

## A re-assessment of the genera *Tridentea* Haw. and *Tromotriche* Haw.

P.V. Bruyns

Bolus Herbarium, University of Cape Town, Rondebosch, 7700 Republic of South Africa

Received 25 November 1994; revised 21 March 1995

The generic delimitation of *Tridentea* Haw. and *Tromotriche* Haw. is considered. Eight species are retained in *Tridentea*: *T. dwequensis* (Lückhoff) Leach, *T. gemmiflora* (Masson) Haw., *T. jucunda* (N.E. Br.) Leach, *T. pachyrrhiza* (Dinter) Leach, *T. parvipuncta* (N.E. Br.) Leach, *T. marientalensis* (Nel) Leach and *T. virescens* (N.E. Br.) Leach. The remaining species are transferred to *Tromotriche*. *Tromotriche engleriana* (Schltr.) Leach is referred back to *Stapelia* as *Stapelia engleriana* Schltr. *Tromotriche* then consists of the following 11 species: *T. aperta* (Masson) Sweet, *T. baylissii* (Leach) Bruyns, *T. choanantha* (Lavrano & Hall) Bruyns, *T. herrei* (Nel) Bruyns, *T. longii* (Lückhoff) Bruyns, *T. longipes* (Lückhoff) Bruyns, *T. pedunculata* (Masson) Bruyns, *T. revoluta* (Masson) Haw., *T. ruschiana* (Dinter) Bruyns, *T. thudichumii* (Pillans) Leach and *T. umdausensis* (Nel) Bruyns. Careful arguments are advanced to justify these changes.

Die generiese begrening van *Tridentea* Haw. en *Tromotriche* Haw. is oorweeg. Agt spesies is behou in *Tridentea*, naamlik *T. dwequensis* (Lückhoff) Leach, *T. gemmiflora* (Masson) Haw., *T. jucunda* (N.E. Br.) Leach, *T. pachyrrhiza* (Dinter) Leach, *T. parvipuncta* (N.E. Br.) Leach, *T. marientalensis* (Nel) Leach en *T. virescens* (N.E. Br.) Leach. Die oorblywende spesies is oorgeplaas na *Tromotriche*. *Tromotriche engleriana* (Schltr.) Leach is terug verander na *Stapelia* as *Stapelia engleriana* Schltr. *Tromotriche* bestaan dan uit die volgende 11 spesies: *T. aperta* (Masson) Sweet, *T. baylissii* (Leach) Bruyns, *T. choanantha* (Lavrano & Hall) Bruyns, *T. herrei* (Nel) Bruyns, *T. longii* (Lückhoff) Bruyns, *T. longipes* (Lückhoff) Bruyns, *T. pedunculata* (Masson) Bruyns, *T. revoluta* (Masson) Haw., *T. ruschiana* (Dinter) Bruyns, *T. thudichumii* (Pillans) Leach en *T. umdausensis* (Nel) Bruyns. Die motivering vir hierdie veranderings word aangebied.

**Keywords:** Stapelieae, taxonomy, *Tridentea*, *Tromotriche*.

### Introduction

There has been a remarkable number of changes at generic level in the Stapelieae over the last 20 years. It is most unfortunate that the present article should have to add to the general nomenclatural 'turmoil' surrounding this group. However, detailed examination of many of the species, in preparation for an account of the tribe as a whole, has revealed that there remain inconsistencies which need to be clarified.

The present article attempts to address one of these problematic areas. In resurrecting *Tridentea* Haw., Leach (1978: 2–3) gave short diagnoses for each of the genera *Stapelia* L., *Tridentea* Haw., *Orbeopsis* Leach and *Orbea* Haw. and mentions in addition that *Tridentea* has 'its closest affinities' with *Orbea* and *Orbeopsis*. In his revision of *Tridentea* (Leach 1980), there is no mention of this 'Orbea-connection' and it is suggested (p. 3) that '*Tridentea* seems most likely to have developed from *Stapelia* Sect. *Gonostemon* (Haw.) Decne.' Here (p. 2) he gives differences between *Tridentea* and *Stapelia*: '*Tridentea* is primarily separated from *Stapelia* by its quite different subtessellately tuberculate and virtually glabrous stems and glabrous, widely-spreading estipulate, subulate leaves or, in some species of sect. *Caruncularia*, leafless'. He also mentions (p. 1) that 'Florally probably the most heterogeneous in the whole tribe, *Tridentea* is nevertheless remarkably homogeneous in its general character, being bound closely together by its vegetative characters which are particularly evident in young growth'.

It is therefore clear that floral characters are not what holds *Tridentea sensu* Leach together. His statement that *Tridentea* is 'most satisfactorily homogeneous' seems to be entirely based on his belief that 'it is the overall characters of the stems and leaves ... which are significant' (Leach 1980: 2). This in turn seems to be derived from the fact that in *Tridentea* Sect. *Tridentea*, leaves are found from large [*T. gemmiflora* (Masson) Haw.] to minute

[*T. pachyrrhiza* (Dinter) Leach], which provides a continuum of variation from the sometimes large leaves in the first two sections to the 'minute ... or absent' leaves of Sect. *Caruncularia*. It is shown here that, when other previously unconsidered characters are taken into account, *Tridentea* is not at all 'satisfactorily homogeneous'.

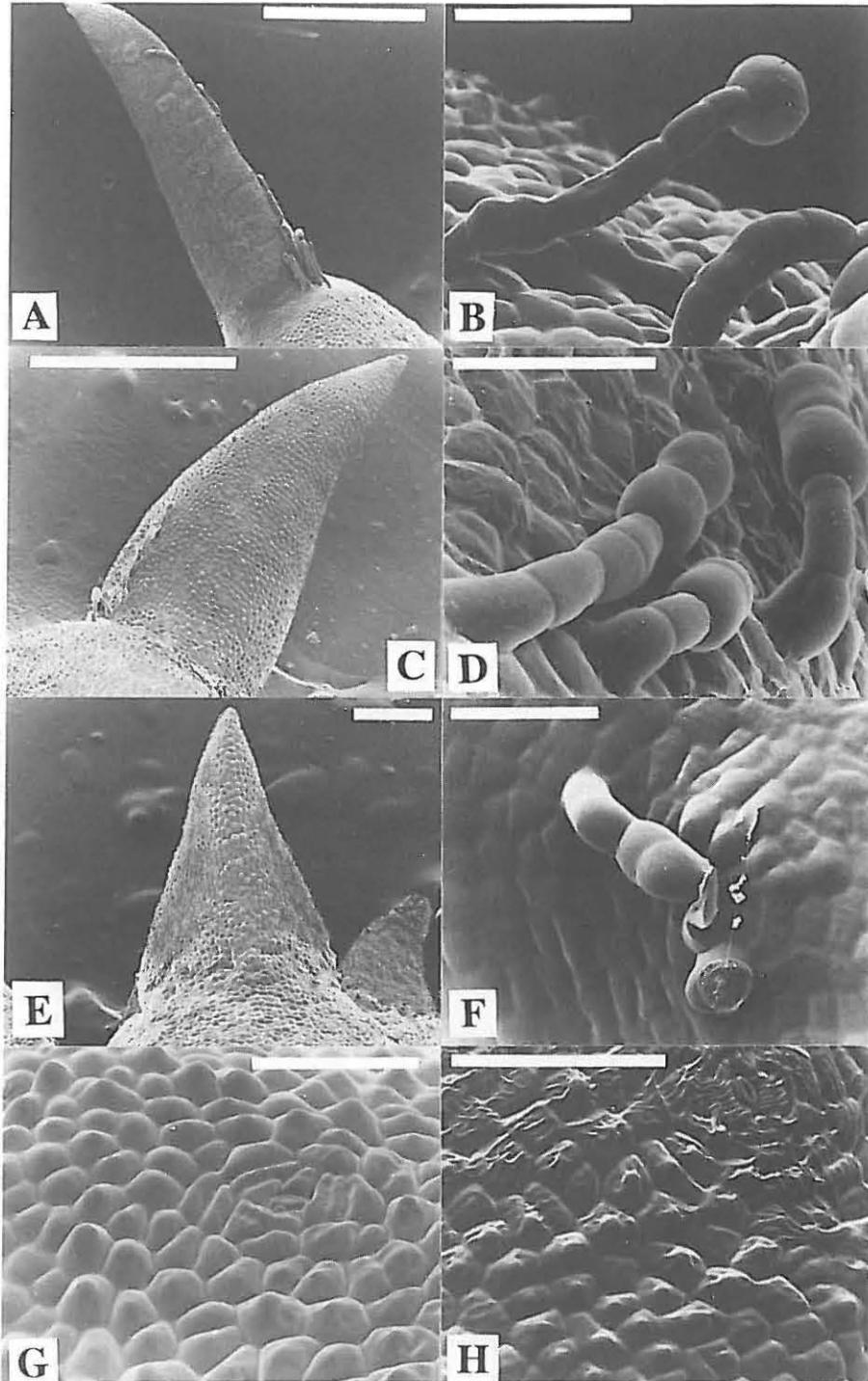
In the revision of *Tromotriche* Haw. (Leach 1984: 550), the diagnostic features are given as 'generally few-stemmed, very sparingly randomly (not sympodially) branched rhizomatous plants with an inflorescence of sessile or subsessile fascicles of shortly pedicellate, strongly revolute flowers, produced randomly along the sides of the stems'. Also 'the three species appear to be more closely related to each other than to any one of the above genera (*Stapelia*, *Tridentea*, *Orbea*, *Quaqua* N.E. Br.); fortunately they exhibit diagnostic characters and correlations which confirm this and are adequate for recognition of the group at generic level'.

Leach (1984: 552) gives a table of characters with a 'numerical summary' which appears to show that the species of *Tromotriche* share more of these characters with each other than with any other group and that they are more closely related to *Tridentea* than to *Stapelia* or *Orbea*. However, there are several points which could shed a rather different light on the issue:

1. The characters 'monopodial stems' and 'corolla strongly revolute' are only partly exclusive to *Tromotriche*. It is not clear why Leach emphasized the 'monopodial, rhizomatous' habit of these species. In the first place, as Meve (1989) pointed out, *T. engleriana* (Schltr.) Leach is not always significantly rhizomatous. Leach (1984: 560) quotes a comment by Acocks that 50% of the plant was underground as evidence for the case of *T. engleriana*. However, it is my experience that this is not usually the situation and plants of *T. engleriana* have a nearly identical growth habit to *Stapeliopsis saxa-*

*tilis* (N.E. Br.) Bruyns: horizontal stems mostly forming interwoven mats on the surface with occasional stems going underground. In the second place, extensively rhizomatous species are found randomly in several genera where most of the other species show no tendency towards this habit: *Duvalia polita* N.E. Br., *Orbea paradoxa* (Verdoorn) Leach, *Orbeopsis gerstneri* (Letty) Leach subsp. *gerstneri*, and *Stapeliopsis exasperata* Bruyns. Therefore, this character

needs to be used with caution in the definition of genera. Thirdly, Leach's use of the term 'monopodial' is not correct. Use of this term implies that the subterranean stems in *Tromotriche* continue growing indeterminately. In Bruyns (1988: 3) it is stated that the vegetative growth in all stapeliads is sympodial (determinate) and this remains true even for these species: here the stem continues growing underground (usually  $\pm$  horizontally) for a considerable distance (up to 1 m,

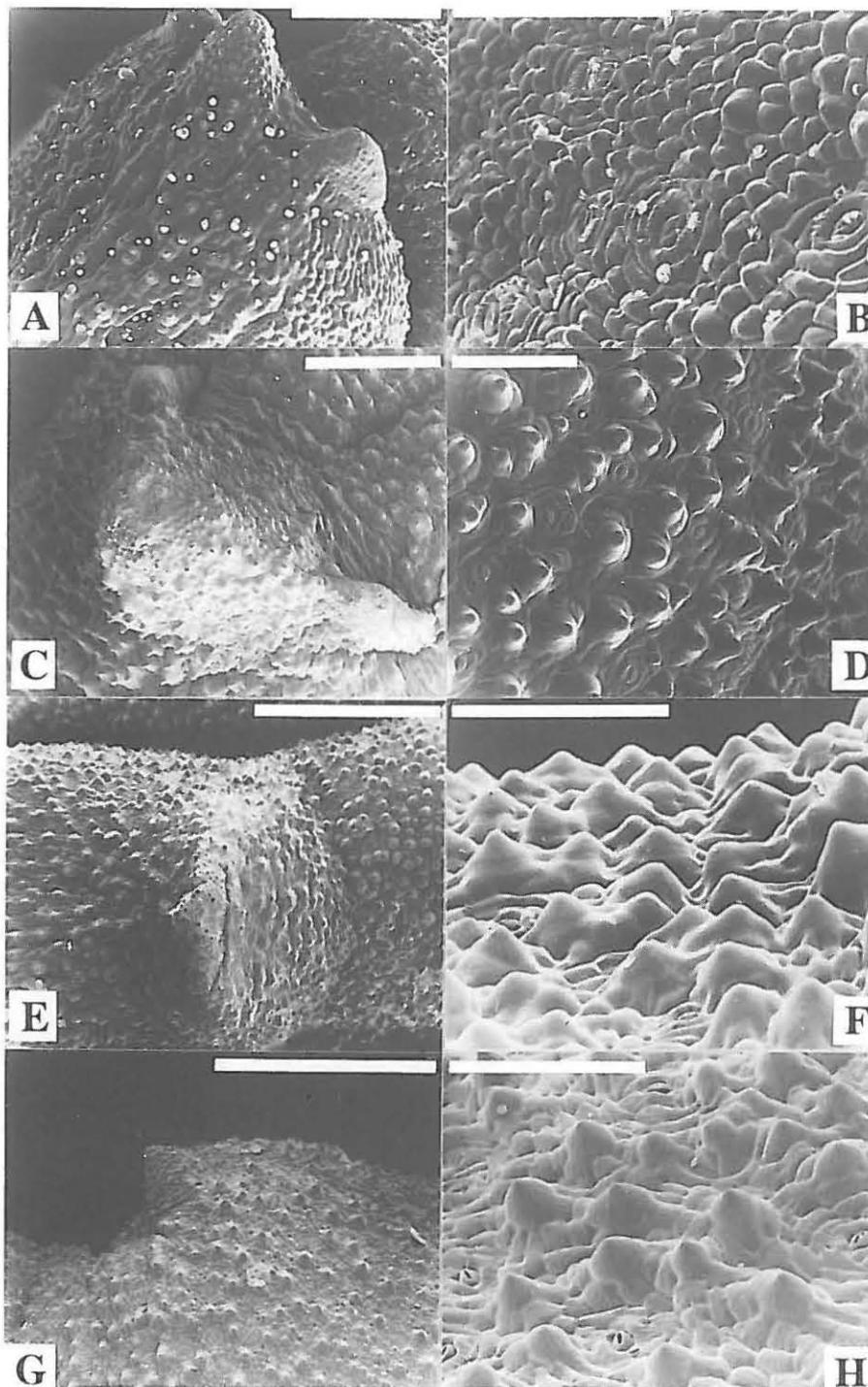


**Figure 1** SEM views of leaves and epidermis of *Tridentea*. *T. gemmiflora*, east of Fraserburg, PVB 4786 (BOL): A, leaf with basal and marginal hairs. B, hairs at base of leaf. *T. jucunda*, south-east of Calvinia, PVB 4291 (no specimen): C, leaf with basal and marginal hairs. *T. parvipuncta* subsp. *truncata*, Botterkloof, Nagel 154 (no specimen): D, hairs at base of leaf. *T. peculiaris*, north of Vanrhynsdorp, Nagel 65 (no specimen): E, leaf, with no hairs visible. *T. pachyrrhiza*, east of Beauvallon, PVB 3945 (no specimen): F, hairs at base of leaf (one  $\pm$  entirely broken off, other with apex broken off). H, surface with nearly flat outer walls of cells. *T. virescens*, east of Beaufort West, PVB 3049 (BOL, NBG). G, surface with nearly flat outer walls of cells. Scale bars: A, C = 1 mm; B, D, F, G = 100  $\mu$ m; E = 250  $\mu$ m; H = 200  $\mu$ m.

rarely more) after which the tip rises above the surface and then is a determinate structure once more.

'Corolla strongly revolute' is shown as occurring in all species of *Tromotriche* and also in *Stapelia erectiflora* Masson. As *Stapelia* is a large genus, one may therefore be led to believe that this character is, to all intents and purposes, diagnostic for *Tromotriche*. However, its occurrence in *Stapelia remota* R.A. Dyer (also with 'shortly pedicellate' flowers) and *Quaqua marlothii* (N.E. Br.) Bruyns indicates that this character is not, after all, diagnostic for *Tromotriche*.

2. The character 'inflorescences randomly produced along the sides of the stems' is not unique to *Tromotriche* at all and the position of the inflorescence is also especially variable in *T. aperta* and *T. undausensis* (see below under Inflorescences).
3. The character 'sessile or subsessile fascicles of shortly pedicellate' flowers is not present in the Table. *Stapelia acuminata* Masson and *Orbea prognatha* (P.R.O. Bally) Leach provide good examples (among many others) which show that this character, too, is not unique to *Tromotriche*. In addition, Figure 5 (p. 560) shows clearly that the pedicels in



**Figure 2** SEM views of leaves and epidermis of *Tromotriche* Sect. *Tromotriche*. *T. revoluta*, Beeswater, Knersvlakte (no specimen): A, leaf with  $\pm$  glandular stipules. B, epidermis. *T. thudichumii*, north of Karooport (no specimen): C, leaf with  $\pm$  glandular stipules. D, epidermis. *T. longii*, Suurberg, PVB 5000 (BOL): E, tubercle. F, epidermis. *T. choanantha*, north of Calitzdorp, PVB 2907 (BOL): G, tubercle. *T. baylissii*, west of Patensie, PVB 1895 (no specimen): H, epidermis. Scale bars: A, C = 500  $\mu$ m; E, G = 1 mm; B, D, F, H = 200  $\mu$ m.

*T. engleriana* are considerably longer than the diameter of the flower and cannot realistically be described as 'short'.

One can conclude, therefore, that Leach's claim, that the three species of *Tromotriche* exhibit diagnostic characters adequate for recognition at generic level, is not true.

This article considers in detail the problem of generic delimitation in *Tridentea* Haw. and *Tromotriche* Haw. An assessment of different characters throughout this group is made, from which characters that are useful for circumscribing the genera are extracted. Rather different conclusions from those of Leach are drawn and the information now available is used to propose a realignment of the species involved into the genera *Tridentea*, *Tromotriche* Haw. and *Stapelia* L. It is possible also, from the evidence presented, to form an opinion on the relationships of these groups to other stapeliads. Finally, a brief but illustrated taxonomic account of *Tridentea* and *Tromotriche* is given. A few additional remarks on individual species are made where new information has become available but descriptions and detailed synonymy are omitted as these were dealt with at length by Leach (1980, 1984). Distribution maps are included: these are based on material cited by Leach and more recent collections made by this author. Citations of new collections are omitted.

## Materials and Methods

Field-collected material has been used for the illustrations and for superficial examination under the dissecting microscope. Where they exist, vouchers for this material are deposited at BOL, NBG or PRE.

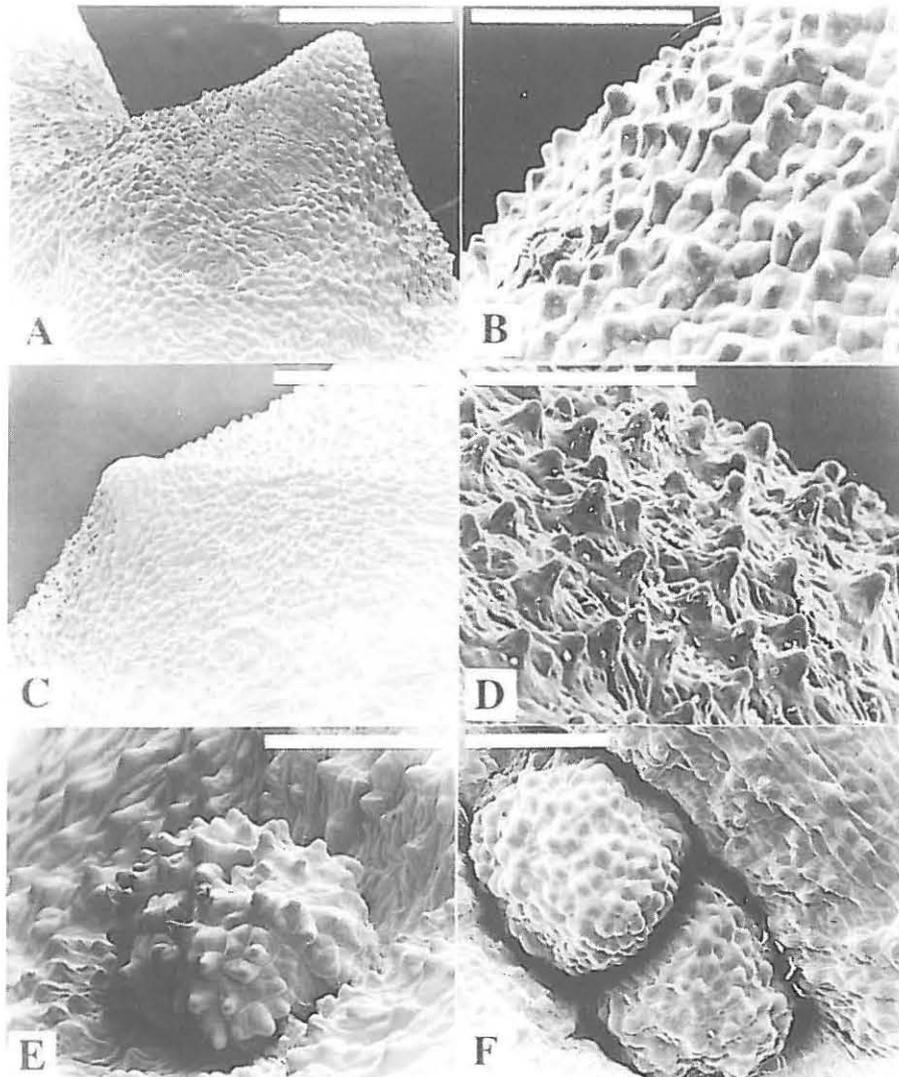
Seeds, either gathered in the field or produced in cultivation by hand pollination, were mounted on stubs, AU/PD coated and examined in a Cambridge S 440 Scanning Electron Microscope at 10 KV. For SEM studies of the epidermis, small pieces were cut from live stems, soaked for 5 mins in chloroform, then dehydrated for up to 1 week in 100% ethanol, critical-point dried and then prepared for examination in the same way as the seeds.

## Results

### Character assessment

So as to simplify the situation, the species involved are divided into four groups. These are labelled A–D as follows:

Group A = *Tridentea dwequensis* (Lückhoff) Leach, *T. gemmiflora* (Masson) Haw., *T. jucunda* (N.E. Br.) Leach, *T. marien-talensis* (Nel) Leach, *T. pachyrrhiza* (Dinter) Leach, *T. parvipuncta* (N.E. Br.) Leach, *T. peculiaris* (Lückhoff) Leach, *T. virescens* (N.E. Br.) Leach. [*Tridentea* Sect. *Tridentea* and Sect. *Parvipunctia* of Leach (1980)].



**Figure 3** SEM views of leaves and epidermis of *Tromotriche* Sect. *Caruncularia*. *T. aperta*, east of Port Nolloth, PVB 4636 (BOL): A, tubercle. B, epidermis. *T. herrei*, east of Eksteenfontein, Heunis & Bruyns 499 (no specimen): C, tubercle. D, epidermis. E, tubercles of emerging axillary bud. *T. ruschiana*, Klinghardt, Hammer (no specimen): F, tubercles of emerging axillary bud. Scale bars: A, C = 500 µm; B, D–F = 200 µm.

