SYSTEMATICS OF PSILOCAULON N. E. BR.

(AIZOACEAE)

by

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SUBMITTED IN FULFILMENT FOR THE DEGREE OF
MASTERS OF SCIENCE

UNIVERSITY OF CAPE TOWN
DEPARTMENT OF BOTANY
OCTOBER 1996

ACKNOWLEDGEMENTS

I would like to thank my supervisor, Prof. H.P. LINDER, for his advice during the preparation of this project. Further I would like to thank Dr. P.V. BRUYNS, Dr. S. PIERCE, Drs. M. & M. GERBAULET and Mr. G.A. VERBOOM for many valuable discussions.

The curators of the following herbaria are being thanked for loan or use of material: B, BM, BOL, COI, GRA, HBG, K, KMG, M, MEL, NMB, P, PRE, S, SAM, STE, UPS, WIND. Dr. Moberg of UPS is thanked especially for having made photographs of the type of *Psilocaulon articulatum*.

Financial support during the course of this thesis had been granted by the University of Cape Town and the Foundation for Research Development.

Additional travel grants were received from the American Cactus and Succulent Society and the Mesemb Study Group. All of them I would like to thank.

CONTENTS

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ABSTRACT

On the basis of herbarium, living and pickled material the morphology and systematics of *Psilocaulon* N. E. Brown *sensu* Ihlenfeldt & Bittrich is investigated. Thirteen species (including one insufficiently known species) are recognized: *P. articulatum*, *P. bicorne*, *P. coriarium*, *P. dimorphum*, *P. dinteri*, *P. foliosum*, *P. gessertianum*, *P. granulicaule*, *P. junceum*, *P. leptarthron*, *P. parviflorum*, *P. salicornioides*, *P. subnodosum*. Species of *Mesembryanthemum*, *Prenia*, *Brownanthus*, *Aspazoma* and *Aptenia* are used as outgroups in a cladistic analysis of *Psilocaulon*. The monophyly of *Psilocaulon* is demonstrated. As a result *P. rapaceum* Jacq. is excluded and transferred to *Caulipsolon* Klak *gen. nov.* The position of *Psilocaulon* and the monotypic genus *Caulipsolon* within the subfamily Mesembryanthemoideae is discussed. However, relationships of *Psilocaulon* and *Caulipsolon* to other genera remain obscure, since no synapomorphies were found to indicate sister relationships. More sampling among outgroups and/or a future molecular study may help to elucidate relationships among the genera of the Mesembryanthemoideae. Geographical distribution patterns for all species and the number of species per half-degree grid square are given. It is discussed how species diversity and geographical distribution in *Psilocaulon* contrasts with or corroborates existing ideas of centres of diversity and distribution patterns in the Mesembryanthema. Each species is described in detail. A description of the genera *Psilocaulon* and *Caulipsolon* is given and a key to the species is provided. Material examined is cited and full synonomy is given.

A. INTRODUCTION

Psilocaulon N.E. Br. is a group of succulent plants in the family Aizoaceae which has its natural distribution in the south-western parts of Southern Africa.

Psilocaulon consists of perennial plants forming erect, much branched shrubs with short-lived leaves, which fall off during dry periods and 4- or 5-locular capsule with valve wings. Whereas most genera in the family are leaf succulents, psilocaulons are stem succulents as well. The only other genera within the subfamily which exhibit stem succulence are *Aspazoma, Brownanthus* and *Aptenia* (GERBAULET 1995). The stems have cylindrical internodes and mostly small whitish, pink, puce or rarely yellow flowers (JACOBSEN 1974).

Based on its central placentation and fruit morphology, the genus is placed in the subfamily Mesembryanthemoideae Ihlenf., Schwantes & Straka (Aizoaceae). Of the five subfamilies currently included in the Aizoaceae, the Mesembryanthemoideae and Ruschioideae form a monophyletic group (BITTRICH & HARTMANN 1988). This group has been referred to by many authors as the Mesembryanthemaceae and controversy still exists as to the level at which it should be recognized. Due to this uncertainty and for convenience, HARTMANN (1991) adopted the term "Mesembryanthema" (a term without taxonomic rank) for the group and this is followed here.

Psilocaulon s.l. (incl. *Brownanthus*) and *Amoebophyllum* N.E. Brown were formerly placed in the Brownanthinae Schwantes or Psilocaulinae Jacobsen respectively (SCHWANTES 1947, JACOBSEN 1974). IHLENFELDT & BITTRICH (1985) excluded *Amoebophyllum* from the Brownanthinae, since it showed characters typical of *Phyllobolus* (*sensu* GERBAULET 1996). However, evidence for either a close or distant relationship between *Brownanthus* and *Psilocaulon* has not yet been established (IHLENFELDT & BITTRICH 1985, BITTRICH 1986).

The genus was established by N.E. BROWN in 1925 with a short diagnosis. Soon afterwards BROWN published a short description of the genus in PHILLIPS' "Genera of South African Flowering Plants" (1926a), as well as in BURTT DAVY'S "Flowering Plants and Ferns" (1926b). The species making up the new genus *Psilocaulon* were those that had been placed by HAWORTH (1821) under *Mesembryanthemum* sect. *Juncea*. FRIEDRICH (1970) was the first to give a taxonomic account of *Psilocaulon s.l.* (incl. *Brownanthus*) in the "*Prodromus einer Flora von Südwestafrika*". However, this is a regional treatment and therefore incomplete. IHLENFELDT & BITTRICH (1985) produced the most recent account of *Psilocaulon*, in which *Brownanthus* Schwantes was re-instated and three other species of uncertain affinities were excluded. Although the authors succeeded in delimiting the genus more closely, they did not show that the species remaining in *Psilocaulon* form a monophyletic group. This is true also for a later treatment of the whole subfamily (BITTRICH 1986).

The type of the genus is *Psilocaulon articulatum* (Thunb.) N.E. Brown. *P. articulatum* was collected by THUNBERG in the south-western Cape and was described in 1791. In the most recent comprehensive account of accepted names, the "Lexicon of Succulent Plants", JACOBSEN (1977) lists 70 species (including *Brownanthus*) under *Psilocaulon*, an astonishingly large number of names. A large proportion of these "species" had been described by L. BOLUS. The characters on which she distinguished them include flower colour, morphology and size, length of internodes, shape and length of leaves and the height of the plant. However, she did not produce a comprehensive taxonomic treatment for this group, as her aim was to document the variability of the species by describing whatever deviant elements she was presented with. In this manner she hoped to lay the basis for critical taxonomic treatments. This, and a pronounced tendency towards polymorphism in the Mesembryanthema (IHLENFELDT 1994), has resulted in a vast proliferation of names and an overdescription of so-called "species" in the group as a whole. So, for example, in *Conophytum*, ± 450 names were reduced to 84 species (HAMMER 1993) and in *Conicosia* ± 20 names were reduced to one species (IHLENFELDT & GERBAULET 1990). These newer treatments, with their much reduced numbers of species, are based on extensive field work. This is particularly important when dealing with xerophytic taxa where many characters are far more variable than previously suspected (BRUYNS & LINDER 1991). Field work, using population samples, is therefore essential to establish the extent of the variability of characters and especially to detect that variability which is a consequence of environmental influences. Herbarium material is often inadequate for these decisions. Furthermore, in the case of poorly collected species, gaps in character variation may prove to be the result of undercollecting.

The conservation and management of the arid Karoo region of southern Africa has been problematic (e.g. HALL *et al.* 1980, ROUX & VORSTER 1986a, HOFFMAN & COWLING 1987). The area has been heavily grazed during historical times and the impact of this on the vegetation is still poorly understood (e.g. ACOCKS 1964, ROUX & VORSTER 1983b, COWLING 1986). In addition, in recent years, many questions regarding biodiversity of the world flora and its management have been raised. However, such questions can only be answered adequately once a sound taxonomic basis has been established for the flora.

This study aims to investigate as broad a range of non-molecular characters as possible within *Psilocaulon* (as delimited by IHLENFELDT & BITTRICH 1985) to establish the limits of the species and to produce a workable taxonomy. The characters commonly used in the existing descriptions are re-evaluated for the purposes of this study.

B. MATERIALS AND METHODS

1. MATERIALS

The study is based on 165 collections of living plants made during numerous fieldtrips in South Africa (1995-1996) and one trip to Namibia (August 1995). Flowers, buds and portions of young and old stems were fixed in FAA [solution of 70% EtOH, formalin, glacial acetic acid, 8.5:1:0.5 by volume). Living material was cultivated in Cape Town in the open along a north-facing wall. The plants were potted in soil taken from their habitats.

In addition, 1000 dried collections from the herbaria: B, BM, BOL, COI, GRA, HBG, K, KMG, M, MEL, NMB, P, PRE, S, SAM, STE, UPS, WIND were investigated. Original drawings kept at BOL were also consulted.

Photographs of living plants and their habitat were taken with a Nikon FM2, using Fujichrome 100 ASA film.

2. METHODS

2.1. Anatomy

The internodal region of young stems was used for the anatomical investigations, since older stems often proved difficult to section due to the increased hardening of the central cylinder. Similarly, the middle region of mature leaves was used. The material was dehydrated in a Sakura tissue processor by agitating the material in two baths each of 70%, 80%, 96%, 100% ethanol N-propanol and N-butanol for 8 hours. Thereafter it was placed in a wax bath and left for 12 hours to allow the wax to penetrate adequately. The material was then imbedded in wax and the wax blocks cooled, trimmed and serially sectioned on a Leitz Wetzlar rotary microtome to a thickness of 10 microns. Sections were placed on microscope slides which had been treated with Haupt's adhesive. The best results were obtained when the sections were first placed in a water bath (30-35° C) to stretch them in order to remove any "crinkles", after which they were placed onto the slide.

The sections were passed through a staining sequence (JOHANSEN 1940): xylene (2 baths, 5 minutes each), 2-methoxy-ethanol (1-2 minutes), 96% ethanol (2 baths, 2 minutes each), safranin (30 minutes), distilled water (brief rinse), 2-methoxy-ethanol (1-2 minutes), fast green (brief rinse), clove oil rinse [clove oil: 100% ethanol: xylene, 2:1:1 by volume] (2-3 minutes), 96% ethanol (2 baths, 2-5 minutes each), N-butanol (2 baths, 1-2 minutes each), and xylene (2 baths, 5 minutes each). The slides were mounted with DPX and covered with a cover slip.

Slides were viewed with a Zeiss standard 25 light microscope using bright field optics and photographs were taken on a Zeiss Axioskop, using PAN F 50 film.

2.2. Cytology

Fifty seeds per species were germinated on wet filter paper without pre-treatment and were checked for emerging roots for three weeks. As most seeds proved to be recalcitrant, the seed coat was slit with a razor blade to enhance water uptake. The root tips of freshly germinated seedlings were pre-treated in α-Bromonaphthalene (1 drop in 30mls) for 1.5 h at room temperature and then fixed overnight in a freshly prepared solution of absolute alcohol, chloroform and glacial acetic acid (6:3:1) at 6° C. The best results were obtained with seedlings that were fixed at ca. 7 am or 6 pm. The chromosomes were stained with carmine: the root tips were left in the stain overnight and then rinsed in water (SNOW 1963). Squashes were then prepared as usual but 45% glacial acetic acid was used as the mounting medium instead of aceto-carmine. This method proved to be far superior to the more commonly used method of DARLINGTON & LA COUR (1960), whereby the chromosomes were stained for only 1-2 min in aceto-carmine with a small amount of iron added at the time of teasing with steel needles.

Counts were made for at least 4, usually 6 to 8 metaphase plates from at least 2, usually 4 to 5 root tips per collection. All collections are deposited at BOL.

The slides were viewed under a Zeiss Axioskop using differential interference optics (DIC).

2.3. Electron Microscopy

The surfaces of leaves, stems, seeds, pollen and nectaries were investigated with a Scanning Electron Microscope. Leaves and stems were prepared for investigation by placing them in chloroform for about 15-20 minutes to remove the wax layer. Thereafter they were dehydrated in a - 50%, 70%, 80%, 90%, 96%, 100% ethanol series, with the specimens left in each solution for 8 hrs. They were then critical-point dried using carbon dioxide as the exchange medium. Seeds were investigated both by conventional means and under the SEM. Pre-treatment of seeds and pollen for removal of any deposits was found to be unnecessary. All samples were sputter-coated with a ca. 25 nm layer of AuPd and examined with a Cambridge S 200 Microscope at 5 - 10 kV.

2.4. Definitions of measurements

At least five individuals or three objects per individual were examined for every measurement or count, where possible selected so as to cover the variation within the taxon. Measurements were made with a ruler under a Zeiss dissecting microscope (x10).

Leaves. Measurements of leaves were made from herbarium material. The length was measured along the longitudinal axes of the leaf and the width measured at its broadest point. Apart from obviously juvenile leaves, selection was random.

Flowers. Diameters of the fully opened flowers were measured.

Fruits. The capsule was divided into two parts: (1) the upper part, which is defined here as that lying between the tip of the columella and the tips of the valves and (2) the lower part which is that between the tip of columella and the inner base of the locules. In order to obtain measurements of these the capsules needed to be cut in half longitudinally (Fig. 1B). The definition of the lower part was chosen since the distinction between the base of the capsule and the apex of the pedicel is often not clear.
To compare taxa with capsules of different sizes, ratios of upper to lower parts were calculated.

Seeds. The length of the seeds was measured along their longest axes.

Graphic displays of available measurements and counts were generated using Statgraphics 6.0.

2.5. Taxonomic concepts

Species delimitations can be made on process data (breeding barriers e.g. MAYR 1970, or pollinators e.g. JOHNSON 1996) or on pattern data (e.g. variation in morphology). However, processes, such as absence of gene flow (which is used to delimit species in the biological species concept) are difficult to test. As it was not possible to gather process data for such a widely dispersed group and as there was no earlier hypothesis of species to be tested, pattern data were used in this thesis. Furthermore a pattern-based species concept makes no assumptions about how evolution has occurred. Therefore processes of speciation may in turn be tested against a proposed phylogeny.

Pattern concepts can be grouped into phenetic and phylogenetic concepts. In this thesis a phylogenetic concept was used, as the data are largely not population samples, but

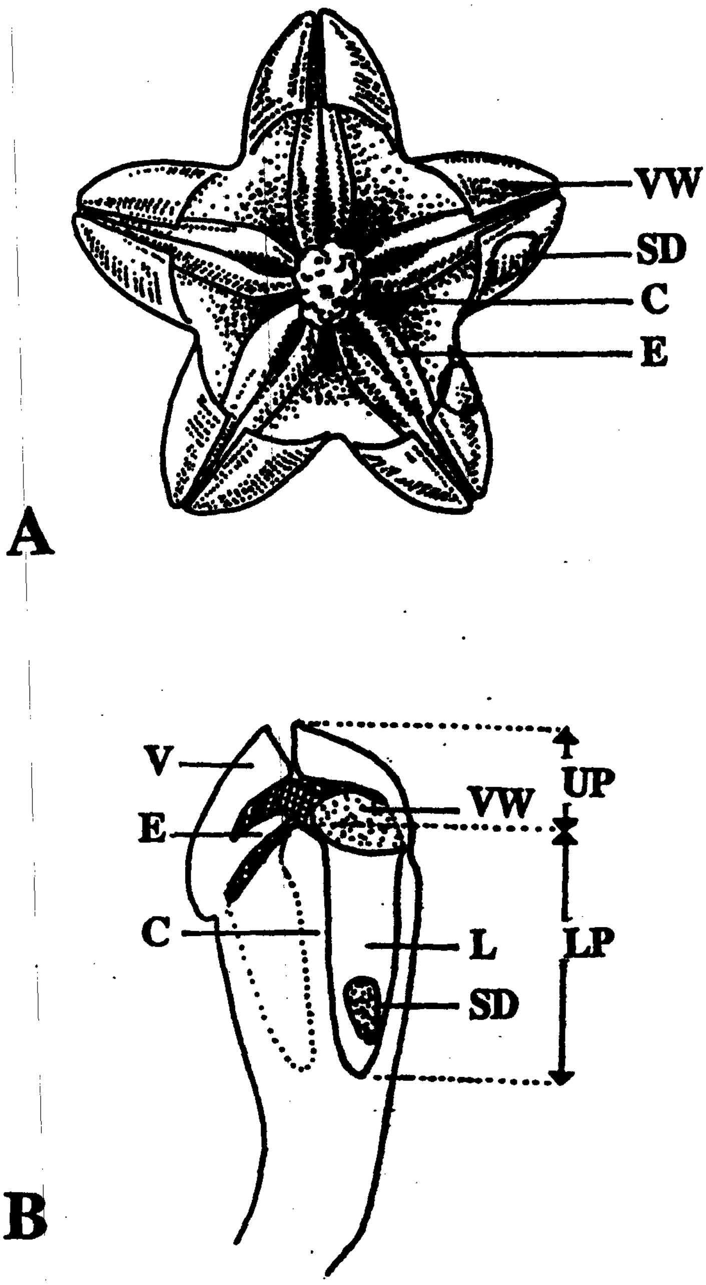

Fig. 1. A. Diagrammatic top view of open capsule of *Psilocaulon*. Fruit with valve wings, with seeds trapped behind them. B. Diagrammatic longitudinal section through closed capsule of *Psilocaulon*. Locules deep with upper part of capsule shorter than lower part. C = columella; E = expanding keels; L = locules; LP = lower capsule part; SD = seed; UP = upper capsule part; V = valves; VW = valve wings.

specimens and it would be too time consuming to score up all the data.

Phylogenetic species concepts either belong to the autapomorphic type (e.g. ROSEN 1979, DE QUEIROZ & DONOGHUE 1988, 1990 and amplified by BAUM & SHAW 1995) or the minimal diagnosable. The latter concept is based on the ideas of NELSON & PLATNICK (1981) and was enlarged by CRACRAFT (1983), NIXON & WHEELER (1990) and DAVIS & NIXON (1992). This latter concept was used as it accounts for all the specimens, while the autapomorphic-based concept cannot account for basal unresolved taxa (metataxa) without complicating the taxonomy. At higher (e.g. genus) level, monophyly is considered a prerequisite for justification of taxonomic rank. In this thesis the concept of monophyly follows HENNIG's (1966) original definition.

The minimal diagnosable species concept is similar to the morphological or taxonomic species concept, in that it finds those characters which are constant within populations, but which can be used to distinguish the species. Thus, in practise, the smallest units with constant character states were sought and assigned species status.

In addition, so as to produce a workable taxonomy only characters that were "easily" recognizable, i.e. visible with no more than a 10x magnification lens were used to delimit species.

2.6. Phylogeny

2.6.1. Characters

The character states in this study were discerned by finding one or more distinct discontinuities in the character values when comparing all species in the genus and/or outgroups. A discontinuity for measurement data is a gap in the ranges of values for a character (cf. STEVENS 1991). Thus they represent essentially qualitative characters. Various methods of transforming more or less continuous characters into character states have been proposed (e.g. BAUM 1988, CHAPPILL 1989, THIELE 1993). However, such methods involve the risk of "false gaps" being used in the delimitation of character states. In this way, continuous characters prevent the discovery of a hierarchical pattern among species ultimately leading to a "false phylogeny". Therefore only measurement characters with clear gaps were included in the analysis.

Autapomorphies, i.e. characters that are not shared by any of the ingroup taxa, are uninformative in terms of ingroup relationships and result in an artificially inflated consistency index (BROOKS *et al.* 1986), suggesting their exclusion from an analysis (CARPENTER 1988). An advantage of including autapomorphies in a data matrix is that they indicate the monophyly of a species (e.g. LINDER 1995, CRISP & CHANDLER 1996), which may enable future workers to assess the support for the ingroup terminals (cf. YEATS 1992). Thus autapomorphies were included in the data matrix, but excluded for the calculation of the statistics (i.e. length of the trees and consistency index).

2.6.2. Choice of outgroup

To date no cladistic analysis has been done in the subfamily Mesembryanthemoideae, consequently the sister-taxa to *Psilocaulon*, which could act as outgroups, are not known. BITTRICH (1986) was uncertain of the position of *Psilocaulon* and placed it between *Brownanthus* and *Mesembryanthemum* subg. *Mesembryanthemum*. GERBAULET (1995) considered the succulent green cortex to be a synapomorphy uniting the genera *Aptenia*, *Aspazoma*, *Brownanthus* (including *Pseudobrownanthus*) and *Psilocaulon*. In the absence of a rigorous cladistic analysis, two to three species from each of these four genera were taken as outgroups in order to establish the position of *Psilocaulon*. In addition, two species of *Prenia* were included. This was necessitated by the very uncertain position of *C. rapaceum*, which in many ways bears a superficial resemblance to some species of *Prenia*. Thus the outgroup consists of the following species: *Mesembryanthemum aitonis* Jacq., *Mesembryanthemum longistylum* DC, *Mesembryanthemum stenandrum* (L. Bolus) L. Bolus, *Prenia pallens* (Aiton) N.E. Br. ssp. *pallens*, *Prenia tetragona* (Thunb.) GERBAULET, *Aptenia geniculiflora* (L.) BITTRICH *ex* GERBAULET, *Aptenia cordifolia* (L. f.), *Aptenia lancifolia* L. Bolus, *Aspazoma amplectens* (L. Bolus) N.E. Br., *Brownanthus arenosus* (Schinz) Ihlenfeldt & Bittrich and *Brownanthus marlothii* (Pax) Schwantes. Live and/or herbarium material was studied for all species. In addition, information concerning the delimitiation of the outgroup genera was extracted from the literature (HERRE 1971, IHLENFELDT & BITTRICH 1985, BITTRICH 1986, GERBAULET 1995, 1996). The sampling and choice of outgroups thus agrees with NIXON & CARPENTER (1993), who emphasize that although only one outgroup is necessary, a more complete sampling of related taxa may increase the expectation of greater stability in future. In addition, outgroups were non-constrained, but treated as all other terminals in order to test the monophyly of the ingroup (NIXON & CARPENTER 1993, originating from FARRIS 1972). *Mesembryanthemum longistylum* was selected to root the outgroups.

2.6.3. Cladistic analysis

Computer programmes of FARRIS (1988), HENNIG86 (options mh*; bb*; ie*) and SWOFFORD (1993), PAUP vers. 3.1 (options swap = global, mulpars), were used to search for the most parsimonious trees. A strict consensus tree was derived from the set of trees of minimal length. In a strict consensus tree only those nodes that are present in all members of the set of most parsimonious trees are retained.

Thirty four morphological characters were assessed.

Characters and character states used in the character matrix are presented in Table 1 and 2 and are briefly discussed (where not self-explanatory) with reference to variation and intermediate states. Variable characters and missing data were coded as "?".

Table 1. Characters used for the cladistic analysis of *Psilocaulon* and the five outgroups, with comments on their definitions and variations. "?" = polymorphic, non-applicable or missing; for characters used to delimit genera of the outgroups the author(s) is(are) given in brackets. Autapomorphies are characters 1, 18. Characters 19, 31 are treated as ordered, all remaining characters are unordered. Additional information for the outgroups was extracted from IHLENFELDT & BITTRICH 1985, BITTRICH 1986 and HERRE 1971.

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1 **Geophytes (0) chamaephytes (1)**

2 **Habit prostrate (0) decumbent - erect (1)**
There were many intermediates between species with a decumbent and/or an erect habit. These have coded as "decumbent - erect". Species (e.g. *P. dinteri*) that were found to have either a prostrate or a decumbent-erect growth form were coded as variable "?".

3 **Persistent green cortex absent (0) present (1)**
Plants with a persistent green cortex shed most of their leaves during the dry season and the stem takes over photosynthesis. In some cases such as *B. marlothii* the leaves remain dried up on the stems. *C. rapaceum*, which has only annual shoots this character is non-applicable.

4 **Stems with no horizontal furrow (0) with furrow (1) between internodes**
No intermediates are present. However, this character cannot be observed in young growth, since it forms only as the stem matures.

5 **Idioblasts on stem protruding (0) much flattened (1)**
Most species can be assigned to one of these character states. Few species such as *P. salicornioides* or *P. dinteri* can have both and have been coded variable.

6 **Shape of idioblast hair-like (0) hexagonal to irregularly polygonal (1) dome-shaped (2)**
No variation in shape of the idioblasts has been observed and no intermediates were found.

7 **Idioblasts scattered (0) closely packed (1) very densely packed (2)**
The character states are illustrated in Fig. 5.

8 **Idioblasts not thickened (0) thickened (1)**
No variation or intermediates were found.

9 **Epidermis on stems and leaves heteromorphic (0) not heteromorphic (1)**
In *Psilocaulon* the epidermis on stems and leaves is very similar. In *Brownanthus*, *Aspazoma* and *Aptenia* the epidermis on the stems is xeromorphically modified and is therefore very different from the one found on the leaves.

10 **Mucro present (0) absent (1)**
Few species of *Psilocaulon* have a mucro on the leaves. Except in *P. articulatum* the presence or absence of a mucro is variable and often difficult to establish once the specimen has been dried. Such cases were coded variable "?".

11 **Leaves in cross section triangular (0) circular to semi-circular (1) dorsi-ventrally flattened (2)**
In *Psilocaulon* most species have cylindrical to semi-cylindrical leaves, often depending on the amount of water stored in the leaves. Dorso-ventrally flattened leaves are only found in some of the outgroup species.

12 **Central water-storing tissue in leaves distinct (0) weakly developed or absent (1)**
P. subnodosum and *P. coriarium* vary in the presence or absence of a central water-storing tissue. However, the transition between non-distinct and distinct water-storing tissue is not entirely obvious in several other species of *Psilocaulon*, since the central parenchymatic cells are usually free of chloroplasts anyhow and may well be somewhat larger than the others. These were coded as "weakly developed or absent".

13 **Flowers few to many together in a dichasium (0) solitary (1)**
In contrast to the outgroup genera this character is variable in *Psilocaulon* and *Caulipsolon*. In *P. salicornioides* which usually has many-flowered dichasia, there are also specimens with solitary flowers. *P. granulicaule*, *P. parviflorum*, *P. leptarthron* and *P. bicorne* have usually solitary flowers, but occasionally also occur with infloresences of 3-7-flowered dichasia. These cases have been coded as variable.

14 **Longer axes with single terminal flower (0) flowers several per axes, single on shorter side shoots (1)**
There is no variation or intermediates known.

15 **Sepals fused (0) free (1)**
No intermediates or variation has been observed.

16 **Sepals upright for duration of anthesis (0) bend down during anthesis (1)**

17 **Colour of flowers yellow or cream (0) pink or puce (1) white (2)**
There are several species that can have pink, puce or white flowers. These have been coded as variable.

18 **Petaloid staminodes present (0) very reduced to absent (1)**
"Very reduced petaloid staminodes" is an autapomorphy for *P. gessertianum*.

19 **Petaloid and filamentous staminodes free (0) shortly fused towards the bases (1) highly fused (2)**
No intermediates or variation within species was found. The different states are illustrated in Fig. 6.

20 **Filamentous staminodes present (0) absent (1)**
No intermediates were found.

21 **Filamentous staminodes gathered into a cone (0) not gathered (1)**
No intermediates. Fig. 6 B & C illustrate the two states.

22 **Filamentous staminodes apically finely incised and transparent (0) apically entire and not transparent (1)**
Characteristic for *Psilocaulon* are finely incised and transparent staminodes. Non-transparent filamentous staminodes with entire margins are found in the outgroups (Fig. 6). No variation within the genus has been observed.

23 **Petaloid staminodes in 1-2 rows, relatively few (0) in 3-5 rows, relatively many (1)**
Psilocaulon has characteristically few petaloid staminodes, usually in only one, rarely in 2 rows. As a consequence there are relatively few (15-40) petaloid staminodes. With respect to the number of petals there is a distinct gap between *Psilocaulon* and *Brownanthus* which forms one group and the remaining taxa forming another (Fig. 7).

24 **Epidermal cells on gynoecium irregular and papillate (0) regular and finely papillate (1)**
No variation was found within *Psilocaulon*.

25 **Styles short (0) long (1)**
The styles are classified as short when most of the stamens are longer than the styles; they are classified as long when most of the stamens are either shorter or as long as the styles.

26 **Nectaries deep (0) shallow or absent (1)**
Deep nectaries were found to be a characteristic of the *Mesembryanthemum* subg. *Mesembryanthemum* and subg. *Opophytum* (BITTRICH 1986). In *Psilocaulon* nectaries are generally very inconspicuous, so that in many cases their presence could not be ascertained. This leads to the character "shallow or absent" being coded as one character.

27 **Capsules 4-locular (0) 5-locular (1)**
In *Psilocaulon* the number of locules is a variable character. Within all species it is common to find both 4- and 5-locular capsules in one specimen, however, one number usually predominates and specimens may be classified as either 4- or 5-locular. Species which may have populations with either 4- or 5-locular capsules (e.g. *P. salicornioides*, *P. coriarium*) were coded "?".

28 **Fruits with shallow locules (0) with deep locules (1)**
This character has been expressed as the ratio of upper to lower capsule parts in order to compare capsules of different sizes (Fig. 1 B). Shallow locules are those where the lower capsule part is shorter than or as long as the upper part, whereas in deep locules the lower capsule part is longer than the upper. There is a distinct gap between *Psilocaulon*, *Prenia* and *Caulipsolon* which form one group and the remaining taxa forming another (Fig. 7 C).

29 **Valve wings of fruits reflexed and fused in pairs (0) inflexed (1)**
No intermediates or variability within species has been observed. Reflexed valve wings are illustrated in Fig. 1 A.

30 **Seed broad (0) compressed (1)**
Neotenic seeds, which are usually small, have an enlarged perisperm region, whereas larger seeds are compressed in this region. The seed of *Aspazoma* is flat on one side and swollen on the other and has therefore been coded "?".

31 **Seed colour ochre or with white perisperm region (0) brown (1) black (2)**
There are few intermediates between the three states, which were coded "?" variable.

32 **Outer walls of testa cells raised into papillae (0) flattened to smooth (1)**
The different states are shown in Fig. 8 A-C. Several intermediates were present, which were coded "?".

33 **Testa cells ordered (0) unordered (1)**
In the ordered state, testa cells are arranged in distinct rows (BITTRICH 1986), whereas in the unordered state testa cells are arranged randomly (Fig. 8 A-C). No intermediates were found.

34 **Testa fold narrow (0) broad (1).**
In *Psilocaulon* the testa fold is always narrow (Fig. 8 A-C), whereas in *Aspazoma* and in *Brownanthus* the testa fold is much broader.

Where three character states are recognized, characters are treated as ordered where the middle state (1) is interpreted as an intermediate step before the adoption of one of the others. So, for example, the "degree of basal fusion of staminodes" (19) and "seed colour" (31) are treated as ordered.

For other multi-state characters, i.e. "shape of idioblasts" (6), "distance between idioblasts" (7) and "flower colour" (17), states are treated as unordered. Here, the middle state (1) is not considered as an intermediate step between the other states (0 and 2). This is obvious for "flower colour" and "the shape of the idioblasts". For the "distance between idioblasts" (7) both states, i.e. "idioblasts scattered" and "idioblasts very densely packed" are considered to be derived from the plesiomorphic type of epidermis with fairly "closely packed idioblasts" (e.g. BITTRICH 1986).

No assumptions of polarity are made (MEACHAM 1984, originating from FARRIS 1970).

Different methods exist for evaluating the degree of confidence in a proposed phylogeny (e.g. "total support index" KÄLLERSJÖ *et al.* 1992, FARRIS *et al.* 1994), as well as for individual clades (e.g. "bootstrap" FELSENSTEIN 1985, BREMER 1988, 1994, DAVIS 1993 a,b) or even for taxa (SIDDALL 1995). The bootstrap is one of the most widely used methods, but was recently strongly critisized (e.g. CARPENTER 1992, HILLIS &

BULL 1993, KLUGE & WOLF 1993, TRUEMAN 1993, BREMER 1994). As an alternative the following tests were performed with the data set:

1. A simplified method after DAVIS (1993 a,b) was used, as a means of assessing the stability of monophyletic groups. Characters are removed one at a time, the data set re-analysed, the character returned, the next character removed and the resulting data set analysed again. Since the removal of more than one character becomes computationally exceedingly difficult, in this thesis only single character removal and certain selected cases of dual character removal were tested. The case of dual character removal specifically investigated the position of *C. rapaceum*, which lacks all of the synapomorphies of the *Psilocaulon* group. Therefore those characters placing it in *Psilocaulon*, i.e. "prostrate growthform" (2), "presence of flattened idioblasts" (5), "flowers several per axis, single on shorter side shoots" (14), "free petaloid staminodes" (19) and "fruits with deep locules" (28) were removed in all possible combinations. The great advantage of this method is that it identifies the particular character or set of characters supporting a clade. BREMER support, or decay analysis (BREMER 1988, 1994) is closely related to methods given by DAVIS (1993 a, b), but instead expresses branch support in terms of character state changes (increase in length required to lose a branch rather than character changes (character deletions required to lose a branch; DAVIS 1993). However, by this method no crucial characters can be identified. Therefore the method of DAVIS (1993 a,b) was chosen.

2. Furthermore, the effect of taxon removal was tested as a means of identifying "critical" taxa, (those whose deletion results in an increase in the total number of trees) and "problematic" taxa (whose removal results in a decrease of the total number of trees) (SIDDALL 1995, originating from earlier ideas of TUKEY 1958 and LANYON 1985). Due to computational limitations, only single taxa were removed. This is called the jack-knife and is similar to character removal, but tests

the effects of taxon removal.

Table 2. Character matrix

M. longistylum	11?0011011010?012011??100010001010
M. aitonis	1??0011011100?012001??000010001010
M. stenandrum	10?0011011010?012011??100010000110
C. rapaceum	00?11???1100?1012001??100111000010
Pr. tetragona	11001???11000?01?02011110101112000
Pr. pallens	10001???11100?01102011110101112000
Ap. geniculiflora	1111012001000001?02011111100112000
Ap. lancifolia	10110120011010111021??111100112000
Ap. cordifolia	10110120011010111021??111100?12000
Asp. amplectens	111101210101100?002011?111?01?01?1
B. arenosus	1111012101010?002011??0001101001?1
B. marlothii	11110121010110002011??0001?01011?1
P. articulatum	1?11000010000?01?00000000111100110
P. bicorne	10111???1?00?1012000000000111101?10
P. coriarium	11111???1?0?0?0120100000001?1101?10
P. dimorphum	1?11?10?100?0?0120?0?0000??1100110
P. dinteri	1?11?2001?0?0?01?0000000011110??10
P. foliosum	110?1???110?0?01201000000111101010
P. gessertianum	1110000010000?01010000000111100110
P. granulicaule	111102001100?101000000000111101110
P. junceum	11111???11000?01?000000001?1101010
P. leptarthron	11111???1100?001200000000111101010
P. parviflorum	10111???1100?101200000000101101010
P. salicornioides	1?10?000100??101?010000001?110??10
P. subnodosum	11101???100?00012010000000111100110

C. RESULTS

1. MORPHOLOGY

1.1. Life-form

The longevity and rootstock structure of plants that were collected in the field and subsequently cultivated in Cape Town is given in Table 3. Plants were collected at different times of the year (between February and August 1995), before coming into flower, and flowered and set seed in Cape Town. None of the specimens that died off after fruiting resprouted in the following vegetative period.

Species with woody stems were found mainly in the winter-rainfall region (*P. dinteri*, *P. foliosum*, *P. junceum*, *P. leptarthron*, *P. parviflorum* and *P. subnodosum*), except for *P. coriarium* and *P. bicorne* which have their main distribution outside the winter-rainfall region. All these species survived after fruiting. In addition, observations made in the field at various times of the year during the period of this study showed that specimens of these species may often form substantial, woody stems. This proves them clearly to be several years old (approximately 4-10 years).

Plants which lacked woodiness did not survive after fruiting. These plants were collected outside the winter-rainfall region.

Table 3. Longevity of plants collected in the field and cultivated in Cape Town between February 1995 and October 1996. W = woody, N-W = non-woody, D = death after fruiting, S = survived after fruiting.

Species	Collector/ Number	Base w/n-w	Locality and Grid	D / S
P. articulatum	*Klak 3*	n-w	Barrydale, 3220DB	D
	Klak 15	n-w	Frazerburg, 3221AC	D
	Klak 50	w	Prince Albert, 3322AA	S

	Klak 53	n-w	Oudtshoorn distr., 3222DD	D
	Klak 55	n-w	Rietbron, 3223CC	D
	Klak 57	n-w	Steytlerville, 3324AD	D
	Klak 40	n-w	18 km E Barrydale, 3322DD	D
	Klak 41	w	St. Helena Bay, 3217DD	S
	Schmiedel 102.245	w	Little Karoo	S
P. bicorne	*Klak 7*	w	Askraal, 3420BB	S
	Klak 47	w	Outol, 3320BD	S
	Klak 167	w	Towsrivier, 3321CC	D
P. coriarium	*Klak 12*	w	Matjiesfontein, 3320AB	S
	Klak 16	w	Frazerburg, 3121CD	S
	Klak 121	w	Maltahöhe, 2416BA	S
P. dinteri	*Klak 10*	w	Karoopoort, 3319BB	S
	Klak 29	w	Van Rhynsdorp, 3118BD	S
	Klak 44	w	Vadrifmond, 3318AB	S
	Klak 115	w	Lüderitz, 2615CA	S
P. foliosum	*Bruyns 6723*	w	Langkloof, 3017DD	S
P. gessertianum	*Klak 124*	w	Klein Karas, 2718AC	D
	Gerbaulet & Struck 50073	n-w	Keetmanshoop - Kl. Karas, 2718AC	D
P. granulicaule	*Klak 134*	n-w	Worcester div., 3319DA	D
P. junceum	*Klak 9*	w	Karoopoort, 3319BA	S
	Klak 66	w	Vanrhynsdorp, 3118AB	S
	Klak 132	w	Sutherland, 3220CB	S
P. leptarthron	*Klak 30*	w	Vanrhynsdorp, 3118DB	S
P. parviflorum	*Klak 6*	w	Dipka, 3420BB	S

P. salicornioides	*Klak 117*	n-w	Schloss Duwisib, 2516BC	D
	Klak 118	n-w	Solitaire, 2416AA	D
	Klak 122	n-w	Sandverhaar, 2617CD	D
	Klak 123	n-w	Sandverhaar, 2617CD	D
	Klak 126	n-w	Kl. Karas, 2718CA	D
	Klak 120	w	Swakopmund, 2215AC	D
P. subnodosum	*Klak 72*	w	Garies, 3017DA	S
	Klak 74	w	Dickdoren, 3017CB	S
	Klak 97	w	Büffelsriver, 2918CC	S
	Klak 127	w	Onseepkans, 2818DB	D

Two species appear to have both annual and perennial forms:

1. Specimens of *P. articulatum* occurring outside the winter-rainfall region were generally short-lived.

2. *P. salicornioides* has short-lived forms occurring inland, south of Swakopmund, Namibia, which are non-woody and relatively small (20-30 cm tall). However, the plants found near Swakopmund have a distinctly woody base and may get much taller (30-50 cm tall).

1.2. Habit

Species of *Psilocaulon* form small (10-15 cm) (Fig. 2 C, D), medium (30-60 cm) (Fig. 3 A) to large (70-150 cm) (Fig. 3 B) shrubs. With respect to their habit they may be classified into two groups: strictly prostrate or decumbent - erect shrubs. The strictly prostrate taxa are *P. parviflorum* and *P. bicorne* (Fig. 2 C, D). However, there are several species in the second group, which have a decumbent - erect habit, which may become prostrate when growing on unstable ground, such as sandy soils (i.e. *P. articulatum*, *P. salicornioides* and *P.*

dinteri, Fig. 3 C). All other species were found to have a decumbent - erect habit. In many cases growth-forms are very variable and there are some species where no clear distinction between strictly decumbent, decumbent - erect or strictly erect can be made.

C. *rapaceum* is remarkable for its tuberous rootstock (Fig. 2 E). Each year it produces long, prostrate, leafy and flowering shoots which die off completely after fruiting (Fig. 2 A). The plant then survives the dry periods under the ground. *P. bicorne* has a similar strategy in that it also makes long, prostrate, annual, flowering shoots which die off after fruiting. However, instead of retreating underground during the dry season the plant consists only of a clump of several short, prostrate stems joined to a rootstock consisting of fibrous roots (Fig. 2 D).

1.3. Stems

1.3.1. Morphology

The axes are circular in cross section. Within the genus the diameter of the stem varies from one 1 to 10 mm. The most slender stems are found in *P. parviflorum* (1-2 mm diameter). In all other species and *Caulipsolon* the stems are usually more than 3 mm thick.

With the exception of *P. foliosum*, all have a persistent, green cortex which allows them not only to store water but also to continue assimilating after the early loss of the leaves. In the perennial species the lower stems become woody with time, but the woodiness generally remains restricted to the base of the plant, with the remaining parts maintaining some degree of succulence.

In *P. foliosum* the green cortex is only present in those parts of the stem where the leaves are still green. With new growth, the stems from the previous year's growth become brown and lose their leaves. The green, leafless stems that are

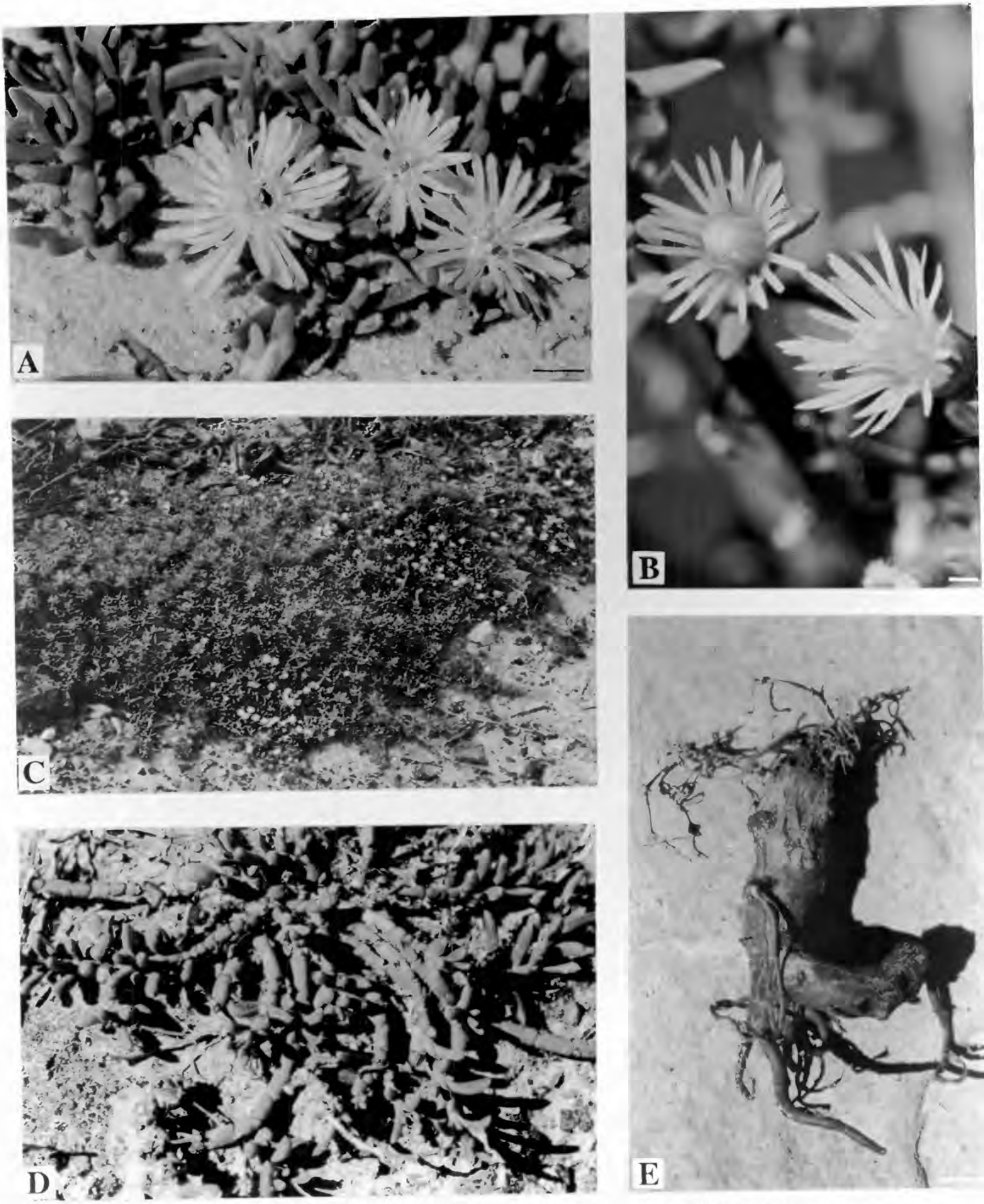


Fig. 2. **A.** *Caulipsolon rapaceum.* The plant has a prostrate habit. The flowers lack filamentous staminodes, scale bar = 5 mm. **B.** *Psilocaulon granulicaule.* The filamentous staminodes are connate, scale bar = 2 mm. **C.** *Psilocaulon parviflorum.* The plant has a characteristic mat-forming habit. **D.** *Psilocaulon bicorne.* The perennial stems form a central clump of short, prostrate stems. Long (to 1 m), annual flowering shoots will emerge at the onset of the rainy season. **E.** *Caulipsolon rapaceum.* Tuberous rootstock by which the plant survives the dry periods, scale bar = 17 mm.

