

A revision and phylogenetic analysis of *Stapeliopsis* (Apocynaceae)

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A survey of morphological characters is carried out for *Stapeliopsis*. The information obtained from this is combined with molecular data from the plastid *trnL-F* DNA region and ITS1 of the nuclear encoded 18S–26S rRNA cistron, to obtain a hypothesis of the evolutionary relationships among the species. It is shown that *Stapeliopsis* is monophyletic in a combined molecular and morphological analysis. *Stapeliopsis* is sister to a clade containing *Huernia*, *Orbea* and *Tromotriche*. The species of *Stapeliopsis* group into two clades. One contains *S. khamiesbergensis*, *S. neronis* and *S. urniflora*, and this is highly supported. The remaining species fall into an unsupported clade in which *S. exasperata* is sister to the others. The genera *Hermanschwartzia* Plowes and *Neopectinaria* Plowes are rejected. It is shown that a synapomorphy for *Stapeliopsis* is the laterally flattened inner corona-lobes, which touch the anthers only at their bases. Eight species of *Stapeliopsis* are recognized, with no subgeneric divisions. © 2005 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2005, 148, 125–155.

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INTRODUCTION

The stapeliads are highly succulent, essentially leafless members of the tribe Ceropegieae (Apocynaceae – Asclepiadoideae), found in the Old World from southern Africa north-eastwards to India and Myanmar. There are some 320 species distributed among 26 genera, with the highest diversity of genera and species in the dry to arid parts of southern Africa. (Bruyns, 2000a, b). A phylogeny of the stapeliads based on morphological characters was proposed in Bruyns (2000a) and this was supplemented by a molecular study by Meve & Liede (2002).

Stapeliopsis was described by N.S. Pillans in 1928 for the single species *S. neronis* Pillans, which has a remarkable and uniquely tubular outer corona. A second species, *S. urniflora* Lavranos, was added in 1966. The concept of the genus was drastically modified when the genus *Pectinaria* Haw. was split up and four of its species were transferred to *Stapeliopsis* (Bruyns, 1981). In the same paper two other species of *Pectinaria* were transferred to a new genus *Ophionella* and

two species of *Caralluma*, *C. longipes* N.E. Br. and *C. maughanii* R.A. Dyer, were transferred to *Pectinaria*. The remarkable, tubular outer corona of *S. neronis* was no longer typical of the genus and the seven species that belong to *Stapeliopsis* are held together by the unusual lateral flattening of the inner corona-lobes and their manner of rising up above the anthers, often in a cage-like structure. This arrangement has been contested by Plowes (2003), who proposed that *Stapeliopsis*, in the new sense, be split into three genera and *Pectinaria* split into two genera. No significant justification was given for these changes.

Several cladistic investigations of the species in *Pectinaria s.l.* involving morphological characters have been carried out. In Bruyns (1999b) it was shown (using most of the species) that the new concepts of *Ophionella*, *Pectinaria* and *Stapeliopsis* are monophyletic. That study (with two species of *Quaqua* as outgroups) revealed that *Stapeliopsis* was sister to a clade consisting of a species of *Orbea* and of *Stapelia* and that *Ophionella* was sister to these. Another investigation (Bruyns, 1999a) found *Pectinaria* (in the new and restricted sense) to be sister to *Notechidnopsis*, with two species of *Quaqua* as sister to this clade. Yet a further investigation (Bruyns, 1999c) showed that

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Quaqua is monophyletic and is sister to a clade containing two species of *Pectinaria* (in the new sense) and *Notechidnopsis*. The molecular investigation of Meve & Liede (2002), involving two species of *Stapeliopsis* and one species of each of *Ophionella* and *Pectinaria*, did not resolve the relationships between them.

Stapeliopsis is endemic to southern Africa. The species, which are mostly rare and poorly collected, are found along the western side of the subcontinent mainly within and on the edges of the winter-rainfall zone of South Africa and Namibia. Records exist from the arid south-western corner of Namibia, through the Richtersveld (where *S. neronis* was originally found) and the gneiss mountains of Namaqualand to the western edge of the Great Karoo around Laingsburg. The genus is especially well represented on the Worcester–Robertson Karoo and the western portion of the Little Karoo. Further east *Stapeliopsis* becomes rare, with a single species found as far east as Somerset East.

In this paper we examine morphological characters in detail in *Stapeliopsis*. The morphological data are combined with molecular data from two DNA regions. Our analyses of these data are used to establish that *Stapeliopsis*, in its present circumscription, is monophyletic and to resolve the relationships among the species of *Stapeliopsis*. In addition we investigate the

relationships of *Stapeliopsis* to other genera of the stapeliads. This enables us to test whether the changes made in Bruyns (1981) were justified as well as to test the hypotheses of relationships among the genera that were proposed in Bruyns (2000a). We are also able to improve substantially on the unresolved situation found by Meve & Liede (2002) and we show that the changes mooted by Plowes (2003) should be rejected.

MATERIAL AND METHODS

Herbarium material from the major southern African Herbaria BOL, GRA, NBG and PRE was examined and this information was used to draw up the distribution maps. The line drawings were made from live material. Pieces of this material were prepared as described in Bruyns (1993) and the micrographs were prepared using a Cambridge S 200 SEM.

The matrix of morphological data included in the analyses is given in Table 1. All known taxa of *Stapeliopsis* were sampled. Two collections of the most widespread species, *S. saxatilis*, were included: one of these is from the mottled- and papillate-stemmed form that occurs on sandstone substrates (*PVB 7045*), while the other (*PVB 6833*) is from soils derived from shales. Two species of *Pectinaria*, *P. articulata* and *P. longipes*, were included as well as *Ophionella arcuata*,

Table 1. Character states for the 25 morphological characters used in the cladistic analysis

| | | | | | |
|------------------------------------------------------|-------|-------|-------|-------|-------|
| <i>Anisotoma cordifolia</i> | ?10?0 | 00100 | 10100 | 0100? | 0???? |
| <i>Brachystelma pygmaeum</i> ssp. <i>flavidum</i> | 100?0 | 00100 | 10?10 | 01000 | 000?? |
| <i>Caralluma arachnoidea</i> var. <i>arachnoidea</i> | 101?1 | 00000 | 10000 | 01001 | 000?0 |
| <i>Frerea indica</i> | 100?0 | 00000 | 10000 | 0?111 | 000?0 |
| <i>Huernia erectiloba</i> | 10101 | 01011 | 10110 | 00001 | 100?0 |
| <i>Neoschumannia kamerunensis</i> | 000?0 | 00000 | 10000 | ?100? | 000?? |
| <i>Notechidnopsis tessellata</i> | 11111 | 11100 | 10?10 | 10111 | 11110 |
| <i>Ophionella arcuata</i> ssp. <i>mirkinii</i> | 11101 | 01111 | 10000 | 01000 | 00001 |
| <i>Ophionella willowmorensis</i> | 11101 | 01111 | 10100 | 01000 | 00011 |
| <i>Orbea namaquensis</i> | 10101 | 01011 | 10000 | 00111 | 100?0 |
| <i>Pectinaria articulata</i> ssp. <i>articulata</i> | 10111 | 11100 | 11110 | 01000 | 01110 |
| <i>Pectinaria longipes</i> ssp. <i>villetii</i> | 10111 | 11100 | 11000 | 01000 | 01110 |
| <i>Quaqua inversa</i> | 10101 | 00100 | 00000 | 01000 | 011?0 |
| <i>Quaqua mammillaris</i> | 10101 | 00100 | 00010 | 01000 | 011?0 |
| <i>Stapeliopsis breviloba</i> | 10101 | 01011 | 10001 | 10000 | 000?0 |
| <i>Stapeliopsis exasperata</i> | 10101 | 0?111 | 10011 | 10000 | 010?0 |
| <i>Stapeliopsis khamiesbergensis</i> | 10101 | 01111 | 10111 | 10000 | 001?0 |
| <i>Stapeliopsis neronis</i> | 10101 | 01111 | 10111 | 10000 | 00110 |
| <i>Stapeliopsis pillansii</i> | 11101 | 01011 | 10001 | 10000 | 010?0 |
| <i>Stapeliopsis saxatilis</i> 1 | 11101 | 01011 | 10001 | 1?000 | 01010 |
| <i>Stapeliopsis saxatilis</i> 2 | 11101 | 01111 | 10001 | 1?000 | 01010 |
| <i>Stapeliopsis stayneri</i> | 11101 | 01011 | 10001 | 10000 | 01010 |
| <i>Stapeliopsis urniflora</i> | 10101 | 01111 | 10011 | 10000 | 001?0 |
| <i>Tromotriche longii</i> | 11101 | 01111 | 10000 | 00111 | 111?0 |

the recently described *O. willowmorensis*, *Notechidnopsis tessellata* and two species of *Quaqua*, *Q. inversa* and *Q. mammillaris*. *Tromotriche longii*, *Orbea namaquensis* and *Huernia erectiloba* were included as representatives of the clade found to be sister to *Stapeliopsis* (Bruyns, 1999b). *Frerea indica* and *Caralluma arachnoidea*, sister to all these taxa (Bruyns, 2000a), were also included. Outgroups *Anisotoma cordifolia*, *Brachystelma pygmaeum* and *Neoschumannia kamerunensis* were chosen from among the non-succulent members of the Ceropegieae which are sisters to the stapeliads (Bruyns, 2000a; Meve & Liede, 2002). The provenance, location of vouchers and GenBank accession numbers for these taxa are given in Table 2.

Two DNA regions were used in this study: the plastid *trnL* (UAA) 5' exon – *trnF* (GAA) gene [including the *trnL* 5' exon, intron, the *trnL* (UAA) 3' exon and the *trnL* 3' – *trnF* intergenic spacer: Taberlet *et al.*, 1991], and internal transcribed spacer 1 (ITS1) region of the 18–26S nuclear ribosomal DNA (Baldwin, 1992).

DNA EXTRACTION, AMPLIFICATION AND SEQUENCING

Total genomic DNA was extracted using the CTAB method described for *Ipomoea* L. (Gawel & Jarret, 1991). Quantities were scaled down for 20 mg of fresh or silica-dried plant material, and slight modifications to the protocol were made as follows. All centrifugation steps were at 11 000 *g*. Samples were ground in a pestle and mortar with 700 µL of extraction buffer and a pinch of polyvinylpyrrolidone (PVP-40). Following incubation, 600 µL of chloroform : isoamyl alcohol (24 : 1 v/v) was added, mixed by inversion for 5 min and spun. The aqueous phase was transferred to a clean microcentrifuge tube. An equal volume of ice-cold isopropanol was added and tubes were stored at –10 °C overnight to precipitate the DNA. After centrifugation the DNA pellet was washed with 75% ethanol and spun. Ethanol was discarded and samples were left to air-dry then resuspended in 50 µL of nanopure water.

Primers *trnC* and *trnF* (Taberlet *et al.*, 1991), and 18KRC (5'-GCACGCGCTACTGA-3') and ITS2 (Baldwin, 1992) were used to amplify the *trn* and ITS regions, respectively. PCRs were performed using 0.75 units of BIOTAQ DNA polymerase (Bioline) in 30-µL volumes also containing 1× NH₄ buffer and 5 mM MgCl₂ (supplied with polymerase), 0.1 mM of each dNTP, and 0.3 µM of each primer, with 3 µL of unquantified DNA template. Thermo-cycling was carried out by using a Hybaid Sprint set to the following thermal conditions: initial denaturation at 97 °C for 2 min, followed by 30 cycles of 97 °C for 1 min, 52 °C for 1 min, 72 °C for 2 min, with a final polymerization step at 72 °C for 7 min.

PCR products were cleaned using the QIAquick PCR purification kit (Qiagen) prior to cycle sequencing with the ABI PRISM Big Dye Terminator v3.0 cycle sequencing Ready Reaction Kit (Applied Biosystems). Amplification primers were also used for sequencing. Cycle sequencing products were resolved on an ABI PRISM 3100 Genetic Analyser.

Sequences were assembled and checked for inaccurate base calling using SeqMan II (LaserGene System Software, DNASTar, Inc.). Consensus sequences were aligned manually using MegAlign (LaserGene System Software, DNASTar, Inc.). The alignment was trimmed in order to exclude the invariant partial 18S region amplified with ITS1 (this region was not available for the sequences obtained from GenBank) and missing data at sequence extremities. Informative indels (five) were coded as present or absent.

Parsimony analyses were conducted using PAUP* 4.0b10 (Swofford, 1998). Data partitions, namely *trn*, ITS and morphology, were analysed separately and as a combined dataset. For each analysis branch and bound searches were performed. All characters were given equal weight and states were unordered. For each dataset, characters were weighted according to their rescaled consistency index. Successively approximated weights were applied until the topology and tree length stabilized over two successive rounds. Nodal support was estimated using the jackknife. Ten thousand jackknife replicates were performed using 33.67% deletion, emulate Jac resampling, random stepwise-addition, TBR swapping and MULPARS on.

MORPHOLOGICAL CHARACTERS AND THEIR CODING IN *STAPELIOPSIS* (DATA FOR THE OTHER TAXA ARE TAKEN FROM BRUYNS, 1999a, b, c, 2000a)

Stems

1. Plant a climber = 0; not climbing = 1.
2. Stems erect to decumbent = 0; horizontal = 1.
Stems in *Stapeliopsis* may be decumbent (*S. neronis*), decumbent with erect apices and basal part sometimes extended into a horizontal, thinner, ± cylindrical underground 'runner', i.e. rhizomatous (*S. breviloba*, *S. exasperata* and *S. urniflora*) or pro-cumbent and with horizontal apices (*S. pillansii*, *S. saxatilis* and *S. stayneri*). They are generally grouped into small clumps or are mat-forming. In thickness and length they are very variable: thickest in *S. neronis*, smallest and thinnest in *S. breviloba*; in the prostrate *S. saxatilis* stems may reach 300 mm or more long and in this species they vary from 6 to 25 mm thick, sometimes on one stem.
3. Stems not angled = 0; stems angled = 1.

Table 2. Taxa employed in molecular analysis with GenBank accession numbers

| Species | Origin | Collector number | GenBank accession number for <i>trnL-F</i> sequence | GenBank accession number for ITS1 (* ITS1 & 2) sequence |
|--------------------------------------------------------------------------------|-----------------------------------|------------------------------|-----------------------------------------------------|---------------------------------------------------------|
| <i>Anisotoma cordifolia</i> Fenzl | South Africa, near Grahamstown | Nicholas 2811 (UDW) | AJ410017 | AJ310780* |
| <i>Brachystelma pygmaeum</i> ssp. <i>flavidum</i> R.A. Dyer | South Africa | Ward (UDW) | AJ410032 | AJ300784* |
| <i>Caralluma arachnoidea</i> (P.R.O. Bally) M. Gilbert var. <i>arachnoidea</i> | Kenya, Rukanga | Meve 934 (UBT) | AJ410038 | AJ310785* |
| <i>Frerea indica</i> Dalz. | India, near Pune | Bruyns 5925 (BOL) | AY780491 | AY790370 |
| <i>Huernia erectiloba</i> L.C. Leach & Lavranos | Mozambique, near Errego | Bruyns 7693 (BOL) | AY780494 | AY790373 |
| <i>Neoschumannia kamerunensis</i> Schltr. | Cameroon, Mt. Cameroon | Meve & Etuge 910 (B, K, UBT) | AJ410053 | AJ310791* |
| <i>Notechidnopsis tessellata</i> (Pillans) Lavranos & Bleck | South Africa, near Nieuwoudtville | Bruyns 7980 (BOL) | AY780491 | AY790371 |
| <i>Ophonella arcuata</i> ssp. <i>mirkinii</i> (Pillans) Bruyns | South Africa, near Steytlerville | Bruyns 7050 (MO) | AY780497 | AY790376 |
| <i>Ophonella willowmorensis</i> Bruyns | South Africa, near Willowmore | Bruyns 6317 (BOL) | AY780496 | AY790375 |
| <i>Orbea namaquensis</i> (N.E. Br.) L.C. Leach | South Africa, near Steinkopf | Bruyns 8825 (MO) | AY780495 | AY790374 |
| <i>Pectinaria articulata</i> (Ait.) Haw. ssp. <i>articulata</i> | South Africa, near Calvinia | Bruyns 7971 (MO) | AY780498 | AY790377 |
| <i>Pectinaria longipes</i> ssp. <i>villetii</i> (C.A. Lückh.) Bruyns | South Africa, near Loeriesfontein | Bruyns 7950 (BOL, NBG, K) | AY780499 | AY790378 |
| <i>Quaqua inversa</i> (N.E. Br.) Bruyns | South Africa, near Bitterfontein | Bruyns 6133 (BOL, K) | AY780509 | AY790388 |
| <i>Quaqua mammillaris</i> (L.) Bruyns | South Africa, near Touwsrivier | Bruyns 6384 (MO) | AY780510 | AY790389 |
| <i>Stapeliopsis breviloba</i> (R.A. Dyer) Bruyns | South Africa, near Worcester | Bruyns 1704 (NBG) | AY780501 | AY790380 |
| <i>Stapeliopsis exasperata</i> (Bruyns) Bruyns | South Africa, near Calvinia | Bruyns 4306 (BOL) | AY780505 | AY790384 |
| <i>Stapeliopsis neronis</i> Pillans | Namibia, near Rosh Pinah | Bruyns 8306 (E) | AY780502 | AY790381 |
| <i>Stapeliopsis pillansii</i> (N.E. Br.) Bruyns | South Africa, near Prince Albert | Bruyns 5070 (BOL) | AY780507 | AY790386 |
| <i>Stapeliopsis saxatilis</i> (N.E. Br.) Bruyns 1 | South Africa, near Vanrhynsdorp | Bruyns 6833 (NBG) | AY780503 | AY790382 |
| <i>Stapeliopsis saxatilis</i> 2 | South Africa, near Steytlerville | Bruyns 7045 (BOL) | AY780504 | AY790383 |
| <i>Stapeliopsis stayneri</i> (M.B. Bayer) Bruyns | South Africa, near Bredasdorp | Bruyns 1263 (BOL) | AY780506 | AY790385 |
| <i>Stapeliopsis urniflora</i> Lavranos | Namibia, near Helmeringhausen | Bruyns 5733 (BOL, K) | AY780500 | AY790379 |
| <i>Stapeliopsis khamiesbergensis</i> Bruyns | South Africa, near Springbok | Bruyns 8249 (BOL) | AY780508 | AY790387 |
| <i>Tromotriche longii</i> (C.A. Lückh.) Bruyns | South Africa, near Kirkwood | Bruyns 4928 (BOL) | AY780493 | AY790372 |

4. Stems 4-angled = 0; stems 6–8-angled = 1.

The tubercles are conical, slightly to prominently laterally flattened (hardly laterally flattened in *S. pillansii*) and arranged into four (rarely five) rows, usually fused into somewhat wing-like ridges along the stem (except in *S. breviloba*, *S. pillansii*).

