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Coryphantha

Cacti of Mexico and Southern USA

With 338 Figures, Including 299 Colour Photos

Springer

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Dedicated to our wifes 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 Sukkulentensammlung 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 Orientàl and the Sierra Madre Occidentàl. 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. wohlschlageri*, *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. *laui*, *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 Ottonis, 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 Orientàl to the Sierra Madre Occidentàl and to the Sierra Madre del Sur. Six species (*C. sulcata*, *C. ramillosa*, *C. recurvata*, *C. robustspina*, *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 Orientàl 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 Orientàl, which mainly consists of calcareous sedimentation and the western and southern zones with the Sierras Madre Occidentàl 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. vaupeliana*, 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. pycnacantha*, *C. hintoniorum* and *C. maiz-tablasensis*, but also to a somewhat lesser degree, for *C. elephantidens* and *C. ottonis*. Today, *C. pycnacantha* 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.

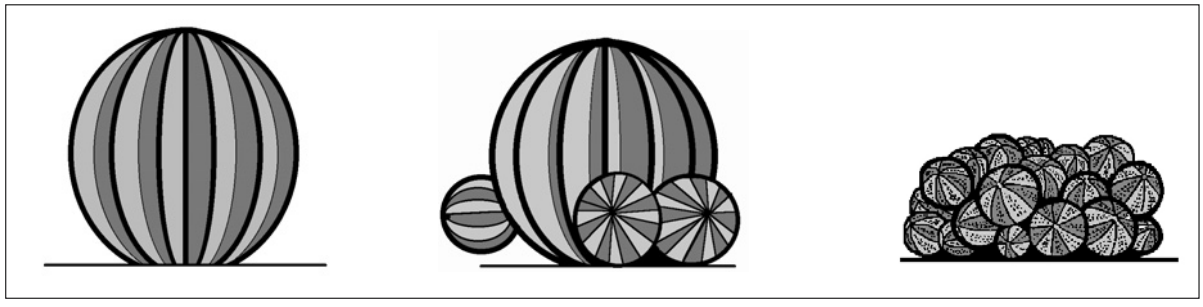

Fig. 1. Formation of groups. *Left* solitary plant, *middle* groups, *right* clusters

