PACHYPODIUM (APOCYNACEAE)

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Pachypodium (Apocynaceae)

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PROEFSCHRIFT
ter verkrijging van de graad van doctor
op gezag van de Rector Magnificus
van de Wageningen Universiteit,
dr. C.M. Karssen,
in het openbaar te verdedigen
op woensdag 27 oktober 1999
des namiddags te half twee in de Aula.

A.A. BALKEMA / ROTTERDAM / BROOKFIELD / 1999

à ma femme
à mes deux filles
'Je dédie ce travail'

Photographs made by W. Röösli 1-13, 15-32, 34-46, 48-68, 72, 74, 79-80; by J.J. Lavranos 69-70, 73, 75, 78; by M. Kroenlein 71; by A.J.M. Leeuwenberg 33, 47; by D. Supthut 14; by J. de Koning 76-77.

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Propositions — Stellingen

1. At present 23 species of *Pachypodium* are recognized, 18 in Madagascar and 5 in the African continent, indicating that the genus originated during a period prior to the separation (some 165 MA ago) of Madagascar from the African continent.

2. The opinion of G.D. Rowley that *Pachypodium inopinatum*, *P. bicolor* and *P. eburneum* do not deserve specific rank is incorrect.
Rowley, G.D., 1999. The Cactus File Handbook 5, Pachypodium & Adenium.

3. The location Horombe Plateau for *Pachypodium densiflorum* as indicated by Allorge is incorrect. This species has never been collected there.
Allorge, L., 1993. Pachypode. Succulentes 3: 24.

4. *Pachypodium geayi*, *P. lamerei*, *P. rosulatum* and *P. rutenbergianum* grow in Leeuwenberg's model, but *P. brevicaule* probably not, as it does not form branchlets.
Hallé, F., Oldeman, R.A.A. & Tomlinson, P.B., 1978. Tropical Trees and Forests.

5. If the present Nature Reserves in Madagascar would be well preserved, the species of *Pachypodium* are protected simultaneously.

6. CITES protects *Pachypodium*. However, in practice the regulations have hampered scientific exchange and did not sufficiently prevent illegal commercial exploitation.

7. The inclusion of the genus *Macoubea* in the tribe Tabernaemontaneae (Apocynaceae) by Boiteau leads to erroneous conclusions in cladistic studies.
Boiteau, P. & Satre, C., 1975. Sur l'arille des Macoubea et la classification des Tabernaemontanoïdées (Apocynacées). Adansonia ser. 2, 15: 239-250.
Endress, M.E., Sennblad, B., Nilsson, S., Civeyrel, L., Chase, M.W., Huysmans, S., Grafström, E. & Bremer, B. 1996. A Phylogenetic analysis of Apocynaceae *s. str.* and some related taxa in Gentianales: a multidisciplinary approach. Opera Bot. Belg. 7: 59-102.

8. To sink *Geissospermum* into *Aspidosperma* (Apocynaceae) was proposed in a cladistic study based on flowers alone, ignoring fruits, seeds and architecture of the trees, which characters point to a separate position.
Potgieter, K. 1997. Abstracts, Congress of North American Botany, Montreal.

9. The seeds of friendship are planted by the moment, but its fruits are harvested during a lifetime.

10. Despite the advanced satellite facilities to pinpoint the exact location of a plant by coordonates, in the case of endangered plants their whereabouts should be reported with restraint.

11. A good plant taxonomist needs both theoretical knowledge and ample field experience.

Stellingen behorende bij het proefschrift, *Pachypodium* (Apocynaceae).
S.H.J.V. Rapanarivo, 27 October 1999.

Table of contents

FOREWORD VII

CURRICULUM VITAE VIII

1 TAXONOMIC REVISION OF *PACHYPODIUM*
SERIES OF REVISIONS OF APOCYNEAE XLVIII 1
Introduction 1
History of the genus 1
Geographical distribution 2
Morphology 3
Relationship with other genera 5
Genus description of *Pachypodium* 6
Key to the species of *Pachypodium* 7
Key to the species of *Pachypodium* endemic to Madagascar 7
Key to the species of *Pachypodium* confined to the African continent 9
Treatment of the species 10
1. *Pachypodium ambongense* Poiss. 10
2. *Pachypodium baronii* Costantin & Bois 12
3. *Pachypodium bicolor* Lavranos & Rapanarivo 14
4. *Pachypodium brevicaule* Baker 17
5. *Pachypodium cactipes* K. Schum. 20
6. *Pachypodium decaryi* Poiss. 24
7. *Pachypodium densiflorum* Baker 26
8. *Pachypodium eburneum* Lavranos & Rapanarivo 30
9. *Pachypodium geayi* Costantin & Bois 33
10. *Pachypodium gracilius* (H. Perrier) Rapanarivo 35
11. *Pachypodium horombense* Poiss. 39
12. *Pachypodium inopinatum* Lavranos 42
13. *Pachypodium lamerei* Drake 44
14. *Pachypodium meridionale* (H. Perrier) Pichon 49
15. *Pachypodium rosulatum* Baker 51
16. *Pachypodium rutenbergianum* Vatke 54
17. *Pachypodium sofiense* (Poiss.) H. Perrier 59
18. *Pachypodium windsorii* Poiss. 60
19. *Pachypodium bispinosum* (L.f.) A.DC. 63
20. *Pachypodium lealii* Welw. 67
21. *Pachypodium namaquanum* (Wyley ex Harv.) Welw. 70

22. *Pachypodium saundersii* N.E.Br. 72
23. *Pachypodium succulentum* (L.f.) A.DC. 76
Excluded species 81
References 81

2 THE HABITATS OF *PACHYPODIUM* SPECIES 83
Introduction 83
Study area, material and methods 83
Results 87
Discussion and conclusions 96
Acknowledgements 101
References 102

3 CULTIVATION OF *PACHYPODIUM* 105
Species list with information 105
Pachypodium ambongense Poiss. 105
Pachypodium baronii Costantin & Bois 106
Pachypodium bicolor Lavranos & Rapanarivo 106
Pachypodium brevicaule Baker 106
Pachypodium cactipes K. Schum. 107
Pachypodium decaryi Poiss. 107
Pachypodium densiflorum Baker 107
Pachypodium eburneum Lavranos & Rapanarivo 108
Pachypodium geayi Costantin & Bois 108
Pachypodium gracilius (H. Perrier) Rapanarivo 108
Pachypodium horombense Poiss. 109
Pachypodium inopinatum Lavranos 109
Pachypodium lamerei Drake 109
Pachypodium meridionale (H. Perrier) Pichon 110
Pachypodium rosulatum Baker 110
Pachypodium rutenbergianum Vatke 110
Pachypodium sofiense (Poiss.) H. Perrier 111
Pachypodium windsorii Poiss. 111

INDEX OF EXSICCATAE 113

INDEX OF SCIENTIFIC NAMES 117

Foreword

The present publication incorporates a taxonomic monograph of the genus *Pachypodium* based on herbarium material and living plants of all species, a detailed study of the habitats and ecological preferences of most species and a chapter on cultivation. The latter describes the successes of artificial propagation, as the ecological conditions have been simulated carefully for the purpose.

The monograph has been written by Rapanarivo, who got essential inputs from the plant explorer Lavranos and the taxonomist Leeuwenberg, world specialist of the Apocynaceae family. The taxonomy is a modern and completely revised update of the publications of Codd (1963) on the continental African species and that of Markgraf (1976) on the Madagascan species, describing 23 species as presently distinguished. All have ornamental value and most can be classified as threatened in the wild, but sustained exploitation is possible through multiplication by seeds. This enables trade without further damaging the natural populations.

The habitats have been studied by Rapanarivo, who travelled to many localities of *Pachypodium* in Madagascar. He could not visit continental Africa, and ecological inputs were contributed for his study by Lavranos.

The author of the chapter on cultivation is Röösli, who grows all species in his private greenhouses from seeds he collected in the wild. He showed all of his living plants to the monographer, which was of great interest for detailed observations, especially for the species not seen by him in the wild. Lavranos and Röösli also made most of the excellent photographs.

L.J.G. van der Maesen

Curriculum vitae

Solo Hery Jean Victor Rapanarivo was born on 25 May 1954. He joined the University of Antananarivo (en Filière Sciences Naturelles) in 1979, where he obtained the certificates 'Licence d'Enseignement en Sciences Naturelles' and 'Maîtrise de Recherche option Biologie Vegetale' in 1988 and 'Diplôme D'Etude Approfondie option Ecologie Végétale' in 1992. He started to work at the Parc Botanique et Zoologique de Tsimbazaza (Botanical and Zoological Park of Tsimbazaza) in Antananarivo in March 1992. He is responsable for the herbarium and is Head of the Flora Departement. Between November 1995 and February 1998, he was affiliated with the Departement of Plant Taxonomy, Wageningen Agricultural University, for a Ph.D. study, made possible by a sandwich grant. He is currently working at the Parc Botanique et Zoologique de Tsimbazaza in Antananarivo. He made collections in the field with various colleagues in Madagascar, among whom his copromotor. He is married and has two daughters.

CHAPTER 1

Taxonomic revision of *Pachypodium* Series of revisions of Apocynaceae XLVIII

S.H.J.V. Rapanarivo & A.J.M. Leeuwenberg

ABSTRACT: The genus *Pachypodium* (Apocynaceae) comprises 23 species. Eighteen are endemic to Madagascar and five occur in continental African (Angola, Botswana, Mozambique, South Africa, Swaziland and Zimbabwe). The study is based on herbarium material and living plants. The varieties *P. baronii* var. *windsorii* and *P. rosulatum* var. *gracilius* are raised to the rank of species and *P. cactipes*, cited as synonym of *P. rosulatum* by Markgraf (1976), is reinstated as a distinct species. Recently three new species have been described: *P. bicolor*, *P. eburneum* and *P. inopinatum* and these have been maintained.

The key consists of an introductory part, keying out the most conspicuous life forms, and leading to the regional keys for Madagascar and for continental Southern Africa.

INTRODUCTION

The present paper is a monographic revision of the genus *Pachypodium* Lindl. The study is based on herbarium material and on living plants in the wild in Madagascar and in cultivation. The authors, in particular Rapanarivo, had the opportunity to make several trips through Madagascar for collecting and field studies and as such they have observed living plants of 10 species in their natural habitat and could study their ecological preferences. In cultivation they have seen living plants of all species in greenhouses in Switzerland, grown from seeds collected in the wild. The greenhouses were of the Städtliche Sukkulentensammlung of the city of Zürich and the perfectly kept private collection of Mr W. Röösli at Zürich. These opportunities enabled them to update the present knowledge of this genus of beautiful plants considerably.

HISTORY OF THE GENUS

Lindley (1830) is the author of the genus *Pachypodium*, based on a single species *P. tuberosum*, which he supposed to be the same as *Echites succulenta* L.f. (1781). G. Don (1837) cited *E. succulenta* as a synonym of a species he called *P. tomentosum* and in the same publication he listed *P. glabrum* with the basionym *Echites bispinosa* L.f. and *P. tuberosum* Lindl. as a synonym.

Subsequently A. de Candolle (1844) described *P. succulentum* based on *E. succulenta* and *P. tomentosum* G. Don. The second species A. de Candolle recognized is *P. bispinosum* with the basionym *E. bispinosa* L.f. and *P. glabrum* G. Don as syno-

nym. The third and last species he accepted is *P. tuberosum* Lindl., to which he added the var. *loddigessii*, which was cited as a synonym of *P. bispinosum* by Codd (1963). The next species to be added were *P. namaquanum* and *P. lealii* proposed by Welwitsch in 1869 and 1871 respectively, and *P. saundersii* N.E. Br. (1892). *P. namaquanum* was initially known as *Adenium namaquanum* Wyley (1863).

The first species from Madagascar that was accepted in this genus is *P. rosulatum* Baker (1882). It was followed by *P. rutenbergianum* Vatke (1885), *P. brevicaule* Baker (1887) and *P. densiflorum* Baker (1887).

The first rather complete treatment of *Pachypodium* was made by Costantin & Bois (1907). They enumerated 17 species, 10 of which are from Madagascar and 7 from continental Africa. Perrier de la Bâthie (1934) distinguished 20 species, 14 from Madagascar and 6 from Continental Africa. Markgraf (1976) accepted 17 species, 12 endemic to Madagascar and 5 belonging to continental Africa.

Lavranos (1996) described *P. inopinatum* and later (1997) added *P. eburneum* and *P. bicolor*, the latter two species he published in cooperation with the first author. In this revision the varieties *P. baronii* var. *windsorii* and *P. rosulatum* var. *gracilius* are raised to the rank of species and *P. cactipes*, cited as a synonym of *P. rosulatum* by Markgraf (1976) is reinstated as a distinct species.

GEOGRAPHICAL DISTRIBUTION

The genus *Pachypodium* has 23 species, 18 in Madagascar, some of which have been discovered recently, and 5 are found in the southern part of the African continent.

In Madagascar, *P. lamerei* is the most widely distributed species extending over an area from Antsingy de Bemaraha in the north to near Toliara in the south. It is also known from near Ihosy to Beloha Sud. *P. rosulatum* occurs in NW and W Madagascar in a region from Maromandia (Sandrakoto) in the north to Malio R. valley, a tributary of Mangoky R. in the south. *P. rutenbergianum* is found in the surroundings of Antsiranana and Ankarana in the north and extends along the NW and W coastal region to near Belo/Tsiribihina in the south and to Mandritsara in the east. *P. densiflorum* occupies the central part of the country between Kandreho in the north and Zazafotsy in the south. *P. meridionale* occurs SW and S from Manja in the north to Ampanihy in the south. *P. horombense* is known from near Ankaramena in the north to Antanimora in the south. *P. geayi* is distributed between the region north of Tuléar and Ampanihy. *P. brevicaule* is known from near Antananarivo in the north to Ambatofinandrahana in the south. *P. baronii* occurs in an area from near Diégo-Suarez in the north to Ambanja and Mandritsara in the south. *P. sofiense* is found near Befandriana Nord and Mandritsara in the north and extends to Antsingy de Bemaraha in the south. *P. gracilius* is known from near Beroroha in the north to Vohitrosy Mts near Anadabolava in the south. *P. decaryi* is found near Diégo-Suarez and in the Ankarana region. *P. cactipes* is known from near Fort-Dauphin. *P. bicolor* is found near Berevo. *P. ambongense* occurs in the Ambongo region. *P. inopinatum* is restricted localities near Tsaratanana. *P. windsorii* is only known from near Diego-Suarez. *P. eburneum* is found on Mt Ibity.

On the African continent *P. succulentum* is the most widely distributed species of *Pachypodium*. It is known from South Africa. It has been collected near Kuruman in the NW Cape Province, and in a region between Matjiesfontein in the Western Cape Province to Albany in the Eastern Cape Province and from the Free State. *P. saunder-*

sii is found in the eastern part of Zimbabwe in the area between Ndanga District in the north to Nuanetsi District in the south, and in the southwestern part of Mozambique near Machaze in the north to Maputo in the south. *P. saundersii* also occurs in South Africa (Kwazulu-Natal and northern and eastern Transvaal) and in Swaziland. *P. lealii* is distributed in SW Angola and NW Namibia from Benguela in Angola to near Waterberg in Namibia. It has also be found near Nokaneng in Botswana. *P. bispinosum* is found from Ladismith District in the west to Albany Division in the east. *P. namaquanum* occupies an area in southern Namibia south of a line from Lüderitz to the east and the extreme NW of Northern Cape Province south to Steinkop.

MORPHOLOGY

Habit

Pachypodium species have various forms from bottle-, cigar- or candelabrum-shaped trees with thick branches to dwarf plants with a very short trunk. *P. namaquanum* is often unbranched. All species are thorny at least on the branchlets except *P. decaryi*, which may be unarmed. *P. brevicaule* has a trunk length not over 8 cm, but it is up to 40 cm in diameter. Many species are shrubs less than 4 m high. However, *P. geayi*, *P. lamerei*, *P. lealii*, *P. meridionale*, and *P. sofiense* are trees that may exceed a height of 5 m. The trees of *P. rutenbergianum* even may become 12 m tall.

Bark

The bark is pale grey to dark brown or grey-green and smooth. It sometimes has leaf scars or protruding lenticels. On section the bark is up to 6 mm thick and usually medium green.

Wood

The wood of *Pachypodium* is cream-coloured and soft.

Spines

Pachypodium has stipules transformed into spines like those in succulent *Euphorbia* species. *P. geayi*, *P. lamerei* and all continental African species have three spines together 2 of which are subequal, while the third is smaller and placed in between them. The other species have paired spines. The length varies from 1 mm in *P. decaryi and P. sofiense* to 75 mm in *P. namaquanum*.

Leaves

The leaves are alternate, sessile or petiolate, confined to the apices of the branchlets, branches or trunk. The petiole is densely pubescent to glabrous. The blade is herbaceous to coriaceous when fresh, papery when dried, ovate to obovate, densely pubescent on both sides with stellate hairs in *P. namaquanum*, glabrous on both sides in *P. rutenbergianum*, pubescent to glabrous above and densely pubescent to glabrous beneath in the other species. The apex is acuminate to rounded or sometimes mucronate in *P. bispinosum*, *P. lamerei* and *P. lealii*. The secondary veins are paired, straight at the base and upcurved upwards, only in *P. bispinosum* they are not visible in dried leaves.

Inflorescence

The inflorescence of *Pachypodium* is terminal, sessile or pedunculate, congested (except in *P. geayi)* and few- to many-flowered. In *P. bispinosum*, *P. lealii* and *P. succulentum* the inflorescence is terminal on minute lateral branchlets and therefore it often seems to be axillary. The bracts are often sepal-like, usually pubescent outside and sparsely so to glabrous inside, except in *P. bispinosum*, *P. rutenbergianum* and *P. saundersii* where they are glabrous on both sides. The peduncle is 0-20 mm long in *P. meridionale*, *P. rutenbergianum*, *P. sofiense* and all continental African species. The longest peduncles are found in *P. horombense* (up to 56 cm long). The flowers are sometimes sessile; the longest pedicels are also found in *P. horombense* (up to 45 mm long).

Flowers

– *Calyx.* The calyx always has five subequal ovate to oblong sepals united at the base and is often persistent in fruit.

– *Corolla.* The corolla is tubular and variously coloured. The lobes are pale red to crimson in *P. baronii* and *P. windsorii*, pure white in *P. meridionale* and *P. rutenbergianum*, yellow in many species of Madagascar and variously coloured in the other species. The head of the mature corolla bud is usually ovoid and has an obtuse apex except in *P. meridionale* and *P. rutenbergianum* which have narrowly ovoid heads and an acuminate apex. The tube is divided in two parts. The basal part is usually cylindrical and often shorter than the upper part, but not in *P. densiflorum*, *P. geayi*, *P. inopinatum* and *P. windsorii*. The upper part may be urceolate in *P. ambongense*, *P. decaryi*, *P. lamerei*, *P. lealii*, *P. rutenbergianum*, and *P. saundersii*, almost cylindrical in *P. baronii*, *P. brevicaule*, *P. sofiense*, *P. succulentum* and *P. windsorii*, and obconical in all other species. There is a pubescent belt below the insertion of the stamens which may continue upwards and may become more densely so at the mouth in *P. baronii* and *P. windsorii* or even extend sometimes all over the lobes as is known in *P. namaquanum*. The length of the corolla tube varies from 9 mm long in *P. succulentum* to 60 mm in *P. sofiense*. The corolla lobes overlap to the right in bud and are slightly twisted only in *P. meridionale* and *P. rutenbergianum*. They are always longer than the tube in *P. meridionale*. They are always shorter in *P. bicolor*, *P. bispinosum*, *P. gracilius*, *P. horombense*, *P. namaquanum*, *P. saundersii* and *P. sofiense*, and shorter or longer than the tube in the other species. They are obliquely ovate or obliquely obovate, recurved in *P. geayi* and undulate in *P. densiflorum*, *P. lealii*, *P. meridionale* and *P. rutenbergianum*. The apex is acuminate to rounded.

– *Stamens and pistil.* The ovary is subglobose and composed of 2 carpels, which are pubescent to glabrous, each carpel contains numerous ovules. The stamens are included in all species except in *P. densiflorum* and *P. geayi* where they are exserted.

Fruit

The fruits are composed of two separate mericarps. The mericarps are pale to dark brown with longitudinal lines or lenticellate outside, whitish to very pale brown inside when dried, glabrous in *P. decaryi*, *P. geayi*, *P. meridionale*, *P. lealii* and *P. saundersii*, densely pubecsent in *P. namaquanum*, pubescent to puberulous in the other species. They are fusiform except in *P. namaquanum* where they are obovoid to ellipsoid.

The seed grains are pale to medium brown and have a smooth to rough testa and bear a single straw-coloured or whitish coma on their apex.

RELATIONSHIPS WITH OTHER GENERA

The easiests characters to recognize Apocynaceae species are opposite leaves without interpetiolar stipules, the presence of white latex, and actinomorphic tubular corollas. Curiously enough only the last of these characters is present in *Pachypodium*. It has alternate leaves with stipules transformed into spines and clear sap. Alternate leaves are also a generic character in *Cerbera*, *Thevetia*, *Plumeria* and *Adenium*. These four genera are placed in 3 tribes (Leeuwenberg 1994), so not intimately related. *Pachypodium* is placed in the tribe Echitae, subtribe Pachypodiinae (Leeuwenberg 1994) not including *Adenium*.

Thevetia and *Cerbera manghas* have scales covering the stamens inside the corolla tube and the fruits are drupes in all *Cerbera* and *Thevetia* species. *Plumeria* is characterized by the infundibuliform corolla with stamens hidden at the base of the tube and dry follicular fruits with winged seeds. *Adenium* has flowers with wide corolla tubes, an obscure corona and stamens with long apical brushes as has *Nerium*, dry follicular fruits and seeds with 2 comas, a basal and an apical one.

Vegetatively *Pachypodium* resembles several succulent *Euphorbia* species by the stipules transformed into spines, and in fact it is a character not found in any other apocynaceous genus. They cannot be confused with *Euphorbia* spp. as these have white latex instead of clear sap.

The only succulent genera in the family Apocynaceae are *Adenium*, *Pachypodium* and *Plumeria*. *Plumeria* belongs to the subfamily of *Plumerioideae*, being its type genus. This subfamily is mainly characterized by the free stamens, anthers entirely fertile or only apically sterile, dry or fleshy fruits and seeds without coma. *Adenium* and *Pachypodium* belong to the subfamily of the *Apocynoideae* of which the anthers are mostly fertile only near the apex and coherent with the pistil head, the fruits are dry and follicular and the seeds bear a coma. *Adenium* and *Pachypodium* have alternate leaves, wide corolla tubes, dry follicles and seeds with coma in common. Therefore they are well placed within the subfamily *Apocynoideae*, the subdivision of which is still under dispute. In his survey of the Apocynaceae Leeuwenberg (1994) placed the two genera next to each other because of their succulence, although clearly separated: *Pachypodium* in the subtribe *Pachypodiinae* in the tribe *Echiteae* and *Adenium* in the subtribe *Neriinae* of the *Wrightieae*. A character supporting the latter conclusion is the presence of stipules in *Adenium*, albeit minute and deciduous. However, *Adenium* species have either clear sap or white latex. *Pachypodium* has persistent stipules transformed into spines and always clear sap.

These conlusions have been voiced earlier in the revision of *Adenium*: '*Adenium* belongs to the tribe *Wrightieae* of the Subfamily *Apocynoideae* and is closely related to *Pachypodium*. *Pachypodium* differs from *Adenium* especially by its spines, which are in fact its stipules; stipules of *Adenium* are early caducous' (Plaizier 1980).

Recently (Sennblad et al. 1998) presented a cladistic analysis of some Apocynaceae even including traditional Asclepiadaceae and the tribe Wrightieae using morphology and molecular data. Of all genera studied only a single species was investigated for molecular (rbcL) data. For morphological data one, two, in a few cases four to six species were investigated (2 for *Pachypodium*). If this approach is considered valid, the cladistic analysis indicates a paraphyletic nature for Wrightieae s.l., and *Pachypodium* appears to be most closely related to *Funtumia*, *Mascarenhasia* and *Holarrhena*, constituting one of the four monophyletic clades within Wrightieae s.l. These four genera are placed in 2 tribes (Leeuwenberg 1994), so not intimately re-

lated. *Pachypodium* is placed in the tribe Echitae, subtribe Pachypodiinae (Leeuwenberg 1994) not including *Adenium*.

GENUS DESCRIPTION

Pachypodium Lindl. in Bot. Reg. 16: t. 1321 (1830); Stapf in Fl. Cap. 4, 1: 515 (1904); Perrier de la Bâthie in Bull. Soc. Bot. Fr. 81: 297-318 (1934); Pichon in Mém. Inst. Sc. Madag., sér. B, 2: 98-125 (1949); in Mém. Mus. Nat. Hist. Nat., II, B, Bot. 1: 46 (1950); Phillips, Gen. South Africa Pl. ed. 2: 587 (1951); Codd in Fl. Southern Afr. 26: 283 (1963). Type species: *Pachypodium tuberosum* Lindl. (= *P. succulentum* (L.f.) A. DC.).

Heterotypic synonym
Belonites E. Mey., Comm. 187 (1837). Lectotype species: *Belonites succulenta* (L.f.) E. Mey., designated here (= *Pachypodium succulentum* (L.f.) A. DC.).

Succulent shrubs or small, mostly candelabrum-shaped trees up to 12 m high with clear non-sticky sap in all parts; in small shrubs trunk cylindrical or usually subglobose; in trees trunk cigar- or less often bottle-shaped; branches and branchlets terete, covered with spines which are paired, or in bundles of three or rarely four or five together (two of them are transformed stipules), very short or absent in *P. decaryi*. *Leaves* alternate, sessile or not, confined to the apices of the branchlets, also on minute lateral branchlets in species from continental Africa except *P. namaquanum*, simple, entire or undulate, deciduous and pubescent to glabrous. *Inflorescence* terminal, pedunculate or sessile, congested (only in *P. geayi* rather lax), with few or many flowers. *Flowers* 5-merous, actinomorphic, except for the subequal sepals, open during the day. *Sepals* free or almost free, subequal, erect, persistent, without colleters. *Corolla* tubular, variously coloured; tube divided in two parts; upper part obconical, urceolate or almost cylindrical; basal part mostly cylindrical; lobes overlapping to the right in bud, spreading or less often suberect or recurved. *Stamens* included or exserted, inserted where the tube starts to widen; anthers sessile, triangular or very narrowly so, acuminate at the apex, sagittate at the base and often pubescent inside at the base of the connective just below they cohere with the pistil head. *Pistil* with apex about halfway along anthers; ovary subglobose, pubescent to glabrous, abruptly narrowed into the style, of 2 separate carpels; disk annular, urceolate, usually composed of 5 ovate often rounded glands which may be partly or entirely fused; style cylindrical, widened at the apex, glabrous or sparsely pubescent; pistil head of 3 parts, an obconical or less often subconical or subcylindrical basal part to the base of which the anthers cohere, a ring-shaped central part and a bilobed stigmoid apex. Ovules numerous. *Fruit* of 2 separate mericarps forming an angle of 5-180°; mericarps pale to dark brown, follicular, fusiform or narrowly oblong, (obovoid to ellipsoid in *P. namaquanum*), straight or curved (much recurved sometimes in *P. baronii*) longitudinally dehiscent with an adaxial slit, glabrous to pubescent. *Seeds* with apex directed towards the apex of the follicle; grain pale to dark brown, ovate or elliptic, rarely ellipsoid or obovoid, lateraly compressed and crescent-shaped on transverse section; testa smooth to rough; coma of straw-coloured or whitish simple hairs. Endosperm mostly thin, mealy, surrounding the embryo. Embryo spathulate; cotyledons and rootlet variously shaped.

Pachypodium counts 23 species, 5 of which are distributed in southern continental Africa and 18 are endemic to Madagascar.

1. KEY TO THE SPECIES OF PACHYPODIUM

1. Dwarf plants with trunk much wider than high; without branches and branchlets; spines all closely together below leaves; Madagascar ..... **P. brevicaule**
   Plants much higher or trunk at least as long as wide; branches and branchlets present; spines variously arranged but never all closely together 2
2. Corolla yellow or red 3
   Corolla creamy, white or pink, or partly white and partly pink 4
3. Unbranched or almost unbranched cactus-like tree; larger spines very thick and stiff, mostly over 3 cm; continental Africa ..... **P. namaquanum**
   Much-branched shrub; larger spines shorter, up to 12 mm long; Madagascar ..... see Key 2
4. Larger spines of a bundle mostly more than 4 × as long as the diameter of the branchlet; continental Africa ..... see Key 3
   Larger spines of a bundle up to 2 × as long as the diameter of the branchlet; Madagascar ..... see Key 2

2. KEY TO THE SPECIES OF PACHYPODIUM ENDEMIC TO MADAGASCAR

1. Stamens exserted 2
   Stamens included 3
2. Corolla lobes bright yellow, spreading, 1-1.3 × as long as wide, small shrub with thick base, 10-50 cm high; inflorescence congested; spines paired, 5-13 mm long ..... 7. **P. densiflorum**
   Corolla lobes cream or yellow-green, recurved, 1.45-1.83 × as long as wide; candelabrum-shaped tree, 4-7 m high; inflorescence rather lax; spines three together, 1.5-20(-50) mm long ..... 9. **P. geayi**
3. Trunk extremely short, much wider than long; branches and branchlets absent; spines closely together below leaves ..... 4. **P. brevicaule**
   Trunk usually at least as long as wide; branches and branchlets present; spines at least along branchlets 4
4. Corolla lobes pale red or crimson 5
   Corolla lobes white, yellow or cream 6
5. Pedicels 8-23 mm long; basal part of the corolla tube 0.39-0.44 of its total length, 7-9 mm long; sepals 0.28-0.75 × as long as the basal part of the corolla tube, 2.5-6 mm long; on gneiss (see Chapter 3) ..... 2. **P. baronii**
   Pedicels 3-5 mm long; basal part of the corolla tube 0.55-0.62 of its total length, 11-17 mm long; sepals 0.18 × as long as the basal part of the corolla tube, 2-3 mm long; on limestone ..... 18. **P. windsorii**
6. Corolla lobes white and tube mostly white as well 7
   Corolla lobes yellow or cream, tube yellow or not white 12
7. Shrub with subglobose trunk, more or less abruptly narrowed into one or several cylindrical branches 8

Candelabrum-shaped tree with mostly straight cigar-shaped or less often bottle-shaped trunk and a distinct crown 9

8. Basal part of the corolla tube 0.5 of the length of the entire tube, 19-21 × 1.5-2 mm; upper part 18-21 mm long; sepals 3-4 mm long; corolla lobes 21-30 × 11-15 mm; spines rigid, 2-10 mm long; leaves densely pubescent beneath ..... 1. **P. ambongense**

Basal part of the corolla tube 0.25-0.35 of the length of the entire tube, 14-18 × 4-6 mm; upper part 26-42 mm long; sepals 6-7 mm long; corolla lobes 32-45(-65) × 16-23(-32) mm; spines rather soft, 1-3 mm long, often absent; leaves sparsely pubescent beneath especially on veins ..... 6. **P. decaryi**

9. Corolla tube with basal part 0.07-0.20(-0.3) of the length of the entire tube; lobes not twisted in bud 10

Corolla tube with basal part 0.26-0.42 of its length; lobes slightly twisted in bud 11

10. Peduncle 20-120 mm long; spines three together, 2.5-27 mm long; upper part of the corolla tube urceolate; entire corolla tube 6.5-12 × as long as the calyx ..... 13. **P. lamerei**

Peduncle 0-12 mm long; spines paired, 1-6 mm long; upper part of the corolla tube almost cylindrical; entire corolla tube 13.7-17.5 × as long as the calyx ..... 17. **P. sofiense**

11. Corolla tube 2-2.3 × as long as the calyx, 17-25(-27) mm long; basal part 5-6(-7) mm long; lobes 1.3-1.6 × as long as the tube; sepals longer than or as long as the basal part of the corolla tube ..... 14. **P. meridionale**

Corolla tube 6-9 × as long as the calyx, 30-47 mm long; basal part 8-15 mm long; lobes 0.75-1.05(-1.4) × as long as the tube; sepals always shorter than the basal part of the corolla tube ..... 16. **P. rutenbergianum**

12. Basal part of the corolla tube 0.55 of the length of the entire tube, 13-15 mm long; sepals 1.5-1.85 × as long as wide; corolla lobes yellowish, tube yellowish-green ..... 12. **P. inopinatum**

Basal part of the corolla tube 0.15-0.38 of the length of the entire tube, 2-10 mm long; sepals 1.75-7 × as long as wide; corolla lobes bright yellow or cream and tube as well or not 13

13. Basal part of the corolla tube 0.3-0.38 of the length of the entire tube; corolla lobes cream and tube as well outside, usually lemon-yellow inside; spines with a conical basal part 0.4-0.5 of its length and a needle-like upper part ..... 8. **P. eburneum**

Basal part of the corolla tube 0.15-0.3 of the length of the entire tube; corolla lobes bright yellow and tube as well or not outside, usually pale yellow inside; spines various 14

14. Corolla tube with upper part urceolate abruptly widened at the base and with again 5-widened parts below the lobes and therefore seemingly 5-winged inside; corolla lobes bright yellow and tube as well ..... 11. **P. horombense**

Corolla tube with upper part obconical and not with again widened part; corolla lobes bright yellow and tube as well or not 15

15. Corolla tube white inside, medium yellow outside with pale green lines below the lobes; sepals 2-3 × as long as wide; near Berevo ..... 3. **P. bicolor**

Corolla tube pale yellow inside, yellowish-green or pale greenish-yellow outside with dark red lines; sepals 3-8(-14) × as long as wide; Mahajanga (W and NW), Fianarantsoa (Isalo) or Toliara (SE) 16

16. Corolla tube 0.8-1.25 × as long as the lobes, 18-30 mm long; basal part of the corolla tube 4-7 mm long; spines 0.5-2 mm wide at the base; Toliara (SE) ..... 5. **P. cactipes**
    Corolla tube 1.3-2 × as long as the lobes, 18-44 mm long; basal part of the corolla tube 3-10 mm long; spines 0.5-5 mm wide at the base; Fianarantsoa (Isalo) and Mahajanga and Toliara 17
17. Spines thin, densely arranged and needle-like; corolla tube 18-26 mm long, inside with a belt of pubescence 1-2 mm below the insertion of the stamens; basal part of the corolla tube 3-5 mm long; Fianarantsoa (Isalo) and Toliara (S center) ..... 10. **P. gracilius**
    Spines usually much thicker, often in some pairs above each other 5-15 mm separate and conical; corolla tube 27-44 mm long, inside with a belt of pubescence 3.5-8 mm below the insertion of the stamens; basal part of the corolla tube (5-)7-10 mm long; Mahajanga (NW and W) and Toliara (W) . 15. **P. rosulatum**

3. KEY TO THE SPECIES OF PACHYPODIUM CONFINED TO THE AFRICAN CONTINENT

1. Shrub with a large tuberous trunk half- to almost fully below soil surface; spines thin, rather soft, often larger two of each group 3-27 mm long and less than 1.5 mm wide at the base, curved or straight 2
   Above ground shrub or small tree; spines much thicker and hard, usually the larger two of each group 8-75 mm long and more than 1.5 mm wide at the base, rarely curved 3
2. Corolla tube glabrous, 2.1-2.7 × as long as the lobes; upper part of the corolla tube obconical; lobes 1.1-1.25 × as long as wide, 5-10 mm long; sepals glabrous on both sides ..... 19. **P. bispinosum**
   Corolla tube pubescent, 0.7-1.7 × as long as the lobes; upper part of the corolla tube almost cylindrical; lobes 2-3 × as long as wide, 10-30 mm long; sepals pubescent outside and glabrous inside ..... 23. **P. succulentum**
3. Unbranched or only once or twice branched tree; corolla tube hirto-pubescent with upper part obconical; leaves densely pubescent on both sides with stellate hairs and margin strongly undulate; sepals hirsute outside, sparsely hirsute to glabrous inside; S Namibia and N Cape Province of South Africa ..... 21. **P. namaquanum**
   Much branched tree or less often shrubs; corolla tube glabrous with upper part urceolate; leaves entire, glabrous to pubescent with simple hairs 4
4. Leaves glabrous on both sides, often with margin ciliolate and midrib sparsely pubescent beneath; sepals not ciliate; Mozambique, South Africa (Kwazulu-Natal and northern and eastern Transvaal), Swaziland and Zimbabwe ..... 22. **P. saundersii**
   Leaves pubescent to almost glabrous on both sides and often slightly mucronate; sepals with margin ciliate; S Angola and N Namibia ..... 20. **P. lealii**

TREATMENT OF THE SPECIES

1. **Pachypodium ambongense** Poiss. in Bull. Acad. Malgache sér.2, 6: 162, pl.5 (1924); Perrier de la Bâthie in Bull. Soc. Bot. Fr. 81: 307 (1934); Pichon in Mém. Inst. Sc. Madag., sér. B, 2: 112 (1949); Markgraf, Fl. Madag. fam. 169: 288 (1976). Type: Madagascar, Majunga (= Mahajanga), Namoroka Res., *Perrier de la Bâthie* 1515 (holotype P). Fig. 1, p. 11; Map 1, p. 12; Plate 1, opposite p. 16.

Shrub 1-2 m high, trunk subglobose, laterally compressed, 10-40 cm in diameter; bark grey-green, smooth or with leaf scars; branched from just below each terminal inflorescence. Branches short, 7-18 cm in diameter; branchlets 18-40 × 5-6 mm, covered with paired straight spines, 2-10 mm long, 0.5-2 mm wide at the base, sparsely pubescent when young. *Leaves* confined near and to the apices of the branchlets, petiolate; petiole 2-10 mm long, sparsely pubescent; blade dark green with midrib pale green above, pale green to pale grey beneath when fresh, papery when dried, ovate to obovate, 1.9-3.4 × as long as wide, 3.5-9 × 1.5-3 cm obtuse to rounded at the apex, cuneate at the base or decurrent into the petiole, margine revolute, glabrous above with impressed reticulate venation, densely pubescent beneath with midrib and secondary veins prominent; secondary veins in 23-32 pairs, straight at the base, upcurved at the apex, forming an angle of 45-85° with the costa; tertiary venation reticulate, hidden by the indumentum beneath. *Inflorescence* sessile or shortly pedunculate, congested, 6-8 × 3-5 cm, 1-8-flowered. Peduncle dark green, 0-5 × 2-4 mm, sparsely pubescent to glabrous; pedicels green, 4-10 mm long, sparsely pubescent to glabrous. Bracts ovate, 2 × 1 mm, acuminate at the apex, pubescent outside, glabrous inside. *Flowers*: *Sepals* pale green, connate at the base for about 0.2 mm, persistent, ovate or narrowly so, 1.5-2 × as long as wide 3-4 × 2-2.2 mm, acuminate and with stiff hairs or not at the apex, sparsely pubescent or glabrous outside, glabrous inside. *Corolla* limb white, tube pale greenish-yellow outside, yellowish-green in the throat, 4.3-6 cm long in the mature bud and forming a comparatively wide broadly ovoid head, 3.8-4.0 of the bud length, 17-23 × 4-10 mm, obtuse at the apex, glabrous outside, with a sparsely pubescent belt inside 7 mm wide just below the insertion of the stamens, otherwise glabrous; tube 10.5-12.3 × as long as the calyx, 1.4-1.8 × as long as the lobes, 3.7-4.2 cm long; basal part narrowly cylindrical, 0.5 of the length of the entire tube, 19-21 × 1.5-2 mm wide; upper part urceolate, clearly narrowed at the throat, 18-21 mm long, 3-4 mm wide at the mouth; lobes obliquely ovate, 0.52-0.7 × as long as the tube, 1.6-2 × as long as wide, 21-30 × 11-15 mm, obtuse at the apex. *Stamens* with apex 6 mm below the mouth of the corolla tube, inserted 0.62 of the length of the corolla tube, at 2.5 cm from the base; anthers very narrowly triangular, 5.25-5.75 × as long as wide, 10.5-11.5 × 2 mm, sparsely pubescent inside at the base of the connective just below where they cohere with the base of the pistil head, fertile part 5 mm long. *Pistil* 2.7 cm long; ovary 2 × 1.3 × 1.2 mm, glabrous, disk urceolate, 2.5 mm high, abruptly narrowed at the throat, 5-lobed at the apex and entirely covering the ovary; style 22.7 mm long, widened at the apex, glabrous; pistil head 2.3 mm high composed of an obconical basal part 1.3 × 0.6 mm, a ring-shaped central part 0.5 × 1.3 mm and a stigmoid apex 0.5 × 0.9 mm. Ovules approximately 50 in each carpel. *Fruit* (*Lavranos*) of 2 mericarps; mericarps dark brown outside, whitish inside when dried, fusiform, c. 15 cm long and c. 1 cm wide; wall thin, 0.5 mm thick. *Seeds*: unknown.

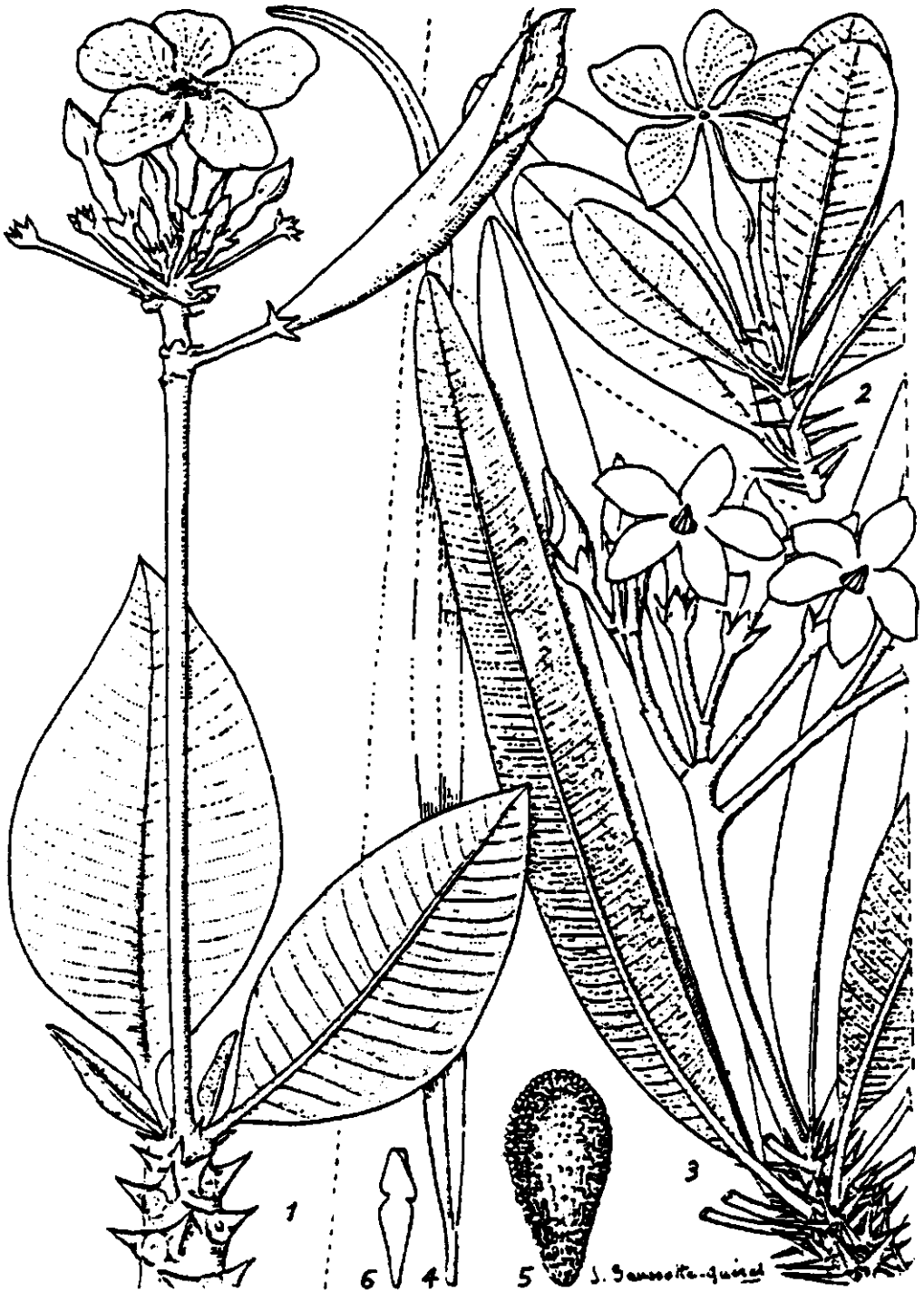
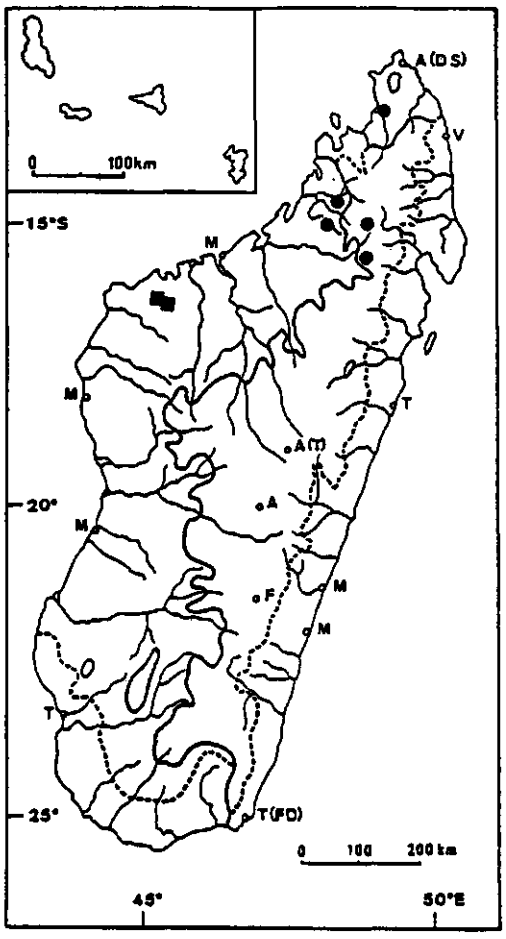
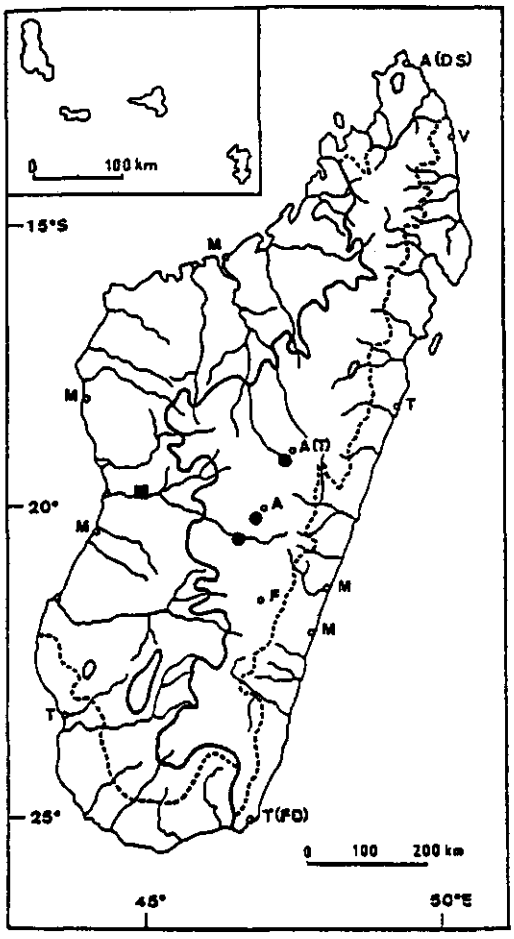


Figure 1. 1) *Pachypodium baronii*: 1 = habit (× 2/3). 2) *P. ambongense*: 2 = habit (× 2/3). 3-6) *P. geayi*: 3 = habit (× 2/3), 4 = other type of leaf, 5 = grain (× 3), 6 = embryo (1 = from Bosser 16733; 2 = from Perrier de la Bâthie 1515; 3-4 = from Decary 16401; 5-6 = from Perrier de la Bâthie 18004).



Map 1. ▪ *Pachypodium ambongense*, • *P. baronii*.



Map 2. ▪ *Pachypodium bicolor*, • *P. brevicaule*.

DISTRIBUTION. Endemic to Madagascar. Rare.

ECOLOGY. Low open deciduous western forest on Mesozoic calcareous rocks. Alt. less than 100 m. Flowering January-March.

Vernacular names: Songosongo or Betono (Sakalava).

Specimens examined:

MADAGASCAR. Mahajanga: Namoroka Res., *Decary* 17893 (P); ibid., *Perrier de la Bâthie* 1515 (P, type); ibid., *Poisson* 1(a) (P); ibid., *Rakotovao* RN 6405 (P); Andranomavo *Randriamiera* RN 8563 (TAN).

CULT. Switzerland. Zürich, from Namoroka, *Röösli* Dec. 1992 (ZSS 16626) & (ZSS 15134); ibid., *Specks* 20 Jun. 1990 (ZSS 903164/a); from c. 55 km S of Soalala, Tsingy de Namoroka, *Röösli* Aug. 1990 (P, ZSS 15092) & (ZSS 15700).

NOTE. The flowers and leaves of cultivated plants are often larger than those of the wild plants. *Röösli* Aug. 1990 (ZSS 15700) has leaves with blades 16-17 × 2.6-3.2 cm, corolla tubes 4.7-5.5 cm long and lobes 4 × 2.3 cm.

2. **Pachypodium baronii** Costantin & Bois in Ann. Sc. Nat. sér. 9, 6: 317 (1907); Perrier de la Bâthie in Bull. Soc. Bot. Fr. 81: 301 (1934); Pichon in Mém. Inst. Sc.

Madag., sér. B, 2: 123 (1949) (all three as *baroni*); Markgraf, Fl. Madag. fam. 169: 289 (1976). Type: Madagascar, sin. loc., *Baron* 5874 (holotype P; isotype K). Fig. 1, p. 11; Map 1, p. 12; Plates 2-4, opposite p. 16.

Heterotypic synonym
Pachypodium baronii var. *erythreum* Poiss. in Bull. Acad. Malgache sér. 2, 6: 166, pl.10 (1924) as *baroni*. Type: Madagascar, Antsiranana, Upper Sofia R., Antsakabary, *Perrier de la Bâthie* 15082 (holotype P).

Shrub 1-3.50 m high; trunk subglobose, mostly narrowed at the base, 20-40 × 20-50 cm, rather abruptly narrowed into one or sometimes several cylindrical branches 30-50 × 4-8 cm tapering to 3-4 cm; bark pale grey or grey-green, smooth or with remains of leaf scars. Branchlets 1.5-7 × 0.8-1.5 cm; covered with paired often curved spines, 2-9(-13) mm long, 1-4(-6) mm in diameter at the base, basal part conical and laterally compressed, 0.33-0.66 of the spine length, often red and pubescent when young, turning medium to dark brown and glabrous. *Leaves* confined to the apices of the branchlets, petiolate; petiole pale reddish-green, 3-25 mm long, pubescent; blade coriaceous, medium green, with midrib pale green and shiny above, pale glaucous beneath with pale green midrib and dark green reticulate venation when fresh, papery when dried, ovate to obovate or narrowly so, 1.4-3 × as long as wide, 3-18 × 1.4-9 cm, acuminate to apiculate at the apex, cuneate to rounded at the base, margin revolute, glabrous to sparsely pubescent above, especially on midrib and secondary veins and with impressed venation, pubescent beneath with midrib and secondary veins prominent; secondary veins in 15-30 pairs, straight, upcurved at the apex, forming an angle of 45-90° with the costa; tertiary venation reticulate. *Inflorescence* pedunculate, congested, 16-40 × 4.5-12 cm, 3-17-flowered. Peduncle pale green, terete, 7-20 × 4-6 mm, glabrescent; pedicels pale reddish-green, 8-23 mm long, sparsely pubescent. Bracts oblong, 2-3.5 × as long as wide, 5-11 × 2-2.5 mm, longer than the sepals, pubescent outside, glabrous inside. *Flowers: Sepals* dark green, connate at the base for about 0.2 mm, persistent, ovate or narrowly so, 1.5-2.5 × as long as wide, 2.5-6 × 1.5-2.5 mm, acuminate at the apex, glabrous to sparsely pubescent outside, glabrous inside. *Corolla* limb crimson, tube with basal part pale green, upper part greenish-red outside, with pale yellow or pale green star or ring inside surrounded by dark red at the throat, 2.5-4 cm long in the mature bud and forming a comparatively wide broadly ovoid head, 0.4-0.5 of the bud length, 1-1.9 × 0.7-1.1 cm, acuminate to obtuse at the apex, glabrous or sparsely and often also partly pubescent outside, glabrous on the part of the lobes covered in bud, glabrous inside for 6-7 mm from the base, with a pubescent belt from 4-7 mm below the insertion of the stamens to the mouth which is more dense at the mouth; tube 4.4-6 × as long as the calyx, 1.13-1.22 × as long as the lobes, 15-23 mm long, basal part almost cylindrical, often conically widened at the base, 0.39-0.44 of the length of the entire tube, 7-9 × 2-4.8 mm; upper part almost cylindrical, 8-14 mm long, slightly narrowed at the mouth, 3-4 mm wide at the mouth; lobes obliquely and broadly obovate, 0.8-0.9 × as long as the tube, 1.35-1.6 × as long as wide, 15-19 × 11-17 mm, rounded at the apex, ciliate the edge not covered in bud. *Stamens* with apex 4-4.5 mm below the mouth of the corolla tube, inserted 0.47-0.6 of the length of the corolla tube, at 1-1.4 cm from the base; anthers very narrowly triangular, 5-6 × as long as wide, 6-6.5 × 1-1.3 mm, pubescent inside at the base of the connective just below where they cohere with the pistil head. *Pistil* 12.5-14.5 mm long; ovary 2-2.5 × 1.8-2.2 × 1.5 mm, pubescent on the part not

covered by the disk; disk of 5 inequal glands, 2 or 2 pairs of which are fused partly or entirely, ovate, 1.7-2 mm high, rounded at the apex, more than half as long as the ovary; style 9.3-11 mm long, sparsely pubescent; pistil head cylindrical, 1-1.3 mm high, composed of an obconical basal part 0.5-0.65 × 0.4-0.5 mm, a ring-shaped central part 0.5-0.7 × 0.6-0.7 mm and a stigmoid apex 0.1-0.2 × 0.3-0.4 mm. Ovules approximately 50 in each carpel. *Fruit* of 2 separate mericarps, sometimes only one developing, with an angle 45-180° at the base (sometimes flowers and fruit on the same inflorescence); mericarps pale reddish-green with longitudinal lines when fresh, pale brown, pale greenish-brown to dark brown outside and whitish to very pale brown inside when dried, 40-115 × 10-20 × 7-10 mm when fresh, straight or recurved, obtuse to acute at the apex, pubescent; wall 1 mm thick. *Seeds:* grain pale brown with margin medium brown when fresh, ovate to elliptic, 6-7 × 3-3.8 mm, rounded at the apex, obtuse at the base, with margin revolute towards the hilar side; testa smooth; coma straw-coloured, 1-1.5 cm long. Embryo whitish, 5-6 mm long; cotyledons ovate, 1.14-1.2 × as long as wide, 3-4 × 2.5-3.5 mm, rounded at the apex, cordate at the base; rootlet 0.6-0.8 × as long as cotyledons, 2-2.5 × 1-1.8 mm.

DISTRIBUTION. Endemic to Madagascar.

ECOLOGY. Low open deciduous western forest on Mesozoic calcareous rocks and granitic or gneissic rocks (metamorphic basement). Alt. 300-1200 m. Flowering mainly September-November and fruiting October-December.

Vernacular name: Bontaka (Tsimihety).

Specimens examined:

MADAGASCAR. Antsiranana: Marivorahona, SW of Manambato, Upper Mahavavy N, Ambilobe District, *Humbert* 25619 (P); Mevahinja near Bejofo, Sambirano, *Perrier de la Bâthie* 8861 (P); Maromandia (Sandrakoto), *Decary* 1102 (P) & 1279 (P). Mahajanga: km 41 Befandriana N-Antsohihy, near Ankobakobaka, *Leeuwenberg & Rapanarivo* 14771 (BR, TAN, WAG); ibid., *Supthut & von Arx* 9324 (G, P, TAN, ZSS); S of Befandriana N, *Razafindratsira* s.n. (ZSS); Upper Sofia R. Antsakabary, Befandriana N, *Perrier de la Bâthie* 15082 (P, type of *P. baronii* var. *erythreum*); 15 km N of Mandritsara, *Röösli & Hoffmann* 16/96 (MO, P, WAG, ZSS); near Mandritsara, *Bosser* 16721 (TAN) & 16733 (P, TAN); ibid., *Decary* 15342 (P); ibid., *Dufournet* anno 1936 (P); ibid., *Supthut & von Arx* 9330 (G, TAN, ZSS); ibid., Herb. Jard. Bot. Tana. 3227 (P). Sin. loc., *Baron* 5874 (K, P, type); *Hofstätter* s.n. (ZSS 04310); *Razafindratsira* s.n. (ZSS 00169).

CULT. Madagascar, Antananarivo, Tsimbazaza Park, *Dorr & Barnett* 3148 (TAN, WAG); ibid., *Leeuwenberg* 13726 (WAG); Tsimbazaza Park, from Ankaizina, Herb. Jard. Bot. Tana. 4939 (TAN). Switzerland, Zürich, Röösli's greenhouse, *Leeuwenberg & Rapanarivo* 14653 (WAG).

