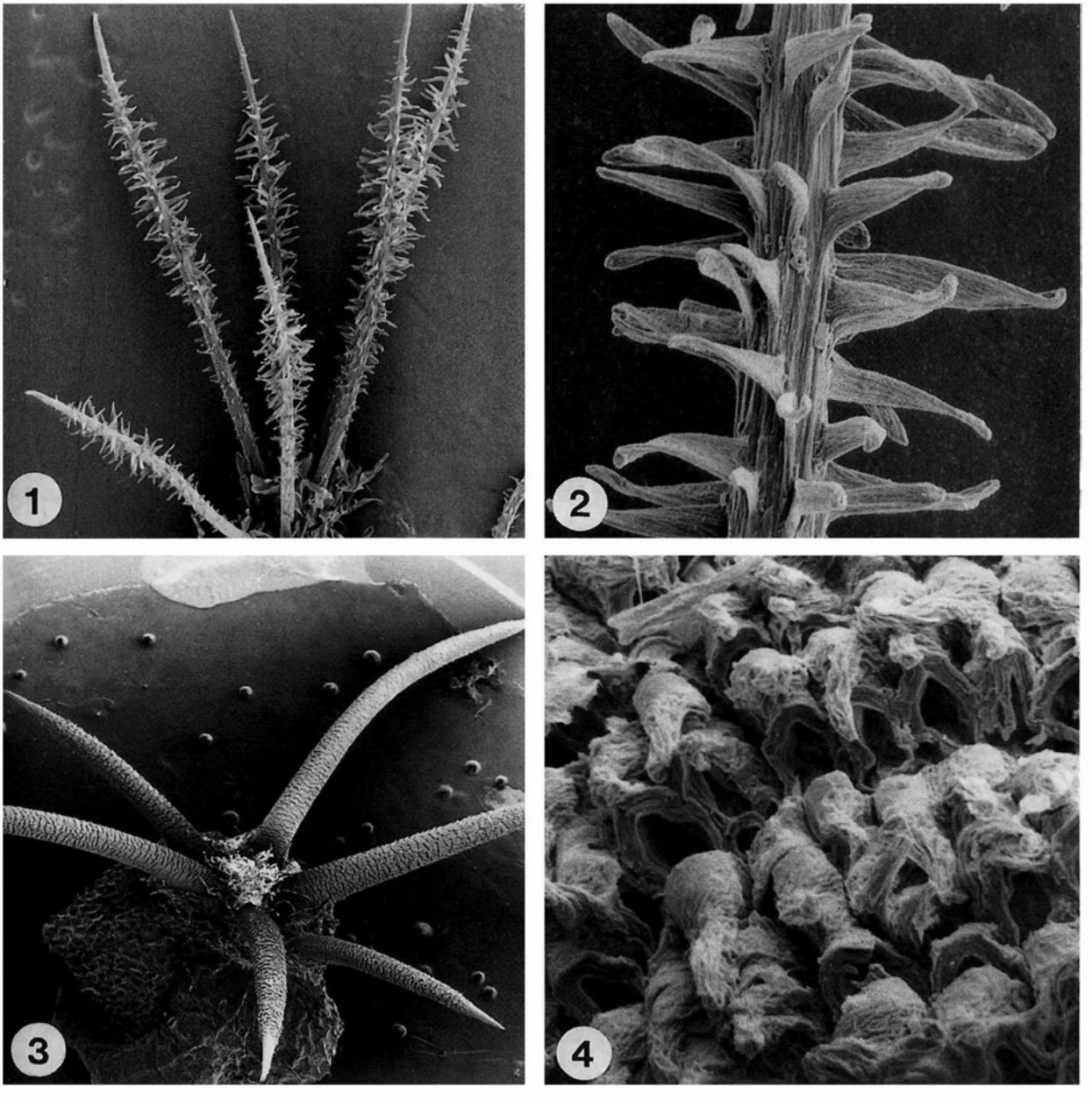
As previously stated, cactus systematics in the past was for the greater part based upon flower characteristics; it was the typical long tubular flower of *Echinocactus haynii* which made Britton and Rose decide to raise the genus *Matucana* and to give this plant a separate position ouside *Echinocactus*.

2.2.1 *The typical Matucana flower*

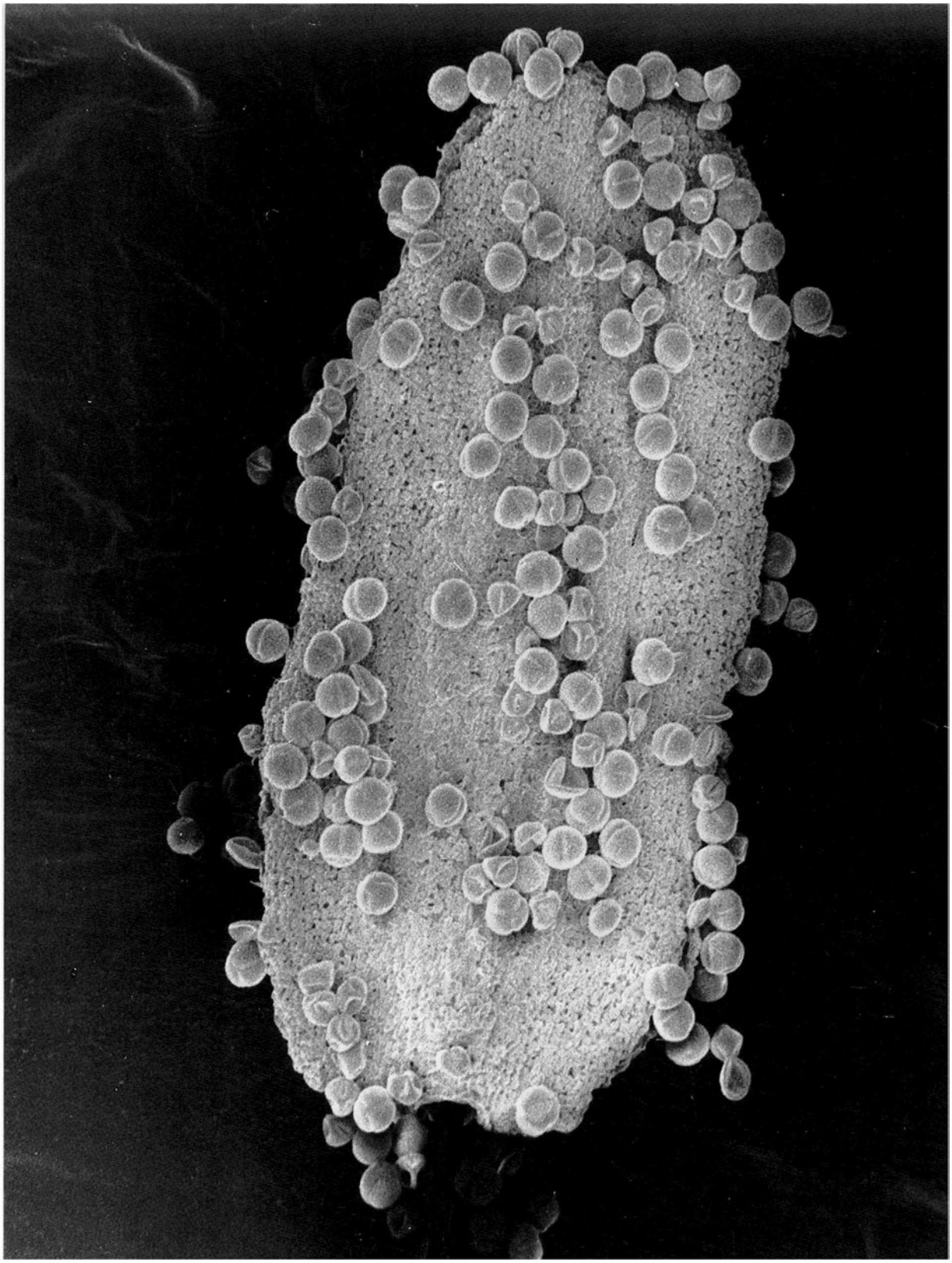
The red, tubular, slightly zygomorphic flower is indeed the most frequent type of flower in *Matucana* encountered (Plate 5). It is odourless and remains fresh for two days under normal circumstances. In a hot greenhouse the flower may wither soon after one day. During flowering the flower does not close, not even at night.

When taking the flower tube between the fingers, one immediately feels its robust construction (which is an adaptation necessary for bird pollination). The floral tube (receptacle) is always firm but varies in width and length. Very long and narrow flowers with a tube of only 5 mm wide are found in *M. krahnii*, *M. madisoniorum* and *M. ritteri*, for example. Wide floral tubes can be found in *M. fruticosa*, *M. aurantiaca* and *M. haynei*. The outside of the floral tube is scaly. The scales are short triangular on the ouside of the ovary and very regularly intermingle into the perianth segments.

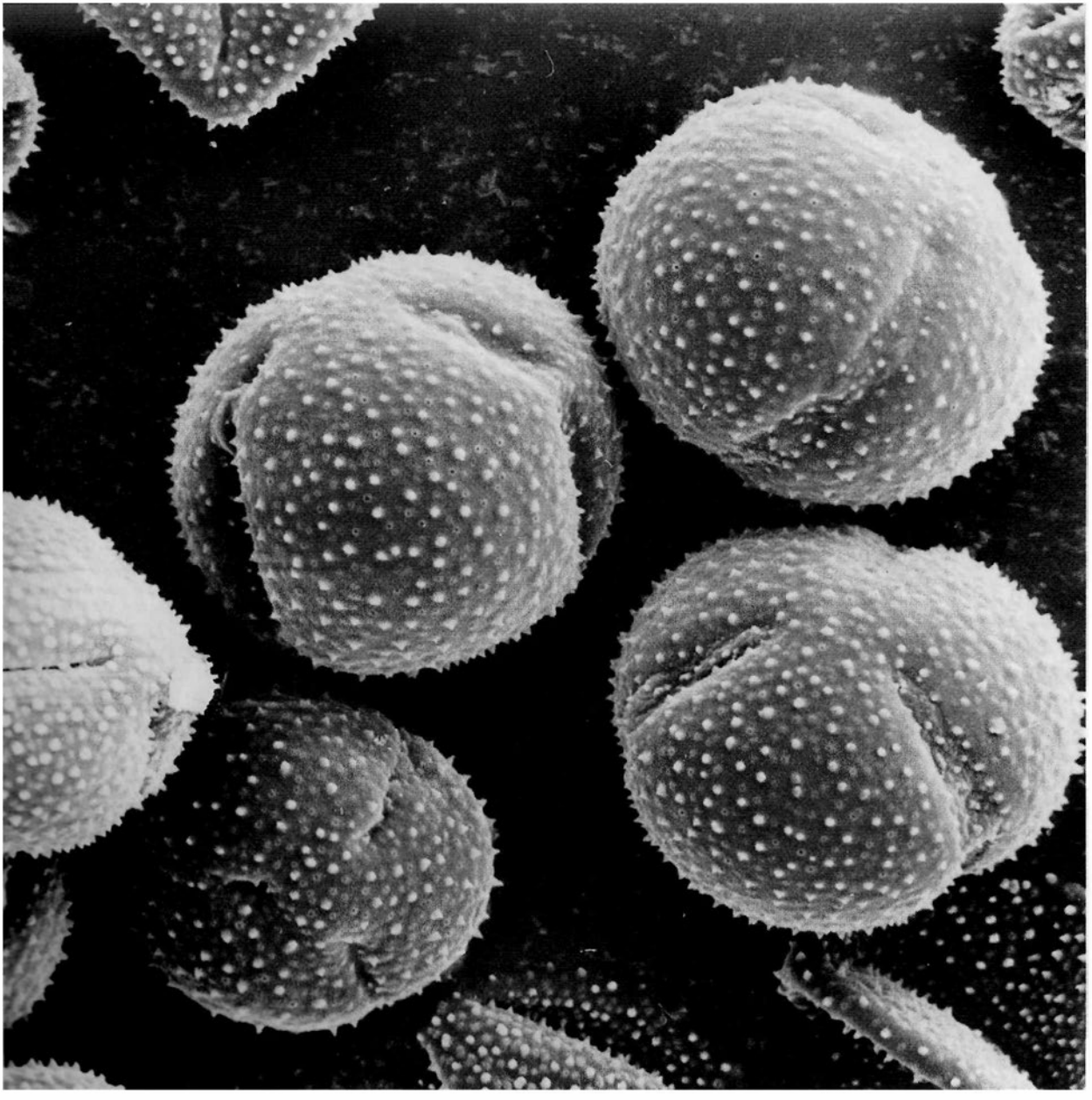
Many species of *Matucana* develop hairs in the axils of the scales on the outside of the floral tube. Backeberg used this feature to distinguish his genus *Submatucana* but unfortunately for him this characteristic turned out to be strongly variable within a single population and therefore taxonomically useless. Both



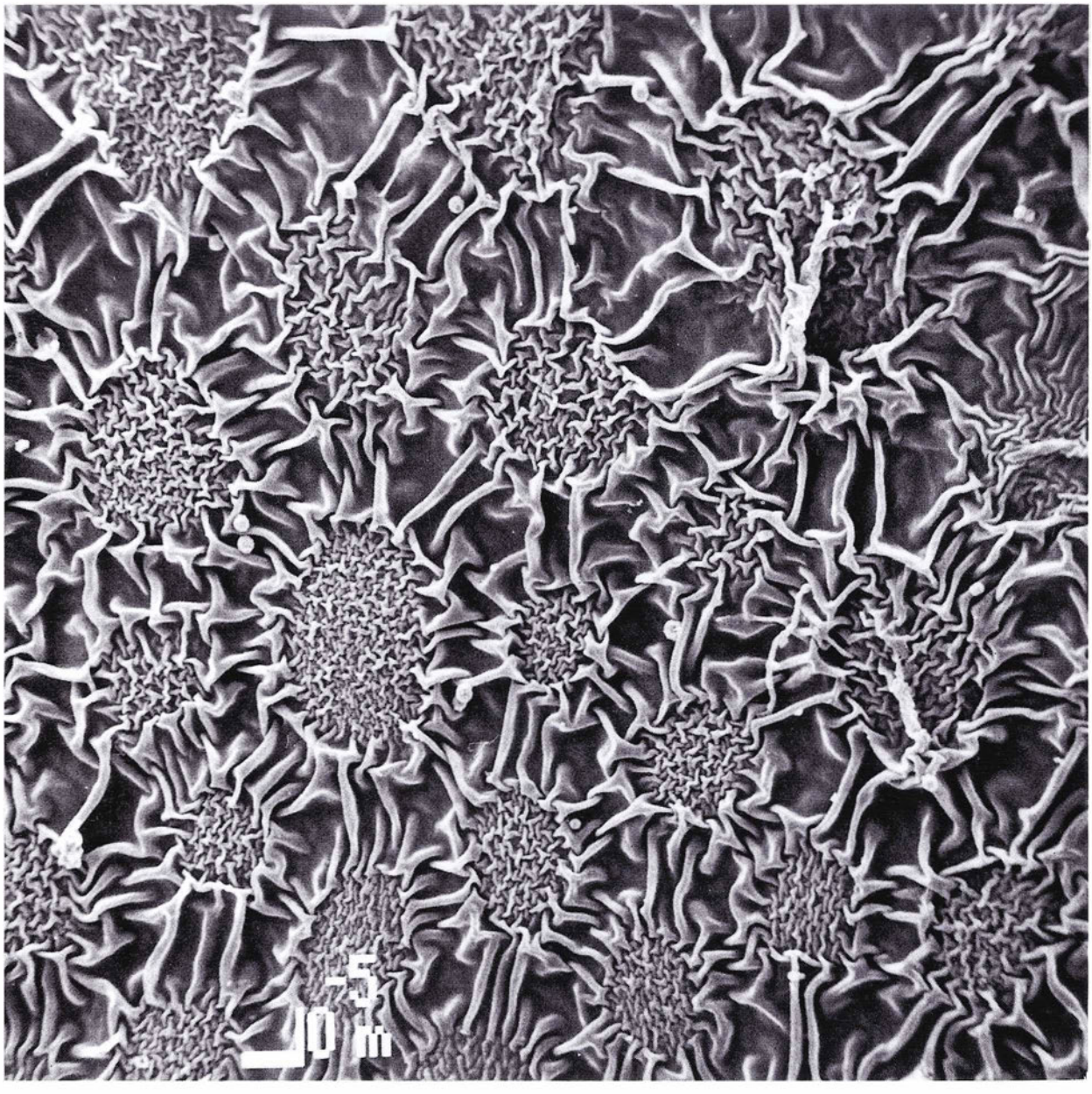
Photograph 2. Scanning electron micrographs of spines of *Matucana paucicostata* (*M. senilis* KK 754). 1. One year old seedling; 30×. 2. Id., in detail; 245×. 3. Mature plant; 10×. 4. Id., in detail; 515×.



Photograph 3. Stamen of *Matucana aurantiaca* (SEM); 160×.



Photograph 4. Pollen grains of *Matucana aurantiaca* (SEM); 2800×.



Photograph 5. Detail of the lateral seed surface of *Matucana tuberculata* (*M. mamillaris* KK 1638) to show the folding pattern of the cuticle.

hairy and naked flower tubes can be found in populations of *M. aurantiaca*, for example. Such receptacle hairs are present in predominantly the northern species (species that belong to the aurantiaca and paucicostata groups, see Chapters 10 and 11 respectively).

The corolla of the flower is bent sideways which enables a pollinating humming bird to stick its bill in the floral tube while hovering. Most perianth segments are curved backwards; a few of the inner ones above the stamens and the stigma, on the other hand, are not. They protect the stamens like a roof in order to keep the pollen dry. Only the stigma is mostly protruding from this protective device.

The stamens (Photograph 3) are devided into two categories depending upon the insertion of the filaments. The primary stamens are inserted in a ring just above the bottom of the tube. The filaments of these stamens usually form a dense bunch around the style and just reach the edge of the floral tube so they can only be observed when looking into the flower. The secondary stamens are inserted at the wall of the floral tube from just above the primary stamens up to the edge of the tube. In most cases there are only a few stamens inserted in the lower part of the tube (sometimes even on the diaphragm) but many are present at the edge to form a ring of stamens which protrude from the throat. The filaments inserted at the wall of the floral tube are variable in length, some of them failing to reach the throat, others reaching far beyond it. The filaments at the edge of the tube are of roughly the same length. The anthers may be yellowish, brownish or purplish, the stigma is mostly olive. The number of stigma lobes varies but in most cases there are six.

The pollen (Photograph 4) is globular in shape and usually contains three parallel grooves (tricolpate). The surface is finely papillate. The pollen may be yellowish or violet, depending upon the species. The pink-flowering species always have violet pollen. Most red-flowering species have yellow pollen, but occasionally it may be violet.

The inside base of the floral tube is the most interesting part of the flower. At the bottom of the tube are nectar glands which are visible as yellowish elongated thickenings on the inside wall. This section of the floral tube is called the nectar chamber. The length of the nectar chamber may vary depending upon the species. *M. haynei* and *M. aurantiaca*, for example, have a rather short nectar chamber (1 mm long); the longest nectar chamber (10 mm long) has been encountered in *M. comacephala* and *M. paucicostata*. Just above the nectar glands there is an outgrowth of the inner tube wall that bears the primary filaments. This outgrowth is called a diaphragm and encloses the nectar chamber almost entirely. Moreover, the bases of the primary filaments are fused resulting in a sort of collar around the style. The degree of fusion of these filaments varies from a few millimeters (like in *M. haynei*) to approximately 2 cm (in *M. krahnii*). The latter situation produces a 2 cm long filament tube around the style.

2.2.2 *Deviating floral features*

Many *Matucana* species produce flowers as outlined above. There are, however, some species with flowers that differ from the basic pattern in structural aspects.

Non-structural differences also exist of course, such as flower colour (yellow in *M. weberbaueri*, orange in *M. oreodoxa*, pink in *M. comacephala* and *M. myriacantha*, even almost white in *M. huagalensis*) and in flower dimensions (short flowers in *M. aureiflora* and forms of *M. haynei* known as *M. breviflora*).

Flower shape

M. aureiflora and possibly *M. oreodoxa* have apparently adapted to another pollination agent. Instead of the typical red bird flowers *M. aureiflora* has yellow, funnelform, radially symmetrical bee flowers, which make this plant look like a Lobivia rather than a Matucana (Plate 6). The long, slender, orange flower of *M. oreodoxa* (Plate 7) is also completely symmetrical and is reminiscent of a Rebutia flower, except that it flowers from the crown rather than from the base of the body.

Several forms of *M. aurantiaca* have actinomorphic flowers: the flower is straight and all petals are spread radially; in *M. comacephala* the flowers are most clearly zygomorphic (Plate 8).

Diaphragm

Only two *Matucana* species, *M. madisoniorum* and *M. oreodoxa*, produce flowers without a diaphragm to protect the nectaries. Also the bunch of primary stamens has been completely lost. The nectar is therefore freely accessible to any animal, whether pollinator or opportunist.

A different situation occurs in *M. comacephala*, where the diaphragm is rudimentary, leaving the nectar chamber open for the greater part. Here the primary filaments take over the protective function of the diaphragm by covering the nectaries.

2.3 FRUIT

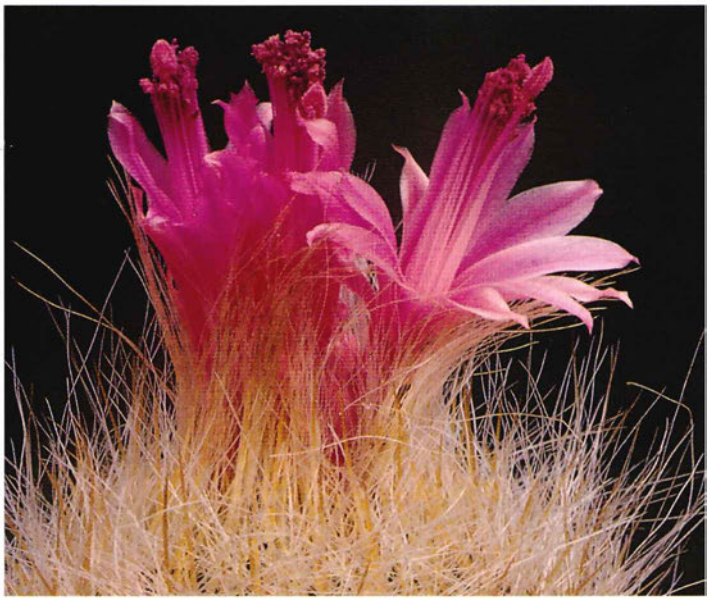
The features of the *Matucana* fruit are significantly responsible for justifying *Matucana* as a separate genus. Both the morphology as well as the mode of dehiscense are reliably typical for the genus.

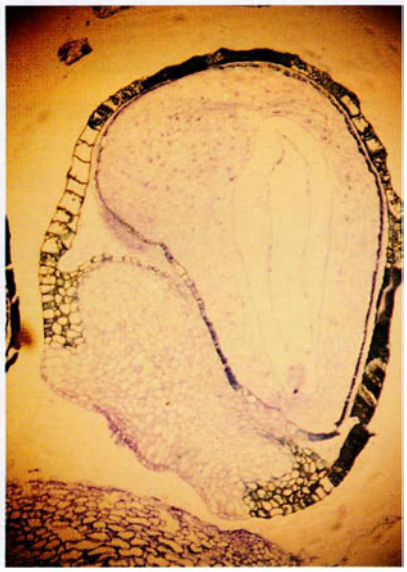
The ripe fruit of all *Matucana* species is dry, hollow, more or less globular in shape, weakly ribbed and provided with some triangular scales (Plate 9). It does not loose its floral remnants. The fruit wall is still firm and somewhat fleshy. The colour is mostly brownish-green (olive, sepia), sometimes with traces of red or

Plates 1-6

1. *Matucana haynei*, the type species of *Matucana*.
2. *M. comacephala* (*M. lutea* KK 1299), a densely spinated species.
3. *M. madisoniorum*, an almost spineless species.
4. *M. polzii*, a strongly offsetting species.
5. The typical *Matucana* flower. Vertical section of a flower of *M. haynei* (*M. blancii*) showing internal morphology.
6. A group of *M. aureiflora* showing the untypical *Matucana* flower. Note the variability in spination.

1	2
3	4
5	6





purple. Later, when the fruit wall has desiccated, the colour turns to brown. Each fruit contains at least three parietal placentae to which the funicles are attached.

The number of seeds per fruit varies greatly. Normally 50-100 seeds are encountered inside a Matucana fruit. Often a fruit contains 120 or more seeds, but also as few as 30 seeds may be counted.

Most characteristic for *Matucana* is the splitting of the ripe fruit by three vertical slits. When mature the inner cell layers of the fruit wall shrink more than the outer fruit wall layers. Because of this pressure the fruit wall cracks along three preformed vertical zones. The edges of the fruit sections become curved inwardly soon after dehiscense, in order to enlarge the slits. Only the basal part of the fruit splits this way; the upper half or 1/3 of the fruit does not dehisce. Now the seeds can easily drop out, or may be washed away by rain, or may be removed by ants.

After the fruit has matured it remains attached to the plant for a few weeks. Then the fruit wall desiccates entirely and turns brown. The fruit remnants may now be detached from the plant by wind, rain or passing animals. So eventually the few seeds that may still be inside the fruit have the opportunity to be dispersed as well.

Although the pattern of fruit rupture is considered to be very characteristic for the genus *Matucana*, it sometimes happens that ripe fruits do not open by three slits but by one or more irregular cracks. It has also been observed that fruits do not dehisce at all, e.g. in *M. intertexta*. Such exceptional occasions will always take place now and then.

2.4 SEED

In addition to the fruit, a number of seed features are also very typical for the genus *Matucana*. Some of these can be recognized by the naked eye, others can only be seen under a microscope or with a magnifying glass. Those micro-features are of course of less importance for the identification of plants. On the other hand, they are very usefull for phylogenetic and ecological studies. Therefore they will be briefly discussed here. In the descriptions of the species as well as in the identification keys only the macro-features of the seeds will be given.

Figure 1 schematically shows a *M. paucicostata* seed grain in lateral view to explain the different components with their terminology. *Matucana* seeds are

7	10
8	11
9	12

Plates 7-12

7. *Matucana oreodoxa*, another species with an untypical *Matucana* flower.
8. Variability in zygomorphy in *Matucana*: the zygomorphic flower of *M. comacephala* (*M. lutea* KK 1299, left) and the almost actinomorphic flower of *M. aurantiaca* (*M. grandiflora* var. *albispina* KK 576, right).
9. *M. pujupatii* showing typical splitting of the ripe fruit.
10. *M. aurantiaca* in habitat on a rocky hill top near Cajamarca.
11. *M. paucicostata*, just fertilized ovule in vertical section, 15 μ thick. Stained with Schiff's reagent and toluidin blue.
12. *M. paucicostata*, vertical section of unripe seed 2 weeks after fertilization. Details as in Plate 11.

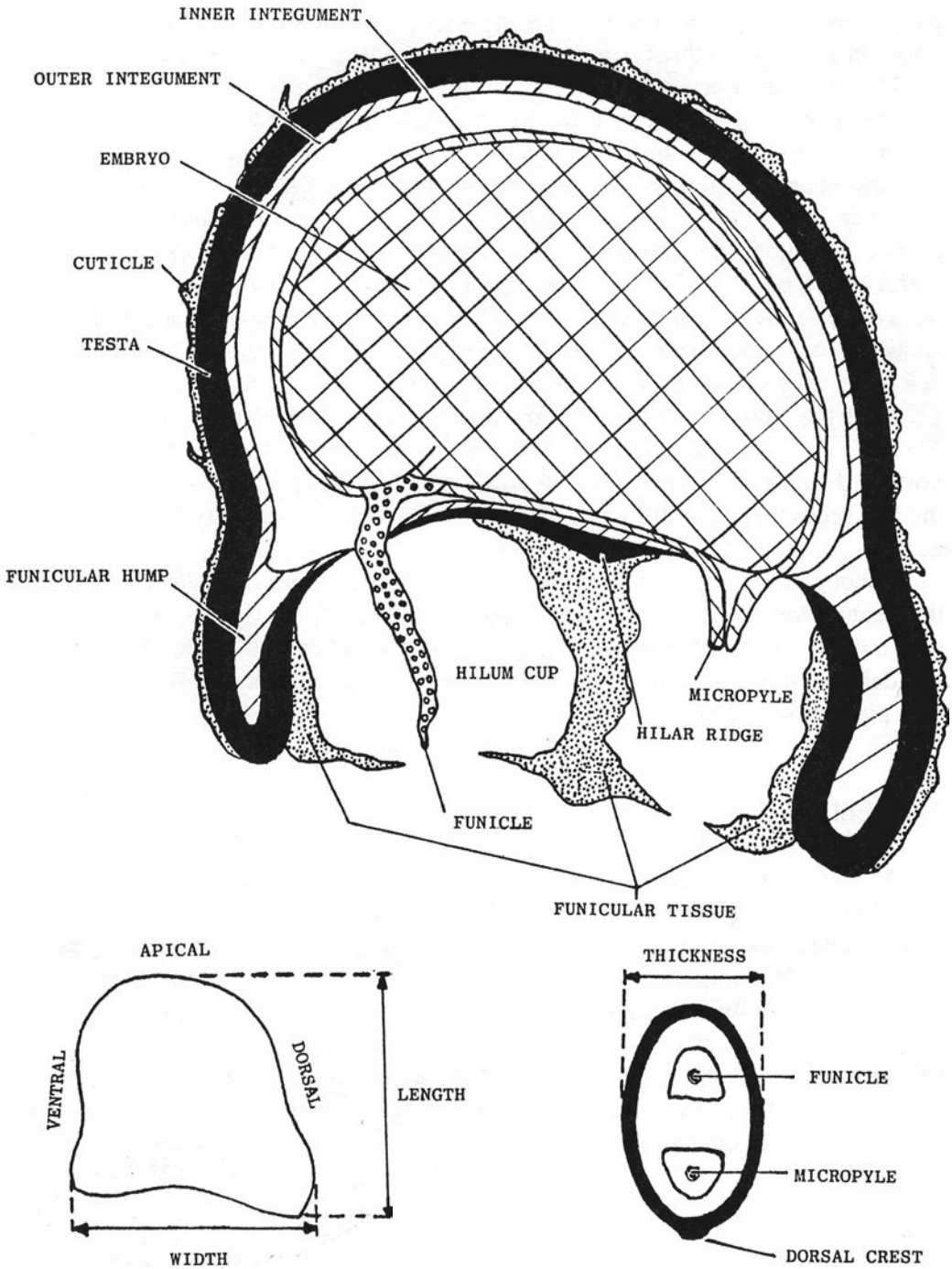


Figure 1. Schematical drawings of seed of *Matucana paucicostata* to indicate terminology.

usually 1 mm long and wide and somewhat less thick. The room occupied by the embryo is separated from the hilar (basal) region by a weak indentation all around the seed.

The seed coat (testa) is formed by one (the outer) epidermal cell layer, of which the outer wall has considerably thickened, sclerified and pigmentated.

These cells are irregularly arranged; only the cells of the dorsal rim are clearly arranged in longitudinal rows. Their surface is weakly convex. On top of the testa is a fatty substance, the cuticle, which is a device to prevent water loss from the seed's interior. In order to enhance this effect, the cuticle is folded in such a way that the folds over the cell walls are parallel but irregular elsewhere (Photograph 5). This folding pattern is not restricted to *Matucana*, occurring in many other South American genera as well. Very frequently the outer layer of the cuticle becomes detached during seed development. In the ripe seed it looks paper-like and gives the seed a yellowish-brown appearance. This remarkable phenomenon is particularly well developed in the species from the Rio Maranon except *M. madisoniorum*. Exceptionally, in *M. haynei*, *M. intertexta* var. *celendinensis* and *M. aurantiaca* it has been observed that the cuticle does not detach at all, so that the seed is dull black all over.

Another important feature of seeds is the structure of the hilum. Actually the hilum is a scar indicating where the seed had been attached to the funiculus. In cacti the entire basal section of the seed is named 'hilum' and includes the micropyle. In *Matucana* it is very large, being as wide as the entire basal seed width. Its shape is broadly elliptical. The hilum of a Matucana seed is depressed. This depression is called the 'hilum cup'; the depth of it is dependant upon the species: this varies from moderate in *M. haynei* to very deep in *M. madisoniorum*. In the dorsal section of the hilum a brownish stump can be found, which is the micropyle. It varies in length; in a group of species it is so long that it protrudes from the basal seed margin. The hilum cup is covered by whitish funicular tissue, which is attached to the hilar margin. The amount of this tissue also varies: in *M. haynei* and *M. aurantiaca* it totally covers the hilum cup, whereas in *M. myriacantha* and *M. paucicostata* one or two holes are present in the hilum. In only one species (*M. madisoniorum*) is the hilum cup completely uncovered.

The embryo is oval in shape. The hypocotyl (stem of the embryo) is the largest portion of it. The cotyledons are short but clearly visible under a magnifying glass; in most species they are weakly bent with respect to the axis of the hypocotyl. Any storage tissue outside the embryo (endosperm or perisperm) is absent.

CHAPTER 3

Geography and ecology

3.1 DISTRIBUTION

The present day distribution of the genus *Matucana* is shown in Figure 2. It covers a long but rather narrow zone in the western Peruvian Andes. The length of the distribution area is about 1000 km, the width varies from about 50 to 150 km.

Matucana occurs on both sides of the western Andean mountain chain (Cordillera occidental), extending from approximately 4°S to 16°S in latitude. The vertical distribution is predominantly between 2000 and 4000 m above sea level with the exception of a group of species growing in the northernmost portion of the distribution area. This group of species, here recognized as the paucicostata group, occurs in the valley of the Rio Maranon and descends even to 400 m altitude (*M. madisoniorum*).

The area of the Cerro de Pasco, situated in the central Peruvian Andes at about 10.5°S, seems to have played a significant role in the distribution pattern of *Matucana*. The Cerro de Pasco is a high plateau where the three major Andean mountain chains (the western, central and eastern Cordilleras) come together. North and south of this place the three Cordilleras run more or less parallel in a SE-NW direction, separated by deeply eroded valleys where rivers use to flow. Because of its altitude of over 4000 m, the Cerro de Pasco plateau has apparently served as a barrier; on both sides of it we find remarkable discontinuity in the distribution of *Matucana*.

South of the Cerro de Pasco almost all *Matucana* localities are restricted to the west-facing slopes of the western Cordillera; in the valleys of the rivers draining to the Pacific to be more exact. In these habitats Matucanas show a striking degree of resemblance. The plants are mostly densely spinated and become elongated in later life. The flowers are always scarlet to purple without hairs in the axils of the receptacle scales.

North of the Cerro de Pasco plateau Matucanas have occupied habitats not only on both sides of the western Cordillera, but on both sides of the central Cordillera as well. Presumably as a result of the greater diversity of habitats, the Matucanas north of the Cerro de Pasco are far more diverse with respect to several characteristics than the relatively uniform species from the south. This northern group of species share a number of characteristics different from the southern

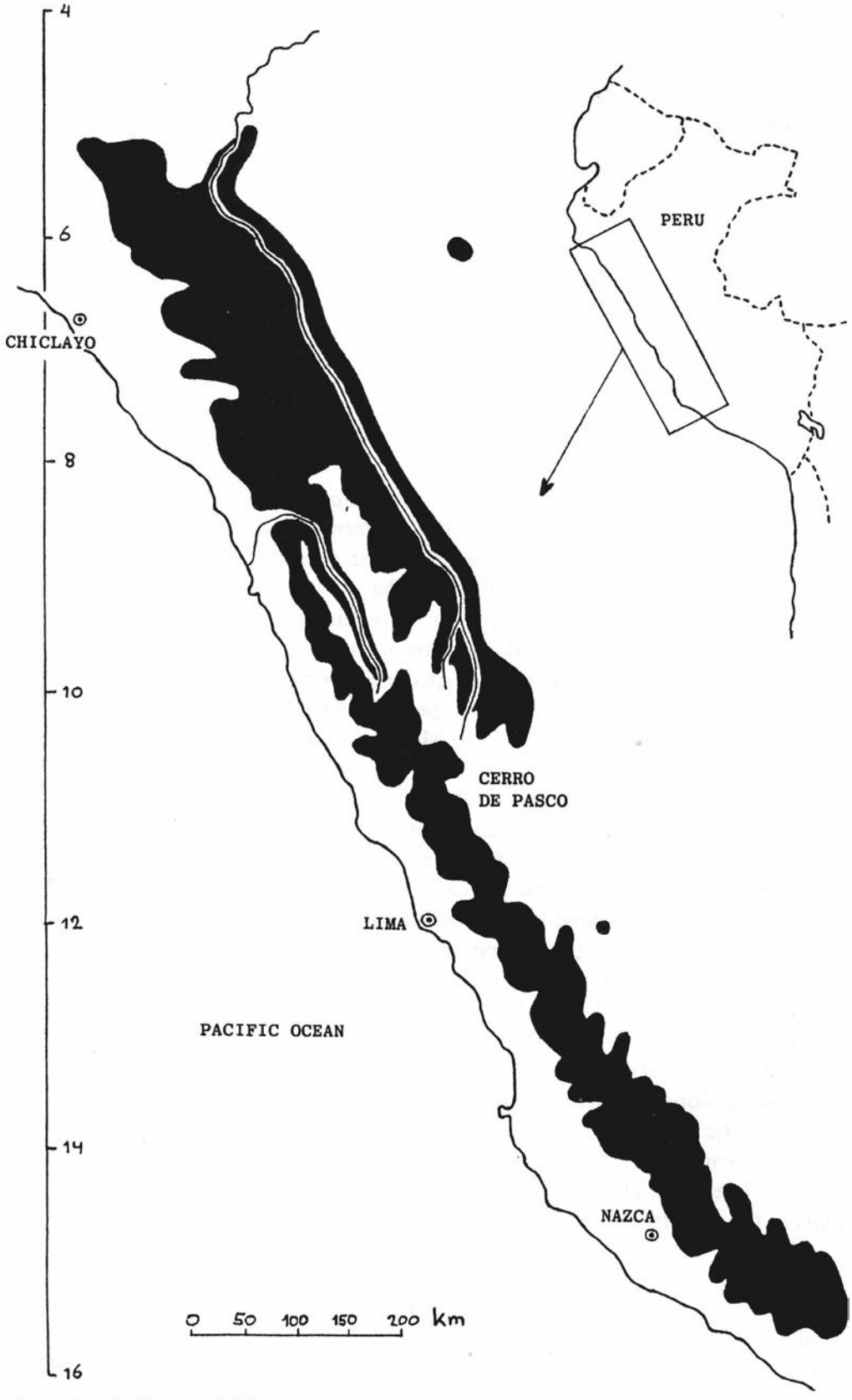


Figure 2. Distribution of *Matucana*.

group, such as the globular habit and the mostly hairy floral tube. Great diversity between northern and southern Matucanas is observed in spination and seed morphology. In terms of the old-fashioned taxonomy according to Backeberg the southern group represents the genus *Matucana* sensu stricto and the northern group the former genus *Submatucana*.

3.2 CLIMATE

As with most plants, the distribution of *Matucana* is (and has been) very much influenced by climatic factors. All habitats are characterized by a rainy season and a dry period which can last several months. The rainy period is usually from November to April. In Figure 3 the Walter climatic diagram of Cajamarca in N. Peru is depicted as an example of a climate suitable for Matucanas. Near Cajamarca are habitats of *M. aurantiaca* and *M. aureiflora*.

The aridity from May to October is caused by two major factors. Firstly the whole of the Andes range provides a rain shadow effect in the inter-Andean valleys and on the western slopes. Rain clouds driven by trade winds from the Amazon rain forest are unable to cross the Andes. The warm and moist air is pressed against the eastern Andean slopes and lifted up. As a result this air is cooled down which causes condensation and precipitation. Thus, the easternmost Andean slopes of Peru receive most of the rain.

The second factor responsible for the periodic lack of precipitation in the *Matucana* habitats is the presence of a cold Antarctic sea current that runs along the coast of Chile and Peru. This current is called the Humboldt current after the German explorer Alexander von Humboldt. Coming from the south it follows the South American coast and deflects to the west at approximately 5°S; at this latitude to be replaced by a warm tropical current coming from the north.

Due to the relatively cold surface water along the Peruvian coast there is no

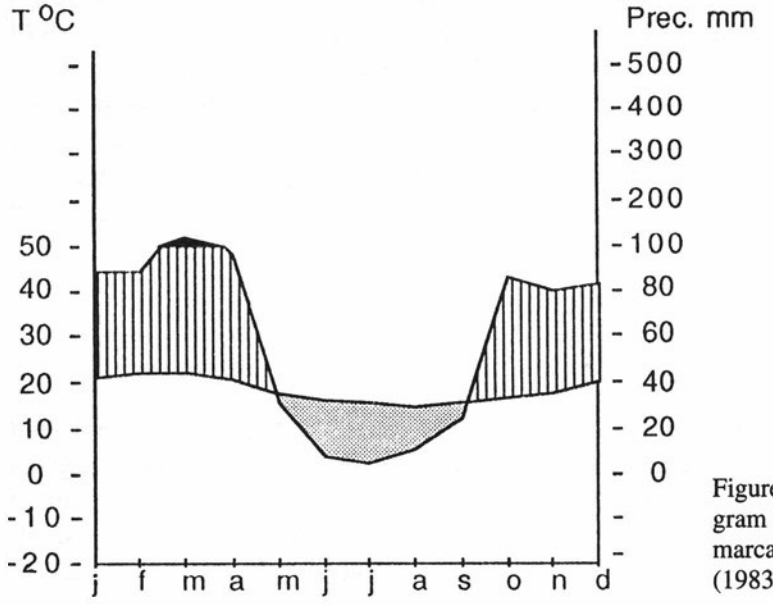


Figure 3. Walter climatic diagram of the town of Cajamarca. Data from Müller (1983).

uplift of humid air and therefore no rapid condensation can take place. Instead, the cold Humboldt current causes humid southwest sea winds to cool down slowly, so that fog is formed. This fog is called 'garua' and occurs in the coastal region of northern Chile and Peru south of 8°S. Vertically the area affected by this fog reaches from almost sea level up to 500 m altitude at 12°S latitude and up to 1000 m at 16°S. So above these upper limits the air is dry and precipitation is almost absent.

There is only sea fog in winter (May to November). In summer (December to April) the cooling effect of the Humboldt current is compensated by the warmer coastal land and no fog occurs. Humid air masses get the chance to be lifted by the warming of the land and therefore rain may occur above 2000-3000 m altitude. In this part of the Andes the precipitation increases with altitude.

The *Matucana* habitats situated on the west side of the western Cordillera are contained within the summer rain zone, which is above the region directly influenced by the 'garua'. This explains why the Matucanas have been unable to occupy west-slope habitats below 2000 m, like they manage in the inter-Andean valleys: since the climatic conditions are entirely different (winter fog and summer aridity).

Because of the events just described, the west-slope *Matucana* habitats are colder than would be expected at these tropical latitudes. Night temperatures may drop well to the freezing point or sometimes below zero, whereas warm tropical conditions are absent and temperatures seldom exceed 30°C. It is also remarkable to note that these relatively cool temperatures are more or less the same all along the coastal area of Peru and N. Chile where the garuas occur. There is only a small difference (of 0.5°C) in average year temperature between 12 and 17°S, which represents a distance of 550 km! (Rauh 1985). Without doubt this is one of the main reasons why the Matucanas from this area are much more similar than the species from the inter-Andean valleys.

In the inter-Andean valleys, where many *Matucana* species have their habitats, the situation is different. Here the Matucanas do not face any abrupt climatic barrier to prevent them from spreading to habitats at lower altitudes. As a result, Matucanas have descended several inter-Andean valleys without problem until the valley floor is reached. Of course, at these lower altitudes temperatures are higher. At the bottom of deeply eroded valleys in particular, such as those of the Rio Maranon and its confluent the Rio Crisnejas, as well as the lower course of the Rio Santa, it may be extremely hot in summer (December to April). Rainfall also occurs in summer; the valleys in the north generally receiving more rain than those in the south.

3.3 VEGETATION AND SOIL

Matucana species occur in various types of vegetation. Most species can be found among open xerophytic vegetation usually on rocky slopes. Here the plants grow frequently in rock crevices with hardly any other vegetation. Quite a number of species occur on grassy hills and take advantage of the periodic absence of shading grasses during the dry period. Inventories of accompanying species are rarely

available, but in any case few other plant species grow together with Matucanas.

Some *Matucana* species seem to have the ability to adapt to habitats influenced by humans such as grazed slopes or terrace walls. A major problem for Matucanas is to compete successfully with grasses. Near the town of Huamachuco in the department of Cajamarca in northern Peru a population of *Matucana calvescens* (= *M. aurantiaca*) was found on a grassy hill slope. The Matucanas flourished, probably because this hill was grazed by cattle, which benefitted the Matucanas since the grass remained short, and also because cattle (but not goats!) usually avoid this kind of cacti. At the base of the slope was a small river with a plantation of *Eucalyptus* trees on the other side. Even by the river side and in the shade of the *Eucalyptus* trees the Matucanas were present (though not very abundant), almost rooting in the river water. The highest density of plants was, as might be expected, on the upper (driest) part of the hill, even though there was evidence that many specimens had been destroyed by farmers. This is often done to encourage grass to grow for cattle grazing in the places previously occupied by cacti. Another threat is the burning of hill slopes and other places where cattle graze as a way to fertilize the soil. This burst of available nutrients is meant to stimulate growth of grass and other herbs in order to serve as cattle food. Several *Matucana* populations were observed to bear traces of burning but the population as a whole did not seem to have suffered very much, neither did the large rozettes of the Bromelias (genus *Dyckia*). Apparently the influx of nutrients by burning also stimulates the development of Matucanas; many young plants and seedlings could be counted.

The above indicates that some *Matucana* species seem to have adapted to habitats influenced by man. In addition they do not seem to be very demanding, bearing in mind the diversity of vegetation within which Matucanas occur. This might be an explanation for the relatively easy cultivation of these plants.

Soil data on *Matucana* habitats is very scarce. One of the few soil analyses was conducted on samples collected at a habitat of *Matucana haynei* beside the Lima-La Oroya road (Table 5). The analytical results indicate that the chemical composition is quite normal for habitats of terrestrial cacti in general. The soil is slighty acidic, contains little nitrogen and calcium but more potassium and phosphorus. The contents of magnesium, iron and manganese are remarkably high. All these data refer to soluble levels of chemical components, for which it is assumed that these nutrients are available to plants. No information is provided about the total amounts of chemicals in the soil, which may be substantially higher, espe-

Table 5. Chemical and physical data of soil, sampled at a habitat of *M. haynei* along the Lima-La Oroya road near Matucana. Values (except those for $CaCO_3$ and humus) expressed in mg soluble components per 100 g of soil (modified after Zecher 1971).

pH (KCl)	6.5	Magnesium	41
$CaCO_3$ (weight %)	< 1	Iron	52
Humus (weight %)	9.4	Manganese	27
Nitrogen (total)	5.7	Zinc	3.2
Phosphorus (as phosphate)	20	Copper	0.6
Potassium	21		

cially for elements that form poorly soluble salts, like calcium.

Generally, the percentage of organic material (humus) in the soil where Matucanas grow may vary; some species grow in almost pure humus, others prefer a more mineral substrate such as clay. In cultivation every species of *Matucana* can be kept successfully in both an organic or mineral substrate, but in nature most plant species have their own preference of substrate. An example of this was observed near Cajamarca city where *M. aurantiaca* and *M. aureiflora* grow almost together, only separated by one hill top. On investigation it turned out that *M. aurantiaca* was growing on a pure organic substrate in cracks and holes between rocks where humus could accumulate (Plate 10), whereas *M. aureiflora* was found on a substrate with a high clay percentage on far more gradual hill slopes.

CHAPTER 4

Reproduction

One of the most fascinating aspects of cultivating plants is to monitor the process of regeneration. Everyone who has himself ever created a second generation of plant individuals subsequently by pollinating a flower, harvesting the seeds, sowing the seeds and bringing the seedlings to mature and flowering specimens, must have experienced that this provides far more satisfaction than just simply buying plants to look at. At the same time it becomes clear that the process of reproduction is very complicated; every step in the course of one generation to the next one presenting its own risks. When we try to germinate seeds, for example, we have to take certain precautions, otherwise there will be no next generation. In nature even more hazards, such as infection by pathogens, predation by animals, habitat destruction by man, drought, volcanic eruptions or landslides and many more, are there to jeopardize regeneration. By the natural selection of those individuals which achieve the best reproductive results, every step in the development of a second generation undergoes the highest possible degree of perfection.

Reproduction may occur either vegetatively or generatively. Matucanas, and most cacti, reproduce mostly generatively (by seed) but sometimes vegetatively by offsets which may become detached from the parent plant to develop into mature plants elsewhere. An extreme example of offsetting is found in *Matucana polzii* (Plate 4). In many other *Matucana* species, both vegetative and generative reproduction occur to minimize risks. If, for example, the main stem of a multi-headed plant is destroyed through the grazing of herbivores, the plant can survive by virtue of its remaining stems. In addition, existing offsets may become detached by the activities of the grazing animal and be transported on the animal's coat, later to become detached, giving the plant species the opportunity to colonize new habitats thus giving rise to a new population. Should, for some reason, seed production fail, then the plant can devote all its energy to the growth of offsets. On the other hand, in years of abundant blooming which gives high seed production, the available energy is put into seed development. Through having the opportunity to utilize generative and vegetative reproduction, put simply in racing terms, the plant has the advantage of being able to bet on two horses.

4.1 POLLINATION

Probably all *Matucana* species but one are pollinated by hummingbirds. The exception is *Matucana aureiflora* which is reported to be pollinated by bees. Largely because of this phenomenon it is the only *Matucana* species with yellow radially symmetric flowers with a short receptacle. Unfortunately it is not known what particular bee species is (or are) involved. The same lack of knowledge applies to the bird pollinated Matucanas; species names of pollinators have so far never been published although published information exists of species of hummingbirds that occur in Peru together with the ranges of altitude in which they operate.

The usually red, purple or pink and slightly zygomorphic tubular flowers of most *Matucana* species indicate a bird pollinating syndrome. Birds are not attributed with a good sense of smell; instead they rely on their superb visual capabilities and red is a colour that they can see very well. The bird pollinators of *Matucana* flowers are attracted by the red colour because for them it has come to represent something that is of benefit to them, namely food in the form of nectar. This substance is nothing more than a solution of mainly sugar which is produced by the nectar glands in the nectar chamber. In most species of *Matucana* the nectar chamber is closed by a protectionary device, the diaphragm. This protects the nectar glands in order to prevent the nectar from being stolen by animals that are not pollinators. A second function of the diaphragm may well be to prevent rain water from entering the nectar chamber, as rain may otherwise cause dilution of the nectar or induce rotting.

In two *Matucana* species only, viz. *M. madisoniorum* and *M. oreodoxa*, the diaphragm is absent so that the nectar chamber is freely accessible. The biological significance of this is not clear but it surely has something to do with pollination.

The hummingbird reaches the nectar chamber by penetrating the diaphragm with its sharply-pointed beak. During the extracting of the nectar, the hummingbird hovers to keep its position by beating its wings up and down at a very high frequency. The high energy content of sugar in chemical terms, more than compensates for the substantial amount of energy that is consumed in carrying out this operation. When sipping the nectar the hummingbird's head and the base of the beak touch the anthers, so that pollen becomes attached to the bird. On the next visit to a *Matucana* flower (preferably to another plant of the same species) the pollen grains are deposited on the stigma, which usually projects beyond the bunch of stamens in order to prevent self-pollination. The outcome of it all is that the bird has performed the task of pollen dispersal for the plant species and has benefitted by receiving high energy food as a reward. If the transferred pollen grains are able to germinate on the stigma surface, they penetrate the style and eventually reach the ovary where fertilization of the ovules can take place. The development of fertilized ovules is outlined below.

4.2 SEED DEVELOPMENT

In *Matucana* the process of development from a fertilized ovule to a ripe seed

grain takes one to two months. Very little is known about the study of the embryos of Matucanas; recently seed development was monitored in *Matucana paucicostata* (Bregman, unpubl.), which is the only *Matucana* species studied in this respect so far. It may be assumed that seed development in other *Matucana* species is to a great extent similar.

Plate 11 shows an ovule of *M. paucicostata* just after fertilization. The ovule consists of the fertilized egg cell embedded in the embryo sack, which is surrounded by nutritious tissue (nucellus) and two protective coverings (inner and outer integuments). (Note that the ovule already has the shape of the ripe seed.) The ovule is attached to the inner fruit wall by a stalk (funicle or funiculus) which contains vascular tissue in order to supply nutrients to the growing embryo.

At about 2 weeks of development (Plate 12) the ovule has almost reached its final dimensions. The outer layer of the outer integument has begun to differentiate into a seed coat; these cells have enlarged, the outer cell wall has become sclerified, thickened and pigmentated. The remaining integumental layers disintegrate. The fertilized egg cell has become an embryo and 'consumes' the surrounding tissue (nucellus).

In the ripe seed the seed coat has turned to black, the embryo occupies almost the entire room inside the seed grain. The funiculus breaks off just below the point of attachment to the seed, leaving some funicular parenchyma to the margin of the hilum. After the fruit has opened, the seed is now ready to be dispersed.

4.3 SEED DISPERSAL

After the ripening of the seed the *Matucana* fruit dehisces to release the seeds. Various causes contribute to how the seeds get out of the fruit. The seeds may be blown out by wind, they may be carried away by ants, or flushed out by rain water, or they may be scattered by the action of birds pecking at the fruit. Seemingly the seeds of most *Matucana* species exhibit no special adaptation to a particular method of seed dispersal but later in this paragraph it will be explained that dispersal by ants and by water are probably involved.

After the seeds have been released, a very risky stage in the reproduction cycle commences. Many causes threaten either to kill a seed or prevent the seed from reaching a suitable place for germination to occur.

The first threat is predation of the seed by all kinds of granivores (birds, rodents like mice, lizards). Often a large portion of the total seed production is destroyed in this way before seed dispersal has even begun. This danger threatens all seed plants but cacti and other plants from seasonally dry habitats are especially vulnerable in this respect because the availability of other edible fruits and seeds is usually not very high. Many *Matucana* specimens already have ripe seed in the beginning of the wet season when most other plants at the same habitat are still at rest. A population of *Matucana intertexta*, for example, was observed to bear ripe seed in the beginning of December when the surrounding grasses had not yet started to produce young shoots. In the same period a population of *Matucana aurantiaca* was visited, growing on a rocky hill top near the town of Cajamarca. There this species dominated the habitat to a large extent; one of the few plants

growing alongside were large bromelias, but these were without fruits or seeds at the time. So in such places *Matucana* seed is a major food source for different kinds of animals.

