

A revision of Hoodia and Lavrania (Asclepiadaceae – Stapelieae)

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Abstract

Hoodia Sweet ex Decne is revised to contain 13 species which are divided into 2 sections. Sect. Hoodia contains H.currorii, H.dregei, H.gordonii, H.juttae and H.parviflora. Sect. Trichocaulon contains H.alstonii, H.flava, H.mossamedensis, H.officinalis, H.pedicellata, H.pilifera, H.ruschii and H.triebneri, all except H.ruschii formerly constituting the section "Eutrichocaulon", the so-called "spiny" species of Trichocaulon. The remainder of Trichocaulon, the section Cactoidea, is transferred to Lavrania Plowes. This genus then consists of the monotypic section Lavrania (L.haagnerae) and Sect. Cactoidea containing L.cactiformis, L.marlothii, L.perlata and L.picta.

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INTRODUCTION

Problem studied

The delimitation of the genera Hoodia Sweet ex Decne and Trichocaulon N.E. Br. have not been re-assessed since they were revised by N.E. Brown (1909) despite the addition of many new species. In addition, Brown placed two vegetatively quite different groups of species in Trichocaulon as he could find no structural difference in their flowers. In this thesis the correct boundary between Hoodia and Trichocaulon is investigated with special consideration given to the vegetative variation.

Theoretical background (1) Species concepts

To decide whether two groups of individuals belong to the same species one needs to have a definition of "species". A precise mathematical definition of this concept does not exist, nor is there unanimity among biologists as to how one ought to define it. Two definitions appear to attract the largest number of adherents (Wiley, 1981).

One is the "biological species concept", where a biological species is defined as a maximal reproductive unit (i.e. the largest possible group of individuals among whom reproduction could take place). The second is the "evolutionary species concept" (see Wiley, 1981, p. 25) which groups individuals that have both a common ancestry ("history of descent") and maintain their identity from other such lineages (i.e. have a unique phylogeny).

While these concepts are philosophically interesting, they are of limited use in deciding what constitutes a species. Nevertheless, indirectly one does apply them: implicit in the search for morphological similarities or differences between individuals is the

assumption (albeit sometimes inaccurate) that phenetically sufficiently similar individuals will interbreed and different ones will not i.e. a discontinuity in the range of a morphological character implies the lack of gene flow. Similarly (and also sometimes inaccurately) one tends to assume that individuals sharing a unique common past history will be morphologically similar and vice versa (i.e. applying the evolutionary species concept).

In practise it is clear that one is dealing with two species when their respective phenotypes differ by two or more consistently different characters (Hedberg 1958). It is in cases where the phenotypes of two groups of individuals differ by one character (which in addition may not always be consistently different) that problems arise. Here two criteria proved to be especially useful. The first is as follows: if two groups of apparently distinct individuals are sympatric, to what extent do they maintain their distinctness in the region of distributional overlap? As Wiley (1981) points out, hybridization may well occur but the question is to what extent the two groups maintain their ecological and evolutionary discreteness. In several closely-related species covered in the present work, partial or complete sympatry has been observed: Hoodia gordonii and H. juttae exhibit complete sympatry with no hybridization at all; H. gordonii and H. currorii exhibit partial sympatry with no hybrids in evidence; Lavrania picta, L. cactiformis also exhibit partial sympatry with no hybridization. Thus in all these cases there is a reproductive barrier between the taxa and these are therefore cases where the biological species concept may be applied.

The second is that continuity in variation in individual characters is important in grouping individuals into species: to delimit species it is important to identify discontinuities in variation (Wiley, 1981, p. 61). I have tried to apply the "field taxonomy" approach advocated by Du Rietz (1930), studying species extensively in the field to compare variation within a population and between populations. This relatively

wide sampling has led me to take a broad view of species, especially in the case of widespread ones like Hoodia gordonii and H.currorii. In general I have maintained as separate species those groups of individuals differing by two or more characters. The only case where two species differ by a single character (shape of corona) is in H.gordonii and H.juttae. Here the peculiar nested distribution of the latter within the distribution of the former and my inability to locate any signs of intergradation between these taxa (despite encountering populations of both flowering simultaneously) has led me to maintain them as separate species.

(2) Supraspecific concepts

At levels above that of species the aim of the taxonomist is to discover the "natural" groupings of species. What is meant by a "natural" system? In the past, naturalness has been determined by an examination of characters and a group of species is said to constitute a "phenetically natural taxon" if all the members are more similar to each other than to anything not included in the group (Davis & Heywood, 1965). One of the problems with phenetic naturalness is that it fails to separate groups which are held together by primitive character states and no derived characters i.e. paraphyletic taxa are not necessarily distinguished. This has led to the development of the concept of the "phylogenetically natural taxon". Such a taxon is one in which the species included share a common ancestor that is not an ancestor of any other group (Wiley, 1981). Thus one arrives at a kind of naturalness defined by genealogy which, unlike characters, cannot be directly observed but must be inferred.

Generally, more is required of a supraspecific taxon: it should be both

phylogenetically natural containing all the descendents of the most recent common ancestor as well as supported by one or more unique derived characters (synapomorphies). Such a taxon is termed monophyletic (Wiley, 1981). It is shown below that the group containing Hoodia and Lavrancia is monophyletic and that this is true of each of these genera as well.

HISTORICAL BACKGROUND

The first species of Hoodia known to science was H.pilifera subsp. pilifera. This appears to have been gathered by Thunberg and Masson between 1772 and 1774 on the Little Karoo north of Mossel Bay and was described in 1781 as Stapelia pilifera. The first Lavrania was collected by William Paterson on 6 or 7 September 1778, probably at Geselskapbank a little south-west of Goodhouse (N.E. Brown 1909, p. 895). Although not seen in flower, this plant was nevertheless described (as Stapelia clavata) as it had a very unusual and distinctive shape. Just a year later, in 1779, Robert Gordon encountered a Hoodia during his journey from Kamieskroon to Pella and Prieska to explore the Orange River for the second time (Gunn & Codd 1981). A figure of this, reputedly by Gordon, was published by Masson in his Stapeliae Novae of 1796, where it was described as Stapelia gordonii.

In 1826, among his first list of plants cultivated in England, Robert Sweet moved Stapelia gordonii tentatively to Gonostemon Haw. He was apparently unhappy about this and, in the 2nd edition of 1830, he moved it to a new genus Hoodia, named after a Mr Hood who was a well-known contemporary grower of succulents in Britain. George Don, apparently unaware of Sweet's name, placed Stapelia gordonii in a new genus Monothylaceum in 1837.

In the meantime the botanical exploration of southern Africa continued and the next person to gather a Hoodia was J. Franz Drège who discovered the rare Hoodia dregei in 1827. Somewhat later Hoodia currorii was collected by the royal navy doctor A.B. Curror. Curror's collections were made during a stop of his ship at the Bay of Elephants in southern Angola in 1840 and were the first documented botanical material to reach Europe from Angola (Mendonssa 1937). Material of Curror's Hoodia was grown at Kew and it was on this that Hooker based his genus Scytanthus of 1844. With the arrival of Friedrich

Welwitsch in Angola in 1853, botanical investigation of this country received an enormous impetus. In the Mossamedes district on 23 rd August 1859, he encountered Hoodia parviflora. He had already discovered the extraordinary gymnosperm Welwitschia and this enormous stapeliad with stems 4–7 feet tall and Cereus-like appearance (Hiern 1898, p.697), which he saw in several places, must have been scarcely less surprising.

The period 1870–77, while Sir Henry Barkly was governor at the Cape of Good Hope, saw a resurgence of interest in stapeliads in Britain. He sent much material, generally collected by other travellers in the interior of South Africa, back to N.E. Brown at Kew who had a special interest in this group of plants. Among Barkly's specimens were several hoodias. Some of these were older species such as H.gordonii but two others were described by W.Thistleton–Dyer as H.barklyi and H.bainii. Among them were also two small-flowered taxa: H.flava and possibly H.officinalis. Brown also at much the same time saw part of Thunberg's Herbarium. Here he found the very fragmentary type of Stapelia pilifera and he decided to place this in a new genus Trichocaulon which he based on Barkly's material of T.flavum. In his account of 1890 of Barkly's stapeliads, Brown extended the definition of Trichocaulon to include Paterson's Stapelia clavata. By then a few more collections of such odd plants as Paterson's had appeared. Carl Zeyher collected a similar plant between 1829 and 1831 (probably in the coastal hills of Namaqualand, west of the escarpment), which flowered at Kew in 1844 and was described by W.J. Hooker as Stapelia cactiformis. Barkly also sent one collection to Kew. Brown assumed that these were the same species as Paterson's. It should be noted clearly that (contrary to the opinion of Plowes, 1990) Brown placed this species under Trichocaulon not because of the existence of the possibly intermediate Trichocaulon pedicellatum but because, despite the lack of spines on the tubercles, he could find "no structural character in the flowers to

justify its separation from that genus" (Brown 1890, sub t. 1905).

Around the turn of the century, when N.E. Brown was preparing for his accounts of the Stapelieae in the Flora Capensis and Flora of Tropical Africa, N.S. Pillans of the Bolus Herbarium and Rudolf Marloth began sending him material. Both collected extensively in Namaqualand and Bushmanland (Marloth also in Namibia) and Pillans also had many unusual plants brought to him by other collectors (Alston, Templeman etc.). Various species of Trichocaulon and Hoodia, several of which were described as new, were made known by their efforts. Pillans was a very careful collector who made ample and well-documented herbarium specimens often from plants cultivated in his garden in Rosebank. Marloth, on the other hand, was very casual both with preserving type material and with noting where specimens had been collected.

Botanical exploration of Namibia, especially of the central and northern parts, was quite independent of collecting activities in the Cape Colony. Little seems to have been collected there of interest until the geologist Friedrich M. Stapff visited the Hope Mine near Walvis Bay in 1885/6 when, among other things, he gathered Hoodia pedicellata. Many of the German settlers were interested in plants on a small scale but it was with the beginning of Kurt Dinter's botanical explorations in 1897 that the region began to become better known. Dinter had an considerable interest in succulents and he found plenty of hoodias and trichocaulons. He soon re-discovered Stapff's H.pedicellata and recorded Curror's H.currorii in Namibia for the first time. His extensive travels in the arid south led to several new species being discovered. Many of his discoveries are documented in his interesting and lively accounts of succulent hunting (Dinter 1923, 1928) but he also left a trail of nomina nuda just mentioned in these books and elsewhere and never validly published. Dinter very carefully preserved herbarium material of many of his collections

(this was part of his job) and his specimens of Hoodia flowers are especially beautifully preserved and widely distributed among herbaria. Areas where Dinter did not venture, such as the extreme north-west, have remained little-known and under-collected to this day. The efforts of W. Giess, over the last 40 years, have greatly improved this in many areas.

Unfortunately this century has seen a vast increase in accessibility of many of the drier areas of southern Africa which has led to large amounts of collecting for private and "public" collections. Remarkably little scientifically useful information has emanated from these collections. The general difficulty of cultivating these plants unless they are cared for with great skill leads to their surviving only briefly in captivity. White & Sloane (1937), for example, mention the enormous collection of hoodias and lavranias amassed by Wilhelm Triebner in Windhoek, Namibia. From this hardly a single herbarium specimen was made so that with the demise of the collection the large amount of potentially very useful and interesting information contained in it vanished without trace. The perennial mania for Lithops has also led to many lavranias being removed from habitat, for these often occur together with lithops but it has not helped at all towards improving the exceptionally poor herbarium record of this genus. Nevertheless, all this collecting has taken people into some unusual areas and this led D.T. Cole, who had a special interest in Trichocaulon, to describe a new species, T.felinum, in 1985. D. Plowes has tried to improve the general lack of records in the stapeliads and has deposited an extensive collection of spirit material in SRGH. This contains some useful data on Hoodia and Lavrania.

Perhaps the most unusual discovery recently was the serendipitous collection by P.Haagner of a piece of a stapeliad at the foot of cliffs in the Sesfontein district of northern Namibia. This single clone was later described as Lavrania haagnerae. I have succeeded

in recollecting this plant and extending its known distribution slightly. Closer observation has shown it to be far more similar to Trichocaulon than was previously realised and so this remarkable cremnophilous plant has been included within the scope of this work.

While this work was nearing completion a publication of Plowes (1992) appeared where many of the changes proposed here were pre-empted. While this article purports to revise the genera Hoodia and Trichocaulon, no type material appears to have been seen, no specimens are cited on which the author's conclusions were based and the genus Leachia Plowes therein described is a later homonym of Leachia Cassini of 1822.

METHODS and MATERIALS

This study is based largely on observations in the field and on material cultivated from these field collections. Herbarium material was seen from all the major southern African and most of the main European herbaria.

For SEM studies of the epidermis of stems and leaves several methods were tried but the most satisfactory was as follows, starting with fresh material. Pieces of stem approx. 5–10 X 5 mm were washed in chloroform for 5 mins to remove the wax covering. These were then placed in 100 % EtOH overnight, then placed in formaldehydedimethylacetal for ± 12 hours and then put in 100 % EtOH again after which they were put through the Critical Point Drying process in 100 % EtOH using CO₂ as carrier medium, Au/Pd coated and finally examined with a Cambridge S 200 microscope at 10 KV. Material examined in this manner (Bruyns collection numbers given) was:

Hoodia alstonii 4646

H.flava 3693

H.gordonii 3188

H.juttae 3526

H.officinalis subsp. officinalis 4178

H.parviflora 4084

H.pilifera subsp. annulata 4963

Lavrania cactiformis 4745, 4633

L.haagnerae 4069

L.marlothii 3475

L.perlata 3229b, 4648

COMPARATIVE ACCOUNT

Rootstock

The rootstock in Hoodia and Lavrania consists of numerous slightly fleshy white roots (\pm 1 mm diam., except in L.marlothii where they are usually 2–3 mm thick). In most hoodias there is a thicker central "tap root" developing from the radicle. This tap root and some of its thicker branches become woody and tough with age and may be as thick as 10 mm. Roots all arise directly from the base of the hypocotyl and in the field it is rare to find roots on any of the side branches (very occasional in Hoodia sect. Trichocaulon). However, virtually all species except H.alstonii root readily from cuttings, if these are taken at the base of a branch and then roots appear between the angles mainly around this basal area.

Stems

In H.pedicellata the stems frequently sprawl with age. In all other hoodias stems are erect to very shortly decumbent with branching mainly around the base. Each branch has a very short, horizontal portion after which it is erect and parallel to the other branches. They therefore exhibit an orthotropic growth form (Albers et al 1989, p. 69) and



Figure 1.—Hoodia parviflora in habitat NW of Opuwa, Namibia, among gneiss boulders.
This plant is 2 m tall (screwdriver at right hand base 450 mm long).

all species are pachycaulous. In Hoodia gordonii, H.curreorii, H.parviflora and H.alstonii they form formidable, thorny, cactus-like shrubs (Figure 1) often a metre or more in height and diameter (in H.parviflora sometimes slightly exceeding 2 m tall). In H.dregei and H.juttae of Sect. Hoodia and the remaining members of Sect. Trichocaulon the stems rarely exceed 0.5 m tall. In these species they are often also only few in a plant but may, as in H.pilifera subsp. annulata, still form large clumps (in this particular case sometimes as large as 2 m diam.) and all have a cactoid appearance (Figure 2B). The stems vary very much in thickness, even within a single species. Thus, for example, in H.gordonii, stems are usually 25–35 mm thick on the Ceres Karoo but in the Namib around Swakopmund are up to 50 mm thick. They are thickest in H.parviflora, the tallest species in the genus, where they may be up to 110 mm in diam. near the base. Large plants of this species are by far the most massive of all stapeliads.

In Lavrana the stems are usually 150 mm or less in height (Fig. 2A) and only occasionally reach 300 mm in L.perlata. In L.haagnerae they have a decumbent (semi-plagiotropic) habit but in the others they are erect, branching from the base (orthotropic). They are fleshy, soft and spineless but become remarkably hard when turgid after rain. In L.haagnerae they form large clusters of up to 100 or more stems. In the other species 1–6 stems per plant is more usual but single-stemmed plants are frequent. In exceptionally vigorous specimens up to 20 stems may develop. Stems vary from 20–30 mm thick in L.haagnerae to 60 mm thick in the other species. Except for L.haagnerae, these plants exhibit a highly specialized, roughly "spherical" growth form (Albers et al 1989, p. 67).

The stems in all lavranias and hoodias are covered with tubercles, each of which bears a leaf. In Hoodia the tubercles are raised, conical, laterally flattened and joined into long narrow rows ("angles") running longitudinally up the stem with the channels between

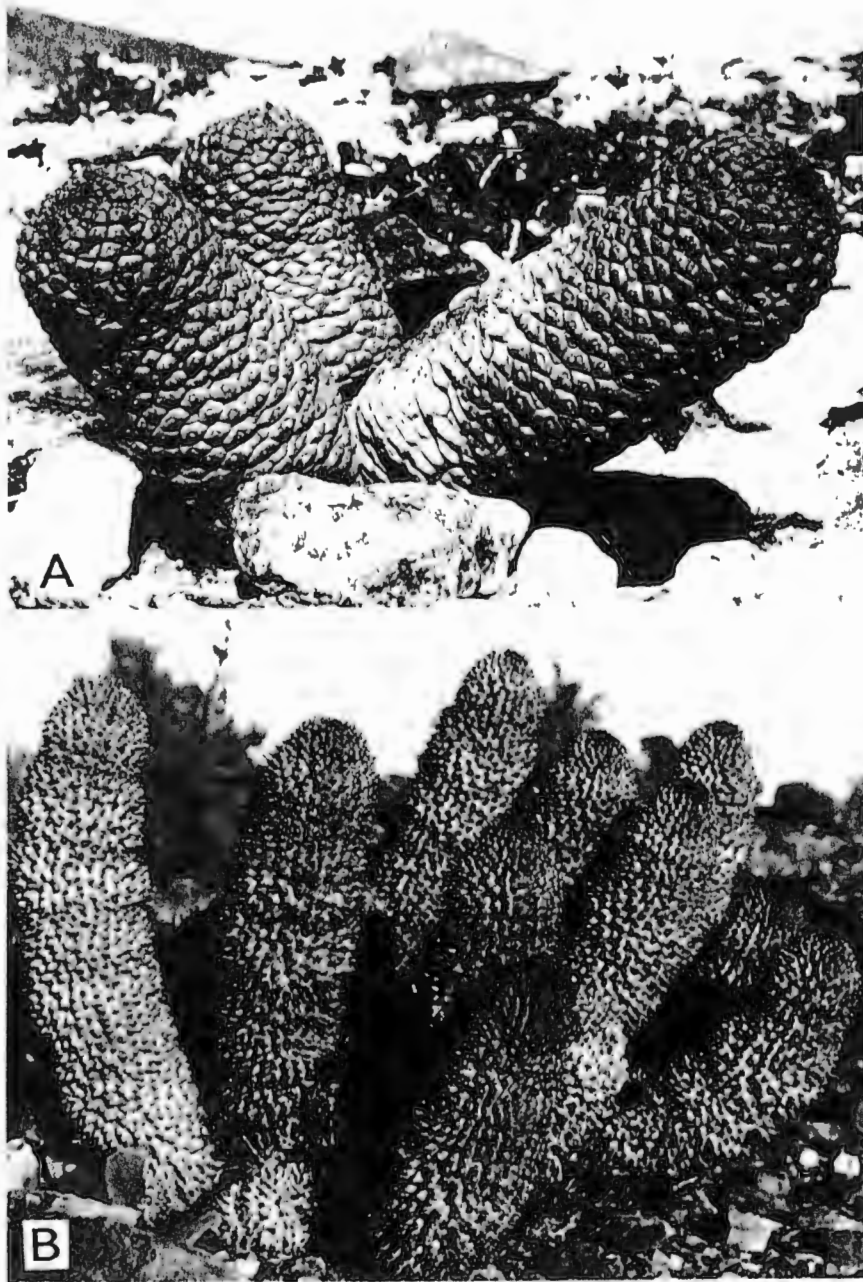


Figure 2.—A, *Lavrania picta* subsp. *picta* in habitat growing fully exposed on quartz patch just east of Witpütz, Namibia. The longest stem is 150 mm long and has been somewhat burnt by the sun on its upper surface. B, *Hoodia pilifera* subsp. *pillansii* in habitat near Kruidfontein, plant 400 mm tall, growing fully exposed among bushes and shale gravel.

these rows much deeper than the grooves between consecutive tubercles in a row. In general in Hoodia the thinner-stemmed species have fewer angles per stem (in H.gordonii and H.triebneri this may be as few as 11–14) while the thicker-stemmed species have many more (up to 34 in H.pilifera). Flowering completely disrupts the arrangement of these angles. In the thinner-stemmed species growth is somewhat faster from one flowering season to the next and so, between bouts of flowering, a portion of stem is produced with regularly arranged tubercles. In the thicker-stemmed species of Sect. Trichocaulon, growth between flowering seasons is usually small and the angles do not recover their ordered arrangement so that they can only be counted at the base of the stem before the first flowers arise. On the tubercle the epidermal cells are ^{flat} ~~flush with the surface~~ (Fig. 4 A–C) or only slightly raised into papillae (Fig. 3 F, H). They are mostly quite regularly polygonal and sometimes there is a slight border around each (Fig. 3 F). Stomata are variably embedded (Fig. 3 E, F taken on same tubercle): sometimes superficial (Fig. 3 H) to sunken and surrounded by a ring of epidermal cells (Fig. 3 E).

In Lavrancia the tubercles are round, usually broader than tall and often somewhat polygonal in outline. They are not joined together into longitudinal rows. Each one has a rounded-truncate summit usually with a depression a little above the centre in which the leaf is situated. In L.haagnerae the inflorescences are few and consequently the 10–12 rows of tubercles are very regular along most of the length of the stem. In the other species even in young stems which have not borne flowers they are often hard to count. Up to 19 rows may occur but 12–16 is the more usual range. On the tubercle many of the epidermal cells are extended into a papilla (Fig. 5 B, H). Groups of these cells may be raised into hills (Fig. 5 G). The stomata are superficial (Fig. 5 H) to sunken (Fig. 5 G) and are deeply sunken in L.haagnerae (Fig. 5 C) where the surrounding cells are strongly folded.

In both genera the stems are thick and the angles much disorganized. Thus it is only in seedlings that one can make observations on the leaf arrangement where the

situation is similar to that in Echidnopsis (Bruyns 1988, p.3). In all seedlings the first leaves above the cotyledons are an opposite pair. Next follows a whorl of 4 rotated through 45° from the initial pair. The next whorl also contains 4, rotated through 45° again so that two of them are directly above the original pair. These alternating 4-leaved whorls may continue for 5 nodes or more, during which the stems are 8-angled, but eventually one or more of the meristems produces two leaves and this begins to increase the number of angles.

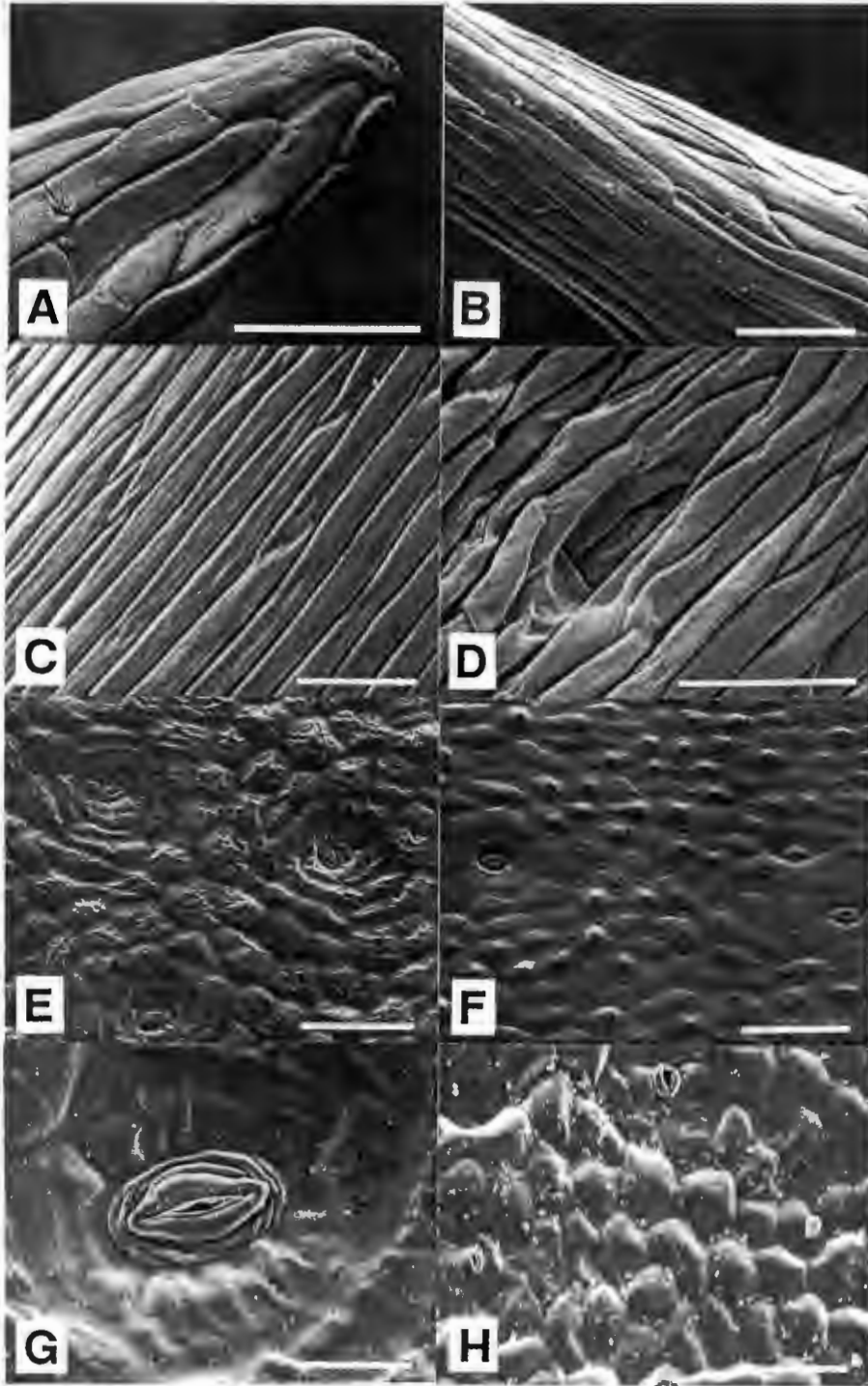
Leaves

In the stapeliads each leaf is borne on a conspicuous phyllopodium or tubercle below the petiole. The only stapeliad with well-developed petiole and lamina is Frerea indica Dalz.. In all others the leaves are reduced to tiny rudiments and the petiole is absent. That the tubercle is part of the stem is demonstrated in Linder & Bruyns (in prep.). In some genera (e.g. Caralluma R.Br., Echidnopsis Hook., Stapelia L.) the leaf rudiment still has a discernable blade and midrib but in many others this is further modified to a conical structure without any discernable differentiation. Hardening of this conical structure into a sharp tooth occurs in Quaqua N.E. Br., Huernia R.Br. (esp. H.hystrix) and in some species of Orbea Haw..

In Hoodia it is only in the first leaves after the cotyledons — usually only in the first pair — where blade and midrib can be distinguished. Here the leaf is somewhat dorsiventrally flattened but even then the blade is minute (see for example Fig. 17 C, E). In subsequent leaves the flattening disappears. The base of the leaf is much swollen and forms a cap-like cover over the summit of the tubercle. This base may occasionally be slightly laterally winged (in H.officinalis, H.flava particularly visible just as the leaves dry out),

Figure 3.—SEM views of epidermis of *Hoodia*. A, tip of spine, surface granular (*H.alstonii*). B, surface of spine (*H.gordonii*). C, surface of spine (*H.juttae*). D, surface of spine with stoma (*H.alstonii*). E, surface of tubercle well below spine (*H.alstonii*). F, surface of tubercle above abscission layer (*H.alstonii*). G, stoma (*H.alstonii*). H surface with superficial stomata (*H.gordonii*).

Scale bars: A–D, H, 50 μm ; E, F, 100 μm ; G, 20 μm .



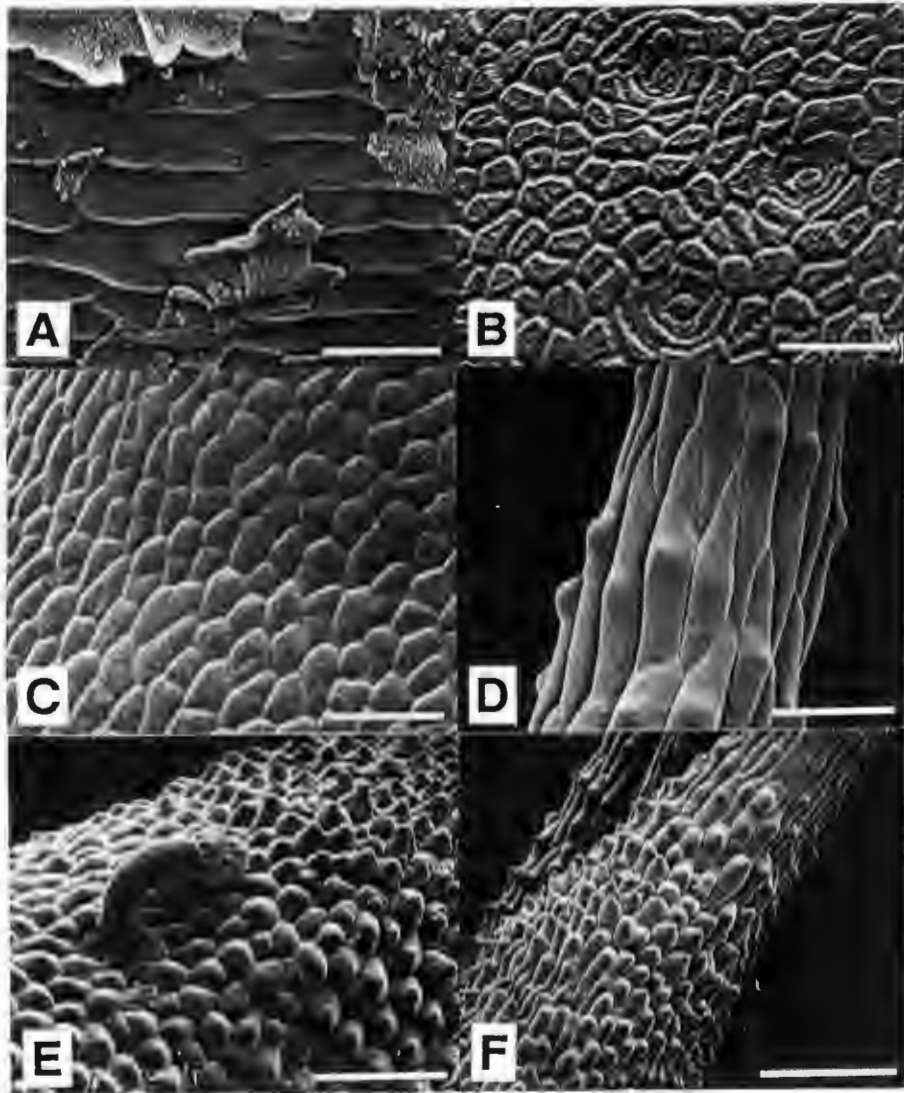


Figure 4.—SEM views of epidermis of *Hoodia*. Surface of tubercle: A, *H.officinalis* subsp. *officinalis*, showing remnants of thick wax covering of epidermis. B, *H.parviflora*. C, *H.pilifera* subsp. *annulata*. Epidermis of seedling (*H.pilifera* subsp. *annulata*): D, spine with long cells with papillae; E, multicellular stipular hair at base of spine; F, transition from small to long cells near base of spine.

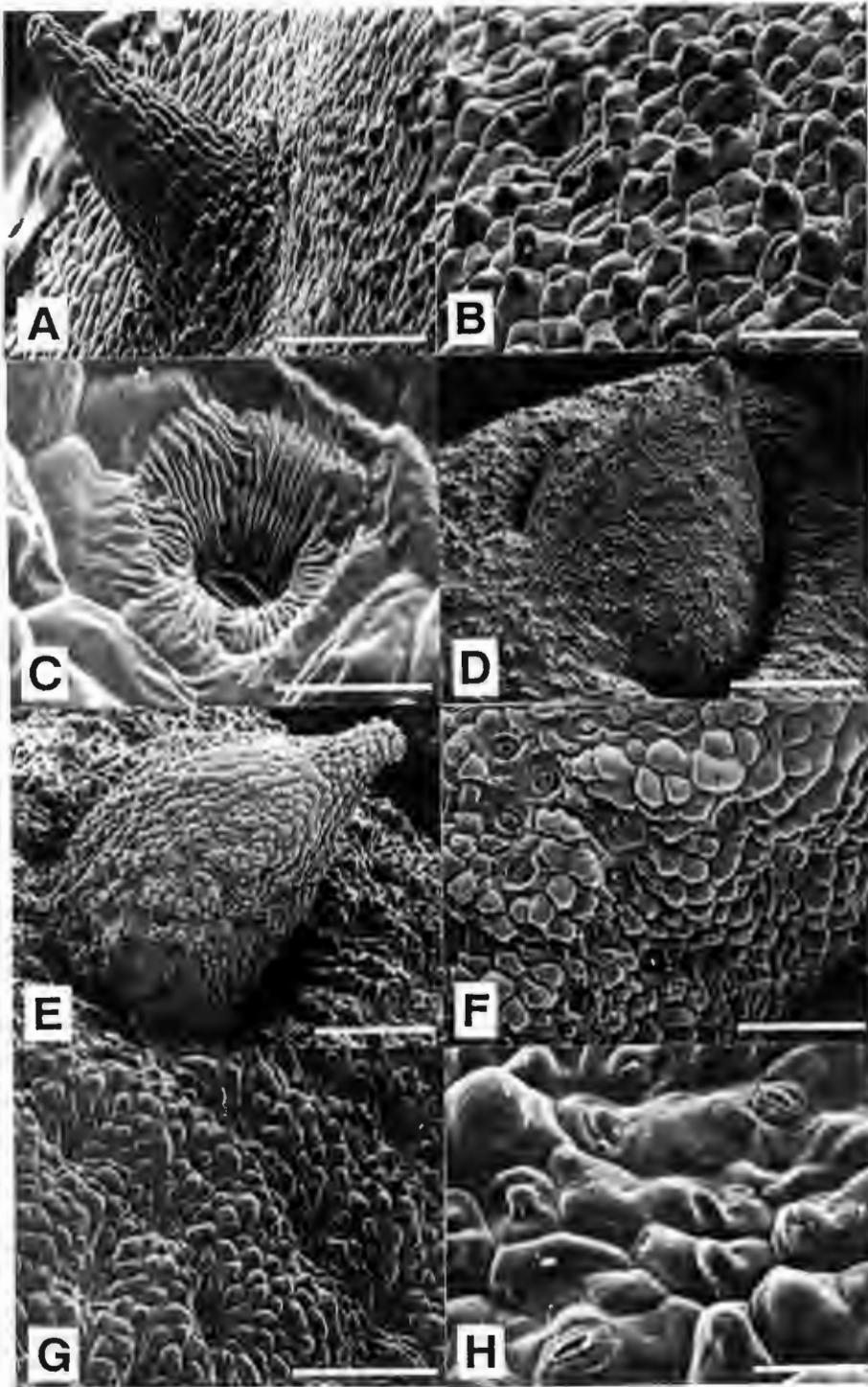
Scale bars: A, D, 50 μm ; B, C, E, 100 μm ; F, 200 μm .

which might represent a trace of the former leaf blade, but it is mostly ± circular in cross-section. Above the basal cap the leaf abruptly narrows and then tapers gradually to a finely rounded tip (Fig. 3 A), all the time remaining circular in cross-section. When young this whole structure is pinkish (often streaked with brown towards the base) to dark brown and is soft and pliable. Soon after, the leaf (including the basal cap) dries out into a sclerified, whitish to brownish spine. Although these spines are normally very hard, they become soft and pliable when moistened, as for example during a nocturnal mist. In Sect. Hoodia, H.ruschii, H.triebneri, H.alstonii, H.officinalis subsp. delatiana (to a lesser extent subsp. officinalis) the spines are stout and hard, usually 6–12 mm long and extremely sharp. In H.flava, H.pilifera and H.mossamedensis they are usually 3–6 mm long, still stiff, but much weaker and more easily broken. In H.pedicellata they are usually less than 3 mm long and, although still sharp, they are weak and soon fall off or are worn off by the weathering action of wind-borne sand. This is the only species where they are not usually persistent. In all species the spine is covered with long, narrow cells running lengthwise (Fig. 3 A–C). Sunken stomata are occasional (Fig. 3 D). The surface of these cells is distinctly granular at > 1000 X in H.alstonii (Fig. 3 A) but smooth in the others.

The surface of the spine in the seedling is rather different. Towards the base the nearly isodiametric epidermal cells are raised into papillae (Fig. 4 D). Stipules have been observed at the base of leaves of seedlings of H.pilifera subsp. pilifera, subsp. annulata (Fig. 4 E) and H.alstonii (Fig. 16 I) and are short, thick, transparent, multicellular hairs (Meve & Albers 1990, type 4).

In Lavrana the minute, persistent, permanently soft leaves are of two kinds. That in L.haagnerae (Fig. 5 A) is conical, seated in a slight depression, covered with rather long

Figure 5.—SEM views of epidermis of *Lavrania*. *L.haagnerae*: A, leaf; B, papillate surface of tubercle with stomata; C, stoma. D, *L.perlata* (4648), leaf with midrib visible. *L.cactiformis*: E, leaf without visible midrib; F, papillae and stomata on leaf; G, surface of tubercle with sunken stomata. H. *L.marlothii*. surface of tubercle



with superficial stomata.

Scale bars: A, G, 200 μm ; B, F, 100 μm ; C, H, 50 μm ; -D, 500 μm ; E, 250 μm .

epidermal cells running lengthwise (reminiscent of those in Hoodia) and apparently lacks stomata. In the others the leaf is slightly (Fig. 5 E) to notably (Fig. 5 D) dorsiventrally flattened and slightly to markedly sunken into a pit. The midrib may be visible (Fig. 5 D). Many stomata are present (Fig. 5 F) except along the midrib and many of the ± round epidermal cells are raised into papillae. Stipules are absent.

Inflorescences

Wertel (1976) discussed the organization, development and position of the inflorescence in Caralluma sensu lato, Stapelia and Huernia. He found that in a typical stapeliad inflorescence a flower terminated the main axis. In many species an axillary shoot continues the florescent axis but, in so doing, it displaces the inflorescence into a lateral position, making the determinate nature of each flowering axis less easy to observe. Wertel indicated a trend of simplification from many-flowered "umbel-like" inflorescences found in some species of Caralluma through (derived) paniculate (p.32) to reduced thyrses in some species of Stapelia (p. 50) and Caralluma (p. 38). He found in addition that this trend of simplification could be traced through several sequences of related species.

Wertel showed as well that the organization of the different inflorescences followed a simple pattern throughout: all are based more or less on a structure such as in Figure 1 (Bruyns 1988) with larger numbers of flowers arising through activation of the axils of various bracts.

Wertel (p. 65) observed that in Huernia and Stapelia the primary stem and first few innovative shoots are sterile (thus indeterminate, though they usually soon cease growth), as is the case in many other genera e.g. Pectinaria Haw., Piранthus R.Br., Duvalia Haw., Tridentea Haw. etc. However, this is not true of all species of Quaqua (especially not of

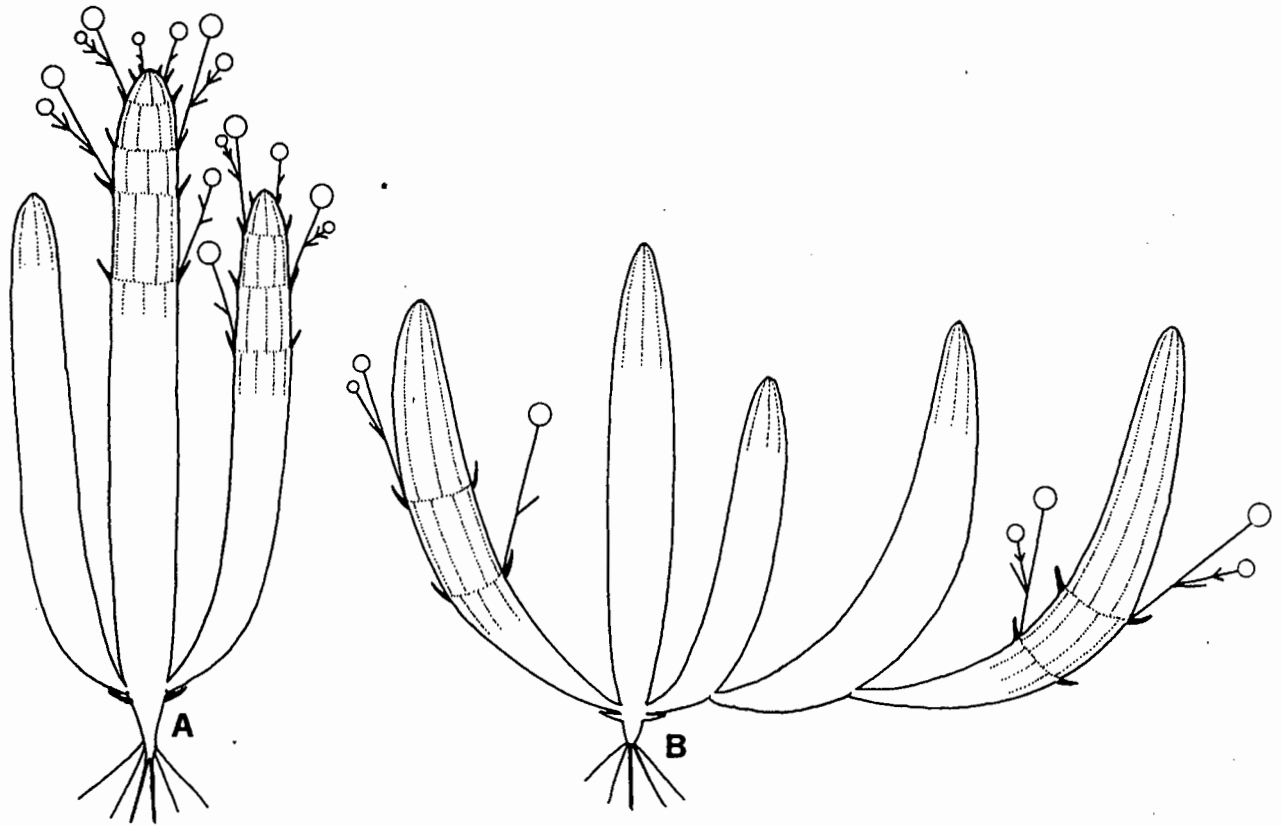


Figure 6
Schematic representation
of growth forms

Figure 6.—Schematic representation of growth forms in Hoodia and Lavrania.

A, orthotropic form of Hoodia and Lavrania Sect. Cactoidea (also some species of Quaqua) with many inflorescences arising on both primary and secondary stems.

B, Decumbent or semi-plagiotropic form of Lavrania haagnerae with few inflorescences arising on secondary stems only.

some members of Sect. Robusticaulon and Q.pruinosa, Bruyns 1983) and, as he indicated, it is not true either for Hoodia or Lavrania (except L.haagnerae).

In both Hoodia and Lavrania the primary stem grows vertically up from between the cotyledons. After it has reached some size, axillary buds near the base give rise to innovative (secondary) shoots. In Hoodia the height at which the primary stem begins to develop innovative shoots varies with species (in H.flava, for example, it may occur when the primary stem is less than 70 mm tall). The primary stem continues to grow, usually keeping up with or exceeding the secondary stems. After a few years (as few as 2–3 in some cases) both the primary and secondary stems begin to bear flowers. This is shown schematically in Figure 6 A.

In one flowering season a stem produces many inflorescences near its apex usually densely and apparently randomly distributed around its circumference for some distance. When flowering stops, vegetative growth resumes and the stem continues to lengthen and will often produce more flushes of flowers higher up in subsequent years. This alternating of inflorescences and vegetative growth continues and thus the primary and secondary stems may reach a considerable length. In all species old inflorescences are able to produce flowers in subsequent years (these arise in the axils of bracts already present in the inflorescence, as observed by Wertel, p. 32–3) but it is the newest inflorescences around the apex of the stem that bear most of the flowers in any given season.

It is now generally accepted that all asclepiad inflorescences develop a terminal flower and that the vegetative shoot continues sympodially past it. In Hoodia and Lavrania the axillary nature of this continuation is obscured by the thickness of the stem. and the only visible evidence for the termination of the axis is that the inflorescence arises at the top of a row of tubercles which does not continue above it.

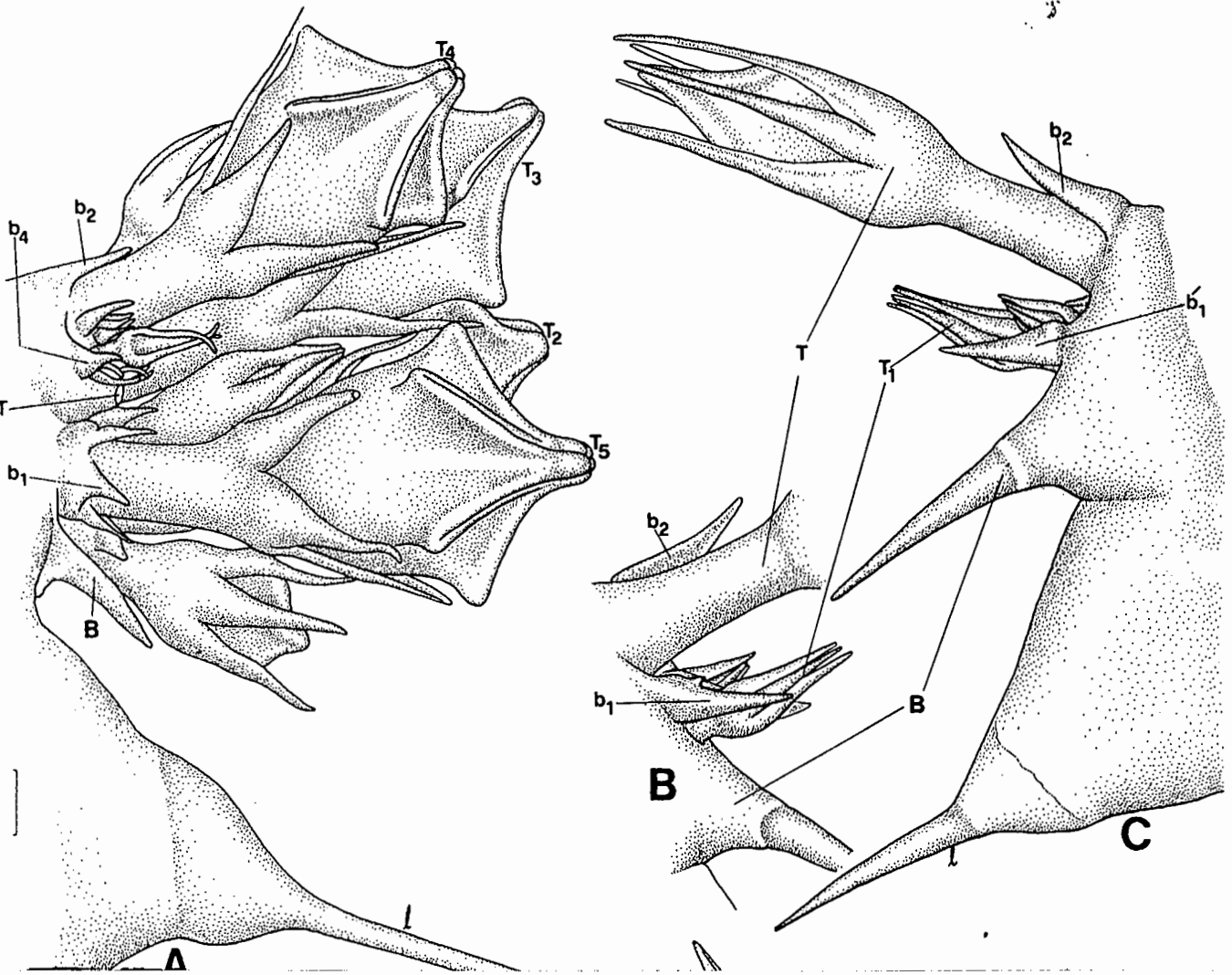


Figure 7.—*Hoodia* inflorescences. A, *H. triebneri*, Bruyns 3632. B, C, *H. currorii* subsp. *currorii*, Bruyns 3624, same inflorescence from opposite sides. D, inflorescence of *H. officinalis* subsp. *officinalis* (Bruyns 3069) with neighboring tubercles removed. E, enlargement of inflorescence of D. F, larger inflorescence on same plant as D. G, inflorescence of *H. pilifera* subsp. *pillansii* (Bruyns 3149) with surrounding tubercles excised. H, rear view of largest bract of G. I, J, face and side views resp. of small bracts in F.

T = first terminal flower, subtended by main (unpaired) bract B, $T_1 - T_5$ are secondary terminal flowers subtended by paired bracts b_i, b'_i . One of the pair of leaves subtending the whole inflorescence is shown in A and C as *l*.

Scale bars: A, B, C, 1 mm (at A); D, 1 mm; E-J, 0.5 mm (at F).



Figure 7
Hoodia
currorii
1964

Figure 8.—Horizontal and vertical plan diagrams of *Hoodia* inflorescences.

A, A', *Hoodia triebneri*, plans of Figure 1 A.

B, B', *Hoodia pilifera* subsp. *pillansii*, plans of Figure 1 G.

C, C', *Hoodia currorii* subsp. *currorii*, plans of Figure 1 B, C.

T = terminating flower of inflorescence subtended by main (unpaired) bract B, T.

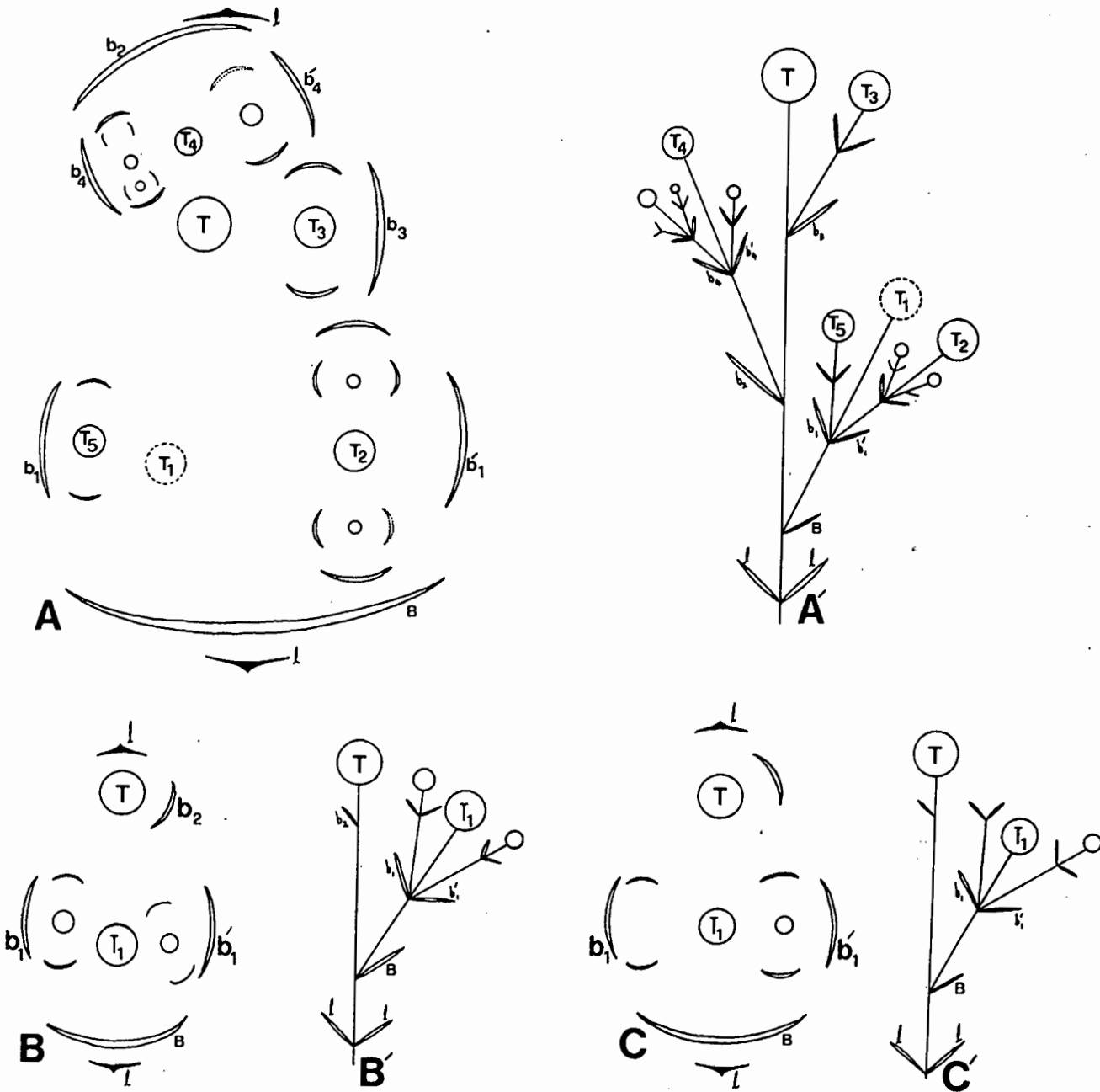


Figure 8
Hoodia inflorescences

= terminating flower of paracladium subtended by paired bracts b_i, b'_i . The pair of leaves subtending the whole inflorescence is indicated by l .

In Hoodia ruschii and H. triebneri the inflorescence often has several flowers open at once with many developing from it in one season. A comparatively large "peduncular patch" of scars is left once flowering is over. The basic pattern shown in Bruyns (1988) for Echidnopsis is present here too, except that the terminal flower (T in Fig. 7, here fallen off) has two bracts b_2 and b_3 on its axis with fertile axils. The bracts here, including the basal one, are all unlike the leaves and are without stipules.

The remainder of the genus shows varying degrees of simplification from this arrangement. The large-flowered species forming Sect. Hoodia all have few-flowered inflorescences where flowers mature successively. The pedicels are thick and even after a few flowers quite a large "peduncular patch" develops. The organization of these inflorescences is as in Bruyns (1988) except once more for the extra bract attached to the axis of the terminal flower. Figure 7 B, C show a very young inflorescence (the main bud is less than 5 mm long) of Hoodia currorii. The terminal flower (T) is obviously the most advanced. The main subtending bract B is difficult to distinguish from a spine (just a little shorter and softer) and it is not flattened or channelled on one side as bracts usually are. The other bracts are a more usual shape and some of them have a stipule on one side.

Fig. 7 D, E, F, G show the more depauperate inflorescences found in other members of Sect. Trichocaulon. In D it can be seen how the young inflorescence is hidden among the tubercles, some of which have been cut away to show it. The same inflorescence is shown in E and another one from the same plant in F (H. officinalis subsp. officinalis). Only one flower is maturing in E and two have matured in F. When more than one develops they do so in succession. G shows an inflorescence of H. pilifera subsp. pillansii. Again some tubercles have been excised. In these taxa the bracts are very unlike the leaves and many of them have one or two stipules at the base (H, I, J). An extra bract is usually attached

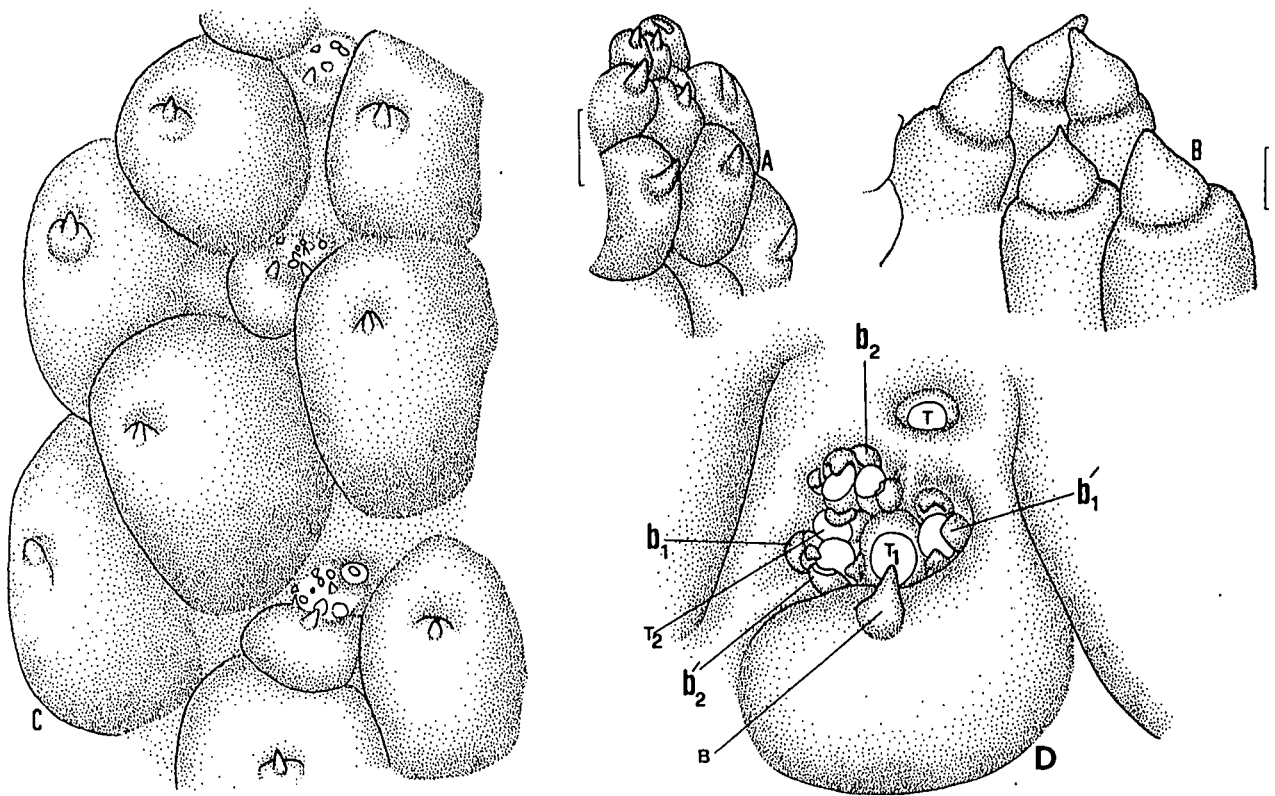


Figure 9
Lavrania
 11. Flowers
 11. 11.

Figure 9.—Leaves and inflorescences of *Lavrania*. A, portion of apex of stem of *L. marlothii*, Heunis 90. B, portion of apex of stem of *L. picta* subsp. *parvipuncta*, Bruyns 4173. C, portion of stem with several inflorescences, *L. marlothii*, Bruyns 3571. D, close-up of lower inflorescence of C.

Labelling in inflorescence as in Figures 7, 8.

Scale bars: A, C, 2 mm (at A); B, D, 0.5 mm (at B).