NOTES. *Leeuwenberg, Rapanarivo, Röösli and Hoffmann* observed in the field, that *P. baronii* suffers extensively from bush fires which are a plague in the country. They observed heavily damaged specimens. The species is therefore endangered.

P. baronii and *P. windsorii* are easily confused. The two species are distinguished mainly by the characters given in number 4 of Key 2.

3. **Pachypodium bicolor** Lavranos & Rapanarivo in Cactus and Succulent Journ. 69: 29-32 (1997). Type: Madagascar, Toliara, along the Tsiribihina R., Bekinankina, W of Berevo, *W. Röösli & R. Hoffmann* 33/96 (holotype P; isotypes MO, TAN, WAG, ZSS). Fig. 2, p. 15; Map 2, p. 12; Plates 5-7, opposite p. 17.

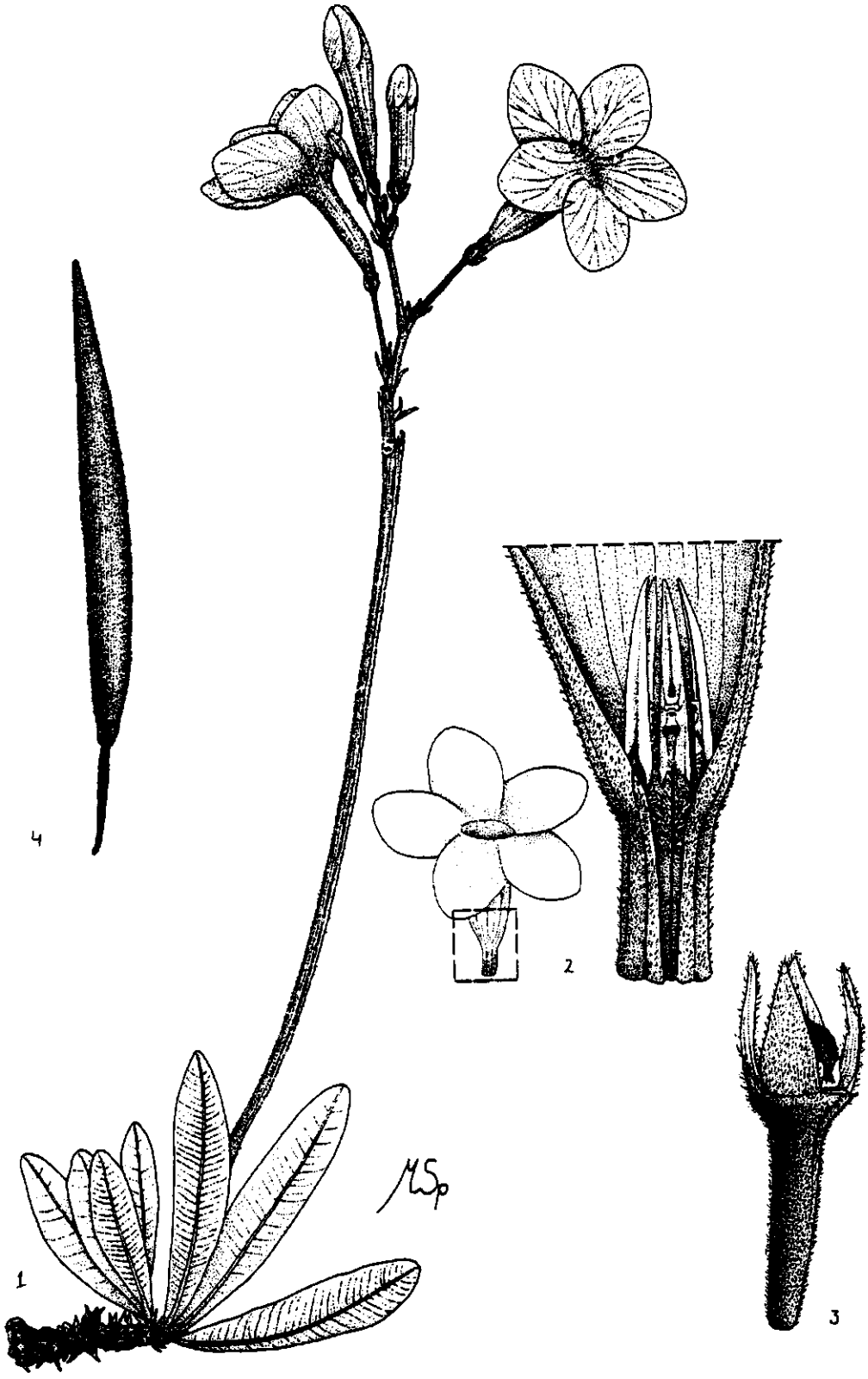
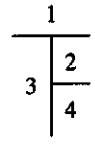


Figure 2. *Pachypodium bicolor*: 1 = habit (× 1), 2 = corolla inside with stamens (× 6), 3 = calyx (× 6), 4 = fruit (× 1) (1-3 = from Röösli & Hoffmann 33/96; 4 = from Röösli & Hoffmann ZSS 16301).

Homotypic synonym
P. rosulatum var. *rosulatum* f. *bicolor* (Lavranos & Rapanarivo) G.D. Rowley in Bradleya 16: 107 (1998) and Pachypodium & Adenium, The Cactus File Handbook 5: 57 (1999), **syn. nov.**

Plant succulent, 25-50 cm high, with a densely branched crown up to c. 50 cm broad; stem cylindrical 6-14 cm in diameter at the base, branched from low down and, like the branches, covered with leaf scars and remains of spines; branches 3.5 cm in diameter; bark pale grey, smooth; branchlets 1.5-5 cm long and 8-12 mm in diameter, covered with paired straight grey-brown spines 2-8 mm long and 1-3.5 mm in diameter at the base, basal part conical 0.6-0.75 of the spine length, young spines and base of young leaves densely white-lanate. *Leaves* subsessile, confined to the apices of the branchlets; petiole 0-2 mm long, pubescent; blade medium green with pale green midrib above, pale green with reticulate venation beneath when fresh, papery when dried, ovate to elliptic or narrowly so, 3-5 × as long as wide, 3-7.5 × 0.8-2 cm, obtuse to rounded at the apex, cuneate at the base, glabrous and with impressed venation above, ciliolate, pubescent beneath, with 14-40 pairs of rather straight secondary veins forming an angle of 45-90° with the costa, tertiary venation reticulate. *Inflorescence* pedunculate, congested, 15-30 × 6-9 cm, 5-8-flowered. Peduncle terete, glaucous, 120-250 × 2-4 mm, pubescent; pedicels pale reddish-green, 12-17 mm long, slightly elongate in fruit to 2.3 cm. Bracts pale green, persistent, narrowly oblong, 4-6 × 1 mm, pubescent outside, sparsely pubescent inside. *Flowers*: *Sepals* pale green, narrowly ovate, 2-3 × as long as wide, 3-5 × 1-2 mm, pubescent outside, glabrous inside, acuminate at the apex. *Corolla* limb medium yellow outside, bright yellow inside, tube pale green at the base, medium yellow outside with 5 very pale green lines to just below the lobes, white inside; 3.5 cm long in the mature bud and forming a comparatively wide broadly ovoid head 0.3 of the bud length, 10 × 8 mm, obtuse at the apex, pubescent outside and glabrous on the part of the lobes covered in bud, pubescent belt inside 2 mm wide just below the insertion of the stamens; tube infundibuliform, 5-10 × as long as the calyx; 1-1.46 × as long as the lobes, 2.5-3 cm long; basal part almost cylindrical, 0.18-0.22 of the length of the entire tube, 3-4 × 2-3 mm, slightly widened at the apex, upper part obconical at base and almost cylindrical above, 21-27 mm long, 8-12 mm wide at the mouth; lobes obliquely obovate, 0.6-0.8 × as long as the tube, 1.2-1.5 × as long as wide, 1.5-2 × 1-1.2 cm, rounded at the apex. *Stamens* with apex 15-16 mm below the mouth of the corolla tube, inserted 0.16-0.2 of the length of the corolla tube, at 5-6 mm from the base; anthers 7-8 × 1 mm, with stiff hairs at the base of the connective just below where they cohere with the pistil head. *Pistil* 7-8.5 mm long; ovary 2 × 2 × 1.5 mm pubescent or sparsely so with short, straight hairs; disk of 5 glands, 2 or 2 pairs of which partly or entirely fused, broadly ovate, 1 mm high, rounded, emarginate or obtuse with irregularly toothed apex which are less than half as long as the ovary; style filiform, gradually thickening into a cy-

Plate 1. *Pachypodium ambongense.*
Plate 2. *Pachypodium baronii*, Mandritsara.
Plate 3. *Pachypodium baronii*, Mandritsara.
Plate 4. *Pachypodium baronii.*



lindrical head; pistil head 1.2 mm high, composed of an obconical basal part 0.6 × 0.7 mm, a ring-shaped central part 0.4 × 0.8 mm and a stigmoid apex 0.2 × 0.4 mm. Ovules approximately 50 in each carpel. *Fruit* of 2 separate mericarps, sometimes only one developing, forming an angle 10-60° at the base (sometimes flowers and fruit in the same inflorescence); mericarps pale brown with longitudinal lines outside, whitish inside, fusiform, 60-100 × 3-6 mm, acute at the apex, pubescent with short hairs; wall c. 0.5 mm thick. *Seeds*: grain pale to medium brown, ovate to elliptic 5 × 2 mm, margin revolute towards the hilar side; testa rough. Embryo 4.5 mm long; cotyledons ovate, 1.22-1.83 × as long as wide, 2.2 × 1.2-1.8 mm, rounded at the apex, subcordate at the base; rootlet 1.04 × as long as the cotyledons, 2.3 × 1-1.5 mm.

DISTRIBUTION. Endemic to Madagascar,

ECOLOGY. Low open deciduous western forest on sandstone. Alt. c. 30 m. Flowering November and fruiting December.

Paratypes:

MADAGASCAR. Toliara: W of Berevo, *Röösli & Hoffmann* Dec.1993 (ZSS 16301).

CULT. Switzerland: Zürich, from W Berevo, *Leeuwenberg & Rapanarivo* 14655 (WAG).

NOTE. *P. bicolor* is distinguished from the other species with yellow corollas by the colour of the tube which is white inside.

4. **Pachypodium brevicaule** Bak. in Journ. Linn. Soc. Bot. 22: 503 (1887); Perrier de la Bâthie in Bull. Soc. Bot. Fr. 81: 303 (1934); Pichon in Mém. Inst. Sc. Madag. sér. B, 2: 122 (1949); Markgraf, Fl. Madag. fam. 169: 299 (1976). Type: Madagascar, sin. loc., *Baron* 4412 (holotype K; isotype P). Fig. 3, p. 18; Map 2, p. 12; Plates 8-10, opposite p. 17.

Broad cactus-like plant when flowering up to 25 cm high; trunk very short, 2-8 cm high, 10-40 cm in diameter; bark pale grey sometimes shiny, smooth, 2-4 mm thick, wood greenish. Branches 1-4 × 2-4 cm when fresh, with paired, rather soft, curved spines at the apices, 2-9 mm long and 1-1.5 mm at the base, pale grey to pale brown, more or less flat, pubescent when young. *Leaves* confined to the apices of the branches, sessile or shortly petiolate; petiole 0-2 mm long, sparsely pubescent; blade herbaceous and glaucous when fresh, papery when dried, ovate to obovate 1.3-3 × as long as wide, 11-30 × 6-12 mm, acuminate to obtuse at the apex, obtuse to rounded at the base, glabrous to sparsely pubescent on both sides, with impressed venation above, with midrib and secondary veins prominent beneath; with 15-30 pairs of secondary veins straight at the base, upcurved at the apex, forming an angle of 45-85° with the costa; tertiary venation reticulate. *Inflorescence* sessile or pedunculate, congested, 2.5-15 × 2-6.5 cm, 1-7-flowered. Peduncle glaucous, terete, 0-120 × 2-4 mm, sparsely pubescent to pubescent; pedicels 0-8 mm long, pubescent. Bracts longer than

5	6
7	9
8	10

Plate 5. *Pachypodium bicolor*, Berevo.
Plate 6. *Pachypodium bicolor*.
Plate 7. *Pachypodium bicolor*, Berevo.
Plate 8. *Pachypodium brevicaule*, Itremo.
Plate 9. *Pachypodium brevicaule*, Mt Ibity.
Plate 10. *Pachypodium brevicaule*, Mt Itongafeno.

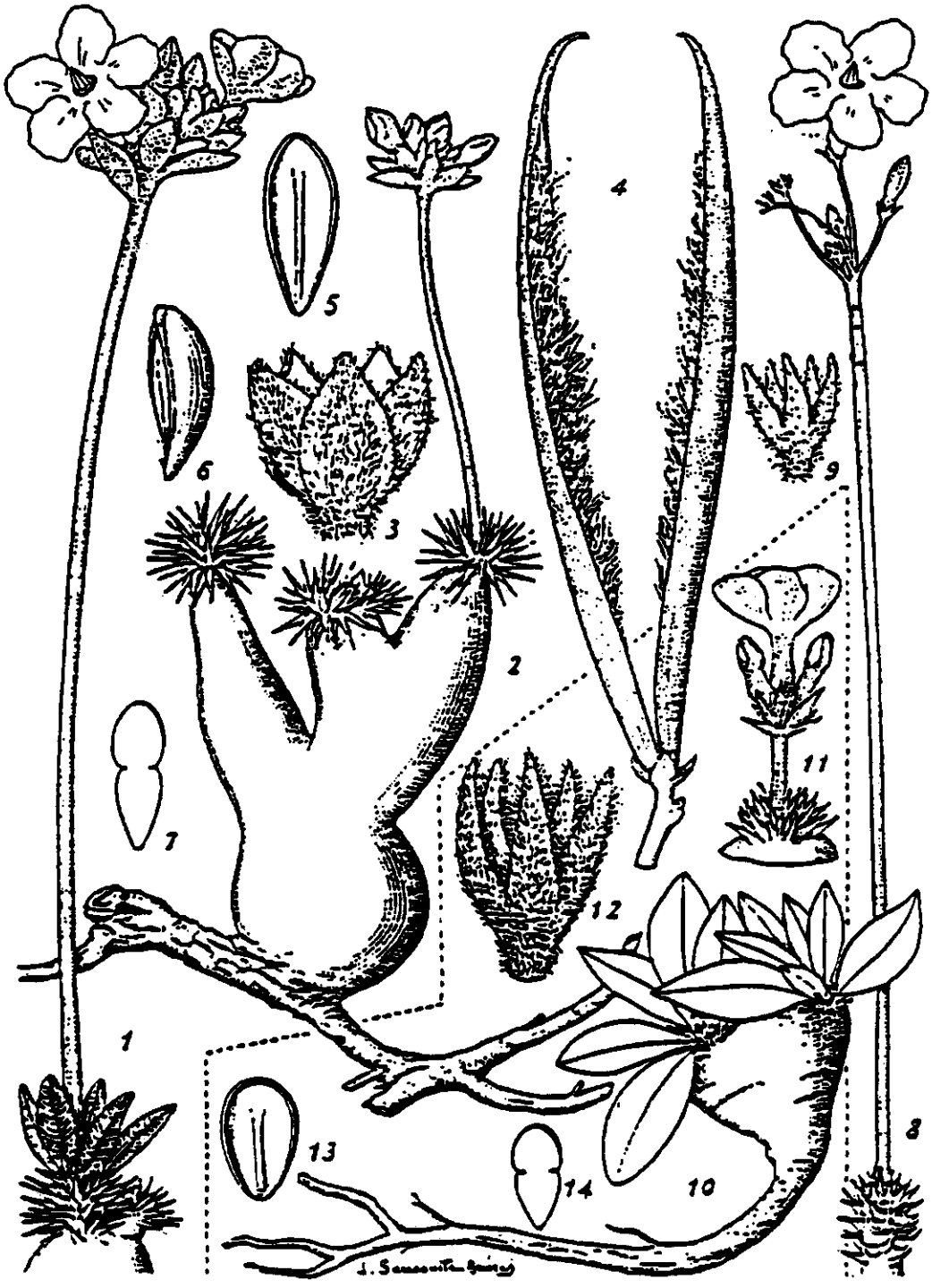


Figure 3. 1-9) *Pachypodium densiflorum*: 1, 2 and 8 = habits (× 2/3), 3 and 9 = calyxes (× 3), 4 = fruit (× 2/3), 5 and 6 = grains (× 4), 7 = embryo (× 4). 10-14) *P. brevicaule*: 10 and 11 = habits (× 2/3), 12 = calyx (× 3), 13 = grain (× 4), 14 = embryo (× 4) (1, 3 and 5-7 = from Perrier de la Bâthie 16549; 2 = from Perrier de la Bâthie 8953; 8 and 9 = from Perrier de la Bâthie 8862; 10, 12 and 14 = from Viguier & Humbert 1510; 11 = from Humbert 4620).

the pedicels, narrowly oblong or narrowly obovate, 3.3-4.3 × as long as wide, 5-13 × 1.5-3 mm, acuminate or acute at the apex, pubescent to sparsely so outside, sparsely pubescent or less so inside. *Flowers*: *Sepals* glaucous, covering the basal part of the corolla tube, connate at the base for about 0.5 mm, narrowly ovate or narrowly oblong, 3-5.5 × as long as wide, 6-11 × 2-3 mm, acuminate or acute at the apex, pubescent outside, often glabrous inside in the lower part and sparsely pubescent near the apex. *Corolla* bright yellow, 17-25 mm long in the mature bud and forming a comparatively wide broadly ovoid head 0.4-0.44 of the bud length, 7-11 × 5-8 mm, obtuse at the apex, pubescent outside but less so on the lobes than on the tube and glabrous on the parts of the lobes covered in bud, pubescent belt inside from 2 mm above to 1 mm below the insertion of the stamens, otherwise glabrous; tube infundibuliform, 1.63-3 × as long as the calyx, 1.05-1.36 × as long as the lobes, 12-18 mm long, basal part almost cylindrical, 0.15-0.18 of the length of the entire tube, 2-3 mm long, 2-2.5 mm wide above the base, upper part almost cylindrical but widened at the throat, 10-15 mm long and slightly widened at the throat, 5.5-7 mm wide at the mouth; lobes obliquely obovate, 0.73-0.94 × as long as the tube, 1.1-1.3 × as long as wide, 9-18 × 8.5-14 mm, rounded at the apex. *Stamens* with apex 4-9 mm below the mouth of the corolla tube, inserted 0.22-0.29 of the length of the corolla tube, at 3.5-4 mm from the base; anthers very narrowly triangular, 5.22-7.14 × as long as wide, 4.7-5.2 × 0.7-0.9 mm, pubescent inside at the base of the connective just below where they cohere with the pistil head, fertile part 2 mm long. *Pistil* 4.8-6.5 mm long; ovary 1.5-1.9 × 1.3-1.6 × 1.2 mm, pubescent; disk composed of 5 broadly ovate glands, 2 of which or 2 pairs of which may be partly fused and which are about half as long as the ovary; style 2.6-3.6 mm long, sparsely pubescent at the base; pistil head 0.7-1 mm high, composed of an obconical basal part 0.4-0.6 × 0.4-0.6 mm, a ring-shaped central part 0.15-0.2 × 0.5-0.7 mm and a stigmoid apex 0.1-0.15 × 0.3-0.5 mm. Ovules approximately 50 in each carpel. *Fruit* of 2 separate mericarps, forming an angle of 5-45°at the base (sometimes with flowers on the same inflorescence); mericarps pale to dark brown with longitudinal lines outside, whitish inside when dried, fusiform, 57-140 × 3-5 × 2-4 mm, obtuse to acute at the apex, pubescent; wall 1 mm thick. *Seeds*: grain pale brown, elliptic, 3.5-3.9 × 1.5-1.8 mm; margin revolute towards the hilar side; testa smooth; coma straw-coloured, 13-21 mm long. Embryo 3.2-3.5 mm; cotyledons ovate, 1.5 × 1.5 mm, rounded at the apex, cordate at the base; rootlet 1.3-1.6 × as long as cotyledons, 2-2.5 × 1.2 mm.

DISTRIBUTION. Endemic to Madagascar.

ECOLOGY. Evergreen sclerophyllous (*Uapaca*) woodland and savanna on quartzitic rocks. Alt. 1300-1900 m. Flowering June-October and fruiting August-November.

Vernacular name: Tsimondrimondry (Merina), Kimondromondro (Betsileo).

Specimens examined:

MADAGASCAR. Antananarivo: near Iharanandriana, Route nat. 7, 38 km S of Antananarivo, *Bosser* 16623 (TAN); ibid., *von Arx & Supthut* 3018 (G, TAN, ZSS); Ambohiponana, *Catat* 1154 (P); Ibity Mt, SW of Antsirabe, *Descoings* 881 (TAN); ibid., *Hofstätter* 070990-4 (ZSS); ibid., *Leeuwenberg & Rapanarivo* 14593 (BR, K, P, TAN, WAG); ibid., *Lewis & Razafimandimbison* 742 (P, PRE, TAN, WAG); ibid., *Perrier de la Bâthie* 8918 (P); ibid., *Viguier & Humbert* 1510 (P); N of Betsileo, Sirabe (= Antsirabe), *Hildebrandt* 3586 (BM, G, K, LE, M, P, W, Z, paratype); Upper Sahatany R. valley, near Antsirabe, *Humbert & Swingle* 4620 (B, G, P); Ambatomenaloha, *Grandidier* anno 1876 (P). Fianarantsoa: S end of Mt Ibity, 25 km S of Manandona, Ambositra, *Fosberg* 52388 (US); Itremo Mts, Ambatofinandrahana, *Bosser*

9716 (TAN); ibid., *Decary* 14993 (P); ibid., *D. Du Puy et al.* 2401 (TAN); W of Itremo, *Humbert* 30004 (P). Sin. loc., *Baron* 4412 (K, P, type); *Camboué* anno 1890 (P); *Rauh* s.n. (M).

CULT. Antananarivo, Tsimbazaza park, *Schlieben* Dec. 1959 (PRE).

NOTES: *Leeuwenberg & Rapanarivo* 14593 grows on quartzite soil with pH c. 4.5 (measured by Röösli) on Ibity Mt. It is surrounded by grasses dominated by *Hyparrhenia* sp. and scattered woody plants as *Uapaca bojeri* Baill. (Euphorbiaceae), *Leptolaena pauciflora* Baker (Sarcolaenaceae). It is found with: *Kalanchoe synsepala* Baker (Crassulaceae), *Aloe capitata* Baker (Aloaceae), *Xerophyta dasylirioides* Baker (Velloziaceae), *Helichrysum ibitiense* R. Vig. & Humbert (Compositae), *Tetradenia fruticosa* Benth. (Labiatae), *Senecio quartzicolus* Humbert (Compositae) and many other plants.

von Arx & Supthut 3018 is accompanied by *Uapaca bojeri* Baill. (Euphorbiaceae) and *Leptolaena pauciflora* Baker (Sarcolaenaceae) near Iharanandriana.

P. brevicaule can easily be distinguished from the other species by the short trunk (2-8 cm hight) with large diameter (10-40 cm) and rather soft spines.

P. brevicaule is not a variable species. The tuberous base has a very short part above the soil and an obconical subterraneous part producing roots penetrating more deeply into the fisssures of the rocks.

5. **Pachypodium cactipes** K. Schum. in Engler & Prantl, Nat. Pflanzenfam. 4, 2: 178 (1895). Type: Madagascar, Toliara, Beravi interior, *J.M. Hildebrandt* 3114 (holotype B†; lectotype Z, designated here; isolectotypes BM, G, K, LE, M, P, W). Fig. 4, p. 21; Map 3, p. 22; Plates 11-13, opposite p. 32.

Heterotypic synonyms

P. rosulatum var. *delphinense* H. Perrier in Bull. Soc. Bot. Fr. 81: 306 (1934); Pichon in Mém.Inst. Sc. Madag. sér. B, 2: 118 (1949). Type: Madagascar, Toliara, Fort-Dauphin, Ifanjahirana, *Decary* 10643 (holotype P).

P. rosulatum var. *stenanthum* ('*stenantha*') Costantin & Bois in Ann. Sc. Nat. sér. 9, 6: 321 (1907); Pichon in Mém. Inst. Sc. Madag. sér. B, 2: 118 (1949). Type: Madagascar, Toliara, sin.loc., *Alluaud* 88 (holotype P).

Shrub up to 1 m high, trunk subglobose and up to 30 cm in diameter or spreading and wider than long; bark grey-green, smooth or with leaf scars. Branches more or less erect; branchlets 5-10 mm in diameter, often with apex pubescent, covered with paired straight spines 2-12 mm long, 0.5-2 mm in diameter at the base, pubescent when young. *Leaves* confined to the apices of the branchlets, shortly petiolate; petiole 1-5 mm long; blade subcoriaceous, dark green above and with midrib pale green, pale green beneath when fresh, papery when dried, ovate to obovate or narrowly so, 2.25-4 × as long as wide, 3.5-8 × 1-2.5 cm, obtuse to rounded at the apex, cuneate at the base, glabrous to sparsely pubescent with short hairs above, densely pubescent to glabrous and often with midrib sparsely pubescent beneath, with midrib and secondary veins prominent, with revolute margin; secondary veins in 14-35 pairs, straight at the base, upcurved at the apex, forming an angle of 45-85° with the costa; tertiary venation reticulate, sometimes hidden by the indumentum. *Inflorescence* pedunculate, congested, 12-37 × 3.5-7.5 cm, 2-13-flowered or more. Peduncle terete, 30-320 × 2-4 mm, sparsely pubescent; pedicels 6-26 mm long, pubescent. Bracts narrowly ovate,

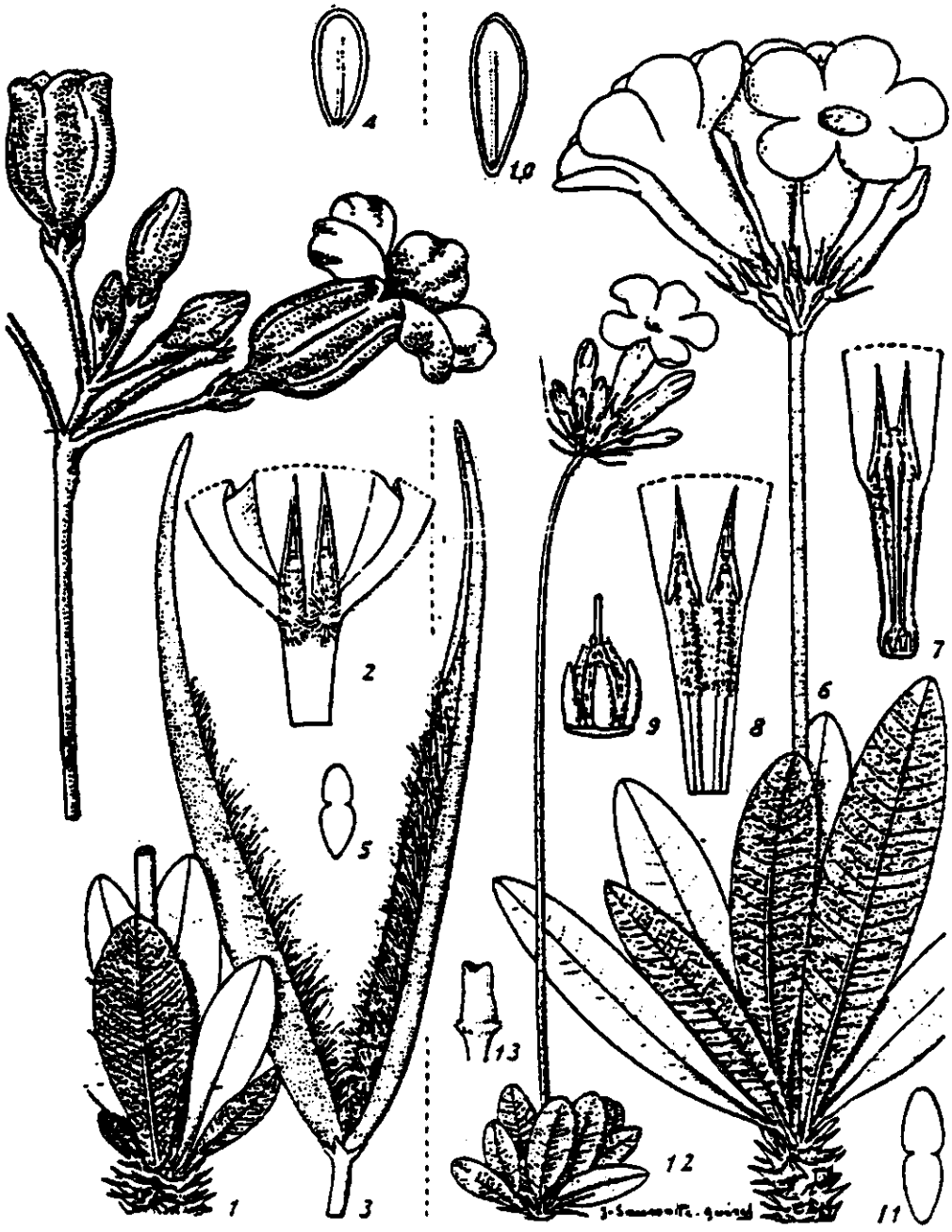
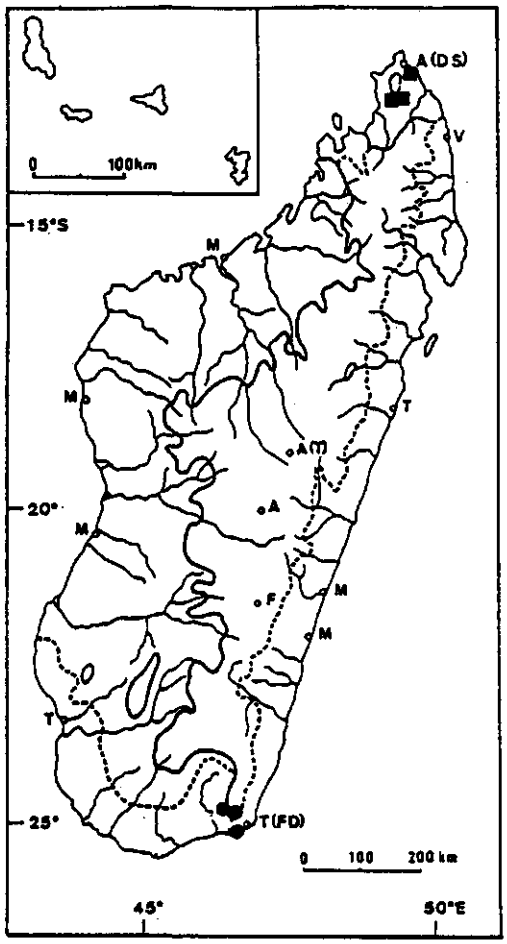
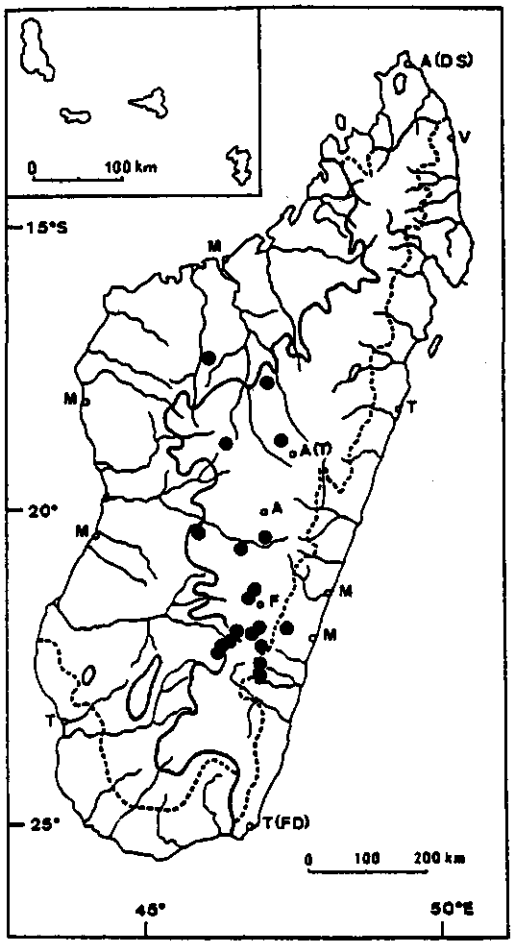


Figure 4. 1-5) *Pachypodium horombense*: 1 = habit (× 2/3), 2 = corolla inside with stamens (× 2), 3 = fruit (× 2/3), 4 = grain (× 3), 5 = embryo (× 3). 6-11) *P. rosulatum*: 6 = habit (× 2/3), 7 = corolla inside with stamens and pistil (× 2), 8 = corolla inside with stamens (× 2), 9 = ovary and disk (× 6), 10 = grain (× 3), 11 = embryo (× 3). 12 and 13) *P. cactipes*: 12 = habit (× 2/3), 13 = pistil head (× 8) (1 = from Seyrig 302; 2 = from Perrier de la Bâthie 16536; 3-5 = from Humbert 2947; 6-11 = from Perrier de la Bâthie 15065; 12 and 13 = from Decary 10643).



Map 3. • *Pachypodium cactipes*, ▪ *P. decaryi*.



Map 4. *Pachypodium densiflorum*.

6.7-12.5 × as long as wide, 10 × 0.8-1.5 mm, pubescent on both sides. *Flowers*: *Sepals* narrowly or very narrowly ovate, 3-5.5 × as long as wide, 5-12 × 1.5-2 mm, acute, pubescent outside, glabrous inside. *Corolla* limb pale yellow outside, bright yellow inside, tube with basal part pale yellowish-green and upper part pale yellow outside, and with dark red lines at the base for two thirds, 27-38 mm long in the mature bud and forming a comparatively wide broadly ovoid head 0.37-0.48 of the bud length, 10-16 × 7-10 mm, obtuse at the apex, pubescent outside, but less dense than the sepals and glabrous on the parts of the lobes covered in bud, pubescent belt inside 2-3 mm wide just below the insertion of the stamens, otherwise glabrous; tube infundibuliform, 2.7-4.7 × as long as the calyx, 0.8-1.25 × as long as the lobes, 18-30 mm long, basal part almost cylindrical, 0.17-0.23 of the length of the entire tube, 4-7 mm long and 2-3.5 mm wide, upper part obconical, 14-23 mm long, 9-13 mm wide at the mouth; lobes obliquely obovate, 0.7-1.22 × as long as the tube, 1-1.5 × as long as wide, 15-24 × 14-25 mm, rounded at the apex. *Stamens* with apex 9-16 mm below the mouth of the corolla tube, inserted 0.2-0.33 of the length of the corolla tube, at 6-7 mm from the base; anthers very narrowly triangular, 5.4-9 × as long as wide, 6.5-9 × 1-1.5 mm, pubescent inside at the base of the connective just below where they cohere with the pistil head. *Pistil* 9-11 mm long; ovary 1.7-2 × 1.5-2 × 1.2-1.6

mm, pubescent, disk composed of 5 broadly ovate retuse glands, 1.4-1.7 mm high, 2 of which or 2 pairs of which may be partly or entirely fused and which are as long as the ovary; style 6.4-8 mm long, sparsely pubescent at the base; pistil head 1-1.3 mm high, composed of an obconical basal part 0.5-0.7 × 0.4-0.6 mm, a ring-shaped central part 0.3-0.35 × 0.5-0.8 mm and a stigmoid apex 0.2-0.25 × 0.3-0.5 mm. Ovules approximately 50 in each carpel. *Fruit* of 2 separate mericarps, sometimes only one developing (sometimes flowers and fruit on the same inflorescence), forming an angle of 10-60°; mericarps medium brown, with longitudinal lines outside, whitish inside when dried, 55-140 × 2.5-4 × 2-3 mm, acute to obtuse at the apex, pubescent; wall 0.5-1 mm thick. *Seeds*: grain pale brown, elliptic, 6-10 × 2-2.3 mm, with margin revolute towards the hilar side; testa with excrescences on the hilar side, smooth at the other; coma whitish or straw-coloured, 8-20 mm long. Embryo 7-9 mm long; cotyledons broadly obovate, 2.3-2.5 × as long as wide, 3.5-5 × 1.5-2 mm, with apex and base rounded; rootlet 0.8-0.9 × as long as the cotyledons, 3.2-4 × 1.3-1.5 mm.

DISTRIBUTION. Endemic to Madagascar.

ECOLOGY. Low open deciduous, dry, southern forest and scrubland on gneissic and granitic rocks. Alt. 2-1800 m. Flowering mainly July-October and fruiting September-December.

Specimens examined:

MADAGASCAR. Toliara: near Fort-Dauphin, *Catat* 4343 (P); ibid., *Cloisel* 52 (BM); ibid., *Ralimanana et al.* 9 May 1997 (TAN); ibid., *Röösli & Hoffmann* 77/96 (BR, K, MO, P, TAN, WAG, ZSS); ibid., *Supthut* 96703 (P); Ifarantsa, *Humbert* 6006 (A, P, US); Upper Manambolo R. valley, *Decary* 9394 (GB, P); middle Mandrare R. valley, *Decary* 4594 (P, S); Amboasaritelo, *Decary* 10514 (BM, C, G, P, PRE, US); Andrahomana, *Decary* 3163 (G, P); Ifanjahirana, *Decary* 10643 (P, type of *P. rosulatum* var. *delphinense*); near Imonty, *Humbert* 14071 (P); ibid., *Leandri* 4265 (P) & 4269 (P); Cap Ste Marie, *Leandri* 4177 (P); Berohanga, near Tranomaro, *Rakotoniaina* RN 2118 (P); ibid., *Seyrig* 853 (P); near Maromiandra, Andohahela Res., parcelle 2, *Phillipson* 2916 (BR, K, MO, P, TAN, WAG); Beravi interior, *Hildebrandt* 3114 (BM, G, K, LE, M, P, W, Z, type); Mts Ambohibato, *Grandidier* 16 Oct. 1901 (P). Sin.loc. *Alluaud* 88 (P, type of *P. rosulatum* var. *stenanthum*).

CULT. Madagascar, Antananarivo, Timbazaza Park, *Dorr & Barnett* 3175 (P). South Africa, Pretoria Bot. Garden, *Hardy* 2916 (PRE). Netherlands, Wageningen Bot. Garden, *van Veldhuizen* 1345 (WAG). Switzerland, Zürich, from near Fort-Dauphin, *Leeuwenberg & Rapanarivo* 14654 (WAG); ibid., *Röösli* s.n. (ZSS 5393).

NOTES. *Röösli & Hoffmann* 77/96 grows on gneiss with soil with pH c. 4.5 (measured by Röösli).

P. cactipes, *P. gracilius* and *P. rosulatum* are very closely allied. The three species can be distinguished from each other according to numbers 16 and 17 of Key 2, although with some difficulty.

Intermediate specimens:

Decary 2351 (P) collected near Morafenobe, Mahajanga, west Madagascar, has a corolla tube 4 × as long as the calyx, 1.23 × as long as the lobes and spines 5 × 2 mm. These characters it has in common with *P. rosulatum*, recognised as species in this publication. The corolla tube is 16 mm long and its basal part 3 mm long by which it resembles *P. gracilius*. Therefore it is an almost perfect intermediate between these two species.

Humbert 12004 (K, P) collected in Kalambatritra, Toliara (SE), has a corolla tube

2.7-3 × as long as the calyx, sepals 9-12 mm long and spines 5-10 × 0.4-1.5 mm, characters almost as in *P. cactipes* but the following characters it has in common with *P. rosulatum*: basal part of the corolla tube 8-9 mm long, anthers 9.5 × 1.8 mm, pistil 15.5 mm long and the pubescent belt 7 mm wide just below the insertion of the stamens. So it cannot be placed in one of these two species as distinguished at present.

Perrier de la Bâthie 8919 (P) collected between Maningoza and Ranobe, Mahajanga (W), has a corolla tube 3.5-3.8 × as long as the calyx, 1.36-1.6 × as long as the lobes and spines 3-6 × 1-3 mm. These characters bring it to *P. rosulatum*, but the 19-21 mm long corolla tube, the 3 mm wide pubescent belt below the insertion of the stamens, the 6.1 mm long style bring it to *P. cactipes*. Therefore this specimen has characters from both *P. cactipes* and *P. rosulatum*.

The intermediate specimens, often collected between the areas of distribution of *P. cactipes*, *P. gracilius* and *P. rosulatum* may illustrate that these species may represent mere forms of a single complex species *P. rosulatum*. For the time being, it is preferred to await more field studies. The information on ecology may elucidate more on the distinction of these 3 species.

6. **Pachypodium decaryi** Poiss. in Bull. Acad. Malgache sér. 2, 3: 235 (1922); Perrier de la Bâthie in Bull. Soc. Bot. Fr. 81: 307 (1934); Pichon in Mém. Inst. Sc. Madag. sér. B, 2: 112 (1949); Markgraf, Fl. Madag. fam. 169: 287 (1976). Type: Madagascar, Antsiranana, Ankarana, *Humbert* 32527 (neotype P, designated by Markgraf). Fig. 5, p. 25; Map 3, p. 22; Plate 14, opposite p. 32; Plates 15-18, opposite p. 33.

Shrub 2-4 m high; trunk subglobose or bottle-shaped; bark pale grey, smooth. Branches not spiny; branchlets 3-9 × 0.5-0.6 cm, at the apex with rare red or dark brown, short or minute, paired straight spines, 1-3 mm long, sometimes lacking. *Leaves* confined to the apices of the branchlets, petiolate; petiole 3-10 mm long, sparsely pubescent to glabrous; blade green, glossy above, pale green beneath with darker reticulate venation (sometimes young leaves reddish-green) when fresh, papery when dried, ovate to oblong or narrowly so, 2-3 × as long as wide, 3-12 × 1.5-5 cm, acuminate at the apex, cuneate at the base or decurrent into the petiole, glabrous above, sometimes with margin sparsely pubescent and with impressed venation, sparsely pubescent beneath especially on veins and with midrib and secondary veins prominent; with 13-36 pairs of secondary veins straight at the base, upcurved at the apex, forming an angle of 45-90° with the costa; tertiary venation reticulate. *Inflorescence* sessile or shortly pedunculate, congested, 6-13.5 × 8.5-13 cm, 1-7-flowered. Peduncle 0-7 × 2-4 mm, glabrous; pedicels 8-18 mm long, glabrous, sometimes lenticellate in fruit. Bracts ovate to oblong, 3.5-7 × as long as wide, 7-14 × 2 mm, acuminate at the apex, glabrous on both sides. *Flowers*: *Sepals* with reddish-brown edges, connate at the base for about 0.5 mm, ovate, 1.5-1.75 × as long as wide, 6-7 × 4-4.3 mm, acuminate at the apex, glabrous on both sides. *Corolla* lobes white inside, sometimes with reddish-brown edge on the part not covered in bud outside, tube pale reddish-green outside, 6.8-10.3 cm long in the mature bud and forming a comparatively wide broadly ovoid head 0.46-0.51 of the bud length, 3.2-5.3 × 0.8-1.1 cm, obtuse at the apex, and glabrous outside, with pubescent belt inside 2-5 mm wide just below the insertion of the stamens, otherwise glabrous; tube 8.57-13.33 × as long as the calyx, 0.92-1.7 × as long as the lobes, 4-6 cm long, basal part almost cylin-

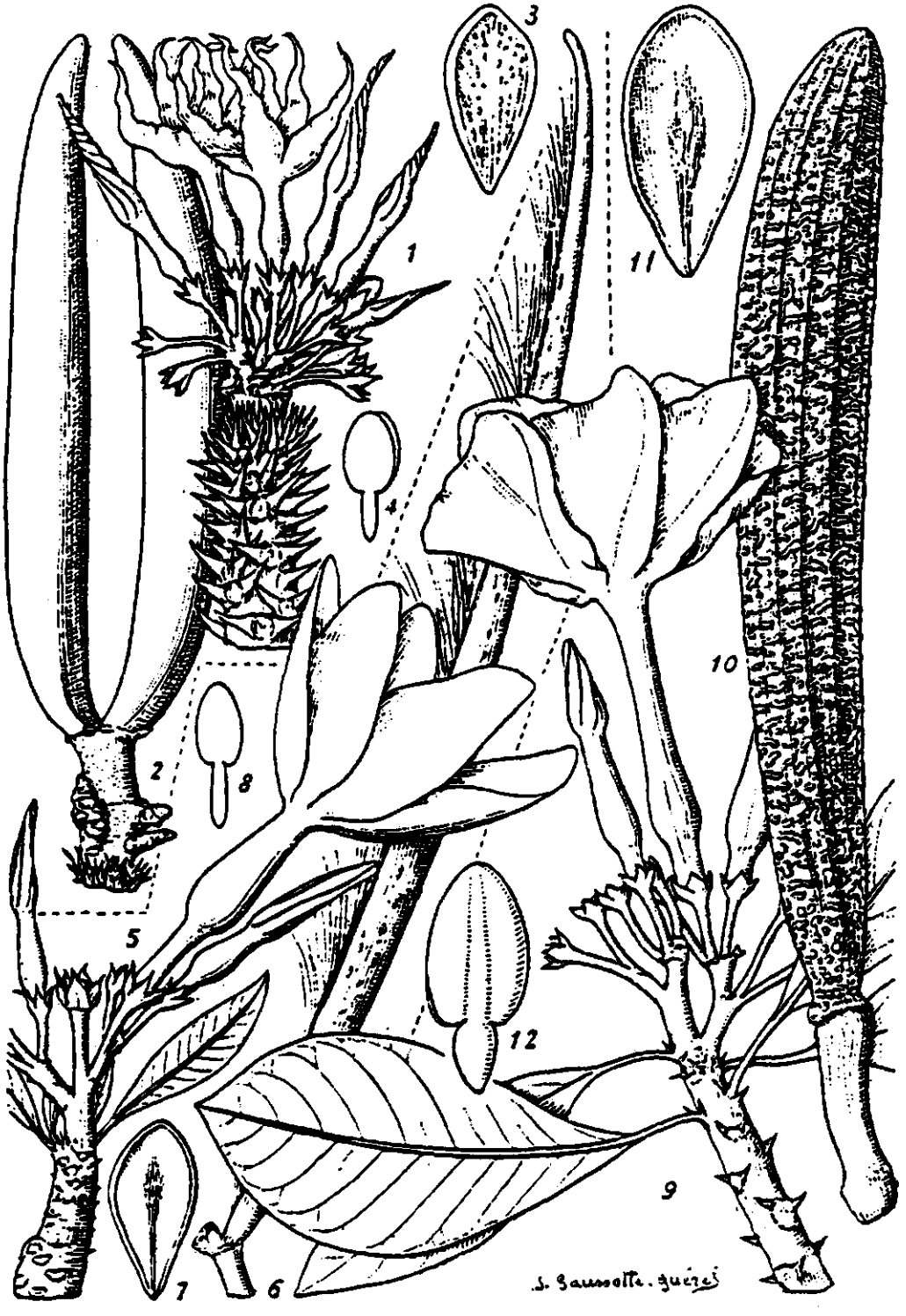


Figure 5. 1-4) *Pachypodium meridionale*: 1 = habit (× 2/3), 2 = fruit (× 2/3), 3 = grain (× 2), 4 = embryo (× 2). 5-8) *P. decaryi*: 5 = habit (× 2/3), 6 = fruit (× 2/3), 7 = grain (× 2), 8 = embryo (× 2). 9-12) *P. sofiense*: 9 = habit (× 2/3), 10 = fruit (× 2/3), 11 = grain (× 2), 12 = embryo (× 2) (1 = from Perrier de la Bâthie 18320; 2-4 = from Boiteau s.n.; 5-8 = from Capuron SF 18981; 9 = from Perrier de la Bâthie 1142; 10-12 from Humbert 11481).

drical, 0.25-0.35 of the length of the entire tube, 14-18 × 4-6 mm wide, upper part conical, 26-42 mm long and 7-10 mm wide at the mouth; lobes obliquely ovate, 0.56-0.78 × as long as the tube, 1.8-2 × as long as wide, 32-45(-65) × 16-23(-32) mm, acute or obtuse at the apex. *Stamens* with apex 1.9-2.3 cm below the mouth of the corolla tube, inserted 0.32-0.4 of the length of the corolla tube, at 2-2.6 cm from the base; anthers very narrowly triangular, 5.35-6.25 × as long as wide, 12.5-15 × 2-2.8 mm, pubescent inside at the base of the connective just below where they cohere with the pistil head. *Pistil* 21.5-22.5 mm long; ovary 3-3.5 × 2.5-3 × 2-2.5 mm, glabrous; disk 1.5-1.7 mm high, 5-lobed, with lobes rounded at the apex which are almost half as long as the ovary; style 17.45-17.65 mm long; pistil head 1.05-1.35 mm high, composed of an obconical basal part 0.6 × 1 mm, a ring-shaped central part 0.4 × 1.4 mm and a stigmoid apex 0.25 × 0.8 mm. Ovules approximately 50 in each carpel. *Fruit* of 2 separate mericarps, sometimes only one developing, with an angle of 30-90° at the base; mericarps pale to medium brown, with longitudinal lines outside, whitish inside when dried, 9-22.5 × 0.8-1 × 0.7-1 cm, obtuse, shortly curved at the apex or not, lenticellate, glabrous; wall 1 mm thick. *Seeds:* grain pale to medium brown with margin dark brown, elliptic to ovate, 10-12 × 4-5 mm, thickened at the margin on the both sides; testa smooth to minutely rough; coma straw-coloured, 2.5-3.2 cm long. Embryo whitish, 9-10 mm long; cotyledons obovate to elliptic, 1.5 × as long as wide, 5.5-6 × 3.8-4 mm, rounded at the apex, cordate at the base; rootlet 0.66-0.69 × as long as the cotyledons, 3.8-4 × 2.5-2.8 mm.

DISTRIBUTION. Endemic to Madagascar.

ECOLOGY. Low open deciduous western forest on Mesozoic calcareous rocks. Alt. 30-350 m. Flowering mainly April-June, fruiting October-November.

Specimens examined:

MADAGASCAR. Antsiranana: Montagne des Français, *Cremers* 2643 (TAN); ibid., *Röösli* s.n. (ZSS 15140); ibid., *Supthut & von Arx* 9308 (G, P, TAN); km 7 Diego-Suarez to Ramena, *Rauh & Heidelberg* 7040 (M); Ankarana Res., *Humbert & Cours* 32527 (P, neotype); ibid., *Jongkind & Rapanarivo* 942 (PRE, TAN, WAG); ibid., *Lewis et al.* 1139 (P); ibid., *Rakotozafy* 1568 (TAN); Andranonakoho R., Ankarana, *Capuron* SF 18981 (P, TEF); Andranonakoho, km 103 Diego-Suarez to Ambilobe Road, *Cours & Humbert* 5529 (P). Sin.loc. *Homolle* 260 (P).

NOTES. *Jongkind & Rapanarivo* 982 near Campement des Anglais, Ankarana Res. grows on calcareous rocks in low open forest. It is found with *Pandanus parkinsonii* Martelli (Pandanaceae), *Ficus reflexa* Thunb. subsp. *reflexa* (Moraceae) and many other species.

P. decaryi is the least spiny species in this genus. The branchlets are whithout or only with minute spines at the apex.

7. **Pachypodium densiflorum** Baker in Journ. Linn. Soc. Bot. 22: 503 (1887); Costantin & Bois in Ann. Sc. Nat. sér. 9, 6: 321 (1907); Perrier de la Bâthie in Bull. Soc. Bot. Fr. 81: 302 (1934); Pichon in Mém. Inst. Sc. Madag. sér. B, 2: 119 (1949); Pernet in Mém. Inst. Sc. Madag. sér. B, 8: 12 (1957); Markgraf, Fl. Madag. fam. 169: 296 (1976). Type: Madagascar, sin. loc., *Baron* 4246 (holotype K; isotype P). Fig. 3, p. 18; Map 4, p 22; Plates 19-23, opposite p. 40.

Heterotypic synonyms

P. densiflorum var. *brevicalyx* H. Perrier in Bull. Soc. Bot. Fr. 81: 303 (1934);

P. brevicalyx (H. Perrier) Pichon in Mém. Inst. Sc. Madag. sér. B, 2: 120 (1949); Markgraf op. cit. 299, **syn. nov.** Type: Madagascar, Mahajanga, Mahakamba R. valley, basin of Mahavavy R. W, *Perrier de la Bâthie* 8862 (holotype P).
Pachypodium × *rauhii* Halda, Cactaceae etc. 3: 108-111 (1997), **syn. nov.** Type: Madagascar, Fianarantsoa, Itremo Mts, Halda 951206 (herb. Halda, n.v.).

Undershrub 10-50 cm high; trunk cactus-like, 10-20 × 4-40 cm; bark pale grey-green, smooth, glossy, 3-5 mm thick; wood greenish. Branches 5-10 cm in diameter; branchlets 0-20 × 1-3 cm, covered with paired straight spines 5-13 mm long, 1.5-3 mm in diameter at the base, basal part conical, laterally compressed, 0.3-0.4 of the spine length. *Leaves* confined to the apices of the branchlets, sessile or shortly petiolate; petiole 0-5 mm long, pubescent; blade herbaceous, medium green, with midrib pale green and shiny above, pale glaucous and with medium green reticulate venation beneath when fresh, papery when dried, ovate to obovate or narrowly so, 1.7-3 × as long as wide, 2-6 × 1-2.5 cm, acuminate to rounded at the apex, cuneate to rounded at the base or decurrent into the petiole, sparsely pubescent to glabrous above and with impressed venation, densely pubescent to almost glabrous beneath, with midrib and secondary veins prominent; with 20-45 pairs of secondary veins, straight at the base, upcurved at the apex, forming an angle of 45-85° with the costa; tertiary venation reticulate, often hidden by the indumentum. *Inflorescence* pedunculate, congested, 6-53 × 2-4.5 cm, 1-10-flowered. Peduncle terete, 30-500 × 3-5 mm, pubescent to sparsely so; pedicels 0-14(-24) mm long, pubescent or sparsely so. Bracts sometimes persistent, obovate, 2-3.5 × as long as wide, 7-12 × 2-6 mm, acuminate at the apex, pubescent outside, sparsely pubescent inside. *Flowers*: *Sepals* pale green with darker green margin, connate at the base for about 0.5 mm, ovate, 1.3-3.33 × as long as wide, 3-9.5 × 1.8-4 mm, under the fruit up to 6 mm wide, acuminate at the apex, pubescent outside, glabrous inside. *Corolla* bright yellow, 12-22 mm long in the mature bud and forming a comparatively wide broadly ovoid head 0.3-0.46 of the bud length, 5-10 × 5-9 mm, obtuse at the apex, pubescent outside but often less dense so than the sepals, glabrous on the parts of the lobes covered in bud, pubescent belt inside 1.5-2 mm wide just below the insertion of the stamens, otherwise glabrous; tube funnel-shaped, 1.8-2.8(-3.33) × as long as the calyx, 0.8-1.5 × as long as the lobes, 9-16 mm long, basal part almost cylindrical, 0.55-0.7 of the length of the entire tube, 6-9 mm long, 2-5.5 mm wide above the base, upper part 3-7 mm long and 5-7 mm wide at the mouth; lobes obliquely and broadly obovate to broadly ovate, 0.9-1.3 × as long as the tube, 1-1.3 × as long as wide, 8-14 × 6.5-11 mm, rounded at the apex, undulate. *Stamens* with apex 2-3 mm above the mouth of the corolla tube, inserted 0.55-0.7 of the length of the corolla tube, at 6-9 mm from the base; anthers narrowly triangular, 3.3-6 × as long as wide, 5-6 × 1-1.8 mm, pubescent inside at the base of the connective just below where they cohere with the pistil head. *Pistil* 10.8-14.2 mm long; ovary 1.8-2 × 1.8-2 × 1.5-1.9 mm, pubescent; disk composed of 5 broadly ovate rounded glands, 2 or 2 pairs of which may be partly or entirely fused and which are slightly more than half as long as the ovary; style 8-11 mm long, sparsely pubescent at the base; pistil head 1-1.1 mm high, composed of an obconical basal part 0.7-0.8 × 0.5 mm, a ring-shaped central part 0.1-0.15 × 0.7-0.9 mm and a stigmoid apex 0.2 × 0.6-0.7 mm. Ovules approximately 50 in each carpel. *Fruit* of 2 separate mericarps, forming an angle of 10-60° at the base (sometime flowers and fruit on the same inflorescence); mericarps erect, immature light green, suffused with dark red when fresh, pale to dark brown and with longitudinally lines when dried, narrowly fu-

siform, 55-180 × 4-10 × 4-6 mm, obtuse to acute at the apex, pubescent; wall 1 mm thick. *Seeds*: grain pale brown, ovate to elliptic, 4.4-6 × 1.8-3 mm; margin revolute towards the hilar side; testa smooth; coma straw-coloured, 10-17 mm long. Embryo thin, 3.8-4.3 mm long; cotyledons ovate, 1.25-1.38 × as long as wide, 1.5-2 × 1-1.6 mm, rounded at the apex, subcordate at the base; rootlet 1.11-1.15 × as long as cotyledons, 2-2.3 × 0.8-1.4 mm.

DISTRIBUTION. Endemic to Madagascar.

ECOLOGY. Evergreen sclerophyllous (*Uapaca*) woodland and savanna on granitic, gneissic or quartzitic rocks. Alt. 200-1750 m. Flowering mainly July-October and fruiting mainly August-November.

Vernacular name: Somo, Somy, somoy or Votaka (Betsileo), Salotra (Sakalava).

