# Bradleya

Yearbook of the British
Cactus and Succulent Society

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## Volume 6/1988

## Contents

*Editors* Nigel Taylor & Colin Walker

*German summaries* Urs Eggli

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The cover design incorporates Richard Bradley's drawing of *Agave americana,* the 'Common American Aloe', from his *Historia Plantarum Succulentarum:* 'The history of succulent plants, containing the Aloes, Ficoids (or Fig-Marygolds), Torch-Thistles, Melon-Thistles, and such others as are not capable of an Hortus Siccus', the work being published in five parts (decades) between 1716 and 1727, in London.

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# A revision of the genus Echidnopsis Hook.f. (Asclepiadaceae)

*P. V. Bruyns*
*Bolus Herbarium, University of Cape Town, 7700*
*South Africa*

*Summary. A revision of the genus Echidnopsis Hook.f. (Asclepiadaceae).* The tropical north-east African and Arabian genus *Echidnopsis* is revised to include *Pseudopectinaria*. Nineteen species are recognised and they are grouped into four new sections. The new taxa *E. scutellata* subsp. *dhofarensis* and *E. scutellata* subsp. *australis* are published and four new combinations are made: *E. scutellata* subsp. *planiflora, E. sharpei* subsp. *ciliata, E. sharpei* subsp. *repens,* and *E. malum.* The following species are accepted: *E. angustiloba, E. archeri, E. ballyi, E. bihendulensis, E. cereiformis, E. dammanniana, E. ericiflora, E. insularis, E. leachii, E. malum, E. mijerteina, E. montana, E. scutellata, E. seibanica, E. sharpei, E. squamulata, E. urceolata, E. virchowii,* and *E. watsonii.* Descriptions, illustrations and distributional data are provided for all the taxa recognised.

*Zusammenfassung. Eine Revision der Gattung Echidnopsis Hook. f. (Asclepiadaceae).* Die im tropischen Nordost-Afrika und in Arabien verbreitete Gattung *Echidnopsis* wird revidiert und umfasst neu auch *Pseudopectinaria.* 19 Arten werden anerkannt und in vier neue Gruppen eingeteilt. *E. scutellata* subsp. *dhofarensis* und *E. scutellata* subsp. *australis* werden als neue Taxa beschrieben. Für die vier Taxa *E. scutellata* subsp. *planiflora, E. sharpei* subsp. *ciliata, E. sharpei* subsp. *repens* und *E. malum* werden die entsprechenden neuen Kombinationen publiziert. Die folgenden Arten werden akzeptiert: *E. angustiloba, E. archeri, E. ballyi, E. bihendulensis, E. cereiformis, E. dammanniana, E. ericiflora, E. insularis, E. leachii, E. malum, E. mijerteina, E. montana, E. scutellata, E. seibanica, E. sharpei, E. squamulata, E. urceolata, E. virchowii* und *E. watsonii.* Für alle akzeptierten Taxa werden Beschreibungen, Abbildungen und Angaben über die Verbreitung gegeben.

## Introduction

*Echidnopsis* Hook.f. is a genus of small-flowered stapeliads mostly found in north-east Africa, with numerous taxa described in recent years. There has been little effort, however, to sort out the resulting miscellany of names, of which many are superfluous. The following account gives a tentative classification based on cultivated material and the extensive spirit collection housed at the Royal Botanic Gardens, Kew. Illustrations are provided demonstrating the variation observed. Unfortunately it has not been possible to support the taxonomic conclusions with field research, rendering the conclusions here more tentative than would otherwise be the case, particularly as collectors active in the relevant regions have shown little inclination to preserve material collected to add to the scanty records.

## Taxonomic history

It was from material in cultivation at Kew and some obtained from the cultivator W. Saunders that Hooker described *Echidnopsis cereiformis* on which he based the genus in 1871. This material seems to have been sent by Georg H. W. Schimper who lived in Ethiopia from 1837 and certainly collected the species as early as 1852. Hooker's new genus was distinguished from other stapeliads by the many-angled, tessellate stems.

The first record of a plant that could be reconciled with *Echidnopsis* is *Stapelia multangula* of Forsskål (1775). This name has been ignored largely, although Schweinfurth suggested that the type collection of *E. nubica* N.E.Br. at Kew represented Forsskål's species. The 'much creeping, 6-9-angled stems' makes its identity as an *Echidnopsis* clear, as was realised by Chiovenda (1923). Unfortunately Forsskål saw no flowers, so it remains impossible to identify his plant with any known species, although it is probable that it is the same as the next-known one which is not uncommon in the southern parts of the Yemen Arab Republic (North Yemen). The next species to be found was *Ceropegia squamulata* Decne, discovered by P. E. Botta in the mountains of the south-west part of North Yemen in 1837 and described in 1838. However, although *Echidnopsis* was created in 1871, it was only in 1957 that Huber pointed out that this *Ceropegia* was probably an *Echidnopsis.* A third species, *Boucerosia cylindrica* Brongniart, was described in 1860. This name too has remained obscure and unused to date.

Species of *Echidnopsis* were collected by both Schweinfurth (travelling in Ethiopia (*E. cereiformis* Hook.f.) and Arabia (*E. scutellata* (Deflers) A. Berger)

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This paper is dedicated to Jo and Bryan.

between 1881 and 1892) and Deflers (travelling in Arabia between 1887 and 1894). Both caused some nomenclatural confusion: Schweinfurth by using the names *E. dammanniana* Sprenger and *E. cereiformis* wrongly (the first for *E. cereiformis* and the second for *E. scutellata*) while Deflers misinterpreted the concept of the genus by considering that its most salient feature was the lack of a conspicuous outer corona. This led him to place *Caralluma quadrangula* (Forsskål) N.E.Br. and *C. penicillata* (Deflers) N.E.Br. in *Echidnopsis* in both of which the outer corona is inconspicuous, though by no means really lacking. At the same time he placed his own discovery, *E. scutellata,* under *Caralluma* on account of its corona being similar to that of *C. armata* N.E.Br., though he noted the similarity of the stems to *E. cereiformis*.

In the final decade of the 19th century *E. dammanniana* Sprenger, *E. virchowii* K.Schum. and *E. nubica* N.E.Br. were added. In addition an *Echidnopsis* was observed for the first time on Socotra by Balfour, Cockburn and Scott in February-March 1880. The situation in the genus was summarized by Berger (1902), although he did not incorporate *E. scutellata*—only doing so in his book of 1910.

White and Sloane (1937) provide the next overview of the genus but added little to our knowledge and no new species. They discussed 10 species of which *E. atlantica* Dinter is now recognised as the intergeneric hybrid *Tridentea ruschiana* (Dinter) Leach × *Trichocaulon delaetianum* Dinter (Lavranos & Barad (1978)).

It is from this date, however, that many new taxa were added. In 1939, *E. sharpei* White & Sloane and *E. repens* R. A. Dyer & Verdoorn were described, being the first of a long series of new species that began to appear with the emergence of relative peace in north-east Africa and the upswing of exploration there by natural historians and collectors. Bally (1942), in one of a series of articles on the succulents of East Africa, gave the first indication of the richness of this area's stapeliad flora and pointed out that species of *Echidnopsis,* mostly new to science, abounded there. Over a period beginning in 1941 and ending in 1962 he described a total of 7 new species, two of which he discovered himself. In addition he discovered the remarkable *E. ballyi* (Marnier-Lapostolle) Bally and was the first to re-collect *E. virchowii* since Hildebrandt discovered it the previous century. He was keenly interested in the genus and published three parts of a series 'The genus *Echidnopsis* in Tropical East Africa' (Bally, 1956, 1957, 1964) in which many of his beautiful illustrations appeared. The last was 'to be continued', but this never took place. These works suffer from an inexplicable disjointedness, brevity and incompleteness: three new names (*E. adamsonii, E. jacksonii* and *E. modesta*) appear in the key in part I but are never mentioned again, thus remaining nomina nuda, and *E. repens* is missing altogether.

Bally's efforts were followed by those of Lavranos who discovered and described 9 new species between 1962 and 1982. With the exception of one from each of South Yemen and Socotra, these all originated in north-east Africa. Another species, *E. radians* Bleck, appeared in 1977.

The majority of these species comes from north-east Africa. For southern Africa White and Sloane (1937) give two species, apart from *E. atlantica*: *E. serpentina* and *E. framesii*. These two were considered synonymous by Bullock (1955) and the number was restored to two only in 1968 when Nel's *Trichocaulon columnare* (discovered by Marloth in 1925) was transferred to *Echidnopsis*. Plowes (1982) mentioned a new species from northern Namibia but this was recently (Plowes, 1986) placed in a new genus, *Lavrania*. Finally Lavranos & Bleck (1985) transferred the two South African species to a new genus *Notechidnopsis*. Thus *Echidnopsis,* as presently circumscribed, is confined to tropical north-east Africa and Arabia.

## Comparative morphology

*Stems.* The plants form small but often very dense clusters of stems growing either under bushes or among rocks. Proliferation of the stems occurs close to the soil surface with branching near the bases. Four species have a repent habit where the entire stem is horizontal, sometimes even terminating slightly beneath the soil and any stems growing initially upwards soon arch back to the soil surface. A typical stem in such a plant is half submerged in the soil with roots arising on the underside along its entire length. The remaining species are all more or less procumbent, i.e. with the stems initially and for only a short distance parallel to the soil surface, then ascending. Despite this 'lowly' habit, soboliferousness is not common: *E. montana* is markedly and consistently soboliferous; *E. scutellata* and *E. ballyi* produce underground shoots but they are few in number and not subterranean for long. Those inhabiting rocky terrain burrow among the stones, but this is not to the extent of *Caralluma europaea* N.E.Br. (an especially soboliferous stapeliad) and the underground stems rise to the surface close to the parent plant. There is, however, a marked increase in underground development of stems in plants in exposed positions.

The stems of all *Echidnopsis* are cylindrical, between 5 and 25mm thick, with the surface divided into shield-like tubercles. These tubercles are arranged in rows lending the stems the tessellate appearance typical of the genus. The number of rows varies from 6 to 20, but the majority has 6 or 8 angles and it is only in *E. urceolata* Bally, *E. bihendulensis* Bally and *E. scutellata* subsp. *planiflora* (Bally) Bruyns where this number is regularly exceeded. Despite the wide range across the genus the number of angles on the stems varies relatively little in individual species.

The stem tubercles vary greatly in shape, although there is a general correlation between their shape and that of the stems—narrower, longer stems with flatter, longer and narrower tubercles. These are almost always 4-6-angled in outline when viewed from above but may be much longer than broad (for example in the long, narrow-stemmed taxa *E. squamulata* Bally and *E. sharpei* subsp. *repens* (R. A. Dyer & Verdoorn) Bruyns) or more or less regularly hexagonal as in *E. sharpei* White & Sloane subsp. *sharpei* and *E. archeri* Bally. They have an unusually narrow shape in *E. malum* (Lavranos) Bruyns, being nearly continuous in the rows with only slight divisions between consecutive tubercles. The degree that these are raised from the surface also varies from very little in *E. squamulata* through a flattened-pyramidal shape in *E. archeri* and *E. sharpei* subsp. *sharpei* to conical in the 'spiny' species, where the tubercle is narrow from the base and confluent with the leaf. In species with flatter tubercles the leaf lies in a sunken area a bit above the middle of the tubercle.

In young growth the surface of the stems of virtually all species is rugulose and/or finely papillose (with minute, densely clustered, sharp-pointed papillae). This rugulosity reaches an extreme form in *E. leachii*, but here the surface is epapillate. In some, as in *E. scutellata* subsp. *planiflora, E. dammanniana, E. virchowii* and *E. cereiformis*, the surface is rough and convoluted as well as papillose. In others, such as *E. squamulata* and *E. archeri*, it is finely papillose or hispid (*E. mijerteina* Lavranos and *E. malum*) but not rugulose. Many (e.g. *E. scutellata* subsp. *planiflora, E. squamulata, E. mijerteina*) not only have a dense covering of papillae but also, between these, a shiny, glass-like epidermis similar to that of *Rhytidocaulon* Bally. Only in *E. montana, E. sharpei* subsp. *sharpei* and *E. scutellata* (in Arabia) is the surface smooth at a magnification of × 30.

*Leaves*. All species possess leaves that are well-developed for stapeliads. Despite the small size (1-5mm long) and often rapidly caducuous nature, these have a definite blade and a midrib visible on the ventral surface. In all except *E. montana, E. sharpei* subsp. *sharpei* and *E. scutellata* subsp. *dhofarensis* the leaves are papillose.

Leaves may be of two kinds: the most common is that found in *E. sharpei* and *E. squamulata* and occurs mainly on species with broader, flatter tubercles, a lower number of stem-angles and often repent habit. Here the leaf is very succulent, broad at the base and abruptly tapers to a sometimes attenuated point, being in total less than 2mm long. In such plants the leaf arises in the terminal bud in an erect position, but rapid growth of the upper part of the tubercle causes it to change its orientation so that the apex points towards the rear of the stem and the leaf becomes adpressed to the tubercle. Exceptions to this orientation are found in *E. cereiformis, E. dammanniana, E. virchowii, E. leachii* and *E. seibanica* where the leaves remain roughly erect (i.e. pointing in the direction of growth of the stem) or spreading in *E. leachii*. In all of these, living leaves are only found in the upper 1-2cm of the stem, after which they dry off and abscise. In most plants with this kind of leaf two small, stipular glands occur on the upper side at the base, each locatable by a small, spherical to elongated, transparent deposit of sap.

The other kind of leaf is found in *E. bihendulensis, E. scutellata* subsp. *planiflora, E. urceolata* and *E. watsonii* to a lesser extent: in the species with more angles to the stems, and a procumbent habit. Here the tubercles are conical and continue directly into the leaf, though the leaf base is visible. Leaves here are 2-5mm long, less succulent, tapering gradually from the base and lacking the stipular secretions. Unlike the shorter leaves, these change orientation from erect only to perpendicular to the direction of growth and remain so until drying up. Usually only the upper 1cm or less has living leaves, after which they dry out but the skeleton is persistent, giving the plant a spiny appearance and texture akin to that of *Hoodia* and *Trichocaulon*.

Two species (*E. ballyi, E. montana*) with long tubercles have short, thick leaves of the first type rather than the longer, persistent kind and both kinds occur in *E. scutellata*.

An examination of many *Echidnopsis* stems shows that the majority has an even number of angles. A careful look at the terminal area will reveal that the leaves and tubercles arise in two alternating whorls each containing half as many leaves as the number of angles on the stem. It appears that the usual asclepiad arrangement of pairs of opposite leaves with consecutive pairs displaced through 90 degrees is replaced by whorls of n leaves with consecutive whorls displaced through an angle of roughly 180/n degrees. This system is, however, frequently disrupted where one whorl fails to produce the same number of leaves as the other and this is how stems with an odd number of angles arise. The initiation of an inflorescence also disrupts this.

*Inflorescence. Echidnopsis* is characterised by a simple synflorescence (Fig. 1) which becomes active shortly after initiation and inactive again soon after. Hence flowers are usually found near the stem apex and a synflorescence produces two or three flowers during its period of activity. Only very occasionally will older synflorescences produce flowers again (a phenomenon most common in *E. cereiformis, E. virchowii* and *E. dammanniana*) and then up to 5 or 6 flowers will have arisen from it in total.

Young, vigorous stems will, at the appropriate time of year, change to 'reproductive phase' after which usually large numbers of the very tiny synflorescences making up an inflorescence arise in close proximity to one another. The opening of the first flower takes place soon after the synflorescence has first appeared. After the development of an inflorescence, even if the stem returns to 'vegetative phase', it elongates relatively little, and further vigorous vegetative growth is taken over by other dormant terminal buds at its base (for the vegetative growth here, as in all stapeliads, is sympodial). Stems that have developed an inflorescence will quite often do so again.

The organization of flowers in a synflorescence is typical of most stapeliads. A terminal flower ($F_1$) appears first, subtended by a bract ($b_1$). While this flower is maturing a second one ($F_2$) surrounded by two bracts usually develops in the axil of the bract $b_1$. In exceptional circumstances the axils of these two subsidiary bracts also become fertile and may give rise to further flowers.

That the flower $F_1$ is terminal is harder to see than in most stapeliads. Synflorescences always lie between the

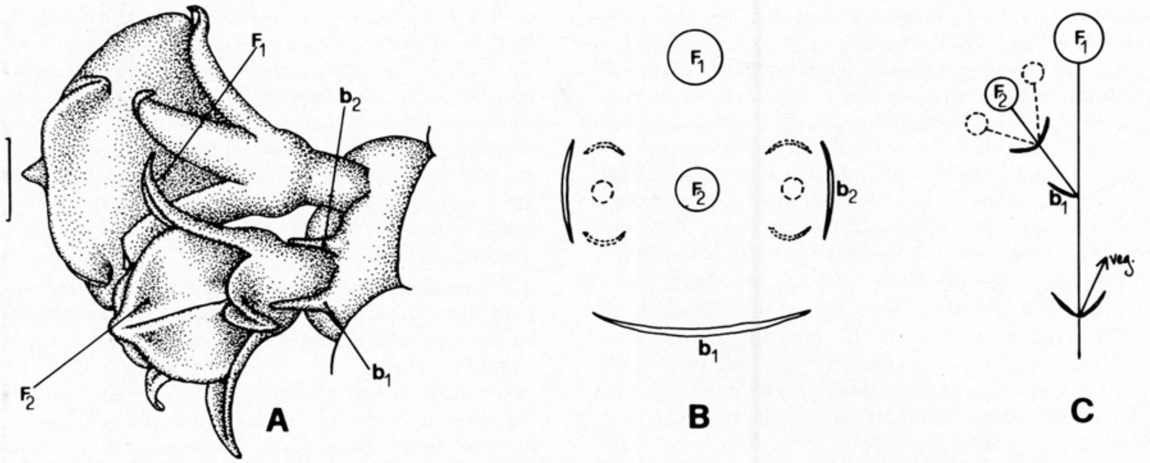


Fig. 1. Typical synflorescence of **Echidnopsis.** A, side view of synflorescence just before anthesis of first flower (scale 1mm); B, horizontal plan diagram of synflorescence showing further development of flowers (usually not achieved) and bract paired with $b_2$ (not visible in A); C, vertical plan diagram of synflorescence. F = flower, b = bract. All drawn from *E. scutellata* subsp. *dhofarensis*, *Butler* s.n.

angles but scarcely disrupt their arrangement so that it is not easy to discern that the stem has been continued from an axillary bud. However, a close examination of the apex of a 'reproductive stem' shows that $F_1$ arises in a terminal position from which it is rapidly displaced by the faster growth of the vegetative continuation.

No species of *Echidnopsis* develops a peduncle even as small as that in *Caralluma dodsoniana*. The bract $b_1$, flower $F_1$ and the others are fused directly to the surrounding tissue at the level of the epidermis and do not remain separate from the surrounding tissue for some distance into the stem as in *Rhytidocaulon*.

*Flowers*. The diameter of the corolla is between 5mm (*E. cereiformis,* the form known as *E. nubica*) and 20-25mm (*E. montana, E. malum*) with most of the species around 10mm. The shape varies from rotate with reflexed corolla-lobes and no significant corolla-tube (*E. dammanniana*) through campanulate (*E. archeri*) to urceolate (*E. ballyi*) and cylindrical (*E. mijerteina*). In the lattermost the corolla is a tube up to 25mm long with lobes reduced to small, spreading flaps at its mouth. In *E. malum* the flower has a most unusual shape as well as having remarkably constructed, inward-pointing corolla-lobes. In all species the corolla is very fleshy, radially symmetric and 5-merous. Intermediate corolla-lobes are formed by small, thick folds between the lobes particularly in *E. squamulata, E. archeri* and *E. ballyi.*

In *E. cereiformis* and *E. dammanniana* the exterior of the corolla is setose, while it is hispid in *E. mijerteina* and papillate in *E. malum,* being more or less glabrous in the others. The interior varies from hairy in *E. malum* and *E. sharpei* subsp. *ciliata* (in both cases with a papillate or setulose indumentum) to glabrous with the surface densely covered with minute, spinescent papillae (setulose) in the majority of species and to slightly projecting but very rounded epidermal cells (i.e. apparently smooth) in *E. scutellata, E. insularis* and *E. leachii.*

The colour of the inside of the corolla is mostly purple-red or yellowish and it is only in the first three species that brown and greenish colours are encountered. The deeply tubular-flowered species all have dark, purple-red interiors lacking the translucent 'window' in the corolla wall often found in *Ceropegia* which illuminates the staminal column and its immediate neighbourhood (Vogel, 1961). Apart from *E. malum,* none of the tubular-flowered species possesses any hairy vesture in the mouth or along the walls of the tube as is found in similarly-shaped flowers in *Dischidia, Ceropegia* and *Stapeliopsis.*

In all species the outer and inner (staminal) coronas are present though the outer one is much reduced in *E. cereiformis.* In this species and *E. dammanniana* the outer corona consists of five free lobes. In all others it is either ring-shaped and shortly cupular (very shallow in *E. virchowii,* and shortly cupular in *E. scutellata* and allies) or deeply cupular as in *E. archeri,* reaching maximum depth in *E. ballyi, E. mijerteina* and *E. malum.* All species (*E. bihendulensis* and *E. insularis* excepted) with deeply cupular outer corona have this ornamented on the inside with stiff, transparent hairs.

The inner corona consists of five free lobes fused to the side and floor of the basin formed by the outer corona, thus dividing this into five compartments. They are always adpressed to the anthers in the lower parts, leaving a narrow channel between adjacent lobes where the tiny anther wings lie. Beneath these wings they close up so that the 'nectarial orifice' is not immediately below and behind the anther wings but situated on the floor of the basin formed by the outer corona. The inner corona-lobes are either short, squat and thick, just touching the anthers or they are dorsiventrally flattened, joined laterally to the outer corona and cover the anthers. In *E. scutellata* and allies they are long, meeting in the centre, then becoming erect over the stigmatic surface.

I have been unable to observe any secretion in the 'nectarial orifices'. Secretions are, however, readily observable on the staminal column forming a pool on the lower, broad, dorsal part of the inner corona-lobes (*E.*

*cereiformis, E. virchowii*) or on the rim of the outer corona (*E. scutellata, E. squamulata, E. ericiflora*). In many such cases the outer corona exudes so much of this substance that the entire column is covered with it. Very occasionally, as in *E. ballyi,* it is secreted on the exterior of the outer corona.

The pollinia are small, nearly spherical and about 0.16-0.22mm diameter. The corpusculum is a little longer than broad and joined to the pollinia by short caudicles which are without wings. The germinating mouth (Schill and Jäkel, 1978), on the inner side of each pollinium, is slightly longer than half the length of the side on which it is situated.

## Distribution

Little attempt has been made to document species distribution which in many cases is still very vague. The occasional odd record indicates that individual species occur much more widely than is currently suspected.

All species occur in arid to very arid parts of the tropics. The easternmost records are of *E. scutellata* from the Jebel Qara in the Dhofar Province of south-west Oman. Three further species are found on the Arabian Peninsula in North Yemen and South Yemen, but the genus does not appear to occur northwards in Saudi Arabia. One species is recorded on the island of Socotra. In north-east Africa records exist from the Red Sea Hills near Port Sudan (the northernmost limit of the genus), in Djibouti and in the eastern and southern sides of Ethiopia, while the main concentrations occur in northern Somalia and the northern parts of Kenya. South of Nairobi the number of species decreases rapidly with only *E. ericiflora, E. archeri, E. sharpei* and *E. watsonii* encountered; with *E. sharpei* subsp. *repens* having its centre of distribution around Mt Kilimanjaro in Tanzania. The very isolated *E. leachii* occurs in the Great Ruaha River Gorge some 900km south of Kilimanjaro and there are unconfirmed reports of an *Echidnopsis*-like plant in the Rovuma River Valley on the Mozambique-Tanzania border.

## Taxonomy

*Infrageneric Groupings*. Bally (1956) subdivided the tropical east African members of the genus informally on the shape of the corolla and the depth of the corolla-tube. This arrangement placed together *E. dammanniana, E. virchowii, E. scutellata* and *E. sharpei* (corolla rotate); *E. cereiformis* and *E. bihendulensis* (rotate-campanulate) etc. A number of species (particularly *E. watsonii* and *E. sharpei* subsp. *repens*) turn out to be so variable in respect of the depth of the corolla-tube and the shape of the corolla, however, that one begins to doubt this approach. Bally's grouping also fails to take account of the remarkable sequence *E. angustiloba, E. scutellata, E. watsonii, E. ericiflora, E. squamulata* in which there is a steadily increasing depth of corolla-tube (from rotate in the first two to urceolate in the lattermost) but with the identical structure of staminal column throughout. A further sequence of this kind—*E. montana, E. sharpei, E. archeri, E. malum, E. ballyi* and *E. mijerteina*—with extremely similar coronas and with corollas varying from rotate to cylindrical, indicates that the geometry of the corolla is particularly fluid in this genus and must be treated with circumspection.

In terms of vegetative features, the group consisting of *E. cereiformis, E. dammanniana* and *E. virchowii* is readily distinguishable, having distinctive stems with broad, rounded angles, rugulose surface and small, broad leaves which remain ascending for their lifetime. The coronas are unusual within the genus and the pollinia are slightly bean-shaped, being similar to those of *Rhytidocaulon*.

That further subdivision on the basis of stems and leaves is not possible is indicated by the presence of virtually identical flowers in the taxa named *E. scutellata, E. planiflora, E. chrysantha* and *E. mariae* as well as in *E. ericiflora, E. squamulata* and *E. urceolata*: in each case some have many-angled, 'spiny' stems (with longer leaves persistent as dried-out spines) and others have shorter, caducuous leaves. The flowers are so similar, though, that these form two complexes of very closely-related species. In fact there is a northward cline from Kenya into Somalia, ranging from taxa with fewer-angled, repent, non-spiny habit to those with procumbent, many-angled, spiny stems. Obvious examples of this are *E. mariae—E. planiflora; E. repens—E. bihendulensis; E. ericiflora—E. urceolata* and to a lesser extent *E. sharpei—E. bavazzani*. It is possible that the more cactoid habit of the northern taxa has been selected preferentially as the genus radiated into more arid environments.

The remaining species must be divided on characters of the corona: (1) there are those in which the outer corona is ring-like, with a flattened, nectar-secreting upper surface, only shallowly cupular and hairless, with long, dorsiventrally flattened inner corona-lobes, encompassing the species related to *E. scutellata*; (2) there are those with the outer corona deeply cupular, hairy on the inner surface, with short, thick inner corona-lobes as in *E. sharpei* and it is probable that the highly-specialized *E. malum* belongs here too.

*Generic Relationships*. The question as to how *Echidnopsis* is related to other stapeliad genera is a most difficult one. Among the stapeliads found north of the equator there are a number of genera which could be related to *Echidnopsis*: *Caralluma* sect. *Caralluma, Desmidorchis, Duvaliandra, Rhytidocaulon* and *Pseudolithos*. Other stapeliads in the area differ particularly by their large and complex pollinaria (e.g. *Orbea, Huernia, Duvalia, Caralluma* 'Ango group' etc.) and mostly also by their much larger flower, solitary synflorescences and the very different leaves.

Of these genera, *Rhytidocaulon* is probably the closest to *Echidnopsis*. Bally (1962) indicated that *Rhytidocaulon* could be separated from it by the upright habit and the nature of the epidermis. However, as pointed out above, a very similar epidermis is found in a number of *Echidnopsis* species and this is just a little more difficult to observe. They are separable, however, by the way the synflorescences are borne and on the shape of the pollinia (in *Rhytidocaulon* this is very much longer than broad with the longer axis perpendicular to the radius of the flower). Florally *R. paradoxum* Bally is most similar to some species of *Echidnopsis* (the other species showing less affinity) and its corona is more or less the same as the form of *E. scutellata* from Djibouti. These two genera are separated, therefore, only on three characters: erect versus creeping to procumbent habit; sunken versus exposed synflorescences, and oval versus usually nearly spherical pollinia, so that the inclusion of *Rhytidocaulon* within *Echidnopsis* at a later stage must be considered.

*Pseudopectinaria* is somewhat less of a problem since its stems and leaves are typically *'Echidnopsis'* (particularly similar to those of *E. mijerteina*), the only difference lying in the indistinct division of the narrower angles into tubercles (a feature of *E. mijerteina* sometimes as well). The flower of *Pseudopectinaria* is indeed most singular when viewed from the exterior but, on dissection, reveals a staminal column in most respects identical to that of *E. ballyi*. The *Pseudopectinaria* flower is unusual in having many hairs on the interior and the corolla-lobes growing back into the tube with only very narrow openings between them. The phenomenon of corolla-lobes growing back into the tube is found also in *Pectinaria articulata* subsp. *articulata,* where it enjoys no special taxonomic recognition, since closely related forms without this feature are well-known. It has also been observed in some freak flowers of *Stapeliopsis saxatilis* (Bruyns, 1986). Despite the more elaborate structure that the corolla-lobes give rise to in *E. malum,* it is felt that this phenomenon is worthy of less taxonomic importance than has been afforded it. *Pseudopectinaria* is thus incorporated into *Echidnopsis*.

The genus *Pseudolithos* Bally, in which growth is restricted to fewer, thicker stems covered with rounded protuberances and flowering concentrated into dense umbels of simultaneously-opening flowers, is also closely related, while *Caralluma dodsoniana* occupies an intermediate position. *Pseudolithos* occurs only in very exposed spots and appears to have achieved extreme reduction in growth so that mostly only a single, central stem arises with rudimentary side-branches. These bear flowers but do not elongate, except in *P. caput-viperae*. All authors to date (Bally et al., 1975) have called these plants leafless, but in fact they bear small, pyramidal leaves in the apical part of the flowering side shoots and even sometimes in the apex of the main stem when this is still young. Thus *Pseudolithos* is mainly distinguished from *Echidnopsis* by the greatly reduced growth, the different form of the synflorescence with umbels of simultaneously-opening flowers and the larger pollinaria with prominent corpusculum. However, the manner in which the synflorescence is borne on highly reduced side shoots in *Pseudolithos* suggests that any apparent similarity that these plants may have to *Echidnopsis* is coincidental and that they have evolved to their much reduced form along different phyletic lines.

*Desmidorchis* and related species still in *Caralluma* differ from *Echidnopsis* by their 4-angled, smooth (never setulose) stems which are not mat-forming, with the angles frequently becoming tipped with a horny, cartilaginous layer with age. The pollinia in this group are extremely variable, much larger than in most *Echidnopis* and usually attached to a more complex corpusculum and caudicles.

*Caralluma* sect. *Caralluma* differs mainly in the organization of synflorescences into a much elongated inflorescence which is at least partially shed after use. In this group the stems are 4-angled with an upright central stem and they are never setulose. I have not examined pollinaria over a wide range in this group so cannot comment on their distinctness or otherwise.

Lavranos & Bleck (1985) have removed the two southern African species from *Echidnopsis*. In justification of this they tabulate seven distinctions between their new genus, *Notechidnopsis* (N), and *Echidnopsis* (E). Of these the first 'roots heavy, wiry' (N)—'roots thin, not wiry' (E) is not valid and the roots of *N. tessellata* are only very slightly thicker than those of other *Echidnopsis*. *N. tessellata* bears flowers singly or in groups of 2-3 (very occasionally 4 or 5 flowers arising simultaneously) so that again it fits into *Echidnopsis* rather than the other on this criterion. *E. cereiformis* and *E. dammanniana* both satisfy the 4th and 5th criteria for *Notechidnopsis* (having bristly upper and lower surfaces to the flower) and *N. tessellata* does not satisfy the 4th criterion for *Notechidnopsis* as the exterior of the corolla is glabrous. A dissection of the corolla-tube of *N. tessellata* reveals that it, too, has a cupular corona, most of which lies within the tube, so that it falls under *Echidnopsis* yet again. In addition neither *E. cereiformis* nor *E. dammanniana* possesses a cupular corona so they would be *Notechidnopsis*. From this it is evident that *N. tessellata* satisfies only three (viz. 2nd, 5th and 7th) of the seven criteria for *Notechidnopsis* and it appears that the authors saw no material of it (the type is not where they cite it either). The seventh criterion is 'distributed in western South Africa' as opposed to 'distributed in north-east Africa' and in view of the enormous disjunctions known in *Huernia* and *Duvalia* in the Stapelieae alone (not to mention any other families—for example in the Polygonaceae a disjunction of 13000km is recorded by Moore (1984) for *Koenigia islandica* L.) it is clear that this ought to be deleted from the list. The conclusions of Lavranos & Bleck are therefore based on inaccurate observations and are not useful in assessing the best generic placing of the two species involved. A closer examination of the two species of *Notechidnopsis* indicates that they are not particularly closely related, and in fact no carefully reasoned argument was ever put forward for moving *N. columnaris* out of *Trichocaulon,* where Nel originally placed it. The flowers of this species are like many of those among the 'spiny-stemmed' species of *Trichocaulon* and are also not much different from some of those in *Quaqua*. It is reasonable to assume that this species represents a stage in vegetative specialization between *Quaqua* and *Trichocaulon* and so

*N. columnaris* has its affinities with these genera. The same probably holds for *N. tessellata* which is, however, florally quite different from *N. columnaris*. The position of these two species is not further dealt with here as they seem to have no particularly close affinity to the northern taxa now in *Echidnopsis*.

It will probably be obvious from the foregoing discussion that one is dealing in the stapeliads with a group of highly evolved plants whose true relationships are difficult to work out on the basis of morphological characteristics alone. This is largely since the plant body, leaves, synflorescence and even the flowers have been much changed by specialization, derivation and reduction in response to both pollinator and environmental pressures. It is strongly suspected that the multi-angled, procumbent to creeping stem form found in *Echidnopsis* has arisen from an upright, 4-angled ancestor. The considerable similarity of some species of *Rhytidocaulon* suggests that these two genera may have shared a recent common origin. However, it must be emphasized that inadequate information is available, so that the conclusions of this paper must be regarded as provisional until studies of seed surface, pollen grain surface, anatomy, ontogeny and possibly also the chemical composition of the plants have been carried out.

### Pollination

As is usual in the Stapelieae, pollination is achieved by the insertion of the germinating mouth of the pollinium into the gap between the anther wings and pulling it upwards in this gap. Since this gap is narrower towards the top, the germinating mouth becomes lodged in it higher up.

Although the agents of pollination of *Echidnopsis* are unknown, it is quite easy to detect attractants for pollinators, especially in the flatter-flowered species. I have been quite unable to detect any scent in *E. squamulata*, or *E. ballyi*, the only urceolate-flowered species on which I have observed many live flowers. However, *E. sharpei* subsp. *ciliata* gives off a sufficiently strong, foetid, excrement-like odour that it can be noticed on a single flower. In the other two subspecies of *E. sharpei* an almost identical, foul odour is exuded but this is more difficult to detect and flowers have to be enclosed in a small bottle for a few minutes. *E. dammanniana* also gives off a foetid, excrement-like odour with a bicarbonate tinge, while in a strikingly yellow-flowered form of *E. scutellata* subsp. *planiflora* (*Plowes* 4909) the flowers smell of horse manure. A scent of dried yeast was detected in some cultivated plants of the form of this taxon known as *E. chrysantha*.

Some of the flowers possess conspicuous, straight hairs on the inner surface of the outer corona and these (as in *Ceropegia*) may serve to direct the insect to the nectarial orifice in such a way as to effect removal of the pollinaria (Vogel, 1961).

Within the stapeliads, similarly urceolate flowers comparable in depth to some *Echidnopsis* are rare and only encountered regularly in the southern African genus *Stapeliopsis*. However, urceolate flowers in *Stapeliopsis* are always held upright with the interior liberally adorned with hairs perpendicular to the corolla surface. Although these hairs do not possess a complicated armature as in *Ceropegia* (Vogel, l.c.), field observations show that the flowers act as traps, keeping prospective pollinators in the flower long enough to effect pollination. This is quite different to *Echidnopsis*, where the flowers are often horizontal or dependent at anthesis and are unable to act as a temporary trap. The one exception to this is *E. malum*. Here the flowers are upright, with narrow openings and large numbers of hairs on the interior so that again the trap mechanism appears and it must be assumed that *E. malum* is florally the most specialized and that the pollinator is different to that in other species.

## SYSTEMATIC TREATMENT

**Echidnopsis** Hook. f. in Bot. Mag. 97: t. 5930 (1871); Schumann in Engl. & Prantl, Pflanzenfam. 4 (2): 274 (1895); A. Berger in Malpighia 16: 1 (1902); N.E.Br. in Fl. Trop. Afr. 4 (1): 474 (1903); White & Sloane, Stap. 3: 975 (1937); Phillips, Gen. S. Afr. Fl. Pl.: 609 (1951); Dyer, Gen. S. Afr. Fl. Pl. 1: 489 (1975). Type: *E. cereiformis* Hook. f.

*Pseudopectinaria* Lavranos in Cact. Succ. J. (US) 43: 10 (1971). Type: *P. malum* Lavranos.

*Virchowia* Vatke ex K.Schum. in Monatsschr. Kakt.-Kunde 3: 101 (1893).

Description. *Plants* forming mats or small clusters of procumbent stems, rarely soboliferous. *Stems* (5-)6-20-angled, 8-25mm diam., surface usually finely papillose, angles divided into more or less hexagonal tubercles topped by a small leaf with clearly defined blade and midrib, stipular glands often present. *Synflorescence* (1-)2-3(-6)-flowered, flowers opening successively, rarely arising from same synflorescence again, without peduncle. *Pedicel* (0.5-)1-5(-15)mm long. *Sepals* mostly less than 2mm long, ovate- or deltoid-acute. *Corolla* (3-)6-15(-20)mm broad, rotate, campanulate to urceolate, globose or cylindrical, glabrous to setulose on inner surface, rarely hairy, exterior glabrous to setose, rarely papillate. *Corona* consisting of two series; outer series rarely of five free lobes (*E. cereiformis, E. dammanniana*), mostly united into cup of varying depth; inner lobes incumbent on anthers, often connivent and rising up above centre of column. *Pollinarium* with very small corpusculum, simple caudicles and mostly nearly spherical, very tiny, yellow (rarely orange) pollinia, 0.16-0.22mm diam.

*Echidnopsis* may be divided into 4 sections. The first, consisting of *E. leachii*, shows affinity to *Rhytidocaulon* in its rather rigidly procumbent-ascending stems with prominently rugose surface, but differs from the second section and from *Rhytidocaulon* in having glabrous (non-papillose) stems. The second section, consisting of three closely related species, also shows affinity to *Rhytidocaulon* but is more typically *Echidnopsis* with very rounded, tessellate stems with rugulose surface not clearly visible to the naked eye. The remaining species can be divided into two closely related sections which show many features of parallel evolution. They are separated on characters of the staminal corona (outlined in the key below). Although this treatment recognises fewer species than some would advocate, facts (such as the variation in the shape of the corolla of *E. watsonii* and *E. urceolata*) suggest that a more radical approach could be justified and the third section reduced to one species. The fourth section has a similar complex of weakly-separated species (here reduced to just two: *E. sharpei* and *E. archeri*) but in addition contains some very distinct and evidently highly specialised plants—*E. ballyi, E. mijerteina* and *E. malum*—whose status as species cannot be doubted and which have diverged substantially from the florally more simple members of the section.

### KEY TO THE SECTIONS OF ECHIDNOPSIS

1. Stem surface rugose but not papillose or leaves remaining erect and outer corona dominated by very broad dorsal areas of inner lobes (as broad as radius of column and broader than outer corona) . . . . . . . . . . . . . 2
Stem surface not rugose; leaves not erect; inner corona not expanding beyond base of limb, dorsal projection of inner lobes narrow, fused into side of cup formed by outer lobes which are broader than dorsal part of inner lobes . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 3
2. Stem surface not papillose; leaves not erect; corona forming shallow cup containing staminal column . . . Sect. **1**
Stem surface papillose; leaves erect; corona not cupular . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . Sect. **2**
3. Outer corona forming shallow cup with broad expanse of tissue at mouth, inner rim of which is formed by outer corona-lobes, remainder by dorsal projection of same, without long hairs on inside; inner corona usually joined to outer cup to level of its mouth, incumbent on and covering anthers, meeting in centre of column and connivent above it . . . . . . . . . . . . . . . . Sect. **3**
Outer corona forming usually deep cup with narrow tissue at mouth (very occasionally bent outwards), no dorsal processes, long white hairs on inner face; inner corona joined to outer cup below middle, usually just touching backs of anthers and not equalling them in length, usually with long white hairs . . . . . . Sect. **4**

1. SECTION GLABRA Bruyns **sect. nov.**
*Caulis rugosus sed non papillosus; folia expansa; corona exterior cupulam non profundam faciens, columnam staminalis continens; pollinia fere sphaerica. Species unica et typica: E. leachii* Lavranos.

1. **E. leachii** Lavranos in Nat. Cact. Succ. J. 27: 69 (1972). Type: Tanzania, Ruaha River Gorge, 48km west of Mikumi, June 1960, *Leach & Brunton* 10143 (EA, holotype [not seen], K).

DESCRIPTION. *Stems* ascending-procumbent, glaucous green becoming brownish with age, 6-angled, up to 150mm long, 8-10mm thick, angles divided into hexagonal, rugose tubercles each bearing a broadly deltoid, rapidly caducuous leaf with acute tip. *Pedicel* less than 1mm long. *Sepals* lanceolate-acute, up to 1.5mm long. *Corolla* shortly campanulate, 4mm long, 4-5mm diam., outside dark purple-pink, glabrous; *tube* 1-2mm long, enclosing whole corona, shallowly bowl-shaped, yellowish; *lobes* ovate-deltoid, ascending, with apices slightly reflexed, margins slightly replicate towards apex, bright purple-pink, 2-2.5mm long, 1.5-1.8mm broad at base. *Corona* yellow suffused with purple towards outside; *outer lobes* united into shallow, pentagonal cup with much indented margin, 2-2.5mm diam.; *inner lobes* fused to outer about ½ way down side of cup, incumbent on backs of anthers, very short with rounded to triangular apex. (Fig. 2)

Probably owing to the inaccessibility of much of Tanzania to collectors—particularly in the southern parts—no records of this species exist other than the type collection. *E. leachii* is extremely isolated from the remainder of the northern species, occurring in the gorge of the Great Ruaha River some 900km south of Mt Kilimanjaro, the southernmost point of the main body of distribution of the genus. At the type locality it occurs in shade on stony slopes among a large number of other succulent plants of various families (Lavranos, l.c.).

The surface of the stem is convoluted and rugose to a degree clearly visible to the naked eye (in most other species it is only visible under a microscope), particularly below the position of insertion of the leaf on the tubercle. The rugosities are rounded or elongated and, though the surface is somewhat transparent, it lacks the papillae (as do the leaves too) typical of *Rhytidocaulon*. Nevertheless, the stems bear a strong resemblance to this genus, further suggested by their somewhat rigid, ascending habit.

Lavranos (l.c.) commented on the very small corolla in relation to the breadth of the column. The column is no broader than that in *E. cereiformis,* for example, and the situation here is comparable to the collection *Darvall* 1 of *'nubica'*. It is quite possible that further collections of *E. leachii* will indicate that this ratio is not typical of the species, as is the case in *E cereiformis*.

The affinities of *E. leachii* within *Echidnopsis* are not at all clear. The rugose stems with ascending habit, deltoid leaves, small, insignificantly-coloured flowers held very close to the stem and low corona with broad bases to the inner corona-lobes suggest affinities with the next three species. However, the outer corona is more cupular than anything found there.

2. SECTION ECHIDNOPSIS
Young stem with erect leaves, papillose; outer corona not cup-shaped, usually consisting of 5 free lobes; pollinia almost spherical.

### KEY TO SPECIES

1. Face of corolla covered with globular, narrow-stalked papillae; corona contained in narrow tube . 4. **E. virchowii**
Face of corolla with spinescent papillae or glabrous; tube broad . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 2
2. Corolla rotate-campanulate; lobes erect to slightly diverging; outer corona reduced to small, not channelled tooth or absent . . . . . . . . . . . . 2. **E. cereiformis**
Corolla rotate; lobes reflexed and adpressed to stem, each outer lobe a conspicuous, channelled, spreading tooth . . . . . . . . . . . . . . . . . . . . . . . . . . . . 3. **E. dammanniana**

2. **E. cereiformis** Hook. f. in Bot. Mag. 97: t.5930 (1871); Penzig in Atti Congr. Bot. Intern.: 40 (1892); A. Berger in Malpighia 16: 160 (1902); N.E.Br. in Fl. Trop. Afr. 4 (1): 475 (1904); White & Sloane, Stap. 3: 978 (1937); Bally in Cact. Succ. J. Gr. Brit. 18: 109 (1956); Cufodontis in Bull. Jard. Bot. Brux. 31, suppl.: 714 (1961); non Deflers in Asclep. Arab. Trop.: 265 (1896) & Schwartz in Mitt. Inst. Allg. Bot. Hamb. 10: 192 (1939). Type: cultivated specimens of unknown origin in Kew Gardens (K).

*E. cereiformis* var. *obscura* A. Berger, l.c.: 160 (1902). Type: not designated.

*E. cereiformis* var. *brunnea* A. Berger, l.c.: 160 (1902). Type: not designated.

*Boucerosia cylindrica* Brongniart in Bull. Soc. Bot. Fr. 7: 900 (1860). Type: Ethiopia, Eritrea, near Halai, *Alfred Courbon,* collected during expedition to Red Sea, 1859-60 (no specimen preserved).

*Echidnopsis tessellata* (Decaisne) K. Schum. in Engl. & Prantl, Pflanzenfam. 4 (2): 274 (1895). *Apteranthes tessellata* Decaisne in Ann. Sc. Nat. ser. 5, 13: 406 (1871). Type: Ethiopia, Eritrea, district of Maschiha below Nahia, 23 Sept. 1852, *Schimper* 805 (P).

*Echidnopsis cylindrica* (Decaisne) K. Schum. l.c.: 274 (1895). *Apteranthes cylindrica* Decaisne l.c.: 406 (1871). Type: Ethiopia, district of Maschiha below Nahia, 23 Sept. 1852, *Schimper* 809 (P).

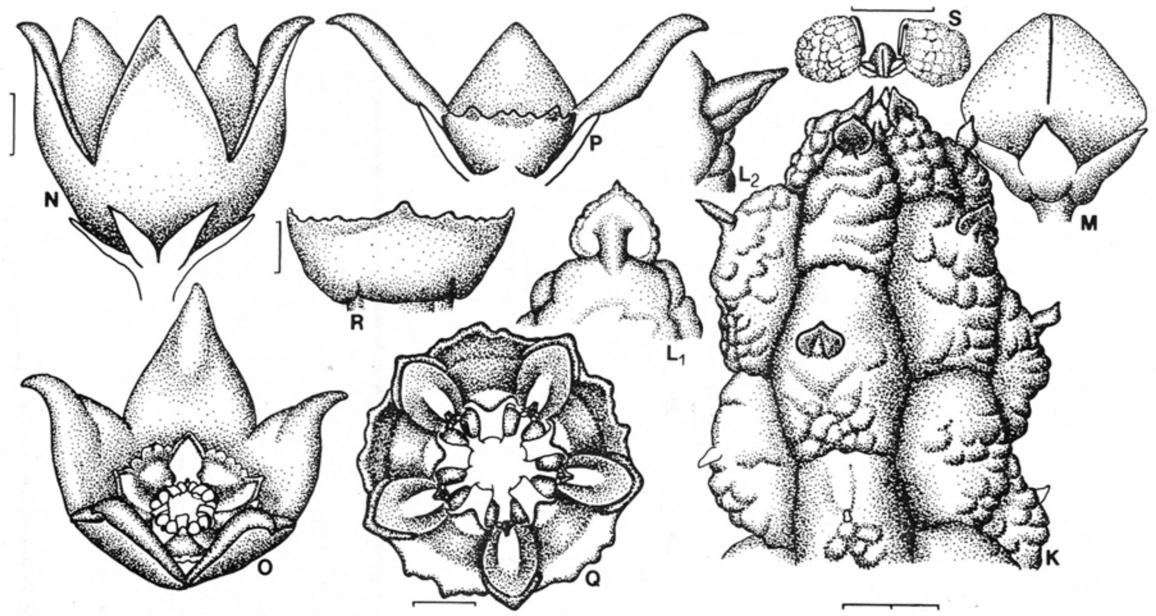


Fig. 2. **Echidnopsis leachii** Lavranos. K, stem apex (scale 2mm); $L_1$, rear view of leaf; $L_2$, side view of leaf; M, bud; N, side view of corolla; O, oblique view of corolla; P, dissected side view of corolla; Q, face view of staminal column (scale 0.5mm; same scale = 1mm for M, N, O, P); R, side view of staminal column (scale 0.5mm as for L); S, pollinarium (scale 0.25mm). All drawn from *Leach & Brunton* 10143.

*Echidnopsis nubica* N.E.Br. in Kew Bull.: 263 (1895) & in Fl. Trop. Afr. 4 (1): 475 (1904); A. Berger l.c.: 160 (1902); Broun & Massey in Fl. Sudan: 256 (1929); White & Sloane l.c.: 977 (1937); Bally in Cact. Succ. J. Gr. Brit. 19 (3): 58 (1957). [*E. dammanniana* sensu Schweinfurth in Gartenflora: 633-637 (1895) non Sprenger; Penzig l.c.: 40 (1892).] Type: Sudan (Nubia), Mt Erkowit, between Suakin and Berber, 15 Sept. 1868, *Schweinfurth* 228 (K).

DESCRIPTION. *Stems* green to brownish, procumbent, up to 600mm long but more usually 50-150mm, 12-20mm thick, finely papillose and faintly rugulose, 8-angled, angles divided into more or less hexagonal, low tubercles, each bearing initially a tiny, thick, deltoid, finely papillose, ascending, rapidly caducuous leaf, with stipular glands on either side. *Pedicel* less than 1mm long. *Sepals* finely papillose, deltoid-acute. *Corolla* exterior setose, interior brown-purple (green background flecked with brown-purple, Schweinfurth, l.c.) to red-brown or bright yellow, rotate-campanulate, (3-)5-8mm diam., setose, with sharp-pointed spikelets or glabrous; *tube* short, saucer-shaped, about 1mm deep, containing column; *lobes* ascending to slightly spreading, ovate-deltoid, very slightly folded in upper half, apex glabrous, rest usually setose, 2-3mm long, 2-2.5mm broad at base. *Corona* bright yellow often with maroon edge along outer rim of backs of inner lobes; *outer lobes* reduced to a linear to deltoid tooth in gap between inner lobes; *inner lobes* broadly triangular often rising abruptly to centre of column, with truncate, dorsiventrally flattened limb incumbent on backs of anthers and mostly exceeding them in length. (Fig. 3)

*Echidnopsis cereiformis* is by far the most common *Echidnopsis* in cultivation and few collections of succulents in Europe are without a specimen of it. It was first collected by G. H. W. Schimper in 1852 and soon afterwards by Courbon and it appears that some of this material arrived in England and was described in 1871 as *E. cereiformis*. Schweinfurth also gathered it (first in 1868) but there have been very few collections this century. This strongly suggests that all the cultivated material is derived from these early collections and this is quite reasonable as it is possibly the easiest of all stapeliads to grow.

Nevertheless, according to Gilbert (pers. comm., 1986) this taxon is not uncommon in the north-east region (Eritrea) of Ethiopia and in the southern parts of the Red Sea Hills south of Port Sudan in south-east Sudan. Schweinfurth seems also to have found it quite plentiful, if the number of specimens that he made is any indication. I was fortunate in having two collections of Gilbert's to examine which indicated that *E. cereiformis* is far more variable than the cultivated material suggests.

*E. cereiformis* is very close to *E. dammanniana,* which it replaces in northern Ethiopia. The two species are most readily separated by the campanulate shape of the corolla in the former which usually does not open further than having the corolla-lobes pointing in the direction in which the flower faces—as opposed to their being reflexed and tightly adpressed to the stem in the latter species. In addition the outer corona is rather different: in *E. dammanniana* the backs of the inner corona run into a ridge running along either side of the tongue-like outer corona-lobe giving it a channelled shape; in *E. cereiformis* the outer corona is reduced to a small tooth situated in the bottom of the gulf between the inner lobes and is not channelled. There is surprising variation in the length of this tooth and further collections may indicate that these two species are the same. From *E. virchowii* it is separated by the same difference in the orientation of the corolla-lobes, by the rather different shape of the column and by the differently-shaped papillae ornamenting the face of the corolla.

This species has been so widely cultivated that it is not surprising that it has an extensive synonymy. Brongniart's name has remained obscure and it was not noticed by Berger. However, Bally (l.c.: 108 (1956)) was indeed aware of Courbon's collection but does not mention Brongniart's name for it. He considered Courbon to have collected *E. dammanniana* and this appears to be a consequence of a note on *E. dammanniana* by Bullock (1955) who was also of this opinion. However, Brongniart mentions a rotate-campanulate corolla and the 'outer corona-lobes fleshy, ovate obtuse, with minute tooth-like lobes inbetween' which is obviously referable to Hooker's *E. cereiformis* rather than *E. dammanniana* and Halai (Halay) is in the area where the former is well-known to occur and is too far north for the latter.

*Echidnopsis nubica* was separated from *E. cereiformis* only by the much smaller corolla. This is not normally as small as Brown and Schweinfurth gave it (2 lin and 3mm resp.) and it is generally 5-6mm in diameter. As the coronas in both are of exactly the

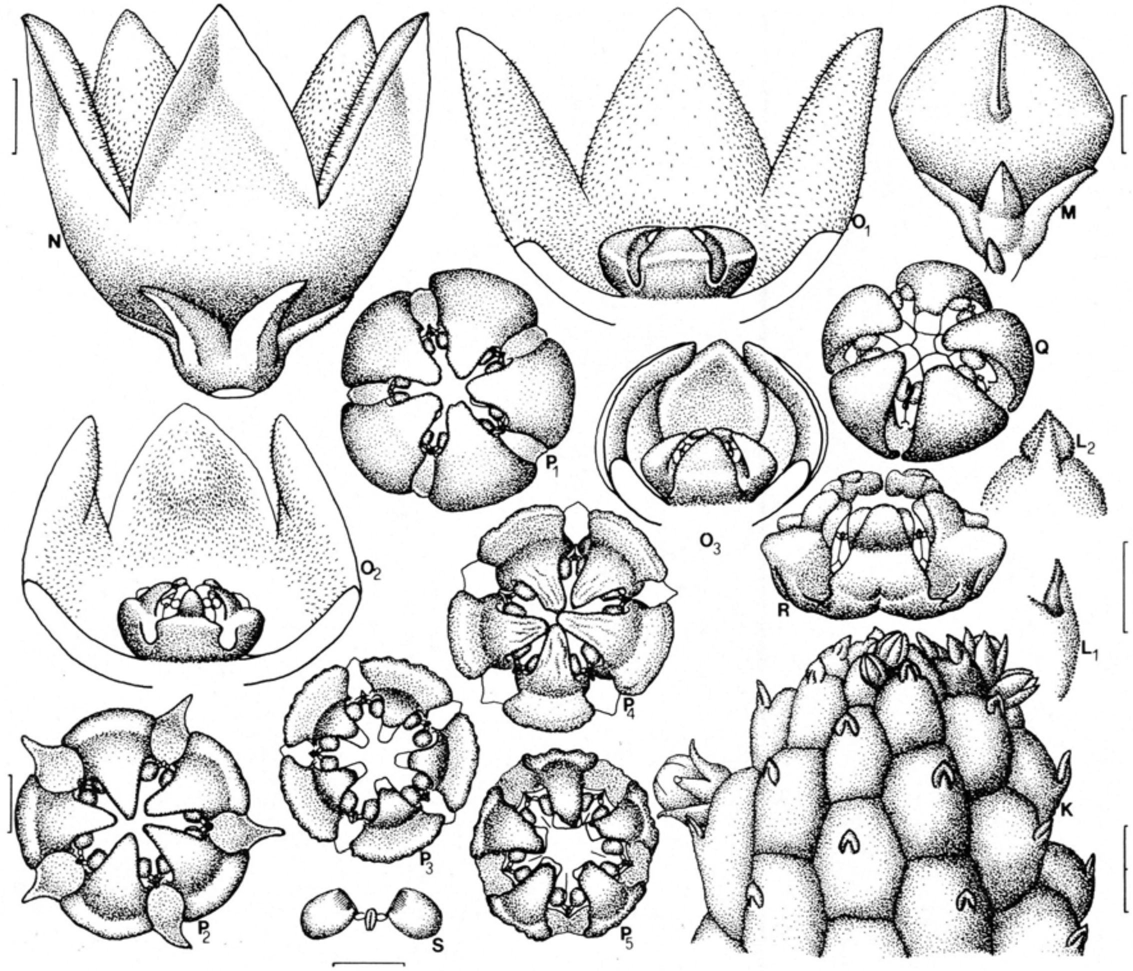


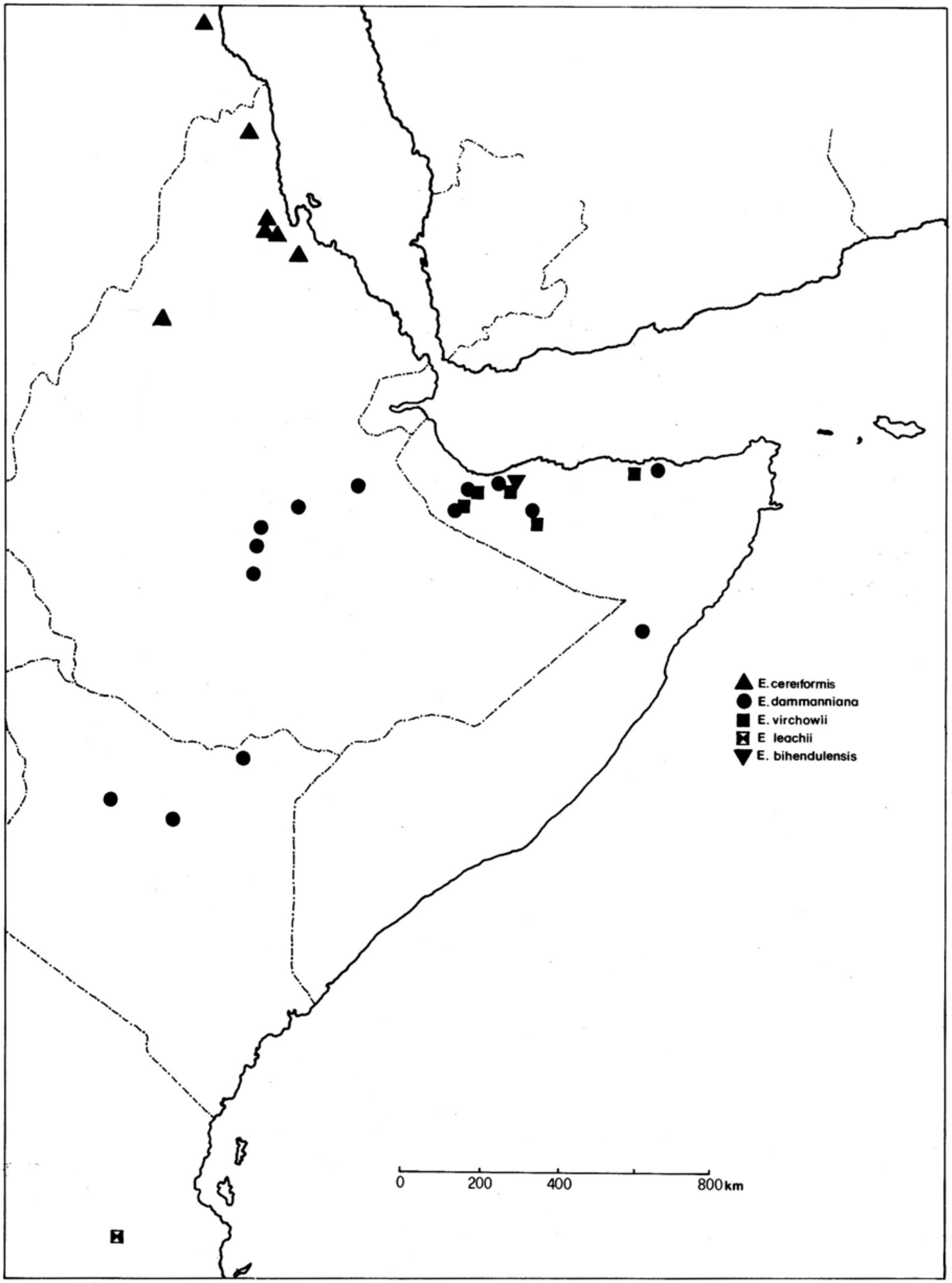
Fig. 3. **Echidnopsis cereiformis** Hook.f. K, apex of stem (scale 2mm); $L_1$, side view of leaf (scale 1mm, as for $L_2$); $L_2$, rear view of leaf; M, bud (scale 1mm); N, side view of corolla (scale 1mm, as for O); O, dissected side view of corolla; P, face view of staminal corona (scale for all as at $P_2$, 0.5mm, as for Q, R); Q, oblique view of staminal corona; R, side view of staminal corona; S, pollinarium (scale 0.25mm). K, L, M, N, $O_1$, $P_1$, S drawn from *Robertson* 1245; $O_2$, $P_2$, $P_3$, $P_4$ from *Gilbert* 2713; $O_3$, Q from *Darvall* 1; $P_5$ from *Gilbert* 2729; R from *Bally* s.n. *Darvall* 1 represents the small-flowered Sudanese form previously known as *E. nubica*; the remainder all correspond to what has previously been termed *E. cereiformis* and are from Eritrea Region, Ethiopia.

same size and shape, this name is discarded. *E. dammanniana* sensu Schweinfurth is the same as *E. nubica* as it was based on his collections from Erkowit ('Erkanit') and Gheleb, the former of which is the type of *E. nubica*. He remarks on the mottling on the corolla of his plants and it seems that this colouring was also the main reason for Decaisne's erecting two species on Schimper's material from Maschiha as there is otherwise no difference between these collections. A perusal of these types reveals the almost complete lack of an outer corona and thus their identity with *E. cereiformis*.

Schweinfurth, Deflers, Berger and Schwartz all mention that *E. cereiformis* is also found in the Yemen. Deflers even cultivated a specimen at Cairo and saw it flower and still maintained that it was this species. The only extant material labelled *E. cereiformis* by Deflers himself is his number 1167 which is the type of *E. scutellata*. Of the material that he collected in the Jebel al 'Urays (Deflers 1895: 424) there appear to be no specimens and so his identification is doubtful. *Schweinfurth* 1324 (near Manakah) is also labelled *E. cereiformis* and this appears to be *E. scutellata*. It seems, therefore, that such reports are without foundation and *E. cereiformis* is confined to Eritrea and the Sudan.

It should be noted that in many (but not all) flowers there is a sudden rise in the inner corona-lobes near their middle. The original illustration of *E. cereiformis* shows this clearly, but it is completely lacking in *Robertson* 1245 and *Darvall* 1 with many intermediates among the Gilbert collections, so this feature is of little taxonomic significance.

In cultivation two forms are found, differing in the colour of the flower—one very bright yellow and the other a pale red-brown or brownish—but both with yellow staminal column. Gilbert (pers. comm., 1986) found dark to light brown flowers in one locality (north of Senafe) and bright yellow flowers at another (near Asmara) and the collection *Robertson* 1245 (also from Asmara area) has reddish-brown flowers. The various colour forms found in European collections are therefore all known to occur in the wild. However, a quite different, pale yellow-brown-flowered taxon with corolla-lobes more spreading than *E. cereiformis* and a blackish staminal column with more prominent outer corona-lobes is also widely cultivated under the name *'maluca'* or



Map 1. Distribution of section 1, section 2 and *E. bihendulensis* in north-east Africa.

*'malaleuca'*. I have been unable to trace the origin of this name, nor does it appear to have been published validly. These plants appear to represent a hybrid *E. dammanniana* × *E. cereiformis* which has appeared in cultivation but is unknown in the wild.

3. **E. dammanniana** Sprenger in Cat. Dammann & Co.: 4, fig. 5 (1892); in Gartenflora 41: 526, fig. 107 (1892) & in Wien. Illustr. Gartenz. 17: 351, fig. 59 (1892); Godefroy-Lebeuf in Le Jardin (Paris) 6: 251 (1892); N.E.Br. in Gard. Chron. ser. 3, 16: 530 (1894) & in Fl. Trop. Afr. 4 (1): 475 (1904); de Duren in Rev. Hort. Belg. 21: 78 (1895); A. Berger in Malpighia 16: 161 (1902); White & Sloane, Stap. 3: 981 (1937); Bullock in Kew Bull.: 587 (1955) pro parte; Bally in Cact. Succ. J. Gr. Brit. 18: 108 (1956); Cufodontis in Bull. Jard. Bot. Brux. 31, suppl.: 714 (1961). Type: Ethiopia, *Dammann & Co.*, based on cultivated material and no specimen preserved. Neotype (designated here): Ethiopia, *Gilbert* 2374 (K).

*E. somalensis* N.E.Br. in Fl. Trop. Afr. 4 (1): 477 (1903); Hemsley in Bot. Mag. 129: t.7929 (1903); Chiovenda in Fl. Somala 2: 222 (1929); White & Sloane l.c.: 980 (1937); Gillett in Kew Bull.: 148 (1941); Bally l.c.: 108 (1956). Type: Somalia, without precise locality, *Mrs Lort Phillips* and *Edith Cole* (K).

DESCRIPTION. *Stems* brownish-green, procumbent, up to 600mm long but more usually 50-150mm, 12-20mm thick, finely papillose and faintly rugulose, 8-angled, angles divided into tetragonal or hexagonal tubercles, each tubercle bearing a short-lived, ascending, finely papillose, thick, deltoid leaf, with stipular glands on either side. *Pedicel* less than 1mm long. *Sepals* deltoid-acute, finely papillose. *Corolla* rotate-reflexed, exterior green-brown, setose, interior purplish- to greenish-brown speckled with dull green-yellow, setose, with sharp-pointed spikelets, 7-11mm diam.; *tube* lacking; *lobes* ovate-deltoid to ovate-lanceolate, reflexed so as to be tightly pressed against stem, 2.5-

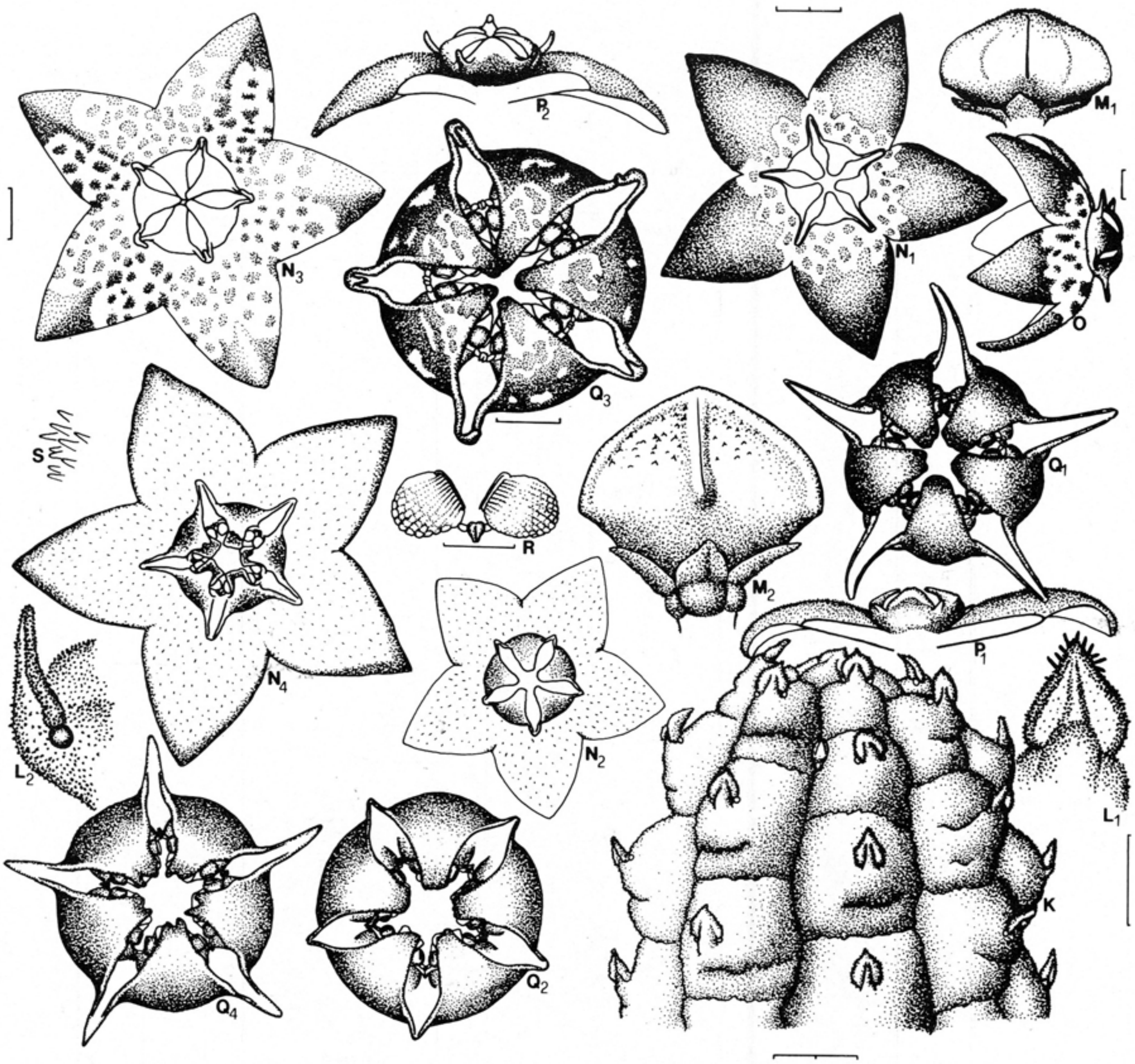


Fig. 4. **Echidnopsis dammanniana** Sprenger. K, apex of stem (scale 2mm); L$_1$, rear view of leaf (scale 1mm, below sketch, as for L$_2$, Q$_1$, Q$_2$, Q$_4$); M, bud; N, face view of corolla (scale at N$_1$ 2mm, as for M$_1$, N$_2$; N$_3$ 1mm, as for M$_2$, N$_4$, P$_2$, P$_1$); O, side view of corolla (scale 1mm); P, dissected side view of corolla; Q, face view of staminal column (scale Q$_3$, 0.5mm); R, pollinarium (scale 0.25mm); S, papillae on surface of corolla (scale at R, 0.5mm). K, N$_3$, P$_2$, Q$_3$, S drawn from *Gilbert & Vollesen* 7932; L, R, M$_2$ from *Bailes* 142 (Somalia, New Sheikh Pass); M$_1$, N$_1$, O, Q$_1$ from *Bailes* 79; N$_2$, Q$_2$ from *Lavranos* 9039; N$_4$ from *Bally* 12399; Q$_4$ from *Lavranos* 12169.

3.2mm long, 2.3-2.5mm broad at base. *Corona* shiny black-purple, sometimes speckled with yellowish; *outer lobes* lanceolate, channelled, ascending towards apices, 0.5mm long; *inner lobes* rising up slightly towards centre of column, outer margin of back confluent with margin of outer lobes, limb small, truncate-deltoid, dorsiventrally flattened, incumbent on and covering anthers. (Fig. 4)

Of all taxa in the genus, *E. dammanniana* has probably the largest distribution in Africa. In Ethiopia it is known from the vicinity of Dire Dawa and along the Awash River south of Addis Ababa. In Somalia it appears to be confined to the mountainous north-western part of the territory particularly between Burao, Hargeisa and Berbera and in Kenya it is well-known in the vicinity of Lake Turkana in the North-west Frontier Province where it was first discovered by Bally. It is very likely, too, that it occurs in the intervening territory as well, the lack of records only being due to the remoteness of much of the area.

Bullock (l.c.) considered that Penzig sent the original material to Dammann & Co. but he seems to have based this only on Penzig's use of the name *'dammanniana'*. However, the use of this name was probably due to Schweinfurth, with whom he travelled on part of the expedition of 1891. Penzig saw his *'dammanniana'* around Gheleb and so this is clearly the same as that illustrated and collected by Schweinfurth (1895). These references ought all to appear under *E. cereiformis* and not under *E. dammanniana* as in Bullock (l.c.).

Sprenger (Wien. Illustr. Gartenz., l.c.) says that Dammann & Co. brought the plant that they grew at their nursery (at San Giovanni a Teduccio, near Naples), from Abyssinia themselves and this is the most likely explanation of its origin. Their plate of the species is not as illuminating as it could be but the 'schwarzbraun' flowers with 'zurückgeschlagenen Zipfeln' (Sprenger, l.c.) make it quite clear that this corresponds with the concept of *E. dammanniana*.

In fact the flowers are not usually as dark as Sprenger gives them and are usually green- or purple-brown flecked with a paler yellow-green in increasingly large quantities as one goes towards the centre. The staminal corona is ornamented similarly, with the outer corona and outermost third of the inner corona a shiny purple-black, the remainder yellowish with large, confluent purple blotches, though sometimes the whole structure is purple-black.

*E. dammanniana* and *E. virchowii* grow together in a number of localities in northern Somalia and many collections from this area contain both species and also, in some cases, what appear to be hybrids. These have short, round-tipped, columnar papillae on the corolla, lacking the narrow neck that each papilla has in *E. virchowii* and the inner corona-lobes are more level from their outer edge to the centre, without a steep rise just after the base of the anthers.

4. **E. virchowii** K.Schum. in Monatsschr. Kakt.-Kunde 3: 98 (1893) & in Engl. & Prantl, Nat. Pflanzenfam. 4 (2): 274 (1895); N.E.Br. in Fl. Trop. Afr. 4 (1): 476 (1904); White & Sloane, Stap. 3: 984 (1937); Bally in J. E. Afr. Nat. Hist. Soc. 16: 163 (1942); in Cact. Succ. J. Gr. Brit. 18: 107, 108 (1956) & in ibid. 19: 60 (1957); Cufodontis in Bull. Jard. Bot. Brux. 31, suppl.: 715 (1961). Type: Somalia, without precise locality, 1875, *Hildebrandt* ('gesammelt in der Gegend von Tanga in D. Ost Afrika' is almost certainly wrong) (K).

*E. stellata* Lavranos in Cact. Succ. J. (US) 46: 182 (1974). Type: Somalia, Erigavo district, escarpment below Tabah Pass, *Lavranos* F342 (FI [not seen]).

*Virchowia africana* Vatke ex K.Schum. nom. nud. in Monatsschr. Kakt.-Kunde 3: 101 (1893).

DESCRIPTION. *Stems* brownish-grey to green, procumbent, 50-200mm long, 12-20mm thick, finely papillose, (6-)8-angled, angles divided into tetragonal tubercles, tubercles bearing short-lived, ovate-deltoid, ascending, thick, finely papillose leaves with stipular glands on either side. *Pedicel* less than 1mm long. *Sepals* ovate-deltoid, 1mm long, finely papillose, green, becoming brownish towards tips. *Corolla* rotate; exterior setose, grey-green; interior purple-brown speckled with pale yellow-green, covered with spherical, stalked, often translucent-white papillae, (6-)8-11(-13)mm diam.; *tube* abrupt beneath column containing most of it so that inner corona-lobes nearly flush with surface of corolla, cupular, less than 1mm deep; *lobes* ovate-deltoid to lanceolate-deltoid, usually reflexed so as to be adpressed to stem, 3-5.5mm long, 2-3mm broad at base. *Corona* purple-brown becoming pale yellow towards nectarial orifice; *outer lobes* enclosing nectarial orifice in basin and appearing as slight indentations or teeth on margins of wall of basin joining backs of inner lobes; *inner lobes* approximately deltoid, with emarginate back confluent with outer corona, limb dorsiventrally flattened, incumbent on anthers, often exceeding them and meeting in centre. (Fig. 5)

Karl Schumann gave this species as native to the vicinity of Tanga in Tanzania which is what he was told by the head gardener at Berlin. Bally l.c. (1942) mentions that it is common on Mt Lasa near Mkomazi but in 1956 he was no longer sure of this and in 1957 he announced its rediscovery in the Al Madu Range in northern Somalia. However, Schweinfurth (1895) had already suspected that it came from Somalia and, as Bally pointed out, Hildebrandt was indeed in northern Somalia in 1875, when this plant arrived in Berlin. Schumann's illustration and notes are very clear and there is no doubt that Bally's collection B11143 is Schumann's species. It is now known to occur in Somalia from Hargeisa to near Erigavo and records indicate that it occurs here only.

Schumann mentions the remarkable spherical papillae on the surface of the corolla in which each little sphere is joined by a narrow neck to the surface of the corolla below. These papillae are usually translucent-clear and are so plentiful—covering nearly the entire surface—that they impart a uniform pinkish-white hue to the corolla. This is not, however, the real colour of the surface of the corolla which is usually purple-brown, mottled increasingly towards the centre with lighter green-yellow. In some cases, though, the papillae are the same colour as the surface underneath and this gives the flower a colour much as in *E. dammanniana*.

Unlike *E. dammanniana*, the column of *E. virchowii* is sunken into an abrupt but very short tube. It is also unlike other members of its group, and more similar to the structure in other groups, in having the outer corona completely intergrown with the backs of the inner corona forming a continuous rim around its edge. From this, the inner corona proceeds horizontally to the centre of the flower usually with an abrupt rise after the base of the anthers. In *E. dammanniana* and *E. cereiformis* the inner corona begins much lower down at its outer extremity and rises up more to the centre.

It appears that Lavranos (l.c.) was unaware of the real identity of *E. virchowii* for he failed to relate his *E. stellata* correctly, allying it instead with *E. dammanniana*. It is peculiar that he considered the dissimilarity in the coronas of *E. stellata* and *E. dammanniana* to 'fall well within the range of . . . such a widespread taxon as *E. dammanniana*' when *E. dammanniana* shows almost no variation in the staminal column over its entire range. Yet he considered the long corolla-lobes of his species not to be within the range of variability of *E. dammanniana*. Variation in the corolla-lobes of *E. virchowii* can be found and it is considered that the long lobes of *E. stellata* (and hence the differently shaped bud) are merely an eastern variant of this species.

The stems of *E. cereiformis*, *E. dammanniana* and *E. virchowii* are superficially similar. However, on a closer examination, those of the lattermost can usually be separated from the other two; they are considerably smoother (less rugulose), more finely setulose and the angles more continuous with the divisions into tubercles usually not continuing right into the groove between adjacent angles. However, the clearest means of separation remains the distinctive papillae and staminal column.

Like the other two species, *E. virchowii* is an easy plant to cultivate and, once established, it thrives and flowers copiously during much of the summer. Plants are long-lived in cultivation so that, for example, Bally's collection of 15th October 1956 is still living at the Städtische Sukkulentensammlung, Zürich.

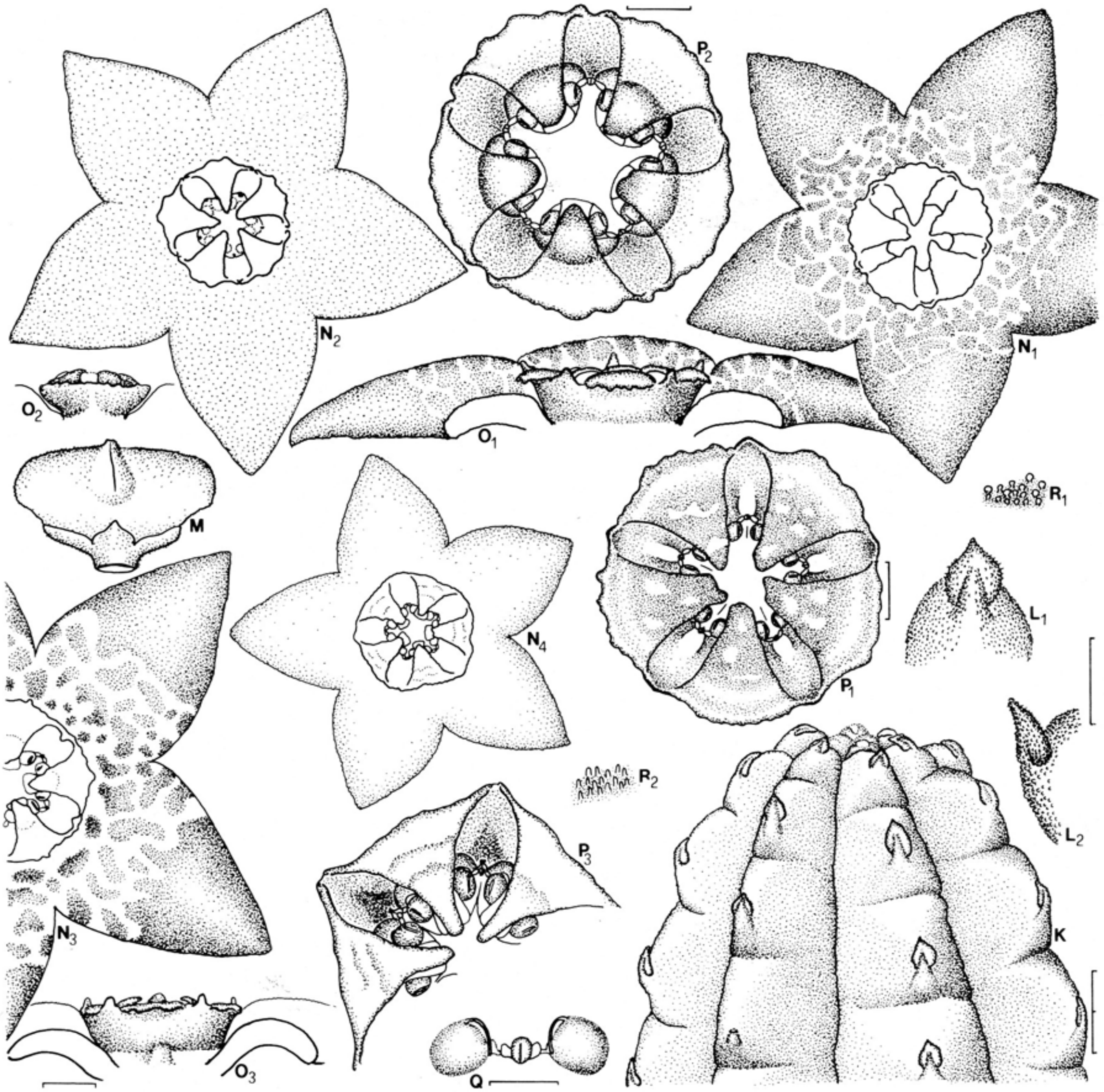


Fig. 5. **Echidnopsis virchowii** K.Schum. and hybrids with *E. dammanniana*. K, apex of stem (scale 2mm); $L_1$, rear view of leaf; $L_2$, side view of leaf (scale 1mm for both); M, bud; N, face view of corolla; O, dissected side view of corolla ($O_1$ scale as for Q, 1mm; $O_3$ scale 1mm, as for $O_2$, N, M); P, face view of staminal column (scale $P_1$ 0.5mm; $P_2$ 0.5mm as for $P_3$); Q, pollinarium (scale 0.25mm); R, papillae on surface of corolla (scale as for Q, 0.5mm). K, L drawn from *Bailes* 79; M, $N_2$, $O_2$, $P_2$ from *Bally* B11143; $N_1$, $O_1$, $P_2$, $R_1$ from *Gillett, Beckett & Watson* 23618; $N_3$, $N_4$, $O_3$, Q from *Bailes* 83; $P_3$, $R_2$ from *Bally* B11699. Most of these collections contain both *E. virchowii* and *E. dammanniana;* $N_4$, $P_3$ and $R_2$ represent the putative hybrid between them.

### 3. SECTION VÄDOSIGORONA Bruyns **sect.nov.**

*Caulis juvenis non rugosus, foliatus; corona exterior cupulam non profundam faciens, ore lato, intus non pilosa; corona interior plerumque ad coronam exteriorem usque orem connata, incumbens in antheras easque celans, in centro columnae connivens; pollinia fere sphaerica. Species typica: E. scutellata* (Deflers) A. Berger.

KEY TO SPECIES

1. Corolla campanulate to rotate; tube only deep enough to contain at most outer corona cup; corolla-lobes as broad as column or > 3× as long as depth of tube ....... 2
   Corolla urceolate to globose; tube at least deep enough to contain entire outer corona cup and most of inner lobes; corolla-lobes narrower than breadth of column, not longer than depth of tube ........................ 3
2. Corolla-lobes < 3× as long as broad at middle; upper rim of outer corona level with, or included within mouth of tube .............................. 6. **E. scutellata**
   Corolla-lobes > 3× as long as broad at middle; tube containing at most lower half of column . 5. **E. angustiloba**
3. Corolla-lobes small at mouth of urceolate tube, much shorter than length of tube ......................... 5
   Corolla-lobes as long as corolla-tube; tube globose ....... 4

4. Corolla-tube pentagonal in cross-section in middle . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 10. **E. urceolata**
Corolla-tube circular in cross-section in middle . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 7. **E. watsonii**
5. Outer corona-tube containing inner corona-lobes; corolla-lobes without outward-pointing fold at base . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 11. **E. insularis**
Outer corona-tube not containing inner corona-lobes; corolla-lobes with outward-pointing folds at base . . . . . . . 6
6. Stems repent, 6-8(-9)-angled; leaves deltoid, caducuous . . 7
Stems procumbent-erect, 12- or more -angled; leaves lanceolate, persistent as dried spine . . . . . 10. **E. urceolata**
7. Pedicel 5-8mm long; corolla-tube pentagonal in cross-section in middle; outer corona with recurved, dentate margin . . . . . . . . . . . . . . . . . . . . . . 9. **E. squamulata**
Pedicel 1-1.5mm long; corolla-tube circular in cross-section in middle; outer corona margin not recurved or dentate . . . . . . . . . . . . . . . . . . . 8. **E. ericiflora**

5. **E. angustiloba** Bruce & Bally in Cact. Succ. J. (US) 13: 180 (1941); Bally in J. E. Afr. Nat. Hist. Soc. 16: 163, fig. 28 (1942); in Flow. Pl. Afr. 26: t. 1003A (1947) & in Cact. Succ. J. Gr. Brit. 19: 58 (1957). Type: Kenya, 5 miles from Archer's Post on road to Isiolo, 17 or 18 Dec. 1939, *Copley* in *Bally* S26 (K, lectotype, designated here, ZSS).

DESCRIPTION. *Stems* 10(-11)-angled, procumbent-erect, 50-100mm long, 10-20mm diam., tubercles conical, leaves with broad base narrowing rapidly, 2-3mm long, finely papillose, soon drying out and persisting as white spines, with stipular glands on either side. *Pedicel* less than 1.5mm long. *Sepals* narrowly ovate-lanceolate, up to 2mm long, glabrous. *Corolla* yellow to yellow-lobed with reddish centre, rotate to slightly campanulate, 10-15mm diam., glabrous outside, inside setulose; *lobes* 3-5mm long, ovate-triangular at base rapidly becoming very narrow with margins strongly folded back for upper ⅔ of length, acute-tipped; *tube* very short, campanulate, about 2mm diam., 1mm deep. *Corona* rounded-pentagonal, pale to bright yellow, 2.3-2.8mm diam.; *outer lobes* united into shallow cup, with slightly to clearly dentate margin, sometimes with a few short hairs on inner surface; *inner lobes* with broad base and narrow, dorsiventrally-flattened, linear limb incumbent on anthers, meeting near centre and rising up, connivent, above column. (Fig. 6)

*Echidnopsis angustiloba* is a very little-known species and Plowes (1980) mentions only one collection other than the type. In 1983 it was collected again near Rumuruti, close to the type locality, by Mrs Patricia Powys and her material enabled the preparation of Fig. 6. Mrs Powys found it growing in red, sandy soil under bushes with a large selection of other Stapelieae (including *Rhytidocaulon paradoxum* and *Echidnopsis sharpei*) and found that both a yellow- and red-flowered form (with yellowish lobes) occurred in the same place. The latter colouring corresponds most closely to Mrs Hugh Copley's original collection.

