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Coryphantha

Cacti of Mexico and Southern USA



Springer

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Cacti of Mexico and Southern USA

With 338 Figures, Including 299 Colour Photos

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Dedicated to our wives Roswitha Dicht and Agnieszka Lüthy

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About this Book

Alexander the Great needed one short moment to cut the Gordian knot. We needed nearly 15 years to solve the nomenclatural confusion of the genus *Coryphantha* and to write this monograph.

Early on, we succumbed to the fascination of cacti. For most genera, specific literature and monographs were available which, despite many contradictions, opened up the background for a plant collection. However, for *Coryphantha* spp., which attracted us especially by their wonderful spination and large flowers, nothing existed.

In the late 1980s, both of us approached the problem of *Coryphantha* spp. independently. Later, by chance, we discovered our common interest during a small discussion at our cactus club, the Solothurn local group of the Swiss Cactus Society, and decided to combine our efforts.

In the beginning, we were very confident and light-hearted and ignored all the warnings of benevolent field researchers and botanists to keep clear of this genus. Fortunately, we only detected the extent of the existing problems as time passed and we were already smitten with the subject.

Had we not worked as a team, we certainly would have given up very early. We will always remember all those innumerable setbacks, but also the joy of discovering new solutions which led us, step by step, and around many detours to the final goal.

It took us several years to gather all the articles, descriptions and combinations (in total, more than 300 since the early nineteenth century), to translate them from five

languages and to classify them correctly, even with the great support of the Städtische Sukkulentsammlung Zürich and Anton Hofer's private library. The discoveries during this period were very thrilling: from the beginning, the history of the genus was full of errors and mistakes, which continued or were made even worse by most authors. To rectify all this, it was necessary for us to work back through the oldest descriptions and delve into the systematic botany and ICBN. We tried to work as conservatively as possible; however, some well-known species names had to be dropped or had to be replaced by valid names.

Several journeys to Mexico were necessary to check the existing species and their distribution. Thousands of photo documents of all known and newly discovered occurrences of *Coryphantha* spp. were the result, which meanwhile, ordered in a card index, became an excellent instrument for the diagnosis of plants and their variability. In the field, measurements of all species were taken and processed into uniform descriptions and, finally, into the key to the genus.

As a surprising bonus, it was possible, despite all the changes in Mexico over the past 150 years, to revisit very old locations and to document once again species lost or forgotten long ago. We even managed to discover and describe some new plants.

We reached our aim, the genus *Coryphantha* has been put into an order following the rules of today's botany and the system of Linné, insofar as a model developed by human beings can describe living nature.

This book cannot deal with the whole diversity of natural forms of *Coryphantha* spp., but we hope it will serve as a basis for the future work of as many enthusiasts of this genus as possible.

During our research, we found open doors and new friends, not only in Mexico, but everywhere, who greatly supported our efforts. To all of them we would like to express our thanks, in particular:

- Anton Hofer, Worben, Switzerland, who was an excellent teacher with his profound general knowledge and his great experience in the field and who allowed us the use of his unique private library
- Jonas Lüthy, whose brilliant knowledge as a botanist and *Mammillaria* specialist was of great benefit, and who made helpful corrections and assisted us in the field
- Urs Eggli, Zurich, who not only supplied us with abundant literature, but also with his great know-how of systematic botany
- Charles Glass, the genial explorer of Mexican cacti with his infallible instinct, who acknowledged us as *Coryphantha* specialists from the beginning and who gave us many new impulses with his unique knowledge about cacti; his field notes made it much easier to find many locations of *Coryphantha* species
- W.A. and Betty Fitz Maurice, San Luis Potosí, our “Mexican fortress”, who took us to many important locations
- George B. Hinton, whose family herbarium was indispensable for our work and who helped us in our research of several species
- Manuel Sotomayor, San Luis Potosí and his “Grupo San Luis”, who gave us many important data and helped us to collect *Coryphantha glassii*
- Andreas Böcker, whose great *Coryphantha* knowledge contributed to our work through an intense exchange of opinions by letter
- Grzegorz F. Matuszewski, our correspondent for Eastern Europe, who gave us much interesting information about locations
- Sidney Woolcock, whose publications on *Coryphantha* in the *Journal of the Mammillaria Society* and personal correspondence often provided inspiration; he spent many hours correcting our English translation of this monograph. Unfortunately, we could not thank him personally, since he died so unexpectedly in July 2001
- David Hunt, Kew, who helped us whenever we asked him and edited our new conspectus of the genus *Coryphantha*
- Ted Anderson, who corrected the areole chapter shortly before his death
- Walter Imber, Günsberg, genial photographer, who improved our photo technique by giving us many hints and tips and, finally
- the wives of the authors, Roswitha Dicht and Agnieszka Lüthy, who were so patient and for understanding the need for our many trips to Mexico and
- Julian R. Dicht, son of R.F. Dicht, who successfully served as our “truffle pig” on three expeditions and proved his aptness in the field

1 Introduction to the Genus *Coryphantha*

Coryphanthas are small to medium-sized globose to short-columnar tubercled cacti from Mexico and the south of the USA, which grow in dry regions and deserts between the Sierra Madre Oriental and the Sierra Madre Occidental. The plant bodies are not partitioned into ribs as e.g., in *Ferocactus*, *Thelocactus* etc., but into tubercles as in the closely related genus *Mammillaria*.

The name *Coryphantha* originates from the Greek *koryphe* = apex and *anthos* = flower and means “flowering from the apex”. The flowers are quite large (3–10 cm diameter) and arise from the new growth, which is in the centre of the plant, contrary to e.g. *Mammillarias*, which flower around the top from the growth of the year before. The flowers often are yellow, but also white or pink. The fruits are green and juicy, with attached flower remnants, the seeds are mostly reniform, brown, with reticulate testa structure.

The tubercles of *Coryphanthas* have a groove on their upper surface which usually reaches from the spine-bearing areole to the axil. The flowers originate from this groove, from which the plants may also sprout. Different types of areole development exist, which gives hints about the possible developmental history of the genus (phylogenesis).

In some species in these grooves and/or the axils, so-called nectary glands are produced which are mostly yellow, orange or red and which produce a sugar-containing sap. This sap may serve to attract ants, which, by their marking, keep plant- and mainly bud-eating animals from the plant.

The genus is characterised by the following three features, which should be present in adult plants:

1. Flowers in the apex of the plant.
2. Flowering tubercles grooved.
3. Seed testa reticulate.

Each cactus with tubercles showing these three features belongs to the genus *Coryphantha*. Moreover, all *Coryphanthas* have the potency to produce extrafloral nectary glands.

Following this definition and mainly due to the seed morphology, the following species have to be separated from *Coryphantha*: all species of the genus *Escobaria* which show foveolate testa cells and *Cumarinia*, with channelled anticlinal boundaries.

Coryphanthas belong to the slow-growing cacti and often are floriferous only after 8–10 years. Formation of a tubercle groove indicates that a plant has become floriferous. Many species pass through several stages, in which they change their appearance repeatedly. In nature, slow growers are heavily influenced by the microclimate at their individual location and, therefore, are surprisingly variable. These are also the main reasons, why up to now, more than 300 supposedly different species or combinations have been published which, as a result of our studies, must be reduced to 43 species and 11 subspecies.

For a better understanding of the genus *Coryphantha*, in addition to their great variability in nature, three particularities must be considered:

1. Many *Coryphantha* species continuously change their appearance during their development from young to adult plants.

Sometimes this change is so marked that, in consequence, floriferous plants of different ages are difficult to identify as belonging to the same species if one does not know their stages of development. Note the following examples: *C. echinus* (whose early form has pure radial spination only and was described as *C. pectinata*), *C. salinensis*, *C. difficilis*, *C. wohlschlagerei*, *C. echinoidea* (see Plate 1).

2. Several *Coryphantha* species occur, even as adult plants, either with or without a central spine.

These variants do not depend on the location. They can be found altogether at one and the same location. Here are some examples: *C. compacta*, *C. nickelsiae*, *C. delicata*, *C. cornifera*, *C. pallida*, *C. erecta*. Repeatedly, plants of the same species with and without a central spine have been described as different species (examples: *C. compacta*/*C. palmeri*, *C. cornifera*/*C. radians*, *C. pallida*/*C. pseudoradians*) (see Plate 3).

3. Extrafloral nectary glands

All *Coryphanthas* have the potential to produce extrafloral nectary glands. Two different types must be differentiated (see Plate 2, photos 1–4):

- Species in which nectary glands are always present, either in the areolar groove and/or in the axil (subgenus *Neocoryphantha*)
- Species with optional nectary glands around the flowering period only, and directly behind the spine-bearing areole only and, moreover, on singular areoles only (subgenus *Coryphantha*). Among them, there are species which were counted among the obligatory gland-bearing *Coryphanthas* by earlier authors (BACKEBERG 1961, H. BRAVO 1991; e.g. *C. pseudechinus* ssp. *pseudechinus*, *C. pulleineana* etc.) as well as other species which until today have been regarded as glandless (e.g. *C. pseudechinus* ssp. *loui*, *C. maiz-tablasensis* etc.).

The differentiation between obligatory and optionally gland-bearing *Coryphanthas* can already be observed in a seedling only a few weeks old, because the species mainly of the series *Clavatae* and section *Otonis*, which will be gland-bearing later on, show strikingly “inflated” and flattened, snow-white small spines, while the first spines of the non-glandular species are much thinner, roundish and yellow-brown (see Plate 4).

Only when considering these three points mentioned above can plants of this genus be judged and classified correctly. Disregard of these points has led to wrong diagnoses in the past and contributed to the general systematic chaos.

2 Ecology of *Coryphantha* spp.

2.1 Geographical Distribution

The 43 *Coryphantha* species are plants of the Mexican highlands, their main distribution area extends from the Sierra Madre Oriental to the Sierra Madre Occidental and to the Sierra Madre del Sur. Six species (*C. sulcata*, *C. ramillosa*, *C. recurvata*, *C. robustispina*, *C. echinus* and *C. macromeris*) also occur on the other side of the Rio Grande in the southernmost states of the USA (Texas, New Mexico and Arizona).

The only species which occurs in some places south of the Sierra Madre del Sur, mainly along the Rio Balsas and South of Oaxaca, is *C. elephantidens* with its ssp. *bumamma*.

The Sierra Madre Oriental is more habitable for *Coryphantha* spp. thanks to the large river valleys towards the Gulf of Mexico. Here, again, it is *C. elephantidens* with its ssp. *greenwoodii*, which has an isolated habitat on the eastern slopes of Puerto del Aire near Acultzingo VER. To the north of the distribution area, *C. macromeris* ssp. *runyonii* reaches the coastal plains along the Rio Grande. In the region in between, in the states of Tamaulipas and Nuevo León, there are two species whose distribution area is exclusively restricted to the eastern slopes of the Sierra and the plains extending below it: *C. salinensis* and *C. nickelsiae*.

The distribution maps are shown on colour Plates 5 and 9–13.

2.2 Climate

The geographical distribution area is identical to the drier zones of Mexico with a maximum precipitation of up to 1000 mm/year. These precipitations, however, are very unequally distributed over the year and mainly occur in the four summer months as heavy thunder showers. The rest of the year is dry. The majority of *Coryphantha* spp. grow in regions with less than 600 mm/year precipitation, i.e. dry and very dry zones, but the marginal areas of distribution are located in moderately humid regions.

Summer in the whole distribution area is very hot, but in the wintertime short cold periods and nightly frosts are not unusual, mainly in the north.

The climatic conditions are shown in Plate 5.

Coryphantha spp. are very well adapted to these conditions of climate. In winter they stop growing in order to withstand the dryness and cold. Growth begins again in spring shortly before or with the first rainfall.

In order to reproduce, *Coryphantha* spp. have two main strategies: either they flower very early in spring or summer so the fruits ripen within the same rainy period (a typical representative of these early flowerers: *C. clavata*). Or they flower in fall only, and the fruits remain dormant and ripen in the following spring when the seeds have a complete rainy season for germination (typical representative of these late flowerers: *C. elephantidens*).

Many *Coryphantha* spp. make use of both strategies and flower several times during the whole summer. In this case, some of the fruits ripen in the same summer, others towards spring.

2.3 Geology

Mexico can roughly be divided into two geological zones: The eastern zone with the Sierra Madre Oriental, which mainly consists of calcareous sedimentation and the western and southern zones with the Sierras Madre Occidental and del Sur which are of volcanic material. *Coryphantha* spp. grow in both zones, but the species are specialised either for lava soils or for calcareous soils. An exception is *C. clavata* which is known to grow on volcanic stone in one location, while otherwise this species grows on calcareous ground.

Coryphantha spp. are not extreme endemites, which occur on strictly defined soil or ground only. Usually, a few main parameters like lava/lime, exposition, incline etc. are sufficient for the occurrence of a species. Most probably, the limits of distribution of the species are caused by climatic factors. This would also explain the rather huge distribution area of certain species like *C. elephantidens* (in this case from southern Oaxaca and Veracruz up to Zacatecas), which can be found wherever their specific demands for a location are fulfilled.

A few species are specialised for special soils:

C. gracilis grows on very characteristic conglomerate soils only, or *C. jalpanensis*, which grows on raw humus on calcareous rocks only. For other species with very limited areas, like *C. pulleineana* or *C. vogtherriana*, the reason for their limited distribution is not known, but it is certainly not caused by geological conditions.

2.4 Habitats

Since many *Coryphantha* spp. are widely distributed, they are practically part of the "basic outfit" of certain floras. Some species, like *C. cornifera* or *C. delicata* occur in masses, while others like *C. hinoniorum* are very scattered over large areas. There are few habitats which are not settled by *Coryphantha* spp.: the highest mountainous regions with pine forests as well as naked rock walls and gypsum hills, but also steep and unstable ground where *Coryphantha* spp. as slow-growing plants can hardly establish themselves.

The classical habitat of a *Coryphantha* is the foot of a hill or a ridge of stony gravel with loose vegetation, or on lava with grass. There, the plants grow partly in the open or slightly to completely protected between or under bushes.

Some species grow in specialised habitats. Among them, *C. macromeris* and *C. maiztablasensis*, both group-forming plants which occur in sandy gypsum, usually dry, nearly bare lagoons only; or *C. pseudechinus* and *C. durangensis*, which form large clusters on quite steep slopes with rocks, and *C. vaupeiana*, which grows on gravel plains. *C. poselgeriana*, *C. pycnacantha* and *C. hintoniorum* occur on flat plains only.

A special form of growth habit is shown by *C. pulleineana* which needs the proximity of a *Hechtia* or *Agave* to support the long, thin sprout.

It is not known yet how *Coryphantha* spp. settle in areas and how they came to be so widely distributed. Moreover, due to its green berry and the fact that, unlike certain *Mammillaria* spp., they are never found on trees, birds as the main distributors of seeds can be excluded with great certainty.

2.5 Conservational Status

The main threat for *Coryphantha* spp. is the fast growth of the population of Mexico and the consequent activities such as construction of settlements and roads, expansion of areas used by agriculture, intensified use of natural resources, deforestation and clearing by fire. Fortunately, most species are only marginally affected by these changes, thanks to their wide distribution and their remote and unfruitful habitats.

However, some *Coryphantha* species are extremely and acutely endangered. The most endangered species is *C. vogtherriana*, of which one single location remains which is extremely threatened by erosion due to deforestation and overpasturing. There are only a few hundred adult plants left and seedlings are never observed.

All those species which need plain, deep soils are heavily threatened by the extension of agriculture. This is true mainly for *C. pycnanantha*, *C. hintoniorum* and *C. maiz-*

tablasensis, but also to a somewhat lesser degree, for *C. elephantidens* and *C. ottonis*. Today, *C. pycnanantha* can only be found in pitiful remnants of habitats between the fields and the roads or near railroad banks.

Certain species suffer from a permanent loss of individuals by the “clearing” of pastures either by burning off the dry vegetation or by intentional removal of the plants, because they are regarded as a source of injury to cattle, as observed for *C. elephantidens* and *C. ottonis*.

Again and again, some habitats are completely destroyed unintentionally or through ignorance. This happened to the only known location of *C. maiz-tablasensis* outside the lagoon of Las Tablas near Matehuala, which was almost completely destroyed by the construction of the new highway. At the location of *C. sulcata* near Monclova COAH, which is right in the centre of a fast-growing industrial zone with continuous construction, there was one single plant left when we last visited (2001).

3 Morphology of *Coryphantha*

In all our definitions, we endeavour to use the same, standardised terms for plant descriptions. For a better understanding of the descriptions of the species, the terms used and their application are explained here.

3.1 Body

Body means the plant as a whole.

Formation of Groups

First, it is always differentiated whether a plant grows alone, or if it forms groups by sprouting, or if it clusters. Groups of three or four and up to about ten shoots are formed either by sprouting or by stolons. Clusters are large groups of about 20 or more sprouts. For a comparison, see Fig. 1.

Body Form, Measurements

Body form describes the form of that part of the plant above the ground. The height is measured from the ground to the apex, the

diameter is related to that of a mature single shoot. The terms used relating to body shape are: depressed globose/semiglobose, globose, clavate/reversed egg-shaped (obovoid), cylindrical, columnar (see Figs. 2 and 3).

Apex

This term refers to the top of a stem. For the shape of the apex the spines towering above are not considered (see Fig. 4). The new growth of a stem arises in the apex and this is often protected initially by wool. Terms used when describing the apex are: rounded, flattened, depressed.

Colour of the Epidermis

It is quite difficult to indicate the colour of the epidermis objectively, because it may depend on the conditions of cultivation or growing conditions, and also on the vegetative stage of the plant. Another criterion describes whether the surface is shiny or dull.

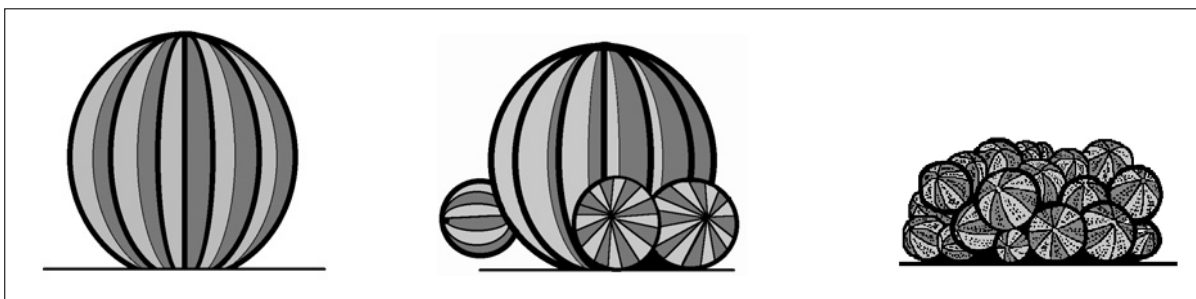


Fig. 1. Formation of groups. *Left* solitary plant, *middle* groups, *right* clusters

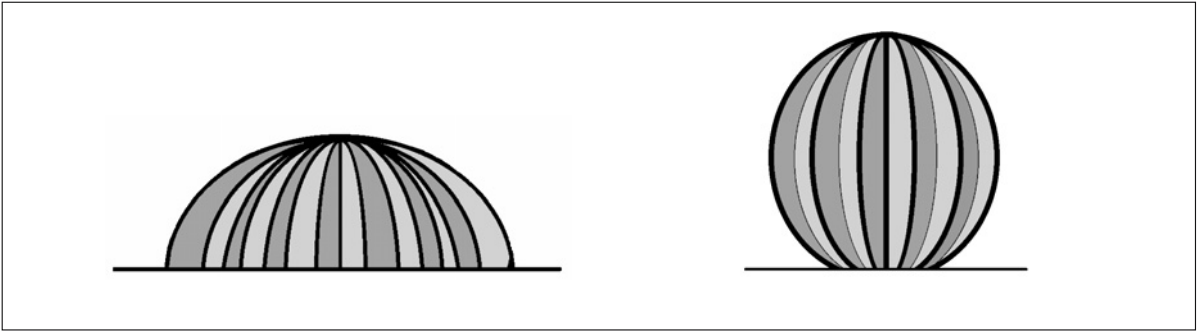


Fig. 2. Body forms. *Left* depressed globose/semiglobose, *right* globose

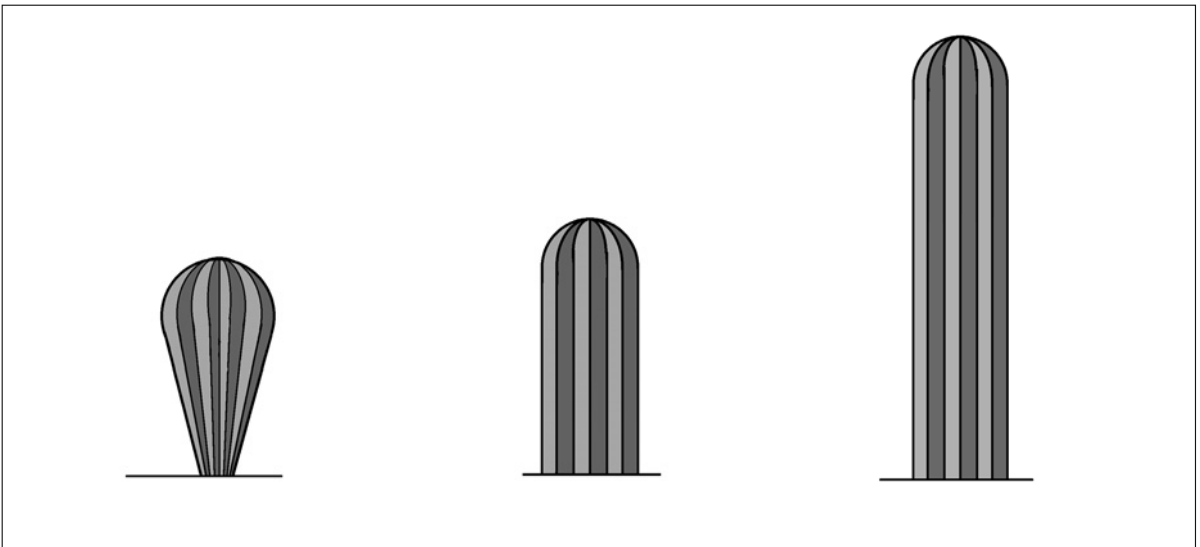


Fig. 3. Body forms. *Left* clavate/obovoid, *middle* cylindrical, *right* columnar

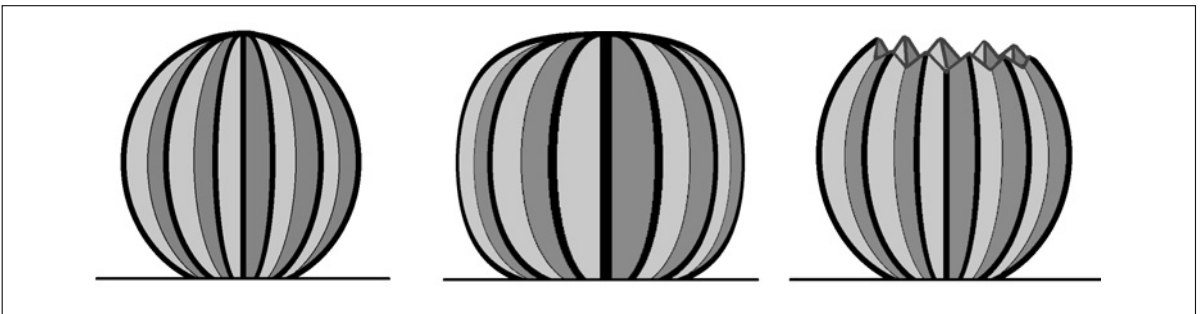


Fig. 4. Apex forms. *Left* rounded, *middle* flattened, *right* depressed

Root

Not all parts below ground level are roots. Sometimes a part of the plant body is in the ground too, tapering more or less continuously into the root. Some species like *C. vaupeiana*, *C. wohlschlageri* or *C. pulleineana* develop a significant “neck” between the tuberous root and the body (see Fig. 5). When cultivated, the root is often deformed. It is generally not permitted to remove plants from their habitat and, therefore, it has become difficult to give an exact description of the root structure of a species. Technical terms for the roots are: fibrous roots, sprouting root, tuberous root.

3.2 Tubercles

The surface of a *Coryphantha* is composed entirely of tubercles. The areoles are no longer arranged on ribs, the ribs have been separated into singular tubercles. The size and the form of the tubercles are important criteria to differentiate between species of *Coryphantha*, since they vary little.

Series

The tubercles of *Coryphantha* spp. are arranged in series, the so-called Fibonacci series. This means the sequences of tubercles when viewing the plant from above into the

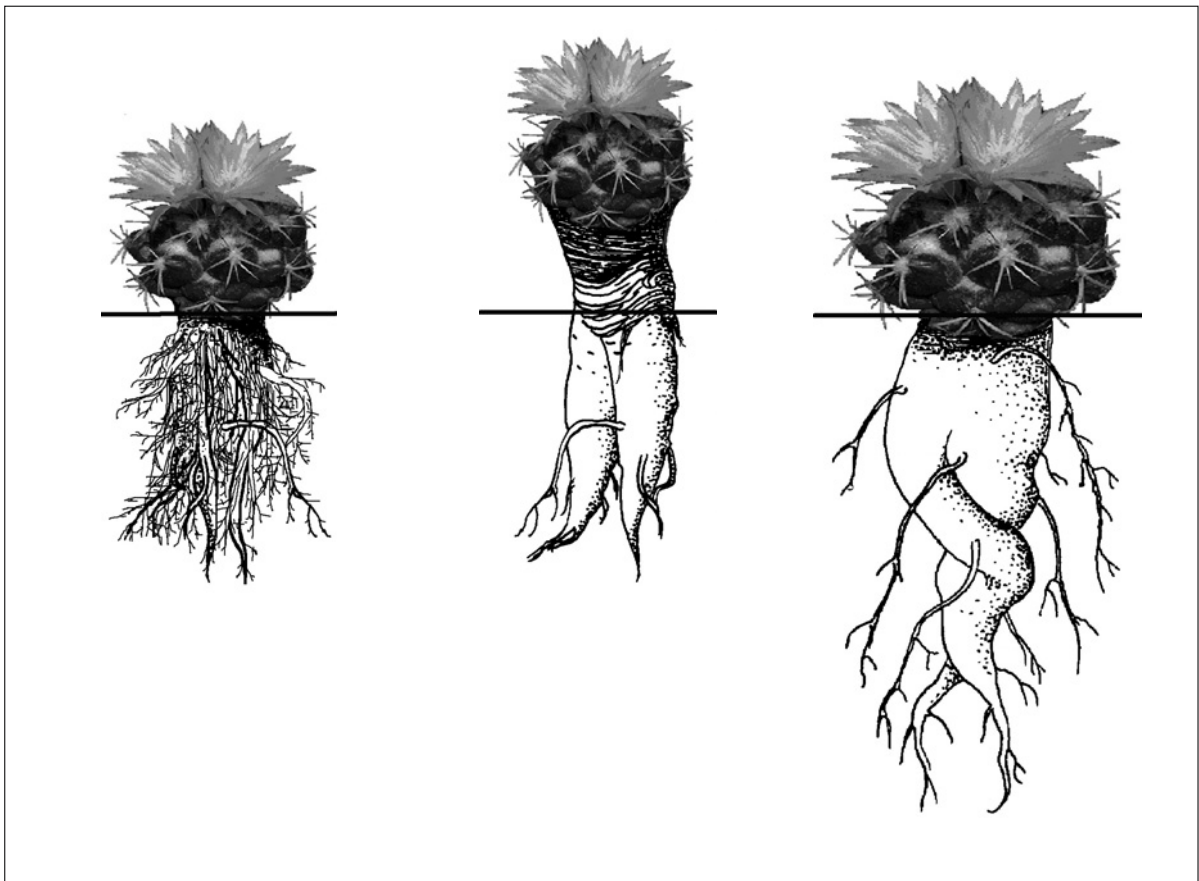


Fig. 5. Roots. *Left* fibrous roots, *middle* sprouting root, *right* tuberous root

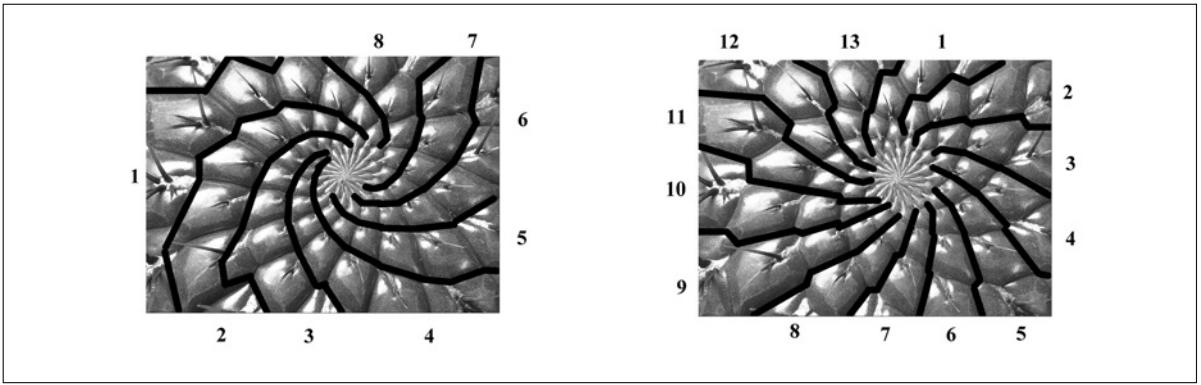


Fig. 6. Tubercle series, example tubercle series 8/13. *Left* counterclockwise, *right* clockwise

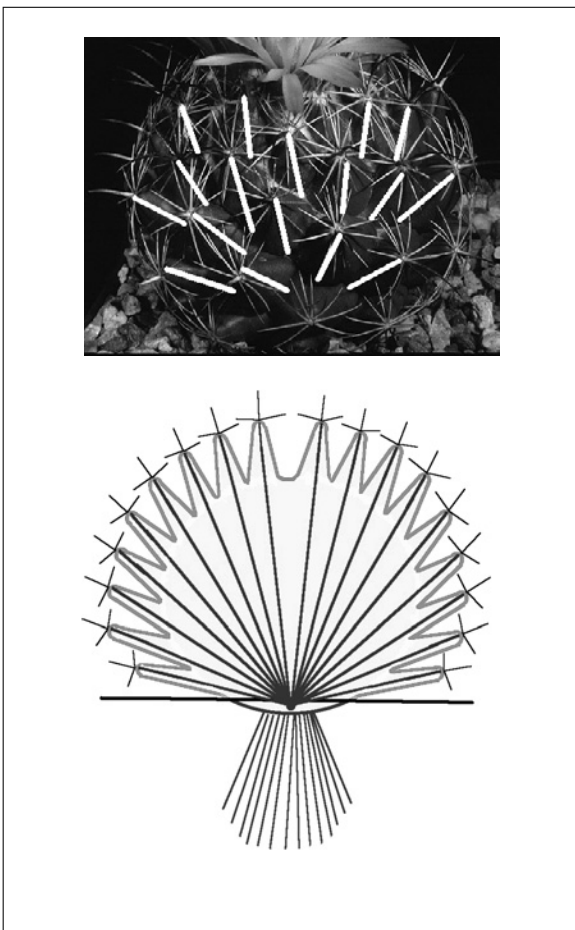


Fig. 7. Direction of tubercle axis, tubercles porrect. Example: *C. cornifera*

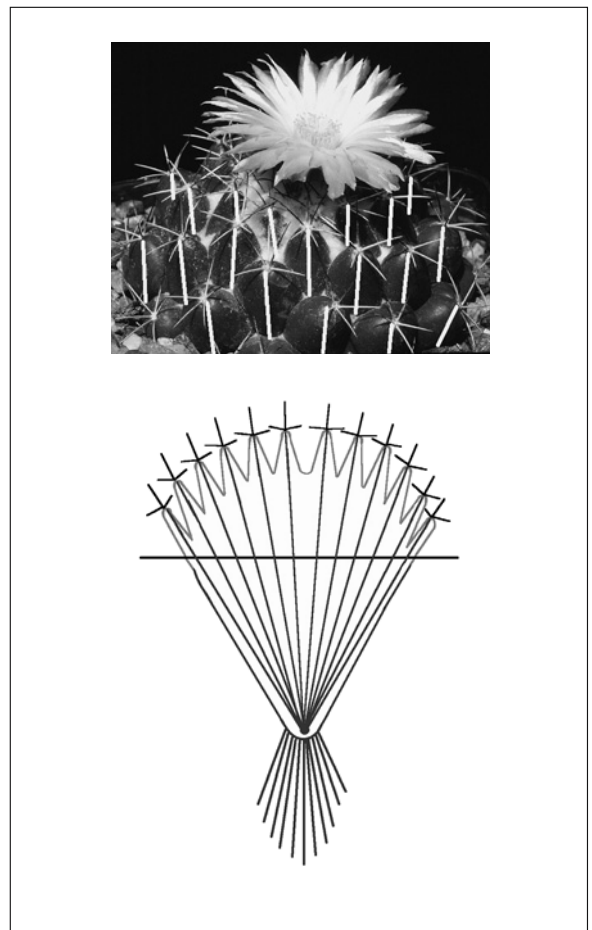


Fig. 8. Direction of tubercle axis, tubercles upright. Example: *C. maiz-tablasensis*

apex, counting the number of tubercles per spiral clockwise and counterclockwise. The numbers counted always correspond to the Fibonacci numbers (1, 2, 3, 5, 8, 13, 21, 34 etc.). *Coryphantha* spp. have tubercle series in a relation of 5/8, 8/13 and 13/21 clockwise/ counterclockwise respectively (see Fig. 6).

Direction of the Tubercle Axis

The axis of the tubercles of *Coryphantha* spp. always points to the centre and to the base of the sprout. For the description of this position of the tubercles, the term “porrect” is used (see Fig. 7).

Within this strict orientation of the tubercle axis, three variations can be differentiated:

- If a part of the plant body is below ground level, the tubercles appear more upright and are described by this term (see Fig. 8).
- In certain species only the base of the tubercle points to the centre of the body, the upper part is more appressed and the direction of the tubercle axis on the whole is tangential to the surface of the plant body. Therefore, for this type, the term “appressed” is used (see Fig. 9).
- In clavate and columnar plants this basal central point becomes more and more elongated and becomes a line (see Fig. 10).

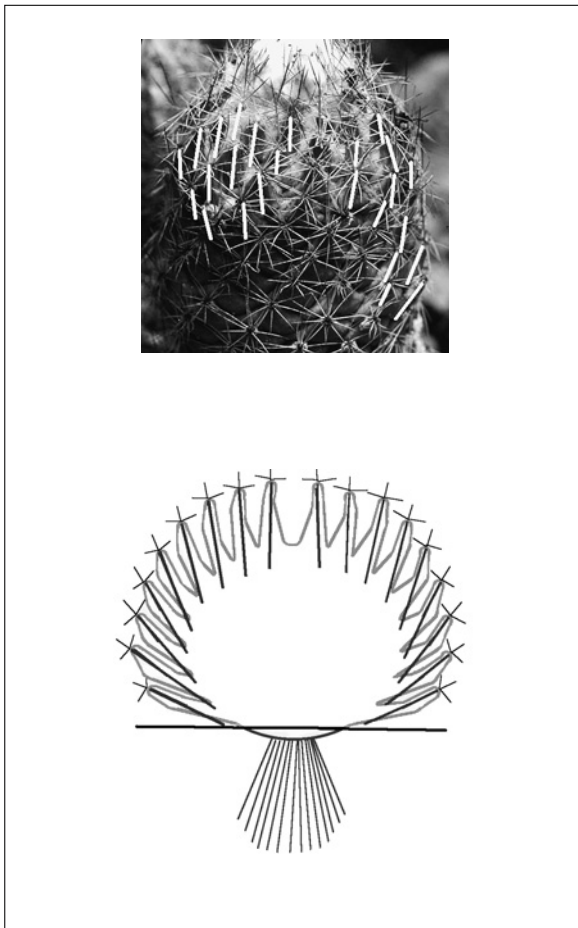


Fig. 9. Direction of tubercle axis, tubercles appressed. Example: *C. durangensis*

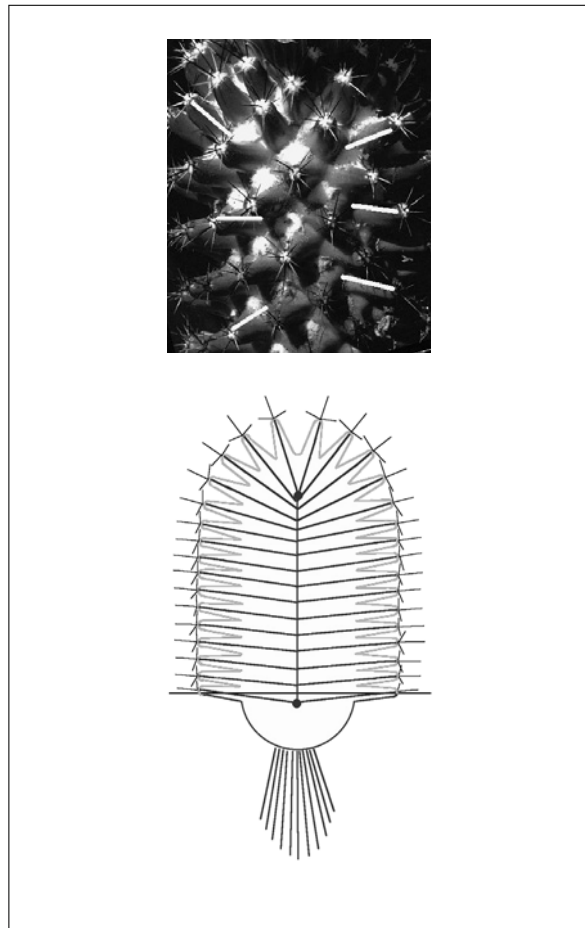


Fig. 10. Direction of tubercle axis, tubercles in clavate and columnar forms. Example: *C. octacantha*

Shape

The tubercle shape of a particular *Coryphantha* species has unique features and is, in fact, one of the best diagnostic features for differentiation between species. In general, tubercles are based on the shape of a cone with the upper part obliquely cut, rounded and more or less edged. The lower part is more or less bulging and sometimes keeled. The base is more or less enlarged. Another typical characteristic feature is the shape of the contour line where the enlarged base of the tubercle joins the plant body. Young tubercles usually are rounder, but develop a more characteristic shape with age. The shapes and measurements given by us always concern tubercles of average age.

Measurements

To describe the size of the tubercles, we use four different measurements and their locations on the plant are shown in Figs. 11 and 12.

3.3 Areoles

As described in Chapter 5, *Position and Delimitation of the Genus Coryphantha*, the areole essentially consists of three different organs: the spiniferous part, the groove, and the axil. In most cactus literature the expression areole is used only for the spine-bearing part. For the whole areole, another word, e.g. podarium, should be used. For clarity and consistency with former publications, we describe the three parts of the podarium separately as areole (spine-bearing part), groove and axil. In the text, the expression 'spiniferous areole' is sometimes used to highlight precisely what specific part of the podarium is under discussion.

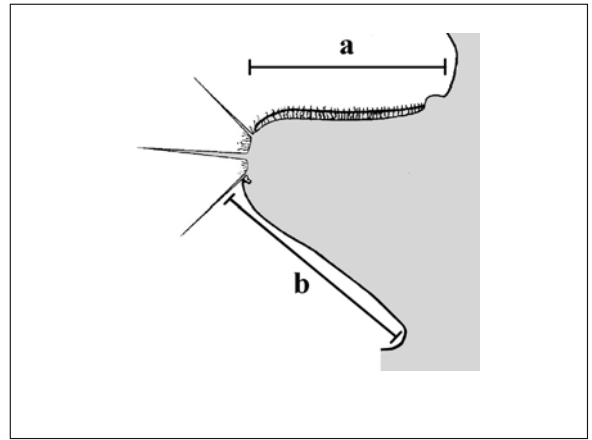


Fig. 11. Measurements of tubercle size, length of upper (a) and lower (b) surface

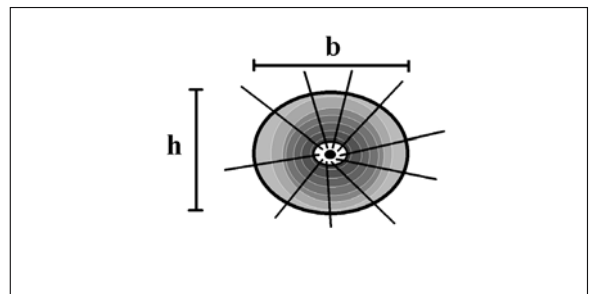


Fig. 12. Measurements of tubercle size, height (h) and breadth (b)

Spiniferous Areoles

Coryphantha areoles are always sterile and never floriferous. The position of the areole is located close to or on the tubercle tip. Usually, areoles are covered by white wool in youth, but this disappears with age. The areole is bordered by the thickened bases of the radial spines in a more or less pectinate manner. The measurements given in the text relate to the diameter, and to the length and breadth within this boundary. The shapes of the areoles can be round or oval. In certain species the shape of the areole is dependent on whether a central spine is produced or not. Without a central spine the areole is oval, whereas with a central spine present, it is round.

Groove

The groove between areole and axil on the upper surface of the tubercle is an organ typical of the genus. The point of time and the way of arrival of the grooves are diagnostic characteristics for certain groups of *Coryphantha* spp. (see Chap. 5). Young grooves often produce white wool which often disappears with age. Another function of the groove is the production of offsets or stolons. *Coryphantha* spp. usually sprout from old tubercles near the ground from the groove directly behind a spine-bearing areole and never from the axil itself. Tubercles which have already reached into the ground may also form stolons in certain species from which young offsets originate some distance from the mother plant (e.g. in *C. tripugionacantha*, *C. glassii*).

Nectary Glands

One group of *Coryphantha* spp. (subgenus *Neocoryphantha*) always produces extrafloral nectary glands. These occur in the groove or in the axil. The nectary glands are round and often bordered by a narrow margin of woolly felt. Their colour varies from red through orange to yellow. In the vegetative period they secrete a transparent, sugar-containing nectar.

The second group of *Coryphantha* spp. (subgenus *Coryphantha*) has the potential to produce optional nectary glands. These are found directly behind the spiniferous areole in the groove and appear during the flowering period of the plant only, otherwise they are invisible (see Plate 2, photos 1–4).

Axil

The axil is the flower-producing part of the areole in the botanical sense and lies, well protected, at the inner (adaxial) end of the groove on the plant body. The flowers are pro-

duced from very young areoles in the apex of the plant. Later on, the axils are sterile and may at most produce nectary glands. Young axils produce a white woolly felt, which may disappear with age.

3.4 Spines

The areoles of *Coryphantha* spp. can produce four series of spines (see Fig. 13). These arise from the centre to the periphery of the spine-bearing areole in the following sequence:

- Central spine(s)
- Subcentral spines
- First layer of radial spines
- Second layer of radial spines

Shape

The spines of *Coryphantha* spp. are usually round or slightly flattened. Most of them are thicker at the base. Spine strength or thickness and the different shapes of spines are shown in Figs. 14 and 15.

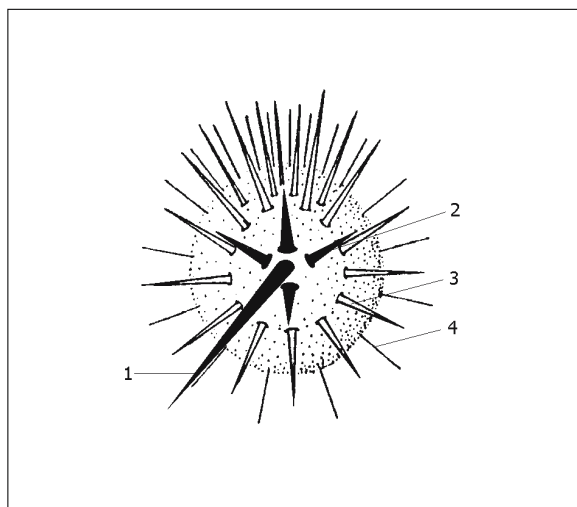


Fig. 13. Scheme of spine formation. Central spine(s) (1), subcentral spines (2), first layer of radial spines (3), second layer of radial spines (4)

Colour

In new growth *Coryphantha* spines are usually intensely coloured, the central spines being darker than the radial spines. Initially, they are red-brown, but soon become darker to nearly black from the tip. This process is then reversed and the spines become grey from the base, either totally or with the exception of the tips. The change in colour to grey

is typical for all species of *Coryphantha*. However, the rate of change varies markedly from one species to another. The radial spines are usually horn-coloured or transparent white at first. Often, the uppermost radials and, more rarely, all radials have dark tips. Moreover, the radial spines become grey from the base, either along the whole length, or with the exception of the tip.

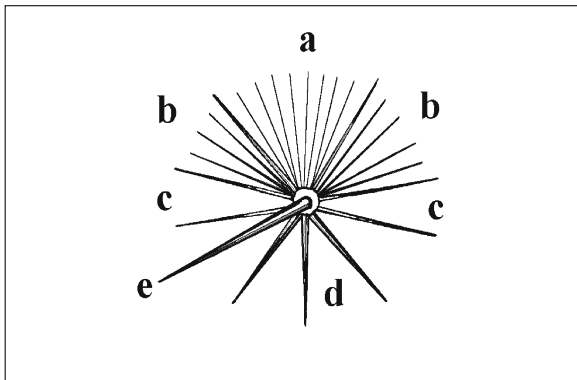


Fig. 14. Spine thickness. Thin needle-like (a) needle-like (b) thick needle-like (c) subulate (d) thick subulate (e)

Central Spine(s)

Coryphantha spp. may produce one dominant central spine and up to six subcentral spines, which, following the established practice, we also named central spines. The subcentral spines arise from the upper half of the areole. All central spines arise from the centre of an areole. Words used to describe the number, direction and position of central spines are explained in Fig. 16.

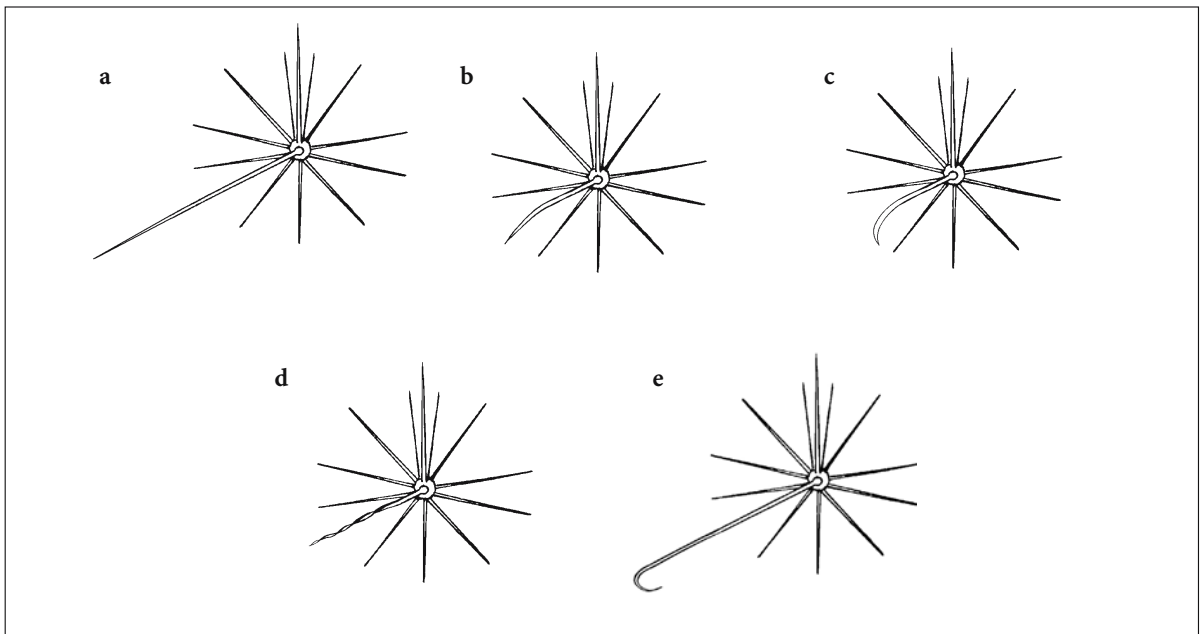


Fig. 15. Shapes of spines. a straight, b slightly curved, c curved, d twisted, e hooked

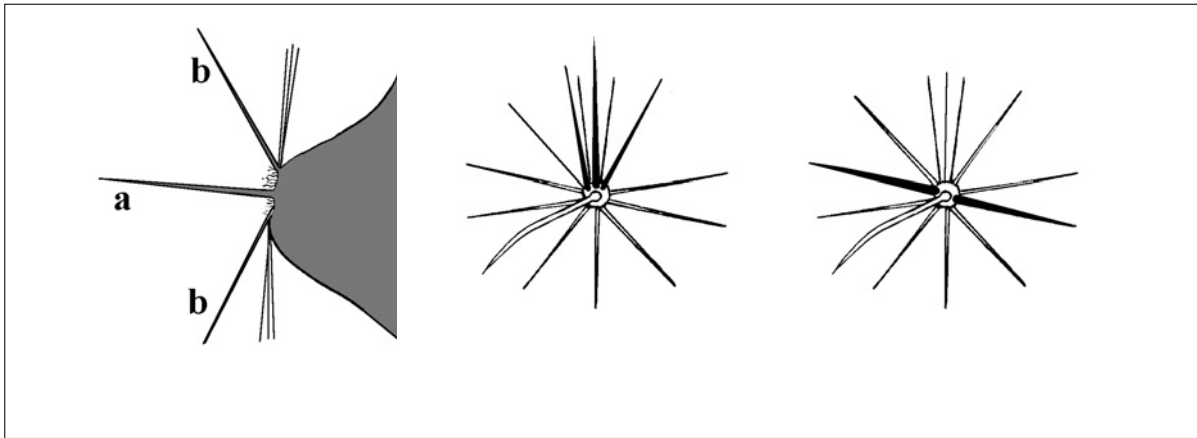


Fig. 16. Direction and position of central spines. *Left* correct (a) and protruding ascending/descending (b), *middle* upwards, *right* sideways

Radial Spines

Often the plants produce one complete layer of radial spines and a second layer in the uppermost part of the areole only. Similarly, it often occurs that the upper radial spines are more densely set. This gives the impression of bundled radial spines in the upper part of the areole. Upper radial spines may also differ in colour, and they are often thinner and longer than the lateral and lower ones. The description concerns the number, direction and position of the radial spines (see Fig. 17).

3.5 Flowers

The flowers of the various species all have the same anatomical details except for size and colour. One further difference to note is that for some species the flower, when fully developed, remains “funnelform”. The size of the flowers can vary depending on flowering time, age of the plant and on variable growing conditions concerning temperature, light, nutrition and humidity. The size can even vary on an individual plant from one flower to the next. Our measurements concern the characteristics shown in Fig. 18.

The colour of the flowers varies noticeably. The intensity of the coloration of the complete flower can vary from pale to saturated. Moreover, singular features, e.g. a red tinge in the throat, may vary from nearly unnoticeable to deep red. In certain species the colour may change with the age of the flower, e.g. a yellow flower turning whitish or pale rose when fading. Some species even have flowers in different colours from yellow through white to magenta.

Perianth Segments

A differentiation is made between inner and outer perianth segments. The number of perianth segments is not indicated. The features used are shown in Figs. 19–21.

Concerning the colour of outer perianth segments, the coloration of the outer surface is meant, for inner perianth segments, the inner surface only is considered. Often perianth segments are not unicoloured, a mid-stripe of a different colour is sometimes present. With regard to the outer perianth segments, the midstripe is usually within the colour spectrum green–red–brown. Inner perianth segments may show a different colour at their base in the throat.

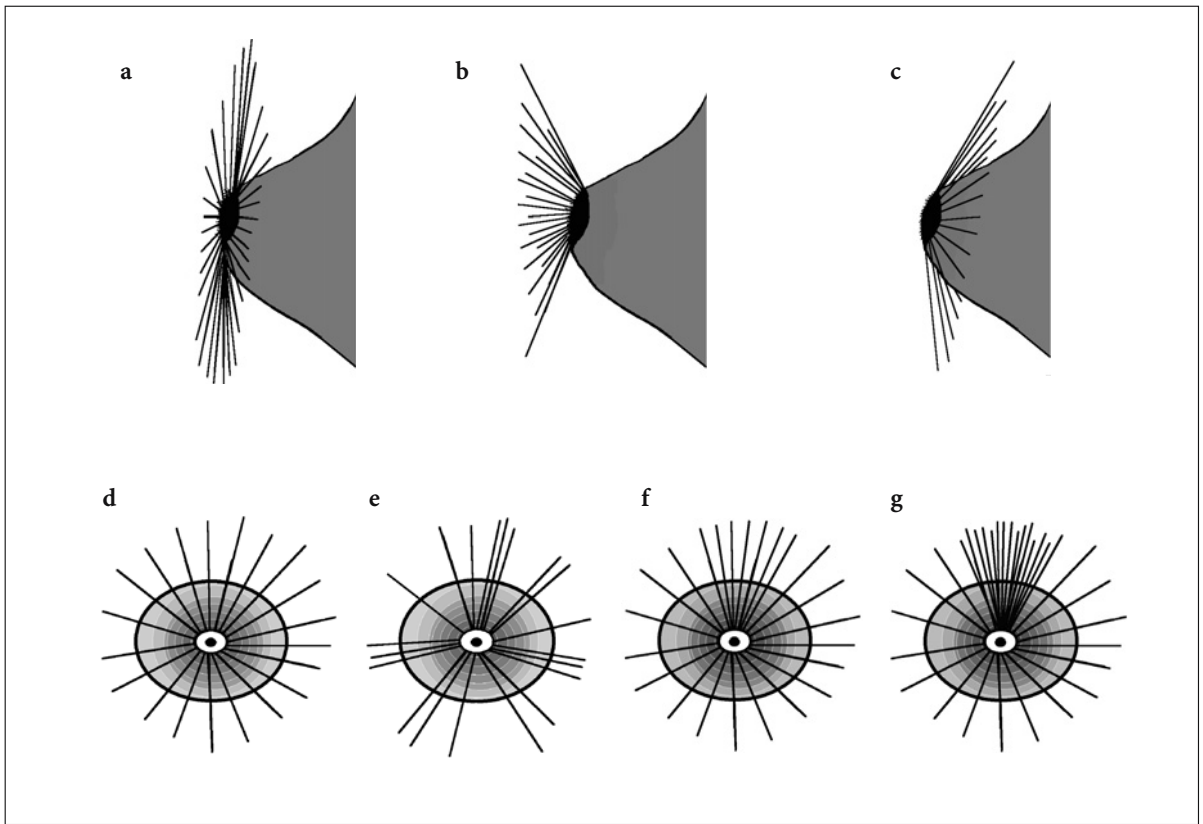


Fig. 17. Direction and position of radial spines. a horizontal, b porrect and c appressed direction, d radiating, e irregularly radiating, f densely set above and g bundled position

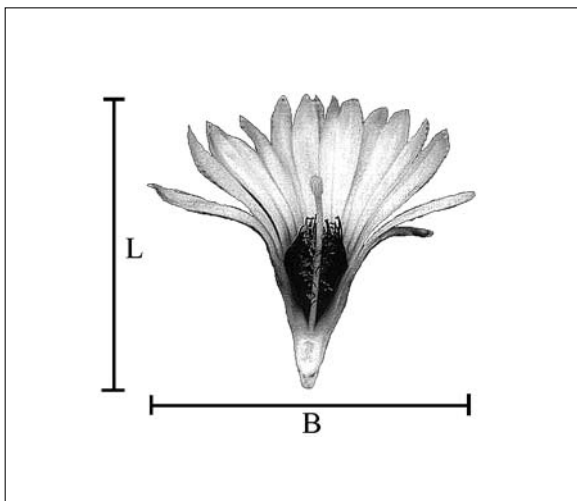


Fig. 18. Flower measurements (open flower). Length (L), breadth (B)

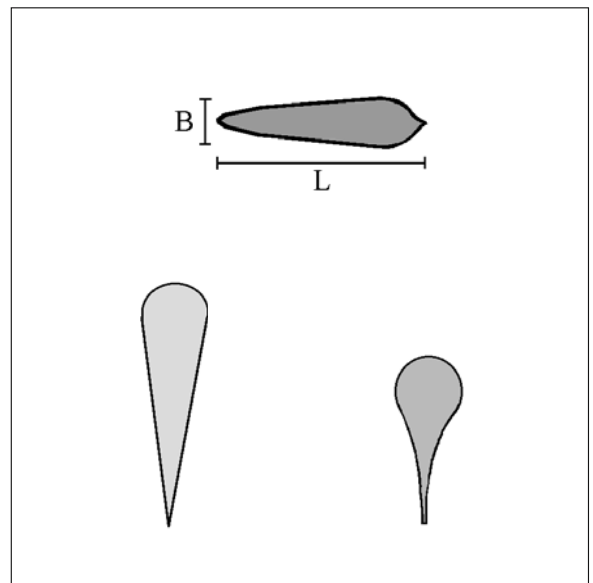


Fig. 19. Measurements and shapes of perianth segments. Above Measurements, length (L)/breadth (B); left ob lanceolate and right spatulate shape

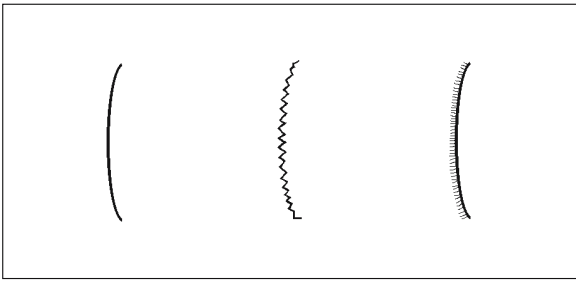


Fig. 20. Margins of perianth segments. *Left* entire, *middle* dentate, *right* ciliate

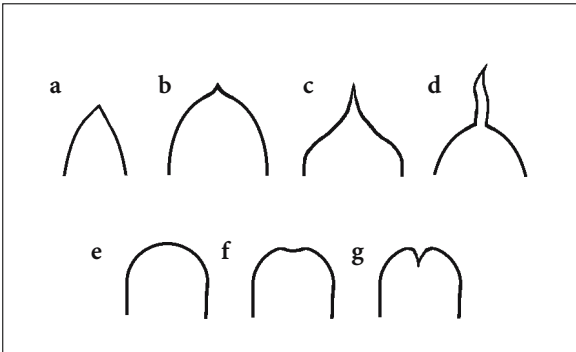


Fig. 21. Shapes of tips of perianth segments. *a* acute, *b* apiculate, *c* acuminate, *d* caudate, *e* rounded, *f* retuse, *g* notched

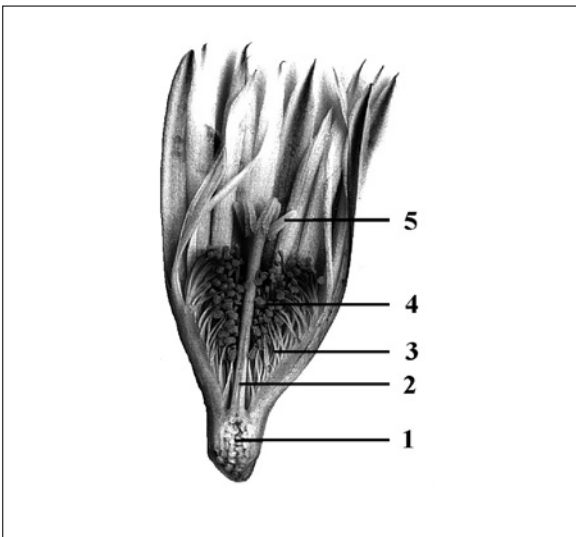


Fig. 22. Flower organs. Ovary (1), style (2), filaments (3), anthers (4), stigma lobes (5)

Remaining Flower Organs

The remaining flower organs are filaments, anthers, style and stigma lobes. The description concerns their colour only, no measurements or numbers are given (see Fig. 22).

3.6 Fruits

The fruits of *Coryphantha* spp. are green, juicy, smooth. They dry very slowly with dried flower remnants remaining attached. The seeds are numerous and embedded in a transparent, greenish, sugar-containing, viscous pulp. In the axil the fruits are attached by a small point and may thus easily be removed. After fertilisation many fruits stop growing for some time and only appear above the spines the following spring. Most fruits are green when ripe, sometimes with a red tinge. Near the base they are paler or nearly white.

The shape of the fruits is cylindrical to round. Measurements in millimetres cover the length and diameter.

Fruits, see Plate 2, photos 5 and 6.

3.7 Seeds

The seeds of *Coryphantha* spp. are generally reniform (only exception: *C. gracilis* with globular hat-like seeds). Sometimes they are somewhat longer or rounder and vary in size.

The measurements given are maximum length and width.

In a rounded impression on the flat side of the seed, there is the hilum and behind, slightly distant, the micropyle. The hilum is narrow and long to oval-shaped. It is slightly depressed and may be surrounded by a bulging prominence, which also includes the micropyle. The region of hilum and micropyle measures about one quarter to one half the length of the seed at the maximum. Characteristics of the seeds are illustrated in

Figs. 23 and 24.

The seeds of *C. gracilis* are very different. They are roundish with a very prominent roll around hilum and micropyle, which gives the impression of a hat or helmet. The hilum is also rounder than in other *Coryphantha* spp. (see Fig. 25).

The colour of the seeds is brown and varies from light to dark, sometimes also reddish. However, the colour of the seeds also depends on their stage of maturity. The surface of the seeds is shiny and smooth.

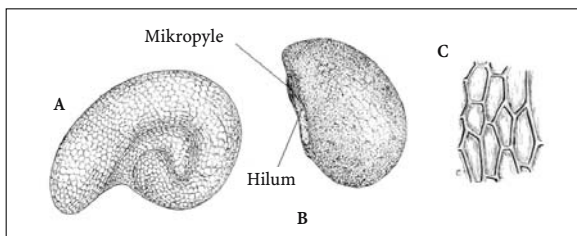


Fig. 23. Scheme of a cactus seed. **A** *Coryphantha poselgeriana*, **B** *Coryphantha salm-dyckiana*, **C** testa cells of *Coryphantha salm-dyckiana*. (From F. Buxbaum in Krainz, 1956–1975)

The borders of the outer testa cells are thick and bulging, which leads to a net-like structure. This form is called reticulate testa, which is obligatory for all *Coryphantha* species. The extent of these net lines varies from very fine (*C. pseudoechinus*) to quite large and prominent as in *C. recurvata*. Moreover, the form of the testa cells varies from nearly regularly hexagonal (*C. pseudoechinus*) to very long as in *C. tripugionacantha*. However, the form of the testa cells and the formation of net lines are not identical on the whole surface of the seeds. Near the hilum they are much smaller and more densely set than on the rest of the surface.

The surface of the testa cells is granularly faceted in some species, but without any granular cuticular structures in others, which means completely smooth (see Figs. 26–29).



Fig. 24. Typical seed shapes. *Left* round, *C. longicornis*, *middle* reniform, *C. octacantha*, *right* longish, *C. retusa*



Fig. 25. Seeds of *C. gracilis*

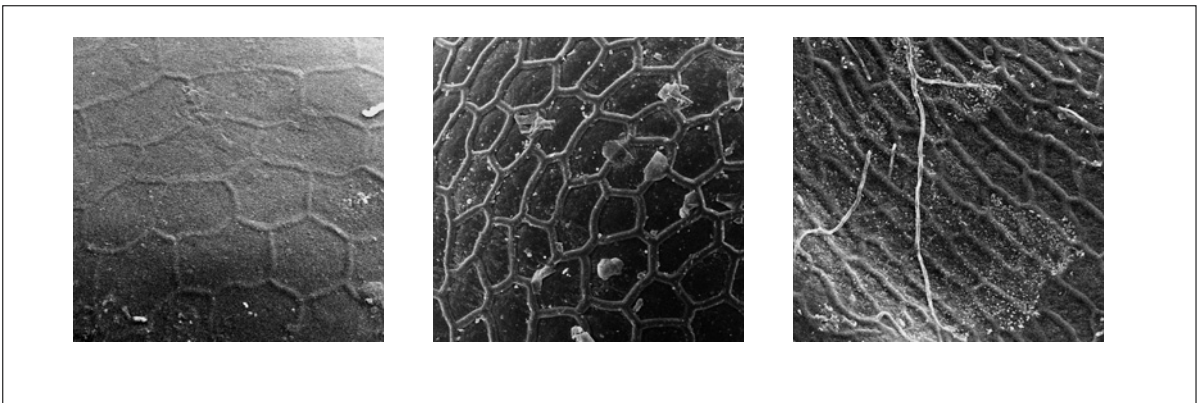


Fig. 26. Structure of testacells. Left *C. pseudoechinus* ssp. *pseudoechinus*, middle *C. recurvata* ssp. *recurvata*, right *C. tripugionacantha*

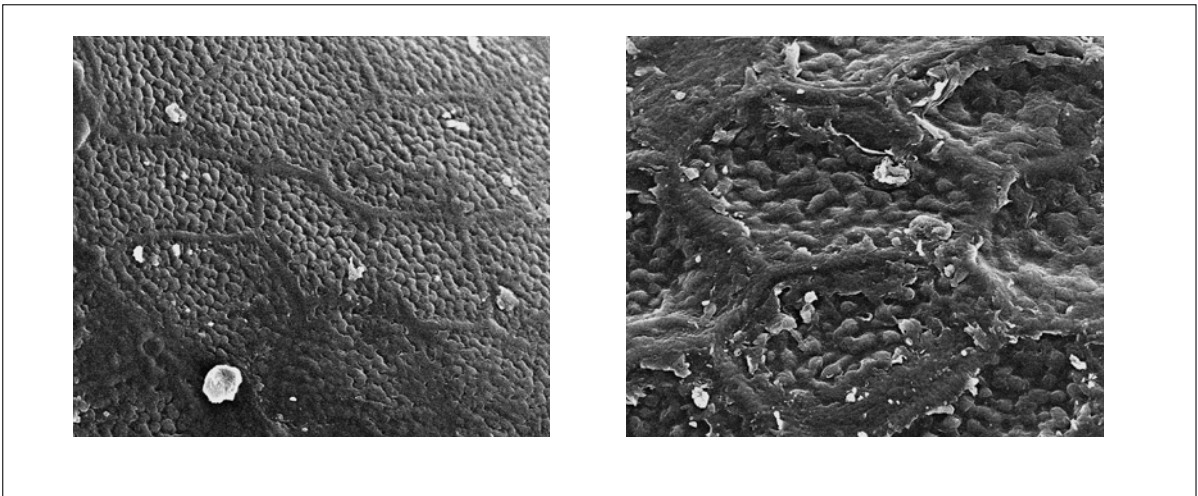


Fig. 27. Surface of testa cells. Left *C. macromeris* ssp. *macromeris*, right *C. elephantidens* ssp. *elephantidens*

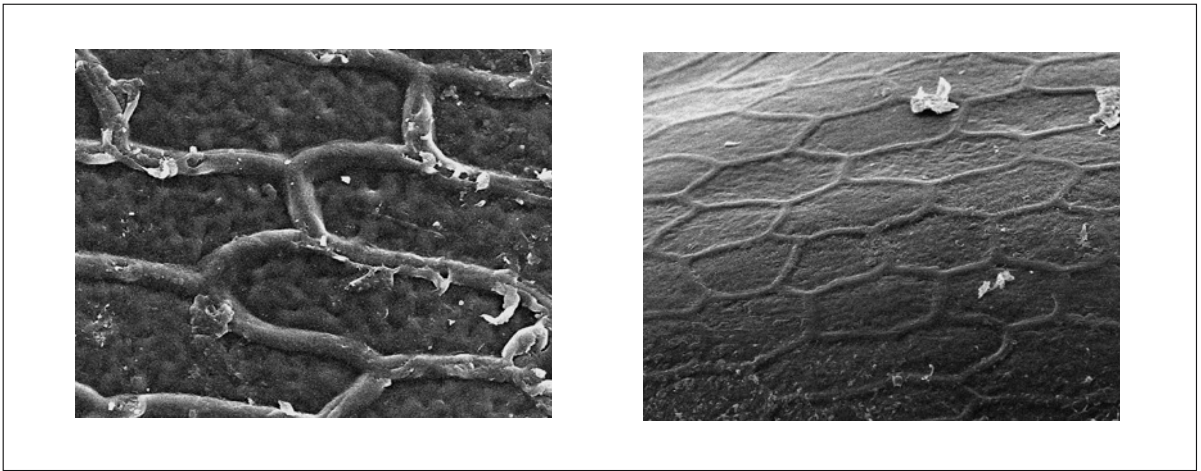


Fig. 28. Surface of testa cells. Left *C. pycnacantha*, right *C. pulleineana*

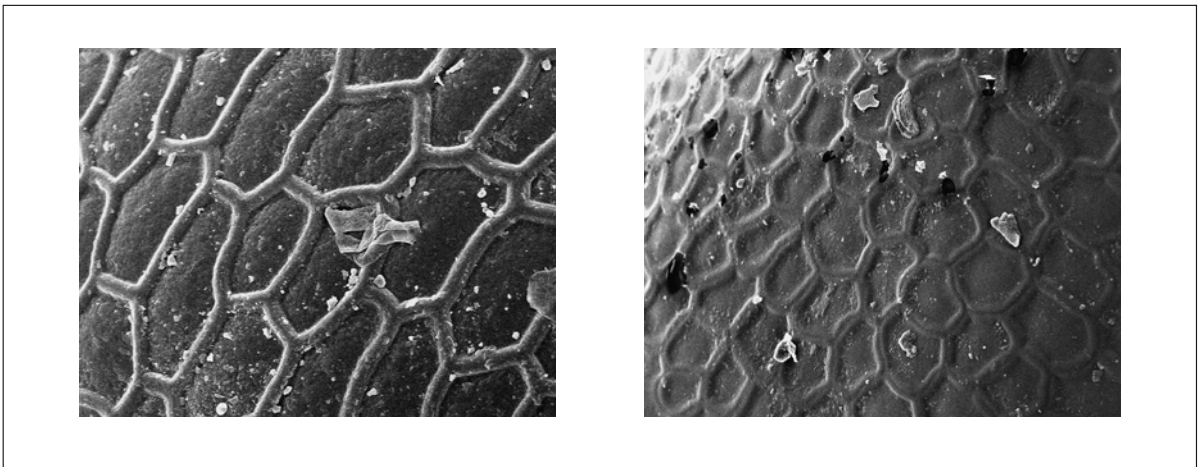


Fig. 29. Surface of testa cells. Left *C. longicornis*, right *C. robustispina* ssp. *robustispina*

4 History of the Genus *Coryphantha*

4.1 Introduction

The systematic and taxonomical history of the genus *Coryphantha*, like that of many other genera of Cactaceae, is characterised by a great number of multiple descriptions and innumerable, sometimes confusing, nomenclatural changes and many errors.

