A taxonomic revision of the genus *Bergeranthus* Schwantes (Mesembryanthemaceae) in South Africa.

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ABSTRACT

The genus *Bergeranthus* Schwantes comprises ten species of leaf-succulent Mesembryanthemaceae that are centred in the Albany centre of endemism and restricted to the Eastern Cape Province of South Africa. No taxonomic revision of the genus, or key to the species of *Bergeranthus,* has been undertaken since its description by Schwantes in 1926. The species concepts are mostly based on single, or at best several, cultivated plants and are notoriously narrow and in some cases incorrect. Louisa Bolus described five of the ten currently recognized species of *Bergeranthus* (as well as *B. cookii, B. firmus, B. glenensis, B. jamesii,* and *B. longisepalus*) from cultivated plants that she had never seen in the wild. This narrow species concept, compounded by morphological change that occurs in response to environmental factors, presents an assemblage of ill-defined and poorly known taxa that have been prioritised for taxonomic attention by various authors. Furthermore, the generic delimitation of *Bergeranthus* with the closely related genera *Rhombophyllum* and *Hereroa* is unclear and requires attention before generic revisions are attempted for all three genera.

The taxonomic revision presented here is based on a study of 210 wild populations of *Bergeranthus* as well as cultivated representatives of these and 135 herbarium specimens. A phenetic analysis based on 36 vegetative characters was initially used to delimit taxa. Thereafter sixty-three macro- and micro- morphological characters were critically assessed for the purposes of species delimitation, amendment of existing species descriptions and the description of two new species. Macro-morphological characters examined included rootstock, leaf (36), inflorescence, floral (nine), fruit (nine), seed germination and seedling characters. Micro-morphological characters examined included leaf anatomy, leaf epidermal wax layer, anther shape and point of adherence, pollen and seed characters. This revision reduces two species into synonymy and two new species, *B. albomarginatus* and *B. nanus*, are described. Existing species descriptions are improved and all species are illustrated. A key to species is provided. The reproductive biology, ecology, phytogeography and distribution data of the genus are discussed towards an improved understanding of the genus.

The generic delimitation of *Bergeranthus* and its closest relatives, *Rhombophyllum* and *Hereroa*, are discussed based on an examination of 25 morphological characters and two phenological characters and a provisional key to genera is provided. A phylogenetic analysis of all 10 species of *Bergeranthus*, both species of *Rhombophyllum* and a single species of *Hereroa* (*H. granulata*) was undertaken to support species and generic delimitation.

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INTRODUCTION

On *Mesembryanthemum s.l.* Haworth (1821) commented '...their actual limits and essential characteristics...lie veiled in difficulties, which escape development and defy research. They will not be fettered.'

The Mesembryanthemaceae is South Africa's largest succulent plant family, comprising 63% of the southern African succulent flora. With an estimated 1 800 species in 120 genera (Smith *et al.* 1997) it is also South Africa's second largest plant family (Chesselet *et al.* 1995). The group is almost entirely endemic to southern Africa (Smith *et al.* 1998). Despite its significance in terms of numbers of genera and species, endemism, arid land agriculture and horticultural appeal the Mesembryanthemaceae remains one of the problem groups of South African botany with only 44 of the 117 genera having been reassessed since publication and only 35% of genera have been treated at species level.[1] (Chesselet *et al.* 1995). As is the case for most succulent plants the Mesembryanthemaceae are poorly collected and a lack of expertise in identification of these has compounded this neglect. Chesselet *et al.* (1995) list 117 genera in the family of which 43 have been revised between 1939 and 1994 and 35 of which, including *Bergeranthus*, require urgent attention.

A confounding problem to the taxonomy of Mesembryanthemaceae is morphological change that occurs in response to environmental factors such as watering regime and light intensity. In his treatment of *Glottiphyllum* Haworth (1821) observed that 'every individual of this section varies in size and gloss, and even in length of peduncle, from being well or poorly fed: and it is only when out of doors, and in unshaded situations, that the true direction of the leaves can be depended on....' The term 'phenotypic plasticity' is often used to describe these responses, but in the Mesembryanthemaceae phenotypic changes do not appear to be fixed during development. The phenotype may change as fast as the environment. Such traits have been termed labile and are physiologically based (Chesselet *et al.* 1995). The poor quality of succulent plant herbarium specimens necessitates the study of living plants. In addition to field studies of plant populations,

[1] A number of important revisions have been undertaken by various authors since 1995 but the reference here serves to illustrate the paucity of taxonomic work on the family.

which are often costly and time-consuming, cultivated plants are usually used for further study. However, in many genera, leaf characteristics such as size, pigmentation and orientation in cultivated plants differ from those of plants grown in their natural habitat. Such drastic changes in cultivation considerably complicate the use of morphological characters in taxonomic studies and emphasize the importance of field observations (Chesselet *et al.* 1995).

The taxonomy of the Mesembryanthemaceae began in 1753 when Linnaeus listed 35 species under the genus *Mesembryanthemum* in his *Species Plantarum* (1753). Sixty-eight years later Haworth described 310 species of Mesembryanthemum in his *Revisiones Plantarum Succulentarum* (1821) but despite his groupings of 69 sections, published only one new genus, *Hymenogyne* Haw.

In 1824 Haworth described *Mesembryanthemum scapigerum* ('the great scaped') in his 'Third Decade of new Succulent Plants' published in the *Philosophical Magazine and Journal* (Haworth 1824). In his letter to the editors Haworth clearly indicates the source of the plant: '...pretty recently discovered in the Cape countries of Southern Africa, by the enterprising zeal of Mr Bowie; and all sent safe to the Royal Gardens of Kew, through his skilful management in the packing and transmittal of succulent seeds and roots.' John Duncanson, a gardener at Kew at the time, was tasked with illustrating newly acquired plants and recently one of his paintings, representing Bowie's plant, was discovered in Kew herbarium (Figure 1). This discovery has allowed for the reassessment of the typification the genus (see taxonomy).

Salm-Dyck also divided the genus *Mesembryanthemum*, together with *Aloe*, into numerous sections in his beautifully illustrated *Monographiae Generum Aloes et Mesembryanthemi* (1836-1863). Here he described *Mesembryanthemum multiceps* (Figure 2) and acknowledges Ecklon from whom the plant was obtained in 1840 and brought into cultivation. *M. scapiger* is also illustrated here (Figure 3) (Salm-Dyck 1854). Unfortunately this work is notorious for lack of structural detail of reproductive organs and misapplied names (Chesselet *et al.* 1995). In 1908 Berger described *Mesembryanthemum vespertinum* from cultivated material in his own garden, La Mortola, and several other gardens where they were incorrectly known as *M. multiceps* (Berger 1908). These three species, grouped together under Mesembrianthemen section Scapigera (Berger 1908) were to become the foundation for *Bergeranthus*.

It was not until 172 years after Linnaeus' (1753) original description that Brown (1925) began assigning species of Mesembryanthemum to various genera. Brown's fundamental distinction between species with axile placentation and those with parietal placentation forms the basis for the separation of the Mesembryanthemaceae into two subfamilies, the Mesembryanthemoideae and Ruschioideae. This discovery encouraged Schwantes (in Germany) and Bolus (in South Africa) to describe new species and genera as prolifically as possible (together with Brown) in what is described by Chesselet *et al.* (1995) as 'the ensuing race to establish genera and describe new species'. Schwantes (1926) described the genus *Bergeranthus* soon afterwards and provided a basic typification of capsules (Schwantes 1952, 1957) and the first supra-generic classification of the group (Schwantes 1960) while Bolus set about describing a total of 1 445 species between 1928 and 1958 (Chesselet *et al.* 1995).

Bolus often named new species after amateur collectors who were encouraged to send material to her from all over South Africa, for example *Bergeranthus leightoniae* and *B. jamesii* are based on single plants sent to her by James Leighton from King William's Town and Henry "Birdie" James from Cradock respectively. Bolus described five of the ten currently recognized species of *Bergeranthus* (as well as *B. cookii, B. firmus, B. glenensis, B. jamesii,* and *B. longisepalus*) from cultivated plants that she had never seen in the wild. Chesselet *et al.* (1995) refer to Bolus' proliferation of species names as the 'Bolusian species concept' and point out that her species concepts have been delimited too narrowly. In this regard Brown (1925) commented: '... species are being described and referred to this or that group or supposed affinity in the most haphazard manner, or are described without any indication of affinity, rendering it almost impossible to identify the species without seeing the type specimen'. This narrow species concept is one of the main causes of the notoriously difficult task of identifying species. Although she has been described as the ultimate splitter, her descriptions of geographical variants are valuable to modern taxonomists (Hammer 1993a). Beautiful drawings and paintings by Mary Page and Beatrice Carter (Figure 4) often accompany her descriptions. The majority of herbarium specimens consulted in this study were those of Mrs Bolus and are housed in the Bolus herbarium in Cape Town (BOL).