Specimens examined:

MADAGASCAR. Mahajanga: Makamba R. valley, basin of Mahavavy R. W, *Perrier de la Bâthie* 8862 (P, type of *P. densiflorum* var. *brevicalyx*); 17 km S of Mahatsinjo, Ankazobe-Maevatanana Road, *Leeuwenberg & Rapanarivo* 14666 (BR, P, TAN, WAG); ibid., *Hofstätter* 040990-2 (ZSS). Antananarivo: Angavo Mts, near Talata, NW of Ankazobe, *Rapanarivo* 368 (TAN); SW of Ankazobe, *Chaurin* 3432 (P); near Ankazobe, *Decary* Sept. 1921 (P); Ambohiby Mts, Tsiroanamandidy, *Descoings* 3590 (TAN, WAG); ibid., *Leandri* 1780 (P); Ibity Mts NW side, *Röösli & Hoffmann* 1/94 (ZSS). Fianarantsoa: km 236 Antananarivo-Ambositra, *Rauh* 7292 (M) & 7292/61 (M); km 2 E of Isorana, *Leeuwenberg & Rapanarivo* 14639 (BR, K, P, TAN, WAG); Itremo, *Bosser* 9715 (TAN) & 18199 (P); ibid., near Ambatofinandrahana, *Decary* 15115 (P) & 15174 (P); ibid., *Labat* 2401 (P); ibid, *Morat* 108 (TAN); between Itremo and Tampina, *Bosser* 9846 (TAN); Antonombato, 28 km S of Fianarantsoa, *von Arx & Supthut* 3037 (G, TAN, ZSS); near Ambalavao, *Decary* 15085 (P, TAN) & 15907 (P); ibid., *Descoing* 3620 (TAN); ibid., *Fosberg* 52392 (US); ibid., *Leeuwenberg & Rapanarivo* 14605 (BR, K, P, TAN, WAG); ibid., *Perrier de la Bâthie* 12582 (P); km 14 Ambalavao-Ihosy, *Leeuwenberg & Rapanarivo* 14605 (BR, K, P, TAN, WAG); km 25 of same road, *Leeuwenberg & Rapanarivo* 14611 (BR, K, P, TAN, WAG); SW of Ambalavao, *Humbert* 4891 (G, P) & 19317ter (P); ibid., *Röösli & Hoffmann* 83/96 (MO, P, WAG, ZSS); Sendrisoa Res., Ambalavao District, *Razafindrakoto* RN 1810 (P) & RN 3087 (P, TAN); 56 km E of Ihosy, *Rapanarivo et al.* 254 (TAN, WAG); Ankaramitomby, *Razafindrakoto* RN 2410 (P, TAN); Vohitsaoka Res., *Razafindrakoto* RN 3120 (P, TAN); Mts Andringitra, *Perrier de la Bâthie* 8916 (P); km 70 Ambalavao-Ihosy, *Leeuwenberg & Rapanarivo* 14612 (BR, K, P, TAN, WAG); Lamboany, *Catat* 4353 (P); near Janjina, *Morat* 3680 (P, TAN); Zazafotsy, *Decary* 1 (P); ibid., *Descoings* 3797 (TAN, WAG) & 3798 (P); ibid., *Grandidier* 9 Aug. 1898 (P), ibid., *Poisson* 674bis (P); SW of Satrokala, near Ranohira, *Röösli & Hoffmann* 57/98 (K, P, WAG); Vohibato, *Decary* 3 (P); 79 km NE of Ihosy, *von Arx & Supthut* 3076 (G, TAN, ZSS); 45 km NE of Ihosy, *Peltier* 2462 (P); 17 km NE of Ihosy, *von Arx & Supthut* 3075 (G, TAN, ZSS); Ivohibe Mt, near Ihosy R., *Perrier de la Bâthie* 8953 (P); Ambinda Mts, W of Ivohibe, *Decary* 5697 (P); near Ihosy, *Descoings* 973 (TAN) & 3604 (TAN). Sin. loc., *Baron* 4246 (K, P, type) & 6939 (K); *Camboué* 11 (P); *Capuron* SF 28904bis (P); *Deans Cowan* anno 1880 (BM, P); *Geay* anno 1909 (P); *Montagnac* 5 (P); *Perrier de la Bâthie* 16535 (P), 16535bis (P) & 16549 (K, P); Acad. Malg. anno 1904 (P).

CULT. Algeria: PQCA, from between Ambalavao-Ihosy Road, 76525 (BM); ibid., from between Antsirabe-Ambositra Road, 75791 (BM). Madagascar: Antananarivo, Tsimbazaza Park, *Dorr & Barnet* 3149 (TAN) & 3150 (TAN, WAG); ibid., Herb.

Jard. Bot. Tana. 534 (P). South Africa: sin. loc., *Hardy* 2940 (PRE).

NOTES. Some specimens have been collected with accompanying species, as listed below. Some remarks have been given on the ecology:

Leeuwenberg & Rapanarivo 14666, near Mahatsinjo, Ankazobe-Maevatanana Road, grows on stratoid granite (Besairie 1984), surrounded by grassland with lateritic soil and quartzite stones with pH c. 3.5 as measured by Röösli with 'System Stoecker', which was at the end of the flowering season in November. *P. densiflorum* is associated here with: *Ischnolepis tuberosa* Jum. & H. Perrier (Asclepiadaceae) *Leeuwenberg & Rapanarivo* 14667, *Dipcadi heterocuspe* Baker (Liliaceae) 14668, *Pentaschistis perrieri* A. Camus (Cyperaceae) 14669, *Euphorbia milii* Des Moul. (Euphorbiaceae) 14670, *Bulbostylis schoenoides* Kunth (Cyperaceae) 14671, *Pellaea goudotii* (Kunze) C. Chr. (Adiantaceae) 14672, *Tetradenia fruticosa* Benth. (Labiatae) 14673.

Leeuwenberg & Rapanarivo 14605, km 14 Ambalavao-Ihosy, near Ampitaha is surrounded by grasses dominated by *Hyparrhenia* sp. (Gramineae) and *Aristida sp.* (Gramineae) with *Catharanthus ovalis* Markgr. (Apocynaceae) 14607, and grows on steep pink granite (Besairie 1984) in association with *Euphorbia milii* Des Moul. (Euphorbiaceae), *Senecio crassissimus* Humb. (Compositae), some Cyperaceae and various other species, mainly grasses which were not identified as they were vegetative and/or dry.

Leeuwenberg & Rapanarivo 14612, km 70 Ambalavao-Ihosy road, surrounded by grasses dominated by *Aristida* sp. and *Hyparrhenia* sp., is found on granite with *Kalanchoe synsepala* Baker (Crassulaceae), *Tetradenia fruticosa* Benth. (Labiatae), *Senecio crassissimus* Humbert (Compositae), *Euphorbia milii* Des Moul. (Euphorbiaceae), *Xerophyta dasylirioides* Baker (Velloziaceae) and *Aloe accutissima* H. Perrier (Aloaceae).

Leeuwenberg & Rapanarivo 14611, km 25 Ambalavao-Ihosy grows on granitic rocks surrounded by grasses (pseudosteppe) dominated by *Aristida sp.* and *Hyparrhenia sp.* with scattered woody plants such as *Ziziphus* sp. (Rhamnaceae), *Sclerocarya* sp. (Anacardiaceae). It is accompanied by *Xerophyta dasylirioides* Baker (Velloziaceae), *Aloe acutissima* H. Perrier (Aloaceae) and other species. It is rather large for the species: 50 cm high, base 30 cm in diameter and crown 2 × 1.5 m.

Röösli & Hoffmann 1/94 from Ibity grows on quartzite (Besairie 1984) with soil of pH c. 4.5.

Sterile *P. densiflorum* and *P. horombense* are similar but flowering they are clearly distinguished. *P. densiflorum* has exserted stamens, a funnel-shaped corolla tube and undulate lobes. *P. horombense* is characterised by included stamens, a tube with upper part widely urceolate and with 5 again widened parts below the lobes and therefore seemingly 5-winged inside and suberect lobes.

We have seen that all specimens observed here from Ibity to near Ihosy have leaves densely pubescent beneath, and between Ankazobe and Kandreho they are sparsely pubescent to almost glabrous (*Chaurin* 3432, *Leeuwenberg & Rapanarivo* 14666 and *Rapanarivo* 368). Usually the leaves appear with or after the flowers. They reach the maximum size at the end of flowering or fruiting seasons. The inflorescence is congested in the beginning and has short pedicels, but when the axis starts to lengthen, the pedicels at the base become longer and the inflorescence is more open.

The pedicels vary from 0 to 24 mm long. Those of *Perrier de la Bâthie* 8862, the type of *P. densiflorum* var. *brevicalyx*, vary from 7 to 24 mm. The sepals vary from 3 to 9.5 mm long. Those of *Perrier de la Bâthie* 8862 are 3 mm long. There is a con-

tinous variation in sepal length from 3 mm in *Perrier de la Bâthie* 8862, the type of var. *brevicalyx*, to 9.5 mm. Therefore the var. *brevicalyx* based on the sepal characters is not maintained here.

When we studied the publication of Halda, we observed that the first and third photographs are of *Pachypodium densiflorum* with the branchlets, long peduncles and exserted stamens. The drawing and the second photograph are of *P. brevicaule* with a flat tuberous trunk, densely crowded spines and leaves, short peduncles and included stamens. The description of the type of *P.* × *rauhii* refers to *P. densiflorum*, while he also gives in an other part a short description of *P. brevicaule*. Therefore it appears that the supposed hybrid has been selected from a population of *P. densiflorum* growing together with one of *P. brevicaule*. Unfortunatelly it was not possible to get the type specimen on loan.

The photographs in Rauh (1995) as *P. brevicaule* Figures 468 and 469 only have shorter peduncles than the one on Figure 471. The variation shown here falls within that of the species. The putative hybrid (Fig. 471) of *P. brevicaule* and *P. densiflorum* therefore is pure *P. brevicaule*.

8. **Pachypodium eburneum** Lavranos & Rapanarivo in Cactus and Succculent Journ. 69: 227-231 (1997). Type: Madagascar, Antananarivo, Mt Ibity, S of Antsirabe, *W. Rööslí & R. Hoffmann* 1/96 (holotype P; isotypes MO, TAN, WAG, ZSS). Fig. 6, p. 31; Map 5, p. 32; Plates 24-27, opposite p. 41.

Homotypic synonym
P. rosulatum var. *eburneum* (Lavranos & Rapanarivo) G.D. Rowley in Bradleya 16: 101 (1998) and Pachypodium & Adenium, The Cactus File Handbook 5: 57 (1999), **syn. nov.**

Succulent shrub 20-40 cm high, base subglobose, up to 20 cm in diameter; bark grey-green, smooth; branches thick, erect or spreading, up to 18 cm long, 5-8 cm in diameter and tapering to 3 cm, often unarmed and with leaf scars in their lower part and in the apical part spiny; branchlets short, 0.5-3 cm long, 1.6-3 cm in diameter, covered with paired straight spines, 5-16 mm long, 2-4 mm in diameter at the base, basal part conical 0.4-0.5 of the spine length and upper part needle-like, pubescent when young. *Leaves* sessile or shortly petiolate, confined to the apices of the branchlets; petiole 0-2 mm long, blade medium green and with pale green midrib above, pale green beneath when fresh; papery when dried, ovate to obovate, 2-3.5 × as long as wide, 3.5-8.5 × 1.5-3.5 cm, shortly acuminate to apiculate at the apex, cuneate at the base, with impressed venation and sparsely pubescent above, pubescent beneath sometimes less so on midrib and margin; with 30-45 pairs of rather straight secondary veins forming an angle of 45-90° with the costa; tertiary venation reticulate, often hidden by the indumentum. *Inflorescence* pedunculate, congested, 45-55 × 6.5-10 cm, 3-12-flowered. Peduncle terete, pale green, 25-50 × 0.3-0.5 cm; sparsely pubescent; pedicels pale green, 3-6 × 1.5 mm, lengthening after anthesis to 15 mm (Lavranos), pubescent. Bracts pale green, obovate, 4-4.5 × as long as wide, 13 × 3 mm, pubescent outside, less so inside. *Flowers*: *Sepals* pale green, longer than the basal part of the corolla tube, narrowly ovate, 2.33-3.33 × as long as wide, 7-11 × 3-4(-5) mm, acuminate at the apex, pubescent outside, glabrous to very sparsely pubescent inside. *Corolla* cream, but usually lemon-yellow inside the tube; 3 cm long in the mature bud

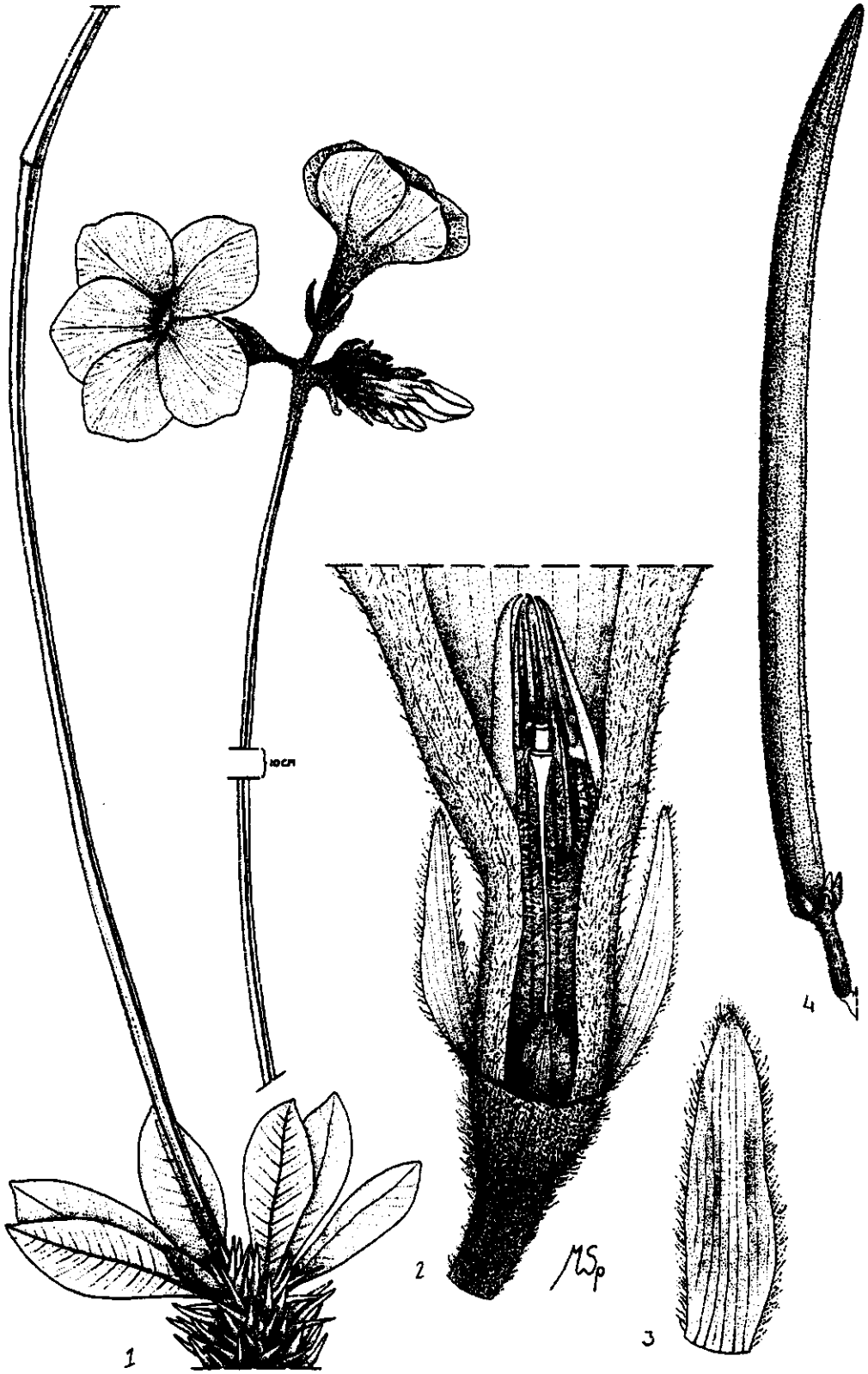
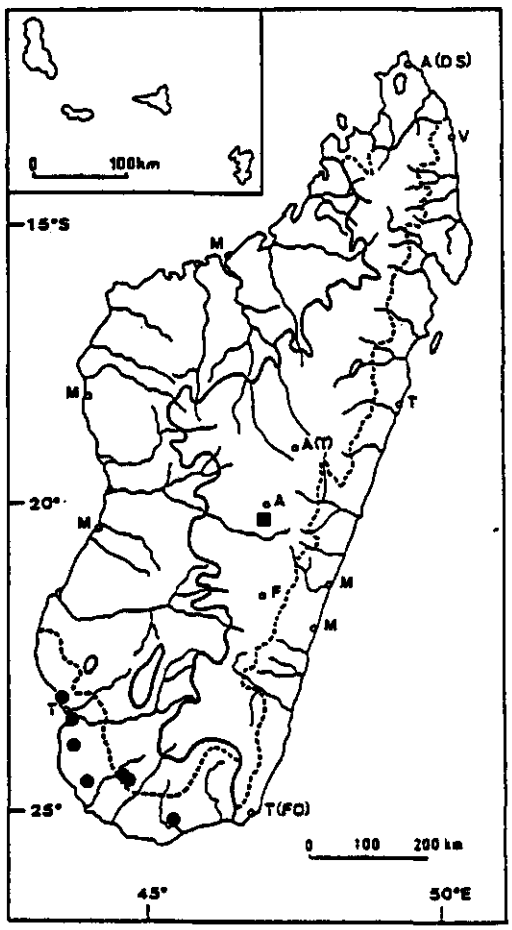
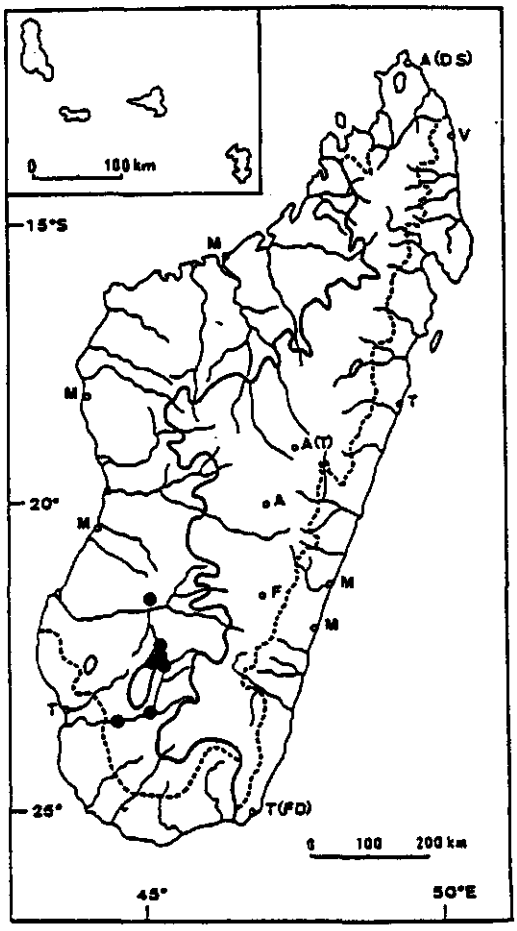


Figure 6. *Pachypodium eburneum*: 1 = habit (× 1), 2 = opened flower (× 6), 3 = sepal inside (× 6), 4 = fruit (× 1) (1 = from Razafindratsira ZSS 15127; 2-3 = from Razafindratsira ZSS 15125; 4 = from Razafindratsira ZSS 16659).



Map 5. ▪ *Pachypodium eburneum*, • *P. geayi*.



Map 6. *Pachypodium gracilius*.

and forming a comparatively wide broadly ovoid head, 0.4 of the bud length, 12 × 7 mm, obtuse at the apex, pubescent outside, glabrous on the part of the lobes covered in bud, pilose-pubescent belt inside 1-3 mm wide just below the insertion of the stamens, with pubescent stripes or not below down to the base, otherwise glabrous; tube infundibuliform, 1.6-3 × as long as the calyx, 0.85-1.1 × as long as the lobes, 16-20 mm long, basal part almost cylindrical, 0.3-0.38 of the length of the entire tube, 5-7 mm long, 3-4 mm wide, upper part obconical, 10-13 mm long, 6-10 mm wide at the mouth; lobes obliquely obovate, 1.1-1.2 × as long as the tube, 1.1-1.15 × as long as wide, 16-22 × 14-20 mm, obtuse at the apex, undulate. *Stamens* with apex 3-5 mm below the mouth of the corolla tube, inserted 0.38-0.42 of the length of the corolla

Plate 11. *Pachypodium cactipes*.
Plate 12. *Pachypodium cactipes*, W of Fort-Dauphin.
Plate 13. *Pachypodium cactipes*.
Plate 14. *Pachypodium decaryi*.

11 | 14
12 |
13

tube, at 7-8 mm from the base; anthers 4-7 × as long as wide, 7-9 × 1-2 mm, pubescent with stiff hairs inside at the base of the connective just below where they cohere with the pistil head. *Pistil* 11 mm long; ovary subglobose, 1.5-2 × 1.5 × 1.2 mm, pubescent; disk of 5 glands, 2 or 2 pairs of which partly or entirely fused, ovate, 1.8 mm high, acuminate at the apex, more than half as long as the ovary; style cylindrical, 8.2 mm long, sparsely pubescent; pistil head 0.8 mm long, composed of an obconical part about 0.5 × 0.4 mm, a ring-shaped central part 0.2 × 0.6 mm and a stigmoid apex 0.1 × 0.4 mm. *Fruit* of 2 separate mericarps, sometimes only one developing; mericarps pale to medium brown, with longitudinal lines outside, whitish inside, fusiform, 100 × 8 × 5 mm, pubescent with short hairs, obtuse at the apex; wall 1 mm thick. *Seeds*: grain unknown; coma whitish to straw-coloured, 9-10 mm long.

DISTRIBUTION. Endemic to Madagascar.

ECOLOGY. Evergreen sclerophyllous (*Uapaca*) woodland on quartzitic rocks. Alt. c. 1700 m.

Paratypes:

MADAGASCAR. Antananarivo, Mt. Ibity, *Razafindratsira* 31 Mar. 1994 (ZSS 15128).

CULT. Madagascar: Antananarivo, Bot. Garden, *Razafindratsira* 27 Apr. 1994 (ZSS 15127). Switzerland: Zürich, Bot. Garden, *Röösli* 17 Jul. 1995 (ZSS 16659).

NOTES. *Röösli & Hoffmann* 1/96 grows on quartzitic rocks with soil c. pH 4.5 (measured by Röösli) and found in association with a.o. *Aloe trachyticola* H. Perrier (Aloaceae), *A. silicicola* H. Perrier and *A. cremersii* Lavranos.

P. eburneum has affinities to *P. inopinatum* but differs clearly by its longer and thicker spines 5-16 mm long, 2-4 mm wide at the base instead of 3-6 mm long and 0.5-1.5 mm wide at the base in *P. inopinatum*. The basal part of the corolla tube of *P. inopinatum* is longer than the upper part. Vegetatively *P. eburneum* can be confused with *P. densiflorum*, that has exserted stamens instead of the included ones of *P. eburneum*.

9. **Pachypodium geayi** Costantin & Bois in Ann. Sc. Nat. sér. 9, 6: 315 (1907); Poisson in Bull. Acad. Malgache sér. 2, 6: 160, pl.2 (1924); Perrier de la Bâthie in Bull. Soc. Bot. Fr. 81: 307 (1934); Pichon in Mém. Inst. Sc. Madag. sér. B, 2: 115 (1949); Markgraf, Fl. Madag. fam. 169: 287 (1976). Type: Madagascar, Toliara, between Mandrarano and Malandry, *Geay* 6064 (holotype P†). Neotype: Madagascar, Tuléar (= Toliara), Mont Eliva Mahafaly Region, *Poisson* 648 bis, 12 Avr.1922 (neotype P, designated here, cited as holotype by Markgraf). Fig. 1, p. 11; Map 5, p. 32; Plates 28-31, opposite p. 56.

Candelabrum-shaped tree, 4-7 m high; trunk cigar- or bottle-shaped, 3-6 m long, 15-30 cm in diameter at the base, gradually thickened above up to 40-80 cm, nar-

16
15 | 18
17

Plate 15. *Pachypodium decaryi*.
Plate 16. *Pachypodium decaryi*.
Plate 17. *Pachypodium decaryi*.
Plate 18. *Pachypodium decaryi*.

rowed again towards the apex; bark grey, grey-green or pale brown, smooth or with leaf scars, 5-6 mm thick, medium green on section; sapwood greenish; branched after, first flowering; branchlets 2.5-3 cm in diameter, often with white-pubescent apex covered with groups of 3 subequal straight spines, 1.5-20(-50) mm long, 1-3 mm in diameter at the base, white pubescent with brown and glabrous apex when young, turning glabrous and medium to dark brown. *Leaves* confined to the apices of the branchlets, petiolate; petiole 1-4 cm long, pubescent or sparsely so; young leaves with pink-tinged midrib, blade dark glossy green above, pale green to pale grey beneath when fresh, papery when dried, narrowly ovate or very narrowly so, 5-21.5 × as long as wide, 6-43 × 1-3.5 cm, acuminate to rounded at the apex, cuneate at the base, decurrent into the petiole, with revolute margin, sparsely pubescent above and with impressed venation, densely pubescent beneath, with midrib prominent; secondary veins in 60-85 pairs, straight at the base, upcurved at the apex if conspicuous, forming an angle of 45-85° with the costa; tertiary venation reticulate, hidden by the indumentum. *Inflorescence* pedunculate, rather lax, 10-22 × 5-17 cm, 6-25-flowered. Peduncle pale green, laterally compressed, 25-110 × 3-8 mm, sparsely pubescent with short hairs; pedicels yellow-green, terete, 10-25 mm, sparsely pubescent. Bracts oblong, 2.3-3 × as long as wide, 3-7 × 1-3 mm, acuminate at the apex, glabrous outside except the midvein, glabrous inside. *Flowers* sweet-scented. *Sepals* pale green, tinged purple when fresh, free, ovate or narrowly so, 1.5-2.33 × as long as wide, 5.5-7 × 3-4 mm, acuminate at the apex, pubescent to sparsely so outside except for the edges at anthesis, sometimes turning glabrous in fruit, glabrous inside, sparsely ciliate or not. *Corolla* lobes cream outside, yellow shading to white inside, tube yellow-green outside, 17-30 mm long in the mature bud and forming a comparatively wide broadly ovoid head, 0.47-0.63 of the bud length 8-15 × 5-10 mm, obtuse at the apex, glabrous on both sides; tube funnel-shaped, 1.8-2.4 × as long as the calyx, 0.68-1.5 × as long as the lobes, 11-16 mm long, basal part almost cylindrical, always longer than the upper part, 0.66-0.76 of the length of the entire tube, 8-11 mm long, 4-6 mm wide above the base, upper part 3-6 mm long, 6-7 mm wide at the mouth; lobes obliquely ovate, 0.66-1.46 × as long as the tube, 1.45-1.83 × as long as wide, 1.2-2.2 × 0.8-1.2 cm, obliquely obtuse at the apex, recurved. *Stamens* with apex 6 mm above the mouth of the corolla tube, inserted 0.8-0.84 of the length of the corolla tube, at 9-12 mm from the base; anthers yellow-brown when fresh, narrowly triangular, 3.8-4.5 × as long as wide, 9-9.5 × 2-2.5 mm, pubescent inside at the base of the connective just below where they cohere with the pistil head, with tails slightly curved at the apex. *Pistil* 13.5-19 mm; ovary 3-4 × 2.5-4 × 2.5-3 mm, glabrous; disk with glands all fused at the lower part, less than half as long as the ovary, but 5-lobed above, lobes broadly ovate, rounded or toothed at the apex and more than half as long as the ovary; style straight, 9.2-13 mm long, glabrous; pistil head 1.3-2 mm high, composed of an obconical part 0.8-0.9 × 0.8-1 mm, a ring-shaped central part 0.3 × 1-1.3 mm and a stigmoid apex 0.2-0.25 × 0.6-0.9 mm. Ovules approximately 50 in each carpel. *Fruit* of 2 separate mericarps; mericarps dark green, shiny when young and fresh, pale to dark brown and with longitudinal lines outside, whitish inside when dried, fusiform, 14-16 × 2 × 1.5 cm, obtuse at the apex, glabrous; wall 2.5 mm thick. *Seeds* unknown.

DISTRIBUTION. Endemic to Madagascar.

ECOLOGY. Low open deciduous, dry, southern forest and scrubland on Tertiary calcareous rocks, sand (dune) and schists. Alt. 2-300 m. Flowering November-April and fruiting September-December.

Vernacular name: Vontaka (Vezo, Antandroy, Mahafaly).

Specimens examined:

MADAGASCAR. Toliara: Mikea Forest, *Debray* 955 (P); 35 km N of Toliara, *Leeuwenberg & Rapanarivo* 14629 (BR, K, P, TAN, WAG); 30 km N of Toliara along Route nat. 9, *Phillipson* 3499 (TAN, WAG); E of Toliara near Arboretum of Petignat, *Leeuwenberg & Rapanarivo* 14624 (TAN, WAG); on 'la Table'= Andatabo Hill, near Toliara, *Röösli & Hoffmann* 69/96 (WAG, ZSS); Toliara, Mont Eliva, Mahafaly, *Poisson* 648bis (P, neotype); Bezaha Mahafaly Res. SW corner of parcelle 1, Betioky, *Phillipson* 2610 (BR, K, P, TAN, WAG); Sakoa R. valley, Onilahy R. basin, *Decary* 16401 (P); ibid., *Humbert* 20215 (G, P) & 20210ter (P); ibid., *Perrier de la Bâthie* 18004 (BM, K, P, PRE, S, TAN, US); Tsimanampetsotsa Res., *B. Du Puy et al.* MB14 (TAN); ibid., *Keraudren* 1413 (P); ibid., *Phillipson* 3151 (K, P, TAN, WAG); near Tsimanampetsotsa Lake, *Bosser* 15861 (P); ibid., *Humbert* 20233 (G, P); ibid., *Perrier de la Bâthie* 8867 (P), 8867A (P) & 8867B (P); between Menarandra and Manambovo, *Perrier de la Bâthie* 18662 (P); near Ampanihy, *Schomerus* Sept. 1962 (M); Tsiombe, *Grandidier* 13 Jul. 1901 (P).

CULT. Germany: Berlin-Dahlem Bot. Gard., *Cubr.* 28431 (B). Madagascar: Antananarivo, Tsimbazaza Park, *Poisson* 1027 (P). South Africa: Nursery B.R.I., from SW of Madagascar, *Hardy* 3545 (PRE).

NOTES. *Leeuwenberg & Rapanarivo* 14629, 35 km N of Toliara, grows on sandy soil (dune ancienne) near the sea (Mozambique Channel) in open dry forest (Didiereaceae forest). It is in association with: *Didierea madagascariensis* Baill. (Didiereaceae), *Alluaudia procera* Drake (Didiereaceae), *Adansonia za* Baill. (Bombacaceae), *Euphorbia stenoclada* Baill. (Euphorbiaceae), *Delonix adansonioides* (R. Vig.) Capuron (Leguminosae), *Cedrelopsis grevei* Baill. (Ptaeroxylaceae), *Fernandoa madagascariensis* (Baker) A.H. Gentry (Bignoniaceae). In this region *P. geayi* is called 'Baobab nain' (= Dwarf Baobab) because it resembles *Adansonia za* Baill.

Röösli & Hoffmann 69/96 is found on calcareous rocks and sandy soil (sable roux comprimé) with pH c. 7 (measured by Röösli) in scrubland on Andatabo Hill, near Tuléar.

B. Du Puy MB14 near Tsimanampetsotsa Lake grows on limestone (calcareous rocks) with a.o. *Delonix* sp. (Leguminosae), *Cassia* sp. (Leguminosae) and *Euphorbia* sp. (Euphorbiaceae).

Humbert 20215 is found on schists in low open forest Onilahy basin near Sakoa.

P. geayi is characterised by the rather lax inflorescence, recurved corolla lobes and exerted stamens. The trunk contains as much as 91.5% water (Koechlin et al. 1974).

The original description given by Costantin & Bois (1907) is very clearly that of a tree of *P. geayi* just as we encountered in the field. Geay collected material of a sterile specimen. So no flowers etc. were described in the protologue. The collection *Poisson* 648bis collected 15 years after Costantin & Bois described the species is one of the two flowering specimens we could trace. This specimen erroneously has been cited as the type by Markgraf (1976). As the holotype seems to be no longer available, the collection *Poisson* 648bis is designated neotype.

10. **Pachypodium gracilius** (H. Perrier) Rapanarivo, **comb. nov.** Type: Madagascar, Toliara, Benenitra Onilahy R., *Perrier de la Bâthie* 8866 (holotype P). Fig. 7, p. 36; Map 6, p. 32; Plate 32, opposite p. 56; Plates 33-35, opposite p. 57.

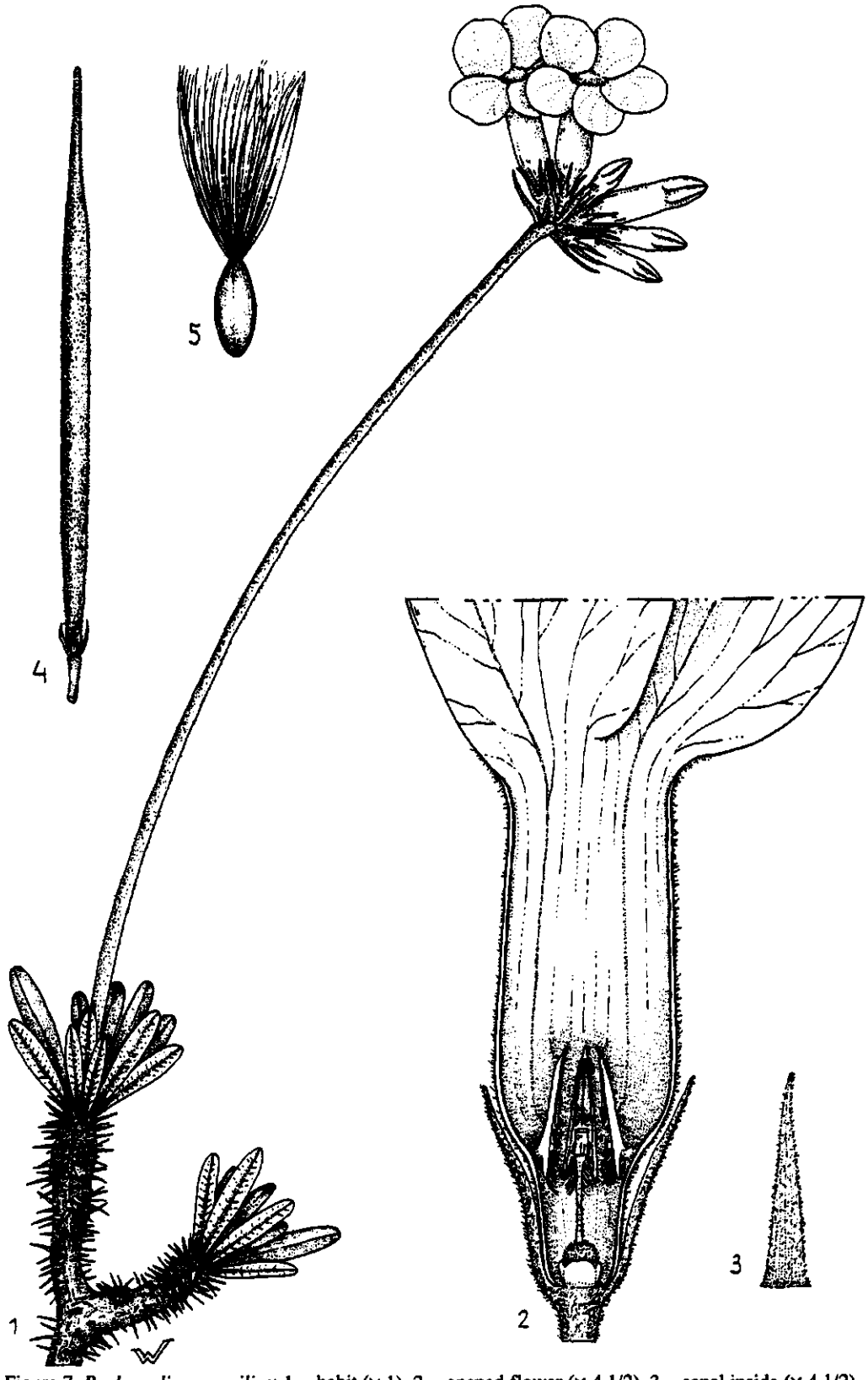


Figure 7. *Pachypodium gracilius*: 1 = habit (× 1), 2 = opened flower (× 4 1/2), 3 = sepal inside (× 4 1/2), 4 = fruit (× 1), 5 = seed (× 3) (1-3 = from Leeuwenberg & Rapanarivo 14613; 4-5 = from Decary 16292).

Basionym

P. rosulatum var. *gracilius* H. Perrier in Bull. Soc. Bot. Fr. 81: 306 (1934); Pichon in Mém. Inst. Sc. Madag. sér. B, 2: 118 (1949); Markgraf, Fl. Madag. fam. 169: 296 (1976).

Undershrub up to 80 cm high; trunk subglobose, laterally compressed and 20-50 cm in diameter or cylindrical and up to 20 cm in diameter; bark smooth, with small protruding lenticels, 5 mm thick; wood greenish-cream. Branches 2-5 cm in diameter; branchlets 5-19 cm long and 1-1.5 cm in diameter, covered with thin, densely arranged and needle-like paired spines 3-10 mm long, 0.5-1.5(-2) mm in diameter at the base. *Leaves* confined to the apices of the branchlets, sessile or shortly petiolate; petiole 0-3 mm long, pubescent; blade pale glaucous with midrib pale green above, pale grey beneath with glaucous reticulate venation when fresh, papery when dried, narrowly ovate to oblong or very narrowly so, 2-8 × as long as wide, 20-80 × 5-20 mm, rounded to acute at the apex, obtuse to acute at the base, margin revolute, sparsely pubescent with short hairs above, often with midrib more densely so and with impressed venation, pubescent to glabrous beneath, with costa and secondary veins prominent; with 15-40 pairs of rather straight secondary veins, forming an angle of 45-85° with the costa; tertiary venation reticulate, sometimes hidden by the indumentum. *Inflorescence* pedunculate, congested, 11-36 × 2.5-6 cm; 2-10-flowered. Peduncle pale green, often partly dark red, terete, 20-300 × 1.5-3 mm, sparsely pubescent; pedicels 3-15 mm long, pubescent. Bracts sepal-like, 9-14 × 0.8-2 mm. *Flowers*: *Sepals* pale green with dark red margin when fresh, curved at the apex when dried, always longer than the basal part of the corolla tube, connate at the base for about 0.5 mm, narrowly ovate to oblong or very narrowly so, 5-8 × as long as wide, 5-9 × 1-1.5 mm, acuminate at the apex, pubescent outside, glabrous inside. *Corolla* limb bright yellow, tube pale yellow outside, with 5 dark red lines at the base for two thirds of their length, 23-31 mm long in the mature bud and forming a comparatively wide broadly ovoid head, 0.3-0.5 of the bud length, 6-10 × 4-7 mm, obtuse at the apex, puberulous outside and glabrous on the parts of the lobes covered in bud, pubescent inside in a belt 1-2 mm wide below the insertion of the stamens, otherwise glabrous; tube infundibuliform, 2.3-3.5 × as long as the calyx, 1.3-1.8 × as long as the lobes, 18-26 mm long, basal part almost cylindrical 0.15-0.25 of the length of the entire tube, 3-5 × 2-2.5 mm, upper part obconical, 13-22 mm long, 6-9(-15) mm wide at the mouth; lobes obliquely obovate to obliquely ovate, 0.5-0.76 × as long as the tube, 1-1.57 × as long as wide, 12-19 × 10-14 mm, rounded at the apex. *Stamens* with apex 9-14 mm below the mouth of the corolla tube, inserted 0.2-0.3 of the length of the corolla tube, at 5-7 mm from the base; anthers triangular or very narrowly so, 3.3-6 × as long as wide, 5-6(-8) × 0.8-1.5 mm, pubescent inside at the base of the connective just below where they cohere with the pistil head. *Pistil* 7-9.5 mm long; ovary 1.5-2 × 1-1.8 × 1-1.5 mm, pubescent; disk composed of 5 broadly ovate rounded or retuse glands, 2 of which or 2 pairs of which may be partly or entirely fused and which are slightly more than half as long as the ovary; style 4.5-6.3 mm long, sparsely pubescent at the base; pistil head 0.9-1.2 mm high, composed of an obconical basal part 0.5-0.6 × 0.4-0.8 mm, a ring-shaped central part 0.2-0.3 × 0.5-0.9 mm and a stigmoid apex 0.15 × 0.25-0.6 mm. Ovules approximately 50 in each carpel. *Fruit* of 2 mericarps, forming an angle of 10-60° at the base; mericarps pale to dark brown, narrowly fusiform, 55-110 × 2-4 × 2-3 mm, obtuse to acute at the apex, pubescent; wall 0.5 mm thick. *Seeds*: grain pale to medium brown, elliptic,

6.5-8 × 2 mm; testa smooth; coma straw-coloured, 10-15 mm long. Endosperm thin. Embryo 4-5.5 mm long; cotyledons ovate, 1.5-2.08 × as long as wide, 1.5-2.5 × 1-1.5 mm, rounded at the apex, subcordate at the base; rootlet 1.2-1.66 × as long as cotyledons, 2.5-3 × 1-1.2 mm.

DISTRIBUTION. Endemic to Madagascar.

ECOLOGY. Evergreen sclerophyllous (*Uapaca*) woodland and savanna on sandstone. Alt. 300-1000 m. Flowering mainly July-October and fruiting mainly September-November.

Vernacular name: Vontaka, Votasitry (Bara, Betsileo).

Use: Against gale (SF 31424 TEF).

Specimens examined:

MADAGASCAR. Fianarantsoa: km 18 road from Amanda along Ihosy R. valley Eastwards, *Descoings* 3751 (TAN); East Isalo Mts, *Schlieben* 8247 (B, BR, M, PRE); Isalo Mts, *Allorge & Veyret* 616 (P); ibid., *Decary* 16292 (P) & 16395 (P); ibid., *Descoings* 1046 (TAN, WAG); ibid., *Keraudren et al.* 24660 (P); ibid., *Paulian* 3 (TAN); ibid., *Rauh* 7413 (M) & M984/59 (M); ibid., SW of Ranohira, *Fosberg* 52414 (US); ibid., *Humbert & Swingle* 4953 (G, P, TAN); ibid., *Jongkind* 743 (WAG); ibid., *Leeuwenberg & Rapanarivo* 14613 (BR, K, P, TAN, WAG); ibid., *Rapanarivo et al.* 240 (TAN, WAG); ibid., *Razafindrakoto* 11212 (P); ibid., *Supthut* 8226 (ZSS); ibid., *von Arx* 3074 (G, TAN, ZSS); ibid., Herb. Jard. Bot. Tana. 4228 (TAN); Ampandrabe, near Ranohira, SF 31424 (TEF); Ranohira-Sahanafo Road, *Cours* 5106 (P); between Voavatalava and Ankaboka, *Poisson* 673 (P); Ilaka (= Ilakaka), *Peltier* 2484 (P); near Fanjahira, *Humbert* 2766 (A, B, G, P). Toliara: Mankay, Mangoky R. basin, *Perrier de la Bâthie* 8921 (P); near Beroroha, Mangoky R. valley, *Humbert* 11353 (G, P); Benenitra, Onilahy R., *Perrier de la Bâthie* 8866 (P, type); 20 km E of Bezaha, Onilahy R., *Röösli et al.* 9 Dec. 1993 (ZSS); Sakaly, near Bezaha, *Röösli & Hoffmann* 40/98 (K, MO, WAG); Vohitrosy Mts, near Anadabolava, *Humbert* 12697 (P). Sin. loc., *Montagnac* 3 (P).

CULT. Germany: Berlin-Dahlem, Bot. Garden, *Cubr* 29384 (B). Switzerland: Geneva, Bot. Garden, *Lambert* Hb.G 236973 anno 1984 (G); Zürich, Bot. Gard., from Isalo Mts, *Röösli* s.n. (ZSS 05392).

NOTES. *Leeuwenberg & Rapanarivo* 14613, S of km 11 Ranohira-Sakaraha, grows on sandstone calcareous rocks where bush fires do not often pass. These rocks are surrounded by grasses dominated by *Hyparrhenia* sp. (Gramineae) and woody plants such as *Uapaca bojeri* Baill. (Euphorbiaceae), *Leptolaena luteola* (H. Perrier) Cavaco and *L. bojeriana* (Baill.) Cavaco (Sarcolaenaceae) and *Mascarenhasia lisianthiflora* A. DC. (Apocynaceae). The species often growing in the proximity of *P. gracilius* are: *Aloe isaloensis* H. Perrier (Aloaceae), *Kalanchoe synsepala* Baker and *K. orgyalis* Baker (Crassulaceae), *Euphorbia milii* Des Moul. (Euphorbiaceae), *Ischnolepis tuberosa* Jum. & H. Perrier (Asclepiadaceae), *Senecio* sp. (Compositae), *Tetradenia fruticosa* Benth. (Labiatae), *Xerophyta dasylirioides* Baker (Velloziaceae) and many other species.

Humbert 11353 (G) grows on sandstone NW of Beroroha and has all characters of *P. gracilius* except its spines that are wider at the base even up to 2 mm, 2 × as long as wide instead of 4-8 × as long as wide.

In Isalo *P. gracilius* has leaves pubescent beneath, (*Decary* 16292 (P), *Leeuwenberg & Rapanarivo* 14613 (BR, K, P, TAN, WAG) and *Rauh* 984/59 (M) & 7413 (M)). Other specimens have glabrous leaves (*von Arx & Suptut* 3074 (G) and *Hum-*

bert 2766 (A, B, G)). Therefore the indumentum can not be used as specific character for *P. gracilius*.

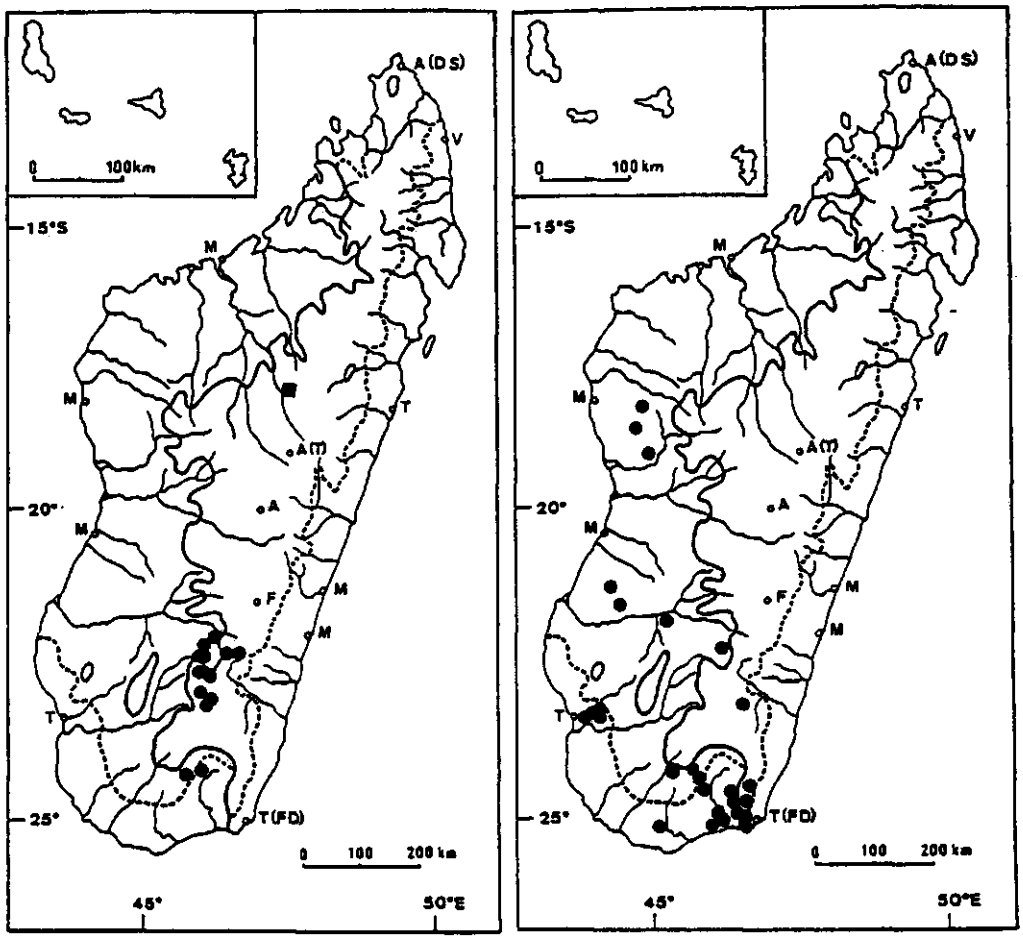
P. gracilius is always found on sandstone. It never grows directly on the sand itself and it forms a long root penetrating the fissures of the rocks at the base of the tuber-like trunk.

P. gracilius is easily confused with *P. cactipes* and *P. rosulatum*. The three species are distinguished mainly by the characters given in numbers 16 and 17 of Key 2.

11. **Pachypodium horombense** Poiss. in Bull. Acad. Malgache sér. 2, 6: 165 (1924); Perrier de la Bâthie in Bull. Soc. Bot. Fr. 81: 304 (1934); Pichon in Mém. Inst. Sc. Madag. sér. B, 2: 119 (1949); Markgraf, Fl. Madag. fam. 169: 292 (1976). Type: Madagascar, Fianarantsoa, Ambatolahy-Kelivondraka Road, *Poisson* 674 (holotype P). Fig. 4, p. 21; Map 7, p. 40; Plates 36-38, opposite p. 57.

Homotypic synonym
P. rosulatum var. *horombense* (Poisson) G. D.Rowley in Nat. Succ. J. 28: 4 (1973).

Shrub up to 60 cm high, 50-70 cm in diameter; trunk cactus-like, 20-30 cm in diameter; bark grey-green, shiny, smooth, medium green on section, 4 mm thick; wood cream. Branches up to 10 cm in diameter; branchlets 20-40 × 6-20 mm, covered with paired straight spines, 3-10 mm long, 1-3 mm in diameter at the base, basal part conical, 0.16-0.42 of the spine length. *Leaves* subsessile, confined to the apices of the branchlets; petiole 1-3 mm long, pubescent; blade medium green and with pale green midrib and secondary veins above, pale grey and with again paler midrib and dark green reticulate venation beneath when fresh, papery when dried, elliptic to oblong or narrowly so, 2.37-3.23 × as long as wide; 25-80 × 10-30 cm, rounded at the apex, cuneate at the base, glabrous to sparsely pubescent above, sometimes with midrib and margin densely so and with impressed venation, pubescent beneath, with midrib and secondary veins prominent; with 25-40 pairs of secondary veins, straight at the base, upcurved upwards, forming an angle of 30-85° with the costa; tertiary venation reticulate, sometimes hidden by the indumentum. *Inflorescence* pedunculate, congested, 15-65 × 3-16.5 cm, 4-11-flowered. Peduncle terete, 100-560 × 3-8 mm, pubescent to sparsely so; pedicels 5-45 mm long, pubescent. Bracts pale green, oblong to obovate or narrowly so, 3-6.2 × as long as wide, 8-25 × 2-6 mm, acuminate at the apex, pubescent outside and sparsely so inside. *Flowers*: *Sepals* pale green, connate at the base for about 0.5 mm, ovate or very narrowly so, 1.75-7 × as long as wide, 6-15 × 2-4 mm, acuminate at the apex, pubescent outside, glabrous inside. *Corolla* bright yellow, 2.5-5.5 cm long in the mature bud and forming a comparatively wide ovoid head 0.25-0.40 of the bud length, 7-18 × 9-14 mm, obtuse at the apex, pubescent outside but often less so than the calyx, glabrous on the part of the lobes covered in bud, with a pubescent belt inside 2-5 mm wide just below the insertion of the stamens, otherwise glabrous; tube with dark red longitudinal lines in bud, pale green in open flowers as sepals at the extreme base, 2.6-4.3 × as long as the calyx, 1.32-2.5 × as long as the lobes, 25-50 mm long, basal part almost cylindrical, 0.2-0.3 × as long as the tube, 6-10 × 3.5-6 mm, abruptly widened where the stamens are inserted into the upper part which is urceolate, 18-40 mm long, 15-26 mm wide at the mouth, with 5 again widened parts below the lobes and therefore seemingly 5-winged inside, sometimes becoming obconical when dried; lobes suberect, obliquely and broadly obovate,



Map 7. • *Pachypodium horombense*, • *P. inopinatum*. Map 8. *Pachypodium lamerei*.

0.3-0.75 × as long as the tube, 1.2-1.6 × as long as wide, 16-27 × 10-20 mm, acuminate with acumen acute at the apex. *Stamens* with apex 9-18 mm below the mouth of the corolla tube, inserted 0.24-0.66 of the length of the corolla tube, at 9-12 mm from the base; anthers very narrowly triangular, 3.66-5 × as long as wide, 8.5-11 × 2-3 mm, fertile part c. 2 mm long, pubescent inside at the base of the connective just below where they cohere with the pistil head. *Pistil* 12-14 mm long; ovary 3-4.5 × 2.5-3.5 × 2-3 mm, pubescent; disk composed of 5 broadly ovate rounded or retuse glands, 2-2.5 mm long, 2 of which or two pairs of which may be partly or entirely fused and which are slightly more than half as long as the ovary; style 6.5-8 mm long, sparsely pubescent from the base to just below the apex; pistil head 1.5-1.95

Plate 19. *Pachypodium densiflorum*, Mt Ibity.
Plate 20. *Pachypodium densiflorum*, Mt Ibity.
Plate 21. *Pachypodium densiflorum*.
Plate 22. *Pachypodium densiflorum*.
Plate 23. *Pachypodium densiflorum*.

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20	23

mm high, composed of a conical or almost cylindrical basal part 0.8-1.4 × 0.9-1.2 mm, an almost cylindrical central part 0.3-0.4 × 0.5-1 mm and a stigmoid apex 0.15-0.2 × 0.4-0.9 mm. Ovules approximately 50 in each carpel. *Fruit* of 2 separate mericarps, forming an angle of 10-60°at the base (sometimes flowers and fruits on the same inflorescence); mericarps pale to medium brown with longitudinal lines, narrowly fusiform, 10-18 × 5-7 × 4-5 mm, obtuse at the apex, pubescent; wall 1 mm thick. *Seeds*: grain pale brown, elliptic, 5.5-7 × 1.5-2.5 mm; testa smooth; coma straw-coloured, 1.2-1.8 cm long. Embryo 5-5.6 mm long; cotyledons ovate, 1.4-2.3 × as long as wide, 2.25-2.28 × 1.2-1.8 mm, rounded at the apex, subcordate at the base; rootlet as long as the cotyledons, 2.25-2.28 × 1-1.5 mm.

DISTRIBUTION. Endemic to Madagascar.

ECOLOGY. Savanna and scrubland on gneissic and granitic rocks. Alt. 400-1100 m. Flowering mainly July-September and fruiting mainly September-November.

Vernacular name: Somo (Betsileo); Vontaka, Vontakakely (Bara).

Specimens examined:

MADAGASCAR. Fianarantsoa: near Ankaramena, *Fosberg* 52401 (US); ibid., *Keraudren et al.* 24636 (P); km 17 Ihosy-Sakalalina Road, *Descoings* 3692 (TAN) & 3694 (TAN); km 18 Ihosy-Ivohibe Road, *Descoings* 3649 (TAN), 3772 (P, TAN, WAG), 3773 (TAN, WAG) & 3374 (TAN); km 43 Ihosy-Ivohibe Road, *Allorge* 577 (P); near Ihosy, *Bernardi* 11244 (BR, E, G, K, NY, P); ibid., *Grandidier* 5 Sept. 1898 (P); ibid., *Leeuwenberg & Rapanarivo* 14634 (BR, K, P, TAN, WAG); ibid., *Miege* 90M (G); km 9 Ihosy-Ranohira Road, *Leeuwenberg & Rapanarivo* 14630 (BR, K, P, TAN, WAG); Ambatolahy, *Decary* 4 (P); Ambatolahy-Kelivondraka Road, *Decary* 4 (P); ibid., *Poisson* 674 (P, type); km 9 Ihosy-Ranohira, *Leeuwenberg & Rapanarivo* 14630 (BR, K, P, TAN, WAG); Horombe Plateau, *Boiteau* 325 (P) & 325B(P); ibid., W of Ihosy R. valley, *Humbert* 2947 (A, B, P); Ivatonarivo, *Deans Cowan* Aug. 1880 (BM, P); Fianarantsoa, *Perrier de la Bâthie* 16536 (K, P). Toliara: Androtsa, Betroka District, *Peltier* 1536 (P, TAN); ibid., *von Arx & Supthut* 3045 (G, TAN, ZSS); Iapety, *Peltier* 2657 (P); 85 km N of Betroka, *Keraudren et al.* 25075 (P); Vohipolaka Mt, N of Betroka, *Humbert* 11615 (G, P, TAN); near Betroka, *Lam et Meeuse* 5527 (K, L, P); between Isoanala and Betioky, *Rauh* 1465/59 (M); Beraketa, *Rauh* M1465 (M); Onilahy R., near Mt Vohibory, *Perrier de la Bâthie* 8869 (P); near Ampandrandava, between Bekily and Tsivory, *Seyrig* 81 (P) & 302 (P); Menarabaka Plain, *Descoings* 991 (TAN); Mts Vohitsiombe, *Decary* 4648 (K, P); near Antanimora, Ambovombe District, *Decary* 3262 (K, P, US); ibid., *Keraudren et al.* 25065 (P); ibid., *Montagnac* s.n. (TAN); ibid., *Röösli & Hoffmann* 52/98 (WAG). Sin. loc., *Baron* 256 (K, rejected type of *P. rosulatum*).