5. Leaves not reduced = 0; leaves reduced to scale-like rudiment = 1.

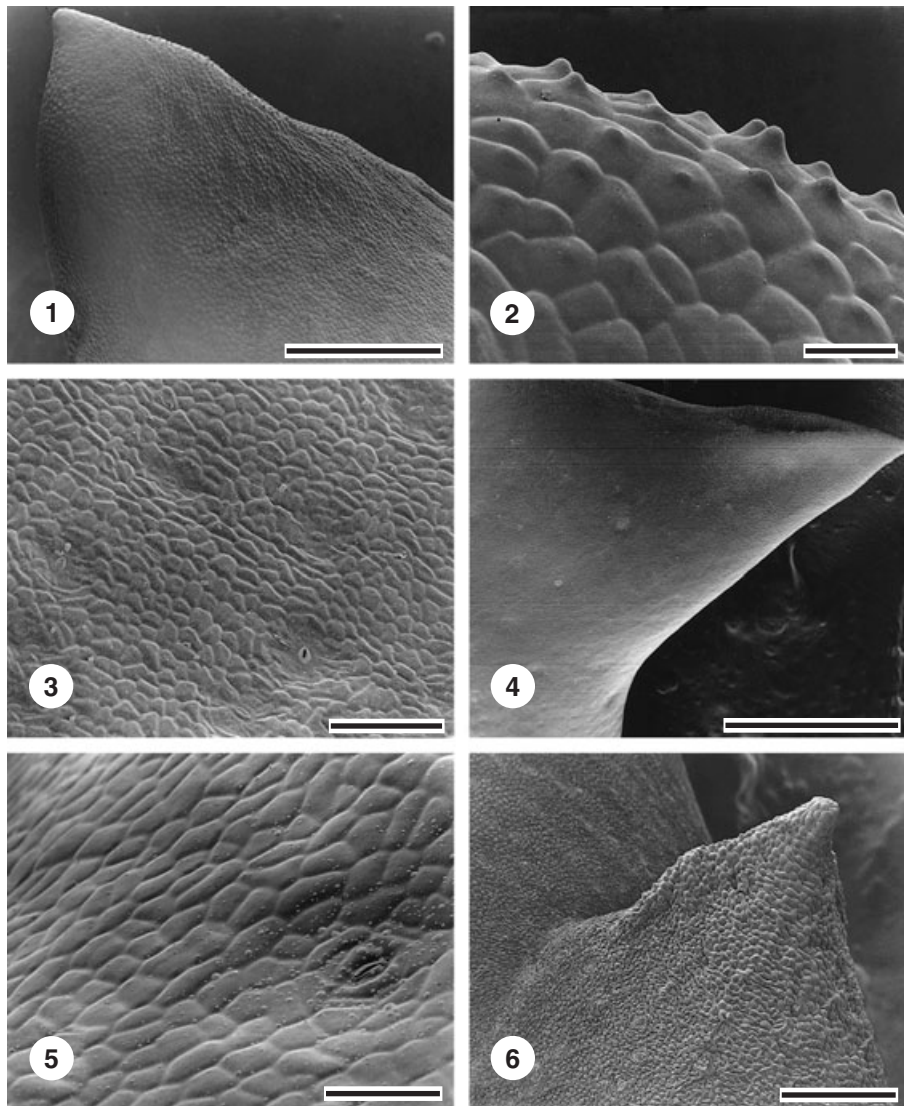
Each tubercle bears a small, conical leaf-rudiment (fairly slender and sharp-tipped in *S. breviloba*,

which shows no differentiation but is usually slightly flattened above and convex below.

6. Leaves decussate = 0; whorled = 1.

7. Stipular denticles present = 0; absent = 1.

In *S. exasperata* each leaf-rudiment is flanked by two fairly obvious stipular denticles (Fig. 9). Faint traces of similar basal protrusions may also be visible in *S. breviloba*, *S. pillansii* and *S. saxatilis*, but these are of very erratic occurrence. The other three are essentially free of stipules and so these six species are treated as stipule-free (cf. Meve & Albers, 1990).



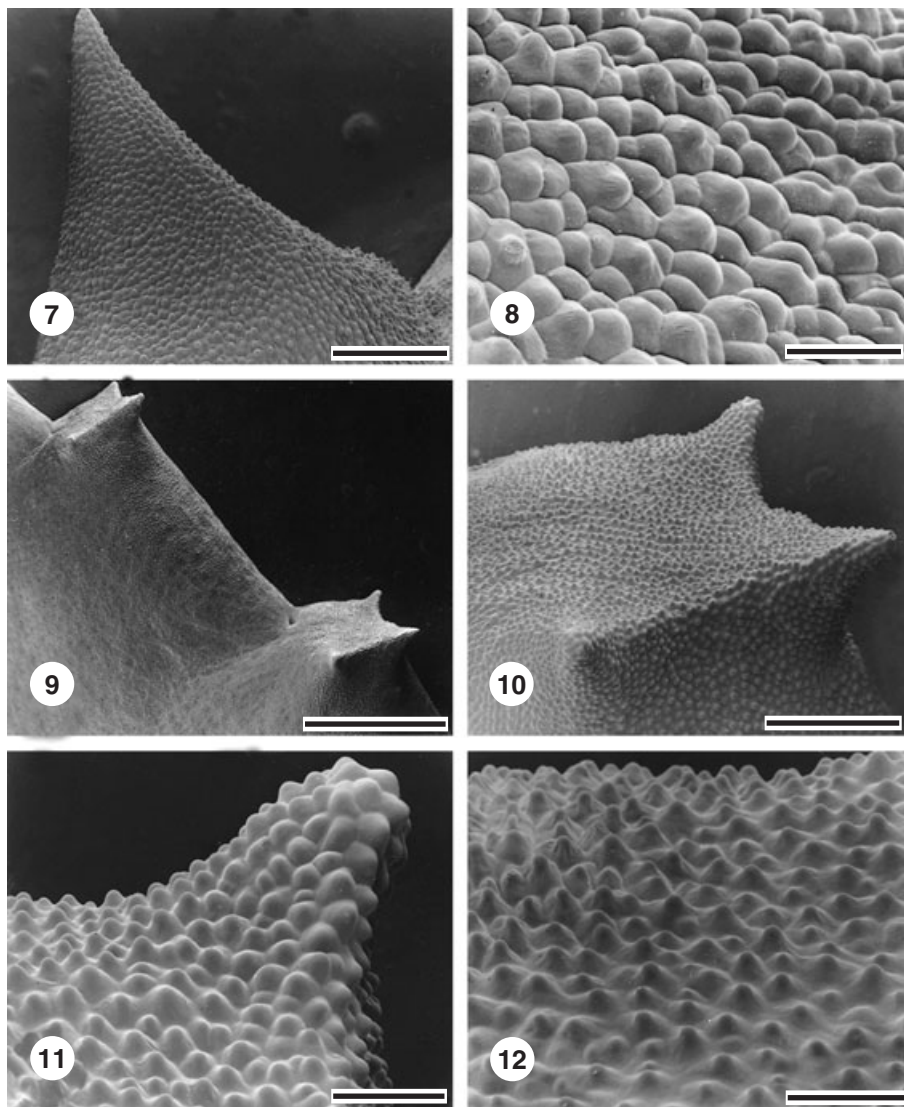
Figures 1–6. SEMs of stems and leaf-rudiments of *Stapeliopsis*: smooth-stemmed taxa. *S. pillansii* (PVB 1561 (NBG)). Fig. 1. Tubercle with leaf-rudiment (from diagonally below). Scale bar = 1 mm. Fig. 2. Outer walls of epidermal cells raised into papillae along upper edge of tubercle near leaf-rudiment. Scale bar = 50 μ m. Fig. 3. Flat outer walls of epidermal cells on stem away from tubercle. Scale bar = 100 μ m. *S. saxatilis* (PVB 4821). Fig. 4. Tubercle with leaf-rudiment, seen from side. Scale bar = 2 mm. Fig. 5. Surface of tubercle below leaf-rudiment. *S. breviloba* (PVB 1704 (MO, NBG)). Fig. 6. Leaf-rudiment from below with slightly papillate 'stipular ridge' along edge. Scale bar = 500 μ m.

8. Epidermal cells on stem with flat outer walls = 0;
outer walls raised into papillae (or hairs) = 1.

The stems in *Stapeliopsis* exhibit a wide variety of epidermis types, even within one species (especially in *S. saxatilis*). To make the position clear this is listed for each species: outer walls of the epidermal cells vary from flat to raised into a prominent, cylindrical, central papilla. In general the papillae become smaller from the base of the leaf to the tip. Stomata are super-

ficial throughout. The species in which the epidermis has been studied are arranged below in order of increasing length of these papillae.

S. pillansii: cells isodiametric, outer walls flat towards tip of leaf-rudiment, slightly raised lower down, raised into quite prominent, central papillae in a line along the margin on the slight 'stipular wing' that develops there, away from leaf-rudiment \pm smooth (Figs 1–3).



Figures 7–12. SEMs of stems and leaf-rudiments of *Stapeliopsis*: papillate-stemmed taxa. *S. saxatilis* (PVB 4905 (BOL)). Fig. 7. Tubercle from side (above = towards upper right) with surface becoming more papillate towards base. Scale bar = 500 μ m. Fig. 8. Outer walls of epidermal cells on tubercle with rounded papillae. Scale bar = 100 μ m. *S. exasperata* (PVB 2820 (BOL, NBG, PRE)). Fig. 9. Two successive tubercles with stipule-bearing leaf-rudiments. Scale bar = 2 mm. Fig. 10. Leaf-rudiment from above with two conspicuous stipules. Scale bar = 500 μ m. Fig. 11. Stipule (above = to right) with outer walls of epidermal cells raised into rounded columnar papillae. Scale bar = 100 μ m. Fig. 12. Outer walls of epidermal cells on tubercle with rounded, columnar papillae. Scale bar = 100 μ m.

S. breviloba: cells isodiametric, outer walls slightly raised all over leaf-rudiment (less so towards tip), with some raised into a central papilla along margin on the slight 'stipular wing' developing towards base (Fig. 6).

S. saxatilis: cells isodiametric to slightly elongated or rectangular, in plants without purple mottling on stems the outer walls are flat with a few small, central papillae along margin of leaf-rudiment (Figs 4, 5); in plants with mottled stems each outer wall is raised into a central papilla decreasing in length towards the tip and away from the leaf-rudiment (Figs 7, 8).

S. exasperata: cells isodiametric, outer walls on and around leaf-rudiment each with a prominent, central papilla (decreasing in prominence slightly towards tip), quite prominent margin of leaf-rudiment running from tip to stipules (Figs 9–12).

S. urniflora: cells isodiametric, outer walls around base of leaf-rudiment each with very prominent, central papilla. These papillae decrease in length to vanish entirely towards tip and become smaller away from leaf-rudiment (Figs 13, 14).

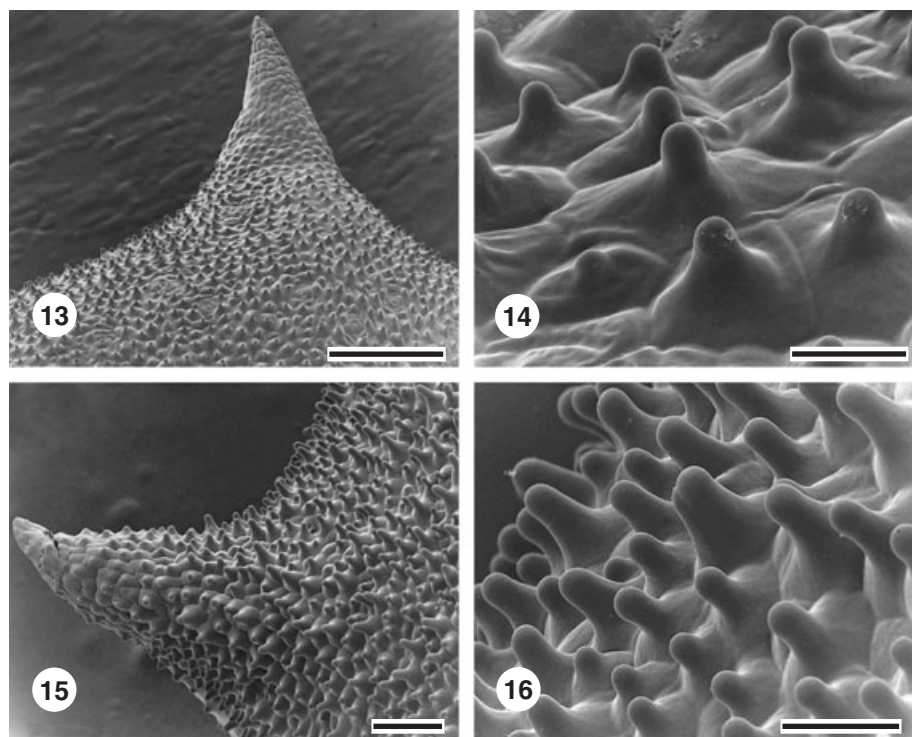
S. neronis: cells isodiametric, outer walls around base of leaf-rudiment each with very prominent, cylindrical, central papilla. These papillae decrease in length to vanish entirely towards tip and become smaller away from leaf-rudiment (Figs 15, 16).

Inflorescence

In *Stapeliopsis* the flowers mature in gradual succession and are organized in the inflorescence in the standard manner of the Ceropegieae (Bruyns, 1988). A small peduncle may develop in *S. neronis* but generally the inflorescence becomes broader with increased activity rather than lengthening into a peduncle. The pedicel is usually slender and horizontal, bending upwards at its end to hold the flower erect in all species except *S. pillansii*. In *S. pillansii* the flower faces horizontally or downwards. In all species except *S. neronis*, the inflorescence is glabrous and smooth. The bracts are without lateral outgrowths.

9. Inflorescences apical on stem = 0; basal = 1.

Inflorescences in *Stapeliopsis* mature near the base of the stem and there is usually only one per stem. In *S. breviloba*, *S. exasperata* and *S. urniflora*, where the stems may be slightly rhizomatous and where the



Figures 13–16. SEMs of stems and leaf-rudiments of *Stapeliopsis*: papillate-stemmed taxa. Figs 13, 14. *S. urniflora* (PVB 5733 (BOL)). Figs 15, 16. *S. neronis* (PVB 2818 (BOL)). Figs 13, 15. Tubercle with leaf-rudiment (upper side to left). Scale bars: 13 = 500 µm, 15 = 250 µm. Figs 14, 16. Outer walls of epidermal cells on tubercle away from leaf-rudiment raised into tall papillae. Scale bars = 50 µm.

lower parts are therefore often well beneath the surface of the soil, the inflorescence frequently develops beneath the ground. The flowers may also end up being partly submerged, in some cases with just the lobes appearing above the surface. In *S. exasperata* this is the usual situation, with the corolla tube beneath the soil and the lobes spreading out on its surface. In *S. pillansii* inflorescences on the lower surface of the stem develop (those on the upper surface tend to remain inactive) and the flowers are pushed downwards into the soil.

10. Inflorescences numerous per stem = 0; single per stem = 1.

In *Stapeliopsis* there is usually only one inflorescence per stem.

11. Inflorescences arranged in vertical rows along upper parts of stem = 0; not arranged in rows = 1.

12. Basal bract in inflorescence not inflated = 0; inflated = 1.

Inflated basal bracts are mainly found in the three species of *Pectinaria* and are unknown in *Stapeliopsis*.

Corolla

The species of *Stapeliopsis* exhibit a remarkably wide range in the shape of the flower from tubular and ellipsoidal to campanulate.

In *S. breviloba*, *S. neronis* and *S. urniflora* the corolla consists primarily of an ovoid or obovoid tube, which narrows towards its mouth where there are five relatively small lobes so that the overall shape is \pm ellipsoidal. In *S. exasperata* and *S. saxatilis* the lobes are nearly as long as the tube: in *S. saxatilis* the tube is cupular to cylindrical or somewhat ovoid and the lobes are mostly joined at their tips, resulting once more in a \pm ovoid corolla; in *S. exasperata* the tube is cylindrical with the lobes usually spreading from the mouth. In *S. pillansii* the corolla is campanulate to pear-shaped with the broadly cupular tube only slightly longer than the lobes. *S. pillansii* is also unusual in that the corolla is exceptionally thick and rigid.

In *Stapeliopsis* none of the species develops a true annulus in the corolla. In *S. neronis* the corolla is considerably thickened around the bases of the lobes; somewhat less thickening is present in *S. urniflora*, *S. khamiesbergensis* and *S. exasperata* and in the others the corolla is not thickened around its mouth. The presence of these occasional thickenings suggests that the whole corolla-tube here is homologous to the tube below the annulus in species such as *Orbea variegata* or *Hoodia gordonii*.

13. Corolla outside without papillae = 0; with papillae = 1.

In *Stapeliopsis* the outside of the corolla is glabrous in all except *S. neronis*, where it is covered with fine, unicellular, acute papillae (Fig. 27) somewhat similar to those on the stems. Although these are coded here the same as the papillae on the outside of the corolla in some species of *Pectinaria* and *Ophionella*, the papillae in those species are multicellular and bear a stoma at their apex.

14. Corolla inside without bristle-tipped papillae = 0; with bristle-tipped papillae = 1.

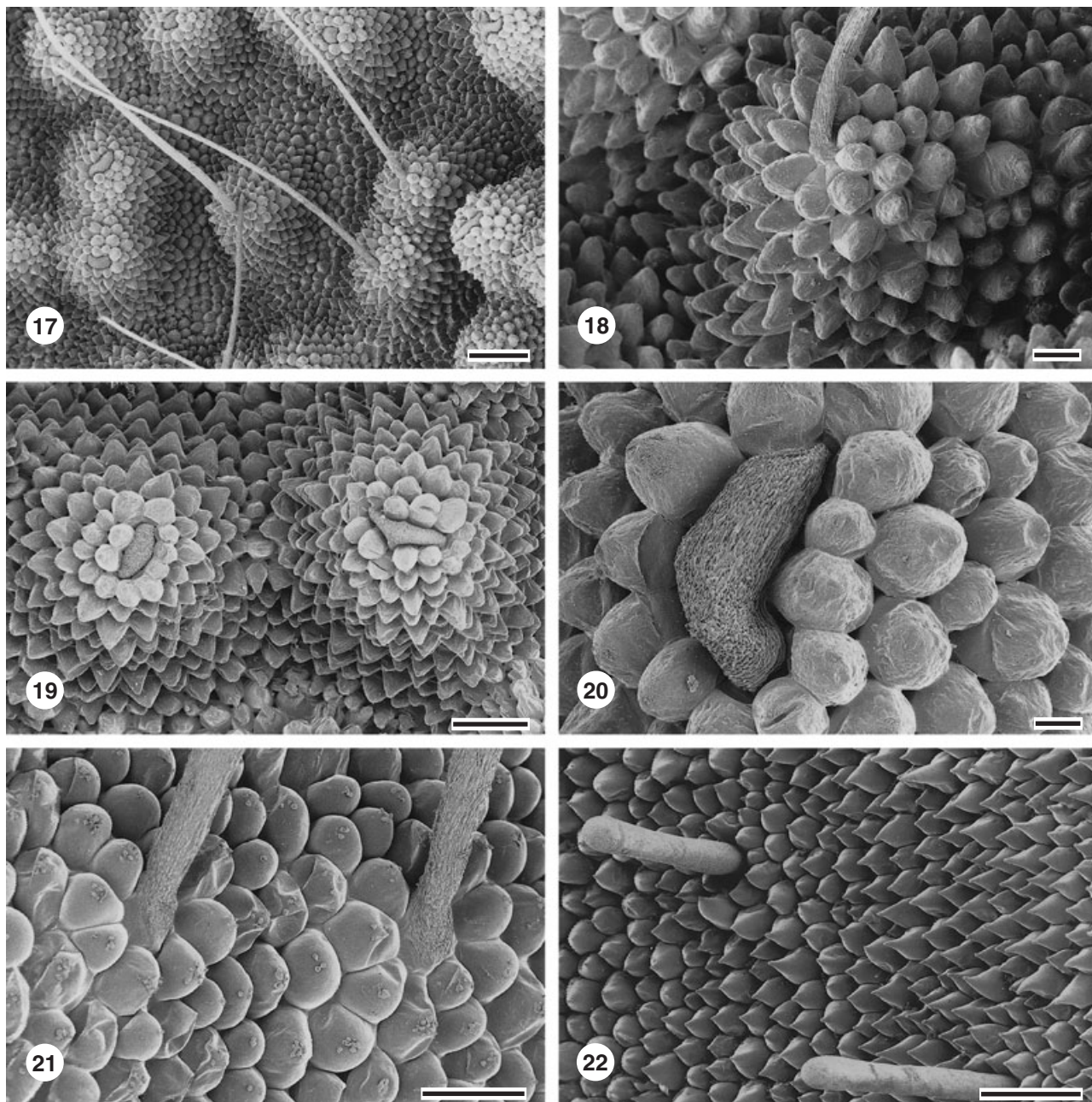
In *Stapeliopsis* prominent, columnar or conical, multicellular papillae festoon the inside of the corolla towards its mouth in *S. exasperata*, *S. khamiesbergensis*, *S. neronis* and *S. urniflora*. Each has a minute, verrucose, apical bristle (Figs 17, 18, 23–25). These apical cells sometimes have a particularly peculiar form in *S. urniflora*, where they may be transversely elongated without projecting from the surface (Figs 19, 20). Further down in the tube the apical bristle becomes progressively longer and the papilla beneath it becomes shorter: in *S. neronis* the papilla disappears entirely towards the base of the corolla but in *S. exasperata*, *S. khamiesbergensis* and *S. urniflora* it is still present right to the base. In *S. breviloba*, *S. pillansii*, *S. saxatilis* and *S. stayneri* (Figs 21, 22) the papillae are more or less absent and only the apical bristles remain as hairs, which are present over most of the lower half of the tube. Consequently, in all species of *Stapeliopsis* the inside of the corolla has these hair-like bristles. The basal epidermal cells between and covering these papillae are variously conical to bottle-shaped, with an unusually long central papilla in *S. neronis* (Fig. 28).

The prominent papillae inside the tube in *S. exasperata* extend onto the lobes. In *S. pillansii* and *S. saxatilis* the lobes possess scattered, small, unicellular, hair-like papillae (as in Fig. 22). Otherwise the lobes in *Stapeliopsis* are glabrous and smooth.

