

THE SYSTEMATIC POSITION OF *RHYTIDOCAULON* (*APOCYNACEAE*–*ASCLEPIADOIDEAE*)

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Rhytidocaulon P.R.O. Bally is reviewed. The relationships with other genera are discussed in the light of the character assessment carried out and it is suggested that it is closest to *Caralluma* R. Br. subg. *Caralluma* and *Echidnopsis* Hook. f. Descriptions of the genus and the eight known species are provided.

Keywords. Arabia, north-east Africa, stapeliads, taxonomy.

INTRODUCTION

In 1962 Bally described *Rhytidocaulon* to accommodate two species with very distinctive vegetative parts and small, but structurally rather different flowers. These had been discovered in Ethiopia and Somalia in 1955 and 1944 respectively. The first collection of a *Rhytidocaulon* that I have been able to locate was made in Somaliland on 27 November 1894 by A. Donaldson Smith (# 278 (BM)). This plant lacks flowers, so that it cannot be assigned to any of the known species, but the stem indicates that it clearly belongs to *Rhytidocaulon*. In 1897 Theodore Bent sent a plant to Kew which flowered on 13 September of that year. N.E. Brown noted that the stems were 'remarkably rugulose from irregular furrows' and he later described it as *Caralluma torta*. Leach (1970) thought that it was probably a *Ceropegia* and it was only in 1990 that Gilbert moved it to *Rhytidocaulon*, where it clearly belongs.

Since Bally's description, several species have been added so that there are now eight names (including *Caralluma torta*) in *Rhytidocaulon*. Plants have rarely been collected and consequently few herbarium records exist so that it is very difficult to assess the true variability of the species or plot their distributions accurately. The only detailed collections appear to be those of I.S. Collenette from Saudi Arabia and I was fortunate to be able to examine many of these in cultivation at ZSS. These showed *R. macrolobum* and *R. sheilae* to be very variable and proved the existence of a host of other plants which could not be placed under either of these names. The taxonomy at the level of species therefore remains uncertain and this article merely lists what has been described with no attempt at a critical assessment. To elucidate the systematic position of the genus, an assessment of characters is carried out.

MATERIAL AND METHODS

Herbarium material was examined at K, BM and ZSS.

For SEM studies of the epidermis of stems and leaves, pieces $\pm 5 \times 5$ mm were

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washed in chloroform for 5–10 minutes to remove the wax covering. These were then placed in 100% EtOH for up to one week after which they were subjected to the Critical Point Drying process in 100% EtOH, mounted on stubs and Au/Pd coated. Examination was carried out with a Cambridge S200 microscope at 5KV. Pieces of flowers were treated the same except that the chloroform bath was omitted and they were instead fixed in 5% formaldehyde solution for 24h. Seeds were mounted and coated directly without any prior treatment.

CHARACTER ASSESSMENT

Plant

The plant in *Rhytidocaulon* consists of a main (primary) stem with a few, shorter side-branches arising well away from the ground. Rooting takes place at the base of the main stem only. The stems are initially erect but tend to spread out horizontally and sometimes the whole plant above the short, erect base is nearly horizontal. Plants are often very small (30–100mm tall) and consist of the main stem with one or two short side-branches. Occasional shrubby plants up to 500mm tall with quite a number of side-branches have been recorded (e.g. Newton, 1980).

Stems vary from 7–25mm thick, the main stem usually somewhat thicker than the side-branches. They tend to taper progressively towards their apices. It is reported in several places (e.g. Bally, 1962) that the stems are sweet and juicy and much sought after by the local inhabitants as food.

The tubercles on the stems are arranged into four rows. On young tissue the stem is quite clearly 4-angled but later this becomes less easy to see and older stems are often more or less cylindrical. The tubercles are roughly rectangular in outline and each bears, near its apex, a leaf. The surface of the tubercles and the zone between the angles is deeply rugose and convoluted (Figs 1A,B, 2C). It is also papillate all over. Young tissue is greyish-green but usually has a translucent outer layer which gives it a glassy appearance.

Leaves are present for a short while and only on young tissue (Figs 1A, 2C). They are relatively conspicuous (2–4mm long), usually ovate-lanceolate, erect and usually nearly adpressed to the stem, fleshy and with a prominent midrib clearly visible on the rear. Sometimes they possess a short petiole but they are usually nearly sessile. At their base on the upper side is a pair of minute, \pm globose, glandular stipules (Fig. 1A). These were not observed by Meve & Albers (1990), who listed *Rhytidocaulon* as 'without stipules'. The leaves are also papillate on both surfaces.

Micromorphological observations (Fig. 1)

The epidermal cells on the stem, tubercles and leaves have \pm flat outer walls with slight indentations marking the divisions between cells. They are isodiametric to slightly rectangular. Scattered over the surface (of the stems, leaves, exterior of sepals and exterior of corolla) are relatively large, cylindrical, decurved papillae: each con-