The first uncertainties were introduced by the incomplete and imprecise descriptions made by early botanists and non-botanist plant collectors. Many of their first descriptions were published in non-professional journals or journals of limited distribution. In consequence, later botanists, unaware of the earlier publications, described many species again under new names.

With regard to the genus *Coryphantha*, the age development (ontogenesis) of many species renders classification difficult: a plant often spends several years in a juvenile state where its physical form is markedly different from that at a mature age, but the plant will often start flowering while still juvenile. This phenomenon has often led botanists to make their first descriptions based on young plants, thinking that they are new species.

Another factor leading to taxonomic problems is the high level of evolutionary development of the Coryphanthae sensu stricto, the *Coryphantha* stage (BUXBAUM 1956). Highly developed plants often become very similar even if they belong to very different branches of the evolutionary tree. This problem relates mainly to the flowers, which may reach such a high degree of simplification that no signifi-

cant differences can be observed. This factor makes a clear differentiation more difficult, considering the great variability.

In spite of all the confusion, today's nomenclature depends on the correct interpretation of the taxonomic history.

4.2 Chronology

The first *Coryphantha* sp. reached Europe in the 1820s. Some of the central Mexican species had been collected by that time in the mining region of the Valle de Mexico by Thomas Coulter (1793–1843) and sent to Geneva to Augustin Pyramus De Candolle (1778–1841), one of the best-known botanists of the period. Coulter worked in the mining region of Real del Monte (today Mineral del Monte) until 1825 and from 1827 at Zimapán. The plants for De Candolle were shipped on, or prior to, 1 May 1828 from Veracruz. Type localities given for these plants were usually “Mexico” or sometimes “Real del Monte” or “Zimapan”.

By the time De Candolle had received the plants, his important work *Prodromus* had already been published and he thus described them under the generic name *Mammillaria* in a lesser known journal in 1828. Unfortunately, De Candolle did not know then which diagnostic criteria for differentiation within the Cactaceae were important and sometimes his descriptions remained so short that it is hard to decide which species Coulter had actually sent him. He also made

the mistake of describing several young plants as separate species. Furthermore, none of the *Coryphantha* sp. described were illustrated and no herbarium material exists.

Consequently, De Candolle's descriptions remain quite dubious, even if well-known species such as *octacantha*, *radians* and *cornifera* are among them and these names have been used for more than a century. Some of the descriptions by De Candolle belonging to the genus *Mammillaria* had to be rejected due to insufficient documentation or justified doubts as *nomina dubia* (HUNT 1981).

Due to De Candolle's shaky base, the chaos of future *Coryphantha* nomenclature was, in a way, preprogrammed.

The first *Coryphantha* species were all subsumed into the genus *Mammillaria* (or *Mamillaria*), which had been proposed by the English expert on succulents Adrian Hardy HAWORTH (1772–1833). He, therefore, separated all cacti with tubercles from all the other globular cacti included at the time in the genus *Cactus*.

In 1827 Heinrich Friedrich LINK (1767–1851) and Friedrich Christian OTTO (1783–1856) proposed *Echinocactus* as a separate genus of certain globular cacti from the similar genus *Melocactus*. However, they did not point out any differentiating criteria to the genus *Mammillaria* and, therefore, some *Coryphantha* sp. were also described as *Echinocactus*.

Until 1848 all publications concerning the genus *Coryphantha* were published in Europe, mainly by Charles Lemaire (1801–1871), Michael Josef Scheidweiler (1799–1861), Friedrich Scheer (1793–1869), Friedr. Chr. Otto (1783–1856), Albert Dietrich (1795–1856), Louis Pfeiffer (1805–1878), Fr. Mühlenpfordt, J. Gerhard Zuccharini (1797–1848), Carl Friedrich Philipp von Martius (1794–1868) and Willem Henrik De Vriese (1806–1862). Most of these descriptions were based on living plants in European greenhouses, often lacking any collection data. Few of these

plants were conserved and most of these taxa are thus as poorly typified as the rudimentary descriptions of De Candolle. Even at this time, none of the above botanists clearly knew what to do with De Candolle's descriptions, hence, new names were published without reference to the earlier names. Most of these new descriptions appeared in the gardening journals of different countries, and because the exchange of literature was quite difficult at that time, all the information was scattered in a manner which made it very difficult for anyone to obtain an overview.

Important information about the distribution area of several Mexican species was given by Karl August EHRENBERG (1801–1849), who lived and studied the botany of Mineral del Monte from 1831 to 1840 and who sent many plants to Europe. His field activities together with plant location details are contained in an article which appeared in the journal *Linnaea* in 1846. This paper remained the most reliable source of locations for many of the plants collected before 1840.

In PFEIFFER's publications (1837a), the *Coryphantha* sp. were still mixed up with *Eumammillaria* sp. in the series Conothelae and Brachythelae. In 1839 LEMAIRE first published the epithet *Aulacothelae* as an infrageneric taxon in which he included those "*Mammillarias*, whose tubercles show a groove on the upper surface". Lemaire also gave a Latin diagnosis and compared the new taxon with *Echinocactus stenogoni*.

At first, the taxon *Aulacothelae* was regarded as a subgenus of *Mammillaria* (G. LAWRENCE 1841). Although Lawrence, in his *Catalogue of the cacti in the collection of Rev. Theodore Williams, at Hendon Vicarage, Middlesex* did not mention Lemaire's name, the list of names clearly relates to Lemaire.

In July 1846 the famous collection of exotic plants of the Baron de MONVILLE (Hippolyte Boissel) was sold by auction. The plants offered for sale were listed in a catalogue, using essentially Lemaire's system.

Here, for the first time, we meet *Aulacothelae* as a separate genus with the spelling *Aulacothele*. Monville did not mention Lemaire's name either, but his list also clearly relates to that of Lemaire.

In 1850 the work of Prince Josef von SALM-DYCK (1773–1861) was published in Europe, entitled *Cacteeae in horto Dyckensi cultae anno 1849*. For the first time, a scientifically based difference between the genera *Mammillaria* and *Echinocactus* was established: in *Mammillaria*, which he allocated to the tribe Melocactaeae, the fruit is at first within the plant body and only protrudes after maturity. The fruit is longish, smooth and crowned by dried perianth segments. In the genus *Echinocactus*, which he allocated to the tribe Echinocactaeae, the fruit protrudes from the beginning and the dried perianth segments are discarded. Since in some of those species, which, because their bodies were covered by tubercles, were counted among *Mammillaria*, and the fruit protrudes from the beginning as in *Echinocactus*, the Prince of Salm-Dyck took LEMAIRE's (1839) *Aulacothelae* and separated it as a subgroup from *Mammillaria*. Certain members of the subgroup were then removed and included within the subgenus *Glanduliferae*. The remainder were left within *Aulacothelae*. By doing this, however, he made the mistake of listing *Mammillaria aulacothele* Lemaire, the type species of Lemaire's *Aulacothelae*, under *Glanduliferae*, thus making this name invalid (ICBN Art. 52.1).

In 1853, Hermann POSELGER (1818–1883) put *Glanduliferae* Salm-Dyck and *Aulacothelae* Lemaire into the genus *Echinocactus*. He did this because the flowers of the reallocated plants are mostly solitary and arise from the top of the plant or at least from younger parts of the top as in *Echinocacti*, as opposed to *Mammillarias* in which the flowers protrude between the tubercles from axils of the year before, or older axils and are mostly arranged in a circle around the top.

From 1848 onwards, publications from George Engelmann (1804–1884) concerning the cacti of the United States followed. Up to this time, all *Coryphantha* sp. were allocated to *Mammillaria*, the generic name being *Aulacothele* (Lemaire) Monville. Although valid, this was not generally recognised and was not referred to after 1846. Engelmann was faced with the nomenclatural chaos described above. In 1856 he suggested the name *Coryphantha* (*Coryphantha* [Greek] ≡ *flowering from the top*) as a subgenus of *Mammillaria* for a group of about 16 species. Incidentally, three of them (*papyracantha*, *pottsii* and *conoidea*) had to be excluded again later. The remainder were from the southern United States and the adjacent regions of Mexico. All other *Coryphantha* species described at that time had originated from Mexico. They were not mentioned by ENGELMANN, which is probably why he did not discuss the *Glanduliferae* of Salm-Dyck, which, of course, should also have been included within *Coryphantha*. Even so, Engelmann's publication is superior to any written about *Coryphantha* at that time. Once again, however, herbarium material was not preserved.

In 1868 the group of plants named *Coryphantha* was raised to generic level by Charles LEMAIRE. In his *Iconographie descriptive des Cactées* (1853), the generic name *Aulacothelae* can still be found. He proposed *Mammillaria sulcolanata* as the type species of this genus (“Typumque sat completum praebet generis *Aulacothelis*, jam ab auctoribus propositum”). In 1868 he finally adopted the name *Coryphantha* from Engelmann, but as a genus and no longer as a subgenus of *Mammillaria*. However, the species listed by the two authors only partly overlapped. Engelmann's list mainly contained species from the United States or the bordering regions of Mexico, whereas Lemaire in his publications mentions mainly Mexican species. In all, Lemaire mentioned 25 names of species (24

species and 1 variety). This list was valid for a long period; 27 years later only one additional species was listed in the Index Kewensis. Today, however, only eight of Lemaire's *Coryphantha* sp. are still in use. All the others are now either synonyms or nomina dubia.

As the lectotype of the genus *Coryphantha*, Lemaire chose *Coryphantha sulcolanata* and this, as we will see later, remained valid until 1976.

Before *Mammillaria* was generally accepted as *nomen conservandum*, John Merle COULTER (1851–1928) in 1894 included all known *Coryphantha* species within the genus *Cactus* as a parallel section to “*Eumammillaria*”. Lemaire's work was probably unknown to Coulter, because in his list of synonyms not a single *Coryphantha* name of Lemaire appears.

In 1898 Karl Moritz SCHUMANN's (1851–1904) *Gesamtbeschreibung der Kakteen* appeared. This is a detailed monograph of the Cactaceae, in which 22 species of *Coryphantha* appeared, considered, however, as a subgenus of *Mammillaria* and divided between the series *Aulacothelae* Lemaire and *Glanduliferae* Salm-Dyck. It was obvious that by this time Lemaire's work was not highly esteemed. Schumann's work contains detailed descriptions, Latin diagnoses and synonyms, but confuses readers by using many catalogue names as first publications, and cultivators of the plants, who had given them any name, as the original species names. Schumann's plants had been preserved in herbaria. However, few specimens survived the World War II (among them not one *Coryphantha*) and, therefore, many of the new names introduced by Schumann must now be regarded as not identifiable nomina dubia.

Post-1900 more first descriptions of *Coryphantha* followed. These mostly originated from German authors and appeared in German journals. To name a few: Leopold Quehl (1849–1922), Walter Mundt (1853–1927), Jos. Anton Purpus (1860–1933), Fried-

rich Bödeker (1867–1937) and Friedrich Vaupele (1876–1927).

In 1919–1923, an important new work appeared, which became an important basis for *Coryphantha* specialists until today: *The Cactaceae* by Nathaniel BRITTON (1858–1934) and Joseph Nelson ROSE (1862–1928). It is the first complete monograph on cactus existing in English. Thanks to their fieldwork and the intensive use of herbaria located worldwide, the fourth volume gives much greater insight into the genus *Coryphantha* than Schumann's *Gesamtbeschreibung der Kakteen*. It is generally known that it was J.N. Rose who studied the small globular cacti of northern America, although both authors, Britton and Rose, are named.

Britton and Rose studied all the existing cactus literature diligently and listed a great number of the earlier *Coryphantha* publications in their work. As “splitters” they did not hesitate to follow Lemaire in accepting *Coryphantha* as a genus. From the former subgenus of Engelmann, they separated three more genera, *Toumeyya*, *Neobesseyya* und *Escobaria*.

In total, Britton and Rose described four new *Coryphantha* species and formally added 16 more to the genus *Coryphantha*, thereby listing 50 species under *Coryphantha*, this number includes four *Neobesseyyas* und eight *Escobarias*.

Most of the type plants of Britton und Rose are correctly named and associated with herbarium material, but it is a pity that most of Rose's descriptions are far too short in general and sometimes superficial or inexact. This led to further confusion later on. They also misapplied several names (e.g., *C. pycnanantha*, *C. salmdyckiana*, *C. sulcolanata*, *C. difficilis* etc.).

After Britton and Rose, the next important publication was that of Alwin BERGER (1871–1931). In his *Monographie der Kakteen* (1929) he gave the infrageneric range within the genus *Coryphantha* to three former gen-

era of Britton and Rose (*Escobaria*, *Neobesseya* and *Neolloydia*). His work lists over 50 species. Among them are many new descriptions of Friedrich Bödeker, who, in the period 1920–1930, described many new cactus species, including some *Coryphantha* sp. In his *Mammillarien-Vergleichs-Schlüssel*, BÖDEKER (1933) mentioned 64 *Coryphantha* species, and he also treated *Neobesseya* and *Escobaria* as separate genera.

After the World War II, the Austrian Franz Buxbaum (1900–1979) published several important scientific works on cacti. As a starting point, he studied Alwin BERGER's *Die Entwicklungslinien der Kakteen* of 1926 where Berger set out to clarify the supposed phylogenetic interrelationship between all the cactus genera acknowledged by Britton and Rose. He did so by using dendrograms.

Buxbaum emphasised the polarisation of characteristics (primitive versus highly derived) and contributed greatly to the analysis of the homology of different taxonomically important features of the Cactaceae. He reclassified several plant groups including *Coryphantha* and *Mammillaria* at the levels of genus/subgenus. He was the first author who transferred the species group *Coryphantha vivipara* from *Coryphantha sensu stricto* to *Escobaria*.

During the same time period, Curt BACKEBERG (1894–1966) worked on his detailed monograph *Die Cactaceae*. In the fifth volume, published in 1961, he devoted 131 pages to the genus *Coryphantha* and its relatives. He considered all publications since Britton and Rose, including seven original descriptions of *Coryphantha* sp.. These had been published in lesser known gardening journals and were introduced to a larger audience by their incorporation into the Cactaceae.

Among all the great cactus monographers, Backeberg was unique in one aspect in that he completely neglected to make herbarium sheets. He did not conserve one single plant; all his descriptions and taxonomic decisions

were based on living plants, which unfortunately no longer exist.

Since most of Backeberg's first descriptions occurred before 1 January 1958, the day when valid nomenclatural rules were introduced, necessitating the indication of a type to achieve a valid description, they are still valid nowadays, but his descriptions after 1 January 1958 are, due to the lack of typification, invalid.

However, Backeberg's work provides a valuable overview of the genus *Coryphantha* and includes all the important publications of the nineteenth and twentieth centuries.

In the years after 1970 Lew Bremer wrote many publications, including 15 first descriptions of *Coryphantha* sp. At present, only three are regarded as good species and two as subspecies, all the others being considered as synonyms only. Many of his species are new descriptions of long-known taxa, but with new names, others are also incorrect applications of names to long-recognised species. It is true that Bremer published excellent descriptions, very detailed and usually photographically well documented. However, on the whole, his work has caused more confusion to taxonomy than contributing to science.

In 1982 a publication appeared, which is regarded as a standard work by the American government and also by most American botanists, namely Lyman BENSON's *The Cacti of the United States and Canada*. Benson accepts 33 species of *Coryphantha* in the USA, although today only 15 can be regarded as good species. In his work some names are incorrectly applied, and some good species are not mentioned.

In 1940 BENSON had retraced the US *Coryphantha* species back to *Mammillaria*. This was at a time when the elevation of *Coryphantha* to genus level by BRITTON & ROSE (1923) was being accepted worldwide. Up to this time, the criteria separating *Coryphantha* from *Mammillaria* contained two

characteristics only, namely the flower position and the areole morphology.

In 1969 BENSON came back to the concept of *Coryphantha* being a natural plant group which had to be separated from *Mammillaria*. Therefore, he raised it to the level of genus and at the same time decided to include all *Escobaria* species within *Coryphantha*.

Over the same period, Del WENIGER (1970) published a book in which he applied Benson's old classification, thus lumping all *Coryphantha* sp. into *Mammillaria*. This classification was followed in Texas only.

It has to be said that the taxonomic work of both Bremer and Benson outlined above caused a lot of confusion among botanists concerned with the classification of the *Coryphantha* species. On the one hand, taxonomy was influenced by Bremer's "splitting" of the species endemic to Mexico, on the other hand, by Benson's "lumping" of the species from USA.

The next large-scale publication is that of Helia BRAVO and Sanchez MEJORADA entitled *Las Cactaceas de Mexico* (1991). Bremer's "splitting" and Benson's "lumping" are presented with equal weight in a non-critical manner in the hope of achieving a compromise. Unfortunately, the outcome is that no progress has been made with classification matters relating to the genus. BREMER's misapplication of names naturally confused matters further.

Allan Dale ZIMMERMAN's dissertation of 1985 entitled *Systematics of the Genus Coryphantha (Cactaceae)*, which was never validly published, proved to be an extremely valuable work on the genus *Coryphantha*. In this work, many of the systematic errors and parallelisms are highlighted and corrected for the first time. Zimmerman evolved an amplified theory of areole development with the differentiation of different areole-types. He recognises 46 species of *Coryphantha*.

The latest complete publication on cacti by E. ANDERSON (2001) widely follows the

work of BRAVO (1991) concerning *Coryphantha*.

4.3 The Generic Name *Coryphantha* and the Type Species

Among the 22 cacti which LINNÉ (1753) mentioned in *Species Plantarum*, only one species is a closer relative of the genus *Coryphantha*: *Mammillaria mammillaris* (in Linné *Cactus mammillaris*), the type species of the genus *Mammillaria*, which itself is the type genus of the tribe Cacteeae of the subfamily Cactoideae of the Cactaceae. In fact, all cacti should be named Mammillariaceae, but the name Cactaceae has been conserved (*nomen conservandum*).

The generic name *Mammillaria* itself is also a *nomen conservandum*, on the one hand, against Linné's genus *Cactus*, on the other hand, against an earlier homonym, the algae-species *Mammillaria*.

Linné's generic name *Cactus* was soon given up, because it included too many species unrelated to each other. Nevertheless, around 1900 two authors (KUNTZE 1891 and J.M. COULTER 1894) restored the genus *Cactus* and combined, with *Cactus mammillaris* as type species, all former *Mammillaria* species, among them many *Coryphantha* sp., to *Cactus*.

With BRITTON and ROSE (1923) only, the generic name *Cactus* was given up definitely, because it also included *Melocactus*, a fact which inevitably led to nomenclatural confusion.

Coryphantha Instead of *Aulacothele*

During the nineteenth century, while all *Coryphantha* sp. were still regarded as *Mammillaria* sp., LEMAIRE (1839) published the name *Mammillaria* [tax. infrag.] *Aulacothelae*, which he defined as follows: "*Mammillarias*, whose tubercles carry a groove on

their upper surface". He also gave a short Latin diagnosis and compared the taxon with *Echinocactus* [tax. infrag.] *stenogoni*. The taxon was first ranked as *Mammillaria* subsect. *Aulacothelae* by LAWRENCE (1841). It is true that by doing so, Lawrence did not mention Lemaire's name as the author of *Aulacothelae*, but the species listed clearly point to Lemaire. Among them was *Mammillaria lehmannii* Otto, a synonym of *Mammillaria aulacothele* Lemaire, the automatic type following ICBN art 22.4. *Aulacothelae*, spelled *Aulacothele* was raised to the rank of a genus by Baron DE MONVILLE in 1846.

The publication of the generic name *Aulacothele* (Lemaire) Monville (1846) must be regarded as valid and, in fact, has priority over *Coryphantha* (Engelmann) Lemaire (1868), based on *Mammillaria* subgenus *Coryphantha* Engelmann (1856).

R. MOTTRAM (1992) proposed the conservation of *Coryphantha* in preference to *Aulacothele*, because the generic name *Aulacothele*, although valid, has never been used by any author since its publication in 1846 and was even given up by its own author, LEMAIRE (1868), in favour of *Coryphantha*. The revival of the generic name *Aulacothele* would also have led to a great number of unfamiliar recombinations.

The Type Species of the Genus *Coryphantha*

When ENGELMANN (1856) proposed *Coryphantha* as a new subgenus of *Mammillaria*, he did not give any indication of a type species. Lemaire, who raised *Coryphantha* to the level of genus, also did not mention any type species (for the genus *Aulacothele*, he had proposed *M. sulcolanata*). One problem was that Lemaire's and Engelmann's lists of species differed markedly. There were, in fact, few species in common.

After typification had been deemed necessary for taxa of any rank, several authors set out to provide a type species for *Coryphantha*.

The first proposal for a lectotype was that of BRITTON and BROWN in 1913 in their paper *An Illustrated Flora of the Northern United States...*, edn. 2, pp. 1–3, Scribner, New York. They proposed *Mammillaria sulcata* Engelmann. This fact had been overlooked by many authors, but was referred to by R. MOTTRAM in 1992. Generally, the lectotypification by BRITTON and MILLSPAUGH (1920) had been regarded as valid. They had proposed *C. sulcolanata* Lemaire, which was referred to in Lemaire's list as the type species. However, *C. sulcolanata* was not mentioned in Engelmann's list and since Lemaire, when proposing the genus *Coryphantha*, had referred to Engelmann, the choice of *C. sulcolanata* as the type species had to be dropped. Moreover, *C. sulcolanata* has not sufficiently been typified and was even used incorrectly (as *C. radians*) by Britton and Rose.

These were reasons why BENSON (1969) proposed a new lectotypification. He chose *Coryphantha vivipara* as the new type species, a species which occurs mainly in the USA and is well known there. It was also mentioned by Engelmann. This was not a good choice and is indeed incorrect, as Hunt details below:

- *C. vivipara* had not been mentioned by Lemaire when he resurrected the genus *Coryphantha*
- due to its flower and seed morphology, *C. vivipara* had rightly been transferred by BUXBAUM (1951) to the genus *Escobaria* Br. & R., which has been accepted in the whole cactus literature since 1923.

If Buxbaum's classification in this point is accepted, as usual today, this would mean that by accepting *C. vivipara* as the type species of *Coryphantha*, then *Escobaria* would become a synonym for *Coryphantha*. In consequence, the correct name for *Escobaria* sensu Buxbaum would have to be *Coryphantha*. A new name for *Coryphantha* sensu Britton & Rose would have to be found.

The confusion would thereby be complete.

In a joint publication, HUNT and BENSON (1976) reached a compromise by proposing to chose a new type species instead of *C. vivipara*. This was to be selected from species jointly present in the lists of Engelmann and Lemaire.

Four species were considered: *C. scheeri* (Mühlenpfordt) Lemaire, *C. scolymoides* (Engelmann) Lemaire, *C. macromeris* (Engelmann) Lemaire und *C. calcarata* (Engelmann) Lemaire.

From these species the first two had to be excluded, because they were “insufficiently typified and problematic”. The third as an “aberrant species” would have led to taxonomic problems similar to those of the former choice of *E. vivipara*.

Therefore, *C. calcarata* was left for consideration. This is a superfluous name published by ENGELMANN in 1850 for *Mammillaria sulcata*. *Mammillaria sulcata* had in fact been described by ENGELMANN in 1845 and this

same plant had been listed by Lemaire as *Coryphantha calcarata* in the sense of *Mammillaria sulcata* Engelmann. Following the rules of the ICBN, the correct name for this type species is *Coryphantha sulcata* (Engelmann) Britton & Rose.

Coryphantha sulcata is based on herbarium material and is treated as that by all modern authors who accept the genus *Coryphantha*. The type of this species was checked by Benson at the Missouri Botanical Garden and considered to be suitable as a type species of the genus. The type locality is recorded as: “Sandstone rocks near Industry (Austin County, Texas,” Lindheimer in July, 1844, MO (specimen sheet and box).

However, the original proposers of *Coryphantha sulcata* Engelmann as the type species of the genus are BRITTON and BROWN. They did this in 1913 and must be named in all published material where appropriate.

5 Position and Delimitation of the Genus *Coryphantha*

5.1 Previous, Traditional Interpretation of the Genus *Coryphantha*

While the opinion prevailed that *Coryphantha* should be treated as a genus separate from *Mammillaria*, authors had to deal with the question of its position within Cactaceae and to decide whether *Coryphantha* should be divided into smaller groups. Consequently, BRITTON & ROSE (1923) separated *Escobaria* and *Neobesseyia* from *Coryphantha*, while BUXBAUM (1956) treated *Escobaria* as a separate genus and, as the first author, included the *Vivipara* complex in *Escobaria*. BENSON (1969) regarded *Escobaria* as a subgroup of *Coryphantha* because of the tubercle grooves, an opinion which persists to this day, especially in America. HUNT (1978) and TAYLOR (1978) continued the European tradition and have treated *Escobaria* and *Coryphantha* as different genera, mainly because of the testa morphology. Similarly, JOHN & RIHA (1981) treated *Escobaria* as a separate genus, with *Neobesseyia* Britton & Rose being one of its subgenera.

In his thesis, *Systematics of the Genus Coryphantha* (Cactaceae), A. ZIMMERMAN (1985) described the genus in detail, defining 169 usable and 30 rejectable characteristics for phenetics. He used them to outline cladograms of the tribus Cactaeae and the genera *Coryphantha* (incl. *Escobaria*) und *Mammillaria*.

Zimmerman derived two phylads from a group corresponding to the *Erianthi* (Berger) (*Echinocactus* Link & Otto, *Homalocephala*

Britton & Rose and *Astrophytum* Lemaire) characterised by flowers with mucronate perianth segments and axillary trichomes:

The first is characterised by convex testa cells (tuberculate seeds), the second by concave to tabular-concave testa cells (foveolate seeds).

This second group he called “*Mammillaria* phylad”, which includes the genera *Ferocactus* Britton & Rose, *Acharagma* (N.P. Taylor) Glass, *Coryphantha* (Engelmann) Lemaire, *Escobaria* Britton & Rose, *Ortegocactus* Alexander and *Mammillaria* Haworth.

According to Zimmerman, this second phylad is not characterised by progressive loss of the perisperm (BUXBAUM 1956–60), but mainly by progressive development of various types of areoles.

Types of Areole Development According to ZIMMERMAN (1985)

1. The **Acharagma type** (“primitive type”): plants producing only non-specialised circular to elliptical areoles even in old age, producing flowers only at the tips of the areoles. Includes all taxa of the subfamilies Opuntioideae and Pereskioideae, and nearly all members of the Cactoideae except the tribus Cactaeae.
2. The **Ferocactus type**: plants flowering from short, broad areolar grooves i.e., from the adaxial extremity of an areole which becomes longer with age.
3. The **Macromeris type**: like type 2, but with gradual development of narrow grooves, these never covering the whole length of the tubercles between the areole and the

axil (about half the length in *Coryphantha macromeris*), and flowering only after the areolar grooves have attained maximum length.

4. The *Escobaria* type: like type 3, producing longer and longer areolar grooves, but flowering only after these have attained maximum length along the whole tubercle from the areole to the axil.
5. The *Neolloydia* type: with an abrupt change from short, sterile areoles to areoles having full length grooves from the areole to the axil, without a transition, with grooves getting longer. Known only for *Neolloydia conoidea*.
6. The *Protomammillaria* type: like type 5, but with a subadult stage with abaxial and adaxial meristem (like *Mammillaria* type), changing abruptly to complete tubercle grooves from the areole to the axil when reaching the adult stage.
7. The *Ortegocactus* type: like 6, but flowering is also possible before production of areolar grooves.
8. The *Leuchtenbergia* type: plants with axillary meristem, but which produce their flowers only at the tips of the areoles.
9. The *Mammillaria* type: like 7, but never make the subsequent switch to grooved tubercles at adulthood.
10. The *Pachycereus* type: like 1, with interareolar lines of trichomes in adulthood.
11. The *Ariocarpus* type: like 9, but without development of the abaxial tubercle part (no spine formation) or groove.

Coryphantha sp. belong to types 3, 4, 6 (most of the species with nectary glands) and 7 (the *Ottonis* sp.).

Because of the common areole types (*Escobaria* type, *Protomammillaria* type) Zimmerman, continuing the American tradition (Benson) concluded that *Escobaria* and *Coryphantha* have to be regarded as sister groups within one and the same genus. Hence, the

older name *Coryphantha* should prevail and *Escobaria* should be positioned as a subgenus, this in spite of the discrepancies concerning flowers and testa morphology. *Protomammillarias* [*Coryphantha chihuahuensis* (Britton & Rose) Berger and *Coryphantha henricksonii* (Glass & Foster) Glass & Foster] are treated by Zimmerman as intermediate between *Escobaria* and *Coryphantha* (see Fig. 30).

However, he does not answer the question whether some of the taxa with grooved tubercles, namely the *Protomammillarias* and the gland-producing group of *Coryphantha* s.str. with *Protomammillaria*-areole type, might originate from a *Mammillaria*-like ancestor or vice versa.

5.2 New Interpretation of the Genus *Coryphantha*

Previous Thesis on the Areole Development and Their Discussion

The areoles of Cactaceae, sometimes referred to as “spine-bearing cushion”, correspond to a shortened lateral shoot with leaves transformed into spines and the disposition of an axillary bud (“sleeping eye”) which may produce either a flower or a shoot. The long-living meristematic region, from which flowers or shoots may develop, is reduced to the adaxial (upper) end of the areole in many Cactaceae.

However, in some genera, among them *Coryphantha*, the areole is elongated in such a way that the insertion of the spine bundle represents a small, clearly demarcated appendage of the whole areole. We often refer to this insertion of the spine bundle as “areole”, because a specific expression for the whole areole does not exist, although an appropriate one would be podarium (Zimmerman). In cactus literature the opinion prevails that in certain genera a serial division of the meristem occurs with production

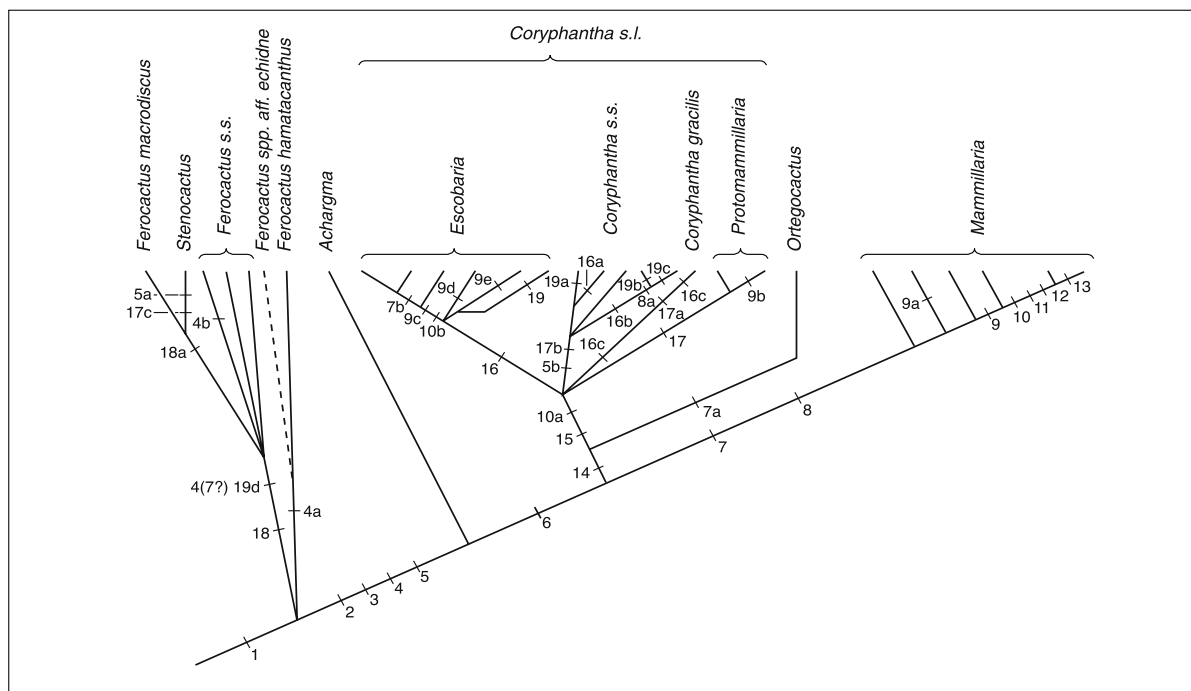


Fig. 30. Interpretation of the *Mammillaria* phylad (from A.D. ZIMMERMAN 1985, Fig. 8). Details of the *Mammillaria* phylad. The treatment of *Ferocactus* is very crude for lack of data from this genus. Numbered apomorphies are as follows: 1 foveolate seeds; 2 adult stems remaining tuberculate (neoteny); 3 loss of scale-like bracts from pericarpel; 4, 4a, 4b indehiscent (and mostly juicy) fruits; 5, 5a suppression of areolar glands; 6 two-parted areoles (*Mammillaria* type); 7, 7a, 7b loss of perisperm; 8 (and 8a in *Coryphantha recurvata*) subapical flowering; 9, 9a, 9b, 9c, 9d, 9e bright red fruits; 10, 10a reddish brown seeds; 10b reversal: secondarily black seeds; 11 strongly sinuate anticlinal walls of testa cells; 12 unique hypodermis in *Mammillaria* spp.; 13 Latex ducts; 14 sporadic presence of areolar grooves on podaria of adults; 15 *Protomammillaria*-type areole sequence; 16, 16a, 16b, 16c *Escobaria*-type areole sequence; 17, 17a, 17b, 17c smooth or weakly reticulate seeds; 18 gigantism; 18a reversal: greatly reduced stem size in *Stenocactus*; 19, 19a, 19b, 19c, 19d multiple hypodermis with glands. Note that this hypothesis would, if correct, imply the re-appearance of perisperm in the most highly derived *Mammillaria* taxa

of an areolar meristem on the one hand, which is transferred on to the tip of the areole by growth and which has the capacity to produce spines, and on the other hand, the production of an axillary meristem which has the potential to produce flowers. This theory was presented by WETTERWALD 1888, and Buxbaum and most other botanists have followed him. Buxbaum in KRAINZ (1956–1960) described the serial division as follows: “...In highly derived *Cereoideae* the top of the axillary shoot is shifted in such a way that

flower- or shoot-producing part a groove develops, which extends on the upper surface along the tubercle (“*Coryphantha* stage”). Ultimately, this serial division is completed in such an early stage of development that an abaxial, areole-forming part and an axial, flower-bearing part, the axil, are separated from the beginning, therefore, no groove develops (“*Mammillaria* stage”).”

Following this interpretation by Wetterwald and Buxbaum, which postulates a serial division, it remains unclear why, during this meristematic division into an outer (areolar)

vegetative part and an inner (axillary) fertile point, the groove formation of *Coryphantha* should take place in an axillopetal direction, i.e. from the spiniferous areole to the axil. This direction of groove development can clearly be verified in species with *Escobaria* areole type, but also with *Macromeris* and *Protocoryphantha* areole types (*C. poselgeriana*, *C. robustispina*). The development of the *Protomammillaria* areole type in which grooves develop after activation of both the areolar and the axillary meristem also remains unexplained, as does the development of the *Ortegocactus* areole type with optional groove formation. Postulation of a division of the meristem completely neglects the appearance of extrafloral nectary glands (morphologically honey spines) in the grooves and their continued secretion until the death of the tubercle. The same is true with regard to the trichomes (woolly hairs) in the grooves.

Two more facts remained unnoticed: 1. The spines of *Coryphanthas* continue to grow after the appearance of flowers and after the tubercles grow from the top of the plant. 2. New shoots arise exclusively from the groove near the spiniferous areole.

A somewhat different interpretation of the development of axils in *Mammillaria* was given by N.H. BOKE (1953) in his very profound histological studies: the axillary meristem develops from the general peripheral meristem after extinction of the areolar meristem, which has moved to the tubercle tip. According to Boke, there is no serial division of the meristem, but a spontaneous formation of buds in a series, as is usually the case for all dicotyledons.

A thesis of areole development which, contrary to the general opinion, does not proceed from a serial division of the meristem and which gives a simple explanation for the axillopetal (from spiniferous areole to axil) direction of the groove development was published in 1968 by Heimo FRIEDRICH: In

his opinion, a separation of the areole meristem does not occur in *Coryphantha*, nor is it the result of such a division present in *Mammillaria*. He postulates that the axillary shoot grows ventrally along the whole length, thus its base immediately follows the rudimentary leaf, and its tip is fixed in the axillary cortex pointing to the top of the shoot. This fixation of the tip meristem has the effect that the leaf spines, produced in an ascending sequence, are pulled away from the axil by continued growth in a downward and outward direction. This process also enforces the vaulting of the tubercle (podarium). He compares the whole areole to a short lateral shoot with a basal leaf rosette, stalk and terminal flower. In its juvenile stage i.e., the vegetative phase, the leaf rosette is formed as a cluster with a species-typical number of spines. Thereafter, the activity of the meristem is exhausted. In floriferous areoles the formation of a "flower-stalk zone" follows with no or with very small hair-like spines, which superficially resemble a groove. At the upper end of this "stalk", which is near the axillary end of the tubercle groove, the flower is finally produced.

New, Extended Thesis of Areole Development

None of the known interpretations of areole development is capable of giving a complete and logical explanation of the specific and pronounced areole development of the genus *Coryphantha*. A phylogenetic analysis of areole development shows that the oldest taxa (e.g. *Ferocactus*) produce only very short grooves close to the spiniferous areole, while the somewhat younger *Macromeres* make shortened grooves which are not transient to the axil. In addition, the *Protocoryphanthae* (*C. poselgeriana*, *C. robustispina*) go through a very long phase with incomplete grooves and in the youngest taxa only the groove develops very fast from the spiniferous areole

to the axil, either in two phases (*Escobaria* type) or in one phase (*Protomammillaria* and *Ortegocactus* type). The individual development (ontogenesis) from the juvenile type to the “two-parted” areole, therefore, reflects the phylogenesis, recapitulating the evolutionary history.

The thesis, which Friedrich postulated as a consequence of his analysis of the *Protomammillaria* areole type (*Coryphantha clavata*), can be applied to all areole types within the *Mammillaria* phylad (mainly the two genera *Coryphantha* and *Mammillaria*), but it needs to be extended, since it originates from observations of *Coryphantha clavata* only.

The separation of peripheral spination from protected flowers positioned inside makes sense ecologically and the transfer of the flowers from the areole to the axils can be understood phylogenetically. According to Friedrich’s interpretation, there is no major difference between the *Coryphantha* and the *Mammillaria* axil; both are homologous organs, however, the *Mammillaria* type is definitely the more advanced type, because it completes the transposition of the flower to the axil in the most perfect way.

To describe the organs of the areole, or the podarium, of the genus *Coryphantha* like the groove on the tubercle surface, the nectary glands in the grooves and axils, but also the trichomes, a continuous meristematic tissue from the spiniferous areole to the axil must be postulated with an axillopetal direction of development and formation of buds in serial sequence. Facing the progression of groove prolongation, such a continuous meristem can easily be inferred for the whole genus and can be confirmed either phylogenetically or ontogenetically.

Finally, at the highest stage of development, the *Mammillaria* areole type, the areole meristem is most differentiated and completely reduced except for the formation of a spine areole and a flower base in the axil. Only here, the possible formation of shoots is

transferred from near the spiniferous areole to the axil and the axillary flower base becomes active only after spine growth has been terminated.

Friedrich’s extended thesis leads to a new interpretation of Zimmerman’s areole theory within the *Mammillaria* phylad, which, following our own observations, must be complemented by a further areole type already mentioned: the *Protocoryphantha* type.

Areole Types According to Zimmermann: New Interpretation

All the areole types are shown on Plates 6 and 7. The morphology is presented on Plate 6 and the appearance on Plate 7:

1. *Ferocactus* type:

Plants flower from short, broad areolar grooves i.e., from the adaxial part of an areole which becomes longer and longer with age. Areoles positioned on ribs. Production of “honey spines” in the grooves. Spine growth continues after flowering.

2. *Macromeris* type:

Resolution of the ribs into individual tubercles, gradual formation of a partial narrow groove (only half-way in *Coryphantha macromeris*) between the spiniferous areole and the axil on the upper surface of the tubercle and flowering only after grooves attain maximum length. Production of nectary glands and trichomes is possible along the whole length of the groove. Offsets occur near the areole.

3. *Protocoryphantha* type:

Like type 2, with production of longer areolar grooves, halting growth at about three-quarters of tubercle length for a long period of time (years) before reaching the adult stage, and persistence of shortened grooves on old tubercles. Flowering only after grooves have reached maximum length along the axil (like type 6).

4. *Ortegocactus* type:

Abrupt groove formation with no transitional stage with grooves getting longer,

floriferous before or after production of grooves. Nectary glands and trichomes in the axil may occur before groove formation, and later also in the groove.

5. *Protomammillaria* type:

Like type 4, but with obligatory tubercle groove when reaching the adult stage. Nectary glands and woolly hairs (trichomes) in the groove.

6. *Escobaria* type:

Production of longer complete grooves extending to the axil within a short period (less than 1 year), without persistence of shortened grooves. Flowering only after attainment of maximum length grooves to the axil. Reduced capacity for producing nectary glands and, if present, only directly behind the spiniferous areole.

7. *Mammillaria* type:

Flowering only after the spiniferous areole stops growing, from a flower base of the meristem in axils of the previous year. Communicating meristem between areole and axil completely inactive and without formation of grooves, trichomes or nectary glands. Offsetting capacity transposed to the axil.

Phylogenetic Interpretation of the Genus *Coryphantha*

The *Ferocactus* line was confirmed by Zimmerman as an evolutionary tribe and the *Coryphantha* and *Neobesseya* lines and the *Mammillaria* line respectively as another phylad which differs from *Ferocacti* by having ribs resolved into tubercles, indehiscent, juicy fruits and loss of bract scales.

This interpretation of the two phylads does not address an important, phylogenetically special feature: production of extrafloral nectary glands. Depending on the weight given to this feature, the resulting systematics are very different, because as a consequence *Coryphantha* s.str. with its capacity to produce nectary glands might well need to be included in the *Ferocactus* phylad.

Development of extrafloral nectary glands is a very original and complex feature. Production of sugar-containing nectar attracts ants, which, by their markings, keep off plant- and bud-eating animals. This is especially important immediately before and during the flowering period. Within the *Mammillaria* phylad, species with concave to tabular-concave testa cells (foveolate seeds), such nectary glands can be found only in *Ferocactus* and *Coryphantha*, but never in any of the other genera. Gland development in *Coryphantha* s.str. clearly shows an evolutionary tendency: in the more primitive *Lepidocoryphanthas* (*C. macromeris*) and also in *Protocoryphantha* (*C. poselgeriana* and *C. robustispina*), it is limited to the whole length of the groove, whereas in the *Protomammillaria* and *Ortegocactus* types it extends to the axil and is finally reduced in the *Escobaria* type, where, around the flowering time, (perifloral) glands if present are only produced near the spiniferous areole.

Since the production of nectary glands is a very complicated process comparable to the Latex syndrome in the genus *Mammillaria* (J. LÜTHY 1995), it has a much greater phylogenetic significance than earlier authors had attributed to it (ZIMMERMAN 1985). Consideration of this leads to the division of the *Mammillaria* phylad into two main branches, the gland-producing genera (*Ferocactus*, *Coryphantha*) and the non-gland-producing genera (*Acharagma*, *Cumarinia*, *Escobaria*, *Mammillaria*).

With its groove development the gland-producing branch represents a continuum having a common ancestor. We observe the formation of very short (*Ferocactus*), half-long (*Macromeris*) and finally complete (*Coryphantha*) tubercle grooves with varying areole developments (*Protomammillaria*, *Ortegocactus*, *Escobaria* areole types).

The non-gland-producing genera follow a parallel development with the formation of shortened grooves (*Cumarinia*), complete

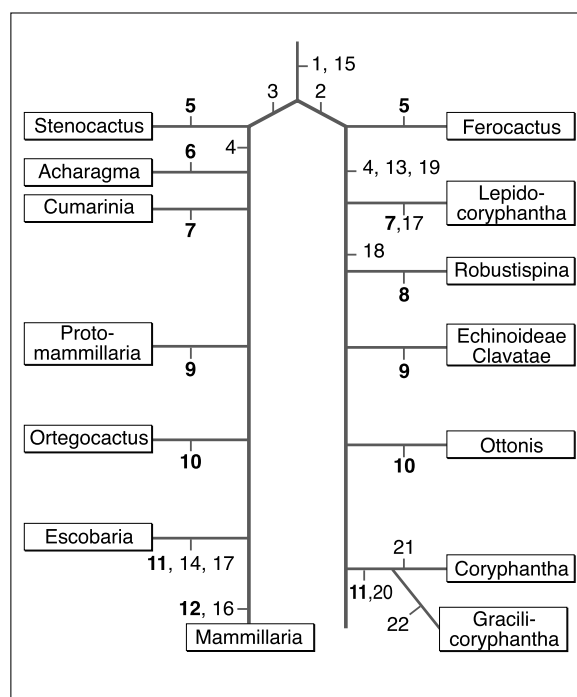
grooves with varying development (*Ortegocactus*, *Escobaria*, *Protomammillaria*) and finally the highest developed form with the absence of groove formation (*Mammillaria*).

This phylogenetic interpretation is ascertained by testa morphology and directs the genus *Escobaria* away from *Coryphantha* and closer to *Mammillaria*. Thus, the differentiation between *Escobaria* and *Coryphantha* is

no longer confined to the testa structure differences (HUNT & TAYLOR 1990), but is extended to the consideration of nectary glands and allocates the two genera into different phylads (*Ferocactus/Coryphantha* line and *Escobaria/Mammillaria* line respectively).

The cladograms in Figs. 31 and 32 show this new interpretation.

Fig. 31. Phylogenetic interpretation of the genus *Coryphantha* (**bold** areole types). 1 Foveolate seeds; 2 potency to produce extrafloral nectary glands; 3 absence of extrafloral nectary glands; 4 tubercles instead of ribs; 5 *Ferocactus*-areole type; 6 *Acharagma*-areole type; 7 *Macromeris*-areole type; 8 *Protocoryphantha* areole type; 9 *Protomammillaria* areole type; 10 *Ortegocactus* areole type; 11 *Escobaria* areole type; 12 *Mammillaria* areole type; 13 smooth, reticulate seeds; 14 dark, "pitted" seeds; 15 apical (central) flowers; 16 subapical flowers; 17 outer perianth segments fimbriate; 18 outer perianth segments entire; 19 extrafloral nectary glands in grooves and/or axils; 20 absence of extrafloral nectary glands except for optional glands close to the areoles; 21 reniform seeds with narrow hilum; 22 globose seeds with large hilum



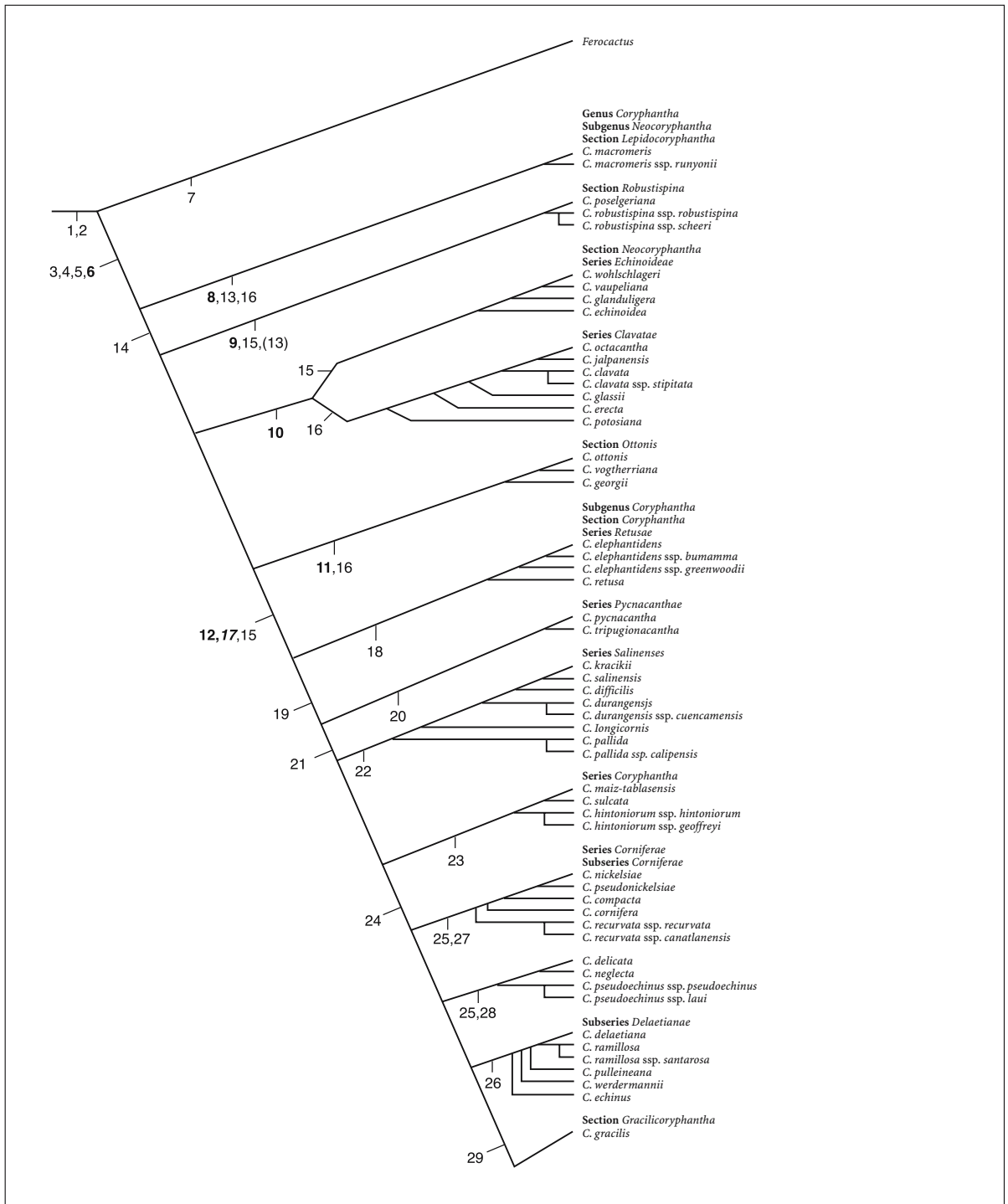


Fig. 32. Phylogenetic interpretation of the genus *Coryphantha* (**bold areole and gland types**). 1 Foveolate seeds; 2 potency to produce extrafloral nectary glands; 3 tubercles; 4 fruits green, juicy, seeds reniform; 5 smooth, reticulate seeds; 6 extrafloral nectary glands in grooves and/or axils; 7 *Ferocactus* areole type; 8 *Macromeris* areole type; 9 *Protocoryphantha* areole type; 10 *Protomammillaria* areole type; 11 *Ortegocactus* areole type; 12 *Escobaria* areole type; 13 fimbriate outer perianth segments; 14 tubercle grooves complete; 15 cortex watery; 16 cortex mucilaginous; 17 reduction of extrafloral nectary glands except for optional glands close to the areole; 18 majority of radial spines subulate; 19 majority of radial spines needle-like; 20 three or more central spines always present, none porrect, all appressed; 21 central spines 0–4, one dominating (if present) porrect; 22 tubercles appressed (“pineapple”); 23 tubercles upright; 24 tubercles porrect; 25 central spines 0–1; 26 central spines always 3–4; 27 tubercles more than 12 mm wide at the base; 28 tubercles up to 12 mm wide at the base; 29 seeds globose, fruits turning red and drying soon

5.3 Systematic Overview of the Genus *Coryphantha*

I. Subgenus *Neocoryphantha* Backeberg emend. Dicht & A. Lüthy

I.A Section *Lepidocoryphantha* (Backeberg) Moran

- 1 a. *C. macromeris* ssp. *macromeris*
- 1 b. *C. macromeris* ssp. *runyonii*

I.B Section *Robustispina* Dicht & A. Lüthy

2. *C. poselgeriana*
- 3 a. *C. robustispina* ssp. *robustispina*
- 3 b. *C. robustispina* ssp. *scheeri*

I.C Section *Neocoryphantha*

I.C.a Series *Echinoideae* Dicht & A. Lüthy

4. *C. wohlschlagerei*
5. *C. vaupeliana*
6. *C. glanduligera*
7. *C. echinoidea*

I.C.b Series *Clavatae* Dicht & A. Lüthy

8. *C. octacantha*
9. *C. jalpanensis*
- 10a. *C. clavata* ssp. *clavata*
- 10b. *C. clavata* ssp. *stipitata*
11. *C. glassii*
12. *C. erecta*
13. *C. potosiana*

I.D Section *Ottonis* Dicht & A. Lüthy

14. *C. ottonis*
15. *C. vogtherriana*
16. *C. georgii*

II. Subgenus *Coryphantha*

II.A Section *Coryphantha*

II.A.a Series *Retusae* Dicht & A. Lüthy

- 17 a. *C. elephantidens* ssp. *elephantidens*
- 17 b. *C. elephantidens* ssp. *bumamma*
- 17 c. *C. elephantidens* ssp. *greenwoodii*
- 18. *C. retusa*

II.A.b Series *Pycnacanthae* Dicht & A. Lüthy

- 19. *C. pycnacantha*
- 20. *C. tripugionacantha*

II.A.c Series *Salinenses* Dicht & A. Lüthy

- 21. *C. kracikii*
- 22. *C. salinensis*
- 23. *C. difficilis*
- 24 a. *C. durangensis* ssp. *durangensis*
- 24 b. *C. durangensis* ssp. *cuencamensis*
- 25. *C. longicornis*
- 26 a. *C. pallida* ssp. *pallida*
- 26 b. *C. pallida* ssp. *calipensis*

II.A.d Series *Coryphantha*

- 27. *C. maiz-tablasensis*
- 28. *C. sulcata*
- 29 a. *C. hintoniorum* ssp. *hintoniorum*
- 29 b. *C. hintoniorum* ssp. *geoffreyi*

II.A.e Series *Corniferae* Dicht & A. Lüthy

Subseries *Corniferae* Dicht & A. Lüthy

- 30. *C. nickelsiae*
- 31. *C. pseudonickelsiae*
- 32. *C. compacta*
- 33. *C. cornifera*
- 34 a. *C. recurvata* ssp. *recurvata*
- 34 b. *C. recurvata* ssp. *canatlanensis*
- 35. *C. delicata*
- 36. *C. neglecta*
- 37 a. *C. pseudoechinus* ssp. *pseudoechinus*
- 37 b. *C. pseudoechinus* ssp. *loui*

Subseries *Delaetianae* Dicht & A. Lüthy

- 38. *C. delaetiana*
- 39 a. *C. ramillosa* ssp. *ramillosa*
- 39 b. *C. ramillosa* ssp. *santarosa*
- 40. *C. pulleineana*
- 41. *C. werdermannii*
- 42. *C. echinus*

II.B Section *Gracilicoryphantha* Dicht & A. Lüthy

- 43. *C. gracilis*

6 Key to the Genus *Coryphantha*

A.1 Extrafloral nectary glands always present in the grooves and/or axils

B.1 Tubercle grooves extending only half-way to the tubercle axil

C.1 Tubercles 15–30 mm long

C.2 Tubercles 10–15 mm long

B.2 Tubercles grooved on whole length between apex and tubercle axil

C.1 Cortex watery

D.1 Upper side of tubercles longer than 20 mm

E.1 Tubercles very broad (35–50 mm), broader than long

E.2 Tubercles very long (25–35 mm), longer than broad

F.1 Tubercles 25–28 mm long

F.2 Tubercles 30–35 mm long

D.2 Upper side of tubercles less than 12 mm long

E.1 Central spines 5–7

E.2 Central spines 1–4

F.1 Radial spines up to 15

F.2 Radial spines more than 17

G.1 Body obovoid to clavate

G.2 Body semiglobose to globose

C.2 Cortex mucilaginous

D.1 Body columnar or cylindrical

E.1 Central spine darker than radial spines

F.1 Tubercles keeled below or bulging

G.1 Upper side of tubercles longer than 18 mm

I. Subgenus *Neocoryphantha*

I.A Section *Lepidocoryphantha*

1.a. *C. macromeris* ssp. *macromeris*

1.b. *C. macromeris* ssp. *runyonii*

I.B Section *Robustispina*

2. *C. poselgeriana*

3.a. *C. robustispina* ssp. *robustispina*

3.b. *C. robustispina* ssp. *scheeri*

I.C Section *Neocoryphantha*

I.C.a Series *Echinoideae*

4. *C. wohlschlagerei*

5. *C. vaupeliana*

6. *C. glanduligera*

7. *C. echinoidea*

I.C.b Series *Clavatae*

8. *C. octacantha*

- G.2 Upper side of tubercles shorter than 10 mm
 - F.2 Tubercles conical, round
 - G.1 Porrect central spine straight
 - G.2 Porrect central spine hooked
 - E.2 Central and radial spines of same colour
 - F.1 Tubercles in 5 and 8 series
 - F.2 Tubercles in 8 and 13 or 13 and 21 series
 - G.1 Spines uniformly yellow
 - G.2 Spines pines dark-brown tipped
 - D.2 Body clavate, globose or depressed-globose
 - E.1 Tubercles in 5 and 8 series
 - F.1 More than 8 radial spines
 - F.2 Less than 7 radial spines
 - E.2 Tubercles in 8 and 13 series
- A.2 Extrafloral nectary glands lacking or optionally present exclusively close to the spiniferous (abaxial) part of the areole**
- B.1 Tubercles at the base more than 7 mm wide, seeds reniform
 - C.1 Majority of radial spines subulate or thin subulate
 - D.1 Radial spines less than 10, majority subulate
 - E.1 Plants solitary
 - E.2 Usually group-forming
 - F.1 Tubercles 25–27 mm wide
 - F.2 Tubercles 18–22 mm wide
 - D.2 Radial spines more than 10, majority thin subulate
 - C.2 Majority of radial spines needle-like
 - D.1 Central spines always present, none porrect, all appressed to the body
 - E.1 5–7 central spines
 - E.2 Always 3 central spines
 - D.2 Central spines, if present, at least one dominating porrect
 - E.1 Tubercles appressed, flat conical or bulging
 - F.1 Two types of radial spines (subulate and needle-like)
 - G.1 Tubercles conical-cylindrical, rounded
 - H.1 Always 5–8 central spines
 - H.2 Maximum 4 central spines
 - G.2 Tubercles flattened, broadly conical

- 9. *C. jalpanensis*
- 10.a. *C. clavata* ssp. *clavata*
- 10.b. *C. clavata* ssp. *stipitata*
- 11. *C. glassii*
- 12. *C. erecta*
- 13. *C. potosiana*
- I.D Section *Ottonis***
- 14. *C. ottonis*
- 15. *C. vogtherriana*
- 16. *C. georgii*

II. Subgenus *Coryphantha*

II. A Section *Coryphantha*

II.A.a Series *Retusae*

- 17.a. *C. elephantidens* ssp. *elephantidens*
- 17.b. *C. elephantidens* ssp. *bumamma*
- 17.c. *C. elephantidens* ssp. *greenwoodii*
- 18. *C. retusa*

II.A.b Series *Pycnacanthae*

- 19. *C. pycnacantha*
- 20. *C. tripugionacantha*

II.A.c Series *Salinenses*

- 21. *C. kracikii*
- 22. *C. salinensis*
- 23. *C. difficilis*

- F.2 Radial spines all needle-like
- G.1 Central spine straight
- H.1 Central spine pointing upward 24.a. *C. durangensis* ssp. *durangensis*
- H.2 1 Central spine porrect 24.b. *C. durangensis* ssp. *cuencamensis*
- G.2 Central spine curved
- H.1 Tubercles 20–22 mm wide 25. *C. longicornis*
- H.2 Tubercles 14–17 mm wide 26.a. *C. pallida* ssp. *pallida*
- H.3 Tubercles 25–30 mm wide 26.b. *C. pallida* ssp. *calipensis*
- E.2 Tubercles upright, conical **II.A.d Series**
Coryphantha
- F.1 No central spine, radial spines less than 7 27. *C. maiz-tablasensis*
- F.2 Central spine always present, radial spines 7–15
- G.1 Central spine(s) never hooked 28. *C. sulcata*
- G.2 Central spine always hooked
- H.1 Tubercles at the base more than 20 mm wide 29.a. *C. hintoniorum* ssp. *hintoniorum*
- H.2 Tubercles at the base up to 12 mm wide 29.b. *C. hintoniorum* ssp. *geoffreyi*
- E.3 Tubercles porrect, conical **II.A.e Series *Corniferae***
Subseries a. *Corniferae*
- F.1 Central spines 0–1
- G.1 Tubercles at the base more than 12 mm wide
- H.1 Upper radial spines bundled
- I.1 Tubercles in 5 and 8 series 30. *C. nickelsiae*
- I.2 Tubercles in 8 and 13 series 31. *C. pseudonickelsiae*
- H.2 Upper radial spines not bundled
- I.1 Plants solitary
- J.1 Upper side of tubercles up to 7 mm long 32. *C. compacta*
- J.2 Upper side of tubercles more than 8 mm long 33. *C. cornifera*
- I.2 Group-forming
- J.1 Central spine curved downward 34.a. *C. recurvata* ssp. *recurvata*
- J.2 Central spine straight, porrect 34.b. *C. recurvata* ssp. *canatlanensis*
- G.2 Tubercles at the base up to 12 mm wide
- H.1 Upper radial spines bundled or densely set
- I.1 Tubercles at the base 7–9 mm wide 35. *C. delicata*

- I.2 Tubercles at the base
11 mm wide
 - H.2 Radial spines radiating regularly
 - I.1 Epidermis greyish-green
 - I.2 Epidermis grass-green
 - F.2 Central spines always 3–4
 - G.1 Tubercles at the base 15–25 mm wide
 - H.1 Upper radial spines bundled
 - H.2 Radial spines radiating regularly
 - I.1 Radial spines 14–20
 - I.2 Radial spines 12–13
 - G.2 Tubercles at the base up to 12 mm wide
 - H.1 Body slender, columnar
 - H.2 Body globose to short-cylindrical
 - I.1 Central spines irregularly protruding
 - I.2 Central spines in bird's foot arrangement
 - B.2 Tubercles at the base less than 7 mm wide, seeds globose
36. *C. neglecta*
- 37.a. *C. pseudoechinus*
ssp. *pseudoechinus*
- 37.b *C. pseudoechinus* ssp.
laui
- Subseries b. *Delaetianae***
38. *C. delaetiana*
- 39 a. *C. ramillosa* ssp.
ramillosa
- 39 b. *C. ramillosa* ssp. *santarosae*
40. *C. pulleineana*
41. *C. werdermannii*
42. *C. echinus*
- II.B Section**
Gracilicoryphantha
43. *C. gracilis*

7 The Genus *Coryphantha* (Engelmann) Lemaire – Descriptions of the Species

Cactées 32, 1868 (*nom.cons.* ICBN 5411 a)
(=) *Aulacothele* (Lemaire) Monville, Cat. Pl.
Exot.:21, 1846.

Basionym: *Mammillaria* subg. *Coryphantha*
Engelmann, Syn. Cact. US, 8, 1856; Proc.
Amer. Acad. 3: 264, 1857.

Lectotype: *Coryphantha sulcata* (Engelmann)
Britton & Rose (Britton, N.L. & Brown, A., An
illustrated Flora of the Northern United
States..., ed. 2, 1–3: 579, 1913; Hunt & Benson,
Cact. Succ. J. (US) 48: 72, 1976).

Synonyms: *Mammillaria* Haworth, Syn. Pl.
Succ.177, 1812 (*pro parte*); *Echinocactus* Link
& Otto, Verh. Ver. Bef. 3: 420, 1827 (*pro parte*);
Mammillaria [tax.infrag.] *Aulacothelae*
Lemaire, Cact. Gen. Nov. 92: 1839; *Mammil-*
laria subsect. *Aulacothelae* (Lemaire)
Lawrence, Gard. Mag. & Reg. Rural Domest.
Improv., ser.3, 6: 313–321, 1841; *Cactus*
Kuntze, Rev. Gen. Pl. 1: 261, 1891 (*pro parte*);
Cactus sect. *Coryphantha* (Engelmann) Coul-
ter, Contr. U.S. Nat. Herb 3 (2): 95, 1894; *Neol-*
loydia Britton & Rose, Bull. Torr. Club. 49: 251,
1922 (*pro parte*); *Lepidocoryphantha* Backe-
berg, Blätter Kakteenforschung 6: 18, 1938;
Escobrittonia Doweld, Sukkulenty, 3 (1): 17,
2000 (*pro parte*).

Definition: Capacity to produce extrafloral
nectary glands. Floriferous tubercles
grooved. Flowers in the plant apex. Fruits
green, juicy. Seeds brown, testa reticulate.

I. Subgenus *Neocoryphantha* Backeberg *emend.* Dicht & A. Lüthy

Jahrb. Dtsch. Kakt. Ges. 2: 61, 1942 (*pro parte*).
Emend. Cact. Syst. Init. (11): 8, 2001

Type: *Coryphantha clavata* (Scheidweiler)
Backeberg.

Synonyms: *Mammillaria* sect. *Glanduliferae*
Salm-Dyck in Walpers [in Suppl.I] Repert.
bot. syst. 2(2): 272, 1843 (*nom.inval.* ICBN art.
52.1, incl. *M. aulacothele* Lemaire, the type
species of the earlier and validly published
Mammillaria sect. *Aulacothelae* Lemaire,
Cact. Gen. Nov. 92, 1839); *Coryphantha* Series
Recurvatae Britton & Rose, Cactaceae 4:24,
1923 (*pro parte*, typ. excl.); *Coryphantha*
series *Glanduliferae* (Salm-Dyck) Bravo &
Sánchez-Mejorada, Las Cactáceas de México
3: 475, 1991 (*nom.inval.* ICBN art 52.1).

Definition: Areoles *Macromeris*-, *Protoco-*
ryphantha-, *Protomammillaria*- or *Ortegocac-*
tus type (ZIMMERMAN 1985, p. 61), with
nectary glands in the tubercle grooves and/or
in the axils. Cortex watery or mucilaginous.
Seeds reniform.

I.A. Section *Lepidocoryphantha* (Backeberg) Moran

Gentes Herb. 8(4): 318, 1953

Basionym: *Lepidocoryphantha* Backeberg,
Blätter Kakteenforschung 6: 18, 1938 (*pro*
gen.)

Type: *Coryphantha macromeris* (Engelmann)
Lemaire.

Synonyms: *Coryphantha* series *Macromeres*
Britton & Rose, Cactaceae 4: 24, 1923.

Definition: Areoles *Macromeris* type (ZIMMERMAN 1985, p. 61): Plants flowering only after attainment of maximum length areolar grooves, which extend only about halfway to the axils. Margins of outer perianth segments fimbriate. Ovary and fruits with few single scales. Cortex mucilaginous.

1 a. *Coryphantha macromeris* subsp. *macromeris* (Engelmann) Lemaire

Cactées 35, 1868

Basionym: *Mammillaria macromeris* Engelmann in Wislizenus, Mem. Tour. North. Mex. 97, 1848.

Lectotype: USA, New Mexico, Donana, 9 May 1846, Wislizenus s.n. (MO); Benson, Cacti US & Canada 959, 1982.

Synonyms: *Echinocactus macromeris* (Engelmann) Poselger, Allg. Gartenz. 21: 102, 1853; *Cactus macromeris* (Engelmann) Kuntze, Rev. Gen. Pl. 1: 260, 1891; *Lepidocoryphantha macromeris* (Engelmann) Backeberg, Cactaceae, Jahrb. DKG 1941 (2): 61, 1942; *Mammillaria heteromorpha* Scheer ex Salm-Dyck, Cact. Hort. Dyck. 1849: 128, 1850; *Echinocactus heteromorphus* (Scheer ex Salm-Dyck) Poselger, Allg. Gartenz. 21: 126, 1853; *Cactus heteromorphus* (Scheer ex Salm-Dyck) Kuntze, Rev. Gen. Pl. 1: 260, 1891; *Mammillaria dactylithele* Labouret, Monogr. Cact. 146, 1853.

Body caespitose, pale-green, globose to short-cylindrical, up to 10–15 cm high and 5 cm diameter, forming large groups up to 50 cm diameter and 20 cm high. Root sprouting in the upper part, terminating in a taproot. **Tubercles** in 5 and 8 series, loosely arranged, conical, rounded, tapering towards the apex, at the base 18 mm wide, 11 mm high, length of upper surface 13–20 mm, of lower surface 17–30 mm, groove never on the whole areole length, extending from the spiniferous areole to the midpoint of the upper surface only or shorter, woolly, often with one or several red glands, one of them at the inner end of the groove. **Areoles** round, 3–4 mm diameter,

with white felt. **Radial spines** 9–15, irregularly arranged and protruding, straight or slightly curved, needle-like, 15–28 mm long, the shortest ones below, dark to light grey, in new growth also reddish-brown. **Central spines** 3–6, irregularly porrect, straight or slightly curved, robust, needle-like, 25–50 mm long, light to dark red-brown, later becoming grey from the base. **Flowers** 3–6 cm in length and diameter, floral tube green with some small scales; outer perianth segments broad lanceolate, acute, dentate towards the tips, fimbriate, 25 mm long, 6 mm wide, purple or light rose with purple-brown central midstripe; inner perianth segments broad lanceolate, acute, dentate towards the tips, margins entire, 30 mm long and 6–9 mm wide, purple or light rose-coloured with darker midstripe, filaments purple-red or rose to nearly white, anthers yellow, stigma yellowish, lobes 7–8, yellowish-white. **Fruit** green juicy berry, 16–25 mm long, 6–9 mm in diameter, with a few small fimbriate scales. **Seeds** reniform, 1.2 mm wide, up to 1.8 mm long, hazel-brown, testa reticulate.

Distribution: USA: south of New Mexico and Texas, along the Rio Grande. Mexico: in the States of Chihuahua, Coahuila and San Luis Potosí.

Habitat: Sandy alluvial plains in open ground or under bushes, 750–1500 m above sea level.