Gynostegium

In all species the gynostegium is at least slightly raised above the base of the tube on a stipe. In *S. neronis*, *S. khamiesbergensis* and *S. urniflora* there is a gradual merging of the stipe into the base of the outer corona-lobes. In *S. neronis* the stipe is slightly broader than the gynostegium at maturity (though narrower in earlier stages) whereas in *S. khamiesbergensis* and *S. urniflora* it is very much broader than the gynostegium, forming a platform on which the corona is seated. In the remaining species the bases of the outer corona-lobes swell outwards and downwards to form a ring into which the stipe fits (Fig. 37).

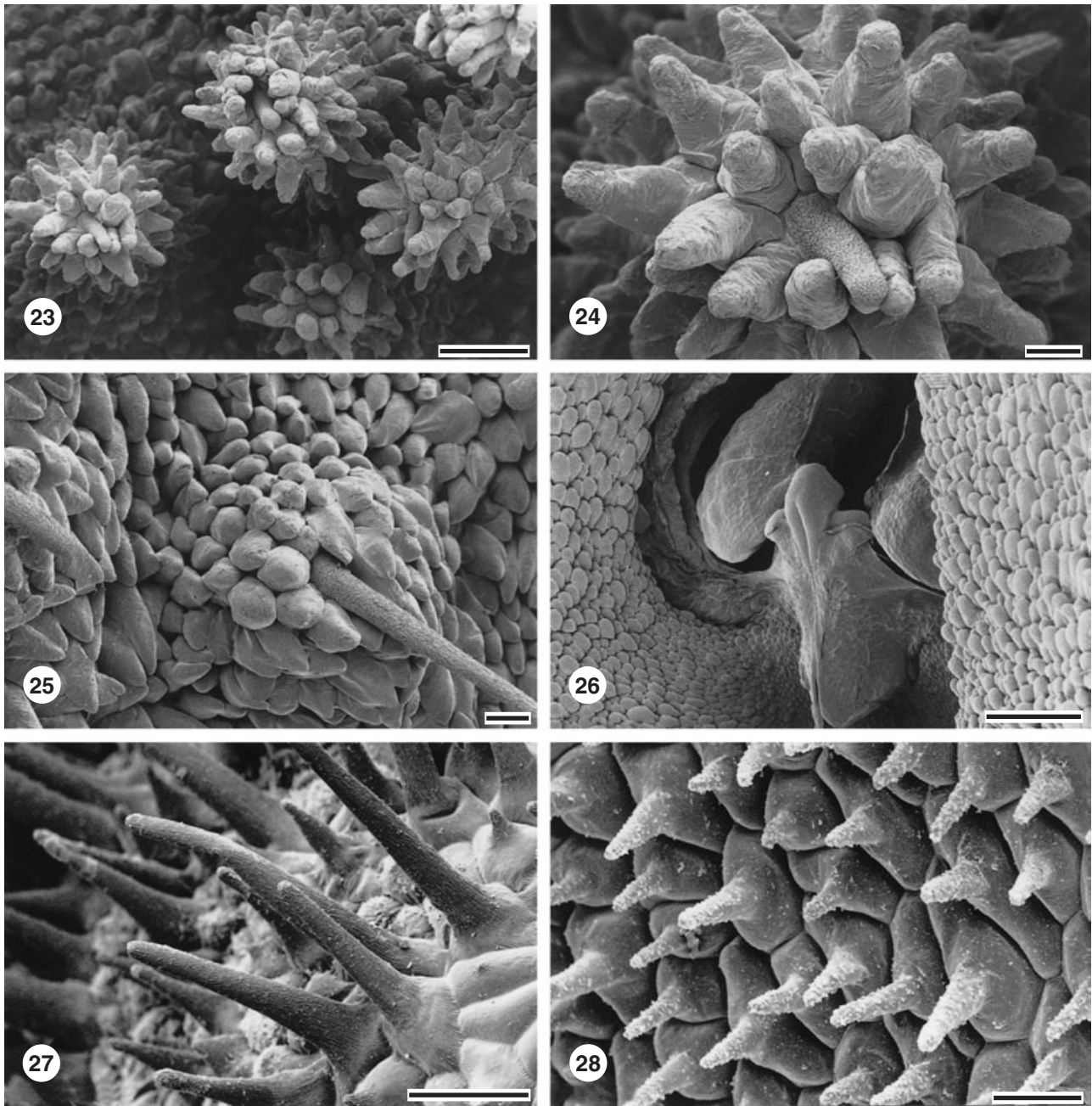
The ontogeny of the corona has been followed in *S. neronis* (Figs 29–32), *S. saxatilis* (Figs 33–36) and



Figures 17–22. SEM views of inner surface of corolla in *Stapeliopsis*. Figs 17–20. *S. urniflora* (PVB 5733 (BOL)). Fig. 17. Papillae in lower half of corolla-tube where individual cells have conical outer walls and apical cell elongated into bristle. Scale bar = 100 μm . Fig. 18. Individual papilla with bristle-like apical cell. Scale bar = 20 μm . Fig. 19. Papillae in upper half of tube with short and spreading apical cell. Scale bar = 60 μm . Fig. 20. Individual papilla with oddly shaped apical cell clearly visible by its different granular texture. Scale bar = 10 μm . Fig. 21. *S. stayneri*. Bristles toward base of corolla-tube, cells here with rounded outer walls, PVB 6262 (BOL). Scale bar = 30 μm . Fig. 22. *S. saxatilis*. Bristles toward base of corolla-tube, cells here with distinctly acute outer walls, PVB 5276 (BOL). Scale bar = 100 μm .

S. urniflora. In *S. neronis* the outer corona begins as five separate lobules beneath the guide-rails (as can just be seen as slight swellings in Fig. 29). These soon spread laterally around the gynostegium, forming a

ridge behind the inner lobes (partly fused to their backs, Figs 30, 31). Then this ring-like structure grows upwards to enclose the whole gynostegium in a cylindrical tube (Fig. 32). In *S. urniflora* the early stages

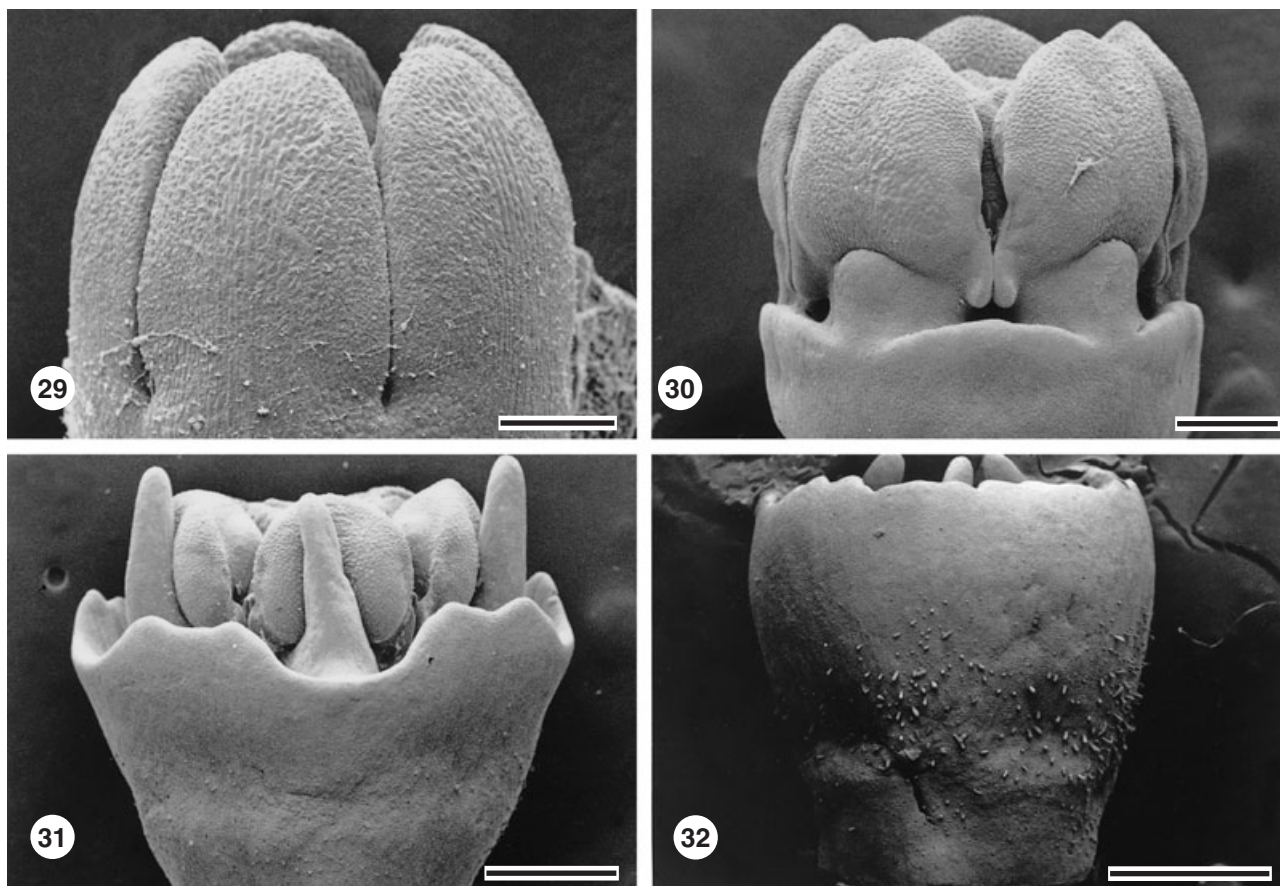


Figures 23–28. SEMs of outer and inner surface of corolla and corona in *Stapeliopsis*. Figs 23–26. *S. exasperata* (PVB 2820 (BOL, NBG, PRE)). Fig. 23. Papillae in upper half of corolla-tube where individual cells have very much extended outer walls but apical cell not larger than the rest. Scale bar = 100 μ m. Fig. 24. Individual papilla with apical cell clearly visible by its different granular texture. Scale bar = 20 μ m. Fig. 25. Smaller papillae towards base of tube with much elongated apical cell. Scale bar = 20 μ m. Fig. 26. Base of inner corona-lobes with view of corpuscle and guide-rail. Scale bar = 100 μ m. Fig. 27. *S. neronis* (PVB 5207 (BOL)). Outer walls of cells on exterior of corolla just beneath sinuses of corolla-lobes. Scale bar = 100 μ m. Fig. 28. Outer walls of cells on inside of corolla-lobes. Scale bar = 50 μ m.

are similar. Again the outer lobes form a ridge behind the inner but now this ridge and the inner lobes grow upwards so that at maturity this ridge is well above the level of the rest of the outer lobes. The part of the

outer lobes beneath the guide-rails rises up at least to the height of the anthers.

In *S. saxatilis* the early stages are again similar (compare Figs 30, 33). The outer corona soon develops



Figures 29–32. SEMs of developing gynostegium in *Stapeliopsis neronis* (PVB 7257 (MO)). Fig. 29 Outer corona just beginning to form below guide-rails and inner corona not present yet. Scale bar = 100 μ m. Fig. 30. Outer corona prominent and broadly spreading below guide-rails and inner lobes developing at bases of anthers. Scale bar = 250 μ m. Fig. 31. Outer corona spreading behind inner lobes but still shorter there than between anthers. Scale bar = 500 μ m. Fig. 32. Tubular outer corona just before inner lobes become hidden. Papillae on outside of outer corona becoming visible. Scale bar = 1 mm.

a further ridge behind each inner lobe (Fig. 34). This ridge grows strongly upwards together with the inner lobe (Fig. 35), to leave the remainder of the outer lobe well below the guide-rail (i.e. hardly developing at all from its early stages, with the guide-rail and anthers visible from the side at maturity) and ends up running from below the level of the guide-rail to well above the anthers (Fig. 36). The inner lobe then consists of the tissue between these ridges and the back of the anther and this rises up high above the anther to form a 'cage' over the gynostegium. The outer corona also grows slightly downwards over the top of the stipe, developing there also most strongly behind the anthers with a slight gap beneath the guide-rail (Fig. 37).

15. Inner corona-lobes dorsiventrally flattened = 0; laterally flattened = 1.

In all species of *Stapeliopsis* the inner corona-lobes are laterally flattened, an unusual situation in the stapeliads.

16. Inner corona adpressed to backs of anthers for most of length of anthers = 0; rising above anthers from near base = 1.

In all species of *Stapeliopsis* the inner corona-lobes rise above the anthers from quite near the base and this is unique to this genus.

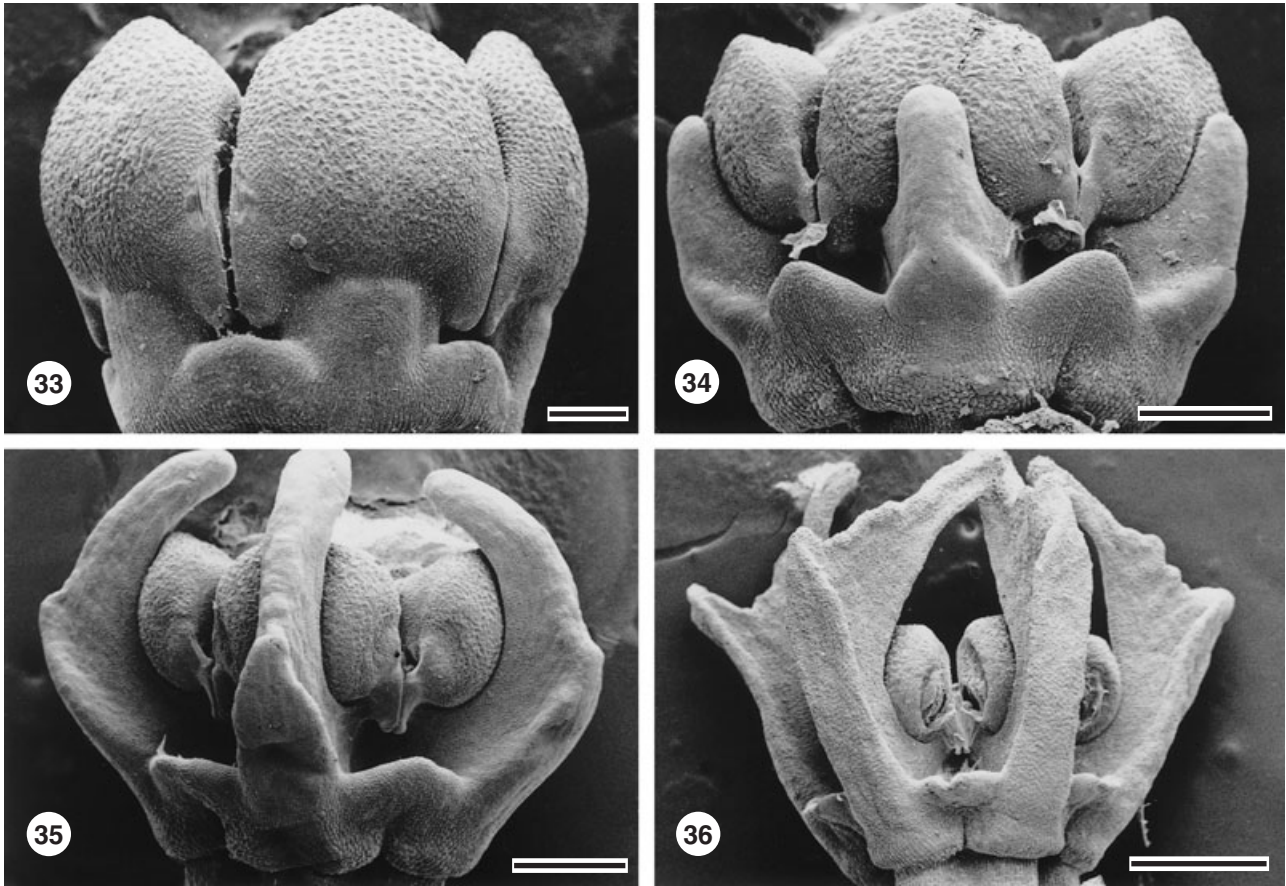
Pollinarium

All species of *Stapeliopsis* have small pollinia which are longer than broad (0.22–0.35 \times 0.18–0.28 mm). The corpusculum is small, in most cases slightly wider above than below, with very small wings (Fig. 26).

17. Pollinia longer than broad = 0; broader than long = 1.

In general the pollinia in *Stapeliopsis* are longer than broad but a few have been seen in *S. saxatilis*, which were slightly broader than long.

18. Pollinia ellipsoidal = 0; D-shaped = 1.



Figures 33–36. SEMs of developing gynostegium in *Stapeliopsis saxatilis* (PVB 4905 (BOL)). Fig. 33 Outer corona already quite prominent and inner just beginning to form below anthers. Scale bar = 100 μ m. Fig. 34. Outer corona developing ridge behind inner lobes to form \pm cupular structure around gynostegium with inner lobes extending along backs of anthers. Scale bar = 250 μ m. Fig. 35. Ridge of outer corona dragged up behind anthers, rest of outer corona not developing further except below around stipe. Scale bar = 500 μ m. Fig. 36. Fully developed gynostegium with ridge of outer lobes forming what looks like dorsal horn of inner lobe. Scale bar = 500 μ m.

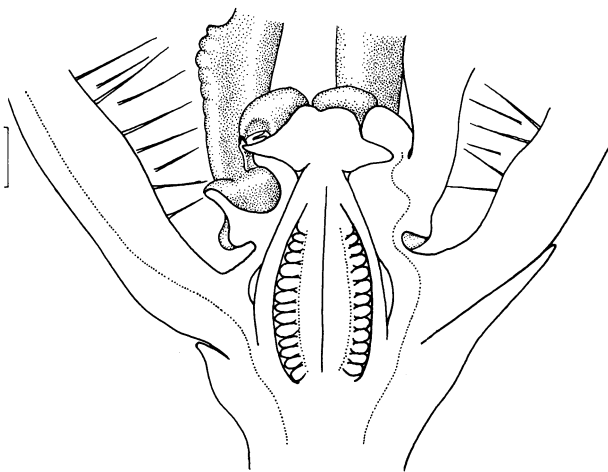


Figure 37. Half-flower in *Stapeliopsis saxatilis*. Scale bar = 0.5 mm. Drawn from PVB 2544 (BOL).

19. Pollinia with insertion-crest along edge = 0; with insertion-crest twisted onto dorsal surface = 1.

In *Stapeliopsis* the germinating mouth of the pollinium lies exactly along the outer edge of each pollinium.

20. Corpuscle small (< 0.15 mm long) = 0; large (> 0.15 mm long) = 1.

21. Caudicle small, attached to ventral side of pollinium = 0; broad and \pm cupular on base of pollinium = 1.

Fruit, seed and seedlings

In all species of *Stapeliopsis* the pedicel elongates to 30–50 mm as the fruit develops. The follicles are 40–80 mm long, slender, mottled longitudinally with purplish on pale green, glabrous (except in *S. neronis*) and diverge from one another at 30–60°. Seeds were

counted in *S. neronis* (130 in two horns) and *S. saxatilis* (48 in two horns).

Seed in *S. neronis* is broadly pear-shaped (4×2 mm), fairly flat, dark brown (without paler margin) and covered all over with conical papillae (Figs 38, 39). In the other species (apart from *S. breviloba*) it is somewhat narrower ($\pm 4.5 \times 1.5$ mm) and more deeply folded (i.e. boat-shaped as in *S. saxatilis*, Fig. 40), pale brown with a paler margin and covered mainly on the margin and lower (convex) surface with low, rounded papillae (Fig. 41). In *S. breviloba* the seed is large ($\pm 6.0 \times 3.5$ mm), brown, broadly pear-shaped, flat, with paler margin folded inwards and all surfaces smooth.