The very long, narrow corolla-lobes and more or less flat flower in this species place it close to *E. scutellata* in this section and possibly between this species and *E. watsonii*. The enormous variability of *E. watsonii* in Kenya suggests that *E. angustiloba* may just be an even flatter-flowered form of this taxon. However, it

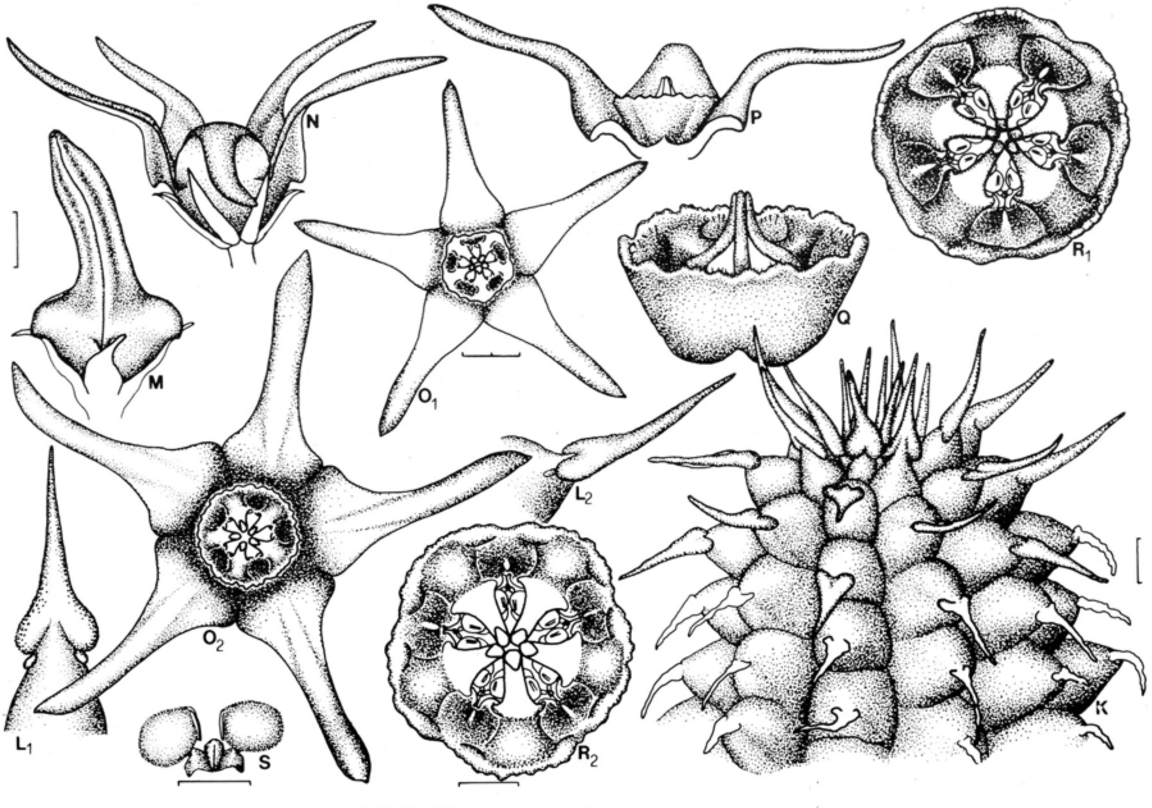


Fig. 6. **Echidnopsis angustiloba** Bruce & Bally. K, stem apex (scale 1mm, as for N, $O_2$, P); $L_1$, face view (dorsal) of leaf (scale that of S = 1mm, as for $L_2$); $L_2$, side view of leaf; M, bud (scale 1mm); N, side view of corolla; O, face view of corolla (scale 2mm); P, dissected side view of corolla; Q, oblique side view of staminal column; R, face view of staminal column (scale for both as at $R_2$ 0.5mm, as for Q); S, pollinarium (scale 0.25mm). All drawn from *Powys* 524. $O_1$, $R_2$ from yellowish-flowered form, remainder from reddish-flowered specimens.

occurs in very much the same general area as *E. watsonii* in Kenya although at present they are not recorded as sympatric. In addition the decrease in size of the corolla-tube (which happens as one proceeds southwards) is generally accompanied by a decrease in the size of the corolla-lobes and thus *E. angustiloba,* which has extremely long lobes in proportion to the tube, would not fit this trend.

It is interesting to note the floral similarity between this species and *E. montana* in the next section. Both have very long, narrow corolla-lobes and a short tube only just containing the column, a further example of the parallel development of the flowers in these two sections.

Bally (1957) gave the stems as 11-angled but, in the plants grown in Oxford, all stems had 10 angles so that this is probably the more usual number.

6. **E. scutellata** (Deflers) A. Berger, Stap. u. Klein.: 26 (1910); Schwartz in Mitt. Inst. Allg. Bot. Hamb. 10: 192 (1939); White & Sloane, Stap. 3: 982 (1937).

*Caralluma scutellata* Deflers in Bull. Soc. Bot. Fr. 43: 114, t.4 (1896) & in Mem. Inst. Egypt. 3: 268 (1896). Type: South–North Yemen border (Bilad Subehi), Wadi M'Adin ('Mo'aden'), 300m, May 1894, *Deflers* 1167 (G).

DESCRIPTION. *Stems* procumbent-erect, 8-15-angled, 30-100(-150)mm long, 6-20mm diam., finely papillose, angles tuberculate with 6-angled to conical tubercles bearing variously-shaped leaves, dark green, with stipular glands on either side. *Pedicel* from 1-10mm long. *Sepals* up to 2mm long, finely papillose, lanceolate. *Corolla* exterior mottled with purple-red and yellow-green to plain yellow-green, glabrous, interior glabrous, from brownish suffused with yellow towards centre to yellowish or bright yellow, 7-10mm diam., rotate to rotate-campanulate to broadly campanulate; *tube* campanulate, containing column up to level of outer corona-lobes or slightly exceeding it; *lobes* ovate-deltoid to deltoid or lanceolate-deltoid, sometimes with slight annulus around base (some Somalian and Djibouti plants) and thickened patch near reflexed apex, margins reflexed, often lined with cylindrical, translucent hairs. *Corona* campanulate to sometimes very shallow (Djibouti material), yellow or red to red-brown, about 2mm diam., circular to rounded-pentagonal; *outer lobes* obscurely divided near middle and flattened on upper surface, sometimes with much toothed, frilly outer margin (particularly in material from North Yemen); *inner lobes* with broad base attenuated into dorsiventrally flattened limb at least covering anthers, usually exceeding them and often connivent for some distance above column.

*Echidnopsis scutellata* provides the best example of a group of closely-allied taxa in which the flowers are not reliably distinguishable, but the stems have a different appearance. A broad view of the species is taken here to give *E. scutellata* both an African and Arabian distribution. Four subspecies are recognised, separable as follows:

### KEY TO THE SUBSPECIES OF E. SCUTELLATA

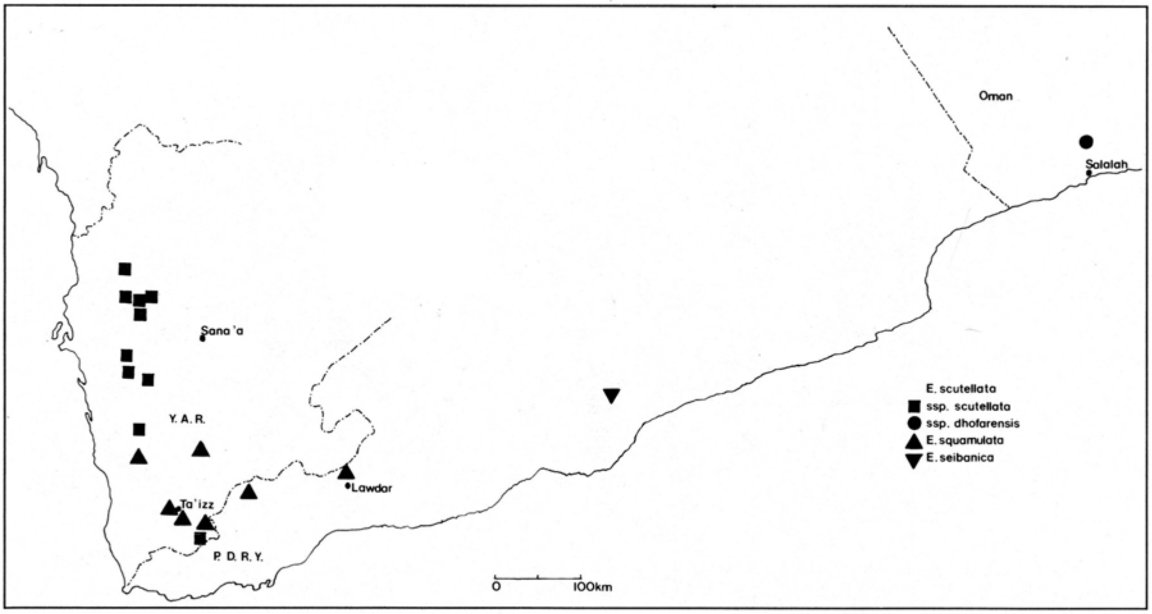
1. Leaves < 2× as long as broad at base, caducuous, not persistent as spines . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 2
   Leaves > 3× longer than broad at base, persistent as spines . . . . . . . . . . . . . . . . . . . . . . . 6d. subsp. **planiflora**
2. Flowers 6-9mm diam., (Kenya) . . . . . . 6c. subsp. **australis**
   Flowers > 10mm diam., (Arabia) . . . . . . . . . . . . . . . . . . . . 3
3. Walls of corolla-tube adpressed to staminal column, corolla flat when fully open . . . . . . . 6b. subsp. **dhofarensis**
   Walls of corolla-tube not touching staminal column, corolla cupular . . . . . . . . . . . . . . . . . . 6a. subsp. **scutellata**

6a. subsp. **scutellata**

DESCRIPTION. *Stems* 8-angled, with thick, rapidly caducuous, finely papillose leaves less than twice as long as broad at base. *Corolla* pale to bright yellow, more than 10mm diam., rotate to campanulate often with purple-red mottling on exterior; *lobes* deltoid to ovate-deltoid usually with reflexed tip, margins reflexed, without cylindrical hairs. *Corona* yellow or red, circular to pentagonal; *outer lobes* much toothed and flat or reflexed to only slightly toothed. (Fig. 7)

Subsp. *scutellata* has been collected in recent years a number of times between Zabid and north of Hajjah in North Yemen. Deflers' original collection was made in the Wadi M'Adin south of the present-day Al Faqarah on the border of North and South Yemen.

Deflers (1895: 424) also recorded an *Echidnopsis* (there called *E. cereiformis*) from the Jebel al 'Urays and it is possible that this, too, represents subsp. *scutellata*.



Map 2. Distribution of *Echidnopsis* in Arabia.

The material from North Yemen (Fig. 7) is of very distinctive appearance with broad corolla-tube deeper than the height of the column and much broader than the column. In addition, there are the purple-red patches on the exterior in many of these plants which make the outside quite brightly coloured. The column is very broad and the outer corona-lobes are especially so with

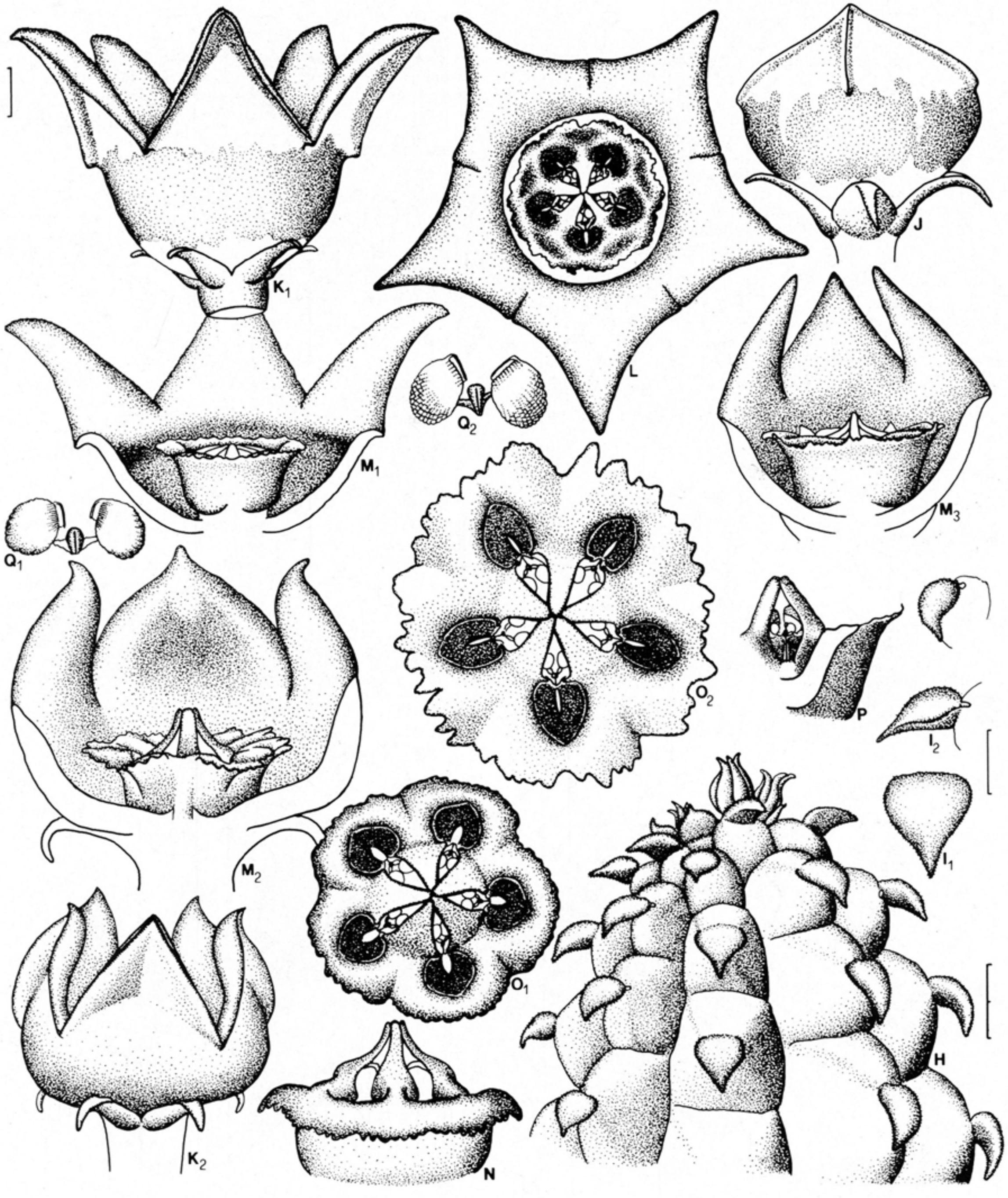


Fig. 7. **Echidnopsis scutellata** (Deflers) A. Berger subsp. **scutellata.** H, stem apex (scale 2mm); $I_1$, face view of leaf; $I_2$, side view of leaf (scale 1mm for both, as for J, $M_2$, $M_3$); J, bud; K, side view of corolla (scale for $K_1$, $K_2$ 1mm, as for L, $M_1$); L, face view of corolla; M, dissected side view of corolla; N, side view of staminal column (scale of I, 0.5mm, as for O, P); O, face view of staminal column; P, side view of part of staminal column with outer corona removed; Q, pollinarium (scale of I = 0.25mm). H, I, $K_2$, $M_2$, $O_2$ drawn from *Miller & Long* 3259; J, $K_1$, L, $M_1$, $M_3$, P, $Q_1$ from *Haig-Thomas* 1; N, $O_1$ from *Miller & Long* 3332; $Q_2$ from *Noltee* 1434.

much-toothed margins sometimes folded back. This much-toothed outer corona, broad corolla-tube (not adpressed to the sides of the column) as well as the blotching with purple on the outside of the corolla corresponds very closely to Deflers' own collection according to his description. However, his drawing suggests a much flatter flower—according to the dimensions he gives the corolla-tube is at least as deep as the length of the corolla-lobes, which is not obvious from sketch number 3 of his plate. Nevertheless the manner in which the staminal column is separated from the sides of the corolla-tube, a characteristic of this subspecies, is clearly visible in Deflers' plate. The relationship with subsp. *australis* is very close. The differences between *E. scutellata* and *E. mariae* that Lavranos (l.c., 1982, see below) listed are mostly invalid or inaccurate (for example it is *E. scutellata* that is more cupular and not the other way round; this species *does* possess recesses between the inner corona-lobe attachments, as do all *Echidnopsis*) and it is really of no use to argue that their geographical separation constitutes a reason for regarding them as separate species, as has been discussed already in a different context.

Deflers (l.c.) included in his description mention of a small patch of red dots in a ring on the corolla near the staminal column. I have not seen this in any of the collections of which live material is available. It may be of interest to note that the corona may be either yellow or red, though there is no structural difference in these colour forms. This colour generally corresponds to that of the corolla-tube which may be pale yellow, yellow or purplish-red. Sometimes the whole of the inside of the flower is purple-red. The colour of the pollinia varies with that of the column—orange pollinia on red column, yellow with a yellow column. A further characteristic of this subspecies is the often very slight extent to which the flowers open, the corolla-lobes frequently not even opening out to be parallel to one another. It is quite uncommon for them to spread out fully, though this does happen.

6b. **E. scutellata** subsp. **dhofarensis** Bruyns **subsp. nov.;** *a subsp. scutellata flore planiore, tubo corollae ad columnam staminalem adpresso; a subsp. australe flore grandiore et a subsp. planiflora foliis dissimilis differt. Holotypus:* Oman, Dhofar Province, on road from Thamarit to Salalah, Agabat al Hatab, 700m, 4 Oct. 1979, *Miller* 2811 (E).

DESCRIPTION. *Stems* 8-angled, not papillose, with thick, rapidly caducuous, glabrous (not papillose) leaves about as long as broad at maximum. *Corolla* pale yellow, 9-10mm diam. when flat; *tube* short, cupular, adpressed to sides of staminal column and just containing it; *lobes* deltoid-ovate, usually with reflexed tip, margins reflexed, without hairs. *Corona* yellow or red. (Fig. 8).

This subspecies is known only from the dry north side of the Jebel Qara in Oman, north of the town of Salalah where it was first collected by Alan Radcliffe-Smith on the 22nd of September 1977 (under the number 5183, Radcliffe-Smith (1980) and pers. comm., 1986).

It is distinguished from subsp. *scutellata* by the flatter flower

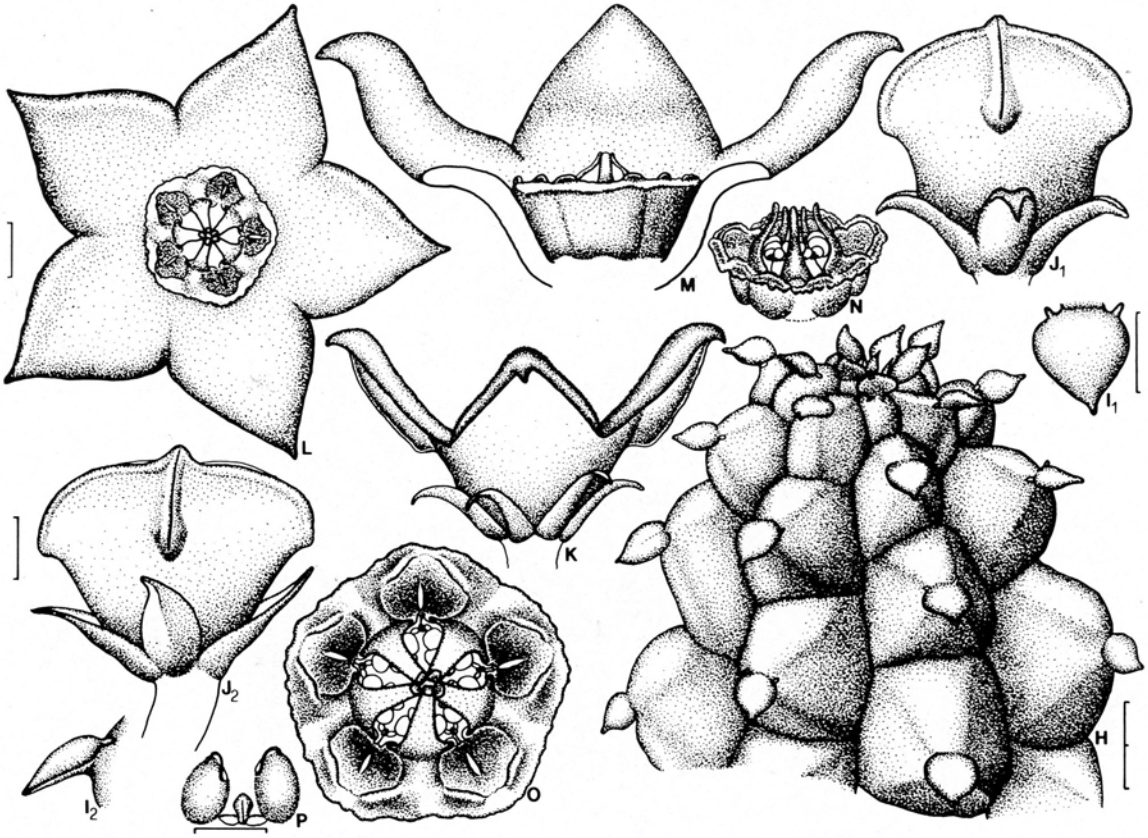


Fig. 8. **Echidnopsis scutellata** subsp. **dhofarensis** Bruyns. H, apex of stem (scale 2mm); $I_1$, face view of leaf (scale 1mm, as for $I_2$); $I_2$, side view of leaf; J, bud (scale 1mm, as at $J_2$); K, side view of corolla (not completely opened out); L, face view of corolla—very flat example (scale 1mm, as for K); M, dissected side view of corolla (scale of P = 1mm, as for N); N, oblique view of staminal column; O, face view of staminal column (scale of P = 0.5mm); P, pollinarium (scale 0.25mm). H, I drawn from *McLeish* 83/52; J from *McLeish* 85/19; K, L, M, O from *Miller* 2811; N, P from *Butler* s.n.

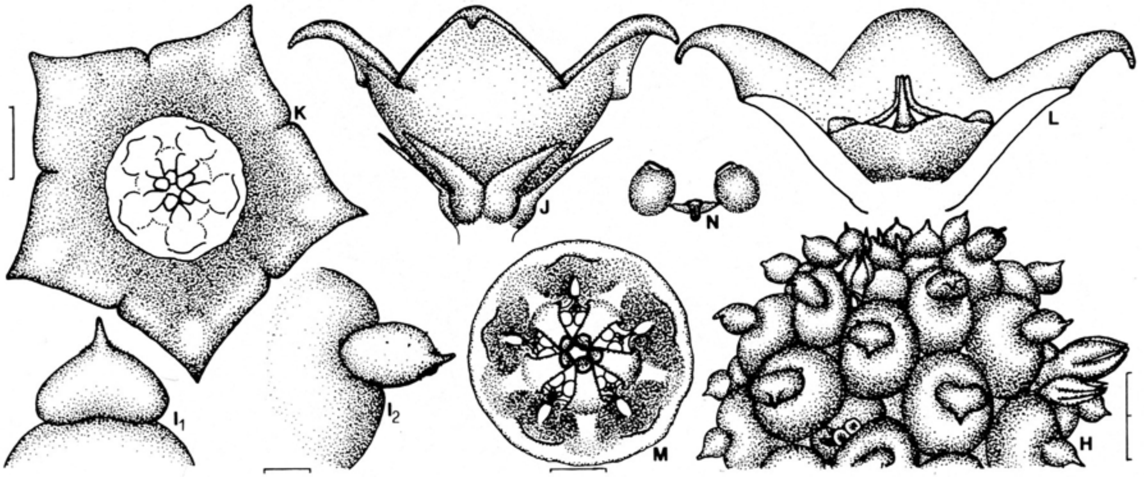


Fig. 9. **Echidnopsis scutellata** subsp. **australis** Bruyns. H, stem apex (scale 2mm); $I_1$, face view of leaf; $I_2$, side view of leaf (scale same for both, 0.5mm); J, side view of corolla; K, face view of corolla (scale 1mm, as for J, L); L, dissected side view of corolla; M, face view of staminal column (scale 0.5mm); N, pollinarium (scale of K = 0.25mm). H, I, L drawn from *Bally* 12565; J, K, N from *Lavranos & Bleck* 19527.

lacking the bowl-shaped, broad tube whose sides are some distance away from the staminal column. The staminal column is also less broad and lacks the dentate margin of subsp. *scutellata*. The flowers are larger than those of subsp. *australis* where the leaves are also finely papillose, a feature lacking in subsp. *dhofarensis*. It is easily separated from subsp. *planiflora* by the different stems, though florally it is similar, particularly to plants previously known as *E. chrysantha*.

Forms with red and with yellow coronas are sometimes found growing together, but there seems to be little variation in the pale yellow colour of the corolla.

6c. **E. scutellata** subsp. **australis** Bruyns **subsp. nov.;** *a subsp. planiflora floribus minoribus et foliis brevibus, latis, mox caducis differt; a subsp. scutellata tubo corollae ad columnam staminalem adpresso discedit. Holotypus*: Kenya, Gof Choba, Marsabit, *Bally* 12565 (K).

*Echidnopsis mariae* Lavranos in Cact. Succ. J. (US) 54: 215 (1982). Type: Kenya, Gof Choba crater, *Lavranos & Bleck* 19527 (neither holotype at E nor isotype at K deposited, enquiries to EA produced no answer and it is presumed no material deposited there either).

*Echidnopsis* sp. *'ethiopica'* Keller in Cact. Succ. J. (US) 43: 163 (illustr. only) (1971).

Description. *Stems* 8-11-angled, with thick, rapidly caducuous, sparsely papillose leaves less than twice as long as broad at base. *Corolla* 6-9mm diam., rotate to rotate-campanulate, pale yellow-brown, exterior pale green; *lobes* deltoid with reflexed tips and margins, sometimes bearing small, cylindrical hairs marginally. *Corona* pale yellow-brown tending to yellow in centre, pentagonal; *outer corona* slightly toothed. (Fig. 9)

This small, inconspicuous plant is known only from the vicinity of the Marsabit mountain and from a single collection (*Gilbert & Thulin* 1635) from the Mandera district. Despite many visits of collectors, the northern parts of Kenya are not botanically well-known and it is quite likely that this subspecies is less rare than these records indicate. As related by Lavranos (l.c.) it was first discovered by Bally in 1971 but remained undescribed until 1982.

The photograph in Lavranos (l.c.) shows two flowers with remarkably flat corolla and it is hard to distinguish this flower, except by its smaller size, from those of subsp. *planiflora*. Mostly, however, the corolla seems to be more campanulate than this (as in Keller, l.c.). From subsp. *scutellata* it is separated by the lack of the broad, bowl-shaped corolla-tube (once again having the sides of the tube adpressed to the corona) and in this it is very similar to subsp. *dhofarensis* from which it differs in the smaller flower with (usually) rather campanulate shape and the slightly papillose leaves.

6d. **E. scutellata** subsp. **planiflora** (Bally) Bruyns **comb. et stat. nov.**

*E. planiflora* Bally in Cact. Succ. J. Gr. Brit. 18: 109 (1956); Cufodontis in Bull. Jard. Bot. Brux. 31, suppl.: 715 (1961). Type: Ethiopia, 2 miles north-west of Dire Dawa, 1943, *Mitford-Barberton* in *Bally* S105 (ZSS).

*Trichocaulon somaliense* Guillaumin in Bull. Hist. Nat. Paris, ser. 2, 10: 628 (1938) & in Cactus (Gent) 9: 19-20 (1939); White & Sloane in Cact. Succ. J. (US) 18: 121 (1946); Cufodontis l.c.: 715 (1961). Type: Djibouti, Gobad and Hanleh Mountains, 1938, *Aubert de la Rue* f.183 (P, photo of stems, incomplete drawing of flower only).

*Echidnopsis chrysantha* Lavranos in Cact. Succ. J. (US) 43: 65 (1971); Horwood in ibid. 49: 13 (1977); Dyer in Flow. Pl. Afr. 45: t. 1767B (1978). Type: Somalia, 4km north-west of Erigavo, 9 Dec. 1969, *Lavranos* 7325 (FI, holotype [not seen], K).

*Echidnopsis chrysantha* var. *filipes* Lavranos in Cact. Succ. J. (US) 46: 184 (1974). Type: Somalia, at top of Dabagha Pass between El Gal and Durbo, *Lavranos & Bavazzano* 8484 (FI, holotype [not seen], E).

Description. *Stems* 8-15-angled, bearing leaves at least 3 times longer than broad at base, persistent as dried-out spines, finely papillose. *Corolla* from brown to brownish suffused with yellow towards centre to bright yellow or green, 7-10mm diam., rotate to rotate-campanulate, exterior pale green, sometimes with raised (not thickened) area around corona (annulus); *lobes* deltoid to lanceolate-deltoid with reflexed tips and margins, often bearing cylindrical hairs near apex. *Corona* yellow to red-brown, *outer corona* pentagonal with smooth to slightly incised margins. (Figs. 10, 11)

Subsp. *planiflora* is found in Ethiopia, Somalia and Djibouti. In Ethiopia it is known from the Shoa and Harerge Regions and occurs from near Awash Station east of Addis Ababa to Borama on the Somalian border. In Somalia it is known from north-west of Borama right to near the north-east tip of the continent south of Alula. In Djibouti the only recent record is from a mountain

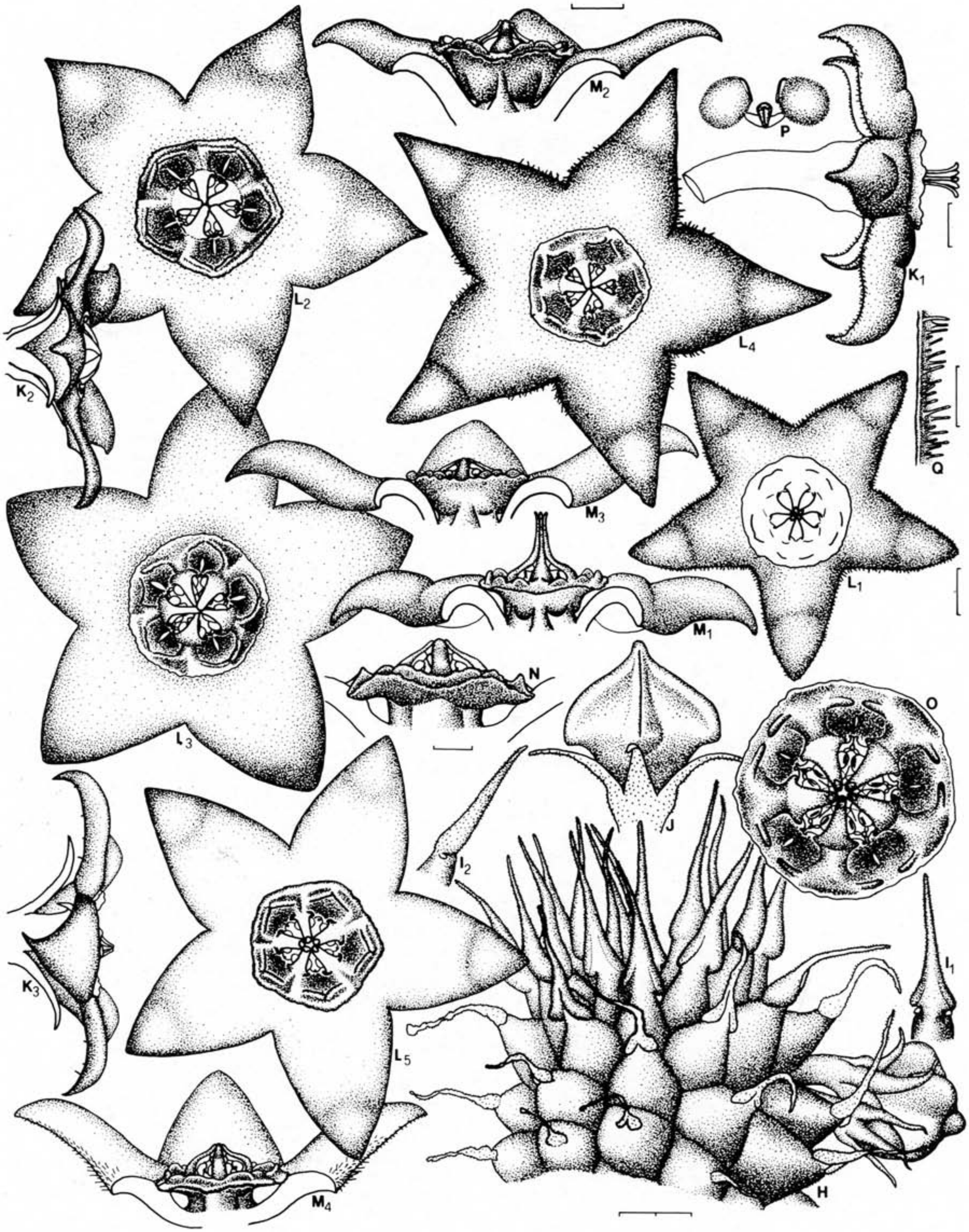


Fig. 10. **Echidnopsis scutellata** subsp. **planiflora** (Bally) Bruyns. H, stem apex (scale 2mm, as for K$_2$, K$_3$); I$_1$, rear view of leaf; I$_2$, side view of leaf (scale of Q = 1mm); J, bud; K, side view of corolla (scale K$_1$ 1mm); L, face view of corolla (scale L$_1$ 1mm, as for J, L$_3$, L$_4$, M$_3$); M, dissected side view of corolla (scale M$_2$ 1mm, as for L$_2$, L$_5$, M$_1$, M$_4$); N, side view of staminal column (scale 0.5mm); O, face view of staminal column (scale of L$_1$ = 0.5mm); P, pollinarium (scale of Q = 0.25mm); Q, hairs along margin of

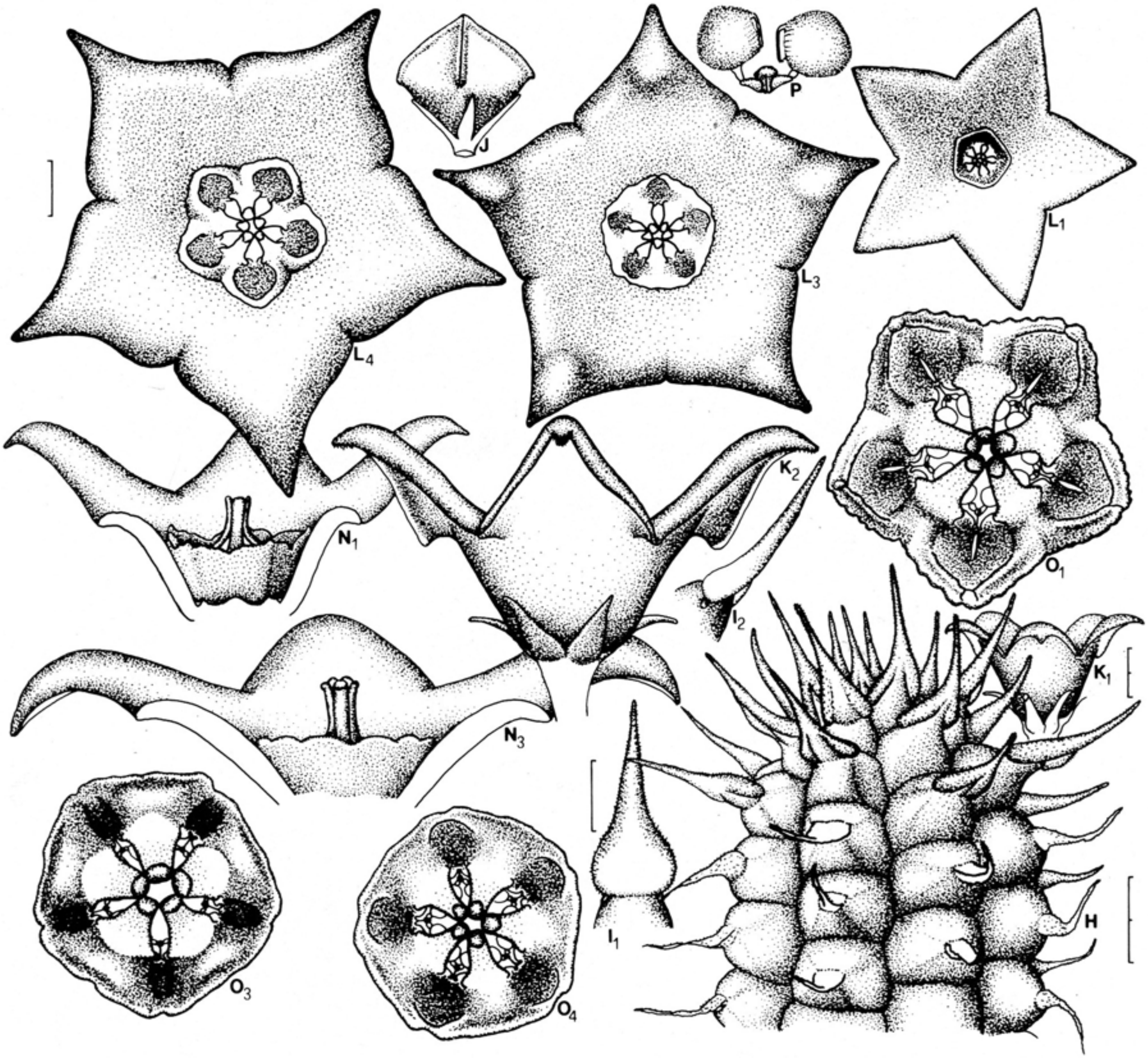


Fig. 11. **Echidnopsis scutellata** subsp. **planiflora** (Bally) Bruyns. Plants previously known as *E. chrysantha* with more campanulate, yellow flowers. H, stem apex (scale 2mm); $I_1$, face view of leaf (scale 1mm, as for $I_2$, $N_3$); $I_2$, side view of leaf; J, bud; K, side view of corolla ($K_1$ scale 2mm, as for J, $L_1$); L, face view of corolla (scale of $L_4$ 1mm, as for $L_3$, $N_1$, $K_2$); N, dissected view of corolla; O, face view of staminal column (scale of $L_4$ = 0.5mm); P, pollinarium (scale of $I_1$ = 0.25mm). H, J, $L_1$ drawn from *Horwood & Lavranos* 10364; $K_1$, $K_2$, $L_4$, $N_1$, $O_1$ from *Plowes* 4909; $L_3$, $O_4$ from *Plowes* 3842; I, $N_3$, $O_3$ from cultivated material ex hort. B. Makin, of unknown origin.

range just south of Lake Assal near the western end of the Gulf of Tajura.

The great variability in the shape of the corolla among Ethiopian and Somalian plants of subsp. *planiflora* has indicated that *E. chrysantha* differs from it only in having slightly more campanulate, bright yellow flowers. However, the flowers of this taxon are themselves very variable in the depth of the corolla-tube and some specimens referable to it have a red exterior to the corolla and greenish-yellow interior (*Plowes* 4909, for example) so that neither of these characters is diagnostic. *E. chrysantha* was described as having 8-angled stems as well, but in fact they vary from 8 to 12 and in *'E. planiflora'* anything from 10 to 16 angles is possible. This is also, therefore, a character of no real assistance.

The flowers of subsp. *planiflora* are particularly variable in shape and colour. Mitford-Barberton's original plants had brownish flowers with the corolla-lobes only slightly reflexed and more or less deltoid in shape. These were collected in Ethiopia around Dire Dawa in Harerge Region and are, according to Gilbert (pers. comm., 1985) typical of plants from this area. Closer to the Somalian border some campanulate-flowered plants are known (*Plowes* 4909) but within Somalia both the campanulate forms with broad corolla-lobes and ones with much narrower and more strongly recurved lobes exist. It would appear, therefore, that this taxon diverges florally in two distinct directions—one towards a much reduced flower with small, pale-coloured corolla with narrow lobes and another towards a deeper flower with

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corolla-lobes (scale 0.5mm). H, I, J, $K_1$, $L_1$, $M_1$, O, Q drawn from *Horwood* 10342; $K_2$ from *Plowes* 4262; $K_3$, $L_3$ from *Robertson* 1367; $L_2$, $M_2$, P from *Gilbert & Vollesen* 7362; $L_4$, $M_3$ from *Plowes* 5054; $L_5$, $M_4$, N from *Newton* 13178.

larger lobes and a bright yellow colour. A further extremely peculiar form is that found in Djibouti. Here the corolla-lobes are very much more rounded in outline though still quite long and the corona is remarkably shallow with a large supporting stipe, bearing a strong resemblance to that of *Rhytidocaulon paradoxum*. As can be seen in the illustrations, the corona varies somewhat in its depth and the stipe in its prominence over the range of the taxon and these features do not seem to warrant taxonomic recognition.

Bally's *E. planiflora* was clearly illustrated when originally published and there is no problem recognising it. However, Guillaumin's *Trichocaulon somaliense* is more of a problem. The pictures of the stems strongly suggest subsp. *planiflora* and the sketch of the corona at Paris suggests the Somalian form of subsp. *planiflora* with narrow, strongly recurved corolla-lobes which is borne out by a number of other features of the description (pilose margins to corolla-lobes, corolla with prominent annulus etc.) although the colour of the corolla does not correspond well to these, but is more reminiscent of that of Bally's original *'planiflora'*.

7. **E. watsonii** Bally in Candollea 18: 343 (1962) & in Cact. Succ. J. Gr. Brit. 18: 108 (1956) in clavi; in ibid. 26: 86 (1964); Cufodontis in Bull. Jard. Bot. Brux. 31, suppl.: 715 (1961). Type: Somalia, 8 miles south-east of Borama, 1600m, 6 Oct. 1954, *Bally & J. M. Watson* B9997 (K).

*Echidnopsis radians* Bleck in Cact. Succ. J. (US) 49: 263 (1977). Type: Kenya near Barsaloi (not Baragoi, Powys, pers. comm., 1986), *Powys* in *Lavranos* 12554 (MO holotype and isotype at E not found, no reply to enquiries from EA).

*E. adamsonii* Bally nom. nud. in Cact. Succ. J. Gr. Brit. 18: 108

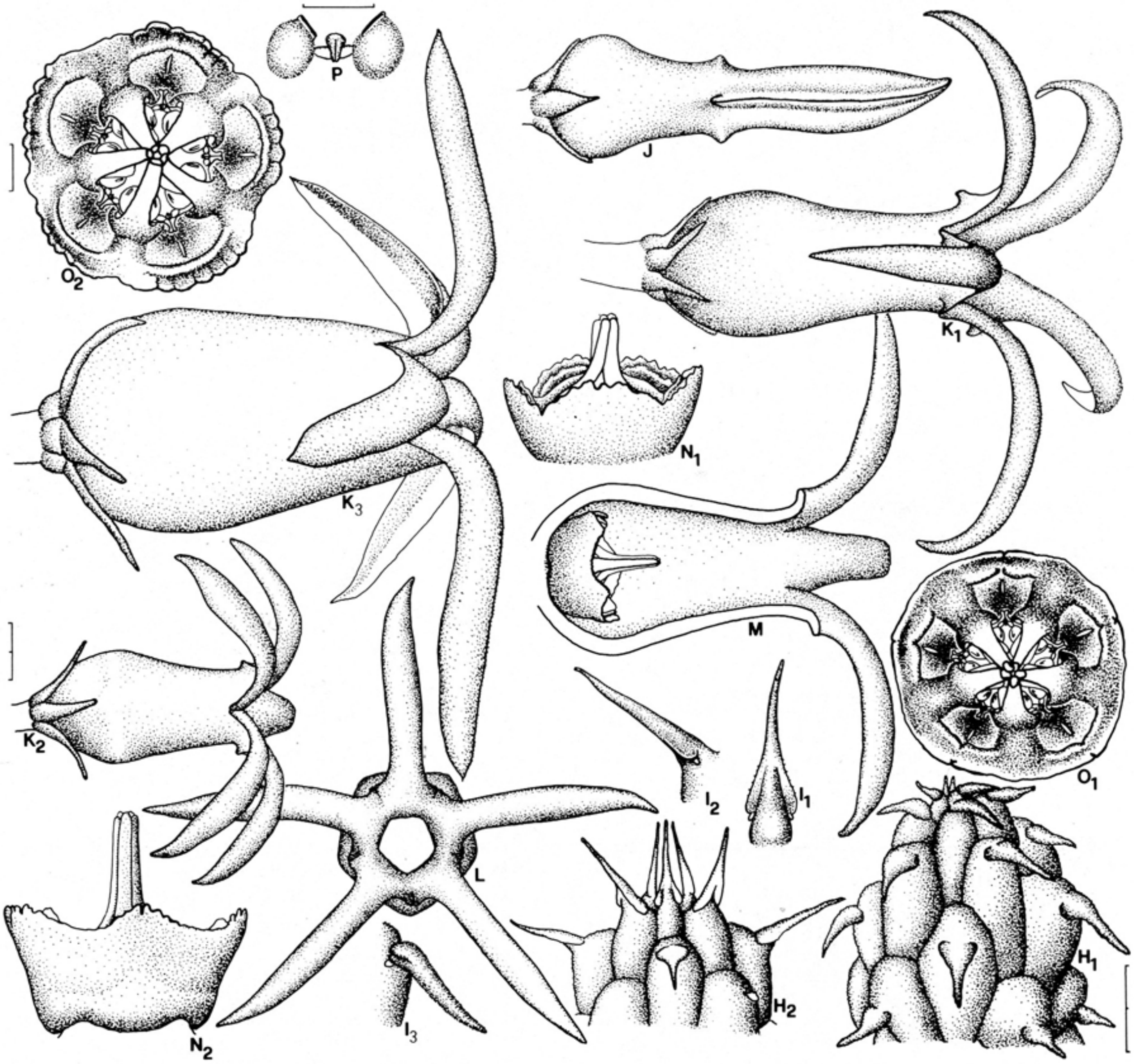


Fig. 12. **Echidnopsis watsonii** Bally. Typical form. H, stem apex (scale 2mm at $H_1$ for both, as for J, $K_1$, $K_2$, $K_3$, M, L); $I_1$, rear view of leaf; $I_2$, $I_3$ side views of leaf (all with scale of P = 1mm); J, bud; K, side view of corolla; L, face view of corolla; M, dissected side view of corolla; N, side view of staminal column (scale $N_1$ that of P = 1mm); O, face view of corolla (scale at $O_2$ 0.5mm for both, as for $N_2$); P, pollinarium (scale 0.25mm). $H_1$, $I_3$, $K_3$, $N_1$, $O_2$ drawn from *Bally* B9997; $H_2$, $I_1$, $I_2$, $K_1$, L from *Lavranos* 10421; remainder from cultivated material ex hort. D. T. Cole.

(1956); in clavi & 'sp. nov.' in J. E. Afr. Nat. Hist. Soc. 16: fig. 30, 164 (1942).

*E. modesta* Bally nom. nud. l.c.: 108 (1956); in clavi & 'sp. nov.' l.c.: fig. 29, 164 (1942). Based on: Kenya, 30-40 miles west of Garissa, 330m, Jan. 1940, *A.T.A. Ritchie* in *Bally* S47 (no specimen located, drawings at K).

DESCRIPTION. *Stems* repent to prostrate-procumbent to procumbent, up to 200mm long, 8-12-angled, tubercles depressed to conical, 4-6-angled, leaves finely papillose, 0.8-2mm long, very thick, deltoid to subulate, becoming reflexed, rapidly caducuous, with stipular gland on either side. *Pedicel* up to 1mm long. *Sepals* up to 3mm long, lanceolate with ovate base. *Corolla* exterior glabrous, dark purplish-red, inner surface setulose, yellow to whitish; *tube* inverted pear-shaped to globose or very shortly cupular, 1.5-11mm long, 2-3mm broad at mouth; *lobes* 2-11mm long, spreading to spreading-reflexed, linear-subulate, margins strongly reflexed. *Corona* sessile or nearly sessile, 1.8-3mm wide,

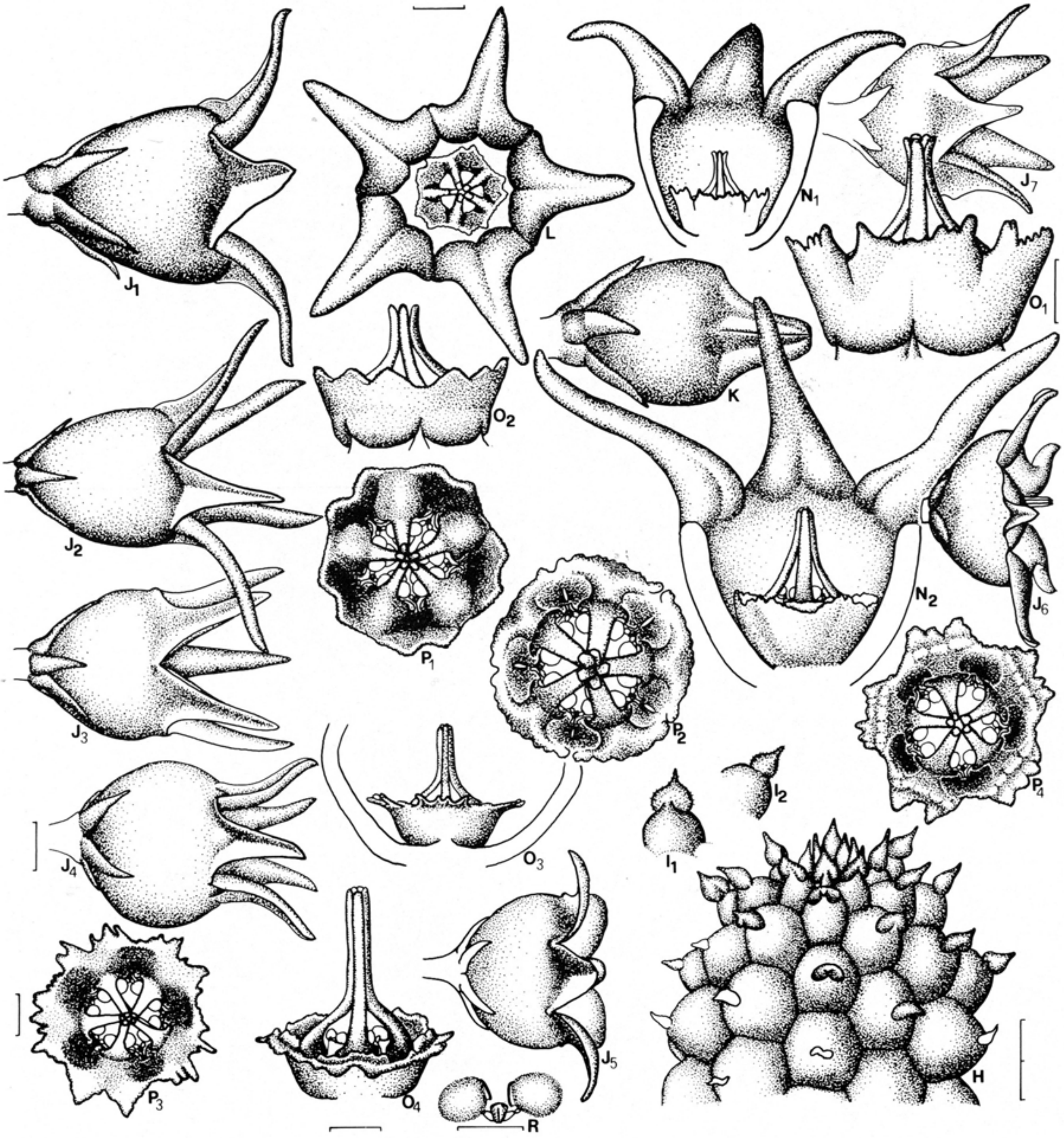


Fig. 13. **Echidnopsis watsonii** Bally. Form previously known as *E. radians*. H, stem apex (scale 2mm, as for I, $J_2$, $J_3$, $J_5$, $J_6$, $J_7$); $I_1$, rear view of leaf; $I_2$, side view of leaf; J, side view of corolla (scale of $J_4$, 1mm); K, bud; L, face view of corolla (scale 1mm, as for $J_1$, K, $N_1$); N, dissected side view of corolla (scale for $N_2$ as for R = 1mm); O, side view of staminal column (scale $O_1$ 0.5mm; $O_4$ 0.5mm, as for $O_2$, $P_1$, $P_2$, $P_4$); P, face view of staminal column (scale of $P_3$ 0.5mm, as for $O_3$); R, pollinarium (scale 0.25mm). H, I, $J_1$, K, L, $N_1$, $O_1$ drawn from cultivated material (ZSS) from Abbey Garden; $J_2$, $O_2$, $P_1$ from *Lavranos* 18616; $J_3$ from *Plowes* 6515b; $J_4$, $O_3$, $P_3$ from *Greenway & Kanuri* 12954; $J_5$, $J_7$, $O_4$, $P_4$, R from *Powys* 789; $J_6$ from *Lavranos & Jenkins* sub Kiel 931 (no specimen); $N_2$, $P_2$ from *Classen* in *Bally* S49A.

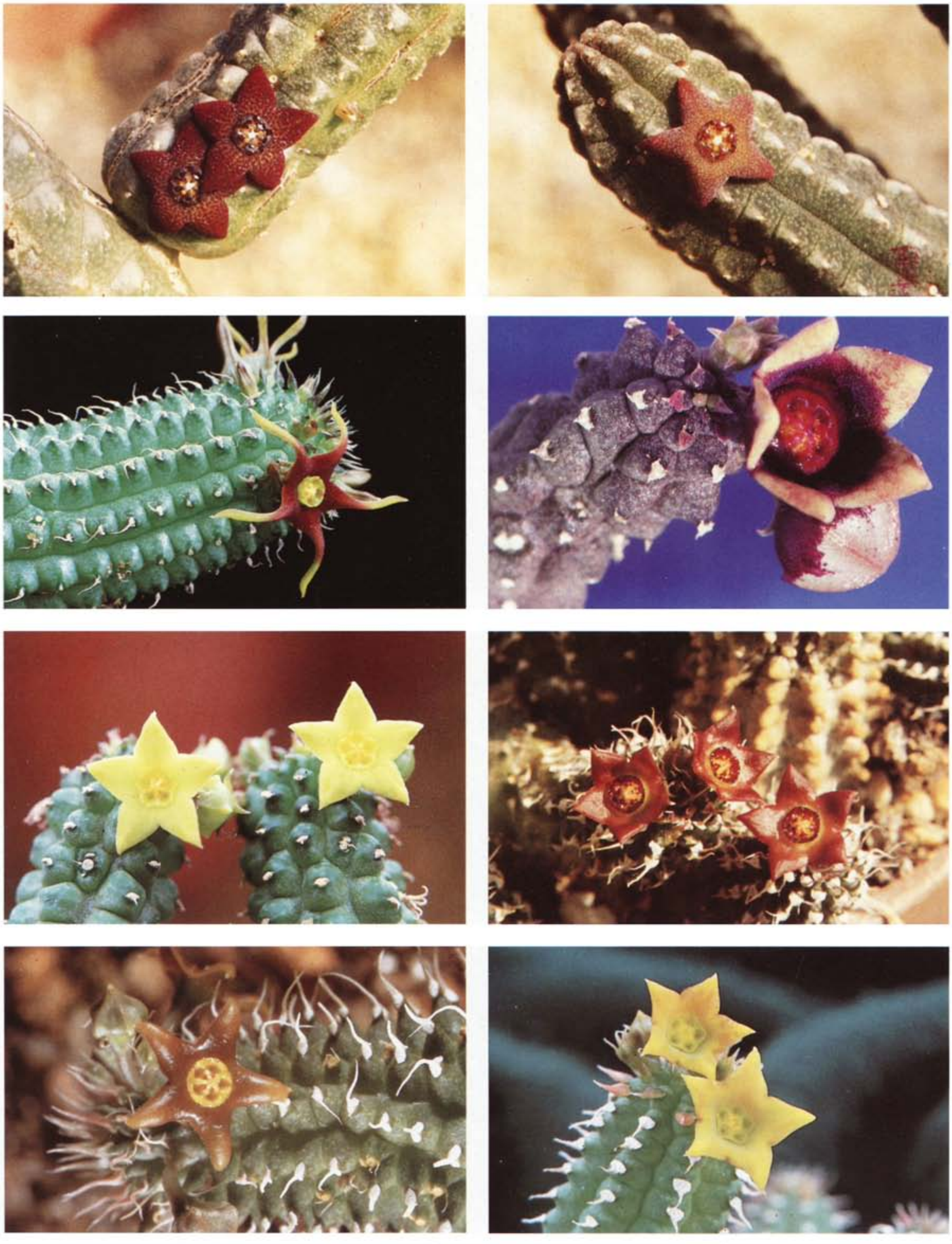


PLATE I. Top row: Left, *E. virchowii*, Somalia, *Gillett et al.* 23618; Right, *E. virchowii*, Somalia, *Bailes* 79. Second row: Left, *E. angustiloba*, Kenya, *Powys* 524 (photo: W. Bosma); Right, *E. scutellata* subsp. *scutellata*, North Yemen, *Noltee* 506 (photo: F. Noltee). Third row: Left, *E. scutellata* subsp. *dhofarensis*, Oman, *Butler* s.n.; Right, *E. scutellata* subsp. *planiflora*, Ethiopia, *Gilbert & Vollesen* 7362. Bottom row, Left, *E. scutellata* subsp. *planiflora*, Somalia, *Horwood* 10342 (photo: D. Supthut); Right, *E. scutellata* subsp. *planiflora*, Ethiopia, *Plowes* 4909.

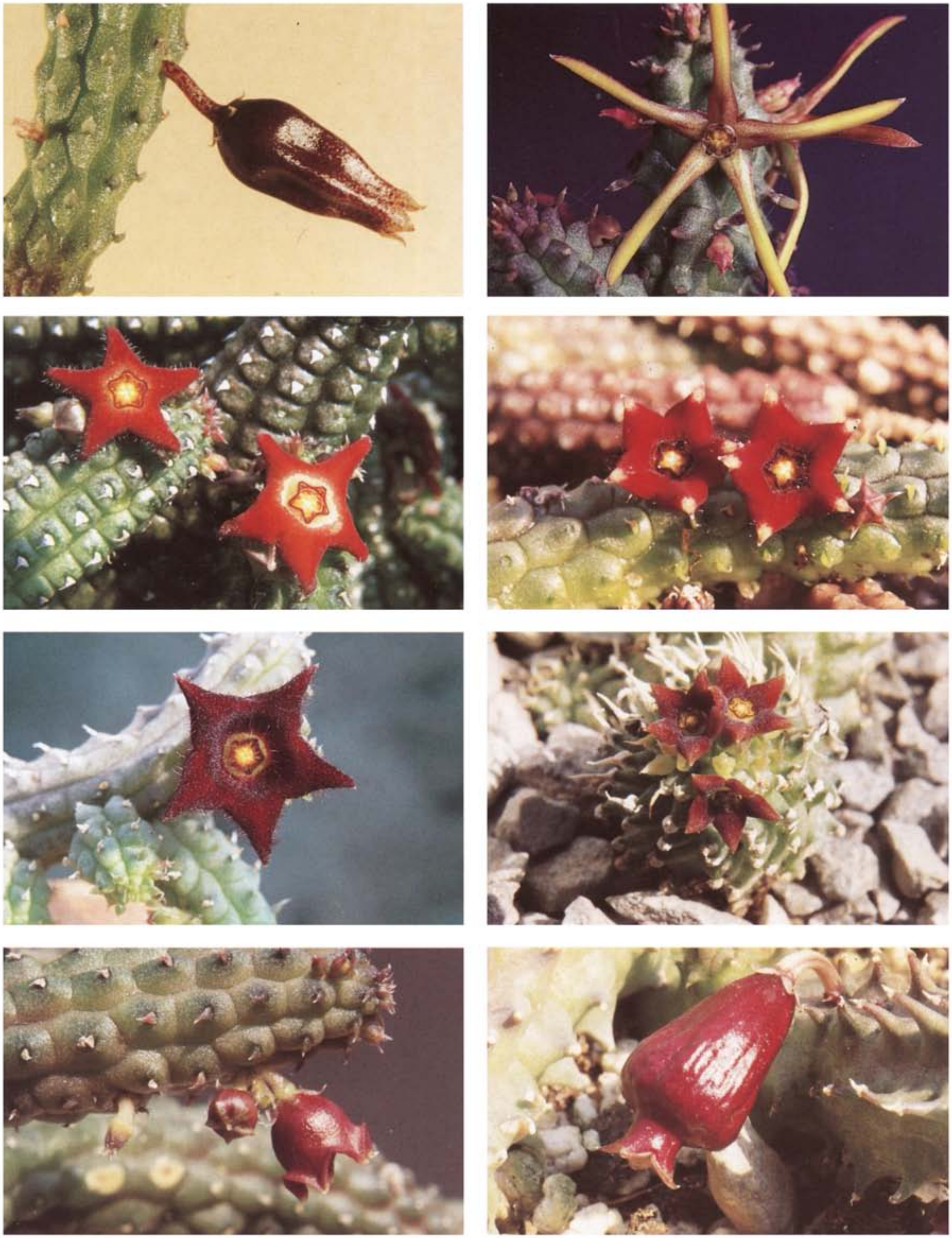


PLATE II. Top row: Left, *E. squamulata*, North Yemen, *Potter* s.n.; Right, *E. montana*, Ethiopia, *Noltee* s.n. (photo: F. Noltee). Second row: Left, *E. sharpei* subsp. *sharpei*, Ethiopia, *Gilbert & Vollesen* s.n.; Right, *E. sharpei* subsp. *repens*, Kenya, ex hort. K. Third row: Left, *E. sharpei* subsp. *ciliata*, Somalia, *Bailes* 134; Right, *E. bihendulensis*, Somalia, *Bailes* 169. Bottom row: Left, *E. archeri*, Kenya, *Classen* s.n.; Right, *E. ballyi*, Somalia, *Bailes* 167.

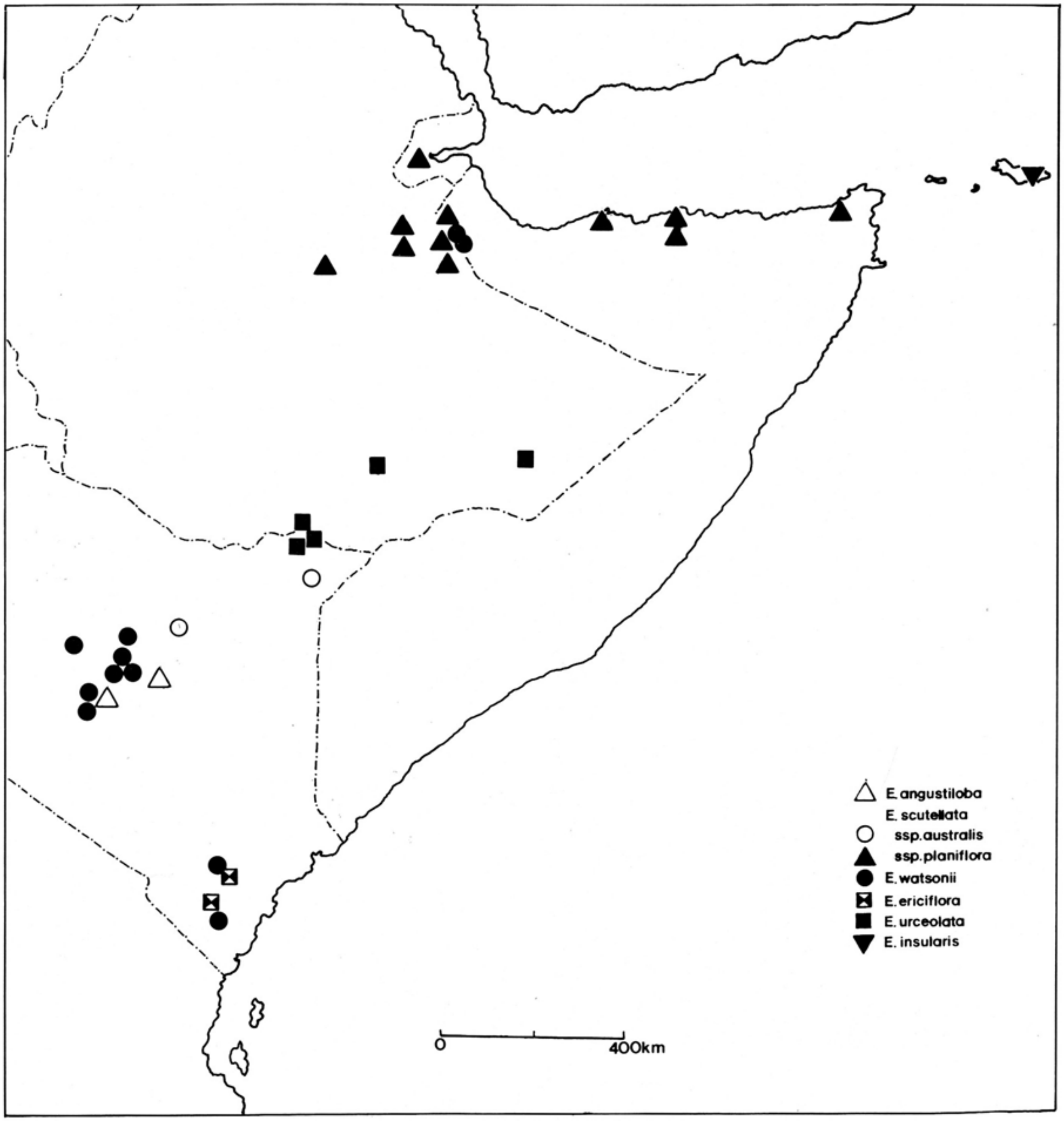
round or obscurely pentagonal, dark purple-red to dark yellow; *outer lobes* forming cup, obscurely divided near middle and often flattened on upper surface, often with margin much toothed; *inner lobes* with broad base becoming linear, dorsiventrally flattened, incumbent on anthers, meeting in centre and rising up, connivent, above column. (Figs. 12, 13)

This species has a wide distribution from the northern part of Somalia to the Tsavo Park north of Mt Kilimanjaro. In general there is a steady decrease in the length of the corolla-tube and corolla-lobes as one progresses southwards, from the largest in the Somalian plants to the shortest along the Galana River and scattered further north in Kenya.

Plants corresponding to Bally's *E. watsonii* (Fig. 12) are known from a small area in northern Somalia in the mountains north-west of Hargeisa. However, even among these few collections considerable variation in the corolla is found. A comparison of Fig. 12 $K_1$ and $K_2$, which are drawn to the same scale, demonstrates the variation in the size of the flower without a change in the proportion of the length of corolla-tube to corolla-lobe. However, Fig. 7 of Boele (1987), based on material collected in the same area shows that sometimes flowers with quite different proportions of corolla-lobe to corolla-tube may occur. These flowers are inseparable from those of *'E. radians'* from Kenya.

Plants which could be accommodated in *'E. radians'* (Fig. 13) are quite widely distributed in Kenya from the area to the south of Lake Turkana, to west of Garissa and to the area just north of Kilimanjaro where two collections are now known.

Over this range the flowers are very variable. The original collection by Powys has a globose corolla-tube with spreading



Map 3. Distribution of section 3 in north-east Africa.

lobes more or less as long as the tube. There is some variation amongst these plants but even in this area the very small-flowered form (corresponding to Bally's *E. modesta*) is found. This is what occurs near Garissa and the same small-flowered plant was collected in November 1985 along the Galana River by Mrs. P. Powys. The position is much complicated by the collection *Greenway & Kanuri* 12954 from the Tsavo Park, which has the corolla very much like those of typical *'radians'* from around Lake Turkana while the corona is more typical of the other southern collections. Most of these southern collections have long, repent stems which are, as Bally commented (1942, l.c.), inseparable from those of *E. sharpei*.

It is fortunate, through Bally's carefully kept card index and numerous sketches, that it has been possible to establish what taxa he intended to describe as *E. adamsonii* and *E. modesta* which were only mentioned in his key (Bally, 1956). His *E. adamsonii* is the same as *'E. radians'* and *E. modesta* is the small-flowered plant with rather narrower, flatter column with more dissected outer corona-lobes and longer inner corona-lobes (as in *Powys* 789). The collection of Greenway and Kanuri is intermediate between *'adamsonii'* and *'modesta'* (having the corolla of the former and the corona of the latter) and is the reason for the abandonment of the latter name. It is noteworthy that the same flattening and increased frilliness of the outer corona occurs in the taxon Bally intended to call *E. jacksonii* which differs from *E. urceolata* otherwise only in having a much shorter flower (and is here included under that species) so that there is possibly some correlation between these characters.

Bleck (l.c.) compared her species with *E. watsonii* but the most important difference—lying in the ratio of the lengths of the corolla-lobes to corolla-tube—falls away when variation among Somalian material is considered.

*E. watsonii* is an extremely attractive plant with the bright purple-red exterior to the corolla and long narrow, yellow corolla-lobes contrasting against this red colour. The stems of Somalian collections are unusual for those bearing long leaves in that they are not procumbent but rather more prostrate, becoming procumbent when of considerable length. They do not, therefore, form the dense clusters that are typical of many Somalian plants. It is noteworthy also that the leaves are not persistent for long and therefore this taxon represents an intermediate between the creeping ones from the southern regions and the procumbent, cluster-forming ones from Somalia.

8. **E. ericiflora** Lavranos in Nat. Cact. Succ. J. 27: 70 (1972). Type: Kenya, 42km from Voi on road to Mombasa, 15 Jan. 1972, *Lavranos* 9305 (EA, holotype [not seen], PRE).

DESCRIPTION. *Stems* repent, rooting throughout their length, 6-8-angled, 4-8mm thick, finely papillose, up to 200mm long, covered with hexagonal tubercles each topped with an ovate-deltoid, rapidly caducuous, finely papillose leaf. *Pedicel* 1-1.5mm long. *Sepals* ovate-acute, 1.5mm long. *Corolla* urceolate, 5-8mm long, exterior wine-red, glabrous, interior reddish to dark red in base of tube, setulose; *tube* 4-4.5mm diam. at maximum narrowing to less than 2mm at mouth (internal measurements); *lobes* yellowish at tips reddening towards base, deltoid, 1-2mm long, erect to slightly spreading when fully open. *Corona* pentagonal, 2.8-3mm diam.; *outer lobes* with slight division towards middle, otherwise entire, enclosing nectarial orifice, with almost black margin, remainder yellowish red-black and yellow around base; *inner lobes* with broad yellowish base, limb dorsiventrally flattened, purple-red, incumbent on anthers, meeting in and rising up above centre, with papillose apices. (Fig. 14)

*Echidnopsis ericiflora* is known only from the south-east corner of Kenya to the east of Mt Kilimanjaro where it has been collected a few times at the type locality on the Voi-Mombasa road and also, in 1985, along the Galana River in the Lali Hills by Mrs. P. Powys. It always appears to grow in deep, red, sandy soil, well-

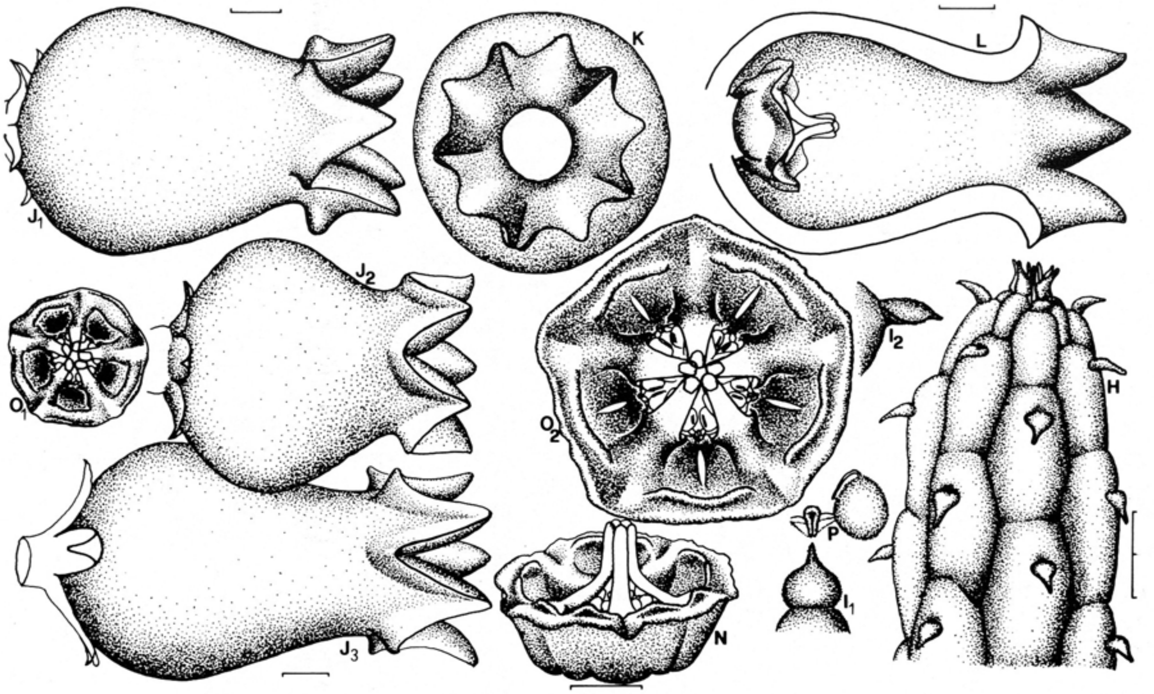


Fig. 14. **Echidnopsis ericiflora** Lavranos. H, stem apex (scale 2mm); $I_1$, face view of leaf; $I_2$, side view of leaf; J, side view of corolla (scales all 1mm, $J_2$ as for $J_3$); K, face view of corolla (scale as for $J_1$); L, dissected side view of corolla (scale 1mm); N, oblique view of staminal column (scale 1mm); O, face view of staminal column (scale of $O_1$ as for L; for $O_2$, scale of L = 0.5mm); P, part of pollinarium (scale of N = 0.25mm). H, $J_1$, K, $O_2$ drawn from cultivated material (ZSS); I, $J_3$, L, $O_1$ from *Lavranos* 9305; $J_2$, N from *Plowes* 3962.

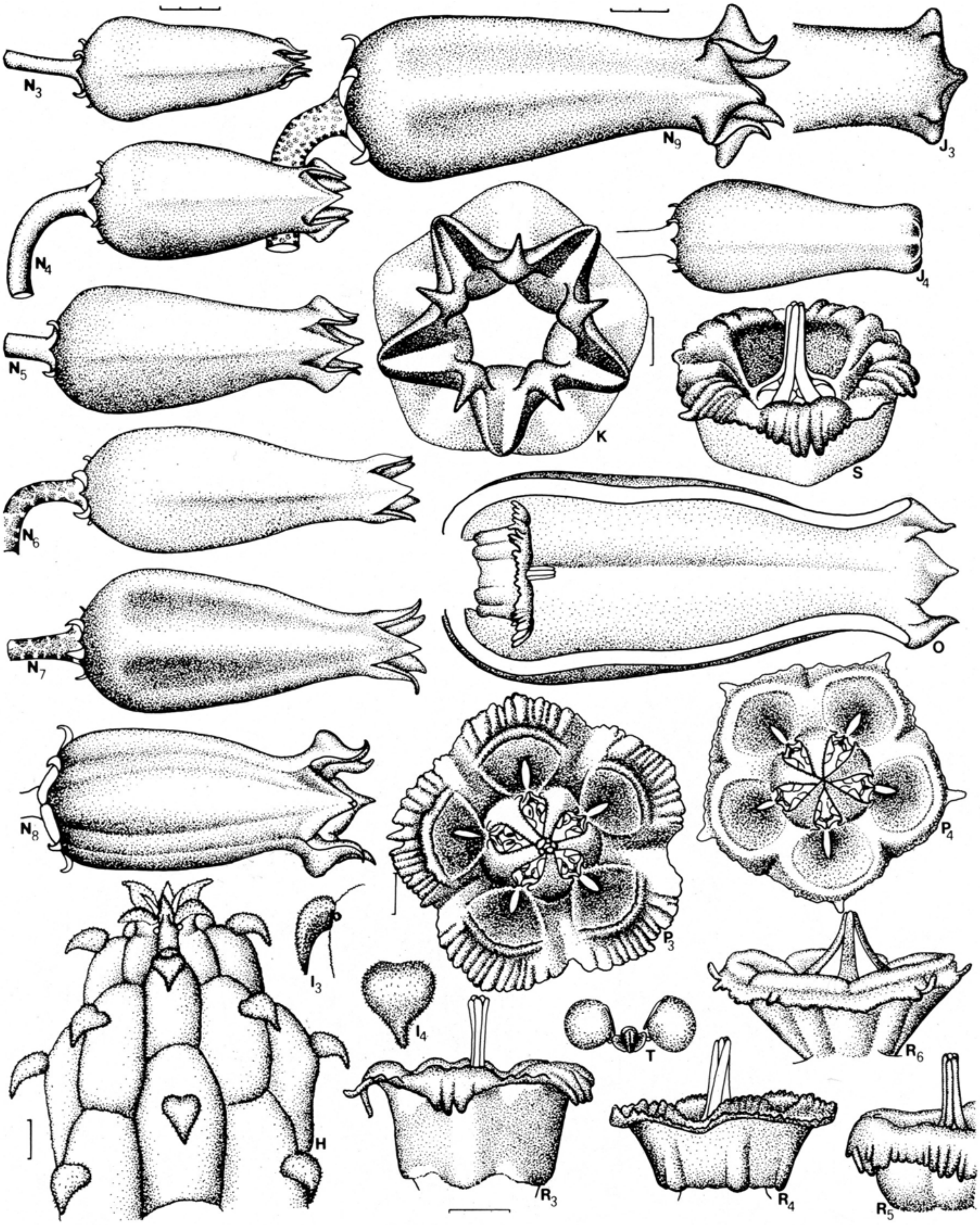


Fig. 15. **Echidnopsis squamulata** (Decne) Bally. H, stem apex (scale 1mm, as for $J_3$); $I_3$, side view of leaf; $I_4$, face view of leaf; J, bud ($J_3$ of a flower as in $N_9$); K, face view of flower (scale 1mm); N, side view of corolla (scale $N_3$-$N_8$, 3mm as for $J_4$; $N_9$, 2mm, as for O); O, dissected side view of corolla; P, face view of staminal column (scale 0.5mm); R, side view of staminal column (scale 1mm at $R_3$, as for I, S); S, oblique view of staminal column; T, pollinarium (scale of $R_3$ = 0.25mm). H, I, $R_3$, S, T drawn from *Potter* s.n.; $J_3$ from *Lavranos* 13101; $J_4$, $N_3$-$N_7$, O from *Miller & Long* 3508; K, $N_9$ from *Lavranos* 1869; $N_8$ from specimen ex hort. J. Swart, Netherlands, origin unknown; $P_3$, $R_4$ from *Barad* 10290; $R_6$, $P_4$ from *Lavranos* 1822; $R_5$ from *Wood* 2593.

hidden under bushes, not being one of those species found in rocky habitats.

This species is very closely allied to *E. squamulata* and *E. urceolata*. It differs from the latter very obviously in the stems and from both it can be separated readily by the circular and not pentagonal cross-section of the flower. It can also be distinguished from these by its rather fleshier flower which has especially thick lobes. Vegetatively it is more or less indistinguishable from *E. squamulata,* having identical leaves and only slightly thinner stems. Apart from the above-mentioned differences the pedicel is also much shorter than in this species.

*E. ericiflora,* with its repent stem, short pedicel and shorter corolla is the most unspecialised of the closely-related group to which it belongs. All three species are of relatively restricted distribution.

9. **E. squamulata** (Decne) Bally in Kakt. and. Sukk. 14: 173 (1963) & in Cact. Succ. J. Gr. Brit. 26: 89 (1964); Lavranos in J. S. Afr. Bot. 30: 15-18 (1964).

*Ceropegia squamulata* Decne in Ann. Sc. Nat. ser. 2, 9: 263, t. 9B (1838) & in DC. Prodr. 8: 644 (1844); Deflers in Voy. Yemen: 11, 168 (1889) & in Mem. Inst. Egypt. 3: 265 (1896); Schwartz in Mitt. Inst. Allg. Bot. Hamb. 10: 192 (1939); Huber in Mem. Soc. Brot. 12: 177 (1957). Type: North Yemen, near Ta'izz, Wadi Sina, 1837, *Botta* (P).

Description. *Stems* repent, rooting along most of length, 6-8(-9)-angled, 5-8mm diam., up to 450mm long, green to brownish-green, finely papillose, divided into low, hexagonal tubercles each bearing an ovate-deltoid, finely papillose, rapidly caducuous, reflexed leaf, with stipular gland on either side. *Pedicel* red-brown spotted, 5-8mm long, about 1mm thick. *Sepals* lanceolate-acute, up to 3mm long, glabrous. *Corolla* urceolate, pentagonal in cross-section, 11-18mm long, 5-8mm broad at widest, 2-3mm broad at mouth (exterior measurements); *tube* exterior red-brown sometimes blotched with pale yellow towards mouth and finely papillate there, otherwise shiny, glabrous, interior red-brown to dark purple or yellow speckled with red, velvety with fine, sharp-pointed papillae (setulose); *lobes* red-brown, speckled with pale yellow outside, red-brown to pale yellow inside, deltoid, erect with abruptly recurved apex, 1.5-2.5mm long, 1.25-2.5mm broad at base. *Corona* pentagonal, 3.5-5mm diam.; *outer lobes* red with yellow patches to red-brown, margins variously toothed, often folded back against column, upper surface wrinkled, covered with nectar, forming entire enclosure around nectarial orifices; *inner lobes* pinkish-red, with broad bases after which dorsiventrally flattened, incumbent on anthers and then rising up above them, connivent. (Fig. 15)

Paul-Emile Botta discovered this plant in the Wadi Sina just below the Jebel Sabir south of Ta'izz in North Yemen. It has since been found to occur from the Jebel Ra's, north-east of Hays in the west to around Ta'izz, where it appears to be plentiful, and is known too from further south in North Yemen, as well as from the Amiri Highlands and the Al Awadhil area north of Lawdar, both in South Yemen. The distribution stretches over a total distance of some 200km.

Plants of *E. squamulata* often occur on the cool, north-facing aspect, where the trailing stems can reach a considerable length among grasses and low bushes (G. S. Barad, pers. comm., 1986). R. G. Potter (pers. comm., 1987), who observed a colony of this species north of Ta'izz over a period of more than a year, found them growing on an inaccessible, much fissured basalt rockface above a watercourse. Plants attached themselves into small pockets of silt and humus washed down from the hillside above, growing 'as if stuck onto the rockface' with stems reaching a length of more than 37cm. The annual rainfall at this locality averaged 1155mm in the years 1970-1973 and the soil in the deeper crevices on the cliff where the plants grew remained moist for most of the year.

The stems of *E. squamulata* are clearly papillose with a shiny epidermis between the papillae and although they are not rugose as in *Rhytidocaulon,* the surface bears a strong resemblance to that in this genus. Florally this species points towards *E. ballyi,* although the corolla is of a simpler construction. The much longer pedicel than either of its closest relatives suggests a tendency towards an arrangement where the mouth of the corolla becomes buried in the soil although this has not been observed and most flowers are held roughly horizontally.

*Echidnopsis squamulata* differs very clearly in its vegetative parts from *E. urceolata*. Florally they are separated easily by the short pedicel (holding the flower obliquely erect) and the more cylindrical corona in the latter. The respective corollas also have slightly different colours but this is not significant, particularly as *E. squamulata* is variable in this respect—the exterior of the mouth of the corolla may vary from red-brown to yellowish. The corolla of *E. squamulata* is extremely variable in its length and the top left hand sketches in Fig. 15, all drawn to the same scale, come from one plant. There is also considerable variation in the staminal corona, particularly in the shape of the outer corona-lobes, the degree to which their upper surface is ridged and the extent to which their extremities are folded over. In some flowers these edges are folded back against the column so that from above the corona has a rounded shape, while normally it is pentagonal with a dentate margin. There is evidence that the corolla-lobes in the North Yemen plants are less strongly recurved at the tips, with thinner fabric and with smaller, outward-pointing folds between adjacent lobes than those from South Yemen. The paucity of material from South Yemen makes it impossible to judge the constancy of these differences.

10. **E. urceolata** Bally in Candollea 18: 342 (1962) & in Cact. Succ. J. Gr. Brit. 26: 86-88 (1964). Type: Kenya, Malka Murri, 600-700m, June 1951, *Williams* in *Bally* B8008 (ZSS).

*E. urceolaris* Bally nom. nud. in Cact. Succ. J. Gr. Brit. 18: 108 (1956).

*E. jacksonii* Bally nom. nud. l.c.: 108 (1956) in clavi. Based on: Ethiopia, El Carre, 920m, April 1943, *T. H. E. Jackson* in *Bally* S112 (K).

Description. *Stems* procumbent-erect, up to 90mm long, 25mm diam., (12-)18-20-angled, covered densely with conical tubercles each tipped with a spreading, lanceolate leaf 3-3.5mm long, rapidly drying off and remaining persistent as a sharp spine. *Pedicel* 1-1.5mm long. *Sepals* lanceolate 1.5-3mm long, 0.7-1.5mm wide at base, tips often recurved. *Corolla* (4.5-)10-18mm long, urceolate; *tube* 4-7mm diam. near base, constricted at mouth to 3-4mm, exterior pale yellow, becoming purple towards base, interior dark purple-red, deeply pentagonal in cross-section; *lobes* deltoid, margins and apex slightly recurved, 1.2-3mm long, pale green-yellowish on inner and outer surface. *Corona* shortly cylindrical, pentagonal, sometimes shortly stipitate, 2.5-3mm wide, 1-2mm high; *outer lobes* widely cupular with dentate, usually erect margin, usually completely enclosing nectarial orifice; *inner lobes* with broad base, then narrow, dorsiventrally flattened, incumbent on anthers and then rising up, connivent, above column. (Figs. 16, 17)

*Echidnopsis urceolata* is, according to M. G. Gilbert, not uncommon in the Mandera district of the north-east corner of Kenya where it has been collected a number of times since it was discovered by J. G. Williams, an ornithologist from Nairobi. It is also known from Ethiopia where it has been collected once in the Ogaden area of Harerge Region (*Gilbert* 2105).

The flowers of *E. urceolata* are extremely variable in size and shape. Even without the inclusion of *'E. jacksonii',* the length of the corolla has been recorded from the 9mm that Bally (1964) gave to 18mm. Further substantial variation in the depth of the bowl formed by the outer corona has been included in the present concept of the species. On account of this variation Jackson's Ethiopian collection is included here. It is felt that further collecting will reveal that the size of the corolla in this plant is not unusual for *E. urceolata*. That the staminal corona of this collection is not considered sufficient on which to base a separate species is justified by the variation observed in Kenyan forms of *E. watsonii* where it also ranges from cupular to nearly flat with horizontal outer corona lobes, this variation being associated with a shortening of the corolla-tube, as in *E. urceolata*. This collection has not been included under *E. watsonii* as the fluting of

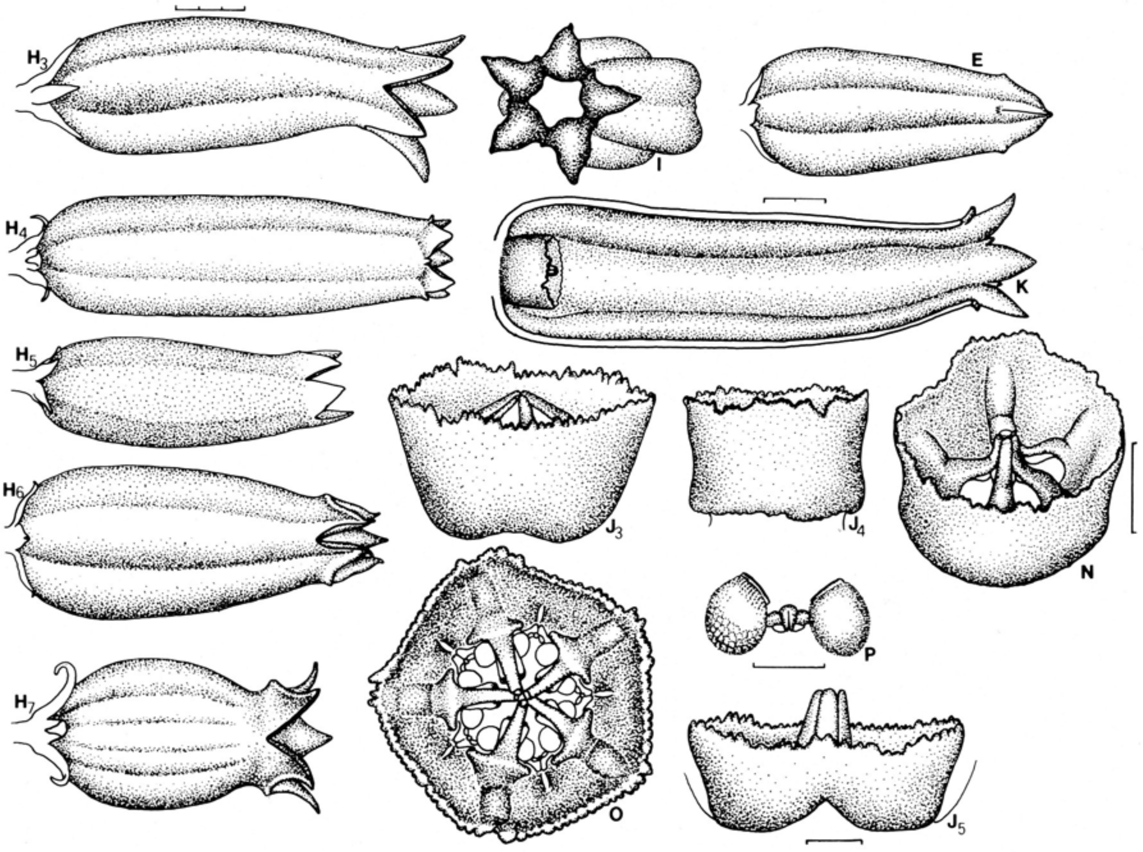


Fig. 16. **Echidnopsis urceolata** Bally. E, bud; H, side view of corolla (scale 3mm, as at $H_3$, as for E, I); I, face view of corolla; J, side view of staminal column (scale $J_4$ that of P = 1mm; $J_5$, 0.5mm as for O); K, dissected side view of corolla (scale 2mm); N, oblique view of staminal column (scale 1mm, as for $J_3$); O, face view of staminal column; P, pollinarium (scale 0.25mm). E, $H_3$, $H_6$, I, $J_3$, $J_5$, O, P drawn from *Lavranos & Newton* 12210; $H_4$, K, $J_4$, N from *Bally* s.n.; $H_5$ from *Bally & Radcliffe-Smith* 14956; $H_7$ from *Williams* in *Bally* B8008.