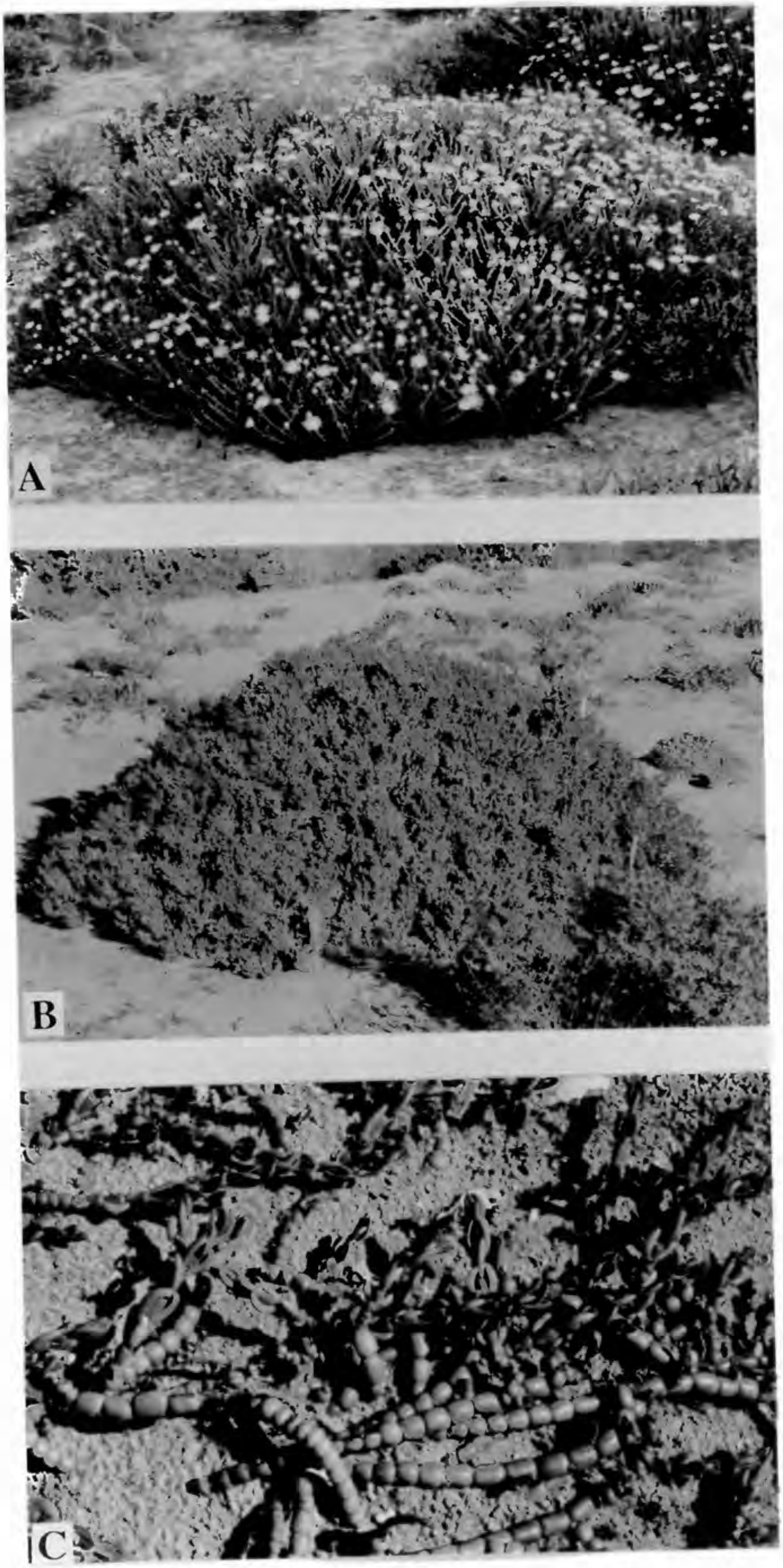


Fig. 3. **A.** *Psilocaulon leptarthron*. Stems erect, appearing almost leafless. **B.** *Psilocaulon foliosum*. Plant with very "leafy" appearance, without stem succulence. The screwdriver placed in front of the shrub is 150 mm tall. **C.** *Psilocaulon dinteri*. In very saline habitats the plants are prostrate and exceedingly succulent with very articulated stems resembling a string of beads.

typical of other psilocaulons are therefore absent. Along with this lack of stem-succulence plants of *P. foliosum* are also notably more leafy than the others (the leaves persist longer -- see below, Fig. 3 B) and they develop a substantial, woody trunk up to 50 mm thick.

The internodes were found to be very plastic both in length and diameter, depending on the water supply. Internodes which are made during dry periods remain short, whereas those that develop when there is sufficient water are much longer. In addition, internodes which remain short due to inadequate water are mostly more articulated than those formed during periods of ample water supply. Under saline conditions the internodes become increasingly articulated (i.e. they are constricted at the nodes) and may even be barrel-shaped (Fig. 3 C, *P. dinteri*). In cultivation plants that have been collected from saline areas tend to retain their barrel-shaped internodes but any new growth is far more slender and less articulated.

The nodes may be emphasized by a fine horizontal furrow separating consecutive internodes (Fig. 4 A, B). The presence or absence of this character is constant in each species of *Psilocaulon*, except in *P. foliosum*. However, this character is unambigiously observed only in mature stems since the furrow often only develops with time.

C. rapaceum also possesses stems with a succulent green cortex and the internodes are separated by a fine furrow. However, since the stems are annual, there is no persistent green cortex.

1.3.2. Anatomy

Psilocaulon and *C. rapaceum* were found to have the "cylinder type" of secondary thickening. Here the epifascicular cambium appears in patches which later merge with the interfascicular cambium to form a single meristematic

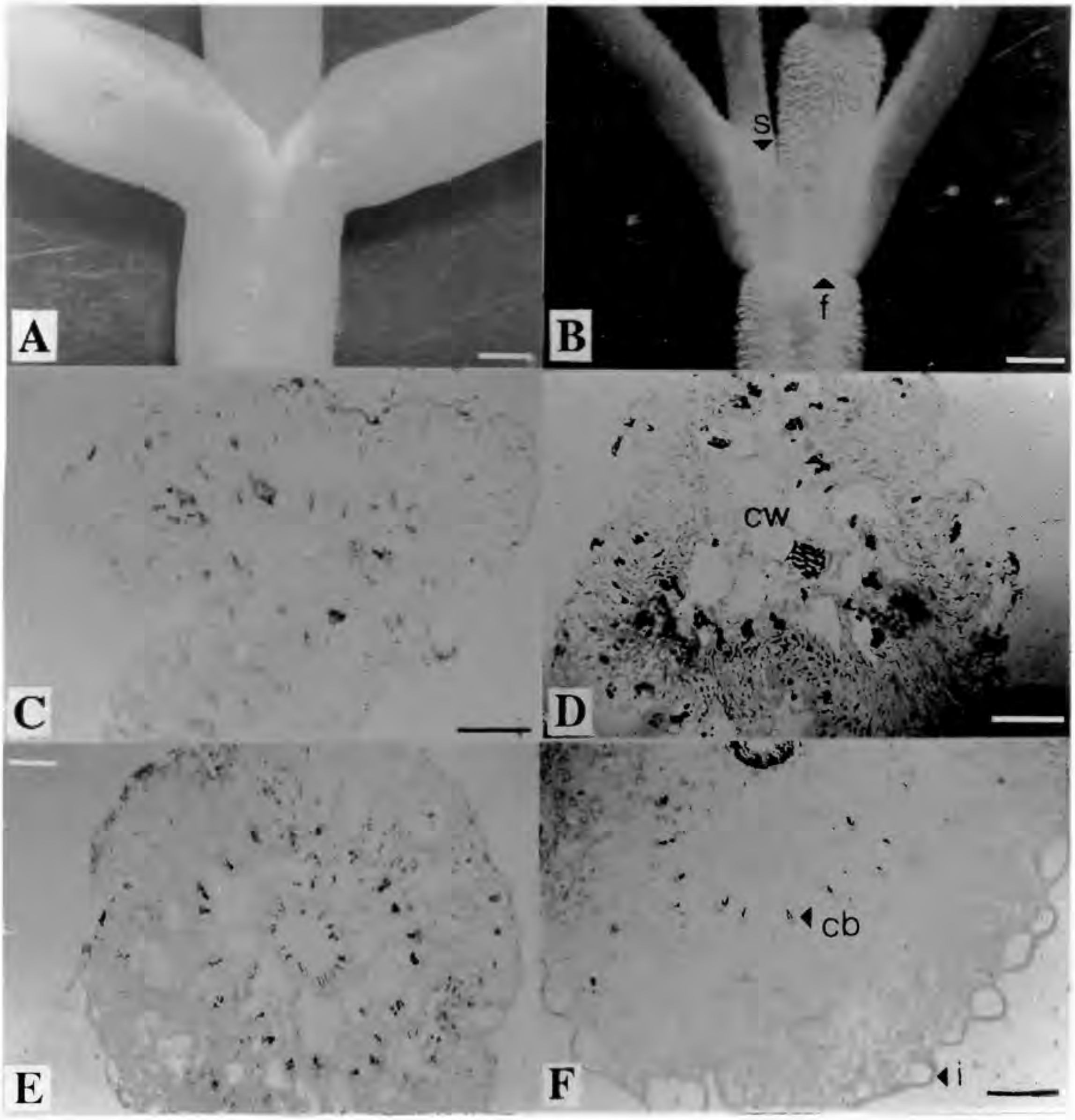


Fig. 4. **A.** Leaves shortly fused towards bases, stems without horizontal furrow (*Psilocaulon subnodosum, Klak 127*), scale bar = 1 mm. **B.** Leaves free towards bases with thin sheath at base, stems with fine horizontal furrow (*Psilocaulon articulatum, Klak 41*), scale bar = 1 mm. **C.** TS section of leaf, no specialized central water-storing tissue present (*Psilocaulon subnodosum, Klak 72*), scale bar = 1 mm. **D.** TS section of leaf, specialized central water-storing tissue present (*Psilocaulon subnodosum, Gerbaulet & Struck 50035*), scale bar = 1 mm. **E.** TS section of stem, with large chloroplast-free cells, plant originating from a saline habitat (*Psilocaulon dinteri, Gerbaulet & Struck 50123*), scale bar = 250 μm. **F.** TS section of stem, parenchyma of cortex without much enlarged cells, cell size increases centripetally, idioblasts dome-shaped, plant originating from a non-saline habitat (*Psilocaulon dinteri, Klak 10*), scale bar = 1 mm. cw = central water-storing tissue; cb = cortical bundles; f = fine horizontal furrow separating the internodes; i = idioblasts; s = leaf sheath.

ring. As a result, a solid xylem cylinder develops, interspersed with scattered islets of phloem.

The cortex is made up of parenchyma cells containing chloroplasts. Thus there is no distinction between palisade tissue and water storing tissue. However, occasionally there are larger water-storing cells found among these parenchyma cells. The size of the cells increases and the number of chloroplasts that they contain decreases towards the centre of the axes (Fig. 4 F). Plants which grow in very saline conditions have much enlarged cells, often with an increased number of raphide bundles (Fig. 4 E). These crystals are enclosed in cells with thickened walls. In several collections of *P. junceum* tannin idioblasts were found.

Particularly noteworthy is the presence of cortical bundles in the cortex. In *Psilocaulon*, cortical bundles are particularly numerous and form a mesh-like structure (Fig. 4 E, F).

The central cylinder has a round to rectangular shape. The shorter sides are positioned below the insertion of the leaves. The primary vascular bundles are gathered into small groups.

The pith contains fairly large cells, which are probably also involved in the storage of water. Between these cells oxalate crystals accumulate. In *P. junceum* the pith contained tannin idioblasts.

1.4. Leaves

1.4.1. Morphology

In *Psilocaulon* and *Caulipsolon* the leaves lack petioles. The leaves are opposite, but frequently become alternate in the inflorescence. They are shed or dry up on the stem as soon as water becomes scarcer. An exception is *P. foliosum*, where the leaves persist longer and are only shed once the stem becomes woody.

The upper side of the leaves is flattened to weakly channelled (Fig. 4 C). The leaves are narrowly linear to lanceolate or weakly oblanceolate with a round to pointed tip or a mucro (e.g. *P. articulatum*). The length of the leaves lies between 2.5 and 28.0 mm and the width between 0.5 and 4.2 mm. Leaf shape, width and length were found to be highly variable and largely dependent on the availability of water during the growing season.

Two different types of leaf-base may be distinguished:

(1) the leaf base may be distinct, i.e. the leaves are free to the base. Often a fine papery sheath is present at the leaf margins and it may overlap with the opposite leaf (Fig. 4 B). Such leaves are only slightly succulent and are shed once they dry out (e.g. *P. articulatum*, *P. granulicaule*).

(2) the leaf base may be indistinct, i.e. the leaves are not clearly separated from the stem. In this case a fine papery sheath is never present. In addition, the leaves may be distinctly fused towards their bases (Fig. 4 A). This may often be clearly observable only in mature leaves. The leaves are conspicuously succulent. They frequently persist after drying out (e.g. *P. subnodosum*, *P. salicornioides*).

C. rapaceum has leaves that are weakly channelled above, narrowly linear to lanceolate or weakly oblanceolate with a round or pointed tip, without a mucro. They are between 11.0 and 38.0 mm long and between 1.5 and 8.5 mm broad and are free to their bases.

The presence or absence of a fine horizontal furrow between the leaf and the stem is always coupled with the presence of free or basally fused leaves respectively. Therefore this character is also variable in *P. foliosum*.

1.4.2. Anatomy

In cross-section the leaves are semi-circular to circular or weakly trigonous.

The epidermis is made up of a single layer of cells. No hypodermis is present. The mesophyll is made up of parenchyma cells which contain chloroplasts and there is no differentiation into a spongy- and palisade-parenchyma (Fig. 4 C).

Generally *Psilocaulon* leaves lack distinct water-storing tissue (Fig. 4 C). However, chloroplasts become fewer towards the centre of the leaf and the transition between distinct and non-distinct, central, water-storing tissue is not always obvious. However, in *P. subnodosum* and *P. coriarium* it appears that specimens with and without central water-storing tissue may occur (Fig. 4 C, D).

Table 4. Central water storing tissue in leaves of *Psilocaulon*.

Species	Collection	Locality and Grid	Water storage tissue
P. coriarium	*Klak 16*	South Africa, Frazerburg, 3121CD	Absent
	Klak 114	Namibia, Aus, 2616CB	Present
P. subnodosum	*Klak 72*	South Africa, Garies, 3017DA	Absent
	Klak 94	South Africa, Ratel Poort,2917BD	Absent
	Klak 127	Namibia, Onseepkans, 2818DB	Present
	Gerbaulet & Struck 50035	Namibia, Ausankehr, 2817AD	Present

It appears as if material from the south-western Cape has no obvious central water-storing tissue (4 C), while material from Namibia exhibited water-storing tissue (4 D). However, wider sampling is needed to support this pattern.

As in the stems, raphide bundles were found in the leaves and, in *P. junceum*, tannin idioblasts were detected.

1.5. Epidermis of stems and leaves

1.5.1. Epidermal waxes

A layer of wax is present on both the stems and the leaves. The thickness of this layer may vary between (e.g. *P. salicorniodes* and *P. parviflorum*) and within species (e.g. *P. subnodosum*, *P. coriarium*). A glaucous colour is usually indicative of a thick covering of wax.

1.5.2. Idioblasts

The idioblasts may be either protruding (i.e. visible with no more than a 10x lens) or completely reduced (i.e. not visible with a 10x lens) to form a more or less smooth surface (e.g. *P. leptarthron* (Fig. 5 C), *P. junceum*). There are several species that are variable with respect to the presence or absence of idioblasts on their stems (i.e. *P. dinteri*, *P. salicornioides*, see discussion below).

In *Psilocaulon* the epidermis of stem and leaves is very similar; these are discussed together. With respect to protruding idioblasts, several characteristics may be distinguished:

In *Psilocaulon* the idioblasts are scattered (Fig. 5 A, B, D), which means that they are separated by numerous "normal" epidermal cells (Fig. 4 F). In *Mesembryanthemum longistylum*, which has been investigated for outgroup comparison, the idioblasts are far less widely spaced (Fig. 5 E), but are not as tightly packed as in a xeromophically modified epidermis (e.g. *Brownanthus*, Fig. 5 F).

The idioblasts of *Psilocaulon* are thin-walled, and collapse when dried. They are found in two shapes: dome-shaped (*P. granulicaule*, *P. dinteri*) (Fig. 5 D) or hair-like (e.g. *P. articulatum*, *P. gessertianum*) (Fig. 5 A, B). In contrast to the density or size of the idioblasts, which may be variable, the shape is constant within species.

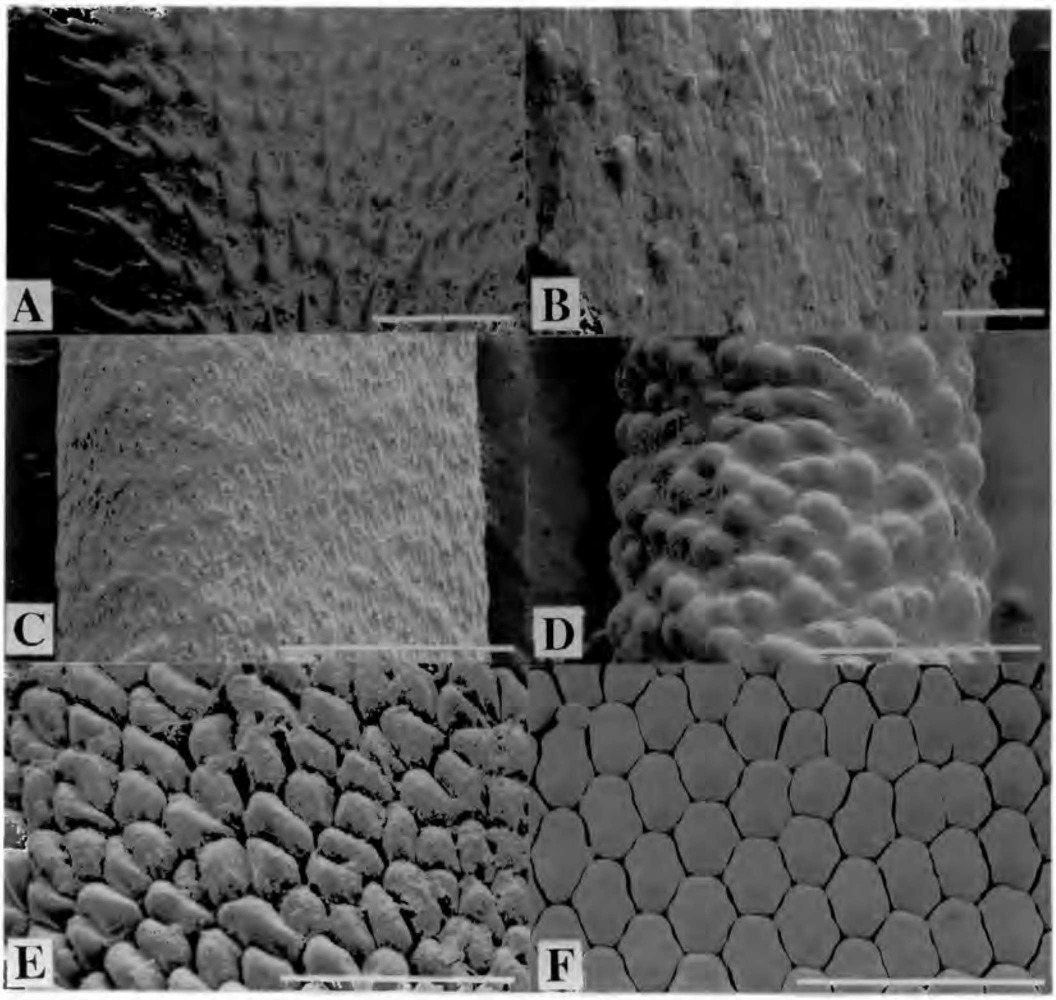


Fig. 5. SEM views of epidermis of stems of *Psilocaulon* (A-D), *Mesembryanthemum* (E) and *Brownanthus* (F). **A.** *P. articulatum* (*Klak 55*), stem covered with hair-like idioblasts, protruding idioblasts are widely spaced, i.e. interspersed by "normal" epidermal cells, scale bar = 500 μm. **B.** *Psilocaulon gessertianum* (*Klak 124*), hair-like idioblasts more widely spaced and shorter than in *P. articulatum* (A), scale bar = 200 μm. **C.** *Psilocaulon leptarthron* (*Klak 30*), idioblasts flattened, stomatal openings parallel to longitudinal axis of stem, scale bar = 1 mm. **D.** *Psilocaulon granulicaule* (*Klak 134*), idioblasts dome-shaped, widely spaced, scale bar = 1 mm. **E.** *Mesembryanthemum longistylum* (*Klak 39*), idioblasts much more closely packed than in *Psilocaulon* but still with some spaces between them, irregularly polygonal, scale bar = 500 μm. **F.** *Brownanthus arenosus* (*Gerbaulet & Struck 94605*), idioblasts very closely packed so as to form another surface above the level of the stem, hexagonal, scale bar = 500 μm.

1.5.3. Stomata

Stomata are sunken or superficial, even on the same specimen. This appeared to be independent of the age of the stems, since stomata were observed to be sunken in the old stems and superficial on some young stems And reversed on others. However, sunken stomata were never observed on the leaves.

The orientation of the stomatal opening was found mostly to be perpendicular to the longitudinal axes of the stems. *P. leptarthron* constituted an exception, since here stomatal openings were observed to be parallel to the longitudinal axes of the stem (Fig. 5 C). Whether this character is constant for *P. leptarthron* is not known, since only one specimen was investigated.

The orientation of the stomata on the leaves was found in most cases to be the same as on the stems, i.e. perpendicular to the longitudinal axes of the leaves.

1.6. Inflorescence

In *Psilocaulon* one finds closed, monotelic inflorescences, i.e. the flowering main- and side-shoots terminate with a flower. The branching of the partial inflorescences is cymose. The inflorescence is loosely arranged in a many-flowered dichasium (e.g. *P. junceum*, *P. articulatum*). There is usually a transition from opposite leaves to alternate leaves from a short distance below the inflorescence. The inflorescences are non-leafy. Often the terminal flower is not exactly positioned at the end of the axis, but is slightly shifted onto one of the side axes.

In some species of *Psilocaulon* (*P. parviflorum*, *P. granulicaule*, *P. leptarthron*) and in *Caulipsolon* the partial inflorescences are usually reduced to single flowers. However, frequently one finds these species also with few (2-3) and, in some rare cases, even with 5-7-flowered dichasia (e.g. *P. granulicaule*). Similarly, *P. bicorne* and *P. salicornioides*, which usually have many-flowered dichasia, are occasionally found with solitary flowers.

Single flowers are present only at the end of the long axis in *P. leptarthron*. In the remaining species of *Psilocaulon* and *Caulipsolon* the single flowers in addition emerge from short side braches along the longer axis.

In perennial specimens the plant usually makes new shoots just below the old inflorescence which, in many cases, dries up completely and eventually falls off. If the whole inflorescence does not die off, new shoots may emerge directly out of the axils of bracts within it.

1.7. Flower

1.7.1. Morphology

The sepals are shortly fused towards their bases. The number of sepals varies between 4 and 5 and equals the number of locules. In four species (i.e. *P. dimorphum*, *P. coriarium*, *P. junceum* and *P. salicornioides*) flowers within a population may have 4 or 5 sepals, while in the other species either 4 or 5 are found, which is species specific. In many species the length of the sepals is variable: 2 (3) of the sepals are longer than the petaloid staminodes or all 4 (5) may be equally long but shorter than the petaloid staminodes. In addition, some of the sepals may be slightly succulent.

The petaloid staminodes are arranged in 1 or rarely 2 rows, so that there are between 15 and 40 of them (Fig. 6 B, Fig. 7 A). The flowers open fully with a diameter of between 5 and 25 mm (Fig. 7 B). The largest flowers are found in *P. leptarthron* (at between 18 and 25 mm). Flower diameter is variable in most species and there is considerable overlap between the species (apart from *P. leptarthron*). *P. gessertianum* is particularly unusual, since it has very reduced staminodes.

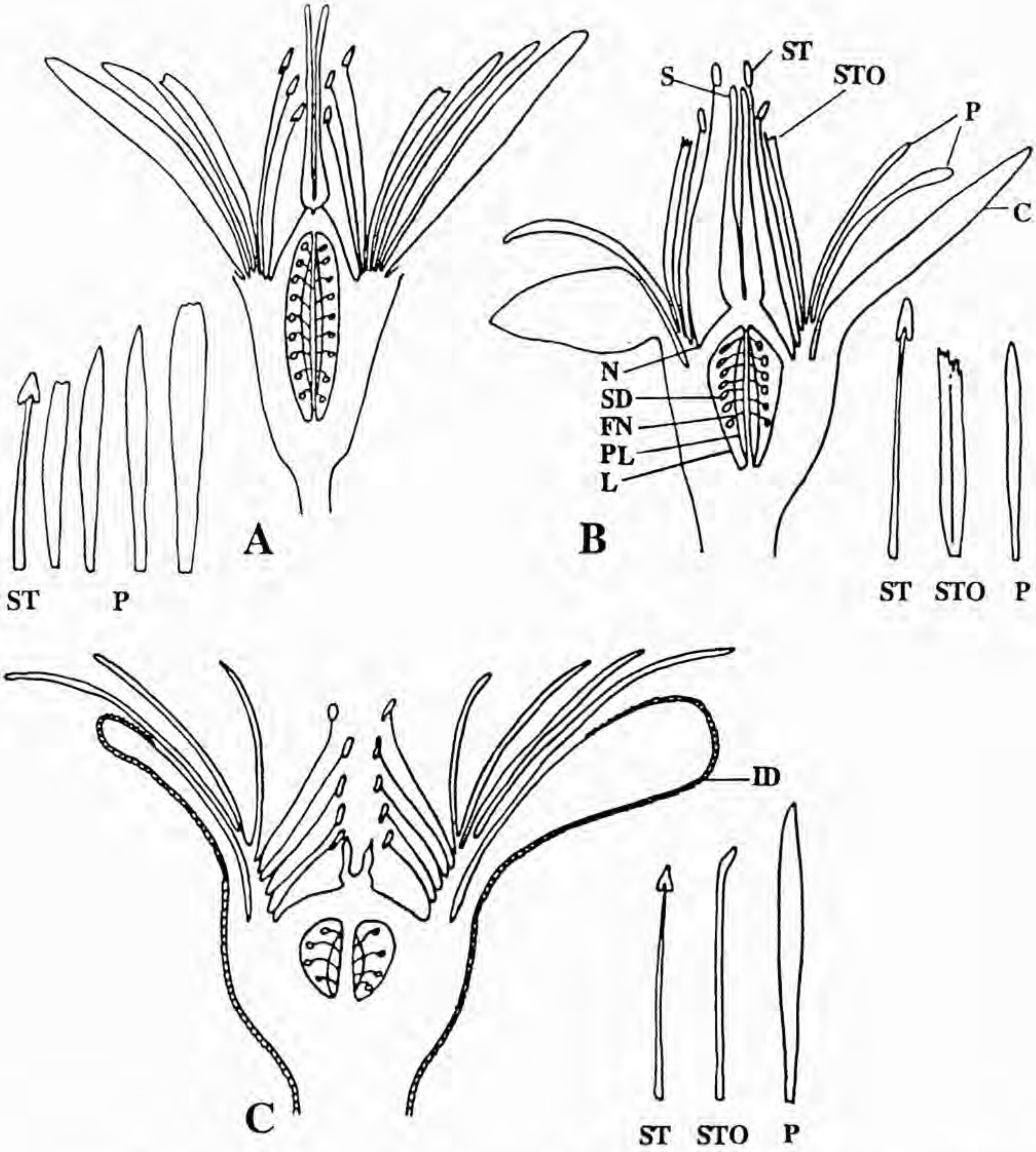


Fig. 6. Flower types of *Psilocaulon*, *Caulipsolon* and one of the outgroups investigated in this study in diagrammatic longitudinal section. **A.** *Caulipsolon rapaceum.* Individual members of the androecium basally free, absence of filamentous staminodes (androecium type 3), styles are as long or longer than stamens. **B.** *Psilocaulon subnodosum.* Individual parts of the androecium basally shortly fused, filamentous staminodes apically lacerate and gathered into a cone (androecium type 2), styles about the same length as stamens. **C.** *Aptenia geniculiflora.* Individual parts of the androecium fused from the base for some distance to form a tube-like structure, petaloid staminodes transform in concentric rings into filamentous staminodes (androecium type 1), the styles are much shortened and are much exceeded by the stamens. C = calyx, FN = funicles, ID = idioblasts, L = locules, N = nectaries, P = petaloid staminodes, PL = placenta, S = styles, SD = seed, ST = stamens, STO = filamentous staminodes.

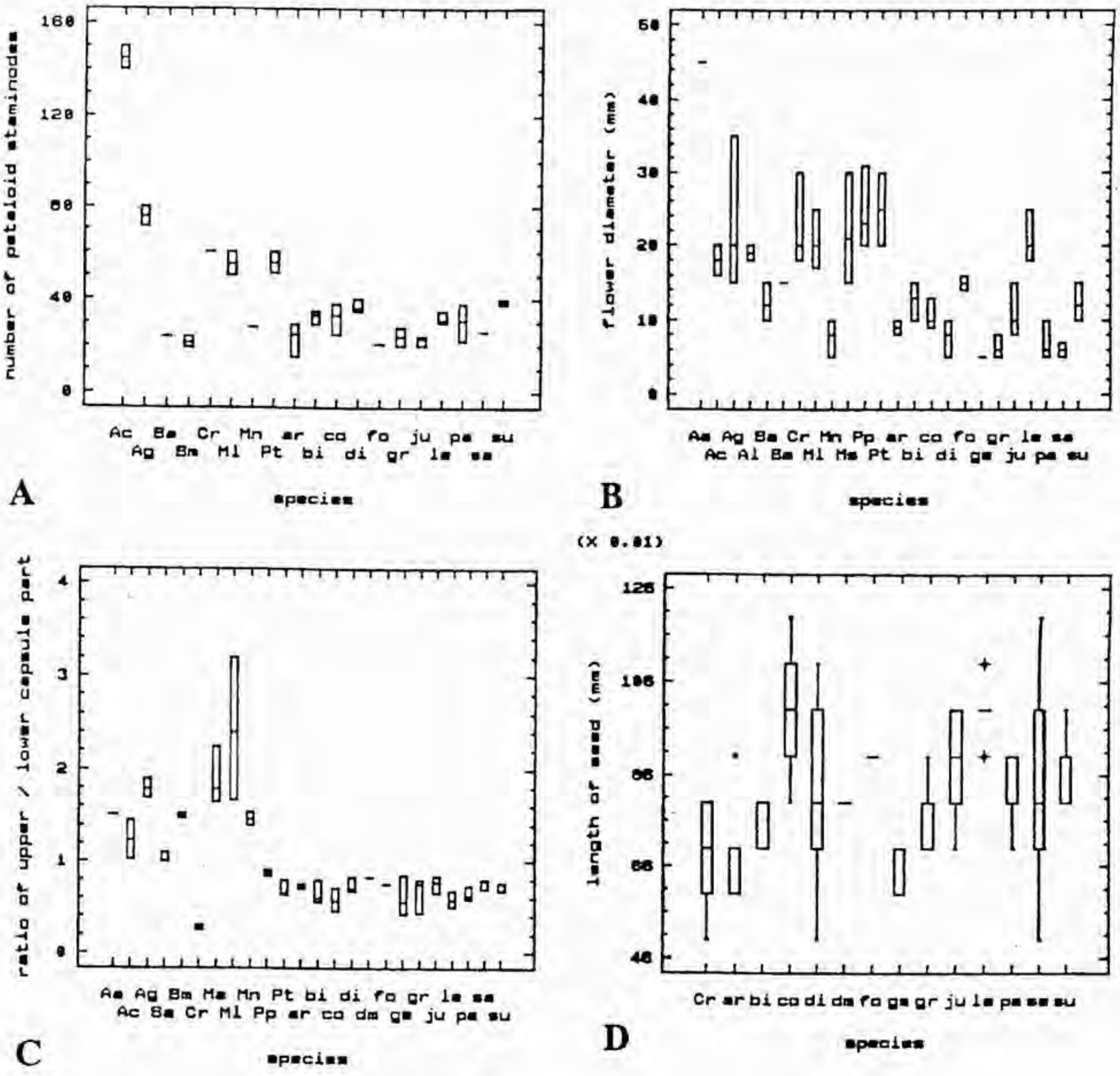


Fig. 7. Multiple box- and whisker plots. **A.** Variation of diameter of flower in *Psilocaulon*, *Caulipsolon* and outgroups. *Psilocaulon leptarthron* has the largest flower in *Psilocaulon*, the remainder having comparatively small flowers. **B.** Based on the number of petaloid staminodes two groups may be distinguished: (1) species with few (< 40) petaloid staminodes and (2) species with many (> 40) petaloid staminodes. **C.** Plotted ratios of upper to lower capsule part indicate a gap between two groups: (1) species with lower capsule parts longer than upper, (2) species with upper capsule parts longer than lower. **D.** Length of seeds of *Psilocaulon*. No distinct gaps between different sizes of seeds evident. Aa = *Aspazoma amplectens*; Ac = *Aptenia cordifolia*; Ag = *A. geniculiflora*, Ba = *Brownanthus* arenosus; Bm = *B. marlothii*; Cr = *Caulipsolon rapaceum*; Ma = *Mesembryanthemum aitonis*; Ml = *M. longistylum*; Mn = *M. nodiflorum*; Pp = *Prenia pallens* ssp. *pallens*; Pt = *P. tetragona*; ar = *Psilocaulon articulatum*; bi = *P. bicorne*; co = *P. coriarium*; di = *P. dinteri*; dm = *P. dimorphum*; fo = *P. foliosum*; ge = *P. gessertianum*; gr = *P. granulicaule*; ju = *P. junceum*; le = *P. leptarthron*; pa = *P. parviflorum*; sa = *P. salicornioides*; su = *P. subnodosum*.

Most species have white flowers, sometimes with a faint tinge of pink at the edge of the petals (i.e. *P. coriarium* and *P. salicornioides*). Puce or pink flowers are less common and are found in *P. salicornioides*, *P. dinteri* and *P. junceum*. Pale yellow flowers are found only in *P. granulicaule* and *P. gessertianum*. Repeated opening and closing of the flowers was observed in most species except in *P. foliosum* where the flowers remain open.

Filamentous staminodes are present and are gathered into a conspicuous cone (Fig. 2 B, 6 B). They are remarkable in being transparent, apart from a thickened middle vein and for having their apices finely incised.

Petaloid and filamentous staminodes may be either free or shortly fused at the base (Fig. 6 B). Highly fused petaloid and filamentous staminodes forming a tube-like structure (e.g. in *Aptenia*), are not found in *Psilocaulon* (Fig. 6 C).

The stigmas are filiform and remain upright for the duration of anthesis. The number of stigmas is always the same as the number of sepals. The length of the stigmas varies between 2 and 5 mm and is fairly long in proportion to the flower diameter -- they have about the same length as the anthers or surpass them.

The placenta is oval, the ovary is half inferior and has a papillate surface (Fig. 8 E). These papillae are irregularly shaped and somewhat convex.

There are small, shallow, koilomorphic mero-nectaries (i.e. structures made up of several single nectaries, Fig. 7 E). In many species nectaries could not be detected and it is possible that they are absent or very reduced in several of them.

C. rapaceum has 5 sepals of unequal size, with 2 or 3 of the sepals longer than the petaloid staminodes. Filamentous staminodes are absent (androecium type 3 *sensu* IHLENFELDT 1960, Fig. 6 A). The petaloid staminodes are white, free to the base and arranged in 3 to 5 rows (Fig. 6 A), becoming shorter towards the centre of the flower. The flowers open fully, reaching between 15 and 25 mm in diameter. The styles are long (between 4 and 6 mm) and are of a similar length to the anthers. However, in contrast to *Psilocaulon*, here they do not remain upright for the duration of anthesis. The flower has definite male and female phases: during the male phase the stigmas are upright and, as the anthers senesce, the stigmas become receptive and spread.

As in *Psilocaulon*, the placenta is oval. The papillae found on top of the ovary are the same as in *Psilocaulon*. There are small, coilomorphic mero-nectaries.

1.7.2. Pollen

Pollen-grains in *Caulipsolon* and the majority of specimens investigated in *Psilocaulon* are tricolpate, spinulose and punctate to micropunctate (Fig. 8 G). The tectum is more or less evenly covered with spinules. The perforations are of about equal size throughout the tectum.

The length of the equatorial side of the pollen of *Psilocaulon* lies between 19.3 μm and 27.5 μm. The polar dimensions measure between 13.5 μm and 20.0 μm. In the case of *P. salicornioides* for which pollen from three different collections were investigated, pollen size varied up to 5 μm.

Two species, *P. coriarium* and *P. salicornioides* vary in their pollen morphology (Table 5), with two of the three specimens investigated for each species differing in having reticulate-foveate, punctate pollen surface (Fig. 7 H). In *P. salicornioides* three of the specimens investigated, which were collected in southern Namibia, show the common pollen morphology, whereas the specimen collected from Swakopmund, Namibia, has reticulate-foveate, punctate pollen.

In addition, in one specimen of *P. salicornioides* an abnormal 6-pericolpate pollen-grain was observed among tricolpate pollen-grains (Fig. 8 F).

Table 5. Variable pollen morphology in two species of *Psilocaulon*.

Species	Collection	Tectum of pollen	Locality, Grid
P. coriarium	*Klak 12*	punctate-microspinulose	South Africa, Matjiesfontein, 3320AB
	Klak 114	reticulate-foveate	Namibia, Aus, 2616CB
	Klak 129	reticulate-foveate	South Africa, Kakamas, 2819DD
P. salicornioides	*Klak 118*	punctate-microspinulose	Namibia, Solitair, 2416AA
	Klak 123	punctate-microspinulose	Namibia, Sandverhaar, 2617CD
	Klak 126	punctate-microspinulose	Namibia, Klein Karas, 2718CA
	Klak 119	punctate-foveate	Namibia, Swakopmund, 2414DA

1.8. Fruit

In *Psilocaulon* the "*Aridaria*" type of capsule is found (*sensu* SCHWANTES 1952), which is characterized by having the valve wings inflexed over the valves (Fig. 1 A).

A different type of fruit is found in *C. rapaceum*. Here the valve wings are reflexed and fused in pairs. This type of fruit is referred to as the "*Halenbergia*" type (*sensu* SCHWANTES 1952).

The fruits of *Psilocaulon* and *Caulipsolon* are characterized by deep locules (Fig. 1 B). Ratios taken of upper to lower capsule parts show that the lower part of the capsule is always longer than the upper part (Fig. 7 C).