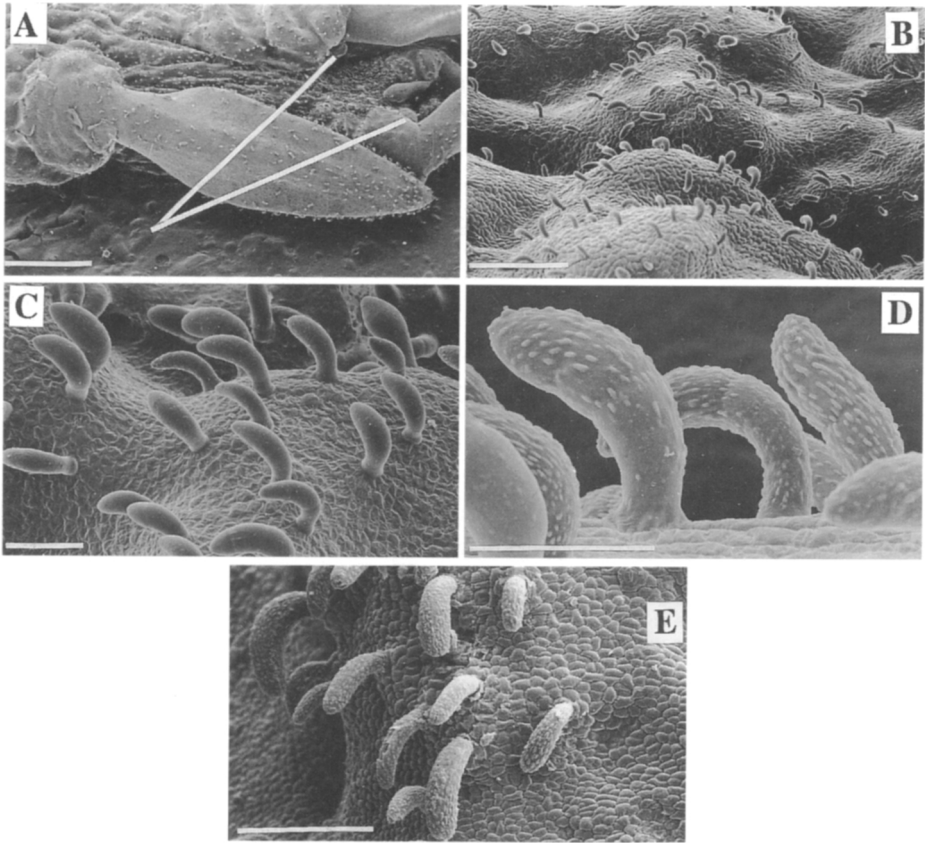


FIG. 1. Leaves, surface of stem and sepals of *Rhytidocaulon* (*R. macrolobum*, ex hort.). A, leaf from rear: the midrib, narrow 'blade' and small petiole are all visible; the much convoluted surface of the stem can be seen above the leaf. Two minute stipules are indicated by the white lines. B, surface away from tubercle – much convoluted and with scattered papillae. C, papillae on surface of tubercle (pointing towards base of stem); the surface of these papillae is smooth, but the surface of those on the leaves is rugose (see D). D, papillae on base of petiole; here it is possible to see on some papillae that they are multicellular. E, papillae on rear of sepals (pointing to base of flower). Scale bars (approx.): A, 1mm; B, 250µm; C, D, 50µm; E, 100µm.

sists of 2–5 cells arising from a single basal cell which is not raised out of the surface by the surrounding cells. The surface of these papillae is often longitudinally verrucose.

Inflorescence

Two unusual features of this genus are that the flowers are found on both the primary stem and on side-branches and that flowering can take place on very small specimens – in fact in some cases within the first year of growth when the plant is still less than 30mm tall.

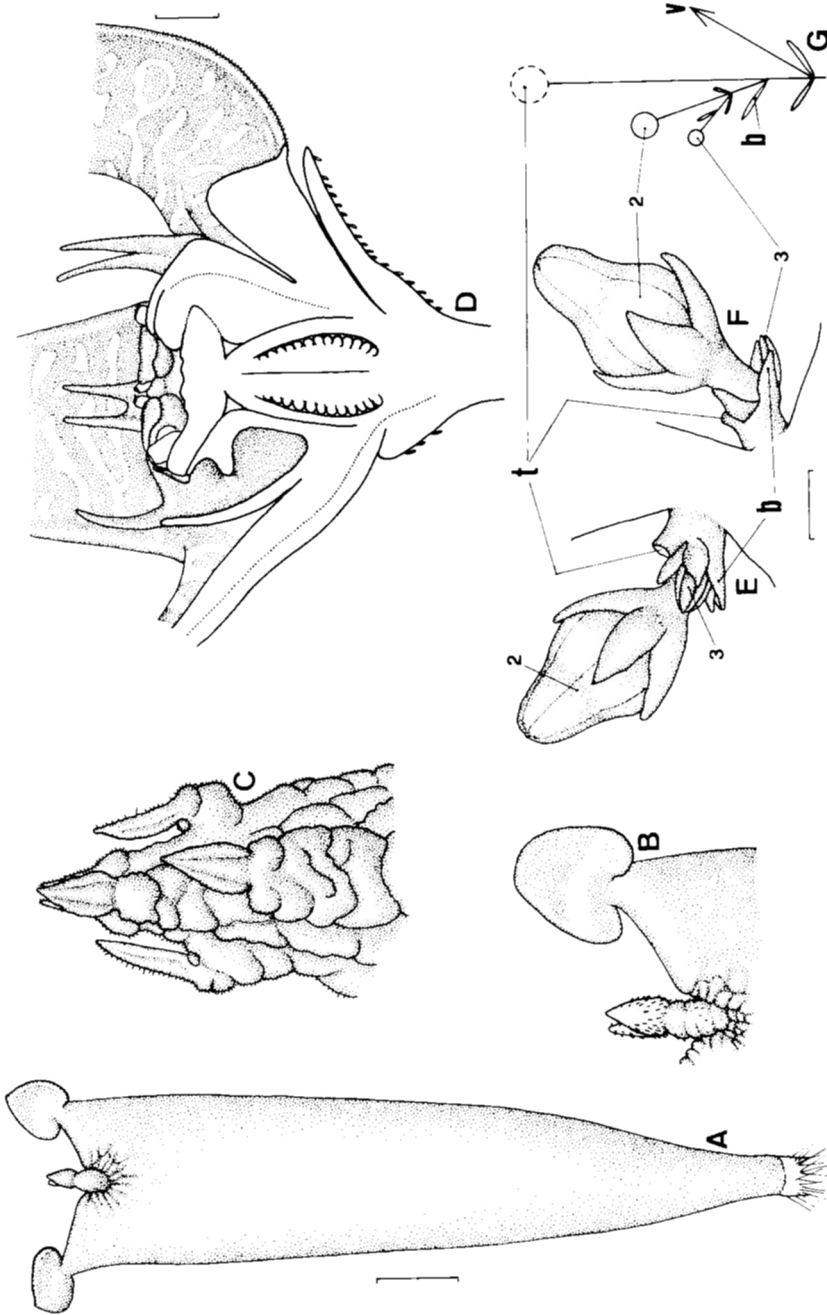


FIG. 2. *Rhytidocaulon* (*R. macrolobum*, ex hort.). A, B, seedling; A, side view of plantlet; B, close-up of apex of plantlet. C, apex of growing stem showing leaves, stipules and wrinkled surface. D, half flower. E-G, inflorescence; E, F, views from opposite sides of inflorescence in *R. macrolobum* with tissue of stem cut away to reveal peduncle; G, plan diagram of inflorescence in E and F. Here t = terminal flower, 2 = second flower, 3 = third flower, b = lowest bract (unpaired) subtending terminal flower, v = vegetative continuation of stem. Scales A, C,

Flowers arise mainly towards the apex of the stem but can also appear on older inflorescences lower down which may remain active.

In *Rhytidocaulon* the inflorescence (Fig. 2E–G) is relatively few-flowered, usually with 1–3 flowers (sometimes slightly more in *R. fulleri*) arising in gradual succession from each peduncle. The inflorescence is usually buried between the folds on the stem which, if cut away, reveal the presence of a short peduncle. Bracts are small and deltoid but are not toothed. The organization of the flowers in an inflorescence follows the usual pattern for the *Stapelieae* (Bruyns, 1988).

Flower

Corolla. In *Rhytidocaulon* the corolla is usually small, with a maximum of 20mm sometimes achieved in *R. macrolobum*. There is much variation in the shape of the corolla: it may be bud-like, with the lobes remaining fused at the tips (*R. fulleri*, *R. tortum*) or it may open out fully to be rotate. In the latter case it is either deeply lobed, with only a very slight disc below the lobes around the corona or the disc may be quite substantial (*R. paradoxum*). In both cases the disc is somewhat thickened and in *R. macrolobum* there is a relatively massively thickened area around the corona. The corolla-lobes are mostly relatively long and narrow and, towards the apex, always have a thickened, cushion-like area which is uniformly coloured on the inside.

The outside of the corolla has the same scattered, multicellular papillae as are found on the stems with \pm flat outer walls of the cells between them. The papillae are concentrated towards the apex of the lobes. The inside of the lobes seems to consist of two zones: one lies at the thickened area where the colour is uniform and here the tightly packed epidermal cells have rounded outer walls (Fig. 3A), the other is lower down on the lobe where it is mottled and barred with a darker colour on a pale background and here the epidermal cells are elongated from broad, tightly packed lower parts into sharp-tipped spikes (Fig. 3B).