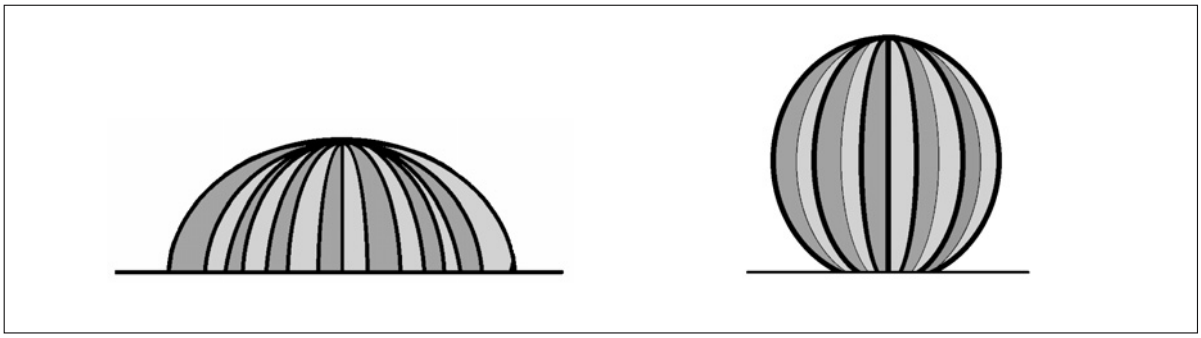

Fig. 2. Body forms. *Left* depressed globose/semiglobose, *right* globose

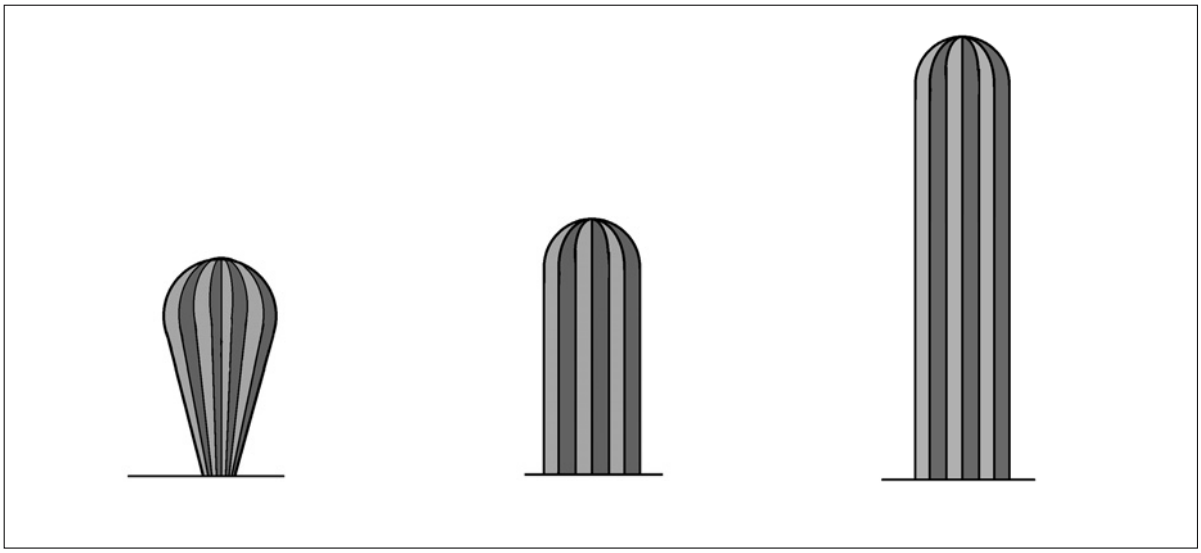

Fig. 3. Body forms. *Left* clavate/obovoid, *middle* cylindrical, *right* columnar

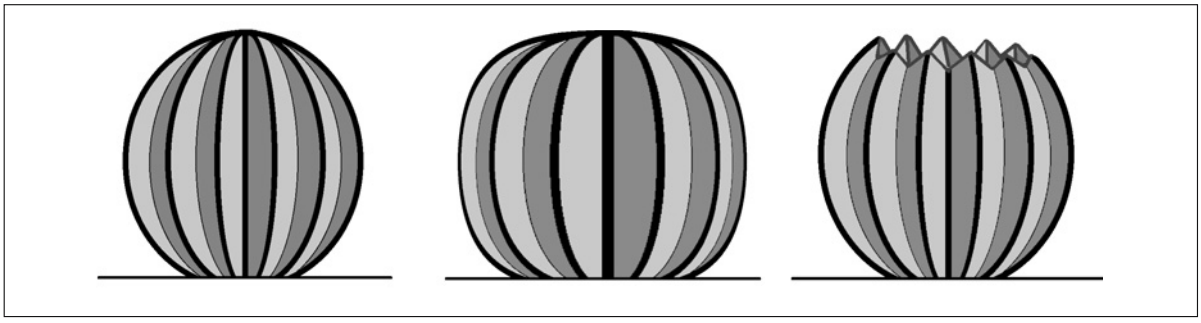

Fig. 4. Apex forms. *Left* rounded, *middle* flattened, *right* depressed

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. vaupeliana*, *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