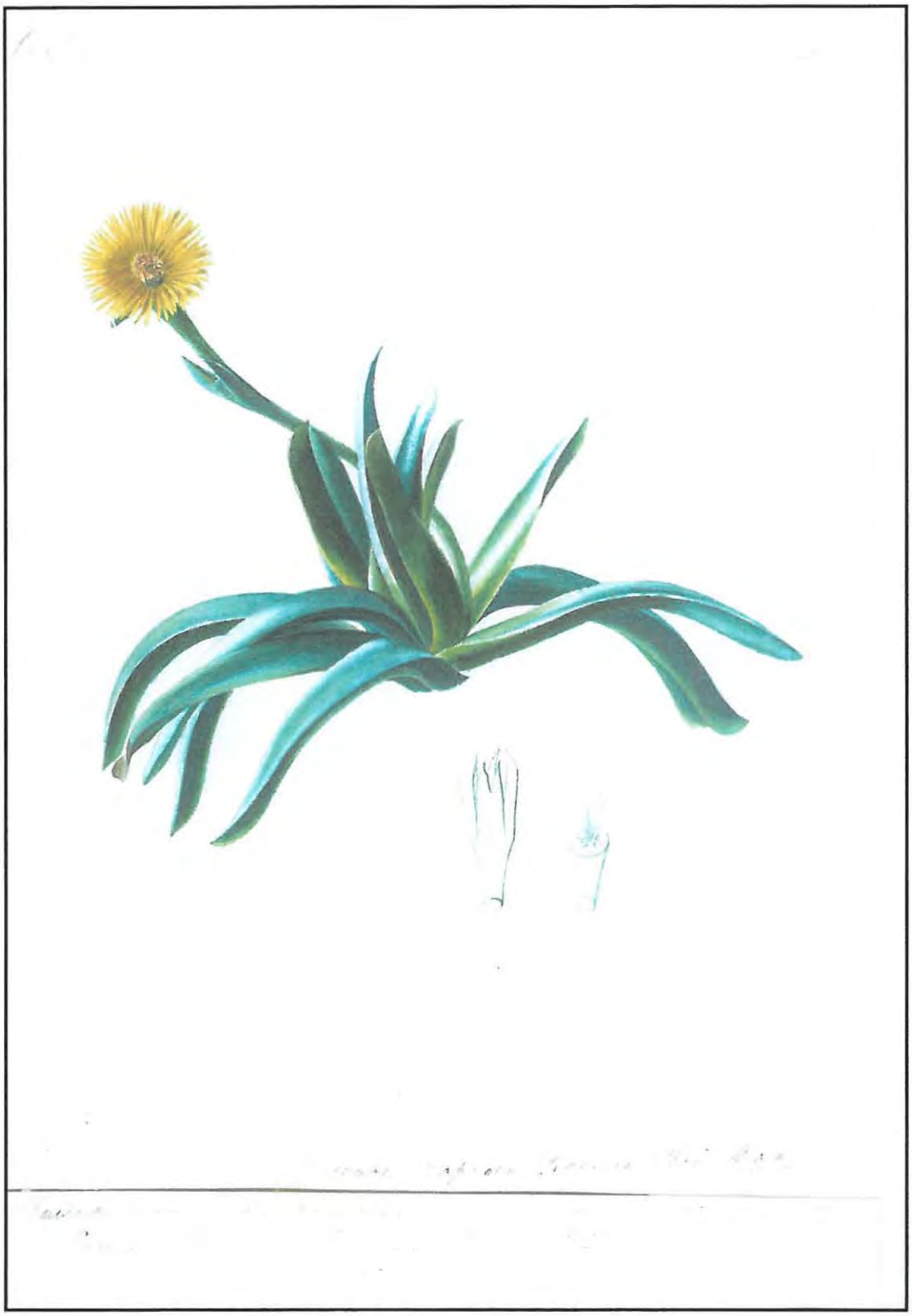

FIGURE 1. —*Mesembryanthemum scapiger* Haw. painted by John Duncanson at Kew, numbered 1006/208, based on material grown from seed collected by Bowie in 1820.

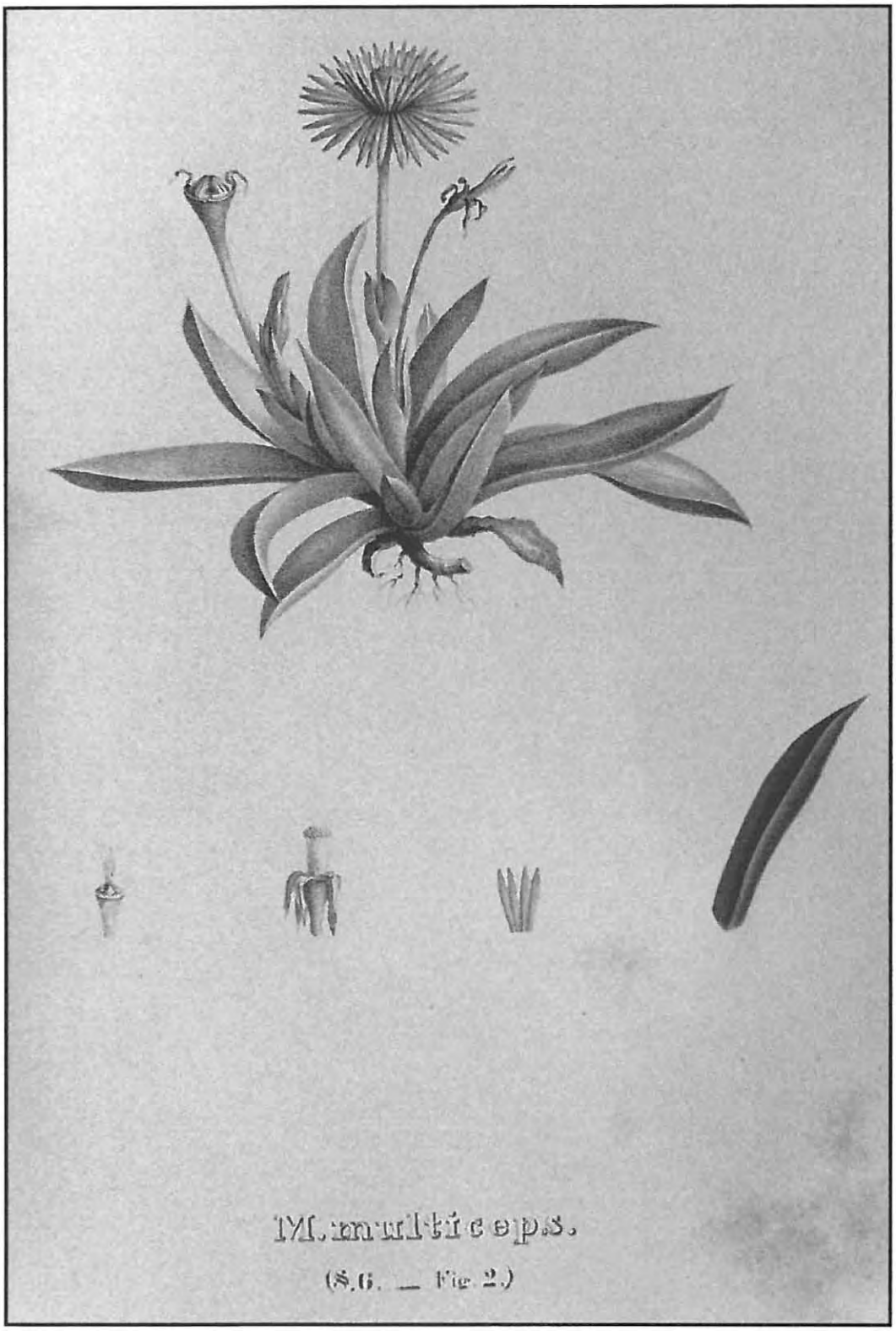

FIGURE 2. —*Mesembryanthemum multiceps* Salm-Dyck drawn by Salm-Dyck in *Monographiae Generum Aloes et Mesembryanthemi*, 1854.