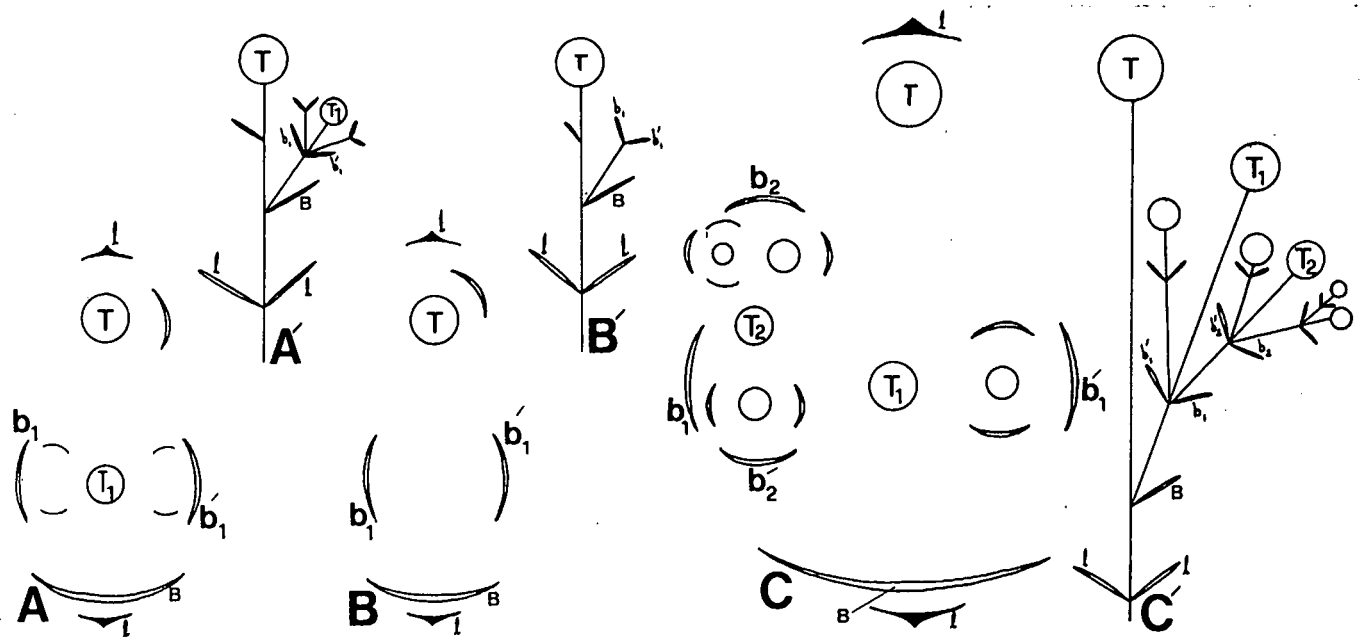


Figure 10
Hoodia + Lavrania
inflorescences

Figure 10.—Plan diagrams of Hoodia and Lavrania inflorescences.

A, A', Hoodia officinalis, plans of Figure 7 F.

B, B', Hoodia officinalis, plans of Figure 7 E.

C, C', Lavrania marlothii, plans of Figure 9 D.

T = terminating flower of inflorescence subtended by main (unpaired) bract
 B, T_i = terminating flower of paracladium subtended by paired bracts b_i, b'_i . The
 two leaves subtending the whole inflorescence are indicated by l .

to the terminal flower but its axil is not fertile. These inflorescences are shown schematically in Figures 8 and 10.

In Lavrania haagnerae few inflorescences are produced. These determinate structures are produced in the very early stages of some of the secondary stems. Their development is suppressed until the axis on which they occur is much longer so that flowers appear in the lower half of the stems (Fig. 6 B). The primary stem does not bear flowers. In all other species of Lavrania the primary stem bears its first flowers after 2–3 years (or more). It is quite common for large, mature plants to consist of the primary stem only but secondary stems may develop from basal axillary buds so as to equal it in height, though they rarely exceed it unless it is damaged. They thus have the same basic structure as shown in Figure 6 A. Exactly as in Hoodia, large numbers of inflorescences are produced near the apex of the stems and they soon produce flowers. Older inflorescences from previous seasons (now lower down on the stem) quite often continue to bear so that flowers are found over most of the surface of the stem though they are concentrated around the apex. After flowering has finished, the stem resumes vegetative growth though it will not reach the length found in Hoodia.

In Lavrania most of the inflorescences are small and bear only a few flowers which develop successively except in L.perlata where several may open simultaneously on one inflorescence. With repeated use over several seasons an inflorescence may develop into a large "peduncular patch".

A typical Lavrania inflorescence is shown in Fig. 9 D and schematically in Fig. 10. The basal bract is seated on a tubercle similar to those bearing leaves and is itself similar to a leaf in shape. The remaining bracts within the inflorescence do not have tubercles beneath them. The terminal flower is separated from the basal bract and all subsequent

development in the inflorescence takes place between them (pushing them ever further apart). No stipules have been seen and the terminal flower lacks an extra bract on its axis.

Flowers

A. Corolla

In Hoodia the fleshy corolla is very variable in size. In Sect. Hoodia it is generally large to very large (25–170 mm but mostly 60–80 mm), saucer shaped to ± flat (funnel-shaped in H.parviflora), with obscure division into 5 broad but short lobes each usually with a distinctive, narrow, tail-like tip (Fig. 21 A shows a typical example). They are borne on a stout pedicel which holds them beyond the spines on the stem. In the centre of the corolla immediately around the gynostegium there is a small cup-like depression. There is always a thickening of the corolla just outside this depression, sometimes appearing as a series of slightly raised islands, but no distinct annulus. Thus this depression appears to be the true corolla tube. In some flowers of H.gordonii and H.currorii the area outside this small central tube may also be cupular (funnel-shaped in H.parviflora). These much expanded "corolla tubes" are not homologous to the small central one. In H.juttae and often in H.gordonii the inner surface of the corolla is smooth and glabrous. In the remainder it is covered inside sparsely to densely with columnar, setulose papillae. The apical cell on the papilla is often extended into a unicellular hair which may be up to 3.5 mm long.

In Sect. Trichocaulon the corolla is less than 15 mm diam. except in H.pilifera (esp. subsp. annulata) and H.ruschii (20–40 mm diam.). The flat to campanulate corolla is deeply lobed, in H.pedicellata practically to the edge of the gynostegium, and the long, narrow tip of the lobes is lacking. In H.pedicellata and H.mossamedensis the pedicel is

long and holds the flower well away from the stem. In most of the others it is extremely short (1mm or less) and the flowers are consequently held between the spines and tubercles and are frequently very misshapen. The corolla tube is abrupt and cup-shaped (very small and shallow in H.flava and H.pedicellata) and there is always a thickening of the corolla just outside the tube (even in the ± flat-flowered H.flava). This thickened area becomes a prominent annulus in H.pilifera. In H.alstonii, H.ruschii and H.triebneri (as in H.parviflora from Sect Hoodia) the corolla is campanulate or funnel-shaped and this thickened ring is some distance into the tubular part. Below the ring the tubular part becomes more steep. Thus this lower steep part is the real corolla tube (homologous to the abrupt tube of H.currorii, for example) and the less steep part outside the "annular" area is equivalent to the flat part outside the tube in H.currorii. The inner surface of the corolla is smooth in H.alstonii, finely setose in H.pedicellata or papillate. In H.officinalis subsp. deletaetiana these papillae are very scattered but in the other taxa they cover the surface densely. They are minute in H.flava (occasionally absent) to large in H.ruschii, H.triebneri and H.pilifera and are covered in setae. The apical seta is usually modified into a short, often horizontally oriented bristle.

In Lavrania the corolla is 5–16 mm diam., campanulate to flat with deeply divided lobes. The pedicel is mostly 1mm long or less. The corolla is slightly thickened around the mouth of the tube in L.cactiformis, L.picta and L.haagnerae but not in L.marlothii or L.perlata. The apparent annulus in L.perlata is caused by the bend at the base of the lobes. The inside of the corolla is smooth in L.marlothii but densely papillate in all the others. These papillae (which are setose) are very low and rounded in L.picta but become conical and tipped with a conspicuous apical seta in L.perlata, L.cactiformis and L.haagnerae. In L.perlata this apical seta is unusual as it is horizontal, thick and

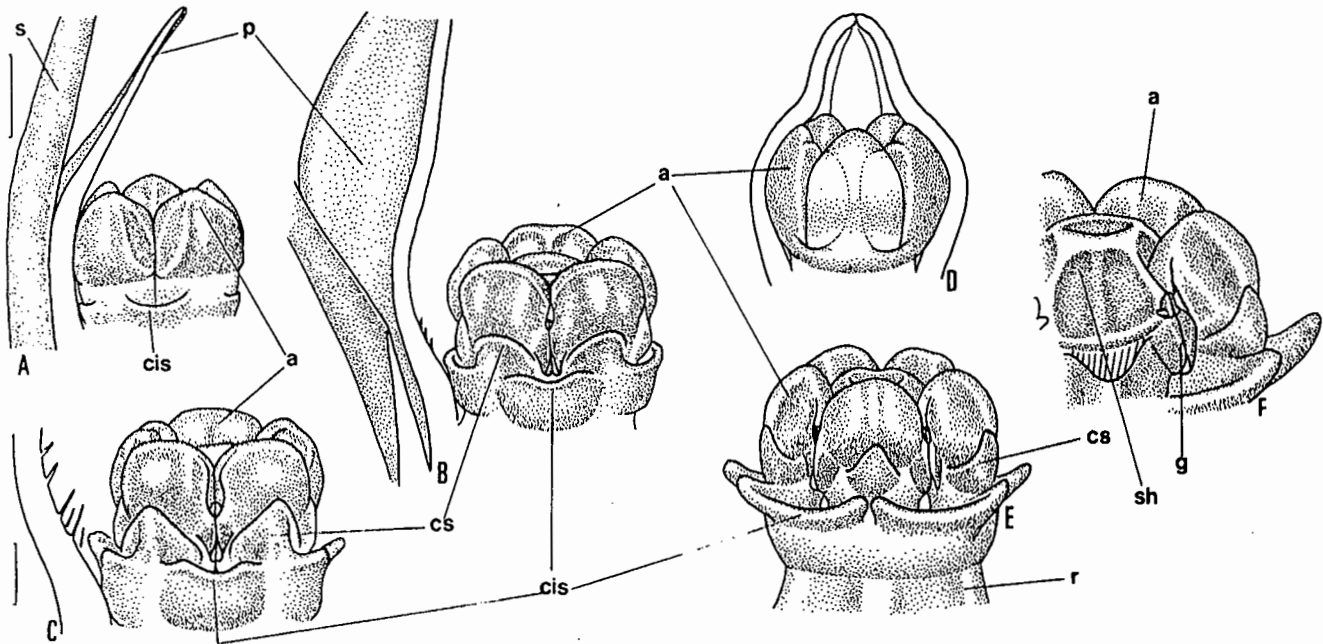


Figure 11
 10. 101
 5/6/21

Figure 11.—Coronal ontogeny in *Hoodia*. A, D, flowers at very early stage (bud in D \pm 1 mm long), only anthers visible with no corona developed. B, E, later stage with inner and outer corona series beginning to develop from base of anthers, hairs of corolla just appearing in B, corpuscle becoming visible and anthers beginning to split laterally to release pollinia. Note that at this stage already the guide rails are fully developed. C, yet later stage. F, close-up of E with one anther removed to show fully developed guide rails and split in anther where pollinium released.

A, B, C drawn from *H. currorii* subsp. *currorii*, Bruyns 3624; D, E, F from *H. flava*, Bruyns 3743.

s = sepal, p = corolla lobe, a = anther, cis = interstaminal (outer) corona, cs = staminal (inner) corona, g = guide rail, sh = style head, r = receptacular stipe.

Scale bars: A, D, F, 0.5 mm (at A); B, C, E, 0.5 mm (at C).

cylindrical with rounded ends. In the others it is as in Hoodia.

B. Gynostegium

Classically, the corona of stapeliads has been divided into two series, an inner series of 5 usually free lobes (inner corona lobes) and an outer series of 5 variously free or fused lobes (outer corona lobes). The five outer lobes are often fused laterally to dorsal projections of the inner lobes to form 5 deep pockets and thus a cupular structure around the whole gynostegium.

It has been shown (Kunze 1982, Hofmann & Specht 1986) that the outer corona arises from an interstaminal meristem while the inner corona lobes arise from meristems situated on the backs of the stamens. On the basis of this different origin Liede & Kunze (1992, in press) have proposed a new classification of coronal structures into interstaminal corona (= outer corona) and staminal corona (= inner corona). In the case of the Stapelieae this new classification does not add anything useful and so, in the taxonomic account here, the old terminology is maintained.

The ontogeny of the corona has been observed in several species of Hoodia (Fig. 11). It has been found to be similar in such different species as H.currorij and H.flava and follows exactly the pattern observed by Kunze (1982, p.145) and Hofmann & Specht (1986) for Ceropegia linearis. The stamens as well as the calyx, corolla and carpels are fairly well differentiated before the corona begins its development. At this stage they are erect, the fertile areas are clearly visible and adjacent anthers have closely adpressed, straight edges. The interstaminal (outer) corona is visible only as 5 small meristematic areas at the base of the free parts of the stamens and above the tube into which the filaments are fused and the staminal (inner) corona has not yet begun to develop (Fig. 11 A, D). The stamens

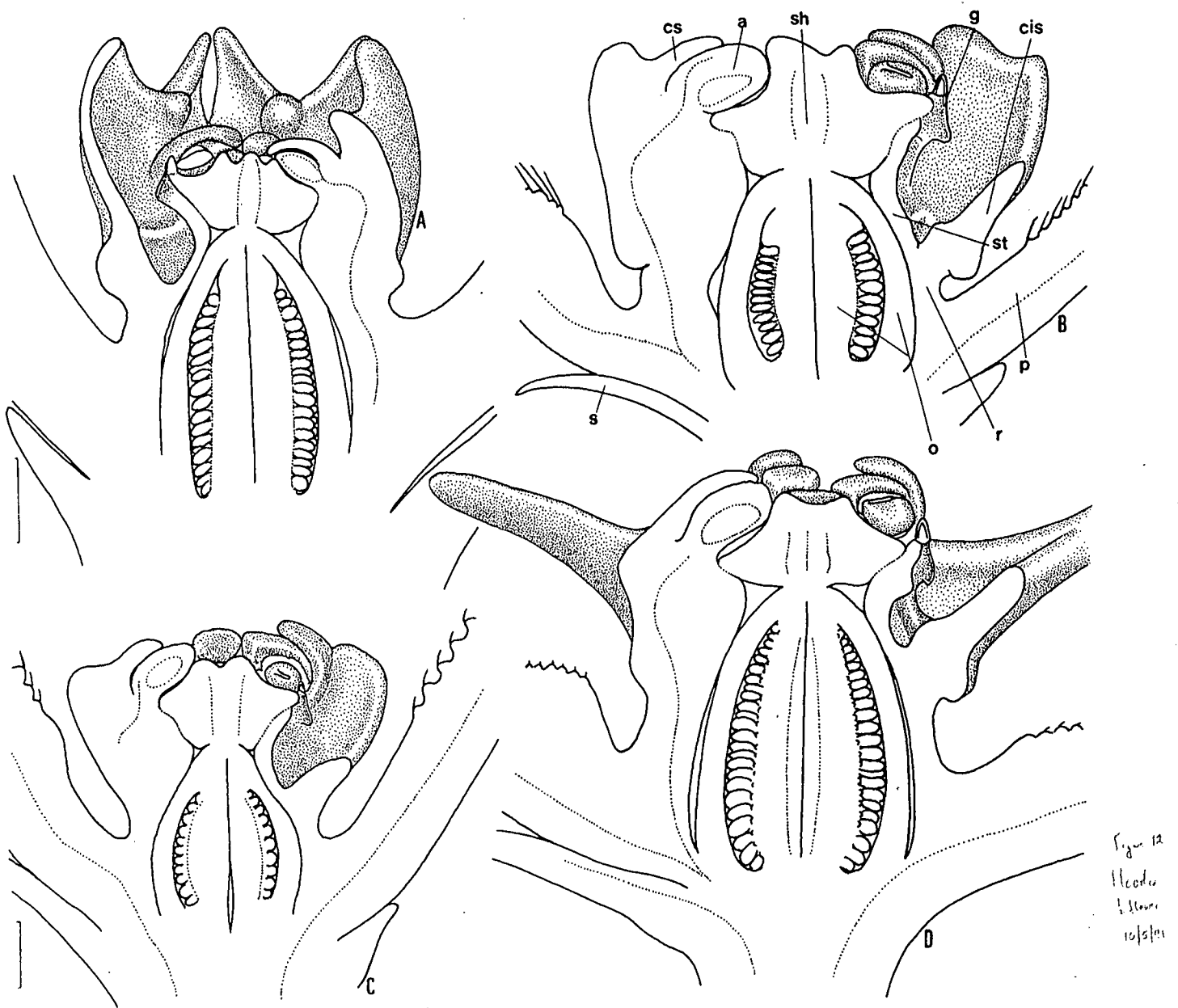


Figure 12.—Half flowers in Hoodia. A, H. currorii subsp. currorii, Bruyns 3624. B, H. officinalis subsp. officinalis, Bruyns 3069. C, H. triebneri, Bruyns 3632. D, H. flava, Bruyns 3070.

In all only the central part of the flower is shown with the gynostegium and the base of the corolla and calyx. Vascular traces and shadow of theca within anther shown with dotted lines. Labelling inserted on B only as follows: s = sepal, p = corolla lobe, a = anther, cis = interstaminal (outer) corona, cs = staminal (inner) corona, g = guide rail, sh = style head, r = receptacular stipe, st = staminal (filament) tube, o = carpel.

Scale bar: A, 1 mm; B, C, D, 0.5 mm (at C).

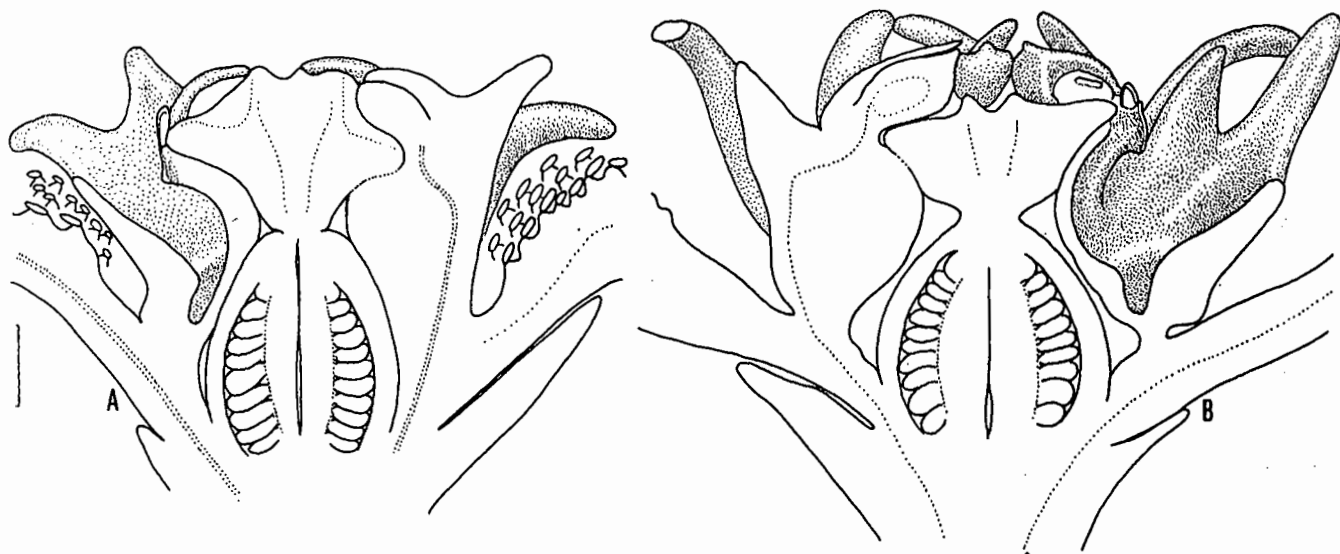


Figure 13.—Half flowers in Lavrania. A, L. perlata, Bruyns 3903. B, L. lactiformis, Heunis 117.

Scale bar: A, B, 0.5 mm (at A).

continue to increase slightly in height with the anthers gradually assuming a more horizontal position (Fig. 11 F). The lower lateral margins of the short, thick anthers expand outwards and downwards to form the guide rails. More or less at the same time slits appear in the sides of the anthers and the development of the corpusculum begins. At this stage the interstaminal corona is clearly assuming a cupular form beneath the guide rails, beginning to form the characteristic "outer corona" while the staminal corona, attached dorsally to the stamens at the base of the anther, is still only just beginning to form (Fig. 11 B). In the mature flower this staminal corona consists of two parts: a lobe adpressed to the back of the anther and a spreading or recurved horn. This horn is the last part of the whole corona to develop. The guide rails (Fig. 11 C, E), the corpusculum and caudicles (Fig. 11 F) soon reach their mature shape. By this stage the whole gynostegium is seated on a stipe (Fig. 11 E) which is presumed to be of receptacular origin (Kunze 1990, p. 38).

From the half-flowers of Figure 12 (Hoodia) and 13 (Lavrania) the structure of the gynostegium is relatively clear and can be seen to be uniformly constructed throughout the two genera.

The ovary is always superior (above the point of fusion of the petals and sepals) and is tightly surrounded by the staminal tube. The two carpels are fused apically and are tightly adnate for most of their length, narrowing towards the apex and joining with the style head. The white style head has a remarkable shape. The apex is truncate and \neq flat, with two small roundish depressions near the middle or a depressed line across the centre. From the apex the head widens out to almost 3 X the apical diameter, dropping slightly in the process. The widened part is traversed by 5 ridges radiating out from the apex and it is on the end of these ridges that the corpusculum is secreted and between them that the

anthers are pressed into the surface of the head. From this widest point it narrows gradually (fused most of the way to the inside of the filaments) to the apex of the carpels. The receptive area is below the widest point and lies opposite the guide rails. Vascular traces showing that it consists of two fused parts are usually clearly visible.

The receptacle gives rise to the small stipe on which the gynostegium of most species is seated (Fig. 11 E shows a good example). In the mature flower the stamen is a little more complicated than at early stages such as Fig. 11 D. The vascular trace in the stamen arches away from the centre of the flower, curving back just below the anther. The area between the trace and the ovary is broad and filled with loose, fragmented tissue with many air pockets. The inner wall of the stamen is closely adherent to the side of the ovary and fused with the lower side of the style head and it appears that the strong and late development of the dorsal horn of the staminal (inner) corona lobe causes a "dragging" of tissue away from the inner wall of the stamen. Hence there is the fragmented tissue in the stamen and the arch in its vascular trace. The guide rails are generally short and vertical and are hard and horny towards the edges.

The interstaminal (outer) corona lobes are deeply cupular and enclose the guide rails and an often deep "nectarial orifice" beneath these rails. In Hoodia Sect. Hoodia, H.officinalis, H.ruschii and H.triebneri they are fused laterally with the dorsal parts of the staminal corona lobes to form a cup around the gynostegium. In the remainder and in Lavrania they are longer and more divided.

The staminal (inner) corona is remarkably uniform in the two genera. The lobes are always adpressed to the backs of the anthers and dorsiventrally flattened. In L.picta and L.marlothii they exceed the anthers and rise up in a column in the centre. There is often a spreading dorsal horn, the lower sides of which are fused to the sides of the interstaminal corona.

C. Pollinarium

Each pollinarium consists of two pollinia, a grooved, dark-brown corpusculum and very small caudicles joining the pollinia to the corpusculum.

The pollinia are generally small, about 0.25 mm broad and long and \pm bean-shaped. Although usually about as long as broad, they may sometimes be a little longer than broad (L. picta, L. perlata) or vice versa in L. marlothii and notably broader than long in H. alstonii. As usual the size of the pollinia is directly related to the breadth of the style head and they are smallest in H. ruschii and H. triebneri where the tops of the gynostegium and the style head are especially small. Each pollinium has a pellucid germinating mouth on the inner side, always shorter than that side and often positioned somewhat towards the upper surface of the pollinium (i.e. not exactly along the inner edge). The corpusculum is small, dark brown, broadest towards the top and with lateral wings a little below the middle. These transparent wings are very variable in length, even within the same species. They are largest in Hoodia Sect. Hoodia and L. haagnerae. They are usually rounded along the edges and become narrower towards the rounded tip. Each pollinium is joined by a short, weak, transparent caudicle to near the tip of the wing.

Pollination

The method of pollination of stapeliad flowers is well known (Bruyns 1988, p. 6). This process has been extensively checked by hand-pollination using a fine pair of tweezers in both Hoodia and Lavrania. It was noted that the angle at which the pollinia have to be oriented for insertion varies greatly among the species. There is also often very little space between the sides of the outer coronal cup and the guide rail (especially in L. marlothii) and this requires delicate manouvering to get the pollinium past this so that the end of the germinating mouth comes into contact with the end of the guide rails. Once this has been

achieved the germinating mouth slips up the rails easily and becomes stuck near the top. It is not necessary for a corpusculum to be in position to hold the pollinium in the rails.

All Hoodia flowers have a foetid odour which is especially strong in H.pilifera, H.ruschii, H.triebneri and H.alstonii. In H.pilifera subsp. pillansii there is a slightly fish-like "tinge" to the odour but in all others it is excrement-like. In Lavrana Sect. Cactoidea the odours are not usually strong except in L.perlata and in some of the small-flowered forms of L.cactiformis. Again a slightly fishy odour was detected in L.cactiformis. Thus it is clear that these plants are all pollinated by flies. The common house fly and blue bottles are often seen on the large flowers of Hoodia Sect. Hoodia and are probably responsible for pollinating them. The same flies have also been observed on L.cactiformis flowers, visiting with frequency and enthusiasm and even doing so while the flowers were being examined under a microscope. Several pollinaria were seen fastened onto hairs on the proboscis, the proboscis itself being far too large to enter the guide rail. Thus it would appear that they may be responsible in at least some cases for pollination in the small-flowered taxa as well.

The large-flowered species of Hoodia mostly have an unusual flesh colour. In H.currorii this colour becomes more intense around the edge of the tube and this area is also shiny. This flesh colour contrasts strongly with the dark purple-black of the corona and it is possible that the whole arrangement mimics a festering wound on an animal. This impression is accentuated in H.currorii further by the hairiness of the flower outside this shiny area.

As is usual in the stapeliads, nectar is produced in the tissue of the filament tube behind the guide rails and, if the flower is kept cool, it will gradually fill up the deep area inside the outer corona lobes.

In both H. flava and L. marlothii droplets of what is probably nectar are produced on the upper surface of both the inner and outer corona lobes.

Follicles & Seed

In all hoodias the fusiform, paired, horn-like follicles are slender with an angle of 30–60° between the horns. Individual horns are circular in cross-section except in H. parviflora where they are slightly flattened above with a slight wing running longitudinally down each edge. The surface is glabrous, often slightly glaucous when young and is uniformly pink to green without purple mottling (very slight mottling occasionally in H. officinalis). The follicles vary greatly in length and in the number of seeds contained within them. Observations are recorded under the species but these should not be taken as diagnostic as they are based on too few cases. A pair of horns 220 mm long in H. currorii contained 414 seeds while a pair 160 mm long contained 505 seeds and a single horn 140 mm long on H. juttae contained 270 seeds. The follicles in Sect. Trichocaulon are mostly shorter with fewer seeds (observed up to 180 mm in H. flava, in this case with 210 seeds in the pair, but usually less than 130 mm). In H. alstonii they are usually only about 40 mm long and a pair may contain as few as 55 seeds.

Follicles in Lavrania are very variable in shape. In L. haagnerae they are slender (3–4 mm thick at maximum). In L. marlothii they are slightly stouter and are the longest in the genus (to 100 mm). They contain relatively few of the large seeds (e.g. only 54 in a single horn 95 mm long). In the other species they are much stouter (up to 10 mm thick). In L. picta, L. haagnerae and L. marlothii the horns diverge at 30–60°. In L. perlata and L. cactiformis they frequently diverge at over 180° and are parallel to or adpressed to the surface of the stem. From the middle they often curve upwards a little towards the apex of

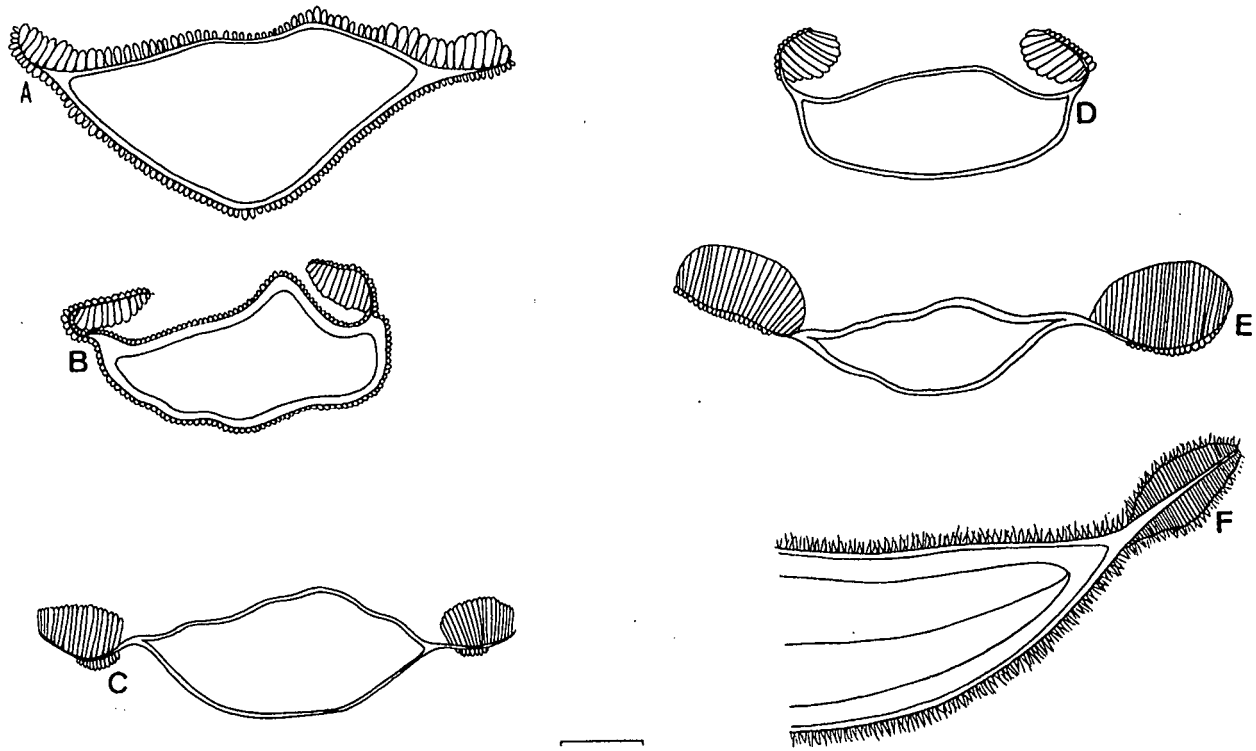


Figure 14
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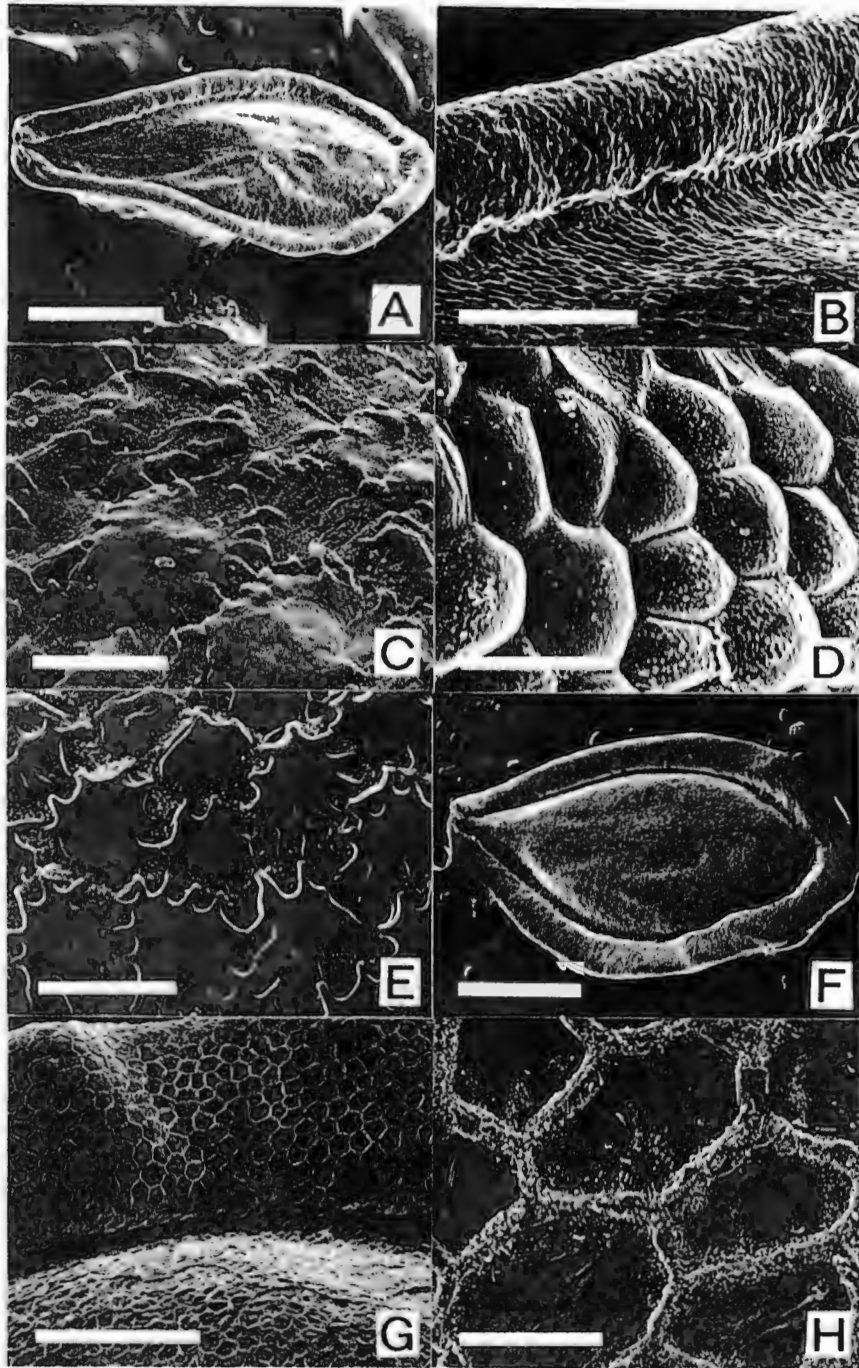
Figure 14.—Transverse sections of several Asclepiad seeds showing margins. A, Quaqua pruinosa (Bruyns 4642). B, Richteranthus columnaris (cult. material). C, Lavrania picta subsp. parvipuncta (Bruyns 3750). D, L. cactiformis (Bruyns 4656). E, Huernia plowesii (Bruyns 3152). F, Pergularia tomentosa (Morocco, Jonkers 215).
 Scale bar: 0.5 mm.

the plant, while remaining \pm parallel to its surface. In L.cactiformis the horns are often only 20–30 mm long and up to 10 mm thick. Nevertheless, they bear a remarkable number of the small seeds: 104 and 70 were observed in 2 single horns 30 and 20 mm long respectively. In L.perlata the pod is usually \pm 50 mm long. In all species of Sect. Cactoidea the follicles become deeply mottled with purple on exposure to bright sunlight and may be \pm uniformly dark purple in L.cactiformis.

Albers & Sylla (1989) have shown that seeds in the Stapelieae are remarkable for their well-developed margin. The seed is circular to pear-shaped with flat to concave ventral surface and \pm convex dorsal surface with a tuft of straight, simple hairs (coma) attached at the micropylar end. Around the perimeter of the seed (except at the micropylar end) the epidermis extends into a brittle, protruding ridge which may project horizontally but is often folded up towards the ventral surface (Figure 14). The cells on the ventral surface of this ridge elongate massively to form a layer of palisade-like translucent tissue, thickest in the middle of the ridge and narrowing to its edges. On the dorsal surface a much smaller elongation occurs. This palisade-like tissue is usually shiny on the surface and differently-coloured from the rest of the seed, lending it the characteristic pale border. The cells are dead (when the seed is released) and their walls are reticulated with pits.

Differently-coloured seed borders are not restricted to the Stapelieae and we have observed them also in Fockea and Pergularia (Marsdenieae). In Fockea the construction is similar to that shown in Abb. 5.B.b (Albers & Sylla 1989, p. 487). In Pergularia (Fig. 14 F) the pilose seeds have a hard, dark brown epidermis (amber-like when cut) and elongated palisade-like cells arise to an equal height in a cluster on both sides of the edge to form a pale border.

Figure 15.—SEM views of *Hoodia* seeds. *H. flava*, Bruyns 3070. A, whole seed ventral view. B, border and surrounding area, ventral. C, border. D, dorsal side.



H. alstonii, Bruyns 4646. E, sculpturing on border. *H. officinalis* subsp. *officinalis*, Bruyns 3179. F, whole seed, ventral. G, border and surrounding area, ventral. H, border, ventral.

Scale bars (approximate): A, F, 2 mm; B, G, 500 μm ; C–E, H, 50 μm .

In southern Africa most stapeliad seeds have a noticeably differently-coloured, shiny border as described above with the rest of the seed \pm smooth. A small group of genera restricted to the south and western Cape (Quaqua, Pectinaria, Notechidnopsis, Richteranthus, Tridentea Sect. Caruncularia) have seeds where the border is indistinguishable from the rest of the seed. In these the seed is \pm uniformly coloured and mostly covered with the same elongated cells making up the border — they are somewhat longer towards the perimeter so that a border is still present, if indistinct. This arrangement seems to lie inbetween the \pm undifferentiated seed of, for example, Microlooma and the typical stapeliad seed where elongation of the epidermal cells is restricted to the margin.

All Hoodia and Lavrania seeds have a well-developed, differently-coloured border. Seeds in Hoodia are all similar, \pm pear-shaped and relatively flat (Fig. 15 A, F). They vary from 7.5–8 mm long in H.ruschii to \pm 5 mm long in H.pilifera subsp. pilifera. The border is cream-coloured to pale brown and is not folded out of sight. The coma hairs are 15–25 mm long and are more readily detached in Sect. Trichocaulon than Sect. Hoodia. The upper wall of each border cell is polygonally partitioned and smooth in H.officinalis subsp. officinalis (Fig. 15 G, H) but variously sculptured in most of the other species (Fig. 15 C, E).

Seeds in Lavrania are less uniform. All have a pale cream border on the upper side and they vary from \pm 7 mm in L.haagnerae to 3 mm long in L.cactiformis. In L.marlothii they are about 6 mm long, flat and grey and this species has the unique arrangement of a narrow band of hairs, slightly shorter than the hairs of the coma extending from the micropyle to half-way around each side (Fig. 16 A–C). These hairs are attached along the perimeter of the epidermis exactly at the edge of the cream border (the thickness of the

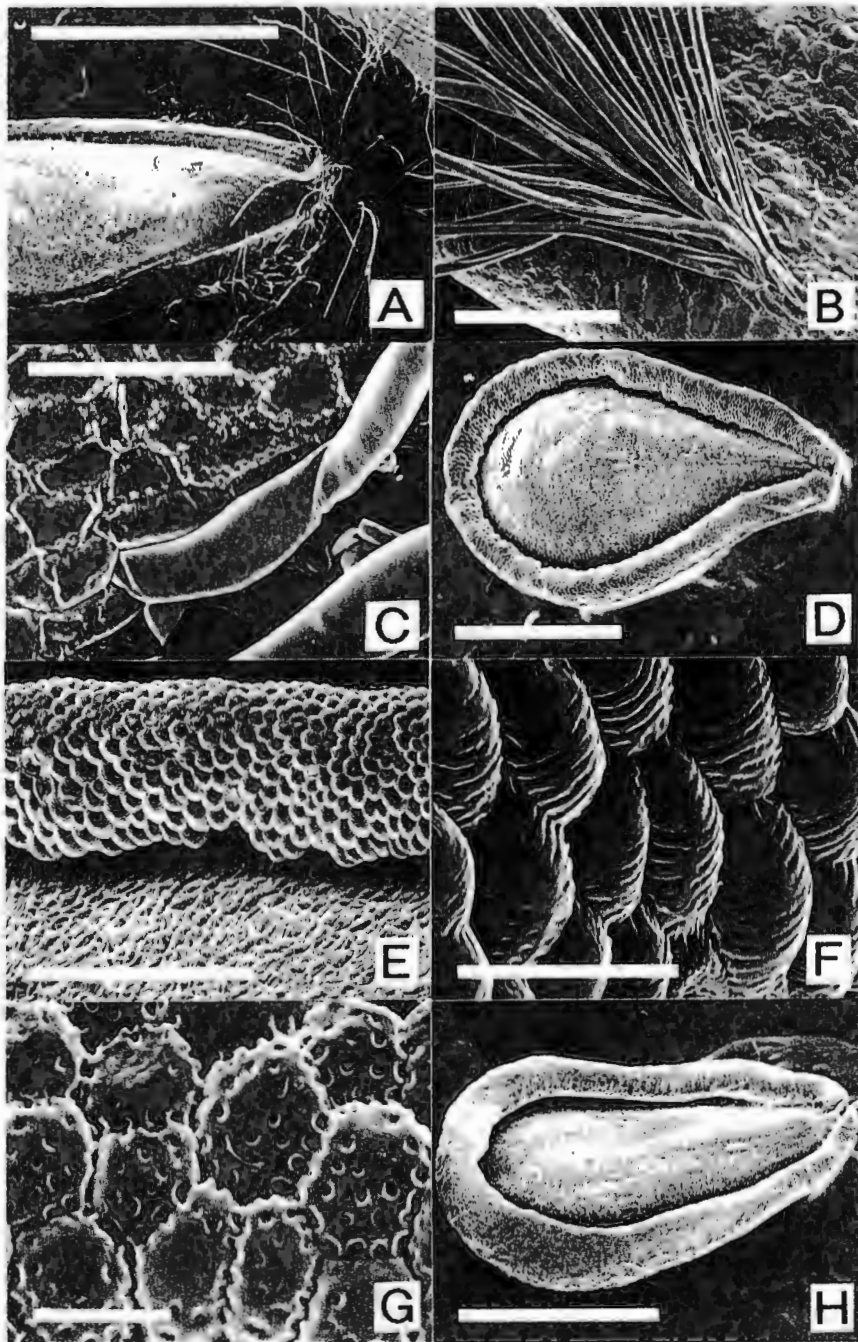


Figure 16.—SEM views of *Lavrania* seeds. *L. marlothii*, Heunis 17. A, whole seed, dorsal view, coma removed. B, hairs extending along margin, dorsal. C, individual hair along margin. *L. picta* subsp. *picta*, Heunis 3. D, whole seed, ventral. E, border and surrounding, ventral. F, border. *L. picta* subsp. *parvipuncta*, Heunis 6. G, border. *L. lactiformis*, Heunis 9. H, whole seed, ventral view.

Scale bars (approximate): A, 5mm; B, 200 μm ; C, F, 100 μm ; D, H, 2 mm; E, 500 μm ; G, 50 μm .

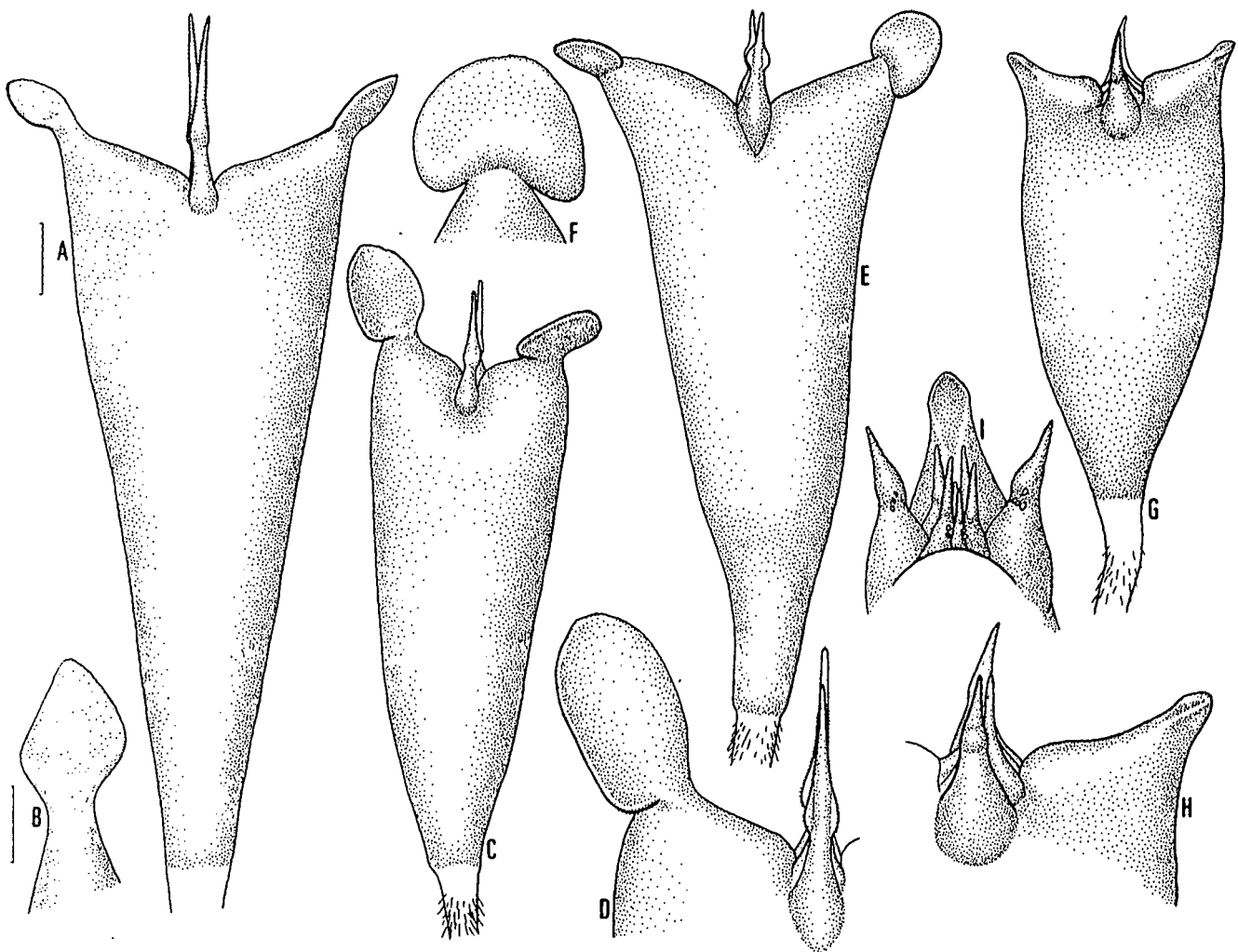


Figure 17
Hoodia
seedlings
10/6/62

Figure 17.—Seedlings of *Hoodia*. *H. parviflora*, Bruyns 4084. A, side view of plant 40 days old. B, close-up of face of cotyledon.

H. officinalis subsp. *officinalis*, Bruyns 3069. C, side view of plant 13 days old. D, close-up of face of cotyledon.

H. pedicellata, E. Erb, Swakopmund. E, side view of plant 26 days old. F, close-up of face of cotyledon.

H. pilifera subsp. *pilifera*, Bruyns 4201. G, side view of plant 23 days old. H, close-up of cotyledon and apical bud from side. I, close-up of face of cotyledon and apical bud. Note stipular glands.

Scale bar: A, C, E, G, 2 mm (at A); B, D, F, H, I, 1 mm (at B).

border makes them appear to arise on the dorsal surface) and each is a single, elongated epidermal cell. The coma of scarcely diverging hairs 13–25 mm long detaches with some difficulty.

In L.perlata the seed is pear-shaped but broad and flat with the rear and upper surface (inside border) reddish-brown. The coma of hairs 7–10 mm long is easily detached. In L.picta (Fig. 16 D) the seed is narrower than in L.perlata but still flat. It is brown on both sides (inside border) with easily detached coma of hairs 12–15 mm long. In L.cactiformis (Fig. 16 H) the tiny pear-shaped seed is folded tightly lengthways so that the cream-coloured border is mostly folded out of sight. It is brown to nearly black on the rear and upper surface with easily detached coma 7–10 mm long. In all except L.cactiformis the outer cell walls of the border were variously sculptured (Fig. 16 E–G).

Seedlings

Observations on the shape of stapeliad seedlings have been made over a broad spectrum of taxa by Spearing (1989, 1990). Since an almost complete collection of Hoodia and Lavrania species has been maintained, it has been possible to pollinate them and examine the seed and seedlings of most.

As with the seed, the shape of the seedling in Hoodia (Fig. 17) is far more uniform than in Lavrania. In all taxa except L.cactiformis, the seedling has an elongated, laterally flattened, cuneiform hypocotyl, widening from ground level towards the cotyledons. The hypocotyl ends \pm at ground level giving way to the radicle which almost immediately bears root hairs. The two cotyledons are perched obliquely on the upper ends of the hypocotyl. Fig. 17 A, C, E show typical Hoodia seedlings with broad, flat hypocotyl, relatively large cotyledons (variable in shape but always with much narrowed base) and the first leaves

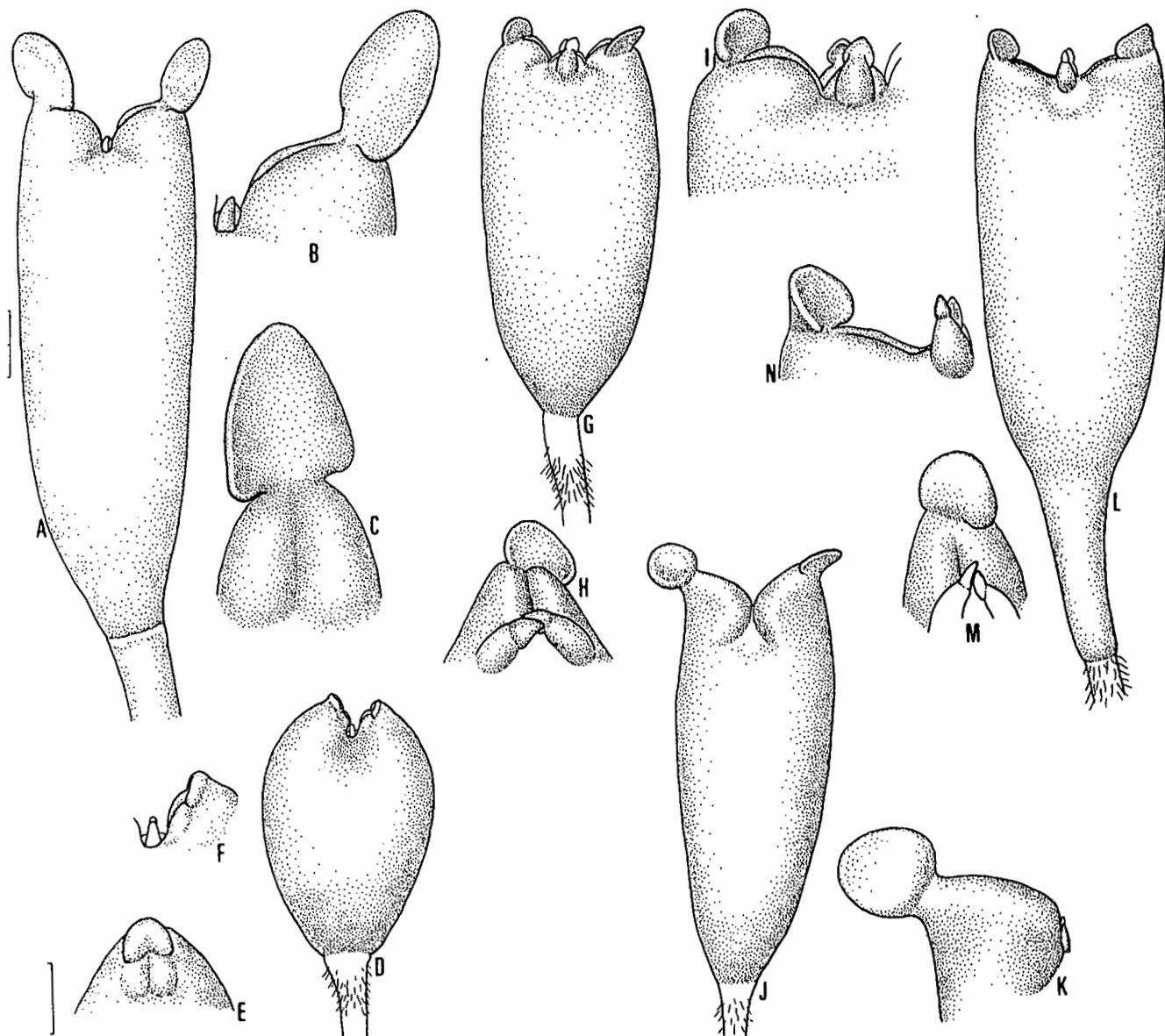


Figure 18
Teredoselen
seedlings
cotyled.

Figure 18.—Seedlings of *Lavrania*. *L.marlothii*, Heunis 1. A, side view of plant 20 days old. B, close-up of cotyledon from side. C, close-up of face of cotyledon.

L.lactiformis, Bruyns 3229a. D, side view of plant 20 days old. E, close-up of face of cotyledon. F, close-up of cotyledon from side.

L.picta subsp. *picta*, Bruyns 3904. G, side view of plant 23 days old. H, close-up of face of cotyledon. I, close-up of cotyledon and apical bud from side.

L.haagnerae, Bruyns 4069. J, side view of plant 20 days old. K, close-up of cotyledon from side.

L.perlata, Bruyns 3942. L, side view of plant 26 days old. M, close-up of face of cotyledon. N, close-up of cotyledon and apical bud from side.

Scale bar: A, D, G, J, L, 2 mm (at A); B, C, E, F, H, I, K, M, N, 1 mm (at E).

(spines) beginning to appear. Fig. 17 G shows the seedling of H.pilifera subsp. pilifera with reduced cotyledons (similar to those of Quaqua), thicker, shorter leaves and tiny stipular glands.

The position in Lavrana (Fig. 18) is more complicated. Seedlings of L.marlothii are similar to Hoodia seedlings with broad, flat, wedge-shaped hypocotyl and broad, semicircular, flat cotyledons. In both L.picta and L.perlata the hypocotyl is parallel-sided (not widening towards the top) and the more succulent cotyledons are smaller and more broadly attached to its summit. L.cactiformis (Fig. 18 D-F) is the most unusual. It is very stout and fat, sometimes nearly spherical in shape and the cotyledons are tiny, very succulent, scarcely separated from the apex of the hypocotyl and very close together. In all these species the apex of the hypocotyl has two grooves running from the bases of the cotyledons inwards towards the terminal bud. In L.haagnerae these grooves are missing but the seedling is otherwise as in L.marlothii.

Uses

Hoodia officinalis was originally imported to the USA for treatment of piles (Brown 1909, p. 894). The more widespread species of Sect. Trichocaulon such as H.flava, H.officinalis and H.pilifera are commonly known as "Ghaap" (a name not unique, though to these plants) and are widely prized by farm-workers and many farmers for their edible stems. Stems are broken or cut off, rubbed on a stone to remove the spines, cut into strips and these strips are eaten. They have a peculiar pervasively spreading sweet taste which is remarkably persistent and is said to quench thirst and hunger for extended periods. We have been told by some farmers that they make a very tasty preserve, but have never seen

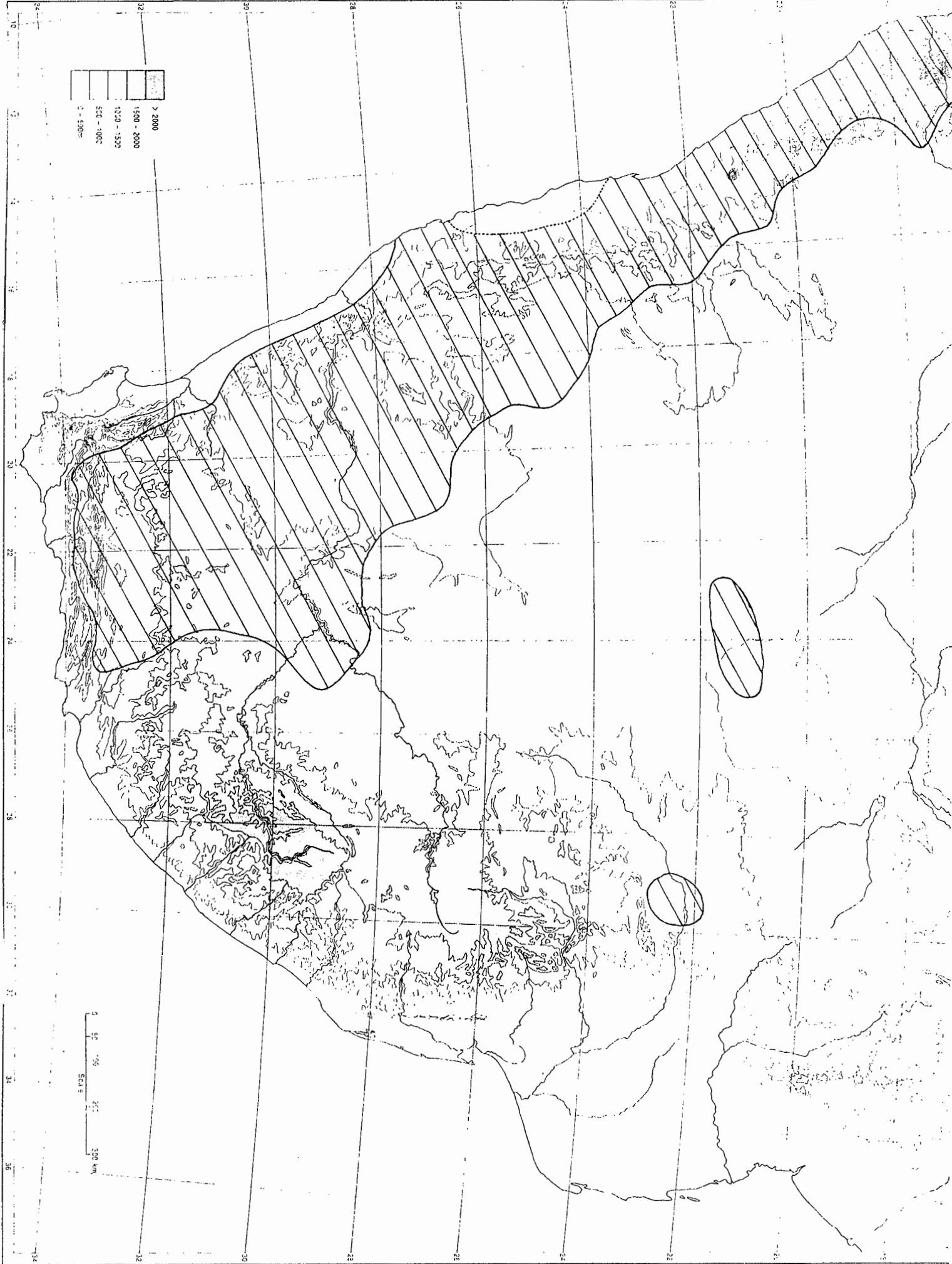


Figure 19 - North Atlantic

this done. As a consequence of their edibility and of the general degradation of vast parts of southern Africa through overgrazing by sheep and goats, these species have practically disappeared in some areas where they were formerly abundant.