22. Seed flat = 0; boat-shaped = 1.

23. Seed coat smooth = 0; papillate = 1.

24. Cells on margin of seed sculptured = 0; not sculptured = 1.

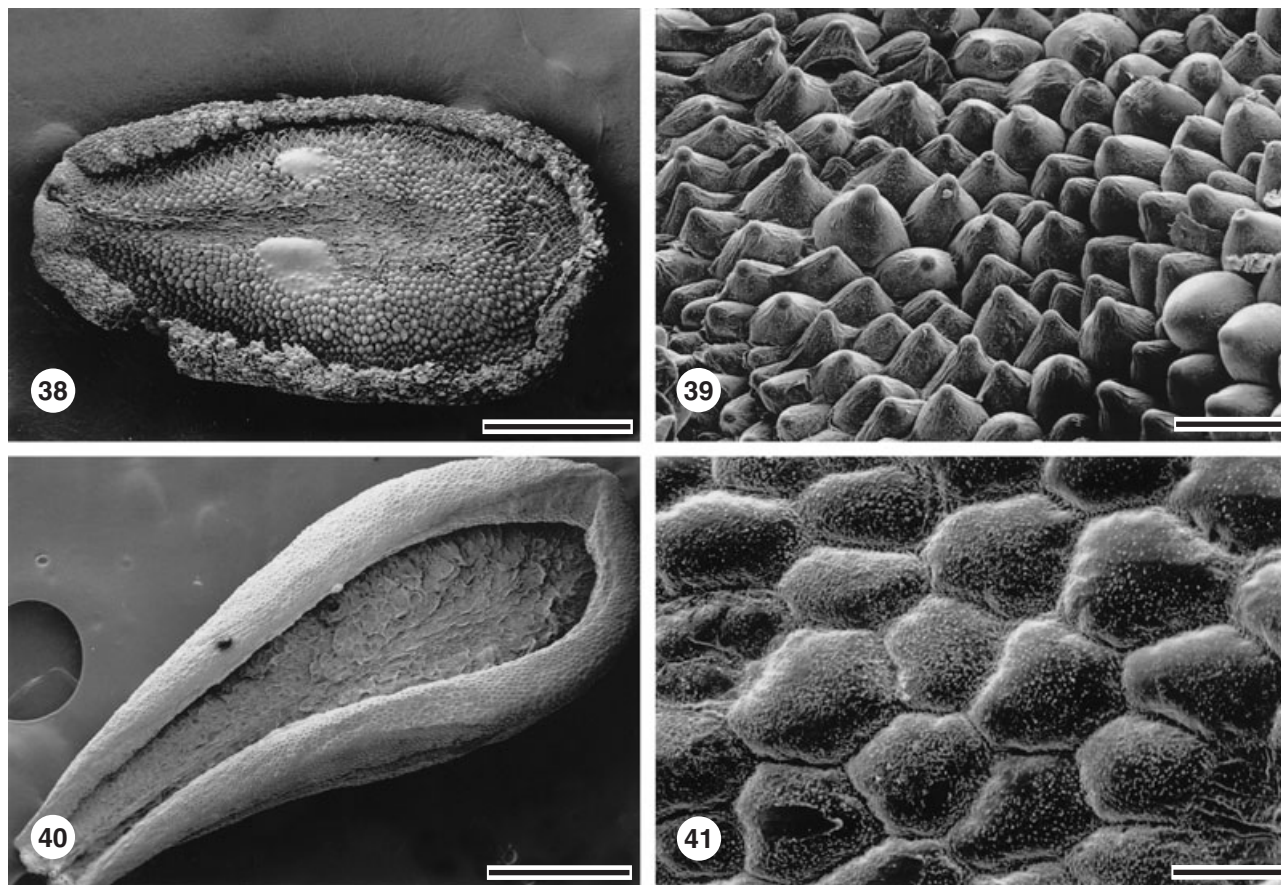
In both *S. neronis* and *S. saxatilis* the marginal cells have smooth (rather than sculptured) outer walls.

25. Hypocotyl wedge-shaped = 0; \pm spherical = 1.

Seedlings have been observed in *S. breviloba*, *S. exasperata*, *S. neronis*, *S. pillansii*, *S. saxatilis* and *S. stayneri* (Fig. 42). They have a relatively short, wedge-shaped hypocotyl with cotyledons barely distinguishable from it (slightly larger in *S. neronis*). The cotyledons are slightly flattened above, as are the leaf rudiments.

Pollination

The flowers of several species of *Stapeliopsis* are deeply urceolate. The mouth of this urn-shaped structure may also be remarkably constricted by the thickened bases of the lobes, as in *S. neronis* (Fig. 56), so that access to the interior of the flower is difficult. In *S. neronis* the pollinia are further hidden away by the cylindrical outer corona.



Figures 38–41. SEMs of seed of *Stapeliopsis*. *S. neronis* (PVB 2818 (BOL)). Fig. 38. Whole seed. Scale bar = 1 mm. Fig. 39. Detail of cell-walls on upper surface between margins. Scale bar = 100 μ m. *S. saxatilis* (PVB 1089 (NBG)). Fig. 40. Whole seed. Scale bar = 1 mm. Fig. 41. Detail of cell-walls along margin. Scale bar = 25 μ m.

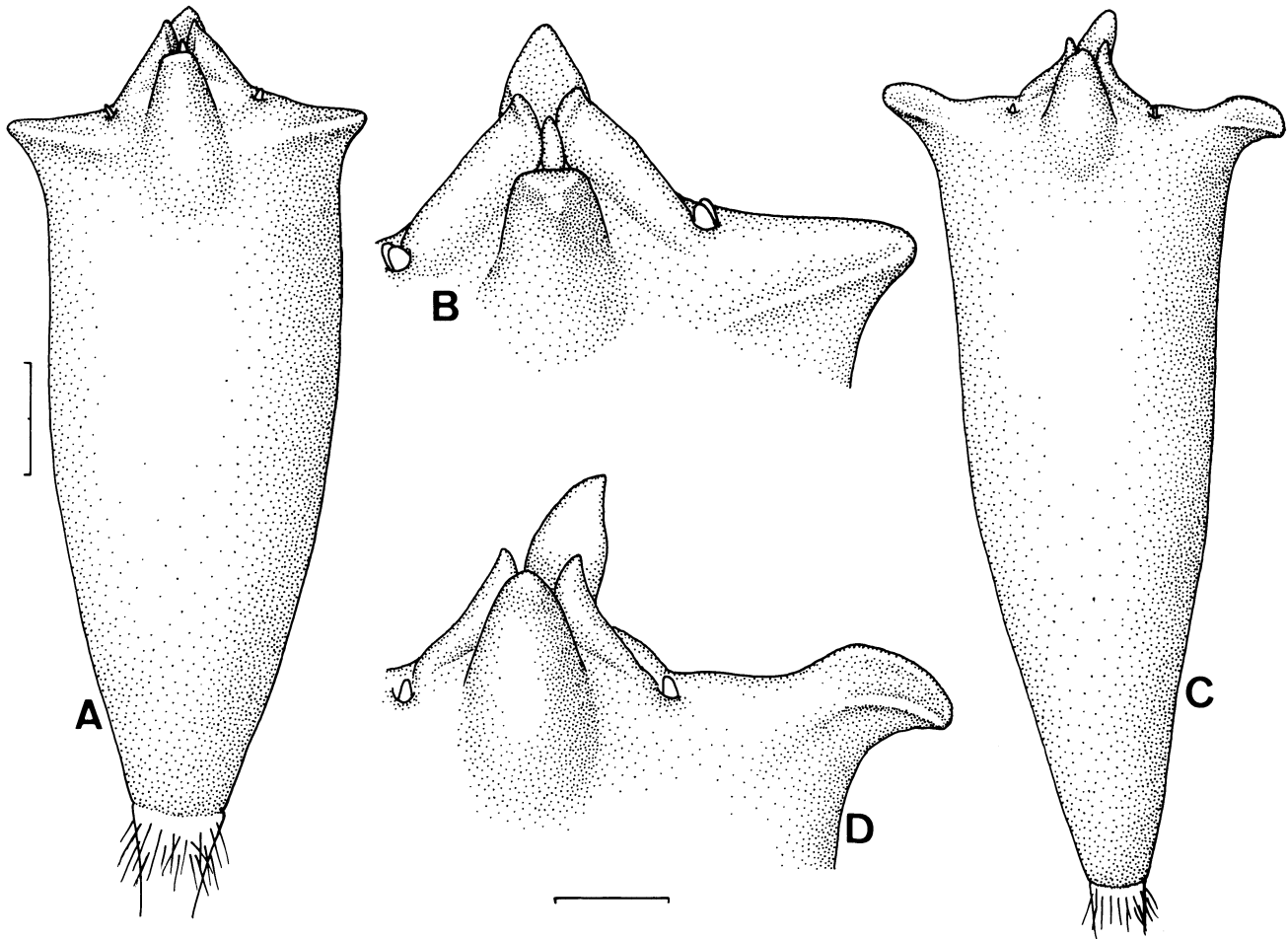


Figure 42. Seedlings of *Stapeliopsis*. *S. saxatilis* (PVB 1089 (NBG)). A, side view of plantlet, 28 days old; B, close-up of apical bud and cotyledon. *S. neronis* (PVB 2818 (BOL)). C, side view of plantlet, 28 days old; D, close-up of apical bud and cotyledon. Scale bars: A, C = 2 mm (at A); B, D = 1 mm (at D).

In *S. exasperata* the somewhat cylindrical flowers are often produced beneath the soil, while in *S. pil-lansii* the campanulate flowers are almost always subterranean.

Direct observations on pollinators are lacking. Vogel (1954) investigated preserved flowers of *S. neronis* and postulated that minute flies were involved in its pollination. We believe that this is correct. We have frequently observed small flies trapped within flowers of species such as *S. breviloba*, *S. neronis*, *S. saxatilis* and *S. urniflora*, which flee their predicament when the flower is cut open for examination (Bruyns, 1979) or die there if the flower is placed in alcohol. We have never checked them for attached pollinia but the small openings to the corolla in these species make it certain that some tiny insect is involved in pollination.

Our evidence is that these flowers act as a trap in a very similar manner to flowers of many species of *Ceropegia*, with the numerous hairs towards the base

of the tube making it difficult for the fly to climb back up the tube. It is even possible that the slippery-slope mechanism of the mouth of the tube (Vogel, 1961) is present here in species such as *S. neronis* and *S. urniflora*. The complex movements of the pedicel in *Ceropegia* to tip the flower and release the trapped insects (Vogel, 1961) have not developed in *Stapeliopsis* and the flies are released once the turgor of the flower subsides and these hairs collapse.

RESULTS

A summary of statistics for the parsimony analyses of separate and combined data sets is given in Table 3.

SEPARATE ANALYSES

After excluding characters, 660 positions were available for analysis in the *trn* dataset. Of these, 57

Table 3. Summary of statistics for parsimony analyses of *Stapeliopsis* and related taxa

| | Inc. | inf. | MPTs | Length | CI | RI | RC |
|------------------------|------|------|------|--------|------|------|------|
| <i>trnL-F</i> | 660 | 37 | 8 | 65 | 0.82 | 0.86 | 0.71 |
| ITS1 | 273 | 48 | 2 | 129 | 0.70 | 0.73 | 0.51 |
| morphology | 25 | 23 | 202 | 57 | 0.42 | 0.74 | 0.31 |
| combined molecules | 933 | 85 | 15 | 136 | 0.91 | 0.93 | 0.85 |
| molecules & morphology | 958 | 108 | 2 | 261 | 0.61 | 0.73 | 0.45 |

Inc., number of characters included; inf., number of informative characters; MPTs, most parsimonious trees; Length, tree length; CI, consistency index; RI, retention index; RC, rescaled consistency index.

were variable and 37 parsimony informative. Within *Stapeliopsis* only seven characters were phylogenetically informative. Unweighted parsimony analysis generated eight most parsimonious trees (MPTs) [length (L) = 65, consistency index (CI) = 0.82, retention index (RI) = 0.86]. A clade comprising all taxa except *Anisotoma cordifolia* and *Neoschumannia kamerunensis* is well supported [jackknife percentage (JK) = 100]. Within this large clade most relationships are unresolved in the strict consensus, except for a well supported (JK = 85) group consisting of *Tromotriche longii*, *Huernia erectiloba* and *Orbea namaquensis*. The latter two are resolved as sisters (JK = 83). A second group consisting of the ingroup taxa, *S. breviloba*, *S. stayneri* and both collections of *S. saxatilis*, is resolved and weakly supported (JK = 65).

For the ITS data 273 characters were available, of which 48 were variable and 48 parsimony informative. Within *Stapeliopsis* only seven were phylogenetically informative. Under unweighted parsimony analysis two MPTs were generated (L = 129, CI = 0.70, RI = 0.73). The strict consensus of these is shown in Figure 43. There is strong support (JK = 91) for a clade consisting of all *Stapeliopsis* taxa, *Pectinaria*, *Ophionella*, *Quaqua*, the *Huernia*–*Tromotriche* clade identified in the *trn* analysis and *Notechidnopsis tessellata*. The placement of *S. pillansii* as sister to the rest of this clade is unsupported. Two main clades are resolved among the remaining taxa of *Stapeliopsis*. One (JK = 84) consists of *S. neronis* as sister to *S. urniflora* + *S. khamiesbergensis* (JK = 65). The second resolved group has *S. breviloba* placed sister (JK = 65) to a strongly supported grouping (JK = 85) of the two *S. saxatilis* accessions. Relationships of these groups to each other and to other members of the larger clade are unresolved.

Owing to the low number of phylogenetically informative characters and the relatively low levels of homoplasy that they display, weighting of characters did not improve resolution within the separate molecular data sets.

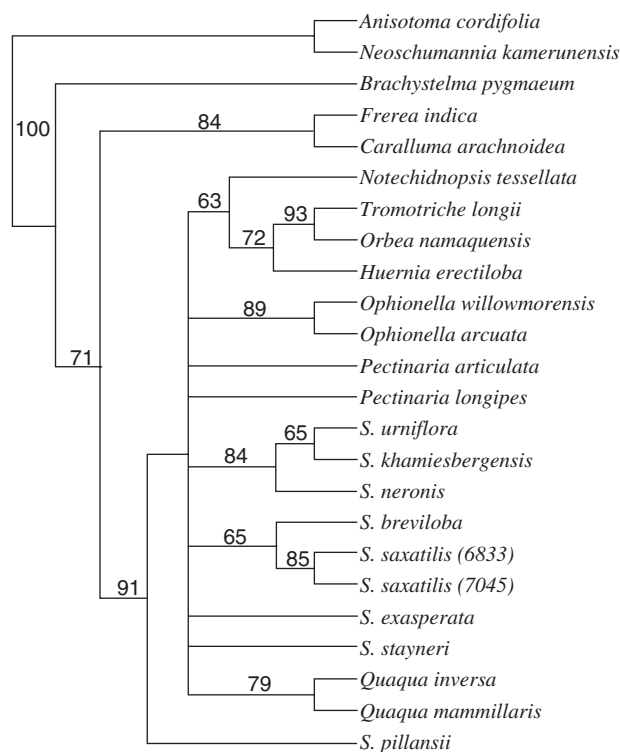


Figure 43. Strict consensus of the two most parsimonious trees from analysis of ITS1 data. Jackknife support values over 60% are indicated above the branches.

MORPHOLOGY

Unweighted analysis of the 23 informative morphological characters recovered 202 MPTs (L = 57, CI = 0.42, RI = 0.74). *Stapeliopsis* is resolved as monophyletic but with low support (JK = 61). Within *Stapeliopsis* relationships are largely unresolved except for a weakly supported (JK = 66) clade comprising *S. urniflora*, *S. neronis* and *S. khamiesbergensis*. A clade comprising *Notechidnopsis tessellata* + *Tromotriche longii* (JK = 66), *Orbea namaquensis* and *Huernia erectiloba* is placed sister to *Stapeliopsis*, but is unsupported.

Tree topology stabilized after two rounds of successive weighting. The strict (weighted) consensus of these is shown in Figure 44. *Stapeliopsis* is recovered as a well-supported monophyletic group (JK = 85), within which, in addition to the clade identified in unweighted analysis (JK = 61), a group is resolved but unsupported, consisting of *S. exasperata* sister to *S. saxatilis* (PVB 7045), which in turn is sister to a trichotomy containing *S. saxatilis* (PVB 6833), *S. stayneri* and *S. pillansii*.

COMBINED ANALYSES

Analysis of the combined molecular data recovered 15 MPTs (L = 136, CI = 0.91, RI = 0.93). The strict consensus of these is identical to the ITS tree with respect to *Stapeliopsis* with the exception that *S. stayneri* and *S. pillansii* resolve as sisters. After three rounds of successively approximated weights there was no change in tree topology (JK = 66).

Unweighted analysis of total evidence (molecular and morphological) identified two MPTs (L = 261, CI = 0.61, RI = 0.73). In the strict consensus *Stapeli-*

opsis forms a monophyletic group (JK = 60). The taxa of *Stapeliopsis* fall into a well-supported clade (JK = 100) that also includes a well-supported *Ophionella* (JK = 99), a group (JK = 98) consisting of *Huernia* as sister to *Orbea* + *Tromotriche* (JK = 61), and an unsupported clade in which *Notechidnopsis* and the two species of *Pectinaria* form a trichotomy that is sister to a well-supported *Quaqua* (JK = 96). Within *Stapeliopsis* one well-supported clade (JK = 98) is recovered in which *S. neronis* is sister to *S. urniflora* + *S. khamiesbergensis* (JK = 70). A second group made up of *S. pillansii*, *S. stayneri*, both *S. saxatilis* accessions and *S. breviloba* is resolved and weakly supported (JK = 67). Two rounds of successive weighting result in the single MPT shown in Figure 45. The monophyly of *Stapeliopsis* is well supported (JK = 86), and relationships within the genus are fully resolved. Two major groupings are recovered. The first places *S. neronis* sister (JK = 99) to *S. urniflora* + *S. khamiesbergensis* (JK = 67) and the second places *S. exasperata* as sister to the remaining *Stapeliopsis* taxa. Within this latter clade the two *S. saxatilis* accessions form a strongly supported

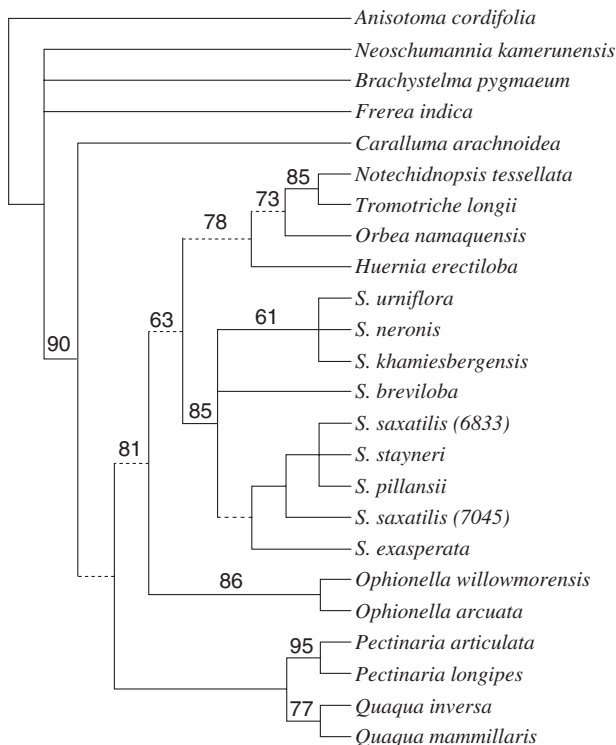


Figure 44. Strict consensus of 202 most parsimonious trees recovered from analysis of 25 morphological characters, following two rounds of successive weighting. Jackknife support values over 60% are indicated above the branches. Branches not supported in the unweighted strict consensus tree are shown as dashed lines.

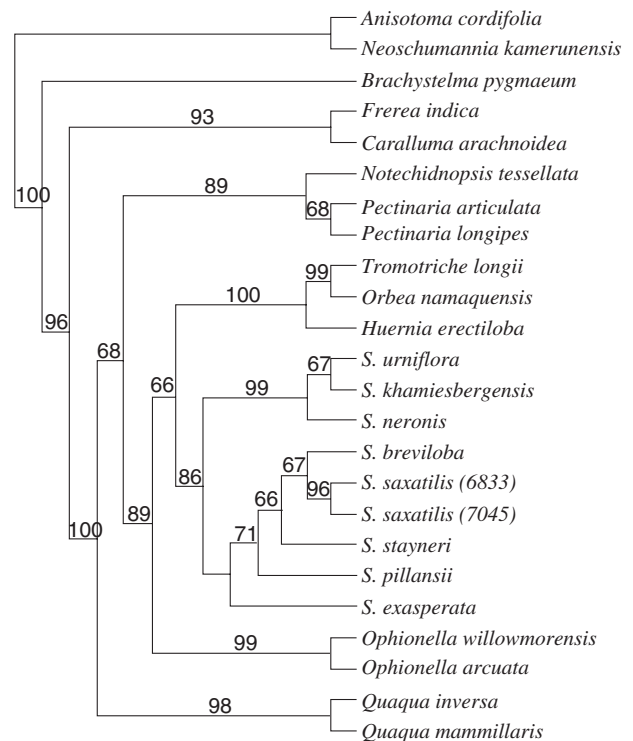


Figure 45. Single most parsimonious tree recovered from analysis of total evidence (i.e. data from two gene-regions and morphological data), following two rounds of successive weighting. Jackknife support values over 60% are indicated above the branches.

group (JK = 96), to which *S. breviloba* (JK = 67), *S. stayneri* (JK = 66) and *S. pillansii* (JK = 71) are successively sister. A well-supported clade (JK = 100) consisting of *Tromotriche*, *Orbea* and *Huernia* is recovered and is sister to *Stapeliopsis*.