As mentioned above, the number of locules is the same as the number of stigmas or sepals in *Psilocaulon*. Usually, specimens which have 4-locular capsules will also have (on the same plant or even branch) some that are 5-locular and vice versa. However, in most cases one locule number predominates

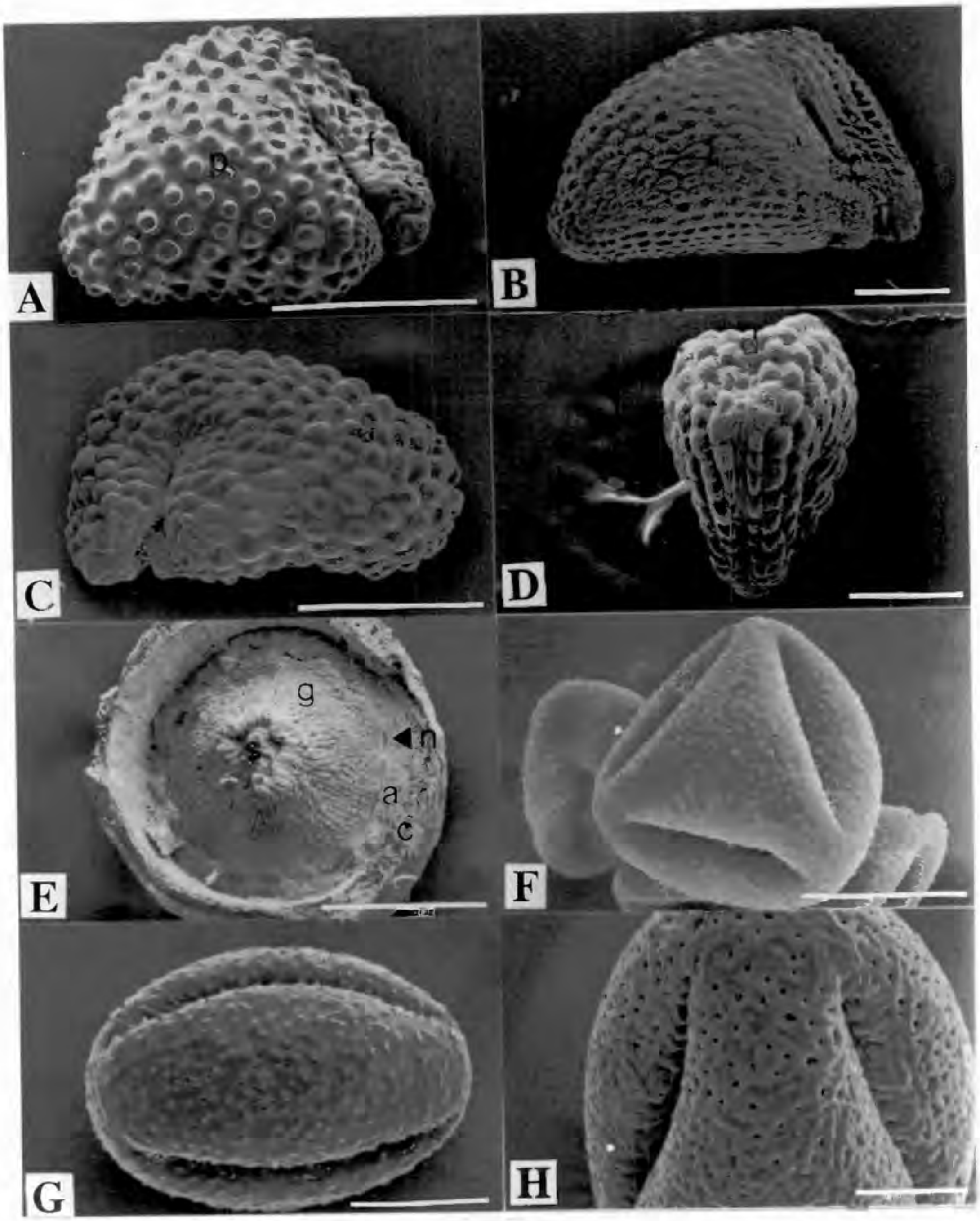


Fig. 8. **A.** Seed of *Psilocaulon junceum* (*Klak 2*), outer walls of testa cells each raised into a rounded, central papillum, scale bar = 500 μm. **B.** Seed of *Psilocaulon granulicaule* (*Wilman* KMG *3407*), outer walls of testa cells flattened, scale bar = 200 μm. **C.** Seed of *Psilocaulon coriarium* (*Klak 121*), outer walls of testa cells each raised into a conspicuous, rounded papillum, scale bar = 500 μm. **D.** Seed of *Psilocaulon articulatum* (*Klak 41*), cells of dorsal region arranged in parallel lines, scale bar = 500 μm. **E.** *Psilocaulon bicorne* (*Klak 135*), view of upper surface of ovary with five separate, small, shallow, coilomorphic nectaries, scale bar = 1 mm. **F.** *Psilocaulon salicornioides* (*Klak 123*), abnormal 6-pericolpate pollen-grain, scale bar = 10 μm. **G.** *Psilocaulon leptarthron* (*Klak 30*), tectum of pollen-grain punctate-microspinulose, scale bar = 10 μm. **H.** *Psilocaulon coriarium* (*Klak 129*), tectum of pollen-grain reticulate-foveate, scale bar = 5 μm. a = androecium (excised); c = calyx (excised); d = dorsal region; f = front region; g = gynoecium; n = small shallow coilomorphic nectary; p = perisperm region; s = styles (excised).

and one can therefore reasonably reliably classify the plants as being either 4- or 5-locular. Nevertheless, in *P. junceum* occasionally about equal numbers of 4- and 5-locular capsules were found. *P. parviflorum* is the only species that is 4-locular. As discussed above with respect to number of sepals, *P. dimorphum*, *P. salicornioides*, *P. coriarium*, *P. junceum* may have populations in which individuals are 4- or 5-locular. For *P. coriarium* it is interesting to note that populations in most parts of Namibia are usually 5-locular, whereas they are usually 4-locular in South Africa and the south-east of Namibia.

1.9. Seeds

Description of seed characteristics follows the terminology of BARTHLOTT & EHLER (1977) and BITTRICH (1986).

1.9.1. Size, shape and colour

Seeds of *Psilocaulon* measure between 0.5 and 1.3 mm in length and between 0.5 and 0.9 mm in height. The size is highly variable within species (Fig. 8 D). No distinct gaps in sizes between species are detectable.

The seeds vary from D-shaped to rarely triangular (Fig. 8 A-C). Such variation may often be observed within a single species.

The colour of the seeds ranges from dark brown to ochre. Although colour was found to be constant in most species it is variable in *P. dinteri* and *P. salicornioides*. In both species ochre and brown seeds occur but seem always to occur in different specimens.

1.9.2. Micromorphology

The arrangement of the testa cells of the perisperm region is unordered (Fig. 8 A-C). The cells of the front region (Fig. 8 A-C) and the middle cells of the dorsal region are always arranged in rows (Fig. 8 D). The testa cells are ± round or elongated, and elongated cells have their longitudinal axes parallel to the long axis of the seed (Fig. 8 B).

The anticlinal cell walls may be straight or undulated. Undulation is omega- or u-shaped. Undulated walls are found in all cells that are flattened at their borders. In contrast the cells of the middle rows of the dorsal region (Fig. 8 D) and the cells around the hilum and the exostome have straight anticlinal walls. The anticlines were found to be sunken in all specimens investigated.

The periclinal cell walls are either flat or partially raised into a central papillum. In numerous species of *Psilocaulon* and in *Caulipsolon* the papillum is confined to a small area in the centre of the testa cell (e.g. *P. junceum*) which gives the seed a rough appearance (Fig. 8 A). In other cases it may take up a much larger area, but the cells are still raised so that the surface of the testa appears to be rough (Fig. 8 C). In some other cases the cells are only slightly raised so that the testa appears to be almost smooth (e.g. *P. granulicaule*, Fig. 8 B).

Most species show no variation with respect to their sculpturing. Exceptions are *P. salicornioides*, *P. dinteri*, *P. coriarium* and *P. bicorne*, which may have rough or almost smooth testa cells.

None of the species of *Psilocaulon* develops a distinct dorsal crest. Nevertheless the outer cells of the dorsal region are usually more papillate than the medium rows.

Within *Psilocaulon* the testa fold reaches above half height of the seed. The direction of the testa fold is variable. It may be at any angle to the long axis of the seed. The testa fold is narrowly linear in *Psilocaulon* and *Caulipsolon*.

Epicuticular structures were absent or near absent.

1.10. Germination and Seedlings

The majority of seeds placed on wet filter paper without prior pre-treatment proved to be highly recalcitrant (Table 6).

Table 6. Percentage germination of seeds of *Psilocaulon* and *Caulipsolon* after two weeks without pretreatment.

Species	Collector & Number	% Germination
P. articulatum	*Klak 15*	0
P. bicorne	*Klak 164*	0
P. coriarium	*Klak 16*	0
	Klak 129	0
P. dinteri	*Klak 29*	1
	Klak 75	0
	Klak 115	99
P. gessertianum	*Gerbaulet & Struck 50073*	5
P. granulicaule	*Klak 134*	0
P. junceum	*Klak 31*	0
	Klak 49	0
P. leptarthron	*Klak 30*	0
P. parviflorum	*Klak 5*	1
P. salicornioides	*Klak 118*	0
	Klak 120	0
P. subnodosum	*Klak 72*	0
	Gerbaulet & Struck 50035	0
C. rapaceum	*Klak 144*	0

With the exception of one collection of *P. dinteri* (*Klak 115*) where 99% of all seeds germinated within the first two weeks, germination results (the number of seeds that germinated out of the total number planted expressed as a percentage) for the other species were poor: few seed germinated in *P. gessertianum* (5%) and *P. parviflorum* (1%) with the remaining species not germinating at all.

After the seeds had been slit with a razor blade, there was almost 100% germination in all species.

The cotyledons stand at an angle of 180° to each other. There is little variation in their morphology between species: they are narrowly linear or broaden slightly towards their base.

2. CYTOLOGY

No diploids were found among the fifteen specimens of *Psilocaulon* investigated (Table 7). Four species were tetraploid (*P. articulatum*, *P. gessertianum*, *P. granulicaule*, *P. Parviflorum*) and three hexaploid (*P. bicorne*, *P. dinteri* and *P. subnodosum*). *P. salicornioides* was found to be tetraploid or hexaploid. Three species (*P. junceum*, *P. coriarium* and *P. leptarthron*) showed very high poidy levels (2n = ± 126).

C. rapaceum and *A. geniculiflora* were found to be tetraploids.

Table 7. List of chromosome counts in *Psilocaulon* and *Caulipsolon*. Counts that have been published for some species of *Psilocaulon* are also listed.

	2n	collector & voucher	2n	author
Aptenia				
geniculiflora	36	*Klak 14*		
Caulipsolon				
rapaceum	36	*Klak 144*		
Psilocaulon				
articulatum	36	*Klak 15*		
bicorne	54	*Klak 164*		
coriarium	ca.126	*Klak 129*		
	ca.142	*Klak 16*		
dinteri	54	*Klak 115*		

	2n	collector & voucher	2n	author
			36	BITTRICH (1986)
gessertianum	36	*Gerbaulet & Struck 50073*		
granulicaule	36	*Klak 134*		
			18	SNOAD (1951)
junceum	ca.126	*Klak 31*		
	ca.126	*Klak 49*		
leptarthron	ca.126	*Klak 30*		
parviflorum	36	*Klak 5*		
salicornioides	36	*Klak 118*		
	54	*Klak 120*		
subnodosum	54	*Klak 72*		
		Gerbaulet & Struck 50035		

3. PHYTOGEOGRAPHY

Psilocaulon is found in the western portion of southern Africa in South Africa, Namibia and Angola (Figs 9-14). It is distributed southwards along the coast from Angola (c. 15°S) to Cape Town (c. 34°40′ S) and extends eastwards from this to ± 27°E.

Within *Psilocaulon* both very widespread and highly localized species are found. The most widespread species are *P. articulatum* (Fig. 10), *P. granulicaule* (Fig. 13), *P. coriarium* (Fig. 9) and *P. salicornioides* (Fig. Fig. 11). *P. granulicaule* is found also occasionally in Namibia as far north as Okahandja and in Australia, Victoria, near Mildura and Birchip where it is likely to have been introduced.

The most localized species are *P. gessertianum*, *P. foliosum* (Fig. 10), *P. parviflorum*, *P. leptarthron* (Fig. 12) and *P. dimorphum*. The lattermost has been recorded between

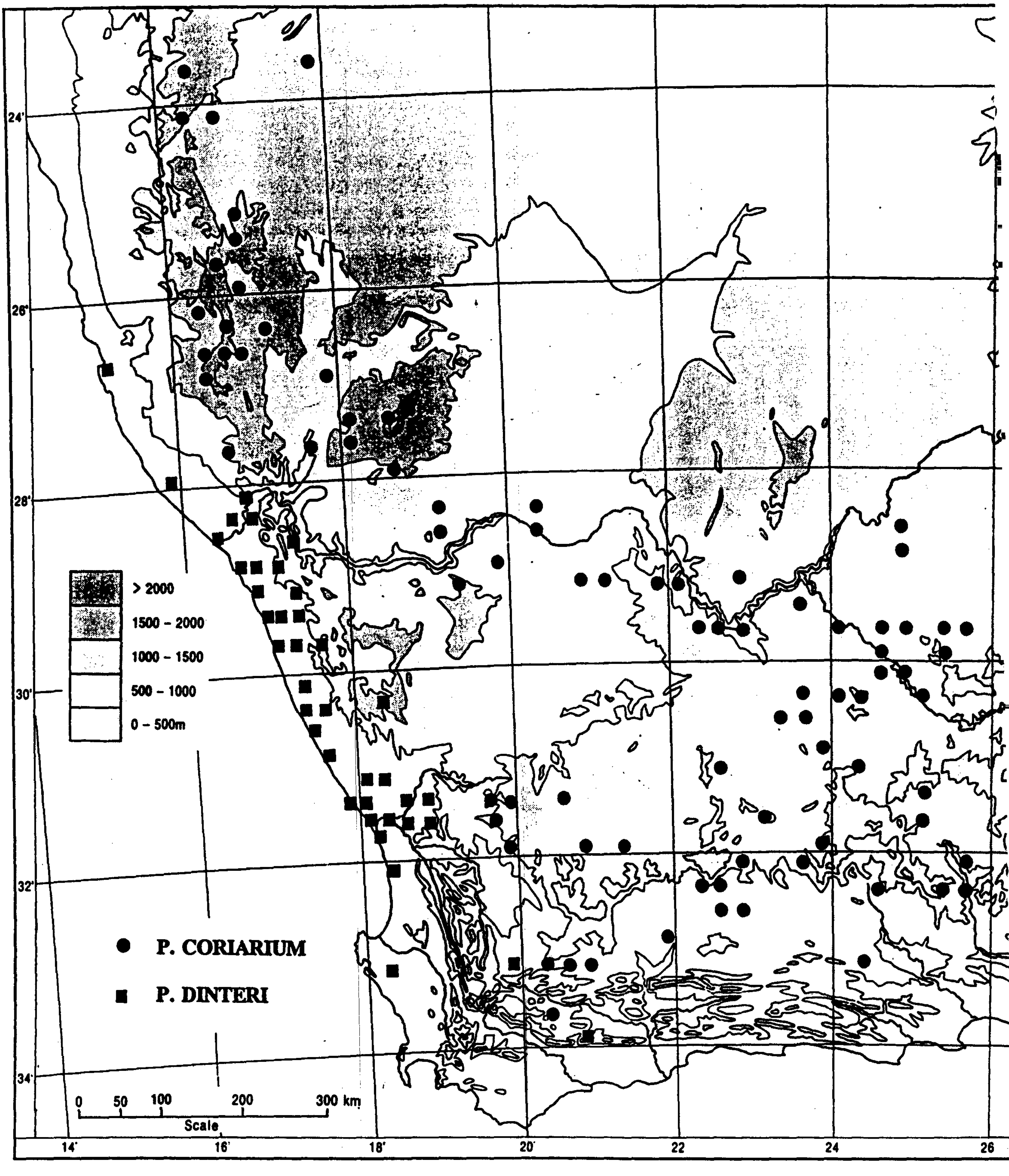


Fig. 9. Distribution of *P. coriarium* (●) and *P. dinteri* (■).

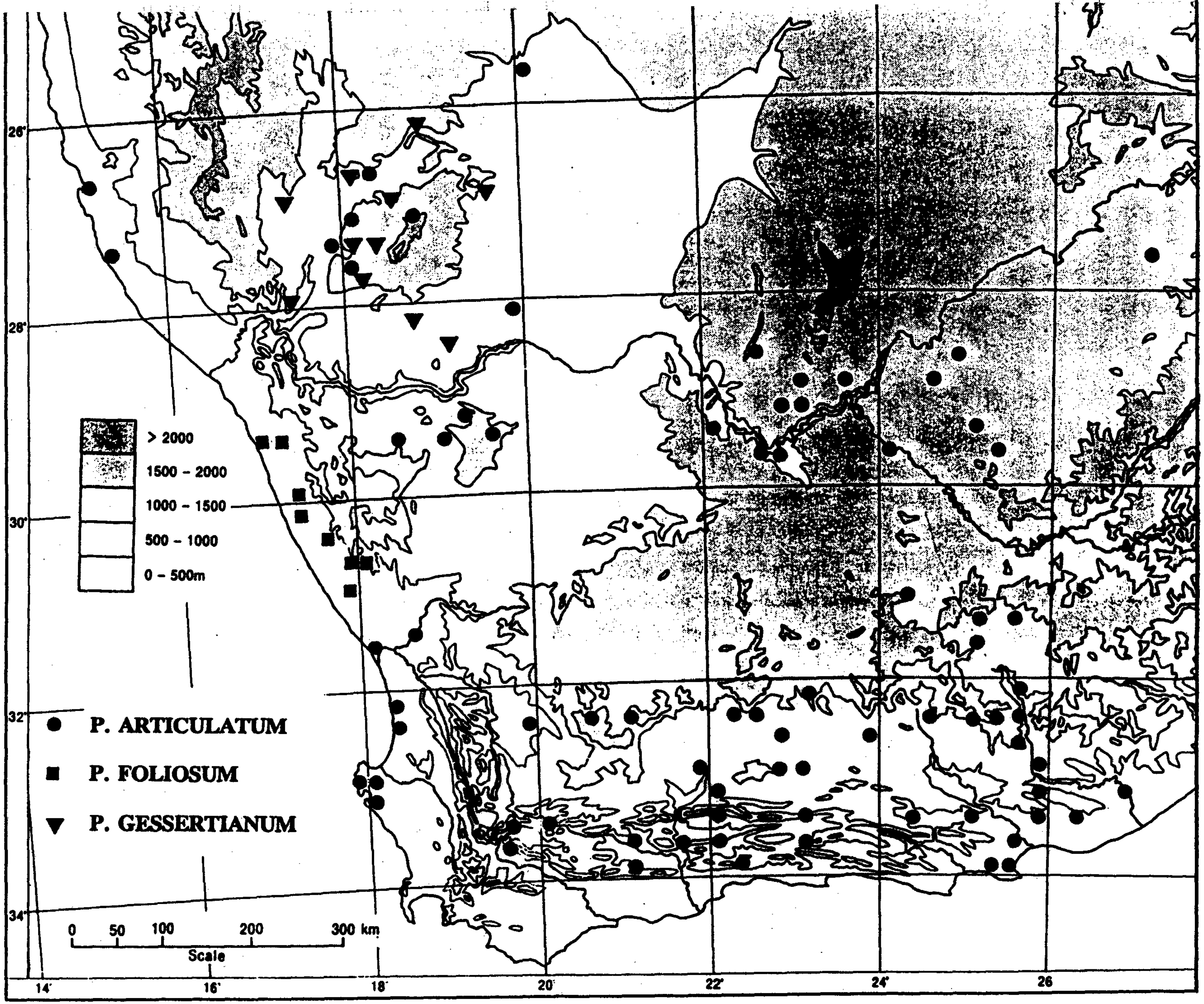


Fig. 10. Distribution of *P. articulatum* (●), *P. foliosum* (■) and *P. gessertianum* (▼).

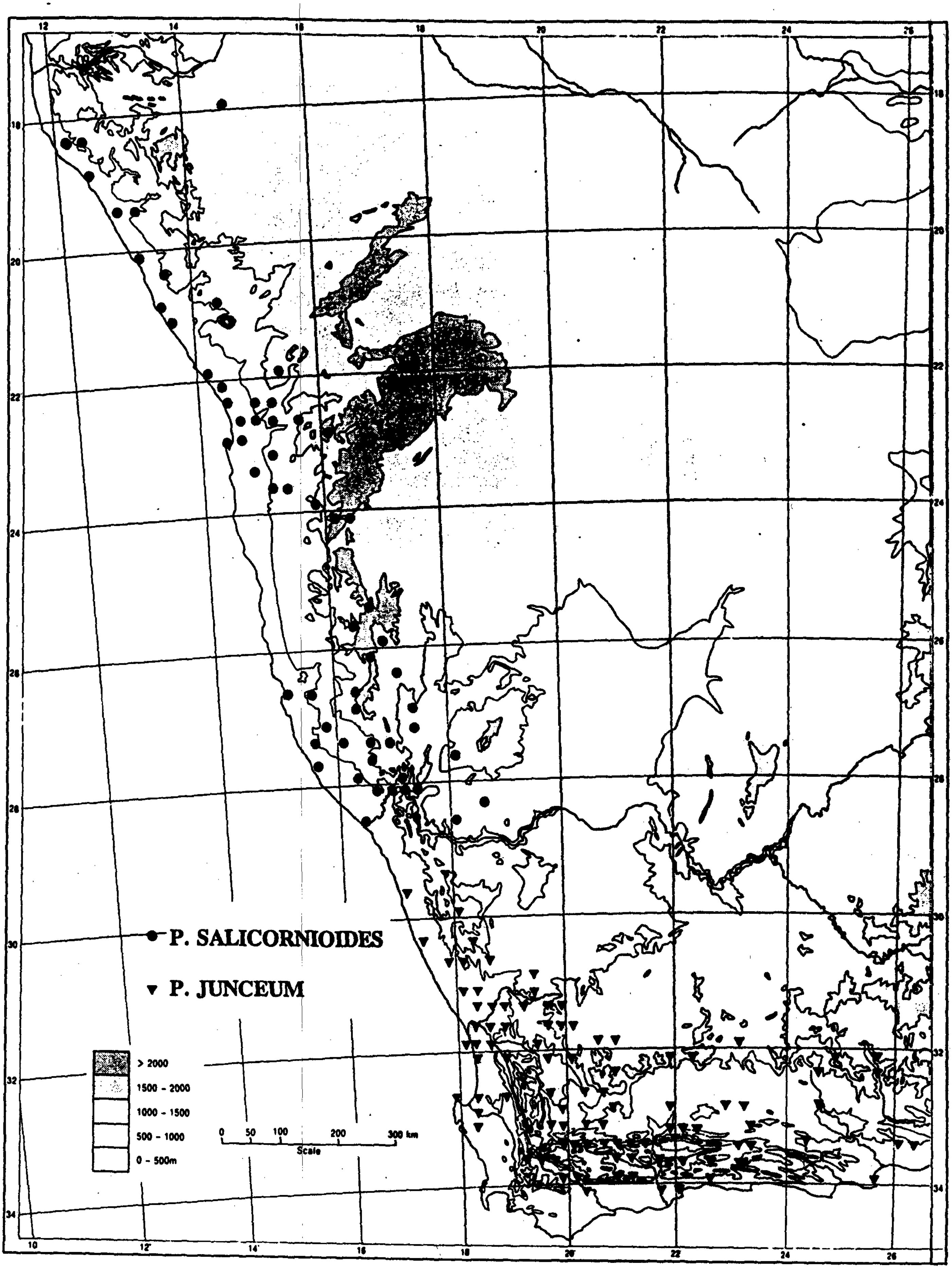


Fig. 11. Distribution of *P. salicornioides* (●) and *P. junceum* (▼

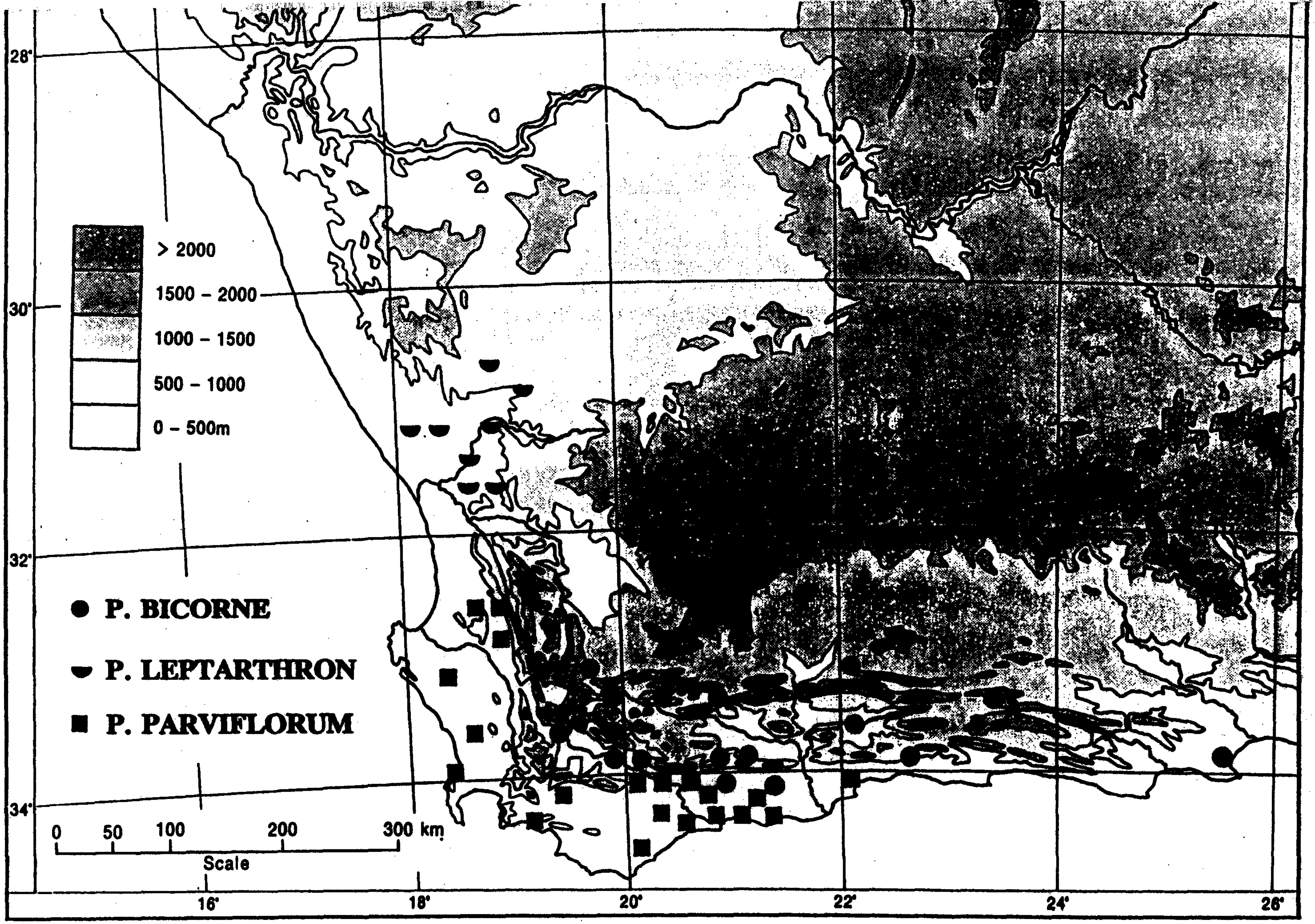
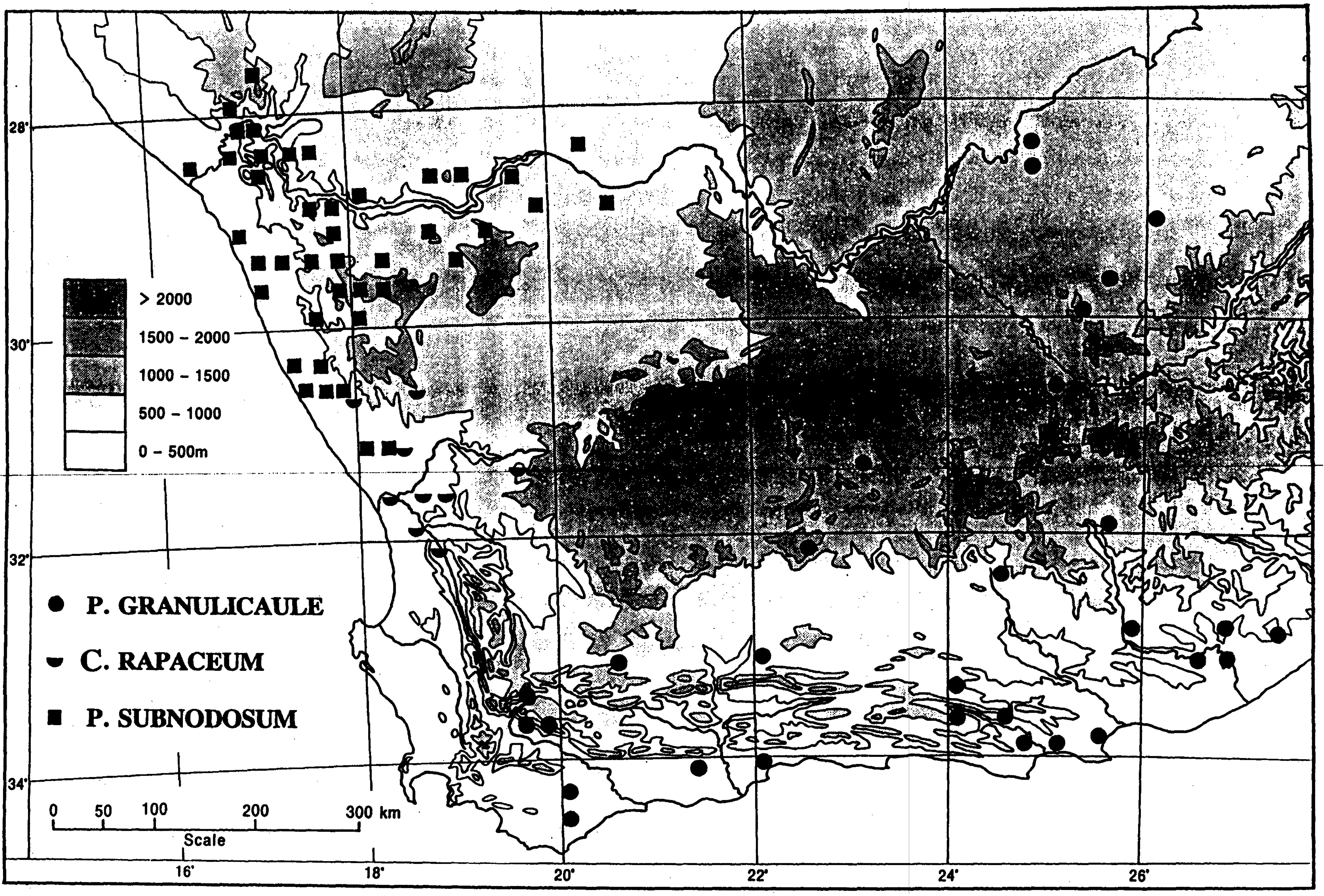


Fig. 12. Distribution of *P. bicorne* (●), *P. leptarthron* (◒) and *P. parviflorum* (■).



> 2000
1500 - 2000
1000 - 1500
500 - 1000
0 - 500m
● P. GRANULICAULE
C. RAPACEUM
■ P. SUBNODOSUM
0 50 100 200 300 km
Scale
28°
30°
32°
34°
16°
18°
20°
22°
24°
26°

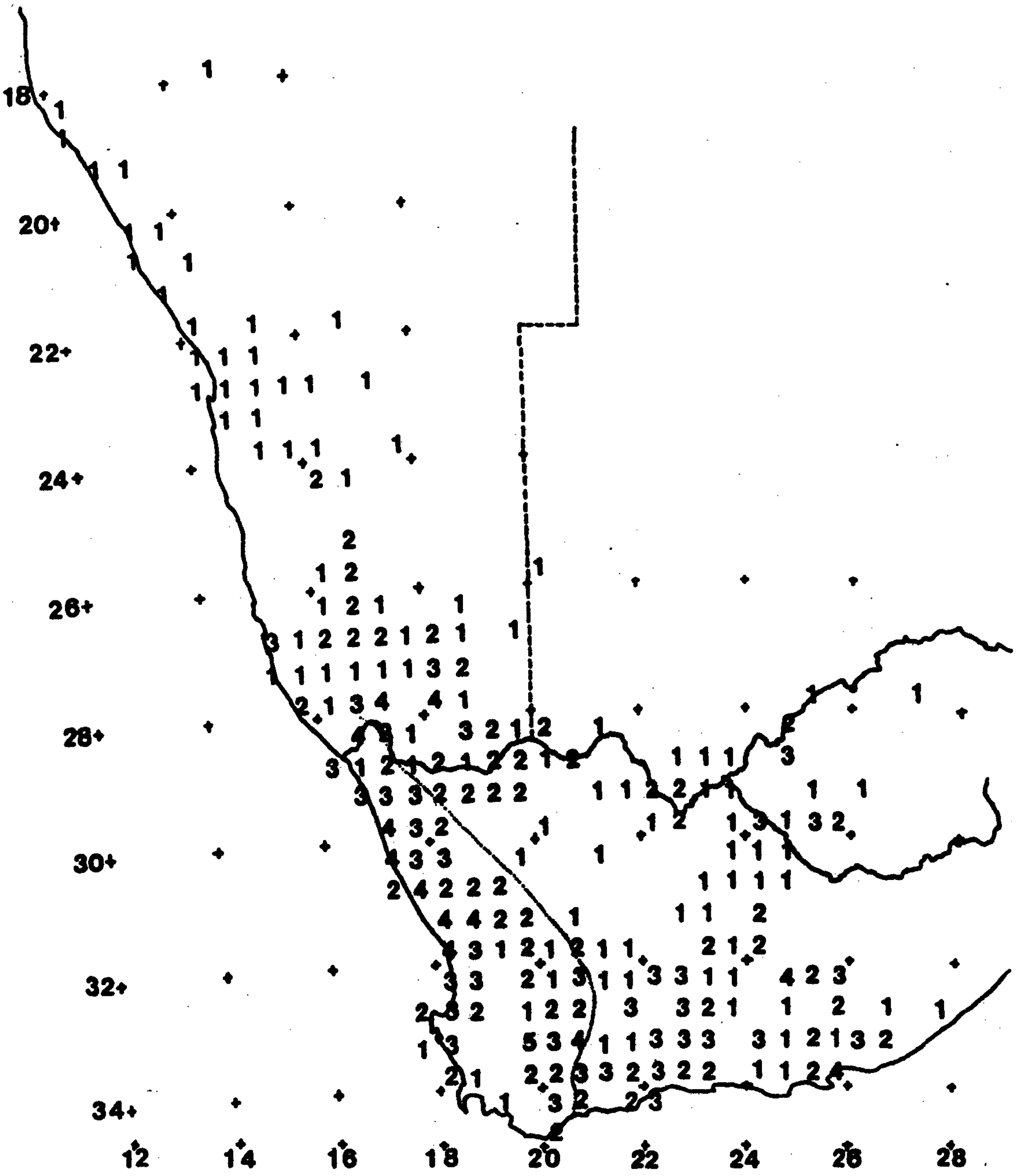


Fig. 14. Density of distribution of the species of *Psilocaulon* in southern Africa per half degree square. To the west the dotted line is the region of winter rains (maximum rainfall in June and July); to the east the maximum rain is received outside winter (simplified from ZUCCHINI & ADAMSON 1984, Fig. 6.6.).

Mossamedes (1412CC) and Porto Alexandre (1511DD).

Caulipsolon is found mostly in the low-lying coastal areas of Namaqualand below 500 m (Fig. 13) although there are some records further north-east from higher altitudes.

A survey based on the frequencies of species in half-degree squares (i.e. 30′ x 30′) indicates that there appear to be no obvious centers of high species richness (Fig. 14).

The frequency of species decreases from about 27° S northwards. Towards the eastern boarder of the distribution of *Psilocaulon*, species are represented often by 2 to 3 species (out of a maximum of 5).

It is further interesting that grids with 5 species (3219DB) can be adjacent to grids without species (3219BC, 3219DA, 3219DC).

4. PHYLOGENY

Twenty eight most parsimonious trees (length = 72 steps, consistency index = 0.51, retention index = 0.77) were found using Hennig86 (option mh*; bb*;). A successively weighted analysis (FARRIS 1989) did not improve the resolution of the network. Two additional trees, raising the total to thirty most parsimonious trees (length = 72 steps, consistency index = 0.51, retention index = 0.77) were found using Hennig86 (option ie*;). However, there was no difference in topology between the strict consensus trees generated from each analysis. The same thirty most parsimonious trees were found using PAUP. The strict consensus tree is presented in Fig. 15.

Mesembryanthemum is assumed as the outgroup and the species of *Mesembryanthemum* are grouped together.

Aspazoma and *Brownanthus* appear as the sister-group to the *Prenia* -*Aptenia* and the *Psilocaulon* clade (node 3). Therefore, *Prenia* and *Aptenia* appear as the sister group to

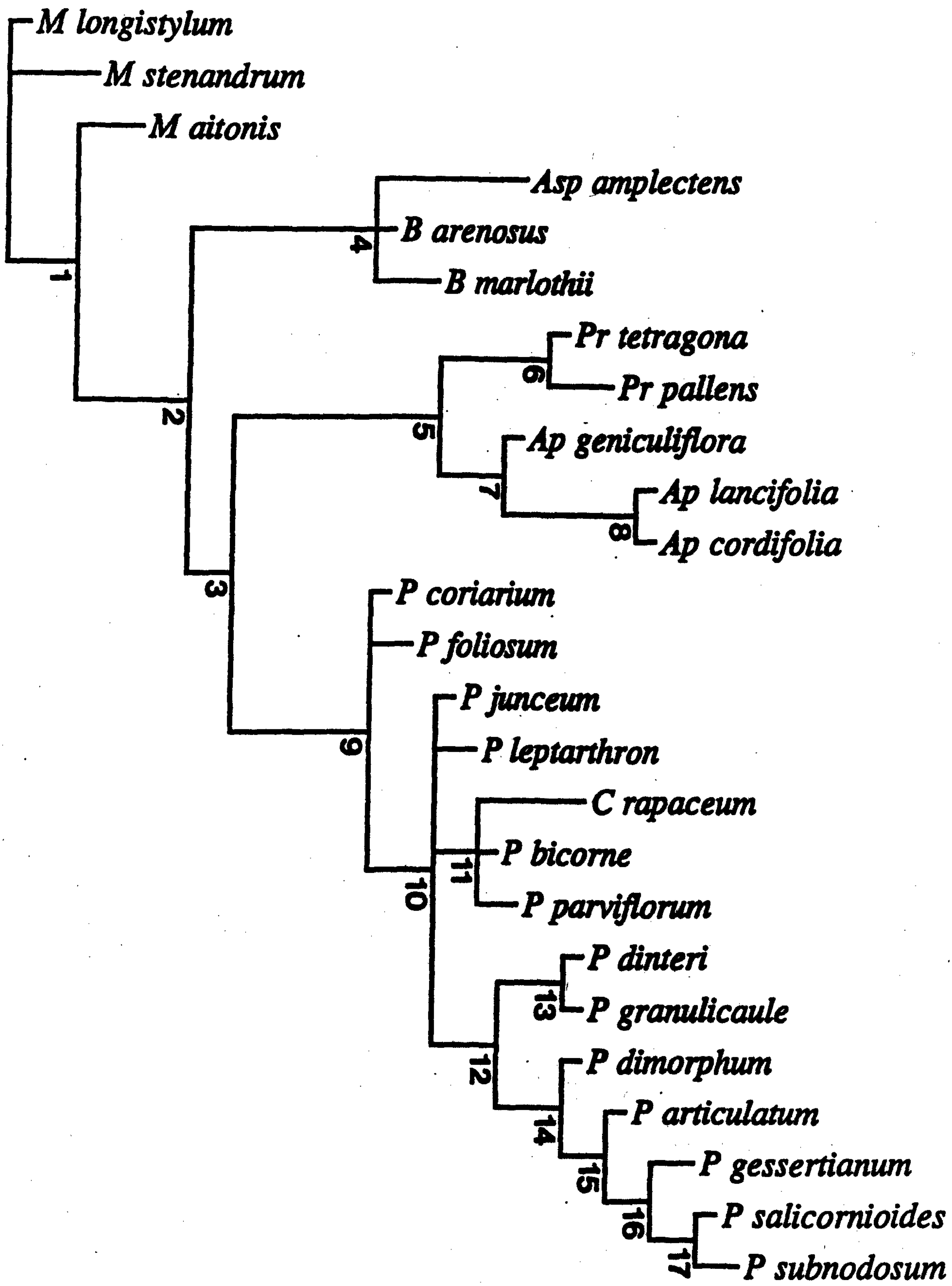


Fig. 15. Strict consensus cladogram.

Psilocaulon.

P. coriarium and *P. foliosum* are at the base of the *Psilocaulon* clade (node 9) and are unresolved. The remaining taxa form a polychotomy consisting of 4 groups (node 10): there are two unresolved taxa (*P. junceum* and *P. leptarthron*) making up two of these groups; *C. rapaceum*, *P. bicorne* and *P. parviflorum* form one clade (node 11) and there remains the "*dimorphum*" subgroup (node 12). The "*dimorphum*" subgroup consists of, in phyletic sequence, the sister pair *P. dinteri* and *P. granulicaule*, *P. dimorphum*, *P. articulatum*, *P. gessertianum* and another sister pair *P. salicornioides* and *P. subnodosum*.

4.1. Character support for the nodes

The sister-group relationship of *Prenia* & *Aptenia* to *Psilocaulon* is supported only by the "presence of filamentous staminodes" (20). This character has evolved in parallel also in *Aspazoma* and reversed twice in *Aptenia* (node 8) and *C. rapaceum* so it has a very low consistency index (0.25).

Mesembryanthemum is the sister to the rest of the study-group, which forms one clade supported by several characters (node 2): "stems with horizontal furrow" transforms to "stems with no horizontal furrow" (reversed at node 16) (4), "loosely packed idioblasts" transforms to "very closely packed idioblasts" (7) "deep nectaries" transforms to "shallow or no nectaries" (26) "valve wings that are reflexed and fused in pairs" become "inflexed" (29) (but reversed in *C. rapaceum*).

To allow detailed examination of support for the monophyly and position of *Psilocaulon* on the cladograms, character state changes for one of the thirty most parsimonious trees are shown in Fig. 16. Three synapomorphies occur at the base of the *Psilocaulon* clade, these are: "widely spaced idioblasts" (7), "filamentous staminodes gathered into a cone" (21) and "filamentous staminodes

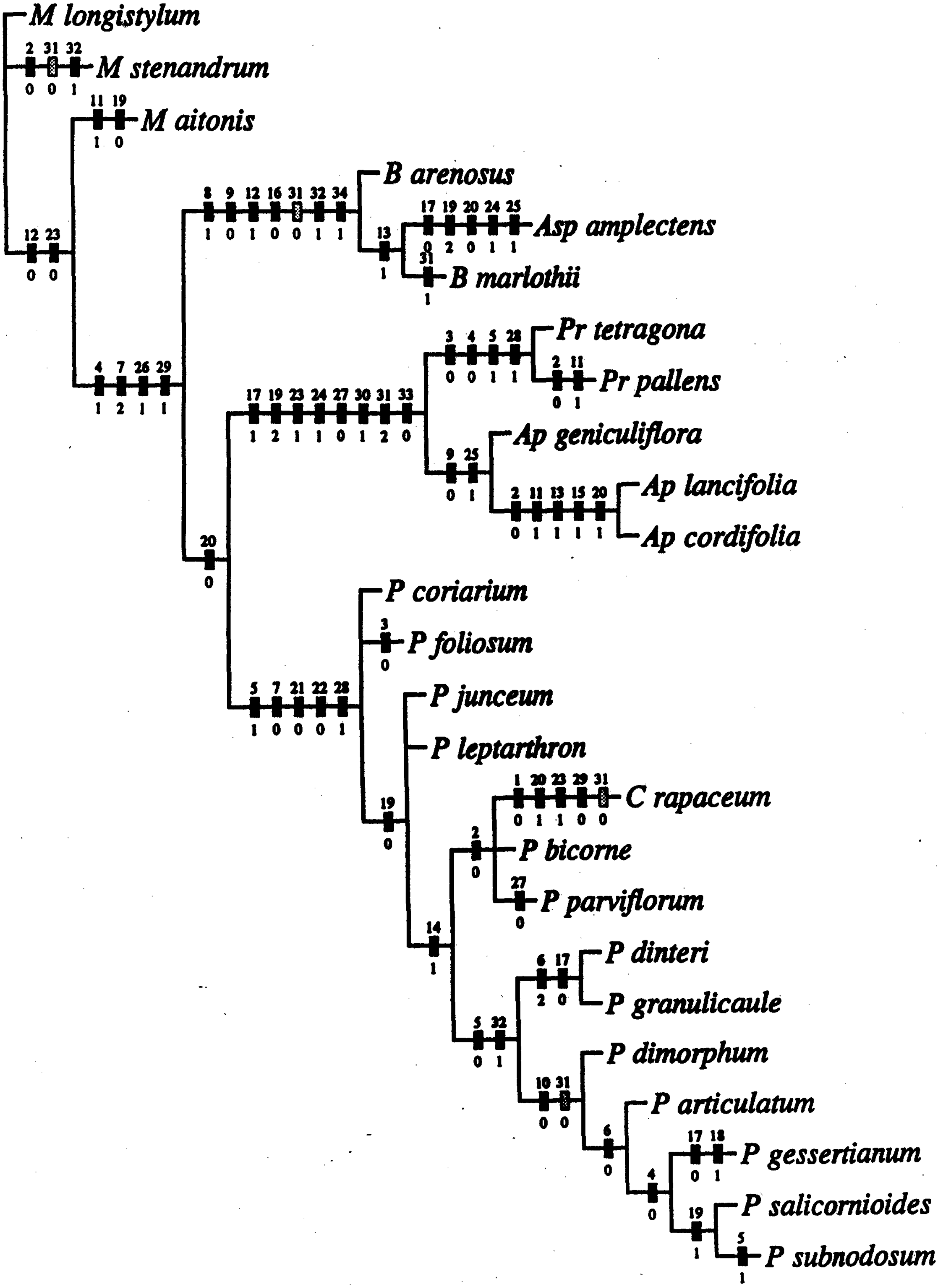


Fig. 16. One of the thirty equally parsimonious solutions showing one possible set of character distributions. Full squares indicate apomorphies, shaded squares indicate homoplasies. The numbers above the squares refer to the characters, the ones below to the character states.

apically lacerate and transparent" (22). Whereas the latter two characters are found in all species of *Psilocaulon* (Table 2), "widely spaced idioblasts" are present in only six species, with a reversal to "idioblasts completely reduced" in the remaining species. The clade is, in addition, supported by two characters which have evolved in parallel in *Prenia*. These are "flattened idioblasts" (5) and "deep locules" (28).