A second serious threat is the danger that the seed does not reach places suitable for germination. It may be flushed into rivers, deposited in places that are too dark, such as deep rock cracks, or under trees, or places that are too wet, or where competition from other plants is too strong, and so on.

To minimize the risk that seed is not given the opportunity to develop into mature plants, seed dispersal syndromes have evolved. As most cacti, including *Matucana*, show a fragmentary distribution pattern of scattered small populations, it is important to rely on both short distance and long distance dispersal. The first strategy enables the plant species to expand the existing population at the same habitat, by increasing the number of plants. This strategy is followed by most *Matucana* species. A number of seeds just drop beside the parent plant and stay there until they can germinate. This has the advantage that the habitat is suitable for the *Matucana* species involved, but a major disadvantage already mentioned remains, in that a high percentage is consumed by animals. There is also competition with the parent plant for room, (sun) light and soil nutrients.

The second strategy is for the seed to be dispersed further away or even outside the influence of the existing population i.e. long distance dispersal. In this way new habitats can be colonized to expand the distribution area and to increase the chances of survival in case the habitat of the parent population is destroyed for some reason. Unfortunately very little information concerning seed dispersal in *Matucana* is available, but two ways of dispersal are likely to occur, viz. dispersal by water currents (hydrochory) and dispersal by ants (myrmecochory).

4.3.1 *Seed dispersal by water*

Dispersal by water has the disadvantage that the direction of seed transport is one-way only, viz. downstream. This may lead to a situation where the seed is flushed into large rivers. In such circumstances seed with a propensity to float well is not helped greatly, as there is a high probability that it will be deposited into a very wet environment or may eventually be flushed into the ocean. As far as *Matucana* seeds are concerned, dispersal by water is probably most successful if acted upon by small, low-velocity streams with a fluctuating water level, and by rain-wash.

A big advantage of dispersal by (fresh) water is that during the transport the seed has the opportunity to imbibe water. This may be important particularly for large seeds, which on the ground may have difficulties in taking up enough water because of their small contact area with the soil. They will have no trouble at all in taking up water when floating. The only concern is not to sink. Another advantage is that at the place where water-dispersed seeds are commonly deposited, there will be (at least temporarily) enough water available for further development after germination. A third advantage, possibly the most important one, is that the seeds are dispersed at the right time, which means at the beginning of the rainy season. Moreover, predation by granivores which is the number one danger affecting seed survival, is considered to be minimal since the time interval between seed ripening and subsequent dispersal is normally short.

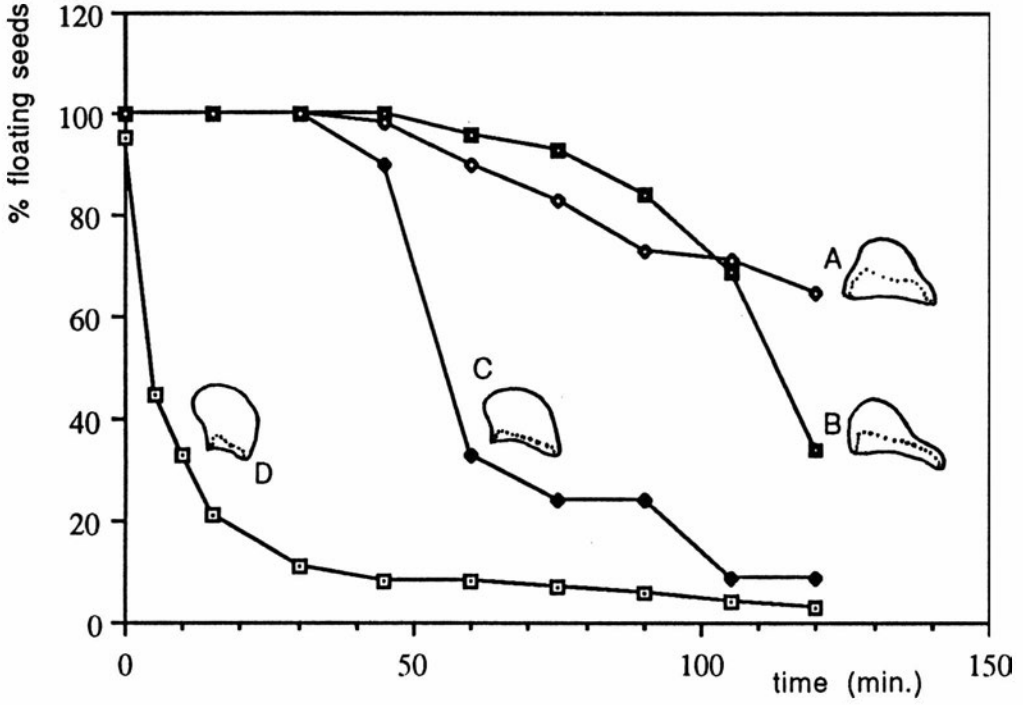


Figure 4. Floating capability of seeds of some *Matucana* species as a function of their hilum structure. Dotted lines in seed drawings indicate hilum cup. A. *M. pujupatii;* B. *M. formosa;* C. *M. aureiflora;* D. *Borzicactus* (*Loxanthocereus*) *sextonianus*, to show the difference with seeds from juicy fruits. In this experiment the water was stirred continuously.

Particularly in deserts or seasonally arid regions the advantages of water dispersal overcome the disadvantages. It is not surprising then that a comparatively large proportion of the seed plant species in deserts are water-dispersed, as was shown for the flora of the Negev desert in Israel (Gutterman 1993).

Seed dispersal by water can be demonstrated by determining the buoyancy of the seeds (Bregman 1988b). This was carried out in the laboratory. Three species of *Matucana* were tested to assess the floating capability of their seeds (Figure 4). The seeds were simply thrown into mechanically agitated water and after a number of time intervals, it was determined how many seeds were still at the surface of the water. Seeds float by utilising the air bubble that is kept in the hilum cup. This is demonstrated by the fact that the seeds turn their hilar side to the surface when thrown into water.

The seeds of a number of *Matucana* species, especially those from the Rio Maranon valley, demonstrate good floating properties. When following this valley from south to north, we see that the hilar region of the seeds of the different *Matucana* species that one comes across becomes broader and broader. In terms of species names the seed of *M. paucicostata*, the southernmost occurring species in this group, possesses the smallest hilum. In *M. krahnii* and *M. formosa*, which grow further north in the valley, the dorsal section of the hilum is expanded and in the northernmost occurring species *M. pujupatii* and *M. madisoniorum* both the dorsal and ventral side of the hilum have enlarged. The wider the hilum becomes for the seed, the more the capacity to float improves: the seeds of *M. paucicostata*

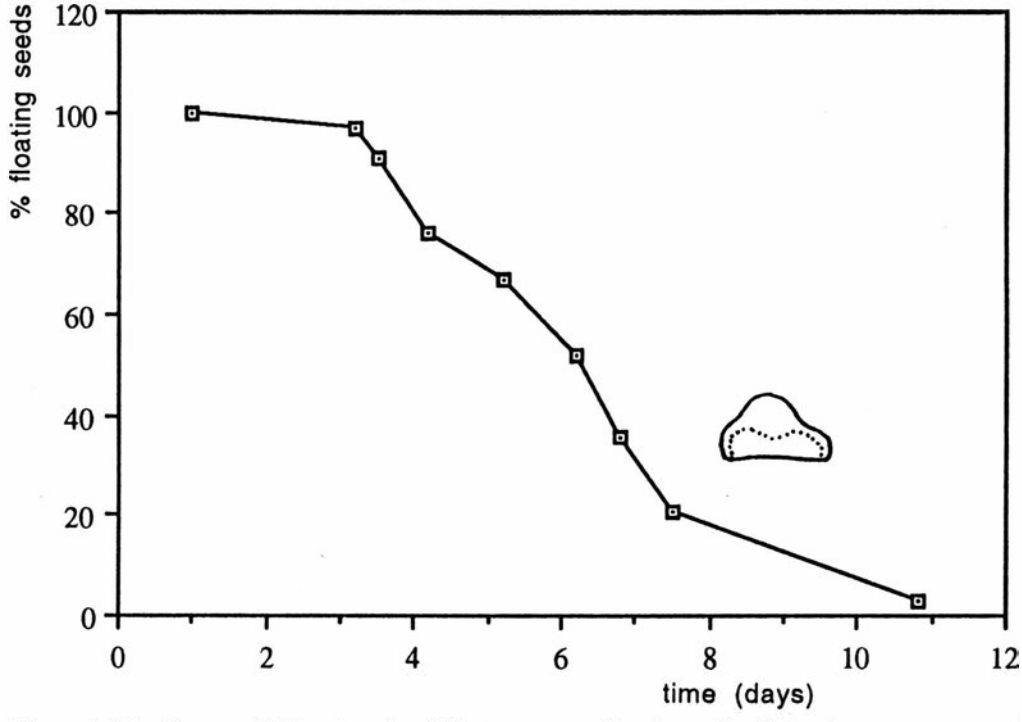


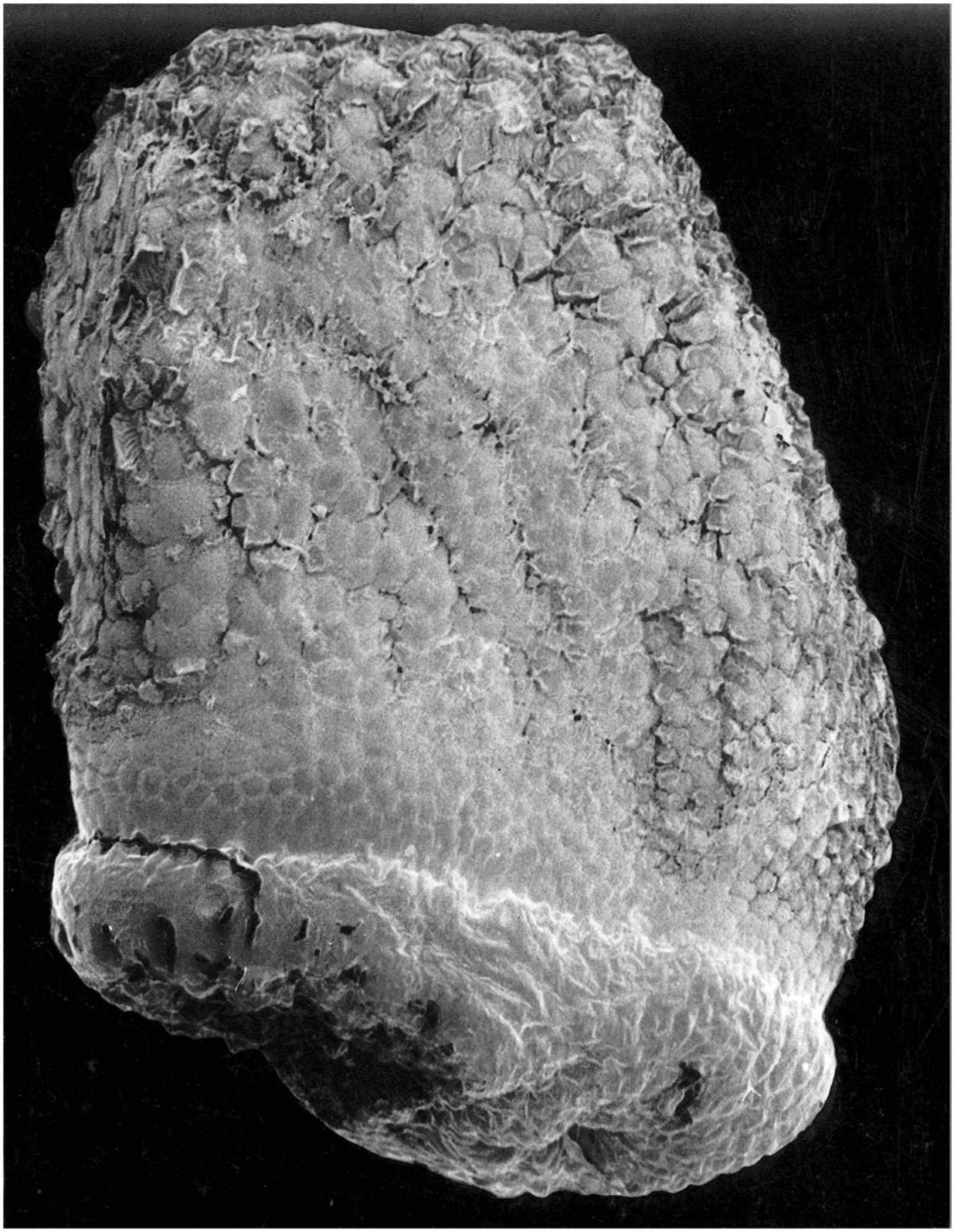
Figure 5. Floating capability of seeds of *Matucana madisoniorum* in still water.

do not float for very long but those of *M. madisoniorum* display excellent buoyancy (Figure 5). The only possible explanation, therefore, is that an increase of the hilum cup has evolved because it improves the buoyancy of the seeds, so that new habitats can be colonized and the advantages of dispersal by water, as discussed above, can be utilised. It is not known whether the Rio Maranon itself is involved as a transporting agent. Maybe this river carries the seeds in times of high water level and deposits the seeds when the water level drops. This might occur, but it does not account for the occurrence of Matucanas at higher levels beyond the influence of the river.

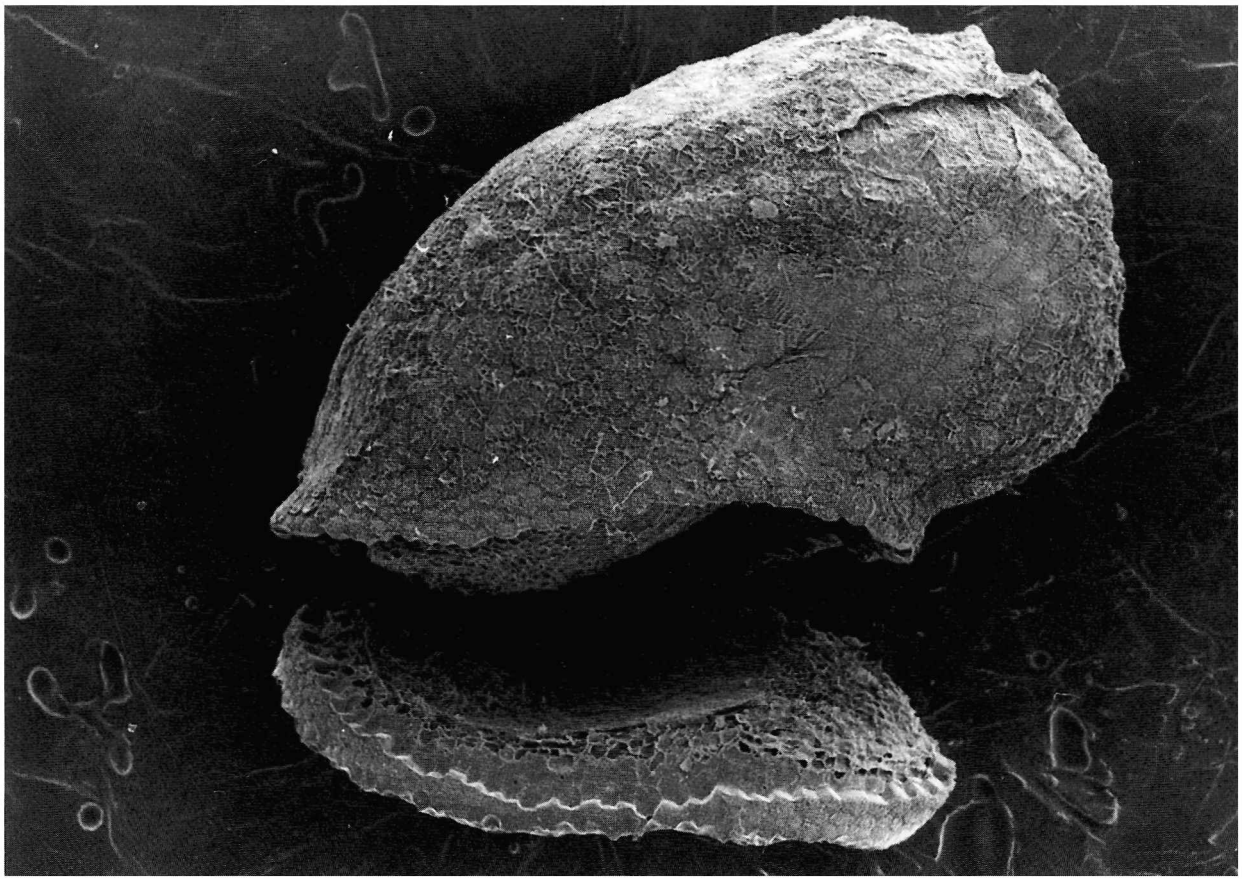
Ritter's (1981) explanation for the broad hilum of *M. madisoniorum* seeds was based upon his assumption that dispersal by the wind might be the basis. This seems unlikely because in the Maranon valley strong winds do not prevail. This is one of the reasons why it is so hot there. Seed of course can be blown away by wind, so wind dispersal cannot be excluded. However, given the adaptation of the seed in combination with the environmental circumstances, then dispersal by water seems to be most probable.

4.3.2 *Seed dispersal by ants*

In a large number of higher plant species ants play a significant role in the dispersal of seed. Almost everyone who cultivates cacti out of doors has found that the seed of many species must be harvested as soon as they are ripe, otherwise they are often carried away by ants. Unfortunately again, very little field data on cactus seed dispersal by ants is on record.



Photograph 6. Seed of *Matucana aurantiaca* with appendage (elaiosome).



Photograph 7. Germinating seed of *Matucana aureiflora* showing operculum.

Seeds are only attractive to ants if they contain nutritious substances such as lipids and sugars. Most ant-dispersed seeds possess appendages containing the ant food. These appendages are called elaiosomes (= oil bodies). Ants usually carry the seeds to their nests where the elaiosome is bitten off to be fed to the larvae. The seed proper with the enclosed embryo remains undamaged. The seeds may be stored anywhere inside the nest, alternatively the ants may remove the seeds from the nest to a 'garbage heap'.

Ant dispersal has a number of advantages for the plant species. If the seeds are burried in the ant nest, the seeds are protected against granivores. Secondly, seeds that germinate in or nearby an ant nest are able to grow faster as a consequence of the higher content of nutrients in the soil. These nutrients result from the decomposition of all kinds of plant and/or animal material which is regularly brought into an ant nest. A third advantage of ant dispersal is that the minor damage to the seed coat caused by the ants, enhances its permeability to water, so that the seed germinates faster.

The seeds of several cacti are provided with appendages which probably serve as elaiosomes (e.g. *Parodia*, *Blossfeldia*, *Aztekium*, some *Mammillaria* species). In other genera the funicles may be swollen (as in *Gymnocalycium* and *Copiapoa,* for instance), or the attractive nutrients may be stored in the funicular tissue inside the hilum cup of the seed.

One of the species of *Matucana* in which a conspicuous elaiosome was observed, is *M. aurantiaca* (Photograph 6). This seed was harvested from a plant raised from seed that was collected near Cajamarca. The elaiosome in this instance is a lateral outgrowth of the funicle at the point of attachment to the seed, and consists of large transparent cells. It is only fresh during a very short time, just after the fruit has split. It soon shrivels when the seed is removed from the fruit. Similar elaiosomes have been observed in *M. intertexta* and *M. paucicostata.*

Most *Matucana* species do not possess distinct elaiosomes. Ant dispersal in *Matucana* has still to be proven and experiments have to be conducted. But there are two arguments which point towards ant dispersal in *Matucana*. The seeds of many species contain a rim of spongy funicular tissue at the edge of the hilum. This tissue is turgorescent when fresh, but it rapidly desiccates. It may regain its turgor when wetted afterwards, though. It is possible that this tissue attracts ants and serves as an elaiosome. It still has to be investigated whether this tissue contains any ant-attracting substances. A second argument for ant dispersal of *Matucana* seeds is the presence of ant nests that were observed on a couple of *Matucana* localities. The finest example of these observations was a habitat of *M. aureiflora* near Cajamarca, where dozens of hill-shaped ant nests could be counted. Several plants were even growing on a nest, in a nest to be more precise, because only the actual heads of the plants were visible; to see the whole plant body it was necessary to remove the surrounding sandy clay particles, from which the nest is formed.

4.4 GERMINATION

Nothing is known about the germination of Matucanas in the wild since this has

never been investigated. From germination tests in the laboratory it may be predicted that the environmental conditions for succesful germination do not differ very much from those for other cacti.

As is the case in many of the other cacti, the seeds of *Matucana* do not require a period of rest. In other words there is no dormancy period. Immediately after ripening, seed is able to germinate, providing there is sufficient water supply and the day temperature is roughly between 15 and 30°C.

When *Matucana* seeds are wetted, water penetrates through the brownish, partly detached, outer cuticular layer. Under experimental conditions seeds of *M. intertexta* imbibed very rapidly. By the end of the first 8 hours of imbibition, more than 90% of the total possible water uptake had already taken place.

The seeds take up water at the hilum region and through the seed coat. In experiments with *M. intertexta* seed, water uptake through the seed coat was found to proceed equally as fast as through the hilum. Water uptake through the seed coat was demonstrated by blocking the hilum of seeds with nail polish.

The uptake of water activates enzymes inside the seed and the embryo starts to grow. The basal part of the embryo, the radicle or first root, presses against the micropylar region of the seed and finally this pressure becomes great enough to split the seed coat. In most cases the pattern of rupture is more or less the same; the seed coat breaks just above the hilum, so that the hilar side of the seed is pushed aside like a lid (Photograph 7). This lid, which is called the operculum, consists of the entire hilum region and the basal portion of the testa. Actually, the operculum in *Matucana* seed is that portion of the seed below the embryo. This is equal to the portion of the testa that envelopes the cavity of the hilum.

The line along which the operculum breaks off the upper section of the seed does not occur by chance. During the development of the seed, a weak zone between two lateral rows of cells at the basal part of the testa is formed. This ruptures when pressure from the inside commences (Bregman & Bouman 1983).

In most *Matucana* species the operculum is relatively small, less than a quarter of the intact seed. In species with a very large and depressed hilum, such as *M. formosa* and *M. madisoniorum*, the operculum is much larger than the remaining seed section.

Once the operculum is discarded, the root first appears from the embryo and bends downward towards the soil. At the boundary of the stem (hypocotyl) and root, there is a whorl of radially spreading hairs. The function of these hairs is probably to fix the embryo to the soil. This ensures that the embryo stands upright so that the root can penetrate the soil. Soon after exposure to daylight the embryo turns green and after a week or so the first spines are formed.

At this stage of the reproduction cycle most of the dangers have been overcome, but not entirely. In nature, most seedlings that succumb do so because they have the misfortune of being in the wrong spot. Even if the position is favourable for growth all manner of animals may destroy the seedlings. In cultivation we also have to take care that fungi, mosses or rotting are controlled. If all these obstacles have been cleared, then eventually the seedling will become a mature plant that is capable of flowering. Only at flowering will the circle have been closed and the cycle of reproduction begin again.

CHAPTER 5

Cultivation

Matucanas are easy to cultivate. They require no special treatment, so anybody with an average knowledge on how to grow plants should be capable of cultivating Matucanas successfully. Of course not every species of *Matucana* requires exactly the same conditions and it depends upon where geographically the plants are grown, as to what treatment should be given. When cultivated in cold and temperate regions, high Andean plants (as many *Matucana* species are) may need additional heating in a greenhouse, whereas in the (sub)tropics they should be cooled or at least be taken out of the greenhouse. The recommendations given here are applicable to the temperate climate of NW Europe.

In the cultivation of cacti and other tropical plants the control of both winter and summer temperatures plays a major role. In this respect the Matucanas may be divided into two groups, which is actually a division according to the altitude of their native habitats. In the genus *Matucana* there is a group of species from high altitudes, which are not cold-sensitive but heat-sensitive, and a second group of species from relatively low altitudes, which exhibit no sensitivity to heat but are cold-sensitive.

The cold-sensitive group consists of all species from the Maranon basin (*M. oreodoxa* , *M. myriacantha*, *M. paucicostata*, *M. tuberculata*, *M. krahnii*, *M. formosa*, *M. pujupatii* and *M. madisoniorum*). All other *Matucana* species are heat-sensitive rather than cold sensitive. General recommendations for succesful cultivation of both groups are given below.

5.1 COLD-SENSITIVE SPECIES

In winter: light aspect; minimum temperature not below 5°C, preferably about 10°C. Special care should be given to *M. formosa* and *M. madisoniorum*, because due to low temperatures these species easily get brown spots where rotting can begin. One should also be careful with *M. oreodoxa* and *M. myriacantha*. In addition, the roots of these species are particularly sensitive to an exceeding amount of moisture.

In summer: as much light and warmth as possible. Temperatures above 40°C will do no harm. Overheating will cause damage only above 50°C. Do not allow

the compost to dry completely. Cultivation outside the greenhouse is not recommended, as these plants usually require a lot of heat.

5.2 HEAT-SENSITIVE SPECIES

In winter: light aspect, minimum temperatures preferably not below freezing point, although well hardened specimens may withstand temperatures down to –5°C.

In summer: as much light as possible; regular watering, not allowing the compost to dry out entirely; maximum air temperature 30°C. If the plants are frequently exposed to temperatures higher than 30°C, they will be extremely susceptible to scorching. Particularly in spring when the plants are just about to start growing, severe and irreversible damage may result from overheating. In appropriate sunny conditions, these plants become beautifully spined when kept outside the greenhouse. Only during long periods of rain does a roof above them become necessary. Another advantage is that plants that can be kept this way are less likely to be affected by mealy bugs, red spider mites and other parasites. The only care needed is to keep out snails and domestic animals.

5.3 FLOWERING

Although Matucanas without flowers are worth looking at, they are naturally at their most beautiful in full bloom. Unfortunately they often refuse to flower, particularly plants from the *M. haynei* complex. It is difficult to predict when a Matucana will flower for the first time. Species that usually flower as juveniles, are to be found almost exclusively in North Peru, such as *M. ritteri*, *M. paucicostata* and *M. intertexta*. Readily flowering species from the south of Peru are some forms of *M. haynei* like *M. hystrix*.

In order to bring the plants to full bloom, correct treatment in summer as well as in winter is absolutely essential. The flowering period of most species covers the spring and the summer periods. A limited number of species, such as *M. oreodoxa*, *M. aureiflora* and *M. ritteri* produce all flower buds more or less at the same time each year. *M. oreodoxa* and *M. aureiflora* may already flower in early spring. The other species may flower throughout the growing season, or they may flower twice a year. *M. weberbaueri* and *M. intertexta* usually start to flower in mid-summer and continue into the autumn. *M. aurantiaca* and forms of *M. haynei* such as *M. breviflora* and *M. villarica* often flower in the spring as well as in the autumn.

5.4 SOWING

Raising Matucanas from seed is the only way to build up a nice and diverse collection. Almost all species are commercially available as seed whereas only approximately half of all species are available as plants. A general method of seed

raising will not be given. This falls outside the scope of this book, and almost any cactus lover will surely have adopted his own way of seed raising, with which he or she has been most successful. Only some recommendations specifically intended for raising Matucanas from seed will be given.

Always use a sterile compost to sow in. Absolutely sterile composts are not for sale, so sterilize it yourself. Any kind of compost, the traditional soil-sand mixture as well as proprietary soiless cactus seed composts are suitable for Matucanas.

Remember that most *Matucana* species are mountain plants, hence their seeds require a moderate day temperature to germinate. Another important fact is the difference between day and night temperatures, which may be extremely great for habitats at high altitudes. Optimum day temperatures for germination are between 20 and 25°C, whereas night temperatures should drop below 10°C for best results. If sown at the end of the winter, around February and March, the seedlings can be planted out in June to July for the first time. The plants will then have dimensions of about 1.5 cm across at the beginning of the winter.

In every sowing there are individuals which obviously cannot keep up with the rest. They mostly grow slower, they flower poorly and they are more liable to catch diseases. Therefore, discard these weak plants.

5.5 GRAFTING

Most *Matucana* species do not need to be and therefore should not be grafted. For Matucanas, grafted plants will not grow faster and will not produce more flowers than well-cultivated plants on their own roots. Moreover, grafted plants adopt an unnatural elongated habit, because growth is forced. Furthermore, the formation of long and strong spines is inhibited.

When ungrafted, the species that belong to the paucicostata group are ready to flower within 5 years after sowing, sometimes the first flowering specimens are only 3 years old. Species from the other groups will normally require more time to flower.

If you still wish to graft Matucanas, then do so as soon as possible on *Peireskiopsis*. When the seedlings have reached a diameter of 1 to 1.5 cm, transfer them to a *Trichocereus spachianus* stem. Plants of 4 to 5 cm across may be removed from this stem to be further cultivated on their own roots.

Grafting as a method for minimizing the risk that difficult species are lost may be advisable for only one *Matucana* species: *M. oreodoxa*. The roots of this plant are fairly sensitive to too much water, so it may be safer to graft it.

CHAPTER 6

Systematics inside *Matucana*
Grouping of species

Genera which contain many species are often divided into subgenera. In practice the use of subgenera may be convenient for the purpose of identification or to facilitate complicated phylogeny of a large genus.

The genus *Matucana* is here proposed to contain 19 species. This makes the genus still rather small. Yet, subgeneric division of *Matucana* was proposed in 1965, when Ritter introduced the subgenus *Incaia* for *M. aureiflora* on the basis of a different flower. He thus divided the genus *Matucana* into two subgenera: subgenus *Incaia*, containing *M. aureiflora* only, and subgenus *Matucana* containing the rest of the species.

Ritter's view is not followed here. Selecting one or two deviating species for infrageneric ranks hardly improves clarity of arrangement. More clarity is achieved by splitting the genus *Matucana* into groups of species which are believed to be closely related. A group is not an official taxonomic rank, so this way of dividing a genus will not cause additional nomenclative confusion.

On the basis of seed features four species groups have been distinguished (Figure 6). These groups can be separated by characteristics dealing with the shape of the seed in lateral view and the structure of the hilum. The four groups are listed below.

1. Haynei group: Shape normal (not broadened dorsally and/or ventrally). Hilum cup covered by funicular tissue. No protruding micropyle.

2. Aurantiaca group: Shape normal. Hilum cup covered by funicular tissue. Micropyle protruding from the hilum.

3. Intertexta group: Shape normal. Amount of tissue in hilum cup reduced; funicular tissue at the hilum margin only; at the position of micropyle and funicle two holes are present in the funicular tissue, sometimes combined into one large hole. Micropyle not protruding from the hilum.

4. Paucicostata group: Seeds broadened by dorsal and/or ventral extension. Funicular tissue in most species reduced; this reduction varies widely from little reduction to complete absence. Hilum cup as large as or larger than the embryo cavity. Micropyle not protruding from the hilum.

After comparison of *Matucana* seeds with those of related genera the conclusion can be drawn that the haynei group is the most primitive, because the seed of this

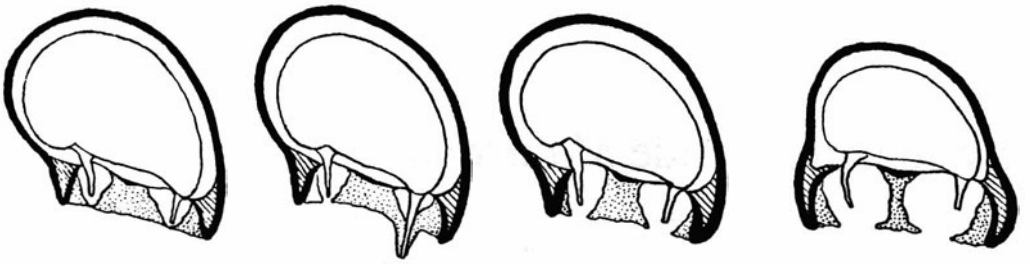


Figure 6. The seeds of the four species groups in *Matucana*, showing the principal differences.

group exhibit the closest resemblance to the seed of related genera.

The aurantiaca group and the intertexta group probably represent two lineages which could have evolved from the haynei group. In the aurantiaca group the uncommon feature of the elongated micropyle has developed. This development could have started in the northern part of the Rio Santa valley, because intermediate forms are found there, not only in seed but also in stem (northern forms of *M. haynei* such as *M. yanganucensis* and *M. megalantha*). More to the east, northern forms of *M. comacephala* also produce seeds intermediate to the haynei group and the aurantiaca group.

In the southern Maranon area the intertexta group could have evolved from the ancestors of *M. comacephala*. This species could have some relationship with the species of the intertexta group, especially the pink-flowering forms. This assumption is based on similarities of spination and flower structure. The only difference in seed between the intertexta group and the haynei group is the amount of funicular tissue.

The paucicostata group probably has a close connection with the intertexta group, particularly with the species from the Maranon valley. Ritter's *M. purpureoalba*, a form of *M. myriacantha* from this region, has seed which looks a lot like that of *M. paucicostata*. This group is most distinct for its broad seeds with a large basal cavity (hilum cup).

In the following chapters the species will be described, beginning with the most ancestral group of *Matucana* species: the haynei group.

CHAPTER 7

Key to all species of *Matucana*

By refering to the key that follows, all species, varieties and forms of *Matucana* as described and discussed in this book, may be identified. For optimal results it is essential that adult plants, flowers and preferably also seeds are available. Focus has deliberately been laid on features concerning the stem and the flowers. References to seed features have been kept to a minimum, but with the use of a magnifying glass these can be very helpful, especially for species that belong to the paucicostata group.

Identification of plants without flowers and seeds may be very difficult or even impossible, as in many species the spination is unfortunately too variable. Only a few species of distinct appearance, such as *M. fruticosa* and *M. madisoniorum*, can be identified in this way. One has to be a specialist to identify some species by their plant body alone (*M. ritteri, M. comacephala, M. paucicostata*, and some others).

In many cases the internal floral morphology of an unknown *Matucana* species must be investigated if the correct choice is to be made using the key. This is best achieved by removing a flower from the plant with a sharp knife or a pair of tweezers. One has to be sure that the entire flower is removed; often the ovarium remains attached to the plant so that the nectar chamber is torn up and can no longer be examined. Once the flower has been removed, it must be cut vertically with a razor or a sharp knife. To preserve the flower for later study, it must be stored in a suitable liquid, for example a mixture of pure ethanol or spirit and water in a 7:3 ratio. The disadvantages of this method are the shrinkage and the discolouration of the material.

Nowadays a large number of hybrids are in cultivation, whether deliberately created or not. When trying to identify such plants with the key presented here, it may not be possible to identify the parent species. So it is recommended to work with pure material, as far as can be anyhow established. Another reason for not arriving at the correct species is when a deviating form is the subject under investigation, such as albinos (e.g. the white-flowering form of *M. madisoniorum*) or other mutants. Such forms are not covered by the key.

7.1 KEY TO IDENTIFICATION

1a. Nectar chamber open (not closed by a diaphragm); primary stamens absent (Figure 7.1) 2
1b. Nectar chamber totally or partly closed by a diaphragm, formed by fusion of the basal filaments and/or a recess of the inner tube wall (Figure 7.2) 3
2a. Perianth orange to red; 0-5 spines per areole; seed broadly cap-shaped, shiny dark-brown (Figure 7.3) ..... *madisoniorum*
2b. Perianth golden to orange; 5-12 spines per areole; seed bag-shaped, dull black with brown-yellow outer layer (Figure 7.4) ..... *oreodoxa*
3a. Receptacle funnelform, regular (Figure 7.5), 30-45 mm long; perianth golden-yellow *aureiflora*
3b. Receptacle tube-shaped (Figure 7.6), 40-105 mm long; perianth white, yellow, pink, orange or red 4
4a. Perianth lemon-yellow ..... *weberbaueri*
4b. Perianth yellow with purple margin and top ..... *aurantiaca (pallarensis)*
4c. Perianth white to pale pink ..... *huagalensis*
4d. Perianth pink to lilac; plant densely spined 5
4e. Perianth orange, salmon, red or red-purple; spination open or dense 6
5a. Floral tube 3-5 mm wide; nectar chamber appr. 10 mm long; seed with no holes in the hilum (Figure 7.7) ..... *comacephala*
5b. Floral tube 5-8 mm wide; nectar chamber appr. 4 mm long; seed with 1 or 2 holes in the hilum (Figure 7.8) ..... *myriacantha*
6a. Single plant body cereoid, 2-6 cm across, strongly offsetting from the base (Figure 7.9) *fruticosa*
6b. Single plant body globose to broadly columnar (Figure 7.10) 7
7a. Perianth segments strongly curved backward, pale orange; spination open, powerful, stiff, centrals up to 7 cm long ..... *hastifera*
7b. Only basal perianth segments curved backward; spination different 8
8a. Plant extremely offsetting, also from lateral areoles (like *Echinopsis*); single plant flat globose, up to 8 cm across; floral tube 8-11 mm wide ..... *polzii*
8b. Plant strongly offsetting from the base; single plant shortly cylindrical, 4-7 cm across; floral tube appr. 6 mm wide ..... *paucicostata*
8c. Plant weakly offsetting to solitary 9
9a. Floral tube with hairs or tufts of wool 10
9b. Floral tube naked 18
10a. Plant flat globose, dark green; spination open (8-16 spines per areole), brown to black *ritteri*
10b. Plant globose to short cylindrical, green to grey-green; spination white to pale brown .. 11
11a. Ribs with elongated tubercles 12
11b. Ribs without tubercles or with flattened tubercles 13
12a. Flower 5-5.5 cm long; floral tube 4-5 mm wide; epidermis grass-green ..... *tuberculata*
12b. Flower up to 8.5 cm long; floral tube appr. 5 mm wide; plant body grey-green ..... *krahnii*
12c. Flower 6-7 cm long; floral tube 6-9 mm wide; plant body grey to grey-green ..... *pujupatii*
13a. Spination dense and fairly long (20-30 spines per areole; floral tube 7-10 mm wide; seed with protruding micropyle (Figure 7.11) 14
13b. Spination dense, short, white (appr. 40 spines per areole); floral tube 5-8 mm wide; seed without protruding micropyle (Figure 7.7) ..... *intertexta*
13c. Spination open (6-20 spines per areole) 15
14a. Ribs 13-17; flower 7-9 cm long; perianth red ..... *aurantiaca*
14b. Ribs 18-30; flower up to 6 cm long; perianth golden ..... *weberbaueri* f. *flammea*
15a. Perianth orange-yellow to orange-red ..... *intertexta*
15b. Perianth crimson 16
16a. Ribs 20-30; flower 8-10 cm long, tube 3-4 mm wide; seed shoe-like, appr. 2 mm wide (Figure 7.12) ..... *formosa*

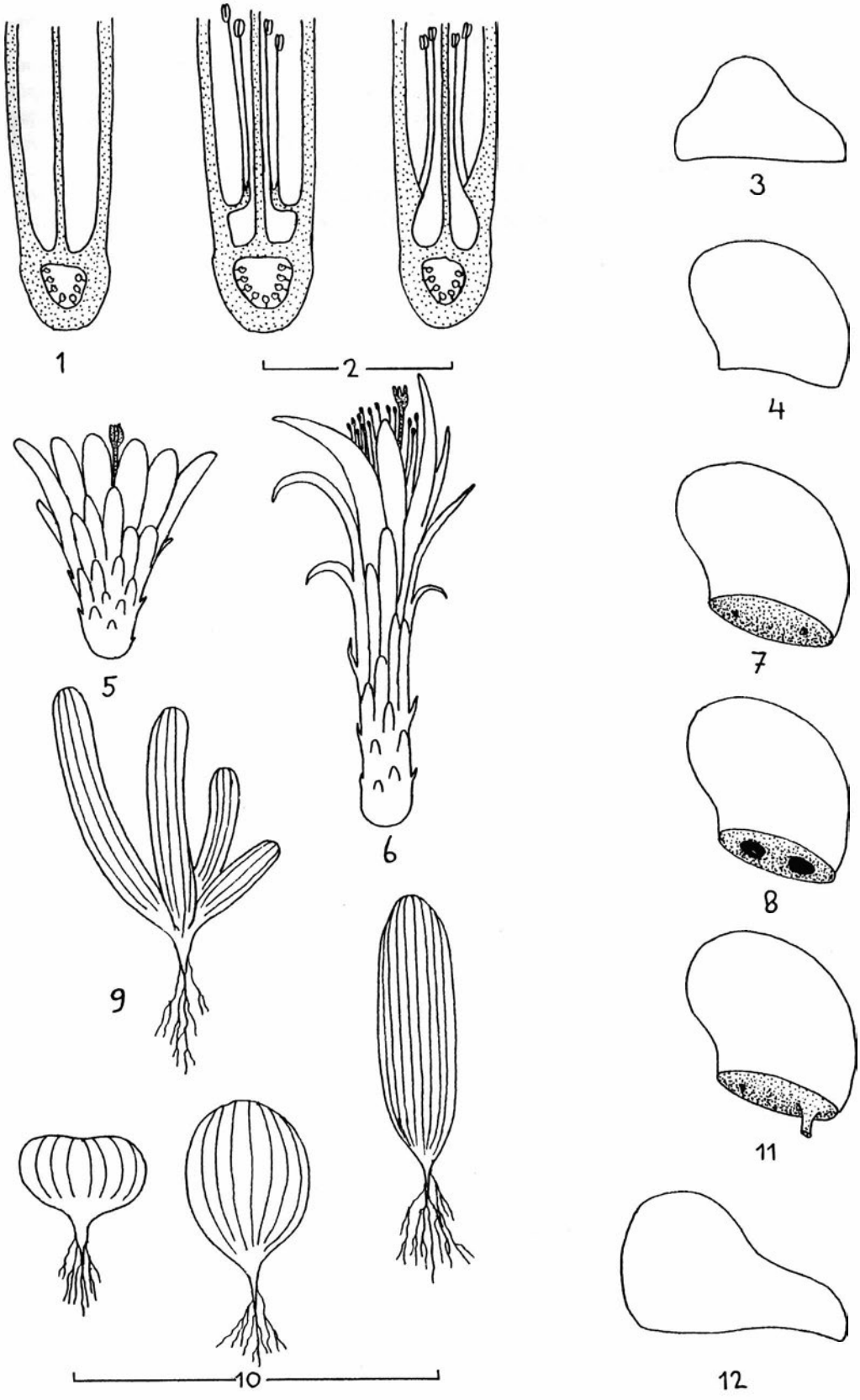


Figure 7. Drawings to elucidate the key to the species.

16b. Ribs 10-22; flower 6-7,5 cm long, tube 5-8 mm wide; seed different 17
17a. Ribs 14-22; epidermis green; 12-20 spines per areole; seed bag-shaped
intertexta var. *celendinensis*
17b. Ribs 10-12; epidermis grey-green; 6-11 spines per areole; seed cap-shaped .....*pujupatii*
18a. Ribs 13-17; seed with protruding micropyle .....*aurantiaca*
18b. Ribs 30-40; seed with 1 or 2 holes in the hilum ..... *myriacantha*
18c. Ribs 14-30; seed with at most weakly protruding micropyle, hilum without holes 19
19a. Floral tube 3-5 mm wide; spination flexible and partly as white hairs ..... *comacephala*
19b. Floral tube 5-10 mm wide; spination flexible to stiff without hairs .....*haynei*

CHAPTER 8

The haynei group

This group comprises all the species that grow in the southern part of the distribution area for *Matucana*, which are predominantly well-known for the dense spination that most of the species have. Surprisingly, according to their seed structure the two atypical Matucanas *M. oreodoxa* and *M. aureiflora* also belong to the haynei group.

As a result of the enormous variability in the haynei group an explosive number of new species and varieties have been introduced during the last 40 years. Most of these combinations were published by Rauh, Backeberg, Ritter and Knize. The majority of these have to be considered as synonyms, and will be dealt with below. Further field investigations are still needed to establish whether the taxonomy proposed here is correct.

8.1 TAXONOMY

Over 70 different names of species and varieties have in total been dedicated to plants that belong to the haynei group, classified in *Arequipa, Borzicactus, Cereus* and *Matucana*. These names are listed below.

8.1.1 *Validly published names*

Borzicactus aurantiacus var. *megalanthus* Donald
Matucana aureiflora Ritter
M. blancii Backeberg
M. blancii var. *nigriarmata* Backeberg
M. breviflora Rauh & Backeberg
M. calocephala Skarupke
M. cereoides Rauh & Backeberg
M. comacephala Ritter
M. crinifera Ritter
M. elongata Rauh & Backeberg
Cereus haynii Croucher
Echinocactus haynii Otto
Matucana haynei Britton & Rose
Borzicactus haynei var. *atrispina* Donald
B. haynei var. *breviflora* Donald
Matucana haynei var. *elongata* Ritter
Arequipa haynei var. *erectipetala* Krainz
Matucana haynei var. *erectipetala* Rauh & Backeberg
Borzicactus haynei var. *perplexa* Donald
Matucana herzogiana Backeberg

M. herzogiana var. *perplexa* Backeberg
M. hystrix Rauh & Backeberg
M. hystrix var. *atrispina* Rauh & Backeberg
M. hystrix var. *umadeavoides* Rauh & Backeberg
M. megalantha Ritter
M. mirabilis Buining
M. multicolor Rauh & Backeberg
M. multicolor var. *breviflora* Ritter
M. multicolor var. *hystrix* (Rauh & Backeberg) Ritter
M. oreodoxa Ritter
M. supertexta Ritter
M. variabilis Rauh & Backeberg
M. variabilis var. *fuscata* Rauh & Backeberg
M. winteri Ritter
M. yanganucensis Rauh & Backeberg
M. yanganucensis var. *albispina* Rauh & Backeberg
M. yanganucensis var. *fuscispina* Rauh & Backeberg
M. yanganucensis var. *longistyla* Rauh & Backeberg
M. yanganucensis var. *parviflora* Rauh & Backeberg
M. yanganucensis var. *salmonea* Rauh & Backeberg
M. yanganucensis var. *setosa* Ritter
M. yanganucensis var. *suberecta* Rauh & Backeberg.

8.1.2 *Invalidly published names (nomina nuda)*

Matucana armillata
M. atrispina
M. aureiflora var. *elata*
M. axiosa
M. blancii var. *platygona*
M. blanicostata
M. breviflora var. *incuiensis*
M. breviflora Pauza
M. carneoflora
M. cephalophora
M. clavispina
M. colorisplendida
M. colorisplendida var. *grandiflora*
M. colorisplendida var. *setosa*
M. comacephala var. *lutea*
M. comacephala var. *luteispina*
M. haynei var. *cereoides*
M. haynei var. *gigantea*
M. haynei var. *grandiflora*
M. hystrix var. *nigrispina*
M. lutea
M. luteispina
M. multicolor var. *armillata*
M. radians
M. robusta
M. setosa
M. villarica
M. violaciflora
M. yanganucensis var. *grandiflora*
M. yanganucensis var. *santiensis*
M. yanganucensis var. *setiflora.*

Most of the *nomina nuda* listed are names from the catalogue of K. Knize, Lima, Peru. Many seeds of these plants have been distributed all over the world and so carry these invalid names.

In the past M. Kimnach and J. Donald have tried to make some sort of order of the plants of the haynei group. Taking *M. oreodoxa* and *M. aureiflora* out of consideration (both species were described in 1965), Kimnach recognized in 1960 one single species: *Borzicactus haynei*. Donald (1970-1971) recognized three species: *Borzicactus haynei* with four varieties (*haynei*, *atrispina*, *perplexa* and *breviflora*), *B. variabilis* and *B. mirabilis*.

The haynei group is here divided into the following four species:

1. *M. haynei* (Otto) Britton & Rose,
2. *M. comacephala* Ritter,
3. *M. aureiflora* Ritter,
4. *M. oreodoxa* (Ritter) Slaba.

The latter 2 species do not seem to fit into the haynei group. In considering the plant body of these species it would be more logical to put them in the aurantiaca group. However, the seed of both species indicates that they belong to the haynei group. All remaining species and varieties are combined into the two species: *M. haynei* and *M. comacephala*.

The *nomina nuda M. brunescens, M. mirabilis, M. blanicostata, M. carneoflora* and *M. rarissima* are not listed because they are insufficiently known to the author.

M. mirabilis (Plate 18, syn. *M. variabilis* var. *mirabilis*) was described by Buining in 1963 but is possibly of hybrid origin. The plant body and the seed looks intermediate between *Loxanthocereus* and *Matucana* (haynei group seed). The flower is typically *Matucana* but with the long nectar chamber of *Loxanthocereus*. The suspected origin of this plant still has to be confirmed by field studies but it is certain that it is not *Arequipa*, as was supposed by Backeberg. According to the *CITES Cactaceae Checklist* (Hunt 1992) it is a hybrid between *Cleistocactus* (*Borzicactus*) *fieldianus* and *Matucana supertexta*.

M. rarissima is a hybrid between *Oreocereus ritteri* and *Matucana multicolor*, according to Ritter.

The remaining three 'species' are not known to the author. The seeds indicate that they belong to the haynei group.

The proposed abandonment of many names may provoke objections from hobbyists and growers but for the present it is simply impossible to recognize any more species. Over the past forty years in particular, many local forms have been described as species or varieties, mainly by Rauh, Backeberg and Ritter. These plants differ only in spination; flower, fruit and seed are almost or entirely identical. However, the natural populations show such a great variability that one local form cannot be separated from another local form by a clear description. To give an example, *M. yanganucensis* is an extremely variable plant. If we were to describe this plant in such a way that all individuals fitted the description, then as a consequence all individuals of *M. haynei* would also fit that description. So *M. yanganucensis* and *M. haynei* s.s. cannot be separated by description. Moreover, all individuals within a population of *M. yanganucensis*, no matter how variable they may be, belong to one breeding community and therefore by definition to one species.

Some authors are suspected of deliberately selecting a plant with deviating features from a variable population to describe it as a new species or variety. Often the deviating characteristics are not constant in following generations. The typical habitat forms of *M. yanganucensis*, *M. hystrix* and *M. breviflora* differ from the typical *M. haynei* and are recognizable by certain features, but if one observes the natural populations or seedlings in the greenhouse, it can be seen that

many individuals differ in appearance from that which is typical for the 'species' in question.

Since *M. haynei* is the first described species of the genus, all other taxa whose descriptions fall within the range of the description of *M. haynei* must be treated as synonyms. Only *M. comacephala* is proposed to retain the rank of species because of differences in flower and spination.

Plants that belong to the haynei group conform with the following description; the features of *M. aureiflora* and *M. oreodoxa*, if relevant, are shown within the brackets ( ).

Spination in general dense (open); radials 14-45 (4-14), bristle-like, white to brownish; centrals 1-20 (0-4), mostly darker coloured than radials.

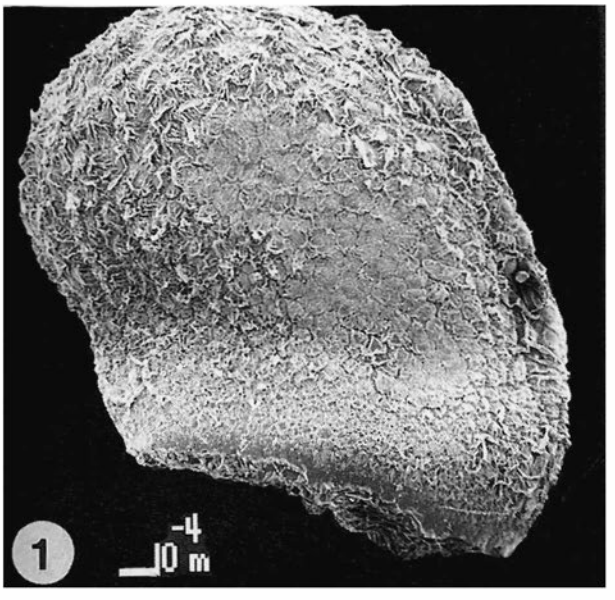
Flower pink to red (yellow to orange), ovary and tube naked (naked or hairy); nectar chamber closed by a diaphragm (no diaphragm in *M. oreodoxa*).

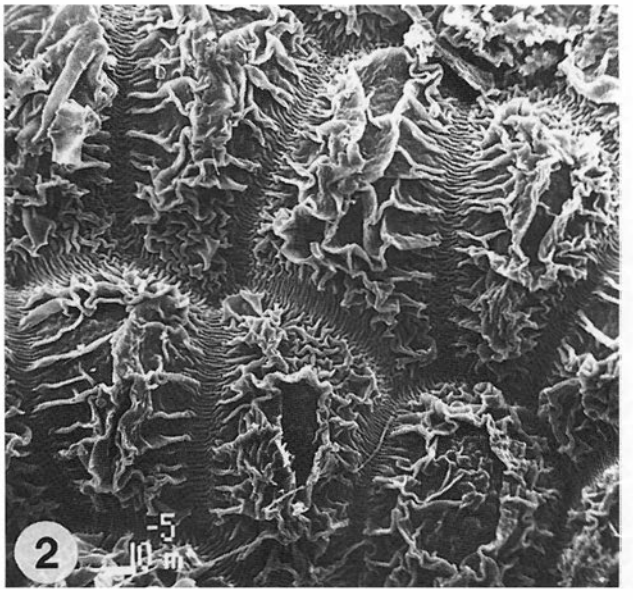
Seed dull black, covered by irregularly ruptured, yellow-brown, paper-like outer layer; about as long as wide, or somewhat longer than wide; dorsally and ventrally little or not expanded; seed surface with irregular grooves and hills; cuticle strongly folded; testa cells in apical region somewhat convex, basally strongly flattened. Hilum mostly somewhat depressed; hilum cup totally covered by funicular tissue; sometimes there is a hole in this tissue at the position of the funicle. Embryo slightly curved.