Locations checked: USA: Texas: Big Bend National Park, Presidio County. New Mexico: Doña Ana County, Eddy County. Mexico: Coahuila: Hipolito, Monclova, Laguna de Meyrán, San Juan de Boquillas, Cuatrociénegas, Benito Juárez, Monterrey-Monclova km 40, Ocampo. Chihuahua: El Sueco, Cuauhtemoc. San Luis Potosí: Villa de Ramos.

Incidence: Least concern.

Illustrations: Distribution see Plate 9, map 1; plant portrait see Plate 14, photos 1 and 3.

1 b. *Coryphantha macromeris* subsp.***runyonii*** (Britton & Rose) N.P. Taylor

Cact. Cons. Init. (6): 15, 1998.

Basionym: *Coryphantha runyonii* Britton & Rose, Cact. 4: 26, 1923.**Lectotype:** USA, Texas, Rio Grande (City), 10 Aug. 1921, Runyon s.n. (US; NY, dupl.). (Benson, Cact. Suc. J.(US) 41: 188, 1969)**Synonyms:** *Mammillaria runyonii* (Britton & Rose) Cory, Rhodora 38: 407, 1936; *Lepidocoryphantha runyonii* (Britton & Rose) Backeberg, Cactaceae 5: 2975, 1961; *Coryphantha macromeris* var. *runyonii* (Britton & Rose) Benson, Cact. Succ. J. (US) 41: 188, 1969; *Lepidocoryphantha macromeris* ssp. *runyonii* (Britton & Rose) Doweld, Sukkulenty 1999 (1): 28, 1999; *Coryphantha pirtlei* Werdermann, Notizbl. Bot. Gart. Berlin-Dahlem 12: 226, 1934.**Body** caespitose, remaining small, maximum size about half that of ssp. *macromeris*, sprouting, forming low clumps of up to 50 cm diameter, greyish-green, with taproot. **Tubercles** loosely arranged, conical, rounded, at the base 11 mm wide, halfway up 5 mm, 10–15 mm long, groove never on the whole areole length, in the areolar half only. **Areoles** round, 1–2 mm diameter, with white woolly felt. **Radial spines** 6–9, irregularly disposed and protruding, straight or curved, 7–20 mm long, shortest ones below, thin needle-like, yellowish-white, some brownish. **Central spines** 1–2, rarely 3, up to 25 mm long, porrect, slightly curved, needle-like, red-brown to dark-brown. **Flowers, fruits and seeds** like ssp. *macromeris*.**Distribution:** along the lower river-course of the Rio Grande, at sealevel, between Brownsville and Rio Grande City (Texas) and parallel on the opposite river side in the Mexican state of Tamaulipas.**Habitat:** Sandy alluvial soils.**Locations checked:** USA: Texas: Jim Hogg County.**Incidence:** Least concern. Collected due to its high content of psychoactive alkaloids.**Comments:** ssp. *runyonii* is about half the size of ssp. *macromeris* in all measurements and grows in an isolated area at the lower course of the Rio Grande on sealevel.Both species and subspecies show some characteristics which are unique within the genus *Coryphantha*:

- tubercle grooves extend only from near the spiniferous areole to about the mid-point of the upper surface, never reaching the axil (*Macromeris* areole type)
- the outer perianth segments are fimbriate
- ovary and fruits with few single scales

These features led BACKEBERG (1938) to form a new genus *Lepidocoryphantha* for the series *Macromeres* of Britton & Rose. BUXBAUM (in KRAINZ 1959) removed this genus and placed the *Macromeres* within *Coryphantha*.With the characteristics mentioned above, the *Macromeres* prove to be the oldest stage within the genus *Coryphantha*. Since other *Coryphantha* species also have fimbriate outer perianth segments (e.g. *Coryphantha robustispina* ssp. *scheeri*) and fruits/ovaries with few single scales (e.g. *Coryphantha clavata*), treatment as an independent subgenus is not justifiable, however, the presence of a unique areole type permits the separation into an independent section.**Illustrations:** Distribution see Plate 9, map 1; plant portrait see Plate 14, photo 2.**I.B Section *Robustispina* Dicht & A. Lüthy**

Cact. Syst. Init. 11: 9, 2001.

Type: *Coryphantha robustispina* (Schott ex Engelman) Britton & Rose.**Definition:** Areoles *Protocoryphantha* type: grooves becoming slowly longer on each newly formed tubercle during the ontogenesis of the individual plant, this process being interrupted for a longer period (years) when the grooves reach about three-quarters of the way to the tubercle axils and incomplete

grooves persist on old tubercles, flowering only after attainment of maximum length areolar grooves reaching the axils. Cortex watery.

2. *Coryphantha poselgeriana* (Dietrich)

Britton & Rose

Cactaceae 4: 28, 1923

Basionym: *Echinocactus poselgerianus* Dietrich, Allg. Gartenz. 19: 346, 1851.

Type: not designated.

Synonyms: *Mammillaria salm-dyckiana* Scheer in Salm-Dyck, Cact. Hort. Dyck 1849:134, 1850 *nom. rejic.* (Dicht 2000); *Mammillaria salm-dyckiana brunnea* Salm-Dyck, Allg. Gartenz. 18:394, 1850 *nom. rejic.*; *Echinocactus salm-dyckianus* Poselger, Allg. Gartenz. 21:102, 1853, *nom. rejic.*; *Cactus salm-dyckianus* Kuntze, Rev. Gen. Pl. 1: 261, 1891, *nom. rejic.*; *Coryphantha salm-dyckiana* (Scheer) Britton & Rose, Cactaceae 4: 28, 1923, *nom. rejic.*; *Coryphantha salm-dyckiana* (Scheer) Britton & Rose var. *brunnea* (Salm-Dyck) Unger, Kakt. and. Sukk. 37(5):85, 1986 *nom. rejic.*; *Echinocactus saltillensis* Poselger, Allg. Gartenz. 21: 101, 1853; *Mammillaria saltillensis* Bödeker, Zeitschr. Sukk-Kunde 3: 268, 1928; *Coryphantha poselgeriana* var. *saltillensis* (Poselger) Bremer, Cact. Suc. Mex. 22:16, 1977; *Mammillaria valida* Purpus, Monatsschr. Kakt. 21: 97, 1911, *nom. illeg.* ICBN Art.53 [Non *Mammillaria valida* Weber, Dict. Hort. Bois 806, 1898. Nec *Mammillaria scheeri* var. *valida* Engelmann, Proc. Amer. Acad.3: 265, 1857 (= *Coryphantha robustispina* subsp. *scheeri* (Lemaire) Taylor)]; *Coryphantha valida* (Purpus) Bremer, Cact. Suc. Mex. 22: 14, 1977 (see ICBN Art. 58.3); *Coryphantha poselgeriana* (Dietrich) Britton & Rose var. *valida* (Purpus) Heinrich ex Backeberg, Cactaceae 5: 3050, 1961 (see ICBN Art. 58.3) [Non *Coryphantha scheeri* (Kuntze) Benson var. *valida* (Engelmann) Benson, The Cacti of Arizona 25, 1969 (= *Coryphantha robustispina* subsp. *scheeri* (Lemaire) Taylor)]; *Mammillaria kieferiana*

Hort. ex Bödeker, Zeitschr. Sukk.-Kunde 3: 270, 1928; *Coryphantha kieferiana* Berger, Kakteen 276, 1929; *Echinocactus salinensis* Poselger 1853 *sensu* Britton & Rose, Cactaceae 4:28, 1923; *Mammillaria difficilis* Quehl 1908 *sensu* Britton & Rose, Cactaceae 4: 28, 1923.

Body solitary, semi-globose to short cylindrical, 10–30 cm high and 13–18 cm in diameter, dull grey-bluish-green, apex rounded, woolly, central thin taproot. **Tubercles** in 8 and 13 series, near the base rounded 4–6-edged, delineated by a groove, near the areole convex-conical, somewhat flattened on the upper surface, rounded at the end, up to 30 mm high and 50 mm wide, younger ones narrower, up to 25 mm long, with a deep, woolly groove with 1–5 yellow-orange glands over the whole length. **Axils** woolly, with gland. **Areoles** round, 7 mm diameter, slightly woolly. **Radial spines** 9–12, with 7–8 of them radiating sideways and downwards, slightly protruding, straight or somewhat curved, strong, thick subulate, the strongest 3–4 below, flattened, edged laterally, 30–40 mm long, in youth whitish, later reddish-brown with dark tips, ultimately grey, blackish on the upper side. Upper 4–5 spines thinner, ascending, slightly curved, in a bundle, slightly shorter, whitish with black tips, ultimately greyish. **Central spine** 1, straight, porrect, in shape, thickness, colour and length similar to lower radial spines. **Flower** funnellform, 6–7 cm diameter, outer perianth segments oblanceolate, margin entire, dentate towards the tip, tips usually acute, light rose to carmine-red with darker, sometimes greenish midstripe. Inner perianth segments oblanceolate, margin entire, dentate towards the tip, pale rose with carmine-red throat. Flower at some locations also yellow. Filaments carmin-red, anthers dark yellow, style reddish, stigma lobes 8–10, 3–5 mm long, greenish-yellow. **Fruit** green, juicy berry with attached flower remnants, oblong to large ovoid, 25–50 mm long and 7–18 mm in diameter. **Seeds** reniform,

2–2.5 mm long and 1.5 mm wide, testa shiny, reticulate, red-brown.

Development: At first, the tubercles are flat and separated from each other by a deep groove only (“sea-urchin”). Later, they are extended and groove development starts. Before the plant is completely adult, sterile faint flowers appear, which never open.

Distribution: Mexico: Coahuila, San Luis Potosí, Durango and Zacatecas.

Habitat: Alluvial plains with sandy-gypsum or gravelly soil, nearly bare.

Locations checked: Mexico: Coahuila: Hipolito, Estacion Marte, Saltillo, Cuatrociénegas, El Papalote, Zona de Minas, La Rosa, Nueva Atalaya, Arteaga, Ocampo. San Luis Potosí: Villa de Ramos, Vanegas, Tolosa. Durango: Santa Clara, Cuencamé, Yerbanis. Zacatecas: Rio Grande, Juan Aldama.

Incidence: Least concern.

Comments: This strongly spined species, reminiscent of an *Echinocactus*, has a long nomenclatural history, like *Coryphantha robustispina* ssp. *scheeri* Br. & R, with which it was confused again and again and, in fact, it should be named *Coryphantha salm-dyckiana*.

As UNGER (1986) correctly stated, this species was first described as *Mammillaria salm-dyckiana* by SCHEER (1850) 1 year before DIETRICH (1851) described it as *Echinocactus poselgerianus*.

Mammillaria salm-dyckiana Scheer ex Salm-Dyck, Cact. Hort. Dyck 1849:134, 1850 was the first description of a globose plant with very large tubercles of 27 mm (one thumb) width (in later years depressed and even up to 40.5 mm [1.5 thumbs] diameter), 8–10 radial spines of 27–40 mm (1–1.5 thumbs) in length and one single central spine of 54 mm (2 thumbs) in length. This, however, is the older description of *Echinocactus poselgerianus* Dietrich 1851, the basionym of *Coryphantha poselgeriana* (Dietrich) Britton & Rose 1923 (UNGER 1986, DICHT 1996).

When Britton and Rose published the new combination *Coryphantha salm-dyckiana*

(Scheer) Britton & Rose in Cactaceae 4:39, 1923 they erroneously applied the name to a different plant with small tubercles (15 mm width), with 15 radial spines of 10–15 mm length and 1–4 central spines (the longest of them 20–25 mm long) corresponding to *Coryphantha delaetiana* (Quehl 1908) Berger 1929, a plant which was listed by BRITTON & ROSE (1923) as one of the synonyms of *Coryphantha salm-dyckiana* (Scheer) Britton & Rose.

Since BRITTON & ROSE (1923), *Coryphantha salm-dyckiana* (Scheer) Britton & Rose has continuously been used in its incorrect sense as a synonym of *Coryphantha delaetiana* (Quehl) Berger (BERGER 1929, BORG 1937, BACKEBERG 1961, GLASS 1975, BRAVO & SANCHEZ-MEJORADA 1991, PRESTON-MAFHAM 1991) and never as the older, but valid synonym of *Coryphantha poselgeriana* (Dietrich) Britton & Rose 1923.

The confusion that would be caused if *Coryphantha salm-dyckiana* (Scheer) were to displace *C. poselgeriana* (Dietrich) Britton & Rose, the lack of an extant type, the difficulty of typifying the name and the evident misapplication of the name by Britton & Rose are sufficient grounds to justify a proposal for rejection of Scheer’s basionym *Mammillaria salm-dyckiana*, thus removing it from contention with *Echinocactus poselgerianus* Dietrich, and adopting *Coryphantha delaetiana* (Quehl) Berger for *Coryphantha salm-dyckiana* Britton & Rose.

This proposal was submitted to the Committee for Spermatophytes in 2000.

Illustrations: Distribution see Plate 9, map 1; plant portrait see Plates 15 and 16.

3 a. *Coryphantha robustispina*

(Schott ex Engelm.) Britton & Rose
subsp. *robustispina*

Cactaceae IV: 33, 1923

Basionym: *Mammillaria robustispina* Schott ex Engelm., Proc. Amer. Acad. 3: 265, 1856.

Type: Mexico: Llanos on the southern side of Baboquivaria mountain, presumably on the Sonora side of the boundary (Schott 4, MO 01443835, holo; F 42679, iso.).

Synonyms: *Cactus robustispinus* (Schott) Kuntze, Rev. Gen. Pl. 1: 261, 1891; *Mammillaria robustissima* Schott, West. Am. Scient. 21, 1900; *Coryphantha muehlenpfordtii* (Poselger) Britton & Rose var. *robustispina* (Schott ex Engelmann) Marshall, Ariz. Cact. 94, 1953; *Coryphantha muehlenpfordtii* Britton & Rose subsp. *robustispina* (Engelmann) Dicht, Kakt. and. Sukk. 47 (12): 252, 1996; *Coryphantha scheeri* (Kuntze) Benson var. *robustispina* (Schott ex Engelmann) Benson, Cact. Arizona 25, 1969; *Coryphantha scheeri* Lemaire var. *robustispina* Benson, cacti of the United States and Canada 820, 1982; *Mammillaria brownii* Toumey, Bot. Gaz. 22: 253, 1896; *Cactus brownii* Toumey, Bot. Gaz. 22: 253, 1896.

Body solitary or group-forming, globose or slightly higher than wide, 5–15 (–20) cm high, dull grey-green, apex flattened. **Tubercles** in 8 and 13 series, conical, rounded, upper surface somewhat flattened, older ones rhomboid, base 20 mm wide, 17 mm high, length of upper surface 22 mm, of lower surface 25 mm, groove on upper surface from spiniferous areole to axil, in youth white-woolly, with small, hidden glands. **Areoles** round, 7 mm in diameter, in youth white-woolly. **Radial spines** 8–12, lower and lateral 6–8 radial, horizontal, straight, subulate, stiff, 30 mm long, upper ones in two layers closely set, somewhat thinner and longer, all brownish in youth, later becoming grey from the base, uppermost lighter with dark tips. **Central spine** 1, more robust, straight, porrect, tip curved to hooked, 30 mm long, colour as for lower radial spines. **Flowers** 5–7 cm diameter, 5–6 cm long, funnellform, outer perianth segments lanceolate, margin fimbriate, acute, dentate towards the tip, yellow with reddish dorsal midstripe, inner perianth segments lanceolate, margin entire, dentate towards the tip, acute, yellow to bronze-coloured, some-

times reddish at the base, filaments reddish, anthers yellow, stigma and stigma lobes light yellow. **Fruit** green, juicy, longish berry, 30–55 mm long, 12–20 mm wide. **Seeds** reniform, 3.2 mm long, 2.5 mm wide, shiny, brown, testa reticulate.

Distribution: South of Arizona in a defined area spreading about 70 km east–west and 80 km north–south and in the adjacent region of the Mexican State Sonora.

Habitat: Flat and sparsely vegetated plains or on flat hilltops in semi-desert grasslands.

Location checked: USA: Arizona: Pima County.

Incidence: Endangered, mainly by urbanisation, constructions, burning off, Lehman's love-grass, illegal collection, off-road vehicles.

This species, popularly known as the Pima Pineapple Cactus, was included in the List of Endangered Species of the USA on 20 April 1992.

Comments: Inclusion of *Coryphantha robustispina* Br. & R as a variety of *Coryphantha muehlenpfordtii* (MARSHALL 1953) and *Coryphantha scheeri* (BENSON 1969), respectively, was not accepted by everybody, since in all the literature, contrary to *Coryphantha scheeri*, it was mentioned as being without any glands. Therefore, it was allocated to the series *Aulacothelae* Lemaire (*Sulcolanatae* Britton & Rose) and not to *Glanduliferae* Salm-Dyck (*Recurvatae* Britton & Rose, *Neocoryphantha* Backeberg).

Our own observations showed that *C. muehlenpfordtii* subsp. *robustispina* clearly does make glands. These are much smaller than those of the typical subspecies and are often hidden by felt in the grooves. Therefore, this species often shows sooty moulds (“black fungus”).

Illustrations: Distribution see Plate 9, map 1; plant portrait see Plate 17, photo 1.

3 b. *Coryphantha robustispina* subsp. *scheeri*

(Lemaire) N.P. Taylor

Cact. Cons. Init. 6: 18, 1998.

Basionym: *Coryphantha scheeri* Lemaire, Cactées 35, 1868.**Lectotype:** Allg. Gartenz. 15 (3): t.2, 1847 (Taylor, CCI 6:18, 1998).

Synonyms: *Mammillaria scheeri* Mühlenpfordt, Allg. Gartenz. 5: 97, 1847 [non *Mammillaria scheeri* Mühlenpfordt, Allg. Gartenz. 13: 346, 1845 (= *Neolloydia conoidea*)]; *Mammillaria scheeri* Mühlenpfordt var. *valida* Engelm., Proc. Amer. Acad. 3: 265, 1856 [non *Mammillaria valida* Weber, Dict. Hort. Bois 806, 1898, nec *Mammillaria valida*, Purpus, Monatsschr. Kakt. 21: 97, 1911, nec *Coryphantha valida* (Purpus) Bremer, Cact. Succ. Mex. 22: 14, 1977]; *Cactus scheeri* (Mühlenpfordt) Kuntze, Rev. Gen. Pl. 1: 261, 1891; *Coryphantha scheeri* (Kuntze) Benson, Cact. Succ. J. (US) 41: 234, 1969; *Coryphantha scheeri* (Kuntze) Benson var. *valida* (Engelm.) Benson, Cact. Arizona 25, 1969; *Coryphantha scheeri* (Kuntze) Benson var. *uncinata* Benson, Cact. Succ. J. (US) 41: 234, 1969; *Coryphantha scheeri* Lemaire var. *uncinata* Benson, Cacti of the United States and Canada: 820, 1982; *Echinocactus muehlenpfordtii* Poselger, Allg. Gartenz. 21: 102, 1853 [non *Mammillaria muehlenpfordtii* Förster, ex Otto & Dietr., Allg. Gartenz. 15: 49, 1847, nec *Echinocactus muehlenpfordtii* Fennel, Allg. Gartenz. 9: 65, 1847 (= *Thelocactus setispinus*)]; *Coryphantha muehlenpfordtii* (Poselger) Britton & Rose, Cactaceae 4 :28, 1923; *Coryphantha muehlenpfordtii* Britton & Rose subsp. *muehlenpfordtii* Dicht, Kakt. and. Sukk. 47 (5): 98, 1996; *Coryphantha muehlenpfordtii* subsp. *uncinata* (Benson) Dicht, Kakt. and. Sukk. 47(5): 98, 1996; *Mammillaria engelmannii* Cory, Rhodora 8: 405, 1936 [non *Coryphantha engelmannii* Lemaire, Cactées 34, 1868, nec *Cactus engelmannii* Kuntze, Rev. Gen. Pl. 1: 261, 1891]; *Coryphantha neoscheeri* Backeberg, Cactaceae 5: 3051, 1961; *Coryphantha robustispina* subsp. *uncinata* (Benson) N.P. Taylor, CCI 6: 18, 1998.

Body solitary, rarely sprouting at the base, globose to egg-shaped, then short cylindrical or somewhat conical, 10–20 cm high and 12 cm in diameter, dull green, apex rounded, slightly woolly. **Tubercles** in 5 and 8 series, prisma-shaped at the base, then cylindrical, at the base 15–19 mm wide, 12 mm high, length of upper and lower surface 30–35 mm, with deep, complete groove with white wool and up to four variously separated reddish-brown glands. **Axils** in youth with white wool, then naked and somewhat broadened. **Areoles** oval, 3.5 mm wide, 5 mm long, in youth woolly, later naked. **Radial spines** 8–11, 3 thinner ones in the upper part of the areole, closer set, the other ones horizontal and radially arranged, straight, stiff needle-like, 20–25 mm long, yellowish-white with dark tips, lower ones sometimes brownish. **Central spines** 1–4, the dominating one straight, porrect, thin-subulate, up to 35 mm long, the others straight upwards and slightly directed outwards, somewhat thinner and shorter, all somewhat darker and more intensely coloured than radials. **Flowers, fruits and seeds:** as *C. robustispina* subsp. *robustispina*.

Distribution: USA: south of New Mexico and Texas. Mexico: in the adjacent regions of Chihuahua.

Habitat: Flat and sparsely vegetated plains or lower hill slopes or on flat hilltops in semi-desert grasslands.

Locations checked: USA: New Mexico: Las Cruces, Carlsbad, Eddy County. Texas: Pecos County. Mexico: Chihuahua: Ciudad Chihuahua, Villa Ahumada, El Sueco und Benito Juarez.

Incidence: Least concern.

Comments: From the beginning, the nomenclatural history of this large-growing, long-tubercled species with its bronze-coloured flowers was characterised by vagueness and confusion. The first description (with illustration) as *Mammillaria scheeri* by MÜHLENPFORDT 1847 was an illegitimate homonym, because under the same name,

MÜHLENPFORDT himself had already described *Neolloydia conoidea* in 1845.

This circumstance may have induced POSELGER in 1853 to publish a new *Mammillaria scheeri* as *Echinocactus muehlenpfordtii*. However, by so doing, he made a similar mistake as Mühlenpfordt before, since this name was in use already: FENNEL in 1839 had described an *Echinocactus muehlenpfordtii* (syn. *Thelocactus setispinus*). Poselger's new name should have replaced *Mammillaria scheeri* Mühlenpfordt as a synonym, but Poselger failed to state which of the two relevant publications of Mühlenpfordt he was referring to in his publication. For this reason, the species name used by Poselger must be considered invalid.

In 1856, ENGELMANN described *Mammillaria scheeri* var. *valida* from Texas without having seen *Mammillaria scheeri* Mühlenpfordt. His knowledge of this species was taken from the description of Prince SALM-DYCK 1850. Engelmann had presumed that his var. *valida* might be just a somewhat larger and more heavily spined northern form of *Mammillaria scheeri* from Chihuahua. When visiting the collection of Prince Salm-Dyck, he found original plants of *Mammillaria scheeri* which corresponded completely with his var. *valida*, thus confirming his initial assumption (cf. J. COULTER 1894).

As Engelmann himself had realised already, var. *valida* does not contain enough distinct criteria to delineate a variety or subspecies, a view which, among others, was also shared by Coulter, Quehl, Britton & Rose und Backeberg.

When LEMAIRE (1868) included *Mammillaria scheeri* in the genus *Coryphantha*, he did not mention Mühlenpfordt as its author, nor did he specify which one of the earlier two versions of *Mammillaria scheeri* he meant.

LEMAIRE (in *Cactées* 35 ff., 1868) pointed out that he referred to SALM-DYCK (1850). In Salm-Dyck's book, *Mammillaria scheeri*

Muehlenpfordt 1847 belonged to the group of species to which, among others, *Mammillaria aulacothelae* also belonged and which Lemaire raised to genus level as *Coryphantha* (Engelmann) Lemaire, while *Mammillaria* (*Neolloydia*) *conoidea* (syn. *M. scheeri* Muehlenpfordt 1845) was put into the same infrageneric group of *Mammillaria* (viz. §6, Centrispinae) by both authors. This fact was overseen by a series of later authors, since it makes *Coryphantha scheeri* Lemaire a valid *nomen novum* (avowed substitute).

KUNTZE (1891) removed *Mammillaria scheeri* Muehlenpfordt to *Cactus scheeri*, naming its author, but without indicating whether the description of 1845 or 1847 was meant. Therefore, this name was also invalid.

In 1923 in *Cactaceae* IV: 28 by BRITTON & ROSE, for the first time *Coryphantha muehlenpfordtii* Britton & Rose appeared as a new combination. These two authors had realised the problems around *Mammillaria scheeri* Muehlenpfordt and, therefore, avoided the name *Coryphantha scheeri*, but obviously they were not aware that *Echinocactus muehlenpfordtii* was also an invalid name and, therefore, the combination *Coryphantha muehlenpfordtii* was inadmissible.

As a valid name we find *Mammillaria engelmannii* Cory 1936, which was used by BENSON (1950) as a synonym of *Coryphantha muehlenpfordtii* sensu Britton & Rose in *The Cacti of Arizona*.

In BACKEBERG's *Cactaceae* V:3051 (1961) one more epithet appears: *Coryphantha neoscheeri*. Probably Backeberg intended to escape the confusion surrounding the name *Coryphantha scheeri*. He had noticed that *Mammillaria scheeri* and *Mammillaria muehlenpfordtii* were both homonyms and he also believed that Lemaire's *Coryphantha scheeri* was invalid, too. In fact, *Coryphantha neoscheeri* is a valid description, but has to be regarded as superfluous.

In 1969, the new combination *Coryphantha scheeri* (Kuntze) L. Benson was published in

Cact. Succ. J. US 41:234 with the contention that following article 72 of the International Code of Botanical Nomenclature *Cactus scheeri* Kuntze, Rev. Gen. Pl. 1:261, 1891 should be regarded as the first valid publication of this species. However, as shown above, the name *Cactus scheeri* Kuntze is invalid because of Mühlenpfordt's imprecise indication of its publication and, therefore, Benson's new combination has to be regarded as invalid, too.

BENSON himself for the first time mentioned the circumstances which make *Coryphantha scheeri* Lemaire a valid *nomen novum* in 1982 (Cacti of the United States & Canada: 959) and consequently recombined the varieties *valida*, *uncinata* and *robustispina*. By doing so, he, like DICHT (1996), also overlooked the fact that *Mammillaria robustispina* Engelm (1856) is an older name than *Coryphantha scheeri* Lemaire (1868) and thus cannot be a subspecies, but must be the real, valid name of the species with Lemaire's *Coryphantha scheeri* as a subspecies. This context was finally rectified by Nigel P. TAYLOR in 1998 (Cactaceae Consensus Initiatives 6: 18) by recombining the two subspecies *scheeri* and *uncinata*. The subspecies *valida* had already been retracted by DICHT (1996).

Finally, the present nomenclature completely corresponds with the rules of the ICBN.

Illustrations: Distribution see Plate 9, map 1; plant portrait see Plate 17, photos 2 and 3.

I.C. Section *Neocoryphantha*

Type: *Coryphantha clavata* (Scheidweiler) Backeberg

Definition: Areoles *Protomammillaria* type (ZIMMERMAN 1985, p. 61) with abrupt transition from a completely grooveless sterile condition to areoles having fully fledged fertile areolar grooves, flowering only after the development of grooves.

I.C.a Series *Echinoideae* Dicht & A. Lüthy
Cact. Syst. Init. 11: 10, 2001.

Type: *Coryphantha echinoidea* (Quehl) Britton & Rose.

Definition: Areoles modified *Protomammillaria* type (ZIMMERMAN 1985) with abrupt transition from a completely grooveless sterile condition with pre-axillary meristematic activity (glands) to areoles having fully fledged fertile areolar grooves. Flowers appearing between the pre-axillary gland and the axil. Cortex watery.

4. *Coryphantha wohlschlagerei* Holzeis
Kakt. and. Sukkulente 41(3): 50, 1990

Type: Mexico, San Luis Potosí, San Francisco, M. Wohlschlagerei WM 223, (WU, holo.).

Body solitary, 10–11 cm high, 6 cm wide, reversed egg-shaped to short-cylindrical, dark olive-green. Tuberos root, up to 7 cm long and 3.5 cm thick, with conspicuously tapering part of often only 5 mm diameter between the root and the above-ground plant body. **Tubercles** in 5 and 8 series, conical to conical-cylindrical, 18–20 mm high, at the base 7–12 mm wide, upper surface 8 mm, lower surface 12–14 mm long, on the upper surface with a complete tubercle groove with red, white-woolly enveloped glands in the third of the groove nearest the axil. **Axils** in youth woolly. **Areoles** round, 2–3 mm diameter, in youth white-woolly, in later years completely naked. **Radial spines** on young plants 7–10, radiating, straight, needle-like, 4–11 mm long, whitish with dark tips. In adult plants up to 20, straight, needle-like radial spines, 3 of them directed downwards, 2 to each side, the other ones towards the apex in a bundle, all whitish with dark tips. **Central spines** on young plants 1 only, but later 5–7, the dominant spine porrect, the others slightly curved onto the body, the longest downward, up to 25 mm long, the others up to 18 mm long, all thin subulate, flattened, horn-coloured with brown tips. **Flower** funnelform, 4 cm long, 5–6 cm diameter, peri-

carpel globose-cylindrical, 5 × 6 mm, light green on the outside, white inside, nectar chamber thick-walled (2.5–3 mm), outer perianth segments lanceolate, 3 mm wide, 8–13 mm long, greenish-yellow with olive-brown midstripe, inner perianth segments light yellow, lanceolate, dentate towards the tip, acute, 4 mm wide, 20–22 mm long, filaments salmon, anthers dark yellow, style 21 mm long, white-yellow, 7–8 white-yellow stigma lobes. **Fruit** juicy berry with attached flower remnants, upper part olive-coloured, lighter below, about 10 mm wide, 20 mm long. **Seeds** reniform, brown, shiny, reticulate, 1.4 mm long, 1 mm wide, hilum on the side below the tip, prominent like an edge, micropyle apical, a little distance from the hilum.

Type locality: In the State San Luis Potosí, northeast of the city of Rio Verde, in the mountains near Rio Verde–San Francisco–Estacion Las Tablas on a hill ridge near bushes and low wood in dry stony soil.

Distribution: Mexico: southeast of the State of San Luis Potosí and adjacent regions of Tamaulipas.

Habitat: Gravel slopes and plains.

Locations checked: Mexico: San Luis Potosí: Angostura, La Gavia, Villa Juárez. Tamaulipas: south of Tula.

Incidence: Least concern.

Differentiation: *C. vaupeliana* (5.): has 8 and 13 tubercle-series, only 3–4 (or less) central spines, tubercles not round, but rounded keeled.

Illustrations: Distribution see Plate 9, map 2; plant portrait see Plate 18, photos 1 and 2.

5. *Coryphantha vaupeliana* Bödeker

Zeitschr. Sukk.-Kunde 3: 206, 1928

Lectotype: Illus. Bödeker l.c. (Dicht & A. Lüthy Cact. Syst. Init. 11: 11, 2001).

Synonym: *Coryphantha daemenoceras Jau-mavei* Fric, Möllers Dtsch. Gartenz. 23: 6, 1925–26, *nom. nud.*

Body solitary or clustering, globose to egg-shaped, up to 7 cm diameter, dull bluish-green, with a thickened taproot and a thinner neck, apex depressed, with connivent spines and a little wool. **Tubercles** in 8 and 13 series, loosely arranged, with 3 edges to nearly conical, with obtuse, oblique tip, porrect, on the lower part a somewhat rounded keel edge, on the upper part more flattened, 16 mm wide, 11 mm high, length of upper surface 8 mm, of lower surface 20 mm, sharp groove naked to slightly woolly, with red, woolly nectary gland near the axil. **Axil** naked to slightly woolly. **Areoles** slightly below the tubercle tip, directed outwards, round, 3 mm diameter, in youth white-woolly. **Radial spines** 12–15, the lower and lateral 8–9 horizontal, radiating, straight to somewhat curved to the body, firm, needle-like, thickened at the base, 8–10 mm long, horn-coloured with brown tips, the upper ones in two layers, bundled, thinner, stiff needle-like, longer, up to 15 mm long, dirty white with brown tips. **Central spines** 4, among them 3 dominant porrect, curved, one downwards, 2 to the sides, subulate, thickened at the base, 13–18 mm long, brown, later horn-coloured with darker tips, the fourth, uppermost, somewhat thinner, less spreading and curved, shorter. **Flower** 5.5 cm diameter, outer perianth segments broad lanceolate, acute, light yellow with green-brown midstripe of 3–4 mm width, inner perianth segments broad lanceolate, acute, slightly fimbriate towards the tip, 30 mm long, shiny light yellow, flower salmon-coloured when fading. Filaments yellow with a reddish tinge, anthers yellow, style yellow with 9 yellow stigma lobes, sweet fragrance. **Fruit** clavate, 16 mm long, 9 mm wide, juicy, green, lighter at the base. **Seeds** reniform, dark brown, shiny, reticulate, 1.5 mm long, 0.8 mm wide.

Distribution: Mexico: Tamaulipas near Jau-mave.

Habitat: Under bushes in sandy-gravelly alluvial soils near the river.

Locations checked: Mexico: Tamaulipas: San Vicente, San Antonio, Palmillas.

Incidence: Least concern.

Differentiation: *Coryphantha wohlschlagerei* (4.): has tubercles in 5 and 8 series, mostly 5–7 central spines and rounder tubercles.

Illustrations: Distribution see Plate 9, map 2; plant portrait see Plate 18, photos 3 and 4.

6. *Coryphantha glanduligera* (Otto) Lemaire Cactées 34, 1868

Basionym: *Mammillaria glanduligera* Otto (in Dietrich), Allg. Gartenz. 16: 298, 1848.

Neotype: Illus. Monatsschr. DKG 1(10): 191, 1929 (Dicht, Kakt. and. Sukk. 48(10): 221, 1997).

Synonyms: *Echinocactus glanduligerus* (Otto) Poselger, Allg. Gartenz. 21: 102, 1853; *Cactus glanduliger* (Otto) Kuntze, Rev. Gen. Pl. 1: 260, 1891; *Coryphantha bergeriana* Bödeker, Monatsschr. DKG 1(10): 191, 1929.

Body solitary, inverted egg-shaped to short clavate, up to 6 cm diameter and 12 cm high, dull dark leaf-green. Apex somewhat depressed, over-towered by a tuft of conivent spines, radial spines mainly, tuberous root with narrow neck. **Tubercles** in 8 and 13 series, loosely arranged, conical, slightly concave, with four edges at the base, 12 mm high, 14 mm wide, length on the upper surface 10 mm, on the lower surface 12 mm, with a naked groove on the upper part and 1–2 red, white-woolly surrounded glands. **Axils** in youth white-woolly, later naked, with 1–2 red glands. **Areoles** oval, 3 mm long, 2 mm wide, slightly woolly initially, later naked. **Radial spines** 17–20, spreading horizontally, stiff needle-like, slightly curved to the body, lower and lateral ones radiating, 10–12 mm long, upper 6–8 bundled in two layers, up to 16 mm long, all yellowish, upper ones often lighter with dark tips. **Central spines** 4, the dominant one straight, porrect, slightly curved downwards, subulate, stiff, 18–20 mm long, the 3 upper ones diverging and slightly spreading,

straight, somewhat thinner and shorter, all yellow-brown with darker tips. **Flower** enlarged funnelform, about 4 cm long and 7 cm maximum diameter, outer perianth segments linear-lanceolate, margins entire, slender and acute, about 2–3 cm long and 3 mm wide, olive-green with yellowish margin. Intermediate layer of perianth segments a little bit longer and broader, same shape, but mucronate, light yellow with brownish dorsal midstripe, inner perianth segments of same length and width, at the base narrower, margins entire, acute, of a pure yellow, filaments yellowish-white, anthers dark yellow, style light yellow with 7–12 expanded, whitish-yellow stigma lobes of about 3 mm length, sweet fragrance. **Fruit** light-green, juicy berry, longish, about 20 mm long, 8 mm wide. **Seeds** reniform, shiny, reticulate, dark brown, 1.3 mm long, 0.7 mm wide.

Distribution: Mexico: In the southwest of Nuevo León and in the adjacent regions of the neighbouring states of San Luis Potosí and Tamaulipas.

Habitat: Hills with calcareous gravel on slopes, sometimes protected by bushes, Agaves or Opuntias.

Locations checked: Mexico: Nuevo León: Nueva Primavera, Ascension-Sandia, Jesus Maria de Aguirre, La Zorra, Salinas del Refugio, north of Dr. Arroyo, El Milagro, Los Pocitos, San Francisco, La Escondida, Mier y Noriega, Sierra las Vaillas. San Luis Potosí: north of Matehuala, El Fraile, Tinaja, Matehuala-Dr. Arroyo, Cedral, Cuatro Milpas. Tamaulipas: La Tapona.

Incidence: Least concern.

Development: seedlings clavate/short columnar, about 3–4 times as high as wide.

Differentiation: *C. echinoidea* (7.): see comparison table in the Appendix.

Comments: The first description, written by OTTO (1848), appeared in an article of Dietrich entitled *Beiträge zur Kakteenkunde* in the Allgemeine Gartenzeitung as *Mammillaria glanduligera* (the incorrect spelling

“*granduligera*” being obviously a misprint). It was supplemented by SALM-DYCK (1850) and reprinted by LABOURET (1858) and FÖRSTER-RÜMPLER (1886) with few modifications. POSELGER (1853) renamed this species *Echinocactus glanduligerus* and LEMAIRE (1868) in *Cactées* made the new combination *Coryphantha glanduligera*.

As QUEHL (1913b) wrote, *Mammillaria glanduligera* had disappeared from all collections when SCHUMANN (1898) had his “Gesamtbeschreibung” in process; this explains why Schumann mentioned the name only without adding any comment or judgment.

After the first description of *Mammillaria echinoidea* by QUEHL (1913a), there was a long discussion in the *Monatsschrift für Kakteenkunde* between QUEHL (1913b, 1914) and E. WEIDLICH (1913, 1914), who regarded the newly described *Mammillaria echinoidea* as a new description of *Coryphantha glanduligera*.

After the appearance of BRITTON & ROSE’s *Cactaceae* (1923), where *Coryphantha glanduligera* was wrongly treated as a synonym of *Coryphantha exsudans*, the name disappeared from cactus literature or was used in the sense of Britton & Rose only. In 1985, ZIMMERMAN resurrected the name *Coryphantha glanduligera*, but only as a synonym of *Coryphantha echinoidea*.

In 1929, BÖDEKER described *Coryphantha bergeriana*, but subsequently, there was no hint in the whole literature that *Coryphantha glanduligera* might be related to this species, or indeed identical to it.

However, new comparison analysis (DICHT 1997) showed that *Coryphantha bergeriana* BÖDEKER (1929) is only a younger synonym of *Coryphantha glanduligera*.

Remark: The flower anatomy and the sweet fragrance of *Coryphantha glanduligera* are very similar to that of *Coryphantha echinoidea*, its closest relative.

In the field putative natural hybrids between *C. glanduligera* and *C. vaupeliana* can be found in the Jaumave-valley (ZIMMERMAN 1985) and also between *C. glanduligera* and *C. echinoidea* to the north of Dr. Arroyo (Nuevo León) and near Mier y Noriega (Nuevo León) (own observations).

Illustrations: Distribution see Plate 9, map 2; plant portrait see Plate 19.

7. *Coryphantha echinoidea* (Quehl)

Britton & Rose

Cactaceae 4: 30, 1923

Basionym: *Mammillaria echinoidea* Quehl, *Monatsschr. Kakt.* 23: 42, 1913.

Lectotype: *Illus. Monatsschr. Kakt.* 23: 42, 1913 (Dicht & A. Lüthy, *Cact. Syst. Init.* 11: 11, 2001).

Body solitary, globose to egg-shaped, 5–6 cm wide and 4.5–6 cm high, dull green, apex topped by spines, with little wool, roots fibrous. **Tubercles** in 8 and 13 series, firstly conical, slightly cut, in later years flattened, becoming rhomboid at the base, 10 mm high, 11 mm wide, length on the upper surface 9 mm, on lower surface 13 mm, top side groove with up to 5 red, woolly glands. **Axils** woolly in youth, later naked, with at least 1 red gland. **Areoles** elliptical, 3 mm long, 2 mm wide. **Radial spines** 20–24 interwoven, lower and lateral ones radiating, horizontal, straight or slightly curved to the body, needle-like, 8–10 mm long, upper 7–9 in two layers, arranged in a bundle, straight or slightly curved to the body, needle-like, flexible, a bit thinner and longer, 12–14 mm, all white, later grey, with dark tips. **Central spines** 1–3, the dominant one porrect, slightly curved downwards, subulate, thickened at the base, 13–15 mm long, 2 others above it, spreading V-like, protruding less, slightly curved to the body, somewhat thinner and shorter, all horn-coloured to brown, darker towards the tips, later becoming grey. **Flower** funnellform, 5–6 cm wide and long, outer perianth segments broad lanceolate, acute, margins entire,

lemon-yellow with green-yellow midstripe on the reverse, inner perianth segments broad lanceolate, acute, margins entire, lemon-yellow, filaments pale greenish-white, reddish towards the base, anthers orange-yellow, style pale yellow-green, 9–10 cream-white stigma lobes 2–4 mm long, sweet fragrance. **Fruit** green, juicy berry with attached flower remnants, broad clavate, 15 mm long and 11 mm in diameter, light dull green to very pale-green at the base, attachment 2 mm in diameter. **Seeds** dark brown, reniform, shiny, 1.3 mm long and 0.8 mm wide.

Distribution: Mexico: San Luis Potosí. Following the first description in the east of the state of Durango, where until today no locations are known.

Habitat: Lower slopes of hills of limestone gravel.

Locations checked: Mexico: San Luis Potosí: Huizache, Monte de Caldera, Sta. Gertrudis, Sta. Teresa, Tulillo, Ventura.

Incidence: Least concern.

Development: seedlings globose, a single, porrect central spine forming at an age of about 3 years, afterwards a second central spine above the first and ultimately a third aside the second.

Differentiation: *C. glanduligera* (6.): see comparison table in the appendix.

Illustrations: Distribution see Plate 9, map 2; plant portrait see Plate 20.

I.C.b Series *Clavatae* Dicht & A. Lüthy

Cact. Syst. Init. 11: 11, 2001

Type: *Coryphantha clavata* (Scheideweiler) Backeberg

Definition: Areoles typical *Protomammillaria* type (ZIMMERMAN 1985). Cortex mucilaginous.

8. *Coryphantha octacantha* (De Candolle)

Britton & Rose

Cact. 4:30, 1923

Basionym: *Mammillaria octacantha* De Candolle, Mém. Mus. Hist. Nat. Paris 17: 113, 1828.

Type: not designated.

Synonym: *Cactus octacanthus* (De Candolle) Kuntze, Rev. Gen. Pl.1:261, 1891; *Mammillaria leucacantha* De Candolle, Mém. Mus. Hist. Nat. Paris 17: 113 1828; *Mammillaria exsudans* Zuccharini ex Pfeiffer, Enum. Cact. 15, 1837; *Aulacothele exsudans* (Zuccharini) Monville, Cat. Pl. Exot., 21, 1846; *Coryphantha exsudans* (Zuccharini) Lemaire ex Rümpler, Handb. Cact. ed.2: 395, 1885; *Cactus exsudans* (Zuccharini) Kuntze, Rev. Gen. Pl. 1: 260, 1891; *Mammillaria curvata* Pfeiffer, Enum. Cact. 15, 1837; *Mammillaria lehmanni* Pfeiffer, Enum. Cact. 15, 1837; *Aulacothele lehmannii* (Otto) Monville, Cat. Pl. Exot., 21, 1846; *Coryphantha lehmannii* (Pfeiffer) Lemaire, Cactées 34, 1868; *Cactus lehmannii* (Pfeiffer) Kuntze, Rev. Gen. Pl.1: 260, 1891; *Mammillaria macrothele* Martius ex Pfeiffer, Enum. Cact 24, 1837; *Echinocactus macrothele* (Martius) Poselger, Allg. Gartenz. 21: 125, 1853; *Mammillaria macrothele lehmanni* Salm-Dyck, Cact. Hort. Dyck 1849: 19, 1850; *Echinocactus macrothele lehmanni* (Salm-Dyck) Poselger, Allg. Gartenz. 21: 125, 1853; *Mammillaria macrothele biglandulosa* Salm-Dyck, Cact. Hort. Dyck 1849: 19, 1850; *Echinocactus macrothele biglandulosus* (Salm-Dyck) Poselger, Allg. Gartenz. 21: 125, 1853; *Cactus macrothele* (Martius) Kuntze, Rev. Gen. Pl. 1: 260, 1891; *Coryphantha macrothele* (Martius ex Pfeiffer) Kümmler, AfM 22(2): 109, 1998; *Mammillaria plaschnickii* Otto ex Pfeiffer, Enum. Cact. 24, 1837; *Aulacothele plaschnickii* (Otto) Monville, Cat. Pl. Exot., 21, 1846; *Mammillaria plaschnickii straminea* Salm-Dyck, Cact. Hort. Dyck 1849: 19, 1850; *Echinocactus plaschnickii* (Otto) Poselger, Allg. Gartenz. 21: 125, 1853; *Cactus plaschnickii* (Otto) Kuntze, Rev. Gen. Pl.1: 261, 1891; *Mammillaria brevimamma* Zuccharini ex Pfeiffer, Enum. Cact. 34, 1837; *Echinocactus brevimammus* (Zuccharini ex Pfeiffer) Poselger, Allg. Gartenz. 21: 102, 1853; *Mammillaria brevimamma exsudans* Salm-Dyck, Cact. Hort. Dyck 1849: 19, 1850; *Coryphantha brevimamma* (Zuccha-

rini) Lemaire ex Rümpler, Handb. Cact. ed.2: 394, 1885; *Cactus brevimmammus* (Zuccharini) Kuntze, Rev. Gen. Pl. 1: 260, 1891; *Mammillaria aulacothele* Lemaire, Cact. Aliq. Nov. 8, 1838; *Coryphantha aulacothele* (Lemaire) Lemaire, Cactées 34, 1868; *Mammillaria aulacothele multispina* Scheidw., Bull. Acad. Sci. Brux. 6:92, 1839; *Mammillaria aulacothele spinosior* Monville ex Lem., Cact. Gen. Nov. Sp. 93, 1839; *Mammillaria aulacothele sulcimamma* Pfeiffer in Walpers, Bot. Repert. 2: 302, 1843; *Mammillaria aulacothele flavispina* Salm-Dyck, Cact. Hort. Dyck.1844: 13, 1845; *Cactus aulacothele* (Lemaire) Kuntze, Rev. Gen. Pl. 1: 260, 1891; *Mammillaria biglandulosa* Pfeiffer, Allg. Gartenz. 6:274, 1838; *Aulacothele biglandulosa* (Pfeiffer) Monville, Cat. Pl. Exot., 21, 1846; *Cactus biglandulosus* (Pfeiffer) Kuntze, Rev. Gen. Pl. 1: 260, 1891; *Mammillaria sulcimamma* Pfeiffer, Allg. Gartenz. 6: 274, 1838; *Mammillaria lehmanni sulcimamma* Miquel, Linnaea 12: 9, 1838; *Aulacothele sulcimamma* (Pfeiffer) Monville, Cat. Pl. Exot., 21, 1846; *Mammillaria martiana* Pfeiffer, Linnaea 12: 140, 1838; *Cactus martianus* (Pfeiffer) Kuntze, Rev. Gen. Pl.1: 261, 1891; *Mammillaria thelocamptos* Lehmann, Linnaea, 13: 101, 1839; *Mammillaria clava* Pfeiffer, Allg. Gartenz. 8: 282, 1840; *Echinocactus clavus* (Pfeiffer) Poselger, Allg. Gartenz. 21:125, 1853; *Aulacothele clava* (Pfeiffer) Monville, Cat. Pl. Exot., 21, 1846; *Coryphantha clava* (Pfeiffer) Lemaire, Cactées 34, 1868; *Cactus clavus* (Pfeiffer) Kuntze, Rev. Gen. Pl. 1: 260, 1891; *Mammillaria schlehtendalii* Ehrenberg, Linnaea 14: 377, 1840; *Aulacothele schlehtendalii* (Ehrenberg) Monville, Cat. Pl. Exot., 21, 1846; *Echinocactus schlehtendalii* (Ehrenberg) Poselger, Allg. Gartenz.21: 125, 1853; *Coryphantha schlehtendalii* (Ehrenberg) Lemaire, Cactées 34, 1868; *Mammillaria schlehtendalii levior* Salm-Dyck, Cact. Hort. Dyck 1849: 127, 1850; *Cactus schlehtendalii* (Ehrenberg) Kuntze, Rev. Gen. Pl. 1: 261, 1891; *Coryphantha clava* var. *schlechtendalii* (Ehrenberg) Heinrich ex

Backeberg, Cactaceae 5: 3040, 1961; *Mammillaria polymorpha* Scheer ex Muehlenpfordt, Allg. Gartenz. 14: 373, 1846; *Mammillaria glanduligera* Otto et Dietr.1848 sensu Britton & Rose, Cactaceae 4: 31, 1923; *Echinocactus glanduligerus* Poselger 1853 sensu Britton & Rose, Cactaceae 4: 31, 1923; *Coryphantha glanduligera* Lemaire 1868 sensu Britton & Rose, Cactaceae 4: 31, 1923; *Cactus glanduliger* Kuntze, Rev. Gen.Pl. 1: 260, 1891 sensu Britton & Rose, Cactaceae 4: 31, 1923; *Mammillaria asterias* Cels ex Salm-Dyck 1850 sensu Britton & Rose, Cactaceae 4: 31, 1923.

Solitary or group-forming, **body** clavate to cylindrical, columnar, up to 50 cm high and 10 cm diameter, dark green, apex slightly depressed with sparse yellowish-white wool. **Tubercles** in 5 and 8 spirals, conical, lower part keeled, often concave lateral parts, upside flattened, nearly 3-edged at the base, towards the top more rounded, obliquely cut, directed outwards and upwards, upper surface 18–25 mm long, lower surface 20–30 mm, at the base 12–18 mm wide, in the grooves, axils or near the areoles with 1–4 red glands with a white, felty border. **Axils** with up to 4 red glands, young with white wool. **Areoles** round, 4 mm diameter, young with white wool. **Radial spines** 7–10, irregularly horizontally radiating or slightly protruding, lower ones shorter, 5–10 mm, upper ones longer, 10–15 mm, first all honey-yellow, then lower ones lighter, often with brown tips, upper ones darker, needle-like, straight. **Central spines** 1–3, longer and stronger, the lower one the longest and strongest up to 25 mm (sometimes 40 mm) long, straight, porrect, thickened at the base, solid, needle-like, upper 1–2 obliquely upwards, up to 18 mm long, all light brown, red-brown or dark brown, then grey with dark tips. **Flowers** 3 cm long, 7 cm diameter, floral tube light green, outer perianth segments lanceolate, 7 mm wide, 26 mm long, yellowish-green with reddish midstripe, inner perianth segments linear-oblong, acute, yellow. Filaments reddish, anthers yolk-yel-

low, style yellowish, stigma lobes 8 mm long, yellow, 6–7 or more. **Fruit** green juicy berry, 20–25 mm long, 10 mm wide, attached dried perianth segments. **Seeds** hazel-brown, 1.8 mm long, 1.2 mm wide, reticulate, reniform.

Distribution: Mexico: Hidalgo and Querétaro, and rarely in San Luis Potosí and Tamaulipas.

Habitat: Limestone gravel, alluvial soil on ridges and foothills.

Locations checked: Mexico: Hidalgo: Pachuca, Actopan-Ixmiquilpan, Patria Nueva, San Francisco, Ixmiquilpan, San Pablo Tetlapayac, San Cristobal. Querétaro: Vista Hermosa, Altamira, Cerro Prieto, Tolantongo. San Luis Potosí: Alaquines. Tamaulipas: José María Morelos.

Incidence: Least concern.

Differentiation: *C. clavata* (10.) and *C. georgii* (16.): see comparison table in the Appendix.

Comments: There is no other species of the genus with as many synonyms as this. In its relatively wide range this species, with its imposing groups, is one of the most striking cacti and, therefore, it was collected and sent to Europe very early. Obviously, there were also many young plants among them which are more sparsely spined than adult plants and thus gave rise to several new descriptions.

The first description, which allows us to identify this species, clearly is *Mammillaria macrothele* Martius ex Pfeiffer 1837. However, Britton & Rose preferred the older basionym *Mammillaria octacantha* De Candolle 1828. Under this name, De Candolle had described a not yet fully developed young plant, a description which does not contradict this species, but would also fit others like e.g., *Coryphantha clavata* (Scheidweiler) Backeberg.

This procedure of Britton & Rose is strengthened by the fact that *Mammillaria octacantha* De Candolle was regarded in the whole important cactus literature of the

twentieth century as identical to all the other synonyms mentioned, of which mainly *Mammillaria lehmannii*, *macrothele*, *plaschnickii* and *aulacothele* were widespread. However, no author mentioned it under *Mammillaria clavata* or its synonym *Mammillaria raphidacantha*. Another circumstance which affirms *Mammillaria octacantha* as the basionym of this species is the fact that it had been collected by Thomas Coulter, who worked at Mineral del Monte and Zimapan, which means in the centre of its range, as number 39 and was sent to De Candolle in Geneva. Among all Coulter's plants described by De Candolle, there is none that fits *Coryphantha octacantha*, and it can be assumed that Coulter would not have overlooked such a dominating species.

In 1840, PFEIFFER described another, as he writes himself, "species of the group *M. octacantha*, *macrothele*, *lehmannii* etc. sent from Mexico by Mr. Ehrenberg" as *Mammillaria clava*. *Coryphantha clava* (Pfeiffer) Lemaire continues to exist in the whole cactus literature until today, although its description does not show any differences to the ones of the complex around *M. octacantha*, *macrothele*, *lehmannii* etc., although the reported range of all these species is identical. Schumann kept *Mammillaria macrothele* and *Mammillaria clava* as valid species, Britton & Rose, Backeberg and Bravo *Coryphantha octacantha* and *Coryphantha clava*. We think that there are no differentiating criteria to maintain two species of this complex. Therefore, *Mammillaria octacantha* De Candolle remains the valid basionym and *Coryphantha octacantha* (De Candolle) Britton & Rose the valid combination under inclusion of *Coryphantha clava* (Pfeiffer) Lemaire as a younger taxonomical synonym.

Compared to other *Coryphanthas*, *Coryphantha octacantha* does not show a greater variety. Of course, in the case of large-growing species their micro-location is more important and leads to a certain range con-

cerning growth form and spine number. However, the distribution of this species is clearly defined and continuous and even the most extreme local forms find a place in our given description. The great number of descriptions of this species from the last century is especially surprising, however, this could mainly be due to the density of its range in a region from where especially many plants came to Europe.

Illustrations: Distribution see Plate 10, map 1; plant portrait see Plate 21.

9. *Coryphantha jalpanensis* Buchenau
Cact. Suc. Mex. 10: 36, 1965

Type: Mexico, Querétaro, in the cerros around Jalpan, 1350 m, Buchenau s.n. (MEXU).

Body branching at the base, forming groups of up to 25 cm diameter, single heads cylindrical up to 15 cm high and 5–6 cm diameter, dull green, apex impressed, few wool. **Tubercles** in 5 and 8 series, cylindrical-conical, somewhat flattened on top, bulging below, ascending, at the base 10–12 mm wide, 9–10 mm high, upper surface 7 mm long. Grooves only on tubercles of older main sprouts, with grey-white felt and 1–2 orange glands. **Axils** with white wool and 1 orange, sometimes red gland. **Areoles** round, 1 mm diameter, in oblique or vertical position below the tip of the tubercle, in youth with white wool, then naked. **Radial spines** 10–12, 6–10 mm long, radiating horizontally, needle-like, somewhat thickened at the base, white with dark tips. **Central spines** 1–3, one of them dominating, 10–17 mm long, porrect, pointing downwards, two others on the sides, upwards, 6–10 mm long, all straight, thickened at the base, brown, then grey, dark-tipped. **Flowers** 4–4.5 cm long and 3–4.5 cm wide, appearing from April to June. Floral tube naked, green, 8 mm long and 5 mm diameter, paler below. Outer perianth segments lanceolate, acute, the lower ones shorter, light yellow with greenish-red centre and tips; inner perianth segments 7 mm wide,

broad lanceolate, fimbriate towards the tip, purely pale yellow. Filaments pale yellow, somewhat reddish, anthers intensely yellow, style pale green to yellowish, 6–7 stigma lobes of 4–5 mm length, pale yellow. **Fruit** juicy berry, upper part olive-green, pale-green below, with dried perianth segments attached, 15–20 mm long and 10–12 mm diameter, appears in October/November. **Seeds** reniform, reticulate, 1.5–1.7 mm long and 1 mm wide, hazel-brown.

Type locality: Hills near Jalpan QRO, at 1350 m above sealevel.

Distribution: Mexico: Querétaro and adjacent regions of San Luis Potosí.

Habitat: On limestone rocks on pastures and in forests in organic material in grooves.

Locations checked: Mexico: Querétaro: Jalpán, Mazcazintla, Landa de Matamoros. San Luis Potosí: Rio Verde-Jalpán km 45, Rayón.

Incidence: Least concern.

Differentiation: *C. glassii* (11.): see comparison table in the appendix.

Illustrations: Distribution see Plate 10, map 1; plant portrait see Plate 22.

10 a. *Coryphantha clavata* subsp. *clavata*
(Scheidweiler) Backeberg

Jahrb. Deutsch. Kakt. Ges. 1941 (2): 61, 1942

Basionym: *Mammillaria clavata* Scheidweiler, Bull. Acad. Sci. Brux. 5: 494, 1838.

Neotype: Mexico, San Luis Potosí, Sierra de Alvarez, Municipio de Villa de Zaragoza, Francisco Rene Sanchez Barra 178 (SLPM 26217).

Synonyms: *Neolloydia clavata* (Scheidw.) Britton & Rose, Cactaceae 4: 15, 1923; *Coryphantha clavata ancistracantha* Marshall, Cact. Succ. J. (US) 19: 10, 1947; *Mammillaria raphidacantha* Lemaire, Cact. Gen. Nov. Spec. 36, 1839; *Aulacothele raphidacantha* (Lemaire) Monville, Cat. Pl. Exot., 21, 1846; *Mammillaria scolymoides raphidacantha* Salm-Dyck, Cact. Hort. Dyck. 1849: 128, 1850; *Echinocactus corniferus raphidacanthus*

Poselger, Allg. Gartenz. 21: 102, 1853; *Coryphantha raphidacantha* (Lemaire) Lemaire, Cactées 34, 1864; *Cactus raphidacanthus* (Lemaire) Kuntze, Rev. Gen. Pl. 1: 261, 1891; *Mammillaria sulcoglandulifera* Jacobi, Allg. Gartenz. 24: 62, 1856; *Cactus maculatus* Coulter, Contr. U.S. Nat. Herb. 3: 117, 1894; *Mammillaria maculata* (Coulter) Vaupel, Monats. Kakt. 56, 1920; *Cactus brunneus* Coulter, Contr. U.S. Nat. Herb. 3: 117, 1894; *Mammillaria brunnea* (Coulter) Vaupel, Monats. Kakt. 56, 1920; *Mammillaria radican-tissima* Quehl, Monatsschr. Kakt. 22: 164, 1912; *Coryphantha unicornis* Bödeker, Zeitschr. Sukk. Kunde 3: 205, 1928. *Coryphantha clavata* var. *radican-tissima* (Quehl) Heinrich ex Backeberg, Cactaceae 5: 2995, 1961.

Body solitary, first globose, then clavate-cylindrical to short columnar, up to 30 cm long and 9 cm diameter, greyish-green, apex woolly, covered by spines. Taproot. **Tubercles** in 5 and 8 or 8 and 13 series, oblique, conical, rounded, flattened on top, length on upper surface 8–12 mm, on lower surface 10–14 mm, one or several red glands in the groove, which is woolly in youth. **Axils** with red gland, in youth woolly. **Areoles** round, 3 mm diameter, in youth with whitish wool. **Radial spines** 8–12, 8–14 mm long, regularly radiating, somewhat protruding, straight, stiff needle-like, whitish, some black from the top. **Central spine** 1, 17–25 mm long, straight, porrect, stronger than radials, thin subulate, dark brown to black, then greyish. Sometimes with 1–2 additional, needle-like central spines of 10 mm length, straight, directed upward and slightly spreading. **Flowers** relatively small, 25–30 mm long, 20–30 mm diameter, whitish-yellow, floral tube naked, outer perianth segments lanceolate, up to 12 mm long, 3.5 mm wide, light yellow with a broad, reddish midstripe, tips red, inner perianth segments narrow lanceolate, to 2 mm wide, inside light yellow to cream-white, outside with a weak purple-red midstripe, filaments yellowish below, upwards

reddish, numerous, irritable, much shorter than perianth segments, anthers yellow, style yellow, on top slightly rose with 5–6 greenish-yellow stigma lobes. **Fruit** first juicy, green, 10 mm long and 5 mm wide, then dries fast, reddish-brown, parchment-like skin, with dried perianth segments attached. **Seeds** 1.4 mm long, 0.8 mm wide, brown, reniform, reticulate.

Juvenile forms: As a young seedling the plant grows thin-columnar and has a taproot. The central spine is absent, there are radial spines of pure white colour only. Seldom flowering before appearance of a central spine.

Distribution: Mexico: San Luis Potosí, Zacatecas, Querétaro and Guanajuato.

Habitat: On lower slopes of limestone hills, often under bushes.

Locations checked: Mexico: San Luis Potosí: Balneario Lourdes, San Anton Martinez, south of Rio Verde, Tolosa, San Luis Potosí Aguascalientes km 28, Villa de Zaragoza. Guanajuato: Cañada Moreno, Queretaro-SLP (km 104), junction San Luis de la Paz-Xichu, San Luis de la Paz-Xichu (km 28), km 110 north-east of San Felipe Torres Rochas, Jofre.

Incidence: Least concern.

Differentiation: *C. octacantha* (8.) and *C. georgii* (16.): see comparison table in the Appendix.

Comments: The first description is very short, but unequivocal all the same because of the characteristics: 1 central spine, 10 radial spines, red glands.

Illustrations: Distribution see Plate 10, map 1; plant portrait see Plate 23, photos 1 and 3.

10 b. *Coryphantha clavata* subsp. *stipitata* (Scheidweiler) Dicht & A. Lüthy

Cact. Syst. Init. 11: 12, 2001.

Basionym: *Mammillaria stipitata* Scheidw., Bull. Acad. Sci. Brux. 5: 495, 1838.

Neotype: Mexico, San Luis Potosí, Municipio de San Luis Potosí, northwest of La Amapola, Rosa Elia Hernandez 282 (SLPM 19396).

Synonyms: *Mammillaria ancistracantha* Lemaire, Cact. Gen. Nov. Sp. 36, 1839; *Aulacothele raphidacantha ancistracantha* (Lemaire) Monville, Cat. Pl. Exot., 21, 1846; *Coryphantha ancistracantha* (Lemaire) Lemaire, Cactées 34, 1864; *Cactus ancistracanthus* (Lemaire) Kuntze, Rev. Gen. Pl. 1: 261, 1891; *Mammillaria raphidacantha humilior* Salm-Dyck ex Förster, Handb. Cact. 244, 1846; *Mammillaria raphidacantha ancistracantha* Schumann, Gesamtb. Kakt. 506, 1898; *Coryphantha clavata* var. *ancistracantha* (Lemaire) Heinrich ex Backeberg, Cactaceae 5: 2995, 1961; *Coryphantha raphidacantha ancistracantha* (Schumann) Ito, 1952.

Shows 1 (rarely –4 !) central always with a hooked tip. The flowers are nearly white and slightly larger (30–35 mm diameter) than in ssp. *clavata*. All the other characteristics are identical to ssp. *clavata*.

Distribution: Mexico: Zacatecas, Guanajuato and Jalisco, mainly around Lagos de Moreno JAL

Habitat: On lower slopes of volcanic hills under bushes, agaves and hechtias.

Locations checked: Mexico: Zacatecas: Villa Garcia, Milagros. Jalisco: Lagos de Moreno. San Luis Potosí: Ojuelos, La Amapola.

Incidence: Least concern.

Comments: Was first described by SCHEIDWEILER (1838) as *Mammillaria stipitata*, one year later by Lemaire as *Mammillaria raphidacantha* and also as *Mammillaria ancistracantha*.

The distribution areas of ssp. *clavata* and of ssp. *stipitata* are always disjunct, they occur nowhere together.

Illustrations: Distribution see Plate 10, map 1; plant portrait see Plate 23, photo 2.

11. *Coryphantha glassii* Dicht & A. Lüthy
Kakt. and. Sukk. 51 (1): 1, 2000.

Type: Mexico, San Luis Potosí, Sanguijuela, Alberto Arredondo 527 (SLPM 28287).

Forming large groups of up to 50 cm diameter by stolons, single heads columnar, up to 30 cm

high, 6 cm diameter, linden-green, apex flat, with very little wool, narrow root-neck proceeding into a taproot with fibrous ramifications. **Tubercles** in 5 and 8 series, loosely arranged, cylindrical-conical, keeled, ascending, at the base 6 mm wide, 14 mm high, upper surface 9 mm long, lower surface 20 mm long, upper side, except in new growth, descending towards the tip or at most horizontal, grooves on tubercles of older main sprouts only, with felt and glands near the areoles. **Axils** with very few wool in youth only, with a yellow-orange gland, surrounded by white wool and very exposed due to the position of the tubercles. **Areoles** round, 1.5 mm diameter, young with much woolly felt. **Radial spines** 10–13; 10–11 lower and lateral ones of them radiating, slightly protruding, lower ones 8 mm long, laterals 7 mm, all needle-like, yellowish-white, often with white dots, upper 1–2 longer, thin, needle-like, straight, 12 mm long, nearly white. **Central spines** 2–3, one of them dominating, straight, porrect, pointing downwards, thick needle-like to subulate, 16–25 mm long, yellowish-brown to horn-coloured, with white dots, the others somewhat thinner, obliquely upwards, 11 mm long, yellowish-brown to horn-coloured. **Flowers** 3.5 cm long, 3 cm in diameter, flower-tube naked, light green. Outer perianth segments oblanceolate, apiculate, margins entire, light yellow with brown-red midstripe on the back. Inner perianth segments oblanceolate, margins entire, denticulate towards the tip, acute, light yellow. Filaments reddish-yellow, anthers yellow, style greenish-yellow, stigma lobes 5–7, yellow, 7 mm long. **Fruit** olive-green, juicy berry with attached dried perianth-segments, very small, 10 mm long, 8 mm wide. **Seeds** reniform, hazel-brown, 1.5 mm long and 1 mm wide.

Distribution: Mexico: Guanajuato and San Luis Potosí.

Habitat: Hills and mountains with calcareous gravel on slopes and tops.

Locations checked: Mexico: Guanajuato: in the region of Xichú. San Luis Potosí: near

Sanguijuela (type location) and San Ciro de Acosta.

Incidence: Least concern.

Differentiation: *C. jalpanensis* (9.): see comparison table in the Appendix.

Comments: The main differences to *Coryphantha jalpanensis* are pointed out in the comparison table (see Appendix) by bold-face letters, mainly:

Taproot, stolons, longer, columnar bodies, narrower, keeled, very loosely arranged tubercles with upper side descending or horizontal towards the tip (except in new growth), clearly visible axillary glands, yellow radial spines and yellowish, longer central spines and smaller fruits.

The growth of *Coryphantha glassii* with its thin columns is reminiscent of *Coryphantha erecta* (Lemaire) Lemaire, which does not have stolons or taproots, but has much smaller, more densely arranged tubercles with higher series, different spination and much larger flowers.

In the closer relationship of *Coryphantha glassii*, there is another species which makes large, columnar groups: *Coryphantha octacantha* (De Candolle) Br. & R. It differs by its much stronger body, the sparse spination, larger flowers and mainly by bigger, more angular tubercles and the missing stolons.

This species has the small, funnelform flowers and the taproot in common with *Coryphantha clavata* (Scheidweiler) Backeberg.

Illustrations: Distribution see Plate 10, map 1; plant portrait see Plate 24.

12. *Coryphantha erecta* (Lemaire) Lemaire
Cactées 34, 1869

Basionym: *Mammillaria erecta* Lemaire ex Pfeiffer, Allg. Gartenz. 5: 369, 1837.

Lectotype: Lemaire, Iconogr. descr. des Cactées, Part 2, t. 3, 1843 (Dicht & A. Lüthy, CSI 11: 13, 2001).

Synonyms: *Aulacothele erecta* (Lemaire) Monville, Cat. Pl. Exot., 21, 1846; *Cactus erectus* Kuntze, Rev. Gen. Pl. 1: 260, 1891;

Echinocactus erectus Poselger, Allg. Gartenz. 21: 126, 1853; *Mammillaria evanescens* Hort. Belg.; *Mammillaria ceratocentra* Berg, Allg. Gartenz. 8: 130, 1840; *Cactus ceratocentrus* (Berg) Kuntze, Rev. Gen. Pl. 1: 260, 1891.

Body cylindrical-columnar, upright, up to 50 cm high and 6–8 cm diameter, branching, forming big groups, apex with white wool, epidermis light-green. **Tubercles** in 8 and 13 or 13 and 21 series, oblique, conical, flattened on top, at the base rhomboid, upper surface 5–7 mm long, at the base 10 mm wide, 9 mm high, most with, some without grooves. **Axils** with white wool and brown glands. **Areoles** elliptical, 3 mm long, 2 mm wide, young with white wool. **Radial spines** 11–17, 8–12 mm long, needle-like, stiff, horizontally radiating, somewhat curved towards the body, yellow, somewhat transparent, interwoven. **Central spines** 0–4, the lower up to 20 mm long, curved downwards, upper ones oblique and slightly protruding, all of same colour as radials, later, darker yellow-brown. **Flowers** 6–7.5 cm diameter, yellow, outer perianth segments lanceolate, acute, narrow, pale yellow, inner perianth segments canary-yellow, greenish at the base, filaments yellow below, upper part reddish, anthers saffron-coloured. **Fruit** intensely green, lighter basally, small, 12 mm long, 8 mm wide. **Seeds** reniform, 1.8 mm long, 1.5 mm wide, hazel-brown, reticulate testa.