Group B = *Tridentea aperta* (Masson) Sweet, *T. baylissii* Leach, *T. choanantha* (Lavranos & Hall) Leach, *T. herrei* (Nel) Leach, *T. longii* (Lückhoff) Leach, *T. longipes* (Lückhoff) Leach, *T. pedunculata* (Masson) Haw., *T. ruschiana* (Dinter) Leach, *T. umdausensis* (Nel) Leach. [*Tridentea* Sect. *Caruncularia* of Leach (1980)].

Group C = *Tromotriche revoluta* (Masson) Haw. and *T. thudichumii* (Pillans) Leach.

Group D = *Tromotriche engleriana*.

### Stems

*Group A*: The stems are decumbent-erect sometimes with a slight tendency to rhizomatous habit in *T. peculiaris* and *T. dwequensis*. Young stems have a soft texture, shiny appearance and are edible (with pleasant lettuce-like flavour and consistency).

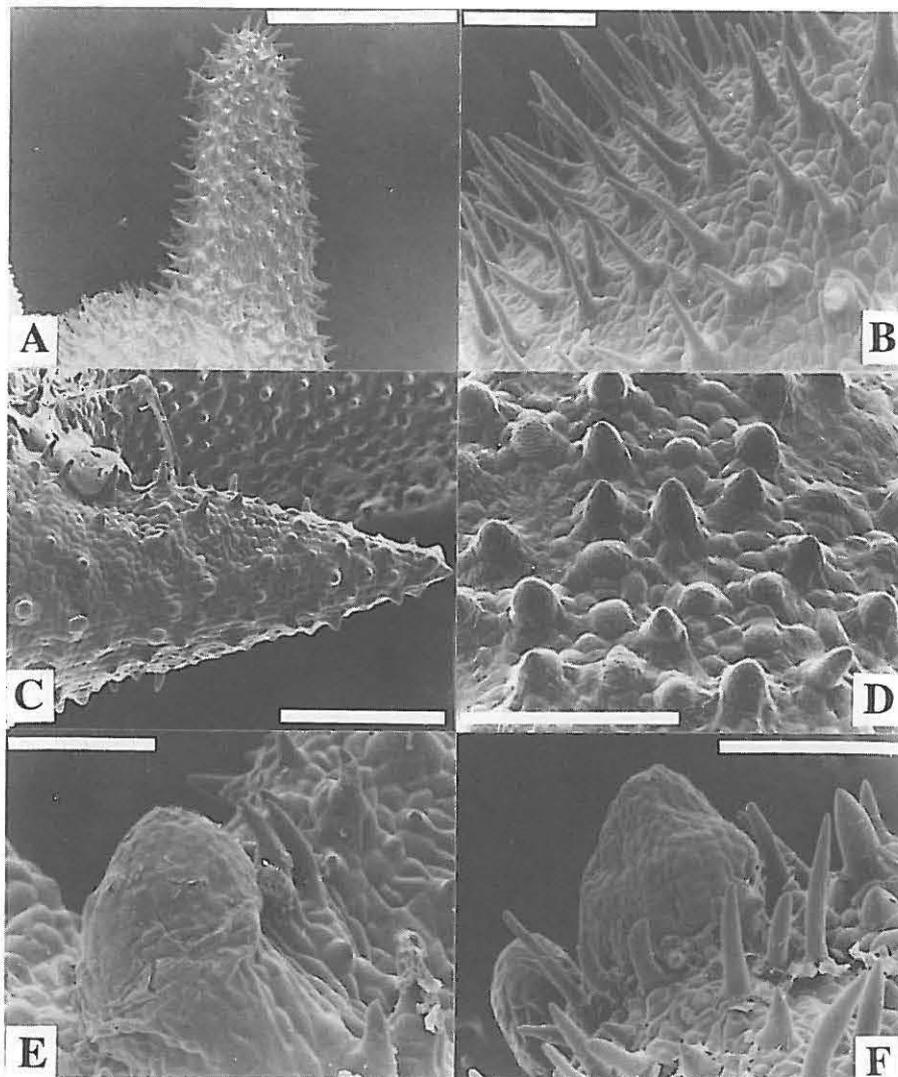
Epidermal cells mostly have flat outer walls (Figure 1F) but scattered cells, mainly on the tubercle just below the base of the leaf, have the outer wall raised into a low, rounded central papilla (Figure 1G).

The tubercles are obtuse, rectangular in outline and taper into the leaf: this tapering is particularly clearly visible in the apical bud when plants are in growth.

*Group B*: Stems here are decumbent-erect to spreading, procumbent or pendulous. In *T. herrei* and *T. umdausensis* the stems are always decumbent-erect with only a short, basally decumbent portion. In *T. aperta*, *T. pedunculata* and, more noticeably, *T. longipes* they have a somewhat spreading to ascending habit with occasional horizontal stems. None of these show any rhizomatous tendency. In *T. baylissii*, *T. choanantha* and *T. longii* the plants are very often (in *T. baylissii* nearly always) pendulous from cliffs and stems may reach 3 m long. However, they do not only grow on cliffs and, when not pendent, *T. choanantha*, for example, has a rhizomatous habit (Lavranos & Hall 1964). The same tendency for the stems to go underground and then emerge some distance away has sometimes been observed in *T. baylissii* in cultivation. Young stems have a firm texture, matt surface and are bitter and more or less inedible.

The outer walls of the epidermal cells are of two kinds:

1. All are  $\pm$  equally raised into rounded, conical papillae (Figures 2B, 3A, B & C);
2. Some cells are raised into larger idioblasts with a short, broad, cylindrical base, then conical above. These are separated by smaller cells whose outer wall is either flat or raised into a conical papilla. The smaller cells around the base of an idio-



**Figure 4** SEM views of leaves and epidermis of *Stapelia*. *S. hirsuta*, Ceres (no specimen): A, leaf. B, epidermis. *S. obducta*, Willowmore, PVB 4977 (BOL): C, leaf (stipular gland partly covered with secretion). D, epidermis. E, stipular gland. *S. garipeensis*, Rosh Pinah, PVB 2772 (BOL): F, stipular glands at base of leaf. Scale bars: A = 1 mm; B, D-F = 200  $\mu$ m; C = 500  $\mu$ m.

blast are often  $\pm$  organized into a ring around it and raise it slightly from the surrounding surface (Figures 2H & 3D, also shown for *T. pedunculata* and *T. ruschiana* by Kusch 1985).

The tubercles are obscure and give the stem a subtessellate, nearly cylindrical appearance.

**Group C:** Stems rhizomatous with slender, horizontal,  $\pm$  cylindrical 'runners' ascending to the surface after which the above-ground parts are erect, 4-angled and thicker. Young stems have a firm texture, matt surface and are bitter and inedible. In *T. thudichumii* they are finely papillate even to the naked eye.

In *T. thudichumii* the outer walls of many of the epidermal cells are raised into idioblasts exactly as described above, with smaller cells around the larger one raising it slightly from the surface (Figure 2D). In *T. revoluta* the surface is covered with rounded, conical papillae (Figure 2B).

In *T. thudichumii* the tubercles are obscure giving the stem a subtessellate, nearly cylindrical appearance (Figure 25A); in *T. revoluta* they are more prominent and the stems are conspicuously 4-winged.

**Group D:** Stems horizontal (procumbent), forming mats on the surface and occasionally going beneath the soil. Young stems are firm, bitter and inedible.

Here the outer walls of some of the epidermal cells are much modified into 'hairs': such a cell has a broad,  $\pm$  conical base above which it is elongated-conical to narrowly cylindrical (Kusch 1985, Abb. 72, exactly as in Figure 4B). The cells between these 'hairs' are small, isodiametric and  $\pm$  flat but those immediately around the 'hair' tend to push it slightly out of the surface.

Tubercles are prominent and stems conspicuously 4-winged.

#### Leaves

**Group A:** Leaf subulate, spreading, very succulent but slightly broader than thick (Figure 1). It is usually impossible to distinguish midrib and blade (though c.f. Figure 1E) and it is likely that the whole structure is reduced to a midrib. Leaves are present

on all young growth but are rapidly caducous, leaving a whitish scar. On either side at their base, mainly concentrated in a 'stipular' position but also scattered along the margin (sometimes nearly to the apex), there is in all species a cluster of one to several hairs. These hairs are  $\pm$  adpressed to the surface, usually 4-6-celled with the lower cells forming a cylinder and 1 or 2 apical cells swollen into a cylindrical or spherical head (Figure 1B, D & F). Kusch (1985) found these hairs to be absent in *T. dwequensis* but in this species they were also observed in the present study. There are no stipules.

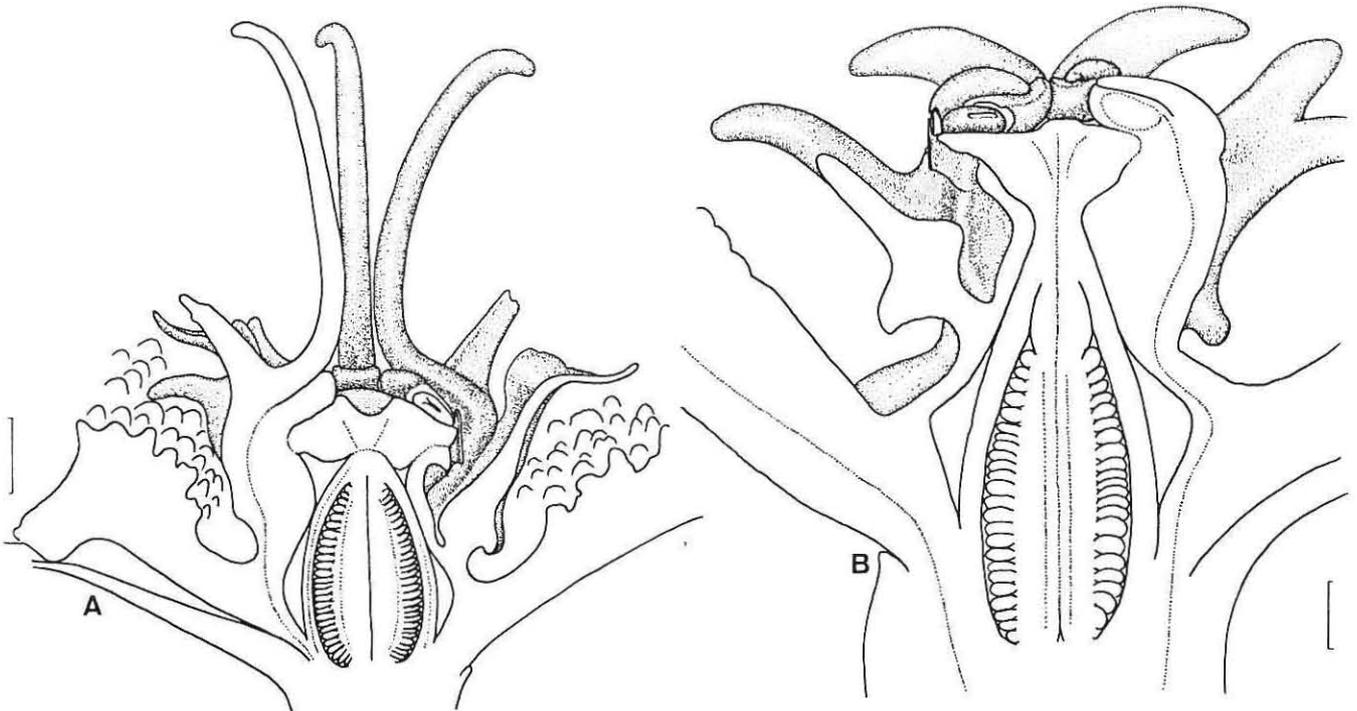
**Group B:** Leaves absent (Figures 2E, G & 3). The extremity of the tubercle, usually raised into a slight ridge, becomes worn with age and covered with a yellow-brown suberized layer. There are no stipules.

**Group C:** Leaf minute,  $\pm$  conical with conical, stipular denticles on either side (Figure 2A, C). It is possible that these stipules are at least partly glandular: their apex is often swollen or covered with a layer of exudate. This whole structure persists but tends gradually to wear down and is progressively replaced by a single, yellow-brown, suberized patch.

**Group D:** Narrow deltoid leaf which is initially erect and later spreading. The leaf is pubescent in the same manner as the stems. It gradually withers and wears away, leaving a round, pale brown scar. Stipules are glandular (rounded structures increasing in size with age, by secretion) and are most easily found on older stems.

#### Inflorescence

In Group A flowers generally mature below the middle of the younger stems. In all other groups the inflorescence may mature anywhere from near the tip of young growth to near its base. In Group B its position is particularly variable in *T. aperta* and *T. umdausensis*. Peduncles in Groups A and B may develop gradually with age to considerable length in some species but in the



**Figure 5** Half-flowers of *Tridentea*. A: *T. virescens*, east of Beaufort West, PVB 3049 (BOL, NBG). Scale: 1 mm. B: *T. parvipuncta*, north of Laingsburg, PVB 3284 (NBG). Scale: 0.5 mm.

others are  $\pm$  absent. The inflorescence is glabrous in all except Group D where it is pubescent.

## Flowers

### Corolla

**Group A:** The flower is mostly rotate with a shallow funnel-shaped depression in the centre (campanulate in *T. dwequensis*). In the united portion the corolla is always somewhat thickened beneath the outer corona lobes (see Figures for species concerned), becoming thinner again towards the base. The dorsal surface (exterior) is glabrous. The ventral surface (interior) is slightly rugulose in *T. parvipuncta* and usually smooth in *T. jucunda* but in all the others is covered, usually very densely, with compound (multicellular) columnar papillae. Epidermal cells on the papillae are raised into short, rounded setae and the apical cell is often extended into a longer seta. In *T. gemmiflora* and more notably in *T. virescens*, these papillae become joined together into ridges but the summits of individual papillae still remain distinguishable. In *T. dwequensis* the papillae are still prominent and sporadically joined together but are shorter. In *T. peculiaris*, very low, irregular heaps are present mainly towards the tips of the lobes which, on closer examination, are found to be complexes of partly to entirely fused compound papillae whose apices remain distinguished by small, dark setae. Groups of these setae occur towards the centre of the flower, indicating other complexes of papillae which have merged with the surface. The margins of the lobes are mostly ciliate.

**Group B:** The flower is mostly campanulate to tubular-campanulate and only in *T. longii* and *T. pedunculata/longipes* is it  $\pm$  rotate with a shallow, funnel-shaped tube. In all species the corolla is distinctly thickened near the base of the tube, often into an inward-descending annulus (Figures 31D, 33C). Between this thickened area and the base of the gynostegium the corolla is much thinner. The dorsal surface is glabrous. The ventral surface

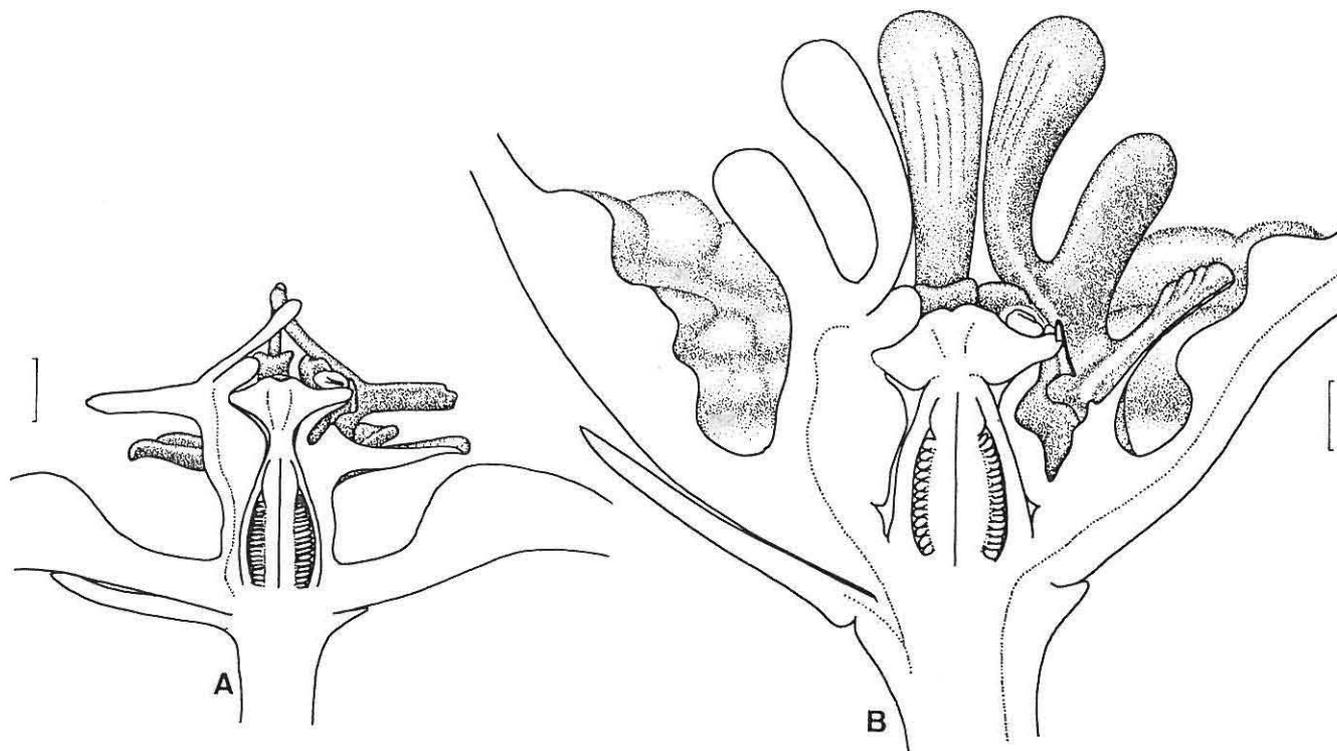
is  $\pm$  smooth in *T. choanantha* and *T. longii*, and shallowly to deeply reticulate-rugose at least in the tube and usually also on the lobes in all others except *T. baylissii* (transverse-rugose in tube, reticulate-rugose on lobes). In several species (*T. aperta*, *T. pedunculata*, *T. ruschiana* and *T. umdausensis* and sometimes in *T. baylissii*), small, unicellular, clavate papillae are common especially around the mouth of the tube. Cilia are often present on the margins of the lobes.

**Group C:** The corolla lobes are strongly revolute. The corolla tube is much thickened – in *T. revoluta* enormously so (Figure 24A, C) – into an annulus around the gynostegium and the annulus is emphasized by the folding back of the lobes. Towards the base below the annulus the corolla becomes thinner. The dorsal surface is glabrous. Small, clavate, unicellular papillae are found sparsely (more densely in the tube) all over the ventral surface of the corolla in *T. thudichumii* and in the base of the tube in *T. revoluta*, but apart from these, the surface is smooth. Cilia are usually present along the margins of the lobes.

**Group D:** The corolla lobes are strongly revolute and the corolla tube is much thickened except for a thinner part towards the base. The dorsal surface is pubescent. The ventral surface is finely transversely rugose and covered sparsely with fine, unicellular setae which increase in size in the flat area immediately around the gynostegium. The corolla lobes usually have fine hairs along their margins towards the base.

### Corona

Throughout these species (and among the majority of stapeliads) there is little variation in the construction of the gynostegium. The depth of the 'nectarial orifice' beneath the guide rails (Schill & Jäkel 1978) and at the base of the interstaminal corona varies very much, as can be seen from the half-flowers shown (Figures 5 & 6 and others among Figures of species), but no pattern can



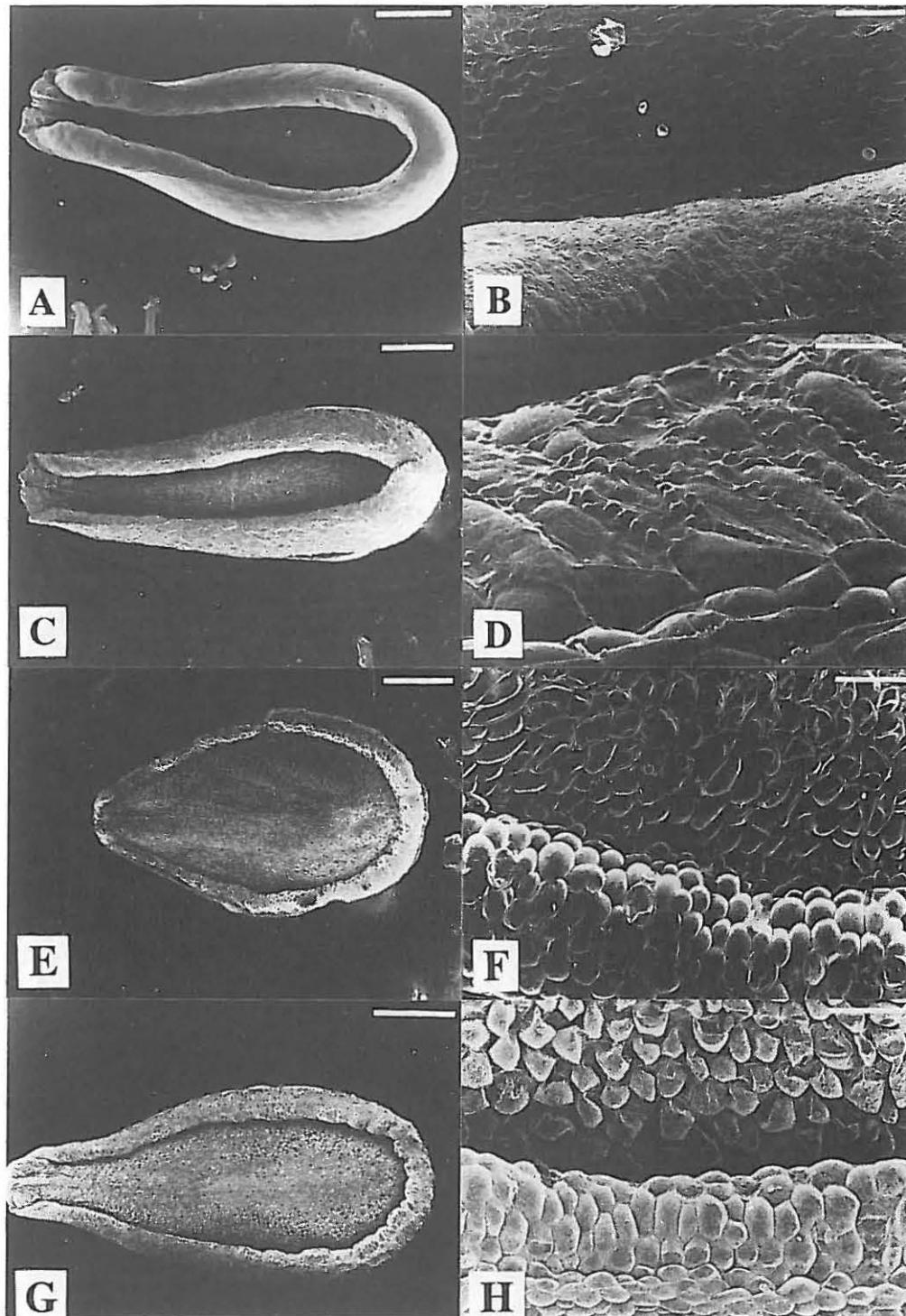
**Figure 6** Half-flowers of *Tromotriche*. A: *T. thudichumii*, north of Karooport (no specimen). Scale: 1 mm. B: *T. herrei*, east of Eksteenfontein, Heunis & Bruyns 499 (no specimen). Scale: 1 mm.

readily be discerned. In Groups B and C the guide rails are often rather short, especially in *T. aperta* and *T. umdausensis*.