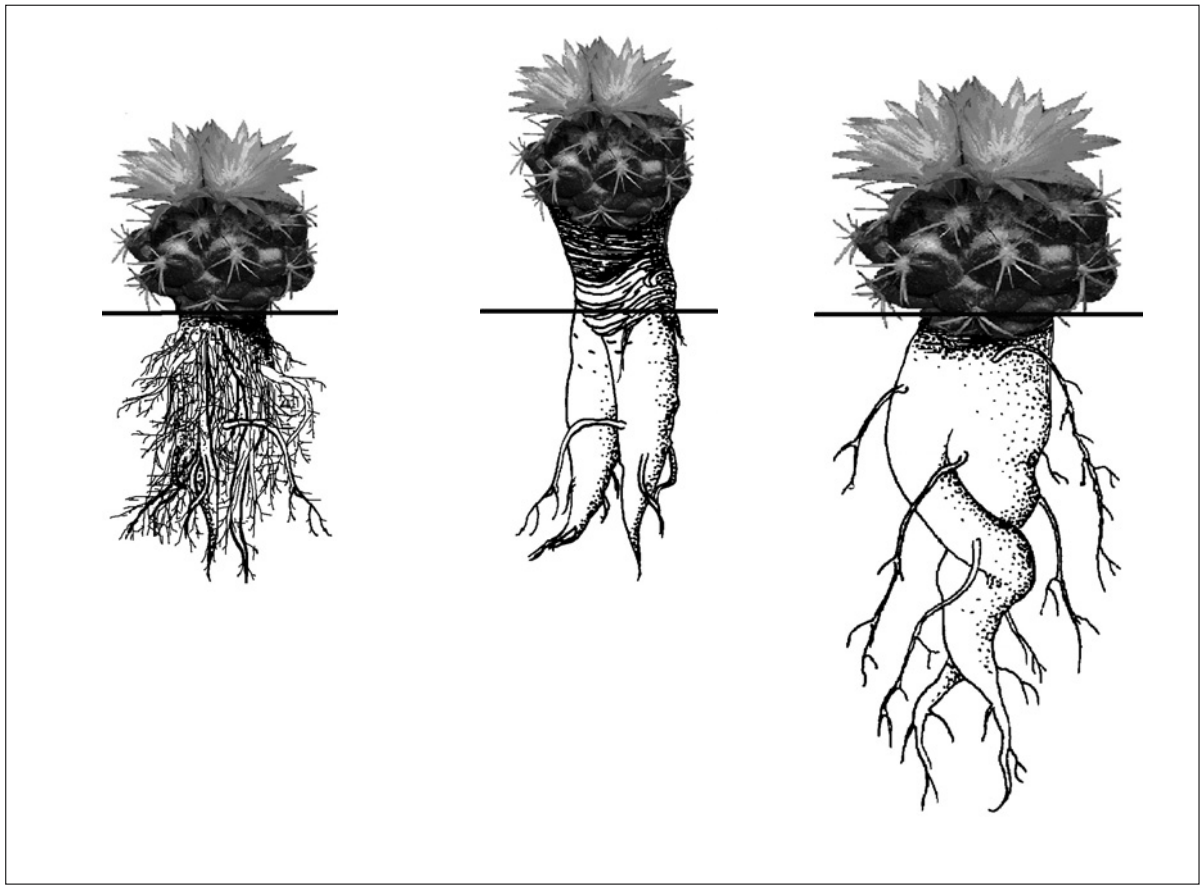

Fig. 5. Roots. *Left* fibrous roots, *middle* sprouting root, *right* tuberous root

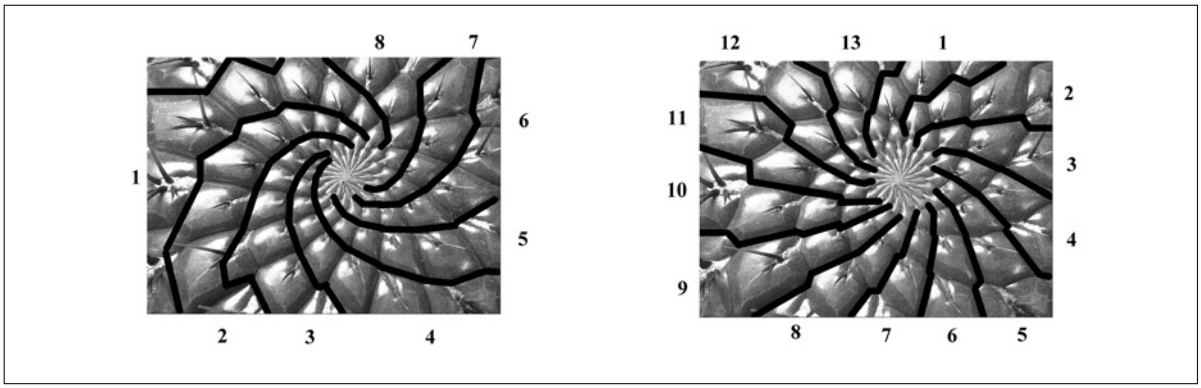

Fig. 6. Tubercle series, example tubercle series 8/13. *Left* counterclockwise, *right* clockwise