The margins of the lobes often have vibratile cilia but these are restricted to a small zone alongside the thickened, apical portion and do not occur right at the tip.

Gynostegium. The inner and outer coronal series are well developed. The outer series consists of five lobes but these almost always spread by a ring of tissue around the bases of the inner lobes to join up adjacent outer lobes. This ring of tissue becomes conspicuous in several species: in *R. paradoxum*, together with the outer lobes, it forms a continuous rampart around the central part of the gynostegium; a similar structure is also found in *R. fulleri* where the parts behind the inner lobes are actually longer than those between the anthers (Fig. 6D); in some others (*R. piliferum*, *R. tortum*) it consists of five discrete lobes in series with the outer lobes; in *R. macrolobum* it is reduced to an indistinct ridge and, in *R. sheilae*, it may even be absent. The inner corona-lobes are always very much dorsiventrally flattened and adpressed

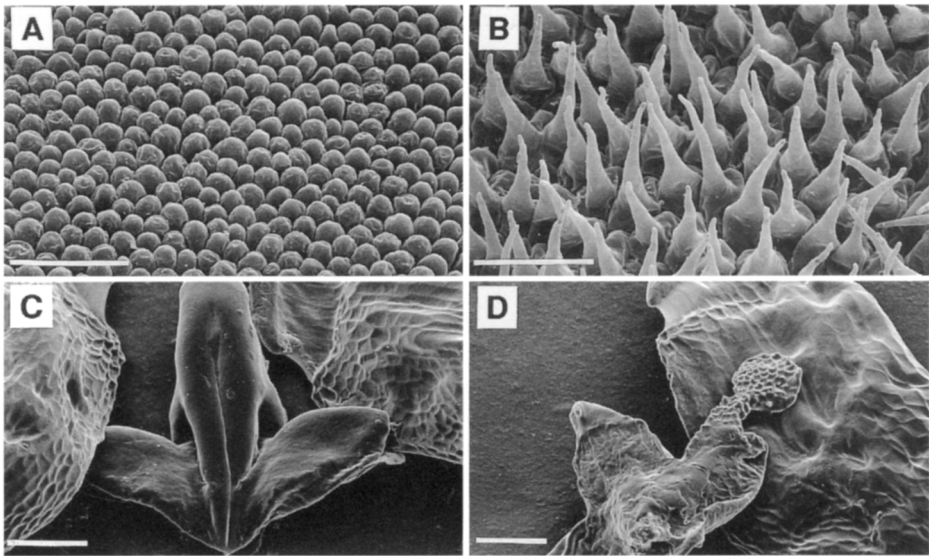


FIG. 3. Inner surface of flower (A, B) and pollinarium (C, D) of *Rhytidocaulon* (*R. macrolobum*, ex hort.). A, upper part of corolla-lobe (uniformly coloured patch); B, lower part of corolla-lobe (mottled part); C, corpusculum; D, underside of corpusculum and one pollinium showing attachment of caudicle. Scale bars (approx.): A, C, 50 μ m; D, 10 μ m.

to the backs of the anthers, sometimes exceeding them slightly. They lack any kind of dorsal appendage.

A half-flower (Fig. 2D) reveals that the carpels are small and short, that the style-head is plate-like (i.e. concave above, very thin and broad) and rises up considerably under the corpusculum, pushing this nearly above the level of the anthers. One finds, too, that the pollinia are pushed up as well near the corpusculum so that the edge with the germinating mouth on it projects a bit above the anthers. The guide rail is short and projects only slightly outwards.

Pollinarium. The pollinaria are small with pollinia 0.18–0.23 \times 0.25–0.40mm, i.e. they are broader rather than long with the germinating mouth exactly along the shorter, outer edge. They have a narrow corpusculum (0.17–0.27mm long; Fig. 3C), relatively small wings and a small, slender caudicle leading to the round adhesive patch underneath the pollinium. The corpusculum seems, at least in some cases, to be unusually sculptured, with a distinct widening above the points of attachment of the wings.

Follicles, seed and seedlings

Follicles. Follicles are erect, slender, paired with horns diverging at 30–60°. They are usually faintly mottled with dark purple.

Seeds. Seeds of *Rhytidocaulon* (Fig. 4) are very distinctive. They vary from 4.5–6.5 \times

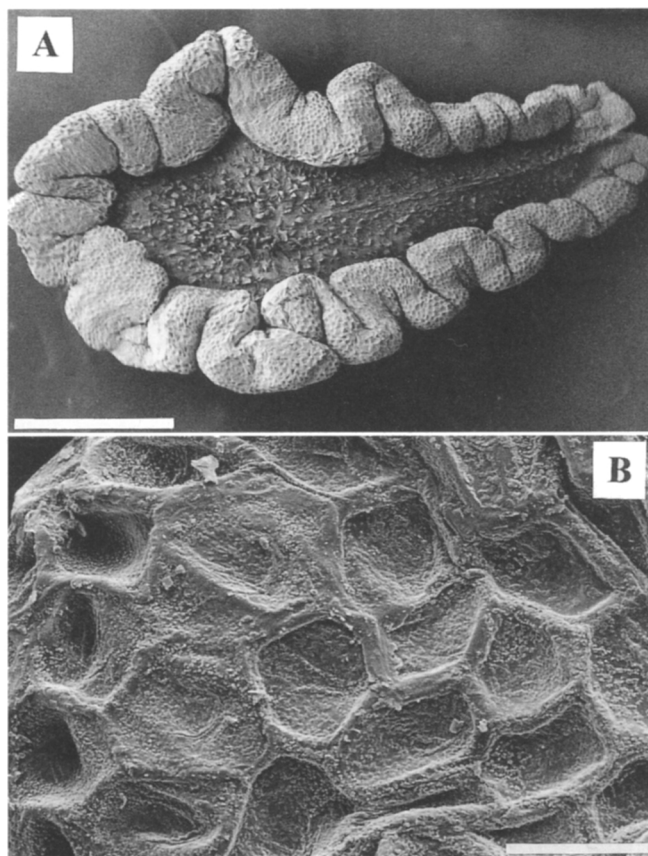


FIG. 4. Seeds of *Rhytidocaulon* (*R. macrolobum*, ex hort.). A, whole seed, ventral side; B, cells on border with sunken outer walls and raised anticlinals. Scale bars (approx.): A, 1mm; B, 50 μ m.

2.0–3.0mm, so are relatively small (largest seen in *R. fulleri* and *R. macrolobum*, smallest in *R. sheilae*) and they are narrowly pear-shaped in outline. They have a pale pinkish brown margin which is thick and extremely convoluted. The testa on the upper (flat/concave) surface is darker and covered with quite long, white, collapsed papillae. The lower (convex) surface is also papillate with similar, though often shorter, white papillae even extending slightly onto the border. The cells on the border have depressed and slightly convex outer walls with the anticlinal walls raised and clearly visible.