*Group A:* There is a prominent ascending-spreading interstaminal (outer) corona with simple (*T. jucunda*) to bifid (*T. parvipuncta*) or obscurely to deeply trifid lobes. Each staminal (inner) corona lobe is dorsiventrally flattened towards the base, often becoming cylindrical towards the tip, and is incumbent on

and covers the anthers. In *T. peculiaris* and *T. parvipuncta* they only just exceed the anthers but in all the others they are produced beyond them, rising up in a column above the centre. They are especially long and slender in *T. dwequensis*. Each lobe usually has a dorsal, laterally flattened horn near the base.

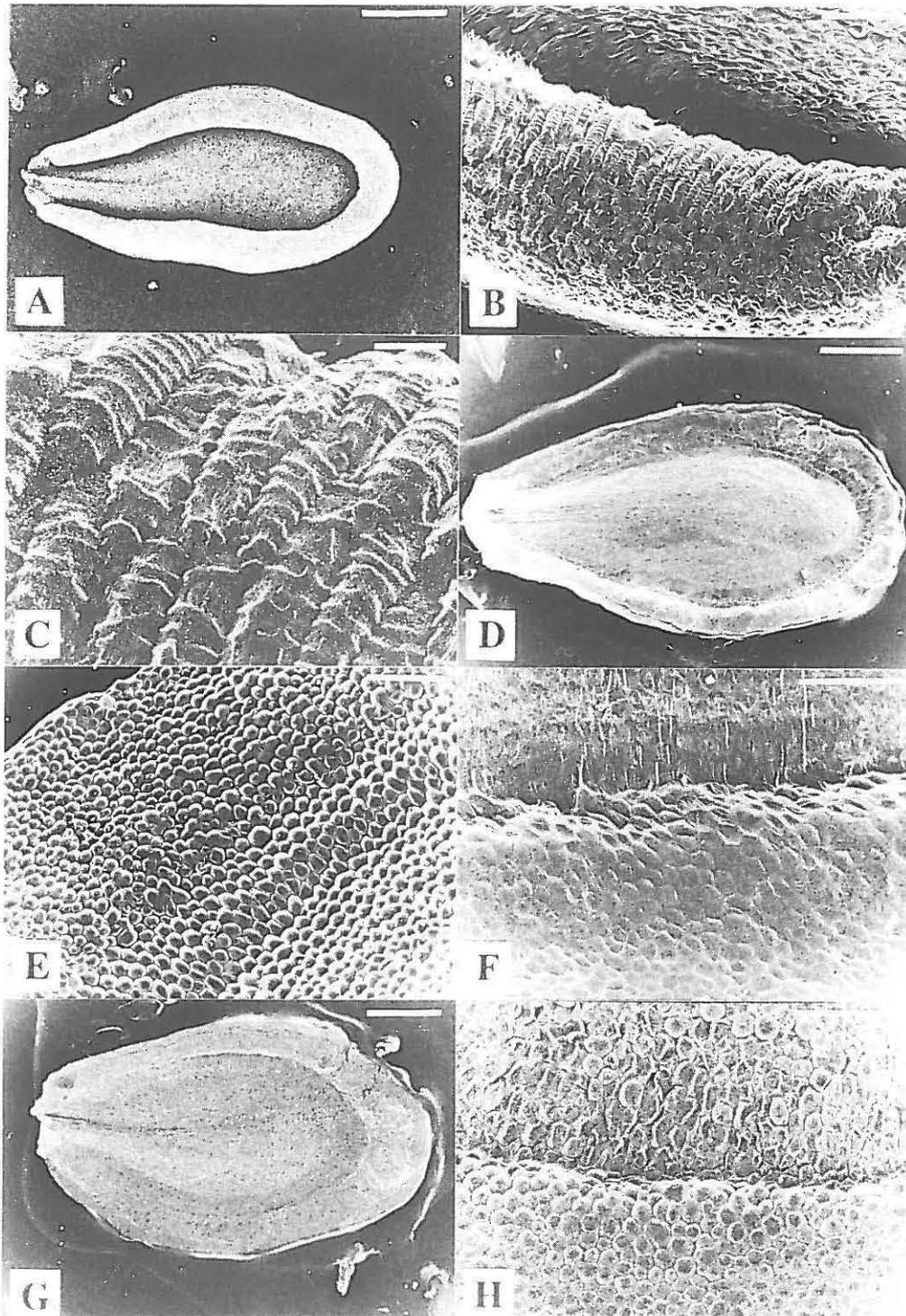
*Group B:* Here the outer corona consists of five lobes which may be discrete and prominently ascending-spreading (*T. baylissii*,



**Figure 7** SEM views of seeds of *Stapelia* and *Tromotriche* Sect. *Tromotriche*. *S. hirsuta*, Ceres (no specimen): A, ventral surface of seed. B, inner edge of border. *S. engleriana*, east of Prince Albert, PVB 3642 (BOL): C, ventral surface of seed. D, inner edge of border. *T. thudichumii*, north of Karooport, PVB 4024 (no specimen): E, ventral surface of seed. F, inner edge of border. *T. choanantha*, north of Calitzdorp, PVB 2907 (BOL): G, ventral surface of seed. H, inner edge of border. Scales: A, E, G = 1 mm; B, F = 150  $\mu$ m; C = 800  $\mu$ m; D = 30  $\mu$ m; H = 120  $\mu$ m.

*T. longii* and *T. choanantha*) or small and ascending (*T. herrei*, *T. longipes*, *T. pedunculata* and *T. ruschiana*) or they may be more or less laterally fused with the backs of the inner lobes into a cup (*T. aperta* and *T. umdausensis*). The inner corona lobes are dorsiventrally flattened at least at their base and cylindrical higher up: in *T. umdausensis* they are much reduced and consist only of the basal, dorsiventrally flattened part adpressed to the anthers (Figure 30C, D); in *T. aperta* they usually consist of sim-

ple lobes slightly thickened and verrucose towards the apex (Figure 31D); in *T. herrei* (Figure 34C, D), *T. longii* (Figure 26B, C), *T. longipes* (Figure 33C), *T. pedunculata* and *T. ruschiana* they consist of connivent-erect then spreading lobes with much thickened, verrucose apices (except in *T. herrei* where the apices are smooth), each with a dorsal horn laterally flattened towards the base, swollen towards the apex and  $\pm$  identical to the lobe itself; in *T. baylissii* (Figure 28C) and *T. choanantha* (Figure 27D, E)



**Figure 8** SEM views of seeds of *Tridentea* and *Tromotriche* Sect. *Caruncularia*. *T. aperta*, north of Soebatsfontein, PVB 5188 (BOL): A, ventral surface of seed. *T. aperta*, east of Port Nolloth, PVB 4634 (PRE): B, C, inner edge of border. *T. virescens*, north of Vanwyksvlei, PVB 3448 (BOL): D, ventral surface of seed. *T. peculiaris*, north of Vanrhynsdorp, Nagel 65 (no specimen): E, inner edge of border. *T. marientalensis* ssp. *albipilosa*, north of Aus, PVB 4220 (BOL): F, inner edge of border. *T. jucunda*, east of Calvinia, PVB 3434 (BOL): G, ventral surface of seed. H, inner edge of border. Scales: A = 800  $\mu$ m; B = 120  $\mu$ m; C = 20  $\mu$ m; D, G = 1 mm; E = 100  $\mu$ m; F, H = 200  $\mu$ m.

they are cylindrical above, slightly thickened and verrucose towards the apex in *T. baylissii*, each with a laterally flattened dorsal horn.

**Group C:** The interstaminal corona consists of five ascending or horizontally spreading,  $\pm$  rectangular lobes, the staminal of basally dorsiventrally flattened lobes which are cylindrical above, becoming thickened and verrucose towards the apex, each with a laterally flattened, dorsal horn (Figures 24B & 25C).

**Group D:** Exactly as in group C.

#### Pollinaria

In all groups the germinating mouth (Schill & Jäkel 1978) lies slightly towards the upper surface of the pollinium. The pollinia are attached by caudicles to the underside of the wings of the corpusculum. These wings appear narrow because of downward-folding of their margins.

**Group A:** Pollinia D-shaped (rather narrowly in *T. gemmiflora*, *T. pachyrrhiza* and *T. marientalensis*), corpusculum  $\pm$  as long as broad and  $\pm$  uniformly broad for whole length, with conspicuous, horizontally spreading wings with downward-folded margins to which the pollinia are attached by a slender, very short caudicle. The pollinaria in *T. gemmiflora*, *T. pachyrrhiza* and *T. marientalensis* are extremely difficult to lay 'flat' i.e. with pollinia and corpusculum both lying horizontally.

**Group B:** Pollinia  $\pm$  circular to nearly elliptical (more narrowly elliptical in *T. choanantha* and *T. baylissii*), corpusculum always at least twice as long as maximum breadth, usually narrow at base then widening to just above wings then shortly deltoid above this. The pollinia are attached to the often broad wing by a slender, short caudicle.

**Group C:** Pollinia D-shaped, very large in *T. revoluta*, much smaller in *T. thudichumii*, corpusculum  $\pm$  twice as long as broad, widening from base to above wings then shortly deltoid above this, wings and caudicles as in Groups A and B.

**Group D:** Pollinaria as in Group C except that the corpusculum does not widen towards the top and the caudicles and wings are extremely broad.

#### Seeds and seedlings

##### Seeds

**Group A:** Flat, ovate, margin mostly practically flat (as in Figure 8E), rarely swollen (Figure 8H). Noticeably larger (9  $\times$  6 mm) than the others in *T. pachyrrhiza*.

**Group B:** Strongly convex beneath with sides folded up so that seed cymbiform, narrowly ovate (more than 2 $\times$  as long as maximum breadth), much-thickened margins folded inwards (Figures 7G, H & 8A, B). Some seeds have marginal cells with sculptured surface (Figure 8C).

**Group C:** Strongly convex, ovate, thick margins folded inwards (Figure 7E, F).

**Group D:** Very narrowly cymbiform, so much folded as to  $\pm$  hide margin altogether (Figure 7C, D). Marginal cells have sculptured edges.

##### Seedlings

**Group A:** Long hypocotyl widening gradually towards apex; cotyledons spreading, from broad and circular to subulate but with flattened upper surface; first pairs of tubercles tapering into

subulate leaves generally with blade and midrib visible and sometimes with marginal hairs (Figure 9).

**Group B:** Hypocotyl swollen around middle to parallel-sided; cotyledons without blade and hardly distinguishable from top of hypocotyl; first tubercles obtuse without any leaves distinguishable at apices (Figure 10).

**Group C:** Hypocotyl broad, widening to apex; cotyledons small, thick, rounded; primary tubercles without distinguishable leaf (Figure 10).

**Group D:** Unknown.

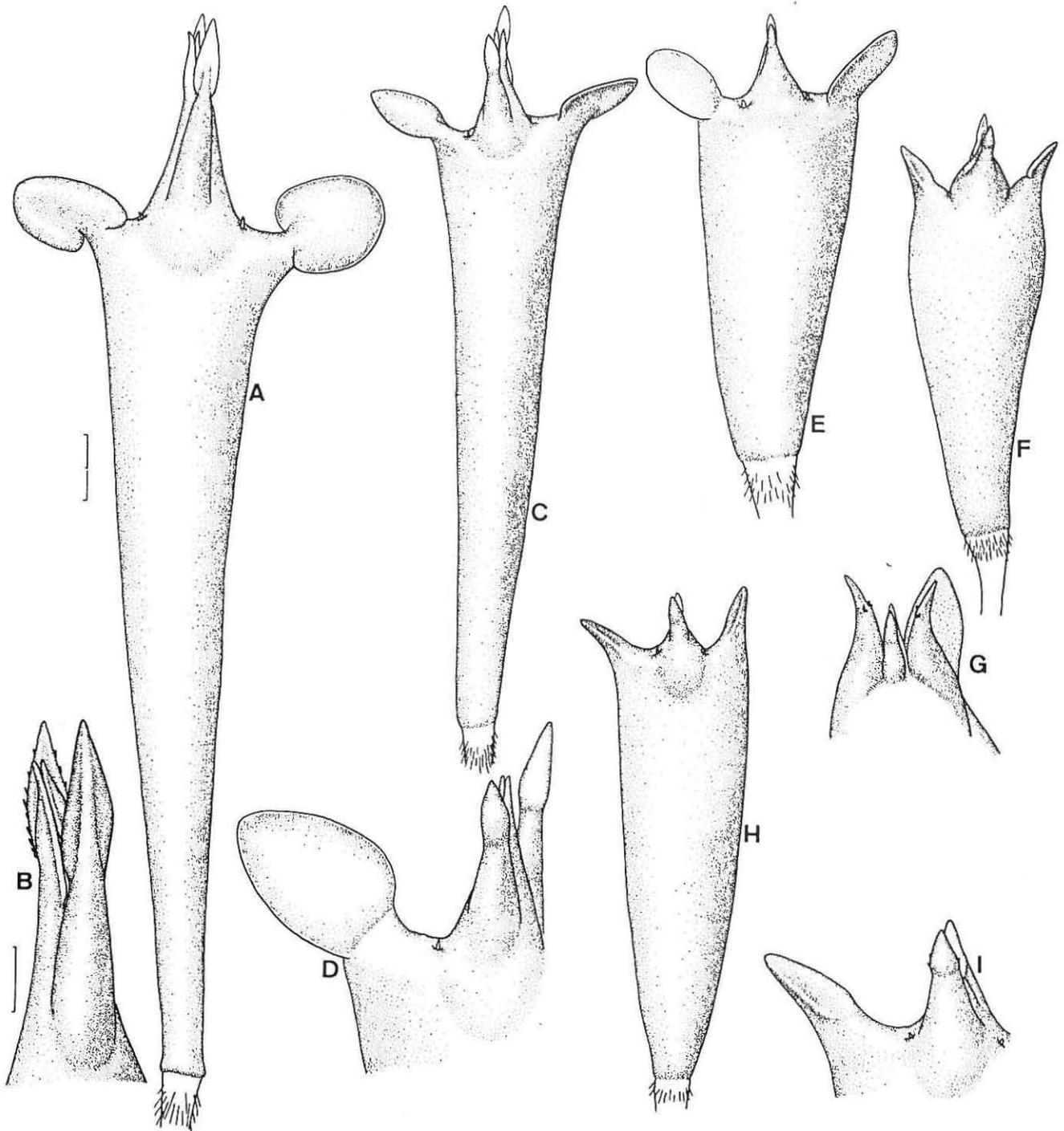
#### Conclusions

Leach (1980) contended that, although the species of *Tridentea* were very different florally, they were nevertheless very similar in vegetative characters (especially in young growth). The various facts (Table 1 and Figures) presented here do not support this contention. In particular, it becomes clear that both in vegetative and floral characters there is very little holding *Tridentea* together. It is therefore necessary to re-assess the arrangement of the various species involved and, as some of them are more closely allied to species of *Tromotriche*, the apportioning of species to this genus also needs to be re-evaluated.

Meve (1989) pointed out that *T. engleriana* has the pubescent stems, inflorescence, exterior of corolla and follicles typical of *Stapelia*. It can be added to this that in *T. engleriana* the tubercles on the stems are laterally flattened and joined into wings along

**Table 1** Comparison of characters in *Tridentea*, *Tromotriche* and *Stapelia*

Character	Group A	Group B	Group C	Group D	<i>Stapelia</i>
Primary tubercle	tapering into leaf	obtuse	obtuse	obtuse	obtuse
Outer wall of cells of stem epidermis	smooth to scattered round/conical	conical-papillate or idioblasts	idioblasts	elongated-papillate ('pubescent')	elongated-papillate ('pubescent')
Leaf	subulate	-	conical	narrowly deltoid	ovate-deltoid
Stipules	multicellular hairs	-	$\pm$ glandular denticles	glandular denticles	glandular denticles
Cotyledons	broad, flat above	not distinguished from hypocotyl	slightly distinguished from hypocotyl	flattened above	flattened above
Papillae on corolla (if present)	compound	swollen unicellular	swollen unicellular	fine unicellular ('hairs')	fine unicellular ('hairs')
Corpusculum	$\pm$ as long as broad, not widened above middle	$\pm$ 2 $\times$ as long as broad, widened above middle	$\pm$ 2 $\times$ as long as broad, widened above middle	> 2 $\times$ as long as broad, widened at apex only	mostly > 2 $\times$ as long as broad, often widened above middle
Seed	flat	boat-shaped	boat-shaped	boat-shaped	boat-shaped



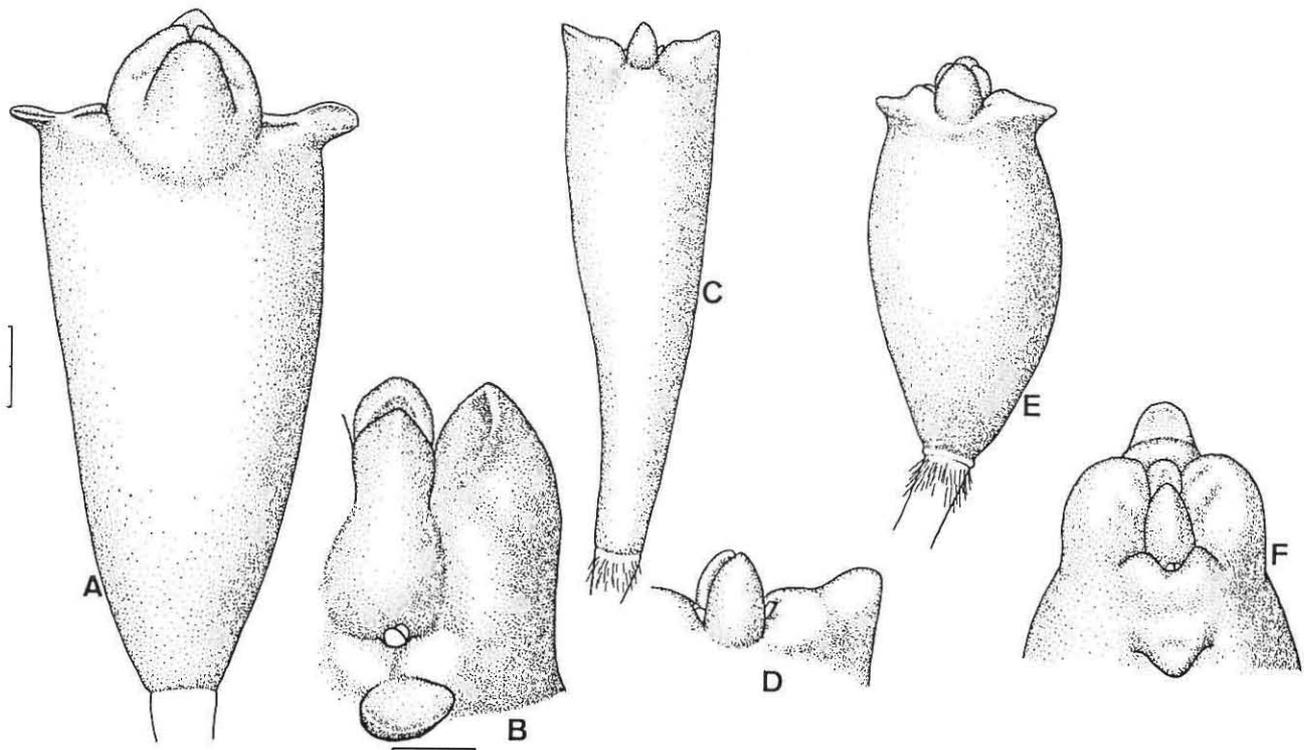
**Figure 9** Seedlings of *Tridentea*. *T. marientalensis* subsp. *marientalensis*, PVB 5466 (no specimen). A, side view of plantlet, 30 days old. B, close-up of primary and secondary leaves. *T. virescens*, PVB 3448 (BOL). C, side view of plantlet, 30 days old. D, close-up of cotyledon and primary leaves. *T. jucunda*, Witpütz, Namibia, Nagel (no specimen). E, side view of plantlet (age not recorded); south-west of Fraserburg, PVB 4797 (PRE). F, side view of plantlet, 28 days old. G, close-up of primary and secondary leaves, with tiny hairs. *T. peculiaris*, north of Vanrhynsdorp, Nagel 65 (no specimen). H, side view of plantlet (age not recorded). I, close-up of cotyledon and primary leaves with tiny hairs. Scales: A, C, E, F, H = 2 mm (at A); B, D, G, I = 1 mm (at B).

the stem, the leaves are subtended by glandular stipular denticles and the corolla is transversely rugose. All of these are characters typical of *Stapelia*.

Reasons for excluding *T. engleriana* from *Stapelia* lie in the procumbent habit of the stems and the spreading leaves: in *Stapelia* (Leach 1978, 1985), the stems are decumbent-erect and the leaves are erect.

Stapeliads appear to be remarkably variable in the orientation (and often also the thickness) of their stems. For example, within *Huernia verekeri* Stent one finds some taxa with procumbent and

others with decumbent-erect stems. Similarly in *Orbeopsis gerstneri* one has one extensively rhizomatous subspecies and one where the stems are superficial. Similar variation is found in *O. valida* (N.E. Br.) Leach (unpublished data). Therefore, there is no reason, because of variation in this character, to question the monophyly of such genera as *Echidnopsis* Hook. f., *Huernia* R. Br., *Stapelianthus* Choux and *Stapeliopsis* Pillans: in each of these, one will encounter species with decumbent-erect stems and others with procumbent or even rhizomatous stems. Similarly, this difference in the orientation of the stems should not be



**Figure 10** Seedlings of *Tromotriche*. *T. thudichumii*, north of Karooport, PVB 4024 (no specimen). A, side view of plantlet, 2 months old. B, close-up of apex of plantlet. *T. aperta*, north of Soebatsfontein, PVB 5188 (BOL). C, side view of plantlet, 30 days old. D, close-up of cotyledon and primary leaves. *T. umdausensis*, west of Gamoep, PVB 4687 (BOL). E, side view of plantlet, 2 months old. F, close-up of apex of plantlet. Scales: A, C, E = 2 mm (at A); B, D, F = 1 mm (at B).

used to separate *T. engleriana* from *Stapelia*. Altogether, the similarities between *T. engleriana* and *Stapelia* outweigh the probably coincidental similarity of its flowers and corona [which, with the supposed monopodial habit, seem to have influenced Leach (1984) strongly in his placing of this species] to *T. revoluta*. *T. engleriana* is therefore referred back to *Stapelia*. *Stapelia* is then defined by 'pubescent stems, inflorescence, exterior of corolla and follicles; tubercles laterally flattened and joined into wings along stem; glandular stipular denticles; corolla mostly transversely-rugose and inside with fine, unicellular hairs'. At this juncture, it should perhaps be noted that the procumbent habit seems always to be the derived state: all stapeliad seedlings known to me have an erect primary stem which, in the procumbent species, is usually of very restricted length. From the secondary stems onwards the procumbent habit begins.

To place Group A and Group B within one phylogenetically acceptable genus, one would have to argue that within Group A a reduction in the size of the leaf and the number of marginal hairs has taken place until they both disappear in Group B, accompanied by an (abrupt) increase in Group B in the size of the papillae on the epidermis and the appearance of the rather unusual idioblasts. Furthermore, if one considers seedlings, one would have to argue that those of Group B are derived from those of Group A (or vice versa): both a reduction in size of the cotyledon and the disappearance of the primary leaf would have to be assumed. However, a simpler, more parsimonious hypothesis is that the seedling structure of Group B is derived from that in Group C. It may be noted that this hypothesis also correlates well with the presence in Group C of epidermal idioblasts, providing an explanation for their presence in Group B.