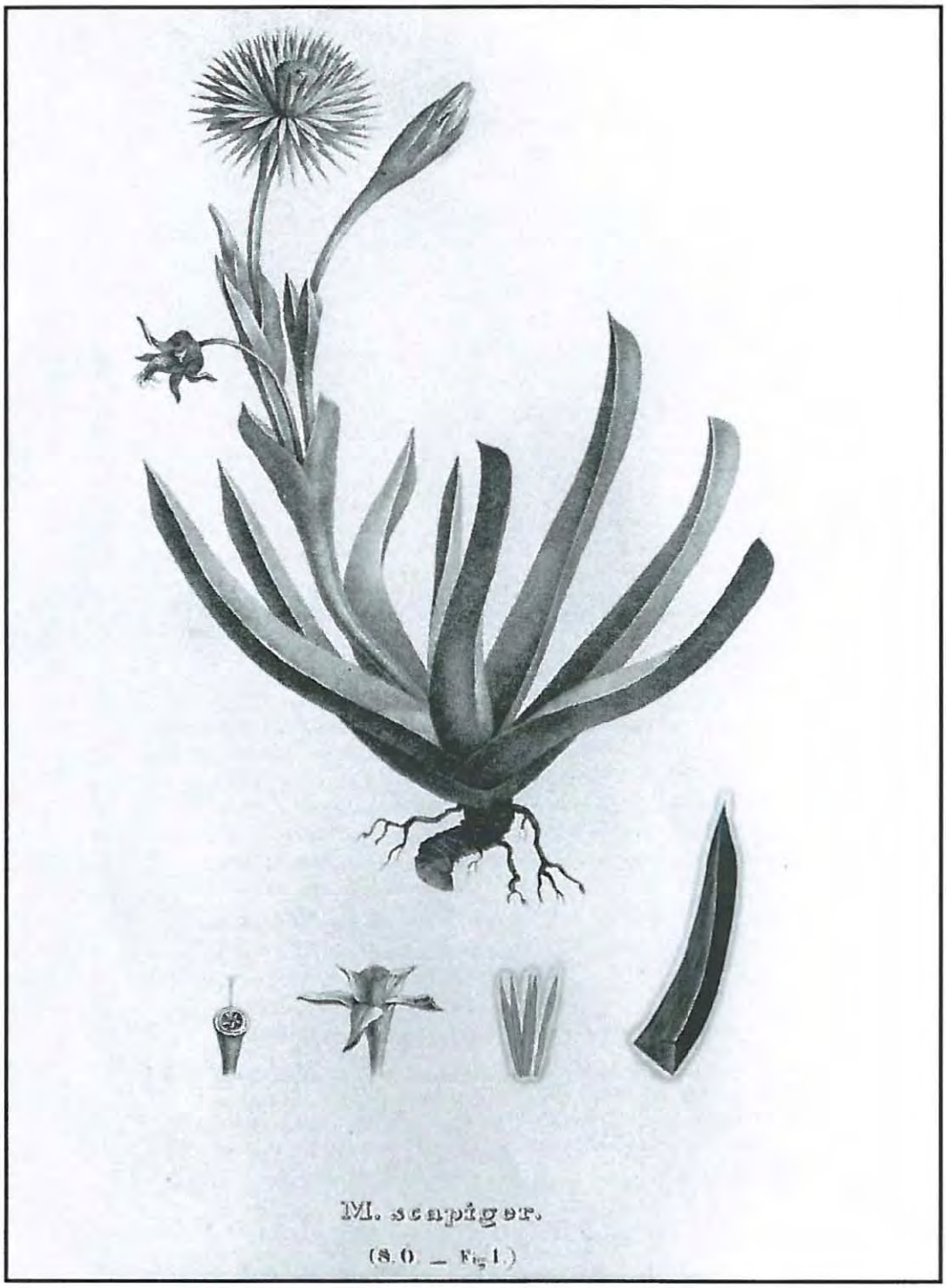

FIGURE 3. —*Mesembryanthemum scapiger* Haw. drawn by Salm-Dyck in *Monographiae Generum Aloes et Mesembryanthemi*, 1854.

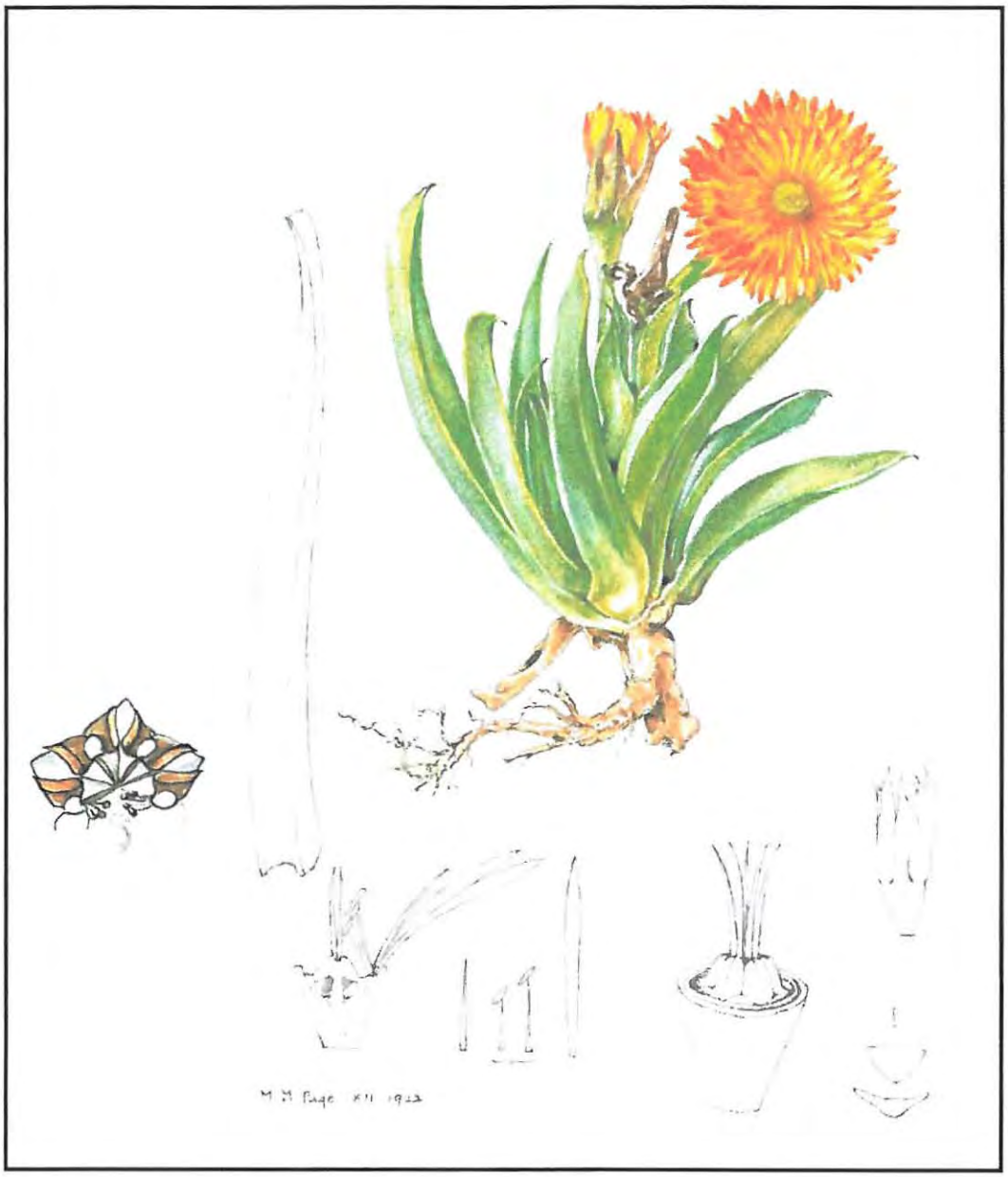

FIGURE 4. —*Bergeranthus scapiger* (Haw.) Schwantes painted by Mary Page in Herre, *The genera of the Mesembryanthemaceae*, 1971.

Since Bolus' time relatively few South African botanists have researched the Mesembryanthemaceae while Hartmann in Germany and Hammer in America have established themselves as leaders in the field. Despite the poor state of taxonomic treatment of the Mesembryanthemaceae reported by Chesselet *et al.* (1995) a renewed interest in the taxonomy and horticulture of the family, with active encouragement form the South African National Botanical Institute, has resulted in many valuable generic revisions (Gerbaulet 1996a, 1996b, 1997; Groen & Van der Maesen 1999; Hartmann & Gölling 1993; Hartmann & Stüber 1993; Hartmann 1992; Klak & Linder 1998; Liede 1989; Wisura & Glen 1993), a novel tribal classification (Chesselet *et al.* 2000b, 2001) and at least four illustrated books (Hammer 1993b, 1999; Smith *et al.* 1998; Van Jaarsveld & De Villiers Pienaar 2000) in the last ten years. *Bergeranthus* however has not been treated since its description in 1926.

Many of these recent revisions, with their much-reduced numbers of species, are based on extensive fieldwork. This is particularly important when dealing with xerophytic taxa where characters are far more variable than previously suspected (Klak & Linder 1998). Fieldwork is therefore essential to establish the extent of variability of characters and detect variability that is a consequence of environmental influences. Herbarium specimens are often inadequate for this interpretation. The current understanding is based on living material, both in wild populations and cultivated material using morphological characters to evaluate species limits within *Bergeranthus* with the aim of a workable taxonomy. The distribution ranges and biology of species are documented. The limits of the genus and its relationships with *Hereroa* and *Rhombophyllum* are investigated. The anatomy, conservation status, ethnobotany, dispersal, phytogeography, and pollination biology are discussed.

MORPHOLOGICAL CHARACTER ASSESSMENT

No taxonomic revision of the genus, or key to the species of *Bergeranthus,* has been undertaken since its description by Schwantes in 1926. Species delimitations are presently based on vegetative characters of, in some cases, a single cultivated plant only, or at best several cultivated plants from the same clone. As a result species descriptions are narrow, and in some cases (*B. artus*) incorrect. Compounding this problem, species seem to merge (i.e. *B. multiceps* and *B. vespertinus*) and are difficult to distinguish in the field. An assessment of 76 macro-and micro-morphological characters of 135 herbarium specimens and 210 living collections of *Bergeranthus* herewith provides a combination of variable characters to delimit species towards a classification of the genus.

Photographs of capsules, ovaries and seedlings were taken in the Rhodes University Electron Microscopy Unit with a Wild M400 Photo Makroskop light microscope using 100 ASA Kodak colour print film. All colour slides of plants in the field were taken with a Canon AE1 SLR camera and a Canon 50 mm 1:3.5 Macro lens (and a series of extension rings: 36 mm, 20 mm & 12 mm where necessary) using *Sensia II*™ ISO100 slide film. Slides were scanned to ± 800 dpi with an Agfa Duoscan scanner.