Seedlings. Plantlets (Fig. 2A,B) of *Rhytidocaulon* have a uniformly green, narrowly wedge-shaped hypocotyl, at the apex of which are two broad, cordate cotyledons. The primary leaves soon appear and are papillate, with the primary tubercles both papillate and rugulose. The rugosities begin to develop just below the terminal bud.

Distribution and habitat

Rhytidocaulon is found in north-east Africa and southern Arabia (Fig. 5) and is recorded so far in the Ogaden of Ethiopia, Kenya, Somalia, south-western Saudi Arabia, Yemen and the Dhofar province of Oman.

Plants (especially smaller ones) bear a close resemblance to dried twigs and this makes them very difficult to spot in their natural habitat (Jonkers, 1989, 1993). They can only be found relatively easily after good rains have fallen. It is likely, therefore, that *Rhytidocaulon* is somewhat more widely distributed than at present known.

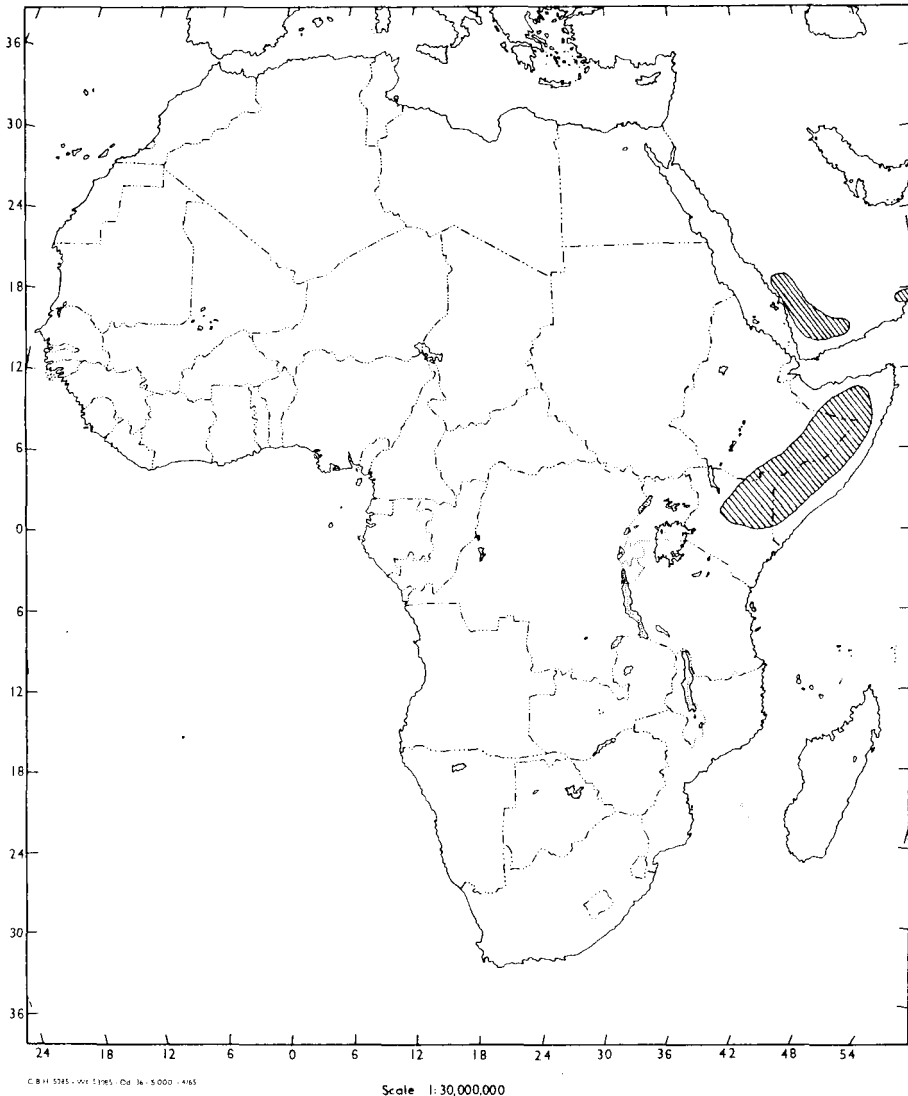


FIG. 5. Known distribution of *Rhytidocaulon*.

It appears that specimens are usually to be found growing well hidden within other, sometimes very spiny, protecting shrubs. Their edibility to both man and grazing animals makes this more or less obligatory for their survival, though occasional large and rather more obvious plants seem to survive (Newton, 1980). Their very rapid attainment of sexual maturity and flowering on the primary stem are also clearly adaptations to severe grazing pressure.

DISCUSSION

Rhytidocaulon shares two characters with *Stapelianthus*: rugulose stems and seedlings and thin, flat style-head. However, they have nothing else in common, so these appear to be purely fortuitous similarities. The long, thin stems, comparatively large leaves and small flowers of *Rhytidocaulon* suggest a relationship to *Caralluma* subg. *Caralluma* (Gilbert, 1990) in which species like *C. adscendens* (Roxb.) Haw. have very similar pollinia to *Rhytidocaulon*. There is also remarkable similarity between the gynostegia of *R. macrolobum* and *C. adscendens*. Again, however, there are many differences: the rugulose stems, the \pm globose stipules without hairs, the sunken inflorescences and also the unusual papillae on the stems, leaves, pedicels, sepals and outside of the corolla.

Bally (1962) suggested that the flowers were most similar to those of *Echidnopsis*. Indeed there are many similarities between these genera: rugulose stems are found in *E. leachii* Lavranos and to a lesser extent in *E. cereiformis* Hook. f. and *E. dammanniana* Sprenger (Bruyns, 1988), similar (though not quite such long) leaves, \pm globose stipules without hairs, small, often flat flowers with papillate exterior of the corolla (e.g. *E. dammanniana*), papillate exterior of the sepals (sometimes in *Echidnopsis*, always in *Rhytidocaulon*) and small pollinaria with very similar shape. The differences between the genera were discussed in Bruyns (1988) and can now be slightly amplified: stems of *Echidnopsis* are 6-20 angled and mat-forming while those of *Rhytidocaulon* are 4-angled and erect; the epidermis in *Echidnopsis* is \pm smooth to papillate with the outer wall of every epidermal cell elongated into a unicellular papilla while in *Rhytidocaulon* the papillae are scattered and multicellular with intervening epidermal cells flat-walled; inflorescence superficial in *Echidnopsis*, sunken in *Rhytidocaulon*.

A cladistic study (Bruyns, in prep.), places *Rhytidocaulon* in a basal position just above *Caralluma* and sharing a clade with *Echidnopsis*.

TAXONOMY

Rhytidocaulon P.R.O. Bally, *Candollea* 18: 336 (1962). *Field*, *Kew Bull.* 36: 51–54 (1981). Type: *R. subscandens* Bally.