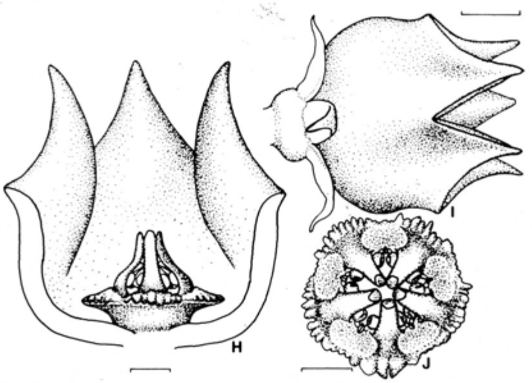


Fig. 17. **Echidnopsis urceolata** Bally. Form provisionally known as *'E. jacksonii'.* H, dissected side view of corolla (scale 0.5mm); I, side view of corolla (scale 1mm); J, face view of staminal column (scale 0.5mm). All drawn from *Jackson* in *Bally* S112.

the walls of the corolla-tube and the shape of the corolla-lobes are quite unlike that in *E. watsonii*.

There is also considerable variation in the colour of the corolla. Bally's illustration shows a flower nearly completely yellow on the exterior with only a narrow purple-red patch near the base. Plowes (1980) illustrated one where just the corolla-lobes are yellowish—the rest being shiny dark purple—and although I have not seen a flower as dark as in *E. squamulata,* this possibility cannot be excluded.

11. **E. insularis** Lavranos in Cact. Succ. J. (US) 42: 136 (1970). Type: Socotra, southern slopes of Hama de Roh, 7 Apr. 1967, *Radcliffe-Smith & Lavranos* 310 (K, holotype, no other specimens appear to exist).

DESCRIPTION. *Stems* procumbent, 20-60mm long, about 5mm diam., 6-angled, brown or brownish-green, finely papillose, each tubercle bearing a minute, triangular, rapidly caducuous leaf. *Pedicel* 2.5-3mm long, about 1mm diam. *Sepals* 1-1.5mm long, green, glabrous with reflexed tips. *Corolla* very fleshy, 9.5-11mm long, 4mm diam. at base, 3mm at mouth of tube, urceolate, outside greenish-yellow, glabrous; *tube* inside greenish-yellow with thin, longitudinal purple lines, 7-8mm long; *lobes* erect, deltoid-acute, 3mm long, 1.75mm broad at base. *Corona* yellow, deeply cupular, pentagonal, 3mm diam.; *outer lobes* forming deep, thick cup containing column, each lobe with deep incision in middle, teeth somewhat reflexed; *inner lobes* with broad, rectangular base then much narrowed into long, nearly cylindrical, subvertical limb touching anthers near base then ascending away from them towards centre but not meeting, much exceeding anthers in length. (Fig. 18)

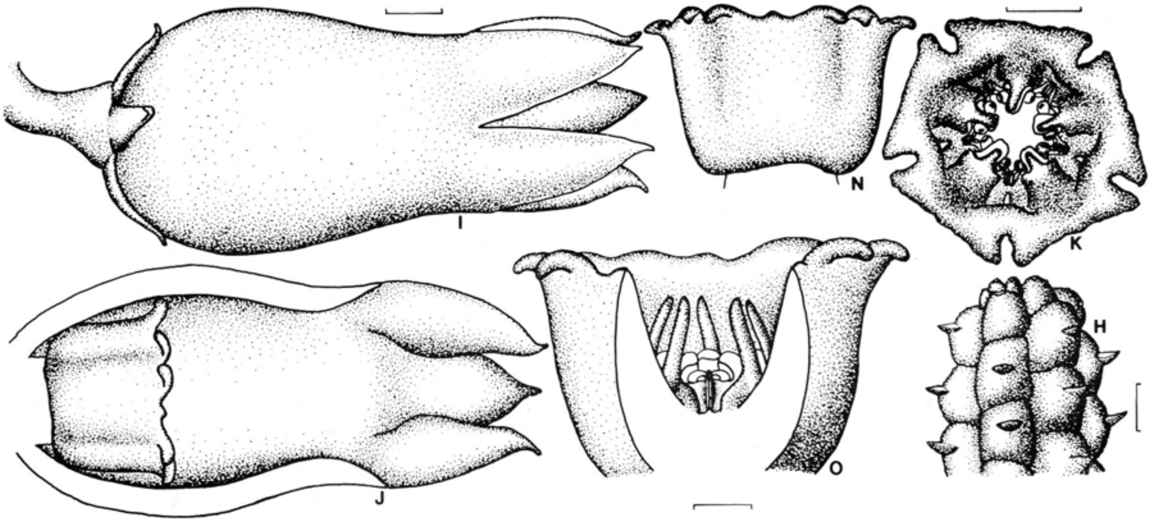


Fig. 18. **Echidnopsis insularis** Lavranos. H, apex of stem (scale 1mm); I, side view of corolla (scale 1mm, as for J); J, dissected side view of corolla; K, face view of staminal column (scale 1mm, as for N); N, side view of staminal column; O, side view of staminal column with part of outer corona removed (scale 0.5mm). All drawn from *Radcliffe-Smith & Lavranos* 310.

This species is known only from the single collection by Radcliffe-Smith and Lavranos of 1967. This collection is not the first record of an *Echidnopsis* from Socotra since one was collected there by Balfour, Cockburn and Scott in February–March 1880 (*Balfour* 617) and another was found in 1897 by Mr and Mrs Theodore Bent. However, none of this material ever flowered and though it was tentatively identified as *E. cereiformis* (Balfour, 1888, 1903), these probably all represented *E. insularis*. In fact Balfour (1888) doubted that their plant was *E. cereiformis,* saying that it was 'considerably more delicate' than this species.

The description above is as in Lavranos (l.c.) except for some small details—in particular, although the inner corona-lobes appear to be shorter than the anthers when viewed from above, when the corona is dissected, they are revealed to be much longer than them. They have a peculiar orientation and rounded shape which is unique in the genus, but it is possible that this is not a reliable feature as I have not been able to examine more material than the small type at Kew.

The affinities of this species are obscure. Despite the depth of the outer corona and the cylindrical inner corona-lobes, the flattening of the outer lobes around the mouth, their thickness lower down and the length and overall shape of the inner corona all suggest that this species belongs to this section. There is an obvious connection with *E. squamulata* in the overall length of the corolla but the corolla lobes, with the complete lack of folding of their margins and their greater length, are very different, as are the respective coronas.

### 4. SECTION PROFUNDICORONA Bruyns **sect.nov.**

*Caulis juvenis non rugosus, plerumque papillosus, foliatus; corona exterior cupulam profundam faciens, textura tenue ad orem, intus pilosa; corona interior ad coronam exteriorem infra medium connata, plerumque dorsum antherarum modo tegens neque antheras aequans, pilosa; pollinia fere sphaerica. Species typica: E. sharpei* White & Sloane.

#### KEY TO SPECIES

1. Corolla shallowly campanulate (much broader than deep) to rotate; tube only deep enough to contain at most outer corona cup ............................ 2
   Corolla deeply campanulate (at least as deep as broad), urceolate, globose or cylindrical; tube at least twice as deep as height of outer corona cup .................... 5
2. Corolla-lobes < 3× as long as broad at base ............ 3
   Corolla-lobes > 3× as long as broad at base . 13. **E. montana**
3. Stems 16-angled; leaves > 3× as long as broad at base; outer corona cup without hairs ..... 15. **E. bihendulensis**
   Stems 10-angled or less; leaves < 2× as long as broad at base; outer corona cup with hairs .................. 4
4. Outer corona cup shallow, not exceeding height of anthers, each lobe with notch in middle; corolla with bristles on rotate part and in tube, without long red hairs, corolla fabric thin ............... 12. **E. seibanica**
   Outer corona cup deep; anthers not visible when cup viewed from side, each lobe with entire rim; corolla velvety with very fine bristles, with long red hairs on lobes and rotate part, corolla fabric thick ... 14. **E. sharpei**
5. Corolla campanulate .................. 16. **E. archeri**
   Corolla globose, urceolate or cylindrical ............... 6
6. Corolla urceolate, exterior glabrous; tubercles on stems attenuated, projecting at least as far as they are broad .................................. 17. **E. ballyi**
   Corolla globose or cylindrical, exterior papillate or hispid; tubercles on stems not attenuated, projecting from stem much less than their breadth ............... 7
7. Corolla globose, corolla-lobes projecting back into corolla-tube, inside of corolla with long hairs, not wrinkled .............................. 19. **E. malum**
   Corolla cylindrical, corolla-lobes projecting out of corolla-tube, inside of corolla without hairs, extensively wrinkled ................ 18. **E. mijerteina**

12. **E. seibanica** Lavranos in J. S. Afr. Bot. 30: 88 (1964). Type: South Yemen, Hadramawt, Mawla Matr, southern slopes of Kor Seiban, 1800m, 21 Aug. 1962, *Lavranos* 1934 (K, holotype).

DESCRIPTION. *Stems* procumbent to decumbent, sometimes soboliferous, 30-150mm long, 6-9mm diam., 6-8-angled, green to brown-green, finely papillose, with hexagonal tubercles each bearing an erect, rapidly caducuous, ovate leaf up to 0.8mm long with stipular gland on either side. *Pedicel* 1mm long, finely papillate. *Sepals* deltoid, 1mm long, adpressed to corolla. *Corolla* shallowly campanulate, 6-7mm diam., exterior finely papillate, cream-coloured, interior setulose, sulphur-yellow with minute red spots in tube and lower ⅓ of lobes; *tube* 0.75mm long, 2mm diam.; *lobes* nearly twice as long as broad, with rounded apex when pressed flat (as in Fig. 20), margins normally reflexed, at first ascending then spreading, 2.5mm long, 1.5mm broad at base. *Corona* circular in outline, 1.5mm diam.; *outer lobes* shallowly bifid, united into cup with erect sides and rounded, red-

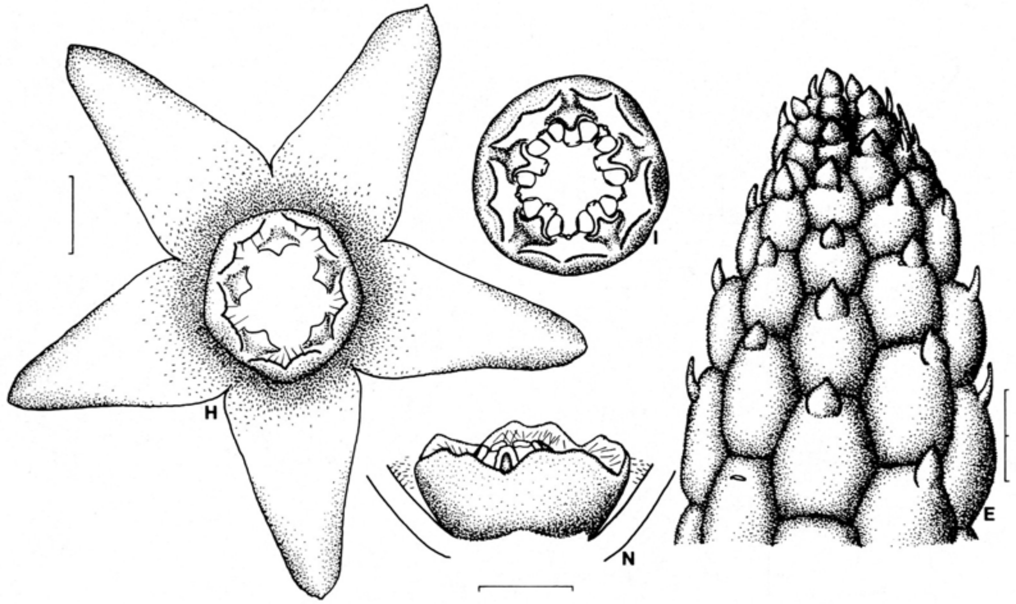


Fig. 19. **Echidnopsis seibanica** Lavranos. E, stem apex (scale 2mm); H, face view of corolla (scale 1mm); I, face view of staminal column; N, side view of staminal column (scale 1mm, as for I). All drawn from *Lavranos* 1934.

purple apices, pinkish with red-purple spots, with transparent, stiff hairs on inner surface; *inner lobes* less than 0.3mm long, whitish with numerous minute, red-purple dots, with broad base and narrow limb incumbent on backs of anthers but shorter than them. (Fig. 19)

*Echidnopsis seibanica* remains known only from the type collection and the type specimen is so small that it gives little impression of the species. This collection is from the mountains south of the Wadi Hadramawt in South Yemen and the only other record of an *Echidnopsis* from near here is Deflers' collection of what he called *E. cereiformis* from the Jebel al 'Urays further to the south-west (Deflers, 1895: 424).

Lavranos allied his species with *E. scutellata*. This is erroneous as it seems to be the only Arabian member of section 4. Despite the shallow coronal cup, this is clearly indicated by the erect, thin outer corona with hairs on the inner face and the small, short inner lobes. Further collecting in this region will put this grouping to the test by showing whether or not these criteria really hold up when the variation of such 'marginal cases' as *E. seibanica* (where the outer corona cup is superficially similar to that in section 3) becomes better known.

13. **E. montana** (R. A. Dyer & E. A. Bruce) Bally in Cact. Succ. J. Gr. Brit. 26: 89 (1964).

*Caralluma montana* R. A. Dyer & E. A. Bruce in Flow. Pl. Afr. 26: t.1034 (1947); Cufodontis in Bull. Jard. Bot. Brux. 31, suppl.: 717 (1961). Type: Ethiopia, Adama Hill, 96km south of Addis Ababa, 2000m, 10 June 1942, *McLoughlin* 835 (PRE, holotype, K, ZSS).

DESCRIPTION. *Stems* procumbent, usually soboliferous, up to 200mm long, 7-15mm diam., 6-angled with prominent, 4-angled tubercles, 1-3mm long, attenuated to a point, each bearing an ovoid-deltoid, rapidly caducuous leaf up to 1.5mm long with stipular gland on either side. *Pedicel* 1-2mm long. *Sepals* ovate to lanceolate, 1-2mm long, finely papillose. *Corolla* greenish-yellow or purplish-brown with greenish-yellow, slightly thickened tips; *tube* short, up to 2mm deep, usually enclosing most of corona; *lobes* 9-10mm long, 2mm broad at base, glabrous, linear, margins replicate nearly to base. *Corona* slightly pentagonal to circular, about 2.5mm diam.; *outer lobes* forming indented cup surrounding column, limb triangular, entire or toothed with few to numerous hairs on inner surface, usually directed inwards or erect, whitish spotted with purple; *inner lobes* with broad base and truncate to deltoid, dorsally flattened tip incumbent on anthers and usually not exceeding them. (Fig. 20)

*Echidnopsis montana* is now known to occur quite extensively in the mountains forming the eastern side of the Rift Valley in Ethiopia. Collections exist from Harar via Adama (Nazareth) to some 50km south of Lake Shala, a total distance of nearly 500km. Most have been made at a height of around 2000m and the species seems to be exclusively a highland one although it does not occur in the highest mountains of this region, which reach to over 4000m.

Dyer and Bruce placed this species in *Caralluma* on the grounds that it was nearest to *Quaqua* (then *Caralluma*) *framesii* (Pillans) Bruyns and *C. baldratii* White & Sloane. However, as Bally realised, there is merely a coincidental resemblance of the corolla-lobes which is not indicative of a close relationship between these species. Such long, narrow corolla-lobes and small, shallow corolla-tube are also known in *E. angustiloba* so that *E. montana* is not unique in this respect. However, its relationship to other species remains a problem. I have placed it at the beginning of this section as the corona fits reasonably well among those here and the flower, with its small corolla-tube and narrow lobes appears to be the least specialized in this section, closely corresponding to the position of *E. angustiloba* in section 3. However, it will be immediately apparent that the outer corona is rather shallow and the inner corona-lobes often longer than is customary and it is possible that it is closer to *E. angustiloba*. The stems of *E. montana* are unusual in being frequently soboliferous, few-angled and bearing long tubercles. In general, species with few-angled stems have much depressed tubercles, while those with many-angled stems have conical tubercles. A further remarkable feature of the stems and leaves is that they are completely glabrous at low magnification (×30). The toothed outer corona is also distinctive.

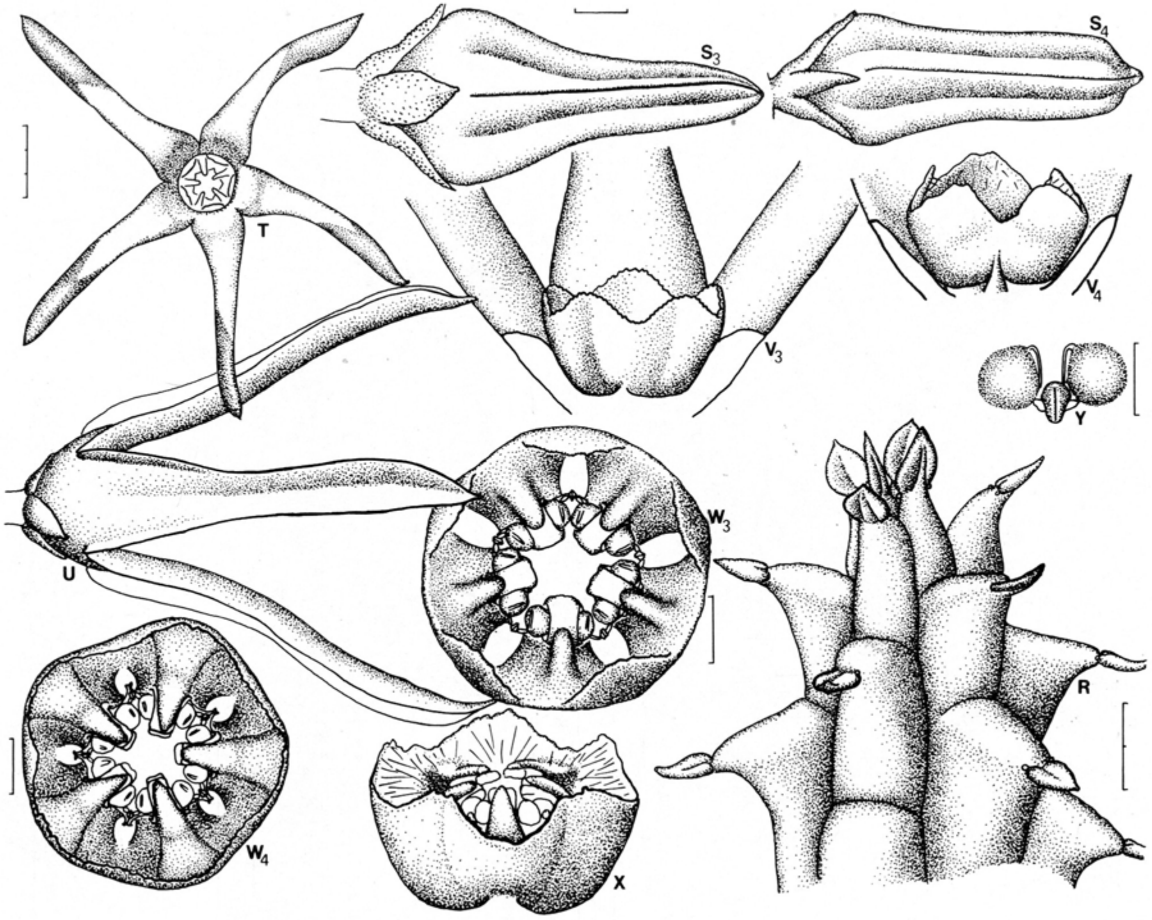


Fig. 20. **Echidnopsis montana** (R. A. Dyer & Bruce) Bally. R, stem apex (scale 2mm, as for $S_4$); S, bud (scale $S_3$ 1mm, as for U); T, face view of corolla (scale 3mm); U, side view of corolla; V, dissected side view of corolla (scale of Y = 1mm); W, face view of staminal column (scale in each case 0.5mm; for X as for $W_4$); X, oblique view of staminal column; Y, pollinarium (scale 0.25mm). R, $S_3$, U, $W_3$ drawn from cultivated material in ZSS, of unknown origin; $S_4$, $V_4$ from *Mason* 139; T, W, X from *Noltee* s.n.; $V_3$ from *Ash* 491; Y from *Plowes* 6684.

14. **E. sharpei** White & Sloane in Cact. Succ. J. (US) 11: 67 (1939); Bally in J. E. Afr. Nat. Hist. Soc. 16: 163, t.27 (1942) & in Cact. Succ. J. Gr. Brit. 18: 107-8 (1956); Dyer in Flow. Pl. Afr. 26: t. 1003B (1947). Type: Kenya, 30 miles south of Lake Turkana, 1937, *Sharpe & Muriel Jex-Blake* (K, lectotype selected here, ZSS).

*E. bavazzani* Lavranos in Cact. Succ. J. (US) 46: 181 (1974); Dyer in Flow. Pl. Afr. 45: t. 1767A (1978). Type: Somalia, Galkudal, approx. 7km south of Las Anod, *Lavranos & Bavazzano* 8428 (FI [not seen]).

DESCRIPTION. *Stems* up to 150mm long, repent to procumbent-erect, 6-15mm thick, 8-10-angled, divided into variously-shaped tubercles each bearing small, finely papillose, rapidly caducuous to persistent leaf up to 2mm long. *Pedicel* 1-3mm long. *Sepals* ovate-lanceolate, 1-1.5mm long. *Corolla* exterior glabrous, 6-15mm diam., shallowly campanulate to rotate, exterior green to green-spotted with purple, inner surface dark maroon to wine-red to purple with scattered to dense hairs up to 1mm long, velvety-setulose; *tube* campanulate, pentagonal; *lobes* ovate-deltoid to ovate or deltoid, 3-6mm long, margins reflexed more or less strongly. *Corona* circular to deeply pentagonal in outline, 2-2.5mm diam.; *outer lobes* cupular, entire, about twice the height of central part of column, with long, white hairs on inner surface; *inner lobes* with broad base arising near middle of outer corona cup and small triangular limb projecting onto backs of anthers but not extending over them, with few erect, dorsal hairs.

Examination of a selection of material has indicated that it is not possible to uphold *E. sharpei* and *E. repens* as distinct species. These two are separated particularly on the shape of the corolla—in *E. sharpei* the corolla-lobes are reflexed and in *E. repens* the flower is campanulate—and the shape of the outer corona cup—narrowed at the mouth in *E. sharpei,* widening at the mouth in the other. In the case of *E. sharpei* the flowers of *Powys* 524 are more akin to those of *E. repens* and the series shown in Fig. 24, as well as the unusual flowers in *Greenway & Kanuri* 12448 show that *E. repens* grades into the shape of *E. sharpei*: in fact from the similarity of the buds it becomes clear that they differ only in the *extent* to which the corolla-lobes spread out. As far as the shape of the outer corona is concerned, it will be obvious from the illustrations that the Gilbert and Vollesen collection from Sidamo has a corona which is inseparable from those of *E. repens*. Thus, although the coronas of the Turkana collections of *E. sharpei* are different from those of *E. repens,* this distinction is obscured further north. A further taxon, *E. ciliata* is also involved. This is most similar to subsp.

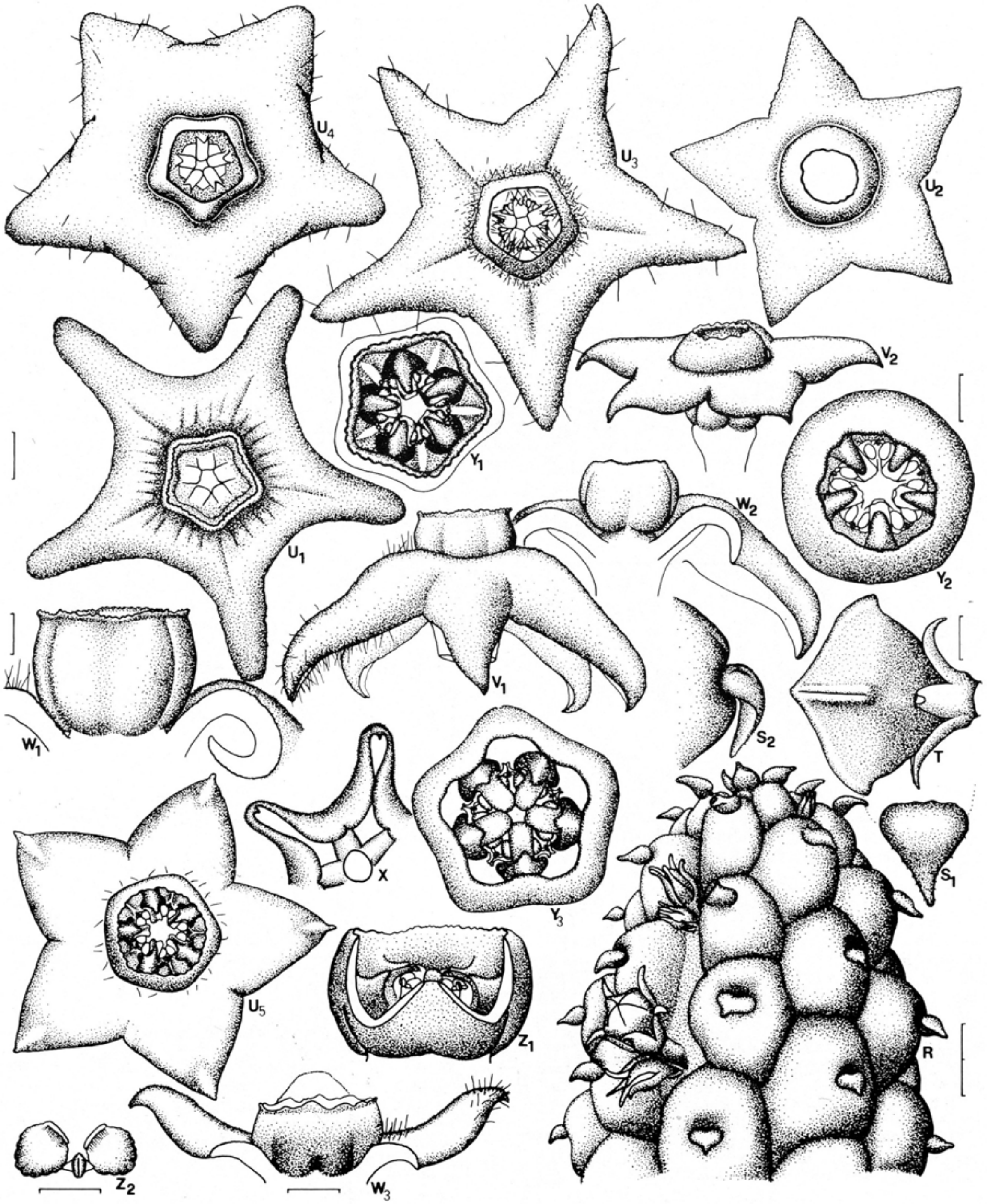


Fig. 21. **Echidnopsis sharpei** White & Sloane subsp. **sharpei.** Kenyan material. R, stem apex (scale 2mm, as for X); $S_1$, face view of leaf; $S_2$, side view of leaf (scale of $Z_2$ = 1mm); T, bud (scale 1mm, as for $W_2$, $U_4$); U, face view of corolla (scale at $U_1$ 1mm, as for $U_2$, $U_3$, $U_5$, $V_1$, $V_2$); V, side view of corolla; W, dissected side view of corolla (scale $W_1$ 0.5mm, as for $Y_1$; $W_3$ 1mm); X, rear view of corolla showing replication of lobes; Y, face view of staminal column (scale at $Y_2$ as for $Y_3$, $Z_1$ 0.5mm); $Z_1$, side view of staminal column with part of outer corona removed; $Z_2$, pollinarium (scale 0.25mm). R, T, $U_4$, $W_2$, $Y_3$ drawn from material cultivated at ZSS of unknown origin; S, $U_3$ from *Jenkins* s.n.; $U_1$, $V_1$, $W_1$, X, $Y_1$ from *Lavranos & Newton* 17698; $U_2$, $V_2$, $Y_2$ from *Williams* in *Bally* S208; $U_5$, $W_3$, $Z_1$ from *Powys* 524A; $Z_2$ from *Powys* 819.

*repens* and differs from it mainly in the larger flower with broader tube. Thus *E. sharpei* is considered to consist of three subspecies, separable as follows:

KEY TO THE SUBSPECIES OF E. SHARPEI

1. Corolla-lobes usually reflexed; corona exserted from corolla-tube; stem tubercles as broad as long . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 14a. subsp. **sharpei**
   Corolla-lobes usually erect to spreading; corona included within tube; tubercles longer than broad . . . . . . . 2
2. Interior of corolla densely hairy; corolla-tube broad, not adpressed to side of staminal column . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 14c. subsp. **ciliata**
   Interior of corolla sparsely hairy; corolla-tube narrower, adpressed to side of staminal column . . 14b. subsp. **repens**

14a. subsp. **sharpei**

DESCRIPTION. *Stems* repent to procumbent-erect, 8-15mm thick, covered with prominent, rounded, approximately regularly 6-angled tubercles each bearing a deltoid, reflexed leaf which is usually rapidly caducuous but may persist as dried-up scale in Somalian material, without stipular glands. *Pedicel* up to 1mm long. *Corolla* 6-12mm diam., with scattered hairs; *tube* short, containing lower half of column and adpressed to its sides, sometimes yellow or white, otherwise red, with many white to red hairs; *lobes* more or less deltoid, apex usually folded right back so that end is obtuse. *Corona: outer lobes* yellow, sometimes with dark red margin and reddish bars on pale yellow to white background, with white hairs on both inner and outer surface, often with narrow mouth, sometimes very deeply indented at join to inner lobes, margin often slightly dentate. (Figs. 21, 22)

Subsp. *sharpei* is a widely distributed taxon. However, its distribution is very poorly known and, despite its discovery as early as 1937, it is only well-documented from just south of Lake Turkana. This is where it was first collected but it has also been collected more than 500km to the south-east near Galole and at Adable in Tanaland. In Ethiopia it is recorded from Ginir (Bale Region), Dire Dawa in the Harerge Region and Negelli in the Sidamo Region while in Somalia it is recorded from Las Anod to the coast at Eil.

Subsp. *sharpei* is also exceedingly variable. In the collections from the Tana River the flowers may be slightly smaller and Bally intended to name this *E. sharpei* var. *exigua* (based on *Bally* S43). However, within the area of the North Frontier Province of Kenya considerable variation occurs too. *Powys* 524A, 819 and *Bally* S208 are remarkably different from the

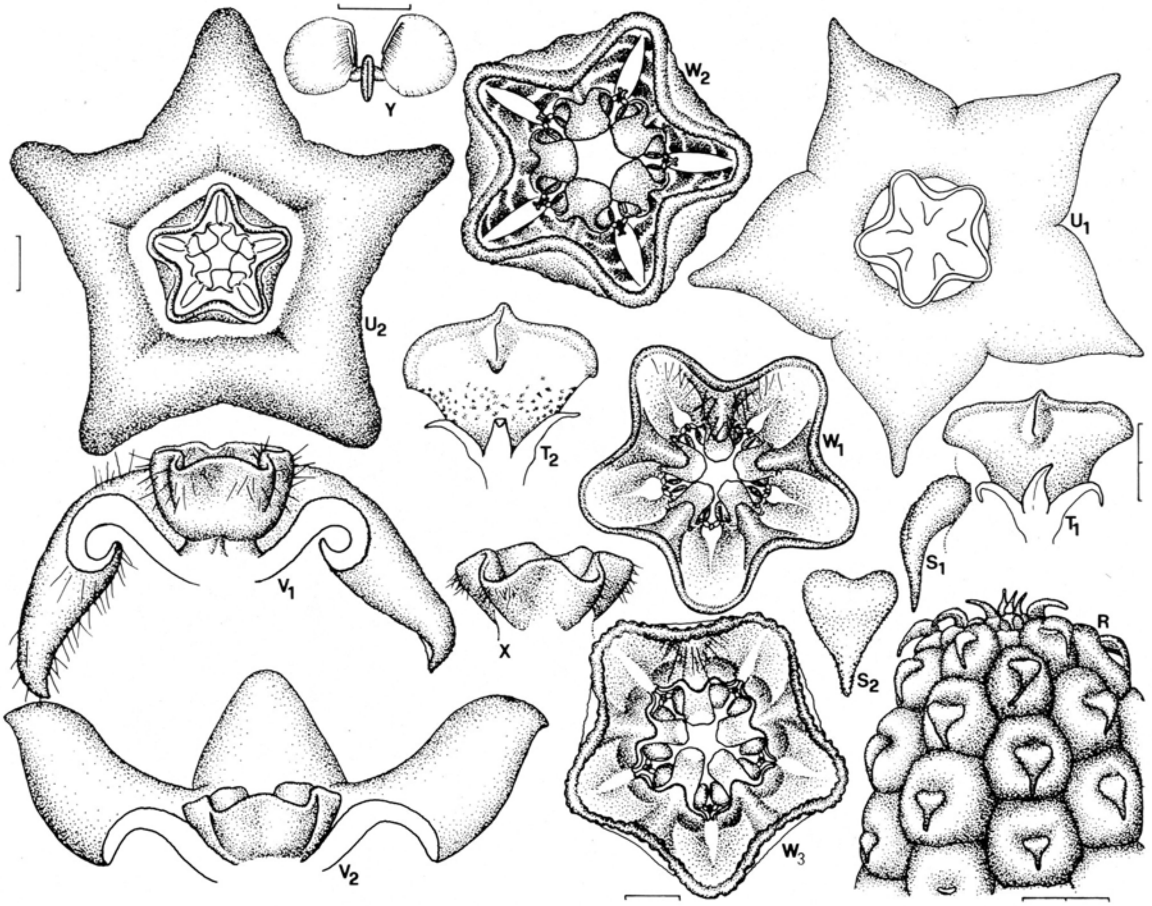
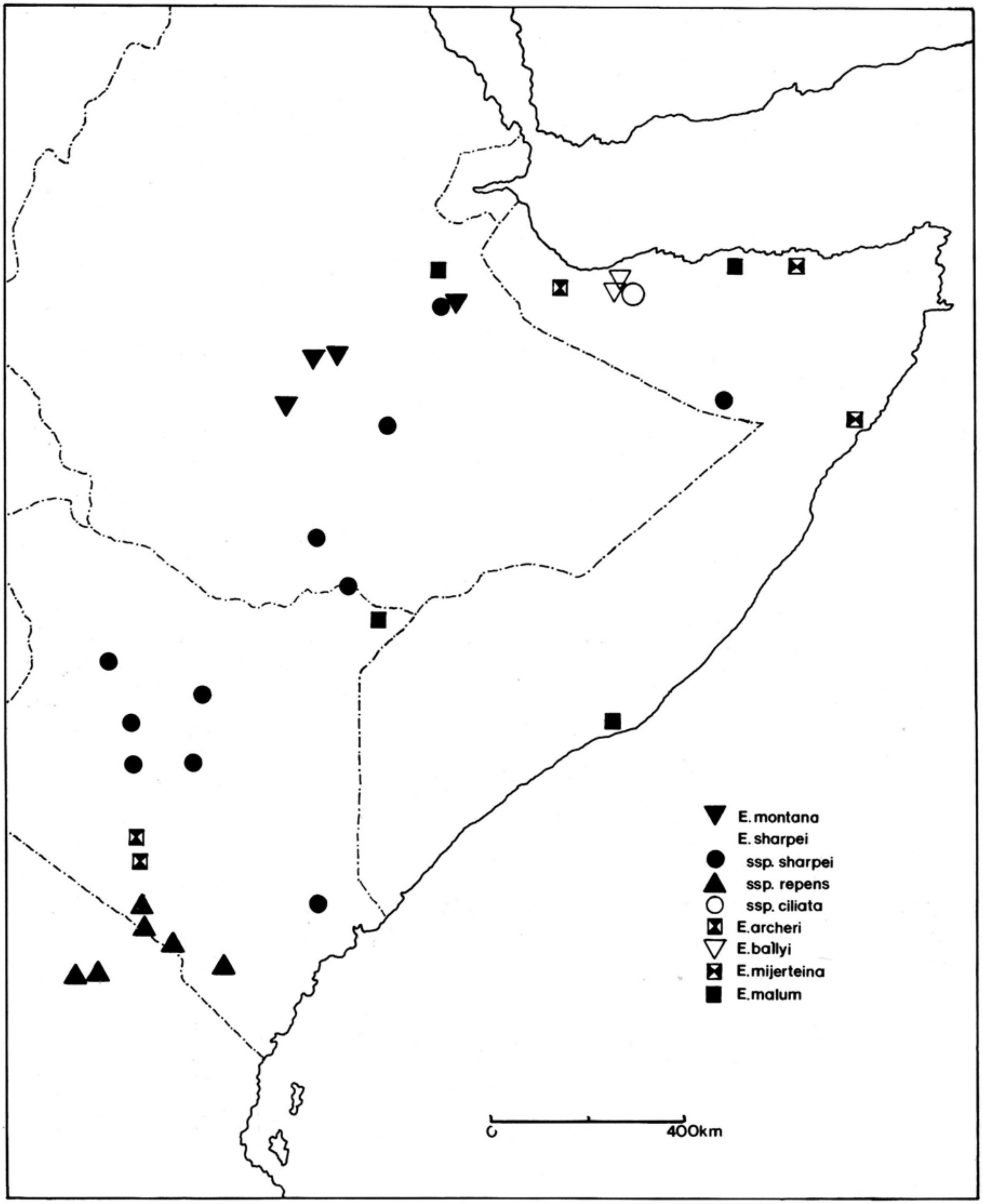


Fig. 22. **Echidnopsis sharpei** White & Sloane subsp. **sharpei.** Somalian and Ethiopian material. R, stem apex (scale 2mm); $S_1$, side view of leaf; $S_2$, face view of leaf (scale of Y = 1mm for both, as for X); T, bud (scale for both as at $T_1$, 2mm); U, face view of corolla (scale 1mm at $U_2$, as for $U_1$, $V_1$, $V_2$); V, dissected side view of corolla; W, face view of staminal column (scale as at $W_3$, 0.5mm); X, side view of staminal column; Y, pollinarium (scale 0.25mm). R, S, $T_2$, $U_2$, $V_1$, $W_2$, Y drawn from *Gilbert & Vollesen* s.n.; $T_1$, $U_1$, $W_1$, X from *Gilbert & Vollesen* 7864; $V_2$, $W_3$ from *Lavranos* 10183.

typical and in S208 the outer corona is nearly closed at the mouth, while in *Powys* 524A the mouth is especially wide open. All of these collections have very small flowers. Considerable variation occurs too among these collections in the outline of the corona (circular to clearly pentagonal) when viewed from above. This is taken further in Ethiopia and reaches an extreme in plants from Somalia. Some of the Ethiopian and Somalian collections have noticeably shallower outer coronas as well (narrowing sometimes from their mouth towards their base), far shallower than that found in most Kenyan material.

*E. bavazzani* differed from *E. sharpei* in having 'short, much thicker stems, a deeply 5-lobed corona and a wholly distinct



Map 4. Distribution of section 4 in north-east Africa.

general aspect'. It is not obvious what the lattermost comment means. As far as the 5-lobed corona and shorter, thicker stems are concerned, it is worth noting the above-mentioned variation in the outline of the corona in face-view (see Fig. 21). In addition, plants from Ethiopia are vegetatively inseparable from the thinner-stemmed, partially repent material from Kenya and yet some of them have flowers with the shallow, 5-lobed corona of *E. bavazzani*. It appears that, once again, the stems change from being long, with a creeping habit to short and upright in response to increasing aridity and they reach an extreme around Eil in Somalia where they are scarcely twice as tall as thick and are more or less erect. It is noteworthy that the distinctive, broad leaves are retained throughout this range.

With its velvety, deep red corolla, *E. sharpei* remains one of the most striking members of the genus. There is not much variation in the colour of the corolla except in *Lavranos & Newton* 17698 where it was very dark maroon and in the northern forms where the corolla-tube is yellow-green to white, and thus different from the rest of the corolla. The outer corona varies considerably in colour. In Kenya it is pale yellow while in Ethiopia and Somalia it is much darker, with a dark red margin and red barring lower down on a yellow background causing a curious dazzling effect.

Vegetatively subsp. *sharpei* is quite distinctive and with its fat, rounded, glabrous, raised tubercles with sunken leaf is nearly always distinguishable from other species and especially from subsp. *repens*.

The flowers, and especially the corona, of this taxon show considerable resemblance to those of *Brachystelma brevipedicellatum* Turrill from southern Africa.

14b. **E. sharpei** subsp. **repens** (R. A. Dyer & Verdoorn) Bruyns **comb. et stat. nov.**

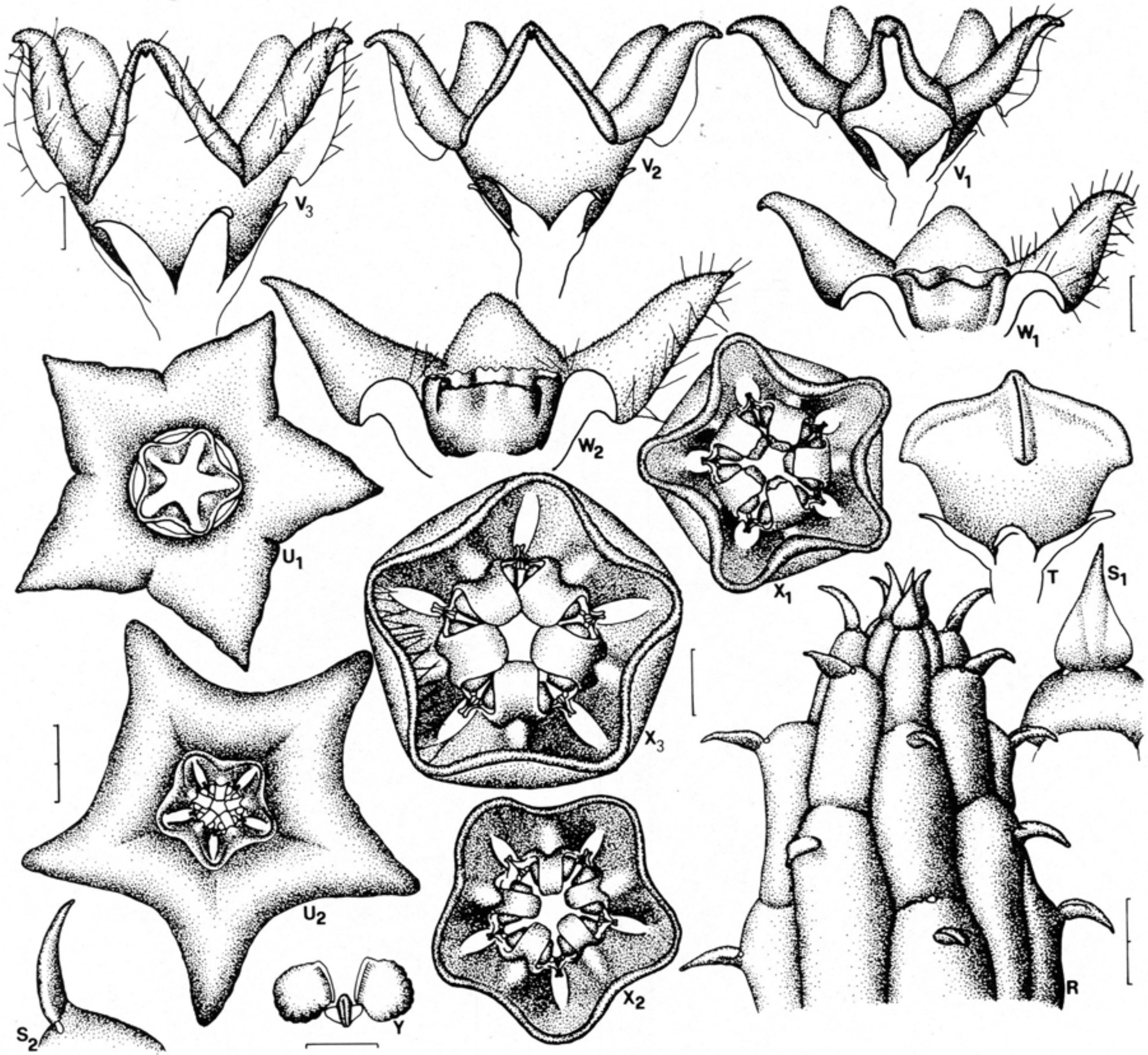


Fig. 23. **Echidnopsis sharpei** subsp. **repens** (R. A. Dyer & Verdoorn) Bruyns. R, stem apex (scale 2mm, as for T, $U_1$, $V_1$, $V_2$, $W_1$); $S_1$, face view of leaf; $S_2$ side view of leaf (scale of Y = 1mm for both); T, bud; U, face view of corolla (scale $U_2$, 2mm); V, side view of corolla (scale $V_3$ 1mm); W, dissected side view of corolla (scale for both as at $W_1$, 1mm); X, face view of staminal column (scale $X_1$, $X_2$ that of $W_1$ = 0.5mm; $X_3$, 0.5mm); Y, pollinarium (scale 0.25mm). R, $V_3$ drawn from *Rauh* Ke276; S, $X_3$ from material ex hort. Kew, of unknown origin; T, $V_2$ from *Richards* 26594; $U_1$, $W_2$, $X_1$, Y from Kiel 551 (no specimen); $U_2$ from *Greenway & Kanuri* 12448; $V_1$, $X_2$ from *Bleck & Lavranos* 19571; $W_1$ from *Barad* 10320.

*E. repens* R. A. Dyer & Verdoorn in Cact. Succ. J. (US) 11: 68 (1939); Bally in J. E. Afr. Nat. Hist. Soc. 16: 163 (1942); Dyer in Flow. Pl. Afr. 25: t. 993 (1946). Type: Tanzania, Aldenyo, near Mt Meru, 1938, *Pole-Evans & Erens* 1020, (PRE, holotype).

DESCRIPTION. *Stems* repent, rooting along most of length, 6-9mm thick, finely papillose, divided into flat, more or less hexangular tubercles much longer than broad each with lanceolate, rapidly caducuous leaf up to 1.5mm long with stipular gland on either side. *Pedicel* 2mm long. *Corolla* 7-9mm diam., outer surface green, inner surface deep wine-red with scattered hairs around margins of lobes and in tube; *tube* containing column, sides adpressed to column, *lobes* ovate-deltoid or ovate, ascending-erect to spreading and occasionally reflexed, sometimes with yellow tips. *Corona* deeply pentagonal; *outer lobes* with red-purple margin becoming lighter coloured towards base. (Fig. 23)

Subsp. *repens* occurs around Mt Kilimanjaro on the Kenya–Tanzania border area where it is of restricted distribution. Jan Erens originally collected it on Mt Meru to the south-west of Kilimanjaro and a number of collections have been made more recently on the same mountain in the Arusha district. It has been collected in the mountains some 100km north-west of Kilimanjaro and Bally (l.c.) mentioned that it has also been found near Maktau some 50km east of the foot of the mountain, where it was collected by MacArthur in 1942. On Kilimanjaro itself it has been gathered a number of times at Loitokitok in Kenya.

Although subsp. *repens* is extremely easy to grow it is very reluctant to flower and this is presumably why the type specimen consists of a large quantity of vegetative material and only three flowers. However, when the flowers do appear, they are extremely beautiful, with the same deep red colour as in subsp. *sharpei*. Even more striking are those forms where each corolla-lobe is tipped with yellow. As pointed out earlier, they are very variable in shape and Fig. 23 shows this clearly. The corona is darker-coloured than in subsp. *sharpei* and seems to be far less variable in shape. In many cases its corona can be distinguished from that of subsp. *sharpei* by the vertical sides and the lack of an incurved rim. It is for this reason that the few remarkably-shaped flowers in *Greenway & Kanuri* 12448, which were among a large number of normal ones, clearly belong to subsp. *repens*. It is only to the north of Kenya that subsp. *sharpei* ceases to have the incurved mouth to the outer corona and then its corona becomes extremely similar to that of subsp. *repens*.

### 14c. **E. sharpei** subsp. **ciliata** (Bally) Bruyns **comb. et stat. nov.**

*E. ciliata* Bally in Cact. Succ. J. Gr. Brit. 19: 58 (1957); Cufodontis in Bull. Jard. Bot. Brux. 31, suppl.: 714 (1961). Type: Somalia, upper Sheikh Pass in an old Mahommedan Cemetery, 1440m, 1 May 1949, *Bally* B7167 (the top figure in Bally l.c.: 59 (1957) is selected as lectotype in absence of preserved specimen of this collection; material preserved under *Bally* 7148 at ZSS is *E. archeri*).

DESCRIPTION. *Stems* repent, 8-angled, tubercles a little longer than broad, bearing fat, rapidly caducuous, lanceolate-deltoid leaves up to 1.2mm long with stipular glands. *Pedicel* 3mm long. *Corolla* 10-15mm diam., exterior green spotted with purple, inside densely hairy, dark purple; *tube* containing column, broadly campanulate and not touching sides of column, with many hairs; *lobes* deltoid, 5-6mm long, 5mm broad, with hairs. *Corona* pentagonal; *outer corona* rim purple-black, becoming reddish around middle and white in lower third; *inner corona* reddish. (Fig. 24)

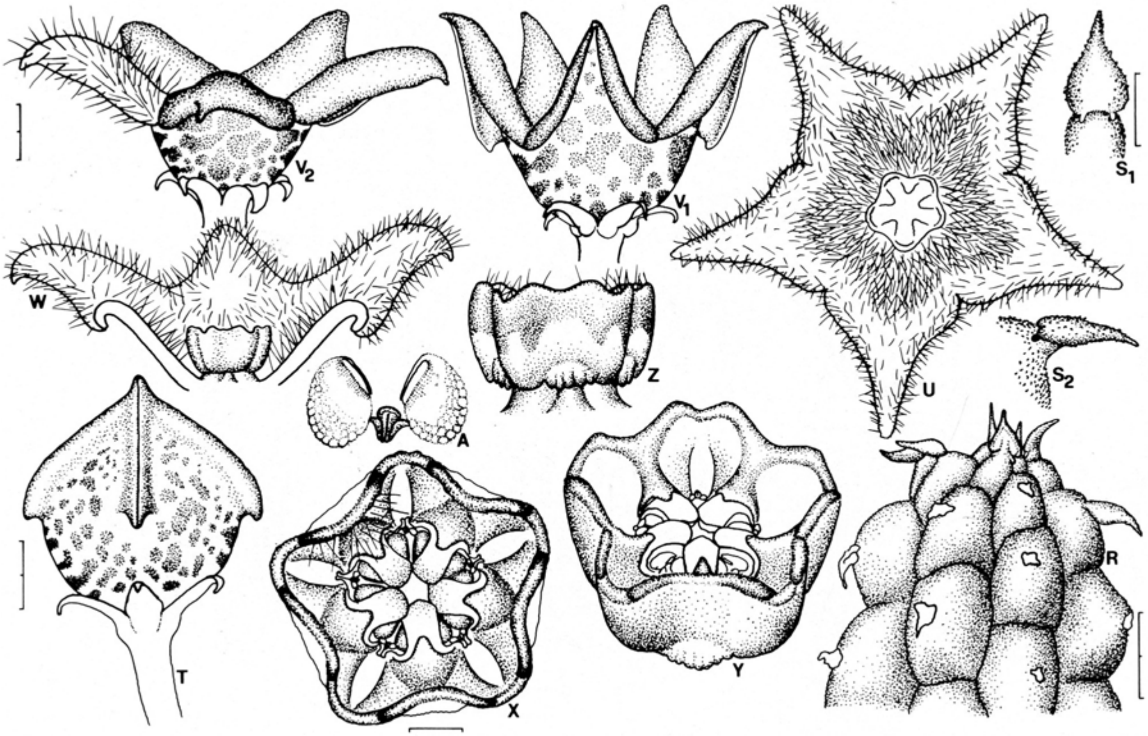


Fig. 24. **Echidnopsis sharpei** subsp. **ciliata** (Bally) Bruyns. R, stem apex (scale 2mm); $S_1$, face view of leaf (scale 1mm, as for $S_2$, Z); $S_2$, side view of leaf; T, bud (scale 2mm); U, face view of corolla; V, side view of corolla (scale $V_2$ 2mm, as for U, $V_1$, W); W, dissected side view of corolla; X, face view of staminal column (scale 0.5mm, as for Y); Y, oblique view of staminal column; Z, side view of staminal column; A, pollinarium (scale of $S_1$ = 0.25mm). All drawn from *Bailes* 134.

Subsp. *ciliata* is known only from the type locality where it was gathered for the first time in 1949 and again in 1981 when it was rediscovered by Brandham, Carter, Johnson and Bailes *(Bailes* 134). A small piece of this collection flowered in Oxford enabling Fig. 24 to be prepared. Bally's photographs (Kew archives) confirmed the identity of this collection. They also showed that a specimen of *Bally* 7148 at ZSS, which he cited as the type (Bally, l.c.:63) represents *E. archeri* and not *E. ciliata*. However, on the drawing cited above, Bally gives the number 7167. At the end of his account of the species Bally (l.c.:63) mentions that the drawing is from the type. This is therefore selected as the lectotype and the specimen of *Bally* 7148 is rejected as having been muddled with *E. archeri*.

The flowers of this taxon are large—as is seen already in the large buds—for any member of this genus and have also more hairs on the interior than is customary in *E. sharpei*. The stems, although shorter and more papillose, retain the repent habit of subsp. *repens*. The depth of the corolla-tube in relation to the overall length of the flower is also typical of subsp. *repens,* as is the corona, though it is very difficult to separate the corona of this taxon from that of some Ethiopian collections of subsp. *sharpei*. Subsp. *ciliata* is separated from both the other subspecies also by the very broad corolla-tube which does not touch the side of the outer corona.

Bally's *E. ciliata* bears some resemblance to the long-lost *E. bentii*. Points of correspondence are the dark purple blotches on a green background on the exterior of the corolla, the campanulate shape of the flower and its colour within. However, the stems are quite different and the corona of *E. bentii* is that of a member of the previous section.

15. **E. bihendulensis** Bally in Cact. Succ. J. Gr. Brit. 19: 58 (1957); Cufodontis in Bull. Jard. Bot. Brux. 31, suppl.: 714 (1961). Type: Somalia, below the Sheikh Pass at Bihendula, 2000′, Jan. 1944, *Bally* S125 (K, holotype, ZSS).

DESCRIPTION. *Stems* grey-green, procumbent-erect, up to 120mm long, 15-25mm thick, finely papillose, 16-angled, angles with deeply divided, conical tubercles, 2-3mm long, tipped with subulate, ascending, finely papillose leaf, 3-3.5mm long, rapidly dying off but remaining persistent as sharp spine, without stipular glands. *Pedicel* less than 1mm long. *Sepals* 1.5-3mm long, finely papillose, lanceolate-acute. *Corolla* 6-7.5mm diam., exterior glabrous, pale green, interior setulose, yellow to red-brown; *tube* campanulate, 1mm deep, just containing but much broader than column; *lobes* 2.5-4mm long, deltoid, erect to spreading, with reflexed apex and margins, margins often with small, thick, sharp-ended, transparent hairs. *Corona* obtusely pentagonal, 1.5-3.3mm diam., 1-1.5mm high; *outer lobes* erect, enclosing anthers in cup, deeply indented at inner lobes on exterior, with brown margin, remainder yellow; *inner lobes* attached to outer lobes just beneath mouth of cup, with broad base and small, rounded limb incumbent on and only rarely nearly as long as anthers, yellow with red margin. (Fig. 25)

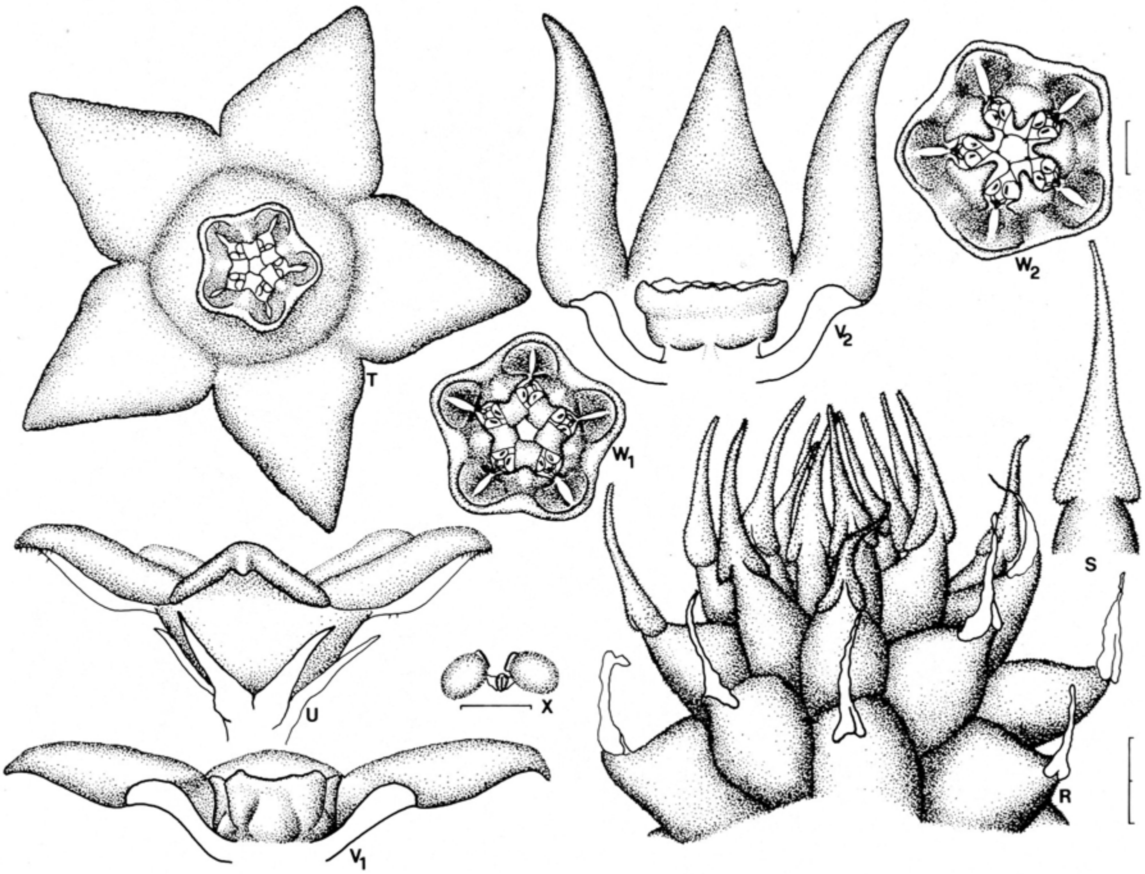


Fig. 25. **Echidnopsis bihendulensis** Bally. R, stem apex (scale 2mm); S, face view of leaf (scale of X = 1mm, as for T, U, V); T, face view of corolla; U, side view of corolla; V, dissected side view of corolla; W, face view of staminal column (scale at $W_2$ = 0.5mm, as for $W_1$); X, pollinarium (scale 0.25mm). R, S, T, U, $V_1$, $W_1$, X from *Bailes* 169; rest from *Bailes* 156.

*Echidnopsis bihendulensis* is known only from the Berbera–Burao road between Bihendula and just south of Hudiso in the Sheikh Pass where it was collected by Bally in 1944 for the first time and again by Bailes *et al.* in February 1981. It is recorded as occurring on stony hillsides in shelter of rocks or bushes.

Bally considered this species to be related to *E. scutellata* subsp. *planiflora*. However, despite the spiny stems—and it is the only member of this section to achieve the spininess typical of many members of section 3—most of the features of the flower suggest a much closer relationship with *E. sharpei,* so that here the affinities suggested by vegetative characteristics are misleading. The setulose corolla is much more akin to that of *E. sharpei* (although some members of section 3 also have setulose corollas, but *E. scutellata* subsp. *planiflora* does not) and the structure of the staminal column with thin outer corona-lobes (lacking broad, flattened top) and very short inner corona-lobes is typical of section 4. Nevertheless, the outer corona is not as deep as it is in many other members of this section, the inner corona-lobes are inserted just below its mouth, higher than is usual and the outer corona is hairless.

Bally recorded both yellowish and brown flowers. I have not seen any with yellowish flowers and all recent collections seem to have brown corollas. Apart from small-flowered forms of *E. sharpei, E. bihendulensis* has the smallest and least attractive flowers in this section.

16. **E. archeri** Bally in Cact. Succ. J. Gr. Brit. 19: 63 (1957) & in ibid. 18: 108 (1956) in clavi. Type: Kenya, Nguruman Escarpment, Oloibitato River near Hayton's Falls, 11 Sept. 1952, *P. G. Archer* in *Bally* S235 (K, lectotype selected here, ZSS).

DESCRIPTION. *Stems* repent with ascending apices, up to 50mm long, 10-15mm thick, 8-angled, finely papillose, tubercles hexagonal, each tipped with acute, reflexed, finely papillose, rapidly caducuous leaf without stipular glands. *Pedicel* glabrous, 1mm long. *Sepals* finely papillose, 1-2mm long, ovate-lanceolate, acute, with reflexed tips. *Corolla* 5-6mm diam., 5-8mm in length, deeply cupular, exterior sparsely papillate to glabrous, purple to red-purple (occasionally pinkish), interior dark purple to crimson, velvety-setulose; *tube* more or less as broad as deep, 3-4mm

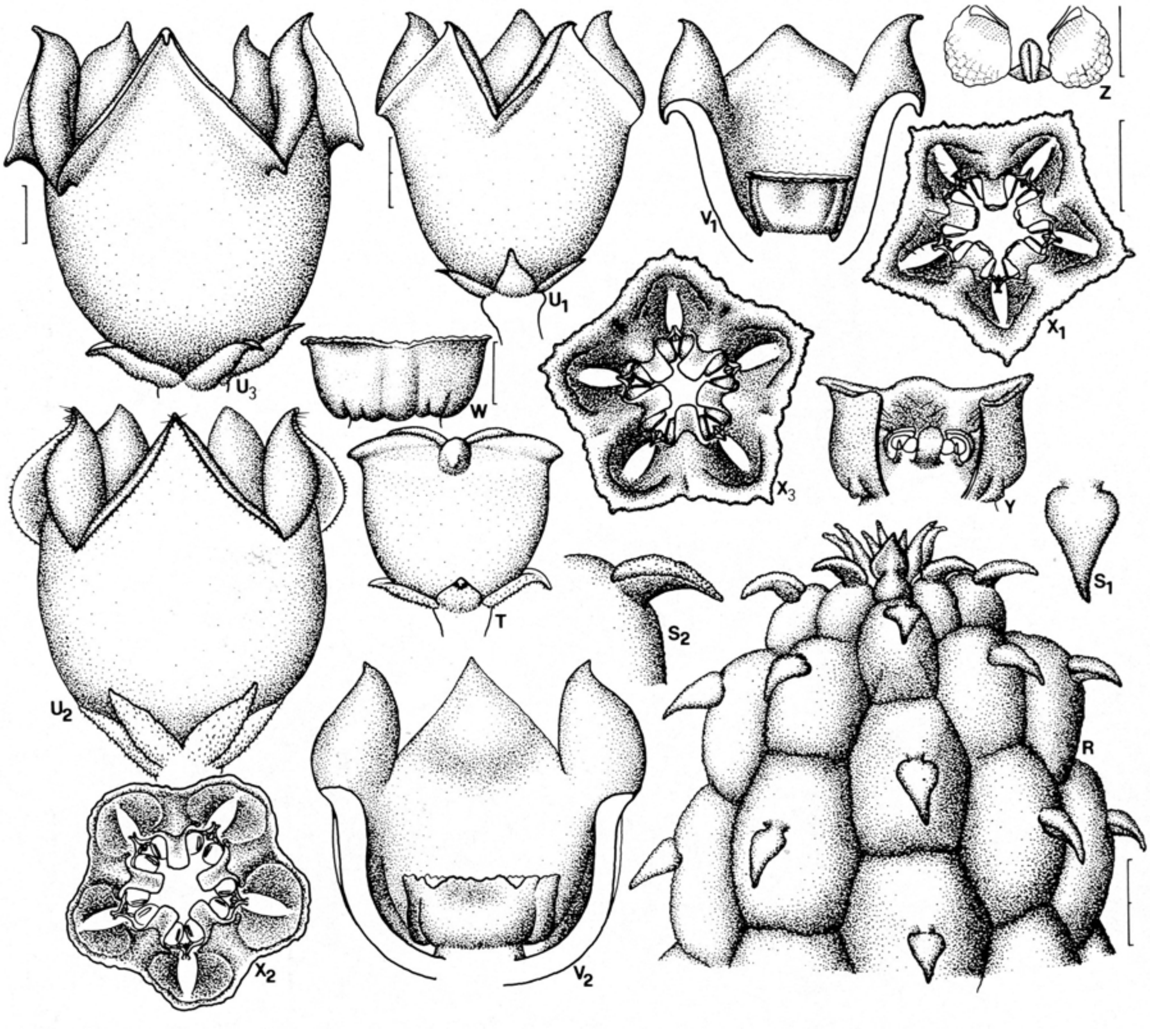


Fig. 26. **Echidnopsis archeri** Bally. R, stem apex (scale 2mm); S$_1$, face view of leaf (scale of Z = 1mm, as for S$_2$, Y); T, bud; U, side view of corolla (scale U$_1$ 2mm, as for T, V$_1$; U$_3$ 1mm, as for U$_2$, V$_2$); V, dissected side view of corolla; W, side view of staminal column (scale 1mm); X, face view of staminal column (all to scale at X$_1$, 1mm); Y, side view of staminal column with part of outer corona removed; Z, pollinarium (scale 0.25mm). R, S, W, X$_3$, Y, Z drawn from *Jenkins* s.n.; T, U$_3$, V$_1$, X$_1$ from *Classen* s.n.; U$_1$ from *Lavranos* s.n.; U$_2$, V$_2$, X$_2$ from *Bally* B11726.

broad at mouth (interior measurement); *lobes* erect, with margins folded back (sometimes finely ciliate) and acute tip reflexed, sometimes with small tuft of hairs at tip on exterior, 3.6-4mm broad at base, 2-2.8mm long. *Corona* 2-2.2mm diam., included within tube, pentagonal; *outer lobes* cupular, twice the height of central part of column, with few long hairs on inner surface, margins toothed, yellow around base to purple around mouth; *inner lobes* with broad base arising near middle of outer corona with small, triangular limb projecting onto backs of anthers but not extending over them, glabrous. (Fig. 26)

*Echidnopsis archeri* is known from two areas: the mountains north-west of Hargeisa in Somalia and the Nguruman Escarpment and Ngong Hills south of Nairobi in Kenya. In Somalia it has been gathered only once at Ga-an Libah by Bally (B11726, which he labelled '*E. archeri*?', apparently with some astonishment) while it is quite well-known from the other area. It is remarkable that both these areas are contiguous to ones where *E. sharpei* occurs.

*E. archeri* is similar to *E. sharpei* subsp. *repens* and differs from this taxon by its much deeper corolla-tube, which is deeper than the length of the corolla-lobes. From this the flower obtains its distinctive bell-shape—for the lobes do not spread out fully, remaining more or less parallel with the tube—and it is held in a dependent attitude. The stems are similar to those of subsp. *repens* in colour and shape of the leaves and differ mainly in being rather thicker and shorter with a slightly more upright habit. Investigations ought to be undertaken to examine more carefully the extent of their respective distributions to find out whether they intergrade.

Bally's material from Somalia differs from that from Kenya in having a more rounded tube to the corolla and small tufts of hairs at the tip of the corolla-lobes as well as small hairs along the margins of the lobes. This plant has not been recollected and it seems likely that *E. archeri* is of restricted distribution in both areas where it occurs.

17. **E. ballyi** (Marnier-Lapostolle) Bally in Kakt. and. Sukk. 14: 190 (1963) & in Cact. Succ. J. Gr. Brit. 26: 89 (1964).

*Stapeliopsis ballyi* Marnier-Lapostolle in Cactus (Paris) 65: 186 (1959). Type: Somalia, 5 miles north of Bihendula, *Bally* B11854, 11 Oct. 1957 (P, holotype in spirit now dried out, ZSS).

DESCRIPTION. *Stems* repent-decumbent with ascending apices, 50-120mm long, 15-25mm diam., 6-8-angled, angles tuberculate, tubercles slightly laterally flattened, more or less 4-angled, up to 7mm long including leaf, tapering into fleshy, rapidly caducuous, papillose leaf with broad base and acute tip and stipular gland on either side, glaucous green. *Pedicel* 10-15mm long, holding flower facing downwards. *Sepals* lanceolate, 2mm long with reflexed tips. *Corolla* dark purple-red inside tube and on exterior; *tube* pyriform-urceolate, up to 10-15mm long, 8-10mm diam. at maximum narrowing to 2mm at mouth (internal measurements), outside glabrous, shiny, with few longitudinal undulations, inside glabrous with longitudinal ridges becoming interlinked near mouth; *lobes* deltoid, erect to spreading, yellow, patched with red on inner face, forming slightly projecting folds in sinuses, margins and apex slightly reflexed. *Corona* 2.25mm diam., pentagonal; *outer lobes* united into deep cup with slightly constricted mouth divided indistinctly into 5 lobes, 2mm high, glabrous outside, within with stiff, translucent hairs, purple-red at base, becoming yellowish towards mouth; *inner lobes* united to outer corona about ½-way up cup, projecting out towards staminal column, touching on and adnate to backs of anthers for short distance, (spathulate) acute, up to 1mm long, 0.4mm wide, yellowish with purple-red blotches. (Fig. 27)

This remarkable species is known from only a few localities to the north of the settlement of Bihendula, some 20 miles south of Berbera on the northern side of the Sheikh Pass in north-western Somalia, where it is reputed to be quite plentiful. It was first collected by Bally on the 18th of January 1944, but the material proved difficult to grow and reluctant to flower. It was only on the third attempt in 1958 that Marnier-Lapostolle managed to persuade a plant to flower, whereupon he described it as *Stapeliopsis ballyi*. Bally himself does not seem ever to have seen live flowers and he went to examine the type in Paris (unfortunately no longer in an examinable state) and decided on the strength of the similarity of the corolla and corona to *E. urceolata* and the 6-7-angled stems, to place it in *Echidnopsis*.

It has been recorded rarely since then and the only documented collections are those of Brandham *et al.*, who collected it at a number of places in February 1981 in the same area as Bally's original collections. This material is still in cultivation at Kew and it has flowered each summer for the past few years, enabling me to examine living examples of its extraordinary flowers.

The stems of *E. ballyi* are unlike those of other northern representatives of the genus (apart from *E. montana*) and bear some resemblance to those of *Notechidnopsis columnaris* from South Africa. They are usually more than 2cm in diameter, bearing large, slightly laterally flattened tubercles which have on their apex a fat, bristly leaf which is shorter than that customary in species with long tubercles. The conspicuous, shiny, purple-red flowers are borne on a pedicel between 10 and 15mm long which is unusually long for this genus. This holds the flower rigidly facing downwards and very often buries the mouth of the corolla for up to 5mm in the loose debris on the surface of the soil. That this phenomenon is not coincidental is indicated by its being observed repeatedly and the fact that the pedicel holds the flower sufficiently firmly in this position as to be damaged by lifting. This may be an adaptation to pollination by a small terrestrial insect though this is unconfirmed, as it is also in two other stapeliads in southern Africa with partially or completely subterranean flowers (*Stapeliopsis pillansii* (N.E.Br.) Bruyns and *S. exasperata* (Bruyns) Bruyns). This orientation causes the corolla-tube to be pressed among small stones and sticks, frequently leading to its being rather misshapen and asymmetric.

Bally l.c. (1963) discussed the removal of this species from *Stapeliopsis,* where its author originally placed it. The superficial floral resemblance to *S. neronis* Pillans is indeed singular but the 4-angled stems, basal inflorescence bearing flowers over many seasons and the typically '*Stapeliopsis*' staminal column of *S. neronis* (Bruyns, 1981), are unlike that of any *Echidnopsis*. *E. ballyi* is the first of the florally highly specialised species and shows this in the complicated shape of the corolla with its broadly inflated base and narrow neck. This is also the first species where the inner surface of the corolla-tube is transversally convoluted, a feature which is considerably further developed in the next species.

18. **E. mijerteina** Lavranos in Cact. Succ. J. (US) 43: 64 (1971). Type: Somalia, Province of Migiurtinia, 60km from Scusciuban on the road to Gardo, 500m, 3 Dec. 1969, *Lavranos* 7268 (FI [not seen]).

*E. mijerteina* var. *marchandii* Lavranos in Cact. Succ. J. (US) 46: 184 (1974). Type: Somalia, Galgalo, 35km from Bender Cassim, 27 Nov. 1971, *Lavranos* 8999 (FI, holotype [not seen], K).

DESCRIPTION. *Stems* repent, rooting along most of length, tips usually ending just beneath soil surface, 8-10-angled, dull green, up to 200mm long, 8-15mm thick, hispid, angles weakly divided into tubercles each tipped by a subulate, hispid, rapidly caducuous leaf, with stipular gland on either side. *Pedicel* 3-6mm long, hispid. *Sepals* 2-3mm long, lanceolate, hispid. *Corolla* cylindrical, curved, 15-25mm long, exterior hispid, white to pale brownish, interior setulose, red-purple, veined; *tube* broadest (4-6mm) at base, constricted then widening very slightly at mouth, transversely ribbed for most of length; *lobes* erect to spreading, 1-2.5mm long, 3-3.5mm broad at base. *Corona* pentagonal, 3mm diam., yellow; *outer lobes* united into deep tube 2-2.5mm deep, distinctly 5-lobed with margins spreading, sometimes slightly toothed, straight hairs on inner surface; *inner lobes* rectangular, truncate, touching on base of anthers. (Fig. 28)

*Echidnopsis mijerteina* is known to occur most of the way up the eastern part of Somalia from just south of Eil to near Bender Cassim but, though Lavranos (l.c., 1971) indicated that it has been collected at many places, no attempt has been made to docu-

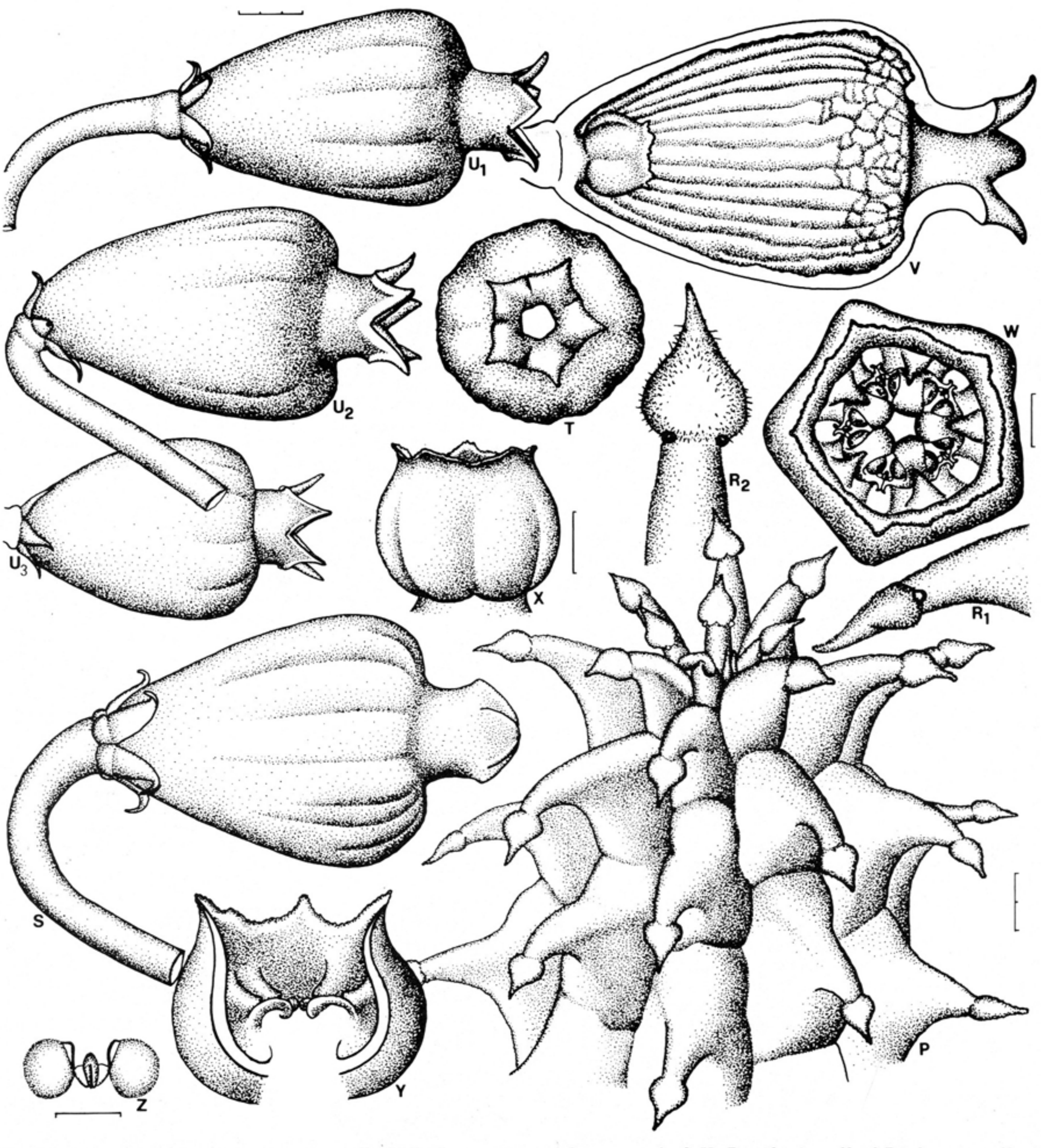


Fig. 27. **Echidnopsis ballyi** (Marnier-Lapostolle) Bally. P, stem apex (scale 2mm, as for S, V); $R_1$, side view of leaf; R2, face view of leaf (scale of Z = 1mm); S, bud; T, face view of corolla; U, side view of corolla (scale for all as at $U_1$ 3mm, as for T); V, dissected side view of corolla; W, face view of staminal column (scale 0.5mm, as for Y); X, side view of staminal column (scale 1mm); Y, side view of column with part of outer corona removed; Z, pollinarium (scale 0.25mm). All drawn from *Bailes* 167.

ment these collections. Plowes (1980) gives a very useful colour picture of it, giving some idea of the shape of the flowers and the nature of the stems.

Lavranos separated his var. *marchandii* from the typical variety by the stouter stems and shorter, proportionally wider flowers. In fact in the much mangled isotype (formerly at ETH and now at K) the flowers appear to be close to 20mm long and so only slightly shorter than in the typical variety. The species also seems to be very variable in the thickness of the stems and plants from Eil with longer flowers are often thicker-stemmed than he gives for the typical variety. In view of the variation in these characters, this taxon is not upheld.

In this species the entire plant is covered with fine, transparent bristles and is in fact more 'hairy' than is customary in the genus. The stems also show, in some cases, a lack of the usual deep division into tubercles and the division is slight, as in the next species, though the angles are not so narrow. The exterior of the flower is also hispid to a degree exceeding that found in the first section, the only other group where it is routinely setose. However, in *E. mijerteina,* the interior of the corolla is setulose,

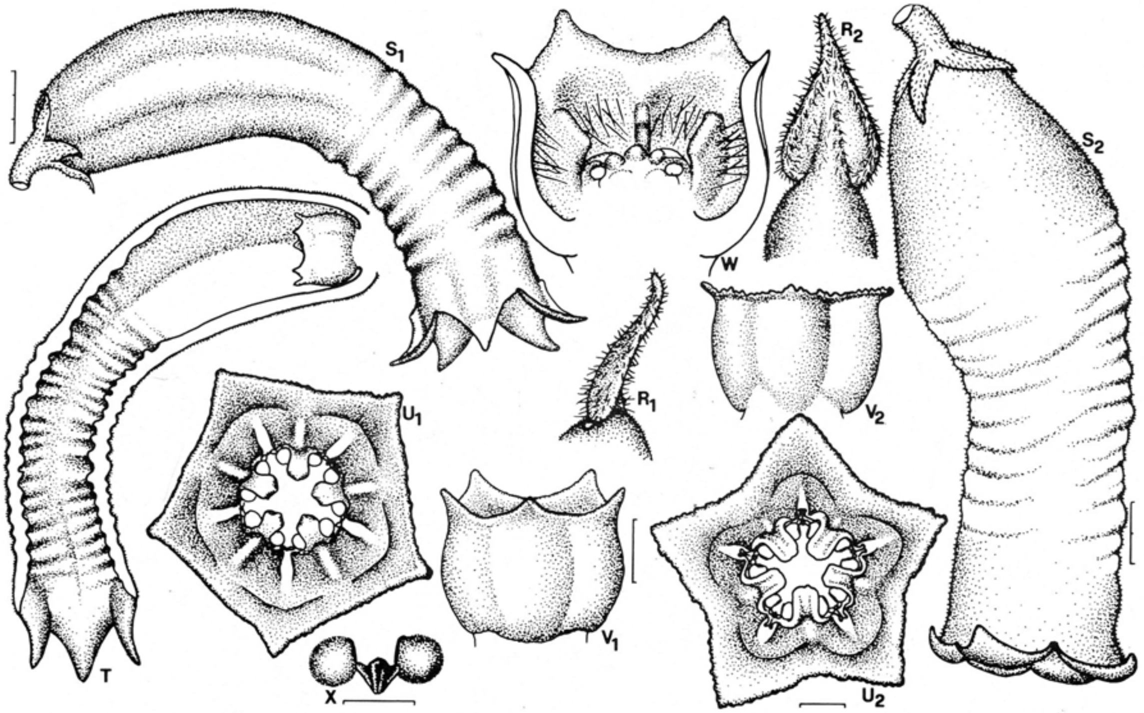


Fig. 28. **Echidnopsis mijerteina** Lavranos. $R_1$, side view of leaf; $R_2$, rear view of leaf (scale of W 1mm); S, side view of corolla (scale $S_1$ 3mm, as for T; $S_2$ 2mm); T, dissected side view of corolla; U, face view of staminal column (scale as at $U_2$ 0.5mm, as for W); V, side view of staminal column (scale as at $V_1$ 1mm); W, side view of column with part of outer corona removed; X, pollinarium (scale 0.25mm). R drawn from *Carter* 23399 (Somalia, 5km north of Eil, no specimen); $S_1$, T, $U_1$, $V_1$, W, X from *Lavranos* 8446; $S_2$, $U_2$, $V_2$ from *Lavranos* 8999.

as is typical of most *Echidnopsis*. The transverse wrinkling of the corolla-tube is also remarkable, being more pronounced than in any other species.

Some photographs of this species indicate the exterior of the corolla to be whitish. However, this is not always the case and it may be a pale greenish-brown. In this case, the flower bears a remarkable resemblance to that of *Ceropegia pygmaea* Schinz and the orientation of the flower, bend in the corolla-tube and the structure of the staminal column (Bruyns, 1984) are extremely similar.

19. **Echidnopsis malum** (Lavranos) Bruyns **comb. nov.**
*Pseudopectinaria malum* Lavranos in Cact. Succ. J. (US) 43: 10 (1971) & in Aloe 9: 31 (1971); Dyer in Flow. Pl. Afr. 41: t. 1626 (1971); Horwood in Cact. Succ. J. (US) 48: 286 (1976); Newton in Asclepiadaceae 17: 2-4 (1979). Type: Somalia, 22km north of Erigavo on road to Mait, 1200m, 27 Sept. 1968, *Lavranos* 6721 (FI [not seen]).

DESCRIPTION. *Stems* repent, rooting along entire length, 30-200mm long, 8-10mm diam., hispid, dark grey-green, 5-6-angled, angles laterally compressed, divided indistinctly into tubercles each tipped with a broadly deltoid, rapidly caducuous, hispid leaf with two glandular stipules on either side. *Pedicels* 10-15mm long, 15mm diam., finely papillose, holding flower erect. *Sepals* 2-3mm long, lanceolate, finely papillose. *Corolla* globose, 14-25mm long, 18-22mm broad, exterior with pale red streaks on grey-green background, covered with rounded papillae, interior dark purple-red, surface rugulose and finely setulose, with white to purple hairs (1-1.5mm long) in base and top, each arising from a broad papilla; *tube* occupying entire length of corolla, with depression in top from which lobes arise; *lobes* connate towards apices, pointing towards base of flower, outer surface small, folded, papillate, inner surface much expanded into broad, thick, deltoid, dark purple-red limb 4mm long and broad, setulose. *Corona* 4mm diam., circular in outline (face view); *outer lobes* red becoming yellow towards apex, united into urceolate tube, 3.5-5mm tall, narrowed at mouth with dentate, recurved margin, inner surface with white hairs; *inner lobes* arising from near base of outer lobes with broad base and narrow limb incumbent on but not exceeding anthers, yellow. (Fig. 29)

*Echidnopsis malum* is known to occur in the mountains north of Erigavo in Somalia, west of there in the area around Dire Dawa (east Ethiopia, Harerge Region), in the Sidamo Region of southern Ethiopia and the neighbouring part of north-east Kenya (Newton, l.c.) as well as from the coastal area near Mogadiscio, Somalia (Kew archives) and so it is of wide distribution in north-east tropical Africa. Over this range *E. malum* shows remarkably little variation.

Lavranos (l.c.) had the following to say in justification of erecting his new genus *Pseudopectinaria*: 'The habit and form of the stems . . . bear a striking resemblance to those of most members of the S. African genus *Pectinaria* Haw. and its flowers . . . have in common with those of its remote S. African relatives a globose corolla with lobes which are connate at their apices'. He adds further on that it 'differs from all other known Stapelieae by its large, globose flowers which are accessible by narrow slits between the corolla lobes which . . . are inflexed. The beautiful, urceolate outer corona is equally distinctive.'