1. **Species delimitation based on vegetative characters**

In the absence of clear species delimitation for *Bergeranthus* (Smith *et al.* 1998) a phenetic analysis of 36 vegetative characters of 126 living plants[2] was undertaken to provide an initial indication of species boundaries. Of these 14 are binary characters, 18 are multistate characters and four are quantitative characters and are briefly discussed below. The data set is provided in Appendix 2.

1.1. **Number of leaves:** 6–12.

The number of leaves on an adult plant varies from six to 12 with considerable variation in some species but is consistent in others.

[2] The phenetic analysis was undertaken early in the study, hence only ± half of the total number of specimens examined were available.

1.2. **Spreading leaf pairs:** 0 = equal length, 1 = unequal length.

Central leaf pairs are equal in length in most species with the exception of *B. scapiger* and *B. vespertinus* that are unequal in length.

1.3. **Unopened leaf pairs:** 1 = central unopened pair with one cradling the other, 2 = central unopened pair of equal size and position.

Young leaves remain tightly held together while emerging from the centre of the plant, most often with apices of equal length and size but in some species with the apex of one leaf incumbent on, and covering, the apex of the other (Figure 5).

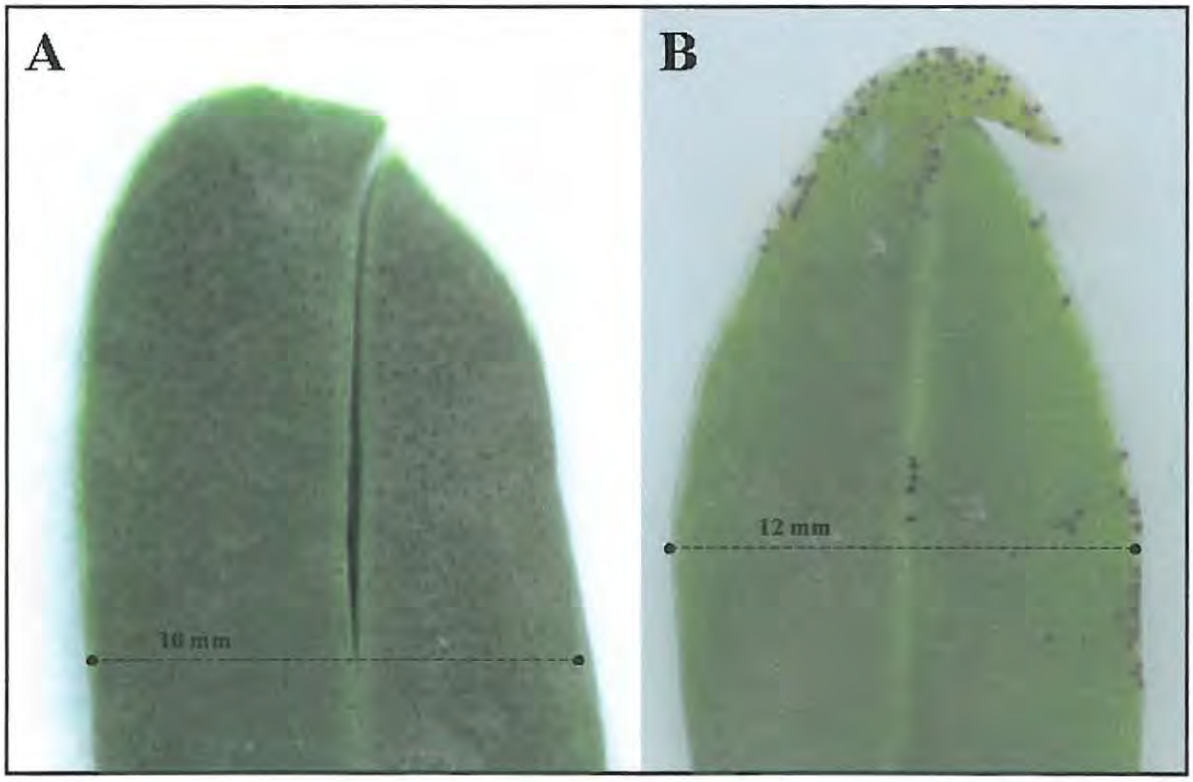

FIGURE 5. —Central *Bergeranthus* leaves "cradling". A. *B. scapiger* (*Dold 4263*), width 10 mm; B. *B. scapiger* (*Dold 4191*), width 12 mm.

1.4. **Leaf shape:** 1 = oblanceolate, 2 = lanceolate, 3 = ovate, 4 = broadly ovate, 5 = linear-lanceolate, 6 = broadly lanceolate.

Six leaf shapes can be described and are illustrated in Figure 6.

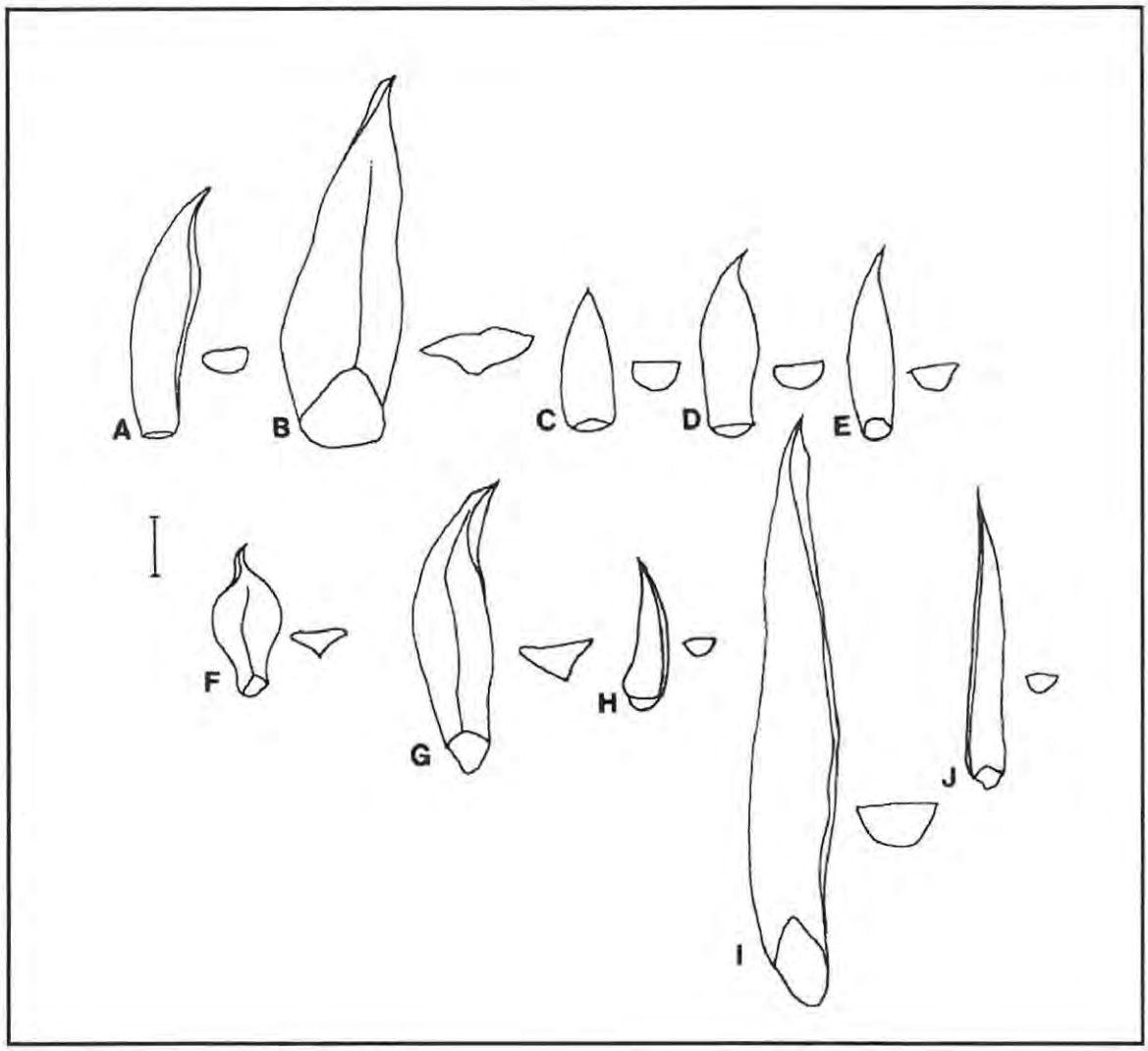

FIGURE 6. —*Bergeranthus* species leaf shapes. A. *B. addoensis* (*Dold 4196*) –oblanceolate; B. *B. albomarginatus* (*Dold 4285*) –ovate; C. *B. artus* (*Dold 4245*) –broadly lanceolate; D. *B. concavus* (*Dold 4251*) –ovate; E. *B. katbergensis* (*Dold 4248*) –lanceolate; F. *B. leightoniae* (*Dold 4232*) –ovate; G. *B. multiceps* (*Dold 4186*) –broadly lanceolate; H. *B. nanus* (*Dold 4271*) –lanceolate; I. *B. scapiger* (*Dold 4202*) –lanceolate, J. *B. vespertinus* (*Dold 4322*) –linear lanceolate. —Cross-section shapes. B –flattened dorsally; F, G – "V"-shaped; A, C, D, E, H, I, J – "D"-shaped. Scale bar 10 mm.

