

Cremnophilous succulents of southern Africa: diversity, structure and adaptations

by

Ernst Jacobus van Jaarsveld

Submitted in partial fulfilment of the requirement for the degree

Philosophiae Doctor

in the Faculty of Natural and Agricultural Sciences
(Department of Plant Science)

University of Pretoria

Pretoria

Promoter: Prof. Dr. A.E. van Wyk

June 2011



Othonna cremnophila [88], from south-facing cliffs of the Rosyntjieberg, Richtersveld, Northern Cape. Artist: Jeanette Loedolff.



DECLARATION

I, Ernst Jacobus van Jaarsveld, declare that the thesis that I hereby submit for the degree Philosophiae Doctor at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

Signature: *Ernst van Jaarsveld*

Date: *9 Julie 2011*

TABLE OF CONTENTS

ABSTRACT	xvi
CHAPTER 1. INTRODUCTION	1
1.1 Objectives, key questions and hypotheses	1
1.2 Succulent riches of South Africa and Namibia	2
1.3 Cliffs and cremnophytes	3
1.4 Cremnophilous succulent plants	5
1.5 Shaped by the cliff	5
1.6 Historical review	6
1.7 Layout of thesis	7
CHAPTER 2. METHODS AND DEFINITIONS	8
2.1 Study area	8
2.2 Methods	8
2.3 Definitions	9
CHAPTER 3. THE CLIFF-FACE HABITAT	14
3.1 Formation of cliffs in southern Africa	14
3.1.1 Cliff bedrock strength	15
3.1.2 Ledges, fissures and cracks	15
3.2 Geology	16
3.2.1 Sedimentary rocks	16
3.2.1.1 Sandstone and quartzitic sandstone	16
3.2.1.2 Conglomerate	17
3.2.1.3 Shale and mudstone	17
3.2.1.4 Dolomite	17
3.2.2 Igneous or magmatic rocks	18
3.2.2.1 Granite and gneiss	18
3.2.2.2 Basalt, dolerite and rhyolite	18
3.3 Cliff weathering and erosion	19
3.3.1 Cliff weathering	19
3.3.2 Cliff erosion	20
3.3.3 Obligate cremnophilous succulents: adaptation to rock type	21

3.4	Cliff moisture-holding capacity (hydrology)	21
3.5	Cliff-face habitat and environment	22
3.5.1	Physiography	22
3.5.1.1	How the cliff-face habitat differs from level-ground habitats (conditions obligate cremnophytes have to face on vertical cliffs)	22
3.5.2	Vertical orientation of the cliff habitat and gravity	23
3.5.2.1	Vertical orientation, gravity and its influence on plant growth	24
3.5.3	Precipitation	25
3.5.3.1	Cliffs and the rain shadow effect	26
3.5.3.2	Water-holding capacity on the cliff	26
3.5.3.3	Dew and fog	27
3.5.3.4	Cremonophytes adapting to a limited water supply	28
3.5.3.4.1	Increase in succulence	28
3.5.3.4.2	Dependence on fog	28
3.5.3.5	Cremonophytes adapting to seasonality of rainfall	28
3.5.3.5.1	Summer-deciduous	29
3.5.3.5.2	Aestivation (summer dormancy)	29
3.5.3.5.3	Winter-deciduous	29
3.5.3.6	Shallow root system	29
3.6	Radiation	29
3.6.1	Effects of sun radiation	31
3.6.1.1	South-facing cliffs	31
3.6.1.2	Leaf presentation and orientation	31
3.6.1.3	Windows	32
3.6.1.4	Anthocyanin production on the abaxial leaf surface	32
3.6.1.5	North-facing cliffs	33
3.7	Wind	34
3.7.1	Wind and succulent cremonophytes	34
3.8	Temperature	35
3.8.1	Temperature and latitude	35
3.8.2	Temperature and altitude	36
3.8.3	Temperature and the coast	36
3.8.4	Temperature and its influence on succulent plant life forms	37
3.8.5	Temperature and growth forms on local cliffs	37