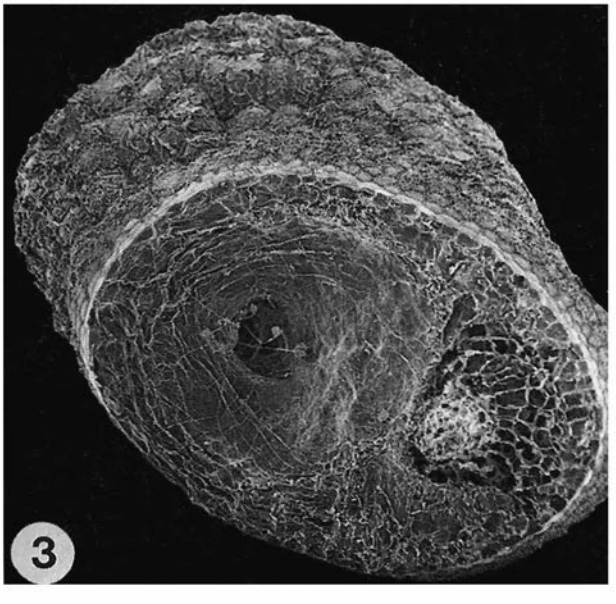
8.2 PHYLOGENY

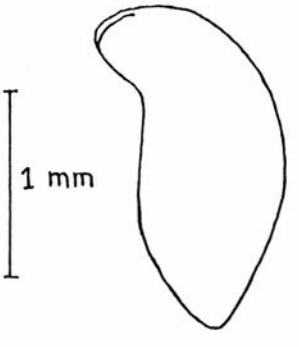
The haynei group is probably the oldest, i.e. the most ancestral species group within the genus *Matucana*. The cereoid species are considered to be less evolved than globular species. So accordingly, *M. haynei* and *M. comacephala* are probably older than *M. aureiflora* and *M. oreodoxa*. This assumption is based upon the similarity in many respects between the cereoid Matucanas and the closely related genus *Oreocereus*. Also the large distribution area of *M. haynei* and its forms supports the argument that points in the direction of a relatively old taxon. It is thus assumed that the haynei group comprises the first plants that became separated morphologically and geographically from its closest relatives, possibly the ancestor of the genus *Oreocereus*. If this assumption is true, this evolution must have started in the area where related genera (*Oreocereus, Oroya*) are still present, i.e. southern Peru. From there, colonization of the western Andean slopes could have proceeded in two directions, to the west where strongly spined forms (*M. multicolor, M. hystrix*) have developed, and to the north where globose forms like *M. blancii* have evolved. This theory is the antithesis of what Buxbaum believed, namely that the southern *Matucana* species are the most developed. His ideas were based on the assumption that *Borzicactus* (*Seticereus*) *icosagonus*, a species from the frontier zone of Peru and Ecuador, is a close relative of *Matucana*. A comparison of the seed of both genera, however, tells us something else.

M. oreodoxa and *M. aureiflora* are difficult species in terms of phylogeny. These species are so different from the typical Matucana that either they must have been isolated for a long period of time, or hybridization must have taken place. For the time being this problem remains unsolved.









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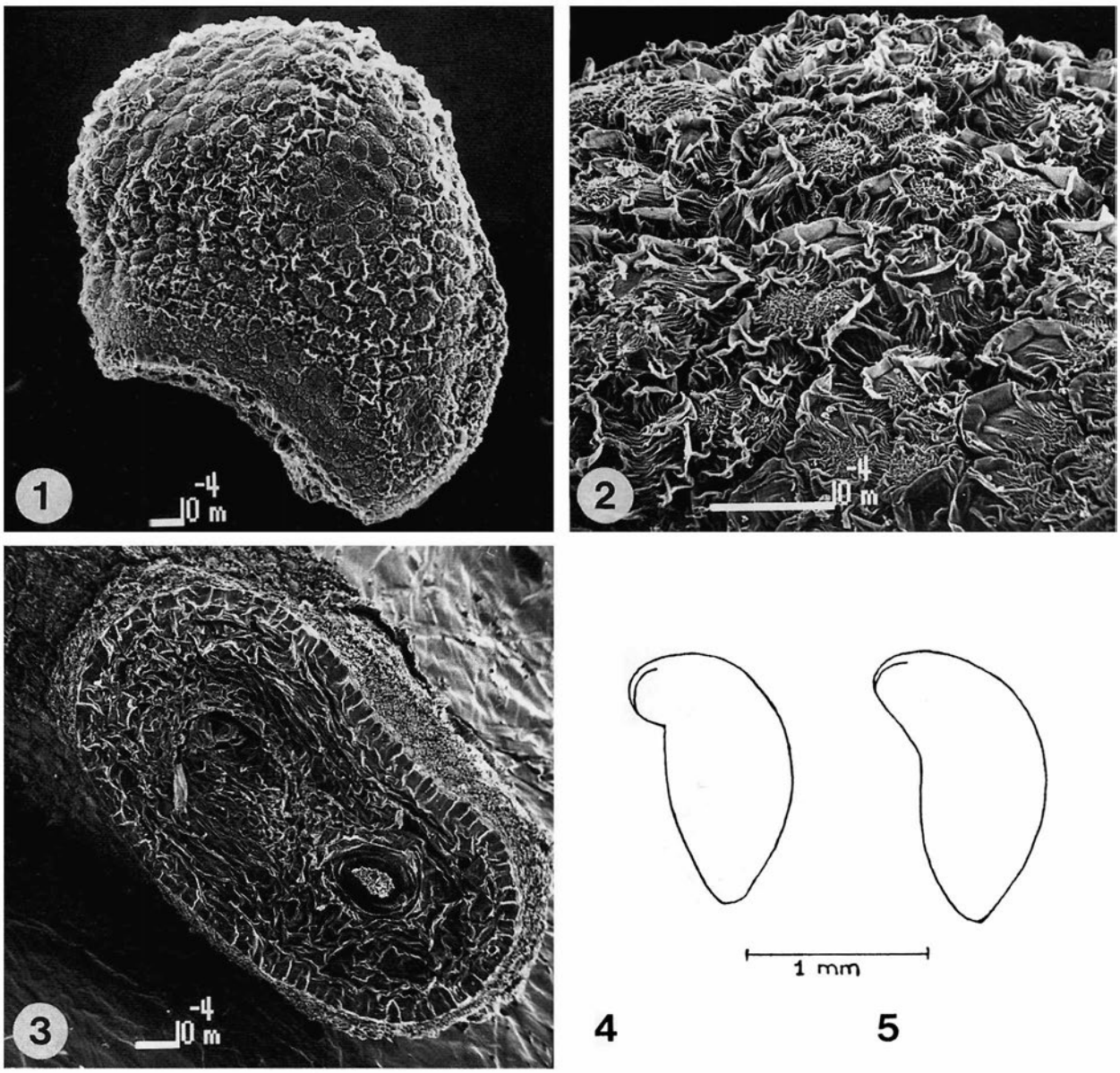
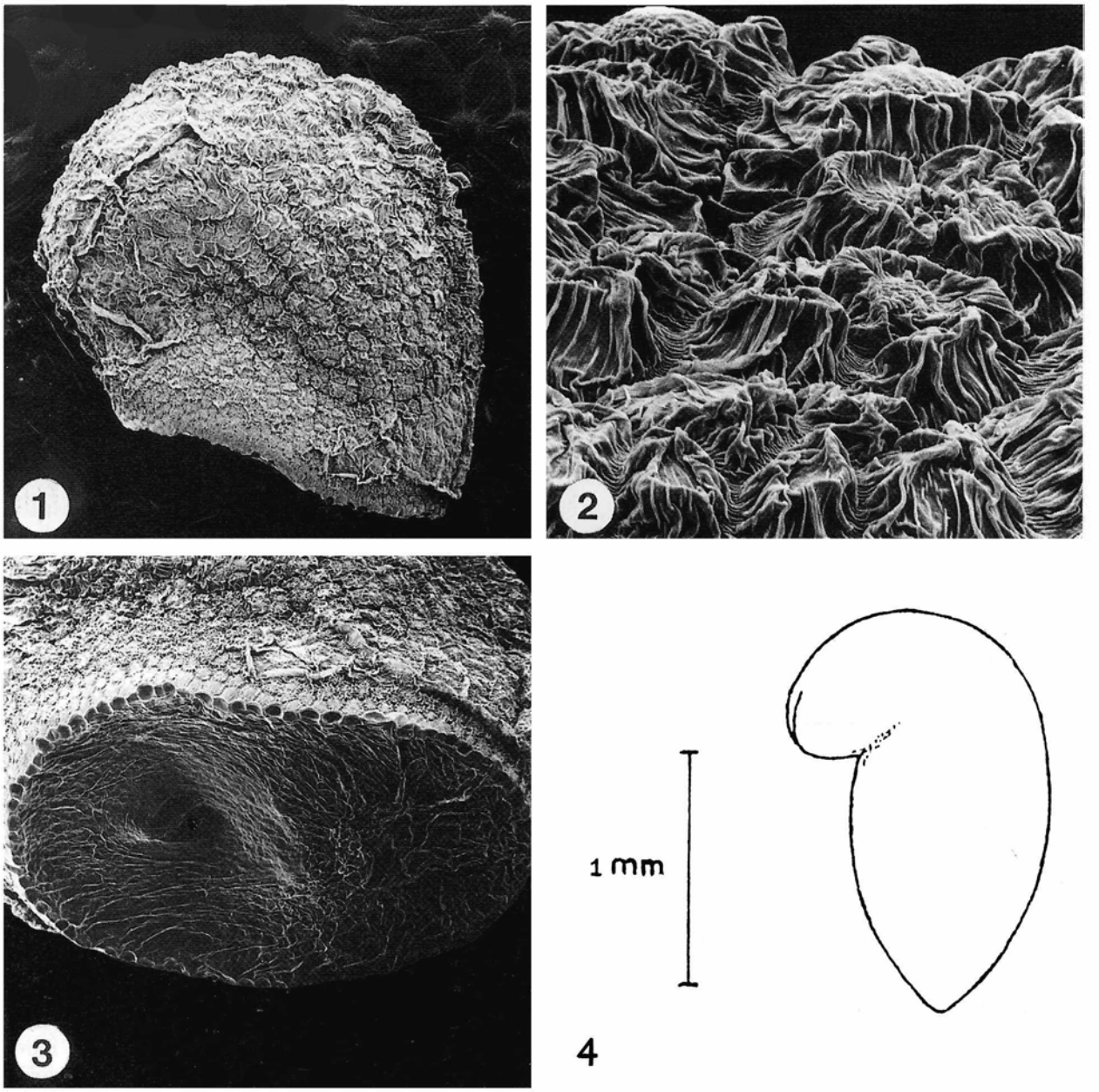
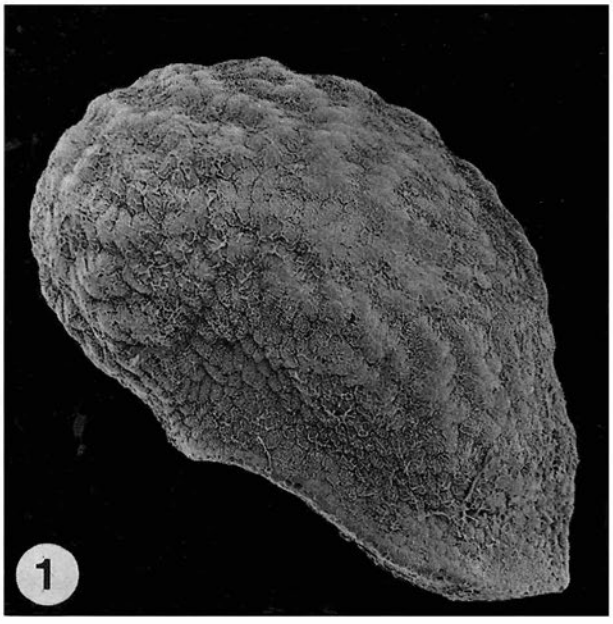
Photograph 8. Seed of *Matucana haynei*. 1. *M. haynei* (Köhres 1984), seed in lateral view; 55×. 2. *M. hystrix* var. *atrispina* (Köhres 1980), detail of the lateral part of the testa; 550×. 3. *M. multicolor* (de Herdt 1984), hilum; 90×. 4. *M. multicolor* (Knize 1982), embryo.

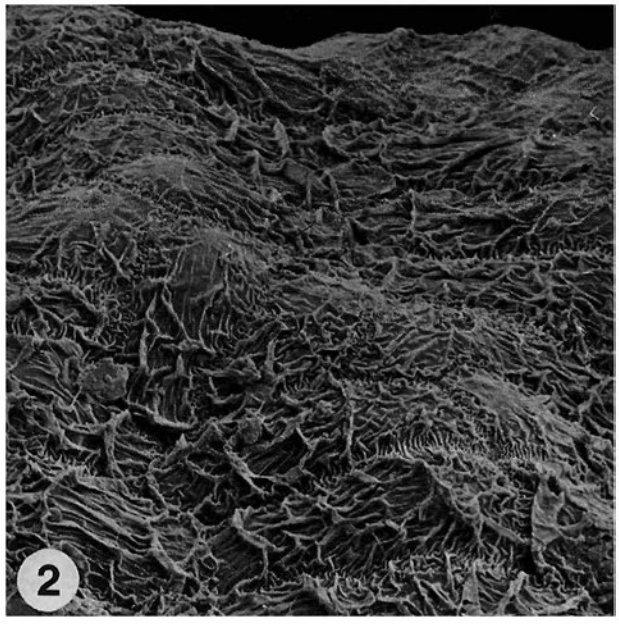


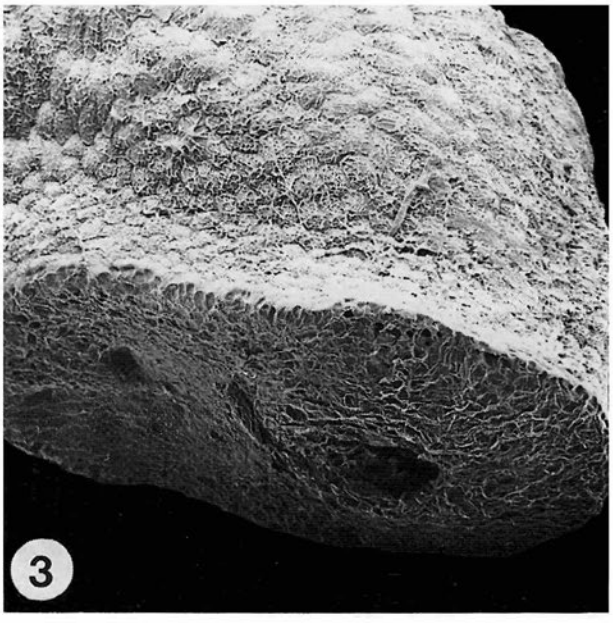
Photograph 9. Seed of *Matucana comacephala*. 1. *M. cephalophora* (Köhres 1981), seed in lateral view; 55×. 2. *Matucana* sp. Pomabamba KK 1776 (Knize 1983), testa in apical region; 220×. 3. *M crinifera* (Köhres 1980), hilum; 80×. 4. *M. cephalophora* (Köhres 1981), embryo. 5. *M. lutea* (Köhres 1984), embryo.

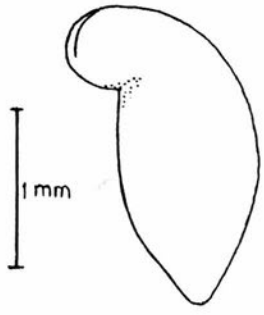


Photograph 10. Seed of *Matucana oreodoxa* (de Herdt 1984). 1. Seed in lateral view; 35×. 2. Testa in apical region; 275×. 3. Hilum; 75×. 4. Embryo.









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Photograph 11. Seed of *Matucana aureiflora* (Cajamarca, 1982). 1. Seed in lateral view; 55×. 2. Testa in apical region; 275×. 3. Hilum; appr.; 75×. 4. Embryo.

8.3 DISTRIBUTION

The distribution area of the species of the haynei group is shown in Figure 8. It covers the largest area of all four species groups. It stretches from approximately 8 to 15°S in a narrow strip along the Pacific slopes of the western Cordillera, but also more to the east.

The four species of the haynei group seem to be geographically separated. *M. haynei* is the only *Matucana* species south of the high plateau of Cerro de Pasco (10°S). Its habitats are solely situated on the western slopes of the western Cordillera. From the area on the other side of this mountain chain south of Cerro de Pasco, only one record of a *Matucana* discovery exists, viz. Knize's *M. villarica* from Huancayo. Due to lack of knowledge of this plant, it has been provisionally placed in *M. haynei*. North of the Cerro de Pasco plateau Matucanas of the haynei group occur on both sides of the western Cordillera, clearly because in Northern Peru this mountain chain seldom exceeds 4000 m altitude, so that the plants can reach the eastern slopes. *M. haynei* has expanded its area further north as far as Santiago de Chuco (Ritter's *M. winteri*), but keeps to the west side of the western Cordillera. On the other hand, *M. comacephala* and *M. oreodoxa* occur on the east side of the western Cordillera.

M. aureiflora is the northernmost occurring species of the haynei group. Its habitat is around the city of Cajamarca, capital of the department with the same name situated in a depression of the western Cordillera. This locality is situated about 120 km away from the nearest habitat of *M. haynei*. Possibly *M. aureiflora* is a relict, its present distribution area now being a small remnant of a much larger distribution area in the past.

8.4 KEY TO THE SPECIES OF THE HAYNEI GROUP

1a. Flower regular, short or elongate funnel-shaped, yellow to orange; 4-8 spines per areole.. 2
1b. Flower oblique, tube-shaped, pink to red; 18-60 spines per areole 3
2a. Flower with diaphragm, 30-45 mm long, yellow; 8-18 spines per areole; plant body with 11-27 ribs ..... *aureiflora*
2b. Flower without diaphragm, 40-60 mm long, orange; 4-12 spines per areole; plant body with 7-12 ribs ..... *oreodoxa*
3a. Flower with weakly developed diaphragm, mostly pink, sometimes red; flower tube 3-5 mm wide; spines bristle-like, erect tuft-like when young, some radials as white hairs *comacephala*
3b. Flower with well developed diaphragm, red to purple; flower tube 5-10 mm wide; radials bristle-like ..... *haynei*

8.5 THE SPECIES OF THE HAYNEI GROUP

Matucana haynei (Otto) Britton & Rose, The Cactaceae 3: 102 (1922)
CITES Cactaceae Checklist: *Matucana haynei, Matucana hystrix, Matucana blancii* p.p., *Matucana myriacantha* p.p.; haynei = named after F.G. Hayne; Plates 1, 5 and 13-17.

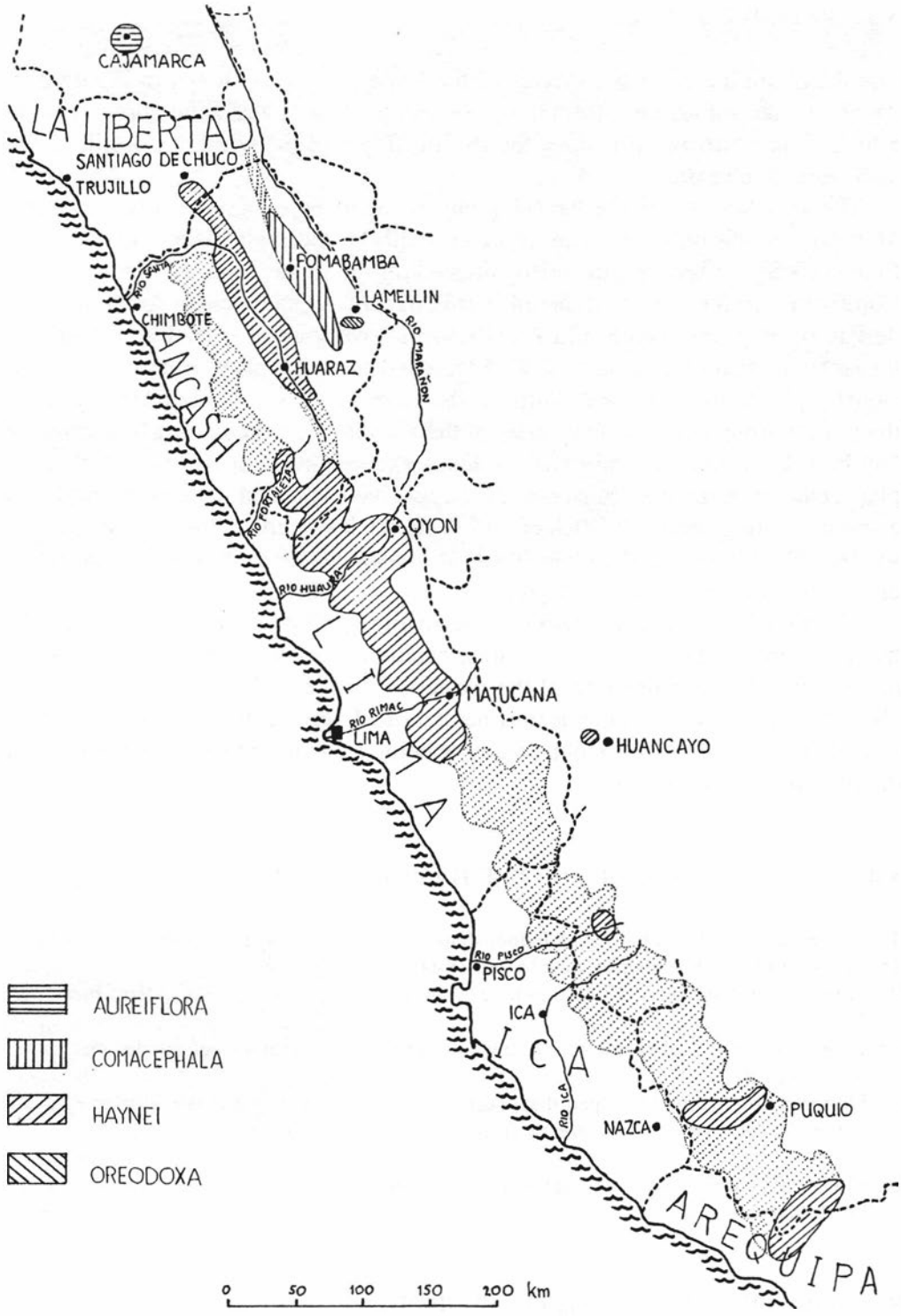


Figure 8. Distribution of the species of the haynei group. Dotted lines indicate probable distributions.

BASIONYM

Echinocactus haynii Otto, in: Salm-Dyck, Cact. Hort. Dyck.: 165 (1850).

SYNONYMS

Borzicactus aurantiacus var. *megalanthus* (Ritter) Donald, Cact. Succ. J. (Gr. Brit.) 26(1): 10 (1971).

Matucana blancii Backeberg, Cact. Succ. J. (Gr. Brit.) 11(4): 70 (1956).

Matucana blancii var. *nigriarmata* Backeberg, Cact. Succ. J. (Gr. Brit.) 11(4): 70 (1956).

Matucana breviflora Rauh & Backeberg, Descr. Cact. Nov.: 18 (1956).

Matucana cereoides Rauh & Backeberg, Descr. Cact. Nov.: 18 (1956).

Matucana elongata Rauh & Backeberg, Descr. Cact. Nov.: 18 (1956).

Arequipa haynei (Otto) Krainz, Die Kakteen I.XI. CVb (1963).

Borzicactus haynei (Otto) Kimnach, Cact. Succ. J. (USA) 32(3): 92 (1960).

Borzicactus haynei var. *perplexa* (Backeberg) Donald, Cact. Succ. J. (Gr. Brit.) 25(4): 111 (1970).

Cereus haynii (Otto) Croucher, Garden 13: 290 (1878).

Borzicactus haynei var. *atrispina* (Rauh & Backeberg) Donald, Cact. Succ. J. (Gr. Brit.) 25(4): 111 (1970).

Borzicactus haynei var. *breviflora* (Rauh & Backeberg) Donald, Cact. Succ. J. (Gr. Brit.) 25(4): 111 (1970).

Matucana haynei var. *elongata* (Rauh & Backeberg) Ritter, Kakteen in Südamerika 4: 1497 (1981).

Arequipa haynei var. *erectipetala* (Rauh & Backeberg) Krainz, Die Kakteen I.XI. CVb (1963).

Matucana haynei var. *erectipetala* Rauh & Backeberg, Descr. Cact. Nov.: 18 (1956).

Matucana herzogiana Backeberg, Cact. Succ. J. (Gr. Brit.) 11(4): 71 (1956).

Matucana herzogiana var. *perplexa* Backeberg, Cact. Succ. J. (Gr. Brit.) 11(4): 71 (1956).

Matucana hystrix Rauh & Backeberg, Descr. Cact. Nov.: 18 (1956).

Matucana hystrix var. *atrispina* Rauh & Backeberg, Descr. Cact. Nov.: 18 (1956).

Matucana hystrix var. *umadeavoides* Rauh & Backeberg, Descr. Cact. Nov.: 18 (1956).

Matucana megalantha Ritter, Succulenta 45(8): 117 (1966).

Matucana multicolor Rauh & Backeberg, Descr. Cact. Nov.: 19 (1956).

Matucana multicolor var. *breviflora* (Rauh & Backeberg) Ritter, Kakteen in Südamerika 4: 1500 (1981).

Matucana multicolor var. *hystrix* (Rauh & Backeberg) Ritter, Kakteen in Südamerika 4: 1499 (1981).

Matucana supertexta Ritter, Kakteen in Südamerika 4: 1504 (1981).

Borzicactus variabilis (Rauh & Backeberg) Donald, Cact. Succ. J. (Gr. Brit.) 25(4): 111 (1970).

Matucana variabilis Rauh & Backeberg, Descr. Cact. Nov.: 19 (1956).

Matucana variabilis var. *fuscata* Rauh & Backeberg, Descr. Cact. Nov.: 20 (1956).

Matucana winteri Ritter, Kakteen in Südamerika 4: 1506 (1981).

Matucana yanganucensis Rauh & Backeberg, Descr. Cact. Nov.: 18 (1956).
Matucana yanganucensis var. *albispina* Rauh & Backeberg, Descr. Cact. Nov.: 18 (1956).
Matucana yanganucensis var. *fuscispina* Rauh & Backeberg, Descr. Cact. Nov.: 18 (1956).
Matucana yanganucensis var. *longistyla* Rauh & Backeberg, Descr. Cact. Nov.: 18 (1956).
Matucana yanganucensis var. *parviflora* Rauh & Backeberg, Descr. Cact. Nov.: 18 (1956).
Matucana yanganucensis var. *salmonea* Rauh & Backeberg, Descr. Cact. Nov.: 18 (1956).
Matucana yanganucensis var. *setosa* Ritter, Kakteen in Südamerika 4: 1507 (1981).
Matucana yanganucensis var. *suberecta* Rauh & Backeberg, Descr. Cact. Nov.: 18 (1956).
Matucana armillata n.n.
Matucana atrispina n.n.
Matucana axiosa n.n.
Matucana blancii var. *platygona* n.n.
Matucana breviflora var. *incuiensis* n.n.
Matucana breviflora Pauza n.n.
Matucana clavispina n.n.
Matucana colorisplendida n.n.
Matucana colorisplendida var. *grandiflora* n.n.
Matucana colorisplendida var. *setosa* n.n.
Matucana haynei var. *cereoides* n.n.
Matucana haynei var. *gigantea* n.n.
Matucana haynei var. *grandiflora* n.n.
Matucana hystrix var. *nigrispina* n.n.
Matucana multicolor var. *armillata* n.n.
Matucana robusta n.n.
Matucana setosa n.n.
Matucana villarica n.n.
Matucana violaciflora n.n.
Matucana yanganucensis var. *grandiflora* n.n.
Matucana yanganucensis var. *santiensis* n.n.
Matucana yanganucensis var. *setiflora* n.n.
Matucana sp. Pisco (Knize).

DESCRIPTION

Body green, globose to broad cylindrical, to 20 cm wide, to 60 cm long, solitary to cespitose, no tap root. Ribs 14-30, 5-10 mm high, tuberculate. Areoles round to elliptic, 3-7 mm long, 2-5 mm wide, with white to brown wool but later naked, 6-12 mm apart. Spination variable in shape, length and colour, grey in later life; radials 14-45, 8-40 mm long, white to pale brown; centrals 1-20, 10-70 mm long.

Flower 4-9 cm long, in anthesis to 4 cm wide, mostly zygomorphic; perianth segments mostly carmine, sometimes salmon or red-purple. Tube 5-10 mm wide,

naked, mostly somewhat curved, reddish. Nectar chamber 1-5 mm long, closed by a diaphragm. Filaments yellow to purple brown, primary filaments at their bases shortly fused to form a collar around the style. Style red to violet, reaching about as far as the anthers; stigma lobes 4-6, 1-3 mm long, yellowish to pale violet.

Fruit globose to club-shaped, 10-15 mm long and wide, reddish green.

Seed as described earlier in this chapter, 1.0-1.7 mm long, 1.2-1.9 mm wide, 0.7-1.1 mm thick.

Remarks

Matucana haynei is the type species of the genus *Matucana* and was originally described in 1850 as *Echinocactus haynii*. The epithet appeared to be misspelled, so was changed to 'haynei' by Schumann because the intention was to name the plant after the German botanist Friedrich Hayne. On comparing this plant with plants of the genus *Echinocactus*, Britton and Rose saw the justification for creating the new genus *Matucana* in 1922, so from then on the plant became known as *Matucana haynei*. It is also the first species described in the genus *Matucana* and the longest known species of the genus.

The tremendous variablitity of this species has already been outlined earlier in this chapter. Again, it should be emphasized that this variability is only found in the appearance of the plant body, more precisely in the spination. Flowers, fruits and seeds exhibit no structural differences. In one population a wide range of different forms in spination can be found, although in most cases one form dominates. Such forms have often been described as separate species in the past. When comparing these plants, the direct consequence of this variability inside a single population is that there is much overlap in characteristics between populations. In other words, populations cannot be sufficiently separated from each other by descriptions. Therefore, they should be treated as ecotypes rather than species. This statement is supported by experience in cultivation. The seed of many taxa listed here as synonyms of *M. haynei* have been sown. The plants grown from these seeds do not, or only partially, possess those features that are stressed in the original descriptions as being typical for the 'species'. The conclusion from this data can only be that several typical features observed in the field are obviously not genetically determined but have developed under the influence of environmental factors such as radiation intensity, soil types, climate, and so on. Therefore we should speak of local modifications or ecotypes. Some of these, still considered as species by many, will be discussed below.

Forms of *Matucana haynei*

One of the best-known forms of *M. haynei* is *M. yanganucensis*, which was described in 1956 after the Rauh expedition to Peru. This plant locally frequents the valley of the Rio Santa, so it is one of the northernmost occurring forms of *M. haynei* s.l. Six varieties were described at the same time. Five of these appeared to be forms within one population; the most extreme forms had simply been selected. This does not conform with taxonomical rules; one of them stipulates that varieties should be geographically isolated.

The typical *M. yanganucensis* (Plate 14) is a broad-cylindrical plant with relatively few, short, glossy, curved spines. On the other hand, densely spinated forms

from the same valley have been described by Ritter as *M. winteri* and *M. megalantha* (Plate 13, syn. *M. herzogiana* var. *perplexa*) and by Backeberg (*M. blancii*). The latter is a high Andean form with dense, short, white spination and a cespitose habit.

More to the south, in the department of Lima, we find forms of *M. haynei* with a dense spination and a cereoid habit. The latter feature is expressed in the names *M. cereoides* and *M. elongata*, both described by Rauh and Backeberg. Another plant from this area is *M. variabilis*, described by the same authors. Unfortunately, the descriptions of these plants are so insufficient that they cannot possibly be separated, not only from each other but even from *M. haynei* s.s. The epithet 'variabilis' is, by the way, most applicable to these plants, but for reasons of priority the correct epithet is 'haynei'.

In 1981 Ritter described *M. supertexta*, a plant unknown to the author. He found this plant near the village of Churin, the same locality where Rauh found his *M. variabilis*. Due to the poor description of *M. variabilis*, Ritter had doubts whether both taxa were identical. The description of *M. supertexta* is a little different from that of *M. haynei* s.s.; the plant is smaller, has less ribs and a stronger spination. These differences, however, fall entirely within the range of variation of *M. haynei* s.l.

The southernmost forms of *M. haynei* s.l. are *M. hystrix* (Plate 16), *M. breviflora* and *M. multicolor*. In general these plants are somewhat more robustly spined; often the centrals are brown to black. In overall habit they resemble *Arequipa*, a former genus (now *Oreocereus*) which occurs not very far from these Matucanas, more to the south in the department of Arequipa and just across the Peru-Chilean border. This resemblance is probably the result of more or less similar environmental conditions. *M. hystrix* and *M. multicolor* were described by Rauh and Backeberg, both again most inadequately. The distribution areas of both taxa are situated between Nazca and Puquio in the department of Arequipa and overlap partly, so these plants are most likely being cross-pollinated. For that reason alone they should be considered conspecific.

M. breviflora, another Rauh finding, is distinct for its small flower (appr. 4 cm long), according to the description. This characteristic was enough reason for Donald to give this plant the rank of variety (*Borzicactus haynei* var. *breviflora*). However, plants raised from imported seed appeared to produce the normal long *haynei* flowers as well as short ones. Hence the short flower in *M. breviflora* has lost its taxonomic significance.

To summarize, the differences between all taxa listed here as synonyms of *M. haynei* are too small to treat them as species. This conclusion is based on the knowledge of a number of specialists with both field and cultivation experience. Naturally there is a lot of field work left to be done in the future. This could yield information to justify that possibly some of the taxa listed should acquire the rank of, maybe, species or, more probable, subspecies or varieties.

Distribution

M. haynei s.l. represents the southernmost species of the genus *Matucana*. Going from north to south, the distribution area sterches from the departments of La Libertad to Arequipa, covering a distance of approximately 800 km (Figure 8). All

habitats but one (*M. villarica* from Huancayo) are located on the western slopes of the western Cordillera, predominantly in valleys of rivers that drain to the Pacific (Rio Santa, Rio Rimac, Rio Pisco, Rio Pilcomayo, Rio Fortaleza, and others). The vertical distribution extends from 2400 m to 4100 m above sea level.

The distribution zone of *M. haynei* is disjunct, which means that large areas within the overall distribution zone are devoid of this species, at least nobody has ever reported observing *M. haynei* in these areas. No doubt many presently unknown habitats of *M. haynei* exist, but due to the inaccessibility of the terrain and the danger of the activities of guerillas, these localities have not yet been discovered.

The type locality is near the town of Matucana, department of Lima, Peru. Rauh and Backeberg recorded an altitude of 2400 m. In this area also grows the variety *erectipetala* at 2500 m altitude. *M. yanganucensis* and its varieties occur in the valley of the Rio Santa, department of Ancash at 2500-3300 m altitude. *M. megalantha* was found by Ritter in the same valley near Caraz. Another plant from this valley is *M. blancii*, growing near Pueblo Libre at 4150 m altitude. For *M. winteri* Ritter reported the locality as Santiago de Chuco, department of La Libertad, at a height of 3500 m. The locality of *M. variabilis* is reported as 10 km north of the town of Churin at an altitude of 2500 m. *M. supertexta* is reported from the same locality, at over 2500 m elevation. *M. elongata* grows in the Cordillera Negra, department of Ancash, at 3800-4150 m elevation. More to the south, in the Rio Pisco valley, department of Huancavelica, *M. cereoides* can be found. The locality of *M. multicolor* is situated between Nazca and Puquio, department of Ayacucho at 4100 m altitude. For *M. hystrix* the area between Nazca and Lucanas is reported. The habitat of *M. breviflora* is located at the foot of the Sarasassa volcano, 30 km west of Incuio.

FIELD NUMBERS

FR 142	*Matucana haynei*
FR 142b	*M. haynei* var. *gigantea*
FR 142c	*M. haynei* var. *elongata*
FR 565	*M. multicolor* var. *hystrix*
FR 592a	*M. yanganucensis* var. *setosa*
FR 593	*M. megalantha*
FR 690	*M. supertexta*
FR 691	*M. winteri*
KK 275	*M. haynei*
KK 460	*M. cereoides*
KK 531	*M. hystrix* var. *nigrispina*
KK 532	*M. multicolor*
KK 560	*M. hystrix*
KK 564	*M. yanganucensis*
KK 564	*M. yanganucensis* var. *grandiflora*
KK 565	*M. herzogiana*
KK 566	*M. elongata*
KK 575	*M. clavispina*
KK 580	*M. villarica*
KK 713	*M. blancii*
KK 730	*M. yanganucensis*
KK 780	*M. breviflora*
KK 794	*M. cereoides*
KK 1035	*M. violaciflora*
KK 1037	*M. yanganucensis*
KK 1040	*M. variabilis*
KK 1044	*M. yanganucensis*
KK 1132*	*M. breviflora* Pauza
KK 1133	*M. multicolor* var. *armillata*
KK 1459	*M. yanganucensis* var. *setiflora*
KK 1548	*M. haynei* var. *grandiflora*
KK 1549	*M. yanganucensis*
KK 1549	*M. yanganucensis* var. *grandiflora*
KK 1550	*M. cereoides*
KK 1551	*M. yanganucensis*
KK 1676**	*M. haynei* var. *grandiflora*
KK 1712	*M. blancii* var. *platygona*
KK 1748	*M. winteri*
L 117	*M. yanganucensis*
L 120	*M. winteriana*
L 166	*M. breviflora*
L 179	*M. variabilis*
L 183	*M. elongata*

L 189	*M. yanganucensis*	WK 24	*M. haynei*
L 192	*M. blancii*	WK 28	*M. variabilis*
L 199	*M. haynei*	WK 30	*M. variabilis*
L 207	*M. multicolor*	WK 31	*M. variabilis*
L 208	*M. hystrix*	WK 130	*M. yanganucensis*
L 209	*M. cereoides*	WK 132	*M. blancii*
L 232	*M. haynei* var. *Aquia*	WK 133	*M. elongata*

*This number is now *Copiapoa minima*.
**This number is now *Cleistocactus santacruzensis*.

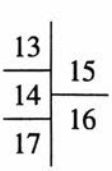
Matucana comacephala Ritter, Succulenta 37(8): 92 (1958)
CITES Cactaceae Checklist: *Matucana myriacantha*, *Matucana blancii* p.p.; comacephala = with apical tuft; Plates 2, 19 and 20.

SYNONYMS
Matucana calocephala Skarupke, Stachelpost 9: 99 (1973).
Matucana crinifera Ritter, Taxon 12(3): 125 (1963).
Borzicactus calocephalus (Skarupke) Donald, Ashingtonia 2(4) (1976).
Matucana cephalophora n.n.
Matucana lutea n.n.
Matucana luteispina n.n.
Matucana comacephala var. *lutea* n.n.
Matucana comacephala var. *luteispina* n.n.
Matucana huarinensis n.n. (Knize).
Matucana radians n.n.
Matucana sp. Pomabamba (Knize).
Matucana sp. Huari (Knize).
Matucana sp. Huari (Lau).
Matucana sp. Pomabamba Huari (Knize).

DESCRIPTION
Body grass green to grey green; first globose, later cereoid, up to 75 cm long (sometimes even longer) and 12 cm thick; seldom offsetting; no tap-root. Ribs 22-30, 4-8 mm high, tuberculate. Areoles circular to elliptical, 4-7 mm long, yellowish to pale brown, 3-10 mm apart; young areoles with white hairs. Spination dense, covering the plant, white to pale yellow, bristle-like, at the top of the plant erect like a tuft; radials 15-20, 1-5 cm long; centrals 5-10, 1-4 cm long.

Flower 5-7 cm long, in anthesis 3-4 cm wide, somewhat oblique; perianth segments mostly pink (sometimes orange red). Tube 3-5 mm wide, naked. Nectar

Plates 13-17. Forms of *Matucana haynei*
13. *M. megalantha* in habitat (Cordillera Blanca, Quebrada Santa Cruz).
14. *M. yanganucensis* in cultivation.
15. *M. herzogiana* KK 565, cultivated specimen.
16. *M. hystrix*, cultivated specimen.
17. *Matucana* sp. Pisco KK 1550, cultivated specimen.



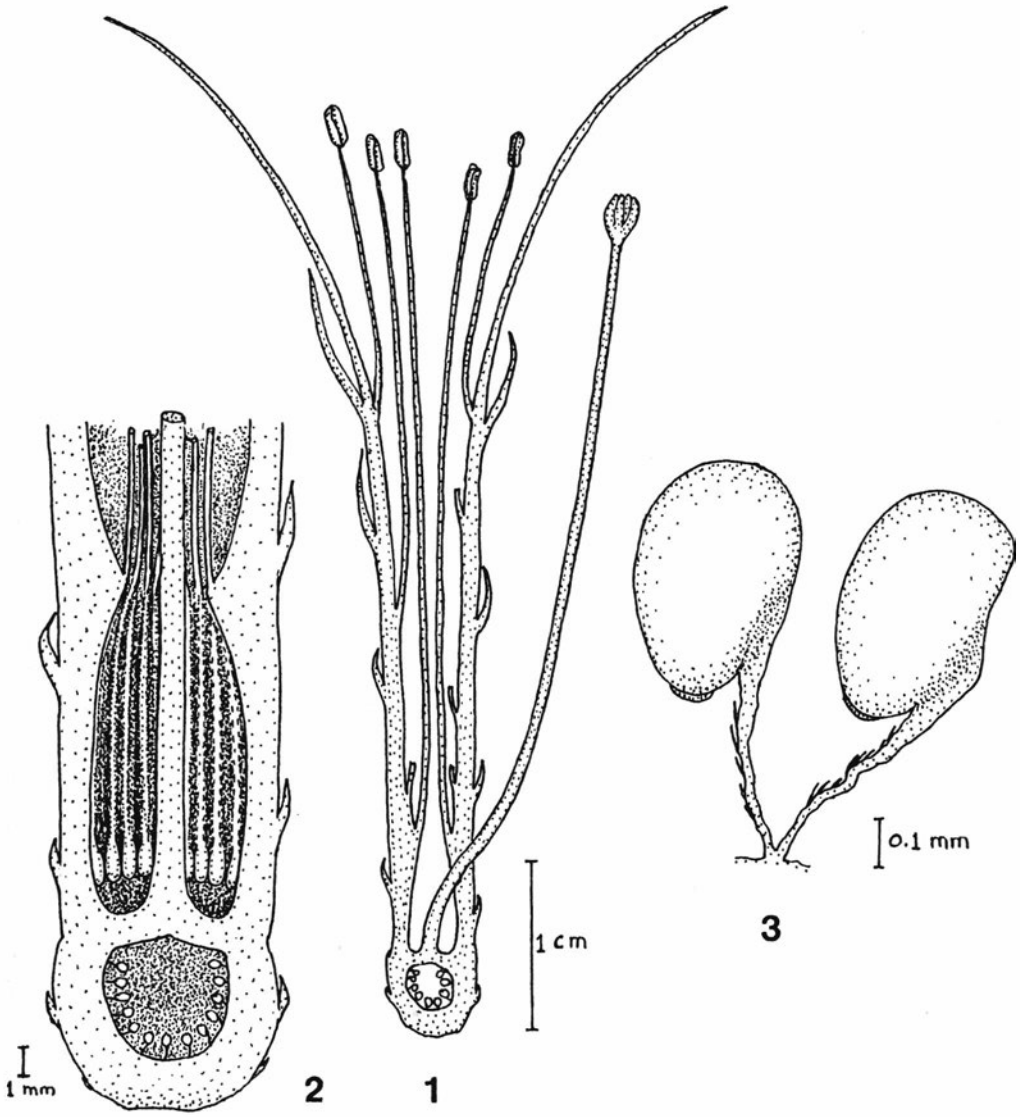


Figure 9. Flower of *Matucana comacephala* (Huari, dept. Ancash, 1986, alcohol-preserved material). 1. Flower in vertical section. 2. Id., showing long nectar chamber. 3. Id., ovules.

18	19	20
21	22	
	23	

Plates 18-23

18. *Matucana mirabilis*, possibly a hybrid between *Matucana* and *Loxanthocereus*.
19. *M. comacephala*, cultivated specimen.
20. *M. comacephala* (*M. huarinensis* KK 573), cultivated specimen.
21. *M. oreodoxa*, cultivated specimen.
22. *M. aureiflora*, cultivated specimen.
23. *M. aureiflora*, large specimen in habitat near Cajamarca.

chamber up to 10 mm long, with weakly developed diaphragm. Filaments cream to red, anthers cream to violet; primary stamens fused at their bases for 2-3 mm. Style orange to carmine, stigma lobes 5, appr. 1.5 mm long.

Fruit oval, up to 2 cm long, appr. 5 mm wide, green.

Seed as described earlier in this chapter, 1.2-2.0 mm long, 1.2-1.4 mm wide, 0.6-0.7 mm thick.

Remarks

Without flowers, this species can be recognized by the upward pointing bristle-like spines of the young areoles, although occasionally this feature is not very conspicuous. In most plants a number of radials have been transformed to white trichomes, which can reach a length of several centimeters. These features are already shown by juvenile specimens. At first glance the pink flower colour was thought to be useful as a diagnostic feature, until in 1963 Ritter described *M. crinifera* as having orange-red flowers. According to Lau (1978-1979) the type localities of *M. comacephala* and *M. crinifera* are very close. This was one of the justifications for him to conclude that both plants should be considered as belonging to one species with a variable flower colour.

There are still some anomalies about a number of flower features in this species. According to the description of *M. comacephala* by Ritter the flower is pink with a long (1 cm) nectar chamber and a diaphragm onto which the primary filaments are inserted. The flower of *M. crinifera*, on the other hand, is red, has a short (1-2 mm) nectar chamber which is also closed by a well developed diaphragm. The flower material studied by the author (*M. comacephala*, *M. crinifera* KK 577 and *M. lutea* KK 1299, all plants in cultivation) is always pink coloured, has a long nectar chamber and a weakly developed diaphragm, which is in fact only a thickening of the inner wall of the flower tube. As a consequence there is a sizeable gap between the primary filaments and the style (Figure 9.2). So the question remains whether *M. crinifera* belongs to *M. comacephala*.

In 1973 E. Skarupke described *M. calocephala*, a pink-flowering and densely spinated plant from the same region as *M. comacephala* and *M. crinifera*. This plant is practically identical to *M. comacephala* sensu Ritter.

The Knize plant *M. radians* is tentatively placed in *M. comacephala*, as for the moment it is insufficiently known.

The seeds of *M. comacephala* betray some affinity to seeds of the species that belong to the aurantiaca group. The micropyle protruding beyond the hilum, which is the main distinguishing character in the aurantiaca group, is sometimes also encountered in seeds of *M. comacephala*, although less clearly. Moreover, only a few seeds from the same fruit have exhibited this feature.

Matucana comacephala was discovered by Ritter in 1956 and described by him in 1958. The holotype is deposited in the herbarium of the 'Städtische Sukkulentensammlung' in Zürich, Switzerland.

Distribution

The type locality of *M. comacephala* is Rahuapampa, department of Ancash, Peru, which is on the eastern slope of the Cordillera Blanca. The species was found there at appr. 2800 m altitude. Probably the range of this species is further

to the east and to the north than we presently know. Perhaps it might even occur in the department of La Libertad. Unfortunately this will be very difficult to verify because the terrain is very inhospitable.

For *M. crinifera*, which is provisionally considered conspecific to *M. comacephala*, Ritter reported the habitat as Machac, department of Ancash. Skarupke gave Llamellin, deparment of Ancash for his *M. calocephala*. Knize mentioned Pomabamba as habitat for KK 1038, 1038a and 1776.

FIELD NUMBERS

FR 142a	*Matucana crinifera*
FR 587	*M. comacephala*
FR 592	*M. crinifera*
FR 592a	*M. crinifera*
FR 594	*M. comacephala*
FR 595	*M. crinifera*
KK 573	*M. huarinensis*
KK 574	*M. comacephala* var. *luteispina*
KK 577	*M. crinifera*
KK 1038	*Matucana* sp. (*supertexta* Ritt.?)
KK 1038a	*Matucana* sp. Pomabamba, Huaura
KK 1299	*M. comacephala* var. *lutea*, *M. lutea*
KK 1710	*M. radians*
KK 1711	*M. comacephala, M. carneoflora*
KK 1776*	*Matucana* sp. Pomabamba
L 184	*M. crinifera*
L 185	*M. comacephala*
WK 530	*M. crinifera*
WK 533	*M. comacephala*

*This number is now *Lobivia* sp.

Matucana oreodoxa (Ritter) Slaba, Kaktusy 22(6): 128 (1986)
CITES Cactaceae Checklist: *Matucana oreodoxa;* oreodoxa = fame of the mountains; Plates 7 and 21.

BASIONYM
Eomatucana oreodoxa Ritter, Kakteen u.a. Sukk. 16(12): 230 (1965).

SYNONYMS
Borzicactus oreodoxus (Ritter) Donald, Cact. Succ. J. (Gr. Brit.) 26(1): 10 (1971).
Matucana oreodoxa var. *turbiniformis* n.n.

DESCRIPTION
Body grass green to dark green, globose, to 80 mm wide. Plant mostly solitary with thick tap root. Ribs 7-12, strongly flattened, 3-6 mm high, with flat circular tubercles. Areoles circular to oval, 1-3 mm long, with little white felt, 8-15 mm apart. Spination flexible, straight to somewhat curved, brownish, turning grey later; radials 4-10, 1-3 cm long; centrals 1-2, 1.5-4 cm long.

Flower 4-6 cm long, in anthesis appr. 3 cm wide, slender funnelform, symmetric, perianth segments ochrous to orange-red. Tube appr. 4 mm wide with thick fleshy wall, greenish to red brown, with notably few scales, practically naked. Nectar chamber open, 8-15 mm long. Filaments white at their bases blending into red, anthers pale yellow; primary stamens absent, secondary stamens only inserted in the upper half of the floral tube, with short filaments, so that they do not reach beyond the perianth. Stigma white to pale green; stigma lobes 4-6, appr. 2 mm long, pale yellow.

Fruit oval, appr. 14 mm long, appr. 8 mm wide, pale green.

Seed as described earlier in this chapter, appr. 1.2-1.7 mm long, 1.3-1.8 mm wide, 0.8-1.0 mm thick; embryo with curved cotyledons.

REMARKS

Matucana oreodoxa is a very untypical Matucana in plant body as well as in flower features. The flower is especially unique for the genus. Morphologically it resembles somewhat the flower of *M. madisoniorum*. The flower of both species has a slender tube, and is radially symmetrical (actinomorphic) and lacks the ring of primary stamens at the base of the tube, which in the remaining *Matucana*

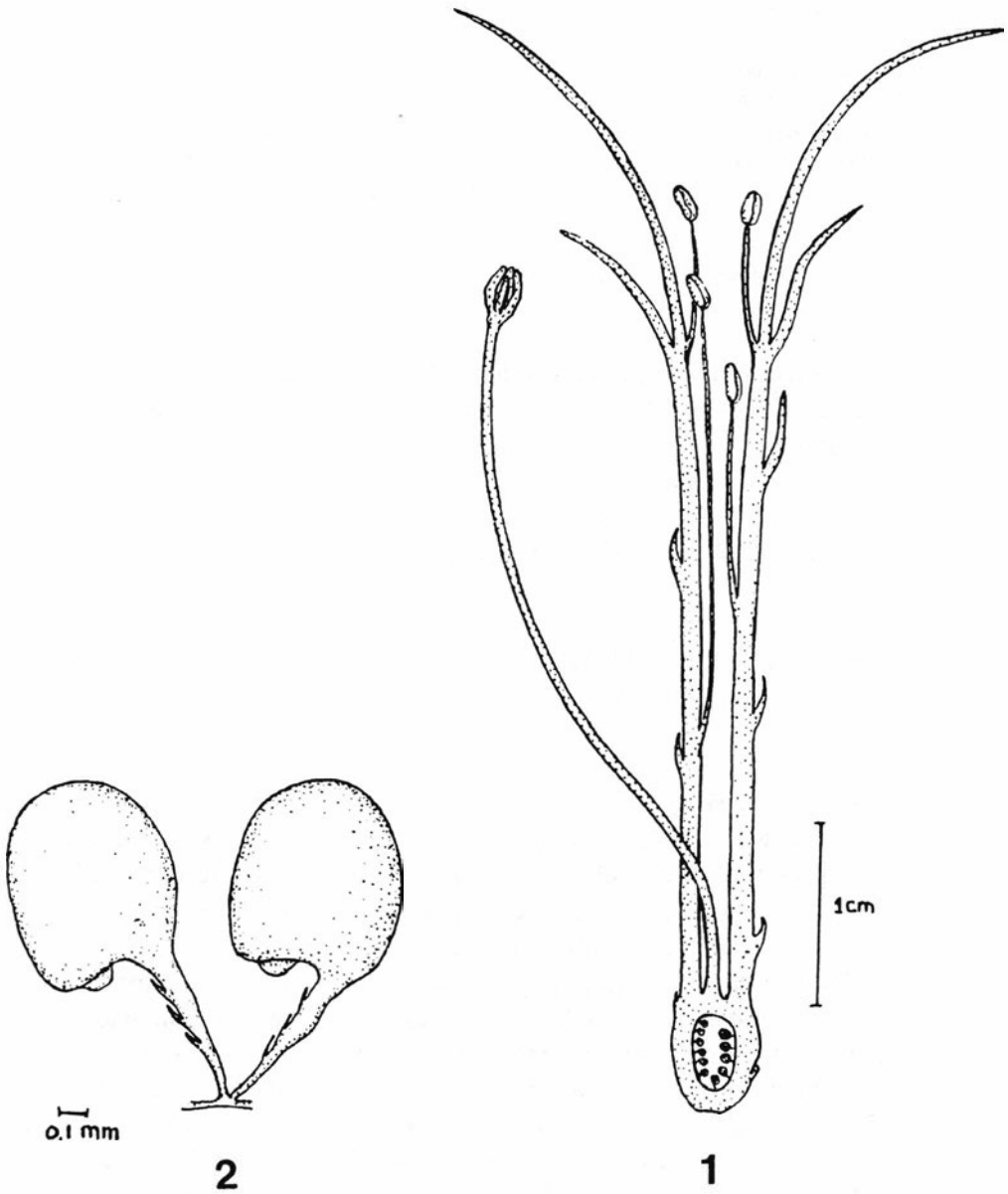


Figure 10. Flower of *Matucana oreodoxa*. 1. Flower in vertical section. 2. Ovules.

species closes the nectar chamber. Based on this similarity Ritter placed both species in a separate genus: *Eomatucana*. It has been already pointed out that this action was incorrect; seed morphology tells us that both species cannot possibly be so closely related. Despite the similarities mentioned above, a number of striking differences can be identified. The flower of *M. oreodoxa* is on the whole very fleshy, even the perianth segments, whereas the flower of *M. madisoniorum* is not so firmly constructed. Secondly, the flower of *M. oreodoxa* closes at night and opens in the morning; that of *M. madisoniorum* remains open night and day.

