Sulcorebutia or Rebutia?

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Ever since Backeberg's description of the genus *Sulcorebutia* in 1951, the question has existed whether the genus is justified. Cárdenas (1966, 1968) never accepted it. Buxbaum (Endler & Buxbaum, 1974) at first could not fit it into his system but then decided to add it as a "primitive side-branch” of his subtribe Gymnocalyciinae. Brandt (1977) placed it into *Weingartia*. Donald (1971, 1977) at first supported the independence of *Sulcorebutia* and emended it with Brederoo (Donald & Brederoo, 1972). Later he adopted Hunt's opinion and preferred merging *Sulcorebutia* and *Weingartia* with *Rebutia.*

The reason for this brief but confusing history of *Sulcorebutia* was the superficial, incomplete, and unconvincing description by Backeberg. Except for Donald and Buxbaum, who looked into the characteristic features of the genus, most authors only made statements or made new combinations without giving reasons for doing so (Hunt & Taylor, 1986).

Hentzschel (1999a, 1999b, 1999c) examined the distinguishing characters of *Sulcorebutia,* together with those of other possibly related groups of species, and emended the genus once again. In order to have an unambiguous reference, a neotype was deposited (Gertel, 1996; Leuenberger, 1989). Hentzschel quoted and commented on the original description (Backeberg, 1951) and the emendation by Donald & Brederoo (1972). He wrote a new description of the genus that took into account the many recent discoveries.

The following remarks are a summary of all the observations made so far on *Sulcorebutia* and its possibly related allies. They will be completed later after we discuss hybridization and the geographic distribution of these plants. In order to carry out a critical comparison with *Rebutia* K. Schum., the most important characters of the genus *Sulcorebutia* must first be presented.

Characteristics of the genus *Sulcorebutia* Back. emend. Hentzschel

Bodies single or offsetting, spherical to shortly elongated, mostly small but sometimes reaching exceptional sizes of more than 10 cm in diameter. They have a sunken apex and the body is divided into spirally-arranged, rhomboidal tubercles that never meet to form straight ribs. The roots are fibrous or swollen, forming a cylindric or conical taproot sometimes narrowed near the body of the plant.

The areoles are sunken into the upper part of the tubercles and merge towards the top into a distinctive, pronounced, slightly slanting epidermal fold, which sometimes may be very short. The areoles are elongated to very extended, thus bearing slightly radiating, but mostly pectinate, spines. Radial and central spines cannot always be distinguished and sometimes centrals are lacking. The spines are hard but straight to curved but never hooked. Their surface is smooth to sometimes very rough.

The flowers are formed from externally naked buds that emerge from the upper part of older areoles but never from near the stema-pex. The open flower is funnel-shaped, rarely campanulate. The color of the flowers is usually magenta, yellow, red or multicolored, rarely white. The base of flower is often magenta. The petals are spatulate to lanceloate, with partially jagged edges. The pericarp and receptacle have fleshy, heart-shaped, differently colored, sometimes slightly protruding scales, which towards the apex of the tube become equal in shape and color to the petals. In the axils of the lowest scales there are some axillary hairs and sometimes a few small bristles or spines, but very rarely are there spiny areoles (such as occur when lateral offsets become converted to flowers). On the inside of the receptacle the stamens are usually uniformly distributed, rarely arranged in two groups. The filaments vary in color and often are even bicolored. The anthers are yellow. The style bears the stigma with its 3 to 13 lobes, which can be white, yellowish or greenish. The style usually reaches the same height as the upper stamens, though in some species it can be considerably shorter or even extend far beyond the stamens and perianth.

The fruit is a spherical or flattened-spherical, fleshy, false berry when mature, bursting open near the middle from the pressure of the swelling funiculi. Sometimes, instead of opening, it dries, appearing almost leathery. The base of the fruit adheres firmly to the body of the plant so that during the dry period the entire fruit or only the lower part, with the seeds enclosed as in a bag, remains protected until the rainy season.

The funiculi are solitary and densely arranged in usually five flattened placentas, which sometimes may be once-branched basally.