DISCUSSION

In a purely morphological cladistical study (Bruyns, 2000a), *Stapeliopsis* was found to be sister to a clade containing many genera such as *Huernia*, *Orbea*, *Stapelia* and others. This was a corroboration of the result of Bruyns (1999b) where only *Orbea variegata* and *Stapelia hirsuta* were included. In Bruyns (1999b) the sister to the clade containing *Orbea* and *Stapeliopsis* was *Ophionella* and sister in turn to all of these was *Pectinaria*. In Meve & Liede (2002, fig. 4), based on molecular data, relationships among the two species of *Stapeliopsis* that they included together with one species of *Pectinaria* and two of *Quaqua* were unresolved. This grouping was itself located in a polytomy made up of a clade consisting only of *Ophionella* and another large polytomy containing, among many other taxa, representatives of *Huernia*, *Orbea*, *Stapelia* and *Tromotriche*. These results are inconclusive regarding the relationships of *Stapeliopsis* to other genera and within the genus. In addition they do not show that N.E. Brown's (1907–9) concept of *Pectinaria* was not monophyletic.

Our results show that the species included in Brown's concept of *Pectinaria* do not form a monophyletic entity. This study corroborates the results of Bruyns (1999b) in showing that *Stapeliopsis*, in the new sense, is monophyletic and we have established that this monophyly has strong statistical support in the weighted analysis of total evidence. Also corroborated is the hypothesis that *Ophionella* is monophyletic and this too is statistically highly supported. Only in the weighted analysis of total evidence is *Pectinaria* found to be monophyletic (with fairly weak support).

Plowes (2003) proposed a monotypic genus *Hermanschwartzia* for *Stapeliopsis exasperata* and another genus *Neopectinaria* for *Stapeliopsis breviloba*, *S. pillansii*, *S. saxatilis* and *S. stayneri*. Our results show that there is no statistical support for monotypic status for *S. exasperata* and that even the other grouping corresponding to *Neopectinaria* is only weakly supported. The strong support for the expanded concept of *Stapeliopsis* (Fig. 45) shows that these new genera are superfluous.

As far as relationships between genera are concerned, our analyses show that *Stapeliopsis* is sister to a very highly supported clade containing *Huernia*, *Orbea* and *Tromotriche* (as found in Bruyns, 1999b, 2000a) and that *Ophionella* is sister to this group

(again as found in Bruyns, 1999b, 2000a). Furthermore, we have shown again that *Pectinaria* and *Notechidnopsis* are sisters and have established that this relationship is strongly supported. Our results show that, among the species sampled, they are sister to *Ophionella*, *Stapeliopsis* and the *Huernia–Orbea–Tromotriche* group (as in Bruyns, 2000a).

Although the morphological data considerably strengthen the support for clades and add greatly to the resolution obtained, no useful new characters with which to separate *Stapeliopsis* from other genera were detected. In *Stapeliopsis* the inner corona-lobes are laterally flattened and they touch the anthers only at their bases. Laterally flattened inner corona-lobes are extremely rare in the stapeliads: the lobes are otherwise always dorsiventrally flattened as they pass over the backs of the anthers, in some cases becoming cylindrical above [cf. *Tromotriche baylissii* (Leach) Bruyns] and frequently with a laterally flattened dorsal horn (e.g. *Stapelia*). Thus this character is a synapomorphy for *Stapeliopsis*.

The total analysis (Fig. 45) yields considerable resolution within the genus. In Bruyns (1981) two sections were recognized, with *S. neronis* and *S. urniflora* in sect. *Stapeliopsis* and the remaining species in sect. *Cageliorona*. In Bruyns (1999b) it was found that *Stapeliopsis* was made up of two clades, one containing *S. exasperata*, *S. neronis* and *S. urniflora* and another embracing *S. breviloba*, *S. pillansii* and *S. saxatilis*. However, the situation is more complex than was recognized then and there is actually considerable morphological transition between these two sections.

In the first place there are characters which *S. urniflora* shares with sect. *Cageliorona* and not with *S. neronis*:

1. smooth corolla outside,
2. lobes coloured the same as the rest of the tube,
3. lobes not much thickened at their bases,
4. inner corona-lobes relatively short and broad.

Secondly there are characters in which there is a cline from *S. neronis* to sect. *Cageliorona*:

1. Habit: very shortly decumbent stems in *S. neronis*; decumbent tending to rhizomatous in *S. urniflora*; stronger tendency to rhizomatousness in *S. exasperata*.
2. Epidermis of stem: papillae largest in *S. neronis*; smaller in *S. urniflora*; smaller again in *S. exasperata*; smaller still to absent in *S. saxatilis* and \pm absent in the others.
3. Outer corona: cylindrical and completely containing the rest of the gynostegium in *S. neronis*; much reduced and exposing most of inner lobes but not the anthers in *S. urniflora*; further reduced and exposing also the anthers in the others.

This considerable morphological transition between these groups can be observed in Figure 44, where the *S. exasperata*–*S. saxatilis* clade is without any statistical support and *S. breviloba* occupies an unresolved position within *Stapeliopsis*. It is interesting that in the analysis of ITS1 data (Fig. 43) the relationship between *S. exasperata* and the other former members of sect. *Cageliorona* is also not resolved. Although the tree (Fig. 45) obtained from total weighted evidence does indicate two groups that correspond to the two sections previously recognized within *Stapeliopsis*, support for some of the nodes is weak and these sections are consequently abandoned. The clade containing *S. neronis* is particularly strongly supported in this analysis, where it was weakly supported in the morphological analysis and much more strongly in the analysis of ITS1 data.

It is revealed here that *Stapeliopsis saxatilis* is not monophyletic if '*stayneri*' is included (as in Bruyns, 1981). A re-examination of the morphological data showed that this view is corroborated by the presence of differences from *S. saxatilis* in two characters. Consequently this taxon is now recognized as a separate species. We have also shown that the inclusion within *S. saxatilis* of the vegetatively distinctive forms that occur on sandstone substrates is strongly supported, despite the differences that were observed in the surfaces of the stems.

The phylogeny proposed here (Fig. 45) suggests that *Stapeliopsis* diversified from an ancestor which occurred possibly widely over the western Cape to produce a 'northern clade' and a 'southern clade'. The 'northern' clade consists of the three species *S. khamiesbergensis*, *S. neronis* and *S. urniflora*, which occur on the northern edge of the generic distribution and two of which are the only species that occur in Namibia. These are the species with the most papillate stems, the most tubular outer corona and the unusual, broad, platform-like stipe below the corona. The remainder of the genus makes up the 'southern' clade. Here the widespread but rare *S. exasperata* is sister to the others. The very localized *S. breviloba* is sister to the widely distributed *S. saxatilis*. All of these 'southern species' have less prominently papillate stems, they have a distinctively reduced outer corona whose sides are dragged upwards by the development of the inner corona and a narrow stipe under the gynostegium. In several morphological features they are considerably more variable than the members of the 'northern clade' and among the molecular characters there are also fewer that hold them together. Perhaps surprisingly, the three 'prostrate-stemmed' species *S. saxatilis*, *S. stayneri* and *S. pillansii* do not form a monophyletic entity. These vegetatively unusual and very similar-looking plants are mainly concentrated on the Little Karoo and in the southern

part of the Great Karoo, only reaching marginally northwards (in the case of *S. saxatilis*) to the southern edge of Namaqualand.

As papillate stems are present throughout the large polytomy in Figure 43 in which the species of *Stapeliopsis* are located (except for *Huernia* and *Orbea*), it is possible that the common ancestor of *S. exasperata* and *S. neronis* had papillate stems. This feature is secondarily lost in some members of the 'southern clade' but is present throughout the 'northern clade'.

A similar evolution may be postulated for the unusual trap-flower pollination syndrome found in several species of *Stapeliopsis*. From the shape of the flower in *S. exasperata*, one may deduce that it too is pollinated by small flies which are trapped in the flowers. It is therefore possible that this trap-mechanism was present in the common ancestor of *S. exasperata* and *S. neronis*. It is almost certainly present throughout the 'northern clade'. Similarly it is almost certainly present throughout the 'southern clade', with the remarkable exception of *S. pillansii*, where it has been secondarily lost and is replaced with an underground flowering habit that is unique in the Asclepiadoideae and probably in the whole of the Apocynaceae.

TAXONOMIC ACCOUNT

Stapeliopsis Pillans, S. African Garden. & Country Life 18: 32 (1928), *non* Choux (1931), *nec* E. Phillips (1932). Type: *Stapeliopsis neronis* Pillans.

Stapeliopsis sect. *Cageliorona* Bruyns, *Cact. Succ. J. Gr. Brit.* 43: 75 (1981). Type: *Stapeliopsis saxatilis* (N.E. Br.) Bruyns.

Hermanschwartzia Plowes, *Excelsa* 20: 11 (2003). Type: *H. exasperata* (Bruyns) Plowes.

Neoplectinaria Plowes, *Excelsa* 20: 12 (2003). Type: *N. saxatilis* (N.E. Br.) Plowes.

Dwarf to small spineless sometimes rhizomatous succulent forming clump or mat. STEMS prostrate to decumbent or erect, when rhizomatous then with erect tips, 4–35 mm thick, ±smooth and glaucous green or brownish (sect. *Cageliorona*), papillate and blue-green mottled with purple (sect. *Stapeliopsis*); tubercles 1–5 mm long, mostly laterally flattened and joined into 4 angles along stem, tapering to small often hard yellowish tooth, rarely with stipular denticles and without any obvious leaf. INFLORESCENCES glabrous to minutely pubescent, 1 (4) per stem arising near base, with 1–10 flowers developing in gradual succession on knobbly peduncle usually short but up to 25 mm long, with lanceolate bracts < 1 mm long. COROLLA ellipsoidal, ovoid to cylindrical or campanulate; outside glabrous and shiny except in *S. neronis*; inside not rugulose, velvety, mostly densely to sparsely papillate especially towards mouth of tube, papillae each with a

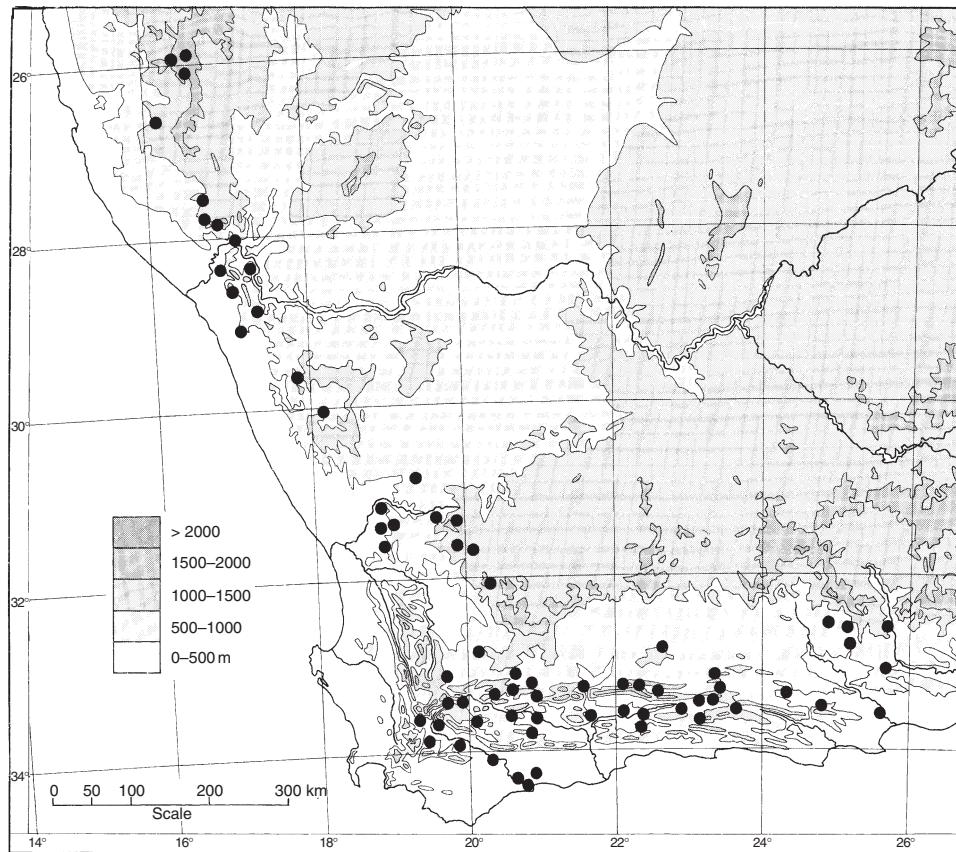


Figure 46. Distribution of *Stapeliopsis* in Southern Africa.

stiff apical seta, these setae usually becoming longer (up to 2 mm) towards base of corolla; tube making up most of length of flower and often narrowing strongly towards mouth; lobes usually considerably shorter than tube, sometimes joined at tips. CORONA raised on short obtusely pentagonal stipe above base of corolla-tube, glabrous outside except in *S. neronis*, consisting of two series of lobes; outer lobes < 1 mm long, emarginate, forming shallow pockets between bases of inner lobes and joined laterally to them (sect. *Cagelio-rona*) or 1–11 mm long and fused into cup from < half of length to exceeding inner lobes (sect. *Stapeliopsis*); inner lobes adpressed to anthers only near base, erect then connivent towards apices, 2–6 mm long, laterally flattened at least in lower half, usually with conspicuous rounded-deltoid dorsal process around middle. ANTHERS horizontal on top of style-head, margins shrinking back to expose pollinia, rectangular. POLLINIUM ellipsoidal, longer than broad, pellucid margin exactly along outer edge, caudicle attached with small \pm circular pad to base. FOLLICLES erect, teretefusiform, borne on considerably elongated pedicel, obclavate, slender, consisting of 2 horns diverging at 30–60°, longitudinally mottled with narrow broken purple stripes, glabrous, smooth.

Distribution and habitat: The species of *Stapeliopsis* are found in southern Namibia and western to southern South Africa. Here they occur mainly within and on the edges of the winter-rainfall zone (Figs 46, 50, 53). In Namibia, records exist from the northern side of the Tiras Mountains (south-west of Helmeringhausen) to the very arid country along the lower reaches of the Orange River. In South Africa records have been made from Namaqualand and the western mountainous edge of Bushmanland (where they are very few and scattered), from above the escarpment between Calvinia and Sutherland to the western edge of the Great Karoo. There are many records from the Worcester-Robertson and Little Karoos but the species become rare once more from Willowmore eastwards to Somerset East.

Plants are usually well hidden, growing under bushes where leaf-litter collects. They are rarely common, except sometimes in the case of *S. saxatilis*.

1. *Stapeliopsis breviloba* (R.A. Dyer) Bruyns, Cact. Succ. J. Gr. Brit. 43: 81 (1981). *Pectinaria breviloba* R.A. Dyer, J. S. African Bot. 20 (4): 155 (1954). *Neopectinaria breviloba* (R.A. Dyer) Plowes, *Excelsa* 20: 12 (2003). Type: South Africa, Cape,

KEY TO THE SPECIES OF *STAPELIOPSIS*

1. Stems papillate, basal stipe of gynostegium broader than rest of gynostegium, outer corona-lobes fused into tube so that anthers not visible from side. 2
2. Outside of corolla sparsely to densely papillate and dull, outer corona enclosing entire column 3
 3. Outside of corolla covered densely with sharp-pointed papillae, outer corona cylindrical with incurved flaps around its mouth 8. *S. neronis*
 3. Outside of corolla sparsely and minutely papillate, outer corona conspicuously broadening towards mouth and vase-shaped without incurved flaps around mouth. 7. *S. khamiesbergensis*
2. Outside of corolla glabrous and shiny, outer corona tube enclosing lower half of column, lobes bifid into small outward-pointing teeth 6. *S. urniflora*
1. Stems not papillate, basal stipe of gynostegium narrower than rest of gynostegium, outer corona-lobe reduced to small tooth between inner lobes and anthers visible from side 4
 4. Plant rhizomatous and underground stems without angles, above-ground stems with erect tips 5
 5. Stems 8–15 mm thick, corolla inside with conspicuous somewhat cylindrical papillae, lobes 6–16 mm long 5. *S. exasperata*
 5. Stems 4–7 (–9) mm thick, corolla inside ± devoid of papillae, lobes 2–3 mm long 1. *S. breviloba*
 4. Plant not rhizomatous and all portions obviously 4-angled and similar in shape, stems horizontal. 6
 6. Corolla thin, folds between lobes minute to absent, flowers above ground and produced facing upwards . . . 7
 7. Corolla with bristles only in lower half of tube, outside pale pink to whitish near base 3. *S. stayneri*
 7. Corolla with bristles over most of inside, outside wholly dark maroon to dark red 2. *S. saxatilis*
 6. Corolla thick and rigid, folds between lobes almost half as broad as lobes, flowers usually subterranean and produced facing horizontally or downwards. 4. *S. pillansii*

Twefontein near Worcester, fl. 1952, *v. Breda 183* (PRE, holo., K, iso.).

Dwarf rhizomatous succulent forming clump 30–80 (–150) mm diameter. STEMS 10–60 mm long, 4–7 (–9) mm thick, decumbent with horizontal portion sometimes spreading up to 150 mm or more underground, above-ground portions erect, glabrous, grey-brown, smooth; tubercles 1–2 mm long, conical, joined near base into 4 obtuse angles along stem, tapering to fine acute spreading tooth. INFLORESCENCE glabrous, usually developing near base of stem at level of soil or below from small often subterranean peduncle; pedicel 3–7 mm long, < 1 mm thick, spreading with ascending apex holding flower facing upwards; sepals ± 2.5 mm long, lanceolate, acute. COROLLA 10–13 mm long, 5.0–6.5 mm diameter, ellipsoidal (broadest near middle); outside glabrous, smooth, somewhat shiny pinkish-brown to reddish towards base; inside pale flesh-coloured around mouth of tube and lobes, below this merging into deep maroon-black, velvety-smooth, with bristles up to 1 mm long in lower half of tube, some arising from low rounded papillae; tube 8–10 mm long, narrowing towards mouth; LOBES 2–3 mm long, 2.0–2.5 mm broad at base, inflexed over mouth of tube, ascending towards and fused at tips, narrowly deltoid, acute. CORONA ± 3 mm tall, 2.5 mm broad, raised on white obtusely pentagonal stipe 0.5–1.0 mm long, deep maroon; outer lobes ± 0.5 mm long, ascending, truncate to finely denticulate, entire to emarginate, forming shallow pouch between bases of

inner lobes and fused laterally to them for entire length; inner lobes 2.0–2.4 mm long, erect then connivent at apices, laterally flattened becoming dorsiventrally flattened near obtuse slightly swollen tips, with obtuse and obscure spreading hump-like dorsal wing near middle (Figs 47, 53).

Always thought to be endemic to the Worcester–Robertson Karoo, *S. breviloba* is also known from a single collection from west of Swellendam. It is most plentiful between Worcester and Robertson especially on the south bank of the Breede River but many of the former localities have been destroyed by the burgeoning viticulture taking over much of this valley.

S. breviloba may be very rhizomatous, often with long, underground stems and short, erect pieces protruding from the soil. This seems to be the response to arid, stony conditions with shallow soils (as seen in some species of *Tromotriche* Haw., Bruyns, 1995): plants growing in more sandy situations where the surrounding vegetation is denser have longer stems above the soil aggregated into clumps and less tendency to spread underground.