Distribution: Hidalgo, Querétaro, Guanajuato and San Luis Potosí.

Habitat: Slopes with calcareous gravel, some trees and agaves.

Locactions checked: Mexico: Hidalgo: Metztitlán. Querétaro: San Joaquín, Colón, Bucareli, Peña Miller, Rio Blanco, Vizarrón. Guanajuato: San Luis de la Paz, Mineral de Pozos, Atarjea, Cañada Morenos. San Luis Potosí: Rio Bagres, Rancho Santa Rita.

Incidence: Least concern.

Illustrations: Distribution see Plate 10, map 1; plant portrait see colour Plates 25 and 26.

13. *Coryphantha potosiana* (Jacobi)

Glass & Foster,

Cact. Succ. J. (US) 43(1): 7, 1971.

Basionym: *Mammillaria potosiana* Jacobi, Allg. Gartenz. 24: 92, 1856 (*non Mammillaria potosina* Britton & Rose, Cact. 4: 99, 1923).**Type:** not designated.

Body cylindrical to short columnar, up to 25 cm high and 8 cm diameter, dark grey-green with fine white dots. **Tubercles** in 13 and 21 series, small, 8 mm long, at the base 7 mm wide, conical, with complete groove with 2–3 yellow-orange glands. **Axils** woolly in youth, with yellow-orange gland. **Areoles** without central spine elliptical, 2 mm wide, 4 mm long, with central spine round, 3 mm diameter, all woolly in youth. **Radial spines** 15–18, 10–12 mm long, needle-like, whitish, yellowish at the base, brownish at the tip, irregularly radiating, interwoven, slightly curved backwards; rarely one **central spine**, straight, porrect, 8–15 mm long, yellowish, base and tip brownish. **Flowers** small, 22 mm long, 20 mm diameter. Outer perianth-segments lanceolate, 2 mm wide, 12 mm long, cream-coloured with large, purple-red mid-stripe. Inner perianth-segments broad lanceolate, margins entire, acute, 4 mm wide, pale yellow to cream-white, filaments reddish, with yellow anthers, style reddish with 6 greenish stigma lobes. **Fruit** dull green, then yellowish, small, 12 mm long, 6 mm diameter, juicy, wall thin. **Seeds** small, 1 mm diameter, light brown.

Distribution: San Luis Potosí.**Habitat:** Flat ridges of lava soil, nearly bare, plants around opuntias and agaves.**Location checked:** San Luis Potosí, near the highway 80 to Aguascalientes.**Incidence:** Least concern.**Differentiation:** Against *Coryphantha clavata* (Scheidweiler) Backeberg: *Coryphantha potosiana* gives a very densely spined impression, because the tubercles are more numerous (13 and 21 series), smaller and denser positioned, moreover, it has many more radial spines.

Another striking feature is the usually missing central spine and the longish, nearly pectinate areoles.

Illustrations: Distribution see Plate 10, map 1; plant portrait see Plate 27.**I.D. Section *Ottonis* Dicht & A. Lüthy**

Cact. Syst. Init. 11: 13, 2001

Type: *Coryphantha ottonis* (Pfeiffer) Lemaire.**Definition:** Areoles *Ortegocactus* type (ZIMMERMAN 1985, p. 61) with abrupt change to full length areolar grooves after a *Mammillaria*-like stage, flowering from areoles characteristic of either stage of development. Cortex mucilaginous.**14. *Coryphantha ottonis* (Pfeiffer) Lemaire**

Cactées 34, 1868

Basionym: *Mammillaria ottonis* Pfeiffer, Allg. Gartenz. 6: 274, 1838.**Type:** not designated.

Synonyms: *Aulacothele ottonis* (Pfeiffer) Monville, Cat. Pl. Exot., 21, 1846; *Echinocactus ottonianus* Poselger, Allg. Gartenz. 21:102, 1853; *Cactus ottonis* Kuntze, Rev. Gen. Pl. 1: 261, 1891; *Mammillaria asterias* Cels ex Salm-Dyck, Cact. Hort. Dyck. 1849: 129, 1850; *Coryphantha asterias* (Cels) Bödeker ex Berger, Kakteen 274, 1929; *Mammillaria bussleri* Mundt, Monatsschr. Kakt. 11: 47, 1902; *Coryphantha bussleri* (Mundt) Scheinvar, Phytologia 49: 3, 1981; *Mammillaria golziana* Haage, Monatsschr. Kakt. 19: 101, 1909; *Mammillaria guerkeana* Bödeker, Monatsschr. Kakt. 24: 53, 1914; *Coryphantha guerkeana* (Bödeker) Britton & Rose, Cact. 4: 29, 1923.

Body solitary, globose to short cylindrical, about 10–12 cm high and 8 cm diameter, dark grey-green, apex depressed, white wool present. **Tubercles** in 5 and 8 series, rounded, broad conical, 18 mm wide, 10 mm high, 10 mm long, groove complete, but sometimes even in adult floriferous plants not on all tubercles, woolly. **Axils** woolly, with red glands. **Areoles** round, 3 mm diameter, white-

woolly in youth. **Radial spines** 8–12, radiating, appressed to irregularly protruding, straight, needle-like, the upper ones somewhat thinner, 9–11 mm long, yellowish-white, tip brown, later grey. **Central spines** 1–3, rarely 4, arranged approximately in cruciform, the lower dominant, straight, porrect, subulate, 1 mm thick, sometimes at the tip curved downwards, nearly hooked, 15–18 mm long, 2–3 upper ones pointing upwards, slightly protruding, thinner, straight, 10–12 mm long, all yellowish-brown, later grey. **Flower** 5 cm diameter, outer perianth segments broad lanceolate, obtuse, with acute tips, on the outside dull brown-red with white margins, inside whitish, with dull brown-red midstripe; inner perianth segments broad lanceolate, with notched tips, pure white. Filaments yellow, anthers saffron-yellow, stigma lobes 10, cylindrical, erect, yellow. **Fruit** green juicy berry, small, roundish, 15 mm long, 10 mm wide. **Seeds** brown, reniform, 1.6 mm long, 0.8 mm wide.

Distribution: Mexico: Puebla, Tlaxcala, Mexico, Hidalgo, Querétaro, Guanajuato, Zacatecas and Durango.

Habitat: Pastures on flat lava soil, sometimes protected between bushes.

Locations checked: Mexico: Tlaxcala: 6 and 11 km west of Tlaxco. Mexico: east of Otumba. Guanajuato: Agustín Gonzales, Xoconoxtle. Zacatecas: El Salto, Monte Escobedo, Rancho Olguín, 48 km north of Cd. Zacatecas, Refugio de los Pozos. Durango: km 5 west of Cd. Durango.

Incidence: Least concern.

Comments: This species shows a wide range of distribution from Puebla to Durango. It also grows near the capital Mexico City and had therefore been collected and first described very early. Southeast of the distribution area (Puebla, Tlaxcala, Mexico, Hidalgo) forms with sparser spination and 1–2 central spines only can be found. These have been described as *Coryphantha asterias* and *Coryphantha bussleri*. However, the tran-

sition to the forms at the centre of distribution (Querétaro, Guanajuato) is continuous and results in more and more heavily spined forms in the northwest (Zacatecas). The latter have been described as *Coryphantha guerkeana* in Zacatecas and Durango.

The main characteristics of all these taxa, growth form, tubercle size and form, number of radial spines, flowers, fruits and seeds are all identical, as are the extrafloral nectary glands and the *Ortegocactus* areole type, the latter having been mentioned indirectly in the first description of *Mammillaria asterias* Cels (“without grooves”).

Illustrations: Distribution see Plate 10, map 2; plant portrait see Plate 28.

15. *Coryphantha vogtherriana*

Werdermann & Bödeker

Monatsschr. DKG 4: 32, 1932.

Lectotype: Illustration (Fig. 1) in first description as cited above (Dicht & A. Lüthy, CSI 11: 13, 2001)

Body usually solitary, later branching and forming groups of up to 30 cm diameter or more, with 15 or more heads. **Body** greyish-green, sometimes bluish, apex somewhat depressed with little wool, depressed-globose, 6–7 cm diameter, 4–5 cm height, in later years also up to 8 cm high, about one quarter of the body is hidden in the soil and grades into a tuberous root. **Tubercles** in 5 and 8 series, 10–14 mm high, up to 20 mm wide and 10–14 mm long, usually pyramidal, rounded in youth, then flatter, rhomboid, with flat surface parallel to the ground, the lower part somewhat bulging, all edges obliquely cut. Complete groove in old plants only, in pre-adult stage no grooves or only short grooves, but plants floriferous before appearance of the grooves, sometimes with a yellow gland at the groove end near the spiniferous areole. **Axils** with white wool, later naked, some with red glands. **Areoles** in youth with white felt, 2–3 mm diameter, slightly angled and descending. **Radial spines** 5–7, straight or

slightly curved to the side, somewhat curved to the body, radiating, upper ones somewhat closer to each other, 5–10 (–15) mm long, stiff, firm, needle-like, in youth whitish-horn-coloured to brown, later greyish-white, often with brown tips. **Central spine** 1, on older plants only, 5–20 mm long, stronger than the radial spines, directed downwards, straight to slightly downward curved, rarely hooked, thickened at the base, brown, soon greyish-white. **Flowers** up to 4 cm diameter, 3.5 cm long, with much wool at the flower-base, 24–34 perianth segments, up to 3 cm long, 2.5–4 mm wide, broad lanceolate, margins entire. Outer perianth-segments with a strong, dark red midstripe (up to 80% of the width). Inner perianth segments white, occasionally yellowish-white, sometimes with a faint pink-coloured midstripe and often with reddish tips. Stigma lobes 5–8, light yellow, anthers dark yellow, ovary small and oval. **Fruit** green juicy berry, very small, 8 mm long, 5 mm diameter, with much white wool at the base and attached flower remnants. **Seeds:** reniform, 1.2×0.8 mm, light brown, testa reticulate.

Distribution: Mexico: San Luis Potosí, near the city of San Luis Potosí.

Habitat: Loamy grasslands with rolling horse pastures crossed by red ditches formed by erosion, anthills often present. Associated cactus: *Mammillaria heyderi*.

Locations checked: Monte de Caldera, about 20 km northeast of the city of San Luis Potosí, Ventura, Fatima and San Antonio del Guia.

Incidence: Critically endangered by erosion and agriculture.

Herbarium specimen: WAF 2401, Monte de Caldera SLP, deposited in the herbarium G.B. Hinton under the number G.B. Hinton et al.27033.

Differentiation: *C. maiz-tablasensis* (27.): has no glands, no central spines, rounder tubercles.

Comments: After the first description of this species, it remained widely unknown and

apparently non-existent. In the whole cactus literature, only a summary of the first description in BACKEBERG (1961) and in BRAVO (1991) can be found.

It was only in the early 1990s that W.A. and Betty FitzMaurice first found plants near Monte de Caldera, about 20 km northeast of the city of San Luis Potosí, of which A. Zimmerman and also Charles Glass supposed that it might well be *Coryphantha vogtherriana*, whose origin was indicated by Bödeker as being “...in the vicinity of the city of San Luis Potosí in somewhat loamy soil at about 2000 m above sea level...”. Our studies at the locality confirmed this supposition. In turgid plants we could verify the presence of the red nectary glands and the mucilaginous cortex, all typical of many gland-bearing *Coryphanthas*. The illustrations with the first description had irritated us before, because they show two plants which were probably damaged during transportation.

This species reminds us of the glandless *Coryphantha maiz-tablasensis* Backeberg. In the first description, BACKEBERG (1949) mentioned a similarity to *Coryphantha vogtherriana*. However, it has a central spine and somewhat more edged, flattened tubercles. Concerning the tubercle groove, this species shows a particular phenomenon which is known in *Ortegocactus* and, within the genus *Coryphantha*, only for *Coryphantha ottonis* and *Coryphantha georgii*: even at flowering age the relatively large tubercles may occur without grooves or possess very short grooves only. The appearance of complete grooves usually occurs only in very old plants. This peculiarity was already mentioned by Werdermann and Bödeker in their first description.

Since the first description, there has been only one correct illustration of this species in literature, namely in PRESTON-MAFHAM (1991).

In cactus literature there is an older first description to be found which fits most aspects of the plants from Monte de Caldera:

Coryphantha cornuta (Hildmann ex SCHUMANN 1898) BERGER (1929). Unfortunately, there is no illustration of this species anywhere in the whole literature, although it has since be mentioned by most authors (BRITTON & ROSE 1923, SCHELLE 1926, BORG 1937, BACKEBERG 1961, BRAVO-HOLLIS 1991). Nevertheless, *Coryphantha cornuta* is described without nectary glands and the name-giving central spine is “curved downwards like a horn”. This spine form is rarely true for *Coryphantha vogtherriana* which usually has a straight or only slightly curved downward-pointing central spine. The discrepancy between these two characteristics precludes a neotypification of *Coryphantha cornuta* by the plants from Monte de Caldera. We think that *Coryphantha cornuta* corresponds to an extreme form of *Coryphantha cornifera* as it grows near Tolantongo in Hidalgo.

Illustrations: Distribution see Plate 10, map 2; plant portrait see Plate 29.

16. *Coryphantha georgii* Bödeker

Monatsschr. DKG 3: 163, 1931.

Lectotype: Illustration in first description as cited above (Dicht & A. Lüthy, CSI 11: 13, 2001).

Synonyms: *Coryphantha villarensis* Backeberg, Feddes Repert. 51: 64, 1942; *Coryphantha grata* Bremer, Cact. Succ. J. (US) 53: 276, 1981.

Body usually solitary, sometimes branching, globose to large clavate, about 13 cm high and 13 cm diameter, shiny dark leaf-green. Apex somewhat depressed, more or less white-woolly, topped by the central spines, which are nearly vertical here. **Tubercles** in 8 and 13 series, conical, oblique, rounded, edges cut, on the lower surface roundish, bulging, width at the base 16–26 mm, 12–15 mm high, length of the upper surface 12–18 mm, groove complete with orange gland near the areole. **Axils** in youth woolly, then naked, with orange-red gland. **Areoles** round, 4 mm diameter, in youth

white-woolly, soon completely naked. **Radial spines** 8–11, lower ones and the ones on both sides regularly arranged, horizontal, 17 mm long, needle-like, straight, dull grey to horn-coloured, upper ones closer to each other, and bundled into two layers, same length and form like the lower radials, but in young growth usually brown, then becoming grey with dark tips. **Central spines** 1 (–4), dominating one porrect, directed slightly downwards, straight to slightly downward curved, up to 28 mm long, robust, needle like, brown, later grey. Sometimes 1–3 additional central spines in the upper part of the areole, slightly spreading, needle like, straight, colour same as dominant spine, but half as long. **Flowers** numerous from the woolly top, about 40 mm long and 40 mm in diameter. Outer perianth segments linear, acute and tipped, 4 mm wide, carmine with yellowish-white margin, the lower ones green with reddish tip. Inner perianth segments broad lanceolate, acute, 8 mm wide, whitish-yellow, with a thin carmine mid-stripe dorsally, inside shiny. Filaments yellowish-white, anthers dark yellow, style 20 mm long, green-white below, with 5–7 greenish stigma lobes. **Fruit** green, juicy fruit, nearly round, 15 mm long, 10 mm wide with attached flower remnants. **Seeds** reniform, 2.1 mm long, 1.3 mm wide, brown, testa reticulate.

Distribution: Mexico: San Luis Potosí, Guanajuato and Tamaulipas.

Habitat: Lava soil on plains and slopes and in oak-forests.

Locations checked: Mexico: San Luis Potosí: Monte de Caldera, Estacion Villar, Rancho Hernandez, Realejos, Armadillo Infante, San Antonio de las Martinez, San José. Guanajuato: km 26 Cañada Morenos-Xichú, Cañada Morenos. Tamaulipas: west of Tula.

Incidence: Least concern.

Differentiation: *C. octacantha* (8.) and *C. clavata* (10.): see comparison table in the Appendix.

Comments: The first description is of a more globose form, as is usually found in sun-ex-

posed locations. The more clavate forms, which were described by BACKEBERG in 1942 as *Coryphantha villarensis*, grow throughout the whole range of distribution, mainly in the shade, especially under bushes. An examination of this species at two locations, particularly near Villar SLP, the type locality of *Coryphantha villarensis*, and near Álvarez, the type locality of *Coryphantha georgii* did not show any differences except for the growth form due to the micro-location. Our experiences in cultivation confirmed the identity of *Coryphantha georgii* and *Coryphantha villarensis*.

Youth form: Only 6 horizontally radiating radials, upper radials and central spines often with a sudden change of colour from brown to a chalky-white tip.

Illustrations: Distribution see Plate 10, map 2; plant portrait see Plate 29.

II. Subgenus *Coryphantha*

Type: *Coryphantha sulcata* (Engelmann) Britton & Rose (type of the genus).

Synonyms: *Mammillaria* Section *Aulacothelae* Salm-Dyck (syn. *Brachythelae* Pfeiffer, *Aulacothelae* Lemaire) in Walpers, Repert. bot. syst., Suppl. 1: 272, 1843; *Coryphantha* series *Sulcolanatae* Britton & Rose, Cact. 4: 24, 1923; *Coryphantha* series *Recurvatae* Br. & R. l.c. pro parte, tantum quoad typ. (Art. 22.6); *Coryphantha* series *Aulacothelae* (Lemaire) Bravo & Sánchez-Mejorada, Cact. Méx. 3: 431, 1991; *Escobrittonia* Doweld, Sukkulenty, 3 (1): 17, 2000, pro parte tantum quoad typ.

Definition: Areoles *Escobaria*-type (ZIMMERMAN 1985), flowering only from full-length narrow areolar grooves after a gradual sterile transition phase. Grooves and axils without nectary glands, except for optional glands close to the spiniferous (abaxial) part of the areole. Seeds reniform or globose. Fruits juicy, green. Cortex watery.

II.A Section *Coryphantha*

Type: *Coryphantha sulcata* (Engelmann) Britton & Rose (Lectotype of the genus).

Definition: Fruits juicy, green. Seeds reniform.

II.A.a Series *Retusae* Dicht & A. Lüthy

Cact. Syst. Init. 11: 14, 2001

Type: *Coryphantha elephantidens* (Lemaire) Lemaire.

Definition: Radial spines mostly subulate.

17 a. *Coryphantha elephantidens* (Lemaire) Lemaire subsp. *elephantidens*

Cactées 35, 1868

Basionym: *Mammillaria elephantidens* Lemaire, Cact. Aliq. Nov. 1, 1838.

Lectotype: Lemaire, Iconogr. descr. des Cactées, Part 5, t. 9, 1841 (Dicht & A. Lüthy, CSI 11: 14, 2001).

Synonyms: *Mammillaria retusa* Pfeiffer, Allg. Gartenz. 5: 369, 1837 (*nom. rejic. prop.*); *Aulacothele elephantidens* (Lemaire) Monville, Cat. Pl. Exot., 21, 1846; *Echinocactus elephantidens* (Lemaire) Poselger, Allg. Gartenz. 21: 102, 1853; *Cactus elephantidens* (Lemaire) Kuntze, Rev. Gen. Pl. 1: 260, 1891; *Coryphantha elephantidens* var. *barciae* Bremer, Cact. Suc. Mex. 18: 55, 1973; *Mammillaria sulcolanata* Lemaire, Cact. aliqu. nov. 2, 1838; *Aulacothele sulcolanata* (Lemaire) Monville, Cat. Pl. Exot., 21, 1846; *Echinocactus sulcolanatus* (Lemaire) Poselger, Allg. Gartenzeitung 21: 102, 1853; *Cactus sulcolanatus* (Lemaire) Kuntze, Rev. Gen. Pl. 1: 261, 1891; *Mammillaria recurvispina* De Vriese, Tijdscht. Nat. Gesch. 6: 53, 1839; *Cactus recurvispinus* (De Vriese) Kuntze, Rev. Gen. Pl. 1: 261, 1891; *Coryphantha recurvispina* (De Vriese) Bremer, Cact. Suc. Mex. 21: 12, 1976; *Coryphantha garessii* Bremer, Cact. Succ. J. (US) 52: 82, 1980.

Body solitary, depressed-globose to globose, apex flattened and strongly white-woolly, about 8 cm high and 10 cm diameter, dull dark-green. **Roots** napiform, deep, secondary roots fibrous. **Tubercles** in 5 and 8 or 8 and 13

series, broad conical, rounded, upper surface flattened, cut at edges, at the base 22–30 mm wide, 15–20 mm high, length on upper surface 14–20 mm, on lower surface 15–20 mm, with a deep, white-woolly groove in youth. **Axils** recessed, longish, 8 × 4 mm, in youth white-woolly. **Radial spines** 8–10, 2–3 of them on each side and 1 below pointing downwards, all subulate, straight, slightly curved to the body, 18–22 mm long, in the upper part of the areole 1–4 much thinner, set back, straight or slightly curved to the side, 12–14 mm long, all radial spines horn-coloured to brown, darker towards the tips, dull, later becoming grey from the base. **Flowers** 5–8 (–10) cm diameter, 5 cm long, light purple or yellow. Outer perianth segments broad lanceolate, acute, purple with light margins or yellow with red-brown midstripe dorsally, inner perianth segments broad lanceolate, margins entire, dentate towards the tip, acute, light purple, lighter to nearly white towards the throat, sometimes yellowish or yellow, in the throat sometimes reddish, filaments purple or whitish or whitish with purple base, anthers yellow, stigma whitish-yellow, stigma lobes small, whitish-yellow. **Fruit** longish, 3.5 cm long, 1 cm diameter, green, juicy berry with attached flower remnants. **Seeds** longish, reniform, 3.5 mm long, 1.5 mm wide, brown, testa reticulate.

Distribution: Mexico: Morelos, Puebla, Oaxaca, Querétaro, Jalisco, Guanajuato, Aguascalientes and Zacatecas.

Habitat: Lava soil in plains and low ridges in grassland, sometimes protected by bushes or Opuntias.

Locations checked: Mexico: Morelos: Zacatepec, Tlatizapan, Yautepec, Las Estacas. Puebla: Tepexco, Izucar de Matamoros, Tejalapa. Oaxaca: ETLA. Querétaro: Humilpán. Guanajuato: Irapuato-Cueramaro. Jalisco: Lagos de Moreno, Huejucar. Zacatecas: Tepetongo.

Incidence: Least concern. At some localities systematically removed from pastures by farmers.

Illustrations: Distribution see Plate 11, map 1; plant portrait see Plates 31 and 32.

17 b. *Coryphantha elephantidens* subsp. *bumamma* (Ehrenberg) Dicht & A. Lüthy

Cact. Syst. Init. 11: 14, 2001.

Basionym: *Mammillaria bumamma* Ehrenberg, Allg. Gartenz. 17: 243, 1849.

Typ: not designated.

Synonyms: *Mammillaria elephantidens bumamma* Schumann, Keys Monogr. Cact. 43, 1903; *Coryphantha bumamma* (Ehrenberg) Britton & Rose, Cact. 4: 33, 1923.

Body globose, somewhat flattened, 13 cm diameter, epidermis slightly bluish-green. Forming large groups of more than 50 cm diameter. **Tubercles** in 8 and 13 series, conical, rounded, upper part flattened, at the base 27 mm wide, 16 mm high, length of upper surface 13 mm, of lower surface 27 mm. **Axils** in youth very woolly, later naked. **Areoles** longish, 5 × 3 mm, slightly woolly. **Radial spines** 3 strong ones to the sides, 16–20 mm long, brown with dark tips, then greyish-brown with dark tips, in upper part of areole 2 more and below 1 more 11 mm long, all subulate, the lower one and the upper ones somewhat thinner than the lateral ones. **Flowers** 5–6 cm diameter, outer and inner perianth segments as for subsp. *greenwoodii* (see 17.c). Filaments reddish at the base, lobes greenish, stigma longer than filaments. **Fruit** claviform, 38 mm long and 13 mm diameter, whitish-green with a reddish tinge. **Seeds** 4 mm long and about 1 mm diameter, light brown.

Distribution: Mexico: Oaxaca and Michoacán.

Habitat: Deep, fine lava-soil with grass, sometimes with *Cereus* forests.

Locations checked: Mexico: Oaxaca: Totolapán. Michoacán: El Paradero.

Incidence: Least concern.

Illustrations: Distribution see Plate 11, map 1; plant portrait see colour Plate 33.

17 c. *Coryphantha elephantidens* subsp.

greenwoodii (Bravo) Dicht & A. Lüthy

Cact. Syst. Init. 11: 14, 2001.

Basionym: *Coryphantha greenwoodii* Bravo, Cact. Suc. Mex. 15: 27, 1970.

Type: Mexico, Veracruz, near Acultzingo, 1600 m, Greenwood s.n. (MEXU).

Body solitary or sprouting, group-forming, flat-globose, about 9 cm diameter, mostly under groundlevel, above ground 5–6 cm high, apex depressed, with much white wool. **Tubercles** in 5 and 8 or 8 and 13 series, obliquely conical, 18–22 mm wide, 17–19 mm high, length of upper surface 11–12 mm, of lower surface 14–20 mm. **Radial spines** somewhat protruding and recurved, 9–10, among them 5 strong ones to the sides, 1 thinner below oblique and 3–4 thinner ones bundled at top. The thinner ones nearly white with dark tip, the stronger ones brown with dark tips. **Flowers** fragrant, 5 cm in height and diameter, outer perianth-segments lanceolate, yellow with reddish midstripe dorsally, inner perianth-segments lanceolate, margins entire, acute, 5 mm wide, yellow, filaments dark yellow, stigma whitish with 4 very small lobes. **Fruits** as for subsp. *elephantidens* (see 17.a). **Seeds** reniform, 1.2 mm wide, 2 mm long, brown, testa reticulate.

Distribution/location checked: Veracruz in the region of Acultzingo, at 1600 m above sea level, on grassy ground.

Habitat: Lava soil with grass and small bushes.

Incidence: Endangered. Small range of distribution, one single location, constant threat by human activities like farming, road construction, clearing of pastures by fire observed.

Comments: This subspecies was named in honour of Ing. Edward W. Greenwood, a cactus and orchid enthusiast and photographer who accompanied H. Bravo on many excursions and who was the first one to discover this taxon.

At first sight, ssp. *greenwoodii* looks quite similar to *Coryphantha pycnacantha*. How-

ever, it has the typical tubercle form of *Coryphantha elephantidens* which is always wider than long (*C. pycnacantha* longer than wide) and therefore was allocated to *Coryphantha elephantidens* by us.

Illustrations: Distribution see Plate 11, map 1; plant portrait see Plate 34.

18. *Coryphantha retusa* Britton & Rose

Cactaceae 4: 38, 1923, *nom. cons. prop.*

Lectotype: Britton & Rose, Cact. 4: 38 (Fig. 36), 1923, Dicht & A. Lüthy, Cact. Syst. Init. 11: 11, 2001).

Synonyms: *Melocactus mammillariaeformis* Salm-Dyck, Allg. Gartenz. 4: 192, 1836 (*nom. rejic. prop.*); *Mammillaria cephalophora* Salm-Dyck, Cact. Hort. Dyck 1849: 137 1850 (*nom. illegit.*); *Echinocactus cephalophorus* (Salm-Dyck) Poselger, Allg. Gartenz. 21: 102, 1853; *Cactus cephalophorus* (Salm-Dyck) Kuntze, Rev. Gen. Pl. 1: 260, 1891; *Coryphantha melleospina* Bravo, An. Inst. Biol. Mex. 25: 526, 1954; *Coryphantha retusa* (Pfeiffer) Britton & Rose var. *melleospina* (Bravo) Bravo, Cact. Suc. Mex. 27: 17, 1982.

Body solitary, flattened-semiglobose to globose with narrowed base, 5–10 cm diameter, 3–8 cm high, dark green, apex depressed, with much white wool, roots fibrous. **Tubercles** in 8 and 13 or 13 and 21 series, conical, rounded, flattened above, below slightly bulging, 13–18 mm wide, 7–12 mm high, upper surface 9–12 mm long, lower surface 12–17 mm long, with deep, complete groove. **Axils** in youth with copious white wool. **Areoles** oblong, 4 mm long, 2 mm wide, in youth woolly. **Radial spines** 10–14 (-19), 3–4 of them on each side, strong, subulate, curved to the body and slightly downwards, radiating, the lowest one repositioned, straight downwards, 3–5 thinner needle-like spines in the upper part of the areole, repositioned, grouped together, directed upwards and slightly to one side, all 14–18 mm long, in new growth pale yellow, then white with darker tips, later turning grey. **Central spine:** occasionally and on some

areoles 1 porrect central spine curved downwards, more rarely upwards, subulate, 18 mm long, colour as radial spines. **Flowers** 4 cm in length and diameter, yellow, all perianth segments lanceolate, acute, filaments reddish, anthers yellow, stigma and lobes whitish-yellow. **Fruit** olive-green, juicy berry, oblong, 28 mm long, 9 mm wide. **Seeds** light brown, oblong, date-shaped, 2.5×1 mm, reticulate.

Distribution: Mexico: Puebla and Oaxaca.

Habitat: Grassland on lava-soil.

Locations checked: Mexico: Puebla: Tehuizingo, Acatlán, Petlalcingo, Xayacatlán. Oaxaca: Saltenango, Etna, 15 km south of Oaxaca, Buenavista, Mitla, Santiago Matatlán, Huajuapán de León, Ocotepc, El Molino, Chazumba, Ocotlán, Cerro Verde.

Incidence: Least concern.

Comments: BACKEBERG described a variety *pallidispina* (Cactaceae VI: 3874, 1962) with the following differences: spines 15, among them 12 more rigid with thickened bases, yellowish, the other 3 much thinner, close to each other and porrect, from horn-coloured to pale grey, with dark tips and yellowish, thickened base. In 1954 BRAVO published a *Coryphantha melleospina*, which she combined to *Coryphantha retusa* var. *melleospina* in 1982. As our field-studies have shown, this is just one form of *Coryphantha retusa*, but with some more radial spines of a golden-yellow colour and somewhat smaller dimensions.

Illustrations: Distribution see Plate 11, map 1; plant portrait see Plates 35 and 36.

Comments relating to the Series *Retusae*

When BRITTON & ROSE (1923–1938) allocated *Mammillaria retusa* Pfeiffer to *Coryphantha*, they obviously misinterpreted the first description. They used this epithet for small-tubercled plants with 12 radial spines, which they had received from various collectors from Oaxaca in 1920, among them Solis, whose plant they illustrated (l.c. Fig. 36). However, Pfeiffer's first description was of a plant with much larger tubercles of more

than 1 in. width and with fewer, but much longer radial spines. It undoubtedly corresponded with what is known as *Coryphantha elephantidens* today. Indeed, *Mammillaria retusa* had been cited as a synonym of *Mammillaria elephantidens* by all authors of the nineteenth century. Thus, following the rules of ICBN the name *Coryphantha retusa* as the oldest and therefore, valid name should be used for *Coryphantha elephantidens*.

A plant as widely distributed as *Coryphantha retusa* would surely have been collected and described early in the nineteenth century. There is, in fact, such a description which matches the plant in all respects: *Melocactus mammillariiformis* Salm-Dyck, Allg. Gartenz. 4: 148, 1836. This first description by Salm-Dyck was very precise and even mentioned the single strong central spine appearing on some areoles only. The very woolly apex of this plant had led Salm-Dyck to regard it as a *Melocactus*, but with a plain cephalium ("cephalium planum"). However, Lemaire and Pfeiffer indicated to him that this would be an error. In consequence, Salm-Dyck redescribed this species, but this time as *Mammillaria cephalophora* in Cact. Hort. Dyck 1849, 1850.

According to the ICBN rules, *Coryphantha retusa* (Pfeiffer) Br. & R. should now be named *Coryphantha mammillariaeformis* and *Coryphantha elephantidens* (Lemaire) Lemaire renamed *Coryphantha retusa*.

However, following Britton & Rose, the name *Coryphantha retusa* has been used by all authors in the sense of Britton & Rose and thus strict application of ICBN rules would lead to negative nomenclatural changes. Therefore, we made a proposal to the Committee for Spermatophytes to conserve *Coryphantha retusa* in the sense of Britton & Rose and to reject *Melocactus mammillariiformis* Salm-Dyck (CSI 10: 19, 2000). This was the only way to ensure continuity of the present nomenclature.

II.A.b Series *Pycnacanthae*

Dicht & A. Lüthy

Cact. Syst. Init. 11: 15, 2001.

Type: *Coryphantha pycnacantha* (Martius) Lemaire.

Definition: 3 or more central spines always present, but none porrect, all appressed.

19. *Coryphantha pycnacantha* (Martius)

Lemaire

Cactées 35, 1868

Basionym: *Mammillaria pycnacantha* Martius, Nov. Act. Nat. Cur. 16: 325, 1832.

Lectotype: Martius, Nov. Act. Nat. Cur. 16: 325, 1832 (Dicht & A. Lüthy, CSI 11: 15, 2001).

Synonyms: *Mammillaria pycnacantha spinosior* Monville ex Salm-Dyck, Hort. Dyck 1844: 4, 1845; *Aulacothele pycnacantha* (Martius) Monville, Cat. Pl. Exot., 21, 1846; *Echinocactus pycnacanthus* Poselger, Allg. Gartenz. 21: 102, 1853; *Cactus pycnacanthus* Kuntze, Rev. Gen. Pl. 1: 261, 1891; *Mammillaria acanthostephes* Lehmann, Allg. Gartenz. 3: 228, 1835; *Aulacothele acanthostephes* (Lehmann) Monville, Cat. Pl. Exot., 21, 1846; *Mammillaria acanthostephes recta* Hort ex Labouret, Monogr. Cact. 138, 1853; *Cactus acanthostephes* Kuntze, Rev. Gen. Pl. 1: 260, 1891; *Mammillaria magnimamma* Otto, Allg. Gartenz. 29: 228, 1835 [non Haworth, 1824]; *Mammillaria magnimamma lutescens* Salm-Dyck, Cact. Hort. Dyck 1849: 121, 1850; *Mammillaria arietina* Lemaire, Cact. Aliq. Nov. 10, 1838; *Mammillaria arietina spinosior* Lemaire, Cact. Gen. Nov. Sp. 94, 1839; *Mammillaria scepontocentra* Lemaire, Cact. Gen. Nov. Sp. 43, 1839; *Cactus scepontocentrus* Kuntze, Rev. Gen. Pl. 1: 261 1891; *Mammillaria winkleri* Foerster, Allg. Gartenz. 15: 50, 1853; *Echinocactus winkleri* Poselger, Allg. Gartenz. 21: 102, 1853; *Cactus winkleri* Kuntze, Rev. Gen. Pl. 1: 261, 1891; *Coryphantha connivens* Br. & R., Cactaceae 4: 34, 1923; *Coryphantha andreae* Purpus & Bödeker, Zeitschr. Sukk.-Kunde 3: 251, 1928.

Body solitary, flat-globose to semiglobose, 9.5 cm diameter, 3.5 cm high, blue-grey green,

apex depressed, woolly. Central part of root nearly a taproot, with lateral fibrous roots. **Tubercles** in 5 and 8 (rarely 8 and 13) series, compressed conical, flattened above, bulging underneath, edges obliquely cut, at the base 17 mm wide, 12 mm high, upper surface 18 mm long, lower surface 22 mm, with deep, woolly groove in youth. **Axils** white-woolly in youth. **Areoles** elliptical, 4 mm long, 2 mm wide, woolly in youth. **Radial spines** 6–15, irregularly radiating, but bundled in the upper part, or merely bundled above, lower and lateral spines 9 mm long, straight, needle-like, the bundled ones above in two layers, some thicker and longer, up to 16 mm, all grey-white with dark tips. **Central spines** 5–7, 2–3 of them on each side, somewhat spreading, curved to the body, thick subulate, 15–21 mm long, 1 downwards, a bit thinner and shorter, in a subcentral position, all pale brown, then greyish with black tips. **Flowers** 30 mm long, 45 mm diameter, outer perianth-segments narrow-lanceolate, acute, 15 mm long, 3 mm wide, lemon-yellow with brown-red dorsal midstripe. Inner perianth segments broad-lanceolate, dentate towards the tip, acute, 24 mm long, 5 mm wide, lemon-yellow. Filaments short, 12 mm long, yellow, anthers yolk-yellow, stigma yellowish, with 5–7 whitish-yellow lobes. **Fruit** green, juicy, oblong berry, 24 mm long, 13 mm wide with attached flower remnants. **Seeds** reniform, 2.5 mm long, 1.5 mm wide, brown, testa reticulate.

Distribution: Mexico, Hidalgo, Puebla, Veracruz.

Habitat: Deep and flat lava soil in gras or besides anthills, together with *Opuntias*.

Locations checked: Mexico: Mexico: Otumba, Cd. Shahogun. Hidalgo: Barranca de Metztilan, San Miguel Regla, Singuilucan, Atonilco, Zempoala. Puebla: Yaltepec. Veracruz: Perote.

Incidence: Endangered. The locations of the plants are deep, plane lava soils, best arable land, and the range of distribution east of

Mexico City is the area of most intensive agricultural production in Mexico. Nearly all potential habitats are cultivated and the populations known are mostly reduced to very small areas along railway tracks, garbage dumps, and so on.

Differentiation: *Coryphantha pycnacantha* is reminiscent of *Coryphantha elephantidens* (Lemaire) Lemaire. However, it has more radial spines, several central spines and smaller rounder, more loosely arranged, longer than broad tubercles than the latter species. Moreover, it has flowers of pure yellow, while the filaments do not have any redness. Finally, the seeds are rounder and reniform.

Comments: *Mammillaria pycnacantha* Martius was imported from Mexico by the Baron L.B. von Karwinski and first described in detail by MARTIUS (1832), with informative illustrations, including a young plant, a flower and the spine-arrangement. Therefore, there are no doubts about the characteristics of the described species, which, contrary to many other descriptions of that time, can clearly be verified. The first description by Martius includes two minor errors: the indicated height of the plant and its origin Oaxaca, where, as we know today, no comparable *Coryphanthas* can be found. Comparing the indicated measurements of the plant with the illustration of Martius, re-measurement shows that the indication of the height applies to the complete length of the plant including the roots. The origin of the species had already been extended in 1843 by PFEIFFER and OTTO by the indication “prope Oajaca & Pachuca: Karw.” In the same publication, these authors stated that this species was very close to the more flat-globose *Mammillaria acanthostephes* Lehmann (1835), which, consequently, was regarded as a synonym of *Mammillaria pycnacantha* Martius in the whole literature of the nineteenth century.

The most important hint as to the effective distribution area of *Coryphantha pycnacantha*

was ultimately given by EHRENBERG, who studied the botany of Mineral del Monte from 1831 to 1840. His article appeared in the journal *Linnaea* in 1846 and is regarded as the most reliable source of the locations of many plants collected before 1840. Ehrenberg found *Coryphantha pycnacantha* near the capital and also mainly in the state of Hidalgo in the plains near Pachuca, near San Mateo, Atotonilco el Grande, Regla and other locations.

The identity of the species, which was allocated to *Coryphantha* by Lemaire in 1868, seems to have been clear in the nineteenth century, although the descriptions vary slightly (Pfeiffer und Otto, Karwinski, Salm-Dyck, Schumann etc.).

The confusion surrounding this taxon only began with BRITTON & ROSE (1923). They reproduced the illustrations of Martius, but in their text they mentioned a completely different plant from the region of Oaxaca, which they had obtained from Prof. Conzatti in 1920. In contrast to the basionym, this plant, besides having 15–20 white radial spines, had 2–3 black, porrect, curved central spines and much smaller tubercles of about 10 mm diameter. In the same publication, Britton and Rose redescribed *Coryphantha connivens* from near the capital, Mexico City, without realising, that this very plant was identical to Martius' *Coryphantha pycnacantha*. However, they did mention that it was very close to *Coryphantha pycnacantha* (Br. & R. Cactaceae V: 34, 1923). The error of Britton & Rose persisted throughout the twentieth century with the result that the name *Coryphantha pycnacantha* was, if ever, used for the wrong species. BÖDEKER (1933), however, discovered this mistake: in 1932 he received from Halbinger in Mexico a plant identical to that received from Prof. Conzatti by Britton & Rose. However, he noticed the discrepancy compared with the first description by Martius and described this plant, which was erroneously named *Coryphantha pycnacantha* by

Britton & Rose, as *Coryphantha reduncuspina* Bödeker. This latter plant today is now included within the variety of *Coryphantha pallida* Br. & R.

In 1928, BÖDEKER was the co-author of a first description which is practically identical to that of *Mammillaria pycnacantha* Martius: *Coryphantha andreae* Purpus & Bödeker. It has to be regarded as merely a younger synonym. This name has been used until today for most specimens of *Coryphantha pycnacantha* in collections.

The first author to rectify the confusion surrounding *Coryphantha pycnacantha* was ZIMMERMAN (1985) who rightly treated *Coryphantha connivens* Br. & R. and *Coryphantha andreae* Purpus & Bödeker as younger synonyms of *Coryphantha pycnacantha*.

Verification at Locations

In this confusing situation, it was important to check the locations of all taxa concerned, especially the old locations listed by Ehrenberg. This was not that easy, since Mexico has changed a lot in the 150 years since Ehrenberg, especially in the regions of the habitats of this species, which prefers plane, deep lava soils. *Coryphantha pycnacantha* is very much endangered today by intensified extensive farming, and has become very rare. We managed to verify some plants in Hidalgo near San Mateo (near Zempoala) and also near Atotonilco and Regla and at locations in the state of Mexico near Otumba and south of Cd. Shahogun. However, our search was only successful in pitiful remnants of habitats such as basureros (garbage dumps) or near railroad dams. In several locations plants with heavily bundled upper radial spines (“connivens”), but with otherwise identical features, can be found in addition to “classical” plants as described by Martius.

In addition, our research affirmed that *Coryphantha andreae*, whose distribution area we studied from Perote VER to the

region of Tecomachalco PUE, is indeed identical to *Coryphantha pycnacantha*.

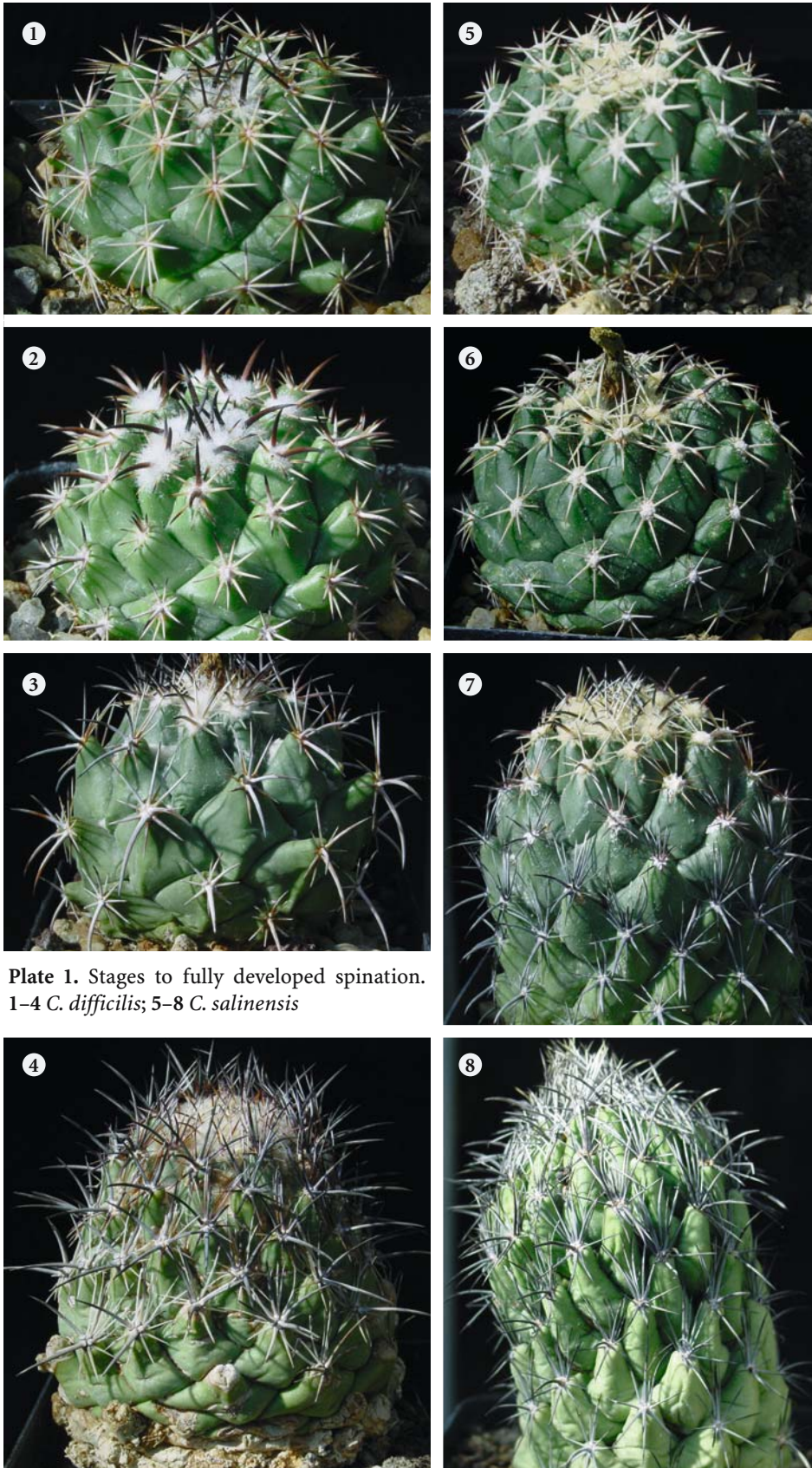
Interestingly, our check on indicated locations of *Coryphantha sulcolanata* (Lemaire) Lemaire published in the twentieth century (Sanchez-Mejorada, Helia Bravo, Steven Brack) always gave the same result: *Coryphantha pycnacantha* and never *Coryphantha sulcolanata*. The latter must be included in the complex around *Coryphantha elephantidens*.

Illustrations: Distribution see Plate 11, map 1; plant portrait see Plates 37 and 38.

20. *Coryphantha tripugionacantha* Lau Cact. Suc. Mex .33: 20, 1988.

Type: Mexico: Zacatecas, San Juan Capistrano, 1000 m, 1983, Lau 1469 (MEXU).

Body solitary, globose to slightly depressed, with much wool, 8–9 cm diameter and 7–9 cm high, epidermis bluish-green, later dull dark green, short taproot with lateral fibrous roots, forming stolons. **Tubercles** in 5 and 8 series, triangular at the base, conical, upper surface flattened, lower part bulging, width at the base 14–20 mm, 15 mm high, length of upper surface 12 mm, of lower surface 18 mm, with complete groove on the upper part. **Axils** in youth white-woolly, later naked. **Areoles** round, 3 mm diameter, in youth with white wool, later naked. **Radial spines** 8–9, radiating, curved towards the body, but without touching it, the 3 lower ones up to 12 mm long, the 5–6 upper ones more closely set, shorter, 8 mm long, all subulate, straight, grey-brown, the lower one darker than the upper ones. **Central spines** 3, none dominant, none porrect, all curved towards the body, the lowest one the longest, 20 mm long, the other two in the upper part of the areole diverging to the sides, up to 18 mm long, all subulate, in new growth black, later becoming grey from below. **Flowers** funnellform, 6–7 cm diameter, cream-yellow; outer perianth segments light yellow with dark red dorsal midstripe, margins entire, at the base 3 mm wide; inner peri-



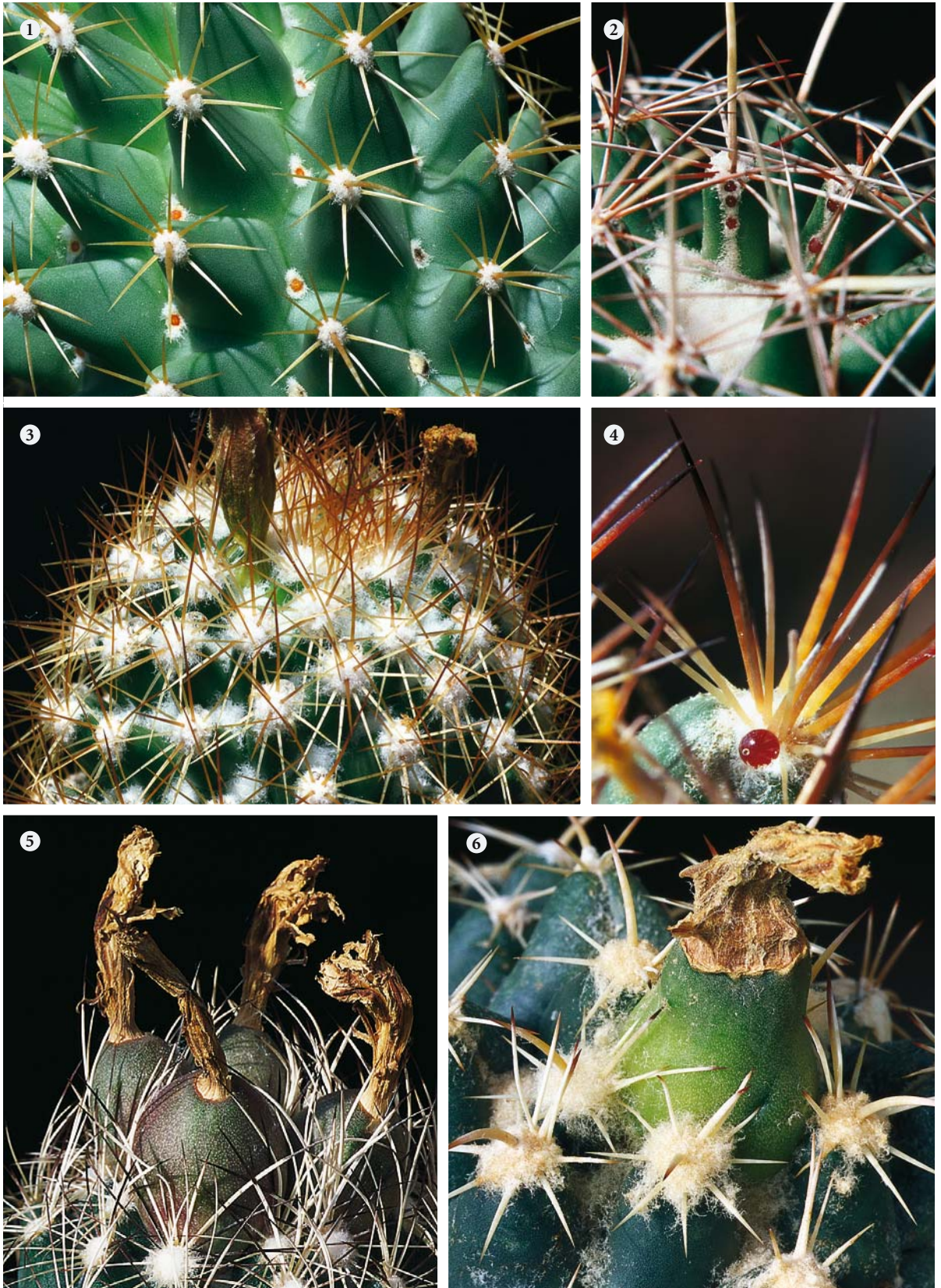


Plate 2. Glands and fruits. 1 Axillary glands of *C. glassii*; 2 glands in the grooves of *C. robustispina* (photo E. Tiefenbacher); 3, 4 glands near the spiniferous areole of *C. erecta* (left) and *C. wohlschlageri* (right); 5, 6 fruits of *C. nickelsiae* (left) and *C. salinensis* (right)



Plate 3. The great variability of the spination. 1-5 *C. cornifera* at one and the same location near Peña Miller QRO

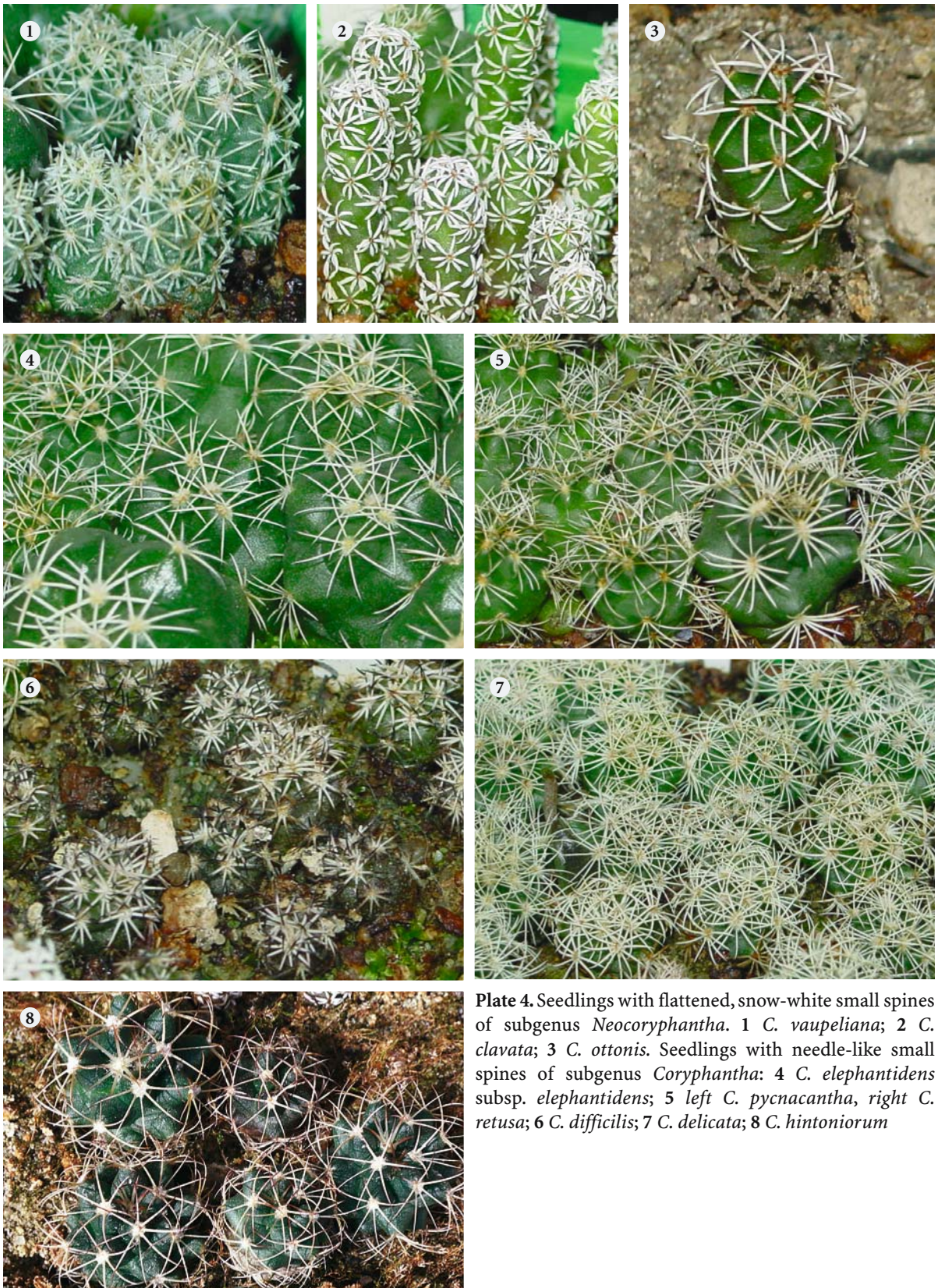


Plate 4. Seedlings with flattened, snow-white small spines of subgenus *Neocoryphantha*: 1 *C. vaupeliana*; 2 *C. clavata*; 3 *C. ottonis*. Seedlings with needle-like small spines of subgenus *Coryphantha*: 4 *C. elephantidens* subsp. *elephantidens*; 5 left *C. pycnacantha*, right *C. retusa*; 6 *C. difficilis*; 7 *C. delicata*; 8 *C. hintoniorum*

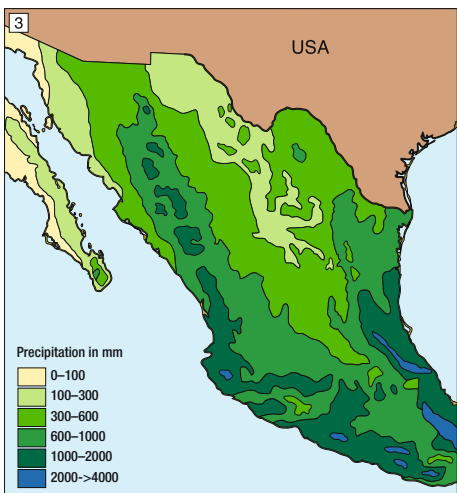
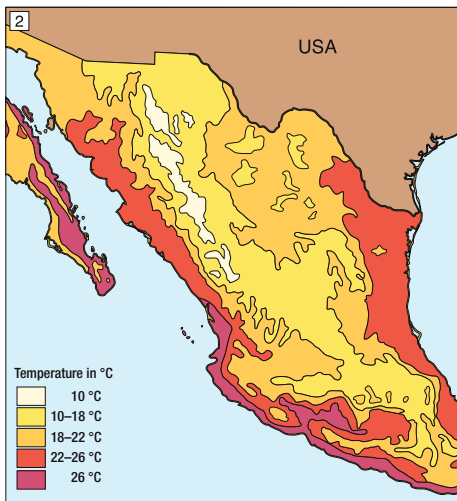
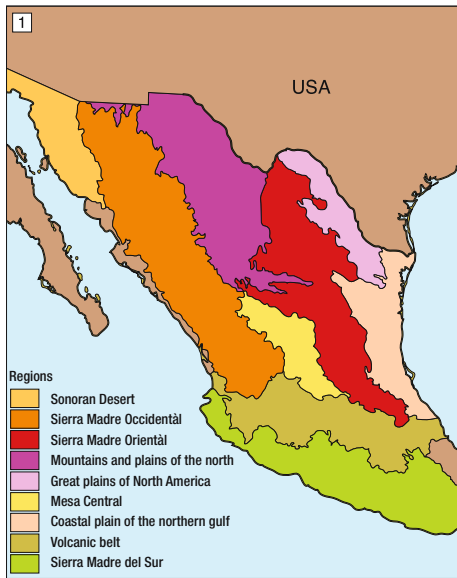
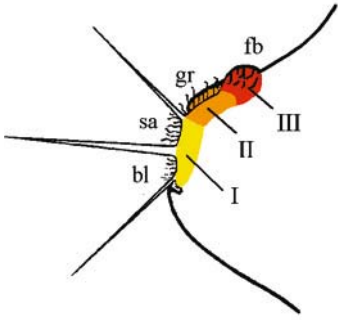


Plate 5. Geographical distribution and climate conditions

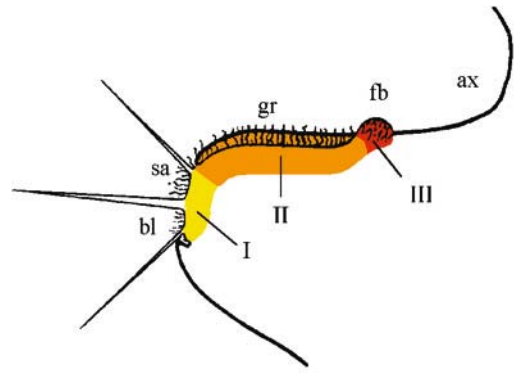
Abbreviations used in the maps of distribution (also for Plates 9–13):

- AGU = Aguascalientes
- CHI = Chihuahua
- COAH = Coahuila
- DGO = Durango
- GRO = Guerrero
- GTO = Guanajuato
- HGO = Hidalgo
- JAL = Jalisco
- MEX = Estado de Mexico
- MICH = Michoacán
- MOR = Morelos
- NL = Nuevo León
- OAX = Oaxaca
- PUE = Puebla
- QRO = Querétaro
- SLP = San Luis Potosí
- SON = Sonora
- TAM = Tamaulipas
- TLA = Tlaxcala
- VER = Veracruz
- ZAC = Zacatecas

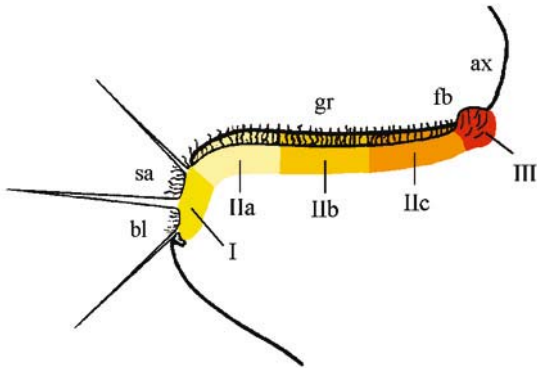
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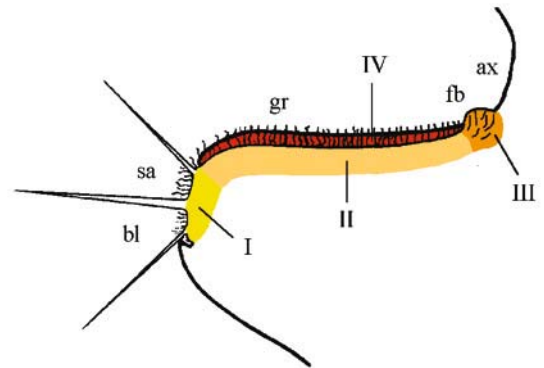
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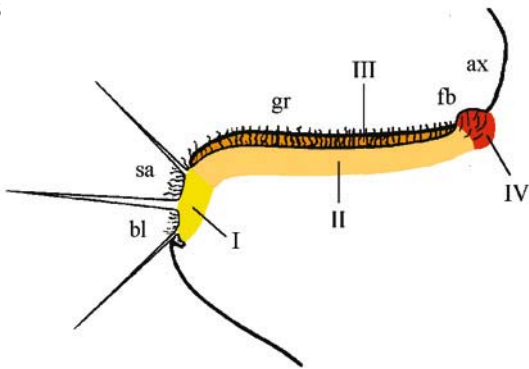
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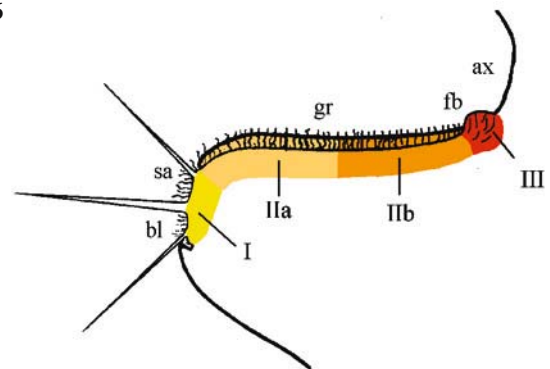
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5



6



7

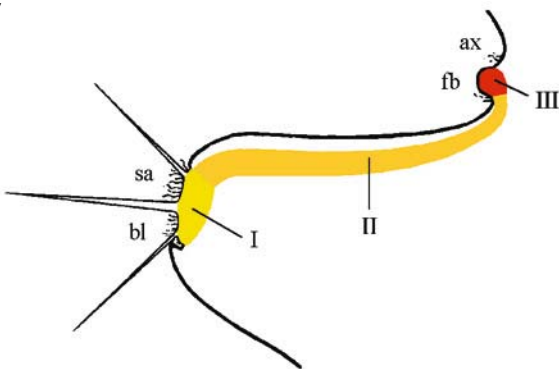


Plate 6. Areole types. 1 *Ferocactus* areole type, 2 *Macromeris* areole type, 3 *Protocoryphantha* areole type, 4 *Ortegocactus* areole type, 5 *Protomammillaria* areole type, 6 *Escobaria* areole type, 7 *Mammillaria* areole type. I-IV Stages of areole development, *bl* basal leaf, *sa* spine areole, *gr* groove, *fb* flower base, *ax* axil

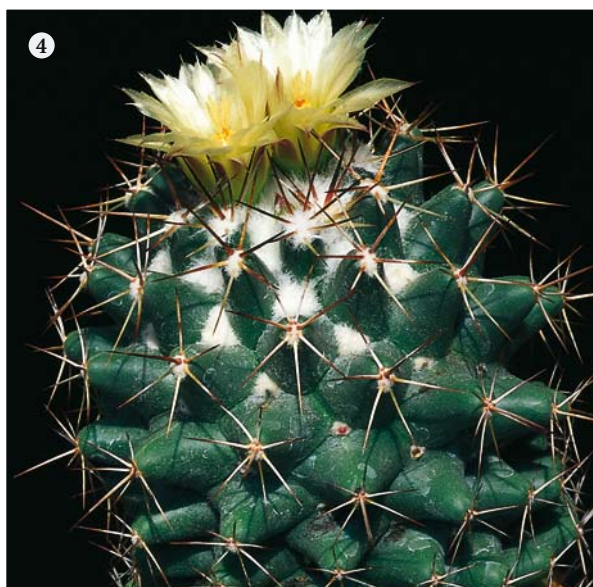


Plate 7. Examples of areole types. 1 *Macromeris* type: *C. macromeris* ssp. *macromeris*; 2 *Protocoryphantha* type: *C. robustispina* subsp. *robustispina* (photo L. Moore); 3 *Protomammillaria* type: *C. vaupeliana*; 4 *Ortegocactus* type: *C. georgii*; 5. *Escobaria* type: *C. elephantidens* ssp. *elephantidens*



Plate 8. A summer with *Coryphantha* sp. 1–3 Flowering *Coryphantha* sp. in cultivation

Plate 9. Distributional maps (see Plate 5 for abbreviations)

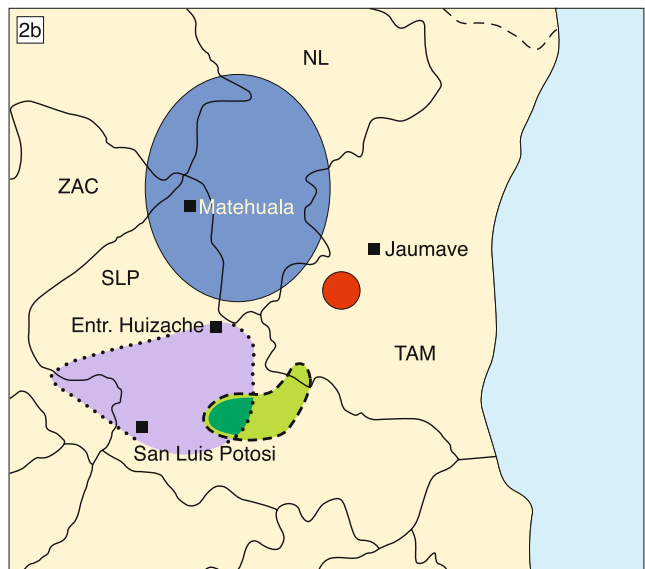
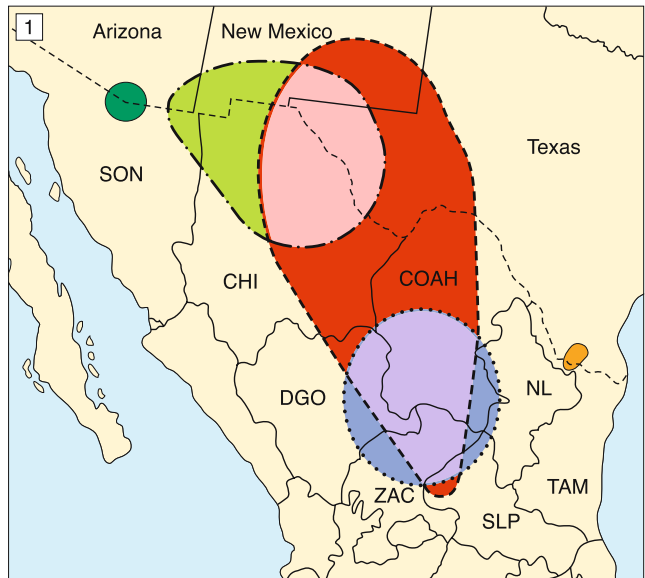
I. Subgenus *Neocoryphantha* Backeberg emend. Dicht & A. Lüthy

I.A. Section *Lepidocoryphantha* (Moran) Backeberg

- Coryphantha macromeris* subsp. *macromeris*
- Coryphantha macromeris* subsp. *runyonii*

I.B. Section *Robustispina* Dicht & A. Lüthy

- Coryphantha poselgeriana*
- Coryphantha robustispina* subsp. *robustispina*
- Coryphantha robustispina* subsp. *scheeri*



I. Subgenus *Neocoryphantha* Backeberg emend. Dicht & A. Lüthy

I.C. Section *Neocoryphantha*

I.C.a. Series *Echinoideae* Dicht & A. Lüthy

- Coryphantha wohlschlageri*
- Coryphantha echinoidea*
- Coryphantha vaupeliana*
- Coryphantha glanduligera*

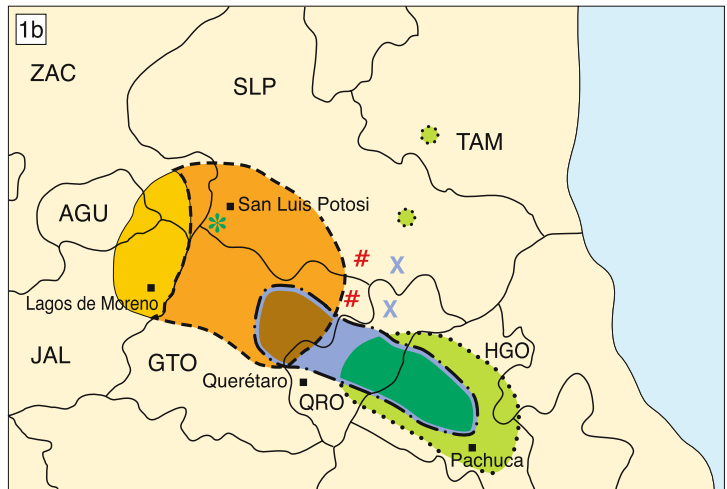


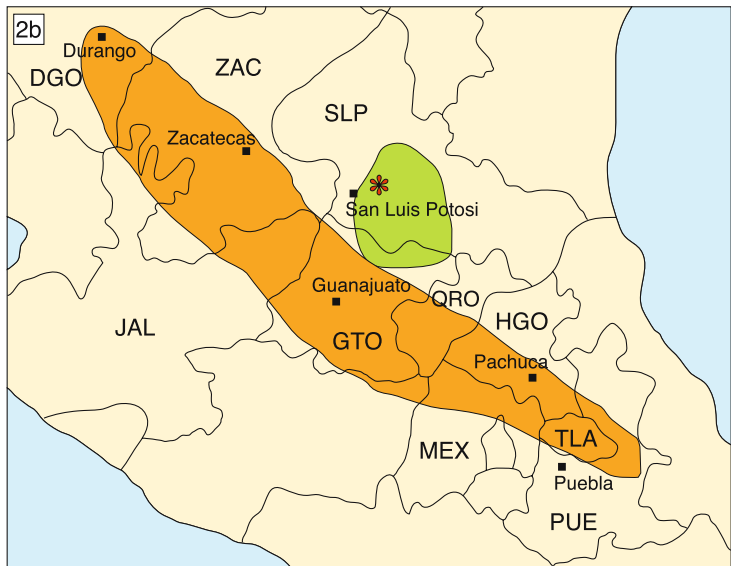
Plate 10. Distributional maps (see Plate 5 for abbreviations)