The habit of *Pseudopectinaria* is indeed very similar to that of *Ophionella* (formerly *Pectinaria*) *arcuata* (N.E.Br.) Bruyns (Bruyns, 1981) but apart from this, there is no vegetative resemblance to any other *Pectinaria*. The habit and form of *Pseudopectinaria* stems is, however, widely found in *Echidnopsis* (*E. sharpei* subsp. *repens, E. mijerteina, E. ericiflora* etc.), differing from most *Echidnopsis* stems only in having more laterally flattened angles indistinctly divided into rather long, narrow tubercles. In fact when *Pseudopectinaria* is grown in exposed, drier conditions the tubercles are shorter and more distinctly divided so that the resemblance to *Echidnopsis* is more pro-

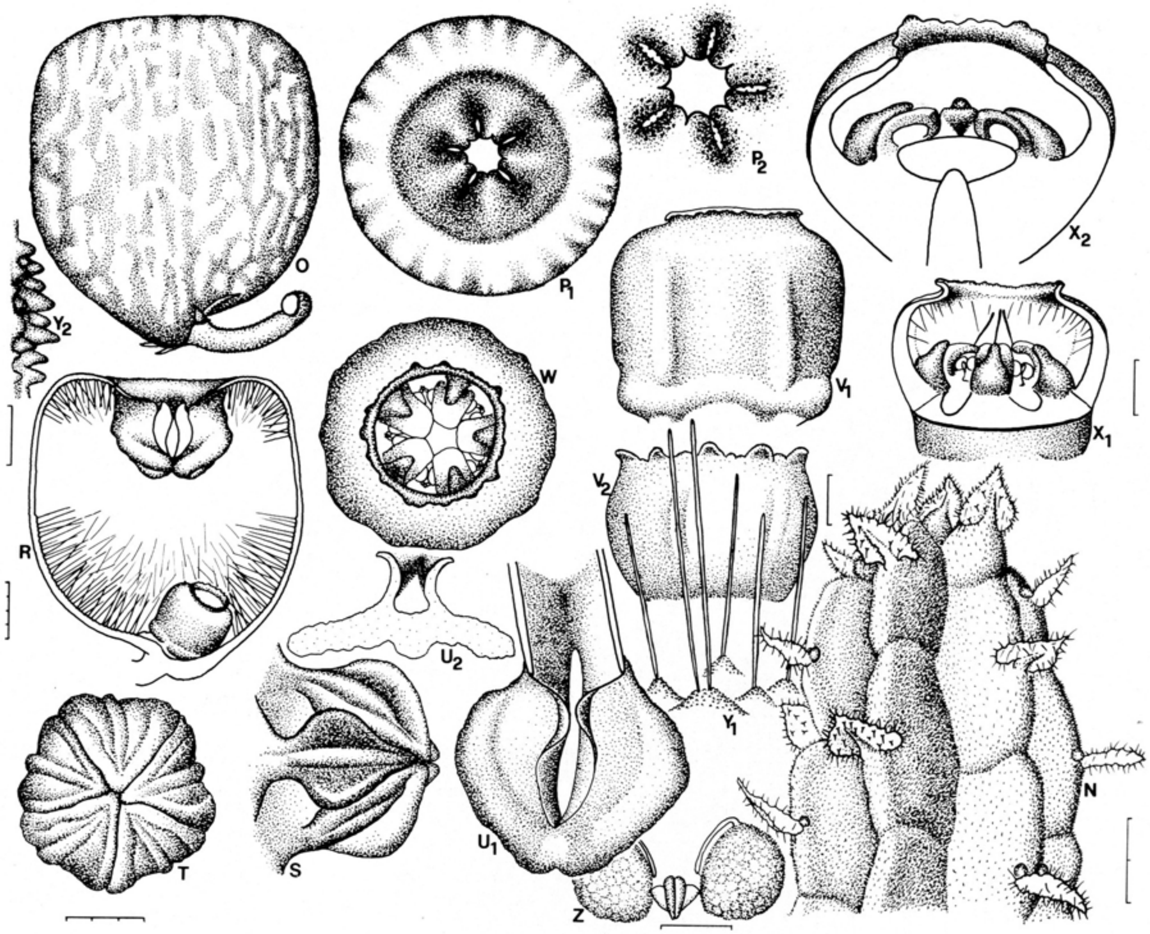


Fig. 29. **Echidnopsis malum** (Lavranos) Bruyns. N, stem apex (scale 2mm, as for U), note the narrow, only slightly divided tubercles; O, side view of corolla; $P_1$, face view of corolla; $P_2$, close-up of opening to corolla with papillae on lobes. (Each of the five, long, narrow incisions corresponds to the long, narrow, unshaded area running down the centre of $U_1$. The point on these incisions furthest from the centre of the sketch ($P_2$) corresponds to the MIDRIB of the respective corolla-lobe. The smaller, curved, V-shaped incisions closer to the centre are where the margins of adjacent lobes have separated from one another). R, dissected side view of corolla with two corolla-lobes removed (scale 4mm, as for O, $P_1$); S, side view of bolus formed by lobes inside corolla-tube. (Access to flower is gained through the space around the base of each lobe, above and slightly to left of letter S). T, face view of same in S. (This bolus remains tightly together during anthesis) (scale 3mm, as for $P_2$, S, $V_1$, W, $X_1$); $U_1$, ventral view of single corolla-lobe. (The two slightly undulating lines down the middle on either side of the long, narrow, unshaded area are the margins of the corolla-lobe. Access to flower is past these flaps into centre of bolus (S, T) after which insect has to climb up and out of bolus through gaps near its base (see S)). $U_2$, cross-section of same. (Margins of lobe are the two narrowest parts at top, ventral surface is the area between them and dorsal surface is the remainder). V, side view of staminal column (scale $V_2$ 1mm); W, face view of staminal column; X, side view of staminal column with outer corona partly cut away (for $X_2$ scale of Z = 1mm); $Y_1$, papillae and hairs on inside of corolla (scale of $Y_2$ = 0.5mm); $Y_2$, papillae on exterior of corolla (scale 0.25mm); Z, pollinarium (scale 0.25mm). $X_2$ from *Gilbert & De Wilde* 443; $V_2$ from *Newton* 12201; remainder all drawn from cultivated material at Karoo Botanic Garden of unknown origin.

nounced. Such long, narrow tubercles are found on some plants of *E. mijerteina* and *E. malum* bears very similar leaves to this species. The stems of *Pectinaria* do not bear any leaves. It appears that the only point of floral similarity between *Pectinaria* and *Pseudopectinaria* is that the former has a taxon (*P. articulata* (Ait.) Haw. subsp. *articulata*) in which the corolla-lobes too are inflexed into the corolla-tube and this seems to have influenced Lavranos unduly in his decision.

Apart from the upright habit of the flower, the main floral difference between *Pseudopectinaria* and *Echidnopsis* lies in the remarkable corolla-lobes. These are short and descend vertically downwards into the corolla-tube, ending in a tightly-knit bolus (viewed from below in Fig. 29 T) made up of the much expanded and thickened dorsal surfaces of the corolla-lobes which remain in this attitude throughout anthesis. The ventral surface is small and much folded (Fig. 29 $U_1$) and provides access to the flower past the small flaps formed by the margins of the lobes. Entry to the main chamber of the flower follows via the gaps around the bases of the lobes (Fig. 29 S).

In *Echidnopsis* the corolla takes on a wide spectrum of forms so that a globose one is not particularly remarkable. Hairs within the corolla-tube are found in *E. sharpei* as well. The claim (Lavranos, l.c.) that the outer corona is distinctive is fallacious and, as Plowes (1980) pointed out, such structures are typical of *E. ballyi* as they are too of *E. mijerteina*. *Pseudopectinaria*, if upheld, would have to be distinguished by the inward-pointing, unusually-shaped corolla-lobes and the narrow stem-angles and, as this is held to be inadequate to separate two genera as well as not indicating the relationships of this species properly, its single species is moved into *Echidnopsis*.

It is interesting to note the very similar growth form found in *Cynanchum rossii* Rauh (Rauh, 1970), a Madagascan species occurring in similar habitats to *E. malum*. This form is not otherwise known in *Cynanchum*.

### Natural hybrids involving species of Echidnopsis

1. *E. scutellata* × *E. sharpei.*
The collection *Gilbert* 2293, made in Harerge Region, Ethiopia, 5km north-east of Dire Dawa on the road to Djibouti (K) and illustrated here in Fig. 30, appears to represent this hybrid. A single plant was found growing under a pile of dead branches at the side of the road. The stems are prostrate, with ascending apices, up to or exceeding 400mm in length and the corolla is a dull brownish-red with red corona flushed with yellow. This plant was found growing with *E. scutellata* subsp. *planiflora* and *E. sharpei* subsp. *sharpei*. The leaves are longer than in the latter and are papillose, but they do not persist. The corolla is very similar in shape to subsp. *sharpei,* but has a brownish hue that clearly comes from subsp. *planiflora* and it is setulose as in the former (and unlike the other parent). The outer corona cup is rather deeper than in subsp. *planiflora,* with narrow rim but has essentially its structure. Hairs are found on both the corolla and the corona. There seems no doubt that Gilbert was correct in his assessment of the hybrid nature of this collection.

2. *E. dammanniana* × *E. virchowii.*
See account of *E. dammanniana* for details of this putative cross.

### Insufficiently known species

1. *E. bentii* N.E.Br. ex Hook. f. in Bot. Mag. 127: t. 7760 (1901); N.E.Br. in Bull. Misc. Inf. Kew: 141 (1901); A. Berger in Malpighia 16: 162 (1902); White & Sloane, Stap. 3: 983 (1937); Schwartz in Mitt. Inst. Allg. Bot. Hamb. 10: 192 (1939). Type: South Yemen, Hadramawt(?), *Bent* s.n., flowered Kew 1899 (K).

DESCRIPTION. *Stems* 120-150mm long, 12-20mm diam., ascending, pale brown, narrowing upwards, 7-8-angled, each rib divided into rounded (?) tubercles, tubercles tipped with ovate, concave, cuspidate leaf about 1.2mm long. *Pedicel* short (< 2mm?). *Sepals* ovate-lanceolate, acute. *Corolla* 12.5mm diam., exterior green, spotted with purple, interior velvety, deep red-purple; *tube* short, campanulate; *lobes* spreading, ovate, margins and acute apex reflexed. *Corona* acutely pentagonal; *outer lobes* united into cup, truncate, purple (with yellow margin?); *inner lobes* erect, conniving, shortly clavate, adnate at base to base of outer corona (Hooker, l.c.).

It is uncertain where Bent collected this and it has not been recollected. A living plant was given to Kew in 1897, in which year he and his wife had been in the Yafei and Fadhli countries to the east of Aden (Bent, 1900) and they may have obtained it there. Many authors have ascribed relationships of their species to *E. bentii,* but nothing like it has even been seen again. The dark-coloured flower, its obviously velvety (setulose) surface and the shape of the tubercles shown by Fitch in Hooker (l.c.) suggest *E. sharpei,* but the corona, as an examination of the type quickly reveals, is not of this species and is similar to that in *E. scutellata* with longer inner corona-lobes and more angular outline.

2. *E. multangula* (Forsskål) Chiovenda in Bull. Soc. Bot. Ital. 1923: 114 (1923).
*Stapelia multangula* Forsskål in Fl. Aegypt. Arab.: 52 (1775); Christensen in Dansk Bot. Arkiv 4 (3): 16 (1922). Type: North Yemen, Wasab (Uahfad), *Forsskål* s.n. (no specimen preserved).

DESCRIPTION. *Stems* branched, much repent, grooved into 6-9-angles, angles toothed (Forsskål l.c.).

Forsskål's locality Uahfad (known as Wasab today) lies in the upper reaches of the Wadi Zabid west of Al 'Udayn and Ibb and unfortunately it has not been possible to ascertain whether any *Echidnopsis* grows there today and which of *E. squamulata* or *E. scutellata* (the most likely candidates) he collected. The 'multum repens' suggests *E. squamulata* strongly but it is impossible to be sure and, in the absence of a type and more information on the area, this species is regarded as insufficiently known.

### Excluded species

1. *E. atlantica* Dinter nom. nud. in Fedde Rep. Sp. Nov. Beih. 23: 56 (1923) & in Fedde Rep. Sp. Nov. 30: 191-192 (1932); Lavranos & Barad in Madoqua 2: 163-165 (1978).

As suggested by Lavranos & Barad (l.c.) this is probably the intergeneric hybrid *Trichocaulon delaetianum* Dinter × *Tridentea ruschiana* (Dinter) Leach, although its true identity remains uncertain, as Dinter never saw any flowers.

2. *E. columnaris* (Nel) R. A. Dyer & Hardy = **Notechidnopsis columnaris** (Nel) Lavranos & Bleck.

3. *E. serpentina* (Nel) White & Sloane = **Notechidnopsis tessellata** (Pillans) Lavranos & Bleck.

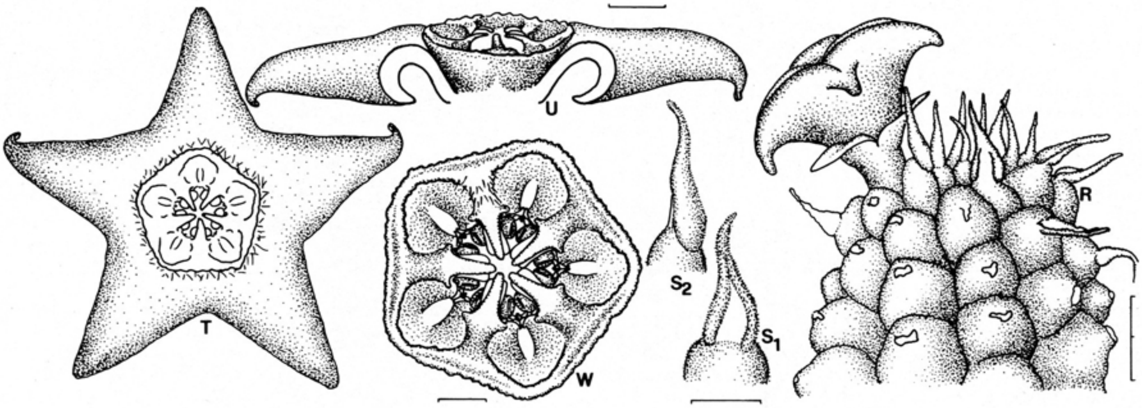


Fig. 30. **Echidnopsis scutellata × Echidnopsis sharpei.** R, stem apex (scale 2mm, as for T); $S_1$, rear view of leaf (scale 1mm, as for $S_2$); $S_2$, side view of leaf; T, face view of corolla; U, dissected side view of corolla (scale 1mm); W, face view of staminal column (scale 0.5mm). All drawn from *Gilbert* 2293.

4. *E. framesii* White & Sloane = **Notechidnopsis tessellata** (Pillans) Lavranos & Bleck.

5. *E. golathii* Schweinfurth ex Deflers in Mem. Inst. Egypt. 3: 267 (1896) = **Caralluma penicillata** (Deflers) N.E.Br.

6. *E. quadrangula* (Forsskål) Deflers in Bull. Soc. Bot. Fr. 43: 113 (1896) & in Mem. Inst. Egypt. 3: 265 (1896). = **Desmidorchis quadrangula** (Forsskål) Gilbert & Raynal.

## Material examined

This is located at The Herbarium, Kew, unless otherwise stated. Taxa are not listed where the only collection is the type. Material is listed from north to south and west to east.

2. **E. cereiformis.** SUDAN. Kassala Prov., Erkowit, 15 Sept. 1868, *Schweinfurth* 228; 21 May 1939, *Darvall* 1. ETHIOPIA. Eritrea Region, above Bab-Agam, 2135m, 2 Sept. 1962, *Mooney* 9437 (ETH); Gheleb, 1891, *Schweinfurth* 1794 (G); 10km south of Asmara towards Arum, 6500′, 5 Oct. 1969, on and between rocks, *Robertson* 1245; 16km from Asmara towards Aduwa, 2230m, steep slope with loose soil, flowers bright yellow, 20 Aug. 1973, *Gilbert* 2729; environs of Acrour, 1900m, 9, 23 Apr. 1892, *Schweinfurth & Riva* 1725 (G); Saganeiti, 2000-2200m, 13 March 1892, *Schweinfurth & Riva* 1273 (K,G); 10km north of Senafe, 2430m, steep limestone slopes with *Juniperus, Tarchonanthus* etc., flowers dark to light brown, 16 Aug. 1973, *Gilbert* 2713; Crater of Adaalanti (Plateau of Kohaito), 1-10 May 1894, *Schweinfurth* 359 (Z); Gonder Region, Maschiha distr., below Nahia, 23 Sept. 1852, *Schimper* 805, 809 (P). Not localised: *Bally* 382/49.

3. **E. dammanniana.** ETHIOPIA. Harerge Region, 7km south of Dire Dawa towards Harar, 14 Apr. 1972, growing inside small *Grewia* bushes, Gilbert 2374 (K, ETH); 10km south of Dire Dawa towards Harar, *Noltee* Eth 23; 5km south of Mojjo (Moja), 1900m, badly eroded area formerly *Acacia* woodland, volcanic ash, *Gilbert & Tewolde* 2453 (K, ETH, MO); 80km south of Addis Abeba, 1952, *Schelpe* s.n.; near Lake Langana, 1650m, 27 Nov. 1978, *Mesfin Tadesse* 496 (ETH); Awash Station, *Gilbert & Vollesen* 7932 (ZSS). SOMALIA. Galgalo, *Lavranos* 9039; Erigavo, *Lavranos* s.n.; Ga-an Libah Plateau, 19 Sept. 1957, *Bally* 11699; Go'o, north-west of Burao, barren rocky hillside, 9 Feb. 1981, *Bailes* 73;79; Hargeisa, Nov. 1961, *Hemming* 2285; Simodi (Semmade?), 5 Nov. 1932, *Gillett* 4570. KENYA. Dandu, *Gillett* 12628 (K, PRE); Mt Kulal, *Bally* 541.57; S176; 26 Nov. 1978, *Hepper & Jaeger* 7143; south of Mt Kulal, 20 Feb. 1979, *Bamps* 6641 (B); Marsabit, June 1942, *J. Bally* in *Bally* S104; Gof Choba, Marsabit, *Bally* B12399. Not localised: Somaliland, *Peck* in *Bally* S128; Somalia, Carbadan, Pozje di Cavernay, *Riva* 943 (Z); *Gillett* 128/55; Kenya, North Frontier District, *Classen* s.n. (PRE 58810).

4. **E. virchowii.** SOMALIA. Al Madu Range, Guri Ijer, 4900′, 15 Oct. 1956, *Bally* B11143; Ga-an Libah Plateau, *Bally* B11699; in rock crevices near precipice edge, 9 Feb. 1981, *Bailes* 83; limestone mountain east of Sheikh, 25 June 1981, *Gillett, Beckett & Watson* 23618; 0.5km south of Go'o, *Bailes* 79; north-east of Hargeisa, *Reynolds* 8479.

5. **E. angustiloba.** KENYA. 8km from Archer's Post towards Isiolo, 18 Dec. 1939, *Copley* in *Bally* S26; Longapito, Rumuruti, 27 Dec. 1983, *Powys* 524.

6a. **E. scutellata** subsp. **scutellata.** NORTH YEMEN. On limestone and rock crevices on slope east of Al Mahabishah, 30 May 1980, *Wood* 3265; road from Kuhlan to Hajjah, dry Wadi bed and sides, 1400m, 27 March 1981, *Miller & Long* 3259 (E); 7km west of Hajjah, 950m, *Noltee* 1434; Wadi Hayle, 8km east of At Tur on sandstone cliff, 450m, 18 Nov. 1982, *King* 167 (E); Wadi Hayle, dry forest on slope, 400m 4 March 1982, *Mueller-Hohenstein & Deil* 96 (BAYR); between Shemsaan Hamman and Rahbaan (Mahwit), Wadi La'ah, 27 Sept. 1978, *Wood* 2534; Wadi Sara, near Jum 'At Sari, 800m, 30 March 1981, *Miller & Long* 3332 (E); Khamis Bana Sa'd, 450m, *Noltee* 506/508; Usil (Uossil), 1400m, 10 Feb. 1889, *Schweinfurth* 1324 (G); Mishrafa, Wadi Rima, Aug. 1979, *Haig-Thomas* 1; SOUTH YEMEN. Wadi M'Aden, May 1894, *Deflers* 1167 (G).

6b. **E. scutellata** subsp. **dhofarensis.** OMAN. Dhofar Province, road from Thamarit to Salalah, Agabat al Hatab, 700m, 4 Oct. 1979, *Miller* 2811 (E); Thamarit to Salalah road, *Butler* s.n.; Jebel Qara, Jan. 1985, *McLeish* 85/19 (E); McLeish 83/52 (E); Ashinshaib to Zeak road, 800m, May 1985, *McLeish* 85/52 (E).

6c. **E. scutellata** subsp. **australis.** KENYA. 48km from Ramu towards El Wak, Mandera district, *Gilbert & Thulin* 1635; Choba Goff, Marsabit, *P. G. Archer* s.n.; collected 9 Mar. 1968, *Bally* 12565; *Lavranos & Bleck* 19527.

6d. **E. scutellata** subsp. **planiflora.** DJIBOUTI. 2km north of Adahala Egueraleyta, just south of Lake Assal, *Newton* 13178. ETHIOPIA. 48km west of Borama, *Plowes* 4909; 17km north-east of Dire Dawa towards Djibouti, on limestone with sparse cover of *Acacia* and *Commiphora,* 8 Apr. 1972, *Gilbert* 2320 (K, ETH, MO); 10km from Dire Dawa towards Djibouti on old road, 1300m, 1970, *Gilbert & De Wilde* in *Bally* 13872; 2 miles north-west of Dire Dawa, 1943, *Mitford-Barberton* in *Bally* S105 (ZSS); Dire Dawa, Sept. 1970, *Robertson* 1297; Marda Pass, Jijiga, *Plowes* 4262; Shewa Region, Awash Station, 1000m, 5 May 1983, *Gilbert & Vollesen* 7362. SOMALIA. Dabagha Pass, Jebel el Kebir, *Lavranos & Bavazzano* 8484; Karin Hills, 30 Oct. 1929, *C. N. Collenette* 207; 33km north of Erigavo, Tabah Pass, 950m, 20 Feb. 1981, *Bailes* 203; 4 miles north-west of Erigavo, Nov. 1970, *Lavranos* s.n. (PRE); 4km north-west of Erigavo, 9 Dec. 1969, *Lavranos* 7325; Jire Tug, near Abdal Qadr (Abdul Ghadir), 8 Nov. 1969, *Robertson* 1367. Not localised: *Plowes* 3842; Somalia, *Horwood & Lavranos* 10342 (ZSS); *Horwood & Lavranos* 10364, yellow form (ZSS).

7. **E watsonii.** SOMALIA. 5km west of Bawn, *Lavranos* 10421; 8 miles south-east of Borama, 6 Oct. 1954, 1600m, *Bally & Watson* B9997. KENYA. Mt Nyiru, north end and lower slopes, May 1940 (and 3 Nov. 1945), *G. Adamson* in *Bally* S49; Kailongol Mountain, *Mathew* 6839; Baragoi, escarpment on lava, Oct. 1960, *Classens* in *Bally* S49A; *Archer* s.n.; 65km north of Maralal on road to Baragoi, Lopet Plateau, 1375m, *Carter & Stannard* 467; near Barsaloi, *Powys* in *Lavranos* 12554; Karpeddo, *Lavranos* 18616; 10km north of Lake Baringo, *Plowes* 6311; Lake Baringo, *Plowes* 6515b; Lali Hills, Galana River, Nov. 1985, *Powys* 789; south-west of Sobo Rock, 42 miles from Voi Gate, Tsavo Nat. Park East, 3 Jan. 1967, *Greenway & Kanuri* 12954.

8. **E. ericiflora.** KENYA. Lali Hills, Galana River, Nov. 1985, *Powys* 793; 42km south-east of Voi on road to Mombasa, 15 Jan. 1972, *Lavranos* 9305 (PRE); *Plowes* 3962.

9. **E. squamulata.** NORTH YEMEN. 84km north of Ta'izz towards Sana'a, 1350m, March 1974, *Potter* s.n.; Jebel Ra's, north-east of Hays, on terrace wall in small cultivated valley, 1400m, 9 Apr. 1981, *Miller & Long* 3508 (E); Ta'izz, 10 Jan. 1977, *Barad* s.n.; Wadi Sina, south of Ta'izz, 1837, *Botta* s.n. (P); 15km east of Ta'izz, *Newton & Lavranos* 13101; in protection of *Acacia,* scrub near Ar Rahidah, 28 Oct. 1978, *Wood* 2593. SOUTH YEMEN. Al Awadhil Plateau, north of Lawdar, 1962, *Lavranos* 1822, 1823, 1841 (PRE); 4 miles north-east of Dhala, Amiri Highlands, *Lavranos* 1869 (PRE, K).

10. **E. urceolata.** ETHIOPIA. Harerge Region, 5km south of junction between Gabredarre–Warder and Gabredarre–Shillave roads, 17 June 1971, *Gilbert* 2105; Bale Region, El Carre, 920m, Apr. 1943, *Jackson* in *Bally* S112. KENYA. Malka Mari, 1951, *Williams* in *Bally* B8008 and S209 (ZSS); *Newton & Lavranos* 12210; 30km on Ramu–Malka road, 400m, limestone valley, very steep in places with much bare rocks, common, 3 May 1978, *Gilbert & Thulin* 1566; 50km west of Ramu at Lag Olla, 580m, 25 Jan. 1972, *Bally & Radcliffe-Smith* 14956.

13. **E. montana.** ETHIOPIA. Harerge Region, Harar, 12 Nov. 1974, *Mason* 139; Shewa Region, 60km south-west of Awash Station, savannah on porous, lava rocks, *De Wilde* 10512 (B, MO); Adama Hill, *McLoughlin* 835 (K, ZSS, PRE); near Adama, *Plowes* 6684; 220km south of Addis Ababa on main road to Nairobi, *Noltee* s.n. Not localised: Ethiopia, *J. W. Ash* 491; *Lavranos* 9206 (PRE).

14a. **E. sharpei** subsp. **sharpei.** ETHIOPIA. Harerge Region, 5km north-east of Dire Dawa on road to Djibouti, *Gilbert* 2497; Bale Region, 3km south of Ginir, on limestone in *Commiphora* woodland, *Gilbert & Vollesen* 7864; Sidamo Region, 60km from Negelli towards Welensu Ranch, *Gilbert & Vollesen* s.n. KENYA. Malka Mari, 920m, June 1951, *Williams* in *Bally* S208 (ZSS); Kerio Valley, *Classen* in *Bally* 12261 (*Bally* 419/60); Marsabit Mtn, 17 Jan. 1972, *Bally & Radcliffe-Smith* 14884; 30 miles south of Lake Turkana, near Baragoi, 1937, *Sharpe & Jex-Blake* in *Bally* S7 (K, ZSS); 59 miles south-east of Maralal, *Newton & Lavranos* 17698; Longapito, Dec. 1983, *Powys* 524A; Nduru, Rumuruti, 1985, *Powys* 819; Adable, Tanaland, Feb. 1940, *Ritchie* in *Bally* S43; 13km from Galole towards Garsen, 10 July 1974, corolla-lobes sometimes tipped with yellow, *Faden* 74/1045 (K, MO). Not localised: SOMALIA, 21 March 1973, *Lavranos* 10183 (PRE).

14b. **E. sharpei** subsp. **repens.** KENYA. 4km south of Ilbisil, *Bleck & Lavranos* 19571; Namanga, Jan. 1972, *Archer* 714; Loitokitok, 1960, *Rauh* Ke 276 (ZSS); Maktau & Lutema Hill, July 1942, without flowers, *MacArthur* in *Bally* S6 (PRE). TANZANIA. Mt Meru, 1938, *Pole-Evans & Erens* 1020 (PRE); Ngare Nanyuki, Arusha District, 20 Mar. 1966, *Greenway & Kanuri* 12448; *Greenway* s.n.; 29 Dec. 1970, *Richards* s.n.

15. **E. bihendulensis.** SOMALIA. Bihendula, below Sheikh Pass, Jan. 1944, *Bally* S125; rocky hill 1km north of Manja Asseh, 15 Feb. 1981, *Bailes* 169; 3.8km south of Hudiso, stony hillside in shade of rocks, 15 Feb. 1981, *Bailes* 156.

16. **E. archeri.** SOMALIA. Ga-an Libah, north slope, 1460m, 19 Sept. 1957, *Bally* B11726. KENYA. Nguruman Escarpment, Oloibitato River near Hayton's Falls, 11 Sept. 1952, *Archer* in *Bally* S235; Nguruman Escarpment, *Lavranos* s.n. (PRE); Ngong Hills, Masai District, Dec. 1959, *P. G. Archer* s.n. Not localised: *Classen* s.n.

17. **E. ballyi.** SOMALIA. Bihendula, beneath rocks, 1957, *Bally* B11854 (ZSS, P); Manja Asseh, rocky hill 1km north, flat exposed area with rock slabs, 15 Feb. 1981, *Bailes* 167 (*Carter* 902, 903); Manja Asseh, sloping rocky hillside with sparse vegetation, *Carter* 908.

18. **E. mijerteina.** SOMALIA. Galgalo, *Lavranos* 8999; 2km south of Eil, *Lavranos* 8446. Not localised: Mar. 1973, *Lavranos* 10182 (PRE).

19. **E. malum.** ETHIOPIA. 5km north-west of Dire Dawa on road to Djibouti, Apr. 1971, *Gilbert & De Wilde* 443. KENYA. 46km west of Mandera. 8 Aug. 1975, *Newton* 12201.

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# Systematic anatomy of the primitive cereoid cactus Leptocereus quadricostatus

*James D. Mauseth*
*Department of Botany, The University of Texas*
*Austin, Texas 78713, U.S.A.*

*and Robert G. Ross*
*Department of Biology, The University of Cayey*
*Cayey, Puerto Rico, U.S.A.*

*Summary. Systematic anatomy of the primitive cereoid cactus Leptocereus quadricostatus.* The genus *Leptocereus* is widely regarded as one of the most primitive of Cactaceae subfamily Cactoideae. It resembles the pereskias in having dense fibrous wood in its trunk and lower branches; this wood lacks vascular tracheids; it has septate protophloem fibres; and the ray cells are all thick walled and lignified. However, it also shows the beginnings of many features which are associated with the more advanced cacti: it has an enlarged, palisade cortex, a system of cortical vascular bundles, and medullary bundles. In addition, the wood of the uppermost portions of many branches is very parenchymatous, unlike the fibrous wood of the trunk. In some portions of the shoot, especially in the cephalia, the wood consists of just parenchyma and vessels, a trait which had been considered quite advanced. It seems reasonable that a strongly dimorphic plant such as *Leptocereus* would be able to give rise to the numerous diverse lines of evolution which exist in the Cactoideae.

*Zusammenfassung. Systematische Anatomie der primitiven cereoiden Kakteenart Leptocereus quadricostatus.* Die Gattung *Leptocereus* wird allgemein als eine der ursprünglichsten der Unterfamilie Cactoideae der Familie Cactaceae betrachtet. Sie ähnelt den Pereskien durch das faserreiche Holz von Stamm und unteren Seitentrieben; diesem Holz fehlen Leitbündel-Tracheiden, es verfügt über septate Protophloem-Fasern, und die Zellen der Markstrahlen sind alle dickwandig und verholzt. Die Art zeigt aber auch Ansätze zu Merkmalen, wie sie bei höher entwickelten Kakteen vorkommen: Sie besitzt einen Cortex mit vergrössertem Palisadenparenchym, ein System von corticalen Gefässbündeln, und medulläre Gefässbündel. Zusätzlich ist das Holz der oberen Teile der Seitentriebe parenchymreich und weicht vom faserreichen Holz des unteren Stammes stark ab. In einigen Teilen der Triebe, vor allem in den Cephalien-tragenden Teilen, besteht das Holz nur aus Parenchym und Gefässen, eine Eigenschaft, die als ziemlich fortgeschritten betrachtet wird. Es erscheint wahrscheinlich, dass eine so stark dimorphe Pflanze wie *Leptocereus* am Ausgangspunkt verschiedener Entwicklungslinien innerhalb der Cactoideae stehen könnte.

## Introduction

The family Cactaceae is considered to be divided taxonomically into three groups: (1) subfamily Pereskioideae contains the species which have retained the greatest number of primitive characters (Leuenberger, 1986). The features include large, planar, photosynthetically active leaves, woody stems which are not at all succulent in many species or only slightly succulent in others (genera *Pereskia* and *Maihuenia* [Gibson, 1977b; Hunt & Taylor, 1986]). (2) The second subfamily (Opuntioideae) contains the large genus *Opuntia* and its close relatives, *Pereskiopsis* and *Quiabentia*. (3) All of the rest of the cacti, which encompass tremendous diversity in their size, habit, habitat, anatomy and ecology, are placed into subfamily Cactoideae.

Although there have been numerous theories presented about the lines of evolution within the Cactoideae, virtually all current investigators agree that the genus *Leptocereus* contains the species which are the least derived; *Leptocereus* has retained many of the characters of the early taxa which arose as the Cactoideae evolved from the Pereskioideae (Figs. 1, 2, 3).

If *Leptocereus* is in fact primitive, then a study of it will provide information about the evolutionary processes which occurred as this family became more succulent, xerophytic and highly specialized. Such processes have been carefully documented already for *Pereskia, Quiabentia* and *Pereskiopsis* (Bailey, all references; Leuenberger, 1986); more recently Gibson has provided extensive anatomical-systematic surveys of the wood of

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many taxa in the Cactoideae of Mexico (Gibson, 1973; Gibson & Horak, 1978). The present study was undertaken to provide detailed information about the intermediate stages between the most primitive cacti (the Pereskioideae) and the more specialized ones; it will also serve as a basis for the analysis of other lines of evolution within the Cactoideae.

## Materials and methods

Samples of *Leptocereus quadricostatus* (Bello) Britton & Rose were collected near Guanica in Puerto Rico. Material was fixed overnight in Randolph's modified Navashin's solution (Johansen, 1940), rinsed in 70% ethanol, then prepared for paraffin microtomy. Some material was treated with hydrofluoric acid to soften it before dehydration. Sections were stained with safranin-fast green as described by Mauseth (submitted for publication). All measurements are given as means, followed by standard deviations, designated SD.

## Observations

***Root.*** *Epidermis.* None of the roots which were examined were young enough to retain epidermis. Seeds were sown, but only a few germinated and the roots of most died before they could be examined.

*Periderm.* The periderm of all older roots is complex, consisting of at least four alternating layers of thick walled sclereids and thin walled phellem cells (Fig. 4). The sclereids are more prominent, having walls that average 6.4μm thick. The cells appear flat in radial section, with a mean height of 16.5μm and width (parallel to the root circumference) of 26.0μm. In tangential view they are irregularly angular (Fig. 5), with shapes ranging from almost square to elongate and narrow (176μm by 30μm). Simple pits occur in all walls, being quite prominent in the tangential walls at a density of 8.8 per 100μm$^2$. There are only three to four sclereids in each file in each layer.

The phellem cells collapse almost completely; each layer is only a few micrometers thick, and it is impossible to count the number of cells present; we estimated that certain areas might have up to 20. In no area of any of the sections did we encounter expanded, uncollapsed phellem cells.

Interior to the innermost dead cells is a layer of large living parenchyma cells (Fig. 6). Because these are aligned with the dead cells, they must have been produced by the phellogen. Consequently we interpret them to be phelloderm cells. They are living and their contents appear to be similar to those of the cortex cells. In some areas the phelloderm is three cells thick, in other areas it is up to seven cells deep. There can be occasional radial divisions within the phelloderm cells. We did not encounter anything that could be interpreted as a lenticel in the root bark.

*Cortex.* The root cortex is about 1.2mm thick and consists of approximately 20 layers of parenchyma cells with diverse sizes. There are numerous air spaces, and druses are abundant throughout, occurring in cross sections at a density of 2.3 per 100μm$^2$.

The most significant feature of the root cortex is the presence of cortical vascular bundles (Figs. 7, 8, 9, 10). These are present in all root cross sections, but they are irregularly distributed: two or three might be near each other whereas in the same section a different sector of cortex would have none. Most are collateral, containing both xylem and phloem (Fig. 8), but in some cross sections, bundles of just phloem (Fig. 9) or of just xylem (Fig. 10) were encountered occasionally. In the collateral cortical bundles, the phloem can be either exterior or interior to the xylem. The number of tracheary elements present at any cross section of a root cortical bundle varies from zero or one up to ten. The xylem consists of small (65μm long by 20μm in diameter) vessel elements with scalariform bordered pits and small circular perforations (Fig. 11). The cortical bundles may turn abruptly, and at these points the vessel elements are short and have irregular shapes.

The phloem of the root cortical bundles contains companion cells, but the nature of the sieve elements could not be determined: some had the shape of sieve tube members, being cylindrical with transverse end walls. However, unequivocal sieve plates could not be found, nor were plugs of either callose or p-protein found. In contrast, the lateral walls of the cells were almost completely covered by sieve areas.

The root cortical bundles are located mostly in the outer regions of the cortex, not next to the stele (Fig. 7). They are connected to the stele, being attached along the interface between a ray and the axial vascular tissue.

Older portions of the roots contain a narrow parenchymatous pith. This is not rich in starch, but individual, isolated vessels did run through it (Fig. 12).

*Stele.* The axial component of the root secondary xylem consists of libriform fibres, vessels and scanty paratracheal parenchyma (Fig. 13). The fibres are living, containing nuclei and abundant starch. Many are septate, and the presence of forked ends indicates that they had undergone intrusive growth (Fig. 14). Pits are few and have elongate, slitlike inner apertures. The libriform fibres are 585 SD 144μm long and 19.6 SD 6.4μm wide. Some are uniformly tapered (spindle shaped) but many have a rather cylindrical central section while both ends are narrow and elongated, somewhat resembling a vessel element with exaggerated tails (Fig. 15). The fibres constitute over half of the cross sectional area of the axial xylem.

The vessel elements in the root secondary xylem all have scalariform bordered pits and simple, round perforations (Fig. 16). In most cases the pits become extremely elongated tangentially, extending around more than half the circumference of the cell. As the pits interdigitate, the wall appears to be helically thickened rather than scalariform. However, it is possible to verify that these are not actually helical walls because the 'helices' branch. The vessel elements average 279 SD 45μm long and 28.7 SD 8.4μm wide; the perforations are 21.9 SD 5.5μm in diameter. Many lack tails completely, but in others the tails are prominent and can be over 12.9μm long. The vessels are mostly solitary, but clusters of two or three are not uncommon.

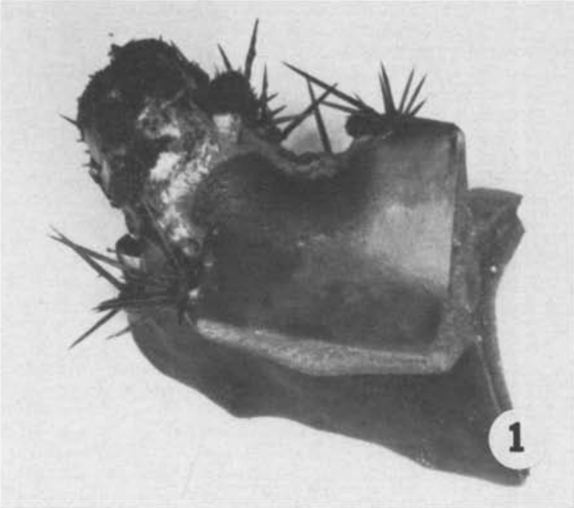
Axial parenchyma is scanty and paratracheal; the parenchyma cells occur as individuals adjacent to vessel elements; they do not constitute a complete sheath (Fig. 17). Even if there are several vessels close together, there are still only a few idioblastic parenchyma cells. Axial parenchyma cells were never observed among the libriform fibres. These parenchyma cells have walls which are thicker than those of the cortex, and they are lignified. They do not seem to contain any more starch than do the libriform fibres.

The rays of the secondary xylem are multiseriate, averaging 5.7 cells wide, but with some being up to 12 cells wide (Fig. 18). The cells are cuboidal and large, about 58μm on each side. The walls are thick (2μm), lignified and have large simple pits which are 2 to 5μm in diameter. None of the ray cells has only thin, primary walls. Adjacent to the secondary walls is an extremely thin layer of material which absorbs fast green and which may be cytoplasm; nuclei are present, but large masses of cytoplasm were never seen even though these samples were collected from living roots and were fixed immediately. Each cell contains several large starch grains.

As the diameter of the root increases with continued secondary growth, new rays are established, presumably by the derivation of new ray initials from existing fusiform initials. When first initiated, the sets of ray initials are uniseriate, but they become multiseriate with age.

The stele contains only a small amount of secondary phloem, and it is entirely axial: the interfascicular cambium is unifacial and does not produce phloem rays (Fig. 13). The axial phloem is scanty, there is just a thin cap of phloem exterior to each group of axial xylem. The caps are only about 10 to 15 cells deep, and

Figs. 1-6. 1. Cephalium and short section of vegetative shoot. ×50. 2. Terminal vegetative shoot, with a short cephalium on left. Three of the four winglike ribs are visible on the vegetative portion, ×0.5. 3. Cephalium, ×3. 4. Periderm of root, showing phelloderm and alternating layers of phellem and sclereids, ×72. 5. Tangential view of root periderm sclereids, ×180. 6. Phelloderm cells of root, ×180.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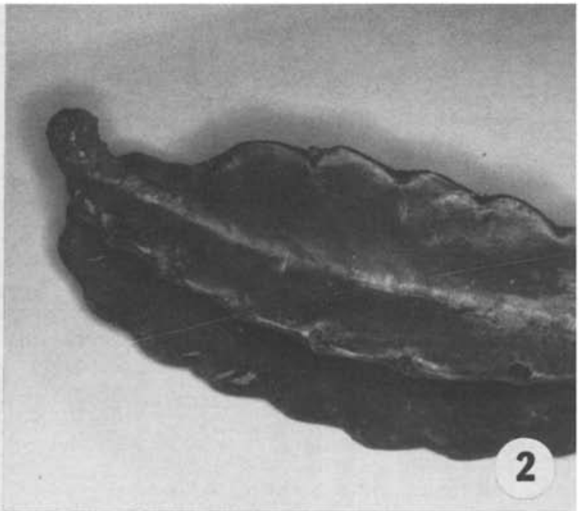
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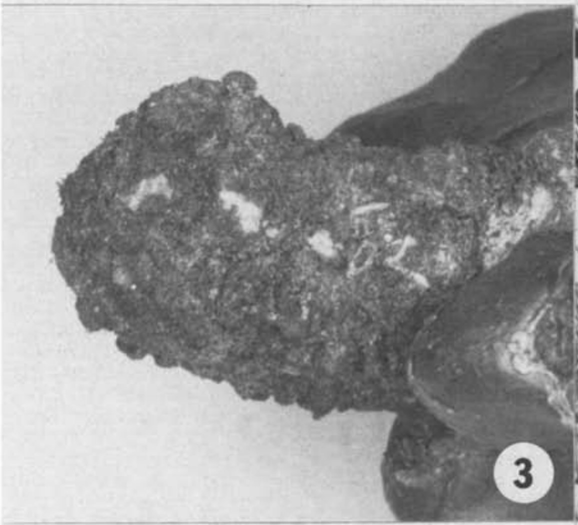
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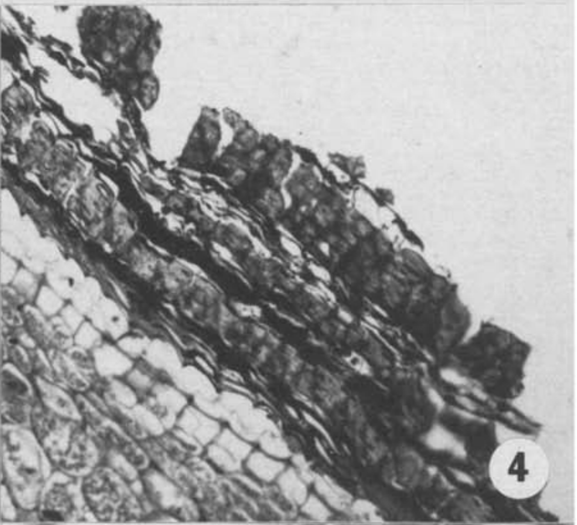
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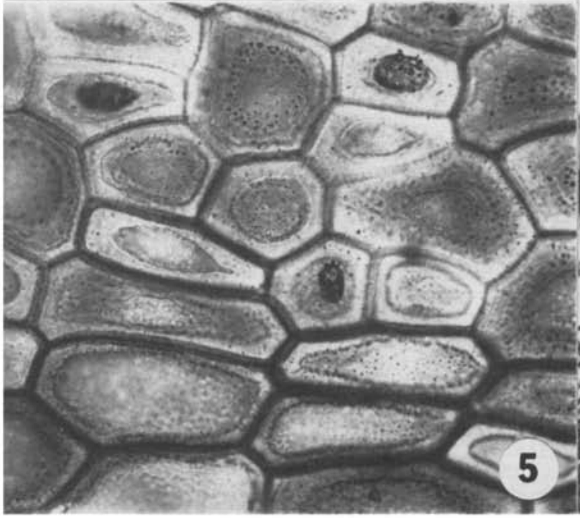
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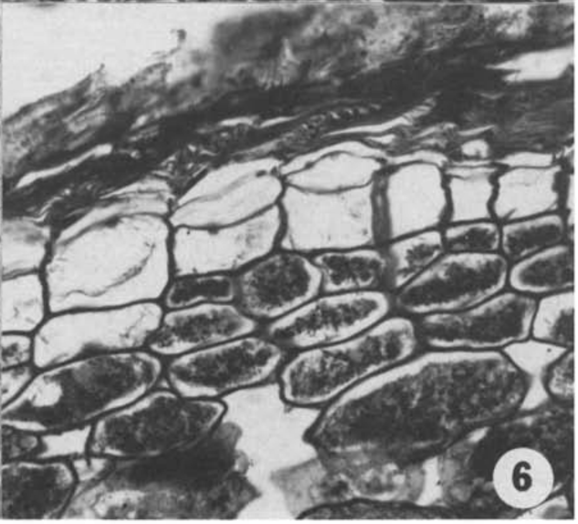
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they contain companion cells, sieve tube members and nonconducting parenchyma cells. Unlike the sieve elements of the root cortical bundles, those of the stele axial system are definitely sieve tube members: they have easily visible sieve plates (15$\mu$m in diameter) with large sieve pores, whereas the lateral sieve areas are small and few (Fig. 19).

There is a layer of collapsed phloem on the outermost side of the phloem mass. No sclerenchyma of any type is associated with either the primary or the secondary phloem in the roots.

***Shoot.*** *Epidermis.* The young shoot is covered by an epidermis that consists of tabular cells approximately 14$\mu$m tall and 16 to 20$\mu$m wide (Figs. 20, 21). The outer periclinal wall is thin and smooth, there are no papillae or projections of any kind. The inner periclinal wall is thickened, as are the adjacent portions of the radial walls. The cuticle is about 3$\mu$m thick. Rhomboidal crystals may be present in many epidermal cells (Fig. 22). Guard cells are smaller than surrounding subsidiary cells and are located near the outer epidermal surface; they are not sunken and do not occur in crypts.

Interior to the epidermis is a hypodermis of three to five layers of flat, thickwalled cells with large pits (Figs. 20, 21). The hypodermal cells have prominent nuclei and abundant cytoplasm, much of which is located in the wide pits. The secondary walls of the hypodermal cells do not stain with safranin and thus are presumably nonlignified. There is a chamber through the hypodermis below each stoma. No crystals were observed in hypodermal cells.

Even while a portion of the shoot is young and photosynthetic, bark may be produced. The phellogen results from an activation of the epidermal cells (except for guard cells), which undergo periclinal divisions and produce phellem. The phellem layer is rather thin and transparent, and it bears the intact cuticle on its outer surface. This precocious cork layer may cover large areas of the shoot or it may occur in small patches. The crystals which had been present in the epidermis persist in the phelloderm, which is only two to three layers thick. With age, a multilayered bark is formed that appears to be virtually identical to that on the roots: collapsed layers of phellem alternate with layers of thick walled, lignified sclereids. We found that portions of a shoot which had five alternating layers; even under such thick bark, the cortex contains abundant chloroplasts, so this periderm may be translucent also. On plants that are extremely old and which have a thick treelike trunk, the base is covered with a flaky bark that is opaque. The bark on the shoot contains lenticels.

*Cortex.* The cortex is composed of an outer chlorenchymatous region and an inner area that lacks chloroplasts. Mucilage cells are abundant. The shape of the cortex is variable: in some specimens the body has low ribs only a few millimetres high; in others the ribs are about 1cm tall (Fig. 2). The outermost cells are columnar and arranged in files perpendicular to the rib surface (Figs. 20, 23); they are apparently produced by a plate meristem, but the developmental stages were not studied.

The cortex contains numerous cortical bundles which are distinct from the areole traces (Figs. 24, 25, 26). They average 83 SD 6$\mu$m in diameter and they contain both xylem and phloem. The xylem consists of tracheary elements with 'scalariform-helical' secondary walls. At a given cross sectional level, each shoot cortical bundle contains between 5 and 14 tracheids. The phloem consists of sieve tube members, companion cells and nonconducting parenchyma. There is no bundle sheath: the cells adjacent to the conducting tissues are large cortex cells and no endodermis was found.

The shoot cortical bundles tend to be larger than those in the root; they also branch profusely and form an extensive network. Presumably their function is similar to that of the minor veins of the leaves of other plants, because the cortical veins permeate a large photosynthetic tissue. Unlike leaves, however, the cortex of these plants is persistant for many years, perhaps hundreds of years on large plants, so the cortical veins must function for long periods. The cortex on old branches is yellow, not green, but the cortical cells are living, they have nuclei and spherical inclusions which may be protein bodies (Fig. 26). The cortical bundles in these old regions (Fig. 26) are slightly larger than those in young branches (Fig. 25): the number of tracheids in each cross section is 16.7 SD 6.7 in the bundles of an old trunk but only 8.4 SD 3.2 in bundles in a young branch. There is a small amount of phloem that appears quite healthy in both old and young cortical bundles. It is difficult to determine if more phloem has been produced, because old phloem collapses. The phloem usually collapses into a flat plate, and the amount of collapsed phloem in old cortical bundles formed a plate 161 SD 94$\mu$m long whereas in young cortical cortical bundles it is only 45 SD 13$\mu$m long. However, the healthy sieve tube members and companion cells did not form files and did not appear to have been formed from a cambium (Fig. 26).

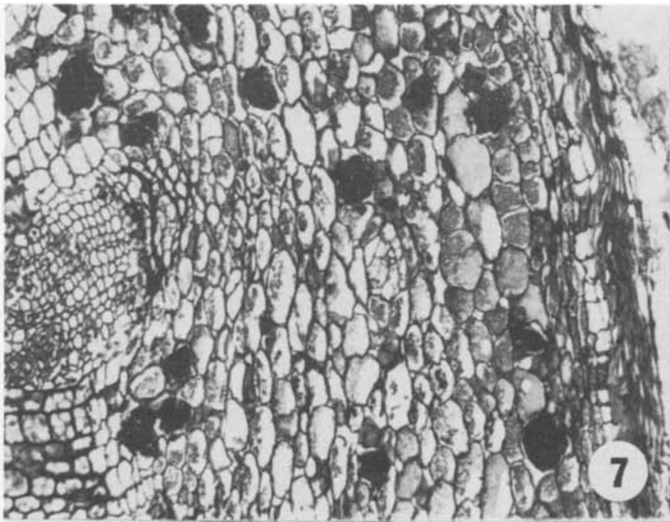
*Stele.* In a young shoot, the stele consists of a set of collateral bundles (about 30 to 60 in number) which surround a parenchymatous pith. The pith of *Leptocereus quadricostatus* is narrow in comparison to the pith of many other cacti, with a diameter of only 1 to 5mm. The shoot sample which had a pith 1mm in diameter was the youngest shoot we collected, having very little secondary xylem; shoots which are older have wider piths. One large plant with a trunk diameter of 60mm had a pith that was 5mm wide. There are medullary bundles present, four in the narrow pith, 12 to 14 being present at any cross section of the older shoots with wider piths (Figs. 27, 28). The medullary bundles are similar to the cortical bundles: they are collateral, the xylem consists of tracheary elements with 'scalariform-helical' secondary walls and the phloem contains sieve tube members, companion cells and nonconducting parenchyma. They have no detectable bundle sheath. In the medullary bundles, the xylem is less prominent than it is in the cortical bundles: one bundle had 12 tracheids at one cross section but most had only three. Conversely, the phloem of the medullary bundles is larger than that of cortical bundles: three to eight conspicuous, healthy sieve tube members being commonly present at each cross section. In the medullary bundles in older shoots, there were no obvious signs of secondary growth. There are no fibres or sclereids associated with medullary bundles.

In addition, the pith contains both mucilage cells and druses, but whereas the druses in the cortex are large (300$\mu$m in diameter, frequently up to 450$\mu$m), those in the pith are small, only rarely being as large as 75$\mu$m in diameter.

The secondary xylem of the shoot stele is somewhat variable. Basically it is similar to that of the root stele in that it contains vessels, scanty paratracheal parenchyma and libriform fibres (Figs. 29, 30, 31). The most significant variation occurs in the amount of lignification of the fibres. In most samples, the fibres have thick (3.7$\mu$m) secondary walls which are heavily lignified (they stain strongly with safranin). The fibres average 804 SD 112$\mu$m long and 19.8 SD 4.5$\mu$m in diameter. They are living and frequently are septate, each fibre having a single septum (Fig. 32). However, in the wood of a vegetative shoot that is immediately below a cephalium, there is very little production of fibres; instead, all of the cells other than vessel elements differentiate as parenchyma cells (Fig. 31). They are short and narrow, with only primary walls. Within these masses of parenchyma, there can be occasional patches of fibres.

The vessel elements in the secondary xylem of shoots average 316 SD 59$\mu$m long and 45 SD 7.5$\mu$m in diameter, thus they are somewhat longer and greatly wider than the vessel elements of roots. They have 'scalariform-helical' bordered pitting and simple, round or oval perforations that average 35 SD 4.5$\mu$m in diameter (Figs. 33, 34, 35). Whereas the vessels of the root are mostly solitary, in the shoot, over half occur in clusters of two or three vessels. In those shoots where the vessels are accompanied by libriform fibres, there is only scanty paratracheal parenchyma; most of the surfaces of the vessels, even in clusters, are in contact with fibres, not parenchyma cells (Fig. 36). However, in

Figs. 7-12. 7. Cross section of root cortex showing stele, periderm and two cortical bundles. The central bundle is shown enlarged in Fig. 8, ×45. 8. Root cortical bundle which has both xylem and phloem, ×180. 9. Root cortical bundle which contains only phloem, ×180. 10. Root cortical bundle which contains xylem but no phloem, ×180. 11. Longitudinal section of root cortical bundle; perforation plates are present, showing that these are vessel elements, ×180. 12. Pith in the root; two individual vessels are visible, ×180.



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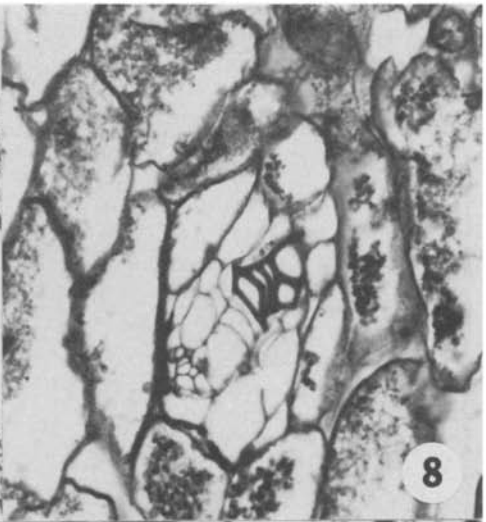

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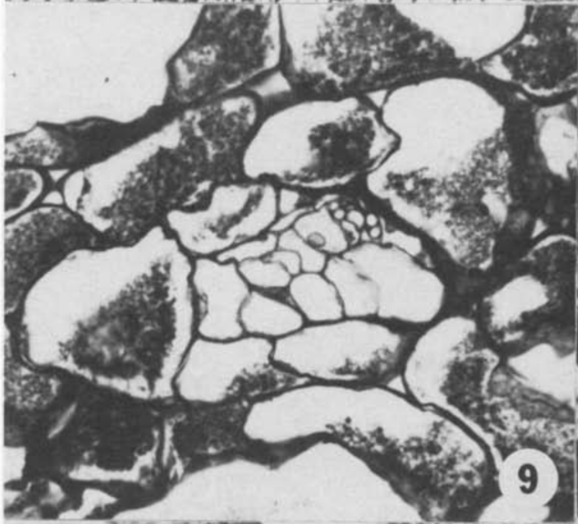

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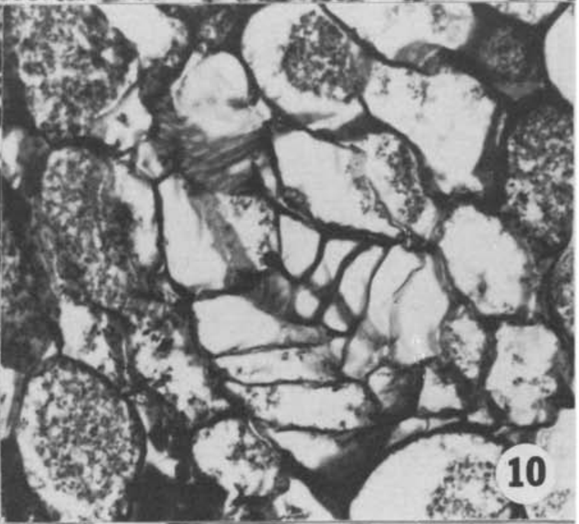

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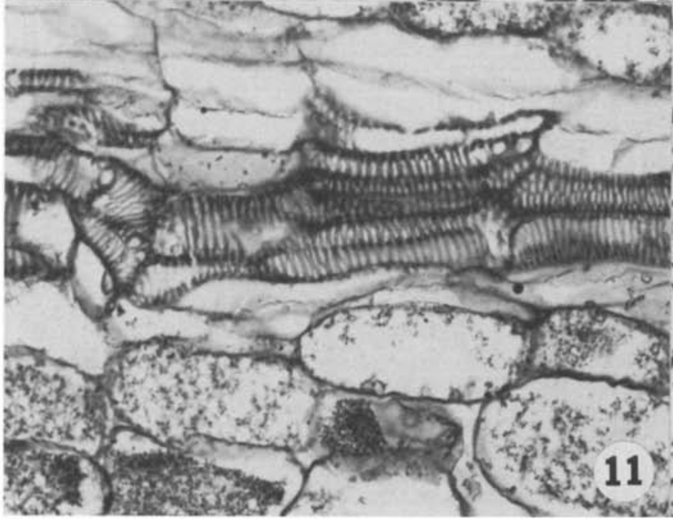

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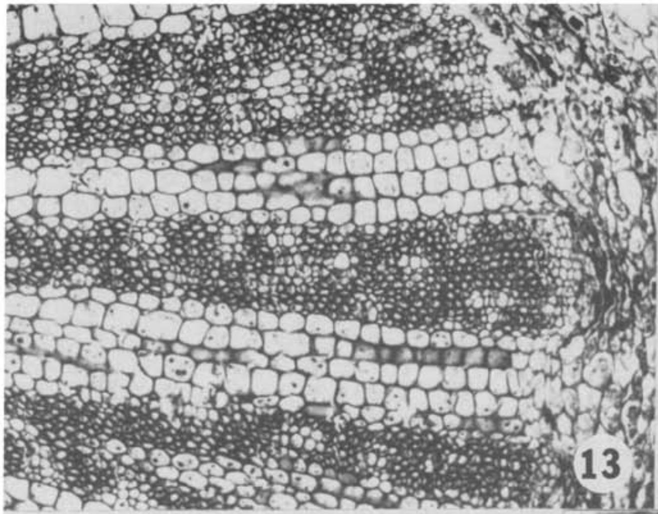
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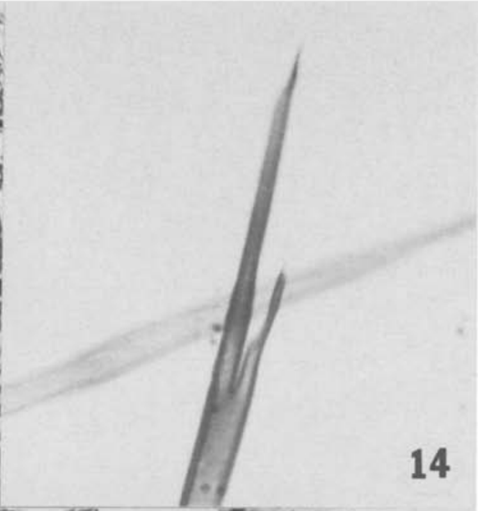
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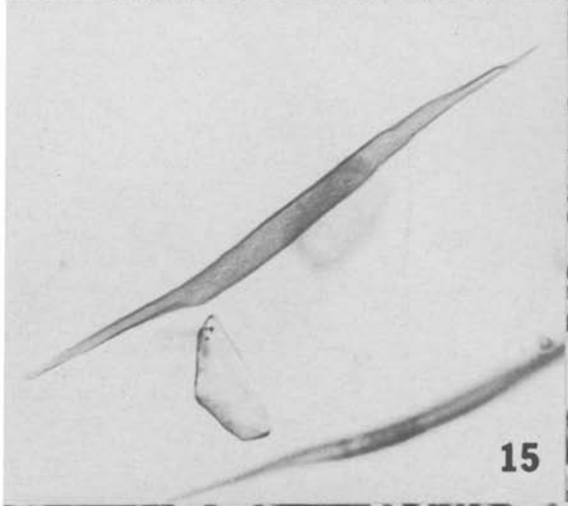
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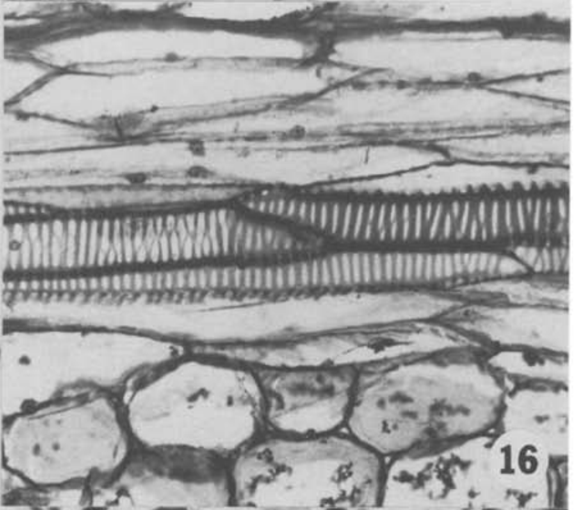
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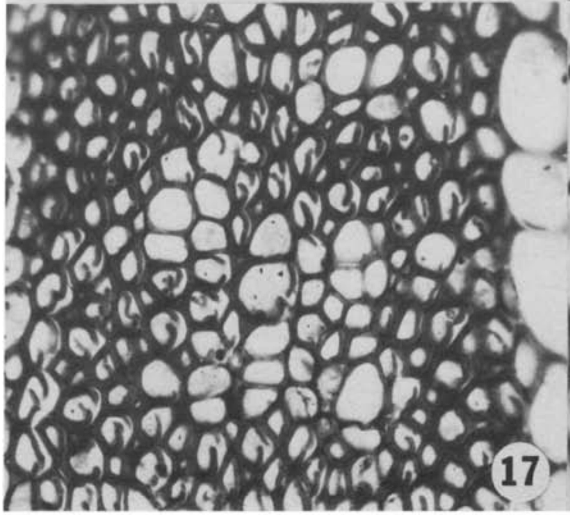
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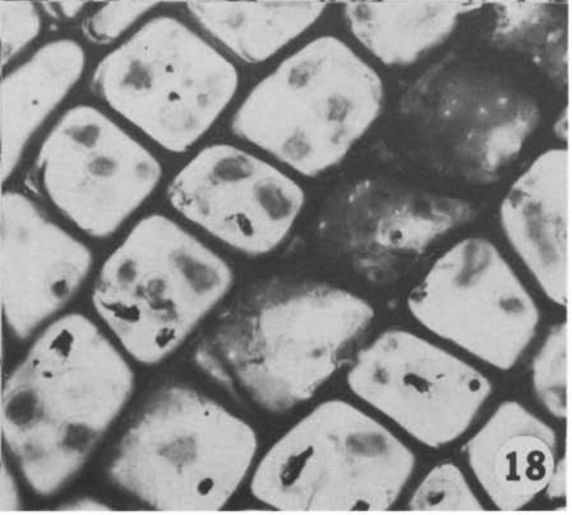
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shoots which terminate in cephalia and which contain parenchyma instead of fibres, vessels are completely surrounded by parenchyma cells.

The axial wood parenchyma in *Leptocereus* is complex; most cells have some lignified secondary wall, often in either scalariform or 'scalariform-helical' pattern, just as occurs on the tracheary elements (Figs. 37, 38). The pits are large and the secondary wall is quite thin. The cells are often septate, being divided into two cells by a lignified secondary wall (Fig. 38). The pair of cells are spindle shaped and thus resembles a septate tracheid. In several instances, these parenchyma cells even have perforations, therefore resembling vessel elements (Fig. 39). These are not merely immature tracheary elements, because they occur surrounded by fully differentiated fibres and vessels, far from the cambium.

Xylem rays in shoots are about eight to ten cells wide (Fig. 40). The cells are heteromorphic: the internal cells are cuboidal: 48 SD 10$\mu$m long radially, 32 SD 8$\mu$m wide tangentially, and 47 SD 10$\mu$m tall whereas the marginal ray cells (those abutting the axial elements) are tall: 48 SD 7$\mu$m long radially, 30 SD 7$\mu$m wide tangentially, but 84 SD 30$\mu$m tall. As in the roots, they all have thick (2.5$\mu$m), lignified secondary walls. In the younger shoots, they contain neither crystals nor starch, but in the trunk, they are filled with starch grains. In those regions of shoot which lack fibres in the axial xylem, the rays are similarly nonlignified and have only thin primary walls (Fig. 31).

The secondary phloem is much more abundant in the shoots than it is in the roots: it can be up to 150$\mu$m deep radially, although much of this is collapsed (Figs. 30, 31). In the noncollapsed phloem, numerous sieve tube member/companion cell pairs are present; sieve plates are large and easily identifiable. There is also some nonconducting parenchyma, and on the outer edge of most protophloem poles there are small masses of fibres (Fig. 30). Each contains from one to 50 fibres at any cross sectional level. These were checked carefully in longitudinal section and are fibres not sclereids.

***Cephalium.*** In *Leptocereus,* a cephalium is an adult, terminal portion of the shoot (Figs. 2, 3), and it is capable of producing flowers. In contrast to the lower, juvenile vegetative portions of the shoot, it is narrow, it does not have winglike ribs, and its internodes are so short that the nodes are closely packed. The cephalia are short, only about 1 to 3cm long, and they appear to be very old, having grown slowly.

*Epidermis.* The cephalium epidermis is quite distinct from that of the vegetative portions of the shoot: in most places it is composed of small cuboidal sclereids with very thick walls (Fig. 41). They are about 16$\mu$m long on each side, and the walls are 3 to 4$\mu$m thick. A distinct cuticular layer is present on the outer surface. In other areas, the cells have basically the same shape and size, but they have thin walls. Rhomboidal crystals are present in many of the epidermal cells. Stomata were not observed in any of the samples, but the material cut poorly, even after treatment with HF, so we cannot be certain that stomata are completely absent. At the areole (axillary bud), the epidermal cells grow out as uniseriate multicellular trichomes, as is true in all other cacti.

Below the epidermis is a layer of sclerenchyma that is three to five cells thick. It was not possible to be certain whether this layer is hypodermis or periderm. Unlike the hypodermis of the shoot, this layer contains cuboidal cells whose walls are lignified and which have narrow pits. In many areas they are aligned with the epidermal cells and it is possible that they were first derived as a periderm from an epidermis, then all cells were converted to sclereids. However, in other areas these cells are not aligned with the epidermal cells and could not possibly have been derived from them. Either way, the epidermis and the adjacent layers of sclereids forms a thick, tough dermal system. On the inner surface is a thin layer of collapsed phellem cells and then a two-layered phelloderm. The epidermis of the cephalium is usually not exposed to the environment, but rather it is hidden by a dense mat of trichomes and short spines that project out from the closely packed areoles.

The cortex of the cephalium is narrow and contains numerous mucilage cells (Fig. 42). Cortical bundles (all collateral) are abundant: in one cephalium that was 12mm in diameter and whose cortex was 3mm deep, there were 48 cortical bundles (Fig. 43). These are small, only 59 SD 8.5$\mu$m in diameter. They have only about eight or nine tracheary elements at any cross section. Most of the tracheary elements of the cortical bundles are vessel elements. All are narrow (only 3 to 7$\mu$m), short and have helical secondary walls. The phloem contains 6 to 16 sieve tubes at each cross section, and each is less than 5$\mu$m in diameter. The bundles are compact, with little or no nonconducting parenchyma associated with the conducting cells.

The pith of the cephalium is striking due to the large number of wide medullary bundles which are present (Figs. 42, 44). In one sample, a pith only 3 to 5mm wide had eleven bundles, each 132 SD 67$\mu$m wide, almost as wide as the axial bundles of the cephalium stele (Figs. 42, 45). The medullary bundle xylem consists of helically thickened vessel elements, ranging from 6 to 12$\mu$m in diameter, and tending to be mostly large. The average number of vessels per bundle is higher for the medullary bundles (13) than for the axial bundles (9.8); this fact, combined with the large number of medullary bundles, suggests that these might be significant for longitudinal conduction throughout the cephalium. The phloem of the medullary bundles consists of narrow sieve tube members, as many as 23 being counted in some bundle cross sections, but in most, the sections were not good enough to count the sieve tubes accurately. This was surprising because adjacent pith parenchyma and xylem had cut well. It may be that much of the phloem had recently collapsed but had not yet become highly chromophilic.

As with the nonstelar bundles of the vegetative shoot, both the medullary and the cortical bundles of the cephalium have little parenchyma and neither type has an obvious sheath. Both types may branch and both are connected to the bundles of the stele.

The stele bundles in the cephalium are collateral and there are about 39 bundles in each cephalium (Fig. 42). Although referred to as bundles, these contain some secondary growth from a fascicular cambium. There is only a small amount of cambial activity, and most of the secondary xylem is unlignified, thin walled parenchyma (Figs. 45, 46). There are only 9.8 SD 3.2 tracheary elements in each, and this is in cephalia that are perhaps several years old; thus only one or two or perhaps no tracheary elements are produced in any particular year. The elements average 15.2 SD 3.3$\mu$m in diameter and 120 SD 45$\mu$m long. They are 'scalariform-helical' vessel elements with simple perforations. There are no fibres present; there is no lignification at all except for the vessel elements. In one cephalium, there was no interfascicular cambium, and the small bundles (182$\mu$m in diameter) were separated by a few enlarged parenchyma cells of the medullary rays (Fig. 45). In a second cephalium, however, a complete cylindrical cambium had developed; it produced a mass of parenchyma to the interior and within the parenchyma were a few vessels (Fig. 46).

The phloem of each axial bundle (even with secondary growth) consists predominantly of several large nonconducting parenchyma cells; only three or four narrow sieve tubes are present in each bundle. There is also very little collapsed phloem on the outside edge of the bundles, and there are no phloem fibres at all.

## Discussion

The concept that *Leptocereus* is a primitive genus within subfamily Cactoideae has been based on several external characters: leptocerei are large treelike plants with a

Figs. 13-18. 13. Cross section of root, showing large, sclerified rays and dense, fibrous wood, ×45. 14. Fibre from root wood; the forked end indicates intrusive growth had occurred, ×180. 15. Fibres from root wood, showing the wide centre and abrupt narrowing at one end, ×72. 16. Vessel elements in root wood; on the right are scalariform bordered pits; on left the pits have expanded and interdigitate, almost appearing helical, ×180. 17. Cross section of root wood showing the living fibres and the scanty paratracheal parenchyma, ×180. 18. Ray cells in roots; they are filled with large starch grains and the walls are thick and lignified, ×180.

heavy, woody, nonsucculent trunk; they branch profusely; and they are restricted to the coastal regions and islands of the Caribbean, the presumed site of origin of the Cactaceae (Gibson & Nobel, 1986). The present study has shown that many features of the anatomy of *L. quadricostatus* support the idea that it contains numerous relictual features. The wood anatomy of the shoot is the most important: first, the wood in the main shoot and most branches is extremely sclerified; the long, septate fibres constitute the bulk of the axial component of the secondary xylem. Although these fibres are long whereas those in many of the more advanced genera are short, Gibson (1973) has shown that fibre length is most strongly correlated with the growth habit of a plant or the various parts of a single plant (Gibson, 1978a).

Throughout most of the shoot wood, the scanty paratracheal parenchyma is the only parenchyma that occurs, and even it has lignified secondary walls. Similarly, the ray cells too have thick lignified walls. Such wood is characteristic of the members of the genus *Pereskia,* which are clearly the most primitive cacti, based on their retention of large, thin leaves, lack of succulence and treelike habit (Bailey, 1962, 1963a; Leuenberger, 1986). On the other hand, all highly advanced cacti have few (*Melocactus* [Mauseth, submitted]) or no fibres in the secondary xylem of the shoot (tribe Cacteae: *Ariocarpus, Astrophytum, Coryphantha, Mammillaria* [Gibson, 1973]).

The vessels of *L. quadricostatus* are few, mostly solitary and their average diameter of 45$\mu$m is smaller than that of most vessels in many other Cactoideae (Gibson, 1973). The vessels have a variety of types of secondary wall: some have rather ordinary scalariform bordered pits, but in many these have become wider and taller while the intervening secondary wall has become reduced. Ultimately, these can be mistaken for helically thickened walls, but the presence of transition forms and the occurrence of frequent forks in the 'helix' show the true scalariform nature of the secondary wall (Gibson & Nobel, 1986). This diversity is interesting because the pereskias have scalariform or circular bordered pits, whereas the more advanced cacti have 'scalariform-helical' walls, either exclusively or almost so (Gibson & Nobel, 1986; Mauseth, submitted). (It should be pointed out here that Anderson and Boke (1969) and Gibson (1973) have stated that they had never encountered a vesselless cactus, and we have not either. Furthermore, none of Bailey's papers states that any cactus is vesselless.)

Another primitive character in the shoot wood is the large amount of axial cells (fibres and vessels) in relation to the radial component of the wood. Although the rays are rather wide and tall, the axial component is still greater than half the volume of the wood; this is similar to the wood of *Pereskia* (Bailey, 1962, 1963a) and *Pereskiopsis* (Bailey, 1964a) whereas in advanced cacti the axial component is less than half the wood volume.

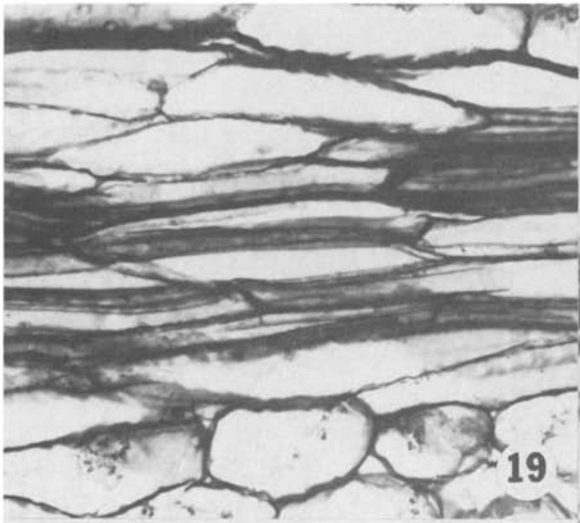
The wood of *L. quadricostatus* lacks vascular tracheids; Gibson (1973) found that these are common in many advanced genera of Cactoideae, but these were predominantly plants which are small at maturity. Genera which are columnar or long and scandent appeared to lack them. In *Melocactus intortus* (Mauseth, submitted), vascular tracheids and fibres tend not to occur together in the same regions of wood; the first layers of secondary xylem consist predominantly of parenchyma, vascular tracheids and vessel elements, later layers of wood contain mostly vessel elements, fibres and parenchyma but no vascular tracheids; later, only parenchyma and vessel elements are produced. If this developmental correlation is valid for cactus wood in general, then a densely fibrous wood like that of *L. quadricostatus* would not be expected to have vascular tracheids. However, because vascular tracheids are not found anywhere at all in the body of *L. quadricostatus* or *Pereskia* plants, it may be that *L. quadricostatus* represents a level that preceded the evolution of vascular tracheids.

Finally, *L. quadricostatus* has a cap of fibres exterior to each strand of protophloem; as in *Pereskia,* the fibres are septate (Bailey, 1961).

Although *Leptocereus* contains many primitive features, it is also obviously more advanced than *Pereskia* in many ways. As was known previously, in *Leptocereus* the leaves are reduced to a microscopic size, there is a formation of a specialized flowering zone, and finally, as the species name indicates, the cortex expands outward into four winglike ribs. Nobel (Gibson & Nobel, 1986) has shown clearly that in leafless stem succulents, the formation of ribs results in a body shape that can efficiently absorb photosynthetically active radiation without greatly increasing transpiration. The outgrowth of the cortex seems to occur by means of a laterally located meristematic region (Boke, 1951, 1957); this results in an outer cortex in which the cells occur in palisades and there is an extensive surface area and apoplastic space. Just as in leaves, this is an optimal organization for the photosynthetic tissues (Mauseth, in press). In all of the very large cacti, the bulk of the body is this type of an expanded cortex (the pith is usually rather narrow), thus the evolution of this cortex expansion mechanism is important.

The enlargement of the cortex results in a large volume of tissues that are separated from the vascular tissues of the stele by a great distance. These tissues must be vascularized, because they are active photosynthetically and metabolically (starch storage and mucilage secretion at least). This may have been the selective pressure that resulted in the development of the system of cortical vascular bundles. These permeate

Figs. 19-24. Phloem in roots, showing the sieve plates which are almost transverse, ×180. 20. Shoot cross section showing dermal system, substomatal chamber and palisade cortex, ×72. 21. Magnification of shoot epidermis and hypodermis; note the thick unlignified walls and the large pits, ×180. 22. Epidermal-hypodermal peel showing the abundant crystals in the hypodermis; the white area on lower right is a substomatal chamber, ×180. 23. Paradermal section of shoot outer cortex, showing its palisade nature and the extensive apoplast, ×72. 24. Cross section of shoot inner cortex showing three shoot cortical bundles (arrows), ×45.



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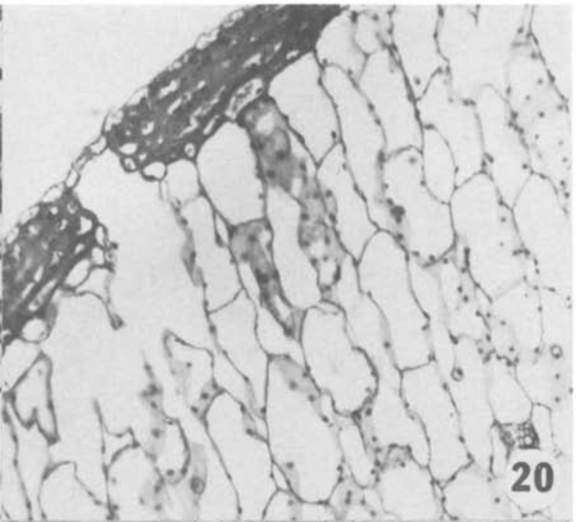

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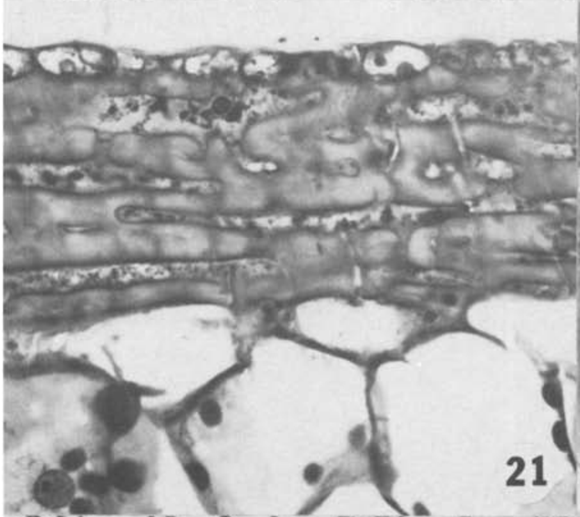

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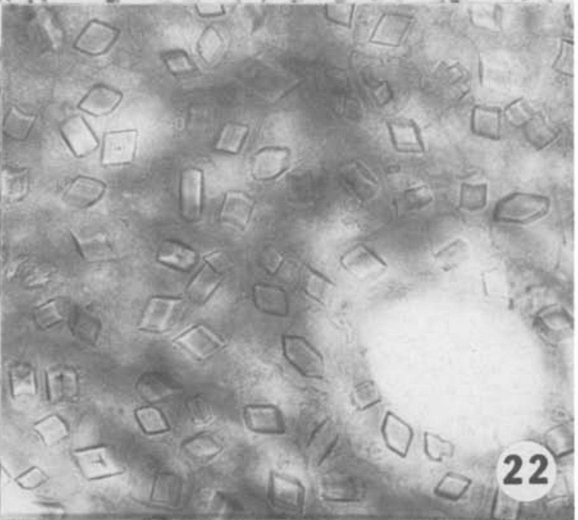

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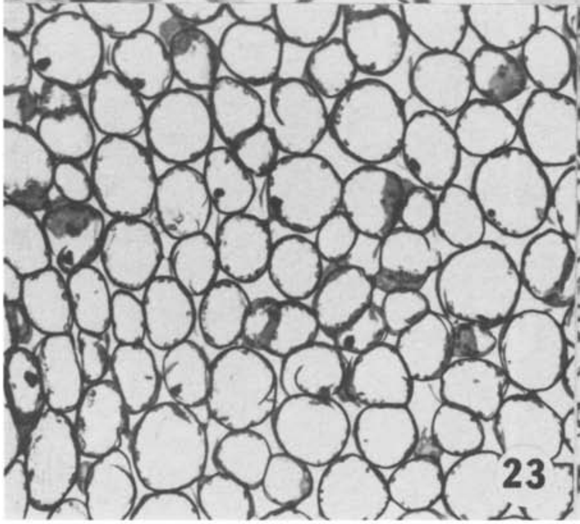

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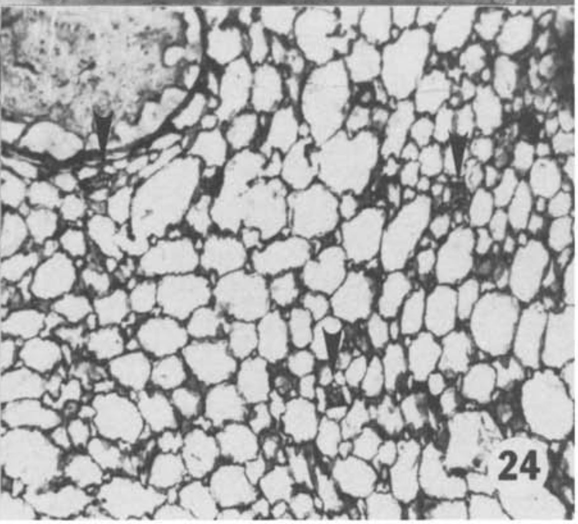

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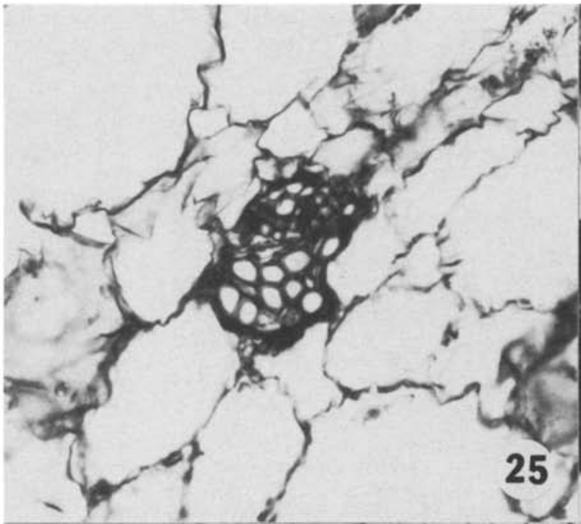
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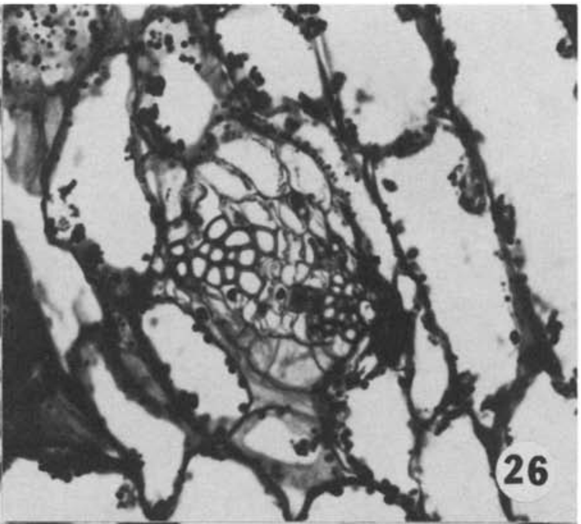
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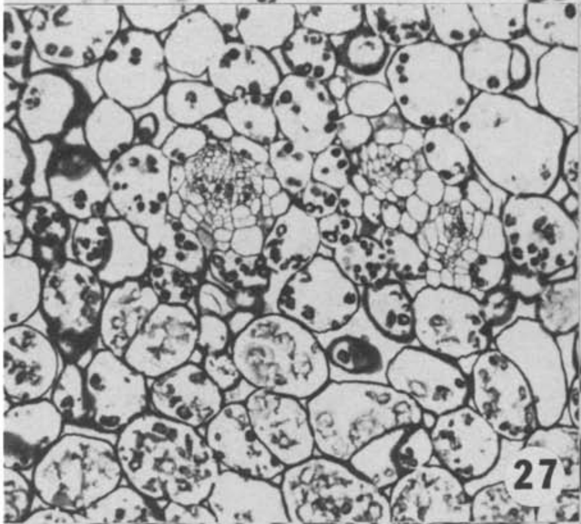
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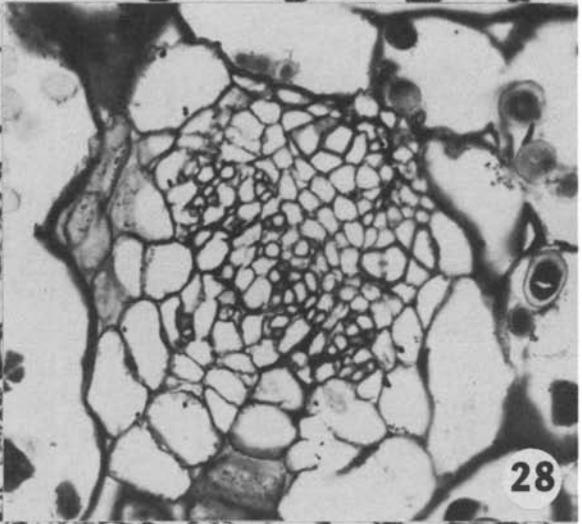
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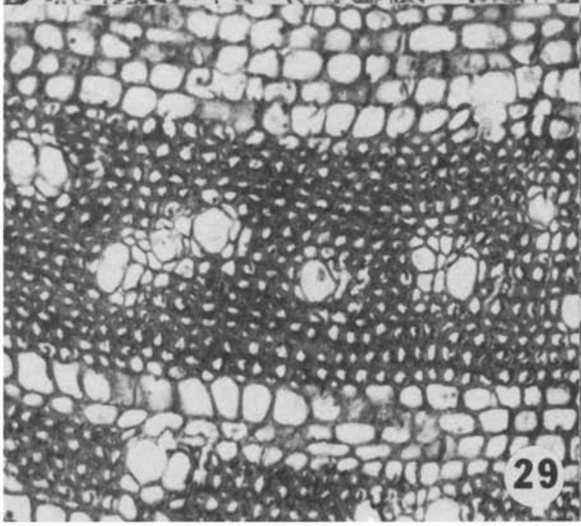
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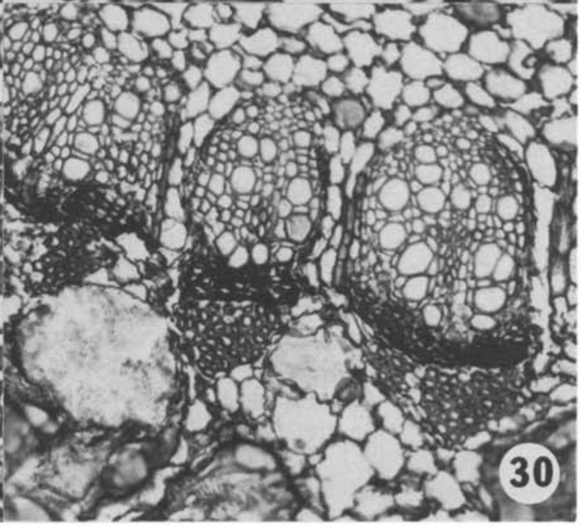
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the cortex and may be important for transporting newly synthesized sugars from the outer cortex to the stele. Because the cortex is persistant and photosynthesizes for many years, the cortical bundles presumably should also be perennially active. There is no production of secondary xylem in the cortical bundles, but there does appear to be continued formation of secondary phloem: the regions of accumulated collapsed phloem are larger in older portions of the cortex as opposed to those in young cortex. The same situation occurs in *Melocactus intortus* (Mauseth, submitted), but in *Melocactus* the production of cortical bundle secondary phloem is much greater, and larger amounts accumulate more quickly. Cortical bundles occur in many members of Cactoideae (Boke, 1951, 1952, 1955, 1980). It is interesting that *Leptocereus* should have an extensive network of cortical bundles capable of secondary growth by means of a unifacial cambium: such a system seems to be completely lacking in *Pereskia, Pereskiopsis,* and *Quiabentia*. Bailey studied these three genera extensively (1961, 1962, 1963a, b, 1964a, b and others cited therein), but he never mentioned the presence of cortical bundles, even though one study centred on the cortex and epidermis (Bailey, 1964b). One of us (JDM) has a large collection of these three genera and has never found cortical bundles in any of them (unpublished obs.).