When in flower *S. breviloba* is quite unmistakable. The flowers may be partially submerged and frequently arise from an underground peduncle. The exterior of the small, ellipsoidal corolla is pinkish-brown with numerous fine, longitudinal, translucent lines. The lobes are shorter than in any other species in the genus and always remain joined at the tips. Inside the flower is bi-coloured – pale around the mouth of the tube and lobes and deep maroon below

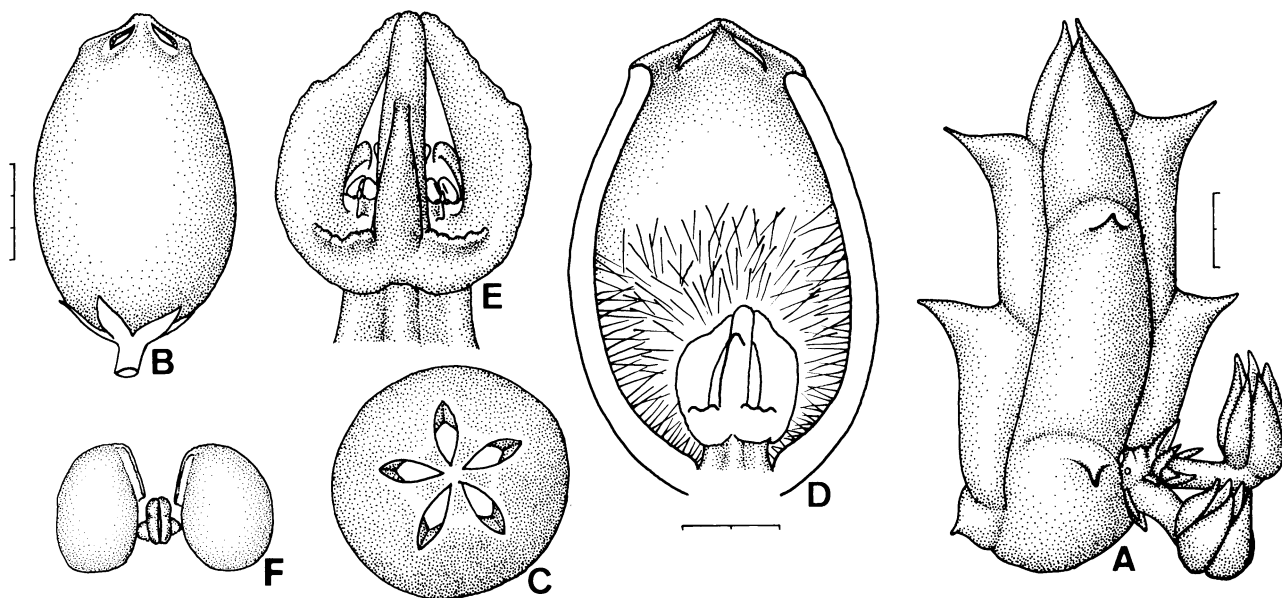


Figure 47. *Stapeliopsis breviloba*. A, young stem with inflorescence. B, side view of flower. C, face view of flower. D, dissected flower. E, side view of gynostegium. Scale bars: A = 2 mm; B, C = 3 mm (at B); D = 2 mm; E = 1 mm (at D). All drawn from PVB 1704 (MO, NBG).

to the base. There are many hairs in the lower half of the tube, a few of them arising from slightly raised papillae.

2. *Stapeliopsis saxatilis* (N.E. Br.) Bruyns, *Cact. Succ. J. Gr. Brit.* 43: 77 (1981). *Pectinaria saxatilis* N.E. Br., *Gard. Chron.* 35: 211 (1904). *Neopectinaria saxatilis* (N.E. Br.) Plowes, *Excelsa* 20: 12 (2003). Type: South Africa, Cape, Zout Kloof, Nov. 1902, *Pillans 115* (K, holo., BOL, iso.).

Pectinaria tulipiflora C.A. Lückhoff, *S. A. Gard.* 24: 101 (1934). *Neopectinaria saxatilis* var. *tulipiflora* (C.A. Lückh.) Plowes, *Excelsa* 20: 12 (2003). Type: Cape, Vanrhynsdorp at foot of Bokkeveld Mtns, *Lückhoff* (no preserved material).

Dwarf non-rhizomatous succulent forming mat up to 300 mm in diameter. STEMS 25–300 mm long, 8–25 mm thick, prostrate, glabrous, initially pale grey-green later often yellowish or reddish green sometimes speckled with purple-red; tubercles 2–5 (–8) mm long, broadly conical, slightly laterally flattened and joined near base into 4 acute angles along stem between which stem concave, tapering to sharp yellow-tipped conical spreading tooth. INFLORESCENCES glabrous, 1 (–3) per stem, with 1–10 flowers developing above surface of soil on knobbly peduncle up to 5 mm long; pedicel 3–12 mm long, 1 mm thick, ascending and holding flower facing upwards; sepals 2–3 mm long, 1 mm broad at base, ovate-lanceolate, acuminate, often with recurved tips. COROLLA

8–21 mm long, 6–11 mm in diameter, ellipsoidal to obovoid or obconical if lobes free; outside glabrous, ± shiny, dark maroon to dark red; inside velvety maroon, red to yellowish pink or pale pink, with many erect straight white bristles from near tips of lobes to near base of tube, towards the base some arising from low conical papillae; TUBE 6–15 mm long, 4–6 mm broad, cupular or widening towards mouth from narrow base, walls less than 0.5 mm thick; LOBES 4–9 mm long, 4–7 mm broad at base, ascending-connivent and fused at tips to ascending-spreading and free at tips, ovate-deltoid to narrowly deltoid, acute. CORONA 3–4 mm tall, 2–3 mm broad, raised on very short stout obtusely pentagonal stipe, shiny dark maroon to pale yellow; outer lobes < 0.5 mm long, ascending-spreading, truncate to emarginate, forming shallow pouch between bases of inner lobes and fused laterally to them for entire length; inner lobes 2.0–3.5 mm long, erect then connivent at apices, laterally flattened in lower half becoming ± terete and sometimes tuberculate above, usually with prominent to obscure obtuse ± deltoid dorsal projection near middle (Figs 33–36, 48, 50).

S. saxatilis is the most widespread species in the genus and from Worcester to Willowmore it is of fairly frequent occurrence. East of Willowmore it is found in a few isolated spots almost to Uitenhage and it also grows sporadically on the Ceres Karoo and northwards to the Hantam Mountains north-east of Calvinia and hillsides to about 50 km north of Nieu-

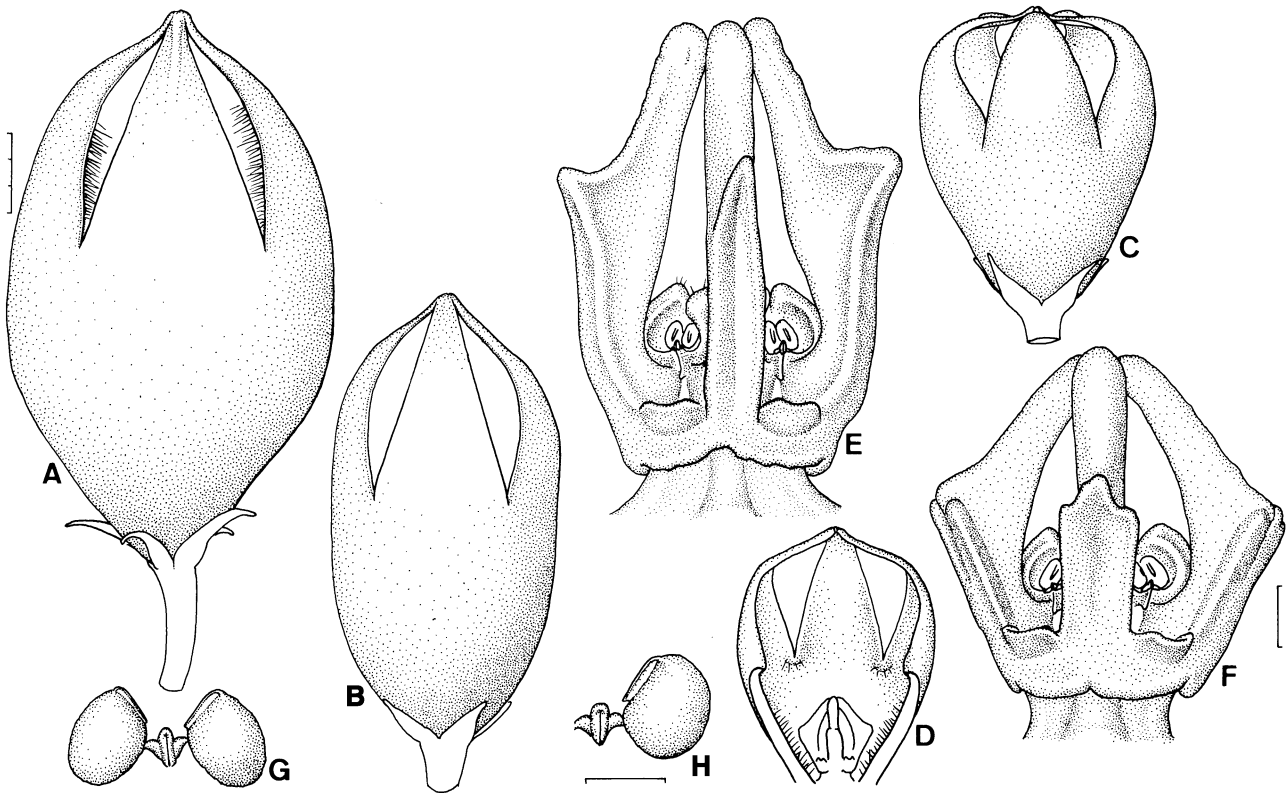


Figure 48. *Stapeliopsis saxatilis*. A–C, side view of flower. D, dissected flower. E, F, side view of gynostegium. G, H, pollinarium. Scale bars: A–D = 3 mm (at A); E, F = 0.5 mm (at F); G, H = 0.25 mm (at H). A, E and G drawn from PVB 2419 (NBG); B from PVB 2544 (BOL); C, D, F and H from PVB 2428 (NBG).

woudtville. It is almost always found on stony slopes and is especially associated with dense stands of *Crassula rupestris* Thunb., which is often the dominant plant on north-facing shale slopes on the Little Karoo. From the Anysberg and eastwards as far as the Groot Winterhoek Mountains around Cockscomb Peak it also grows in soils derived from sandstones. In these situations it is associated with *Crassula rupestris*, the small fern *Cheilanthes hirta* or grass tufts, growing in small pockets of soil among rocks or on outcrops. Plants in these situations have purple-mottled stems and rather weak points on the tubercles as well as distinctly more papillate stems (Figs 7, 8). Nevertheless, our results show that these are very closely related to the smooth-stemmed forms without surface mottling that are found on shale substrates.

With its prostrate stems and tubercles flattened into continuous angles along the stem, *S. saxatilis* is invariably identifiable even when sterile. Florally it is also distinctive but the shape of the corolla, its colour, the length of the lobes and especially the shape of the corona-lobes are all very variable. Many of the flowers emit quite a strong dung-like odour and this is the

only member of the genus where any odour has been detected.

3. *Stapeliopsis stayneri* (Bayer) Bruyns, Aloe 39: 82 (2003). *Pectinaria stayneri* Bayer, J. S. African Bot. 41 (3): 166 (1975). *S. saxatilis* ssp. *stayneri* (Bayer) Bruyns, Cact. Succ. J. Gr. Brit. 43: 79 (1981). *Neopectinaria stayneri* (M.B. Bayer) Plowes, *Excelsa* 20: 12 (2003). Type: Cape, about 8 km inland from Infanta on bank of Breede River, *Stayner sub KG 731/71* (NBG).

Dwarf non-rhizomatous succulent forming mat up to 300 mm in diameter. STEMS 25–300 mm long, 8–10 mm thick, prostrate, glabrous, initially pale grey-green later often yellowish or reddish green sometimes speckled with purple-red; tubercles 2–5 (–8) mm long, broadly conical, slightly laterally flattened and joined near base into 4 acute angles along stem between which stem concave, tapering to sharp yellow-tipped conical spreading tooth. INFLORESCENCES glabrous, 1 (–3) per stem, with 1–10 flowers developing above surface of soil on knobby peduncle up to 5 mm long; pedicel 3–12 mm long, 1 mm thick,

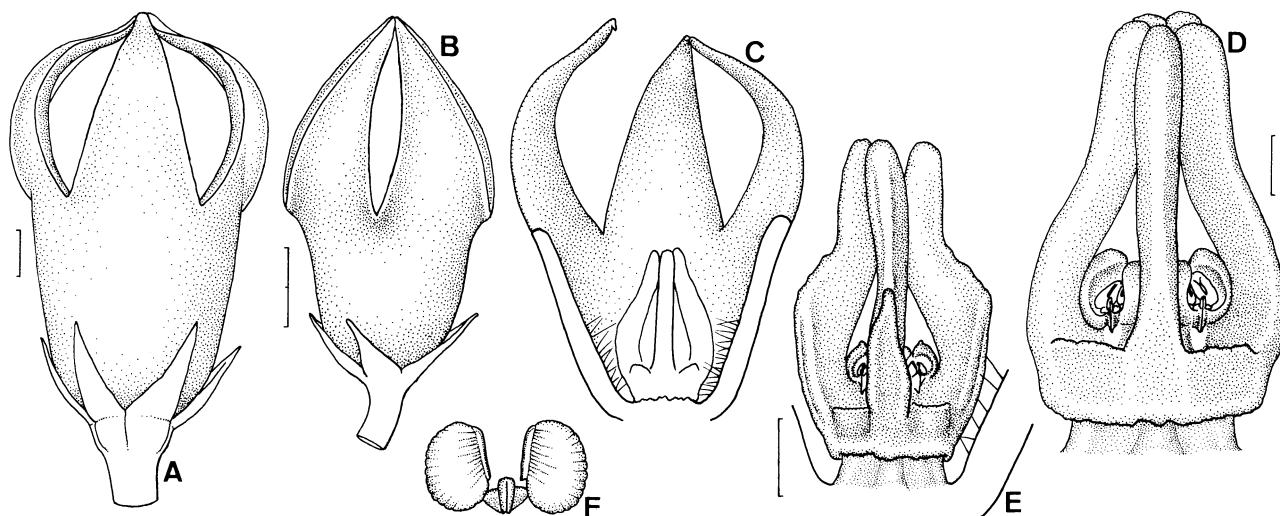


Figure 49. *Stapeliopsis stayneri*. A, B, side view of flower. C, dissected flower. D, E, gynostegium. F, pollinarium. Scale bars: A, C = 1 mm (at A); B = 2 mm; D = 0.5 mm; E = 1 mm; F = 0.25 mm (at E). A, C, D and F drawn from PVB 1262 (NBG); B and E from PVB 6262 (BOL).

ascending and holding flower facing upwards; sepals 2–3 mm long, 1 mm broad at base, ovate-lanceolate, acuminate, often with recurved tips. COROLLA 8.5–9.0 mm long, 5–6 mm in diameter, obconical and widest about half way down lobes; outside glabrous, ± shiny, dark flesh-coloured to pale pink becoming whitish near base; inside pink on lobes changing to pale yellow in lower half of tube, with many erect straight white bristles ± 0.5 mm long in lower half of tube only; tube 4–6 mm long, 3.0–4.5 mm broad, cupular but widening slightly towards mouth from narrow base, walls less than 0.5 mm thick; LOBES 4–6 mm long, ± 3 mm broad at base, occasionally united at tips, narrowly deltoid, acute. CORONA 3–4 mm tall, 2–3 mm broad, raised on very short stout obtusely pentagonal stipe, yellow becoming reddish towards tips of inner lobes; outer lobes < 0.5 mm long, ascending-spreading, truncate to emarginate, forming shallow pouch between bases of inner lobes and fused laterally to them for entire length; inner lobes 2.5–3.5 mm long, erect then connivent at apices, laterally flattened in lower half becoming ± terete above, dorsal projection ± absent (Figs 49, 50).

This species is found south of the Langeberg to the south and south-east of Swellendam and is restricted to the lower 20 km of the Breede River and a few patches along the Duiwenhoks River. It inhabits dry, rocky, usually steep, north- or east-facing shale slopes with *Crassula rupestris*, *Euphorbia heptagona* L. and other succulents. Such habitats form locally very arid, karroid enclaves surrounded by *renoster*.

S. stayneri is separated from *S. saxatilis* by the smaller, subcampanulate flowers with the widest

point of the flower about half-way down the lobes. The flowers are pale pink becoming whitish towards the base. A further distinction is found in the hairs inside the corolla-tube, which are present in only the lower half of the tube in *S. stayneri* and over most of the inside in *S. saxatilis*. As shown in Figure 45, it appears to be more closely related to *S. pillansii* than to *S. saxatilis*.

4. *Stapeliopsis pillansii* (N.E. Br.) Bruyns, Cact. Succ. J. Gr. Brit. 43: 81 (1981). *Pectinaria pillansii* N.E. Br., Fl. Cap. 4 (1): 869 (1909). *Neopectinaria pillansii* (N.E. Br.) Plowes, *Excelsa* 20: 12 (2003). Type: South Africa, Cape, Glen Avon Estate, Somerset East, July 1903, *Pillans 180* (BOL, K).

Dwarf non-rhizomatous succulent forming mat up to 150 mm in diameter. STEMS 20–150 mm long, 15–20 mm thick, prostrate, glabrous, grey- to purplish above, paler and often pinkish beneath; TUBERCLES 2–5 mm long, conical and joined into 4 obtuse angles along stem when young, later stem swelling to become ± convex between 4 rows of tubercles of which only an acute, hardened, pale yellow, spreading to slightly recurved tooth remains. INFLORESCENCES glabrous, 1 (–3) per stem, usually developing on underside of stems at or just below surface of soil on short knobby peduncle up to 5 mm long; pedicel 2–3 mm long, 1 mm thick, reddish, descending or spreading holding flower facing horizontally or downwards; sepals ± 2 mm long, ovate-lanceolate, acuminate, pinkish. COROLLA 6–10 mm long (7–) 12–14 mm in diameter, pear-shaped to campanulate; outside glabrous, smooth, red to maroon; inside red to maroon, with many erect

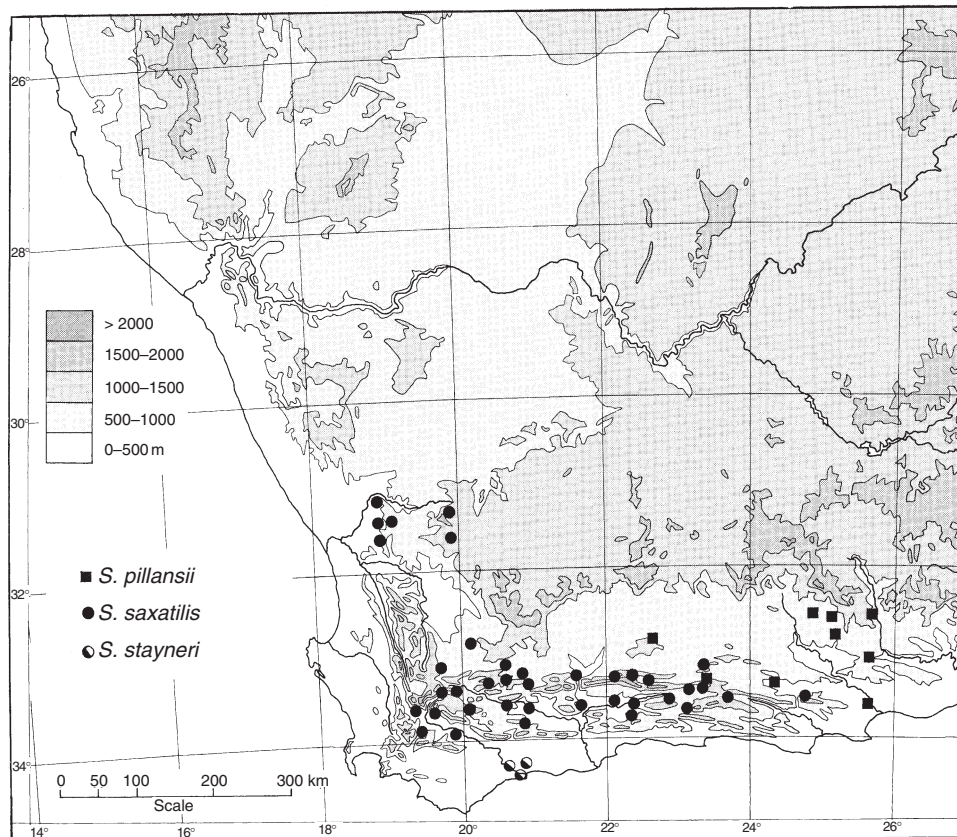


Figure 50. Distribution of *Stapeliopsis pillansii*, *S. saxatilis* and *S. stayneri* in Southern Africa.