M. madisoniorum is surely a highly evolved species rather than an Eomatucana (= ancestral Matucana), but *M. oreodoxa* may very well be descended from an ancestral form. The plant grows in a small remote region not very far from other 'primitive' *Matucana* species and up till now no close relatives have been encountered. In addition, the embryo of *M. oreodoxa* exhibits some ancestral features: e.g. the cotyledons are more curved than in other *Matucana* species. In that respect the embryo of *M. oreodoxa* somewhat resembles *Cleistocactus*, one of the most ancestral genera within the subtribe Borzicactinae.

In evolutionary terms it is defendable to put *M. oreodoxa* in a separate genus *Eomatucana*. However, the differences in floral characteristics are insufficient to merit recognition of this taxon at the rank of genus. Fruit and seed of *M. oreodoxa* conform in every respect with *Matucana*.

Knize has caused confusion with his names *Submatucana eriodisa* KK 1591 and *S. eriodisa* var. *echinata* KK 1431. The first-mentioned plant is *M. oreodoxa*, whereas var. *echinata* is most likely a form of *M. paucicostata* (Plate 61)!

Matucana oreodoxa was discovered by Ritter in 1964 and described by him the following year. The holotype labelled FR 1311 is deposited in the herbarium of the University of Utrecht, Netherlands.

Distribution

M. oreodoxa occupies a small distribution area in the valley of the Rio Puchca, which is a tributary of the Rio Maranon. The type locality is on the slopes on both sides of the Rahuapampa canyon, Dept. Ancash, Peru. According to Ritter the elevation is 3000 m above sea level. *M. oreodoxa* seems to be rare in nature; many people have searched for it in vain. Habitats other than the type locality are unknown.

Cultivation

This species is not very easy to cultivate. On his own roots the plant will rot fairly often; therefore grafting is recommended. When grafted, the plant provides no problems if winter temperature is not below 5°C. If this temperature exceeds 10°C, the plant will flower less abundantly. In NW Europe it blooms readily in early spring, mostly with many flowers simultaneously.

Field numbers

FR 1311 *Eomatucana oreodoxa*
KK 1591 *Submatucana eriodisa*
L 273 *Eomatucana oreodoxa*

Matucana aureiflora Ritter, Kakteen u.a. Sukk. 16(12): 229 (1965)
CITES Cactaceae Checklist: *Matucana aureiflora*; aureiflora = with golden flowers; Plates 6, 22 and 23.

SYNONYMS

Submatucana aureiflora (Ritter) Backeberg, Kakteenlexikon: 459 (1966).
Borzicactus aureiflorus (Ritter) Donald, Cact. Succ. J. (Gr. Brit.) 26(1): 10 (1971).
Matucana aureiflora var. *elata* n.n.
Submatucana aureiflora var. *elata* n.n.
Submatucana aureiflora var. *incaica* n.n.
Matucana incaica n.n.
Submatucana incaica n.n.
Oroya incaica n.n. var. *aureiflora* n.n.

DESCRIPTION

Body glossy dark green, occasionally mid-green, flattened-globose, up to 13 cm wide; plant mostly solitary, with short tap root. Ribs 11-27, 3-7 mm high, very blunt with flat tubercles. Areoles oblong, 5-8 mm long, appr. 2 mm wide, with little white wool, 7-11 mm apart. Spination firm, curved, brown to black at the base, yellow to brown yellow at the top; radials 8-14, 7-18 mm long, pectinately arranged; centrals 0-4, 12-25 mm long. Young areoles sometimes exhibit the beginnings of vestigial leaves, which disappear later.

Flower 3-4.5 cm long, appr. 4 cm wide in anthesis, broadly funnelform, symmetrical, perianth segments golden. Tube at the base 3-5 mm wide, red brown with small tufts of white wool. Nectar chamber appr. 1 mm long, without nectar. Filaments yellow, anthers pale pink; primary stamens fused at their bases to create an appr. 2 mm long collar around the style. Style yellow; stigma lobes 5-7, appr. 3 mm long, pale yellow to pale green.

Fruit oval, appr. 14 mm long and 10 mm wide, purplish, greenish at the top.

Seed as described earlier in this chapter, appr. 2.0 mm long, appr. 1.3 mm wide, appr. 1.0 mm thick, often with a very long hilum.

REMARKS

Like *M. oreodoxa*, *M. aureiflora* is different from the typical Matucana in flower and plant body. Here again, one may suggest that this species is a 'relict species', which has remotely developed for a long period of time. Considering the resemblance with *Oroya* it could also be possible that *M. aureiflora* is a descendant of a transitional form between *Matucana* and *Oroya*. To resolve this problem further investigation is needed.

Indeed, the spination makes this plant look like an Oroya. The flower is also very atypical for *Matucana*, it more resembles the flower of a Lobivia or a Mila.

Because of the deviating flower, Ritter introduced for this species the subgenus *Incaia* (at first erroneously spelled 'Incaica'). This is one step lower in rank than *Eomatucana*, which was described as a genus to include only those Matucanas without a diaphragm in the flower. Apparently Ritter ascribed a high taxonomic value to the absence of the diaphragm. In *M. aureiflora* the diaphragm is

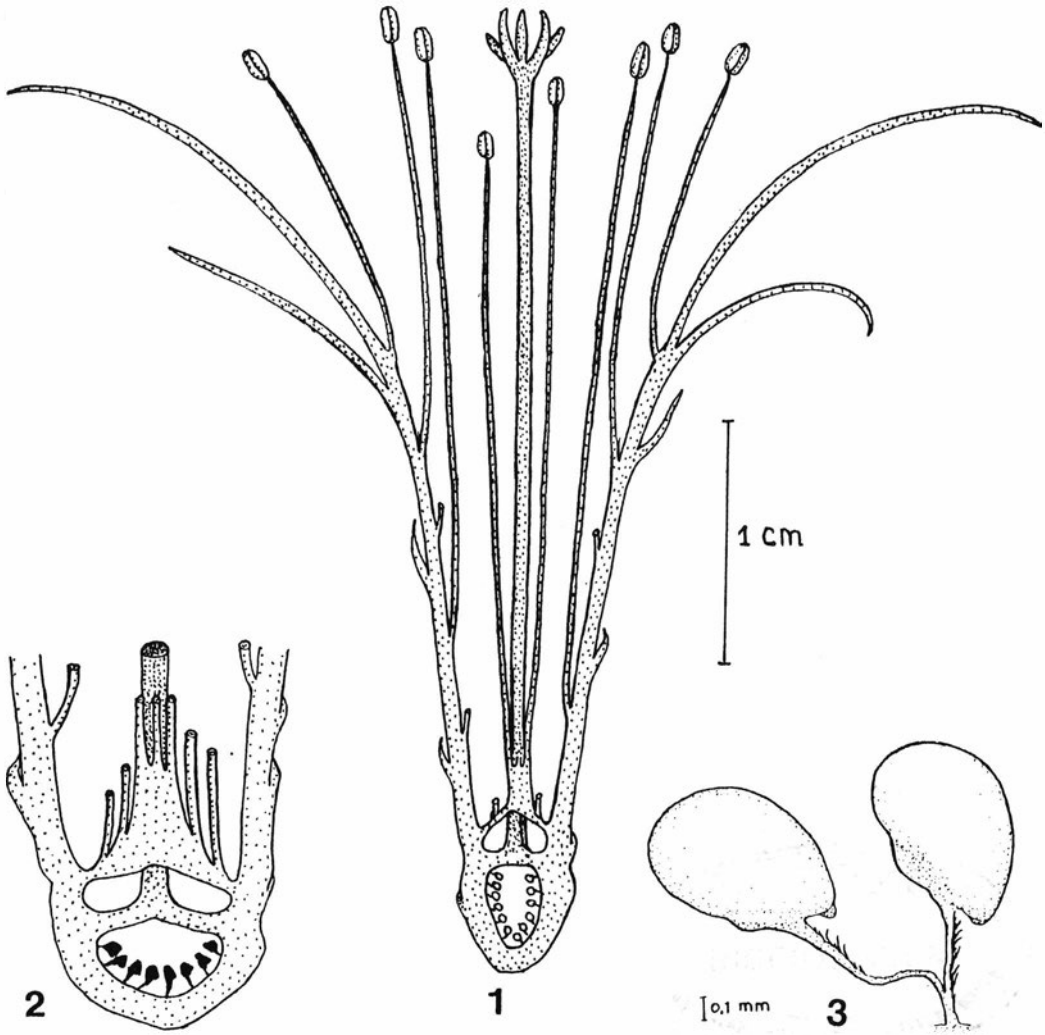


Figure 11. Flower of *Matucana aureiflora* (Cajamarca, 1982). 1. Flower in vertical section. 2. Detail of flower showing diaphragm. 3. Ovules.

present but functionless, since no nectar is produced. Ritter stated that this species is pollinated by pollen collecting bees, not by nectar-sucking hummingbirds, as is the case in all other *Matucana* species. This seems to be a plausible explanation for the disappearance of the red flower colour; the colour red is more noticeable to birds than to bees.

M. aureiflora was discovered by Ritter in 1964 and described by him in 1965. The holotype is deposited in the herbarium of the University of Utrecht, Netherlands.

Distribution

M. aureiflora is only known from the direct vicinity of the city of Cajamarca. The type locality is Banos del Inca, near Cajamarca city, dept. Cajamarca, Peru. Consequently, *M. aureiflora* is the northernmost occurring species of the haynei group. In the same area, populations of *M. aurantiaca* occur, too, which may have

a lot to do with the statement by Ritter that *M. aureiflora* is closely related to *M. aurantiaca*. Often, as in this case, the link between a close habitat and a close relationship is stated too readily. In the case of *M. aureiflora* and *M. aurantiaca* there is probably no direct relationship, not only by virtue of their distinctly different characteristics, but also because of the ecological differerence. *M. aureiflora* is found on grassy slopes with a mineral substrate. On the other hand, the plants of *M. aurantiaca* that occur near Cajamarca (given this species has a far wider distribution), grow between rocks where humus has accumulated. This difference in soil preference is displayed by the root system: *M. aureiflora* has a tap root, *M. aurantiaca* has a superficial and finely branched root system.

Cultivation

M. aureiflora is easy to cultivate. The plant requires lots of fresh air and can be cultivated succesfully outside in a sunny spot, as long as the temperature does not drop below zero and the plant is kept dry in winter until the floral buds appear. Sometimes complaints are heard about its poor blooming. The plants do not usually flower when young, but adult specimens should flower normally, which takes place in late spring to early summer.

Field numbers

FR 1310 *Matucana aureiflora*
KK 776 *Submatucana aureiflora* var.
KK 777 *S. aureiflora*
KK 1315 *S. aureiflora* var. *elata*
L 104 *S. aureiflora*
WK 124 *Matucana aureiflora*

CHAPTER 9

The aurantiaca group

This species group contains a number of collectors plants which are easy to grow and flower readily. Many species are very popular. In many collections they are still labelled as *Submatucana* because most plants produce flowers with a hairy tube. The group is named after the best-known species *Matucana aurantiaca*.

9.1 TAXONOMY

Many names and field numbers are given to plants that belong to this group. Here it is also evident that many epithets are just names and not species, apparently as a result of the great variability in spination and flower. The seeds, on the other hand, are very similar; they all possess the remarkably enlarged micropylar stump that reaches beyond the hilum cup, as was already discussed in Chapter 6. As they have this feature, the following taxa belong to the aurantiaca group:

Matucana aurantiaca	*M. aurantiaca* var. *densispina* n.n.
M. calvescens	*M. bagalaensis* n.n.
M. fruticosa	*Submatucana calvescens* var. *seminuda* n.n.
M. hastifera	*S. grandiflora* n.n.
M. pallarensis	*S. grandiflora* var. *albispina* n.n.
M. polzii	*S. grandiflora* var. *densispina* n.n.
M. ritteri	*S. intermedia* n.n.
M. weberbaueri	*Matucana variicolor* n.n.
M. weberbaueri var. *flammea*	

These plants can be characterized as follows:

Body bright green to dark green, epidermis smooth; moderately to strongly offsetting. Ribs 10-30, more or less resolved into tubercles. Spination needle-like, yellowish to dark brown.

Flower yellow to red; nectar chamber closed by a diaphragm formed by the fused bases of the primary filaments.

Seed dull black, longer than wide, with few irregular cuticular remnants, dorsally and ventrally little or not extended. Seed surface with irregular grooves and

humps. Cuticle strongly folded. Funicular tissue well developed, micropyle reaching beyond the hilum cup. Embryo somewhat curved.

From the taxa listed above the following six species can be selected:

1. *M. aurantiaca*
2. *M. fruticosa*
3. *M. ritteri*
4. *M. hastifera*
5. *M. weberbaueri*
6. *M. polzii.*

M. aurantiaca and *M. weberbaueri* have already been known since the beginning of this century, both originally classified in *Echinocactus*. Not until the 1950s were a number of new species described in this group, predominantly as a consequence of the collecting activities of Friedrich Ritter. These species were *M. ritteri*, *M. fruticosa*, *M. currundayensis* and *M. calvescens*. In 1981 *M. hastifera* and *M. pallarensis* followed, and finally in 1986 *M. polzii*.

The Ritter species *M. currundayensis* (Plate 26) and the invalid names *M. bagalaensis* (Plate 27) and *M. variicolor* (Plate 28) are so much like *M. aurantiaca* that these plants do not deserve a distinct taxonomic rank, not even that of variety. The same applies to *M. calvescens* (Plates 29 and 30), described as *Borzicactus calvescens* by Kimnach and Hutchison in 1957. These authors listed the differences of this taxon to *M. aurantiaca* in a table, but these are so minimal that no clear separation can be traced.

M. fruticosa (Plate 36) and *M. hastifera* (Plates 40 and 41), both discovered by Ritter, are plants that are conspicuously identifiable by their characteristically elongated plant bodies. On the other hand, they resemble *M. aurantiaca* so much in flower, fruit and seed that in the future possibly these taxa should be treated as subspecies or varieties of *M. aurantiaca.* Regrettably, very little is known about *M. hastifera* and, here also, further data is needed.

M. weberbaueri (Plates 38 and 39) is a story on its own. Something on this subject is mentioned in Section 9.6. The true *M. weberbaueri* blooms with lemon-yellow flowers. Plants with a similar habit but with orange flowers were found by Lau and described by Donald as *Borzicactus weberbaueri* var. *flammea*. However, the flower colour is really the only feature of this plant that is different from *M. weberbaueri*, so the rank of this plant has been lowered from variety to form (Bregman et al. 1986-1990).

M. pallarensis (Plate 31) is a southern form of *M. aurantiaca*. According to Ritter, this plant is densely spinated and has a yellow flower. In cultivated specimens, raised from habitat collected seed, these features do not appear to be stable. Therefore until further notice this taxon is considered as a synonym of *M. aurantiaca*.

M. pallarensis may be an intermediate between *M. weberbaueri* and *M. aurantiaca*, because it combines features of the former (dense spination, yellow flower) and the latter (thick flower tube).

M. polzii (Plates 4 and 37) is an interesting species in that it produces lots of offsets. These detach easily and therefore the plant is already widely spread amongst hobbyists. It is a recently described species, on which not very much information is available yet.

The position of the Knize discoveries *Submatucana grandiflora* (Plate 32) and its varieties *albispina* (Plate 33) and *densispina*, all unvalid names, is equivocal

because these plants are insufficiently known. Awaiting further data these plants have been scheduled as synonyms of *M. aurantiaca* because the seeds have a protruding micropyle. The flower, however, is more like that of *M. intertexta.*

9.2 PHYLOGENY

The aurantiaca group on the whole probably has a close affinity with the northernmost occurring taxa of the haynei group (*M. winteri*, *M. yanganucensis*).

On floral and seed morphology the aurantiaca group can be divided into two subgroups. The first species group is composed of *M. aurantiaca, M. fruticosa, M. hastifera* and *M. polzii*, all species with a broad and firm floral tube, usually yellow at the base with red perianth segments and relatively large seeds. The second subgroup contains *M. ritteri* and *M. weberbaueri*, which are distinct from the first subgroup by their slender flowers and smaller seeds.

9.3 SEED MORPHOLOGY

The seeds of the species of the aurantiaca group are defined by their protruding micropyle (see Chapter 6). This feature can sometimes be encountered in a few species of the haynei group, but it is less well developed, so here there seems to be a transitional situation. For example, a minority of the seeds inside a fruit of *M. aureiflora* and *M. comacephala* were found to also exhibit a weakly protruding micropyle. To conclude, this remarkable feature has probably developed in the areas of overlap of the haynei and the aurantiaca groups, and has for a reason yet to be explained, become regularly identifiable in the latter.

As to the remaining seed features the aurantiaca group is close to the haynei group. The hilum cup is entirely covered by funicular tissue, which is also the case for the haynei group. In the other groups, i.e. the intertexta and the paucicostata groups, there are one or two holes in this tissue.

The seeds of the 6 species recognized here are morphologically very similar. The size is the only seed feature that varies: *M. fruticosa* has the largest seeds, *M. ritteri* and *M. weberbaueri* the smallest ones.

9.4 DISTRIBUTION

The distribution of the species of the aurantiaca group is shown in Figure 12.

M. aurantiaca covers a large area. This species reaches from Huancabamba (Department of Piura) in the north, to Santiago de Chuco and El Pallar (Department of La Libertad) in the south, which is a distance of roughly 400 km. It is thus not surprising that *M. aurantiaca* is very variable. Furthermore, this species is often quite abundant. The other 5 species are in fact only known from their type localities and their direct surrounding areas.

M. hastifera and *M. polzii*, coming from the Departments of Ancash and Huanuco respectively, are the southernmost representatives of the aurantiaca

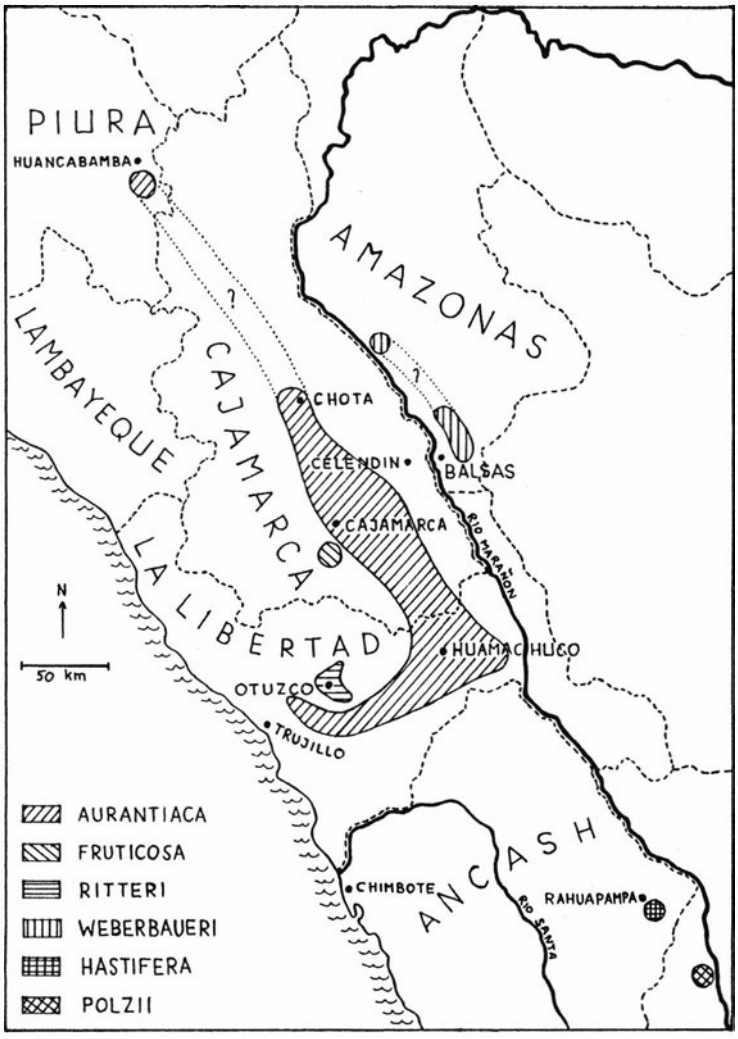


Figure 12. Distribution of the species of the aurantiaca group. Dotted lines and question mark indicate probable distribution.

group. *M. weberbaueri* is the only species of this group to occur east of the Rio Maranon. The most westerly occurring species is *M. ritteri* near Otuzco (Department of La Libertad). Between the localities of *M. aurantiaca* and the southern species *M. hastifera* and *M. polzii* there is a large area for which no data is available, probably due to the absence of roads. It is suspected that the eastern slope of the Cordillera Blanca constitutes a connection between the taxa mentioned. From this remote area only *Matucana* sp. Pomabamba (KK 1038 and 1776 from Knize) have been recorded. These plants, however, are definitely forms of *M. comacephala* and thus belong to the haynei group.

There are some Matucanas that are borderline cases between the aurantiaca and the haynei groups and are therefore difficult to place in either group, because they seem to occupy an intermediate position. Such plants are the forms of *M. yanganucensis* from the northern Rio Santa valley and *M. winteri* from the area near Santiago de Chuco. Their seeds show a weakly protruding micropyle indicative of the first phase of development of this feature. The same was observed in

seeds of *M. oreodoxa*. This plant comes from Huari which lies at the eastern border zone between the two groups mentioned.

Generally speaking, the species of the aurantiaca group occur at higher elevations than do those of the intertexta and paucicostata groups. This is also a point in favour of a close affinity between the aurantiaca group and the haynei group rather than with the intertexta and paucicostata groups.

9.5 KEY TO THE SPECIES OF THE AURANTIACA GROUP

1a. Flower lemon-yellow, shorter than 60 mm ..... *weberbaueri*
1b. Flower golden to red, 50-90 mm long 2
2a. Spines robust (to 70 mm long); all outer perianth segments strongly curved backward *hastifera*
2b. Spines less robust (short stiff to long flexible); only lower perianth segments curved backward 3
3a. Plant slender cereoid (to 6 cm across) ..... *fruticosa*
3b. Plant broadly cereoid to globose (to 12 cm across) 4
4a. Floral tube appr. 4 mm wide; centrals brown-black ..... *ritteri*
4b. Floral tube appr. 5-12 mm wide; centrals yellowish to brownish 5
5a. Plant extremely offsetting from the lateral areoles ..... *polzii*
5b. Plant solitary or weakly offsetting from the base 6
6a. Flower up to 60 mm long, tube to 8 mm wide 7
6b. Flower 70-90 mm long, tube 8-10 mm wide ..... *aurantiaca*
7a. Flower golden-orange, tube naked ..... *weberbaueri* f. *flammea*
7b. Flower red, tube mostly pubescent ..... *aurantiaca*

9.6 THE SPECIES OF THE AURANTIACA GROUP

Matucana aurantiaca (Vaupel) Buxbaum, in: Krainz, Die Kakteen 1.IX (1973)
CITES Cactaceae Checklist: *Matucana aurantiaca*, *Matucana currundayensis*, *Matucana pallarensis*; aurantiaca = flowering orange; Plates 24-33.

BASIONYM
Echinocactus aurantiacus Vaupel, Bot. Jahrb. Engler 50 Beibl. 111: 23 (1913).

SYNONYMS
Arequipa aurantiaca (Vaupel) Werdermann, Kakteenkunde 5: 77 (1939).
Borzicactus aurantiacus (Vaupel) Kimnach & Hutchison, Cact. Succ. J. (USA) 29(2): 46 (1957).
Submatucana aurantiaca (Vaupel) Backeberg, Die Cactaceae 2: 1061 (1959).
Borzicactus calvescens Kimnach & Hutchison, Cact. Succ. J. (USA) 29(4): 111 (1957).
Borzicactus aurantiacus var. *calvescens* (Kimnach & Hutchison) Donald, Cact. Succ. J. (Gr. Brit.) 26(1): 10 (1971).
Submatucana calvescens (Kimnach & Hutchison) Backeberg, Die Cactaceae 2: 1061 (1959).
Matucana calvescens (Kimnach & Hutchison) Buxbaum, in: Krainz, Die Kakteen 1.IX (1973).

Submatucana calvescens var. *seminuda* n.n.
Matucana aurantiaca var. *densispina* n.n.
Submatucana aurantiaca var. *densispina* n.n.
Matucana currundayensis Ritter, *Succulenta* 37(12): 139 (1958).
Submatucana currundayensis (Ritter) Backeberg n.n.
Matucana currundayii n.n.
Matucana pallarensis Ritter, Kakteen in Südamerika 4: 1501 (1981).
Matucana variicolor n.n.
Matucana weberbaueri var. *pallarensis* n.n.
Submatucana bagalaensis n.n.
Submatucana grandiflora n.n.
Submatucana grandiflora var. *albispina* n.n.
Submatucana grandiflora var. *densispina* n.n.
Submatucana catamarcensis n.n.
Submatucana nivosa n.n.
Submatucana calmada n.n.
Submatucana sp. Cajamarca n.n.

DESCRIPTION

Body freshly green to dark green; globose to broadly cylindrical, up to 35 cm long and 15 cm wide; offsetting little at the base in general; root system superficial, strongly branched without tap root. Ribs 13-17, broad, straight, with transverse grooves that divide the rib more or less clearly into hexagonal tubercles. Areoles oval, 5-10 mm long, 3-5 mm wide, with white to grey felt, 10-15 mm apart. Spination very variable in colour and length, mostly ochrous to dark brown, turning grey later, straight; radials 12-20, 5-40 mm long; centrals appr. 9, 20-70 mm long.

Flower 7-9 cm long, in anthesis 5-7 cm wide, little oblique to straight; perianth segments orange-yellow to red, margin sometimes violet. Tube 8-10 mm wide, greenish to orange-red, with whitish to brownish pubescence, sometimes naked. Nectar chamber appr. 6 mm long, closed by a pink diaphragm. Filaments white at the base, blending to violet at the top, anthers pale yellow; primary filaments fused at the base over 1-5 mm. Style white at the base blending to pink at the top, stigma lobes 6-7, 2-3 mm long, olive.

Fruit globose, up to 20 mm across, green.

Seed as described earlier in this chapter, 1.3-2.2 mm long, appr. 1.5 mm wide and 0.8 mm thick.

M. pallarensis (Plate 31) is a southern form of *M. aurantiaca*. It differs, according to the original diagnosis by Ritter, in the following features (translated from the original German text):

Ribs appr. 21; spination in general more dense (about 40 spines per areole), yellow to brown-yellow, 8-25 mm long, areoles closer to each other than in *M. aurantiaca.*

The differences mentioned turn out not to be constant. In other words, aurantiaca-like plants also grow from pallarensis seed. Awaiting further field data *M. pallarensis* is considered to be synonymous with *M. aurantiaca.*

REMARKS

The typical aurantiaca flower (a wide, robust, yellowish floral tube with red perianth) is dominant in the northern populations, a.o. from the area of Chota (Department of Cajamarca). In other localities slightly deviating flower forms may be encountered. Southern populations consist of plants with an entirely red flower.

There is still confusion about how far north *M. aurantiaca* has actually reached. According to Backeberg Matucanas from the Huancabamba region near Sondor (Department of Piura) should possess a woolly ring (modified stamens) inside the floral tube, a characteristic that has never been observed in any Matucana by the author. This locality had been mentioned by Blossfeld, who collected there in 1940. His material does not exist anymore. However, progeny is still in cultivation and Kimnach and Hutchison used it in 1957 as the basis for their description of *Borzicactus aurantiacus*. But it is strange that after Blossfeld nobody has ever re-located *M. aurantiaca* near Sondor. This locality is approximately 200 km north of Chota. Moreover, between Chota and Sondor *M. aurantiaca* has never been found. Bearing in mind that the woolly ring in the floral tube is a common feature in the genus *Borzicactus* s.s., a genus from the Ecuador-Peruvian border and also occurring near Sondor, two still unanswered questions remain:

1. Did Backeberg indeed talk about a Matucana or did he in fact have a Borzicactus in front of him, or perhaps a natural hybrid?

2. Did the plants that Kimnach and Hutchison based their description of *B. aurantiacus* on, really come from Sondor?

In the neighbourhood of the city of Cajamarca grows a densely spinated form of *M. aurantiaca* (Plates 10 and 24), Ritter's variety *densispina*, a taxon which has never been formally described. In two populations of this taxon a comparitively small and slender flower that was red all over was encountered. It is uncertain whether this flower type is also present in all members of these populations, and whether it is also present in other populations. Unfortunately, at the time of visiting the site, only one flowering specimen could be found. These plants were in fact not always as densely spined as Ritter claimed; i.e. specimens with 'normal' spination were growing there also.

M. calvescens (Plates 29 and 30) from the area near the town of Huamachuco represents the southernmost populations of *M. aurantiaca*. Its flower is red all over too, but the tube is much wider than in the plants from Cajamarca. An exceptional occasion was the finding of an almost yellow flowering specimen. Donald and Ritter pointed out the little differences between *M. calvescens* and *M. aurantiaca*, which made them decide to treat both taxa as conspecific.

M. currundayensis (Plate 26), a Ritter plant, is also too similar to *M. aurantiaca* to recognize it as a good species. The same applies to *M. bagalaensis* (Plate 27) and *M. variicolor* (Plate 28), both *nomina nuda*. *M. grandiflora* and *M. grandiflora* var. *albispina* (Plate 33) are Knize names; these plants have in general a weaker spination and a more orange flower than the typical *M. aurantiaca*. Both taxa have been brought into circulation under the same field number.

M. aurantiaca is a common species that frequently occurs in nature. It usually grows on rocky slopes where organic material is able to accumulate in crevices and furrows between the rocks. It is also found on grassy hills. The plants root su-

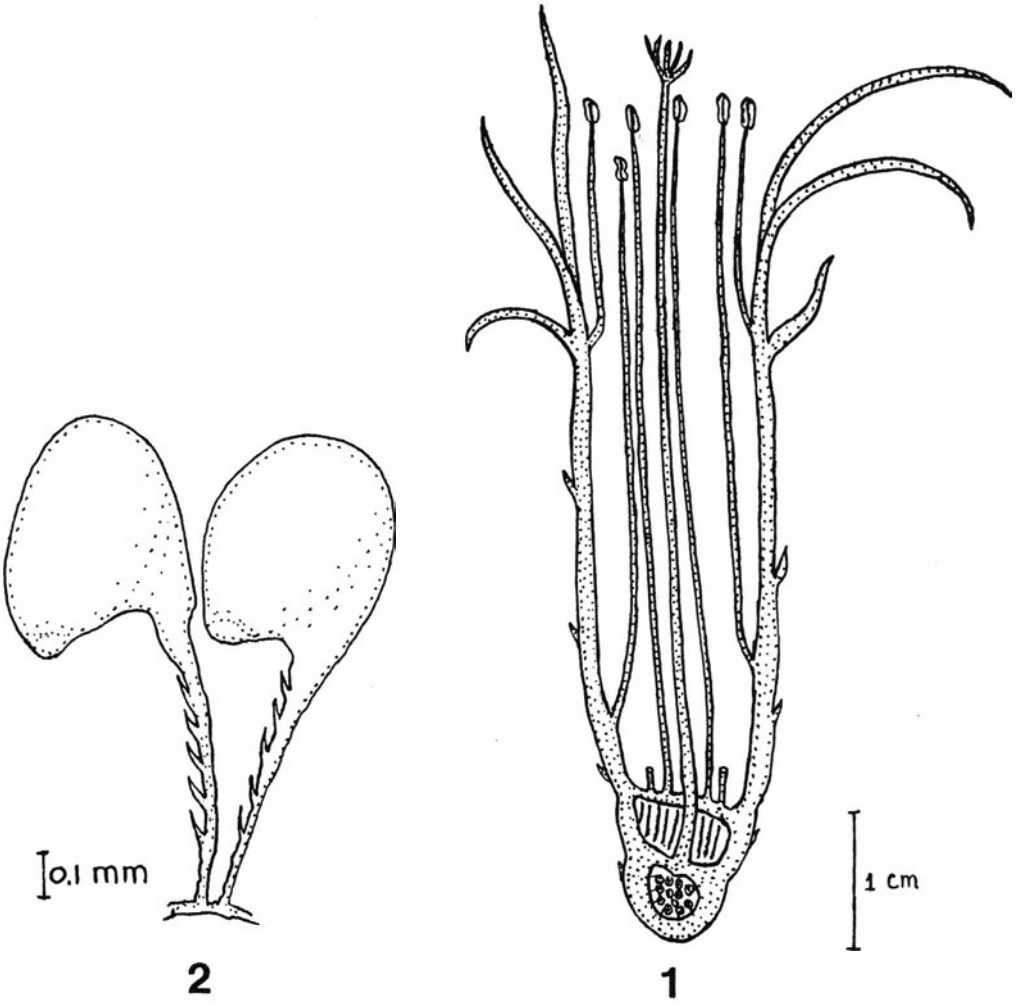


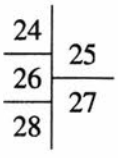
Figure 13. Flower of *Matucana aurantiaca.* 1. *M. calvescens* (Huamachuco), vertical section of the flower. 2. Id., ovules with remarkably long funicles.

perficially because the humus layer is mostly rather shallow. Near Huamachuco the plants seem to be less choosy about their habitat; there they grow almost anywhere, not only on rocky slopes with other low vegetation but also in the shade of Eucalyptus plantations with their roots almost in the water of streams.

M. aurantiaca flowers very easily, but only when the plant has reached a reasonable size. It does not flower as a young plant. Usually a ring of flowers around

Plates 24-28. Forms of *Matucana aurantiaca*

24. *M. aurantiaca* in habitat near Cajamarca; form with a relatively small crimson flower.
25. *M. aurantiaca* in cultivation.
26. *M. currundayensis* in cultivation.
27. *M. bagalaensis*, cultivated specimen.
28. *M. variicolor*, cultivated specimen.



the growing point is produced. In NW Europe the flowering periods are in spring (May) and late summer (August-October).

The original type material, deposited by Weberbauer in the herbarium of the University of Berlin, Germany, was lost during the Second World War. A new type specimen should be collected, preferably at the original type locality.

DISTRIBUTION

The total area of distribution of *M. aurantiaca* is rather large. This species stretches from Huancabamba (Department of Piura) in the north to Santiago de Chuco and El Pallar (Department of La Libertad) in the south. The type locality is near San Pablo, Department of Cajamarca, Peru. The vertical distribution is between 2000 and 3700 m altitude.

FIELD NUMBERS

Blossf. 96	*Echinocactus aurantiacus*	KK 1902	*S. calmada*
DM 23	*Matucana calvescens*	KK 1903	*S. cajamarcensis*
DM 40	*M. currundayensis*	KK 1904	*S. nivosa*
DM 63	*M. pallarensis*	KK 1952	*S. subterranea*
FR 164	*M. currundayensis*	L 115	*S. calvescens*
FR 596	*M. aurantiaca*	L 118	*S. aurantiaca* var. *densispina*
FR 596a	*M. aurantiaca* var. *densispina*	L 171	*S. currundayensis*
FR 1076	*M. pallarensis*	L 172	*S. calvescens*
KK 455	*Submatucana aurantiaca*	L 177	*S. aurantiaca*
KK 576	*S. grandiflora*	L 225	*S. pallarensis*
KK 576	*S. grandiflora* var. *albispina*	UCBG 53486	*Borzicactus aurantiacus*
KK 729	*S. currundayensis*	UCBG 371101	*B. calvescens*
KK 753	*S. calvescens*	Weberb. 3846	*Echinocactus aurantiacus*
KK 778	*S. calvescens* var. *seminuda*	Weberb. 4222	*E. aurantiacus*
KK 1470	*S. calvescens* var. *seminuda*	WK 123	*Matucana aurantiaca*
KK 1901	*Submatucana* sp.		

Matucana fruticosa Ritter, Succulenta 45(8): 117 (1966)
CITES Cactaceae Checklist: *Matucana fruticosa*; fruticosa = bushy; Plate 36.

SYNONYM

Borzicactus fruticosus (Ritter) Donald, Cact. Succ. J. (Gr. Brit.) 26(1): 10 (1971).

DESCRIPTION

Body grass green, cereoid, 10-50 cm long, 3-6 cm wide; strongly offsetting mostly from the base, thus forming multi-headed groups up to 1 m across; no tap

29 30 31 32 33

Plates 29-33. Forms of *Matucana aurantiaca*
29. *M. calvescens* near Huamachuco; form with a thick floral tube.
30. *M. calvescens* near Huamachuco; the only yellow-flowering specimen of a red-flowering population.
31. *M. pallarensis*, cultivated specimen.
32. *M. grandiflora*, natural specimen in cultivation.
33. *Submatucana grandiflora* var. *albispina* KK 576, cultivated specimen.

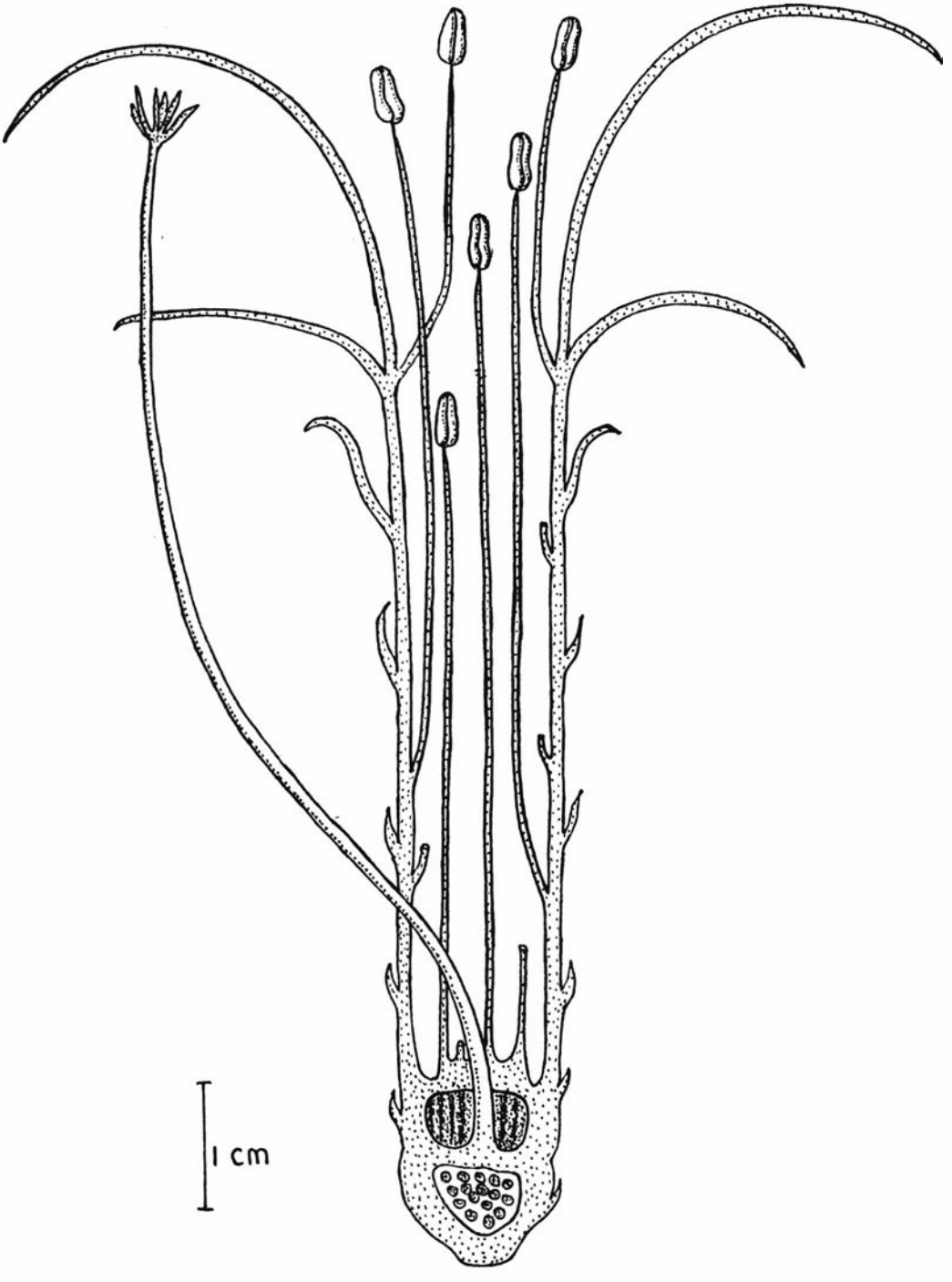


Figure 14. Flower of *Matucana fruticosa*. Flower in vertical section.

root. Ribs 10-21, straight, with transverse grooves. Areoles oval, 2-3 mm long, white, 5-10 mm apart. Spination straight, needle-like, yellow to brown, turning grey in later life; radials 5-10, 8-60 mm long.

Flower 7-9 cm long, in anthesis 4-5 cm wide, a little oblique to straight; perianth segments golden at the base blending to carmine. Tube 6-10 mm wide,

brown-green to yellow, with grey to black hairs. Nectar chamber 3-5 mm long, closed by a white to pink diaphragm. Filaments white at their bases blending to red, anthers yellow; primary filaments fused at their bases over 1.5 mm forming a collar around the style. Style yellow to reddish; stigma lobes 5, appr. 2 mm long, greenish.

Fruit globular with vertical ribs, 10-15 mm across, green, yellowish when over-ripe.

Seed as described earlier in this chapter, appr. 2 mm long and wide, appr. 1 mm thick.

REMARKS

This species is distinct for its conspicuous growth habit. As to flower, fruit and seed features though, it is identical to *M. aurantiaca.*

There seem to be two forms of *M. fruticosa* in cultivation: plants with firm erect stems and plants with weaker stems that bend after some time. The first-mentioned form is the original one, the second has shown up in the 1970s. The origin of the latter is not known.

M. fruticosa is easy to cultivate, although the number of flowers per stem is mostly low (1 to 3). In NW Europe the flowering period is in late summer (August to October).

M. fruticosa was found by Ritter in 1964. He described the species two years later. The holotype is deposited in the herbarium of the University of Utrecht, Netherlands.

DISTRIBUTION

M. fruticosa comes from San Juan, Department of Cajamarca, Peru. The species is only known from the type locality.

FIELD NUMBER

FR 1307 *Matucana fruticosa*

Matucana ritteri Buining, Succulenta 38(1): 2 (1959)

CITES Cactaceae Checklist: *Matucana ritteri*; ritteri = named after F. Ritter; Plates 34 and 35.

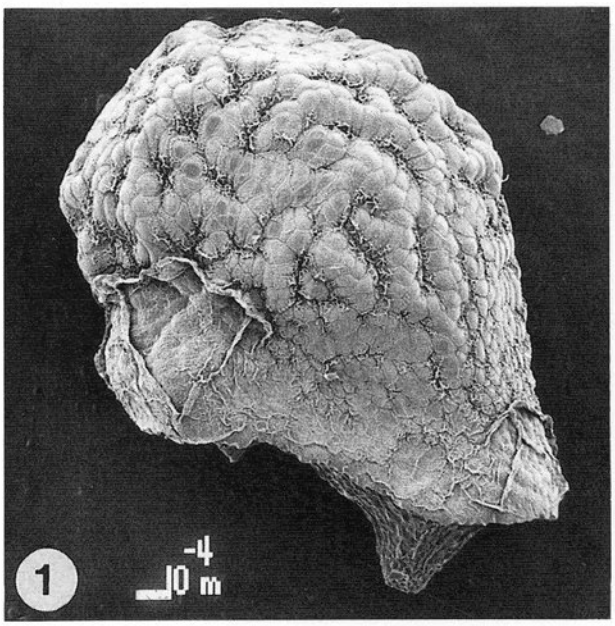
SYNONYMS

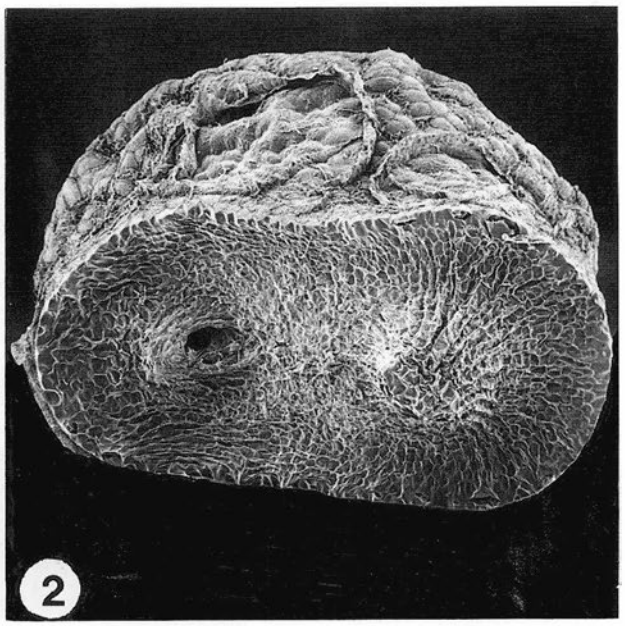
Borzicactus ritteri (Buining) Donald, Cact. Succ. J. (Gr. Brit.) 26(1): 10 (1971).
Submatucana ritteri (Buining) Backeberg.
Submatucana ritteri fa. Agallpampa n.n.

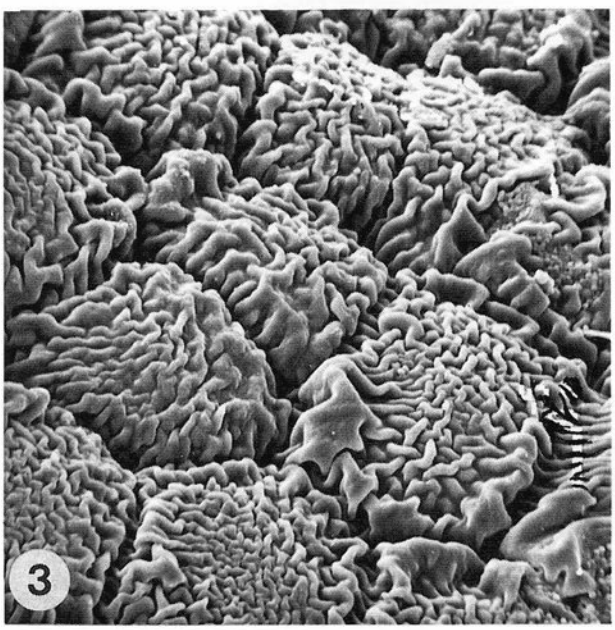
DESCRIPTION

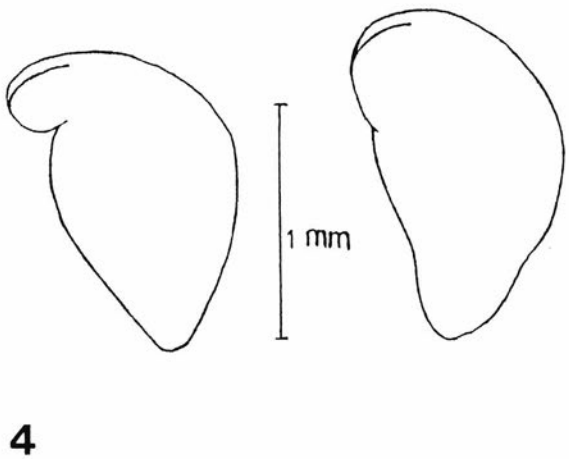
Body glossy dark green, flattened-globose, 3-5 cm tall (in cultivation taller), 5-10 cm wide; hardly offsetting from the base. Weakly developed tap root. Ribs 12-22, appr. 10 mm wide, blunt. Areoles oval, 5-10 mm long, 3-6 mm wide, with grey felt, 10-20 mm apart. Spination brownish black when young, turning grey later,

Figure 15. Flower *Matucana ritteri*. 1. Flower in vertical section. 2. Ovules.

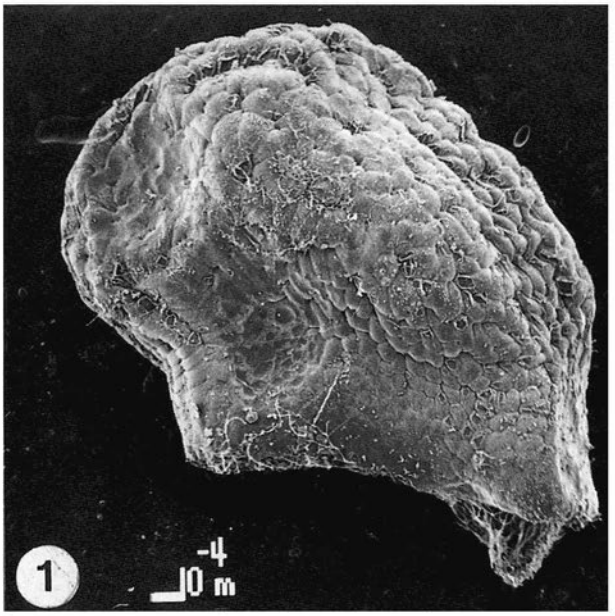


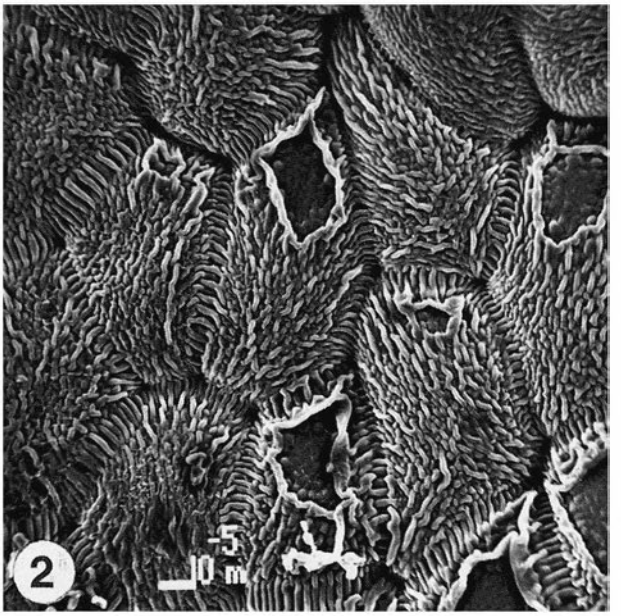


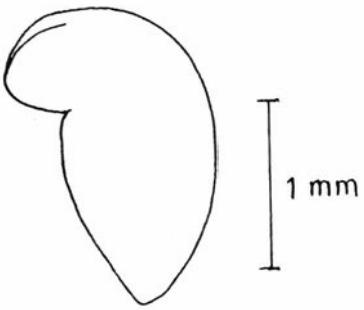




Photograph 12. Seed of *Matucana aurantiaca*. 1. *M. currundayensis* (Köhres 1983), seed in lateral view; 45×. 2. Id., hilum; 60×. 3. *M. aurantiaca* (Cajamarca, 1982), testa in lateral region; 875×. 4. Embryos of *M. calvescens* (Huamachuco) left and *M. aurantiaca* (Cajamarca) right.