The base of the 4-taxon polychotomy (node 10) is supported by two characters:

(1) "flowers several per axis, single on shorter side shoots" (i.e. character 14): this character is lost in *P. leptarthron*.

(2) "free petaloid and filamentous staminodes" (i.e. character 19): this character is reversed at node 17 which supports the sister group relationship of *P. salicornioides* and *P. subnodosum*. This character has evolved several times in the Mesembryanthemoideae (e.g. in *M. aitonis*).

The *C. rapaceum*, *P. bicorne* and *P. parviflorum* clade is supported by a single character, i.e. "prostrate habit" (2). This has evolved in parallel in other groups, e.g. in *Prenia* and *Aptenia* which gives this character a consistency index of only 0.33.

The "*dimorphum*" subgroup (node 12) is supported by a reversal from "flattened idioblasts" (5) to "protruding idioblasts" and "presence of flattened testa cells" (32), which has evolved in parallel in several other groups (*M. aitonis*, *Aspazoma* and *Brownanthus*) resulting in a low consistency index of 0.33.

The sister-group relationship of *P. dinteri* and *P. granulicaule* is supported by a synapomorphy, i.e. "presence of dome-shaped idioblasts" (6).

The basal node to *P. dimorphum* (node 14) is supported by two characters, i.e. "presence of a mucro" (10) and "ochre seeds" (31). The latter character has evolved in parallel in several taxa (*Brownanthus*, *Aspazoma* and *M. aitonis*) and so has a low consistency index (0.33).

P. articulatum, *P. gessertianum* and *P. salicornioides* are united by the "presence of hairy-like idioblasts" (6) (node 15). (This character does not apply to *P. subnososum* since it has flattened idioblasts.)

P. gessertianum, *P. salicornioides* and *P. subnodosum* are grouped together by a reversal from "stems with a horizontal furrow at node" (4) to "stems without horizontal furrow at node".

4.2. Infrageneric relationships: strength of support for the clades

4.2.1. Single character removal

Characters whose removal results in the loss of the same node(s) are being discussed together.

Removal of "habit" (2, ci = 0.33) causes the collapse of node 11 (Appendix 2).

Exclusion of "stems with or without a horizontal furrow" (4, ci = 0.33) or "presence or absence of mucro" (10, ci = 100) causes the collapse of all nodes within *Psilocaulon*, except nodes 10, 12 and the two sister groups *P. dinteri* & *P. granulicaule* (node 13) and *P. salicornioides* & *P. subnodosum* (node 17).

Exclusion of "idioblasts on stem protruding or much flattened" (5) results in considerable lack of resolution, retaining only the *Aspazoma* & *Brownanthus* clade (node 4), the *Prenia* and *Aptenia* clade (node 5) and the "*dimorphum* subclade" (node 12). This leaves the relationship of seven (i.e. *P. coriarium*, *P. foliosum*, *P. junceum*, *P. leptarthron*, *C. rapaceum*, *P. bicorne* and *P. parviflorum*) of the twenty five species uncertain.

Removal of "shape of idioblasts" (6) causes the collapse from node 10 to 15 and only node 16 and 17 are retained.

Removal of "idioblasts not thickened or thickened" (8), "central water storing tissue present or absent" (12), "fruits with shallow or deep locules" (28), "colour of the seed" (31), "outer walls of testa cells raised into papillae or flattened to smooth" (32) and "testa fold narrow or broad" (34) causes the collapse of nodes 3, 4, 5 and 7, leaving the relationships among the genera *Prenia*, *Aptenia*, *Brownanthus* and *Aspazoma* ambivalent. Removal of character 31, in addition to the loss of the above mentioned nodes, leads to a lack of resolution in the "*dimorphum* subclade" due to the collapse of nodes 14, 15 and 16, retaining only the two sister taxa *P. dinteri* & *P. granulicaule* and *P. salicornioides* & *P. subnodosum*.

The node basal to the *Psilocaulon* clade (node 9) is lost if any one of the following seven characters is removed: "idioblasts on stem protruding or flattened" (5, ci = 0.25), "idioblasts thickened or not thickened" (8, ci = 100), "presence or absence of central water storing tissue" (11, ci = 0.33), "fruits with shallow or deep locules" (28, ci = 0.50), " colour of seeds" (31, ci = 0.33), "testa rough or smooth" (32, ci = 0.33), "testa fold narrow or broad" (34, ci = 100).

Exclusion of "position of single flowers" (14) or "degree of connateness of filamentous and petaloid staminodes" (19) leads to the collapse of node 10. Exclusion of character 19 causes, in addition to the collapse of node 10, the collapse of node 17. Although character 14 is uniquely derived (ci = 1.00), supporting node 10, removal of the homoplasious character 19 (ci = 0.40) alone leads to the collapse of node 10, indicating little overall support for this node.

Removal of "presence or absence of filamentous staminodes" (20, ci = 0.25) results or "presence of short or long styles" (25, ci = 0.50) results in the collapse of node 3 and leaves the sister group relationship to *Psilocaulon* ambivalent.

4.2.2. Dual character removal

Five characters place *C. rapaceum* in *Psilocaulon*. Three of these have a very low consistency index viz. "prostrate habit" (2, ci = 0.25), "idioblasts on stem flattened" (5, ci = 0.25) and "free petaloid staminodes" (19, ci = 0.40). Similarly, the other two characters, i.e. "deep locules" (28, ci = 0.50) and "position of single flowers" (15, ci = 0.50), also show some homoplasy since deep locules are also found in *Prenia* and character 15 reverses once in *Psilocaulon*.

Exclusion of pairs of characters showed that removing characters 2 and 14 or 2 and 19 lead to the exclusion of *C. rapaceum* from *Psilocaulon*, placing it between the *Brownanthus* - *Aspazoma* clade and the *Prenia* - *Aptenia* clade, but not as sister taxon to *Psilocaulon* (Fig. 17, Table 8). The rest of the topology remains largely unchanged, but there is loss of resolution at node 11 and 17. Exclusion of any other combinations of two of the five characters results in all but one case in a loss of resolution and the position of *C. rapaceum* remains uncertain (for character pairs 2 - 5, 2 - 28, 5 - 14, 5 - 19, 5 - 28, 14 - 28, 19 - 28). Removal of characters 14 and 19 results in an increase in resolution of the ingroup.

Table 8. Results of selected dual character removal

excluded	length	trees	ci	ri	position of *Caulipsolon*
2 + 5	64	2420	0.54	0.78	unresolved
2 + 14	66	196	0.53	0.78	outside *Psilocaulon*
2 + 19	62	2424	0.54	0.78	outside *Psilocaulon*
2 + 28	66	1594	0.53	0.77	unresolved
5 + 14	67	418	0.52	0.77	unresolved
5 + 19	63	2419	0.53	0.77	unresolved
5 + 28	65	114	0.53	0.77	unresolved
14 + 19	65	6	0.52	0.77	inside *Psilocaulon*
14 + 28	69	841	0.50	0.75	unresolved
19 + 28	65	2419	0.52	0.76	unresolved

However, in most cases, exclusion of characters causes a considerable increase in the number of trees, indicating the importance of these characters for the resolution of the

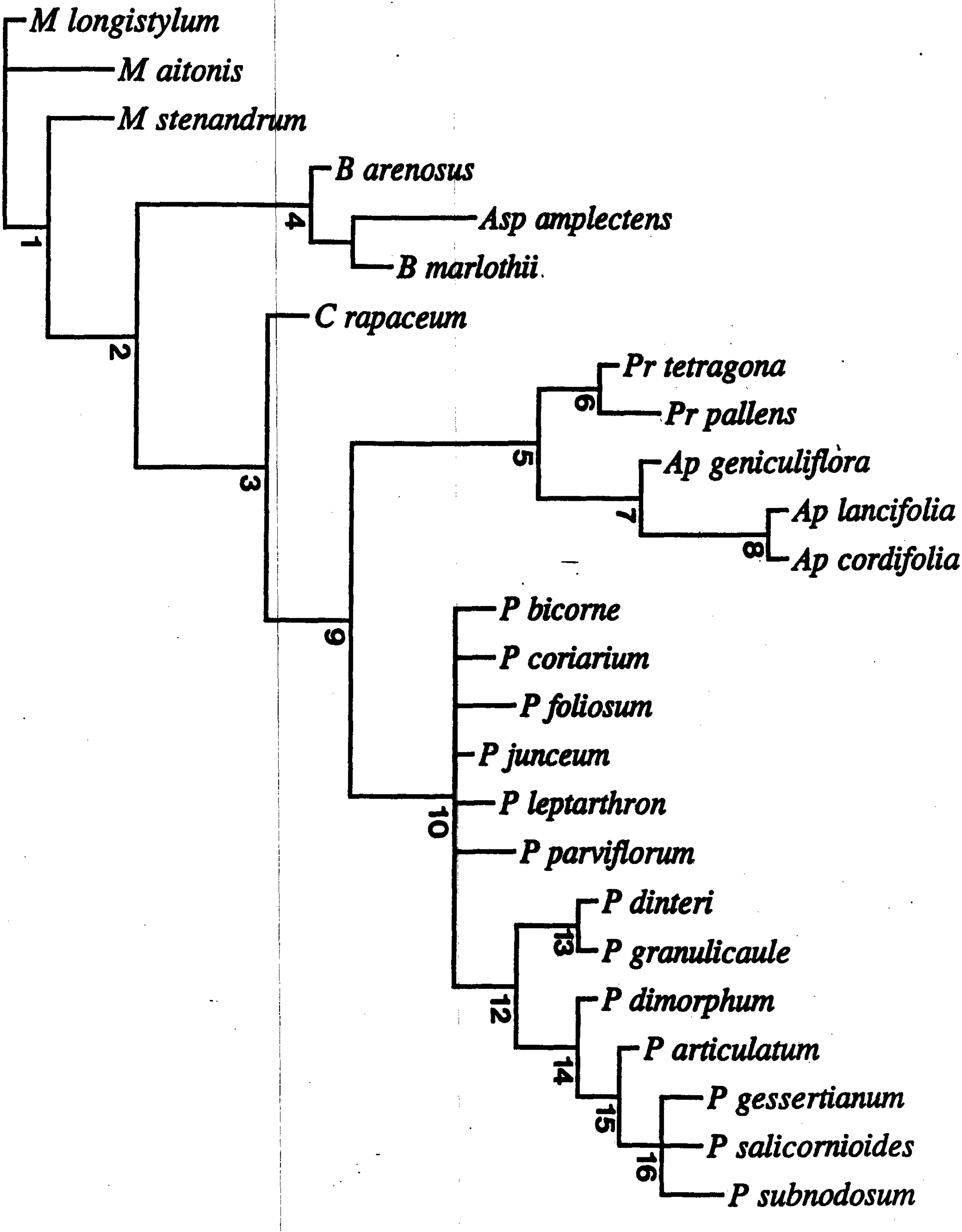


Fig. 17. Strict consensus cladogram generated after removal of characters 2 and 14. Removal of characters 2 and 19 produces the same result.

cladogram.

4.2.3. Taxon removal

Exclusion of either *P. dimorphum* or *P. granulicaule* results in a considerable increase in the total number of trees obtained (Table 9): Exclusion of *P. dimorphum* increases the total number of trees obtained when all taxa are included from 28 to 254. Similarly, exclusion of *P. granulicaule* causes an even greater increase, i.e. to 2508 (overflow). This indentifies these two species as crucial to the resolution of the cladogram. It shows, in addition, that these two species (in particular *P. granulicaule*) possess the character combinations characteristic for *Psilocaulon*. In contrast, removal of any of *P. coriarium*, *P. foliosum* or *P. junceum* leads to a decrease in the total number of trees, suggesting that these species are problematic: they possess character combinations which are unusual for *Psilocaulon*.

It is also noteworthy that the exclusion of numerous taxa among the outgroup increases the numbers of trees obtained which leads to a loss in resolution in the strict consensus tree. This suggests that a wider sampling among outgroup taxa may increase the resolution of the ingroup.

Table 9. Effect of taxon removal on pseudoreplicates in jackknife using Hennig86 (option mh*, bb*).

Taxon deleted	length	ri	trees
none	72	77	28
Mesembryanthemum longistylum	72	75	142
M. aitonis	69	77	42
M. stenandrum	69	77	28
C. rapaceum	68	78	28
Prenia tetragona	72	75	212
P. pallens ssp. *pallens*	70	76	28
Aptenia geniculiflora	72	75	140
A. lancifolia	72	74	28

A. cordifolia	72	74	28
Aspazoma amplectens	66	78	70
Brownanthus arenosus	71	76	118
B. marlothii	71	76	80
Psilocaulon articulatum	72	76	28
P. bicorne	72	76	28
P. coriarium	72	76	10
P. dimorphum	72	76	254
P. dinteri	72	76	28
P. foliosum	71	77	10
P. gessertianum	71	76	28
P. granulicaule	71	76	2514
P. junceum	72	76	6
P. leptarthron	72	76	24
P. parviflorum	71	77	28
P. salicornioides	72	76	28
P. subnodosum	71	77	28

D. DISCUSSION

1. CYTOLOGY

The basic chromosome number for the Mesembryanthema is n = 9 (e.g. WULFF 1940, DE VOS 1947, ALBERS & HAAS 1978), in contrast to the other subfamilies of the Aizoaceae where it is n = 8 (e.g. SUGIURA 1936a, b, BITTRICH 1986). For the Mesembryanthemoideae relatively few chromosome counts have been made. Several of these were made more than 40 years ago (e.g. DE VOS 1947, SNOAD 1951) and the identity of the material investigated is not certain. Within both subfamilies diploid conditions are most frequently recorded (e.g. WULFF 1940, DE VOS 1947, ALBERS & HAAS 1978, HARTMANN 1984, 1986, BITTRICH 1986). Nevertheless tetraploids occur in about 30% of the species in the well-analysed genera (e.g. *Gibbaeum*, WULFF 1944, *Cephalophyllum*, HARTMANN 1986). Hexaploids, on the other hand, are very rare (e.g. in *Brownanthus*, BITTRICH 1986 and in *Cephalophyllum*, HARTMANN 1986).

In this study no diploids were detected in *Psilocaulon* (Table 7). SNOAD (1951) recorded *P. granulicaule* as diploid, although the identity of the specimen on which this count was made could not be verified. Nevertheless, the presence of diploid populations cannot be ruled out as the number of collections investigated in the present study was small and much variation was found within species (Table 7 and below).

A surprising ± 40% of the specimens investigated was found to be tetraploids, ± 17% were hexaploids and a further ± 17% were either tetra- or hexaploids. Although intraspecific variability is known for other genera, it is generally rare (HARTMANN 1988a). So far, *Cephalophyllum* is known to show the largest variation in chromosome numbers within species or specimens (HARTMANN 1986, HARTMANN 1988a). In this study, the sample size was too low to establish the extent of the variability in *Psilocaulon*.

Particularly unusual is the occurrence of very high ploidy levels in three species of *Psilocaulon* with 2n = ± 126-142. High chromosome numbers were found previously by DE VOS (1947) in *Phyllobolus spinuliferus* (Haw.) Gerbaulet with n = ± 54-63.

Polysomaty of the root periblem (WULFF 1940), a phenomenon whereby chromosome sets double or multiply in certain cells of the root, has been known to make the establishment of somatic counts difficult. The technique used in this study does not allow for the recognition of the different cell types. However, a comparison of several samples allows for some confidence in the results (Table 7). Polysomaty of the root periplem has been observed in *Cephalophyllum*, but is apparently absent in *Psilocaulon*. However, the chromosome numbers vary between populations, as they do in some species of *Cephalophyllum* (HARTMANN 1983b, HARTMANN 1986, 1988a).

WULFF (1944) reported an overall correlation between ploidy level and morphology, such as degree of succulence. However, in *Psilocaulon* there seems to be no relationship between the degree of succulence and the chromosome numbers and for *Jordaaniella* H.E.K. Hartmann a negative relationship was found between succulence and ploidy levels (HARTMANN 1984). However, at a higher taxonomic level it appears that polyploids are particularly apparent among the stem succulents in the subfamily (i.e. in *Aptenia*, *Brownanthus* and *Psilocaulon*), whereas fewer polyploids are found among the remaining genera (cf. BITTRICH 1986). *Phyllobolus spinuliferus*, which was found to have a high ploidy level, has exceedingly succulent stems (GERBAULET, in press). On the other hand, numerous species of *Brownanthus* and *Aptenia cordifolia* are diploids, indicating that stem succulence is not induced by polyploidy only. This view is further supported by a comparison with other groups in the Centrosperms: for example in the Didieraceae the numbers range from 2n = 48 to 2n = ± 240 (SCHILL *et al.* 1974).

As well as correlations between succulence and ploidy levels, certain growth forms have been associated with different ploidy levels: in the Poaceae, polyploidy is widespread among rhizomatous species giving them the ability to colonize new habitats, whereas diploidy prevails in caespitose and annual species (STEBBINS 1971). Although *Psilocaulon* makes no adventitious roots, several species of *Psilocaulon* have a creeping habit (i.e. *P. bicorne*, *P. parviflorum*) whereas others are even able to adopt both a creeping and decumbent to upright habit (i.e. *P. dinteri*, *P. salicornioides*, *P. articulatum*). For *P. dinteri* and *P. salicornioides* it is known that their chromosome number is variable. However, it is not known whether this variability may correlate with the environment or whether the variability may simply allow for greater adaptability to the different requirements of the habitat. In *Cephalophyllum* the majority of species with a creeping habit were tetraploids, although diploids were also found among creeping species and therefore it is evident that the creeping habit is not induced by polyploidy alone (HARTMANN 1986, 1988a).

The sample size investigated in this study has been very small and correlations to morphology or habit may therefore be incidental. In order to circumvent this it would be necessary to either include phylogenetic information in the analysis or to compare polyploidy within one species. Thus for a future study the sample size would need to be increased so as to cover the variation within the taxon.

It has been recognized that polyploidy is a significant factor in plant evolution (e.g. GRANT 1981). Within the Aizoaceae *s.l.* WULFF (1944) found 36% to be polyploid, which is considerably higher compared to other succulent groups such as the Stapelieae (Asclepiadaceae) where only 16% are polyploid (ALBERS 1983). Previously it was considered that polyploids mostly arose through hybridization and consequently autopolyploidy was thought to be extremely rare compared to allopolyploidy (Stebbins 1950). However, more recent research showed that autopolyploidy is not that rare (e.g. LUMARET &

BARRIENTOS 1990, SOLTIS *et al.* 1989, WOLF *et al.* 1990). Indeed, recent research on the evolutionary dynamics of polyploid plants has drawn attention to the biological diversity of polyploid origins and establishment and the need to recognize polyploidy as an integral component in the evolution and maintenance of biodiversity, which may or may not involve the generation of new species (THOMPSON & LUMARET 1992).

In the Mesembryanthema there are examples that may corroborate the idea that polyploidy is involved in the generation of new species: in *Cephalophyllum* the highest proportion of tetraploids occurs where the highest diversity of species and the highest number of endemic species were found (HARTMANN 1988). Two areas are involved: one north of 29°S (Richtersveld and Southern Namib), and second between 31°-31°30'S and 18°-18°45'E (Knersvlakte). It was therefore suggested that both areas represent evolutionary centres and it seems that polyploidy developed independently in both regions. This interpretation points towards the hypothesis that in *Cephalophyllum* -- in contrast to other genera in the family -- chromosomal evolution may have taken place (HARTMANN 1988). A similar situation is found in *Brownanthus*: here the centre of diversity is in the Richtersveld (BITTRICH 1986) which is also where the highest number of polyploids is found.

In *Psilocaulon* there are no centres of diversity. Therefore, correlations between diversity and ploidy levels cannot be found. Instead it appears that polyploidy may have contributed to the great adaptability of *Psilocaulon*: its distribution range covers almost the entire area in southern Africa where the Mesembryanthema occur. It occurs in a wide variety of habitats, with almost an equal number of species found inside the winter-rainfall area as outside it (see below for detailed discussion).

An increase in heterozygosity has been found likely to provide genetic advantage to polyploids (SOLTIS & RIESENBERG 1986). This may enable them to colonize different habitats, since increased internal genetic variation should improve the ability of individuals to respond to different environmental conditions. However, further experiments are needed to determine the contribution of increased heterozygosity to the maintenance of fitness over a range of environments (THOMPSON & LUMARET 1992). Thus, despite the ubiquity of polyploidy in plants, the population processes influencing the evolutionary dynamics of polyploids remain poorly understood.

Despite the low sample size that has been investigated, it appears that *Psilocaulon* is another genus where evolution at a chromosomal level has taken place, and this may have contributed to its success. On the other hand, variability in chromosome numbers in a species is closely linked to character introgression. This may lead, as in *Cephalophyllum*, to difficulties in naming material, particularly if it is incomplete (HARTMANN 1988).

Chromosome numbers were not included in the phylogenetic analysis due to uncertainty as to how variable these were within species. In addition, as was suggested for *Cephalophyllum*, polyploidy may have arisen several times, so that species with the same chromosome number may not necessarily be closely related.

2. PHYTOGEOGRAPHY

It is evident that the distribution area of *Psilocaulon* is remarkably wide compared with those of most genera in the Mesembryanthema, which have mostly very local distribution patterns (IHLENFELDT 1994). Other widespread genera are *Aptenia*, *Brownanthus*, *Phyllobolus*, *Mesembryanthemum* and *Delosperma* (BITTRICH 1986, HARTMANN 1991). *Brownanthus* is noteworthy in that most of its distribution area coincides with that of *Psilocaulon* (BITTRICH 1986). Both genera belong to the Mesembryanthemoideae and their distribution illustrates a remarkable characteristic of this subfamily: although it consists of only ten genera (out of ± 119), it covers two thirds of the entire area of the family (BITTRICH 1986, HARTMANN 1991).

1. CHARACTERISTICS OF THE BOUNDARY AREAS

The frequency of species decreases from about 27° S northwards. The same situation is found in the Mesembryanthemoideae as a whole (BITTRICH 1986). North of Lüderitz the genus is represented by only three species: of these *P. salicornioides* and *P. coriarium* are sympatric in many areas as far north as ± 24°S. In the northern parts of Namibia only *P. salicornioides* has been recorded. Remarkable, however, is the occurrence along the southern coast of Angola of another species, *P. dimorphum*, which is restricted to the northernmost edge of the distribution area of the genus. Such marginal speciation has also been observed in other genera such as *Leipoldtia* L. Bol. (HARTMANN 1987). As the southern coastal area of Angola is very poorly collected, it is quite possible that *P. dimorphum* and *P. salicornioides* are sympatric. Apart from a single species of *Lithops*, only members of the Mesembryanthemoideae (in fact only *Mesembryanthemum*, *Brownanthus* and *Psilocaulon*) occur as far north as Angola. In contrast to *Psilocaulon*, *Brownanthus* and *Mesembryanthemum* are represented in this area by widespread species such as *B. kuntzii* (Schinz) Ihlenf. & Bittrich (BITTRICH 1986), *M. crystallinum* L., *M. cryptanthum* Hook.f., *M. gürichianum* Pax (GERBAULET in press).

Along the eastern boundary of the distribution area the genus is often represented by two to three species (out of a maximum of five). Therefore, along this zone the number of species does not gradually decrease and the genus disappears quite abruptly.

The number of species is low in the northern Great Karoo, Bushmanland and Gordonia, where *Psilocaulon* is mostly represented by a single species or is often absent. This phenomenon has been shown to be typical for the Mesembryanthema as a whole (HARTMANN 1991). Possible explanations may be sought in the ecological requirements of the taxa (see discussion below), rather than in low collection density.

There is also a notable absence of *Psilocaulon* from the high-rainfall, mountainous areas of the south-western Cape. A possible explanation for this may be found in the geology of this area: although tolerant of a wide variety of soils, *Psilocaulon* is never found growing on soils derived from Table Mountain sandstones.

2. CENTRES

There is a remarkable absence of distinct centres of diversity in *Psilocaulon*: five species per 30′x 30′ square is found once (Worcester - Robertson Karoo, in the half-degree grid square 3319B), while a density of four species is found in many, widely scattered, half-degree squares in the western portion of southern Africa. Examples of two other widespread genera indicate that distribution patterns are specific to a genus (cf. HARTMANN 1987): *Brownanthus* has its highest diversity of about eight species (out of 11) in the Gariep centre (*sensu* NORDENSTAM 1969), with several species endemic to this area (BITTRICH 1986). *Cephalophyllum* N.E. Br. exhibits two centres of diversity, the Vanrhynsdorp centre (*sensu* NORDENSTAM 1969) and the Gariep centre. Both areas have been identified as centres of generic diversity for the Mesembryanthema as a whole (HARTMANN 1991) and were, in addition, "important for the succulent Karoo flora" generally (NORDENSTAM 1969). These centres were shown to be a consequence of the intersection of distribution areas of widely distributed taxa with those of endemic or relatively localized taxa (e.g. subtribe Leipoldtiinae Schwantes ex H.E.K. Hartm., HARTMANN 1987).

In *Psilocaulon* there are no highly localized species: most are adapted to a wide range of ecological requirements (cf. ecology) and consequently their distribution areas are fairly large. This may explain the absence of centres of high species density in *Psilocaulon*.

3. LOCALIZED SPECIES

Despite the absence of highly localized or endemic species, there are species with a limited distribution area. Two are restricted to Namaqualand:

(1) *P. leptarthron* is largely confined to the Knersvlakte (degree grid square 3118) with a few outliers towards the north-east (Fig. 12);

(2) *P. foliosum* is restricted to the western region of Namaqualand (2917, 3017) along the low-lying (0-500m) coastal strip (Fig. 10).

One species, *P. parviflorum*, is confined to the south-western Cape. It is found in low-lying areas not exceeding 500m. *P. dimorphum* is restricted to the coastal areas of south-western Angola.

In contrast to these, *P. gessertianum* is restricted to the central parts of Southern Namibia (Fig. 10). Whereas the first three species are confined to the winter-rainfall area (defined here as the area receiving a maximum of rainfall between June and July) the latter two are found in areas receiving maximum precipitation in March (Fig. 6.6 in ZUCCHINI & ADAMSON 1984).

The phylogeny that has been generated for *Psilocaulon* (Fig. 15) shows *P. dinteri* - *P. granulicaule*, *P. salicornioides* - *P. subnodosum* and *P. bicorne* - *P. parviflorum* as pairs of sister species. Although great care has to be taken in interpreting a phylogeny of a group as young as this (discussed in more detail below), it is interesting to note that in each of the above pairs of sister species the members of the pair occur allopatrically (Fig. 18). Consequently *Psilocaulon* can be described as a genus whose species are mostly widespread but also largely vicariant. Correlations to certain ecological patterns, such as seasonality of rainfall, are most closely associated with these trends

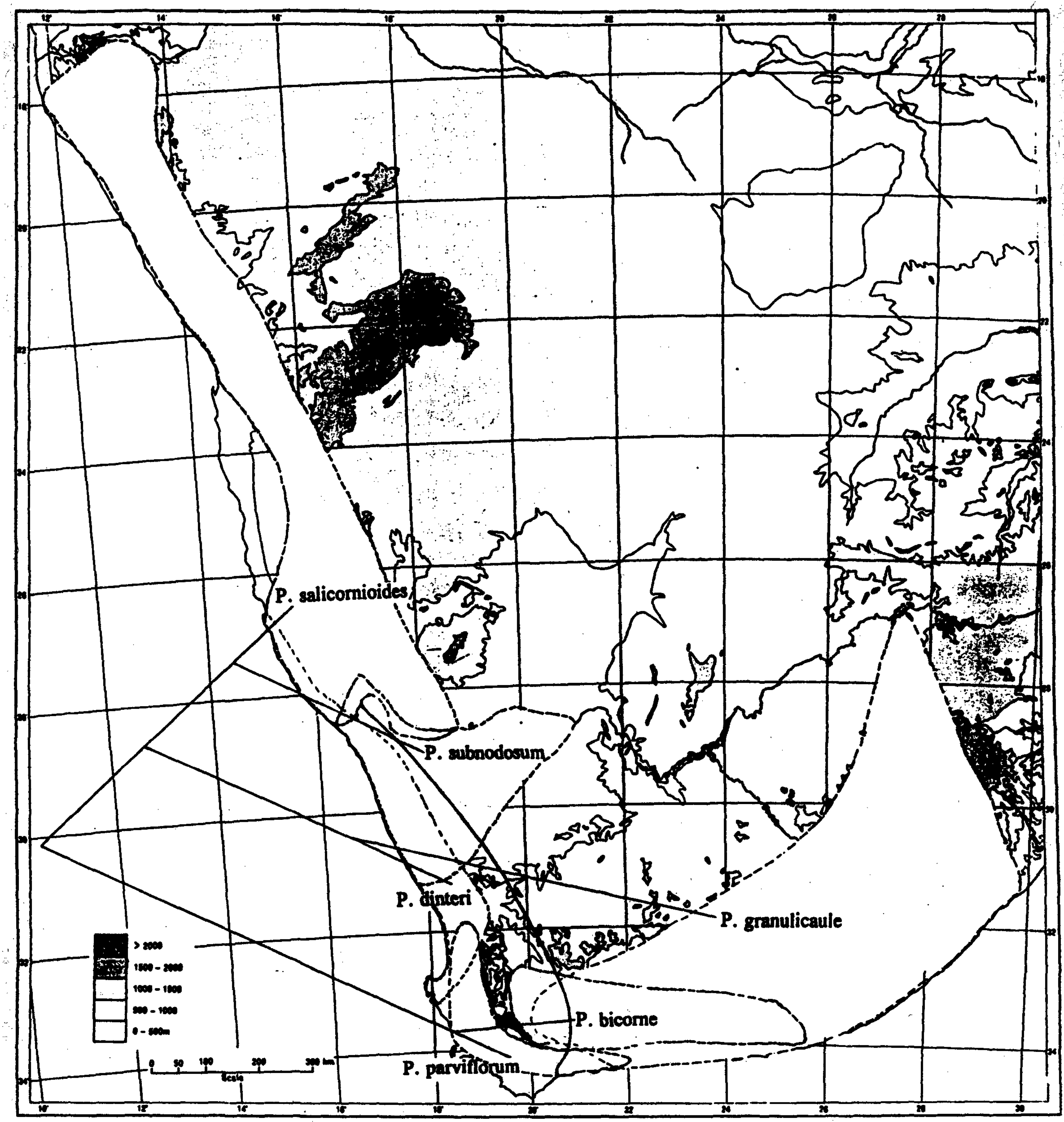


Fig. 18. Distribution of sister species of *Psilocaulon* in southern Africa. Most sister species are widespread, but also vicariant with each member of a pair being found in a different rainfall regime. The dashed lines indicate the boundaries of the distribution area of a species. To the west of the solid line is the region of winter rains (maximum rainfall in June and July); to the east the maximum rain is received outside winter (simplified from ZUCCHINI & ADAMSON 1984, Fig. 6.6.).

(discussed in more detail below).

3. ECOLOGY

3.1. Habitat

The distribution of *Psilocaulon* can only be understood in connection with the ecology of the genus (cf. JÜRGENS 1987, 1990).

Psilocaulon consists of weedy or pioneering plants, which are hardly ever found in undisturbed vegetation. The species show a preference for disturbed habitats, which may be either artificially created (e.g. roadsides, overgrazed areas by livestock) or natural (e.g. "heuweltjies", coastal sands, overgrazing and/or trampling by game) (IHLENFELDT & BITTRICH 1985, ESLER 1993).

Possibly as a consequence of their weedy nature, plants grow on a wide variety of soils. Although most species have been observed to be tolerant of some salinity, very saline coastal sands appear to have been most successfully exploited by *P. dinteri* and *P. salicornioides*, which may then often form monospecific stands (cf. IHLENFELDT & BITTRICH 1985). At these localities, *P. dinteri* is often found growing amongst species of *Arthrocnemum* (Chenopodiaceae), to which it bears a striking superficial resemblance.

In contrast *P. parviflorum*, which only occurs within 60 km of the coast of the south-western Cape, appears to be unable to colonize sandy habitats and remains restricted to loamy - clayish soils, often with a covering of quartz gravel. Similarly, *P. leptarthron* prefers firm, red, calcareous loams of the Knersvlakte.

Although preferences for certain edaphic factors can be observed in some species of *Psilocaulon*, these factors seem to be relatively minor in determining distribution patterns. In terms of soil factors, it has been shown for other genera that patchy occurrence can be correlated to differences in soil characters, such as ion content, pH and conductivity (JÜRGENS 1987). In fact high generic frequencies in the Gariep centre have been attributed to the rugged mountains and rich geological diversification offering numerous microclimates (JÜRGENS 1987). In contrast the Little Karoo and Vanrhynsdorp centres are less varied from the point of view of topography and it was shown that the edaphic and related ecological mosaic give rise to the diversity (JÜRGENS 1987).

Precipitation patterns are generally considered to have a large-scale influence on the distribution of the Mesembryanthema (JÜRGENS 1987, HARTMANN 1991). An abundance of succulents was shown to be associated with areas of low but predictable rainfall (ELLENBERG 1981, HOFFMAN 1987, BURGESS & SHMIDA 1988, VON WILLERT *et al.* 1992, COWLING *et al.* 1994). In addition, COWLING *et al.* (1994) found that seasonality of rainfall, particularly the occurrence of winter-rainfall, was the strongest predictor of the total number of succulents per site (cf. WERGER 1978).

In the Mesembryanthema it has been shown that the most speciose area may be correlated with winter-rainfall of less than 200 mm per year combined with the presence of sea fogs, coinciding largely with the leaf-succulent zone defined by JÜRGENS (1987). In addition, JÜRGENS (1990) related the extent of the leaf-succulent zone to temperature and showed that it coincides with the area circumscribed by the 32 °C isoline. He argued that CAM, the phytosynthetic pathway by means of which most Mesembryanthema assimilate (e.g. VON WILLERT 1979), operates best under these conditions. In contrast, higher mean maximum temperatures (≥ 32,5 °C) are more favourable for large stem-succulents (JÜRGENS 1990). *Psilocaulon* occurs within this leaf-succulent zone, but extends well beyond it as well (Fig. 14). *Psilocaulon* appears to be one of the most tolerant genera in the Mesembryanthemoideae with respect to amounts and seasonality of rainfall, but is absent from regions receiving ≥ 500 mm median annual rainfall (Fig. 6.2 in ZUCCHINI & ADAMSON 1984).

Similarly, the distribution patterns of individual species may be best understood in terms of the precipitation patterns and two groups may be delimited:

(1) species which only occur in the winter-rainfall region, or have at least their main distribution in the winter-rainfall zone and may extend further beyond it. These are *P. leptarthron*, *P. parviflorum*, *P. foliosum*, *P. dinteri*, *P. junceum* and *P. subnodosum*.

(2) species which either occur only outside this area (i.e. *P. gessertianum*, *P. dimorphum*) or have their main distribution outside the winter-rainfall area (i.e. *P. articulatum*, *P. bicorne*, *P. coriarium*, *P. granulicaule* and *P. salicornioides*).

About half the species of *Psilocaulon* occur outside the winter-rainfall zone. This is the first case of its kind to be reported for the Mesembryanthema. Some genera may be distributed exclusively outside the winter-rainfall region (e.g. *Khadia* N.E. Br., *Aptenia*). There are also a few genera (*Delosperma*, *Hereroa* and *Lithops*) most of whose species occur outside the winter-rainfall area with a few extending into it. Most of the remaining genera have the majority of their species in the winter-rainfall area with possibly a few members extending beyond this or restricted to areas outside it (e.g. *Brownanthus*).

The unusually high proportion of species that have adapted to a non-winter-rainfall pattern gives further support to the idea that *Psilocaulon* has a particularly high ability to adapt to diverse environmental conditions. This may, in turn be a consequence of its genetic variability (cf. cytology).

As shown above, sister species are largely vicariant and different rainfall regimes are associated with these patterns: in each of the above pairs of sister species the members of the pair occur in areas subject to different rainfall regimes (Fig. 18). Thus differentiation does not seem to have occurred first into winter- and non-winter-rainfall species (which would have implied that all winter-rainfall species were more closely related to each other than to the non-winter-rainfall species). Instead, differentiation into winter-rainfall and non-winter-rainfall elements seems to have occurred several times. Therefore, different precipitation regimes appear to have influenced the speciation events in *Psilocaulon* strongly.

3.2. Ecological factors influencing the morphology and habit of the stems.

3.2.1. Saline habitats

Stems of *P. dinteri* were found to be far more articulated and succulent when growing in a saline environment (Fig. 3 C). This corresponds with the findings of Friedrich (1961, unpublished notes on herbarium sheet, *Jensen s.n.* (M)) who found that plants of *P. salicornioides* that were grown from seed and watered with a saline solution (2/000) were found to have thicker stems than those that had been given tap water. The observations made for *Psilocaulon* are largely based on field observations. In order to substantiate the above findings controlled experiments are necessary to establish how much variability is due to environmental influences or may be due to genetic impacts.

3.2.2. Solar radiation

The thickness of the waxy layer is thought to be a function of ecological conditions, in particular of the amount of solar radiation the plant receives (OBERSTEIN 1910, HARTMANN 1978, 1979). This theory is confirmed in the present study, where specimens of *P. subnodosum* which were collected in Namibia had a far more glaucous colour than those growing in Namaqualand. This suggests that the role of the waxy cover lies in protecting underlying tissue from solar radiation (cf. ELLER 1979, BARTHLOTT & WOLLENWEBER 1981). In this study no measurements of the thickness of the wax layer was made, so that the apparent pattern needs to be substantiated by experimental evidence.

3.2.3. Availability of water

According to IHLENFELDT & HARTMANN (1982) the density of distribution of idioblasts on the surface of the stems varies between widely spaced and very closely packed idioblasts.

In *Psilocaulon* the idioblasts are widely spaced. However, there are slight differences in density both within and between species. The density of protruding idioblasts may be influenced by the availability of water (cf. BITTRICH 1986). Although it is possible that variation in density and presence or absence of idioblasts is genetically determined, it appears likely that the idioblasts function as water storage cells and may therefore diminish as soon as the stored water is translocated. This idea is certainly supported by the observation that in some species, with an otherwise smooth epidermis on their stems, idioblasts are found in the inflorescence (on and just below the calyx). These idioblasts disappear as the flower and later the fruit mature (see also BITTRICH 1986). In the case of the idioblasts of the stem it was noted in *P. dinteri* that they may become undetectable to the naked eye, but vestiges can still be detected under the SEM (IHLENFELDT & BITTRICH 1985). This indicates that they may only change their size.

The variations in stem morphology which have been discussed above are mainly based on field observations. No experimental work which may test the impacts of environmental influences have been done in this study. However, it shows that care needs to be taken in interpreting features, such as a thick wax cover, for use in a phylogenetic study (e.g. GERBAULET 1995). Thus, more experimental work is needed to show how stem morphology may be modified by selected environmental factors.

3.3. Pollination

The flower of *Psilocaulon* belongs to the *Ruschia*-type (*sensu* VOGEL 1954). Such flowers are pollinated by insects while they forage for pollen ("head pollination" *sensu* VOGEL 1954). The apparent lack of nectaries or their very small size suggests that the insect may only be rewarded with pollen.

Pollination biology in the Mesembryanthema has received very little attention. Certain species of bees and butterflies are known to visit the flowers (STRUCK 1995, JÜRGENS pers. comm.). The white flowers of *P. foliosum*, which remain open at night, may also be visited by moths.

3.4. Dispersal

In the Mesembryanthema dispersal is achieved by water or rain (ombrohydrochory), wind (anemochory) or animals (zoochory), although ombrohydrochory is most common (HARTMANN 1991).

1. Ombrohydrochoric dispersal starts with the hygrochastic opening of the capsule, brought about either by rain or by moisture in the air such as that brought by fog or mist. The seeds are washed out by water which has collected in the capsule and are carried further by the water (wash-out dispersal, HARTMANN 1988b). Alternatively, seeds are removed by the splash-cup mechanism (BRODIE 1951), whereby raindrops which fall into the centre of the open capsule are reflected, taking with them one or more seeds. Both modes of dispersal are short-range and the seeds remain in the vicinity of the mother plant. This has been interpreted as an adaptation to arid environments: conditions near the mother plant are likely to be advantageous

(ZOHARY 1937). Hygrochastic capsules are interpreted as antetelechoric structures (STOPP 1958, ELLNER & SHMIDA 1981), in which removal of seeds during dry periods is prevented. However, several structures have evolved to inhibit the escape of seeds even during wet periods, allowing for a more gradual dispersal from the capsule (e.g. IHLENFELDT 1959, 1983). In *Psilocaulon* this may be achieved by the presence of valve wings, which are inflexed to form a pocket. They are thought to retain some of the seeds (SCHWANTES 1952, IHLENFELDT 1959, BITTRICH 1986, Fig. 1 A). However, such pockets are not closed and so all seeds may eventually escape.

Seed retention is furthermore achieved by the deepening of the capsules (Fig. 1 B). In the case of *Caulipsolon* the locules are as much as 10 mm deep and it appears likely that many of the seeds will only escape once the capsule has decomposed (STOPP 1962).

2. Dispersal by wind of entire dried plants, which are rolled along the ground, was reported for some *Psilocaulon* species growing in flat areas in Bushmanland, northern Cape (BITTRICH 1986). If this were the case, seeds would be distributed over a larger area since the less stable capsules will fall off or be destroyed in the rolling process (BITTRICH 1986). This mode of dispersal may contribute to the species' wide distribution range. However, I have been unable to verify the existence of this phenomenon in *Psilocaulon*.