The seeds are globular to irregularly oblong to ovoid, ranging in size between 1 and 2 mm, laterally broadened, dull brownish black, with an irregular surface formed mostly by a thick cuticle of very variable structure. The hilum and micropyle are surrounded by a joint wall of very small, flattened testa cells. These cells are more or less isodiametric, brownish black, and have finely warted, slightly convex, outer cell-walls. The hilum-micropylar region (HMR) is covered with a slack, yellowish white tissue. The mature seed contains a very simplified embryo without distinctly visible cotyledons. Endosperm and perisperm are not detectable.

Further details can be found in Augustin et al. (2000).

All this shows that *Sulcorebutia* is a very variable genus, but it is possible to recognize certain consistent characters needed for a differential diagnosis:

1. The oblong to very elongated areoles are clearly shifted apically and somewhat sunken on top of the rhomboid, spirally arranged tubercles. Ribs are never formed.
2. The buds are covered completely with fleshy, heart-shaped scales. Hairs cannot be found in the bud stage.
3. These characteristic scales, often auriculate at the base, later cover the pericarp and the lower part of the receptacle of the unopened flower. They are still visible on the mature fruit. Usually some axillary hairs and bristles can be found underneath the more basal scales.
4, The flowers always originate from older areoles, often even near the base of the stem, but never from the apex.
5. The fruit consists of a fleshy, multilayered, outer and inner pericarp. At maturity, fruits split equatorially to subequatorially because the area of the inner pericarp that will later open had earlier become partially dissolved. In cases where the fruit dries off and appears leather-like, the inner pericarp did not dissolve and the outer pericarp always remains.
6. The funiculi are solitary, only at their base sometimes becoming once branched.
7. The seeds are spherical to oblong-ovate, 1-2 mm long, with a defined cuticular fold and always with plano-convex, periclinal testa cell-walls.

By means of these seven groups of characters, *Sulcorebutia* can be easily distinguished from all other genera of cacti.

Differentiation of *Sulcorebutia* from other genera

The essential differences from *Rebutia* sensu lato will next be discussed, as well as possible relatives or ancestors of *Sulcorebutia* and cacti that have been confused with it.

1. Differences from *Rebutia* sensu lato

Before the treatment by the I.O.S Working Group (Hunt & Taylor, 1986; Hunt, 1999), the genus *Rebutia* K. Schumann was already a conglomeration of different groups of cacti. Therefore not all of the following comparisons of characters is correct for all the *Rebutia* species.

Sulcorebutias always have rhomboid tubercles, whereas they are roundish in *Rebutia*. Sulcorebutias always have an elongated areole positioned and sunken in the upper part of the tubercle (adaxial). In *Rebutia* the mostly round areole is positioned at the apex of the tubercle. Some populations of the *Rebutia padcayensis-margarethae* group also have adaxial, sunken areoles. A distinct epidermal fold also exists. To distinguish those plants clearly from *Sulcorebutia,* one needs to especially examine the flowers, fruits, and seeds.

The spines of sulcorebutias are hard but flexible, while in rebutias they are brittle and break easily. Investigations of the fine structure of the spines that could explain these differences have not yet been made.

The flowers of *Sulcorebutia* and *Rebutia* are shaped quite differently, according to the group they belong to. Those of *Sulcorebutia* have fleshy bud scales located on the apex of tubercles; these scales have a broad base and often bear lateral auricules. *Rebutia,* on the other hand, has fragile, acute, triangular bud scales that develop axillary hairs and spines. Both of these characters result in the protection of the buds: in *Sulcorebutia* the buds are protected by the scales and in most species of *Rebutia* by the axillary hairs.

Within the *Rebutia padcayensis—margarethae* group and in *R. minuscula* and its allies, relatively broad scales are formed, but they almost never have hairs or spines. The fruits and the testa structure of the seeds clearly show features typical of *Rebutia* sensu stricto.