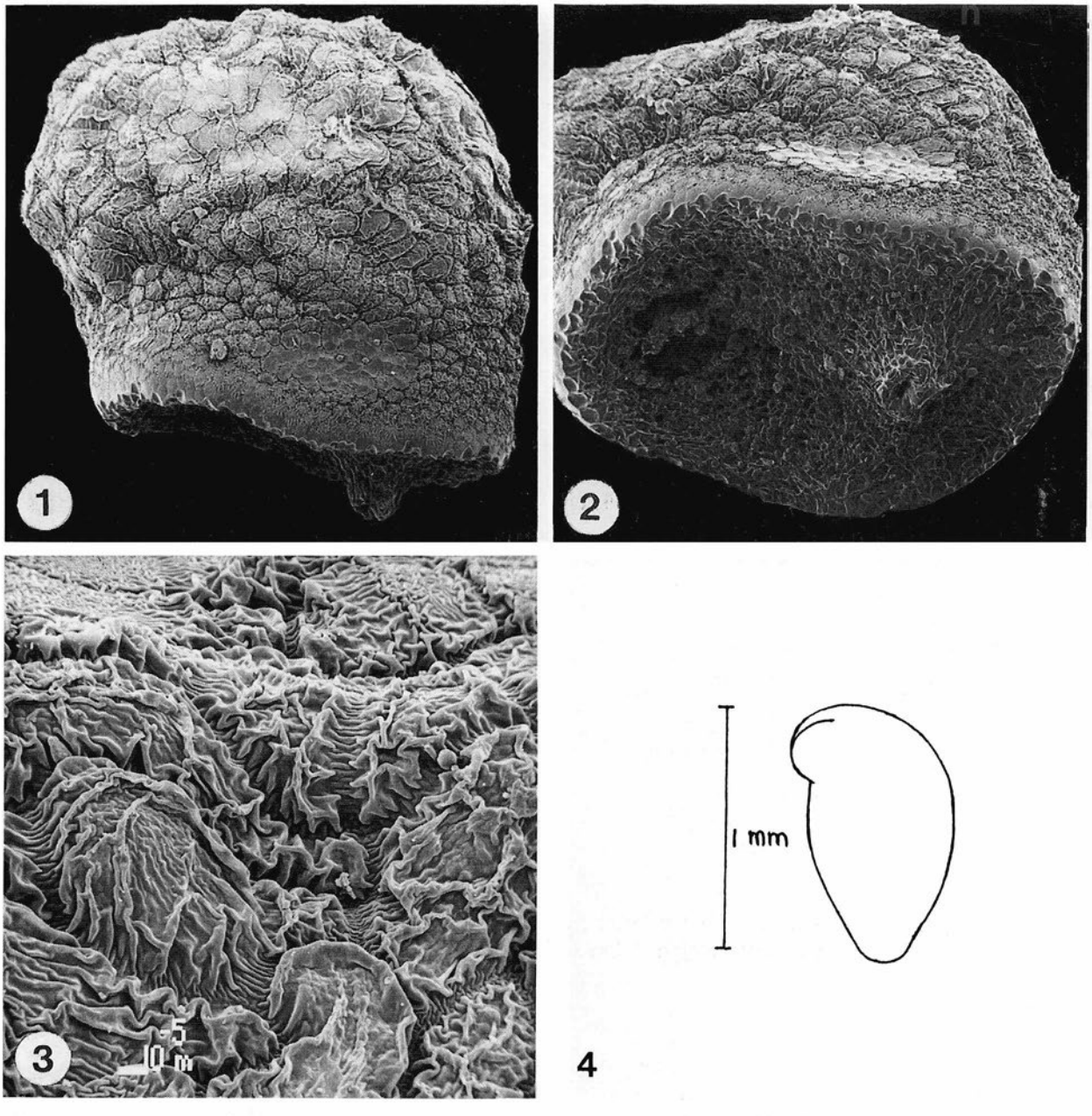




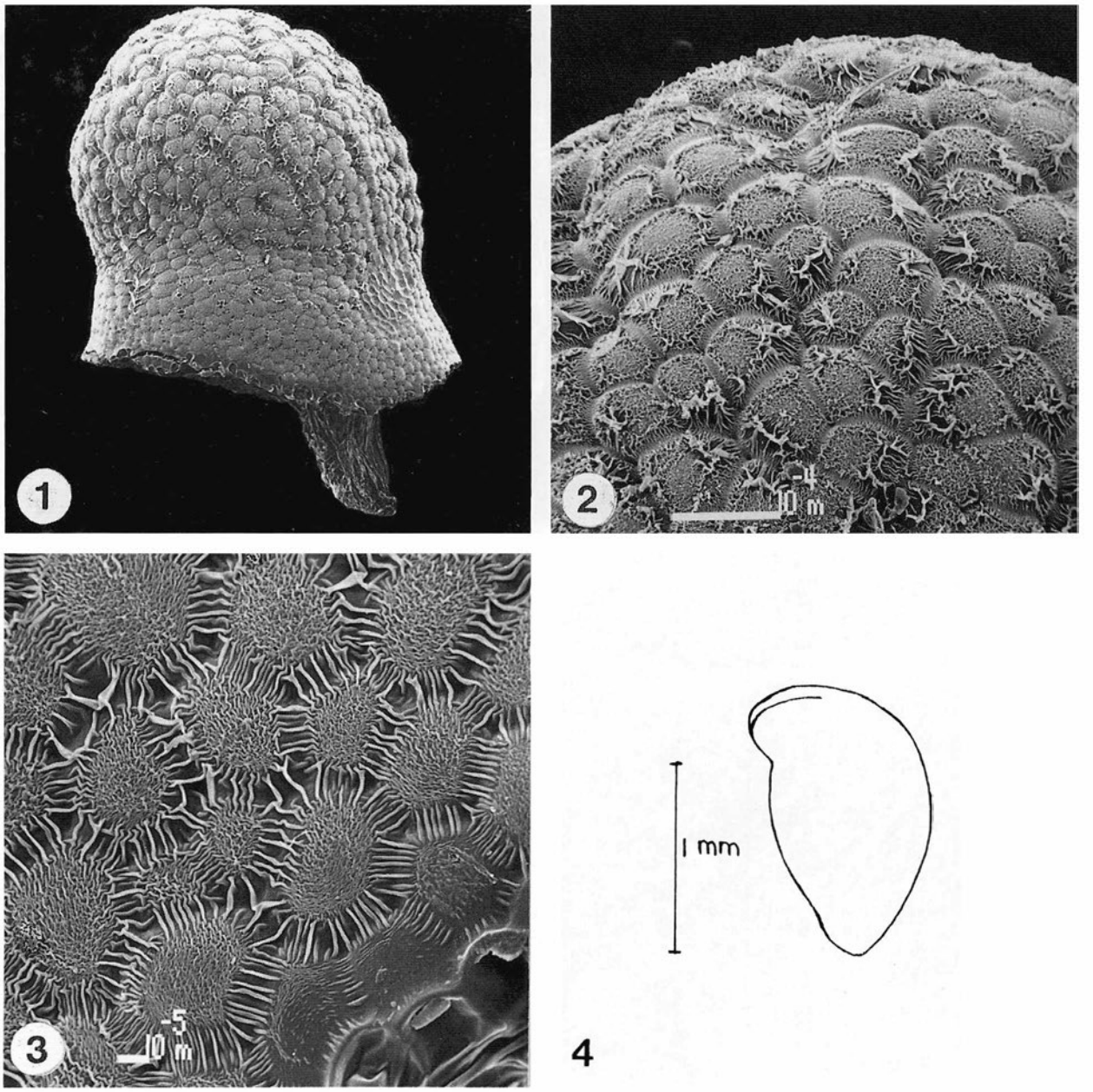


3

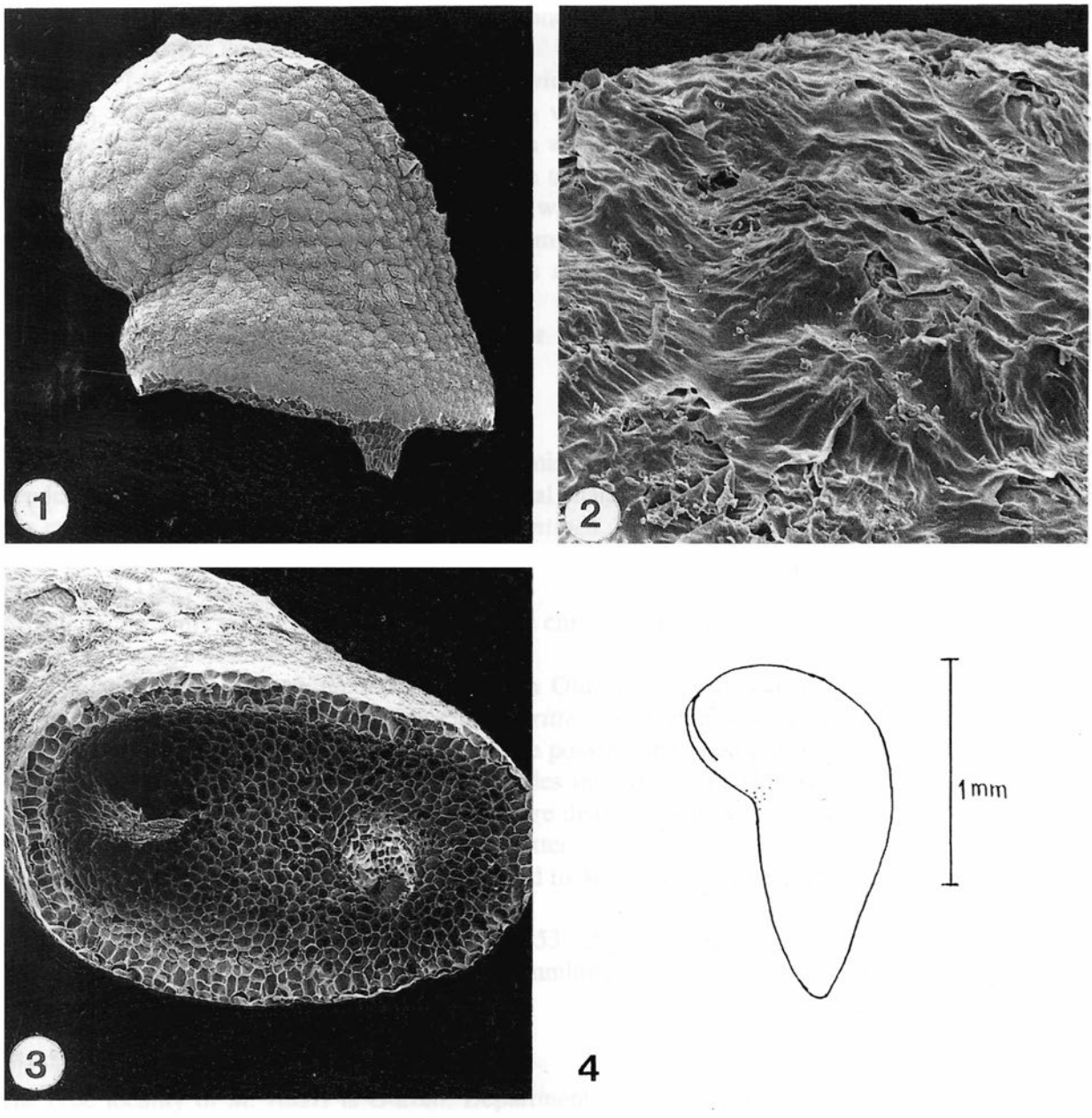
Photograph 13. Seed of *Matucana fruticosa*. 1. Seed (Köhres 1984) in lateral view; 50×. 2. Testa in lateral region; 550×. 3. Embryo.



Photograph 14. Seed of *Matucana ritteri*. 1. Seed (*Clichéfonds Succulenta*, 1980) in lateral view; 60×. 2. Id., hilum; 80×. 3. Id., testa in apical region; 460×. 4. Embryo (Köhres 1984).



Photograph 15. Seed of *Matucana weberbaueri* (Köhres 1984). 1. Seed in lateral view; 50×. 2. Id., apical region; 185×. 3. Id., detail of basal region; 500×. 4. Id., embryo.



Photograph 16. Seed of *Matucana polzii* (ex-habitat specimen). 1. Seed in lateral view; 30×. 2. Id., testa in apical region; 250×. 3. Id., hilum; 50×. 4. Id., embryo.

straight to slightly bent; radials 7-10, sometimes more (11-14), 1-3 cm long; centrals 1-2, sometimes up to 5, 2-4 cm long.

Flower 7-9 cm long, in anthesis 4.5-5 cm wide, oblique, carmine, perianth segments with violet margin. Tube appr. 4 mm wide, red, with white tufts of wool. Nectar chamber 2-4 mm long, closed by a white to pink diaphragm. Filaments white at the base blending to violet at the top, anthers ochrous to cream-violet; primary stamens only fused at their bases without forming a collar around the style. Style violet; stigma lobes 5-6, appr. 2 mm long, reddish green.

Fruit shiny red and green, with small scales and tufts of wool, 10-15 mm across.

Seed as described earlier in this chapter, appr. 1.2 mm long and wide, appr. 0.7 mm thick.

Remarks

This species is distinct for its dark green epidermis, almost black spines and the slender, totally red and curved floral tube. In floral characteristics *M. ritteri* deviates rather considerably from the typical *M. aurantiaca*. The flowers appear readily, mostly more than one simultaneously. In NW Europe the flowering period is in the spring (May-June).

Due to the shiny dark green epidermis and the curved spines young specimens of *M. ritteri* are very similar to *M. aureiflora*.

Populations of *M. aurantiaca* occur between Otuzco and Cajamarca. Some specimens of these show a resemblance to *M. ritteri*. Unfortunately nothing is known about the flower of these plants. It is quite possible that, going from Cajamarca to Otuzco, *M. aurantiaca* more or less fades into *M. ritteri*. However, the typical *M. aurantiaca* and the typical *M. ritteri* are distinct plants which are easy to distinguish. Field study could elucidate this matter.

According to Buining *M. ritteri* is most related to *M. currundayensis*, which is a synonym of *M. aurantiaca*.

The species was discovered by F. Ritter in 1953. The holotype is deposited in the herbarium of the 'Städtische Sukkulentensammlung' in Zürich, Switzerland, under number FR 299.

Distribution

The type locality of *M. ritteri* is Otuzco, Department of La Libertad, Peru. The altitude is 2500 m above sea level.

Both Buining and Ritter stated that *M. ritteri* is only known from the type locality. Knize has distributed plants and seeds from Agallpampa (KK 1045), which is not very far away from Otuzco. These plants are reported to become very large (30-40 cm across). *M. ritteri* has also been recorded from the area between Agallpampa and Usquil.

Field numbers

FR 299 *Matucana ritteri*
KK 711 *Submatucana ritteri*
KK 1045 *S. ritteri* Agallpampa
L 116 *S. ritteri*
WK 546 *Matucana ritteri*
WK 546a *M. ritteri*

Matucana weberbaueri (Vaupel) Backeberg, Beitr. Sukk. 1939: 42 (1939)
CITES Cactaceae Checklist: *Matucana weberbaueri*; weberbaueri = named after A. Weberbauer; Plate 38.

BASIONYM
Echinocactus weberbaueri Vaupel, Bot. Jahrb. Engler 50, Beibl. 111: 26 (1913).

SYNONYMS
Submatucana weberbaueri (Vaupel) Backeberg.
Borzicactus weberbaueri (Vaupel) Donald, Cact. Succ. J. (Gr. Brit.) 26(1): 10 (1971).

DESCRIPTION
Body green, (flattened) globose to slightly cylindrical, up to 20 cm tall and 12 cm wide, seldom offsetting; no tap root. Ribs 18-30, divided into tubercles by transverse grooves. Areoles circular to oval, up to 7 mm long and 5 mm wide, with short cream-coloured felt, appr. 10 mm apart. Spination golden to dark brown, no clear difference between radials and centrals, 25-30 spines per areole, 10-50 mm long, straight, needle-like.

Flower up to 6 cm long, in anthesis appr. 3 cm wide, straight to slightly oblique, perianth segments lemon-yellow. Tube appr. 8 mm wide, greenish-yellow, naked or very weakly pubescent. Nectar chamber 2-4 mm long, nectar glands parietal. Filaments white at the base, blending to violet at the top, anthers lilac-pink; primary filaments fused at their bases over appr. 2 mm, thus forming a very short collar around the style. Style white; stigma lobes 5-6, appr. 2 mm long, greenish.

Fruit oval, green and red, appr. 8 mm across.

Seed as described earlier in this chapter, 1.2-1.8 mm long, 1.2-1.4 mm wide, 0.8-1.1 mm thick.

REMARKS
For several decades *M. weberbaueri* was thought to have disappeared in nature. After a long and thorough search Lau relocated the spot where Weberbauer found this species in the beginning of this century. So since the late 1960s plenty of seed of this conspicuously flowering species is available again.

In stem appearance this species is very similar to *M. aurantiaca*. *M. weberbaueri* is densely spinated but this also can occur in *M. aurantiaca*. *M. weberbaueri* has a more slender floral tube and generally smaller seeds. The most dinstinctive feature of *M. weberbaueri* is the lemon-yellow flower, a colour that is unique to the genus *Matucana*.

All type material of Matucanas deposited by Vaupel in 1913 was lost in the Second World War. Hence, like *M. aurantiaca* and *M. myriacantha*, a new type specimen (neotype) of *M. weberbaueri* should be designated. Preferably one of the plants collected by Lau should be selected.

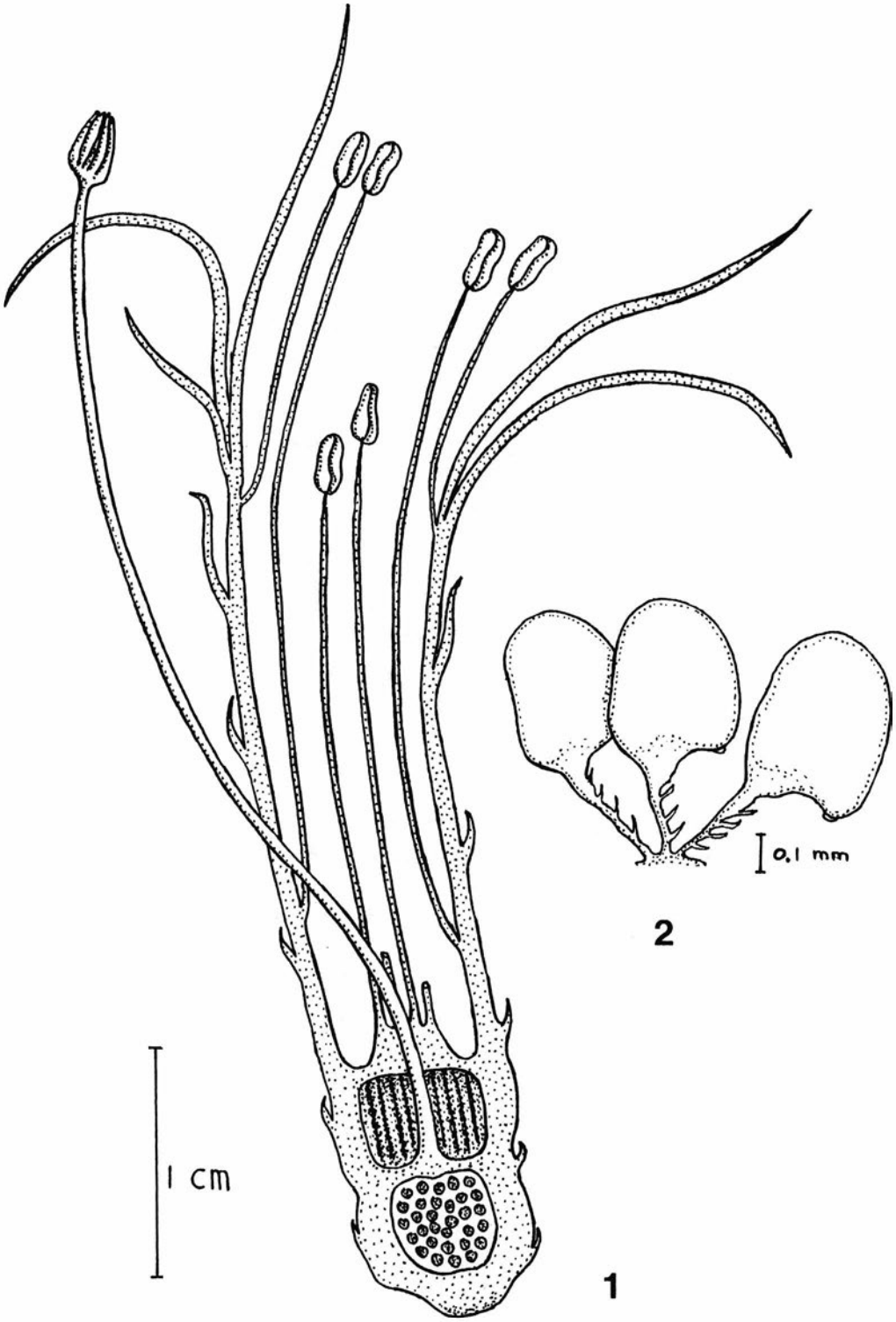


Figure 16. Flower of *Matucana weberbaueri*. 1. Flower in vertical section (f. *flammea*). 2. Id., ovules.

DISTRIBUTION

This species was discovered in 1904 by Weberbauer east of the Rio Maranon at 2000-2100 m altitude. The type locality is near the village of Balsas, Department of Amazonas, Peru.

M. weberbaueri is the only species in the aurantiaca group to occur on the east side of the Rio Maranon. Presumably the total distribution area extends further south from the type locality near Balsas.

FIELD NUMBERS

FR 1304	*Matucana weberbaueri*
L 218	*M. weberbaueri*
Weberb. 4271	*Echinocactus weberbaueri*

Matucana weberbaueri (Vaupel) Backeberg forma **flammea** (Donald) Bregman, Melis, Meerstadt et Pullen, Succulenta 68(6): 143 (1989)
CITES Cactaceae Checklist: *Matucana weberbaueri*; flammea = flaming red; Plate 39.

BASIONYM

Borzicactus weberbaueri var. *flammeus* Donald, Ashingtonia 1(9): 100 (1974).

SYNONYM

Matucana myriacantha sensu Ritter.

REMARKS

This plant is distinct for its golden-orange flower colour. It was described in 1974 by Donald as a variety of *Borzicactus weberbaueri*. However, the only difference between them is the colour of the flower, so the rank of variety has been changed to form. In addition, Donald mentioned a little difference in spine length, but this could not be confirmed by the author.

In cultivation many specimens of this plant still bear the wrong label *M. myriacantha*. An understandable situation, because plants were brought into circulation under that name. This confusion began after the collecting work by Lau in the late 1960s. At the time he was searching near Balsas for the long disappeared *M. myriacantha* and *M. weberbaueri*. After finding *M. weberbaueri* f. *flammea*, Lau initially thought that he had relocated the true *M. myriacantha*, but, as Lau himself subsequently noticed, the flower colour did not match the original description. After this material had been sent to England, Donald correctly placed the plant under *M. weberbaueri* and not under *M. myriacantha*.

Also Ritter mixed this plant up with *M. myriacantha*. In his book *Kakteen in*

Plates 34-37
34-35. *Matucana ritteri*, cultivated specimens.
36. *M. fruticosa*, cultivated specimen.
37. *M. polzii*, natural specimen in cultivation.

34	35
36	37

Südamerika the description of *M. myriacantha* is in reality that of *M. weberbaueri* f. *flammea*.

In cultivation this orange flowering form seems to be somewhat easier than the yellow flowering *M. weberbaueri*. The plants seem to be stronger in their winter cold resistance and flower more readily, although the number of flowers that appear simultaneously is mostly low.

The holotype is deposited in the herbarium of the University of Heidelberg, Germany, under number L 109.

DISTRIBUTION

M. weberbaueri f. *flammea* is only known from one locality near the village of Balsas, Department of Amazonas, Peru.

FIELD NUMBERS

FR 1305	*Matucana myriacantha*	L 109	*Borzicactus weberbaueri* var. *flammeus*
KK 457	*Submatucana myriacantha*	PCH 4953	*B. weberbaueri*
KK 779	*S. weberbaueri*	WK 77	*M. weberbaueri* var. *flammea*

Matucana hastifera Ritter, Kakteen in Südamerika 4: 1496 (1981)
CITES Cactaceae Checklist: *Matucana hastifera*; hastifera = bearing spears; Plates 40 and 41.

DESCRIPTION

Body green, broad cereoid, up to 50 cm long, 6-12 cm wide, offsetting from the base, erect or creeping; no tap root. Ribs 13-19, blunt, weakly tuberculate, 7-12 mm high, 10-12 mm wide at the base of the plant. Areoles oval, 8-15 mm long, 3-6 mm wide, with white felt, 8-22 mm apart. Spination piercingly robust, straight, yellow to reddish brown; radials 14-20, 8-25 mm long; centrals 4-8, 20-70 mm long.

Flower 6.5-8 cm long, in anthesis appr. 5 cm wide, straight; outer perianth segments strongly bent backward, pale orange with red tip. Tube 8-10 mm wide, naked. Nectar chamber 4-5 mm long. Filaments white at the base blending to red at the top, anthers cream-coloured; primary filaments fused at their bases like a collar around the style. Style white at the base blending to red at the top; stigma lobes 4-5, 4-5 mm long.

Fruit globular, dark green to yellowish.

Seed as described earlier in this chapter, appr. 2.2 mm long, appr. 1.6 mm wide, appr. 1.2 mm thick.

38 39
40 41

Plates 38-41
38. *Matucana weberbaueri*, cultivated specimen.
39. *M. weberbaueri* f. *flammea*, cultivated specimen.
40. *M. hastifera*, ex-habitat specimen.
41. *M. hastifera*, cultivated specimen.

REMARKS

Due to lack of data the description given above is entirely derived from the original description by Ritter. According to him this species is distinct for its strongly developed centrals and its backwardly curled perianth segments.

In Dutch collections this species seems to be very rare; only one specimen could be traced. This plant has the stem as described by Ritter but a 'normal' aurantiaca-like flower without the strongly curved perianth segments (Plate 41). Additional data is needed.

Seeds from the field or from field-collected plants were not available. Nowhere in the seed catalogues from commercial enterprises and nurseries are seeds of this species being offered. The seeds from the specimen in cultivation mentioned above appeared to be somewhat larger than those of *M. aurantiaca*, like in *M. fruticosa.*

The holotype is deposited in the herbarium of the University of Utrecht, Netherlands under number FR 1306. Unfortunately the type material contains no flowers, no fruits and no seeds. The holotype itself is in a bad shape, as was remarked by an employee of the herbarium.

DISTRIBUTION

The type locality of *M. hastifera* is east of the Cordillera Blanca, south of Rahuapampa, Province of Huari, Department of Ancash, Peru. The altitude is appr. 3500 m. Up till now no other localities have been reported.

FIELD NUMBERS

FR 1306 *Matucana hastifera*
L 272 *M. hastifera*

Matucana polzii Diers, Donald & Zecher, Kakteen u.a. Sukk. 37(6): 114 (1986)
CITES Cactaceae Checklist: *Matucana polzii*; polzii = named after F. Polz; Plates 4 and 37.

DESCRIPTION

Body green, flattened-globose, up to 5 cm tall and 8 cm wide, strongly offsetting laterally; root system superficial. Ribs 9-16, flat and rounded, mostly straight, with a transverse groove above each areole. Areoles oval, up to 8 mm long, 2-3 mm wide, with cream-white wool that turns grey with age, 5-9 mm apart. Spination flexible, white to brown-yellow with black tip, sometimes black all over, turning grey in later life. Radials 6-12, 6-18 mm long; centrals 1-3, up to 25 mm long.

Flower 5-7 cm long, in anthesis 3.5-5 cm wide; perianth segments carmine with paler margin. Tube somewhat curved, 8-12 mm wide, red, with white to brown hairs. Nectar chamber appr. 1 mm long. Filaments white at the base shading to red-violet, anthers yellow; primary stamens fused at their bases over 1-3 mm like a collar around the style. Style white at the base shading to red-violet; stigma lobes 5-6, appr. 2 mm long, yellowish-green.

Fruit reverse-egg-shaped, purple-brown, up to 12 mm long, 5-7 mm wide, with white to brown hairs.

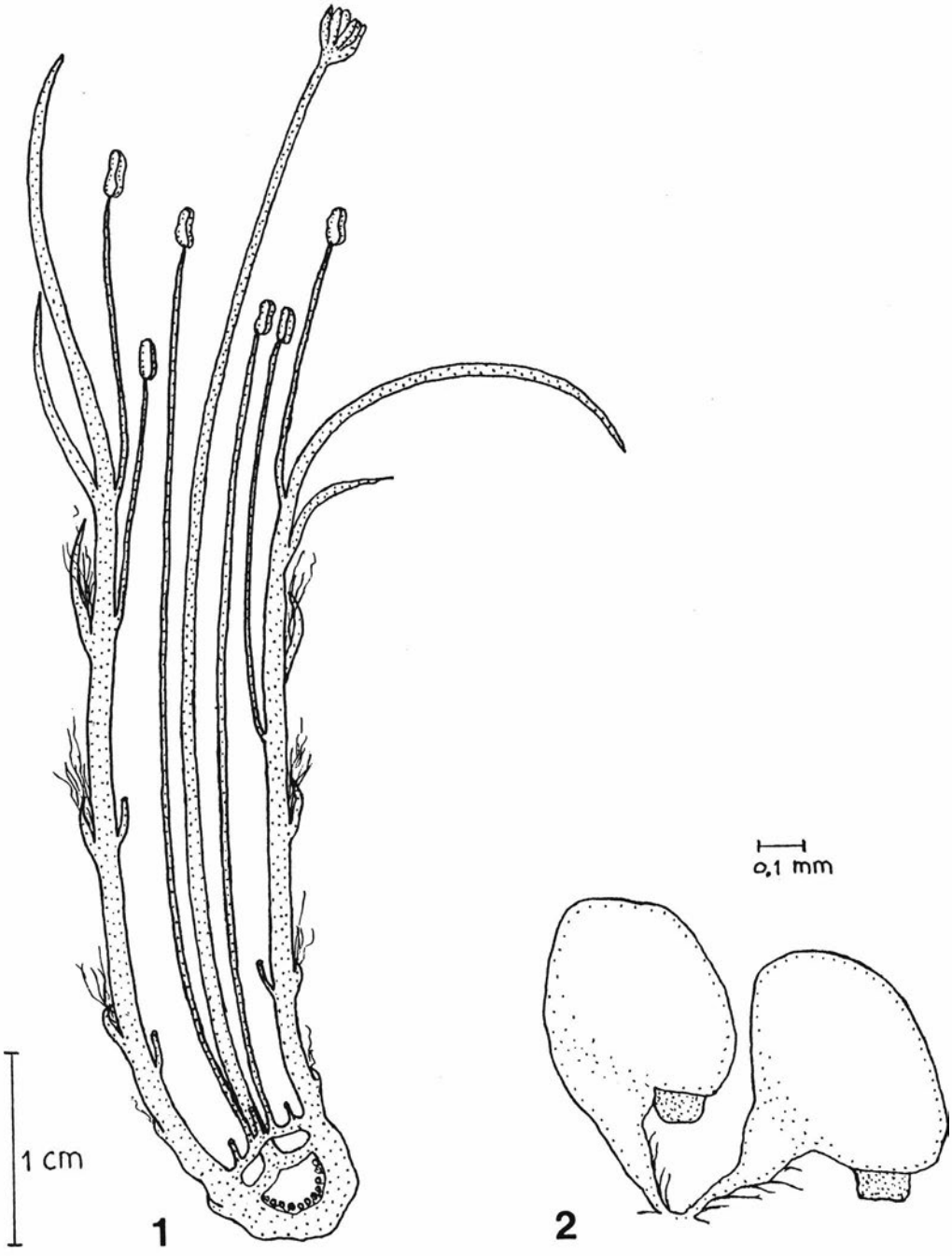


Figure 17. Flower of *Matucana polzii*. 1. Flower in vertical section. 2. Id., ovules.

Seed as described earlier in this chapter, 1.8-2.0 mm long, 1.4-1.5 mm wide, 0.9-1.0 mm thick.

REMARKS

This latest described *Matucana* species is remarkable for its propensity to offset; without flowers the plant could be easily mixed up with an Echinopsis. Even on

young (2 year old) areoles offsets are produced. That is why it is not surprising that this species is distributed on a large scale among cactophiles through offsets. A single plant is capable of producing a few dozen offsets each year. As far as applies to the Netherlands, probably all the specimens kept in collections are derived from this mode of propagation. No seeds have been offered by commercial traders so far. The seeds used for the drawings and SEM micrographs were obtained by cross-pollination with another species.

Another similarity with *Echinopsis* is the poor capacity to flower. This is understandable due to the fact that *M. polzii* reproduces merely by its offset rather than by seed, hence the need to produce many seeds, and thus many flowers, is not very high. The plant may be stimulated to flower if all the offsets are removed as soon as possible, and the plant has reached a size of appr. 8 cm across.

The authors of this species stated that it is most closely related to *M. paucicostata*. This statement is not confirmed by seed morphology. So they probably based their conclusion on the fact that the habitats of both species are not very far away from each other. According to seed characteristics *M. polzii* belongs to the *M. aurantiaca* complex.

Distribution

The type locality of *M. polzii* is near the upper reaches of the Rio Maranon, in the south-west of the Department of Huanuco, Peru, in 2100-2300 m altitude. The holotype is deposited in the herbarium of the University of Cologne, Germany, under number EZ 762.

Field numbers

No field numbers exist.

CHAPTER 10

The intertexta group

10.1 TAXONOMY

This group, named after the best-known species in this group, *Matucana intertexta*, contains a number of taxa with an insufficiently known systematic position. Further study has to be conducted to find out which taxa should obtain the rank of species, subspecies, variety or form.

Considering the number of names brought into circulation, whether or not validly published, the intertexta group is the smallest group of the genus *Matucana*. Based on seed structure, as outlined in Chapter 6, the following taxa belong to the intertexta group:

Matucana intertexta	*M. roseoalba*
M. celendinensis	*Matucana* sp. Lau 103
M. myriacantha	*Matucana* sp. Lau 103a
M. purpureoalba	*Matucana* sp. Lau 173
M. huagalensis	*Matucana* sp. Lau 224.
M. mentosa	

All the taxa listed above meet the following description:

Body grass green, globose to shortly cylindrical, seldom offsetting. Ribs 14-40, partly or totally divided into tubercles. Spination variable; centrals 1-10, 10-40 mm long; radials 8-26, 7-20 mm long.

Flower orange, red or pink, mostly with a pubescent tube; nectar chamber closed by a diaphragm formed by the fused bases of the primary filaments.

Seed dull black to brown, somewhat longer than wide, with irregular cuticular remnants, dorsally and ventrally little or not expanded; seed surface with irregular grooves and bumps; cuticle strongly folded; there are two small holes in the funicular tissue at the positions of micropyle and funiculus. Testa cells convex in apical region, strongly flattened in the basal section of the seed. Embryo somewhat curved.

The order of the taxa that belong to the intertexta group is as follows:

1. *M. intertexta* var. *intertexta*
2. *M. intertexta* var. *celendinensis*
3. *M. huagalensis*

4. *M. myriacantha.*

M. celendinensis (Plates 48 and 50) was originally described as a species by Ritter in 1966, but was reduced to the rank of variety by Donald in 1971. The present author follows this view, as both taxa differ in flower colour and flower length only.

M. myriacantha (Plate 51) had posed a problem for years because the species seemed to have vanished in the wild. At one time an entirely different plant (*M. weberbaueri* f. *flammea*) was by mistake considered to be *M. myriacantha* because it was collected at almost the same locality. After the (probably) true *M. myriacantha* had been recollected by Lau, a number of more or less identical plants were brought into circulation by Ritter and Lau under field numbers and/or (provisional) epithets. These are *M. purpureoalba* Ritter (Plate 52), *M. roseoalba* n.n. and the Lau field numbers 103, 103a, 173 (Plate 53) and 224. All these plants share a relatively dense spination and a pink flower, only with exclusion of Lau 173 which blooms with a short scarlet flower. One could say that the plants mentioned belong to a myriacantha complex of plants.

Possibly the Lau 173 taxon deserves the rank of variety because of its different flower. Further field study is needed prior to doing so. For the time being this taxon will be treated as a synonym of *M. myriacantha.*

Another problem plant is *M. huagalensis* (Plate 49), which is remarkable for its white flower, a colour that is unique not only in *Matucana* but also in the subtribe Borzicactinae. Actually the flower colour is a very pale pink. However, seed distributed under that name yield red-flowering plants identical to *M. intertexta* (Plate 50). Here also, additional field study is needed.

10.2 PHYLOGENY

The intertexta group is probably closely related to the paucicostata group. This conclusion can be drawn from similarities in seed structure and distribution area. Also the preference of a relatively warm habitat is a common feature of both *M. myriacantha* and the species of the paucicostata group.

According to seed morphology *M. intertexta* shows more affinity to the seed type found in the haynei group, whereas *M. myriacantha* seems to be closer to the seed type of the paucicostata group, especially to that of *M. paucicostata* itself. *M. huagalensis* is probably very close to *M. intertexta*, perhaps just a local form of it.

At first glance *M. intertexta* and *M. myriacantha* have little in common; both species differ substantially in plant body and flower. Yet, both species have been placed in the same group because of similarities in the seed. On second thoughts the difference in plant body is not so great; juvenile specimens of *M. intertexta* exhibit a dense white spination (which disappears in mature specimens) so that they look like *M. myriacantha.*

M. intertexta var. *celendinensis* looks a lot like *M. aurantiaca.* As the nearest populations of *M. aurantiaca* are fairly close by, a hybrid origin of var. *celendinensis* cannot be excluded. Another such possible crossing could have lead to

Knize's *M. grandiflora* n.n. from Balsas which has an intertexta flower but aurantiaca seeds (see Chapter 9).

10.3 SEED MORPHOLOGY

The seeds of the species of the intertexta group, as described in Chapter 6, are distinct in only a few features. The seeds are very much like those of the haynei group; the difference is the reduced funicular tissue inside the hilum cup. As a result, two holes are present in the hilum, while there are no such holes in the seed of the haynei group. These holes indicate that the hilum cup is covered only by a thin layer of funicular tissue; Thus, the hilum cup is just a cavity with an air bubble enclosed at the base of the seed grain. The air bubble enhances the floating capability of the seeds which may be advantageous to seed dispersal by water.

The seeds of *M. myriacantha* show some similarities to those of *M. paucicostata.* The holes in the hilar tissue are large and, when looking at the seeds in lateral view, a beginning of the typical broad seed shape of the paucicostata group is already visible. In *M. intertexta*, on the other hand, the holes in the funicular tissue are smaller; also the dorsal extension of the seed is absent.

10.4 DISTRIBUTION

The known localities of the species and varieties of the intertexta group are shown in Figure 18. The distribution area is rather small, in relation to the area covered by the remaining species groups. The plants can be found in the valley of the Rio Maranon and its tributary stream Rio Crisnejas as well in their immediate surrounding areas. So, not only phylogenetically but also geographically the intertexta group is close to the paucicostata group. As to the altitude, the localities are relatively low, which means in practice that most populations are not very far away from the river banks.

Within this group *M. intertexta* occupies the largest area. This species is also fairly abundant; it's not very difficult to find. When traveling by bus from Cajamarca to Cajabamba, one can often see this species along the road side, especially during the flowering period. It is not known whether this species occurs also more to the north where its variety *M. intertexta* var. *celendinensis* grows. Probably it does.

The habitats of *M. myriacantha* and its forms follow the slopes of the Rio Maranon valley, just like the species of the paucicostata group do. According to present knowledge *M. myriacantha* is restricted to the Maranon area between Balsas and Aricapampa in the Departments of Amazonas, Cajamarca and La Libertad. From this region also species of the paucicostata group are recorded but usually closer to the river. In any case both groups occur separated and without apparent genetical exchange, at least as far as we know now. In 1978 A. Lau discovered four localities of myriacantha-like plants: Balsas (L 103), Huagal (L 103a), Crisnejas (L 173) and Aricapampa (L 224). The plants bearing the last-mentioned field number are probably identical to Ritter's *M. purpureoalba*. When comparing

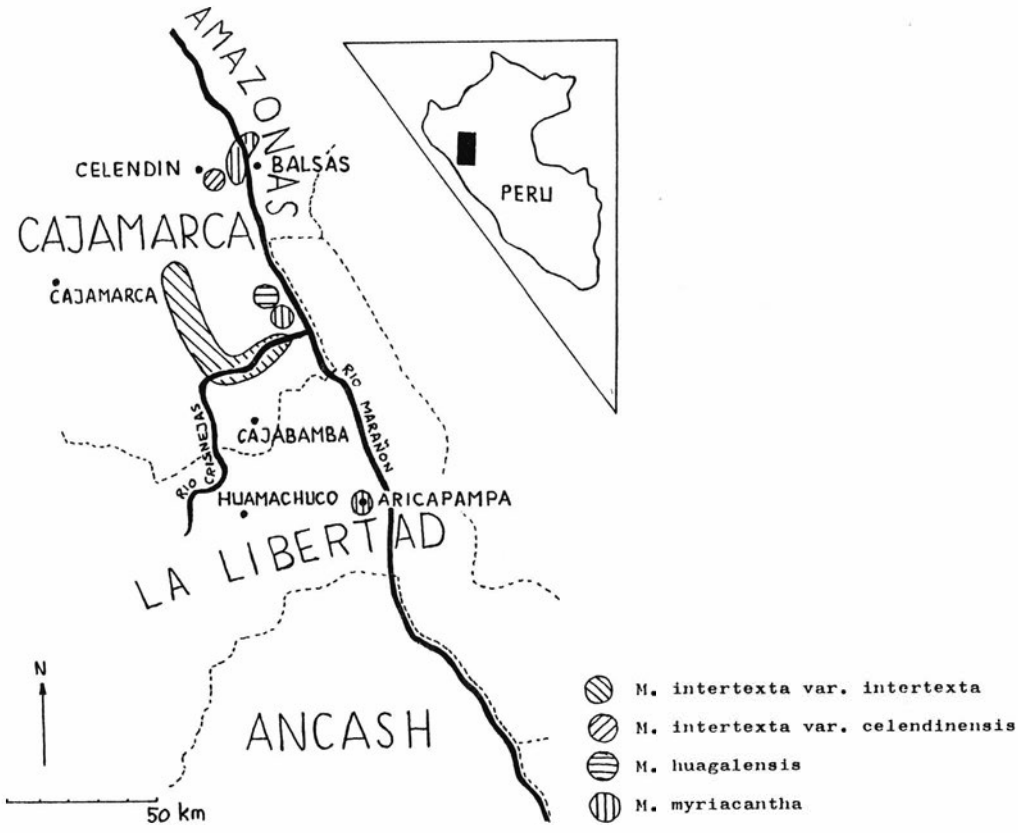


Figure 18. Distribution of the species and varieties of the intertexta group.

photographs and descriptions of both taxa they are probably conspecific and should be taken as a local form of *M. myriacantha*.

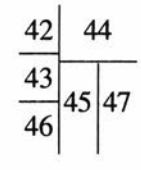
M. huagalensis, as the epithet already indicates, comes from Huagal, just north of the junction of the Rio Crisnejas and the Rio Maranon. This plant is most likely known from one locality only.

10.5 KEY TO THE SPECIES AND VARIETIES OF THE INTERTEXTA GROUP

1a. Ribs 14-25; spination relatively open, 9-24 spines per areole 2
1b. Ribs 30-40; spination relatively dense, 30-50 spines per areole ..... *myriacantha*

Plates 42-47. Forms of *Matucana intertexta* var. *intertexta*

42. *M. intertexta* var. *intertexta* in habitat near the bridge over the Rio Crisnejas.
43. *M. intertexta* var. *intertexta* in habitat beside the road from Cajamarca to Cajabamba.
44-46. *M.intertexta* var. *intertexta*, cultivated specimens.
47. *M. intertexta* 'var. nov.', cultivated specimen.



2a. Flower white to pale pink; ribs not clearly tuberculate ..... *huagalensis*
2b. Flower orange to red; ribs more or less clearly tuberculate 3
3a. Flower pale orange to vermilion, longer than 7.5 cm ..... *intertexta* var. *intertexta*
3b. Flower scarlet, shorter than 7.5 cm ..... *intertexta* var. *celendinensis*

10.6 THE SPECIES OF THE INTERTEXTA GROUP

Matucana intertexta Ritter var. **intertexta**, Succulenta 67(4): 89 (1988)
CITES Cactaceae Checklist: Matucana intertexta; intertexta = interweaved; Plates 42-47.

BASIONYM
Matucana intertexta Ritter, Taxon 12(3): 125 (1963).

SYNONYMS
Submatucana intertexta (Ritter) Backeberg, Descr. Cact. Nov. 3: 14 (1963).
Borzicactus intertextus (Ritter) Donald, Cact. Succ. J. (Gr. Brit.) 26(1): 10 (1971).
Submatucana intertexta var. *cinerascens* n.n.
Matucana intertexta var. *loranzensis* n.n.
Matucana mentosa n.n.
Submatucana mentosa n.n.

DESCRIPTION
Body green, solitary, globose to broadly cylindrical, 7-18 cm wide, up to 30 cm tall. Ribs 15-25, 7-15 mm high, very blunt with flattened tubercles. Areoles oval, 5-8 mm long, 3-4 mm wide, with little brown to grey wool, 1-2 cm apart. Spination in juveniles densely white, in adult specimens more open, stronger, darker coloured ; radials first appr. 20, 5-10 mm long, later 8-12, 7-20 mm long, pointing sideways, straight; centrals first appr. 20, 5-10 mm long, later 1-4, 20-35 mm long, straight or somewhat bent, brown with black tip, turning grey with age.

Flower 7.5-10.5 cm long, in anthesis 5-8 cm wide, oblique; perianth segments pale orange to vermilion. Tube 6-8 mm wide, almost naked to whitish pubescent. Nectar chamber 1-3 mm long, closed by a diaphragm. Filaments white at the base blending into carmine; anthers brown; primary filaments fused over 2-4 mm at their bases hugging the style like a collar. Style white at the base, pale yellow at the top; stigma lobes 6-8, 3-6 mm long, yellowish.

48	50
49	51
53	52

Plates 48-53
48. *Matucana intertexta* var. *celendinensis*, cultivated specimen.
49. *M. huagalensis*, ex-habitat specimen collected on the type locality.
50. *M. intertexta* var. *celendinensis*, cultivated specimen raised from seed sold as *M. huagalensis*.
51. *M. myriacantha*, cultivated specimen.
52. *M. myriacantha* (*M. purpureoalba*), cultivated specimen.
53. *M. myriacantha* (*Matucana* sp. Lau 173), cultivated specimen.

Figure 19. Flower of *Matucana intertexta* var. *intertexta* (Puente Crisnejas, 1982). 1. Flower in vertical section. 2. Id., ovules.

Fruit globular, 10-18 mm across, with white tufts of wool.

Seed as described earlier in this chapter, 1.2-1.8 mm long, 1.3-1.8 mm wide, 0.7-0.9 mm thick. Hilum oval; funicular tissue with two small holes at the positions of funiculus and micropyle, sometimes without such holes.

REMARKS

F. Ritter discovered this species in 1957. His description followed in 1963. The holotype is deposited in the herbarium of the University of Utrecht, Netherlands, under number FR 693.

The invalidly published names *Matucana mentosa* and *Submatucana mentosa* have been recorded from catalogues, for example those of Uhlig and Whitestone Gardens. *Submatucana intertexta* var. *cinerascens* is an invalid name introduced by Knize (KK 1054). In the 1983 plant list of Bisnaga the invalid name of *M. intertexta* var. *loranzensis* appeared. All these names should be abandoned.

Juveniles of this species differ substantially in appearance from mature specimens. The juvenile form is usually densely spinated, in the mature plant the number of spines per areole has considerably decreased. This difference is less clear in cultivation.

M. intertexta is found in different biotopes. They grow often in the shade of xerophytic shrubs but also in open grassy spots. In nature the plants flower in November and December when the grasses have not yet begun to form young shoots. The flower colour at the type locality near Puente Crisnejas is mostly vermilion; near Huagal, more to the east, it is slightly darker red.

Ritter reported to have found a natural hybrid between *M. intertexta* and *Espostoa lanianuligera*.

DISTRIBUTION

The type locality of this species is near Puente Crisnejas, Department of Cajamarca, Peru. This appears to be the southern part of the actual distribution which is far more extensive (Figure 18). This streches approximately to Matara in the north and to Huagal near the Rio Maranon in the east. The altitudes of the habitats are between 1500 and 2300 m.

FIELD NUMBERS

FR 693	*Matucana intertexta*
KK 1036	*Submatucana intertexta*
KK 1054	*S. intertexta* var. *cinerascens*
KK 1085	*Submatucana* sp.
KK 1153	*S. intertexta*
KK 1316	*S. intertexta*
L 108	*S. intertexta*
L 175	*S. intertexta*
WK 548	*Matucana intertexta*

Matucana intertexta var. **celendinensis** (Donald) Bregman, Meerstadt, Melis et Pullen, Succulenta 67(5): 100 (1988)

CITES Cactaceae Checklist: *Matucana aurantiaca*; celendinensis = from Celendin; Plates 48 and 50.

BASIONYM

Matucana celendinensis Ritter, Succulenta 45(8): 118 (1966).

SYNONYMS

Borzicactus intertextus var. *celendinensis* Donald, Cact. Succ. J. (Gr. Brit.) 26(1): 10 (1971).

Submatucana celendinensis Celendin n.n.

S. huagalensis sensu Knize.

DESCRIPTION

Body green, globose to broad cylindrical, 10-12 cm wide, rarely offsetting. Ribs 14-22, appr. 1 cm high, very broad and blunt, with flat tubercles. Areoles narrow elliptic, 5-8 mm long, 3-5 mm wide, grey, 1-2 cm apart. Spination brown with darker tip, grey in later life, erect; radials 10-15, 7-15 mm long, pointing sideways; centrals 2-5, 20-40 mm long.

Flower 7-7.5 cm long, in anthesis appr. 3.5 cm wide, a little oblique; perianth segments scarlet with violet margin. Tube 5-8 mm wide, with white to black hairs. Nectar chamber 1.5-4 mm long, closed by a diaphragm. Filaments white blending into purple; anthers yellow; primary filaments fused at their bases along 2-5 mm like a collar around the style. Style reddish; stigma lobes 4-7, 4-6 mm long, pale green to yellowish.

Fruit globose, green.

Seed as described earlier in this chapter, somewhat larger than in *Matucana intertexta* var. *intertexta*, appr. 2 mm long, appr. 1.5 mm wide, appr. 1 mm thick.

REMARKS

This plant is frequently mixed up with *M. aurantiaca*. The most important differences are found in the flower, the spination and the seeds. In *M. aurantiaca* the spines are longer and more numerous, the floral tube is wider and the seed possesses the protruding micropylar stump, which is so typical for the aurantiaca group.

Both morphologically and geographically this variety is somewhere in between *M. intertexta* and *M. aurantiaca*. So it cannot be excluded that var. *celendinensis* may be of hybrid origin.

Ritter discovered this plant in 1957 and described it in 1966. The holotype is deposited in the herbarium of the University of Utrecht, Netherlands, under number FR 692.

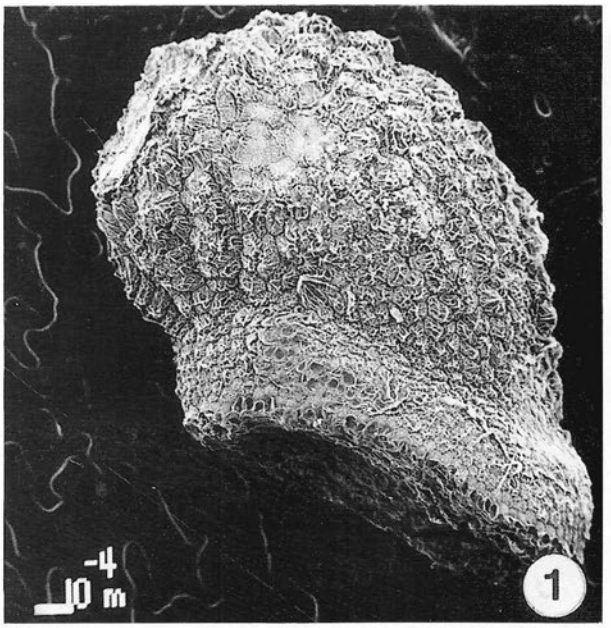
DISTRIBUTION

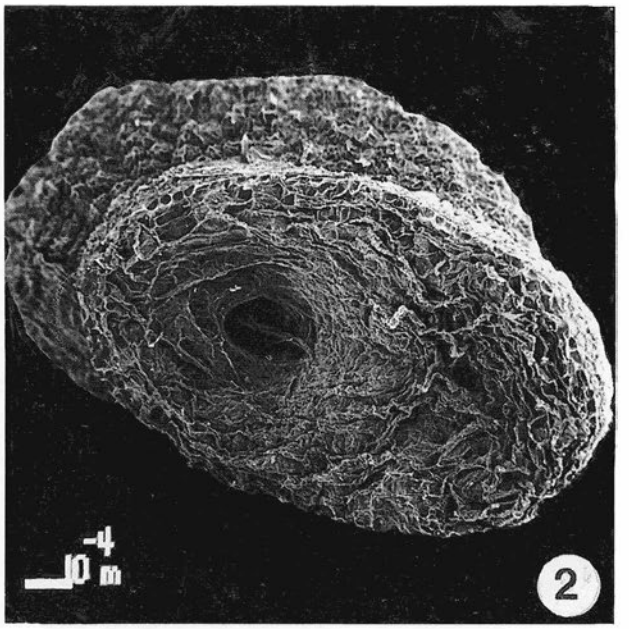
The type locality is situated between Celendin and Balsas, Department of Cajamarca, Peru, at appr. 2300 m altitude.

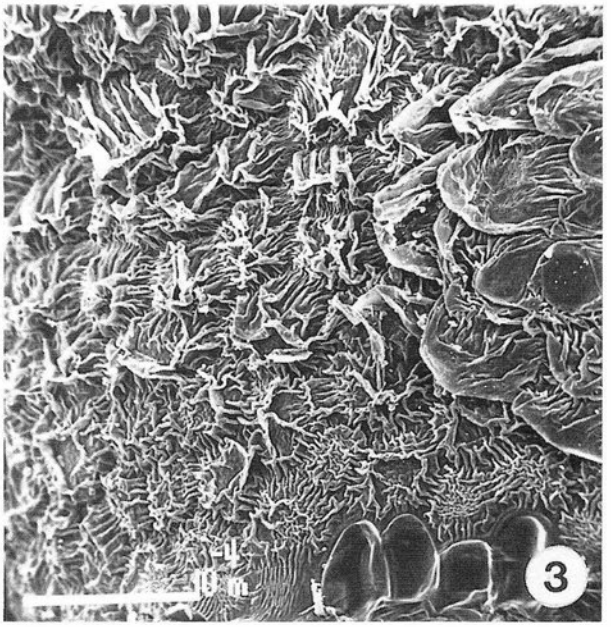
This plant seems to be rare in nature. Very little is known about its distribution outside the type locality, which is probably small.