3. Epizoochory has been described by DEAN *et al*. (1990) for several Mesembryanthema, amongst them species of *Psilocaulon*. Twigs with either fruits or short shoots have been found among material used in the construction of nests. These are thought to have been collected for their interlocking capacity to serve as the basic building material of the nests. MILTON (1992) also reported endozoochory for several members of Mesembryanthema (e.g. *Sceletium* sp., *Phyllobolus* sp.) by leopard tortoises

(*Geochelone pardalis*) in the southern Karoo. Several genera of Mesembryanthema found during that study remained unidentified. However, it appears likely that parts of *Psilocaulon* are eaten and dispersed by tortoises (MILTON, pers. comm.).

The modes of dispersal found in *Psilocaulon* are diverse: They include both short and long range dispersal. In addition, several structures promote seed retention through time. Thus, the presence of such diversity is likely to have contributed to the wide distribution of the genus.
Again, some comment on the need for experimental verification of these anecdotal observations. Seems to be the bottom line is that we understand rather little about the biology of the mesembryanthema

3.5. Germination

Most seeds of *Psilocaulon* are recalcitrant and are therefore difficult to germinate, confirming earlier observations (IHLENFELDT & BITTRICH 1985, BITTRICH 1986). Only *P. dinteri* and *P. gessertianum* were found to show "reduced recalcitrance" (IHLENFELDT & BITTRICH 1985), although the exact percentage of seeds which germinated was not stated. Differences in degree of recalcitrance between species has been observed previously in e.g. *Brownanthus* (IHLENFELDT & BITTRICH 1985). The observation made here in *P. dinteri*, however, suggests that in *Psilocaulon* there is also variation within species, since the population near the sea showed a lack of recalcitrance whereas populations from further inland did not germinate unless pretreated.
Differences in germination behaviour among different populations has previously been recorded in *Vanzijlia annulata* (A. Berger) L. Bolus (HARTMANN 1983a). There the population near the coast had a slight lag phase compared to those growing inland. The difference was attributed to adaptation to the different

habitats. In contrast, in *P. dinteri* the pattern is reversed. So clearly the explanation given for *Vanzijlia* cannot be extrapolated to this genus.

Psilocaulon plants are relatively short-lived plants. It is therefore remarkable that occasionally there are specimens with seeds germinating in large numbers within a short period of time, which is a characteristic of long lived plants (IHLENFELDT 1985).

The mechanisms that lead to the different degrees of recalcitrance are far from being fully understood. Recalcitrance may be a result of the "hardseededness" (GILL 1977), which may prevent either water or oxygen (cf. VAN STADEN & BROWN 1977) from penetrating the seed coat. Treatment of the seed with KOH (50 g in 100 ml water), which corrodes the seed coat (LEISTNER 1959), or by slitting it with a razor blade is known to increase the number of germinating seeds in recalcitrant Mesembryanthema (e.g. IHLENFELDT & STRUCK 1987, LIEDE 1990).

The natural equivalent to these treatments may be found in the abrasion of the seed coat by external factors such as sand (IHLENFELDT 1985). However, there is evidence that recalcitrance may be a consequence of internal, physiological factors (GUTTERMANN 1980). In the case of *Psilocaulon*, slitting of the seed coat resulted in almost 100% germination, which indicates that external factors may be responsible for recalcitrance.

4. PHYLOGENY

4.1. Relationships to other genera

IHLENFELDT & BITTRICH (1985) originally thought a close relationship between *Psilocaulon* and *Brownanthus* possible due to the presence of neotenic seeds in both genera. However, BITTRICH (1986) remained uncertain about the position of *Psilocaulon* and suggested a position between *Brownanthus* and *Mesembryanthemum* subg. *Mesembryanthemum*, without giving details of his reasoning.

GERBAULET (1995) suggested that *Aspazoma*, *Brownanthus*, *Aptenia* and *Psilocaulon* were most closely related due the presence of succulent stems in all four genera. In addition, GERBAULET (1996) argues that *Aspazoma*, *Brownanthus* and *Aptenia* are more closely related to each other than they are to *Psilocaulon*. She bases this relationship on the similarity of the epidermis of the stems.

The relationships of *Psilocaulon* to other genera of the Mesembryanthemoideae may be discussed under five major headings:

1. STEMS

The stems are of particular importance in evaluating the relationships of *Psilocaulon*, since (with one exception) they are succulent and this character state is considered to be derived from scarcely succulent stems (BITTRICH 1986, GERBAULET 1995). Numerous characteristics are associated with the stems and some of them indicate relationships to other taxa.

Some species of *Ruschia*, especially those of the *Ruschia grisea* (L. Bol.) Schwant. - *Ruschia crassa* (L. Bol.) Schwant. alliance have stems that appear to be succulent and superficially resemble those of *Psilocaulon* - the resemblance between those and *P. subnodosum* in the drier parts of its distribution may be quite striking. However, in *Ruschia* it is the leaf sheath which forms a cylinder around the stem for some distance and from this the stem derives its succulent appearance.

(1) Anomalous secondary thickening is well known for the Mesembryanthema (e.g. REGNAULT 1860, FALKENBERG 1876, DANNEMANN 1883). Two types of secondary thickening, i.e. the concentric type and the cylinder type were found in the Mesembryanthemoideae (BITTRICH 1986, GERBAULET 1995). The cylinder type was found to be widespread, while the concentric type appears to be restricted to species of *Phyllobolus* (GERBAULET 1995). Thus the type of anomalous secondary thickening is uninformative on the relationships of *Psilocaulon*.

(2) Particularly noteworthy is the presence of cortical

bundles. These were recorded for the first time by DANNEMANN (1883) in *Sphalmanthus splendens* and SOLEREDER (1899) in *Mesembryanthemum crystallinum*. In species with a persistent green cortex, such as *Psilocaulon*, *Brownanthus*, *Aptenia* and *Aspazoma*, cortical bundles are particularly numerous and form a mesh-like structure (BITTRICH 1986). Such cortical bundles are widespread in the Mesembryanthemoideae, but are absent in most of the Ruschioideae and in the remaining subfamilies of the Aizoaceae (BITTRICH 1986). Within the Mesembryanthemoideae they are completely reduced only in *Aridaria* and in *Phyllobolus lignescens* (L. Bolus) Gerbaulet (GERBAULET 1995). In contrast, there are relatively few in woody species (GERBAULET 1995). The presence of cortical bundles is, however, not restricted to the Mesembryanthema, but appears to be a feature of stem-succulents in numerous families within the Centrospermeae, such as the Cactaceae and Chenopodiaceae, e.g. *Arthrocnemum* (FAHN 1982).

Previously stem-succulence had been one of the major guidelines, apart from small flower size, for placing a species in *Psilocaulon s.l.* (including *Brownanthus*) (IHLENFELDT & BITTRICH 1985). However, in more recent generic delimitations based on common ancestry, stem-succulence was shown to be a characteristic of several genera (IHLENFELDT & BITTRICH 1985).

One species, *P. foliosum*, was found to lack stem-succulence and has instead evolved a more woody growth. It has been suggested (BITTRICH 1986) that it is possible for an ancestral weakly succulent stem to have advanced in two wholly distinct directions: one towards highly succulent stems and the other towards more woody, less succulent stems. This exception re-emphasizes the fact that the presence of stem-succulence in two taxa need not be indicative of a close relationship between them. Indead, it is possible that it may have evolved several times as an adaptation to arid environments. Convergent evolution of stem-succulence in unrelated plant families, for example in the Cactaceae and Euphorbiaceae is well known (e.g. JÜRGENS 1985).

Thus the recent suggestion of GERBAULET (1995) that stem succulence is a synapomorphy uniting *Aspazoma*, *Brownanthus*, *Aptenia* and *Psilocaulon* is questionable.

(3) Whereas stem-succulence is fairly widespread among plant families, the presence of bladder-cells in the epidermis on leaves and stems has been established as a synapomorphy for the Aizoaceae Rudolphi *sensu stricto* (BITTRICH & HARTMANN 1988).

HAWORTH (1821) and DE CANDOLLE (1828) were the first to recognize the two fundamentally different epidermal types in the Mesembryanthema: papillate and non-papillate. Much later this observation was confirmed by IHLENFELDT & HARTMANN (1982), who showed that the family may be subdivided in terms of these two different epidermal types: the idioblast (papillate) type of epidermis and the xeromorphic (non-papillate) type of epidermis.

The idioblast type of epidermis, which is present in all members of the Mesembryanthemoideae, is generally characterized by thin-walled idioblasts, superficial stomata and a high rate of transpiration (IHLENFELDT & HARTMANN 1982, IHLENFELDT & BITTRICH 1985, BITTRICH 1986), with some modifications of this basic type. A detailed analysis of the different epidermis types and their ecological significance is given by IHLENFELDT & HARTMANN (1982), IHLENFELDT & BITTRICH (1985), BITTRICH (1986) and JÜRGENS (1985).

Mesembryanthemum has the mesomorphic type of epidermis, i.e. the idioblasts are fairly closely packed, but are interspersed by "normal" epidermal cells and the idioblasts are thin-walled. In *Brownanthus*, *Aptenia*, *Aspazoma*, *Psilocaulon* and *Prenia* the mesomorphic type of epidermis is modified. In *Psilocaulon* the idioblasts are also thinwalled, but size and density is reduced. In several cases the idioblasts are completely flattened in *Psilocaulon*, which is a characteristic also of *Prenia*.

Brownanthus (except *B. pseudoschlichtianus* Pierce & Gerbaulet (JÜRGENS 1986)), *Aptenia* and *Aspazoma* have idioblasts which are very closely packed so that they form another surface above the level of the surface of the stem, which is functionally equivalent to the xeromorphic type of epidermis (termed the "xeromorphic idioblast type", IHLENFELDT & HARTMANN 1982, IHLENFELDT & BITTRICH 1985). However, in these three genera, the epidermis has been xeromophically modified only on the axes. As a consequence the epidermis of the stem and the leaves are different (e.g. IHLENFELDT & HARTMANN 1982, IHLENFELDT & BITTRICH 1985). The presence of this heteromorphism is thought by some to be indicative of a close relationship (GERBAULET 1996). In addition, in *Brownanthus* (IHLENFELDT & BITTRICH 1985, BITTRICH 1986) and *Aspazoma* the idioblasts are thick-walled (e.g. REULE 1937), with the thickest wall at their outermost edge (cf. IHLENFELDT & HARTMANN 1982, IHLENFELDT & BITTRICH 1985). As a consequence they retain their shape even when dried (e.g. IHLENFELDT & HARTMANN 1982). In contrast they are thin-walled in *Psilocaulon* and *Aptenia* and usually collapse when dried.

The modifications of the epidermis may again be interpreted as an adaptation to an arid environment and may therefore not neccessarily be indicative of a close relationship.

2. LEAVES

It was thought that only *Aspazoma*, *Brownanthus* and *Mesembryanthemum* subg. *Mesembryanthemum* and *Mesembryanthemum* subg. *Opophytum* possess distinct water storing tissue in the leaves (BITTRICH 1986). However, this was also occasionally found in *Psilocaulon*. The presence of water storing tissue is variable within some species of *Psilocaulon* and there is evidence that specimens found in more arid parts of the distribution area have developed a central water storing tissue, whereas it is absent in specimens from the wetter parts. Thus it is possible that central water-storing tissue may have evolved in response to a more arid environment. However, more material needs to be investigated to support this apparent pattern.

Convergent evolution of leaf and epidermal characters is known in families containing leaf succulents (e.g. IHLENFELDT 1985, JÜRGENS 1985). Therefore also in the case of *Azpazoma*, *Brownanthus* and *Psilocaulon* the existence of water-storing tissue in the leaves may not be indicative of a close relationship between them.

3. FLOWERS

The surface of the gynoecium is covered with finely papillate and regularly arranged cells in *Prenia, Aptenia* (IHLENFELDT & BITTRICH 1985) and *Aspazoma*. In contrast, the papillae are irregular in shape and somewhat convex in *Psilocaulon, Brownanthus* (IHLENFELDT & BITTRICH 1985) and in the *Mesembryanthemum* subg. *Mesembryanthemum*.

An increased number of petaloid staminodes occurs in *Prenia* and *Aptenia* (i.e. where the petaloid staminodes are arranged in 3-5 rows) but this is widespread and occurs also in the *Mesembryanthemum* subg. *Mesembryanthemum*. In *Psilocaulon* they are arranged in one or rarely two rows and are always in two rows in *Brownanthus* (IHLENFELDT & BITTRICH 1985). Thus, in both genera the number of petaloid staminodes is low. However, a reduced number of petaloid staminodes is found also in *M. nodiflorum* (cf. GERBAULET in press).

In *Prenia* and *Aspazoma* the petals transform through a series of concentric rings into filamentous staminodes (androecium type 1 *sensu* IHLENFELDT 1960). The presence of filamentous staminodes supports the sister group of *Prenia* - *Aptenia* to *Psilocaulon*. However, since the relationship is supported only by the presence of filamentous staminodes (20), a character state that is widely distributed among the mesembryanthemoid genera (Fig. 16) there is little confidence in this relationship. Removal of any of the characters 5, 8, 12, 28, 31, 32 and 34 leads to the collapse of node 3, providing further evidence for the weakness of this relationship.

Aptenia, Mesembryanthemum subg. *Mesembryanthemum* and *Brownanthus* lack filamentous staminodes altogether (androecium type 3 *sensu* IHLENFELDT 1960). Although the absence of filamentous staminodes is considered a derived character (IHLENFELDT 1960), it is widespread among mesembryanthemoid genera and is therefore likely to have arisen several times.

Similarly, petaloid and filamentous staminodes that are free or shortly fused towards their bases are present in *Psilocaulon*, *Brownanthus* and *Aptenia*, but are also found in the *Mesembryanthemum subg*. *Mesembryanthemum*. Petaloid and filamentous staminodes, which are fused from their bases for a considerable length to form a tubular structure, occur in *Aptenia*, *Aspazoma* and *Prenia* (Fig. 6 C).

Long styles (i.e. the styles are longer than or as long as most of the anthers) are present in *Brownanthus* and *Psilocaulon*, but are also found in *Prenia* and *Mesembryanthemum*. *Aptenia* and *Aspazoma* have short styles (i.e. the styles are shorter than most of the fertile anthers, Fig. 6 C). Nevertheless short styles are also found in *Sceletium* and *Phyllobolus* (BITTRICH 1986).

From these considerations, it is apparent that among the characters of the flower there is no unambiguous support for the hypothesis that *Aspazoma*, *Brownanthus*, *Aptenia* and *Psilocaulon* are most closely related.

In the present analysis several floral characters indicate a close relationship between *Prenia* and *Aptenia*: these are "highly fused staminodes" (19), "petaloid staminodes in 3-5 rows" (23) and "epidermal cells on gynoecium regular and finely papillate" (24). However, all three characters are homoplasious. Therefore additional characters are needed to support this apparent relationship.

4. FRUITS

Inflexed valve wings (29) are common among numerous mesembryanthemoid genera and are therefore not useful in revealing close relationships. Two of the three subgenera of *Mesembryanthemum*, i.e. *Mesembryanthemum* subg. *Mesembryanthemum* and *Mesembryanthemum* subg. *Opophytum* are distinguished from the remaining genera of Mesembryanthemoideae by having valve wings that are reflexed and fused in pairs. Within the

Mesembryanthemoideae this characteristic is otherwise only present in one species of *Phyllobolus* (i.e. *Phyllobolus digitatus* (Aiton) Gerbaulet.) and in *Caulipsolon*.

Deep locules are characteristic of species of *Psilocaulon* and are in the Mesembryanthemoideae otherwise only found in *Prenia* and in *Caulipsolon*. In *Brownanthus* (IHLENFELDT & BITTRICH 1985), *Aspazoma*, *Aptenia* and in *Mesembryanthemum* (BITTRICH 1986) the locules are shallow.

The presence of 4-locular capsules relates *Prenia* most closely to *Aptenia*. However, this character is found in several species of *Psilocaulon* and *Phyllobolus* and in *Aridaria* (GERBAULET 1995).

5. SEEDS

Both *Brownanthus* and *Psilocaulon* were formerly placed on their own in the subtribe Brownanthinae Schwantes (SCHWANTES 1947). *Brownanthus*, which had previously been included in a broader concept of *Psilocaulon* (e.g. FRIEDRICH 1970), was shown to be clearly distinct from it (IHLENFELDT & BITTRICH 1985). However, these authors thought that a close relationship between *Brownanthus* and *Psilocaulon* was possible, because of the presence of neotenic seeds in both of them (cf. BITTRICH 1986). However, neotenic seeds are also present in *Mesembryanthemum* subg. *Mesembryanthemum*, which might have lead BITTRICH (1996) to suggest a close relationship of *Psilocaulon* to this group to be equally possible. However, *Mesembryanthemum* subg. *Opophytum* also possess neotenic seeds and it is not clear which characters BITTRICH (1986) used to support his arguments for a possible close relatioship between the *Psilocaulon* and *Mesembryanthemum* subg. *Mesembryanthemum*.

A characteristic of all neotenic seeds is their swollen perisperm region (BITTRICH 1986). In contrast, the seeds of *Aptenia* and *Prenia* are flattened in the perisperm region. *Aspazoma* was found to have a flattened and a swollen side, which might be related to the position of the seed in the fruit

(BITTRICH 1986). Linked to this characteristic of neotenic seeds is the absence or near absence of epicuticular verrucose structures, which are present in *Aptenia*, *Aridaria* and *Prenia* (BITTRICH 1986).

Whereas in *Brownanthus* and *Aspazoma* the testa fold is very broad (BITTRICH 1986), it is narrow in *Psilocaulon* and in the *Mesembryanthemum* subg. *Mesembryanthemum*.

The present analysis shows *Aptenia* to be most closely related to *Prenia*. The relationship is supported by seed characters (i.e. "compressed" (30), "black seeds" (31), with a "central papillate testa, with cells arranged in more or less distinct concentric rows" (33) and floral characters (cf. discussion above).

However, *Prenia* is believed to be most closely related to *Aridaria* (GERBAULET 1995). This putative relationship is based on the reduced bladder idioblasts and a thick and clearly visible epidermal wax layer. However, these characters are also found in *Psilocaulon* (GERBAULET 1995). Since *Aridaria* was not included in the present study it remains unknown how much support there would remain for a relationship between *Prenia* and *Aptenia* if *Aridaria* were included.

The arguments presented in the discussion indicate that the relationships of *Psilocaulon* to the remaining genera of Mesembryanthemoideae remain ambivalent.

In the most recent publication on *Phyllobolus* N.E. Br. *emend*. Bittrich, uncertainty about intergeneric affinities is clearly evident in the relationships of *Sceletium* to *Phyllobolus s.str.*, *Aridaria* and *Prenia* and between the latter two genera (GERBAULET 1995). Although the generic boundaries appear to be well defined and are supported by numerous unique characters, relationships among genera are either poorly supported or could not be detected at all. Thus the sister group relationship of *Sceletium* to *Phyllobolus s.str.* is supported by only one character ("seeds with convex, papillose testa cells") which is absent from the remaining genera of the Mesembryanthemoideae. On the other hand *Aridaria*, which has evolved at least four other derived characters in common with *Phyllobolus s. str.*, is suggested as being more closely related to *Prenia*, due to the absence of convex, papillose testa cells and the presence of two shared, but not uniquely derived characters (see above). Unfortunately, when GERBAULET 's list of characters and the distribution of characters on her network were analysed using Hennig86 (options: mh*, bb*;) the relationships that she proposed between these genera could not be retrieved. It is therefore uncertain how much support exists for the proposed relationships that she suggested.

The above considerations suggest that a more comprehensive analysis including all the mesembryanthemoid genera is needed to establish relationships among the genera. In the present study sampling among the outgroups merely sufficed to establish the monophyly of *Psilocaulon*. Therefore in addition to a morphological study including a much wider range of species, a molecular analysis of the subfamily may be needed to help elucidate the phylogeny.

4.2. *Psilocaulon* and *Caulipsolon*

All species of *Psilocaulon* are united in one clade in the cladistic analysis, with *C. rapaceum* being part of this clade. However, several facts suggest that this arrangement may be fortuitous:

1. None of the uniquely derived characters that are characteristic for *Psilocaulon* (i.e. "filamentous staminodes gathered into a cone" (21), "filamentous staminodes apically lacerate" (22), "idioblasts widely spaced" (8)) are present in *C. rapaceum*. Although numerous species of *Psilocaulon* lack protruding idioblasts, this character state is not uniquely

derived in the Mesembryanthemoideae and therefore does not unambiguously place *C. rapaceum* in *Psilocaulon*.

The lack of filamentous staminodes is not otherwise found in *Psilocaulon*, but has evolved several times in other genera of the Mesembryanthemoideae. Thus on the basis of this character alone no deductions can be made on which taxon *C. rapaceum* is most closely allied to.

2. Five characters are common to *C. rapaceum* and *Psilocaulon* and these lead to the placement of *C. rapaceum* as sister species to *P. bicorne* and *P. parviflorum*. Since a "prostrate growth form" has evolved several times (ci = 0.25), it is likely that *P. parviflorum*, *P. bicorne* and *C. rapaceum* have been grouped on homoplasious characters only and so there is little evidence that the three species are closely related.

The other four characters show similarly high levels of homoplasy. Exclusion of pairs of characters shows that removing "growth form" (2) with either "position of single flowers" (14) or "extent to which staminodes are fused" (19) results in a different topology, in which *C. rapaceum* is placed between the *Brownanthus* - *Aspazoma* clade and the *Prenia* - *Aptenia* clade, but not as sister taxon to *Psilocaulon* (Fig. 17).

3. Three characters are reversed in *C. rapaceum*, which may indicate possible links to other taxa: these are "filamentous staminodes absent" (20), "petaloid staminodes in 3-5 rows" (23), and "valve wings that are reflexed and fused in pairs" (29).

Thus the presence of *C. rapaceum* in *Psilocaulon* (Fig. 15, 16) is interpreted to be the result of a superficial resemblance to some species of *Psilocaulon* (*P. bicorne* and *P. parviflorum*), rather than of any close relationship between them. This suggests that placing it outside *Psilocaulon* is more satisfactory (Fig. 17) despite the total evidence arguments which would indicate that the inclusion of *C. rapaceum* in *Psilocaulon* is required to satisfy the monophyly arguments.

The relationship of *C. rapaceum* to other genera is discussed below in more detail.

The monophyly of *Psilocaulon* is well supported by several synapomorphies: *Psilocaulon* is characterized by the conspicuous gathering of the filamentous staminodes into a cone. Although not present in any other genus within the Mesembryanthemoideae, this characteristic is found in the Ruschioideae (e.g. *Ruschia*). However, in *Psilocaulon* the filamentous staminodes are apically lacerate and are remarkable in being transparent (apart form a thickened middle vein). In contrast, the filamentous staminodes found in *Aptenia*, *Prenia* and *Aspazoma* have entire margins and are not transparent (cf. IHLENFELDT & BITTRICH 1985).

Although only five of the thirteen species possess protruding idioblasts, wide spacing of the idioblasts is unique to *Psilocaulon*. Their small size and spacing -- compared to other genera such as *Mesembryanthemum* where the idioblasts are both larger and more closely packed -- may indicate that they are in a transitional state towards becoming completely flattened.

The clade uniting the species of *Psilocaulon* (node 9) was reasonably robust to character removal. In all but one case, where the monophyly of *Psilocaulon* was not retrieved, only the position of *P. foliosum* and *P. coriarium* remained unresolved. However, both species show the characteristic flower morphology of *Psilocaulon*, so that their accommodation in *Psilocaulon* is unquestionable.

4.3. Relationships among species of *Psilocaulon*

Numerous relationships among species of *Psilocaulon* remain unresolved (Fig. 15). Parallel evolution, hybridization and young groups (where little extinction among and within species has occurred) might make the finding of a hierarchical pattern difficult (e.g. MANKTELOW 1996).

Infraspecific variation in several characters made the finding of resolved relationships among species of *Psilocaulon* particularly difficult. Some of the variation appears to be at least partly due to ecological conditions (e.g. stems, epidermis, cf. discussion above), but some characters appear to be polymorphic.

1. An example of a polymorphic character is the pollen. As in most Centrosperms (SKVARLA & NORWICKE 1976, NORWICKE & SKVARLA 1977, 1979) a tricolpate, spinulose and punctate to micropunctate pollen is most common and the same is true of the Mesembryanthema (e.g. DUPONT 1977, BITTRICH 1986). In the Mesembryanthmoideae relatively little variation in the morphology of the pollen has been observed, particularly in *Psilocaulon*, *Brownanthus* and *Mesembryanthemum* (BITTRICH 1986). Nevertheless, infraspecific variation was observed in two species. This variation may be correlated to the geographical distribution, although a larger sample size needs to be investigated to demonstrate this conclusively. Similar infraspecific variation has been observed previously in *Conophytum minusculum* ssp. *minusculum* and *Jensenobotrya lossowiana* (DUPONT 1977).

The occasional occurrence of a 6-pericolpate pollen grain in *Psilocaulon* provides another example. This has previously been found in *Ruschia perfoliata* (Mill.) Schwant. (DUPONT 1977) and *Conophytum gratum* (N.E. Br.) N.E. Br. (DUPONT 1980). According to DUPONT (1977, 1980) this abnormality may be due to hybridization. However, hybridization among Mesembryanthema is thought to be rare (e.g. HAMMER & LIEDE 1990). On the other hand the mechanisms of gene flow (including pollination and breeding systems) and genetic potentials (cf IHLENFELDT 1994) within the Mesembryanthema are little known and the subject of hybridization is not adequately understood.

2. Seed characters were similarly polymorphic. IHLENFELDT & BITTRICH (1985) consider that the size of the seed is specific to a species. According to their observations large seeds measure 1.0 X 0.8 mm and small ± 0.6 X 0.5 mm. However, in this study no gaps were found between the different sizes of seeds, so that a distinction between large and small seeds for use in a taxonomic study cannot be upheld.

3. Furthermore, (IHLENFLEDT & BITTRICH 1985) found that stomata in *Psilocaulon* are almost always sunken on both leaves and axes and they used this characteristic to separate *Psilocaulon* from *Brownanthus* . However, in the present study this character was found to be variable within species of *Psilocaulon* and therefore unsuitable also for distinguishing *Psilocaulon* and *Brownanthus*. In addition, sunken stomata were never observed on the leaves. IHLENFELDT & BITTRICH also found that the stomatal openings were parallel to the longitudinal axes of the leaves. This was not confirmed in the present study, which therefore establishes that both orientation of stomatal openings and the depth of the stomata are also variable characters in *Psilocaulon*.

As a consequence of the plasticity or polymorphousness of numerous characters, very few were useful for a cladistic analysis.

Characters indicative of phylogenetic relationships (i.e. characters whose removal results in a considerable loss of resolution) are: "presence or absence of a horizontal furrow on the stems" (4); "presence or absence of protruding idioblasts" (5), "shape of the idioblasts" (6); "presence or absence of a mucro" (10), " petaloid and filamentous staminodes free, shortly fused, or highly fused" (19) and "colour of the seed" (31).

However, it should be borne in mind that several of these characters have a high degree of homoplasy: these are characters 5 (ci = 0.25), 19 (ci = 0.40), 31 (ci = 33) which evolved or reversed several times. Therefore they, too, must be used with circumspection..

Whereas "presence or absence of protruding idioblasts" is a highly homoplasious character, the two different "shapes of the idioblasts" appears to be uniquely derived and is thus thought to be indicative of a close relationship. The shapes of the idioblasts have received considerable attention in the literature (e.g. IHLENFELDT & HARTMANN 1982), but little use has been made of them in taxonomic treatments, particularly at species level. This situation may change since recently, the shape of the idioblasts in *Brownanthus* was used in a key to the species (GERBAULET & PIERCE in press).

Reticulate distribution of characters may strongly impede cladistic analysis at all taxonomic levels (IHLENFELDT 1994). At the level of species, relationships in *Psilocaulon* are, in many cases, poorly supported or remain unresolved. The "*dimorphum*" subclade, comprising the majority of species occurring outside the winter-rainfall area (node 12), however, is relatively stable (cf. Appendix 2). This indicates that speciation may have occurred first into winter-rainfall (species below node 12) and non-winter-rainfall species. The sister-group relationships retrieved in this study are also well supported (see above). Therefore, it appears that subsequently winter- and non-winter rainfall species evolved in both groups.

It has been suggested above that adaptation to a non-winter-rainfall regime is likely to have evolved several times. However, in the case of *P. dinteri* and *P. subnodosum*, it appears that these two species re-adapted to a winter-rainfall regime (winter-rainfall species are at the base of the clade, node 9). This theory is supported by the presence of idioblasts (although in many cases reduced) in *P. dinteri*, which is a characteristic feature of the non-winter-rainfall species. Similarly, the absence of idioblasts in *P. bicorne* and *P. coriarium* may be taken as an indication that they originated from the winter-rainfall region.

Unfortunately, much of the above remains speculative. A molecular analysis, which is often able to generate a much larger number of phylogenetically informative characters and where characters are thought to be independent of environmental influences, may be needed to elucidate the evolution of *Psilocaulon*.

4.4. Evolution of growth- and life-forms

The succulent stems are of particular importance in *Psilocaulon*, since they take over assimilation once the leaves are shed. The shedding and drying up of the leaves not only assists in the survival of the mother plant, but also facilitates the ripening of the fruit. When the leaves begin to shrivel, water is thought to be relocated to the ripening fruits (BITTRICH 1986). This suggests that the leaves only assist with assimilation during the wetter periods and they are shed as soon as conditions become drier.

In the relatively long-lived, slow-growing species of *Psilocaulon* idioblasts on the stems are completely flattened. The epidermis therefore corresponds functionally to the xeromorphic type of epidermis (e.g. IHLENFELDT & BITTRICH 1985). These species may display a double strategy, which enables them to survive dry periods after the shedding of the leaves (cf. IHLENFELDT & BITTRICH 1985).

Protruding idioblasts on the stem are rarer and are typical of the small herbaceous species. These species have their main distribution outside the winter-rainfall region and may be very short-lived.

An exception to this pattern is found in *P. dinteri*. This species also possesses protruding idioblasts, but is a perennial with its main distribution in the winter-rainfall area and beyond it. However, idioblasts are particularly prominent in specimens found outside the winter-rainfall area and in the dryer parts receiving winter rain. Thus, the evolution of the epidermal structures on the stems appears to be closely linked to their distribution and their life-forms.

Most species of *Psilocaulon* appear to be relatively short-lived perennials (4-10 years). IHLENFELDT & BITTRICH (1985), reported that the smaller shrubs like *P. parviflorum* and *P.*

gessertianum were annuals or biennials, whose longevity most likely depends on the water supply. As a consequence they may live longer under greenhouse conditions, where the water supply may be regulated optimally. However, the observations made in this study, based on field observations and on plants grown in Cape Town, suggest a somewhat different situation.

It appears likely that within a given species one may find forms which are strictly annual (irrespective of the availability of water) and others that have the potential to survive several years. This behaviour was particularly apparent in *P. articulatum*, of which reasonable amounts of material from various parts of South Africa had been collected and grown: those specimens collected outside the winter-rainfall region (e.g. around Prince Albert, Steytlerville and Rietbron) were found, with one exception, not to survive after fruiting, despite being carefully tended and watered. In contrast, other specimens collected in the south-western Cape (near St. Helena Bay, winter-rainfall area) and in the Little Karoo (transition zone between winter-rainfall and summer-rainfall region) were found to survive the dry period and into the next rainy season easily. The presence of one specimen collected outside the winter-rainfall region, which was woody and survived after fruiting indicates that a divisions between winter-rainfall and non-winter-rainfall forms is not clear.

The predictability of rainfall, especially winter-rainfall, has been recognized as an important factor contributing to the richness of succulents in the south-western parts of southern Africa (e.g. COWLING *et al*. 1994). It is possible that longer-lived lifeforms have evolved in response to predictable winter-rainfall. The annual lifeform, on the other hand, evolved in those parts of the country where rainfall is both much lower and, more importantly, far more erratic. This theory is supported by a consideration of other species found outside the winter-rainfall region (especially *P. gessertianum*, *P. salicornioides*, *P. granulicaule*). Of these, none survived after having fruited in Cape Town, (despite having been watered frequently) whereas specimens of species that occur in the winter-rainfall area survived. So the annual and perennial form appears to be genetically entrenched.

P. salicornioides also appears to have both perennial and annual forms: very short lived specimens appear to occur inland, in the southern parts of Namibia (Fig. 11), whereas plants coming from the fog-zone of the Skeleton coast of Namibia appear to be perennials. Again this can be explained by the presence of a reliable water supply (cf. VON WILLERT *et al.* 1992). The theory is further corroborated by the fact that *P. parviflorum*, which is a small shrub occurring within the winter-rainfall region (again reliable rainfall), is a relatively long-lived perennial - directly contradicting the opinion of IHLENFELDT & BITTRICH (1985).

An exception to this pattern is *P. coriarium*, which also occurs mainly outside the winter-rainfall region (Fig. 9). *P. coriarium* differs from the others discussed above in being substantially woody. In addition, in this species the idioblasts are completely reduced, whereas the other species possess idioblasts. Thus the difference in morphology may explain the presence of a perennial growth-form in *P. coriarium*.

Unfortunately, much of the above is speculative and the proposed hypothesis should be tested further. This may be achieved by growing the plants from seeds under controlled conditions.

5. USES

Parts of the plants of *P. coriarium* used to be dried, burnt and the ashes so obtained used in the making of soap. Due to this practice *Psilocaulon* is known among the Afrikaans-speaking people in South Africa as "*asbos*", meaning ash-bush. The soap was further used to soften hard water, as stock lick and for defurring boilers, engines and kettles. WATT & BREYER-BRANDWIJK (1962) also report the use of "*P. parviflorum* Schwantes" by the African and Khoi peoples for making soap. In addition, in the Worcester area, the ash of this species has been used to make a lye (*loog*) in which grapes are soaked when making raisins. Consequently the plant is sometimes called "*loogbos*". However, it is unlikely that these authors meant *P. parviflorum* (Jacq.) Schwantes, since the plants in this species are rather small and it is not found in the Worcester area. Instead it is likely that they referred to *P. junceum*, since it is a fairly large plant which occurs in great abundance over much of the country.

Most species are unpalatable to livestock. Observations in the field indicate that *Psilocaulon* is probably not grazed at all or only to a small extent (MILTON, pers. comm.). *P. coriarium* has been recorded as causing stock poisoning in the Willowmore district. The two chemical compounds identified as being responsible for death were piperidine and oxalic acid (WATT & BREYER-BRANDWIJK 1962).

E. TAXONOMY

1. PSILOCAULON

Psilocaulon N.E. Br., Gard. Chron., ser. 3, **78:** 433 (1925); Ihlenfeldt & Bittrich, Bot. Jahrb. Syst. **105:** 289-322 (1985); Bittrich, Mitt. Inst. Allg. Bot. Hamburg **21:** 5-116 (1986). Type: *Psilocaulon articulatum* (Thunb.) N.E.Br.

Plants prostrate, forming decumbent to erect shrubs, perennial to short-lived or annual, roots fibrous. **Stems** with at least younger parts succulent and remaining green, usually articulate, epidermis of stems and leaves similar, cortex with additional vascular bundles. **Leaves** circular, semi-circular to slightly trigonous in cross-section, decussate, fused towards the base or free, often with membranous margins at leaf sheaths, short-lived, either caducous or drying up and persistent, mostly without water-storing cells in centre, epidermis with distinct, hair-like, dome-shaped or flattened mesomorphic bladder cells, stomata sometimes sunken. **Flowers** in dichasia, rarely solitary, 5-25 mm diam.; calyx 4-5-lobed, lobes fused into a short tube; petals pink, puce, yellow or white, few or rarely almost none, either very shortly fused or free; filamentous staminodes present, transparent except for a middle vein, apically lacerate, connate; nectaries narrowly shell-shaped or absent. **Fruit** with valve wings inflexed over valves, 4-5-locular, often deep (1.4-6.0 mm); seeds 0.5-1.2 mm long, D-shaped, ochre or brown with dark warts, testa rough to ± smooth with dome-shaped cells, without distinct crest.

Key to the species of Psilocaulon:

1. Green stems soon withering and becoming woody, with a trunk up to 50 mm diam.............................**2. P. foliosum**
- Stems with persistent succulent green stems, scarcely woody..2

2. Nodes conspicuous with fine horizontal furrow at nodes present..3
- Nodes inconspicuous: without fine horizontal furrow, leaves shortly fused...12
3. Stems with hair-like papillae...........**10. P. articulatum**
- Stems glabrous or warty...4
4. Side branches very slender (< 2 mm diam.), flowers white, capsule 4-locular, prostrate.............**6. P. parviflorum**
- Stems ≥ 3 mm diam., flowers white, pink or yellow, capsule 4-5-locular, prostrate or decumbent to erect..............5
5. Flowers usually solitary..6
- Flowers in few- to many-flowered dichasia.................7
6. Flower 18-25 mm diam., capsules 4.5-6.0 mm diam., petals white, stems glabrous.........................**4. P. leptarthron**
- Flower 5-8 mm diam., capsules 3.0-3.5 mm diam., petals pale yellow, stems with dome-shaped papillae...**8. P. granulicaule**
7. Stems conspicuously constricted at the nodes, flowers puce, pink or rarely white, stems often with dome-shaped papillae or shiny ....**7. P. dinteri**
- Stems inconspicuously constricted at the nodes, flowers white or pink, stems smooth, never shiny.................8
8. Plants prostrate or decumbent, small shrubs...............9
- Plants erect, medium to large shrubs (30-150 cm).........10
9. Plants prostrate, stems forming central clump and long prostrate annual shoots......................**5. P. bicorne**
- Plants decumbent, small shrubs...............**9. P. dimorphum**
10. Plants (50-)70-150 cm tall, petals 0.5-1.0 mm broad...**1. P. coriarium**
- Plants 30-50(-60) cm tall, petals 1-2 mm broad...**3. P. junceum**
11. Flowers yellow, petals very reduced......**13. P. gessertianum**
- Flowers white or pink, petals present....................12
12. Stems prostrate to decumbent, small shrubs to 25 (-35) cm tall, flower up to 10 mm diam..........**12. P. salicornioides**
- Stems decumbent to erect, shrubs to 50 (-80) cm high, flower 10 to 15 mm diam..........................**13. P. subnodosum**

1. Psilocaulon coriarium (Burchell ex N.E. Br.) N.E. Br., Gard. Chron. SER. 3, **84:** 254 (1928).
Mesembryanthemum coriarium Burchell ex N.E. Br., J. Linn. Soc. **45:** 127 (1920). - *Ruschia coriaria* (Burchell ex N.E. Br.) Schwantes, Zeitschr. Sukkulentenk. **3:** 20 (1927). - Type: South Africa, Philipstown division, near Petrusville, March 1813, *Burchell 2679* (K!, holo).
Mesembryanthemum mentiens Berger, Bot. Jahrb. Syst. **57:** 630 (1922). - *Psilocaulon mentiens* (Berger) N.E. Br., Gard. Chron. SER. 3, **84:** 254 (1928). - Type: Namibia, Rosh Pinah district, near Klein Aub, *Dinter 2148a* (B! holo; BOL!, K!, SAM!).
Psilocaulon absimile N.E. Br., Man. Fl. Pl. & Ferns Tvl **1:** 49, 157 (1926). - Type: South Africa, Transvaal, Christiana, *Burtt*

Davy 10809 (K! holo; BOL!, PRE!, SAM!).
Psilocaulon uncinatum L. Bolus, Notes Mesembryanthemum 2: 60 (1929). - Type: Namibia, near Aus, *Compton NBG 1831/27* (BOL! holo; M!).
Psilocaulon stenopetalum L. Bolus, Notes Mesembryanthemum 2: 171 (1930). - Type: South Africa, near Prieska, November - December 1929, *Bryant 712* (BOL! holo; PRE!).

Plant forming decumbent to erect shrubs, to 1.5 X 3.0 m. **Stems** succulent, articulate, nodes conspicuous with fine horizontal furrow, smooth. **Leaves** free, short, often not longer than 5 mm, occasionally with short mucro, bladder cells flattened. **Flowers** several together in dichasia, up to 10 (13) mm diam., calyx 4-5-lobed, petals white or pale pinkish, usually thread-like 0.5-1.0 mm broad, petals and filamentous staminodes shortly fused. **Fruit** 4-5-locular, 3.1-4.0 mm diam., 3.1-3.5 mm deep; seed brown, testa mostly rough, rarely reduced.

DISTRIBUTION: Central and Southern Namibia; South Africa: Northern Cape, eastern Namaqualand, Kenhardt, Prieska, Phillipstown; Western Cape, from Ceres to Beaufort West (Fig. 9).

ECOLOGY: The main distribution lies outside the winter-rainfall area, at high altitudes (500 - > 2000 m) and it is never found in low lying areas (i.e. < 500 m). A few localities fall within the winter-rainfall area. It is found on a wide variety of soils.

Plants of *Psilocaulon coriarium* often develop into large shrubs which are second in size only to those of *P. foliosum*. Nevertheless, *P. coriarium* is very variable in stature and some of the smaller specimens may bear a superficial resemblance to *P. junceum*.

The distribution areas of *P. coriarium* and *P. junceum* overlap to some extent, although each has its main distribution in different rainfall regimes. However, where the two species are sympatric, *P. coriarium* always forms much more substantial shrubs than *P. junceum*. *P. coriarium* can further be distinguished by its smaller flowers (8-10 mm diam.), usually with thread-like petals (0.5-1.0 mm wide), whereas *P. junceum* has usually larger flowers (to 15 mm diam.) and broader petals (1.0-2.0 mm wide).

The number of locules in the capsules of *P. coriarium* varies from 4 to 5. Broadly speaking, 5-locular capsules are found in Namibia from Rosh Pinah to Windhoek, while 4-locular capsules are found on plants from the south-eastern corner of Namibia (Warmbad district) and in South Africa. However, especially in South Africa, the number of locules is not constant; consequently this character is of no taxonomic value.

2. Psilocaulon foliosum L. Bolus, Notes Mesembryanthemum **2**: 100, 142 (1929). - Type: South Africa, Namaqualand, on north facing slopes around Wallekraal, October 1924, *Pillans BOL 17813* (BOL!, holo).

Plant a large shrub to 1.0 X 1.0-2.0 m, densely and regularly branched. **Stems** initially green, soon becoming woody, up to 50 mm thick, smooth, young stems indistinctly articulate with inconspicuous nodes with or without fine horizontal furrow. **Leaves** fused towards the base or free, soon caducous (as the stem becomes woody), without mucro, bladder cells flattened. **Flowers** several together in dichasia, up to ± 15 mm diam., calyx 5-lobed, petals white, ± 1 mm broad, petals and filamentous staminodes shortly fused. **Fruit** 5-locular, ± 3.0 mm diam., 1.4-2.6 mm deep; seeds brown, testa rough.

DISTRIBUTION: South Africa: Northern Cape, Namaqualand, from Bitterfontein westwards to the sea and northwards to Port Nolloth (Fig. 10).

ECOLOGY: This species is restricted to the winter-rainfall area and only grows at low altitudes (0 - 500 m) on firm reddish, often gneissic loam.