Sparsely branched succulent with branches usually much shorter than primary (main) stem, branching well above ground and rooting at base of primary stem only. *Stems* erect often later spreading horizontally, 30–500 \times 5–25mm, grey to grey-green or

purplish, rugose, sparsely papillate, with translucent epidermis; tubercles indistinctly rectangular, joined into 4 (–6) angles along stem or obscure with stem cylindrical; *leaves* 2–4 × 1mm, erect, ovate to lanceolate, fleshy, with distinct midrib on rear, papillate, subtended by two glandular stipules on either side at base, rapidly caducous. *Inflorescences* many, mainly in upper parts of primary stem and branches, sunken into surface and ± without peduncle, each with 1–3 (–6) flowers maturing in gradual succession, bracts narrowly deltoid < 1mm long, glabrous; *pedicel* 0.5–2.0 × 0.5–1.0mm, papillate; *sepals* 1.2–3.0 × 0.4–1.3mm, narrowly deltoid, papillate on outside only, usually adpressed to corolla. *Corolla* ± rotate and 6–20mm diam. or bud-like with lobes fused at apices and then 5–17 × 4–5mm; outside papillate especially towards apices of lobes, usually greyish with faint darker red or purple spots or bars; inside ± smooth; *tube* very short (< 1.0mm) and containing only lower part of gynostegium; *lobes* linear to ovate-deltoid, spreading to connivent at apices, usually speckled or banded in lower half and uniformly coloured in upper half where distinctly thickened, margin often with cilia towards apex and folded back towards base so that lobes convex above base. *Corona* (1.5–) 2.5–4.0mm diam., consisting of two series, often somewhat papillate on outer lobes but otherwise glabrous, raised on slight stipe to sessile; *outer lobes* sometimes united into ring around column, more usually consisting of 5 free ± erect bifid lobes; *inner lobes* rectangular to deltoid from broad base, dorsiventrally flattened, adpressed to backs of anthers and sometimes meeting in centre, without dorsal projections.

Key to species

- 1a. Corolla-lobes connivent, remaining fused at tips to form bud-like flower — 2
 1b. Corolla-lobes spreading, not remaining fused at tips ————— 3
- 2a. Corolla-lobes twisted together into long thin column; outer corona-lobes deeply bifid into cylindrical teeth, with simple tooth behind inner lobes ————— **R. tortum**
- 2b. Corolla-lobes not twisted; outer corona shallowly bifid, forming channelled projections behind inner lobes ————— **R. fulleri**
- 3a. Corolla-lobes uniformly coloured, covered in upper half with fine twisted hairs ————— **R. richardianum**
- 3b. Corolla-lobes mottled with red or purple on whitish to green towards base, sometimes with marginal cilia towards apex but otherwise glabrous ————— 4
- 4a. Outer coronal series with conspicuous parts behind inner lobes ————— 5
 4b. Outer coronal series without conspicuous parts behind inner lobes ————— 6
- 5a. Outer corona fused into continuous ring around gynostegium — **R. paradoxum**
 5b. Outer corona with 10 erect lobules, and discrete lobules behind inner lobes ————— **R. piliferum**

- 6a. Corolla-lobes deltoid, 3×2 mm, eciliate (Somalia) _____ **R. subscandens**
 6b. Corolla-lobes lanceolate, usually ciliate towards tips (Arabia) _____ 7
 7a. Corolla-lobes $3-5 \times$ up to 1.5mm _____ **R. sheilae**
 7b. Corolla-lobes $5-9 \times 2$ mm _____ **R. macrolobum**

1. **R. fulleri** Lavranos & Mortimer, Natl Cact. Succ. J. 25: 3 (1971). Jonkers, Asklepios 60: 31–34 (1993). Type: Oman, Dhofar Province, north of Rakhyut, 900m, 14 xi 1968, *Fuller sub Lavranos & Mortimer* 7133 (PRE! holo.). **Fig. 6.**

Stems erect to spreading, sometimes almost prostrate, 100–400 \times 15–25mm, obscurely to very clearly 4-angled. *Pedicel* 1.0×0.5 mm; *sepals* $1.5-3.0 \times 0.5$ mm. *Corolla* 5–10mm long, 4–5mm diam. at base, narrowing to obtuse apex where corolla lobes fused; outside greyish white with faint reddish dots or bars; inside on lower half of lobes white to pale yellow irregularly transversely barred with brownish red, on upper half uniformly brownish red; *tube* \pm absent; *lobes* \pm lanceolate, connivent and remaining fused at obtuse apices, thickened in upper half, margins folded back strongly in lower half, eciliate. *Corona* 2.5–3.5mm diam., reddish above becoming cream towards base; *outer lobes* bifid into broad \pm deltoid erect lobules forming obtuse emarginate channel behind inner lobes which spreads into gap between bases of corolla-lobes; *inner lobes* broadly deltoid, truncate to emarginate, adpressed to backs of and often covering anthers.

Jonkers (1993) has shown that this rare species occurs between Marbat and Rakhyut in the Dhofar province of Oman, from the coastal plain at 100m to 1150m on the northern slopes of the Jebel Qamar. Its presence in the eastern part of the former South Yemen is not unlikely.

I have not been able to find any evidence of cilia on the lobes ('their margins ciliate' according to the original description) and photographs by Jonkers and v. Donkelaar show the flowers to be eciliate. Photographs of Jonkers also show that quite substantial peduncular patches may develop so that up to six flowers may arise from each inflorescence. The flowers are remarkably attractive inside, mottled with red on whitish (these markings are not indicated in Fig. 6 which were drawn from preserved material, in which they had vanished).

The outer corona forms a continuous ring around the gynostegium and is, in this respect, similar to that in *R. paradoxum*. However, here spreading channels are formed behind the inner lobes and these channels fit fairly closely into the spaces between the bases of the corolla-lobes.

2. **R. macrolobum** Lavranos, Cact. Succ. J. (U.S.) 39: 3 (1967). Type: South Yemen, Lodar, 1000m, 19 i 1966, *Lavranos* 4366 (K holo.; PRE, G, P iso.). **Fig. 7.**

Stems erect, becoming horizontal above, sparsely branched, up to 250 \times 20mm, obscurely 4-angled. *Pedicel* 1.3×1 mm; *sepals* $1.2-2.0 \times 0.6$ mm. *Corolla* 10–20mm diam., \pm rotate, lobed nearly to base but usually with thickened raised area at mouth of tube around column; outside white to grey flecked finely with purple except