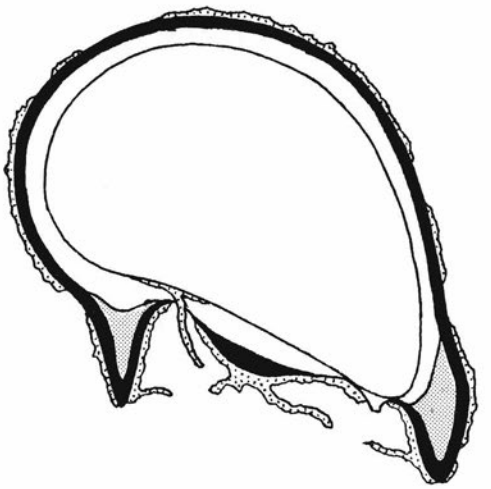
FIELD NUMBERS

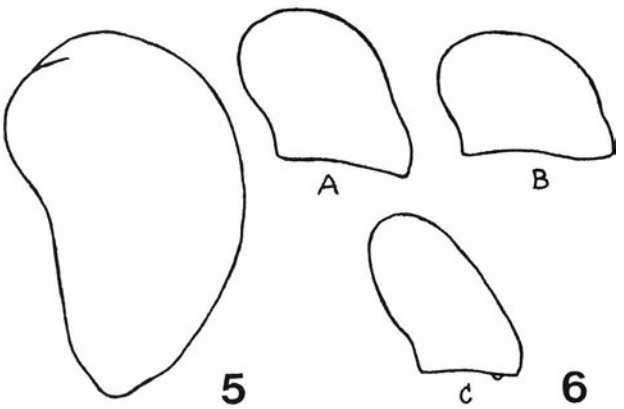
DM 21	?	KK 773a	*Submatucana huagalensis*
DM 22	?	KK774	*S. huagalensis* var. *bruneispina*
FR 692	*Matucana celendinensis*	KK 1039	*S. celendinensis*



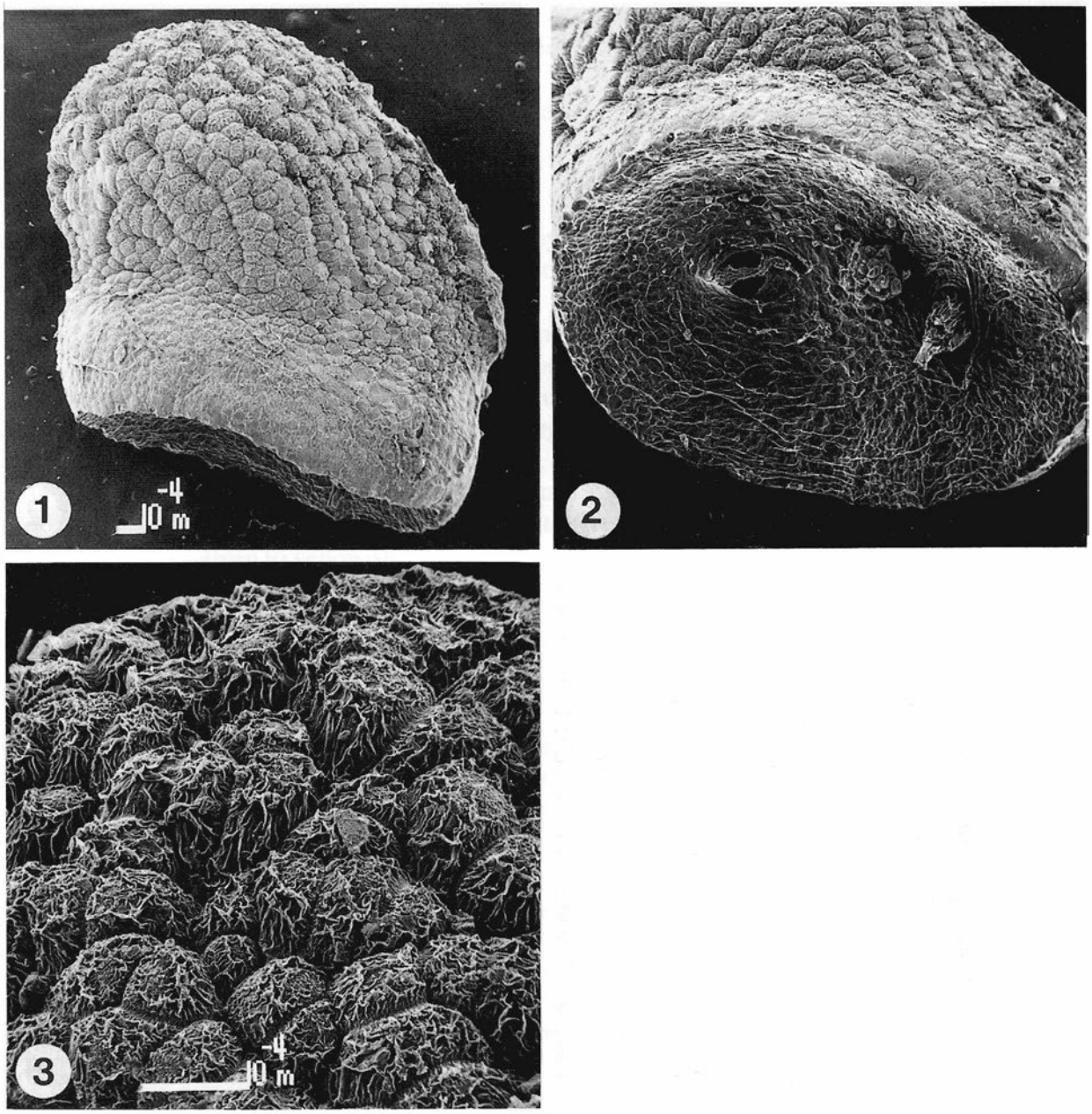




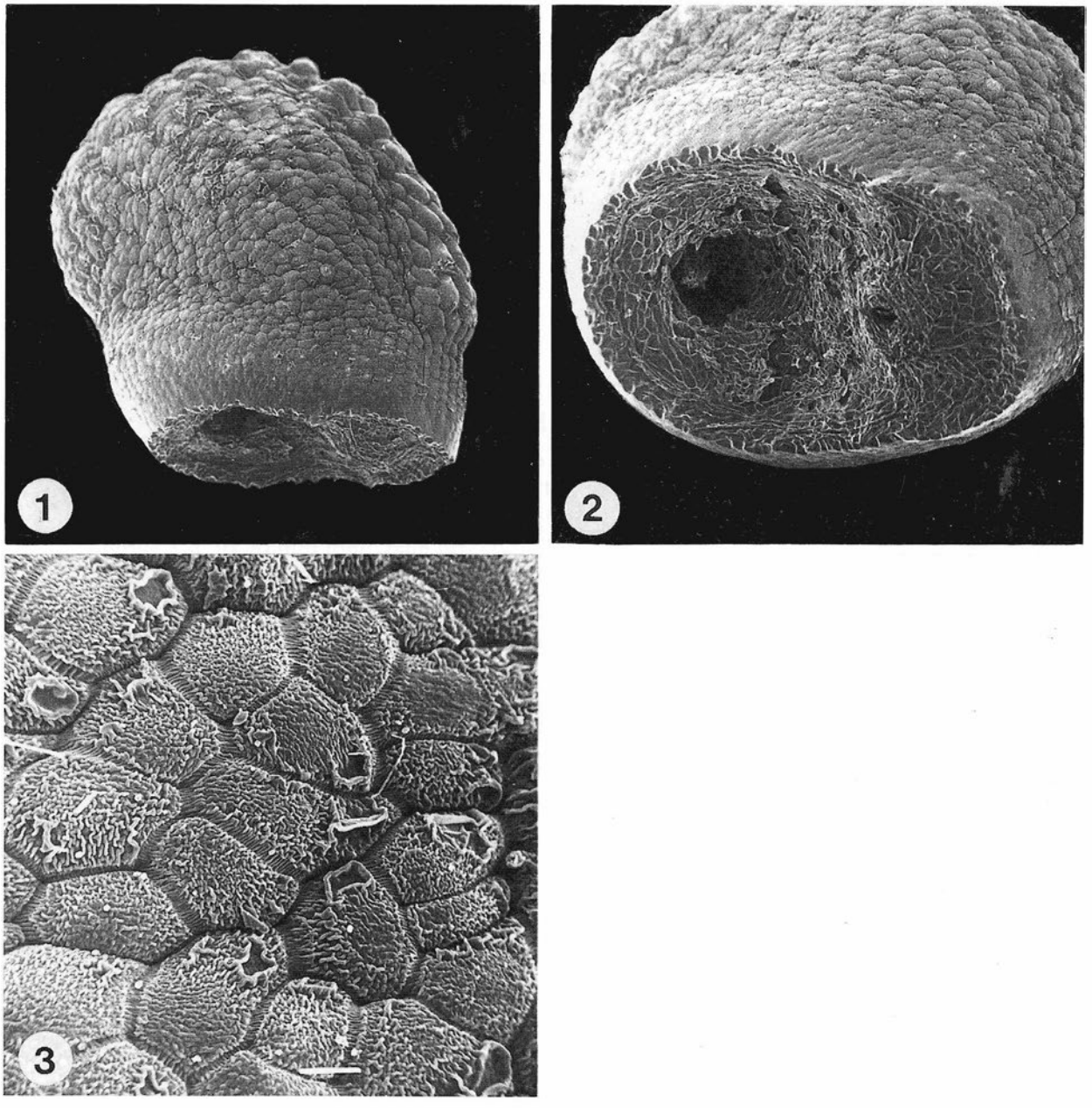




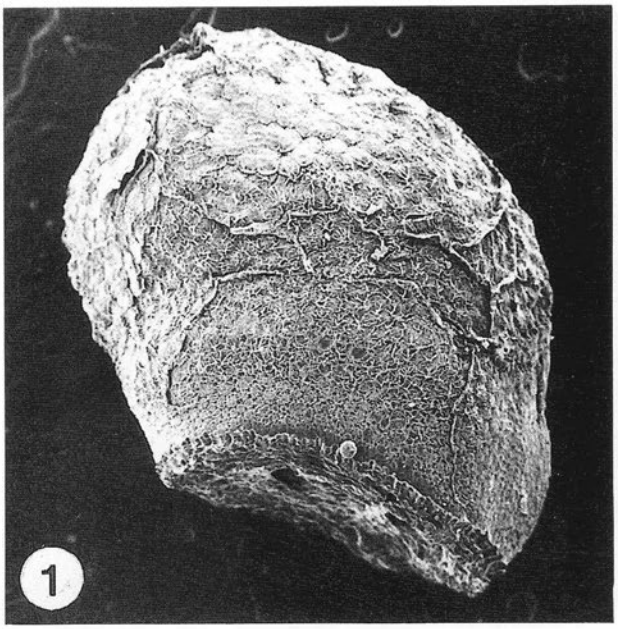
Photograph 17. Seed of *Matucana intertexta* var. *intertexta* (Puente Crisnejas, 1982). 1. Seed in lateral view; 45×. 2. Id., hilum; 60×. 3. Id., testa in basal region; 260×. 4. Id., vertical section; funicular tissue and detached cuticle stippled; 25×. 5. Id., embryo. 6. Id., variability of seed form at the type locality; type A is common, types B and C are exceptional.

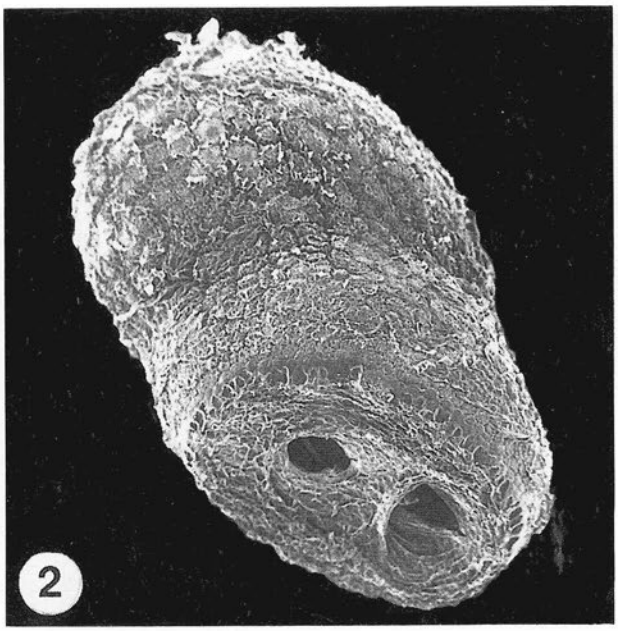


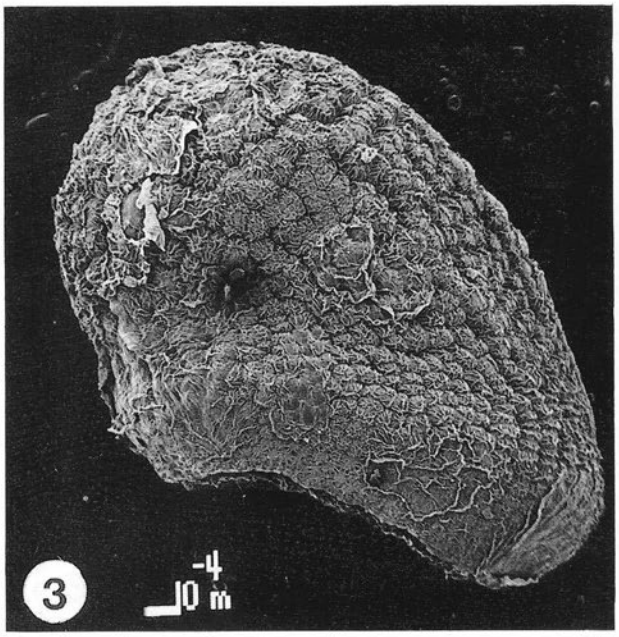
Photograph 18. Seed of *Matucana intertexta* var. *celendinensis* (KK 1039; Knize 1983). 1. Lateral view; 45×. 2. Id., hilum; 55×. 3. Id., apical region; 185×.

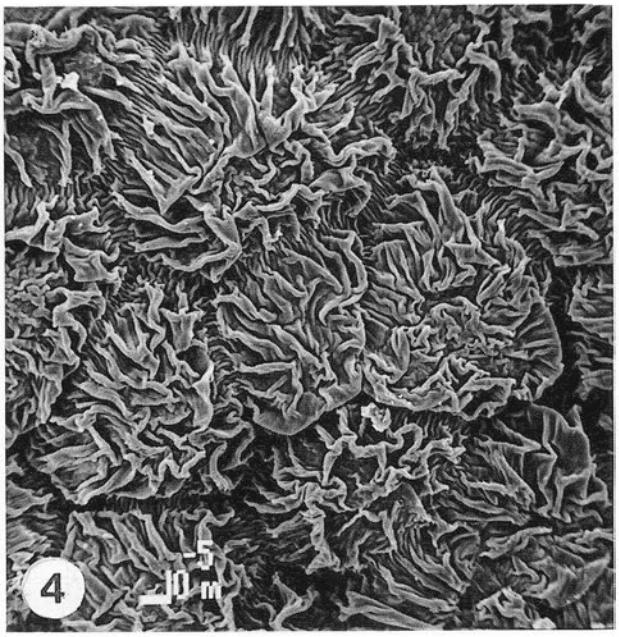


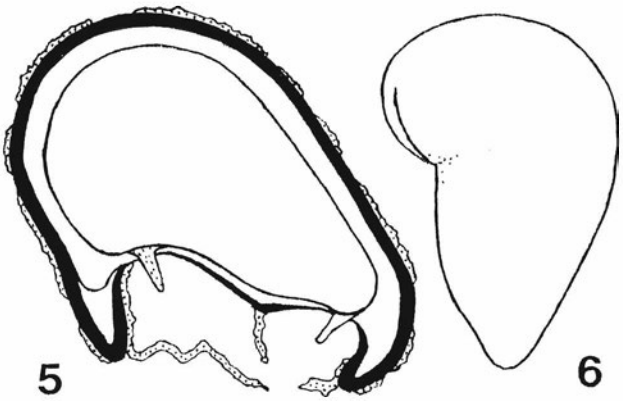
Photograph 19. Seed of *Matucana huagalensis* (Köhres 1981). 1. Lateral view; 50×. 2. Id., hilum; 60×. 3. Id., testa in lateral region; 460×. It is doubtful whether the seeds investigated and illustrated are *M. huagalensis*, but rather *M. intertexta* var. *celendinensis* (see text).











Photograph 20. Seed of *Matucana myriacantha*. 1. Seed (*Matucana* sp. Lau 103; Andreae 1980) in lateral view; 50×. 2. Seed (*Matucana* sp. Lau 173; Andreae 1980) in lateral-basal view showing characteristic holes in the hilum; 55×. 3. Seed (*M. purpureoalba*, de Herdt) in lateral view; 55×. 4. Id., testa in lateral region; 460×. 5. Id., vertical section; funicular tissue and detached cuticle stippled; 40×. 6. Id., embryo.

Matucana huagalensis (Donald & Lau) Bregman, Meerstadt, Melis et Pullen, Succulenta 67(7/8): 155 (1988)
CITES Cactaceae Checklist: *Matucana huagalensis*; huagalensis = from Huagal; Plate 49.

BASIONYM
Borzicactus huagalensis Donald & Lau, Cact. Succ. J. (Gr. Brit.) 25(2): 33 (1970).

SYNONYM
Submatucana huagalensis n.n.

DESCRIPTION
Body green; flattened globose to broad cylindrical, up to appr. 25 cm tall, up to appr. 15 cm wide, hardly offsetting. Ribs appr. 18, straight, relatively acute, with circular tubercles. Areoles oval, 3-4 mm long, 3 mm wide, young areoles with dark wool, appr. 15 mm apart. Radials 18-20, 10-20 mm long, white to pale brown; centrals 3-4, to 40 mm long, pale brown with darker tip.

Flower up to 10 cm long, somewhat oblique; perianth segments pale pink to almost white. Tube pink, appr. 10 mm wide, pubescent.

Fruit globose, green.

Seed as described earlier in this chapter, appr. 1.3 mm long and wide, appr. 0.9 mm thick.

REMARKS
This species was discovered by Alfred Lau in 1968 and described in 1970 by Donald and Lau as *Borzicactus huagalensis*. The holotype is deposited in the herbarium of the University of Heidelberg, Germany, under number L 174.

It seems to be the case that all the seed commercially sold in Europe under the epithet 'huagalensis' comes from *M. intertexta* rather than from the true *M. huagalensis*. Most cultivated plants named *M. huagalensis* have been raised from seed supplied by Knize, not by Lau. These plants (Plate 50) produce the 'normal' red flowers instead of the typical almost white flower of the true *M. huagalensis*. This mix-up is, by the way, understandable since *M. intertexta* has also been recorded from Huagal. Therefore, *Submatucana huagalensis* KK 773a, distributed by Knize, must be considered as a synonym of *M. intertexta.*

Most likely *M. huagalensis* is only known from one locality, and Dr Lau has been the only one who collected there. After his activities no reports have appeared from other persons who claimed to have found *M. huagalensis*. Because of this, *M. huagalensis* is a poorly known species, that is if it is a species and not a white-flowering form of *M. intertexta.* Additional field study is urgently needed to resolve this problem.

DISTRIBUTION
The type material was collected by Lau near the Hacienda Huagal, close to the junction of the Rio Maranon and its confluent Rio Crisnejas, in the Department of

Cajamarca, Peru. The plants were reported as growing upon steep grassy slopes facing east. *M. huagalensis* is only known from this locality.

FIELD NUMBERS
This taxon was brought into circulation solely under number L 174 as *Borzicactus huagalensis*.

Matucana myriacantha (Vaupel) Buxbaum, in: Krainz, Die Kakteen 1.IX (1973)
CITES Cactaceae Checklist: *Matucana myriacantha*; myriacantha = with numerous spines; Plates 51-53.

BASIONYM
Echinocactus myriacanthus Vaupel, Bot. Jahrb. 50, Beibl. 111: 25 (1913).

SYNONYMS
Arequipa myriacantha (Vaupel) Britton & Rose, The Cactaceae 3: 101 (1922).
Submatucana myriacantha (Vaupel) Backeberg, Die Cactaceae 2: 1063 (1966).
Borzicactus weberbaueri var. *myriacanthus* (Vaupel) Donald, Cact. Succ. J. (Gr. Brit.) 26(1): 10 (1971).
Borzicactus myriacanthus (Vaupel) Donald, Ashingtonia 1(9): 100 (1974).
Matucana purpureoalba Ritter, Kakteen in Südamerika 4: 1502 (1981).
Matucana roseoalba n.n.

DESCRIPTION
Body green, globose to broad cylindrical, up to appr. 30 cm tall, 7-12 cm wide; rarely offsetting. Ribs 30-40, divided into 5-8 mm high conical tubercles. Areoles circular to oval, 2.5-4 mm long, 4-7 mm apart. Spination dense, flexible, for the greater part covering the stem epidermis; spination of young areoles standing straight up. Radials and centrals often hard to separate, 25-50 spines per areole, 1-3 cm long; radials white to pale brown; centrals variable in colour (white, yellowish to foxy red) with darker tip.

Flower 5-7 cm long, in anthesis 4-5.5 cm wide, a little oblique; perianth segments pale lilac with darker median stripe. Tube 7-8 mm wide, dark pink, naked or weakly pubescent. Filaments purple at their bases blending to white at the tops, anthers dark lilac to carmine; primary filaments fused at their bases for appr. 7 mm surrounding the style like a collar. Style at the base white, blending to purple at the top; stigma lobes 5, appr. 3 mm long.

Fruit globose, green, appr. 10 mm across.

Seed as described earlier in this chapter, 1.3-1.8 mm long, 1.1-2.0 mm wide, 0.7-1.1 mm thick. At the positions of micropyle and funiculus there are two small to fairly large holes in the hilum. Hilum cup relatively deep, which makes the seed resemble to some degree that of *M. paucicostata*.

REMARKS
This species was discovered in 1904 by Weberbauer and described by Vaupel in 1913. In 1974 Donald overcame the deficiencies in Vaupel's original description

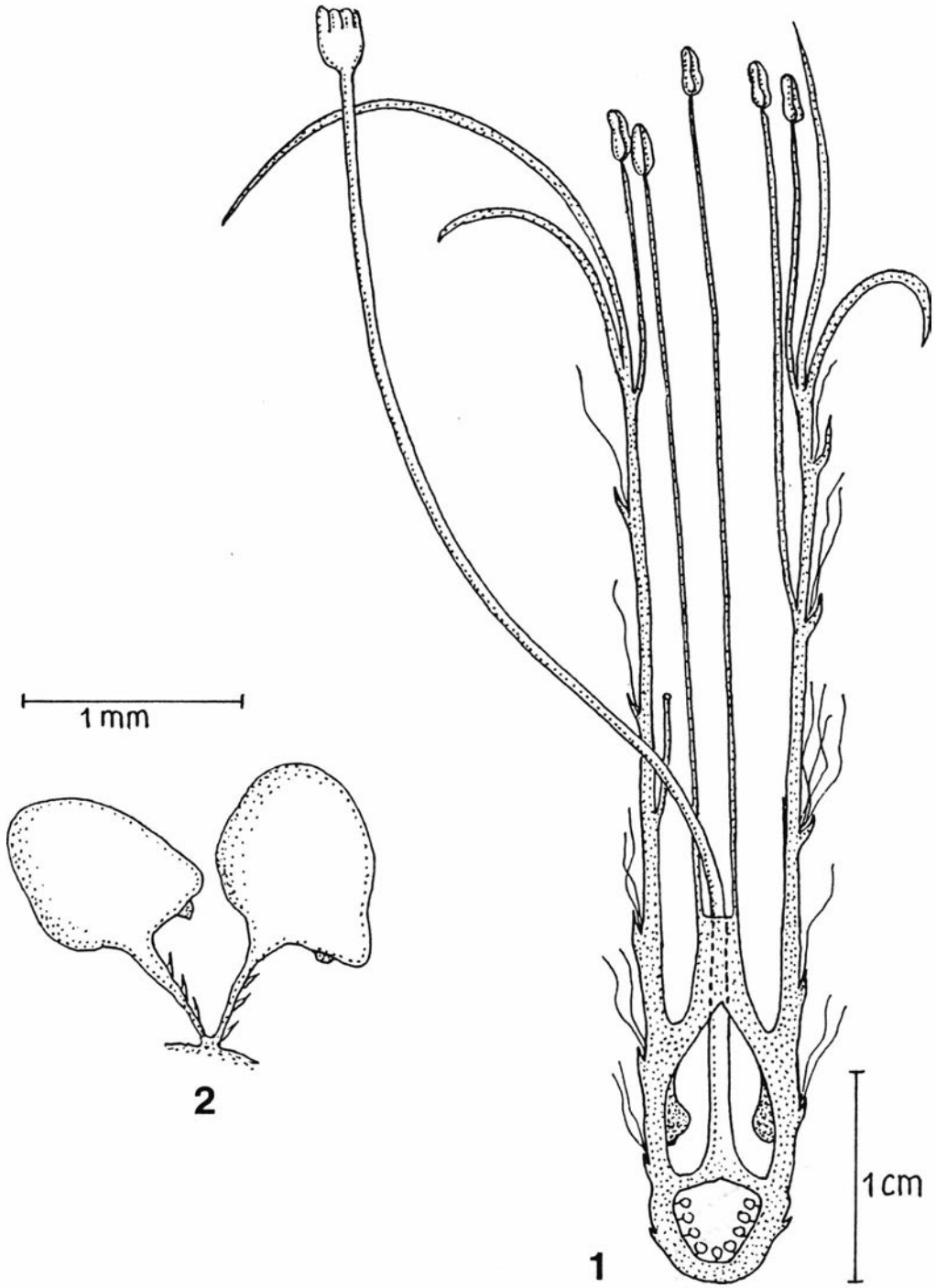


Figure 20. Flower of *Matucana myriacantha* (*Matucana* sp. Lau 173). 1. Flower in vertical section. 2. Id., ovules.

by including additional data from plants collected by Lau (L 103). Unfortunately, the original type material was lost during the Second World War. Consequently, a new type should be designated, which preferably should be selected from Lau 103 plants.

M. myriacantha is highly variable. Flat globular and short spined forms, mostly under the name *Matucana roseoalba* exist, as well as broad cylindrical and longer spined forms. In between these extremes a wide range of intermediate forms are found, so there is no justification for setting up varieties. An exception in this respect may perhaps be made for the plants that bear the Lau fieldnumber L 173 (Plate 53). This taxon has already been briefly discussed earlier in this chapter. Only cultivated specimens from different suppliers are known to the author, which all share a similar cylindrical habit, a dense yellowish spination and, most remarkably, a short orange-red flower.

The Ritter epithet *roseoalba* has never been validly published. *M. purpureoalba* (Plate 52), another Ritter finding and indeed validly published, surely belongs to the myriacantha complex, but additional information is needed to decide whether it deserves to become a subspecies or a variety of *M. myriacantha*. When comparing the original descriptions of *M. myriacantha* and *M. purpureoalba*, it becomes clear that both taxa are very similar; only the colour of the spination and the length of the flower are different, which is not sufficient justification for recognizing separate species. These differences are, however, less distinct in specimens in cultivation. Therefore, awaiting further data, *M. purpureoalba* is thought to represent the southernmost occurring form of *M. myriacantha*.

Distribution

Vaupel (1913) gave the type locality as 'near Balsas, on the eastern bank of the Rio Maranon, at 2200 m altitude, province of Chachapoyas, Department of Amazonas, Peru.' In the 1970s Lau searched there in vain. He did find myriacantha-like plants on the other side of the river, i.e. on the west bank. On that side of the Rio Maranon the distribution of *M. myriacantha* stretches from Balsas in the north to Aricapampa in the south. At the latter locality Ritter found his *M. purpureoalba*.

Field numbers

FR 1063	*Matucana purpureoalba*
KK 1041	*Matucana* sp. (*purpureoalba*)
L 103	*M. myriacantha*
L 103a	*M. roseo-alba*
L173	*Matucana* sp. Rio Crisnejas
L 224	*M. roseo-alba*
WK 537	*M. myriacantha*?

CHAPTER 11

The paucicostata group

Finally the paucicostata group will be discussed. This group is named after the well-known species *M. paucicostata*, perhaps the best-known *Matucana* species of all. It is a rather homogeneous group of species from comparitively warm habitats. It is also the group formerly placed in Backeberg's genus *Submatucana*, as all species have flowers with a hairy tube. The general ease of flowering makes the paucicostata group the most popular group of all the Matucanas.

11.1 TAXONOMY

Plants with the following epithets (validly described taxa and *nomina nuda*) belong to the paucicostata group (published in combination with *Borzicactus*, *Matucana* or/and *Submatucana*):

caespitosa
calliantha
calliantha var. *gigantea*
callianta var. *prolifera*
eriodisa var. *echinata*
formosa
formosa var. *longispina*
formosa var. *minor*
huaricensis
huarinensis
joadii
krahnii
krahnii f. *gracilis*
krahnii var. *major*
krahnii var. *prolifera*
madisoniorum
madisoniorum var. *asterium*
madisoniorum var. *caespitosa*
madisoniorum var. *horridispinum*
madisoniorum var. *pujupatii*
madisoniorum var. *uyupanii*
mamillaris
paucicostata
paucicostata var. *curvispina*
paucicostatus f. *robustispinus*
paucispina
pujupatii
senile
senilis
sp. Chagual
sp. Corral Quemado
sp. Llamellin
sp. Tarapoto
tarapotensis
tuberculata
tuberculosa
turbiniformis.

From this long list, 6 species have been selected:

1. *Matucana paucicostata*
2. *M. tuberculata*
3. *M. krahnii*
4. *M. formosa*
5. *M. pujupatii*
6. *M. madisoniorum.*

These species can be defined by the following description:

Body grey-green (except in *M. tuberculata*), globose to short cylindrical, mostly offsetting at the base. Ribs more or less tuberculate.

Spination in general open, centrals 0-4, radials 0-15.

Flower red; tube relatively slender, mostly pubescent; nectar chamber closed by a diaphragm (except in *M. madisoniorum*) that is formed by fusion of the bases of the primary filaments.

Seed dull black to glossy dark-brown, as wide as or wider than long, more or less cap-shaped; considerably extended dorsally, little to considerable extension ventrally. Seed surface without furrows and humps. Cuticle smooth to strongly folded, outer cuticular layer paper-like and partly fragmented and detached (except in *M. madisoniorum*). Hilum large; funicular tissue strongly reduced. At the positions of funiculus and micropyle there are two large holes in the hilum; sometimes these holes fuse into one large hole, resulting in a deep cavity to the basal side of the seed.

M. krahnii is perhaps better known as *M. calliantha*. For reasons of priority the first mentioned epithet is the correct one.

M. pujupatii was originally described as a variety of *M. madisoniorum*, but differences in stem, flower and seed justify the rank of species.

M. mamillaris Knize n.n. (KK 1638, Plates 65 and 66) is in seed structure in-between *M. krahnii* and *M. paucicostata.* The plant appearance, on the other hand, shows more affinity to *M. tuberculata.* Possibly this plant is a transitional form between *M. paucicostata* and *M. tuberculata.* Awaiting further information this plant is treated here as a synonym of *M. tuberculata.*

Submatucana turbiniformis, S. eriodisa var. *echinata, S. paucispina, S. caespitosa, S. huaricensis* and *S. senilis* are all synonyms of *M. paucicostata.*

An interesting taxon is the Knize finding *Submatucana tarapotensis* n.n. (KK 1602), initially distributed under the name *Submatucana* sp. Tarapoto. Seed, stem and flower indicate that it is very close to *M. pujupatii.* Hence, it is here brought under that species.

11.2 PHYLOGENY

The species of the paucicostata group are considered here to be the most developed group of the genus *Matucana.* They could evolve only after the time that its ancestors reached the upper course of the Rio Maranon. It follows that the most southerly and at highest altitude occurring species (*M. paucicostata*) is most likely the least developed species of this group. This species has seeds that exhibit some similarities with the other species groups of *Matucana*, particularly with those species of the intertexta group that also come from the Rio Maranon valley.

From the above it is deduced that the evolution of the other species of the paucicostata group has taken place from south to north, 'simply' by following the Rio Maranon downstream. The seed and the flower structure of the species from south to north, change gradually. The outcome is that the seeds of the southernmost species, i.e. *M. paucicostata* from Huari, look very different from those of the northernmost species, i.e. *M. madisoniorum* from Bagua. However, studying the seeds of *M. tuberculata, M. krahnii, M. formosa* and *M. pujupatii* in that order, confirms that the morphology of the seed changes gradually. This will be further explained in Section 11.3.

Another common characteristic of the species of the paucicostata group is the requirement for heat in the growing season. Of course this is due to the relatively low altitude of the habitats. The altitude in this section of the Rio Maranon valley decreases from 2500 m to only 400 m above sea level. So in altitude only *M. paucicostata* is comparable to the other species groups of *Matucana*; the other members of the paucicostata group are warm tropical species which therefore require more attention during the winter when cultivated in the cold and temperate regions of the globe.

According to seed morphology *M. tuberculata* is the closest relative of *M. paucicostata*. The other 4 species have seeds that display a changing shape, which has been brought about by different stages of dorsal and/or ventral broadening of the seed. In *M. krahnii* the dorsal part of the seed is starting to extend, whereas in *M. formosa* the dorsal extension is considerable. The two most developed species of all are *M. pujupatii* and *M. madisoniorum*, both having dorsally and ventrally extended seed structures.

Ritter stated that *M. madisoniorum* is closely related to *M. oreodoxa* since both have an open nectar chamber. This conclusion is most likely to be incorrect for two reasons: firstly, the seeds are entirely different, and, secondly, between the habitats of both species there is a large area of approximately 500 km.

11.3 SEED MORPHOLOGY

The species of the paucicostata group make interesting subjects for seed studies. In the other species groups of *Matucana* the differences between the seeds of two species groups are generally small and in most cases the species cannot be identifed by their seeds alone. Conversely, in the paucicostata group each species has its own typical seed features or typical combination of seed features. Depending on the species the seeds may vary in the following characteristics:

1. Shape in lateral view, possession of dorsal and/or ventral extensions.
2. Dimensions of the hilum (which is a consequence of the preceding feature).
3. Mode of hilar depression, in other words the depth of the hilum cup.
4. Mode of funicular tissue reduction.
5. Thickness of the testa.
6. Folding of the cuticle.
7. Dimension and shape of the embryo.

In *M. paucicostata* all the seed features listed above are in their plesiomorphic (original, ancestral) state of development. Hence, the seed shows a weak dorsal

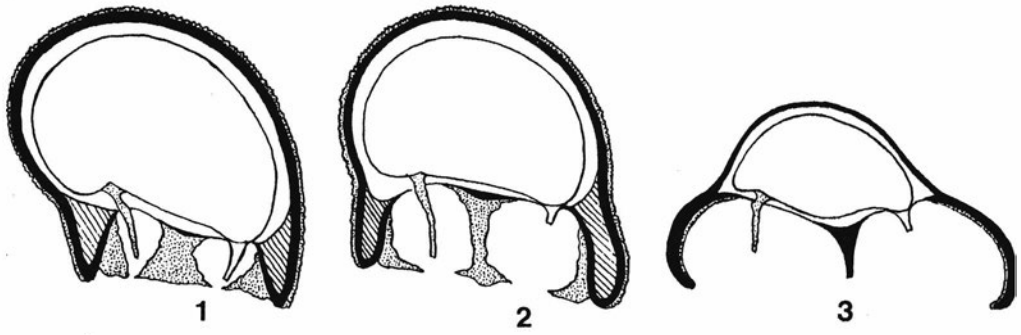


Figure 21. Seeds of *Matucana haynei* (1), *M. paucicostata* (2) and *M. madisoniorum* (3) in vertical section to show seed development in the paucicostata group: increase of the hilum cup, reduction of funicular tissue and development of a transverse ridge inside the hilum cup. Funicular tissue and outer cuticular layer stippled.

and almost no ventral extension, the hilum is not very much larger than in the other species groups, the hilum cup is still rather shallow, the testa is thick, the cuticle is strongly folded and the embryo has bent cotyledons. Many of these characteristics are also found in the species of the intertexta group, most conspicuously in *M. myriacantha*. In contrast to *M. paucicostata, M. madisoniorum* has very large seeds with strongly developed dorsal and ventral extensions. Consequently, the hilum is very large. Furthermore, the hilum cup in this species is very deep, the funicular tissue has entirely disappeared, the testa is thin and the embryo is much smaller and has straight cotyledons. Many of these changes are illustrated in Figure 21. The remaining four species of the paucicostata group exhibit seeds with an intermediate morphology. The reason for these changes in seed structure must be looked for in a different mode of seed dispersal, as was discussed in Chapter 4.

Donald (1979) asked the question as to whether we are dealing here with one variable species. The seed features discussed above as well as certain flower characteristics are constant in all six species recognized here. As far as is generally accepted currently, there is only variation in seed between species, and hardly at all within a species. That means that there is no genetic exchange between the species, which is one of the principle conditions for treating taxa as separate species. A second plea for rejecting the one species concept is the difference in flower and seed between the two extreme 'forms', viz. *M. paucicostata* and *M. madisoniorum*. Even the most fanatical 'lumper' would refuse to combine these two into the one species.

11.4 DISTRIBUTION

As has already been pointed out, the species of the paucicostata group grow in the valley of the Rio Maranon, a major tributary of the Amazon, running in a northwest direction between the western and the central Cordilleras in northern Peru. The habitats of the species are drawn in Figure 22. These localities have been based upon data from long published literature. During the last 20 years many

Figure 22. Distribution of the species of the paucicostata group.

habitats have been plundered by commercial collectors, so it is doubtful whether the distribution map still represents the actual situation. Fortunately, though, many terraces along the Maranon basin are as good as inaccessible,which is in fact a favourable situation for allowing plant species to survive. For example, the distribution of *M. formosa* is known to consist of two areas widely separated by an unexplored region; its habitats are very likely to be connected in some way. Also, much more information is needed about the distribution of *M. paucicostata* and *M. tuberculata*. These species are recorded as from both sides of the Rio Ma-

ranon, but it is to be expected that in reality the gap between the two known distribution zones of these species is much smaller.

One of the puzzling aspects concerning the distribution of the paucicostata group is the distribution of the plants that grow near Tarapoto in the Department of Amazonas. If this is in fact the Tarapoto in question, then these *M. pujupatii*-like plants were discovered by Knize in a region far away from the Maranon valley, the nearest *Matucana* species being *M. krahnii* rather than *M. pujupatii*. Nothing is known about the presence of Matucanas in the intervening area, which does not generally seem to be very suitable for the support of cacti anyway, since it is mostly covered by tropical rainforest. Solving this puzzle may be a challenge for future explorers.

Figure 22 shows that all species but one grow in the direct vicinity of the Rio Maranon; only *M. krahnii* comes from a region farther away from the river.

11.5 KEY TO THE SPECIES OF THE PAUCICOSTATA GROUP

1a. Plant with only a few spines per areole or spineless; flower without a diaphragm; seed glossy dark brown with very large hilum devoid of funicular tissue ..... *madisoniorum*
1b. Plant with radials and/or centrals; flower with diaphragm; seed dull black with brownish cuticular remnants, hilum with funicular tissue 2
2a. Ribs 20-30; seed with large dorsal recess (seed 'shoe-shaped') ..... *formosa*
2b. Ribs 7-15; seed with smaller dorsal recess (seed cap-shaped or bag-shaped 3
3a. Plant with bright green epidermis; spines straight; flower relatively short (appr. 5 cm long) *tuberculata*
3b. Plant with dark green to grey green epidermis; spines curved; flower longer than 6 cm ... 4
4a. Radials 8-15; flower up to 85 mm long, tube narrow (appr. 5 mm wide), primary filaments fused at the base over appr. 15 mm ..... *krahnii*
4b. Radials 4-8; flower up to 70 mm long, tube 6-8 mm wide; primary filaments fused at the base over appr. 5 mm 5
5a. Seed bag-shaped, hilum cup shallow ..... *paucicostata*
5b. Seed cap-shaped, hilum cup deep ..... *pujupatii*

11.6 THE SPECIES OF THE PAUCICOSTATA GROUP

Matucana paucicostata Ritter, Taxon 12(3): 124 (1963)
CITES Cactaceae Checklist: *Matucana paucicostata*; paucicostata = with few ribs; Plates 54-61.

SYNONYMS

Submatucana paucicostata (Ritter) Backeberg, Descr. Cact. Nov. 3: 14 (1963).
Borzicactus paucicostatus (Ritter) Donald, Cact. Succ. J. (Gr. Brit.) 26(1): 10 (1971).
Borzicactus paucicostatus fa. *robustispinus* Donald & Lau, Cact. Succ. J. (Gr. Brit.) 26(3): 71 (1971).
Submatucana paucicostata var. *curvispina* n.n.
Submatucana caespitosa n.n.
Submatucana huaricensis n.n.

Submatucana huarinensis n.n.
Submatucana paucispina n.n.
Submatucana senile n.n.
Submatucana senilis n.n.
Submatucana sp. Llamellin
Submatucana eriodisa var. *echinata* n.n.
Submatucana turbiniformis n.n.

DESCRIPTION

Body dark grey-green, globose to short cylindrical, 7-15 cm tall, 4-7 cm wide; strongly offsetting at the base; short thick tap-root. Ribs 7-11, broad, straight, divided into conical tubercles. Areoles circular to oval, 2-3 mm long, grey, 10-15 mm apart. Spination reddish brown when young, turning grey later, curved, somewhat flexible; radials 4-8, 5-30 mm long; centrals 0-1, up to 30 mm long.

Flower appr. 6 cm long, in anthesis appr. 3 cm wide, carmine. Tube slightly curved, appr. 6 mm wide, with whiteish pubescence. Nectar chamber appr. 10 mm long, closed by a diaphragm. Nectar glands yellow, beneath the diaphragm. Filaments purple; anthers orange; primary filaments fused at the base over appr. 5 mm forming a collar around the style. Style red, stigma lobes 4-5, appr. 2 mm long, green.

Fruit green, appr. 8 mm long and 11 mm wide.

Seed dull black with irregular brown-yellow cuticular remains, 1.1-1.3 mm long, 1.0-1.4 mm wide, 0.7-1.2 mm thick, weakly extended ventrally and dorsally. Hilum broadly elliptical; funicular tissue pale yellow, attached to the hilar margin leaving one or two holes in the centre of the hilum. Testa cells slightly convex with strongly folded cuticle. Embryo pear-shaped, slightly bent.

REMARKS

M. paucicostata is a variable species. Ritter selected only one phenotype from a highly variable population (Donald 1979). The holotype is deposited in the herbarium of the University of Utrecht, Netherlands, under number FR 597.

The forma *robustispina* differs from the type in having a greener epidermis and stronger spination. These features do not exceed the natural range of variation and it is merely a phenotype as well. The same applies to *Submatucana paucicostata* var. *curvispina*, which is distinguishable from the type by a greener epidermis and more clearly developed tubercles (Skarupke 1974).

Knize has collected at many locations. Even the slightest variations have been given different names which are all invalid (*nomina nuda*). For example, the four 'species' *Submatucana turbiniformis, S. huaricensis* (Plate 56), *S. caespitosa* (Plate 57) and *S. senilis* (Plate 58) cannot be separated from *M. paucicostata*. Their flowers, fruits and seeds are identical, so these four names have been brought under *M. paucicostata*.

Confusion exists about the Knize plants *Submatucana eriodisa* and its 'variety' *echinata*. The former is without doubt *M. oreodoxa*, but the latter is very similar to *M. paucicostata*. Var. *echinata* (Plate 61) is a weakly spined plant with a flower which is slightly longer and more slender than in *M. paucicostata*. Further information is needed.

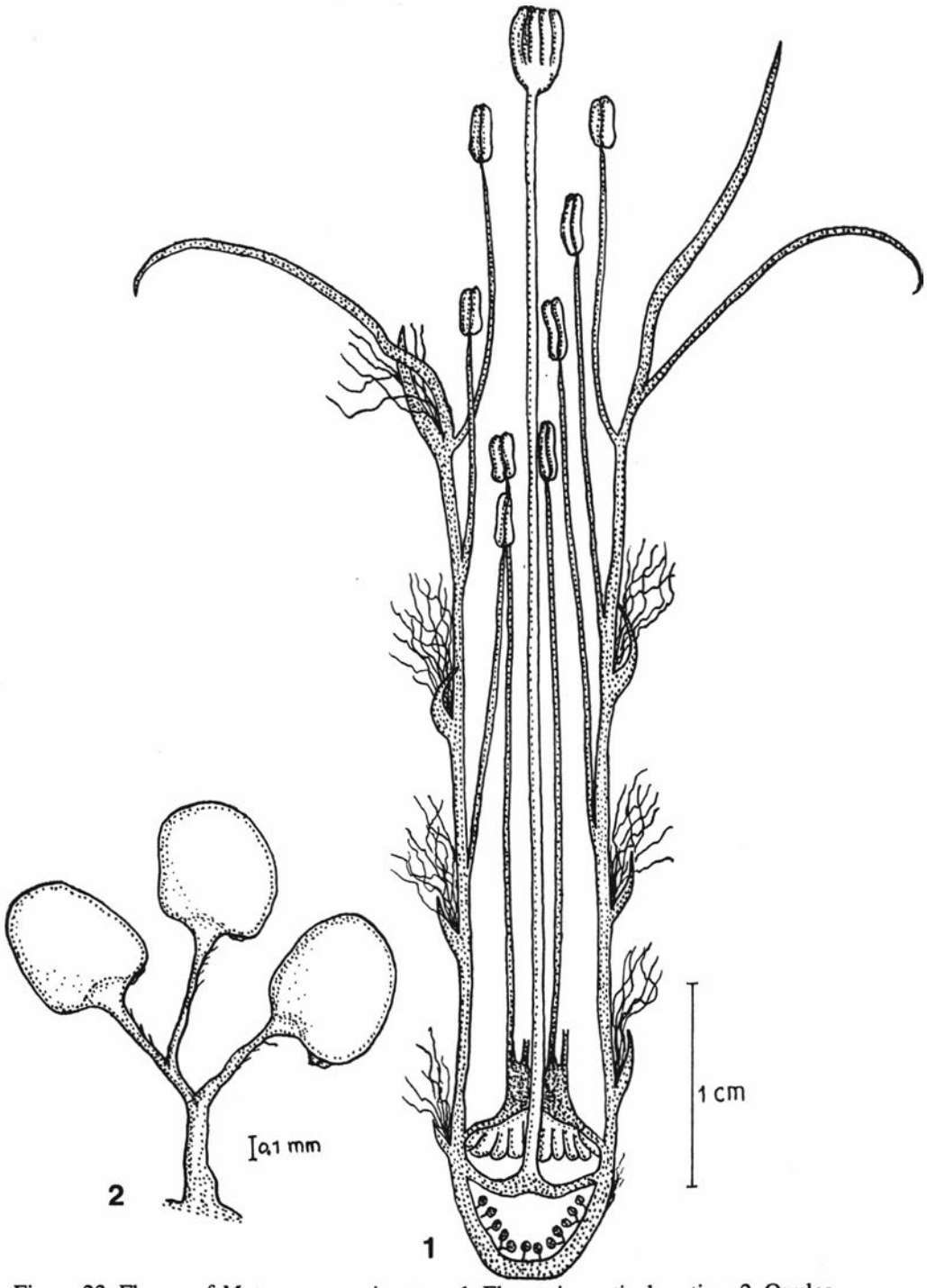
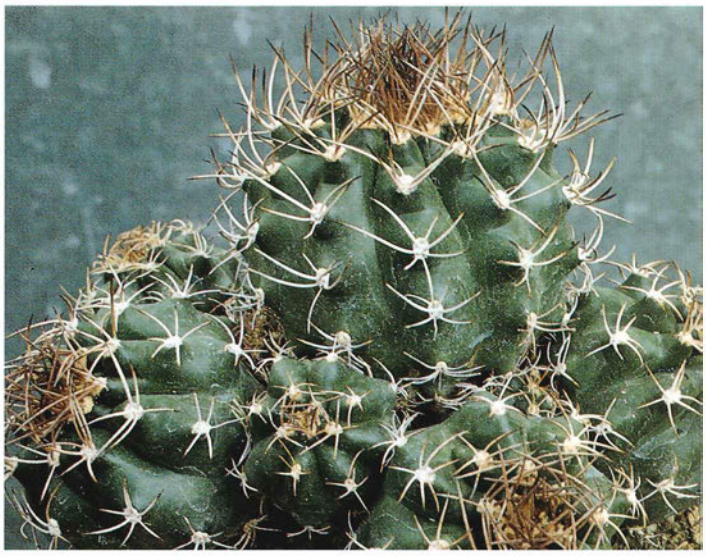


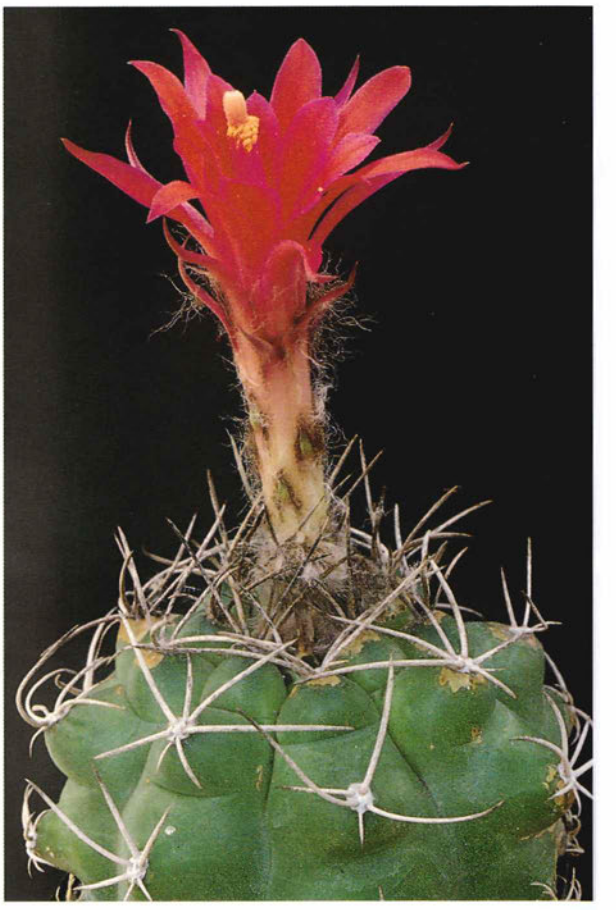
Figure 23. Flower of *Matucana paucicostata*. 1. Flower in vertical section. 2. Ovules.

Plates 54-57. Forms of *Matucana paucicostata*

54. *M. paucicostata*, cultivated specimen.
55. *M. paucicostata*, ex-habitat specimen in the Heidelberg Botanic Garden under number 30970.
56. *Submatucana huaricensis*, raised from Köhres 2294 seed.
57. *S. caespitosa* KK 1317, cultivated specimen.

54	55
56	57





DISTRIBUTION

Ritter discovered this species in 1956. The type locality is Rahuapampa, province of Huari, Department of Ancash, Peru.

M. paucicostata is reported to occur in the provinces Huari and Antonio Raymondi. The plants grow in the valleys of the Rio Puchca, Rio Mosna and Rio Huari. In this area also *M. oreodoxa, M. comacephala, M. crinifera* and the KK plants *M. lutea* and *M. luteispina* can be encountered. The altitude is between 1800 and 2800 m above sea level, being much higher than the altitudes for the remaining species of the paucicostata group. It should otherwise be noted that many of the altitudes given by Knize in his field number list are incorrect; more than half of his data on altitudes is too high.

M. paucicostata was also discovered on the other side of the Rio Maranon, in the Department of Huanuco. Little is known about the size of this distribution.

Lau reported the habitat of *M. paucicostata* as between Huari and the Rio Puchca. The altitude given for this locality, 288 m, must be a printing error. Knize listed the following localities: San Marcos, 2800 m; Huari, 2500 m; Aczo, province of Antonio Raymondi, 2800 m; Llamellin, 1800 m. For the forma *robustispina* too, the locality 'Rio Puchca, 2800 m' is given.

FIELD NUMBERS

DM 29	*M. paucicostata*
FR 597	*Matucana paucicostata*
KK 728	*Submatucana turbiniformis*
KK 754	*Submatucana* sp. Llamellin
KK 754	*S. senile*
KK 754	*S. senilis*
KK 755	*S. paucicostata*
KK 791	*S. paucicostata*
KK 1317	*S. caespitosa*
KK 1431*	*S. eriodisa* var. *echinata*
KK 1450	*S. huarinensis*
KK 1471	*S. paucicostata*
KK 1768**	*S. paucicostata*
KK 1777	*Submatucana* sp.
KK 1778	*Submatucana* sp.
KK 1779	*Submatucana* sp.
L 187	*Borzicactus paucicostatus* fa. *robustispinus*
WK 534	*Matucana paucicostata*

*This number is now *Neochilenia* sp.
**This number is now *Cintia napina*.

The German firm of G. Köhres has sold seeds of plants under different names that are definitely forms of *M. paucicostata*. These are:

Köhres 2289	*Submatucana paucispina*
Köhres 2294	*S. huaricensis*
Köhres 3773	*Submatucana* sp. Llamellin

58 | 59
60 | 61

Plates 58-61. Forms of *Matucana paucicostata*

58. *Submatucana senilis* KK 754, cultivated specimen.
59. *S. paucispina*, cultivated specimen raised from Köhres 2289 seed.
60. *Submatucana* sp. Llamellin, cultivated specimen raised from Köhres 3773 seed.
61. *S. eriodisa* var. *echinata* KK 1431, cultivated specimen.

Matucana tuberculata (Donald) Bregman, Meerstadt, Melis et Pullen, Succulenta 66(9): 175 (1987)
CITES Cactaceae Checklist: *Matucana tuberculata*; tuberculata = tuberculate; Plates 62-66.

BASIONYM
Borzicactus tuberculatus Donald, Cact. Succ. J. (USA) 51(2): 155 (1979).

SYNONYMS
Matucana tuberculosa Ritter, Kakteen in Südamerika, Band 4: 1505 (1981).
Matucana chagualensis n.n.
Submatucana tuberculosa n.n.
Submatucana mamillaris n.n.
Submatucana sp. Chagual n.n.

DESCRIPTION
Body bright green, globose to oval, appr. 10 cm tall, 4-7 cm wide, strongly offsetting at the base or higher up the stem, no tap-root. Ribs 14-18, fairly broad, straight to somewhat twisted, divided into tubercles; tubercles conical, up to 10 mm long. Areoles circular, 2-3 mm across, white, 4-12 mm apart. Spination white to yellowish, straight; radials 8-12, 5-10 mm long; centrals 1-4, with dark-brown tip, 10-20 mm long.

Flower 5-5.5 cm long, in anthesis 3.5-4 cm wide, perianth segments orange-red with violet margin. Tube straight to curved, 4-5 mm wide, with white to brown hairs. Nectar chamber appr. 4 mm long and 3 mm wide, closed by a diaphragm. Nectar glands yellowish and parietal. Filaments white at the base blending to purple at the top, anthers reddish, primary filaments fused at the base over appr. 2 mm. Style reddish; stigma lobes 7-8, 1.5 mm long, reddish.

Fruit globular, green and red-brown, appr. 6 mm across.

Seed dull black with brown-yellow irregular cuticular remnants, 1.1-1.3 mm long, 1.0-1.4 mm wide, 0.7-1.2 mm thick; ventrally not extended, dorsally moderately extended. Hilum circular to oval; funicular tissue pale yellow, attached to the hilar margin, with one oval or two circular holes. Testa cells slightly convex with weakly folded cuticle. Embryo pear-shaped.

REMARKS
Ritter discovered this species in 1960 but it was not until 1981 that he described it as *Matucana tuberculosa*. Unfortunately for him, he was too late, because 2 years earlier the same plant had already been described by Donald as *Borzicactus tuberculatus*. This description was made from material that had been collected by Hutchison, Wright and Straw in 1964. *Matucana tuberculosa* Ritter and *Borzicactus tuberculatus* Donald turned out to be the same species, although the diagnoses of both plants do not totally match. For example, Donald stated that the nectar chamber is open, but that must be an error. For reasons of priority, the correct epithet of this plant must be *tuberculata*.

The holotype is in Pomona, USA, under number PCH 6218.