P. foliosum is the only species of *Psilocaulon* which does not have persistent, succulent, green, leafless stems. The leaves persist even during the dry season so that the plants are permanently green to grey-green. Once the plant makes new shoots, the leafy parts of the stems (i.e. the previous year's growth) soon become woody and lose their leaves.

Plants form very substantial shrubs which may have several robust, woody trunks up to 50 mm thick. They usually grow socially and are invariably the dominant element where they occur.

Despite the large size of the plants, few collections of this species have been made. This may be due to the relatively small distribution area. So far it has been recorded as far north as Port Nolloth. However, it is likely that the distribution range reaches still further north, possibly as far as the Orange River.

Although vegetatively *P. foliosum* looks very different from any other species of *Psilocaulon*, the flowers are typical of the genus. The filamentous staminodes are gathered into a cone and are transparent and apically lacerate. All these features clearly place it in *Psilocaulon*. An unusual characteristic of this species is that the flowers remain open, whereas in the other species they are able to open and close repeatedly.

3. **Psilocaulon junceum** (Haw.) Schwantes, Gartenflora **77:** 69 (1928).
Mesembryanthemum junceum Haw., Misc. Nat.: 59 (1803). - *Peratetracoilanthus junceus* (Haw.) Rappa & Camarrone, Lav. Ist. Bot. Giard. Colon. Palermo **18:** 23 (1960). - Type: Drawing, lecto, Salm-Dyck, Monographia generum Aloes et Mesembryanthemi, Mesembryanthemorum congestus, **45,1** (1836-1863).
Mesembryanthemum junceum var. *pauciflorum* Sonder, in Harvey & Sonder, Fl. Cap. **2:** 434 (1862). - *Psilocaulon pauciflorum* (Sonder) Schwantes, Repert. Spec. Nov. Regni Veg. **43:** 229 (1938). - Type: South Africa, Karoo, in Zwartsland and near Olifantriver and Gauritzriver, Bosjesveld, Springbokkeel, *Zeyher 2957* (S!, holo; P!).
Mesembryanthemum simile var. *namaquense* Sonder, in Harvey &

Sonder, Fl. Cap. 2: 435 (1862). - *Psilocaulon namaquense* (Sonder) Schwantes, Gartenflora **77:** 69 (1928). - Type: South Africa, Namaqualand, *Schlicht s.n.* (MEL!, lecto); *Wyley s.n.* (syn, missing).
Mesembryanthemum simile Sonder, in Harvey & Sonder, Fl. Cap. **2:** 435 (1862). - *Psilocaulon simile* (Sonder) Schwantes, Gartenflora **77:** 69 (1928). - Type: South Africa, Uitenhage, Zwartkopsriver, *Zeyher 2618* (MEL!, holo; B!, K!, P!, PRE!).
Mesembryanthemum acutisepalum Berger, Bot. Jahrb. Syst. **57:** 629 (1922). - *Psilocaulon acutisepalum* (Berger) N.E. Br., Gard. Chron. SER. 3, **84:** 253 (1928). - Type: South Africa, Clanwilliam division, Troe - Troe, February 1884, *Bachmann 329* (B, holo, missing; K!, lecto; BOL!).
Psilocaulon pageae var. *pageae* L. Bolus, Ann. Bolus Herb. **4:** 106 (1927). - Type: South Africa, Montagu division, Montagu Baths, October 1921, *Page BOL 17167* (BOL!, holo).
Psilocaulon bijliae N.E. Br., Gard. Chron. SER. 3, **84:** 254 (1928). - Type: South Africa, Prince Albert division, Abrahams Kraal, *Van der Bijl 30* (K!, holo).
Psilocaulon levynsiae N.E. Br., Gard. Chron. SER. 3, **84:** 254 (1928). - Type: South Africa, Calvinia division, foot of Blauwkrantz Pass, September 1926, *Levyns 1722* (K!,holo; BOL!).
Psilocaulon squamifolium N.E. Br, Gard. Chron. SER. 3, **84:** 254 (1928). - Type: Riverbed between Loeriesfontein and Grauwater, *Pearson 3273* (K!, holo; BM!, BOL!).
Psilocaulon rogersiae L. Bolus, Notes Mesembryanthemum **2:** 30 (1928). - Type: South Africa, Cradock, near town, *Rogers BOL 18856* (BOL!, holo).
Psilocaulon pageae var. *grandiflorum* L. Bolus, Notes Mesembryanthemum **2:** 30 (1928). - Type: South Africa, Vanrhynsdorp district, January 1928, *Frames NBG 159/28* (BOL!, holo).
Psilocaulon laxiflorum L. Bolus, Notes Mesembryanthemum **2:** 157 (1929). - Type: South Africa, between Vanrhynsdorp and Nuwerus, October 1929, *Godman BOL 19004* (BOL!, holo).
Psilocaulon utile L. Bolus, Notes Mesembryanthemum **2:** 157 (1929). - Type: South Africa, Laingsburg district, near Whitehill, *Compton BOL 19005* (BOL!, holo).
Psilocaulon framesii L. Bolus, Notes Mesembryanthemum **2:** 190 (1930). - Type: South Africa, Little Karoo, between Touwsriver and Ladismith, October 1929, *Frames BOL 19112* (BOL!, holo).
Psilocaulon delosepalum L. Bolus, Notes Mesembryanthemum **2:** 174 (1930). - Type: South Africa, Vanrhynsdorp, between Zoutrivier and Nuwerus, August 1929, *L. Bolus BOL 19050* (BOL!, holo).
Psilocaulon semilunatum L. Bolus, Notes Mesembryanthemum **2:** 174 (1930). - Type: South Africa, locality uncertain, probably between Zoutriver and Bitterfontein, August 1929, *L. Bolus BOL 19051* (BOL!, holo).
Psilocaulon calvinianum L. Bolus, Notes Mesembryanthemum **2:** 410 (1933). - Type: South Africa, near Calvinia, *Du Plessis NBG 2267/32* (BOL!, holo).
Psilocaulon candidum L. Bolus, J. S. African Bot. **27:** 116 (1961).

- Type: South Africa, Namaqualand, Ratelpoort, October 1959, *Littlewood KG 631/59* (BOL!, holo).
Psilocaulon imitans L. Bolus, Notes Mesembryanthemum **2:** 429-430 (1934). - Type: South Africa, St. Helenafontein, November 1933, *L. Bolus BOL 21038* (BOL!, holo).
Psilocaulon subintegrum L. Bolus, Notes Mesembryanthemum **2:** 429 (1934). - Type: South Africa, St. Helenafontein, November 1933, *L. Bolus BOL 21034* (BOL!, lecto); South Africa, Malmesbury district, near Hopefield, November 1933, *Lavis BOL 21035* (BOL!, syn).
Psilocaulon lewisiae L. Bolus, Notes Mesembryanthemum **2:** 492 (1935). - Type: South Africa, Swellendam district, near Bonnievale, September 1934, *Lewis NBG 2011/33* (BOL!, holo).
Psilocaulon leightoniae L. Bolus, Notes Mesembryanthemum **3:** 14 (1936). - Type: South Africa, Laingsburg district, near Matjiesfontein, at foot of Witteberg, *Leighton BOL 21643* (BOL!, holo).
Psilocaulon planisepalum L. Bolus, Notes Mesembryanthemum **3:** 160-161 (1939). - Type: South Africa, Bushmanland, 10-35 miles from Nieuwefontein on road to Pofadder, October 1938, *Esterhuysen BOL 21855* (BOL!, holo).
Psilocaulon oculatum L. Bolus, J. S. African Bot. **27:** 118 (1961). - Type: South Africa, near Clanwilliam, October 1959, *Littlewood KG 640/59* (BOL!, holo).
Psilocaulon simulans L. Bolus, J. S. African Bot. **27:** 119 (1961). - Type: South Africa, Beaufort West district, 21 miles south of Beaufort West on road to Klaarstroom, November 1960, *Stayner KG 806/60a* (BOL!, holo).
Psilocaulon stayneri L. Bolus, J. S. African Bot. **27:** 119 (1961). - Type: South Africa, Calvinia district, 30 miles north of Nieuwoudtville, December 1959, *Stayner KG 893/59* (BOL!, holo).

Plant a decumbent to erect shrub, (0.10-) 0.30-0.45 (-0.60) m high. **Stems** articulate with fine horizontal furrow at nodes, smooth. **Leaves** free, without mucro, bladder cells flattened. **Flowers** several together in dichasia, to 15 mm diam., calyx 4-5 lobed, petals white, pink or pale pink, 1-2 mm broad, petals and filamentous staminodes free to the base. **Fruit** 4-5-locular, ± 2.1-4.7 mm diam., 2.1-3.6 mm deep; seed dark brown, testa rough.

DISTRIBUTION: South Africa: Northern Cape, Namaqualand, Calvinia; Western Cape, from Beaufort West to Oudtshoorn; Eastern Cape, Willowmore to Graaff Reinet (Fig. 11).

ECOLOGY: Found mainly in the winter-rainfall area, but also extends beyond it, grows mainly between 0 - 1000 m and along the edge of the South African escarpment (to 2000 m), found in a variety of soils, occasionally also in very saline spots.

NOMENCLATURAL NOTES: The isotype at Kew was chosen as the lectotype for *P. acutisepalum* (Berger) N.E. Br., since it provided the best match for the description.

P. junceum is one of the most common, most widely distributed and also one of the most variable species of *Psilocaulon*.

Plants found growing above the escarpment, i.e. at altitudes above 1000 m, are dwarf and usually do not exceed 300 mm in height and diameter. At lower altitudes i.e. below 1000 m, it may be much larger, both in height and diameter -- as much as 60 X 120 cm. However, in situations where the plant is under environmental stress (e.g. limited water supply, shallow ground or very saline habitats) the plant will also remain fairly small (< 300 mm in height and diameter).

Psilocaulon junceum usually has showy flowers: their diameter may reach 15 mm, the petals are often a rich pink and they are fairly broad (1-2 mm diam.). However, petals may also be white or pale pink, so that the colour of the flowers is yet another variable feature. In addition, if the plants are under environmental stress the diameter of the flowers may be much smaller (7-10 mm).

In many cases in *Psilocaulon* the length of the sepals was used to distinguish between species. The case of *P. junceum* demonstrates very well how unreliable this character is. Here, depending on the number of locules, two or three of the sepals may be longer than the petals. However, they may also all be of equal length or shorter than the petals and may even be slightly succulent.

The number of locules was previously used to distinguish between species. Thus, for example, *P. junceum* was said to be 4-locular, whereas *P. simile* was supposed to be 5-locular. However, the number of locules may vary: in most cases an individual will produce both 4- and 5-locular capsules. However, one locule number usually predominates so that it is possible to classify plants as either 4- or 5-locular. In some rare cases specimens had about equal numbers of 4- and 5-locular capsules. Specimens that are 4-locular may be found growing next to specimens that are 5-locular. No additional characters were found which could be used to separate the 4-locular from the 5-locular specimens.

The large variability found among and within populations has led to the sinking of the astonishingly large number of 26 names under *P. junceum*.

Despite this broad variability, the plants are easily identified from other species of *Psilocaulon* by their decumbent or erect (never prostrate) habit, a smooth epidermis and broad petals. The species bears similarity to *P. coriarium* (for differences see under *P. coriarium*) and *P. dinteri*. From *P. dinteri* it differs in having smooth stems (the stems are usually covered with dome-shaped papillae in *P. dinteri*) and seeds which are usually a darker brown than those of *P. dinteri*.

As with *P. coriarium*, dried plants were burnt and the ashes used in making soap.

4. Psilocaulon leptarthron (Berger) N.E. Br., Gard. Chron. SER. 3, **84:** 254 (1928).
Mesembryanthemum leptarthron Berger, Bot. Jahrb. Syst. **57:** 628 (1922). - Type: South Africa, Knersvlakte, *Schlechter 8151* (B!, holo; BOL!, BM!, GRA!, K!, P!).
Psilocaulon album L. Bolus, S. African Gard. **17:** 365 (1927). - Type: South Africa, near Vanrhynsdorp, October 1926, *Compton NBG 1475/26* (BOL!, holo).

Plant erect, forming very regularly branched shrubs, up to 0.5 X 1.0 m. **Stems** succulent, straight, distinctly articulate, nodes conspicuous with fine horizontal furrow, smooth. **Leaves** free, without mucro, bladder cells flattened. **Flowers** solitary terminating long side branches, rarely few together in dichasium, up to 25 mm diam., calyx 5-lobed, petals white, 1-3 mm broad, petals and filamentous staminodes free to base. **Fruit** 5-locular, 4.5-6.0 mm diam., 4.5-6.0 mm deep; seeds brown, testa rough.

DISTRIBUTION: South Africa: Western Cape, restricted to the Knersvlakte and the basin of the Sout River. Found from Klawer in the south to as far north as Bitterfontein and eastwards towards Loeriesfontein and Kliprand (Fig. 12)

ECOLOGY: This species only occurs in the winter-rainfall area at altitudes of between 0 and 1000 m. *P. leptarthron* is one of the few species of *Psilocaulon* which shows a preference for a certain soil type: it prefers firm, red, calcareous loams of the kind especially associated with the basin of the Sout River north of Vanrhynsdorp.

Psilocaulon leptarthron is probably the species with the most restricted distribution in the genus. It also does not exhibit the weedy tendency of most of the others and, although it will also grow in disturbed spots, it is more often found in undisturbed veld.

It has notably stout, very straight side branches and the plants are usually quite sparsely branched. In contrast to the other species of *Psilocaulon* which may occasionally produce solitary flowers, the single flowers in this species are positioned terminally. The flowers are the largest in the genus, reaching 25 mm diameter and the petals are fairly broad (1-3 mm diam.). As a consequence *P. leptarthron* is one of the most showy species of *Psilocaulon*.

5. **Psilocaulon bicorne** (Sonder) Schwantes, Gartenflora 77: 69 (1928).
Mesembryanthemum bicorne Sonder, in Harvey & Sonder, Fl. Cap. 2: 434 (1862). - Type: South Africa, fields near Zwartkopsriver, *Zeyher 2616* (S!, holo; BOL!, K!, MEL!, P!, PRE!, SAM!).

Plant prostrate with cluster of short stems in the centre and long trailing flowering shoots. **Stems** succulent, articulate, nodes conspicuous with fine horizontal furrow. **Leaves** free to base, with short mucro, bladder cells flattened. **Flowers** few together in dichasium or solitary on short side-shoots, to 15 mm diam., calyx 5-lobed, petals white, ± 1 mm broad, petals and filamentous staminodes free to base. **Fruit** 5-locular, ± 3.5 mm diam., 2.8 mm deep; seeds brown, testa usually smooth with flattened, elongated, dome-shaped cells, occasionally rough.

DISTRIBUTION: South Africa: Western Cape, from Worcester and Caledon to Beaufort West and Uniondale; Eastern Cape, from Willowmore to Port Elizabeth (Fig. 12).

ECOLOGY: *P. bicorne* mainly occurs outside the winter-rainfall region, but also extends into it. It grows at altitudes of 0 - 1000 (-1500) m, in a variety of soils.

P. bicorne forms a cluster of short stems which radiate from the centre of the plant and this is how it remains for most of the year. When the rainy season begins (usually April to May) long prostrate shoots start to grow out of the short, perennial stems and these may eventually reach a length of one metre. These long shoots flower from about October to November and then the plant is very conspicuously covered with white flowers. The perennial stems are usually sterile. After fruiting the annual stems are shed.

The smooth stems clearly distinguish it from *P. articulatum*. It is occasionally found growing with *P. parviflorum*. However, *P. bicorne* is easily identified by its much stouter stems, thicker leaves and 5-locular capsules -- *P. parviflorum* has a more densely mat-forming habit, slender stems, fine leaves and 4-locular capsules.

6. **Psilocaulon parviflorum** (Jacq.) Schwantes, Gartenflora

77: 69 (1928).
Mesembryanthemum parviflorum Jacq., Hort. Schönb. **3:** 15 t. 278 (1798). - *Peratetracoilanthus parviflorus* (Jacq.) Rappa & Camarrone, Lav. Ist. Bot. Giard. Colon. Palermo **18:** 23 (1960). - *Mesembryanthemum micranthon* Haw., Syn. Pl. Succ.: 257 (1812). nom. illeg. - *Psilocaulon micranthon* L. Bolus, S. African Gard. **17:** 365 (1927). nom. illeg. - Iconotype: Jacquin, Hort. Schönb. **3:** 15 t. 278! (1798).
Mesembryanthemum tenue Haw., Rev. Pl. Succ.: 175 (1821). - *Psilocaulon tenue* (Haw.) Schwantes, Gartenflora **77:** 69 (1928). - Type: Drawing (K, lecto, Photograph!).
Psilocaulon implexum N.E. Br., Kew Bull. Misc. Info **2:** 60 (1929). - Type: South Africa, Riversdale division, near the Kaffirkuils River, *Muir 4234* (K!, holo; BM!, BOL!).

Plant prostrate, mat-forming. **Stems** succulent, articulate, very slender in young stems (1-2 mm thick), glabrous, nodes conspicuous with fine horizontal furrows. **Leaves** free, without mucro, bladder cells flattened. **Flowers** few to solitary on shorter side-branches, 5-10 mm diam., calyx 4-lobed, petals white, ± 1 mm broad, petals and filamentous staminodes free to base. **Fruit** 4-locular, ± 2.5 mm diam., 2.7 mm deep; seed brown, testa rough.

DISTRIBUTION: South Africa: Western Cape, from Clanwilliam to Malmesbury and Mosselbay (Fig. 12).

ECOLOGY: *P. parviflorum* is restricted to the winter-rainfall area and grows in low lying areas between 0 and 500 m. It is found only in clayish - loamy, slightly saline soils, often with a covering of quartz gravel.

This species has the most slender stems in the genus (young stems are 1-2 mm diam.), which makes it readily distinguishable from any other *Psilocaulon*. The branches may reach 1 m in length and eventually form a dense mat.

It is a common plant in small remnant patches of disturbed natural vegetation between wheat fields in the "Swartland" north of Cape Town and eastwards to Mossel Bay. It usually grows in hard ground towards the foot of hills or in flat areas and is especially associated with patches of gravel and clay.

In a letter to N.E. BROWN, MUIR noted about this species: "when the sun has dried everything up here (near Riversdale) to a brown waste it forms dark green patches visible at a distance". He furthermore notes: "*M. micranthum* here can stand some shade and is one of the last indigenous plants to be shaded out by *Eucalyptus globulus* and *E. cladocalyx* F.v.M. In such sun-demanding plants this ecological note may be worth recording" [Kew archives]. These notes indicate that *P. parviflorum* appears to be one of the more tolerant species with respect to requirements of light. However, with respect to soils it is more fussy than most species of *Psilocaulon*, showing a preference for clayish-loam.

Plants found east of Cape Town have usually shorter (5-10 mm), narrower (± 1 mm) leaves and are more leafy than those north of Cape Town, which have usually fewer leaves per axes and the leaves are also longer (10-15 mm) and broader (1-2 mm).

7. **Psilocaulon dinteri** (Engler) Schwantes, Gartenflora **77**: 69 (1928). *Mesembryanthemum dinteri* Engler, Bot. Jahrb. Syst. **43**: 197 (1909). - Type: Namibia, on rocks next to Swakop River, July 1897, *Dinter 954* (B!, lecto; BOL!).
Mesembryanthemum marinum Berger ex Engler, in Engler and Drude, Vegetation der Erde 9 Band 3 (1): 153 (1915). - Type: Namibia, Diaz Point, *Klak 115* (BOL!, neo).
Psilocaulon fasciculatum N.E. Br., Gard. Chron. SER. 3, **84**: 254 (1928). - Type: South Africa, Namaqualand, October 1924, *Pillans BOL 17767* (K!, holo; B!, BOL!).
Psilocaulon godmaniae L. Bolus var. *godmaniae*, Notes Mesembryanthemum **2**: 143-144 (1929). - Type: South Africa, between Vanrhynsdorp and Nuwerus, October 1929, *Godman BOL 18979* (BOL!, holo).
Psilocaulon godmaniae var. *gracile* L. Bolus, Notes Mesembryanthemum **2**: 174 (1930). - Type: South Africa, between Zout River and Bitterfontein, October 1929, *Godman BOL 19049* (BOL!, holo).
Psilocaulon variabile L. Bolus, Notes Mesembryanthemum **2**: 190-191 (1930). - Type: South Africa, Namaqualand, near Hondeklip Bay, October 1924, *Pillans BOL 17769* (BOL!, holo).
Psilocaulon littlewoodii L. Bolus, J. S. African Bot. **27**: 117 (1961). - Type: South Africa, 8 miles north of Vanrhynsdorp,

October 1959, *Littlewood KG 591/59* (BOL!, holo).
Psilocaulon littlewoodii forma L. Bolus, J. S. African Bot. **27:** 118 (1961). - Type: South Africa, 6 miles east of Vredendal, September 1959, *Littlewood KG 629/59* (BOL!, holo).
Psilocaulon herrei L. Bolus, J. S. African Bot. **29:** 47 (1963). - Type: South Africa, Vanrhynsdorp district, Platbakkies, August 1961, *Herre STE 14675* (BOL!, holo).
Psilocaulon baylissii L. Bolus, J. S. African Bot. **29:** 47 (1963). - Type: South Africa, Namaqualand, 20 miles from Grootmist on the road to Port Nolloth, November 1962, *Bayliss 988* (BOL!, holo).

Plant an erect, decumbent to prostrate shrublet, up to 0.25 m tall. **Stems** succulent, distinctly articulate, nodes conspicuous with fine horizontal furrow, older stems often very succulent with internodes becoming barrel-shaped in saline coastal areas, otherwise internodes cylindrical, smooth or warty. **Leaves** free to base, occasionally with mucro, bladder cells flattened. **Flowers** few to many together in dichasia, 5-10 mm diam., calyx 5-lobed, petals puce or pink, 1-2 mm broad, petals and filamentous staminodes free to base. **Fruit** 5-locular, ± 2.7-4.5 mm diam., 2.7-3.9 mm deep; seeds ochre, testa usually rough, rarely smooth with flattened dome-shaped or completely flattened cells.

DISTRIBUTION: Southern Namibia; South Africa: Northern Cape, Namaqualand; Western Cape, north of Cape Town from the Piquetberg to Clanwilliam, Vanrhynsdorp and Vredendal and eastwards in the Ceres Karoo and Barrydale (Fig. 9).

ECOLOGY: *P. dinteri* is found in the winter-rainfall area, at low altitudes (0 - 500 m). Occasionally it grows further inland also at higher altitude (500 - 1000 m). Along the coast it tolerates conditions of high salinity and is often found within a few metres of the high-water mark. Further inland it is often found in and around patches of quartz gravel.

NOMENCLATURAL NOTES: In the original description, Engler cited two specimens for *Mesembryanthemum dinteri* of which only one is a *Psilocaulon*, the other being *Brownanthus kuntzei*. The name *M.*

marinum was validly published but no type was cited in the protologue. Therefore a neotype has been selected here.

P. dinteri is a highly variable species. Along the coast, it may occur right next to the shore and well within the range of wind-borne spray. Under these and similarly saline conditions the internodes of the stem are up to 10 mm thick, barrel-shaped and the stem often resembles a short string of fattish beads. In these situations the plants are always prostrate to decumbent with a bright red colour. The epidermis is often shiny. Further inland, in less saline conditions, the stems are usually decumbent to erect, the internodes are less barrel-shaped and the plant is green to faintly suffused with red. In addition, the epidermis of the stems is no longer shiny, but mostly covered by fairly widely-spaced, dome-like or warty papillae.

The flowers of *P. dinteri* are often very small -- only 5 mm across -- but despite this they may be a strikingly deep puce. Pink flowers may also be found but white is a rare colour in *P. dinteri*.

P. dinteri was previously considered to occur only along the coast (IHLENFELDT & BITTRICH 1985) but has also been found further inland during the course of this study. These authors may have been not aware of the great variability of this species and only identified plants which have the characteristic barrel-shaped stems as *P. dinteri*. However, plants with exceedingly bead-shaped internodes are to be found also further inland. What is remarkable is the close association of *P. dinteri* with quartz patches, which are mostly saline environments in which these plants appear to thrive.

The considerable variability in this species -- as outlined above -- has led to much confusion and there are ten valid names for this species, all of which are reduced to synonymy here under *P. dinteri*.

8. Psilocaulon granulicaule (Haw.) Schwantes, Gartenflora **77:** 69 (1928).
Mesembryanthemum granulicaule Haw., Till. Phil. Mag. **64:** 427 (1824). - *Perapentacoilanthus granulicaulis* (Haw.) Rappa & Camarrone, Lav. Ist. Bot. Giard. Colon. Palermo **18:** 31 (1960), nom. invalid. - Type: Drawing, lecto, in Salm-Dyck, Monographia generum Aloes et Mesembryanthemi, Mesembryanthemorum congestus, **45,2**! (1836-1863).
Psilocaulon pauper L. Bolus, Notes Mesembryanthemum **2:** 191-192 (1930). - Type: South Africa, Prince Albert, in hills near the town, November 1905, *H. Bolus 11906* (BOL!, holo).

Plant a decumbent to erect shrublet, up to 0.25 m tall. **Stems** succulent, articulate, nodes conspicuous with fine horizontal furrow, with dome-shaped or warty idioblasts. **Leaves** free to base, without mucro, bladder cells flattened. **Flowers** solitary or rarely several together in dichasia, several per axis, single on shorter side shoots, 5-8 mm diam., calyx 5-lobed, petals pale yellow or cream, 1-2 mm broad, petals and filamentous staminodes free to base. **Fruit** 5-locular, ± 3.5 mm diam., 2.5 mm deep; seed brown, testa smooth with flattened, elongated, dome-shaped cells.

DISTRIBUTION: South Africa: Northern Cape, Kimberley; Western Cape, from Worcester to Uniondale; Free State, Fauresmith; Eastern Cape, from Willowmore, Steytlerville to Graaff-Reinet (Fig. 13). Australia: Victoria, Mildura, Birchip, probably introduced.

ECOLOGY: The distribution lies mainly outside the winter-rainfall region, but with outliers within the winter-rainfall area. It occurs from 0 - 2000 m, in a wide variety of soils.

Psilocaulon granulicaule had previously been treated as a synonym of *P. articulatum* by authors such as FRIEDRICH (1970) and JACOBSEN (1986). Only recently BITTRICH & HARTMANN (1990) noted that *Psilocaulon granulicaule* had yellow flowers, a rare colour in *Psilocaulon*. They concluded that it was distinct from *Psilocaulon articulatum*, but believed it to be rare. However, *Psilocaulon granulicaule* is in fact widespread. It has been introduced in Australia, where it is now common. As well as various collections from South Africa, it is also known from three widely separated localities in Namibia, one of them as far north as Okahandja.

Like most other species of *Psilocaulon*, this species has very inconspicuous flowers. They are small (usually 5-8 mm diam.) but are exceptional in having pale yellow petals. The flowers are usually solitary and arise on short side-shoots along the longer axes.

The stems are covered with dome-shaped papillae that are visible to the naked eye. Such dome-shaped papillae are also found in *P. dinteri* and consequently these two are thought to be most closely related. Apart from the differently coloured flowers, a further difference between them is that *P. granulicaule* is an annual and is therefore not at all woody, whereas *P. dinteri* is perennial with stems that become distinctly woody towards their bases.

9. Psilocaulon dimorphum (Welw. ex Oliver) N.E. Br., Gard. Chron. SER. 3, **84:** 254 (1928).
Mesembryanthemum dimorphum Welw. ex Oliver, Fl. Trop. Africa **2:** 582 (1871). - Type: *Welwitsch 2377* (BM!, holo; B!, COI!, K!).

Plant a decumbent shrub. **Stems** succulent, articulate, nodes conspicuous with fine horizontal furrow, usually with flattened idioblasts, occasionally with protruding idioblasts. **Leaves** free to base, with mucro, bladder cells usually flattened. **Flowers** several together in dichasia, to 15 mm diam., calyx 4- to 5-lobed, petals white. **Fruit** 4-5-locular, ± 3.0 mm diam., 3.0 mm deep; seeds ochre, testa smooth, flat.

DISTRIBUTION: Along the coast of Southern Angola, between Mossamedes and Porto Alexandre.

ECOLOGY: The species has been recorded as growing in saline sandy soils, in coastal regions.

P. dimorphum is very poorly known, since the area where it occurs has become inaccessible so that no recent collections have been made. It most closely resembles *P. salicornioides*, but differs from the latter in having leaves which are free to the base.

In the protologue it is mentioned that "the glaucous, glabrous" stems become "rigid pubescent" after three or four years. This gradual change of the epidermis would be unique in *Psilocaulon*, but details of this need to be verified.

10. Psilocaulon articulatum (Thunb.) N.E. Br. in Phillips, Gen. S. African Flow. Pl.: 248 (1926).
Mesembyanthemum articulatum Thunb., Nov. Act. Ephem. Nat. Curios. **8**: 10 App. (1791). - Type: *Thunberg 11947a* (UPS, holo; Photograph!).
Mesembryanthemum secundum Thunb., Mus. Naturalium Acad. Ups.: 12 (1827), nom. nud.
Mesembryanthemum mucronulatum Dinter, Neue Pfl. Deutsch-Südwest Africa: 42 (1914). - *Psilocaulon mucronulatum* (Dinter) N.E. Br., Gard. Chron. SER. 3, **84**: 254 (1928). - Type: Namibia, Klein Karas, October 1913, *Jutta Dinter 3176* (K! lecto; SAM!).
Psilocaulon annuum L. Bolus, Notes Mesembryanthemum **2**: 29-30 (1928). - Type: South Africa, Middelburg district, Grootfontein, November 1928, *Gill 254* (BOL!, holo).
Psilocaulon asperulum N.E. Br., Gard. Chron. SER. 3, **84**: 254 (1928). Type: South Africa, Prince Albert district, near Abrahams Kraal, 1926, *van der Bijl 31* (K!, holo).
Psilocaulon pubescens N.E. Br., Gard. Chron. ser. 3, **84**: 254 (1928). - Type: South Africa, near Uitenhage, November 1926, *Muir 3978* (K!, holo).
Psilocaulon hirtellum L. Bolus, Notes Mesembryanthemum **2**: 191 (1930). - Type: South Africa, between Malmesbury and Hopefield, November 1929, *Pillans BOL 19010* (BOL!, holo).
Psilocaulon bryantii L. Bolus, Notes Mesembryanthemum **2**: 173 (1930). - Type: South Africa, around Prieska, November 1926, *Bryant 708* (BOL!, holo; B!).
Psilocaulon dejagerae L. Bolus, Notes Mesembryanthemum **2**: 236-237 (1931). - Type: South Africa, Beaufort West district, February 1930, *De Jager BOL 19382* (BOL!, holo).
Psilocaulon puberulum Dinter, Repert. Spec. Nov. Regni Veg. **29**: 163 (1931). nom. nud.

Psilocaulon duthiae L. Bolus, Notes Mesembryanthemum **2:** 331-332 (1932). - Type: South Africa, Cradock district, near Baroda, June 1931, *Duthie STE 9547* (BOL!, holo).
Mesembryanthemum granulicaule var. *purpurascens* Berger ex Range, Repert. Spec. Nov. Regni Veg. **36:** 18 (1934). nom. nud.
Psilocaulon roseoalbum L. Bolus, Notes Mesembryanthemum **2:** 493 (1935). - Type: South Africa, Griqualand West, between Kimberley and Kenilworth, December 1934, *Power BOL 21458* (BOL!, holo).
Psilocaulon liebenbergii L. Bolus, J. S. African Bot. **30:** 77 (1964). - Type: South Africa, Alexandria district, Addo Elephant Nat. Park, January 1964, *Liebenberg 7390* (BOL!, holo).

Plant a decumbent to erect shrub, becoming prostrate in loose or sandy soil, ± 0.1-0.3 m tall. **Stems** succulent, articulate, nodes conspicuous with fine horizontal furrow, bladder cells hair-like. **Leaves** free to base, with mucro, bladder cells hair-like. **Flowers** several together in dichasia, up to 10 mm diam., calyx 5-lobed, petals dark to pale pink or white, 1-2 mm broad, petals and filamentous staminodes free to base. **Fruit** 5-locular, 3.0-3.3 mm diam., 2.0-2.1 mm deep; seed light brown, testa smooth with flattened, dome-shaped cells.

DISTRIBUTION: Southern Namibia; South Africa: Western Cape, from Clanwilliam to Malmesbury and Beaufort West; Eastern Cape, from Middelburg to Steytlerville and Albany; Northern Cape, from Colesberg to Prieska and Kimberley (Fig. 10).

ECOLOGY: *P. articulatum* is mainly found outside the winter-rainfall area. Nevertheless, it also extends into the winter-rainfall area of the western Cape. It is found between 0 and 2000 m and tolerates a wide variety of soils.

NOMENCLATURAL NOTES: For *P. mucronulatum* a lectotype was selected, since it was not clear which of the herbarium sheets DINTER used to base his description on. The isotype at K was chosen as lectotype, since it represented best the description given in the protologue.

P. articulatum is very variable in habit. While it is prostrate in loose, sandy soil, it forms small, decumbent to erect shrubs in denser soils. In parts of the country outside the winter-rainfall region, it appears to be an annual. However, within the winter-rainfall region of the south-western Cape, plants may live for several years.

As with most of the other species, the lack of experience in the field and the failure to examine variation in populations by those describing species led to a misunderstanding of the extent of variability within and among populations of *P. articulatum*. The result of this here, as elsewhere, was a proliferation of names most of which are now reduced to synonymy.

The large distribution area and the great adaptability of this species (as with most of the others) may account for the variability in its morphology. *P. articulatum* is nevertheless easily recognized by the fine, hair-like papillae which cover the stems and are visible to the naked eye, lending them a somewhat rough texture. Two other species, i.e. *P. gessertianum* and *P. salicornioides* may also have stems which are covered with hair-like papillae. However, in *P. articulatum* the leaves are free to the bases and the nodes are separated by a fine horizontal furrow. In the two other species with which it may be confused, the leaves are fused for a short distance and the nodes are without a horizontal furrow.

11. Psilocaulon gessertianum (Dinter & Berger) Dinter & Schwantes, Gartenflora **77:** 69 (1928).
Mesembryanthemum gessertianum Dinter & Berger, in Dinter Repert. Spec. Nov. Regni Veg. **19:** 189 (1924). - Type: Namibia, Sandverhaar, January 1910, *Dinter 1195* (B, holo, missing; BOL!, lecto; K!).
Psilocaulon luteum L. Bolus, Notes Mesembryanthemum **1:** 141 (1928). - Type: Namibia, near Keetmanshoop, *Coetzee 17171* (BOL!, holo; B!).

Plant a decumbent to erect shrublet, up to 0.25 m tall. **Stems** succulent, indistinctly articulate, nodes inconspicuous without fine horizontal furrow, covered with fine hair-like idioblasts. **Leaves** shortly fused towards the base, with mucro, bladder cells flattened or with pointed tips when young. **Flowers** several together in few- to many-flowered dichasia, ± 5 mm diam., calyx 5-lobed, petals very reduced, filamentous staminodes yellow, free to base. **Fruit** 5-locular, 2.8-3.5 mm diam., 1.4-2.6 mm deep; seed ochre, testa smooth with flattend, dome-shaped cells.

DISTRIBUTION: Southern to south-eastern Namibia (Fig. 10).

ECOLOGY: *P. gessertianum* is restricted to areas outside the winter-rainfall region and grows at between 1000 - 2000 m, in a variety of soils.

NOMENCLATURAL NOTES: The holotype of *P. gessertianum* was at Berlin, but appears to have been lost. Therefore a lectotype has been selected here. The isotype at the BOL was chosen as lectotype, since it represented best the description given in the protologue.

Psilocaulon gessertianum is remarkable for its minute flowers with very reduced petals, the latter being unique in *Psilocaulon*. Thus, the most conspicuous part of the flower is the cluster of pale yellow, translucent filamentous staminodes. These are gathered into a cone, holding the bright yellow, exserted anthers and stamens in place.

If the plant is not flowering it may be confused with two other species occurring in the same area. From *P. articulatum* it differs in that the leaves are shortly fused towards their bases and the nodes lack a fine horizontal furrow. However, in both species the leaves have a mucro and the stems are covered with short, fine, hair-like papillae. Although the density of papillation is often influenced by environmental factors, the stems of *P. gessertianum* are usually the less papillate of the two.

P. gessertianum cannot be separated from *P. salicornioides* unless it is flowering, since both species have papillate stems and mucronate leaves that are shortly fused at their base.

12. Psilocaulon salicornioides (Pax) Schwantes, Gartenflora **77:** 69 (1928).
Mesembryanthemum salicornioides Pax, Bot. Jahrb. Syst. **19:** 133 (1895). -
Type: Namibia, at the river mouth of the Kuisib near Walfishbay, *Gürich 149* (B!, holo; K!).
Mesembryanthemum glareosum Berger, Bot. Jahrb. Syst. **57:** 630 (1922). - *Mesembryanthemum sinus-redfordiani* Dinter, Repert. Spec. Nov. Regni Veg. Beih. **23:** 44 (1923), nom. nud. - *Psilocaulon sinus-redfordiani* Dinter ex Range, Repert. Spec. Nov. Regni Veg. **36:** 17 (1934), nom. nud.
Psilocaulon glareosum Dinter & Schwantes, Gartenflora **77:** 69 (1928). - Type: Namibia, Aus, *Dinter 1104* (B, holo, missing, K!, lecto; BOL!, SAM!); *Marloth 5044* (B, syn, missing).
Psilocaulon fimbriatum L. Bolus, Ann. Bolus Herb. **4:** 105 (1927). - Type: Namibia, north of Sendlings Drift, *Pillans 5284* (BOL!, holo; HBG!).
Psilocaulon inconspicuum L. Bolus, Notes Mesembryanthemum **2:** 36 (1929). - Type: South Africa, Namaqualand, near Orange River, *Erni BOL 18863* (BOL!, holo).
Psilocaulon inachabense L. Bolus, Notes Mesembryanthemum **3:** 336 (1958). - Type: Namibia, near Inachab, June 1955, *Gessert STE 13637* (BOL!, holo).
Psilocaulon planum L. Bolus, Notes Mesembryanthemum 2: 173-174 (1930). - Type: South Africa, Orange River Mouth, January 1930, *Frames BOL 19048* (BOL!, holo; HBG!).
Mesembryanthemum trothai Engler, Bot. Jahrb. Syst. 43: 196 (1909). - *Psilocaulon trothai* (Engler) Schwantes, Gartenflora **77:** 69 (1928). - Type: Namibia, river bed of Khan River, *Trotha 48a* (B!, holo; K!).
Psilocaulon woodii L. Bolus, Notes Mesembryanthemum **2:** 393 (1933). - Type: Namibia, Pforte, January 1933, *Harcourt-Wood BOL 20449* (BOL!, holo).

Plant a decumbent to erect shrub, up to 0.40 m tall, becoming prostrate on loose/sandy soil. **Stems** succulent, in coastal form distinctly articulate, inland indistinctly so, nodes inconspicuous without fine horizontal furrow. **Leaves** fused towards the base, with short mucro. **Flowers** several together in dichasia, rarely solitary along short side branches, up to 10 mm diam., calyx 4-5-lobed, petals white, pale pink to puce, usually thread-like (0.5-1.0 mm broad), petals and filamentous staminodes fused towards base. **Fruit** 4-5-locular, 2.5-3.1 mm diam., 1.7-2.0 mm deep; seeds ochre or brown, testa rough or smooth with flattened, dome-shaped cells.

DISTRIBUTION: Namibia: it is distributed along the western coastal areas and extends towards the north to the Cunene River. Towards the south it extends as far as the lower Orange River region (Fig. 11).

ECOLOGY: The distribution lies outside the winter-rainfall region only marginally extending into it. It mainly grows at low altitudes (0 - 500 m) in coastal areas, but also occurs at much higher altitudes (-2000 m). It is found in saline habitats, in sand or loam, sometimes between granite outcrops.

NOMENCLATURAL NOTES: The isotype of *P. glareosum* at the Kew was chosen as lectotype, since it represented best the description given in the protologue.

P. salicornioides is a very variable taxon:

The habit depends on the substrate: in loose, sandy soil it is often prostrate, whereas in more loamy soils it is decumbent to erect. Young plants may also be first prostrate and then become decumbent. In saline habitats the stems are more articulated compared to plants growing in less saline soils further inland.

This species was previously thought to occur only along the coast (IHLENFELDT & BITTRICH 1985). However, it does occur also further inland and in fact the distribution of this species is very large, with records from many parts of Namibia (Fig. 11). North of Swakopmund the plants are only found in the fog-zone of the Skeleton Coast. Here they are often noticeably woody compared to those further south. Due to the dependability of the water supply (despite the small quantities involved), plants are able to survive for several years. In the south, where the rainfall is unpredictable, specimens are rarely woody and appear to be annuals.

P. salicornioides most closely resembles *P. articulatum*, *P. gessertianum* (for differences between them see under these two species) and *P. subnodosum*. *P. subnodosum* and *P. salicornioides* are sympatric in southern Namibia. For differences between them see under *P. subnodosum*.

13. Psilocaulon subnodosum (Berger) N.E. Br., Gard. Chron. SER. 3, **84:** 254 (1928).
Mesembryanthemum subnodosum Berger, Bot. Jahrb. Syst. **57:** 628 (1922). - Type: South Africa, Namaqualand, on hills near the Buffelsriver, *Schlechter 11274* (B!, holo; BOL!, K!, S!).
Mesembryanthemum clavulatum Berger, Bot. Jahrb. Syst. **57:** 630 (1922). - *Psilocaulon clavulatum* (Berger) N.E. Br., Gard. Chron. SER. 3, **84:** 254 (1928). - Type: South Africa, Karoechas, *Schlechter 11393* (B!, holo; BOL!, GRA!).
Psilocaulon filipetalum L. Bolus, Notes Mesembryanthemum **2:** 491-492 (1935). Type: South Africa, between Khamieskroon and Springbok, September 1934, *L. Bolus BOL 21425* (BOL!, holo).
Psilocaulon inconstrictum L. Bolus, Notes Mesembryanthemum **3:** 160 (1939). - Type: South Africa, Bushmanland, between Kakamas and Bladgrond, October 1938, *Esterhuysen BOL 21854* (BOL!, holo).

Plant a decumbent to erect shrub, up to 0.70 m tall. **Stems** succulent, indistinctly articulate, nodes inconspicuous, without fine horizontal furrow, glabrous, glaucous. **Leaves** fused towards the base, with short mucro. **Flowers** several together in dichasia, 10-15 mm diam., calyx 5-lobed, petals white or pale pink, usually thread-like (0.5-1.0 mm broad), petals and filamentous staminodes fused towards base. **Fruit** 5-locular, 2.8-3.2 mm diam., 2.1-2.5 mm deep; seeds ochre, testa smooth with flattened, dome-shaped cells or completely flattened cells.

DISTRIBUTION: Southern Namibia: Lower Orange River Valley; South Africa: Northern Cape, Namaqualand, Gordonia, Kenhardt (Fig. 13).

ECOLOGY: *P. subnodosum* has its main distribution in the winter-rainfall area, but also extends well beyond it. It grows at between 0 and 1500 m, in a variety of soils.