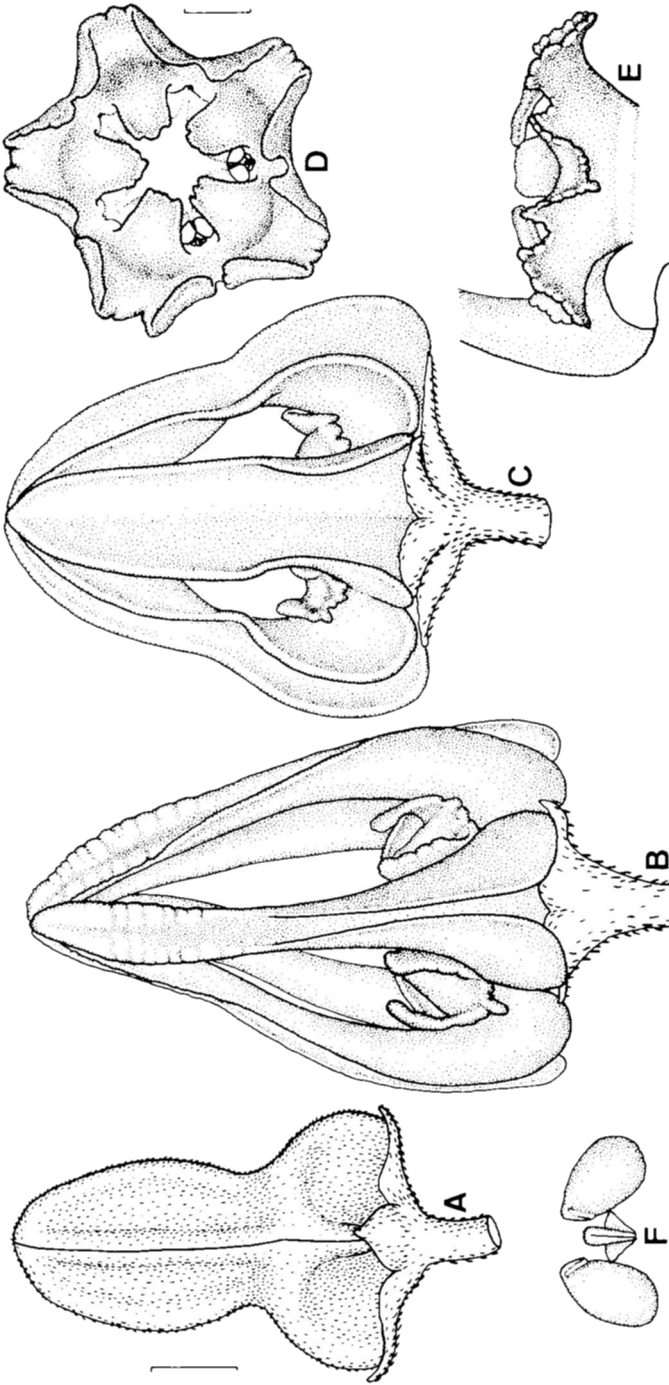


FIG. 6. *Rhytidocaulon fulleri*. A, bud; B, C, side view of corolla; D, face view of gynostegium; E, side view of gynostegium; F, pollinarium. Scales: A-C, E, 1 mm (at A); D, 0.5 mm; F, 0.25 mm (at A). Drawn from: A, B, D, *Miller* 6112, Oman (E); C, E, F, *Jonkers* 145 (no specimen).

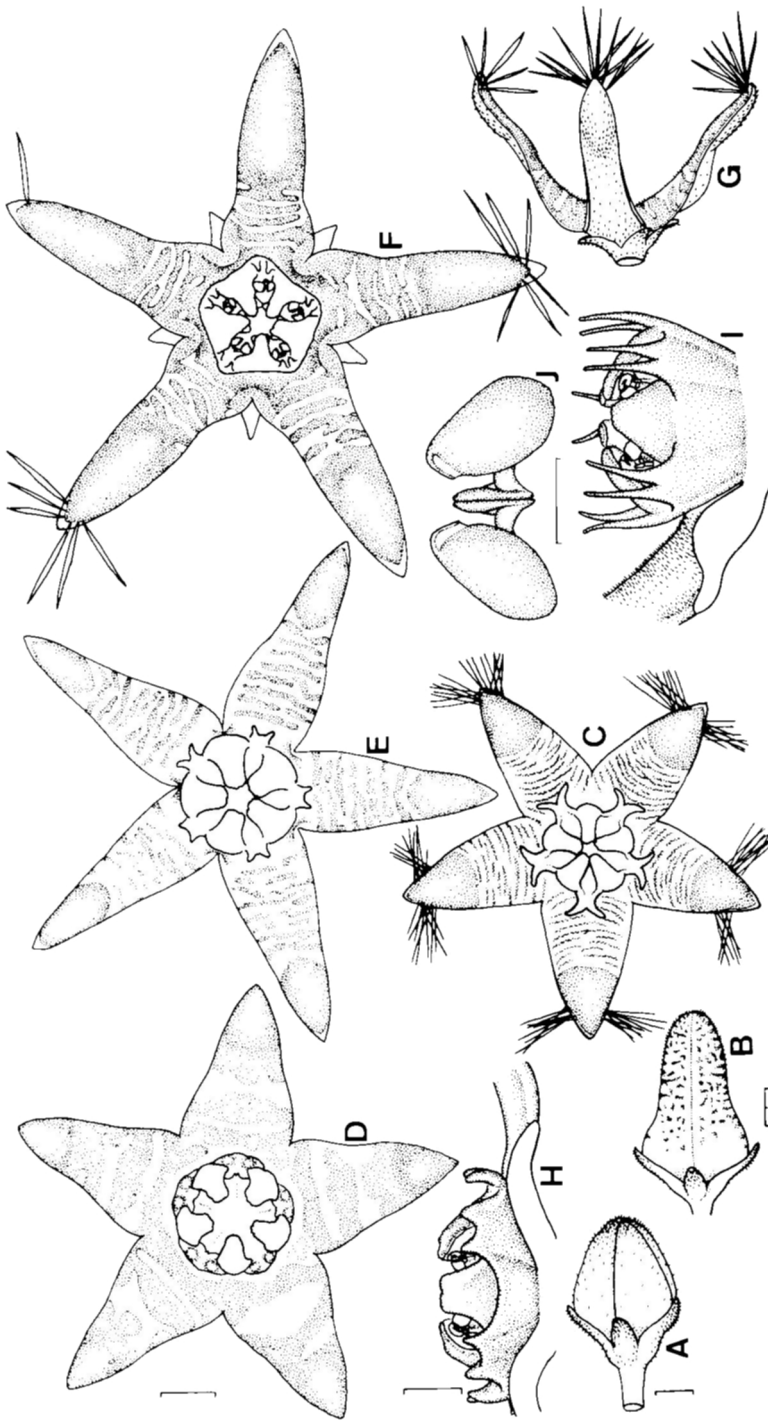


FIG. 7. *R. macrolobum*, *R. sheilae*, *R. subscandens*: A, B, buds; C-F, face view of corolla; G, side view of corolla; H, I, side view of gynostegium; J, pollinarium. Scales: A, G, 1mm (at A); B, 2mm; C-F, 1mm (at D); H, I, 0.5mm (at H); J, 0.25mm. *R. macrolobum* subsp. *minimum*: A, C, Saudi Arabia, Manfah, 6200'; *Collenette* 3301 (ZSS). *R. macrolobum* subsp. *macrolobum*: B, F, G, I, Saudi Arabia, Jabal Fayfa, 5200'; *Collenette* 3600 (ZSS); J, Yemen, 6km W of Hajdah, \pm 1200m, *Noltee* 366 (no specimen). *R. sheilae*: E, Saudi Arabia, Mukaylah, 2000'; *Collenette* 2705 (ZSS). *R. subscandens*: D, H, Somaliland, between Hargeisa and Burao, *Bally & Peck* S 111 (ZSS).

towards base; inside whitish to green towards base; *tube* < 1mm long; *lobes* initially ascending then spreading, \pm lanceolate, 5–9 \times 2mm, inside often lined all round with purple, lower half transversely and irregularly barred with dark purple, upper half uniformly dark purple or grey, margins slightly recurved towards base only, usually with a cluster of narrow cilia 2–3mm long on either side towards apex. *Corona* \pm 2.5mm diam.; *outer lobes* deeply bifid into narrow erect to diverging cylindrical lobules often setose towards apices, fused lower down to backs of inner lobes to form deep cup around anthers; *inner lobes* adpressed to backs of anthers, purple-red, broadly deltoid from base to truncate or emarginate apex, often exceeding anthers and meeting in centre.