From the Table, it is clear that Groups B and C differ only in the leaves and stipules. In addition the following three facts are relevant:

1. *T. thudichumii* bears a strong resemblance vegetatively to most species of Group B (cf. Figures 25A & 27A). In *T. revoluta*, where the angles are more pronounced and consequently the stem more square, the stems are most similar to those of *T. baylissii*, which are also more square (with less rounded angles) than is usual in Group B. The elongated subterranean 'rhizomes' of Group C suggest the long stems produced by *T. choanantha* and *T. baylissii*, a fact reinforced by the occasionally rhizomatous habit of *T. baylissii* and *T. choanantha*.
2. In Group B the corona is usually campanulate but is rotate in *T. pedunculata* and rotate with the lobes slightly reflexed in *T. longii*. Therefore, the more strongly reflexed corolla lobes of Group C could be considered as more extreme examples in this range.
3. The coronal structure of *T. revoluta* is almost identical to that of *T. baylissii* (cf. Figures 24A & 28C): in the latter the main difference lies in the more steeply ascending outer lobes and the longer dorsal 'fin' on the inner lobes, both relatively minor variations probably correlated with the more tubular corolla.

There is, therefore, a remarkable degree of agreement in many features between Groups B and C and sufficient evidence exists to regard them as congeneric.

Group A differs from Group B + C in the following characters:

1. Primary tubercle tapering into leaf: primary tubercle obtuse;
2. Leaves subulate: leaves deltoid or absent;
3. Multicellular hairs present on leaf: hairs absent;
4. Epidermal cells on stem slightly papillate to flat: epidermis papillate, or raised idioblasts present;
5. Papillae on corolla compound: papillae on corolla unicellular [if present];
6. Corpusculum  $\pm$  as long as broad, not widening above middle:

corpusculum  $\pm 2\times$  as long as broad, much widened above middle.

In consequence of this, it is proposed that Group A be retained in *Tridentea* while Group B + C be placed in an expanded *Tromotriche*.

The phylogeny of the Stapelieae is still little understood. Nevertheless it is possible to postulate rather different ancestries for *Tridentea* and *Tromotriche*.

Flat, relatively broad cotyledons, tapering primary tubercles, subulate primary and secondary leaves and multicellular hairs near the base of the leaf have been observed in some seedlings of *Hoodia* Sweet ex Decne. (Bruyns 1993). Relatively flat outer walls of epidermal cells on the stems, compound papillae on the corolla and flat seeds are also features common to both *Hoodia* and *Tridentea*. It seems clear, therefore, that these two genera are closely related, with *Lavrana* Plowes also sharing many of these characters (Bruyns 1993). Elsewhere, multicellular hairs on and around the base of the leaves are known in *Edithcolea* N.E. Br. (Meve & Albers 1990) and have also been observed in many species of *Caralluma* R. Br. In particular, the very widespread (and presumably relatively ancient) *Caralluma adscendens* (Roxb.) Haw. shares these hairs with *Hoodia* and *Tridentea*, as well as flat, relatively broad cotyledons, tapering primary tubercles, subulate primary and secondary leaves and relatively flat outer walls of epidermal cells on the stems.

Hints on the relationships of *Tromotriche* are provided by two vegetative characters: the presence in two species of slightly glandular stipular denticles and the epidermal idioblasts. The first character is clearly common with *Stapelia* (Table 1, Figure 4). In *Stapelia* most species have conspicuously pubescent stems (Figure 4) but a few are glabrous to the naked eye. One such species, *Stapelia obducta* Leach, is illustrated (Figure 4C–E) and, while a few larger 'hairs' (such as are typical in 'pubescent-stemmed' species) are found around the stipules, most of these are reduced to idioblasts exactly as in, for example, *T. choanantha*. Therefore, both these characters indicate a relationship with *Stapelia* and this is further supported by the unicellular hairs on the corolla and the cymbiform seeds. Some of the evidence presented here suggests that the pubescent condition in *Stapelia* is plesiomorphic: a few longer papillae are found around the stipules in *S. obducta*; tubercles of *Tromotriche* tend to emerge in the bud with larger papillae than they have later (Figure 3E, F); there are rather more pubescent species in *Stapelia* and they are generally widely distributed and more plentiful.

### Distribution

The distributions of *Tridentea* (Figure 11) and *Tromotriche* (Figure 12) exhibit quite different patterns. That of *Tridentea* is broad, with the bulk of known localities falling between the eastern boundary of the winter-rainfall region and west of the true summer-rainfall zone, that is, mainly in the arid area receiving rainfall peaks in March and November (Hartmann 1991: Figure 6). This is a similar pattern to that of *Hoodia* (Bruyns 1993) apart from the fact that *Hoodia* extends northwards into the tropics. There are five species with wide and generally rather scattered distributions (though this diffuseness is certainly in part still due to lack of collecting): *T. gemmiflora*, *T. marientalensis*, *T. jucunda*, *T. virescens* (in order of decreasing area of occurrence) with *T. dwequensis* and *T. parvipuncta* more restricted, and *T. peculiaris* and *T. pachyrrhiza* rather localized. The last two are the only ones occurring exclusively within the winter-rainfall region of the Western Cape Provinces and south-western Namibia.

*Tromotriche* occurs almost exclusively within the winter-rainfall zone of the Western and Northern Cape Provinces and south-western Namibia. It also appears to be fairly strictly contained by

the western and southern edge of the Karoo Dolerites (except for *T. thudichumii*, which occurs on doleritic slopes on the north-eastern Ceres Karoo and beyond). The genus with most similar distribution to this is *Quaqua*: the extremities of the two distributions coincide almost exactly (including, in both genera, outliers in the Suurberg, Eastern Cape), though *Quaqua* is more common in the southern and south-western part of the Western Cape and shows some tolerance for dolerites on the Roggeveld Plateau (as far east as Fraserburg). In *Tromotriche*, only *T. pedunculata* could be considered as widely distributed. Several species (such as *T. aperta*, *T. herrei*, *T. longipes* and *T. umdausensis*) have rather restricted (though generally well-documented) distributions. *T. baylissii*, *T. choanantha*, *T. longii* and *T. ruschiana* are very localized and the first three appear to be highly specialized cremnophilous endemics found only on sandstones of the fold mountains of the southern parts of the Western and Eastern Cape Provinces.

### Taxonomy

In one case, the status of taxa has been altered from that in Leach (1980): in *Tridentea parvipuncta* the two varieties are changed to subspecies.

In the application of the ranks variety and subspecies, I follow Du Rietz (1930): 'A subspecies is a population of several biotypes forming a more or less distinct regional facies of a species' and 'A variety is a population of one or several biotypes forming a more or less distinct local facies of a species'. In *T. parvipuncta* var. *truncata* I do not think that the term 'local facies' could be reasonably applied.

**I. TRIDENTEA** Haw. Syn. Pl. Succ.: 34 (1812). Leach, Proc. Trans. Rhod. scient. Ass. 59: 3 (1978), Excelsa Tax. Ser. 2: 4 (1980). Lectotype (Leach 1980): *Tridentea gemmiflora* (Mason) Haw.

*Plant* a dwarf succulent, tufted, forming compact clumps, rarely slightly rhizomatous. *Stems* obtusely 4 (–6) angled, (20) 50–150 (200)  $\times$  (7) 10–20 (25) mm, softly fleshy, glabrous to naked eye, tubercles submammosse each bearing a thick glabrous subulate

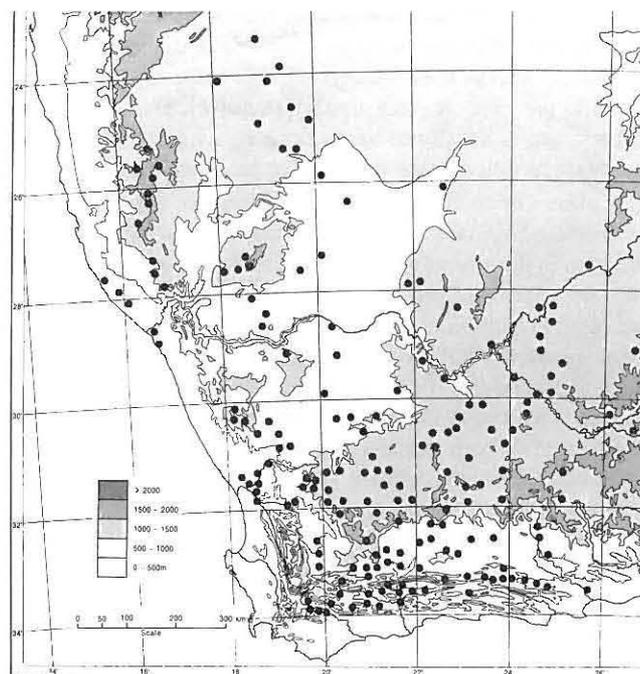


Figure 11 Distribution of *Tridentea*.

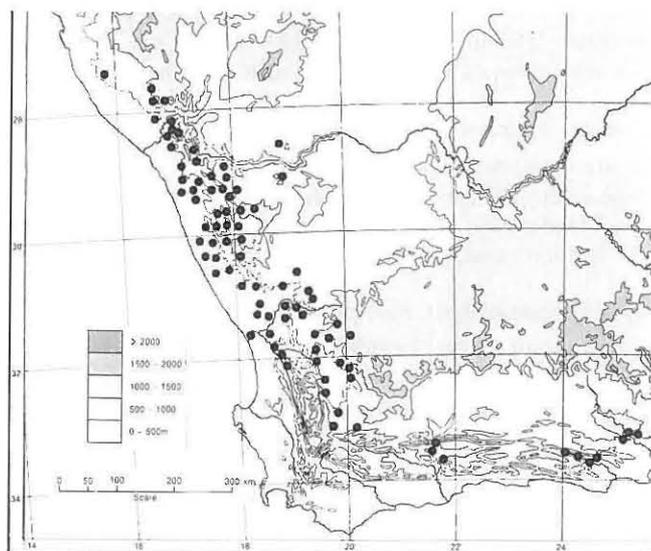


Figure 12 Distribution of *Tromotriche*.

widely spreading caducous leaf 1.5–10.0 mm long (leaving a whitish scar) subtended by a patch of stipular hairs on either side sometimes extending along margin. *Flowers* developing successively on a gradually lengthening peduncle arising near base of stem. *Pedicel* 25–80 × ± 2 mm, spreading to ascending. *Calyx* 5-lobed, glabrous or with few marginal cilia. *Corolla* 20–100 mm diam., usually lobed to about half of radius or less, rotate to campanulate, with shallow funnel-shaped depression in centre, outside glabrous, inside glabrous and smooth to slightly rugose or papillate (papillae often with apical 'hair'), margins usually ciliate. *Corona* consisting of two series arising from staminal column, glabrous; *outer corona* of 5 ascending to spreading dorsiventrally flattened simple to bifid or trifold lobes, fused only at base to bases of inner lobes; *inner lobes* incumbent on anthers, usually much exceeding them and rising up above centre of style-head, dorsiventrally flattened at least towards base (often cylindrical above), often with laterally flattened ± deltoid dorsal 'fin' in lower half. *Staminal column* arising near base of corolla tube on short stipe. *Anthers* incumbent on top of style-head, subquadrate, horizontal, without apical or lateral appendages. *Pollinia* solitary, nearly horizontal in each anther-theca, with short caudicles, D-shaped, attached to winged corpusculum ± as long as broad. *Style-head* not produced beyond anthers, truncate depressed at apex. *Follicles* terete-fusiform, slender, paired, with horns diverging at 30–60°, mottled with purple, glabrous, smooth.

This genus contains the eight species placed by Leach (1980) in *Tridentea* Sect. *Tridentea* and Sect. *Parvipunctia* Leach. Leach placed *Tridentea peculiaris* in Sect. *Tridentea* on account of its 'tridentate outer corona lobes' but admitted that 'on the evidence of its relatively small leaves, obscurely mottled corolla, the shape of its inner corona lobes and ... the relatively broad ... pollinia' it appears to belong to Sect. *Parvipunctia*. I maintain the two sections recognized by Leach – the extensive overlapping in their distributions suggests that one is indeed dealing with two distinct taxa – but also wish to make the infrageneric classification more phylogenetically acceptable so have moved this species to Sect. *Parvipunctia*.

Key to sections of *Tridentea*

1. Outer corona lobes deeply trifold ..... 2.  
Outer corona lobes bifid or simple ..... Sect. *Parvipunctia*
2. Surface of corolla densely and roughly papillate Sect. *Tridentea*  
Surface of corolla nearly smooth. .... Sect. *Parvipunctia*

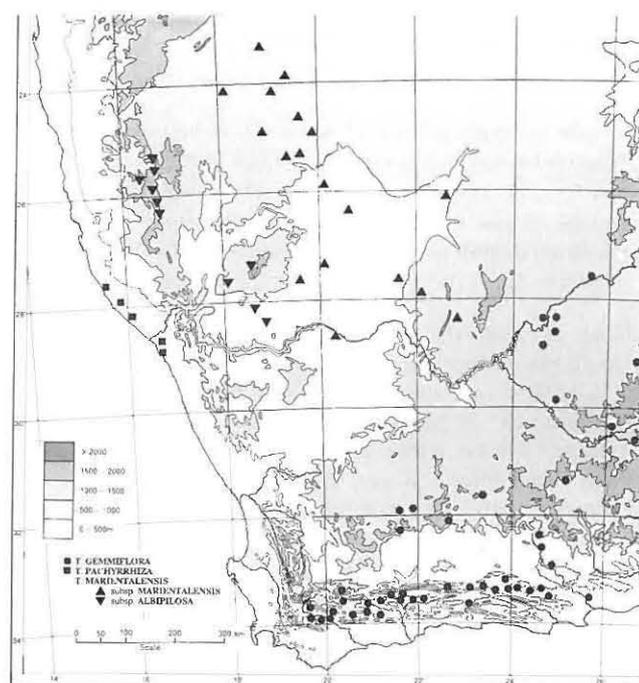


Figure 13 Distribution of *Tridentea gemmiflora*, *T. marientalensis* and *T. pachyrrhiza*.

A. Sect. *Tridentea*

*Leaves* up to 10 mm long (except *T. pachyrrhiza*). *Corolla* on ventral surface densely papillate, obscurely mottled towards centre or uniformly coloured. *Corona*: *outer lobes* deeply trifold; *inner lobes* with dorsal 'fin'. *Pollinia* often much longer than broad.

Key to species of Sect. *Tridentea*

1. Flowers uniformly bright greenish-yellow or yellow, 25–30 mm diam. .... *T. virescens*  
Flowers reddish-brown, brown or black, 45–100 mm diam. . . . . 2.
2. Corolla lobes with edge folding upwards, pedicels mostly < 50 mm long, papillae on corolla ± without apical seta ..... 3.  
Corolla lobes without upward-folding edge, pedicels mostly > 70 mm long, papillae on corolla each tipped with a long seta .  
..... *T. marientalensis*
3. Lateral teeth of outer corona lobes at least half as long as central, leaves up to 10 mm long. .... *T. gemmiflora*  
Lateral teeth of outer corona lobes < one-third length of central, leaves < 2 mm long ..... *T. pachyrrhiza*

1. *Tridentea gemmiflora* (Masson) Haw., Syn. Pl. Succ.: 34 (1812). Figures 13, 14.

This species is now known from several localities between Sutherland and Beaufort West on the western part of the Great Karoo where formerly it had not been recorded.

In *T. gemmiflora* the papillae on the corolla are usually partially fused into clusters as in *T. virescens*. There is usually only a dark dot at the apex of each papilla rather than a conspicuous apical seta as in *T. marientalensis*.

Plants from between Sutherland and Beaufort West [e.g. PVB 4000 (BOL)] have pale yellow flowers finely flecked with purple rather than the customary dark brown to purple-black.

2. *Tridentea pachyrrhiza* (Dinter) Leach, Excelsa Tax. Ser. 2: 14 (1980). Figure 13.

3. *Tridentea marientalensis* (Nel) Leach, Proc. Trans. Rhod. scient. Ass. 59: 3 (1978). Figures 13, 15.

Two subspecies are recognized and may be separated as follows:

Corolla sparingly yellowish towards centre, becoming reddish to blackish beyond, tube short, more or less funnel-shaped . . . . .

..... 3a. subsp. *marientalensis*

Corolla yellow to cream except towards upper half of lobes which are reddish to blackish, campanulate to bowl-shaped (tube cup-shaped) . . . . . 3b. subsp. *albipilosa*

Subsp. *marientalensis* is far more common and widespread in the south-eastern portion of Namibia than earlier records indicate. It is found to the north and east of the Great Karas Mountains (Figure 13). In Namibia it grows on reddish Kalahari sand or calcrete, not on dunes but in the firmer, low-lying areas between them among stands of *Rhigozum trichotomum*. It is sometimes locally very common, with individual specimens forming clumps up to 0.5-m diameter.

*T. marientalensis* subsp. *albipilosa* (Gies) Leach is found from the west between Maltahöhe and Aus eastward to the western flank of the Great Karas Mountains (Figure 13). While it was observed in a few cases to grow on stony slopes, plants in such places were rare. Larger populations were seen in flat areas on firm reddish sand among dense patches of *Rhigozum trichotomum*. There is, therefore, very little difference, if any, between the type of habitat that the two subspecies occupy.

Flowers in western localities seem very different from subsp. *marientalensis*. There is only a small, dark patch in the upper half of each corolla lobe and the rest of the corolla is pale yellow or cream-coloured. The corolla tube is usually somewhat asymmetrically bowl-shaped, with the tube slightly longer on the side closest to the ground. This causes the flower to face partially upwards but with the corona facing horizontally.

Material from south and south-east of the Great Karas Mountains in Namibia is somewhat difficult to place into either of these two subspecies. Photographs of a specimen collected near Ariamsvlei and cultivated at Münster, Germany (*Albers 2348*) showed flowers with a rather shallow, bowl-shaped tube at the centre with cream speckled finely with red on most of the corolla and reddish-black towards the tips of the lobes. This would seem to be subsp. *albipilosa* as well but is far less brightly yellow-cream and tubular than flowers from further west. It is possible that one is dealing here with only a single, quite variable taxon rather than two subspecies: similar variation from pale to dark flowers is found in the closely allied *T. gemmiflora*.

The papillae on the inner surface of the corolla seem always to be discrete and each is usually tipped with a long, slightly clavate seta which may reach nearly five times the length of the papilla itself.

4. *Tridentea virescens* (N.E. Br.) Leach, Proc. Trans. Rhod. scient. Ass. 59: 3 (1978). Figures 16, 17.

*Tridentea virescens* has an extremely wide distribution over the drier parts of the Northern Cape and northern parts of the Eastern Cape. Several new records (Figure 17) have been gathered since Leach's account.

While *T. virescens* clearly belongs in *Tridentea* and also in Sect. *Tridentea* (longer leaves, large papillae on the corolla, trifold outer corona), the unusually coloured flowers are smaller than is typical of this section and they are deeply 5-lobed so that there is only a small united portion around the corona. There is a shallowly bowl-shaped tube in the centre containing the lower half of the corona. The flowers have a strong foetid odour somewhat resembling that of old human excrement.

The papillae on the corolla surface are especially prominent in this species and are fused into ridges with only the apices free. Each usually has an inconspicuous, small apical seta.

B. Sect. *Parvipunctia* Leach, Excelsa Tax. Ser. 2: 5 (1980).

Corolla papillate to smooth on ventral surface, mottled over whole surface except sometimes for dark border. Corona: outer lobes simple, bifid or trifid; inner lobes often without dorsal 'fin'. Pollinia broadly D-shaped.

Key to species of Sect. *Parvipunctia*

1. Inner corona lobes incumbent on anthers and not produced above them . . . . . 2.
- Inner corona lobes much exceeding anthers, initially incumbent on them then rising above centre in narrow column . . . . . 3.
2. Outer corona lobes distinctly trifid. . . . . *T. peculiaris*
- Outer corona lobes ± truncate to deeply bifid . . . *T. parvipuncta*
3. Corolla covered with columnar papillae, outer corona lobes linear-lanceolate with broad ascending lateral flaps at base . . . . . *T. dwequensis*
- Corolla ± smooth inside, outer corona lobes without broad basal flap . . . . . *T. jucunda*

5. *Tridentea parvipuncta* (N.E. Br.) Leach, Proc. Trans. Rhod. scient. Ass. 59: 3 (1978). Figures 18, 19.

Leach maintained two varieties: var. *parvipuncta* and var. *truncata*. As can be seen from the distribution map (Figure 19), var. *truncata* is found only some distance to the north-west of var. *parvipuncta*. The two varieties are separated by somewhat unreliable characters (Leach 1980: 29), although I have never seen specimens where it was not possible to assign them to one or other of the varieties. Since there appears to be distinct regional separation of the various populations into two elements, the rank of subspecies is most appropriate. The two subspecies are separated as follows:

- Margins of corolla lobes without cilia, outer corona lobes ± truncate . . . . . 5b. subsp. *truncata*
- Margins of corolla lobes ciliate, outer corona lobes usually deeply bifid. . . . . 5a. subsp. *parvipuncta*

The inner surface of the corolla is faintly and irregularly rugose but seems always to be without papillae.

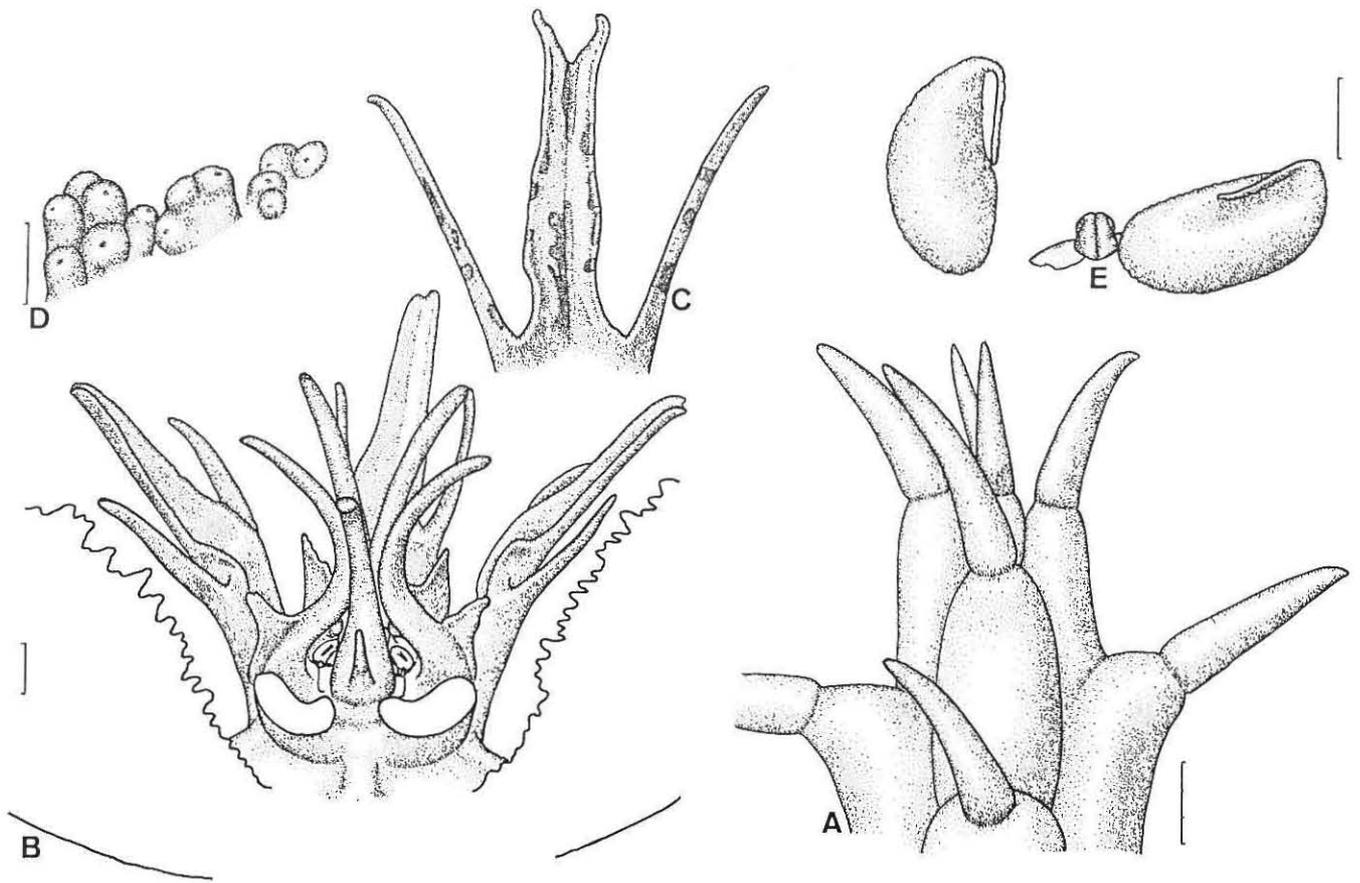
5a. *T. parvipuncta* subsp. *parvipuncta*

This subspecies is found from around Matjiesfontein eastwards in the Great Karoo to near Beaufort West. The isolated locality from Douglas (Leach 1980: 30) is extremely doubtful and has been left off the distribution map.