The larger, hard-spined species such as H.gordonii, H.curreorii and H.alstonii are more rarely eaten. Their lower status as a food is indicated by names like "muishondghaap" or "jakkalsghaap". They have a more bitter flavour which spreads around the mouth and is difficult to get rid of. As with all species, though, the young pods are much sought after for their sweetness.

Lavranias are never eaten. They have an extremely strong, bitter taste and are widely (but probably falsely) considered poisonous. Nevertheless they are mostly well-known where they occur. Their phallic shape has led to all manner of delightful colloquial names such as "hondebal", "perdebal" and "perdepiel". They are sometimes known too as "bobbejaan seep".

Distribution

As shown in Figures 19, 20, Hoodia and Lavrania are both closely associated with the whole length of the Namib Desert, occurring especially along its edges and in the dry, stony "Pro Namib" region bounding the desert on the eastern side. They are also extensively associated with the valley of the Orange River along which they advance far to the east and are exclusively plants of arid to very arid regions.

In south-western Angola they occur south of 13° S (Hoodia only) mainly within 100 km of the coast. In Namibia they are found along the whole length of the western seaboard

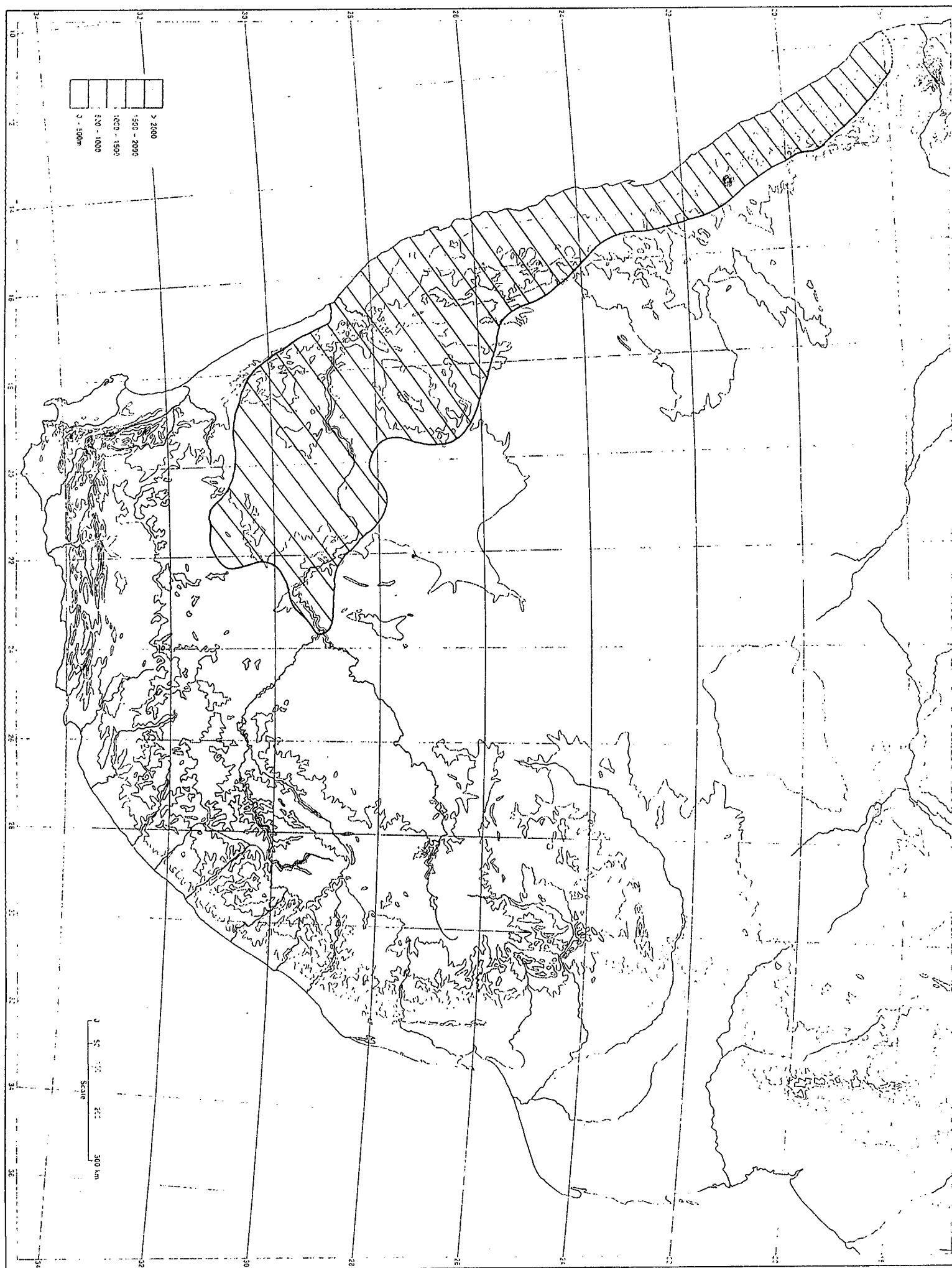


Figure 20.—Distribution of *Lavrania*.

in a belt which is narrow in the north but broadens out south of the high region around Windhoek to include most of the arid south. In South Africa both genera occur mainly in the Cape Province in Namaqualand and Bushmanland. A few species come further south across the Great Karoo, reaching 33° S and there are a few records from the dry western portion of the Orange Free State (H.gordonii, H.officinalis). The very isolated H.currorii subsp. lugardii occurs in a small area in the northern Transvaal (South Africa) and is the only species of either genus recorded from Botswana and Zimbabwe.

In Sect. Hoodia, H.gordonii and H.currorii cover the whole distribution of the genus and are only sympatric in a small area (Swakopmund to Karibib, Namibia). H.parviflora, which is closely related to H.currorii, is more local to the mountains of SW Angola and NW Namibia and occurs just adjacent to H.currorii. H.dregei and H.juttae are very local and grow within the distribution of H.gordonii, to which both are closely allied. In Sect. Trichocaulon the situation is more complex but the two "basic" species appear to be H.flava and H.officinalis. The rather specialized but quite widely distributed H.pedicellata and the very local H.ruschii and H.triebneri are all closely allied to H.officinalis. H.alstonii and H.pilifera occur around the edges of the distribution area of H.flava. H.pilifera subsp. pilifera and H.alstonii occur mainly within the winter rainfall belt of the western Cape Province and H.officinalis subsp. delatiana occurs exclusively within it. All the others occur in the regions of all year or summer rainfall.

In Lavrania, L.marlothii covers nearly the whole distribution area, with the papillate-flowered taxa occurring ± allopatrically with it — L.haagnerae very local in Damaraland (N Namibia), L.perlata and L.cactiformis in the winter rainfall zone and L.picta in the all year/summer rainfall parts.

As in the case of Microloma (Bruyns & Linder 1991) all the species are found within the "extended winter rainfall" area of Bayer (1984). Unlike Microloma, they are much

more resilient and thus, where the retreat of the winter rainfall and increasing aridity have left Microlooma confined to certain high mountains in the Namib region, Hoodia and Lavrana have remained widespread.

Taxonomy

Infrageneric relationships

Hoodia is divided into two sections. Hoodia Sect. Hoodia consists of those species formerly in Hoodia except for H.ruschii. It is characterised by the generally thin stems relative to their length (though H.parviflora of this section has the thickest stems of all Hoodia spp.), forming robust, free-standing shrubs with the tubercles on the stems arranged into 11–18, usually quite readily observable rows. The spines on the tubercles are sharp and hard. Flowers are borne on thick pedicels and are large, saucer- to funnel-shaped and only obscurely five-lobed. The corona is uniformly cupular, only varying somewhat between the species in the height of the outer corona lobes. Within this section the differences between species are often small. The distinctions between H.gordonii and H.currorii are subtle in some areas but where they occur near one another they can easily be separated. It is even more difficult to separate H.juttae and H.gordonii in a key but in the field no problems arise in distinguishing the two.

Hoodia Sect. Trichocaulon includes Hoodia ruschii and all the "spiny" members of the former genus Trichocaulon. In this section the stems are mostly much thicker and shorter and less robustly shrub-forming. In H.triebneri the tubercles are arranged into 12–14 angles but in the others 16–34 angles can be found on the stems. The spines on the tubercles are mostly weak (H.alstonii, H.ruschii and H.triebneri excepted). Flowers are borne on pedicels < 1 mm thick, often less than 1 mm long as well and are small, always with 5

deltoid lobes. The corona varies from a cupular structure very similar to that in Sect. Hoodia (H.officinalis, H.ruschii, H.triebneri) to ones with more deeply bifid and widely spreading outer lobes which lend it a quite different appearance (H.pilifera, H.flava). In this section species are mostly very distinctive. In the case of H.pilifera intermediates have been found between the former T.piliferum, T.pillansii and T.annulatum and consequently their status is changed. Also it is considered that Trichocaulon officinale and T.delaetianum are too similar to be maintained as distinct species. The difference between them in the papillae on the surface of the corolla is similar to the variation in these papillae found in H.gordonii except that in H.officinalis it is more clearly geographically determined. Thus subspecies is considered here to be the most appropriate rank.

The remainder of the former genus Trichocaulon, the so-called "spineless species", has been moved to Lavrancia which was monotypic. This genus now consists of two sections. One monotypic section contains the type species, L.haagnerae. Here the cylindrical stems are produced in prolific clusters of up to 100 or more, the flowers arise in relatively few inflorescences in the lower half of the stem and in upper parts the stem has neat, regular rows of tubercles arranged in 10–12 angles. The flower is similar to that in the next section. The four species transferred from Trichocaulon make up the section Cactoidea. Here the stems are fewer per plant and many plants consist of a single stem only. The stems are clavate and flowers are produced in many inflorescences concentrated towards the apex of the stem. The rows of tubercles cannot be distinguished in the upper parts of the stems. Species of this section are not readily separated vegetatively. The flowers of L.perlata, with longitudinally folded corolla lobes, a false annulus and unusually-shaped papillae are the most unusual. The flowers of L.marlothii, L.picta and L.cactiformis are very similar and care has to be exercised to separate them. In particular

this is true of L.cactiformis and L.picta. However, the seeds and seedlings of these two are quite different so that they must be maintained as distinct species despite their floral similarity. It is also interesting to note that where these two species occur together the floral distinctions quite clearly separate them but it is in areas where they are not sympatric that these floral differences may occasionally be difficult to apply.

Intergeneric relationships

In the families Euphorbiaceae and especially the Cactaceae, plants with highly succulent, ± leafless, angled stems are numerous and there are many species and many whole genera where the stems are mostly more than 4-angled. In the Cactaceae it may even happen that plants with 4 or fewer angles on the stems are the adult forms of juveniles with higher numbers of angles (e.g. Taylor 1985, p.61).

However, among the ± 400 species of Stapelieae s.s., plants with more than 4-6-angled stems are relatively rare. The genera Echidnopsis, Huernia, Stapelianthus Choux, Tavaresia Welw. and Notechidnopsis each contain a few. In Hoodia (13 species) and Lavrania (5 species) all have stems with 10 or more angles. With their spiny to smooth, cylindrical stems and cactoid appearance they are thus very unusual within the group. Some of them, especially in Lavrania, are dwarf, globose to shortly cylindrical plants consisting of only a single stem. This, too, is a rare growth form among the stapeliads which is otherwise only known in Whitesloanea Chiov. and Pseudolithos Bally from north-east Africa (again in contrast to the Cactaceae, where it is common). In Hoodia, Lavrania and Pseudolithos the stems are completely covered with tubercles but, as shown in Bruyns (1990), these are quite different in Pseudolithos where the stems are actually 4-angled.

Similar leaf-spines to those of Hoodia are found only in Tavaresia. SEM investigations of the surface of these spines show them to be identical in these two genera

(and identical to that found on spines of some of the most primitive Cactaceae, see Schill et al, 1973). Under the SEM the epidermis of the tubercle in Tavaresia and Hoodia is also similar.

The leaves and epidermis of Lavrania are quite different to those of Hoodia and the sunken leaves of Lavrania Sect. Cactoidea are unique in the tribe. The papillate epidermis of all species of Lavrania is very similar to that in Pectinaria and Notechidnopsis but also to the leaves of seedlings of Hoodia. Pectinaria and Lavrania haagnerae also share the folded cells around the stomata.

Several genera (viz. Echidnopsis, Notechidnopsis s.l., Pectinaria, Piarranthus, Quaqua) share with Hoodia and Lavrania the small inflorescences mostly concentrated towards the apices of the stems (the lower inflorescences of L.haagnerae are aberrant but similar to the situation in Quaqua armata subsp. arenicola (N.E. Br.) Bruyns and need not be over-emphasized). These appear to represent a transitional stage between the much elongated inflorescences in some species of Caralluma and the few, ± basal inflorescences typical of, for example, Tavaresia, Huernia and Duvalia.

The shape and colour of the corolla in Hoodia Sect. Hoodia is quite different to that in any other stapeliad while the size, colour, surface texture and smell of flowers of Sect. Trichocaulon (especially H.pilifera, H.ruschii and H.triebneri) show similarity to those of Quaqua Sect. Robusticaulon. In Quaqua (stems 4–5–angled) the leaves are modified to hardened, conical teeth and in a few cases these may become sharp and spine-like, suggestive of the spines of Hoodia. In Quaqua stipules may be present in various forms (Meve & Albers, 1990). Although Meve & Albers give Hoodia (Trichocaulon) as stipule-less, they are in fact found (as glandular hairs) in young plants of H.pilifera and H.alstonii. In addition in H.pilifera the cotyledons have no blade, as is the case throughout

Quaqua and the papillate surface of the leaves of young plants has been observed on the teeth of some species of Quaqua. There is thus some indication that Hoodia and Quaqua may be closely allied.

Assessment of characters and cladogram

The stapeliads are monophyletic on account of the possession of at least two probable synapomorphies. These are:

- (1) the raising of each leaf onto a tubercle and the arrangement of these tubercles into vertical ridges up the stem
- (2) the reduction of the leaf to a minute rudimentary structure without a petiole

Character 0 in Table 1, that is "stems with tubercles arranged into 10–30 vertical rows or angles" is also derived. This is deduced from the fact that seedlings start off with 4 angles, the condition found in all other stapeliads. Thus there is a single synapomorphy supporting Hoodia and Lavranaia as monophyletic. There are some reasons to suspect that the sister group to our group might be Tridentea (the very similar seeds, seedlings, the remarkable stipules present in Tridentea (unpublished data) and in some seedlings of Hoodia) but I am unsure of this. Thus for the purpose of this study the sister group is assumed to be unknown and the outgroup is taken as the rest of the stapeliads.

In the present study the following 8 characters were used to define genera and sections. Each character is assigned the states 0, 1 or 2 for the four groups and the outgroup (see Table 1) and reasons for assigning these values are given below. From these a single cladogram^(Figure 20 A) of shortest length (with two optimizations of character 7) is derived. It has length 10, consistency index 100 and retention index 100. From this it can be seen that my assumption concerning the evolutionary series for character 1 is not supported by the cladogram. It is also possible to assume that character 4 was in the advanced state at node G and suffered a reversal on the left hand side of the tree, remaining in the advanced state for nodes C and D.

Character	<u>Hoodia Sect.</u>	<u>Hoodia Sect.</u>	<u>Lavrania Sect.</u>	<u>Lavrania Sect.</u>	Outgroup
	<u>Hoodia</u>	<u>Trichocaulon</u>	<u>Lavrania</u>	<u>Cactoidea</u>	
0	1	1	1	1	0
1	2	2	1	0	0
2	0	0	1	1	0
3	0	0	1	1	0
4	0	0	1	1	?
5	0	0	1	0	?
6	0	0	1	0	?
7	0	1 (0)	1	1	?
8	1	0	0	0	0

TABLE 1. Character states for Hoodia and Lavrania.

Characters

1. Leaf a flattened body less than 1 mm long (0); a conical body < 1 mm long (1); a sharp spine 3–15 mm long.

Minute flattened leaves are found in most other stapeliads except for a few cases outside our group where again a sharp spine develops. In seedlings of plants which later develop sharp spines the first few leaves are also flattened. Thus it is deduced that the primitive state (0) should be assigned to flattened leaves and the derived state is the sharp spine.

2. Base of spine raised on tubercle (0); leaf sunken into apex of tubercle (1)

"Leaves raised on tubercles" is found throughout the stapeliads, with sunken leaves unique to Lavrania. Seedlings of Lavrania do not have leaves sunken into apex of tubercle hence this is taken as derived.

3. Tubercles joined into ridges up stem (0); tubercles discrete, not joined into ridges (1).

States are assigned by reference to the outgroup, the first being the condition throughout the rest of the stapeliads.

4. Epidermal cells flat (0); epidermal cells raised into papillae (1).

Unpublished data has shown that in several groups in the stapeliads there is a cline from flat epidermal cells to cells raised into hairs, with all intermediate stages. It is assumed that the situation with cells raised into hairs is the most derived state and that parallel evolution of this character occurs in several groups in the stapeliads.

5. Flowers arising in upper half of stem (0); flowers arising near base of stem (1)

All inflorescences in the Asclepiadaceae are terminal. The second state is caused by inhibition of development of the inflorescence, probably by the adjacent axillary bud (see

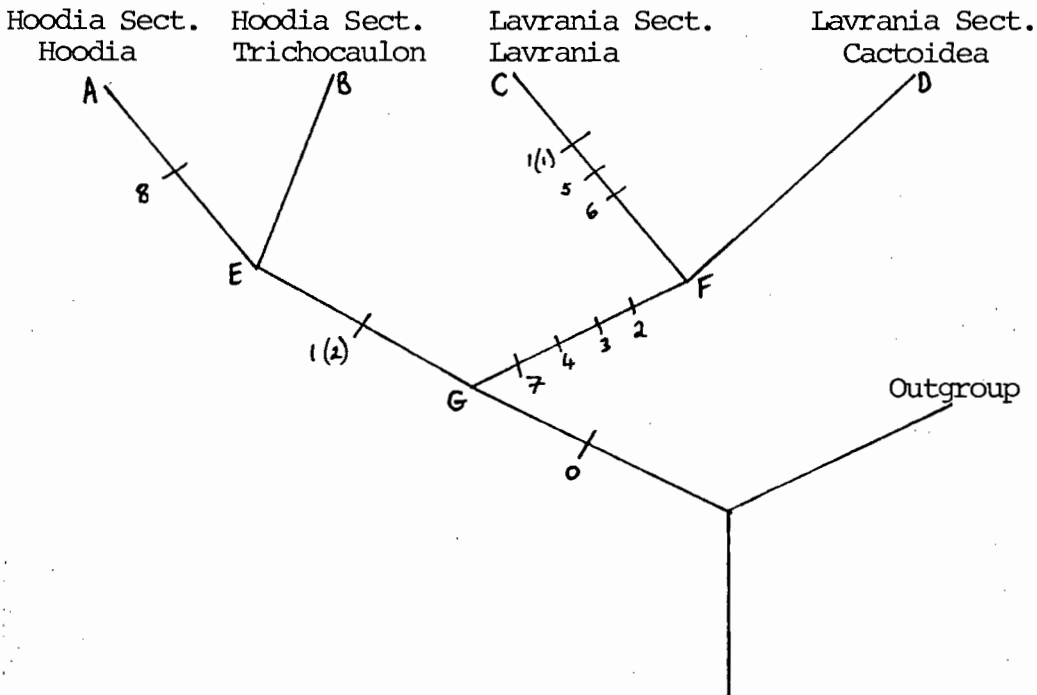
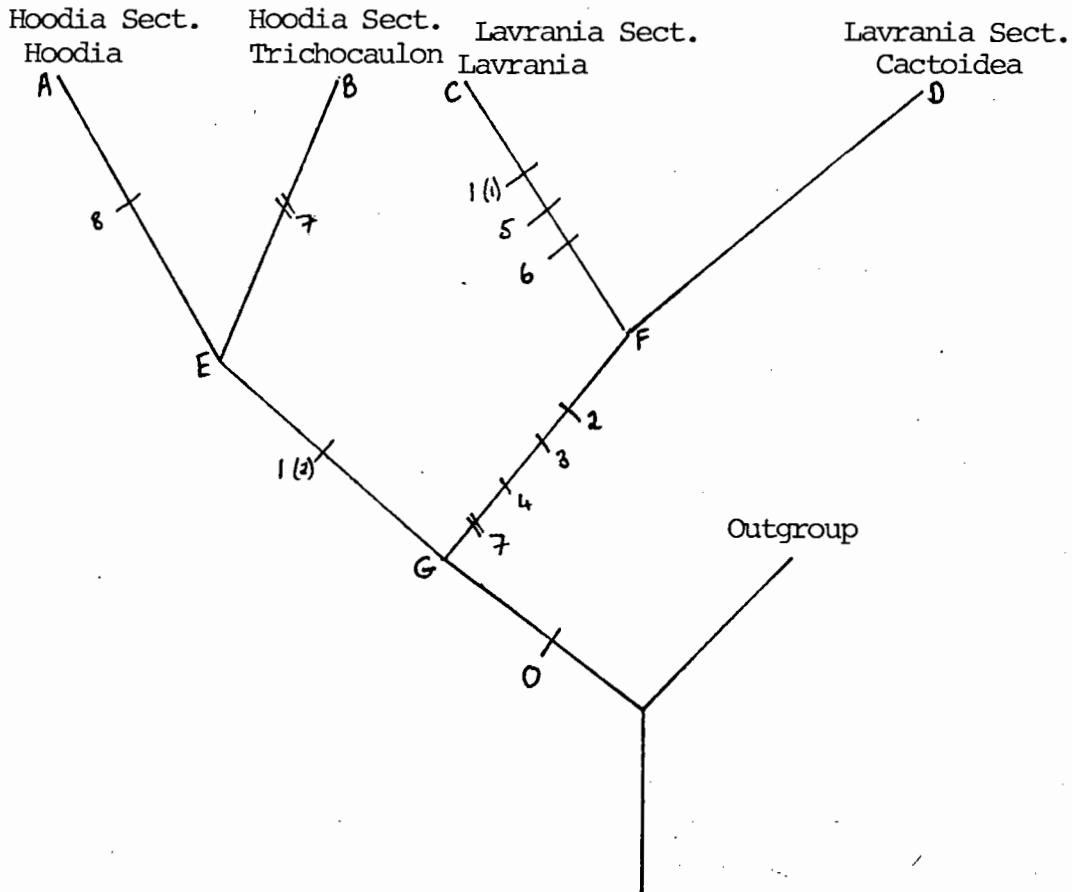


Figure 20A Cladograms of genera and sections from character data in Table 1.

discussion on inflorescences above). Thus it is assumed derived. As in character 4, both states are found widely in the stapeliads but it is not clear what the primitive state in the outgroup is and hence "?" is used.

6. Inflorescences more than 5 per stem (0); inflorescences 1–4 per stem (1).

It is here assumed that reduction in numbers is a derived state. Both states are found widely in the tribe (the former in Echidnopsis, Caralluma, the latter in Stapelia, Huernia).

7. Flowers 25–170 mm diameter, pedicels 2–4 mm thick (0); flowers 8–20 mm diam., pedicels < 1 mm thick (1).

It is generally found in the stapeliads that larger flowers are held on thicker pedicels, hence the placing together of these characters. As in the case of character 4, it is often found among the stapeliads that there is a cline among closely related species from large (sometimes very large) flowers to small flowers. Here it is assumed that a reduction in size is derived. In Sect. Trichocaulon a single subspecies (of H. pilifera) has large flowers, hence the coding of "1 (0)" in the table.

8. Flowers deeply divided by lobes, lobes deltoid to deltoid–ovate, without filiform tip (0); flowers nearly circular in outline with narrow, filiform tips to lobes (1).

The first state is found throughout the stapeliads except in species with urceolate corollas and the second is unique to Hoodia sect. Hoodia and thus is assumed derived.

TAXONOMIC ACCOUNT

Key to the genera

1. Tubercles on stems each tipped with spine or stiff bristle (1.5) 3–12 mm long initially green but rapidly drying out to grey or brownish, base of spine/bristle not depressed into apex of tubercle.....A. Hoodia
1. Tubercles on stems each tipped with small conical persistent leaf < 1 mm long, remaining grey–green and not drying out, usually sunken into apex of tubercle.....B. Lavrania

A. Hoodia Sweet ex Decne in DC. Prodr. 8: 644 (1844). – K. Schum. in Engl. & Prantl, natürl. Pflanzenfam. 4 (2): 274 (1895). – N.E. Br. in Fl. Trop. Africa 4 (1): 490 (1903) et in Fl. Cap. 4 (1): 896 (1909). – White & Sloane, Stap. 3: 1050 (1937) – Bullock in Kew Bull. 1956: 508 (1957). – Huber in Prodr. Fl. SWA 114: 33 (1967). – Dyer in Gen. Southern African Flow. Pl. 1: 489 (1975). Stapelia L. pro parte S.gordonii Masson. Type: Hoodia gordonii (Masson) Sweet ex Decne.

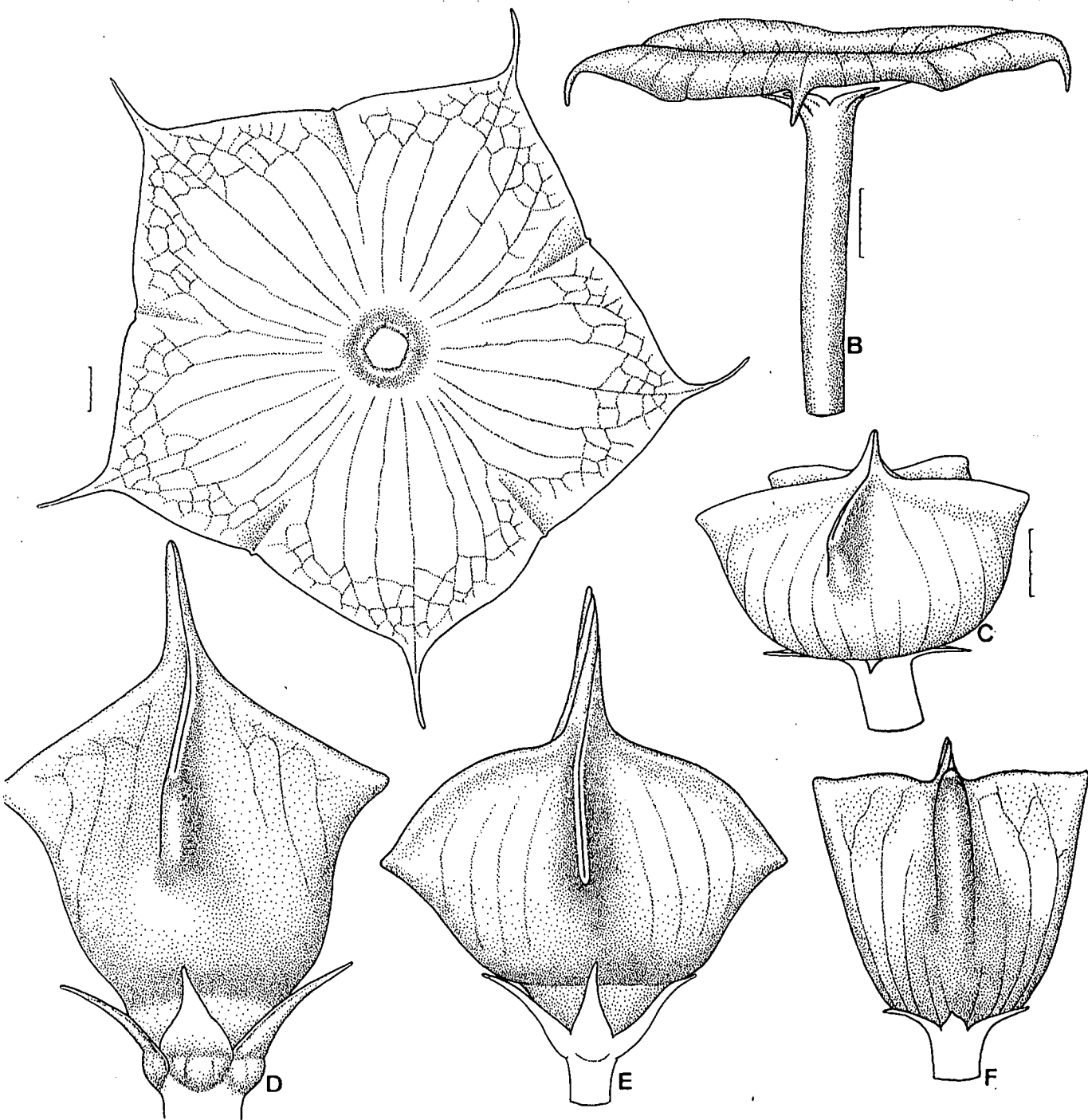


Figure 21
 Hoodia
 2/1/50

Figure 21.—Hoodia Sect. Hoodia. A, face view of flower (H. currorii subsp. currorii, Bruyns 3592), this flower rather more deeply lobed than usual. B, side view of flower (H. juttae, Bruyns 3508), showing typical shallow saucer-shape. Buds: C, H. juttae, Bruyns 3508. D, H. parviflora, Bruyns 4084. E, H. currorii subsp. lugardii, Bruyns 4471. F, H. gordonii, near Beaufort West..

Scale bar: A, 10 mm; B, 5 mm; C–E, 3 mm; F, 5 mm.

Gonostemon Haw. pro parte G.gordonii (Mass.) Sweet, Hort. Brit. Ed. 1: 278 (1826).

Monothylaceum G.Don, Gen. Syst. 4: 116 (1837), nom. nud.

Scytanthus W.J. Hooker in Hook. Icon. Pl. 7: t. 605-6, 625 (1844). Type: S. currorii
Hook.

Trichocaulon N.E. Brown in J. Linn. Soc. 27: 164 (1878), in Fl. Trop. Africa 4 (1): 489
(1903) et in Fl. Cap. 4 (1): 888 (1909). — K. Schum. in Engl. & Prantl, natürl.
Pflanzenfam. 4 (2): 275 (1895). — White & Sloane, Stap. 3: 991 (1937). —
Huber in Prodr. Fl. SWA 114: 66 (1967). — Dyer in Gen. Southern African Flow.
Pl. 1: 490 (1975), pro parte Sect. Eutrichocaulon White & Sloane. Stapelia L. pro
parte S.pilifera Masson. Type: Trichocaulon flavum N.E. Br.

Plant a spiny succulent consisting of (few-) many erect (rarely prostrate) stems forming
shrub, branching from base. Stems cylindrical, 25-60 (-110) mm thick, covered with obtuse
tubercles vertically arranged into 11-31 rows, each tubercle tipped with a weak to hard
sharp spine 3-12 mm long, glabrous. Flowers 1-many in groups, opening successively
(rarely simultaneously), near apex of stem. Calyx 5-lobed, lobes overlapping slightly at
broad bases, glabrous. Corolla 8-170 mm diam., small and deeply lobed to large flat and
saucer- to shallowly cup-shaped, lobes valvate in bud, glabrous outside and inside, within

papillate to smooth. Corona consisting of two series, arising from staminal column, mostly glabrous; outer corona at least basally cupular, emarginate or bifid towards apex; inner corona of 5 dorsiventrally-flattened lobes incumbent on backs of anthers, dorsally connected to outer lobes. Staminal column arising near base of corolla tube. Anthers incumbent on top of style head, subquadrate, without apical appendage. Pollinia solitary, \neq horizontal in each anther-theca, with short caudicles. Style head not produced beyond anthers, truncate-depressed at apex. Follicles terete-fusiform, slender, paired, with horns somewhat diverging ($30^{\circ} - 60^{\circ}$), uniformly-coloured, glabrous, smooth.

Two sections are recognised and may be separated as follows:

Key to sections

1. Pedicel 2–4 mm thick, flowers (20–) 25–170 mm diam., never dark red–brown to purple–black, mostly saucer–shaped with broad flat to bowl–shaped united part, rarely funnel–shaped (H. parviflora), with small tube just enclosing gynostegium, lobes much less than half as long as broad (excluding narrow tip) and shorter than breadth of united part of corolla outside corolla tube.....Sect. Hoodia
1. Pedicel \leq 1 mm thick, flowers 8–20 mm diam., if larger (20–40 mm) then dark red–brown to purple–black, if saucer–like then without small tube enclosing gynostegium, lobes more than half as long as broad and much longer than breadth of united part of corolla outside tube.....Sect. Trichocaulon

I. Section Hoodia

Key to the species

1. Corolla covered with fine hair–like bristles.....3.

1. Corolla glabrous.....2.
2. Corolla 20–55 mm diam., limb of outer corona adpressed to corolla just outside tube.....2. H. juttae
2. Corolla 50–100 mm diam., outer corona just touching side of corolla tube near mouth, not adpressed to corolla outside tube.....1. H. gordonii
3. Outer corona lobes exceeding height of inner lobes.....4.
3. Outer corona lobes not exceeding height of inner lobes.....5.
4. Corolla 28–48 mm diam., densely covered with soft white hair–like bristles obscuring colour of surface, outer corona lobes touching surface of corolla outside tube.....3. H. dregei
4. Corolla 50–100 mm diam., hairs not dense nor obscuring colour of surface, outer corona touching corolla tube near mouth and not outside tube.....1. H. gordonii
5. Corolla funnel–shaped, usually yellow or orange, stems matt bluish–green.....5. H. parviflora
5. Corolla bowl–shaped to flat, not yellow or orange, stems grey–green to brownish–green.....6.
6. Corolla (50–) 60–170 mm diam., pedicels > 12 mm long, plants from Namibia or Angola.....4a. H. currorii subsp. currorii
6. Corolla 40–75 mm diam., pedicel < 7 mm long, plants from east of 24° E.....4b. H. currorii subsp. lugardii

1. Hoodia gordonii (Masson) Sweet ex Decne in DC. Prodr. 8: 665 (1844). – N.E. Br. in Gard. Chron. 4: 452 (1875), in Hook. Icon. Pl. 20: page 3 sub t. 1905 (1890) et in Fl. Cap. 4 (1): 899 (1909). – Th.–Dyer in Bot. Mag. 102: t. 6228 (1876) et in J.

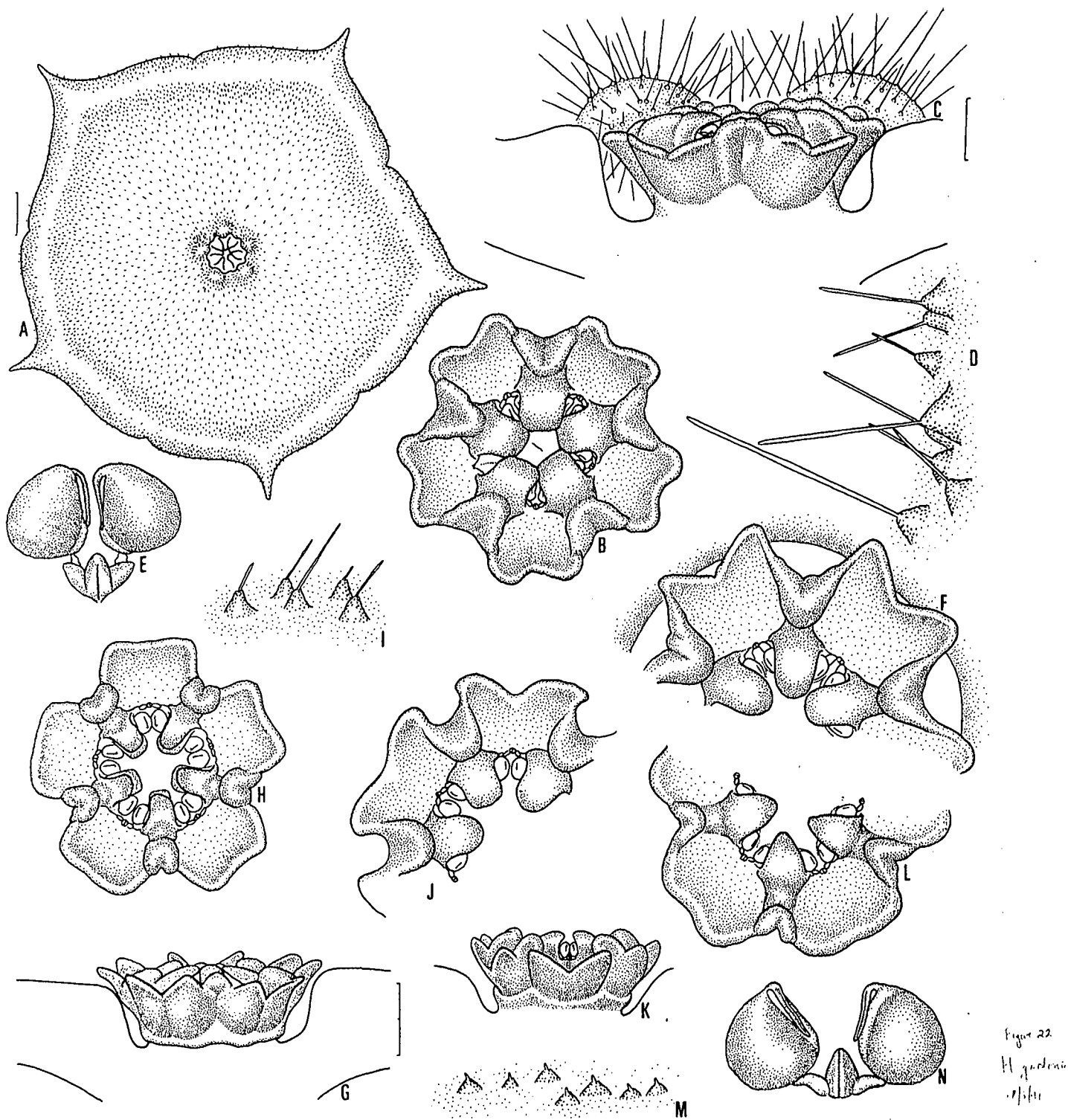


Figure 22
Hoodia gordonii
 N. J. M.

Figure 22.—*Hoodia gordonii*. A, face view of flower. B, F, H, J, L, face view of gynostegium. C, G, K, side view of gynostegium. D, I, M, papillae on corolla. E, N, pollinaria.

Drawn from: A, B, C, D, E, Cole 101, Namibia, near border east of Aroab; F, G, Bruyns 2620 (Tanqua Karoo); H, I, Bruyns 3575 (near Koës, Namibia); J, K, Bruyns 2720 (Steinkopf, Namaqualand); L, M, N, Bruyns 2621 (Tanqua Karoo).

Scale bar: A, 5 mm; B, C, F, H, J, L, 1 mm (at C); G, K, 2 mm (at G); D,

I, M, 0.5 mm (at C); E, N, 0.25 mm (at C).

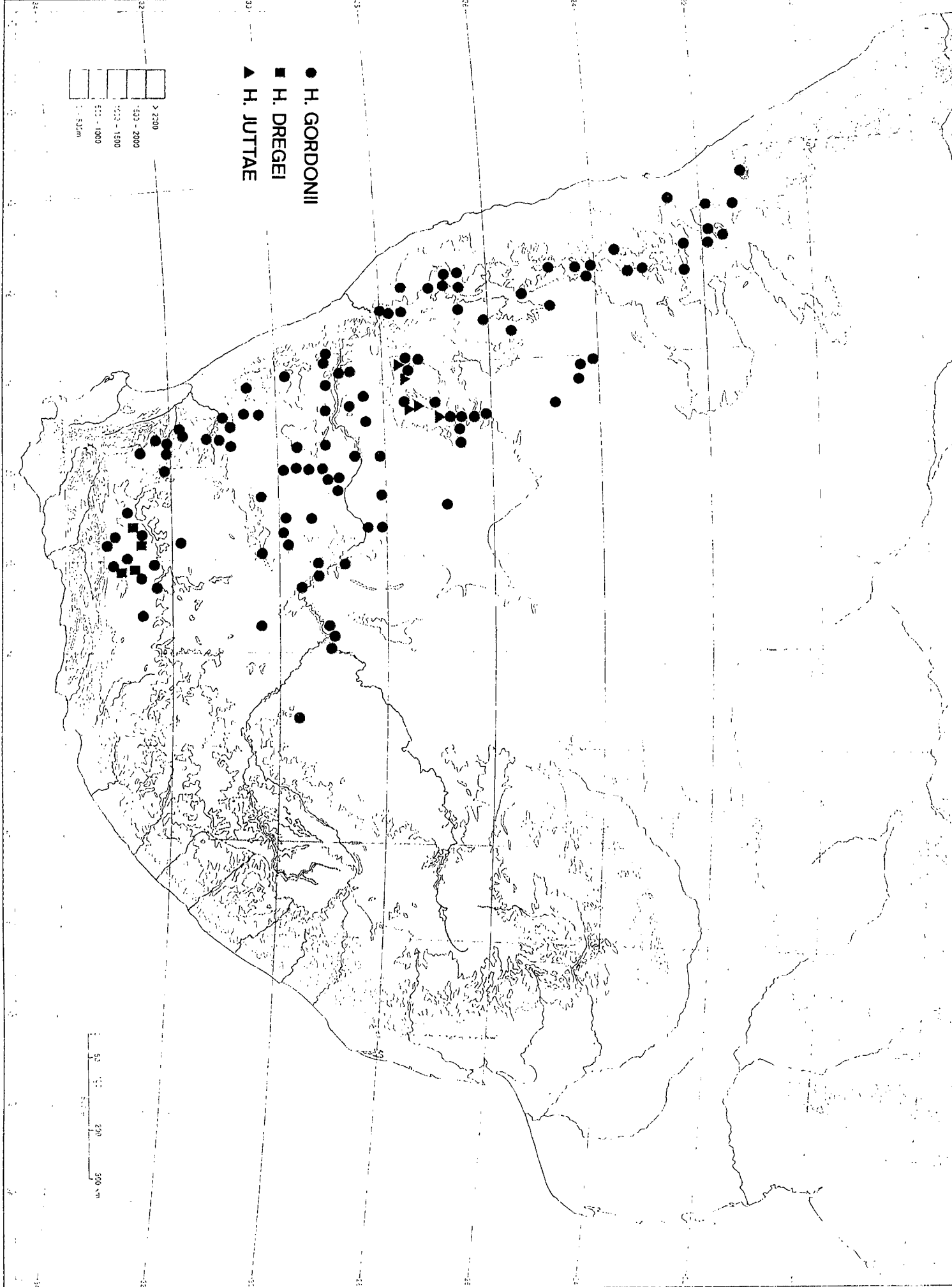


Figure 23.—Distribution of *Hoodia gordonii*, *H. dregei* and *H. juttiae*.

Th.—Dyer in Bot. Mag. 102: t. 6228 (1876) et in J. Linn. Soc. 15: 252, t. 5, fig. 1 (1876). — K. Schum. in Monatsschr. Kakt. 3: 57, fig. (). — Schltr in J. Bot.: 475 (1898). — Marloth, Das Kapland: fig. 127b (1908). — Berger, Stap. u. Klein.: 36 (1910). — White & Sloane, Stap. 3: 1076 (1937). — Lückhoff, Stap.: 267 (1952). — Huber in Prodr. Fl. SWA 114: 36 (1967). Scytanthus gordonii (Masson) W.J. Hooker in Hook. Icon. Pl. 7: t. 625 (1844). Gonostemon gordonii (Masson) Sweet, Hort. Brit. Ed. 1: 278 (1826). Monothylaceum gordonii (Masson) G. Don, Gen. Syst. 4: 116 (1837). Stapelia gordonii Masson, Stap. Nov.: 24, t. 40 (1796). — Willd., Sp. Pl. 1: 1285 (1798). — Pers., Syn. Pl. 1: 279 (1805). — Poir., Encycl. 7: 383 (1806). — Haw., Syn. Pl. Succ.: 25 (1812). — Schultes, Syst. Veg. 6: 25 (1820). — Sprenger, Syst. Veg. 1: 840 (1824). — Loudon, Encycl.: 200 (1836). — Dietr. Syn. Pl. 2: 886 (1840). Type: South Africa, Namaqualand, near Orange River, R.J. Gordon, collected between 1777 and 1780 (no material preserved). Lectotype: Masson, Stap. Nov.: t. 40 (designated here).

Hoodia barklyi Th.—Dyer in J. Linn. Soc. 15: 252 (1876). — N.E. Br. in Hook. Icon. Pl. 20: page 3 sub t. 1905 (1890) et in Fl. Cap. 4 (1): 897 (1909). — K. Schum. in Engl. & Prantl, Pflanzenfam. 4 (2): 275 (1897). — Schltr in J. Bot.: 475 (1898). — Berger, Stap. u. Klein.: 38 (1910). — White & Sloane, Stap. 3: 1086 (1937). Type: South Africa, Karoo, 1873, Lycett comm. McGibbon & Barkly (K¹)

Hoodia bainii Th.—Dyer in Bot. Mag. 34: t. 6348 (1878). — N.E. Br. in Hook. Icon. Pl. 20: page 3 sub t. 1905 (1890) et in Fl. Cap. 4 (1): 897 (1909). — K. Schum. in Engl. & Prantl, Nat. Pflanzenfam. 4 (2): 275 (1897). — Schltr in J. Bot.: 475 (1898). — Berger, Stap. u. Klein.: 38 (1910). — Pole Evans in Flow. Pl. S. Africa 3: t. 93

(1923). — Marloth in Fl. S. Africa 3 (1): 92, fig. 44, t. 21c (1932). — White & Sloane, Stap. 3: 1084 (1937). — Lückhoff, Stap.: 269, 270 (1952). — Huber in Prodr. Fl. SWA 114: 35 (1967). Type: South Africa, Uitkyk on road to Beaufort West, autumn 1876, Bain 11 (K!)

Hoodia pillansii N.E. Br. in Fl. Cap. 4 (1): 898 (1909). — White & Sloane, Stap. 3: 1081 (1937). — Dyer in Flow. Pl. Africa 45: t. 1768 (1978). Type: South Africa, Prince Albert region, Grootfontein, Jan. 1904, Pillans 164 (K, holo. BOI)

Hoodia burkei N.E. Br. in Fl. Cap. 4 (1): 899 (1909). — White & Sloane, Stap. 3: 1083 (1937). Type: South Africa, Beaufort West region, near Gamka River, Burke 464 (K!)

Hoodia rosea Obermeyer & Letty in Flow. Pl. S. Africa 16: t. 615 (1936). — White & Sloane, Stap. 3: 1071 (1937). — Huber in Prodr. Fl. SWA 114: 36 (1967). Type: South Africa, Cape, Rietvlei (Gordonia), Lang & E.Schweickerdt in Tvl Mus. 34896 (PRE!)

Hoodia langii Obermeyer & Letty in White & Sloane, Stap. 3: 1067 (1937). Type: South Africa, about 90 miles west of Upington, April 1933, Lang & E.Schweickerdt in Tvl Mus. 32843 (PRE!)

'Hoodia lugardii' sensu Phillips in Flow. Pl. S. Africa 16: t. 617 (1936).

Hoodia husabensis Nel in White & Sloane, Stap. 3: 1069 (1937). — Huber in Prodr. Fl. SWA 114: 36 (1967). Type: Namibia, Husab gorge, June 1935, Boss sub SUG 6920 (no material preserved). Lectotype: Figure 1145 of White & Sloane, l.c. (designated here).

Hoodia whitesloaneana Dinter ex White & Sloane, Stap. 3: 1071–2, nom nud. Based on: Namibia, Kuankib between Gurub and Tschamis, 24 Dec. 1934, E.Rusch sub Dinter 8272 (BOI! Z! G!)

Hoodia dinteri Schltr ex Dinter in Feddes Rep. sp. nov. 18: 425 (1922), nom. nud. Based on: Namibia, between Witvley and Mariental, Dinter 1969 (SAM!)

Stapelia gordonii sensu Hook. in London J. Bot.: 164 (1843) et in Icon. Pl.7: t. 605, 606 (1844).

Scytanthus gordonii sensu Hook. in Icon Pl.7: t. 625 (1844) et in London J. Bot.: 111 (1846).

Plant a spiny succulent consisting of many erect stems forming shrub to 0.75 m tall, 0.5 m diam., branching from base. Stems 25–50 mm thick with prominent obtuse tubercles vertically arranged into 11–17 angles, each tubercle tipped with a sharp spine 6–12 mm long, grey–green to grey–brown. Flowers arising in groups of 1–4, opening successively on each peduncular patch, near apex of stem. Pedicel 8–30 mm long, 2–3 mm thick, oval in cross–section, glabrous. Sepals 5–6 mm long, 2–4 mm broad at base, ovate– to broadly ovate–lanceolate and overlapping, acuminate, glabrous, adpressed to corolla. Corolla (40–) 50–100 mm in diam., ± circular to quite clearly 5–lobed, outside pale flesh–coloured with darker veins, inside flesh–coloured to purple–red usually with darker veins, outside glabrous and smooth, inside glabrous and smooth to covered with fine conical papillae each tipped with a hair–like bristle up to 2 (2.5) mm long, papillae sometimes red around mouth of tube; tube 1–1.5 mm deep, 4.5–6 mm broad across mouth, containing most of gynostegium; lobes broadly ovate, up to 15 mm long (excluding tip), 50 mm broad at base, tipped with narrow subulate point 3–6 mm long. Corona purple–black, glabrous, 4–6 mm broad across top, 1.5–2 mm tall, usually just touching side of tube at mouth; outer lobes basally cupular, erect, entire and truncate or emarginate to bifid up to halfway down into two spreading–erect obtuse teeth less than 1 mm long; inner lobes about 1 mm long, linear, usually with truncate slightly depressed touching apices, dorsally connected by broad ridge to outer lobes. Follicles 90–115 mm long, 180–190 seeds per horn. Figure 22.

Material examinedNamibia

- 2114: Numasschlucht (-BA), Bruyns 3647 (BOL); Trichter (-BA), Bruyns 3596 (WIND).
- 2115: 64 km towards Uis from Usakos (-AC), Bruyns 3594 (WIND); Klein Spitzkopje (-CC), Boss sub Tvl Mus. 35813 (PRE); Ekuta (-DB), Bruyns 3619 (WIND); near Usakos (-DC), Marloth 1453 (BOL, PRE).
- 2116: 3 km W Friedrichsfelde (-CC), Bruyns 3590 (WIND).
- 2214: Palmenhorst (-DB), Giess 11630 a (WIND).
- 2215: Ukuib bei Otjimbingwe (-BD), Dinter 1649 (SAM).
- 2216: Nomatsaus (-AD), Bruyns 3633 (WIND).
- 2315: Donkerhoek (-DB), Volk 2787 (M).
- 2316: Djab (-AB), Giess 9128 (WIND, PRE, M); Gamsberg (-AD), Giess 4798 (WIND).
- 2416: Tsamis-Ost (-AA), Müller 1017 (WIND, PRE); Blässkrantz (-AB), Volk 923 (M); Onis (-AC), Giess 11560 (WIND; M); Neuhof Reserve (-CC), Giess et al 5172 (WIND, M); Daweb (-DD), Giess 11629 (WIND); Namseb (-DD), Giess et al 5197 (WIND, M).
- 2418: 50 km N Stampriet (-AA), Bruyns 3585 (WIND); Witvley (-AC), Dinter 1969 (SAM); 6 km S Stampriet (-AD), Bruyns 3580 (WIND); 3 km N Gochas (-DD), Bruyns 3579 (BOL).
- 2516: Duwisib (-BC), Giess 4780 (WIND).
- 2517: Eidsamub (-CB), Giess 8393; 9045 (WIND).
- 2616: Tiras (-BA), not collected, July 1988; 16 miles W of Aus (-CA), Giess & v. Vuuren 856 (WIND, M); Aus (-CB), Lewis sub NBG 3014/17 (BOL); Kubub (-CB), Range 1298 (SAM); Tsirub (-CC), Dinter 1045 (Z); 17 miles S of Aus

- (-CD), Leippert sub Volk 4827 (WIND, M); Kuibis (-DB), Erni 293 (PRE);
Kuibis-Nord (-DB), Giess et al 5484; 5484 a; 5484 b (WIND, M).
- 2617: Gurub-Tschamis (-AA), E.Rusch jnr sub Dinter 8272 (S, BOL, G, Z, WIND, M);
Dinter 8273 (BOL, G, Z, M).
- 2619: Aandblom (-AA), Giess 10493 (WIND); Springboktrek Suid (-AC), Bruyns 3575
(NBG); Aroab, Keetmansh., Koës intersection (-CA), Bruyns 3567 (BOL, WIND);
Straussennest (-CB), Giess 9046 (WIND, M); Vensterkop (-CC), Bruyns 3565
(WIND); Mullersrust (-DA), Barnard 42 (WIND).
- 2716: Pockenbank (-AB), Giess et al 5319 (WIND, PRE, M); Weissequartzkuppe (-CB),
Bruyns 3213 (NBG); Witpütz (-DA), v.Berkel 495 (NBG); Namuskluft (-DD),
Giess 12919 (WIND, PRE, M); Giess & Müller 14359 (WIND, PRE, M); Bruyns
3188 (NBG).
- 2717: Holoog (-BD), Krause sub Marloth 5957 (PRE); Karios (-DB), Giess 10320 (PRE,
M); Holoogberg (-DB), Wiss sub Giess 8386 (WIND).
- 2718: Kochena (-BB), Giess 2452 (WIND); Pieterskloof (-BB), Bruyns 3559 (BOL,
WIND); Klein Karas (-CA), Dinter 5073 (S); 5072 (S, KMG, SAM, BOL, G, Z,
PRE); Vredenhof (-DB), Bruyns 3507 (BOL, WIND).
- 2816: Lorelei Kupfermine (-BB), De Winter & Giess 6380; Giess 12919; Giess et al 5432
(WIND, M); Giess 12989 (S, PRE).
- 2818: 11 km W Warmbad (-BC), Bruyns 4188 (BOL); Warmbad (-BC), Smithers sub
NBG 1537/35 (BOL); Kromrivier (-CA), Giess et al 7007 (WIND, M);
Sperlingpütz (-CA), S.Bleissner 277 (M).
- 2819: 42 km NW Orange R. from Onseepkans (-AC), Davidse & Loxton 6219 (PRE).

South Africa

- 2620: Cromdale (-DD), Rood s.n. (NBG).
- 2818: Goodhouse (-CC), Marloth 13282 (PRE).
- 2819: 90 miles W Upington (-BB), Lang & Schweickerdt sub Tvl Mus. 32843 (PRE); 30 miles W Augrabies (-DB), Werger 158 (WIND, S, PRE).
- 2820: Koegoekoep (-BA), Bruyns 3485 (BOL).
- 2821: 18 miles NE Upington (-AB), Stayner sub KG 147/64 (NBG); Sultanaoord (-AD), Hardy & Bayliss 1214 (PRE).
- 2822: Buchuberg (-CC), Acocks 1795 (KMG).
- 2917: Umdaus (-BA), Bruyns 2720 (BOL); Uranoep (-BB), Hall 863 (NBG).
- 2918: 48 miles NE Springbok (-AB), Schlieben 9079 (PRE, M); Hytkoras (-CC), Bruyns 4692 (BOL).
- 2921: Kenhardt (-AC), Long sub NBG 963/27 (BOL); 36 miles S Kenhardt (-CC), Hutchinson & Pillans 962 (PRE); Diemansput Suid (-DC), Bruyns 3452 (BOL).
- 2922: Marydale (-AC), Lindeberg 1156 (KMG); Koegas (-AD), Acocks 8633 (BOL, PRE); Prieska (-DA), Bryant 886 (STE); Marloth 5956 (PRE); comm. v.d. Bijl 130 (BOL); Stofbakkies (-DA), Bryant sub KMG 5966 (KMG); Hafström 1156 (PRE).
- 2923: Read's Drift (-AB), Acocks 2537 (KMG, PRE); Mazelsfontein (-BA), Anderson sub KMG 3312 (KMG); St Clair (-BB), Orpen (PRE); Douglas (-BB), Anderson 587 (BOL); near Douglas (-BB), Orpen sub MacOwen 3397 (BOL); 6 m SE Douglas (-BB), Reynolds 1675 (PRE).
- 2925: Dassiepoort (-CB), Henrici (PRE).
- 3018: W Bitterfontein (-BD), no specimen, Aug. 1992; Stofkraal(-CB), Bruyns 4744,

- (BOL); 5 km W of Langeberg (–DB), Bayer 2776 (NBG).
- 3020: Rietkolk Oos (–BC), Bruyns 3436 (NBG).
- 3021: Holboskolk (–BA), Le Roux & Lloyd 58 (PRE); Van Wyksvlei (–BD), Alston sub Pillans 18 (BOL); Alston sub Pillans 127 (BOL).
- 3023: N Voëlgeraas (–AA), Bruyns 3025 (BOL).
- 3118: Kalkgat Noord (–BB), Boucher 5127 (STE).
- 3119: Bloukrans (–AB), Stirton 11007 (STE); Tweefontein (–AD), Bruyns 4327 (BOL); Doornbos (–CC), Compton 19481 (NBG); v. Breda (PRE); near Doornbosch (–CC), Pillans 7008 (BOL); Doorn River Bridge (–CC), Hall sub NBG 1386/48 (NBG); W Doorn R. Bridge (–CC), Galpin 12937 (PRE); Botterkloof (–CD), Hall 724 (NBG); N. Doringbos (–CD), Bayer 1592 (NBG).
- 3121: Fraserberg (–DC), v.d. Bijl sub Nat. Herb. 2592 (PRE).
- 3219: Biedouw Valley (–AB), Maguire 1884 (NBG); Tra–Tra R. Gorge (–AD), Bruyns 2621 (NBG); 80–90 km N Karooport (–BC), Hall 723 (NBG); 67 km N Karooport (–DA), Bruyns 2620 (NBG); 9 miles N Tulpfontein (–DA), Acocks 14174 (PRE).
- 3220: S. Gannaga Pass (–AA), Bayer s.n. (NBG); near foot of Gannaga Pass (–AA), Levyans 5088 (BOL); 1 km towards Klipfontein (–DD), Bruyns 3094 (NBG).
- 3221: Spitzkop (–CB), Bruyns 4864 (PRE); Kruidfontein (–DD), Pillans s.n.; v.d. Bijl s.n. (BOL).
- 3222: Rietkuil (–AC), Bayer 2413 (NBG); 1 km W Beaufort West (–BC), Shearing K4 (PRE); Kaatjieskop (–BC), Hardy 280 (PRE); Letjesbosch (–CB), Maddison (PRE).
- 3223: Rooidam (–CA), Bruyns 2951 (BOL).

3321: Koup (-AB), Joubert s.n. (NBG); Archer 849 (BOL); Grootfontein (-AB),
Marloth 5955a; 4670 (PRE); Gamka Poort (-BC), Laidler 623 (STE).

3322: Prince Albert (-AA), Marloth 5955b (PRE).

Without precise locality

Asbestos Mountains, Marloth 2084 (STE, PRE); between Beaufort West and Prince
 Albert, Nel 9039 (STE); between Prieska & Marydale, Hafström 1156 (S); Pakhuis –
 Botterkloof, Barker 1014 (NBG); between Prince Albert & Seven Weeks Poort (3321 B),
Joubert 152 (BOL) .

Namibia, Giess 8390 (WIND); west of way to Kuiseb Canyon, Giess 9130 (WIND, M);
 between Aiais & Klein Karas, de Winter 6684 (WIND); Kleinfontein, Dinter 6262 (M).