This species was originally discovered in the former South Yemen. Today it is known widely in what was formerly North Yemen through the collections of F.K.A. Noltee and J.R.I. Wood and has been found as well in several localities in Saudi Arabia by I.S. Collenette.

R. macrolobum is a very variable species. The buds usually have a narrow beak above a broad base but may be nearly cylindrical (Collenette 2919 (ZSS)). The corolla may be green or whitish mottled inside with purple. The outer corona is very variable also, with lobules from erect to widely diverging. These outer corona-lobes are remarkably similar to those found in *Caralluma adscendens* and *Quaqua parviflora* (Masson) Bruyns and seem to be quite common in small-flowered stapeliads.

R. macrolobum subsp. **minimum** Meve & Collenette, *Edinb. J. Bot.* 56: 79–84 (1999). Type: Saudi Arabia, Collenette 7565 (holo. K, in alc.).

Several small-flowered plants very similar to *R. macrolobum* have been collected in Yemen and Saudi Arabia, often with fairly tall, stout stems, which have a more conspicuous, white outer corona and a slightly different pattern of colours on the corolla (see Fig. 7A,C). These have recently been published as *R. macrolobum* subsp. *minimum* Meve & Collenette.

3. **R. paradoxum** P.R.O. Bally, *Candollea* 18: 339 (1962). Bruyns, *Bradleya* 4: 29–38 (1986). Jonkers, *Succulenta* 68: 225, 227–231 (1989). Type: Ethiopia, Ogaden, west of Shillave, 400m, xi 1955, *Ellis* 405 (K! holo.; ZSS! iso.). **Fig. 8.**

Stems up to 120 \times 15mm, obscurely 4-angled. *Pedicel* < 1mm long; *sepals* 2mm long, deltoid. *Corolla* 8–9mm diam., lobed to about half of radius with united portion somewhat thickened towards edge of corona; outside greyish to faintly pinkish; inside speckled with pale red on whitish except towards tips of lobes where solid pale red; *tube* very shallow; *lobes* spreading to adpressed to stems, broadly ovate-deltoid, 2.5–3.0 \times 3.0mm. *Corona* 3.5–4.0mm diam., pale orange around edge, rest greenish brown; *outer lobes* forming continuous flat ring around column with toothed edge \pm adpressed to corolla and five short slightly incurved lobes rising up from this which are bifid into broad rounded flaps, exterior of ring papillate, interior smooth:

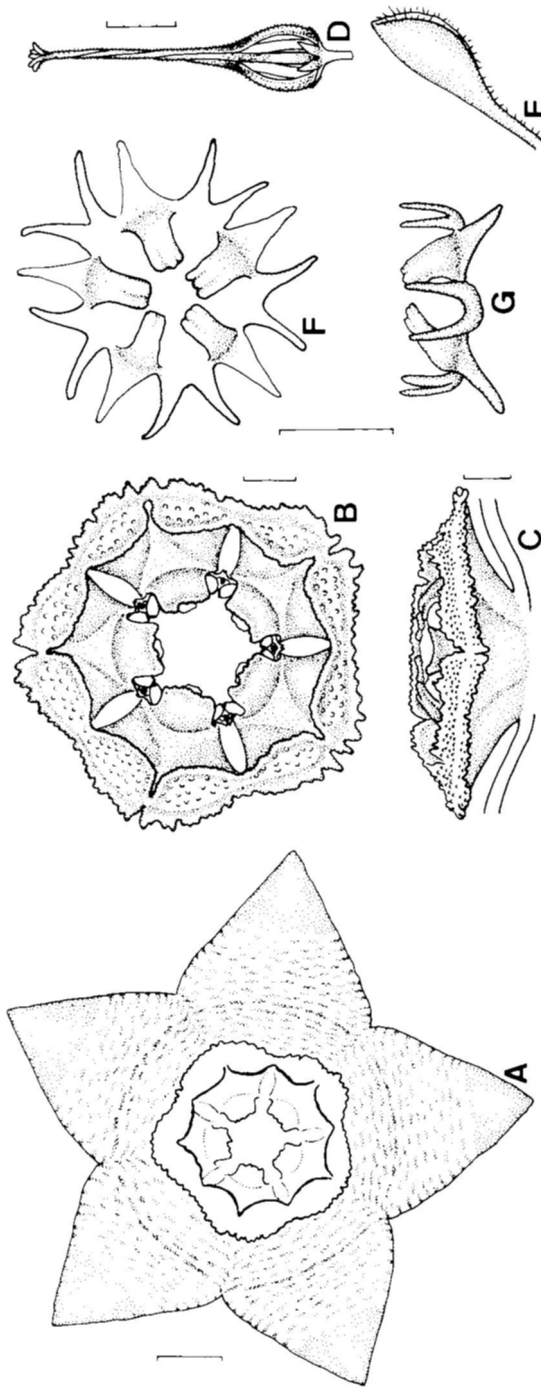


FIG. 8. *R. paradoxum*. *R. tortum*: A, flower, face view; B, gynostegium, face view; C, gynostegium, side view. D, side view of corolla; E, tip of corolla-lobe; F, face view of gynostegium; G, side view of part of gynostegium. Scales: A, 1mm; B, 0.5mm; C, 0.5mm; D, 4mm; E, 0.5mm (at F); F, G, Imm. *R. paradoxum*: Kenya, near Rumuruti. *Poirivix* 520 (no specimen). *R. tortum*: D copied from White & Sloane, 1937; E-G, rough sketches from type specimen (K).

inner corona nearly rectangular from broad base, adpressed to backs of anthers and \pm equalling them, truncate, emarginate.

This species is now known from three localities, one each in Ethiopia, Kenya and Somalia.

R. paradoxum has remarkable, more or less flat flowers with an unusual, pale red colour. The corona is particularly unusual, with the outer corona lobes joined into a continuous, almost uniformly broad ring around the column. A similar outer corona has been observed in some collections of *Echidnopsis scutellata* subsp. *planiflora* (P.R.O. Bally) Bruyns (Bruyns, 1988).

4. **R. piliferum** Lavranos, Cact. Succ. J. (U.S.) 43: 62–3 (1971). Type: Somalia, between Lower Sheikh and Bihendulla, near Manja Asseh, 700m, 16 xii 1969, *Lavranos* 7365 (FT holo., now useless (Meve, 1989)).