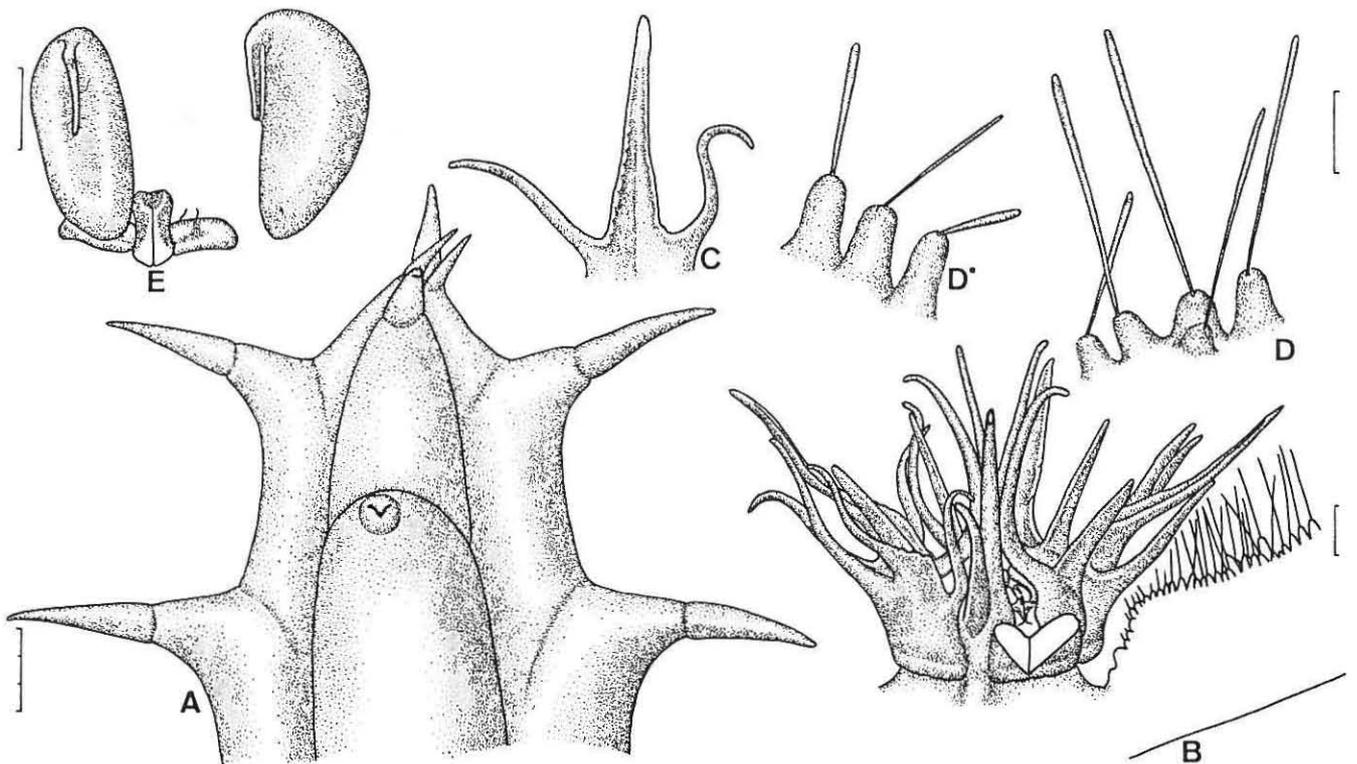
5b. *T. parvipuncta* subsp. *truncata* (Lückhoff) Bruyns, stat. nov. *Tridentea parvipuncta* var. *truncata* (Lückhoff) Leach, Excelsa Tax. Ser. 2: (1980). *Stapelia parvipuncta* var. *truncata* Lückhoff, White & Sloane, Stap. ed. 2, 3: 1145 (1937). Type: Cape, Ceres Karoo, Dwequa River, J. Lückhoff (missing). Neotype (Leach 1980): Cape, Botterkloof, Hall sub NBG 229/56 (NBG).

*Tridentea pusilla* Frandsen, Aloe 29: 40 (1992). Type: Cape, Botterkloof, Frandsen FR5 (PRE).

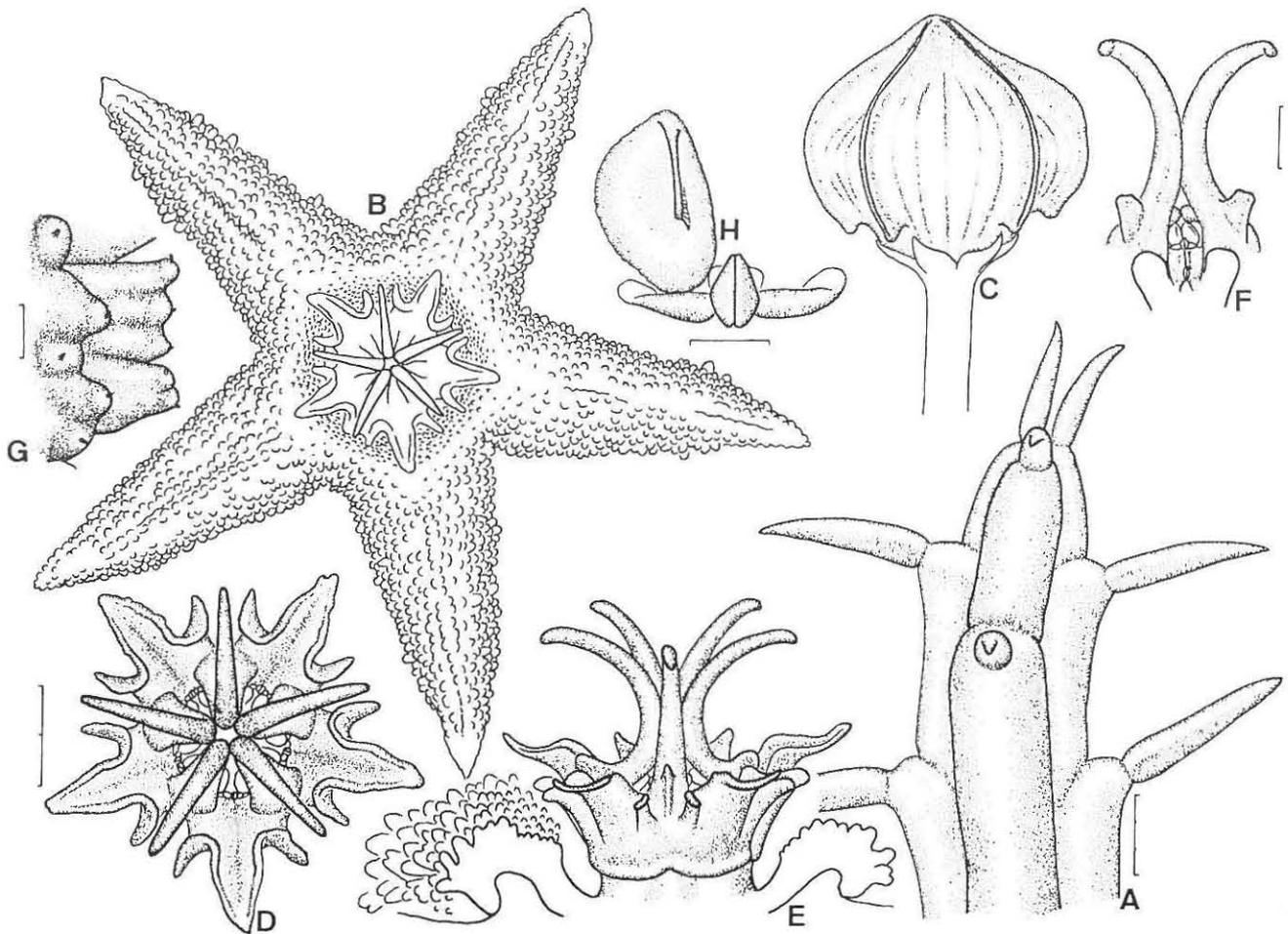
It is not at all clear why *Tridentea pusilla* was described. It does not differ from subsp. *truncata* except for the smaller flowers. Notably smaller flowers are often produced in this genus (and others) if the plant is unhealthy or not properly established or towards the end of the flowering period. Small flowers have been seen on plants of this species from several localities and



**Figure 14** *Tridentea gemmiflora*. A, apex of stem with leaves. B, corolla dissected to show thickened fabric beneath corona, gynostegium with 2 outer corona lobes removed. C, outer corona lobe, dorsal view. D, papillae on corolla. E, pollinarium (one pollinium broken off). Scales: A = 3 mm; B, C = 1 mm (at B); D = 0.5 mm; E = 0.25 mm. Drawn from: A, B, E, south-east of Touwsriver, PVB 2615 (NBG); C, D, Fraserburg, PVB 4786 (BOL).



**Figure 15** *Tridentea marientalensis* subsp. *albipilosa*. A, apex of stem with leaves. B, dissected flower with one outer corona lobe removed. C, outer corona lobe, dorsal view. D, papillae on corolla. E, pollinarium (one pollinium broken off). Scales: A = 3 mm; B, C = 1 mm; D = 0.5 mm; E = 0.25 mm. Drawn from: A-E, north of Aus, PVB 4220 (BOL); D\*, north of Helmeringhausen, PVB 4169 (BOL).



**Figure 16** *Tridentea virescens*, A, apex of stem with leaves. B, flower. C, bud. D, gynostegium, face view. E, gynostegium, side view showing slightly thickened corolla above base. F, bases of inner corona lobes (outer lobe removed). G, papillae on corolla lobes. H, pollinarium (one pollinium broken off). Scales: A–C = 3 mm; D, E = 2 mm; F = 1 mm; G = 0.5 mm; H = 0.25 mm. Drawn from: east of Beaufort West, PVB 3049 (BOL, NBG).

there is no justification for maintaining *T. pusilla* as a distinct species.

**6. *Tridentea jucunda*** (N.E. Br) Leach, Proc. Trans. Rhod. scient. Ass. 59: 3 (1978). Meve, Asklepios 44: 2–7 (1988). Lectotype (Leach 1980): Cape, near Douglas, *Pillans 644* (BOL).

*Tridentea jucunda* var. *cincta* (Marl.) Leach, Excelsa Tax. Ser. 2: 33 (1980). Type: Cape, Nuweveld Mtns near Beaufort West, *Marloth 5116* (PRE).

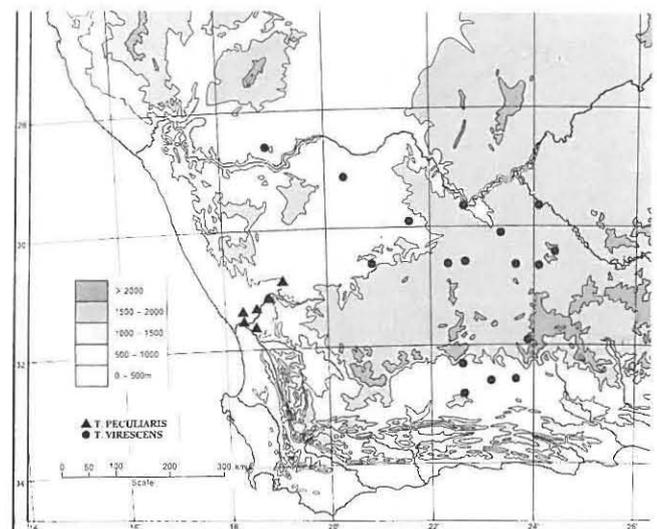
*Tridentea jucunda* var. *dinteri* (Berger) Leach, Excelsa Tax. Ser. 2: 34 (1980). Type: Namibia, Klein Karas, *J. Dinter sub Dinter 3247* (SAM). Figures 19, 20.

Leach (1980: 32) considered his arrangement of three varieties within *T. jucunda* as 'perhaps somewhat unsatisfactory'. Meve (1988) has also pointed out that 'the obvious overlapping and mixing of characters which still exists certainly appears not to allow the convincing use of three different taxa'. I have illustrated here (Figure 20) two collections which I was unable to assign satisfactorily to any one of the varieties recognized by Leach.

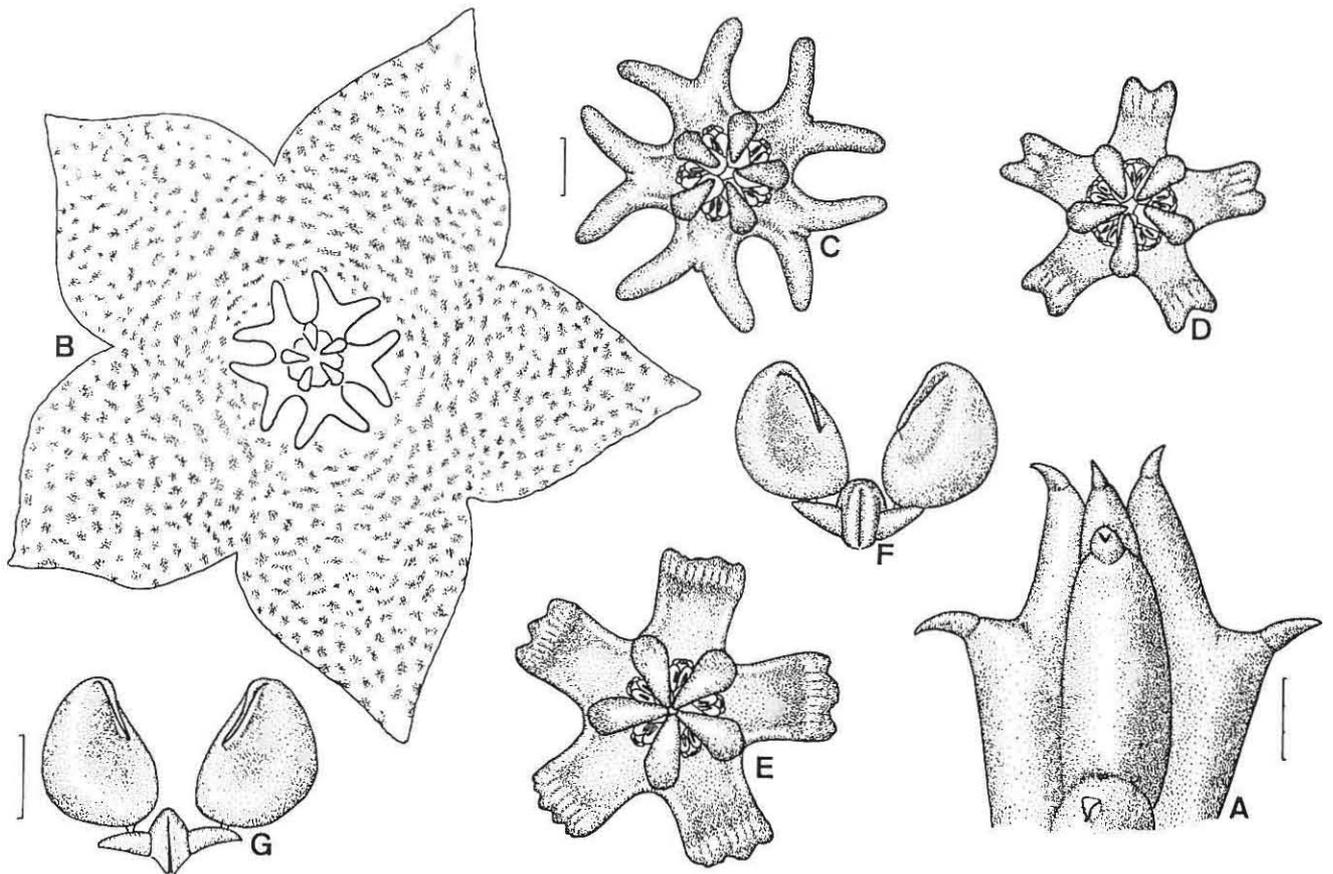
The first collection (PVB 3908) came from south-east of Witpütz, Namibia in an area where one would expect var. *dinteri*. Its acute outer corona lobes, the presence of a few cilia in the sinuses between the lobes and the 'not at all clavate' inner corona lobes place it under var. *jucunda*. There is no trace of the 'wing-

like dorsal horn or gibbosity' on the inner corona lobes and the outer lobes have quite the wrong shape for var. *dinteri*.

The second collection (PVB 3318), from south of Prieska, lacked cilia on the margins of the lobes and had inner corona lobes slightly recurved and slightly thickened towards the apex.



**Figure 17** Distribution of *Tridentea peculiaris* and *T. virescens*.



**Figure 18** *Tridentea parvipuncta*. A, apex of stem with leaves. B, flower. C-E, gynostegium. F-G, pollinaria. Scales: A, B = 3 mm; C-E = 1 mm; F, G = 0.25 mm. Drawn from: subsp. *parvipuncta*: A, near Rietbron, PVB 3246 (BOL); B, C, F, north of Laingsburg, PVB 3284 (NBG). Subsp. *truncata*: D, E, G, north of Karooport, PVB 4274 (no specimen).

Therefore it would probably key out as var. *cincta*, although geographically it should be under var. *jucunda*.

Meve (1988) provided several other examples of similar anomalies. It appears therefore that three different taxa are not involved here and that one is dealing with one rather variable and very widespread species.

The inner surface of the corolla in *T. jucunda* is usually smooth. Nevertheless, in some collections (e.g. PVB 3318) there are a few, low papillae in the corolla tube, each tipped with a seta.

**7. *Tridentea dwequensis*** (Lückhoff) Leach, *Excelsa Tax. Ser. 2*: 35 (1980). Figures 19, 21.

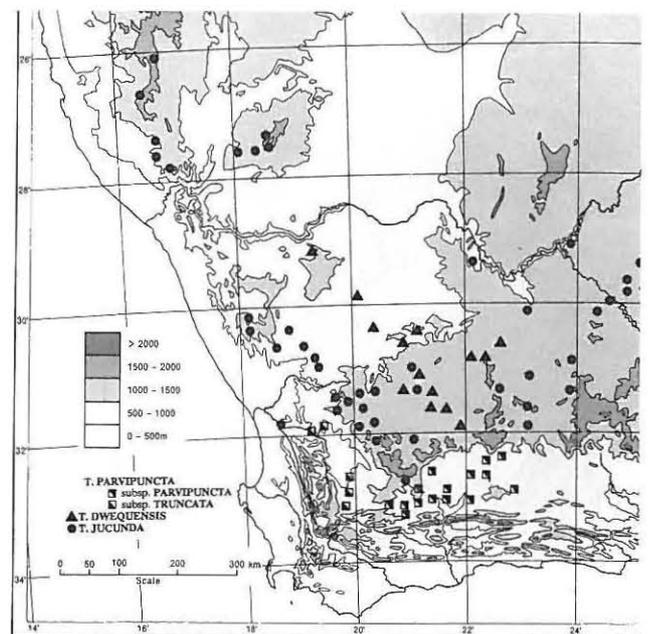
Little-known at the time of Leach's publication, *T. dwequensis* has been proved, by more recent exploration, to be quite widespread and frequent in the arid parts between Brandvlei, Williston, Carnarvon and Fraserburg and a much more complete picture of its distribution can now be given (Figure 19).

The corolla in this species is covered, especially towards the tips of the lobes, with columnar papillae. Towards the tips of the lobes these appear to be always discrete but in the mouth of the corolla tube they sometimes become fused together as in Sect. *Tridentea*. The flower is always campanulate, with the corona entirely contained within the tube. The corolla lobes usually have a few small cilia along the margins near the base (cf. Leach 1980: 36).

The outer corona lobes have a broad flap on either side at the base which is folded upwards (Figure 21C, D). This is almost certainly homologous to the lateral lobules of the trifid corona lobes of Sect. *Tridentea*. The inner corona lobes are exceptionally long and slender from a broad base and appear always to be without any dorsal 'fin'.

In cultivation, the stems have been found sometimes to exhibit a slight tendency towards a rhizomatous habit.

**8. *Tridentea peculiaris*** (Lückhoff) Leach, *Proc. Trans. Rhod. scient. Ass.* 59: 4 (1978). Figures 17, 22.



**Figure 19** Distribution of *Tridentea dwequensis*, *T. jucunda* and *T. parvipuncta*.

*T. peculiaris* is associated with the deep red sands found along the Sout, Doring and Hol Rivers and the lower Olifants River, from Koekenaap in the west to the foot of the Langeberg (north-west of Loeriesfontein) in the north-east. Plants do not grow on loose sand and are found in firm soil, usually among colonies of various species of *Ruschia* and other succulents.

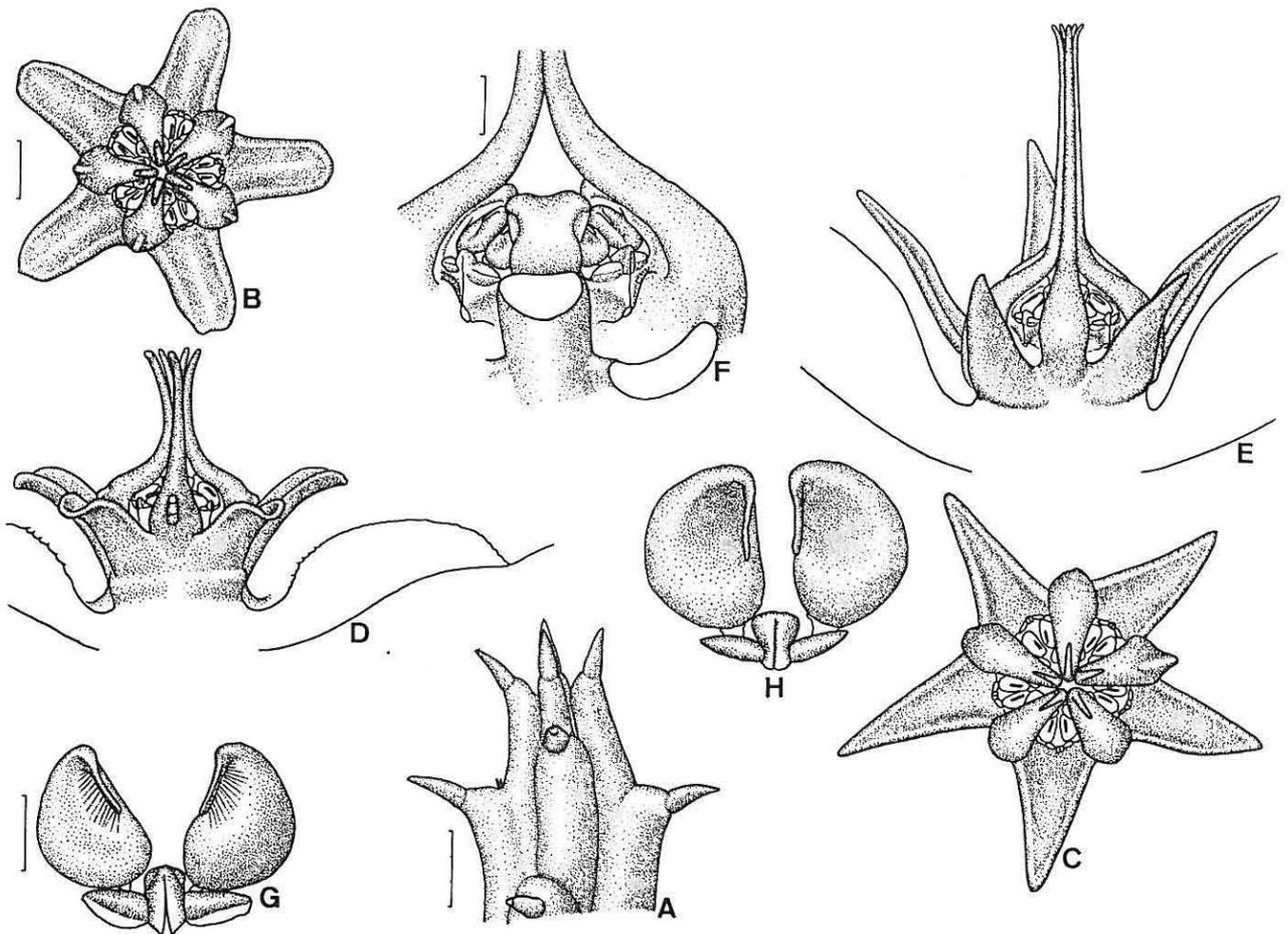
*T. peculiaris* often exhibits a rhizomatous habit, to an extent unusual for *Tridentea*, though it is not as pronounced as in *Tromotriche revoluta*. Apart from this the plants are typical for the genus with the usual, soft, edible stems with subulate leaves on young tissue.