The structure of the fruits is also important. In *Sulcorebutia* both cellular layers of the outer pericarp are completely intact at the time of maturity. At this time the central portion of the inner pericarp is already dissolved, so that the fruit tears open due to the pressure of the swelling funiculi. In *Rebutia* the inner pericarp, the funiculi, and the placentas are converted into a sticky pulp at quite an early stage of development, while the seeds are still brown. Also the outer pericarp decomposes and disintegrates, except in the *Rebutia aureiflora* group. In the latter group the fruit tears open transversely, but the plants are easily recognized as rebutias by their narrow scales with tufts of axillary hair.

2. Differences from *Rebutia fidaiana, R. neumanniana* and *R. neocumingii*

These plants are better known as members of the genus *Weingartia* Werd. One group can be distinguished as a northern group *(Rebutia neocumingii* (Back.) Hunt and related taxa) and another as a southern group *(R. fidaiana* (Back.) Hunt, *R. neumanniana* (Werd.) Hunt).

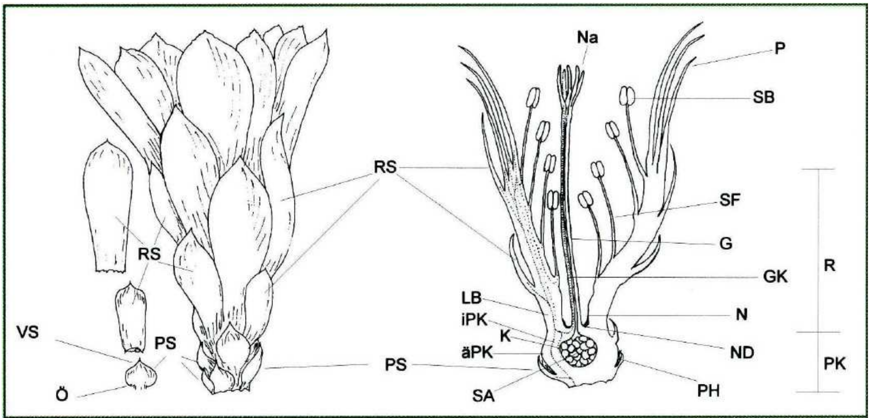
During their juvenile stage the northern forms resemble certain *Sulcorebutia* species, having rhombic, spirally-arranged tubercles. They only form ribs, if they do so at all, when very old. The southern forms soon develop broad flat ribs similar to those of *Gymnocalycium*.

The structure of the tubercles is comparable to that of *Sulcorebutia*. The areoles are mostly round to ovate, with tougher spines than those of *Sulcorebutia*, and have elongated areoles and mostly pectinate spines.

Buds, bud scales and petals are very similar to those of *Sulcorebutia* but on the whole are more fleshy. Bud scales and petals have a broader base than in *Sulcorebutia* and their basal lateral auricules are even more pronounced; the structure of these auricules resembles those of *Gymnocalycium*.

The inner and outer structure of the flower and fruit of the southern forms is comparable to that of *Sulcorebutia*. The northern forms differ from the former in several significant characters. The fruits of the southern weingartias tear open equatorially by the pressure of the swelling whereas the fruits of the northern forms decompose by the dissolving of the pericarp and funiculi.

It is also interesting that in *Weingartia*, as in *Sulcorebutia*, mostly unbranched funiculi are formed, normally in five placentas. The placentas of the northern forms are linear, those of the southern ones are broader. The funiculi are often placed so close together that a branching



Drawing 1: Floral structure of *Sulcorebutia* species. (after Donald and Brederoo, 1972, enlarged and revised)
Na = Papillate stigmatic lobe. **G** = Style. **Gk** = Stylar canal. **P** = Perianth. **Sb** = Anther. **SF** = Filament. **R** = Flower tube (receptacle). **Pk** = Pericarp. **iPk** = Inner pericarp. **äPk** = Outer pericarp. **PS** = Pericarp scales. **PH** = Axillary hair tuft. **K** = Carpel tissue (very thin and incompletely developed). **SA** = Ovules. **N** = Nectary. **ND** = Nectar-gland (not always developed). **LB** = Vascular bundle (shown are only the most important vascular bundles). **VS** = Apex of scale. **Ö** = auriculate scale-base.

of funiculi is simulated, though not actual (Hentzschel, 1999a; Augustin et al., 2000). The northern *Weingartia* species form more numerous funiculi than the southern ones and the sulcorebutias. Therefore they develop more numerous seeds. which are considerably smaller than those of sulcorebutias and the southern weingartias.