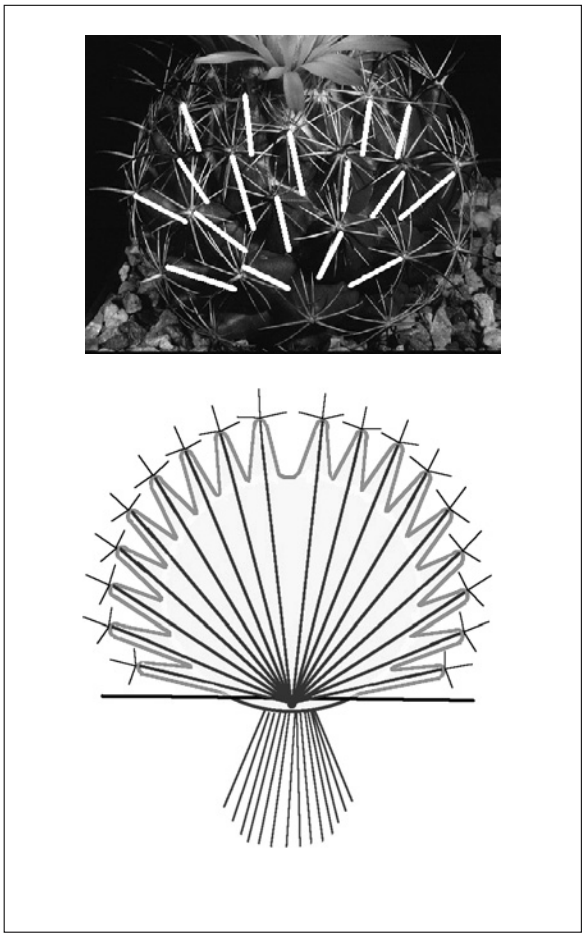

Fig. 7. Direction of tubercle axis, tubercles porrect. Example: *C. cornifera*

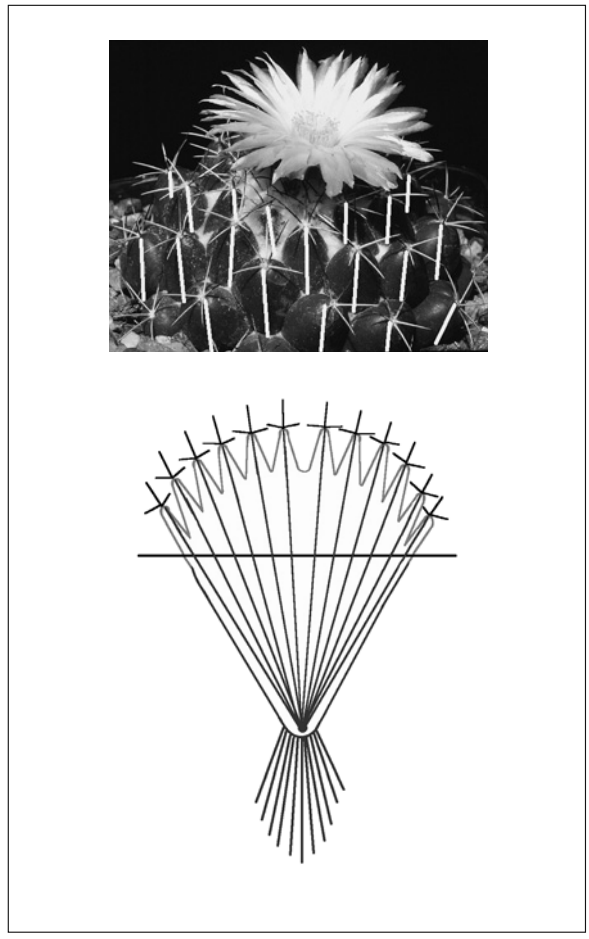

Fig. 8. Direction of tubercle axis, tubercles upright. Example: *C. maiz-tablasensis*

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).