Whereas the large volume of the expanded cortex seems to require the development of cortical bundles, the pith does not appear to be so large as to necessitate medullary bundles. The largest pith we observed was only 5mm in diameter, and many of the pereskias and quiabentias have large piths but no medullary system (JDM, unpublished obs.). The selective advantage of the medullary bundles is not known, but perhaps their abundance in the cephalium is significant: the flowers and fruits of *L. quadricostatus* are large and must require relatively great conduction of water and nutrients during their development. They are borne one at a time on the side of the cephalium; the medullary bundles may be a means of integrating the entire cephalium stele such that conduction can occur to the single site where there is great demand. Without the medullary bundles, it might not be possible to transfer sufficient material circumferentially through the axial elements of the stele. Although some genera of Cactoideae have a system of cortical bundles but no medullary ones, no genus is known to have only a medullary system (Boke, 1980).

Another advanced character of *Leptocereus* wood is its tendency to have regions which are relatively unlignified and parenchymatous. Whereas the trunk and main branches have a dense, fibrous, primitive wood, many of the terminal vegetative shoots and all of the cephalia have a wood which consists of vessels and unlignified parenchyma only; there are no fibres at all. This has been a critical aspect of cactus evolution, as shown by extensive, detailed surveys (Gibson, 1973; Gibson & Horak, 1978; summarized in Gibson & Nobel, 1986). One of the most characteristic features of increased succulence and reduced body size in the cacti has been the parenchymatization of the wood. This not only involves the loss of fibres, but actually the reduced lignification of all elements: the amount of secondary wall on individual vessel elements is greatly reduced, and the wood matrix is composed of parenchyma and vascular tracheids (Bailey, 1963b; Gibson, 1973, 1977a, 1978b; Mauseth, submitted). As a result, a large mass of wood consists almost exclusively of unlignified walls with only occasional secondary thickenings of any type. This general reduction of lignification on a cellular level results in a complete spectrum of cell types ranging from libriform fibres and vessel elements to parenchyma cells. In the root wood of *Leptocereus,* the axial parenchyma cells all have lignified secondary walls and the libriform fibres are living, thus there is probably little functional or biological distinction between the two. As lignification is lessened, the parenchyma cells become more parenchymatous (with just thin primary walls) and the living fibres have such thin secondary walls it is better to consider them, on a functional basis, to be parenchyma rather than sclerenchyma. Ultimately the fibres produce no secondary wall at all and have been completely converted to parenchyma. In several cases, parenchyma cells were found that had both secondary wall and perforations: this suggests that the entire suite of genes which control wall development in wood cells was changing at the time that *Leptocereus* evolved. Gibson (1977b) has suggested that the levels of endogenous hormones may have been dramatically altered as the cacti became leafless, and these new levels of hormones may not be able to induce or control extensive lignification; this is certainly an intriguing idea and deserves the attention of developmental physiologists.

A final major advancement in *Leptocereus* is the presence of a multilayered hypodermis of thickwalled collenchyma cells. This is completely absent in most species of *Pereskia* (Bailey, 1964b; *P. aculeata* does have a slightly collenchymatous hypodermis, JDM pers. obs.), and although not universal in more advanced Cactoideae (Anderson & Boke, 1969; Boke, 1959; Boke & Anderson, 1970), it certainly is common (Anderson, 1962; Gibson & Nobel, 1986; Mauseth, submitted; Mauseth et al., 1985). The evolution of the extended cortex may have contributed to the selective pressure for such a hypodermis: a collenchymatous hypodermis provides a tough barrier that not only protects the cortex from pathogens but also gives it support and maintains its shape. As the cortex becomes larger, this support is more important, and as the plant becomes 'leafless', it is more advantageous to protect the perennially photosynthetic cortex.

Figs. 25-30. 25. Cortical bundle from a young shoot, ×180. 26. Cortical bundle from very old portion of shoot; note lack of secondary xylem, but some accumulation of collapsed phloem, ×180. 27. Pith of shoot showing three medullary bundles, ×45. 28. Large medullary bundle in shoot pith, ×180. 29. Outermost wood from base of trunk of very old plant; the wood is heavily fibrous and contains only paratracheal parenchyma; the ray cells have thick, lignified walls, ×72. 30. Young sympodia from young shoot; the fibres have rather thin walls and the ray cells are not lignified; caps of primary phloem fibres are visible, ×72.

Assuming that our conclusions are correct and that *Leptocereus* is one of the most primitive members of subfamily Cactoideae, then its anatomy could explain some of the later remarkable morphological divergence within the subfamily. The cactoideae contains giant trees *(Dendrocereus, Carnegiea),* miniature plants (*Blossfeldia* is less than 0.5cm tall and in diameter when reproductively mature), scandent vines *(Selenicereus, Hylocereus),* epiphytes *(Aporocactus, Rhipsalis),* and short columnar cacti *(Haageocereus).* All of these lines of evolution have been considered to be centred on *Leptocereus* (Barthlott, 1979; Hunt & Taylor, 1986). The idea of one taxon giving rise to such totally different lines of evolution is difficult to accept, unless that taxon is dimorphic and quite heterogeneous internally. With the evolution of *Leptocereus,* morphogenic control mechanisms in the cacti had evolved which could establish a vertical woody shoot (the trunk) or an elongate, scandent shoot (the branches) or a short dwarf shoot (the cephalium). The cortex could be expanded into ribs or kept small; fibrous or nonfibrous wood could be established; the epidermis could be persistant or a phellogen could arise precociously (as in the cephalium). The morphogenetic mechanisms for controlling the ontogeny of cortical and medullary bundles was established. Thus a rapid radiation out of a plant like *Leptocereus* would be possible, certain characters being dominant in different lines of evolution. Carlquist (1975) has already shown that characters present in one part of a plant can be expressed in other parts (his theory of paedomorphosis). Such expression of existing genomes in new organs or tissues has been important in plant evolution (Mauseth, 1988).

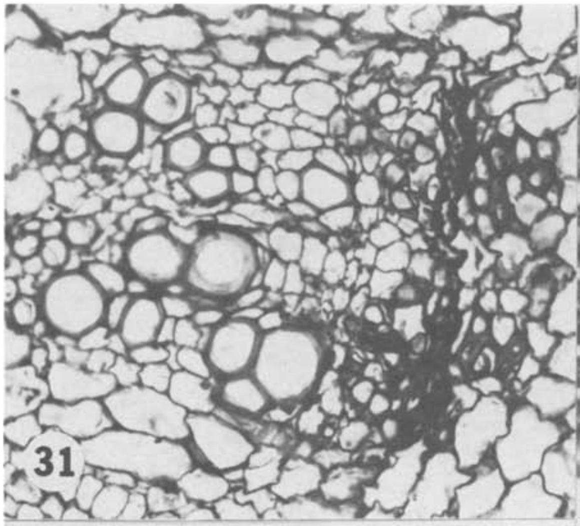
The most primitive pereskias (*P. sacharosa, P. bleo, P. grandifolia;* Bailey, 1962, 1963a) are very homogeneous internally and are lacking many advanced cactus characteristics: they are not succulent, have no expanded cortex, have no ribs or tubercles, have no cortical or medullary bundles, etc. Therefore, a multidirectional, rapid divergence from them would not seem probable.

In addition to *Pereskia,* two other genera are considered especially primitive because of their sparse succulence and retention of large leaves. These are *Pereskiopsis* and *Quiabentia*; they are members of subfamily Opuntioideae because they produce the characteristic glochids (fine deciduous spines) and arillate seeds of the well-known genus *Opuntia* (Britton & Rose, 1919). Bailey has studied these carefully (1964a), and in many ways *Leptocereus* seems to resemble *Pereskiopsis* much more than it resembles any *Pereskia*. Like *Leptocereus, Pereskiopsis* has a multistratose, collenchymatous hypodermis; a somewhat expanded palisade cortex; some vessel elements have scalariform bordered pits; and in both genera the trend to 'scalariform-helical' walls is well-developed. *Pereskia* contains characteristic sclerenchyma in its cortex and secondary phloem (Bailey, 1961), but this is lacking in both *Leptocereus* and *Pereskiopsis*. One of the main anatomical differences between *Leptocereus* and *Pereskiopsis* is that the latter contains vascular tracheids whereas *Leptocereus* and *Pereskia* do not.

Perhaps most importantly, although there are some trends towards less lignification and increased parenchymatization in some of the pereskias, these trends occur in their *roots* whereas in *Leptocereus* and *Pereskiopsis* they occur in their *shoots*. Only the vining Caribbean species *Pereskia aculeata* has some signs of parenchymatization of the shoot wood (Bailey, 1962). In this regard it may be important that the roots of *Leptocereus* are fully lignified, and contain only scanty paratracheal parenchyma; even the root rays are sclerified. Thus, these trends to advancement in *Pereskia* may be typical only of the individual species in which they occur, not in the ancestral stock that gave rise to *Leptocereus* and *Pereskiopsis*. The rest of the Cactoideae is like *Leptocereus* in having more parenchymatous shoot wood and more fibrous root wood: in *Melocactus intortus* (Mauseth, submitted), which is advanced, the stem wood is quite parenchymatous while the root wood is strongly sclerenchymatous. Thus, although *Leptocereus* and *Pereskia* do share a few trends toward advancement, these trends occur in different organs in each genus.

It appears as if *Pereskia* evolved to a point at which it was almost leafless, there was some parenchymatous tendencies in the shoot wood, and it had a collenchymatous hypodermis but there were no vascular tracheids. At this point its anatomy would resemble that of *P. aculeata* but it would have been larger and would have had almost enough characters to call it either *Leptocereus* or *Pereskiopsis;* because *Pereskiopsis* and all the other Opuntioideae have leaves, it might be that they diverged at this time and the remaining plants evolved into *Leptocereus* and the other Cactoideae. Because vascular tracheids do not occur in *Leptocereus,* this would mean that they either had to be lost in *Leptocereus* or evolve independently in all three subfamilies; Gibson (Gibson & Nobel, 1986) has suggested that they have actually evolved at least seven times, five times in the Cactoideae. Therefore, the anatomical data seem consistant with the idea that *Leptocereus* is indeed one of the least derived members of Cactoideae. Because both *Leptocereus* and *Pereskiopsis* are each quite different from *Pereskia,* it would be easy to assume that each is somewhat advanced within its own subfamily and that the most primitive stages are extinct. However, because *Leptocereus* and *Pereskiopsis* resemble each other so strongly anatomically, they must both be extremely basal within their own subfamilies, representing the

Figs. 31-36. 31. Young sympodia from young shoot; this sympodium occurred in the same microtome section as that of Fig. 30; however, this sympodium is less lignified, there is much axial parenchyma and only a few axial xylary fibres, ×180. 32. Longitudinal section of shoot wood, showing septate libriform fibres, ×180. 33. Vessel macerated from shoot wood; note the simple perforations, the 'scalariform-helical' secondary walls and the pair of septate parenchyma cells, ×180. 34. Single vessel element and its accompanying pair of paratracheal septate parenchyma cells, ×180. 35. Vessels from shoot, showing true helical secondary walls (top two vessels) and 'scalariform-helical' secondary wall (bottom vessel). 36. Paratracheal parenchyma cells with starch, ×285.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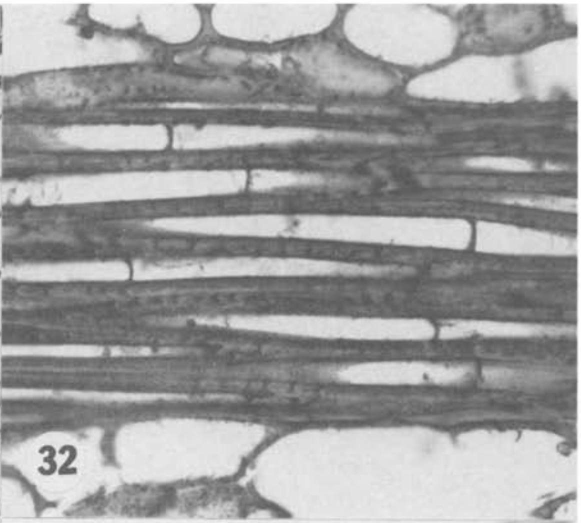
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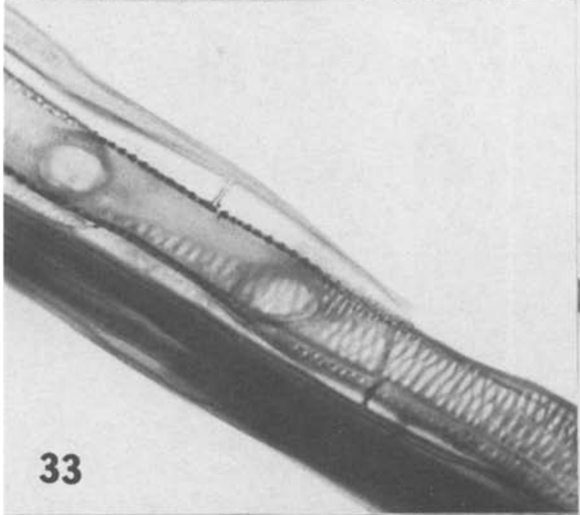
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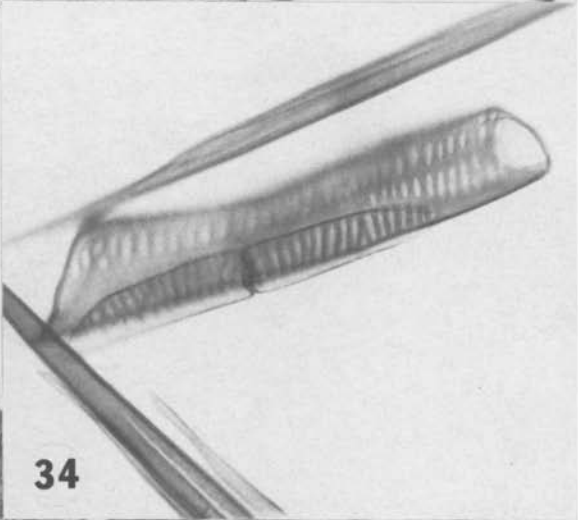
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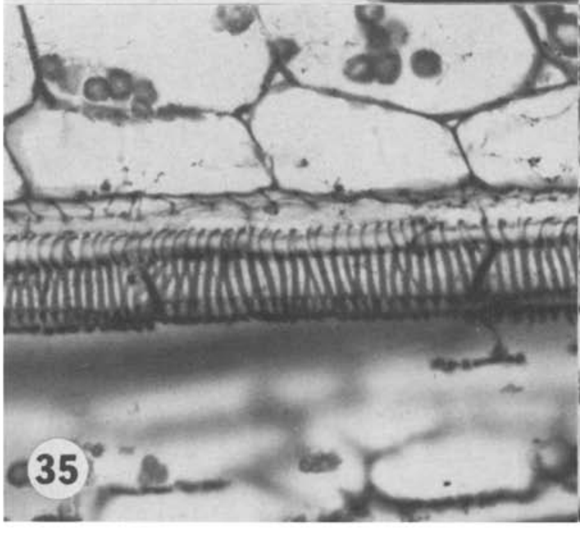
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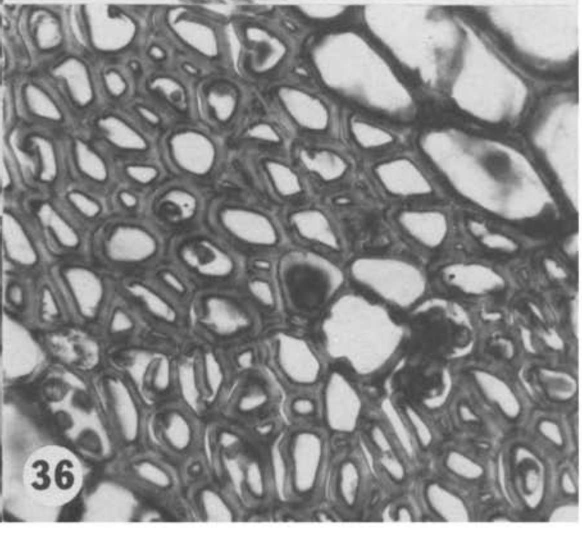
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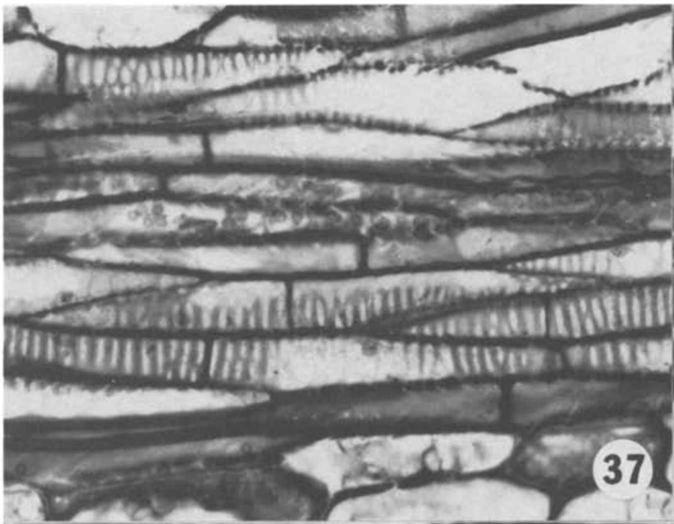
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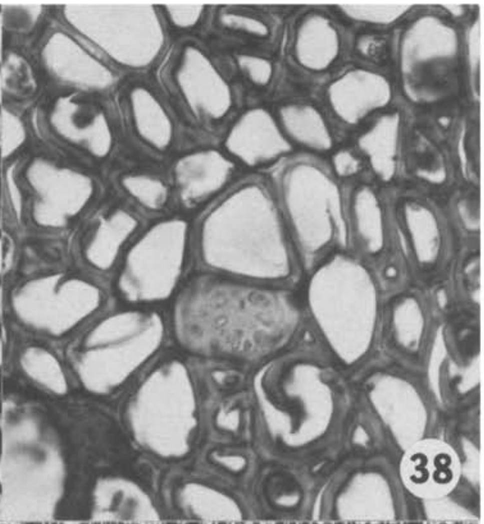
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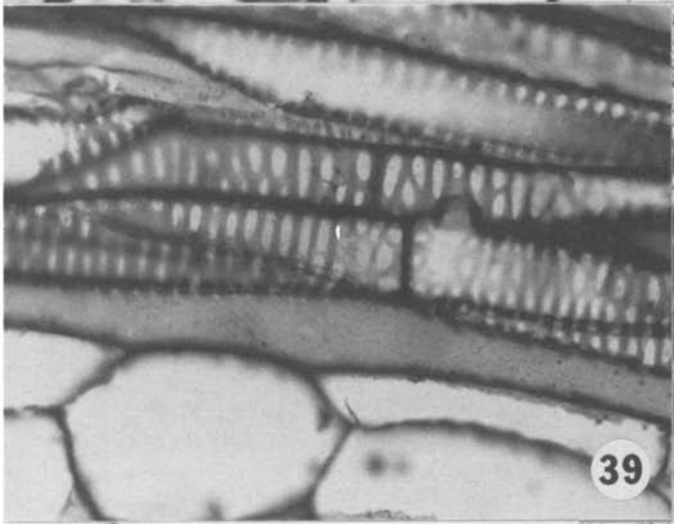
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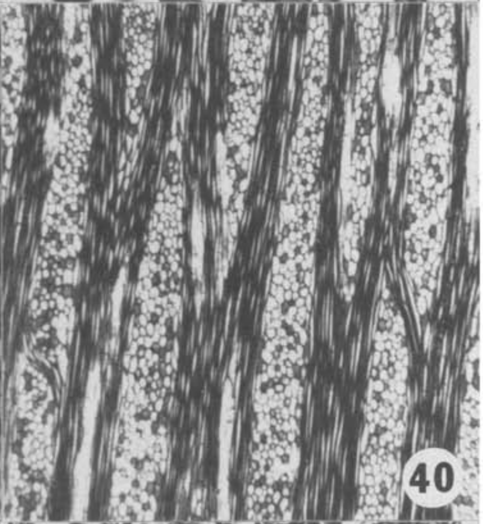
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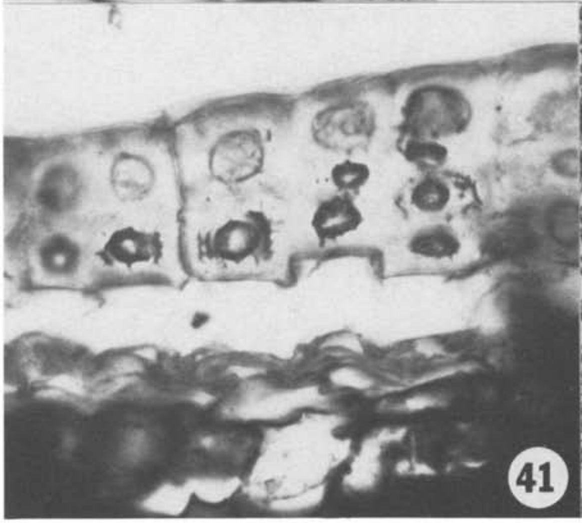
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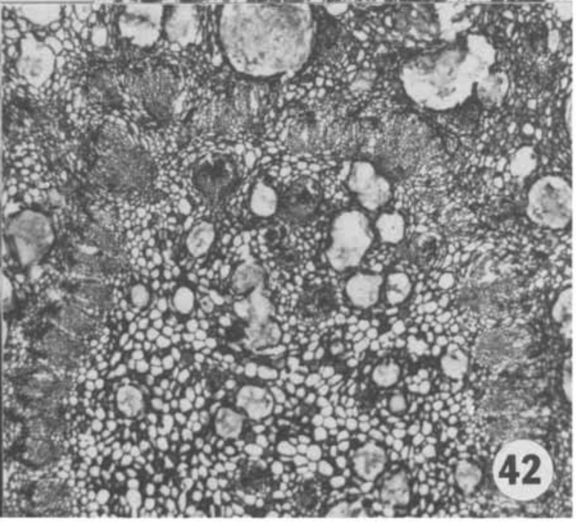
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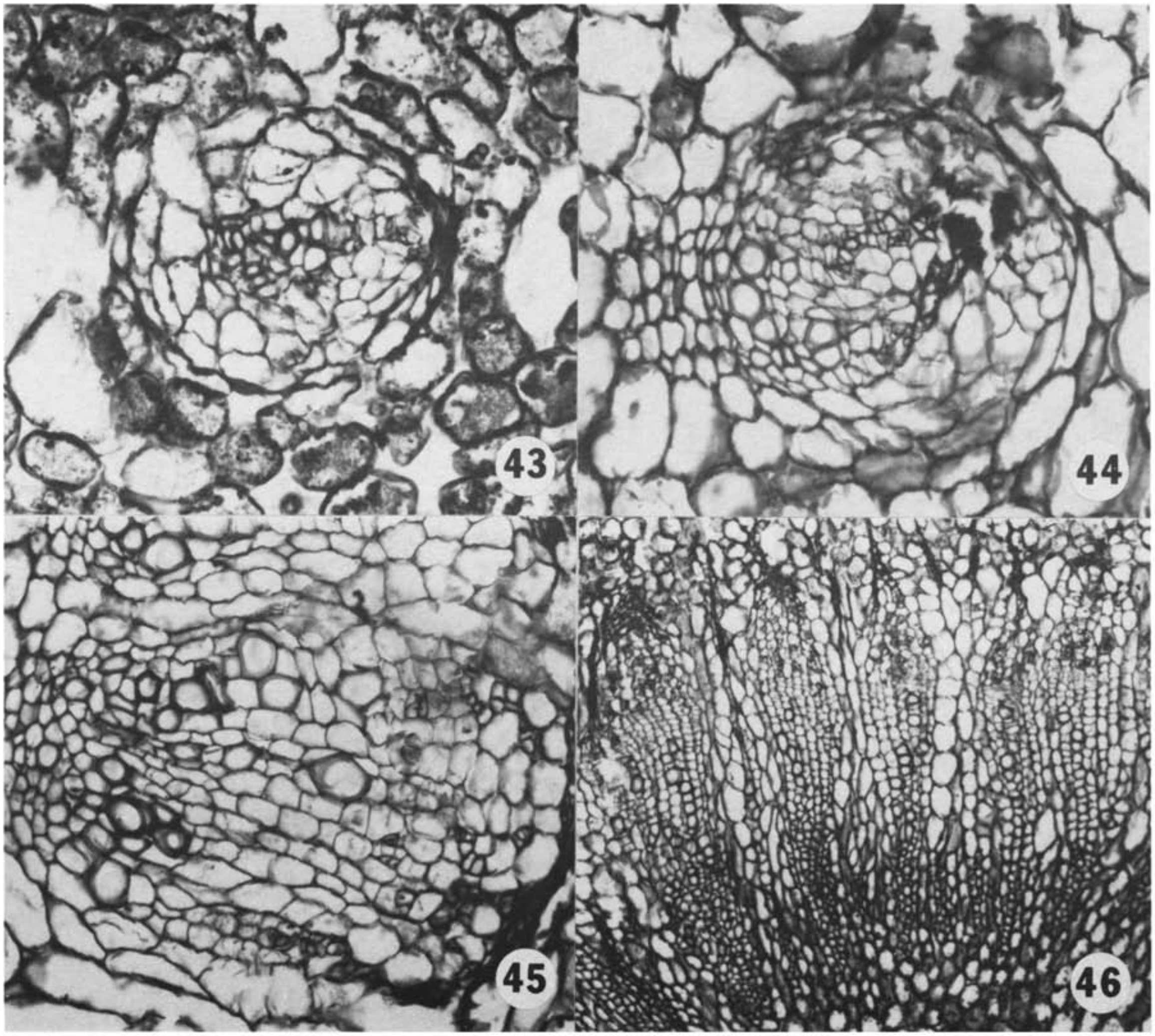

Figs. 43-46. 43. Cephalium cortical bundle, ×180. 44. Cephalium medullary bundle, ×180. 45. Cephalium sympodium; the wood contains only vessels and parenchyma; there are no xylary fibres; the phloem is relatively abundant, ×180. 46. Cross section of cephalium stele; in contrast to the cephalium of Fig. 42, this one has formed a larger amount of wood, and new cells are added to the primary rays; this wood also contains only vessels and parenchyma, ×180.

stage of evolution which occurred just at the two subfamilies diverged. The stages which are extinct would be the most advanced pereskias.

Figs. 37-42. 37. Longitudinal view of septate parenchyma cells with lignified secondary walls (mostly in a modified scalariform pattern), ×180. 38. Face view of septum between a pair of paratracheal septate parenchyma cells, ×285. 39. Parenchyma cells with modified scalariform secondary walls, septa and a perforation (arrow), ×285. 40. Tangential section of outermost wood of a very old shoot; the rays are extremely tall, ×18. 41. Cephalium epidermis; note the presence of a cuticle on uppermost sclereids, indicating that they are the epidermal cells; several layers of collapsed phellem are visible near the bottom of the photograph, ×285. 42. Cross section of cephalium stele, showing the parenchymatous wood and the large medullary bundles, ×18.

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# Supplementary notes on Mexican Echinocereus (1)

*N.P. Taylor*

*Royal Botanic Gardens, Kew*
*Richmond, Surrey TW9 3AB, U.K.*

*Summary.* The first part of a series of notes and new taxa supplementary to the author's *The Genus Echinocereus* (1985) is presented. The following new names, based on the results of studies in the field and of documented plants in cultivation, are published: *Echinocereus cinerascens* var. *septentrionalis* (var. nov.), *E. cinerascens* var. *tulensis* (stat. nov.), *E. stramineus* var. *occidentalis* (var. nov.), *E. parkeri* (sp. nov.), *E. parkeri* var. *gonzalezii* (var. nov.), *E. rayonesensis* (sp. nov.), *E. longisetus* var. *delaetii* (stat. nov.) and *E. polyacanthus* var. *huitcholensis* (stat. nov.). In addition, the circumscription of *E. viereckii* var. *morricalii* is substantially expanded, *E. freudenbergeri* is reinstated as a species, and *E. knippelianus* is tentatively referred to Sect. *Echinocereus*, E. VIRIDIFLORUS Group. The grouping of species in Sect. *Echinocereus* is revised, and the descriptions of various species in Sections 1-4 amplified.

*Zusammenfassung.* Dies ist der erste Teil einer Reihe von ergänzenden Angaben und neuen Taxa zur Veröffentlichung *"The Genus Echinocereus"* (1985) des Autors. Aufgrund von Feldarbeit sowie der Untersuchung von dokumentiertem Kulturmaterial werden die folgenden neuen Namen veröffentlicht: *Echinocereus cinerascens* var. *septentrionalis* (var. nov.), *E. cinerascens* var. *tulensis* (stat. nov.), *E. stramineus* var. *occidentalis* (var. nov.), *E. parkeri* (sp. nov.), *E. parkeri* var. *gonzalezii* (var. nov.), *E. rayonesensis* (sp. nov.), *E. longisetus* var. *delaetii* (stat. nov.) und *E. polyacanthus* var. *huitcholensis* (stat. nov.). Zusätzlich wird die Umschreibung von *Echinocereus viereckii* var. *morricalii* erheblich erweitert, und *E. freudenbergeri* wird wieder als Art anerkannt. *Echinocereus knippelianus* wird vorläufig in die E. VIRIDIFLORUS-Gruppe der Sektion *Echinocereus* gestellt. Die Gruppierung der Arten der Sektion *Echinocereus* wird revidiert. Schliesslich werden die Beschreibungen verschiedener Arten der Sektionen 1 bis 4 erweitert.

## Introduction

In the three years since my book, *The Genus Echinocereus* (1985), was sent to press, a considerable body of new information has been amassed. Most of this has been acquired either by field studies in Mexico or through the study of documented material in cultivation, especially that housed at Birmingham, U.K., as the Echinocereus Reference Collection. I would have preferred to delay publication of the 'Kew Magazine Monograph' until the last three years' studies were complete, but alas my publishers were not in a position to wait. Thus, with apologies to any purchasers of my book who now realize that it is rather out-of-date, I offer the first instalment of supplementary notes which may eventually find their way into a second edition of the monograph.

The information presented below mainly concerns individual species and attempts to document more fully the variety of plants seen in the field and, increasingly, in cultivation. My preoccupation, however, is with attempting to understand the broader interrelationships between the species, species groups and sections. To do this justice it is necessary to have as complete as possible an overview of the genus in respect of all pertinent sources of information. In particular, comprehensive surveys of pollen, floral pigment chemistry and chromosomes promise to greatly assist our understanding of the evolution of the genus, but to date these are all major projects which have scarcely been touched. Numerous Scanning Electron Microscope photographs of seeds have been published in recent years, but in a family where so many taxonomic decisions have been helped by seed characters, *Echinocereus* seems to be the exception that proves the rule.

One subtle but important change made below, is the order in which I list the sections: Sect. *Echinocereus* now comes after Sect. *Erecti*, not after Sect. *Triglochidiatus*. This is intended to reflect my suspicion that the genus may be capable of being resolved into two long-independent evolutionary lines: the first comprising sections *Morangaya*, *Erecti* and *Echinocereus*, the second sections *Triglochidiatus*, *Reichenbachii*, *Wilcoxia* and *Pulchellus*. At present I can see connecting links between the sections within each of these lines, but no hint of any connexion between the lines themselves. However, only wide-ranging surveys of the kind suggested above are likely to corroborate such hunches, since a reliance on gross morphological characters alone increases the risk of wrongly associating the products of convergent evolution.

## Acknowledgements

In addition to those earlier acknowledged in my book, the following have assisted the production of these notes: the late Hernando Sanchez-Mejorada R. (MEXU); Rodrigo Gonzalez G., Ulises Guzman, Ruth E. Taylor and Sabina G. Knees (companions during field studies); Myron Kimnach (HNT), G. Freudenberger (Bad Rappenau, BRD; preserved flowers and photographs); and the R.B.G. Kew Photographic Department for some of the illustrations reproduced below. However, once again the greatest contribution has been that of David Parker, manager of the Echinocereus Reference Collection, Birmingham, whose patience with my endless requests for more material and ability as a grower and seed-raiser I really admire.

## Taxonomic notes

NB. In the descriptions and documentation of materials which follow, unqualified measurements refer to length (except where the context indicates otherwise), those connected by a multiplication sign to length followed by diameter, and e.g. 'E.R.C. 792' stands for Echinocereus Reference Collection accession number 792. All materials cited have been seen by the author.

### 1. Section MORANGAYA

DIAGNOSTIC CHARACTERS. Stems elongate, to >1m, aerial roots freely produced; ribs 8-10; areoles of indefinite growth, subtended by small yet visible scale leaves when young. Flower-buds developed at the areoles; flowers displaying hummingbird pollination syndrome (tubular, bright red, very large nectar-chamber and copious nectar); perianth-segments turning brownish in alcohol-formalin preservative; anthers large for the genus, to 3.5mm; stigma-lobes whitish. Fruit fleshy, pulp red. Seeds to 2mm, testa tubercles poorly differentiated. Monotypic (S Baja California Sur, Mexico).

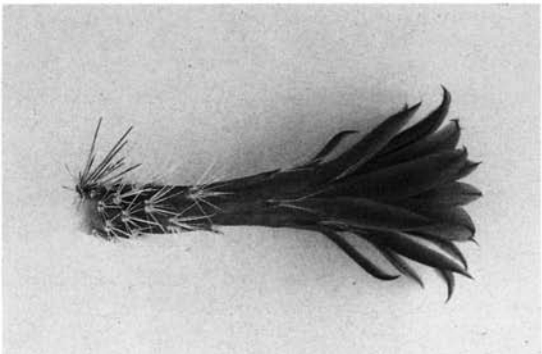
**Echinocereus pensilis** (K. Brandegee) J. Purpus

There are a few points to add to what I wrote about *E. pensilis* in my book. The first is a correction concerning the comparison made with species of *Nyctocereus*, where it was unfortunate that I mentioned *N. chontalensis* Alexander. Recent and as yet unpublished research by Prof. A.C. Gibson (Univ. of California) suggests that this species may belong elsewhere. A better choice, and one which resembles *E. pensilis* even more closely, is *N. oaxacensis* Britton & Rose. The stems of *E. pensilis* also resemble those of some species of *Harrisia*, and thus it is interesting to note that Prof. W. Barthlott, in a new classification of Cactaceae (Beitr. Biol. Pflanz. 63: 17-40, 1988), places *Echinocereus* (including *E. pensilis*) in Tribe Echinocereeae along with *Leptocereus*, *Harrisia*, *Acanthocereus* and *Peniocereus* (incl. *Nyctocereus*). When compared with these, *Echinocereus (Morangaya) pensilis* still seems closest to *Echinocereus*, at least in terms of its flowers and seeds, and I remain to be convinced that it deserves a genus of its own. One important aspect of *E. pensilis*, as yet unknown, is its seedling morphology. The seedlings of other *Echinocereus* species have reduced cotyledons, in keeping with their adult stem morphology, which is derived relative to other genera of Echinocereeae.

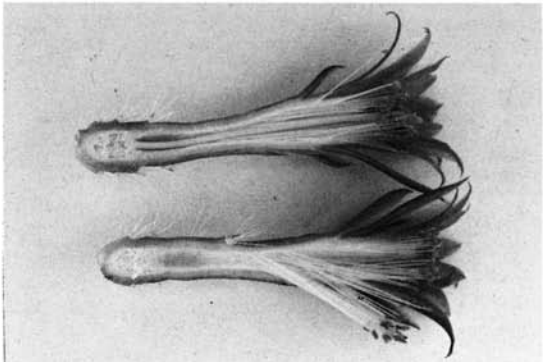
Although I am not prepared to accept *Morangaya* as a genus, *E. pensilis* does seem to merit its own section, since it lacks any really close allies. Nevertheless, its flower can be compared with that of *E. maritimus* (Sect. *Erecti)*, which agrees in its surprisingly elongate receptacle and nectar-chamber and, more significantly, in having perianth-segments which turn brown in alcohol-formalin preservative. The elongate stems of *E. pensilis* are more unusual in the genus, although equally eccentric and sometimes quite elongate stems are found in *E. brandegeei*, another member of Sect. *Erecti*. Certainly, it may be no coincidence that these species of Sect. *Erecti* from Baja California, the home of *E. pensilis*, have flower-buds which develop directly at the stem's areoles (rather than bursting through its epidermis), and *E. brandegeei* often has flowers with whitish stigma-lobes. Both of these features are characteristic of *E. pensilis*, though it must be stressed that they are not the derived state for the genus and therefore cannot be held as definitely indicating a relationship between sections *Morangaya* and *Erecti*.

Looking further afield, there is also a quite marked agreement between the flowers of *E. pensilis* and *E. scheeri* (Sect. *Triglochidiatus*), especially in perianth-segment shape and in their large nectar-chambers and anthers. However, these features may simply reflect a shared pollination syndrome—that of hummingbirds—and there is no reason to suppose that this syndrome should have evolved only once in the genus.

The following floral details can be added to my earlier description (from a flower of *Lau* 50, cult. R. Mottram, RM112.1, Thirsk, U.K., Jun 1986, K—in spirit): flower to 6.9cm, pericarpel and tube to 43mm, pericarpel to 11×8.5mm; nectar-chamber to 13×3mm, lower 7mm secretory, upper 6mm contracted, nectar copious and running out of the flower if tube directed downwards; perianth-segments sometimes attenuate acute at apex, turning brown when flower preserved in alcohol-formalin mixture; anthers to 3.5mm long; stigma-lobes 6-9, 3.5-7×1mm. Seed: for a Scanning Electron Microscope photograph see G.R.W. Frank in Kakt. and. Sukk. 37: 132 (1986)—as *Morangaya pensilis*.



Flower of *E. pensilis* (*Lau* 50), measuring 6.9×3.9cm.



(*photos: R. Mottram*)

## 2. Section ERECTI

DIAGNOSTIC CHARACTERS. Stems elongate or short and stout, sometimes unbranched, to 1m or less, not normally producing aerial roots; ribs 8-23; areoles of finite growth, subtending scale leaves not visible to naked eye. Flower-buds developing at the areoles or bursting through the stem epidermis above them; flowers broadly funnelform, variously coloured including yellow, >4.5cm; tube and base of perianth-segments conspicuously thickened and/or flower-buds not bursting through stem epidermis; nectar-chamber small or narrow and filled by style base; perianth-segments yellow *in vivo* or non-yellow and becoming colourless in alcohol-formalin preservative, outermost rather narrow and dark coloured; anthers 1-3mm. Fruit large, fleshy or juicy, pulp red or white, fragrant, indehiscent. Seeds <2mm, testa tubercles well defined. 8 species (NW & cent.-N Mexico, SW United States).

There are a few amendments required to the classification of this Section as presented in my book. First, I was in error placing *E. barthelowanus* Britton & Rose in the E. ENGELMANNII Group; greater familiarity with this species leads me to place it next to *E. ferreirianus* H. Gates in the E. FENDLERI Group. Secondly, I can confirm the last-minute placement of *E. papillosus* A. Linke ex Ruempler next to *E. fendleri* in this Section (Gen. Echinocer. 85. 1985, footnote).

G.R.W. Frank (Kakt. and. Sukk. 37: 90-98, 122-125. 1986) has proposed a classification of the Echinocerei of Baja California, including five species I place in Sect. *Erecti*. His scheme is based largely on flower colour and seems highly artificial, so that I do not feel obliged to discuss it much further (the same applies to the scheme for the whole genus by H. Kunzmann in ibid. 36: 72-81. 1985). However, it should be noted that all members of this Section have flowers with two (or more) zones of differing colour or colour tone, including both *E. engelmannii* and *E. maritimus* (in these there is a distinct change in colour tone and intensity between the upper half of each perianth-segment and its middle or base, giving the flower a deeper coloured centre or throat).

E. ENGELMANNII Group:

**Echinocereus brandegeei** (J. Coulter) K. Schum.
The flowers of this species vary in size as follows: 5.5-9.5×4.0-8.3cm (measurements by David Parker of E.R.C. 634 and Roy Mottram of RM138.1).

**Echinocereus maritimus** (M.E. Jones) K. Schum.
My description of its flowers can be supplemented as follows: pericarpel and tube to 36mm, pericarpel to 19×9-12mm, tube c. 7mm diam. near base, flared to c. 16mm at apex, walls 2-2.5mm thick; perianth-segments to 27-30×10mm, turning brownish in alcohol-formalin preservative; nectar-chamber 5×2mm; stamens to 14mm; style c. 24×1.5mm, stigma-lobes 6.5×1mm; ovary locule c. 8.5×4.5mm (undocumented material cult. Holly Gate Nursery Reference Collection, 8 Sep 1985, K—fl. in spirit).

E. FENDLERI Group:

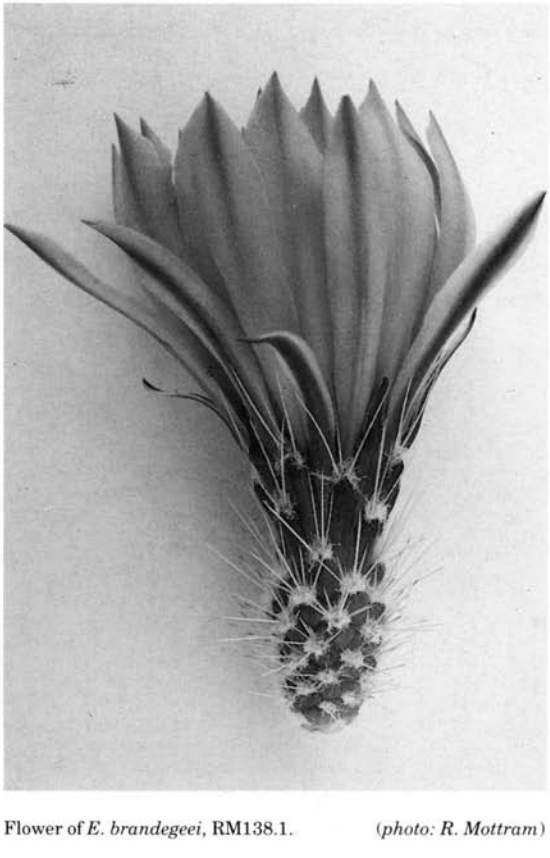
**Echinocereus barthelowanus** Britton & Rose
G.R.W. Frank has published excellent photographs of this species in Kakteen und andere Sukkulenten 37: 90, 123 (Abb. 17) stem & flowers, 124 (Abb. 19) fruit, 125 (Abb. 24 & 25) seed (1986). It is a pity that, having had access to flowering material, Frank has not made available an amplified description to supplement that of Britton & Rose.

**Echinocereus ferreirianus** H. Gates var. **lindsayi** (Meyran) N.P. Taylor
It is a pleasure to note that this threatened plant has recently been sighted again in habitat, and that it is becoming more freely available in cultivation through the tremendously successful artificial propagation practised by a number of amateur and professional growers.

The following details relate to plants flowering at the Städtische Sukkulenten-Sammlung, Zürich, 3 May 1984 & 25 Apr 1986 (ZSS 833316, K—in spirit): flower 6-7.6×7cm; pericarpel and tube 32-35mm, areoles with white to red spines to 12mm, pericarpel 16-20×10-12mm, tube 9mm diam. at base, flared to 20mm at apex; nectar-chamber 3.5-4×2mm, filled by style base; perianth-segments to 28-41×9mm, outermost narrowly oblanceolate, very dark; style 22-23×2mm, stigma-lobes 10-12, 4-6×0.7mm; ovary locule 7-9×3-5mm.

**Echinocereus fendleri** (Engelm.) F. Seitz, Cat. cactearum cultarum, 11 (1870)
The varieties of this species show a wide amplitude of variation in flower size, var. *bonkerae* having the smallest, var. *kuenzleri* (including the Mexican *E. hempelii*) the largest. In the following, the lower figure in each range of measurement refers to the former variety (*Nase* 1, cult. E.R.C. 316, 9 May 1985, K—fl. in spirit), the upper figure to the latter var. (cult. E.R.C. 326, 8 Jun 1985, K—in spirit): pericarpel and tube 21-50mm, pericarpel 12-23×12mm, tube 12mm diam. at base, flared to 18-25mm at apex, to 4.5mm thick; nectar-chamber 2-8×3.5mm; perianth-segments 29-45×8.5-14mm; stamens 7-18mm, anthers 1.5-3mm; style to 19-35×2-4mm, stigma-lobes 10-21, 6-8×1-1.5mm; ovary locule 3-14×3.5-5mm.

**Echinocereus pectinatus** (Scheidw.) Engelm. var. **pectinatus**
At the southern limits of its range, in the state of Guanajuato (S of Pozo Hondo, NW of San Luis de la Paz, 1986, *G.A. Navarro A.*, MEXU), this variety is represented by an extreme form with stems only 16-ribbed and areoles with 0-2 central spines. Also, the range of var. *pectinatus* extends some distance beyond both eastern and western limits of the Chihuahuan Desert (the basis for the outline on my 1985 distribution map) and it has been recorded at altitudes in excess of 2500 metres (Reppenhagen, Die Gattung Mammillaria, 38. 1987).



Flower of *E. brandegeei*, RM138.1. (*photo: R. Mottram*)

*E. pectinatus* var. *pectinatus*: a large clump near El Rodeo, Durango. (*photo: Taylor*)

## 3. Section ECHINOCEREUS

DIAGNOSTIC CHARACTERS. Stems, flowers and fruits as in Sect. *Erecti*, but: ribs 4-24, flower-buds always bursting through stem epidermis, perianth-segments turning brown in alcohol-formalin preservative or flowers <4.5cm; outermost perianth-segments various. Seeds 1.1-2.2mm, testa tubercles well defined. 13 species (Cent.-N & E Mexico, cent.-S United States).

There can be no doubt that hitherto Sect. *Echinocereus* has been the least well understood assemblage of species in the genus. In the notes which follow two species are removed to other sections, the status of two others is altered, two are described as new (besides various new varieties), and another species is tentatively transferred here from Sect. *Pulchellus*. On balance, this leaves the section with one more species, bringing the total to 13. I continue to recognize three informal species groups (which could be named as series if the number of included taxa were not so small), but their composition is rather different from my earlier scheme (1985), hopefully reflecting better the situation seen in the field.

The first group in my 1985 treatment recognized the uncertain position of the single species it housed, *Echinocereus pentalophus* (DC.) Lemaire. This interesting taxon will be discussed in relation to *E. subinermis*, in Sect. *Reichenbachii*, where it clearly belongs (see Part 2).

Following the removal of *E. papillosus* to the E. FENDLERI Group of Sect. *Erecti*, the E. CINERASCENS Group requires division. The closest allies of *E. cinerascens* seem to be *E. enneacanthus* and *E. berlandieri*; their distribution areas are complimentary (allopatric) and converge in SW Tamaulipas, where all three can be found within a 50km radius of the town of Palmillas: *E. cinerascens* var. *tulensis* near Tula (*N.P. Taylor* 184, K), *E. enneacanthus* var. *enneacanthus* west of Miquihuana, near La Perdita (*N.P. Taylor* 188A, K) and *E. berlandieri* near Jaumave (*Bravo-Hollis* in 1959, MEXU). These three, then, constitute a redefined E. CINERASCENS Group, whose geographical range overlaps with that of the related, but larger and more complex E. STRAMINEUS Group, and there are instances where contrasting members of the two groups actually grow together. The E. STRAMINEUS Group includes the remainder of the former group, plus *E. freudenbergeri* and *E. longisetus* (incl. *E. delaetii*) from the former E. VIRIDIFLORUS Group. Unlike the last mentioned, these two groups share the peculiarity of their flowers turning brown when preserved in Kew's alcohol-formalin solution—a unique feature within the genus (excepting *E. maritimus* and *E. pensilis*, which show a weak yet similar reaction). I am making efforts to get the biochemistry of this interesting phenomenon investigated. Depending on the outcome is the question of whether the E. CINERASCENS and E. STRAMINEUS Groups deserve recognition as a separate section. (N.B. a name at this rank is available: *Cereus* sect. *Costati* Engelm. in Mem. Amer. Acad., ser. 2, 4: 50, in adnot. (1849). Lectotype: *E. enneacanthus* Engelm.)

E. CINERASCENS Group:

**Echinocereus cinerascens** (DC.) Lemaire var. **septentrionalis** N.P. Taylor **var. nov.** a *var.* cinerascenti *caulibus in cumulis compactis aggregatis, floribus minoribus differt. Holotypus:* Mexico, Edo San Luis Potosi, 10 July 1986, *N.P. Taylor* 281 (MEXU, K iso).

DESCRIPTION. Caespitose, forming compact sub-hemispheric mounds of short branches; stems to c. 20×6cm, light yellowish-green; ribs 6-8, tuberculate, rounded; areoles c. 25mm apart. Spines pale yellow to brownish, subulate to acicular; centrals 4-6, 25-50mm or more, stout; radials 8-13, to 20-45mm. Flowers 6-7×7-10cm, pink, white in the throat; pericarpel and tube 30-35mm, walls very thick, pericarpel c. 13-15×17mm, tube flared to c. 27mm diam. at apex, its areoles with up to 9 pale, to 15mm spines; nectar-chamber 5-6×4mm, more than half filled by style base; perianth-segments oblanceolate, the largest c. 30-40×15mm, apex rounded-apiculate, margins finely serrate; stamens 5-11mm, lowermost shortest; style very stout, 22-25×3-4mm; stigma-lobes 9-15, 5-10mm, dark to somewhat grey-green; ovary locule 4.5-6×5mm. Fruit not available. Seeds 1.3-1.4×1.0mm. 2n=22, *fide* Pinkava & Parfitt in Bull. Torrey Bot. Club 109: 123 (1982).

Distribution. San Luis Potosi and adjacent part of Zacatecas, on the plateau of N central Mexico; Chihuahuan Desert and its higher margins to the west, 1250-2300(-2550)m.

Material examined. SAN LUIS POTOSI. Between La Bonita (S of Matehuala) and Charcas, 1800m, 18 Jun 1986, *N.P. Taylor* 204 (K—photos); Entronque Huizache (junction of Hwy Fed. 57 & 80), flat valley bottom, muddy soil under *Larrea,* 1250m, 10 Jul 1986, *N.P. Taylor* 281 (MEXU, K—dried stem, fl. in spirit, photos); Hwy Fed. 57, 5km NE of San Lorenzo, flats with *Larrea* and *Prosopis*, c. 1500m, 28 Oct 1978, *Leuenberger & Schiers* 2582 (MEXU); 30km NE of San Luis Potosi, beside Hwy Fed. 57, limestone flats, 1800m, 2 Jun 1986, *N.P. Taylor* 179 (K—dried fls, fl. in spirit, photos); c. 1km along road to Tinajas from Hwy 57, KM28 NE of San Luis Potosi, 19 Jul 1988, *W. A. FitzMaurice* s.n. (K—areoles, seeds); KM89 from San Luis Potosi towards Zacatecas (Hwy Fed. 49), May 1965, *Bravo-Hollis* 37 (MEXU); ibid., KM94, c. 2km before turnoff to Salinas, 2100m, 26 Jun 1986, *N.P. Taylor* 211A (K—photos). ZACATECAS. Hwy Fed. 54, 117km from city of Zacatecas towards Saltillo, 2300m, 2 May 1973, *Sanchez-Mejorada* 1765 (MEXU); (?) near Pinos, cf. Reppenhagen, Die Gattung Mammillaria, 38. 1987 *('E. merkeri')*.

*Echinocereus cinerascens* var. *cinerascens* is found in the central Mexican states of Queretaro, Hidalgo and Mexico. Plants encountered by the writer at various localities in Hidalgo and Queretaro, as well as in cultivation, form broad loose mats of sprawling stems and produce very large pinkish-magenta flowers, to 10×12cm. Towards the north-western edge of the species' range, in the southern part of the Chihuahuan Desert *(sensu stricto)* and its higher western margins, a markedly different variety is common, recognizable for its compact mounds of short stems and smaller, paler flowers. This variety, named above, shows as much affinity to *E. enneacanthus* as to var. *cinerascens* in habit and stem form, but its flowers have the characteristic white throat of the latter (flowers unicolorous or throat darker in *E. enneacanthus)*. Var. *septentrionalis* is, without doubt, the taxon that links the two species and, with a broader species concept, would be the reason for reducing *E. enneacanthus* to infraspecific status.

To the east of Entronque Huizache, the type locality of var. *septentrionalis*, this variety begins to intergrade with the following:

**E. cinerascens** var. **tulensis** (H. Bravo-H.) N.P. Taylor **stat. nov.**

*E. tulensis* H. Bravo-H. in Cact. Suc. Mex. 18: 110-111 (1973) excl. fig. 63. Type: Mexico, Edo San Luis Potosi, 4 May 1973, *Sanchez-Mejorada* 2085 (MEXU).

[*E. berlandieri* (Engelm.) Hort. F.A. Haage sensu N.P. Taylor, Genus Echinocereus, 82-83 (1985) pro parte.]

Description. Caespitose, spreading in flat clumps 1-3m diam.; stems prostrate or with the tip ascending, to 100×4-6cm, light to dark green; ribs (4-)5-7, with low tubercles; areoles c. 20mm apart. Spines pale yellow to brownish; centrals 1-4(-6), to 30mm, stout; radials 8-12, to 32mm, acicular. Flowers 6.7-10×8-12cm, reddish- to pinkish-magenta, darkening or changing to white in the throat; pericarpel and tube 40-50mm, walls very thick especially around nectar-chamber, pericarpel 21-27×15-17mm, tube flared to c. 30mm diam. at apex, its areoles with up to 7 pale, to 18mm spines; nectar-chamber 9-10×3mm, all but completely filled by style base; perianth-segments oblanceolate, the largest c. 50×20mm, apex rounded-apiculate, margins finely serrate-denticulate; stamens 6-13mm, lowermost shortest; style 26-33×2-4mm; stigma-lobes 6-9, 5-8mm, dark green; ovary locule oblong, 11-14×5-6mm. Fruit globose, to c. 30×30mm, green, bearing stout whitish spines. Seeds 1.2-1.3×1.0-1.2mm, black.

Distribution. SW Tamaulipas and adjacent San Luis Potosi; easternmost segment of the Chihuahuan Desert, on flats chiefly under *Prosopis* or *Larrea,* 1000-1200m.

Material examined. TAMAULIPAS. NW of Tula, between the town and Hwy Fed. 101, 1200m, 3 Jun 1986, *N.P. Taylor* 184 (K—fls in spirit, photos). SAN LUIS POTOSI. Beside Hwy Fed. 80, KM15-16 from Entronque Huizache, 1200m, 10 Jul 1986, *N.P. Taylor* 282 (K—fl. in spirit, photo); junction of Hwy Fed. 80 & 101, 1100m, 2 Jun 1986, *N.P. Taylor* 181 (K); ibid., 10 Jul 1986, *N.P. Taylor* 283 (K—fr. in spirit, photos, seeds); ibid., 4 May 1973, *Sanchez-Mejorada* 2085 (MEXU); KM95 on Hwy Fed. 80, 37km SE of junction with Hwy Fed. 101, 1000m, 10 Jul 1986, *N.P. Taylor* 284 (K—fr. in spirit, seeds).

This distinctive variety, with its elongate creeping stems, I earlier mistakenly included in the synonymy of *E. berlandieri,* to which, nevertheless, it is closely related. Indeed, the northernmost population, around the town of Tula, includes forms with flowers lacking the white throat of typical *E. cinerascens,* which look at first much closer to those of *E. berlandieri* and *E. enneacanthus.* One of these was the only plant of this taxon I had seen flowering in cultivation when my book went to press. Var. *tulensis* is also easily confused with some forms of *E. cinerascens* var. *cinerascens,* which, however, usually has shorter stems with a higher average rib count. The latter occurs at twice the altitude and its ecology is less specific than that of var. *tulensis.* Even more like var. *tulensis,* both in habit and ecology, is var. *ehrenbergii,* an ecotype of *E. cinerascens* from shady thickets in the barrancas of Hidalgo. This plant, however, usually bears glassy-white spines and in other respects seems closer to var. *cinerascens,* its immediate neighbour.

In my book I referred '*E. spinibarbis*' Hort. F.A. Haage ex Backeb., nom. inval. (Arts 36 & 37) (*E. spinibarbis* Hort. F.A. Haage 1900, nom. nud., non (Pfeiffer) K. Schum.) to *E. cinerascens* var. *ehrenbergii.* Through the kindness of Herr E. Meier (BRD), I have received a colour slide of what purports to be Haage's plant in flower, which has confirmed that it belongs to *E. cinerascens,* though probably not to var. *ehrenbergii.* This curious and, according to Herr Meier, very slow-growing, plant is of unknown wild origin and is best regarded as a cultivar.

**Echinocereus enneacanthus** Engelm. var. **enneacanthus.**
The following are the southernmost records of this taxon's range in Mexico known to me:

Material examined. TAMAULIPAS. West of Miquihuana, near La Perdita, 1500m, 4 Jun 1986, *N.P. Taylor* 188A (K—photos). NUEVO LEON. KM80 from Matehuala, beside road between Doctor Arroyo and La Escondida, 1500m, 16 Jun 1986, *N.P. Taylor* 203A (K—photos). SAN LUIS POTOSI. KM28 from Matehuala towards San Tiburcio on Hwy Fed. 62, 1700-1790m, 1987, *Sanchez-Mejorada et al.* (MEXU—living plants). DURANGO. Hwy Fed. 40, 2-3km SW of Cuencame, 1650m, 8 Oct 1987, *N.P. Taylor & S.G. Knees* 478 (K—areole, photos).

**E. enneacanthus** var. **brevispinus** (W.O. Moore) L. Benson
Two Mexican records of this variety, both from Coahuila, are worth noting, since they deviate from the description given in my book. The first is a form found growing with *E. longisetus* at 500-600m in the mountains just west of Melchor Muzquiz (7 Jul 1986, *N.P. Taylor* 266, MEXU, K). Its stems are c. 4.5cm diam. with 6-7 ribs, areoles 20-25mm apart; central spine 1, to 13-50mm; radial spines 3-7, to 13mm, except for the lowermost, to 19-33mm. The second occurs NW of Cuatrocienegas, at 1000m (1987, *Sanchez-Mejorada et al.* 4083, MEXU—living plants), and has unusually stout stems,

8cm diam., with 7-8 ribs; areoles to 30mm apart. Its spination is quite typical for this variety (centrals 1-2, to 20-35mm; radials 5-7, to 10mm).

**Echinocereus berlandieri** (Engelm.) Hort. F.A. Haage
As noted above, the thick-stemmed form mentioned in my book, which corresponds to *E. tulensis* H. Bravo-H., is now to be excluded from the circumscription of this species. Taking this into account, and also some undocumented material cultivated as E.R.C. 792 (K—fl. in spirit) and at Berlin-Dahlem (fruit), the following amendments and additions can be made to my earlier description: stem 1.5-3cm diam., dark or purplish-green; flowers to 7cm or more; pericarpel and tube 30mm, pericarpel 13×10-11mm, tube 11mm diam. at base, flared to 19mm at apex, walls 2-3mm thick, nectar-chamber 4×1.5mm; perianth-segments oblanceolate, the largest to 40×11mm; stamens to c. 10mm, filaments greenish-gold, anthers c. 1mm; style 25×1.5-3mm, stigma-lobes c. 8, 6-10×1.5-2mm; ovary locule 6×5mm; fruit 19×17mm, becoming reddish.

The range of *E. berlandieri* remains very poorly known. The northernmost record is that of the type (nr Nueces River, SE of Mathis, Texas), while the southernmost has been mentioned already (Valley of Jaumave, Tamaulipas, Mexico). This scanty information suggests an altitudinal range of 0-600m.

E. STRAMINEUS Group:
This group now comprises 7 species, four of which are subdivided into varieties. Four of the 11 named taxa accepted here are formally described for the first time. The newly described taxa are remarkably distinct and it is surprising that they have remained unnamed for so long. Some have clearly been in cultivation for many years under invalid or misapplied names, which may explain why they have remained unrecognized. On the other hand, some of the longer-established names in this group represent taxa that are proving hard to distinguish, now that their variability in the field is becoming better understood. Although a linear order can never give a really satisfactory representation of relationship, the sequence in which the species are dealt with below is intended to indicate their closest affinity.

**Echinocereus stramineus** (Engelm.) F. Seitz, Cat. cactearum cultarum, 11 (1870)
Typical *E. stramineus* ranges from near the northern end of the Chihuahuan Desert southwards to northern San Luis Potosi, at altitudes of 450-1800m (the southernmost record I have is 61km along Hwy Fed. 62 from Matehuala towards San Tiburcio, 1987, *Sanchez-Mejorada et al.* 4025, MEXU—living plants). It forms compact hemispherical mounds of stems armed with long, glassy-white to dirty straw-coloured spines, and bears large flowers, to at least 12cm long and broad. Despite its considerable range, *E. stramineus* remains a remarkably constant taxon, though it does begin to vary in habit and flower size in E Durango and central W Nuevo Leon (e.g. S of Providencia).

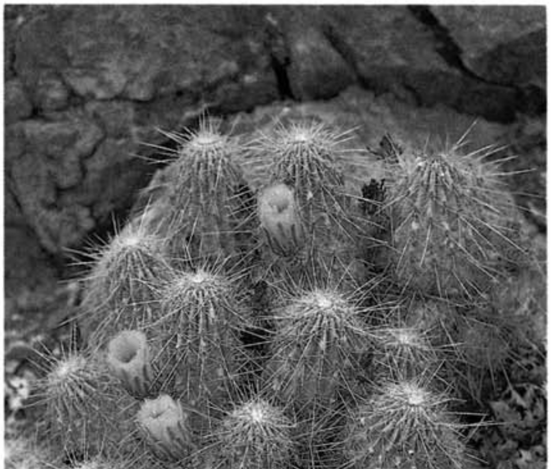
West of the area occupied by *E. stramineus* var. *stramineus* in central northern Mexico, a relatively local yet quite distinct variety can be recognized. It flowers up to a month later, but intergrades with forms of var. *stramineus* at its easternmost locality, so that its description as a new species does not seem appropriate.

**E. stramineus** var. **occidentalis** N.P. Taylor **var. nov.** *a var.* stramineo *caulibus cumulos compactos non formantibus, spinis centralibus superis deficientibus vel brevibus, floribus minoribus, segmentis perianthii angustis differt. Holotypus:* Mexico, Edo Durango, 1 July 1986, *N.P. Taylor* 240B (MEXU, K iso).

DESCRIPTION. Caespitose to 60cm diam., not forming compact mounds; stems erect, cylindric or slightly tapered towards apex, to 30×5-6.5cm, yellowish- to light green; ribs 12-17, rounded, tuberculate; areoles 10-15mm apart. Spines straight, glassy-white or some brownish tipped; centrals 1-3, the lowermost longest, to 40-55mm, directed downwards, upper 1-2 centrals when present much shorter, to 10-30mm, brownish; radials 9-12, to 15-20mm. Flowers 5-7×5-7cm, deep pink to pinkish-magenta; pericarpel and tube 25-35mm, areoles with c. 1-10, to 19mm, glassy-white spines, pericarpel 11-15×10-14mm, tube flared to 15-20mm diam. at apex; nectar-chamber 3-4.5×1.7-2.7mm, nearly filled by style base; perianth-segments oblanceolate, the largest 24-30×4-10mm, apex attenuate-acuminate to rounded-apiculate, margins entire to finely lacerate; stamens 6.5-14mm, anthers oblong, 0.6-0.8mm; style 21-24×1.5-2.2mm; stigma-lobes 10-14, 3.5-6×0.8mm, bright green; ovary locule obovoid-oblong, 5-8.5×3-4.5mm. Fruit globose, c. 30×30mm, green with numerous white spines at first, later pinkish-red. Seeds 1.3-1.4×1.0-1.2mm, black.

DISTRIBUTION. Durango, in the drainage of the Rio Nazas; Chihuahuan Desert on volcanic and limestone rocks, 1200-1800m.

MATERIAL EXAMINED. DURANGO. SE of La Cuesta, KM140 N of city of Durango on Hwy Fed. 45, volcanic rocks, 1400-1450m, 1 Jul 1986, *N.P. Taylor* 240B (MEXU, K—dried stem, fl. & fr. in spirit, photos), 240C (K—dried stem), 240D, E, F (K—fls from different plants in spirit, photos); loc. cit., KM141, volcanic cliff, 1600m, 10 Oct 1987, *N.P. Taylor & S.G. Knees* 495 (K—areole, seeds); S of El Rodeo, 2.5km E of Hwy Fed. 45 near road to Nazas, 1275m, *N.P. Taylor & S.G. Knees* 499C (K—photos); loc. cit. ['Chihuahua'], 1959, *Bravo-Hollis* s.n. (MEXU); KM199 on Hwy Fed. 45 N of Durango, N of Rio Nazas, cliff, 1800m, 1 Jul 1986, *N.P. Taylor & R. Gonzalez G.* 241 (MEXU, K); KM65 W of Bermejillo on Hwy Fed. 30, rocky hillside on limestone, 1650m, 1 Jul 1986, *N.P. Taylor* 243 (K—fr. in spirit, photos); 48km W of Mapimi, just SW of



*E. stramineus* var. *occidentalis* in habitat, 11km SW of Chocolate, Durango, *Taylor* 246A. (*photo: Taylor*)

26°N/104°W, *Leuck* 354 (K—photos); Hwy Fed. 40, KM192 from city of Durango, 11km SW of Chocolate, small limestone barranca, 1200m, population of plants including intermediates with var. *stramineus*, 2 Jul 1986, *N.P. Taylor* 246A (K—photos).

This distinctive plant was mentioned and illustrated as a *sp. nov. prov.* by Breckenridge & Miller in Syst. Bot. 7: 365-378, figs 8 & 9 (1982). Another illustration is the colour photo in M. Pizzetti, Piante grasse le Cactacee, no. 63 (1985), misidentified as '*E. longisetus*'. It is regrettable that plants at the type locality were found to have been severely damaged by fire in October 1987. Fortunately, this variety is relatively abundant at various sites between KM128 and KM199 on Hwy 45, as well as along parts of Hwy 30 west of Mapimi. Recently collected seed should enable it to become better known in cultivation.

**Echinocereus viereckii** Werderm. var. **morricalii** (Riha) N.P. Taylor

Field studies and examination of various herbarium and documented living collections convince me that the circumscription of this variety must be considerably expanded. It is particularly unfortunate that Riha's name was founded on a spineless, slender-stemmed race, since it is now seen to be the ultimate extreme of a variable taxon including some very long-spined, stout-stemmed forms. Spine development seems to be strongly influenced by ecological factors: the spiniest forms occurring in exposed, sunny situations, the less spiny or spineless in shady, forested habitats, cliffs and canyons. Thus, as one drives from Montemorelos, N.L., towards Rayones, through a spectacular, deep and shady canyon marking the eastern edge of the Sierra Madre Oriental, a very weakly-spined form is first encountered; then, having passed Rayones, travelling either towards Galeana or up the broad valley to the NW, one finds long- and even fiercely-spined forms in open sunny places. Further north, in the vicinity of Monterrey, similar contrasting forms can be found short distances from one another. These differing forms seem to be genetically determined, since they maintain their characteristics once brought into cultivation under uniform conditions.

As emended here, var. *morricalii* has a much greater geographical range than before and at its northern limit intergrades with *E. stramineus* in an embarrassing way. The northern forms (Hidalgo, N.L.) appear to flower earlier in the season than those from the south (e.g. *circa* Rayones), likewise *E. stramineus* and *E. viereckii* var. *viereckii*, resp., and the change in both stem and flower character north to south indicates that var. *morricalii* represents a cline connecting the two species. This said, it would be justifiable to synonymize *E. viereckii* with the much older *E. stramineus*, but I am against doing so, since that would create a rather diverse assemblage of forms that even the enlightened hobbyist-grower would find hard to accept as one species. As it is, the variety of forms comprising my expanded concept of *E. viereckii* var. *morricalii* may prove unacceptable to some. However, those who doubt the wisdom of placing together such spineless and spiny extremes should see the complete range of intermediate documented plants at the Echinocereus Reference Collection, as well as the situation in habitat.

It should be noted that spiny forms of var. *morricalii* are easily confused with *E. enneacanthus* var. *brevispinus* by the non-specialist. However, the former have more slender spines and more slender, paler green stigma-lobes.

DESCRIPTION. Caespitose, forming broad clusters of loose to densely arranged branches; stems erect or prostrate below, cylindric, 10-30×3-6cm, pale to dark green; ribs (5-)6-13, straight, acute, well defined, frequently with transverse wrinkles or creases (as if dehydrated and shrinking), not or scarcely tuberculate; areoles 10-24mm apart. Spines absent or weakly to well developed, all rather fine and slender, terete; centrals 1-4, to 1-80mm, pale whitish- to golden yellow; radials 4-10, to 1-40mm, whitish. Flowers 6-11×6-10cm, magenta; pericarpel and tube 20-45mm, areoles with 6-13, to 13-21mm spines, pericarpel to 23×14mm, tube 11-12mm diam. at base, flared to 27mm at apex; nectar-chamber to 6×3-4mm; perianth-segments oblanceolate, the largest to 45-50×12-21mm, apex broadly acute-acuminate to rounded-apiculate, margins finely serrate; stamens 10-14mm, anthers oblong, slightly >1mm; style c. 27×2-3.5mm; stigma-lobes 7-13, to 12×1mm, light green; ovary locule oblong, c. 14×6mm. Fruit 25-30×18-30mm, red or green, strawberry-flavoured. Seeds 1.2-1.6mm, black.

ILLUSTRATION. Hirao, H., Colour Encyclopaedia of Cacti, 159, no. 633 (1979)—as '*E. enneanthus*'.

DISTRIBUTION. Nuevo Leon, eastern drainage of the Sierra Madre Oriental; Chihuahuan Desert vegetation on limestone and forested cliffs and canyons E of the C.D. region, 350-1000m or higher.

MATERIAL EXAMINED. NUEVO LEON. NE of Hwy Fed. 53, N of Hidalgo (between Monterrey and Monclova), 475m, 12 Jun 1986, *N.P. Taylor* 198 (K—photos, seeds); WNW of Monterrey, just outside city limits, 1978, *Preston-Mafham* 62, cult. E.R.C. 146, Mar 1988 (K—stem in spirit); Grutas Garcia, nr Monterrey, Apr 1957, 22 Apr 1958 & no date, *Bravo-Hollis* (MEXU—flowering stems, on 3 sheets); Cañon de Huasteca, W of Monterrey, [no date or collector], cult. E.R.C. 748, 7 Jul 1986 (K—fl. in spirit, photos); ibid., growing with *E. enneacanthus* var. *enneacanthus*, [no date], *G. Freudenberger* s.n. (K—photo); Chipinque (just S of Monterrey), 1 Jul 1947, *T.A. Barkley & G.L. Webster* 7121 (MEXU); Barranca de las Garrapatas, [no date], *J. Riha*, cult. E.R.C. 157, 5 Jun 1985 (K—fl. in spirit); between Rayones and Casillas, valley of Rayones, 11 Jun 1986, *N.P. Taylor* 196 (K—photos); Cañon de Rayones, 15km W of Hwy Fed. 85 on Hwy N.L. 6, 550m, among rocks and shrubs in partial shade, 9 Jun 1986, *N.P. Taylor* 192 (K—flowering stem in spirit); 5km along dirt road from Rayones towards Galeana, 1000m, 9 Jun 1986, *N.P. Taylor* 194 (K—dried stem, photos).

The extreme, nearly spineless type form of *E. viereckii* var. *morricalii*. (*photo: Fröhlich*)

Having emended var. *morricalii* to include spiny forms, the following key is required:

Ribs 6-13, acute, not or scarcely tuberculate; areoles 8-24mm apart; spines absent or present, centrals 1-4, 10-80mm (Nuevo Leon: Galeana northwards) .............................. var. **morricalii**
Ribs 6-9, rounded, tuberculate; areoles 5-12mm apart; spines present, centrals (3-)4-5, to 20mm (SW Tamaulipas) ..................
.............................................................................. var. **viereckii**

**E. viereckii** var. **viereckii**
The altitudinal range given by Werdermann (1500-2000m), who collected the plant on the road between Ciudad Victoria and Jaumave, Tamaulipas, seems exaggerated. The pass between the two places is at 1450-1500m and *E. viereckii* is abundant on cliffs and rocks in the forest beside the road from 650-1400m on the Cd Victoria side. Lau's collection between 'El Mirador' and Dulces Nombres (*Lau* 1295) may be the highest record we have, at 1700m. His form is notable for producing variably sized flowers, with perianth-segments 30-50 ×7.5-12mm (cult. E.R.C. 167, Jul 1984 & cult. N.P. Taylor, 1988, K—in spirit). Plants at the first-mentioned locality flower in early June (*N.P. Taylor* 191A—photos, 6 Jun 1986).

The following new taxa represent a complex of forms allied to *E. stramineus* and *E. viereckii* on the one hand, and to *E. nivosus* on the other.

**Echinocereus parkeri** N.P. Taylor **sp. nov.** *a* Echinocereo viereckii *spinis albis, ineunte vere florentibus, floribus minoribus, segmentis perianthii angustis differt. Holotypus:* Mexico, Edo Nuevo Leon, 26 March 1976, *B. Hansen et al.* 3863 (MEXU).

? *E. barcena* Rebut ex A. Berger, Kakteen, 175-176 (1929). Type apparently not preserved; known only from the very brief original description.

DESCRIPTION. Caespitose, forming compact mounds or spreading clumps, branching above or below ground; stems tapering or cylindric, to 15×2-6cm; ribs (6-)7-10, 8-30mm wide, weakly to strongly tuberculate; areoles 9-12(-14)mm apart, circular, c. 3.5mm. Central spines (1-)2-5, acicular, dark at first, especially the uppermost 1-2, soon glassy-white to slightly yellowish, often dark tipped, lowermost longest, to 20-65mm; radial spines similar, 6-14(-16), very slender, to 7-12mm. Flowers 4.5-5.5×4.5-6cm, magenta to deep pink, white in the throat, rarely entirely white; pericarpel and tube to 27mm, areoles c. 2mm diam., with 3-14 glassy-white, to 17mm spines, pericarpel to 13×12mm, tube 8-10mm diam. near base, flared to 14mm at apex, walls 2.5mm thick; nectar-chamber 4×3-3.5mm; perianth-segments oblanceolate, largest 20-32×4-8mm, apex acute to acuminate, margins serrate; stamens very numerous, densely inserted inside tube, to 6.5mm long, anthers oblong, 0.8-1.0mm; style c. 20×1.3-2.0mm; stigma-lobes 7-10, to 8×1mm, pale to mid-green; ovary locule obovoid-obconic, c. 6.5×4mm. Fruit nearly globose, to 20-23×20mm, green or green tinged red, with glassy-white spines at first, pulp white. Seeds rather large, 1.6-2.2mm, black.

DISTRIBUTION. S Nuevo Leon, SW Tamaulipas, N San Luis Potosi and NE Zacatecas, in the Sierra Madre Oriental; open coniferous or mixed woodland, grassland and Chihuahuan Desert type vegetation, 1000-2750m.

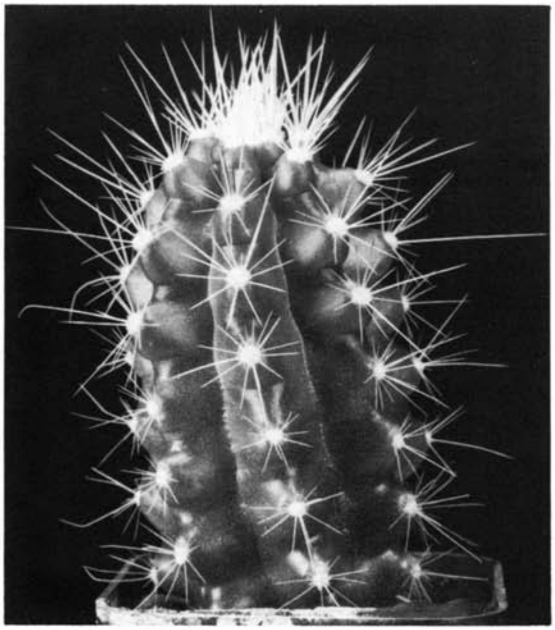
var. **parkeri**

DESCRIPTION. Stems in compact mounds, branching above ground, to 6cm diam., markedly tapered towards apex; ribs 7-9, strongly tuberculate. Central spines (1-)2-4(-5), to 20-25mm; radial spines 10-13.

DISTRIBUTION. SE Nuevo Leon, 1000-1800m.

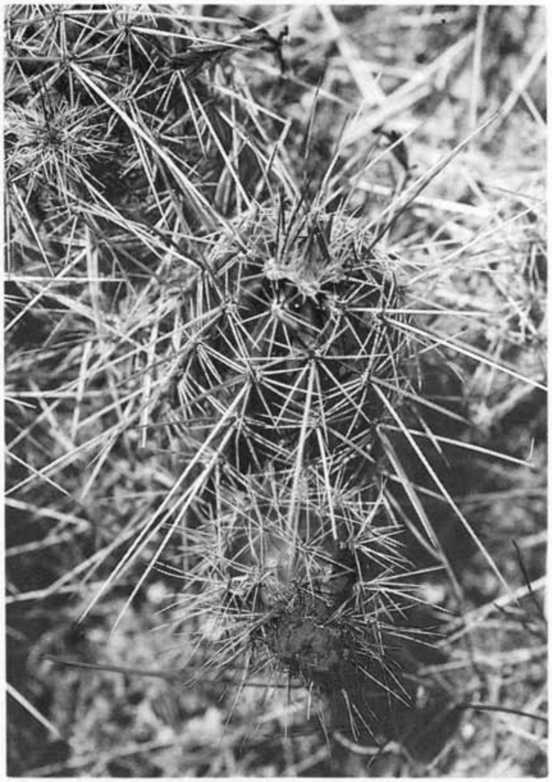
MATERIAL EXAMINED. NUEVO LEON. Between La Poza and Puerto de los Pastores, E of Hwy N.L. 31, 2km S of turnoff to Galeana, 24°46'N/100°2'W, 1400-1500m, in rock crevices of walls of canyon, grey limestone, 26 Mar 1976, *B. Hansen et al.* 3863 (MEXU—flowering stem); Ascension, [no date], *Lau* 1546, cult. E.R.C. 1209, Jan 1988 (K—areole, photos); S of La Escondida, KM99 on highway from Matehuala, 1650-1700m, on rocks in oak forest, 9 Jul 1986, *N.P. Taylor* 279 (MEXU, K—dried stem, seeds, photos); El Morro, 6km S of Aramberri, 1000m, 9 Jul 1986, *N.P. Taylor* 277 (MEXU, K—stem, photos).


*E. viereckii* var. *viereckii, Lau* 1295 (E.R.C. 167). *(photo: Parker)*


*E. parkeri* var. *parkeri*: 18 month old seedling raised from *Taylor* 279. *(photo: RBG Kew ©)*

Left, two contrasting forms of *E. viereckii* var. *morricalii* from Nuevo Leon: above, in the canyon between Montemorelos and Rayones, *Taylor* 192; below, near dirt road c. 5km south of Rayones, *Taylor* 194. *(photos: Taylor)*

*E. parkeri* var. *parkeri*, south of Aramberri, NL, *Taylor* 277. (*photo: Taylor*)

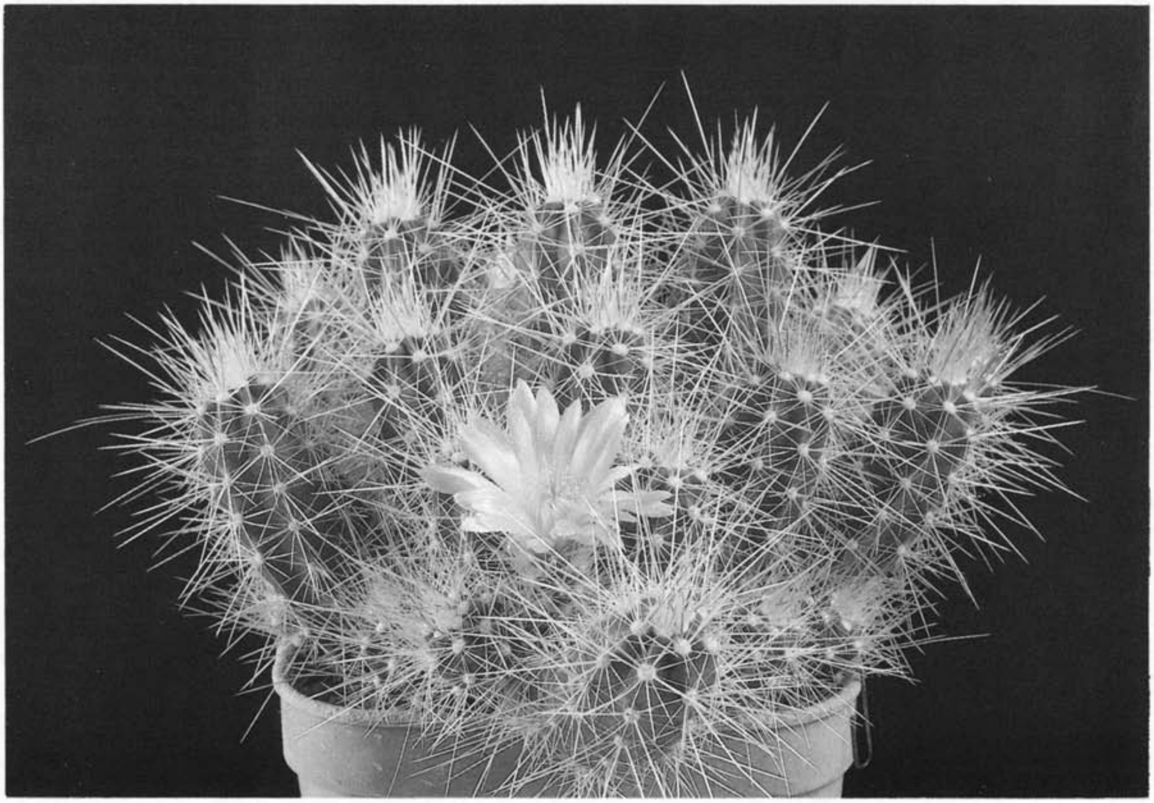


**E. parkeri** var. **gonzalezii** N.P. Taylor **var. nov.** *a var.* parkeri *ramis ex parte subterraneis, costis vix tuberculatis, spinis centralibus longioribus. Holotypus:* Mexico, Edo Tamaulipas, *Gonzalez Medrano* 8515 (MEXU).

DESCRIPTION. Stems usually not forming compact mounds, branching above and below ground (suckering by means of slender rhizomes), to c. 4.5cm diam., only gradually tapered towards apex; ribs (6-)7-10, scarcely tuberculate. Central spines 3-5, to 30-55mm; radial spines 10-14.

DISTRIBUTION. SE Nuevo Leon, SW Tamaulipas and N San Luis Potosi, 1700-2500m.

*E. parkeri* var. *gonzalezii*: above right, between La Bonita and Charcas, SLP, *Taylor* 204A (*photo: Taylor*); below, *Lau* 1375 flowering in cultivation (*photo: RBG Kew* ©).



Material examined. NUEVO LEON. Dulces Nombres, 2500m, [no date], *Lau* 1375, cult. A.J. Ward, Scarborough, U.K., 1987 (K—photo); ibid., cult. W. Blum, Bietigheim, W Germany, 1987 (K—photo); ibid., cult. S. Plath, California, U.S.A., May 1987 (K—photo); ibid., cult. N.P. Taylor, Woking, U.K., May 1988 (K—flowering stem in spirit). TAMAULIPAS. Between Palmillas and Miquihuana, ridge top W of road, *G. Freudenberger* s.n., cult. G. Freudenberger, Bad Rappenau, W. Germany, 26 May 1985 (K—fl. in spirit); 13km W of Palmillas on Hwy Fed. 101, 1700m, in hollow of flat rock beside piñon pines, 6 Jun 1986, *N.P. Taylor & R. Gonzalez G.* 191 (MEXU—dried stem, K—seeds); ibid., *Sanchez-Mejorada et al.* 3678 (MEXU); Sierra de las Vacas, 4km NE of San Jose d'Llano (nr border with Nuevo Leon), 1750m, *F. Gonzalez Medrano* 8515 (MEXU). SAN LUIS POTOSI. Between La Bonita and Charcas, 1900-2000m, grassy hillslope with flat rocks, 18 Jun 1986, *N.P. Taylor* 204A (K—photos).

**E. parkeri** var. (unnamed)

Description. Stems in compact mounds, branching above ground, to 4cm diam.; ribs 8-10, tuberculate. Central spines 3-4, to 65mm; radial spines 6-8. (Flowers not seen.)

Distribution. NE Zacatecas, c. 2750m.

Material examined. ZACATECAS. 6-8km E of Mazapil, Dec 1974, *Glass & Foster* 4043, cult. S. Plath, California, U.S.A., Oct 1985 (K—photo); 0.3km from El Cobre, nr Mazapil, 2750m, pine forest, 1987, *Sanchez-Mejorada et al.* 4041 (MEXU).

It gives me great pleasure to name this species in honour of David Parker, founder of the Echinocereus Reference Collection (Birmingham, U.K.) and friend of all who grow plants of this genus. His work in building up the Collection and furnishing Kew and other recipients with valuable documented material provides a fine example to the managers of other specialist collections. It is only by means of such living collections, and with knowledge of plants in the field, that real progress in the taxonomy of succulents can be achieved.

This new species, which comprises three varieties (the last unnamed for lack of floral details confirming its affinity), is not well known in cultivation at present, though it is possible that it was first introduced to European collections late last century as '*E. barcena*' Rebut. All three varieties are currently available, however, as either Lau, Taylor or Glass & Foster field numbers (see above).

*Echinocereus parkeri*, as noted already, has points in common with *E. viereckii*, *E. stramineus* and *E. nivosus*. It is between them in both taxonomic and geographic senses, and leaves no room for doubt that they and their other allies discussed below form a natural species complex. No single feature distinguishes *E. parkeri* from the remainder of the E. STRAMINEUS Group, but its combination of 6-10-ribbed, moderately spiny stems, small flowers with narrow perianth-segments expanding in early spring, and unusually large seeds (to 2.2mm!), is unique.

From *E. viereckii* it differs in its longer, whitish spination and earlier flowering period (e.g. fruit of *E. parkeri* var. *gonzalezii*, *Taylor* 191, which yielded viable seeds, was collected the same day as *E. viereckii* var. *viereckii* was observed in flower—6 June 1986). The flowers of *E. parkeri* are also smaller in most respects, though there is a slight overlap in perianth-segment width. From the geographically adjacent *E. stramineus*, *E. parkeri* differs in its lower rib count, by being smaller in all its parts, except seeds, and ecologically in its generally wetter, higher elevation, and mostly non-Chihuahuan Desert habitat.