I. Subgenus *Neocoryphantha* Backeberg emend. Dicht & A. Lüthy

I.C. Section *Neocoryphantha*

I.C.b. Series *Clavatae* Dicht & A. Lüthy

- Coryphantha octacantha*
- Coryphantha erecta*
- Coryphantha clavata* subsp. *clavata*
- Coryphantha clavata* subsp. *stipitata*
- Coryphantha jalpanensis*
- Coryphantha glassii*
- Coryphantha potosiana*



I. Subgenus *Neocoryphantha* Backeberg emend. Dicht & A. Lüthy

I.D. Section *Otonis* Dicht & A. Lüthy

- Coryphantha ottonis*
- Coryphantha georgii*
- Coryphantha vogtherriana*

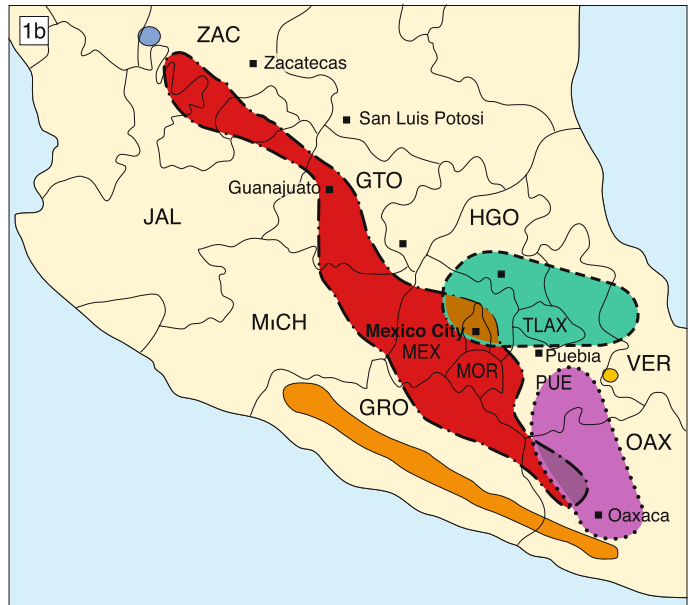






Plate 11. Distributional maps (see Plate 5 for abbreviations)



II. Subgenus *Coryphantha*

II.A. Section *Coryphantha*

II.A.a. Series *Retusae* Dicht & A. Lüthy

-  *Coryphantha elephantidens* subsp. *elephantidens*
-  *Coryphantha elephantidens* subsp. *bumamma*
-  *Coryphantha elephantidens* subsp. *greenwoodii*
-  *Coryphantha retusa*









II.A.b. Series *Pycnananthae* Dicht & A. Lüthy

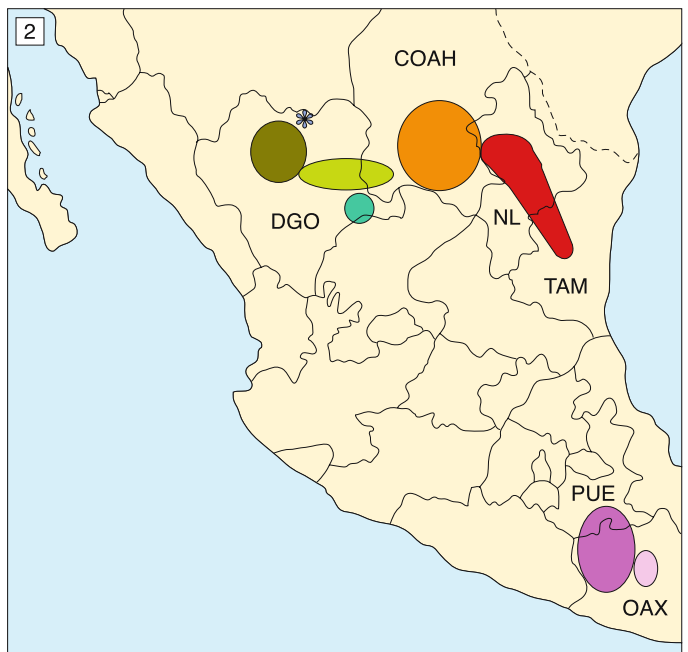
-  *Coryphantha pycnanantha*
-  *Coryphantha tripugionacantha*

II. Subgenus *Coryphantha*

II.A. Section *Coryphantha*

II.A.c. Series *Salinenses* Dicht & A. Lüthy

-  *Coryphantha kracikii*
-  *Coryphantha salinensis*
-  *Coryphantha difficilis*
-  *Coryphantha durangensis* subsp. *durangensis*
-  *Coryphantha durangensis* subsp. *cuencamensis*
-  *Coryphantha longicornis*
-  *Coryphantha pallida* subsp. *pallida*
-  *Coryphantha pallida* subsp. *calipensis*



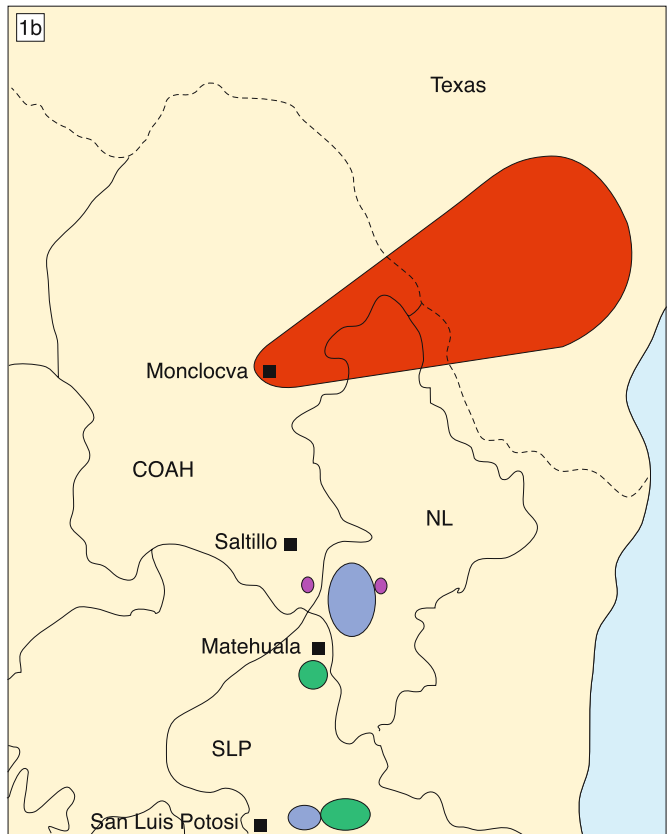
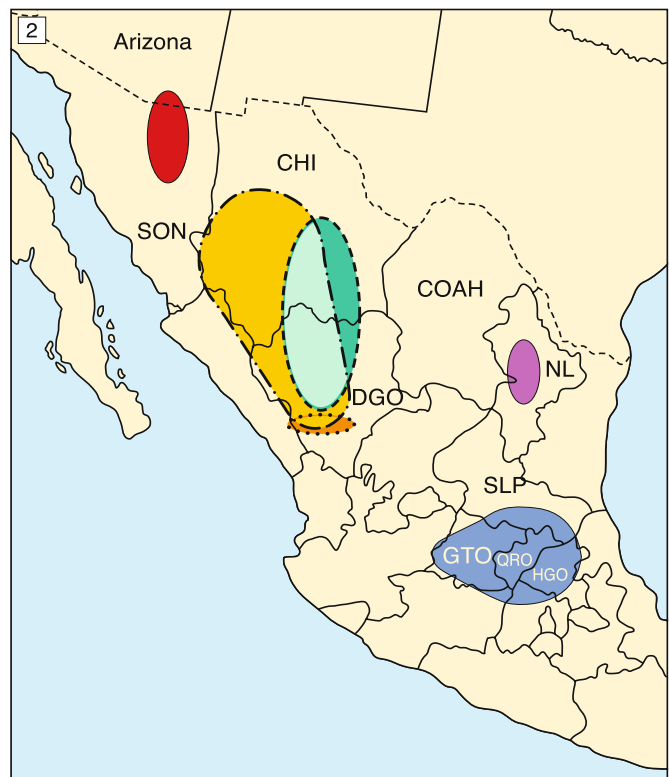


Plate 12. Distributional maps (see Plate 5 for abbreviations)

II. Subgenus *Coryphantha*
 II.A. Section *Coryphantha*
 II.A.d. Series *Coryphantha*

- *Coryphantha maiz-tablasensis*
- *Coryphantha sulcata*
- *Coryphantha hintoniorum* subsp. *hintoniorum*
- *Coryphantha hintoniorum* subsp. *geoffreyi*





II. Subgenus *Coryphantha*
 II. A. Section *Coryphantha*
 II.A.e. Series *Corniferae* Dicht & A. Lüthy
 Subseries *Corniferae*, part 1

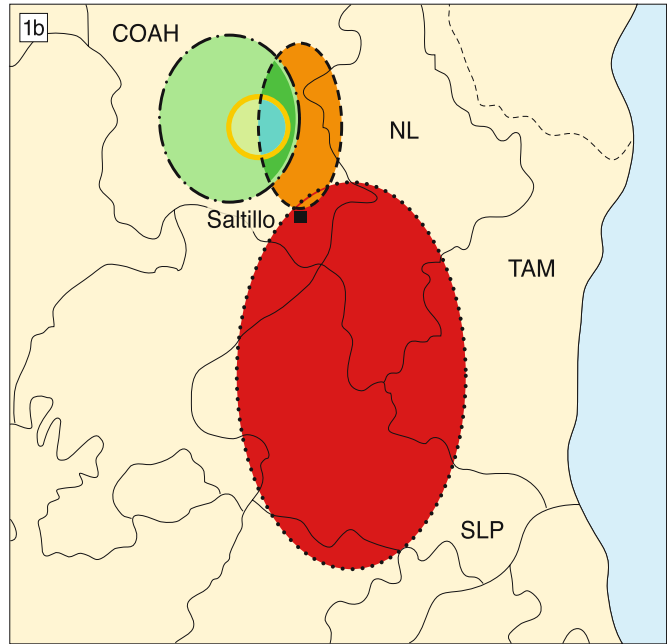
- *Coryphantha nickelsiae*
- *Coryphantha pseudonickelsiae*
- *Coryphantha compacta*
- *Coryphantha cornifera*
- *Coryphantha recurvata* subsp. *recurvata*
- *Coryphantha recurvata* subsp. *canatlanensis*





Plate 13. Distributional maps (see Plate 5 for abbreviations)

II.A.e. Series *Corniferae* Dicht & A. Lüthy
Subseries *Corniferae*, part 2







-  *Coryphantha delicata*
-  *Coryphantha neglecta*



-  *Coryphantha pseudoechinus* subsp. *pseudoechinus*
-  *Coryphantha pseudoechinus* subsp. *loui*



II.A.e. Series *Corniferae* Dicht & A. Lüthy
Subseries *Delaetianae*

-  *Coryphantha delaetiana*
-  *Coryphantha ramillosa* subsp. *ramillosa*
-  *Coryphantha ramillosa* subsp. *santarosa*
-  *Coryphantha pulleineana*
-  *Coryphantha werdermannii*
-  *Coryphantha echinus*

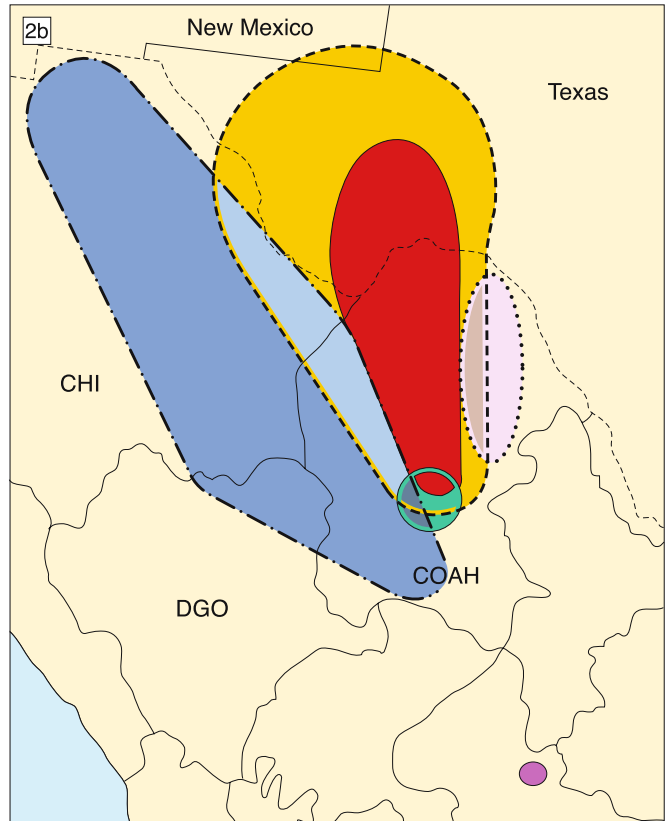




Plate 14. *Coryphantha macromeris*. 1 *C. macromeris* subsp. *macromeris* (cultivar). 2 *C. macromeris* subsp. *runyonii* (cultivar). 3 *C. macromeris* subsp. *macromeris* at km 40 of the road Monterrey–Monclova COAH

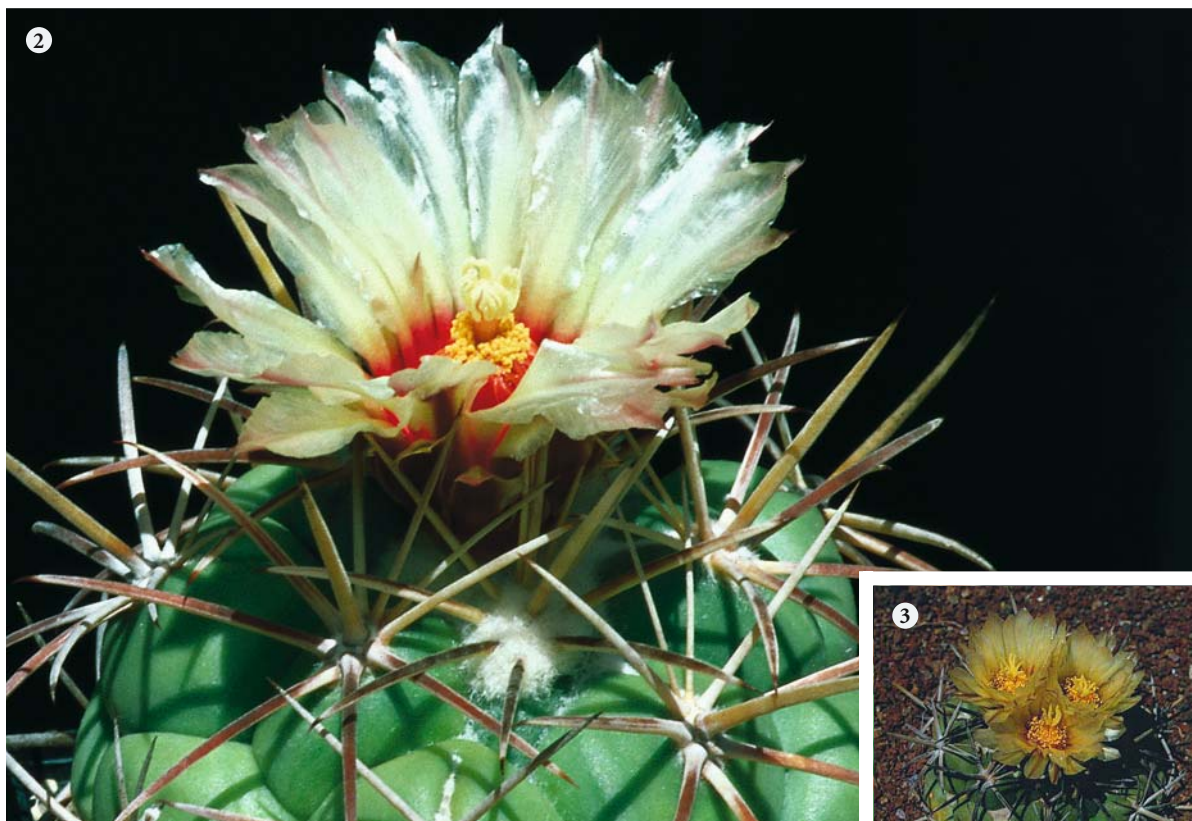


Plate 15. Flower colours of *Coryphantha poselgeriana*. 1–3 The flower colour of *C. poselgeriana* varies from red to yellowish-white. 3 Flowers of pure yellow near Villa de Ramos SLP. (Photo M. Sotomayor)

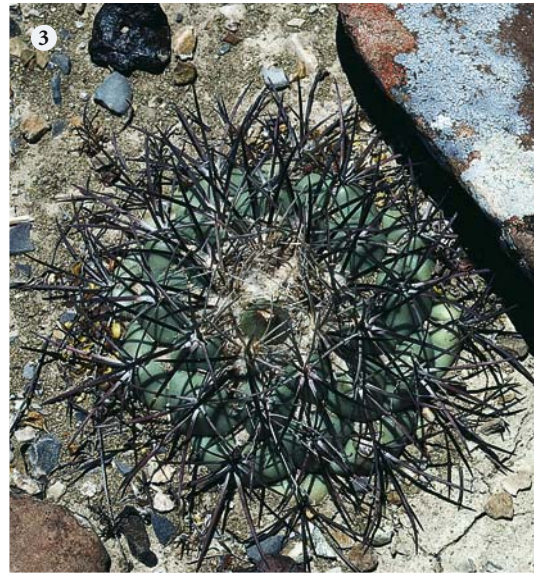


Plate 16. Forms of *Coryphantha poselgeriana* at different locations. 1 Cuatrociénegas COAH. 2 Saltillo COAH. 3 Hipolito COAH. 4 Hipolito COAH. 5 Cuencamé DGO



Plate 17. *Coryphantha robustispina*. 1 *C. robustispina* subsp. *robustispina*, Pima County, Arizona, USA (photo L. Moore). 2 *C. robustispina* subsp. *scheeri* in flower (cult. and photo A. Böcker). 3 *C. robustispina* subsp. *scheeri*, Benito Juarez CHI. (Photo R. Römer)

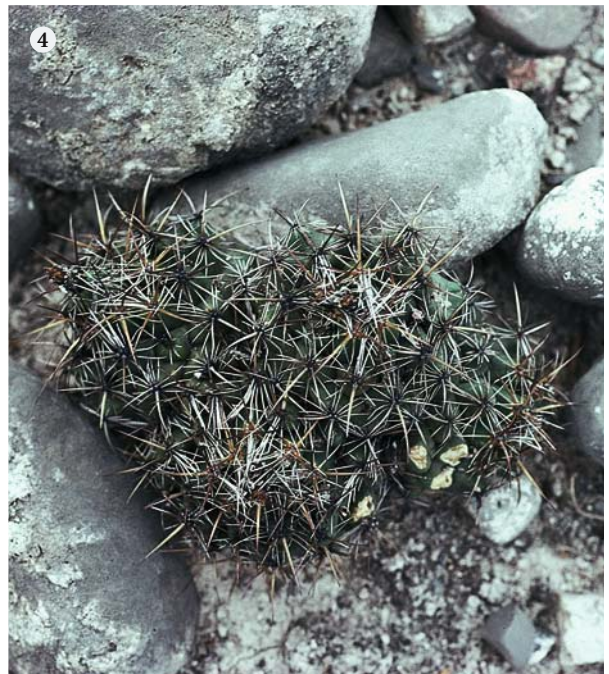


Plate 18. *Coryphantha wohlschlagerei* and *Coryphantha vaupeliana*. 1 Seedling of *C. wohlschlagerei*, Villa Juarez SLP. 2 *C. wohlschlagerei*, Angostura SLP. 3 Seedling of *C. vaupeliana*, San Antonio, TAM. 4 *C. vaupeliana*, San Antonio TAM

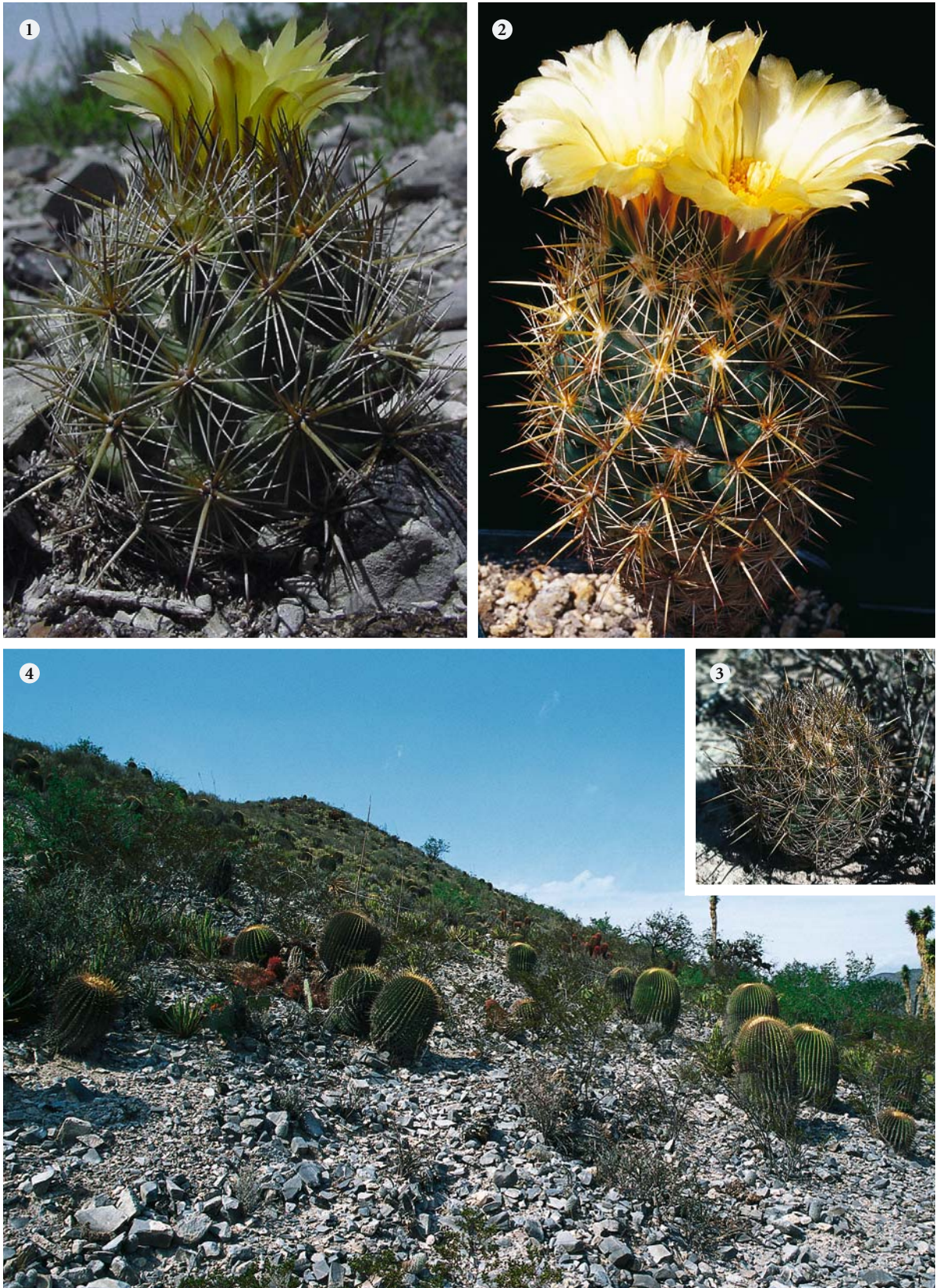


Plate 19. *Coryphantha glanduligera*. 1 *C. glanduligera*, San Rafael NL (photo G. Hinton). 2 *C. glanduligera* (cultivar), Matehuala SLP. 3 *C. glanduligera*, Sandia NL. 4 The location of *C. glanduligera* near Sandia NL

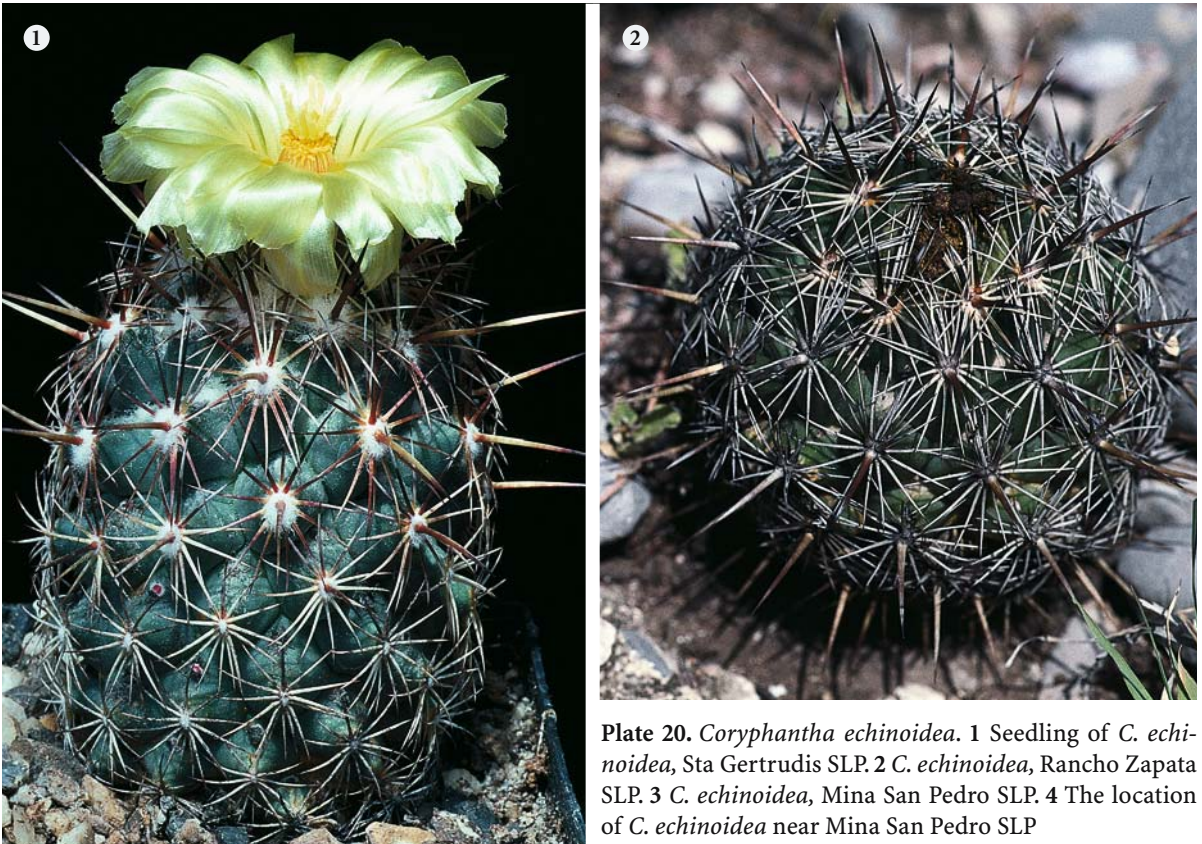




Plate 21. *Coryphantha octacantha*. 1 *C. octacantha* (cultivar). 2 *C. octacantha* (cultivar). 3 *C. octacantha*, Pachuca HGO. 4 *C. octacantha*, Pachuca HGO. 5 *C. octacantha*, Vista Hermosa QRO

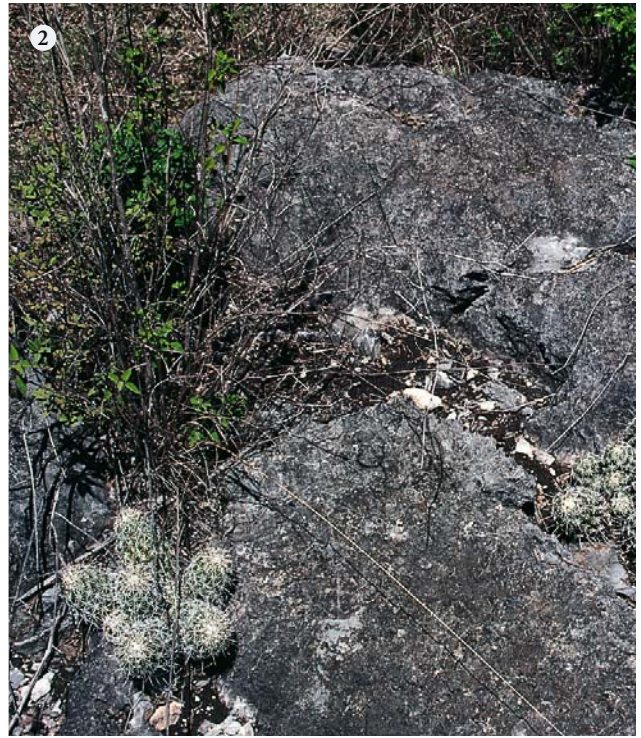


Plate 22. *Coryphantha jalpanensis*. 1 *C. jalpanensis* (cultivar). 2 Location of *C. jalpanensis* on calcareous rocks, Mazcazintla QRO. 3 *C. jalpanensis*, Mazcazintla QRO



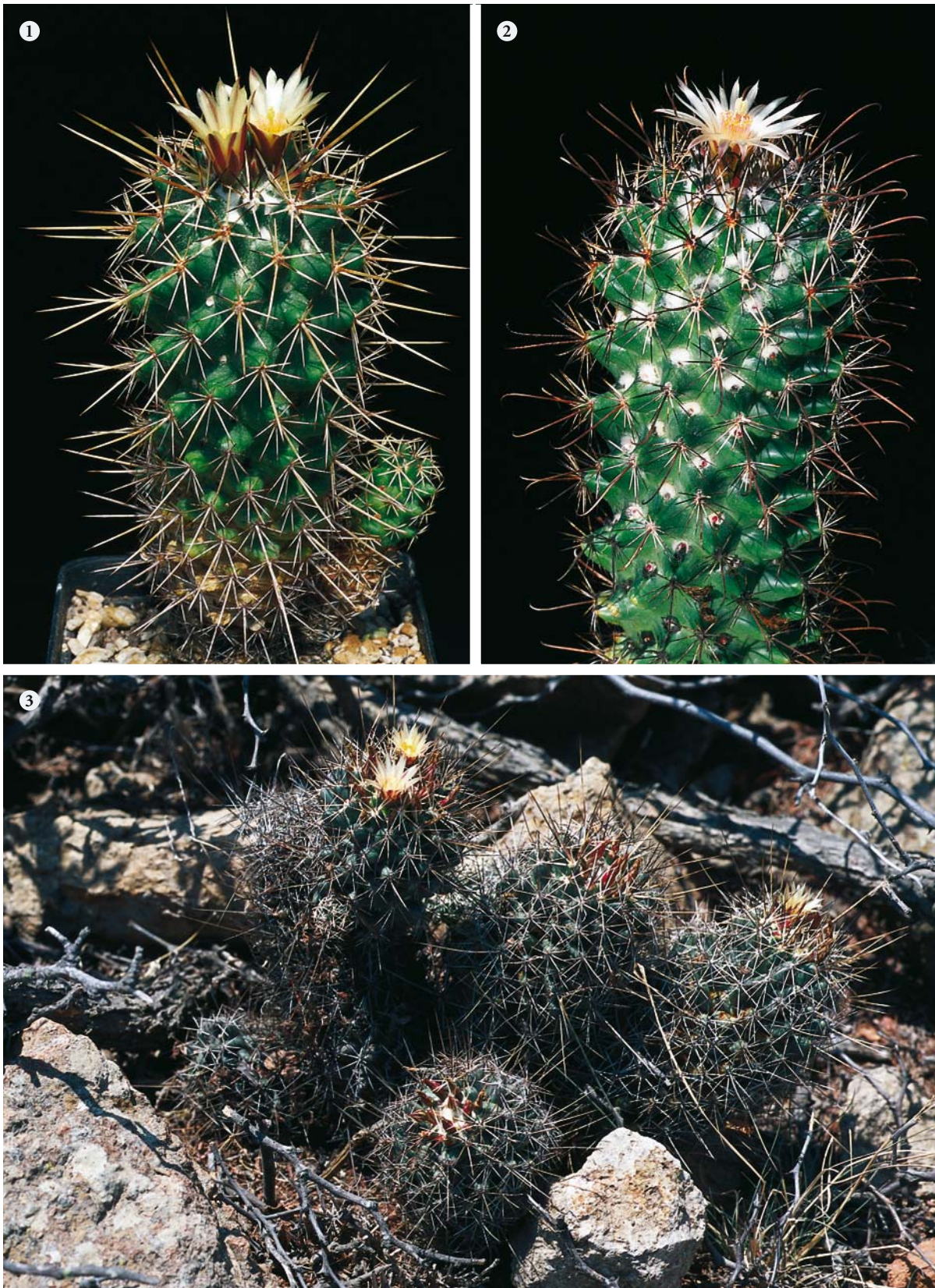


Plate 23. *Coryphantha clavata*. 1 *C. clavata* subsp. *clavata* (cultivar). 2 *C. clavata* subsp. *stipitata* (cultivar). 3 *C. clavata* subsp. *clavata*, Cañon de las Calabassas SLP



Plate 24. *Coryphantha glassii*. 1 *C. glassii* with the hoe of its discoverer Charles Glass, Xichù GTO. 2 *C. glassii* with flowers (photo: M. Sotomayor). 3 *C. glassii* at the type locality, Sanguijuela SLP. 4 *C. glassii*, Las Magdalenas SLP

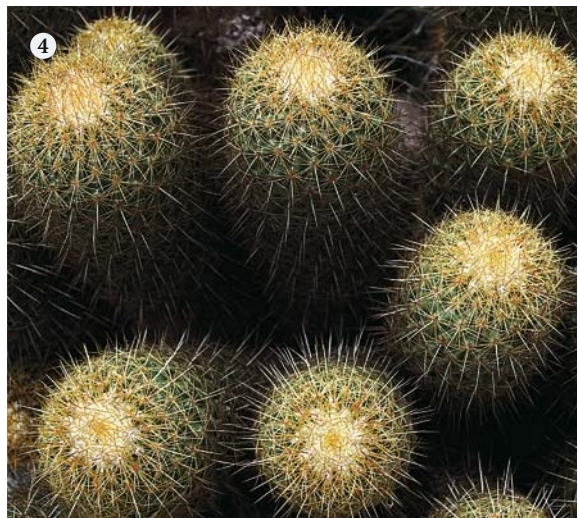


Plate 25. *Coryphantha erecta*. 1 Flowers of *C. erecta* (cultivar). 2 *C. erecta*, San Joaquín QRO. 3 *C. erecta*-group, San Luis de la Paz GTO. 4 *C. erecta*, San Luis de la Paz GTO. 5 *C. erecta* near Jalpàn QRO



Plate 26. *Coryphantha erecta*. 1,2 Groups of *C. erecta* at the location near San Joaquín QRO



Plate 27. *Coryphantha potosiana*. 1–4 *C. potosiana* at the type locality near the road from San Luis Potosí to Aguascalientes SLP



Plate 28. *Coryphantha ottonis*. 1 *C. ottonis* ("bussleri" form), Tlaxco TLX. 2 *C. ottonis* Otumba MX. 3 *C. ottonis* (cultivar). 4 *C. ottonis* (cultivar). 5 *C. ottonis* ("guerkeana" form), Rancho Olguin ZAC. 6 *C. ottonis* ("guerkeana" form), La Providencia ZAC

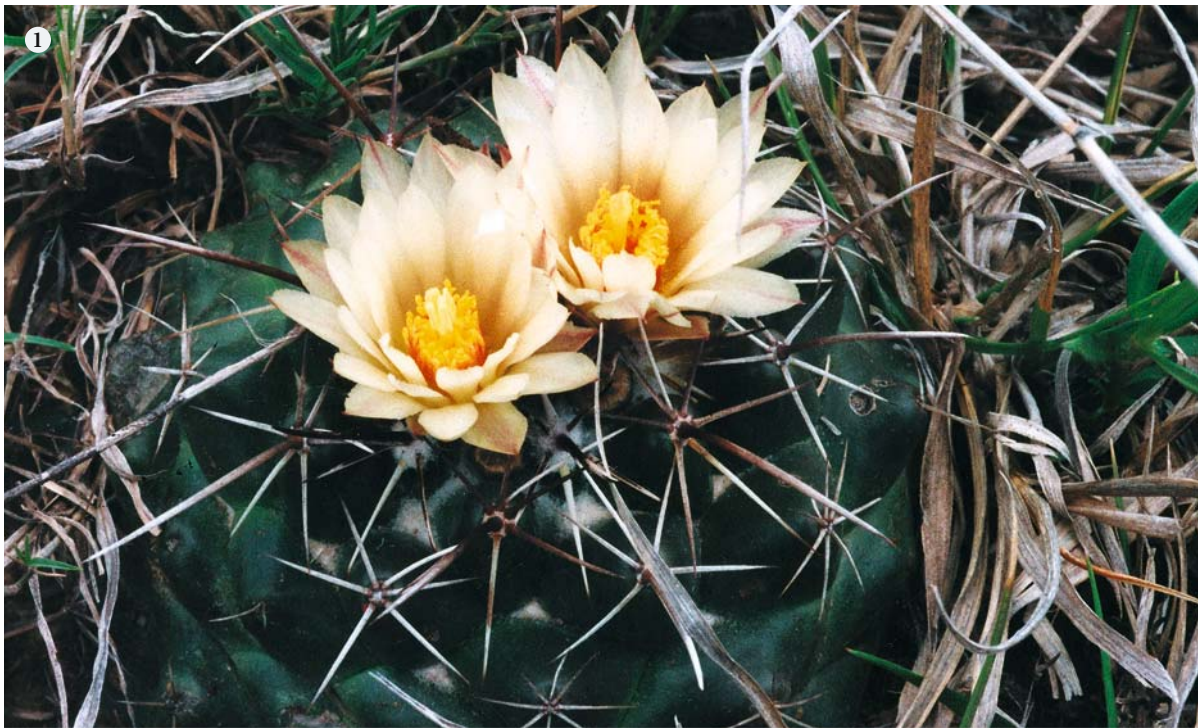


Plate 29. *Coryphantha vogtherriana*. 1, 3 and 4 *C. vogtherriana*, Monte Caldera SLP (photos: W.A. FitzMaurice). 2 Location near Monte Caldera, with Betty and W.A. FitzMaurice

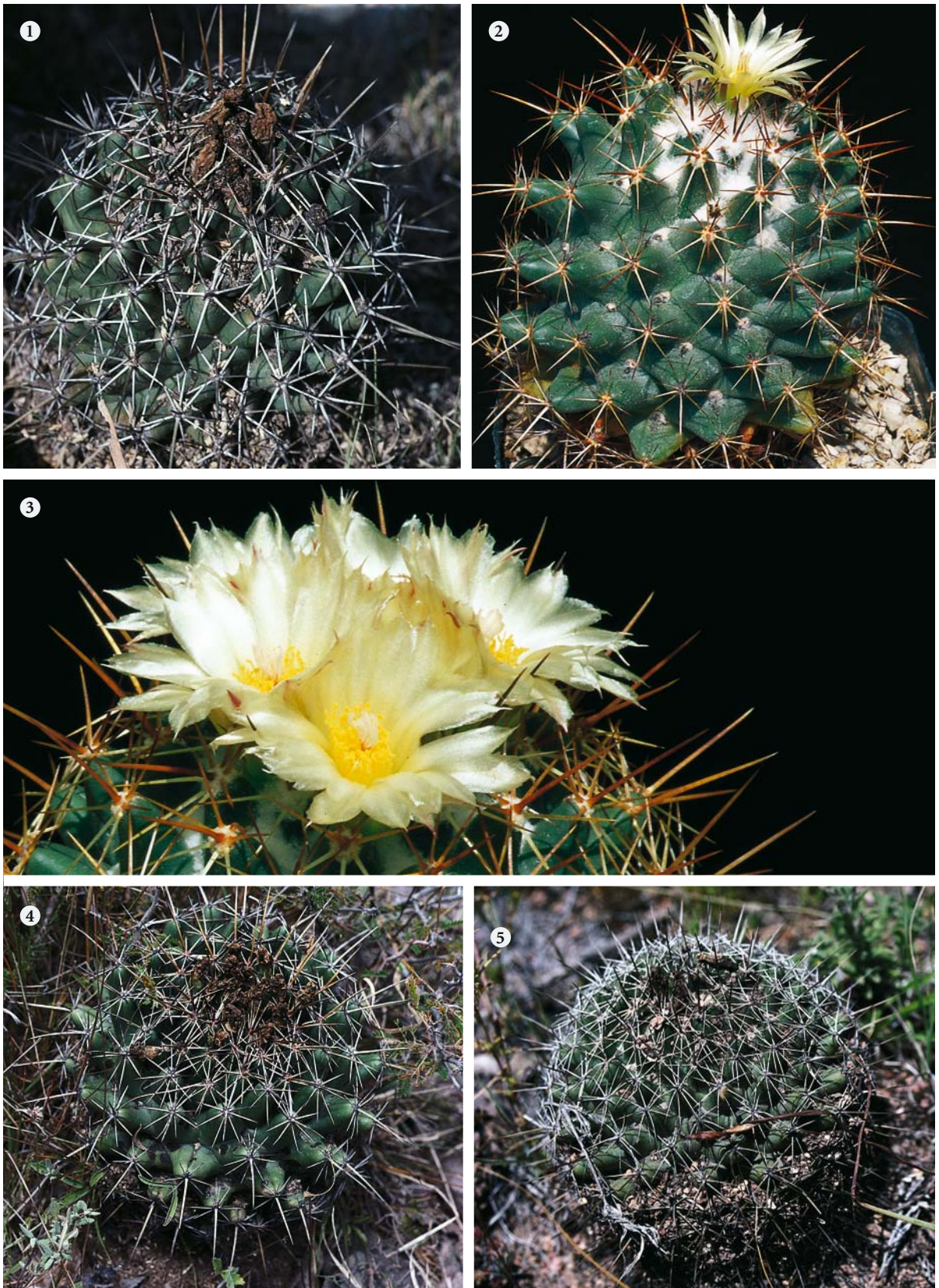


Plate 30. *Coryphantha georgii*. 1 *C. georgii*, Estación Villar SLP. 2 *C. georgii* (cultivar). 3 *C. georgii* (cultivar). 4 *C. georgii*, Monte Caldera SLP. 5 *C. georgii* near the road to Xichú GTO

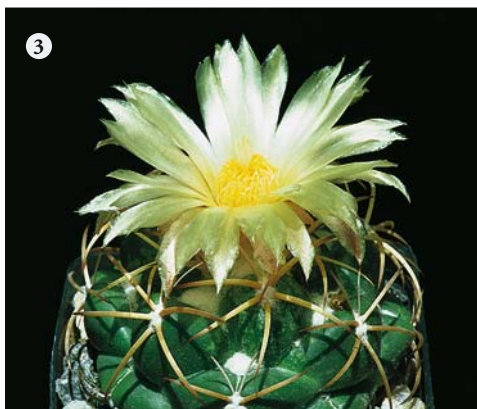


Plate 31. Flower colour of *Coryphantha elephantidens*. 1–4 The variability of flower colour of *C. elephantidens* subsp. *elephantidens* from red to yellow

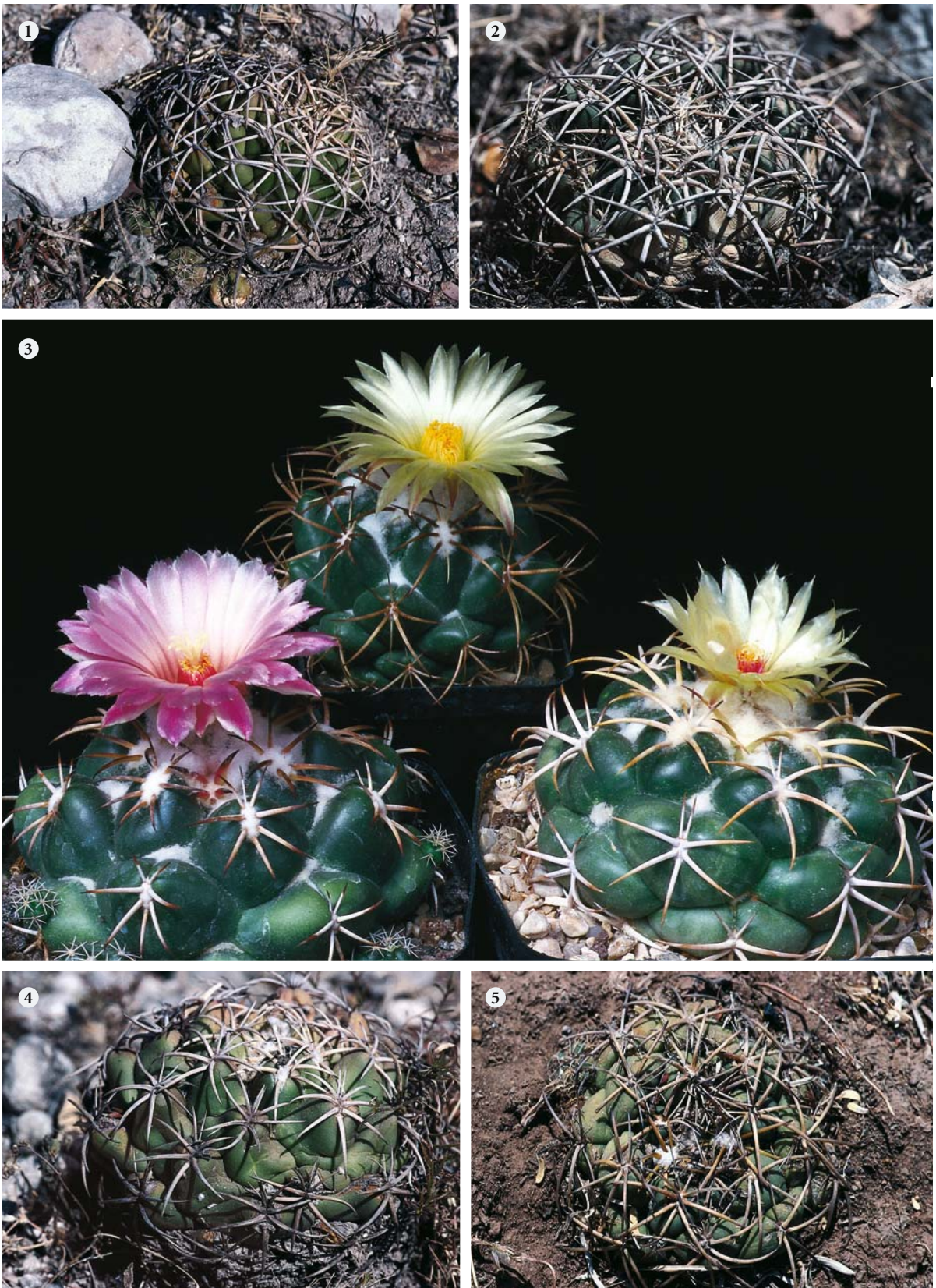


Plate 32. *Coryphantha elephantidens*. 1 *C. elephantidens* subsp. *elephantidens*, Tepalcingo MOR. 2 *C. elephantidens* subsp. *elephantidens*, Zacatepec MOR. 3 *C. elephantidens* subsp. *elephantidens* (the two in front) in comparison with *C. elephantidens* subsp. *greenwoodii* (behind). 4 *C. elephantidens* subsp. *elephantidens*, Las Estacas MOR. 5 *C. elephantidens* subsp. *elephantidens* ("garessii" form), Tepetongo ZAC

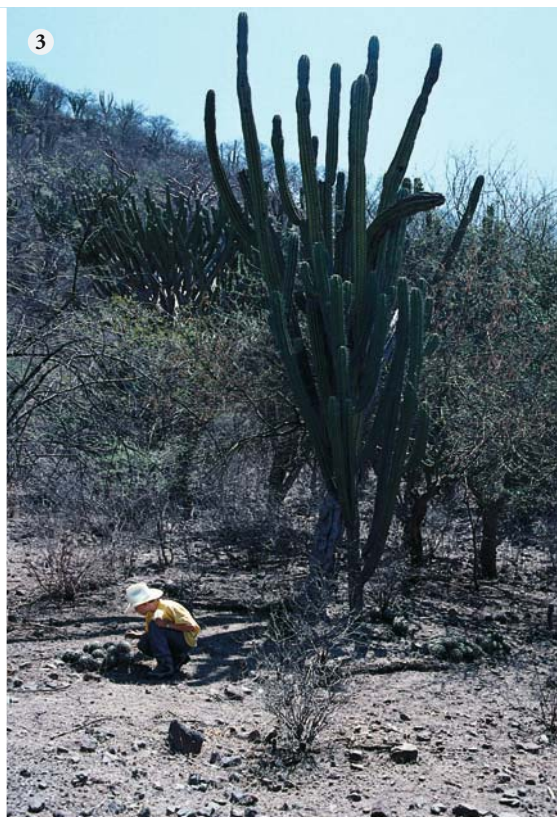


Plate 33. *Coryphantha elephantidens*. 1 *C. elephantidens* subsp. *bumamma* (cultivar from Felix Krähenbühl). 2 *C. elephantidens* subsp. *bumamma* detailed view, Totolapán OAX. 3 Location of *C. elephantidens* subsp. *bumamma* near Totolapán OAX with Julian Dicht. 4 *C. elephantidens* subsp. *bumamma* group, Totolapán OAX



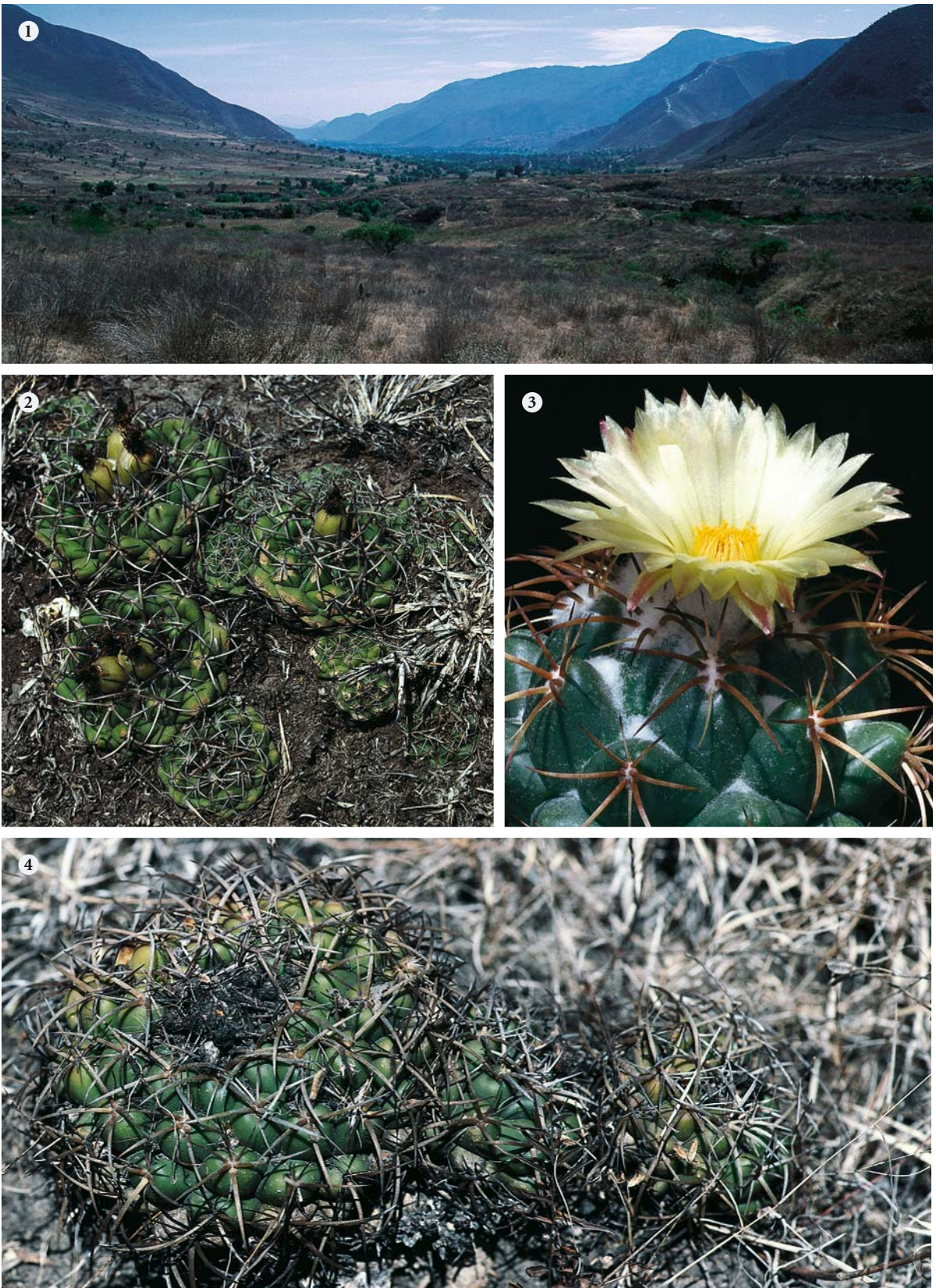


Plate 34. *Coryphantha elephantidens*. 1 Type locality of *C. elephantidens* subsp. *greenwoodii* near Acultzingo VER. 2 *C. elephantidens* subsp. *greenwoodii* with fruits, Acultzingo VER. 3 *C. elephantidens* subsp. *greenwoodii* (cultivar). 4 *C. elephantidens* subsp. *greenwoodii*, Acultzingo VER



Plate 35. *Coryphantha retusa*. 1 Typical habitat of *C. retusa* near Ocotepc OAX. 2, 3 Two times *C. retusa* in flower (cultivars Felix Krähenbühl), Petalcingo PUE

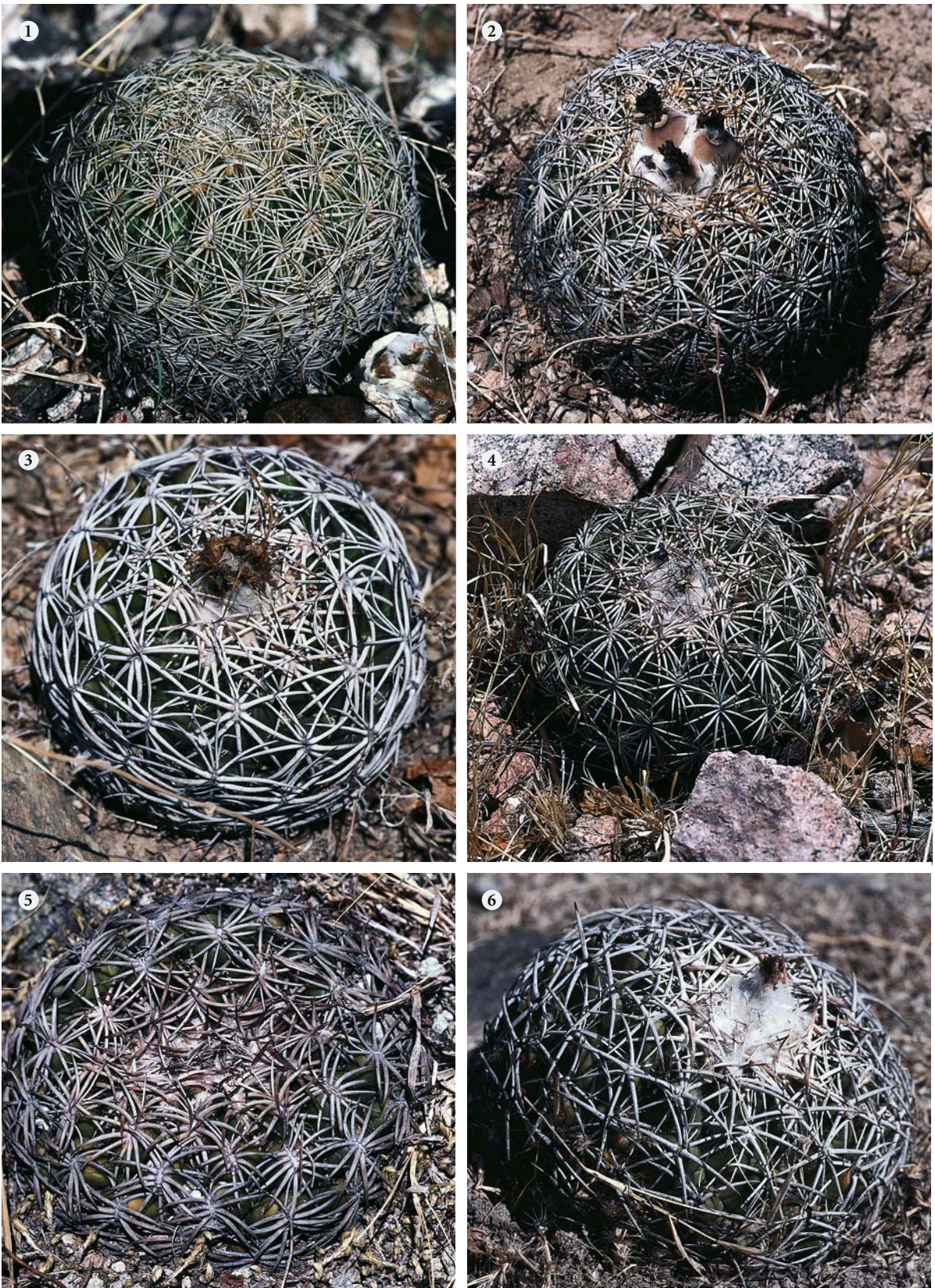


Plate 36. The variability of the spination of *Coryphantha retusa* at different locations. 1 Chazumba OAX. 2 Acatlán PUE. 3 north of Acatlán PUE. 4 Xuyacatlán PUE. 5 Ocoatepec OAX. 6 Tehuiztingo PUE



Plate 37. *Coryphantha pycnantha*. 1 *C. pycnantha* east of Tecamachalco PUE. 2 *C. pycnantha* south of Ciudad Shahogun HGO. 3 A habitat of *C. pycnantha* near Zempoala HGO, destroyed by men. 4 *C. pycnantha* south of Zempoala HGO. 5 *C. pycnantha* with fruits, San Miguel Regla HGO



Plate 38. *Coryphantha pycnantha*. 1-3 *C. pycnantha* with flowers and fruits (cultivars)





Plate 39. *Coryphantha tripugionacantha*. 1 *C. tripugionacantha* at the type locality San Juan Capistrano ZAC (photo: J. Chalet). 2 *C. tripugionacantha* in flower (cult. and photo A. Böcker). 3 Seedlings of *C. tripugionacantha*. (Photo: A. Böcker)



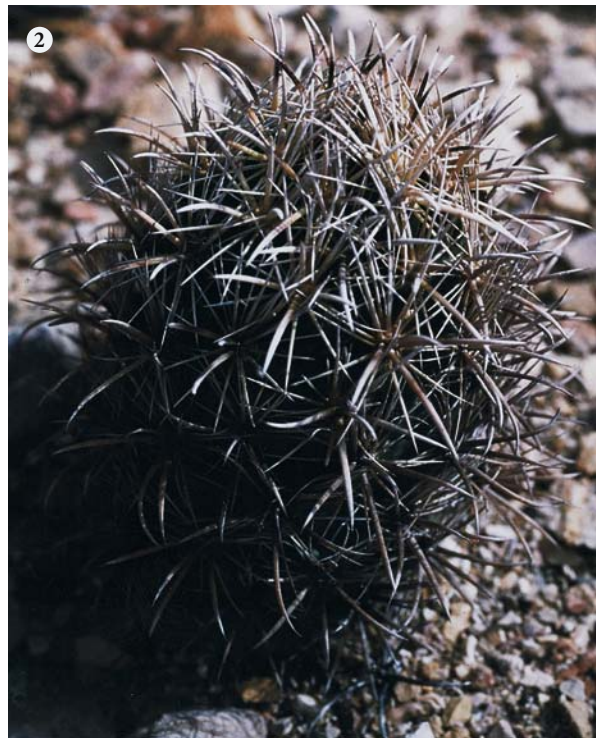


Plate 40. *Coryphantha kracikii*. 1 *C. kracikii* in flower (cult. and photo: K. Kracik). 2, 3 *C. kracikii* at the type locality El Diamante DGO. (Photos: K. Kracik)

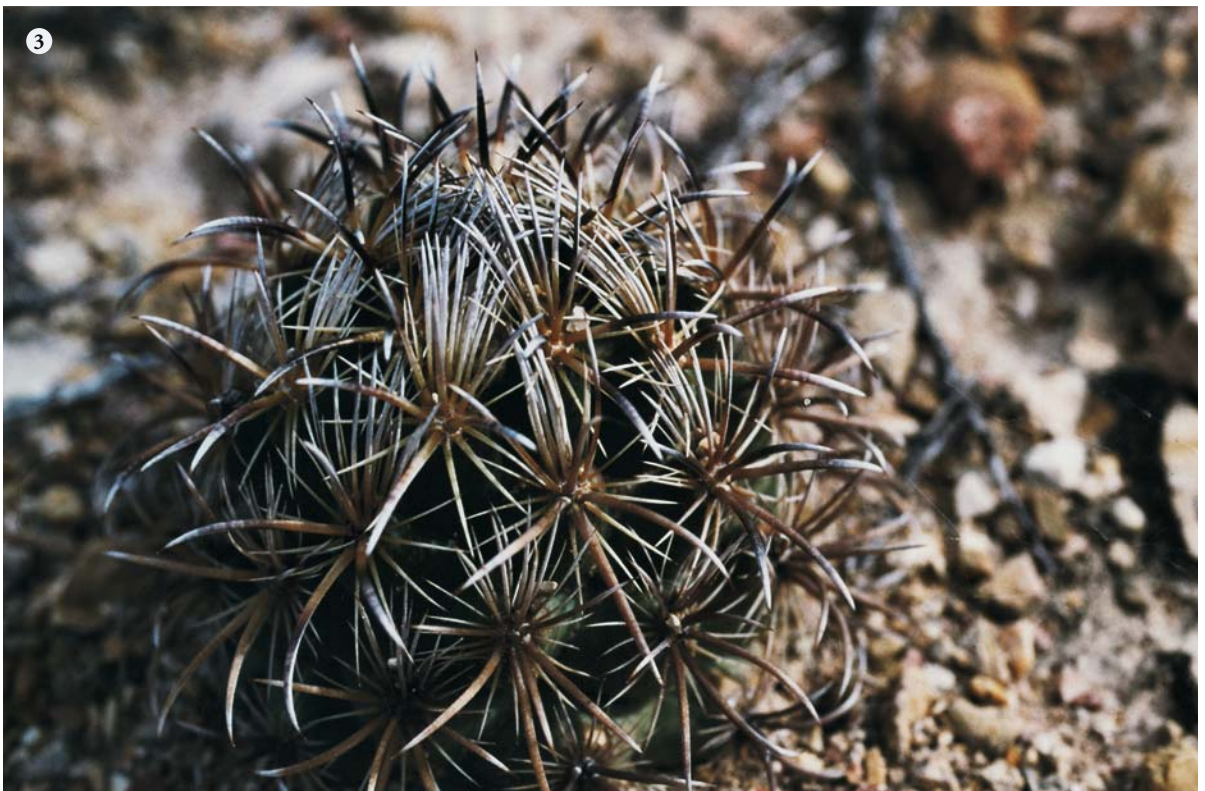




Plate 41. *Coryphantha salinensis*. 1,2 Different stages of development of the spination of *C. salinensis* near Microondas Pedernales NL. 3 *C. salinensis* in flower (cultivar). 4 Very old plant of *C. salinensis*, Candela COAH



Plate 42. *Coryphantha salinensis*. 1 Type locality of *C. salinensis* near Salinas Victoria NL (photo: J. Lüthy). 2 Old plant of *C. salinensis* in flower (cultivar). 3 Young plant of *C. salinensis* in flower (cultivar). 4 *C. salinensis*, Las Cruces TAM. 5: Flower of *C. salinensis* (cultivar)

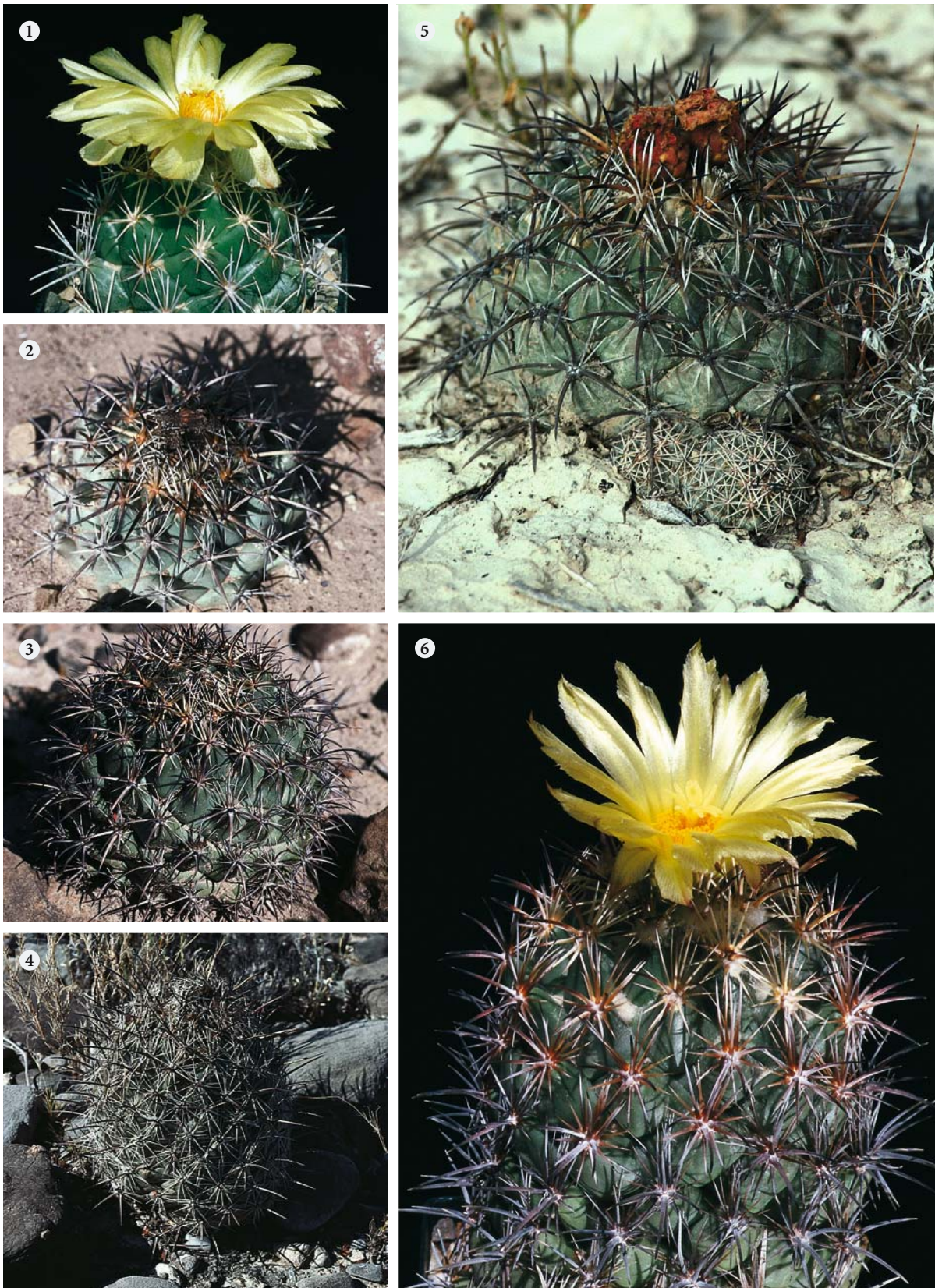


Plate 43. *Coryphantha difficilis*. 1 Young plant of *C. difficilis* with flower (cultivar). 2, 3 *C. difficilis*, La Rosa COAH. 4 *C. difficilis* in the Sierra Paila COAH. 5 *C. difficilis*, Hipolito COAH. 6 Old plant of *C. difficilis* in flower (cultivar)



Plate 44. *Coryphantha durangensis*. 1 Habitat of *C. durangensis* subsp. *durangensis* near Nazas DGO. 2 *C. durangensis* subsp. *durangensis* with erect central spine, Nazas DGO. 3 *C. durangensis* subsp. *durangensis* (cultivar SB 453, Lerdo DGO). 4 *C. durangensis* subsp. *durangensis* without central spine, Nazas DGO