4.5.2.2	Stems abbreviated, resulting in reduced growth	54
4.5.2.2.1	Cliff huggers	54
4.5.2.2.1.1	Stems abbreviated; congested, bulbous cremnophytes	55
4.5.2.2.1.2	Stems abbreviated; compact, globose to mat-forming clusters	55
4.5.3	Stem succulence on the cliff	56
4.5.3.1	Stem and leaf succulence	57
4.5.3.2	Succulent internodes and phyllopodia	57
4.5.3.3	Caudex	58
4.5.3.4	Stems and fog-trapping hairs	58
4.6	Leaves	58
4.6.1	Leaf succulence on the cliff	59
4.6.1.1	Long-lived perennial leaves	59
4.6.1.2	Succulent leaves annually replaced	59
4.6.1.2.1	Deciduous leaves	59
4.6.1.2.2	Summer-aestivating leaves	60
4.6.1.3	Leaf shape as an adaptation to the cliff	60
4.6.1.3.1	Cylindrical leaves	61
4.6.1.4	Bulbous cremnophytes; leaf and bulb scales	61
4.6.1.4.1	Bulb scales and their modification	62
4.6.1.4.1.1	Tunicate bulbs	62
4.6.1.4.1.2	Bulb scales	62
4.6.1.4.2	Bulb leaves	62
4.6.1.4.2.1	Leaves ascending	62
4.6.1.4.2.1.1	Leaves few, narrow	63
4.6.1.4.2.1.2	Leaves numerous	63
4.6.1.4.2.2	Bulbs with drooping leaves.....	63
4.6.1.4.2.2.1	Leaves drooping due to epinastic growth	64
4.6.1.4.2.2.2	Leaves drooping due to gravity	64
4.6.2	Leaf duration on the cliff	64
4.6.3	Assimilating organs other than leaves	64

4.6.4	Leaves of non-bulbous succulent geophytes	64
4.6.4.1	Succulent plants (non-bulbous) with leaves in acaulescent rosette	65
4.6.4.1.1	Pendent leaves from acaulescent rosette due to epinastic growth ..	65
4.6.4.1.2	Leaves becoming pendent due to gravity	65
4.6.4.1.3	Leaves in a rosette (or rosette-like clusters), short, non-drooping	66
4.6.4.1.4	Leaves in pendent caulescent rosettes (pendent megachamaephytes) with non-assimilating stems	67
4.6.4.1.5	Succulent leaves on a leafy stem	68
4.6.4.1.5.1	Leaves arranged in a subcylindrical body (internodes short)	68
4.6.4.1.5.2	Leaves evenly spread (internodes extended)	68
4.6.4.1.6	Leaves in drooping clusters	69
4.6.4.1.7	Leaves in ascending clusters	69
4.6.5	Leaf epidermis	69
4.6.5.1	Epicuticular waxes	69
4.6.5.2	Colour	69
4.6.5.3	Papillae	70
4.6.5.4	Epidermal hairs	70
4.6.5.4.1	Epidermal hairs reducing moisture loss	70
4.6.5.4.2	Epidermal hairs and fog-trapping abilities	71
4.6.5.4.3	Epidermis glabrous	71
4.6.5.5	Stomata	71
4.6.5.6	Changeable epidermis	72
4.6.5.7	Windows	72
4.6.6	Leaf margin	73
4.7	Succulent cremnophyte growth rate and life cycle	73
4.7.1	Monocotyledons	73
4.7.2	Dicotyledons	74
4.8	Cremonophyte defence	75
4.8.1	Armour	75
4.8.2	Camouflage	75
4.8.3	Chemical defence	76