CULT. Germany: Berlin-Dahlem Bot. Garden., *Schwerdtfeger* 15952 (B). Madagascar: Antananarivo, Tsimbazaza Park, *Dorr & Barnett* 3149 (BR, K, P, PRE, TAN, WAG); ibid., *Leeuwenberg* 13727 (WAG).

NOTES. *Leeuwenberg & Rapanarivo* 14634, km 9 Ihosy-Ranohira, grows on gneiss

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Plate 24. *Pachypodium eburneum*, Mt Ibity.
Plate 25. *Pachypodium eburneum*, Mt Ibity.
Plate 26. *Pachypodium eburneum*, Mt Ibity.
Plate 27. *Pachypodium eburneum*, Mt Ibity.

(Baiserie 1984) surrounded by savanna dominated by *Aristida sp*, *Heteropogon contortus* (Roem. & Schult.) P. Beauv. and *Hyparrhenia* sp. (Gramineae). It is often found with: *Kalanchoe orgyalis* Baker (Crassulaceae), *Catharanthus longifolius* (Pichon) Pichon *Leeuwenberg & Rapanarivo* 14631 (Apocynaceae), *Euphorbia* sp. (Euphorbiaceae), *Aloe* sp. (Aloaceae), *Stapelianthus* sp. (Asclepiadaceae), *Tetradenia* sp. (Labiatae) and *Xerophyta dasylirioides* Baker (Velloziaceae). When leafless, *P. horombense* resembles *Euphorbia milii* Des Moul. (Euphorbiaceae) which has white latex instead of clear sap. Near Ihosy *P. horombense* is also found with *P. lamerei* (*Leeuwenberg & Rapanarivo* 14636).

P. horombense is characterised by the urceolate upper part of the corolla tube, which has 5 widened parts below the lobes. This character state is unique in the genus.

12. **Pachypodium inopinatum** Lavranos in Cactus and Succulents Journ. 60: 171-176 (1996). Type: Madagascar, Mahajanga, Tsaratanana District, near Telomitra (= Telomita), *Röösli & Hoffmann* 46/93 (holotype ZSS, n.v.; isotypes P, TAN, WAG). Fig. 8, p. 43, Map 7, p. 40; Plates 39-43, opposite p. 64.

Homotypic synonym
P. rosulatum var. *inopinatum* (Lavranos) G.D. Rowley in Bradleya 16: 101 (1998) and Pachypodium & Adenium, The Cactus File Handbook 5: 59 (1999), **syn. nov.**

Shrub 15-40 cm high, base subglobose 10-20 cm in diameter, stem cylindrical 5-15 cm in diameter; bark grey-green, smooth; branches thick, often unarmed in the lower part, 5-6 cm in diameter and tapering to 2-3 cm, branchlets sometimes erect, 1-1.5 cm in diameter, covered with paired straight spines, 3-6 mm long, 0.5-1.5 mm in diameter, basal part conical, laterally compressed, 0.33-0.5 of the spine length. *Leaves* subsessile, confined to the apices of the branchlets; petiole 0-2 mm long, pubescent; blade medium green and with pale green midrib above, pale green beneath and with glaucous reticulate venation when fresh, narrowly elliptic to narrowly obovate, 4.4-7.5 × as long as wide, 2-5.3 × 0.3-1 cm, obtuse to rounded at the apex, obtuse to cuneate at the base, margin revolute, glabrous or glabrescent above, often with margin and midrib sparsely pubescent, glabrous beneath except for the sparsely pubescent and prominent midrib; with 30-40 pairs of rather straight secondary veins forming an angle of 45-85° with the costa. *Inflorescence* pedunculate, congested, 15-25 × 5-5.5 cm, 3-5-flowered. Peduncle pale green, terete, 10-19 cm long, 4-5 mm wide at the base, narrowed to 3 mm wide at the apex, pubescent; pedicels pale green, about 7-10 mm long, 1-2 mm in diameter, pubescent. Bracts pale green, narrowly obovate to oblong, 1.5-3.5 × as long as wide, 5-10.5 × 3-6 mm, acuminate at the apex, pubescent outside and less so inside. *Flowers: Sepals* pale green, ovate, 1.5-1.85 × as long as wide, 9-11 × 3-6 mm, acuminate at the apex, pubescent outside and less so inside. Corolla limb yellowish, tube with upper part yellowish-green and basal part pale green outside 3-3.2 cm long in the mature bud and forming a comparatively wide broadly ovoid head, 0.5 of the bud length, 15-16 × 6-7 mm, obtuse at the apex, pubescent outside but glabrous on the part of the lobes covered in bud, pubescent belt inside 5 mm wide just below the insertion of the stamens, otherwise glabrous; tube infundibuliform, 2.45-2.8 × as long as the calyx, 1-1.2 × as long as the lobes, 25-28 mm long, basal part almost cylindrical, 0.55 of the length of the entire tube, 13-15 mm long and

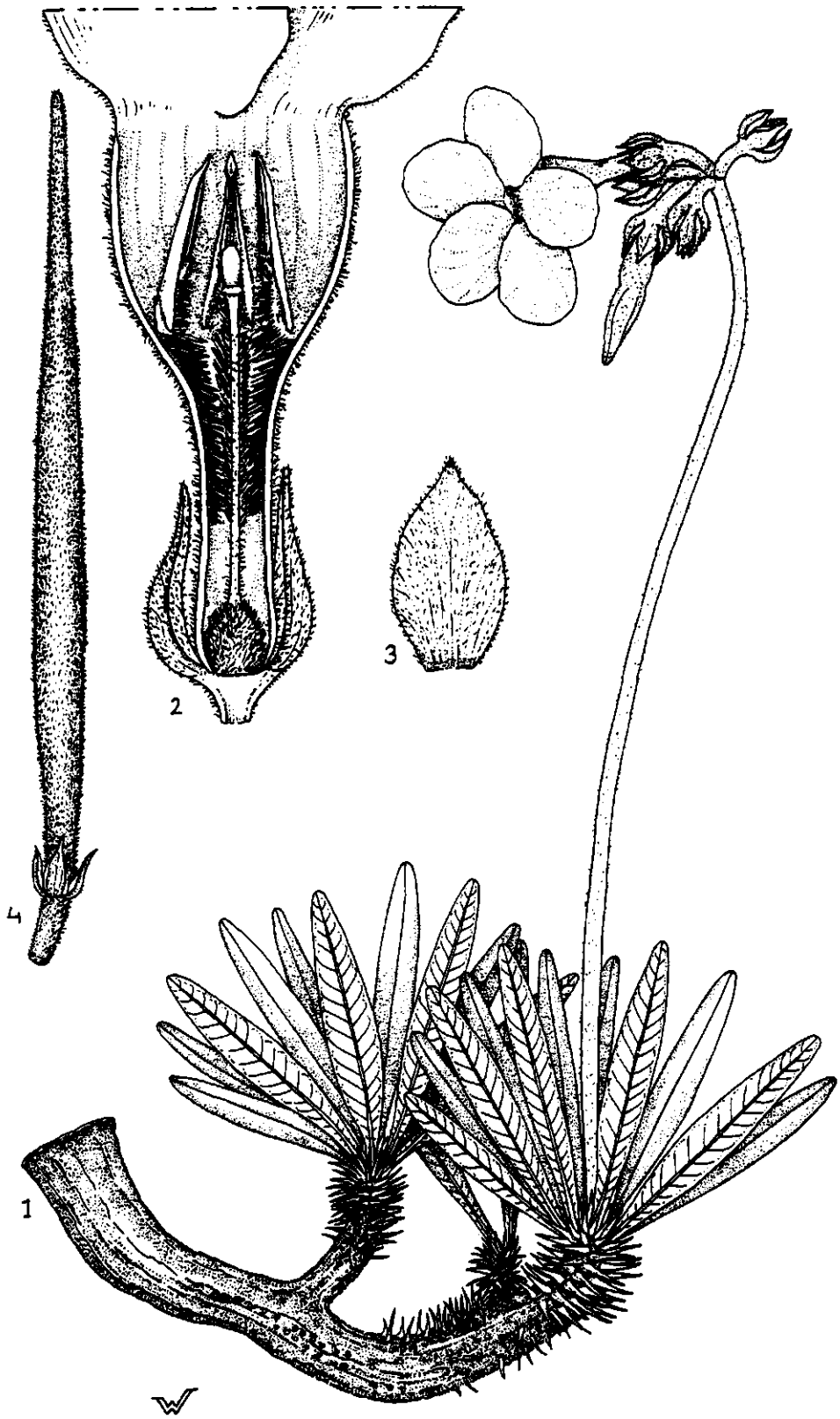


Figure 8. *Pachypodium inopinatum*: 1 = habit (× 1), 2 = opened flower (× 4.6), 3 = sepal inside (× 4.6), 4 = fruit (× 1) (1 and 4 = from Röösli & Hoffmann ZSS 15697; 2 and 3 = from Röösli & Hoffmann 46/96).

4 mm wide, upper part obconical, 12-13 mm long and 14 mm wide at the mouth; lobes obliquely and broadly ovate, 0.6-0.9 × as long as the tube, 1.25-1.3 × as long as wide, 22-25 × 17-20 mm, rounded at the apex. *Stamens* with apex 5 mm below the mouth of the corolla tube, inserted 0.6 of the length of the corolla tube, at 14 mm from the base; anthers narrowly triangular, 4.5 × as long as wide, 9 × 2 mm, pubescent inside at the base of the connective just below where they cohere with the base of the pistil head. *Pistil* 18.5 mm long; ovary 2.5 × 2 × 1.6 mm, pubescent; disk of 5 glands, 2 or 2 pairs of which partly or entirely fused, lobes broadly ovate, 1 mm high, rounded and toothed at the apex, which are less than half as long as the ovary; style filiform, 14.5 mm long, sparsely pubescent; pistil head 1.5 mm high, composed of an obconical basal part 0.9 × 0.8 mm, a ring-shaped central part 0.4 × 0.5 mm and a stigmoid apex 0.2 × 0.4 mm. Ovules approximately 50 in each carpel. *Fruit* of 2 mericarps; mericarps pale brown and with longitudinal lines outside, whitish to pale brown inside, fusiform, 140 × 4 × 2 mm, narrowly obtuse at the apex, pubescent. *Seeds*: grain pale brown, elliptic, 7-8 × 2.5 mm; testa smooth, margin revolute towards the hilar side, with hilum medium brown; coma straw-coloured, 19 mm long. Embryo 6-7 mm long; cotyledons broadly ovate, 1.1-1.25 × as long as wide, 2.5-3 × 2-2.8 mm, rounded at the apex, cordate at the base; rootlet 1.33-1.6 × as long as the cotyledons, 4 × 1.8-2.5 mm.

DISTRIBUTION. Endemic to Madagascar.

ECOLOGY. Savanna on granitic rocks. Flowering and fruiting in December. Alt. c. 1450 m.

Specimens examined:

MADAGASCAR. Mahajanga, near Tsaratanana District, near Telomita, *Rapanarivo* 369 (TAN); ibid., *Röösli & Hoffmann* 46/93 (P, TAN, WAG, ZSS (n.v.), type) & Dec. 1993 (ZSS 15697).

NOTES. *Rapanarivo* 369 grows on granite (Besairie 1984). It is surrounded by grasses dominated by *Aristida* sp. (Gramineae) and some woody plants (remains of sclerophyllous forest), *Leptolaena bojeriana* (Baill.) Cavaco (Sarcolaenaceae) and *Weinmannia* sp. (Cunoniaceae). Other accompaning species are *Aloe capitata* Baker (Aloaceae), *Kalanchoe synsepala* Baker (Crassulaceae), *Coleochloa setifera* (Ridl.) Gilly (Cyperaceae), *Dionycha bojeri* Naudin (Melastomataceae), *Euphorbia milii* Des Moul. (Euphorbiaceae), *Tetradenia* sp. (Labiatae) and *Pellaea goudotii* (Kunze) C. Chr. (Adiantaceae).

13. **Pachypodium lamerei** Drake in Bull. Mus. Hist. Nat. 5: 308 (1899); Costantin & Bois in Ann. Sc. Nat. sér. 9, 6: 311 (1907); Perrier de la Bâthie in Bull. Soc. Bot. Fr. 81: 308 (1934); Pichon in Mém. Inst. Sc. Madag. sér. B, 2: 113 (1949); Markgraf, Fl. Madag. fam. 169: 279 (1976). Type: Madagascar, sin. loc., *Lamère* s.n. (holotype P†). Neotype: Madagascar, Toliara, Andohahela Res., Parcelle 2, *Leeuwenberg, Malcomber, Rapanarivo & Randriamampionona* 14169, 29 Nov.1991 (neotype P, isoneotypes BR, K, PRE, TAN, WAG). Fig. 9, p. 45; Map 8, p. 40; Plates 44-48, opposite p. 65.

Homotypic synonym

P. rutenbergianum var. *lamerei* (Drake) Poiss. in Bull. Acad. Malgache sér. 2, 6: 162, pl. 4 (1924).

Figure 9. 1-4) *Pachypodium lamerei*: 1 = habit (× 2/3), 2 = leaf (× 2/3), 3 = grain (× 2), 4 = embryo (× 2). 5-8) *P. rutenbergianum*: 5 = habit (× 2/3), 6 = leaf (× 2/3), 7 = grain (× 2), 8 = embryo (× 2) (1 = from Capuron SF 320; 2 = from Capuron SF 22202; 3 and 4 = from Leandri 2182; 5 = from Decary 14557; 6 = from Decary 1179; 7 and 8 = from Decary 15604).

Heterotypic synonyms
P. ramosum Costantin & Bois in Ann. Sc. Nat. sér. 9, 6: 316 (1907); Perrier de la Bâthie in Bull. Soc. Bot. Fr. 81: 141 (1934). *P. lamerei* var. *ramosum* (Costantin & Bois) Pichon, l.c. Type: Madagascar, Tuléar (= Toliara), Behara, near Amboasary, *Grandidier* 8 Jul. 1901 (holotype P).
P. menabeum Leandri in Bull. Soc. Bot. Fr. 81: 141 (1934). Type: Madagascar, Mahajanga, Bemaraha Res., *Leandri* 1009 (holotype P).
P. champenoisianum Boiteau in Bull. Acad. Malgache sér. 2, 24; 82 (1942). Type: Madagascar, Fianarantsoa, near Ambohibe, near Manambovony and Manatanana Rs. junction, *Champenois* in Herb. Jard. Bot. Tana. 4922 (holotype P).

Small candelabrum-shaped tree 2-5 m high; trunk bottle- or cigar-shaped 10-30 cm in diameter; bark grey-green or pale to medium brown, smooth or with leaf scars; branches covered with straight spines in groups of three, two of which subequal, 2.5-27 × 1-3.5 mm and in between them a small one 2.5-9 × 0.8-2 mm, fused at the base and forming an obconical and laterally compressed excrescence; branchlets 2-3 cm in diameter, spiny. *Leaves* petiolate, confined to the apices of the branchlets; petiole 1.2-6 cm long, sparsely pubescent or glabrous; blade coriaceous, medium to dark green and sometimes glossy, with pale green midrib and secondary veins above, pale glaucous with pale green midrib and with dark green reticulate venation beneath when fresh, papery when dried, narrowly ovate to oblong or very narrowly so, 2.3-7 × as long as wide, 9-41 × 2.4-11 cm, acuminate to rounded at the apex and mucronate (1-3 mm) or not, cuneate to rounded at the base, sometimes decurrent into the petiole, mostly with margin slightly revolute, glabrous above, with midrib and secondary veins prominent or all venation impressed, pubescent to glabrous beneath, with midrib and sometimes secondary veins prominent; with 45-90 pairs of secondary veins, straight at the base, upcurved at the apex, forming an angle of 45-85° with the costa; tertiary venation reticulate, sometimes hidden by the indumentum. *Inflorescence* pedunculate, congested, 9-22 × 5-19 cm, 4-23-flowered. Peduncle terete or fluted, 20-120 × 4-15 mm, glabrous to sparsely and shortly pubescent; pedicels 4-15 mm long, glabrous to sparsely pubescent. Bracts ovate or narrowly so, 1.3-3(-3.3) × as long as wide, 3.5-6(-13) × 1.5-2(-4) mm, acuminate at the apex, glabrous to sparsely pubescent outside, glabrous inside but sometimes with small stiff hairs at the apex. *Flowers* fragrant. *Sepals* dark green when fresh, connate at the base for about 0.5 mm, ovate or narrowly so, 1.3-3.5 × as long as wide, 3-7 × 1.5-3.5 mm, acuminate at the apex, glabrous or very sparsely pubescent outside, glabrous inside, ciliate or not near and at the apex. *Corolla* limb white, rarely with reddish edge, tube greenish outside, yellow in the throat, 3-7 cm long in the mature bud and forming a comparatively wide broadly ovoid head, 0.41-0.66 of the bud length, 13-30 × 4-11 mm, obtuse at the apex, glabrous outside, pubescent belt inside 1-1.5 mm wide below the insertion of the stamens, otherwise glabrous; tube 6.5-12 × as long as the calyx, 0.70-1.5 × as long as the lobes, 26-60 mm long, basal part almost cylindrical, 0.07-0.2(-0.3) of the length of the entire tube, 2-7 × 2.5-4.5 mm; upper part urceolate, 23-53 mm long, 4-7 mm wide at the mouth; lobes obliquely ovate to obliquely obovate, 0.67-1.42 × as long as the tube, 0.84-2.76 × as long as wide, 25-68 × 17-41 mm, acute or dolabriform and with an acute and a rounded apex. *Stamens* with apex 1.2-3.2 cm below the mouth of the corolla tube, inserted 0.1-0.2 of the length of the corolla tube, at 3-9 mm from the base; anthers very narrowly triangular 3.8-6 × as long as wide, 9-12 × 2-2.5 mm, pubescent at the base of the connective just below

where they cohere with the pistil head. *Pistil* 9.5-14.5 mm long; ovary 2.5-3.5 × 2-3 × 1.8-2 mm, glabrous; disk 1.25-2.5 mm high, 5-lobed; style 4.5-8.9 mm long, sparsely pubescent at the base; pistil head 1.2-1.6 mm high, composed of an obconical basal part 0.8-1.2 × 0.5-1 mm, a ring-shaped central part 0.2-0.5 × 0.8-1.2 mm and a stigmoid apex 0.2-0.5 × 0.5-1 mm. Ovules approximately 50 in each carpel. *Fruit* of 2 separate mericarps, sometimes only one developing, forming an angle of 45-180° at the base; mericarps with an indented line of dehiscence, smooth when fresh, pale to dark brown outside, with longitudinal lines, whitish inside when dried, fusiform, 9-26 × 2.5-5.5 × 2-4 cm, glabrous; wall 2.5-5 mm thick. *Seeds*: grain pale brown, ellipsoid, 14-15 × 4-6 × 3 mm; testa rough; coma straw-coloured, 1.5-4.5 cm long. Endosperm thick. Embryo almost ovate, 12 mm long; cotyledons broadly ovate, 1.7 × as long as wide, 6-6.8 × 3.5-4 mm, rounded at the apex, cordate at the base; rootlet 1.03-1.16 × as long as the cotyledons, 7 × 3-3.5 mm.

DISTRIBUTION. Endemic to Madagascar.

ECOLOGY. Low open deciduous dry western and southern forest and scrubland on Mesozoic or Tertiary calcareous rocks, gneiss, granite, sand, sandstone and sandy soil. Alt. 10-1200 m. Flowering November-April and fruiting October-December.

Vernacular name: Vontaka (Antanosy and Sakalava), Vontaky, Hazotavohangy (= tree bottle) (Sakalava); Votasitry (Antanosy).

Specimens examined:

MADAGASCAR. Mahajanga: Tsingy de Bemaraha, *Leandri* 1009 (P, type of *P. menabeum*); ibid., *Morat* 4829 (TAN); ibid., 11 km E of Antsalova, *Klackenberg* 93.03.12-23 (P); near Ambodiriana R., 1 km E of Ambinda (Res. Nat. 9), near Antsalova, *Labat & Deroin* 2310 (K, P, PRE, TAN, WAG); ibid., *Leandri & Saboureau* 2182 (P) & 2733 (P); ibid., *Rabarison* 235 (Faculté des Sciences, Université Antananarivo); ibid., *Villier et al.* 4859 (P); near Bekopaka, *B. Du Puy et al.* MB808 (P, TAN); ibid., SF 25096 (TEF). Fianarantsoa: Near Ambohibe, near Manambovony and Manantanana Rs. junction, *Champenois* in Herb. Jard. Bot. Tana. 4922 (P, type of *P. champenoisianum*); Upper valley of Menarahaka R., E of Ihosy, *Humbert* 28617 (P); near Ihosy, *Röösli & Hoffmann* 87/96 (WAG, ZSS); 6 km S of Ihosy, *Leeuwenberg & Rapanarivo* 14636 (BR, K, P, WAG). Toliara: near Beroroha, *Humbert* 11281 (P); Mangoky R. basin, *Perrier de la Bâthie* 12860bis (P) & 12860ter (P); Malio R. basin, *Humbert* 19321 (G, P); E slope of Analavelona Mts, W of Mitia, *Capuron* SF 22201 (P) & SF 22202 (P, TEF); 28 km S of Manja, *Röösli & Hoffmann* 53/96 (WAG, ZSS); 30 km N of Tuléar along Route nat. 9, *Phillipson* 3499 (G, K, P, TAN, WAG); Gorges of Fiherenana R., Anjamala, *Capuron* SF 22234 (K, P, TEF, WAG); ibid., *Humbert* 19890 (G, P); ibid., *Röösli & Hoffmann* 4/94 (P, ZSS) & 63/96 (P, WAG, ZSS); Fiherenana R. valley, NE of Tuléar, near Beantsy, *B. Du Puy et al.* MB18 (TAN); ibid., *Phillipson & Rabesihanaka* 3106 (K, P, TAN, WAG); lower valley of Fiherenana R., *Humbert* 11581 (G, P); 37 km from Tuléar, Fiherenana R., *Leeuwenberg & Rapanarivo* 14628 (BR, K, P, TAN, WAG); ibid., *Röösli & Hoffmann* Sept. 1993 (ZSS); 16 km S of Bereketa along Route nat. 13, *Röösli et al.* Dec. 1993 (ZSS 015702); Ambia Mts, Tsiterempeky Region, *Decorse* probably anno 1901 (P); near Ampandrandava, *Seyrig* 395 (P); Tsivory, Anadabolava, *Humbert* 12294 (P); near Imonty, *Keraudren* 1504 (P); ibid., *Leandri & Saboureau* 4200bis (K, P); S of Imonty, *Leandri & Saboureau* 4264 (P); Fangidraty, *Decary* 9331 (P); between Antanimora and Bereketa, *Croat* 32026 (TAN, WAG); Andalatanosy, near Antanimora, *Röösli & Hoffmann* 72/96 (WAG, ZSS); near Bekily, *Capuron* SF 320 (P); Upper Mandrare R., Manambolo R. valley, *Humbert* 6756 (B, G, K, P, TAN); Ima-

nombo, *Bosser* 3801 (P, TAN, WAG); Antanimora, *Bosser* 13961 (TAN); ibid., *Decary* 3824 (P, US); Vohibala Canton, near Fort-Dauphin, *Rakotoson* RN 10791 (P); near Ranofotsy Lake, 30 km W of Fort-Dauphin, *Röösli & Hoffmann* 79/96 (P, WAG, ZSS); Andohahela Res., parcelle 2, *Clement et al.* 2111 (E, K, P, PRE, TAN); ibid., *Leeuwenberg et al.* 14169 (BR, K, P, PRE, TAN, WAG, neotype); ibid., *Ramarokoto* RN 2753 (P); ibid., *Randriamampionona* 167 (P, WAG); N of Amboasary, road to Ihazofotsy, *Pillipson* 2682 (BR, C, K, P, S, TAN, WAG); Behara, near Amboasary, *Grandidier* 8 Jul. 1901 (P, type of *P. ramosum*); ibid., *Jaonarivelo* RN 6450 (P); near Fort-Dauphin, *Cloisel* 40 (P); ibid., *Ralimanana et al.* 99 (TAN); Imonty R., Mananara R., tributary of Mandrare R., *Bosser 15720* (TAN); Andrahomana, *Alluaud* 11 (P); Berenty Res., Mandrare R., 15 km of Amboasary, *Leeuwenberg et al.* 14039 (TAN, WAG); Sakoa R. basin, *Perrier de la Bâthie* 18572 (P); Elakelaka, Ambovombe District, *Decary* 2878 (P); Angavo Mt, *Decary* 8844 (P); Ambovombe, *Decary* 2611 (K, P, TAN), 2852 (P) & 8355 (P); ibid., *Descoings* 1374 (TAN); Manombo S, *Perrier de la Bâthie* 8868 (P); Tsiombe-Ambovombe Road, *Dumetz* 1258 (K, P, PRE, WAG); near Beloha (Androy), *Humbert* 20317 (G). Sin.loc, *Boiteau* 375B (P); *Homolle* 1433 (P) & 1676bis (P); *Montagnac* 4 (P).

CULT. Madagascar: Mahajanga, from near Tuléar, *Perrier de la Bâthie* 17806 (P). South Africa: Bot. Garden of Univ. Stellenbosch, introduced from Madagascar, *Twinen* 25 March 1976 (WAG); Pretoria, from Tuléar area, *Rauh* 10491a (PRE) & 10491b (PRE); ibid., from near Fort-Dauphin, *Hardy* 2908 (PRE). Germany: Berlin-Dahlem Bot. Gart., *Schwerdtfeger* 2360 (B), 15317 (B), 15318 (B) & 16254 (B); München-Nymphenburg Bot. Garden, from S Madagascar, 5 Aug.1976 (M). Switzerland: Geneva Bot. Garden, *Lambert* Hb.G. 159076 (G).

NOTES. *Leeuwenberg & Rapanarivo* 14628, *Phillipson* 3106 and *Röösli & Hoffmann* 63/96, about 35 from Tuléar, left bank Fiherenana R., grow on calcareous rocks with soil with pH c. 7 (measured by Röösli) in low open forest. They are in association with *Euphorbia* sp., (Euphorbiaceae), *Delonix adansonioides* (R. Vig.) Capuron (Leguminosae), *Commiphora orbicularis* Engl. (Burseraceae) and *Plectaneia stenophylla* Jum. (Apocynaceae).

Rabarison 235, Antsingy de Bemaraha is found on calcareous rocks in low open forest (Végétation claire semée xérophytique (Rabarison Harison, pers. comm.). It is often in association with: *Euphorbia milii* Des Moul., *E. turricalli* L. and *E. viguieri* Denis (Euphorbiaceae), *Cynanchum eurychitoides* K. Schum. (Asclepiadaceae), *Neoharmsia madagascariensis* R. Vig. (Leguminosae), *Hildegardia erythrosiphon* Baill. (Sterculiaceae), *Commiphora aprevalii* Guill. (Burseraceae), *Apaloxylon tuberusum* R. Vig. (Leguminosae) and *Kalanchoe gastonis-bonnieri* Raym.-Hamet & H. Perrier (Crassulaceae).

Röösli & Hoffmann 53/96, near Manja, grows on calcareous rocks with soil with pH c. 7 (measured by Röösli) in an open forest. It is sometimes found with *P. meridionale*.

Leeuwenberg & Rapanarivo 14636, 6 km S of Ihosy, is found on granite, surrounded by grasses and deciduous forest destroyed by bushfire. It is in association with: *Euphorbia milii* Des Moul. (Euphorbiaceae), *P. horombense* Poiss. (Apocynaceae), *Kalanchoe orgyalis* Baker (Crassulaceae), *Xerophyta sp.* (Velloziaceae), *Aloe* sp. (Aloaceae), *Stapelianthus* sp. (Asclepiadaceae) and *Tetradenia* sp. (Labiatae).

Röösli & Hoffmann 87/96, near Ihosy, grows on gneiss (Besairie 1984) with soil with pH c. 4.5-5 (measured by Röösli).

Röösli & Hoffmann 72/96, Andalatanosy, grows on gneiss with soil with pH c. 4.5

(measured by Röösli). It is found with *P. horombense*. Besairie didn't indicate the presence of gneiss at Andalatanosy. He only marks 'Andalatanosy. The road is on Leptynite with pyroxenite and amphibolite'. In Rapanarivo's opinium probaly *P. lamerei* grows there on leptynite but not on gneiss as Röösli & Hoffmann thought. So *P. horombense* can grow also on leptynite.

Leeuwenberg et al. 14169, Andohahela Res., near Ihazofotsy, grows on granitic rocks in xerophyllous bush dominated by *Alluaudia procera* Drake (Didiereaceae).

Phillipson 3499, 30 km N of Tuléar is, found on sandy substrate in low open forest dominated by *Didierea madagascariensis* Baill. (Didiereaceae).

Leeuwenberg et al. 14039, Berenty Res., Mandrare R., grows on white sand in open dry forest.

B. Du Puy et al. MB808, 1 km E of the ferry crossing at Bekopaka R., grows on calcareous rocks under a low open deciduous forest canopy.

Humbert 19321, Malio R. valley, tributary of Mangoky, grows on sand and sandstone in scrubland.

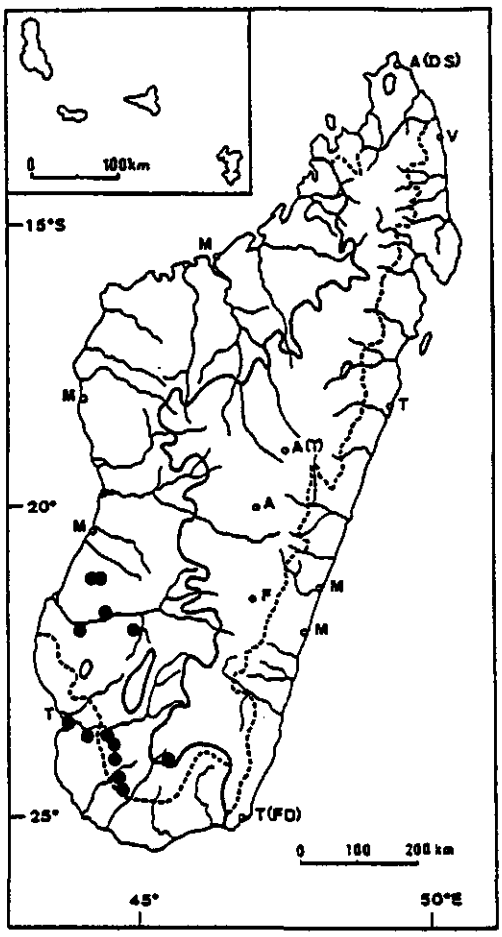
The leaves of *P. lamerei* may be glabrous or pubescent beneath near Tuléar. Near Fort-Dauphin they are always pubescent, as far as is known.

Without leaves *P. lamerei* is sometimes confused with *P. sofiense* by their short basal part of the corolla tube which is often less than 0.2 × as long as the tube. It is observed that the two species are distinguished mainly by the characters given in number 10 of Key 2.

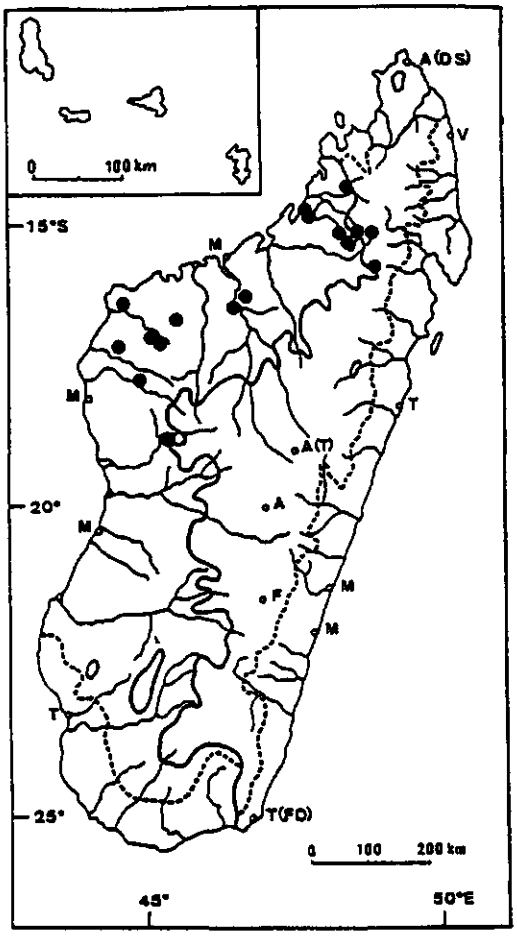
14. **Pachypodium meridionale** (H. Perrier) Pichon in Mém. Inst. Sc. Madag. sér. B, 2: 109 (1949); Markgraf, Fl. Madag. fam. 169: 284 (1976). Type: Madagascar, Tuléar (= Toliara), Mangoky R. basin, *Perrier de la Bâthie* 8954 (holotype P). Fig. 5, p. 25; Map 9, p. 50; Plates 49-52, opposite p. 80.

Basionym
Pachypodium rutenbergianum var. *meridionale* H. Perrier in Bull. Soc. Bot. Fr. 81: 311 (1934).

Candelabrum-shaped tree 2-8 m high, slightly branched; trunk bottle-shaped, up to 50 cm in diameter; bark grey. Branches covered with spines as the branchlets; branchlets 5-18 mm in diameter, covered with paired straight or sometimes curved spines, 4-11 mm long, 2-7 mm in diameter, basal part conical, 0.12-0.5 of the spine length, rarely less and spines minute. *Leaves* confined to the apices of the branchlets, petiolate; petiole 1-2.5 cm long, glabrous; blade very narrowly oblong, 3.7-8.33 × as long as wide, 8.4-26 × 1.6-7 cm, obtuse to acuminate with acumen acute at the apex, cuneate at the base and decurrent into the petiole, glabrous above, glabrous to pubescent beneath, sometimes with margin slightly revolute; secondary veins in 25-65 pairs, straight at the base, upcurved at the apex, forming an angle 45-90° with the costa; tertiary venation reticulate. *Inflorescence* congested, 6-8 × 5-7 cm, 6-17-flowered. Peduncle 0-3 mm long; pedicels 7-13 mm, glabrous. Bracts oblong or narrowly so, 3.5-3.75 × as long as wide, acuminate at the apex, glabrous out- and inside. *Flowers* sweet-scented. *Sepals* free, about as long as or longer than the basal part of the corolla tube, ovate, 1.5-1.7 × as long as wide, 4-8 × 2-2.5 mm, acuminate at the apex, glabrous on both sides. *Corolla* limb white, tube green-yellow or red-pink outside, 4.5-5.7 cm long in the mature bud and forming a comparatively wide very narrowly ovoid



Map 9. *Pachypodium meridionale.*



Map 10. *Pachypodium rosulatum.*

head, 0.44-0.56 of the bud length, 27-32 × 8-10 mm, narrowly acuminate at the apex, glabrous outside, with a pubescent belt inside 3 mm wide just below the insertion of the stamens, otherwise glabrous; tube 2-2.3 × as long as the calyx, 0.4-0.6 × as long as the lobes, 17-25(-27) mm long, basal part almost cylindrical, 0.22-0.3 of the length of the entire tube, 5-6(-7) mm long, upper part almost cylindrical, 13-15(-20) mm long, 6-7 mm wide at the mouth; lobes obliquely and narrowly ovate, 1.3-1.6 × as long as the tube, 1.8-3.4 × as long as wide, 27-35 × 8-19 mm, acuminate at the apex, often twisted in bud, undulate. *Stamens* with apex 4-5 mm below the mouth of the corolla tube, inserted 0.3-0.4 of the length of the corolla tube, at 5-7 mm from the base; anthers very narrowly triangular, 5-7 × as long as wide, 11-12 × 1.7-2 mm, pubescent at the base of the connective just below where they cohere with the pistil head. *Pistil* 12.5-14 mm long; ovary 3.5-6 × 3-4 × 2.5-3.5 mm, glabrous; disk annular, slightly 5-lobed, lobes broadly ovate rounded, teethed at the apex, 1-2 mm high and less than half as long as the ovary; style 6.5-8.1 mm long, but at the apex first widened, then narrowed and again widened just below the pistil head, glabrous; pistil head 1.4-1.5 mm high, composed of an obconical part c. 0.8-0.9 × 0.6-0.7 mm, a ring-shaped central part 0.4-0.5 × 0.9-1.2 cm and a stigmoid apex 0.2-0.3 × 0.5-1 mm. Ovules approximately 50 in each carpel. *Fruit* of 2 separate mericarps, forming an angle of

30-60° at the base; mericarps medium to dark brown outside, 10-25 × 1-2 × 1-1.5 cm, obtuse at the apex, glabrous; wall 1-1.5 mm thick. *Seeds*: grain pale brown, elliptic, 10.5-11 × 3-6 mm; testa rough; coma whitish to straw-coloured, 3-4.5 cm long. Embryo 2.7-5.5 mm long; cotyledons broadly obovate, 1.65-1.7 × as long as wide, 1.2-2.5 × 0.7-1.5 mm, rounded at the apex, subcordate at the base, rootlet 1.18-1.25 × as long as cotyledons, 1.3-1.5 × 0.5-0.6 mm.

DISTRIBUTION. Endemic to Madagascar.

ECOLOGY. Low open deciduous dry western and southern forest and scrubland on Mesozoic or Tertiary calcareous rocks and sandstone. Alt. 40-700 m. Flowering July-October and fruiting September-November.

Specimens examined:

MADAGASCAR. Toliara: Belo sur Tsiribihina, *Phillipson* 2281 (K, P, TAN, WAG); 30 km N of Manja, *Röösli & Hoffmann* 40/96 (MO, P, WAG); between Manja and Andranopasy, *Rauh* 7348/61 (M); 10 km N of Befandriana S, *Appert* 167 (Z); Mangoky R. basin, *Perrier de la Bâthie* 8871 (P), 8954 (P, type) & 12860 (P); near Ampandrandava, *Seyrig* 394 (P) & 394B (P); Manakaralahy, *Peltier* 2573 (P); near Bekily, *Boiteau* anno 1972 (P); 3 km S of Tongobory, *Phillipson* 3755 (P, TAN); SW of 'la Table'= Andatabo Hill, near Tuléar, *Röösli & Hoffmann* 66/96 (WAG); Bezaha Mahafaly Res., near Betioky, *van der Werff et al.* 12709 (P, TAN, WAG); ibid., *Phillipson* 2358 (BR, K, P, TAN, WAG); Sakoa R., *Perrier de la Bâthie* 17350 (P), 18303 (P) & 18320 (P); Onilahy R. basin, *Perrier de la Bâthie* 18571 (P); 20 km N Ampanihy, near Ankilibao, SF 19165 (P, TEF).

NOTES: *Phillipson* 2358 and *van der Werff et al.* 12709, Bezaha Mahafaly Res., grow on calcareous rocks in a low open forest dominated by *Alluaudia procera* Drake (Didiereaceae).

Röösli & Hoffmann 40/96, 30 km N of Manja is found on calcareous rocks with *P.lamerei* Drake in a low open forest.

Rauh 7348/61, between Manja and Andranopasy, in a low open forest, is accompanied by *Adansonia grandidieri* Baill. (Bombacaceae).

Röösli & Hoffmann 66/96, SW of 'la Table'= Andatabo Hill, near Tuléar, grows on calcareous rocks with soil pH c. 7 (measured by Röösli). It is the only specimen almost without spines seen there.

P. meridionale and *P. rutenbergianum* resemble each other so much, that they were often confused. The two species are distinguished mainly by the characters given in number 11 of Key 2. In addition *P. meridionale* is found in the south of Madagascar but *P. rutenbergianum* in the north.

15. **Pachypodium rosulatum** Baker in Journ. Bot. 20: 219 (1882); Poisson in Bull. Acad. Malgache sér. 2, 6: 165, pl. 6 (1924); Perrier de la Bâthie in Bull. Soc. Bot. Fr. 81: 305 (1934); Pichon in Mém. Inst. Sc. Madag. sér. B, 2: 116 (1949); Markgraf, Fl. Madag. fam. 169: 294 (1976); Leeuwenberg & Rapanarivo, Taxon 48: 181 (1999). Rejected type: Madagascar, sin.loc. (probably Fianarantsoa Province), *Baron* 256 (K). Type: Madagascar, Mahajanga, km 40 Antsohihy-Befandriana N Road, *Leeuwenberg & Rapanarivo* 14766 (holotype WAG; isotypes BR, P, TAN), typ. cons. prop. Fig. 4, p. 21; Map 10, p. 50; Plates 53-54, opposite p. 80; Plates 55-56, opposite p. 81.

Heterotypic synonym

P. drakei Costantin & Bois in Ann. Sc. Nat. sér. 9, 6: 319 (1907); Perrier de la Bâthie

in Bull. Soc. Bot. Fr. 81: 305 (1934). *P. rosulatum* var. *drakei* (Costantin & Bois) Markgr. in Adansonia sér. 2, 12: 590 (1972), **syn. nov.** Type: Madagascar, Mahajanga, near Tsitondroina, Ambato Boeny, *Perrier de la Bâthie* 968 (holotype P).

Shrub 1-2.5 m high; trunk subglobose and 15-30 cm or cylindrical and 10-20 cm in diameter; crown up to 3 × 2 m; bark grey or grey-green, smooth or with leaf scars. Branches 9-12 cm in diameter; branchlets often thin, 15-42 × 4-10 mm, often pale brown-pubescent at the apex, covered with paired spines 3-10 mm long, 1-5 mm in diameter at the base, basal part conical, 0.25-0.85 of the spine length, often in some pairs above each other 5-15 mm separate, pubescent or not when young, turning glabrous and less acute. *Leaves* confined to the apices of the branchlets, petiolate; petiole 1-10 mm long, pubescent; blade softly coriaceous, dark green and with midrib pale green above, pale glaucous, with pale green midrib and sometimes dark green reticulate venation beneath when fresh, papery when dried, ovate to elliptic or narrowly so, 2-9 × as long as wide, 28-180 × 4-45 mm, acuminate to rounded at the apex, cuneate at the base, sometimes decurrent into the petiole, margin revolute, glabrous to sparsely pubescent above, with costa densely so and with impressed venation, pubescent to glabrous beneath and with midrib and secondary veins prominent; secondary veins in 24-60 pairs, straight at the base and upcurved upwards, forming an angle of 45-85° with the costa; tertiary venation reticulate, sometimes hidden by the indumentum. *Inflorescence* pedunculate, congested, 10-50 × 3-10 cm, 2-16-flowered. Peduncle terete, 44-330 × 2-5 mm, sparsely pubescent or almost glabrous; pedicels pale or reddish-green, terete, 5-20 mm long, pubescent. Bracts sepal-like, 4-16 × 0.8-1.6 mm. *Flowers*: *Sepals* light green, connate at the base for about 0.5 mm, narrowly ovate or oblong or very narrowly so, 3-5(-7) × as long as wide, 3-7(-14) × 0.8-1.5(-2) mm, acuminate at the apex, pubescent outside, glabrous inside. *Corolla* lobes bright yellow, tube greenish-yellow with red stripes outside, often at basal part suffused with dark red, 30-44 mm long in the mature bud and forming a comparatively wide broadly ovoid head, 0.2-0.4 of the bud length, 10-15 × 6-10 mm, obtuse at the apex, pubescent outside but glabrous on the parts of the lobes covered in bud, with a pubescent belt inside 3.5-8 mm wide just below the insertion of the stamens, otherwise glabrous; tube infundibuliform, 3-10 × as long as the calyx, 1.4-2 × as long as the lobes, 27-44 mm long, basal part almost cylindrical, 0.16-0.26 of the length of the entire tube, (5-)7-10 × 2-4 mm, upper part obconical, 20-34 mm long, 10-18 mm wide at the mouth; lobes obliquely obovate to obliquely ovate, 0.47-0.7 × as long as the tube, 1-1.6 × as long as wide, 16-23 × 12-18 mm, rounded at the apex. *Stamens* with apex 13-22 mm below the mouth of the corolla tube, inserted 0.2-0.37 of the length of the corolla tube, at 7-12 mm from the base; anthers very narrowly triangular, 4-6.5 × as long as wide, 6-9 × 1-1.8 mm, pubescent at the base of the connective just below where they cohere with the pistil head. *Pistil* 10-16.7 mm long; ovary 1.8-2.5 × 1.5-2 × 1.2-1.8 mm, pubescent; disk composed of 5 broadly ovate rounded or retuse glands, 2 of which or 2 pairs of which may be partly or entirely fused and which are slightly more than half as long as the ovary; style 7.2-12.8 mm long, sparsely pubescent at the base; pistil head 1-1.4 mm high, composed of an obconical basal part 0.5-0.7 × 0.4-0.8 mm, a ring-shaped central part 0.3-0.4 × 0.6-1 mm and a stigmoid apex 0.2-0.3 × 0.4-0.8 mm. Ovules approximately 50 in each carpel. *Fruit* of 2 separate mericarps, sometimes only one developing, forming an angle of 10-60° (sometimes flowers and fruit on the same inflorescence); mericarps green or pale reddish-green when fresh, pale to dark brown with longitudinal lines outside, whitish in-

side when dried, 90-185 × 6-9 × 3-5 mm, sometimes curved, acute to obtuse at the apex, pubescent; wall 0.5-1 mm thick. *Seeds*: grain pale to medium brown, ovate to elliptic, 6.2-9.5 × 1.6-2.4 mm, margin revolute towards the hilar side; testa slightly rough at the hilar side and smooth at the other; coma straw-coloured, 15-25 mm long. Embryo 4.8-6.5 mm long; cotyledons broadly ovate, 1.35-1.66 × as long as wide, 2.3-3 × 1.5-2 mm, rounded at the apex, subcordate at the base; rootlet 1-1.3 × as long as the cotyledons, 2.5-3.5 × 1-1.8 mm.

DISTRIBUTION. Endemic to Madagascar.

ECOLOGY. Low open deciduous western forest and scrubland on sand (unconsolidated sands), gneissic or granitic rocks and basalt. Alt. 100-600 m. Flowering mainly July-October and fruiting mainly September-November.

Vernacular name: Bokalahy, Saribotaka (Sakalava); Boadaka, Songosongo (Tsimihety).

Specimens examined:

MADAGASCAR. Mahajanga: Maromandia, Sandrakoto, *Decary* 1148 (P), 1193 (P), 1277 (P), anno 1922 (P) & s.n. (BM, G, P, PRE, S); Ambalavary, Antsakabary, *Cours* 3944 (P, TAN); 30 km S of Antsakabary, *Röösli & Hoffmann* 26/96 (WAG, ZSS); Antsohihy District, *Harizo* RN 1756 (P); 40 km E of Antsohihy-Befandriana N, *Leeuwenberg & Rapanarivo* 14766 (BR, P, TAN, WAG, type cons. prop.); ibid., *Röösli & Hoffmann* 27/96 (WAG, ZSS); ibid., *Supthut & von Arx* 9325 (G, P, TAN, ZSS); near Befandriana N, *Bosser* 17110 (P, TAN); ibid., *Supthut & von Arx* 9333 (G, P, TAN, ZSS); Ambato-Befandriana N, Herb. Jard. Bot. Tana. 5474 (TAN); 20 km S of Mandritsara, *Röösli & Hoffmann* 17/96 (MO, P, WAG, ZSS); km 33 Ankerika-Analalava, *Leeuwenberg & Rapanarivo* 14727 (BR, P, TAN, WAG); ibid., *Supthut & von Arx* 9335 (G, TAN, ZSS); ibid., *Rauh* 23260 (B); Antsohihy, between Androhibe and Antanimbaribe, *Hofstätter* 260890 (ZSS); ibid., RN 1748 (P); near Antsohihy, *Rauh* 6069 (M) & 6069/61 (M); ibid., *Harizo* RN 1756 (P); Masokoamena, Upper Bemarivo R., *Perrier de la Bâthie* 8145 (P) & 8968 (P); Ambatomainty, *Perrier de la Bâthie* 8849 (P); near Mandritsara, *Humbert* 18061 (P); ibid., *Perrier de la Bâthie* 15065 (P); 36 km N of Port Berge, Sofia R., *Cremers* 2423 (TAN); Ambatorekitra (or probably Ambatoraikitra), Mahajanga District, *Decary* 15407 (K); Ankarafantsika, *Perrier de la Bâthie* 8064 (P); ibid., SF 63 (K, P, TAN, US); S edge of Ankarafantsika Res., Marovoay District, *B. Du Puy et al.* MB115 (TAN); Tsaramandroso, *Ramamonjisoa* RN 1641 (P); near Bevazaha, *Harizo* RN 1020 (P); ibid., *Ramamonjisoa* SF 13044 (P, TEF); near Ambonara, Cap St André, *Perrier de la Bâthie* 8910 (P); Ambongo, near Benetsy, Mahavavy R., *Capuron* SF 24267 (P, TEF); Manongarivo, near Ambongo, *Perrier de la Bâthie* 968bis (P); between Mahatsinjo and Andriba, Ikopa R. valley, *Hofstätter* June 1989 (ZSS 04310); Bokarafa (= Bekarafa), near Bekodoka, *Decary* 2247 (P), 8119 (P, S) & 8124 (K, P, TAN, US); near Tsitondroina, Ambato Boeny, *Perrier de la Bâthie* 968 (P, type of *P. drakei*); near Morafenobe, *Decary* 2347 (P) & 8236 (P). Toliara: Bongolava, near Ankavandra, *Decary* 7950 (BM, P, PRE); Malio R. valley, tributary of Mangoky R., Humbert 19374 (P). Sin. loc., *Baron* 5730 (K, P) & 6827 (K); *Paulian* 4 (TAN) & 5 (TAN); Acad. Malg. Oct. 1904 (P); Herb. Jard. Bot. Tana. 4911 (TAN); SF 78 (P).

CULT. Madagascar: Antananarivo, Tsimbazaza Park, *Dorr* 3175 (TAN, WAG); ibid., *Leeuwenberg* 13728 (WAG). Germany: Berlin-Dahlem Bot. Garden, *Schwerdtfeger* 24913 (B). Switzerland: Zürich, Staedtliche Sukkulenten-sammlung, *Leeuwenberg & Rapanarivo* 14649 (WAG) & 14650 (WAG).

NOTES. *Leeuwenberg & Rapanarivo* 14727, km 33 Ankerika-Analalava, grows on

white quartz sand with pH 4-5 (measured by Röösli) in low open deciduous forest. It is found with: *Protorhus deflexa* H. Perrier (Anacardiaceae) 14728, *Memecylon boinense* H. Perrier (Melastomataceae) 14730, *Tabernaemontana coffeoides* Bojer ex A. DC. (Apocynaceae) 14732, *Erythroxylum pervillei* Baill. (Erythroxylaceae) 14733, *Breonia sp.* (Rubiaceae) 14734, *Carphalea sp.* (Rubiaceae) 14735, *Hugonia breweri-oides* Baker (Linaceae) 14736, *Commiphora marchandii* Engl. (Burseraceae) 14731, *Forsythiopsis vincoides* (Lam.) Benoist (Acanthaceae) 14737, *Mascarenhasia lisianthiflora* A. DC. (Apocynaceae) 14738, *Plectaneia thouarsii* Roem. & Schult. (Apocynaceae) 14739 & 14744; *Pachypodium rutenbergianum* Vatke (Apocynaceae) 14740, *Rauvolfia media* Pichon (Apocynaceae) 14741, *Tabernaemontana stellata* Pichon (Apocynaceae) 14742, *Ancylobotrys petersiana* (Klotzsch) Pierre (Apocynaceae) 14743. (numbers of coll. *Leeuwenberg & Rapanarivo*). *P. rosulatum* is protected here because the bushfire can not enter the forest in absence of Gramineae, therefore the forest on sand is stable.

Leeuwenberg & Rapanarivo 14766, km 40 Antsohihy-Befandriana N, grows on a steep granitic rock among shrubs. It is found with *P. rutenbergianum* 14767, *Euphorbia milii* Des Moul. (Euphorbiaceae), *Kalanchoe synsepala* Baker (Crassulaceae) and many other plants, particularly Gramineae.

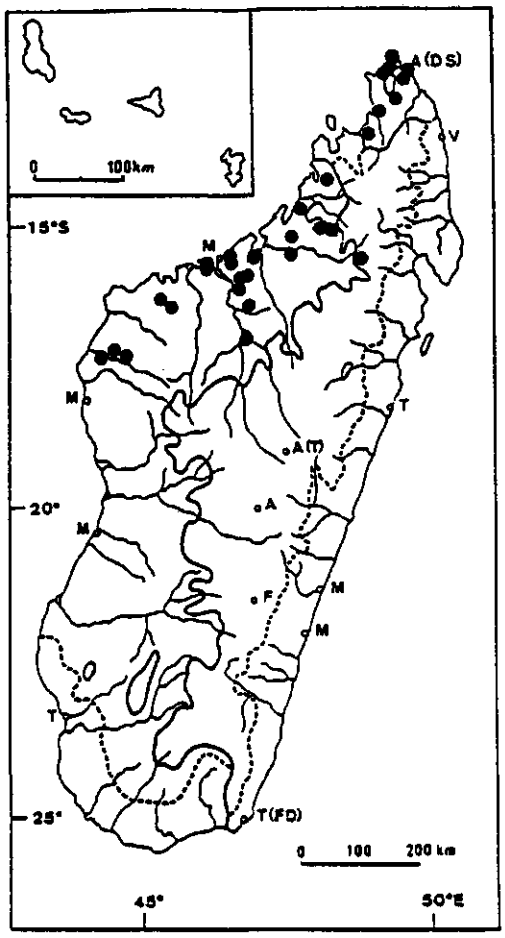
B. Du Puy MB115, Ankarafantsika, grows on white sand in low open forest. It is found with *Dalbergia* sp. (Leguminosae), *Holmskioldia* sp. (Verbenaceae) and *Terminalia* sp. (Combretaceae).

P. rosulatum is easily confused with *P. cactipes* and *P. gracilius*. See number 17 of Key 2.

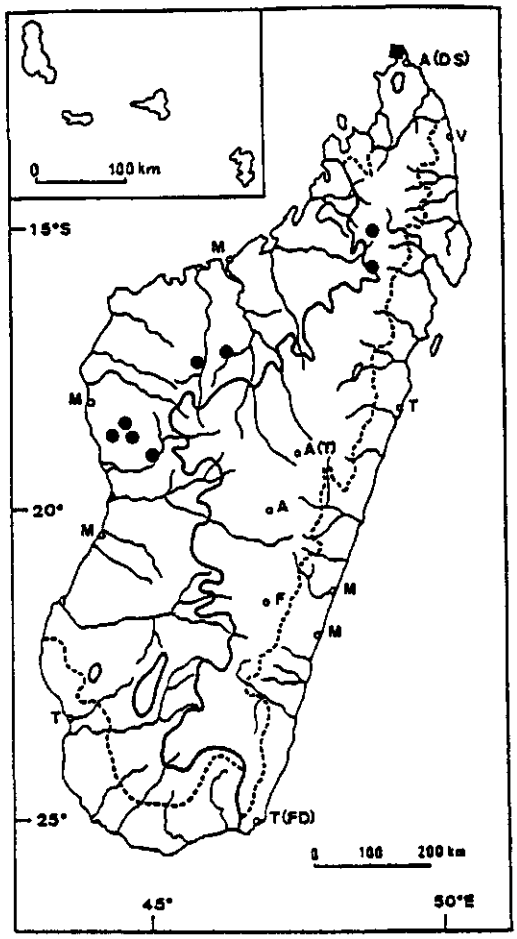
The unicate Baron 256 is a poor specimen in bud. It was the holotype of *P. rosulatum*, but it is recognized by Rapanarivo as belonging to *P. horombense*. Both species *P. horombense* and *P. rosulatum* are well-known in cultivation. Therefore it is proposed to reject *Baron 256* as type of *P. rosulatum* and to take *Leeuwenberg & Rapanarivo* 14766 as conserved type and to conserve the name *P. horombense* over the original *P. rosulatum*, as both species are extensively cultivated as ornamental plants.

16. **Pachypodium rutenbergianum** Vatke in Abh. Naturv. Ver. Bremen 9: 125 (1885); Costantin & Bois in Ann. Sc. Nat. sér. 9, 6: 310 (1907); Perrier de la Bâthie in Bull. Soc. Bot. Fr. 81: 311 (1934); Pichon in Mém. Inst. Sc. Madag. sér. B, 2: 108 (1949); Pernet in Mém. Inst. Sc. Madag. 8: 12 (1957); Markgraf, Fl. Madag. fam. 169: 282 (1976). Type: Madagascar, Mahajanga, Mojangà (= Mahajanga), *Hildebrandt* 3037 (K lectotype designated here; isolectotypes BM, LE, P). Fig. 9, p. 45; Map 11, p. 55; Plates 57-60, opposite p. 81; Plate 64, opposite p. 88.