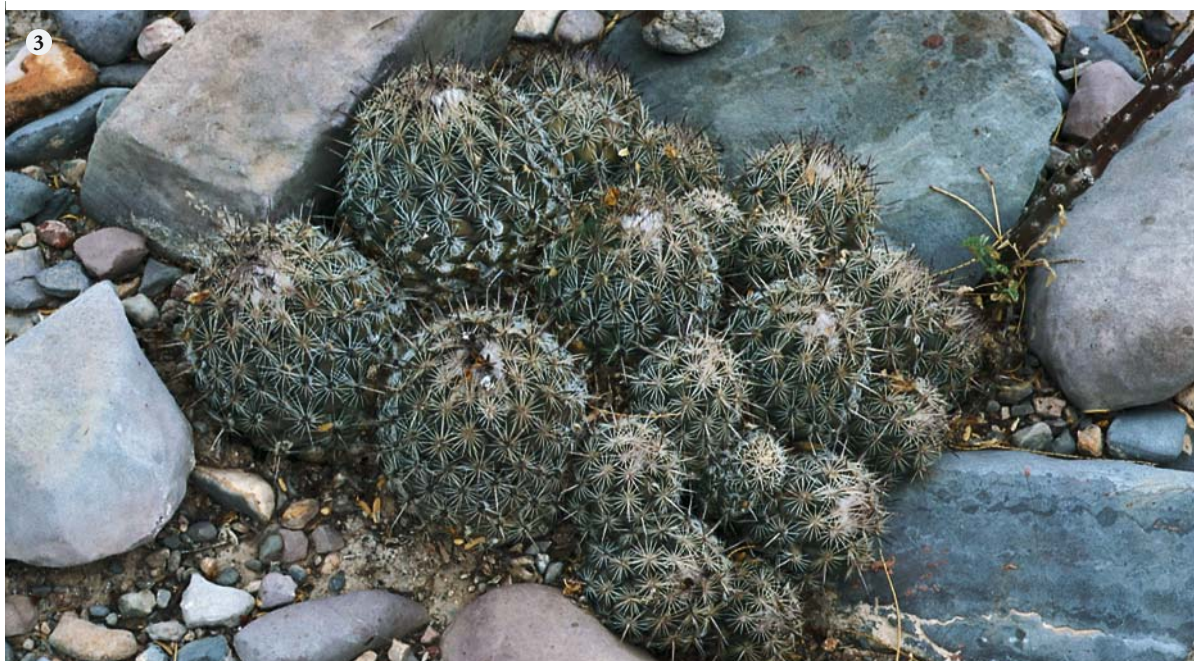


Plate 45. *Coryphantha durangensis*. 1, 2 Comparison of *C. durangensis* subsp. *durangensis* (left) with *C. durangensis* subsp. *cuencamensis* (right). 3 *C. durangensis* subsp. *cuencamensis* at the type locality Cuencamé DGO. 4 Habitat at the type locality Cuencamé DGO

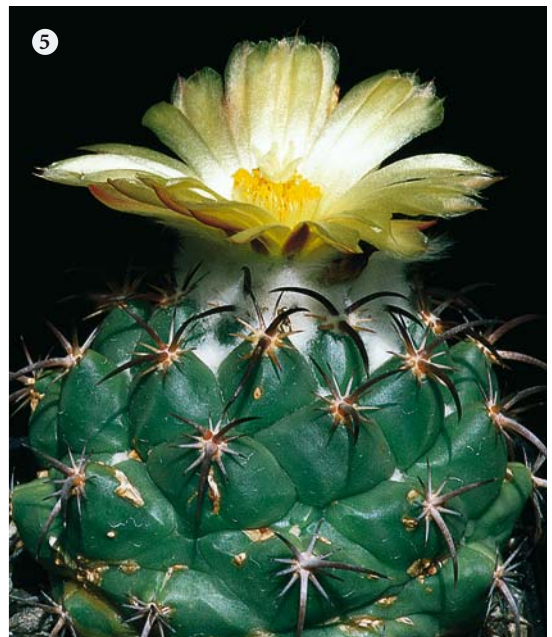
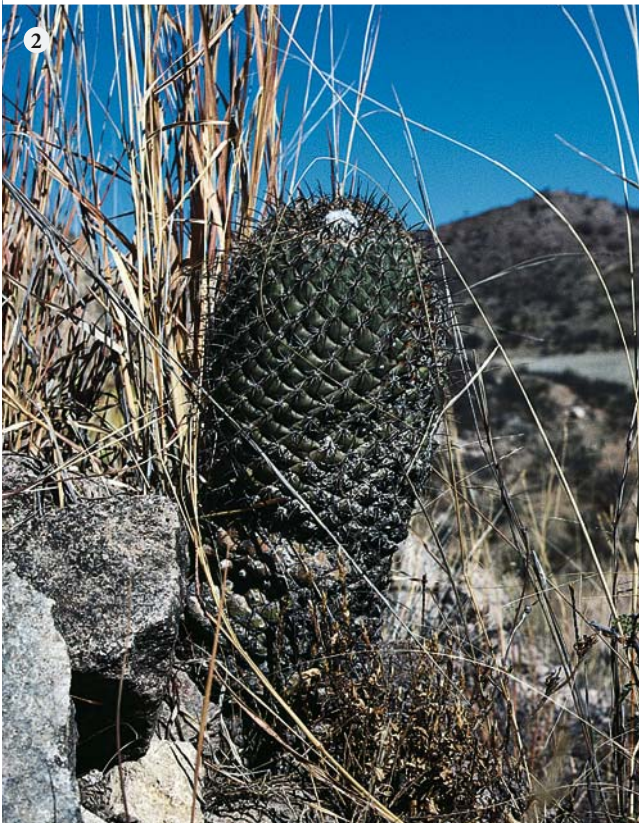
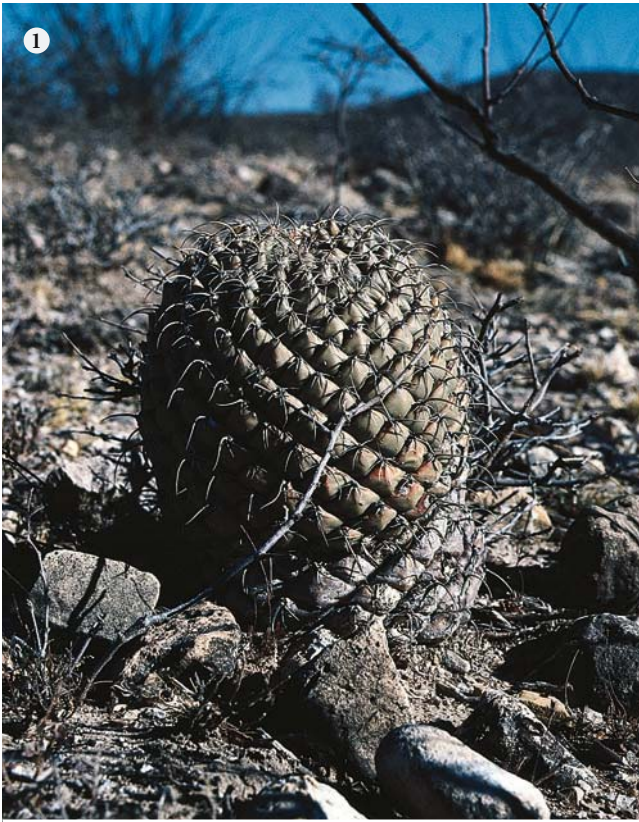


Plate 46. *Coryphantha longicornis*. 1, 2 *C. longicornis* ("grandis" form), El Palmito DGO (photos: J. Lüthy). 3 *C. longicornis*, La Bufa de Indé DGO. 4 *C. longicornis*, Abasolo DGO. 5 *C. longicornis* with flower (cultivar)

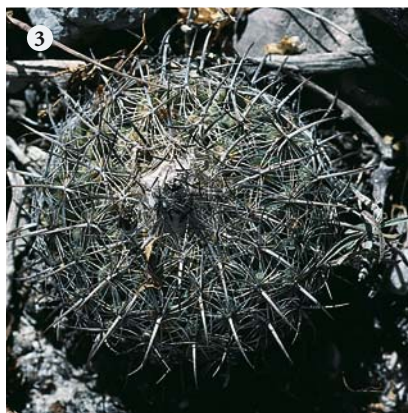


Plate 47. *Coryphantha pallida*. 1 *C. pallida* subsp. *pallida* with flower (cultivar). 2 Habitat with forests of cereus near Zapotitlán de las Salinas PUE. 3, 4 *C. pallida* subsp. *pallida* with 2 and with 3 strong central spines near Zapotitlán PUE. 5 *C. pallida* subsp. *pallida* "classical" form south of Tehuacan PUE



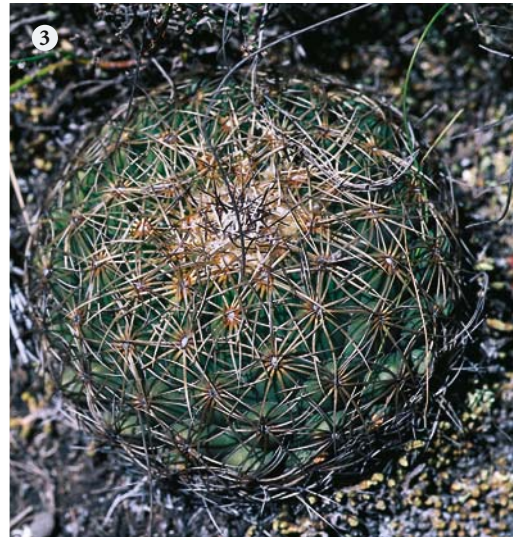


Plate 48. *Coryphantha pallida*. 1–5 The variability of the spination of *C. pallida* subsp. *pallida* with or without up to 3 central spines near Azumbilla PUE, together with flowering *Mammillaria napina*

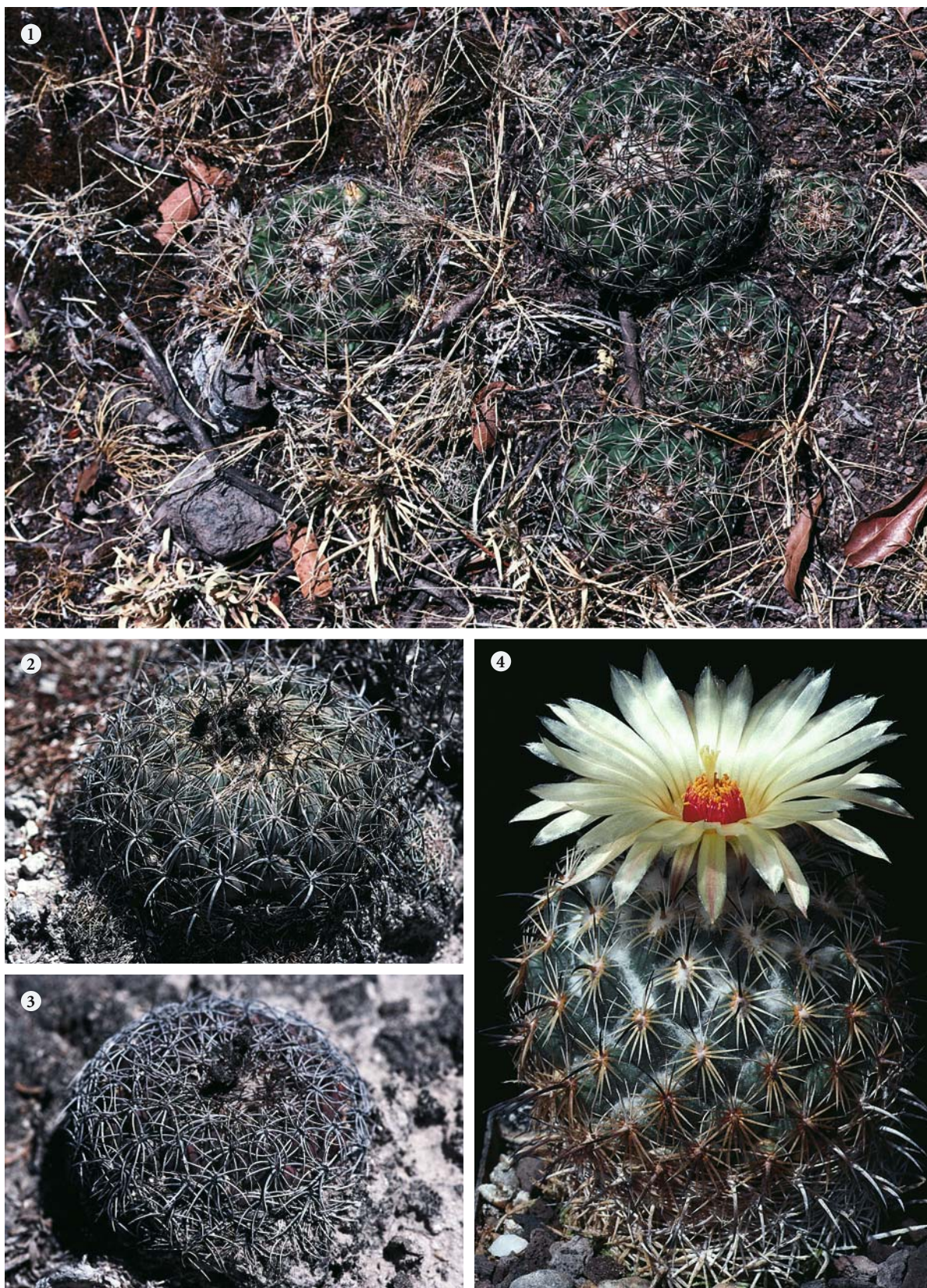


Plate 49. *Coryphantha pallida*. 1 *C. pallida* subsp. *pallida* at the type locality of *C. pseudoradians* near Suchixtlahuaca OAX. 2, 3 *C. pallida* subsp. *pallida* with and without central spine, Nochixtlán OAX. 4 *C. pallida* subsp. *pallida* in flower (cultivar)

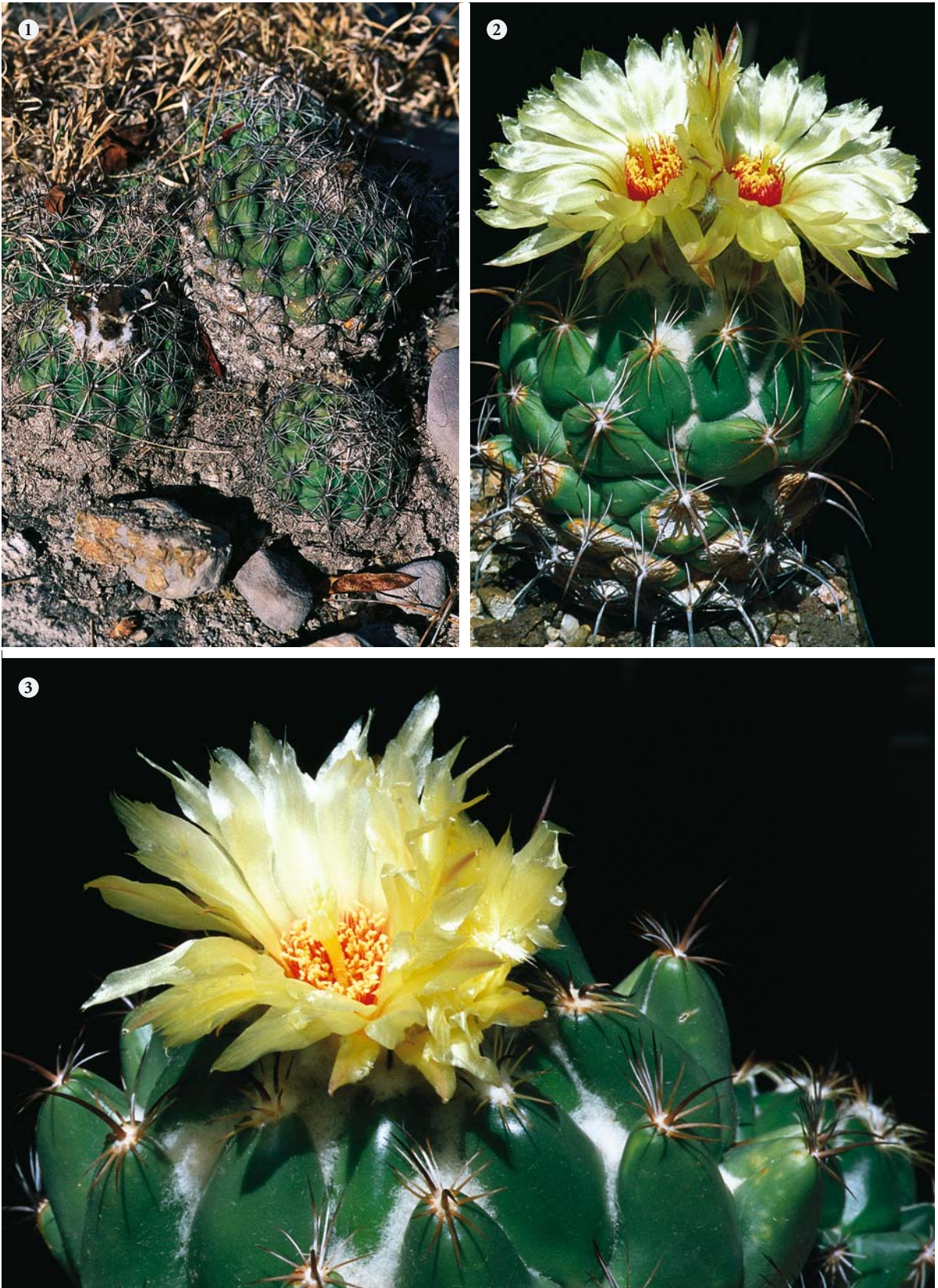


Plate 50. *Coryphantha pallida*. 1 *C. pallida* subsp. *calipensis*, Chilac PUE. 2, 3 *C. pallida* subsp. *calipensis* with flowers (cultivars)

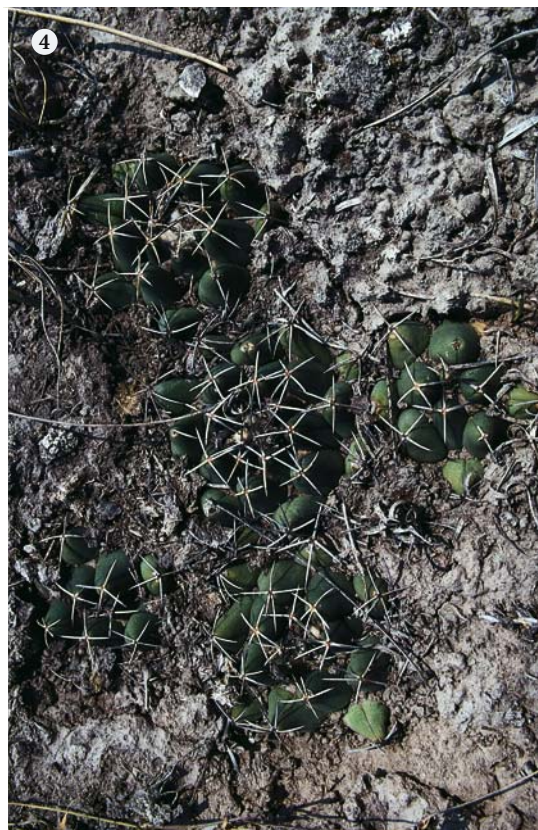


Plate 51. *Coryphantha maiz-tablasensis*. 1 *C. maiz-tablasensis* with flowers (cultivar). 2 Habitat of *C. maiz-tablasensis* north of Rio Verde SLP. 3 northern form of *C. maiz-tablasensis* (cultivar) near Matehuala SLP. 4, 5 *C. maiz-tablasensis* in the lagoon of Las Tablas SLP

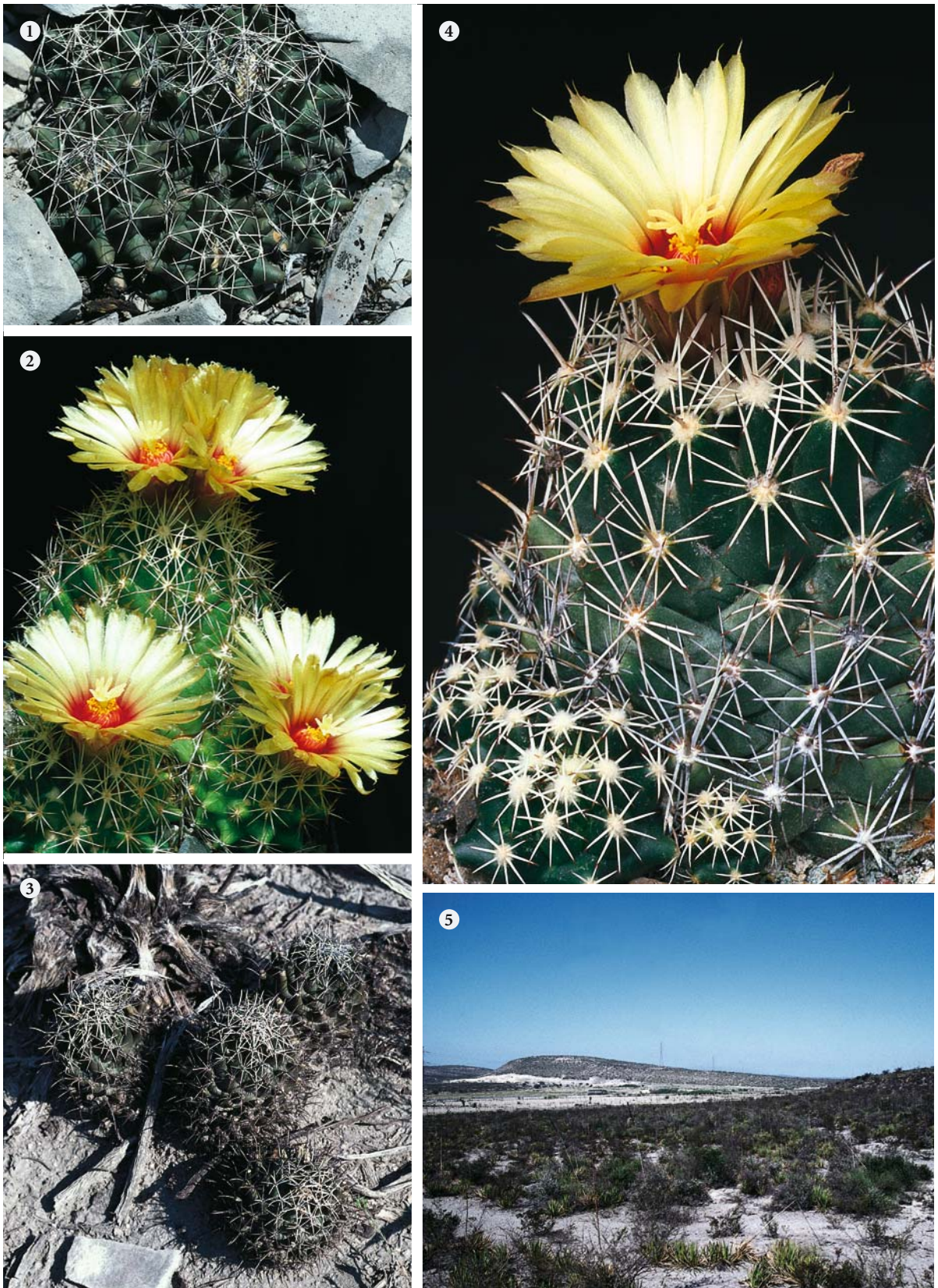


Plate 52. *Coryphantha sulcata*. 1 *C. sulcata* San Alberto COAH. 2, 4 *C. sulcata* in flower (cultivars SB 486, Val Verde County, Texas, USA). 3 *C. sulcata* ("speciosa" form) Villafrontera COAH. 5 Habitat of *C. sulcata* in the industrial zone of Villafrontera COAH



Plate 53. *Coryphantha hintoniorum*. 1–3 *C. hintoniorum* subsp. *hintoniorum* at the type locality San Rafael NL (photo 1: G. Hinton). 4 Habitat of *C. hintoniorum* subsp. *hintoniorum* in the prairie near San Rafael NL

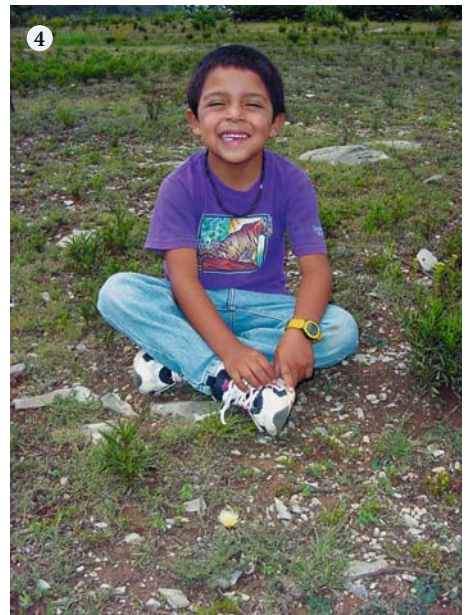


Plate 54. *Coryphantha hintoniorum*. 1 *C. hintoniorum* subsp. *geoffreyi* (photo: G. Hinton). 2: Geoffrey Hinton (photo: G. Hinton). 3–5 *C. hintoniorum* subsp. *geoffreyi* at the type locality San Pedro Sotolar NL, together with *Echinocereus knippelianus*.

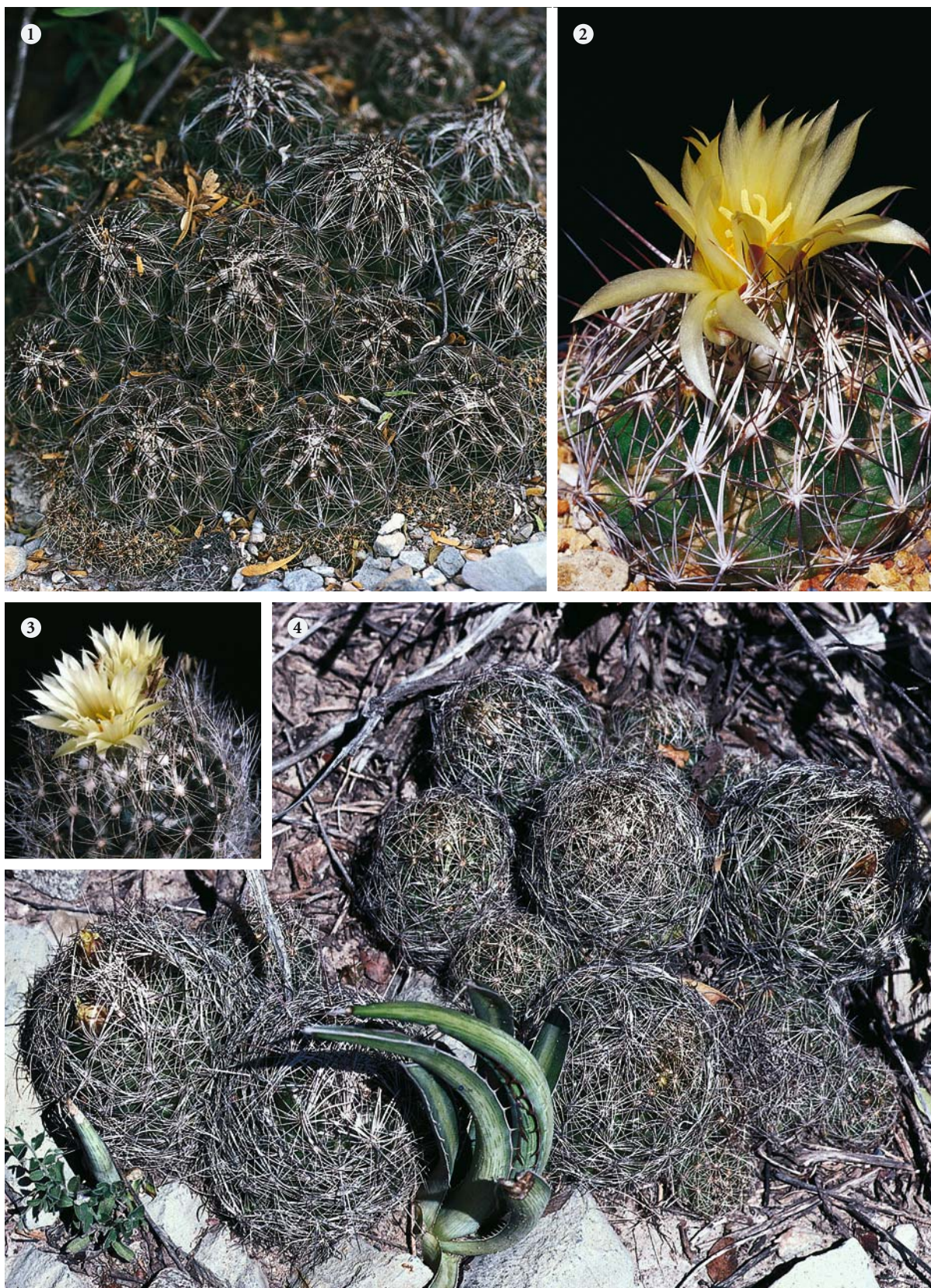


Plate 55. *Coryphantha nickelsiae*. 1 *C. nickelsiae*, Huasteca Cañon NL. 2, 3 *C. nickelsiae* with flowers (cultivars). 4 *C. nickelsiae*, Candela COAH

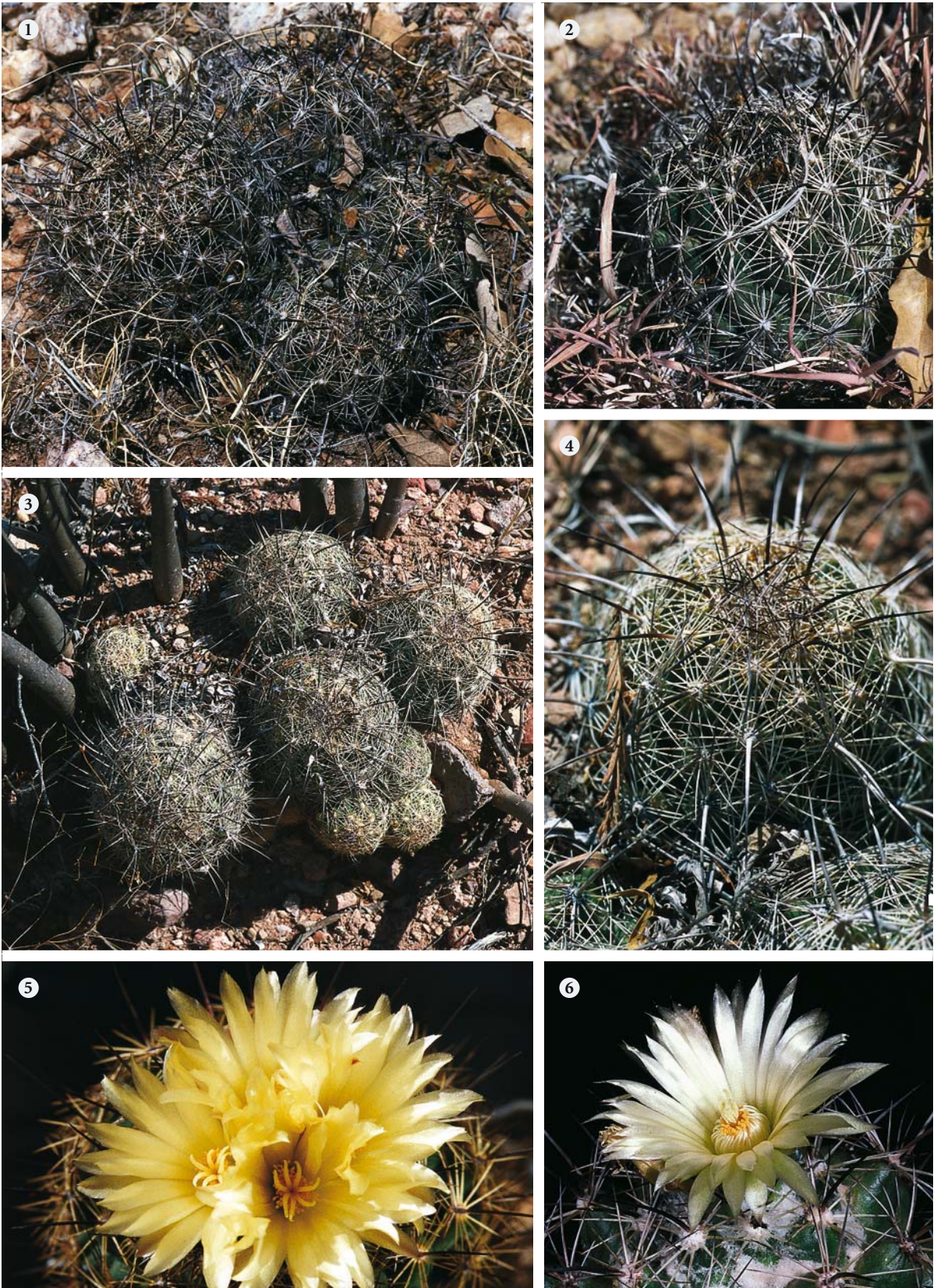


Plate 56. *Coryphantha pseudonickelsiae*. 1, 2 *C. pseudonickelsiae* near Indé DGO. 3, 4 *C. pseudonickelsiae*, Abasolo DGO. 5, 6 Flowers of *C. pseudonickelsiae* (cultivars)

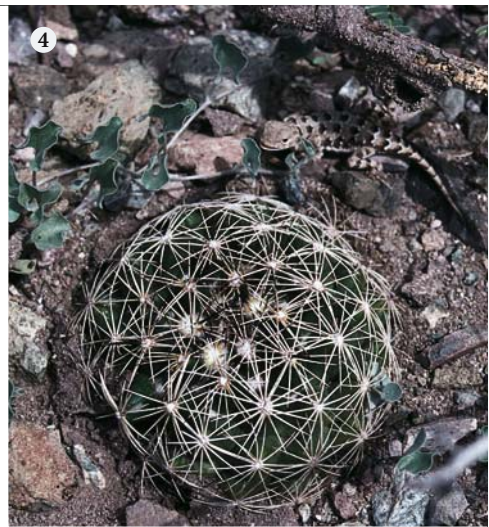


Plate 57. *Coryphantha compacta*. 1 *C. compacta* with flower (cultivar). 2, 3 *C. compacta* with and without central spine, Ciudad Durango DGO. 4, 5 *C. compacta* with and without central spine, Valle de Olivos CHI. 6 *C. compacta*, Valle de Rosario CHI

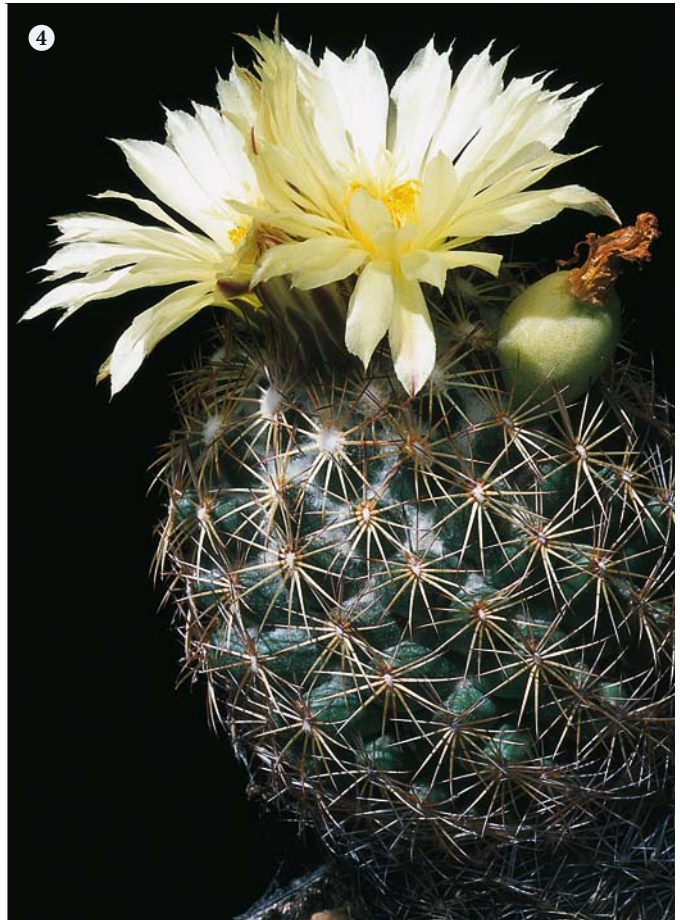


Plate 58. *Coryphantha cornifera*. 1 *C. cornifera*, Tolantongo HGO. 2 *C. cornifera* ("schwarziana" form), San Felipe GTO. 3-5 Flowering *C. cornifera* with different spination (cultivars)

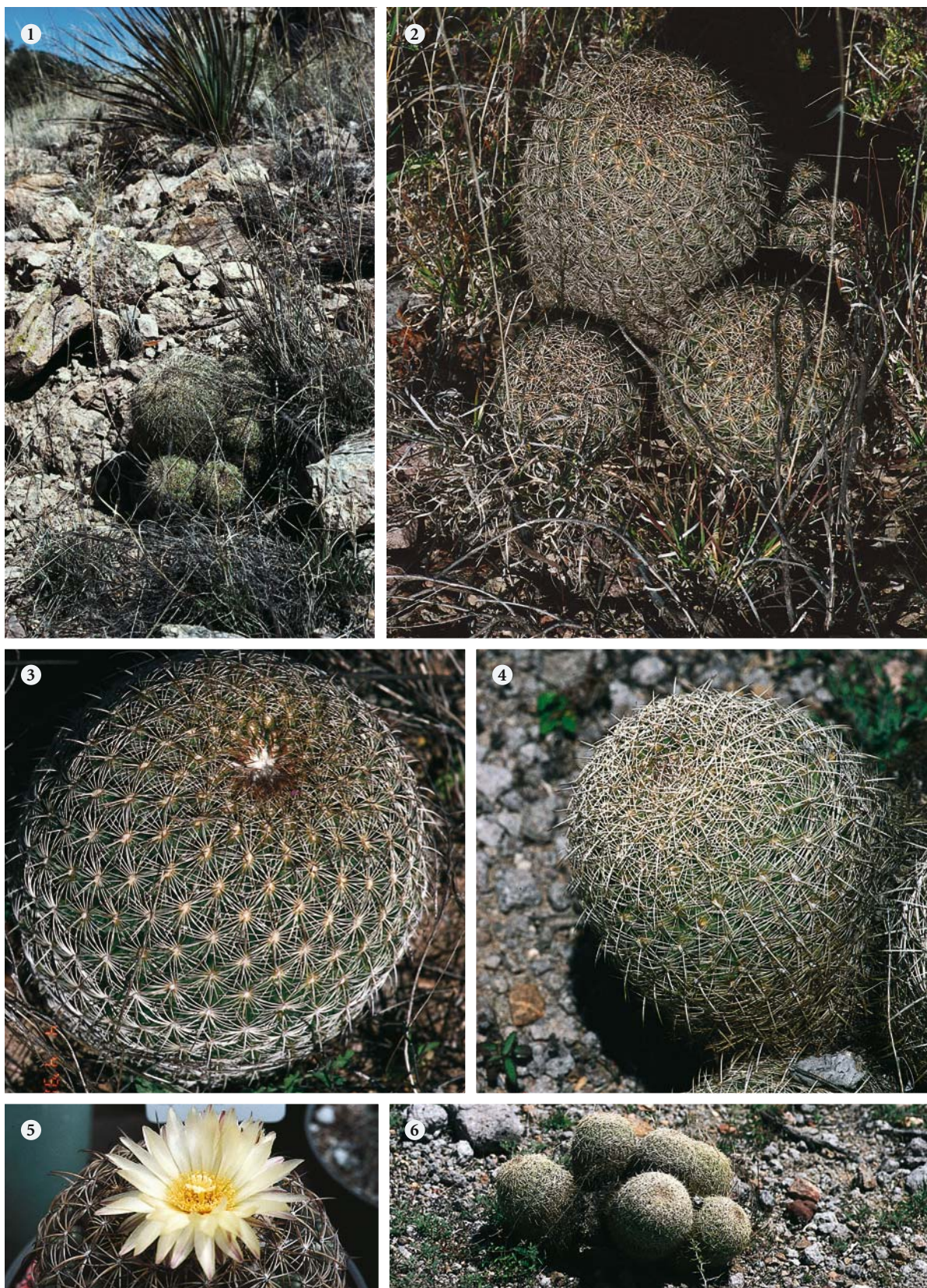


Plate 59. *Coryphantha recurvata*. 1 *C. recurvata* subsp. *recurvata*, Sycamore Canyon, Arizona, USA (photo: J. Lüthy). 2 *C. recurvata* subsp. *recurvata*, Moctezuma SON (photo: R. Römer). 3, 4 Varying spination of *C. recurvata* subsp. *recurvata* near Moctezuma SON (photos: R. Römer). 5 Young plant of *C. recurvata* subsp. *recurvata* with flower (cultivar). 6 *C. recurvata* subsp. *recurvata*, Nacoziari SON. (Photo: R. Römer)



Plate 60. *Coryphantha recurvata*. 1 Habitat of *C. recurvata* subsp. *canatlanensis* west of Ciudad Durango DGO. 2 *C. recurvata* subsp. *canatlanensis* west of Ciudad Durango. 3 *C. recurvata* subsp. *canatlanensis* with the single, straight central spine (cultivar). 4 *C. recurvata* subsp. *canatlanensis* with flower buds around the top, west of Canatlàn DGO (photo: C. Glass). 5, 6 *C. recurvata* subsp. *canatlanensis* at the type locality west of Canatlàn DGO



Plate 61. *Coryphantha delicata*. 1 *C. delicata*, San Antonio TAM. 2 *C. delicata*, Palmillas TAM. 3 *C. delicata*, Entronque Huizache SLP. 4 *C. delicata*, La Escondida NL. 5 Flowering *C. delicata* with and without central spine (cultivars). 6: *C. delicata*, San Francisco SLP

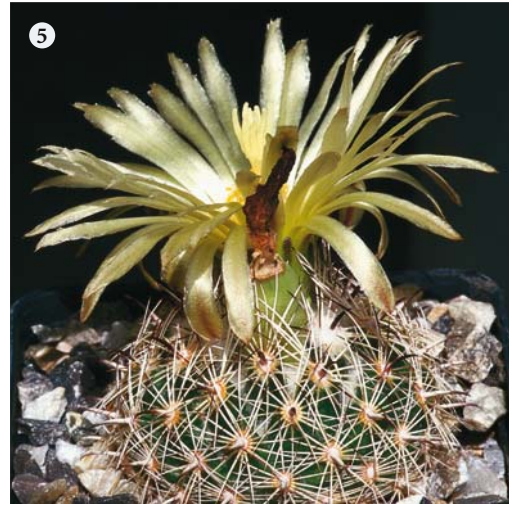


Plate 62. *Coryphantha delicata*. 1 Large group of *C. delicata*, La Escondida NL. 2 *C. delicata* with and without central spine near Arteaga COAH. 3-6 Different forms of flowering *C. delicata* (cultivars)



Plate 63. *Coryphantha neglecta*. 1, 2 *C. neglecta*, Casas Coloradas COAH. 3 *C. neglecta* at the type locality near El Sago COAH. 4 *C. neglecta*, El Sacrificio COAH. 5 *C. neglecta* west of Cuatrociénegas COAH. 6 *C. neglecta* in flower (cultivar)



Plate 64. *Coryphantha pseudoechinus*. 1–4
C. pseudoechinus subsp. *pseudoechinus* in
the Sierra Paila COAH



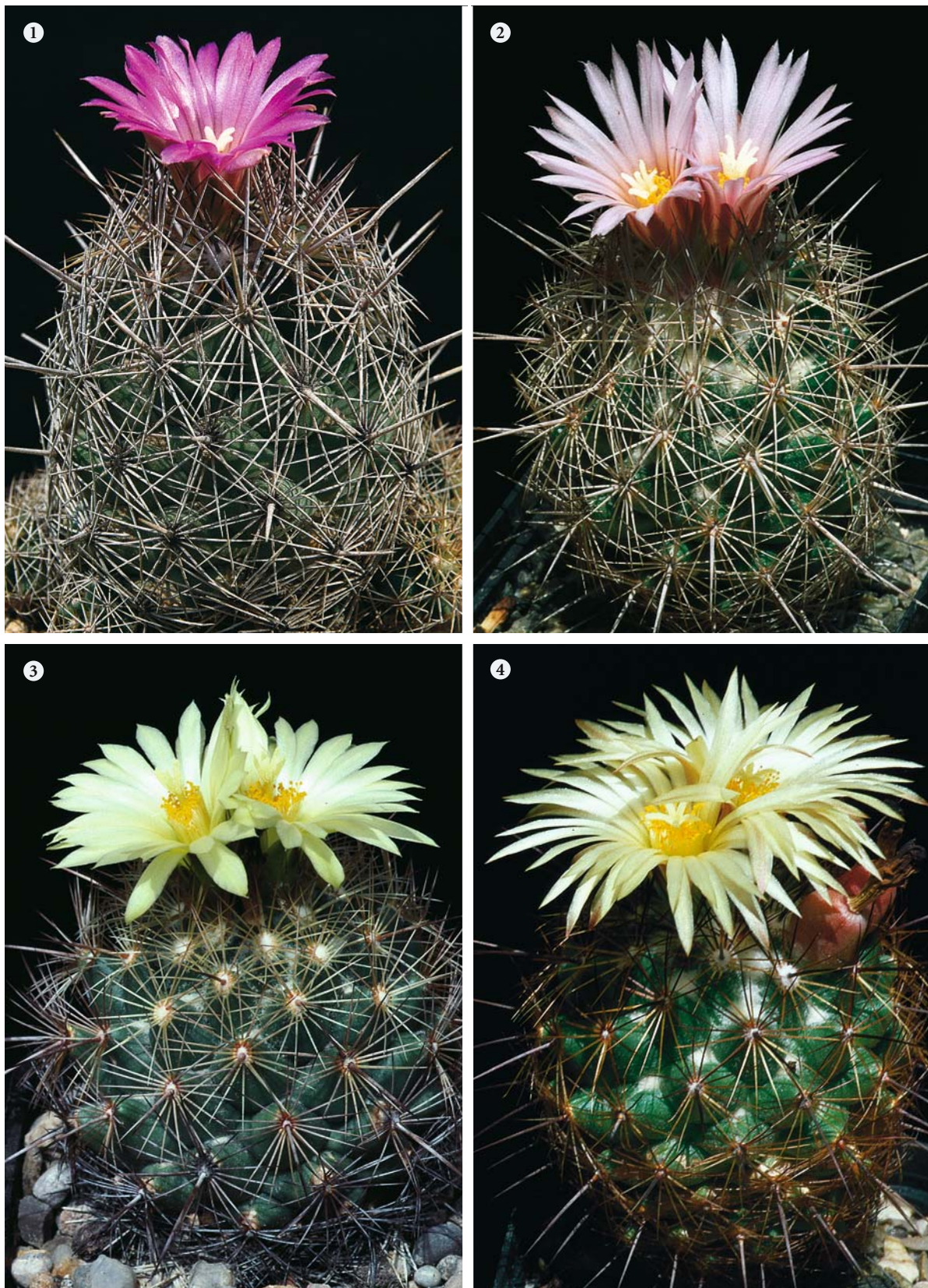


Plate 65. *Coryphantha pseudoechinus*. 1, 2 *C. pseudoechinus* subsp. *pseudoechinus* with typical red flower (cultivars). 3, 4 *C. pseudoechinus* subsp. *laui* with typical yellow flower (cultivars)

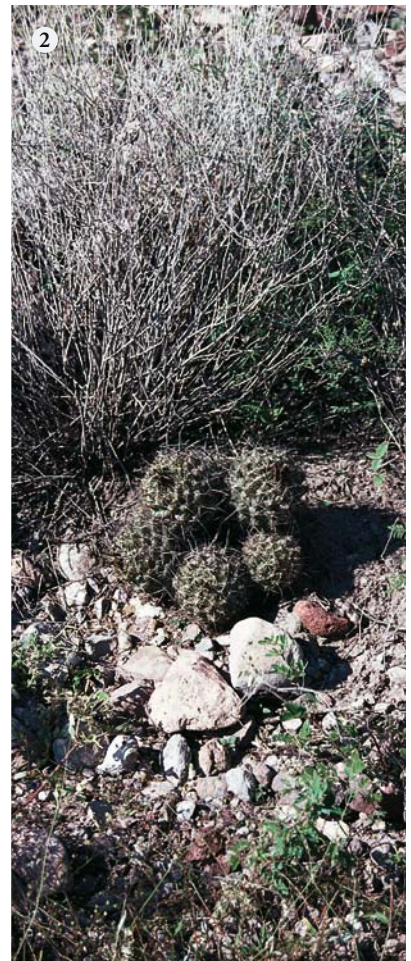


Plate 66. *Coryphantha delaeliana*. 1 *C. delaeliana*, Escalón CHI. 2 *C. delaeliana*, Ciudad Chihuahua CHI. 3 *C. delaeliana* in flower (cultivar). 4 *C. delaeliana* at the type locality near Parras COAH



Plate 67. *Coryphantha ramillosa*. 1 *C. ramillosa* subsp. *ramillosa* west of Cuatrociénegas COAH. 2 The habitat of *C. ramillosa* subsp. *ramillosa* near Cuatrociénegas COAH. 3, 4 *C. ramillosa* subsp. *ramillosa* with pink flower (cultivars SB 908, Brewster County, Texas, USA)

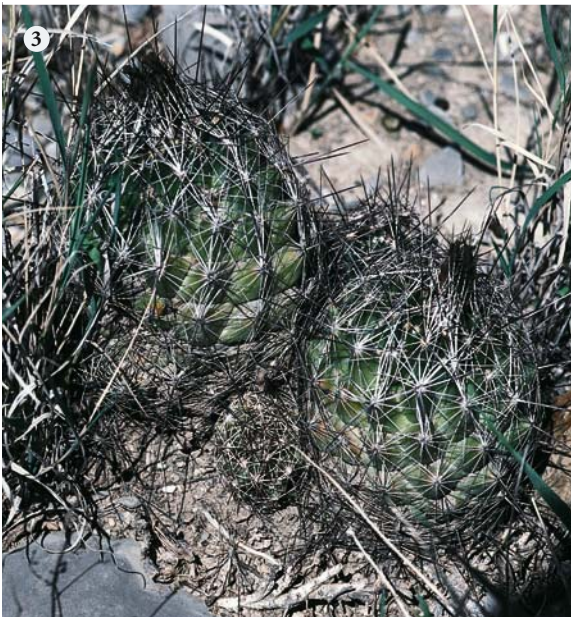


Plate 68. *Coryphantha ramillosa*. 1 *C. ramillosa* subsp. *ramillosa* east of Cuatrociénegas COAH. 2 *C. ramillosa* subsp. *santarosa*, San Alberto COAH. 3 *C. ramillosa* subsp. *santarosa*, Minas de Barroterán COAH. 4 *C. ramillosa* subsp. *santarosa* with yellow flower (cultivar). 5 *C. ramillosa* subsp. *santarosa* at the type locality near La Babia COAH

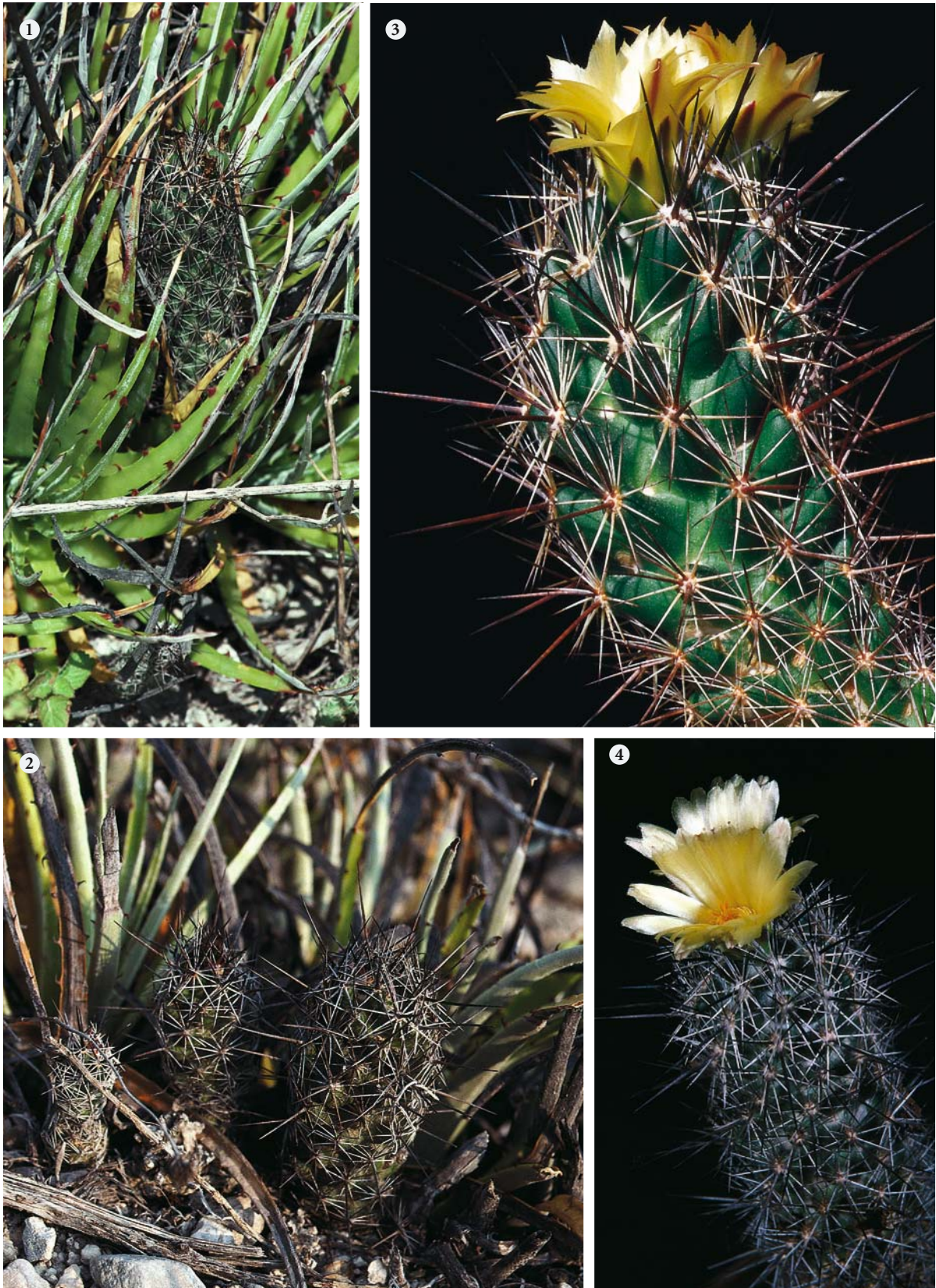


Plate 69. *Coryphantha pulleineana*. 1, 2 *C. pulleineana* at the type locality near Entronque Huizache SLP. 3, 4 *C. pulleineana* with flowers (cultivars)

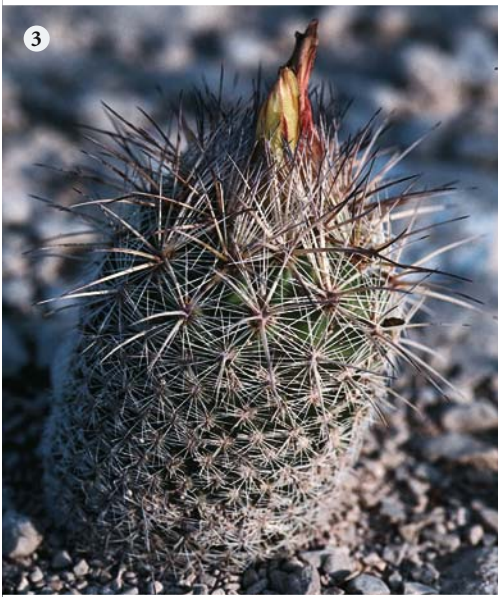


Plate 70. *Coryphantha werdermannii*. 1–4 *C. werdermannii* west of Cuatrociénegas COAH, from youth form to very old plant. 5 *C. werdermannii* in flower (cultivar)



Plate 71. *Coryphantha echinus*. 1, 2 *C. echinus* in the habitat Cuatrociénegas. 3, 4 *C. echinus*, El Paradero CHI (photos: G. Matuszewski). 5, 6 Flowering *C. echinus* SB 391 Pecos County, Texas, USA



Plate 72. *Coryphantha gracilis*. 1, 5 *C. gracilis* in flower (cultivars). 2 *C. gracilis* at the type locality Rancho Pelayo CHI. 3-5 The fruit of *C. gracilis*, turning red. 6 The habitat of *C. gracilis* at the type locality Rancho Pelayo CHI

anth segments linear-lanceolate with thinner, 2 mm long tip, 3–3.5 cm long and 3 mm wide, whitish-yellow. Filaments red, yellow towards the tips, 10–12 mm long, anthers yellow, stigma green with 9 whitish lobes. **Fruit** oblong green juicy berry with attached flower remnants, 35 mm long and 10 mm diameter. **Seeds** light brown, reniform, 1.3 mm long, 1.1 mm wide, testa reticulate.

Distribution: only at the **type locality** = **location checked:** Mexico: San Juan Capistrano, Zacatecas, growing under small shrubs of *Bursera* and other xerophyte plants, not plentiful, on humid slopes and on arcillose soil, at 1000 m above sealevel.

Habitat: On plain ground or slight declines in clayish soil.

Incidence: Least concern.

Illustrations: Distribution see Plate 11, map 1; plant portrait see Plate 39.

II.A.c Series *Salinenses* Dicht & A. Lüthy

Cact. Syst. Init. 11: 15, 2001.

Type: *Coryphantha salinensis* (Poselger) Dicht & A. Lüthy

Definition: Tubercles appressed (“pineapple”-like), majority of radial spines needle-like, dominating central spine (if present) porrect.

21. *Coryphantha kracikii* J. J. Halda,
J. Chalupa et P. Kupcak

Cactaceae etc. 1 :12, 2002

Type: PR no. JJH 4709; leg. H. Swoboda 10. 06. 1982.

Body single, globose to short columnar, 9 cm diameter, up to 17 cm high, dull grey-green, top depressed, white-woolly, topped by bundled, interwoven spines, strong, long main root and fibrous roots. **Tubercles** in 5 and 8, occasionally in 8 and 13 series, broad at the base, conical-cylindrical, rounded, flattened above, obliquely cut, appressed, at the base 24 mm wide, 16 mm high, length of upper surface 12 mm, length of lower surface 16 mm, with fine groove. **Axils** woolly in

youth. **Areoles** round, 4 mm diameter, white-woolly in youth, completely bald in later years. **Radial spines** 24–26, lower and lateral 7–9 radiating, strong, thick needle-like, up to 15 mm long, light to horn-coloured with dark tips, upper 12–17 bundled, longer, up to 25 mm, somewhat thinner, white with dark tips, later all turning grey. **Central spines** 5–8, the longest downward, slightly protruding and curved downwards, up to 25 mm long, on each side 1–2 obliquely protruding, somewhat shorter, all thick, subulate, at first black with light tips, then light brownish with dark tips and turning grey, in the upper part of the areole up to 3 more central spines, hardly protruding, directed upwards with the radial spines, slightly curved, subulate, light with dark tips. **Flowers** funnellform, 4–8 cm diameter, outer perianth segments broad lanceolate, acute, yellow with purple-red, broad mid-stripe, inner perianth segments spatulate, acute, dentate towards the tips, shiny yellow, deep red in the throat, filaments reddish, anthers yolk-yellow, stigma white-yellow, 7–8 yellowish lobes. **Fruit** juicy berry, olive-coloured above, lighter below, with dried floral remnants attached, 15 mm diameter, 25 mm long. **Seeds** reniform, brown, shiny, reticulate, 1.8 mm long, 1 mm wide, hilum long and white.

Distribution/Location checked: Mexico: Durango: El Diamante. Only one location known.

Habitat: On hills in limestone gravel, 1400 m above sea level.

Differentiation: With the 5–8 strongly curved, stout central spines this species is reminiscent of *C. pycnacantha* and *C. tripugionacantha*, but the centrals are porrect and as regards tubercle form and arrangement (covering above) this species is closest to *C. salinensis* und *C. difficilis*. The flower with the red throat is also very similar to the one of *C. salinensis*.

Comments: This wonderful species has been recently discovered in the region of El Diamante DGO and named in honour of the

Czech cactus grower and researcher Karel Kracik, who was the first one to study this species carefully at its location and to document it.

Illustrations: Distribution see Plate 11, map 2; plant portrait see Plate 40.

22. *Coryphantha salinensis* (Poselger)

Dicht & A. Lüthy

Kakt. and. Sukk. 49 (11): 253, 1998.

Basionym: *Echinocactus salinensis* Poselger, Allg. Gartenz. 21: 106, 1853.

Neotype: Mexico, Nuevo León, Salinas Victoria, 20. 5. 1996, Hinton et al. 27113 (herb. Hinton).

Synonym: *Coryphantha borwigii* Purpus, Gartenflora 1927: 338, 1927.

Body solitary, globose-cylindrical, 8–15 cm high, 7–9 cm diameter, dark grey-green, apex depressed, white-woolly, bundled and interwoven spines overtowering the apex, roots fibrous. **Tubercles** in 8 and 13 series, oblong conical-cylindrical, roundish, in later years pyramidal, appressed and edges obliquely cut, width at the base 17 mm, length of upper surface 8 mm, of lower surface 18–22 mm, with complete, in youth wooly groove. **Axils** woolly in youth. **Areoles** round, 3 mm diameter, woolly in youth. **Radial spines** 12–20, lower and lateral 5–7 spines stronger, firm, needle-like, straight, radiating, 10–15 mm long, light grey to horn-coloured with dark tips, upper 7–13 bundled, longer, 16–20 mm long, needle-like, straight, whitish with dark tips. **Central spines** 1–4, the lower one dominant, porrect, curved downwards like a horn, subulate, 15–21 mm, first horn-coloured to brownish, then becoming black from the tip on both sides, on the upper surface initially. 2–3 upper ones slightly protruding, curved to the sides, 2 laterals 15–18 mm long, colour as dominant central spine, the central one, if present, straight upwards, colour as radial spines, up to 21 mm long, all upper central spines thinner. **Flowers** 5–6 cm diameter, outer perianth segments spatulate, margins

entire, dentate near the tip, acuminate, yellow with greenish-brown dorsal midstripe, inner perianth segments of the same shape, but shiny yellow, throat deep red, filaments red, anthers yellow, stigma whitish-yellow, lobes greenish-yellow. **Fruit** green juicy berry with attached flower remnants, 25 mm long, 10 mm diameter. **Seeds** brown, reniform, 1.8 mm long, 1 mm wide, testa reticulate.

Distribution: Mexico: Coahuila, Nuevo León und Tamaulipas.

Habitat: Alluvial plains and limestone gravel at the foot of the eastern slopes of the Sierra Madre Oriental.

Locations checked: Mexico: Tamaulipas: Las Crucitas. Coahuila: Candela, Higueras. Nuevo León: Bustamante, Codornices, Salinas Victoria, Sabinas Hidalgo, Rinconada, Monterrey-Monclova km 40 and km 70.

Incidence: Least concern.

Comments: The basionym *Echinocactus salinensis* was first described by POSELGER (1853) with the indication “in the plains between Monterrey and Salinas”. Subsequently, this name was missing from the literature until A. ZIMMERMAN’s dissertation in 1985 where it was mentioned as *Coryphantha salinensis* comb.nov.ined. It also appeared in Alfred LAU’s list of field numbers (1983) as Lau Nr. 1387 *Coryphantha salinensis*, Las Crucitas, Tamaulipas.

In 1997, we managed to rediscover this species of Poselger at its type locality Salinas Victoria (Coahuila). We compared it with A. Lau’s *Coryphantha salinensis* (L 1387), whose location near Las Crucitas (Tamaulipas) Alfred Lau had shown us personally. It did not show any important differences. Compared to *Coryphantha salinensis* from the type locality, the plants from Tamaulipas have flowers with a darker red throat and stronger spines, but all other features are within the variability of the type plants.

Coryphantha borwigii Purpus and *Coryphantha obscura* SB 714 turned out to be synonyms.

For this very variable species several names have, in the past, been used, especially *Coryphantha scolymoides* (Scheidweiler) A. Berger and *Coryphantha daimonoceras* (Lemaire) Lemaire. These two taxa must be considered as *nomina dubia* for the following reasons:

- ***Coryphantha scolymoides*** (Scheidweiler) A. Berger

The first description by SCHEIDWEILER (1841) was very rudimentary. No type exists and this species was never illustrated during the nineteenth century. The only features described were “pale green, tubercles ascending like tiles, spines numerous, lower one radiating, flesh-coloured, upper ones bundled, white, blackish at the tips, stiff, one single central spine recurved, black, grey at the base”. These details fit several species of the genus *Coryphantha*, mainly at the juvenile stage. More precise descriptions can be found in FÖRSTER (1846) and also in SALM-DYCK (1850), but they differ in several aspects, so that one wonders whether they were describing the same plant. Another description of *Coryphantha scolymoides*, which corresponds best to today’s *Coryphantha ramillosa* Cutak (see BENSON 1982) was published by ENGELMANN (1856) as did Coulter’s description (1894). BRITTON & ROSE (1923) made it a synonym of *Coryphantha cornifera* De Candolle, as did SCHELLE (1926), while K. SCHUMANN (1898) mentioned it as a synonym of *Coryphantha radians* De Candolle.

The situation with regard to *Coryphantha scolymoides* (Scheidweiler) A. Berger is thus so confusing and this species so badly documented that it seems better to regard this epithet as a historical name only.

It is apparent that the descriptions published by FÖRSTER (1846) and by SALM-DYCK (1850) may fit the plants growing in Salinas Victoria. However, the name *Coryphantha scolymoides* (Scheidweiler) A.

Berger cannot be applied to these, since the first description given by Scheidweiler does not fully match any phase of their development: *Coryphantha salinensis* (Poselger) Dicht & A. Lüthy at the stage of growth where one single central spine exists has uniform radial spines only. Two types of radial spines (lower radiating horn-coloured and upper bundled spines whitish) appear only after the development of a second or even third central spine.

- ***Coryphantha daimonoceras*** (Lemaire) Lemaire

LEMAIRE’s (1838) illustrative first description as *Mammillaria daimonoceras* was soon interpreted in a number of different ways: FÖRSTER (1846) regarded it as a synonym of *Mammillaria cornifera* De Candolle, although two different types of radial spines were described. SALM-DYCK (1850) treated it as being identical to *Mammillaria scolymoides* Scheidweiler, although its upper central spines were described as “curved forward like a devil’s horns”, which was in contrast to his own plants which had, as he wrote, “upper central spines appressed to the plant, usually interwoven with the radial spines”. LABOURET (1858) also treated *Mammillaria daimonoceras* Lemaire as a synonym of *Mammillaria cornifera* De Candolle, while BRITTON & ROSE (1923), probably following K. SCHUMANN (1898), referred to it as a synonym of *Coryphantha radians*.

Finally, the first description of *Mammillaria daimonoceras* also fits *Coryphantha difficilis* (Quehl) A. Berger. We can only conclude that a specific interpretation of this taxon is impossible nowadays.

The two taxa *Coryphantha scolymoides* and *Coryphantha daimonoceras* have therefore been proposed to the committee of spermatophytes as *nomina rejicienda* (Dicht, Cact. Syst. Init. 10: 20, 2000).

Illustrations: Distribution see Plate 11, map 2; plant portrait see Plates 41 and 42.

23. *Coryphantha difficilis* (Quehl) A. Berger
Kakteen 271, 1929

Basionym: *Mammillaria difficilis* Quehl,
Monatsschr. Kakt. 18: 107, 1908.

Lectotype: Fig. Monats. Kakt. 18: 107, 1908
(Dicht & A. Lüthy, CSI 11: 15, 2001).

Synonym: *Coryphantha densispina* Werder-
mann in Feddes Repert. 30: 57, 1932.

Body solitary, initially semiglobose, in later years also short-cylindrical, 8 cm diameter, 8 (-14) cm high, dull bluish-green, apex slightly depressed, white-woolly, fibrous roots. **Tubercles** in 8 and 13 series, flattened broad-conical, appressed, tip slightly directed outwards, edges obliquely cut, in later years rhomboid and edged below, width at the base 24 mm, length of upper surface 10 mm, of lower surface 21 mm, upper surface grooved. **Axils** white-woolly. **Areoles** round, 3 mm diameter, white-woolly in youth. **Radial spines** 14–16 (-20), lower and lateral 6–9 strongest and shortest, subulate, straight, radiating and horizontally arranged, 8–10 mm long, the upper 7–10 in a bundle, firm, needle-like, straight, 16–18 mm long, in new growth light horn-coloured with dark tips, then becoming brown from the base, later turning grey. **Central spines** 4 (-6), the three lower ones spreading, porrect, curved downwards, strong, subulate, the upper one slightly curved, protruding, thinner, all 16–20 mm long, in new growth brown, darker towards the tips, later turning grey from the base. **Flowers** funnel-shaped, 6–8 cm diameter, outer perianth segments broad lanceolate, acute, yellow with reddish-brown dorsal mid-stripe, inner perianth segments broad lanceolate, acute, dentate towards the tip, shiny yellow, filaments yellowish, anthers yellow, stigma yellowish, 7–8 whitish lobes. **Fruit** green juicy berry with attached flower remnants, roundish, 18 mm long, 14 mm diameter. **Seeds** reniform, brown with reticulate testa, 1.5 mm long, 0.9 mm wide.

Distribution: Mexico: Coahuila, in and around the Sierra de la Paila.

Habitat: Alluvial plains and slopes of Sierra Paila in limestone gravel.

Locations checked: Mexico: Coahuila: Hipolito, La Paila, La Rosa, El Sacrificio, Casas Coloradas, Las Imágenes, Las Palomas, Parrial de la Paila, Zona de Minas, Mount Paila, Saltillo, Laguna de Meyrán, San Ildefonso, San José de la Paila, Estacion Marte, Sierra los Alamitos.

Incidence: Least concern.

Comments: The plants were discovered in Mexico by Purpus and sent to De Laet. Quehl wrote that this beautiful species had problems adjusting to the European climate and easily rot in culture. He, therefore, named it *difficilis* (difficult, difficult to treat).

Coryphantha densispina Werdermann in Fedde, Rep. 30:57, 1932 has been allocated to *Coryphantha werdermannii* by several authors. Hence, the described tubercle form and size correspond to *Coryphantha difficilis*. The name-giving density of spination is reminiscent of *Coryphantha werdermannii*, but is also well-known in *Coryphantha difficilis* from locations at higher sealevels.

Illustrations: Distribution see Plate 11, map 2; plant portrait see Plate 43.

24 a. *Coryphantha durangensis*

(Runge ex Schumann) Britton & Rose
subsp. *durangensis*

Cactaceae 4: 42, 1923.

Basionym: *Mammillaria durangensis* Runge
ex Schumann, Gesamtb. Kakt. 478, 1898.

Type: Mexico, Durango, near Villa Lerdo on the Rio Nazas, coll. Runge, Mathsson; not designated.