Though it will not be immediately obvious, *E. parkeri* comes close to *E. nivosus*, via a seemingly intermediate population encountered near the border of the states of Coahuila and Nuevo Leon (30km E of Arteaga on dirt road to Las Vigas, 2250m, rocks above pine forest, 14 Jun 1986, in fruit, *U. Guzman* in *Sanchez-Mejorada* 3807, MEXU). The salient features of this plant are: stems 4-14×3.3-3.7cm; ribs 10, very low, to 13mm wide; areoles 3-9mm apart; spines hairlike, white, centrals 4-5, lowermost to 55mm, radials 14-16, to 11mm; fruit 10×10mm, covered in fine white bristles to 12mm. These details should be compared with those of *Lau* 739A (from 300m above Cinco de Mayo, Coahuila, which is discussed under *E. nivosus*, q.v.) and with the following species.

By far the closest ally of *E. parkeri*, and one which is much better known in cultivation, is *Lau* 1101, named as *E. rayonesensis sp. nov.* below. I have agonized for some time as to the rank at which to describe this distinctive plant. While the average *Echinocereus* enthusiast will have no difficulty in recognizing it as a species, careful analysis of its characters shows that it could equally well be treated as a further variety of *E. parkeri*. Certainly, there are no reliable floral distinctions to separate them, so that we must rely on weaker vegetative differences and the lack of any hint of intermediates as justification for accepting specific rank. I am also strongly influenced by the fact that the valley of Rayones is noted for its unique cactus flora, including such remarkable endemics as *Aztekium ritteri* and *Ariocarpus scapharostrus*, besides various unusual forms of other more widespread taxa. Thus, it comes as no surprise that the E. STRAMINEUS Group should have its own special representative apparently restricted to this valley. More importantly, the publication of *E. rayonesensis* makes more apparent the need to designate this valley as a nature reserve, preferably with provision for its plant treasures to be guarded by wardens.

**Echinocereus rayonesensis** N.P. Taylor **sp. nov.** *a* Echinocereo parkeri *costis 10-15 spinis centralibus 5-9 spinis radialibus 15-25 differt. Holotypus:* Mexico, Nuevo Leon, *Lau* 1101, cult. R. Mottram, Jun 1987 (K).

[*E. longisetus* sensu Werderm. in Blühende Kakt. and. Sukk. Pfl., Lfg 7, t. 25 (1932) non (Engelm.) Lemaire.]

Holotype of *E. rayonesensis* (*Lau* 1101) prior to preservation; flower 2.7×2.8cm. (*photo: R. Mottram*)

Description. Caespitose, branching at ground level or by means of underground suckers; stems erect, cylindric, 12-28×2.5-4.5cm, epidermis obscured by spines; ribs 10-15, to 4-8mm high, 7-10mm wide, tuberculate; areoles 5-13mm apart, circular, 1.5-3mm diam. Central spines 5-9, glassy-white to pale yellowish, darker at base and apex, hairlike to slender needlelike, lowermost much longer than the others, 30-50mm, directed downwards; radial spines 15-25 or more, glassy-white, hairlike to finely bristlelike, to 7-15mm. Flowers 2.7-5.4(-6.0)×2.8-5.3(-6.0)cm, purplish-magenta, white in the throat; pericarpel and tube 18-20mm, areoles 1.5-2mm diam., with 6-40, to 13-20mm, fine glassy-white bristle-spines, pericarpel 8-11×7-10mm, tube flared to 7-10mm diam. at apex, walls 2-3mm thick; nectar-chamber 2-4×2-3mm; perianth-segments narrowly oblanceolate, the largest 19-35×3-5mm, apex attenuate-acute, margins serrulate; stamens 4.5-7mm, anthers broadly oblong, 0.8mm; style c. 15×1-2mm; stigma-lobes c. 8-10, to 6×0.7mm, yellow-green; ovary locule obovoid, 6.5×4mm. Fruit c. 17×8mm, olive green to brownish, pulp colourless. Seeds 1.5mm, black.

Illustrations. Kakteen und andere Sukkulenten 27: 32 (1976); ibid. 39: 110 (1988).

Distribution. S central Nuevo Leon (valley of Rayones); Chihuahuan Desert type vegetation on limestone, c. 1000m.

Material examined. NUEVO LEON. Valley of Rayones near Rayones, c. 1974, *Lau* 1101, cult. G. Freudenberger, Bad Rappenau, W. Germany, 26 May 1985 (K—fl. in spirit); ibid., cult. R. Mottram, Thirsk, U.K., Jun 1987 (K—flowering stem in spirit); ibid., cult. E.R.C. 213, 1987 (K—photos).

The above description is based on cultivated material of *Lau* 1101, supplemented with details from the Lau habitat specimen described by Piltz in Kakt. and. Sukk. 27: 34 (1976), the data of Unger in ibid. 39: 110 (1988) and that of Werdermann, loc. cit. At least one other form of the species is circulating in cultivation at present, but is without any documentation. Like Werdermann's plant, described in 1932 from long-cultivated material at Berlin, this form has been labelled '*E. longisetus*', to which *E. rayonesensis* bears a very strong resemblance, vegetatively speaking. Though both clearly belong in the E. Stramineus Group, they are not directly related, but connect via *E. parkeri*, *E. nivosus* and *E. freudenbergeri*. The flowers of the true *E. longisetus* are larger, a paler pinkish-magenta with a more obvious white throat, and have perianth-segments twice as broad. A similar comparison could be made between *E. rayonesensis* and *E. nivosus*, but while the floral differences are somewhat less, the altitudinal separation is greater, viz. c. 1000 vs 1900-2300m.

Leaving taxonomic considerations aside, both new species described above seem easy to grow and flower, providing ample sunlight is available. Furthermore, their attractive spination makes up for their generally small flowers.

**Echinocereus nivosus** Glass & Foster

The beautiful type locality form of this species seems rare at present in cultivation, where *Lau* 739 is better known. The former has stems with up to 15 ribs, covered in extremely numerous, dense spines, and branches both above and below ground (by suckers), forming mounds or spreading clumps (Coahuila, SW of General Cepeda, Sierra El Rancho, Pico El Chino, mountain pass N of El Cinco, 1900-2300m, limestone rocks with occasional *Arbutus* and *Juniperus*, 13 Jun 1986, *N.P. Taylor* 200, K—seeds, photos). The latter has 10-12 ribs and fewer spines per areole. It comes from farther east, south of Carneros pass, and at higher elevations in this habitat Lau has found a form (*L.* 739A) whose relatively sparse spination hints at a relationship with *E. parkeri* (q.v.), via an intermediate taxon discussed above. *Lau* 739A has 10-ribbed stems, areoles c. 7mm apart, central spines 10, to 18mm, radials c. 16, to 11mm (E.R.C. 1204, Jan 1988, K—areole, photos).

**Echinocereus freudenbergeri** G.R.W. Frank in Kakt. and. Sukk. 32: 102-105 (1981).

*E. delaetii* var. *freudenbergeri* (G.R.W. Frank) N.P. Taylor, Genus Echinocer. 97 (1985).

'*E. setosus*' hort., nom. nud.

In my book (1985) I chose to submerge *E. freudenbergeri* into *E. delaetii*, as a variety, basing my decision on the apparent lack of any significant difference in their reproductive structures and habit. In July 1986 I was able to study *E. freudenbergeri* in the field, at a locality north-west of Cuatrocienegas, Coahuila, where it was growing side by side with *E. longisetus*. (Frank, loc. cit., reports that his species was found growing with *E. delaetii*, which I now regard as a synonym of *E. longisetus*, in the Sierra de la Paila—a considerable distance to the south of my locality.) Though these two agree so closely in flower and seed morphology, some mechanism must operate to prevent them interbreeding, since I could find no evidence of intermediates at this locality, where they were easily distinguished by their striking divergence in stem and spine length. Therefore, until the biological barriers which appear to prevent interbreeding are understood, I prefer to recognize *E. freudenbergeri* G.R.W. Frank as a species and accept that it breaks the general rule that closely related species in the Cactaceae do not grow together.

Although I am presently prepared to accept that *E. freudenbergeri* may be distinct from *E. longisetus sens. lat.*, it is far from certain how it can be differentiated from the very similar *E. nivosus*. The variability displayed by *E. nivosus* at its type locality (see above) means that neither habit nor rib number can be used to distinguish them, and their spination completely intergrades. There are, however, small differences in the relative proportions of their flower parts, and Frank illustrates somewhat different seeds, but it is possible that a wider range of material will show these already small

Right, *E. nivosus* at the type locality, *Taylor* 200. (*photo: Taylor*) distinctions to be worthless. It would not surprise me if the allopatric *E. freudenbergeri* and *E. nivosus* relate in the same way as do *E. longisetus* and *E. delaetii*, which are synonymized below.

The following description is based on that of Frank, loc. cit., amplified with details taken from the materials cited below.

DESCRIPTION. Stem to 15×4-6cm, cylindric, tapered at apex, freely branching by means of slender underground suckers; ribs of mature stems 13-18, c. 3mm high and 9mm wide, tuberculate; areoles c. 6-10mm apart, oval, to 3mm long. Spines 20-35 per areole, bristle-like, all white or creamy-yellow, or centrals reddish to brownish, occasionally all spines brownish; centrals 6-9 or more, lowermost longest, to 18-25mm; radials 15-20 or more, lowermost to 15mm. Flowers c. 6-7.5×6-9cm, slightly purplish pink, throat white; pericarpel and tube 29-35mm, with numerous areoles bearing 7-15 to 19mm, white spines, pericarpel 12-16×12-14mm, tube 10-13mm diam. at base, flared to 17-21mm at apex, walls c. 2-4mm thick; nectar-chamber 3.5-5.5×2.5-3mm; perianth-segments oblanceolate, largest 31-43×8-10mm, apex attenuate-acuminate, margins coarsely serrate; stamens very numerous and densely inserted within tube, 7-12mm, anthers oblong, to 1.4mm; style c. 25×1.5mm; stigma-lobes 11-15, to 7×0.7-1.0mm, yellow-green; ovary locule c. 5.5×6.5mm. Fruit 20-25×15-20mm, carmine red, very spiny. Seeds c. 1.5×1mm, dull black.

ILLUSTRATION. Kakteen und andere Sukkulenten 32: 102 (1981).

DISTRIBUTION. Central and S Coahuila; Chihuahuan Desert type vegetation on limestone, 1300-1800m.

MATERIAL EXAMINED. COAHUILA. At base of mountains c. 25km SW of Cuatrocienegas–Ocampo highway, having first travelled 28.5km from Cuatrocienegas, 1300m, with *Echinocereus longisetus*, 8 Jul 1986, *N.P. Taylor* 276B (K—dried stem, photos), s.n. (MEXU); vicinity of Cuatrocienegas, *Glass & Foster*, cult. E.R.C. 208, Apr 1988 (K—areoles); 12km S of Cuatrocienegas, *G. Freudenberger* s.n. (ZSS, holo); ibid., cult. G. Freudenberger, Bad Rappenau, W Germany, 26 May 1985 (K—fl. in spirit); Sierra de la Paila, 1800m, *Lau* 1032, cult. E.R.C. 1123, May 1988 (K). Locality unknown: cult. R. Mottram, Jun 1988 (K—fl. in spirit, seeds, photos).

**Echinocereus longisetus** (Engelm.) Lemaire var. **longisetus** Having observed this species at its type locality and further south, where it begins to resemble var. *delaetii*, and having obtained liquid preserved flowers from plants in cultivation, the following amplified description is offered.

DESCRIPTION. Branching from base to form large sprawling clumps to 1m diam.; stems erect or partly prostrate, to 30-50×3.5-6.0(-7.5)cm, cylindric; ribs 11-17, rather low, 12mm or more wide, tuberculate; areoles 8-13mm apart. Central spines 4-9, uppermost 2-3 to 10-35mm, white, pink or brownish, lowermost much longer, to 45-70mm, whitish, bristle-like to hairlike, straight, directed downwards; radial spines c. 15-20, lowermost to 10-18.5mm, white, acicular. Flower 5.6-7×6-7.2cm, slightly purplish pink, throat white; pericarpel and tube 36mm, with areoles bearing numerous white, to 23mm spines, pericarpel c. 14×17cm, tube 13mm diam. at base, flared to 19mm at apex, walls 3.5-4.5mm thick; nectar-chamber 5-6.5×2.5-3.5mm; perianth-segments oblanceolate, largest to 34×10mm, rather fleshy at base, apex attenuate-acute, margins coarsely to finely serrate; stamens very numerous and densely inserted within tube, 8-13mm, anthers oblong, c. 1.3mm; style 25-29×2-2.5mm; stigma-lobes 11-14, to 9.5×1mm; ovary locule 6.5×7mm. Fruit not available. Seeds 1.5mm, black.

*E. freudenbergeri* in habitat, *Taylor* 276B. (*photo: Taylor*)

Illustration. Haustein, E., Der Kosmos-Kakteenfuhrer, 233 (1983).

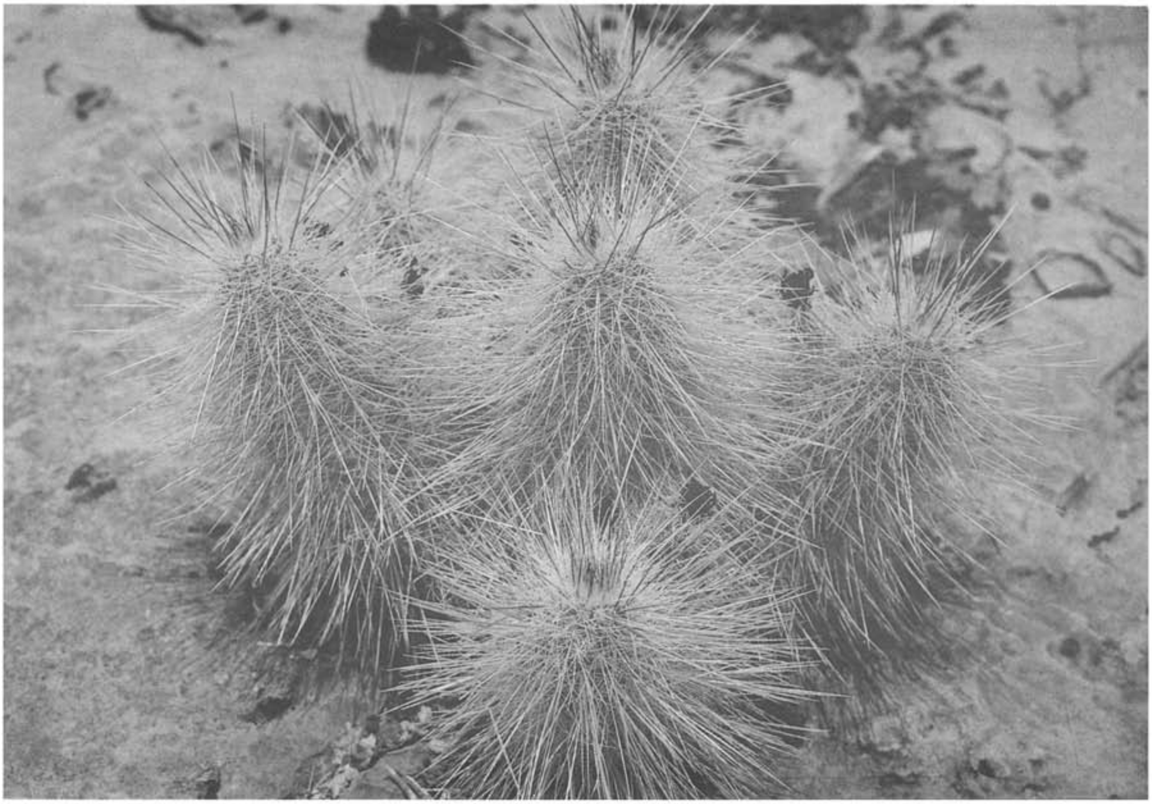
Distribution. Central and N Coahuila, ? Texas (Big Bend); Chihuahuan Desert and rocks in selva baja, 500-1500m.

Material examined. COAHUILA. Sierra del Carmen, c. 29° N/102°30′W, 1400m, [no date], *Lau* 1538 (K—seeds); Nueva Rosita, 1986, [no collector], cult. E.R.C. 1159, Jan 1988 (K—areole); mountains SW of Melchor Muzquiz *(locus classicus)*, 500-600m, with *Echinocereus enneacanthus* var. *brevispinus*, valley floor clearing in selva baja, 7 Jul 1986, *N.P. Taylor* 265 (MEXU—dried stem, K—photos); at base of and on cliffs of mountains c. 25km SW of Cuatrocienegas–Ocampo highway, having first travelled 28.5km from Cuatrocienegas, 1250-1500m, with *Echinocereus freudenbergeri*, 8 Jul 1986, *N.P. Taylor* 276A (K—photos). Locality unknown: cult. E.R.C. 1177, 25 May 1987 (K—fl. in spirit, photos); cult. R. Mottram RM250.1, Jun 1987 (K—fl. in spirit).

Var. *longisetus* ranges both north and south of its type locality near Melchor Muzquiz (Santa Rosa). To the north it may even reach into the Big Bend of Texas (I have heard at least two independent reports that this is so but have seen only a poorly documented photograph to date), while to the south, Backeberg, relying on a photograph of Zehnder (Die Cact. 6: 3845-3846, Abb. 3484. 1962), has recorded it from the Sierra de la Paila, S Coahuila. This identification, however, is in error, since Zehnder's plant seems to be the same as a distinctive, long-spined, half-starved form of *E. stramineus*, which I have encountered about 30km north of Est. Marte.

From the collections of true *E. longisetus* made in the last few years it is clear that it is rather variable in its spination.

*E. longisetus* var. *longisetus*: above right, stem at the type locality, *Taylor* 265; below, form approaching var. *delaetii, Taylor* 276A. *(photos: Taylor)*



Half-starved, long-spined form of *E. stramineus* var. *stramineus* from 30km N of Est. Marte, Coah., which may be the plant misidentified as *E. longisetus* by Backeberg. *(photo: Taylor)*

The southernmost collection cited above has stems with up to 17 ribs and hairlike central spines to 70mm. In these respects it clearly approaches *E. delaetii* and there seems to be little other than minor quantitative differences to separate them. The following change of status seems to reflect their relationship more accurately:

**E. longisetus** var. **delaetii** (M. Gürke) N.P. Taylor **stat. nov.**

*Cephalocereus delaetii* M. Gürke in Monatsschr. Kakt.-Kunde 19: 116 (1909). Lectotype (Taylor, Gen. Echinocer. 97. 1985): illustration in Gürke, loc. cit., 119 (1909).

*Echinocereus delaetii* (M. Gürke) M. Gürke in ibid., 131 (1909).

Differs from var. *longisetus*: stems to 8cm diam.; ribs 17-24; central spines to 100mm, hairlike and variously wavy or curled; flowers 5.7-10×5.8-12.5cm, perianth-segments to 55×15mm.

ILLUSTRATION. Cactaceas y Suculentas Mexicanas 31(4): front cover, fig. 36 (1986).

DISTRIBUTION. Cent.-S and SE Coahuila; Chihuahuan Desert and piñon pine forest, c. 1800-2000m.

MATERIAL EXAMINED. COAHUILA. Sierra de la Paila, c. 1973, *Lau* 798, cult. E.R.C. 204, May 1988 (K—areole). Locality unknown: cult. A.J. Ward, Scarborough, U.K., 1984 (K—fl. in spirit, photos); cult. R. Mottram, Thirsk, U.K., 1985 (K—photos); cult. E.R.C. 205, May 1988 (K—areole).

E. VIRIDIFLORUS Group:

**Echinocereus knippelianus** Liebner

In my book I indicated it was possible that this highly specialized species might be convergent with *E. pulchellus* (Gen. Echinocer. 150. 1985). Further observations of them, both in cultivation and in the field, have reinforced my earlier suspicions so that I am now prepared to exclude *E. knippelianus* from Section *Pulchellus.* Previously, it was hard to see any obvious connexion for this species elsewhere in the genus. However, David Parker recently acquainted me with an interesting hybrid raised between *E. knippelianus* and *E. viridiflorus* var. *davisii*, which has drawn attention to the fact that there are considerable similarities between these two. Both display a semi-geophytic lifestyle, have a tuberous rootstock, a few-ribbed, dark blue-green stem, remarkably similar flower morphology, and few-seeded, very quickly ripening purplish fruits. Thus, for the present, I am placing *E. knippelianus* in the E. VIRIDIFLORUS Group of Sect. *Echinocereus*, where it represents the most specialized lifeform attained in the related sections 1-3 of the genus.

Observation of var. *knippelianus* at two localities in SE Coahuila, 25 and 30km E of Arteaga (*N.P. Taylor* 201, 202), and of liquid preserved flowers from cultivated material of all three named varieties (E.R.C. 293 & 296; G. Freudenberger, 26 May 1985, all K) suggests the following additions to my earlier description: stem small, apex flush with ground surface (open meadow habitats), or stem large, half exserted (in forest); ribs 5-8, flat or markedly raised; pericarpel and tube 9-15mm, pericarpel 3.5-7×4-9mm, tube areoles with 1-5 spines, nectar-chamber 1-1.5×1.5-2mm; perianth-segments oblanceolate, 15-25×3-6mm; stamens to c. 9mm, anthers to c. 2mm; style 9-13×0.8-1.2mm, stigma-lobes 5-11, 4-6×0.5-1.0mm.

## 4. Section TRIGLOCHIDIATUS

DIAGNOSTIC CHARACTERS. Stems elongate to short and stout but densely branched, <0.6m; ribs 4-16; vegetative characteristics otherwise as in Sect. *Erecti*. Flower-buds bursting through stem epidermis; flowers displaying hummingbird pollination syndrome as in Sect. *Morangaya*, but perianth-segments pink, orange or red, remaining colourless in alcohol-formalin preservative and stigma-lobes bright green; anthers to 3mm. Fruit as in the preceding sections, indehiscent or splitting open when ripe. Seeds to 2mm, testa tubercles well defined. 3-4 species (W & N-cent. Mexico, SW United States).

**Echinocereus scheeri** (Salm-Dyck) Scheer

The following variety, listed as 'unnamed' in Taylor (1985: 63), has now been formally described. It is probable that the name *Echinocereus ortegae* Rose ex J. Gonzalez Ortega (1929) refers to this plant, but there are discrepancies between the original description and a photograph at K (ex US) of Gonzalez Ortega's material—casting doubt on whether the latter represents the type. My earlier opinion, that *E. ortegae* was a synonym of *E. scheeri* var. *scheeri*, was influenced by Gonzalez Ortega's original description, which calls for a plant with only 7-8 ribs, whereas the photograph depicts a specimen with at least 10 ribs.

Also included here is an isosyntype of *Wilcoxia papillosa* Britton & Rose, a species apparently founded on disparate elements. The detached flowers cited below (*Gonzalez Ortega* 848) are clearly referable to this *Echinocereus*, while the vegetative material described by the American monographers (*C.A. Purpus* UC160654—lectotype, here designated, K—photo) represents a species of *Peniocereus*, which awaits rediscovery.

**E. scheeri** var. **koehresianus** G.R.W. Frank in Kakt. and. Sukk. 39: 186-189, with figs. (1988). Type: Mexico, Edo Sinaloa, 1975, *Lau* 1143 (ZSS).

*Wilcoxia papillosa* Britton & Rose, Cact. 2: 112 (1920) pro parte.

? *Echinocereus ortegae* Rose ex J. Gonzalez Ortega, Apuntes para la Flora Indigena de Sinaloa [unpaged] (1929). Type: cf. photograph cited below (the whereabouts of Gonzalez Ortega's herbarium is not known).

'*E. koehresii*' hort., nom. nud.

'*E. koehresianus*' hort., nom. nud.

'*E. scheeri* var. *australis*' N.P. Taylor, ined.

DESCRIPTION. Caespitose, forming dense clusters 30cm broad of up to 50 or more branches; stems erect or sometimes pendent when old and elongated, 10-20(-40)×2.5-4cm, dark green; ribs 10-16, to 2.5mm high × 4-8mm broad, tuberculate; areoles 2-6mm apart, circular, only 1-2mm diam. Spines 14-21 per areole, finely needle-like or bristle-like, white or dirty white to dark brownish, especially at base, more or less hiding the stem surface in habitat plants; centrals 3-6, to 9(-22)mm; radials 10-15, to 8mm. Flowers tubular-funnelform, nearly regular to somewhat zygomorphic (weakly S-shaped), 6.5-9(-10)×4.5-6(-10)cm, brilliant scarlet, sometimes with a bluish cast, remaining open all day; flower-buds sharply pointed; pericarpel and tube c. 45-55mm, areoles with short inconspicuous whitish trichomes and up to 15, 4-11mm, dark brown, pale tipped bristle-spines; pericarpel 11-16×9-12mm, dark green to purplish-brown; nectar-chamber 5×3-4mm, narrowed above, sometimes protected by the incurved bases of the lowermost stamens; tube narrowed to 7.5-10mm diam. above ovary, flared to 15-18mm at apex, dark red; perianth-segments obovate to oblong-oblanceolate, the largest 25-35×6.5-10mm, apex broadly acute to acuminate-apiculate or aristate, margins entire to irregularly serrate; stamens 20-40mm, filaments magenta in upper half, pollen pale yellow; style 55-70×1.2-1.5mm, equalling or exceeding stamens by up to 20mm; stigma-lobes 9-12, 4-6×1mm, erect, yellowish- or bright green; ovary locule broadly ovoid to oblong, 5-11×5-6mm. Fruit ovoid, c. 22×18mm, dark green. Seeds black, 1.3-1.5×0.8-1.0mm.

ILLUSTRATIONS. Kakteen und andere Sukkulenten 38: 306 (1987); ibid. 39: 186-189 (1988).

DISTRIBUTION. S Sinaloa and W Durango, in the Sierra Madre Occidental; cliffs in forest, c. 600-2400m.

MATERIAL EXAMINED. SINALOA. About 5km E of El Espinal (c. 110km N of Mazatlan), Sierra de Pinal, c. 600m, with *Echinocereus subinermis* var. *ochoterenae*, 30 Jan 1976, *Kimnach* 1920, cult. Huntington Bot. Gard. (HNT, K—photos); loc. cit., 14 Nov 1977, *Kimnach & Sanchez-Mejorada* 2258 (HNT); San Ignacio, 1340m, 20 May 1919, *Gonzalez Ortega* 848 (K— fls only; isosyntype of *Wilcoxia papillosa* Britton & Rose); between El Carrizo and Loberas, near Hwy Fed. 40, east-facing cliff in mixed pine/broadleaved forest, 1850m, with *Echinocereus polyacanthus* var., 29 Jun 1986, *N.P. Taylor & R. Gonzalez G.* 231A (K—fl. & fr. in spirit, photos), 231B (MEXU, K—stem); loc. cit., 21 Sep 1987, *N.P. Taylor & S.G. Knees* 389 (K—photos, seeds); loc. cit., 1975, *A. Lau* 1143, cult. R. Simpson, Kidderminster, U.K., Aug 1985 (K—fl. in spirit); ibid., cult. N.P. Taylor, Woking, U.K., Jul 1987 (K—stem & fls. in spirit). DURANGO. Cuenca del Rio Tamazula, Sianori, 800m, c. 1924, *Gonzalez Ortega* s.n. (K—photo; type of *Echinocereus ortegae* Rose ex J. Gonzalez Ortega?); between El Palmito and Puente Buenos Aires, on inaccessible cliff above Hwy Fed. 40, 2400m, with *E. polyacanthus* var., 9 Oct 1987, *N.P. Taylor* (obs. only).

*Echinocereus scheeri* is one of the most variable species known to the writer and deserves detailed study in the field throughout its range. The southernmost member of this complex, described above, is rather unusual and may eventually prove worthy of specific rank. However, its cylindrical stems bear the small areoles and spines characteristic of *E. scheeri*, and when compared with red-flowered forms of var. *scheeri* from Chihuahua, its differences are seen to be less significant. These include the stem's higher rib count, the more numerous spines, and the scarcely woolly areoles bearing dark brown bristles on the pericarpel and tube. Other floral features, such as the relatively short tube, the tendency towards zygomorphy, the development of a nectar-chamber protected by incurved stamen bases, and a long-exserted style, can be found in other forms of the species, or have proved rather inconstant now that a range of material has been studied. Perhaps its most important difference, which concerns its ability to exchange genes with the remainder of the species, is that it appears to flower later in the season—a characteristic maintained when it is cultivated with other *E. scheeri* forms under uniform conditions.

The variability of var. *koehresianus* is not so obvious in cultivation, where *Lau* 1143 is the only widely grown form at present. It should be noted that the wild population represented by Lau's introduction has generally larger flowers than plants known from the other Sinaloan localities

*E. scheeri* var. *koehresianus* on a cliff between El Carrizo and Loberas, Sinaloa, *Taylor & Knees* 389. (*photo: Taylor*)

Flower of *E. scheeri* var. *koehresianus* (*Lau* 1143).
(*photo: RBG Kew* ©)

cited above. At Lau's site, beside the Mazatlan–Durango highway, and higher up across the state border into Durango, var. *koehresianus* grows with another member of Sect. *Triglochidiatus*, namely *E. polyacanthus* Engelm. *sensu lato*. Some collectors have failed to recognize the differences between these two, and in a W German nursery I have seen a plant 'identified' as *Lau* 1143 which was the *E. polyacanthus* form. In the wild it flowers up to two months before *E. scheeri* var. *koehresianus* (in April-May or earlier vs. June/July), the flower-buds are more or less blunt at apex (sharply pointed in typical *E. scheeri* forms), there are numerous rows of perianth-segments, and the floral areoles are conspicuously woolly. The stem areoles are much larger and woollier too, whereas those of var. *koehresianus* are very small and soon become nearly glabrous.

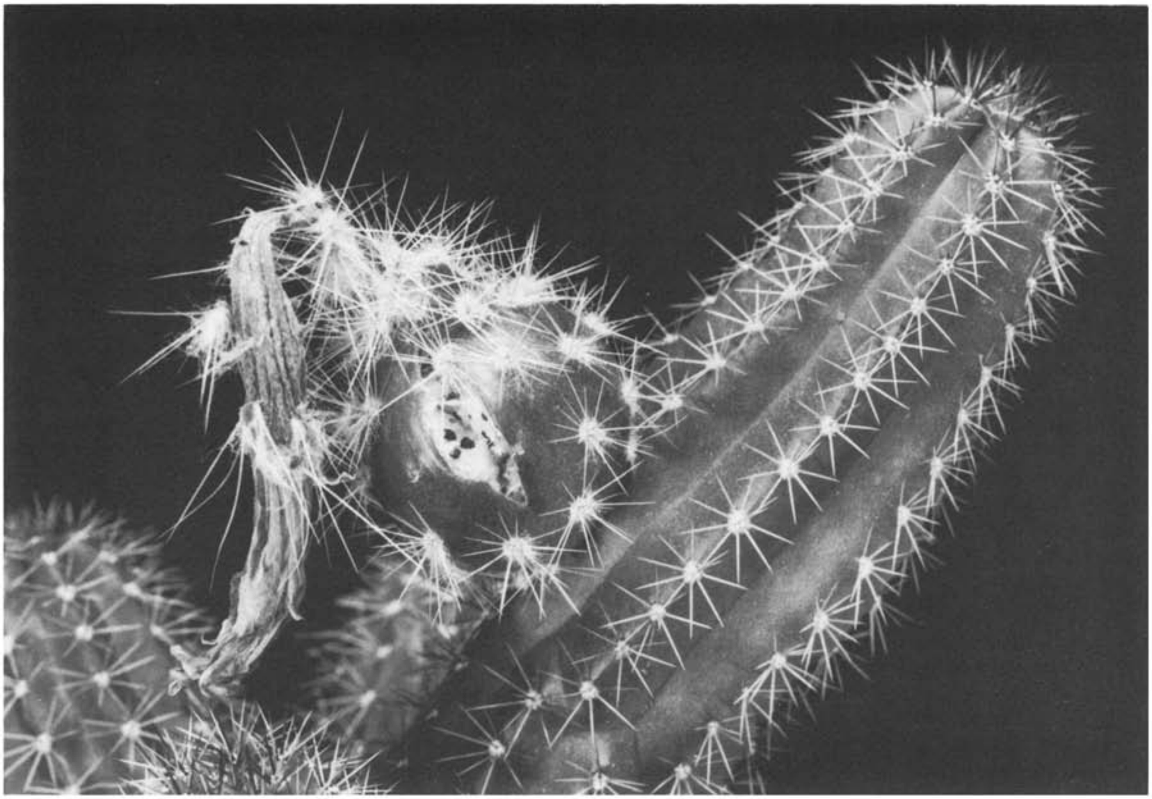
**E. scheeri** var. **scheeri**

Typical *E. scheeri* var. *scheeri*, as defined by the designation of *Lau* 84 (K) as neotype of the species (Taylor in Kew Mag. 1: 154. 1984), is a plant with elongate tubular-funnelform flowers ranging in colour from pink to orange. The neotype form has flowers of an intermediate pinkish-orange and thus the traditional use of the name *E. salm-dyckianus* Scheer for orange- as opposed to pink-flowered forms seems unwarranted, and the name is best abandoned in any case for lack of adequate typification (Taylor in Brit. Cact. Succ. J. 4: 25-26. 1986). At least three red-flowered clones of var. *scheeri* are in cultivation at the Echinocereus Reference Collection (E.R.C. 13, 704 & 713), each with slightly different flower forms, but with uniform stems scarcely distinguishable from those of certain orange-pink-flowered plants. Two of these clones are said to have originated in Chihuahua and I have no reason to suppose that they are not naturally occurring forms of the species. Certainly, there is nothing, apart from flower colour, to justify their exclusion from any reasonable concept of var. *scheeri*.

More important than variation in flower colour, however, is the range observed in flower size and shape. Various forms of interest in this respect have entered cultivation from the region known as the Sierra Obscura, in W Chihuahua, through the work of Alfred Lau. One such produces large orange flowers measuring 8-10×7.5-9.5cm, in which the tube and nectar-chamber are unusually short but broad. The latter is protected by the bases of the lowermost stamens, as in some flowers of var. *koehresianus*. The fruits of this form measure to 27×26mm. The most interesting forms are those which appear to have been distributed under the Lau numbers 90 and 91, though there seems to be confusion over which number applies to which plant! The plant in the E.R.C. as *Lau* 91 is of a clone that produces relatively small tubular flowers striped with pale to deep yellow and pink. Its stems are fairly typical of var. *scheeri*. *Lau* 90, as labelled at E.R.C., has long spines atypical of the species and superficially resembles *E. polyacanthus* until it flowers.

Omitted from the synonymy of var. *scheeri* in my monograph is *E. salm-dyckianus* var. *noctiflorus* Heid in Leafl. West. Bot. 4: 27 (1944), based on a collection from Cerocahui, SW Chihuahua. The tendency of flowers of this species to partially close during the hottest part of the day (this falsely giving the impression that they are nocturnal) is well known, but I do not believe this characteristic to be particularly reliable. According to Peter Schatzle (Kakt. and. Sukk. 38: 306. 1987), var. *koehresianus* (i.e. *Lau* 1143) is not related to *E. scheeri*, since its flowers lack this diurnal rhythm. While this appears to be so, it is not the only form differing in this respect. Furthermore, I have received reports that some of the larger-flowered plants referable to *E. polyacanthus sens. lat.* also bear flowers displaying a diurnal

*E. scheeri* var. *scheeri*, *Lau* 84, the neotype clone.
(*photo: RBG Kew* ©)



*E. scheeri* var. *scheeri* (*Lau* 84), showing longitudinal dehiscence of its ripe, green fruit, 3×2.5cm (K—in spirit). (*photo: RBG Kew* ©)

rhythm, so that this characteristic may not be restricted to *E. scheeri*. Thus, for the present, I am discounting this feature as a means of distinguishing var. *koehresianus* from its allies.

The present state of the infraspecific taxonomy of *Echinocereus scheeri* may be summarized in the following key:

1. Stems 4-10-ribbed; spines <14 per areole; pericarpel and tube of flower with conspicuously woolly areoles bearing pale bristle-spines (E Sonora & W to SW Chihuahua) ............2
   Stems 10-16-ribbed; spines 14-21 per areole; pericarpel and tube areoles almost devoid of wool, bristle-spines dark brown except at apex (S Sinaloa & W Durango) .................................................................................. var. **koehresianus**
2. Stems 4-5(-7)-ribbed; spines absent, minute or to c. 2mm; flowers pink; pericarpel and fruit with spines to 3mm .......................................................................................... var. **gentryi**
   Stems (6-)7-10-ribbed; spines >2mm; flowers pink to orange or scarlet; pericarpel and fruit with spines to 8mm .......................................................................................... var. **scheeri**

**Echinocereus polyacanthus** Engelm.

Like the preceding, this species is highly variable and in need of detailed field study. My earlier circumscription of the large-flowered var. *densus* (Gen. Echinocer. 65, footnote), which tentatively included *E. huitcholensis* and '*E. matthesianus*', has proved to be rather broad and it can now be divided into western and eastern taxa, as follows:

**E. polyacanthus** var. **huitcholensis** (F.A.C. Weber) N.P. Taylor **stat. nov.**

*Cereus huitcholensis* F.A.C. Weber in Bull. Mus. Hist. Nat. Paris 10: 383 (1904). Type: Mexico, Edo Jalisco, May 1900, *L. Diguet* (P—on 3 sheets, 2 with admixture of *E. spinigemmatus* A. Lau). Lectotype (designated here): the sheet including stems and fls of *C. huitcholensis* only (P).

*Echinocereus huitcholensis* (F.A.C. Weber) M. Gürke in Monatsschr. Kakt.-Kunde 16: 23 (1906).

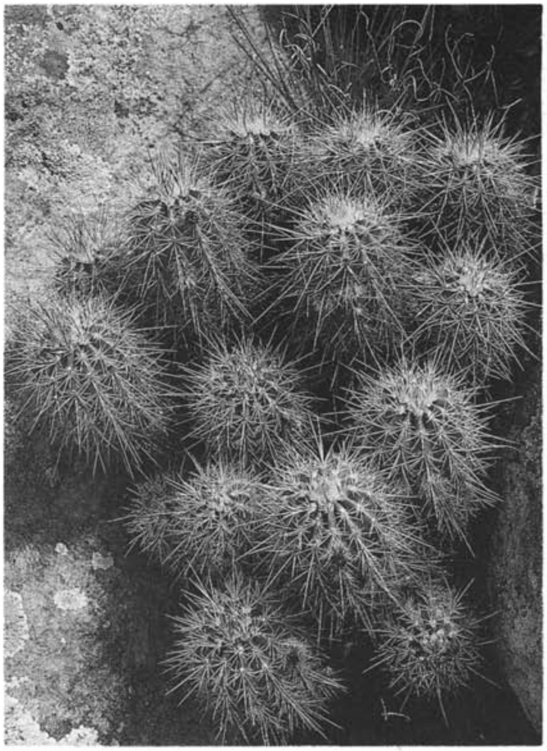
? '*E. matthesianus*' Backeb., Descr. Cact. Nov. 3: 6 (1963); Kakteenlexikon, Abb. 90 (1966) nom. inval. (Arts 9.5 & 37.1).

Description. Stems becoming slender-cylindric, 2-5(-6)cm diam.; ribs 10-13, rather low, 2-5mm high. Central spines 1-7, to 10-15mm; radial spines 9-15, to 5-10mm. Flowers 5.5-15×4.5-8cm, light to deep pink, orange-red or scarlet; tube nearly straight to strongly S-shaped, gradually tapered to base, rather stout, c. 10-15mm diam. in region of nectar-chamber, c. 20-25mm at apex, areoles very woolly and conspicuous; nectar-chamber broad, c. 4-5mm diam.; perianth-segments often broadly rounded, apiculate, not widely spreading.

Illustration. Kakteen und andere Sukkulenten 39: 63 (1988).

Distribution. Sinaloa, SW Durango, Nayarit and NW Jalisco, Pacific drainage of the Sierra Madre Occidental; rocks and cliffs in forest, 1600-2400m.

Material examined. SINALOA. N Sinaloa (?), between Choix and San Vicente (Chihuahua), *Lau* (K—photo of flowering pl. in habitat); S Sinaloa, Plomosas, *Lau* 768, cult. E.R.C. 743, 1985 (K—fl. in spirit, photos). DURANGO. Mazatlan–Durango Hwy, [collector?], cult. E.R.C. 44, 1985 (K—photos); Pueblo Nuevo, *Lau*, cult. Huntington Bot. Gard., May 1981 (HNT1548); loc. cit., 1600-1800m, *Lau* 768A, cult. E.R.C. 1213, Mar 1988 (K). NAYARIT. Locality unknown, *Lau*, cult. E.R.C. 1161, 1987 (K—fl. in spirit, line drawing, photos). JALISCO. Sierra de Nayarit (Sierra de los Huitcholes), 1800m, May 1900, *L. Diguet* (P); 'Macata', on rocks in arroyo, found planted in Guadalajara garden, Feb 1970, *Boutin & Kimnach* 3243, cult. Huntington Bot.



*E. polyacanthus* var. *densus* in habitat in Zacatecas, *Taylor & Knees* 473. *(photo: Taylor)*

Gard., Mar 1972 (HNT1536). Without locality: cult. Holly Gate Cactus Nursery, Sussex, U.K., 1984 (K—fl. in spirit, photos).

Var. *huitcholensis* is a distinctive variety which could be, and sometimes is, confused with *Echinocereus scheeri* until it comes into bud and flowers. Then, the blunt-ended buds and row upon row of rounded perianth-segments immediately distinguish the former from varieties of the latter.

**E. polyacanthus** var. **densus** (Regel) N.P. Taylor in Kew Mag. 1: 159, Plate 20 (1984).

*Echinopsis valida* var. *densa* Regel in Gartenflora 1: 295 (1852). Lectotype (Taylor, loc. cit.): Regel, loc. cit., t. 29 (1852).

*Cereus acifer* Otto ex Salm-Dyck, Cact. Hort. Dyck. 1849, 189 (1850).

*Echinocereus acifer* (Otto ex Salm-Dyck) Hort. F.A. Haage, Cacteen-Verzeichniss, 19 (1859).

'*E. marksianus*' F. Schwarz ex Backeb., Die Cact. 4: Abb. 1956 (1960); Kakteenlexikon, 124 (1966) nom. inval. (Arts 9.5 & 37.1).

DESCRIPTION. Stems stoutly cylindric, to 5-8cm diam.; ribs 10-15, >5mm high. Central spines (1-)3-5, to 25-100mm; radial spines 10-13, to 10-25mm. Flowers 8-14×7cm, brilliant light red; tube usually straight (but limb sometimes oblique), abruptly tapered towards base, only c. 7-8mm diam. in region of nectar-chamber, c. 15-20mm at apex, areoles not conspicuously woolly; nectar-chamber narrow, c. 2-2.5mm diam., nearly filled by style; perianth-segments acute, acuminate or rounded, expanding fully.

ILLUSTRATION. Taylor, The Genus Echinocereus, pl. 4 (1985).

DISTRIBUTION. Zacatecas, SW San Luis Potosi, NE Jalisco and Guanajuato, on the high plateau of N central Mexico; bare rocky places and open pine/oak woodland, 2100-2500m.

MATERIAL EXAMINED. ZACATECAS. Between Jerez and Fresnillo, 35km from the former, rocks c. 1km W of road, 2300m, 7 Oct 1987, *N.P. Taylor & S.G. Knees* 473A&B (K—areoles, photos). SAN LUIS POTOSI. Region of San Luis Potosi, 22°N, 1878, *Parry & Palmer* 278 (K). GUANAJUATO. 20km NE of city of Guanajuato, pine/oak forest, *J. Meyran* 3283 (MEXU). Without locality: cult. G.E. Cheetham, Kent, U.K., Jun 1983 (K—fl. & areole in spirit, drawings, photos).

Varieties *huitcholensis* and *densus* are linked by populations intermediate in character, found along the famous Mazatlan–Durango highway (from El Salto westwards), between 1850 and 2500m altitude. Some of the forms along this route are included in var. *huitcholensis*, but others seem closer to var. *densus*. Plants in cultivation from *Lau* 1082, loc. cit., are variable, representing more or less intermediate forms as well as those closer to var. *huitcholensis*. Another intermediate population can be seen in crevices and ledges of the spectacular rocks at Mexiquillo, south of La Ciudad, Durango, 2500m (*N.P. Taylor* 228, *N.P. Taylor & S.G. Knees* 405, K—photos, seeds). From further east, near El Salto, I have a plant raised from seed collected by Steven Brack, received as '*E. scheeri*'. Although it is yet to flower, its vegetative characteristics agree with var. *huitcholensis*.

Both varieties are geographically close to the smaller flowered var. *polyacanthus*, which occurs on rocky outcrops in pine/oak/arbutus forest beside Highway 40 east of El Salto; see Hunt in Curtis's Bot. Mag. 183(3): 103-105, tab. 818 (1981). In connexion with this variety, I have previously discussed (1985) the poorly known entity, *E. leeanus* (Hooker) Lemaire (*Cereus leeanus* Hooker in ibid. 75: tab. 4417. 1849), whose original description calls for an exceptionally large stem, 10cm in diameter, with 14 ribs. Plants in agreement with this occur west of Canatlan, Durango, on lichen-covered lava at only 1950m altitude (*N.P. Taylor* 235, K—photos, seeds), and clearly belong to var. *polyacanthus*. Seedlings are being reared in cultivation.

*E. polyacanthus* var. *polyacanthus* (syn. *E. leeanus*) in habitat, *Taylor* 235. *(photo: Taylor)*

Top row: Left, *E. maritimus*, S of El Rosario, BCN; Right, *E. cinerascens* var. *septentrionalis*, *Taylor* 179. Second row: Left, *E. cinerascens* var. *tulensis* near Tula, *Taylor* 184; Right, *E. stramineus* var. *occidentalis* at type locality, *Taylor* 240B. Third row: Left, *E. viereckii* var. *morricalii*, *Taylor* 192 (*photos: Taylor*); Right, *E. parkeri* var. *gonzalezii*, *Lau* 1375 (*photo: RBG Kew* ©). Bottom row: Left, *E. scheeri* var. *koehresianus*, small-flowered form from c. 5km E of El Espinal, c. 600m, *Kimnach* 1920 (*photo: Kimnach*); Right, *E. scheeri* var. *scheeri*, ex Sierra Obscura, Chihuahua (*Lau*), form with flowers to 10×9.5cm (*photo: RBG Kew* ©).

**Bradleya 6/1988**
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# On the taxonomy of Brazilian Cereeae (Cactaceae)

*Pierre J. Braun*
*Hauptstrasse 83, D-5020 Frechen 1*
*West Germany*

*Summary.* A brief commentary on the genera of tribe Cereeae is presented, with diagnoses of some genera, notes on the circumscription of subgenera and comments on several infrageneric and infraspecific taxa. A key to genera and a phylogenetic dendrogram are presented. Various new names in *Cereus, Pilosocereus, Arrojadoa, Coleocephalocereus* and *Melocactus* are published. Species relationships in *Melocactus* are briefly discussed.

*Zusammenfassung. Zur Taxonomie brasilianischer Cereeae (Cactaceae).* Kurzen Kommentaren und Diagnosen zu einigen Gattungen der Tribus Cereeae folgen Umschreibungen der Untergattungen, Kommentare zu einigen infragenerischen und infraspezifischen Taxa, Neu- und Umkombinationen in *Cereus, Pilosocereus, Arrojadoa, Coleocephalocereus* und *Melocactus.* Einige Verwandtschaftsverhältnisse innerhalb der Gattung *Melocactus* werden kurz skizziert. Ein Schlüssel der Tribus und ein phylogenetisches Dendrogramm werden vorgestellt.

*Resumo. Sôbre a Taxionomia da Tribo Cereeae Brasileiras (Cactaceae).* Breves comentários e diagnoses sôbre alguns gêneros da tribo Cereeae são seguidos de circunscrições dos subgêneros, de discussões sôbre alguns taxas infragenéricos e infraespécificos, novas combinações em *Cereus, Pilosocereus, Arrojadoa, Coleocephalocereus* e *Melocactus* são apresentadas. Algumas relações de parentesco em *Melocactus* são brevemente descritas. São apresentados uma chave da tribo e um dendrograma filogenético.

## Introduction

In the wake of the I.O.S. Working Party's report and recommendations on the generic classification of Cactaceae (Hunt & Taylor, eds 1986; Hunt & Taylor 1987) and with reference to forthcoming reviews of certain Brazilian cactus genera by the present author, it is necessary to revise the taxonomic status and nomenclature of several taxa.

Virtually all of the genera mentioned in this paper have been studied thoroughly in their natural habitats and, during a period of 15 years, also in cultivation. Between 1979 and 1987 the author travelled extensively in Brazil, visiting most of its states in order to observe and thoroughly document nearly all described and many till now undescribed species of Cactaceae. Plants, flowers and fruits were studied in detail, seeds and pollen by SEM (Scanning Electron Microscopy) and light microscopy. In addition to these investigations, the micromorphological surveys of seedcoats by Barthlott & Voit (1979) and Diers & Buining (1974), and of pollen by Leuenberger (1976), have been taken into consideration. Field collected specimens have mostly been deposited at KOELN and ZSS; living material studied was also donated to the botanical garden of the University of Bonn, West Germany, as part of the permanent living collection.

## Phylogenetic relationships of Brazilian Cereeae

The phylogeny of Brazilian genera of Cereeae is summarized in Figure 1, below.

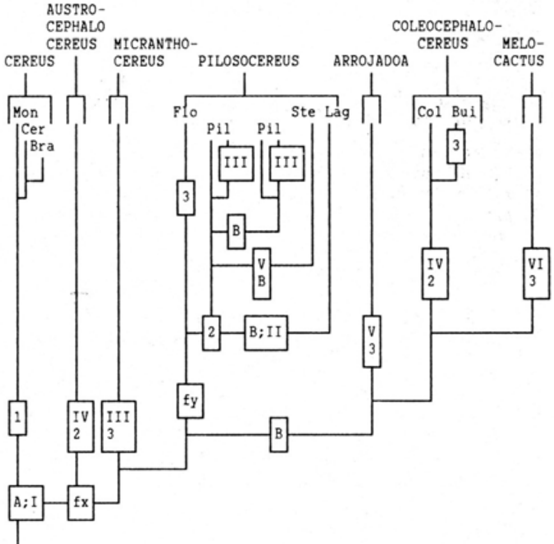

Fig. 1. Supposed relationships of Brazilian Cereeae.

Key. Infrageneric taxa: Mon, *Monvillea*; Cer, *Cereus*; Bra, *Brasilicereus*; Flo, *Floribunda*; Pil, *Pilosocereus*; Ste, *Stephanocereus* (NB. has priority over *Pilosocereus* unless or until the latter is conserved); Lag, *Lagenopsis*; Col, *Coleocephalocereus*; Bui, *Buiningia*. Seeds: A = seedcoat smooth, B = seedcoat tuberculate with cuticular folds. Floral syndrome: 1, sphingogamous; 2, chiropterogamous; 3, ornithogamous. Fruit: fx, globose to clavate, smooth, pink to red, indehiscent; fy, depressed-globose, wrinkled and deeply folded/grooved at apex,

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greenish, blue or reddish-pink when ripe, laterally dehiscent, walls thick, mucilaginous, fleshy. Habit: I, lacking both pseudo- and true cephalium, and without tufts of wool at flower-bearing areoles; II, bipartition of vegetative and generative stages; III, pseudocephalium present; IV, lateral cephalium present; V, terminal ring cephalium present (flowers exserted), plants columnar with branched jointed stems; VI, true terminal cephalium present (flowers sunken), plants globular to short columnar, stems single, not normally branching.

## Key to genera of tribe Cereeae

*Note*. According to Rauh (1984), a true cephalium ('echtes Cephalium') is produced after completion of the vegetative phase of development. The photosynthetic part of the stem ceases to grow except in width. This can be regarded as a feature of high organizational specialization. A restimulation of the vegetative phase is impossible, except after injury or as a consequence of viral infection. This true cephalium occurs in *Melocactus* and *Discocactus* only; all other cephalioid zones are termed pseudocephalia.

In the key presented below, the author uses the word 'cephalium' in a somewhat modified sense. It is employed for (a) the true terminal cephalium, (b) the ring cephalium which terminates each successive vegetative joint ('durchwachsenes Pseudocephalium' of Rauh 1984) and (c) the continuous lateral cephalium with the podaria of the stem's ribs reduced, which is more or less sunken in the stem.

1. Cephalium, pseudocephalium or flowering areoles with woolly tufts present . . . . . . . . . . 2
   Cephalium lacking, the flowering areoles without woolly tufts . . . . . . . . . . 8
2. Plants developing a cephalium . . . . . . . . . . 3
   Plants developing a pseudocephalium . . . . . . . . . . 9
3. Cephalium terminal . . . . . . . . . . 4
   Cephalium lateral, continuous . . . . . . . . . . 6
4. Globular to shortly cylindric plants . . . . . . . . **Melocactus**
   Columnar plants . . . . . . . . . . 5
5. Flowers small, ornithogamous, coloured; fruits small, globular, mostly reddish to pink . . . . . . . . . . **Arrojadoa**
   Flowers large, chiropterogamous, pericarpel and tube green, perianth white; fruits very large, bluish-green; stems covered in white spines . . . . . . . . **Stephanocereus**
6. Seedcoat tuberculate, with cuticular folds . . . . . . . . . . 7
   Seedcoat smooth . . . . . . . . . . **Austrocephalocereus**
7. Flower with completely coloured perianth, ornithogamous, small, ± tubular **Coleocephalocereus** subg. **Buiningia**
   Flowers with white inner perianth, chiropterogamous . . . . . . . . . **Coleocephalocereus** subg. **Coleocephalocereus**
8. Flowers ornithogamous, small (to 4cm), coloured, tubular, or strongly chiropterogamous, campanulate . . 9
   Flowers sphingoid, with large white perianth and often elongate tube; seedcoat smooth . . . . . . . . . . 12
9. Flowers ornithogamous, small, tubular, coloured . . . . . 10
   Flowers chiropterogamous . . . . . . . . . . 11
10. Plants developing a pseudocephalium. . **Micranthocereus**
    Plants lacking a pseudocephalium . . . . . . . . . . **Pilosocereus** subg. **Floribunda**
11. Stem bottle-like, lacking a pseudocephalium . . . . . . . . . . **Pilosocereus** subg. **Lagenopsis**
    Stem cereoid, branched **Pilosocereus** subg. **Pilosocereus**
12. Flowers to 25cm, tube elongate, almost naked . . . . . . . . . . **Cereus** subg. **Cereus**
    Flowers to 6.5cm, tube short, scaly . . . . . . . . . . **Cereus** subg. **Brasilicereus**

CEREUS Miller 1754
Lectotype: *C. hexagonus* (L.) Miller 1768 (Hunt & Taylor 1986). About 25 species in Brazil, including those referred here from *Monvillea* and *Brasilicereus*.

**Cereus** subg. **Cereus**
The following new combinations are required for taxa described by Ritter (1979) under the synonymous generic name *Piptanthocereus* Riccob. 1909.

**Cereus lanosus** (Ritter) P. J. Braun **comb. nov.** Basionym: *Piptanthocereus lanosus* Ritter, Kakteen in Südamerika 1: 259-260 (1979).

**Cereus sericifer** (Ritter) P. J. Braun **comb. nov.** Basionym: *Piptanthocereus sericifer* Ritter, tom. cit. 232 (1979).

**Cereus goiasensis** (Ritter) P. J. Braun **comb. nov.** Basionym: *Piptanthocereus goiasensis* Ritter, tom. cit. 234 (1979).

**Cereus calcirupicola** var. **cabralensis** (Ritter) P. J. Braun **comb. et stat. nov.** Basionym: *Piptanthocereus cabralensis* Ritter, tom. cit. 235-236 (1979).

**Cereus calcirupicola** var. **cipoensis** (Ritter) P. J. Braun **comb. nov.** Basionym: *Piptanthocereus cipoensis* Ritter, tom. cit. 236 (1979).

**Cereus neonesioticus** (Ritter) P. J. Braun **comb. nov.** Basionym: *Piptanthocereus neonesioticus* Ritter, tom. cit. 237 (1979).

**Cereus neonesioticus** var. **interior** (Ritter) P. J. Braun **comb. nov.** Basionym: *Piptanthocereus neonesioticus* var. *interior* Ritter, tom. cit. 237-238 (1979).

**Cereus alacriportanus** Pfeiffer var. **bageanus** (Ritter) P. J. Braun **stat. et comb. nov.** Basionym: *Piptanthocereus bageanus* Ritter, tom. cit. 238 (1979).

**The status of Monvillea**
The Brazilian species of *Monvillea* Britton & Rose 1920 are difficult to separate from *Cereus*. They intergrade in floral features (e.g. *C. crassisepalus* Buining & Brederoo and *Praecereus* (=*Monvillea*) spp.) and in view of *C. insularis* Hemsl. even the slender climbing habit of *Monvillea* cannot be regarded as a reliable difference. Therefore, *Monvillea* should be sunk into *Cereus*. Further investigations, including the type* and other extra-Brazilian species will probably show that *Monvillea* should be regarded as a subgenus of *Cereus*. The following new combinations are required for the Brazilian taxa involved:

**Cereus campinensis** (Backeberg & Voll) P. J. Braun **comb. nov.** Basionym: *Pilocereus campinensis* Backeberg & Voll in Arq. Jard. Bot. Rio de Janeiro 9: 162 (1949). Syn. *Monvillea campinensis* (Backeberg & Voll) Backeberg, Die Cactaceae 4: 2313 (1960).

**Cereus campinensis** var. **piedadensis** (Ritter) P. J. Braun **comb. et. stat. nov.** Basionym: *Monvillea piedadensis* Ritter, Kakteen in Südamerika 1: 114-115 (1979).

**Cereus alticostatus** (Ritter) P. J. Braun **comb. nov.** Basionym: *Monvillea alticostata* Ritter, tom. cit. 251-252 (1979).

**Cereus adelmarii** (Rizzini & Mattos) P. J. Braun **comb. nov.** Basionym: *Monvillea adelmari* Rizzini & Mattos in Rev. Brasil. Biol. 45(3): 301 (1985).

**Cereus saddianus** (Rizzini & Mattos) P. J. Braun **comb. nov.** Basionym: *Monvillea saddiana* Rizzini & Mattos in Rev. Brasil. Biol. 45(3): 304 (1985).

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*See note by D. R. Hunt in Bradleya 6: 100 (1988).

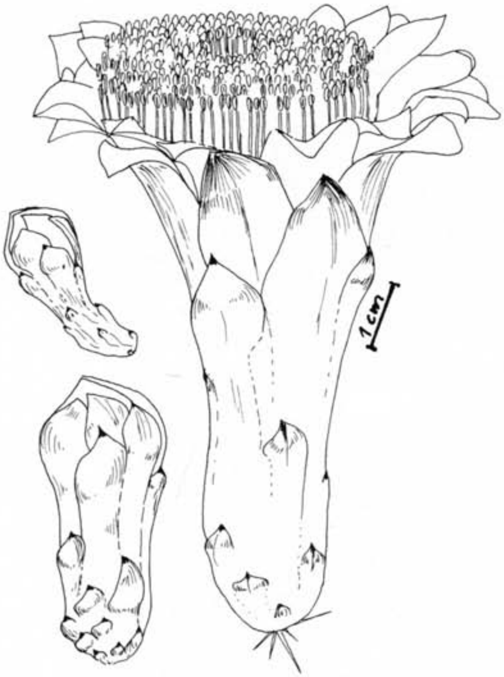

Fig. 2. Flowers of *Cereus campinensis* var. *piedadensis*.

**Cereus** subg. **Brasilicereus**
It has been proposed (Hunt & Taylor, eds 1986) that *Brasilicereus* Backeb. 1938 should be sunk into *Monvillea*, but its classification as a subgenus of *Cereus* seems to be the more practical solution. Subgenus *Brasilicereus* differs from subg. *Cereus* by the very short, reduced, scaly flowers.

**Cereus** subg. **Brasilicereus** (Backeb.) P. J. Braun **stat. nov.** Basionym: *Brasilicereus* Backeb., Blätt. Kakt.-Forsch. 1938, 6: 20 (1938). Type: *Cereus phaeacanthus* Gürke in Monatsschr. Kakt.-Kunde 18: 57 (1908).

Besides the type, subg. *Brasilicereus* includes the following:

**Cereus phaeacanthus** var. **breviflorus** (Ritter) P. J. Braun **comb. et stat. nov.** Basionym: *Brasilicereus breviflorus* Ritter, Kakteen in Südamerika 1: 228 (1979).

**Cereus markgrafii** (Backeb. & Voll) P. J. Braun **comb. nov.** Basionym: *Brasilicereus markgrafii* Backeb. & Voll in Arq. Jard. Bot. Rio de Janeiro 9: 155 (1949).

PILOSOCEREUS Byles & Rowley 1957
Type: *Pilocereus leucocephalus* Poselger.

DESCRIPTION. *Plants* columnar, erect or semi-erect, single or branched, very variable in height and shape, epidermis green, grey or blue; roots branched; stems with 4-26 ribs; areoles round or oval, sometimes with long hairs, spination acicular, very variable in quantity, length, colour and thickness; mostly with a pseudocephalium consisting of continuous lateral or irregularly positioned tufts of wool and/or long bristles out of generative areoles. *Flowers* campanulate or funnelform (subgen. *Floribunda* tubular), 1.5-9 cm long and up to 6 cm wide (subgen. *Floribunda* with a scarcely opening tubular perianth), very often ribbed, nocturnal, chiropterogamous (subgen. *Floribunda* ornithogamous), with a bad smell; pericarpel ± globular, naked or with some spines or hairs; receptacle in the lower part tubular or funnel-shaped, in the upper part funnel-shaped or campanulate, whitish-green, bluish-green, green, olive, brownish, reddish or red, naked, strong, fleshy, sometimes with fleshy scales; receptacle wall mostly mucilaginous; transitive segments fleshy, outer perianth-segments coloured or white, often fleshy, inner perianth-segments thin, white; between nectar-chamber and basal stamens very often a 'channelled zone'; nectar-chamber open, or closed by diaphragm formed from primary stamens. *Fruit* (berry) ± globular to depressed-globose, 0.6-6.0 cm in diameter, green, bluish-green, violet or red, mostly naked, sometimes with few hairs or spines, wrinkled, folded and grooved (especially at the top), wall ± fleshy, flower remains persistent, 'cupule' more or less deepened in the overgrowing fleshy epicarp of the fruit; when ripe dehiscing lengthwise; pulp white, pink or red. Seeds black or brown, 0.8-2.3 mm long, about 1 mm wide, obliquely ovoid, hat-shaped or pear-shaped, testa smooth or tubercled, sometimes with cuticular folds, hilum-micropylar-region basal to subbasal, ± oval.

DISTRIBUTION. Tropical Central America, Caribbean Islands, Venezuela, Colombia, Ecuador, Peru, NE Paraguay, Brazil (states of Rio de Janeiro, Espirito Santo, Minas Gerais, Bahia, Sergipe, Alagoas, Rio Grande do Norte, Paraiba, Ceara, Piaui, Pernambuco, Maranhao, Goias, Mato Grosso do Sul, Mato Grosso, Rondonia, Para, Roraima).

**Pilosocereus** subg. **Pilosocereus**
The author agrees with the IOS Working Party report (Hunt & Taylor, eds 1986) that *Pseudopilocereus* F. Buxbaum 1968 is a synonym of *Pilosocereus*. The diagnostic feature, the 'channelled zone' (kannelierte Zone) according to Buxbaum (1957, 1968a, 1968b, 1975), can be present or absent in the Brazilian species, with all intergrading forms.

Fig. 3. *Pilosocereus parvus*, the dwarf representative of the genus, at the type locality in the Serra Geral de Goias, 1983, *Braun* 317.

The following three *Pseudopilocereus* taxa are transferred to *Pilosocereus*, since these combinations will be needed for a key to all Brazilian pilosocerei (a separate publication is in preparation):

**Pilosocereus diersianus** (Esteves) P. J. Braun **comb. nov.** Basionym: *Pseudopilocereus diersianus* Esteves in Kakt. and. Sukk. 32: 90 (1981).

**Pilosocereus parvus** (Diers & Esteves) P. J. Braun **comb. nov.** Basionym: *Pseudopilocereus parvus* Diers & Esteves in Kakt. and. Sukk. 33: 104 (1982).

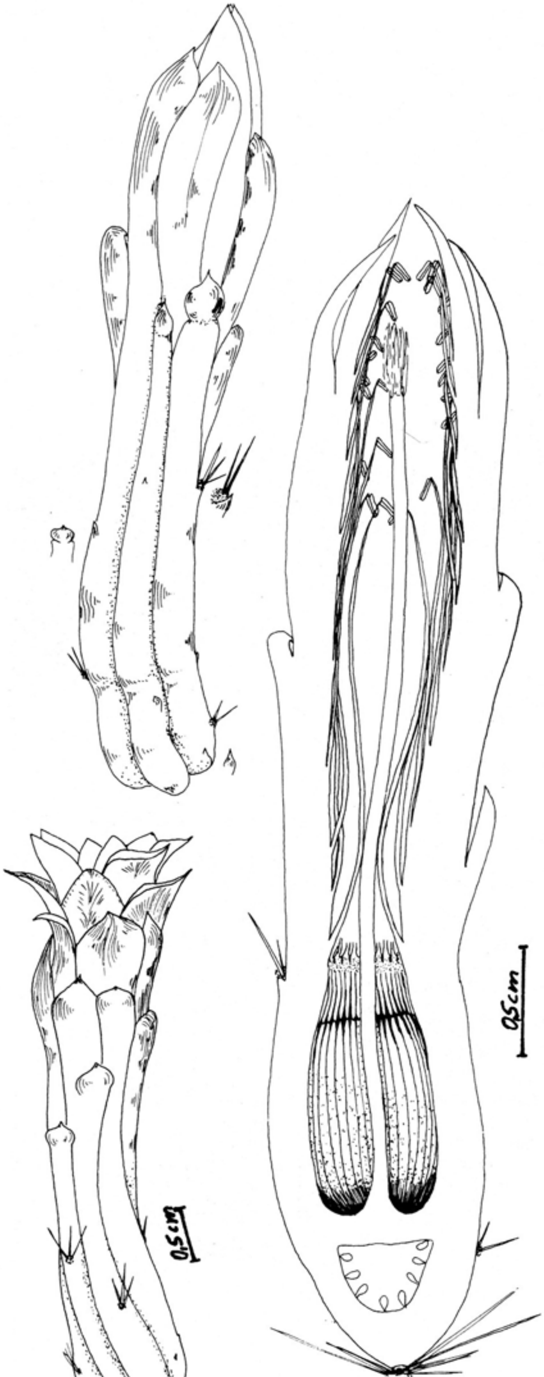

Fig. 4. Flowers of *Pilosocereus pleurocarpus*.

**Pilosocereus vilaboensis** (Diers & Esteves) P. J. Braun **comb. nov.** Basionym: *Pseudopilocereus vilaboensis* Diers & Esteves in Kakt. and. Sukk. 34: 111 (1983).

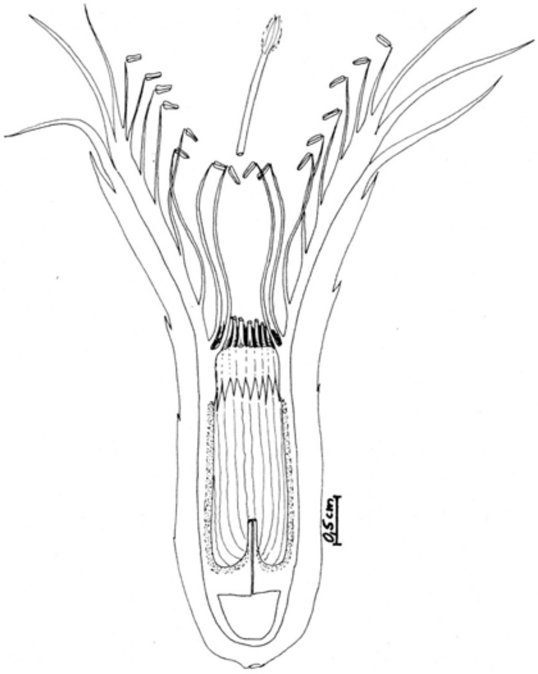

Fig. 5. Flower of *Pilosocereus minensis*.

All known and some new habitats of *Cipocereus* Ritter have been visited by E. Esteves Pereira and the author. With a knowledge of the plants, flowers, fruits and seeds it becomes most difficult to maintain the genus. The distinguishing characteristics mentioned by Ritter (1979) are present, but certainly they are not significant enough to segregate *Cipocereus* from *Pilosocereus*. From unpublished studies of a perhaps undescribed species it has become evident that the .transfer of *Cipocereus* species to *Pilosocereus* is now necessary.

In addition, it is not practical to accept *Cipocereus* as an infrageneric taxon, since it cannot be keyed out satisfactorily. The ribbed pericarp and receptacle, sometimes with reduced areoles, are also present in *Pilosocereus*, and the general outer appearance and the inner structure of the flower have no distinguishing features. The very tuberculate seedcoat with cuticular folds can also be found in *Pilosocereus* (e.g. *P. aureispinus* (Buin. & Bred.) Ritter (cf. Buining & Brederoo 1974), *P. juaruensis* (Buin. & Bred.) P. J. Braun (cf. Braun & Arzberger 1986) and others). A characteristic of *Cipocereus* is the absence of both pseudocephalium and woolly tufts at the flowering areoles. This is also true of the mature stems of *P. gaturianensis* Ritter (1979) and *P. multicostatus* Ritter (1979).

The species involved are:

**Pilosocereus pleurocarpus** (Ritter) P. J. Braun **comb. nov.** Basionym: *Cipocereus pleurocarpus* Ritter, Kakteen in Südamerika 1: 54-55 (1979).

**Pilosocereus minensis** (Werdermann) Byles & Rowley (*Cereus minensis* Werderm.; *Cipocereus minensis* (Werdermann) Ritter).

**Pilosocereus** subgenus **Lagenopsis**
Knowing *Cereus luetzelburgii* Vaupel from several Brazilian habitats, and in cultivation, I am in no doubt that it belongs to *Pilosocereus*. Its flowers, depressed-globose greenish fruits and seeds are typical for *Pilosocereus*, but not *Coleocephalocereus*. The most significant characteristic of the subgenus is a transition from a globular juvenile stage into a columnar fertile stage:

the mature plant then has a bottle-like appearance. This habit (without the production of a cephalium) is unique in the Cactaceae and justifies the rank of subgenus for this taxon.

It differs from subgenus *Pilosocereus* by the bottle-shaped stems and the strong bipartition of vegetative and generative growth. Distribution: Brazil, central to south-central parts of Bahia.

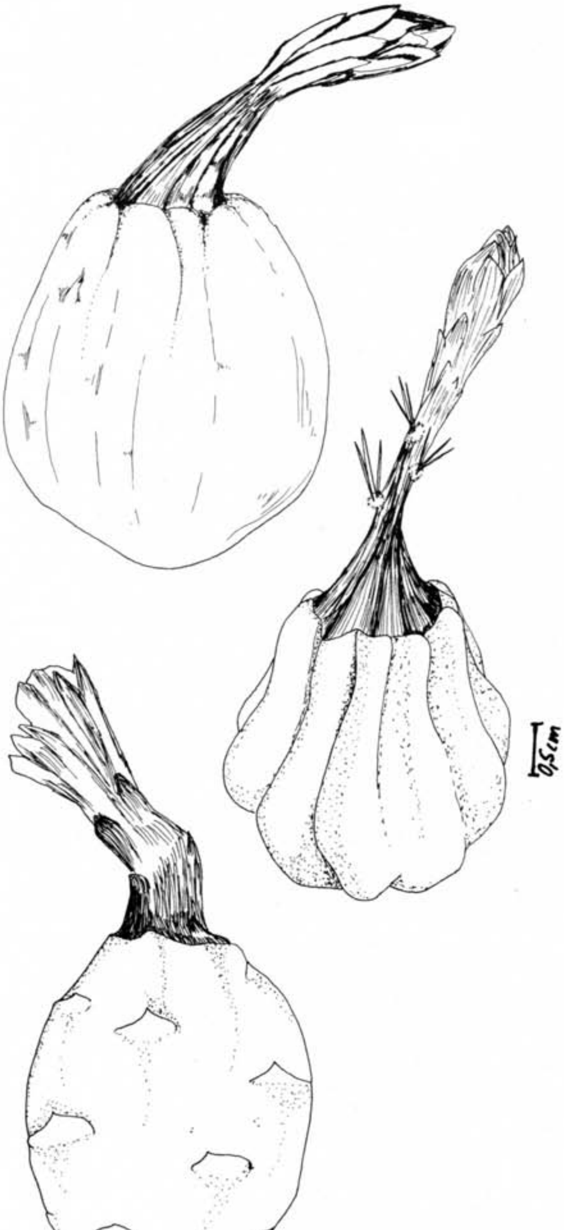

Fig. 6. Fruits of *Pilosocereus minensis* (above), *P. pleurocarpus* (middle), *Cereus campinensis* var. *piedadensis* (below).

Fig. 7. *Pilosocereus* (subg. *Lagenopsis*) *luetzelburgii*, mature and young plant (*Austrocephalocereus purpureus* behind), Seabra, 1986, *Braun* 623.

**Pilosocereus** subg. **Lagenopsis** (F. Buxbaum) P. J. Braun **comb. nov.** Basionym: *Coleocephalocereus* subg. *Lagenopsis* F. Buxbaum in Krainz, Die Kakteen, Lieferung 48-49 (1972). Type: *Pilosocereus luetzelburgii* (Vaupel) Byles & Rowley (*Cereus luetzelburgii* Vaupel: *Coleocephalocereus luetzelburgii* (Vaupel) F. Buxbaum).

**Pilosocereus** subg. **Floribunda**

Another recently described genus is *Floribunda* Ritter 1979, which resembles *Micranthocereus* at a first, superficial examination. After more critical, detailed observations the close relationship to *Pilosocereus* becomes obvious. The habit of *Floribunda* and *Cipocereus* is identical, the fruit is typical for *Pilosocereus* (another species with very small fruits is *P. pusillibaccatus* Braun & Esteves 1986) and the flower with the ribbed, coloured pericarpel and receptacle is reminiscent of the flower of *P. pleurocarpus*. Ritter mentioned differences between the seeds of *Cipocereus* and *Floribunda*, but the presence (*Cipocereus* and some *Pilosocereus* spp.) or absence (*Floribunda* and some *Pilosocereus* spp.) of tubercular testa cells is quite common in several genera. As we now know, there exists a great variation in seed microstructure in *Pilosocereus*. There are completely smooth seedcoats (cf. SEM-illustrations of *P. rosae* P. J. Braun (1984b), *P. supthutianus* P. J. Braun (1985a), *P. albisummus* Braun & Esteves (1987a), *P. schoebelii* P. J. Braun (1987f) and *P. cristalinensis* Braun & Esteves (1987b)), there are mamilla-like testas with cuticular folds (e.g. *P. aureispinus* (Buin. & Bred.) Ritter, *P. pusillibaccatus* Braun & Esteves and others) and there are those with all intermediate structures.

On the other hand, the very small ornithogamous (hummingbird), little expanded flowers of *Floribunda* (also in *P. pleurocarpus*, cf. Buining 1974) with a specialized internal structure (deep small, globular nectar-chamber) justify a separate subgenus. *Pilosocereus* subg. *Floribunda* seems to be the link to *Micranthocereus*.

It differs from subgenus *Pilosocereus* and subgenus *Lagenopsis* by the non-hairy stems, without a pseudocephalium, and very small tubular, purple, ornithogamous flowers with a ± tubular scarcely expanding perianth and very small 0.6-1.3 cm fruits. Distribution: Brazil, northern Minas Gerais.

**Pilosocereus** subg. **Floribunda** (Ritter) P. J. Braun **stat. nov.** Basionym: *Floribunda* Ritter, Kakteen in Südamerika 1: 58 (1979). Type and only species:

**Pilosocereus pusilliflorus** (Ritter) P. J. Braun **comb. nov.** Basionym: *Floribunda pusilliflora* Ritter, tom. cit. 58 (1979).

STEPHANOCEREUS A. Berger 1926

Type and only species: *Stephanocereus leucostele* (Gürke) A. Berger (*Cereus leucostele* Gürke).

DESCRIPTION. Differing from *Pilosocereus* by more or less single or hardly branched stems, which are totally covered by dense white hairs and white spines, and which are jointed by bristly fertile zones (terminal cephalium) terminating each successive vegetative section. *Flowers* very large, receptacle green, perianth white. Fruit large, blue.

DISTRIBUTION. Brazil, S to SE Bahia.

This monotypic genus could be combined with *Pilosocereus*, since its flowers and fruits are identical. Some differences in the seedcoat and the terminal ring cephalium (which resembles *Arrojadoa*; jointed stems with woolly and bristly fertile cephalloid zones terminating each successive vegetative section) could justify the retention of *Stephanocereus* at generic rank. While there is no sound theoretical basis for separating *Pilosocereus* and *Stephanocereus*, Berger's name has priority, and it does not make sense to transfer all *Pilosocereus* taxa to *Stephanocereus*.

Fig. 8. *Stephanocereus leucostele* near Brumado, with white, chiropterogamous flowers.

ARROJADOA Britton & Rose 1920

Type: *Cereus rhodanthus* Gürke.

DESCRIPTION. *Plants* slender, columnar; stems 0.5 to about 5 cm thick, up to 2 m long, mostly branched from the base, erect, semierect or creeping, epidermis green; roots branched, tuberous or napiform; apical cephalia terminating each successive section of vegetative growth; cephalium with white wool and reddish bristles. *Flowers* ornithogamous, seminocturnal (opening in the evening and closing late next morning, hummingbird-pollination), fleshy, naked, up to 4.5 cm long; receptacle tubular, purple to pinkish red; perianth scarcely expanding, mostly ± tubular, outer perianth-segments fleshy, purple to pinkish red, inner perianth-segments thinner, pinkish, rose, violet, white or yellow; nectar-chamber globular to pear-shaped, sometimes closed by the bases of the primary stamens; filaments of primary stamens very long and strong, those of secondary stamens shorter, the uppermost filaments only 1-3 mm long. *Fruit* (berry) globose to pear-shaped, to 20 mm in diameter, naked, epicarp smooth, purple, pink, rose or red, if pear-shaped sometimes bi-coloured (lower part greenish, upper part rose to reddish), pulp ± white. *Seeds* to 1.5 mm long, obliquely ovoid or pear-shaped, sometimes hat-shaped; testa ± black, tuberculate, with cuticular folds.

DISTRIBUTION. Brazil, central and northern part of Minas Gerais, Bahia, Pernambuco, Piaui.

A preliminary species list has already been published (Braun 1978) and a review of the genus is in preparation.

It seems practical to transfer the following taxa to *A. rhodantha*. Ritter (1979) proposed to do the same with *A. aureispina*, but this does not seem to be desirable, because *A. aureispina* is easy to distinguish and is divisible into three varieties itself (Braun & Esteves 1988b).

**Arrojadoa rhodantha** var. **theunisseniana** (Buining & Brederoo) P. J. Braun **stat. nov.** Basionym: *Arrojadoa theunisseniana* Buining & Brederoo in Krainz, Die Kakteen, Lieferung 52 (1973).

**Arrojadoa rhodantha** ssp. **canudosensis** (Buining & Brederoo) P. J. Braun **stat. nov.** Basionym: *Arrojadoa canudosensis* Buining & Brederoo in Cact. Succ. J. (US) 44: 111 (1972).

*List of recognized species*

The genus *Arrojadoa* can be divided into two major groups:

1. Plants without tuberous or rhizomatous rootstocks, with purple flowers, a globular nectar-chamber and a red, globular fruit.

1. A. rhodantha (Gürke) Britton & Rose
    - ssp. rhodantha
        - var. rhodantha
        - var. occibahiensis P. J. Braun .
        - var. theunisseniana (Buining & Brederoo) P. J. Braun
    - ssp. canudosensis (Buin. & Bred.) P. J. Braun
    - ssp. reflexa P. J. Braun
2. A. horstiana Braun & Heimen
3. A. aureispina Buining & Brederoo
    - var. aureispina
    - var. anguinea Braun & Esteves
    - var. guanambensis Braun & Heimen
4. A. penicillata (Gürke) Britton & Rose
    - var. penicillata
    - var. decumbens Backeberg & Voll
    - var. spinosior Buining & Brederoo

2. Plants very often with tuberous, napiform or rhizomatous rootstocks, with short, mostly white spined stems (sometimes covered with white hairs), with a bicoloured flower (inner

perianth yellow, white or violet), a more or less pear-shaped nectar-chamber and with a more or less oval to pear-shaped, very often bicoloured (sometimes greenish) fruit.

5. A. eriocaulis Buining & Brederoo
    var. eriocaulis
    var. albicoronata van Heek et al.
6. A. dinae Buining & Brederoo
    var. nov. (*Braun* 415)
7. A. multiflora Ritter
8. A. sp. nov. (*Braun* 830)
9. A. albiflora Buining & Brederoo

### MICRANTHOCEREUS Backeberg 1938

Type: *Cephalocereus polyanthus* Werdermann.

Description. *Plants* columnar, up to 6 cm thick, erect, to 1.5 m high, branched from the base, epidermis green or blue, ribs many, rounded, spination dense, with long curled bristle-like spines at the base of the stems; roots branched; pseudocephalium lateral, oriented to one side, sometimes interrupted, areoles of the pseudocephalium with tufts of white wool and long red, yellowish or grey/brownish bristles. *Flowers* ornithogamous, to 4 cm long, mostly appearing in large numbers near the stem apex, in serried rows and blooming at the same time; pericarpel very small, ± globular; receptacle naked, fleshy, tubular, purple, pinkish, rose, orange-red, violet-red or yellow, perianth-segments short, the outer ± fleshy, mostly erect and not expanded (except *M. auri-azureus*); nectar-chamber small, ± globular, sometimes closed by the bases of the primary stamens, very often with staminodes between the nectar-chamber and the basal filaments; all stamens very short and thin. *Fruit* (berry) very small, to 1.8 cm long, globose, naked, smooth, pink, purple or rose-greenish; pulp whitish. *Seeds* ± 1 mm long, obliquely ovoid, testa black, smooth, shining, without cuticular folds.

Distribution. Brazil, northern, central and southern Bahia, northern Minas Gerais.

*Arrojadoa* is characterized by a terminal ring-cephalium (like *Stephanocereus*), which is overgrown periodically by the vegetative stem, whereas *Micranthocereus* bears a continuous lateral pseudocephalium. There is no periodical and morphological change between vegetative and generative growth. The morphology of the small, tubular, coloured hummingbird-flowers is similar to those of *Pilosocereus* subgen. *Floribunda*, and fruits of some *Micranthocereus* have features of the sculpturate, fleshy *Pilosocereus* fruit; the seedcoat is also unspecialized. Consequently, *P.* subgen. *Floribunda* seems to be the closest relative of *Micranthocereus*, and latter could represent the link between *Pilosocereus* and *Austrocephalocereus*.

Contrary to this, *Arrojadoa* with more specialised seeds and a terminal cephalium, with a strong bipartition of vegetative and generative stages, seems to be derived directly from a *Pilosocereus (Stephanocereus)*—*Coleocephalocereus* line.

Some species of *Micranthocereus* and *Arrojadoa* have very similar flowers, but this should be interpreted as parallel adaptation towards hummingbird pollination. The suggestions of Hunt & Taylor (1986, 1987)*, that *Micranthocereus* should be sunk into *Arrojadoa*, is not followed here. Both genera are easy to circumscribe and seem to have a different phyletic origin.

*List of recognized species*

1. M. auri-azureus Buining & Brederoo
2. M. densiflorus Buining & Brederoo (coloured illustration in Braun 1987c)
3. M. flaviflorus Buining & Brederoo
4. M. polyanthus (Werdermann) Backeberg (*Cephalocereus polyanthus* Werdermann; *Arrojadoa polyantha* (Werderm.) D. Hunt)
5. M. streckeri van Heek & van Criekinge (may belong to *M. ruficeps* Ritter; see Braun 1987d)
6. M. violaciflorus Buining (coloured illustration in Braun 1987e)

*Synonyms and names of uncertain status*

*M. aureispinus* Ritter seems to be synonym of *Austrocephalocereus albicephalus* Buining & Brederoo.

*M. haematocarpus* Ritter = *Austrocephalocereus purpureus* (Gürke) Backeberg.

*M. monteazulensis* Ritter = *Austrocephalocereus albicephalus* Buining & Brederoo.

*M. ruficeps* Ritter. Recollection of this species is necessary; if it is identical with *M. streckeri*, the name *M. ruficeps* has priority, but according to the short description (without any illustration) the species may also belong to *Austrocephalocereus*.

*M. uilianus* Brederoo & Bercht may be only a subspecies or variety of *M. flaviflorus;* see also P. van Veen (1985).

### AUSTROCEPHALOCEREUS Backeberg 1938

Type: *Cephalocereus purpureus* Gürke.

This Brazilian genus consists of columnar species with continuous, longitudinal cephalia. Looking at the habit of the plants, the cephalium, the long, funnel-shaped, chiropterogamous flowers with an expanding white perianth and the fruits, it is rather difficult to accept Ritter's general transference of all *Austrocephalocereus* taxa to *Micranthocereus* (Ritter 1979). Nevertheless, the genus, as we understand it today, appears to be artificial (a paper on this subject is in preparation).

*List of recognized species*

Group 1. Plants branching, covered by dense white hairs; flower white; fruit large, fleshy, whitish and wrinkled.

1. A. dybowskii (Goss.) Backeberg

Group 2. Plants branching; flowers large, chiropterogamous, reddish; fruits smaller, epicarp smooth, purple, when ripe a large turgescent berry, not opening, falling out of the cephalium.

2. A. purpureus (Gürke) Backeberg (probable syn. *Micranthocereus haematocarpus* Ritter)
3. A. albicephalus Buining & Brederoo (cf. Braun 1983b) (probable syn. *Micranthocereus aureispinus* Ritter; *M. monteazulensis* Ritter)

Group 3. Plants simple, very stout, epidermis bluish, very tough, strictly continuous non-interrupted cephalium; fruits very small, not fleshy, very thin, ± paper-like epicarp, drying in the cephalium, opening at the bottom, not falling out of the cephalium; seeds sometimes very elongated. Found on calcareous rocks only.

4. A. dolichospermaticus Buining & Brederoo (cf. Braun 1983a, 1987b)
5. A. estevesii Buining & Brederoo (cf. Braun 1983a)
6. A. sp. *Esteves* 122 (Minas Gerais)
7. A. sp. *Esteves* 149 (N Goias)

### COLEOCEPHALOCEREUS Backeberg 1938

Type: *Cereus fluminensis* Miquel.

Description. *Plants* columnar, erect, semi-erect or creeping on rocks, to 5 m high, simple or branched (mostly from the base), epidermis green; roots branched; ribs (6-35) ± rounded, spines acicular, yellow, brown, grey, black or red; sometimes with up to 45 cm long curled bristle-like spines at the base; cephalium continuous, lateral, normally not interrupted, ± sunken in the stem, directed to one side (depending on the species), with whitish wool and long, ± strong, yellow, orange, red, black, brownish or grey bristles. *Flowers* nocturnal, ± near the apex of the cephalium, naked, tubular, funnelform, sometimes campanulate, chiropterogamous, c. 2-8 cm long; pericarpel very small, globular or conical, naked, creamy or white, sometimes with a few minute scales; tube long tubular or funnelform, sometimes in the upper part campanulate, naked, sometimes with minute scales, creamy, white, yellowish, greenish, green, brownish-olive, reddish-rose or purple; nectar-chamber globular, oval or pear-shaped, open or ± closed by the primary stamens; primary

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*During the IOS Inter-Congress-Meeting, Zürich, 21-22 July 1985, a proposal for the submergence of *Micranthocereus* in *Espostoa* was discussed. The author stressed his opinion that there is a closer affinity to *Arrojadoa*, but without leaving doubts as to its distinctness as a genus. Several comments and observations were presented and the possible existence of a natural hybrid (*Arrojadoa multiflora* Ritter) was mentioned. Unfortunately these aspects may have led to the misunderstanding that *Micranthocereus* could be submerged into *Arrojadoa*.

stamens long, secondary stamens progressively shorter, uppermost stamens only a few mm long; filaments white, anthers yellow; stigma-lobes near the top of the flower. *Fruit* (berry) globose, oval-globose or ovoid, sometimes shortly clavate, to 25 mm long, naked, smooth, purple; when ripe not opening or opening at the base, pulp ± white. *Seeds* about 1 mm long, globular to pear-shaped (*C. goebelianus*), testa black, tuberculate, with cuticular folds.