Hoodia gordonii is extremely widely distributed (Fig. 23). It occurs from the
 Brandberg in Namibia (about 21° S) southwards into the Cape Province where it is of
 scattered occurrence over much of the Great Karoo to the Tanqua Karoo in the south-west
 and the Prince Albert district (33° S) in the extreme south. It is found as far east as near
 Kimberley. Generally Hoodia gordonii avoids the winter rainfall areas, only occurring
 towards their drier margins where some summer rainfall is received – for example it is
 hardly recorded at all from Namaqualand. One notable exception to this is along the
 Doorn River from the 'Ceres'/Tanqua Karoo north of Tulpfontein to Doringbos within the
 northern Cedarberg. This is also the only area where it will be found occasionally growing
 on sandstone soils.

With such a vast range the species grows in a wide variety of habitats from very
 dry, rocky places to sandy spots in river beds. Plants often form quite extensive colonies of
 robust shrubs and grow in the open, having long outgrown the protecting shrub in which

they generally begin their existence.

Hoodia gordonii has been subjected to more unjustified splitting than any other species in this genus and a great deal of rather useless material has been written on how to separate all the various species sunk above. The reason for this chaotic state of affairs seems to lie mainly in collectors gathering single plants from populations which are then grown and, on flowering, found to differ in all manner of details. No attempt ever appears to have been made to observe whole populations in flower to see how these details fit into general patterns of variation in the species and thus how much relevance they ought to be accorded. The identification of material in herbaria also seems to have been very haphazard: some herbaria use only the name H.gordonii while in others material has been placed more or less at random under various names.

Most flowers of H.gordonii have a flesh colour which is pale pink to somewhat yellowish, fading to pinkish as the flower ages. A few collections exist of much darker-flowered plants: Giess et al 5172, 5179 from the Tsaris Mountains west of Maltahöhe had 'intense violet-red' flowers and purple-red flowers were observed in the Auob River Valley near Gochas (Bruyns 3579). This intensity fades to a paler pink/flesh colour as the flowers age.

Flowers of this species are also very variable in size. This has much to do with the state of health of the plant as a specimen in cultivation which has not rooted properly often produces abnormally small flowers. Flowers also decrease in size as the flowering period advances with the largest often appearing first. There is also much variation from plant to plant and in any population of reasonable size flowers between 50 and 100 mm diam. can usually be found.

There is also much variation in the shape of the flowers: in some the united portion

may be deeply cup-shaped while in others it is only shallow or ± flat to even slightly convex. The lobes vary from very indistinct (flower ± circular in outline) to clearly defined lending the flower a definite 5-lobed shape although this is not usually as clear as in some forms of H.currorii.

The corolla tube is usually somewhat pentagonal in outline. The tissue around its mouth is much thickened and raised into 5 slight mounds opposite the inner corona lobes. Towards the centre the flower often becomes lighter coloured (though sometimes darker if covered with reddish papillae) with the raised area at the mouth of the tube always significantly paler than beyond, highlighting the purple-black corona. This is different from H.currorii where the mouth of the tube is darker than the surrounding tissue and noticeably shiny.

The differences between H.gordonii and H.juttae are discussed under the latter.

From the various forms of H.currorii in central western Namibia (Swakopmund northwards to Khorixas and eastwards to the Erongo Mountains) and Botswana, H.gordonii is usually easily separated when sterile by its erect parallel stems forming a neat shrub — in H.currorii in these areas the stems have an untidy spreading habit. In northern Damaraland and the Kaokoveld of Namibia H.currorii is not so easy to distinguish vegetatively from H.gordonii as the stems are more rigidly erect. Florally the two differ significantly: H.currorii has much longer bristles (hairs) on the corolla, a conspicuous shiny, livid mouth to the corolla tube, the gynostegium is completely contained within the tube (in H.gordonii at least the top of the gynostegium protrudes from the tube and sometimes most of it is exerted). Also the respective coronas look rather different: in H.currorii the outer lobes are erect with incurved margins and they considerably exceed the height of the inner lobes (in H.gordonii the outer lobes are spreading-erect without

incurved margins and they do not exceed the height of the anthers).

One of the characters that appears to have given rise to an especially large amount of confusion is the presence or absence of papillae on the inner surface of the corolla (c.f. Plowes 1982). These papillae usually have an apical bristle which varies from extremely short to 2 mm long or even longer on rare occasions. In the southern part of the distribution such papillae are rarely found – in one large colony, for example, on the Tanqua Karoo only one plant was seen with them and they were bright red and thus clearly visible against the flesh-coloured background of the corolla. As one progresses northwards the flowers become steadily more frequently papillate and over most of the summer rainfall parts of Namibia papillate flowers predominate. However, even here there is a tendency for flowers to vary greatly from smooth to papillate ± without bristles (papillae often bright red) to papillate with quite long bristles lending the flower a ± hairy appearance [see comments on Giess, Volk & Bleissner 5484 (WIND)]. In the winter rainfall part of Namibia (the extreme south-west) smooth-flowered plants are again common but occasionally papillate ones occur and at one spot just east of Witpütz quite conspicuously 'hairy-flowered' plants [bristles on papillae up to 2.5 mm long] have been reported several times. In the south-east corner of Namibia and eastwards to Upington finely downy-flowered plants are also prevalent.

2. Hoodia juttae Dinter in Neue u. wenig bekannte Pflanzen D. SWAs: 34 (1914) et in Sukkulentenforschung 2: 91 (1928). – White & Sloane, Stap. 3: 1082, fig. 1155, 1161, 1162, 1163 (1937). – Lückhoff, Stap.: 268 (1952). Hoodia bainii var. juttae (Dinter) Huber in Mitteil. Bot. Staatss. München 4: 33 (1961) et in Prodr. Fl. SWA 114: 35 (1967). Type: Namibia, Klein Karas, Oct. 1913, Jutta Dinter 3203 (SAM, holo! S, iso!)

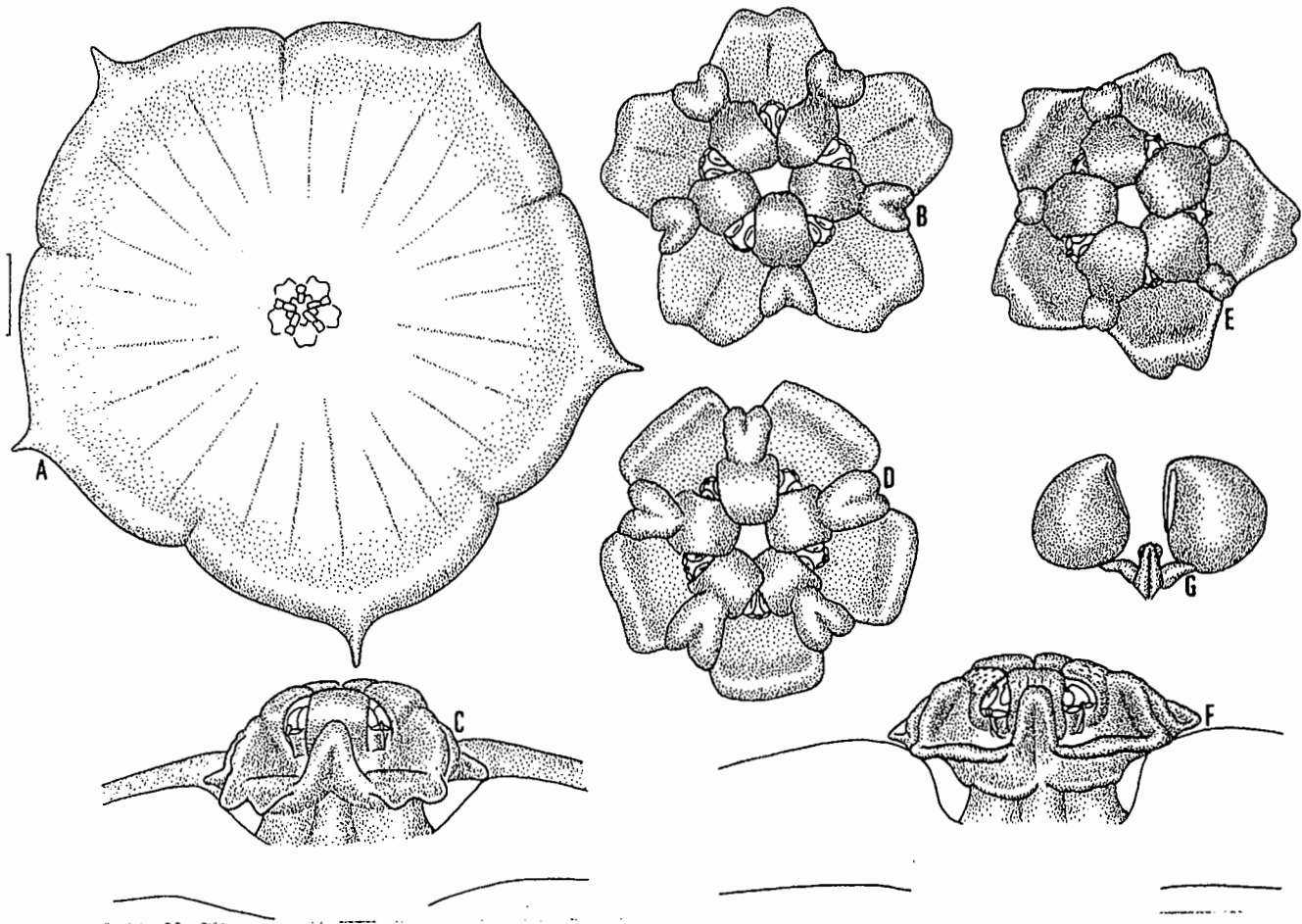


Figure 24.—*Hoodia juttae*. A, face view of flower. B, D, E, face view of gynostegium. C, F, side view of gynostegium. G, pollinarium.

Drawn from: A, B, C, Bruyns 3508; D, E, F, G, Bruyns 3526, both from eastern side of Great Karas Mountains.

Scale bar: A, 5 mm; B–F, 1 mm (at A); G, 0.25 mm (at A).

Plant a spiny succulent consisting of many erect stems forming shrublet to 300 X 500 mm, branching mainly from base. Stems 30–50 mm thick, with prominent obtuse tubercles vertically arranged into 15–17 angles, each tubercle tipped with a stiff spine 8–11 mm long, pale grey–green. Flowers in groups of 1–4, opening successively, in upper parts of stems. Pedicel 10–30 mm long, 2.5–4 mm thick, slightly oval in cross–section, glabrous. Sepals 3–5 mm long, ± 2 mm broad at base, acuminate, glabrous. Corolla 20–55 mm diam., outside pale yellow–brown, inside pale yellow–brown to dark flesh–pink with darker veins, flat to very shallowly saucer–shaped, slightly and broadly 5–lobed, glabrous and smooth outside and inside, slightly depressed around corona lobes outside tube; tube cup–shaped, 1 mm deep with corolla much thickened around mouth; lobes broadly ovate, obtuse, 4–8 mm long (excluding narrow tip), 15–25 mm broad at base with subulate point 2–5 mm long. Corona dark purple–black, glabrous, 3–4.5 mm across top; outer lobes basally cupular then spreading, transversely oblong truncate–emarginate to shortly bifid, ± 1.5 mm broad at base, up to 1 mm long, limb adpressed to corolla; inner lobes broadly linear, obtuse, incumbent on backs of anthers and slightly exceeding them, usually slightly overlapping laterally near tips, dorsally adnate to outer lobes with obtuse projection. Follicles 140 mm long, 270 seeds per horn. Figure 24.

Material examined

2619: Arus (–CC), de Winter 6683 (WIND).

2718: Garis (–BD), Bruyns 3526 (BOL); Klein Karas (–CA), J. Dinter 3203 (S, SAM); 12 miles W Grünau (–CA), Bayer (NBG); Vredenhof (–DB), Bruyns 3508 (BOL, WIND).

Without precise locality: Namibia, Herre sub SUG 1134 (BOL).

Hoodia juttæ is known only from around the base of and within the Little and Great Karas Mountains of southern Namibia (Fig. 23) and has relatively rarely been collected. In the Great Karas Mountains it occurs both around the foot of the mountains and also on some of the high, flat-topped summits that make up this range. After excellent rains which fell in December 1988 in this region, many plants were seen in flower and it was found not to be particularly rare.

H. juttæ presents a difficult taxonomic problem. While flowering specimens look quite remarkably distinctive, in fact the differences between them and the ubiquitous H. gordonii are subtle and small. In addition it occurs together with H. gordonii: in one of the localities found in Jan. 1989 it was significantly rarer than H. gordonii and in the other rather more common. Both species were flowering profusely and no intermediates or hybrids were seen.

Vegetatively there is not much difference between them. In H. juttæ the stems are often a bit stouter, they never attain the height of H. gordonii and the plant has a slightly more compact habit. Florally there are various subtle differences. The flowers of H. juttæ are always much smaller than those of H. gordonii: those of H. gordonii may be small but this is usually due to lack of water or ill health and under these conditions H. juttæ produces flowers as small as 20 mm across which is far smaller than any in H. gordonii. In H. juttæ flowers are held roughly erect and well away from the stem on a relatively long, thick pedicel while in H. gordonii they are held closer to the stem and tend to wrap around and cover it up when produced in numbers. In colour they are variable from yellow-brown to a deep flesh-pink and the veins are always clearly visible (in H. gordonii in this area they are a much paler flesh-pink) while in shape they show the usual variation for this section from circular with the tips of the lobes attenuated into 5 fine points to quite deeply

5-lobed.

The main difference between the two lies in the corona: in H.juttae the outer lobes form only a shallow cup with the limb actually adpressed to the surface of the corolla just outside the tube (this is very clear in Lückhoff's photo but can also be made out in Dinter's). They spread away from the gynostegium ± horizontally at a level the same as that of the surface of the corolla. This is never seen in H.gordonii where they form a pouch much lower on the gynostegium and rise up from this level to touch the side of the corolla tube obliquely and do not lie on the surface at its mouth.

This very subtle difference leads one to suspect that Huber's treatment of H.juttae as a variety of H.bainii (= H.gordonii) is eminently sensible. Nevertheless I prefer to maintain this taxon as a separate and distinct species especially in view of its intimately interlinked distribution with H.gordonii and the complete lack of intermediates between them. If such are in due course found to exist, the position will need to be reviewed.

3. Hoodia dregei N.E. Br. in Fl. Cap. 4 (1): 897 (1909). — Marloth in Fl. S. Africa 3 (1): 92, fig. 45 (1932). — Pole Evans in Flow. Pl. S. Africa 17: t. 670 (1937). — White & Sloane, Stap. 3: 1064, fig. 1139–1141 (1937). — Lückhoff, Stap.: 264 (1952). Type: South Africa, Cape, zwischen Dweka und Swartbulletjie, März 1827, Drege 5616 (K!)

Plant a spiny succulent consisting of 3–8 or more erect stems forming shrublet, branching from base. Stems 25–60 mm thick, usually not more than 200 mm tall but sometimes up to 0.5 m, with 16–24 rows of vertically arranged prominent laterally flattened tubercles, each tubercle tipped with a weak spine 5–7 mm long (dark purple–brown when young).

Flowers in groups of 1–5, opening successively, in upper part of stem. Pedicel 7–12 mm long, 2–3 mm thick, glabrous. Sepals 3–4 mm long, 1.5 mm broad at base, lanceolate–subulate, glabrous. Corolla 28–48 mm diam., dark flesh–coloured to greenish–yellow, flat to saucer–shaped, slightly and broadly 5–lobed, glabrous outside, inside densely covered with soft white hair–like bristles 1–2 mm long each arising from a small red columnar papilla; tube 1 mm deep, 3.5–4 mm diam. across mouth, mouth formed by annulus of 5 pinkish slightly shiny bulges at base of corolla

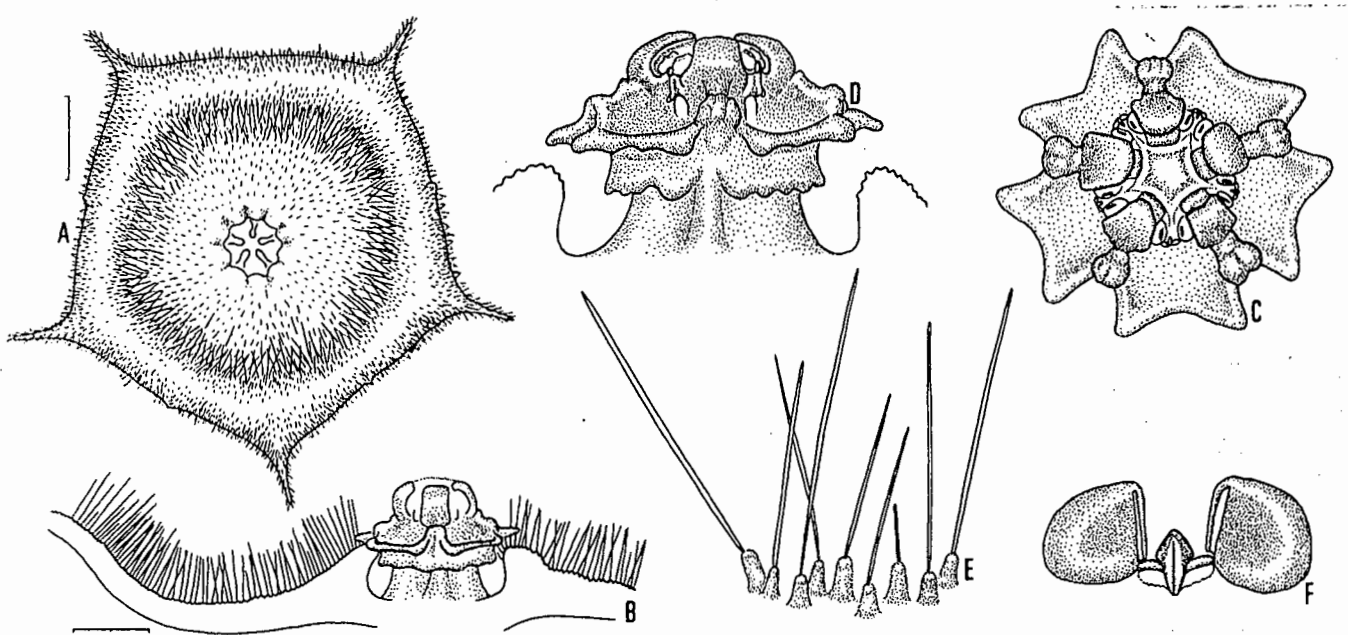


Figure 25
H. dregei
20/5/10

Figure 25.—*Hoodia dregei*. A, face view of flower. B, side view of centre of dissected flower. C, face view of gynostegium. D, side view of gynostegium. E, papillae on inner surface of corolla. F, pollinarium.

All drawn from Bruyns 1258, east of Merweville.

Scale bar: A, 5 mm; B, 2 mm; C, D, 1 mm (at A); E, 0.5 mm (at A); F, 0.25 mm (at A).

around gynostegium; lobes broadly ovate, obtuse, 4–7 mm long (excluding narrow tip), 12–18 mm broad at base with subulate point 3–6 mm long. Corona dark purple–black, glabrous, 3–4 mm broad across top; outer lobes basally cupular horizontally spreading, transversely oblong, truncate–emarginate to shortly and broadly bifid, 1–1.7 mm broad at base, < 0.5 mm long; inner lobes 1 mm long, broadly linear, obtuse, incumbent on backs of anthers and not exceeding them, dorsally adnate to outer lobes with obtuse projection.

Figure 25.

Material examined

3221: near Merweville (–CB), Bayer 2412 (NBG); S of Merweville (–CB), Bruyns 4817 (BOL); east of Merweville (–DA), Bruyns 1258 (NBG); 10 miles SE Merweville (–DC), Dec. 1935, Broom sub Tvl Mus. 34944 (PRE).

3222: Letjesbos (–CB), 1925, Haymes (BOL); fl. Dec. 1935, Madison sub Tvl Mus. 34898 (PRE).

3322: Prince Albert (–AA), Oct. 1924, Broom sub Marloth 6281 (PRE).

Without precise locality: Smithers (BOL).

Hoodia dregei is a rare species known only on the Great Karoo between Merweville, Beaufort West and Prince Albert (Fig. 23). Discovered by J.F. Drège in 1827 north of Prince Albert, it was rediscovered nearly 100 years later by the paleontologist Robert Broom in 1924. It remains known from very few collections.

In the field plants of this species are usually small (< 200 mm tall) with only a few stems with a short, thick–set stature rather like that of species in Sect. Trichocaulon. With 16–24 rows of tubercles, the stems are far more angled than in any other in this section (normally 11–17–angled stems) and they generally also have much weaker spines

on the tubercles.

Florally H.dregei is very distinctive looking. The flowers are small (< 25 mm diam.), shallowly saucer-shaped to more or less flat with circular to very slightly 5-lobed perimeter and each lobe is attenuated into a narrow point. Thus, despite their size, they are the usual shape for this section. They are covered densely with white hairs, each of which arises at the apex of a small, conical papilla and represents a much modified apical cell exactly as do the much shorter versions in species like H.pilifera. The corona is typical for the section: a shallowly cup-shaped outer corona with broad, truncate lobes and broad inner lobes incumbent on but not exceeding the anthers. The basal cupular part of the outer corona is not as deep as in H.gordonii and the outer lobes spread perpendicular to the axis of the flower, usually somewhat above the annulus forming the mouth of the corolla tube. This arrangement is very similar to that in H.juttae and it is probably to this species that H.dregei is most closely allied.

4. Hoodia currorii (Hook.) Decaisne in DC. Prodr. 8: 665 (1844). — Hooker, Niger Fl.: 458 (1849). — Th.—Dyer in J. Linn. Soc. 15: 251, t. 5, fig. 2 (1876). — N.E. Br. in Hook. Icon. Pl. 20: page 3 sub t. 1905 (1890) et in Fl Trop. Afr. 4 (1): 491 (1903). — Berger, Stap. u. Klein.: 40 (1910). — Dinter in Neue u. wenig bekannte Pflanzen D.—SWAs: 33—4, fig. 26 (1914). — White & Sloane, Stap. 3: 1059, not fig. 1134 (1937). — Lückhoff, Stap. 262 (1952). — Huber in Prodr. Fl. SWA 114: 35 (1967). All as 'currori'. Scytanthus currori W.J. Hooker in Icon. Pl. 7: t. 605—606 (1844). Type: Angola, barren sparingly sandy mountains at Elephant's Bay, 1840, A.B.
Curror (K!)

Two subspecies are recognised.

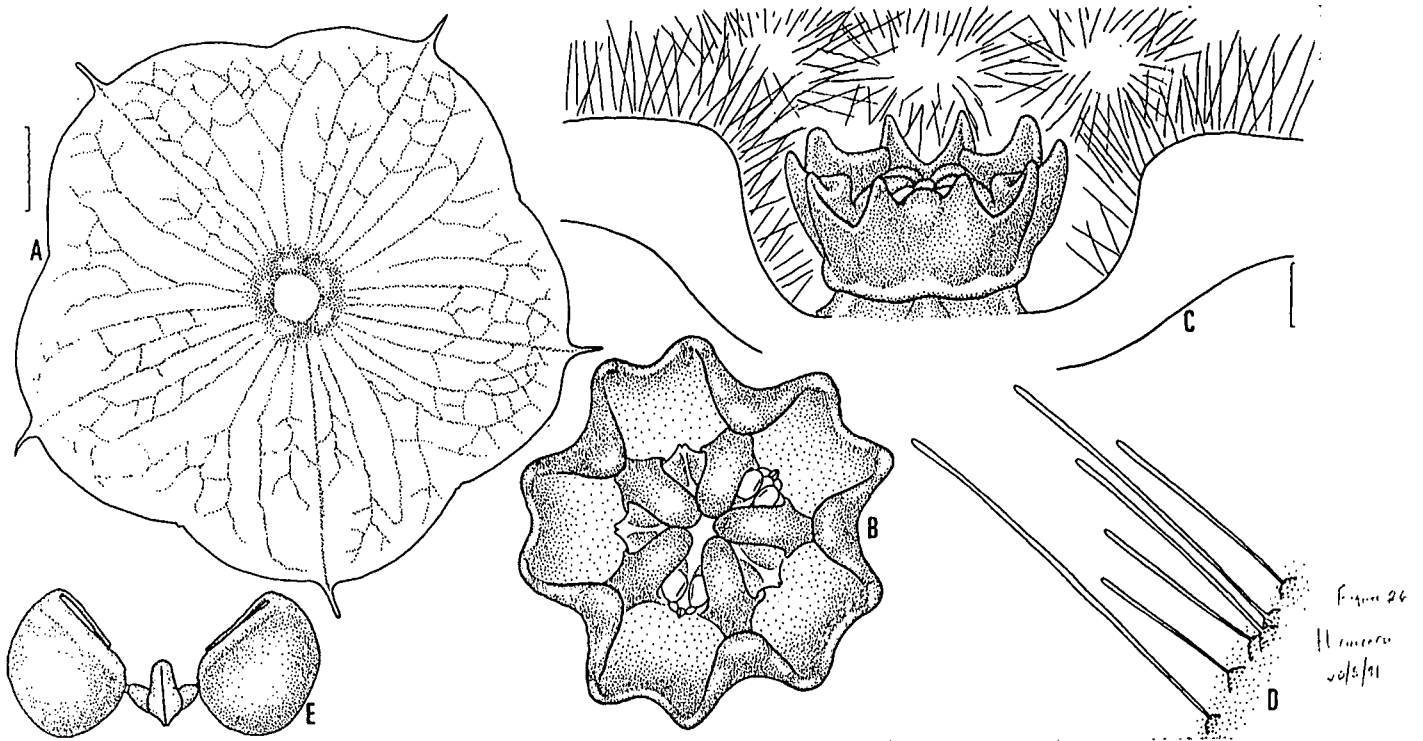


Figure 26.—*Hoodia currorii* subsp. *currorii*. Form from northern Damaraland with rather shallow corolla tube. A, face view of flower. B, face view of gynostegium. C, side view of gynostegium. D, papillae with apical hairs, taken from near mouth of tube. E, pollinarium.

All drawn from Bruyns 4060, west of Kamanjab.

Scale bar: A, 15 mm; B, 1 mm (at A); C, 1 mm; D, 0.5 mm (at A); E, 0.25 mm (at A).

4a. Hoodia currorii subsp. currorii.

'Scytanthus burkei' Hooker, Icon. Pl. 7: t. 625 (1844).

Hoodia macrantha Dinter in Neue u. wenig bekannte Pflanzen D.–SWAs: 35, fig. 52, 53 (1914) et in Sukkulantenforschung 2: 92, 109 (1928). – White & Sloane, Stap. 3: 1055 (1937). Type: Namibia, Onguati am Füsse der Erongoberge, Dinter 1648 (SAM!)

Hoodia gibbosa Nel in White & Sloane, Stap. 3: 1061 (1937). Type: Namibia, Sphinx, ± 70 miles E of Swakopmund, Boss sub SUG 6921 (STE!)

Hoodia montana Nel in White & Sloane, Stap. 3: 1063 (1937). – Huber in Prodr. Fl. SWA 114: 36 (1967). Type: Namibia, Brandberg, Nov. 1935, Nel sub SUG 6916 (no material preserved)

Hoodia currorii var. minor Dyer in Flow. Pl. Africa 37: t. 1474 (1966). Type: Namibia, 26 miles NE Hentjies Bay, Hardy & de Winter 1508 (PRE!)

Adenium 'namaquarium' Henslow in The Gardener: 1194, fig. 16 (1901).

Plant a spiny succulent consisting of many erect to spreading stems, forming shrub 0.15–1 m tall, 0.15–1 m or more in diam., branching from base. Stems 40–60 (–80) mm thick with prominent obtuse laterally flattened tubercles vertically arranged into 11–16 (–24) angles, each tubercle tipped with a sharp spine 6–10 mm long, grey– to brown–green. Flowers arising in groups of 1–4, opening successively, near apex of stem. Pedicel 12–50 (–60) mm long, 4–6 mm thick, oval in cross–section, glabrous. Sepals 4–8 mm long, 3 mm broad at base, ovate–lanceolate, acuminate, glabrous, adpressed to corolla. Corolla (50–) 60–170 (–180) mm diam., ± circular to clearly 5–lobed, outside pale flesh–coloured usually with narrow red–pink patch at base of tube among sepals, inside deep reddish to flesh–pink or yellowish–pink usually with darker veins, with orange–livid shiny area around mouth and inside tube, outside glabrous and smooth, inside covered with pink to

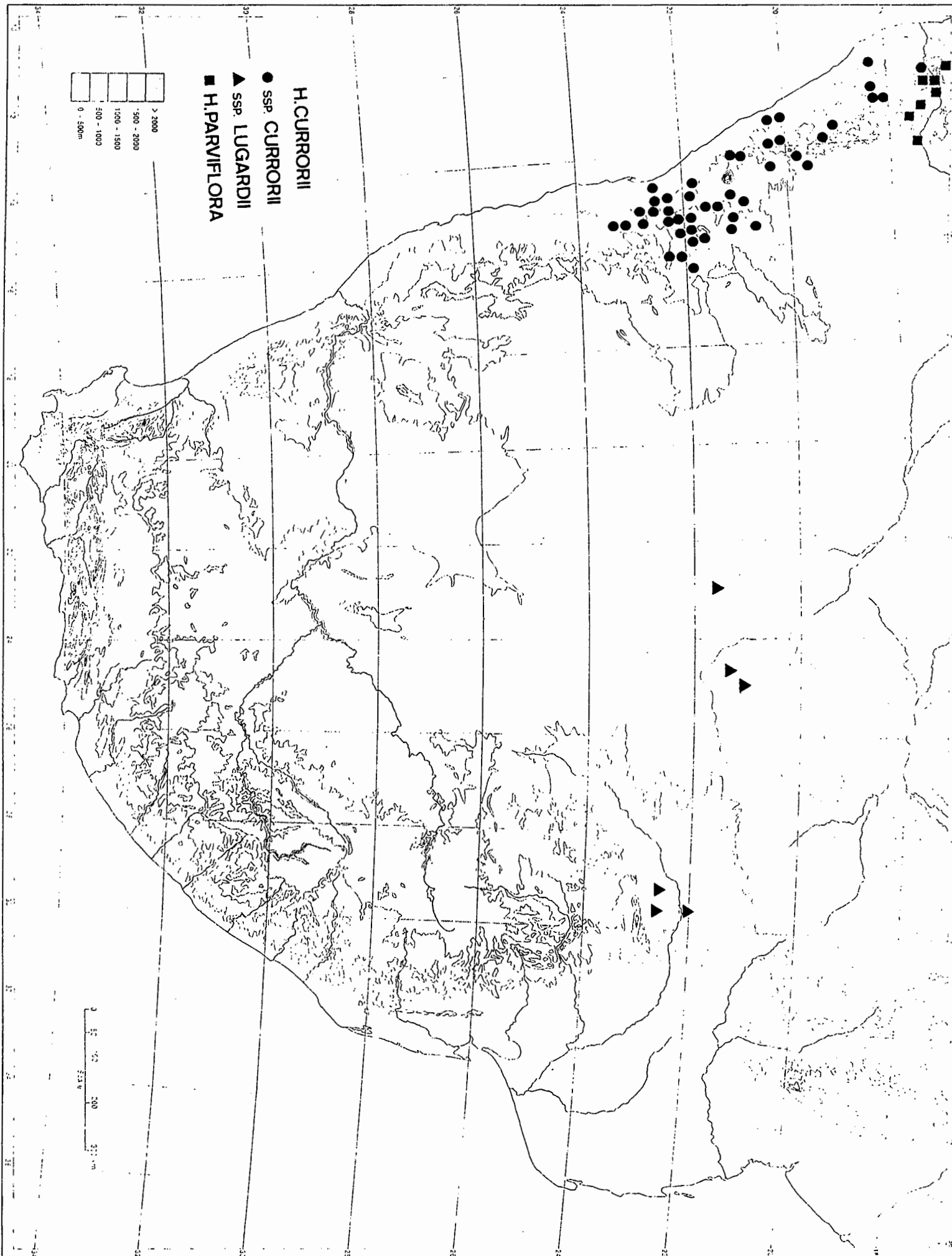


Figure 27.—Distribution of *Hoodia currorii* and *H. parviflora* in southern Africa.

purple hairs 0.5–3.5 mm long each arising from a flattened–conical papilla (papillae becoming larger towards lobes and vanishing towards centre, hairs longest towards centre); tube (2.8–) 3–6 mm deep, 6–9 mm broad at mouth, pentagonal with 5 mounds in corolla at mouth, containing whole of gynostegium and much broader than it; lobes broadly ovate to broadly deltoid, ± 10–25 mm long (excluding narrow tip), ± 55–75 mm broad at base, with narrow subulate point 6–20 mm long. Corona deep red–purple or –brown, shiny, glabrous to sparingly pilose on exterior, 3.8–5 mm broad across top, 2–3 mm tall, well separated from side of corolla tube; outer lobes forming a 5–lobed cup from slightly taller than style head to nearly twice as tall as style head, bifid for less than half of length into erect obtuse–truncate to deltoid teeth with outer margin folded inwards; inner lobes linear, obtuse, incumbent on backs of anthers and mostly exceeding them to meet in centre. Follicles recorded at 155, 160, 220 mm long with resp. 252, 505, 414 seeds per pair. Figure 26, 28, 29.

Material examined

Angola

1312: Elephant's Bay (–BA), Curror (K).

1412: Sao Nicolau (–AD), Mendes 420 (LISC); Dois Irmaos (–DC), Carp sub Santos 181 (LISC).

1512: Giraul (–AA), Menezes et al 2958 (PRE, LISC); Caraculo (–BA), Santos & Henriques 401 (PRE); 2 km from Caraculo towards Mossamedes (–BA), Clara Couto 373 (LISC); Sao Joao do Sul (–CC), Torre 8416 (LISC, M).

Namibia

1712: Kapupa Valley (–BC), Story 5880 (PRE).

1812: near Sechumib R. between Orupembe & Sarusas (–AD), Kers 1735 (S); 7 km N Okonjambo (–BB), Giess 9417 (WIND, PRE, M).

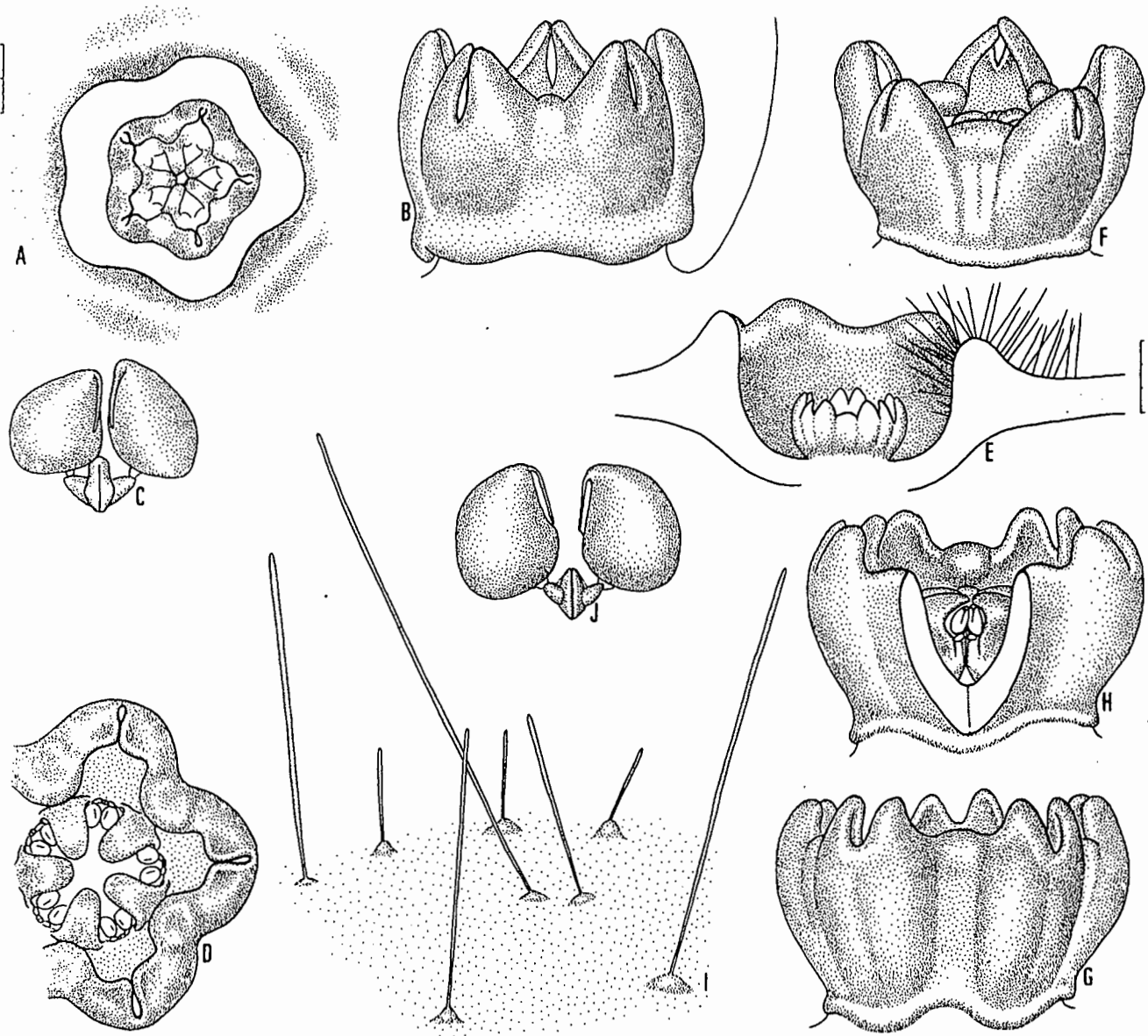


Figure 28
macrantha
6/7/60

Figure 28.—*Hoodia currorii* subsp. *currorii*. Material from eastern edge of Namib Desert and Erongo Mountains usually known as *H. macrantha*. A, face view of centre of flower. B, F, G, side view of gynostegium. D, face view of gynostegium. E, dissection of centre of flower. H, gynostegium with one outer corona lobe cut away. I, papillae on surface of corolla. C, J, pollinaria.

A, B, C, drawn from Bruyns 3624, Erongo mountains; rest from Bruyns 3592, N of Usakos.

Scale bar: A, 2 mm; B, D, F, G, H, 1 mm (at E); E, 3 mm; I, 0.5 mm (at E); C, J, 0.25 mm (at E).

- 1813: Otjiu (–AA), Merxmüller 1420 (M); Okumutati (–AC), Viljoen 412 (WIND).
- 1913: Sesfontein (–BA), Thorne sub SAM 35701 (SAM); Khowarib Gorge (–BD), Bruyns 4062 (BOL).
- 1914: farm Grootberg (–CB), Giess 7774 (WIND); 83 km W Kamanjab (–CC), Bruyns 4060 (BOL); 96 km W Kamanjab (–CC), Bruyns 4061 (PRE).
- 2013: Obob–Unjab R Junction (–AB), Müller & Loutit 1179 (WIND); 14 miles E Torra Bay (–AD), Giess et al 6283a (WIND); Wereldsend (–BB), Merxmüller & Giess 30606 (M); Driefontein (–BD), Müller & Giess 382 (WIND, M).
- 2014: Austerlitz (–AD), Giess et al 6136 (WIND); Bloemhof (–BC), Müller & Giess 386 (WIND); near Brandberg Wes (–CC), Craven 1503 (WIND).
- 2015: Otjijhorongo Reserve (–CC), Giess & Müller 11757 (WIND, M); Elim (–DA), Bruyns 4049 (BOL).
- 2114: 74 miles N Hentjies Bay (–AA), Barnard 108 (WIND); 8 km E Uis (–BB), Bruyns 3607 (NBG); 10 miles N Neineis (–BD), Wiss 1775 (WIND); Ränder am Omaruru, ± 32 km flüssaufwärts (–DC), Giess 9952a (WIND); 26 miles E Hentjies Bay (–DC), Hardy & de Winter 1508 (PRE); Kleinsiedlung Grüttemeyer (–DC), Giess 10894 (WIND); 35 miles E Hentjies Bay (–DD), Merxmüller & Giess 1725 (WIND, M).
- 2115: Omatjette (–AB), Volk 2700 (M); Neineis (–AC), Bruyns 3595 (BOL, NBG, WIND); Ohere (–BA), Giess 9200 (WIND, M); N Usakos (–CA), Bruyns 3592 (BOL, WIND); W Usakos (–CD), Giess 10456 (WIND, PRE, M); Kuduberg (–DB), Bruyns 3624 (BOL, WIND, NBG); Krantzberg (–DC), NBG 1627/27 (BOL) Goabeb (–DC), Giess 8453 (WIND); 6 km W Usakos (–DC), Jankowitz 517 (WIND); Usakos (–DC), Dinter 1648 (SAM); Karibib (–DD), Dinter 6835

- (BOL, G, Z, M); Volk 11855 (M); Etiro (-DD), Dinter 7018 (WIND, S, PRE).
- 2116: Wilhelmstal (-CD), Volk 2790 (M).
- 2214: 49 km E Swakopmund (-BD), Leuenberger et al 3363 (WIND); Arandis (-BD), Boss sub Tvl Mus. 35812 (PRE); Rössing (-DB), Dinter 2825 (SAM); just N of Rössing Mtns (-DB), Craven 1484 (WIND); before crossing of Swakop R. (-DB), Craven 2444 (WIND).
- 2215: Aukas siding (-AB), Bradfield 564 (PRE); 80 km E Swakopmund (-AC), Giess 3425 (WIND, PRE, M); Sphinx (-AD), Boss sub SUG 6921 (STE); Sebraberg (-AD), Kers 1801 (S); Ubib (-BA), Kers 1669 (S); Husab (-CA), Kers 705 (S); Merxmüller 1757 (M); Südausläufer der Witportbergen (-CC), Giess 9552 (WIND); 8 miles S Blutkuppe (-CD), Giess 8771 (WIND).
- 2216: Otjosandu (-AA), v.Koenen 385 (WIND); v. Koenen sub Giess 15455 (PRE); S Karibib (-AC), de Winter 2657 (WIND, PRE, M).
- 2315: 50 miles SE Walvis Bay (-AA), Barnard 94 (WIND, M); 58 miles E Walvis Bay (-AB), Giess et al 5143 (WIND, M).

Without precise locality

Namibia, 6 km ö. Swakopmund am Kan (-DA), Rusch (Z); Pesch 1 (STE); Brandberg, Oritsaub (2114), Giess 2124; Merxmüller & Giess 1689 (WIND); hills & flats between Brandberg & Uis (2114B), Merxmüller & Giess 2142b (WIND); im Kan (2214D), Dinter 55 (Z).

Hoodia currorii subsp. currorii is found in Namibia and Angola from 13° S to just below 23° S, south of Walvis Bay. In Angola it appears to be restricted to the very arid parts of the coastal Namib Desert (Fig. 30). In Namibia it also occurs in this arid zone but

advances eastwards as well (Fig. 27). It occurs furthest east in the dry, short, mopane 'forest' of the Ugab River Valley south-west of Outjo (Vingerklip area) more than 250 km from the coast and also in dry Acacia scrub in the Erongo Mountains and south-east of these beyond Karibib (also about 200 km from the coast).

Curror's plant was illustrated (Hooker 1844, probably a little less than natural size) as having shallowly saucer-shaped, \pm circular flowers 120–140 mm diam., with corolla tube \pm 8 mm diam. and apparently at least twice as deep as the height of the corona. The corona has a very broad cup formed by the outer lobes which are only slightly taller than the anthers. Curror's specimen came from 13° S in Angola. A more recently collected specimen from 13° S [Santos & Henriques 401 (PRE)] had one flower nearly 160 mm and another \pm 100 mm in diam., both with very broadly deltoid lobes and thus a distinctly pentagonal flower very similar to some material usually called Hoodia macrantha. It is also interesting to note that, on the basis of Curror's material, N.E. Brown (1903) had no hesitation in placing a collection of Palgrave from Otjimbingwe under H.currorii: under current usage this would be assigned to H.macrantha.

In the light of these facts it is necessary to examine carefully what has been written about the names H.currorii and H.macrantha.

Dinter does not give precise differences between his 'macrantha' and 'currorii' except to say that it has larger flowers and 'differs substantially'. Huber (1967) reproduces a resumé of the differences between the two by W.Giess which may be summarized as follows:

H.currorii: Stems 300–400 mm tall, corolla mostly only 70–90 mm broad, shallowly plate-like with sharply-defined, almost hemispherical tube, commonly yellowish flesh-coloured, fairly densely violet-haired.

H. macrantha: Stems 600–800 mm tall, corolla mostly 120–150 mm broad, crateriform, without clearly-defined corolla tube, bright purple to brown-violet, thinly violet-haired mainly in the outer half of the radius.

While the taxon growing in the coastal Namib Desert from Swakopmund up to Khorixas satisfies Giess' definition of H. currorii, Hooker's type does not fit it and corresponds better to H. macrantha: even the height of the plant given by Giess is not valid for Curror's material which Hooker gives as 2 feet (600 mm) or more. Thus the small, somewhat yellowish- and small-flowered plants from Swakopmund to Khorixas which are widely referred to as H. currorii both in cultivation and in herbaria are not typical of the species. It seems that botanists have generally followed Dinter (who figured such plants for the first time in 1914) in calling such material H. currorii. In this Dinter was wrong and his H. macrantha is actually H. currorii in the sense of Hooker while the material he illustrated as H. currorii is a southern coastal variant of this. In view of the variation seen within H. currorii and usually found within species of this genus this variant is not given any taxonomic recognition here.

Mature specimens of H. currorii from south of 20° S have a distinctive shape with the stems spreading untidily outwards. The same growth habit is found in plants from the coastal districts of Angola (photograph of plant in habitat, Mendes 420). This can readily be used to distinguish it from H. gordonii where the two occur together: as for example in the Erongo Mountains, the Brandberg and further southwards towards the Swakop River. However, in northern Damaraland and in the Kaokoveld H. currorii has a much more rigidly erect habit and plants can easily be mistaken for H. gordonii which, however, is not recorded from north of the 21 st parallel.

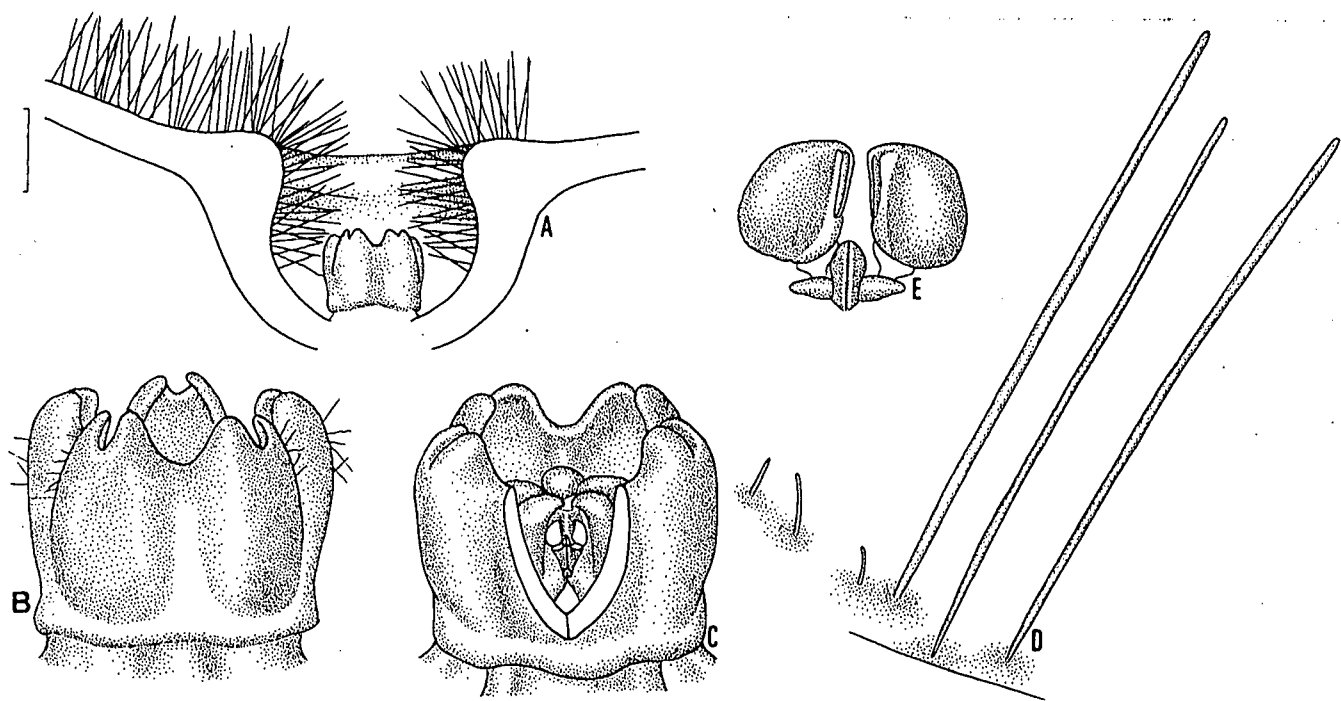


Figure 29
 currorii
 6/1/90

Figure 29.—*Hoodia currorii* subsp. *currorii*. Material from southern coastal Namib.

A, dissection of centre of flower. B, side view of gynostegium. C, gynostegium with one outer corona lobe removed. D, hairs on corolla near centre. E, pollinarium.

Drawn from Russel, E of Torra Bay.

Scale bar: A, 3 mm; B, C, 1 mm (at A); D, 0.5 mm (at A); E, 0.25 mm (at A).

In the brief diagnoses by Giess quoted above H.macrantha is given as lacking a well-defined corolla tube. It would appear that Giess is referring to the united portion of the corolla. In this treatment the corolla tube is taken as the cupular depression in the centre of this united portion immediately surrounding and containing the gynostegium (see page 15). In H.currorii this corolla tube is always present but, unlike in H.gordonii, it is usually about twice as deep as the height of the gynostegium. This is true of Curror's material and of all that occurring in the southern part of the range. However, plants in northern Damaraland sometimes have shorter tube, only slightly exceeding the height of the gynostegium.

In plants from the southern end of the distribution, the gynostegium is completely contained within a deep cup formed by the erect outer corona lobes. This cup varies considerably in breadth, being somewhat narrower in the coastal material and broader in that usually called 'macrantha'. In Curror's original plant the outer corona is much shorter and only slightly exceeds the height of the inner lobes. This is found also in material from northern Damaraland and the Kaokoveld and in some of these plants the corona suggests that of H.gordonii. However, these plants are better placed under H.currorii: the very hairy corolla, bright, shiny, livid-orange area around the mouth of the corolla tube, the wide separation of the sides of the corolla tube from the gynostegium and the more cupular outer corona with incurved margins to the lobes all indicate closer affinity with H.currorii.

Nel distinguished his H.gibbosa from H.currorii by differences in the outer corona: 'gibbosa' is supposed to have the outer corona forming a 5-starred cup with quadrate, obtuse, emarginate lobes while in 'currorii' it is a regular oblong cup with linear and acute lobes. We have examined the type of H.gibbosa and its outer corona is clearly the same as

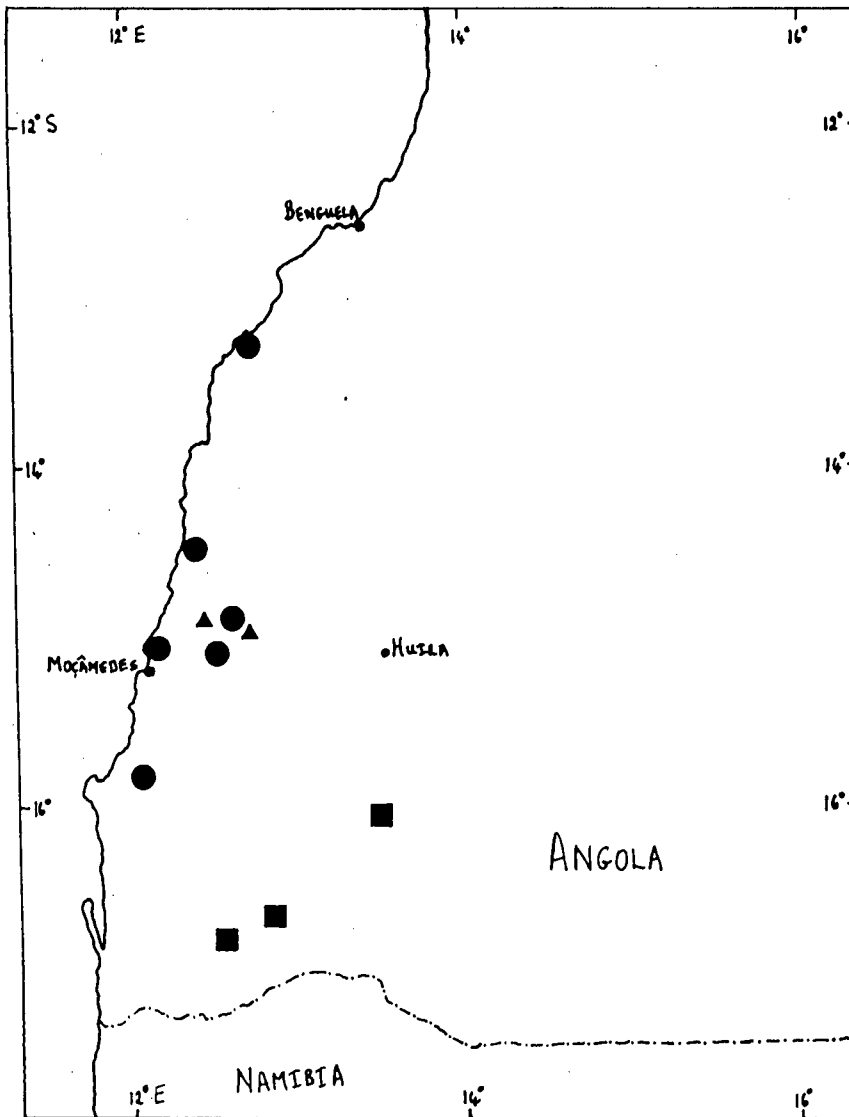


Figure 30.—Distribution of *Hoodia currorii* (circle), *H. parviflora* (square) and *H. mossamedensis* in south-western Angola.

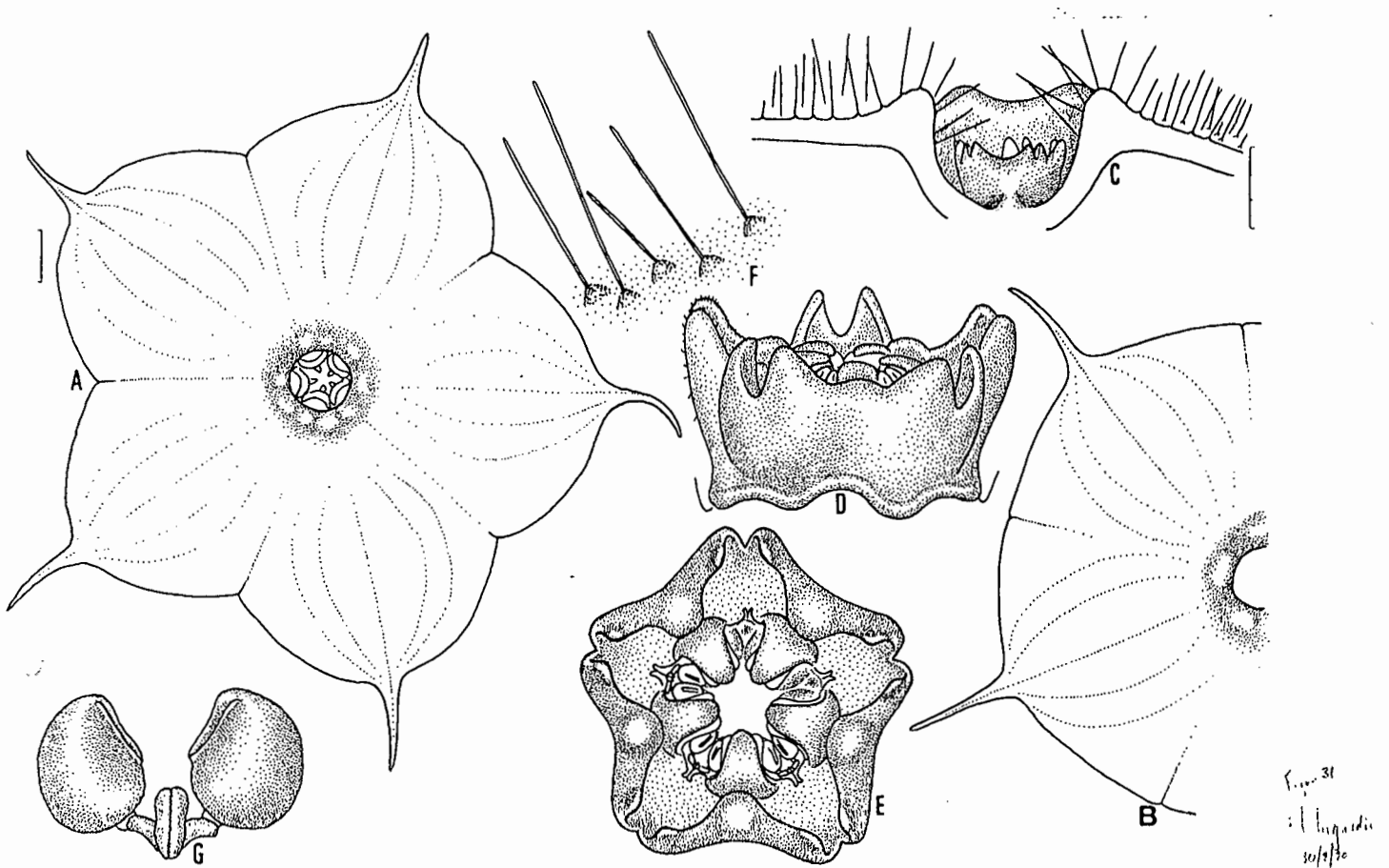


Figure 31.—*Hoodia currorii* subsp. *lugardii*. A, B, face view of flower. C, dissection of centre of flower. D, side view of gynostegium. E, face view of gynostegium. F, hairs on corolla taken from united part. G, pollinarium.

B drawn from Leach 15085, Zimbabwe; rest from Fourie 26446 (no data).

Scale bar: A, B, 5 mm (at A); C, 3 mm; D, E, 1 mm (at C); F, 0.5 mm (at C); G, 0.25 mm (at C).

some of the broader ones found among 'macrantha' flowers. The excellent photographs in White & Sloane also verify this view and so this species is sunk with 'macrantha' under H.currenii.

H.montana is given as having very similar outer corona to H.currenii but differing by its longer pedicels. He gave the stems as 20–24–ribbed as well, which is much more than is normal in H.currenii. This may have been an error and the flowers are so similar to those of H.currenii that there is no point in upholding this species. Unfortunately no type material was deposited.

H.currenii var. minor is also abandoned as recommended by Huber. Variation in the size and shape of flowers in hoodias is so prevalent that a taxon based purely on this character is quite useless. Dyer (1966, see above) evidently intended describing it as a new species. However, over two successive flowering seasons, he observed considerable variation in the shape of the corolla of the one plant in cultivation on which this name is based. This led him eventually to describe it only as a variety of H.currenii.

It should be noted that the spelling 'currenii' is used here, the single 'i' being reserved for names ending in a vowel or 'er' [ICBN, Recommendation 73 C. 1(a)].

4b Hoodia currenii subsp. lugardii (N.E. Br.) Bruyns comb. et stat. nov.