CHAPTER 5. REPRODUCTION ON THE CLIFF	77
5.1 Sexual reproduction	77
5.1.1 Pollination	77
5.1.1.1 Insect pollination	78
5.1.1.2 Bird pollination	79
5.1.1.3 Rich flowering	79
5.1.2 Dispersal	81
5.1.2.1 Seed	81
5.1.2.1.1 Wind (anemochorous diaspores)	81
5.1.2.1.1.1 Flattish or disk-like winged diaspores	82
5.1.2.1.1.2 Diaspores with a single lateral wing	83
5.1.2.1.1.3 Seed with a parachute (plumed diaspores)	83
5.1.2.1.1.4 Dust diaspores	83
5.1.2.1.1.5 Wind-ballists (anemoballists)	84
5.1.2.1.2 Water dispersal (hydrochory)	84
5.1.2.1.2.1 Wash-out dispersal	84
5.1.2.1.3 Bird-dispersed diaspores	85
5.1.2.1.4 Autochory (<i>in situ</i> dispersal)	85
5.1.2.1.5 Dimorphic dispersal strategy (amphicarpy) of semisucculent cremnophytes	85
5.2 Vegetative (asexual) reproduction	87
5.2.1 Bulbil propagules	87
5.2.2 Winged bulbils	87
5.2.3 Inflorescence propagules	87
5.2.4 Leaf propagules	87
5.2.5 Bulb scale propagules	88
5.2.6 Dividing or proliferating clusters	88
5.2.7 Active growth	88
5.3 Establishment	89
5.3.1 Crevices	89
5.3.2 Cliff-face lichen fields	89
5.3.3 Germination	90

CHAPTER 6. PHYTOGEOGRAPHY OF OBLIGATE SUCCULENT AND BULBOUS CREMNOPHYTES	93
6.1 Background	93
6.2 Size of the cliff face	93
6.3 Plant size	94
6.4 Endemism	95
6.5 South African and Namibian cliff faces	95
6.5.1 The cliffs of the Great Escarpment and inland	96
6.5.1.1 Cliffs of Mpumalanga Drakensberg (northeastern Great Escarpment)	97
6.5.1.2 Cliffs of KwaZulu-Natal and Eastern Cape Drakensberg (eastern Great Escarpment)	97
6.5.1.3 Nuweveld and Roggeveld Mountains (southern Great Escarpment)	98
6.5.1.4 Kamiesberg	98
6.5.1.5 Namibia	98
6.5.2 Cliffs of the marginal zone	99
6.5.2.1 Cape zone (Cape Supergroup, Cedarberg–Suurberg)	99
6.5.2.2 Greater Namaqualand zone	100
6.5.2.3 Kaoko marginal zone	101
6.5.2.4 Limpopo zone	101
6.5.2.5 Mpumalanga to KwaZulu-Natal zone (Mpumalanga–Thukela)	102
6.5.2.6 Pondoland and Eastern Cape zone (Durban–Great Fish River)	102
6.5.2.7 Riverine cliffs of the marginal and other zones (between Great Escarpment and the sea)	103
6.5.2.7.1 Levuvu Gorge (Savanna)	103
6.5.2.7.2 Olifants River (Savanna)	104
6.5.2.7.3 The Kaap River (Savanna)	104
6.5.2.7.4 Umbeluzi (Swaziland), Pongola, White Mfolozi and Mkuze Rivers (all KwaZulu-Natal) (Savanna)	104
6.5.2.7.5 Thukela River (Savanna)	104
6.5.2.7.6 Umgeni River and its tributaries (Indian Ocean Coastal Belt)	104