DISTRIBUTION. Brazil, states of Sao Paulo, Rio de Janeiro, Espirito Santo, Bahia, Minas Gerais.

### **Coleocephalocereus** subgenus **Buiningia**

Ritter's proposal to submerge *Buiningia* F. Buxbaum into *Coleocephalocereus* is followed here, because it is most difficult to accept the smallness and the colouration (adaptation to pollination by hummingbirds) of the flowers as distinguishing criteria. Amongst species of *Coleocephalocereus, C. braunii* Diers & Esteves and *C. pluricostatus* Buining & Brederoo possess similar short flowers (about 3 cm) and the receptacle and the outer perianth-segments of the flower of *C. braunii,* which seems to link the subgenera *Coleocephalocereus* and *Buiningia,* is intense green like some *Buiningia* flowers (cf. Esteves 1988).

The more or less closed, tubular perianth of *Buiningia* is an adaptation to hummingbird pollination. Very similar flowers can be found in *Melocactus* (e.g. the flower of *Melocactus warasii* very much resembles a *Buiningia* flower).

The reduction of the *Buiningia* stem and the precocious development of the cephalium are also not relevant criteria for separation; *C. braunii* (Diers & Esteves 1985) begins to form a cephalium at a height of only 15 cm.

Nevertheless, the bird pollination syndrome is evident and, therefore, *Buiningia* is best classified as a subgenus, as suggested in Braun (1984a).

The author also agrees with the proposal that *Melocactus* derives from this group (Barthlott 1979, Ritter 1968, 1979). *Coleocephalocereus* (incl. *Buiningia*) can be regarded as the closest phylogenetic relative of the highly specialized, ± globular genus *Melocactus. Coleocephalocereus* itself shows many intergrading stages of reduction and specialization: reduction of cereoid columnar growth (*C. braunii, C. decumbens, C. estevesii, Buiningia*); precocious development of the cephalium (*C. braunii, Buiningia*); prolonged globular juvenile growth (*C. goebelianus, C. estevesii, Buiningia*); colouration of flower (greenish: *C. braunii*; green: *Buiningia aurea*; green-brownish: *C. diersianus*; reddish: *C. decumbens*; red: *Buiningia purpurea*); reduction of flower length (*C. braunii, C. pluricostatus, Buiningia*); not or less expanded tubular perianth (*Buiningia,* sometimes *C. braunii*); hummingbird-pollination (*Buiningia*).

The naked, red fruits resemble those of *Melocactus,* but they are bigger and more globular than the clavate *Melocactus* fruits. The seeds do not show significant differences in size and structure. In spite of all the links and many points in common with *Melocactus* the retention of *Coleocephalocereus* at generic rank is justified by its lower level of progression. The high specialization of *Melocactus* with a strong morphological and physiological bipartition of vegetative and fertile structures (terminal cephalium) is not present in *Coleocephalocereus,* which has a less specialized longitudinal, lateral cephalium and continuous vegetative growth.

**Coleocephalocereus** subg. **Buiningia** (F. Buxbaum) P. J. Braun **stat. nov.** Basionym: *Buiningia* F. Buxbaum in Krainz, Die Kakteen, Lieferung 46-47 (1971). Type: *Buiningia brevicylindrica* Buining.

Differing from subg. *Coleocephalocereus* by globular, short cylindrical to short columnar (up to 1 m) stems, and by small, completely coloured (yellow, green or purple) ornithogamous flowers with a ± tubular, scarcely expanded perianth, sometimes with a whitish to transparent diaphragm closing the nectar-chamber. Distribution: Brazil, NE and NE-central Minas Gerais.

*Buiningia brevicylindrica* var. *brevicylindrica* may be regarded as a short columnar to globular, scarcely offsetting subspecies of *Coleocephalocereus aureus,* but there are several floral differences which require further study. *Buiningia brevicylindrica* var. *elongata* is considered as a distinct species because of its giant habit (up to 1 m; cf. Braun 1981a) and distinct internal floral features (absence of a diaphragm in contrast to *B. brevicylindrica,* more tubular receptacle, more and slender perianth-segments); *B. brevicylindrica* var. *longispina* could be reduced to a lower rank or into synonymy. From the author's point of view it is only a local long-spined form.

**Coleocephalocereus elongatus** (Buining) P. J. Braun **stat. nov.** Basionym: *Buiningia brevicylindrica* Buining var. *elongata* Buining in Krainz, Die Kakteen, Lieferung 46-47 (1971); *Coleocephalocereus brevicylindricus* var. *elongatus* (Buining) Ritter.

*List of recognized species*

Subgenus Coleocephalocereus

Group 1. Base of stem lacking long curled spines.

1. C. fluminensis (Miquel) Backeberg
    - var. fluminensis
    - var. braamhaarii P. J. Braun
2. C. decumbens Ritter
3. C. diersianus Braun & Esteves
4. C. paulensis Ritter (perhaps a ssp. of *C. fluminensis*)
5. C. pluricostatus Buining & Brederoo

Group 2. Stem with long curled spines at base.

6. C. braunii Diers & Esteves
7. C. buxbaumianus Buining & Brederoo
8. C. estevesii L. Diers
9. C. flavisetus Ritter

Group 3. Seeds elongate, pear-shaped.

10. C. goebelianus (Vaupel) Buining

Subgenus Buiningia (F. Buxbaum) P. J. Braun

11. C. aureus Ritter
12. C. brevicylindricus (Buining) Ritter (see notes above)
    - var. brevicylindricus
    - var. longispinus (Buining) Ritter
13. C. elongatus (Buining) P. J. Braun
14. C. purpureus (Buining & Brederoo) Ritter

### MELOCACTUS Link & Otto 1827

Type: *M. communis* (Aiton) Link & Otto (see Hunt & Taylor eds. 1986).

DESCRIPTION. *Plants* globular to short-columnar, mostly single, differing in size and habit, epidermis green or blue; roots branched; number and form of ribs very variable; areoles round or oval, at first with white wool, later naked; spines acicular, in colour, length and quantity very variable, mostly a visible bipartition of central and radial spines usually differentiated; vegetative growth of the stem ceases with the development of a true terminal cephalium, flattened, globular or columnar, up to 1 m high, with dense ± white wool and mostly many reddish to brown bristles. *Flowers* very small, up to 40 mm long and, ± hidden in the cephalium, only the perianth arising out of the cephalium, ornithogamous (hummingbird pollination), naked; pericarpel small, ± globular to conical, naked; receptacle ± tubular, with some scales; nectar-chamber globular, open; perianth-segments pink, red, orange, purple. *Fruit* naked, smooth, clavate to cylindrical, 15-40 mm long, white, rose, pink, purple, red or bicoloured (lower part white, upper part reddish, pink, purple), perianth remains persistent, when ripe not opening. *Seed* ± globular or hat-shaped, 0.8-1.5 mm in diameter; testa black, tuberclate or smooth, sometimes with cuticular folds.

DISTRIBUTION. Tropical America: S Mexico, Central America, Caribbean islands, Colombia, Ecuador, Peru, Venezuela, Brazil (N Amazonas, states of Rio de Janeiro, Minas Gerais, Bahia, Espirito Santo, Pernambuco, Piaui, Sergipe, Alagoas, Paraiba, Ceara, Rio Grande do Norte, Maranhao).

An annotated alphabetic list of Brazilian *Melocactus* species is presented below. The author is conscious of the disadvantage that the observations and classifications are only based on a knowledge of the Brazilian taxa, which is based on very thorough and extensive investigations and field research.

Up to now about 60 species of *Melocactus* have been described

PLATE I. Top row: Left, *Cereus markgrafii* at Botomirim, 1987, *Braun* 846; centre, *Micranthocereus auri-azureus* at Grao Mogol, 1987, *Braun* 858; right, *Austrocephalocereus dolichospermaticus*, SW Bahia, 1986, *Braun* 673. Middle row: Left, *Pilosocereus* sp.nov., an intergrading species between *P. minensis* and *P. pleurocarpus*, Serra de Itacambira, 1987, *Braun* 831; right, *Arrojadoa aureispina* at Riacho de Santana, 1979, *Braun* 76 (left), and *A. horstiana* at Mato Verde, 1979, *Braun* 83 (right). Bottom row: Left, *Austrocephalocereus albicephalus* at Mato Verde, 1986, *Braun* 86; centre, *Pilosocereus vilaboensis* at type locality near Goiás, 1987, *Braun* 801; right, *P. vilaboensis*, *Esteves* 19.

from Brazil. Nearly all type localities, whether mentioned in the original descriptions, or from information deposited with the holotypes or received by personal communication with the authors or discoverers, have been visited. Numerous further habitats and intergrading populations were studied and compared. Great numbers of flowers, fruits and seeds were observed and it seems to be necessary for future research to pay more attention to floral structures. Though it is most difficult to isolate these little flowers, mostly hidden deep in the cephalium, a comparison between them is of high taxonomic value.

The surveys on *Melocactus* published by Buining (1974b), Rizzini (1982) and Taylor (1980, 1982) have been taken into consideration. The author accepts currently 7 species groups, comprising a total of 25 species and 1 natural hybrid. Fifteen species are reduced to infraspecific rank. A better knowledge of some uncertain taxa and further investigations including the non-Brazilian species, may have the consequence that further reductions will become necessary.

An asterisk (*) indicates a species which is insufficiently known.

**M. acispinosus* Buining & Brederoo

**M.** × **albicephalus** Buining & Brederoo (pro spec.) in Krainz, Die Kakteen, Lfg. 52 (1973) (*M. pruinosus* × *M. oreas* ssp. *cremnophilus* f. *erythracanthus*); hybrid status first suggested by Braun (1981b) and Taylor (1982).

**M. amethystinus** Buining & Brederoo
*M. lensselinkianus* Buining & Brederoo
*M. griseoloviridis* Buining & Brederoo
*M. glauxianus* Brederoo & Bercht
*M. ammotrophus* Buining et al.
All the taxa mentioned above were observed at their type localities, and it is impossible to distinguish them. Only *M. glauxianus* may be considered as a forma. *M. amethystinus* was the first name of this species, which is very widely distributed in NE Minas Gerais, up to south-central Bahia (Jacaraci and Caitite (*HU* 124), '*M. caititensis*' nom. nud.) and down to central Minas Gerais, near Itamarandiba (*M. griseoloviridis*). North of Diamantina it starts at Itacambira and has an extensive area at Cristalia/Grao Mogol/Virgem da Lapa (*M. ammotrophus*), further to the north at Salinas (*HU* 173, '*M. salinensis*' nom. nud.) and to the east at Itaobim (*M. lensselinkianus* and *M. glauxianus*). These plants represent a very distinct species, which cannot be combined with *M. salvadorensis* (Taylor 1980) or with *M. bahiensis* (Ritter 1979). From the author's point of view this species seems to be a member of the M. OREAS Group. According to Taylor (1982) it belongs to the M. BREDEROOIANUS Group. The two illustrations (showing ribs and areoles) in the description of *Melocactus amethystinus* (in Krainz, Die Kakteen, Lieferung 50-51. 1972) show *M. ferreophilus* (reprinted in the description of *M. ferreophilus* Buining & Brederoo in Krainz, Die Kakteen, Lieferung 52. 1973).

*M. ammotrophus* = *M. amethystinus*

**M. arcuatispinus* Brederoo & Eerkens

*M. axiniphorus* = *M. pruinosus*

*M. azulensis* see *M. oreas* ssp. *ernestii*

**M. azureus** Buining & Brederoo
var. **krainzianus** (Buining & Brederoo) P. J. Braun **stat. nov.** Basionym: *Melocactus krainzianus* Buining & Brederoo in Krainz, Die Kakteen, Lfg. 62 (1975). (Colour pictures in Braun 1986b.)

*M. bahiensis* (Britton & Rose) Luetzelb. If *M. bahiensis* was the plant recollected by Buining and Horst, the taxon should not be combined with *M. oreas*.

**M. brederooianus* Buining

*M. canescens* see *M. zehntneri*

**M. conoideus** Buining & Brederoo
A distinct species, which does not seem to belong to the M. OREAS Group.

*M. concinnus* = *M. pruinosus* var. *concinnus*

*M. cremnophilus* = *M. oreas* spp. *cremnophilus*

*M. curvicornis* = *M. zehntneri* var. *curvicornis*

**M. deinacanthus** Buining et Brederoo
ssp. **longicarpus** (Buining & Brederoo) P. J. Braun **stat. nov.** Basionym: *Melocactus longicarpus* Buining & Brederoo in Cact. Succ. J. (US) 46: 191-194 (1974) (see also Braun 1980).

Plants with long, flexible, not very curved spines and large, bicoloured fruits.
f. **mulequensis** (Buining & Brederoo) P. J. Braun **stat. nov.** Basionym: *Melocactus mulequensis* Buining & Brederoo in Succulenta 55: 46 (1976).

Depressed-globose, local form from southern Bahia.

ssp. **florschuetzianus** (Buining & Brederoo) P. J. Braun **stat. nov.** Basionym: *Melocactus florschuetzianus* Buining & Brederoo in Ashingtonia 2: 27 (1975) (see Braun 1981c).

This plant with strong, reddish and basally bulbous spines belongs, without any doubt, to the M. DEINACANTHUS Group; it is not identical with *M. azulensis* as stated by Taylor (1980, 1982). Further investigations may show that *M. montanus* is a later name for this taxon.

**M. depressus* Hooker
For a very long time this 'species' was of uncertain affinity, but after the discovery of *Melocactus HU* 482 in 1978 by Horst & Uebelmann the name was reinstated by Strecker et al. (1980) (the author participated in this working group). Since then our knowledge of Brazilian melocacti has increased considerably and the author now has doubts, in contradiction to Taylor (1982), whether it would not be better to place this taxon in the *M. violaceus* complex. This 'species' could be the link between the M. VIOLACEUS and M. ZEHNTNERI Groups.

**M. diersianus** Buining & Brederoo
Related to *M. levitestatus*, yet distinct.
f. **rubrispinus** (Ritter) P. J. Braun **stat. nov.** Basionym: *Melocactus rubrispinus* Ritter, Kakteen in Südamerika 1: 135-136 (1979).

Scarcely differing from *M. diersianus*, but seeds smaller. (A separate paper is in preparation.)

**M. douradaensis* Hovens & Strecker = *M. zehntneri*

*M. ernestii* = *M. oreas* ssp. *ernestii*

*M. erythracanthus* see *M. oreas* ssp. *cremnophilus*

**M. ferreophilus** Buining & Brederoo
Belongs to *M. azureus* complex, but rather distinctive and worthy of specific rank.

*M. florschuetzianus* = *M. deinacanthus* ssp. *florschuetzianus*

**M. giganteus** Buining & Brederoo
Related to *M. zehntneri*, but a distinct species; further information in Braun (1982).

*M. glaucescens* = *M. pruinosus*

*M. glauxianus* = *M. amethystinus*

*M. griseoloviridis* = *M. amethystinus*

**M. helvolilanatus* Buining & Brederoo may be a variety of *M. zehntneri*

**M. horridus* Werdermann.
Up to now not rediscovered, but seems to be a distinct species of the M. ZEHNTNERI Group, and not of the M. OREAS Group as suggested by Taylor (1982). The author has received photographs of the holotype (B) through the kindness of Dr. B. E. Leuenberger of the Botanical Garden and Museum, Berlin—Dahlem.

*M. inconcinnus* Buining & Brederoo
Contrary to Ritter's statements this taxon is *not* identical with *M. permutabilis* Ritter nom. nud.; the latter belongs to *M. salvadorensis* without any doubt. *M. inconcinnus sensu* Buining should not be combined with *M. salvadorensis*.

*M. interpositus* = *M. oreas* ssp. *rubrisaetosus*

*M. krainzianus* = *M. azureus* var. *krainzianus*

**M. lanssensianus** P. J. Braun
A cleistogamous-flowered species from Pernambuco; seems to link the M. ZEHNTNERI and M. SALVADORENSIS Groups.

*M. lensselinkianus* = *M. amethystinus*

**M. levitestatus** Buining & Brederoo

*M. longicarpus* = *M. deinacanthus* ssp. *longicarpus*

*M. longispinus* = *M. oreas* var. *longispinus*

*M. macrodiscus* Werdermann
Up to now Werdermann's plant has not been rediscovered. Rizzini (1982) makes many reports on *M. macrodiscus* and several illustrations are published. Unfortunately his plant material is rather heterogeneous. Buining and Horst could not find this plant. *HU* 269, '*M. macrodiscus*' is nothing more than a local form of *M. zehntneri* ssp. *robustispinus* (cf. Braun 1986a)

*M. macrodiscus* var. *minor* Ritter

**M. margaritaceus* Rizzini and varieties

*M. melocactoides* auctt. = *M. violaceus*

*M. melocactoides* f. *exsanguis* Rizzini

*M. melocactoides* var. *itaipuassuensis* Rizzini

**M. montanus** Ritter
Following field work it became obvious that *M. neomontanus* van Heek & Hovens is a synonym; *M. montanus* is more related to *M. deinacanthus* than *M. oreas,* but seems to link both groups.

*M. mulequensis* see *M. deinacanthus* ssp. *longicarpus*

*M. neomontanus* = *M. montanus*

**M. neryi** K. Schumann
*M. schulzianus* Buining & Brederoo and *M. smithii* (Alexander) Buining may be conspecific.

*M. nitidus* Ritter = *M. azulensis,* not *M. florschuetzianus* (Taylor 1980, 1982)

**M. oreas** Miquel
ssp. **oreas**
var. **longispinus** (Buining et al.) P. J. Braun **stat. nov.** Basionym: *Melocactus longispinus* Buining et al. in Succulenta 56: 137 (1977).

ssp. **ernestii** (Vaupel) P. J. Braun **stat. nov.** Basionym: *Melocactus ernestii* Vaupel in Monatsschr. Deutsche Kakt.-Ges. 30: 8 (1920).

Large subspecies with long brownish to yellowish spines in the Rio das Contas valley, S to SE Bahia.

f. **azulensis** (Buining et al.) P. J. Braun **stat. nov.** Basionym: *Melocactus azulensis* Buining et al. in Kakt. and. Sukk. 28: 156 (1977). Syn. *Melocactus nitidus* Ritter.

Small, flat, local form in NE Minas Gerais.

ssp. **rubrisaetosus** (Buining et al.) P. J. Braun **stat. nov.** Basionym: *Melocactus rubrisaetosus* Buining et al. in Succulenta 56: 161 (1977). Syn. *Melocactus interpositus* Ritter.

Globular plants with less ribs and strong, scarcely curved, red spines, in S Bahia.

ssp. **cremnophilus** (Buining & Brederoo) P. J. Braun **stat. nov.** Basionym: *Melocactus cremnophilus* Buining & Brederoo in Cact. Succ. J. (US) 44: 3 (1972).

Subspecies from central Bahia, surrounding Morro de Chapeu.
f. **erythracanthus** (Buining & Brederoo) P. J. Braun **stat. nov.** Basionym: *Melocactus erythracanthus* Buining & Brederoo in Cact. Succ. J. (US) 45: 223 (1973).

Local form with extremely long spination, on the western slopes of the Serra do Espinhaço, central Bahia.

**M. pachyacanthus** Buining & Brederoo
Though the habit of *M. pachyacanthus*, with its bluish epidermis (Braun 1986c), is rather reminiscent of *M. azureus*, the proposal to combine these taxa as varieties (Taylor 1982) does not seem to be practical. From the author's point of view it seems to be more realistic that *M. pachyacanthus* represents a link between the M. ZEHNTNERI Group (on crystalline rocks of the Serra do Espinhaço, northern Minas Gerais up to Ceará and Rio Grande do Norte) and the M. AZUREUS Group, which is locally restricted to precambrian, but only recently exposed, flat outcrops of calcareous 'Bambui' rocks in the Rio Sao Françisco and Rio Salitre basins (cf. Braun 1987a), and never growing together with representatives of the M. ZEHNTNERI Group.

The flower (especially the perianth) is different from *M. azureus,* and the plant body and spination are reminiscent of the holotype of *M. horridus* Werdermann (B). Summarizing all these aspects, *M. pachyacanthus* seems to be worthy of specific rank.

**M. paucispinus** Heimen & Paul is allied to *M. pruinosus*.

**M. pruinosus** Werdermann
Following the rediscovery of this species, *M. glaucescens* Buining & Brederoo has proved to be a synonym; a more detailed report about its rediscovery and identity with *M. glaucescens* has been published recently (Braun 1988).

var. **concinnus** (Buining & Brederoo) P. J. Braun **stat. nov.** Basionym: *Melocactus concinnus* Buining & Brederoo in Kakt. and. Sukk. 23: 7 (1972).

After rediscovery of *M. pruinosus,* and with knowledge of many more local populations, *M. concinnus* must be combined with *M. pruinosus*; another variety could be *Melocactus axiniphorus* Buining & Brederoo in Succulenta 55: 193-197 (1976).

*M. robustispinus* = *M. zehntneri* ssp. *robustispinus*

*M. rubrisaetosus* = *M. oreas* ssp. *rubrisaetosus*

*M. rubrispinus* = *M. diersianus* f. *rubrispinus*

**M. salvadorensis** Werdermann

*M. saxicola* Diers & Esteves
Up to now this very isolated species is of uncertain affinity. It may belong to the M. ZEHNTNERI Group; further information can be found in Diers & Esteves (1984).

*M. schulzianus* = *M. neryi*

**M. securituberculatus** Buining & Brederoo
An ally of *M. levitestatus,* but more research is necessary.

*M. smithii* (Alexander) Buining = *M. neryi*

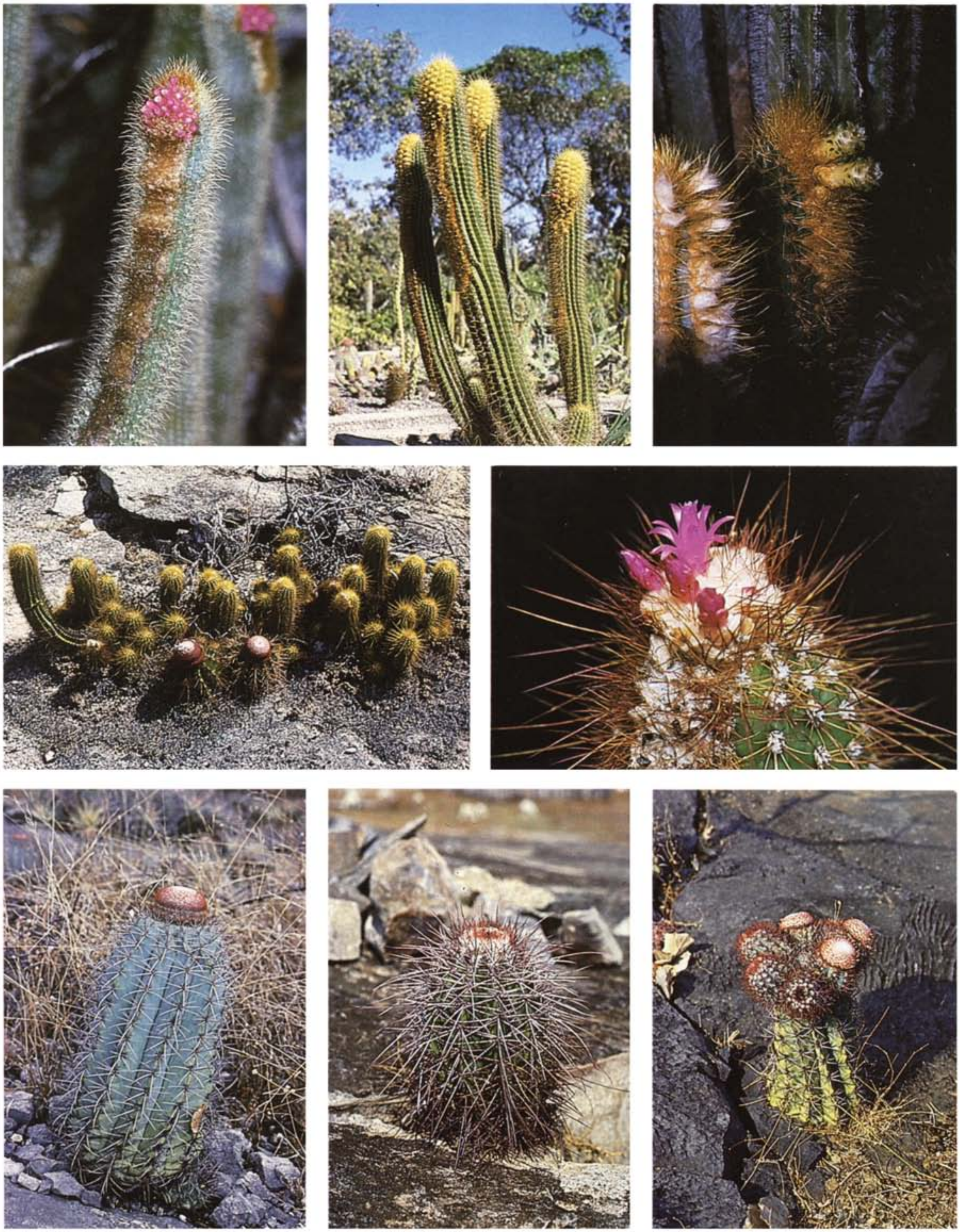

PLATE II. Top row: Left, *Micranthocereus streckeri* at Seabra, 1986, *Braun* 615; centre (*Horst, Braun & Esteves* 4) and right (*Braun* 470) *Coleocephalocereus braunii* from type locality, W Espirito Santo. Middle row: Left, *C.* (subg. *Buiningia*) *aureus* at type locality, 1987, *Braun* 872, together with *Melocactus oreas* ssp. *ernestii* f. *azulensis* at Itaobim, 1987, *Braun* 873; right, *C. purpureus* at Itinga, *Braun* 29. Bottom row: Left, *Melocactus azureus*, large plant, S of type locality, 1986, *Braun* 717; centre, *M. deinacanthus* ssp. *longicarpus*, N of Porteirinha, 1983, *Braun* 393; right, *M. warasii*, SW Bahia, 1983, *Braun* 361.

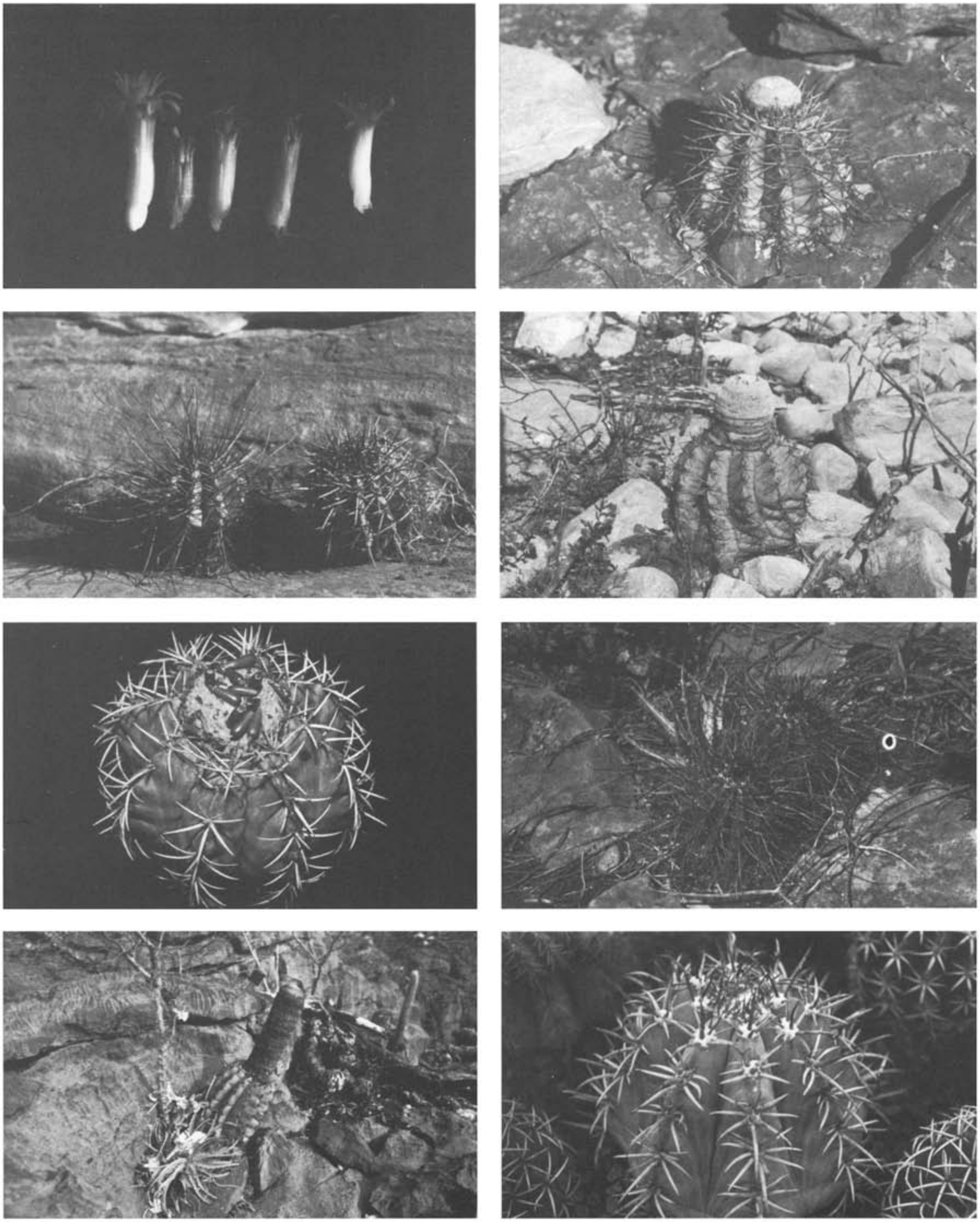

PLATE III. Top row: Left, *Melocactus* flowers ex type localities (from left to right): *M. deinacanthus* ssp. *longicarpus* (*Braun* 393), *M. diersianus* f. *rubrispinus* (*B* 431), *M. diersianus* f. *diersianus* (*B* 433), *M. warasii* (*B* 361), *M. oreas* ssp. *rubrisaetosus* (*B* 196); right, *M.* × *albicephalus* at type locality near Morro de Chapeu, 1986, *Braun* 634. Second row: Left, young plants of *M.* × *albicephalus* (left) and *M. oreas* ssp. *cremnophilus* f. *erythracanthus* (right) at above locality, 1986; right, *M. pruinosus* (at type locality of *M. glaucescens*), Morro de Chapeu, 1986, *Braun* 639. Third row: Left, *M. pruinosus* (*HU* 635), near Ventura, 1985; right, *M. oreas* ssp. *cremnophilus* f. *erythracanthus* at Morro de Chapeu, 1979, *Braun* 61. Bottom row: Left, *M. levitestatus* at the type locality, SW Bahia, 1983, *Braun* 328; right, *M. pachyacanthus* (*HU* 407).

**M. uebelmannii** P. J. Braun
A relative of *M. levitestatus,* but easy to distinguish, having less ribs and self-fertile flowers; synopsis in Braun (1985b).

**M. violaceus** Pfeiffer
According to Taylor (1980) the name *M. melocactoides* should be abandoned; several infraspecific taxa were described by Rizzini (1982).

**M. warasii** Pereira & Bueneker
An ally of *M. levitestatus,* but distinct species even in juvenile stage.

**M. zehntneri** (Britton & Rose) Luetzelb.
ssp. **zehntneri**
var. **viridis** Ritter
var. **curvicornis** (Buining & Brederoo) P. J. Braun **stat. nov.** Basionym: *Melocactus curvicornis* Buining & Brederoo in Kakt. and. Sukk. 23: 35 (1972).

ssp. **canescens** (Ritter) P. J. Braun **stat. nov.** Basionym: *Melocactus canescens* Ritter, Kakteen in Südamerika 1: 134 (1979).

Large, globose plants with flat cephalium, from south-central Bahia.

ssp. **robustispinus** (Buining et al.) P. J. Braun **stat. nov.** Basionym: *Melocactus robustispinus* Buining et al. in Succulenta 56: 119 (1977).

Very small plants with a flat cephalium, from south-central Bahia and northern Minas Gerais; often sympatric with *M. zehntneri* ssp. *canescens, M. amethystinus* and a southern population of *M. salvadorensis* (= *M. permutabilis* Ritter).

*Melocactus species groups*
I. M. NERYI Group
1. neryi (syn. schulzianus, smithii)
2. violaceus ('melocactoides')
   depressus?

II. M. ZEHNTNERI Group
3. giganteus
4. zehntneri
   horridus?
   helvolilanatus?
5. macrodiscus
6. pruinosus
7. paucispinus
8. saxicola (link to Gp VII?)
9. lanssensianus (link to Gp III?)

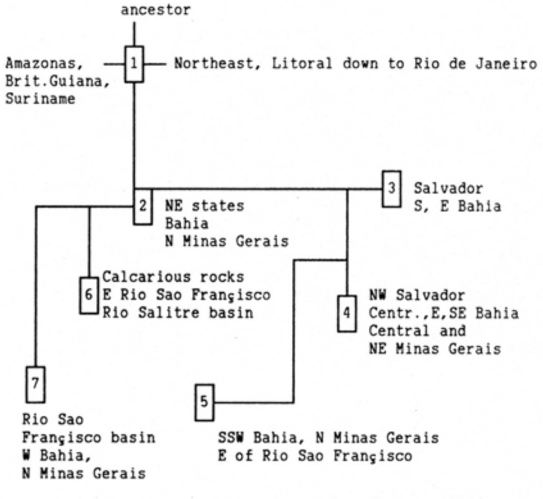

Fig. 9. Hypothetical relationships and distribution of *Melocactus* species groups in Brazil.

III. M. SALVADORENSIS Group
10. conoideus
11. inconcinnus
12. salvadorensis
    brederooianus

IV. M. OREAS Group
13. bahiensis
14. amethystinus
15. oreas

V. M. DEINACANTHUS Group
16. montanus (link to Gp IV)
17. deinacanthus

VI. M. AZUREUS Group
18. pachyacanthus (link to Gp II?)
19. ferreophilus
20. azureus

VII. M. LEVITESTATUS Group
21. diersianus
22. securituberculatus
23. levitestatus
24. uebelmannii
25. warasii

VIII (Hybrid: Gp II/IV)
26. M. × albicephalus

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# New and unfamiliar names for use in the European Garden Flora: Addenda and Corrigenda

*David Hunt*

*Royal Botanic Gardens, Kew*
*Richmond, Surrey TW9 3AE, U.K.*

Three errors have come to light in the list of new names to be used in the *European Garden Flora* (Hunt & Taylor 1987). These are corrected below, although it may not be possible to make corrections to the Flora treatment. Comments are appended on the genera *Monvillea* and *Micranthocereus*.

CARNEGIEA Britton & Rose
The following new combination was omitted from the earlier list:

**Carnegiea polylopha** (DC.) D. Hunt **comb. nov.** Basionym: *Cereus polylophus* DC. in Mem. Mus. Nat. Hist. Paris 17: 115 (1828); *Neobuxbaumia polylopha* (DC.) Backeb.

CLEISTOCACTUS Lemaire
Mr Roy Mottram has pointed out that the name *C. aureispinus* (Ritter) D. Hunt is a homonym of *C. aureispinus* Fric in Möllers Deutsche Gärtner-Zeitung 43: 267 (1928). The following replacement is therefore proposed:

**Cleistocactus winteri** D. Hunt **nom. nov.**: *C. aureispinus* (Ritter) D. Hunt in Bradleya 5: 92 (1987) non Fric; *Winteria aureispina* Ritter in Kakt. and. Sukk. 13: 4 (1962); *Hildewintera aureispina* (Ritter) Ritter.

ECHINOPSIS Zucc.
The combination *Echinopsis thionantha* was earlier made by Werdermann, as follows: **Echinopsis thionantha** (Spegazzini) Werdermann in Notizbl. Bot. Gart. Berlin 11: 264 (1931).

MICRANTHOCEREUS Backeberg
Braun (1988) claims that the submergence of *Micranthocereus* by the IOS Working Party (Hunt & Taylor, eds. 1986) was based on a misunderstanding. The merger was certainly made in the belief that it had Braun's consent, but will be reconsidered at a future 'Consensus' discussion.

MONVILLEA Britton & Rose
Largely for practical reasons, this genus was accepted by the IOS Working Party and has been included in the account for the European Garden Flora, but its taxonomic status, and the correct name of '*M. cavendishii*' are arguable.

Ritter (1979) drew attention to the compelling argument presented by Weingart (1914) for believing that the original *Cereus cavendishii* Monv. ex Lem. was a species of *Acanthocereus*. The tentative suggestion by Schumann (1897) that *C. cavendishii* and the better-known *C. paxtonianus* Monv. ex Salm-Dyck were the same was adopted by J. D. Hooker and led to the selection of *C. cavendishii* as the type of *Monvillea* by Britton & Rose.

Ritter treated *Monvillea cavendishii* sensu B. & R. as a synonym of *M. paxtoniana* "(sensu Schumann) Borg", which is inadmissible. If, as seems very probable (although no original material is extant), *C. cavendishii* was indeed a species of *Acanthocereus*, application of the current edition of the *International Code of Botanical Nomenclature* (Art. 10.2) renders *Monvillea* a synonym of *Acanthocereus*, the case being comparable with that of *Mitrocereus*. *Monvillea,* in Britton & Rose's intended sense, is left without a valid generic name.

Taxonomically, however, the case for '*Monvillea*' as a genus is weak, resting on habit and fruit characters, and Braun (1988) recommends that it be submerged in *Cereus*. Braun (l.c., fig. 1) implies that *Cereus* should consist of three subgenera, *Brasilicereus* (formally proposed in his paper), *Cereus* (autonym) and *Monvillea,* but does not make the reduction or include the group in his key to genera and subgenera.

In view of the nomenclatural problem, it is desirable that *Monvillea* should be rejected as the name of the group as a whole when it is treated at subgeneric rank. Two other valid names are available: *Ebneria* Backeb. and *Hummelia* Backeb., proposed simultaneously (along with *Eumonvillea*, which must be corrected to subg. *Monvillea*) by Backeberg (1948). Theoretically, either name would serve, but since the species of *Hummelia* have been transferred to a separate genus, *Praecereus* Buxbaum, I propose to select *Ebneria*:

**Cereus** subg. **Ebneria** (Backeb.) D. Hunt **comb. nov.** Basionym: *Monvillea* subg. *Ebneria* Backeb. in Sukkulentenkunde 2: 54 (1948). Type: *Cereus spegazzinii* F.A.C. Weber. Syn. *Monvillea* subg. *Hummelia* Backeb., l.c.

This choice does not affect the availability of *Hummelia* if a further subgeneric name is required. Its type is *Monvillea maritima* B. & R., which was included in *Praecereus* by Buxbaum. The type of *Praecereus* is *Cephalocereus smithianus* B. & R., but if (as seems likely) the two species are referable to the same group, *Hummelia* would be the correct subgeneric name.

The correct name for *Monvillea cavendishii* hort. remains in doubt. If, as Weingart claimed, *Cereus paxtonianus* Monv. ex Salm-Dyck was also an *Acanthocereus,* the earliest relevant names for 'monvilleas' of localized origin appear to be *C. saxicola* Morong and *C. euchlorus* F.A.C. Weber ex Schumann.

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# Conophytum: an annotated checklist (A-C)

*Steven A. Hammer*
*c/o Karoo Botanic Garden, P.O. Box 152*
*Worcester 6850, South Africa*

*Summary.* The author introduces an annotated list of *Conophytum* names to be completed in about four instalments. Authorities, places of publication, details of typification and essential synonyms are cited for all bi- and trinomials listed. Accepted species are accompanied by a statement of their provisional infrageneric placement, a brief description, distributional data and discussion.

*Zusammenfassung. Conophytum: Eine kommentierte Liste (A-C).* Für die Gattung *Conophytum* wird eine kommentierte Liste der veröffentlichten Namen begonnen, die in voraussichtlich drei Fortsetzungen beendet sein wird. Für alle aufgenommenen Namen werden Autor, Publikationsort, Details der Typifizierung und wichtigste Synonyme angegeben. Akzeptierte Artnamen werden von Angaben zur infragenerischen Zugehörigkeit, einer kurzen Beschreibung, Verbreitungsinformationen und kritischen Bemerkungen begleitet.

## Introduction

Since its creation in 1922 the genus *Conophytum* N.E.Br. has been subject to a prodigious inflation of names. There are several reasons for this unfortunate predicament, some of them historical. The principal European workers (N. E. Brown in England, A. Tischer and G. Schwantes in Germany) suffered from a paucity of material and from murky collection data; L. Bolus, the remarkably industrious South African conophile, had a uniquely narrow species concept. The lines of communication between the various parties were not always clear, with the result that many species were repeatedly redescribed.

The extreme variability of many species—both in the field and in cultivation—also contributed to many misunderstandings. None of the European workers visited South Africa; they collected by remote control and had little concept of the actual range of the genus. A similar situation obtained with *Lithops,* of course, but these have usually been propagated by seeds, so that some of the inherent variability was inescapably revealed; conophytums have traditionally been propagated by division, with the attendant danger of artificial uniformity. On the other hand, many *Conophytum* species are so amazingly mutable that different environments can reveal aspects previously unsuspected; the same clone, sent to Kew and to Kiel, could diverge to the point of unrecognizability after a few seasons.

Confusion was inevitable in such a situation; the *olla podrida* reached its peak in the late 'fifties. By that time, Tischer began to receive adequate collection samples, which caused his previously-neat schemes great difficulties; Schwantes was ill and essentially out of the picture. Brown, of course, was long dead, though he can be regarded as the most modern of these workers—the most involved, and at the same time, the most detached. Plants from his extensive collection lingered on, not always accurately labelled; many of his ms. names were never published, though they circulated widely. Bolus was still very much alive; she continued her formidable output until 1967. She was greatly concerned with the necessity of preserving type specimens within South Africa; her other aim was the recording of variation. Rather than emending old descriptions, she simply coined new species, trusting that posterity would separate the genuine from the spurious. Her prolixity has been much critized, and yet some of her late species are among the most interesting in the genus; the penultimate, *C. burgeri,* is extraordinary.

In the early 'sixties, Rolf Rawe, a German immigrant to South Africa, and Dr. H. W. de Boer, the Dutch mesemb specialist, began to turn their close attentions to the genus. Rawe's field work, conducted sporadically over two decades, led to numerous reductions published in *Kakteen und andere Sukkulenten* and the *Cactus and Succulent Journal* (US). Rawe extended the known range of most species and rediscovered many lost ones. He also discovered several remarkable new species, some still unpublished. De Boer's work was published in *Succulenta;* it is a pity that he died just as he was obtaining a clearer picture of the genus, in 1970. The study of the genus had already suffered a loss with the death of R. C. Littlewood, an English immigrant to South Africa, in 1967. Littlewood had hoped to conduct field surveys

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throughout Namaqualand; his early death cut short much promising work.

In 1973, A. R. Mitchell began a comprehensive field study of the genus. The abundant and literal fruits of his work are still being studied, by Mitchell and the present writer. Meanwhile, in view of the great confusion which prevails on paper and in collections, I have decided to publish an annotated checklist of the species named to date. Accepted species are printed in bold type; readers may be surprised by the paucity of these. It will be noticed that the species richest in synonyms is *C. bilobum* (Marloth) N.E.Br., which has always been the most collectible species, because of its size and ubiquity.

Measurements are based upon cultivated specimens grown in good light. Most exceed field measurements, though it should be noted that in a 'good year' plants in the wild take advantage of all available moisture, ballooning to surprising proportions. Corolla length is also tricky, as it depends so much upon exposure; and of course the flowers of most species continue to expand after anthesis. Capsule locularity is partly a function of nutrition and maturity, as is seed size.

Place-names pose a three-fold problem of their own. Those of Nama origin go under a variety of spellings; European-derived names tend to be repetitious (requiring further qualification); and an impressive number of place-names—of whatever origin—have become firmly established in botanical literature, despite the fact of their never having appeared on any officially published map! My main aims have been to avoid ambiguity, and to standardize spelling throughout.

## Notes on the infrageneric classification of Conophytum

Before briefly discussing infrageneric classification, I should first give a description of *Conophytum*. In 1925 (Gard. Chron. 78:450) N. E. Brown gave a description which improves upon the original given in 1922 (Gard. Chron. 71:198), and it can still be used, with some modifications which are inserted in brackets:

> 'Very small succulent perennial, tufted [rarely single] plants, usually stemless, but with a few species developing short stems with age, with the growths crowded into a clump. Roots very short. Each growth consists of a small, fleshy body, obconical, globose, ovoid, oblong, or subcylindric in shape, formed of two opposite leaves fused into one body, and convex, flat, depressed, notched or two-lobed at the top, with a small orifice resembling a closed mouth at the centre or between the lobes. Flower solitary [very rarely appearing in pairs], growing up from the interior of the growths through the central orifice. Calyx with a distinct elongated, slender, membranous [or fleshy] tube above the ovary, four-to-six-lobed at the top, included in or partly or entirely exserted from the orifice. Corolla with a distinct slender or funnel-shaped tube as long as or longer than the calyx-tube, and usually numerous, sometimes few lobes or petals [petaloid staminodes], spreading or recurved, in one to several series, the inner series at the mouth of the tube in some species smaller and differently coloured ([filamentous] staminodes?). Stamens, few or many, erect, included in or partly exserted from the corolla-tube. Style [fused portion of the stigmas] long or short, rarely nearly or quite absent; stigmas four to six [to eight], filiform. Ovary inferior, flat or convex or conical at the top, with a crenulate ring of connected [or separate] glands at its margin, four-to-six-[to eight]-celled; placentas on the floor or outer wall of the cell [or very rarely central]. Capsule small, with four to seven [eight] valves and cells; valves with a central expanding keel continuous with the cell-partitions; cells open, without cell-wings or tubercles [minute rims often present]. Seeds minute, ovoid, with a nipple at one end, smooth'.

In 1926 Brown mentioned a further trait: the presence of bracts upon the pedicel (q.v. *C. bilobum*). The bracts—and the fusion of the petals into a tube—are the essential characters which separate *Conophytum* from *Lithops*, the other large genus of 'body-forming' mesembs. We should note that the cotyledons of all members of both genera form small bodies; to quote Brown (loc. cit. 1922): 'the only known plants that are almost alike in form in both the cotyledonary and adult stages, the only practical difference between the two stages being that of size.' After a few months, the 'bodies' dry into a resting sheath or tunic. With adult Conophyta, this sheath is usually present during at least part of the annual cycle. The sheaths of many *Conophytum* species are highly diagnostic; the texture (continuous, perforated, ribbed, reticulate), colour (from pure white to blackish-brown), maculation (from tanniniferous idioblasts or various chromoplasts) and degree of persistence of the sheaths, are very useful traits.

In the latest scheme, proposed by Rowley in 1978 (Nat. Cact. Succ. J. 33(1):7-8), *Conophytum* is divided into five subgenera: *Conophytum*, *Fenestrata* (N.E.Br.) Tischer, *Berrisfordia* (L. Bolus) Schwantes, *Ophthalmophyllum* (Dinter & Schwantes) G. Rowley and *Oophytum* (N.E.Br.) G. Rowley. The last-named is not accepted here, because of its closer connection with the *Mitrophyllinae*. In Tischer's concept (Kakt. and. Sukk. 17(4):71-75. 1966), subgenera *Fenestrata* and *Conophytum* were further subdivided into sections; these were based upon the earlier, somewhat fragmented, arrangement into series proposed by Schwantes. These series, and Tischer's sections, were based upon a combination of macroscopic traits and geographical distribution; the latter was very incompletely understood, but most of the sections do represent natural groupings, and with some modification they are provisionally accepted here. Unfortunately, some of Tischer's infrageneric names were not validly published for want of Latin diagnoses; I have cited such names in inverted commas, preferring to wait until the classification of the genus is better researched before publishing them formally. Others, e.g. sect. *Cordiformia*, must be replaced by earlier names, while the remainder, which were invalid for lack of proper basionym citations, are validated at the end of this discussion.

Tischer divided subgenus **Fenestrata** into two sections. The first, **Pellucida** (Schwantes) Tischer ex Hammer, is characterized by partially windowed bodies, which are usually warted or pitted, and, especially, by floral peculiarities: golden to orange, shortened inner filamentous staminodes, which form a 'ring' at the mouth of the corolla-tube. The stamens and stigmas are so short as to be concealed at the mouth of the very narrow corolla-tube. Section two, **'Subfenestrata'** Tischer, also has windowed bodies, but these are smooth on the apex. In this section, the flowers are 'normal', i.e., the anthers and stigmas are well-exserted. In both sections the flowers are exclusively diurnal and usually scentless. Note that 'windowing' is found in other sections of the genus, but in those it is restricted to the tissue surrounding the fissure.

Subgenus **Conophytum** is a much larger and far more heterogenous assemblage. Tischer divided it into nine sections. The first, *'Cordiformia'* (A. Berger) Tischer (correctly sect. **Biloba** N.E.Br.) consisted of three subsections: *'Eubiloba'* Tischer, *'Ovigera'* Tischer, and *'Saxetana'* (Schwantes) Tischer. **'Eubiloba'** contained not only *C. bilobum* and its myriad micro-variants, but also many other species not florally allied, though they do share a tendency toward incomplete fusion of leaf-pairs. I suggest that *'Eubiloba'* should be limited to those yellow- (rarely white, orange, or pink) flowered species which have large corollas, no filamentous staminodes, long stigmas and dark woody capsules.

Subsection **'Ovigera'** is separated tenuously from *'Eubiloba'*; the principal differences involve smaller bodies with a greater degree of leaf-fusion, and smaller corollas, with a greater colour range (to magenta). The fact that eubilobas and ovigeras co-occur at several colonies, maintaining their separate existences, suggests retention of the subsections, though I note that they cross freely in cultivation. **Saxetana,** unlike the previous two, consists of night-flowering species. These are so distinct in their pollination syndrome and floral peculiarities (small, cream to copper-coloured corollas, very long, often exserted stigmas, and heavy scent) that I regard them as an independent section. Some species do show a vegetative convergence toward *C. taylorianum* Dinter & Schwantes, which was hitherto regarded as a member of *'Eubiloba'.* but which actually belongs, with its several relatives (some undescribed) in a new section, which will be described in the near future.

Section *'Truncatella'* (Schwantes) Tischer must be renamed section **Conophytum,** as it includes the type species of the genus. Species in the section are closely allied, not only to each other but also to members of section *'Colorata'* Tischer. All the 'Truncatellas' have truncate to sub-bilobed bodies, a maculate, generally greenish epidermis, and nocturnal flowers, with narrow, usually cream-coloured petals and short stigmas. Most of the species are native to the Oudtshoorn and Little Karoos; these are the southernmost members of the genus.

Species in section **Tuberculata** are, for the most part, native to the Clanwilliam and Vanrhynsdorp districts. They are characterized by elaborate, often raised epidermal markings, and (frequently) by a glossy, non-papillate epidermis; these traits provide a superficial distinction from the comparatively dull southeastern species of section *Conophytum,* but the flowers show no essential distinctions. Epidermal studies currently underway may help us to determine the boundaries between these sections.

Section **Wettsteinia** (Schwantes) Tischer ex Hammer (*'Wettsteiniana'* Tischer), is a well-founded group. The bodies are turbiniform to (rarely) globose; a few species have a vegetative resemblance to *C. truncatum* (Thunb.) N.E.Br., but when in flower there is no mistaking them. They bear large, diurnal flowers with broadened petals which are white, yellow, pink, or purple. Often the filaments are brilliantly coloured as well. Tischer divided the section into two subsections; the lion's share of the species went to subsection *'Longistyla'* Tischer, which is characterized by long styles and short, often hardly discernible, stigmas (i.e. the fused portion of the stigmas was very long in proportion to the free ends). Subsection *'Minuta'* Tischer consists of a very few species which were grouped together because of their floral structure, which is similar to that described above for section *Pellucida.* Indeed, Littlewood had grouped these with the *Pellucida* in his subgenus *'Celatistamina',* named for its 'concealed' stamens. Tischer wisely rejected the subgenus because of the wide vegetative disparities between *'Minuta'* and *Pellucida.* I have large reservations about subsection *'Minuta',* because there are colonies which have traits intermediate between it and subsection *'Longistyla'.*

Section *'Cataphracta'* Tischer is the most uniform of all the groups discussed here. Though very widespread, its members are all closely related. They can be recognised by their tough, absolutely smooth bodies, which are invariably glabrous; even the fissure zone is devoid of cilia or papillae (a character they share with *Lithops,* but with no other Conophyta). The strongly-scented nocturnal flowers have very short stigmas. The petals, oddly, are usually coloured bright yellow to reddish, a contrast to the shades found in the other nocturnal sections (in these pale yellow and white are the predominant shades, and golden yellow is unknown).

Section **Minuscula** (Schwantes) Tischer ex Hammer is also well-founded; the (usually) dwarf bodies, with their glossy raised lines, and the surprisingly large diurnal flowers, brilliant magenta to (rarely) white or fluorescent pink, are very easily recognized. Two flower structures are seen in this group: long petals, with concealed anthers and stigmas, or shorter sparser petals, with exserted anthers and stigmas.

Section **'Costata'** (Schwantes) Tischer is easily recognized by the thickened, sulcate to tuberculate tunics found in most species. The section is divided into two groups, subsection *'Costifera'* Tischer, with small nocturnal flowers, and subsection *'Verrucosa'* Schwantes, with larger diurnal flowers. Some species in the latter group have epidermal structures close to those seen in sect. *Minuscula,* but the floral structures are quite distinct. It is interesting to note that *'Costata'* occupies the Bushmanland and Richtersveld; *Minuscula* is found further south: they do not overlap.

Section **'Barbata'** (Schwantes) Tischer is probably the most distinctive of all; all members have a remarkable covering of long hairs. The floral structure is close to that seen in subsection *'Costifera',* with very short, acute, petals. The flowers open at night, and in one species, they last only a short time.

In his 1966 grouping, Tischer placed section **Cylindrata** Schwantes at the very end. In the 1970 Lexicon he shifted it from subgenus *Conophytum* to subgenus *Fenestrata,* an odd move, considering the opaque bodies of *C. cylindratum.* It was perhaps motivated by considerations of body shape. In 1974 Rawe (Excelsa 4:73) suggested that the section be abolished, placing its members in subsection *'Verrucosa'.* Since 1974, however, *C. cylindratum* and its surprisingly numerous allies have been better investigated, and they form a very distinct group, with soft bodies, which have a prolonged juvenile stage. The flowers are peculiar too, viz. few-petalled, lacking the 'showy' quality seen in *'Verrucosa',* and in at least one case, protogynandrous. Greyish-brown seed capsules, often quite fragile, are also a peculiar trait of this group.

Evidence for justifying the recognition of sections in *Conophytum* is provided by the frequent occurrence of sympatric populations of several species, with no evident hybridization. At Augrabies, for example, I have seen a species of *'Ovigera',* a *Wettsteinia,* a *'Barbata'* and a *'Cataphracta',* all growing together, and this is by no means unusual. However, the sections as they are given above cannot quite accommodate all known species. There are a number of species—usually known from small endemic populations—which are so aberrant that their placement frankly puzzles me (see *C. concavum*). Ben Groen of Wageningen is working on this very complex aspect of *Conophytum.*

Brief discussions of subgenus **Ophthalmophyllum** will be found under *C. acutum, C. burgeri, C. caroli* and *C. concordans.* Here I will note only that the key given by Rowley (loc.cit.) is incomplete; many Ophthalmophylla lack the specified broad fissure and well-developed window. These non-fitting species have another peculiarity—nocturnal flowers—and it would seem that subgenus *Ophthalmophyllum* needs two sections. Niko Sauer is working on this group and we eagerly await his conclusions.

As for subgenus **Berrisfordia,** it seems odd to have a subgenus which contains only a single species (the former *B. khamiesbergensis* L. Bolus) but then that species is very odd. It flowers in late winter (unlike all other species, except *C. smorenskaduense* de Boer); its capsule is extremely slow to ripen and partly axile in its placentation; its leaves bear curious 'encrustations' and moreover they smell like raspberries!; and its mode of branching is particularly unusual—the flowering branches bear a single flower which is usually flanked by two leaf-pairs. On the other hand, the species has points of connection with members of the sect. *Cylindrata.*

### Validation of infrageneric names

**Conophytum** sect. **Pellucida** (Schwantes) Tischer ex Hammer **stat. nov.** Basionym: *C.* ser. ('Reihe') *Pellucida* Schwantes in Gartenflora 76:425 (1927). Type: *C. pellucidum* Schwantes.

**Conophytum** sect. **Saxetana** (Schwantes) Hammer **stat. nov.** Basionym: *C.* ser. ('Reihe') *Saxetana* Schwantes in Gartenflora 76:425 (1927). Type: *C. saxetanum* (N.E.Br.) N.E.Br.

**Conophytum** sect. **Wettsteinia** (Schwantes) Tischer ex Hammer **stat. nov.** Basionym: *C.* ser. ('Reihe') *Wettsteinia* Schwantes in Gartenflora 76:424 (1927). Type: *C. wettsteinii* (A. Berger) N.E.Br.

**Conophytum** sect. **Minuscula** (Schwantes) Tischer ex Hammer **stat. nov.** Basionym: *C.* ser. ('Reihe') *Minuscula* Schwantes in Gartenflora 76:425 (1927). Type: *C. minusculum* (N.E.Br.) N.E.Br.

**Conophytum** sect. **Tuberculata** (Schwantes) Tischer ex Hammer **stat. nov.** Basionym: *C.* ser. ('Reihe') *Tuberculata* Schwantes in Gartenflora 76:425 (1927). Type: *C. obconellum* (Haw.) Schwantes. [=*C. obcordellum* (Haw.) N.E.Br.].

**Acknowledgements**
I am grateful to A. R. Mitchell for reading through various drafts of this paper and making many helpful suggestions and improvements. Nigel Taylor has assisted with matters nomenclatural.

## Checklist of Conophytum names A-C

*C. absimile* L. Bolus, Notes on Mesemb. 3:309-310 (1958). Type: 'On the road between Springbok and Spektakel', *P. van Heerde* (BOL 26214). *C. absimile* f. *major* L. Bolus, ibid. Type: as above (BOL 26215). *C. absimile* f. *umbrosum* L. Bolus ('umbrosa'), ibid. Type: as above (BOL 26216).

*C. absimile* was named for its asymmetrical lobing. Redundant in itself, it was saddled with two forms, which grew in shade or in the open. The locality is close to the distribution centre of 'the elishae complex', into which Tischer suggested that it be placed. That dubiously-defined entity fits into the expanded concept of *C. bilobum* favoured here.

**C. acutum** L. Bolus, Notes on Mesemb. 3:189, pl.42, fig.D (1950); and ibid. 3:264 (1954); Tischer in Cact. Succ. J. Gr. Brit. 15(4):81 (1953); 16(3):264 (1954). Type: 'near Bokkraal ('Bushmanland')', R.Primos in NBG 1352/36 (BOL).

Plant single or branching in age; tunic yellowish, membranous, impersistent; bodies cylindric, narrowing toward the truncate apex, 12-25×7-12×5-7mm, yellowish-green, fenestrate at the apex; fissure 2-4mm. Flowers nocturnal, strongly scented; calyx-tube hyaline, scarcely projecting beyond the fissure; corolla-tube 13-30[!]×6-8mm, ivory white, petals 26-30, acute, outer very brief, hardly differentiated from the tube, inner in 1-2 series, 5-6mm; stamens 19-25, 2-seriate, c. 5-7mm; stigmas 4, thin, 4-6mm, shortly united at the base. Capsule 4-locular; seeds very numerous, golden-brown, 0.55mm.

In 1953, Tischer transferred this poorly-known species to *Ophthalmophyllum,* because of its 'total habit', concave ovary, broad disc, and long stigmas. As the original description is incomplete, Tischer, who had seen no specimens, was unable to determine whether or not the calyx- and corolla-tubes were partially fused, which would have provided a useful determining character. *Ophthalmophyllum,* by definition, must have partially adnate calyx- and corolla-tubes; in *Conophytum,* the tubes are free. Unfortunately, this neat distinction breaks down in the nocturnal ophthalmophyllums. If the genera are to be separated—which I do not suggest at present—other characters must be used. When Tischer wrote 'total habit', he meant: this looks like an *Ophthalmophyllum*! Bolus rejected this judgment, without advancing any reasons; note that she maintained *C. maughanii* N.E.Br. (which, like *C. acutum,* flowers at night) in *Conophytum* as well. Certainly these two species are vegetatively close to *Ophthalmophyllum,* having the pulpy, quasi-translucent tissues usually associated with that genus.

The material I have seen of *C. acutum* (collected by Buys Wiese c. 15km east of Bitterfontein, in the Knersvlakte) matches the dried material seen at the Bolus Herbarium very well. Both collections have membranous, free, calyx tubes, unlike the fleshy calyx tubes of diurnal ophthalmophyllums, and remarkably long corolla tubes, with only a small degree of segmentation at the apex. The capsules produced by Wiese's plants are also remarkable; they are pyriform, reluctant to open fully, and their placentation is axile-basal, traits quite foreign to (subgenus) *Ophthalmophyllum,* but found in several conophytums.

It should also be noted that the very narrowly cylindric seedlings of *C. acutum* are unique. Altogether the species is quite aberrant, fitting none of the described sections in *Conophytum,* but it is certainly not an *Ophthalmophyllum*. It is uncertain which of the various Bushmanland Bokkraals Primos referred to, but there is a Bokkraal c. 35km north of Wiese's colony, and this spot is very likely terrain for the species.

*C. admiraalii* L. Bolus in J. S. Afr. Bot. 31(2):170-171 (1965); Rawe in Cact. Succ. J. (US) 54(5):220 (1982). Type: '31 miles from the main road (Port Nolloth-Steinkopf) along the Kliphoogte road', *J. Admiraal* in *P.A.B. van Breda* 2073/64 (BOL).

This taxon has a short but muddled history. In her original description, Bolus suggested no section, which poses a problem as plants distributed by Hall shortly after the first collection belong to section *Wettsteinia*. The Hall-derived plants have purple corollas and although the description gives the colour as 'in siccis albidis', purple in a living flower may fade to whitish, on death and drying.

In 1969 Rawe distributed material (*RR*758) from Doringrivier, near Admiraal's locality, as *'C. admiraalii-orbicum'*. *C. admiraalii* is indeed very close to *C. orbicum* N.E.Br. ex Tischer, which does belong to section *Wettsteinia*, and which probably came from Kubus, north of Doringrivier. Both taxa have pyriform, obscurely keeled, and minutely asperulous bodies. In floral structure, they match completely; there is no reason to retain Bolus's taxon. Nonetheless, in 1982 Rawe suggested that it was a member of the subsection *'Ovigera'*, following Tischer's idea that it was a variety of *C. meyeri* N.E.Br.

*C. advenum* N.E.Br. in Gard. Chron. 78:451 (1925); Bolus, Notes on Mesemb. 3:145-146 (1939); ibid. 3:208, pl.44, fig.I (1950); Tischer in Cact. Succ. J. Gr. Brit. 18(3):56 (1956); Bolus in J. S. Afr. Bot. 31(2):173 (1965). Type: 'Montague [sic] division', *M. Michell* in NBG 991/18 (K; BOL, iso).

Bolus and Brown received this species at about the same time. Brown's plants failed to flower, but Bolus was luckier and in 1939 she described the petals as 'copper-red outside and paler and more yellow on the inside', which reminded her of *C. piluliforme* (N.E.Br.) N.E.Br. Bolus remarked that the species were closely related, and Rawe's placement of *C. advenum* as a variety of *C. piluliforme* followed from this. (Rawe in Cact. Succ. J. (US) 54(6):283-284. 1980). He distinguished the variety by its glabrous epidermis and its flower colour—very fine distinctions, especially considering the minuteness of the papillae of *C. piluliforme*. Rawe remarked that the taxa can hardly be separated in the field; a simple union would be the best solution.

*C. aequale* L. Bolus, Notes on Mesemb. 3:265-266 (1954). Type: 'Numees', *H. Hall* in NBG 689/53 (BOL).

This large bilobe was named for the fact that its height matched its diameter. Such equality is not unusual though the apparent uniformity of *C. aequale* is striking; Rawe's collection, also from Numees, is likewise isometric. Otherwise, *C. aequale* can hardly be distinguished from *C. bilobum* in one of its glabrous manifestations.

*C. aequatum* L. Bolus in J. S. Afr. Bot. 28(3):221 (1962). Type: 'Steinkopf', *H. Hall* in NBG 847/48 (BOL).

This species was only distinguished by the equal length of its 'style' and stigmas. Rawe (in Cact. Succ. J. (US) 47(4):183. 1975) sunk it into *C. breve* N.E.Br., which typically lacks a 'style'. What Bolus termed a style is better regarded as the lower fused portion of the stigmas; the degree of fusion varies greatly within a taxon, and sometimes within the various flowers of a single plant. Unfortunately, the length of the 'style' was very often used as a taxonomic character, especially by Bolus.

*C. aggregatum* (N.E.Br.) N.E.Br. in Gard. Chron. 72:8 (1922); *Mesembryanthemum aggregatum* N.E.Br. in J. Linn. Soc. 45:91-92 (July 1920). Type: Locality and collector unknown; photo and painting by N. E. Brown (K).

*C. aggregatum* has a tangled history. Brown attempted to re-identify the old *'Mesembryanthemum aggregatum'*, a name known to and used by Haworth (Obs. Mesemb. 131, 419. 1794), though he never formally published it. The name referred to two species, ambiguously; at least one belonged to the present-day genus *Gibbaeum*. Brown first saw the plant he later named *M. aggregatum* in Saunders's collection, in 1865. It was certainly a species belonging to *Conophytum*, but upon transferring it to that genus, Brown noted that he had, inexplicably, mixed two descriptions in 1920: the body of one species *(M. aggregatum)*, with the flowers of another *(M. piluliforme)*. *C. aggregatum* always attempted to flower so late in the season that complete floral development was impossible.

In 1957 Tischer (in Kakt. and Sukk. 8:89) sunk *C. aggregatum* into *C. piluliforme* (N.E.Br.) N.E.Br. (*Mes. piluliforme* N.E.Br. July 1920!—same journal, p. 98) though it did have some distinctive characters: the bodies were truncate, and irregularly hexagonal in outline; the flowers were a dark saturated red (as his 'clonotype' plant had recently shown). These characters were insufficient to justify its retention. It is worth noting that Brown's 'clonotype' of *C. aggregatum* was given to him by Saunders; the material probably dated from the 1820s at the latest.

*C. albertense* (N.E.Br.) N.E.Br. in Gard. Chron. 71:261 (1922) and ibid. 78:500 (1925); *Mesembryanthemum albertense* N.E.Br. in J. Linn. Soc. Bot. 45:92 (1920). Type: 'Prince Albert Road' *H. H. W. Pearson & H. W. R. Marloth* (not preserved); photo and painting by N. E. Brown (K).

This completed its taxonomic existence within five years: from *M. albertense* to *C. albertense*, to synonymy under *C. purpusii* (Schwant.) N.E.Br. Brown synonymized it because *M. purpusii* antedated *M. albertense;* both were collected near Prince Albert. *C. purpusii* itself has been subsumed into *C. truncatum* (Thunb.) N.E.Br.

*C. albescens* N.E.Br. in Gard. Chron. 79:12 (1926). Type: 'Near Chubiessis?', *H. H. W. Pearson* (not found; cf. fragments of *Marloth* 6919, also N.E.Br. painting of same, K).

At first, Brown thought that this might have come from Chubiessis [Chabiesies], because it was sent with *C. cauliferum* N.E.Br. (q.v.), which Pearson collected southwest of that place. However, in his unpublished notes, Brown identified a plant from Kubus (*Marloth* 6919) as *C. albescens*. Some of the bilobes from Kubus do fit Brown's description: a rather large plant with terete lobes, conspicuously tomentose, but such plants are also found near Chabiesies, and these cannot be distinguished from *C. bilobum* (Marloth) N.E.Br. *sensu stricto*.

*C. albescens* N.E.Br.; photo ex N.E.Br. coll. © RBG Kew.

*C. albifissum* Tischer in Cact. J. (Croydon) 3(4):63 (1935) and in Cact. Succ. J. Gr. Brit. 14(3):56-57 (1952); Rawe in Cact. Succ. J. (US) 52(6):283-284 (1980). Type: Locality and collector unknown; 'clonotype' is still in cultivation at HBG.

Rawe's suggestion that this 'lost' species belongs near *C. piluliforme* (N.E.Br.) N.E.Br. is interesting. In 1952 Tischer placed it in his subseries *'Picta'*, not in his subseries *'Piluliformia'*. The plant I know, which stemmed from Tischer, does suggest the smaller, less ornately-marked Pictas—these also have ciliate white fissures—and there is much evidence that the smaller Pictas intergrade with the Piluliformias; all these belong in sect. *Tuberculata*. The Tischer clone can plausibly be seen as a pale-flowered variant of *C. piluliforme;* almost certainly it originated in the western Little Karoo.

*C. altile* (N.E.Br.) N.E.Br. in Gard. Chron. 72:83 (1922); *Mesembryanthemum altile* N.E.Br. in J. Linn. Soc. 45:92 (1920). Type: Locality and collector unknown, painting by N.E.Br., without data (K).

*C. altile* (N.E.Br.) N.E.Br.; photo of type ex N.E.Br. coll. © RBG Kew.

According to Brown, this was readily distinguished by its bloated, shining, appearance, which it retained year after year. Littlewood (in J. S. Afr. Bot. 32:205-206. 1966) recognized that fatness was common in the 'ficiforme group', and he wisely sunk the whole lot into *C. ficiforme* (Haw.) N.E.Br. In habitat, particularly when growing in shaded crevices, that species can be surprisingly obese. By inference, *C. altile* must have been collected in the vicinity of Worcester (the Breede River Valley), possibly by Thomas Cooper, Brown's father-in-law.

*C. altum* L. Bolus, in S. Afr. Gard. 17:294-295 (1 Aug. 1927) and Notes on Mesemb. 1:21,130 (1928). Type: 'Richtersveld, hill south of Brakfontein', *N. S. Pillans* 5687 (BOL).

This taxon was named for its height; it forms stems with age, unlike many of the bilobes. Typically, it is rather thin-bodied, especially in its wild state. The short lobes with reddish keels place it unmistakably in the bilobes, but its constant caulescent habit, at least, distinguishes it from *C. bilobum* proper, and calls for further examination. Plants resembling *C. altum* can be observed in several highly variable colonies, along with more robust plants; I have also seen colonies in which the plants, and especially their flowers, were quite uniformly depauperate.

*C. altum* var. *plenum* L. Bolus, Notes on Mesemb. 3:86 (1937) and ibid. 3:139, pl.20, fig.C (1939). Type: 'Near Port Nolloth', *P. van Heerde* (BOL 21964). Bolus distinguished this from typical *C. altum* by its total lack of red keel margins and by the far greater number of its petals (50-68 vs. 17-18).In the 1939 *Notes,* she expressed some doubt as to the correct placement of var. *plenum,* and its position—as with other coastal bilobes—is still unclear. The watercolour, by B. O. Carter, suggests synonymy with *C. bilobum,* in one of its coastal manifestations.

*C. ampliatum* L. Bolus in J. S. Afr. Bot. 27:178 (1961). Type: '4 miles south of Nababeep', *R. C. Littlewood* in KG 715/59 (BOL).

This was named for its shape; it had an 'enlarged' girth toward the middle of its body. According to Tischer, who received specimens from Littlewood, this was simply *C. elishae* (N.E.Br.) N.E.Br., which I include in *C. bilobum*. The locality is close to that of *C. absimile,* making *C. ampliatum* a double redundancy.

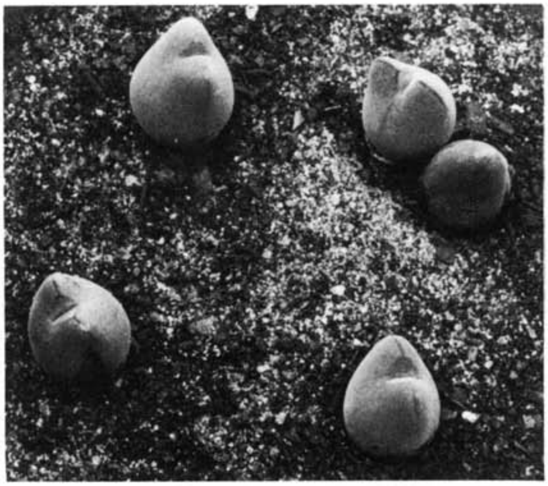
*C. amplum* L. Bolus, Notes on Mesemb. 3:87 (1937) and ibid. pl.36, fig.G (1950). Type: 'Richtersveld, Vlakmyn', *P. van Heerde* (BOL 21965).

This 'ample' species was placed as a variety of *C. obtusum* N.E.Br. by Rawe (in Kakt. and. Sukk. 20(3):58-59. 1969). He recognized two distinct populations in the Vlakmyn area: *C. obtusum* var. *obtusum* easy of the road, and *C. obtusum* var. *amplum,* with larger bodies and longer lobes, to the west. These characters can be seen in A. R. Mitchell's recent collections from the same area, but there is a good deal of intergrading as regards shape. Plants from *ARM* 1216 do show a remarkably smooth, shining, light green epidermis, corresponding well to Bolus's description of *C. amplum* and producing a superficial distinctiveness, but similar tendencies can be seen in so many bilobe populations. It should be noted that *C. obtusum* was discovered in the Soebatsfontein-Wallekraal area, c. 150km south of Vlakmyn (central Richtersveld). The identification of Vlakmyn plants with *C. obtusum* began with Tischer's comparison with *C. vlakmynense* L. Bolus (in Cact. Succ. J. Gr. Brit. 18:56. 1956). If we are to use one name to identify so widespread a genotype, then *C. bilobum* will serve; both *C. obtusum* and *C. amplum* are unnecessary.

*C. andausanum* N.E.Br. in Gard. Chron. 81:32 (1927); Labarre, Mesembryanthema, 139, fig. 38 (1931); Bolus, Notes on Mesemb. 3:198-199 (1950). Type: 'Andaus Poort near Anenous', *H. W. R. Marloth* 6908, flower fragments and N. E. Brown painting (K).

This rather small greyish-green bilobe is one of several reported from the Anenous area. The 1931 photograph gives a poor idea of *C. andausanum;* the translucent dotting, described by Brown, is invisible, though it is conspicuous on the 'clonotype', which is still in cultivation. Brown likened this species to his *C. diversum*—collected near Anenous (*Marloth* 6908), and published at the same time—but his suggestion that both had an alliance with *C. gracilistylum* (L. Bolus) N.E.Br. seems far-fetched, except that they all share a low, clustering habit.

*C. andausanum* var. *immaculatum* L. Bolus, Notes on Mesemb. 3:87 (1937); 3:198, pl.38, fig.E (1950); and in J. S. Afr. Bot. 27(3):178 (1961). Type: 'Ezelsfontein' on the road from Springbok to 'Spektakel', *P. van Heerde* (BOL 21966). In 1950 Bolus expressed doubt as to the placement of this 'immaculate' bilobe. By 1961, she had decided that it was 'erroneously associated' with *C. andausanum,* and was perhaps a variety of her new taxon *C. ampliatum,* thus putting the cart before the horse. Both cart and horse can comfortably be housed in the ample stable of *C. bilobum,* however.



*C. andausanum* N.E.Br.; photo ex N.E.Br. coll. © RBG Kew.

**C. angelicae** (Dinter & Schwantes) N.E.Br. in Gard. Chron. 78:451 (1925); Rawe in Excelsa 4:70-71 (1974); *Mesembrianthemum (Conophytum) angelicae* [sic] Dinter & Schwantes in

Zeitschr. Sukk.-Kunde 2:27 (1925). Type: 'South West Africa, Eendoorn, near Warmbad', *K. Dinter* (not known to have been preserved; neither Dinter nor Schwantes mentioned a number for this collection).

Sect. 'COSTATA' subsect. 'COSTIFERA'. Plant caespitose, stems densely aggregated in age, internodes invisible; tunic whitish, squamous, impersistent at apex; bodies obconic, concave, truncate to convex at apex, 8-18×4-10×3-7mm; nearly smooth to sulcate; epidermis glabrous, of 'dull waxen' appearance, yellowish-grey to olive-green. Flowers nocturnal, inconspicuous, powerfully scented; calyx-tube thin, 1-2mm, 4-6-lobed; corolla-tube projecting 2-4mm beyond the calyx tube, petals 15-28, acute, reddish-maroon to dull orange, 2-3mm; stamens 12-20, 1.5-3mm; stigmas 0.5-1.5mm, very shortly united at base. Capsule often exserted beyond the fissure while still green, 4-6-locular; seeds reddish-brown, 0.65mm.

*C. angelicae* is undoubtedly strange, distinct, and elusive. Its buckled surface, 'waxen' appearance, and ochreous nocturnal flowers cannot be confused with any other species. Unlike other *Conophytum* species, *C. angelicae* is rare in its habitat, especially in SWA. Dinter for all his repeated searching of suitable terrain only found one plant. The collector Wilhelm Triebner took specimens from the Warmbad area and others as far afield as Grünau, in the 40s and 50s. I know of only two recent collections from this area ('Eendoorn', *E. E. Fritz s.n.*, 1970, and 'Witsand', *S. Hammer SH* 480/87). In July 1982 A. R. Mitchell discovered a substantial colony at Aggenys c. 40km SSW of Eendoorn—south of the Orange River and thus within the republic of South Africa proper. These plants match the SWA form closely. Possibly Mitchell's discovery was anticipated by Hans Herre, who sent a collection from 'Bushmanland' (SUG 10030) to N. E. Brown. In 1933 Brown proposed the name *'C. hansii'* for SUG 10030, but it was one of many names left unpublished upon his death in 1934.

In 1974 Rawe reported a striking new form of the species. 'A single plant obviously related [to *C. angelicae*] but with uniformly square bodies! The collector [H. Horn] could not recall the locality but stated that it was extremely rare.' The location of Horn's colony is still a mystery, but it is known that he collected mesembs extensively in the vicinity of the Little Helskloof, at the time in question. Mitchell and I have recently found several colonies of *C. angelicae* in this area (southern Richtersveld). In this Richtersveld form, the angular tendencies of the typical Aggenys/Eendoorn form are considerably exaggerated, the apex is sometimes remarkably concave, or divided into a few pits, and the bodies are often elongated. Crossing experiments between the 'forms' suggest a degree of incompatibility, but in floral structure, our various collections match closely.

When Schwantes published the species, he placed it both in *Mesembry[i]anthemum* and (parenthetically) in *Conophytum*. At the time Dinter still regarded *Mesembryanthemum* as a 'wonderful' (if gigantic) natural genus; Schwantes was influenced by this, though he soon acknowledged many of Brown's segregates.

*C. angustum* L. Bolus, Notes on Mesemb. 3:25 (1936) and ibid. 3:388 (1958). Type: 'Nutabooi, Buffelsrivier', *A. G. J. [H.] Herre* in SUG 10238 (BOL).

Bolus originally overlooked the fact that Brown had already employed her epithet in 1931, but in 1958, she reduced *C. angustum* L. Bolus to synonymy under *C. nutaboiense* Tischer (1937), another species collected by Herre at Nutabooi. Tischer's 'species' is perilously close to *C. angustum* N.E.Br.

*C. angustum* N.E.Br. in Cact. Succ. J. (US) 2(9):427 (1931); Tischer in Kakt. and. Sukk. 6(2):127 with photo of 'clonotype' (1955). Type: 'Little Namaqualand,' *M. Brown* 1047 (not preserved); N. E. Brown painting (K).

Tischer placed this in the 'form-circle' of *C. elishae* (N.E.Br.) N.E.Br., distinguishing it by its 'slender' body and large flower. It is known to collectors as the 'thin form' of *C. elishae,* a species which could easily accommodate it, though the distinction between *C. elishae* and *C. bilobum* is also rather slender.

*C. angelicae* (Dinter & Schwantes) N.E.Br. in habitat, Richtersveld.

*C. anjametae* de Boer in Succulenta 49(3):43-44, with 2 photos (1970) nom. inval. (Arts. 37.1 & 9.5). Type: 'Karamoep', collector unspecified, not preserved at time of publication (deposited at WAG by Boom in 1972).

This was sent to de Boer, 'under a wrong name', from 'Karamoep'; probably it was labelled *C. karamoepense,* under which name de Boer originally distributed the plant. The repetition of Bolus's spelling error is curious; I wonder if the collector ever got near Haramoep, Bushmanland, as nothing like *C. anjametae* is known to occur there. Probably the collector switched his labels, but it is possible that he deliberately deceived de Boer. By this time, strict conservation laws were in force and some collectors chose to operate furtively, as the paucity of their habitat data would seem to suggest.

*C. anjametae* greatly resembles *C. violaciflorum* Schick & Tischer, a species from Springbok, of which it might well be a large-bodied, sharply-keeled, freak, or possibly a hybrid. Note that de Boer's photographs suggest a similarity to *C. karamoepense* L. Bolus; his plant had grown bloated after its hemispherical switch. However, my material, which comes from de Boer, has slimmed down considerably and now has a well-developed keel. It also has the capsule of *C. violaciflorum,* which is quite distinct from that of *C. karamoepense.*

*C. anomalum* L. Bolus in J. S. Afr. Bot. 29(2):46 (1963). Type: 'Kleinzee, near Grootmist', *R. Bayliss & D. Hardy* 1163 in NBG 1040/62 (BOL).

Rawe (in Cact. Succ. J. (US) 54(5):219,222. 1982) correctly suggested that this was needlessly published; but he sunk it into the wrong taxon, *C. ecarinatum* var. *candidum* (L. Bolus) Rawe. It is not 'in all respects' identical with that variety—*C. anomalum* had yellow flowers—but it is indistinguishable from the likewise yellow-flowered *C. approximatum* Lavis, not to mention some of the other coastal 'species'. The trifling 'anomaly' was that it had six stigmas and five sepals; normally the numbers match.

*C. apertum* Tischer in Succulenta 13(3):52-53 (1931) and in Kakt. and. Sukk. 11(9):135-136 (1960). Type: '28 miles northeast of Port Nolloth on the way to O'okiep', collector unknown, not known to have been preserved.

Despite the rather vague locality data, this taxon was sunk painlessly by Tischer (1960) into *C. retusum* N.E.Br.; the localities were close and the plants virtually identical.

*C. apiatum* (N.E.Br.) N.E.Br. in Gard. Chron. 72:83 (1922); Labarre, Mesembryanthema, 140, fig. 39 (1931); *Mesembryanthemum apiatum* N.E.Br. in J. Linn. Soc. 45:64-65 (1920). Type: 'Western slopes of a ridge between Daunabs and Bethany Drift [Sendelingsdrift]', *H. H. W. Pearson* 6058, flower only and N. E. Brown painting (K).

The photograph in Labarre, loc. cit. gives a good idea of this large, well-dotted, whitish-green, asperulous bilobe. Plants I have seen at Remhoogte (a ridge which lies between Daunabis and Bethany Drift) match Brown's description very well, but they can hardly be distinguished from *C. bilobum,* which may vary from glabrous to asperulous in a single population! Other *C. bilobum* variants were later described from Remhoogte—a locality well-known to field botanists for many years.

*C. apiculatum* N.E.Br. in Cact. Succ. J. (US) 2(9):427 (1931). Type: 'Between Springbok and Port Nolloth', *M. Brown* 1050, preserved specimen and N. E. Brown painting (K).

This was originally characterized by a small upturned point at the apex of the lobes, a subtlety not constant even on a single plant. Tischer (in Kakt. and. Sukk. 17(11):204-205. 1966) placed *C. apiculatum* as a form of *C. meyerae* Schwantes, distinguishing it by its 'bowed' leaf-tips and broadened keel-lines, equally inconstant refinements. Maughan Brown's locality information is too general to be helpful, but plants corresponding to *C. apiculatum* are common around Lekkersing, northeast of Port Nolloth. Tischer reduced *C. lekkersingense* L. Bolus to synonymy under his *C. meyerae* f. *apiculatum.* The Lekkersing plants do have one idiosyncracy: they flower in early summer, long before most bilobes. Otherwise they cannot be distinguished from *C. meyerae,* which I include in *C. bilobum.*

*C. approximatum* Lavis in S. Afr. Gard. 22: 257 (1932). Type: 'Grootmist near Springbok', *de Villiers* in SUG 8289 (BOL).

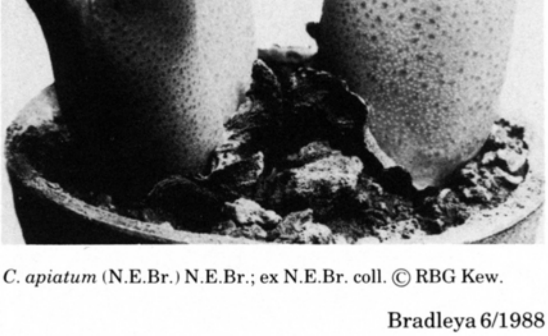
Rawe (in Cact. Succ. J. (US) 54(5):221-222. 1982) reduced this species, one of the first coastal Ovigeras, to form status under *C. auctum* N.E.Br., noting that size was the only real difference between these taxa. Size is a most unreliable character, however, and *C. approximatum* can be safely dispensed with, a conclusion reached earlier by Rawe himself in 1972, in a note written to M. Kimnach. Its ultimate resting place is in question, as *C. auctum* itself will probably be merged with *C. ovigerum* Schwantes.

*C. archeri* Lavis in Bolus, Notes on Mesemb. 2:378 (1933); Bolus, ibid. 3:146 (1939). Type: 'Near Montagu' *J. Archer* 613 (BOL).

This is one of several species reported from the 'Montagu' area. At the Bolus Herbarium, Archer's specimen cohabits with specimens collected by M. Glickman near Baden, NW of Montagu. These plants show not only the reported 'wine-red', but also yellow flowers. Intrigued by this, I recently visited Baden and found a small colony of very old plants which showed unusual variability; some resembled *C. piluliforme* (N.E.Br.) N.E.Br. (which has wine-red petals), other plants—much larger, differing in pattern and epidermal colour as well—suggested *C. muirii* N.E.Br. or even *C. placitum* N.E.Br. It was interesting that the plants occurred on sandstone, rather than the shale often associated with the other Little Karoo species.

Lavis distinguished her new species from *C. advenum* by its larger bodies and 'translucent' appearance, and Bolus noted that it was 'quite distinct' from all its neighbours. Size is an unreliable trait, however, and as for the translucence, many species acquire this as they approach dormancy—the epidermis has the look of grease paper! More research is necessary in the western Little Karoo before the status of *C. archeri* can be determined. I know of several populations which show introgression in this area and suggest that *C. archeri* might be one of these.

*C. archeri* var. *stayneri* L. Bolus in J. S. Afr. Bot. 31(2):171 (1965). Type: 'Petrusfontein, 14 miles northeast of Montagu', *F. J. Stayner* in KG 823/59 (BOL). In 1982 Rawe (in Cact. Succ. J. (US) 54(4):167,169) reduced this taxon to synonymy under *C. muirii* N.E.Br., with which its whitish flowers agree. At least one other interpretation is possible, however; the description matches that of Bolus's *C. longitubum,* reported from Avondrus, some 40km north of Montagu. The status of *C. longitubum* itself is problematic; it is another of the introgressing populations which are still poorly understood. It should be noted that Petrusfontein is not on maps available to me; did Stayner mean Pietersfontein, which is c. 12 miles *northwest* of Montagu?



*C. apiatum* (N.E.Br.) N.E.Br.; ex N.E.Br. coll. © RBG Kew.

*C. areolatum* Littlewood in J. S. Afr. Bot. 29(3):139,141 (1963). Type: '18 miles north of Kamieskroon', *R. C. Littlewood* in KG 707/59 (BOL).