Hoodia lugardii N.E. Br. in Fl. Trop. Africa 4 (1): 491 (1903). – Berger, Stap. u. Klein.: 41 (1910). – White & Sloane, Stap. 3: 1066 (1937). – Dyer in Flow. Pl. Africa 25: t. 977 (1946) 'lugardii'. Non Pole Evans in Flow. Pl. S. Africa 16: t. 617 (1936).

Type: Botswana, Chukutsa Salt-Pan, 2300', Lugard 303 (K!)

Plant forming shrub 0.3–1 m tall, 0.3–1 m or more in diameter. Stems pale

grey-green, erect to spreading. Pedicel 3–7 mm long, 2–2.5 mm thick, green. Corolla 40–75 mm diam., concave-rotate, broadly 5-lobed to circular, outside deep red-pink on exterior of tube rest pale pink or flesh-coloured, inside brick-red to pale flesh-pink livid shiny pink-red around mouth and inside tube, covered on inside with erect hairs 0.5–2.5 mm long each arising from a small reddish conical papilla; lobes broadly ovate-deltoid to deltoid, ± 5–11 mm long (excluding narrow tip), 20 mm broad at base, terminated by subulate point 5–7 mm long; tube 5–6 mm broad across mouth, ± 4 mm deep. Corona 4 mm broad across top, ± 2.5 mm tall, usually sparsely pilose on exterior; outer lobes shortly cupular, erect, bifid to less than half of length into deltoid teeth with margins folded inwards. Otherwise as in subsp. currorii. Figure 31.

Material examined

Botswana

2122: 80 miles E Ghanzi (–DB), Plowes 2589 (SRGH).

2124: Mopipi (–BB), Allen X 369 (PRE); 40 km ESE Rakops (–BC), Wild & Drummond 7319 (PRE).

Zimbabwe

2229: ± 30 miles W Beit Bridge (–BA), Leach & Knott 15085 (BOL, WIND, SRGH, PRE, M, LISC).

South Africa

2229: near Alldays (–CA), Bruyns 4471 (BOL); SE of Alldays (–DA), Bruyns 4475 (BOL).

Without precise locality: Fourie 26446 (PRE); Botswana, Mkgadigadi, Drummond 8844 (SRGH).

Hoodia currorii subsp. lugardii is found further east than any other hoodia and occurs in the low-lying, calcareous region along the Botletle River south of the Mgadi-gadi salt pan of central Botswana (Fig. 27). Here it was discovered by Major Edward Lugard in 1896 or 1897. In about 1943 it was collected for the first time in the relatively low-lying and also rather calcareous region along the valley of the Limpopo River in the far northern Transvaal north of the Soutpansberg where it is now known to occur from Alldays to Messina. In 1973 it was gathered on the northern banks of the Limpopo in rather similar country in southern Zimbabwe. Throughout its range it has been rarely collected but it seems to be much more common than the herbarium records indicate.

Plants grow on calcareous ground among small trees of Acacia tortilis and Copaifera mopane in fairly open bushveld usually forming a shrub around the base of a tree. They may grow to as large as 1 m X 1 m and the stems have a somewhat spreading habit similar to that in H.curreorii. The plant usually has a rather paler grey colour than the Namibian H.curreorii.

Florally Hoodia lugardii differs very little from H.curreorii: the pedicels are shorter, the flowers are smaller and flatter with longer acuminate points on the lobes (though fig. 1132 of White & Sloane shows that such long points sometimes occur in Namibian plants too); the 'hairs' on the corolla are a little shorter than those in subsp. curreorii, the corolla tube is similarly slightly shallower than in subsp. curreorii and the gynostegium is ornamented with shorter outer corona lobes. Some flowers also have a striking deep red-pink exterior of the corolla tube. However, none of these distinctions is absolutely reliable. In view of the variation in H.curreorii (especially in the corona and the size and shape of the flower), the overall similarity between the plants, the similar corolla with the typical bright livid area around the mouth of the tube and especially in the shape of the

corona (compare figures 26 and 31), Hoodia lugardii is treated as a subspecies of H. currorii.

5. Hoodia parviflora N.E. Br. in Kew Bull. misc. inf.: 265 (1895) et in Fl. Trop. Afr. 4 (1): 491 (1903). — Hiern in Cat. Afr. Pl. Welw. 1 (3): 697 (1898). — Schltr in Warburg (edit.), Kunene-Sambesi Expedition: 344, t. 6 (1903). — Berger, Stap. u. Klein.: 41 (1910). — White & Sloane, Stap. 3: 1075 (1937). Gossweiler, Carta Fitogeográfica Angola: 147, 191 (1939). — Lückhoff, Stap.: 267 (1952). — Giess in Mitteil. Bot. Staatss. München 6: 239–243 (1966). — Huber in Prodr. Fl. SWA 114: 36 (1967).
Type: Angola, Mossamedes district, near Pomangala, 1500', Welwitsch 4265 (K[!] holo.; G, iso[!]).

Plant a spiny succulent consisting of few to many erect stems forming medium to large shrub 0.3–2.2 m tall, 0.3–1 m diam., branching from base. Stems 35–110 mm thick with prominent obtuse laterally flattened tubercles vertically arranged into 14–18 angles, each tubercle tipped with a stout spine 6–10 mm long, usually strikingly matt bluish–green (violet–green). Flowers in groups of 1–4, opening successively, near apex of stem. Pedicel 2–4 mm long, 3–4 mm thick, oval in cross–section, glabrous. Sepals 5–6 mm long, nearly 3 mm broad at subcordate base, ovate–lanceolate, acuminate, glabrous, adpressed to corolla in lower third only, spreading with reflexed tips. Corolla 30–55 mm diam., outside whitish with darker veins, inside yellow to brownish–orange with darker (usually reddish) veins, conical–campanulate, slightly 5–lobed, smooth and glabrous outside, inside covered with obconical papillae each tipped with a hair–like bristle up to 3.5 mm long; tube broadly cup–shaped, slightly darker than corolla (pink–orange), ± 7 mm broad across mouth, 3–4 mm deep, corolla with 5 raised mounds around mouth, containing

gynostegium; lobes broadly ovate, ± 10 mm long (excluding narrow tip), 20–27 mm broad at base, tipped by subulate point 5–7 mm long. Corona purple–black, glabrous, 4–4.5 mm broad across top, 2–2.5 mm tall, not touching sides of corolla tube; outer lobes basally cupular, erect, bifid to half–way down into two erect deltoid to truncate, obtuse teeth up to 1 mm long; inner lobes linear, obtuse, incumbent on backs of anthers and shorter than them, dorsally connected by ridge of flat tissue to outer lobes. Figure 32.

Material examined

Angola

- 1512: Mossamedes district near Pomangala, Welwitsch 4265 (G).
 1612: 49 km from Oncócuá towards Iona (–DB), De Menezes, Barroso & Sousa 4881 (LISC); Iona Nat. Park, S spur of Caionone (–DC), Ward 71 (WIND, NU).
 1613: Zwischen Umpupe (Ompupa) und Palmfontein beim Aufstieg in den Shellabergen (–AB), 25 Aug. 1899, Baum 20 (G, Z)Huila, Curoca, near Rio Elefantés (–C), De Menezes & Henriques 7 (LISC).

Namibia

- 1712: Baynesberge, im Rivierlauf zwischen Felsen unterhalb der Quelle von Okombambi (–BB), Giess 8972 (PRE, WIND, M); Okombambi, 8 miles from Cunene (–BB), Goyns 2 (PRE); Otjomborombonge, near bed of main kloof to south (–BA), Leistner et al 165 (PRE).
 1713: 7 Meilen südlich Epupa Fälle am Wege nach Otjijanjasemo (–AA), Giess 3969 (PRE, WIND, M); 35 miles from Otjijanjasemo towards Epupa (–AA), Meyer 1293 (M); near Epupa Falls (–AA), Leach & Cannell 15037 (BOL, WIND); 20 km S Epupa Falls (–AA), Giess 3264 (WIND); Otjijanjasemo (–AD), Leach &

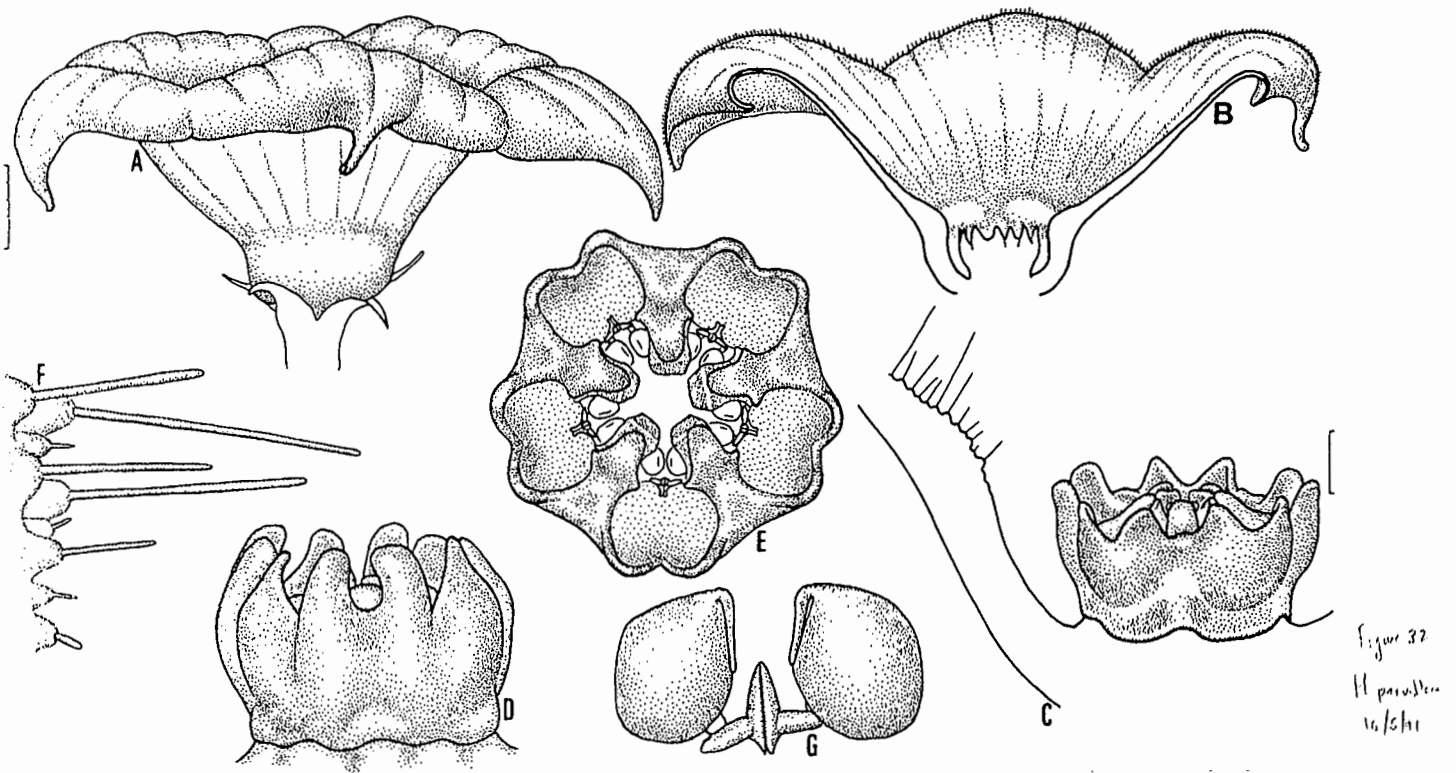


Figure 32.—*Hoodia parviflora*. A, side view of flower. B, dissection of flower. C, D, side views of gynostegium. E, face view of gynostegium. F, papillae on united part of corolla. G, pollinarium.

A, B, D, F drawn from Bruyns 4084; C, E, G from Oliver et al 19.

Scale bar: A, B, 5 mm (at A); C, 1 mm; D, E, 1 mm (at A); F, 0.5 mm (at A); G, 0.25 mm (at A).

Cannell 15031 (PRE, M, LISC); Owen-Smith 170 (WIND); Epembe (—DA),
Viljoen 558 (WIND).

1714: 6 km SW Ruacana Falls (—AC), Leistner et al 19; 20 (PRE).

Without precise locality: Angola: Dec. 1938, Otzen (BOL).

Namibia: Cunene R., Barnard 664 (SAM).

Hoodia parviflora is found in the south—western corner of Angola west of the Chela Mountains and to the south of Mossamedes (Fig. 30). In 1959 material was sent to Windhoek by S. Triebner which he had collected while working in the Kaokoveld, north—western Namibia. There are now quite a few collections known from along the Cunene River and the surrounding parts of the Kaokoveld (Fig. 27), though it is much more plentiful in Namibia than the records suggest. It occurs more or less continuously from west of Ruacana Falls past Sodalite to Epupa Falls along the Cunene River and in minor, usually dry river beds up to 5 km away from the main valley (Tribe, in litt.).

Around Okonguati (Otjijanjasemo) H. parviflora is very common indeed. Here it occurs with a variety of peculiar trunk succulents (Adenium obesum (Forssk.) Römer & Schultz, Pachypodium lealii Welw., Sesamothamnus benguellensis Welw.) and plenty of other succulents and geophytes among scattered mopane trees. Plants grow on heavily weathered granite apparently with a high calcareous content in the soil brought about by extensive seepage in the wet months. They reach a remarkable size and several specimens slightly over 2 m tall were seen (Fig. 1), making this the largest of all stapeliads. In other localities plants are not always so large and they may average 0.5 m or less. Along the Cunene R. it occurs on calcrete deposits a little distance from the sandy floodplain of the

river, well beyond the denser riverine vegetation, usually where the sand starts merging with rocks at the foot of surrounding hills but not in the hills themselves (Tribe, in litt.).

As far as members of this section go, H. parviflora is distinctive and easily recognised. The stems are thicker and taller than in any other and have exceedingly long, uninterrupted rows of tubercles (angles). This suggests that flowering only takes place after a certain, in some cases quite considerable, height has been reached. The epidermis has a characteristic matt bluish hue and is only greenish in the apical bud.

Hoodia parviflora has an unusual flowering time. Flowering has been reported in June, July and August which, where it grows, is the beginning of the driest part of the year. The flowers are very distinctive: the pedicels are markedly shorter than normal and rather thick for the small size of the flowers; the corolla is deeply funnel-shaped and relatively small, although it is not usually as small as the dimensions that Brown gave. The flowers have an unusual yellow or orange colour with a reddish centre, unmatched in any other species. The follicles of H. parviflora have a slightly angled shape with a slight ridge running longitudinally along each edge. In the field they are reported to develop quickly after flowering so that some release their seeds already before the first rains of late October to November (Tribe, in litt.). Maturing pods were, however, observed at Okonguati in mid-January 1990.

The considerable size of specimens should not lead to the conclusion that they reach a great age. If the locality at Okonguati is anything to judge by, they tend to grow at the base of ridges where temperatures are high but a fair amount of seepage water is available. Plants from 10 mm to over 2 m tall were seen so that both regeneration and the collapsing and dying off of old plants could be seen. It appeared that plants could increase anything from 150 to 300 mm or more in a single season if reasonable rains fell.

II. Section Trichocaulon (N.E.Br.) Bruyns stat. nov.

Trichocaulon N.E. Brown in J. Linn. Soc. 27: 164 (1878), in Fl. Trop. Africa 4 (1): 489 (1903) et in Fl. Cap. 4 (1): 888 (1909). — White & Sloane, Stap. 3: 991 (1937). — Huber in Prodr. Fl. SWA 114: 66 (1967). — Dyer in Gen. Southern African Flow. Pl. 1: 490 (1975), excl. Sect. Cactoidea White & Sloane. Type: T. flavum N.E. Br.

Note: N.E. Brown (1878) states that Thunberg's specimen of T. piliferum was "too imperfect to construct a genus from" so that he "derived the generic character chiefly" from T. flavum. This species is therefore the type of Brown's genus Trichocaulon. White & Sloane (1937) assumed that the type of Trichocaulon is T. piliferum (Mass.) N.E. Br and this was followed uncritically by Farr et al (1979), Huber (1967) and Plowes (1992) from which it is clear that none of these authors consulted Brown's original publication. This lectotypification was based therefore on a "mechanical method of selection" and is here set aside in favour of T. flavum (Greuter et al, 1988).

Key to the species

1. Horns of outer corona lobes adherent laterally to dorsal part of inner lobes for entire length.....2.
1. Horns of outer corona lobes not adherent laterally to dorsal part of inner lobes for more than half of length.....5.
2. Corona 2–2.2 mm broad across top, corolla tube conical with sides of tube touching sides of gynostegium.....3.
2. Corona 3–4 mm broad across top, corolla tube saucer-shaped, sides of tube not touching sides of gynostegium.....4.

3. Stems 22–28–angled, corolla 20–40 mm diam.....10. H.ruschii
3. Stems 12–14–angled, corolla 11–15 mm diam.....9. H.triebneri
4. Corolla 10–14 mm diam., inside densely covered with small papillae.....6a. H.officinalis subsp. officinalis
4. Corolla 14–20 mm diam., inside with few very scattered papillae or smooth.....6b. H.officinalis subsp. deilaetiana
5. Pedicel 4–15 mm long, flowers never yellow.....6.
5. Pedicel \leq 2 mm long (if longer, flowers bright yellow).....7.
6. Stems erect with persistent spines, corolla tube containing three quarters of gynostegium, outer corona lobes bifid for less than half of length.....7. H.mossamedensis
6. Stems usually sprawling, spines only present on young growth, corolla tube only containing lower quarter of gynostegium, outer corona lobes divided nearly right to base.....8. H.pedicellata
7. Corolla tube campanulately funnel–shaped to cup–shaped, completely containing gynostegium (except sometimes for tips of outer corona lobes).....8.
7. Corolla tube \pm absent, containing only basal stipe of gynostegium, united part of corolla flat to slightly saucer–shaped,11. H.flava
8. Corolla smooth inside, corolla tube campanulately funnel–shaped, pollinia broader than long.....12. H.alstonii
8. Corolla densely papillate within, corolla tube cup–shaped, pollinia longer than broad.....9.
9. Corolla without raised annulus around mouth of tube, yellow, greenish–yellow to pale pinkish, corona yellow.....13c. H.pilifera subsp. pillansii

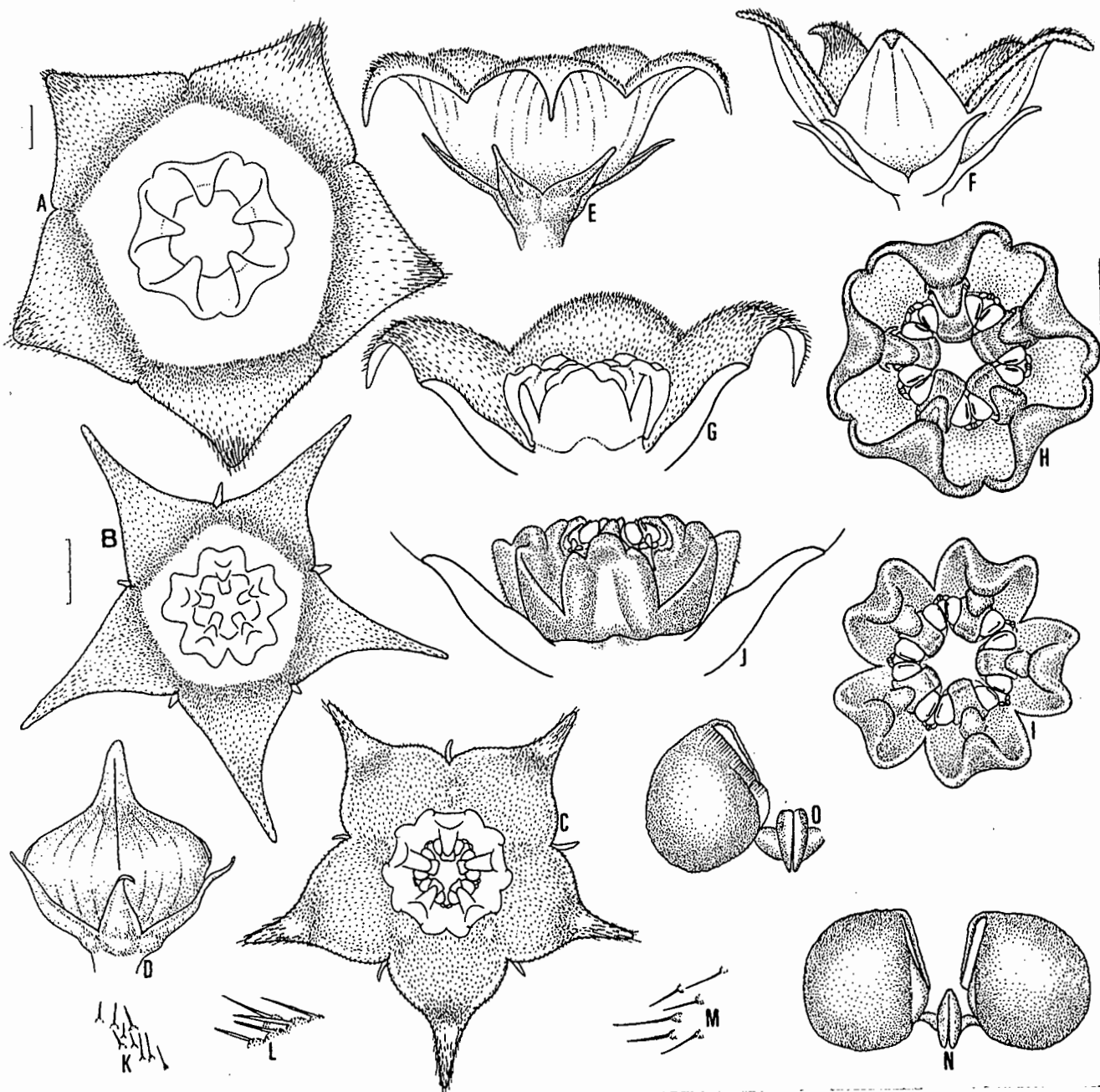


Figure 33
H. officinalis
officinalis

Figure 33.—*H. officinalis* subsp. *officinalis*. A, B, C, face view of flower. D, bud. E, F, side view of flower. G, side view of dissected flower. H, I, face view of gynostegium. J, side view of gynostegium. K, L, M, papillae on corolla: K in base of corolla tube; L, M at end of lobes. N, O, pollinaria.

A, E, G, H, O drawn from specimen from SE of Gamsberg, Namibia, Kratz; B, I, J, K, N, Nabibis, Tiras mountains, Namibia, Bruyns 1511; C, D, F, Bruyns & Heunis 3179; L, Bruyns 3570; M, Bruyns 3069.

Scale bar: A, G, 1 mm (at A); B–F, 2 mm (at B); H–J, 1 mm (at H); K–M, 0.5 mm (at H); N, O, 0.25 mm (at H).

9. Corolla with raised annulus around mouth of tube, purple brown/black to pinkish-brown, corona dark purple-brown/black.....10.
10. Corolla (15) 20–30 mm diam., dark purple-black, lobes spreading and usually adpressed to stem, plants from east of 22° E.....13b. H. pilifera subsp. annulata
10. Corolla 16–20 mm diam., sometimes pinkish-brown, lobes erect to spreading, plants from west of 22° E.....13a. H. pilifera subsp. pilifera

6. Hoodia officinalis (N.E. Br.) Plowes in *Asklepios* 56: 9 (1992).

Trichocaulon officinale N.E. Br. in *Kew Bull. misc. Inf.*: 264 (1895), in *Fl. Trop. Africa* 4 (1): 489 (1903) et in *Fl. Cap.* 4 (1): 893 (1909). – Schltr in *J. Bot.*: 475 (1898). – Berger, *Stap. u. Klein.*: 32 (1910). – Dinter in *Neue u. wenig bekannte Pflanzen D. SWAs*: 58 (1914) et in *Feddes Rep. sp. nov.* 24: 16 (1927). – Marloth in *Fl. S. Africa* 3 (1): t. 22 G (1932). – White & Sloane, *Stap.* 3: 1016, fig. 1081, 1083, 1086 but not 1082 (1937). – Dyer in *Flow. Pl. S. Africa* 23: t. 896 (1943). – Lückhoff, *Stap.*: 249 (1952). – Huber in *Prodr. Fl. SWA* 114: 69 (1967). Type: Botswana?, material imported to America as remedy for piles, some slices of stem with flowers attached presented to Kew by Mr E.M. Holmes of the Pharmaceutical Society (K!)

Two subspecies are recognised.

6a. Hoodia officinalis subsp. officinalis

Trichocaulon pubiflorum Dinter in *Feddes Rep. sp. nov.* 30: 192 (1932). – White & Sloane, *Stap.* 3: 1018 (1937). – Lückhoff, *Stap.*: 250 (1952). Type: Namibia, Velloor, east of Warmbad, 29 Mar. 1924, Dinter (not located).

T. rusticum N.E. Br. in *Fl. Cap.* 4 (1): 891 (1909). – White & Sloane, *Stap.* 3: 1005 (1937). Hoodia rustica (N.E. Br.) Plowes in *Asklepios* 56: 10 (1992). Type: South Africa, Kenhardt, Marloth 3764 (not located).

Plant forming shrub to 0.3 X 0.5 m but mostly much smaller, branching from base. Stems 35–65 mm thick with (14–) 17–22 rows of vertically–arranged tubercles, each tubercle ending in a brown spine up to 6 mm long. Flowers in groups of 1–3 mostly in upper half of stem. Pedicel mostly < 1 mm long, glabrous. Sepals 2.5–3.5 mm long, ovate–lanceolate, acuminate, glabrous. Corolla 10–14 mm diam., rotate to somewhat campanulate with broad shallow saucer–shaped tube, glabrous and smooth outside, within covered with small papillae each tipped with a fine bristle, pale green with brownish veins outside, within red–brown to yellow–brown with tube much paler and yellowish behind corona; lobes spreading with recurved tips, 3–5 mm long, 3.5–5.5 mm broad at base, ovate–deltoid, acuminate. Corona mostly yellow sometimes suffused with fine red dots and inner lobes brownish, about 4 mm diam., 1.5–2 mm tall, usually finely pubescent on exterior; outer lobes forming pouch between inner lobes, divided in centre nearly to base into 2 obtuse erect teeth laterally adnate to and not exceeding dorsal part of inner lobe; inner lobes mostly less than 0.5 mm long, dorsiventrally flattened, incumbent on anthers and usually much shorter than them with broad obtuse erect dorsal projection joined laterally to outer lobes. Follicles 115–125 mm long, 164–292 seeds per pair. Figure 33.

Material examined

2316: Nauchas (–CB), Bruyns 4140 (BOL).

2317: Rehoboth (–AC), comm. Herre sub SUG 6009 (BOL).

2416: Onis (–AC), Bruyns 4153 (); Neu Onis (–AD), Bruyns 4151 (); Swartmodder (–CD), Bruyns 4165 (BOL); Zwischen Hoodien kurz vor Nomtsas (–DB), Dinter 3138a (SAM).

2417: Kalkrand (–BA), Hall sub NBG 506/55 (NBG); Mariental (–DB), Dreyer sub NBG 775/32 (BOL).

- 2418: N of Stampriet (–AA), Bruyns 3581 (BOL).
 2517: Alsuma (–CC), Bruyns 4178 (PRE).
 2616: Tiras (–BA), Bruyns & Heunis 3179 (BOL).
 2619: Springboktrek–Suid (–AC), Bruyns 3570 (BOL); Vensterkop (–CC), Bruyns 3564 (BOL).

2718: Kuduberg (–CA), Tölken s.n. (NBG).

[2819: Velloor (–CA), Dinter s.n. (not located but included on distribution map)]

South Africa

- 2820: Biesjespoort, (–BC), Herre sub SUG 5992 (BOL); Keimoes (–DB), Wilmot 107 (BOL); Kakamas (–DC), Fuller 128 (BOL).
 2821: Vollgraafsig (–DB), Hardy (PRE).
 2822: Paardekloof (–DA), Bruyns 4528 (); Rudesheim (–DD), Bruyns 4490 (BOL).
 2823: Papkuil (–BC), Wilman 17073 (BOL).
 2920: Graafwater (–AB), Bruyns 5257 (BOL).
 2921: 20 miles N Kenhardt (–AA), Acocks 18840 (PRE); Kenhardt (–AC), Fuller sub NBG 353/26 (BOL).
 2922: Kruispad (–BB), Bruyns 4544 (BOL); Kloof (–BD), Bruyns 3069 (BOL); 11 km S Niekerkshoop (–BD), Bruyns 3746 (BOL); Prieska (–DA), Dunker 6609 (PRE).
 2923: Mazelsfontein (–BA), Anderson 541 (BOL, STE); Anderson sub KMG 2228 (KMG); Florisfontein (–BA), Bruyns 3276 (BOL); Douglas (–BB), Herre sub SUG 6025 (BOL); Vlakpan (–DC), Bruyns 5127 (BOL).
 2924: Vetberg (–AC), Wilman 17152 (BOL); Thornhill (–AC), Leistner 1423 (PRE, KMG); Jacobsdal (–BB), Hall sub NBG 290/53 (NBG); Kalkpoort (–DC), Bruyns 5123 (BOL).

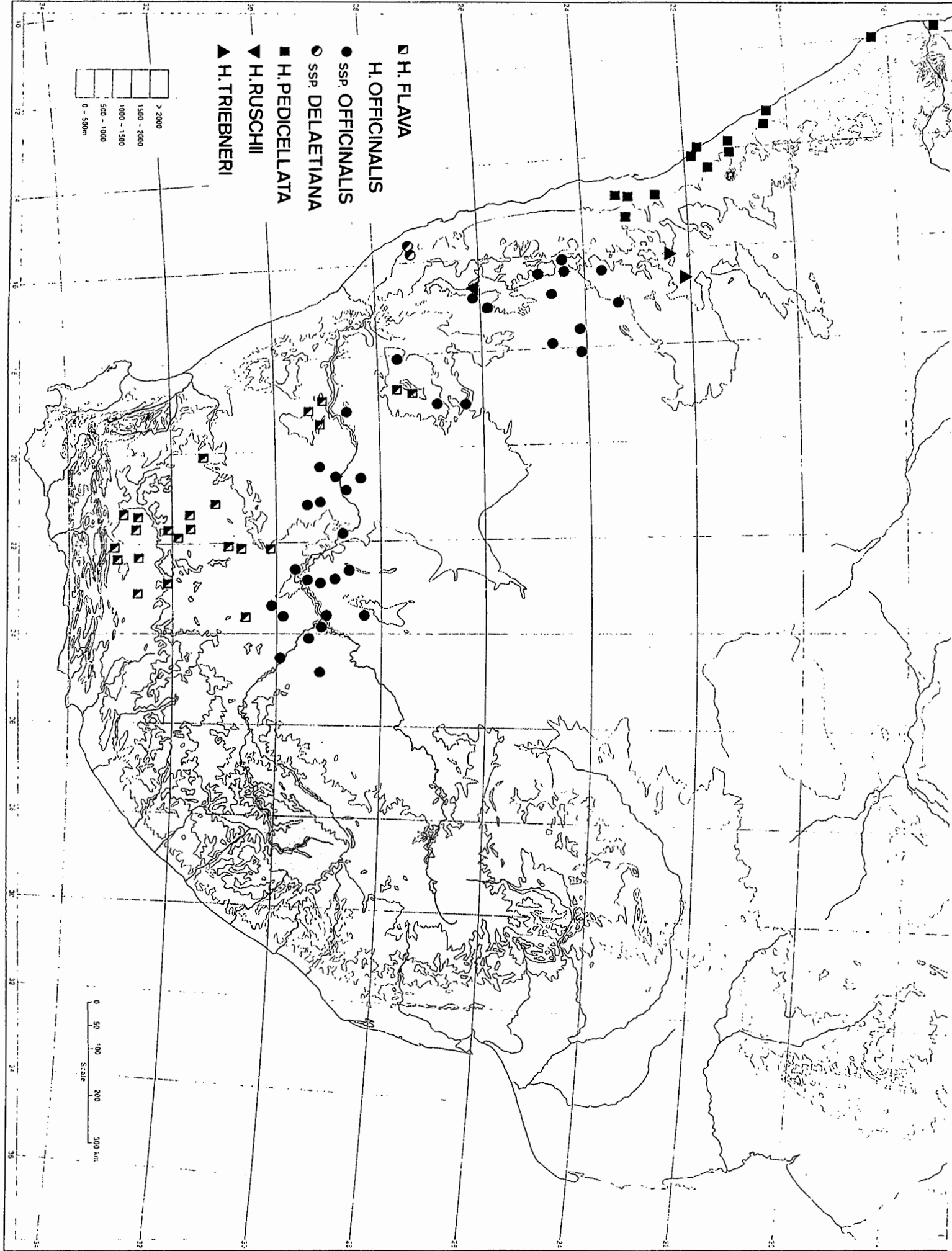


Figure 34.—Distribution of *Hoodia flava*, *H. officinalis*, *H. pedicellata*, *H. ruschii*, *H. triebneri*.

3023: Ruitjiesvlakte (–AB), Bruyns 5136 (BOL).

Without precise locality: Phillipstown district (3024 A), v.d. Walt sub PRE 26507 (PRE);
I.L.Drège sub Marloth 5983 (PRE).

H.officinalis subsp. officinalis is the most widespread species in this section (Fig. 34). It occurs from a little south of Windhoek more or less throughout southern Namibia except in the south–western winter rainfall area and in the deep sands of the Kalahari in the east. From here it occurs eastwards to Griqualand West near Douglas and Kimberley and just enters the western part of the Orange Free State at Jacobsdal (with one inexact recorded collection from further east near Phillipstown). Only in one locality (just south of the Naukluft Mountains in Namibia) was it found to be plentiful. Mostly it is of sporadic occurrence, though it is not necessarily rare. Plants are almost always found growing inside bushes in flattish or gently sloping areas and they are often associated with patches of the 'driedoring' Rhigozum trichotomum.

Specimens of this subspecies vary very much in size and thickness of the stems. The largest (up to 300 mm tall and 65 mm thick, forming robust shrubs up to 0.5 m diam.) were seen in a year of good rainfall in the Aroab district (Namibia). These were exceptional and mostly they are much smaller (150 mm tall) and only 35–50 mm thick. The corolla is variable in colour from a deep pinkish–brown to yellow–brown and usually has a paler whitish to yellowish centre behind and around the gynostegium which itself varies from deep, bright yellow to pale yellow. The corolla lobes are also somewhat variable in shape and especially around the Tiras Mountains they have rather longer, more acuminate tips than elsewhere where they tend to be more shortly acute. The lobes will

often be observed to have a silvery sheen towards their tips and this is caused by the bristles which tip the papillae on the surface being \pm horizontal in these parts. Elsewhere (for they cover \pm the entire inner surface of the corolla) they are more erect and are not visible to the naked eye. A curious feature of the corona is the crystalline, sharp-tipped, colourless to reddish setae found on the outside usually especially densely below the backs of the inner lobes. This has been observed in specimens throughout southern Namibia but not in any South African material. This phenomenon is unknown otherwise in this section but is seen occasionally in Hoodia currorii.

The stems of subsp. officinalis have slightly fewer rows of broader, more rounded (less laterally flattened) tubercles with slightly stouter, darker spines than in H.flava. Thus, although these two are vegetatively similar they can actually be distinguished without flowers. However, when flowers do appear there is no confusing them at all: the virtually flat flower of H.flava with its mandible-like outer corona lobes lacking the 'pubescence' of subsp. officinalis is quite different. Thus these two do not appear to be especially closely related despite their curiously superimposed distribution: in southern Namibia and Bushmanland H.flava actually crosses over the distribution range of H.officinalis, although there are no known localities where they occur together and H.officinalis seems to be absent in the area from the Great Karas Mountains to Pofadder where H.flava occurs. I have tried to cross-pollinate these two species. The brown pollinia of H.officinalis are much larger than those of H.flava (which are yellow) and there is insufficient space below the guide rails of H.flava to fit one in. However, the pollinia of H.flava fit in readily to the rails of H.officinalis but no seeds were produced from this.

The structure of the gynostegium in H.officinalis is very similar to that in

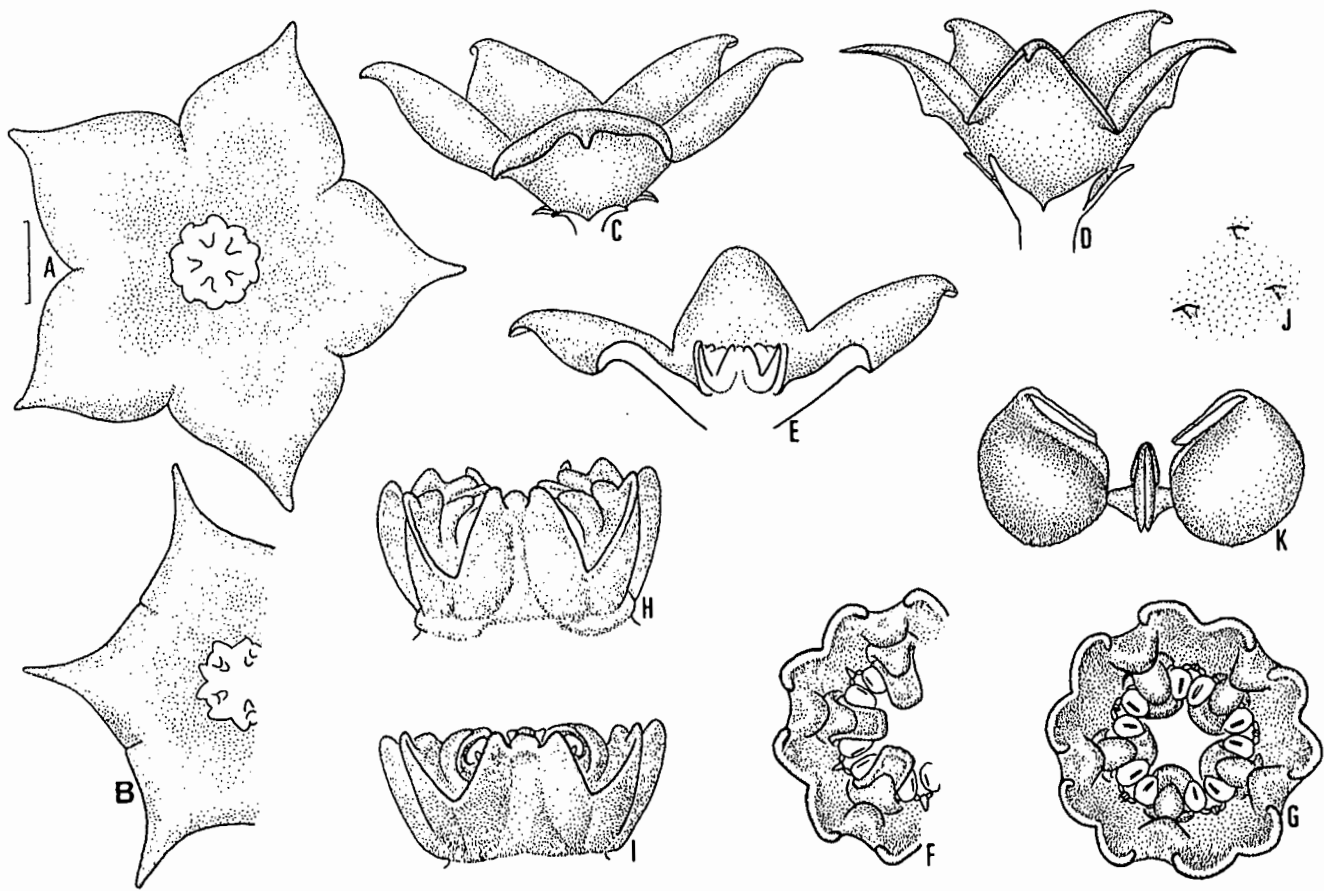


Figure 35
 T. del. 1977
 10/12/90

Figure 35.—*H. officinalis* subsp. *delaetiana*. A, B, face view of flower. C, D, side view of flower. E, side view of dissected flower. F, G, face view of gynostegium. H, I, side view of gynostegium. J, papillae on united part of corolla. K, pollinarium.

A, C, E, G, H, J, drawn from Karoo Garden 553/77; B, D, F, I, K, from Bayer 3858.

Scale bar: A–E, 3 mm (at A); F–I, 1 mm (at A); J, 0.5 mm (at A); K, 0.25 mm (at A).

H.triebneri, H.pedicellata and H.ruschii and it appears that this species is more closely related to these more northern taxa.

T.pubiflorum is quite clearly the same as subsp. officinalis as Figure 1083 in White & Sloane (1937) shows. It is supposed to differ from 'officinale' only in having longer and denser pubescence on the inner surface of the corolla and in the pubescence on the outside of the outer corona. The latter has been observed many times and I have also noted variation in the length of the bristles on top of papillae on the corolla. Thus I have no hesitation (as did Huber) in including this name under H.officinalis subsp. officinalis.

In T.rusticum the 'distinct campanulate tube' of the flower, the 'microscopic pubescence, invisible when wetted' on the inner surface of the corolla lobes and the outer corona lobes 'erect deeply bifid ... rising to about the level of the top of the staminal column' all strongly suggest H.officinalis subsp. officinalis. The type has not been located but Marloth 5983 (from "I.L. Drège") at PRE was annotated by Marloth as T.rusticum and this is H.officinalis subsp. officinalis.

6b. H.officinalis subsp. delaetiana (Dinter) Bruyns comb. et stat. nov.

Trichocaulon delaetianum Dinter in Feddes Rep. sp. nov. 19: 155 (1923). — White & Sloane, Stap. 3: 1019, fig. 1084, 1085 but not 1086 (1937). — Lückhoff, Stap.: 250 (1952). — Huber in Prodr. Fl. SWA 114: 68 (1967) sub T.alstonii. — Dyer & Hardy in Flow. Pl. Africa 47: t. 1845 (1982). Type: Namibia, Klinghardt Mountains, Dinter 4735 (not located). Hoodia delaetiana (Dinter) Plowes in Asklepios 56: 8 (1992) as "delaetii".

Neotype: Namibia, Klinghardt Mountains, Merxmüller & Giess 32150 (WIND! M!)

Plant consisting of several erect to sprawling stems to 400 mm tall, forming shrub. Stems

40–70 mm thick, with 19–23 rows of vertically arranged tubercles, each tubercle tipped with sharp brown spine up to 12 mm long. Pedicel 1–2 mm long, glabrous. Sepals (1–) 2–2.5 mm long, about 1.5 mm broad at base, acuminate, glabrous. Corolla (12–) 14–20 mm diam., inside with few scattered papillae each tipped with short bristle or smooth, broadly campanulate, outside reddish–brown, inside brownish–yellow to yellow; tube broadly saucer–shaped, 2–3 mm deep; lobes ovate, acuminate, 4–6 mm long, 5–7 mm broad at base, with tips recurved. Corona dark red–brown to reddish, 3–3.5 mm broad, glabrous; inner lobes incumbent on anthers and about half as long as them, obtuse. Otherwise as in subsp. officinalis. Figure 35.

Material examined

2715: Klinghardt Mountains (–B), Lavranos & Barad (NBG); (–BC), Müller 719a (WIND); Merxmüller & Giess 32150 (WIND); Paradise Valley (–BD), Bayer 3858 (NBG).

H.officinalis subsp. delaetiana is known only from the Klinghardt Mountains in the ‘diamond area’ about 100 km SSE of Lüderitz in the south–western corner of Namibia (Fig. 34). It is apparently quite common there and is the only member of this section found there, surrounded to the north–east and south–east by populations of H.alstonii. The nearest populations of subsp. officinalis are some 150 km away to the north–east and out of the strictly winter–rainfall area where subsp. delaetiana occurs.

This taxon has an identical gynostegium to subsp. officinalis. The plant is generally a little more stoutly spined and more robust than in subsp. officinalis, the flowers are larger with a broader and much flatter tube to the corolla. They vary in colour from

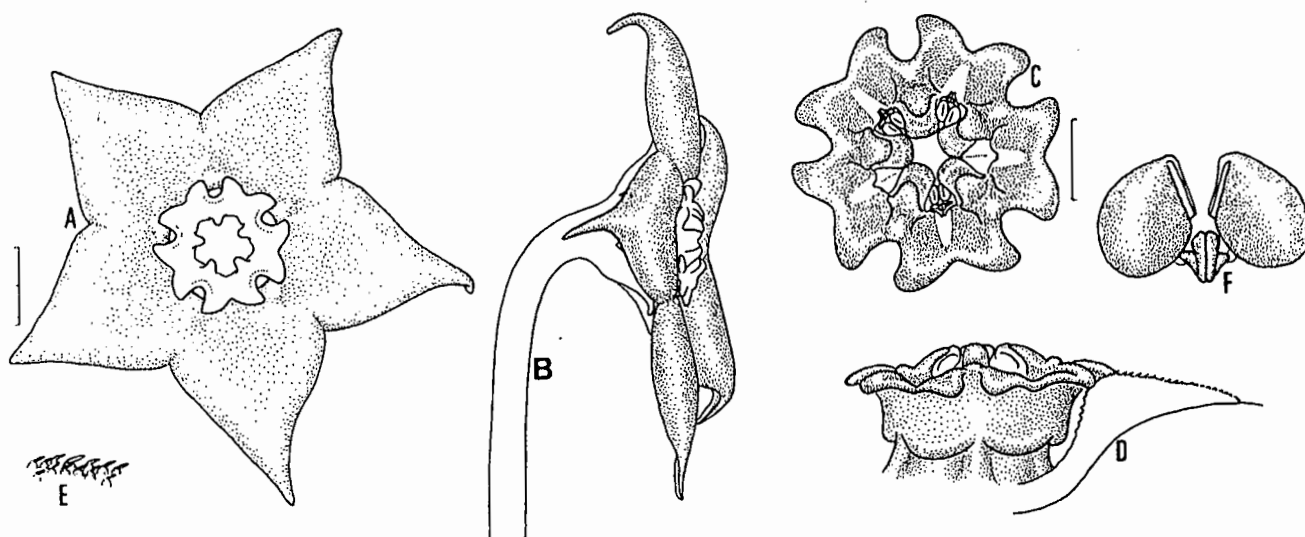


Figure 36
H. mossamedensis
 Rabl

Figure 36.—*H. mossamedensis*. A, face view of flower. B, side view of flower. C, face view of gynostegium. D, side view of gynostegium. E, papillae on corolla just beyond mouth of tube. F, pollinarium.

All drawn from Horwood, Downes & Chambers, Angola.

Scale bar: A, B, 2 mm (at A); C, D, 1 mm (at C); E, 0.5 mm (at C); F, 0.25 mm (at C).

yellow to dark brownish—yellow but are never the brownish—pink often seen in subsp. officinalis. Although the inside of the corolla has been given as smooth this is not always true and it may have scattered papillae on the surface. These are also armed with a small, apical bristle which is, however, never as long as that in subsp. officinalis.

The geographic separation of these two taxa (one of extremely restricted distribution in the winter rainfall region of Namibia and the other widely spread over the drier, subtropical, summer rainfall parts of southern Africa) and the rather weak differentia on which they may be distinguished suggests that they have relatively recently separated into two disjunct taxa, a situation best reflected by classifying them as subspecies of one widespread species.

7. Hoodia mossamedensis (Leach) Plowes in *Asklepios* 56: 9 (1992).

Trichocaulon mossamedense Leach in *J. S. African Bot.* 40: 15 (1974). — Horwood in *Cact.*

Succ. J. (US) 46: 262–264 (1974). — Dyer in *Flow. Pl. Africa* 44: t. 1736 (1977).

Type: Angola, Mossamedes district, Leach & Cannell 14690 (LISC[!] holo.; SRGH, iso[!])

Plant consisting of 1–4 erect stems, up to 300 mm tall, branching at or near base. Stems 40–50 mm diam., with 16–20 rows of vertically arranged compressed conical tubercles, each tubercle 4–7 mm high tipped with brown spine up to 6 mm long. Flowers in groups of 1–4, developing successively from an eventually knob-like persistent peduncle, mainly in upper part of stem. Pedicel 10–18 mm long, about 1 mm diam., glabrous, spreading to ascending. Sepals 2.5–3 mm long, ± 1 mm broad at base, very slightly overlapping at bases, deltate, acuminate. Corolla campanulate, rotate or with lobes slightly reflexed, 9–18

mm diam., dark maroon, glabrous outside and inside, smooth outside, inside covered with minute papillae each tipped with a horizontally-spreading thick bristle; tube ± 1.5 mm deep, cupular, often slightly thickened around mouth; lobes ovate, acuminate, ± 4 mm long, 3.5 mm broad at base, margins slightly recurved. Corona glabrous, maroon-black, shallowly cup-shaped, ± 1.5 mm tall, 3.5 mm diam.; outer lobes spreading with slightly recurved tips, ± 0.75 mm long, 1.25 mm broad, shallowly bifid, joined laterally to inner lobes; inner lobes oblong, obtuse, incumbent on backs of anthers and slightly shorter than them, with small obtuse erect dorsal projection where joined to outer lobes. Figure 36.

Material examined

Angola

1412: 10 km towards Lucira from Mossamedes (–CD), Leach & Cannell 14690 (LISC, SRGH); 30 km N Mossamedes (–CD), Horwood, Downes & Chambers (PRE); about 45 km from Mossamedes towards Dois Irmaos (–DC), Mendes 3845 (LISC).
Not located on map: ± 21 km N Chapeu Armado, Leach & Cannell 14697 (M, K).

Because of the war in southern Angola, it seems that this species has not been gathered since it was described. In the collection illustrated here the inner corona lobes are much shorter than those shown by Leach (1974, see above) and the pollinarium has a much smaller wing on the corpusculum. For known distribution see Figure 30.

This species and H. pedicellata are closely related and the differences between them are discussed under the latter.

8. Hoodia pedicellata (Schinz) Plowes in *Asklepios* 56: 9 (1992).

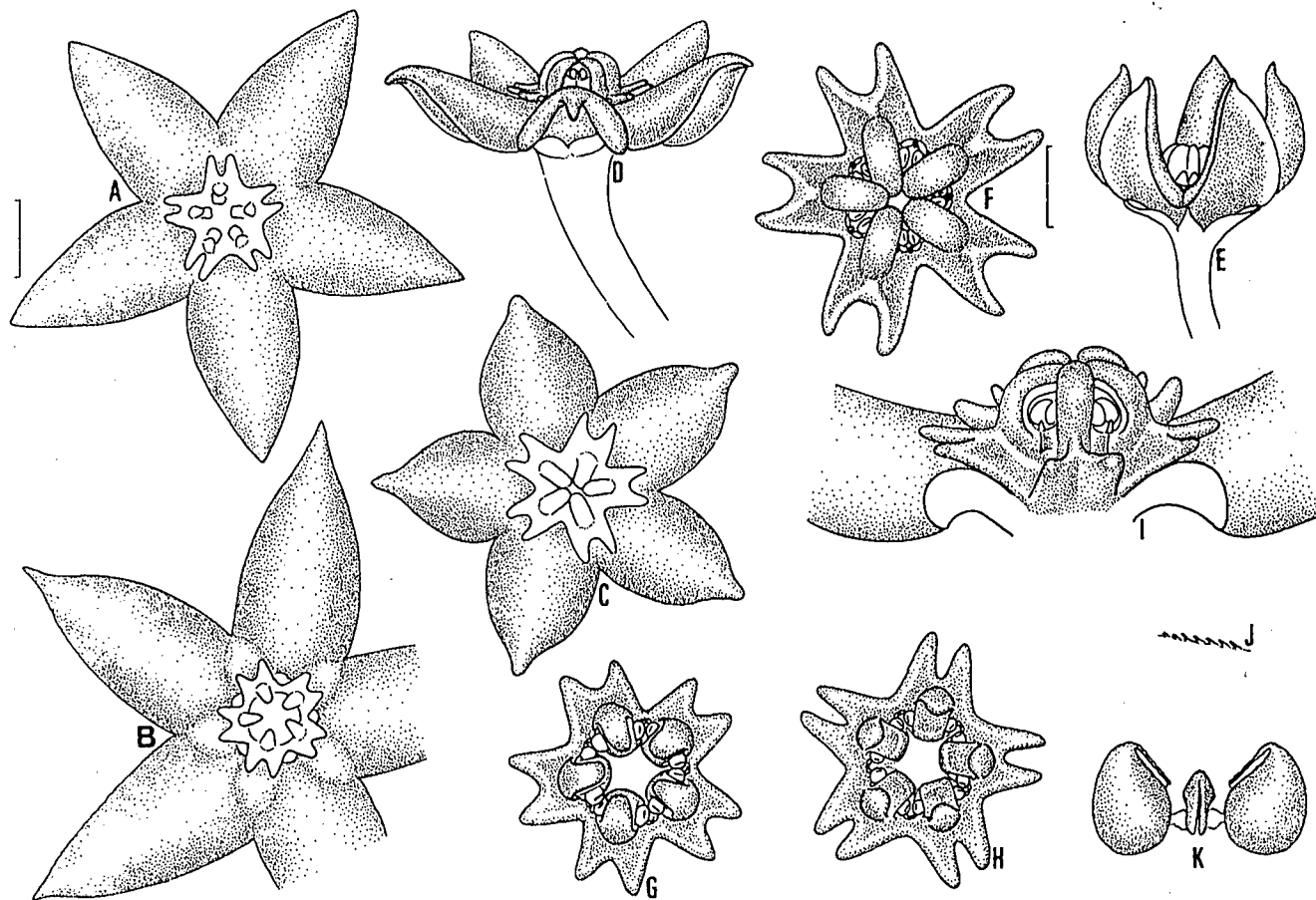


Figure 37
H. pedicellata
 7/6/90

Figure 37.—*H. pedicellata*. A, B, C, face view of flower. D, E, side view of flower. F, G, H, face view of gynostegium. I, side view of gynostegium. J, papillae on corolla lobes. K, pollinarium.

Drawn from: A, H, 72 miles N Swakopmund, M. Visagie; B, G, Codd 10585; C, D, F, I, 40 km E Swakopmund, cult. Windhoek; E, J, Cape Cross, collector unknown (PRE).

Scale bar: A–E, 2 mm (at A); F–I, 1 mm (at F); J, 0.5 mm (at F); K, 0.25 mm (at F).

Trichocaulon pedicellatum Schinz in Verhandl. Bot. Verein Brandenb. 30: 266 (1888). — N.E. Br. in Fl. Trop. Africa 4 (1): 490 (1903). — Berger, Stap. u. Klein.: 35 (1910). — Dinter in Feddes Rep. sp. nov. 24: 16 (1927). — White & Sloane, Stap. 3: 1014, fig. 1078, 1079, 1080, 1118 (1937). — Lückhoff, Stap.: 247 (1952). — Huber in Prodr. Fl. SWA 114: 69 (1967). — Horwood in Cact. Succ. J. (US) 46: 264, photos (1974). — Giess in Dinteria 15: 61 (1981). — Jacobsen & Moss in Dinteria 19: 53 (1987).
 Type: Namibia, probably near Hope Mine, Stapff (K!)

Plant consisting of up to 20 or more stems, branching from base. Stems erect when young, later sometimes horizontally creeping, 100–250 (–500) mm long, 25–50 mm thick, with 11–20 rows of vertically arranged tubercles, each tubercle tipped by a dark spine 1.5–3 mm long soon weathered off by sand so that spines usually only found at growing tip of stem. Flowers in groups of 1–4, mainly in upper parts of stem, developing successively. Pedicel 4–12 mm long, glabrous, dependent. Sepals 1.5–2 mm long, lanceolate, acuminate, glabrous. Corolla 8–14 mm diam., nodding, finely papillate within, glabrous inside and outside, inside maroon or light to dark purple–brown, with slight bulges just below sinuses of lobes; tube usually < 1 mm long, just enclosing base of corona; lobes erect to spreading, 3–6 mm long, 2.5–3 mm broad at base, often widening slightly towards middle, lanceolate, acuminate, margins recurved. Corona purple–brown or yellow, glabrous, 3–3.5 mm diam.; outer lobes spreading horizontally from middle of gynostegium, bifid nearly right to base into two widely diverging very short teeth laterally joined to backs of inner lobes; inner lobes rising up from level of outer lobes, incumbent on backs of anthers, obtuse, very variable in length but often meeting in centre. Figure 37.

Material examinedAngola

1711: 30 km from Foz do Cunene towards Espinheira (–BB), Mendes 1281 (LISC).

Namibia

1811: Angra Fria (–BD), Plowes 5286 (SRGH).

1912: (–BD), Jacobsen & Moss (l.c. 1987, see above).

2013: ± 20 km ö. Torra Bay (–AD), Giess 8015 (PRE, WIND); 17 miles E Torra Bay
(–BC), Hardy & de Winter 1477 (PRE).

2014: S of Ugab River Station (–DD), Müller & Loutet 1103 (WIND) [very doubtful
locality, not included on map].

2113: S of Ugab (–BB), Giess 15323 (WIND); Cape Cross (–DD), Hall sub NBG 513/55
(NBG).

2114: hills E of Cape Cross (–AA), Oliver & Müller 6654 (PRE); 25 miles E Cape Cross
(–CB), Triebner sub NBG 625/50 (NBG); 28 miles N Hentjies Bay (–CC),
Barnard 100 (WIND); Lagunenberg (–CC), Giess 3547a (PRE, WIND).

2214: Rössing (–DB), Dinter 8429 (G, Z).

2314: near Vogelfederberg (–BB), Jensen 254 (WIND); 36 miles SSE Walvis Bay (–BD),
Giess 3027 (WIND).

2315: 50 miles SE Walvis Bay (–AB), Barnard 95 (WIND).

Without precise locality: near Cape Cross, 1932, Harcourt–Wood (BOL).

Hoodia pedicellata occurs exclusively in the coastal mist–belt of the tropical Namib Desert from south of Swakopmund at least to a little north of Foz do Cunene in SW Angola (see Fig. 34). It seems to be found only within 80 km of the coast. The southern

portion of the distribution is well documented but beyond the Ugab River Mouth little is known and it is probably much more common than the few records indicate.

H.pedicellata is an extremely distinctive species. The stems often sprawl among rocks and may be pendulous (as in the exceptionally large plant shown by Giess 1981, see above). The spines are usually only found near the growing apex of the stem as they are weak and soon weathered off by windblown sand, leaving the tubercle spineless. Stems which are spineless bear some resemblance to those of Lavrania. White & Sloane (1937, pp. 991, 1014) use this resemblance to suggest that this species represents an intermediate between the "spiny" Trichocaulons and the "spineless" species. This hypothesis is clearly wrong since both seedlings and all young, growing shoots show the spines typical of Hoodia. The flowers of H.pedicellata and H.mossamedensis are remarkable for their nodding habit on long pedicels which keeps the flowers from being misshaped by the neighbouring spines and tubercles. They have an extremely beautiful dark, velvety, maroon to purple-brown colour and unusual, relatively narrow corolla lobes with the margins well folded back. The velvety texture is caused by very fine papillae on the surface of the corolla. The flowers are very variable in size and the extent to which the lobes fold out. Much variation has also been seen in the corona: both in the shape and length of the outer lobes and in the length of the inner lobes.