3. Differences from *Echinopsis* sensu lato

All cacti grouped together in the genus *Echinopsis* Zucc. normally differ considerably from *Sulcorebutia* and *Weingartia* in body, flower and fruit. Therefore there have been very few cases of confusion.

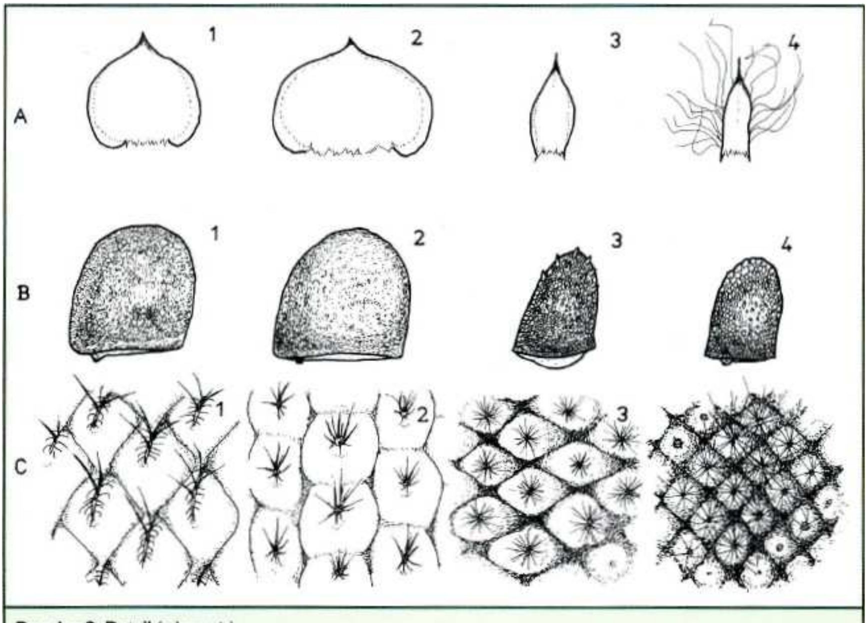
In some places forms of *Echinopsis cinnabarina* (Hooker) Labouret grow together with *Sulcorebutia purpurea* (Donald & Lau) Brederoo Donald and have been confused due to their similar appearance during the rest period, but with the first onset of flowers the error becomes obvious. Some luxuriantly sprouting and rarely flowering forms of *E. schieleana* (Back.) Hunt and *Sulcorebutia krugerae* var. *hoffmannii* Augustin & Hentzschel were sometimes confused as well. In this case, too, the mistake was soon realized by observing the large, hairy flowers of *E. schieleana* with their triangular bud scales.

Generally one can say that cacti with woolly buds and acute triangular scales can never be *Sulcorebutia* or *Weingartia* species but according to their other characters could be *Echinopsis* (sensu lato) species, matucanas or Chilean globular cacti.

Observations from hybridization

The importance of cross-pollination experiments with cacti is generally underrated. Unsuccessful hybridization of cacti may have many causes and cannot be assessed conclusively. A successful hybridization on the other hand, if the offspring are able to reproduce, means there is a high genetic similarity of the mating partners—an indication of close relationship.

As self-fertility is to be avoided in hybridization, experiments with *Sulcorebutia* and *Weingartia* are made easier because of their selfsterility. In *Rebutia* sensu stricto self-fertility is widespread. But whether this differente has tax-



Drawing 2: Detail (schematic)
A = Pericarp scale. **B** = Seed. **C** = Tubercle and rib arrangement.
1: *Sulcorebutia steinbachii* (Werd.) Back. (*Rebutia steinbachii* Werd.). **2:** *Weingartia neumanniana* Werd. (*Rebutia neumanniana* (Werd.) Hunt). **3:** *Rebutia minuscula* Schumann. **4:** *Rebutia hoffmannii* Diers & Rausch (*R. spinosissima* Back.).

onomic significance is not known at present.