This newcomer to the pellucidum pack has some interesting traits: extremely small bodies, and relatively opaque 'windows' which have a honeycomb-like appearance, to use Littlewood's simile. The ciliate fissure is another peculiarity, though this is also seen in colonies of *C. pellucidum* Schwantes which border the type locality. A recent exploration of the farm Silverfontein, a few kilometres northeast of Littlewood's spot, yielded a small colony referable to *C. areolatum* (*SH* 50/86). The plants lacked only the reddish points mentioned in the description; such idiosyncracies can be remarkably localized. All the evidence I have seen suggests that *C. areolatum*, and the much older *C. terricolor* Tischer, grade into *C. pellucidum;* the flowers of these three are indistinguishable. If we attempt to accord taxonomic status to these, we will need even more names, because *C. pellucidum* abounds in local variants throughout its wide range.

The *'C. areolatum'* presently represented in horticulture is from Rawe's collection 20 miles *south* of Kamieskroon, it should be noted. These plants are very glossy, with non-ciliate fissures and a tendency to pink flowers. Only in their relatively small size do they suggest the 'species' discussed here. They are much closer to *C. lilianum*, another variant of *C. pellucidum*, also described by Littlewood.

*C. asperulum* L. Bolus, Notes on Mesemb. 3:306 (1958). Type: '5 miles north of Wallekraal', *H. Hall* in NBG 374/54 (BOL).

This was one of a spate of Bolus bilobes from the Soebatsfontein-Wallekraal area. Rawe (in Kakt. and. Sukk. 20(5):88-89. 1969) sunk it into *C. lavisianum* L. Bolus, though *C. simplum* N.E.Br., the oldest name for a Soebatsfontein bilobe, would have been the better choice. All of these should be merged into *C. bilobum*, which frequently shows the rough-textured epidermis described by Bolus for *C. asperulum*.

C. asperulum var. *brevistylum* L. Bolus, Notes on Mesemb. 3:306 (1958). Type: '5 miles north of Wallekraal' *H. Hall* in NBG 374/54a (BOL). This is a minor variant of *C. asperulum* named for its smaller overall dimensions, and for other small differences (shorter 'styles') which do not depart from the pattern of variability shown by *C. bilobum*. The footnote to Bolus's description, referring to a 'transparent waxy covering', is quite curious, however. Bilobes do have a wax layer, but it rarely flakes off in the manner of e.g. *Glottiphyllum regium* N.E.Br., and is usually invisible.

*C. assimile* N.E.Br. in Gard.Chron. 78:451 (1925); Labarre, Mesembryanthema, 141, pl.40 (1931); *Mesembryanthemum assimile* N.E.Br. in J. Linn. Soc. 45:92 (1920). Type: Locality and collector unknown; photograph annotated by N. E. Brown (K).

This plant was familiar to Schwantes, who likened it to *C. scitulum* N.E.Br. in his book 'Flowering Stones and Mid-day Flowers'. Both species were described from single clones, which inevitably caused Brown to exaggerate their idiosyncracies. To me the photo, however, strongly suggests *C. ficiforme* (Haw.) N.E.Br. in one of its many forms, an opinion shared by L. Bolus and expressed in a letter to Littlewood (June 1963). If any reader has a piece of Brown's 'clonotype', I would be very glad to see it.

*C. assimile* N.E.Br.; photo of type ex N.E.Br. coll. © RBG Kew.

**C. astylum** L. Bolus in J. S. Afr. Bot. 29:135 (1963) and Notes on Mesemb. 3:205, pl.42, fig.B (1950) (as *C. pellucidum*). Type: 'Near Vanrhynsdorp', *P. Ross Frames* (BOL 24116).

Sect. PELLUCIDA. Plant caespitose; tunic pale brown, finely wrinkled, glossy on the inner surface, persistent; body oblong to obovate, convex on the upper surface, 7-12×7-9×5-7mm; epidermis deep brownish green to reddish, very finely pitted and 'shingled', marked with concentric pigmented bands at the apex; fissure short, ciliate. Flower diurnal, scentless; calyx-tube 2-3mm, 4-lobed; corolla-tube 8-12mm, petals 5-12mm, rose-pink, inner petals (filamentous staminodes) short, crowded, whitish-pink, occluding the tube; stamens entirely concealed, 3-5mm; stigmas 4, extremely short, free. Capsule 4-locular; seeds very numerous, 0.45mm.

This species was illustrated long before it was christened. The 1950 plate shows a beautiful example of the Frames collection, as *C. pellucidum* N.E.Br. Bolus mentioned that its rose-pink petals and short fissure were unusual, but at the time she defined *C. pellucidum* in the broadest terms. In 1952 Tischer (in Kakt. and. Sukk. 3:19) queried the name given to plate 42 fig. B, suggesting that the painting bore a resemblance to his *C. cupreatum* but rejecting its inclusion in that species on grounds of petal colour and geography. (He believed, erroneously, that *C. cupreatum* occurred in the area between Gamoep and Namies, and that the species was exclusively white-flowered.)

In 1963, stimulated by Tischer's arguments and by Littlewood's recent collections of pellucid species, Bolus published BOL 24116 as *C. astylum*. Since absence of a 'style' is common among members of sect. *Pellucida*, the epithet is not

*C. astylum* L. Bolus, ex Brakfontein, Bushmanland.

specially relevant, but the species is nonetheless distinct. The plants have a truncate, finely wrinkled upper surface, with a peculiar marbled pattern. The floral structure is particularly odd; it suggests both *C. minutum* (Haw.) N.E.Br. and *C. koubergense* L. Bolus.

Two collections subsequent to Frames's should be recorded here. In 1962 Stayner discovered a colony 56km west of Loeriesfontein [actually c. 30km northwest] (KG 1313/62), and in 1968 Rawe discovered similar plants 4 miles south of Brakfontein, southwest of Kliprand (*RR* 964). Tischer proposed the name *'C. rawei'* for the latter collection, but never published it. Comparison of dried material of *RR* 964 with the *C. astylum* material at the Bolus Herbarium suggests that Tischer's restraint was wise. Probably, Frames's locality was near the district boundary, and not the town, of Vanrhynsdorp, in which case the modern localities are not far from the original one as cited.

*C. auctum* N.E.Br. in Cact. Succ. J. (US) 2(9):429, with fig. (1931); Rawe in ibid. 54(5):221-222, fig.15 (1982). Type: 'Little Namaqualand', *M. Brown* 1055, no specimen preserved; pencil sketch by N. E. Brown (K).

This was described without locality, but the collection number suggests that Maughan Brown may have been in the vicinity of Kleinzee or Grootmist. Plants close to *C. auctum* are common there; they are nearly globose, immaculate, shining light green, and weakly lobed. Note that N. E. Brown's figure (published with the description) shows a definite keel. However, the lobing and the acuteness of the keel can change considerably in cultivation. *C. auctum* is separated from the older *C. ovigerum* Schwantes by a few tenous characters; they share a glabrous epidermis and rather short chrome-yellow petals. It is curious that many of the coastal 'Ovigeras' have white petals, unlike the larger inland bilobes, which very rarely show such variation.

**C. auriflorum** Tischer in Zeitschr. Sukk.-Kunde 3(7):122 (1927). Type: 'Near Steinkopf', collector unknown [probably G. Meyer], contemporaneous material under SUG 8898 (BOL); Tischer's 'clonotype' preserved at NBG, and painted by N. E. Brown (K).

Sect. 'COSTATA' subsect. 'VERRUCOSA'. Plant densely caespitose; tunic yellowish-brown, persistent; bodies barrel-shaped to cylindric, 10-15×4-6×4-5mm; epidermis dark green to reddish-green, glabrous, shining, immaculate or sparsely dotted, minutely pitted, conspicuously covered with white raphides; fissure 1-1.5mm, surrounded by a dark green band. Flowers diurnal; calyx-tube 4-lobed, 2-3mm, greenish; corolla-tube 8-12mm, petals 6-8mm, golden-yellow; stamens numerous, exserted beyond the mouth of the tube; 'style' 7-15mm, stigmas 4, 0.5-1.5mm. Capsule 4-locular; seeds yellowish-brown, 0.50-0.60mm.

A distinct and peculiar little species, which has been observed at only a few localities. The cited origin 'near Steinkopf' is almost certainly an error or an exaggeration. Rev. G. Meyer, the probable first collector, served the Komaggas mission before moving to Steinkopf, and the species does indeed occur near Komaggas—there is a small colony on quartzite rocks at Templekloof—just above the town. Another colony occurs at Koringhuis, nearer Springbok; these plants have a much darker epidermis than the Komaggas plants. Rawe's *C. turbiniforme*, found in the Spektakel Pass, northeast of Komaggas, is very close to *C. auriflorum*, and probably represents an outlying truncate form of it.

There is an apparent natural hybrid between *C. auriflorum* and *C. velutinum* Schwantes, another Komaggas species. The plant has the epidermal sheen of *C. auriflorum*, the pubescence of *C. velutinum*, and the orange petals usually produced in such yellow-purple crosses.

*C. australe* L. Bolus, Notes on Mesemb. 3:317 (1958). Type: '20 miles west of Vanrhynsdorp', *J. Luckhoff* in SUG 10153 (BOL).

This was named for its locality; *C. australe* would certainly be the southernmost *'Ovigera'* if the locality were correct, but as Rawe noted, it is quite implausible. In a letter to Littlewood (1963), Tischer had the same reaction. Bolus read the letter and added the firm comment: 'Given by Dr. Luckhoff'. At any rate, 20 miles west of Vanrhynsdorp puts us near the coast, and *C. australe*, on the sheet, does resemble the coastal 'Ovigeras' very closely, so Rawe's reduction to *C. auctum* makes sense (Rawe in Cact. Succ. J. (US) 54(5):221-222. 1982). Note that *C. australe* never entered cultivation.

*C. avenantii* L. Bolus in J. S. Afr. Bot. 31(3):237-238 (1965). Type: 'Die Hoop, Richtersveld', *H. Hall* 1299 in NBG 95/58 (BOL).

This is known from just two collections: Hall's, which was distributed to a few English collectors, and Rawe's (*RR* 596, Little Helskloof, some 70km southeast of Avenant's farm Die Hoop). Hall's material is difficult to distinguish from *C. wettsteinii* (A. Berger) N.E.Br., but the Rawe material—which was widely distributed, through the ASPS—has some floral peculiarities: a very long corolla tube, white petals, and deep red filaments. However, *C. wettsteinii* and its ally, *C. gratum* (N.E.Br.) N.E.Br., vary considerably in tube length, and in petal and filament colour. Vegetatively, the two collections mentioned here are close; rather small for *C. wettsteinii*, but not otherwise distinctive.

**C. barbatum** L. Bolus, Notes on Mesemb. 3:302-303 (1958); Rawe in Kakt. and. Sukk. 22(7):127 (1971). Type: 'Augrabies', *H. Hall* in NBG 239/56 (BOL).

Sect. WETTSTEINIA? Plant caespitose, internodes short; tunic tan-brown, shining, parchment-like, persistent; bodies clavate, 12-15×4-6×4-6mm, apex truncate; epidermis deep green, nearly immaculate, irregularly covered at the apex with fine papillae; fissure short, deepened, 'densely barbed'. Flowers diurnal; calyx-tube membranous, 7-8mm, 4-lobed; corolla-tube 9-12mm, unusually narrow, petals c. 20-22, 2-3-seriate, rose-purple; stamens 22-25, barely exserted from the tube; 'style' c. 9mm, stigmas 4, very short. Capsule 4-locular; seeds not available (only one clone is known).

A remarkable number of purple-flowered conophytums have been reported from Augrabies: *C. barbatum*, *C. marlothii*

*C. barbatum* L. Bolus, ex Augrabies.

N.E.Br., *C. obscurum* N.E.Br., *C. wettsteinii* (A. Berger) N.E.Br., and *C. intrepidum* L. Bolus. *C. barbatum* can be distinguished from all of these by its deep green, nearly immaculate, finely pubesecent epidermis. Rawe conjectured that it was a dwarf form of *C. intrepidum*, which grows above it, toward the summit. However, in several respects the two species are quite distinct: *C. barbatum* forms small cushions, and bears its slender-tubed flowers in autumn; *C. intrepidum* forms dense, flat mats, its epidermis is densely papillate, and it flowers in early summer. Note that after 25 years in cultivation, the two species retain their peculiarities, which include distinct resting sheaths: *C. barbatum* produces a tough, thickened sheath, unlike the thin friable sheath of its neighbour. Hall's collection is apparently unique, though Augrabies has long attracted collectors.

*C. barkerae* L. Bolus, Notes of Mesemb. 3:312 (1958). Type: 'Soebatsfontein', *W. F. Barker* in NBG 282/45 (BOL).

In 1969 Rawe (in Kakt. and. Sukk. 20(5):88-89) sunk a quartet of Bolus bilobes: *C. asperulum, C. barkerae, C. inclusum* and *C. indefinitum*, into an older species, *C. lavisianum* L. Bolus. All four dated from 1958 and came from the Soebatsfontein-Wallekraal area. Their sinking was fully justified, though Rawe would have chosen a still-older name, *C. simplum* N.E.Br., had he known the true provenance of that species. It is a pity that Bolus employed Barker's name in vain, for Miss Barker found a really distinctive species in 1950, the so-called 'red form' of *C. roodiae* N.E.Br., which would have made a splendid '*C. barkerae*'.

*C. batesii* N.E.Br. in Gard. Chron. 78:468 (1925). Type: Locality and collector unknown (K).

This is one of many 'species' in subsection *'Picta'* published without locality. Recent finds from the Laingsburg area correspond well to *C. batesii*, but they also correspond to several other Brown Pictas, including *C. petraeum, C. polulum* and *C. pictum* itself, *C. batesii* being the plainest of the lot. Its gaping fissure ('lips rising to the top') gives it a superficial distinction, but this feature can be seen in other Pictas. In any case, *C. batesii* is known from only a single clone, perpetuating a uniform image and behaviour. (Seeds of '*C. batesii*' do appear in the trade now and then, courtesy of promiscuous moths.)

**C. bicarinatum** L. Bolus, Notes on Mesemb. 3:152 (1939). Type: 'Near Ceres', *Els* in NBG 1862/37 (BOL).

Sect. MINUSCULA. Plant caespitose, forming dense clusters, internodes very short; tunic papery, brown, persistent towards the base; bodies obovate, 12-25×8-15×5-10mm, lobe tips free, acute, doubly or triply keeled; epidermis appearing glabrous but covered with very minute papillae, glaucous green to reddish, heavily marked with purple lines. Flowers diurnal, occasionally paired (two per body); calyx-tube 8-10mm, 4-5-lobed; corolla-tube 10-12mm, whitish to pale yellow, petals 2-3-seriate, inner white, acute, 2-5mm, outer magenta, 10-30mm; stamens 3-4-seriate, included within the tube; stigmas 4-5, 1.5-3mm, united for one-third their length. Capsule 4-5-locular; seeds 0.60mm.

*C. bicarinatum* is presently known from two kloofs at the very edge of the Swartruggens, some 60km NE of Ceres. With its keeled, bilobed bodies and its interlacing reddish lines, *C. bicarinatum* is very close to various forms *C. luckhoffii* Lavis, distinguished mainly by its enormous size and its lighter green colour. Polyploidy has often been suspected for this giant among Minusculas, but *C. bicarinatum* has the same count as *C. luckhoffii*: 2n=18.

The species has frequently been collected at Skitterykloof; the material in cultivation shows surprisingly little variation. Recently, Mitchell discovered a second colony further south, in similar terrain. In 1987 P. V. Bruyns discovered plants which are probably referable to *C. bicarinatum* near the Tra-tra river, east of Wuppertal (*PVB* 2627). This is surprisingly far out for the species, and indeed the plants are not 'typical': the epidermis has a heavy coat of long papillae, linking the plants with the Wuppertal forms of *C. leipoldtii* N.E.Br.

**C. bilobum** (Marloth) N.E.Br. in Gard. Chron. 72:83 (1922); *Mesembryanthemum bilobum* Marloth in Trans. S. Afr. Phil. Soc. 18(1):44, pl.5, fig.2 (1907). Type: 'Little Namaqualand', *R. Marloth* 3750 (not preserved). Lectotype (designated here): Marloth, loc. cit. pl.5, fig.2 (1907).

Sect. BILOBA. Plant caespitose, stemless to caulescent in age; tunic brown, papery to leathery, persistent, smooth to asperulous, immaculate or maculate from tanniniferous idioblasts; bodies (10-)15-50(-70)×10-28×10-15mm or larger in cultivation, cuneate-oblong, laterally compressed to subcylindric, free leaf tips 3-20(-25!)mm, terete to ovate in cross-section, often keeled, keel margins often reddish to deep purple; epidermis whitish-green, yellow-green, to deep blue-green, glossy to velvety to harshly asperulous, immaculate to heavily maculate, partially fenestrate below the fissure zone; fissure ciliate, gaping or not. Flowers diurnal, scentless, large; calyx-tube 3-10mm, herbaceous, with 4-7 lobes; corolla-tube exceeding the calyx-tube, petals 24-60, 10-25mm, 2-4-seriate, pale yellow to deep golden-yellow tipped reddish, occasionally ivory to pure white; stamens numerous, 4-6-seriate, 4-15mm; 'style' 1-10mm, stigmas 4-7, equalling the stamens or exserted beyond them. Capsule woody, deep brown to maroon or blackish, persistent, 4-7-locular; seeds 0.60-0.85mm.

This has had as many interpretations as Hamlet. It is the oldest member—I may soon say, the only member—of the group familiarly known as the 'bilobes', those large-bodied, yellow-flowered, rabbit-eared species in which the fusion of the leaves is incomplete. Marloth's *M. bilobum* had rounded, short lobes, with a pale bluish-green, minutely papillate epidermis; Brown's *C. bilobum*, which was sent to him from the 'plains between Stinkfontein and Chubiessis' by Pearson (no. 6203), had slightly longer lobes, with a yellowish-green, glabrous epidermis. Between these and, for example, Brown's *C. apiculatum*, with its 'waxen' epidermis and long pointed lobes, there is an enormous range of forms, which have acquired some 100 names. Their delimitation is quite impossible, so fluid is the shifting from form to form. There *is* some regional pattern to bilobe variation—an unlabelled plant can often be placed within 20km—but some of the forms have taken surprisingly large leaps.

In 1926 Schwantes proposed the separation of the then-known bilobes into a new genus, *Derenbergia*, which was quickly demolished by Brown, who pointed out that one of the determining characters, the absence of bracts, was entirely false. The bracts in *C. bilobum* are simply well-concealed, as they surround the base of the pedicel, which is deeply buried within the plant body. It is nonetheless interesting to note that most collectors spurn the bilobes, hardly regarding them as conophytums, unlike Brown, for whom they were the 'aristocrats' of the genus!

*C. bilobum* (Marloth) N.E.Br.; ex N.E.Br. coll. © RBG Kew.

*C. bilobum* (Marloth) N.E.Br. in habitat, Swartwater, Richtersveld.

**C. blandum** L. Bolus, Notes on Mesemb. 3:88 (1937) and ibid. 3:141, pl.21, fig.A (1939). Type: 'Geselskapbank', *P. van Heerde* (BOL 21967).

Plant caespitose, internodes very short; tunic whitish, thickened, tough, persistent; bodies oblong, bilobed, 17-30×10-15×6-10mm, leaf tips free, strongly keeled, apiculate; epidermis minutely and densely papillate, whitish-green, occasionally flushed with red, margins marked with pellucid dots at irregular intervals; fissure densely ciliate. Flower diurnal, very long-lasting, strongly scented (like *Lobularia maritima*), produced late in autumn; calyx-tube fleshy, greenish-white, 7-9mm, 6-lobed; corolla-tube 8-10mm, outer petals broadened, to 15mm, white or pale to rose pink, inner petals white, dense, filamentous; stamens partly exserted, 3-4-seriate, very numerous; 'style' absent, stigmas 6, 12-22mm. Capsule 6-locular, very pale, borne on an extremely persistent pedicel; seeds pale tan, 0.70mm.

A very distinct species from the Bushmanland, this has several peculiarities: a very pale epidermis, reminding one of *Ruschia dualis* (N.E.Br.) L. Bolus, honey-scented diurnal flowers with crowded, partly filamentous petals, and long, free stigmas. The remarkably tough pedicel and capsule, so close to *Herreanthus meyeri* Schwantes, are also unusual. The nearest alliance is apparently with the long-lost *C. semivestitum* L. Bolus, reported from Jakkalswater, southwest of Geselskapbank. (The bogus *C. semivestitum* common in European cultivation is a form of *C. blandum*, or possibly a hybrid involving that species.) It is particularly interesting to compare seedlings of *C. blandum* with those of *Herreanthus meyeri*. For the first two years, there is virtually no difference; both form sharply-keeled little bodies which sheathe completely. Later *Herreanthus* loses its sheathing ability—or acquires free leaves, depending upon one's point of view—while *C. blandum* continues to make sheaths. Another difference is the ciliate fissure of the latter, absent in the former. And yet both species have an apiculus at the leaf-tips, a highly unusual character.

In 1939 Bolus mentioned an affinity with her *C. regale*, which occurs further southwest, at Ratelpoort. *C. regale* is readily distinguished by its soft green bodies, which bear large windowed 'pustules' next to the fissure zone. The conophytums mentioned here form an interesting group of pink-flowered 'pseudo-bilobes'.

*C. bolusiae* Schwantes in Gartenwelt 33(2):25 (1929). Type: 'Between Vanrhynsdorp and Nuwerus', *M. Schlechter*, not known to have been preserved.

In 1956 Tischer (in Kakt. and. Sukk. 7(2):25-28) reduced this to synonymy under *C. fibuliforme* (Haw.) N.E.Br., a species of uncertain provenance, described briefly but cogently by Haworth. The reduction was plausible; the main puzzle here involves locality, for nothing resembling *C. bolusiae* has been found in the reported area for sixty years. It is extremely probable that Max Schlechter collected his plants at Augrabies, which harbours an extensive colony of *C. fibuliforme*, better known by its later name, *C. intrepidum* L. Bolus (1959). This supposition is strengthened by the fact that Schlechter lived close to Augrabies and knew it well. Perhaps he confused dormant plants of *C. bolusiae* with *C. pearsonii* N.E.Br., which does occur near Nuwerus.

There is no question that *C. bolusiae* is identical with *C. intrepidum*. Schwantes described his species without knowledge of its flower, but he gave a plant to Tischer, who flowered it in 1955 and later compared it with material of *C. intrepidum*. The plants had the same peculiar habit of flowering in early summer, and were identical in all other respects. Note that only one locality—Augrabies (c. 25km east of Port Nolloth)—is known for *C. intrepidum*.

*C. boreale* L. Bolus in J. S. Afr. Bot. 29(3):135 (1963); cf. idem, Notes on Mesemb. 3:205 (1950). Type: 'Between Kakamas and Augrabies Falls', *C. L. Leipoldt* 4414 (BOL).

*Leipoldt* 4414 was first mentioned by Bolus in the 1950 Notes, in the course of a discussion of *C. pellucidum* Schwantes. At the time, Bolus took that to be a highly variable species (and very rightly too!), but she later described as separate species three of the collections mentioned in 1950. *C. boreale* is the furthest out of the three, indeed Augrabies Falls (not to be confused with the Augrabies mentioned above) seems implausibly remote for a *Conophytum,* though not, perhaps, for (Subgenus) *Ophthalmophyllum;* the area lies well within the summer rainfall zone.

*C. boreale* has not been seen with certainty since Leipoldt's 1936 collection, though a recent report of a small 'mesemb' growing *in moss* near the Falls (which echoes Leipoldt's report) gives us some hope. I recently explored various granite formations between Kakamas and the Falls and learned that Leipoldt's brother surveyed the area c. 1935. It seems likely that Leipoldt's locality data is authentic—the terrain is suitable; probably he found a relict population.

*C. boreale* was described partly from dried material, and the description is incomplete and ambiguous. In the dried state, the window was not 'well seen', though its short lines, and all the floral details, strongly suggest *C. pellucidum.* Until its rediscovery, this is best left in limbo; I can only add that mossy rocks gather many conophytums but no ophthalmophyllums, in my experience.

*C. braunsii* Schwantes in Zeitschr. Sukk.-Kunde 3(9):178 (1928). Type: 'Vanrhynsdorp District', *H. Brauns* in SUG 8114; not preserved.

According to Tischer (in Kakt. and. Sukk. 7(6):93-94. 1956), this was identical with Brown's *C. pearsonii* var. *minor;* as imported, it was quite small (10×10mm). However, Tischer believed—as I do—that the variety was quite unnecessary, so he placed both it and *C. braunsii* in the synonymy of *C. pearsonii* N.E.Br.

The *C. ectypum* var. *'braunsii'* that circulates freely in England arises from a double corruption—of spelling (brownii), and of breeding (*C. ectypum* var. *brownii* (Tischer) Tischer × *C. ectypum* var. *tischleri* (Schwantes) Tischer, in all likelihood). This interesting mongrel has beautiful orange corollas and, not incidentally, closely resembles *C. marnierianum* Tischer & Jacobsen, which, like *C. braunsii,* was collected by a well-known entomologist. *C. marnierianum* is a natural hybrid (probably *C. bilobum* × *C. ectypum*) with an ill-fitting flower.

**C. breve** N.E.Br. in Gard. Chron. 78:468 (1925); Rawe in Cact. Succ. J. (US) 47(4): 183-187 (1975). Type: 'Near Steinkopf', *G. Meyer* in *Marloth* 6513 (K).

Sect. 'CATAPHRACTA'. Plant caespitose, internodes invisible to short; tunic pale to deep brown (not eggshell white), smooth, persistent; bodies obconic, truncate or weakly convex at the circular top, 8-15×8-12×8-11mm; epidermis glabrous, pale glaucous-green to whitish yellow-green (not pale blue), reddish toward the base, immaculate to densely maculate; fissure hairless, frequently dimpled at each end, often surrounded by a reddish ring, very short to (rarely) extending over most of top surface. Flowers nocturnal, powerfully scented; calyx-tube 2-4mm, 'rather stout', lobes 5-6, 2-3mm; corolla-tube not or shortly exceeding the calyx, petals sparse to numerous, 1.5-5mm; stamens 20-28, 2-5mm; 'style' absent or very short, stigmas (4-)5-6(-8), 0.5-1.5mm. Capsule (4-)5-6(-8)-locular, seeds 0.55-0.65mm.

In the original description, Brown mentioned that his new species was allied with *C. minutiflorum*(Schwantes) N.E.Br. He distinguished *C. breve* from *C. minutiflorum* (and from his *C. pageae* as well) by its indistinctly dotted bodies, stout calyx tube, uniformly exserted stamens, and prominent ovary top. He described the flower from dried material, and gave dimensions comparable with those of *C. minutiflorum,* which was somewhat misleading, as that species has peculiarly depauperate flowers. Tischer thought that *C. breve* was 'merely a form' of *C. minutiflorum,* with longer petals, and Rawe put it the other way round, with his combination *C. breve* var. *minutiflorum* (see below).

The problem of distinguishing *C. breve* from the older *C. pageae* is considerable; the species have very often been confused. As originally described, *C. pageae* was the larger of the two. Why Rawe reversed this in his 1975 key (which is handy if artificial) is not clear, though he was probably following Tischer. For the moment, I retain both names, *sensu* Rawe, pending a regional resolution of the conflict.

Meyer almost certainly collected *C. breve* near the Geelvlei plateau, northwest of Steinkopf. *Marloth* 6512, which became Brown's *C. tantillum,* is known only from the plateau, and it is possible that Meyer collected the two species at the same time; they socialize.

*C. breve* var. *minor* L. Bolus, Notes on Mesemb. 3:303 (1958). Type: 'Namaqualand, Alexander Bay', *H. Hall* in NBG 620/512 [sic] (BOL). In 1975 Rawe (in Cact. Succ. J. (US) 47(4):185) reduced this to synonymy under *C. pageae* (N.E.Br.) N.E.Br., as its diminutive dimensions suggested *C. pageae* (*sensu* Rawe in 1975!). What puzzles me, however, is the locality data; from Alexander Bay I know only *C. graessneri* Schwantes. When Hall entered 620/52 in the NBG register (9/9/52, along with 22 other Conophytums collected over a wide area of Namaqualand), he provided a tentative (but shrewd) identification: *C. saxetanum* (N.E.Br.) N.E.Br. (arguably equal to *C. graessneri*). Hall could not possibly have confused a *'Cataphracta'* species with a *Saxetana;* therefore, a later slip must have occurred.

*C. breve* var. *minutiflorum* (Schwantes) Rawe in Cact. Succ. J. (US) 47(4):184 (1975); *C. minutiflorum* (Schwantes) N.E.Br. in Gard. Chron. 78:484 (19 Dec. 1925); *Mesembryanthemum calculus minutiflorum* Schwantes in Monatsschr. Kakt.-Kunde 30(6):81 (1920); *M. minutiflorum* (Schwantes) Schwantes in ibid. 32(6):81-82 (1922). Type: 'Near O'okiep in the Kamiesberg range', *R. Marloth* 11950, probably not preserved; 'clonotype' is at HBG. Schwantes's original placement of this taxon is interesting: it was the second *'Cataphracta'* he encountered, and he recognized the essential similarities which bind this group together. The differences—involving foliar habits (shape and colour) and small floral variations—can be tied to geography to some extent. Plants corresponding to *C. minutiflorum* (mid-size, truncate, immaculate bodies, small corollas) can be observed in the area between Springbok and Steinkopf, but they venture much further, in several directions. In my view, taxonomic recognition for floral depauperants is unnecessary; these are common throughout the genus.

*C. breve* var. *vanzylii* (Lavis) Rawe in Cact. Succ. J. (US) 47(4):184 (1975); *C. vanzylii* Lavis in Bolus, Notes on Mesemb. 2:267-268 (1931). Type: 'Pofadder', *G. van Zyl.* (Also, *C. vanzylii* forma, L. Bolus in J. S. Afr. Bot. 29(2):47 (1963)—a pink-flowered variant.) Rawe's combination is invalid under Art. 33, and I am leaving it that way. Lavis herself noted a closeness to *C. breve,* but a connection with *C. calculus* (A. Berger) N.E.Br. is also evident; from the latter, *C. vanzylii* is geographically well-separated. Its traits include a pinkish-tan epidermis (sometimes a remarkable pale blue), an occasional reddening of the fissure zone, and, rarely, pink corollas! Typically, the bodies are globose, as in *C. calculus*—but they are generally much smaller. Flatter forms are also seen, and I despair of separating these from *C. subrisum* N.E.Br., which is typically truncate. That slightly despairing adage: mesembs are identified by their *locality,* is especially apt here.

*C. brevilineatum* Tischer in Kakt. and. Sukk. 10(7):102 (1959). Type: 'Ceres Division?'. *W. Triebner* 16/143 (SSM).

On the evidence presented by Tischer, this almost certainly came from the Ceres Karoo, though he later identified plants from north of Bitterfontein (Bolus's *C. stenandrum*) as this species, which would give *C. brevilineatum* a most disjunct and unlikely distribution. A collection from Patatsrivier (*van Breda,* KG 269/76) matches Tischer's photograph uncannily well; Patatsrivier is located between the Ceres and the Little Karoos, which confirms Tischer's information.

In 1975 Rawe (in Kakt. and. Sukk. 26(9):199-200) reduced *C. brevilineatum* to synonymy under *C. ceresianum* L. Bolus. Given a very broad definition of that species, the reduction makes sense, but it should be noted that the Patatsrivier plants show multiple influences: *C. ceresianum sensu stricto, C. pictum* (N.E.Br.) N.E.Br., and *C. polulum* N.E.Br.; these occur to the northwest, east, and southwest of Patatsrivier. My recent collections north of Matjiesfontein, Little Karoo, suggest introgression between *C. ceresianum* and *C. pictum,* and some of them match *C. brevilineatum.*

*C. brevipes* L. Bolus in J. S. Afr. Bot. 30(4):233-234 (1964). Type: 'Anenous Pass', *H. Hall* 2769 in NBG 248/64 (BOL).

This came from the same area as the older but equally superfluous *C. circumpunctatum* Schick & Tischer. Neither is sufficiently distinct from *C. wettsteinii* (A. Berger) N.E.Br.; *C. brevipes* was only notable for its short pedicel. Such brevity is common in *C. wettsteinii*, especially when the plants are grown in bright situations.

*C. brevipetalum* Lavis in Bolus, Notes on Mesemb. 2:290 (1931); Bolus, ibid. 3:145, pl.23, fig.B (1939); Rawe in Cact. Succ. J. (US) 52(6):283 (1980). Type: 'Probably Little Karoo', *R. Morgan* in NBG 768/30 (BOL).

In her description Lavis mentioned the close affinity of this taxon with *C. piluliforme* (N.E.Br.) N.E.Br. Bolus and Rawe also noted the similarities while nonetheless maintaining the taxon. Rawe placed it as a variety of *C. piluliforme*, though the slightly shorter petals seems an inadequate distinction, and the 'glabrous' epidermis hardly differs from the (very) minutely papillate epidermis of Brown's species. (And in fact both taxa are papillate, it is simply a question of papillae length.) The slightly domed bodies of *C. brevipetalum* to provide a trait for 'micro-identification', and suggest the forms of *C. piluliforme* common north of Montagu. In a letter to Littlewood, Tischer suggested that *C. brevipetalum* was identical with *C. piluliforme*, with which I agree.

*C. brevisectum* L. Bolus in J. S. Afr. Bot. 30(4):232 (1964). Type: 'Nakamas [sic], 15 miles east of Port Nolloth and south toward Grootmist', *P. van Heerde* (BOL 27615).

This was named for a minute distinction: the unusually short calyx segments (sepals). I have seen many specimens from Nakanas; Rawe distributed these widely as *'C. brevisectum-stylosum'* (*RR* 1136), and am unable to distinguish these from *C. stylosum* (N.E.Br.) Tischer. For that matter, I am unable to distinguish *C. stylosum* from *C. bilobum*, or rather, am unwilling to take the differentia seriously. The interesting thing about *C. brevisectum* is the fact that so ordinary a bilobe occurs so close to the coast.

*C. brevitubum* Lavis in Bolus, Notes on Mesemb. 2:292 (1931); *C. truncatum* var. *brevitubum* (Lavis) Tischer in Kakt. and. Sukk. 19(6):115-118 (1968); Rawe in Cact. Succ. J. (US) 54(4):166 (1982). Type: 'At the entrance to Seven Week's Poort', *J. Luckhoff* 1 (BOL).

In 1982 Rawe retained Tischer's 1968 combination, *C. truncatum* var. *brevitubum*, regarding this as an isolated and distinct variety. I agree about the isolation, though not entirely convinced about the distinctiveness, because plants similar to typical 'brevitubums' are found at other *C. truncatum* localities, having the proper reduced bodies and greyed-pink corollas.

*C. brownii* Tischer in Möll. Deuts. Gärtnerz. 41:257-258 (1926); *C. ectypum* var. *brownii* (Tischer) Tischer in Kakt. and. Sukk. 4(2):30 (1953); Rawe in Cact. Succ. J. (US) 47(3):129-130 (1975). Type: 'Near Steinkopf', *G. Meyer* (NBG).

Brown (in Gard. Chron. 81:32. 1927) regarded this as a 'mere form' of *C. ectypum* N.E.Br., with a few more lines; Tischer, however, later held that it deserved at 'least' varietal status, and published the combination *C. ectypum* var. *brownii* in 1953. He distinguished the variety by its crowded conspicuous lines and its rich bronze colour. He might also have mentioned its well-developed keel, a feature seen in the 'clonotype', which is still in cultivation. *C. ectypum*, however, is such a widespread and variable species that I agree with Brown's view; Tischer was emphasizing individual, not specific, traits (q.v. *C. chloratum*).

Rawe's statement that typical *C. ectypum* var. *brownii* is found only at Ratelpoort (south of Steinkopf) needs some qualification. Other colonies, at Eenriet and especially at Concordia, have much the same phenotype, though they lack the heavily sulcate resting sheath of the Ratelpoort plants. Incidentally, those plants have not only the 'deep rose' corollas mentioned by Rawe, but also paler pink, yellow and (very rarely) orange. The keeled form of *C. ectypum* is most common west of Steinkopf, at Anenous Pass; these plants have been circulating as *C. ectypum* var. *limbatum* (N.E.Br.) Tischer, but they strongly suggest the clonotype of *C. brownii*, especially in their rich epidermal colours.

**C. burgeri** L. Bolus in J. S. Afr. Bot. 33(4):305 (1967); cf. also idem, Notes on Mesemb. 2:204 pl.42, fig.A (1950) (as *C. pillansii*). Type: 'Aggenys', *H. C. Kennedy* in NBG 339/65 (BOL).

Subg. OPHTHALMOPHYLLUM. Plant single or rarely caespitose (in cultivation); tunic whitish, squamous, persisting in patches; body globose, broadened toward the base, 13-25×20-25×20-25mm; epidermal cells remarkably convex and translucent, pale grey-green to deep purple-red; fissure narrow, inconspicuous, 2-4mm. Flower diurnal, opening in the late afternoon, sweetly scented (like *C. fulleri*); calyx-tube 4-5mm, 6-lobed, greenish-white, thin; corolla-tube slightly exceeding the calyx-tube, petals 7-18mm, purple-rose; stigmas 6, 10-14mm. Capsule 6-locular; seeds extraordinarily minute, 0.25-0.35mm.

An astonishing species. In particular, its strange, continuously-flaking sheath, its complete translucence, the perfect fusion of its leaves, and its minute seeds, nearly as small as those of *Dinteranthus*, set it apart. Bolus apparently decided to place it in *Conophytum* rather than *Ophthalmophyllum* because of its free corolla-tube; otherwise its floral and capsule structures strongly suggest (subgenus) *Ophthalmophyllum*. Its seedling structure—resembling a raspberry!—is unduplicated in either group. I have considered the possibility of a separate genus for this oddity, but logic would then dictate other segregates; *C. concavum* L. Bolus and *C. pillansii* Lavis are almost as weird, and equally difficult to place infragenerically.

Material from Achenhuis, Bushmanland (*R. Primos*, NBG 1361/36), painted by B. O. Carter and shown in the 1950 Notes, is certainly *C. burgeri* or a variant thereof, though it was determined, with reservations, as *C. pillansii*. The plants died soon after their introduction, otherwise Bolus would surely have realized that this *'C. pillansii'* had little to do with the well-known Knersvlakte species. Note that Achenhuis is an older spelling of Aggenys (now modernized to Aggeneys!); the pronunciations are the same. The Primos material differed from Kennedy's (which is remarkably uniform) in at least one respect: the concave fissure zone. H. Horn collected similar material c. 1965, but he kept the locality a secret; I mention this collection as evidence that *C. burgeri* is not entirely *sui generis*.

**C. calculus** (A. Berger) N.E.Br. in Gard. Chron. 70:231 (1922); *Mesembryanthemum calculus* A. Berger, Mesemb. Portulac. 289 (1908). Type: 'Hardeveld', *R. Marloth* 4573 (preserved?).

Sect. 'CATAPHRACTA'. Plant caespitos, internodes invisible; tunic smooth, pale brown, persistent, blackening in age; bodies globose, 15-35×10-30×10-30mm, remarkably firm in substance; epidermis entirely glabrous, immaculate, chalky-green to pale yellowish-green; fissure 3-5mm, non-papillate. Flower

*C. calculus* (A. Berger) N.E.Br.; ex N.E.Br. coll. © RBG Kew.

nocturnal, heavily scented (like cloves); calyx-tube 4-7mm, 5-6-lobed; corolla-tube 5-10mm, petals filiform, 6-22mm, pale yellow to deep orange; stamens exserted, numerous; stigmas 5-6, 1-2mm. Capsule 5-6-locular; seeds numerous, light brown, 0.75-0.80mm.

The oldest member of its section, this is undoubtedly distinct. Its globose, pebble-like bodies, completely unmarked, cannot be confused with those of any other species, except, perhaps, *C. vanzylii* Lavis. Those species are well-separated geographically: *C. calculus* is a denizen of the Knersvlakte; *C. vanzylii* occurs far to the northeast, in the Bushmanland, and it differs in its epidermal colours and markings.

*C. calculus* var. *komkansicum* (L. Bolus) Rawe in Kakt. and. Sukk. 21(10):199 (1970); *C. komkansicum* L. Bolus in J. S. Afr. Bot. 28(3):221 (1962). Type: 'Komkans', *H. Hall* in NBG 898/54 (BOL). *C. komkansicum* L. Bolus was reduced to varietal status under *C. calculus* by Rawe, who distinguished it from the type variety by its 'barrel-shaped' bodies. I regard it simply as a northwestern outlier of *C. calculus,* especially as there are intermediate forms between Komkans and Nuwerus.

*C. calculus* var. *protusum* L. Bolus, Notes on Mesemb. 3:189,191, pl.32, fig.B (1950). Type: 'Komkans, 18 miles south of Bitterfontein', *V. S. Peers* (BOL 24077). Bolus distinguished this from *C. calculus* var. *calculus* by its smaller size and protruding fissure lips. The colour plate shows clearly that the fissure is outlined in red, but Bolus makes no mention of this detail, not seen in typical *C. calculus* though common in *C. pageae* (N.E.Br.) N.E.Br., *C. breve* N.E.Br., and *C. subrisum* N.E.Br. Mitchell and I recently rediscovered *C. calculus* var. *protusum* at localities south of Komkans (Koekenaap and Booisberg); the plants were highly variable as regards fissure protrusion. Many of the plants were indistinguishable from typical *C. subrisum,* and none suggested *C. calculus* to us, though it is possible that the Komkans 'protrusums' have a connection with the former *C. komkansicum.* Note that a remarkable form of *C. pageae,* with deeply red fissures (and pink corollas) occurs at Komkans as well.

*C. calitzdorpense* L. Bolus (*'calitzdorpensis'*), Notes on Mesemb. 3:21-22 (July 1936) and ibid. 3:147, pl.23, fig.I (1939). Type: 'Calitzdorp', *J. Luckhoff* in SUG 10151 (BOL).

In her 1939 Notes, Bolus proposed that this might be merely a 'form' of *C. muirii* N.E.Br. Rawe (in Cact. Succ. J. (US) 54(4):167,169. 1982), however, saw it as a stable and very small relative of *C. truncatum* (Thunb.) N.E.Br. It is partly a question of looking east or west. I see it as a dwarf form of *C. truncatum,* with an affinity to the *C. truncatum* var. *brevitubum* (Lavis) Rawe population found some 30km to the northwest of Calitzdorp.

Tischer independently published Bolus's epithet two months after her, based on the same collection (Cact. Succ. J. Gr. Brit. 5(1):13. Sept. 1936).

*C. candidum* L. Bolus, Notes on Mesemb. 3:267 (1954); *C. ecarinatum* var. *candidum* (L. Bolus) Rawe in Cact. Succ. J. (US) 54(5):219,222 (1982). Type: '20 miles south of Port Nolloth', *H. Hall* in NBG 736/53 (BOL).

In 1953 Hall discovered a gaggle of white-flowered bilobes (including 'Ovigeras' as well) on the coastal strip between Port Nolloth and Grootmis. A year later, Bolus published five taxa based on Hall's collections. Rawe reduced these to two: *C. ecarinatum* var. *ecarinatum,* and *C. ecarinatum* var. *candidum* (L. Bolus) Rawe, distinguishing var. *candidum* by its shorter lobes. Since lobe length is wildly inconstant in this group—and since these taxa were found within 5 miles—one might suggest that a simple synonymy is the best solution, but I hesitate, because our knowledge of these populations is quite limited. Hall's slides suggest marked differences in habit, and the sheets at the Bolus Herbarium confirm this. The Port Nolloth-Grootmis area has at least as many diamonds as conophytums, and unfortunately I have been able to explore only its fringes.

At several colonies, white and yellow bilobes mingle freely; absence of yellow is apparently controlled by a single recessive gene, and I have seen several plants with ivory-white flowers, intermediate between golden and pure white. I am therefore reluctant to attach any taxonomic importance to these flower colours. The coastal populations illustrate another taxonomic difficulty: the separation of the 'bilobes' (large bodies with well-developed lobes) from the 'Ovigeras' (smaller bodies, often globose, with nearly connate leaves). *C. ecarinatum* suggests the former group, *C. candidum,* the latter.

**C. caroli** Lavis in Bolus, Notes on Mesemb. 2:378 (1933) and Bolus in ibid. 3:208-210 pl.44, fig.J (1950); *Ophthalmophyllum caroli* (Lavis) Tischer in Kakteenkunde 4:86 (1935) and in Cact. Succ. J. Gr. Brit. 15(2):33 (1953). Type: 'South border, about 100 miles southeast of Springbok', *C. Luckhoff* (BOL 20429).

Subg. OPHTHALMOPHYLLUM. Plant solitary (in cultivation caespitose with age); sheath brownish-yellow, persistent; body cylindric, bilobed at apex, 22-30×18-25×7-12mm, lobes turret-shaped, truncate above, fenestrate; epidermis purple-brown, glabrous, smooth to rugose above; fissure 4-10mm. Flowers diurnal, non-scented or slightly sweet; calyx-tube herbaceous, 3mm, lobes 6, 3-5mm; corolla-tube partially adnate to the calyx tube, 6-10mm, petals 10-15mm, white to ivory or pale yellow, inner segments filamentous; stamens c. 30, 4-seriate; stigmas 6, 10-20mm. Capsule 6-locular; seeds 0.55mm, very numerous.

In 1935, Tischer transferred this species to *Ophthalmophyllum* because of its floral structure, in particular, the partial fusion of its calyx and corolla tubes. Commenting on this manoeuvre in 1950, Bolus noted that the species seemed to be a 'connecting link' between the two genera, having the body structure of an *Ophthalmophyllum,* but lacking the 'prolongation of the receptacle into a tube between the top of the ovary and the insertion of the disk' typical of that genus. The material I have seen strongly suggests *Ophthalmophyllum;* this is one of the points where the two groups approach each other most closely. The placement problem will be solved if *Ophthalmophyllum* is accepted as a well-defined subgenus *within Conophytum.*

Tischer's 1953 article defended his transfer and also provided a quasi-precise locality: Bokkraal. Unfortunately, Bushmanland has several Bokkraals, two of them near Kliprand; another in the Knersvlakte. The latter is near a colony of *C. acutum* L. Bolus, which resembles *C. caroli* quite strongly. The two have different flowering syndromes, however (nocturnal vs. diurnal), and distinct capsule structures. *O. australe* L. Bolus, from Kliprand, is almost certainly a synonym of *C. caroli,* which confirms the provenance of that species.

**C. carpianum** L. Bolus, Notes on Mesemb. 3:264-265 (1954). Type: 'Doornpoort, Richtersveld', *H. Hall* in NBG 704/53 (BOL).

Sect. SAXETANA. Plant caespitose, internodes hardly visible; tunic greyish-brown to whitish, membranous, flaking; body subcylindric to subquadrate or obovate, 6-15×4-8×3-4mm, leaf tips free for 1-2mm, keeled, often retuse; epidermis dirty grey-green, maculate. Flowers at first nocturnal, after a few nights remaining open during the day, sweetly scented; calyx-tube herbaceous, 4-lobed; corolla-tube 5mm, petals 20-35, 2-seriate, 2-4mm; stamens 10-15, well-exserted; 'style' 3-6mm, stigmas 4, 6-10mm,

*C. caroli* Lavis, ex Kliprand, Bushmanland.

*C. carpianum* L. Bolus, ex Doornpoort, Richtersveld.

extremely slender, often well-exserted. Capsule 4-locular; seeds dark brown, unusually large, 0.80-0.95mm.

This is known from only two adjacent localities: above the watering hole at Dooringpoort (Doornpoort), and a few km south of it (*A. R. Mitchell* 1328); at both, it grows with lichens on granite rock faces. Its habitat preference is so similar to that of *C. hallii,* described by Bolus at the same time as *C. carpianum,* that she was inspired to compare the species, though they have no actual affinities. *C. carpianum* is a montane relative of *C. saxetanum* (N.E.Br.) N.E.Br.; the relationship is clearly shown by their floral structures. The peculiar things about *C. carpianum* are its greyed epidermis and its narrowly-wedged bodies, which call to mind the shapes of *C. luckhoffii* Lavis and *C. helenae* Rawe, species far removed from *C. carpianum* florally. It is interesting to note such similar vegetative habits in distinct sections of the genus.

*C. catervum* (N.E.Br.) N.E.Br. in Gard. Chron. 72:8 (1922); *Mesembryanthemum catervum* N.E.Br. in J. Linn. Soc. 45:93 (1920). Type: 'Near Grootfontein', *I. B. Pole-Evans* 4975 (K).

In his 1982 review of section *Conophytum* (*'Truncatella'*), in Cact. Succ. J. (US) 54(4):165-169, Rawe omitted all mention of this taxon, which was named for its 'crowded' bodies. It came from the same locality as Brown's *C. viridicatum* var. *punctatum,* a variety completely sunk by Rawe into *C. viridicatum* (N.E.Br.) N.E.Br. *C. catervum* should share the same fate. All the above taxa have ridged, angled bodies, shapes commonly seen in the Grootfontein–Laingsburg corner of the Little Karoo.

The 'clonotype' of *C. catervum* has gained very wide circulation because of its indestructible vigour; this clone has an attractive light grey-green colour, which distinguishes it from the darker green 'clonotype' of *C. viridicatum.* Both plants have peculiarly white sheaths, reminiscent of eggshells.

*C. cauliferum* N.E.Br. in Gard. Chron. 72:84,83, fig. 37 (1922). Type: 'Upper northwestern slopes of a hill southwest of Chubiessis', *H. H. W. Pearson* 6176 (K).

Brown distinguished this from *C. bilobum* (*sensu* Brown) by its dots, shorter lobes, and stem-forming habit. The first two characters are trivial, but the last is of some significance, given the acaulescent nature of many bilobes. (That is an uncertain character, since it concerns a potential which can only be expressed in age; many wild bilobes do not live long enough to acquire the legginess seen in long-cultivated plants.)

In 1927 two more caulescent bilobes were published: *C. altum* L. Bolus and *C. frutescens* Schwantes. Brown at first considered the latter to equal his *C. cauliferum,* but this synonymy has never been accepted, probably because the reddish flowers of *C. frutescens,* which appear early in the summer, make it memorably distinct. It should be noted that other bilobes flower early, e.g. *C. compressum* N.E.Br., which also forms stems. The flowers of *C. compressum* (and *C. cauliferum*) are golden when young; with age they redden slightly. The buds of *C. frutescens* are vivid reddish-pink, a colour matched only by *C. notabile* N.E.Br. (1930), which Brown himself finally regarded as a synonym of *C. frutescens* (as attested by a note in his album of Gardener's Chronicle clippings at K).

*C. cauliferum,* in my view, can be safely included in *C. bilobum*—Chubiessis is quite close, after all, to the locality Brown gave for *C. bilobum; C. frutescens,* however, has enough distinguishing traits to justify retention.

*C. cauliferum* var. *lekkersingense* L. Bolus, Notes on Mesemb. 3:315 (1958). Type: 'Lekkersing', *H. Meyer* in SUG 9747 (BOL). Bolus distinguished this from the type variety, which occurs some 30km southeast of Lekkersing, by its longer lobes, longer corolla tube, and much shorter 'style', trifling distinctions which can vary even on a single plant. It had the same caulescent habit as the type variety. Bolus's *C. lekkersingense* (1936), found by R. Smithers at Lekkersing, was described as having 'abbreviated branches'; perhaps Bolus described SUG 9737 so as to amplify her previous description. Both 'lekkersingenses' are pleonasms; two more synonyms of *C. bilobum*.

**C. ceresianum** L. Bolus, Notes on Mesemb. 3:82-83 (1937); Rawe in Kakt. and. Sukk. 26(9):198-200 (1975) and in Cact. Succ. J. (US) 55(1):5,7-8 (1983). Type: 'Ceres Karoo', *V. S. Peers* (BOL 21981).

Sect. TUBERCULATA. Plant caespitose, densely aggregate, internodes invisible; tunic rusty-brown, persistent; bodies obovate to obconic, round to oval seen from above, 10-30×12-22×5-8mm, often depressed toward the fissure; epidermis pale green to purple-red, glabrous, not glossy, covered with dots and fine lines; fissure short, frequently rhomboidal, ciliate. Flowers nocturnal, sweetly scented (reminiscent of *C. ficiforme*); calyx-tube 3-4mm, 4-6-lobed; corolla-tube 4-6mm, petals numerous, 6-20(!)×0.4-1.2mm, yellowish white to pink or deep crimson-magenta; stamens numerous, 3-seriate; stigmas 4-6, 2.5mm, united for c. ½ their length. Capsule 4-6-locular, seeds pale tan, 0.80mm.

This variable species is frequently encountered between Karoopoort and Skitterykloof, in the Ceres (Tanqua) Karoo. To the northwest it intergrades to a disconcerting extent with *C. obcordellum* (Haw.) N.E.Br. In its 'classic' form, it is easily recognized by its finely-divided lines, which run down the sides of the (often) asymmetrical bodies, and by its large, heavily-scented nocturnal flowers. The petals vary in shade from straw yellow to pink, to a wonderfully deep magenta, the darkest shade of any southern night-flowering *Conophytum.* (It is interesting to note that all of the species of the Tanqua, Little and Kammannasie Karoos are exclusively nocturnal.)

*Conophytum ceresianum* var. *divergens* (L. Bolus) Rawe in Kakt. and. Sukk. 26(9):198-200 (1975); *Conophytum divergens* L. Bolus, Notes on Mesemb. 3:83 (1937). Type: 'Karroopoort [sic]', *Mrs. M. Pollock* in NBG 630/33 (BOL). At first, Rawe regarded *C. divergens* as a variety of *C. ceresianum,* separating it by its epidermal colour. In 1982, however, he included it within that species without distinction; he might also have included *C. ursprungianum* var. *stayneri* L. Bolus, a montane outlier. Instead, he placed this as a form of *C. obcordellum* var. *mundum* (N.E.Br.) Rawe, which is arguably close to the intergrading obcordellums mentioned above. Another link is provided by *C. spectabile* Lavis, which occurs just south of the Ceres Karoo, in mountainous terrain.

*C. chloratum* Tischer in Möll. Deuts. Gärtnerz. 43:150 (1928); Jacobsen in Kakt. and. Sukk. (Berlin) 2:46 (1938). Source: 'Near Steinkopf', collector unknown.

This was named for its greenish bodies; Tischer himself suggested its sinking into *C. limbatum* N.E.Br. He had a piece of Brown's 'clonotype' and presumably compared it with his own material. It should be noted that 'clonotype' material of *C. limbatum* is also a lively, non-bronzing, green, and it is not particularly well-keeled.

In the original description Tischer likened *C. chloratum* to *C. tantillum* N.E.Br., another greenish element in the 'ectypum complex', found near Steinkopf. It is possible that *C. chloratum* was introduced along with *Herreanthus meyeri* Schwantes (1928), first collected by Meyer at Umdaus, northwest of Steinkopf. In the neighbourhood of that species there are at least two odd forms of *C. ectypum*—one with moderately striate bodies, crescent-shaped in outline, the other with very green, hardly striate bodies, round in outline.

*C. christiansenianum* L. Bolus in J. S. Afr. Bot. 29(1):12-13 (1963); Jacobsen, Lex. Succ. Plants, pl.153, fig.2 (1974). Type: '22 miles south of Springbok', *R. C. Littlewood* in KG 965/61 (BOL).

When Tischer received KG 965/61 from Littlewood, he wrote back: 'probably a form of *C. strictum* . . . ' (another Bolus bilobe). It is odd that he did not identify it with *C. muscosipapillatum* Lavis, found some 35km west of *C. christiansenianum* and virtually identical with it, though Lavis's species is rather more stout. The crenate margin seen in the Lexicon photo is common to both 'species', and they share a papillate epidermis; both can be absorbed into *C. bilobum*. It should be noted that Rawe's *C. christiansenianum* material (*RR* 1058), circulated by the ASPS, came from the type locality, not from '22 miles north of Springbok' as reported—though three other Bolus bilobes are reported from there as well!

*C. cibdelum* N.E.Br. in Gard. Chron. 78:468 (1925); Labarre, Mesembryanthema, 192-193 with fig. (1931). Type: Locality and collector unknown (K?).

In 1925 Brown wrote that this resembled a small-scale *C. truncatellum* (Haw.) N.E.Br., but in 1927 it developed larger growths which convinced him that it was merely a 'state, not a variety', of that species (now placed in *C. truncatum* (Thunb.) N.E.Br.).

*C. circumpunctatum* Schick & Tischer in Succulenta 13(3):53-54, with illus. (1931). Type: 'Little Namaqualand, road to the south of Anenous', collector unknown [G. Meyer?], not preserved.

This is a southern *C. wettsteinii* (A. Berger) N.E.Br., slightly smaller than the 'classic' form of that species, but not otherwise distinct; the circumpunctate fissure is not at all unusual. Tischer mentioned that it had the same form and size as *C. flavum* N.E.Br., not the only time these species have been compared. They are presently separated by flower colour—purple vs. yellow, a thin division which invites closer scrutiny. Their easily-accomplished union produces orange-flowered offspring. Note that *C. flavum* has a chromosome count of 2n=36, double the number of *C. wettsteinii* and most other species checked to date. Rawe's collection from south of Kosies, circulated by the ASPS as *C. circumpunctatum,* produced yellow flowers, as have my own collections from Kosies; *C. wettsteinii* occurs further south in the Pass itself.

*C. citrinum* L. Bolus, Notes on Mesemb. 3:26 (1936) and ibid. 3:139, pl.20, fig.B (1939). Type: 'Kubus', *R. Smithers* in NBG 2882/35 (BOL).

Bolus described three papillate, short-lobed bilobes from Kubus in the July 1936 Notes: *C. citrinum, C. latum,* and *C. piriforme*. The first-named has one slightly odd feature: its lemon-yellow petals, which stand out from the usual chrome-yellow sea. Otherwise, it was simply a rather small *C. bilobum*.

*C. clarum* N.E.Br. in Gard. Chron. 81:32 (1927); *C. uvaeforme* var. *clarum* (N.E.Br.) Rawe in Aloe 18(1-2):10,13 (1980). Type: 'Calvinia division: foothills of the Langeberg range', *I. B. Pole-Evans* 6022 (K).

Brown described this as 'a bright-looking little species', and Rawe, in reducing it to varietal status under *C. uvaeforme* (Haw.) N.E.Br., also emphasized its small bodies. In Rawe's sense, *C. uvaeforme* var. *clarum* denotes the Bushmanland 'extension' of *C. uvaeforme*. I find, however, that a division between the small Bushmanland forms of *C. uvaeforme* and the larger Knersvlakte forms is quite impractical; when the plants are cultivated, the size distinctions disappear. In 1980 I collected several extremely minute specimens of *C. clarum* southwest of Kliprand, and within two years the plants were indistinguishable from Vanrhynsdorp *C. uvaeforme*. The comma-shaped markings so typical of the latter are common in the former, though they are often reduced to prominent points, which tend to flatten out in cultivation.

*C. clavatum* L. Bolus in J. S. Afr. Bot. 30(2):77 (1964). Type: 'Richtersveld, 10 miles southwest of Brakfontein', *R. C. Littlewood* in KG 1327/62 (BOL).

A late redescription of *C. obscurum* N.E.Br., as noted by Rawe in Cact. Succ. J. (US) 47(3):131 (1975). The given locality is close to Augrabies, the *locus classicus* for *C. obscurum*. Bolus remarked upon the small size of *C. clavatum,* but *C. obscurum* is frequently Lilliputian.

*C. colorans* Lavis in Flow. Pl. S. Afr. 13:509, pl.509a (1933). Type: 'Probably Little Namaqualand', *N. S. Pillans* in NBG 416/16 (BOL).

At the risk of beating a dead horse, I wonder why Tischer (in Kakt. and. Sukk. 7(5):77-78. 1956 and in Nat. Cact. Succ. J. 26(2):51. 1971) was so certain that *C. colorans* equalled *C. uvaeforme* (Haw.) N.E.Br. From Mary Page's excellent watercolour, and from Lavis's suggestion that it was 'closely allied' with *C. purpusii* (Schwantes) N.E.Br., I would have deduced an Oudtshoorn origin for *C. colorans,* i.e. it would belong with *C. truncatum* (Thunb.) N.E.Br. However, if Pillans did in fact collect NBG 416/16 in Little Namaqualand, then *C. uvaeforme* is the only plausible name. The plant died at least fifty years ago, so the question has interest only as a point of historical curiosity.

*C. complanatum* L. Bolus in J. S. Afr. Bot. 27(2):111-112 (1961). Type: 'Laingsburg', *R. C. Littlewood* in KG 803/59 (BOL).

Bolus's comments give a mixture of affinities: she places *C. complanatum* in the *'Piluliformia',* and suggests an alliance with *C. calitzdorpense* L. Bolus, but the actual description—especially the elevated keel and the obscure dots—strongly suggests *C. viridicatum* (N.E.Br.) N.E.Br. In 1982 Rawe (in Cact. Succ. J. (US) 54(4):166,169) sunk *C. complanatum* into that species; the text was unfortunately garbled by the printer, but the key (p. 169) makes Rawe's intention clear.

*C. compressum* N.E.Br. in Cact. J. (Croydon) 3(2):37 (1934); Tischer in Kakt. and. Sukk. 8(3):44-45 (1957); Jacobsen, Handb. Succ. Plants 3:1052, fig.1259 (1960). Type: 'Near Alexander Bay', *A. G. J. Herre* in SUG 8460, not preserved (Tischer, loc. cit. gives a photo of Brown's 'clonotype').

'Lateral compression' is common in the bilobes. The bodies of *C. compressum* were thin, but bilobes from Jenkin's Kop (north of Eksteenfontein, Richtersveld, *A. R. Mitchell* 726) are even thinner; this variation is simply another aspect of the polymorphic *C. bilobum*. The involute lobes seen in the Handbook photo are also common, particularly on bodies which surround ripening capsules. The locality given by Brown is a mystery—bilobes are unknown here; I can only suggest that 'Alexander Bay' refers not only to a place, but also to a map sheet (which pertains, of course, to the Richtersveld).

**C. comptonii** N.E.Br. in Gard. Chron. 81:32, with fig. (1927); Rawe in Kakt. and. Sukk. 22(7):126-127 (1971) and in Cact. Succ. J. (US) 55(1):5,8 (1983). Type: 'Near Nieuwoudtville', *H. Compton* in NBG 1502/26?).

Sect. TUBERCULATA. Plant dwarf, caespitose, internodes invisible; tunic deep brown, persistent; body shortly obconic, truncate to shortly convex on top, 2.5-5×1.2-4×1.2-4mm, often faintly keeled; epidermis glabrous except at the fissure, brownish to greyish metallic green to blackish-green, markings numerous, narrow, reddish-brown to deep grey, faintly elevated; fissure short, whitish from crowded papillae. Flowers nocturnal, very sweetly scented, often self-fertile; calyx-tube 1.5-2mm, membranous, 4-5-lobed; corolla-tube 2mm, petals 22-30, acute, c. 2mm, yellowish-pink to pale orange to brownish; stamens c. 20, not exceeding the petals; stigmas 4-5(-6), 0.5-0.7mm. Capsule 4-5-locular; seeds few per loculus, 0.60mm.

Brown noted that *C. comptonii* was a 'very distinct' species, allied with none of the others. His statement still holds, in the sense that no other species closely resembles it in body. *C. comptonii* has been much shunted around within the genus, but Rawe's eventual choice of [sub]section *Tuberculata* seems the happiest. In his 1983 key, he placed it next to *C. rauhii* Tischer, another aberrant species. A demonstrated affinity between these two would be very interesting; their distribution areas are some 200km apart.

*C. comptonii* has a wider distribution than previously reported. It is found at several spots near Vanrhynspas, near the edge of the escarpment, and also on the Matsikamma. Some specimens seen at the latter colony (*SH* 115/85) were extraordinarily minute: the bodies were a mere 1mm in diameter, making this one of the smallest species. Several plants had a nearly black epidermis, a deeper colour than the usual metallic grey. The bodies of *C. comptonii* are always covered with a fantastically delicate tracery of fine lines; this species demands a good lens for its appreciation.

**C. concavum** L. Bolus, Notes on Mesemb. 3:23 (1936) and ibid. 3:141, pl.21, fig.C (1939). Type: 'Near Hondeklip Bay in the direction of Riethuis', *P. van Heerde* in NBG 679/34 (BOL).

Plant caespitose, slowly forming clusters of 6-10 bodies, internodes invisible; tunic whitish, irregularly wrinkled, spotted; bodies sub-obconic, concave toward the fissure, 20-35×15-22×12-15mm, soft in substance; epidermis pale green to dusky reddish-grey, velvety; fissure depressed, gaping, 3-8mm, surrounded by a greenish pellucid zone. Flower opening late in the afternoon, with a strong honey-like scent; calyx-tube 3-5mm, pale green to ruddy, 5-6-lobed; corolla-tube 2-4mm, petals 18-25, to 12mm, white to cream-coloured; stamens numerous, exserted, 4-seriate; stigmas 5-6, 6-8mm. Capsule 5-6-locular; seeds 0.55mm.

It is difficult to relate *C. concavum* to other species; its soft, velvety, depressed-globose and partially translucent bodies are highly unusual. Bolus made an intriguing comparison with her *C. regale,* another quartz-lover. That species also has soft, papillate bodies, translucent near the fissure; both species have scented flowers, with spathulate petals and free stigmas. In *C. concavum,* the leaves are completely fused, with only a trace of a keel; *C. regale* is conspicuously bilobed though it is not a member of the bilobe complex, in my view. Another possible link is provided by *C. schlechteri* Schwantes, which, like *C. concavum,* grows level with the soil.

*C. concavum* is one of the few species known to have a chromosome count of 2n=36. *C. pillansii* Lavis has the same count and the same ground-hugging habit. It is interesting to note that both species have some degree of fenestration; they have the look and growth habit of *Ophthalmophyllum,* but they lack its flower structure. *C. intrepidum* L. Bolus (*C. bolusiae* Schwantes, q.v.), another very odd species, also has the 2n=36 count, but it has no fenestration at all. It may well be allied with *C. concavum.*

*C. concinnum* Schwantes in Möll. Deuts. Gärtnerz. 42:27 (1927). Type: 'Near Steinkopf', *G. Meyer,* not preserved; 'clonotype' at HBG.

Brown considered this to be distinct from his slightly older *C. flavum,* and used the name in his private notes for several collections by Herre and M. Brown. Tischer, however, recognized that *C. flavum* is a variable species, which can easily accommodate *C. concinnum* (and a good deal else). At his suggestion, Jacobsen sank *C. concinnum* in 1938 (in Kakt. and. Sukk. (Berlin) 2:46).

*C. concordans* G. Rowley in Nat. Cact. Succ. J. 33(1):7 (1978); *Ophthalmophyllum villetii* L. Bolus in J. S. Afr. Bot. 28:225 (1962). Type: 'Brakwater', *Villet* (BOL).

In 1978 Rowley suggested the placement of all the *Ophthalmophyllum* species within *Conophytum.* Eighteen transfers were necessary; the remaining *Ophthalmophyllum* species had already been juggled between the genera. Because the epithet *C. villetii* already existed, Rowley coined a new one for Villet's discovery, which is, unfortunately,. the most poorly-known species in *Ophthalmophyllum.* It is likely that 'Brakwater' actually indicates the Brakfontein near Loeriesfontein, where *Ophthalmophyllum* does occur. There is a similar confusion of 'fontein' and 'water' in regard to two Bushmanland species of *Aloinopsis* collected during the same period. However, there is a Brakwater in the Kamiesberge; I hope to explore it soon, though it is unlikely to yield any ophthalmophyllums. Meanwhile I can only suggest that *C. concordans* is probably a variant of *C. caroli* Lavis, and should be found on the sort of limestone formations favoured by that species.

*C. connatum* L. Bolus, Notes on Mesemb. 3:88 (1937) and ibid. 3:119, pl.18, fig.F (1938). Type: Locality uncertain, *A. G. J. Herre* in SUG 27 (BOL); for the paratype, SUG 8364, which Bolus considered to be the same: '28 miles from Port Nolloth on the road to O'okiep', *A. G. J. Herre.*

If a name were required for the bilobes with nearly connate leaves, several earlier ones exist. It is significant that many of these came from the area west of Steinkopf, along the main road; remoter areas were (and continue to be) so difficult of access as to skew our picture of distributions.

At the end of the description, Bolus mentioned that plants collected by Erni 'near Wittputs' might be *C. connatum.* Erni and Wittputs are both associated with South West Africa, and so the supposed occurrence of *C. connatum* within that country has taken root in the literature. Bilobes are completely unknown north of the Orange River; did Erni collect at a Wittputs within South Africa, south of the river—or did Bolus confuse *C. quaesitum* (N.E.Br.) N.E.Br., which is mildly bilobed, and abundant near Wit[t]putz, SWA, with her new species?

*C. conradii* L. Bolus, Notes on Mesemb. 3:89 (1937). Type: 'Breekpoort', *C. Herre* in SUG 10216 (BOL).

A courtesy taxon, made at the suggestion of Hans Herre to honour his father Conrad. Now that all the parties involved are dead, this can be painlessly relegated, along with the three other Eenriet-Breekpoort bilobes, to *C. bilobum.* Plants at Breekpoort vary considerably in size and pubescence, but their shape—'classic meyerae'—is fairly constant.

*C. convexum* L. Bolus, Notes on Mesemb. 3:26 (1936). Type: 'Little Namaqualand, Richtersveld, Nieuwe Mine', *R. Smithers* (BOL 21461).

Every good concavum deserves its convexum, and Bolus published these as a pair in 1936. *C. concavum* is indeed distinct; *C. convexum,* however, was wholly superfluous. The locality data is a puzzle. I cannot find Nieuwe Mine on any of my maps; did Smithers mean Numees Mine? And another puzzle: why does Schwantes's 'Flowering Stones' give 'white' as the flower colour, when Bolus specifies yellow for this quite ordinary bilobe? In Jacobsen's Lexicon, this taxon was relegated to synonymy under *C. cordatum* Schick & Tischer (q.v.), probably at Tischer's suggestion.

*C. corculum* Schwantes in Gartenwelt 33:68 (1929). Type: '35km east of Port Nolloth', *M. Schlechter,* not preserved; 'clonotype' at HBG.

This was named for the outline of its bodies: 'like a little heart'. *C. corculum* greatly resembles *C. meyeri* N.E.Br.; it differs principally by its slightly brighter, yellow-green epidermis. That distinction can hardly be taken seriously, especially as *C. corculum* is known only from a single clone. Plants referable to *C. corculum* are common at Augrabies, 25km east of Port Nolloth. These plants usually circulate as *C. meyeri* N.E.Br. (or as its var. *quinarium* L. Bol.). It should be noted that the Augrabies plants do differ from Brown's laxly-sprawling *C. meyeri* in one non-trivial respect; they form tight clusters, and *C. corculum* shares this habit.

*C. cordatum* Schick & Tischer in Zeitschr. Sukk.-Kunde 3(8):152-153 (1927). Type: 'Mountains south of the Port Nolloth-Anenous railway', collector unknown (not preserved). Lectotype (designated here): illustration in Schick & Tischer, loc. cit.

The much-rounded lobes of this bilobe produced a heart-shaped contour. Plants collected 35km east of Port Nolloth (KG 1104/62) match the description very well, and the same shape can be seen (along with myriad other shapes) at a colony east of Hondeklip Bay (*A. R. Mitchell* 622). Indeed, the fact that the same genotype has spread so far (c. 120km), with so many intervening colonies, gives us an idea of the extraordinarily 'plastic' nature of the bilobes. Some specimens from *ARM* 622 are very close to the classic *C. cordatum;* others, with larger elongate bodies, match Brown's *C. simplum;* all can be subsumed under *C. bilobum.*

*C. cordatum* var. *macrostigma* L. Bolus, Notes on Mesemb. 3:89 (1937) and ibid. 3:140, pl.20, fig.F. (1939); *C. macrostigma*

(L. Bolus) Schwantes, Flowering Stones and Mid-day Flowers: 274 (1957). Type: 'Tussen-in-Berge [Skimmelberg]', *P. van Heerde* (BOL 21968). According to Bolus, this differed from the type variety chiefly by the greater length of its petals and stigmas. Schwantes, inspired also by the 'larger plant body', suggested that it was a separate species, which is puzzling, as the given body dimensions are equivalent. Note that Skimmelberg is about 30km northwest of the (rather vague) locality of *C. cordatum*. At any rate, this too is *C. bilobum*.

*C. coriaceum* L. Bolus, Notes on Mesemb. 3:312-313 (1958). Type: 'Between Helskloof and de Koei', *F. Leighton* 2334 (BOL).

This is one of several bilobes reported from the northern Richtersveld. 'Leathery' (coriaceous) old sheaths are common in the bilobes, and I believe that sheath texture is at least partly environmentally induced. Leighton's material varied in this respect; some of the old sheaths were 'pergamentaceous' or 'papyraceous'. In short, *C. coriaceum* was a quite typical northern *C. bilobum*—rather large, slightly papillate, and well-marked on its keels.

*C. corniferum* Schick & Tischer in Zeitschr. Sukk.-Kunde 3(8):151-152, with illus. (1927); Labarre, Mesembryanthema, 147, with fig. (1931). Source: Locality and collector unknown.

This was named for its horn-bearing bodies, a character not well seen in Schick's photograph (published with the description). It is one of the 'smaller forms' of *C. bilobum;* both bodies and flowers are much reduced. Such forms are seen growing with more larger, strongly bilobed, plants, especially at Steenbok and Augrabies. *C. corniferum* has been widely distributed from Rawe's collection at Nakanas (*RR* 1137). These plants have a caulescent tendency which brings them very close to *C. altum* L. Bolus (q.v.).

*C. crassum* L. Bolus, Notes on Mesemb. 3:308-309, pl.97 (1958). Type: 'Ratelpoort', *H. Hall* in NBG 476/52 (BOL).

Bolus described this from a single, monstrously large specimen, which Hall had discovered growing among the normal Ratelpoort bilobes; she noted that it was among the largest she had ever seen. I imagine that this gargantuan plant had found an especially favoured spot. Its descendents, raised from seed of doubtful purity (collected in cultivation), are still thriving at Kirstenbosch; their proportions are quite modest.

Hall sent cuttings of the original clone to various collections; I note that the Jardin D'Exotique offered 'crassum' seed on its 1984 list! In cultivation many bilobes are weakly self-fertile, but they eagerly accept pollen from their potted neighbours.

*C. craterulum* Tischer in Cact. Succ. J. Gr. Brit. 18(2):31,36, with plate (1956); *C. velutinum* var. *craterulum* (Tischer) Rawe in Cact. Succ. J. (US) 54(5):218,222 (1982). Type: 'Little Namaqualand', collector unknown (SSM, Mes. no. 198—deposited c. 1956, but the sheet is now lost).

This has an odd history. 'Several plants' of this species were given to Tischer, without information as to their natural origin, though one plant arrived as *C. velutinum* Schwantes. Tischer decided that the specimens represented a new species, distinguished from *C. velutinum* by its greater size, paler body colour, 'crater-like' fissure zone, and broader, lilac-pink, petals. My piece of the 'clonotype' (ex Tischer!) has proven itself false; it has yellow petals, though it matches the vegetative description. Rawe believes that *C. craterulum* was probably no more than an extreme form of that species, but he cautiously produced the combination *C. velutinum* var. *craterulum* in 1982.

The case of *C. craterulum* exemplifies Tischer's difficulties with the genus. The vagueness of the essential habitat data is in sad contrast to the laborious and minute description of individual plants; only toward the end of his writing life did Tischer begin to receive adequately representative samples, from documented collections. Note that Tischer distributed another pink-purple quasi-bilobe, as '*C. cinereo-viride*', in the 'sixties. This is certainly nothing more than *C. velutinum,* and should not be confused with '*C. cinereum*', a corruption of *C. senarium* L. Bolus (=*C. karamoepense* L. Bolus), which also circulates in European collections. Another 'European' '*C. cinereum*' is a bilobe of the *C. muscosipapillatum* Lavis ilk.

As for the provenance of *C. craterulum:* for some time, a pink-flowered, pubescent quasi-bilobe has been known from Rosyntjieberg in the central Richtersveld. Some material, collected by van Jaarsveld, Kritzinger, and van der Westhuizen, corresponds in part to the *C. craterulum* description, though the plants tend to alter with age. It is very unfortunate that there is no authentic Tischer material for comparison. The Rosyntjieberg plants do represent a taxon distinct from *C. velutinum,* which occurs well south of the Richtersveld, near Komaggas. Both Rosyntjieberg and Komaggas were explored botanically in the 1930s, but the explorations were by no means complete.

*C. cuneatum* Tischer in Succulenta 14(5):113-114 (1932). Source: Locality and collector unknown.

This was sunk by Jacobsen (in Kakt. and. Sukk. (Berlin) 2:46. 1938) at Tischer's suggestion into *C. halenbergense* (Dinter) N.E.Br., which is a peculiarly mutable species in cultivation. Its bodies are often cuneate.

**C. cupreatum** Tischer in Succulenta 18(3):33-34 (1936) and in Kakt. and. Sukk. 3(2):19 (1952). Source: 'Little Namaqualand', *Dr. Luckhoff,* not preserved. Neotype: 'S of Kliprand, *R. Rawe* 864 (BOL).

Sect. PELLUCIDA. Plant caespitose, internodes invisible; tunic deep brown, thin, persistent toward the base; bodies obconic to subcylindric, 10-25×8-10×4-7mm, truncate to convex on the upper surface; epidermis deep green to brownish, nearly glabrous to densely covered with trichomes (papillae), partially fenestrate toward the fissure, ornamented by 'islands' of a yellowish-orange to orange-tan colour with a slight metallic lustre; fissure very short (or, rarely, dividing the body into two lobes), ciliate. Flower diurnal, appearing mid-summer; calyx-tube 2-3mm, 4-lobed; corolla-tube 5-15mm, petals 15-30, very narrow to broadly spathulate, outer 6-10mm, white, pale rose-pink or rarely magenta, inner 4-5mm, golden to reddish-orange; stamens entirely enclosed, numerous; stigmas 4-5(-6), 1-2mm. Capsule 4-5(-6)-locular; seeds very numerous, 0.50-55mm.

In the original description, Tischer mentioned an affinity with *C. pellucidum* Schwantes, distinguishing his new species by its copper-coloured bodies and non-rugose upper surface. *C. cupreatum* can also be distinguished by its incomplete fissure and nearly circular outline (as seen from above), and especially by its fine papillae, which give the upper surface a slightly matt appearance. The flowers of *C. cupreatum* are very like those of *C. pellucidum* in structure; a ring of yellow to reddish-orange staminodes is found at the mouth of the corolla tube. Tischer gave the petal colour as 'shining white', and that is the dominant colour at the many colonies we have examined, but pink-tipped to entirely pinkish-purple petals are also seen.

In 1952 Tischer narrowed the locality to 'between Gamoep and Namies', which is still a wide area, north of all colonies known to me. Perhaps Namies was a mistake for Garies—this is a frequent confusion; *C. cupreatum* certainly is found between Gamoep and Garies (e.g. at Vaalputs). To the north of Gamoep, *C. koubergense* L. Bolus occurs; that has been confused with *C. cupreatum* since 1951 at least. *C. cupreatum* is abundantly present in the area around Kliprand; as the species goes north, it intergrades more and more with *C. pellucidum,* but on its own turf, it seems distinctive, so I refrain from a merger. It should be noted that *C. terrestre,* described by Tischer in 1960 from material collected near Aalwynsfontein (northeast of Kliprand), is a vicariant of *C. cupreatum* with longer papillae (trichomes) and curiously pitted sides.

*C. cupreiflorum* Tischer in Cact. Succ. J. Gr. Brit. 17(4):79 (1955). Type: 'Probably Little Namaqualand', collector unknown, not preserved; SSM, Mes. no. 195—photograph only.

Tischer received a single cutting of this in 1951, from Dr. de Boer, the Dutch conophile. Since then *C. cupreiflorum* (and its various simulacrums) have travelled around the world. Seed has even been offered, yielding yellow-, purple-, and copper-flowered progeny. I have the strongest suspicion that the original clone was a natural or artificial hybrid involving *C. elishae* (N.E.Br.) N.E.Br. and *C. violaciflorum* Schick & Tischer. There is a mixed colony of these two species at Springbok, so a natural origin is possible; their flowering times overlap. Certainly a reddish-flowered *Conophytum* would have attracted a collector's eye.

In Tischer's unpublished monograph on *Conophytum* (preserved at PRE), there is an interesting clue to the origin of this taxon: 'Bushmanland, *P. van Heerde* SUG 12242, 1949'. This has a curious echo in the seed collection of G. Schwantes; a packet from SUG has the following data: *C. cupraefolium* [sic] Tisch. SUG 12249 [sic] 'O'okiep' (just north of Springbok). The packet is undated, but it is probably contemporaneous with Schwantes's 'Flowering Stones' (1957). *C. cupreiflorum* was the newest of the *Conophytum* taxa treated in the book; the text contains the erroneous and puzzling information that the species flowers at night. Schwantes's capsules, incidentally, are very close to those of *C. elishae,* and the seeds I discovered in them match that species as well.

Another quite unexpected clue is found in Stefan Vogel's 1954 paper on pollination syndromes (Blutenbiologische Typen der Sippengliederung, Botanische Studien Heft 1, Jena 1954). On page 139, Vogel refers to an orange-flowered, still unnamed 'species', which he saw *in* Springbok and which opened only between 13:00 and 17:00. Since most of the mesembs mentioned in the paper were observed in habitat, one would like to assume that this one was as well—but it is possible that Vogel visited van Heerde's garden at Springbok, where the recently-collected—and very strikingly coloured—*C. cupreiflorum* would have been conspicuous. Only one other species—*C. marnierianum* Tischer & Jacobsen—could fit all Vogel's particulars.

Reconciling the bits of information, we can assume that van Heerde regarded O'okiep as part of Bushmanland—after all, Herre did—and that Tischer gleaned the locality data given in his monograph after 1955. It seems reasonable to assume that van Heerde was the source of the original plant, that it was probably a unique specimen, and that it was of wild origin—though I cannot preclude the idea that van Heerde passed off a garden hybrid as a species; he was often mysterious about the origin of his material.

Previously I inclined to the view that the locality data should read: 'northern Europe', but the evidence of South African origin is too strong. Nonetheless, many or most of the *'C. cupreiflorum'* plants in cultivation are very obviously European hybrids, involving the original *C. cupreiflorum, C. bilobum,* and *C. velutinum* Schwantes (this species contributed the pubescence seen on many of the hybrids; Tischer's plant was glabrous). There is even a rash of grotesque Japanese hybrids, but these have more horticultural than taxonomic interest, with their fire-engine red flowers and enormous bodies.

It is worth noting that all of the yellow × purple mesemb crosses known to me have produced copper to salmon-coloured flowers (e.g. *Gibbaeum* × *Glottiphyllum, Argyroderma* × *Argyroderma* [natural and artificial], and the orange conophytums mentioned above [q.v. *auriflorum, braunsii, brownii*]). Rawe (pers. comm. 1987) has told me of a single orange-flowered *Conophytum* which he found many years ago, at Eenriet. The plant resembled a giant *C. ectypum;* I imagine that the plant was a hybrid between the pinkish *C. ectypum* form common at Eenriet, and *C. bilobum,* which occurs with it. It should be noted that while orange is a common enough colour in the night-flowering species, it is extremely rare in those which flower by day.

*C. curtum* L. Bolus, Notes on Mesemb. 3:313-314 (1958). Type: 'Doornpoort', *R. Smithers* 11 (BOL).

Product of a late house-cleaning, this large northern bilobe taxon gets short shrift from me; it was only differentiated by its 'curt' calyx tube. Such brevity, however, is common in *C. bilobum*; *C. curtum* was entirely redundant. Once again, Bolus published such taxa as this one not to record actual new species, but rather to record variation in existing ones. As she wrote to Littlewood: 'I dare not call them new species!'

*C. cylindratum* Schwantes in Gartenwelt 33:69 (1929); Rawe in Cact. Succ. J. (US) 47(3):126 (1975). Type: 'Little Namaqualand, Alexander Bay', *M. Schlechter,* not preserved.

Schwantes was so struck by this species that he created a section for it: *Cylindrata* Schwantes. He described the species without knowledge of its flowers, but a plant in Bates's collection flowered in Oct. 1929, and Brown's watercolour of it, preserved at Kew, gives us an excellent idea of the original *C. cylindratum.* If Schwantes had seen the flower—and if he had disregarded the bogus locality data—he might well have recognized that his new species had an affinity with *C. roodiae* N.E.Br., described in 1926.

*C. cylindratum* had a hemispherical or slightly depressed upper surface, quite smooth and yellowish-green; *C. roodiae* had a light green or slightly yellowish green, unequally-lobed body, with small pellucid idioblasts and a peculiarly 'crystalline' surface. It is notable that *C. roodiae* in its juvenile stages is quite lobeless, a state which can persist for years, despite early floral maturity.

In Rawe's 1975 article, he suggested the inclusion of Sect. *Cylindrata* within the subsection *Verrucosa;* he also suggested that *C. hallii* L. Bolus, Notes on Mesemb. 3:263-264 (1954) was conspecific with the much earlier *C. cylindratum.* Since 1975, very much more material has turned up, especially *C. roodiae* in various forms (including the original form, which was unknown to Rawe, Tischer, Bolus and Schwantes). This material demonstrates that while *C. hallii* is certainly close to *C. cylindratum,* it is also close to *C. roodiae*; if one accepts the union of the first two, their inclusion in the third is tempting. The curious thing is that I have seen *C. hallii, C. roodiae* and *C. cylindratum* growing within a few km of each other, maintaining distinct behaviours.

One could characterize *C. cylindratum* as a robust pan plant, *C. hallii* as a depauperate dome plant (it grows at steep angles in granite among mosses), and *C. roodiae* as a crevice plant—but this is an oversimplification. In cultivation *C. hallii* may attain the size (and even something of the colour) of *C. cylindratum.* But *C. cylindratum* is usually easily distinguishable from *C. roodiae,* which often has the shape one associates with *C. pellucidum.*

Schlechter's locality data was queried by Tischer and Rawe; it is certainly false. *C. cylindratum* is found between Kamieskroon and Springbok, extending no further north, so far as I know. There is a conspicuous colony near Die Drif crossing (near the Buffelsrivier bridge at N7), and I assume that Schlechter collected his plants here: the plants are accessible, and they match Schwantes's description (and Bates's plant, which must have come from Schlechter via Haage). *C. roodiae* was originally reported from near 'Vanrhynsdorp', but that report is just as problematic as Schlechter's. Perhaps Mrs. Rood meant the district boundary; that comes close to colonies of *C. roodiae* found within the Kamiesberge.

*Conophytum cylindratum* var. *primosii* (Lavis) Rawe in Cact. Succ. J. (US) 47(3):126,132 (1975); *C. primosii* Lavis in Bolus, Notes on Mesemb. 2:267 (1931); Bolus in Notes on Mesemb. 3:135, pl.21, Fig.K (1939). Type: 'Mesklip in montibus Komaggas', *R. Primos* in NBG 1973/30 (BOL). Rawe distinguished this from the type variety by the very pronounced warty top surface of the lobes as well as the somewhat better developed 'lobes'. The curious thing is that Lavis said nothing about wartiness; she mentioned only a degree of 'turreting' of the lobes. Rawe based his combination on material he collected at Mesklip. It is unlikely that he hit upon Primos's spot, though that was indeed at Mesklip, in the mountains southeast of Springbok, not in the Komaggas mountains. (Lavis's notes make this clear; she refers to the Vogelklip mountains, which are part of the old Mesklip farm.) Rawe must have come across one of the rather verrucose forms of *C. roodiae* prevalent in the Mesklip area. What Lavis described was one of the smoother forms, better known as *C. hallii.* East of Mesklip I have seen smooth and verrucose forms growing together, which inclines me to regard them all as *C. roodiae.* It should be noted that even the 'classic' *C. cylindratum*—normally very smooth at the apex—can show a verrucose tendency. One of my mature specimens changed from smooth to verrucose after a few seasons in a very hot glasshouse!

# Guidelines for Authors

Contributions for publication in 'Bradleya' are invited on any aspect of succulent plant study and should be submitted to Nigel Taylor, c/o The Herbarium, Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AE, England, or to Colin Walker, Biology Dept., The Open University, Walton Hall, Milton Keynes MK7 6AA, England.

It is a condition of acceptance that contributions are the original work of the author, have not been previously published, and are not under consideration for publication elsewhere. The editors reserve the right to refuse any contribution and to make minor textual changes without reference to the author.

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