H.pedicellata is probably most closely related to H.mossamedensis with which it shares the remarkably long pedicels. Both have similar corona structure to H.officinalis, H.ruschii and H.triebneri. H.pedicellata differs from all of them in the stems which, in the others, are erect and more persistently spiny. Apart from the differences in the stems, H.mossamedensis is distinguished mainly by the differently shaped corolla lobes (more deltoid than lanceolate), the deeper tube with thickened mouth containing most of the

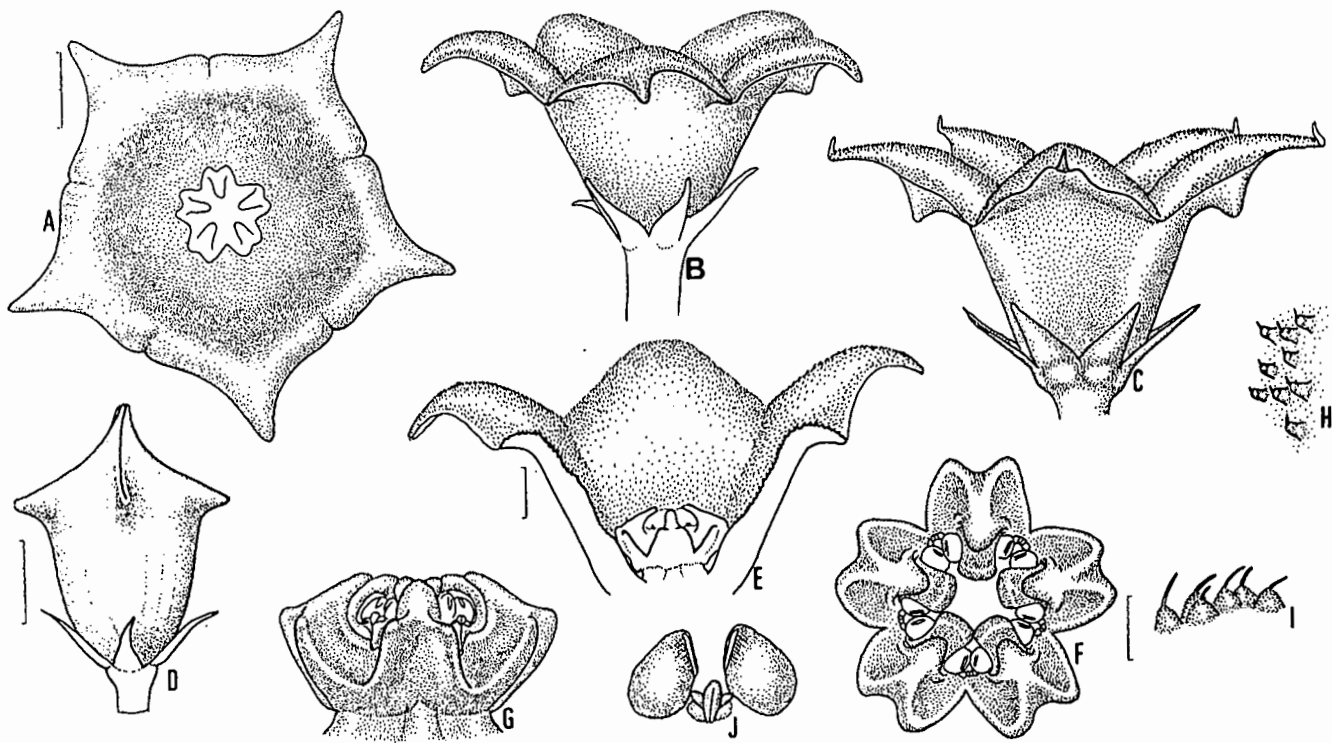


Figure 38
Hoodia triebneri
 n. sp.

Figure 38.—*Hoodia triebneri*. A, face view of flower. B, C, side view of flower. D, bud. E, side view of dissected flower. F, face view of gynostegium. G, side view of gynostegium. H, I, papillae on corolla: H, in tube; I on lobe. J, pollinarium.

C, D, H, I drawn from Bruyns 3632; rest from M. Visagie sub Giess 15303

Scale bar: A–C, 2 mm (at A); D, 3 mm; E, 1 mm; F, G, 0.5 mm (at F);

H, I, 0.5 mm (at H); J, 0.25 mm (at H).

gynostegium, the slightly larger papillae on the corolla (with obvious apical bristle) and the only very slightly divided outer corona lobes. In H. pedicellata the inner corona lobes and anthers rise up much higher above the level of the outer corona lobes.

The material at Kew which was annotated by N.E. Brown as 'part of type specimen' is further annotated as having been gathered by Hans Schinz on 3 March 1890. However, by this date neither Stapff nor Schinz was still in Namibia (Gunn & Codd 1981) and so this specimen was probably sent by Schinz to Brown, arriving at Kew in 1890 and is most likely then to be part of Stapff's collection. Unfortunately I have been unable to examine this specimen.

Dinter annotated several specimens of this species from the Swakopmund district as 'Trichocaulon bossii' but never published this name.

9. Hoodia triebneri (Nel) Bruyns comb. nov. non Hans Schuldt in Desert: 92 (1933) nom. nud..

Trichocaulon triebneri Nel in Kakteenkunde: 117 (1935). — White & Sloane, Stap. 3:

1003, fig. 1071, 1072, 1082 (1937). — Lückhoff, Stap.: 246 (1952). — Huber in Prodr. Fl. SWA 114: 70 (1967). — Plowes in Asclepiadaceae 21: 23–26 (1980). Hoodia foetida Plowes in Asklepios 56: 9 (1992). Type: Namibia, near Okandu, 120 km E Swakopmund, 1933, W. Triebner sub SUG 6020 (BOL!)

Plant a spiny succulent consisting of 10–30 erect stems forming a shrub to 300 mm tall, 450 mm broad, branching mainly near base. Stems 25–40 mm thick, with 12–14 (–16) rows of vertically arranged prominent conical tubercles, each tubercle tipped with a pale spine 5–6 mm long. Flowers in groups of 6–12, often several on each eventually knob-like persistent peduncle opening simultaneously, mainly in upper part of stem. Pedicel 3–4 mm

long, a little more than 1 mm thick, glabrous. Sepals 2.2–2.5 mm long, \pm 1 mm broad at base, ovate–acuminate, glabrous. Corolla 11–15 mm diam., campanulate, outside reddish–green, inside blackish red–purple (paler in base of tube), glabrous outside and inside, outside smooth, inside covered with obconical papillae each tipped with a slender spreading bristle; tube 3.5–4 mm long, conical, slightly thickened around gynostegium and touching sides of it; lobes 3–4.5 mm long, 4–5 mm broad at base, deltoid–acuminate, spreading, sometimes with fine erect tip. Corona dark purple–black, glabrous, about 1 mm tall, 2.2 mm broad; outer lobes divided nearly right to base into two erect obtuse lobules laterally fused for whole length to dorsal part of inner lobes and not exceeding them; inner lobes obtuse, oblong, incumbent on backs of anthers and about half as long as them. Follicles 105 mm long, 66 seeds per horn. Figure 38.

Material examined

2216: Otjimbingwe (–AC), Bruyns 3632 (BOL, PRE, K, STE); Rūdenau–Nord (–BA), Visagie sub Giess 15303 (WIND).

Hoodia triebneri only occurs along the Swakop River from west of Okahandja to near Otjimbingwe and Karibib (see Fig. 34). Very occasionally it is locally common but it is normally rare.

H. triebneri is a most unusual species. The plants, with their slender, strongly spiny, 12–14–angled stems, resemble Hoodia gordonii closely. The appearance of flowers, however, immediately dispels any confusion. H. triebneri is the first of the small–flowered, summer rainfall species to flower and in cultivation large numbers of flowers are usually produced for about 5 weeks in October and November. They arise in clusters with several

of the flowers in a cluster opening simultaneously. These clusters of flowers develop from flat 'peduncular patches' which are more complicated (Fig. 7) than in any other Hoodia except H.ruschii. The flowers are dark blackish red–purple, covered densely inside with columnar papillae and are exceedingly foul–smelling. They are somewhat funnel–shaped with the very small corona sitting in the base of the tube surrounded quite closely by the thickened lower part of the tube.

This species is very close to H.ruschii under which this is discussed.

The present Hoodia triebneri should not be confused with that of Hans Schuldt for which no description was ever published and which consequently remains an invalid name.

The tiny specimen at BOL was sent by H.Herre in October 1934 without any information other than its originating in Namibia. There is no mention in White & Sloane (1937) of any other collections of this species other than those of Triebner, who seems to have seen it at several places. Herre sent pieces of many of the type plants of Nel's new species to BOL and it is assumed that this is what happened here. This piece is then taken as the holotype.

10. Hoodia ruschii Dinter in Feddes Rep. sp. nov. 30: 192 (1932). — White & Sloane, Stap. 3: 1074, fig. 1150, 1151 (1937). — Huber in Prodr. Fl. SWA 114: 37 (1967). Type: Namibia, Tiras Mtns, 1931, E.Rusch jnr sub Dinter 7976 (BOL, holo!; S{ PRE| Z| G}).

Plant a spiny succulent consisting of many erect stems forming shrub to 450 X 500 mm, branching mainly from base. Stems 40–60 mm thick, with prominent conical laterally flattened tubercles vertically arranged into 22–28 angles, each tubercle bearing a

stiff spine 6–8 mm long, brownish to grey–green. Flowers in groups of 4–10, often several on each knob–like persistent peduncle opening simultaneously, mainly in upper half of stem, extremely foul–smelling. Pedicel 2–4 mm long, 2 mm thick, glabrous. Sepals 2–4 mm long, 1–2 mm broad at base, acute–lanceolate, glabrous. Corolla 20–40 mm diam., broadly campanulate, outside pale green to reddish towards base, inside red–brown, glabrous outside and inside, outside smooth, inside covered with conical papillae each tipped with a slender spreading bristle; tube 6–8 mm long, 8–10 mm broad across mouth, broadly conical, slightly thickened around gynostegium and touching sides of gynostegium; lobes 8–14 mm long, 9–14 mm broad at base, deltoid–acute (slightly ovate at base), spreading with slightly recurved tips. Corona dark purple–black, glabrous, slightly over 1 mm tall, 2.2 mm broad across top; outer lobes divided nearly right to base into two erect obtuse lobules laterally fused for whole length to dorsal part of inner lobes and not exceeding them; inner lobes obtuse, oblong, incumbent on backs of anthers and about half as long as them. Figure 39.

Material examined

2616: Tiras (–BA), Bruyns 1475 (BOL); Tiras mountains, without precise locality, E.Rusch jnr sub Dinter 7976 (BOL; S; PRE; Z; G).

Hoodia ruschii is at present known only from the eastern flank of the Tiras Mountains some 70 km north of Aus (Fig. 34). Here it grows on steep, granite slopes among rocks and small bushes. Plants are not uncommon but are of rather scattered occurrence.

Specimens of H.ruschii may reach a size of 0.5 m diameter and more or less the same in height. The stems are stout (40–60 mm thick) and densely covered with sharp, hard

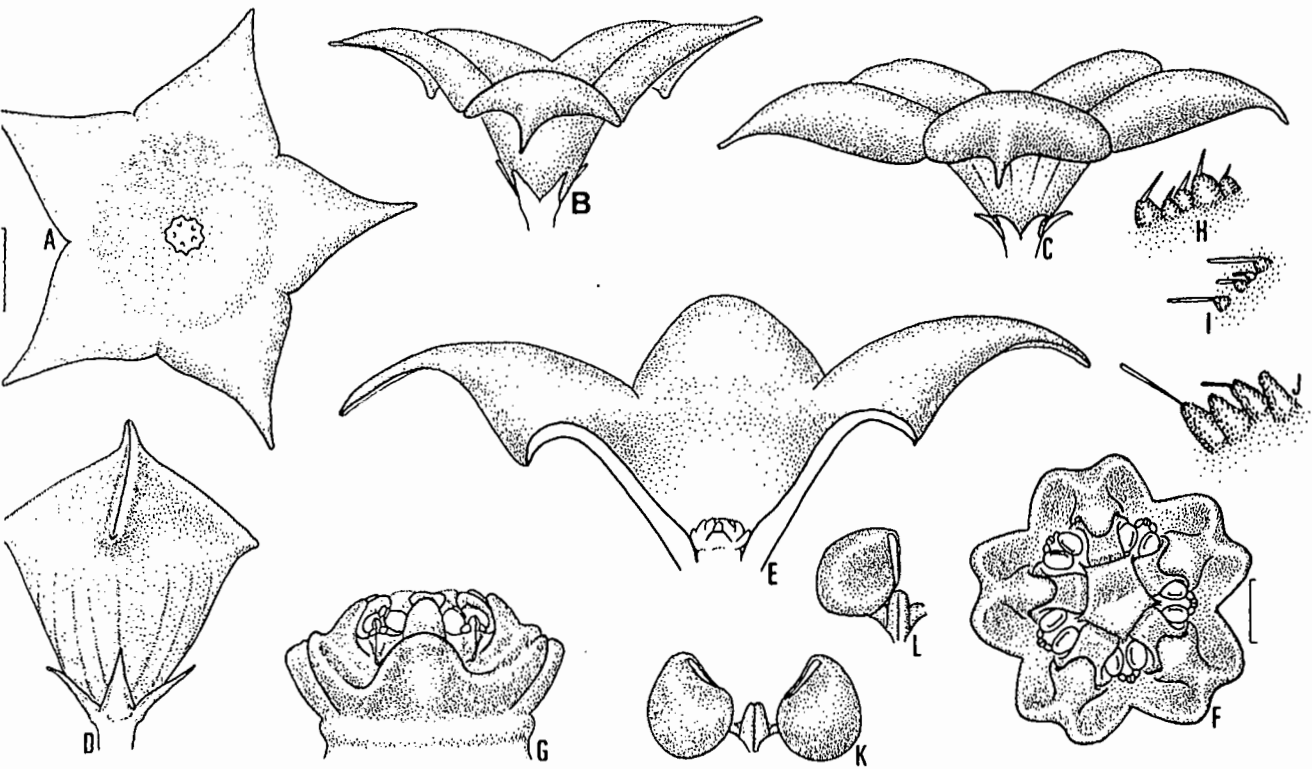


Figure 39
 H. ruschii
 25/1/75

Figure 39.—*Hoodia ruschii*. A, face view of flower. B, C, side view of flower (B one of first flowers produced, plant not properly rooted; C more normal size). D, bud. E, side view of dissected flower. F, face view of gynostegium. G, side view of gynostegium. H–J, papillae on corolla: H, J, from sinuses of lobes; I in base of tube. Apical bristles directed towards mouth of tube. K, L, pollinaria.

Drawn from Bruyns 1475.

Scale bar: A–C, 5 mm (at A); D, E, 3 mm (at A); F, G, 0.5 mm (at F); H–J, 0.5 mm (at A); K, L, 0.25 mm (at A).

spines. In the field they assume a brownish colouring but they are usually paler green in cultivation. Hoodia ruschii is remarkably floriferous and the upper parts of the stems can be covered with flowers if the plant is healthy (as in Figure 1151 of White & Sloane). Flowering seems, in cultivation at least, to continue for most of the summer months. The flowers are a deep red–brown colour and have a dreadful and extremely strong smell: a single flower can be smelt readily from 30 cm away when it is placed under the microscope for drawing.

Dinter thought that this species was related to H. dregei, probably on account of the small flowers. However, it is not closely allied to any of the species formerly in Hoodia and but rather to H. triebneri. In both the flowers arise from relatively large 'peduncular patches' with a complicated organization (Fig. 7) often with several flowers on each patch open simultaneously. The flowers are funnel–shaped with the unusually small gynostegium seated in the thickened basal portion of this funnel, the true corolla tube (page 16). In both the inside of the corolla is conspicuously and densely papillate with conical papillae.

H. ruschii and H. triebneri are readily distinguished: In H. ruschii the stems are 40–60 mm thick with 22–28 angles, in H. triebneri 25–40 mm thick with 12–14 angles; in H. ruschii the flowers are red–brown, 20–40 mm diam., with large papillae, in H. triebneri blackish, 11–15 mm diam., with smaller papillae.

11. Hoodia flava (N.E. Br.) Plowes in *Asklepios* 56: 8 (1992).

Trichocaulon flavum N.E. Br. in *J. Linn. Soc.* 17: 165, t. 11, fig. 2–4 (1878), in Hook.

Icon. Pl.: t. 1905 (1890) et in *Fl. Cap.* 4 (1): 893 (1909). — K. Schum. in *Engl. & Prantl, Nat. Pflanzenfam.* 4 (2): 275 (1895). — Schltr in *J. Bot.*: 475 (1898). — Berger, *Stap. u. Klein.*: 34 (1910). — Marloth in *Fl. S. Africa* 3 (1): t. 22H (1932).

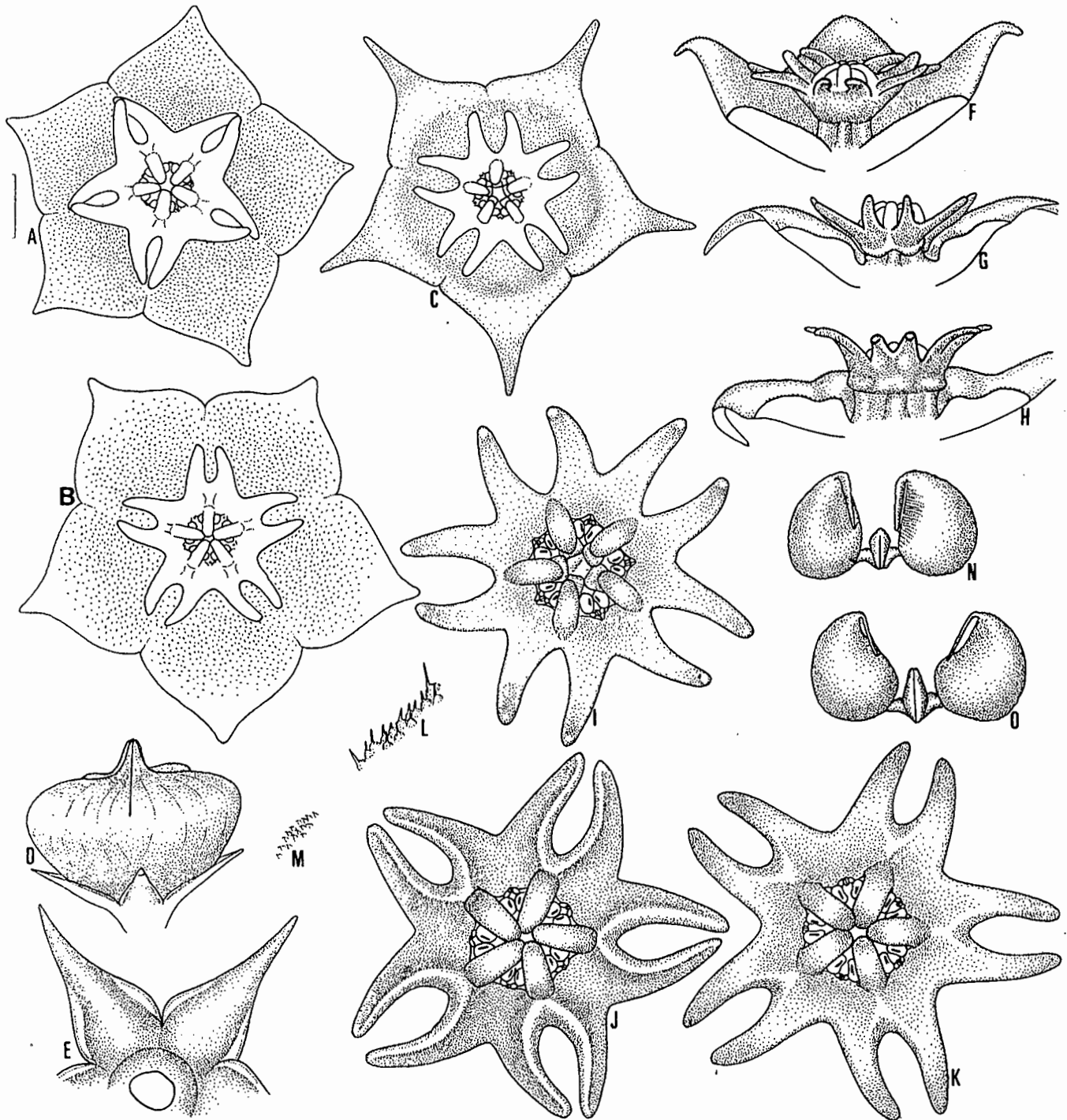


Figure 40.—*Hoodia flava*. A, B, C, face view of flower. D, bud. E, view from rear of calyx. F–H, side view of dissected flower showing minute tube just enclosing stipe of gynostegium. I–K, face view of gynostegium. L, M, papillae on inner surface of corolla, both taken from just below base of corolla lobes. N, O, pollinarium.

Drawn from: A, E, F, J, M, Bruyns 1122; B, D, H, K, O, Bruyns 3050; C, G, I, L, Bruyns 3494 (Namibia); N, Bruyns 1259.

Scale bar: A–H, 2 mm (at A); I–K, 1 mm (at A); L, M, 0.5 mm (at A); N, O, 0.25 mm (at A).

— White & Sloane, Stap. 3: 1021 (1937). — Lückhoff, Stap.: 251 (1952). Type: South Africa, Karoo, without locality, Bain (K!)

Trichocaulon karasmontanum Dinter in Feddes Rep. sp. nov. 24: 16 (1927), nom. nud. [collected in Us River Valley, ± 29 km NE of Kanus, 2 May 1913 (no material preserved)].

Plant forming shrub to 0.5 X 0.3 m but mostly much smaller, branching at base. Stems 20–70 mm thick with 18–31 rows of vertically–arranged tubercles, each tubercle tipped with a pale to dark brown weak spine 4–6 mm long. Flowers in groups of 1–3 mostly in upper half of stem. Pedicel 0.5–1 mm long, glabrous. Sepals 2.5–3 mm long, tapering from 1–1.5 mm broad ovate base to narrow apex, glabrous, adpressed to corolla. Corolla 11–13 mm diam., lobed to half–way down, glabrous on both sides, eciliate, smooth outside, minutely papillate (papillae rounded with fine apical bristle) or smooth inside, greenish–yellow or greenish–yellow with brown tips to lobes or wholly brown; tube absent, united part flat to slightly saucer–shaped with slight depression around base of gynostegium; lobes spreading, 2.5–4 X 3.5–5 mm, broadly ovate–deltoid, sometimes with long narrow point, abruptly acuminate. Corona yellow (very occasionally faintly brownish–translucent), glabrous; outer lobes spreading, 1.6–2.2 mm long, divided below middle into two broadly and slightly dorsiventrally–flattened linear horns (those of adjacent lobes usually connivent); inner lobes 0.6–1 mm long, linear, obtuse, dorsiventrally flattened, clearly incumbent on backs of anthers and shorter than or longer than them (sometimes meeting in centre). Follicles 75–180 mm long, 55–105 seeds per horn. Figure 40.

Material examinedNamibia

2718: Narudas (-BD), Bruyns 3519 (BOL); Vredenhof (-DB), Bruyns 3494 (BOL).

South Africa

2918: Witberg (-BB), Bruyns 5247 (BOL).

2919: Pofadder (-AB), v.Breda 255 (PRE); Achab (-AC), v.d. Heever s.n. (BOL).

3022: NE of Vanwyksvlei (-AA), Stayner sub KG 1387/62 (NBG); 128 km S Prieska (-CA), Bruyns 3743 (BOL); Michounia (-CC), Bruyns 3077 (BOL); Vaalhoek (-CC), Bruyns 3278 (BOL).

3023: Twyfelhoek (-DA), Bruyns 3050 (BOL).

3120: Stuurmans (-AC), Bruyns 1122 (BOL).

3121: 24 miles NNE Williston (-AA), Acocks 18252 (Z, PRE); N Williston (-AA), Bruyns & Nagel 4887 (); Korfplaas (-CB), Bruyns & Nagel 4876 ();

Bakhovenskraal (-DA), Bruyns 4001 (BOL); S of Stofkraal (-DA), Bruyns 4519 (BOL); E of Fraserburg (-DD), Bruyns 4792 (BOL).

3221: 20 km E Fraserburg (-BA), Bruyns 3070 (BOL); Spitzkop (-CB), Bruyns 1259 (BOL); 45 km N Koup (-CD), Bruyns & Heunis 3759 (BOL); Merweville (-DA), Broom s.n. (PRE).

3222: Rhenosterkop (-BB), Foster sub Pillans 171 (BOL); Riemhoogte (-BB), Bruyns 4227 (BOL); Sonop (-CB), Bruyns 3680 (BOL).

3223: Eensaam (-CA), Snyman s.n. (BOL).

3322: Prince Albert (-AA), Slabbert sub SUG 1135 (STE); Tierberg (-AB), Bruyns 3693 (BOL).

Without precise locality: near Prince Albert, Marloth 2105 (PRE); SWA, May 1936, N.J.G. Smith sub PRE 7909 (PRE).

H. flava is widely and rather patchily distributed from the eastern and southern flanks of the Great Karas Mountains of Namibia across the Cape Province just east of the winter rainfall region from Pella and Pofadder in Bushmanland to Prince Albert and near Rietbron on the southern edge of the Great Karoo (Fig. 34). It is quite plentiful in some localities between Britstown and Beaufort West but becomes rare further south towards Prince Albert and Rietbron. It appears to have become very rare (perhaps due to degradation of the veld and consequent persistent droughts) between Pofadder and Vanwyksvlei where there is a gap in the documented distribution.

Plants often grow on gentle, gravelly slopes or summits of hills inside bushes but have also been found several times in flat areas ± devoid of stones growing well hidden inside shrubs. They are often associated with colony-forming Ruschia species in western localities, Rhigozum trichotomum further east and further south with R. obovatum.

As with H. officinalis, H. flava is very variable in size and one may occasionally find a large plant up to 500 mm tall forming a robust shrub within another bush. However, most plants are smaller and they will often be found flowering in the field at a height of 75 mm or less which is probably achieved after 2 years from seed if conditions are favourable. The flowers of H. flava are usually greenish yellow with brownish tips to the lobes. Two localities in Namibia both yielded plants with deep brown flowers and others with the usual greenish yellow but sometimes also greenish-yellow without the characteristic brownish tips to the lobes. Neither of these colour variants has been observed in South Africa but in Figure 1089 of White & Sloane it appears as though the flowers may also have been brown. The corona is normally bright yellow but in brown-flowered plants it is translucent yellow-white or slightly suffused with brown.

Hoodia flava differs from all others by its almost flat flower (occasionally

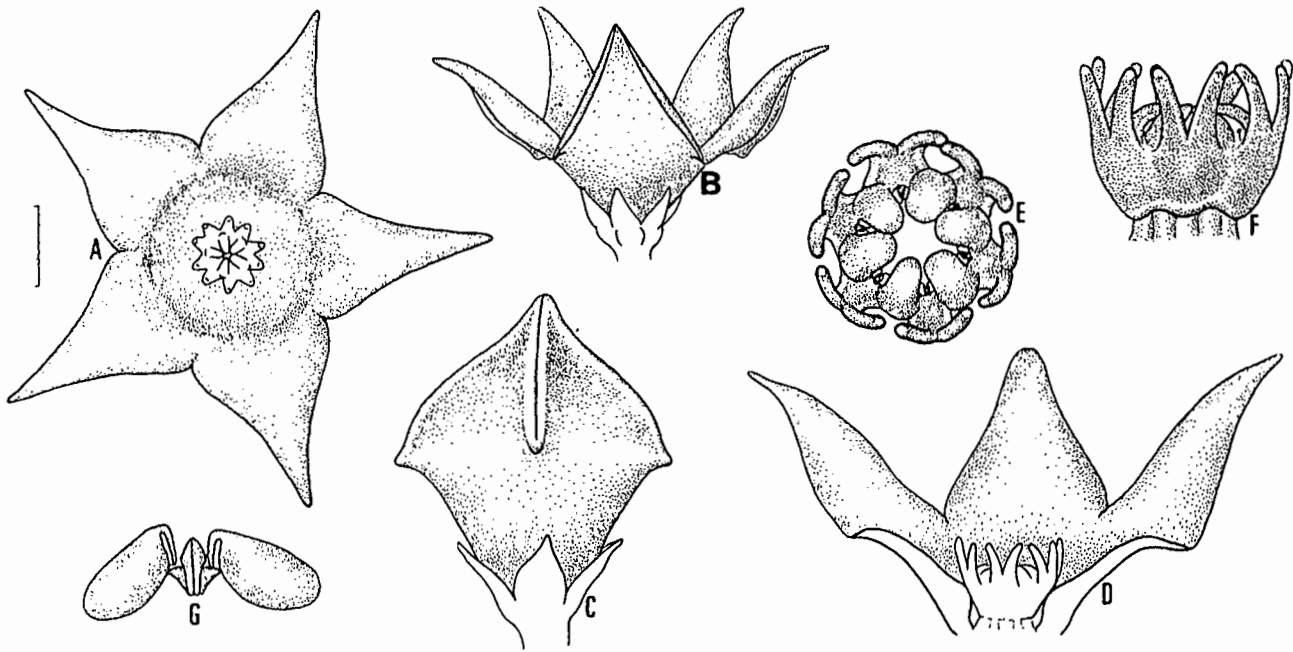


Figure 41
T. Alston
2/15/54

Figure 41.—*Hoodia alstonii*. A, face view of flower. B, side view of flower. C, bud. D, side view of dissected flower. E, face view of gynostegium. F, side view of gynostegium. G, pollinarium.

A drawn from material from Hahlenberg, Namibia, M. Visagie; rest from Bruyns 1327 (Sendeling's Drift, South Africa).

Scale bar: A, B, 3 mm (at A); C, D, 2 mm (at A); E, F, 1 mm (at A); G, 0.25 mm (at A).

campanulate from pressure of surrounding tubercles and spines) with only very minute papillae on the inner surface and widely spreading outer corona lobes. The structure of the corona is quite similar to that of H. pilifera but there the outer corona lobes rise up steeply and thus are far more deeply cupular around the base of the gynostegium. In the other bright yellow-flowered species, H. alstonii, the outer corona lobes are also much more erect, the flower is always campanulate, completely devoid of papillae and the pollinia are an unusual shape (Fig. 41 G). The pollinia of H. flava and members of the H. pilifera complex are similar and it is probably to these that H. flava is most closely allied.

This species has been exceptionally rarely recorded in Namibia. It appears that it was first observed there in April 1913 by Kurt Dinter and Geheimrat Adolf Engler who collected a thorny Trichocaulon 'with insignificant flowers' at the mouth of the Us River gorge at the southern end of the Great Karas Mountains (Dinter 1921, p.108). Dinter dubbed these plants 'T. karasmontanum'. I have not located a specimen of this collection but it is almost certainly H. flava rather than H. officinalis, which he knew well (Dinter 1914) and which does not appear to occur around the foot of these mountains. It was gathered again in May 1936 in Namibia by N.J.G Smith (PRE records).

12. Hoodia alstonii (N.E. Br.) Plowes in *Asklepios* 56: 7 (1992).

Trichocaulon alstonii N.E. Br. in *Kew Bull. misc. inf.*: 166 (1906) et in *Fl. Cap.* 4 (1): 891

(1909). — White & Sloane, *Stap.* 3: 1008, fig. 1075, 1077 (1937). — Lückhoff, *Stap.*: 246 (1952). — Huber in *Prodr. Fl. SWA* 114: 68 (1967) pro parte excl.

T. delaetianum. — Dyer & Hardy in *Flow. Pl. Africa* 47: t. 1846 (1982). Type:

South Africa, in stony fields near Namies, 900 m, Alston sub MacOwan 2017 (K!)

T. halenbergense Dinter in *Feddes Rep. sp. nov.* 29: 163 (1931) Rowley & Hall in *Nat.*

Cact. Succ. J. 14: 48, 50 (1959), nom. nud.

Plant forming often dense shrub to 1 X 0.5 m, branching from base. Stems 40–80 mm thick with 20–22 rows of vertically arranged tubercles, each tubercle tipped by a stout sharp pale–brown spine (6–) 8–10 mm long, whitish grey–green. Flowers in groups of 1–8 mostly in upper parts of stem, arising in time from short stumpy peduncle. Pedicel 1–2 (–4) mm long, glabrous. Sepals 2–2.5 mm long, about 1 mm broad at base, ovate, acuminate, glabrous. Corolla glabrous and smooth inside and outside, yellow, very foul–smelling, 10–18 mm diam.; tube 2–3 (–4) mm deep, campanulately funnel–shaped, usually whitish towards base inside; lobes (4–) 6–8 mm long, 4–5 mm broad at base, ovate and usually very acute, spreading–ascending. Corona pale yellow, glabrous; outer lobes divided at least to level of base of inner lobes into two erect gradually tapering (to obtuse apex) teeth usually 1–1.5 mm long; inner lobes incumbent on backs of anthers and usually exceeding them, oblong, obtuse, about 0.75 mm long. Follicles 30–40⁵ mm long, 55 seeds per ^{horn} pair. Figure 41.

Material examined

Namibia

- 2615: Sturmhaube (–BC), Bruyns 3165 (NBG); Hahlenberg (–DA), Dinter 6010 (BOL, Z); Sander s.n. (WIND); Tschaukaib (–DA), Bruyns 3169 (NBG).
- 2816: Lorelei copper mine/ Kahanstal (–BB), Dinter 8151 (WIND, S, BOL, G, Z, PRE); Giess 10207 (WIND, PRE); de Winter & Giess 6379 (WIND, PRE).
- 2817: near Gamkab R. mouth (–AB), Bruyns 3890 (BOL).

South Africa

- 2816: Swartpoort (–BB), Bruyns 1327 (BOL); SE of Sendelingsdrift (–BB), Pillans 5003

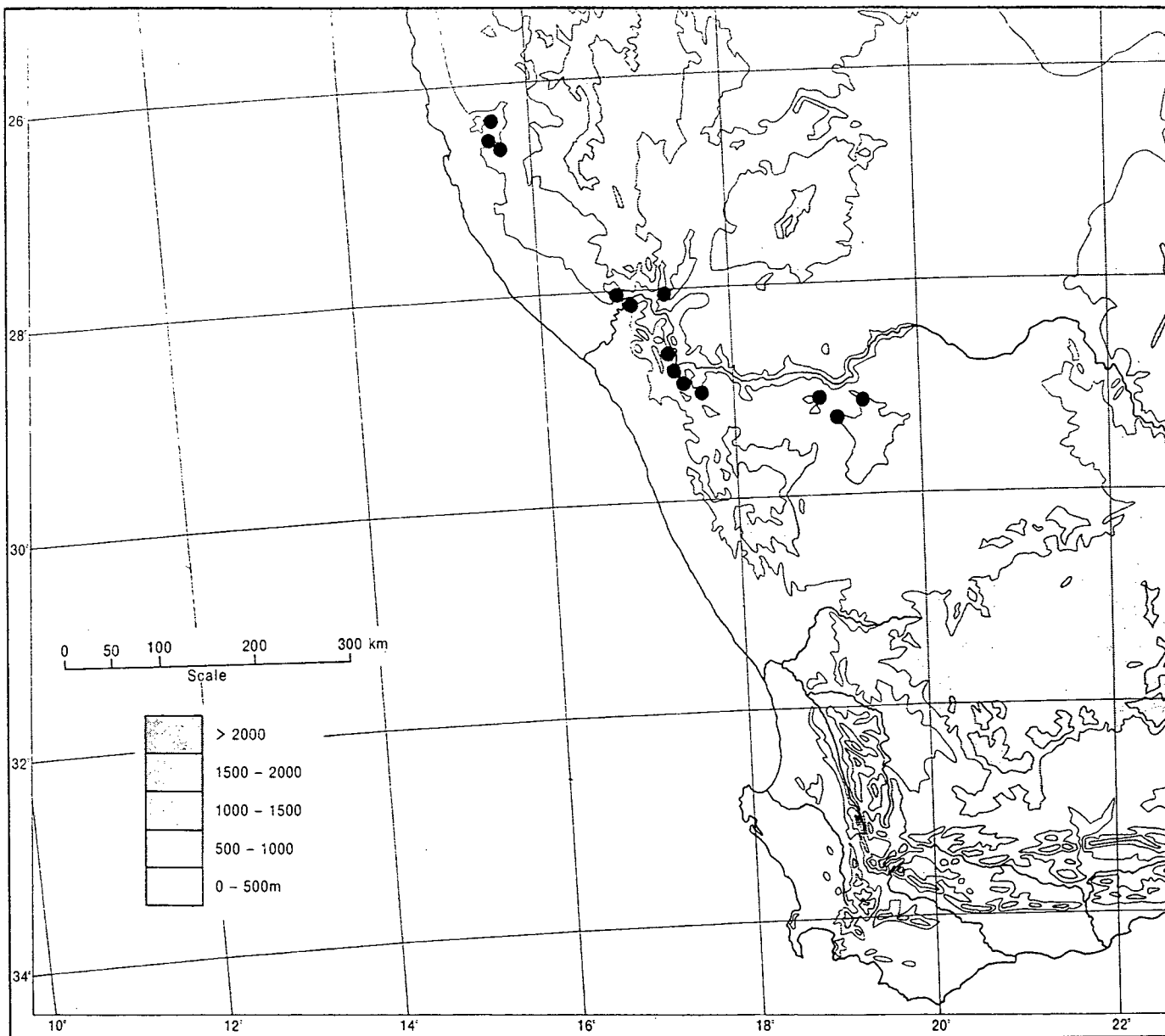


Figure 42.—Distribution of *H. alstonii*.

(BOL); Sendelingsdrift (–BB), Hall (BOL); Munro (PRE); Hardy 556 (PRE).

2817: W of Mt Stewart (–CB), seen Dec. 1991, not collected; W of Rooiberg (–CD), Bruyns 4948 (BOL); Klipbok (–CD), Bruyns & Heunis 4646 (BOL, PRE).

2917: Umdaus (–BA), Hall sub NBG 715/49 (NBG, BOL).

2918: Witberg (–BB), Bruyns 5240 (BOL).

2919: Pofadder (–AB), Horn s.n. (NBG); v. Zyl s.n. (BOL); Achab (–AC), no specimen deposited.

Hoodia alstonii has an unusual distribution within the winter rainfall region of southern Namibia and the north–western Cape. It occurs in three apparently discrete areas which are separated at their nearest points by some 150 km (Fig. 42). The northernmost of these consists of several gravelly hillsides (quartz and schist) to the north and south of the road from Aus to Lüderitz, 30 to 50 km east of Lüderitz. Plants are extremely common on the Hahlenberg, roughly in the centre of this area, but are much rarer on other similar prominences nearby and the species may be more widely distributed in these parts than the records show. The other two areas where it occurs are along the lower reaches of the Orange River. The more extensive of these is the mountainous country along the lower Orange River from Umdaus north of Steinkopf to Sendelingsdrift. Here H. alstonii grows on both banks of the river and is mainly found on schist slopes and outcrops (occasionally on quartz). The remaining area is in the flat–topped quartz mountains of the Aggenys – Pella – Pofadder area where it seems to occur mainly on the summits of these ridges, but in this case only on the south bank of the river. Plants in this area seem to be markedly smaller than further west, starting to flower when only 80 mm

tall and rarely exceeding 300 mm in height.

H.alstonii inhabits remarkably arid places. Plants of any size generally grow fully in the open on rocky slopes or stony flat areas. Several times they have been seen rooted in the most unlikely narrow crevices in rock outcrops where they still manage to reach a considerable size. They are often very scattered but occasionally small localised colonies are found.

Specimens of H.alstonii may reach a height of 1 m or slightly more and thus they are by far the tallest of this section. The stems are armed with extremely hard, sharp spines much like those of H.gordonii. The whitish, grey-green colour of the stems is also distinctive.

Flowers are produced in large numbers on the upper parts of the stems, arising on peduncles which eventually may elongate to a few millimetres. They are bright yellow, becoming slightly paler towards the centre and make quite a show, covering the top of the plant with yellow. Their beauty is rather offset, however, by their strong, dung-like odour. They are peculiar for the very thin texture of the corolla, without papillae on the inner surface. The corolla lobes are also narrower than in most of the Cape species but the structure of the corona is similar, for example, to that in H.pilifera. Another significant difference is the shape of the pollinium which is much broader than long with the germinating mouth on the short side: in all other species it is as long as broad or slightly longer with germinating mouth on the longer side. Perhaps most surprising is the fact that this robust species produces the smallest follicles in the genus. These are often only 30 mm long with about 60 seeds per pair.

On herbarium material Dinter used the manuscript name T.halenbergense for plants from both Hahlenberg and Kahanstal (Lorelei). Several of these specimens have been seen from which it is clear that this is N.E. Brown's T.alstonii.

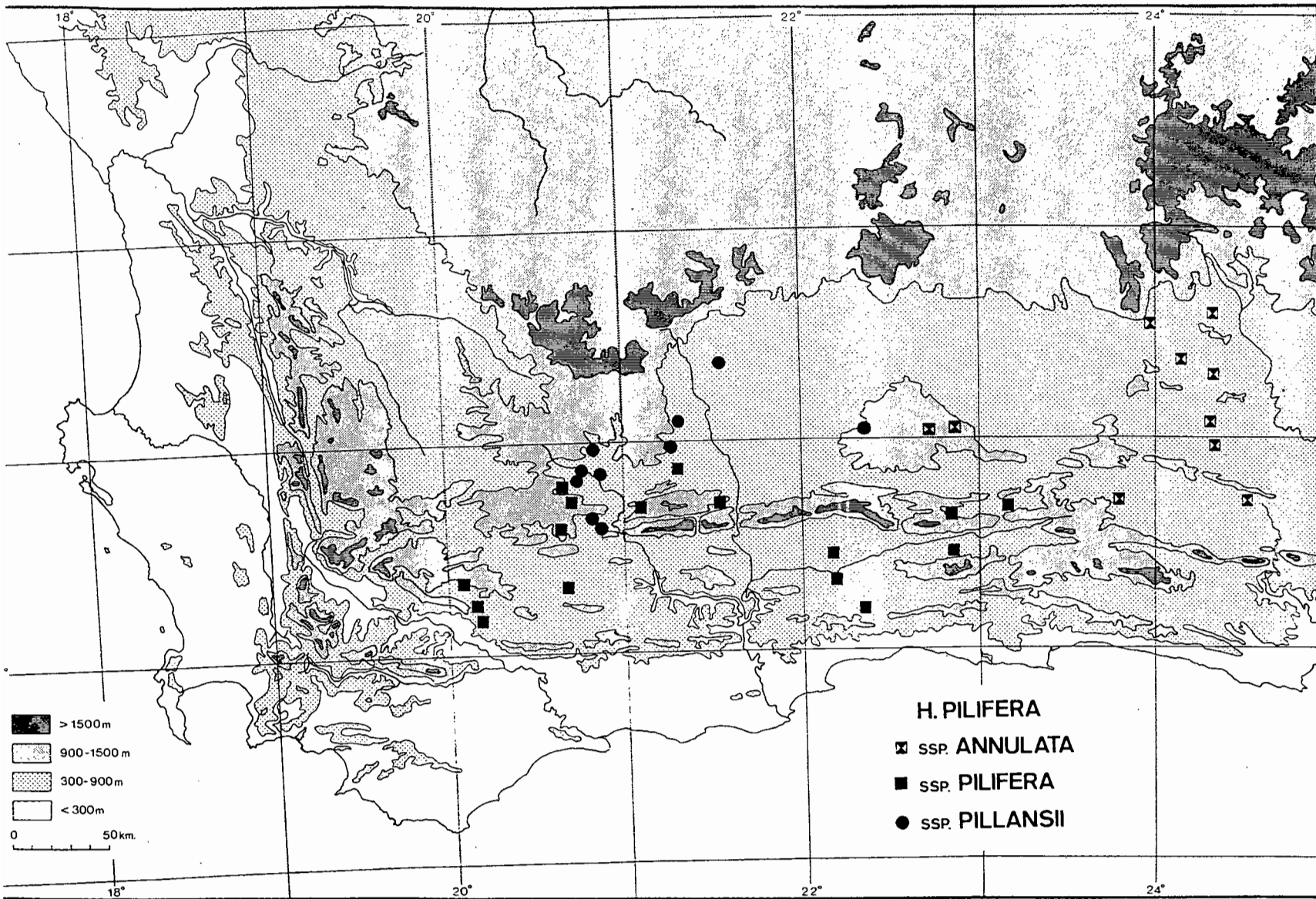


Figure 43.—Distribution of *H. pilifera*.

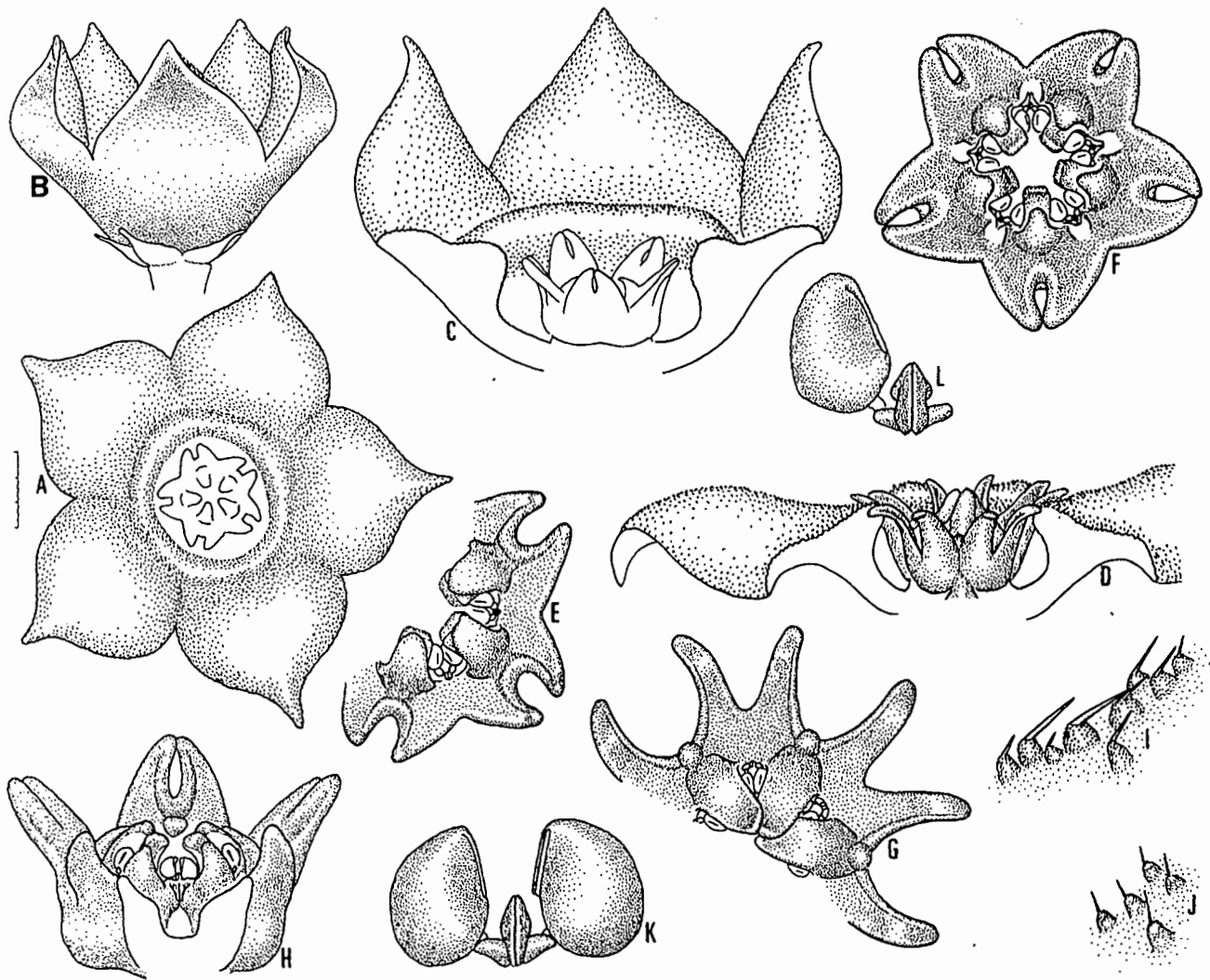


Figure 44.
Hoodia pilifera
 29/1/10

Figure 44.—*Hoodia pilifera* subsp. *pilifera*. A, face view of flower, flattened out. B, side view of flower showing usual shape. C, D, side view of dissected flower. E–G, face view of flower showing usual shape. C, D, side view of dissected flower. E–G, face view of gynostegium. H, side view of gynostegium with one outer corona lobe removed. I, J, papillae on inner surface of corolla. K, L, pollinarium.

A, E, H, J, K drawn from Bayer 2449; B, C, F from Bruyns 924; D, G, I, L from SW of Laingsburg, Kratz.

Scale bar: A, B, 3 mm (at A); C, D, 2 mm (at A); E–H, 1 mm (at A); I, J, 0.5 mm (at A); K, L, 0.25 mm (at A).

13. Hoodia pilifera (L.f.) Plowes in *Asklepios* 56: 10 (1992).

Trichocaulon piliferum (L.f.) N.E. Br. in *J. Linn. Soc.* 17: 164 (1878) et in *Fl. Cap.* 4 (1): 890 (1909). — J.D. Hooker in *Bot. Mag.* 110: t. 6759 (1884). — Berger, *Stap. u. Klein.*: 33 (1910). — Marloth in *Fl. S. Africa* 3 (1): t. 22 K (1932). — Pole Evans in *Flow. Pl. S. Africa* 15: t. 594 (1935). — White & Sloane, *Stap.* 3: 1000 (1937). — Lückhoff, *Stap.*: 243, 244 (1952). Piaranthus piliferus (L.f.) Sweet, *Hort. Brit. Ed.* 2: 359 (1830) et in *Ed.* 3: 463 (1839). Stapelia pilifera L.f., *Suppl.* 171 (1781). — Masson, *Stap. nov.*: t. 23 (1797). — Thunb. *Prodr. fl. cap.*: 46 (1794) et *Fl. cap.* 1: 239 (1823). — Sweet, *Hort. Brit. Ed.* 1: 278 (1827). — Loudon, *Encycl.*: 200 (1836).

Type: South Africa, Cape, in Karoo beyond Hartequas Kloof, Thunberg 6332 (UP, *photo!*)

Three subspecies are recognised. Their distribution is shown in Figure 43.

13a. Hoodia pilifera subsp. pilifera.

Plant a spiny succulent forming shrub to 800 mm tall, branching from base. Stems 30–60 mm diam., with 21–34 rows of vertically arranged prominent slightly laterally–flattened tubercles each tipped with a stiff grey to brown spine 5–9 mm long, dark green, slightly glaucous. Flowers in groups of 1–3, opening successively, in upper parts of stem, with strong bad odour. Pedicel 0.5–1.5 mm long, glabrous. Sepals 2–3 mm long, ovate at base, acuminate, glabrous. Corolla 16–20 mm diam. when fully expanded, usually somewhat campanulate with lobes only slightly spreading, reddish–green outside, inside dark purple–brown to pinkish–brown, glabrous, outside smooth, inside covered with obtuse papillae each tipped with a sharp–pointed horizontally–spreading bristle, usually with a raised annulus around mouth of tube; tube cup–shaped, often with slightly constricted,

subpentagonal mouth 4–5 mm broad, 2–2.5 mm deep, often smooth inside; lobes erect to spreading, 4–6 mm long, 6–7 mm broad at base, broadly deltoid–ovate, acuminate, margins slightly folded back. Corona dark purple–brown (reddish towards base), glabrous, 4–5 mm broad across top; outer lobes basally cupular, divided to well below middle into spreading to sub–erect diverging dorsiventrally–flattened lobes 1–1.5 mm long; inner lobes 0.5–1 mm long, linear–oblong, closely incumbent on backs of anthers and very variable in length (shorter than, equalling or occasionally much exceeding them and rising up in centre). Figure 44.

Material examined

- 3320: Matjiesfontein (–BA), Hall 936 (NBG); Whitehill (–BA), Compton 9309 (NBG); Ezelsfontein (–BC), Bayer 2449 (NBG); Tapfontein se Kloof (–BC), Bruyns 4553 (BOL); 11 km N Montagu (–CA), Joubert sub KG 283/73 (NBG); NE of Montagu (–CC), A Joubert s.n. (NBG); E of Montagu (–CC), Bruyns & Heunis 4724 (BOL); 35 miles NE Montagu (–DA), Bruyns 924 (BOL).
- 3321: Koup (–AB), Archer 841 (BOL); Langwater (–AC), Bruyns 4201 (BOL); Bosluiskloof (–BC), Bruyns 3711 (BOL).
- 3322: E Klaarstroom (–BD), Bruyns 4957 (BOL); Oudtshoorn (–CA), Lückhoff (BOL, PRE); near Zebra (–CD), v.d. Bijl sub Fourcade 4739 (BOL); Buffelsklip (–DB), Schwegmann (NBG).
- 3323: near Vondeling (–AC), Bruyns 4961 (BOL).
- Without precise locality: near Barrydale, Muir 4907 (BOL).

Hoodia pilifera subsp. pilifera is confined to the south–western corner of the distribution of the genus (Fig. 43). It is found on the Little Karoo from Montagu to west

of Uniondale and on the southern edge of the Great Karoo from Matjiesfontein eastwards to Laingsburg and Gamka Poort. East of Gamka Poort towards Prince Albert it disappears but re-appears in the valley east of Klaarstroom. Records are few and sparse and it appears to be quite rare, probably due to the degradation of habitat by overgrazing and the eating of plants by humans. Plants are usually found growing inside bushes on steep shale slopes, often on the hotter northern to eastern aspect but I have seen the occasional specimen in flat areas and on cooler south slopes.

Two records are known from far outside this area: Huber (1967) cites a specimen of Range from the Arasabkuppe near Lüderitz in Namibia and Steenkamp & Vahrmeyer record it from Botswana (without exact locality, specimen in PRE). I have not seen Range's specimen but these are both certainly errors.

On the western end of the Little Karoo, *H. pilifera* subsp. *pilifera* is quite distinctive with relatively small flowers which are very dark purple-brown (practically black – becoming paler around and inside the tube). The flowers usually do not open fully and are kept partially closed by pressure from the surrounding stem-tubercles. They have a prominent annulus forming an abrupt mouth to the corolla tube. The corona is usually as dark as the corolla and the deeply bifid outer lobes are fused at the base into a cup around the gynostegium. The inner lobes are usually shorter than the anthers but closely adhere to them. Plants with identical flowers to these (except for the smooth inside of the corolla tube) are found in the dry valleys east of Klaarstroom and around Oudtshoorn.

Within the Witteberg range from west of Laingsburg to Gamka Poort specimens produce larger flowers which usually open fully and are a pinkish-brown colour. The corona is still practically black, often with long inner lobes which touch in the centre and may rise up as a small column. These flowers have a broad, flat, united portion to the

corolla and there is a considerable annulus forming the mouth of the tube. The broad corolla and long inner corona lobes suggest that these plants could be referred to subsp. annulata but geographically they fit better into subsp. pilifera. The well-developed annulus and the blackish corona insure that these specimens are not confusable with subsp. pillansii.

13b. Hoodia pilifera subsp. annulata (N.E. Br.) Bruyns comb. et stat. nov.

Trichocaulon annulatum N.E. Br. in Fl. Cap. 4 (1): 889 (1909). — White & Sloane, Stap. 3: 997 (1937). — Dyer in Flow. Pl. S. Africa 22: t. 872 (1942). — Lückhoff. Stap.: 243 (1952). Hoodia annulata (N.E. Br.) Plowes in Asklepios 56: 8 (1992). Type: South Africa, Klipplaat, coll. 1908, Lee sub Pillans 135 (BOL[!])

Plant a spiny succulent forming large shrub up to 450 mm tall and up to 2 m diam., branching at base. Stems cylindric, erect, 30–50 mm thick, with 20–22 (–30) rows of vertically arranged prominent conical tubercles each tipped with a stiff brown spine 3–5 (–6) mm long. Flowers in groups of 1–3, opening successively, in upper parts of stem. Pedicel < 1 mm long (flower practically sessile), glabrous. Sepals 2–2.5 mm long, 1.5 mm broad at ovate base, acuminate, glabrous. Corolla (15–) 20–30 mm diam., rotate, with prominent central annulus forming cup-shaped tube up to 5 mm deep completely containing gynostegium, exterior glabrous, smooth except for slightly raised veins, reddish–purple to greenish towards base, interior glabrous and densely covered with conical papillae (up to 0.5 mm long) each tipped with an erect to horizontal bristle, dark purple–black; lobes 5–7 X 8–9 mm at base, spreading and usually adpressed to stem, broadly deltoid–ovate, shortly acute, with margins slightly recurved. Corona 5–6 mm diam., 4 mm tall, glabrous, dark purple–black, cupular; outer lobes basally erect, divided

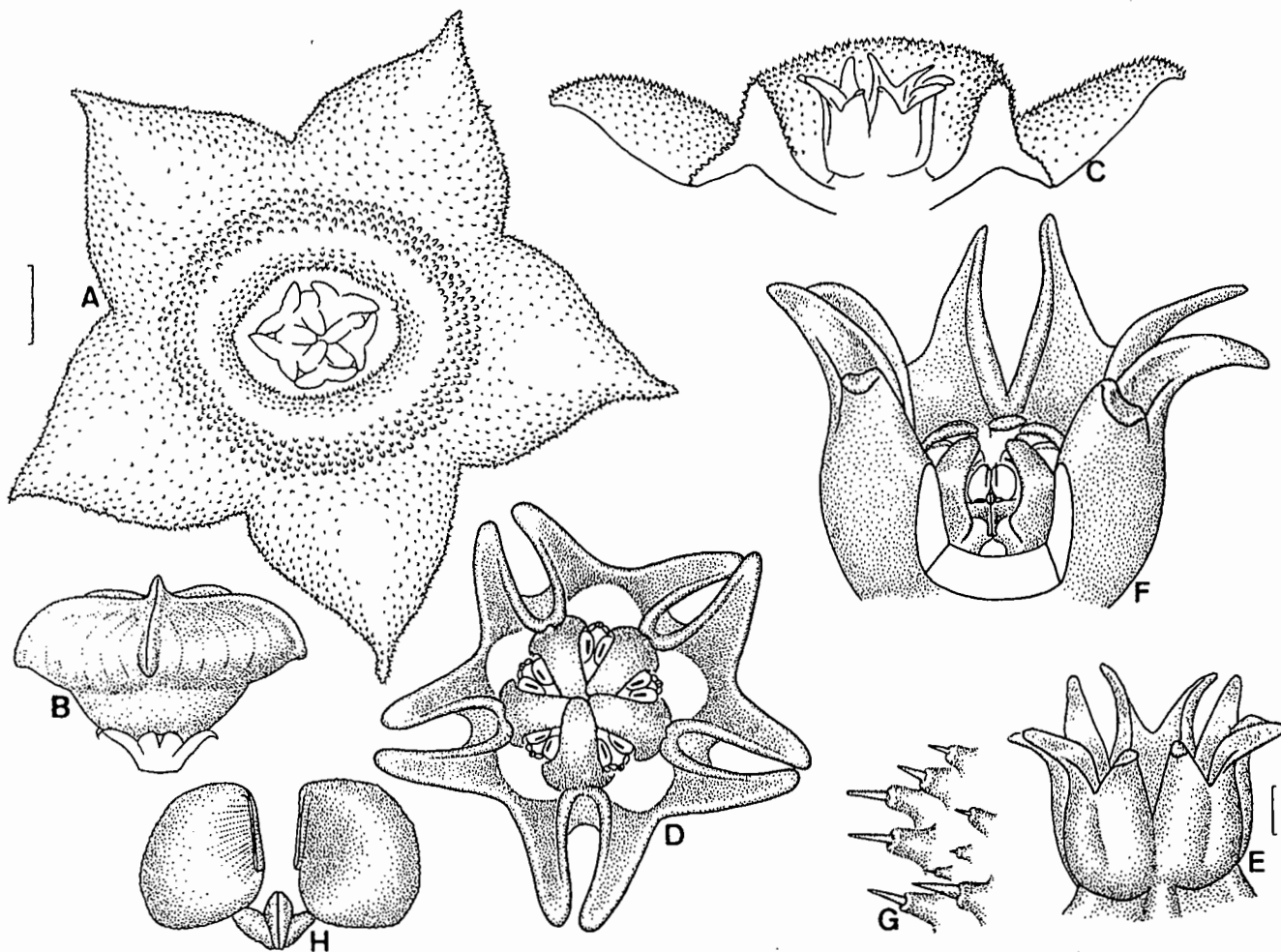


Figure 45
T. annulata
 27/6/70

Figure 45.—*Hoodia pilifera* subsp. *annulata*. A, face view of flower. B, bud. C, side view of dissected flower. D, face view of gynostegium. E, side view of gynostegium. F, side view of gynostegium with one outer corona lobe removed. G, papillae taken on annulus. H, pollinarium.