Body sprouting at the base, group-forming, egg-shaped to columnar, up to 7 cm diameter and more than 15 cm high, greyish-green, apex egg-shaped, rounded, with much white wool. **Tubercles** in 5 and 8, rarely 8 and 13 series, rhomboid, very flat, slightly keeled, appressed like tiles, at the base 12–15 mm wide, length of upper surface 4–6 mm, of lower surface 12–14 mm, completely

grooved. **Axils** much woolly in youth. **Areoles** round, 1 mm diameter, woolly in youth. **Radial spines** 9–16, most of them radiating, sometimes some bundled over body apex, horizontal, fine, needle-like, straight, lower and lateral ones 7–10 mm long, upper ones up to double this length and somewhat thinner, all dull white, more or less dark tipped, upper ones nearly black, then all turning grey. **Central spine** (0)–1, directed upwards, slightly protruding (or rarely single spines up to nearly right-angled to the radials spines), straight, needle-like, stiff, 13–18 mm long, black, then turning grey from the base. **Flower** funnel-shaped, 3 cm long, 3–4 cm wide, light yellow, outer perianth segments narrow lanceolate, margins entire, yellow with broad purple midstripe, inner perianth segments lanceolate, acute, margins entire, shiny light yellow, filaments whitish-yellow, anthers yellow, stigma and 3–5 lobes whitish-yellow. **Fruit** light green juicy berry, with attached flower remnants, 12–15 mm long and 5–7 mm wide. **Seeds** reniform, brown, 1.2 mm long, 0.8 mm wide, testa reticulate with oblong testa cells.

Distribution: Mexico: eastern Durango and adjacent Coahuila.

Habitat: Slopes and rocky parts of volcanic hills.

Locations checked: Mexico: Durango: Nazas, Lerdo (location of the first description), El Chocolate, Cuatillos. Coahuila: Viesca, Cruz de Malto.

Incidence: Least concern.

Differentiation: *C. durangensis* ssp. *cuencamensis* (24.b): see comparison table in the appendix.

Illustrations: Distribution see Plate 11, map 2; plant portrait see Plates 44 and 45, photo 1.

24 b. *Coryphantha durangensis* subsp. *cuencamensis* (Bremer) Dicht & A. Lüthy

Cact. Syst. Init. 11: 18, 2001.

Basionym: *Coryphantha cuencamensis* Bremer, Cact. Succ. J. (US) 52: 183, 1980.

Type: Mexico, Durango, east of Cuencamé, Route 49, about 15 km from the junction with Route 46, 1800 m, 26.3. 1979, Bremer Nr.379–4 (ASU).

Body sprouting at the base, group-forming, egg-shaped-globose to cylindrical, up to 10 cm diameter and up to 16 cm high, dull greyish-green, apex flat or slightly vaulted, strongly white-woolly. **Tubercles** in 13 and 21, more rarely in 8 and 13 series, rhomboid, conical towards the apex, at the base 12–15 mm wide, length of upper surface 10 mm, of lower surface 13–15 mm, completely grooved. **Axils** white-woolly in youth. **Areoles** round, white-woolly in youth. **Radial spines** 14–17, radiating, horizontal, 15–17 mm long, in the upper part of the areole 4–5 longer ones bundled, all needle-like, straight, whitish with black tips.

Central spines 1–3, the dominant porrect, at a right angle to the radial spines (never directed upwards), 17 mm long, subulate, stiff, straight or slightly curved downwards, at first dark brown to black, then turning grey from the base. Sometimes 2 additional central spines, shorter, thinner, slightly protruding obliquely upwards, same colour as radial spines. **Flower, fruit and seeds** as for *Coryphantha durangensis* subsp. *durangensis*.

Distribution: Type locality only (checked): east of Cuencame, Durango, near the carretera Nr. 49, on flat ground and gentle hills.

Habitat: Lower slopes of calcareous hills, on gravelly places under bushes.

Incidence: Vulnerable.

Differentiation: *C. durangensis* ssp. *durangensis* (24 a.): see comparison table in the Appendix.

Illustrations: Distribution see Plate 11, map 2; plant portrait see Plate 45, photos 2–4.

25. *Coryphantha longicornis* Bödeker

Monatsschr. DKG 3: 249, 1931.

Lectotype: Illustration in first description as cited above (Dicht & A. Lüthy, CSI 11: 18, 2001).

Synonym: *Coryphantha grandis* Bremer, Cact. Succ. J.(US) 50: 124, 1978.

Body solitary or group-forming by sprouting, broad-globose, then cylindrical, up to 10 cm diameter and more than 20 cm high, dull green, apex slightly depressed, very woolly. **Tubercles** in 8 and 13 or 13 and 21 series, conical in youth, then flat conical and rhomboid, tip slightly curved, slightly keeled, appressed, at the base 20–22 mm wide, 17 mm high, length of upper surface 8 mm, of lower surface 18–22 mm, with marked, in youth woolly groove. **Axils** woolly. **Areoles** round, 2 mm diameter, woolly in youth, soon bald. **Radial spines** 11–14, upper 3–4 closer to each other, thin subulate, straight or slightly curved, lateral and lower ones 7–9 mm, upper ones up to 14 mm long, whitish-horn-coloured in youth with dark tips, later grey. **Central spines** 3, the dominant one porrect, curved downward, subulate to thick-subulate, 15–20 mm long, upper 2 slightly protruding and curved to each side, subulate, 10–14 mm long, in youth red-brown, darker towards the tips, then black. **Flowers** broad funnellform, 4 cm wide, 2 cm long, yellow, outer perianth segments broad lanceolate, acute, fimbriate towards the tips, yellow with strong, red midstripe. Inner perianth segments broad lanceolate, acute, fimbriate towards the tips, light yellow, filaments light yellow, anthers yellow, stigma and lobes (6) light yellow. **Fruit** green juicy berry, 9 mm wide, 15 mm long, clavate, with attached flower remnants. **Seeds** globose-reniform, 1.5 mm long, 1 mm wide, brown, testa reticulate with rounded testacells.

Distribution: Mexico: northwestern part of Durango

Habitat: Lava gravel on hills and slopes, often under bushes or oaks

Locations checked: Mexico: Durango: Abasolo, El Palmito, Mina Navidad, Zarcas, Indè.

Incidence: Least concern.

Illustrations: Distribution see Plate 11, map 2; plant portrait see Plate 46.

26 a. *Coryphantha pallida* Britton & Rose
subsp. *pallida*

Cactaceae 4: 40, 1923.

Type: Mexico, Puebla, near Tehuacán, 1901, J.N. Rose Nr. 5583 (US).

Synonyms: *Coryphantha reduncispina* Bödeker, Kakteenk. 1933: 153, 1933 (as “*reduncuspina*”); *Coryphantha pseudoradians* Bravo, An. Inst. Biol. Mex. 25: 228, 1954; *Coryphantha radians* var. *pseudoradians* Bravo, Cact. Suc. Mex. 27: 17, 1982; *Coryphantha pycnacantha* sensu Arias et al., Flora del Valle de Tehuacán-Cuixatlàn 10–12, 1997.

Body solitary, later also forms groups by sprouting, semiglobose to globose, 7–9 cm diameter, 4–6 cm high, dull olive-green, apex slightly depressed, very white-woolly. **Tubercles** in 8 and 13 or 13 and 21 series, closely set, flattened conical, slightly bulging, edges obliquely cut, appressed, at the base 14–17 mm wide, 6–8 mm high, length of upper surface 6–9 mm, of lower surface 13–16 mm, completely grooved with white wool. **Axils** woolly. **Areoles** round, 2 mm diameter, if central spines present or, without central spines, oval, 3.0 × 1.5 mm, woolly. **Radial spines** 13–21, about two-thirds of them radiating to both sides and downwards, horizontally arranged, needle-like, straight or slightly curved, transparent, white to yellowish, 11–13 mm long, the rest more closely set and pointing upwards, dirty white with dark tips, longer, up to 16 mm. **Central spines** 0–3, usually 1 dominant porrect, curved downwards, sometimes also to the side, subulate, 15–17 mm long, 1–2 upper ones straight or slightly upwards and to the sides or curved ahead, thinner, a bit shorter, all dark brown to black, then becoming grey from the base. Sometimes the porrect one and/or one or both of the two upper ones are missing. **Flowers** 4 cm long, 7 cm diameter, outer perianth segments linear lanceolate, acute, outside red with yellow margins, inner perianth segments narrow lanceolate, acute, margins entire, dentate towards the tip, 35 mm long, 6 mm wide,

yellow, filaments deep red, anthers yolk-yellow, stigma yellow with 7–9 whitish lobes. **Fruit** green juicy berry with attached flower remnants, 25 mm long, 9 mm wide. **Seeds** reniform, brown, 2.3 mm long, 1 mm wide.

Distribution: Mexico: Puebla and Oaxaca.

Habitat: Limestone gravel, alluvial soil on foothills and ridges.

Locations checked: Mexico: Puebla: Tepeji de Rodriguez, Tecamachalco, Cañada Morelos, Tehuacan, Copàn, Azumbilla, Zapotitlán de las Salinas, San Lorenzo, Salitrillo. Oaxaca: Tamazulapan, Tejupan, Coixtlahuaca, Teposcolula, Nochixtlán, Buenavista, Molcaxac, San Pedro Tetitlán.

Incidence: Least concern.

Comments: It is quite surprising that such a widespread and common species like *C. pallida* had not been collected and described before the beginning of the twentieth century, mainly in view of the fact that all other *Coryphantha* species of this part of Mexico had been described nearly 100 years earlier. In fact, there is a description of a *Coryphantha loricata* (MARTIUS) Lemaire of 1837 which, in all characters, fits *C. pallida* completely and is considered to belong to the series *Aulacothelae*, the *Coryphanthas* without glands. However, the origin of this plant was indicated with “Mexico” only and there is no type existing. Because the description of *C. loricata* could as well fit some of the forms of *Coryphantha sulcata* (Engelmann) Britton & Rose or *Coryphantha salinensis* (Poselger) Dicht & A. Lüthy, it is impossible today to say which one of these three species was meant and *C. loricata* has to be classified as a historical name without any nomenclatural meaning nowadays.

Another old name which might fit *C. pallida* is, as CRAIG (1945) claimed, *Mammillaria incurva* SCHEIDWEILER of 1839. However, the origin of *M. incurva* is indicated as Guanaquato and it had red nectary glands.

Therefore, the official history of this species starts in 1923 when BRITTON &

ROSE first described *Coryphantha pallida* from a plant collected near Tehuacán PUE in 1901 by J.N. Rose. According to these authors, C.G. Pringle had collected the same plant too, and distributed it under the name *Mammillaria pycnacantha*. To prove the difference between these two species, BRITTON & ROSE published a picture of their *C. pallida* together with the drawing of the original publication of Martius of *M. pycnacantha*. However, in the same book, in the appendix to the description of *C. pycnacantha*, they mentioned a plant which Dr. Rose had received from Dr. Conzatti from Oaxaca in 1920, which was more or less identical to their description of *C. pallida* and due to this fact, the identity of *C. pycnacantha* got mixed up with that of *C. pallida*, a confusion that still continues.

BÖDEKER (1933) was the first one to detect Britton & Rose’s error when he received the same plants from Oaxaca from Halbinger. He noticed that these plants were not *C. pycnacantha*, but he did not realise they were identical to *C. pallida* and re-described these plants in 1933 as *Coryphantha reduncuspina*, herewith creating a younger synonym of *C. pallida*.

In fact, northwest of Oaxaca, we could detect plants which are identical to Bödeker’s description, but we classify them as *C. pallida*.

S. ARIAS Montes, S. GAMA Lopez and L.U. GUZMAN Cruz from UNAM continued the old confusion with *C. pycnacantha* in their publication “Flora del Valle de Tehuacán-Cuicatlán” (1997). They too were misled by the wrong indication of the type locality in the first description of *C. pycnacantha* and the contradictory indications of Britton & Rose. They published a drawing of *C. pycnacantha* which is identical to *C. reduncuspina* Bödecker. To differentiate between *C. pallida* and *C. pycnacantha*, they unfortunately used the shape of the tubercles, a character which is identical for all forms of *C. pallida*. When we visited their indicated locations

in Oaxaca for *C. pycnacantha*, we found nothing else but forms of *C. pallida*.

Between Tejupan und Suchixtlahuaca OAX, on volcanic soils in oak forests, Helia BRAVO detected a population of plants often in clusters, usually without central spines which she first described in 1954 as *Coryphantha pseudoradians*. In 1982 she included this species as a variety of *Coryphantha radians* (Lem.) Lem. From Helia Bravo's indicated type locality it is only a few kilometers to Tejupan where *C. pallida* grows with its normal number of central spines from 0–3 and as this link and the otherwise identical features of *C. pseudoradians* and *C. pallida* prove, it is impossible to differentiate between these taxons.

Illustrations: Distribution see Plate 11, map 2; plant portrait see Plates 47, 48 and 49.

26 b. *Coryphantha pallida* subsp. *calipensis*

(Bravo ex Arias et al.) Dicht & A. Lüthy

J. Mamm. Soc. 40 (4): 50, 2000.

Basionym: *Coryphantha calipensis* Bravo ex Arias et al., Cact. Succ. Mex. 37: 71, 1992.

Type: Mexico, Puebla, Calipan, S of Tehuacán, 1960, Bravo s.n. (MEXU 60655).

Synonyms: *Coryphantha calipensis* Bravo, Cact. Succ. Mex. 9: 79, 1964, *nom. inval.* (Art. 37.1); *Coryphantha pycnacantha* var. *calipensis* Arias et al., Flora del Valle de Tehuacán – Cuixcatlán 12–13, 1997.

Body group-forming by sprouting, globose to cylindrical, 6–9 cm diameter, apex rounded with abundant white wool. **Tubercles** loosely set in 5 and 8 series, flattened conical, bulging, rhomboid at the base, appressed to body, very large, at the base 25–30 mm wide, 20 mm high, length of upper surface 13–15 mm, of lower surface 25–35 mm, with deep woolly groove. **Axils** white woolly. **Areoles** round, 2 mm diameter, woolly in youth. **Radial spines** 10–16, 7–8 of them radiating, horizontally arranged, straight to slightly curved, needle-like, transparent, white to yellowish, then grey, 10–12

mm long, the other ones in the upper part of the areole more densely set, dirty white with dark tips, longer, up to 18 mm. **Central spines** 1–3, one dominant porrect, curved downwards, subulate, 15 mm long, usually 1–2 additional centrals straight or slightly to both sides upwards, slightly protruding, straight or a bit curved to the side or the front, thinner, slightly shorter, all dark brown to black with lighter base, later becoming grey from the base. **Flower, fruits and seeds:** as for *Coryphantha pallida* ssp. *pallida*.

Distribution: Mexico: Puebla and Oaxaca.

Habitat: Limestone gravel, alluvial soil on foothills and ridges.

Locations checked: Mexico: Puebla: Zinacantepec, Coxcatlán, San José Tilapa, San Gabriel Chilac. Oaxaca: Teotitlán del Camino, Cuicatlán, San Juan Tonaltepec.

Comments: The main differences between ssp. *calipensis* and ssp. *pallida* are the larger tubercles, the slightly fewer and shorter radial spines and its form of growth with larger and more cylindrical bodies and its strong clustering habit. In its distribution area in the valley of the Rio Salado between Chilac PUE and San Juan Batista OAX, its characteristics are very stable and identical. The distribution area of ssp. *calipensis* is east of ssp. *pallida*, without any interference between the two forms.

In her first description of *Coryphantha calipensis*, BRAVO (1964) forgot to designate one of her herbarium specimens deposited in MEXU as the holotype. Allan D. ZIMMERMAN (1985) noticed this fact and therefore, regarded the taxon as a *nomen nudum* and identical to *C. pallida*. S. ARIAS Montes, S. GAMA Lopez and L.U. GUZMAN Cruz (1992) from UNAM completed Helia Bravo's description of *C. calipensis* by designating herbarium specimens of the author, deposited at MEXU, as the holotype and a paratype. Later, in their publication "Flora del Valle de Tehuacán-Cuicatlan" (1997) they combined *C. calipensis* as a variety with what they called *C.*

pycnacantha. This erroneous combination had already been proposed by BRAVO (1991) in “Las Cactáceas de Mexico”.

Illustrations: Distribution see Plate 11, map 2; plant portrait see Plate 50.

II.A.d Series *Coryphantha*

Type: *Coryphantha sulcata* (Engelmann) Britton & Rose (type of the genus).

Definition: tubercles upright, majority of radial spines needle-like, dominating central spine (if present) porrect.

27. *Coryphantha maiz-tablasensis*

Backeberg

Blätt. Sukk.-Kunde 1:5, 1949

Type: not designated.

Body sprouting, forming large groups, flat-globose, 5–7 cm diameter, 3 cm high, 75% of the plant underground, merging into a long taproot (up to 50 cm length), apex depressed, white-woolly, epidermis dull dark-green.

Tubercles in 5 and 8 series, conical, somewhat flattened above, somewhat bulging below, upright, at the base 14 mm wide, 11 mm high, length of upper surface 9 mm, of lower surface 14 mm, with a fine groove above. Sometimes glands are present immediately behind the spiniferous areole. **Axils** woolly in youth. **Areoles** less than 1 mm diameter, white-woolly in youth. **Radial spines** 4–7, irregularly radiating, horizontal, straight, stiff needle-like, 7–10 mm long, upper 1–3 in new growth brown-black, then turning grey from the base, the rest grey-white, some with dark tips.

Central spine absent. **Flowers** funnelform, 3.5 cm long, 4 cm diameter, outer perianth segments broad lanceolate, acute, reddish-green with yellow-green margin, inner perianth segments lanceolate, acute, margin dentate towards the tip, cream-white, filaments white, anthers yolk-yellow, stigma white, lobes white. **Fruit** green juicy berry, 24 mm long, 10 mm diameter, with attached flower remnants. **Seeds** reniform, brown, 1.8 mm long, 0.9 mm wide, testa reticulate.

Distribution: Mexico: in the lagoon plain around Las Tablas in the state of San Luis Potosí, in a region which is used more and more for farming which leads to the destruction of many plant locations. Some isolated locations can be found north of the type locality.

Another, more remote location, has been detected by Charles Glass south of Matehuala near El Retorno, this is about 200 km north of the type locality. The plants there tend to propagate by underground stolons, but are otherwise very similar to the type plants. This location has practically been destroyed by road construction.

Habitat: Dry lagoon in gypsum soil with grass.

Locations checked: Mexico: San Luis Potosí: Las Tablas, Los Adobes, Rio Verde, Angostura, San Bartolo, El Retorno.

Incidence: Vulnerable.

Illustrations: Distribution see Plate 12, map 1; plant portrait see Plate 51.

28. *Coryphantha sulcata* (Engelmann) Britton & Rose

Cactaceae 4: 48, 1923

Basionym: *Mammillaria sulcata* Engelmann, Bost. J. Nat. Hist. 5: 246, 1845 [non Pfeiffer ex Förster, Handb. Cact. 255, 1846, *nom.nud.*]

Type: USA, Texas, Austin County, sandstone rocks near industry, July 1844, *Lindheimer* (MO) (Hunt & Benson, Cact. Succ. J. (US) 48: 72, 1976).

Synonyms: *Mammillaria strobiliformis* Muehlenpfordt, Allg. Gartenz. 16: 19, 1848 [non Engelmann in Wislizenus, Mem. Tour. N. Mex. 14, 1848]; *Mammillaria calcarata* Engelmann, Bost. J. Nat. Hist. 6: 195, 1850; *Coryphantha calcarata* (Engelmann) Lemaire, Cactées 35, 1868; *Cactus calcaratus* (Engelmann) Kuntze, Rev. Gen. Pl. 1: 259, 1891; *Cactus scolymoides* (Scheidweiler) Kuntze var. *sulcatus* Coulter, Contr. U.S. Nat. Herb. 3: 116, 1898; *Mammillaria radians* De Candolle var *sulcata* Schumann, Gesamtb.

Kakt. 496, 1898; *Cactus sulcatus* Small, Fl. SE U.S. 812, 1903; *Coryphantha radians* Br. & R. var. *sulcata* Yto, Cacti 115, 1952; *Coryphantha roederiana* Bödeker, Monatsschr. DKG 1: 153, 1929; *Coryphantha speciosa* Bödeker, Monatsschr. DKG 2: 23, 1930; *Coryphantha obscura* Bödeker, Monatsschr. DKG 2: 25, 1930.

Body group-forming, globose to egg-shaped, up to 12 cm high and 10 cm diameter, dark green, apex woolly. **Tubercles** in 8 and 13 series, oblong, conical, very large at the base, edges obliquely cut, upright, at the base 13–17 mm broad, 9 mm high, from the centre 6 mm diameter, length of upper surface 14–20 mm, of lower surface 18–27 mm, with complete, woolly groove above. **Axils** woolly. **Areoles** round, 2 mm diameter, with white wool in youth. **Radial spines** 7–12, lower and lateral ones radiating, upper ones more densely set to bundled, horizontal, needle-like, stiff, straight, unevenly thick, lower ones 10–13 mm long, upper ones up to 18 mm, grey-white, most upper ones have dark tips. **Central spines** 1–4, the dominant spine porrect, slightly curved downwards, subulate, 12–17 mm long, brownish above, greyish below, tip black, the other ones straight upwards, slightly protruding, same colour as radial spines, but somewhat stronger and longer. **Flowers** 5–6 cm diameter, outer perianth segments lanceolate, margins entire, acute, greenish-yellow with green-brown midstripe, inner perianth segments lanceolate, margins entire, tips fimbriate, acute, golden-yellow, red in the throat, filaments reddish, anthers yellow, stigma yellowish, lobes yellowish-white. **Fruit** green juicy berry, 25 mm long, 12 mm diameter. **Seeds** reniform, brown, shiny, 1.8 mm long, 1.2 mm wide, reticulate.

Distribution: USA: Texas, from Tarrant to Uvalde, Austin and Duval. Mexico: Tamaulipas, Coahuila, Nuevo León.

Habitat: Alluvial plains and flat ridges with limestone gravel.

Locations checked: USA: Texas: Val Verde County, Kimble County. Mexico: Coahuila: Villafrontera, San Alberto.

Incidence: Least concern.

Comments: *Coryphantha sulcata* was first described as *Mammillaria sulcata* by ENGELMANN in 1845. When FÖRSTER (1846) mentioned a *Mammillaria sulcata* Pfeiffer, ENGELMANN (1850) unnecessarily changed its name to *Mammillaria calcarata*. Pfeiffer's name was the younger one and, moreover, without any description. The allocation to *Coryphantha sulcata* by BRITTON & ROSE (1923), with *Coryphantha calcarata* Lemaire as a younger synonym was therefore justified.

There are populations of small plants which have finer spination as e.g., SB 486 from Val Verde County, Texas, and in Texas more robust plants can be found (BENSON 1982). An excellent picture of such a plant is shown by WENIGER (1984), who states that *Coryphantha sulcata* usually has flowers with a red throat, and rarely, there are plants with a greenish-yellow throat without any red in the centre.

Our field studies showed that three taxa described by Bödeker, namely *C. roederiana*, *C. speciosa* and *C. obscura*, which we rediscovered in the field in 1997 (DICHT & A. LÜTHY 1998), are identical in form to the above robust plants. The distribution of this species thus extends into the Mexican states of Coahuila and Nuevo León.

Illustrations: Distribution see Plate 12, map 1; plant portrait see Plate 52.

29 a. *Coryphantha hintoniorum* Dicht & A. Lüthy ssp. *hintoniorum*

Kakt. and. Sukk. 50 (1): 13, 1999

Type: Mexico, Nuevo León, Galeana, San Gerardo, 1850 m, 28.9.1997, Hinton et al. 27111 (Herb. Hinton).

Body usually group-forming, but sometimes solitary, globose to short-columnar, often reaching more than 10 cm in diameter and 9–15 cm in height, apex slightly depressed,

with little wool, root fibrous, group formation by stolons from the lower areoles, epidermis dark green. **Tubercles** in 13 and 21 series, broad at the base, then cylindrical-conical, nearly round, bulging a bit towards the outside, upright to slightly appressed, edges obliquely cut, with a complete groove without glands, at the base 22 mm wide, at half the length about 10 mm diameter, 15 mm high, length of upper surface 22 mm. **Axils** woolly in youth. **Areoles** round, 3 mm diameter, woolly in youth. **Radial spines** 11–12, the lower 6 radiating, horizontally protruding, 9–12 mm long, the upper 5–6 bundled in two layers, up to 18 mm long, all thickened at the base, greyish-white, horn-coloured at the base and some tipped black. Radial spines on the underside of the bundle sometimes flattened, curved and twisted. **Central spine** 1, porrect in direction of the tubercle-axis, 14–18 mm long, straight, always hooked, base of spine thickened, base horn-coloured, lower part of the hook black. **Flower** 45 mm long, 40 mm diameter. All perianth segments lanceolate, acute, with entire margins. Outer perianth segments 20 mm long, 7 mm wide, yellowish-white to gold-bronze with red-brown midstripe, changing at the base into a green/ red-brown flower tube. Inner perianth segments yellowish-white, 27 mm long, 5 mm broad, with a silver-white, shiny throat at the base. Filaments greenish-white, 12 mm long, anthers yellow, stigma greenish-white, 25 mm long, 10 yellow lobes, 7 mm long. **Fruit** green juicy berry with attached flower remnants, 27 mm long, 10 mm wide. **Seeds** numerous, reniform, red-brown, with reticulate testa. **Distribution:** Mexico: Nuevo León, at about 1850 meters above sea level in the prairies west of Cerro Potosí, and also at a few locations in San Luis Potosí. **Habitat:** Sandy-loamy alluvial plains with a high content of gypsum. **Locations checked:** Mexico: Nuevo León: San Gerardo, San Raphael, Los Adobes, San Pablo,

Cienega del Toro. San Luis Potosí: San Francisco, Agua de Enmedio.

Incidence: Vulnerable. Plants very scattered. Constant loss of plants by agricultural cultivation observed in the last few years. The size of the untouched prairie is diminishing from year to year.

Development: As a juvenile plant *Coryphantha hintoniorum* has fewer and only white radial spines each having a dark tip. The hooked central spines soon appear and this is followed in the near-adult phase by another layer of radials situated in the upper region of each spine cluster only.

Comments: *Coryphantha hintoniorum* ssp. *hintoniorum* is somewhat similar to *Coryphantha sulcata* (Engelmann) Britton & Rose, particularly in relation to growth, form of body and the radial spination. The main differences are the shape of the tubercles, their arrangement and also the central spine.

The tubercles of *Coryphantha hintoniorum* ssp. *hintoniorum* are broad at the base, but reduced in cross section to become almost rounded a short distance from the base. A bulge in the outer surface is also apparent. The tubercles remain almost round, even in later years and, therefore, never cover each other as tiles. Because the form of the tubercles remains constant and because they are evenly separated, the plant has an even, regular, globose appearance. *Coryphantha hintoniorum* ssp. *hintoniorum* always has one single, always hooked central spine, which already appears on very young plants. Moreover, the flower of *Coryphantha hintoniorum* is yellowish-white, nearly silvery, and there is no redness in the throat.

In some aspects *Coryphantha hintoniorum* ssp. *hintoniorum* also reminds one of *Coryphantha delicata* Bremer, mainly because of the single, hooked central spine and the regular body shape. There are, however, differences in body-size, form and dimensions of tubercles and the taproots which is wanting

in *Coryphantha hintoniorum* ssp. *hintoniorum*. *Coryphantha delicata* also has many more radial spines (14–20). These are always arranged in a single layer in the upper part of an areole only.

A description which fits many of the characteristics of *Coryphantha hintoniorum* ssp. *hintoniorum* is that of *Coryphantha roederiana*. However, the former has tubercles which are about twice the size of those of the latter. Moreover, *Coryphantha hintoniorum* ssp. *hintoniorum* always has a hooked central spine, while in *Coryphantha roederiana* it is not hooked. Unfortunately, *Coryphantha roederiana* is no longer positively identifiable since the type no longer exists. However, as mentioned earlier, we came across plants in Coahuila which seem to have the characteristics of both *Coryphantha roederiana* and *Coryphantha sulcata*. Therefore, we have come to the conclusion that *Coryphantha roederiana* is a synonym of *Coryphantha sulcata*.

Coryphantha hintoniorum ssp. *hintoniorum* grows in the State of Nuevo León in the valley along the Carretera Mex 57 between Entronque San Roberto and the border to Coahuila, west of the Cerro Potosí to the Sierra las Mazmorras. Recently, it has been reported in the region north of the Carretera MEX 70 near Rio Verde, San Luis Potosí.

The nearest location of *Coryphantha sulcata* (Engelmann) Britton & Rose we found is near Monclova in the State of Coahuila (DICHT & LÜTHY 1998).

The distribution of *Coryphantha delicata* Bremer overlaps that of *Coryphantha hintoniorum* ssp. *hintoniorum*. It extends from Tamaulipas to the north of Saltillo in Coahuila.

Coryphantha hintoniorum ssp. *hintoniorum* was named in honour of the Hinton family. The Hintons have been excellent botanists and active field scientists for the last three generations. Their hacienda is situated in the centre of the distribution area of this species.

George Hinton has known the plant for a long time and showed us a specimen growing near his house. The holotype was deposited as one of more than 27,000 specimens in the herbarium G.S. Hinton et al.

Illustrations: Distribution see Plate 12, map 1; plant portrait see Plate 53.

29 b. *Coryphantha hintoniorum* Dicht & A. Lüthy subsp. *geoffreyi*

Kakt. and. Sukk.54 (2):43, 2003.

Type: Mexico, Nuevo León, San Pedro Sotolar: Grassy saddle with *Echinocereus knip-
pielianus*, *Mammillaria heyderi* and *Stenocactus* sp., July 11, 1998, Hinton et al. 27206 (Holotype: Herbarium G.B. Hinton).

Body mostly sprouting, forming groups of more than 30 heads, flat globose, diameter up to 6 cm, height 2 cm, top slightly depressed, with little wool, sprouting root leading into a taproot, group formation by stolons from the lower areoles, epidermis dull dark green. **Tubercles** in 5 and 8 or 8 and 13 series, upright, conically rounded, slightly bulging, flattened above, obliquely cut, grooved on upper part, at the base 11 mm wide, 7 mm high, length of upper part 11 mm, of lower part 12 mm. **Axils** woolly in youth. **Areoles** round, 2 mm diameter, white woolly in new growth. **Radial spines** 14–15, lower ones on both sides radiating, upper up to 4 closer set, all horizontal, slightly interwoven, needle-like, upper ones somewhat thinner, all straight, 8–10 mm long, upper ones up to 11 mm, yellowish-white, then becoming grey, upper ones often with black tips. **Central spine** 1, porrect, straight, hooked, stiff needle-like, 9–10 mm long, dark brown-black, then becoming grey from the base, lower part of hooks remaining dark for a longer period. **Flowers, fruits and seeds** like ssp. *hintoniorum*.

Distribution: Mexico: Nuevo León, Coahuila.

Habitat: grassy, deep, red soils, pastures surrounded by pine forests, 2560 m above sealevel, together with *Echinocereus knip-
pielianus*, some agaves and opuntias.

Locations checked: Mexico: Nuevo León: type locality. Coahuila: Huachichil.

Incidence: Vulnerable. Low incidence, habitats potentially of use for farming.

Comments: Discovered by George S. Hinton and his son George Boole (*Turbincarpus booleanus*), who suggested naming this plant after his younger brother Geoffrey, both being members of the fourth generation of the botanical dynasty Hinton.

Illustrations: Distribution see Plate 12, photo 1; plant portrait see Plate 54.

II.A.e *Series Corniferae* Dicht & A. Lüthy ser.nov.

Diagnosis: Tuberculis porrectis, conicis; majoritas spinarum radialium aculeiformis; spina centralis dominans porrecta (sicut praesens).

Definition: Tubercles porrect, conical. Majority of radial spines needle-like, dominating central spine (if present) porrect.

Type: *Coryphantha cornifera* (De Candolle) Lemaire

Subseries *Corniferae* Dicht & A. Lüthy

Cact. Syst. Init. 11: 19, 2001.

Definition: Central spines 0–1.

30. *Coryphantha nickelsiae* (K.Brandegee)

Britton & Rose

Cactaceae 4: 35, 1923.

Basionym: *Mammillaria nickelsiae* K. Brandegee, Zoe 5:31, 1900.

Lectotype: USA, Texas, across from Laredo, 1893, Anna B. Nickels s.n. (F 260723) (Benson, Cact. Succ. J. (US) 41: 188, 1969).

Synonyms: *Coryphantha calochlora* Bödeker, Mamm. Vergl. Schlüss. 7, 1933; *Coryphantha sulcata* (Engelmann) Br. & R. var. *nickelsiae* (K. Brandegee) Benson Cact. Succ. J. (US) 41: 188, 1969.

Body sprouting, group-forming, globose, 6 cm high, 5 cm diameter, apex depressed, with a little white wool, epidermis dull green, short taproot with fibrous attachments. **Tubercles** in 5

and 8 series, conical, slightly flattened above, width at the base 15 mm, 13 mm height, length of upper surface 9 mm, of lower surface 15 mm, groove on upper surface. **Axils** white woolly. **Areoles** oval, 2 mm long, 1.5 mm wide when central spine absent, round, 1.5 mm diameter when central spine present, with white wool in youth. **Radial spines** 14–18, lower and lateral ones radiating, straight, horizontally interwoven, 10–12 mm long, fine needle-like, yellowish-white, upper third of spines bundled in two layers, straight or slightly curved, thicker, needle-like, sometimes 2–3 of them flattened and twisted, up to twice as long as lower radial spines, mostly white with brown tips, some also completely brown or reddish-brown. **Central spines** 0–1, usually on single areoles only, straight, porrect, needle-like, 18–20 mm long, dark brown to black. **Flower** funnellform, 4.5 cm long, 5 cm diameter, outer perianth segments narrow lanceolate, acute, yellow with red dorsal midstripe. Inner perianth segments narrow lanceolate, acute, margins entire, yellow, filaments yellowish-white, anthers yellow, stigma and stigma lobes yellowish-white. **Fruit** short clavate, green juicy berry, 15 mm long, 8 mm diameter, with attached flower remnants. **Seeds** roundish-reniform, brown, 1.4 mm long, 1 mm wide, testa reticulate.

Distribution: Mexico: Coahuila and Nuevo León, on eastern slopes of the Sierra Madre Oriental

Habitat: Limestone gravel, alluvial soil on foothills and ridges, protected under bushes.

Locations checked: Mexico: Nuevo León: Huasteca Canyon, north of Monterrey, Monterrey-Monclova km 40, Salinas Hidalgo-Villaldama, Bustamante, Rinconada, Microondas Pedernales. Coahuila: Candela, between Candela and Monclova, west of Monclova, Monclova-Piedras Negras km 59, Villafrontera, Buenaventura, Campamento San Lazaro.

Incidence: Least concern.

Illustrations: Distribution see Plate 12, map 2; plant portrait see Plate 55.

31. *Coryphantha pseudonickelsiae*

Backeberg

Blätt. Sukk.-Kunde 1:8, 1949.

Lectotype: Illustration in first description (Dicht & A. Lüthy, CSI 11: 19, 2001).**Synonym:** *Coryphantha indensis* Bremer, Cact. Suc. Mex. 22 (4): 75, 1977.

Body solitary or group-forming, globose, 6 cm high, 7 cm diameter, lime-green, apex depressed, with white wool, roots fibrous. **Tubercles** in 8 and 13 series, initially conical, later rounded pyramidal, flattened above, width at the base 15 mm, 12 mm high, length of upper surface 9 mm, of lower surface 14 mm, pronounced groove on upper surface, sometimes with a gland directly behind the spiniferous areole. **Axils** in youth with white wool. **Areoles** round, 2 mm diameter, white wool in youth. **Radial spines** 14–17, radiating, upper 2–3 more closely set, all horizontal to slightly protruding, interwoven, straight, needle-like, stiff, 12–16 mm long, lower ones horn-coloured, later grey, upper ones brownish, later turning grey from the base. **Central spine** 1, sometimes appearing very late, not necessarily appearing on all areoles, porrect, curved downward, thick needle-like, stiff, 16–20 mm long, at first brown-black, later becoming grey from the base. **Flower** funnelform, 30 mm long, 35 mm wide, outer perianth segments lanceolate, margins entire, yellow with reddish midstripe dorsally, inner perianth segments lanceolate, margins entire, yellow, filaments whitish, anthers light yellow, stigma and stigma lobes yellowish. **Fruit** green, juicy berry with attached flower-remnants, 20 mm long, 8 mm wide. **Seeds** reniform, brown, 1.5 mm long, 1 mm wide, testa reticulate.

Distribution: Mexico: To the northeast of Durango.**Habitat:** Lava gravel on hills and slopes.**Locations checked:** Mexico: Durango: Indé, Mina Navidad, Mapimi, La Zarca, Yerbanis.**Incidence:** Least concern.**Illustrations:** Distribution see Plate 12, map 2; plant portrait see Plate 56.**32. *Coryphantha compacta* (Engelmann)**

Britton & Rose

Cactaceae 4: 36, 1923.

Basionym: *Mammillaria compacta* Engelmann in Wislizenus, Mem. Tour. N Mex. 105, 1848.**Type:** not designated.**Synonyms:** *Cactus compactus* (Engelmann) Kuntze, Rev.Gen.Pl. 1: 260, 1891; *Coryphantha palmeri* Britton & Rose, Cact. 4: 39, 1923.

Body solitary, flattened globose, apex depressed, woolly, 5–8 cm diameter, 3–6 cm high, dark green, short taproot. **Tubercles** in 8 and 13 series, conical, rounded, somewhat flattened above, rhomboid at the base, edges obliquely cut, width at the base 13–15 mm, height 9 mm, length of upper surface 7 mm, of lower surface 10 mm, groove on upper surface. **Axils** in youth woolly. **Areoles** oval, 2 mm long, 1 mm wide, in youth woolly. **Radial spines** 14–16, radiating, upper 2–4 more closely set, straight, interwoven, needle-like, 10–15 mm long, upper ones somewhat thinner and longer, horn-coloured, later grey-white, sometimes with darker tips. **Central spine** 0 (–1), rarely on all areoles, porrect, slightly curved, tip sometimes hooked, subulate, black, later becoming grey from the base. **Flower** broad funnelform, 3.5 cm wide, 3 cm long. Outer perianth segments greenish-yellow with broad, brown-red dorsal midstripe, lanceolate, acute, margin entire. Inner perianth segments greenish-yellow, throat greenish tinged, lanceolate, acute, margins entire. Filaments glassy white, anthers yellow, stigma pale yellow, with 7 pale green stigma lobes. **Fruit** conical, dull green, juicy berry with attached flower-remnants, 2 cm long and 1 cm diameter. **Seeds** reniform, brown, 1.7 mm long, 1 mm wide, testa reticulate.

Distribution: Mexico: Chihuahua and Durango.**Habitat:** Plains and ridges of low hills in grassland in volcanic soils.**Locations checked:** Mexico: Chihuahua: Cosihuiriachic, Independencia y Reforma, Valle de

Olivos, Pelayo, Valle de Zaragosa, south of Hidalgo del Parral. Durango: Rio Florida, Cd. Durango, Sombrerete.

Incidence: Least concern.

Comments: *Coryphantha compacta* was first described as *Mammillaria compacta* by Engelmann in 1848 and later reallocated to *Coryphantha* by BRITTON & ROSE (1923) after recollection of the plant at the type locality Cosihuiriachic CHI by Dr. Rose. The first description by Engelmann is very precise and describes a form without a central spine. Eight years later, however, ENGELMANN (1856) himself completed this description by indicating that often the porrect central spine is wanting. This indication of the occasionally appearing central spine was continued by all subsequent authors.

Coryphantha compacta is very widespread in northwestern Mexico and therefore, very variable. Mostly, it has no central spines, but is capable of producing central spines, either on single areoles of a plant only, but also on all areoles. From one population to another, the frequency of occurrence of the single, strong and curved to hooked central spine varies very much.

In 1923, BRITTON & ROSE described a supposedly different plant, *Coryphantha palmeri*, using their concise style as usual: a small globose plant with 13 tubercle series and 11–14 quite strong, horizontally radiating radial spines, small, pale yellow to nearly white flowers of only 3 cm diameter and one single, strong and hooked central spine. As the origin of the holotype they indicated: “On stony ridge near Durango, Mexico”. However, as we know today, near Durango City only two species of the genus *Coryphantha* occur: *Coryphantha compacta* (Engelmann) Britton & Rose and *Coryphantha ottonis* (Pfeiffer) Lemaire (syn. *Coryphantha guerkeana* (Bödeker) Britton & Rose).

ZIMMERMAN (1985) noticed the inconsistency with *Coryphantha palmeri* Br. & R. He

treated it as a synonym of *Coryphantha guerkeana*. Our field studies near the city of Durango showed that here *Coryphantha ottonis* (Pfeiffer) Lemaire (syn. *Coryphantha guerkeana* (Bödeker) Britton & Rose) has up to 11 radiating radials only, tubercles series of 5:8 and up to 4 central spines and therefore, does not correspond to *Coryphantha palmeri* Br. & R. However, we also found plants near Durango with which we are familiar, mainly from the state of Chihuahua, which completely correspond to the description of *Coryphantha palmeri*, but which we classify as forms of *Coryphantha compacta*. Usually they show 14 radial spines, tubercles in 13 series and at most one single, sometimes hooked central spine which is often wanting.

In fact, there is more or less no difference between the descriptions of *Coryphantha compacta* (Engelmann) Britton & Rose and *Coryphantha palmeri* Britton & Rose. *Coryphantha palmeri* Br. & R. including its holotype is nothing else than a younger description of *Coryphantha compacta* (Engelmann) Br. & R. and therefore, as a younger synonym, invalid.

A. BERGER (1929) gave a very different meaning to the name *Coryphantha palmeri* Br. & R. by his illustration of another plant from San Vicente, Tamaulipas, under the name *Coryphantha palmeri*. His illustrated plant had 18 radial spines! Consequently, this very hook-spined species, whose correct name is *Coryphantha delicata* Bremer (see 35.), was erroneously named *Coryphantha palmeri* by all authors to come.

BRITTON & ROSE (1923) mentioned two more plants under *Coryphantha palmeri* which had been collected by Dr. Palmer near Saltillo COAH in October 1904 (Nr. 438) and July 1905 (Nr. 703), which, as we know today, correspond to Berger’s *Coryphantha palmeri*, but not to its holotype from Durango.

More comments: see *C. delicata* (35.).

Illustrations: Distribution see Plate 12, map 2; plant portrait see Plate 57.

33. *Coryphantha cornifera* (De Candolle)
Lemaire

Cactées 35, 1868.

Basionym: *Mammillaria cornifera* De Candolle, Mém. Mus. Hist. Nat. Paris 17: 112, 1828.

Type: not designated.

Synonyms: *Mammillaria radians* De Candolle, Mém. Mus. Hist. Nat. Paris 17: 111, 1828; *Mammillaria impexicoma* Lemaire, Cact. Aliq. Nov. 5, 1838; *Mammillaria radians globosa* Scheidweiler, Bull. Acad. Sci. Brux. 5: 494, 1838; *Mammillaria pfeifferiana* De Vriese, Tydschr. Nat. Geschr. 6: 51, 1839; *Aulacothele cornifera* (De Candolle) Monville, Cat. Pl. Exot., 21, 1846; *Aulacothele radians* (De Candolle) Monville, Cat. Pl. Exot., 21, 1846; *Mammillaria cornifera impexicoma* Salm-Dyck, Cact. Hort. Dyck. 1849: 20, 1850; *Echinocactus corniferus* (De Candolle) Poselger, Allg. Gartenz. 21: 102, 1853; *Echinocactus corniferus impexicomus* (Salm-Dyck) Poselger, Allg. Gartenz. 21: 102, 1853; *Echinocactus corniferus longisetus* Poselger, Allg. Gartenz. 21: 102, 1853; *Echinocactus corniferus nigricans* Poselger, Allg. Gartenz. 21: 102, 1853; *Echinocactus radicans* (De Candolle) Poselger, Allg. Gartenz. 21: 107, 1853; *Cactus corniferus* (De Candolle) Kuntze, Rev. Gen. Pl. 1: 260, 1891; *Cactus pfeifferianus* (De Vriese) Kuntze, Rev. Gen. Pl. 1: 261, 1891; *Cactus radians* (De Candolle) Kuntze, Rev. Gen. Pl. 1: 261, 1891; *Cactus radians pectinoides* Coulter, Contr. U.S. Nat. Herb. 3: 144, 1894; *Mammillaria radians impexicoma* Schumann, Gesamtb. Kakt. 495, 1898; *Mammillaria cornuta* Hildmann ex Schumann, Gesamtb. Kakt. 496, 1898; *Coryphantha radians* (De Candolle) Britton & Rose, Cactaceae 4: 36, 1923; *Coryphantha cornuta* (Hildmann) Berger, Kakteen 268, 1929; *Coryphantha schwarziana* Bödeker, Mamm. Vergl. Schlüss. 12, 1933; *Coryphantha radians* (De Candolle) Britton & Rose var. *pectinoides* (Coulter) Bravo, Cact. Suc. Mex. 27 (1): 17, 1982; *Coryphantha maliterrarum* Bremer, Cact. Succ. J. (US) 56: 71, 1984; *Coryphantha bernalensis* Bremer, Cact. Succ. J. (US) 56: 165, 1984.

Body solitary, rarely sprouting, globose, 6 cm high and 8 cm diameter, dull olive-green, apex depressed, with white wool, fibrous roots. **Tubercles** in 5 and 8 series, conical, rhomboid at the base, obliquely cut, grooved above, width at the base 12–16 mm, height 8–14 mm, length of upper surface 8–10 mm, of lower surface 12–18 mm. **Axils** in youth with white wool. **Areoles** oval, 3 mm long, 1.5 mm wide when central spine absent, round, 2 mm diameter when central spine present, in youth with white wool, pectinate. **Radial spines** 12–18, irregularly radiating, horizontal, interwoven, thick needle-like, straight or slightly curved, occasionally 3–4 thinner spines more densely set, all 14–16 mm long, horn-coloured to yellowish-white, sometimes darker tipped. **Central spines** 0–1 (–4), the dominant spine straight, porrect, curved downward, the other two centrals protruding laterally and curved, all subulate, 14–18 mm long, dark brown, becoming grey from the base. **Flower** funnelform, 6 cm in length and diameter, outer perianth segments narrow lanceolate, acute, margins entire, yellow with strong red dorsal midstripe; inner perianth segments narrow lanceolate, acute, margins entire, 40 mm long, 4 mm wide, light yellow, sometimes reddish at the base, filaments yellow to reddish-yellow, anthers yolk-yellow, stigma pale yellow, stigma lobes whitish. **Fruit** green juicy berry with attached flower remnants, 25 mm long, 10 mm wide. **Seeds** reniform, brown, 1.3 mm long, 0.8 mm wide, shiny, testa reticulate.

Distribution: Mexico: Hidalgo, Querétaro, Guanajuato, San Luis Potosí, Jalisco and eastern Zacatecas.

Habitat: Limestone gravel on low hills and plains.

Locations checked: Mexico: Hidalgo: Pachuca, Ixmiquilpan-Actopan, Tolantongo, El Cubo, Zempoala, Cardonal, Patria Nueva, Tepetitlan, Naxteay, Lagunilla, Santiago Tlautla. Querétaro: Peña Miller, Vista Hermosa, San Joaquin, Huimilpan, Peña Blanca, Bucareli, Boye, Bernal, Maria Puerto del Cielo,

Colón, Rancho Nuevo, Higuerillas. Guanajuato: La Cañada, San Felipe, Guanajuato, Agustín González, Dolores Hidalgo, Xoco-noxtle, Jofre. San Luis Potosí: Balneario Lourdes, Tullillo, Santa Gertrudis, Santa María del Río, San Antonio, La Granja, 19 km north of SLP, Monte de Caldera, Villa de Reyes, Mesa la Mula, Santa Teresa, Ventura, Tolosa. Jalisco: Ojuelos. Zacatecas: Piños.

Incidence: Least concern.

Comments: At most locations adult plants can be found with and without central spines. When present, the central spines vary in number from 1 (more usual) to 4. The arrangement of the centrals is variable, spines being symmetrically arranged on some plants and set totally irregularly on others. Spines vary from straight to strongly curved downwards. Plants without centrals are identical in all respects (form and size of the tubercles, number and arrangement of the radial spines, flowers, fruits and seeds) to centrally spined plants apart from the centrals, of course. There is no justification in separating them and giving them their own species name, e.g. *C. radians*.

When cultivated in non-ideal light conditions, plants originally with strong central spines can revert to pure radial spination, but still maintain normal body growth and flower production.

The number of radial spines is very variable, in extreme cases from 8–22, with the same arrangement, i.e. purely radial to bundled above.

C. cornifera was first described in 1828 by De Candolle as one of the first species of *Coryphantha*. Apparently, De Candolle had received plants with and without central spines within the same shipment and published them as *Mammillaria cornifera* and *Mammillaria radians* respectively. The astonishing variability of this species led to many new descriptions. We prefer the name *cornifera* as opposed to *radians*, because several species of *Coryphantha* which show cen-

tral spines later go through a stage when only radials are present (e.g. *C. echinoidea*, *salinensis* etc.). Other species may only have radial spines when adult (e.g., *C. pallida*, *compacta*, *delicata* etc.) and might therefore, be confused with this species.

Comments about *Coryphantha cornuta*: see *Coryphantha vogtherriana* (15.).

Illustrations: Distribution see Plate 12, map 2; plant portrait see colour Plate 3 and 58.

34 a. *Coryphantha recurvata* (Engelmann)

Britton & Rose ssp. *recurvata*

Cactaceae 4: 27, 1923.

Basionym: *Mammillaria recurvata* Engelmann, Trans. St. Louis Acad. 2: 202, 1863.

Lectotype: Mexico, Sonora, Sierra del Pajarito, 1855, Schott s.n. (MO), F 42678, ISC (Benson, Cacti US & Canada 962, 1969).

Synonyms: *Mammillaria recurvispina* Engelmann, Proc. Amer. Acad. 3: 266, 1856 (*non* De Vriese 1839); *Cactus recurvatus* Kuntze, Rev. Gen. Pl. 1: 259, 1891; *Cactus engelmannii* Kuntze, Rev. Gen. Pl. 1: 260, 1891; *Mammillaria nogalensis* Runge ex Schumann, Gesamtb. Kakt. 494, 1898.

Body: Plant sometimes solitary, mostly group-forming by sprouting at the base, forming large mounds of more than 1 m diameter, **body** globose, up to and over 20 cm in height and 10–20 cm diameter, apex slightly depressed with sparse white wool, epidermis dull green, fibrous roots. **Tubercles** in 8 and 13, later 13 and 21 series, conical, rhomboid at the base, 12–14 mm width, 8–9 mm height, length of upper surface 6–7 mm, of lower surface 8–9 mm, naked groove on upper surface. **Axils** with sparse white wool in youth. **Areoles** elliptical, 4 mm long and 2 mm wide, with white felt in youth. **Radial spines** 17–20, radiating, slightly protruding, interwoven, straight or slightly curved, 8–14 mm long, needle-like, stiff, horn-coloured to white, brown towards the tip. **Central spine** 0–1, seldom 2, slightly

downwards pointing, somewhat protruding and curved, 10–17 mm long, needle-like to strong needle-like, brown, becoming grey from the base, the second central spine, when present, directed upwards. **Flowers** often several at the same time near the top, funnelform, outer perianth segments lanceolate, margins entire, acute, yellow with brown-red midstrip, inner perianth segments lanceolate, margins entire, yellow with brownish tips, filaments pale yellow, anthers yellow, stigma and stigma lobes yellow. **Fruit** globose, juicy green berry with attached flower remnants, 9 mm diameter. **Seeds** small, 1.2 mm long and 0.8 mm wide, roundish-reniform, brown, testa reticulate.

Distribution: Mexico: Sonora. USA: Arizona.

Habitat: Open grassland on lava soil.

Locations checked: USA: Arizona: east of Nogales. Mexico: Sonora: Nacozari, south of Moctezuma, Mazocahui.

Incidence: Least concern.

Comments: Common name: golden-chested beehive.

Engelmann (1859: 12) mentioned a great similarity to *Coryphantha compacta*, whose flowers, as he stated, always appear right in the centre of the top, while in *Coryphantha recurvata* they are arranged around the centre of the top.

Illustrations: Distribution see Plate 12, map 2; plant portrait see Plate 59.

34 b. *Coryphantha recurvata* (Engelmann)

Britton & Rose subsp. *canatlanensis*

Dicht & A. Lüthy

Kakt. and. Sukk. 54 (3): 57, 2003.

Type: Mexico, Durango, west of Canatlàn DGO, G.S. Hinton s.n. (Herbarium Hinton 27666)

Plant sometimes solitary, mostly group-forming by sprouting at the base, **body** globose, up to 15 cm high, 13 cm diameter, apex slightly depressed with sparse white wool, epidermis dull green, thick taproot. **Tubercles** in 8 and 13, later 13 and 21 series, conical, rhomboid at

the base, 12–14 mm width, 8–9 mm height, length of upper surface 8 mm, of lower surface 10 mm, naked groove on upper surface. **Axils** with sparse white wool in youth. **Areoles** pectinate, elliptical, 3 mm long and 1 mm wide, with white wool in youth. **Radial spines** 17–19, radiating, appressed, only slightly protruding, interwoven, straight or slightly curved, 14 mm long, needle-like, stiff, pale horn-coloured, upper ones whitish with dark tips. **Central spine** 0–1, on some areoles only, stiff needle-like, straight, porrect at a right angle to the radial spines, 13 mm long, dark brown, later turning grey from the base. **Flowers, fruit and seeds:** like ssp. *recurvata*.

Distribution: Mexico: Durango, Sinaloa.

Habitat: Open grasslands on lava soils.

Locations checked: Mexico: Durango: west of Canatlàn and west of Cd. Durango (km 34–36).

Incidence: Least concern.

Comments: The locations of ssp. *canatlanensis* are about 1000 km south of the most southern known locations of ssp. *recurvata*. The distribution area is west of the line Cd. Durango-Canatlàn, on the eastern slopes of the Sierra Madre Occidental, while single locations have also been reported from the western slopes (Charles Glass, field notes), where this species, the only *Coryphantha*, also grows in the State of Sinaloa.

Ssp. *canatlanensis* differs mainly by the always completely straight, dark brown central spine, which never occurs on all areoles and which is porrect in the prolongation of the tubercle axis. It also differs by the whiter colour of the radial spines and the very thick taproot.

The other characteristics are identical to ssp. *recurvata*, the single heads remain somewhat more globular and the groups do not reach the measurements of those of the northern form.

The plants have been known for a longer time period, they were collected west of Durango by George Lindsay and Charly Mieg

(BRAVO 1991) and erroneously published as *Coryphantha radians* var. *pectinoides* (Coulter) Bravo by H. BRAVO (1982).

Illustrations: Distribution see Plate 12, map 2; plant portrait see Plate 60.

35. *Coryphantha delicata* Bremer

Cact. Succ. J. (US) 51: 76, 1979.

Type: Mexico, Tamaulipas, Palmillas, e. 4700 ft (1430 m), 11.4.1976, Bremer 476–7A (ASU).

Synonyms: *Coryphantha jaumavei* Fric, Möllers Deutsche Gärtnerztg. 12: 140, 1926 *nom.nud.*; *Coryphantha palmeri* Britton & Rose *sensu* Berger, Kakteen 269, 1929; *Coryphantha panarottoi* Halda & Horáček, Acta Mus. Richnov. Sect. Nat. 6 (3): 235, 1999.

Body solitary or group-forming by sprouting, semi-globose to globose, 5–6 cm diameter, 4–5 cm high, dark green, apex flattened with sparse white wool, body tapers into a taproot.

Tubercles in 8 and 13 series, densely set, conical, round, oval and slightly enlarged at the base, with complete, fine groove, width at the base 7–9 mm, height 5–6 mm, length of upper surface 6–8 mm, of lower surface 7–9 mm.

Axils in new growth with sparse white wool.

Areoles without central spine are oval, 2.5 mm long and 1.5 mm wide, with central spine present round, 2 mm diameter, in new growth slightly woolly. **Radial spines** 17–22, radiating, upper 6–8 more densely set to bundled in several layers, all strongly interwoven, needle-like, nearly straight, lower and lateral radials 9–10 mm, upper ones sometimes longer, up to 15 mm, white or yellowish-horn-coloured with dark tips, uppermost ones in new growth often brown, later white, dark tipped.

Central spine 0–1, porrect, tip curved to hooked, thin subulate, 6–12 mm long, in new growth brown to nearly black, later becoming pale and then grey from the base. **Flower** funnellform, yellow, 5 cm long and wide, outer perianth segments lanceolate, acute, margins entire, yellow with a reddish dorsal midstripe outside, inner perianth segments lanceolate, acute, margins entire,

40 mm long, 6 mm wide, whitish-yellow. Filaments greenish-white, anthers yellow, stigma and stigma lobes whitish. **Fruit** green juicy berry with attached flower remnants, 25–30 mm long, 12 mm diameter. **Seeds** brown, reniform, 1.6 mm long, 1 mm wide, testa reticulate.

Distribution: Very common in Tamaulipas, San Luis Potosí, Nuevo León, Coahuila, Durango and Zacatecas.

Habitat: Limestone gravel on plains, lower slopes and tops of hills.

Locations checked: Mexico: Tamaulipas: Jaumave, Nogales, San Antonio, Palmillas, junction to Bustamante, La Taponá, La Perdida, San Vicente. San Luis Potosí: Ventura, Las Tablas, Monte de Caldera, north of Matehuala, Rio Verde, Entronque Huizache, El Sauz, San Martín, San Francisco, Cedral-Catorce, Salinas, north of Santa Rita, Cerritos, La Monalla, San Antonio Trojes, Venado, San Isidro etc. Nuevo León: Ascension-Sandia, Dr. Arroyo, Mier y Noriega, La Trinidad, Jesus Maria de Aguirre, San Antonio de Alamitos, Sandia el Grande, La Zorra, Cerros Blancos, La Soledad, La Escondida, Aramberri, Rinconada, Higuera, San Francisco, San Roberto etc. Coahuila: east of General Cepeda, Arteaga, El Tule, Las Imágenes etc. Zacatecas: near Tiburción, Panuco, Villa García. Durango: Cuencamé.

Incidence: Least concern.

Variability/differentiation: *Coryphantha delicata* Bremer has a very wide distribution and therefore its appearance varies: in the Jaumave Valley, there are whitish and strongly spined forms, single or in groups; in San Luis Potosí and Nuevo León, there are more yellowish forms with finer and longer spines which often form large clusters; and in Coahuila, mainly in the region of Saltillo-General Cepeda, there are more multi-coloured forms with yellow, brownish-red and white spines, usually without central spines, growing as single plants.

The most striking features are the very small, only 7–9 mm broad tubercles, which,

with the exception of *Coryphantha gracilis*, are the smallest tubercles within the genus *Coryphantha*, the needle-like, densely interwoven 17–22 radial spines, the single central spine always hooked, the relatively large flower of 5 cm diameter and the big taproot.

Comments: The first illustration of this species appeared in A. BERGER's Kakteen (1929) under the name *Coryphantha palmeri* Br. & R. However, the holotype (Palmer 557) of *Coryphantha palmeri* Br. & R. was from near the city of Durango and its first description was nothing less than a redescription of *Coryphantha compacta* (Engelmann) Br. & R. which grows there, occasionally with a single central spine present. However, *Coryphantha compacta* has larger tubercles, lesser radial spines and smaller flowers than *Coryphantha delicata*.

Another illustration of *Coryphantha delicata* was given by FRIC in Möllers Deutscher Gartenzeitung Nr. 12: 140, 1926 as *Coryphantha Jaumavei*, Fric. Sp.n. However, a valid description of *Coryphantha Jaumavei* was never published, therefore, this name must be discarded as being a *nom.nud.*

At several locations this species grows without any central spines e.g., in the region of Saltillo SLP, near Aramberri SLP, north of Dr. Arroyo NL and also in the Jaumave valley. This form, which, except for the absence of central spines, cannot be differentiated from centrally spined forms, was newly described by Bremer in 1979 as *Coryphantha delicata*. Therefore, this is the only valid name of this species with its usually hooked central spines.

Illustrations: Distribution see Plate 13, map 1; plant portrait see Plates 61 and 62.

36. *Coryphantha neglecta* Bremer

Cact. Suc. Mex. 24: 3, 1979.

Type: Mexico, Coahuila, north of Cuesta la Muralla, km 151 Carr. Fed. 57 Monclova-Piedras Negras, 700 m., Bremer 978–1 (MEXU).

Body solitary, later sprouting from the base or from old tubercles, forming large groups, globose, about 7 cm in width and 6 cm height, dull dark green, apex slightly depressed, somewhat woolly. **Tubercles** in 8 and 13 series, conical, rhomboid at the base, slightly bulging, 11 mm wide, 7 mm high, length of upper surface 8 mm, of lower surface 13 mm, with complete, slightly woolly groove. **Axils** in youth woolly, later naked. **Areoles** oval, 1.5 mm wide and somewhat longer, with sparse felt in youth. **Radial spines** 16–20, the lower and lateral ones radiating horizontally and interwoven, straight, stiff, needle-like, 11–16 mm long, in the lower half pale yellow, the laterals dark brown, soon all becoming grey, the 4–6 upper spines longer, usually bundled together in two layers, curved, sometimes broader and flatter, 16–20 mm long, whitish with black tips. **Central spines** 0–1 (never more), if present thin subulate, straight, porrect, 13–18 mm long, initially dark brown with paler base, soon becoming grey with dark tips. **Flower** funnelform, 4.5 cm in length and diameter, outer perianth segments linear lanceolate, acute, margins entire, pale yellow with greenish-brown midstripe and red-brown tip, inner perianth segments linear lanceolate, acute, margins entire, notched towards the tip, pale yellow, filaments cream-white, anthers yellow, stigma greenish, stigma lobes 7–8, white. **Fruit** pale green juicy berry, 21 mm long, 10 mm diameter, with attached flower remnants. **Seeds** reniform, 1.2 mm long, 1.0 mm wide, shiny hazel-brown, testa reticulate. **Distribution:** Mexico: western slopes of the Sierra Madre Oriental in Nuevo León and Coahuila.

Habitat: Limestone gravel, alluvial soil on foothills and ridges.

Locations checked: Mexico: Nuevo León: Monterrey, Monterrey-Monclova, Casas Colradas, Sabinas Hidalgo-Villaldama, Rancho San Gabriel. Coahuila: Dolores, Bonanza, Candela, west of Cuatrociénegas, Microondas El Zago, Castaños, El Sacrificio, km 151 Mon-

clova-Saltillo (type locality), Loma Verde, Las Palomas.

Incidence: Least concern.

Differentiation: This species is often confused with either *Coryphantha nickelsiae* (30.) or with *Coryphantha pseudoechinus* (37 a.), also forming large groups and sometimes sharing the same habitats.

Illustrations: Distribution see Plate 13, map 1; plant portrait see Plate 63.

37 a. *Coryphantha pseudoechinus* Bödeker subsp. *pseudoechinus*

Monatsschr. DKG 1: 17, 1929

Lectotype: Illustration in first description (Dicht & A. Lüthy, CSI 11: 20, 2001).

Synonym: *Coryphantha pusilliflora* Bremer, Cact. Succ. J. (US) 54: 133, 1982.

Body sprouting from the base, forming large groups, ovoid to short cylindrical, 7–12 cm high and 5 cm in diameter, dark green, apex slightly depressed with some wool. **Tubercles** in 5 and 8 series, conical, somewhat flattened on the upper side, rhomboid at the base, 10 mm wide, length of upper surface 8 mm, of lower surface 13 mm, with sharp, narrow groove, woolly in youth and with yellow glands near the spiniferous areole. **Axils** in youth woolly. **Areoles** round, 2 mm diameter, in youth with white wool, later naked, vaulted, with a ring-like boundary represented by the dark bases of the radial spines. **Radial spines** 18–20, radiating, straight, stiff, needle-like, 10–15 mm long, mostly greyish-white, frosted, or, mainly the uppermost radial spines, initially presenting the whole spectrum from yellow, brown to nearly black, then all greyish. **Central spines** 0–1, porrect, in the direction of the tubercle axis i.e., usually obliquely upwards, but occasionally also displaced laterally and/or even slightly downwards, 14–18 mm long, thick needle-like, brown to black, soon greyish and frosted. **Flowers** often several simultaneously open, situated near apex, flattened funnellform, 2 cm long and 3 cm in diameter, outer peri-

anth segments lanceolate, dark red-brown with a rose margin, greenish at the base, 3 mm wide, 11 mm long, inner perianth segments narrow lanceolate, violet-rose, lighter towards the base, 3 mm wide, 22 mm long, filaments numerous, whitish, anthers yellow, style whitish with 5–6 whitish stigma lobes. **Fruit** oblong, ovoid, when mature reddish with attached flower remnants, 15 mm long and 7 mm wide. **Seeds** 1 × 1.2 mm, reniform, smooth, brown, testa reticulate.

Distribution: Mexico: Coahuila, in the Sierra de la Paila.

Habitat: Hillsides with limestone gravel and rocks.

Locations checked: Mexico: Coahuila: Casas Coloradas, San José de la Paila, Zona de Minas, north of Estacion Marte, Mount Paila, Las Palomas, San Pedro, El Sacrificio, Pareños, Cuatrociénegas-San Pedro de Las Colonias, west of Hipolito.

Incidence: Least concern.

Differentiation: *C. pseudoechinus* subsp. *loui* (37 b.), *C. neglecta* (36.).

Comments: *Coryphantha pseudoechinus* has always been treated as an obligatory gland-forming species. More precise observations confirmed the indication of the first description that “glands are only produced during active growth and formation of buds” and this immediately behind the spine-bearing areole only. Although glands are more often present than in most other species of subgenus *Coryphantha*, it completely fits the definition of the latter.

Illustrations: Distribution see Plate 13, map 1; plant portrait see Plates 64 and 65, photos 1 and 2.

37 b. *Coryphantha pseudoechinus* subsp. *loui* (Bremer) Dicht & A. Lüthy

Cact. Syst. Init. 11: 20, 2001.

Basionym: *Coryphantha loui* Bremer, Cact. Succ. J. (US) 51: 278, 1979.

Type: Mexico, Coahuila, 30 miles (48 km) N of El Marte, 2000–2200 m, Bremer 476–3 (ASU).

Body solitary or group-forming, globose to ovoid, apex slightly depressed, white woolly, 5.5 cm diameter and up to 5 cm height, grass-green. **Tubercles** in 5 and 8 series, conical, somewhat flattened on the upper side, rhomboid at the base, 10 mm wide, length of upper surface 8 mm, of lower surface 13 mm, with narrow groove on upper surface, having white wool initially, sometimes with yellowish glands near the areoles. **Axils** woolly in youth. **Areoles** round, 2 mm diameter, in youth white woolly, later naked, vaulted. **Radial spines** 18–20, radiating, horizontal to slightly ascending, straight or slightly curved, thin needle-like, often bristly, flexible, 10–14 mm long, yellowish-horn-coloured, those from the upper half of an areole red-brown at first, some slightly greyish in later years. **Central spine** 0–1, straight, porrect or slightly curved downwards, thick needle-like, 14–16 mm long, reddish-brown to dark mahogany, becoming lighter to grey on older tubercles. **Flowers** funnellform, 3.5 cm long, 3 cm diameter, outer perianth segments linear lanceolate, tips acute, margins entire, light yellow with green near the tip, reddish-brown dorsal midstripe, inner perianth segments linear lanceolate, acute, margins entire, light yellow, filaments glassy white, anthers light orange, style pale green with 5–7 cream-white stigma lobes. **Fruit** small, ovoid jade-green juicy berry with attached flower remnants, 18 mm long and 8 mm wide. **Seeds** light brown, reniform, smooth, shiny, testa reticulate, 1 × 1.2 mm.

Distribution: Mexico, Coahuila, Sierra la Paila.

Type locality (checked): The higher mountain ridges in the region of the fluorite mines at 2000–2200 m above sea level, 30 miles north of El Marte, Coahuila, a railway station on the railroad parallel to route 40, the Saltillo-Torreon road.

Habitat: On hilltops with limestone gravel and rocks.

Incidence: Least concern.

Illustrations: Distribution see Plate 13, map 1; plant portrait see Plate 65, photos 3 and 4.

Subseries *Delaetianae* Dicht & A. Lüthy
Cact. Syst. Init. 11: 20, 2001

Type: *Coryphantha delaetiana* (Quehl) Berger

Definition: central spines always 3–4.

38. *Coryphantha delaetiana* (Quehl) Berger
Kakteen 270, 1929

Basionym: *Mammillaria delaetiana* Quehl, Monatschr. Kakt. 18, 1908.

Lectotype: Fig. Monats. Kakt. 18, 1908 (Dicht & A. Lüthy, CSI 11: 20, 2001).

Synonyms: *Mammillaria gladiispina* Bödeker, Zeitschr. Sukk.-Kunde 2: 120, 1925; *Coryphantha gladiispina* (Bödeker) Berger, Kakteen 271, 1929; *Coryphantha salm-dyckiana* (Scheer) Br. & R. sensu Britton & Rose, Cact. 4: 39, 1923; *Coryphantha borwigii* sensu Bremer, Cact. Suc. Mex. 15: 69, 1980.

Body irregularly group-forming by sprouting from the lower and middle part of the body, globose, 8 cm in height, 8 cm diameter, epidermis dull dark green, apex slightly depressed with a little white wool. **Tubercles** in 8 and 13 series, conical, rhomboid at the base, flattened above, obliquely cut, 15 mm wide at the base, 10 mm height, length of upper surface 9 mm, of lower surface 11 mm, groove complete, with little wool in youth. **Axils** white woolly in youth. **Areoles** slightly oval, 1.5 mm wide and somewhat longer, white woolly in youth. **Radial spines** 16–20, about two-thirds of them radiating to the sides and downwards, slightly protruding, straight, needle-like, interwoven, 11–15 mm long, the upper ones more densely set, slightly longer, all transparent yellowish to white, upper ones darker tipped. **Central spines** 3 (–4), dominant one straight porrect, somewhat curved downwards, thin subulate, 18–22 mm long, other centrals from obliquely upwards to nearly sideways protruding, slightly curved, somewhat thinner and

shorter, all dark brown to black, later becoming grey. **Flower** funnellform, 4.5 cm diameter, 4 cm long, outer perianth segments lanceolate, acute, margins entire, yellow with strong red-green dorsal midstripe, inner perianth segments broad lanceolate, acute, margins entire, whitish-yellow, 25 mm long, 4 mm wide, filaments whitish-yellow, anthers yellow, stigma whitish-yellow, 13 mm long, with 6 stigma lobes of same colour. **Fruit** green juicy berry, 20 mm long, 9 mm diameter, thinner towards the base, with flower remnants attached. **Seeds** reniform, dark brown, 1.3 mm long, 0.9 mm wide, testa reticulate.