1.5. **Central pair of leaves:** 0 = erect, 1 = spreading, 2 = declinate, 3 = recurved.
The central leaf pair separates when almost fully grown and remains erect or becomes spreading, declinate or recurved when fully developed.

1.6. **Outermost pair of leaves:** 0 = erect, 1 = spreading, 2 = decumbent, 3 = recurved.

The outermost (oldest) pair of leaves may remain erect or become spreading, decumbent or recurved.

1.7. **Leaf curving:** 0 = inwards (falcate), 1 = curving outwards, 2 = not curving, 3 = curving outwards and back "S" shaped, 4 = reflexed.

Fully developed leaves may curve inwards (falcate), outwards, outwards and back in an "S" shape, curve sharply downwards (reflexed) or not curve at all.

1.8. **Leaf colour:** 0 = dark green, 1 = pale yellow-green, 2 = yellow-green, 3 = blue-green, 4 = grey-green, 5 = lime-green 6 = pale whitish green.

1.9. **Leaf surface:** 0 = matt, 1 = glossy.

1.10. **Leaf surface:** 0 = waxy, 1 = with a bloom, 2 = smooth, 3 = rugose.

1.11. **Leaf surface:** 0 = turgid (swollen from fullness), 1 = rugose, 2 = defined raised dots, 3 = smooth/unmarked, 4 = noticeable darker green-black flecks (not raised), 5 = noticeable maroon flecks (not raised).

1.12. **Leaf texture:** leaves may be described as 1 = succulent (turgid-swollen), 2 = fleshy 3 = leathery.

1.13. **Leaf pliability:** 0 = brittle, 1 = pliable.

Leaves may be brittle when bent, breaking easily, or pliable.

1.14. **Leaf length** (average of 4 leaves per plant): 11–100 mm.

1.15. **Broadest part of leaf:** 0 = base, 1 = middle, 2 = above middle.

Species can be distinguished by having leaves that are broadest at the base, at the middle or above the middle of the blade.

1.16. **Broadest part of leaf** (average of 4 leaves per plant): 4–22 mm.

1.17. **Cross-section height at thickest part** (average of 4 leaves per plant): 2–10 mm.

1.18. **Cross-section thickest at:** 0 = base, 1 = middle, 2 = above middle.

The cross section of the leaf from keel to upper surface can be thickest at the base of leaf (proximally), the middle of leaf or above the middle of leaf (distally).

1.19. **Margins** may be: 1 = inconspicuous, 2 = thickened (± cartilaginous), 3 = with a dense concentration of epidermal cells.

1.20. **Margin angle:** 0 = acute, 1 = rounded.

1.21. **Margin colour:** 0 = whitish, 1 = darker green than the leaf, 2 = the same colour as the leaf, 3 = tinged reddish in colour.

1.22. **Keel:** 0 = extending the entire length, 1 = distal half only.

1.23. **Keel texture:** 0 = inconspicuous, 1 = thickened (± cartilaginous).

1.24. **Keel angle:** 0 = acute, 1 = rounded.

1.25. **Distal keel:** 0 = "chinned", 1 = not "chinned" (Figure 7A).

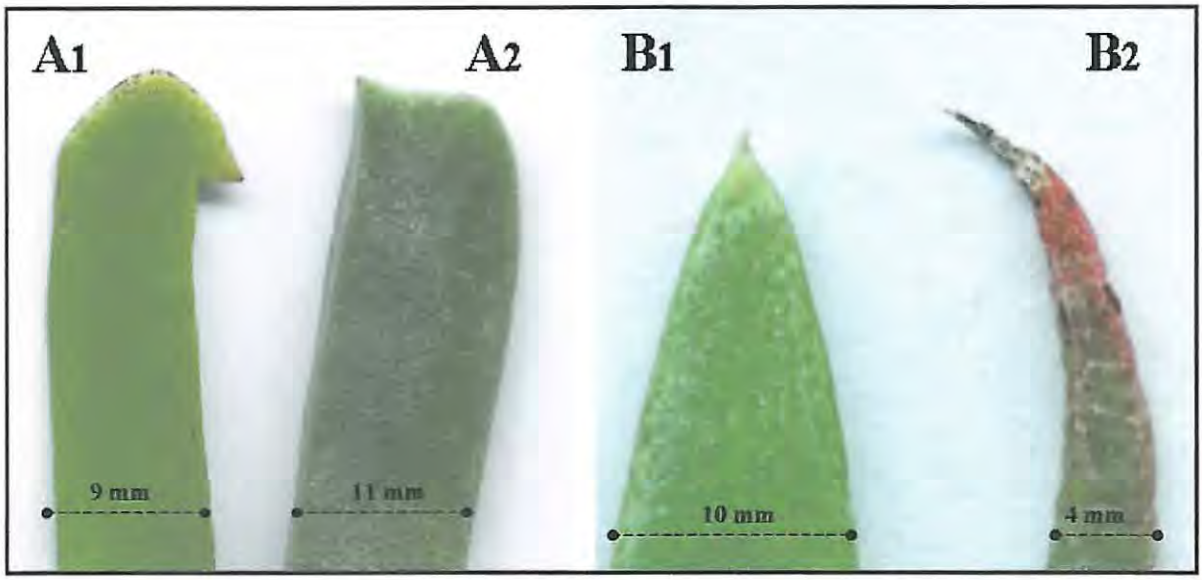

FIGURE 7. —*Bergeranthus* leaf characters. A1. Leaf distally "chinned" (*B. scapiger, Dold 4296*), width 9 mm; A2. Leaf distally "chinned" (*B. scapiger, Dold 4263*), width 11 mm; B1. Apex mucronate (*B. artus, Dold 4245*), width 10 mm; B2. Apex aristate (*B. vespertinus, Dold 4260*), width 4 mm.

1.26. **Apices:** 0 = acuminate, 1 = shortly acute, 2 = acute (drawn out), 3 = obtuse.

1.27. **Apices:** 0 = inwardly hooked, 1 = outwardly hooked, 2 = straight.

1.28. **Apices:** 0 = mucronate, 1 = without an awn or seta, 2 = aristate (Figure 7B).

1.29. **Leaf cross-section:** 0 = flattened dorsally (top to bottom), 1 = triangular ("V"-shaped), 2 = "D"-shaped, 3 = broadly/shallowly "D"-shaped (Figure 6).

1.30. **Central leaf tissue** (without magnification)**:** 1 = with a conspicuous central vascular bundle, 2 = without a conspicuous central vascular bundle.

1.31. **Upper surface:** 0 = flat, 1 = concave, 2 = convex, 3 = broadly "V"-shaped.

1.32. **Leaf base:** 0 = truncate, 1 = tapering abruptly, 2 = tapering gradually.

1.33. **Leaf tips:** 1 = tinged reddish, 2 = not tinged reddish.

Although the degree of reddish tinge is seasonally stress related it is unmistakable in certain species but never occurs in other species.

1.34. **Lower basal leaf surface:** 0 = pustulate (blistered), 1 = not pustulate.

Occurring in only two species (*B. katbergensis* & *B. multiceps*) but inconsistently.

1.35. **Older leaf colour:** 0 = becoming pale (as a result of minute whitish dots) with age, 1 = not becoming pale (whitish) with age.

Occurring in a single species (*B. katbergensis*) but age related developing in older leaves.

1.36. **Leaf twist:** 0 = twisted, 1 = not twisted.

Occurring in *B. addoensis* only, in older (outer) leaves but inconsistently.

2. **Phenetic analysis of vegetative characters**

The data set for the phenetic analysis was constructed in an Excel™ spreadsheet and imported into NTSYS-pc™ version 2.02k. A triangular matrix of similarity was constructed using the Simple Matching co-efficient, and a phenogram constructed from this using the UPGMA (Unweighted Pair Group Method using Arithmetic averages) algorithm. This analysis, represented by means of a phenogram graphically displayed using the GRAPHICS TREEPLOT option in NTSYS™ (Figure 8) clearly groups the plants examined into assemblages that coincide with current species concepts and thereby provides a basis from which to delimit existing species and describe new species. *Bergeranthus addoensis* is represented by six specimens, *B. concavus* by six specimens, *B. katbergensis* by 23 specimens, *B. leightoniae* by 12 specimens and *B. scapiger* by 22 specimens. Species names were allocated based on type specimens, descriptions and illustrations. Two species however, *B. multiceps* and *B. vespertinus*, represented by 51 specimens together, are not clearly distinguished in the phenogram and are grouped with some overlap that confirms the difficulty in separating these two species in the field (i.e. based on vegetative characters alone). This is elaborated on in the section on taxonomic treatment. Two distinct groups that do not conform to known species concepts are described as *B. albomarginatus*, represented by two specimens, and B. *nanus*, represented by a single specimen, in this revision (see taxonomic treatment). Although this result is based on vegetative morphology alone additional morphological characters (see 2.1 macro-morphology and 2.2 micro-morphology) have been used to confirm and clarify the taxa recognized by the phenetic analysis.