B drawn from Abelshoek, Heunis; rest from Bayer sub Karoo Garden 142/72.

Scale bar: A–C, 3 mm (at A); D, F, 1 mm (at A); E, 1 mm; G, 0.5 mm (at A); H, 0.25 mm (at A).

to middle into two sublanceolate spreading–diverging–recurved canaliculate teeth up to 1.5 mm long; inner lobes about 1 mm long, obtuse, linear, closely incumbent on backs of anthers, equalling or exceeding them. Figure 45.

Material examined

3222: Wolwekraal (–DC), seen Jan. 1992, not collected; Prutkraal (–DD), Bruyns & Snyman 3744 (BOL).

3323: W Aberdeen (–BD), Bruyns 4242 (PRE).

3224: 21 km E Aberdeen (–AD), Bruyns 3078 (BOL); ; S Wallacedale (–CA), Bruyns 4243 (BOL); Aberdeen Road (–CB), Bayer 1604 (NBG); 10 km N Klipplaat (–CD), Bruyns 4256 (BOL).

3323: near Knoetze (–BD), Bruyns 4963 (BOL).

3324: Klipplaat (–AB), Lee sub Pillans 135 (BOL); near Abelshoek (–BC), Heunis (BOL).

Hoodia pilifera subsp. annulata is found on the flat plains and low rolling hills of the Great Karoo from Rietbron to Aberdeen and Graaf Reinet and southwards towards Klipplaat, Steytlerville and Willowmore (Fig. 43). Plants are often very scattered with several hundred metres or more from one large plant to the next but occasionally quite substantial colonies occur. One east of Willowmore was found to contain more than 50 large plants. Specimens may become enormous and although the stems are rarely taller than 300 mm, they branch extensively from the base to form a low shrub sometimes exceeding 2 m in diameter with hundreds of stems. The areas where it occurs are mostly covered with short Pentzia bushes (Euphorbia ferox is also often present) and there are few

shrubs exceeding 300 mm in height. Thus, although specimens start off as tiny seedlings protected by a shrublet, they soon outgrow this protection and are fully exposed to the elements: in most places where it was seen, the plants were the largest shrubs and were visible from a considerable distance. Regeneration seems to be poor. Whereas large plants of Hoodia gordonii are often covered with pods, the much larger specimens of H. pilifera subsp. annulata bear very few pods (1–4 per plant, if any). Even in large populations, few small specimens were seen.

Subsp. annulata has dark purple–black flowers which open out fully against the stems despite the extremely short pedicel: in this case the corolla tube is sufficiently long to place the rest of the flower beyond the tubercles and spines so that it can spread out. Usually 20–30 mm in diameter, they are rivalled in size only in H. ruschii and are the largest among the Cape species in the section. However, this is subject to much variation and they may be as small as 15 mm diameter. They also have by far the most prominent annulus which usually has an irregular, ± elliptical mouth (due to pressure from the surrounding tubercles). The inner surface of the corolla (including the annulus) is covered densely with papillae which are clearly visible to the naked eye. As with most dark-flowered stapeliads, the flowers emit an unpleasant, foetid odour.

This subspecies is most similar to subsp. pilifera. It differs mainly in the habit [growing in flats (very rare for subsp. pilifera) and forming huge clumps growing fully in the open] and in the much larger flowers: the corolla is larger and the corona is also larger with a more prominent and deeper cup formed by the outer lobes which are more erect. However, pale-flowered plants of subsp. pilifera from around Laingsburg begin to approach subsp. annulata in the size of the flowers and it is only the small-flowered forms of subsp. pilifera from the west around Montagu that are clearly and easily separable from subsp. annulata.

13c. Hoodia pilifera subsp. pillansii (N.E. Br.) Bruyns comb. et stat. nov.

Trichocaulon pillansii N.E. Br. in Gard. Chron. 35: 242 (1904) et in Fl. Cap. 4 (1): 892

(1909). — Marloth, Das Kapland: fig. 96 (1908) 'T. piliferum'. — Berger, Stap. u.

Klein.: 31 (1910). — White & Sloane, Stap. 3: 1010, fig. 1076 (1937). — Dyer in

Flow. Pl. S. Africa 22: t. 850 (1942). Hoodia colei Plowes in Asklepios 56: 8

(1992) Type: South Africa, Cape, SE of residence of Sout Kloof farm, 1902, Pillans 9

(K, holo!; BOL, iso!).

T. pillansii var. major N.E. Br. in Gard. Chron. 35: 242 (1904) et in Fl. Cap. 4 (1): 892

(1909). Type: SE of Sout Kloof farmhouse, Pillans 160 (BOL).

T. grande N.E. Br. in Fl. Cap. 4 (1): 892 (1909). — White & Sloane, Stap. 3: 1013 not fig.

1077 (1937). Hoodia grandis (N.E. Br.) Plowes in Asklepios 56: 9 (1992). Type:

South Africa, after descent on northern slopes of Klein Swartberg on

Ladismith—Laingsburg road, Pillans 668 (K, holo!; BOL, iso!).

Plant a spiny succulent, forming shrub to 300 (–600) mm tall and up to 500 mm diam., branching from base. Stems 30–60 mm thick, with 25–34 rows of vertically arranged prominent slightly laterally–flattened tubercles each tipped with a greyish spine 5–6 mm long, glaucous green. Flowers in groups of 1–3, opening successively, in upper parts of stem, with very bad slightly fish–like odour. Pedicel 1–1.5 mm long, about 1–1.5 mm thick, glabrous. Sepals 1.5–2.5 mm long, ovate, very acuminate, glabrous. Corolla 8–20 mm diam., inside pale yellow to greenish–yellow to pinkish, outside pale pinkish–green, glabrous and smooth outside, inside glabrous but covered with obtuse columnar papillae each tipped with a tiny horizontally–spreading bristle; tube cup–shaped, with somewhat thickened mouth sometimes beginning to form slight annulus, 3.5–5 mm diam. at mouth on inside, 2–3 mm deep; lobes spreading, 3.5–9 mm long, 3–7 mm broad at base, broadly ovate–deltoid, very acute, often with margins strongly folded back. Corona yellow (usually

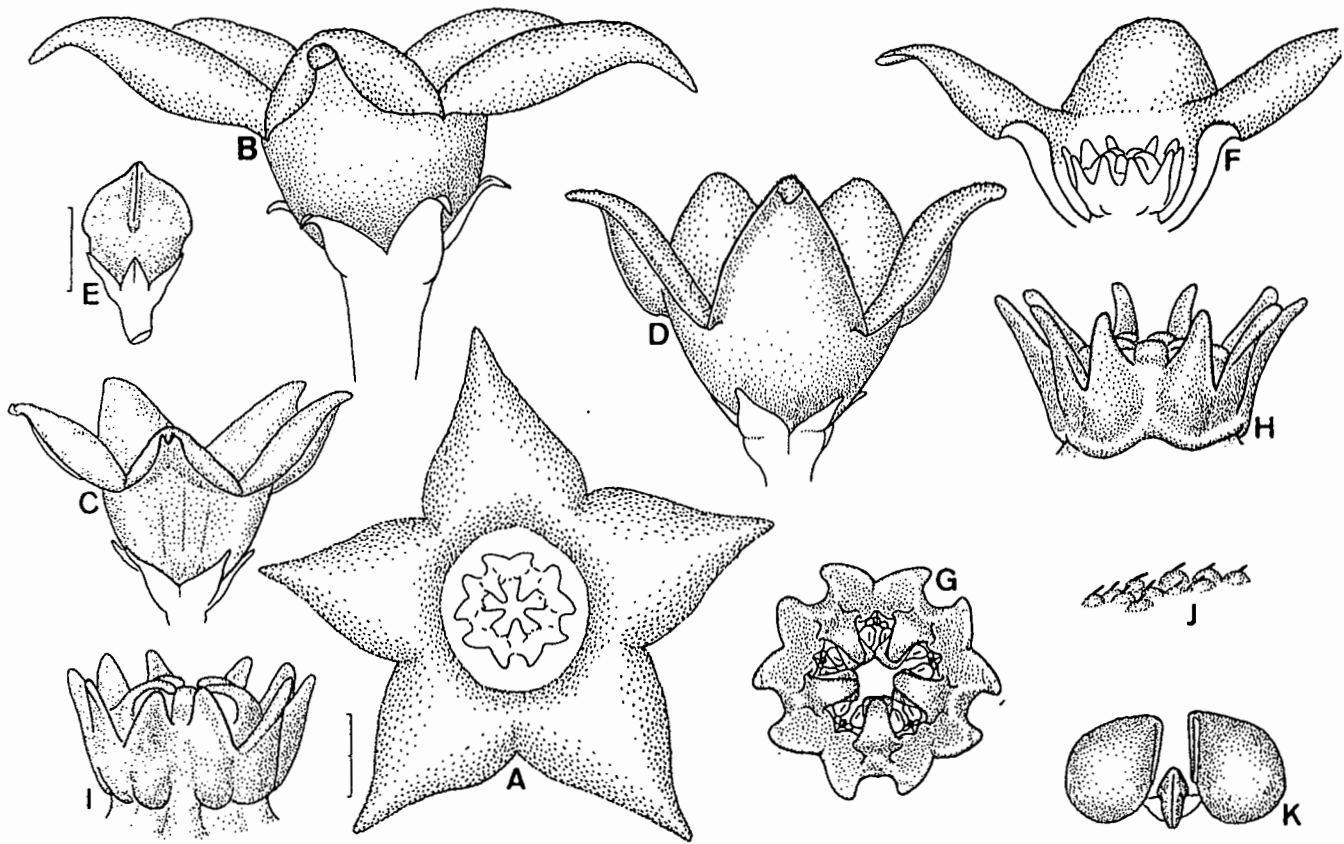


Figure 46
T. pillansii
 5, 1911

Figure 46.—*Hoodia pilifera* subsp. *pillansii*. A, face view of flower. B–D, side view of flower. E, bud. F, side view of dissected flower. G, face view of gynostegium. H, I, side view of gynostegium. J, papillae, taken on corolla lobe, apical bristle pointing towards tip of lobe. K, pollinarium.

A, D, F, G, I, drawn from Bruyns 3804; B, H, from Bruyns 1260; C, E, J, from Bruyns 3149.

Scale bar: A, B, C, D, F, 2 mm (at A); E, 3 mm; G–I, 1 mm (at A); J, 0.5 mm (at A); K, 0.25 mm (at A).

brighter than corolla), glabrous, 3–4 mm diam. across top; outer lobes basally cupular, divided to just below half their length into erect sometimes slightly diverging somewhat dorsiventrally flattened lobes, 1–2 mm long; inner lobes 0.5–1 (–1.5) mm long, linear–oblong, obtuse, from half as long as anthers to equalling them (rarely connivent and rising up in centre), somewhat dorsiventrally flattened. Figure 46.

Material examined

- 3221: Schoppelmaakraal (–CD), Bruyns 1255 (NBG); Merweville (–DA), Stayner s.n. (NBG).
- 3222: near Kruidfontein (–CD), Bruyns 3149 (BOL).
- 3320: near Matjiesfontein (–BA), Watt & Breyer–Brandwijk 2147 (PRE); N side Ngaapkop (–BA), Compton 9240 (NBG); Pillans 9 (BOL); Archer 847; 848 (BOL); Soutkloof se Berg (–BA), Bruyns 3804 (BOL); Klipgat (–BB), Bruyns 1231 (NBG); SE Soutkloof farm (–BB), Pillans 9 (BOL); Pillans 160 (BOL); Keurfontein (–BD), Bruyns 1357 (NBG); Bruyns 1959 (NBG); northern slopes of Klein Swartberg (–BD), Pillans 668 (BOL).
- 3321: S of Schoppelmaakraal (–AA), Bruyns 1260 (NBG); (locality doubtful, not included on map) 5 miles S of Calitzdorp (–DA), NBG 1260/49 (NBG).

Hoodia pilifera subsp. pillansii occurs east of the Roggeveld Plateau from just south of Merweville to the northern slopes of the high tillite/shale ridge running parallel to and north of the Witteberge from Matjiesfontein to Laingsburg. Outliers exist south of the Witteberge west of the Rooinek Pass and another prolific, isolated population exists east of Kruidfontein on the Great Karoo. This distribution interlinks partially with that of

H. flava which is also found south of Merweville and occurs in several widely scattered spots east and south of Kruidfontein.

Subsp. pillansii is usually found on gentle to steep, stony slopes. Plants up to 0.5 m diam. have been seen and individual stems may reach a length of 0.6 m (though 0.3 m is more usual) so that specimens may form quite substantial shrubs (Fig. 2B).

H. pilifera subsp. pillansii is usually easily recognised and distinctive, especially in the northern part of its range and down to the Soutkloof area north of Laingsburg (where it was first collected). The flowers are usually small (8–12 mm diam.) and pale yellow with a slight suffusion of pink along the margins towards the tips of the lobes. However, even in this area they may be up to 20 mm in diameter so that size is not reliable. The corolla lobes are relatively narrow and the margins are recurved, giving them a convex shape. The corolla tube is deep and cupular but there is no thickening at the mouth (i.e. no annulus is present). The bright yellow corona has erect, scarcely diverging outer lobes. Its flowers have a strong, evil, slightly fish-like odour.

Plants in the outlying population east of Kruidfontein conform closely to the above. However, those west of the Rooinek Pass show unexpected variability and present somewhat of a taxonomic puzzle. These plants are cut off from the main body of the distribution of subsp. pillansii by the populations with pinkish-brown flowers around Laingsburg which are referable to subsp. pilifera. It is possible that the extreme variation that they show is a consequence of intergradation or perhaps even hybridization with subsp. pilifera. A representative from this area was described by N.E. Brown as Trichocaulon grande. Flowers from here are somewhat larger than is usual for subsp. pillansii. They are very variable in colour [from greenish-brown through yellowish-pink to quite bright pink or purple-brown in Bruyns 1959], have more broadly deltoïd corolla lobes

which are also less convex and there is a slight thickening around the mouth of the corolla tube giving rise to traces of an annulus. The corona is usually pale yellow and has spreading—erect outer lobes which are scarcely diverging.

B. Lavrania Plowes in Cact. Succ. J. (US) 58: 122 (1986). Type: L.haagnerae Plowes.
Trichocaulon N.E. Brown in J. Linn. Soc. ~~27~~¹⁷: 164 (1878), in Fl. Trop. Africa 4 (1): 489
(1903) et in Fl. Cap. 4 (1): 888 (1909). — White & Sloane, Stap. 3: 991 (1937). —
Huber in Prodr. Fl. SWA 114: 66 (1967). — Dyer in Gen. Southern African Flow.
Pl. 1: 490 (1975), pro parte Sect. Cactoidea White & Sloane. Type: T.cactiforme
(Hook.) N.E. Br.
Leachia Plowes in Asklepios 56: 11 (1992) nom. illegit. Type: L.cactiformis (Hook.)
Plowes.

Plant a spineless succulent consisting of 1—many erect to spreading stems forming small shrub up to 300 mm tall, branching from base. Stems cylindrical to clavate, 20–60 mm thick, covered with flattened—rounded polygonal tubercles arranged roughly into 10–19 rows each with small conical persistent leaf < 1 mm long usually sunken into depression near apex, glabrous. Flowers in groups of 1–6 (–12), opening successively (rarely simultaneously), arising all over stems though usually more towards apex (rarely basal only). Calyx 5-lobed, lobes overlapping slightly at broad bases, glabrous (occasionally with ciliate margins). Corolla (5–) 7–16 mm diam., shallowly campanulate, rotate or with strongly reflexed lobes, deeply lobed, lobes valvate in bud, glabrous outside and inside, inside papillate to smooth. Corona consisting of two series, arising from staminal column, glabrous; outer corona basally cupular, emarginate to deeply bifid, lobes usually spreading; inner corona of 5 dorsiventrally flattened lobes incumbent on backs of anthers and sometimes much exceeding them, dorsally connected to outer lobes. Staminal column arising from near base of corolla tube. Anthers incumbent on top of style head, subquadrate, without apical appendage. Pollinia solitary, ± horizontal in each anther theca, with short caudicles. Style head not produced beyond anthers, truncate—depressed at apex. Follicles terete—fusiform, often very short, paired, horns diverging from 30° – 180°, glabrous, smooth.

Two sections are recognised which may be separated as follows:

1. Flowers arising in few inflorescences in lower half of stem, upper part of stem with neat, regular rows of tubercles.....Sect. *Lavrania*
1. Flowers arising in many small inflorescences concentrated towards apex of stem, rows of tubercles not distinguishable in upper part of stem.....Sect. *Cactoidea*

I. Section Lavrania

This section is monotypic.

1. Lavrania haagnerae Plowes in Cact. Succ. J. (U.S.) 58: 123 (1986). "Echidnopsis sp. nov." Plowes in Excelsa 10: 11 (1982). Type: Namibia, Khowarib Gorge on Hoanib River SE of Sesfontein, Haagner sub Plowes 5046 (PRE).

Plant a spineless succulent usually only 150 mm tall but very occasionally reaching 300 mm, forming dense clusters of 20 – 100 or more stems, branching from base. Stems cylindrical, 20–30 mm thick with 10–12 rows of flattened polygonal tubercles each with a small conical persistent leaf < 1 mm long, grey–green, glabrous. Flowers in groups of 3–15, arising on "peduncular patches" near base of stem, developing successively. Pedicel 2–3 mm long, glabrous. Sepals 2.5 mm long, 1.5 mm broad at ovate base, acute, glabrous. Corolla 13–16 mm diam., ± rotate, pale whitish–green, glabrous and smooth outside, inside red–spotted on yellow background, glabrous, covered densely with obtuse papillae (except in tube) each tipped with a small obtuse to acute "bristle"; tube shallowly cup–shaped and

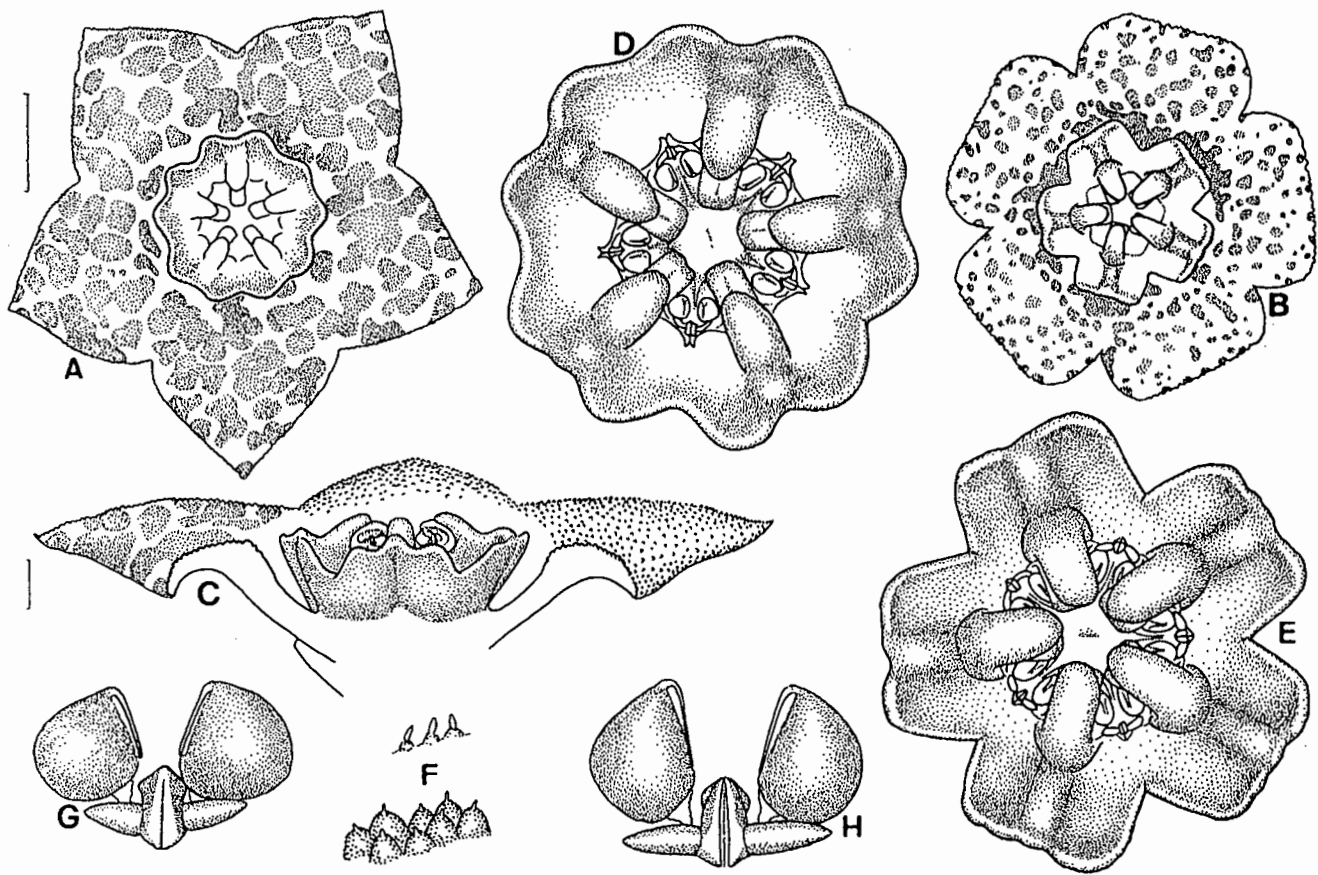


Fig 47
L. haagnerae
 4/12/41

Figure 47.—*Lavrania haagnerae*. A, B, face view of flower. C, side view of dissected flower. D, E, face view of corona. F, papillae on face of corolla; upper from near tip of lobe, lower from united part outside tube. G, H, pollinaria.

A, C, D, F, G drawn from Haagner sub Plowes 5046; B, E, H from Bruyns 4069.

Scale bar: A, B, 3 mm (at A); C, 1 mm; D, E, 1 mm (at E); F, 0.5 mm (at E); G, H, 0.25 mm (at E).

just containing gynostegium, a little over 1 mm deep, very slightly thickened at mouth; lobes 3 mm X 6 mm (at base), broadly ovate–deltoid, acuminate, margins slightly folded back. Corona pink–red, glabrous, ± 5 mm broad across top; outer lobes basally cupular, divided to middle into erect very obtuse lobes laterally adnate for nearly whole of length to dorsal projection of inner lobe, margins all somewhat rough; inner lobes incumbent on anthers and shorter than them, slightly less than 1 mm long, linear–obtuse, with obtuse erect dorsal projection confluent with and slightly taller than outer lobes. Follicles ± 70 mm long, divergent at 30–60°. Figure 47.

Material examined

1913: Sesfontein (–BA), Bruyns 4069 (BOL); Khowarib Gorge (–BD), Haagner sub Plowes 5046 (PRE).

L.haagnerae is found on the Damaraland–Kaokoveld border in the mountains around Sesfontein in north–west Namibia (Fig. 48). Plowes (1986, see above) gives a dramatic and interesting account of the fortuitous discovery of this plant by P. Haagner – a piece was found lying at the foot of some cliffs – and the failure of all attempts to recollect it. He maintained that the locality at which it was gathered by Haagner was unique. However, neither that nor the claims that this was the type and sole known locality for the little–known Aloe dewinteri Giess are correct. L.haagnerae is now known from two localities separated by about 40 km, but it is probably not uncommon in other precipitous spots in the area, of which there are many.

At both its known localities L.haagnerae occurs only on vertical dolomite cliffs with large quantities of Aloe dewinteri and very little other vegetation. Like this aloe, the plants are of quite unbelievably difficult access: the joy of being the first person to see this

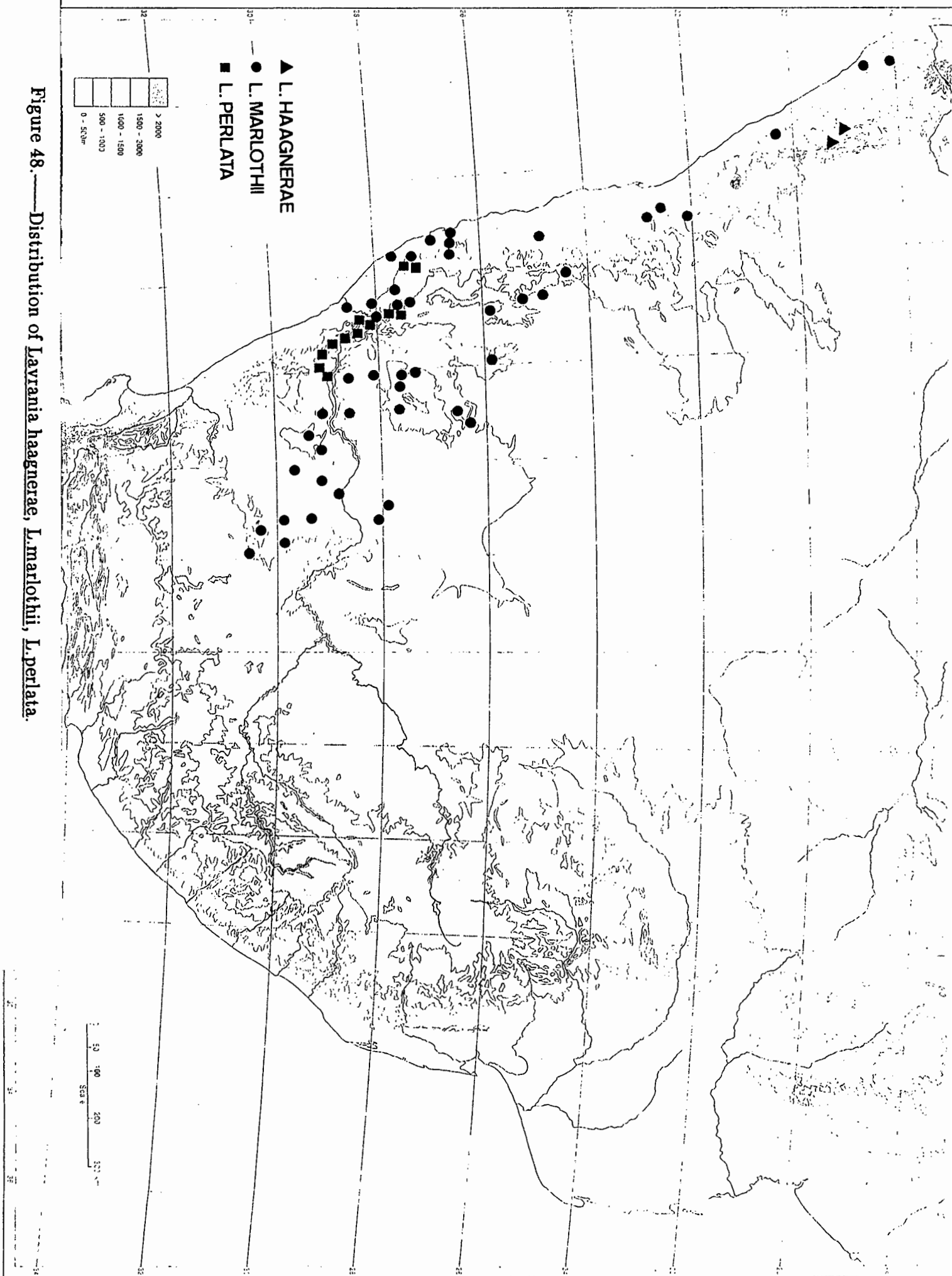


Figure 48. Distribution of *Lavarania haagnerae*, *L. marlothii*, *L. perlata*.

plant growing in its natural habitat was somewhat marred by the horror of having to edge out along ledges and past overhangs 20–60 m up sheer cliffs to collect specimens for cultivation. Plants are not uncommon and they form often quite large clumps in narrow crevices and small ledges on rock faces. They are quite shallowly rooted in small pockets of soil and they seem well able to spread along small veins of ground which enables them to become quite large: one clump about 150 mm broad and nearly 1 m long was noticed in January 1990.

L.haagnerae is the only member of this genus found in such precipitous habitats. A number of other ± obligatory cliff-dwelling stapeliads are known (Bruyns 1989). Unlike these, the stems of L.haagnerae are always rigidly erect and never have the creeping to pendulous habit of the others. They therefore never reach the enormous length of some of the other cremnophilous species and most of the stems are 100–150 mm long though one plant was seen with a few stems to 300 mm long.

Lavrania haagnerae differs from all others in this genus in having few (up to 10) inflorescences on each stem. They mature and bear flowers long after they are produced and thus flowers are mainly found in the lower half of the stem though inflorescences may be found most of the way up a floriferous axis. In all others the inflorescences are very numerous and bear flowers immediately after they are produced so that flowers are mainly found in the upper half of the stem: in fact many of these inflorescences remain active for a long time and so flowers can be seen practically anywhere on the stem, though most of them arise near the apex. The few inflorescences in L.haagnerae leaves the stem tubercles neatly arranged into 10–12 rows – in the others they are only neatly arranged in young plants that have not yet flowered. The flowers of L.haagnerae are notable for their intense and regular mottling with red spots and their unusually strong odour reminiscent of rock-rabbit dung and urine. The corona forms a much broader cup than in any of the

others and the slightly roughened upper margin of the outer lobes is unusual. The wings on the corpusculum of the pollinarium are also better developed than in other species. Apart from these, L. haagnerae is not very unusual florally in this genus.

In his article of 1986, Plowes (1986, see above) provides little justification for the erection of a monotypic genus. He gives two main distinguishing features: (1) the ± basally produced flowers and (2) the uniqueness of its "bristle-tipped papillae". The first distinction has been discussed above. In view of the great variability of the position of the inflorescences in a genus such as Stapelia, this cannot be used to distinguish other genera, especially when this new genus is florally so similar to the species formerly in Trichocaulon Sect. Cactoidea. As far as the second criterion is concerned, it is shown in this paper that bristle-tipped papillae are practically universal throughout Hoodia (Plowes concedes that they "do occur in some of the spiny species" of Trichocaulon, now in Hoodia) and that they are found in Lavrancia cactiformis, L. picta and L. perlata.

II. Sect. Cactoidea (White & Sloane) Bruyns comb. nov. Type: L. cactiformis (Hook.)

Bruyns.

Trichocaulon N.E. Br. Sect. Cactoidea White & Sloane, *Stap.*, 3: 991 (1937). Type:

T. cactiforme (Hook.) N.E. Br.

Leachia Plowes in *Asklepios* 56: 11 (1992), nom. invalid. Type: L. cactiformis (Hook.)

Plowes.

Key to the species

1. Corolla lobes strongly reflexed to press against stem, margins folded back, papillae on inner surface each tipped with horizontally-spreading cylindrical appendage.....5. L.perlata
1. Corolla not as above, papillae if present without apical appendage or appendage erect and very minute.....2.
2. Flowers entirely without papillae on inner surface, inner corona lacking dorsal projection.....2. L.marlothii
2. Flowers papillate on inner surface, at least in mouth of corolla tube, inner corona with conspicuous dorsal projection confluent with horns of outer lobes.....3.
3. Inner corona lobes usually meeting in centre, rising up into column at least as tall as horizontal part of anthers.....3a. L.picta subsp. picta
3. Inner corona lobes either horizontally adpressed to anthers and scarcely exceeding them or just meeting in centre but not rising up in column as above.....4.
4. Corolla with fine reddish dots on cream background and dark red patch on apex of lobes, horns of outer lobes strongly diverging, plants from Namibia north of Aus.....3b. L.picta subsp. parvipuncta
4. Corolla with white to yellow and purple-red bars to ± uniformly purple- or wine-red (without conspicuous dark apical patch), horns of outer corona lobes ± straight, plants from south of Orange River.....4. L.cactiformis

2. Lavrania marlothii (N.E. Br.) Bruyns comb. nov.

Trichocaulon marlothii N.E. Br. in Fl. Cap. 4 (1): 894 (1909). — Berger, Stap. u. Klein.: 353 (1910). — Dinter in Feddes Rep. sp. nov. 24: 16 (1927). — White & Sloane,

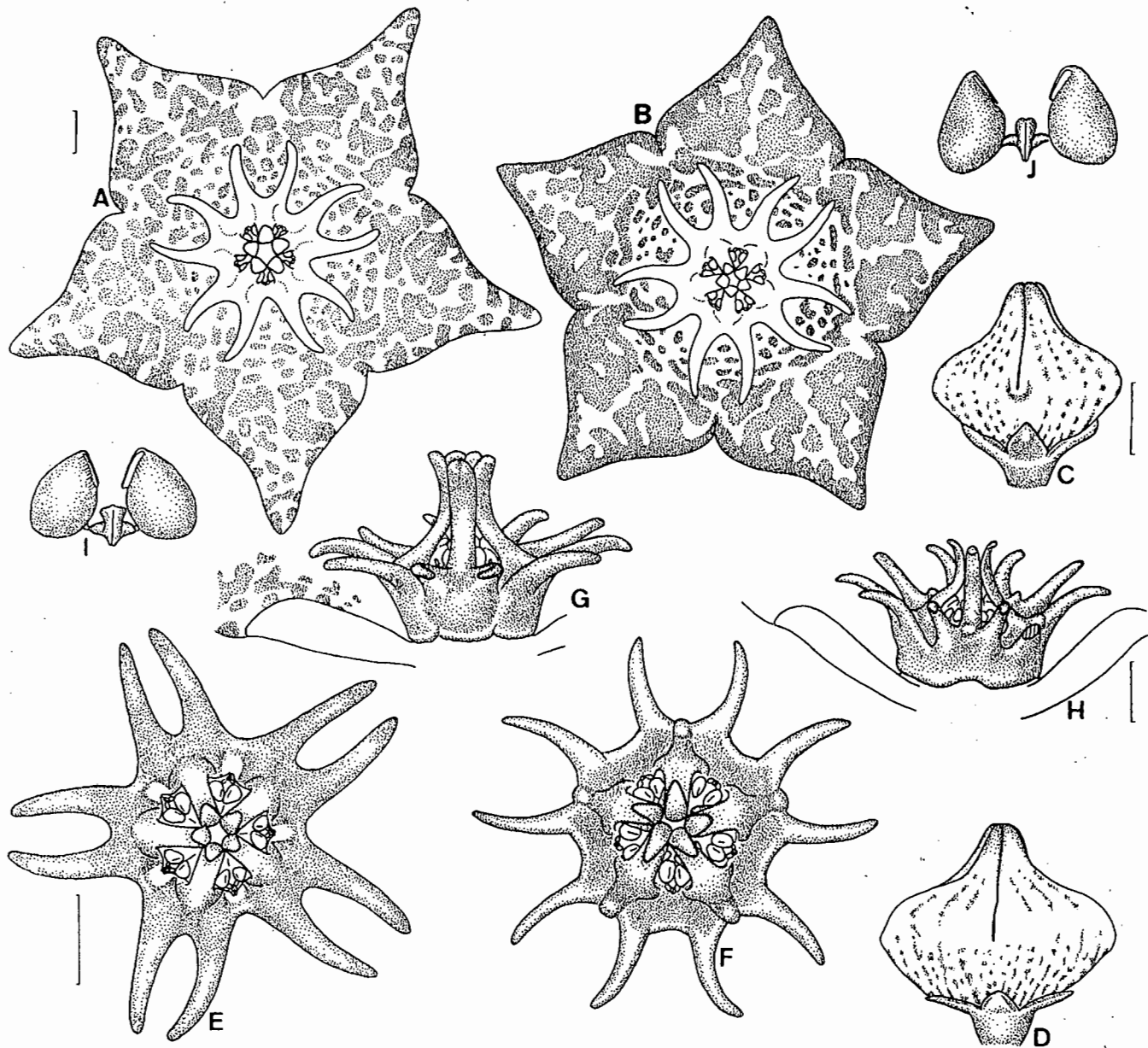


Figure 49
 T. van der
 11/7/19

Figure 49.—*Lavrania marlothii*. A, B, face view of flower. C, D, bud. E, F, face view of gynostegium. G, H, side view of gynostegium. I, J, pollinaria.

A, G drawn from Bruyns 3478; B from Bruyns 3571; C from Bruyns 3569; D from Pretorius (Eendorn); E, I, from Heunis & Bruyns 28; F, H, J, from Heigums, SE Aus, Kratz.

Scale bar: A, B, 1 mm (at A); C, D, 2 mm (at C); E, F, 1 mm (at E); G, H, 1 mm (at H); I, J, 0.25 mm (at C).

Stap. 3: 1043 (1937). — Pole Evans in Flow. Pl. S. Africa 18: t. 681 (1938). — Lückhoff, Stap.: 255 (1952). — Cole in Asklepios 31: 75–77 (1984). Leachia marlothii (N.E. Br.) Plowes in Asklepios 56: 12 (1992). Type: South Africa, near Kenhardt, Marloth 3763 (not located).

T.dinteri Berger, Stap. u. Klein.: 30 (1910). — Dinter in Neue u. wenig bekannte Pflanzen D.–SWAs: 55 (1914) et in Feddes Rep. sp. nov. 24: 16 (1927). — White & Sloane, Stap. 3: 1036 (1937). Leachia dinteri (Berger) Plowes in Asklepios 56: 12 (1992). Type: Namibia, Kalkhügel in der Namib 82 km ö. Swakopmund, Dinter 3136a (SAM!)

T.keetmanshoopense Dinter in Neue u. wenig bekannte Pflanzen D. SWAs: 57 (1914) "keetmanshoopensis" et in Feddes Rep. sp. nov. 24: 16 (1927). — White & Sloane, Stap. 3: 1041 (1937). — Lückhoff, Stap.: 254 (1952). Type: Namibia, zwischen Keetmanshoop u. Aroab auf Karooschiefer in der Rhigozum–Steppe, Jan. 1910, Dinter 3258 (not located).

T.sinus-luederitzii Dinter in Neue u. wenig bekannte Pflanzen D. SWAs: 59 (1914) et in Feddes Rep. sp. nov. 24: 16 (1927). — White & Sloane, Stap. 3: 1031 (1937). Type: Namibia, auf Strandfelsen nördlich von Lüderitzbucht, zuerst 1897 wieder Jan. 1910 gesammelt, Dinter 3163 (not located).

Included in the present concept of L.marlothii are Figures 1101, 1107, 1109, 1111, 1112 (left only) of White & Sloane (1937).

Plant a spineless succulent usually not more than 150 mm tall, branching from the base with 3–20 stems. Stems cylindrical, clavate or ovoid, erect to spreading, 20–55 (65) mm thick covered with flattened–rounded polygonal tubercles each tipped with a small conical leaf < 1 mm long seated in a small depression, tubercles crowded but arranged into ± 12–19 rows, grey–green, glabrous. Flowers arising in groups of 1–5 mostly in upper parts

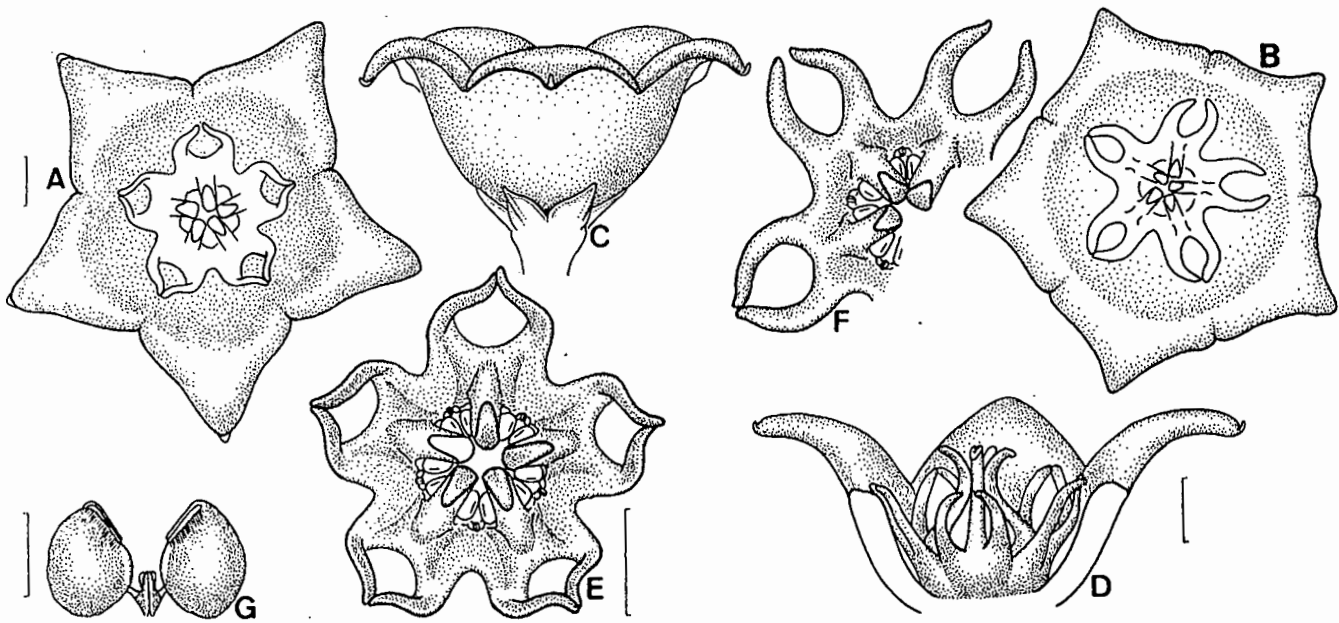


Figure 50.—Lavrania marlothii. Material from north of Swakopmund formerly known as T.dinteri. A, B, face view of flower. C, side view of flower. D, side view of dissected flower. E, F, face view of gynostegium. G, pollinarium.

A, D, E, G, drawn from Russel 39; B, C, F, from southern foot of Brandberg, van Rensberg.

Scale bar: A–C, 1 mm (at A); D, 1 mm; E, F, 1 mm (at E); G, 0.25 mm.

of stem but sometimes evenly spread over plant, developing successively. Pedicel up to 1 mm long, glabrous. Sepals 1.5–2 mm long, 1 mm broad at ovate base, acute, glabrous. Corolla 8–16 mm diam., campanulate to ± rotate, green spotted with reddish outside, inside variously mottled with red to dark red–brown on cream background, sometimes nearly uniformly dark purple–brown (in north), inside and outside smooth and glabrous; tube very shallowly saucer–like, < 1 mm deep to cup–shaped up to 3 mm deep, scarcely to not at all thickened at mouth; lobes spreading, often with recurved tips, 2–5 X 3–5 mm (at base), broadly ovate, acuminate, margins very slightly recurved. Corona irregularly spotted and lined with pink to maroon on cream background, often with droplets of nectar accumulating on upper surfaces, glabrous, 3.5–4.5 mm broad across top; outer lobes basally cupular, divided to well below middle into two slender ± cylindrical widely divergent spreading to spreading–erect obtuse horns 1–1.5 mm long; inner lobes incumbent on anthers meeting in centre and connivent–erect above it sometimes diverging at tips, obtuse, linear, nearly 2 mm long, dorsiventrally flattened, occasionally with small obtuse dorsal projection at base of teeth of outer lobes. Follicles 50–95 mm long, 35–54 seeds per horn, horns diverging at 30–60°. Figure 49, 50.

Material examined

Namibia

1812: Munutum River (–AB), Plowes 5287 (SRGH); Ogams (–CB), Plowes 5288 (SRGH).

2013: 26 miles W Wereldsend (–BC), Merxmüller & Giess 30607 (M); ± 25 km E of Torra Bay (–BC), Russel 39 (BOL).

2214: 3 km SW Rössing Stn (–DB), Plowes 4348 (SRGH).

- 2215: 82 km ö. Swakopmund (–AA), Dinter 3136a (SAM); 65 km E Swakopmund, south of river (–CC), Plowes 4941 (SRGH).
- 2415: Witberg Mtn (–CD), Seely & Ward 5 (WIND).
- 2416: Urikos (–AC), Bruyns 4156, no specimen preserved; Bergplaas (–DC), Bruyns 4162 (BOL).
- 2516: Rooiberg Suid (–BC), Bruyns 4172 (BOL); 5 km SE Helmeringhausen (–DD), Heunis 7 (BOL).
- 2517: Beerseba (–DD), Giess et al. 6883 (WIND).
- 2615: N of Lüderitz (–CA), Giess & v. Vuuren 687 (WIND); N of Nautilus (–CA), Metz (WIND); Rotekuppe (–CB), Dinter 3137a (SAM); Kowisberge (–CB), Heunis & Bruyns 24 (BOL); 22 km SE Lüderitz (–CD), Plowes 4945a (SRGH); Hahlenberg (–DA), Archer 545 (BOL); Heunis 5 (BOL).
- 2618: Keetmanshoop (–CA), STE 9040 (STE); Dinter s.n. (SAM).
- 2619: Springboktrek Suid (–AC), Bruyns 3571 (BOL); Koës intersection (–CA), Bruyns 3569 (BOL).
- 2715: Western edge of Klinghardt Mtns (–BC), Plowes 4948b (SRGH); 23 km S Schlafkuppe (–BD), Hardy 4689 (PRE); Buntveldschuh (–DA), Plowes 4955b (SRGH).
- 2716: Pockenbank (–AB), Heunis 2 (BOL); Rooiberg (–CB), Heunis & Bruyns 28 (BOL); Witpütz–Nord (–DA), Heunis 1 (BOL).
- 2718: Gründorn (–AC), Giess & Müller 12318 (WIND); Onverwag (–CA), Bruyns & Heunis 4338 (BOL); Quarzriff (–CB), Giess & Müller 12062 (WIND, M); Vredenhof (–DB), Bruyns 3495 (BOL).
- 2816: Schakalsberg (–BA), Hardy 4832, 4819 (PRE); Lorelei (–BB), Giess 12988

(WIND).

2818: Norachas (-AA), Giess et al 6900 (WIND, M); Sperlingpütz (-CA), Giess & Müller 12272 (PRE, WIND); Eendorn (-DB), Giess & Müller 12199 (WIND, M); Pretorius s.n. (BOL); Hardy 202 (PRE).

South Africa

2720: Kalkpoort (-DD), Bruyns 3475 (BOL).

2816: Sendelingsdrift (-BB), Hardy 565 (PRE); Grootderm (-DA), Pillans 5812 (BOL); Pillans 5329 (BOL); E of Oppenheimer bridge (-DA), Leistner 3434 (PRE).

2820: Kakamas (-DC), Wilmot (BOL); Fuller (BOL).

2821: Ghams (-AA), Bruyns 3478 (BOL).

2918: Rosynebos (-BB), Bruyns 5235 (BOL).

2919: Kykgate (-AC), Heunis 17 (BOL); SW Kwaggaskop (-BA), Bruyns 5250 (BOL).

2920: Droëgrond (-AB), Bruyns 5256 (BOL); Klippoort (-CA), Bruyns 5260 (BOL).

2921: Kenhardt (-AC), Hardy 868 (PRE); SW Kenhardt (-AC), Bruyns 4541 (PRE); Vaderlandspan (-CC), Dean s.n. (BOL); Diemansput Suid (-DC), Bruyns 3449 (BOL).

3021: Isaacskolk (-AD), Bruyns 3440 (BOL); Vanwyksvlei (-BD), Bruyns 3441 (BOL); Hardy 867 (PRE).

From the records cited and the map, it is clear that Lavrania marlothii is the most widely distributed in the genus (Fig. 48). It occurs along practically the whole length of Namibia from the mouth of the Cunene River to the Orange (it may well exist in Angola too) in and on the fringes of the Namib Desert. It is found more or less throughout the dry southern part of Namibia and extends eastwards as far as Upington and Vanwyksvlei.

Plants are quite common and characteristic in some of the coastal regions of the southern Namib especially along the Orange River from the Lorelei (Kahanstal) to Alexander Bay. In such places they mostly grow in the shelter of small stones in windswept flat places: windblown sand often filling many of the spaces between the stones and sometimes partly covering the plants. Further east it occurs under bushes of a colony-forming Ruschia or more frequently under Rhigozum trichotomum bushes in flat gravelly or sandy areas. Around Pofadder it has been seen a few times growing close to plants of L. picta or L. cactiformis: nevertheless they appear to be edaphically quite discrete with L. marlothii on the sandier areas and the others on hard ground among quartz pebbles.

L. marlothii is quite variable over this vast distribution. In the eastern part of its range the plants are usually more slender with a dark grey colour and deep grooves between the tubercles. They usually have at least 3 stems and may have up to 20 in some instances. The corolla lobes are relatively long and narrow (with broad base) and the whole corolla has a characteristic reddish patterning on a cream background which varies only slightly in intensity (Fig. 49). In the southern, winter rainfall part of the Namib the plants are mostly not more than 30 mm tall, with one or two stems (though even here they may have up to 20 stems). The stems are usually at least partially covered with a pale grey corky layer caused by blasting by sand. They are also thicker and the tubercles are much flatter with hardly any grooves between them. Especially at Lorelei and towards Alexander Bay enormous variation in the colour patterns on the corolla is found.

In the northern part of the range from Swakopmund northwards the corolla is more deeply campanulate (Fig. 50). It is also smaller, with shorter, more deltoid lobes and is frequently (though not always) more darkly coloured — in some cases a nearly uniform purple-black.

From the other species L.marlothii may often be distinguished by its more slender dark grey stems with deep grooves between the tubercles. However, this distinctiveness breaks down as one moves out of the Rhigozum—steppe westwards into the Namib. L.marlothii is distinguished from all others in the genus by its entirely smooth (papillae-free) corolla and by the nearly total lack of any dorsal projection on the inner corona lobes (a minute round one may occasionally be present). The striking distinctiveness of the seed has already been discussed (Figures 16, 18).

Trichocaulon dinteri was described from material collected 82 km E of Swakopmund. Dinter's photo (Dinter 1914) is not very clear but the rather campanulate flowers can be seen and he comments (page 56) on the nearly uniformly dark colour of the corolla lobes. They have been seen both darker and lighter than this but have not been noted to open up to be nearly as flat as those of L.marlothii. It is not quite clear, therefore, how material such as that illustrated by Cole (1984, page 76) comes to be called T.dinteri. Although plants from further south normally have practically flat flowers, occasionally more campanulate ones do appear. Thus there is no reliable character on which to separate the two and specimens referable to T.dinteri are considered to fall within the range of variation of L.marlothii. I can find no characters at all on which to separate either T.sinus-luederitzii or T.keetmanshoopense.

3. Lavrania picta (N.E. Br.) Bruyns.

Trichocaulon pictum N.E. Br. in Kew Bull. misc. inf.: 307 (1909) et in Bot. Mag.

140: t. 8579 (1914). — White & Sloane, Stap. 3: 1045 (1937). Leachia picta (N.E. Br.) Plowes in Asklepios 56: 14 (1992). Type: South Africa, Little Namaqualand, Marloth 4596 (K, specimen apparently lost). Neotype: t. 620 in Flow. Pl. S. Africa (1936), designated here.

Two subspecies are recognised.

3a. Lavrania picta subsp. picta

T. meloforme Marloth in Trans. Roy. Soc. S. Africa 2: 239 (1912). — Dinter in Feddes Rep.

sp. nov. 24: 16 (1927). — White & Sloane, Stap. 3: 1038 (1937). — non Lückhoff,

Stap.: 253 (1952). Leachia meloformis (Marl.) Plowes in Asklepios 56: 12 (1992).

Type: Namibia, between granite boulders near Aus, 1400 m, Marloth 4874 (PRE!)

T. engleri Dinter in Neue u. wenig bekannte Pflanzen D.—SWAs: 56 (1914) et in Feddes

Rep. sp. nov. 24: 16 (1927). — White & Sloane, Stap. 3: 1039 (1937). — Lückhoff,

Stap.: 254 (1952). Type: Namibia, Us Tal, nord-östlich von Kanus, Engler 3083 =

Dinter 3136 (SAM!)

T. simile sensu Marloth in Fl. S. Africa 3 (1): 94, fig. 47 (left hand part) (1932). — Pole

Evans in Flow. Pl. S. Africa 16: t. 620 (1936). — White & Sloane,

Stap. 3: 1034 (1937). — Cole in Asklepios 31: 79 (1984), non N. E. Brown.

Included in the present concept of L. picta subsp. picta are Figures 1062, 1099, 1100, 1104,

1105, 1106, 1114 of White & Sloane (1937).

Corolla (8) 12–16 mm diam., with ± round purple–brown spots on pale yellow background, covered within with low rounded papillae rarely with apical bristle; tube pentagonal with inward–pointing bulges opposite anthers, cup–shaped; lobes spreading, with strongly reflexed tips, usually with purple–brown patch on apex. Corona whitish spotted with purple–black; outer lobes up to 2 mm long, basally shallowly cupular, bifid almost to base into widely divergent ascending–spreading slightly dorsiventrally flattened horns; inner lobes incumbent on anthers and connivent–erect in centre, rising up in column up to 2 mm tall often with tips diverging, dorsiventrally flattened. Follicles 45 mm long with 82 seeds per horn, horns divergent at 30–60°. Otherwise as in L. cactiformis. Figure 51.

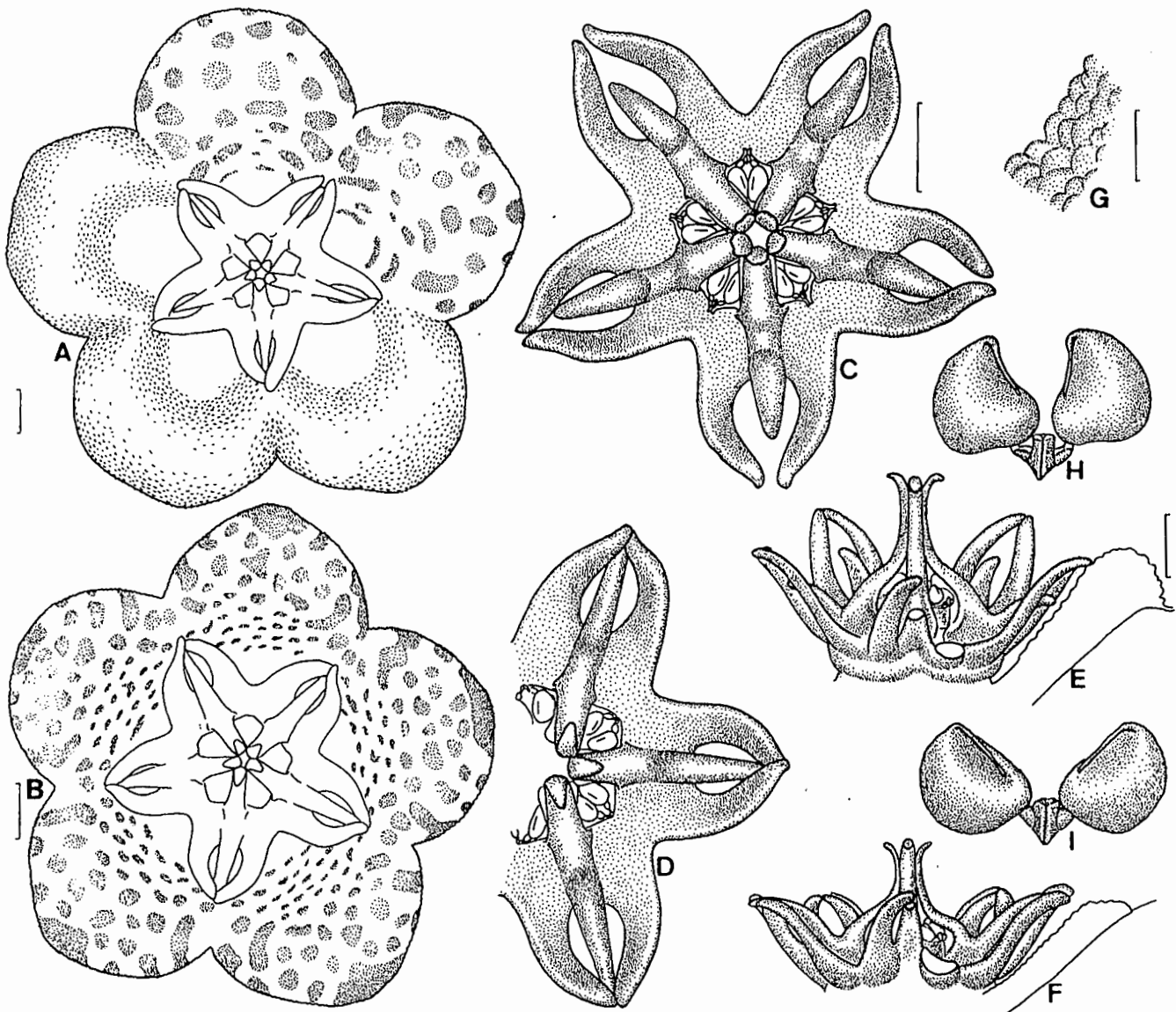


Figure 51
L. picta
 26/8/10

Figure 51.—*Lavrania picta* subsp. *picta*. A, B, face view of flower. C, D, face view of gynostegium. E, F, side view of gynostegium. G, papillae inside corolla tube. H, I, pollinaria.

A, C, E, H, G, drawn from Heunis 3; rest from Bruyns 3747.

Scale bar: A, B, 1 mm; C, D, 1 mm (at C); E, F, 1 mm (at E); G, 0.5 mm; H, I, 0.25 mm (at G).