Submatucana mamillaris n.n. (KK 1638, Plates 65 and 66) is thought to be-

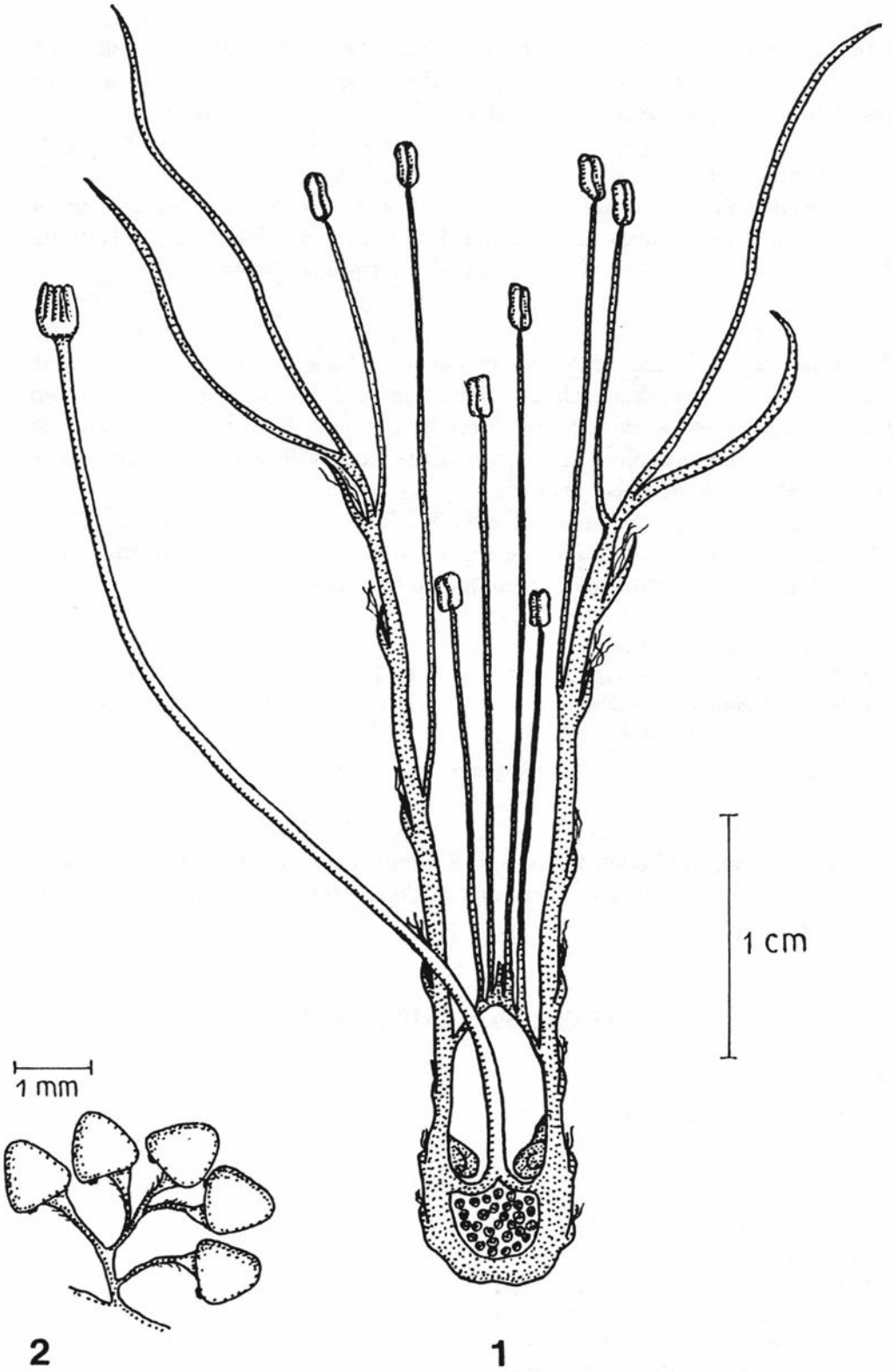


Figure 24. Flower of *Matucana tuberculata*. 1. Flower in vertical section. 2. Ovules.

long to *M. tuberculata* due to its green epidermis and its short flower. Its seed, however, is slightly different in having a strongly folded cuticle, similar to the seed of *M. krahnii* and *M. paucicostata*. This is not surprising when one realises that KK 1638 comes from the Maranon area in the Department of Huanuco. So based on seed morphology and habitat localization KK 1638 could be a transitional form between *M. paucicostata* and *M. krahnii*.

As well as the tuberculate form with short white spines a less tuberculate form with longer yellow spines has appeared in collections (Plate 63). In every other feature it is *M. tuberculata*. The origin of this form is unknown.

DISTRIBUTION

The type locality is the west-bank of the Rio Maranon 18 km south of Aricapampa, province of Huamachuco, Department of La Libertad, Peru. Another finding place is in the same valley 5 km more south. Both Ritter and Lau mentioned the mountains above El Chagual as the locality. The vertical distribution is from 1800 to 2400 m above sea level.

In the same area but at lower altitude, *M. formosa* occurs. Populations of *M. tuberculata* and *M. formosa* are separated by appr. 200 m difference in altitude. Despite this short distance, there are no reports of hybridization.

FIELD NUMBERS

FR 1073	*Matucana tuberculosa*	L 223	*S. tuberculata*
KK 1638	*Submatucana mamillaris*	PCH 6218	*Borzicactus tuberculatus*
KK 1653*	*Submatucana* sp. Chagual	PCH 6223	*B. tuberculatus*

*This number is now *Cleistocactus orthogonus*.

Matucana krahnii (Donald) Bregman, Kakteen u.a. Sukk. 37(12): 253 (1986)
CITES Cactaceae Checklist: *Matucana krahnii*, *Matucana calliantha*; krahnii = named after W. Krahn; Plates 67-71.

BASIONYM

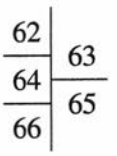
Borzicactus krahnii Donald, Cact. Succ. J. (USA) 51(2): 52 (1979).

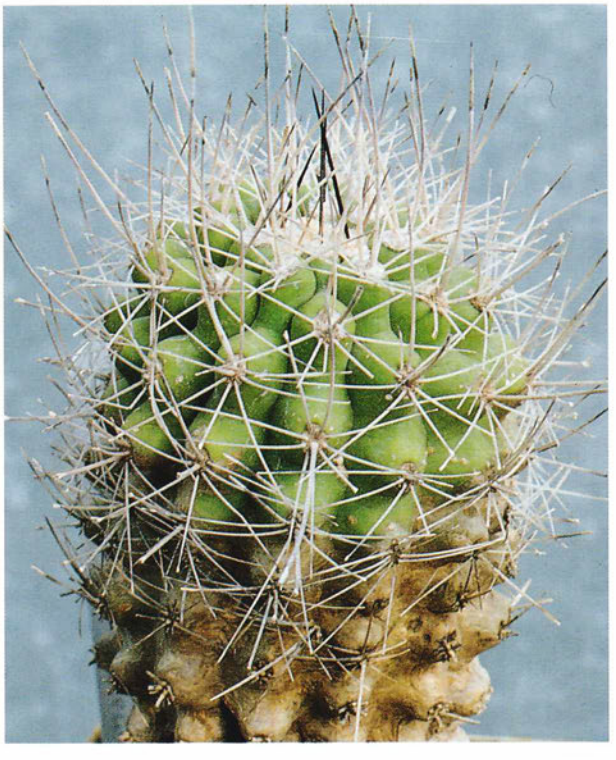
SYNONYMS

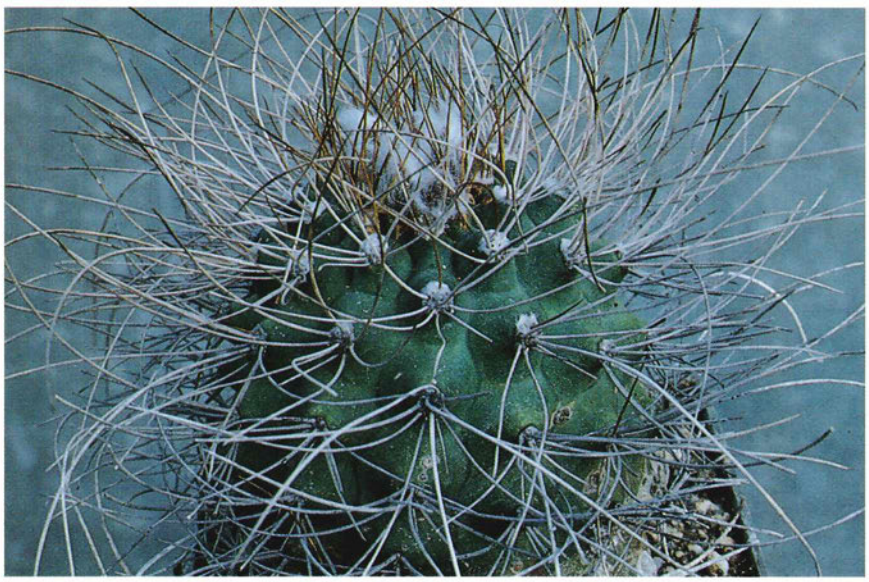
Borzicactus krahnii fa. *gracilis* n.n.

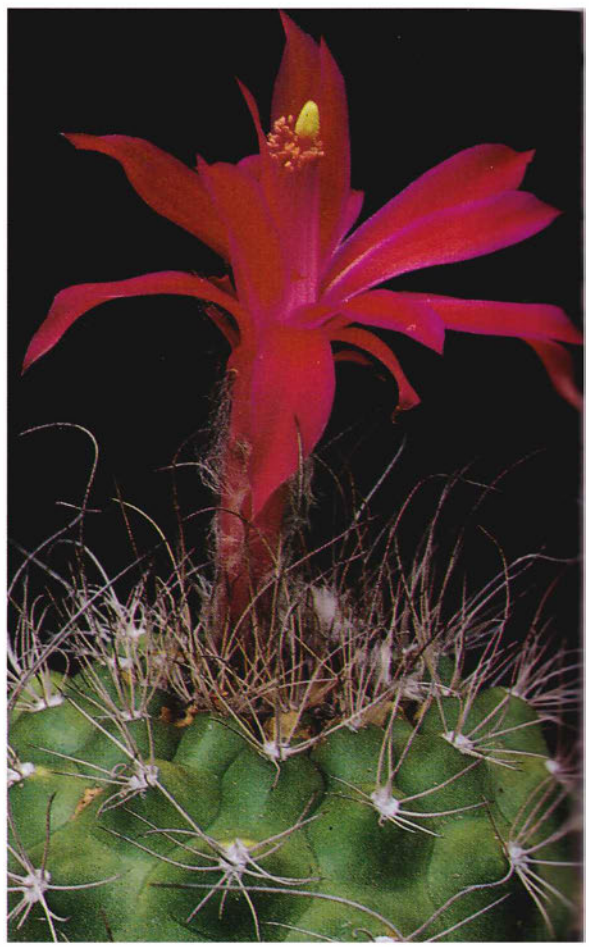
Plates 62-66

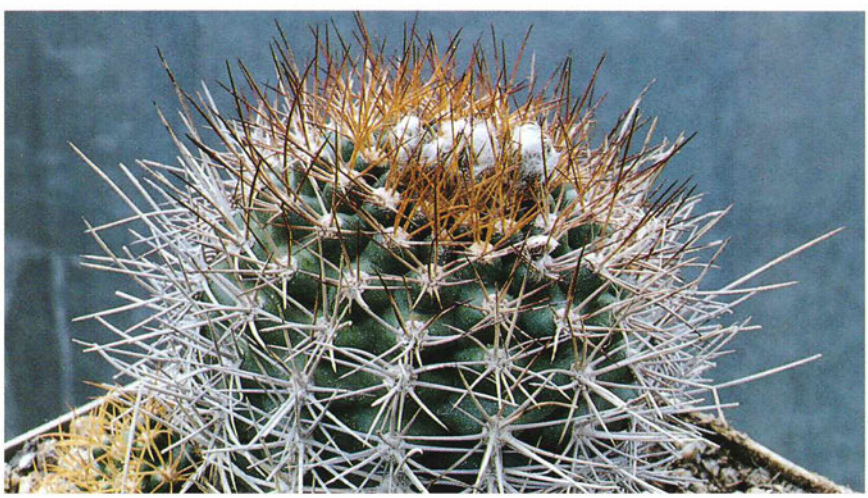
62. *Matucana tuberculata*, cultivated specimen.
63. *M. tuberculata*, form with long yellow spines in cultivation.
64. *M. tuberculata*, natural specimen from El Chagual in the Heidelberg Botanic Garden, labelled '*M. chagualensis*, nr. 54273'.
65. *M. tuberculata* (*Submatucana mamillaris* KK 1638) in cultivation.
66. *Matucana tuberculata* (*Submatucana mamillaris*), ex-habitat specimen collected near the Rio Maranon, dept. Huanuco, numbered 54299 in the Heidelberg Botanic Garden.











Matucana calliantha Ritter, Kakteen in Südamerika, Band 4: 1490 (1981).
Matucana calliantha var. *gigantea* n.n.
Matucana calliantha var. *prolifera* Ritter, Kakteen in Südamerika, Band 4: 1491 (1981).
Submatucana calliantha n.n.
Submatucana calliantha var. *gigantea* n.n.
Submatucana krahnii n.n.
Submatucana krahnii var. *major* n.n.
Submatucana krahnii var. *prolifera* n.n.

Description

Body grey-green, flattened globose to short cylindrical, 10-14 cm tall, 5-10 cm wide, mostly weakly offsetting at the base, no tap-root. Ribs 10-18, broad, straight, divided into tubercles; tubercles conical, up to 10 mm long. Areoles circular, 2-4 mm across, with white wool, 7-10 mm apart. Spination yellow-brown, turning grey in later life, mostly curved, flexible; radials 8-15, 15-50 mm long; centrals 1-4, mostly 20-80 mm long, sometimes up to 150 mm long.

Flower up to 8.5 cm long, in anthesis up to 7 cm wide, carmine. Tube straight to weakly bent, appr. 5 mm wide, with whitish pubescence. Nectar chamber appr. 2 mm long and 3 mm wide, closed by a diaphragm. Nectar glands parietal, weakly developed. Filaments purple, anthers orange-yellow; primary stamens fused at the base over appr. 15 mm. Style purple; stigma lobes 6-7, 3 mm long, greenish yellow.

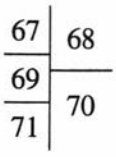
Fruit globular, green with brown-red spots, appr. 10 mm across.

Seed dull black with irregular brown-yellow cuticular remnants, 1.2-2.0 mm long, 1.0-1.3 mm wide, 0.7-1.0 mm thick, ventrally not extended, dorsally strongly extended. Hilum oval; funicular tissue with one large oval hole or two circular smaller holes, pale yellow, attached to the hilar margin. Testa cells slightly convex, cuticle strongly folded. Embryo pear-shaped.

Remarks

This species is possibly better known under its improper name *M. calliantha*. It was discovered more or less simultaneously by both Hutchison and Ritter. The material collected by Hutchison was first published in 1979 as *Borzicactus krahnii*, so *krahnii* should be the correct epithet, as Ritter was two years late with his name *calliantha*.

Plates 67-71
67-68. *Matucana krahnii*, cultivated specimens.
69. *M. krahnii*, ex-habitat specimen with unusually long spination, kept in the Heidelberg Botanic Garden under number 52768. The precise locality is unknown, the label only says '*Matucana krahnii*, 1200 m, Peru'.
70. *M. krahnii* (*Submatucana calliantha* var. *gigantea* KK 758), cultivated specimen.
71. *Matucana krahnii*, ex-habitat specimen in the Heidelberg Botanic Garden, labelled RH 178.



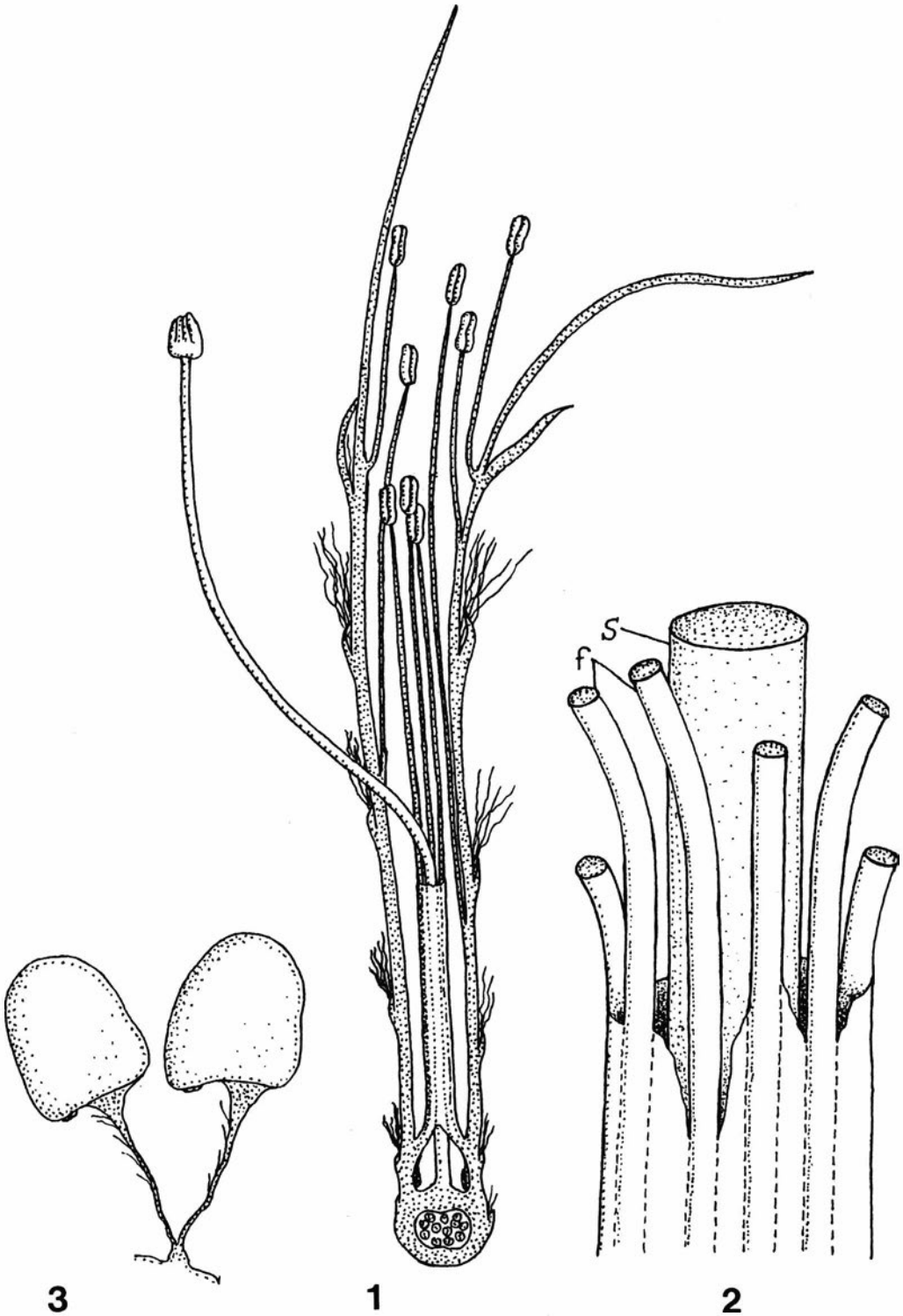


Figure 25. Flower of *Matucana krahnii*. 1. Flower in vertical section. 2. Id., detail of fused bases of the primary filaments; s = style, f = filaments. 3. Ovules.

Ritter recognized a variety *prolifera*, which should be different from the type by virtue of the following features:

Body smaller, 2-3 times as tall as wide, extremely offsetting. Flower smaller, up to 7 cm long; basal fusion of primary filaments only 4 mm. Seed larger (2 mm wide).

Imported seeds of this taxon proved to be identical to those of the type, in contrast to the diagnosis by Ritter. The other discriminating features have not been observed in cultivated material, therefore until further notice this taxon deserves no special rank.

Donald (1979) wrote that three phenotypes can be distinguished. The forma *gracilis*, the forma *minor* and, of course, the typical form (forma *krahnii*). The forma *gracilis* is distinct in having a smaller and more slender body, and the forma *minor* is relatively strongly tuberculate with shorter spines. Clearly these are just phenotypes as Donald stated, i.e. variations induced by environmental differences. Therefore, they do not deserve an infraspecific rank either. The same applies to the Knize varieties *major* and *gigantea*.

All epithets combined with the generic name *Submatucana* have not been validly published. Yet, they still appear frequently in seed and plant catalogues.

The holotype is in Pomona, USA, under number PCH 4954.

DISTRIBUTION

The type locality is situated on the east-bank of the Rio Maranon, 16 km to the north of Balsas, in the province of Chachapoyas, Department of Amazonas, Peru. The plants grow on steep, rocky slopes of sandstone at 1650-1750 m altitude. This species seems to be rather limited in both its horizontal and vertical distribution.

FIELD NUMBERS

DM 19	*Matucana krahnii*	KK 758	*S. krahnii*
DM 65	*M. krahnii* fa. *gracilis*	KK 758a	*S. krahnii* var. *major*
FR 1308	*M. calliantha*	L 178	*S. krahnii*
FR 1308a	*M. calliantha* var. *prolifera*	L 178a	*S. krahnii* var. *prolifera*
KK 758	*Submatucana calliantha*	PCH 4954	*Borzicactus krahnii*
KK 758	*S. calliantha* var. *gigantea*	WK 108	*Matucana krahnii*

Matucana formosa Ritter, Taxon 12(3): 125 (1963)
CITES Cactaceae Checklist: *Matucana formosa*; formosa = nice; Plates 72-75.

SYNONYMS

Submatucana formosa (Ritter) Backeberg, Descr. Cact. Nov. 3: 14 (1963).
Borzicactus formosus (Ritter) Donald, Cact. Succ. J. (Gr. Brit.) 26(1): 10 (1971).
Loxanthocereus formosus (Ritter) Buxbaum, in: Krainz, Die Kakteen CVc (1974).
Submatucana formosa var. Pai-Pai n.n.
Submatucana formosa var. *longispina* n.n.
Submatucana formosa var. Bolivar n.n.
Matucana formosa var. *minor* Ritter, Taxon 12(3): 125 (1963).

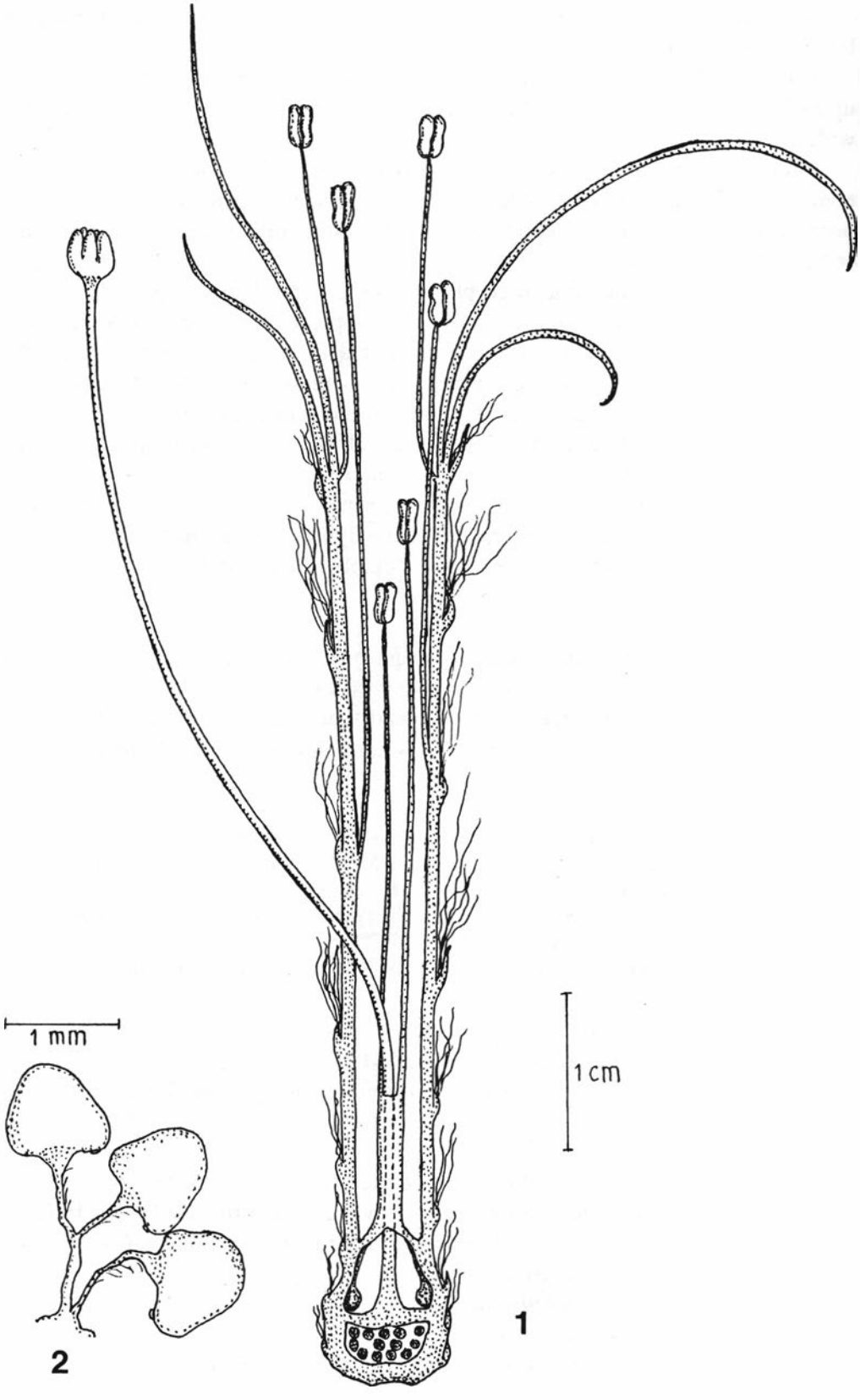
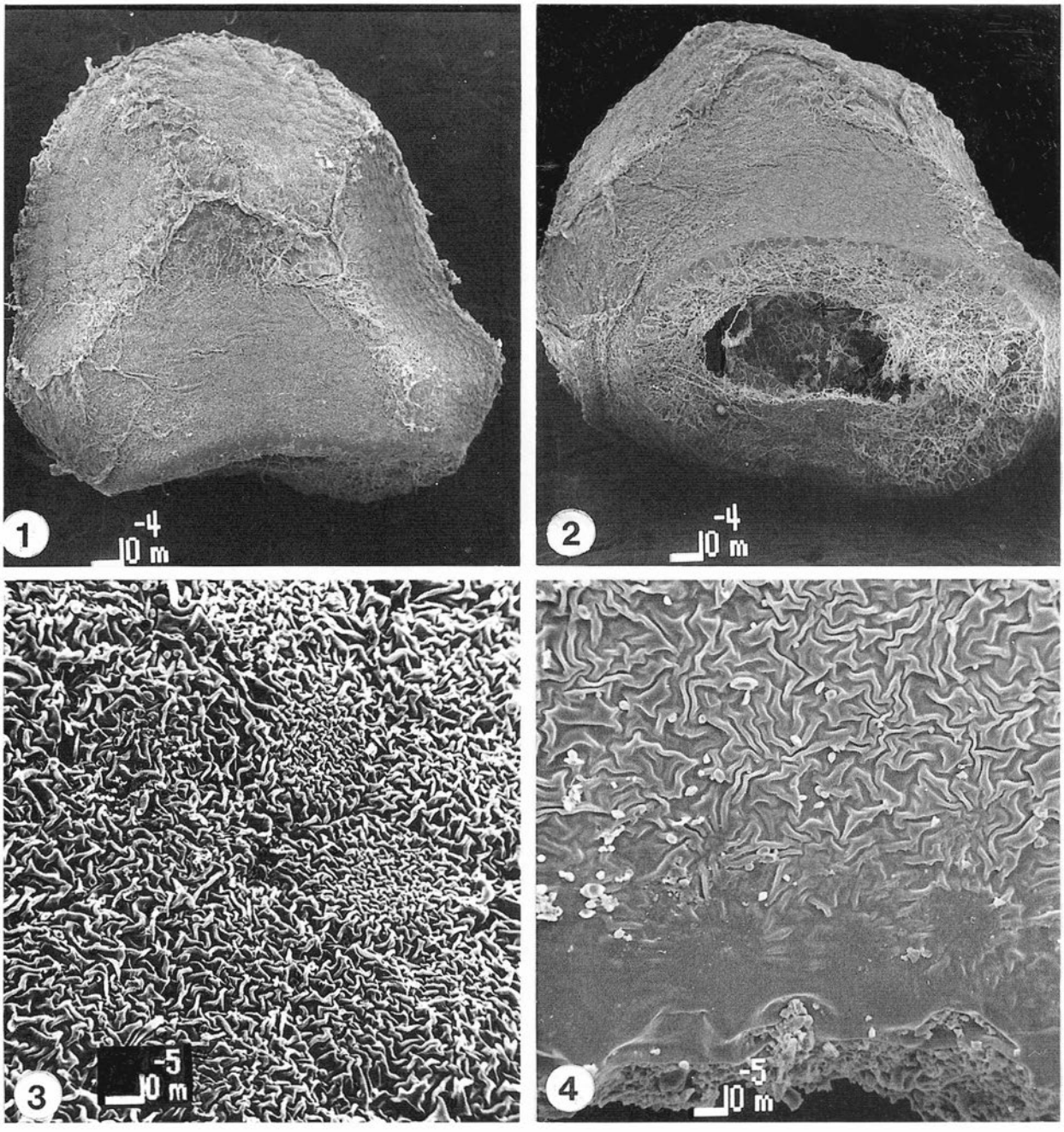


Figure 26. Flower of *Matucana formosa*. 1. Flower in vertical section. 2. Ovules.



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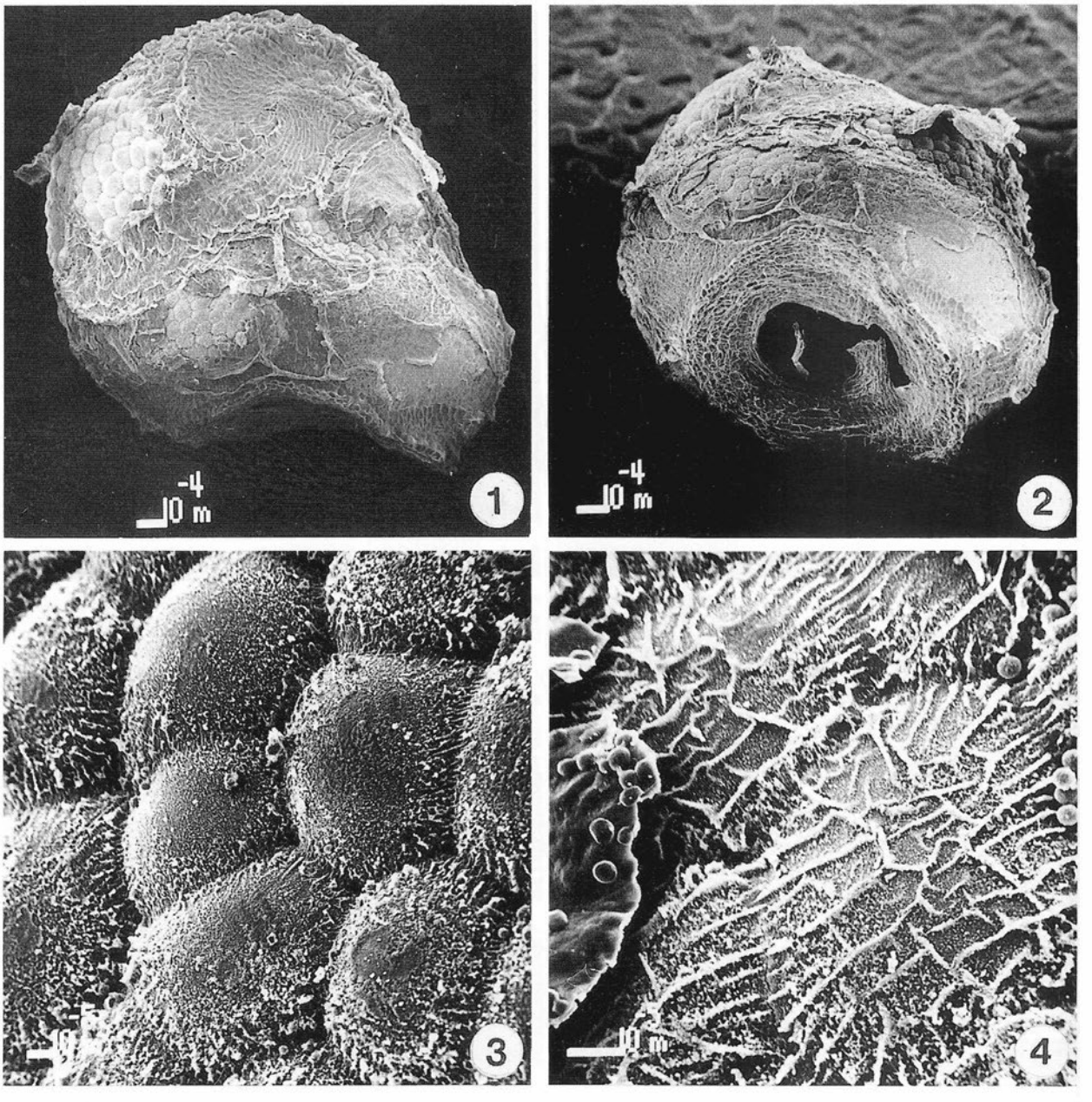
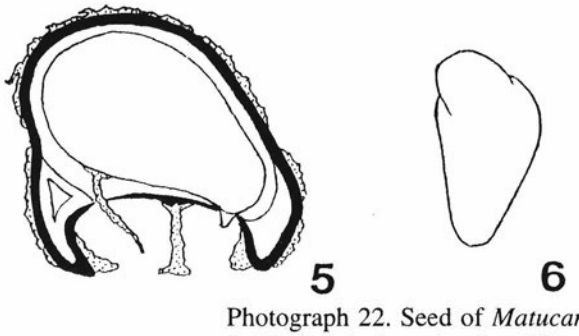
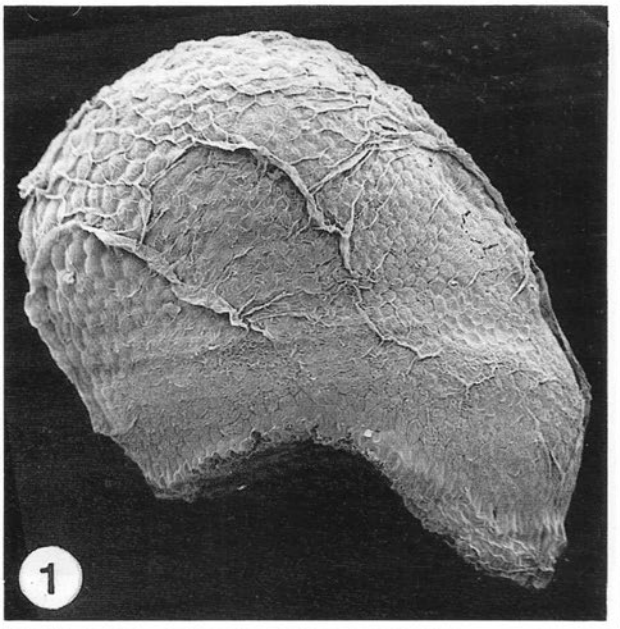
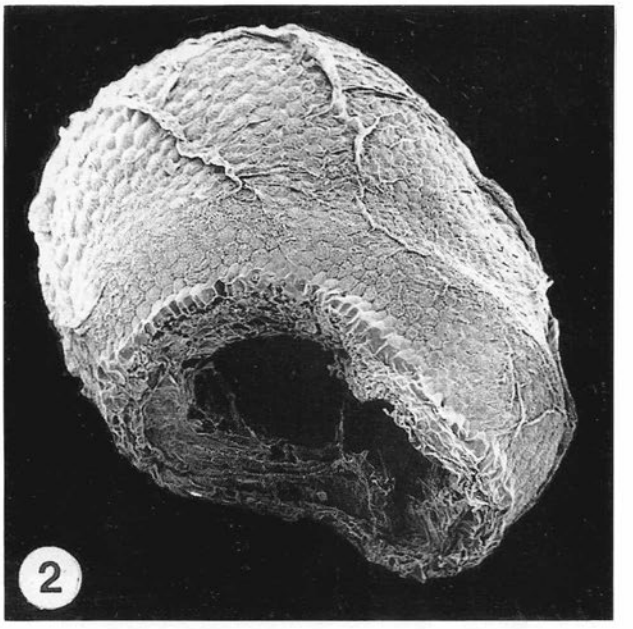
Photograph 21. Seed of *Matucana paucicostata* (Knize 1982). 1. Seed in lateral view; 40×. 2. Hilum showing large hole in the funicular tissue; 45×. 3. Testa in apical region; 415×. 4. Testa in basal region; 455×. 5. Embryo.

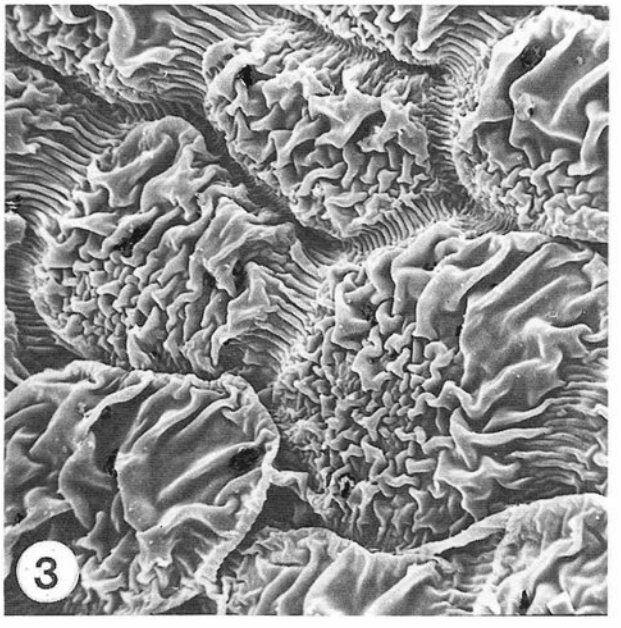


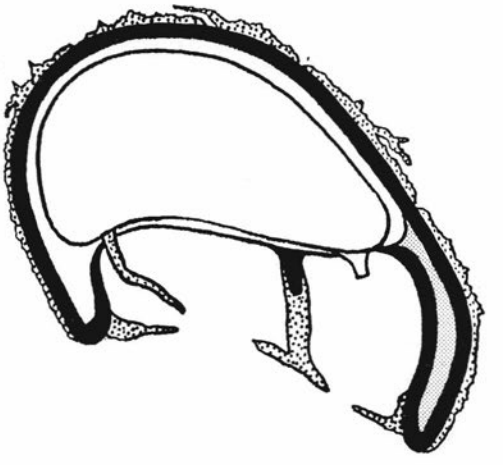


Photograph 22. Seed of *Matucana tuberculata* (Andreae 1980). 1. Seed in lateral view; 45×. 2. Id., basal view showing hilum; 50×. 3. Testa in apical region with weakly folded cuticle; 460×. 4. Testa in basal region with somewhat stronger folded cuticle; on the left is the detached cuticular layer just visible; 920×. 5. Seed in vertical section; funicular tissue and outer cuticular layer stippled; 30×. 6. Embryo.









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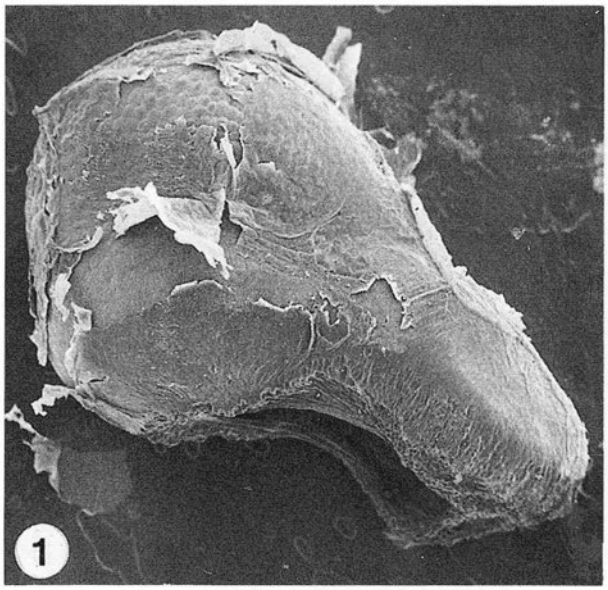
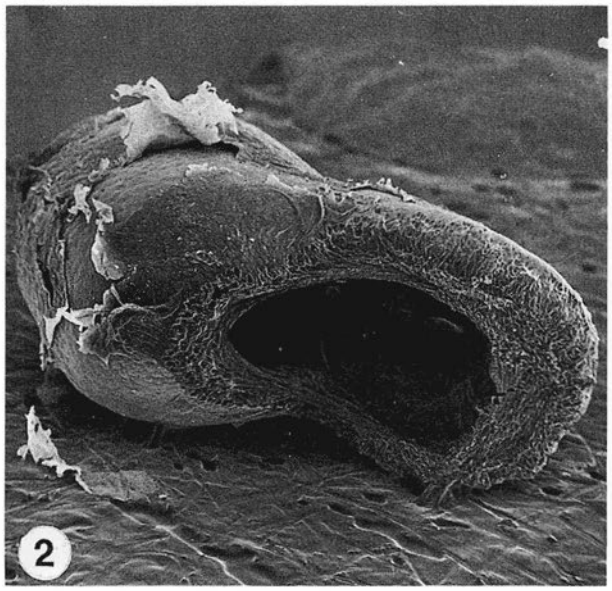
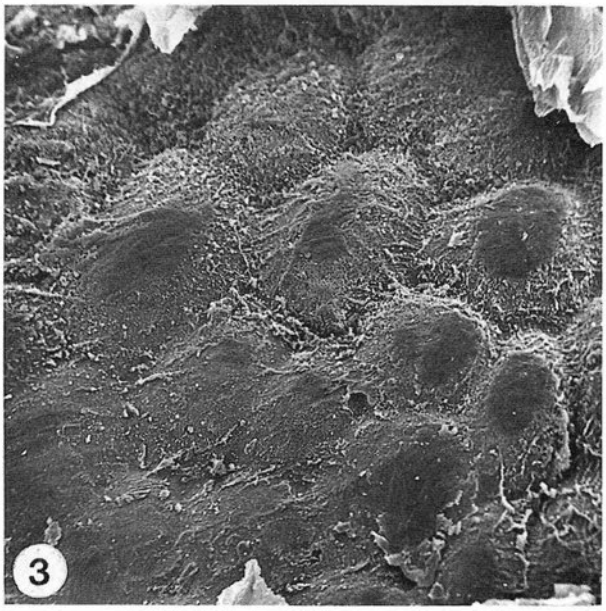
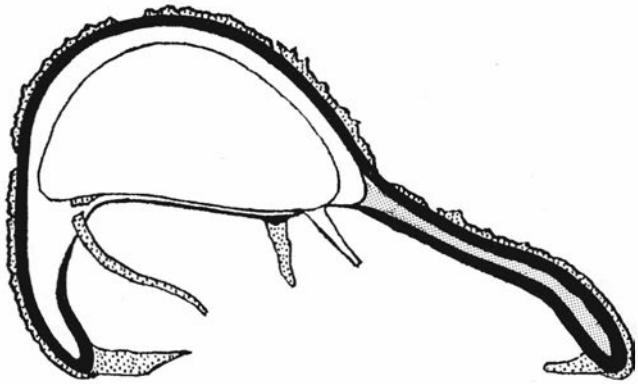
Photograph 23. Seed of *Matucana krahnii* (*Clichéfonds Succulenta*, 1980). 1. Seed in lateral view; 50×. 2. Id., lateral-basal view showing hilum; 45×. 3. Testa in basal region; 920×. 4. Vertical section of seed; funicular tissue and outer cuticular layer stippled; 45×. 5. Embryo.









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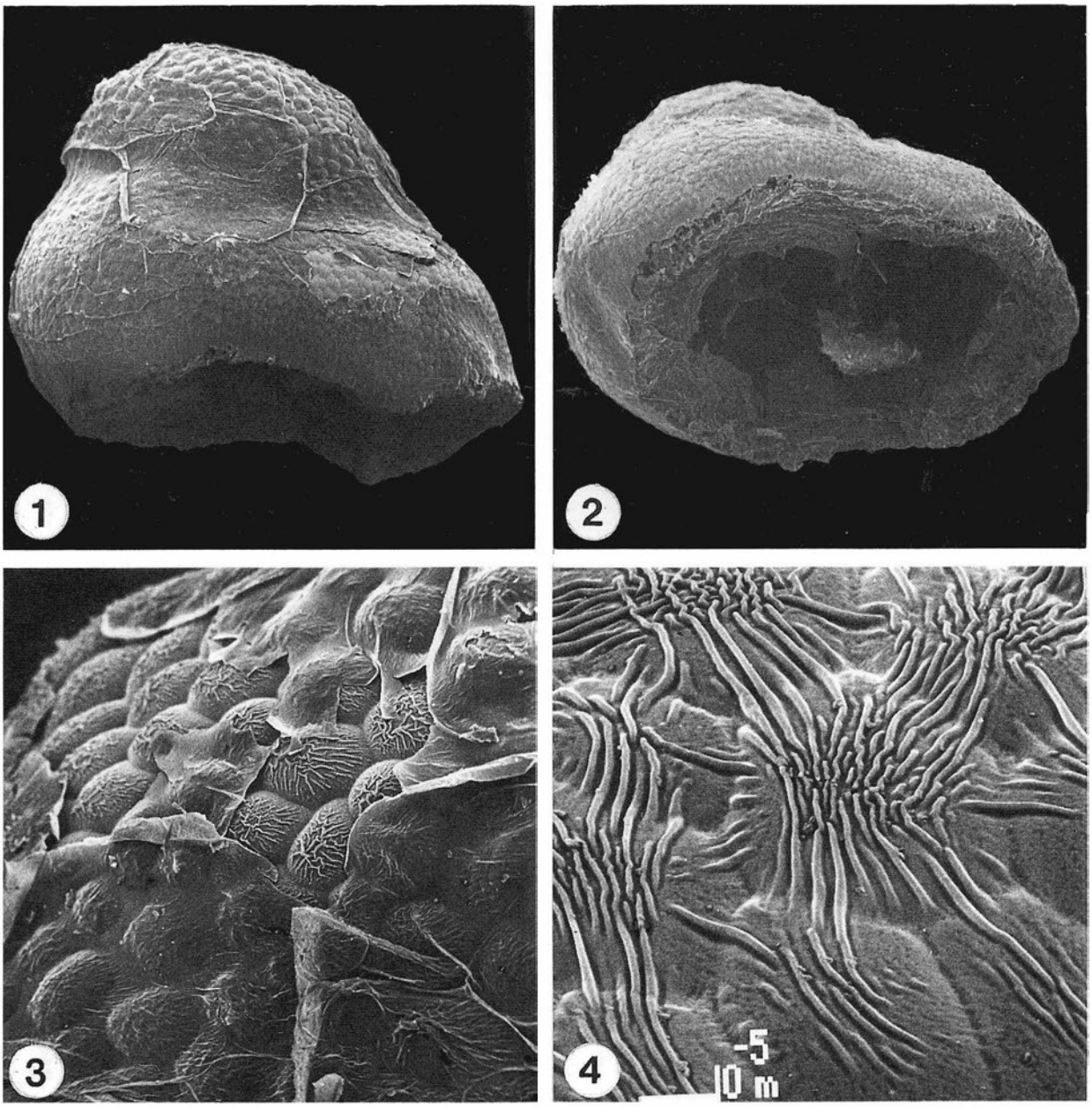
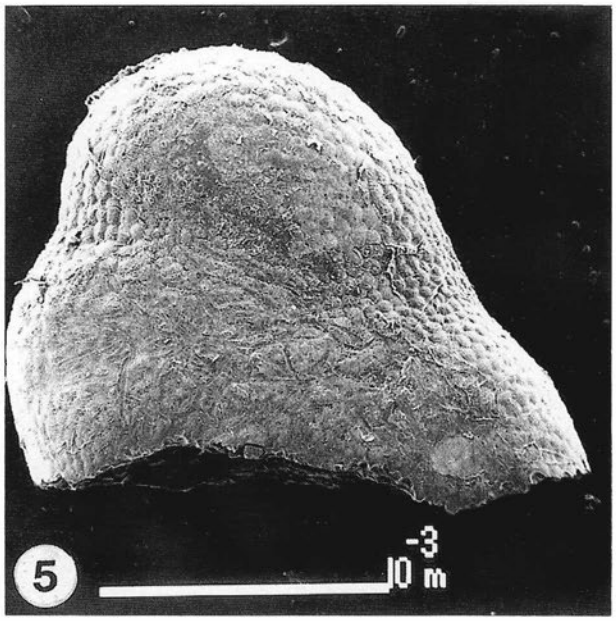
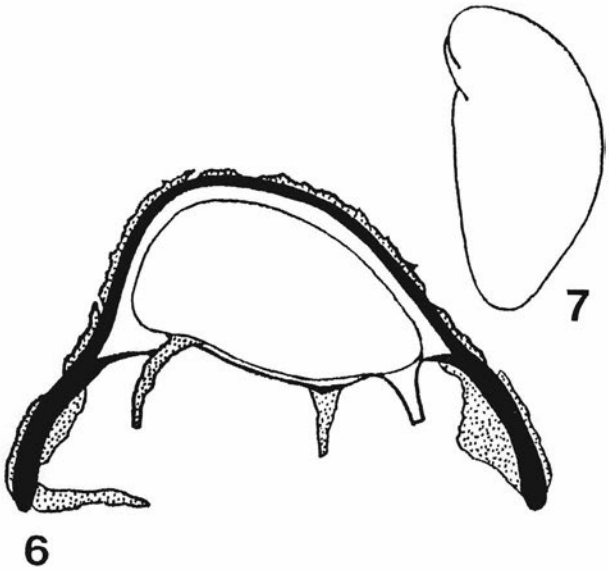
Photograph 24. Seed of *Matucana formosa* (Köhres 1980). 1. Seed in lateral view showing extreme detachment of outer cuticular layer; 35×. 2. Hilum; 35×. 3. Testa in apical region; 400×. 4. Seed in vertical section; funicular tissue and outer cuticular layer stippled; 30×. 5. Embryo.

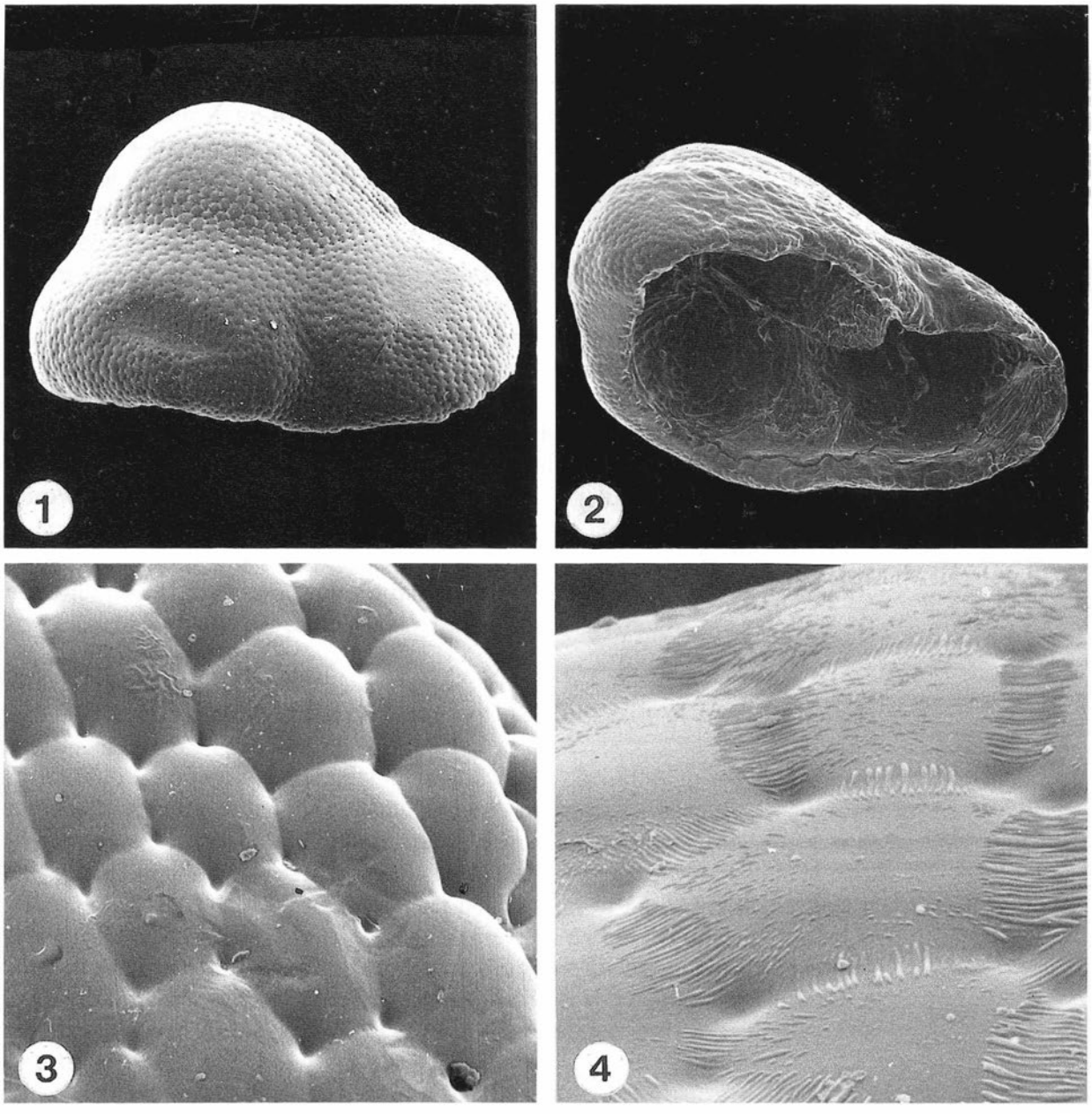


Photograph 25. Seed of *Matucana pujupatii*. 1. Seed (Köhres 1980) in lateral view; 30×. 2. Id., hilum; 30×. 3. Testa in apical region with partly torn up outer cuticular layer; 185×. 4. Testa in basal region, cuticular folds somewhat stronger; 920×.