In this species one can see a gradual change in the morphology from the drier to the wetter parts of its distribution area. In the drier parts there are fewer leaves, they are more succulent and are fused for more of their length. Also, in drier areas the plants have a thicker covering of wax on the stems and leaves and this gives them a noticeably glaucous appearance. Forms found in some of the drier parts superficially resemble some species of *Ruschia* such as *Ruschia grisea*.

P. subnodosum most closely resembles *P. salicornioides*, but differs in being a larger shrub, usually with larger flowers. In both species the petals are usually thread-like (0.5 mm broad). In *P. subnodosum* (in contrast to *P. salicornioides*), the stems are always smooth. However, the calyx and that part of the stem just below the flower is often papillate. These papillae disappear as the flower and fruit mature. Thus their function may be to provide water reserves for the flower and fruit to ensure the completion of the reproductive cycle.

2. CAULIPSOLON

Caulipsolon rapaceum is noteworthy for possessing unusual, mostly derived character states (which it shares with several genera, including *Psilocaulon*) but for having none of the synapomorphies of *Psilocaulon* (Fig. 16).

Characters shared with *Psilocaulon* are its articulated stems with free leaves, which are otherwise only found in *Aptenia* and *Brownanthus*. *Caulipsolon* has stems with reduced bladder idioblasts, a character present not only in numerous species of *Psilocaulon* but also in *Prenia* and *Aridaria* (*sensu* GERBAULET 1995). The locules are very deep, as is typical of most species of *Psilocaulon*. However, deep locules are also characteristic for *Prenia*. The seeds of *Caulipsolon* are relatively small and have a rough testa with irregularly arranged cells. This character is found not only in *Psilocaulon*, but also in *Mesembryanthemum* and *Brownanthus* and is absent from all other genera of the Mesembryanthemoideae.

It differs from *Psilocaulon* in having a geophytic life form, with deciduous stems, a characteristic of numerous species of *Phyllobolus* (GERBAULET 1995). In addition, the flowers lack filamentous staminodes, but instead have an increased number of petaloid staminodes. In contrast to *Psilocaulon*, the styles spread when fertile. Flowers without filamentous staminodes are found in several genera, including *Phyllobolus*. However, in *Phyllobolus* the stigmas are concealed by the petaloid staminodes (GERBAULET 1995). Very peculiar is also the presence of reflexed valve wings that are fused in pairs ("*Halenbergia*" type *sensu* SCHWANTES 1952), which are otherwise only found in two of the three subgenera of *Mesembryanthemum* (i.e. *Mesembryanthemum* subg. *Opophytum* and subg. *Mesembryanthemum*) and in *Phyllobolus digitatus* (Aiton) Gerbaulet.

A future cladistic study including all the genera of the Mesembryanthemoideae may well show that *Caulipsolon rapaceum* may be placed in some other genus of the Mesembryanthemoideae. However, the evidence put forward in this study suggests that the peculiar combination of characters that it possesses does not link it to any particular genus. It is therefore necessary to move it out of Psilocaulon and create a new monotypic genus, **Caulipsolon**, for it.

Caulipsolon Klak **gen. nov.**

A Psilocaulo radice tuberosum, caulibus caducis, staminodiis filamentosis destitutis, stigmatibus expansis, fructibus cum valvis reflexis et binatis connatis; a Brownantho, Mesembryanthemo, Apteniaque epidermide glabra; a Prenia seminibus cum cellulis testae non serialis differt.

Caulipsolon rapaceum (Jacq.) Klak, **comb. nov.**

Mesembryanthemum rapaceum Jacq., Jacq. fragm.: 43 t. 52 f. 1. (1800-1809). - *Psilocaulon rapaceum* (Jacq.) Schwantes, Gartenflora 77: 69 (1928). - Type: Drawing, holo, in Jacq. fragm.: 43 t. 52 f. 1. (1800-1809).
= *Psilocaulon longipes* L. Bolus, Notes Mesembryanthemum 2: 101 (1929). - Type: South Africa, Namaqualand, along road between Hondeklip Bay and Walle Kraal, October 1924, *Pillans Bol 17917* (BOL, holo).

Plant with tuberous rootstock and prostrate annual stems. **Stems** articulate, epidermal bladder cells flattened, nodes conspicuous with fine horizontal furrow. **Leaves** free to base, without mucro, epidermal bladder cells flattened. **Flowers** several together in dichasia or solitary, several per axis, single on shorter side branches, 20-30 mm diam., calyx 5-lobed, petals white, in 3-5 rows becoming shorter towards centre of flower, free to base, filamentous staminodes absent, stigmas spreading when fertile. **Fruit** 5-locular, ± 4.0-4.5 mm diam., 8-10 mm deep, valve wings reflexed and fused in pairs; seed ochre, testa rough.

DISTRIBUTION: South Africa: Northern Cape, Namaqualand, Calvinia; Western Cape, Vanrhynsdorp (Fig. 13).

ECOLOGY: Typically found in disturbed areas, such as along road sides or overgrazed areas. No preference for a particular soil type has been observed. Its distribution range lies within the winter-rainfall zone and it grows at altitudes between 0 and 1000 m.

C. rapaceum is a very common plant in Namaqualand, from Klawer in the south to Garies and Hondeklip Bay in the north. It is especially plentiful on the Knersvlakte but also occurs in the sandveld close to the shore.

Plants are conspicuous when growing and become covered with white flowers from June until September after which the aerial shoots die back, break off and are blown away so that they disappear without trace until the next growing season.

Excluded species

Psilocaulon arenosum (Schinz) L. Bolus = *Brownanthus arenosus* (Schinz) Ihlenf. & Bittrich

Psilocaulon caducum (Aiton) N.E. Br. = *Mesembryanthemum nodiflorum* L.

Psilocaulon ciliatum (Aiton) Friedrich = *Brownanthus ciliatus* (Aiton) Schwantes ssp. *ciliatus*

Psilocaulon corallinum (Thunb.) Schwantes = *Brownanthus corallinus* (Thunb.) Ihlenf. & Bittrich

Psilocaulon distinctum N.E. Br. = *Aptenia geniculiflora* (L.) Bittrich ex Gerbaulet

Psilocaulon diversipapillosum (Berger) N.E. Br. = *Brownanthus arenosus* (Schinz) Ihlenf. & Bittrich

Psilocaulon gymnocladum (Schlechter & Diels) Dinter & Schwantes = *Brownanthus arenosus* (Schinz) Ihlenf. & Bittrich

Psilocaulon kuntzei (Schinz) Dinter & Schwantes = *Brownanthus kuntzei* (Schinz) Ihlenf. & Bittrich

Psilocaulon lindequistii (Engler) Schwantes = *Aridaria noctiflora* (L.) Schwantes ssp. *noctiflora*

Psilocaulon marlothii (Pax) Friedrich = *Brownanthus marlothii* (Pax) Schwantes

Psilocaulon melanospermum (Berger) N.E. Br. = *Aptenia geniculiflora* (L.) Bittrich ex Gerbaulet

Psilocaulon namibense (Marloth) Friedrich = *Brownanthus namibensis* (Marloth) Bullock

Psilocaulon otzenianum (Dinter) L. Bolus = *Drosanthemum otzenianum*?

Psilocaulon peersii L. Bolus = *Brownanthus corallinus* (Thunb.) Ihlenf. & Bittrich

Psilocaulon pfeilii (Engler) Schwantes = *Prenia tetragona* (Thunb.) Gerbaulet

Psilocaulon pillansii (L. Bolus) Friedrich = *Brownanthus pubescens* (N.E. Br. ex Maass) Bullock

Psilocaulon pomeridianum L. Bolus = *Mesembryanthemum stenandrum* (L. Bolus) L. Bolus

Psilocaulon rapaceum (Jacq.) Schwantes = *Caulipsolon rapaceum* (Jacq.) Klak

Psilocaulon schlichtianum (Sonder) Schwantes = *Brownanthus arenosus* (Schinz) Ihlenf. & Bittrich

Insufficiently known species

Psilocaulon densum is known only from the type and one other collection, both of which were probably collected at the same locality near Steinkopf. N.E. BROWN in 1928 published the name with a very short diagnosis: "Flowers in dense leafy masses". A more detailed description, however, was never published. The specimens are indeed very leafy and the stems appear to be non-succulent. In addition, it is difficult to assess whether the leaves are fused towards the base or free. In the leafyness and lack of succulence it most closely resembles *Psilocaulon foliosum*, which also lacks the otherwise typical succulent stems. However, the capsules which are very small and 5-locular in *Psilocaulon foliosum* are, in comparison, much larger and are 4-locular in *Psilocaulon densum*. The characteristics of the flower could not be investigated. The locules are relatively deep and the seeds neotenic, which are characteristics found in *Psilocaulon*. However, without more information on the floral characteristics its placement in *Psilocaulon* is uncertain. Hybrids are rare in the Mesembryanthema, so that a hybrid origin for these specimens is unlikely, although not impossible. Until more data are available the status of "*Psilocaulon densum*" has to remain uncertain.

Psilocaulon densum N.E. Br., Gard. Chron. SER. 3, **84:** 254 (1928). - Type: South Africa, near Steinkopf, Schakalswater, November 1897, *M. Schlechter 1* (K!, holo; BOL!).

Plant a decumbent to erect shrub. **Stems** smooth, woody, indistinctly articulate, nodes inconspicuous, with or without fine horizontal furrow at nodes. **Leaves** shorty fused or free towards base, no mucro, bladder cells flattened. **Flowers** in dichasia, ± 15 mm diam., calyx 4-lobed, petals free. **Fruit** 4-locular, ± 5.0 mm diam., ± 2.6 mm deep; seeds ochre with white perisperm region, testa almost smooth.

DISTRIBUTION: South Africa: Northern Cape, Namaqualand, near Steinkopf.

ECOLOGY: Winter-rainfall area.

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INDEX

Accepted specific epithets are printed in bold face and synonyms in italics. The page numbers listed refer only to the major reference(s) of each taxon concerned.

List of synonyms

Accepted specific epithets are printed in bold face and synonyms in italics.

Psilocaulon absimile = **Psilocaulon coriarium**
Psilocaulon acutisepalum = **Psilocaulon junceum**

Psilocaulon album = **Psilocaulon leptarthron**
Psilocaulon annuum = **Psilocaulon articulatum**
Psilocaulon arenosum = **Brownanthus arenosus**
Psilocaulon asperulum = **Psilocaulon articulatum**
Psilocaulon baylissii = **Psilocaulon dinteri**
Psilocaulon bijliae = **Psilocaulon junceum**
Psilocaulon bryantii = **Psilocaulon articulatum**
Psilocaulon caducum = **Mesembryanthemum nodiflorum**
Psilocaulon calvinianum = **Psilocaulon junceum**
Psilocaulon candidum = **Psilocaulon junceum**
Psilocaulon ciliatum = **Brownanthus ciliatus** ssp. **ciliatus**
Psilocaulon clavulatum = **Psilocaulon subnodosum**
Psilocaulon corallinum = **Brownanthus corallinus**
Psilocaulon dejagerae = **Psilocaulon articulatum**
Psilocaulon delosepalum = **Psilocaulon junceum**
Psilocaulon distinctum = **Aptenia geniculiflora**
Psilocaulon diversipapillosum = **Brownanthus arenosus**
Psilocaulon duthiae = **Psilocaulon articulatum**
Psilocaulon fasciculatum = **Psilocaulon dinteri**
Psilocaulon filipetalum = **Psilocaulon subnodosum**
Psilocaulon fimbriatum = **Psilocaulon salicornioides**
Psilocaulon framsii = **Psilocaulon junceum**
Psilocaulon godmaniae var. *godmaniae* = **Psilocaulon dinteri**
Psilocaulon godmaniae var. *gracile* = **Psilocaulon dinteri**
Psilocaulon gymnocladum = **Brownanthus arenosus**
Psilocaulon herrei = **Psilocaulon dinteri**
Psilocaulon hirtellum = **Psilocaulon articulatum**
Psilocaulon imitans = **Psilocaulon junceum**
Psilocaulon implexum = **Psilocaulon parviflorum**
Psilocaulon inachabense = **Psilocaulon salicornioides**
Psilocaulon inconspicuum = **Psilocaulon salicornioides**
Psilocaulon inconstrictum = **Psilocaulon subnodosum**
Psilocaulon kuntzei = **Brownanthus kuntzei**
Psilocaulon laxiflorum = **Psilocaulon junceum**
Psilocaulon leightoniae = **Psilocaulon junceum**
Psilocaulon levynsiae = **Psilocaulon junceum**
Psilocaulon lewisiae = **Psilocaulon junceum**
Psilocaulon liebenbergii = **Psilocaulon articulatum**
Psilocaulon lindequistii = **Aridaria noctiflora** ssp. **noctiflora**
Psilocaulon littlewoodii = **Psilocaulon dinteri**
Psilocaulon littlewoodii forma = **Psilocaulon dinteri**
Psilocaulon longipes = **Caulipsolon rapaceum**
Psilocaulon luteum = **Psilocaulon gessertianum**
Psilocaulon marlothii = **Brownanthus marlothii**
Psilocaulon melanospermum = **Aptenia geniculiflora**
Psilocaulon mentiens = **Psilocaulon coriarium**
Psilocaulon micranthon = **Psilocaulon parviflorum**
Psilocaulon mucronulatum = **Psilocaulon articulatum**
Psilocaulon namaquense = **Psilocaulon junceum**
Psilocaulon namibense = **Brownanthus namibensis**
Psilocaulon oculatum = **Psilocaulon junceum**
Psilocaulon otzenianum = **Drosanthemum otzenianum?**
Psilocaulon pageae var. *grandiflorum* = **Psilocaulon junceum**
Psilocaulon pageae var. *pageae* = **Psilocaulon junceum**
Psilocaulon pauciflorum = **Psilocaulon junceum**

Psilocaulon pauper = **Psilocaulon granulicaule**
Psilocaulon peersii = **Brownanthus corallinus**
Psilocaulon pfeilii = **Prenia tetragona**
Psilocaulon pillansii = **Brownanthus pubescens**
Psilocaulon planisepalum = **Psilocaulon junceum**
Psilocaulon planum = **Psilocaulon salicornioides**
Psilocaulon pomeridianum = **Mesembryanthemum stenandrum**
Psilocaulon puberulum = **Psilocaulon articulatum**
Psilocaulon pubescens = **Psilocaulon articulatum**
Psilocaulon rapaceum = **Caulipsolon rapaceum**
Psilocaulon rogersiae = **Psilocaulon junceum**
Psilocaulon roseoalbum = **Psilocaulon articulatum**
Psilocaulon schlichtianum = **Brownanthus arenosus**
Psilocaulon semilunatum = **Psilocaulon junceum**
Psilocaulon simulans = **Psilocaulon junceum**
Psilocaulon sinus-redfordiani = **Psilocaulon salicornioides**
Psilocaulon squamifolium = **Psilocaulon junceum**
Psilocaulon stayneri = **Psilocaulon junceum**
Psilocaulon stenopetalum = **Psilocaulon coriarium**
Psilocaulon subintegrum = **Psilocaulon junceum**
Psilocaulon tenue = **Psilocaulon parviflorum**
Psilocaulon trothai = **Psilocaulon salicornioides**
Psilocaulon uncinatum = **Psilocaulon coriarium**
Psilocaulon utile = **Psilocaulon junceum**
Psilocaulon variabile = **Psilocaulon dinteri**
Psilocaulon woodii = **Psilocaulon salicornioides**
Mesembryanthemum acutisepalum = **Psilocaulon junceum**
Mesembryanthemum articulatum = **Psilocaulon articulatum**
Mesembryanthemum bicorne = **Psilocaulon bicorne**
Mesembryanthemum clavulatum = **Psilocaulon subnodosum**
Mesembryanthemum coriarium = **Psilocaulon coriarium**
Mesembryanthemum dimorphum = **Psilocaulon dimorphum**
Mesembryanthemum dinteri = **Psilocaulon dinteri**
Mesembryanthemum gessertianum = **Psilocaulon gessertianum**
Mesembryanthemum glareosum = **Psilocaulon salicornioides**
Mesembryanthemum granulicaule = **Psilocaulon granulicaule**
Mesembryanthemum granulicaule var. *purpurascens* = **Psilocaulon articulatum**
Mesembryanthemum junceum = **Psilocaulon junceum**
Mesembryanthemum junceum var. *pauciflorum* = **Psilocaulon junceum**
Mesembryanthemum leptarthron = **Psilocaulon leptarthron**
Mesembryanthemum marinum = **Psilocaulon dinteri**
Mesembryanthemum mentiens = **Psilocaulon coriarium**
Mesembryanthemum micranthon = **Psilocaulon parviflorum**
Mesembryanthemum mucronulatum = **Psilocaulon articulatum**
Mesembryanthemum parviflorum = **Psilocaulon parviflorum**
Mesembryanthemum rapaceum = **Caulipsolon rapaceum**
Mesembryanthemum salicornioides = **Psilocaulon salicornioides**
Mesembryanthemum secundum = **Psilocaulon articulatum**
Mesembryanthemum simile = **Psilocaulon junceum**
Mesembryanthemum simile var. *namaquense* = **Psilocaulon junceum**
Mesembryanthemum sinus-redfordiani = **Psilocaulon salicornioides**
Mesembryanthemum subnodosum = **Psilocaulon subnodosum**
Mesembryanthemum tenue = **Psilocaulon parviflorum**
Mesembryanthemum trothai = **Psilocaulon salicornioides**

Ruschia coriaria = **Psilocaulon coriarium**

Appendix 1

Index to numbered exsiccatae investigated in this study. Only exsiccatae with collectors name are listed. The numbers given in brackets refer to the following species: *Psilocaulon articulatum* (1), *P. bicorne* (2), *P. coriarium* (3), *P. dimorphum* (4), *P. dinteri* (5), *P. foliosum* (6), *P. gessertianum* (7), *P. granulicaule* (8), *P. junceum* (9), *P. leptarthron* (10), *P. parviflorum* (11), *P. salicornioides* (12), *P. subnodosum* (13), *P. densum* (14), *Caulipsolon rapaceum* (15).

Acocks 3: (13), 2284: (1), 11911: (3), 11912: (9), 14725: (15), 14787: (15), 14860: (9), 14929: (6), 15052: (9), 15072: (1), 15077: (3), 15083: (1), 15085: (3), 15101: (13), 15110: (5), 15145: (3), 15225: (9), 15249: (9), 15285: (9), 15290: (3), 15311: (1), 16237: (9), 16500: (13), 17317: (3), 24247: (11); Acocks & Hafström 1341: (1), H 1336: (3); Anderson 113: (1), 142: (1), 382: (1), 475: (1); Arbuthnot BH 21546: (8); Archer 169: (9); Archibald 563: (1), 3122: (3), 3683: (3), 3732: (1), 4920: (9);

B.R. BH 12919: (8), BH 12923: (1); Bachmann 329: (9); Badenhorst 111: (3); Balkwill & Balkwill 4157: (3), 4506: (13); Balsinhas & Kersberg 1958: (9), 2032: (1); Barbosa 9468: (4); Barclay 962: (1); Barker 2: (9), 3: (2), 14: (1), BH 20846: (9); Bayliss 623: (11), 998: (5), 6932: (8); Bean 541: (5), 542: (5), 562: (5), 1247: (10), 1660: (9); Bean & Viviers 1475: (3); Bean, Vlok & Vivien 1627: (9); Bengis 429: (3); Blake 21979: (8); Blyth 2498/33: (9); Bohnen 7412: (11), 8405: (9), 8735: (9), 8974: (9), 8993: (2); H. Bolus 102: (3), 6708: (9), 11497: (9), 11906: (8), 112: (9), 793: (8), 6709: (9), 6711: (9), 8650: (11), 13121: (1); L. Bolus 32/03: (6); 19050: (9), 19051: (9), 21034: (9), 21038: (9), 21425: (13), BH 18846: (9), BH 19096: (9), BH 19324: (15), BH 20841: (2), BH 32101: (9), BH 32102: (15), BH 32105: (11), NBG 2693/17: (1); Botha 6590: (8); Boucher 2681: (11), 3617: (1), 4042: (1), Bradfield 514: (8); Brink 242: (8), 287: (1); Brito Teixeira 975: (4); Britten 3018: (9), BH 100: (9); Brueckner 113: (8); Bruyns 6389: (3), 6390: (3), 6391: (3), 6651: (3), 6652: (3), 6653: (3), 6654: (3), 6714: (5), 6715: (10), 6716: (9), 6717: (5), 6722: (5), 6723: (6), 6733: (6), 6737: (6), 6739: (5), 6762: (6), 6772: (6); Bryant 8: (1), 560: (3), 708: (1), 712: (3), 718: (1), 768: (1), 947: (1), J 167: (3), J248: (1), KMG 3621: (3), KMG 5834: (1), STE 18277: (1); Burchell 665: (11), 2679: (3), 6408: (11); Burger 108: (10); Burgers 95: (2), 1432: (11), 2531: (11); Burtt-Davy 9958: (8), 9962: (3), 10809: (3), 11960: (8), 13513: (3);

Carrisso & Sousa 221: (4), 246: (4); Codd 5895: (7); Coetzee 17171: (7); Compton 3906 :(8), BH 18593: (8), BH 19005: (9), BH 27231: (12), BH 32108: (12), NBG 1475/26: (10), NBG 1831/27: (3), NBG 1861/26: (3), NBG 1861/27: (3); Cooke KMG 6308: (1); Cooper 2381: (1); Craven 1573: (12), 1606:

(12); Craven & Craven 242: (12), 265: (12);

Dahlstrand 2298: (9), 3556: (9), Daly 1033: (8); De Jager BH 19382: (1), BH 27241: (8); De Winter & Giess 6079: (3); Dinter 954: (5), 1104: (12), 1195: (7), 1331: (5), 2148a: (3), 2801: (12), 3176: (1), 3745: (12), 3755: (5), 3778: (12), 3780: (12), 3780b: (12), 3877: (3), 3879: (3), 4083: (5), 4935: (1), 4941: (12), 4942: (3), 4953: (1), 4967: (12), 4973: (1), 5041: (7), 6002a: (5), 6013: (12), 6017: (1), 6431: (3), 6509: (5), 6575: (5), 7865: (8); Dold 398: (9); Drege 238: (1), 276: (8), 313: (9), 484: (8), 764: (8), 1089: (1), 3113: (8); Du Plessis 182: (2), s.n.: (9), 2267/32: (9), BH 3157/32: (9), Du Toit s.n.: (8), BH 21437: (1), BH 23402: (3); Duthie 9547: (1);

Eckert H.1783/67: (8); Eichler 17811: (8), 18297: (8); Engler 6694: (3), 6839: (5), Erni BH 18863: (5); Esterhuysen 2874: (9), 5638: (9), 6359: (1), 13269: (8), 19552: (11), 21854: (13), 21855: (9), BH 27230: (3), BH 32106: (11); Evrard 8826: (1), 9025: (13), 9228: (7);

Fellingham 460: (9); Flanagan 1481: (1), Flanagan 1482: (3); Foley 111: (9); Forbes 541: (8); Fourcade 1818: (8), 3420 (1), 3458: (9), 3546: (8), 4046: (11), 4280: (9), 4289: (1), 4290: (9), 4302: (9), 4368: (9), 4510: (9), 4514: (8), 5846: (9), 5850?: (8), 5850B: (1); Francis 8: (1); Friedrich 254: (11), 516: (12), 697: (3), 723: (12), 743: (3), 744: (7), 748: (13), 756: (13);

Galpin 4049: (11), BH 19860: (11); Gerbaulet & Struck 24713: (15), 24936: (9), 24943: (1), 24963: (15), 24973: (2), 24978: (2), 50012: (1), 50014: (1), 50022: (9), 50035: (13), 50047: (12), 50054: (5), 50059: (3), 50066: (3), 50067: (12), 50068: (3), 50073: (7), 50074: (3), 50076: (7), 50081: (12), 50083: (13), 50086: (13), 50090: (13), 50097: (13), 50108: (10), 50123: (5), 50161: (6); Germishuizen 2426: (1); Gess & Gess A 7677: (9), A 7683: (9); Gessert SUG 13637: (12); Giess 2263a: (12), 2282: (3), 2301: (12), 2320: (5), 2363: (12), 2369: (3), 2433: (3), 3068: (12), 3411a: (12), 3411b: (12), 3550: (12), 7978: (12), 10695: (3), 10838: (12), 13775: (12), 13840: (12); Giess & Leippert 7393: (12), 7446: (12), 7504: (12); Giess & Mueller 12243: (12); Giess & Van Vuuren 701: (5); Giess, Volk & Bleissner 5297: (3), 5369: (12), 5457: (3), 7019: (7), 7031: (3); Giffen 954: (8); Gill 254: (1), 255: (8); Glen 881: (5), 936: (9), 942: (1); Godman 639: (9), BH 18979: (5), BH 19004: (9), BH 19049: (5); Goldblatt 7086: (9); Greuter 20302: (12), 20898: (8), 21609: (13), 21632: (13), 21633: (13), Greuter 21799: (9); Grillarmod 7678: (9); Grobelar BH 23139: (5); Growers Assw. s.n.: (3); Gubb 514: (3), 1031: (3), KMG 12429: (3); Guerich 149: (12); Guillamod 5404: (9); H. 11944: (1);

Hafström 1263: (1), 1264: (3), 1280: (8), 1341: (1), KMG 5625: (11), KMG 5626: (11); Hahndiek D 165: (8); Hampden s.n.: (5); Hanekom 224: (8); Harcourt-Wood 20449: (12), BH 20845: (12); Hardy 6947: (3); Hartzer 31: (9); Henrici 1452: (3), 3397: (9), 3840: (3), 4735: (3), 4738: (3), 4999: (9), 5151: (3), 5152: (3), PRE 53608: (3); Herbert 2: (3); Herre s.n.: (1), 14675: (5), SUG 8503: (10), SUG 10096: (1), SUG 11002: (9); Hilton-Taylor 1566: (9), 17770: (9); Hoffman 596: (9), 928: (1); Hook 678/22: (1); Horn PRE 53681: (9); Hosken 56: (9); Humbert 16387: (4); Hutchinson 1518: (1);

Ihlenfeldt 1019: (11), 1062: (9) 1096: (15), 1110: (5), 1188: (5), 1389: (13), 1471: (5); Ihlenfeldt, de Winter &

3891: (11), 3978: (1), 4222: (9), 4234: (11), 4725: (3), 5154: (11);

Noel 10301: (1);

O'Callaghan 322: (5), 1152: (5), Oertendahl 292: (13), 641: (12); Olivier 202: (9), Owen-Smith 1277: (3); Owen-Smith & Malan 383: (12); BH 17166: (9), BH 17167a: (9), Page BH 17167: (9);

Parker KMG 46: (8); Parsons 507: (9); Paterson 2154: (2), 2162: (9); Pearson 508: (5), 572: (6), 3062: (9), 3063: (10), 3273: (9), 3846: (3), 3918: (9), 4164: (5), 4443: (3), 4719: (3), 4879: (9), 6127: (5), 8038: (3), 8568: (1), 8585: (1), 8586: (1), 9034: (3), 9184: (12), 9286: (12), 9398: (1), 9703: (1); Penther 1804: (1); Perold 2214: (9); Peter 47112: (3), 47116: (3), 50817: (1), 50819: (1), 50861: (1); Pierce 59: (5), 76: (5); Pillans 4022: (1), 5024: (5), 5031: (5), 5185: (13), 5284: (12), 5439: (5), 5969: (12), 6144: (1), 6382: (13), 6583: (12), 17769: (5), 17813: (6) BH 17762: (5), BH 17767: (5), BH 17805: (5), BH 17921: (5), BH 19010: (1), BH 32109: (11), 17917: (15); Pole-Evans 8010: (1), PRE 18817: (3); Pont 396: (1); Power KMG 426: (1), BH 21458: (1), Primos sub Marloth 13670: (11);

R.H. 1475/26: (10); Range 156: (7), 180: (12), 204: (12), 762: (1), 1189: (12), 1298: (12), 1633: (1), 278a: (3), 278b: (12); Retief & Reid 284: (1); Roesch & Le Roux 217: (13); Rogers 198: (12), 3486: (9), 4505: (9), 17795: (11), A 7684: (12), BH 17176: (1), BH 18856: (9), BH 27236: (1), BH 27604: (1), BH 32100: (2), BH 32107: (12); Ross Frames 19048: (12), BH 19112: (9), NBG 159/28: (9); Roux & Parsons 6: (5); Rycroft 2478: (12);

Salter 3838: (10), Sanday BH 27237: (3); Schinz 276: (3); Schlechter 1: (14), 96: (13), 126: (14), 168: (13), 181: (13), 5715: (11), 8151: (10), 11274: (13), 11393: (13); Schlieben 9103: (13), 11445: (5); Schlieben & Van Breda 9831: (9), 9870: (9), Schmidt 240: (9), 396: (9), 1021: (12); Schmiedel FNR 102018: (5); Schyf 33: (3); Scott 505: (8); Seely 2060: (12); Seydel 609: (12), 1111: (12), 1677: (12); Shaw 7: (1), 13: (3); Shearing 688: (9); Sim 1146: (8); Smith 2360: (3) 2368: (3), 2409: (8), 5233: (1), 4112A: (3), BH 27232: (11); Stayner 893/59: (9), KG 993/59: (9), KG 806/60a: (3); Stephens & Glover 8730: (11); Story 7: (3); Strohbach 96: (13), 127: (5), 203: (12), 279: (12), 512: (13); Swan KMG 43: (1);

Theron 547: (3), 3095: (9), 3811: (12), 3929: (1), 3950: (3), 3953: (3); Theron & Van der Schijff 2337: (3); Thode 3776: (1); Thompson 3141: (9); Thorne 54075: (7); Thorold 2049: (4); Tijmens SUG 14787: (9); Toelken & Hardy 612: (3); Trotha 48A: (12); Troughton 120: (9); Tyson 42: (3);

Van Blerk 13: (9); Van Breda 199: (9), 2174/64: (11), 2202/64: (1); Van Jaarsveld 1714: (3), 4624: (1), 12747: (9), 13752: (1); Van Vuuren 1178: (3); Van Wyk 515: (9), 6512: (13); Van der Merwe 67: (9), 1414: (3), 1875: (8); Van den Eynden 14.2e: (12); Van der Bijl 30: (9), 31: (1), 43: (11), 59: (9), 60: (8), 60A: (1); Vanderplank A 7679: (1); Venter 8615: (5); Verdoorn 1166: (1), 1452: (3), 1536: (3), 1569: (8), 1594: (3), 2037: (8); Viljoen 381: (12); Visser A 7681: (3); Volk 719: (12), 928: (12), 930: (12), 12812: (3), 12832: (5);

Walter & Walter 139: (7), 1727: (3), 2564: (3), 2606: (3); Walters 75: (9); Ward 219: (12), 9214: (12), 9243: (12); Ward & Seely 10211: (12), 10235: (12); Watmough 852: (12);

Welwitsch 2377: (4); Wendt 33: (13), sub Giess 14733: (12), sub Giess 14745: (12), sub Giess 14704: (3); Werdermann & Oberdieck 537: (9), 619: (9); Werger 119: (3), 128: (3), 169: (1), 437: (13); Williamson 3152: (13), 3156: (13), 3174: (5), 3204: (13), 3207: (13), 3209: (13), 3219: (13), 3230: (5), 3232: (13); Wilman 34: (8), 4049: (8), Wilman KMG 44: (3), BH 21544: (3), BH 27234: (1), BH 32110: (13), KMG 3399: (3), KMG 3407: (8), KMG 4042: (3), KMG 6307: (3); Wiss 2081b: (12); Wolley Dod 2130: (11);

Young 14201: (8), Young sub Moss 15295: (8);

Zeyher 192: (9), 704: (9), 705: (1), 1079: (9), 2615: (11), 2616: (2), 2617: (1), 2618: (9), 2957: (9), 2957: (8); Zeyher & Ecklon 2037: (9), 2041: (9), 2042: (9), 2044: (2), 2045: (2), PRE 20951: (9), Zietsman & Zietsman 614: (3), 678: (13), 689: (13), 697: (1), 766: (13), 839: (5), 1225: (9), 1636: (9).

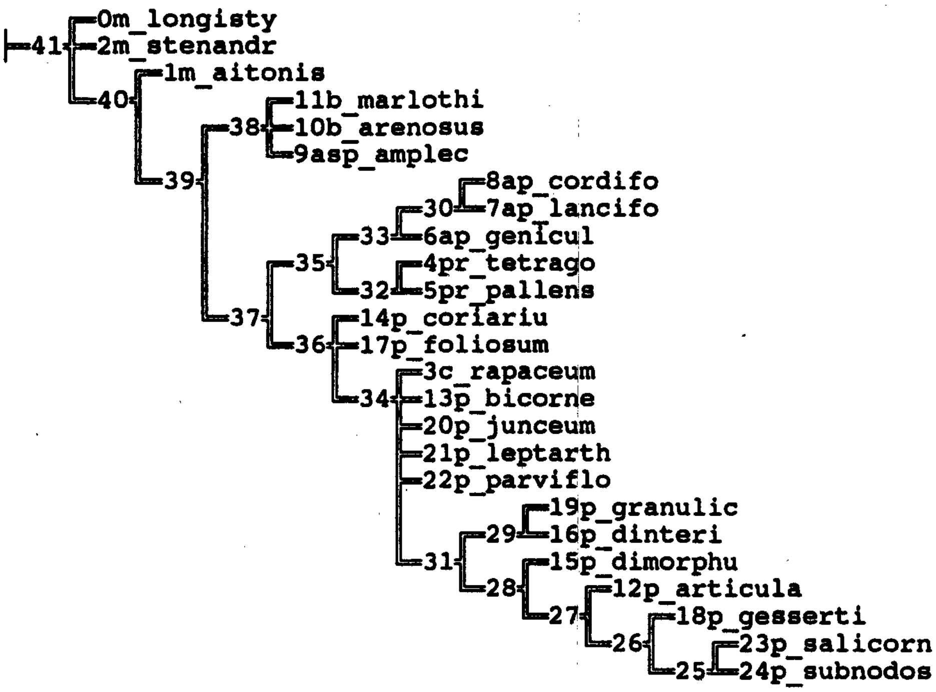
Vouchers studied for the outgroups.

Aspazoma amplectens:
Bruyns 6751 (BOL), *Pillans 5698* (BOL).
Aptenia cordifolia:
Strey 5310a (BOL), *Van Zijl 883* (BOL).
Aptenia geniculiflora:
Gerbaulet & Struck 50063 (BOL); *Klak 14* (BOL), *17* (BOL), *131* (BOL).
Aptenia lancifolia:
Riley NBG 372159 (BOL), *Strey 6031* (BOL).
Brownanthus arenosus:
Pierce 60 (BOL), *68* (BOL).
Brownanthus marlothii:
Dinter 6419 (BOL); *Giess & Van Vuuren 702* (BOL).
Prenia pallens ssp. *pallens*:
Gerbaulet & Struck 24768 (BOL), *24736* (BOL).
Prenia tetragona:
Gerbaulet & Struck 24920 (BOL), *24957* (BOL).
Mesembryanthemum aitonis:
Gerbaulet & Struck 50002 (BOL), *Glen 847* (BOL).
Mesembryanthemum longistylum:
Gerbaulet & Struck 50131 (BOL), *Klak 39* (BOL).
Mesembryanthemum nodiflorum:
Guthrie 17165 (BOL), *Van Breda 1934* (BOL).

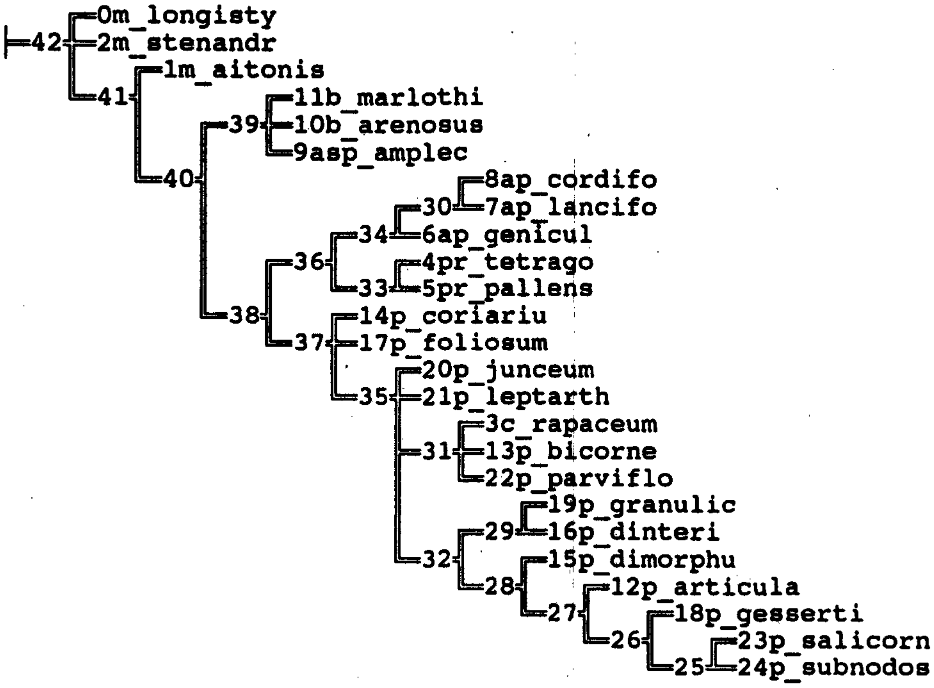
Appendix 2

Effect of exclusion of single characters. The consistency index of the exluded character is given as well as the length, consistency index (ci), retention index (ri) and the number of trees calculated using Hennig86 (option mh*; bb*;). A strict consensus tree was calculated for each character removal.