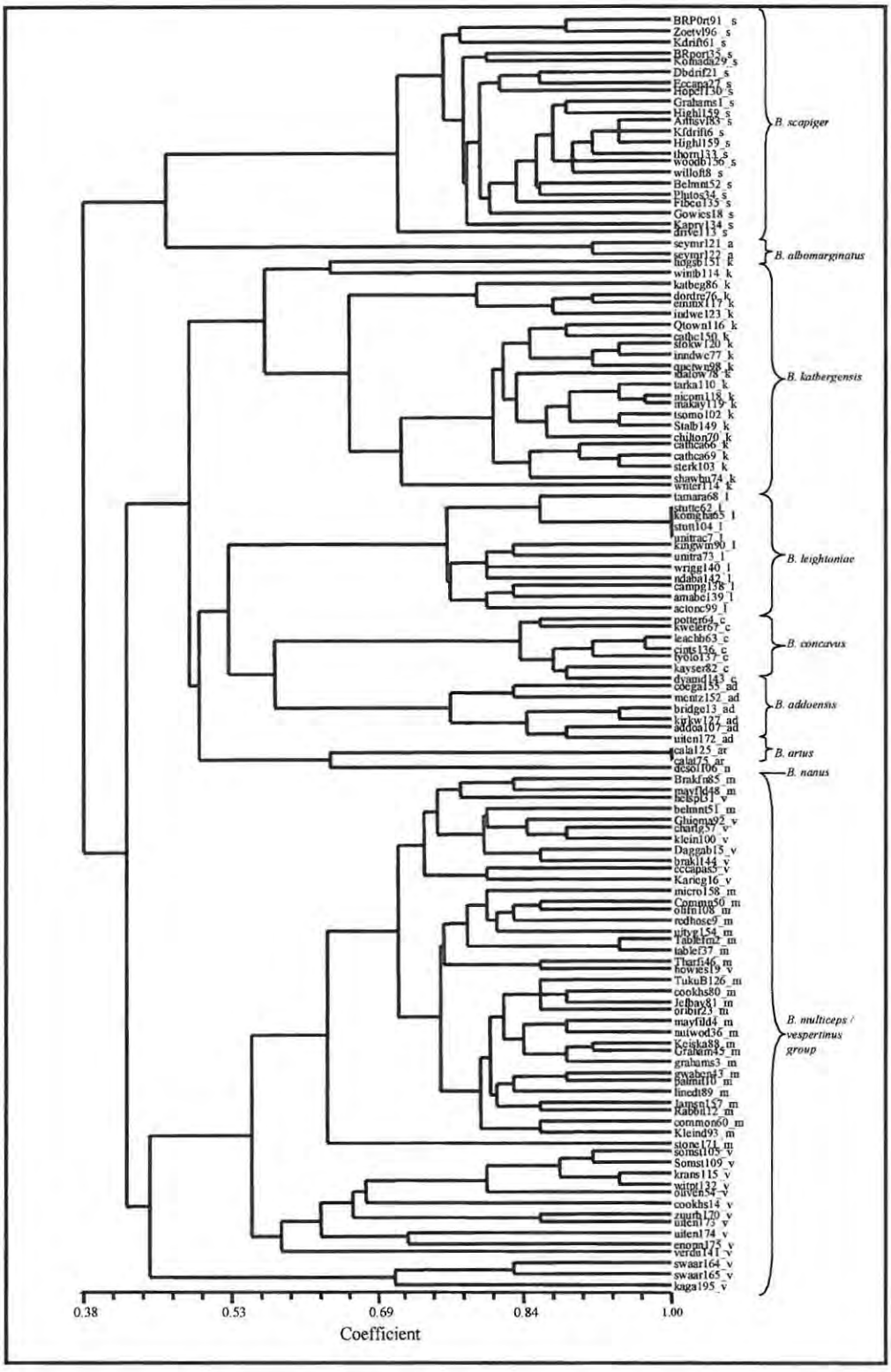

FIGURE 8. —Phenetic representation of vegetative characters of *Bergeranthus* species.

3. **Species delimitation—the search for additional characters**

Further investigation of vegetative, floral, capsule, seed and seedling characters was undertaken at both macro- and micro- level to help distinguish and describe taxa identified in the phenetic analysis based on vegetative characters. An additional 84 living collections were available for this assessment and together with 135 herbarium specimens (B, BLFU, BOL, G, GRA, K, MO, NBG, PEU, PRE, TCD, UFH & WAG listed in Appendix 1) a total of 345 specimens were examined. These characters are discussed and clarified individually and although not all characters proved useful they are included here for completeness sake.

3.1. **Macro-morphology**

3.1.1. **Rootstock:** *Bergeranthus* has a unique rhizomatous root formation that serves as a storage system. Immediately below the above-ground parts of the plant is a thickened woody taproot and numerous spreading fibrous roots. The single taproot develops a smooth, woody, flattened lateral body on one side from which new vegetative parts may arise (Figure 9). Three-year-old seedlings show no sign of this formation and it is clear that it is age related. Although this character has been used for generic delimitation (Herre & Volk 1971) it is not useful at species level. The term "woody rootstock" may be interpreted as "woody stem" and may lead to a misinterpretation and according to Hartmann (1991a) a clarification of the terminology is needed. Bittrich & Struck (1989) report that thickened storage roots such as found in *Phyllobolus* N.E.Br. and *Trichodiadema* Schwantes represent at higher level of organization and are therefore derived. This interpretation may be applied to *Bergeranthus* with its well-developed rhizomatous rootstock.

FIGURE 9. —*Bergeranthus* rootstock. *B. multiceps* (*Dold 4186*). Scale bar 100 mm.

3.1.2. **Inflorescence:** The cymose inflorescence may be branched or unbranched, is taller than the vegetative parts, and is strongly persistent in some species. The pedicel and peduncle are considerably flattened ("two-edged" *sensu* Hartmann pers. comm. 2000). The bracts and bracteoles are large and leaf-like (Figure 10A). Inflorescence characters vary considerably between and within species and are not considered taxonomically useful.

3.1.3. **Flowers:** *Bergeranthus* flowers are protandrous, melittophilous flowers (Figure10B) that are classified by Hartmann (1991a) as Stamen Carpet Flowers when in their female state but as Central Cone Flowers when in their male state. However, *B. artus* retains its cone-like arrangement of stamens throughout and falls clearly within Hartmann's Central Cone Flower classification. Flowers are mostly diurnal and scentless with the exception of *B. artus* that is nocturnal and has a sweet lemon scented flower, these unique characters are therefore useful when considering this species. Some species open characteristically earlier in the day than

others, this being a taxonomically useful character. Flower opening is dependant on, and controlled by, weather conditions and open only in dry, warm weather. It has been established that pollen fertility is negatively affected through contact with water and flowers do not open in wet conditions or high humidity (see pollination biology).

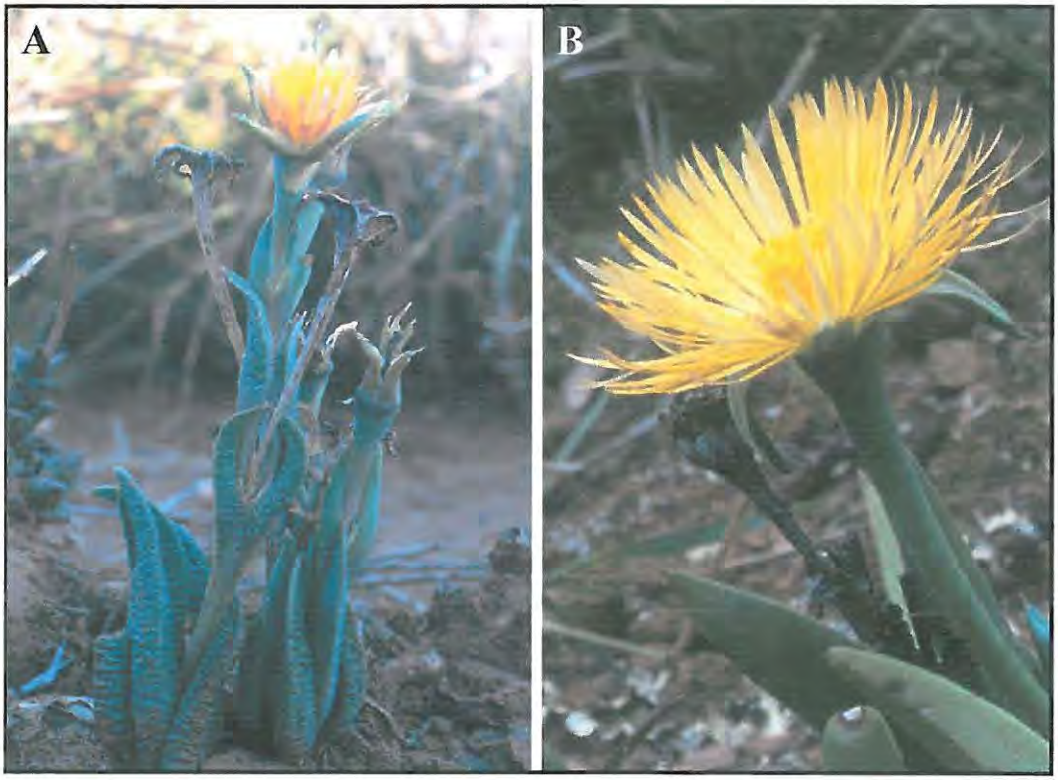

FIGURE 10. —*Bergeranthus* flowers. A. *Bergeranthus vespertinus* (*Dold 4212*), a cymose inflorescence with flattened peduncle and leaf-like bracts; B. *Bergeranthus scapiger* (*Dold 4262)*, protandrous, melittophilous flower.