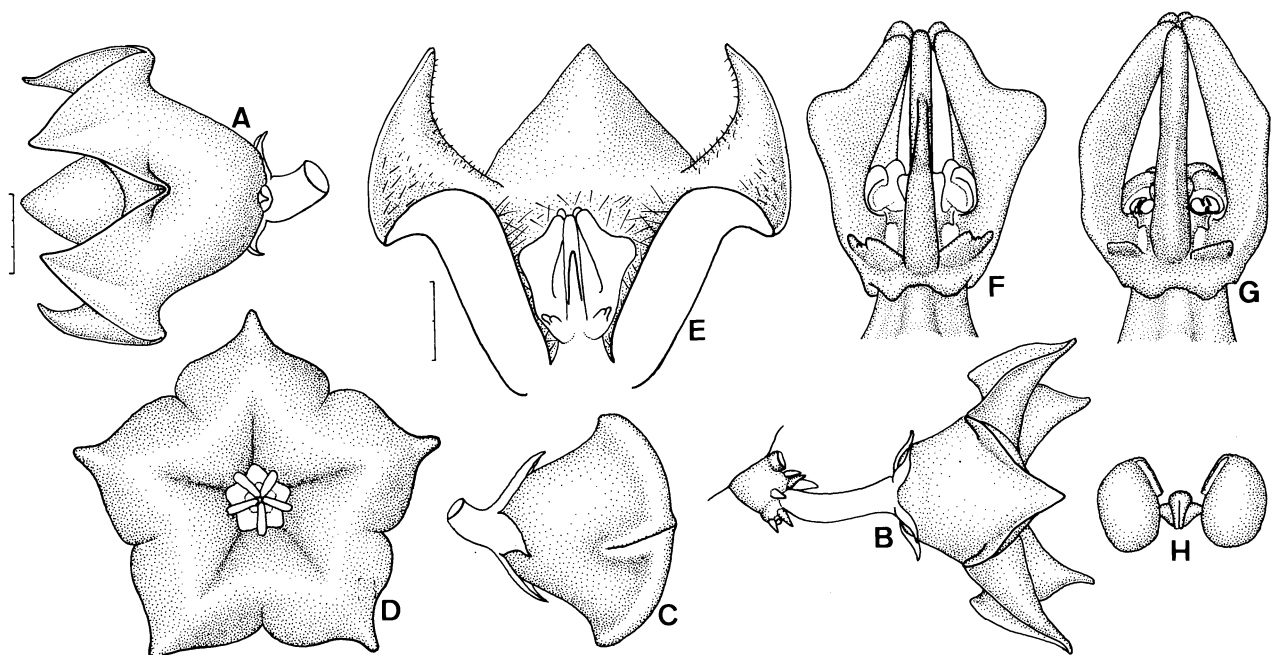


Figure 51. *Stapeliopsis pillansii*. A, B, side view of flower. C, bud. D, face view of flower. E, dissected flower. F, G, side view of gynostegium. H, pollinium. Scale bars: A–D = 3 mm (at A); E = 2 mm; F, G = 1 mm (at G); H = 0.25 mm (at G). C drawn from PVB 1805 (NBG); rest from PVB 1589 (NBG).

straight white bristles up to 0.5 mm long from tips of lobes to base of tube (longest around mouth) but without papillae; tube 2–4 mm long, \pm 4 mm broad, pentagonal, V-shaped with lower part closely enclosing base of gynostegium and stipe, walls 1.5–2.0 mm thick from near base to mouth; lobes \pm 4 mm long, 4–6 mm broad at base, ascending and remaining connate at tips to erect or widely spreading, deltoid, acute, thick and rigidly fleshy. CORONA 2.5–3.0 mm tall, \pm 3.5 mm broad, raised on stout obtusely pentagonal stipe \pm 1 mm long, dark maroon with blackish edges; outer lobes \pm 1 mm long, ascending-spreading, channelled above, narrowing slightly to truncate to emarginate apex, fused laterally to inner lobes only near base; inner lobes 2.3–3.0 mm long, erect then connivent at apices, laterally flattened becoming dorsiventrally flattened or terete near obtuse slightly swollen tips, with slight to prominent obtuse spreading \pm deltoid dorsal wing near middle (Figs 50, 51).

As seems to be typical in this genus, *S. pillansii* has a fairly wide distribution but is uncommon. It has been collected from west of Rietbron sporadically eastwards to near Somerset East, Kommadagga and Port Elizabeth. Plants are usually few at any one locality and have almost always been observed growing on low, stony ridges or flat gravelly areas under small shrubs which may be anything from *Lycium* L. or small composites to *Euphorbia ferox* Marl.

The prostrate fairly thick stems of *S. pillansii* resemble those of *S. saxatilis*. However, they have a harder, shinier epidermis with more conical, slightly recurved tubercles. The tubercles are fused into 4 angles along the stem when it is young but as they mature there remain only 4 rows of teeth along the stem without any sign of the tubercle-base. When turgid, the stem becomes convex while in *S. saxatilis* it remains somewhat concave.

S. pillansii mainly produces its flowers beneath the soil and only on lifting up a plant will they be seen. Flowering seems to be especially prolific in loose soil with a high leaf-mould content. Peduncles are produced on both the upper and the lower sides of the stem but usually only those on the lower surface mature to produce flowers. Unlike the other species, where the \pm urceolate flowers are erect, in *S. pillansii* the flowers are campanulate (if the lobes spread out) or more or less pear-shaped and are held horizontally or facing downwards. The entire flower is a deep maroon with the corona even darker and edged with blackish. This reddish colour continues into the pedicels and peduncle. Both the corolla-lobes and the rather pentagonal tube are unusually thick, rigid and fleshy. The combined molecular and morphological data show that this species is more closely related to *S. stayneri* than to *S. saxatilis*, though this relationship is not strongly supported.

5. *Stapeliopsis exasperata* (Bruyns) Bruyns, Cact. Succ. J. Gr. Brit. 43: 82 (1981). *Pectinaria exasperata* Bruyns, J. S. African Bot. 44 (2): 153 (1978). *Hermanschwartzia exasperata* (Bruyns) Plowes, *Excelsa* 20: 17 (2003). Type: South Africa, Cape, 20 miles north of Calvinia, *Bruyns 1345* (NBG).

Dwarf rhizomatous succulent forming clump to 150 mm in diameter. STEMS 10–60 (–100) mm long, 8–15 mm thick, decumbent, erect above soil often from horizontal subterranean runner up to 150 mm or more long, glabrous, grey-green, smooth (to naked eye); tubercles 2–4 mm long, conical, slightly laterally flattened and joined near base into 4 obtuse angles along stem, tapering to deltoid spreading tooth somewhat flattened above and subtended by two stipular denticles. INFLORESCENCES glabrous, 1–4 per stem, usually developing beneath surface of soil, each with 1–10 flowers; pedicel 2–5 (–10) mm long, 1 mm thick, spreading with ascending apex holding flower facing upwards; sepals 2–3 mm long, 1 mm broad at base, lanceolate, acute, often with recurved tips. COROLLA 16–28 (–32) mm long, 18–25 mm in diameter, \pm cylindrical with lobes spreading at mouth of tube; outside glabrous, smooth, pinkish-red to cream; inside pale pinkish to cream or white with dark maroon patch in base, with somewhat cylindrical obtuse bristly papillae on lobes (from base at least to middle) and in tube, largest around mouth of tube and base of lobes (becoming very short towards base of tube) each with an apical bristle, bristle increasing to 1 mm long towards base of tube; tube 10–18 mm long, 4–7 mm broad, cylindrical, often widest near base and narrowing slightly towards mouth; lobes 6–16 mm long, 2.0–4.5 mm broad at base, usually widely spreading but occasionally remaining fused at tips, lanceolate-acuminate, without thickening in corolla around mouth. CORONA 3.0–3.5 mm tall, 3–4 mm broad, raised on very short yellow obtusely pentagonal stipe, dark maroon; outer lobes ascending, broadly obtusely bifid near apex, < 0.5 mm long, forming shallow pouch between bases of inner lobes and fused laterally to them for entire length; inner lobes \pm 2.5 mm long, erect then connivent at apices, laterally flattened becoming dorsiventrally flattened near obtuse slightly swollen tips, with prominent obtuse spreading \pm deltoid dorsal wing near middle (Figs 52, 53).

This species is also widely distributed but only relatively few collections are known and our knowledge of this rare species remains patchy.

Vegetatively *S. exasperata* is distinctive. The horizontally spreading underground parts of the stems are thin and rounded. They become abruptly thicker just before emerging from the soil. The stem appearing above the surface is erect, square or pyramid-shaped, with small, deltoid teeth, each subtended by two obvi-

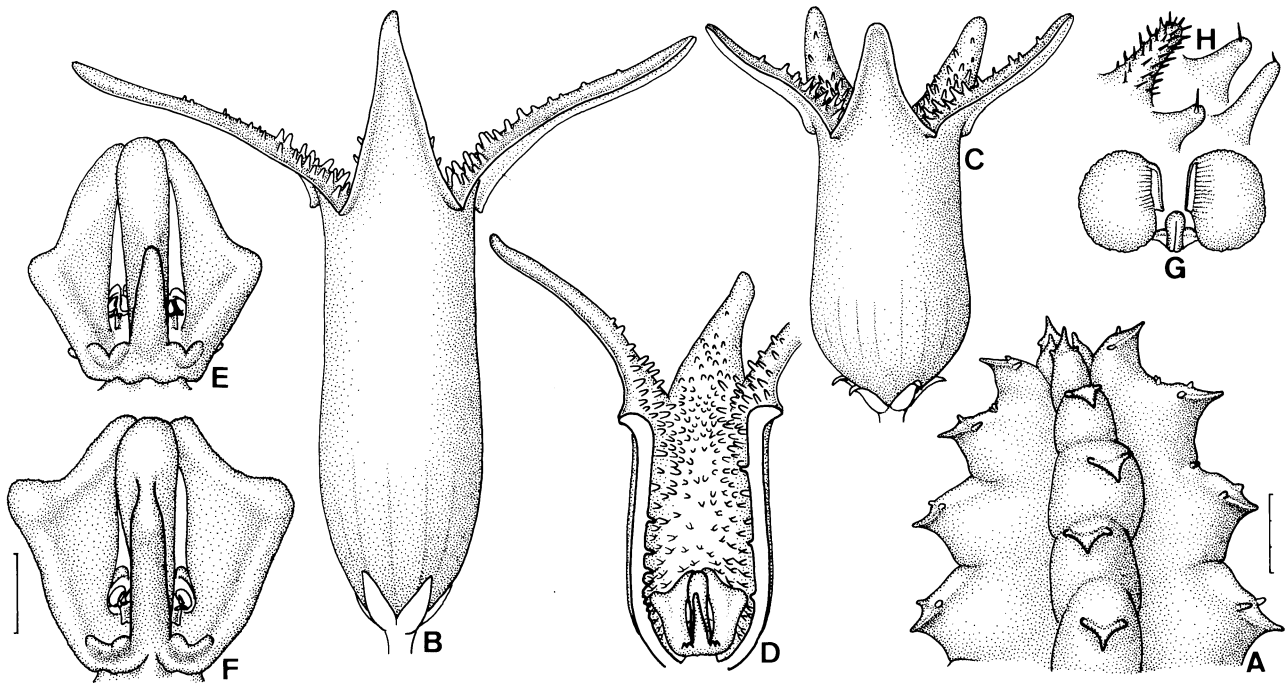


Figure 52. *Stapeliopsis exasperata*. A, apex of young stem. B, C, side view of flower. D, dissected flower. E, F, side view of gynostegium. G, pollinarium. H, papillae (three tall papillae from mouth of tube, all spinescent as in extreme left; shorter one from base of tube, not as spinescent as others). Scale bars: A–D = 3 mm (at A); E, F = 1 mm (at F); G, 0.25 mm (at F); H, 0.5 mm (at F). All drawn from PVB 1345 (NBG).

ous, stipular denticles. The peduncle arises beneath the soil and flowers may also be completely submerged but usually at least the lobes project from the ground rather like minute flowers of the parasitic genus *Hydnora*. Very occasionally the lobes are joined at their tips – normally they are free and spread out horizontally on the surface of the soil.

Florally *S. exasperata* could also not be confused with any other species: the lanceolate corolla lobes with prominent papillae on their inner surface and more or less cylindrical tube are sufficient to separate it from all others. As in *S. breviloba*, the inside of the tube is bi-coloured but in *S. exasperata* the dark patch is restricted to the base of the tube around the gynostegium. In this darker area the papillae are tipped with a slender, hair-like apical seta. Elsewhere the apical seta is not distinguishable from the other epidermal cells of the papilla, which are relatively long and lend the papillae a bristly appearance.

6. *Stapeliopsis urniflora* Lavranos, J. S. African Bot. 32: 195 (1966) as *urnaeflora*. Type: Namibia, Tiras Mtns, *Lofty-Eaton sub Lavranos 2536* (PRE).

Dwarf slightly rhizomatous succulent forming clump to 150 mm in diameter. STEMS 20–70 (–200) mm long, 6–20 mm thick, decumbent with horizontal (and often quite slender) portion sometimes spreading up to

60 (–100) mm underground, silvery green to green with dark green to purplish mottling, minutely papillate (glabrous to naked eye); tubercles 1–3 mm long, broadly deltoid, laterally flattened and joined near base into 4 narrowly obtuse angles along stem, tapering abruptly to minute conical tooth. INFLORESCENCE glabrous, usually developing at level of surface of soil or beneath it, with several lanceolate bracts up to 1 mm long on short broad peduncle (occasionally up to 30 mm long); pedicel 5–8 mm long, 1 mm thick, spreading then erect holding flower facing upwards; sepals 2.0–2.5 mm long, 1 mm broad at base, ovate-lanceolate, acuminate. COROLLA 9–18 mm long, 5–11 mm in diameter, ovoid with somewhat flattened base; outside glabrous, smooth, shiny purple-red; inside paler velvety (matt) purple-red, densely covered with conical obtuse papillae on inside of tube only, longest (up to 0.5 mm) towards mouth and shortest towards base, each with an apical bristle (very short in upper half of tube, up to 2 mm long in lower half); tube 6–16 mm long, 8–10 mm broad near base narrowing to 2.0–2.5 mm inside slightly thickened mouth, ovoid; lobes 2.0–3.5 mm long, 2.0–2.5 mm broad at base, erect to spreading, deltoid, acute. CORONA \pm 3 mm tall, 4.0–4.5 mm broad, raised on circular stipe \pm 1.5 mm long and 5–6 mm thick narrowing above into gynostegium, purplish red becoming yellowish at base of inner

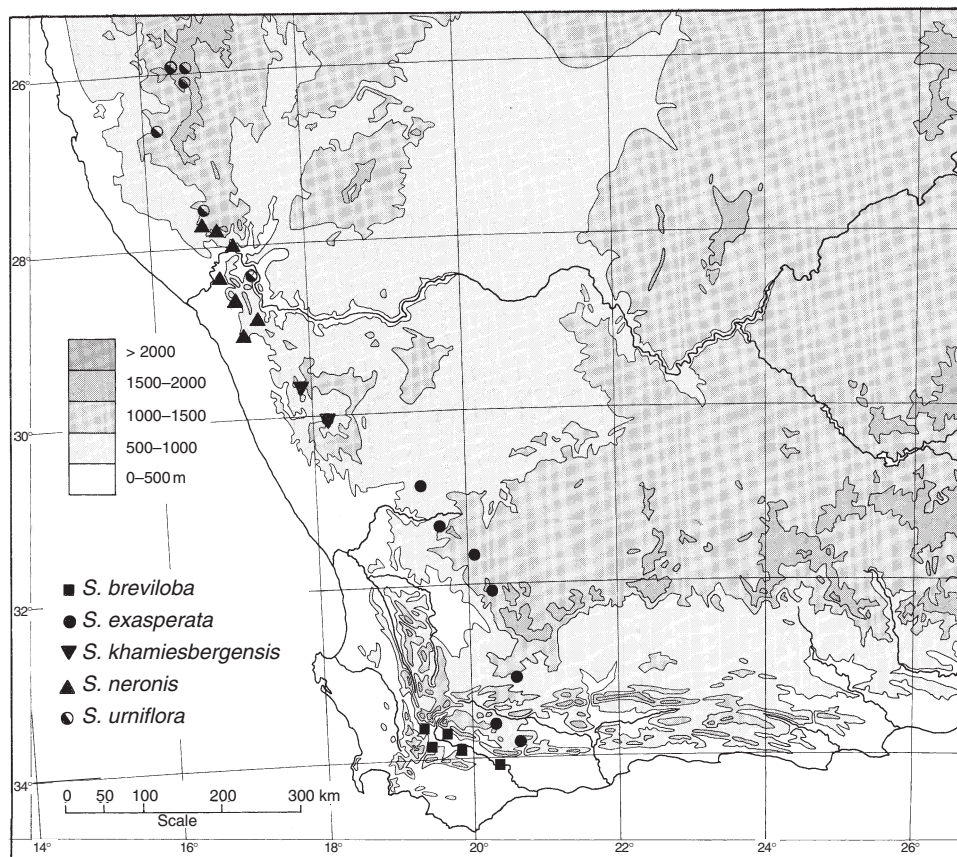


Figure 53. Distribution of *Stapeliopsis breviloba*, *S. exasperata*, *S. khamiesbergensis*, *S. neronis* and *S. urniflora* in Southern Africa.

lobes, glabrous; outer lobes 1.0–1.5 mm tall, fused laterally with sides of inner lobes into cylindrical to bowl-shaped tube 3 mm broad at base and 3.0–4.5 mm broad around mouth, with pairs of nearly erect to spreading deltate lobules 0.5–0.7 mm long alternating with inner lobes; inner lobes 2.0–2.3 mm long, erect then connivent at broadly obtuse apices, laterally flattened, slightly broadened in lower half but otherwise without dorsal appendage (Figs 53, 54).

Previously believed to be endemic to Namibia (Bruyns, 1981; Plowes, 1993), this very little-known species has been found to occur as far south as the northern Richtersveld. This gives it a fairly wide distribution but, like *S. exasperata*, it is very inconspicuous and so is almost certainly more common than the few and scattered records indicate. It mostly grows on granite or gneiss, sheltering between stones and under small bushes and grass tufts. The only area where it seems to be fairly plentiful is in the Tiras mountains south-west of Helmeringhausen.

Vegetatively one can usually tell *S. urniflora* and *S. neronis* apart. Stems of *S. neronis* are stouter and grow only on the surface of the soil. In *S. urniflora* the stems have a distinctly rhizomatous tendency and the

narrower underground portions are without obvious angles. Although they are also papillate and mottled, they have a somewhat silvery, slightly more shiny colour and the papillae covering them are finer so that they are glabrous to the naked eye and more or less smooth to the touch. The peduncle often arises beneath the soil. This and the rhizomatous habit clearly indicate its affinities with *S. exasperata*.

Florally *S. urniflora* is distinctive. The ovoid corolla is glabrous and shiny purple-red outside, inside matt and slightly lighter purple-red. It is not thickened at the mouth nor are the lobes different in colour from the remainder of the flower. The inside is covered with a forest of prominent papillae which, as usual, are larger towards the mouth of the tube and vanish towards the base. They are not found on the lobes at all. The gynostegium resembles that found in the species that have already been discussed, except for the fact that it is seated on a broad pedestal-like stipe.

7. *Stapeliopsis khamiesbergensis* Bruyns, *Aloe* 39: 82 (2003). Type: South Africa, east of Springbok, Bruyns 8249 (BOL).