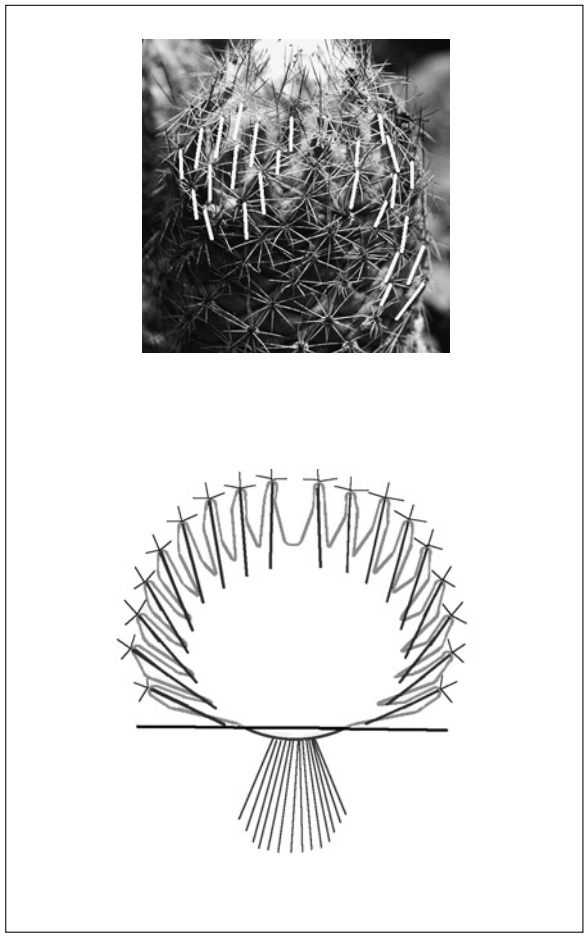

Fig. 9. Direction of tubercle axis, tubercles appressed. Example: *C. durangensis*

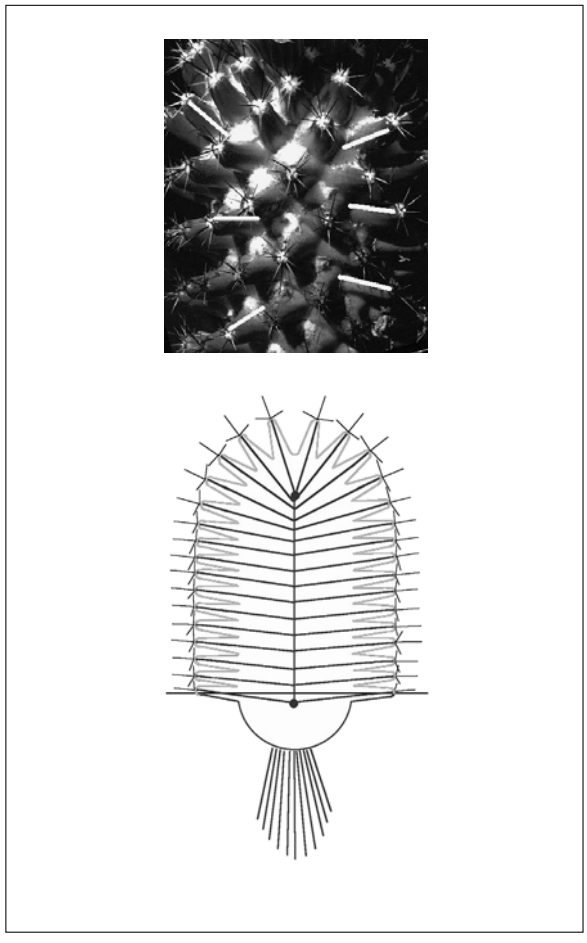

Fig. 10. Direction of tubercle axis, tubercles in clavate and columnar forms. Example: *C. octacantha*

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.