Hybridization experiments by the author with *Sulcorebutia, Weingartia, Rebutia* and *Echinopsis* have produced the following results:

1. Most, perhaps all, *Sulcorebutia* species can hybridise with each other.
2. All experiments of crossing *Sulcorebutia* and *Weingartia* have resulted in an F. 1 generation capable of surviving. The plants grew normally, but some were partially chlorotic.
3. Cross-pollinating experiments of *Sulcorebutia* and *Echinopsis chamaecereus* H. Friedrich & Glaetzle were carried out in various combinations but did not produce an Fl-generation. From time to time, fruits developed with barren seeds. On the other hand, hybridization between *Rebutia* and *E. chamaecereus* succeeded many times.
4. Hybridization failed between *Sulcorebutia* and rebutias of the *R. padcayensis* group, which closely resemble *Sulcorebutia*. With several other Rebutia species it was also not possible to produce an F1 -generation. The only exception, a hybrid produced by John Donald between *Sulcorebutia krahnii* and *Rebutia gracilispina*, was reported by Gröner (1997).

Although investigations have not been concluded, the following conclusions can be made:

1. The genetic distance between *Sulcorebutia* species is very small.
2. *Sulcorebutia* and *Weingartia* are closely related.
3. The genetic distance between *Sulcorebutia* and *Echinopsis* is large.
4. The genetic distance between *Rebutia* and *Echinopsis* is smaller than between *Sulcorebutia* and *Echinopsis*.
5. There is a relatively large genetic distance between *Sulcorebutia* and *Rebutia*.

Geohistorical distribution

In observing plants and their areas of present distribution, one has to bear in mind that these areas and the plants that now occur there are the result of major geological changes. This is especially true for areas with such rapid and intense tectonic changes as in the Andes. As in Europe, the flora and fauna of North and South America, especially throughout the Andes and Patagonia, have been strongly influenced by the ice ages. It is evident by terminal moraines of the cordilleras that glaciation occurred four times during the quaternary. Throughout the area of lakes and salt lakes, a four-fold change of glacial and interglacial periods is obvious. During the strongest glaciation the shield of ice extended from the Andes over Chile as far as Tierra del Fuego and in the east as far as the Atlantic Ocean.

The whole region of southern South America and especially that of the central and southern Andes, except for a few refuge areas, was scoured of plants and was repopulated again between and after the ice ages. The repopulation came from different refuge areas. At the same time, inevitable genetic exchange between closely related groups occurred in the overlapping areas, leading to an increase of variability and to a strengthening of the genetic drift.

The extremely variable *Sulcorebutia* populations are the result of these postglacial introgressions, a process that can also be observed in a multitude of other Andean, Patagonian and North American plant populations. This also applies to *Rebutia* and particularly for a possible genetic interchange between *Rebutia* and *Sulcorebutia.*

On the basis of the differing main distribution areas of these two genera, one can assume that they each immigrated from different refuge areas. In spite of geographical introgression of both genera, no genetic interchange with consequent hybrid populations is known up to now between *Sulcorebutia* and *Rebutia*. This fact lets us assume that only a minor relationship exists between these genera.

Because of the morphological similarities of *Sulcorebutia* and the *R. padcayensis* group, the southern overlapping region of both genera should be investigated even more intensively.

Conclusions

On the basis of important shared or similar characters in *Sulcorebutia* and *Weingartia* it is justified to unite both with the older genus *Weingartia*. Both genera can be regarded as extremely neotenic, highly derived plant groups. They have a lot of characters in common with *Gymnocalycium* as well, so it would be conceivable to integrate *Sulcorebutia* and *Weingartia* as subgenus Weingartia into the genus *Gymnocalycium.*

On the whole, the genus *Rebutia* has more morphologic characters in common with *Echinopsis* and could be regarded as a highly derived group within that genus.

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