The corolla is remarkable for its unusual colours and the presence of a thickened, raised annulus around the corona. However, the illustrations here show that in most species the corolla is thickened around the mouth of the tube and the main reason for the conspicuousness of the annulus in *T. peculiaris* is the manner in which the corona lobes are partly reflexed. The margin of the corolla lobes are somewhat folded upwards towards the base after the manner of *T. gemmiflora*. The papillae on the corolla (Figure 22D) are discussed earlier, under the heading Flowers (page 7).

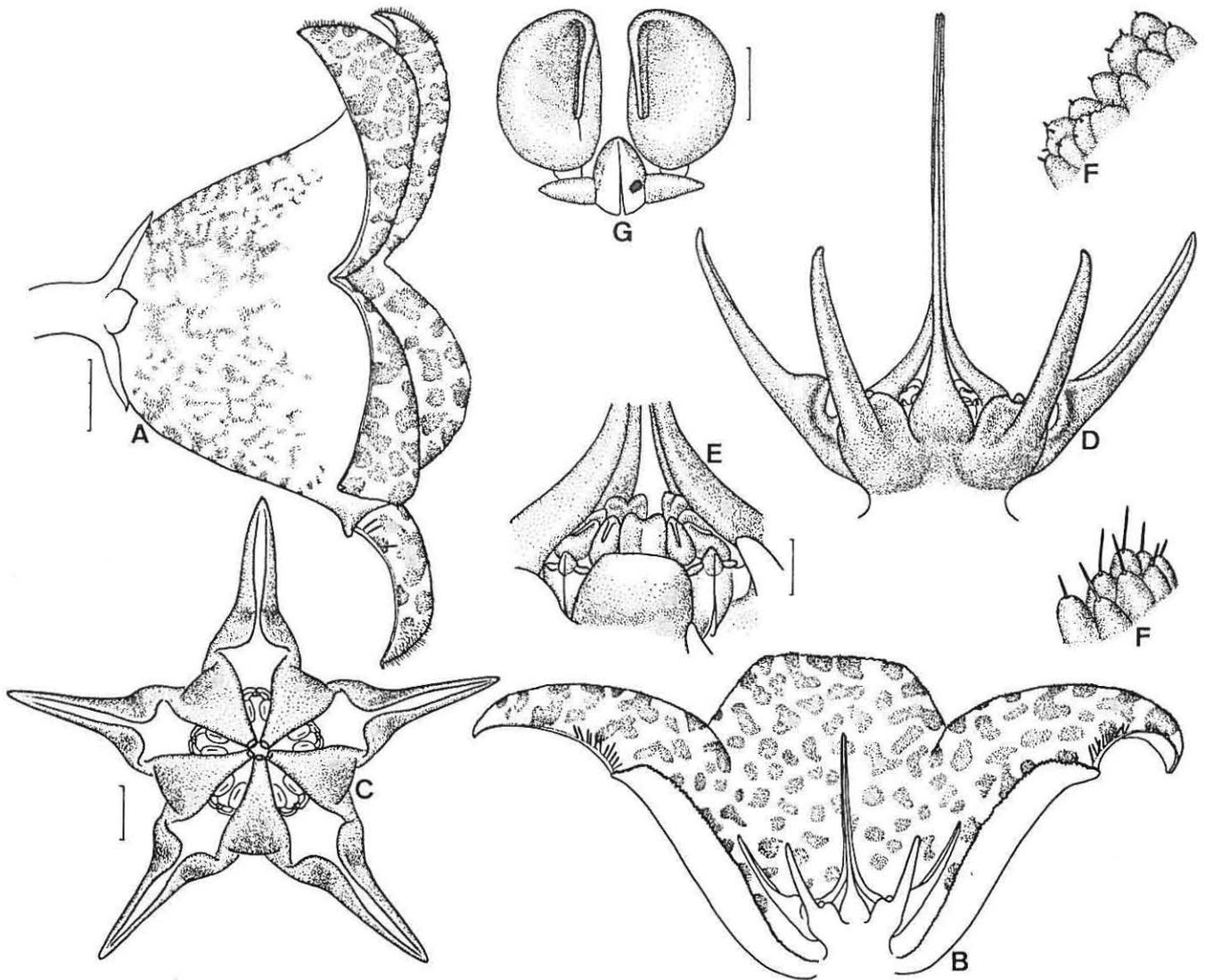
**II. TROMOTRICHE** Haw., Syn. Pl. Succ.: 36 (1812), excl. *T. pruinosa*. Leach, JI S. Afr. Bot. 50: 549–562 (1984), excl. *T. engleriana*. Lectotype (Leach 1984): *T. revoluta* (Masson) Haw.

*Caruncularia* Haw., Syn. Pl. Succ.: 333 (1812). Type: *C. pedunculata* (Masson) Haw. *Stapelia* Sect. *Caruncularia* (Haw.) Decne., DC. Prodr. 8: 658 (1844). *Tridentea* Sect. *Caruncularia* (Haw.) Leach, Excelsa Tax. Ser. 2: 5 (1980). Type: *T. pedunculata* (Masson) Leach.

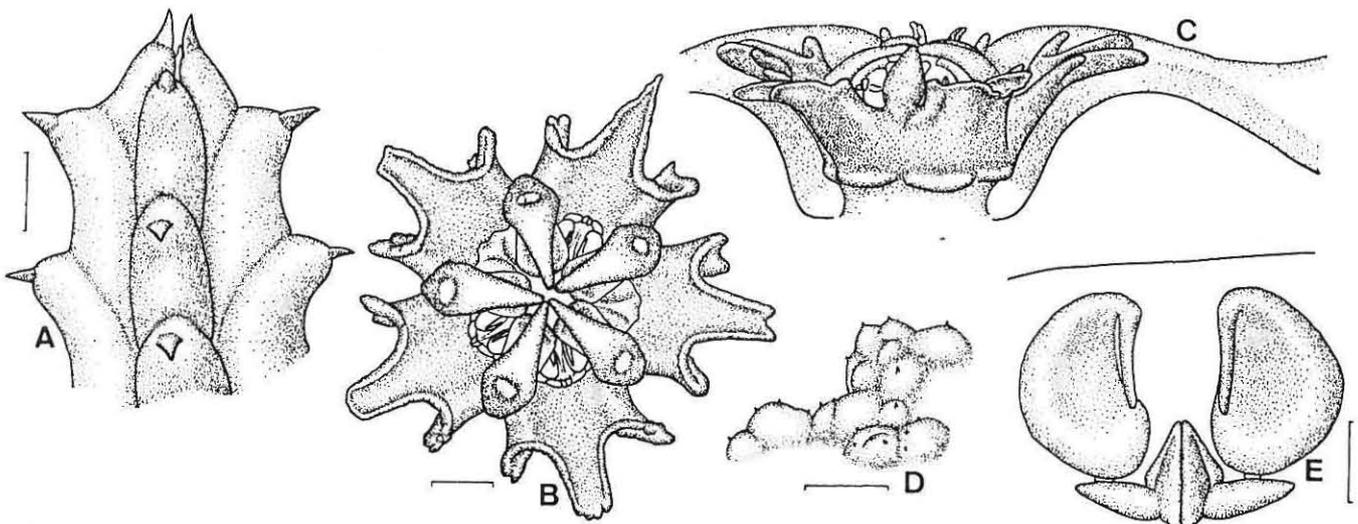
*Plant* a dwarf succulent, tufted, sometimes forming compact clumps, sometimes extensively rhizomatous with widely separated above-ground stems, occasionally with long stems pendulous from cliffs or stems creeping. *Stems* 4 (–6)-angled, very variable in length, 6–25 mm thick, fleshy, with matt surface, subtessellate, tubercles obscure and obtuse, with small deltoid leaf subtended by two stipular denticles to leafless and without stipules. *Flowers* developing successively on gradually lengthening peduncles randomly situated on stem. *Pedicel* (6) 10–190 mm long, spreading to ascending, glabrous. *Calyx* 5-lobed, glabrous. *Corolla* (12) 15–70 mm diam., revolute to rotate to tubular-campanulate, deeply to shallowly lobed, inside often reticulately to transversely rugose usually with small unicellular papillae especially in tube. *Corona* consisting of two series arising from staminal column, glabrous; *outer corona* of five ascending to spreading dorsiventrally flattened simple lobes fused to inner lobes at base or fused laterally to lower sides of inner lobes to form cup around column; *inner lobes* incumbent on anthers, usually much exceeding them and rising up above centre of style-head, dorsi-ventrally flattened at least towards base (often cylin-



**Figure 20** *Tridentea jucunda*. A, apex of stem with leaves. B, C, face view of gynostegium. D, E, side view of dissected flower. F, gynostegium with 2 outer and one inner corona lobes excised. G, H, pollinaria. Scales: A = 3 mm; B–E = 1 mm; F = 0.5 mm; G–H = 0.25 mm. Drawn from: A, B, D, G, south of Prieska, PVB 3318 (NBG); C, E, F, H, south-east of Witpütz, PVB 3908 (BOL).



**Figure 21** *Tridentea dwequensis*. A, flower. B, dissected flower showing broad tube. C, face view of gynostegium. D, side view of gynostegium. E, part of gynostegium with outer corona lobes and one inner lobe removed, showing rather broad guide rails. F, papillae on corolla: upper ones from mouth of tube, lower from near tips of lobes. G, pollinarium. Scales: A–B = 3 mm; C–D = 1 mm; E–F = 0.5 mm; G = 0.25 mm. Drawn from: Williston townlands, PVB 3320 (BOL).



**Figure 22** *Tridentea peculiaris*. A, apex of stem. B, face view of gynostegium. C, side view of centre of dissected flower showing thickened annulus. D, papillae on corolla taken towards tips of lobes. E, pollinarium. Scales: A = 3 mm; B, C = 1 mm (at B); D = 0.5 mm; E = 0.25 mm. Drawn from: north of Vanrhynsdorp, Nagel 65 (no specimen).

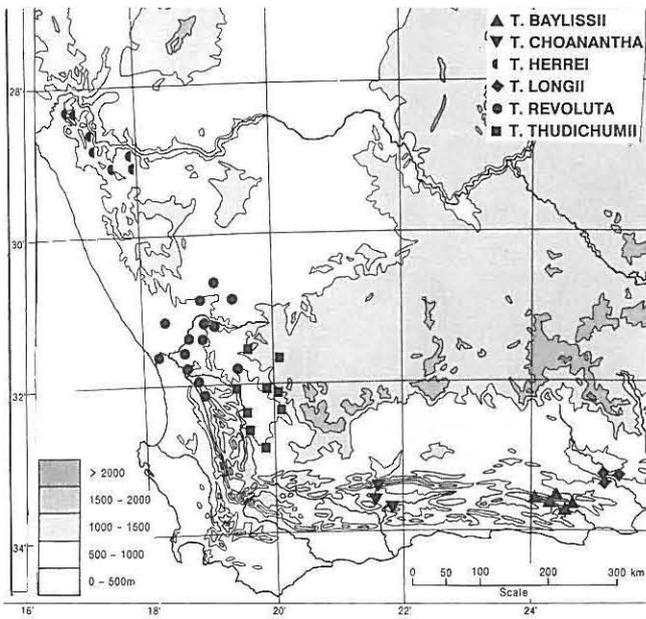


Figure 23 Distribution of *Tromotriche baylissii*, *T. choanantha*, *T. herrei*, *T. longii*, *T. revoluta* and *T. thudichumii*.

drical or clavate and variously tuberculate above), mostly with laterally flat-tened deltoid to clavate dorsal 'fin' in lower half. Otherwise as in *Tridentea*.

*Tridentea* Sect. *Caruncularia* was divided into three subsections: Subsect. *Caruncularia*, Subsect. *Apertae* Leach and Subsect. *Pendentes* Leach (Leach 1980).

The first two were distinguished by the two-horned inner corona lobes in Subsect. *Caruncularia*, as opposed to the one-horned lobes in Subsect. *Apertae* and the cup-like structure formed by the outer lobes in Subsect. *Apertae*. However, in Subsect. *Apertae* the outer corona is very variable (especially in *T. aperta*) and sometimes a discrete lobe is present with the crenulate-papillose margin which is often found in Subsect. *Caruncularia*. The inner corona varies from short and incumbent on the anthers only (*T. umdausensis*) to rising up in the centre with a single to sometimes two-horned clavate lobe (*T. aperta*) to two clavate lobes in Subsect. *Caruncularia*. I view this as a continuum of variation in both these characters and so place all these species in a single section *Caruncularia*. The species of Subsect. *Pendentes* and the two from *Tromotriche* are placed in Sect. *Tromotriche*.

With the exception of *T. umdausensis*, all species of Sect. *Caruncularia* have inner corona lobes rather swollen towards the apex and often (except in *T. herrei*) with rather verrucose apex.

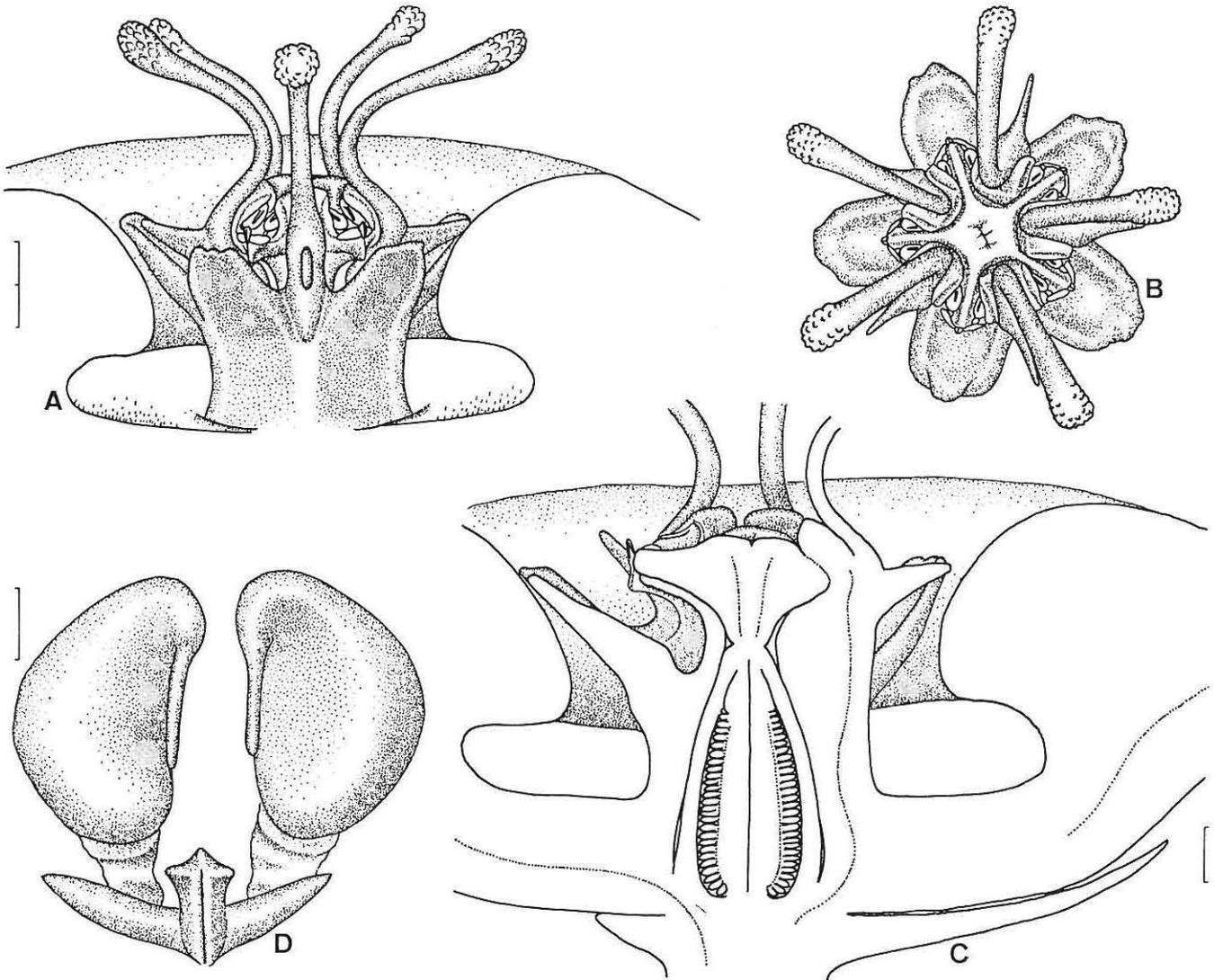
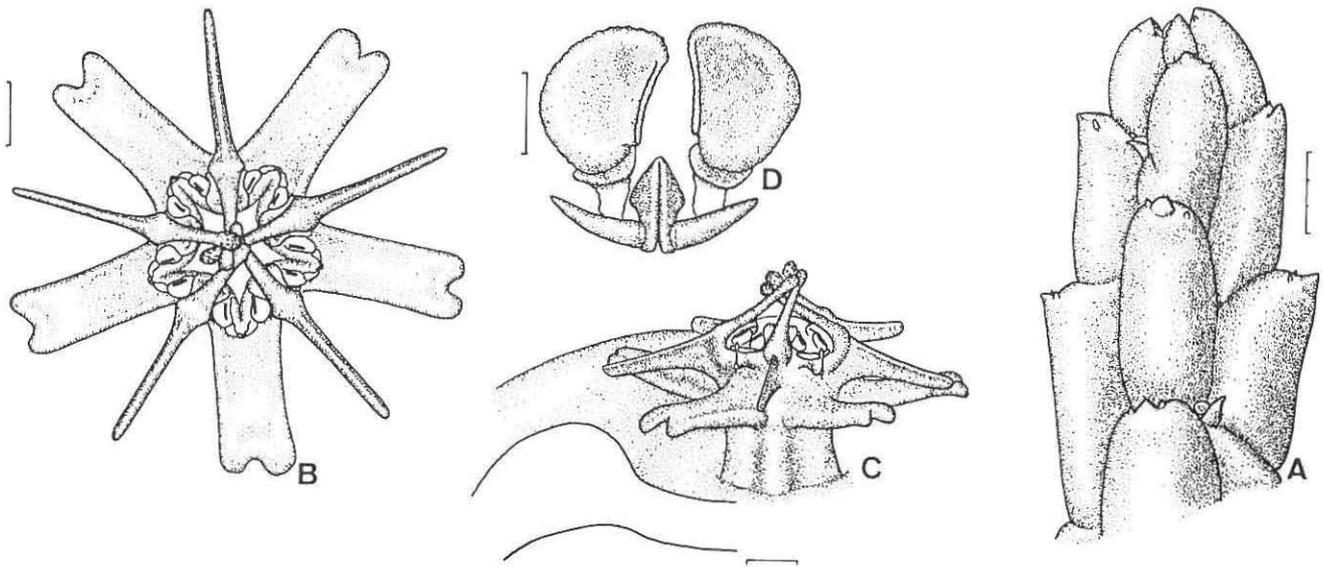
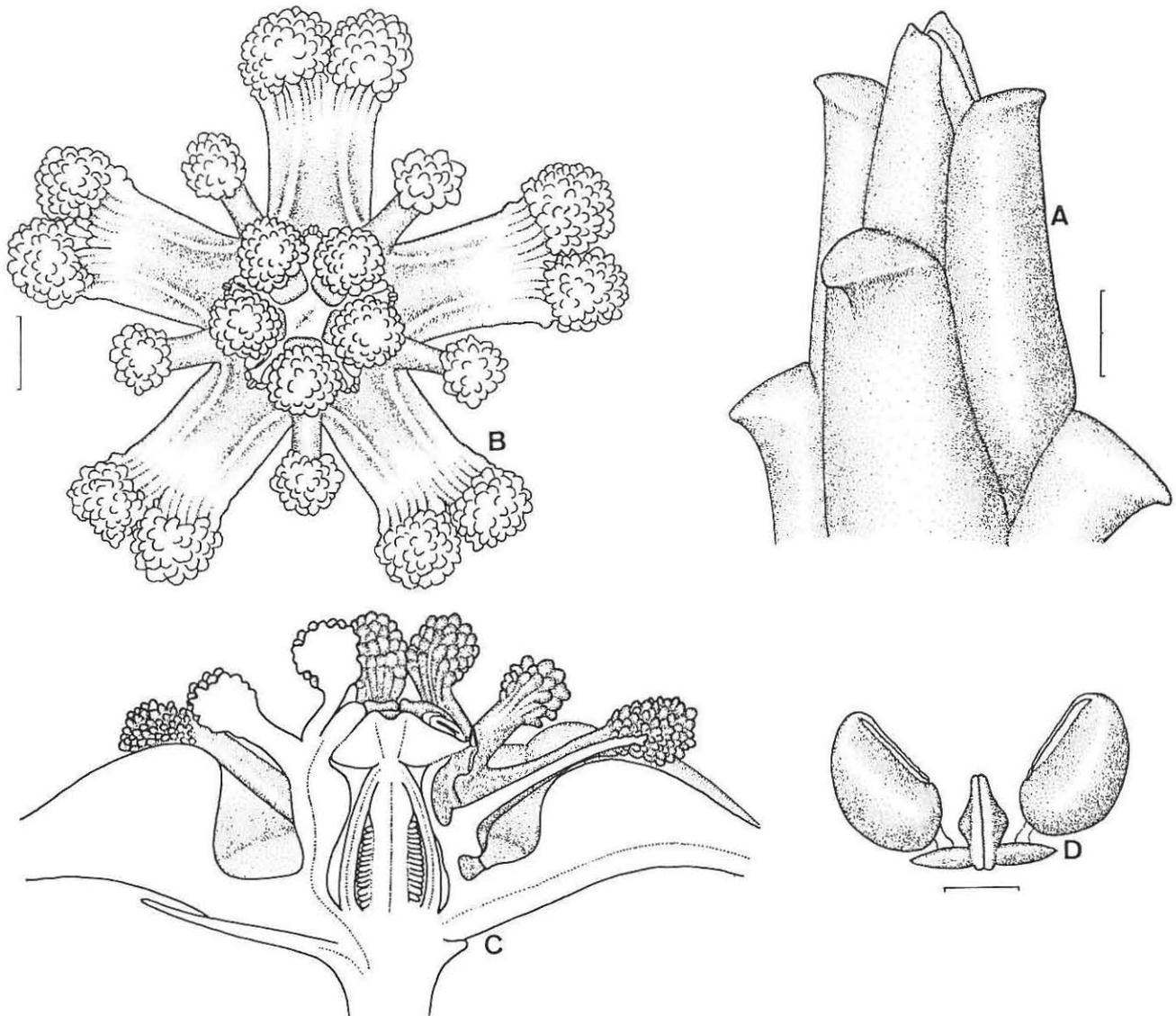