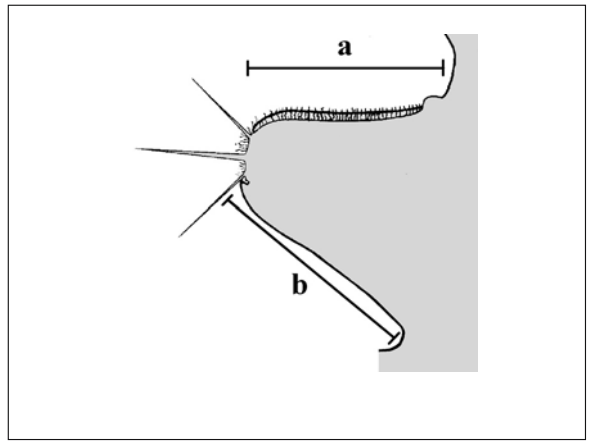

Fig. 11. Measurements of tubercle size, length of upper (*a*) and lower (*b*) surface

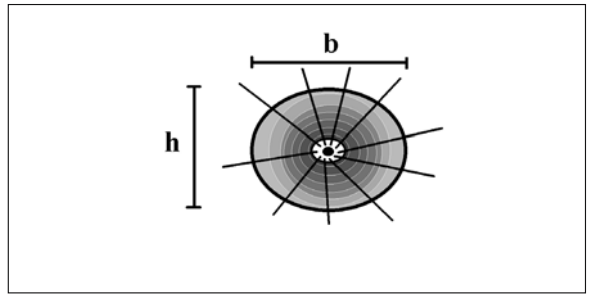

Fig. 12. Measurements of tubercle size, height (*h*) and breadth (*b*)

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.

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 produced 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.

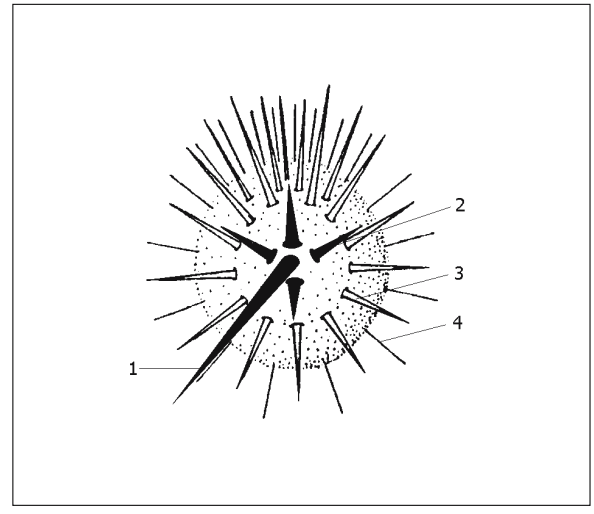

Fig. 13. Scheme of spine formation. Central spine(s) (*1*), subcentral spines (*2*), first layer of radial spines (*3*), second layer of radial spines (*4*)

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.

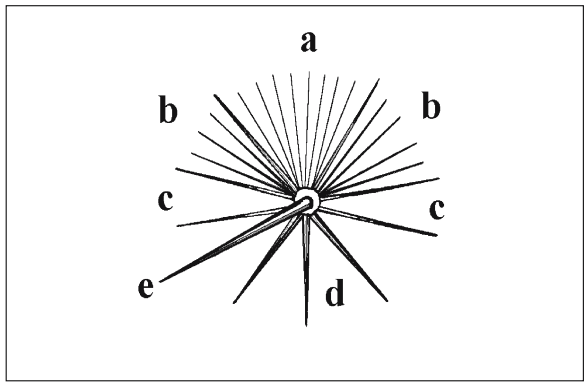

Fig. 14. Spine thickness. Thin needle-like (*a*) needle-like (*b*) thick needle-like (*c*) subulate (*d*) thick subulate (*e*)

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.