Distribution: Mexico: Coahuila, Durango and Chihuahua.

Habitat: Alluvial soils on plains and flat ridges.

Locations checked: Mexico: Coahuila: Road junction to Parras de la Fuente, Las Palomas. Durango: Minas Navidad, Sierra de la Muerte, Conejos, Mapimi, Bermejillo. Chihuahua: Escalón, El Morrion, Aldama, División del Norte.

Incidence: Least concern.

Illustrations: Distribution see Plate 13, map 2; plant portrait see Plate 66.

39 a. *Coryphantha ramillosa* Cutak subsp. *ramillosa*

Cact. Succ. J. (US) 14: 163, 1942.

Type: USA, Texas, Brewster County, Reagan Canyon, Cutak s.n. (MO 1242260)

Body solitary or group-forming, flattened-globose, grey-green, 3–8 cm height and 6–9 cm diameter, apex with white wool.

Tubercles quite large, 20 mm long, widened at the base, 15–25 mm wide, groove on upper surface from tip to base. **Areoles** round, initially with white felt, later naked. **Radial spines** 14–20, radiating, somewhat flattened or angular and slightly curved, 10–15 mm long, radiating. **Central spines** 4, longer and thicker than radial spines, but still relatively weak, 25–28 mm long, initially all chocolate-

brown in colour with white base, later grey with darker tips, the lower one usually porrect or slightly curved downwards; the upper 3 straight and ascending, sometimes with sharpish curve. **Flower** large, 6.5 cm long and 5 cm diameter when fully opened, colour changing from light rose to purple, outer perianth segments lighter and larger than inner ones, light green dorsal midstripe; pericarpel greenish, eventually with a purple tinge; inner perianth segments 25 mm long, 2 mm wide in the lower half and 4 mm wide in the upper third, margins entire, white, upper half rose or purple; filaments short, white, anthers orange, stigma slender, white, stigma lobes 6 or 7. **Fruit** egg-shaped, 2–2.5 cm long, green, with attached flower remnants. **Seeds** reniform, 1.4 mm long, 1 mm wide, brown, testa reticulate.

Distribution: USA: Texas: Brewster County and Big Bend National Park near the Rio Grande. Mexico: Coahuila: adjacent regions of Coahuila and Chihuahua near Rio Grande.

Habitat: Limestone gravel, alluvial soil on foothills and ridges.

Locations checked: USA: Texas: Brewster County. Mexico: Coahuila: Sierra del Carmen, Cuatrociénegas, Ocampo, San Miguel, San José de las Piedras, Piedritas. Chihuahua: Coyame.

Incidence: Least concern.

Illustrations: Distribution see Plate 13, map 2; plant portrait see Plates 67 and 68, photo 1.

39 b. *Coryphantha ramillosa* subsp. *santarosana* Dicht & A. Lüthy

Kakt. and. Sukk. 51(6): 141, 2000.

Type: Mexico, Coahuila, La Babia, G.S. Hinton s.n. (herb. Hinton 25792).

Body solitary, also group-forming, 7 cm diameter, 3–4 cm height, semi-globose with apex flattened, grass-green. **Tubercles** rounded, pyramidal, later flattened, 20 mm width at the base, 13 mm height, 10 mm long, grooved. **Axils** woolly. **Areoles** 2.5 mm diame-

ter, round, in youth with white felt. **Radial spines** 11–13, lateral and lower ones horn-coloured, upper ones whitish with brown tips, often bundled, all straight to slightly curved laterally, 9–12 mm long, needle-like. **Central spines** up to 4, the longest lower one up to 28 mm long, porrect, slightly curved downwards, two laterals pointing to the sides and upwards, slightly protruding, needle-like, dark brown, later grey. The fourth pointing straight upwards with the radial spines, coloured like upper radial spines, slightly thicker than radials. **Flower** 6.5 cm long, 5 cm diameter, yellow. Outer perianth segments yellow with greenish red-brown midstripe, at the base 3 mm wide, towards the tip 4 mm. Inner perianth segments yellow, 35 mm long, up to 5 mm wide, margins entire, apiculate, filaments light yellow, anthers dark yellow, stigma 23 mm long, whitish-yellow, stigma lobes 5–6, up to 5 mm long, ovary whitish, 10 mm long. **Fruit** dark green globose juicy berry, somewhat lighter and reddish at the base, 16 mm wide, 20 mm long, with attached flower remnants. **Seeds** 1.2 mm long, 1 mm wide, brown, reniform, testa reticulate.

Distribution: Mexico: to the north of Coahuila.

Habitat: Hills and ridges of alluvial material, mostly with pebbles

Locations checked: Mexico: Coahuila: Minas de Barroteràn, La Babia, San Alberto, San Blas, Buenaventura, Lomas de los Angeles, La Peña, El Mélon, El Berrendo.

Incidence: Least concern.

Comments: In his seed catalogue of 1989, Steven Brack offered a yellow-flowering form of *Coryphantha ramillosa* from Allende Coahuila (SB 600) for the first time. The same plant was found by Anton Hofer and Adrian Lüthy in 1990 near La Babia, Coahuila. In 1997, we thoroughly searched the region northeast of Coahuila for *Coryphantha ramillosa* Cutak and always found the yellow-flowering form at various locations within the triangle Monclova–Piedras Negras–Boquillas del Carmen.

The most southern location we checked was San Alberto, Coahuila, about 60 km northeast of Monclova. The densest populations are in the Sierra Hermosa de Santa Rosa.

The flower colour alone would not justify a delineation of the plant as a subspecies, but there are other differences such as body colour, tubercle size, number of radial spines and length of all the spines.

The plants usually grow solitarily or as small groups in calcareous gravel on gentle slopes like hill tops. Associative flora is the typical Chihuahuan Desert flora with *Opuntias*, *Yuccas*, *Agave lechuguilla* and low, sparsely disposed bushes. Other cacti found were: *Echinocereus dasyacanthus*, *Echinocereus longisetus*, *Echinocereus triglochidiatus* var. *paucispinus*, *Escobaria tuberculosa*, *Glandulicactus uncinatus* var. *wrightii* and *Neolloydia conoidea*.

An analysis of cactus literature has confirmed that this yellow-flowering form was collected in the nineteenth century by Dr. Bigelow near Santa Rosa, Coahuila (ENGELMANN 1859, BENSON 1982), which is south of the Rio Grande opposite Big Bend National Park. ENGELMANN's description of *Mammillaria scolymoides* Scheidweiler in 1859 fits this subspecies in practically all respects. However, Engelmann's description does not correspond to the first description of Scheidweiler of *Mammillaria scolymoides* in any respect and the supplementary data by SALM-DYCK (1850) and FÖRSTER (1846) relevant to this latter species diverge completely (DICHT & A. LÜTHY 1998). Engelmann's *Mammillaria scolymoides* must, therefore, be regarded as a homonym. The discrepancies to Scheidweiler's first description mean that this name cannot be used for the *Coryphantha ramillosa* subspecies.

We chose the name *santarosa* because of its main distribution area, the Sierra Hermosa de Santa Rosa, and also because of Santa Rosa, Coahuila, to highlight the historical facts referred to above.

Illustrations: Distribution see Plate 13, map 2; plant portrait see Plate 68, photos 2–5.

40. *Coryphantha pulleineana* (Backeberg)

Glass

Cact. Succ. Mex. 13(2): 34, 1968.

Basionym: *Neolloydia pulleineana* Backeberg, The Spine 1:4, 106, 1948.

Neotype: Mexico, San Luis Potosí, Entronque Huizache, Foster 276 A (POM) (Glass, loc.cit.).

Body usually solitary or with few branches, at the base thin and nearly serpentine, then cylindrical-clavate, up to 20 cm long and 4.5 cm diameter, dark green. Taproot up to several decimetres long with potential for generation of further plant bodies. **Tubercles** in 5 and 8 series, 12 mm long, slender, conically rounded, curved upward, obliquely cut, groove complete, sometimes with glands, but near the spiniferous areole only. Old tubercles become desiccated, woody, and finally drop off. **Axils** woolly in youth or grey felted, without glands. **Areoles** round, 3 mm diameter, in youth with dense wool. **Radial spines** 13–18, lower 7–8 of them 10 mm long, needle-like, stiff, radiating horizontally, upper ones bundled into two layers, variably thick and long, the ones behind shorter and thinner, those in front thicker and longer (up to 19 mm). All radials dirty grey-white with dark tips. **Central spines** 1–3, the strongest one straight, porrect, up to 25 mm long, stiff, dark brown, then grey, the other 1–2 smaller, 16 mm long, disposed a little sideways and upward. **Flowers** 3–4 cm diameter, light-yellow to orange-yellow; outer perianth segments yellow with reddish-brown midstripe; inner perianth segments lanceolate, acute, margins entire, 3 mm wide, pure yolk-yellow, filaments and style yellow, stigma lobes 5, yellow. **Fruit** green juicy berry, 1 cm diameter. **Seeds** 1.5 mm long, 1 mm wide, reniform, testa reticulate, bright reddish-brown.

Distribution (checked): Mexico: San Luis Potosí near Entronque Huizache.

Habitat: On lower hillsides and on the top of limestone gravel in hechtias and bushes.

Incidence: Least concern.

History of the species: The plant was described in 1948 by Backeberg as a *Neolloydia* and named after Dr. R.H. Pulleine of Adelaide, Australia, a “friend of all succulent-fanciers”. Inclusion in the genus *Coryphantha* followed in 1968 by Charles Glass (Cact. Suc. Mex. 13:34, 1968). This was because the species differs from the definition of the genus *Neolloydia* as given by Britton & Rose in The Cactaceae in several respects. With its central flowers, the grooved tubercles, the juicy green fruits and its seeds being typical of *Coryphantha*, it clearly belongs to the genus *Coryphantha*. A unique feature is the extremely long taproot (several decimetres) with potential for regeneration of new plant bodies.

Illustrations: Distribution see Plate 13, map 2; plant portrait see Plate 69.

41. *Coryphantha werdermannii* Bödeker

Monatsschr. DKG 1: 155, 1929.

Lectotype: Illustration in first description (Dicht & A. Lüthy, CSI 11: 20, 2001).

Body solitary, egg-shaped to columnar, up to more than 20 cm height, 7 cm diameter, dull light grey-green, apex slightly depressed, white-woolly, over-towered by dense bundles of spines, superficially spreading fibrous roots. **Tubercles** in youth in 13 and 21 series, densely set, conical, slightly enlarged at the base, width at the base 6 mm, height 3 mm, length of upper surface 3 mm, of lower surface 5 mm. Abrupt transition to the adult stage with 8 and 13 series, more loosely set, conical, cut, 11 mm width, 7 mm height, length of upper surface 6 mm, of lower surface 12 mm, in new growth longer and narrower, grooved on upper surface. **Axils** white-woolly in youth. **Areoles** longish in youth, 1.5 mm long, 1 mm wide, when adult round, 3 mm diameter, white-woolly in youth. **Radial spines** in youth 16–18, most of them side-

ways, horizontal, interwoven, fine needle-like, straight, 6 mm long, white. In adult stage 22–30, irregularly radiating and protruding, upper ones more densely set, interwoven, needle-like, straight, upper ones 20 mm, lower and lateral ones shorter, all white, but upper ones with dark tips. **Central spines** 4, only in adult stage, irregularly porrect, slightly curved, the lowest stronger and longer, 18–10 mm long, the others 16–18 mm long, the uppermost somewhat finer, all dark brown with lighter base, later becoming grey from below. **Flower** flat funnellform, 7 cm diameter. Outer perianth segments narrow lanceolate, margins entire, yellow with fine, reddish dorsal midstripe. Inner perianth segments narrow lanceolate, dentate towards the tips, acute, shiny yellow. Filaments yellow, anthers yellow, stigma and stigma lobes whitish-yellow. **Fruit** green juicy berry, 25 mm long, 15 mm diameter. **Seeds** reniform, brown, 1.3 mm long, 0.8 mm wide, testa reticulate.

Distribution: Mexico: Coahuila, in the valley of Cuatrociénegas.

Habitat: Gravel slopes and plains

Locations checked: Mexico: Coahuila: Cuatrociénegas-San Pedro de Las Colonias (diverse locations).

Incidence: Least concern.

History of the species: Discovered by Friedrich Ritter in 1928 who sent several plants to Friedrich Bödeker. Dedicated to the head of the German Cactus Society of that time, Dr. E. Werdermann.

Illustrations: Distribution see Plate 13, map 2; plant portrait see Plate 70.

42. *Coryphantha echinus* (Engelmann)

Britton & Rose

Cactaceae 4: 42, 1923.

Basionym: *Mammillaria echinus* Engelmann, Proc. Amer. Acad. 3: 267, 1856.

Lectotype: USA, W Texas, 1849, Wright s.n. (MO 115174) (Benson, Cact. Succ. J. (US) 41: 189, 1969).

Synonyms: *Mammillaria pectinata* Engelmann, Proc. Amer. Acad. 3: 266, 1856; *Cactus echinus* (Engelmann) Kuntze, Rev. Gen. Pl. 1: 260, 1891; *Cactus pectinatus* (Engelmann) Kuntze, Rev. Gen. Pl. 1: 260, 1891; *Mammillaria radians echinus* Schumann, Gesamtb. Kakt. 496, 1898; *Coryphantha pectinata* (Engelmann) Britton & Rose, Cact. 4: 34, 1923; *Coryphantha radians echinus* Ito 1952; *Coryphantha cornifera* (DC) Britton & Rose var. *echinus* Benson, Cact. Succ. J. (US) 4: 189, 1969; *Mammillaria scolymoides* Scheidweiler sensu Del Weniger, Cacti of Texas and neighboring states: 165, 1984.

Body solitary, later also sprouting, globose to egg-shaped, later short-cylindrical, 5–6 cm diameter, up to 7 cm height, dull grey-green, apex flattened, with sparse wool, fibrous roots. **Tubercles** in 8 and 13 series, conical, rounded, width at the base 10–11 mm, height 8 mm, length of upper surface 8 mm, of lower surface 10 mm. **Axils** naked. **Areoles** round, 1.5 mm diameter, in youth white-woolly. **Radial spines** 17–28, lower and lateral ones radiating, horizontal, interwoven, 10–12 mm long, upper ones more densely set and bundled, longer, up to 25 mm, all needle-like, straight, in youth yellowish, later greyish-white. **Central spines** 4, the dominant porrect, straight or curved downwards, thick needle-like, 16 mm long, initially yellow-brown with dark tip, later becoming grey from the base. The 3 other central spines spreading upwards, appressed, sometimes somewhat curved, thinner, colour and length as upper radial spines. **Flower** 5–6 cm diameter, outer perianth segments lanceolate, brownish-green with yellow margin, inner perianth segments lanceolate, acute, dentate towards the tips, yellow. Filaments reddish, anthers yolk-yellow, stigma whitish-yellow, 6 white stigma lobes. **Fruit** green juicy berry with attached flower remnants, 2.5 × 1 cm. **Seeds** reniform, brown, 1.7 mm long, 1 mm wide, testa reticulate.

Youth form: As a young plant this species has pectinate radial spines only. It was therefore

described as an independent species with the name *Mammillaria pectinata*. In later years the central spines appear on young areoles step by step. Flowers may appear even on young plants with solely pectinate spination.

Distribution: USA: region of Big Bend, Texas. Mexico: adjacent regions of Coahuila and Chihuahua.

Habitat: Alluvial plains with limestone gravel.

Locations checked: USA: Texas: Pecos County, Howard County, Terlingua, Val Verde County, Presidio County. Mexico: Coahuila: Cuatrociénegas, San Miguel, Sierra El Granizo, La Morita. Chihuahua: El Cariño, El Paradero, Rancho Blanco, Paso de San Antonio, El Diamante, Villa Ahumada.

Incidence: Least concern.

Illustrations: Distribution see Plate 13, map 2; plant portrait see Plate 71.

II.B Section *Gracilicoryphantha* Dicht & A. Lüthy

Cact. Syst. Init. 11: 21, 2001.

Type: *Coryphantha gracilis* Bremer & Lau.

Synonym: Subgenus *Escobrittonia* Doweld, Sukkulenty, vol. 3 (1): 17, 2000 (*pro parte*).

Definition: Seeds globose with a broad basal hilum. Fruits at first juicy and green, but soon turning red and drying out.

43. *Coryphantha gracilis* Bremer & Lau

Cact. Succ. J. (US) 49: 71, 1977.

Type: Mexico, Chihuahua, Pelayo, hills E of Rancho El Toro, 1800 m, 10.8.1972, Lau 645 (MEXU)..

Body solitary, rarely sprouting from the base and group-forming, globose to short-cylindrical, 3.5–4 cm diameter, up to 8 cm height, apex flattened, with white wool, epidermis light greyish-green, in later years losing the basal spines and becoming corky, very long taproot, up to 12 cm long. **Tubercles** in 8 and 13 series, conical, round at the base, later rhomboid, directed slightly upwards, at the base 7 mm width, 6 mm height, length of upper surface 7 mm, of lower surface 10 mm,

with thin groove on upper surface. **Axils** in youth with white wool, later naked. **Areoles** oval, 1 mm wide and 1.5 mm long, in youth with short white wool, later naked. **Radial spines** 12–18, radiating, horizontal, interwoven, straight to slightly curved, fine needle-like, stiff, 5–8 mm long, the longer ones in the upper part of the areole in two layers, the other radials shorter towards the lower part of the areole, light horn-coloured to dirty white, at the base yellow-brown, the lowest somewhat flattened and yellowish-tinged. **Central spine** 0 (–1), on older plants only, in the upper part of the areole perpendicularly upwards in front of the radial spines, length and colour as upper radial spines. **Flower** broad funnelform, 4–5 cm wide, outer perianth segments shiny pale-yellow to cream-coloured, with brown-green midstripe, lanceolate, acute, margins dentate, 2.5 cm long, 6–7 mm wide, inner perianth segments shiny pale-yellow to cream-colored, greenish in the throat, lanceolate, tips acute, margins dentate. Filaments white, anthers yolk-yellow, stigma pale green-white, with 6 cream-coloured stigma lobes of 4 mm length. **Fruit** relatively small, dull green juicy berry with a reddish tinge at the tip, with attached flower remnants, 12 mm long, less than 9 mm diameter. After 1 month swelling up and turning red from above, finally completely dull purple-red. After one more month completely dried out. **Seeds** roundish to ovoid-truncate, with a very thick border, chocolate-brown, 1.3 mm long and 1.3 mm wide, testa reticulate. 40–50 seeds per fruit.

Distribution: Mexico: Chihuahua, near Pelayo [**Type locality** (checked)], on hills east of Rancho El Toro, on southeastern slopes, 1800 m above sea level. Also north of Rosario CHI.

Habitat: Calcareous gravel on flat ridges on hills with little grass.

Incidence: Least concern.

Illustrations: Plant portrait see Plate 72.

8 *Coryphantha* sp. in Cultivation

Most *Coryphantha* spp. are rather easy to cultivate. Thanks to their undemanding nature, they willingly display their numerous large flowers from summer to late autumn.

Nevertheless, a lot of patience is required to cultivate *Coryphantha* spp.: they grow very slowly and the time from germination to the first flower may take more than 10 years. To obtain plants with fully developed spination, another couple of years may pass. On the other hand, the happiness and pride in succeeding to cultivate such a jewel is reward enough. Observing such a plant over this growing period is very interesting, especially in this genus, because many species constantly change their appearance during this process and the grower can always detect something new.

Species, whose natural habitat are the more southern regions of Mexico, are the easiest to grow in cultivation, whereas those from the more northerly Mexican states and the USA are usually more difficult. The latter category includes *C. robustispina*, *C. poselgeriana* or *C. werdermannii*.

When cultivated, almost all *Coryphantha* spp. flower regularly as soon as they have reached a certain size and maturity, which is indicated by the appearance of tubercle grooves. Exceptions are *C. erecta* and *C. glassii*, which are slow flowerers in cultivation. Much patience is needed for *C. recurvata*, but once it starts to flower, it displays several flowers at once.

8.1 Optimum Cultivation Conditions

In general, the optimum cultivation conditions for *Coryphantha* spp. do not differ from those of other North American genera. The easiest way to cultivate *Coryphantha* spp. is to grow them in a greenhouse. However, some species, especially those of southern and central Mexico, can be grown on a windowsill as well as in the garden, if protected from rain and frost. They are quite undemanding as regards the climate of their surroundings. In summer, they like enough light and warmth and can be watered frequently. In winter, they need a rest for several months and should not be watered. They do not need to stand directly under glass, but in a place with a lot of light and direct sun exposure. They are very rarely burnt by the sun, on the contrary, they protect themselves with a lot of wool and longer and denser spination, which makes them more attractive to the grower. However, sufficient ventilation or circulation of air is necessary.

In winter, if the plants are hardy and the pots are completely dry, they can withstand freezing temperatures. However, temperatures from 4 to 12 °C are ideal.

8.2 Soils and Pots

Mixtures of mineral components are well received. A precise mixture of ingredients of the soil for *Coryphantha* spp. is not very important as long as some general characteristics of the soil are considered. The more

northern the origin of the species, the less organic components the soil should contain. It should be friable and not lumpy and not too finely grained. Soil should never stay wet over a long period of time, however, the roots should always be kept a little moist. The optimum soil mixture is around pH 7.

Deep plastic containers are suitable. Clay pots are not suitable as the fine roots growing along the walls of the pot are exposed to the cold of evaporating moisture. Many *Coryphantha* spp. have thick roots, taproots or bulbous roots. Therefore, they should be planted in pots of sufficient depth. It is preferable to plant them in a pot which is a little too big than too small. Planting more than one plant per pot should be avoided because *Coryphantha* spp. are strong competitors and when they are potted together only one of the plants will grow, the others will die sooner or later. To obtain good drainage some bigger stones should be put into the pot first. In addition, the soil should be covered with some bigger stones as well to allow the base of the plants to dry more easily (important mainly for species with a thin root "neck" like *C. wohlschlagerei*, *C. glanduligera*, *C. pulleineana* etc.).

Replanting is possible during the entire period of vegetation. However, the best time is early spring before the start of vegetation. Since the plants grow slowly, it is enough to replant them every few years.

8.3 Watering and Fertilization

From spring to autumn *Coryphantha* spp. need to be watered regularly and the soil should never dry out completely. In summer, weekly watering may be necessary, in spring and autumn a bit less, depending on the weather. Some species from northern Mexico and all species with taproots, e.g. *C. gracilis*, are very sensitive to over-watering and their roots can rot very easily. After watering, the plant body should dry as fast as possible.

Therefore, the optimum time to water them is early in the morning. During the hottest time of summer, they may also be watered in the evening. Watering from above reduces excessive production of wool on the plant. The water should not contain too much lime. Occasional watering with limy water does not harm the plants, but watering with rainwater proved to be better. Rainwater has to be controlled, however, because it should not be contaminated by environmental dirt, i.e. copper from the roof and so on.

As soon as the *Coryphantha* spp. start to grow in spring, they need fertilizer. Until the end of June they need about four to six applications; later on, fertilization should be stopped completely to allow the new sprouts to mature before wintertime.

Normal liquid fertilizers, which are available for all kinds of flowers, will do well for *Coryphantha* spp. The indicated concentration for cacti must be observed and the plants should not receive too much nitrate.

8.4 Pests and Illnesses

Coryphantha spp. are quite resistant to pests and are rarely the first cacti to be attacked in a greenhouse.

One should be aware of mealybugs, since they can hide very well in the woolly apex and axils of the plants. Mealybugs on the roots and larvae of *Sciara* flies can be a threat, especially for young seedlings. Therefore, it is important to control seedlings regularly.

Some of the species are favoured by the red spider mite, which leave ugly traces of their damage on new sprouts of the plants. As the plants grow slowly, the damage is visible for a long time.

A treacherous enemy are the nematodes. Excessive watering transfers them from pot to pot and they propagate in the fleshy and tuberous roots where they prosper. They damage the roots with poisonous products of

their metabolism and block the vessels, leading to the death of the whole plant. In spring, if a plant does not fill out and start to grow similarly to all the others, this may be a very suspicious sign for nematodes. In this case, repotting the plant is indicated. Infected roots should be cut off completely, the plant disinfected, left to dry (2–3 weeks) and repotted in fresh soil.

Coryphantha spp. are quite resistant to fungus diseases as long as the air around them is kept circulating. On the other hand, all species with nectary glands normally have black fungus, the so-called sooty mould, mainly around the glands. This fungus does not harm the plants and is only an aesthetic problem. If wasps and ants are allowed to collect the nectar from the glands or if the plants are watered regularly from above, the problem will be diminished.

8.5 Sowing and Propagation

The easiest method of propagation can be performed with sprouting *Coryphantha* spp. The sprouts may be picked from the mother plant and planted into separate pots.

Another, somewhat more complicated, method is derived from the fact that all *Coryphantha* spp. have dormant vegetative centres in their grooves. If a tubercle of a *Coryphantha* is grafted onto any usual grafting stock, after maybe 1–3 years, it will sprout from the groove and a new plant will appear. This method also serves to rescue sick or dying plants.

The growth of seedlings can be accelerated by early grafting onto fast-growing stocks like *Pereskia*. In fact, such plants flower much earlier, but later on they show a somewhat different, usually lesser spined appearance.

In general, the grafting of *Coryphantha* spp. can be performed without major problems. However, in view of their easy cultivation, grafting is usually unnecessary.

The most common method of propagation is by seeds. Seeds are available from retailers, but it is only worth sowing seeds of documented origin, e.g. seeds with a collector's number. It is difficult to get well-documented and correctly diagnosed seeds and plants from nurseries. In our experience, most nursery supplies or seed lists have incorrect labels, or are invented names, or turn out to be undefinable cultivation hybrids. Another possibility is to sow self-produced seeds, if someone has two plants of the same origin and avoids hybridization when pollinating the plants. Sowing hybridized seeds under the name of the mother plants should be avoided. Too many such hybrids exist already and have contributed a lot to the confusion within the genus *Coryphantha* in the past.

With a few exceptions *Coryphantha* seeds germinate within 10 days. The best time to sow is spring because the seedlings can grow without a break during the whole summer. To protect them from fungus and bacterial diseases, it is wise to disinfect the seeds and the soil with a disinfectant like Chinosol. One of the best soils for sowing is fine-grained pumice. Initially, constant humidity of the soil and the air should be guaranteed and this is easily obtained in a closed container. The temperature should vary between about 20 and 32 °C. In their first or second year, the seedlings should be planted into a deep bowl to develop their root system easily. Later, after 3 or 4 years of growth, it is important to cultivate each seedling in its own pot to avoid competition between the plants, which may hinder growth.

Most *Coryphantha* seedlings are about 3–5 mm in diameter after 1 year. Some species need a high light intensity, otherwise they grow upwards very fast, forming very long, thin, weak columns which may die early. This tendency towards long growth can be seen e.g., in *C. clavata*, *C. wohlschlagerei* und *C. glanduligera*.

The time period from sowing to flower production is different from one species to another. In our experience, the fastest flowerers are *C. clavata* and *C. pulleineana* (3–4 years). However, many species need about 5–7 years (e.g. *C. echinoidea*, *C. vaupeliana*, *C. delae-tiana*, *C. nickelsiae*, *C. sulcata*, *C. neglecta*),

others 8–10 years (e.g. *C. ottonis*, *delicata*, *pseudoechinus*, *hintoniorum*) and some even longer (e.g. *C. difficilis*, *salinensis*, *poselgeri-ana*, *robustispina*, *recurvata*).

Despite this long time period, propagation of *Coryphantha* species remains a thrilling task.

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Appendix

Comparison Tables

Table 1. *Coryphantha echinoidea*/*Coryphantha glanduligera*

	<i>Coryphantha echinoidea</i> (Quehl) BR. & R.	<i>Coryphantha glanduligera</i> (Otto) Lemaire
Body	Globose, 6 cm Ø, 5.5 cm high	Reversed egg-shaped to short clavate, up to 6 cm Ø and 12 cm high
Roots	Fibrous	Tuberous
Tubercles	Conical-cone-shaped	Concave-conical
Radial spines	20–24, white, dark tips	18–20, yellowish, then greyish-white
Central spines	1–3, mostly 2, up to 15 mm long, horn-coloured to brown	3–4, 15–20 mm long, yellowish-horn-coloured with brown tips
Seedlings	Globose	Clavate/short columnar

Table 2. *C. clavata*/*C. octacantha*/*C. georgii*

	<i>Coryphantha clavata</i>	<i>Coryphantha octacantha</i>	<i>Coryphantha georgii</i>
Growth form	Cylindrical – columnar	Columnar	Globose or clavate
Tubercles	In 5 and 8 or 8 and 13 series; small (1/2), round	In 5 and 8 or 8 and 13 series; large, keeled	In 5 and 8, 8 and 13 or 13 and 21 series; large round, somewhat bulgy, not keeled
Radial spines	Epidermis grass-green Regularly radiating All ± same length	Epidermis grass-green All irregularly disposed Upper ones longer Upper ones not bundled	Epidermis dark-green Lower ones regularly and horizontally disposed All ± same length Upper ones very close/bundled
Central spines	Usually 1	1–3 brown/white	1–3, especially in young plants two-coloured
Flowers	Small (2.5–3 cm Ø)	Large (7 cm Ø)	Medium size (3.5–4 cm Ø)

Table 3. *Coryphantha jalpanensis*/*Coryphantha glassii*

	<i>Coryphantha jalpanensis</i> Buchenau	<i>Coryphantha glassii</i> Dicht & A. Lüthy
Body	Sprouting at the base, forming groups of up to 25 cm Ø, single heads cylindrical or short-clavate, up to 15 cm height and 5–6 cm Ø, dull green, apex depressed, slightly woolly, fibrous roots	Forming large groups of up to 50 cm Ø by stolons, columnar heads up to 30 cm height, 6 cm Ø, lime-green, apex flat, very sparse wool, taproot with narrow neck
Tubercles	In 5 and 8 series, cylindrical-conical, flattened above, bulging below, ascending, width at the base 10–12 mm, height 9–10 mm, upper surface 7 mm long, lower surface 13 mm, upper part ascending outwards, tubercle grooves on old main sprouts only, with grey-white felt and 1–2 orange glands	In 5 and 8 series, cylindrical-conical, keeled below, ascending, width at the base 6 mm, 14 mm height, upper surface 9 mm, lower surface 20 mm long, upper part, except in new growth, descending outwards horizontally at maximum, tubercle grooves on old main sprouts only, with felt and glands near the areoles
Axils	With white wool and 1 hidden, orange, sometimes red gland	Wool in new growth only, with one clearly visible yellow-orange gland
Radial spines	10–12, 6–10 mm long, white with dark tips	10–13, 10–11 lower ones 8 mm long, lateral ones 7 mm, yellowish-white, often white-dotted, upper 1–2 longer, 12 mm long, nearly white
Central spines	1–3 (-4), one of them dominating, 10–17 mm long, protruding slightly downwards, two additional lateral spines upwards, 6–10 mm long, brown, later grey, dark tipped	2–3, one of them dominating, straight, porrect, directed downwards, thick needle-like, 16–25 mm long, yellow-brown-horn-coloured, white dotted, the others obliquely upwards, 11 mm long, yellow-brownish-horn-coloured
Flowers	4–4.5 cm long and 3–4.5 cm wide	3.5 cm long, 3 cm wide
Fruit	15–20 mm long and 10–12 mm diameter	10 mm long, 8 mm diameter

Table 4. *Coryphantha durangensis* ssp. *durangensis*/ssp. *cuencamensis*

	<i>Coryphantha durangensis</i> subsp. <i>durangensis</i>	<i>Coryphantha durangensis</i> subsp. <i>cuencamensis</i>
Body	Egg-shaped to columnar, up to 7 cm wide and over 15 cm high, apex egg-shaped-rounded	Egg-shaped globose to cylindrical, up to 10 cm wide and 16 cm high, apex flat
Tubercles	In 5 and 8, rarely 8 and 13 series, very flat, slightly keeled, length of upper surface 4–6 mm, of lower surface 12–14 mm	In 13 and 21, rarely 8 and 13 series, conical towards the top, length of upper surface 10 mm, of lower surface 13–15 mm
Radial spines	9–16, lower and lateral ones 7–10 mm long, upper ones double	14–17, 15–17 mm long, upper ones up to 18 mm
Central spines	(0-)1, pointed upwards, slightly protruding or rarely a single central spine nearly at a right angle to the radials	Always 1, porrect, at a right angle to the radials (never pointed upwards)

Table 5. *Coryphantha ramillosa* ssp. *ramillosa*/ssp. *santarosa*

	<i>Coryphantha ramillosa</i> subsp. <i>ramillosa</i> Cutak	<i>Coryphantha ramillosa</i> subsp. <i>santarosa</i> Dicht & A. Lüthy
Body	6 cm Ø, 5 cm high, grass-green	7 cm Ø, 3–4 cm high, grass-green
Tubercles	Up to 15–5 mm wide, 20 mm long	At the base up to 20 mm wide, 10 mm long
Radial spines	14–20, 10–35 mm long	11–13, 9–12 mm long, upper ones often bundled
Central spines	4, the lower longest one up to 40 mm long, all thick needle-like	–4, the lower longest one, up to 28 mm long, needle-like
Flowers	65 mm long, 50 mm wide, colour varying from pale pink to deep rose to purple. Outer perianth segments lighter, broader, with light green midstripe. Inner perianth segments white, upper one-half to one-third pink to purple, filaments short, white, anthers golden to orange	65 mm long, 50 mm Ø, yellow. Outer perianth segments yellow with greenish red-brown mid-stripe, at the base 3 mm, towards the tip 4 mm wide. Inner perianth segments yellow, filaments light yellow, anthers dark yellow
Distribution	Calcareous soils in the neighbourhood of the Rio Grande from Brewster County, Texas, to Big Bend, USA, and in the neighbouring Mexican states of Chihuahua and Coahuila	In the north of the Mexican State Coahuila. Type locality: La Babia

Synonyms and Valid Names

Bold: valid names of species recognized by the authors and described in detail in this book.
nom. rejic. (nomen rejiciendum) = rejected names

Synonym

Actual plant name

<i>Aulacothele acanthostephes</i> (Lehmann)	<i>C. pycnacantha</i>
<i>Aulacothele biglandulosa</i> (Pfeiffer) Monville	<i>C. octacantha</i>
<i>Aulacothele clava</i> (Pfeiffer) Monville	<i>C. octacantha</i>
<i>Aulacothele cornifera</i> (De Candolle) Monville	<i>C. cornifera</i>
<i>Aulacothele elephantidens</i> (Lemaire) Monville	<i>C. elephantidens</i> ssp. <i>elephantidens</i>
<i>Aulacothele erecta</i> (Lemaire) Monville	<i>C. erecta</i>
<i>Aulacothele exsudans</i> (Zuccarini) Monville	<i>C. octacantha</i>
<i>Aulacothele lehmannii</i> (Otto) Monville	<i>C. octacantha</i>
<i>Aulacothele ottonis</i> (Pfeiffer) Monville	<i>C. ottonis</i>
<i>Aulacothele plaschnickii</i> (Otto) Monville	<i>C. octacantha</i>
<i>Aulacothele pycnacantha</i> (Martius) Monville	<i>C. pycnacantha</i>
<i>Aulacothele radians</i> (De Candolle) Monville	<i>C. cornifera</i>
<i>Aulacothele raphidacantha</i> (Lemaire) Monville 1846	<i>C. clavata</i>
<i>Aulacothele raphidacantha ancistracantha</i> (Lemaire) Monville	<i>C. clavata</i> ssp. <i>stipitata</i>
<i>Aulacothele schlechtendahlII</i> (Ehrenberg) Monville	<i>C. octacantha</i>
<i>Aulacothele sulcimamma</i> (Pfeiffer) Monville	<i>C. octacantha</i>
<i>Aulacothele sulcolanata</i> (Lemaire) Monville	<i>C. elephantidens</i> ssp. <i>elephantidens</i>
<i>Cactus acanthostephes</i> (Lehmann) Kuntze 1891	<i>C. pycnacantha</i>
<i>Cactus ancistracanthus</i> (Lemaire) Kuntze 1891	<i>C. clavata</i> ssp. <i>stipitata</i>
<i>Cactus aulacothele</i> (Lemaire) Kuntze 1891	<i>C. octacantha</i>
<i>Cactus biglandulosus</i> (Pfeiffer) Kuntze 1891	<i>C. octacantha</i>
<i>Cactus brevimmammus</i> (Zuccharini) Kuntze 1891	<i>C. octacantha</i>
<i>Cactus brownii</i> Toumey 1896	<i>C. robustispina</i>
<i>Cactus brunneus</i> Coulter 1894	<i>C. clavata</i> ssp. <i>clavata</i>
<i>Cactus calcaratus</i> (Engelmann) Kuntze 1891	<i>C. sulcata</i>
<i>Cactus cephalophorus</i> (Salm-Dyck) Kuntze 1891	<i>C. retusa</i>
<i>Cactus ceratocentrus</i> (Berg) Kuntze 1891	<i>C. erecta</i>
<i>Cactus clavus</i> (Pfeiffer) Kuntze 1891	<i>C. octacantha</i>
<i>Cactus compactus</i> (Engelmann) Kuntze 1891	<i>C. compacta</i>
<i>Cactus corniferus</i> (De Candolle) Kuntze 1891	<i>C. cornifera</i>
<i>Cactus echinus</i> (Engelmann) Kuntze 1891	<i>C. echinus</i>
<i>Cactus elephantidens</i> (Lemaire) Kuntze 1891	<i>C. elephantidens</i> ssp. <i>elephantidens</i>
<i>Cactus engelmannii</i> (Lemaire) Kuntze 1891	<i>C. recurvata</i> ssp. <i>recurvata</i>
<i>Cactus erectus</i> (Lemaire) Kuntze 1891	<i>C. erecta</i>
<i>Cactus exsudans</i> (Zuccharini) Kuntze 1891	<i>C. octacantha</i>
<i>Cactus glanduliger</i> (Otto) Kuntze 1891	<i>C. glanduligera</i>

- Cactus heteromorphus* (Scheer) Kuntze 1891
Cactus lehmannii (Otto) Kuntze 1891
Cactus loricatus (Lemaire) Kuntze
Cactus macromeris (Engelmann) Kuntze 1891

Cactus macrothele (Martius) Kuntze 1891
Cactus maculatus Coulter 1894
Cactus martianus (Pfeiffer) Kuntze 1891
Cactus octacanthus (De Candolle) Kuntze 1891
Cactus ottonis (Pfeiffer) Kuntze 1891
Cactus pectinatus (Engelmann) Kuntze 1891
Cactus pfeifferianus (De Vriese) Kuntze 1891
Cactus plaschnickii (Otto) Kuntze 1891
Cactus pycnacanthus (Martius) Kuntze 1891
Cactus radians Kuntze (De Candolle) 1891
Cactus radians pectinoides Coulter 1894
Cactus raphidacanthus (Lemaire) Kuntze 1891
Cactus recurvatus (Engelmann) Kuntze 1891
Cactus recurvispinus (De Vriese) Kuntze 1891

Cactus retusus (Pfeiffer) Kuntze 1891
Cactus robustispinus (Schott) Kuntze 1891

Cactus salmdyckianus (Scheer) Kuntze 1891
Cactus scepontocentrus (Lemaire) Kuntze 1891
Cactus scheeri (Muehlenpfordt) Kuntze 1891
Cactus schlechtendalii (Ehrenberg) Kuntze 1891
Cactus scolymoides (Scheidweiler) Kuntze 1891
Cactus scolymoides sulcatus Coulter 1894
Cactus sulcatus Small 1903
Cactus sulcolanatus (Lemaire) Kuntze 1891

Cactus winkleri (Poselger) Kuntze 1891
Coryphantha ancistracantha Lemaire 1864
Coryphantha andreae Purp. et Boed. 1928
Coryphantha asterias (Cels) Boedeker ex Berger 1929
Coryphantha asterias Cels ex Salm-Dyck 1850 sensu Br. & R.
Coryphantha aulacothele Lemaire 1868
Coryphantha bergeriana Boedeker 1929
Coryphantha bernalensis Bremer 1984
Coryphantha borwigii Purpus 1927 nom. nud.
Coryphantha borwigii sensu Bremer 1980
Coryphantha brevimamma Lemaire ex Foerster 1885
Coryphantha bumamma (Ehrenberg 1849) Br. & R. 1923

C. macromeris ssp.
macromeris
C. octacantha
Nom. rejic. (see *C. pallida*)
C. macromeris ssp.
macromeris
C. octacantha
C. clavata ssp. *clavata*
C. octacantha
C. octacantha
C. ottonis
C. echinus
C. cornifera
C. octacantha
C. pycnacantha
C. cornifera
C. cornifera
C. clavata ssp. *clavata*
C. recurvata
C. elephantidens ssp.
elephantidens
C. retusa
C. robustispina ssp.
robustispina
C. poselgeriana
C. pycnacantha
C. robustispina ssp. *scheeri*
C. octacantha
nom. rejec. (see *C. salinensis*)
C. sulcata
C. sulcata
C. elephantidens ssp.
elephantidens
C. pycnacantha
C. clavata ssp. *stipitata*
C. pycnacantha
C. ottonis
C. octacantha
C. octacantha
C. glanduligera
C. cornifera
C. salinensis
C. delaetiana
C. octacantha
C. elephantidens ssp.
bumamma

<i>Coryphantha bussleri</i> (Mundt) Scheinvar 1981	<i>C. ottonis</i>
<i>Coryphantha calcarata</i> Lemaire 1868	<i>C. sulcata</i>
<i>Coryphantha calipensis</i> Bravo 1964	<i>C. pallida</i> ssp. <i>calipensis</i>
<i>Coryphantha calcarata</i> (Engelmann) Lemaire 1868	<i>C. sulcata</i>
<i>Coryphantha calochlora</i> Boedeker 1933	<i>C. nickelsiae</i>
<i>Coryphantha clava</i> (Pfeiffer) Lemaire 1868	<i>C. octacantha</i>
<i>Coryphantha clava</i> var. <i>schlechtendalii</i> (Ehrenberg) Heinr. ex Backeberg 1961	<i>C. octacantha</i>
<i>Coryphantha clavata</i> (Scheidweiler) Backeberg 1942 ssp. <i>clavata</i>	
<i>Coryphantha clavata</i> ssp. <i>stipitata</i> (Scheidweiler) Dicht & A. Lüthy 2001	
<i>Coryphantha clavata ancistracantha</i> Marshall 1947	<i>C. clavata</i> ssp. <i>stipitata</i>
<i>Coryphantha clavata</i> var. <i>ancistracantha</i> (Lemaire)	<i>C. clavata</i> ssp. <i>stipitata</i>
<i>Coryphantha compacta</i> (Engelmann) Br. & R. 1923	
<i>Coryphantha conimamma</i> (Linke) Berger 1929	<i>C. pycnacantha</i>
<i>Coryphantha connivens</i> Br. & R. 1923	<i>C. pycnacantha</i>
<i>Coryphantha cornifera</i> var. <i>echinus</i> (Engelmann) Benson 1969	<i>C. echinus</i>
<i>Coryphantha cornifera</i> var. <i>scolymoides</i> (Scheidw.) Borg 1951	nom. rejic. (<i>C. salinensis</i> ?)
<i>Coryphantha cornuta</i> (Hildmann) Berger 1929	<i>C. cornifera</i>
<i>Coryphantha cornifera</i> (De Candolle 1828) Lemaire 1868	
<i>Coryphantha cuencamensis</i> Bremer 1980	<i>C. durangensis</i> ssp. <i>cuencamensis</i>
<i>Coryphantha daemenoceras</i> Jaumavei Fric 1926	<i>C. vaupeliana</i>
<i>Coryphantha daimonoceras</i> Lemaire 1868	nom. rejic. (see <i>C. salinensis</i>)
<i>Coryphantha delaetiana</i> (Quehl) Berger 1929	
<i>Coryphantha delicata</i> Bremer 1979	
<i>Coryphantha densispina</i> Werdermann 1932	<i>C. difficilis</i>
<i>Coryphantha difficilis</i> (Quehl) Berger 1929	
<i>Coryphantha durangensis</i> (Runge ex Schumann) Br. & R. 1923 ssp. <i>durangensis</i>	
<i>Coryphantha durangensis</i> ssp. <i>cuencamensis</i> (Bremer) Dicht & A. Lüthy 2001	
<i>Coryphantha echinoidea</i> (Quehl) Br. & R. 1923	
<i>Coryphantha echinus</i> (Engelmann) Br. & R. 1923	
<i>Coryphantha elephantidens</i> (Lemaire) Lemaire 1868 ssp. <i>elephantidens</i>	
<i>Coryphantha elephantidens</i> ssp. <i>bumamma</i> (Ehrenberg) Dicht & A. Lüthy 2001	
<i>Coryphantha elephantidens</i> ssp. <i>greenwoodii</i> (Bravo) Dicht & A. Lüthy 2001	
<i>Coryphantha elephantidens</i> var. <i>barciae</i> Bremer 1977	<i>C. elephantidens</i>
<i>Coryphantha erecta</i> (Lemaire) Lemaire 1868	
<i>Coryphantha exsudans</i> (Zuccharini) Lemaire ex Foerster 1885	<i>C. octacantha</i>

- Coryphantha garessii* Bremer 1980
C. elephantidens ssp. *elephantidens*
- Coryphantha georgii* Boedeker 1931**
Coryphantha gladiispina (Boedeker) Berger 1929
***Coryphantha glanduligera* (Otto et Dietrich) Lemaire 1868**
Coryphantha glanduligera Lemaire 1868 sensu Br. & R.
Coryphantha glanduligera Otto et Dietr. 1848 sensu Br. & R.
***Coryphantha glassii* Dicht & A. Lüthy 2000**
***Coryphantha gracilis* Bremer et Lau 1977**
Coryphantha grandis Bremer 1978
Coryphantha grata Bremer 1981
Coryphantha greenwoodii Bravo 1970
C. longicornis
C. georgii
C. elephantidens ssp. *greenwoodii*
C. ottonis
- Coryphantha guerkeana* (Boedeker) Br. & R. 1923
Coryphantha hintoniorum* ssp. *hintoniorum
Dicht & A. Lüthy 1999
***Coryphantha hintoniorum* ssp. *geoffreyi* Dicht & A. Lüthy 2003**
Coryphantha indensis Bremer 1972
***Coryphantha jalpanensis* Buchenau 1965**
Coryphantha Jaumavei Fric 1926
Coryphantha kieferiana Berger ex Backeberg 1961
Coryphantha laui Bremer 1979
Coryphantha lehmannii Lemaire 1868
***Coryphantha longicornis* Boedeker 1931**
Coryphantha loricata Lemaire 1868
***Coryphantha macromeris* (Engelmann) Lemaire 1868**
ssp. *macromeris*
***Coryphantha macromeris* ssp. *runyonii* ((Britton & Rose)**
Taylor 1998
Coryphantha macromeris var. *runyonii* (Br. & R.) Benson 1969
Coryphantha macrothele (Martius ex Pfeiffer) Kümmler 1998
***Coryphantha maiz-tablasensis* Backeberg 1949**
Coryphantha maliterrarum Bremer 1984
Coryphantha melleospina Bravo 1954
Coryphantha muehlenpfordtii (Poselger) Britton & Rose 1923
Coryphantha muehlenpfordtii Br. & R. ssp. *uncinata* (Benson)
C. pseudonickelsiae
C. delicata
C. poselgeriana
C. psuedechinus ssp. *laui*
C. octacantha
- Coryphantha muehlenpfordtii* (Poselger) Br. & R.
 var. *robustispina* (Schott) Marshall 1953
Coryphantha muehlenpfordtii Br. & R. ssp. *robustispina*
 (Engelmann) Dicht 1996
***Coryphantha neglecta* Bremer 1979**
Coryphantha neoscheeri Backeberg 1961
***Coryphantha nickelsiae* Brandege 1900**
Coryphantha obscura Boedeker 1930
***Coryphantha octacantha* (De Candolle) Br. & R. 1923**
Nom. rejic. (see *C. pallida*)
C. macromeris ssp. *runyonii*
C. octacantha
C. cornifera
C. retusa
C. robustispina ssp. *scheeri*
C. robustispina ssp. *scheeri*
C. robustispina ssp.
robustispina
C. robustispina
C. robustispina ssp. *scheeri*
C. sulcata

- Coryphantha ottonis* (Pfeiffer) Lemaire 1868**
Coryphantha pallida* Br. & R. 1923 ssp. *pallida
***Coryphantha pallida* ssp. *calipensis* (Bravo ex Arias et al) Dicht & A. Lüthy 2000**
Coryphantha palmeri Br. & R. 1923 *C. compacta*
Coryphantha palmeri Br. & R. sensu Berger 1929 *C. delicata*
Coryphantha panarottoi Halda & Horacek 1999 *C. delicata*
Coryphantha pectinata (Engelmann) Br. & R. 1923 *C. echinus*
Coryphantha pirtlei Werdermann *C. macromeris* ssp. *runyonii*
***Coryphantha poselgeriana* (Dietrich) Br. & R. 1923**
Coryphantha poselgeriana var. *saltillensis* (Poselger) Bremer 1977 *C. poselgeriana*
Coryphantha poselgeriana var. *valida* (Purpur) Heinr. Ex Backeb. *C. poselgeriana*
***Coryphantha potosiana* (Jacobi) Glass et Foster 1970**
Coryphantha pseudoechinus* Boedeker 1929 ssp. *pseudoechinus
***Coryphantha pseudoechinus* ssp. *loui* (Bremer) Dicht & A. Lüthy 2001**
***Coryphantha pseudonickelsiae* Backeberg 1949**
Coryphantha pseudoradians Bravo 1954 *C. pallida* ssp. *pallida*
***Coryphantha pulleineana* (Backeberg) Glass 1968**
Coryphantha pusilliflora Bremer 1982 *C. pseudoechinus* ssp. *pseudoechinus*
***Coryphantha pycnacantha* (Martius) Lemaire 1868**
Coryphantha pycnacantha sensu Br. & R. 1923 *C. pallida* ssp. *pallida*
Coryphantha radians (De Candolle) Br. & R. 1923 *C. cornifera*
Coryphantha radians echinus Ito 1952 *C. echinus*
Coryphantha radians var. *pectinoides* (Coulter) Bravo 1982 *C. cornifera*
Coryphantha radians var. *pseudoradians* (Bravo) Bravo 1982 *C. pallida* ssp. *pallida*
Coryphantha radians var. *sulcata* Ito 1952 *C. sulcata*
Coryphantha ramillosa* Cutak 1942 ssp. *ramillosa
***Coryphantha ramillosa* ssp. *santarosa* Dicht & A. Lüthy 2000**
Coryphantha raphidacantha ancistracantha (Schumann) Ito 1952 *C. clavata* ssp. *stipitata*
Coryphantha raphidacantha (Lemaire) Lemaire 1864 *C. clavata* ssp. *clavata*
Coryphantha recurvata* (Engelmann) Br. & R. 1923 ssp. *recurvata
***Coryphantha recurvata* ssp. *canatlanensis* Dicht & A. Lüthy 2003**
Coryphantha recurvispina (De Vriese) Bremer 1976 *C. elephantidens* ssp. *elephantidens*
Coryphantha reduncuspina Boedeker 1933 *C. pallida* ssp. *pallida*
***Coryphantha retusa* Br. & R. 1923**
Coryphantha retusa var. *melleospina* (Bravo) Bravo 1982 *C. retusa*
Coryphantha robustispina* (Schott) Br. & R. 1923 ssp. *robustispina
***Coryphantha robustispina* ssp. *scheeri* (Lemaire) Taylor 1998**
Coryphantha robustispina ssp. *uncinata* (Benson) Taylor 1998 *C. robustispina* ssp. *scheeri*
Coryphantha roederiana Boedeker 1929 *C. sulcata*
Coryphantha runyonii Br. & R. 1923 *C. macromeris* ssp. *runyonii*
***Coryphantha salinensis* (Poselger) Dicht & A. Lüthy 1998**

- Coryphantha salm-dyckiana* (Scheer) Britton & Rose 1923
Coryphantha scheeri Lemaire 1868
Coryphantha scheeri (Kuntze) Benson 1969
Coryphantha scheeri Lemaire var. *robustispina* Benson 1982

Coryphantha scheeri var. *robustispina* (Schott) Benson 1969
Coryphantha scheeri var. *scheeri* (Kuntze) Benson 1969
Coryphantha scheeri (Kuntze) Benson var. *uncinata* Benson 1969
Coryphantha scheeri Lemaire var. *uncinata* Benson 1982
Coryphantha scheeri (Kuntze) Benson var. *valida*
(Engelmann) Benson 1969
Coryphantha schlehtendahlia (Ehrenberg) Lemaire 1868
Coryphantha schwarziana Boedeker 1933
Coryphantha scolymoides (Scheidweiler) Berger 1929
Coryphantha speciosa Boedeker 1930.
***Coryphantha sulcata* (Engelmann) Br. & R. 1923**
Coryphantha sulcata var. *nickelsae* (Brandege) Benson 1969
Coryphantha sulcolanata (Lemaire) Lemaire 1838

***Coryphantha tripugionacantha* Lau 1988**
Coryphantha unicornis Boedeker 1928
Coryphantha unicornis sensu Bremer 1978
Coryphantha valida (Purpus) Bremer 1977
***Coryphantha vaupeliana* Boedeker 1928**
Coryphantha villarensis Backeberg 1942
***Coryphantha vogtherriana* Werdermann et Boedeker 1932**
***Coryphantha werdermannii* Boedeker 1929**
***Coryphantha wohlshlageri* Holzeis 1990**
Echinocactus brevimammus Poselger 1853
Echinocactus cephalophorus (Salm-Dyck) Poselger 1853
Echinocactus clavus Poselger 1853
Echinocactus corniferus raphidacanthus Poselger 1853
Echinocactus corniferus impexicomus Poselger 1853
Echinocactus corniferus longisetus Poselger 1853
Echinocactus corniferus nigricans Poselger 1853
Echinocactus corniferus Poselger 1853
Echinocactus corniferus scolymoides Poselger 1853
Echinocactus elephantidens Poselger 1853

Echinocactus erectus Poselger 1853
Echinocactus glanduligerus (Otto) Poselger 1853
Echinocactus glanduligerus Poselger 1853 sensu Br. & R.
Echinocactus heteromorphus (Scheer ex Salm-Dyck)
Poselger 1853
Echinocactus macromeris (Martius) Poselger 1853

C. delaetiana
C. robustispina ssp. *scheeri*
C. robustispina ssp. *scheeri*
C. robustispina ssp.
robustispina
C. robustispina ssp. *scheeri*
C. robustispina ssp. *scheeri*
C. robustispina ssp. *scheeri*
C. robustispina ssp. *scheeri*
C. robustispina ssp. *scheeri*

C. octacantha
C. cornifera
Nom. rejic. (see *C. salinensis*)
C. sulcata

C. nickelsiae
C. elephantidens ssp.
elephantidens

C. clavata ssp. *clavata*
C. ottonis
C. poselgeriana

C. georgii

C. octacantha
C. retusa
C. octacantha
C. clavata ssp. *clavata*
C. cornifera
C. cornifera
C. cornifera
C. cornifera
C. cornifera
C. cornifera
C. elephantidens ssp. *elephantidens*
C. erecta
C. glanduligera
C. exsudans
C. macromeris ssp.
macromeris
C. macromeris ssp.
macromeris

<i>Echinocactus macrothele biglandulosus</i> Poselger 1853	<i>C. octacantha</i>
<i>Echinocactus macrothele lehmanni</i> Poselger 1853	<i>C. octacantha</i>
<i>Echinocactus macrothele</i> Poselger 1853	<i>C. octacantha</i>
<i>Echinocactus muehlenpfordtii</i> Poselger 1853	<i>C. robustispina</i> ssp. <i>scheeri</i>
<i>Echinocactus ottonianus</i> Poselger 1853	<i>C. ottonis</i>
<i>Echinocactus plaschnickii</i> Poselger 1853	<i>C. octacantha</i>
<i>Echinocactus poselgerianus</i> Dietrich 1851	<i>C. poselgeriana</i>
<i>Echinocactus pycnacanthus</i> Poselger 1853	<i>C. pycnacantha</i>
<i>Echinocactus radicans</i> Poselger 1853	<i>C. cornifera</i>
<i>Echinocactus salinensis</i> Poselger 1853	<i>C. salinensis</i>
<i>Echinocactus salinensis</i> Poselger 1853 sensu Br. & R. 1923	<i>C. poselgeriana</i>
<i>Echinocactus salm-dyckianus</i> Poselger 1853	<i>C. poselgeriana</i>
<i>Echinocactus saltillensis</i> Poselger 1853	<i>C. poselgeriana</i>
<i>Echinocactus schlechtendalii</i> (Ehrenberg) Poselger	<i>C. octacantha</i>
<i>Echinocactus sulcolanatus</i> Poselger 1853	<i>C. elephantidens</i> ssp. <i>elephantidens</i>
<i>Echinocactus winkleri</i> Poselger 1853	<i>C. pycnacantha</i>
<i>Escobrittonia gracilis</i> (Bremer) Doweld 2000	<i>C. gracilis</i>
<i>Lepidocoryphantha macromeris</i> (Engelmann) Backeber 1938	<i>C. macromeris</i> ssp. <i>macromeris</i>
<i>Lepidocoryphantha macromeris</i> ssp. <i>runyonii</i> (Br. & R.) Doweld 2000	<i>C. macromeris</i> ssp. <i>runyonii</i>
<i>Lepidocoryphantha runyonii</i> (Br. & R.) Backeberg 1961	<i>C. macromeris</i> ssp. <i>runyonii</i>
<i>Mammillaria acanthostephes</i> Lehmann 1835	<i>C. pycnacantha</i>
<i>Mammillaria acanthostephes recta</i> Hort ex Labouret 1853	<i>C. pycnacantha</i>
<i>Mammillaria ancistracantha</i> Lemaire 1839	<i>C. clavata</i> ssp. <i>stipitata</i>
<i>Mammillaria arietina</i> Lemaire 1838	<i>C. pycnacantha</i>
<i>Mammillaria arietina spinosior</i> Lemaire 1839	<i>C. pycnacantha</i>
<i>Mammillaria asterias</i> Cels ex Salm-Dyck 1850	<i>C. ottonis</i>
<i>Mammillaria aulacothele flavispina</i> Salm-Dyck 1845	<i>C. octacantha</i>
<i>Mammillaria aulacothele</i> Lemaire 1838	<i>C. octacantha</i>
<i>Mammillaria aulacothele multispina</i> Scheidw. 1839	<i>C. octacantha</i>
<i>Mammillaria aulacothele spinosior</i> Monville ex Lem. 1839	<i>C. octacantha</i>
<i>Mammillaria aulacothele sulcimamma</i> Pfeiffer 1843	<i>C. octacantha</i>
<i>Mammillaria biglandulosa</i> Pfeiffer 1838	<i>C. octacantha</i>
<i>Mammillaria brevimamma exsudans</i> Salm-Dyck 1850	<i>C. octacantha</i>
<i>Mammillaria brevimamma</i> Zuccharini 1837	<i>C. octacantha</i>
<i>Mammillaria brownii</i> Toumey 1896	<i>C. robustispina</i> ssp. <i>robustispina</i>
<i>Mammillaria brunnea</i> (Coulter) Vpl. 1920	<i>C. clavata</i> ssp. <i>clavata</i>
<i>Mammillaria bumamma</i> Ehrenberg 1849	<i>C. elephantidens</i> ssp. <i>bumamma</i>
<i>Mammillaria bussleri</i> Mundt 1902	C. ottonis
<i>Mammillaria calcarata</i> Engelmann 1850	C. sulcata
<i>Mammillaria cephalophora</i> Salm-Dyck 1850	<i>C. retusa</i>
<i>Mammillaria ceratocentra</i> Berger 1840	<i>C. erecta</i>

<i>Mammillaria clava</i> Pfeiffer 1840	<i>C. octacantha</i>
<i>Mammillaria clavata</i> Scheidw. 1838	<i>C. clavata</i> ssp. <i>clavata</i>
<i>Mammillaria compacta</i> Engelman 1848	<i>C. compacta</i>
<i>Mammillaria conimamma</i> Linke 1857	<i>C. pycnacantha</i>
<i>Mammillaria cornifera</i> De Candolle 1828	<i>C. cornifera</i>
<i>Mammillaria cornifera impexicoma</i> Salm-Dyck 1850	<i>C. cornifera</i>
<i>Mammillaria cornuta</i> Hildmann ex Schumann 1898	<i>C. cornifera</i>
<i>Mammillaria curvata</i> Pfeiffer 1837	<i>C. octacantha</i>
<i>Mammillaria dactylithele</i> Labouret 1853	<i>C. macromeris</i> ssp. <i>macromeris</i>
<i>Mammillaria daimonoceras</i> Lemaire 1838	<i>nom. rejic.</i> (see <i>C. salinensis</i>)
<i>Mammillaria delaetiana</i> Quehl 1908	<i>C. delaetiana</i>
<i>Mammillaria difficilis</i> Quehl 1908 sensu Br. & R. 1923	<i>C. poselgeriana</i>
<i>Mammillaria durangensis</i> Runge ex Schumann 1898	<i>C. durangensis</i> ssp. <i>durangensis</i>
<i>Mammillaria echinoidea</i> Quehl 1913	<i>C. echinoidea</i>
<i>Mammillaria echinus</i> Engelman 1856	<i>C. echinus</i>
<i>Mammillaria elephantidens bumamma</i> Schumann 1903	<i>C. elephantidens</i> ssp. <i>bumamma</i>
<i>Mammillaria elephantidens</i> Lemaire 1838	<i>C. elephantidens</i> ssp. <i>elephantidens</i>
<i>Mammillaria engelmannii</i> Benson ex Marshall 1953	<i>C. robustispina</i> ssp. <i>scheeri</i>
<i>Mammillaria engelmannii</i> Cory 1936	<i>C. robustispina</i> ssp. <i>scheeri</i>
<i>Mammillaria erecta</i> Lemaire ex Pfeiffer 1837	<i>C. erecta</i>
<i>Mammillaria evanescens</i> H.belg.	<i>C. erecta</i>
<i>Mammillaria exsudans</i> Zuccharini ex Pfeiffer 1837	<i>C. octacantha</i>
<i>Mammillaria gladiispina</i> Boedeker 1925	<i>C. delaetiana</i>
<i>Mammillaria glanduligera</i> Otto et Dietrich 1848	<i>C. glanduligera</i>
<i>Mammillaria golziana</i> Haage 1909	<i>C. ottonis</i>
<i>Mammillaria guerkeana</i> Boedeker 1914	<i>C. ottonis</i>
<i>Mammillaria heteromorpha</i> Scheer ex Salm-Dyck 1850	<i>C. macromeris</i> ssp. <i>macromeris</i>
<i>Mammillaria impexicoma</i> Lemaire 1838	<i>C. cornifera</i>
<i>Mammillaria kieferiana</i> Hort.ex Boedeker 1928	<i>C. poselgeriana</i>
<i>Mammillaria lehmanni</i> Otto ex Pfeiffer 1837	<i>C. octacantha</i>
<i>Mammillaria lehmanni sulcimamma</i> Miquel 1838	<i>C. octacantha</i>
<i>Mammillaria leucacantha</i> De Candolle 1828	<i>C. octacantha</i>
<i>Mammillaria loricata</i> Martius 1837	<i>nom. rejic.</i> (see <i>C. pallida</i>)
<i>Mammillaria macromeris</i> Engelman 1848	<i>C. macromeris</i> ssp. <i>macromeris</i>
<i>Mammillaria macrothele</i> Martius in Pfeiffer 1837	<i>C. octacantha</i>
<i>Mammillaria macrothele biglandulosa</i> Salm-Dyck 1850	<i>C. octacantha</i>
<i>Mammillaria macrothele lehmanni</i> Salm-Dyck 1850	<i>C. octacantha</i>
<i>Mammillaria maculata</i> (Coulter) Vaupel 1920	<i>C. clavata</i> ssp. <i>clavata</i>
<i>Mammillaria magnimamma lutescens</i> Salm-Dyck 1850	<i>C. pycnacantha</i>

<i>Mammillaria magnimamma</i> Otto 1835	<i>C. pycnacantha</i>
<i>Mammillaria martiana</i> Pfeiffer 1838	<i>C. octacantha</i>
<i>Mammillaria nickelsae</i> Brandegee 1900	<i>C. nickelsiae</i>
<i>Mammillaria nogalensis</i> Ruenge ex Schumann 1898	<i>C. recurvata</i> ssp. <i>recurvata</i>
<i>Mammillaria octacantha</i> De Candolle 1828	<i>C. octacantha</i>
<i>Mammillaria ottonis</i> Pfeiffer 1838	<i>C. ottonis</i>
<i>Mammillaria pectinata</i> Engelman 1856	<i>C. echinus</i>
<i>Mammillaria pfeifferiana</i> De Vriese 1839	<i>C. cornifera</i>
<i>Mammillaria plaschnickii</i> Otto ex Pfeiffer 1837	<i>C. octacantha</i>
<i>Mammillaria plaschnickii straminea</i> Salm-Dyck 1850	<i>C. octacantha</i>
<i>Mammillaria polymorpha</i> Scheer ex Muehlenpfordt 1846	<i>C. octacantha</i>
<i>Mammillaria potosiana</i> Jacobi 1856	<i>C. potosiana</i>
<i>Mammillaria pycnacantha</i> Martius 1832	<i>C. pycnacantha</i>
<i>Mammillaria pycnacantha spinosior</i> Monville ex Salm-Dyck 1845	<i>C. pycnacantha</i>
<i>Mammillaria radians daimonoceras</i> Schumann 1898	<i>nom. rejic</i> (see <i>C. salinensis</i>)
<i>Mammillaria radians</i> De Candolle 1828	<i>C. cornifera</i>
<i>Mammillaria radians echinus</i> Schumann 1898	<i>C. echinus</i>
<i>Mammillaria radians globosa</i> Scheidw. 1838	<i>C. cornifera</i>
<i>Mammillaria radians impexicoma</i> Schumann 1898	<i>C. cornifera</i>
<i>Mammillaria radians scolymoides</i> Schelle 1926	<i>C. cornifera</i>
<i>Mammillaria radians sulcata</i> Schumann 1898	<i>C. sulcata</i>
<i>Mammillaria radicanissima</i> Quehl 1912	<i>C. clavata</i> ssp. <i>clavata</i>
<i>Mammillaria raphidacantha ancistracantha</i> Schumann 1898	<i>C. clavata</i> ssp. <i>stipitata</i>
<i>Mammillaria raphidacantha humilior</i> Salm-Dyck ex Foerster 1846	<i>C. clavata</i> ssp. <i>stipitata</i>
<i>Mammillaria raphidacantha</i> Lem. 1839	<i>C. clavata</i> ssp. <i>clavata</i>
<i>Mammillaria recurvata</i> Engelman 1863	<i>C. recurvata</i> ssp. <i>recurvata</i>
<i>Mammillaria recurvispina</i> De Vriese 1839	<i>C. elephantidens</i> ssp. <i>elephantidens</i>
<i>Mammillaria recurvispina</i> Engelman 1856	<i>C. recurvata</i> ssp. <i>recurvata</i>
<i>Mammillaria retusa</i> Pfeiffer 1837	<i>C. elephantidens</i> ssp. <i>elephantidens</i>
<i>Mammillaria robustispina</i> Schott ex Engelman 1856	<i>C. robustispina</i> ssp. <i>robustispina</i>
<i>Mammillaria robustissima</i> Schott 1900	<i>C. robustispina</i> ssp. <i>robustispina</i>
<i>Mammillaria runyonii</i> Cory 1936	<i>C. macromeris</i> ssp. <i>runyonii</i>
<i>Mammillaria salm-dyckiana brunnea</i> Salm-Dyck 1850	<i>C. robustispina</i> ssp. <i>scheeri</i>
<i>Mammillaria salm-dyckiana</i> Scheer ex Salm-Dyck 1850	<i>C. robustispina</i> ssp. <i>scheeri</i>
<i>Mammillaria saltillensis</i> Boedeker 1928	<i>C. poselgeriana</i>
<i>Mammillaria scepontocentra</i> Lemaire 1839	<i>C. pycnacantha</i>
<i>Mammillaria scheeri</i> Muehlenpfordt 1847 (non 1845 ! = <i>N. conoidea</i>)	<i>C. robustispina</i> ssp. <i>scheeri</i>
<i>Mammillaria scheeri</i> Muehlenpfordt var. <i>valida</i> Engelman 1856	<i>C. robustispina</i> ssp. <i>scheeri</i>
<i>Mammillaria schlehtendahlia</i> Ehrenberg 1840	<i>C. octacantha</i>

- Mammillaria schlechtendalii* levior Salm-Dyck 1850
Mammillaria scolymoides longiseta Salm-Dyck 1850
Mammillaria scolymoides nigricans Salm-Dyck 1850
Mammillaria scolymoides raphidacantha Salm-Dyck 1850
Mammillaria scolymoides Scheidweiler 1841
Mammillaria stipitata Scheidweiler 1838
Mammillaria strobiliformis Muehlenpfordt 1848
Mammillaria sulcata Engelmann 1845
Mammillaria sulcimamma Pfeiffer 1838
Mammillaria sulcoglandulifera Jacobi 1856
Mammillaria sulcolanata Lemaire 1838

Mammillaria sulcolanata var. *macracantha* Lemaire 1841

Mammillaria thelocamptos Lehmann 1839
Mammillaria valida Purpus 1911
Mammillaria winkleri Poselger 1853
Mammillaria impexicoma Lemaire 1838
Melocactus mammillariaeformis Salm-Dyck 1836
Neolloydia clavata (Scheidweiler) Br. & R. 1923
Neolloydia pulleineana Backeberg 1948

C. octacantha
Nom.rejic. (see *C. salinensis*)
Nom.rejic. (see *C. salinensis*)
C. clavata ssp. *clavata*
Nom.rejic. (see *C. salinensis*)
C. clavata ssp. *stipitata*
C. sulcata
C. sulcata
C. octacantha
C. clavata ssp. *clavata*
C. elephantidens ssp. *elephantidens*
C. elephantidens ssp. *bumamma*
C. octacantha
C. poselgeriana
C. pycnacantha
C. cornifera
C. retusa
C. clavata ssp. *clavata*
C. pulleineana

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