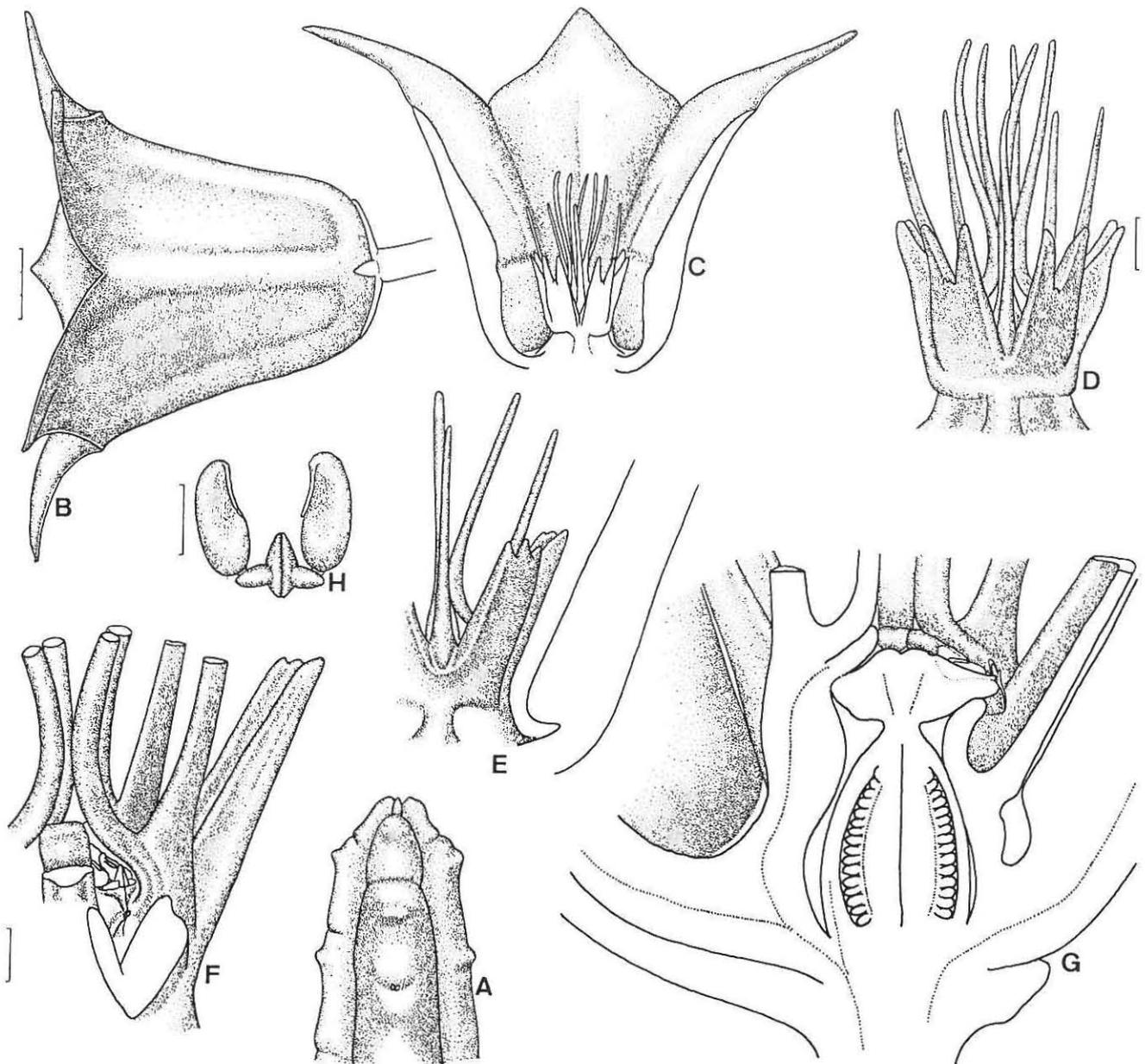
Figure 24 *Tromotriche revoluta*. A, side view of dissected flower showing massive annulus. B, face view of gynostegium. C, half-flower. D, pollinarium. Scales: A, B = 2 mm (at A); C = 1 mm; D = 0.25 mm. Drawn from: Beeswater, Knersvlakte (no specimen).



**Figure 25** *Tromotriche thudichumii*. A, apex of stem. B, face view of gynostegium. C, side view of dissected flower showing thickened 'annulus'. D, pollinarium. Scales: A = 3 mm; B = 1 mm; C = 1 mm; D = 0.25 mm. Drawn from: north of Karooport (no specimen).



**Figure 26** *Tromotriche longii*. A, apex of stem. B, face view of gynostegium. C, half-flower. D, pollinarium. Scales: A = 2 mm; B, C = 1 mm; D = 0.25 mm. Drawn from: A, Sondagrivier, PVB 4928 (BOL.); B-D, north of Kirkwood, PVB 1593 (NBG).



**Figure 27** *Tromotriche choanantha*. A, apex of stem. B, flower. C, dissected corolla. D, gynostegium. E, part of dissected corolla showing much thickened 'annulus' above base beneath outer corona lobe, also rather different outer corona lobes from D. F, gynostegium with outer corona and inner corona lobe excised. G, half-flower. H, pollinarium. Scales: A–C = 3 mm (at B); D–E = 1 mm (at D); F–G = 1 mm (at F); H = 0.25 mm. Drawn from: A–C, E–G, west of Calitzdorp, PVB 2216 (NBG). D, H, north of Calitzdorp, PVB 2907 (BOL).

However, this character is not unique to these species and consequently has not been used: it is found in *T. revoluta*, to a lesser degree in *T. thudichumii* and *T. baylissii* and in the otherwise unrelated *Stapelia clavicornata* Verdoorn and *S. engleriana*.

From Figures 2 and 3 it can be seen that the outer walls of the epidermal cells of Sect. *Tromotriche* and Sect. *Caruncularia* may be somewhat different. In Sect. *Tromotriche* (except for *T. revoluta*) there are larger idioblasts with smaller  $\pm$  flat cells in between. *T. revoluta* is exceptional in the section in having all the outer walls raised more or less equally into low papillae, though this becomes irregular around the leaf base (Figure 2A).

Prominent idioblasts are found more sporadically in Sect. *Caruncularia*: They are just distinguishable in Figure 3D in *T. herrei* and were observed by Kusch (1985) in *T. pedunculata* and *T. ruschiana*. In *T. umdausensis* and *T. aperta* more or less every cell may have its outer wall raised into a papilla. The sur-

face was never observed, though, to have the neat, flat cells such as are usually seen in *Tridentea* away from the leaf.

The first two species of Sect. *Tromotriche* exhibit an extremely rhizomatous habit. One might suppose that this is a response to sandy habitats. If this were the case for *T. revoluta*, one would expect it to be common in the 'sandveld' from Elands Bay to Port Nolloth or in the deep red sands along the lower Olifants River. However, my own investigations have not turned it up in these areas at all: north of the Olifants River it is most common on the Knersvlakte on small stony outcrops (where its stems can rise up from among the rocks over an area of 2–3 m<sup>2</sup>) and on rocky, often steep slopes on the eastern boundary of the Knersvlakte from north of Vanrhyns Pass southwards to near Clanwilliam. *T. thudichumii* grows among stones (dolerite boulders on the northern and eastern boundaries of the Ceres Karoo) or in hard loam in flat areas (usually with various colony-forming, sometimes spiny ruschias) and I have never found it in sand.

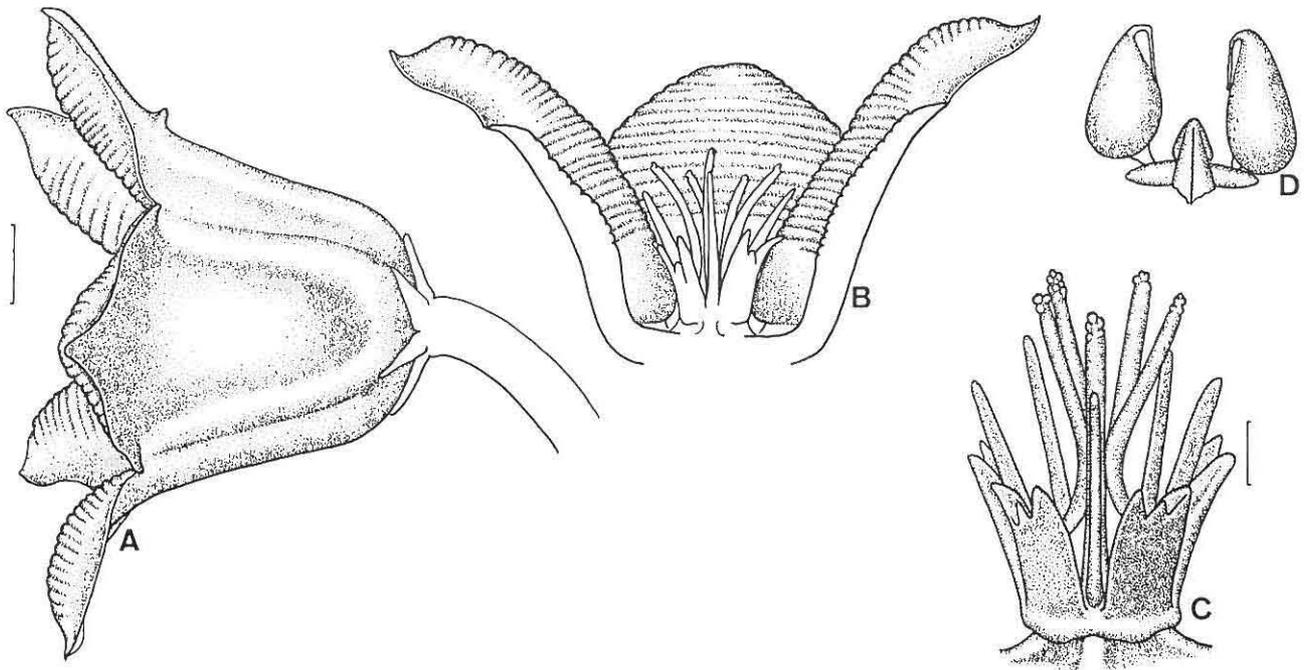


Figure 28 *Tromotriche baylissii*. A, flower. B, dissected flower. C, gynostegium. D, pollinarium. Scales: A–B = 3 mm; C = 1 mm; D = 0.25 mm. Drawn from: west of Patensie, PVB 1895 (no specimen).

Neither rockiness nor hardness of the soil seem to have the slightest inhibiting effect on the rhizomatousness of plants and there appear to be no grounds at all for believing that this growth form is invariably a response to sandy habitats.

Key to sections of *Tromotriche*

1. Inner corona lobes with laterally flattened dorsal horn ..... **Sect. *Tromotriche***  
 Inner corona lobes with clavate dorsal horn or horn lacking. . . . . 2.
2. Outer corona lobes with much thickened apex, longer than inner corona lobes ..... **Sect. *Tromotriche***  
 Outer corona lobes without thickened apex, much shorter than inner corona lobes ..... **Sect. *Caruncularia***

A. Sect. *Tromotriche*

*Plants* pendulous from cliffs, creeping or rhizomatous. Leaves minute and deltoid subtended by stipular denticles to absent. *Corolla* revolute to tubular-campanulate. *Corona*: outer lobes simple or bifid and thickened near apex, dorsiventrally flattened; inner lobes dorsiventrally flattened at least at base, becoming cylindrical above, often with thickened apex, usually with laterally flattened dorsal horn (clavate in *T. longii*).

Key to species of Sect. *Tromotriche*

1. Corolla tubular-campanulate ..... 2.  
 Corolla revolute or ± rotate with short tube ..... 3.
2. Inner surface of corolla smooth, inner corona lobes attenuate . . . . . ***T. choanantha***  
 Inner surface of corolla transversely rugose, inner corona lobes slightly thickened towards apex. . . . . ***T. baylissii***
3. Outer corona lobes bifid, thickened and irregularly tuberculate towards apex, inner lobes and their dorsal horn both clavate and tuberculate ..... ***T. longii***  
 Corona not as above. . . . . 4.
4. Corolla 20–30 mm diam., inner corona lobes shorter than outer with dorsal horn of equal or greater length . . . . . ***T. thudichumii***  
 Corolla 40–70 mm diam., inner corona lobes much larger than outer, with short dorsal horn. . . . . ***T. revoluta***

1. ***Tromotriche revoluta*** (Masson) Haw, Syn. Pl. Succ.: 36 (1812). Leach, JI S. Afr. Bot. 50: 553 (1984). *Stapelia revoluta* Masson, Stap. Nov.: 12, t. 10 (1796). Lectotype (Leach 1984): Masson, Stap. Nov.: t. 10. Figures 23, 24.

A very extensive synonymy is given by Leach (1984) and will not be repeated here.

*T. revoluta* is widespread along the Olifants River valley from Clanwilliam northwards onto the Knersvlakte where it is also found from near the coast at Papendorp to a little south-east of Kliprand.

Most notable features of the flowers are the extreme thickening of the corolla at the annulus and the very large pollinaria (Figure 24).

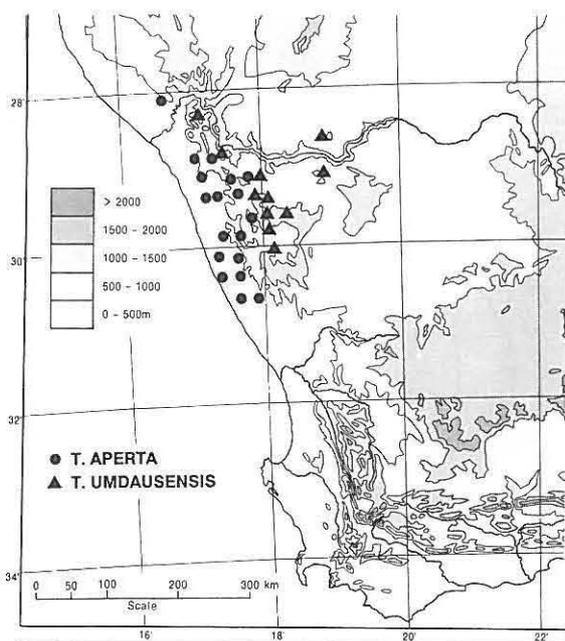


Figure 29 Distribution of *Tromotriche aperta* and *T. umdausensis*

2. *Tromotriche thudichumii* (Pillans) Leach, JI S. Afr. Bot. 48: 425 (1982), *ibid.* 50: 556 (1984). *Stapelia thudichumii* Pillans, JI S. Afr. Bot. 25: 375 (1959). Type: Cape, Ceres Karoo, Uitkomst, *Thudichum sub BOL 26740* (BOL). Figures 23, 25.

Again a very rhizomatous species like *T. revoluta*, *T. thudichumii* is mainly found around the edges of the Ceres Karoo, except in the south and east. It has also been collected more recently outside the Ceres Karoo on the high area north of Middelpos [PVB 4300 (BOL)].

While the coronas of *T. thudichumii* and *T. revoluta* are of a similar size, the corolla of *T. thudichumii* is much smaller with a rather shallow tube and only slightly raised annulus (Figures 6A, 25C). The pollinarium is also smaller. The inner corona is most unusual. There is a comparatively large, spreading dorsal horn, usually about the same size as the lobe itself, while the lobes spread obliquely towards the centre of the flower and do not rise up in the centre as is usual. The nectarial orifice (Figure 6A) is unusually narrow.

The flower emits a slight putrid smell.

3. *Tromotriche longii* (Lückhoff) Bruyns, *comb. nov. Tridentea longii* (Lückhoff) Leach, Proc. Trans. Rhod. scient. Ass. 59: 4 (1978), *Excelsa Tax. Ser. 2: 63* (1980). *Stapelia longii* Lückhoff, S. Afr. Gard. 25: 95-6 (1935). Type: Cape, Klein Winterhoek Mtns, Paardepoort, *Long sub Lückhoff 220* (missing).

Neotype (Leach 1980): Paardepoort, *Leach & Bayliss 15680* (K, PRE, SRGH). Figures 23, 26.

This remarkable species has always been known only from the type locality, Paardepoort, in the Klein Winterhoek Mountains south of Jansenville. More recent collecting has revealed its presence at several other precipitous places nearby in these mountains and also in gorges in the western end of the Suurberg. The pendulous habit observed in Paardepoort (Leach 1980, Figure 37) was not seen elsewhere and plants were mainly creeping in leaf litter under bushes. Specimens were noted often to be associated with shrubs of *Crassula rupestris*.

Stems of *T. longii* are always 6-8 mm thick and so are more slender than in any other *Tromotriche*. In addition they have quite an obvious tooth on each tubercle (Figures 2E, 26A) and are not as rounded as in many of the other species. The corolla is somewhat similar to that of *T. thudichumii* but the corona, with its clavate-tuberculate lobes, is rather more similar to that in the species of Sect. *Caruncularia*. A half-flower (Figure 26C) shows clearly the conspicuous annulus which is partly divided into five islands. However, *T. longii* is unique in its bifid outer corona lobes with clavate-tuberculate apices. The pollinia are somewhat narrow, suggestive of the next two species.

4. *Tromotriche choanantha* (Lavranos & Hall) Bruyns, *comb. nov. Tridentea choanantha* (Lavranos & Hall) Leach,

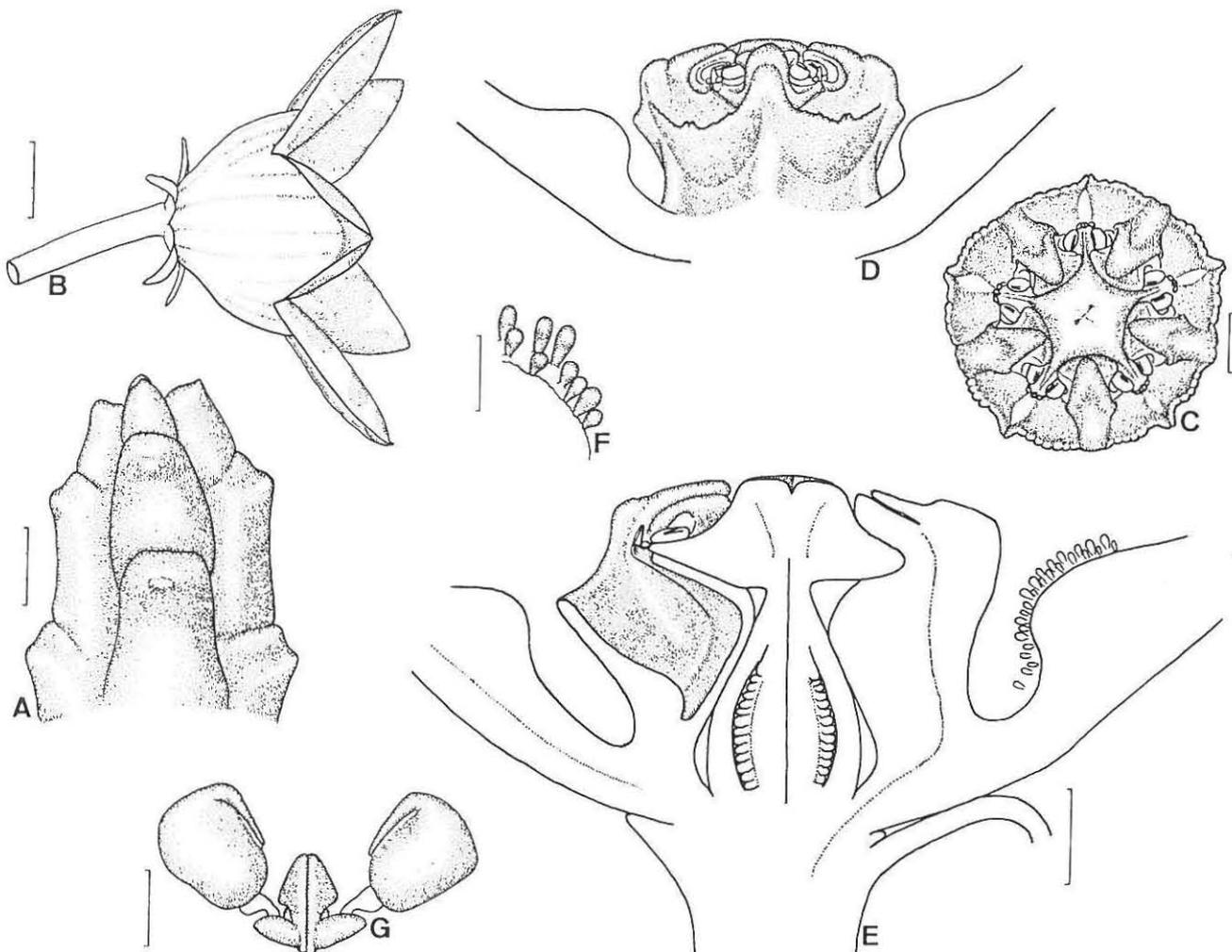


Figure 30 *Tromotriche umdausensis*. A, apex of stem. B, flower. C, face view of gynostegium. D, dissected corolla with gynostegium and thickened 'annulus'. E, half-flower. F, papillae on corona around 'annulus'. G, pollinarium. Scales: A = 3 mm; B = 5 mm; C, D = 1 mm; E = 1 mm; F = 0.5 mm; G = 0.25 mm. Drawn from: north of Steinkopf, PVB 1337 (NBG).