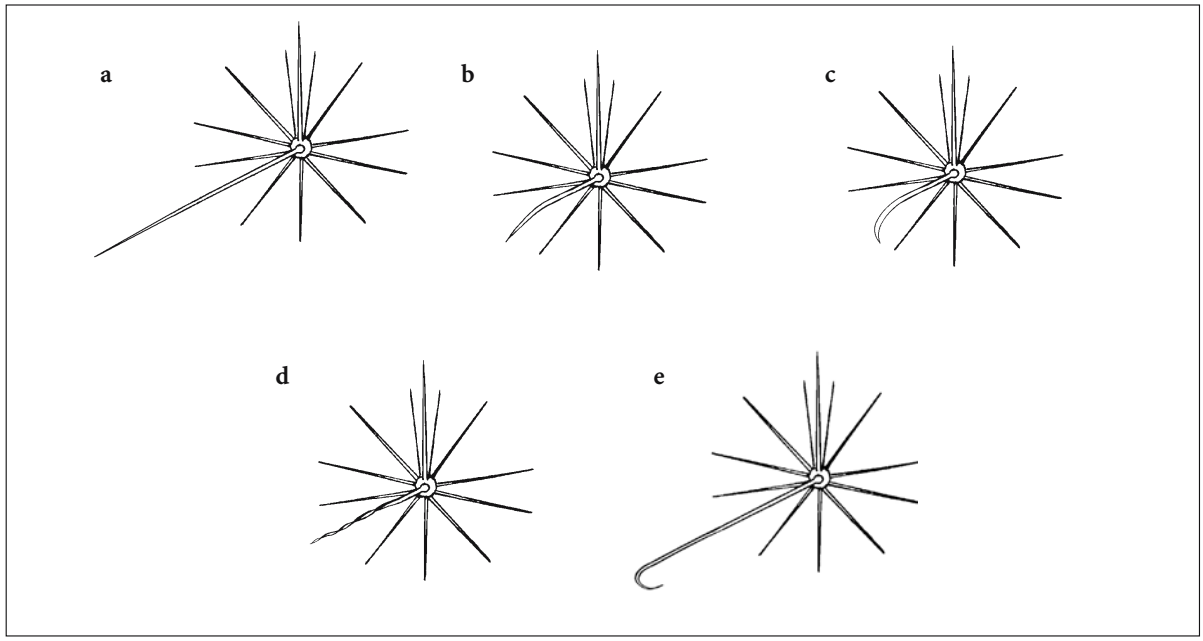

Fig. 15. Shapes of spines. **a** straight, **b** slightly curved, **c** curved, **d** twisted, **e** hooked

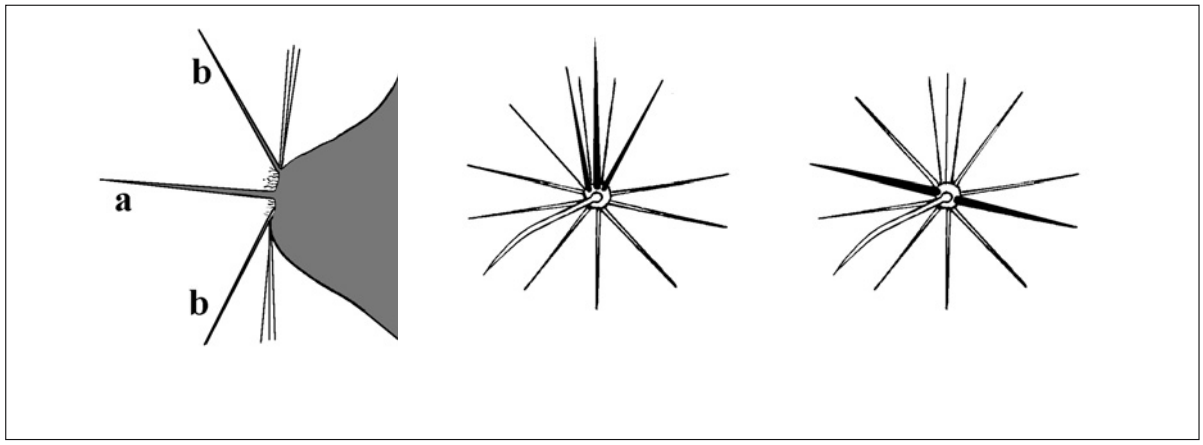

Fig. 16. Direction and position of central spines. *Left* porrect (*a*) and protruding ascending/descending (*b*), *middle* upwards, *right* sideways

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 midstripe 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.