Candelabrum-shaped tree, 3-12 m high; trunk bottle- or cigar-shaped, 15-100 cm in diameter; bark grey, grey-green or pale brown, smooth or with leaf scars; first branches often very narrowly ovoid, 5-20 cm in diameter at the base and tapering to 4-9 cm at the apex. Branchlets 1-3.5 cm in diameter, covered with paired straight or rarely curved spines, 3-15 mm long, 1-10 mm wide at the base, basal part conical and laterally compressed, 0.1-0.4 of the spine length, sometimes in between them one or two minute spines. *Leaves* confined to the apices of the branchlets, petiolate; petiole 5-60 mm long, up to 5 mm in diameter when fresh, 1-3 mm when dried, glabrous; blade softy coriaceous or softy herbaceous, shiny and with pale green midrib on both sides, with pale reticulate venation above, with dark reticulate venation beneath when



Map 11. *Pachypodium rutenbergianum.*



Map 12. • *Pachypodium sofiense*, ▪ *P. windsorii.*

fresh, papery when dried, narrowly obovate or very narrowly so, 2-10 × as long as wide, 3-45 × 1-8 cm, acuminate at the apex, cuneate at the base, often decurrent into the petiole, glabrous on both sides, midrib prominent beneath; secondary veins in 35-75 pairs, straight at the base, upcurved upwards, forming an angle of 45-90° with the costa, prominent or not above; tertiary venation reticulate if conspicuous. *Inflorescence* sessile or shortly pedunculate, congested, 7-20 × 7-15 cm, 3-30-flowered. Peduncle 0-20 × 4-20 mm, glabrous, lenticellate, with 1-4 branches pale green and which may be about 10 cm long and 1.5 cm in diameter near the end of the flowering season and covered by pedicel scars (*Leeuwenberg & Rapanarivo* 14752 WAG); pedicels 10-20 × 3-4 mm when fresh, glabrous. Bracts elliptic to oblong, 1.8-2.8 × as long as wide, 4.5-7 × 2-3 mm, acuminate at the apex, glabrous on both sides. *Flowers* sweet-scented. *Sepals* pale green, sometimes with brown edges when fresh, connate at the base for about 0.5 mm, always shorter than the basal part of the corolla tube, ovate, 1.33-2.5 × as long as wide, 4.5-6.5 × 2-4.5 mm, acuminate at the apex, glabrous on both sides. *Corolla* limb white, tube pale green outside, sometimes pale greenish-yellow inside in the throat, 5-7.5 cm long in the mature bud and forming a comparatively wide narrowly ovoid head, 0.4-0.5 of the bud length, 2-3.8 × 0.8-1.1(-1.6) cm, acuminate at the apex, glabrous outside, with a pilose-

pubescent belt inside 3-7 mm wide just below the insertion of the stamens, otherwise glabrous; tube fleshy, 6-9 × as long as the calyx, (0.7-)0.9-1.33 × as long as the lobes, 30-47 mm long, basal part almost cylindrical, 0.22-0.33 of the length of the entire tube, 8-15 mm long, upper part conical, 22-32 mm long and 6-8 mm wide at the mouth; lobes obliquely ovate to obliquely obovate, 0.75-1.05(-1.4) × as long as the tube, 1.52-2.14(-2.36) × as long as wide, 31-45(-53) × 17-25 mm, narrowly and obliquely acuminate to acute at the apex, slightly fleshy and often slightly auriculate at the base at the right side, undulate at the other, slightly twisted in bud. *Stamens* with apex (7.5-)10-15 mm below the mouth of the corolla tube, inserted 0.28-0.41 of the length of the corolla tube, at 1.1-1.5(-1.9) cm from the base; anthers very narrowly triangular, 4.8-7.5 × as long as wide, 12-15 × 2-2.5 mm, pilose-pubescent at the base of the connective just below where they cohere with the pistil head, fertile part 5 mm long. *Pistil* 1.5-1.95 cm long; ovary 4-4.5 × 2.5-3.5 × 2-2.5 mm, glabrous; disk 5-lobed 1.2 mm high, less than half as long as the ovary; style filiform, 9.5-13 mm long; pistil head 1.5-2 mm high, composed of an obconical part 0.8-1.3 × 0.7-1 mm, a ring-shaped central part 0.4-0.5 × 1.2 mm and a stigmoid apex 0.2-0.3 × 0.5-1 mm. Ovules approximately 50 in each carpel. *Fruit* of 2 separate mericarpes, sometimes only one developing, forming an angle 10-90° at the base; mericarps green, sometimes with apex dark red, turning dark brown when ripe, straight, smooth outside, pale brown inside, valves often curved or curled when dry, fusiform, 18-48 × 3-4.5 × 2-2.5 cm, acute to obtuse at the apex, glabrous; wall 2-3 mm thick. *Seeds*: grain pale to medium brown, elliptic, 11-15 × 5-8 mm, thickened at the margin on both sides; testa minutely rough or with excrescences on the hilar side, smooth at the other side, with minute excrescences near the apex and on the edges; coma straw-coloured or pale brown, 3-6 cm long. Endosperm thick. Embryo 10-14 mm long; cotyledons obovate, 1.6-1.8 × as long as wide, 7-9.5 × 4-6 mm, slightly rounded at the apex, sucordate to obtuse at the base; rootlet 0.36-0.54 × as long as the cotyledons, 3.5-5 × 1.2-2 mm.

DISTRIBUTION. endemic to Madagascar.

ECOLOGY. Low open deciduous western forest, coastal bush, scrubland and savanna on Mesozoic or Tertiary calcareous rocks, sand (dune and unconsolidated sands), sand with laterite and granitic rocks. Alt. 2-400 m. Flowering April-August (-November) and fruiting August-November.

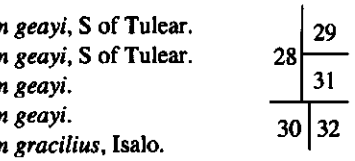
Vernacular names: Boadaka, Bontaka, Vontaka, Vohely (Antakarana, Sakalava, Tsimihety).

Use: Textiles are made of a mixture of the bark with the leaf pinnae of *Raphia* (*Ramamonjisoa* RN 1628 (P)).

Specimens examined:

MADAGASCAR. Antsiranana: Windsor Castle, NW of Diégo-Suarez, *Leeuwenberg & Rapanarivo* 14764 (TAN, WAG); NW of Diégo-Suarez, near Ambodimadiro, *Leeuwenberg & Rapanarivo* 14762 (BR, P, TAN, WAG); near Montagne des Fran-

Plate 28. *Pachypodium geayi*, S of Tulear.
Plate 29. *Pachypodium geayi*, S of Tulear.
Plate 30. *Pachypodium geayi*.
Plate 31. *Pachypodium geayi*.
Plate 32. *Pachypodium gracilius*, Isalo.



çais, *Supthut & von Arx* 9307 (G); ibid., SF 29256 (TEF); W of Diégo-Suarez, along road to Andramahimba, *B. Du Puy et al.* MB224 (P, TAN); Orangea, 17 km from Diégo-Suarez, *Humbert & Cours* 32250 (P, WAG); ibid., *Leeuwenberg et al.* 14408 (BR, P, TAN, WAG); Anivorano N, *Humbert* 32325 (P); Ankarana, near Ambondromifehy, *Capuron* SF 24724 (P, TEF, WAG); Ankarana Res., *Jongkind & Rapanarivo* 982 (PRE, TAN, WAG); ibid., *Leeuwenberg et al.* 14393 (P, TAN, WAG); Ampasimbingy, *Humbert* 18899bis (P); Nosy Mitsio, *Perrier de la Bâthie* 18802 (P); km 9 Ambilobe-Vohemar, W of Ankinadoso, *Leeuwenberg & Rapanarivo* 14752 (BR, P, TAN, WAG); Marovato, Ambanja District, *Sajy* RN 5743 (P) & RN 5748 (TAN); Maromandia, *Decary* 2177 (P) & 14489 (P); Presqu'Ile Radama, *Decary* 1179 (P); sin.loc. *Baron* 6289 (K). Mahajanga: km 30 Ankerika-Analalava, near Befandrama, *Leeuwenberg & Rapanarivo* 14740 (BR, P, TAN, WAG); km 40 Befandriana N-Antsohihy, *Leeuwenberg & Rapanarivo* 14767 (BR, P, TAN, WAG); km 48 Antsohihy-Befandriana N, *Supthut & von Arx* 9334 (G, TAN, ZSS); 34 km N of Port Berge, near Andrevorevo, *Leeuwenberg & Rapanarivo* 14712 (BR, P, TAN, WAG); 22 km N of Port Berge, near right bank Sofia R., *Leeuwenberg & Rapanarivo* 14709 (P, TAN, WAG); 3 km W of Mandritsara, *Röösli & Hoffmann* 18/96 (WAG); 3 km E of km 14 Port Berge-Mampikomy, near Ambopitika, E side of Bongolava, *Leeuwenberg & Rapanarivo* 14720 (BR, P, TAN, WAG); Marovato, near Mahajanga, *Rapanarivo* 365 (TAN); Nosingidro near Mahajanga, *Rapanarivo* 366 (TAN); Mojangà (= Mahajanga), *Hildebrandt* 3037 (BM, K, LE, P, lectotype); ibid., *Perrier de la Bâthie* 18570 (P); 1 km E of Mahajanga, *Leeuwenberg & Rapanarivo* 14681 (BR, P, TAN, WAG); Katsepy, Mahajanga District, *Kaudern* May 1912 (S); 24 km S of Katsepy, *B. Du Puy et al.* MB344 (MO, P, TAN); near Marovoay, *Perrier de la Bâthie* 18569 (P); ibid., *Rapanarivo* 363 (TAN) & 364 (TAN); km 47 Mahajanga-Tsaramandroso, *Leeuwenberg & Rapanarivo* 14680 (BR, P, TAN, WAG); 40 km WNW of Ambondromamy, along road to Majunga, *Leeuwenberg* 13887a (WAG); Ankarafantsika Res., E.F.A. 63 (P); ibid., SF 61 (P); 12 km W of Tsaramandroso, *Phillipson* 1942 (K, P, PRE, TAN, WAG); Bevazaha, Tsaramandroso, *Ramamonjisoa* RN 1628 (P); Anjiajia, District Ambato Boeny, *Bosser* 3384 (TAN); Soalala Region, *Decary* 7787 (P); ibid., *Rakotozafy* 1906A (TAN); Faranta, Soalala, SF 3978 (P, TEF); Antsingimavo, District Maintirano, *Decary* 15604 (P); Andranomavo, Res. Nat. 8, *Rakotovao* RN 4114 (P); ibid., *Randriamiera* RN 8003 (P); ibid., SF 30 (P); Antanimena Plateau, *Perrier de la Bâthie* 8845 (P); Ankara Mts, *Decary* 14557 (P); near Maevatanana, *Perrier de la Bâthie* 934 (P) & 934bis (P). Toliara: Ankirisa Forest, near Belo/Tsiribihina, *Mabberley* 753 (K); N of Morondava, *Röösli & Hoffmann* 31/96 (P, WAG). Sin.loc. *Alluaud* 1 (P); *Bosser* 5759 (TAN); *Decary* 903 (P); *Lother* 161 (M); *Perrier de la Bâthie* 934ter (P).

CULT. South Africa: Pretoria, from 16 km E of Diégo-Suarez, *Hardy* 3601 (PRE). USA: Florida, Miami Fairchild Tropical Gard., *Gillis* 11193 (S).

33 | 35
34 | 36
37 | 38

Plate 33. *Pachypodium gracilius*, Ranohira.
Plate 34. *Pachypodium gracilius*.
Plate 35. *Pachypodium gracilius*, Bezaha.
Plate 36. *Pachypodium horombense*, N of Betroka.
Plate 37. *Pachypodium horombense*.
Plate 38. *Pachypodium horombense*, N of Betroka.

NOTES. *P. rutenbergianum* is found in very diverse ecological situations. It can grow in areas with soils pH 4-7 (measured by Röösli).

Leeuwenberg & Rapanarivo 14680, km 47 Mahajanga-Antananarivo Road, grows on calcareous rocks in scrubland. It is found with a.o. *Rhopalocarpus lucidus* Bojer (Sphaerosepalaceae) and *Sclerocarya caffra* Sond. (Anacardiaceae).

Between Mahajanga-Anjohibe *P. rutenbergianum* is found on calcareous rocks with soil with pH c. 7 (Röösli & Hoffmann) in scrubland with: *Strophanthus boivinii* Baill. (Apocynaceae) 14695, *Tabernaemontana coffeoides* Bojer ex A. DC. (Apocynaceae) 14694, *Rauvolfia media* Pichon (Apocynaceae) 14698, *Ancylobotrys petersiana* (Klotzsch) Pierre (Apocynaceae) 14697. In this area *P. rutembergianum* has a trunk up to 1 m in diameter.

Leeuwenberg & Rapanarivo 14709, 22 km N of Port Berge, right bank Sofia R., grows on sand in low open deciduous forest. It is found with: *Catharanthus trichophyllus* (Baker) Pichon (Apocynaceae) 14711, *Plectaneia thouarsii* Roem. & Schult. (Apocynaceae) 14710, *Tabernaemontana calcarea* Pichon (Apocynaceae) 14708, among other species.

Leeuwenberg & Rapanarivo 14720, near Ambopitika, S of Port Berge, grows on laterite in low open deciduous forest. It is found with: *Carissa edulis* Vahl (the name will be syn. of *C. spinarum L.* in forthcoming monograph of the genus by Leeuwenberg & van Dilst) (Apocynaceae) 14718, *Ancylobotrys petersiana* (Klotzsch) Pierre (Apocynaceae) 14717.

Leeuwenberg & Rapanarivo 14767, km 40 Befandriana N-Antsohihy, grows on granite in scrubland with *P. rosulatum* and other species (see *P. rosulatum* Baker, *Leeuwenberg & Rapanarivo* 14766).

Leeuwenberg & Rapanarivo 14740, km 30 Ankerika-Analalava, is found on white quartz sand with pH c. 4.5 (Röösli & Hoffmann) in low open forest sometimes with *P. rosulatum* and other plants (see *Leeuwenberg & Rapanarivo* 14727).

Leeuwenberg et al. 14408, Orangea, near Diégo-Suarez, grows on sand (dune) in coastal bush (secondary littoral forest). It is found with: *Strophanthus boivinii* Baill. (Apocynaceae), *Plectaneia thouarsii* Roem. & Schult. (Apocynaceae) and *Sclerocarya* sp. (Anacardiaceae).

Leeuwenberg & Rapanarivo 14681, near Mahajanga, grows on sandy soil with laterite (sable roux) in savanna. It is found with: *Strychnos spinosa* Lam. (Loganiaceae), *Mascarenhasia arborescens* A. DC. (Apocynaceae), *Caesalpinia bonduc* Roxb. (Leguminosae).

Leeuwenberg & Rapanarivo 14752, km 9 Ambilobe-Vohémar, is found on sandy soil in savanna with *Petchia erythrocarpa* (Vatke) Leeuwenb. (Apocynaceae) 14753, *Plectaneia thouarsii* Roem. & Schult. (Apocynaceae) 14754 and *Mascarenhasia lanceolata* A. DC. 14755.

Jongkind & Rapanarivo 982, Ankarana Res., grows on calcareous rocks in scrubland dominated by *Zizyphus jujuba* Lam. (Rhamnaceae).

B. Du Puy MB344, 24 km S of Katsepy, is found on limestone with short Burseraceae and Sapindaceae trees, and *Hyphaene* sp. (Palmae).

The paired spines are longitudinally cleft in 2 or 3 parts when the branches grow thicker. Leaves appear after flowering.

P. rutenbergianum can be easily confused with *P. meridionale*. It is observed that the two species are distinguished mainly by the characters given in number 11 of Key 2.

17. **Pachypodium sofiense** (Poiss.) H. Perrier in Bull. Soc. Bot. Fr. 81: 311 (1934); Pichon in Mém. Inst. Sc. Madag. sér. B, 2: 110 (1949); Markgraf, Fl. Madag. fam. 169: 286 (1976). Type: Madagascar, Mahajanga, near Antsakabary, Upper Sofia R. basin, *Perrier de la Bâthie* 15030 (holotype P). Fig. 5, p. 25; Map 12, p. 55; Plates 61-63, opposite p. 88.

Basionym
P. rutenbergianum var. *sofiense* Poiss. in Bull. Acad. Malgache sér.2, 6: 162, pl.3 (1924).

Heterotypic synonym
P. rutenbergianum var. *perrieri* Poiss. in op. cit. 162, pl. 4 (1924). Type: Madagascar, Mahajanga, Ankara Mts, *Perrier de la Bâthie* 1142 (holotype P).

Small bottle- or candelabrum-shaped tree 2-8 m high, slightly branched; trunk more or less straight, 10-50 cm in diameter; bark silver-grey. Branchlets 17-25 × 5-11 mm, covered with paired straight spines, 1-6 mm long, 1-3 mm in diameter at the base, basal part conical, 0.25-0.6 of the spine length. *Leaves* confined to the apices of the branchlets, petiolate; petiole 7-50 mm long, sparsely pubescent to almost glabrous; blade coriaceous, bright green above, pale green beneath when fresh, papery when dried, elliptic to obovate or narrowly so, 1.7-3.2 × as long as wide, 8.5-24.5 × 2.4-10.5 cm, acuminate to obtuse at the apex, cuneate at the base, sometimes decurrent into the petiole, glabrous above and with impressed venation or not, sparsely pubescent beneath, especially on veins, with midrib and secondary veins prominent; with 10-25 pairs of secondary veins straight at the base, upcurved upwards, forming an angle of 30-85° with the costa; tertiary venation reticulate. *Inflorescence* sessile or shortly pedunculate, congested, 7-12 × 9-14 cm, 6-21-flowered; peduncle 0-12 × 4-6 mm, glabrous; pedicels pale green, 10-25 mm long, 1-2 mm in diameter at anthesis and when fruiting up to 8 mm in diameter, glabrous. Bracts oblong, 2-3 × as long as wide, 3.5-6 × 1.7-3 mm, acuminate with straight white hairs at the apex, glabrous on both sides. *Flowers* sweet-scented. *Sepals* cream when fresh, connate at the base for about 0.5 mm, ovate, 1.2 × as long as wide, 3-5 × 2.5-4 mm, acuminate, ciliate or not, glabrous on both sides. *Corolla* limb white, tube cream, 6-8.5 cm long in the mature bud and forming a wide very narrowly ovoid head, 0.35-0.5 of the bud length, 22-42 × 10-14 mm, obtuse at the apex, glabrous outside, with a pubescent belt inside 1-3 mm wide just below the insertion of the stamens, otherwise glabrous; tube 13.7-17.5 × as long as the calyx, 1.40-1.77 × as long as the lobes, 44-60 mm long; basal part almost cylindrical, 0.1-0.17 of the length of the entire tube, 6-9 × 3-5 mm; upper part almost cylindrical, 38-51 mm long and 7-12 mm wide at the mouth; lobes obliquely ovate, 0.56-0.7 × as long as the tube, 1.32-1.46 × as long as wide, 27-38 × 19-28 mm, acute at the apex. *Stamens* with apex 2.8-4 cm below the mouth of the corolla tube, inserted 0.14-0.2 of the length of the corolla tube, at 8-10 mm from the base; anthers very narrowly triangular, 5-6 × as long as wide, 12-12.5 × 2-2.5 mm, sparsely pubescent inside at the base of the connective just below where they cohere with the pistil head. *Pistil* 9.7-11.7 mm long; ovary 2.5-4 × 2-3 × 1.5-2.2 mm, glabrous; disk annular, 0.75-1.2 mm high; style 6 mm long, glabrous; pistil head 1.2-1.7 mm high, composed of an obconical basal part 0.7-1 × 0.6-0.8 mm, a ring-shaped central part 0.3-0.4 × 1-1.2 mm and a stigmoid apex 0.2-0.25 × 0.7-0.8 mm. Ovules approximately 50 in each carpel. *Fruit* of 2 sepa-

rate mericarps, sometimes only one developing; mericarps pale brown, densely lenticellate outside, narrowly obovoid 17-18 × 2-2.5 × 1.5-2.5 cm, glabrous; wall 2-3 mm thick. *Seeds*: grain medium brown, ellipsoid to ovoid, 15-19 × 6.5-8 × 2-3 mm; testa smooth; coma straw-coloured, 3.55 cm long. Embryo 13 mm long; cotyledons elliptic, 1.58-1.83 × as long as wide, 9.5-11 × 6 mm, rounded at the apex, cordate at the base; rootlet 0.5 × as long as the cotyledons, 4.5-5.5 × 2.5-3 mm.

DISTRIBUTION. Endemic to Madagascar.

ECOLOGY. Low open deciduous western forest or scrubland on Mesozoic calcareous rocks and gneissic rocks. Alt. 20-600 m. Flowering June-September and fruiting October.

Vernacular name: Bontana (Tsimihety).

Use: bark used as textile fibre (Herb. Jard. Bot. Tana. 5319 (TAN)).

Specimens examined:

MADAGASCAR. Mahajanga: near Antsakabary, Upper Sofia R. basin, *Perrier de la Bâthie* 15030 (P, type); Befandriana Nord, Andavakaka Pass, Herb. Jard. Bot. Tana. 5319 (TAN); 6 km NW of Mandritsara, *Röösli & Hoffmann* 14/96 (P, WAG); Kelifely Mts, *Perrier de la Bâthie* 8967 (P); Ankara Mts, *Perrier de la Bâthie* 1142 (P, type of *P. rutenbergianum* var. *perrieri*); Bemaraha Mts, c. 20 km W of Marerano, Manambolo R., *B. Du Puy et al.* MB759 (TAN); Bemaraha Res., near Antsalova, *Morat* 92 (K, P, TAN), 778 (TAN, WAG) & 4829 (TAN); ibid., *Phillipson* 2219 (BR, K, P, PRE, TAN, WAG); Antsalova-Tsiandro Road, *Bosser* 18188 (P, TAN) & 18191 (P); near Tsiandro, *Leandri & Capuron* 2367 (P); ibid., *Lowe* 20 Jul. 1929 (BM); near Ambalarano, *Rabarison* anno 1992 (Faculté des Sc. Univ. Antananarivo); Tsiribihina R. valley, Bemaraha, *Humbert* 11481 (P).

NOTES. *Rabarison* s.n., near Ambalarano, Antsingy de Bemaraha, grows on calcareous rocks in low open forest. It is found with *Delonix adansonioides* (R. Vig.) Capuron (Leguminosae), *Gyrocarpus americanus* Jacq. (Combretaceae), *Diospyros* sp. (Ebenaceae), *Dalbergia* sp. (Leguminosae), *Erythroxylum seyrigii* H. Perrier (Erythroxylaceae), *Commiphora aprevalii* Guill. (Burseraceae) and *Hildegardia erythrosiphon* Baill. (Sterculiaceae).

Röösli & Hoffmann 14/96, near Mandritsara, grows on gneiss with soil with pH c. 4 (measured by Röösli). They found here the thickest trunk which is up to 50 cm in diameter.

B. Du Puy et al. MB759, c. 20 km W of Marerano on the Manambolo R., grows on limestone in low open deciduous forest under a canopy of *Bussea* sp. (Leguminosae).

P. sofiense is easly confused with *P. lamerei*. See number 10 of Key 2.

18. **Pachypodium windsorii** Poiss. in Bull. Acad. Malgache sér. 2, 3: 237 (1922); Perrier de la Bâthie in Bull. Soc. Bot. Fr. 81: 302 (1934). Type: Cult. Tsimbazaza Park, Antananarivo, Madagascar, collected at Windsor Castle rock, near Diego Suarez, Antsiranana Province, or from seed collected there, *Perrier de la Bâthie* s.n. (holotype P). Fig. 10, p. 61; Map 12, p. 55; Plate 64, opposite p. 88; Plates 65-68, opposite p. 89.

Homotypic synonym

P. baronii var. *windsorii* (Poiss.) Pichon in Mém. Inst. Sc. Madag. sér. B, 2: 123 (1949) (as *baroni* and *windsori*); Markgraf, Fl. Madag. fam. 169: 290 (1976).

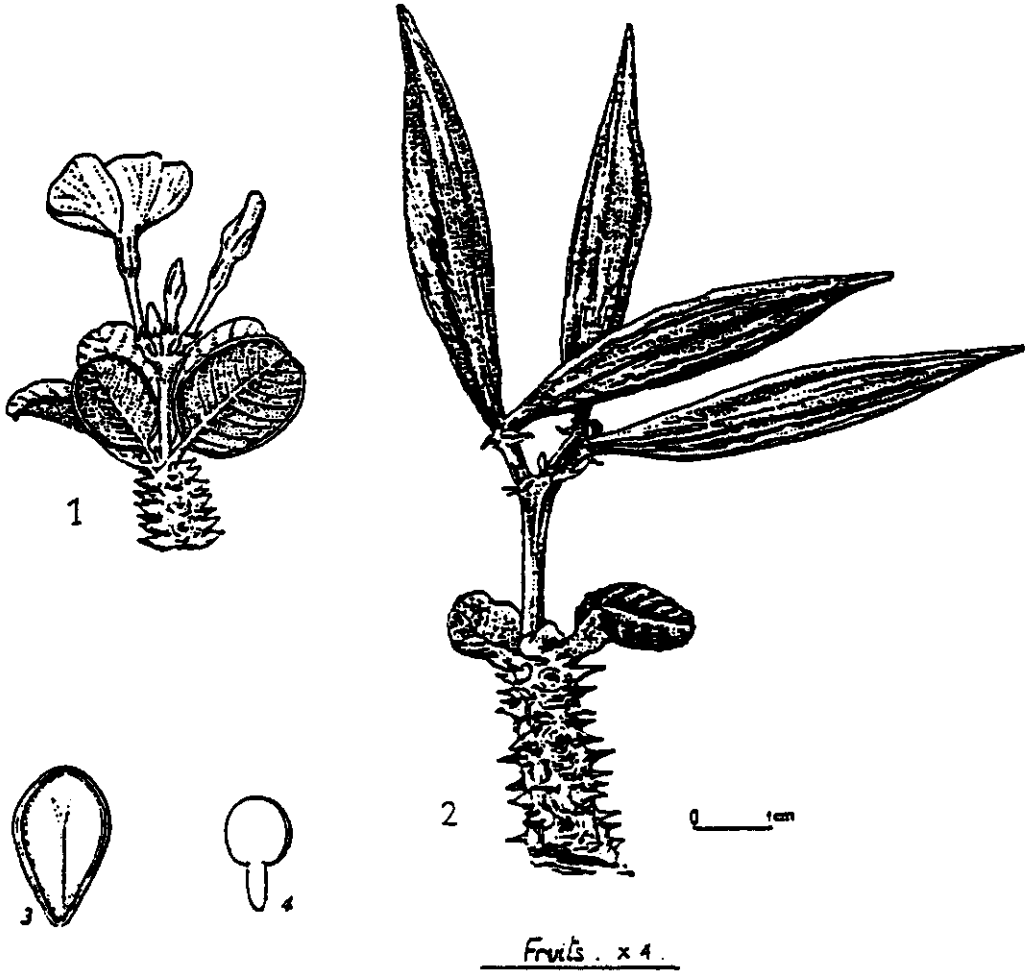


Figure 10. *Pachypodium windsorii*: 1 and 2 = habits (× 1), 3 = grain (× 3), 4 = embryo (× 3) (1 and 2 = from Leeuwenberg & Rapanarivo 14763; 3 and 4 = from SF 12058).

Shrub 0.50-1.50 m high; trunk subglobose or ovoid 30-50 × 35-60 cm; bark grey or grey-green, smooth or with leaf scars; with 1-5 branches from the apex and/or the side of the trunk, swollen at the base into a subglobose or ovoid part up to 5 × 8 cm, above terete, 10-80 cm long, often overhanging, 1.5-3 cm in diameter and branched or not; branchlets 7-13 mm in diameter, covered with paired straight or slightly curved spines, 2-6 mm long, 1-5 mm wide at the base, basal part conical and laterally compressed, 0.33-0.71 of the spine length, pubescent with red apex when young, turning glabrous and less acute. *Leaves* confined to the apices of the branchlets, shortly petiolate; petiole 2-10 mm long, 2-5 mm in diameter, pubescent; blade subcoriaceous, dark green, bullate, shiny, with midrib and secondary veins pale green and tertiary venation reticulately impressed above, pale glaucous with darker venation beneath when fresh, papery when dried, ovate to elliptic, 1.1-2.5 × as long as wide, 3-11 × 2-7.7 cm, shortly acuminate, apiculate, emarginate or rounded at the apex, acute to rounded at the base, sparsely pubescent to glabrous above, sometimes with midrib and secondary veins densely so, pubescent to sparsely so beneath with costa and secondary veins prominent; secondary veins in 13-20 pairs, straight at the base,

upcurved upwards, forming an angle of 45-90° with the costa; tertiary venation reticulate, sometimes hidden by the indumentum. *Inflorescence* pedunculate, congested, 6-13 × 2-6.7 cm, 3-7-flowered. Peduncle 12-80 × 3-5 mm when fresh, sparsely pubescent or glabrous; pedicels short, 3-5 mm long, slightly elongate in fruit up to 8 mm, sparsely pubescent. Bracts ovate, 2-2.5 × as long as wide, 3-5 × 1.5-2 mm, acuminate at the apex, sparsely pubescent outside, glabrous inside. *Flowers*: *Sepals* pale green, connate at the base for about 0.2 mm, ovate, 1.33-1.5 × as long as wide, 2-3 × 1.5-2 mm, obtuse to acuminate at the apex, sparsely pubescent outside, ciliolate, glabrous inside. *Corolla* limb pale red to crimson, tube with upper part reddish-green and basal part pale green and with longitudinal reddish lines outside, with yellow or pale green star inside surrounded by dark red in the throat, 3-3.5 cm long in the mature bud and forming a comparatively wide broadly ovoid head, 0.4-0.42 of the bud length, 13-14 × 6-7 mm, obtuse to rounded with a blunt tip and ciliate near and at the apex at the side not covered in bud, pubescent outside in longitudinal stripes up to the base of the lobes, glabrous on the part of the lobes covered in bud, glabrous inside on the basal 7-8 mm, with a pubescent belt from 8-10 mm below the insertion of the stamens to the mouth, even densely so at the mouth; tube 7-12 × as long as the calyx, 0.92-1.33 × as long as the lobes, 20-27 mm long, basal part almost cylindrical, 0.55-0.62 of the length of the entire tube, 11-17 mm long, 2-3.5 mm wide above the base; upper part almost cylindrical, 9-11 mm long, 4-6 mm wide at the mouth; lobes obliquely and broadly obovate, 0.73-1.1 × as long as the tube, 1.1-1.44 × as long as wide, 15-26 × 12-21 mm, rounded at the apex. *Stamens* with apex 3-5 mm below the mouth of the corolla tube, inserted 0.62-0.72 of the length of the corolla tube, at 16-17 mm from the base; anthers very narrowly triangular, 6.5-7 × 1 mm, sparsely pubescent inside at the base of the connective just below where they cohere with the pistil head. *Pistil* 18-20 mm long; ovary 2-2.3 × 2 × 1.5-1.8 mm, pubescent on the part not covered by the disk; disk 1 mm high, 5-lobed, with lobes rounded at the apex, less than half as long as the ovary; style 15-16.7 mm long, sparsely pubescent; pistil head 1 mm high, composed of an obconical part 0.5-0.6 × 0.6-0.7 mm, a ring-shaped central part 0.3 × 0.7-0.8 mm and a stigmoid apex 0.1-0.2 × 0.5 mm. Ovules approximately 50 in each carpel. *Fruit* of 2 separate mericarps, sometimes only one developing, with an angle 20-90° at the base (sometimes with flowers on the same inflorescence);

mericarps pale green or pale reddish-green when fresh, pale brown outside and whitish to very pale brown inside when dried, with longitudinal lines, fusiform, 40-65 × 10-12 × 10 mm, obtusely acuminate at the apex, puberulous outside; wall 1 mm thick. *Seeds*: grain pale to medium brown, elliptic to ovate, 5-8 × 3-5 mm; testa smooth; coma straw-coloured 1-1.3 cm long. Embryo 5.5-6 mm long; cotyledons orbicular, 1-1.4 × as long as wide, 2-4 × 1.8-3.5 mm; rootlet 1-1.2 × as long as the cotyledons, 3 × 0.8-1 mm.

DISTRIBUTION. Endemic to Madagascar.

ECOLOGY. Low open deciduous western forest on Mesozoic calcareous rocks. Alt. 270-390 m. Flowering and fruiting November-December.

Specimens examined:

MADAGASCAR. Antsiranana: Windsor Castle, near Diégo-Suarez, *Capuron* SF 12058 (P, TEF) & SF 11322 (P, TEF); ibid., *Labat* 2879 (P, TAN, WAG); ibid., *Leeuwenberg & Rapanarivo* 14763 (BR, P, TAN, WAG); ibid., *Supthut & von Arx* 9302 (G, TAN, ZSS).

CULT. Madagascar: Antananarivo, Tsimbazaza Park, from Windsor Castle near

Diégo-Suarez, *Perrier de la Bâthie* s.n. (P type). Germany: München-Nymphenburg Bot. Garden, from near Diégo-Suarez, s.coll. s.n. (M).

NOTES. *Leeuwenberg & Rapanarivo* 14763 grows on calcareous rocks in low open forest. It is found with: *Aloe* sp. (Aloaceae), *Tetradenia* sp. (Labiatae), *Ancylobotrys petersiana* (Klotzsch) Pierre (Apocynaceae), *Euphorbia* sp. (Euphorbiaceae) and *P. rutenbergianum* Vatke *Leeuwenberg & Rapanarivo* 14764.

Röösli took photographs of *P. windsorii* at the Montagne de Français and collected only seeds there.

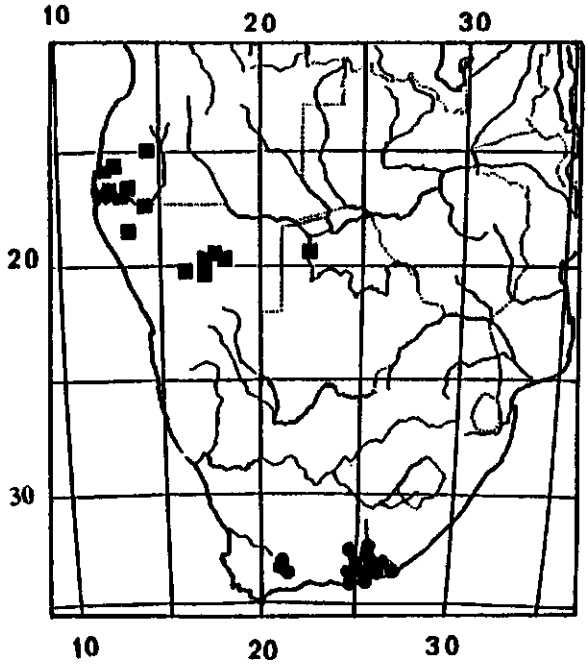
P. windsorii is easily confused with *P. baronii*. The two species are distinguished mainly by the characters given in number 5 of Key 2.

19. **Pachypodium bispinosum** (L.f.) A. DC., Prodr. 8: 424 (1844); Stapf in Fl. Cap. 4, 1: 516 (1907); Codd in Fl. S. Afr. 26: 284 (1963). Type: South Africa, W Cape Province, *Thunberg* (lectotype S, designated by Codd). Fig. 11, p. 66; Map 13, p. 64; Plates 69-70, opposite p. 89.

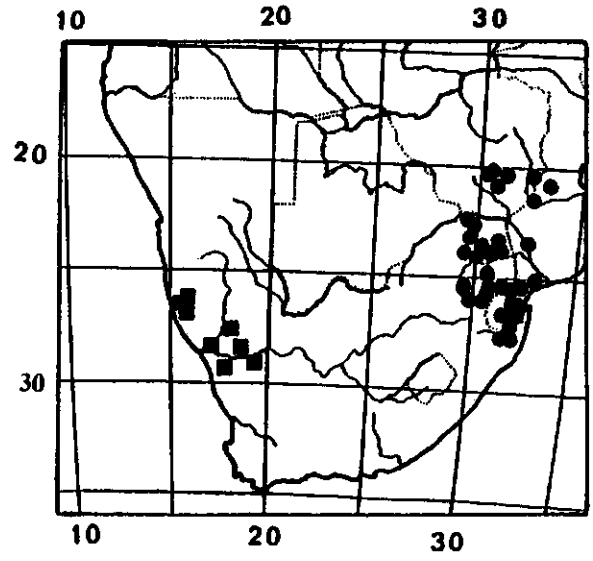
Basionym and homotypic synonyms
Echites bispinosa L.f., Suppl. 167 (1781); Thunberg, Prodr. 37 (1794); *Belonites bispinosa* (L.f.) E. Mey., Comm. 188 (1837). *Pachypodium glabrum* G. Don, Gen. Syst. 4: 77 (1837).

Heterotypic synonyms
P. tuberosum Lodd., Bot. Cab. 17: t. 1676 (1830), non Lindley (1830). *Pachypodium tuberosum* var. *loddigessii* A.DC., l.c. Type: icon. cit.

Shrub with a large, half- to almost fully submerged tuberous stem 14-18 cm in diameter bearing several to numerous slender branches. Branches erect or spreading, simple or sparingly branched, 12-45 cm long and 5-10 mm in diameter (from Codd 1963); branchlets pubescent, turning glabrous 1-8.5 cm long, 3-5 mm in diameter, covered with paired straight or curved spines, 3-25 × 0.4-1.5 mm, sometimes in between them a third small one, 0.5-8 × 0.1-0.5 mm, fused at the base and forming a subconical and laterally compressed excrescence 2-4 × 1-3 × 0.5-3 mm, with in the centre a rounded depression on which the leaf is inserted. *Leaves* sessile, blade medium green, with midrib pale green above, pale green beneath when fresh, papery when dried, ovate to oblong or narrowly so, 2.6-5 × as long as wide, 15-40 × 4-8 mm, acuminate and mucronate (mucro 0.5-1 mm) at the apex, cuneate at the base, glabrous to sparsely pubescent above, glabrous to pubescent beneath and with midrib prominent, with revolute margin; secondary veins in up to 7 pairs, rather straight (visible only in fresh leaves) forming an angle of 30-80° with the costa; tertiary venation not visible. *Inflorescence* terminal, congested; 2-4 × 1-2.5 cm, 1-5-flowered. Peduncle obsolete; pedicels pale green, 1-5 mm long, glabrous. Bracts oblong or narrowly so, 2.5-5 × as long as wide, 2.5-4 × 0.7-3 mm, acuminate at the apex, glabrous out- and inside. *Flowers*: *Sepals* pale green, connate at the base for about 0.5 mm, ovate or narrowly so, 1.75-2.5 × as long as wide, 3.5-5 × 0.7-1 mm, acuminate at the apex, glabrous on both sides. *Corolla* limb purple to pale pink, tube with basal part pale green and upper part dark pink outside and at the throat inside, 1.1-2.5 cm long in the mature bud and forming a comparatively wide broadly ovoid head, 0.3-0.4 of the bud length, 4-8 × 3-9 mm obtuse to rounded at the apex, glabrous outside, with a belt in-



Map 13. • *Pachypodium bispinosum*, ▪ *P. lealii*.



Map 14. ▪ *Pachypodium namaquanum*, • *P. saundersii*.

side of stiff hairs directed downwards 3 mm wide just below the insertion of the stamens, otherwise glabrous; tube infundibuliform, 3-6.8 × as long as the calyx, 2.1-2.7 × as long as the lobes, 13-27 mm long, basal part almost cylindrical, 0.29-0.47 of the length of the entire tube, 4-8 mm long, 2-4 mm wide, upper part obconical; 7-19 mm long, 6-12 mm wide at the mouth, lobes broadly obovate to broadly ovate, 0.37-0.42 × as long as the tube, 1.1-1.25 × as long as wide, 5-10 × 4-9 mm, rounded to slightly apiculate at the apex. *Stamens* with apex 3-13 mm below the mouth of the corolla tube, inserted 0.37-0.52 of the length of the corolla tube, at 6-10 mm from the base; anthers very narrowly triangular, 4.4-5 × as long as wide, 3.5-5 × 0.8-1 mm, pubescent inside at the base of the connective just below where they cohere with the pistil head. *Pistil* 8-10 mm long; ovary 1.5-2 × 1.2-1.5 × 1-1.5 mm, glabrous; disk 0.6-1.3 mm high, deeply 5-lobed with lobes retuse at the apex, often less than half as long as the ovary; style 6-6.2 mm long, glabrous; pistil head 0.6-1 mm high, composed of a conical or subcylindrical basal part 0.3-0.6 × 0.4-0.6 mm, a ring-shaped central part 0.2-0.25 × 0.3-0.6 mm and a stigmoid apex 0.1-0.15 × 0.3-1 mm. Ovules approximately 20 in each carpel. *Fruit* of 2 mericarps, sometimes only one developing, forming an angle of 5-30° at the base; mericarps pale to dark brown or pale greenish-brown when dried, obovoid 50-65 × 9-12 × 7-10 mm, acute at the apex,

Plate 39. *Pachypodium inopinatum*.
Plate 40. *Pachypodium inopinatum*.
Plate 41. *Pachypodium inopinatum*.
Plate 42. *Pachypodium inopinatum*.
Plate 43. *Pachypodium inopinatum*.

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41

glabrous or puberulous; wall 0.5 mm thick. *Seeds*: grain pale brown, elliptic, 5 × 2 mm; coma straw-coloured, 2 cm long. Embryo: cotyledons orbicular, 1.5 × 1.5 mm; rootlet 2.5 × 1.2 mm.

DISTRIBUTION. Endemic to the Western and Eastern Cape Provinces of South Africa.

ECOLOGY. Fynbos, Grassland, Nama Karoo, Savanna and Thicket on clay, gravel quartzite and sand. Alt. 20-800 m. Flowering February-July and fruiting August-December.

Vernacular names: Bobbejaankos, Kafferkambroo, -Kamkoo, -Kamoo, Kambroo, Kamoa, Kragman, Sterk- (Smith 1966).

Specimens examined:

SOUTH AFRICA. Western Cape: between Zuurberg Range and Klein Bruintjes Hoogte, Somerset Div., *Drège* anno 1837 (K, PRE, S); Blauwkrantz, *Schönland* 399 (PRE); Ladismith Div., *Baker & Lewis* 20342 (K); 27 km E of Landismith, *Liebenberg* 710 (PRE); S of Ladismith, *van Jaarsveld & Marthinus* 7878 (PRE); sin. loc., *Thunberg* anno 1775 (S, lectotype). Eastern Cape: Albany, Graaff Reinet, *Thode* A 595 (GH, K, PRE); ibid., *Bolus* 113 (K); Farm Langplaas, Somerset E Distr. *Schoeman* 8 Oct. 1986 (PRE); near Winterfontein, *Hafström & Acocks* 11998 (K, PRE); N of Steytlerville, *Vorster* 2424 (PRE); Carlisle Bridge, Albany Distr., *Bayliss* 3103 (UC) & 3639 (NY, UC); Jagersdrift, between Bushman and Karega Rs., Albany Region, *Ecklon & Zeyher* Oct. probably anno 1830 (28.10) (B, BP, C, E, F, G, GH, HBG, L, LE, NY, P, PRE, UPS, US, W, Z); Ecca Pass, *Bayliss* 7593 (BR, HBG, WAG); Pluto's Vale, *Bayliss* 5558 (A, C, WAG); ibid., *Dyer* 1156 (L); Fish R., Albany Distr., *Dyer* 132 (K, PRE); ibid., *Esterhuysen* 13267 (P); ibid., *Lotsy et Goddijn* 71 (L) & 175 (L); 21 km N of Grahamstown, *Galpin* 13262 (PRE); 14 km from Grahamstown to Fort Beaufort, *Arnold* 627 (PRE); near Alicedale, *Bayliss* 8059 (BR, G, HBG, WAG); ibid., *Archibald* 5979 (PRE); near Grahamstown, *Humbert* 10367 (K, WAG); ibid., *Kleinhoonte* 475 (L); ibid., *Rogers* 27823 (A, NY, S, Z); ibid., *Taylor* 1824 (NY); Loerie R., *Penther* 2006 (M, W); Groendal Res., *Scharf* 1944 (PRE); Swartkops R., Uitenhage District, *Marloth* 13132 (PRE); ibid., *Zeyher* 261 (BM, E, K, PRE, W) & 3412 (S); Spring Nature Res., *Olivier* 2042 (WAG); near Port Elizabeth, *Dahlstrand* 345 (GB, PRE), 1781 (C, GB) & 3125 (PRE); ibid., *Fries* 1017 (P); ibid., *Groen* 1120 (WAG); ibid., *Peter* 50801 (B); ibid., *v. Wettstein* 1929 (M); near Peddie, *Sim* 19696a (PRE); near Humansdorp, *Burtt-Davy* 12046 (PRE); Gowies Kloof, Grahamstown, *Sidey* 1220 (S); Ecca R., *Taylor & Edward* 8743 (PRE); Great Fish R. Region, Grahamstown, *Sørensen* 530 (C) & 542 (C); near Addo Drift, *Fries* 746 (PRE); ibid., *Hutchinson* 1510 (K); ibid., *Lam & Meeuse* 4745 (L); ibid., *Long* 248 (K); near Uitenhage, *Burchell* 3880 (K, PRE); ibid., *Hafström & Lindelberg* 8 Aug. 1936 (S); ibid., *Schlechter* 6078 (Z); ibid., *Thode* A 679 (PRE). Sin. loc., *Fraser* 18 (E); *Oldenburg* 920 (BM).

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Plate 44. *Pachypodium lamerei*, Bevaketa.
Plate 45. *Pachypodium lamerei*, Tulear.
Plate 46. *Pachypodium lamerei*, Tulear.
Plate 47. *Pachypodium lamerei*, Andohahela.
Plate 48. *Pachypodium lamerei*, W of Fort-Dauphin.

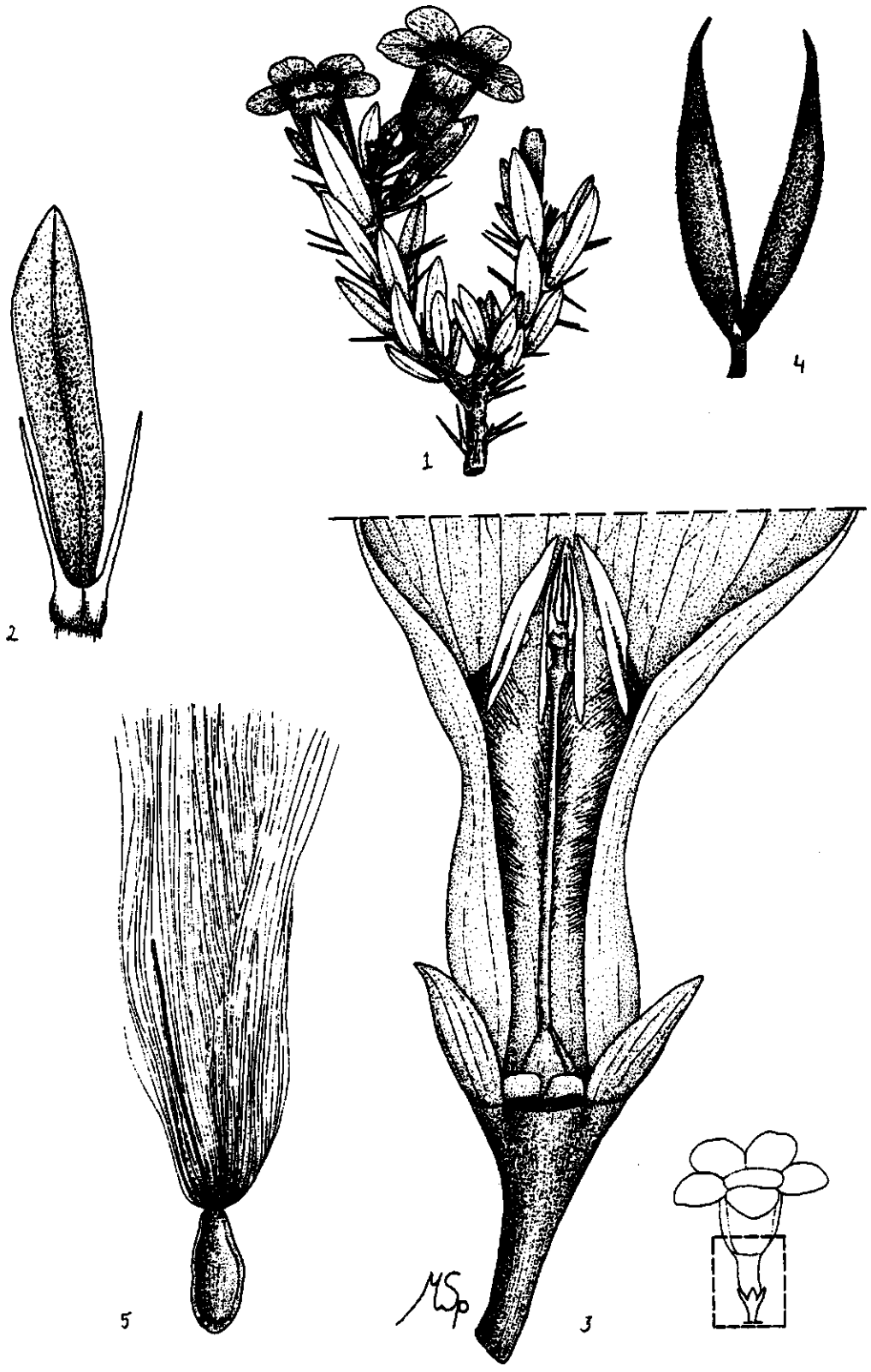


Figure 11. *P. bispinosum*: 1 = habit (× 1), 2 = leaf and spines (× 3), 3 = opened flower (× 9), 4 = fruit (× 1), 5 = seed (× 4.1/2) (1 and 3 = from Penther 2006; 2 = from Sidey 1220; 4 and 5 = from Burtt-Davy 12046).

NOTE. Sometimes *P. bispinosum* and *P. succulentum* are similar. The two species are distinguished mainly by the characters given in number 2 of Key 3.

20. **Pachypodium lealii** Welw. in Trans. Linn. Soc. 27: 45 (1871); Stapf in Fl. Trop. Afr. 4, 1: 230 (1902); Markgraf in Notizbl. Bot. Gart. Berlin 15: 457 (1941); Codd in Fl. S. Afr. 26: 287 (1963). Type: Angola, Huila, Bumbo District, near Quitibe (= Quiteve), *Welwitsch* 1510 (holotype BM, isotypes G, K, P). Fig. 12, p. 68; Map 13, p. 64; Plate 71, opposite p. 96.

Heterotypic synonym
P. giganteum Engl. in Bot. Jahrb. 19: 147 (1895). Type: Namibia, Otjitambi, Pforten Mts, Gürich 15 (holotype B†). Neotype: Namibia, Kaokoveld, 10 km WSW of Epupa Falls, *Leistner et al.* 261 (neotype K, designated here; isoneotypes PRE (n.v.), SRGH, WAG).

Shrub or candelabrum-shaped tree 2-10 m high. Trunk 10-40 cm in diameter at the base; bark grey to pale brown, smooth or with leaf scars; wood soft. Branches glabrous; branchlets 4.5-17 cm long, 6-8 mm in diameter, covered with straight or rarely curved spines in groups of three, two of which subequal, 8-40 mm long, 1.5-3.5 mm wide at the base, often in between them the third small one 3-30 × 0.5-2 mm, fused at the base and forming a subconical and laterally compressed excrescence 2-10 × 0.5-10 × 1-7 mm, leaf scar not at the apex between the two spines but outside near the base. *Leaves* confined to the apices of the branchlets, sessile or shortly petiolate, also on minute lateral branchlets; petiole 0-5 mm long, pubescent or sparsely so; blade papery and sometimes greenish-brown when dried, elliptic to obovate or narrowly so, 1.6-4 × as long as wide, 2.3-9.5 × 1-4.3 cm, shortly acuminate to apicute, often mucronate (mucro 0.5-1 mm long), rarely rounded at the apex, cuneate at the base or decurrent into the petiole, pubescent to almost glabrous on both sides, with secondary veins often impressed (in dried leaves), midrib prominent beneath; secondary veins in 9-20 pairs, rather straight at the base, upcurved upwards, forming an angle of 30-70° with the costa; tertiary venation reticulate if conspiscuous. *Inflorescence* terminal, sessile or shortly pedunculate, congested, 4-10 × 6-12 cm, 6-20-flowered or more. Peduncle 0-12 × 3-6 mm, glabrous or nearly so; pedicels 1-5 mm long at anthesis, elongate up to 8 mm under the fruit, glabrous or nearly so. Bracts ovate, 1-1.5 × as long as wide, 2-3 × 1.5-2 mm, acuminate at the apex, sometimes fringed with minutes hairs and turning glabrous out- and inside. *Flowers* sweet-scented. *Sepals* connate at the base for about 0.5 mm, ovate, 1-1.33 × as long as wide, 3-4 × 3 mm, acuminate at the apex, margin ciliate, glabrous out- and inside. *Corolla* limb white inside, white and tube sometimes greenish-cream outside, often suffused with dark red, especially in bud, 50-60 mm long in the mature bud and forming a comparatively broadly ovoid head, 0.4-0.5 of the bud length, 23-31 × 8-15 mm, acuminate at the apex, glabrous outside, glabrous inside for 3-6 mm just above the base, pubescent from 11-14 mm below the insertion of the stamens with indumentum becoming sparsely so upwards and ending 2-3 mm below the throat; tube 8-11 × as long as the calyx, 1-1.45 × as long as the lobes, 30-40 mm long, basal part almost cylindrical, (0.16-)0.32-0.45 of the length of the entire tube, (5-)11-17 mm long, upper part 18-23 mm long, 7-10 mm wide at the mouth; lobes broadly and obliquely ovate 0.69-1 × as long as the tube, 1.27-1.9 × as long as wide, 23-38 × 18-24 mm, rounded

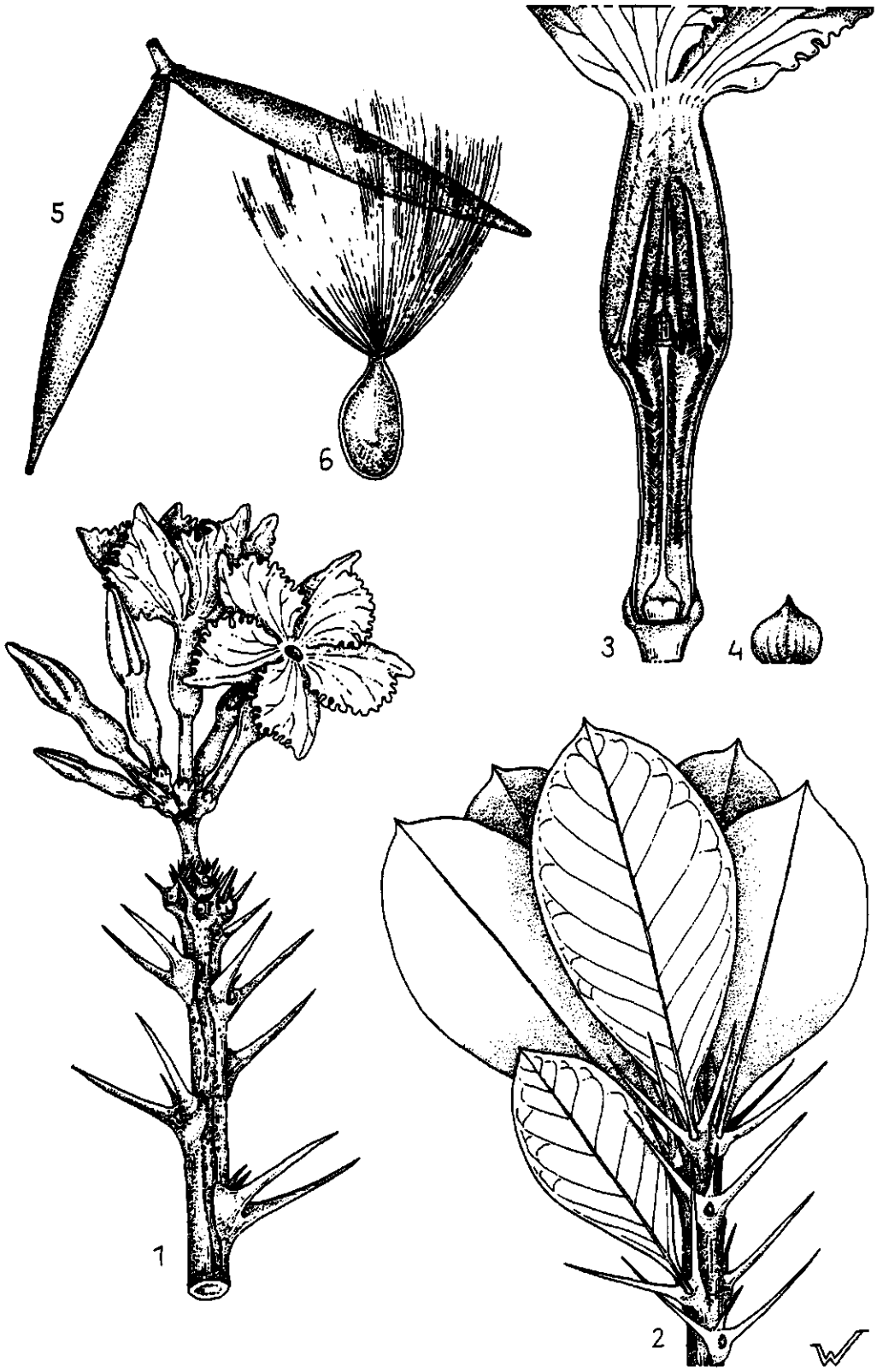


Figure 12. *P. lealii*: 1 and 2 = habits (× 1), 3 = opened flower (× 3), 4 = sepal inside (× 6), 5 = fruit (× 1), 6 = seed (× 3) (1, 3 and 4 = from Leistner et al. 75; 2 = from Dinter 1899; 5 and 6 = from Humbert 16524).

at the apex, undulate. *Stamens* with apex 4-8 mm below the mouth of the corolla tube, inserted 0.45-0.53 of the length of the corolla tube, at 15-18 mm from the base; anthers very narrowly triangular, 5-8 × as long as wide, 11-16 × 2-2.5 mm, pubescent inside at the base of the connective just below where they cohere with the pistil head. *Pistil* 12-17 mm long; ovary 3-4 × 2.5 × 2-2.5 mm, glabrous; disk 1.2-2 mm high, 5-lobed, with lobes rounded at the apex which are less than half as long as the ovary; style 1-1.55 mm long, glabrous; pistil head 1.5-1.55 mm high, composed of an obconical basal part 1 × 0.8 mm, a ring-shaped central part 0.3-0.5 × 1.4-1.5 mm and a stigmoid apex 0.15-0.2 × 1 mm which is sometimes obscure. Ovules approximately 50 in each carpel. *Fruit* of 2 separate mericarps, sometimes only one developing, forming an angle of 45-180° at the base (sometimes with flowers on the same inflorescence); mericarps dark to pale brown, whitish to very pale brown inside when dried, fusiform, 4.5-11 × 1-1.2 × 1 cm, obtuse at the apex, glabrous; wall 1 mm thick. *Seeds*: grain medium to dark brown, elliptic to ovate, 7-10 × 4-5.5 mm; testa rough; coma whitish to straw-coloured, 1-2.3 cm long. Endosperm thin. Embryo 6-9.5 mm long; cotyledons broadly obovate to orbicular, 1.1-2 × as long as wide, 4-6.5 × 2-4.5 mm, rounded at the apex, cordate at the base; rootlet 0.5-0.62 × as long as the cotyledons, 2-3 × 1-2 mm.