3.1.4. **Calyx:** Sepal length varies from 6–17 mm and width (basal) from 2–7 mm. Margins are transparently broadly or narrowly membranous winged (Figure 11a, 11b). Sepals are rounded or indistinctly keeled at the distal ends only and may have a small dorsal apiculus on the lower distal keel that sometimes extends beyond the sepal apex (Figure 11c). Inner and outer sepals are equal in length; outer sepals are only slightly broader than inner.

Sepals control the opening and closing of the flower by means of applying pressure against the petals. If the sepals are removed the petals open immediately. The presence or absence of a dorsal apiculus on the calyx lobe is of taxonomic importance at species level.

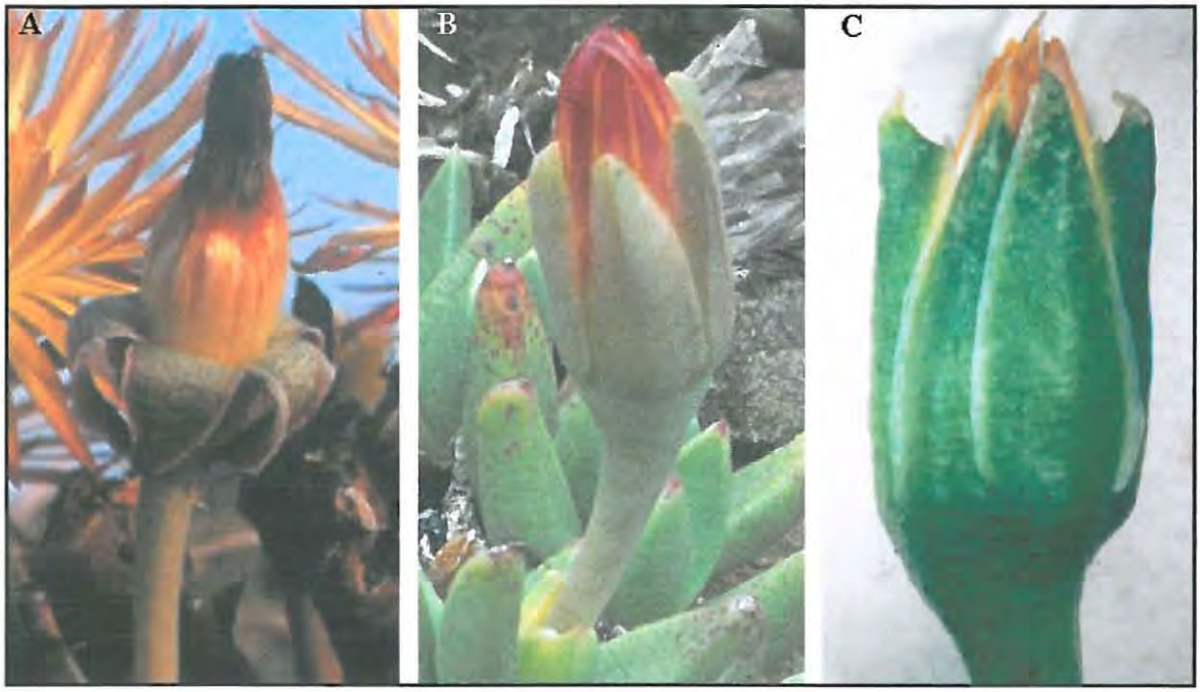

FIGURE 11. —Sepals of *Bergeranthus* species. A. *B. multiceps* (*Dold 4186*), broadly winged margin of sepals of open flower; B. *B. artus* (*Dold 4245*), narrowly winged margin of sepals without a dorsal apiculus on closed flower; C. *B. leightoniae* (*Dold 4232*), dorsal apiculus protruding beyond apex of sepal.

3.1.5. **Petals:** Petals are two to three seriate and the number of petals per flower varies from 50–316 (Figure 12). The outermost (fully developed) petals may be described as linear-acute, oblanceolate or lanceolate and vary in length from 7–26 mm (Figure 13) and in width from 1–3 mm. Petals are yellow becoming orange or red tinged below with age. Apices are acute, occasionally emarginate. Outer petals are spreading in most species with the exception of *B. artus* where they are reflexed partially obscuring the calyx. Some differences between the species occur in the number of petals per flower (Figure 12). Petal number is not considered a useful taxonomic character.

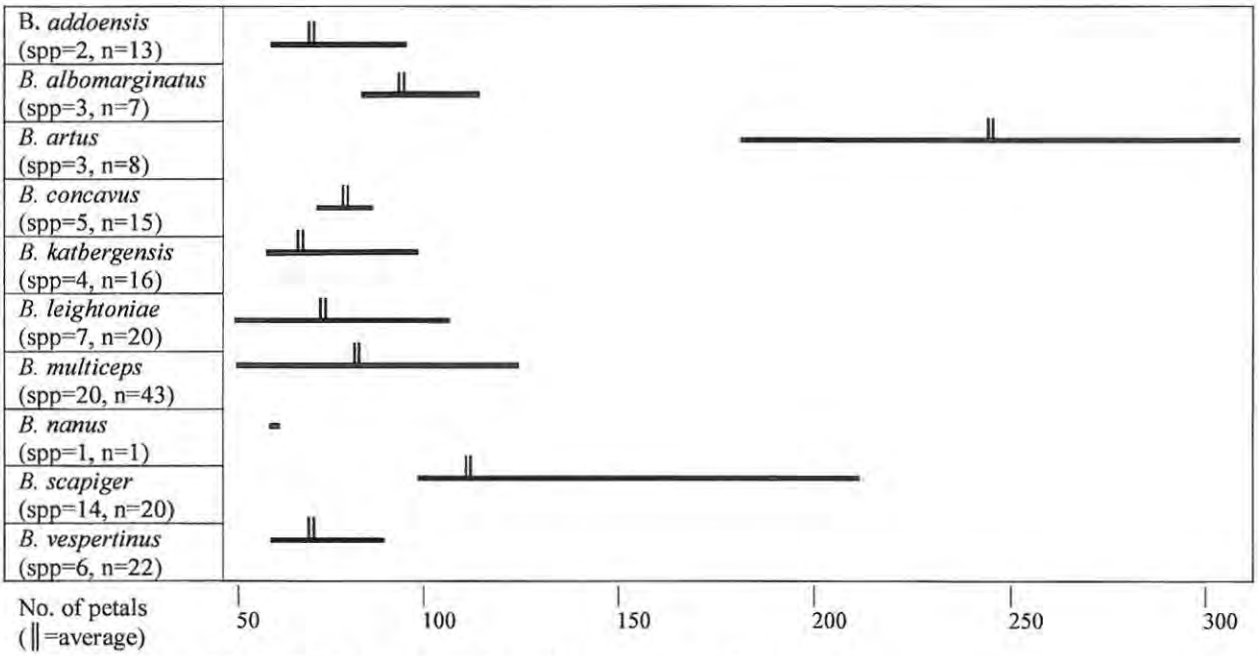

FIGURE 12. —Variation in number of petals of *Bergeranthus* species.

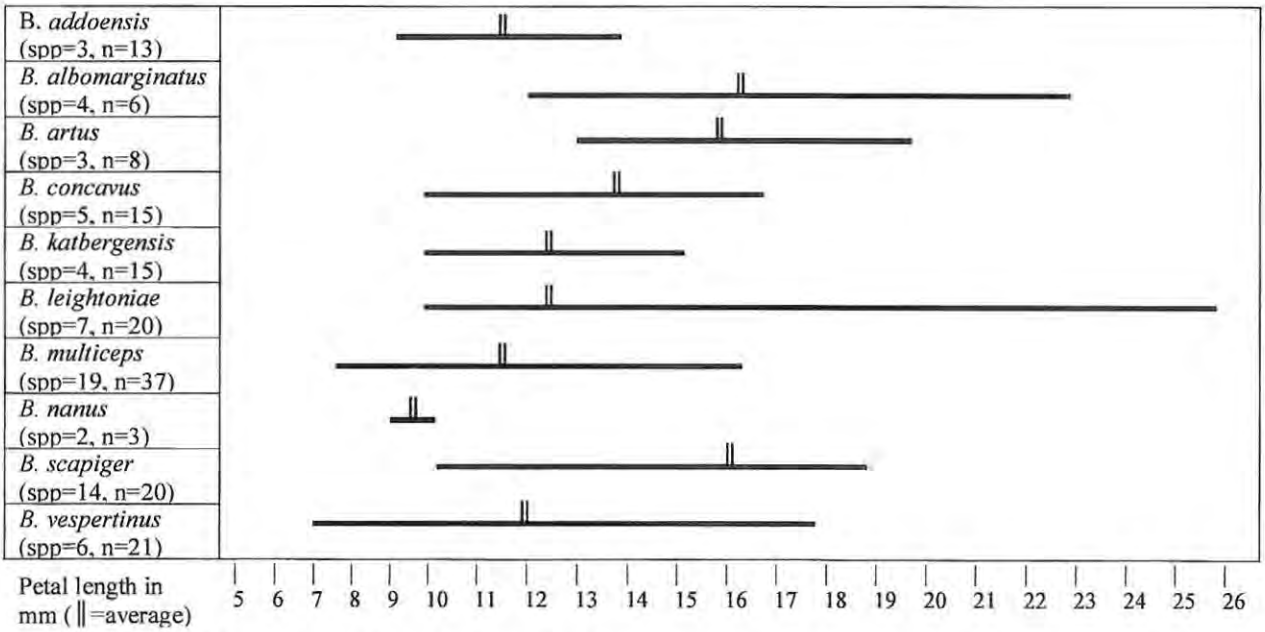

FIGURE 13. —Variation in length of petals of *Bergeranthus* species.