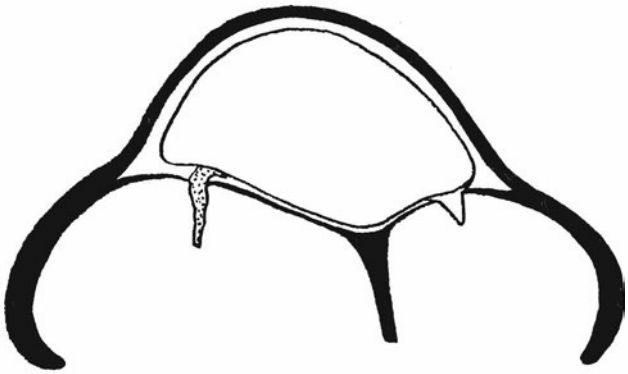




Photograph 25 (continued). 5. *Matucana* sp. Tarapoto KK 1602 (Knize 1983), seed in lateral view, 40×. 6. Seed of *M. pujupatii* in vertical section; funicular tissue and outer cuticular layer stippled. 7. Embryo.



Photograph 26. Seed of *Matucana madisoniorum* (Köhres 1980). 1. Seedin lateral view; 35×. 2. Id., basal view showing hilum with transverse crest inside the hilum cup; 35×. 3. Testa in ventral region with almost smooth cuticle; 460×. 4. Testa in apical region showing only a few cuticular folds; 780×.



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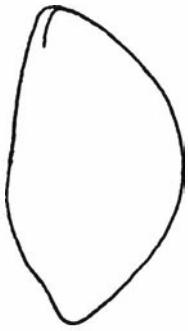

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Photograph 26 (continued). 5. Seed in vertical section; note the hilar crest and the absence of funicular tissue. 6. Embryo.

DESCRIPTION

Body grey green, globose, 10-15 cm tall and wide, weakly offsetting at the base, no tap-root. Ribs 20-30, fairly narrow, straight, weakly tuberculate; tubercles short, oval or conical, up to 10 mm long. Areoles oval, 3-6 mm long, brownish, later grey, 10-20 mm apart. Spination dark brown with black tip when young, later turning grey, straight to somewhat curved, rather stiff; radials 6-11, up to 30 mm long; centrals 1-4, 20-50 mm long.

Flower 8-10 cm long, in anthesis 4-7.5 cm wide, carmine. Tube a little curved, 4-5 mm wide, with grey hairs. Nectar chamber 3-4 mm long, appr. 4 mm wide, closed by a diaphragm. Nectar glands parietal, yellow. Filaments white at the bases blending to purple at their tips, anthers brown; primary filaments fused at their bases to beyond 15 mm like a collar around the style. Style reddish; stigma lobes 5-8, 3-5 mm long, greenish yellow.

Fruit globose, green and red, appr. 15 mm long and 10 mm wide.

Seed very peculiar in shape (like a shoe in lateral view), dull black with irregular brown-yellow cuticular remains, appr. 1.5 mm long, appr. 2.3 mm wide, appr. 1.0 mm thick; ventrally not extended, dorsally with a large duck bill-shaped extension. Hilum pear-shaped; funicular tissue pale yellow, attached to the hilar margin leaving a large oval hole in the centre of the hilum. Testa cells slightly convex to tabular; cuticle weakly folded. Embryo almost straight, pear-shaped.

REMARKS

The holotype is deposited in the herbarium of the University of Utrecht, Netherlands, under number FR 658.

Ritter (1981) described a variety *minor* which is, according to the description, distinct in having the following characteristics:

Body smaller; ribs 13-21. Flower up to 65 mm long, collar of the fused filaments up to 3 mm long. Seed identical to the type.

This taxon represents the southernmost populations of *M. formosa*. At most it can be considered as a local form whose features fall within the range of variation shown by *M. formosa*. Therefore, there is no need to consider this plant as a variety. To confirm this view, cultivated specimens do not show any major difference to *M. formosa* var. *formosa*. It has yet to be investigated if there is any genetic connection between var. *minor* and var. *formosa*.

DISTRIBUTION

The type locality of *M. formosa* is near the village of Balsas, on the west bank of the Rio Maranon, Department of Cajamarca, Peru. The species occurs on both sides of this river in the Departments of Cajamarca and Amazonas at 800-1000 m altitude. Ritter's variety *minor* was found more to the south, near El Chagual, Department of La Libertad at 900 m altitude.

FIELD NUMBERS

DM 20	*Matucana formosa*
FR 658	*M. formosa*
FR 1072	*M. formosa* var. *minor*
KK 276	*Submatucana formosa*
KK 276	*S. formosa* var. Bolivar
KK 276a	*S. formosa* var. *minor*
KK 276b	*S. formosa* var. *longispina*
L 105	*S. formosa*
L 221	*S. formosa* var. Pai-Pai
L 226	*S. formosa* var. *minor*
PCH 4957	*Matucana formosa*
WK 79	*M. formosa*

FR 1315 labelled material may exist in cultivation. According to Ritter this is a natural hybrid between *M. formosa* and *Thrixanthocereus blossfeldiorum*.

Matucana pujupatii (Donald & Lau) Bregman, Willdenowia 17(1): 173 (1988) CITES Cactaceae Checklist: *Matucana madisoniorum*; pujupatii = named after Shawintu Pujupat Dagses; Plates 9, 76 and 77.

BASIONYM

Borzicactus madisoniorum var. *pujupatii* Donald & Lau, Cact. Succ. J. (Gr. Brit.) 26(3): 71 (1971).

SYNONYMS

Matucana madisoniorum var. *pujupatii* (Donald & Lau) Rowley, Rep. Pl. Succ. 22: 10 (1971).
Borzicactus madisoniorum var. *caespitosa* n.n.
Matucana madisoniorum var. *uyupanii* n.n.
Submatucana joadii n.n.
Submatucana sp. de Corral Quemado.
Submatucana sp. Tarapoto.
Submatucana tarapotensis n.n.

DESCRIPTION

Body grey green to bluish grey, globose to oval, up to 15 cm tall and 10 cm wide, weakly offsetting at the base, no tap-root. Ribs 10-12, broad, straight, with up to 20 mm long conical tubercles. Areoles circular to oval, 3-4 mm long, white to grey, 10-20 mm apart. Spination brown with ochrous base when young, turning grey in later life, curved, flexible; radials 6-9, 5-20 mm long; centrals 0-2, up to 50 mm long.

Flower 6-7 cm long, in anthesis 4-5 cm wide, perianth segments carmine. Tube slightly curved, 6-9 mm wide, with white to brownish hairs. Nectar chamber 2-3 mm long, closed by a diaphragm; nectar glands weakly developed, parietal. Filaments white at the base blending to carmine, anthers yellow; primary stamens fused at their bases over appr. 7 mm; many stamens sterile. Style carmine; stigma lobes 5-7, appr. 2 mm long, green.

Fruit globose to oval, purplish green, appr. 10 mm across.

Seed cap-shaped, dull black, with irregular yellow-brown cuticular remains, appr. 1.2 mm long, appr. 1.8 mm wide, appr. 1.2 mm thick, ventrally and dorsally, strongly extended. Hilum oval, very large, hilum cup very deep; funicular tissue pale yellow, attached to the hilar margin, strongly reduced so there is mostly one large hole and sometimes two smaller holes in it. Testa cells fairly flattened, cuticle weakly folded. Embryo pear-shaped, somewhat bent.

REMARKS

This plant was originally described by Donald in 1971 as *Borzicactus madisoniorum* var. *pujupatii*. A. Lau dedicated it to Shawintu Pujupat, a Peruvian boy who found this plant in 1969 during the Lau expedition to Peru. Before that, the

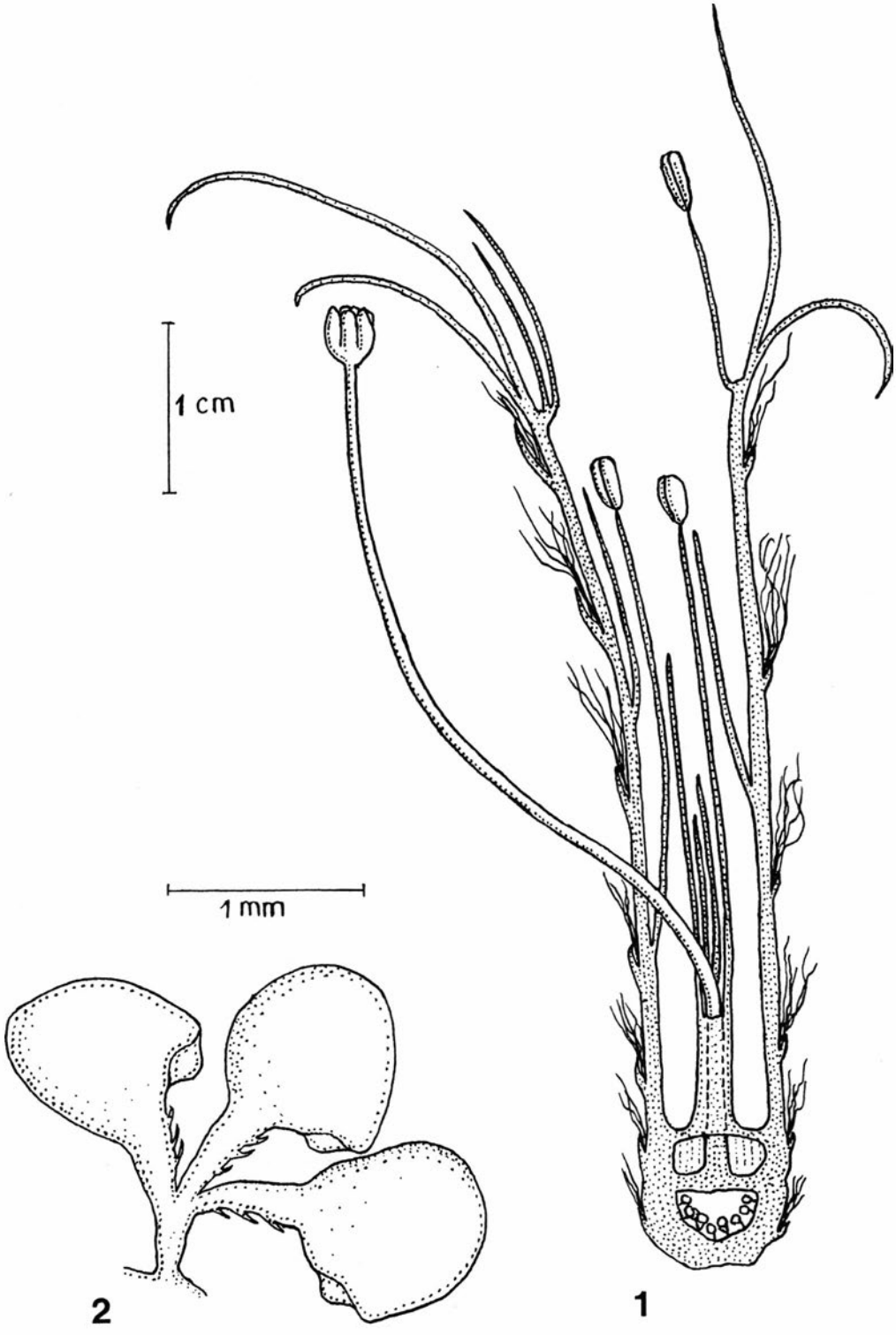


Figure 27. Flower of *Matucana pujupatii*. 1. Flower in vertical section showing sterile stamens. 2. Ovules.

Table 6. Differences between *M. pujupatii* and *M. madisoniorum*.

Character	*M. pujupatii*	*M. madisoniorum*
Number of spines per areole	6-11	0-5
Maximum spine length	50 mm	30 mm
Totally spineless	Never	Often
Flower length	60-70 mm	80-100 mm
Flower colour	Carmine	Orange-red
Floral tube shape	Tubular	Narrowly funnelform
Floral tube width	6-9 mm	Appr. 5 mm
Primary stamens	Present	Absent
Nectar chamber	Closed	Open
Seed colour	Dull black	Shiny red-brown
Cuticular remnants	Present	Absent
Funicular tissue	Present	Absent
Transverse partition in hilum (hilar ridge)	Weakly present	Conspicuous
Cuticular folding	Weak	Absent
Testa cracking at germination	Regular	Irregular

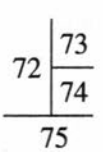
plant had been found by Krahn and Hutchison. The latter gave it the provisional name *Borzicactus madisoniorum* var. *caespitosa* n.n. This combination, however, has never been validly published.

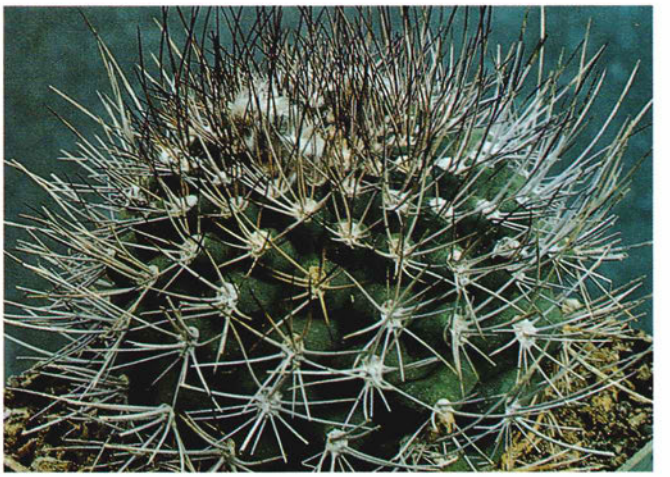
In the same year as the original description, 1971, the plant was placed in the genus *Matucana* by Rowley, still as a variety. Field study has shown that the differences with *M. madisoniorum* are too substantial for a variety, thus the plant has been classified as a species (Bregman 1988a). The differences in plant body are somewhat minor, particularly in cultivation, but on the other hand remarkable differences in flower and seed can be observed, as is listed in Table 6.

M. pujupatii is not only geographically intermediate between *M. formosa* and *M. madisoniorum*, but also in a phylogenetic sense. Particularly the flower and the seed exhibit a number of features that are also found in *M. formosa* but have disappeared in *M. madisoniorum*. A conspicuous example concerns the ring of primary stamens, whose bases close the nectar chamber. In all species of the paucicostata group but one, this feature is present; only in *M. madisoniorum* is it entirely absent. An intermediate stage of this characteristic is found in *M. pujupatii*. In this species notably, many stamens were found to be sterile because the anthers were missing. (Four flowers from four habitat collected specimens were examined). This is another clear indication in support of the theory that *M. madi-*

Plates 72-75

72. *Matucana formosa*, cultivated specimen.
73. *M. formosa*, ex-habitat specimen collected near Balsas, in the Heidelberg Botanic Garden.
74. *M. formosa*, ex-habitat specimen in the Heidelberg Botanic Garden under number 19200.
75. *M. formosa* in habitat near Balsas.





soniorum is at the end of the evolutionary lineage represented by the species of the paucicostata group. Therefore, Ritter was in error when he stated that *M. madisoniorum* is one of the most primitive *Matucana* species. On the contrary, it probably is the most evolved one!

There is no reference whatever of the plant of *M. pujupatii* in Ritter's work *Kakteen in Südamerika*. It could be that he never found the plant, for otherwise he would definitely have described the plant as a new species. Another possibility may be that Ritter chose deliberately not to mention the plant because, still being a variety of *M. madisoniorum* at the time, it did not fit into his genus *Eomatucana*. After all, *Eomatucana* had been erected for those Matucanas with an open nectar chamber (*M. madisoniorum* and *M. oreodoxa*), whereas *M. pujupatii* has a closed one. In any event it does seem strange that Ritter does not make any mention of this noteworthy plant.

The variety name 'uyupanii' is a corruption of *pujupatii*; nevertheless, this name will still be present on many labels. According to Donald (1976) *Submatucana joadii* n.n. is identical to *M. pujupatii*; the same applies to Knize's *Submatucana* species de Corral Quemado.

Another Knize finding, KK 1602, distributed as 'species Tarapoto' and *Submatucana tarapotensis*, is still a mystery. The flowers and the seeds of this plant are very similar to those of *M. pujupatii*; the body also. This plant was collected between Tarapoto and Lamas at 1000 m altitude. This is a locality roughly 300 km east of the distribution of the paucicostata group as a whole. This intervening area is largely covered by tropical rain forest, so at this moment it is not clear how these plants have reached the Tarapoto region. Perhaps the distribution of *M. pujupatii* is much larger than we know now and extends far more to the east. It is possible that there may be another locality called Tarapoto within the widely accepted distribution area for *Matucana*. If this is so, it is not known to the author despite some searching. Another subject for further study.

In cultivation *M. pujupatii* is not a species that excels abundantly in flowering, a characteristic it has in keeping with *M. formosa*. Its other close relative, *M. madisoniorum*, on the other hand, flowers very easily.

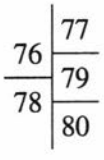
The holotype of this species is deposited in the herbarium of the University of Heidelberg under number Lau 107 as *Borzicactus madisoniorum* var. *pujupatii*.

DISTRIBUTION

The type locality is reported to be Puente 24 Julio, beside the road from Chamaya

Plates 76-80

76. *Matucana pujupatii*, natural specimen collected at Corral Quemado, in cultivation.
77. *M. pujupatii* in habitat at Corral Quemado.
78. *M. madisoniorum*, cultivated specimen.
79. *M. madisoniorum*, ex-habitat specimen in the Heidelberg Botanic Garden under number 54274.
80. *M. madisoniorum*, white-flowering form from Mesa Garden Nurseries, USA.



to Bagua, in 1300 m altitude. It is also recorded from Corral Quemado. Both localities are in the Department of Cajamarca, Peru.

FIELD NUMBERS

DM 38	*Matucana madisoniorum* var. *pujupatii*
DM 38a	*M. madisoniorum* var. *pujupatii*
KK 712	*Submatucana madisoniorum* var. *pujupatii*
KK 1602	*Submatucana* sp. Tarapoto
KK 1602	*S. tarapotensis*
L 107	*Borzicactus madisoniorum* var. *pujupatii*
WK 66	*Matucana pujupatii*

Matucana madisoniorum (Hutchison) Rowley, Rep. Pl. Succ. 22: 10 (1971)
CITES Cactaceae Checklist: *Matucana madisoniorum*; madisoniorum = named after Mr. and Mrs. Madison; Plates 3 and 78-80.

BASIONYM

Borzicactus madisoniorum Hutchison, Cact. Succ. J. (USA) 35(6): 167 (1963).

SYNONYMS

Submatucana madisoniorum (Hutchison) Backeberg, Kakteenlexikon: 412 (1966).

Loxanthocereus madisoniorum (Hutchison) Buxbaum, in: Krainz, Die Kakteen CVc (1974).

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

Submatucana madisoniorum var. *asterium* n.n.

Submatucana madisoniorum var. *horridispinum* n.n.

DESCRIPTION

Body dull grey-green, flattened globose to broad-columnar, up to 15 cm tall and 10 cm wide, weakly offsetting at the base, short thick tap-root. Ribs 7-12, broad, straight, very flat, with transverse grooves. Areoles circular to oval, 1-3 mm long, white to grey, 10-20 mm apart. Spines per areole 0-5, up to 30 mm long, black-brown with ochrous base when young, later turning grey, curved, flexible, easily detachable.

Flower 8-10 cm long, in anthesis 4-5.5 cm wide, orange-red. Tube narrowly funnelform, appr. 6 mm wide at the base, with white to brown hairs. Nectar chamber open. Filaments purple, anthers yellow. Style yellowish, pink above; stigma lobes appr. 8, appr. 3 mm long, yellow.

Fruit globose, with short pubescent hairs, appr. 2 cm across.

Seed very distinctive glossy dark-brown without cuticular remnants, appr. 1.3 mm long, appr. 2.0 mm wide, appr. 1.2 mm thick, ventrally and dorsally strongly extended. Hilum very large, oval to 'shoe-sole-shaped', with a transverse partition in the middle, funicular tissue absent. Testa cells tabular, cuticle almost flat. Embryo small, oval, straight.

REMARKS

Due to large-scale commercial collecting this remarkable species has become

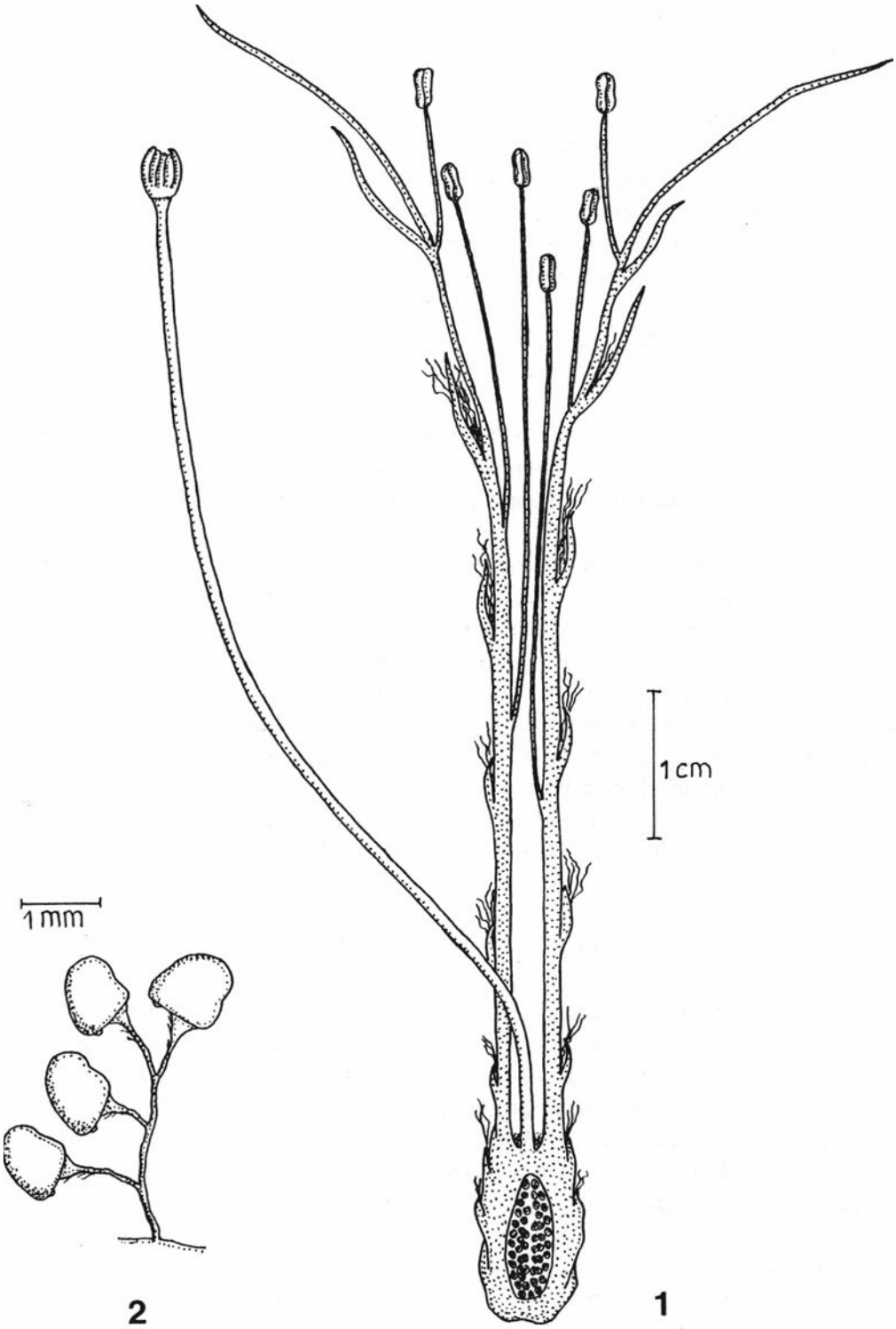


Figure 28. Flower of *Matucana madisoniorum*. 1. Flower in vertical section. 2. Ovules.

threatened in nature. The Peruvian government should urgently take measures to prevent extinction.

M. madisoniorum is best known in its spineless form; without flowers it even resembles *Lophophora williamsii*, the very familiar 'peyote' from Mexico. In many cases some spines can begin to form in the young areoles, but they detach so easily that most specimens are unarmed except for the apical zone.

The Knize names *horridispinum* and *asterium* should be discarded. The first name was used for plants covered in spines, the second for spineless ones. Since this variability is present in populations of the 'normal' *M. madisoniorum*, these Knize names are superfluous.

In view of the differences in stem, flower and seed, the variety *M. madisoniorum* var. *pujupatii*, described in 1971, was raised to the rank of species in 1988 (Bregman 1988a).

Recently a white-flowering form has appeared in Mesa Garden nurseries, USA (Plate 80). This is probably an albino form arising from a spontaneous mutation. Sometimes such deviant plants spring up in nature as well, but they are often less robust.

The flower of *M. madisoniorum* is distinct for the absence of a diaphragm inside the floral tube. The only other *Matucana* species that exhibits this feature is *M. oreodoxa* (see Section 8.5). This feature was ascribed great taxonomic importance by Ritter, who placed both species in a separate genus *Eomatucana*.

As well as the diaphragm, the entire ring of primary stamens has also been lost in the flower of *M. madisoniorum*. It is speculative to explain the cause of this. Ritter (1981) stated that perhaps the flowers are pollinated by insects with a long tongue such as certain diurnal butterflies.

The holotype of *M. madisoniorum* is deposited in the herbarium of the University of California, Berkeley, USA, under number UC 1188467.

Distribution

M. madisoniorum was found in 1957 by P. Hutchison near the village of Nazareth, province of Bagua, Department of Amazonas, Peru. The total distribution is proportionally small and is located on the east side of the Rio Maranon north-east of the village of Bagua. Lau reported Rentema as the place where he located the plants. The vertical distribution is between 400 and 1000 m above sea level.

The plants were reported as growing on steep sandstone cliffs in company with *Melocactus bellavistensis*, *Armatocereus rauhii*, *Peperomia dolabriformis* (Piperaceae) and the silvery rosettes of *Deuterocohnia longipetala* (Bromeliaceae) (Hutchison 1963, Rauh 1966).

Field numbers

DM 36	*Matucana madisoniorum*	KK 1766	*S. madisoniorum* var. *asterium*
KK 456	*Submatucana madisoniorum*	L106	*S. madisoniorum*
KK 537*	*S. madisoniorum* var. *horridispinum*	WK 565	*Matucana madisoniorum*

*This number is now *Islaya brevicylindrica*.

CHAPTER 12

Checklist

All names of infraspecific epithets, which have ever been associated with *Matucana*, are listed below alphabetically. The accepted epithets are printed in bold.

armillata = **haynei**
atrispina = **haynei**
aurantiaca
aurantiaca var. *calvescens* = **aurantiaca**
aurantiaca var. *densispina* = **aurantiaca**
aurantiaca var. *megalantha* = **aurantiaca**
aureiflora
aureiflora var. *elata* = **aureiflora**
aureiflora var. *incaica* = **aureiflora**
axiosa = **haynei**
bagalaensis = **aurantiaca**
blancii = **haynei**
blancii var. *nigriarmata* = **haynei**
blancii var. *platygona* = **haynei**
blanicostata = **haynei**
breviflora = **haynei**
breviflora var. *incuiensis* = **haynei**
breviflora Pauza = **haynei**
brunescens = **haynei**
caespitosa (sensu Ritter) = **paucicostata**
caespitosa (sensu Hutchison) = **pujupatii**
cajamarcensis = **aurantiaca**
calliantha = **krahnii**
calliantha var. *gigantea* = **krahnii**
calliantha var. *prolifera* = **krahnii**
calmada = **aurantiaca**
calocephala = **comacephala**
calvescens = **aurantiaca**
calvescens var. *seminuda* = **aurantiaca**
carneoflora = **haynei**
catamarcensis = **aurantiaca**
celendinensis = **intertexta** var. **celendinensis**
cephalophora = **comacephala**
cereoides = **haynei**
clavispina = **haynei**
colori-splendida = **haynei**
colorisplendida = **haynei**
comacephala
comacephala var. *lutea* = **comacephala**
comacephala var. *luteispina* = **comacephala**
crinifera = **comacephala**
currudayii = **aurantiaca**
currundayensis = **aurantiaca**
elongata = **haynei**
eriodisa = **oreodoxa**
eriodisa var. *echinata* = **paucicostata**
formosa
formosa var. *longispina* = **formosa**
formosa var. *minor* = **formosa**
formosa Bolivar = **formosa**
formosa Pai-Pai = **formosa**
fruticosa

grandiflora = **aurantiaca**
grandiflora var. *albispina* = **aurantiaca**
grandiflora var. *densispina* = **aurantiaca**
hastifera
haynei
haynei Aquia = **haynei**
haynei var. *cereoides* = **haynei**
haynei var. *elongata* = **haynei**
haynei var. *erectipetala* = **haynei**
haynei var. *gigantea* = **haynei**
haynei var. *grandiflora* = **haynei**
haynei var. *multicolor* = **haynei**
haynei var. *perplexa* = **haynei**
haynii = **haynei**
haynii var. *erectipetala* = **haynei**
herzogiana = **haynei**
herzogiana var. *blancii* = **haynei**
herzogiana var. *perplexa* = **haynei**
huagalensis
huagalensis (sensu Knize) = **intertexta** var. **celendinensis**
huagalensis var. *bruneispina* = **intertexta** var. **celendinensis**
huaricensis = **paucicostata**
huaricensis var. *bruneispina* = **paucicostata**
huarinensis = **paucicostata**
huarinensis (sensu Knize) = **comacephala**
humboldtii = **Borzicactus (Seticereus) humboldtii**
hystrix = **haynei**
hystrix var. *atrispina* = **haynei**
hystrix var. *nigrispina* = **haynei**
hystrix var. *umadeavoides* = **haynei**
icosagona = **Borzicactus (Seticereus) icosagonus**
incaica = **aureiflora**
incaica var. *aureiflora* = **aureiflora**
incaica var. *flaviflora* = **aureiflora**
intermedia = **aurantiaca**
intertexta = **intertexta** var. **intertexta**
intertexta var. **celendinensis**
intertexta var. *cinerascens* = **intertexta** var. **intertexta**
intertexta var. **intertexta**
intertexta var. *loranzensis* = **intertexta** var. **intertexta**
intertexta Huagal = **intertexta** var. **intertexta**
intertexta Matara Cajamarca = **M. intertexta** var. **intertexta**
intertexta Rio Crisnejas = **intertexta** var. **intertexta**
joadii = **pujupatii**
krahnii
krahnii f. *gracilis* = **krahnii**
krahnii var. *major* = **krahnii**
krahnii f. *minor* = **krahnii**
krahnii var. *prolifera* = **krahnii**
lutea = **comacephala**
luteispina = **comacephala**
madisoniorum
madisoniorum var. *asterium* = **madisoniorum**
madisoniorum var. *caespitosum* = **pujupatii**
madisoniorum var. *horridispinum* = **madisoniorum**
madisoniorum var. *pujupatii* = **pujupatii**
madisoniorum var. *uyupanii* = **pujupatii**
mamillaris = **tuberculata**
megalantha = **haynei**
mentosa = **intertexta** var. **intertexta**
mirabilis (is possibly a hybrid)
multicolor = **haynei**
multicolor var. *armillata* = **haynei**
multicolor var. *breviflora* = **haynei**
multicolor var. *hystrix* = **haynei**
myriacantha
myriacantha (sensu Ritter) = **weberbaueri** f. **flammea**
nigricantha = **weberbaueri**
nivosa = **aurantiaca**
oreodoxa
oreodoxa var. *turbiniformis* = **oreodoxa**
pallarensis = **aurantiaca**
paucicostata
paucicostata var. *curvispina* = **paucicostata**
paucicostata var. *robustispina* = **paucicostata**

paucispina = **paucicostata**
polzii
purpureoalba = **myriacantha**
radians = **comacephala**
rarissima is a hybrid between *Oreocereus ritteri* and *Matucana haynei*
ritteri
ritteri f. Agallpampa = **ritteri**
robusta = **haynei**
roseiflora = **?**
roseoalba = **myriacantha**
senilis = **paucicostata**
setosa = **haynei**
sp. Cajamarca = **aurantiaca**
sp. Caraz = **haynei**
sp. Carhuaz = **haynei**
sp. Chagual = **tuberculata**
sp. de Corral Quemado = **pujupatii**
sp. Huaraz = **haynei**
sp. Huari = **comacephala**
sp. Llamellin = **paucicostata**
sp. Pisco = **haynei**
sp. Pomabamba = **comacephala**
sp. Pomabamba Huari = **comacephala**
sp. Tarapoto = **pujupatii**
subterranea = **aurantiaca**
supertexta = **haynei**
tuberculata
tuberculosa = **tuberculata**
turbiniformis = **paucicostata**
variabilis = **haynei**
variabilis var. *fuscata* = **haynei**
variicolor = **aurantiaca**
villarica = **haynei**
violaciflora = **haynei**
weberbaueri
weberbaueri var. *blancii* = **weberbaueri**
weberbaueri f. **flammea**
weberbaueri var. *flammea* = **weberbaueri** f. **flammea**
weberbaueri var. *myriacanthus* = **myriacantha**
winterae = **haynei**
winteri = **haynei**
winteriana = **haynei**
yanganucensis var. *albispina* = **haynei**
yanganucensis var. *fuscispina* = **haynei**
yanganucensis var. *gilesii* = **haynei**
yanganucensis var. *grandiflora* = **haynei**
yanganucensis Lago Yanganuco = **haynei**
yanganucensis var. *longistyla* = **haynei**
yanganucensis var. *parviflora* = **haynei**
yanganucensis var. *roseiflora* = **haynei**
yanganucensis var. salmonea = **haynei**
yanganucensis var. *santiensis* = **haynei**
yanganucensis var. *setosa* = **haynei**
yanganucensis var. *suberecta* = **haynei**
yanganucensis Casma Pass = **haynei**

CHAPTER 13

Complete list of field numbers

A list of all field numbers associated with *Matucana* is given below in alphabetical order. The abbreviation before each number refers to the collector or person who has brought seeds and/or plants under that name into circulation. These are: Blossf. = Blossfeld, Germany; DM = De munter, Belgium; EZ = Zecher, Switzerland; FR = Ritter, Germany; KK = Knize, Peru; L = Lau, Mexico; PCH = Hutchison, USA; R = Rausch, Austria; UCBG = University of California Botanic Garden, USA; Weberb. = Weberbauer, Germany; WK = Krahn, Germany. The first name shown against each field number is the correct species name, according to the author. The second name is the name used for the originally distributed material together with the locality data, if available.

Field number	Name	Original name	Locality
Blossf. 96	*aurantiaca*	*aurantiaca*	Sondor, 3500 m
DM 19	*krahnii*	*krahnii*	?
DM 20	*formosa*	*formosa*	Balsas, 900 m
DM 21	*intertexta* var. *celendinensis*	?	?
DM 22	*intertexta* var. *celendinensis*	?	?
DM 23	*aurantiaca*	*calvescens*	Angasmarca
DM 29	*paucicostata*	*paucicostata*	?
DM 36	*madisoniorum*	*madisoniorum*	?
DM 38	*pujupatii*	*madisoniorum* var. *pujupatii*	Chamaya
DM 38a	*pujupatii*	*madisoniorum* var. *pujupatii*	Chamaya
DM 40	*aurantiaca*	*currundayensis*	Cerro Currunday
DM 63	*aurantiaca*	*pallarensis*	?
DM 65	*krahnii*	*krahnii* f. *gracilis*	?
EZ 762	*polzii*	*polzii*	Upper course Rio Maranon, Huanuco, 2200 m
FR 142	*haynei*	*haynei*	Pisco valley
FR 142a	*comacephala*	*crinifera*	?
FR 142b	*haynei*	*multicolor*	Galeras, west of Nazca
FR 142c	*haynei*	*haynei* var. *elongata*	Fortaleza valley
FR 164	*aurantiaca*	*currundayensis*	Samne, Otuzco, Currunday mountains, 3000 m

Field number	Name	Original name	Locality
FR 299	*ritteri*	*ritteri*	Otuzco, La Libertad, 2500 m
FR 565	*haynei*	*multicolor* var. *hystrix*	North of Quicacha, Arequipa
FR 587	*comacephala*	*comacephala*	Rahuapampa, Ancash
FR 592	*comacephala*	*crinifera*	?
FR 592a	*haynei*	*yanganucensis* var. *setosa*	?
FR 592b	*comacephala*	*crinifera*	?
FR 593	*haynei*	*megalantha*	Caraz, Ancash
FR 594	*comacephala*	*comacephala*	?
FR 595	*comacephala*	*crinifera*	Machac, Huari, Ancash
FR 596	*aurantiaca*	*aurantiaca*	San Pablo, Cajamarca/La Libertad
FR 596a	*aurantiaca*	*aurantiaca*	San Pablo, Cajamarca/La Libertad
FR 597	*paucicostata*	*paucicostata*	Rahuapampa
FR 658	*formosa*	*formosa*	Balsas, Cajamarca, 900 m
FR 690	*haynei*	*supertexta*	Churin
FR 691	*haynei*	*winteri*	Santiago de Chuco
FR 692	*intertexta* var. *celendinensis*	*celendinensis*	Between Celendin and Balsas
FR 693	*intertexta*	*intertexta*	Puente Crisnejas, Cajamarca
FR 911	*haynei*	*multicolor* var. *hystrix*	North of Quicacha, Arequipa
FR 1063	*myriacantha*	*purpureoalba*	Aricapampa
FR 1072	*formosa*	*formosa* var. *minor*	El Chagual, La Libertad
FR 1073	*tuberculata*	*tuberculosa*	El Chagual, 2400 m
FR 1076	*aurantiaca*	*pallarensis*	El Pallar, Rio Chuscon
FR 1304	*weberbaueri*	*weberbaueri*	East of Balsas, 2300 m
FR 1305	*weberbaueri* f. *flammea*	*myriacantha*	East of Balsas, 2300 m
FR 1306	*hastifera*	*hastifera*	Rahuapampa, Huari, Ancash
FR 1307	*fruticosa*	*fruticosa*	San Juan, Cajamarca
FR 1308	*krahnii*	*calliantha*	Balsas, Amazonas, 1700 m
FR 1308a	*krahnii*	*calliantha* var. *prolifera*	Balsas, Maranon, Cajamarca, 900 m
FR 1310	*aureiflora*	*aureiflora*	Banos del Inca, Cajamarca
FR 1311	*oreodoxa*	*oreodoxa*	Rahuapampa, Ancash, 3000 m
KK 275	*haynei*	*haynei*	Matucana, 2000-2200 m
KK 276	*formosa*	*formosa*	Balsas, 1500 m
KK 276	*formosa*	*formosa* var. Bolivar	Bolivar
KK 276a	*formosa*	*formosa* var. *minor*	El Chagual, 1000 m
KK 276b	*formosa*	*formosa* var. *longispina*	Balsas, 1000 m
KK 455	*aurantiaca*	*aurantiaca*	Hualgayoc, Chota, 2200 m
KK 456	*madisoniorum*	*madisoniorum*	Bagua Chica/Rentema, Maranon, 1000 m
KK 457	*weberbaueri* f. *flammea*	*myriacantha*	Balsas, 1300-1500 m
KK 460	*haynei*	*cereoides*	Rio Pisco, 2000-2200 m
KK 530	*haynei*	*hystrix*	Lucanas, 4000 m
KK 531	*haynei*	*hystrix* var. *nigrispina*	Pampa de Galeras, 3800 m
KK 532	*haynei*	*multicolor*	Lucanas, 4000-4200 m
KK 537*	*madisoniorum*	*madisoniorum* var. *horridispinum*	?

Field number	Name	Original name	Locality
KK 564	*haynei*	*yanganucensis*	Lago Yanganuco, 3800 m
KK 564	*haynei*	*yanganucensis* var. *grandiflora*	Lago Yanganuco, 3800 m
KK 565	*haynei*	*herzogiana*	Cordillera Negra, 3200 m
KK 566	*haynei*	*elongata*	Lago Yarinacocha, Cordillera Negra, 3800 m
KK 573	*comacephala*	*huarinensis*	Huari, 3200 m
KK 574	*comacephala*	*comacephala* var. *luteispina*	Chavin, 3800 m
KK 574	*comacephala*	*luteispina*	Chavin, 3800 m
KK 575	*haynei*	*clavispina*	Coracora volcano, 3500 m
KK 576	*aurantiaca*	*grandiflora*	Balsas, 1200-1500 m
KK 576	*aurantiaca*	*grandiflora* var. *albispina*	Balsas, 1200-1500 m
KK 577	*comacephala*	*crinifera*	Machac, 2500 m
KK 580	*haynei*	*villarica*	Huancayo, Villarica, 3800-4000 m
KK 711	*ritteri*	*ritteri*	Otuzco, 2800 m
KK 712	*pujupatii*	*madisoniorum* var. *pujupatii*	Rio Chamaya, Maranon, 1300 m
KK 712	*pujupatii*	*madisoniorum* var. *uyupani*	Rio Chamaya, Maranon, 1300 m
KK 713	*haynei*	*blancii*	Caraz, Cordillera Negra, 3800 m
KK 727	*comacephala*	*comacephala*	Chavin, Cordillera Blanca, 3300-4000 m
KK 728	*paucicostata*	*turbiniformis*	Llamellin, 2600 m (or 1800 m?)
KK 729	*aurantiaca*	*currundayensis*	Samne, 2500 m
KK 730	*haynei*	*yanganucensis*	Yunguyo, Cordillera Blanca, 3800 m
KK 730	*haynei*	*yanganucensis* var. *roseiflora*	Yunguyo, Cordillera Blanca, 3800 m
KK 753	*aurantiaca*	*calvescens*	Angasmarca, 2600 m
KK 754	*paucicostata*	*senilis*	Llamellin, 2000-2600 m
KK 755	*paucicostata*	*paucicostata*	San marcos, Huari, 2500-2800 m
KK 758	*krahnii*	*calliantha*	Balsas, 1600-1800 m
KK 758	*krahnii*	*calliantha* var. *gigantea*	?
KK 758	*krahnii*	*krahnii*	Balsas, 1600-1800 m
KK 758a	*krahnii*	*krahnii* var. *major*	?
KK 773	*intertexta* var. *celendinensis*	*huagalensis*	Huagal, Cajamarca, 1800 m
KK 773a	*intertexta* var. *celendinensis*	*huagalensis* f.	Huagal, 1800 m
KK 774	*intertexta* var. *celendinensis*	*huagalensis* var. *bruneispina*	Huagal-Cajamarca, 2800 m
KK 776	*aureiflora*	*aureiflora* var. *elata*	Cajamarca, 2500 m
KK 777	*aureiflora*	*aureiflora*	Cajamarca, 2500 m
KK 778	*aurantiaca*	*calvescens* var. *seminuda*	Santiago de Chuco, 2800-3000 m
KK 779	*weberbaueri* f. *flammea*	*weberbaueri*	Balsas, Chachapoyas, 1600 m
KK 780	*haynei*	*breviflora*	Inquio, Pauza, 4000 m
KK 791	*paucicostata*	*paucicostata* var.	Huari, 2500 m

Field number	Name	Original name	Locality
KK 794	*haynei*	*cereoides*	Rio Pisco, Castrovirreyna, 3800 m
KK 1035	*haynei*	*axiosa*	Santiago de Chuco, 2800 m
KK 1035	*haynei*	*violaciflora*	Santiago de Chuco, 2800 m
KK 1036	*intertexta* var. *intertexta*	*intertexta*	Rio Crisnejas, 1300 m
KK 1037	*haynei*	*yanganucensis*	Caraz, Cordillera Blanca, 3800 m
KK 1038	*comacephala*	sp.	Pomabamba, Huaura valley, 3800 m
KK 1038a	*comacephala*	sp. Pomabamba	Pomabamba, Huari
KK 1039	*intertexta* var. *celendinensis*	*celendinensis*	Celendin, 2000 m
KK 1039	*intertexta* var. *celendinensis*	*celendinensis* f. Bolivar	Celendin, 2000 m
KK 1040	*haynei*	*variabilis*	Churin, 2200 m
KK 1041	*myriacantha*	*purpureoalba*	Aricapampa, 2800 m
KK 1044	*haynei*	*yanganucensis*	Carhuaz, Cordillera Blanca
KK 1045	*ritteri*	*ritteri* var.	Agallpampa, Libertad, Otuzco, 3000 m
KK 1054	*intertexta* var. *intertexta*	*intertexta* var. *calmada*	Ichocan, Cajamarca, 1500 m
KK 1054	*intertexta* var. *intertexta*	*intertexta* var. *cinerascens*	Ichocan, Cajamarca, 2000 m
KK 1085	*intertexta* var. *intertexta*	sp.	Cayday, Cajamarca, Crisnejas, 1800 m
KK 1132*	*haynei*	*breviflora*	?
KK 1132*	*haynei*	*breviflora* var.	Pauza, 4000 m
KK 1133	*haynei*	*multicolor* var. *armillata*	Lucanas, 4200 m
KK 1153	*intertexta* var. *intertexta*	*intertexta* var.	Rio Crisnejas, 1500 m
KK 1299	*comacephala*	*comacephala*	?
KK 1299	*comacephala*	*comacephala* var. *lutea*	Uchupata, 2800 m
KK 1299	*comacephala*	*lutea*	Uchupata, 2800 m
KK 1315	*aureiflora*	*aureiflora* var. *elata*	Cajamarguilla, Cajamarca, 2800 m
KK 1316	*intertexta* var. *intertexta*	*intertexta* var.	Matara, Cajamarca, 2200 m
KK 1317	*paucicostata*	*caespitosa*	Huari, 2800 m
KK 1431*	*paucicostata*	*eriodisa* var. *echinata*	?
KK 1450	*paucicostata*	*huarinensis*	Huari, 2800 m
KK 1459	*haynei*	*yanganucensis* var. *setiflora*	Recuay, 3600-3800 m
KK 1459	*haynei*	*yanganucensis* var. *setosa*	Recuay, 3600-3800 m
KK 1470	*aurantiaca*	*calvescens* var. *seminuda*	San Marcos, Cajamarca, 2500 m
KK 1471	*paucicostata*	*paucicostata* var.	Aczo, Raimondi, 2800 m
KK 1548	*haynei*	*haynei* var. *grandiflora*	Matucana, 2200 m
KK 1549	*haynei*	*yanganucensis*	Rio Santa, 3500 m
KK 1549	*haynei*	*yanganucensis* var. *grandiflora*	Rio Santa, 3500 m

Field number	Name	Original name	Locality
KK 1550	*haynei*	*cereoides*	Rio Pisco, 2800 m
KK 1551	*haynei*	*yanganucensis* f.	Rio Santa, Huaraz, Cordillera Blanca, 3000 m
KK 1591	*oreodoxa*	*eriodisa*	Huari, Llamellin, 1800 m
KK 1602	*pujupatii*	*tarapotensis*	Tarapoto-Lamas, 1000 m
KK 1638	*tuberculata*	*mamillaris*	Prov. Raimondi, 1500 m
KK 1653*	*tuberculata*	sp. Chagual, Rio-Maranon	?
KK 1676*	*haynei*	*haynei* var. *grandiflora*	?
KK 1710	*comacephala*	*radians*	Prov. Raimondi, 1800 m
KK 1710	?	sp. nov.	Santiago de Chuco
KK 1711	*comacephala*	*carneoflora*	Machac, Chavin, Cordillera Blanca, 3800 m
KK 1711	*comacephala*	*comacephala*	Machac, Chavin, Cordillera Blanca, 3800 m
KK 1712	*haynei*	*blancii* var. *platygona*	Cordillera Negra, Aija, 3000 m
KK 1748	*haynei*	*winteriana*	Santiago de Chuco, 2500 m
KK 1766	*madisoniorum*	*madisoniorum* var. *asterium*	Rio Maranon, Bagua, 1300 m
KK 1767	?	*roseiflora*	Rio Crisnejas-Maranon, 1300 m
KK 1768*	*paucicostata*	*paucicostata*	?
KK 1777	*paucicostata*	sp.	Llamellin, Maranon, 1500 m
KK 1778	*paucicostata*?	sp.	Llamellin, Maranon, 1600 m
KK 1779	*paucicostata*	sp.	Llamellin, Rio Maranon, 1800 m
KK 1793	*aurantiaca*	*intermedia*	Rio maranon, 1500 m
KK 1901	*aurantiaca*	sp.	Santiago de Chuco, 2800 m
KK 1902	*aurantiaca*	*calmada*	Rio Crisnejas, 2800 m
KK 1903	*aurantiaca*	*cajamarcensis*	Cajamarca, 2800 m
KK 1904	*aurantiaca*	*nivosa*	Angasmarca, 2800 m
KK 1952	*aurantiaca*	*subterranea*	Huamachuco, 2800 m
L 103	*myriacantha*	*myriacantha*	Balsas, Rio Maranon
L 103a	*myriacantha*	*roseoalba*	Huagal
L 104	*aureiflora*	*aureiflora* var. *incaia*	Cajamarca
L 105	*formosa*	*formosa*	Balsas
L 106	*madisoniorum*	*madisoniorum*	Rentema
L 107	*pujupatii*	*madisoniorum* var. *pujupatii*	Bagua, Corral Quemado
L 108	*intertexta* var. *intertexta*	*intertexta*	Crisnejas
L 109	*weberbaueri* f. *flammea*	*weberbaueri* var. *flammeus*	Balsas
L 115	*aurantiaca*	*calvescens* var.	West of Cajamarca
L 116	*ritteri*	*ritteri*	Otuzco
L 117	*haynei*	*yanganucensis* var.	Casma Pass
L 118	*aurantiaca*	*aurantiaca* var. *densispina*	Namora
L 120	*haynei*	*winterae*	Santiago de Chuco
L 166	*haynei*	*breviflora*	?
L 171	*aurantiaca*	*currundayensis*	Otuzco, Cerro Currunday
L 172	*aurantiaca*	*calvescens*	Angasmarca
L 173	*myriacantha*	*roseo-alba*	Rio Crisnejas
L 174	*huagalensis*	*huagalensis*	Hazienda Huagal
L 175	*intertexta* var.?	*intertexta* var. Huagal	Huagal

Field number	Name	Original name	Locality
L 177	*aurantiaca*	*aurantiaca*	San Pablo
L 178	*krahnii*	*calliantha*	Balsas
L 178a	*krahnii*	*calliantha* var. *prolifera*	Chancillos
L 179	*haynei*	*variabilis*	Oyon
L 183	*haynei*	*elongata*	Rio Fortaleza
L 184	*comacephala*	*crinifera*	Huari
L 185	*comacephala*	*comacephala*	Huaytuna
L 187	*paucicostata*	*paucicostata* var. *robustispina*	Huari, Rio Puchca, 2800 m
L 189	*haynei*	*yanganucensis*	Catac
L 192	*haynei*	*blancii*	Parron
L 197	*haynei*	sp.	Caraz
L 199	*haynei*	*haynei*	Eulalia valley
L 207	*haynei*	*multicolor*	Nazca-Puquio
L 208	*haynei*	*hystrix*	Nazca-Puquio
L 209	*haynei*	*cereoides*	Pisco valley
L 218	*weberbaueri*	*weberbaueri*	Carrizal-Bagua, 2100 m
L 221	*formosa*	*formosa* var.	Pai-pai
L 223	*tuberculata*	*tuberculosa*	Chagual
L 224	*myriacantha*	*roseo-alba*	Aricapampa
L 225	*aurantiaca*	*pallarensis*	El Pallar
L 226	*formosa*	*formosa* var. *minor*	Chagual
L 232	*haynei*	*haynei* var.	Aquia
L 272	*hastifera*?	sp. *hastifera*?	Huari, Puchca valley, 3700 m
L 273	*oreodoxa*	*oreodoxa*	Huari
PCH 4953	*weberbaueri* f. *flammea*	*weberbaueri*	?
PCH 4954	*krahnii*	*krahnii*	?
PCH 4957	*formosa*	*formosa*	?
PCH 6218	*tuberculata*	*tuberculatus*	18 km south of Aricapampa, 2100 m
PCH 6223	*tuberculata*	*tuberculatus*	23 km south of Aricapampa, 1900 m
R 379	*haynei*	*haynei*	?
R 442	*haynei*	*hystrix*	?
UCBG 53486	*aurantiaca*	*aurantiaca*	Sondor, 3500 m
UCBG 371101	*aurantiaca*	*calvescens*	Angasmarca, La Libertad, 3700 m
Weberb. 3846	*aurantiaca*	*aurantiaca*	San Pablo, Cajamarca, 2300 m
Weberb. 4222	*aurantiaca*	*aurantiaca*	Between Chota and Hualgayoc, 3550 m
Weberb. 4271	*weberbaueri*	*weberbaueri*	?
WK 24	*haynei*	*haynei*	Rimac valley, 2500 m
WK 28	*haynei*	*variabilis*	Above Churin, 2600 m
WK 30	*haynei*	*variabilis*	6 km below Oyon, 3200 m
WK 31	*haynei*	*variabilis*	Above Oyon, 3700 m
WK 66	*pujupatii*	*madisoniorum* var. *pujupatii*	Chamaya, 450 m
WK 77	*weberbaueri* f. *flammea*	*weberbaueri* var. *flammea*	? 1680 m
WK 79	*formosa*	*formosa*	Balsas, 900 m
WK 108	*krahnii*	*krahnii*	? 1680 m

Field number	Name	Original name	Locality
WK 123	*aurantiaca*	*aurantiaca*	Cajamarca, 2800 m
WK 124	*aureiflora*	*aureiflora*	West of Cajamarca, 2900-3200 m
WK 130	*haynei*	*yanganucensis*	Catac
WK 132	*haynei*	*blancii*	?
WK 133	*haynei*	*elongata*	Rio Fortaleza valley, 3200 m
WK 530	*comacephala*	*crinifera*	Machac, 3200-3400 m
WK 533	*comacephala*	*comacephala*	?
WK 534	*paucicostata*	*paucicostata*	East of Huaytuna, 2250 m
WK 537	*myriacantha*?	*myriacantha*?	Andamayo, 3000 m
WK 546	*ritteri*	*ritteri*	Otuzco, 3000 m
WK 546a	*ritteri*	*ritteri*	Near Usquil, 3150 m
WK 548	*intertexta* var. *intertexta*	*intertexta*	Puente Crisnejas, 2000 m
WK 565	*madisoniorum*	*madisoniorum*	East of Bagua Chica

*In the Knize list 1987 these numbers represent other plants.

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