DISTRIBUTION. Angola, Botswana, Namibia.

ECOLOGY. Xerophyllous forest, Low Mopane scrub, on sandy soil, dolomite, granite and quartzite. Alt. 50-1600 m. Flowering May-August and fruiting July-December.

Use: Parts of the tree have been used to prepare arrow poison and it is now known to contain a glucoside, pachypodium, with an action similar to that of digitalis (Coates Palgrave 1983).

Specimens examined:

ANGOLA. Benguela: Lengue, *Gossweiler* 9685 (BM, K, US); Loanda, Cazengo, *Gossweiller* 4950 (BM, K) . Huila: Sin. loc., *Antunes* 879 (P); Humpata, *Fritzsche* 205 (S); Oncócua-Pediva, Tchihihua, *Teixeira* 354 (BM, PRE); near Quitibe (= Quiteve), Bumbo District, *Welwitsch* 1510 (BM, G, K, P, type). Namibe (= Moçâmedes): km 30 of Arriaga- Moçâmedes, *Humbert* 16524 (BM, G, P); km 13 Caraculo-Virei Mts Road, *Henriques & Brites* 1111 (K, PRE); km 8 of same road, *Menezes et al.* 2992 (PRE, SRGH); Humbia, *Carrisso & Sonsa* 204 (BM); Tampa, *Exell & Mendonça* 2442 (BM); Cahinde, near Sá da Bandeira, *Brain* 6 (PRE).

BOTSWANA. Nokaneng, Ngamiland, *Gibson* 74 (US).

NAMIBIA. Kaokoveld: Onjamu, 88 km NW of Orotjitombo, Kaokoveld Res., *Edwards* 4469 (PRE); near Otjitanda, *Meyer* 1247 (M); Onandera Hills, NW Boundary, *Le Roux* 582 (PRE); 160 km NW of Ohopoho, *Davies et al.* 31 (PRE); 86 km Ohopoho-Anabib Road, *Story* 5680 (PRE); Otjijadjasema, *Leistner et al.* 191 (K); 10 km WSW of Epupa Falls, *Leistner* 261 (K, SRGH, WAG, neotype of *P. giganteum*); Giraffenbergen, near Otjue, *Merxmüller* 1473 (M). Ovambo: Kunene R., near Ruacana Falls, *Leistner* 75 (K, PRE, SRGH); ibid., *de Winter* 3655 (K, M, PRE); Tsumeb, *Dinter* Aug.1929 (B); ibid., *Giess* 10484 (M, PRE); ibid., *Nägelsbash* 10 (M) & Aug.1933 (PRE); ibid., *Obermeyer* 30 Aug. 1934 (PRE); ibid., *Pillans* 5900 (K); ibid., *Range* R22(4342) (HBG); ibid., *Volk* 636 (M); ibid., *Walter* 567 (B); 10 km S of Tsumeb, *Peter* 47336 (B); ibid., *Leach & Cannell* 13816 (PRE); near Outjo, *Hardy* 2076 (PRE); ibid., *van Greuning* 270 (PRE); km 21 Tsumeb-Grootfontein Road, *de Winter* 3690 (K, M, P). Herero: N of Grootfontein, Otjirukaka, *Leistner* 2119 (L); 45 km W of Otavi, Grootfontein District, *de Winter* 3011 (K, PRE); Ouros, Otavi, *Dinter*

5671 (B); near Grootfontein, *v. Wettstein* 350 (M); near Waterberg, *Giess & Hoffmann* 13900 (M, PRE); near Otjikoware, *Berger & Kinges* 2140 (K); between Umpupe and Palmfontein, *Baum* 21 (BM, E, G, HBG, K, M, S, W, Z); Ontjo District, Klippenberg, *Schwerdtfeger* 1/310 (B); Gunatseb, *Volk* 2442 (M); sin.loc. *Dinter* anno 1899 Z); *Volk* 520b (M).

NOTES. *Davies et al.* 31 and *Giess* 10484 have almost no spines.

P. lealii and *P. saundersii* resemble each other very much. The two species are distinguished mainly to the characters given in number 4 of Key 3.

21. **Pachypodium namaquanum** (Wyley ex Harv.) Welw. in Trans. Linn. Soc. 27: 45 (1869); Stapf in Fl. Cap. 4, 1: 515 (1907); Marloth, Fl. S. Afr. 3, 1: 62-66, t. 18, figs 25-28 (1932); Phillips in Fl. Pl. S. Afr. 20: t. 771 (1940); Codd in Fl. S. Afr. 26: 283 (1963). Type: South Africa, West Northern Cape Province, Namaqualand, *A. Wyley* anno 1860 (holotype TCD, n.v.; isotype K). Fig. 13, p. 71; Map 14, p. 64; Plates 72-75, opposite p. 96.

Basionym
Adenium namaquanum Wyley ex Harv., Thes. Cap. 2: 11, pl. 117 (1863).

Cactus-like plant, 1.5-5 m high; trunk subcylindrical, unbranched or once or sometimes twice branched, 10-30 cm in diameter at the base, tapering to 8-10 cm in diameter at the apex; bark grey-green to dark brown, smooth or with remains of leaf scars; upper part of trunk and branches covered with straight or curved spines in groups of three, two of which subequal, 1.5-7.5 cm long, 1-3 mm in diameter at the base, in between them the third small one 0.5-4 cm long, 0.5-2 mm in diameter, fused at their base and forming a conical or subconical and laterally compressed excrescence, 4-5 × 4-3 × 3-2 mm, leaf scar between the two spines near the base, rarely the small spine absent, erect at the apex of trunk or branches, later recurved and shed, leaving the basal excrescences. *Leaves* sessile, confined to the apices of trunk and branches, pale green when fresh, often yellowish-green when dried, ovate to obovate, 2-3.4 × as long as wide, 4-14 × 2-5.5 cm, acuminate or rounded at the apex, cuneate at the base, densely pubescent on both sides with stellate hairs, with margin strongly undulate, with midrib and secondary veins prominent beneath; with 6-15 pairs of secondary veins straight at the base, upcurved at the apex if conspicuous, forming an angle of 30-70° with the costa; tertiary venation not visible. *Inflorescences* several together at the apices of the trunk and branches, sessile or shortly pedunculate, congested, 3-6.5 × 2.5-6.5 cm, 3-10-flowered. Peduncle terete, 0-10 × 3-5 mm, densely pubescent; pedicels 0-7 mm long, densely hirto-pubescent. Bracts ovate or obovate, 1.4-2.33 × as long as wide, 7-13 × 3-8 mm, acute or rounded at the apex, sometimes with a toothed margin near the apex, hirsute outside, sparsely pubescent to almost glabrous inside. *Flowers*: *Sepals* almost free, oblong to obovate or narrowly so, 1.33-2.87 × as long as wide, 4-11 × 3-4 mm, acuminate to apiculate at the apex, hirsute outside, sparsely hirsute to glabrous inside. *Corolla* red or red and yellow outside, 3-4 cm long in the mature bud and forming a comparatively wide broadly ovoid head, 0.16-0.25 of the bud length, 5-9 × 8-11 mm, obtuse to rounded at the apex, hirto-pubescent outside, sometimes with lobes sparsely so, glabrous inside for 3.5-5 mm above the base, pubescent from 4-7 mm below the insertion of the stamens, less so upwards and ending 2-3 mm below the mouth or all over the lobes; tube

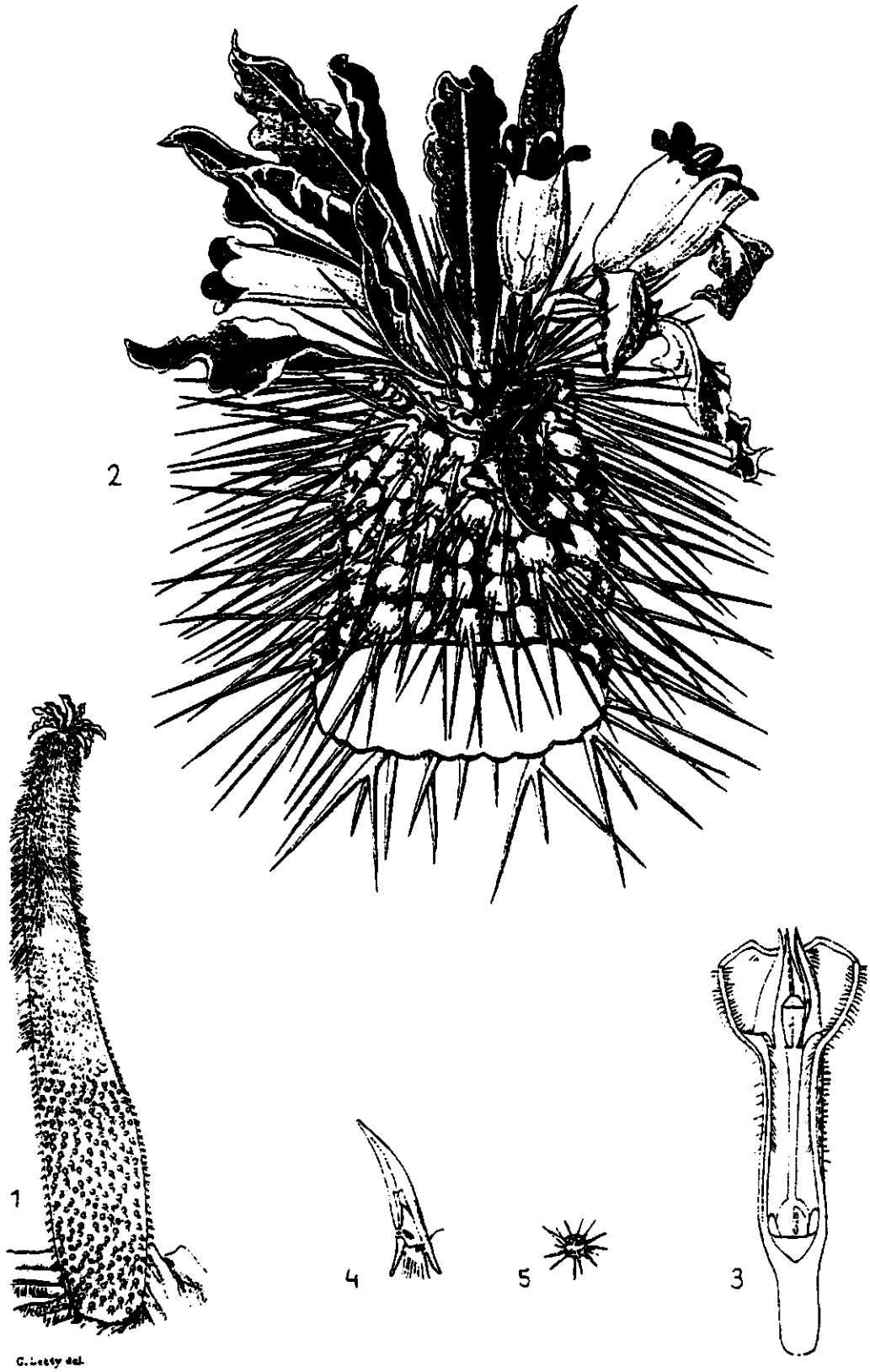


Figure 13. *P. namaquanum*: 1 and 2 = habits, 3 = opened flower, 4 = stamen, 5 = stellate hair (1-5 = from Phillips, E.P. 1940. The flowering plants of South Africa 20: plate 771).

1.75-8.6 × as long as the calyx, 2.66-5.4 × as long as the lobes, 25-40 mm long, basal part almost cylindrical, 0.18-0.3 of the length of the entire tube, 5-9 mm long, 2-4 mm wide, upper part obconical to slightly obovoid, 20-35 mm long, 10-15 mm wide at the mouth; lobes broadly ovate to orbicular, 0.23-0.34 × as long as the tube, 1-2 × as long as wide, 5-10 × 3.5-8 mm, rounded at the apex. *Stamens* with apex 11-17 mm below the mouth of the corolla tube, inserted 0.31-0.4 of the length of the corolla tube, at 7-12 mm from the base; anthers very narrowly triangular, 3.5-5.4 × as long as wide, 6-8 × 1.2-2 mm, pubescent inside at the base of the connective just below where they cohere with the pistil head. *Pistil* 10.2-14.4 mm long; ovary 2.5-3 × 2 × 1.8-2 mm, glabrous; disk 1-1.2 mm high, 5-lobed with rounded lobes, less than half as long as the ovary; style 6.8-10 mm long, glabrous; pistil head 0.9-1.4 mm high, composed of an obconical or conical basal part 0.5-0.8 × 0.6-1 mm, a ring-shaped central part 0.2-0.4 × 0.8-1.2 mm and a stigmoid apex 0.15-0.2 × 0.5-0.8 mm. Ovules approximately 50 in each carpel. *Fruit* of 2 separate mericarps, sometimes only one developing, forming an angle of 5-90° at the base; mericarps pale brown to pale greenish-brown, obovoid to ellipsoid, 27-45 × 10-15 × 10-15 mm, densely pubescent; wall 1 mm thick. *Seeds*: grain pale brown, ovate, 5-7 × 2-3 mm; testa slightly rough; coma straw-coloured, 11 mm long. Embryo small, 2-2.5 mm long; cotyledons orbicular or broadly obovate, 1-1.4 × as long as wide, 0.7-1 × 0.5-1 mm, apex and base rounded; rootlet 1.5-1.85 × as long as the cotyledons, 1.3-1.5 × 0.8 mm.

DISTRIBUTION. Namibia and South-Africa (West Northern Cape Province).

ECOLOGY. Nama Karoo and Succulent Karoo on sand, schist, granitic or quartzitic rocks. Alt. 300-900 m. Flowering July-October and fruiting September-December.

Vernacular name: Halfmense (Hottentots) and Elephant's trunk (English).

Specimens examined:

NAMIBIA. Lorelei Copper Mine, Lüderitz District, *de Winter & Giess* 6341 (M, PRE); ibid, *Merxmüller* 2500 (M); Namuskluft, Lüderitz, *Merxmüller & Giess* 28555 (M); ibid., *Mittendorf* 79 (PRE); Nanusberge, Lüderitz, *Leuenberger* 3270 (B); Klein Karras, Keetmanshoop District, *Wallace* 19 Sept. 1926 (PRE); 69 km SW of Sperlingspütz, Warmbad District, *Dyer & Verdoorn* 3641 (PRE); Kahanstal, *Dinter* 8071 (B, G, HBG, K, M, Z).

SOUTH AFRICA. West Northern Cape Province: Namaqualand, Lower Orange R., *Pillans* 6545 (K); ibid., *Rodin* 1567 (F, K, PRE, UC, US); near Pella, *Henrici* 2233 (PRE, US); ibid., *Pole-Evans* 2251 (PRE); ibid., *Schlieben* 9140 (PRE); 30 km N of Steinkopf, *Leistner* 800 (K, PRE); SE of Sendlings Drift, *Pillans* 5000 (K); Richtersveld, *Brown* Nov.1962 (PRE); ibid., *Krapohl* 5367 (BM, K, PRE); ibid., *Werdermann & Oberdieck* 577 (B, K); Witpütz, *Evrard* 9186 (BR); sin. loc., *Brown* s.n. (K); *Herre* anno 1962 (UC, US); *Wyley* anno 1860 (K, type).

CULT. Germany. München Bot. Garden., from Sperlingspütz, Namibia, *Giess* 12328 (M).

NOTE. *P. namaquanum* is distinguished from the other species by its mostly unbranched trunk covered with long spines. Leaves are densely pubescent on both sides with stellate hairs and with margin strongly undulate.

22. **Pachypodium saundersii** N.E. Br. in Kew Bull. 1892: 126 (1892); Stapf in Fl. Cap. 4, 1: 516 (1907); Pole Evans in Fl. Pl. S. Afr. 4: pl. 123 (1924); Codd in Fl. S. Afr. 26: 286 (1963); Kupicha in Fl. Zambesiaca 7, 2: 464 (1985). Type: South Africa,

Kwazulu-Natal, Bombo (= Lebombo) Mts, *Saunders* s.n. (holotype K; isotype Z). Fig. 14, p. 74; Map 14, p. 64; Plates 76-77, opposite p. 97.

Homotypic synonym
P. lealii subsp. *saundersii* (N.E.Br.) G.D.Rowley in Nat. Cac. Succ. J. 28: 4 (1973).

Shrub 0.5-1.5(-5) m with a large tuberous base, 20-100 cm in diameter, partly above the soil; bark grey or grey-green. Branches thick at the base; branchlets 5-8 mm in diameter, covered with long, paired straight, rarely curved spines, 10-45 mm long, 1-4 mm wide at the base, often in between a small third one, 3-13 mm long and 0.5-2 mm wide at the base, fused at their base and forming a subconical and laterally compressed excrescence, 3-7 × 1-4 × 1-5 mm, on which the leaf is inserted in a depression in the centre. *Leaves* sessile, rarely petiolate, confined to the apices of the branchlets, also on minute lateral branchelets; petiole 0-7 mm long; blade glossy green above, pale green beneath when fresh, papery when dried, obovate to elliptic or narrowly so, 1.75-5 × as long as wide, 2-8 × 1-4 cm, apiculate to slightly acuminate with acumen acute at the apex, cuneate at the base or decurrent into the petiole, glabrous on both sides or with midrib sparsely pubescent beneath, often with margin ciliolate; secondary veins in 6-10 pairs, straight at the base, upcurved upwards, forming an angle of 30-70° with the costa, often not visible in dried leaves; tertiary venation not visible. *Inflorescence* terminal, sessile, congested; 3-6 × 2.7-9 cm, 4-20-flowered. Pedicels 2-5 mm long, glabrous. Bracts oblong, 2.3 × as long as wide, 3.5 × 1.5 mm, acuminate at the apex, glabrous out- and inside. *Flowers*: *Sepals* dark red, connate at the base for about 0.5 mm, ovate, 1.1-1.5 × as long as wide, 2-5 × 1-3.5 mm, acuminate at the apex, glabrous out- and inside. *Corolla* limb white, tube often greenish at the base, reddish outside or partly so, 3.5-6 cm long in the mature bud and forming a comparatively wide broadly ovoid head 0.3-0.4 of the bud length, 12-25 × 6-9 mm, acuminate to obtuse at the apex, glabrous outside, glabrous inside for 4-6 mm at the base, pubescent in a belt from 5-8 mm below the insertion of the stamens to the mouth; tube 7-12 × as long as the calyx, 1.2-2.2 × as long as the lobes, 23-45 mm long, basal part almost cylindrical, 0.22-0.43 of the length of the entire tube, 8-15 × 1-3 mm; upper part conical, 10-30 mm long, 4-8 mm wide at the mouth; lobes obliquely obovate, 0.44-0.84 × as long as the tube, 1-2 × as long as wide, 16-35 × 12-25 mm, acuminate to rounded at the apex, undulate but often less so than in *P. lealii*. *Stamens* with apex 8-12.5 mm below the mouth of the corolla tube, inserted 0.4-0.57 of the length of the corolla tube, at 11-16 mm from the base; anthers very narrowly triangular, 4-5.5 × as long as wide, 10-11 × 2-2.5 mm, sparsely pubescent inside at the base of the connective just below where they cohere with the pistil head. *Pistil* 15-18.5 mm long; ovary 3-3.5 × 2.5 × 2 mm, glabrous; disk annular, 1.3-1.5 mm high, with 5 crenate lobes which are less than half as long as the ovary; style 10.5-13.2 mm long, glabrous; pistil head 1.5-1.9 mm high, composed of an obconical basal part 0.9-1.2 × 0.8 mm, a ring-shaped central part 0.4-0.5 × 1-1.2 mm and a stigmoid apex 0.2 × 1-1.2 mm. Ovules approximately 50 in each carpel. *Fruit* of 2 separate mericarps, sometimes only one developing (sometimes flowers and fruit on the same inflorescence), forming an angle of 20-180° at the base; mericarps brown, fusiform, 95-125 × 10-17 × 10 mm, obtuse at the apex, glabrous. *Seeds*: grain dark to medium brown, ovate to elliptic, 7-8 × 5-5.5 mm, acute at the apex, rounded at the base; testa rough, thickened at the margin on both sides; coma whitish, sometimes straw-coloured, 2-3 cm long. Endosperm thick. Embryo 7-7.5 mm long; cotyledons

Figure 14. *P. saundersii*: 1 and 2 = habits, 3 = opened flower (1-3 = from Pole Evans, I.B., 1924. The flowering plants of South Africa 4: plate 123).

orbicular, 1-1.25 × as long as wide, 4.5-5 × 4-5 mm, rounded at the apex, cordate at the base; rootlet 0.66-0.8 × as long as the cotyledons, 3-4 × 1.8-2.3 mm.

DISTRIBUTION. Mozambique, South-Africa, Swaziland, Zimbabwe.

ECOLOGY. Savanna on granite, limestone, basalt, rhyolite, sandstone and sand. Alt. 70-1200 m. Flowering January-July and fruiting May-August.

Vernacular name: Impalalelie, Keodeo-; Impala lily, Kudu-, Rathbonia (Smith 1966).

Specimens examined:

MOZAMBIQUE. Sofafa: Mossurize between Maringa and Machaze, *Pedro & Pedragão* 7861 (PRE); 10 km N of Sabi R., Maringa District, *Chase* 2247 (BM, K, SRGH). Gaza: near Mavue, *Drummond* 7964 (SGRH); near Combomune, *Correia & Marques* 1196 (WAG). Maputo: near Maputo, *Balsinhas* 1264 (WAG); ibid., *Humbert* 14546 (P, WAG); ibid., *Marques* 2117 (WAG); ibid., *Schäfer* 6734 (WAG).

SOUTH AFRICA. Kwazulu-Natal Province: Abercorn Drift, Usutu R., Bella Vista District, *Stephen* 740 (PRE); Jozini Dam, Ubombo District, *Crawford* 250 (PRE); ibid., *Ward* 5656 (PRE); ibid., *Wearne* 38 (PRE); Mkuzi, Ubombo District, *Moll* 3157 (PRE); ibid., *Ward* 3072 (M, PRE); Pongolo Poort, Ubombo District, *Ward* 4115 (PRE); Bombo (= Lebombo) Mts, *Saunders* s.n. (K, Z, type); ibid., *Strey* 6584 (PRE). Northern Transvaal Province: Wylliespoort, Soutpansberg, Messina District, *Galpin* 14935 (PRE); ibid., *Hartmann* 1045 (HBG); ibid., *Meeuse* 10229 (PRE, S, SRGH); ibid., *Schweickerdt & Verdoorn* 668 (K, PRE); ibid., *Schlieben & Hartmann* 12032 (K); Soutpansberg, c. 8 km above Louis Trichardt, *Anteobus* 10 Apr.1919 (PRE); ibid., *Rodin* 3982 (F, K, PRE, UC, US); ibid., *Gettliffi* 9644 (PRE); Olifants R., Letaba District, *McNeil* s.n. (PRE); Blyde R. Canyon, *Olivier* 7319 (PRE); Swadini Nature Res., *Venter* 8500 (PRE); 14 km S of Phalaborwa, *Retief* 342 (PRE); Klaserie R., W of Game Res., *Smuts* 2381 (PRE). PWV Province: near Pretoria, *Marloth* 9519 (PRE). Eastern Transvaal Province: c. 5 km E of Burgersfort, Lydenburg District, *Codd* 10494 (K, M, PRE); Erasmus Pass, Lydenburg District, *Strey* 3315 (K, M, PRE, W) & 3869 (PRE); Komatipoort, Barberton Div., *Rogers* 22208 (PRE, Z); Crocodile Poort, *Dyke* 5393 (A, PRE); near Nelspruit, *Barker* 48 (B, K); ibid., *v. d. Merve* 15.06.1932 (PRE); ibid., *Mogg* 7 Apr. 1925 (K, PRE); near Kaapmuiden, Barberton District, *Mogg* 9 Jan.1938 (PRE); ibid., *Pole Evans* 4679 (PRE); near Malelane, Kruger National Park, *Codd* 5225 (K, PRE) & 6064 (K); Abercorn Pont, Usutu R., Ingwavuma District, *Codd & Dyer* 2855 (K, PRE); near Olifants Gorge, Kruger National Park, *Story* 3955 (PRE); Shabin, Kruger National Park, *v. d. Schyff* 660 (K, PRE); near Barberton, *Williams* 8207 (PRE); between Souetti and Louw's Creek, *Sypkens* 18 Mar.1948 (PRE); Louw's Creek, *Edwards* 5 (PRE); Gravalotte District, *Bayliss* 1136 (G, Z).

SWAZILAND. Near Umbuluzi Gorge, Lebombo Mts, *Culverwell* 722 (PRE); near Jilobi Forest, Lebombo Mts, Lebombo District, *Kemp* 820 (US, WAG); Mbuluzi Poort, Stegi District, *Compton* 31441 (PRE); Blue Lay Ranch, Stegi District, *Compton* 29757 (PRE); Lebombo Mts, Stegi District, *Compton* 27848 (PRE); ibid., *Dyer* 3470 (K, PRE); Signal Hill, *Pole Evans* 3478 (K, PRE).

ZIMBABWE. Chionja Hills, Ndanga District, *Phipps* 2898 (K, PRE, SRGH); near Rimayi, Sabi valley, Chipinge District, *Plowers* 2685 (K, PRE, SRGH); 72 km S of Fort Victoria on Beitbridge Road, *Rushworth* 329 (SRGH); Chibi, *Wild* 5457 (K, PRE, SRGH); ibid., *Biegel & Pope* 3250 (B, K, PRE, SRGH); S of Lundi R. Bridge in Fort Victoria-Beitbridge Road, *Leach* 10801 (BM, K, SRGH) & 11645 (K, SRGH); 32 km N of Sabi-Lundi Rs. junction, *Chase* 2362 (BM, K, SRGH); near Sabi

R., *Whellan* 508 (K, SRGH); Chiribira Falls, Sabi-Lundi District, *Wild* 3414 (K, SRGH); near Lundi, *Pole Evans* 2701 (PRE); Christmas day Hill, Lundi R., Nuanetsi District, *Davies* 1740 (SRGH).

CULT. England: Royal Bot. Gard. Kew, from Goba, Mozambique, *Pickering* Nov. 1970 (K). Germany: Berlin-Dahlem Bot. Garden, *Schwerdtfeger* 14737 (B); ibid., *Cubr.* 27579 (B). South Africa: Durban Bot. Gard. *Olgilvin & Schweicherdt* May 1939 (K); Pietersburg, Division of Botany, *Kirton* 2736 (K, PRE); Bot. Garden of Pretoria Univ., *Leeuwenberg* 11025 (WAG); Lowveld Bot. Gard. from Blyde R. Canyon, *Buitendag* 1010 (PRE). Zimbabwe: Brichenough Bridge, from Lower Sabi, *Stock* 23359 (SRGH).

NOTES. *Venter* 8500, Swadini Nature Res. next to dam, grows on light brown sandy loam in high montane scrub forest with *Olinia* sp. (Oliniaceae), *Pterocelastrus* sp. (Celastraceae) and *Faurea* sp. (Proteaceae).

Culverwell 722, Blue Jay Ranch, c. 6 km S of W entrance to Umbuluzi Gorge Lumbombo Mt, is found on rhyolite. It is in association with: *Indigofera* sp. (Leguminosae), *Huernia* sp. (Asclepiadaceae) and *Plectranthus cylindraceus* Hochst. ex Benth. (Labiatae).

Biegel & Pope 3250, Chibi District, grows on granite in *Combretum apiculatum* Sond. (Combretaceae) woodland with *Sclerocarya caffra* Sond. (Anacardiaceae) and *Afzelia quanzensis* Welw. (Leguminosae).

P. saundersii is easily confused with *P. lealii*. See number 4 of Key 3.

23. **Pachypodium succulentum** (L. f.) A. DC., Prodr. 8: 424 (1844); Stapf in Fl. Cap. 4, 1: 517 (1907); Pole Evans in Fl. Pl. S. Afr. 1: t. 21 (1921); Marloth, Fl. S. Afr. 3, 1: 62, t. 18, Fig. 23 (1932); Dyer in Fl. Pl. Afr. 33: t. 1306 (1959); Codd in Fl. S. Afr. 26: 285 (1963). Type: South Africa, Cape Province, *Thunberg* anno 1775 (lectotype S, designated by Codd). Fig. 15, p. 77; Map 15, p. 78; Plates 78-80, opposite p. 97.

Basionym and homotypic synonyms

Echites succulenta L.f., Suppl. 167 (1781); Thunberg, Prodr. 37 (1794). *P. tuberosum* Lindl. in Bot. Reg. 16: t. 1321 (1830). *Belonites succulenta* (L.f.) E. Mey., Comm. 187 (1837). *P. tomentosum* G. Don, Gen. Syst. 4: 78 (1837).

Heterotypic synonyms

P. griquense L. Bolus in S. Afr. Gard. 22: 84 (1932). Type: Cult., South Africa, W Cape, Kirstenbosch (N.B.G. 991/22), from Moritzfontein, Kimberley, *William* 11 Dec. 1931 (holotype BOL, n.v.; isotype K).

P. jasminiflorum L. Bolus in S. Afr. Gard. l.c. (1932). Type: South Africa, Williston, Fraserburg, *Engelbrecht* s.n. (holotype BOL, n.v.).

Shrub 0.6-2 m hight, with a large half-submerged tuberous trunk 20-50 × 10 cm; bark dark brown and smooth, creamy and soft on section. Branches terete, erect, often thin, 25-40 cm long, up to 2 cm diameter; branchlets 12-20 × 3-4 mm covered with paired straight or often curved spines, 4-27 mm long, 0.5-2 mm in diameter, often in between of them a third small one, 1-15 × 0.2-1 mm, fused at the base and forming a subglobose or subconical and laterally compressed excrescence, 2.5-5 × 1-4 × 1.5-2 mm, with depressed leaf scar on the top, white pubescent when young, often turning

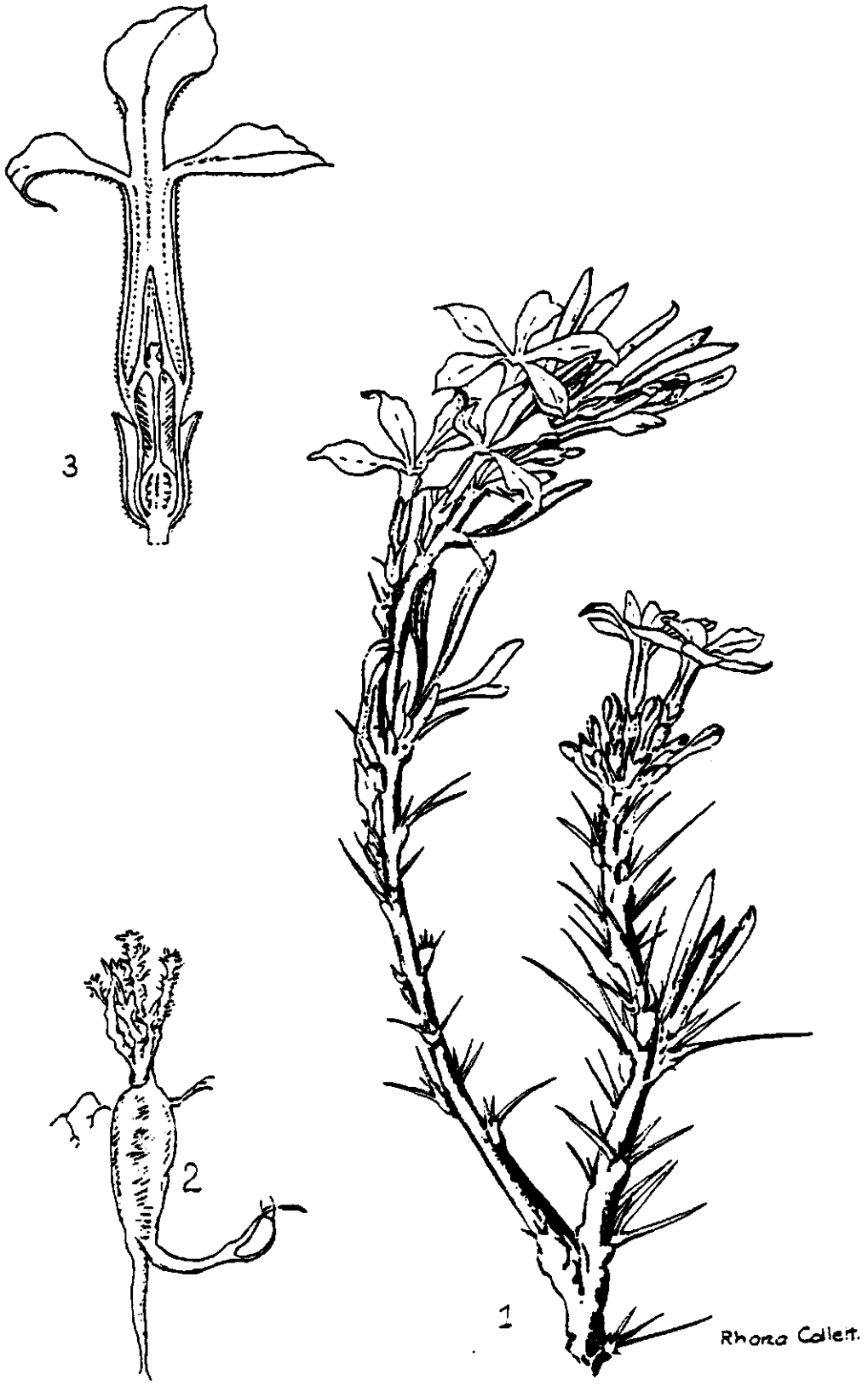
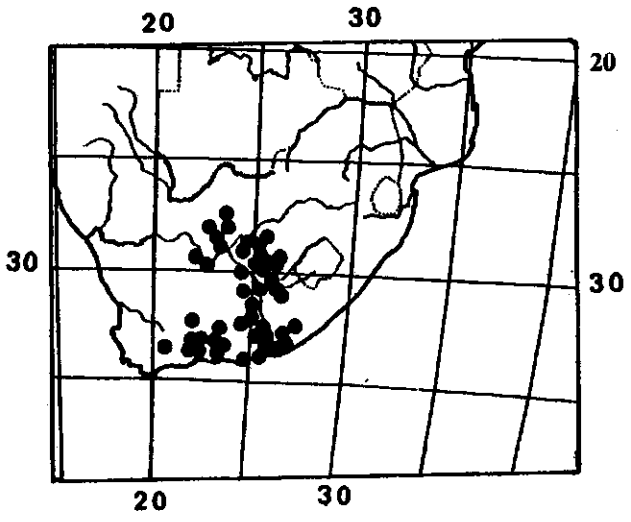


Figure 15. *P. succulentum*: 1 and 2 = habits, 3 = opened flower (1-3 = from Dyer, R.A., 1959. The flowering plants of Africa 33: plate 1306).



Map 15. *Pachypodium succulentum.*

less so and dark brown to blackish. *Leaves* sessile, confined to the apices of the branchlets, glaucous and dull above, pale green beneath when fresh, papery when dried, elliptic to oblong or very narrowly so, 2-17 × as long as wide, 13-70 × 2.5-16 mm, acuminate to rounded at the apex, cuneate at the base, with revolute margin, pubescent to sparsely so above, densely pubescent beneath and with midrib prominent; secondary veins up to 9 pairs, rather straight (inconspicuous in dried leaves), forming an angle of 45-85° with the costa; tertiary venation not visible. *Inflorescence* sessile or shortly pedunculate, congested, 2.5-5 × 2-3.5 cm, 1-9-flowered or more. Peduncle 0-7 × 1.5-2 mm, pubescent; pedicels 2-10 mm long, up to 2.5 mm in diameter when fruiting, pubescent. Bracts narrowly oblong, 3.66-6 × as long as wide, 5.5-6 × 1-1.5 mm, acuminate at the apex, pubescent outside, sparsely pubescent inside especially below the apex. *Flowers*: *Sepals* green, ovate or narrowly so, 2-3.25 × as long as wide, 4-6.5 × 2-2.5 mm, acuminate at the apex, pubescent outside, glabrous inside, elongate under the fruit to 7 mm long. *Corolla* lobes white with pink or red lines, especialy in a median stripe, outside and white or pale pink inside, tube with basal part pale green and upper part marron-red or darker deep cerise-pink, 12-35 mm long in the mature bud and forming a comparatively wide ovoid head, 0.33-0.5 of the bud length, 6-18 × 3-5 mm, obtuse at the apex, pubescent outside, often glabrous on the edges of the lobes, glabrous inside, with a pubescent belt 3-5 mm wide just below the insertion of the stamens; tube 2.4-4.4 × as long as the calyx, 0.7-1.7 × as long as the lobes, 9-20 mm long, basal part almost cylindrical, 0.25-0.5 of the length of the entire tube, 4-7 × 2-2.5 mm, upper part almost cilyndrical, 5-15 mm long, 3-7 mm wide at the mouth; lobes narrowly obovate, 0.6-1.5 × as long as the tube, 2-3 × as long as wide, 10-30 × 5-10 mm, rounded at the apex. *Stamens* with apex 2-5 mm below the mouth of the corolla tube, inserted 0.37-0.55 of the length of the corolla tube, at 5-7.5 mm from the base; anthers very narrowly triangular, 3-5.5 × as long as wide, 5-5.5 × 1-1.6 mm, sparsely pubescent to glabrous inside at the base of the connective just below where they cohere with the pistil head. *Pistil* 6-9.5 mm long; ovary 1.5-2 × 1-1.5 × 1 mm, sparsely pubescent at the apex, otherwise glabrous; disk 0.5-0.6 mm high, composed of 5 inequal broadly ovate rounded or retuse glands, 2 of which or 2 pairs of which may be partly or entirely fused, which are less than half as long as the ovary; style 4.5-6 mm long, glabrous; pistil head 0.8-1.4 mm high, com-

posed of an obconical or conical basal part, 0.5-0.8 × 0.4-0.8 mm, a ring-shaped central part 0.2-0.4 × 0.6-0.8 mm and a stigmoid apex 0.1-0.2 × 0.3-0.6 mm. Ovules approximately 50 in each carpel. *Fruit* of 2 separate mericaps, sometimes only one developing, with an angle often of 10-60° at the base; mericarps pale grey and suffused with dark red when fresh, medium to dark brown and with longitudinal lines outside when dried, fusiform, 50-90 × 9-11 × 8-10 mm, acute at the apex, pubescent, *Seeds*: grain pale brown, ovate, 6-7 × 2.5-3.2 mm; testa rough; coma whitish, 1.6-2 cm long. Embryo 5.5-6.5 mm long; cotyledons broadly ovate, 0.78-0.83 × as long as wide, 2.5 × 3-3.2 mm, rounded at the apex, cordate at the base; rootlet 1.2-1.6 × as long as the cotyledons, 3-4 × 2.2-2.8 mm.

DISTRIBUTION. Endemic to South Africa.

ECOLOGY. Grassland, Nama karroo, savanna, succulent karoo and thicket on dolerite, dolomite, quartzite, sandstone and sand. Alt. 50-1400 m. Flowering mainly September-November and fruiting October-December.

Vernacular name: Bergkambroo, Bobbejaan-, -Kos, Bottelboom; Bottle tree, Dikvoet, Kafferkambroa, -Kambroo, Ystervark-, -Kos (Smith 1966).

Specimens examined:

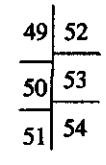
SOUTH AFRICA. Western Cape: Braam R., near Joubertina, Unimodale Div., *Esterhuysen* 16299 (PRE); Uniondale Hot Springs, *Esterhuysen* 6265 (K); Avontuur, *Horn* Sept.1960 (PRE); Montagu Pass, *Castelnau* 17 (P); near Matjesfontein, *Foley* 155 (PRE); Outeniquas, at Moeras R., Oudtshoorn Div., *Esterhuysen* 19446 (PRE); Prince Albert, *Bolus* 11605 (PRE); Ganska Pass, *Hardy* & Bayliss 995 (PRE); near Beaufort West, *Brown* Oct.1935 (PRE); Karoo Nat. Park, Beaufort West, *Bengis* 308 (PRE) & 324 (PRE); ibid., *Cloete* 11 Dec. 1931 (K); Kouga Mts, near Geelhoutboschkloof, *Volk* 1295 (PRE). Northern Cape: Langberg, Kuruman District, *Sitwell* 43 (P, PRE); Langkloof, c. 19 km NW of Olifantshoek, *Leistner* 2100 (PRE); c. 40 km from Olifantshoek, *Burgoyne* 1456 (PRE); km 17 Postmasburg-Papkuil Road, *Hafström & Acocks* 1126 (PRE, S); Asbestos Hill, Griquatown, *Acocks & Hafström* 1054 (PRE, S); Griqualand W, *Burchell* 1719 (K) & 1918 (K); Ouplaas farm, *Gubb* 25 Apr. 1981 (PRE); Klipfontein, Barkly West, *Acocks* 730 (PRE); Pniel, Vaal R. near Barkly West, *William* 13621 (PRE); near Plooysburg, *Hafström & Acocks* 893 (PRE, S); S of Koegas, *Hardy* 6971 (NY); ibid., *Leistner* 1191 (K, M, PRE, S); Buisvlei NW of Prieska, *Wall* 22 Sept.1938 (GB, S); Bushmans R., *Daly* 797 (PRE); near Prieska, *Acocks* 2549 (K); *Marloth* 2006a (PRE) & 2006b (PRE); ibid., *Bryant* 5164 (PRE); c. 26 km WNW of Prieska, *Leistner* 2920 (K, M, PRE); Asbestos Mts, between Griquastad and Prieska, Hay District, *Merxmüller* 687 (M); ibid., *Burchell* 1662 (GH, K, P). Eastern Cape: Culmstock, Middelburg District, *Southey* 5597 (PRE); Grootfontein, *Theron* 363 (K, PRE); near Middelburg, *Bolus* 70 (Z); Katberg, *She* 430 (K); near Graaff Reinet, *Bolus* 115 (K, PRE) & 16296 (BM); ibid. *Hilliard & Burtt* 10732 (E); near Hankey, *Bayliss* 7956 (US); ibid., *Fourcade* 2775 (K); between Port Elisabeth and Graaff Reinet, *Peter* 50814 (B); ibid., *Schröter* 14 Sept.1926 (Z); ibid., *Thode* NH17799 (PRE) & A596 (K, PRE); near Somerset East, *Bowker* s.n. (BM, K); ibid., *Schoeman* 8 Oct.1986 (PRE); Enon, *Thode* A2704 (K, PRE); Dam Nat. Res. 40 km E of Cradock, *Palmer* 816 (PRE); near Cradock, *Cooper* 1288 (BM, E, K, W, Z); ibid., *Zietsman* 1290 (PRE); Bruintjieshoogte, *Mac Owan* 641 (Z); near Komgha, *Flanagan* 1039 (PRE); Begha R. valley, Peddie Div., *Acocks* 11855 (E, PRE); Peddie District, *Sim* 19696 (PRE), anno 1899 (PRE); 24 km N of Bedfort, *Theron* 1813 (K, PRE); Fort Beaufort, *Giffen* 1291 (PRE); near Breakfast Vlei, *Dyer* 660 (L, PRE); ibid., *Giffen* 1203 (PRE); ibid., *Hafström & Acocks* 1109 (PRE); ibid., *Taylor* 1720

(NY); Piggot Bridge, Albany, *Bayliss* 7872 (NY); near Albany, *Bowker* 23 Feb. 1883 (K); ibid., *Burchell* 4181 (K); ibid., *Lindsted* 27 (PRE); Carlisle Bridge, *Bayliss* 3122 (A); Great Fish R. Region, Grahamstown, *Marloth* 10881 (PRE); ibid., *Sørensen* 554 (C); near Grahamstown, *Mac Owan* 841 (GH); ibid., *White* 1122 (G, Z); Alicedale, *Rogers* 12026 (Z); Willowmore-Steytlerville Road, *Bayliss* 3629 (NY, US, Z); km 5 Paterson-Addo Road, *Retief* 239 (PRE); near Addo, *Drege* s.n. (S); ibid., *Krest* Dec. 1932 (K); ibid., *Long* 246 (K, PRE) & 247 (K, PRE); Addo Nat. Park, Alexandrie District, *Liebenberg* 6622 (PRE); Jansenville, Port Elizabeth District, *Marloth* 6075 (PRE); near Port Elizabeth, *Penther* 2003 (M, W); ibid., *Rogers* 28220 (Z); ibid., *West* 23 (K); ibid., *v. Wettstein* 1929 (M); km 21 Port Elisabeth-Uitenhage, *Hutchinson* 1509 (BM, K, PRE); Lueri R., *Penther* 2007 (W); between Sunday and Swartkops Rs., Uitenhage Disrtrict, *Zeyher* 262 (E, G, M, W); Swartkops R., *Zeyher* 3411 (BP, P, S, Z); between Zuurbergen and Klein-Bruintjeshoogte, *Drege* s.n. (G, HBG, L, P, S); near Uitenhage, *Ecklon & Zeyher* 2.1 (B, BM, BP, C, E, F, G, GH, HBG, L, LE, S, US, W, Z); ibid., *Schlechter* 6079 (Z); ibid., *Thode* A680 (K, PRE); ibid., *Zeyher* 282 (BM, K). Sin.loc. *Alexander* anno 1847 (BM); Burchell 4410 (BM, K); *Bryant* 164 (K); *Fraser* 18 (E); *Mocquin* anno 1837 (G); *Pole Evans* 2357 (PRE) & 2358 (PRE); *McPregor* 19118 (PRE); *Repton* 3073 (PRE); *Scholl* 319 (W); *Scott Elliot* Nov.1884 (E); *Thunberg* anno 1775 (lectotype S); *Webb* 311 (P); *Zeyher* 25 (G, L, P). Free State: Bestersput, Bloemfontein District, *Welti* 57 (Z); Boshof, *Brueckner* 888 (PRE); km 15 Bloemfontein-Petrusburg Road, *Leeuwenberg* 12386 (WAG); Klipnek, Fauresmith District, *Marais* 118 (PRE) & 128 (PRE); Heuningberg, *Marais* 173 (PRE); Langerberg Plateau, *Smith* 945 (PRE); Veld Res., *Henrici* 1806 (PRE); ibid., *Verdoorn* 870 (PRE) & 1122 (K, PRE); Fauresmith Bot. Res., *Smith* 923 (PRE) & 973 (PRE); near Fauresmith, *Coetzee* 790 (PRE); ibid., *Verdoorn* 951 (K); ibid., *Lam & Meeuse* 4794 (L); Le Roux Dam, Luckhoff District, *Bourquin* 840 (PRE); km 11 Berthulie-Venterstad Road, *Werger* 1459 (PRE); Bergplaats Hills, *van der Merve* 1463 (PRE); Norvalspont, *Nutt* May 1900 (E).

CULT. South Africa: W Cape, Kirstenbosch (N.B.G. 991/22), from Moritzfontein, Kimberley, *William* 11 Dec. 1931 (K, type of *P. griquense*); D.B.O., from near Koffiefontein, *Liebenberg* 7 Nov.1958 (PRE); Pretoria Bot. Garden 1797, from near Port Elisabeth, 10 Nov.1919 (PRE). Germany: Berlin-Dahlem Bot. Garden, *Schwerdtfeger* 11832 (B), 17776 (B) & 17778 (B). Switzerland: Zürich, Staedtliche Sukkulentten-sammlung, *Leeuwenberg & Rapanarivo* 14651 (WAG) & 14652 (WAG). Probably Scotland, Edinburgh: from Natal South Africa, *Lace* acc. 521287 (K, UC, US).

NOTE. *P. succulentum* is easily confused with *P. bispinosum*. The two species are distinguished mainly by the characters given in number 2 of Key 3.

Plate 49. *Pachypodium meridionale*, Manja.
Plate 50. *Pachypodium meridionale*, Tulear.
Plate 51. *Pachypodium meridionale*, Manja.
Plate 52. *Pachypodium meridionale*, Tulear.
Plate 53. *Pachypodium rosulatum*, Mandritsara.
Plate 54. *Pachypodium rosulatum*, Mandritsara.



EXCLUDED SPECIES

Pachypodium obesum G. Don ex A.DC., Prodr. 8: 424 (1844) = *Adenium obesum* Roem. & Schult. as was mentioned there. G. Don did not make this combination.

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55 | 56
57 | 59
58 | 60

Plate 55. *Pachypodium rosulatum*, Analalava.
Plate 56. *Pachypodium rosulatum*, Befandriana Nord.
Plate 57. *Pachypodium rutenbergianum*, Mahajanga.
Plate 58. *Pachypodium rutenbergianum*, Mandritsara.
Plate 59. *Pachypodium rutenbergianum*, Mahajanga.
Plate 60. *Pachypodium rutenbergianum*, Mahajanga.

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CHAPTER 2

The habitats of *Pachypodium* species

S.H.J.V. Rapanarivo

INTRODUCTION

Many authors have published accounts of the succulent genus *Pachypodium*, but often on the taxonomic issues only. No complete ecological study for all species of *Pachypodium* exists as yet. Recent references regarding the biotope of *Pachypodium* are those by Koechlin (1969): Contribution à l'étude morphologique du genre *Pachypodium*; Koechlin et al. (1974): Flore et Végétation de Madagascar; Rowley (1983): The *Adenium* and *Pachypodium* handbook; Rauh (1995): Succulent and xerophytic plants of Madagascar; and Lavranos & Röösli (1996): The habitat of *Pachypodium* in Madagascar.

In this chapter, the available information acquired during field studies and from literature on the preferred sites of all *Pachypodium* species is brought together. It is quite clear from the detailed information on at least some species that site definition may help to distinguish among species, especially when the available plant material is incomplete.

STUDY AREA, MATERIAL AND METHODS

The complete ecological study of species of *Pachypodium* is outside the scope of the present study. No complete sampling or mapping of ecosystems or syntaxonomic units was included among our aims; let alone numerical, computer-assisted model building. Our observation methods, and the plant material sampled are the tools to define the immediate environment of our plants (Oldeman 1990). The immediate environment is the habitat which constitutes the direct interface between an organism and the surrounding world. Rossignol et al. (1998), in their book on stress and adaptation, compare it to an 'ecological coat' worn by an organism.

The immediate environment of our plants is indicative of the adaptive architectures evolved by *Pachypodium* species, at the organisation level of morphological characters and their variability. This is particularly relevant in the species of this genus, because their habitat is part of a number of micro-environments within larger vegetation types discerned. The latter are barely relevant for the adaptive behaviour of *Pachypodium* species, although we will see that there are vegetation types with and without *Pachypodium* habitats.

Pachypodium indeed is found very often in rocky habitats. Although methods exist for inventories by quadrats or transects on steep and sloping rocks for the description and numerical analysis of Alpine or Andean vegetation (cf. Cleef 1981), such meth-

ods do not fit our aims as stated above. Because no large homogenous areas are present with regard to *Pachypodium*, the use of statistics is not possible (see Van Rompaey 1993).

During our field work in Madagascar, we (Rapanarivo and Leeuwenberg, and/or Jongkind, Lavranos, Röösli and Hoffmann) collected *Pachypodium* and as many fertile companion plants as possible. We identified the species, the genera and the families, and the physiognomic characteristics of the vegetation, to indicate the vegetation types surrounding the particular substrate where *Pachypodium* species grow, as this is often different from the substrate of the surrounding vegetation. We also registered the presence of certain particular genera of especially but not uniquely succulent and xerophytic plants accompanying *Pachypodium* itself, such as *Aloe* (Aloaceae), *Euphorbia* (Euphorbiaceae), *Kalanchoe* (Crassulaceae), *Senecio* (Compositae), *Tetradenia* (Labiatae), *Xerophyta* (Velloziaceae). The succulents are often easier to identify to genus and species level than other plants in the sterile stages, and have similar preferences as *Pachypodium*. Such companion species (= espèces compagnes) can be analysed as differentiating elements of micro-habitats or as members of 'ecological groups', especially to obtain precise geographical or ecological information (Gehu & Rivas-Martinez 1981).

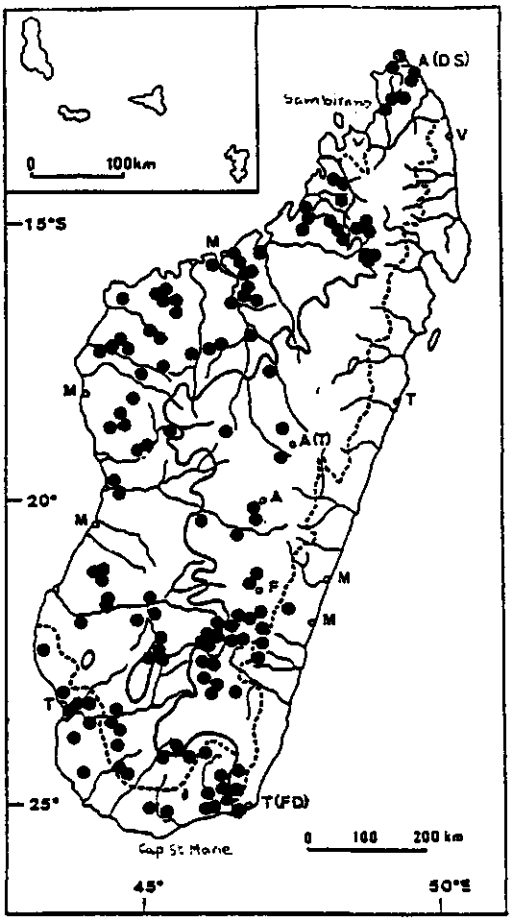
For instance, *Uapaca bojeri* (Euphorbiaceae) is a species characteristic of 'Evergreen, Sclerophyllous (*Uapaca*) Woodland (800-1800 m) occurring on sandstone and quartzite' (Du Puy & Moat 1996). Didiereaceae and *Euphorbia*, characteristic of 'Deciduous, Dry, Southern Forest and Scrubland (0-300 m) are occurring principally on Tertiary limestones, unconsolidated sands, sandstones, basalt and metamorphic rocks' (Du Puy & Moat 1996). Another example, Dry western forest 'série à *Commiphora-Hildegardia-Dalbergia*' (Humbert 1965) is included in 'Deciduous, Seasonally Dry, Western Forest (0-800 m) occurring principally on Mesozoic calcareous, unconsolidated sand, sandstones and metamorphic basement' (Du Puy & Moat 1996).

For Madagascar, climatic data were obtained mainly from the 'Service de la Météorologie Nationale' in Antananarivo. For some species, soil pH was measured directly in the field by W. Röösli with the 'System Stoeker'. Measurement of the pH was colorimetric, the colour of the obtained solution being compared with a standard sample card belonging to the System. For the African continent, *Vegetation of South Africa, Lesotho and Swaziland* by Bredenkamp et al. (1996) provided us with the relevant vegetation types and simple climatic data. Lavranos (pers. comm.) added some information on the biotopes of the continental African species of *Pachypodium*.