6.5.2.7.7	Mzimkulu, Mtamvuna, Mzamba, Mtentu and Msikaba Rivers (KwaZulu-Natal and Eastern Cape) (Indian Ocean Coastal Belt)	105
6.5.2.7.8	Mzimvubu River (Eastern Cape) (Valley Bushveld)	105
6.5.2.7.9	Bashee River (Eastern Cape) (Valley Bushveld)	105
6.5.2.7.10	Kei River and its tributaries (Eastern Cape) (Valley Bushveld)	106
6.5.2.7.11	Great Fish River, Keiskamma River (Eastern Cape) (Albany Thicket)	106
6.5.2.7.12	Gamtoos River and its tributaries (Eastern Cape) (Albany Ticket)	106
6.5.2.7.13	Gourits River and its tributaries (Eastern Cape) (Albany Thicket)	107
6.5.2.7.14	Berg, Breede and Olifants Rivers (Western Cape) (Fynbos) ...	107
6.5.2.7.15	Buffalo River and its Skaaprivier tributary (Namaqualand) (Succulent Karoo)	107
6.5.2.7.16	Orange (Gariiep) River (Richtersveld) (Desert and Succulent Karoo)	108
6.5.2.7.17	Kunene River (Desert and Savanna)	109
6.5.3	Inselberg cliffs	109
6.5.4	Coastal cliffs	109
6.6	Representation of obligate succulent cremnophytes in biomes	110
6.6.1	Winter rainfall	110
6.6.1.1	Fynbos Biome	110
6.6.1.2	Succulent Karoo Biome	111
6.6.2	Rainfall in summer and winter	113
6.6.2.1	Desert Biome	113
6.6.2.2	Albany Thicket Biome	114
6.6.3	Summer rainfall	116
6.6.3.1	Nama-Karoo Biome	116
6.6.3.2	Grassland Biome	118
6.6.3.3	Savanna Biome	119
6.6.3.4	Indian Ocean Coastal Belt	121
6.6.3.5	Forest Biome	123

CHAPTER 7. EVOLUTION OF CREMNOPHYTES	126
7.1 Introduction	126
7.2 Evolution of cremnophytes	127
7.3 Adaptive trends	131
7.4 Convergence of cremnophytes	133
7.5 Distribution patterns (historical and present)	133
7.5.1 Distribution and representation	133
7.6 Evolutionary history and origin of southern African cremnophytes	134
7.6.1 Uplift events and the creation of cliffs during the Neogene	136
7.6.2 Origin of Albany Thicket	138
CHAPTER 8. CONSERVATION OF CLIFFS AND SUCCULENT CREMNOPHYTES IN SOUTH AFRICA AND NAMIBIA	139
8.1 Introduction	139
8.2 Why cliffs should be protected	140
8.3 Threats to obligate cremnophilous succulent plants in the study area	140
8.3.1 Habitat loss	140
8.3.1.1 Dam construction	140
8.3.1.2 Mining	141
8.3.1.3 Recreation	141
8.3.1.3.1 Hikers and climbers	141
8.3.1.3.2 Plant collectors	142
8.3.1.3.2.1 Gathering of medicinal plants	142
8.3.1.3.2.2 Plant enthusiast collectors	142
8.4 Natural disturbances on the cliff face	143
8.4.1 Rock falls	143
8.4.2 Fire	143
8.4.3 Storm damage	143
8.4.4 Mammals	143
8.5 <i>Ex situ</i> conservation	144
8.5.1 Propagation in botanical gardens and other institutions	144