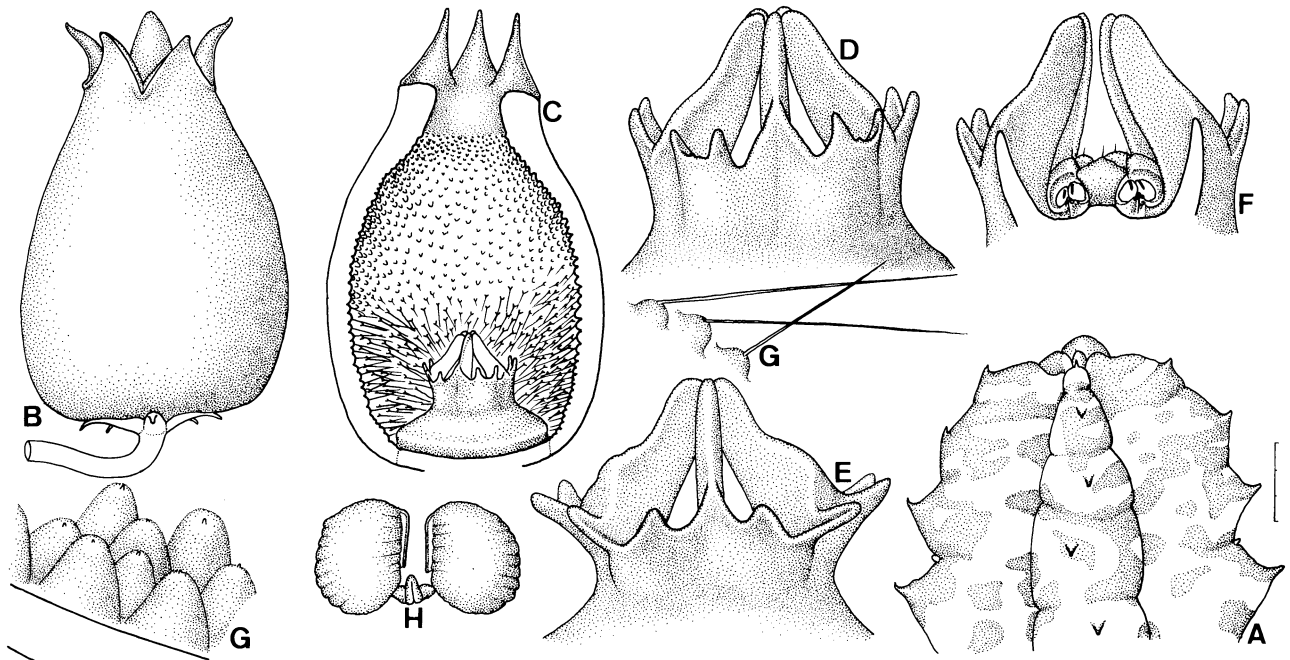


Figure 54. *Stapeliopsis urniflora*. A, apex of young stem. B, side view of flower. C, dissected flower. D, E, side view of gynostegium. F, dissected gynostegium. G, papillae inside corolla tube (those with long setae from base of tube; large papillae from just above middle of tube). H, pollinarium. Scale bars: A–C = 3 mm (at A); D–F = 1 mm (at A); G, 0.5 mm (at A); H, 0.25 mm (at A). E drawn from Nabibis, Tiras Mountains, Namibia, *Cumming 0225* (no specimen); rest from *PVB 1477* (K, NBG).

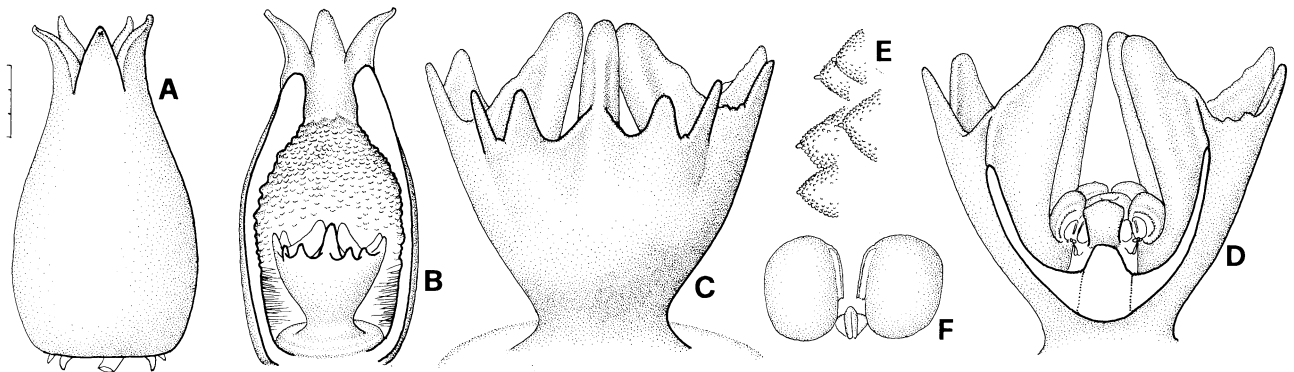


Figure 55. *Stapeliopsis khamiesbergensis*. A, side view of flower. B, side view of dissected flower. C, side view of gynostegium. D, side view of gynostegium with one inner and two outer corona-lobes removed. E, papillae inside corolla from just above middle of tube. F, pollinarium. Scale bars: A, B = 3 mm (at A); C, D = 1 mm (at A); E, 0.5 mm (at A); F, 0.25 mm (at A). All drawn from *PVB 8249* (BOL).

Small rhizomatous succulent to 300 mm in diameter. STEMS 30–200 mm long, 3–20 mm thick, decumbent with horizontal (and often very slender) portion spreading up to 100 mm underground, silvery green to green with purplish mottling, minutely papillate (glabrous to naked eye); tubercles 1–3 mm long, broadly deltoid, laterally flattened and joined near base into 4 narrowly obtuse angles along stem, taper-

ing abruptly to minute conical tooth. INFLORESCENCE glabrous, usually developing at level of surface of soil or beneath it, with several lanceolate bracts up to 1 mm long on short broad peduncle (occasionally up to 30 mm long); pedicel 2–3 mm long, 1 mm thick, purplish, spreading then sometimes erect, holding flower facing upwards or outwards; sepals 3 mm long, 0.5 mm broad at base, lanceolate, acuminate, with

spreading apices. COROLLA 10–12 mm long, 5–7 mm in diameter, urceolate with somewhat flattened base; outside finely papillate, dull purple-maroon; inside maroon in tube, reddish yellow on lobes, densely covered with conical obtuse papillae on inside of tube only, longest (up to 0.5 mm) towards mouth and shortest towards base, each with an apical bristle (very short in upper half of tube, up to 2 mm long in lower half); tube 10–12 mm long, 5–7 mm broad around middle narrowing to 2 mm inside slightly thickened mouth, ovoid; lobes 2.5 mm long, 1.5–2.0 mm broad at base, erect to spreading, deltoid, acute. CORONA 5 mm tall, 5 mm broad, raised on low circular stipe < 1 mm long and \pm 5 mm broad narrowing abruptly above into gynostegium, purplish red, glabrous; outer lobes \pm 3 mm tall, fused laterally with sides of inner lobes into vase-shaped tube < 2 mm broad at base widening to 5 mm broad at apex, with pairs of nearly erect deltate lobules 0.6 mm long at mouth of tube alternating with inner lobes; inner lobes 3 mm long, erect and then connivent at obtuse apices, laterally flattened, slightly broadened in lower half but otherwise without dorsal appendage (Figs 53, 55).

This new species is known only from the Khamiesberg. Two collections have been made in the vicinity of Springbok and it occurs as far south as north-east of Khamieskroon on the western edge of Bushmanland.

In both localities where they were observed around Springbok, plants of *S. khamiesbergensis* were seen growing in dense clumps of *Polymita albiflora* (L. Bol.) L. Bol. on low gneiss outcrops, with only the tips of the stems peeping out from among the twigs of the sheltering clump. The larger specimens of *Polymita* appear to be the most important nurse-plants in these hills, providing shelter for a range of small succulents belonging to genera such as *Adromischus* Lem., *Anacampteros* L., *Crassula* L., *Larryleachia* Plowes, *Stapelia* L. and *Stapeliopsis*.

S. khamiesbergensis is, for the most part, vegetatively indistinguishable from *S. urniflora* in that the stems are similarly coloured and of similar dimensions. In *S. khamiesbergensis*, however, the basal horizontal part of the stem can be remarkably slender and is often considerably longer than has ever been observed in *S. urniflora*.

It is in subtle features of their flowers that these two species are most clearly distinct. In *S. urniflora* the exterior of the flower is always shiny and smooth whereas in *S. khamiesbergensis* it is dull and papillate and, in this respect, the surface is more like that in *S. neronis*. In addition, the inside of the corolla-lobes is reddish yellow and different in colour from the rest of the inside of the tube, rather than the same purple-red as the rest that one finds in *S. urniflora*. Again in this respect, *S. khamiesbergensis* is reminiscent of *S. neronis*. In *S. khamiesbergensis* the vase-shaped tube

formed by the outer corona is considerably more substantial than that in *S. urniflora*. In *S. khamiesbergensis* it is about 3 mm tall and expands from quite a slender base, whereas in *S. urniflora* it does not exceed 1.5 mm tall and is often cylindrical. Our combined molecular and morphological data show that it is most similar to *S. urniflora*.

8. *Stapeliopsis neronis* Pillans, S. African Garden. & Country Life 18: 32 (1928). Type: South Africa, Cape, Richtersveld, Annisfontein, October 1926, Pillans 5728 (BOL).

Small non-rhizomatous succulent forming clump 100–300 mm in diameter. STEMS 40–150 (– 300) mm long, 20–35 mm thick, decumbent, blue-green mottled with purple, minutely pubescent; tubercles 1–4 mm long, broadly deltoid, laterally flattened and joined into 4 narrowly obtuse angles along stem, tapering abruptly to minute conical tooth. INFLORESCENCE minutely pubescent, arising near base of stem on peduncle gradually elongating to 10 mm or more, with lanceolate bracts < 2 mm long; pedicel 5–10 mm long, \pm 2 mm thick, spreading then erect holding flower facing upwards; sepals 2–4 mm long, ovate-lanceolate, acuminate, with recurved apices. COROLLA 17–28 mm long, 11–16 mm in diameter, ellipsoidal to nearly spherical (narrowing \pm equally to both ends); outside finely pubescent with acute papillae, deep purple usually with many darker longitudinal veins; inside velvety white on lobes and mouth of tube, deep purple below, densely covered with conical obtuse papillae on inside of tube only, longest (< 0.5 mm) towards mouth and disappearing towards base, each with apical bristle (very short in upper half of tube, up to 1.25 mm long towards base); tube 12–24 mm long, 13–15 mm broad at middle narrowing to 1.0–1.5 mm inside very much thickened mouth, ellipsoidal; lobes 4–5 mm long, \pm 3 mm broad at base, erect to slightly spreading, narrowly deltoid, acute, very much thickened at base, with margins somewhat folded back so that inner surface strongly convex. CORONA 7–11 mm tall, \pm 5 mm broad, raised on circular stipe \pm 2 mm long and 5–6 mm broad (only slightly broader than outer coronal tube near base), dark purple; outer lobes 7–11 mm tall, fused into erect cylinder \pm 5 mm broad which entirely hides rest of gynostegium, with 5 incurved broadly obtuse to emarginate flaps at mouth alternating with inner lobes, outside of cylinder finely setose towards base, inside smooth with 5 longitudinal ridges joining towards base to dorsal surface of inner lobes; inner lobes 4.5–6.0 mm long, erect then connivent in upper half, laterally flattened, linear, tapering to slender terete obtuse apex, dorsally broadened towards base and for \pm lower 1.5 mm fused there to sides of outer corona-tube (Figs 29–32, 53, 56).

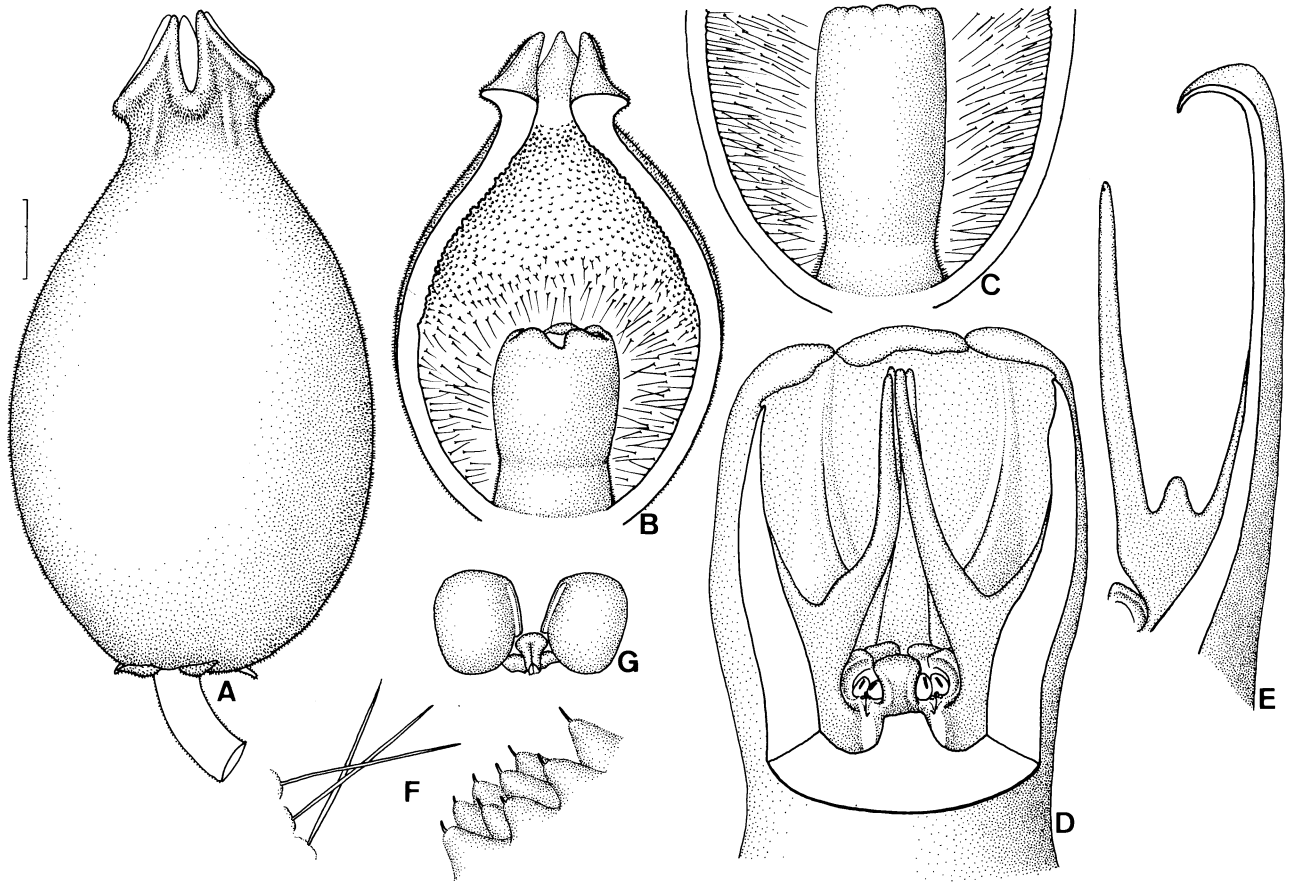


Figure 56. *Stapeliopsis neronis*. A, side view of flower. B, C, dissected flower. D, E, dissected gynostegium. F, papillae inside corolla: those with long seta from base of tube, large papillae from just beneath mouth of tube. G, pollinarium. Scale bars: A–C, 3 mm; D, E, 1 mm (at A); F, 0.5 mm (at A); G, 0.25 mm (at A). A, B and D drawn from PVB 1385 (NBG); C, E, F and G from PVB 2818 (BOL).

S. neronis is rare and known from relatively few collections. It has been found in the mountains just north of Rosh Pinah and scattered localities are known to as far south as Lekkersing.

S. neronis occurs mainly on steep slopes among the highly succulent vegetation (nearly entirely succulent Aizoaceae and Crassulaceae) that covers the western aspects of the mountains of the Richtersveld facing the sea.

The square, stout, velvety stems with their blue-green background colour mottled with purple are some of the most distinctive and beautiful among the stapeliads. This colour enables them to blend in well with their surroundings and, despite the plant reaching a diameter as large as one-third of a metre, it can be extremely inconspicuous. The stems also often become covered with mud splashed onto them by rain and this further adds to their camouflage.

The almost perfectly ellipsoidal flower with tiny lobes at its apex is just as remarkable and striking as

the stems. The exterior has a velvety appearance caused by an indumentum of small, acute setae. The mouth is considerably thickened so that there is only a narrow, cylindrical entrance to the cavernous interior. Although most of the flower, both inside and outside, is deep purple, the inside of the lobes and this narrow entrance are white. *S. neronis* has a singular, cylindrical outer corona (Figs 32, 56) and it was on this character that Pillans established the genus in 1928. Such highly evolved outer coronas are found randomly throughout the tribe: *Brachystelma gymnopodium* (Schltr.) Bruyns, various species of *Echidnopsis* Hook. f. such as *E. ballyi* (M.-Lapostolle) P.R.O. Bally and *E. malum* (Lavranos) Bruyns and in the two species of *Tavaresia* Welw. They are usually associated with tubular flowers. Among all of these, that of *S. neronis* is the longest relative to its breadth. The inner corona-lobes are rather frail and do not succeed in emerging from within this massive outer corona, which therefore has to be dissected to see them. They

have the typical laterally flattened, erect shape for the genus, occasionally with a small, dorsal lobule and are fused, also dorsally, to the sides of the outer coronal cylinder.

DOUBTFUL AND EXCLUDED NAMES

Pectinaria villetii C.A. Lüekh., *nom. nud.*
Stapeliopsis ballyi M.-Lapostolle = *Echidnopsis ballyi*
 (M.-Lapostolle) P.R.O. Bally
Stapeliopsis cooperi (N.E. Br.) E. Phillips = *Orbea cooperi* (N.E. Br.) L.C. Leach
Stapeliopsis madagascariensis Choux = *Stapelianthus madagascariensis* (Choux) Choux.

REFERENCES

- Baldwin BG. 1992.** Phylogenetic utility of the internal transcribed spacers of nuclear ribosomal DNA in plants: an example from the Compositae. *Molecular Phylogenetics and Evolution* **1**: 3–16.
- Brown NE. 1907–9.** Asclepiadeae in Thistleton-Dyer. *Flora Capensis* **4**: 518–1036. London: Lovell Reeve
- Bruyns PV. 1979.** Some observations on *Pectinaria breviloba* R.A. Dyer. *Asclepiadaceae* **18**: 7–9.
- Bruyns PV. 1981.** A review of *Pectinaria* Haw., *Stapeliopsis* Pillans and a new genus, *Ophionella* (Asclepiadaceae). *Cactus and Succulent Journal of Great Britain* **43**: 61–83.
- Bruyns PV. 1988.** A revision of the genus *Echidnopsis* Hook.f. (Asclepiadaceae). *Bradleya* **6**: 1–48.
- Bruyns PV. 1993.** A revision of *Hoodia* and *Lavrania* (Asclepiadaceae–Stapelieae). *Botanische Jahrbücher für Systematik* **115**: 145–270.
- Bruyns PV. 1995.** A re-assessment of the genera *Tridentea* Haw. & *Tromotriche* Haw. *South African Journal of Botany* **61**: 180–208.
- Bruyns PV. 1999a.** A systematic analysis with notes on the taxonomy of *Notechidnopsis*. *Kew Bulletin* **54**: 327–345.
- Bruyns PV. 1999b.** A systematic assessment of *Ophionella*. *Botanical Journal of the Linnean Society* **131**: 383–398.
- Bruyns PV. 1999c.** The systematic position of *Quaqua* (Apocynaceae–Asclepiadoideae) with a critical revision of the species. *Botanische Jahrbücher für Systematik* **121**: 311–402.
- Bruyns PV. 2000a.** Phylogeny and biogeography of the stapeliads. 1. Phylogeny. *Plant Systematics and Evolution* **221**: 199–226.
- Bruyns PV. 2000b.** Phylogeny and biogeography of the stapeliads. 2. Biogeography. *Plant Systematics and Evolution* **221**: 227–244.
- Gawel NJ, Jarret RL. 1991.** A modified CTAB DNA extraction procedure for *Musa* and *Ipomoea*. *Plant Molecular Biology Reporter* **9**: 262–266.
- Meve U, Albers F. 1990.** Die Stipularrudimente der Stapelieae. *Beiträge zur Biologie der Pflanzen* **65**: 99–107.
- Meve U, Liede S. 2002.** A molecular phylogeny and generic re-arrangement of the stapelioid Ceropegieae (Apocynaceae–Asclepiadoideae). *Plant Systematics and Evolution* **234**: 171–209.
- Plowes DCH. 1993.** Two new stapeliads from Namibia and variation in *Hoodia gordonii*. *British Cactus and Succulent Journal* **11**: 56–59.
- Plowes DCH. 2003.** An examination of *Stapeliopsis* Pillans, *Pectinaria* Haw. and *Ophionella* Bruyns: Ceropegieae (Asclepiadoideae). *Excelsa* **20**: 1–20.
- Swofford DL. 1998.** *PAUP*: phylogenetic analysis using parsimony (*and other methods)*, Version 4. Sunderland, MA: Sinauer.
- Taberlet P, Gielly L, Pautou G, Bouvet J. 1991.** Universal primers for amplification of three non-coding regions of chloroplast DNA. *Plant Molecular Biology* **17**: 1105–1109.
- Vogel S. 1954.** Blütenbiologische Typen als Elemente der Sipplgliederung. *Botanische Studien* **1**.
- Vogel S. 1961.** Die Bestäubung der Kesselfallenblüten von *Ceropegia*. *Beiträge zur Biologie der Pflanzen* **36**: 159–237.