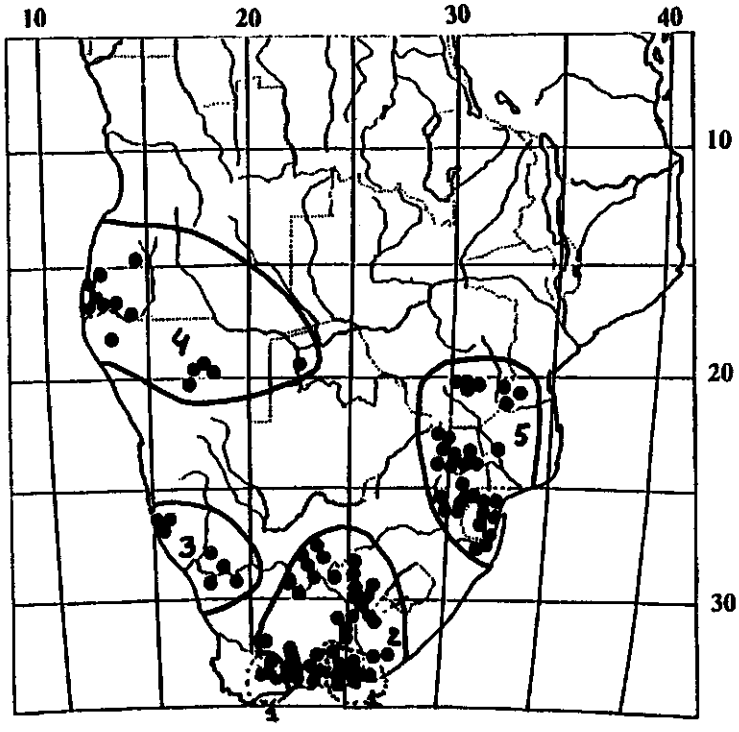
We have no specific information on the vegetation in Botswana, Mozambique, Namibia and Zimbabwe as far as *Pachypodium* is concerned. For *Pachypodium ambongense* and *P. bicolor* detailed habitat information is also lacking.

In conformity with the aims set out above, we restricted our study area to places where *Pachypodium* specimens actually have been found (Maps 16-17, p. 85). Species of the genus occur in Angola, Botswana, Madagascar, Mozambique, Namibia, South Africa, Swaziland and Zimbabwe (see Map 18, p. 86). It is approximately limited to an area between 12°11′ and 34°00′S, and 12°52′ and 49°20′E. In Madagascar it extends from near Cap St Marie in the south to near Antsiranana (= Diégo-Suarez) in the north excepting the humid eastern and Sambirano regions. In continental Africa *Pachypodium* is found more often in South Africa than in the other countries.

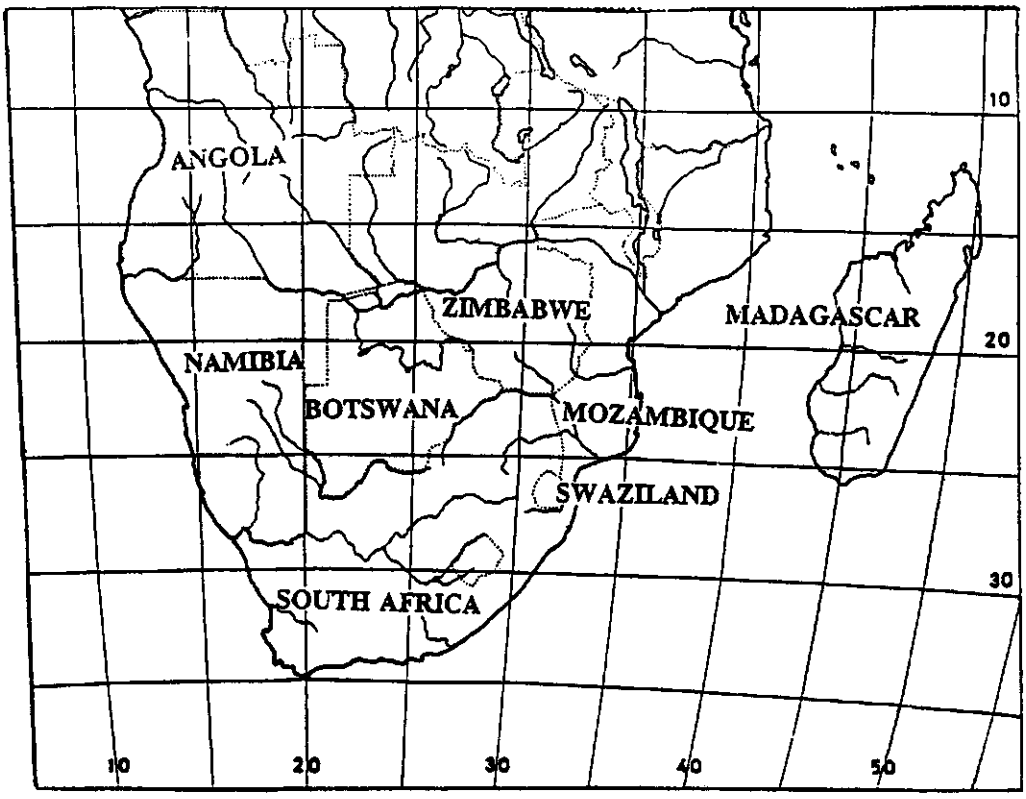
The precise latitude and longitude where the species are found are not indicated here for obvious reasons: particularly the rare species should be protected from visits of plant robbers. General area indications are given. This presents a particular case in



Map 16. *Pachypodium* in Madagascar.



Map 17. *Pachypodium* in Southern Africa.
1. *P. bispinosum*
2. *P. succulentum*
3. *P. namaquanum*
4. *P. lealii*
5. *P. saundersii*



Map 18. Countries where *Pachypodium* species occur.

Table 1. Selected climatic data for the main distribution areas of *Pachypodium* species of Madagascar (source: Service de la Météorologique Nationale d'Antananarivo).

Regions	Stations	Average temperature Coldest month	Average temperature Warmest month	Rainfall (mm)	Number of dry months
Semi-humid	Antananarivo	14.5	22.2	1354	5
	Ambilobe	24.5	28.3	1872	6
	Marovoay	24.2	29	1520	6
	Befandriana Nord	22.2	27.2	1985	6
Sub-semi-humid	Diégo-Suarez	25.1	28.3	902	7
	Maintirano	25.7		840	7
	Manja	21.2	27.5	896	7
	Ranohira	14.8	28.4	912	7
	Ihosy	17.4	24.5	842	7
	Mandritsara	21.2	26.7	1149	7
Semi-arid	Bezaha	19.9	28.6	517	8
	Ejeda	18.3	27	582	8
	Ampanihy	19.8	28.3	581	7
	Amboasary	19	28.7	499	9
	Beloha Sud	19.3	28	457	9
	Tsihombe	19.4	27.8	506	8
Sub-arid	Tuléar = Toliara	19.9	27.4	344	10
	Faux Cap	20.2	26.4	344	10

the ethics of science, supposed to demand that the truth shall be revealed whatever the cost. We solved this moral problem by deciding that the price of truth should not include the risk of extinction of the species studied.

RESULTS

The results of the biotope studies are presented by a downward, zoom-like movement, from the broad geographical and climatological scales down to the habitat of *Pachypodium* species. Thus, we will first give information on the species in relation to e.g. altitude, precipitation, temperatures, followed by habitat information per species. The data at the widest scales are from literature and other existing sources, whereas the data on specific habitats are the result of our own observations, unless stated otherwise. Table 1 presents information on selected climates in Madagascar.

1. *Altitude*

In Madagascar *Pachypodium* species are found from sea level (*P. cactipes*, *P. geayi* and *P. rutenbergianum*) to an altitude of 1900 m (*P. brevicaule*). In the African continent they are known from sea level (*P. bispinosum*) to 1600 m (*P. lealii*).

2. *Temperature extremes*

The average annual temperature regime, as established by the parametric temperatures varies approximately from 13°C where *Pachypodium brevicaule*, *P. densiflorum*, and *P. eburneum* occur, to 26.7°C in the habitats of *P. decaryi*, *P. rutenbergianum* and *P. windsorii*. In the central part of Madagascar frost occurs occasionally. Antsirabe has recorded an absolute minimum of –2.6°C and Ambohibary one of –6.3°C (Lavranos & Röösli 1996). In the sub-arid region the maximum temperature may reach up to 40°C (Rauh 1986). In continental Africa the extreme temperatures range from an occasional –10°C for *Pachypodium succulentum* sites to as much as 45°C for those of *P. bispinosum*, *P. lealii* and *P. namaquanum*. In winter some snow may fall sometimes in the South-eastern Mountain Grassland (Lubke et al. 1996). The continental African species live in areas with a heat regime exhibiting greater amplitudes than those of Madagascar.

3. *Precipitation*

In the southern part of the African continent the rainfall varies from 75 mm per annum in the sites of *P. namaquanum* to 800 mm per annum in *P. saundersii* sites (J.J. Lavranos, pers. comm.). Along the west coast of South Africa and Namibia, the yearly rainfall is less than 100 mm but the fog coming in from the Atlantic Ocean plays a very important role in the maintaining plant diversity (Bredenkamp et al. 1996). In Madagascar precipitation varies from 344 mm per annum for the region of the habitats of *P. geayi*, *P. lamerei* and *P. meridionale* to 1985 mm per annum for those of *P. baronii*, *P. rosulatum* and *P. rutenbergianum*.

4. *Number of dry months per year*

Pachypodium is very much a representative element of the dry flora of continental Africa and Madagascar (Schnell 1970). *Pachypodium* grows in areas where the number of dry months varies from 5 (*P. brevicaule*) to 10 or more (*P. cactipes*, *P. geayi*, *P. lamerei* and *P. meridionale*).

Vegetation zones of Madagascar and southern Africa
(Maps 16-17, p. 85; Map 18, p. 86)

The data presented here are mainly geographical and their ecological significance is limited to the localization of surfaces covered by certain vegetation types (Bredenkamp et al. 1996, Du Puy & Moat 1996), coinciding with the areas of distribution of *Pachypodium* species. These data do not directly explain the occurrence of *Pachypodium* species, an aspect that will figure amply in the discussion.

The vegetation types have been listed in Tables 2 and 3. In Madagascar *P. ambongense*, *P. baronii*, *P. bicolor*, *P. decaryi*, *P. rosulatum*, *P. rutenbergianum*, *P. sofiense* and *P. windsorii* occur mainly in low open Deciduous Western Forest. *P. brevicaule*, *P. densiflorum*, *P. eburneum*, and *P. gracilius* are found on rocky outcrops in Evergreen Sclerophyllous (*Uapaca*) Woodland or Savanna. *P. horombense* is known from Scrubland and Savanna. *P. catipes* and *P. geayi* are known mainly from low open Deciduous, Dry, Southern Forest and Scrubland. *P. lamerei* and *P. meridionale* occur both in low open Deciduous Western Forest and low open Deciduous, Dry, Southern Forest and Scrubland. In the African continent *Pachypodium lealii* is known in Low Mopane Scrub and Xerophyllous Forest, *P. saundersii* in Savanna and *P. nama-*

Table 2. Vegetation types associated with *Pachypodium* species in Madagascar.

Species	Vegetation types					
	Low open deciduous W. Forest 0-800 m	Evergreen scleroph. Uapaca Woodland 800-1800 m	Savanna	Low open deciduous dry S. Forest and Scrubland 0-300 m	Scrubland	Coastal Bush (Western)
P. ambongense	+					
P. baronii	+					
P. bicolor	+					
P. brevicaule		+	+			
P. cactipes				+		
P. decaryi	+					
P. densiflorum		+	+			
P. eburneum		+				
P. geayi				+		
P. gracilius		+	+			
P. horombense			+		+	
P. inopinatum			+			
P. lamerei	+			+	+	
P. meridionale	+			+		
P. rosulatum	+				+	
P. rutenbergianum	+		+		+	+
P. sofiense	+				+	
P. windsorii	+					

Plate 61. *Pachypodium sofiense*, Mandritsara.
Plate 62. *Pachypodium sofiense*, Mandritsara.
Plate 63. *Pachypodium sofiense*, Mandritsara.
Plate 64. *Pachypodium rutenbergianum* and *P. windsorii*, Windsor Castle.

61 | 63 / 64
62

Table 3. Vegetation types associated with *Pachypodium* species in Angola and South Africa.

Biomes	Vegetation types	Species				
		bispinosum	*lealii*	*namaquanum*	*saundersii*	*succulentum*
Fynbos	Mountain fynbos	+				
Grassland	Rocky highveld					+
	Dry sandy highveld					+
	N-eastern Mountain	+				
	S-eastern Mountain					+
Nama Karoo	Central Lower	+				
	Eastern Mixed	+				+
	Great					+
	Orange River			+		+
	Upper					+
Savanna	E. Thorn Bushveld	+				+
	Kalahari Mountain Bushveld					+
	Kimberley Thorn Bushveld					+
	Lebombo Arid Mt Bushveld				+	
	Mixed Bushveld				+	
	Mixed Lowveld Bushveld				+	
	Mopane Bushveld				+	
	Natal Lowveld Bushveld				+	
	South Lowveld Bushveld				+	
	South Arid Mt Bushveld				+	
	Sweet Lowveld Bushveld				+	
Succ. Karoo	Little					+
	Upland			+		
Thicket	Dune Thicket	+				
	Mesic Succulent Thicket	+				
	Spekboom Succ. Thicket	+				
	Valley Thicket	+				+
	Xeric Thicket	+				+
Angola	Xeroph. Forest and Low Mopane Scrub		+			

quanum in Nama Karoo and Succulent Karoo. The rest is distributed in many different biomes but *P. bispinosum* occurs mainly in Thicket and *P. succulentum* in Grassland, Nama Karoo, Savanna, and Thicket.

From the general context of climates, landscapes and vegetation types we now descend to the more detailed scale of precise habitats of the species of *Pachypodium*.

65 | 67
66 | 68
69 | 70

Plate 65. *Pachypodium winsorii*, Windsor Castle.
Plate 66. *Pachypodium windsorii*, Windsor Castle.
Plate 67. *Pachypodium windsorii*.
Plate 68. *Pachypodium windsorii*.
Plate 69. *Pachypodium bispinosum*, near Willowmore.
Plate 70. *Pachypodium bispinosum*, Laingsburg, Cape.

5. *Substrate*

Pachypodium grows on various types of substrates (Tables 4 and 5). Some species occur on one single type of substrate, such as *P. ambongense*, *P. decaryi* and *P. windsorii* growing exclusively on calcareous rocks. *P. brevicaule* and *P. eburneum* are restricted to quartzite. *P. bicolor* and *P. gracilius* prefer sandstone and *P. inopinatum* grows on granite. *P. cactipes*, *P. densiflorum* and *P. horombense* occur mainly on gneiss and granite. *P. rutenbergianum* can grow on varying substrates, particularly on sand with laterite or on sand such as *P. geayi* and *P. rosulatum*. In continental Africa *P. namaquanum* grows mainly on granite, quartzite and sand. The other species are found on various different substrates.

6. *Soil pH*

The pH was measured by Röösli for the substrates of half the number of species endemic to Madagascar. The pH ranges approximately from 3.5 to 7 (Table 6). Strictly acid soils, with a pH from 3.5 to 5, are preferred by *P. brevicaule*, *P. cactipes*, *P. densiflorum*, *P. eburnum* and *P. rosulatum*. Acid to almost basic soils, with a pH between

Table 4. Nature of substrates of Madagascan *Pachypodium* species.

Species	Substrates										
	Mesoz. limestone	Granite	Gneiss	Sand-stone	Quart-zite	Sand	Schist	Tert calc.	Sandy soil	Basalt	Sandy loam
ambongense	+										
baronii	+	+	+								
bicolor				+							
brevicaule					+						
cactipes		+	+								
decaryi	+										
densiflorum		+	+		+						
eburneum					+						
geayi						+	+	+			
gracilius				+							
horombense		+	+								
inopinatum		+									
lamerei	+	+	+	+		+		+	+		
meridionale	+			+				+			
rosulatum		+	+			+				+	
rutenbergianum	+	+				+		+			+
sofiense	+		+								
windsorii	+										

Table 5. Nature of substrates of *Pachypodium* species belonging to the African continent.

Species	Substrates												
	Quart-zite	Sand-stone	Clay	Gravel	Sandy soil	Dolo-mite	Granite	Schist	Basalt	Lime-stone	Rhylite	Sand stone	Dole-rite
bispinosum	+	+	+	+									
leâlii	+				+	+	+						
namaquanum	+	+					+	+					
saundersii		+					+		+	+	+	+	
succulentum	+	+				+						+	+

Table 6. Values of soil pH for some Madagascan *Pachypodium* species.

Species	pH values				
	3.5	4	4.5	5	7
ambongense					
baronii					
bicolor					
brevicaule					
cactipes			+		
decaryi					
densiflorum	+		+		
eburneum			+		
geayi					+
gracilius					
horombense			+		
inopinatum					
lamerei			+	+	+
meridionale					+
rosulatum		+		+	
rutenbergianum			+		+
sofiense		+			
windsorii					

4.5 and 7, are suitable for *P. lamerei* and *P. rutenbergianum*. *P. meridionale* can grow on neutral soil of pH 7, and *P. sofiense* will grow on calcareous soils but also on acid soil (with a pH of 4). *P. lealii* grows on outcrops of granite in fairly fertile, acid soil (Rawé 1968, as *P. giganteum*).

Description of the habitats of species of Pachypodium

In the discussion, the following data on specific biotopes immediately surrounding *Pachypodium* species will be linked to adaptive morphological features. The morphological data required for this fitting together of both pieces of the puzzle are given in the taxonomic part of this book, there also the geographical distribution of the species is presented.

The following pages contain the physiognomic description of the habitats of *Pachypodium* species of Madagascar and Southern Africa in alphabetical order.

P. ambongense grows on Mesozoic calcareous rocks in the low open Decidous Western Forest zone. According to Rauh (1995), this species is associated here with *Adenia firingalavensis* Harms (Passifloraceae), *Aloe* sp., *Cissus* sp. (Vitaceae), *Euphorbia viguieri*, *Lomatophyllum* sp. (Liliaceae), *Pachypodium rutenbergianum*, *Pandanus* sp., *Uncarina* sp. (Pedaliaceae), and *Xerosicyos perrieri* (Cucurbitaceae). It occurs at altitudes of less than 100 m above sea level.

P. baronii grows on Mesozoic calcareous rocks and outcrops of the metamorphic basement gneiss and granite in clefts or crevices. It is usually found in the low open Deciduous Western Forest zone, but sometimes it is found at high altitudes up to 1200 m (*Humbert* 25619). *P. baronii* lives in an area with a high annual rainfall which ranges from 900 to 1985 mm (semi-humid region). The number of dry months ranges from 6 to 7 per year. The average monthly temperatures vary from 27.2° to 21.2°C, average annual temperatures vary from 24.7° to 23.9°C. *P. baronii* occurs at altitudes from 300 to 1200 m.

P. bicolor grows on outcrops of sandstone in the Deciduous Western Forest zone. Average monthly temperatures here range from 30° to 19.8°C (Morondava, Bastian 1967).

P. brevicaule grows in crevices between outcrops of quartzite. It is strictly adapted to acid soil with pH varying from 3.5 to 4.5. It is found in the Evergreen Sclerophyllous (*Uapaca*) Woodland or Savanna zone dominated by *Hyparrhenia* sp. and scattered woody plants such as *Leptolaena pauciflora*, *Uapaca bojeri* and many other plants. *P. brevicaule* grows associated with *Aloe capitata*, *Helichrysum ibitiense*, *Tetradenia fruticosa*, *Xerophyta dasylirioides* and according to Rauh (1995) also with *Aloe alfredii*, *Euphorbia quartziticola* and *Pachypodium densiflorum*. It occurs in an area with an annual rainfall of 1354 mm and a number of dry months of 5 per year. The average monthly temperature varies from 17° to 9 °C according to Anonymous (1973). The average annual temperature varies from 18.4° to 13°C. *P. brevicaule* is found at high altitudes between 1300 to 1900 m.

P. cactipes grows on outcrops of gneiss and granite in fissures or crevices in acid soils of pH c. 4.5. It is usually found in low open Deciduous, Dry, Southern Forest and Scrubland zones with Didiereaceae such as *Alluaudia procera*. Sometimes this species is also found at high altitudes up to 900 m in the Mananara River basin, in the Mandrare River system (*Humbert* 14071). *P. cactipes* grows commonly together with species of *Aloe* and *Xerophyta*. The annual rainfall is comparatively low and varies between 340 and 530 mm (sub-arid to semi-arid). The number of dry months amounts to 9 or 10 months or more per year. The average monthly temperature varies from 28.7° to 19°C. The average annual temperature varies from 23.9° to 23.6°C.

P. decaryi grows on Mesozoic calcareous rocks in the Deciduous Western Forest zone. It is associated with *Ficus reflexa* subsp. *reflexa*, and *Pandanus parkinsonii*. Annual rainfall is high and ranges between 900 and 1872 mm (semi-humid region). The number of dry months is 6 to 7 per year. The average monthly temperature varies from 28.3° to 24.5°C. The average annual temperature varies from 26.7° to 26.4°C at low altitudes between 30 and 350 m.

P. densiflorum grows on outcrops of gneiss, granite and quartzite in fissures or clefts. It is adapted to very acid soil with pH between 3.5 and 4.5. *P. densiflorum* is found in the Evergreen Sclerophyllous (*Uapaca*) Woodland or Savanna zone. Grasses here are dominated by *Aristida* and *Hyparrhenia*, and in the savanna some scattered woody plants such as *Sclerocarya* sp., *Uapaca bojeri* and *Ziziphus* sp. are conspicuous. *P. densiflorum* is associated with *Aloe accutissima*, *Bulbostylis schoenoides*, *Dipcadi heterocuspe*, *Euphorbia milii*, *Ischnolepis tuberosa*, *Pellaea goudotii*, *Pentaschistis perrieri*, *Senecio crassissimus*, *Tetradenia fruticosa* and *Xerophyta dasylirioides*. According to Koechlin et al. (1974), *Coleochloa setifera*, *Euphorbia oncoclada*, *Senecio decaryi* are growing in association. Rauh (1995) refers to the following associated species: *Cynanchum pycnoneuroides*, *Aloe conifera*, *A. deltoideodonta* var. *candicans*, *A. fievetii*, *Euphorbia didiereoides* and *E. fianarantsoae*. The annual rainfall is c. 1820 mm and the average monthly temperature varies between 17° and 9°C (Antsirabe area, Anonymous 1973). Other data show a range of 22.2° to 14.5°C (Antananarivo area). Average annual temperatures vary from 18.8° to 13 °C. *P. densiflorum* is known from 200 to 1750 m above sea level.

P. eburneum grows in fissures on outcrops of quartzite. It is adapted to acid soils with pH 4.5. *P. eburneum* is found in a remnant of Evergreen Sclerophyllous (*Uapaca*) Woodland. Associated species recorded are *Aloe cremersii*, *A. silicicola* and *A. trachyticola*. The annual rainfall is 1350 mm and the average annual tempera-

ture is about 13°C (Antsirabe, see Anonymous 1973). *P. eburneum* occurs up to an altitude of c. 1700 m.

P. geayi grows on Tertiary calcareous rocks, sand (dunes) and schists. The soil on the calcareous rock has a pH of 7. This species occurs mainly in the low open Deciduous, Dry Southern Forest and Scrubland zones, associated with *Adansonia za*, *Alluaudia procera*, *Cassia* sp., *Cedrelopsis grevei*, *Delonix adansonioides*, *Didierea madagascariensis*, *Euphorbia stenoclada* and *Fernandoa madagascariensis*. The annual rainfall is low: from 344 to 581 mm (sub-arid and semi-arid). The number of dry months is between 8 and 10 months or more per year. The average monthly temperature varies from 28.3° to 20.2°C. The average annual temperature varies from c. 24.1° to 23.3° C, which corresponds with altitudes from sea level to about 300 m. The altitude indicated by *Poisson* 648 (P) as 657 m is incorrect because the highest mountain between Ejeda and Ampanihy attains only 317 m.

P. gracilius grows on outcrops of sandstone in fissures, crevices or clefts, and is found in open Evergreen Sclerophyllous (*Uapaca*) Woodland or Savanna dominated by *Aristida* sp. and *Hyparrhenia* sp., and some woody plants such as *Leptolaena bojeriana*, *L. luteola*, *Mascarenhasia lisianthiflora* and *Uapaca bojeri*. On top of the outcrops it is associated with *Aloe isaloensis*, *Euphorbia milii*, *Kalanchoe orgyalis*, *K. synsepala*, *Ischnolepis tuberosa*, *Tetradenia fruticosa*, *Xerophyta dasylirioides*. In addition Rauh (1995) mentions *Ceropegia dimorpha*, *Coleochloa setifera* and *Cynanchum microlobum*. The rainfall is 912 mm per year and the number of dry months is 7 per year (Ranohira Region). The average monthly temperature varies between 28.4° and 14.8°C, an average 21.6°C on yearly basis. *P. gracilius* occurs from 300 to 1000 m above sea level.

Pachypodium horombense grows on outcrops of gneiss and granite in crevices or fissures. This species is found in Scrubland or Savanna dominated by *Aristida* sp., *Heteropogon contortus* and *Hyparrhenia* sp. Associated species include *Catharanthus longifolius*, *Kalanchoe orgyalis*, *Pachypodium lamerei*, *Stapelianthus* sp., *Tetradenia* sp., *Xerophyta dasylirioides*. In addition Rauh (1995) refers to *Euphorbia horombensis*. The annual rainfall is 842 mm and the number of dry months is 7 per year (Ihosy District). The average monthly temperature varies between 24.5° and 17.4°C, an average 21.5°C per year. *P. horombense* is known from altitudes between 400 and 1100 m.

Pachypodium inopinatum grows on lower montane outcrops of granite in fissures and clefts surrounded by Savanna dominated by species of *Aristida* and *Hyparrhenia*, and some woody plants such as *Leptolaena bojeriana* and *Weinmannia* sp. (remains of Sclerophyllous Forest). Accompanying species are *Aloe capitata*, *Coleochloa setifera*, *Dyonicha bojeri*, *Euphorbia milii*, *Kalanchoe synsepala*, *Pellaea goudotii*, and *Tetradenia* sp. The rainfall is 1820 mm per year and the average monthly temperature varies from 22.2° to 14.5°C, the average annual temperature is about 18.8°C (Station forestière de Manankazo, Rakotondrainibe 1989). *P. inopinatum* has been reported at altitudes of about 1450 m.

P. lamerei is geography – wise the most widely distributed species in Madagascar and has been found on a variety of substrates. *P. lamerei* grows on sand and sandy soils, Mesozoic and Tertiary calcareous rocks and on outcrops of gneiss, granite and sandstone. It is adapted to acid as well as almost basic soil with pH values ranging from 4.5 to 7. The species is mainly known from zones with low open Deciduous Western Forest and low open Deciduous, Dry, Southern Forest and Scrubland, but occasionally up to an altitude of 1200 m (*Humbert* 6756 from Upper Mandrare R.). It

may be in association with *Aloe* sp., *Alluaudia procera*, *Apaloxylon tuberosum*, *Commiphora aprevalii*, *Cynanchum eurychitoides*, *Didierea madagascariensis*, *Euphorbia milii*, *E. tirucalli*, *E. viguieri*, *Hildegardia erythrosiphon*, *Kalanchoe gastonis-bonnieri*, *Neoharmsia madagascariensis*, *Pachypodium horombense*, *P. meridionale*, and some species of *Stapelianthus*, *Tetradenia*, and *Xerophyta*. According to Jongkind (pers. comm.) *Cyphostemma sakalavense* (Asclepiadaceae), *Uncarina leptocarpa* (Pedaliaceae) and *U. sakalava* are also found in association with *P. lamerei*. It occurs in a region with a low rainfall between 344 and 896 mm. The number of dry months varies from 7 to 10 months or more per year (dry to very dry). The average monthly temperatures vary from 28.7° to 17.4 °C, the latter corresponding to an altitude of 1200 m. Average annual temperatures lie between 24° and 21°C. In arborescent species of *Pachypodium* the bottle-shaped or cigar-shaped trunk may act as a water reservoir, with *P. lamerei* as a good example. The wood of the succulent trunks is soft and juicy, and contains much parenchyma and few wood elements (Rauh 1986).

Pachypodium meridionale grows on sandstone and Mesozoic and Tertiary calcareous rocks with a soil of pH 7 in the low open Deciduous Western Forest zones, and in the low open Deciduous, Dry, Southern Forest and Scrubland zones. It grows together with *Adansonia grandidieri*, *Alluaudia procera* and *P. lamerei*. The rainfall varies from 344 to 896 mm per year. The number of dry months varies between 7 and 10 or more per year (sub-arid, semi-arid and sub-semi-humid). The average monthly temperature varies from 28.6° to 19.9°C at altitudes of 40-700 m, the yearly averages are stable between 24.4° and 24°C.

P. rosulatum grows on sand or on outcrops of granite and gneiss. It is adapted to acid soils of pH 4-5. It is found in the low open Deciduous Western Forest and Scrubland zone. It is accompanied by *Aloe* sp., *Ancylobotrys petersiana*, *Breonia* sp., *Carphalea* sp., *Commiphora marchandii*, *Dalbergia* sp., *Erythroxylon pervillei*, *Euphorbia millii*, *Forsythiopsis vincoides*, *Holmskioldia* sp., *Hugonia brewerioides*, *Kalanchoe synsepala*, *Mascarenhasia lisianthiflora*, *Memecylon boinense*, rarely *Pachypodium rutenbergianum*, *Plectaneia thouarsii*, *Protorhus deflexa*, *Rauvolfia media*, *Tabernaemontana coffeoides*, *T. stellata*, *Terminalia* sp. and according to the label of *Hofstätter* 260890 also by *Euphorbia guillauminiana*. The rainfall ranges between 840 and 1985 mm per year. The number of dry months varies from 6 to 7 in the year (semi-humid region). The average monthly temperatures range from 29° to 21.2°C, the average annual temperatures vary from 26.6° to 24°C. *P. rosulatum* occurs from 100 to 600 m above sea level.

Pachypodium rutenbergianum grows on Mesozoic and Tertiary calcareous rocks, sand, sand with laterite and on outcrops of granite. This species may occur on acid to almost basic soils with pH values ranging from 4.5 to 7. *P. rutenbergianum* is found in the zones of low open Deciduous Western Forest, and Scrubland and Savanna. Associated species are *Ancylobotrys petersiana*, *Caesalpinia bonduc*, *Carissa edulis* (= *C. spinarum*), *Catharanthus trichophyllus*, *Euphorbia milii*, *Kalanchoe synsepala*, *Mascarenhasia arborescens*, *M. lanceolata*, *Pachypodium rosulatum*, sometimes *P. windsorii*, *Petchia erythrocarpa*, *Plectaneia thouarsii*, *Rauvolfia media*, *Rhopalocarpus lucidus*, *Sclerocarya caffra*, *Strophanthus boivinii*, *Strychnos spinosa*, *Tabernaemontana calcarea* and *Ziziphus jujuba*. Rauh (1995) added as companion species also *Euphorbia guillauminiana* and *Hyphaene schatan*. The annual rainfall varies between 840 and 1985 mm per year. The number of dry months is from 6 to 7 (semi-humid region). The average monthly temperatures vary from 31.8° (Majunga region,

see Bastian 1967) to 21.2°C. Average annual temperatures vary from 26.7° to 24°C. *P. rutenbergianum* occurs from sea level to 380 m.

P. sofiense grows on Messozoic calcareous rocks and on outcrops of gneiss. The soil on top of the outcrops with gneiss has a pH of 4. It is found in low open Deciduous Western Forest and Scrubland. On calcareous rocks *P. sofiense* is associated with *Bussea* sp., *Commiphora aprevalii*, *Dalbergia sp.*, *Delonix adansonioides*, *Diospyros* sp., *Erythroxylum seyrigii*, *Gyrocarpus americanus* and *Hildegardia erythrosiphon.* The mean annual rainfall is 1149 mm and 7 dry months per year are recorded (Mandritsara area). The annual average temperatures vary from about 26.7° to 21.2°C (Mandritsara area), with an average of about 24°C per annum. *P. sofiense* is known from near sea level up to 600 m.

P. windsorii grows on Mezozoic calcareous rocks in the low open Deciduous Western Forest zones. It has been found associated with *Ancylobotrys petersiana*, *Euphorbia* sp., *Tetradenia* sp., while *Aloe suarezensis*, *Euphorbia bulbispina* and *E. viguieri* may also be associated (Rauh 1995). The annual rainfall is c. 902 mm with 7 dry months of the year (Diégo-Suarez = Antsiranana Distict). The average monthly temperature varies from 28.3° to 25°C, corresponding to a yearly average of about 26.7°C. *P. windsorii* is reported between 270 to 380 m above sea level.

As far as the *Pachypodium* species of continental Africa concerns, *P. bispinosum* grows on clay, sand, gravel or on outcrops of quartzite. The species has been documented in Mountain Fynbos, North-eastern Mountain Grassland, Central Lower Nama Karoo and Eastern Mixed Nama Karoo, Savanna (Eastern Thorn Bushveld) and all subdivisions of Thicket (Dune Thicket, Mesic Succulent Thicket, Spekboom Succulent Thicket, Valley Thicket and Xeric Thicket). According to the information on herbarium labels, *P. bispinosum* may occur in association with the following species: *Aloe* sp. (Aloaceae), *Crassula* sp. according to *Bayliss* 3103; *Ceropegia africana* (Asclepiadaceae), *Bayliss* 3639; *Delosperma lehmanii* (Aizoaceae), *Euclea* sp. (Ebenaceae), *Faucaria felina* (Aizoaceae), *Senecio* sp. (Compositae), *Groen* 1120; *Capparis* sp. (Capparidaceae), *Carissa haematocarpa* (= *C. bispinosa*) (Apocynaceae), *Gasteria nitida* (Aloaceae), as indicated on the sheet *Marloth* 13132, and *Euphorbia mammillaris* (Euphorbiaceae), *Portulacaria afra* (Portulacaceae) and *Rhus undulata* (Anacardiaceae), see specimen *van Jaarsveld et al.* 7878. The rainfall varies from 100 to 900 mm annually. In the western part of its distribution area some 40% of the total rain falls in the winter months (March-September) while at the eastern end of its distribution winter rains represent only 20% of the precipitation (J.J. Lavranos, pers. comm.). The temperature varies between extremes of –2°C and 42°C with a moderate average of 18°C. *P. bispinosum* occurs from sea level to 800 m.

Pachypodium lealii grows on outcrops and hillsides of dolomite (limestone), granite or quartzite and sandy soil. The substrates are mainly acid (J.J. Lavranos, pers. comm.). This species has been found in Xerophyllous Forest or Low Mopane Scrub. The rainfall ranges from 150 to 500 mm per year, falling almost exclusively in summer. The temperature ranges from about 5° to 45°C (J.J. Lavranos, pers. comm.). The altitudinal range is between 50 and 1600 m.

Pachypodium namaquanum grows on sand or on outcrops of granite, quartzite and schists. This *Pachypodium* species is mostly found in Orange River Nama Karoo and Upland Succulent Karoo. The rainfall here is low (between 75 and 150 mm per year) and the temperatures range from slightly above freezing to about 45°C (J.J. Lavranos, pers. comm.). *P. namaquanum* occurs between 300 and 900 m in arid regions both north and south of the Orange R. on rocky slopes, often with their roots wedged

tightly between large boulders or in rock crevices (Phillips 1940). Apparently the plants are strongly phototropic, they grow in areas where the sun is always to their north and most characteristically they curve their apex northwards. This species particularly fascinates gardeners, but although the seed germinates fairly readily, it generally does not thrive away from its natural desertlike conditions (Coates Palgrave 1983).

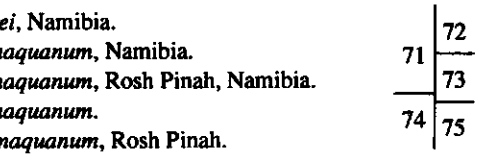
Pachypodium saundersii grows on basalt, granitic rocks, limestone, sand and sandstone. This species occurs in a number of Savanna biomes in South Africa: Lebombo Arid Mountain Bushveld, Mixed Bushveld, Mixed Lowveld Bushveld, Mopane Bushveld, Natal Lowveld Bushveld, Sour Lowveld Bushveld, Soutpansberg Arid Mountain Bushveld, and Sweet Lowveld Bushveld. It is found in association with *Afzelia quanzensis*, *Combretum apiculatum*, *Faurea* sp., *Huernia* sp., *Indigofera* sp., *Olinia* sp., *Plectranthus cylindraceus*, *Ptercelastrus* sp., *Sclerocarya caffra*, and according to *Correia & Marques* 1196 also with *Colophospermum mopane* (Leguminosae), *Strychnos* sp. (Loganiaceae) and *Sansevieria* sp. (Dracaenaceae). The rainfall is approximately between 300 and 800 mm per year. The temperature varies from about 5°C to well over 40°C (J.J. Lavranos, pers. comm.). *P. saundersii* occurs at altitudes of 100 to 1000 m.

Pachypodium succulentum is a quite widely distributed species endemic to South Africa. It grows on various substrates such as dolerite, dolomite, quartzite, sand or sandstone. *P. succulentum* is also found in many vegetation types: Rocky Highveld Grassland, Dry Sandy Highveld Grassland, South-eastern Mountains Grassland, Eastern Mixed Nama Karoo, Great Nama Karoo, Orange River Nama Karoo, Upper Nama Karoo, Eastern Thorn Bushveld, Kalahari Mountains Bushveld, Kimberley Thorn Bushveld, Little Succulent Karoo, Valley Thicket and Xeric Succulent Thicket. The following species are companions: *Aloe* sp. (Aloaceae) according to the label of *Drège* 3150; *Portulacaria afra* (Portulacaceae) is mentioned on *Liebenberg* 6622. *Marloth* 6075 adds *Capparis* sp. (Capparidaceae), *Euphorbia mammillaris* (Euphorbiaceae) and *Gasteria nitida* (Aloaceae). The rainfall is in the order of 300 to 500 mm per year. *P. succulentum* has an enormous underground storage trunk found growing in the sandy regions of the Kalahari and can survive for years without any water uptake (Walter 1979). The temperatures range between –13°C and 41°C. During the winter severe frosts occur at higher altitudes, but little snow falls in South-eastern Mountain Grassland (Lubke et al. 1996). *P. succulentum* is found from sea level up to 1400 m.

DISCUSSION AND CONCLUSIONS

The wide as well as the immediate environments of *Pachypodium* species will be discussed in this order. First, the general context will be sketched, with the aim to pin-

Plate 71. *Pachypodium lealei*, Namibia.
Plate 72. *Pachypodium namaquanum*, Namibia.
Plate 73. *Pachypodium namaquanum*, Rosh Pinah, Namibia.
Plate 74. *Pachypodium namaquanum*.
Plate 75 . *Pachypodium namaquanum*, Rosh Pinah.



point the few general environmental factors that bear upon the aptitude of larger areas to host *Pachypodium* species. Then we will discuss the specific habitats of the species, with particular attention to their comparison with corresponding biotopes elsewhere. Finally, there is a strong indication of the adaptive history and strategy of the plants belonging to the genus.

The larger context

The information obtained from our own fieldwork and from literature shows that *Pachypodium* species grow in dry areas and in different vegetation zones (Tables 1-3), mainly in rocky habitats (Tables 4 and 5). In Madagascar *Pachypodium* is absent from the eastern zone of the island the domain of the Evergreen, humid forests at low altitude and Sambirano (0-800 m), the Evergreen, humid forest at mid-altitude (800-1800 m), the Evergreen, humid forest at lower montane (1800-2000 m) and the montane (>2000 m) scrubland often dominated by *Phillipia* (= *Erica*).

Arborescent *Pachypodium* species such as *P. geayi*, *P. meridionale*, *P. rutenbergianum* and *P. sofiense* do not surpass an altitude of 800 m in Madagascar except the most widely spread *P. lamerei* that can reach 1200 m, while dwarf plants (*P. brevicaule*) and shrubs (such as *P. eburneum* and *P. inopinatum*) are only known from areas above 1000 and up to 1900 m. In the African mainland, *P. bispinosum* and *P. namaquanum* are known from sites up to an altitude of 900 m and *P. lealii* may even reach 1600 m. According to Koechlin et al. (1974) *Pachypodium* is absent above 2000 m altitude.

The species of *Pachypodium* usually grow in frost-free areas, except *P. bispinosum* and *P. succulentum*; these sometimes withstand temperatures of –10°C in winter. According to Chapman & Reiss (1992) most succulents do not survive the cold at subzero temperatures.

The ecological profile of the general regions where, in Madagascar and the Southern parts of Africa, one may expect to find *Pachypodium* biotopes, may now be sketched. Such regions are situated between sealevel and 2000 m and are also generally defined by temperature. However, all species of *Pachypodium* share sunny and xeric habitats. Their exclusion from humid, dense forest vegetation – except on inselbergs surging above the forest canopy – shows that adaptive evolution of *Pachypodium* species was concentrated on open, dry, xeric habitats. The xerophytic or succulent morphology of many species supports this general conclusion.

Rupicolous shrublands are preferred by *Pachypodium* species and here they occur on outcrops of various types of parent rock throughout Madagascar, although most commonly in the central highlands. *Pachypodium* is absent from the eastern humid part of Madagascar and from the high mountains with an altitude over 2000 m. As edaphically arid islands the inselbergs support a plant cover dramatically different from their surroundings. They are particularly frequent in Angola extending to Namibia, Zimbabwe and Central Madagascar (Barthlott & Porembski 1996).

76

77 | 79

78 | 80

Plate 76. *Pachypodium saundersii*, Goba, Mozambique.
Plate 77. *Pachypodium saundersii*, Goba, Mozambique.
Plate 78. *Pachypodium succulentum*, 53 km E of Grahamstown.
Plate 79. *Pachypodium succulentum*.
Plate 80. *Pachypodium succulentum*.

The little that is known about seed dispersal by *Pachypodium* species fits in with such a scattered set of outcrop/inselberg habitats. The seeds of *Pachypodium* spp. are provided with awns suggesting that dispersal is by wind. However, according to Keraudren (1963) wind dispersal may not be very effective because the awns of the seeds separate easily or even as soon as the fruit follicles open, and the seeds will fall on the ground near the mother plant. In addition, it is possible that insects, birds and also small rodents may disperse the seeds. During our study seedlings were only found close to where the mother plant presumably has been established for a long time. The occurrence of *P. densiflorum* from Kandreho to Zazafotsy in between inselbergs or outcrops shows that distribution is restricted. Other examples are *P. eburneum, P. windsorii, P. inopinatum* and *P. decaryi*, that have a more or less restricted distribution in this way too. Chorological aspects are among the most interesting and urgent items for research, as the true situation is unclear.

The habitat of Pachypodium species

The key to understanding the particular morphology and architecture of the species hence lies in detailed environmental study of the special, scattered habitats of these species in the different ecological zones known to host them.

Often *Pachypodium* species occur on rocky outcrops, steep hills and on inselbergs. In these places the microclimatic conditions are quite different from the general climate of the region as reported by standard meteorological records (Clarke 1954). Microclimatically and edaphically these habitats can be considered as arid islands, even in perhumid zonobiomes. Indeed, they have a flora entirely different from the surrounding vegetation (Barthlott & Porembski 1994).

According to Rauh (1986), temperature reaches 50° to 70°C on bare rocks. On inselbergs and even on smaller rocky outcrops in the perhumid Taï rain forest in SW Ivory Coast this was confirmed, as the temperature of the air over sun-exposed rocky surfaces was found to exceed 50°C, whereas the temperature in the surrounding forest understorey remained under 30°C. In the same locality the relative humidity of the air drops to 30% in relation to almost 90% in the surrounding forest understorey (Barthlott & Porembski 1996). Vegetation on rocks exposed to the sun may be heated up to temperatures of 50° to 60°C, which may approach lethal limits. During the long rainless periods insolation is very intense. A rock substrate (e.g. black in colour) is the hottest substrate here. Consequently, most plants occur only in fissures of rocks (Warming 1909). Even sand surfaces may warm up to a temperature of 60°C by day (Walter 1979).

On outcrops, the plants are subjected to fluctuating moisture, high winds and temperature extremes, due to shallow soil and exposed situation. The evaporation of water from the exposed shallow soil is maximal. The only plants that can survive such conditions are those which have some special adaptation to extreme drought (Higgins 1950). These plants must be regarded as constituting a small to moderately sized well-defined formation of their own, because the composition and architecture of the community is strongly affected by the climatic factors of the locality (cf. Oldeman 1990). These plants must be able to resist long periods of drought, and this is achieved chiefly by means of special morphological adaptations. There are different ways of adaptation. Examples of some adaptive structures conveying resistance against such conditions are: succulent leaves such as in species of *Aloe* and *Kalanchoe*, stem and root succulence in shrubs such as in species of *Cynanchum* and *Tetradenia*, spinescent and succulent trunks like those in species of *Euphorbia* and *Pachy-*

podium and numerous species of *Pellaea* and *Xerophyta* spp., and many other such genera. *Pachypodium* species display a water-storing trunk or stems. The name means 'Thickfoot' (*Pachys* = thick; *podium* = foot), as in some species the trunk remains underground, e.g. in *P. bispinosum* and *P. succulentum*. *P. gracilius* (Plate 33, opposite p. 57) has a globular trunk, *P. baronii* (Plate 2, opposite p. 16) has a bottle-shaped one and *P. lamerei* (Plate 45, opposite p. 65) a cigar-shaped trunk.

Pachypodium rutenbergianum can grow directly on sand with laterite and also on sand as do *P. bispinosum*, *P. geayi*, *P. lamerei*, *P. namaquanum*, *P. rosulatum*, *P. saundersii* and *P. succulentum*. The sand body can store water because the rain is readily taken up and there is less evaporation from the top layer that rapidly dries out. However, deep sand bodies lose water rather soon by seepage. Shallow sandy soils do not dry out so much if water accumulates on deeper, impermeable layers. When the upper 5 cm of the sandy layer have dried out, this would involve a loss of only 10% of the available water (Walter 1979). In both shallow and deep sands *Pachypodium* can have access to water. In the first case when *Pachypodium* species grow on sand dune close to the sea (e.g. *P. geayi* near Tuléar and *P. rutenbergianum* in NW and W coastal regions of Madagascar), the water table is relatively close to the surface and can be tapped by the long roots. In the second case where *Pachypodium* spp. grow on sand over laterite (e.g. *P. rosulatum* and *P. rutenbergianum* near Antsohihy and Ankarafantsika), the relatively impermeable laterite traps the water, and provided the sand is not too deep, this water source is available to the species.

On outcropping rocks, *Pachypodium* species are rooted in clefts, fissures and crevices. Their roots penetrate deeply in the soil accumulated in the crevices. On rocky ground with small cracks, the water may penetrate quite deeply, possibly to 100 cm or more. Under such circumstances, there is almost no evaporation, and nearly all rain water is retained. Fissured, rocky ground provides a 'very wet habitat' if there is no appreciable runoff from the rock surface and when there is enough fine soil accumulated in the cracks to retain the water (Walter 1979). In those conditions, *Pachypodium* species may store large amounts of water in the trunk and can easily survive a dry period of five months or more.

In the coastal region of Namibia, the annual rainfall is very low. However, the soil there is slightly but frequently moistened by fog or dew (Walter 1979). The fog can also condense on the spines of *P. namaquanum* which are pointing downward and the resulting water will drip onto the ground, which can be quite wet by the early morning. The moisture is taken up by the superficial root system. Whenever drought prevails for a very long period, the trunk of *Pachypodium* species becomes soft and the plants eventually die.

Soil pH values measured did not show much difference compared with those known from literature. Dajoz (1970) described the pH of calcareous soils as close to 8. Hence *Pachypodium* species are found throughout a range of pH conditions: from strictly acid soils (pH 3.5) to those quite alkaline (pH between 7 and 8). Of course all species growing on gneiss, granite, sand and quartzite are adapted to acid soil. Those on calcareous rocks are adapted to alkaline soil. There are some species tolerating either condition. We cannot indicate here a definite trend because our data are not complete. However, the great difference between the mean acidity of the soils under one large vegetation type, and the acidity in each of the immediate biotopes of a *Pachypodium* plant must be emphasized. The general means are without relevance at the scale that is important to these plant species.

Stebbins (1952) and van Jaarsveld (1987) draw attention to three important reasons

why evolution accelerates in a dry climate. Firstly, in a dry climate the diversity of geology and topography has a much greater effect on plants than in a high rainfall climate. Secondly, the broken geological formation of a locally dry site tends to break up populations into smaller units, each of which is still able to interbreed and eventually give rise to new genotypes or taxa (species). Thirdly, these taxa develop specialized xeromorphic structures at some architectural organisation levels, of which succulents are one good example at the whole plant level, and dew-dripping spines another at the level of organs. These plants so cope with dry conditions. The diversity of *Pachypodium* in Madagascar is a consequence of this. According to Koechlin et al. (1974) the remarkable form of micro-endemism that exists in Madagascar in so many taxa is due to actual speciation aided by isolation of plants in specific, very small but very differentiated climatic and edaphic immediate environments. Some such areas of distribution are extremely limited, sometimes restricted to a single granitic outcrop.

I did not find information on fosssils of *Pachypodium*, except for a fragmentary record on the origin of succulent plants by van Jaarsveld (1987). He wrote that the subtropical succulents probably had their origin at the fringe of the tropics in the late Cretaceous, but became more widespread during the Tertiary, with the onset of drier and cooler conditions. Succulent genera which probably originated from the southern fringe include *Aloe* (van Jaarsveld 1987), *Talinum*, *Euphorbia*, *Pachypodium*, *Cyphostemma*, *Cissus*, *Ceropegia*, *Sesamothamnus*, *Pterodiscus*, *Plectranthus*, *Kalanchoe*, *Adansonia*, *Thorncroftia* and *Aeollanthus*. We can safely assume that these succulents existed before or close to the separation of Madagascar (at the end of the Cretaceous, c. 65 million years ago), since most of these genera are represented on the island as well as in continental Africa.

The Mesozoic limestones were formed between c. 195-100 MA and the Tertiary limestones during the Eocene c. 54-38 MA but they are old enough for the evolution of new taxa to have taken place (Du Puy & Moat 1996).

The adaptation mechanisms in Pachypodium

Koechlin's hypothesis of micro-endemism (1974) was cited above: the speciation in small particular habitats aided by isolation. But how does speciation work in these conditions? Examining the illustrations of *Pachypodium* species in the taxonomy chapter, remarkable strongly specialised, precisely built organs can be seen to coexist with flexible whole plants without clear architecture. They often are not branched, except at their base, and in other cases grow branches without any clearly defined system, wherever necessary.

As postulated by Vester (1997) and Oldeman & Vester (in press), one of the expressions of the adaptive mechanism is the coexistence of structural flexibility at some organisation levels with architectural severity or stereotypy at others. This is exactly what is found in *Pachypodium*. Only the precise morphological study, reported in the above chapter on taxonomy, could demonstrate this point by providing documentation on structures.

Indeed, the size of the larger *Pachypodium* species is such, that they can easily grow out of the micro-habitat of their germination. The environment the young plant meets outside this minuscule seedling niche is unpredictably diverse. Hence the adaptation resides in extreme flexibility of opportunistic branching patterns. Oldeman (1990) described this mechanism in various stressed environments, e.g. in the forest zones inhabited by Northern European oaks (*Quercus robur, Q. petraea*). The architectural flexibility of these oaks also is a heritage of their tumultuous past during the

Glaciations. *Pachypodium* has had more time to speciate, in view of the enormous age of their substrates mentioned above and the vicissitudes of the geological and climatic changes over that long period.

Many old genera of flowering plants in stressed environments have organs built with all-but mechanical precision to cope with the stresses and even to use them as resources. This is the case with most *Pinus* species, the fascicules of needles of which are strongly stereotyped, metabolically efficient and cheap to produce in terms of solar energy and nutrients invested. Another example are the *Acacia* species of the dry savannahs in East Africa and the Sahel, which, except for short shoots, also built compound leaves which are adjustable to water stress but precisely shaped. All illustrations of *Pachypodium* species in the present book show that these typical characteristics of organs that cope with highly variable stress of a few factors – water and soil – are rife in our genus.

The existence of species of *Pachypodium* on infertile substrates is not in danger as far as its flexible adaptability is concerned. It is rather compromised because its habitat can easily change abruptly. Any environmental change that brings the ecological conditions of the habitat outside the brackets of *Pachypodium* flexibility is a menace of extinction. Deterioration of the habitat can come in the disguise of agricultural improvement, such as higher soil fertility or less drought. Usually *Pachypodium* species occur in small populations within small niches. Young plants are often rare or absent. Collection with the purpose to sell plants as ornamentals, improvement of the land for human use, and yearly bush fires are endangering many species of *Pachypodium* today in the wild. The easy germination of the seeds in cultivation may provide an escape to extinction. However, protecting the plants in the wild is the best method of conservation, because diversity can not be conserved as such, as if it were a constant property of some protected ecosystem. It has to be reproduced by living organisms. The ways to cultivate *Pachypodium* species in greenhouses are treated in Chapter 3 by our colleague W. Röösli.

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CHAPTER 3

Cultivation of *Pachypodium*

W. Röösli

All *Pachypodium* species are succulent and cactus-like. They have large showy flowers in various beautiful colours. The well known *P. namaquanum* in the Western Cape Province of South Africa and Southern Namibia, called 'halfmense'in Afrikaans, is strictly protected with good reason, as it is a rather large, showy, mostly unbranched cactus-like tree in an open landscape. The four other continental African species are relatively easily grown, and they have been propagated successfully for many years in various botanic gardens. Nota: Of all the continental species *P. lealii* is *by far* the most difficult to cultivate.

The various species have greatly differing areas of distribution in nature. This is caused by their ecological requirements, that have been studied especially for the Madagascan species. For that purpose many localities throughout the country have been visited by a number of expeditions. It then turned out, that widely spread species have a great tolerance in this respect, e.g. *P. lamerei* and *P. rutenbergianum*. Other species with much smaller areas of distribution, usually require a very special ecology.

The author, who had the opportunity to collect seeds of all species, made elaborate observations of all environmental and growing conditions, as light, air-temperature during the day and during the night in dry and rainy seasons, and temperature, structure, humidity (also in the different seasons), chemical composition and pH of the soil. The plants were always watered with lukewarm water as rain is not cold in most tropical countries, as is often overlooked by people growing pot plants. The author has been quite succesfull in growing *Pachypodiums*. He planted the seeds in rows in low greenhouses and after they reached a reasonable size potted them individually. He managed to raise flowering plants of all species by respecting meticously their ecological requirements. On several plants he even obtained fruits after hand-pollination of species of which only some poorly preserved fruits were avaiable in old herbarium specimens. Of others he found dehisced and shrivelled fruits in the field when collecting seeds.

SPECIES LIST WITH INFORMATION

Pachypodium ambongense Poiss.
Fig. 1, p. 11; Map 1, p. 12; Plate 1, opposite p. 16.
DISTRIBUTION. Namoroka Res. Nat. 8.

HABIT. Shrub with bottle-shaped stem and few branches at c. 1 m height. It can reach a height of 2 m.

ECOLOGY. On strongly eroded calcareous rocks, the fissures of which are filled with humus. Alt. 70-100 m. On sunny or half-shaded places in deciduous dry forest. Accompanied by *Pachypodium rutenbergianum*, *Euphorbia viguieri*, *Uncarina sakalava*, *U. perrieri*, *Lomatophyllum* sp., *Commiphora* sp., and *Cyphostemma* sp.

CULTIVATION. Substrate loose peat with a little lime gravel. Temperature spring to autumn: nocturnal at least 18°C and diurnal up to 38°C. Wintering: nocturnal 15°C and diurnal 20°C or more. It flowers at the end of the dry season. It needs much water when it is growing. During the resting time it should be moistened a little bit when the soil is drying out too much.

REPRODUCTION. By seeds.

Pachypodium baronii Costantin & Bois

Fig. 1, p. 11; Map 1, p. 12; Plates 2-4, opposite p. 16.

DISTRIBUTION. Befandriana Nord to Mandritsara.

HABIT. Shrub with robust, globose to bottle-shaped trunk, much branched, up to 3.50 m high.

ECOLOGY. On steep gneiss rocks. Alt. 350-1000 m. Mostly in full sun, sometimes in open dry forest in light shade. Accompanied by *Pachypodium sofiense*, *Uncarina* sp., *Aloe bulbillifera*, *Euphorbia milii*, *Kalanchoe gastonis-bonieri*, *Urera* sp. and *Ischnolepis* sp.

CULTIVATION. Substrate loose peat with gneiss sand, pH 4. Temperature from spring to autumn: nocturnal 12°C and diurnal up to 40°C. Wintering: nocturnal 12°C and diurnal 20°C or more. It flowers profusely in spring. It needs larger pot sizes than other species. It requires much water when it is growing, very little during the resting time only to prohibit drying out of the roots.

REPRODUCTION: By seeds. It can flower when it is 4 years old.

Pachypodium bicolor Lavranos & Rapanarivo

Fig. 2, p. 15; Map 2, p. 12; Plates 5-7, opposite p. 17.

DISTRIBUTION. East of Belo sur Tsiribihina.

HABIT. Low shrub with thickened trunk and numerous ramifications, partly creeping.

ECOLOGY. On porous sandstone, only in full sun. Alt c. 50-60 m. Accompanied by *Euphorbia* aff. *pedilanthoides*, *E. viguieri*, *Uncarina leandrii* var. *rechbergeri*, *Aloe* sp., Orchidaceae and *Kalanchoe* spp.

CULTIVATION. Substrate loose peat with quartz gravel, pH 4.5. Temperature from spring to autumn: nocturnal 20°C and diurnal up to 40°C. Wintering: nocturnal 16°C and diurnal 20°C. It flowers in spring. It needs very dry conditions, during the resting period occasionally a little of water.

REPRODUCTION. By seeds and cuttings.

Pachypodium brevicaule Baker

Fig. 3, p. 18; Map 2, p. 12; Plates 8-10, opposite p. 17.

DISTRIBUTION. South of Antananarivo to the Itremo Mts.

HABIT. Flat tuberous plant with several leaf rosettes.