CHAPTER 9. COMPENDIUM OF SUCCULENT CREMNOPHYTES

AND THEIR FEATURES	150
9.1 Diagram (dendrogram) of obligate succulent cremnophyte growth forms	150
9.1.1 Cliff growth form formula	150
9.1.2 Explanation of symbols	152
9.1.3 Descriptive dichotomous key to the schematic Diagram 9.1	154
9.2 Descriptions of growth forms according to Diagram 9.1	155
9.2.1 Extended stem growth (E, 94 taxa)	156
9.2.1.1 Cremnophytes with rudimentary foliage (E:Ex, 5 taxa)	156
9.2.1.1.1 Decumbent growth (E:Ex:De, 1 taxon)	156
9.2.1.1.2 Pendent growth (E:Ex:P, 4 taxa)	157
9.2.1.2 Foliated cremnophytes (F, 88 taxa)	157
9.2.1.2.1 Trees and shrubs (facultative cremnophytes, 8 species)	157
9.2.1.2.2 Ascending herbaceous and succulent-stemmed, foliated shrubs or shrublets (E:F:As:S/H, 29 taxa)	158
9.2.1.2.3 Ascending, woody stemmed shrublets (E:F:As:W, 7 taxa) ...	158
9.2.1.2.4 Pendent stems (E:F:P, 51 taxa)	159
9.2.1.2.4.1 Pendent rosettes (E:F:P:R, 14 taxa)	159
9.2.1.2.4.2 Pendent leafy stems (E:F:P:Els, 39 taxa)	159
9.2.2 Abbreviated or truncated stem growth (A, 126 taxa)	159
9.2.2.1 Bulbous cremnophilous succulent plants (A:B, 30 taxa)	160
9.2.2.1.1 Bulbs with perennial leaves (A:B:Lper, 21 taxa)	160
9.2.2.1.2 Bulbs with leaves that are deciduous or replaced annually (A:B:D, 9 taxa)	161
9.2.2.2 Non-bulbous succulents (A:S, 96 taxa)	161
9.2.2.2.1 Compact succulent plants, leaves annually replaced (deciduous or aestivating leaves) (A:S:Lar, 27 taxa)	161
9.2.2.2.1.1 Compact growth with fused leaves, the genus <i>Conophytum</i> (A:S:Lar:Lf, 19 taxa)	161
9.2.2.2.1.2 Compact cluster, succulent-stemmed, leaves deciduous during the long dry summer season, the genera <i>Tylecodon</i> and <i>Othonna</i> (A:S:Lper:D, 8 taxa)	162

9.2.2.2.1.3 Compact succulent plants with perennial leaves (clustered, crowded leaves, or in dense rosettes) (A:S:Lper, 69 taxa)	162
9.2.2.2.2 Compact succulent plants with leaves crowded, the genera <i>Adromischus</i> , <i>Pyrrosia</i> and <i>Streptocarpus</i> (A:S:Lper:Lc, 10 taxa)	162
9.2.2.3 Plants with leaves in tight (rarely loose) rosettes (A:S:Lper:R, 59 taxa) ...	162
9.2.2.3.1 Plants with solitary rosettes (A:S:Lper:R:So, 3 taxa)	163
9.2.2.3.2 Plants with leaves in a tight rosette in dense to loose clusters (A:S:Lper:R:C, 56 taxa)	163

CHAPTER 10. CHECK LIST OF OBLIGATE AND NEAR-OBLIGATE

CREMNOPHILOUS TAXA (220 TAXA, 203 SPECIES)	164
10.1 Introduction	164
10.2 Explanation of the check list	164
10.3 The list is still growing	165
10.4 Layout of Table 10.1	165

CHAPTER 11. GENERAL DISCUSSION AND CONCLUSIONS 223

11.1 General observations	223
11.2 Main findings of this study	225
11.2.1 Obligate or near-obligate cremnophytes	225
11.2.2 New taxa	225
11.2.3 Growth modification traits (morphological adjustment to the cliff habitat)	225
11.2.3.1 Increase in succulence and other drought-adapted traits	226
11.2.3.2 Decrease in size and weight	226
11.2.3.3 Adjustment of growth form	226
11.2.3.4 Leaves and sun radiation	227
11.2.3.5 Decrease in defence (armament)	227
11.2.4 Reproductive traits	227
11.2.4.1 Vegetative reproduction	227
11.2.4.2 Rich flowering	228
11.2.4.3 Seed dispersal	228
11.2.5 Taxonomic representation	228
11.2.6 Representation of cremnophytes in the various biomes	229
11.2.7 Representation of cliffs	229