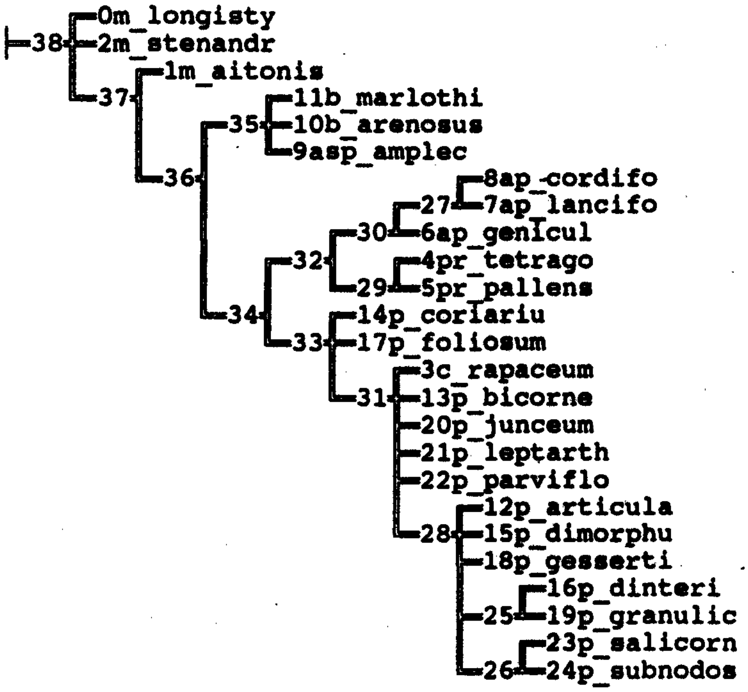
Character 2 ("habit") excluded, ci = 0.25, length 68 ci 52 ri 78 trees 514



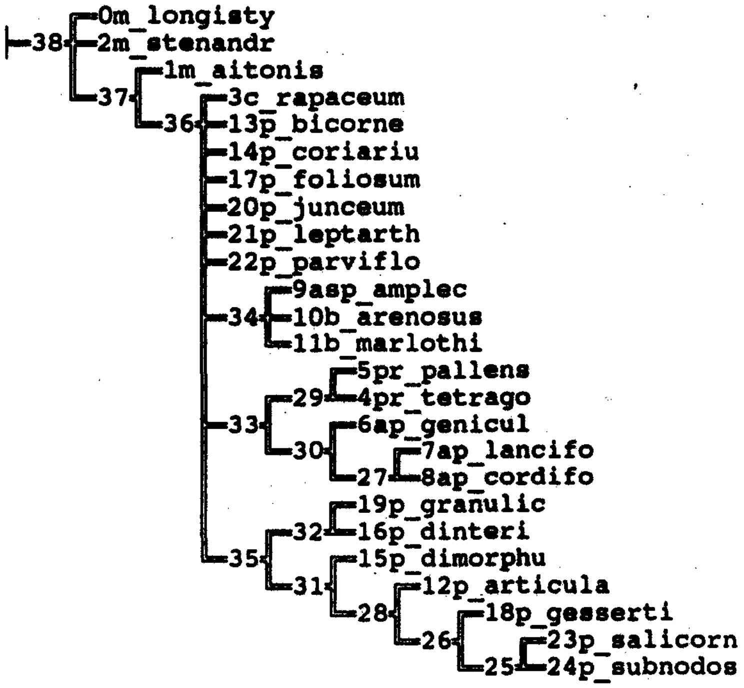
Character 3 ("presence or absence of a persistent green cortex") excluded, ci = 0.50, length 70 ci 51 ri 77 trees 28



Character 4 ("stems with or without horizontal furrow") excluded, ci = 0.33, length 69 ci 52 ri 77 trees 196



Character 5 ("idioblasts on stem protruding or flattened") excluded, ci = 5, length 68 ci 52 ri 77 trees 142



Character 6 ("shape of idioblasts") excluded, ci = 100, length 70 ci 50 ri 76 trees 248

```
     ┌─0m_longisty
├─37─┼─2m_stenandr
     │    ┌─1m_aitonis
     └─36─┤
          │         ┌─11b_marlothi
          │    ┌─34─┼─10b_arenosus
          │    │    └─9asp_amplec
          └─35─┤
               │                   ┌─8ap_cordifo
               │              ┌─26─┴─7ap_lancifo
               │         ┌─29─┴─6ap_genicul
               │    ┌─31─┤    ┌─4pr_tetrago
               │    │    └─28─┴─5pr_pallens
               └─33─┤    ┌─14p_coriariu
                    └─32─┼─17p_foliosum
                         │    ┌─3c_rapaceum
                         └─30─┼─12p_articula
                              ├─13p_bicorne
                              ├─15p_dimorphu
                              ├─16p_dinteri
                              ├─19p_granulic
                              ├─20p_junceum
                              ├─21p_leptarth
                              ├─22p_parviflo
                              │    ┌─18p_gesserti
                              └─27─┤    ┌─23p_salicorn
                                   └─25─┴─24p_subnodos
```

Character 7 ("distance between protruding idioblasts"), ci = 100, length 70 ci 50 ri 76 trees 6

```
     ┌─0m_longisty
├─42─┼─2m_stenandr
     │    ┌─1m_aitonis
     └─41─┤
          │         ┌─11b_marlothi
          │    ┌─39─┼─10b_arenosus
          │    │    └─9asp_amplec
          └─40─┤
               │                   ┌─8ap_cordifo
               │              ┌─30─┴─7ap_lancifo
               │         ┌─34─┴─6ap_genicul
               │    ┌─36─┤    ┌─4pr_tetrago
               │    │    └─33─┴─5pr_pallens
               └─38─┤    ┌─14p_coriariu
                    └─37─┼─17p_foliosum
                         │    ┌─20p_junceum
                         └─35─┼─21p_leptarth
                              │    ┌─3c_rapaceum
                              ├─31─┼─13p_bicorne
                              │    └─22p_parviflo
                              │         ┌─19p_granulic
                              │    ┌─29─┴─16p_dinteri
                              └─32─┤    ┌─15p_dimorphu
                                   └─28─┤    ┌─12p_articula
                                        └─27─┤    ┌─18p_gesserti
                                             └─26─┤    ┌─23p_salicorn
                                                  └─25─┴─24p_subnodos
```

Character 8 ("idioblasts thickened or not thickened") excluded, ci = 100, length 71 ci 50 ri 76 trees 98

```
      ┌──0m_longisty
├──37─┼──2m_stenandr
      │    ┌──1m_aitonis
      └─36─┤
           │    ┌──6ap_genicul
           └─35─┼──9asp_amplec
                ├──10b_arenosus
                ├──11b_marlothi
                ├──14p_coriariu
                ├──17p_foliosum
                │    ┌──4pr_tetrago
                ├─32─┴──5pr_pallens
                │    ┌──7ap_lancifo
                ├─33─┴──8ap_cordifo
                │    ┌──20p_junceum
                └─34─┼──21p_leptarth
                     │    ┌──3c_rapaceum
                     ├─30─┼──13p_bicorne
                     │    └──22p_parviflo
                     │         ┌──19p_granulic
                     │    ┌─29─┴──16p_dinteri
                     └─31─┤    ┌──15p_dimorphu
                          └─28─┤    ┌──12p_articula
                               └─27─┤    ┌──18p_gesserti
                                    └─26─┤    ┌──23p_salicorn
                                         └─25─┴──24p_subnodos
```

Character 9 ("epidermis on stems and leaves heteromorphic"), ci = 0.50, length 70 ci 51 ri 77 trees 28

```
      ┌──0m_longisty
├──42─┼──2m_stenandr
      │    ┌──1m_aitonis
      └─41─┤         ┌──11b_marlothi
           │    ┌─39─┼──10b_arenosus
           │    │    └──9asp_amplec
           └─40─┤              ┌──8ap_cordifo
                │         ┌─30─┴──7ap_lancifo
                │    ┌─34─┴──6ap_genicul
                │    │    ┌──4pr_tetrago
                │ ┌─36─┤
                ...
```

Character 10 ("presence or absence of mucro") excluded, ci = 100, length 71 ci 50 ri 76 trees 268

```
    ┌─0m_longisty
├─38┼─2m_stenandr
    │   ┌─1m_aitonis
    └─37┤       ┌─11b_marlothi
        │   ┌─35┼─10b_arenosus
        │   │   └─9asp_amplec
        └─36┤               ┌─8ap_cordifo
            │           ┌─27┴─7ap_lancifo
            │       ┌─30┴─6ap_genicul
            │   ┌─32┤   ┌─4pr_tetrago
            │   │   └─29┴─5pr_pallens
            └─34┤   ┌─14p_coriariu
                └─33┼─17p_foliosum
                    │   ┌─3c_rapaceum
                    └─31┼─13p_bicorne
                        ├─20p_junceum
                        ├─21p_leptarth
                        ├─22p_parviflo
                        │   ┌─12p_articula
                        └─28┼─15p_dimorphu
                            ├─18p_gesserti
                            │   ┌─16p_dinteri
                            ├─25┴─19p_granulic
                            │   ┌─23p_salicorn
                            └─26┴─24p_subnodos
```

Character 11 ("shape of cross section of leaves") excluded, ci = 0.33, length 69 ci 52 ri 78 trees 28

```
    ┌─0m_longisty
├─42┼─2m_stenandr
    │   ┌─1m_aitonis
    └─41┤       ┌─11b_marlothi
        │   ┌─39┼─10b_arenosus
        │   │   └─9asp_amplec
        └─40┤               ┌─8ap_cordifo
            │           ┌─30┴─7ap_lancifo
            │       ┌─34┴─6ap_genicul
            │   ┌─36┤   ┌─4pr_tetrago
            │   │   └─33┴─5pr_pallens
            └─38┤   ┌─14p_coriariu
                └─37┼─17p_foliosum
                    │   ┌─20p_junceum
                    └─35┼─21p_leptarth
                        │   ┌─3c_rapaceum
                        ├─31┼─13p_bicorne
                        │   └─22p_parviflo
                        │       ┌─19p_granulic
                        │   ┌─29┴─16p_dinteri
                        └─32┤   ┌─15p_dimorphu
                            └─28┤   ┌─12p_articula
                                └─27┤   ┌─18p_gesserti
                                    └─26┤   ┌─23p_salicorn
                                        └─25┴─24p_subnodos
```

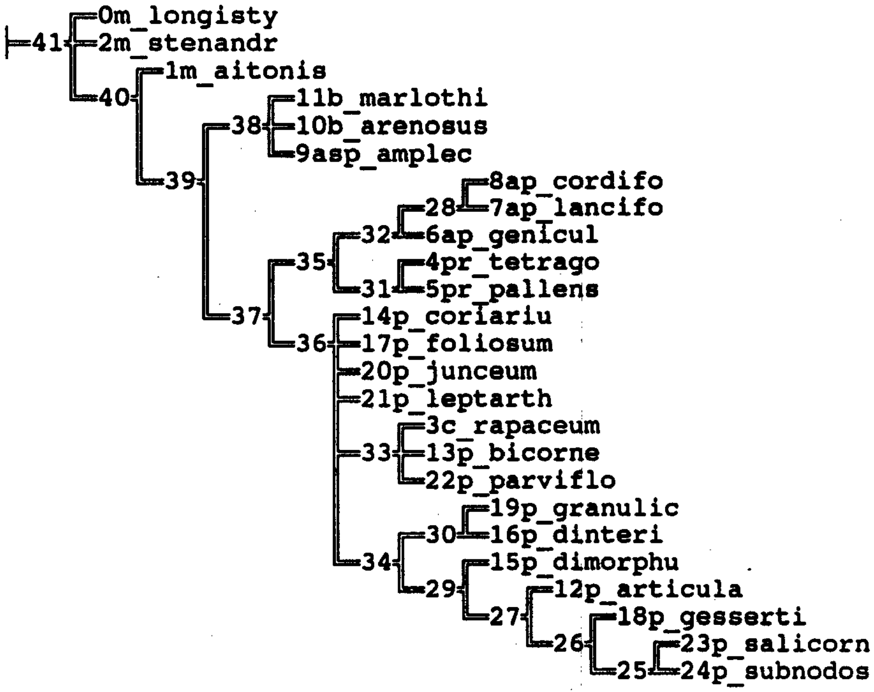
Character 12 ("presence or absence of a central water storing tissue in leaves") excluded, ci = 0.50, length 70 ci 51 ri 77 trees 76

```
      ┌─0m_longisty
├─37──┼─2m_stenandr
      │    ┌─1m_aitonis
      └─36─┤    ┌─6ap_genicul
           └─35─┼─9asp_amplec
                ├─10b_arenosus
                ├─11b_marlothi
                ├─14p_coriariu
                ├─17p_foliosum
                │    ┌─4pr_tetrago
                ├─32─┴─5pr_pallens
                │    ┌─7ap_lancifo
                ├─33─┴─8ap_cordifo
                │    ┌─20p_junceum
                └─34─┼─21p_leptarth
                     │    ┌─3c_rapaceum
                     ├─30─┼─13p_bicorne
                     │    └─22p_parviflo
                     │         ┌─19p_granulic
                     │    ┌─29─┴─16p_dinteri
                     └─31─┤    ┌─15p_dimorphu
                          └─28─┤    ┌─12p_articula
                               └─27─┤    ┌─18p_gesserti
                                    └─26─┤    ┌─23p_salicorn
                                         └─25─┴─24p_subnodos
```

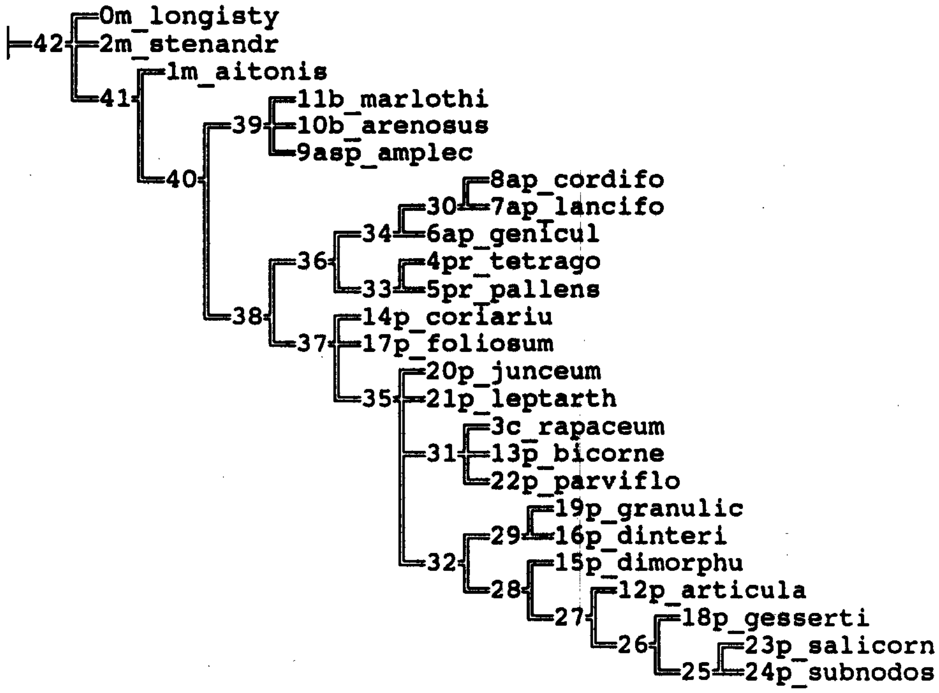
Character 13 ("Inflorescence a few-flowered dichasium or solitary flowers") excluded, ci = 0.33, length 69 ci 52 ri 78 trees 14

```
      ┌─0m_longisty
├─43──┼─2m_stenandr
      │    ┌─1m_aitonis
      └─42─┤              ┌─10b_arenosus
           │         ┌─38─┴─9asp_amplec
           │    ┌─40─┴─11b_marlothi
           └─41─┤                   ┌─8ap_cordifo
                │              ┌─30─┴─7ap_lancifo
                │         ┌─34─┴─6ap_genicul
                │    ┌─36─┤    ┌─4pr_tetrago
                │    │    └─33─┴─5pr_pallens
                └─39─┤    ┌─14p_coriariu
                     └─37─┼─17p_foliosum
                          │    ┌─20p_junceum
                          └─35─┼─21p_leptarth
                               │    ┌─3c_rapaceum
                               ├─31─┼─13p_bicorne
                               │    └─22p_parviflo
                               │         ┌─19p_granulic
                               │    ┌─29─┴─16p_dinteri
                               └─32─┤    ┌─15p_dimorphu
                                    └─28─┤    ┌─12p_articula
                                         └─27─┤    ┌─18p_gesserti
                                              └─26─┤    ┌─23p_salicorn
                                                   └─25─┴─24p_subnodos
```

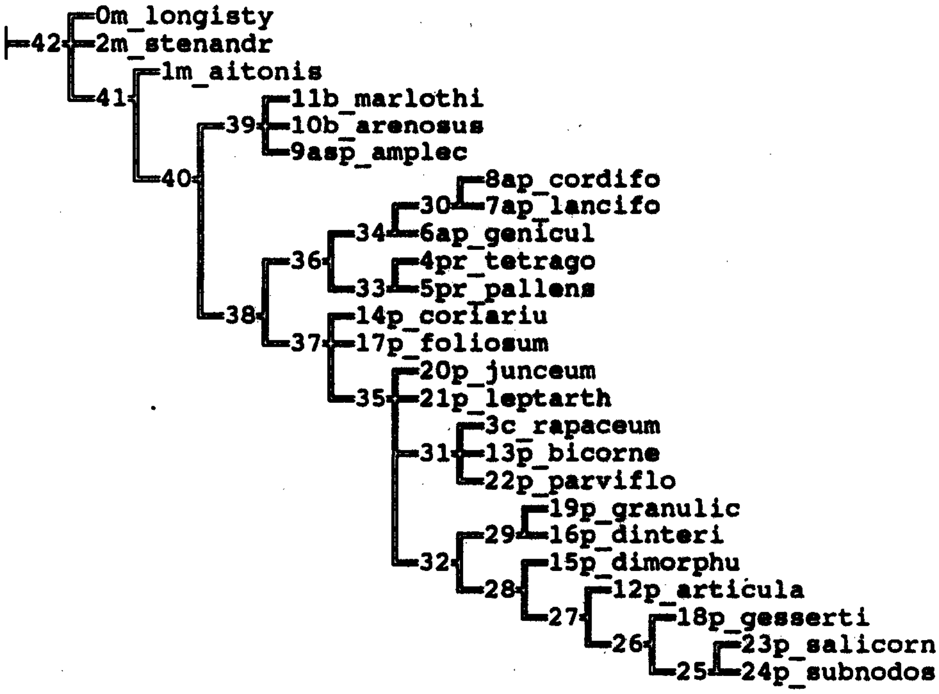
Character 14 ("position of single flowers") excluded, ci = 0.50, length 71 ci 50 ri 76 trees 80



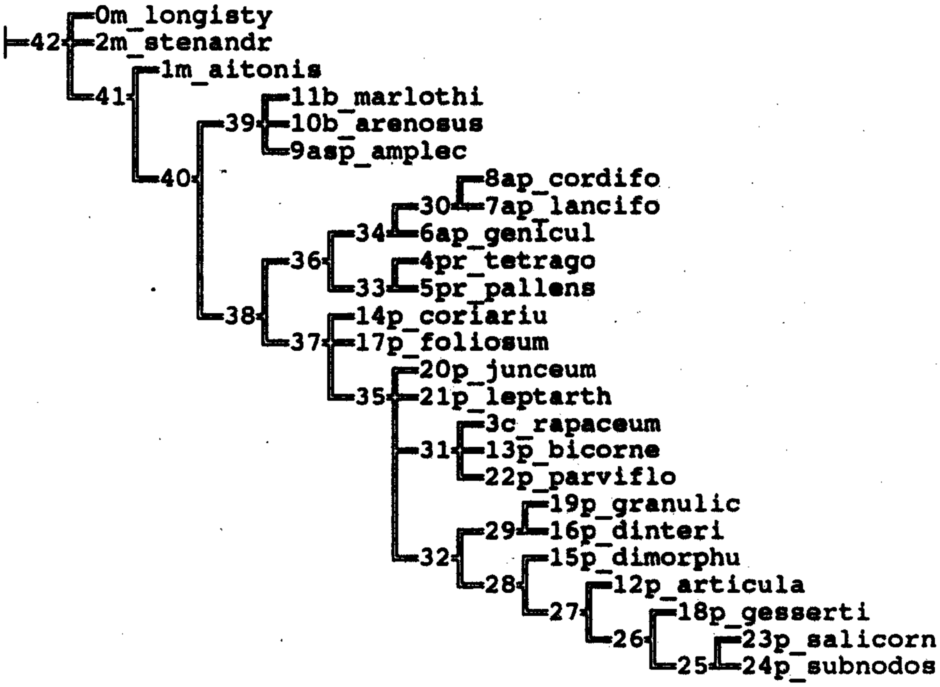
Character 15 ("sepals connate or free") excluded, ci = 100, length 71 ci 50 ri 76 trees 28



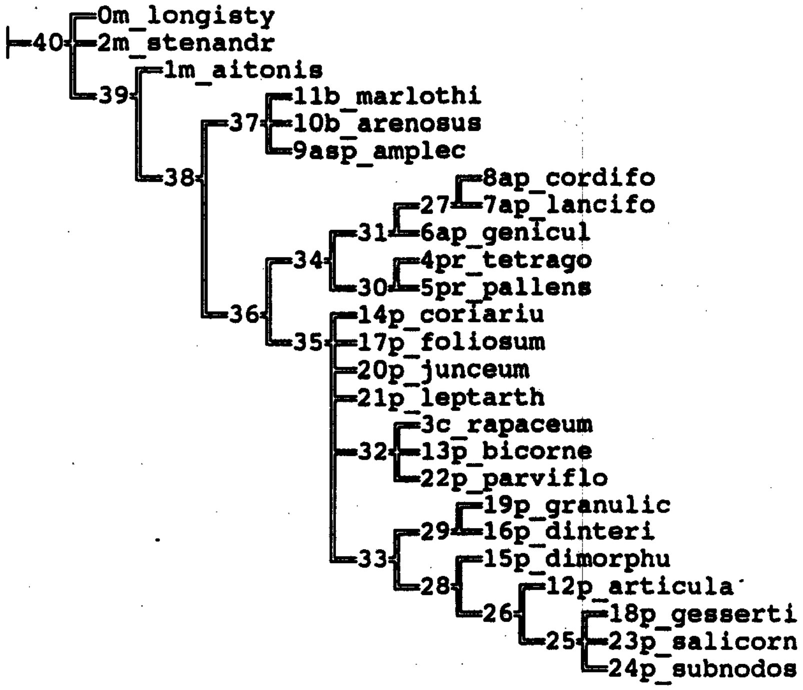
Character 16 ("sepals upright or bend down during entire anthesis") excluded, ci = 100, length 71 ci 50 ri 76 trees 28



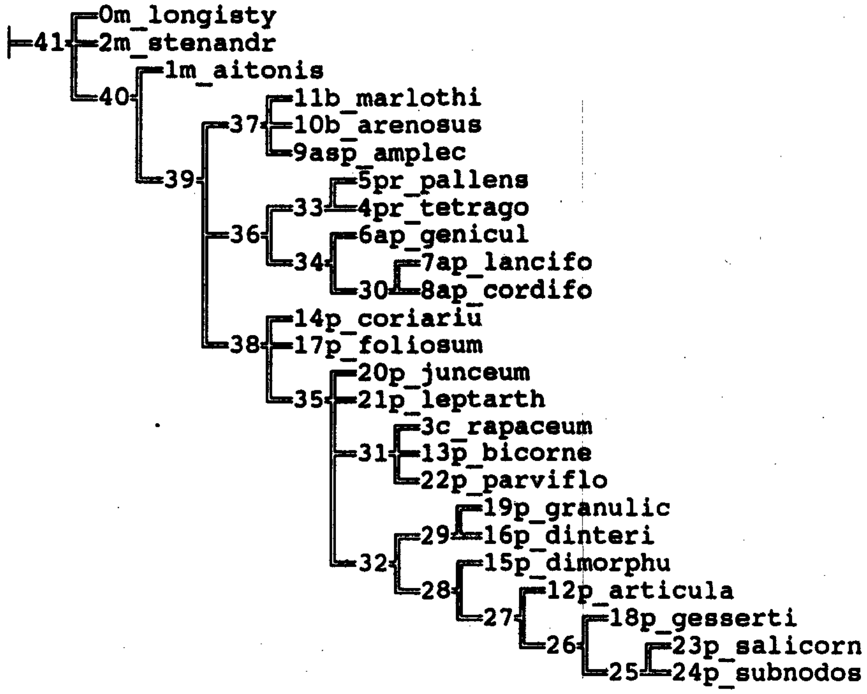
Character 17 ("flower colour") excluded, ci = 0.50, length 68 ci 51 ri 77 trees 28



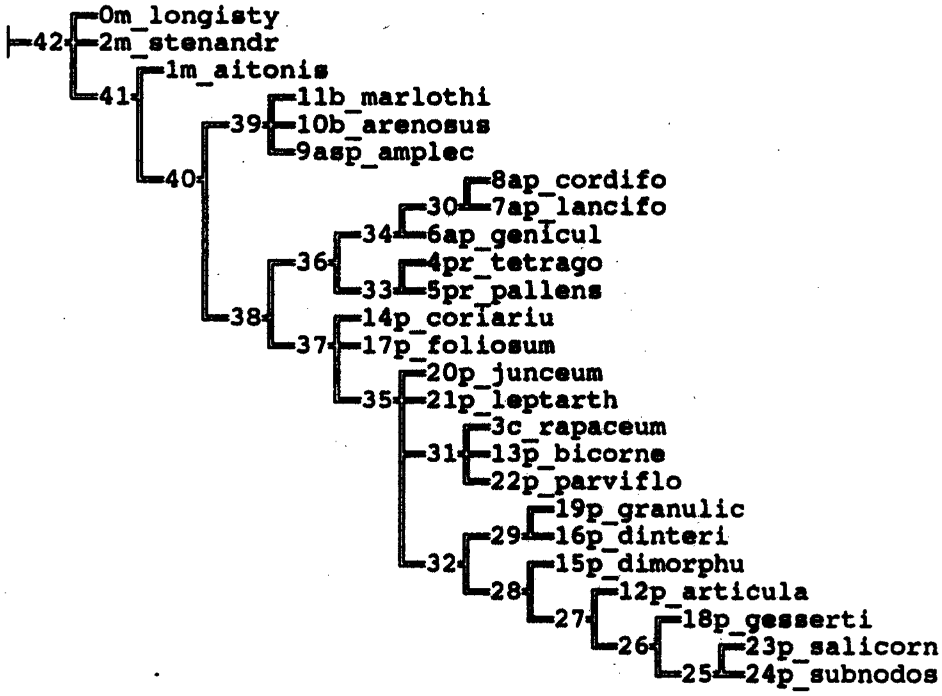
Character 19 ("petaloid and filamentous staminodes free, shortly connate or highly connate") excluded, ci = 0.40, length 67 ci 52 ri 76 trees 1468



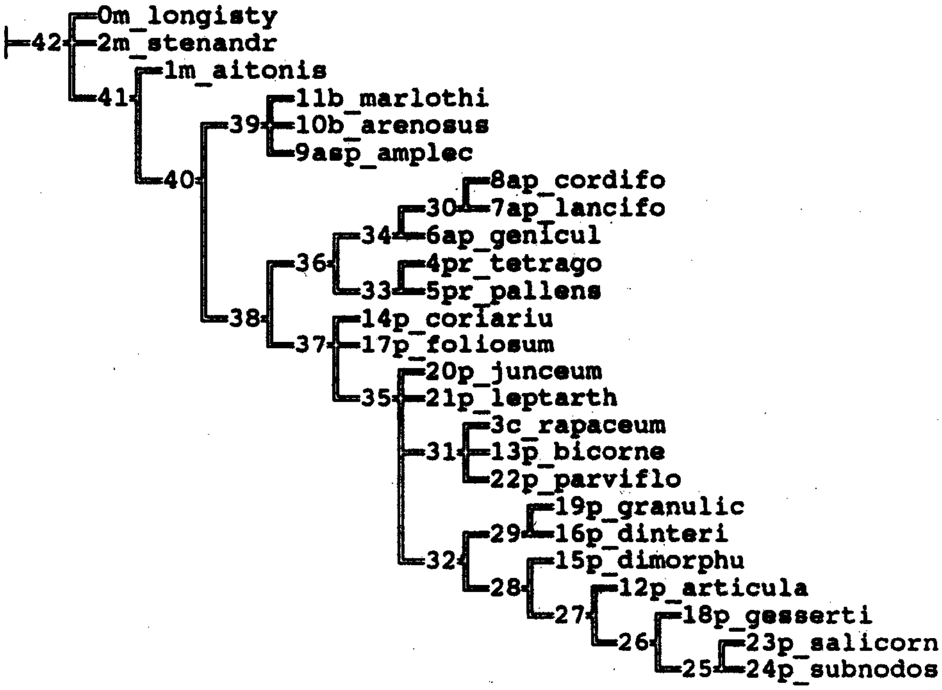
Character 20 ("presence or absence of filamentous staminodes") excluded, ci = 0.25, length 68 ci 52 ri 78 trees 84



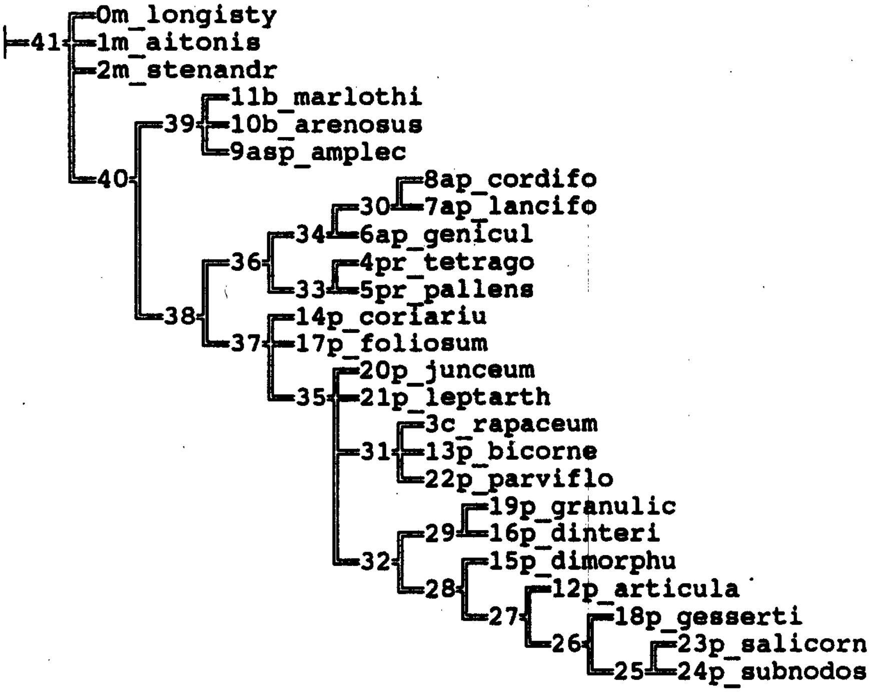
Character 21 ("filamentous staminodes (not) gathered into a cone") excluded, ci = 100, length 71 ci 50 ri 76 trees 28



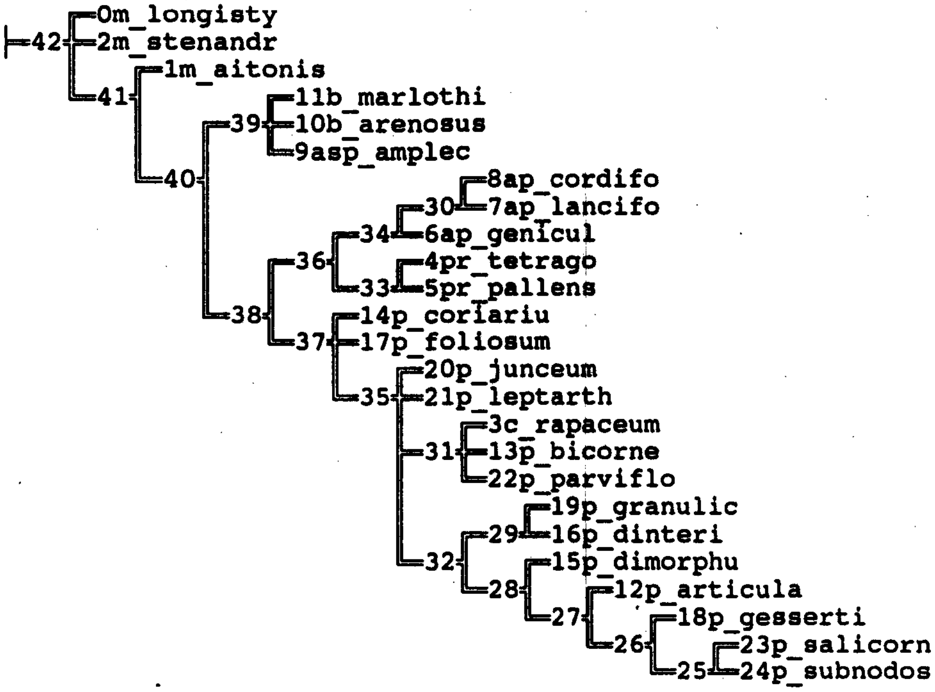
Character 22 ("filamentous staminodes apically lacerate and transparent or margins entire") excluded, ci = 100, length 71 ci 50 ri 76 trees 28



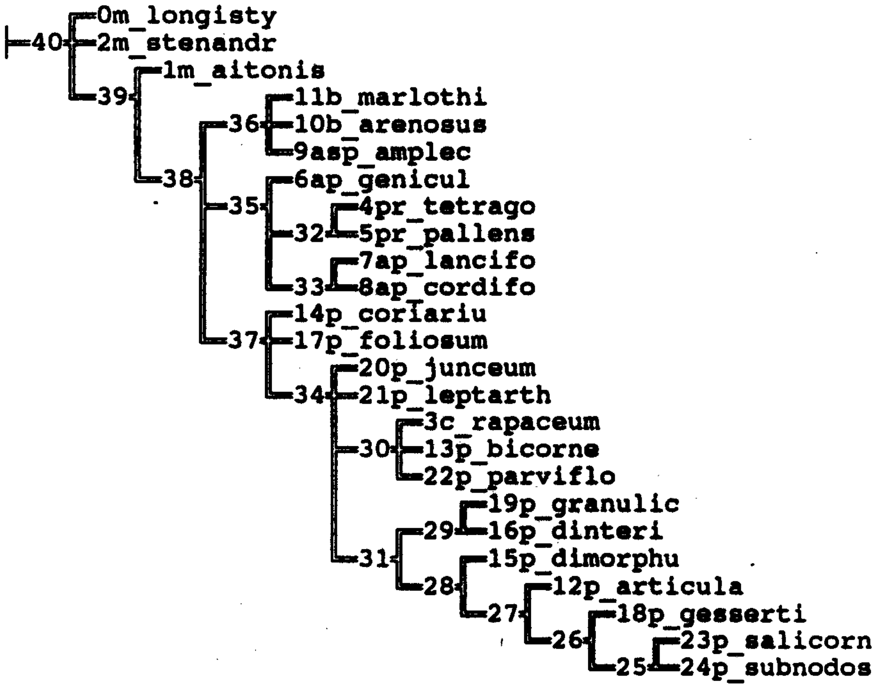
Character 23 ("petaloid staminodes in 1-2 or in 3-5 rows") excluded, ci = 0.33, length 69 ci 52 ri 77 trees 84



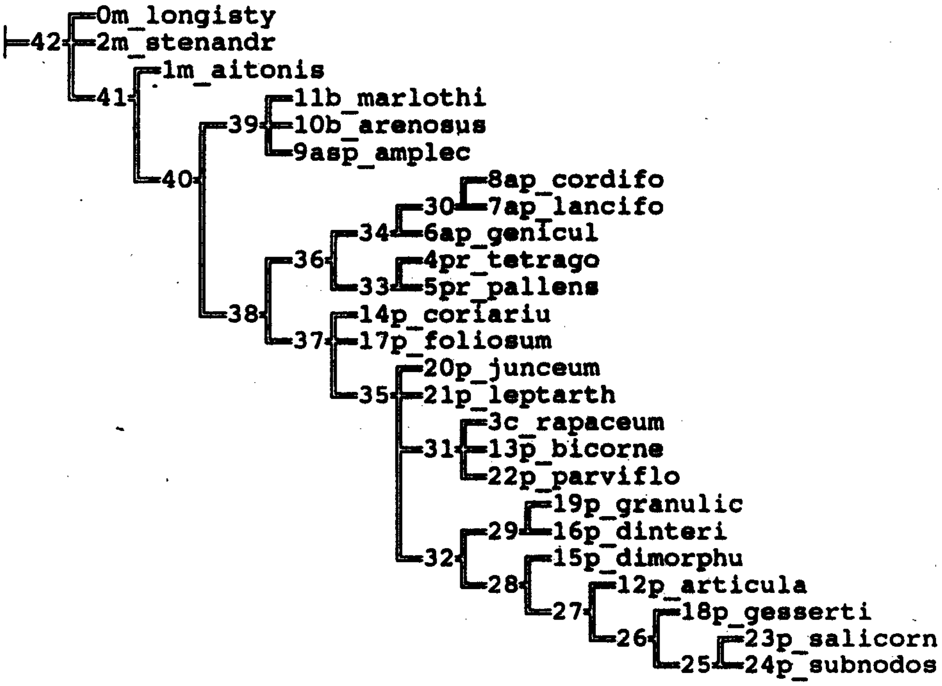
Character 24 ("shape of epidermal cells on gynoecium") excluded, ci = 0.50, length 70 ci 51 ri 77 trees 28



Character 25 ("styles long or short") excluded, ci = 0.50, length 70 ci 51 ri 77 trees 56



Character 26 ("nectaries deep, shallow or absent") excluded, ci = 100, length 71 ci 50 ri 76 trees 28



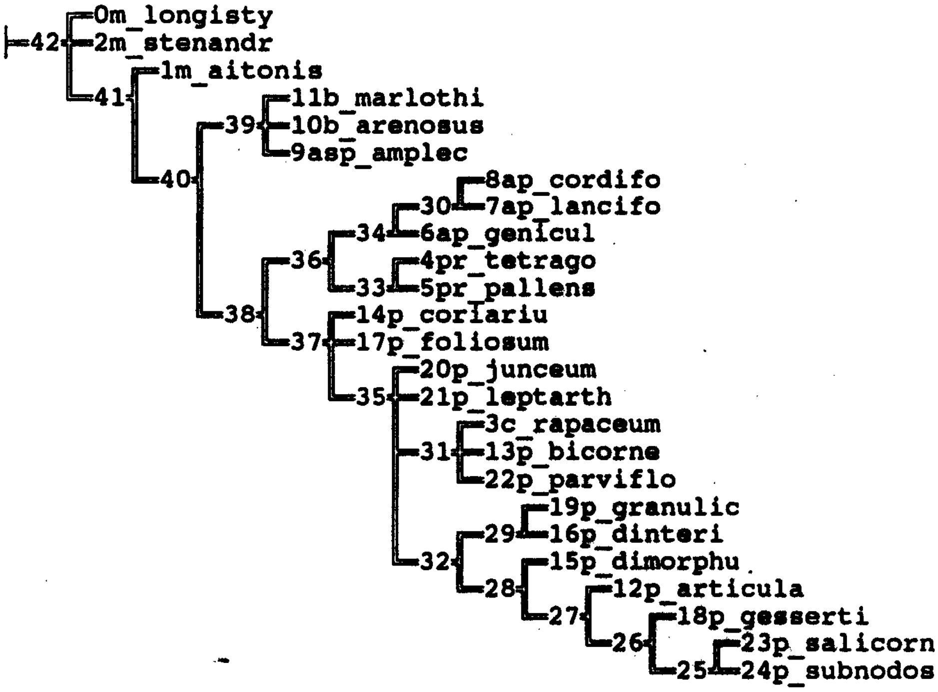
Character 27 ("capsules 4- or 5-locular") excluded, ci = 0.50, length 70 ci 51 ri 77 trees 28

```
    ┌─0m_longisty
├─42┼─2m_stenandr
    │   ┌─1m_aitonis
    └─41┤       ┌─11b_marlothi
        │   ┌─39┼─10b_arenosus
        │   │   └─9asp_amplec
        └─40┤               ┌─8ap_cordifo
            │           ┌─30┴─7ap_lancifo
            │       ┌─34┴─6ap_genicul
            │   ┌─36┤   ┌─4pr_tetrago
            │   │   └─33┴─5pr_pallens
            └─38┤   ┌─14p_coriariu
                └─37┼─17p_foliosum
                    │   ┌─20p_junceum
                    └─35┼─21p_leptarth
                        │   ┌─3c_rapaceum
                        ├─31┼─13p_bicorne
                        │   └─22p_parviflo
                        │       ┌─19p_granulic
                        │   ┌─29┴─16p_dinteri
                        └─32┤   ┌─15p_dimorphu
                            └─28┤   ┌─12p_articula
                                └─27┤   ┌─18p_gesserti
                                    └─26┤   ┌─23p_salicorn
                                        └─25┴─24p_subnodos
```

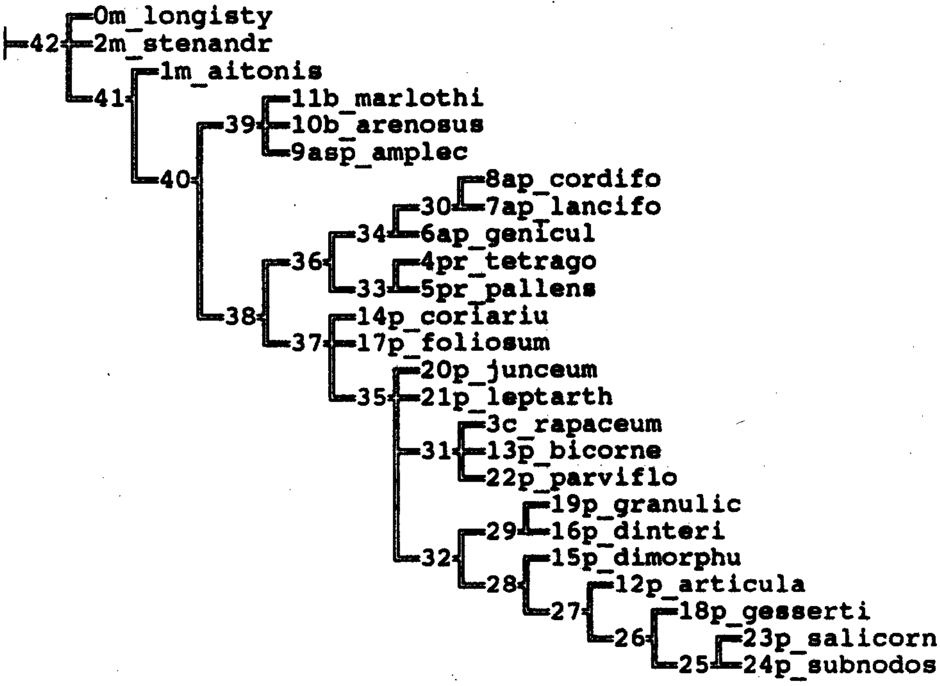
Character 28 ("fruits with shallow or deep locules") excluded, ci = 0.50, length 70 ci 51 ri 76 trees 142

```
    ┌─0m_longisty
├─38┼─2m_stenandr
    │   ┌─1m_aitonis
    └─37┤   ┌─3c_rapaceum
        └─36┼─13p_bicorne
            ├─14p_coriariu
            ├─17p_foliosum
            ├─20p_junceum
            ├─21p_leptarth
            ├─22p_parviflo
            │   ┌─9asp_amplec
            ├─34┼─10b_arenosus
            │   └─11b_marlothi
            │       ┌─5pr_pallens
            │   ┌─29┴─4pr_tetrago
            ├─33┤   ┌─6ap_genicul
            │   └─30┤   ┌─7ap_lancifo
            │       └─27┴─8ap_cordifo
            │       ┌─19p_granulic
            │   ┌─32┴─16p_dinteri
            └─35┤   ┌─15p_dimorphu
                └─31┤   ┌─12p_articula
                    └─28┤   ┌─18p_gesserti
                        └─26┤   ┌─23p_salicorn
                            └─25┴─24p_subnodos
```

Character 29 ("valve wings reflexed and fused in pairs or inflexed") excluded, ci = 0.50, length 70 ci 51 ri 77 trees 28



Character 30 ("seed broad or compressed") excluded, ci = 100, length 71 ci 50 ri 76 trees 28



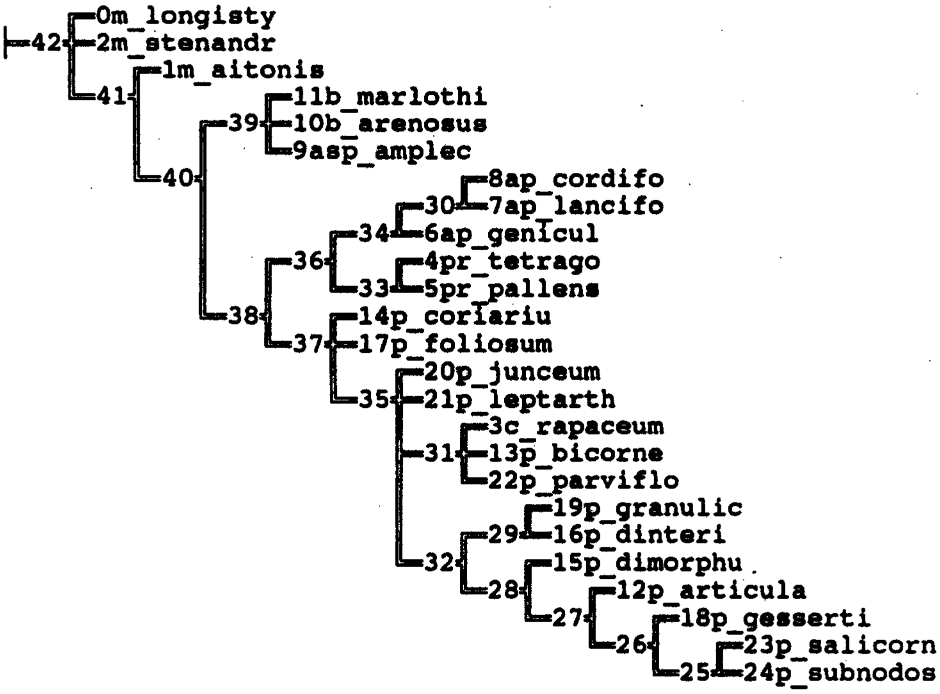
Character 31 ("seed colour") excluded, ci = 0.33, length 66 ci 53 ri 78 trees 288

```
    ┌─0m_longisty
├─34┼─2m_stenandr
    │   ┌─1m_aitonis
    └─33┤   ┌─6ap_genicul
        └─32┼─9asp_amplec
            ├─10b_arenosus
            ├─11b_marlothi
            ├─14p_coriariu
            ├─17p_foliosum
            │   ┌─4pr_tetrago
            ├─29┴─5pr_pallens
            │   ┌─7ap_lancifo
            ├─30┴─8ap_cordifo
            │   ┌─20p_junceum
            └─31┼─21p_leptarth
                │   ┌─3c_rapaceum
                ├─27┼─13p_bicorne
                │   └─22p_parviflo
                │   ┌─12p_articula
                └─28┼─15p_dimorphu
                    ├─18p_gesserti
                    │   ┌─16p_dinteri
                    ├─25┴─19p_granulic
                    │   ┌─23p_salicorn
                    └─26┴─24p_subnodos
```

Character 32 ("testa rough or smooth") excluded, ci = 0.33, length 69 ci 52 ri 77 trees 98

```
    ┌─0m_longisty
├─37┼─2m_stenandr
    │   ┌─1m_aitonis
    └─36┤   ┌─6ap_genicul
        └─35┼─9asp_amplec
            ├─10b_arenosus
            ├─11b_marlothi
            ├─14p_coriariu
            ├─17p_foliosum
            │   ┌─4pr_tetrago
            ├─32┴─5pr_pallens
            │   ┌─7ap_lancifo
            ├─33┴─8ap_cordifo
            │   ┌─20p_junceum
            └─34┼─21p_leptarth
                │   ┌─3c_rapaceum
                ├─30┼─13p_bicorne
                │   └─22p_parviflo
                │       ┌─19p_granulic
                │   ┌─29┴─16p_dinteri
                └─31┤   ┌─15p_dimorphu
                    └─28┤   ┌─12p_articula
                        └─27┤   ┌─18p_gesserti
                            └─26┤   ┌─23p_salicorn
                                └─25┴─24p_subnodos
```

Character 33 ("testa cells ordered or unordered") excluded, ci = 100, length 71 ci 50 ri 76 trees 28



Character 34 ("testa fold narrow or broad") excluded, ci = 100, length 71 ci 50 ri 76 trees 98