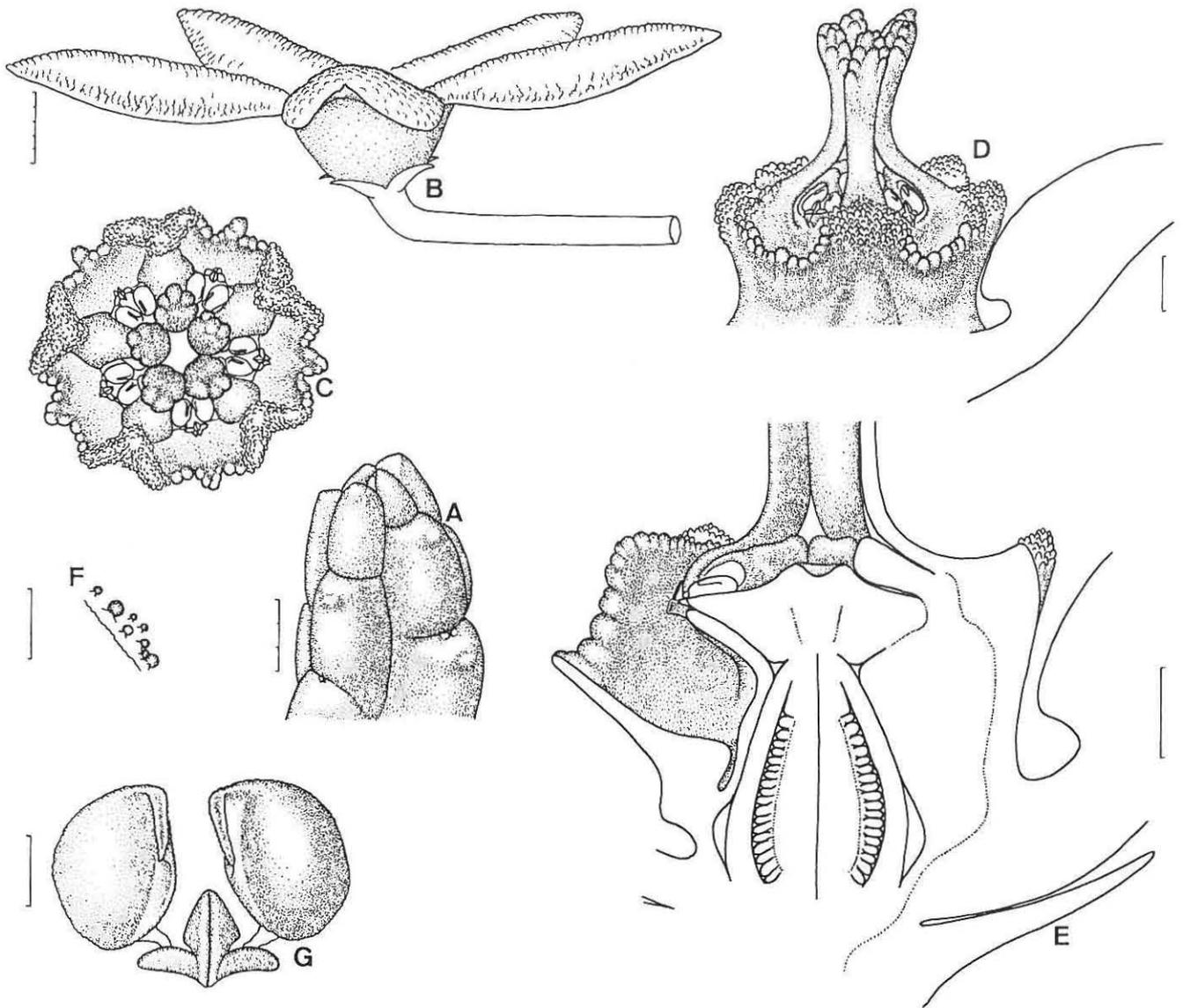


Figure 31 *Tromotriche aperta*. A, apex of stem. B, flower. C, face view of gynostegium. D, side view of dissected flower showing thickened 'annulus'. E, half-flower. F, papillae on corolla in mouth of tube. G, pollinarium. Scales: A = 3 mm; B = 5 mm; C, D = 1 mm (at D); E = 1 mm; F = 0.5 mm; G = 0.25 mm. Drawn from: east of Port Nolloth, Bayer & Bruyns 830 (NBG).

Proc. Trans. Rhod. scient. Ass. 59: 4 (1978), Excelsa Tax. Ser. 2: 58 (1980). *Stapelianthus choananthus* (Lavranos & Hall) R.A. Dyer, Flow. Pl. Afr. 37: t. 1459 (1966). *Stapelia choanantha* Lavranos & Hall, Jl S. Afr. Bot. 30: 107 (1964). Type: Cape, Huis River Pass, Hall 2579 (BOL). Figures 23, 27.

This species was also, until recently, only known from the type locality, where it grows on steep rock faces in a deep, sheltered gorge. It has now been found in several other similar gorges in the Huis River Mountains as well as somewhat further north along the Gamka River and further south in similar places in the Rooiberg. Many of the deep ravines in this area are of very difficult access and the species may well be more widespread.

*T. choanantha* is closest to *T. baylissii*, which grows in similar precipitous habitats. It differs by its more rounded stems, smooth rather than rugose interior of the corolla, slender rather than apically thickened inner corona lobes and the production of flowers only near the base of the stems. These two species appear superficially to be very different, both vegetatively and florally, from others in *Tromotriche*. However, the young stems are identical to those of others in *Tromotriche* and their occasional rhizomatous habit is also similar to such species as *T. thudichumii*. Although

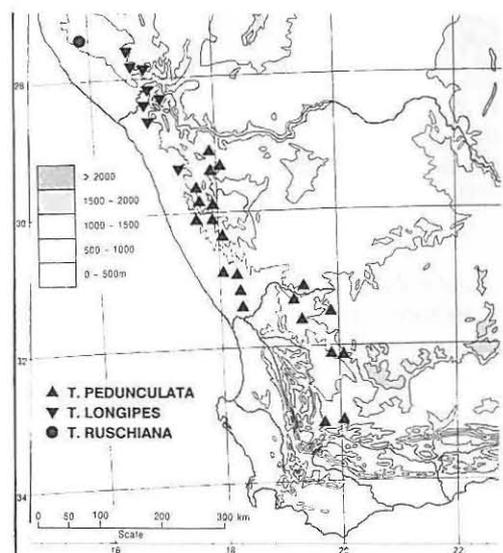
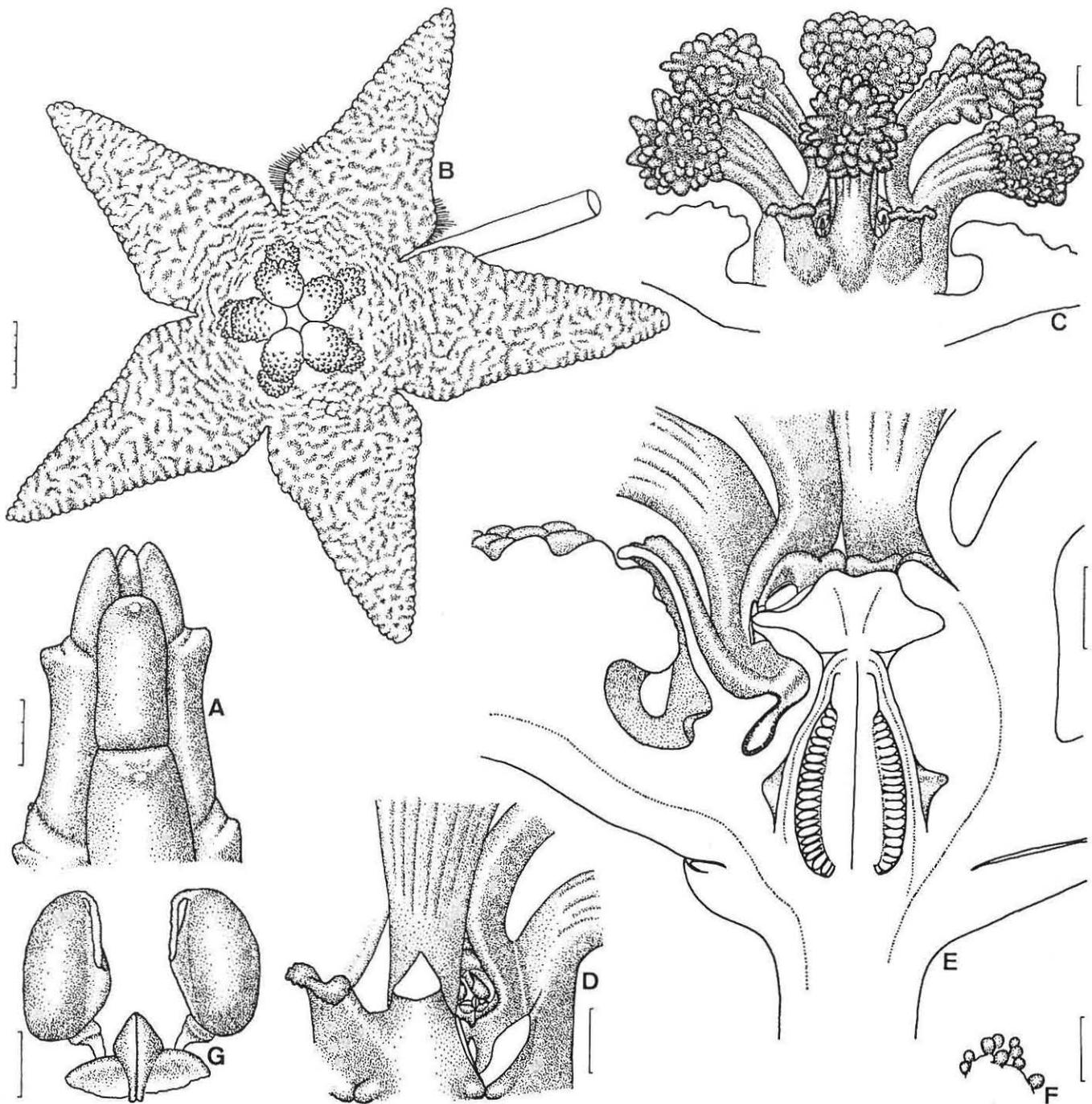


Figure 32 Distribution of *Tromotriche longipes*, *T. pedunculata* and *T. ruschiana*.



**Figure 33** *Tromotriche longipes* and *T. pedunculata*. A, apex of stem. B, flower. C, side view of centre of dissected flower with 'annulus' and gynostegium. D, gynostegium with outer corona lobe and dorsal horn of inner lobe removed. E, half-flower. F, papillae on corolla at mouth of tube (on 'annulus'). G, pollinarium. Scales: A = 3 mm; B = 5 mm; C = 1 mm; D = 1 mm; E = 1 mm (at right middle); F = 0.5 mm; G = 0.25 mm. Drawn from: *T. longipes*: B–D, F, near Rosh Pinah, PVB 3184 (NBG); *T. pedunculata*: A, E, G, north of Steinkopf, PVB 1388 (BOL).

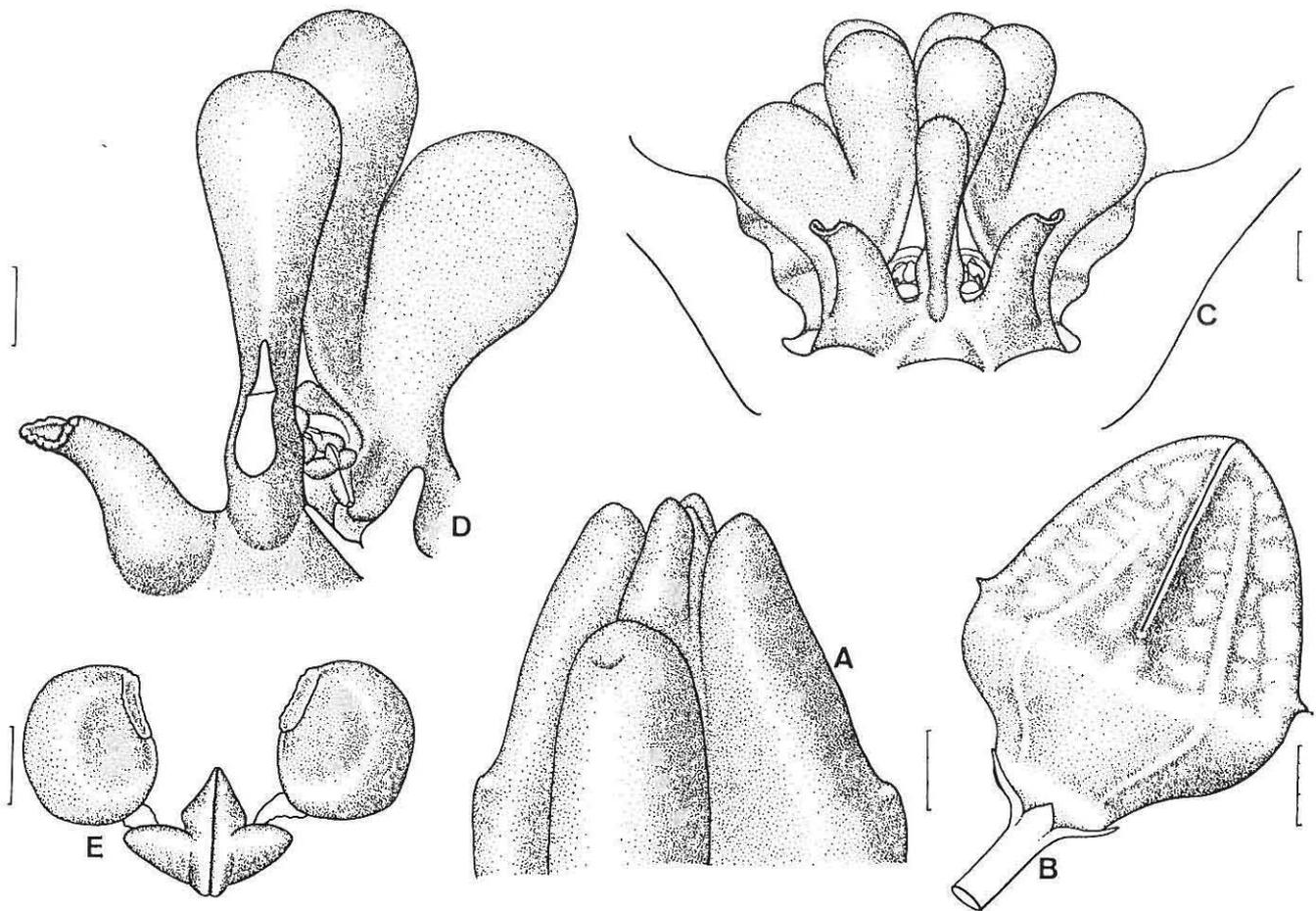
the corolla has a different shape, the corona is rather similar to that of *T. revoluta* (inclusive of the clavate tips of the inner corona lobes in *T. baylissii*). The small, unicellular, nearly spherical papillae found on the inside of the corolla in many species of *Tromotriche* are sometimes present in *T. baylissii*. The pollinia are unusually narrow in *T. choanantha* but somewhat less so in *T. baylissii*. Therefore, although arguments could be advanced to place them in their own genus, they are better regarded as slightly aberrant members of *Tromotriche*.

**5. *Tromotriche baylissii*** (Leach) Bruyns comb. nov. *Tridentea baylissii* (Leach) Leach, Proc. Trans. Rhod. scient. Ass.

59: 4 (1978). *Stapelianthus baylissii* Leach, Jl S. Afr. Bot. 34: 135 (1968). Type: Cape, south-eastern end of Baviaanskloof, Leach & Bayless 13617 (K, NBG, PRE, SRGH).

*Tridentea baylissii* var. *ciliata* Leach, Excelsa Tax. Ser. 2: 62 (1980). Type: Cape, western end of Baviaanskloof, Rawlinson sub Plowes 4792 (PRE). Figures 23, 28.

*T. baylissii* occurs in most of the deep 'kloofs' in the western part of the Baviaanskloof and is quite common also in the eastern parts west of Patensie and along the Groot and Kouga River gorges. Stems of *T. baylissii* are more or less always pendulous and may reach a considerable length – I have seen them nearly 3 m long on occasion.



**Figure 34** *Tromotriche herrei*. A, apex of stem. B, bud. C, dissected corolla showing thickened 'annulus' and gynostegium. D, part of gynostegium with outer corona lobe and dorsal horn of inner lobe removed. E, pollinarium. Scales: A = 3 mm; B = 5 mm; C = 1 mm; D = 1 mm; E = 0.25 mm. Drawn from: east of Eksteenfontein, *Heunis & Bruyns 499* (no specimen).

At the time of Leach's account, 'only three populations (possibly two)' (Leach 1980: 62) were known and the westernmost one was described as a new variety, based on the presence of cilia and various other minor quantitative differences. The corolla of the western plants does appear to be more bell-shaped and less pentagonal than the eastern ones but variation in the shape of the corolla has also been observed in *T. choanantha*. I view these differences in the eastern and western populations as part of the variation occurring within the species and therefore have not recognized this variety.

**B. Sect. *Caruncularia***

*Plants* tufted, stems erect to occasionally prostrate. *Leaves* absent. *Corolla* rotate to bicampanulate. *Corona*: *outer lobes* dorsiventrally flattened, simple and spreading often with crenulate margin especially towards apex or fused laterally with inner lobes to form cup; *inner lobes* simple and incumbent on anthers in *T. umdausensis*, otherwise dorsiventrally flattened only at base, incumbent on anthers then rising above them, cylindrical above with clavate and usually tuberculate apex, usually with clavate-tuberculate dorsal horn.

The species of this section are concentrated within the Richtersveld of the Northern Cape Province. However, more recent collecting has shown that, apart from *T. herrei*, none of them is restricted to the 'Gariiep Centre' (cf. Leach 1980: 37).

**Key to the species of Sect. *Caruncularia***

1. Inner corona lobes and their dorsal horns both nearly equal in length and both clavate .....2.  
Inner corona lobes simple or only with small dorsal gibbosity .5.
2. Corolla rotate .....4.  
Corolla campanulate. ....3.
3. Corolla lobes ciliate, with small unicellular papillae in tube . . . . .*T. ruschiana*  
Corolla eciliate, tube glabrous inside . . . . . *T. herrei*
4. Corolla ± obscurely rugose, lobes with strongly recurved margins, bearing clavate to subclavate marginal cilia . . . . .  
..... *T. pedunculata*  
Corolla deeply rugose, lobes with slightly recurved margins bearing fusiform marginal cilia . . . . . *T. longipes*
5. Inner corona lobes incumbent on anthers and only rarely slightly produced above them . . . . . *T. umdausensis*  
Inner corona lobes much exceeding anthers, produced above them and somewhat clavate towards tips . . . . . *T. aperta*

**6. *Tromotriche umdausensis*** (Nel) Bruyns, comb. nov. *Tridentea umdausensis* (Nel) Leach, Proc. Trans. Rhod. scient. Ass. 59: 4 (1978), *Excelsa* Tax. Ser. 2: 56 (1980). *Caralluma umdausensis* Nel, Kakt. Jahrb.: 22 (1936). Type: Cape, Umdaus, *Herre sub STE 6079* (missing). Neotype (Leach 1980): *Herre sub STE 7068* (STE). Figures 29, 30.

This species is separated from all the others by its very short inner corona lobes which are incumbent on the anthers and mostly do not exceed them. The pollinia also are rather small and

somewhat rectangular. Leach (1980: 57) pointed out that the distinctive colouring of the flowers is subject to much variation and is not always reliable in separating it from *T. aperta*.

*T. umdausensis* has a more easterly distribution than *T. aperta* and has now been recorded from near Eksteenfontein to Pofadder in Bushmanland and Warmbad in south-eastern Namibia southwards to the eastern (and much drier) flanks of the Khamiesberg east of Khamieskroon.

Flowers have been noted to emit a mild smell of bad breath or excrement.

**7. *Tromotriche aperta*** (Masson) Sweet, Hort. Brit. ed. 2: 359 (1830). *Tridentea aperta* (Masson) Leach, Proc. Trans. Rhod. scient. Ass. 59: 4 (1978). *Caralluma aperta* (Masson) N.E. Br., Hook. Icon. Pl. 20: t. 1905 A (1890). *Stapelia aperta* Masson, Stap. Nov.: 23, t. 37 (1796). Lectotype: Masson, Stap. Nov.: t. 37 (1796). Figures 29, 31.

The corona of *T. aperta* is intermediate between that of *T. umdausensis* and the remaining species in this section with more complex coronas. The outer lobes, while usually fused into a cup such as in *T. umdausensis*, may consist of five small lobes and always have the crenulate margin seen in some of the other species. The inner lobes are much longer than in *T. umdausensis* and are slightly clavate towards the apices, there is sometimes a dorsal gibbosity and Leach (1980: 55) records one case where the dorsal gibbosity had developed into a horn similar to, though much shorter than, the inner lobes.

**8. *Tromotriche pedunculata*** (Masson) Haw., Syn. Pl. Succ.: 333 (1812). *Tridentea pedunculata* (Masson) Leach, Proc. Trans. Rhod. scient. Ass. 59: 4 (1978). *Stapelia pedunculata* Masson, Stap. Nov.: 17, t. 21 (1796). Lectotype (Leach 1980): Masson, Stap. Nov.: t. 21 (1796). Figures 32, 33.

Recent collections have extended the distribution of *T. pedunculata* to north of Steinkopf (PVB 1388) so that it too nearly enters the Gariiep centre (cf. Leach 1980: 42). This brings it far closer to the distribution area of *T. longipes* than was previously thought to be the case.

Flowers of PVB 1388 (*T. pedunculata*) were observed to emit a strong, sharp smell of urine. The nectarial orifice in this species is quite labyrinthine and is lined with a layer of larger secretory cells over much of its interior.

**9. *Tromotriche longipes*** (Lückhoff) Bruyns comb. nov. *Tridentea longipes* (Lückhoff) Leach, Excelsa Tax. Ser 2: 43 (1980).

*Stapelia longipes* Lückhoff, S. Afr. Gard. 24: 245 (1934). Type: Namibia, Witpütz, *E. Rusch sub Lückhoff 194* (missing). Neotype (Leach 1980): *E. Rusch sub BOL 31684* (BOL.) (Figure 32).

**10. *Tromotriche ruschiana*** (Dinter) Bruyns comb. nov. *Tridentea ruschiana* (Dinter) Leach, Proc. Trans. Rhod. scient. Ass. 59: 4 (1978). *Stapelia ruschiana* Dinter, Repert. Sp. Nov. Regni. Veg. 19: 177 (1923). Type: Namibia, Klinghardt Mtns, *Dinter 3963* (missing). Neotype (Leach 1980): *Plowes 4988* (PRE). Figure 32.

**11. *Tromotriche herrei*** (Nel) Bruyns comb. nov. *Tridentea herrei* (Nel) Leach, Proc. Trans. Rhod. scient. Ass. 59: 4 (1978). *Stapelia herrei* Nel, Kakteenkunde: 69 (1933). Type: Cape, Eksteenfontein, *Herre sub STE 6002* (missing). Neotype (Leach 1980): *STE 1571* (STE). Figures 23, 34.

## References

- BRUYNS, P.V. 1988. A revision of the genus *Echidnopsis* Hook. f. *Bradleya* 6: 1–48.
- BRUYNS, P.V. 1993. A revision of *Hoodia* and *Lavrania*. *Bot. Jb. Syst.* 115: 145–270.
- DURIETZ, G.E. 1930. The fundamental units of biological taxonomy. *Svensk bot. Tidskr.* 24: 333–428.
- HARTMANN, H.E.K. 1991. Mesembryanthema. *Contr. Bol. Herb.* 13: 75–157.
- KUSCH, G. 1985. Morphologische Studien an Arten des Verwandtschaftskreises *Stapelia* sowie einiger verwandter Gattungen von extrem trockenen Standorten. Diploma thesis, University of Münster.
- LAVRANOS, J.J. & HALL, H. 1964. A new *Stapelia* from the western Cape Province. *Jl S. Afr. Bot.* 30: 107–110.
- LEACH, L.C. 1978. On the classification of Stapelieae and the re-instatement of *Tridentea* Haw. *Proc. Trans. Rhod. scient. Ass.* 59: 1–5.
- LEACH, L.C. 1980. A review of *Tridentea* Haw. *Excelsa Taxon. Ser.* 2: 1–68.
- LEACH, L.C. 1984. A revision of *Tromotriche* Haw. *Jl S. Afr. Bot.* 50: 549–562.
- LEACH, L.C. 1985. A revision of *Stapelia* L. *Excelsa Taxon. Ser.* 3.
- LÜCKHOFF, C.A. 1952. The Stapelieae of southern Africa. A.A. Balkema, Cape Town.
- MEVE, U. 1988. The differing status of varieties in the Stapelieae. *Asklepios* 44: 2–7.
- MEVE, U. 1989. *Tromotriche thudichumii* (Pillans) Leach. *Kakteenu. Sukkulenten* 40: 74–76.
- MEVE, U. & ALBERS, F. 1990. Die Stipularrudimente der Stapelieae. *Beitr. Biol. Pfl.* 65: 99–107.
- SCHILL, R. & JÄKEL, U. 1978. Beitrag zur Kenntnis der Asclepiadaceen-Pollinarien. *Trop. u. subtrop. Pflanzenwelt* 22.