11.3 Conclusions	229
11.3.1 Adaptation to the cliff habitat	229
11.3.2 Isolation of the cliff habitat	230
11.3.3 Cliffs as refugia	231
11.3.4 Cliffs as living laboratories	231
11.3.5 The vertical habitat as a driving force in evolution	231
11.3.6 Horticultural application and conservation	232
CHAPTER 12. SPECIES TREATMENT (Enumeration of the 220 obligate or near-obligate cremnophilous succulent and bulbous taxa)	243
Descriptions	243
Colour plates	800
Figures	897
Distribution maps	1331
SUMMARY	1369
ACKNOWLEDGEMENTS	1375
CURRICULUM VITAE	1376
REFERENCES	1379
APPENDICES	
APPENDIX 1: DISCOVERY OF OBLIGATE CREMNOPHYTES NEW TO SCIENCE ON EXPEDITIONS BY THE AUTHOR AND COLLEAGUES	1392
APPENDIX 2: NEW CREMNOPHILOUS PLANT TAXA IN SOUTH AFRICA AND NAMIBIA DESCRIBED BY THE AUTHOR OR IN COLLABORATION WITH OTHER AUTHORS.....	1393
APPENDIX 3: LIST OF PUBLICATIONS ON SUCCULENT AND BULBOUS SUCCULENT CREMNOPHYTES AS WELL AS ON OTHER SUCCULENT PLANT TAXA BY THE AUTHOR OR IN COLLABORATION WITH OTHER AUTHORS	1395

ABSTRACT

Cremnophilous succulents of southern Africa: diversity, structure and adaptations

Ernst Jacobus van Jaarsveld

Submitted in partial fulfilment of the requirement for the degree

Philosophiae Doctor

In the Faculty of Natural and Agricultural Sciences (Department of Plant Science)

University of Pretoria

June 2011

Promoter: Prof. Dr. A.E. van Wyk

The vertical cliff-face habitat is renowned for many specifically adapted plant species that exhibit a high degree of local endemism. Over a period of nine years the succulents and bulbous succulents on cliff faces in South Africa and Namibia were systematically surveyed and documented. Distinction was made between succulents growing on cliffs as part of a wider habitat and those found only on cliffs (obligate cremnophytes). Most major cliff-face habitats in the study area were visited and all plants were documented. A check list and descriptions (including adaptive traits) of the 220 obligate cremnophilous taxa are provided.

During the study some 45 new cremnophilous succulent taxa were discovered and named, representing almost 20% of the total and proving that cliff habitats are some of the least studied environments, not only in southern Africa but globally. Among the newly described cremnophilous taxa is the genus *Dewinteria* (Pedaliaceae).

Using stem length, three basic cliff-face growth forms are identified—compact or cluster-forming ‘cliff huggers’, cliff shrublets or ‘cliff squatters’ and pendent ‘cliff hangers’. Compact growth (often tight clusters or mats) is mainly associated with the winter-rainfall

Succulent Karoo and Thicket regions, especially Namaqualand. However, further north the same compact growth forms are associated with an increase in altitude such as the Drakensberg Escarpment and other northern mountains. Most pendent growth forms are associated with the eastern and southeastern summer-rainfall regions; a number of smaller pendent shrublets occur on the high quartzitic sandstone mountains of the Western Cape. The degree of specialisation varies from highly adapted (smaller percentage) to less specialised (often eco-forms), and some taxa have no obvious adaptations.

This study revealed a general increase in succulence in most obligate cremnophilous succulent species (compared to closely related species in other habitats), a reflection of their xeric habitat, and plants tend to be more compact. Also, there is a shift in reproductive output, including an increase in vegetative reproduction (backup), wind-dispersed seed and enriched flowering associated with certain species. Most obligate cremnophilous succulent plants in the study area have cliff-adapted features, ensuring long-term survival.

Keywords: adaptations, biogeography, cliff-adapted features, cliff face, cremnophytes, ecology, evolution, flora, specialisation, succulent plants.