ECOLOGY. On quartz, rarely on granite, in full sun. Alt. 1250-2000 m. Accompanied by *Pachypodium densiflorum*, *P. eburneum*, *Aloe compressa*, *A. capitata*, *Kalanchoe integrifolia*, *Euphorbia quartzicola*, *Lycopdium* sp., Orchidaceae, Gramineae, Bryophyta and Lichenes.

CULTIVATION. Substrate loose peat with much quartz sand and gravel, pH 3.5. Temperature spring to autumn: nocturnal 12°C and diurnal up to 35°C. Wintering: nocturnal 5-10°C and diurnal 15-2°C. It needs much water during the growth period. During the resting period the substrate may be moistened carefully. It flowers during the entire growth period. It is recommended to repot it yearly, to remove all dead roots and to use new loose potting mixture.

REPRODUCTION. By seeds.

Pachypodium cactipes K. Schum.

Fig. 4, p. 21; Map 3, p. 22; Plate 11-13, opposite p. 32.

DISTRIBUTION. Northwest of Fort-Dauphin.

HABIT. Shrub-like, with short tuberous trunk, much branched, up to 1 m high, diameter up to 1.50 m.

ECOLOGY. On gneiss rocks, in full sun. Alt. from 70 m. Accompanied by *Aloe schomeri*, *A. bakeri*, *Tetradenia* sp., *Euphorbia milii* and *Rhipsalis baccifera*.

CULTIVATION. Substrate loose peat with some gneiss sand, pH 4.5. Temperature from spring to autumn: nocturnal 15°C and diurnal up to 32°C. Wintering: nocturnal 12°C and diurnal 15°C or more. It flowers in spring with many inflorescences. It needs much water during the growing period. The leaves drop late and therefore it needs also occasionally water during the dry season.

REPRODUCTION. By seeds.

Pachypodium decaryi Poiss.

Fig. 5, p. 25; Map 3, p. 22; Plate 14, opposite p. 32; Plates 15-18, opposite p. 33.

DISTRIBUTION. Falaise d'Ankarana, Montagne des Français.

HABIT. Shrub-like with robust trunk and few ramifications, up to 4 m high.

ECOLOGY. Strongly eroded limestone rocks. Sunny places in dry forest. Alt. 200-400 m. Accompanied by *Pachypodium windsorii*, *P. rutenbergianum*, *Euphorbia aureo-viridiflora*, *E. pachypodioides*, *Talinella* sp., *Uncarina peltata*, *Impatiens tuberosa*, *Aloe suarezensis* and *Cyphostemma sakalavense*.

CULTIVATION. Substrate loose with sand and some lime gravel. Temperature from spring to autumn: nocturnal 18°C and diurnal 40°C. Wintering: nocturnal 16°C and diurnal 20°C or more. It flowers during the the dry season, December to February. It needs much water during the growing period but requires hardly any water during the resting period.

REPRODUCTION. By seeds.

Pachypodium densiflorum Baker

Fig. 3, p. 18; Map 4, p. 22; Plates 19-23, opposite p. 40.

DISTRIBUTION. East of Ihosy to Mahatsinjo (South of Andriba). Over this distance of 550 km it shows slight differences in morphology from South to North.

HABIT. Tuberous plant with thick branches and with few ramifications. Height up to 50 cm, width up to 1 m. In the southern part of the area of distribution the flowers are very small, between Antsirabe and Andriba, the northern part of the area of distribution, the flowers are larger.

ECOLOGY. On steep gneiss and quartz rocks. Alt. 750-2000 m. Accompagnied by *Pachypodium brevicaule*, *Aloe ibitiensis*, *Cynanchum perrieri*, *Ischonolepsis tuberosa*, *Kalanchoe tomentosa*, *Cynorkis incarnata*, *Euphorbia quartziticola*, *E. milii*, *E. didiereoides* and *Xerophyta* sp.

CULTIVATION. Substrate loose peat, pH 3.5-4. Temperature from spring to autumn: nocturnal 14°C or more, diurnal 20-35°C. Wintering: nocturnal 5-10°C and diurnal 15-25°C. It flowers in spring. Much water when it is growing. In the dry season moisten the substrate occasionally a little.

REPRODUCTION. By seeds.

Pachypodium eburneum Lavranos & Rapanarivo

Fig. 6, p. 31; Map 5, p. 32; Plates 24-27, opposite p. 41.

DISTRIBUTION. Mt Ibity.

HABIT. Tuberous plant with thick branches and few ramifications, up to 40 cm high.

ECOLOGY. On quartz rocks in sandy humus. Alt. c. 1600 m, in full sun. Accompanied by *Pachypodium densiflorum*, *P. brevicaule*, *Aloe laeta* and *Aloe trachyticola*.

CULTIVATION. Substrate loose peat with quartz sand, pH 3.5. Temperature from spring to autumn: nocturnal 15°C and diurnal 25°C or more. Wintering: nocturnal 5°C and diurnal 15°C or more. It flowers in early spring. It needs much water during the growth period and should not be too dry during the resting time.

REPRODUCTION. By seeds.

Pachypodium geayi Costantin & Bois

Fig. 1, p. 11; Map 5, p. 32; Plates 28-31, opposite p. 56.

DISTRIBUTION. Morombé to Fort-Dauphin.

HABIT. Tree up to 7 m high, with thick trunk, branching from 3 m height or more.

ECOLOGY. On sand in low dry forest. Alt. 0-100 m. Accompanied by *Pachypodium meridionale*, *Uncarina stellulifera*, Didiereaceae, *Delonix* sp., *Moringa hildebrandtii*, *Commiphora* sp. and *Operculicarya pachypus*.

CULTIVATION. Good porous sandy substrate, pH 7.0. Temperature from spring to autumn: nocturnal 15°C or more and diurnal 25-45°C. Wintering: nocturnal 10°C or more and diurnal 18°C or more. It requires occasionally a large quantity of water during the growth period and should be kept dry during the resting time.

REPRODUCTION. By seeds.

Pachypodium gracilius (H. Perrier) Rapanarivo

Fig. 7, p. 36; Map 6, p. 32; Plate 32, opposite p. 56; Plates 33-35, opposite p. 57.

DISTRIBUTION. Isalo Mts, between Ranohira and Onilahy River.

HABIT. Shrub-like plant up to 80 cm high, with mostly subglobose thickening of trunk and few branchings; in the southern part of its area of distribution much more branched.

ECOLOGY. On sandstone rocks. Alt. 100-1000 m, in full exposure. Accompanied by *Ceropegia dimorpha*, *Cynanchum marnierianum*, *Aloe contigua*, *A. isaloensis*, *A. deltoideodonta* var. *brevifolia* and *Euphorbia milii* (with yellow cyathea).

CULTIVATION. Substrate loose peat with a little sand. Temperature from spring to autumn: nocturnal 15°C and diurnal 35°C. Wintering: nocturnal 6°C or more and diurnal 20°C or more. It flowers profusely in spring. It requires much water during the growth period. In the resting time it should be kept rather dry.

REPRODUCTION. By seeds.

Pachypodium horombense Poiss.

Fig. 4, p. 21; Map 7, p. 40; Plates 36-38, opposite p. 57.

DISTRIBUTION. Between Ihosy and Antanimora.

HABIT. Tuberous plant up to 60 cm high, with numerous thick branches.

ECOLOGY. Mostly on bare gneiss rocks in full sun. Alt. from 750 m. Accompanied by *Pachypodium lamerei*, *Aloe betsileensis*, *Euphorbia horombensis*, *E. milii*, *Alluaudia dumosa*, *Stapelianthus* sp. and *Tetradenia* sp.

CULTIVATION. Substrate loose peat with a little gneiss, pH 4.5. Temperature from spring to autumn: nocturnal 15°C and diurnal 35°C. Wintering: nocturnal 10°C and diurnal 18°C. It flowers in spring. It requires much water during the growth period. During the resting time occasionally moisten the substrate when needed.

REPRODUCTION. By seeds.

Pachypodium inopinatum Lavranos

Fig. 8, p. 43; Map 7, p. 40; Plates 39-43, opposite p. 64.

DISTRIBUTION. South of Telomina.

HABIT. Tuberous plant up to 40 cm high which branches very much when aging.

ECOLOGY. In fissures of steep crystalline rocks in full exposure. Accompanied by *Euphorbia milii* and *Polystachya* sp.

CULTIVATION. Substrate loose peat with quartz sand. Temperature from spring to autumn: nocturnal 15°C and diurnal 35°C. Wintering: nocturnal 5°C and diurnal 18°C or more. It flowers in spring. It requires much water during the growth period and it should be kept rather dry in the resting period.

REPRODUCTION. By seeds.

Pachypodium lamerei Drake

Fig. 9, p. 45; Map 8, p. 40; Plates 44-48, opposite p. 65.

DISTRIBUTION. Antsingy de Bemaraha to Fort-Dauphin.

HABIT. Cactoid plant with sturdy stem. Branching 1.5-5 m high, according to locality.

ECOLOGY. Area of distribution very extensive with often strongly divergent forms. On limestone or gneissose rocks, in dry forest or in full sun and at alt. from sea level to 750 m. Accompained by *Pachypodium meridionale*, *P. horombense*, *Uncarina leptocarpa*, *U. grandidieri*, *U. roeoesliana*, *Euphorbia moratii*, *E. enterophora*, *E. millii*, *Alluaudia dumosa*, *Aloe viguieri*, *Kalanchoe orgyalis*, *Adenia monadelpha*, *Stapelianthes* sp., etc.

CULTIVATION. Substrate loose peat, with a little sand. Temperature from spring to

autumn: nocturnal 17°C and diurnal up to 38°C. Wintering: nocturnal 12°C and diurnal 20°C. It should be watered regularly during the growth season. During the resting period it ought to be kept rather dry.

REPRODUCTION. By seeds.

Pachypodium meridionale (H. Perrier) Pichon

Fig. 5, p. 25; Map 9, p. 50; Plates 49-52, opposite p. 80.

DISTRIBUTION. Between Manja and Ampanihy.

HABIT. Tree 2-8 m high, with thickened trunk and much branched crown. Branches densely spiny.

ECOLOGY. On limestone rocks and sandy soil. in dry forest. Alt. 30-250 m. Accompanied by *Pachypodium geayi*, *P. lamerei* (var. *ramosum*), *Uncarina stellulifera*, *Alluaudia* spp., *Erythrophysopsis aesculina*, *Delonix* sp., *Commiphora* sp., *Euphorbia obcordata* and *Cassia meridionalis*.

CULTIVATION. Subtrate: humus with sand, pH 7.0. Temperature from spring to autumn: nocturnal 18°C and diurnal 40°C. Wintering: nocturnal 12°C and diurnal 20°C. It requires occasionally very much water during the growth period and it should be kept dry in the rest period.

REPRODUCTION. By seeds.

Pachypodium rosulatum Baker

Fig. 4, p. 21; Map 10, p. 50; Plates 53-54, opposite p. 80; Plates 55-56, opposite p. 81.

DISTRIBUTION. Ankarafantsika, Befandriana Nord to Mandritsara.

HABIT. Shrub-like plant with tuberous base, varying in size depending on the ecology.

ECOLOGY. Between Ankarafantsika and Analalava on quartz sand in dry forest up to 2.50 m high and at alt. 70-150 m. Between Befandriana Nord and Mandritsara on gneiss rocks and plants low, much branched, creeping, 50 cm high and at alt. 300-500 m. Accompanied by *Pachypodium rutenbergianum*, *Uncarina peltata*, *Kalanchoe gastonis-bonnieri*, *Euphorbia pauliana* and *E. pedilanthoides*.

CULTIVATION. Substrate loose peat with gneiss or quartz sand, pH 4.5-6. Temperature from spring to autumn: nocturnal 18°C and diurnal 35°C. Wintering: nocturnal 15°C and diurnal 20°C. It flowers in spring. It requires much water in the growth period and it should be kept dry in the rest period.

REPRODUCTION. By seeds.

Pachypodium rutenbergianum Vatke

Fig. 9, p. 45; Map 11, p. 55; Plates 57-60, opposite p. 81; Plate 64, opposite p. 88.

DISTRIBUTION. From Diego-Suarez to Morondava.

HABIT. Tree 3-12 m high, with conspicous thickening of trunk.

ECOLOGY. This species is widely spread. It grows on limestone or gneiss rocks and also on pure quartz sand, mostly in dry forests. Alt. 0-400 m. Accompanied by *Pachypodium windsorii*, *P. decaryi*, *P. rosulatum*, *P. sofiense*, *P. ambongense* or *P. bicolor*, depending on the ecology of the species listed here.

CULTIVATION. Porous humose or sandy substrate. Temperature from spring to autumn: nocturnal 17°C and diurnal 40°C. Wintering: nocturnal 15°C and diurnal

18°C or more. It requires much water during the growth period and it should be kept dry in the rest period.

REPRODUCTION. By seeds.

Pachypodium sofiense (Poiss.) H. Perrier

Fig. 5, p. 25; Map 12, p. 55; Plates 61-63, opposite p. 88.

DISTRIBUTION. Befandriana Nord, Ansakabary, Mandritsara and Antsingy de Bemaraha.

HABIT. Tree 2-8 m high, with thickened trunk, forming a crown.

ECOLOGY. On steep gneiss or limestone rocks in dry forest. Alt. 400-1000 m. Accompanied by *Pachypodium baronii*, *P. lamerei* (var. *ramosum*), *Aloe bulbilifera*, *Amorphophallus hildebrandtii*, *Adenia* sp., *Cissus* sp., *Oeceoclades* sp. and *Uncarina* sp.

CULTIVATION. Substrate porous peat with a little sand, pH 4.0 (in Mandritsara). Temperature from spring to autumn: nocturnal 15°C and diurnal up to 40°C. Wintering: nocturnal 12°C and diurnal 20°C or more. It requires much water during the growth period and it should be kept rather dry in the rest period.

REPRODUCTION. By seeds.

Pachypodium windsorii Poiss.

Fig. 10, p. 61; Map 12, p. 55; Plate 64, opposite p. 88; Plates 65-68, opposite p. 89.

DISTRIBUTION. Known from Windsor Castle and Montagne de Français, two localities 25 km apart.

HABIT. Shrub up to 1.50 m high, with globose thickening of trunk, with few branches.

ECOLOGY. On strongly disintegrated hard limestone rocks with fissures filled with humus, In well exposed places. Alt. 150-390 m. Accompanied by *Pachypodium rutenbergianum*, *Adansonia suarezensis*, *Aloe suarezensis*, *Euphorbia bulbispina*, *E. aureo-viridiflora*, *E. viguieri*, *E. ankarensis*, *Uncarina peltata*, *Dracaena* sp., *Adenia* sp. and Orchidaceae.

CULTIVATION. Substrate loose peat with some lime gravel. Temperature from spring to autumn: nocturnal 16°C and diurnal 38°C. Wintering: nocturnal 15°C and diurnal 20°C or more. It flowers in spring. It requires much water during its growth and should be kept rather dry in the resting time.

REPRODUCTION. By seeds.

Detailed information on cultivation of continental African species may be derived from the information given in the chapter on the biotopes of *Pachypodium*.

Index of exsiccatae

This is a list of herbarium specimens studied. The names are the names of the collectors. The specimens have been numbered by the collectors during collecting or afterwards. The specimens are also given with each description of the relevant species together with the locality in which they were collected. In addition the acronyms given between brackets after the numbers cited with each description indicate the herbaria where the specimens are kept. In this list, the index of exsiccatae, the species to which the specimens belongs is given after each number, e.g. *Pachypodium ambongense* is given as Pa. The following example may help: In this list: Leeuwenberg 14593 (Pbr) belongs to *Pachypodium brevicale* and is cited after the relevant description as: *Leeuwenberg & Rapanarivo* 14593 (BR, K, P, TAN, WAG).

BR means the Herbarium of the National Botanic Garden of Belgium, Meise, north of Brussels;
K means the Herbarium of the Royal Botanic Garden at Kew, near London;
P means the Herbarium of the Laboratoire de Phanérogamie at Paris;
TAN means the Herbarium of the Parc de Tsimbazaza at Antananarivo, Madagascar;
WAG means the Herbarium of Plant Taxonomy, Agricultural University of Wageningen, Netherlands;
† means that the specimens got lost;
B† means lost during the second World War in Berlin.

The herbaria of the World are listed in the *Index Herbariorum – The Herbaria of the World*, 8th edition, New York, 1990.

Pachypodium ambongense (Pa), *P. baronii* (Pba), *P. bicolor* (Pbc), *P. bispinosum* (Pbp) *P. brevicaule* (Pbr), *P. cactipes* (Pc), *P. decaryi* (Pdc), *P. densiflorum* (Pds), *P. eburneum* (Pe), *P. geayi* (Pge), *P. gracilius* (Pgr), *P. horombense* (Ph), *P. inopinatum* (Pi), *P. lamerei* (Plm), *P. lealii* (Ple), *P. meridionale* (Pm), *P. namaquanum* (Pn), *P. rosulatum* (Pro), *P. rutenbergianum* (Pru), *P. saundersii* (Psa), *P. sofiense* (Pso), *P. succulentum* (Psu), *P. windsorii* (Pw).

Acocks, J.P.H., 730, 2549, 11855 (Psu)
Allorge, L., 577 (Ph), 616 (Pgr)
Alluaud, C., 11 (Plm), 88 (Pc)
Anteobus, A.E., N.G. 3936 (Psa)
Antunes, P.J.M., 879 (Ple)
Appert, P.O., 167 (Pm)
Archibald, E.E.A., 5979 (Pbp)
Arnold, T.H., 627 (Ppb)

Baker, W., 20348 (Pbp)
Balsinhas, A., 1264 (Psa)
Barker, W.R., 48 (Psa), 105 (Psu)
Baron, R., 256 Ph), 4246 (Pds), 4412 (Pbr), 5730 (Pro), 5874, 5879 (Pba), 6289 (Pru), 6827 (Pro), 6939 (Pds)
Baum, H., 21 (Ple)
Bayliss, R.D.A., 1136 (Psa), 3103 (Pbp), 3122, 3629 (Psu), 3639, 5558, 7593 (Pbp), 7872, 7956 (Psu), 8059 (Pbp)
Bengis, B.K., 308, 324 (Psu)
Berger, J., 2140 (Ple)
Bernardi, L., 11244 (Ph)
Biegel, H.M., 3250 (Psa)
Boiteau, P., 325, 325B (Ph), 375B (Plm)
Bolus, F., 70 (Psu), 113 (Pbp), 115, 11605, 16296 (Psu)
Bosser, J., 3384 (Pru), 3801 (Pro), 5759 (Pru), 9715 (Pds), 9716 (Pgr), 9846 (Pds), 13961, 15720 (Plm), 15861 (Pge), 16623 (Pbr), 16721, 16733 (Pba), 17110 (Pro), 18188, 18191 (Pso), 18199 (Pds)
Bourquin, O., 840 (Psu)
Brain, C.K., 6 (Ple)
Brueckner, A.E., 888 (Psu)
Bryant, E.G., 164, 5164 (Psu)
Buitendag, E., 1010 (Psa)
Burchell, W.J., 1662, 1719 1918 (Psu), 3880 (Pbp), 4181, 4410 (Psu)
Burgoyne, 1456 (Psu)
Burtt-Davy, J., 12046 (Pbp)

Camboué, 11 (Pds)
Carrisso, L.W., 204 (Ple)
Castelnau, F. de, 17 (Psu)
Catat, L.D.M., 1154 (Pbr), 4343 (Pc), 4353 (Pds)
Chase, N.C., 2247, 2362 (Psa)
Chaurin, 3432 (Pds)
Clement, R.A., 2111 (Plm)
Cloisel, J., 40 (Plm), 52 (Pc)
Codd, L.E., 2855, 5225, 6064, 10494 (Psa)

Coetzee, J.Q., 790 (Psu)
Compton, R.H., 27848, 29757, 31441 (Psa)
Cooper, T., 1288 (Psu)
Correia, M.F., 1196 (Psa)
Cours, G., 3944 (Pro), 5106 (Pgr), 5529 (Pdc)
Crawford, R., 250 (Psa)
Cremers, G., 2423 (Pro), 2643 (Pdc)
Croat, T.B., 32026 (Plm)
Cubr, 27579 (Psa), 28431 (Pge), 29384 (Pgr)
Culverwell, J., 722 (Psa)

Dahlstrand, I., 345, 1781, 3125 (Pbp)
Daly, M., 797 (Psu)
Davies, R.M., 31 (Ple), 1740 (Psa)
Debray, M.M., 955 (Pge)
Decary, R., 1, 3 (Pds), 4 (Ph), 56, 97 (Pgr), 903 (Pru), 1102 (Pba), 1148 (Pro), 1179 (Pru), 1193, 1277 (Pro), 1279 (Pba), 2177 (Pru), 2247, 2347 (Pro), 2611, 2852, 2878 (Plm), 3163 (Pc), 3262 (Ph), 3824 (Plm), 4594 (Pc), 4648 (Ph), 5697 (Pds), 7787 (Pru), 7950, 8119, 8124, 8236 (Pro), 8355, 8844, 9331 (Plm), 9394, 10514, 10643 (Pc), 14489, 14557 (Pru), 14993 (Pbr), 15085, 15115, 15174 (Pds), 15342 (Pba), 15407 (Pro), 15604 (Pru), 15907 (Pds), 16292, 16395 (Pgr), 16401 (Pge), 17893 (Pa)
Descoings, R., 881 (Pbr), 973 (Pds), 991 (Ph), 1046 (Pgr), 1374 (Plm), 3590, 3604, 3620 (Pds), 3649, 3692, 3694 (Ph), 3751 (Pgr), 3772, 3773, 3774 (Ph), 3797, 3798 (Pds)
Dinter, K., 5671 (Ple), 8071 (Pn)
Dorr, L.J., 3148 (Pba), 3149 (Ph), 3150 (Pds), 3175 (Pro)
Drège, J.L., 28.10 (Pbp), 3150 (Psu)
Drummond, R.B., 7964 (Psa)
Dumetz, N., 1258 (Plm)
Du Puy, B.S., MB14 (Pge), MB18 (Plm), MB115 (Pro), MB224, MB344 (Pru), MB759 (Pso), MB808 (Plm)
Du Puy, D.J., 2401 (Pbr)
Dyer, R.A., 132 (Pbp), 660 (Psu), 1156 (Pbp), 3470 (Psa), 3641 (Pn)
Dyke, E., 5393 (Psa)

Ecklon, C.F. & Zeyher, C.L.P., 2.1 (Psu), 28.10 (Pbp)
Edwards, D., 4469 (Ple)
Edwards, E.B., 5 (Psa)
Esterhuysen, E., 6265 (Psu), 13267 (Pbp), 16299, 19446 (Psu)
Evrard, C. 9186 (Pn)
Exell, A.W., 2442 (Ple)

Flanagan, H.G., 1039 (Psu)
Foley, W.G., 155 (Psu)
Fosberg, F.R., 52388 (Pbr), 52392 (Pds), 52401 (Ph), 52414 (Pgr)
Fourcade, H.G., 2775 (Psu)
Fraser, J.A., 18 (Pbp)
Fries, Th. C.E., 746, 1017 (Pbp)
Fritzsche, B., 205 (Ple)

Galpin, E.E., 13262 (Pbp), 14935 (Psa)
Gettliffi, G.F., 9644 (Psa)
Gibson, G.D., 74 (Ple)
Giess, W., 10484 (Ple), 12328 (Pn), 13900 (Ple)
Giffen, M.H., 1203, 1291 (Psu)
Gillis, W.T., 11193 (Pru)
Gossweiler, J., 4950, 9685 (Ple)
Groen, L.E., 1120 (Pbp)

Hafström, A., 893, 1054, 1109, 1126 (Psu), 11998 (Pbp)
Hardy, D.S., 995 (Psu), 2076 (Ple), 2908 (Plm), 2916 (Pc), 2940 (Pds), 3545 (Pge), 3601 (Pru), 6971 (Psu)
Hartmann, H., 1045 (Psa)
Henrici, M., 1806 (Psu), 2233 (Pn)
Henriques, C., 1111 (Ple)
Hildebrandt, J.M., 3037 (Pru), 3114 (Pc), 3586 (Pbr)
Hilliard, O.M., 10732 (Psu)
Hofstätter, 040990-2 (Pds), 070990-4 (Pbr), 260890 (Pro)
Homolle, A.M., 260 (Pdc), 1433, 1676bis (Plm)
Humbert, H., 2766 (Pgr), 2947 (Ph), 4620 (Pbr), 4891 (Pds), 4953 (Pgr), 6006 (Pc), 6756 (Plm), 10367 (Pbp), 11281 (Plm), 11353 (Pgr), 11481 (Pso), 11581 (Plm), 11615 (Ph), 12294 (Plm), 12697 (Pgr), 14071 (Pc), 14546 (Psa), 16524 (Ple), 18061 (Pro), 18899bis (Pru), 19317ter (Pds), 19321 (Plm), 19374 (Pro), 19890 (Plm), 20210ter, 20215, 20233 (Pge), 20317 (Plm), 25619 (Pba), 28617 (Plm), 30004 (Pbr), 32250, 32325 (Pru), 32527 (Pdc)
Hutchinson, J., 1509 (Psu), 1510 (Pbp)

Jongkind, C.C.H., 743 (Pgr), 942 (Pdc), 982 (Pru)

Kemp, E.S., 820 (Psa)
Keraudren, M., 1413 (Pge), 1504 (Plm), 24636 (Ph), 24660 (Pgr), 25065, 25075 (Ph)
Kirton, J., 2736 (Psa)
Klackenberg, J., 93.03.12.-23 (Plm)
Kleinhoonte, A., 475 (Pbp)
Krapohl 5367 (Pn)
Krest, 97/26 (Psu)

Labat, J.N., 2310 (Plm), 2401 (Pds), 2879 (Pw)
Lace, PRE 521287 (Psu)
Lam, H.J., 4745 (Pbp), 4794 (Psu), 5527 (Ph)
Lambert, M., Hb.G. 159076 (Plm)
Leach, L.C., 10801, 11645 (Psa), 13816 (Ple)
Leandri, J., 1009 (Plm), 1780 (Pds), 2182 (Plm), 2367 (Pso), 2733 (Plm), 4177 (Pc), 4200bis, 4264 (Plm), 4265, 4269 (Pc)
Leeuwenberg, A.J.M., 11025 (Psa), 12386 (Psu), 13726 (Pba), 13727 (Ph), 13728 (Pro), 13887a (Pru), 14039, 14169 (Plm), 14393, 14408 (Pru), 14593 (Pbr), 14605, 14611, 14612 (Pds), 14613 (Pgr), 14624 (Pge), 14628 (Plm), 14629 (Pge), 14630, 14634 (Ph), 14636 (Plm), 14639 (Pds), 14649, 14650 (Pro), 14651, 14652 (Psu), 14653 (Pba), 14654 (Pc), 14655 (Pbc), 14666 (Pds), 14680, 14681, 14709, 14712, 14720 (Pru), 14727 (Pro), 14740, 14752, 14762 (Pru), 14763 (Pw), 14764 (Pru),

14766 (Pro), 14767 (Pru), 14771 (Pba)
Leistner, O.A., 75, 191, 261 (Ple), 800 (Pn), 1191, 2100 (Psu), 2119 (Ple), 2920 (Psu)
Le Roux, P.J., 582, 1018 (Ple)
Leuenberger, B., 3270 (Pn)
Lewis, B., 742 (Pbr), 1139 (Pdc)
Liebenberg, L.C.C., 710 (Pbp), GN 1509, 6622 (Psu)
Lindstedt, G., 27 (Psu)
Long, F.R., 246, 247 (Psu), 248 (Pbp)
Lother, A., 161 (Pru)
Lotsy, J.P., 71, 175 (Pbp)

Mabberley, D.J., 753 (Pru)
Mac Owan, P., 641, 841 (Psu)
Marais, E., 118, 128, 173 (Psu)
Marloth, R., 2006a, 2006b, 6075, 9519, 10881 (Psu), 13132 (Pbp), 13621 (Psu)
Marques, A., 2117 (Psa)
McPregor, 19118 (Psu)
Meeuse, A.D.J., 10229 (Psa)
Menezes, A., 2992 (Ple)
Merxmüller, H., 687 (Psu), 1433 (Ple), 2500, 28555 (Pn)
Meyer, P.G., 1247 (Ple)
Miège, J., 90M (Ph)
Mittendorf, H., 79 (Pn)
Moll, E.J., 3157 (Psa)
Montagnac, P., 3 (Pgr), 4 (Plm), 5 (Pds)
Morat, P., 92 (Pso), 108 (Pds), 778 (Pso), 3680 (Pds), 4829 (Plm)

Nägelsbash, E., 10, PRE 32754 (Ple)

Obermeyer, A.A., PRE 32803 (Ple)
Ogilvin, PRE 29846 (Psa)
Oldenburg, F.P., 920 (Pbp)
Olivier, E.G.H., 2042 (Pbp), 7319 (Psa)

Palmer, A.R., 816 (Psu)
Paulian, R., 3(Pgr), 4, 5 (Pro)
Pedro, E., 7861 (Psa)
Peltier, J. & M., 1536 (Ph), 2462 (Pds), 2484 (Pgr), 2573 (Pm), 2657 (Ph)
Penther, A., 2003 (Psu), 2006 (Pbp), 2007 (Psu)
Perrier de la Bâthie, J.M.H.A., 934, 934bis, 934ter (Pru), 968, 968bis (Pro), 1142 (Pso), 1515 (Pa), 8064, 8145 (Pro), 8845 (Pru), 8849 (Pro), 8861 (Pba), 8862 (Pds), 8866 (Pgr), 8867, 8867A, 8867B (Pge), 8868 (Plm), 8869 (Ph), 8871 (Pm), 8910 (Pro), 8916 (Pds), 8918 (Pbr), 8921 (Pgr), 8953 (Pds), 8954 (Pm), 8967 (Pso), 8968 (Pro), 12582 (Pds), 12860 (Pm), 12860bis, 12860ter (Plm), 15030 (Pso), 15065 (Pro), 15082 (Pba), 16535, 16535bis (Pds), 16536 (Ph), 16549 (Pds), 17350 (Pm), 17806 (Plm), 18004 (Pge), 18303, 18320 (Pm), 18569, 18570 (Pru), 18571 (Pm), 18572 (Plm), 18662 (Pge), 18802 (Pru)
Peter, A., 47336 (Ple), 50801 (Pbp), 50814 (Psu)
Phillipson, P.B. 1942 (Pru), 2219 (Pso), 2281, 2358 (Pm), 2610 (Pge), 2682 (Plm), 2916 (Pc), 3106 (Plm), 3151 (Pge), 3499 (Plm), 3755 (Pm)
Phipps, J.B., 2898 (Psa)
Pillans, N.S., 5000 (Pn), 5900 (Ple), 6545 (Pn)
Plowers, D.C.H., 2685 (Psa)
Poisson, H., 1(a) (Pa), 648bis (Pge), 673 (Pgr), 674 (Ph), 674bis (Pds), 1027 (Pge)
Pole Evans, J.B., 2251 (Pn), 2357, 2358 (Psu), 2701 (Ple), 3478, 4679 (Psa)
Pretoria Bot. Gard., 1797 (Psu)
Puff, Chr., N.Mad. 965 (Pgr), N.Mad. 1095, N.Mad. 1096 (Pge), SA-7779(7781) (Pbp)

Rabarison, H., 235 (Plm)
Rakotozafy, A., 1568 (Pdc), 1906A (Pso)
Ralimanana, H., 99 (Plm)
Range, P., A22 (4342) (Ple)
Rapanarivo, S.H.J.V., 240 (Pgr), 254 (Pds), 363, 365, 366 (Pru), 369 (Pi)
Rauh, W., M984/59 (Pgr), M1465, M1465/59 (Ph), 6069, 6069/61 (Pro), 7040 (Pdc), 7292, 7292/61 (Pds), 7348/61 (Pm), 7413 (Pgr), 10491a, 10491b (Plm), 23260 (Pro)
Razafindratsira, A., 00169 ZSS, 05386 ZSS (Pba)
Repton, J.E., 3073 (Psu)
RN (= Réserves Nationales), 1020 (Pro), 1628 (Pru), 1641, 1748, 1756 (Pro), 1810 (Pds), 2118 (Pc), 2410 (Pds), 2753 (Plm), 3087, 3120 (Pds), 4114, 5743, 5748 (Pru), 6405 (Pa), 6450 (Plm), 8003 (Pru), 8563 (Pa), 10791 (Plm), 11212 (Pgr)
Retief, E., 239 (Psu)
Retief, I.M., 342 (Psa)
Rodin, R.J., 1567 (Pn), 3982 (Psa)
Rogers, F.A., 12026 (Psu), 22208 (Psa), 27823 (Pbp), 28220 (Psu)
Röösli, W., 46/93 (Pi), 1/94 (Pds), 4/94 (Plm), 1/96 (Pe), 14/96 (Pso), 16/96 (Pba), 17/96 (Pro), 18/96 (Pru), 26/96, 27/96 (Pro), 31/96 (Pru), 33/96 (Pbc), 40/96 (Pm), 53/96, 63/96 (Plm), 66/96 (Pm), 69/96 (Pge), 72/96 (Plm), 77/96 (Pc), 79/96 (Plm), 83/96 (Pds), 87/96 (Plm), ZSS 05386 (Pba), ZSS 05393 (Pc), ZSS 15092, ZSS 15134 (Pa), ZSS 15140 (Pdc), ZSS 15697 (Pi), ZSS 15700 (Pa), ZSS 15702 (Plm), ZSS 16301 (Pbc), ZSS 16626 (Pa), ZSS 16659 (Pe)
Roussel, S., 28 (Plm)
Rushworth, J.E., 329 (Psa)

Schäfer, P.A., 6734 (Psa)
Scharf, H.T. 1944 (Pbp)
Schlechter, R., 6078 (Pbp), 6079 (Psu)
Schlieben, H.J., 8247 (Pgr), 9140 (Pn), 12032 (Psa)
Scholl, G., 319 (Psu)
Schönland, S., 399 (Pbp)
Schweickerdt, H.G.W.J., 668 (Psa)
Schwerdtfeger, G., 2360 (Plm), 11310 (Ple), 11832 (Psu), 14737 (Psa), 15317, 15318 (Plm), 15952 (Ph), 16254 (Plm), 17776, 17778 (Psu), 24913 (Pro)
SF (= Service Forestier de Madagascar), 30, 61 (Pru), 63, 78 (Pro), 320 (Plm), 3978 (Pru), 11322, 12058 (Pw), 13044 (Pro), 18981 (Pdc), 19165 (Pm), 22201, 22202, 22234

(Plm), 24267 (Pro), 24724 (Pru), 25096 (Plm), 28904bis (Pds), 29256 (Pru), 31424 (Pgr)
Seyrig, A., 81, 302 (Ph), 394, 394B (Pm), 395 (Plm), 853 (Pc)
Sidey, J.L., 1220 (Pbp)
Sim, T.R. 19696 (Psu), 19696a (Pbp)
Sitwell, H., 43 (Psu)
Smith, C.A., 923, 945, 973 (Psu)
Smuts, J.C., 2381 (Psa)
Sole, M., 430 m.D (Psu)
Sørensen, T., 530, 542 (Pbp), 554 (Psu)
Southey, C., 3 (Psu)
Specks, ZSS 03336 (Pa)
Stephen, J., 740 (Psa)
Stock, R.B., SRGH 23359 (Psa)
Story, R., 3955 (Psa), 5680 (Ple)
Strey, R.G., 3315, 3869, 6584 (Psa)
Supthut, D.J., 8226 (Pgr), 9302 (Pw), 9307 (Pru), 9308 (Pdc), 9324 (Pba), 9325 (Pro), 9330 (Pba), 9333 (Pro), 9334 (Pru), 9335 (Pro), 9337 (Pru), 96703 (Pc)

Tana. Herb. Jard. Bot. (= TAN= Antananarivo), 534 (Pds), 3227 (Pba), 4228 (Pgr), 4911 (Pro), 4914 (Ph), 4922 (Plm), 4939 (Pba), 5319 (Pso), 5474 (Pro) .
Taylor, L.E., 1720 (Psu), 1824, 8743 (Pbp)
Teixeira, J.B., 354 (Ple)
Theron, G.C., 363, 1813 (Psu)
Thode, J., A595 (Pbp), A596 (Psu), A679 (Pbp), A680, A2704 (Psu)

van der Merve, C.V., 1463 (Psu)
van der Schyff, W.P., 660 (Psa)
van der Werff, H., 12709 (Pm)
van Greuning, J.V., 270 (Ple)
van Jaarsveld, E., 7878 (Pbp)
van Velduizen, J., 1345 (Pc)
Venter, F., 8500 (Psa)
Verdoorn, I.C., 870, 951, 1122 (Psu)
Viguier, R., 1510 (Pbr)
Villier, A., 4859 (Plm)
Vlok, J.H.K., 1295 (Psu)
Volk, O.H., 520b, 636, 2442 (Ple)
von Arx, B., 3018 (Pbr), 3037 (Pds), 3045 (Ph), 3074 (Pgr), 3075, 3076 (Pds)
von Wettstein, F., 350 (Ple), 1929 (Pb)
Vorster, P., 2424 (Pbp)

Walter, E. & H., 567 (Ple)
Ward, C.J., 3072, 4115, 5656 (Psa)
Wearne, W.P., 38 (Psa)
Webb, P.B., 311 (Psu)
Welti, G. A., 57 (Psu)
Welwitsch, F.M.J., 1510 (Ple)
Werdermann, E., 577 (Pn)
Werger, M.J.A., 1459 (Psu)
West, E., 23 (Psu)
Whellan, J.A., 508 (Psa)
White, G., 1122 (Psu)
Wild, H., 3414, 5457 (Psa)
William, M., NBG 991/22 (Psu)
Williams, J., 8207 (Psa)
Winter, B. de, 3011, 3655, 3690 (Ple), 6341 (Pn)

Zeyher, C.L.P., 25 (Psu), 261 (Pbp), 262, 282, 3114 (Psu), 3412 (Pbp)
Zietsman, L. & P.C. 1290 (Ps)

Index of scientific names

New names in **bold face**, synonyms in *italics*. Page numbers of principal entries are in **bold face**, those of figures, plates and maps in *italics* (*op* = opposite).

Acacia L. 101
Acanthaceae Juss. 54
Adansonia L. 100
  grandidieri Baill. 51, 94
  suarezensis H. Perrier 111
  za Baill. 35, 93
Adenia Forsk. 111
  firingalavensis Harms 91
  monadelpha H. Perrier 109
Adenium Roem. & Schult. 5
  namaquanum Wyley ex Harv. 2, 70
  obesum Roem. & Schult. 81
Adiantaceae (C. Presl) Ching 29, 44
Aeollanthus C. Mart. 100
Afzelia Sm.
  quazensis Welw. 76, 96
Aizoaceae Rudolphi 95
Alluaudia Drake 110
  dumosa Drake 109
  procera Drake 35, 49, 51, 92, 93, 94
Aloaceae Batsch. 20, 29, 33, 42, 44, 48, 63, 84, 95, 96
Aloe L. 42, 48, 63, 84, 91, 92, 94, 95, 96, 98, 100, 106
  accutissima H. Perrier 29, 92
  alfredii Rauh 92
  bakeri Scott-Elliot 107
  betsileensis H. Perrier 109
  bulbillifera H. Perrier 106, 111
  capitata Baker 20, 44, 92, 93, 107
  compressa H. Perrier 107
  conifera H. Perrier 92
  contigua (H. Perrier) Reynolds 109
  cremersii Lavranos 33, 92
  deltoideodonta Baker
    var. candicans H. Perrier 92, 109
  fievetii Reynolds 92
  ibitiensis H. Perrier 108
  isaloensis H. Perrier 38, 93, 109
  laeta Berger 108
  schomeri Rauh 107
  silicicola H. Perrier 33, 92
  suarezensis H. Perrier 95, 107, 111
  trachyticola (H. Perrier) Reynolds 33, 92, 108
  viguieri H. Perrier 109
Amorphophallus Blume
  hildebrandtii (Engl.) Engl. & Gehrm. 111
Anacardiaceae Lindl. 29, 54, 58, 76, 95
Ancylobotrys Pierre
  petersiana (Klotzsch) Pierre 54, 58, 63, 94, 95
Apaloxylon Drake
  tuberosum R. Vig. 48, 94
Apocynaceae Juss. 5, 29, 38, 42, 48, 54, 58, 63, 95
Apocynoideae 5
Aristida L. 29, 42, 44, 92, 93
Asclepiadaceae R. Br. 29, 38, 42, 48, 76, 92, 94, 95

Belonites E.Mey. 6
  bispinosa (L.f.) E.Mey. 63
  succulenta (L.f.) E.Mey. 6, 76
Bignoniaceae Juss. 35
Bombacaceae Kunth 35, 51
Breonia A. Rich. ex DC. 54, 94
Bryophyta 107
Bulbostylis Kunth
  schoenoides Kunth 29, 92
Burseraceae Kunth 48, 54, 58
Bussea Harms 60, 95

Caesalpinia L.
  bonduc Roxb. 58, 94
Capparidaceae Juss. 95, 96
Capparis L. 95, 96
Carissa L.
  bispinosa (L.) Desf. ex Brenan 95
  edulis Vahl 58, 94
  haematocarpa A. DC 95
  spinarum L. 58, 94
Carphalea Juss. 54, 94
Cassia L. 35, 93
  meridionalis R. Vig. 110
Catharanthus G. Don
  longifolius (Pichon) Pichon 42, 93
  ovalis Markgr. 29
  trichophyllus (Baker) Pichon 58, 94
Cedrelopsis Baill.
  grevei Baill. 35, 93
Celastraceae R. Br. 76
Cerbera L. 5
  manghas L. 5
Ceropegia L. 100
  africana R. Br. 95
  dimorpha Humbert 93, 109
Cissus L. 91, 100, 111
Coleochloa Gilly
  setifera (Ridl.) Gilly 44, 92, 93
Colophospermum J. Kirk ex Benth.
  mopane (J. Kirk ex Benth.) J. Léonard 96
Combretaceae R. Br. 54, 76
Combretum Loefl.
  apiculatum Sond. 76, 96
Commiphora Jacq. 84, 106, 108, 110
  aprevalii Guill. 48, 94, 95
  marchandii Engl. 54, 94
  orbicularis Engl. 48
Compositae Giseke 20, 29, 38, 84, 95
Crassulaceae DC. 20, 29, 38, 42, 44, 48, 54, 84

Crassula Dill. ex L. 95
Cucurbitaceae Juss. 91
Cunoniaceae R. Br. 44
Cynanchum L. 98
  eurychitoides K. Schum. 48, 94
  marnierianum Rauh 109
  microlobum Jum. & H. Perrier 93
  perrieri Choux 108
  pycnoneuroides Choux 92
Cynorkis Thours
  incarnata 108
Cyperaceae Juss. 29, 44
Cyphostemma (Planch.) Alston 100, 106
  sakalavense Desc. 94, 107

Dalbergia L. f. 54, 84, 94, 95
Delonix Raf. 35, 108, 110
  adansonioides (R. Vig.) Capuron 35, 48, 93, 95
Delosperma Schwantes
  lehmanii Schwantes 95
Didiera Baill.
  madagascariensis Baill. 35, 49, 93, 94
Didieraceae Drake 35, 49, 51, 84, 108
Dionycha Naudin
  bojeri Naudin 44, 93
Diospyros L. 95
Dipcadi Medik.
  heterocuspe Baker 29, 92
Dracaena L. 11
Dracaenaceae R.A. Salisbury 96

Ebenaceae W.R. Guerke 95
Echiteae G. Don 5
Echites P. Br.
  bispinosa L.f. 1, 63
  succulenta L.f. 1, 76
Erica L. 97
Erythrophysopsis Verdc.
  aesculina (Baill.) Verdc. 110
Erythroxylaceae Kunth 54
Erythroxylum P. Browne
  pervillei Baill. 54, 94
  seyrigi H. Perrier 95
Euclea L. 95
Euphorbia L. 3, 5, 35, 42, 48, 63, 84, 95, 98, 100
  ankarensis Boiteau 111
  aureo-viridiflora (Rauh) Rauh 107, 111
  bulbispina Rauh & Razafindratsira 95, 111
  didiereoides Denis ex Leandri 92, 108
  enterophora Drake 109
  fianarantsoae Ursch & Leandri 92
  guillauminiana Boiteau 94
  horombensis Ursch & Leandri 93, 109
  mammillaris L. 95, 96
  milii Des Moul. 29, 38, 42, 44, 48, 54, 92, 93, 94, 106, 107, 108, 109
  moratii Rauh 109
  obcordata Denis 110
  oncoclada Drake 92
  pachypodioides Boiteau 107
  pauliana Ursch & Leandri 110
  pedilanthoides Denis 106, 110
  quartziticola Leandri 92, 107, 108
  stenoclada Baill. 35, 93
  turricali L. 48, 94
  viguieri Denis 48, 91, 94, 95, 106, 111
Euphorbiaceae Juss. 20, 29, 35, 38, 42, 44, 48, 54, 63, 84, 95, 96

Faucaria Schwantes
  felina Schwantes 95
Faurea Harv. 76, 96
Fernandoa Welw. ex Seem.
  madgascariensis (Baker) A.H. Gentry 35, 93
Ficus L.
  reflexa Thunb.
    subsp. reflexa 26, 92
Forsythiopsis Baker
  vincoides (Lam.) Benoist 54, 94
Funtumia Stapf 5

Gasteria Ser.
  nitida (Salm-Dyck) Haw. 95, 96
Gramineae Juss. 20, 29, 38, 42, 44, 54, 107
Gyrocarpus Jacq.
  americanus Jacq. 95

Helichrysum Mill.
  ibitiense R. Vig. & Humbert 20, 92
Heteropogon Pers.
  contortus (L.) Roem. & Schult. 42, 93
Hildegardia Schott & Endl. 84
  erythrosiphon Baill. 48, 94, 95
Holarrhena R. Br. 5
Holmskioldia Retz. 54, 94
Huernia R. Br. 76, 96
Hugonia L.
  brewerioides Baker 54, 94
Hyphaene Gaertn. 58
  schatan Bojer 94
Hyparrhenia E. Fourn. 20, 29, 38, 42, 92, 93

Impatiens L.
  tuberosa H. Perrier 107
Indigofera L. 76, 96
Ischnolepis Jum. & H. Perrier 106
  tuberosa Jum. & H. Perrier 29, 38, 92, 93, 108

Kalanchoe Adans. 84, 98, 100, 106
  gastonis-bonnieri Raym.-Hamet & H. Perrier 48, 94, 106, 110
  integrifolia Baker 107
  orgyalis Baker 38, 42, 48, 93, 109
  synsepala Baker 20, 29, 38, 44, 54, 93, 94
  tomentosa Baker 108

Labiatae Juss. 20, 29, 38, 42, 44, 48, 63, 76, 84
Leguminosae Juss. 35, 48, 54, 58, 60, 76, 96
Leptolaena Thouars
  bojeriana (Baill.) Cavaco 38, 44, 93
  luteola (H. Perrier) Cavaco 38, 93
  pauciflora Baker 20, 92
Lichenes 107
Liliaceae Juss. 29, 91
Linaceae Gray 54
Loganiaceae C. Mart. 58, 96
Lomatophyllum Will. 91, 106
Lycopodium L. 107

Mascarenhasia A. DC. 5
  arborescens A. DC. 58, 94
  lanceolata A. DC. 58, 94
  lisianthiflora A. DC. 38, 54, 93, 94
Melastomataceae Juss. 44, 54
Memecylon L.
  boinense H. Perrier 54, 94
Moraceae Link 26
Moringa Adans.
  hildebrandtii Engl. 108

Neoharmsia R. Vig.
  madagascariensis R. Vig. 48, 94
Neriinae Boiteau 5
Nerium L. 5

Oeceocladus Lindl. 111
Olinia Thunb. 76, 96
Oliniaceae Arn. ex Sond. 76
Operculicarya H. Perrier
  pachypus Eggli 108
Orchidaceae Juss. 106, 107, 111

Pachypodiinae Pichon ex Leeuwenb. 5
Pachypodium Lindl. 1, 2, 5, **6**, 7, 83, 84, *85*, *86*, 88, 89, 94, 95, 97, 98, 100, 101, 105, 111
ambongense Poiss. 2, 4, 8, **10**, *11*, *12*, *op. 16*, 84, 88, 90, 91, 105, 110
baronii Costantin & Bois 2, 4, 6, 7, *11*, **12**, 14, *op. 16*, 63, 87, 88, 90, 91, 99, 106, 111
var. *erythreum* Poiss. 13, 14
var. *windsorii* (Poiss.) Pichon 1, 2, 60
bicolor Lavranos & Rapanarivo 1, 2, 4, 8, *12*, **14**, *15*, *op. 17*, 17, 84, 88, 90, 91, 92, 106, 110
bispinosum (L.f.) A. DC. 1, 2, 3, 4, 9, **63**, *64*, *66*, 67, 87, *op. 89*, 89, 90, 91, 95, 97, 99
brevicalyx (H. Perrier) Pichon 27
brevicaule Baker 2, 3, 4, 7, *12*, *op. 17*, **17**, *18*, 20, 30, 87, 88, 90, 91, 92, 97, 106, 108
cactipes K. Schum. 1, 2, 9, **20**, *21*, *22*, 23, 24, *op. 32*, 39, 54, 87, 88, 90, 91, 92, 107
champenoisianum Boiteau 46, 47
decaryi Poiss. 2, 3, 4, 6, 8, *22*, **24**, *25*, 26, *op. 32*, *op. 33*, 87, 88, 90, 91, 92, 98, 107, 110
densiflorum Baker 2, 4, 7, *18*, *22*, **26**, 29, 30, 33, *op. 40*, 87, 88, 90, 91, 92, 98, 107, 108
var. *brevicalyx* H. Perrier 26, 28, 29, 30
drakei Costantin & Bois 51, 52, 53
eburneum Lavranos & Rapanarivo 1, 2, 8, **30**, *31*, *32*, 33, *op. 41*, 87, 88, 90, 91, 92, 93, 97, 98, 107, 108
geayi Costantin & Bois 2, 3, 4, 6, 7, *11*, *32*, **33**, 35, *op. 56*, 87, 88, 90, 91, 93, 97, 99, 108, 110
giganteum Engl. 67, 69
glabrum G. Don 1, 63
gracilius (H. Perrier) Rapanarivo 2, 4, 9, 23, 24, *32*, **35**, *36*, 38, 39, 54, *op. 56*, *op. 57*, 88, 90, 91, 93, 99, 108
griquense L. Bolus 76, 80
horombense Poiss. 2, 4, 8, *21*, 29, **39**, *40*, 42, 48, 49, 54, *op. 57*, 88, 90, 91, 93, 94, 109
inopinatum Lavranos 1, 2, 4, 8, 33, *40*, **42**, *43*, *op. 64*, 90, 91, 93, 97, 98, 109
jasminiflorum L. Bolus 76
lamerei Drake 2, 3, 4, 8, *40*, 42, **44**, *45*, 49, 51, 60, *op.65*, 87, 88, 90, 91, 93, 94, 97, 99, 105, 109, 110, 111
var. *ramosum* (Costantin & Bois) Pichon 46, 110, 111
lealii Welw. 2, 3, 4, 9, 64, **67**, *68*, 70, 76, 87, 88, 90, 91, 95, *op. 96*, 97, 105
subsp. *saundersii* (N.E.Br.) G.D. Rowley 73
menabeum Leandri 46, 47
meridionale (H. Perrier) Pichon 2, 3, 4, 8, *25*, 48, **49**, *50*, 51, 58, *op. 80*, 87, 88, 90, 91, 94, 97, 108, 109, 110
namaquanum (Wyley ex Harv.) Welw. 2, 3, 4, 6, 7, 9, *64*, **70**, *71*, 72, 87, 88, 90, 91, 95, *op. 96*, 97, 99, 105
obesum G. Don ex A.DC. 81
ramosum Costantin & Bois 46, 48
x rauhii Halda 27, 30
rosulatum Baker 1, 2, 9, *21*, 23, 24, 39, 41, *50*, **51**, 54, 58, *op. 80*, *op. 81*, 87, 88, 90, 91, 94, 99, 110
var. *delphinense* H. Perrier 20
var. *drakei* (Costantin & Bois) Markgr. 52
var. *eburneum* (Lavranos & Rapanarivo) G.D. Rowley 30
var. *gracilius* H. Perrier 1, 2, 37
var. *horombense* (Poiss.) G.D. Rowley 39
var. *inopinatum* (Lavranos) G.D. Rowley 42
var. *rosulatum*
f. *bicolor* (Lavranos & Rapanarivo) G.D. Rowley 16
var. *stenanthum* Costantin & Bois 20, 23
rutenbergianum Vatke 2, 3, 4, 8, *45*, 51, **54**, *55*, 58, 63, *op. 81*, 87, 88, *op. 88*, 90, 91, 94, 95, 97, 99, 105, 106, 107, 110, 111
var. *lamerei* (Drake) Poiss. 44
var. *meridionale* H. Perrier 49
var. *perrieri* Poiss. 59, 60
var. *sofiense* Poiss. 59
saundersii N.E.Br. 2, 3, 4, 9, *64*, 70, **72**, *74*, 76, 87, 88, 90, 91, 96, *op. 97*, 99
sofiense (Poiss.) H. Perrier 2, 3, 4, 8, *25*, 49, *55*, **59**, 60, 88, *op. 88*, 90, 91, 95, 97, 106, 110, 111
succulentum (L.f.) A.DC. 1, 2, 4, 6, 9, 67, **76**, *77*, *78*, 87, 89, 90, 91, 96, 97, *op. 97*, 99
tomentosum G. Don 1, 76
tuberosum Lindl. 1, 2, 6, 76
var. *loddigessii* A. DC. 2, 63
tuberosum Lodd. 63
windsorii Poiss. 2, 4, 7, 14, *55*, **60**, *61*, 63, 87, 88, *op. 88*, *op. 89*, 90, 91, 94, 95, 98, 107, 110, 111
Palmae Juss. 58
Pandanaceae R. Br. 26
Pandanus Parkinson 91
parkinsonii Martelli 26, 92
Passifloraceae Juss. ex Kunth 91
Pedaliaceae R. Br. 91, 94
Pellaea Link 99
goudotii (Kunze) C. Chr. 29, 44, 92, 93
Pentaschistis (Nees) Spach
perrieri A. Camus 29, 92
Petchia Livera
erythrocarpa (Vatke) Leeuwenb. 58, 94
Philippia Klotzsch 97
Pinus L. 101
Plectaneia Thouars
stenophylla Jum. 48
thouarsii Roem. & Schult. 54, 58, 94
Plectranthus L'Hér. 100
cylindraceus Hochst. ex Benth. 76, 96
Plumeria L. 5
Plumerioideae K. Schum. 5
Polystachya Lindl. 109
Portulacaceae Juss. 95, 96
Portulacaria Jacq.
afra Jacq. 95, 96
Proteaceae Juss. 76
Protorhus Engl.
deflexa H. Perrier 54, 94
Ptaeroxylaceae J.-F. Leroy 35
Pterocelastrus C.F.W. Meissn. 76, 96
Pterodiscus Hook. 100

Quercus L.
petraea (Mattuschka) Lieblein 100
robur L. 100

Rauvolfia L.

media Pichon 54, 58, 94
Rhamnaceae Juss. 29, 58
Rhipsalis Gaertn.
baccifera (J.S. Mill.) Stearn 107
Rhopalocarpus Bojer
lucidus Bojer 58, 94
Rhus L.
undulata Jacq. 95
Rubiaceae Juss. 54

Sansevieria Thunb. 96
Sapindaceae Juss. 58
Sarcolaenaceae Caruel 20, 38, 44
Sclerocarya Hoscht. 29, 58, 92
caffra Sond. 58, 76, 94, 96
Senecio L. 38, 84, 95
crassissimus Humbert 29, 92
decaryi Humbert 92
quartzicolus Humbert 20
Sesamothamnus Welw. 100
Sphaerosepalaceae Tiegh. 58
Stapelianthus Choux ex A. White & B. Sloane 42, 48, 93, 94, 109
Sterculiaceae Bartl. 48
Strophanthus DC.
boivinii Baill. 58, 94
Strychnos L. 96
spinosa Lam. 58, 94

Tabernaemontana L.
calcarea Pichon 58, 94
coffeoides Bojer ex A. DC. 54, 58, 94
stellata Pichon 54, 94
Talinella Baill. 107
Talinum Adans. 100
Terminalia L. 54, 94
Tetradenia Benth. 42, 44, 48, 63, 84, 93, 94, 95, 98, 107, 109
fruticosa Benth. 20, 29, 38, 92, 93
Thevetia L. 5
Thorncroftia N.E. Br. 100

Uapaca Baill. 28, 33, 38, 84, 88, 92, 93
bojeri Baill. 20, 38, 84, 92, 93
Uncarina (Baill.) Stapf 91, 106, 111
grandidieri (Baill.) Stapf 109
leandrii Humbert
var. rechbergeri Lavranos 106
leptocarpa (Decne.) Ihlenf. & Straka 94, 109
peltata (Baker) Stapf 107, 110, 111
perrieri Humbert 106
roeoesliana Rauh 109
sakalava Humbert 94, 106
stellulifera Humbert 108, 110
Urera Gaud. 106

Velloziaceae Endl. 20, 29, 38, 42, 48, 84
Verbenaceae J. St-Hil. 54
Vitaceae Juss. 91

Weinmannia L. 44, 93
Wrightieae G. Don 5

Xerosicyos Humbert
perrieri Humbert 91
Xerophyta Juss. 48, 84, 92, 94, 99, 108
dasylirioides Baker 20, 29, 38, 42, 92, 93

Ziziphus Mill. 29, 92
jujuba Lam. 58, 94