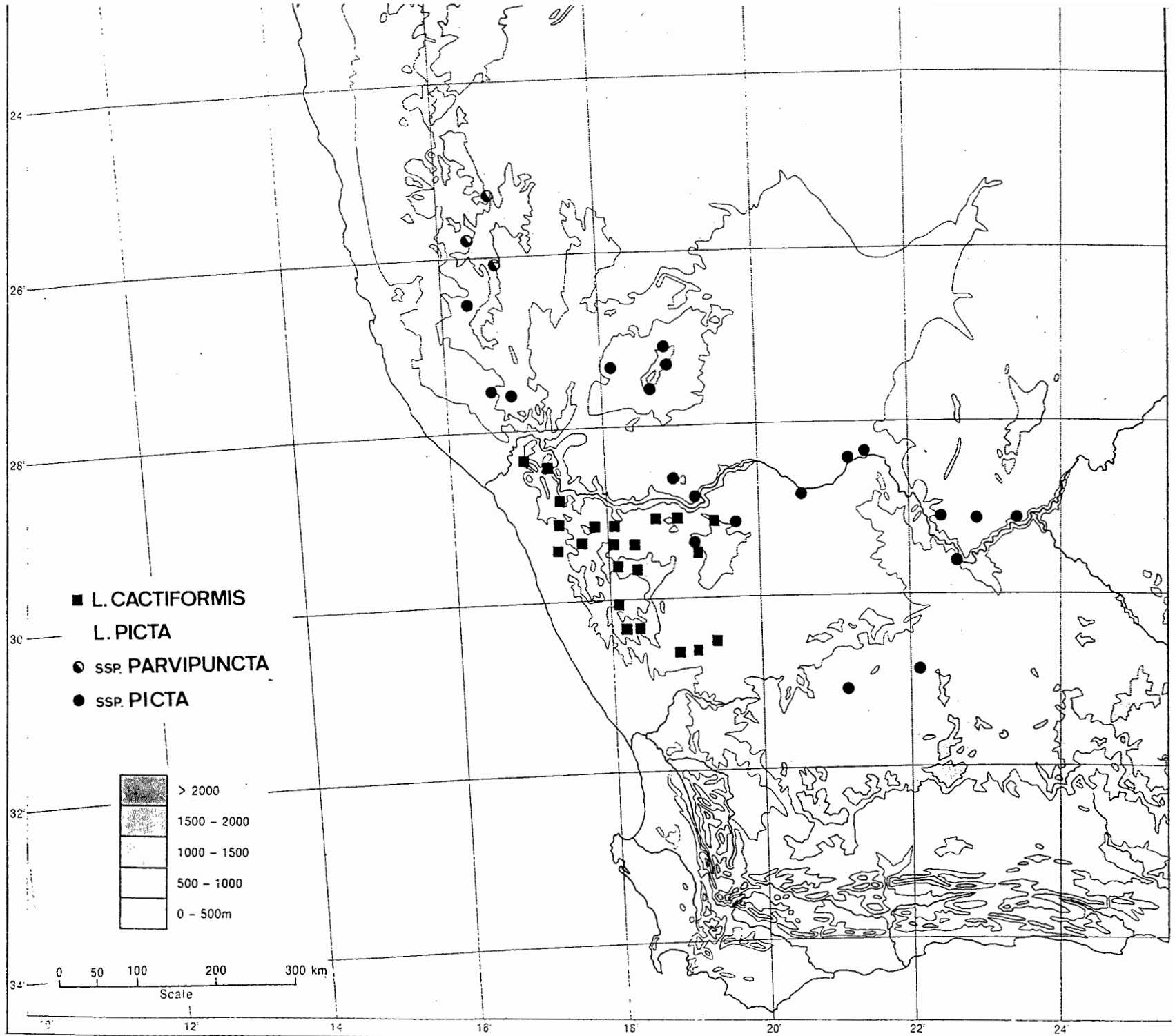


Figure 52.—Distribution of *Lavrania cactiformis* and *L. picta*.

Material examinedNamibia

- 2616: Aus (-CB), Heunis 3 (BOL); Marloth 4874 (PRE); cult. PRE 9979 (PRE).
- 2716: 4 km N Witpütz (-DA), Heunis & Bruyns 27 (BOL); 2 miles SE Witpütz (-DA), v.d. Merwe (PRE); Witpütz (-DA), cult. PRE 9981 (PRE); Sebrafontein (-DB), Bruyns 3904 (BOL).
- 2718: above Pass leading down to Gründorn (-AC), Pearson 4358 (BOL); Kraikluft (-BB), Pearson 8470 (BOL); Garis (-BD), Bruyns 3520 (BOL); Us-Tal, n.-ö. von Kanus (-DA), Dinter 3136 (SAM).
- 2818: Eendorn (-DB), Heunis 12 (BOL).
- 2819: Keimas (-CC), Heunis 14 (BOL).

South Africa

- 2820: Kakamas (-DC), Fuller 176 (BOL).
- 2821: Uppington Townlands (-AC), Pole Evans 2159 (PRE); Sultana-Oord (-AD), Visser (BOL).
- 2919: Namies (-AC), Heunis 16 (BOL); 16 km E Pofadder (-BA), Hardy 3889 (PRE).
- 2922: Lelikstad (-AB), Acocks 8634 (PRE); Kruispad (-BB), collected by farm labourer (BOL); Glen Allan (-DA), Bryant 587 (KMG).
- 2923: Read's Drift (-AB), Anderson 542 (KMG, BOL); Brakkies (-AB), Bruyns 4539 (); Oranjeoord (-AB), Bruyns 4535 ().
- 3022: Vaalhoek (-CC), Bruyns 3747 (BOL).
- 3121: N of Williston (-AA), Bruyns & Nagel 4884 ().

Without precise locality: Namibia, Compton sub NBG 1818/27 (BOL); NBG 5153/14.

(BOL); v. Son 11/1933 (PRE); Schlieben 8946b (PRE); Griquatown (-CD), cult. PRE 1739 (PRE); 9983 (PRE).

Lavrania picta subsp. picta is distributed along the eastern edge of the winter rainfall region from Aus to Witpütz in south-western Namibia via the Great Karas Mountains (where it grows both around the foot of the mountains and on some of the highest ridges) to Griqualand West (as far east as Douglas) and then south to Carnarvon (Fig. 52). There do not seem to be any records at all for Namaqualand.

Flowers of L.picta subsp. picta are generally large for this genus with a yellow background colour, numerous ± round, evenly distributed purple-brown spots and a purple-brown apex to each lobe. The apex of the lobe is usually folded back once the flower is fully open so that this dark patch is only visible as the flowers open. The corolla tube has a broad inward bulge at the sinuses of the lobes which gives the tube a distinctly pentagonal shape (this is rarely found in L.cactiformis). As is commonly the case in the genus, the inner surface of the corolla is covered with broad, rounded papillae but here they often have a dark apical cell and there is rarely an apical bristle. The corona is extremely variable. Usually the horns of the outer lobes are divergent and spreading so as to lie close to (sometimes adpressed to or curling round) the long dorsal projection of the inner lobe giving the appearance of 5 trifold lobes; occasionally they do not diverge at all and the 15 horns (10 outer corona horns and 5 dorsal projections on the inner lobes) are more or less equally spaced. This taxon has long inner corona lobes. They are initially incumbent on the anthers, then connivent and then erect, rising up in a column above the centre of the flower. In a few cases they form a cage above the anthers i.e. incumbent on anthers only near base then rising above them and meeting in centre to form small vertical column.

Although both the seed and seedlings are very different in L.cactiformis and L.picta subsp. picta (Fig. 16, 18), in their vegetative and floral parts the two are remarkably similar, a result presumably of convergence. Florally the two are most readily separable by the long inner corona lobes of L.picta subsp. picta. There are other minor and less reliable distinctions discussed under L.cactiformis.

There has been considerable confusion in the recent popular literature (Plowes 1982; Cole 1979; 1984) as to which names apply to the taxon here called L.picta subsp. picta. These plants have mostly been called Trichocaulon simile but it was uncertain whether Trichocaulon pictum is synonymous. In herbaria much of the preserved material has been called Trichocaulon meloforme and very occasionally T.engleri. It is worth clarifying the position by quoting in each case the relevant piece (on the inner corona lobes) from the original description.

T.cactiforme: "segments of inner (corona) ... rather short and incurved upon the gynostegium" (Hooker).

T.simile: "inner corona-lobes ... ascending-connivent, closely pressed to backs of anthers and shortly exceeding them" (Brown).

T.pictum: "Coronae interiores ... antheras excedentes apicibus connivento-erectis" (Brown). [inner corona ... exceeding anthers with apices connivent-erect]

T.meloforme: inner corona lobes "elongated ... reach(ing) to the level of the outwards corona segments" (Marloth).

T.engleri: "Die Abschnitte der inneren Korona den Antheren aufliegend und als Säule dieselben weit überragend" (Dinter). [the segments of the inner corona lying on the anthers and reaching far above them as a column]

Hooker's remarks on the inner corona of T.cactiforme are not illuminating but the figure accompanying this description is extremely clear. The type of T.cactiforme is missing but nevertheless this figure makes the application of this name unambiguous.

The diagnosis for the inner corona of T.simile fits T.cactiforme rather than the taxon we are now dealing with. The type of T.simile is a single flower which was kindly examined for me by A.Nicholas and D.Goyder at Kew. When it was reconstituted it was found to have short inner corona lobes adpressed to the anthers and only slightly exceeding them. Thus it is clear that T.simile is a synonym of T.cactiforme.

Brown's "connivent—erect" for the inner corona lobes of T.pictum is a much better fit for the taxon we are now dealing with. However, the type of this name (Marloth 4596) is missing. On the type sheet at K is a note by N.E. Brown dated 1 July 1909 that "the flowers are at present in fluid, waiting to be figured". There is no trace of this preserved material at K nor any figure of it. Further confusion is caused by the illustration in Curtis' Bot. Mag. (Brown 1914, see above). According to the accompanying account, this figure is based on a collection of Pearson (no number given) from quartzite hills SW of Chubiesis, which flowered for the first time in June 1912. On the same sheet as the type of T.pictum is Pearson 6192, determined by N.E. Brown on 30 June 1912 as T.pictum. Pearson's notebooks (BOL archives) reveal that 6192 was collected on a hill SW of Chubiesis so that this is definitely the specimen referred to in the account. This specimen was kindly examined for me by A.Nicholas and D Goyder. The inner corona lobes are adnate to and slightly shorter than the backs of the anthers, barely meeting in the centre. Thus Pearson 6192 is a collection of T.cactiforme. In the figure in Curtis' Bot Mag. (t.8579, fig. 2, 3) the inner corona lobes are produced far above the style head and are much longer than the anthers. Brown gives them as "connivent—erect" in the accompanying description.

Consequently it is clear that some confusion has occurred and this figure is not of Pearson 6192. It is quite possible that it is the one that was supposed to be made from Marloth 4596. To add to the uncertainty it is rather crude as the corolla tube is not shown and the dorsal projections on the inner lobes are abnormally variable. It is therefore better to select the detailed figure in Pole Evans (1936, see above), reproduced as Plate 33 and Figure 1100 in White & Sloane (1937) as neotype.

In most of the recent popular literature it has been assumed that T. pictum and T. simile are the same and that both represent the present taxon (consequently called T. simile, the earlier valid name). This can now clearly be seen to be incorrect. It appears that this confusion can be traced back to the plate that appeared in Flowering Plants of South Africa in 1936 which was said to represent T. simile. This in turn may have been induced by the confusing amendment of Brown's description of T. simile by Rudolf Marloth (cited above, page 94) where he gives the inner corona as "one half the length of the outer, each lobe terminating in a globose, chrome-yellow knob". The first part of this amendment suggests T. cactiforme but the second is inexplicable. Marloth muddled things further as his illustration of T. pictum seems to be T. cactiforme. White and Sloane (1937) followed all the above uncritically and prominently displayed the plate from Flowering Plants of South Africa as T. simile and thus probably entrenched the error.

The diagnosis for T. meloforme suggests the present taxon. Unfortunately Marloth's paper was accompanied by an unclear photograph and the type specimen (PRE) is sterile.

The diagnosis of T. engleri and Figure 64 (Dinter 1914, see above) leave no doubt that this represents the present taxon. It is assumed that Engler 3083 = Dinter 3136 as Dinter (see above, p. 57) informs us that Engler gave him the only plant that they collected along the banks of the Us River north-east of Kanus (Dinter 1921, p. 107) and this appears to be the only time that Dinter visited this spot.

3b. Lavrana picta subsp. parvipuncta Bruyns subsp. nov., a subspecie picta, planta parva uno caule, corolla subtiliter rubri–parvipuncta, coronae lobis interioribus conniventes–adscendentibus non conniventis–erectis differt. Type: Namibia, Heunis 6 (BOL, holo).

Plant consisting mostly of a single erect stem 30–80 mm tall (occasionally branching from base), 20–35 mm diam., 12–16–angled, grey–green. Pedicels 0.5–1 mm long, 1 mm thick. Sepals 2 mm long, 1 mm broad at middle, lanceolate–ovate, keeled towards apex, glabrous, pale green faintly suffused with red. Corolla 8–9 mm diam., papillate within (papillae each tipped with minute bristle), greenish spotted with red outside, inside cream finely spotted with red and with dark red area near apex of each lobe; tube \pm 2 mm deep, shallowly cup–shaped; lobes spreading, 2 mm long, 3 mm broad at base. Corona pale yellow spotted with red; outer lobes ascending–spreading, \pm 1.5 mm long, divided nearly right to base into two widely divergent terete horns with recurved tips; inner lobes \pm 2 mm long, incumbent on backs of anthers, connivent in centre and rising up together for \pm 0.5 mm or less, linear with rounded apex, with conical spreading dorsal projection just less than 1 mm long. Follicles 55 mm long with 78–100 seeds per horn, horns divergent at 30–60°. Otherwise as in L.cactiformis. Figure 53.

Material examined

Namibia

2516: Rooiberg (–BC), Bruyns 4173 (BOL); Landsberg (–CD), Heunis 6 (BOL).

2616: Tiras (–BA), Bruyns 3750 (BOL).

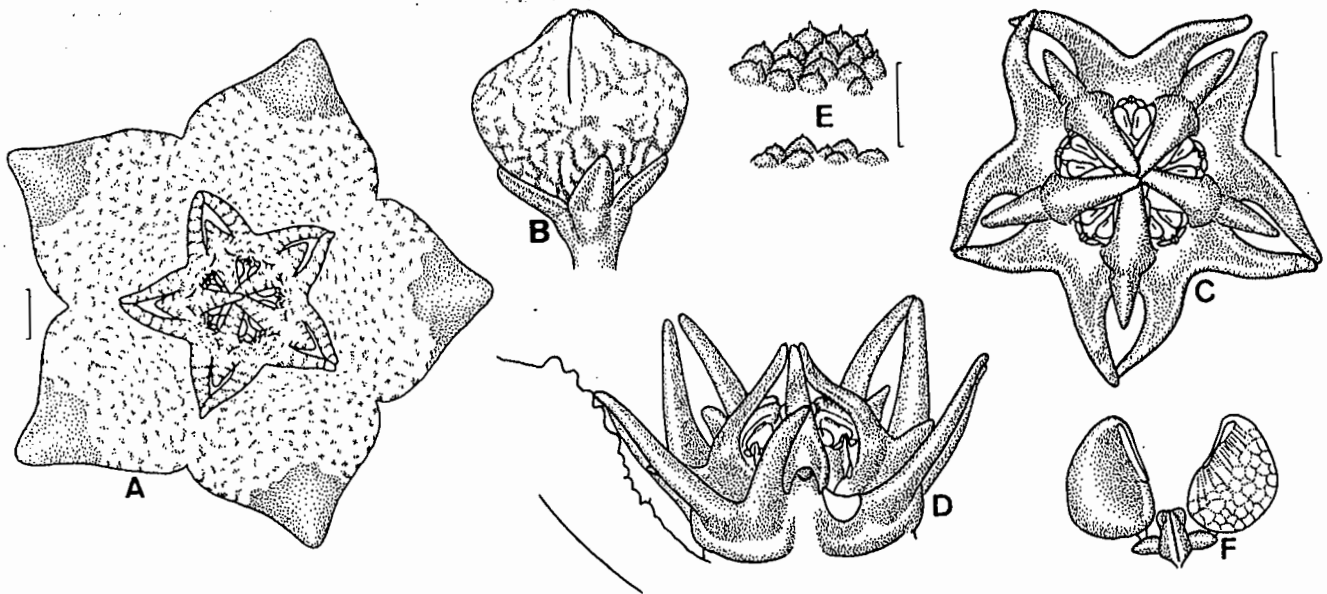


Figure 53.—*Lavrania picta* subsp. *parvipuncta*. A, face view of corolla. B, bud. C, face view of gynostegium. D, side view of gynostegium. E, papillae on inner surface of corolla: upper from deep in tube, lower from base of lobes. F, pollinarium.

A, B, E drawn from Bruyns 4173; C, D, F from Bruyns 3750.

Scale bar: A, B, 1 mm (at A); C, D, 1 mm (at C); E, 0.5 mm; F, 0.25 mm (at E).

Lavrania picta subsp. parvipuncta is evidently widespread around the base of and within the Tiras Mountains some 70 km north of Aus. It is also common on the Rooiberg about 80 km further north and has been reported by Plowes (Plowes 1982, page 21) at Tsamis West in the Naukluft Mountains although no material has been preserved (for documented distribution see Figure 52).

The plants are generally small and in the wild consist of one short unbranched stem only. They may thus also be quite short-lived, although this has not proved to be the case in cultivation. The flowers are smaller than is usual for L.picta and are cream with very fine spotting of red. The tips of the corolla lobes are also red. The main difference from subsp. picta is in the inner corona lobes which are shorter and connivent-ascending in the centre rather than connivent-erect into a small column.

In the corona this subspecies resembles L.cactiformis closely. It has, however, the very long, widely diverging outer corona horns typical of L.picta. The inner corona lobes rise up slightly in the centre (more so than is usual for L.cactiformis) and they have a more spreading dorsal horn than is usual in L.cactiformis where it is normally erect. This dorsal horn is, however, not as long as it usually is in subsp. picta. The very fine spotting of the corolla with red and the dark red tips to the lobes are both more typical of L.picta rather than L.cactiformis where the colours are barred against one another. Most important are the seed and seedlings (Fig. 16, 18), which are indistinguishable from those of L.picta subsp. picta and not similar to those of L.cactiformis.

4. Lavrania cactiformis (Hooker) Bruyns comb. nov.

Trichocaulon cactiforme (Hook.) N.E. Br. in Hook., Icon. Pl. 20: t. 1905 (1890)

"cactiformis" et in Fl. Cap. 4 (1): 895 (1909). — Berger in Stap. u. Klein.: 29

(1910). – Dinter in Feddes Rep. sp. nov. 24: 15 (1927). – Marloth in Fl. S. Africa 3 (1): 94 (1932). – White & Sloane, Stap. 3: 1032, fig. 1102, 1103 (1937). – Lückhoff, Stap.: 253 [lower figure, not T.meloforme as given] (1952). – Cole in Asklepios 31: 79 [the figure of CX 84 on page 78 is T.cactiforme not T.pictum] (1984). Stapelia cactiformis W.J. Hooker in Bot. Mag. 71: t. 4127 (1845). Leachia cactiformis (Hook.) Plowes in Asklepios 56: 12 (1992). Type: Little Namaqualand, Zeyher fl. Aug. 1844 (no material preserved).

Lectotype: t. 4127 in Bot. Mag. 71 (1845).

T.simile N.E. Br. in Fl. Cap. 4 (1): 895 (1909). Leachia similis (N.E. Br.) Plowes in Asklepios 56: 14 (1992). Type: South Africa, near Vanrhynsdorp, Marloth 4571 (K!)

T. felinum Cole in Aloe 22: 6 (1985). Leachia felina (Cole) Plowes in Asklepios 56: 12 (1992). Type: South Africa, Richtersveld, near summit of Rosyntjie Mtn, July 1978, Cole X 441 (PRE!)

Included in the present concept of L.cactiformis are Figures 1098, 1102, 1103 of White & Sloane (1937).

Plant a spineless succulent up to 150 (rarely 200) mm tall, single-stemmed or branching from base. Stems cylindrical-clavate, 30–60 mm thick, covered with flattened–rounded polygonal tubercles each tipped with small conical leaf < 1 mm long, tubercles crowded but arranged into ± 12–16 rows, whitish–green, glabrous. Flowers arising in groups of 1–5 near apex of stem, developing successively. Pedicel up to 1 mm long, glabrous. Sepals 1.5 mm long, ovate, acute, glabrous except for cilia sometimes on margins. Corolla 6–15 mm diam., glabrous outside and inside, outside smooth, inside covered with obtuse papillae, usually each with a small apical bristle, white to pale yellow barred (rarely spotted) with purple–red to ± uniformly purple– or wine–red; tube shallowly to quite deeply cup-shaped, containing most of gynostegium; lobes spreading, usually with recurved tips,

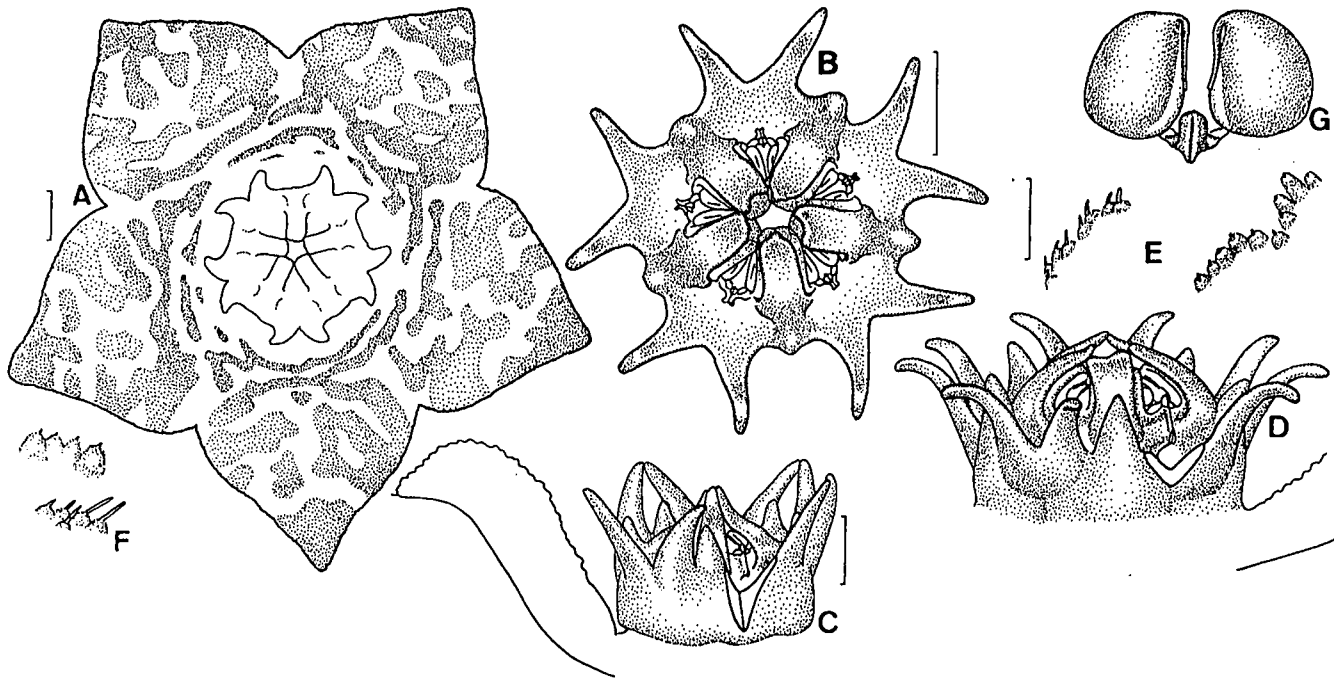


Figure 54.—*Lavrania cactiformis*, large-flowered forms. A, face view of flower. B, face view of gynostegium. C, D, side view of gynostegium. E, F, papillae on corolla: ones with longer bristles from near tips of lobes, others near mouth of tube. G, pollinarium.

A, F, drawn from Heunis 11; B, D, E, G from Kennedy (Kweekfontein); C from Heunis 112.

Scale bar: A, 1 mm; B, D, 1 mm (at B); C, 1 mm; E, F, 0.5 mm (at E); G, 0.25 mm (at E).

2–3.5 X 2.5–5.5 mm (at base), very broadly ovate, abruptly acuminate. Corona variously spotted and lined with red on yellowish background, glabrous, 3–4.5 mm broad across top; outer lobes basally cupular, divided to well below middle into two spreading–erect diverging slightly flattened obtuse horns; inner lobes sometimes white with red margins, otherwise as for corona, usually not produced beyond anthers (sometimes meeting in centre and slightly overlapping), acute to truncate–emarginate, with ± deltoid erect to slightly spreading dorsal projection laterally attached to outer lobes. Follicles 20–30 mm long with 35–52 seeds per horn, horns usually diverging at 180°. Figure 54.

Material examined

Namibia (both doubtful, not included on map)

? 2616: Aus (–CB), v.d. Merwe 18 (PRE).

? 2716: Witpütz (–DA), v.d. Merwe sub PRE 9019 (PRE).

South Africa

2816: Numees mine to Hellskloof (–BD), Pearson 6088 (BOL).

2817: Rosyntjie Mountain (–AC), Cole 47; 441; 443 etc (PRE); Oliver, Tölken & Venter 376 (PRE); Klipbok (–CD), Bruyns 4649 (BOL).

2820: Kakamas (–DC), Fuller 155 (BOL) (doubtful, not included on map).

2917: N. Grasvlakte (–AB), Bruyns 3749 (BOL); 29 miles SE Port Nolloth (–AD), Acocks 14232 (PRE); Naroegas (–AD), Bruyns & Heunis 4633 (); Eenriet (–BB), Heunis 117 (BOL); Steinkopf (–BC), Archer 713 (BOL).

2918: Geselskapbank (–AA), Bruyns & Heunis 4656 (); Witbank (–AC), Bruyns 5200 (BOL); Naip (–AD), Bruyns & Heunis 4661 (); Haramoep (–BA), Strey 3900 (PRE); Rosynebos (–BB), Bruyns 5239 (BOL); Kweekfontein (–CA), Kennedy

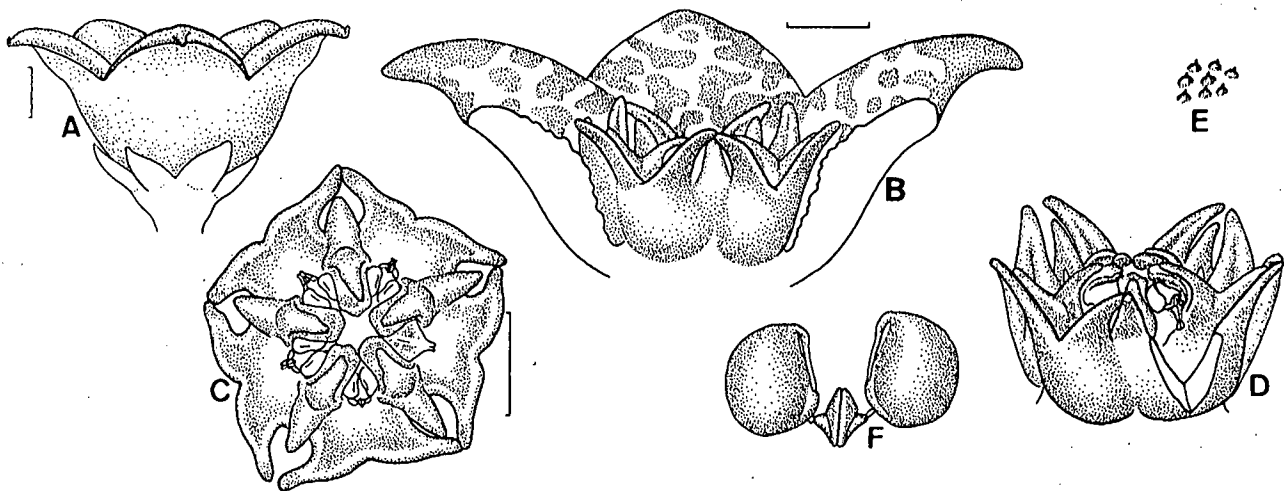


Figure 55.—*Lavrania cactiformis*, small-flowered forms sometimes referred to '*T.felinum*'. A, side view of flower. B, side view of dissected flower. C, face view of gynostegium. D, side view of gynostegium with half of outer corona lobe removed. E, papillae on inner surface of corolla near base of lobes. F, pollinarium.

E drawn from Cole 442; rest from Bruyns 3229a.

Scale bar: A, 1 mm; B, 1 mm; C, D, 1 mm (at C); E, 0.5 mm (at B); F, 0.25 mm (at B).

(BOL); Kangnas (–CB), Bruyns & Heunis 4679 ().

2919: Namies (–AC), Heunis 15 (BOL).

3018: Goraap turnoff (–AA), Heunis 112 (); W of Paulshoek (–AC), Bruyns 5340 (BOL);
E of Roodekloof (–AD), Bruyns 5334 (BOL); W of Platbakkies (–AD), Bayer 1603
(NBG); Sterkstroom (–AD), Bruyns 4745 (); E of Kliprand (–DB), Bruyns 5307
(BOL).

3019: Taaiboshoek (–CA), Heunis 9 (BOL); Brakfontein (–CB), Heunis 21 (BOL).

Without precise locality: Port Nolloth, Hardy 2546 (PRE); Schlieben 8946a (PRE).

Lavrania cactiformis is less widespread than most of its congeners (Fig. 52). It occurs over most of Namaqualand from near Sendelingsdrift to south of Port Nolloth on the coastal plain, usually occurring here on quartzitic hillsides. Further east it is of sporadic occurrence in the Khamiesberg and other Namaqualand mountains from Steinkopf to as far south as near Garies. It is quite common on many of the quartz hills of western Bushmanland (east of Springbok to Aggeneys and Pofadder). There are a few alcohol specimens at PRE from south–western Namibia but these are considered to be due to a confusion of cultivated specimens and L.cactiformis does not appear to grow in Namibia.

L.cactiformis is very similar indeed to L.picta and the two occur together at several localities (especially to the W and SW of Pofadder). There are several weak characters by which they may be separated: in L.picta subsp. picta the flower is larger with small, nearly circular, purple–brown spots on pale yellow (usually elongated, transverse bands on whitish background in L.cactiformis); in subsp. picta the corolla tube is usually quite clearly pentagonal and it has a shallower, broader gynostegium with more widely divergent outer

corona lobes and a longer dorsal projection on the inner lobes; the papillae on the inside of the corolla are also usually more flattened and rarely have an apical bristle. They are most reliably distinguished by the different inner corona lobes. In L.cactiformis these are incumbent on the backs of the anthers and mostly shorter than them but may exceed them slightly to meet in the centre. In one collection (Heunis 112) they were found to rise up slightly in the centre (Figure 34 C) but this was only in one plant and this is the only locality where this was seen. L.cactiformis is much less easily separated from L.picta subsp. parvipuncta and this is discussed under that taxon.

L.cactiformis shows considerable variation. Plants with flowers similar to that illustrated by William Fitch predominate (Fig. 54). Usually they are quite broad and often nearly rotate with transverse bands of purple-brown on a whitish background and a noticeably rugose inner surface with comparatively large papillae. The inner corona lobes are mostly as long as the anthers with truncate to acute apices.

In the extreme north-western Cape from the Rosyntjie Mountain to just north of Steinkopf an extraordinary range of variants occurs. Some of the more extreme of these found on the Rosyntjie Mountain (Fig. 55) were given the name Trichocaulon felinum Cole. In this area flowers vary from the normal size of 12–15 mm down to 6 mm in diameter and in colour from the usual to deep reds and maroon with hardly any of the normal white background. The flowers have a relatively deeper, often more pentagonal corolla tube and consequently the horns of the inner corona lobes rise more steeply. They are also sometimes less papillate than normal with the papillae restricted to the tube. The inner corona lobes are usually narrower towards the apices. While the flowers of the original T.felinum were extremely distinctive looking, subsequent collections on the Rosyntjie Mountain have not proved nearly as singular, as the flowers have been far less dark, more

lightly banded with red and larger. Material from the Klipbok and Eenriet areas also contains a host of intermediates between T.felinum and normal "cactiformis".

It should be noted that in Lavrania marlothii similar variation from ± rotate flowers to small campanulate ones (the former T.dinteri), also accompanied by intensification and darkening of the colours occurs and could be regarded as a typical trend within the genus T.felinum is therefore not upheld as a distinct species.

5. Lavrania perlata (Dinter) Bruyns comb. nov.

Trichocaulon perlatum Dinter in Feddes Rep. sp. nov. 19: 155 (1923). — White &

Sloane, Stap. 3: 1027, fig. 1094 (1937). — Huber in Prodr. Fl. SWA 114: 69 (1967).

— Cole in Aloe 17: 72–73 (1979) et in Asklepios 31: 81–82 (1984). Leachia perlata

(Dinter) Plowes in Asklepios 56: 14 (1992). Type: Namibia, Klinghardt

mountains, at various places, fl. Sept. 1922, Dinter 4734 (B)

T.cinereum Pillans in S. African Gard. 18: 62 (1928). — White & Sloane, Stap. 3: 1028

(1937). Type: South Africa, Cape, north part of Richtersveld, Oct. 1926, Pillans

5781 (BOL!)

T.kubusense Nel in Kakteenkunde: 70 (1933). — White & Sloane, Stap. 3: 1025, Fig. 1092,

1093 (1937). — Lückhoff, Stap.: 253 (1952). — 'kubusanum' Jacobsen, Succ. Pl. :

291 (1935). Type: South Africa, Cape, under bushes at altitude of 400 m, Kubus,

Oct. 1930, Herre sub SUG 6007 (not located).

T.truncatum Pillans in White & Sloane, Stap. 3: 1029, fig. 1096 (1937). Type: South

Africa, Uranoep on Goodhouse road, Smithers sub BOL 21725 (BOL!)

Included in the present concept of L.perlatum are Figures 1092–1096, 1112 (right hand only), 1117 of White & Sloane (1937).

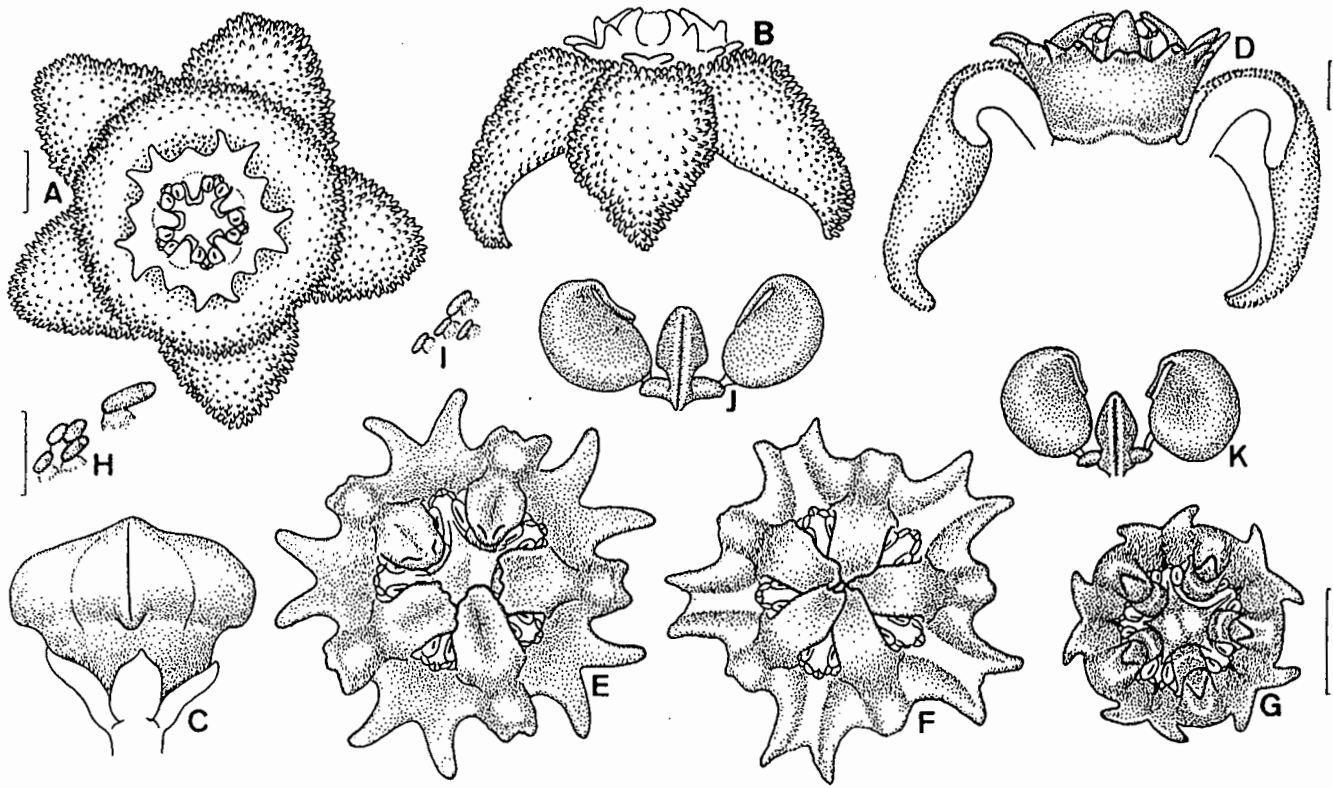


Figure 56
L. perlata
 19/6/90

Figure 56.—*Lavrania perlata*. A, face view of flower. B, side view of flower. C, bud. D, side view of dissected flower. E–G, face view of gynostegium. H, I, papillae on corolla face, taken near base of lobes. Apical appendage pointing to tip of lobe. J, K, pollinaria.

A, B, H, drawn from cultivated material (ZSS); C, E, J, from Bruyns 3229b; D, F, I, K, from Cornellskop, Russel; G from Richtersveld, without precise locality, Van Jaarsveld.

Scale bar: A, B, 1 mm (at A); C, D, 1 mm (at D); E–G, 1 mm (at G); H, I, 0.5 mm (at H); J, K, 0.25 mm (at H).

Plant a spineless succulent up to 300 mm tall, branching from base. Stems cylindrical-clavate, 25–60 mm thick with 12–14 rows of flattened rounded polygonal tubercles each with small conical persistent leaf < 1 mm long initially at apex and later near middle, grey–green, glabrous. Flowers in groups of 3–6 (–12) on often large ‘peduncular patches’, in upper parts of the stem, often several per cluster open at once, with strong excrement odour. Pedicel 0.5–2 mm long, glabrous. Sepals 1–1.5 mm long, 0.5–1 mm broad at broadly ovate base, acute, margins usually ciliate with transparent thick hairs, otherwise glabrous. Corolla (5) 7–10 mm diam., yellow–green glabrous outside, inside greenish–white to spotted with red to entirely deep red, outside smooth, inside covered densely with obtuse papillae each tipped with a horizontally–spreading cylindrical obtuse appendage; tube shallowly cup–shaped, containing gynostegium up to level of base of inner lobes (about 1 mm deep), not thickened at mouth; lobes strongly reflexed and pressed against stems with bases raised into ‘annulus’ around mouth of tube, 3–4.5 mm long, 2–2.5 mm broad at base, (narrowly) ovate–deltoid, acuminate; margins folded back. Corona irregularly red– to maroon–spotted on yellow to whitish background, glabrous, 2–3.5 mm broad across top; outer lobes basally cupular, divided to near middle into bifid divergent spreading dorsiventrally–flattened teeth up to 0.5 mm long or emarginate and truncate; inner lobes incumbent upon anthers, broadly oblong, truncate, often emarginate, incumbent on anthers and sometimes exceeding them, occasionally with erect apices, with broad truncate ± erect dorsal projection in series with outer lobes. Follicles with horns ± 60 mm long, usually divergent at 180°. Figure 56.

Material examined

Namibia

2715: 110 km SE Lüderitz (–BC), Plowes 4952c (SRGH); Schlafkuppe (–BD), Hardy 4689 (PRE).

2716: Sebrafontein (–DB), Giess 12415, Giess 13923 (WIND).

South Africa

2816: Swartpoort (–BB), Bruyns 1326 (NBG); Hellskloof (–BD), Hall sub NBG 679/53 (NBG); Hardy 3895 (PRE); S of Remhoogte (–BD), Bruyns 3942 (BOL); 10 km S Hellskloof (–BD), Hardy 3907 (PRE).

2817: Rosyntjie Mountain (–AC), Bruyns 3229b (BOL); W of Mt Stewart (–CB), Bruyns 4949 (); Kliphoogte (–CD), Hardy 699 (PRE); Klipbok (–CD), Bruyns 4648 ().

2917: Umdaus (–BA), Herre sub STE 15792; 15793 (STE); Hardy 646 (PRE); Uranoep (–BB), Hall 613 (NBG); Smithers s.n. (BOL); Smithers sub BOL 21725 (BOL); 29 km N Steinkopf (–BB), Hardy 3914 (PRE).

Without precise locality: Steinkopf, Meyer sub STE 9041 (STE); near Violsdrift, Archer 572 (BOL); Nosabis, near Violsdrift, Galpin (BOL); north part of Richtersveld, Pillans 5781 (BOL).

Lavrana perlata is found on both sides of the Orange River from near Goodhouse to near Sendelingsdrift and north of this in the mountains east of Rosh Pinah. It reaches its southernmost station in the dry valley of the Wyepoort River a little north of Steinkopf. It is found apparently entirely isolated from the main body of its distribution in the Klinghardt Mountains in the coastal Namib Desert about 100 km south of Lüderitz (Fig. 48).

Although some plants of L. perlata may be small, stems of this species may reach a

length of 300 mm. Plants consisting of 3 to 10 such stems form quite an impressive shrublet. Specimens of this size have been seen in several places: especially around Hellskloof, the lower slopes of the Rosyntjie Mountain and east of Eksteenfontein. They grow fully in the open, often wedged between rocks or growing out of a small crevice in an outcrop of rock.

The flowers of Lavrana perлата are remarkably variable in colour. They may be a uniform greyish-yellow, almost cream to grey-pink to more or less densely spotted with red. In spotted flowers the spots are often missing on a line down the middle of each lobe and on the 'annulus'. Occasionally ± uniformly deep maroon-red flowers are found. They are also variable in size and plants bearing flowers only 5 mm across are encountered (usually 7-10 mm). However, despite the variability they have a very distinctive shape and indumentum. The corolla lobes are always convex, with the margins folded back and the limb recurved, usually very strongly so as to form a fold around the mouth of the tube which gives rise to the apparent annulus: unlike in the annulus of Hoodia pilifera, for example, there is no thickening of the tissue at the mouth of the tube. Under the microscope the surface of the corolla is found to be covered with papillae each of which is tipped by a cylindrical bristle which is rounded at both the front and the rear and lies ± horizontally on top of the papilla facing the perimeter of the flower. The corona is also somewhat variable in shape, especially in the extent to which the outer lobes are bifid. It always seems to be yellow, densely and irregularly spotted with red or maroon.

In L. perлата the flowers arise in larger clusters than in the other species. The 'peduncular patches' from which they develop may become very large indeed (10 mm or more in diameter) and often will have one or more knobbly, scarred 'peduncles' projecting for up to 3 or 4 mm from it. More than one flower will often develop concurrently on each

patch. This is not known in any of the other species.

Huber (1967) was the first to advocate some of the synonymy above by recommending that Trichocaulon kubusense be sunk under T.perlatum. Cole (1984) went much further and his synonymy is followed here. The various different species described appear to be no more than colour variants of a single rather variable species.

No material of Dinter 4734 seems to have been preserved. Figure 1094 in White & Sloane (1937) was taken by Dinter of a plant from the same area as the type collection and may well be of this collection so is designated as lectotype.

EXCLUDED SPECIES

Trichocaulon columnare Nel = Notechidnopsis columnaris (Nel) Lavranos & Bleck

Trichocaulon decaryi Choux = Stapelianthus pilosus Lavranos & Hardy

Trichocaulon somaliense Guillaumin = Echidnopsis scutellata subsp. planiflora (Bally)

Bruyns.

INSUFFICIENTLY KNOWN SPECIES

1. Trichocaulon clavatum (Willd.) Druce in Rep. Bot. Soc. Exch. Club Brit. Isles: 651 (1917). Huber in Mitteil. Bot. Staatss. München 4: 35 (1961). Stapelia clavata Willdenow, Sp. pl. 1: 1295 (1798). – White & Sloane, Stap. 3: 1032 (1937).

Stapelia Paterson, Narr. journ. Hottentot.: figure opposite page 60 (1789). Type: no material appears to have been preserved and the cited figure of Paterson is here designated the lectotype.

Willdenow based the diagnosis of this name on William Paterson's Stapelia,

collected in September 1778 in Namaqualand on Paterson's second journey. Paterson's figure is of a fruiting plant and, as White & Sloane point out, it is not possible to identify this accurately with any known species.

N.E. Brown (1909, p.895) seems to have had information that Paterson found his plant at Geselskapbank. I have been unable to verify this. If this were true then his assumption that Paterson had collected what later came to be called Trichocaulon cactiforme is correct.

2. Trichocaulon sociarum White & Sloane, Stap. 3: 1175 (1937). Leachia sociarum (White & Sloane) Plowes in *Asklepios* 56: 14 (1992) as "sociara". Type: Namibia, on the Brandberg, Triebner 1717A (no material preserved). Lectotype designated here: Figure 1224 of White & Sloane (1937).

The figure in White & Sloane selected here as the lectotype shows the pale yellow inner corona lobes with dark (red-brown) margins quite clearly. These lobes are incumbent on the anthers and just seem to meet in the centre. The corolla also appears to be papillate inside, although White & Sloane do not mention this in their description. The flowers resemble those of L.cactiformis quite strongly, despite their peculiar colouration. However, L.cactiformis is not known from Namibia and it may be that the origin given for this plant is erroneous. No plants like this have been recorded again from the Brandberg.

PUTATIVE INTERSPECIFIC HYBRIDS

Hoodia gordonii X H.pedicellata Giess in *Dinteria* 10: 35 (1974).

2214: Palmenhorst (-DB), Giess 11630 (WIND, PRE, M).

This hybrid was described and figured in detail by Giess. The single known plant

was discovered by Mr H. Bachran on his farm and it was observed to bear many seed pods so appears to be fertile. In habit this plant bears more resemblance to H.gordonii.

Hoodia gordonii X H.flava Bruyns in Nat. Cact. Succ. J. 35: 102–6 (1980).

3120: Stuurmans (–AC), Bruyns 1123 (NBG, PRE).

This hybrid was observed in 1975 and 1976 and several plants were found. Recent searches (1989) at the locality, however, have failed to find it at all. Cuttings brought into cultivation produced plenty of seed and these were found to be back crosses mostly with H.flava, one of the parents. Although thicker–stemmed than H.gordonii at this locality, vegetatively the hybrid bears more resemblance to it than to H.flava.

PUTATIVE INTERGENERIC HYBRIDS

Hoodia gordonii X Orbeopsis lutea subsp. vaga (N.E. Br.) Leach

Hoodiopsis triebneri Lückhoff in S. African Gard. & Country Life 23: 231 (1933). – White

& Sloane, Stap. 3: 1092 (1937). – Lückhoff, Stap.: plate 5 (1952). – Huber in

Prodr. Fl. SWA 114: 37 (1967). – Plowes in Excelsa 10: 15 (1982). Type:

Namibia, Triebner sub herb. Lückhoff 183 (no specimen preserved). Lectotype:

Figure by Lückhoff in S. African Gard. & Country Life 23 (1933), designated here.

Hoodiopsis triebneri var. ciliata Lückhoff in White & Sloane, Stap. 3: 1094 (1937) et in

Stap.: 272 (1952). Type: Namibia, Triebner (no material preserved).

Material examined

Namibia

2718: Narudas (–BD), Bruyns 3542 (BOL).

South Africa

2918: W of Pofadder (-BB), Bruyns 5230 (BOL).

According to White & Sloane (1937 p. 1093), this hybrid was gathered several times by William Triebner. However, as is usual with Triebner collections, no precise localities were given. Huber (1967) suspected it of being a garden hybrid involving a Hoodia. Plowes (1982) suggested a possible parentage for it and mentions that it was 'apparently collected SE of Warmbad' where both putative parents are plentiful.

A single plant was found in flower in January 1989 on the eastern side of the Great Karas Mountains. On the same farm a very large selection of stapeliads was observed: Hoodia gordonii, H. juttae, H. flava, Lavrana picta, Orbeopsis lutea, O. albocastanea, Stapelia schinzii, S. flavopurpurea, S. pearsonii, Huernia hallii, H. zebrina, Caralluma lugardii and Orbea rangeana. Despite this confusing array of species, it would appear that H. gordonii and Orbeopsis lutea were the parents. A further plant was collected more recently west of Pofadder. Here again there was a large selection of stapeliads —12 species were found — among which were the putative parents.

Although the plants bear sharp spines on the tubercles, they are relatively short-stemmed (<200 mm tall) and the stems are pale green with reddish-purple mottling. They root readily on the side branches forming clumps to 400 mm in diameter. The tubercles on the stems are arranged into 6–8 regular rows. Several large brick-red flowers with slight yellowish mottling and rugulose inner surface were open at once on one peduncle on the Namibian specimen.

Hoodia gordonii X Stapelia arenosa Lückhoff

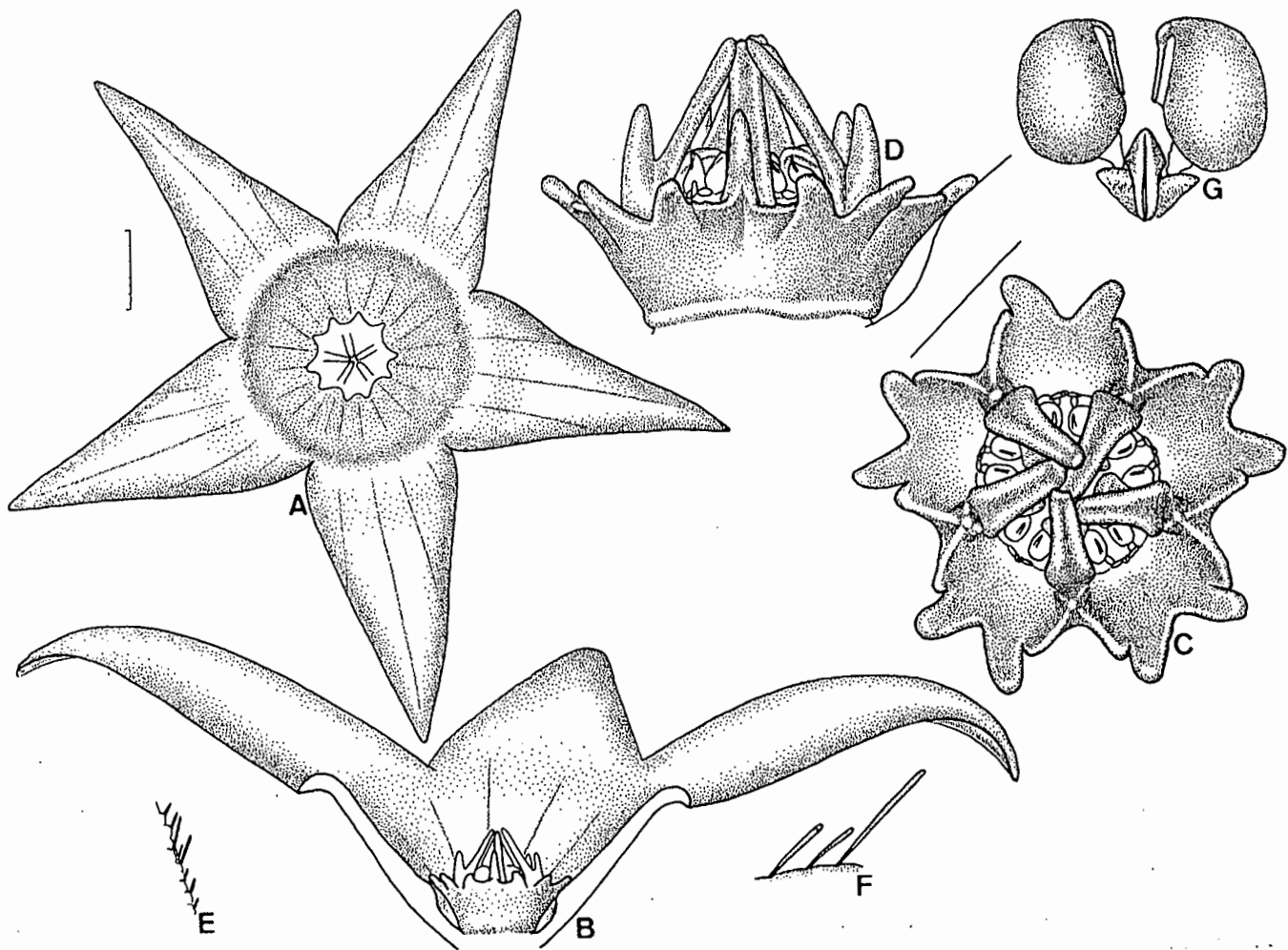


Figure 57
 1. Hoodia
 2. Tridentea
 3. Pollinia

Figure 57.—*Hoodia officinalis* subsp. *delaetiana* X *Tridentea ruschiana*. A, face view of flower. B, side view of dissected flower. C, face view of gynostegium. D, side view of gynostegium. E, papillae on face of corolla around mouth of tube (i.e. at level of ends of outer corona lobes). F, clavate (later flat) cilia scattered along margin of corolla lobes. G, pollinarium.

All drawn from Hammer, Klinghardtgebirge (BOL).

Scale bar: A, 5 mm; B, 3 mm; C, D, 1 mm; E, F, 0.5 mm; G, 0.25 mm

(all at A).

Lueckhoffia beukmanii (Lückhoff) White & Sloane in S. African Gard. & Country Life 25: 37 (1935) et in Stap., 3: 1097 (1937) 'Lueckhoffia'. – Lückhoff, Stap.: 275 (1952).
Stapelia beukmanii Lückhoff in S. African Gard. & Country Life 24: 101 (1934) non Lückhoff in ibid. 25: 96 (1935). Type: South Africa, Cape, near Doringbos, Beukman sub herb. Lückhoff 191 (BOL).

Material examined

Clanwilliam district, Leipoldt 4426 (BOL).

C. Beukman originally found several plants in 1933. A single flower was deposited by Dr J. Lückhoff at BOL which was produced in their garden in April 1935. Since Lückhoff does not seem to have re-collected it in the field it is assumed that this was from one of Beukman's plants and therefore can be taken as the holotype. Its probable hybrid origin seems to be quite clear and was known to Dr J. Lückhoff and his son Carl. Leipoldt's collection seems to be the only other one ever made.

It should be noted that many of the plants in cultivation under this name are not actually this hybrid.

Hoodia officinalis subsp. delaetianum X Tridentea ruschiana (Dinter) Leach. Barad & Lavranos in Madoqua 2: 163–5 (1978). Figure 57.

The collection cited in this article is 2715: Klinghardt Mtns (–B), Lavranos & Barad 15451 but no material appears to have been preserved.

REFERENCES

ALBERS, F. et al. 1989. Lebensformen der Ceropegieae und Stapelieae in ariden Zonen

- Afrikas. Beitr. Biol. Pflanzen 64: 59–74.
- Albers, F. & Sylla, T. 1989. Samenentwicklung und Samenmorphologie krautiger und sukkulenter Asclepiadaceae. Bot. Jahrb. Syst. 110: 479–492.
- BAYER, M.B. 1984. The Cape Flora & Karoo – A winter rainfall Biome versus Fynbos Biome. Veld & Flora 70: 17–19.
- BROWN, N.E. 1878. Stapelieae of Thunberg's Herbarium. J. Linn. Soc. (Bot.) 17: 162–172.
- . 1890. Stapelieae Barklyanae. Hooker's Icon. Pl. 20.
- . 1903. Asclepiadaceae in Th.–Dyer, Fl. trop. Africa 4 (1).
- . 1909. Asclepiadaceae in Th.–Dyer, Fl. cap. 4 (1).
- BRUYNS, P.V. 1983. Resurrection of Quaqua N.E. Br. Bradleya 1: 33–78.
- . 1988. A revision of the genus Echidnopsis. Bradleya 6: 1–48.
- . 1989. Caralluma staintonii Hara. Bradleya 7: 63–68.
- . 1990. A review of Pseudolithos. Bradleya 8: 33–37.
- & LINDER, H.P. 1991. A revision of Microlooma. Bot. Jahrb. Syst. 112: 453–527.
- COLE, D.T. 1979. Preliminary thoughts on some Trichocaulons. Aloe 17: 67–74.
- . 1984. Trichocaulon – The smooth-stemmed species. Asklepios 31: 73–83.
- DAVIS, P.H. & HEYWOOD, V. 1965. Principles of Angiosperm taxonomy. Oliver & Boyd, Edinburgh.
- DINTER, M. K. 1914. Neue und wenig bekannte Pflanzen D.–SWAs. Okahandja.
- . 1921. Botanische Reisen. Feddes Rep. sp. nov. Beih. Band 3.
- . 1923. Sukkulenteuforschung I. ibid. Beih. Band 23.
- . 1928. Sukkulenteuforschung II. ibid. Beih. Band 53.
- DU RIETZ, F. 1930. The fundamental units in Taxonomy. Svensk Bot. Tidskr. 29: 333.
- FARR, E.R. et al. (edit.) 1979. Index Nominum Genericorum (Plantarum).
- GREUTER, W. et al. 1988. International Code of Botanical Nomenclature. Junk, The Hague.
- GUNN, M. & CODD, L.E. 1981. Botanical Exploration in southern Africa. Govt. Printer, Pretoria.

- HEDBERG, O. 1958. *The taxonomic treatment of vicarious taxa. Systematics of today. Uppsala Univ. Årsskr. 6: 193.*
- HIERN, W. P. 1898. *Catalogue of the African Plants collected by Dr F. Welwitsch. 1 (3).*
British Museum, London.
- HOFMANN, U. & SPECHT, A. K. 1986. *Der morphologische Charakter der Asclepiadaceencorona. Beitr. Biol. Pflanzen 61: 79–85.*
- HOOKER, W. J. 1844. *Scytanthus currorii*. In *Icon. Pl. 7: t. 605–6.*
- HUBER, H. 1967. *Asclepiadaceae* in H. Merxmüller, *Prodr. Fl. SWA.*
- KUNZE, H. 1982. *Morphogenese und Synorganisation des Bestäubungsapparates einiger Asclepiadaceen. Beitr. Biol. Pflanzen 56: 133–170.*
- . 1990. *Morphology and Evolution of the Corona in Asclepiadaceae and related families. Trop. u. subtr. Pflanzenw. 76.*
- KUSCH, G. 1985. *Morphologische Studien an Arten des Verwandtschaftskreises Stapelia sowie einiger verwandter Gattungen von extrem trockenen Standorten.*
Unpublished Diploma Thesis, Wilhelms-Universität, Münster.
- LIEDE, S. & KUNZE, H. *A descriptive system for corona analysis in Asclepiadaceae and Periplocaceae. Preprint.*
- MENDONSSA, F. A. 1937. *Conspectus Florae Angolensis 1 (1).*
- MEVE, U. & ALBERS, F. 1990. *Die Stipularrudimente der Stapelieae. Beitr. Biol. Pflanzen 65: 99–107.*
- PLOWES, D.C.H. 1982. *The stapeliads of South West Africa/Namibia. Excelsa 10: 5–26.*
- . 1990. *An introduction to stapeliad genera. Cact. Succ. J. (US) 62: 111–129.*
- . 1992. *A preliminary re-assessment of the genera Hoodia and Trichocaulon. Asklepios 56: 5–15.*
- SCHILL, R., BARTHLOTT, W. & EHLER, N. 1973. *Mikromorphologie der*

- Cactaceen—Dornen. Trop. subtrop. Pflanzenwelt 6.
- SPEARING, J.K. 1989. A contribution to the study of Stapeliad seedling morphology I. Asklepios 46: 65–70.
- . 1990. ibid. II. Asklepios 49: 63–72.
- TAYLOR, N.P. 1985. The genus Echinocereus. Collingridge, Middlesex.
- WERTEL, H.P. 1974. Bau und Stellung der Infloreszenzen bei einiger Stapelieen—Gattungen. Trop. u. subtr. Pflanzenw. 17.
- WHITE, A. & SLOANE, B.L. 1937. The Stapelieae 3. Abbey San Encino Press, California.
- WILEY, E.O. 1981. *Phylogenetics. The theory and practice of phylogenetic systematics.* John Wiley & sons. New York.

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