Stems ascending to erect, up to 400×5 –12mm. *Pedicels* ± 2 mm long; *sepals* deltoid. *Corolla* \pm rotate, 10mm diam.; *tube* 1×2 mm; *lobes* 4mm long, spreading, with deltoid base then rest narrow, inside lower half white with irregular transverse dark purple bands, upper half thickened and dark purple, bearing cluster of dark purple vibratile cilia (± 1 mm long) near apex, margins recurved. *Corona* dark purple; *outer lobes* bifid nearly to base into ascending \pm cylindrical lobules, with bifid flattened spreading lobule behind inner lobes; *inner lobes* broadly truncate, adpressed to backs of anthers.

The corolla, with its narrow lobes and cilia resembles those of *R. macrolobum* and *R. sheilae* from Arabia and the corona has deeply bifid outer lobes as in those species. Nevertheless, the outer corona produces also a conspicuous, spreading, bifid lobule behind each inner lobe and this structure is lacking in both these Arabian species.

5. **R. richardianum** Lavranos, Cact. Succ. J. (U.S.) 63: 167 (1991). Type: Somalia, 75km NNW of Eil on road to Sinujif, 550m, 24 xi 1986, *Lavranos et al.* 24895 (UPS).

Stems 50 – 80×7 mm. *Pedice*l $\pm 1.5 \times 0.6$ mm; *sepals* 1.2×0.4 mm, deltoid, acute. *Corolla* nearly rotate, lobed nearly to base; inside uniformly yellow-green; *tube* $< 1.0 \times 2.0$ mm; *lobes* $\pm 4.5 \times 2.0$ mm (at base, narrowing to 1.6mm just above middle then widening slightly before acute apex), slightly rugulose within on lower half, upper half distinctly thickened, covered with long fine purple twisted and entangled hairs. *Corona* ± 1.5 mm diam.(?), reddish purple becoming paler towards tips of lobes; *outer lobes* divided nearly to base into two erect slightly dorsiventrally flattened lanceolate acute lobules, basal part slightly spreading, papillate; *inner lobes* \pm rectangular from broad base, adpressed to backs of anthers, truncate-emarginate.

No other species has uniformly coloured flowers with fine hairs covering the upper surface of the lobes. It is most unfortunate that the description of this new species is particularly brief. The drawings accompanying it are somewhat fanciful and completely without scales and it is further accompanied by a very poor photograph, so that further comparisons are not possible.

6. ***R. sheilae*** D.V. Field, Kew Bull. 36: 51 (1981). Type: Saudi Arabia, 15km SE Khamis Mushayt, 7 iv 1979, *I.S. Collette* 1304 (K! holo.). **Fig. 7.**

Stems ascending to erect, up to 200×7 –15mm, side branches often \pm horizontally spreading. *Pedicels* $\pm 2.0 \times 0.5$ mm, descending; *sepals* deltoid, 1.0×0.5 mm. *Corolla* rotate, 6–10mm diam.; outside greyish speckled faintly with pale purple; *tube* up to 0.5×1.5 mm, pale cream inside, slightly thickened around mouth; *lobes* 3.0 – 5.0×0.7 – 1.5 mm, narrowly acuminate-deltoid, basal half with narrow purple-green to brown-green bars and margin on green to whitish background, upper part slightly narrower, thickened, pale brown-green to cream, margins slightly recurved and often with a few cilia near apex. *Corona* 1.25–2.00mm diam., purple-black; *outer lobes* erect to spreading, slightly bifid at tips, very short (just reaching height of base of guide rail) laterally joined to broad base of inner lobes, sometimes with slight ridge below bases of inner lobes; *inner lobes* broadly deltoid, adpressed to backs of anthers and often exceeding them slightly.

Very closely allied to *R. macrolobum*, *R. sheilae* differs by its generally smaller, less robust, more horizontally spreading plant, smaller flowers facing downwards with few cilia towards the end of the lobes and very short outer corona-lobes. The bud is usually deltoid from the base and without a constriction below the middle.

It is in fact a rather variable taxon especially in the colour of the flowers and even in their size. In one plant (*Collette* 2705 (ZSS)), the corolla-lobes sometimes remained fused at their apices.

Whether this is actually a distinct species or merely a form of *R. macrolobum* is impossible to judge from the material seen.

7. ***R. subscandens*** P.R.O. Bally, Candollea 18: 337 (1962). Type: Somalia, between Hargeisa and Burao, Jan. 1944, *Bally & Peck* S 111 (G holo.; K!, ZSS! iso.). **Fig. 7.**

Stems up to 110×15 mm, erect to spreading horizontally. *Pedicel* $0.5 \times \pm 0.5$ mm, descending; *sepals* 2.50×1.25 mm, deltoid-lanceolate. *Corolla* 9mm diam., rotate; outside green; inside barred with red on whitish up to middle of lobes, rest of lobes uniformly red; *tube* \pm absent; *lobes* 3×2 mm, deltoid, acute, with noticeably thickened tip, eciliate. *Corona* ± 3 mm diam.; *outer lobes* erect, very short and bifid, laterally fused to bases of inner lobes, sometimes forming ridge below bases of inner lobes; *inner lobes* broadly deltoid, with obtuse emarginate apices, adpressed to backs of anthers.

This species is known only from a gathering of Jackson in the Ogaden Province of Ethiopia and the type collection from Somalia.

It is very closely allied to *R. macrolobum* and even more so to *R. sheilae*, differing from the former by the smaller, eciliate flowers and from the latter by the broader corolla-lobes.

8. ***R. tortum*** (N.E. Br.) M.G. Gilbert, Bradleya 8: 29 (1990). *Caralluma torta* N.E. Br., Kew Bull. Misc. Inform. 1901: 142 (1901). White & Sloane, Stap. ed. 2, 1: 258 (1937). Type: Arabia or Socotra, sent to Kew 1897, flow. ix 1897, *Bent* (K! holo.). **Fig. 8.**

Stems 8–11mm thick. *Pedicels* <1mm long; *sepals* 1.5–2.1mm long, reflexed. *Corolla* 16–17mm long; inside glabrous, lobes green spotted with purple-brown at base;

tube ± absent; *lobes* linear, spreading at base then erect and connivent, twisted together into long thin column, thickened at tips, margins very much reflexed at base, ciliate. *Corona* ± 3mm diam., purple-brown, apices of lobes pale; *outer lobes* almost 1mm long, erect from spreading base, deeply bifid into ± cylindrical lobules, with spreading lanceolate-deltoid lobule behind inner lobes ± equalling bifid part; *inner lobes* nearly rectangular from broad base, truncate-emarginate, adpressed to backs of and exceeding anthers.

Characters of the stem clearly place this species in *Rhytidocaulon*. Examination of the type revealed that the drawing by S. Ross-Craig (White & Sloane, 1937) is not very precise: there is a distinct outward folding of the margins of the corolla lobes towards their bases (this is not shown in Fig. 8A, which was copied from that of S. Ross-Craig) and each lobe has a thickened apex. This then suggests a much closer affinity to *R. fulleri* than was formerly obvious. The corona is, however, not that similar: the inner lobes are typical of *Rhytidocaulon* generally. The outer lobes are divided almost to their bases into cylindrical lobules (whereas they are broad and flat in *R. fulleri*) and they produce a spreading tooth behind each inner lobe rather than the broad channel found in *R. fulleri*.

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