3.1.6. **Stamens:** These vary in number from 94–460 and filaments vary from 3–12 mm in length. In the majority of species filaments vary from 3–9 mm in length. *B. artus* is an exception that varies from 5–12 mm in length. Filament length is not considered a useful character.

Stamens are three to four seriate and develop centripetally therefore only mature outer filament length was measured. The number of stamens per species is variable and overlaps thus reducing the value of stamen number as a taxonomic character (Figure 14). *B. artus* has an exceptionally high number of stamens. Stamens are mostly arranged in a solid brush-like column with the exception of *B. artus* that is arranged in a distinct ring-like erect cylinder (Figure 15A). This character is shared with *Hereroa granulata*, also a nocturnal flowering species, and is most likely a function of pollination.

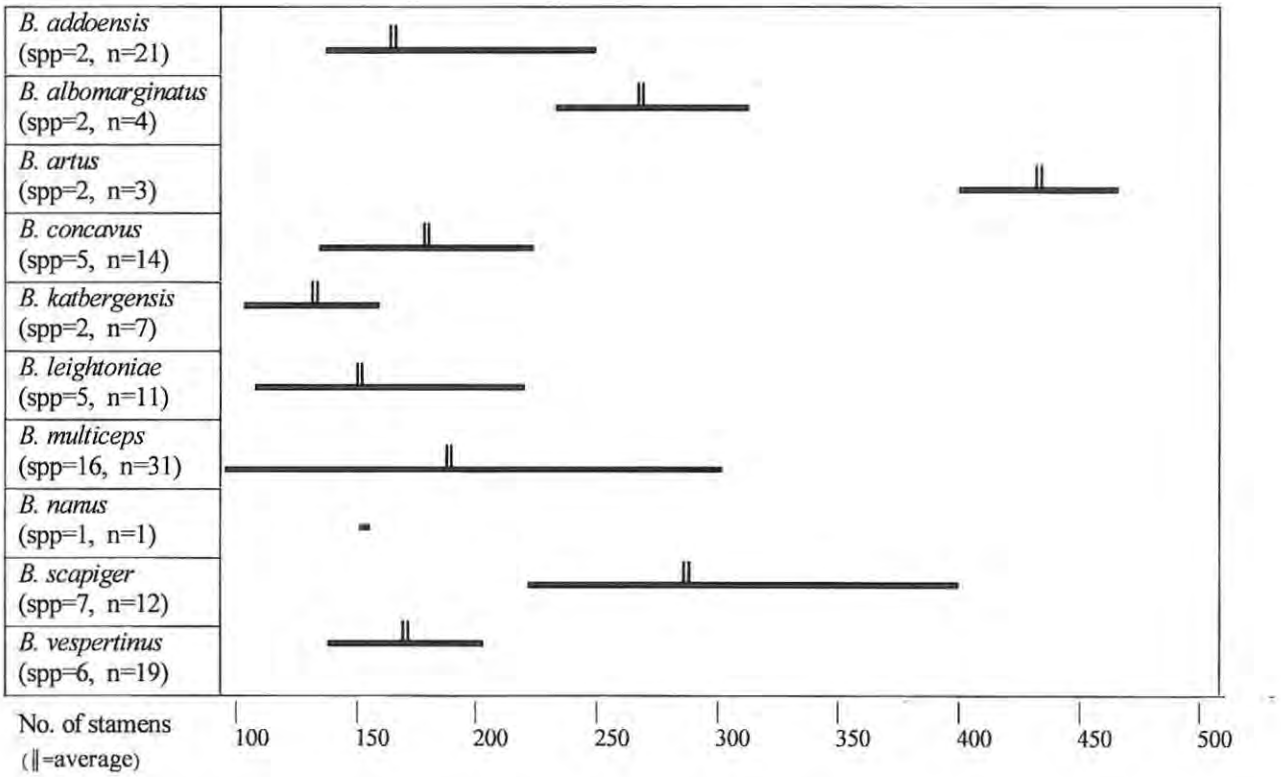

FIGURE 14. —Variation in number of stamens of *Bergeranthus* species.

3.1.7. **Filament vesture:** Filaments may be glabrous or basally (sparsely) white lanulose on the inner surface of the central series only (Figure 15B2). This character is of limited taxonomic value as vesture develops with age. Hartmann (1991a) reports that most genera in the Ruschioideae possess papillae on the base of androecial elements but does not report the presence of hairs. Bittrich & Struck (1989) interpret glabrous filaments as a primitive state and those clad with hairs at the base as derived.

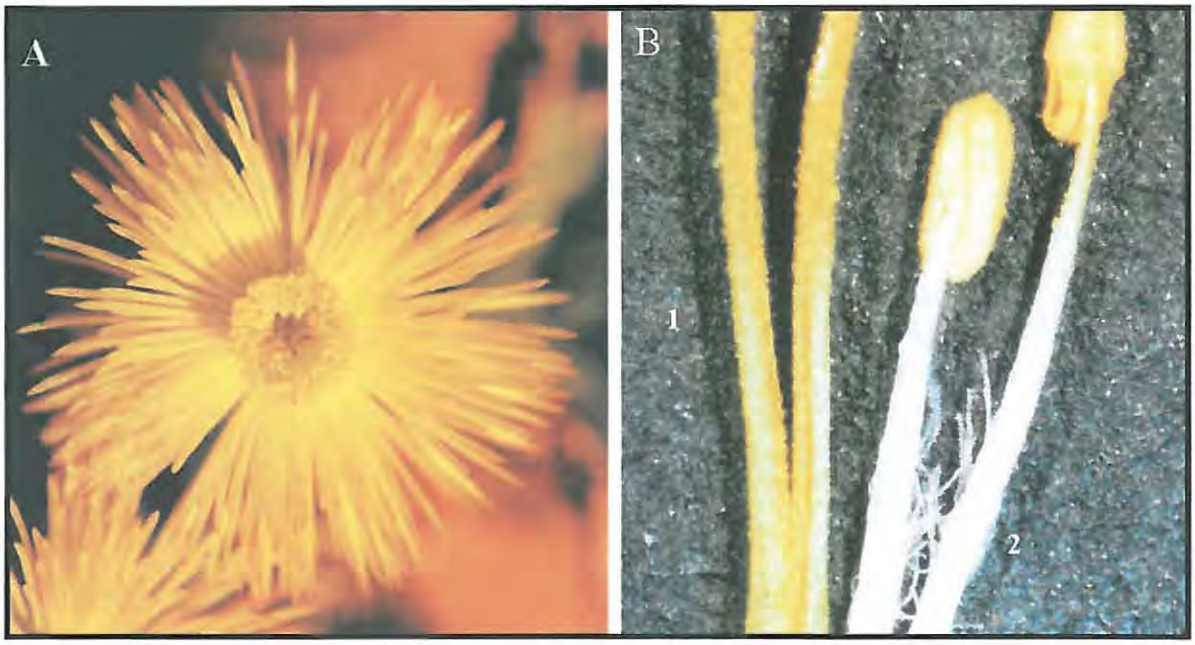

FIGURE 15. —Floral parts of *Bergeranthus* species. A. *B. artus* (*Dold 4245*), stamens arranged in an erect cylinder with ovary and stigmata visible; B. *B. albomarginatus* (*Dold 3943*), 1 = papillate stigmata, 2 = central series of filaments sparsely white antrose-lanulose on inner surface.

3.1.8. **Stigma shape and vesture:** The linear stigmata may be basally glabrous, papillate or sparsely puberulous (Figure 15B1, 16Ae). The young stigmata are erect and loosely cohering in the male stage (Figure 16Ae) that is later followed by the female stage where the stigmata separate and spread to ± 45° and the apices eventually recurve. Stigma vesture may be of taxonomic value although further study is needed to clarify this. It has been established that the tip of the stigma not only spreads and later recurves with age but that the tip swells to form a globose head with age. It is therefore possible that the basal vesture may also be age related.

3.1.9. **Ovary shape and diameter:** The upper portion of the ovary is raised to form a slight cone (Lockyer 1932) (Figure 16Aa & 16B). This character is of taxonomic importance at a generic level only. The diameter of the top surface of the ovary varies within species from 2–7 mm. This character is not of taxonomic value.

3.1.10. **Ovary septa:** The septa of the ovary are raised and distinctly marked where the valve margin will develop on the capsule (Figure 16Bb). These characters of the septa are of

taxonomic importance at a generic level (see section on relationships with other genera) but not at a specific level in *Bergeranthus.*

3.1.11. **Floral nectary:** The nectaries of all species of *Bergeranthus* are lophomorphic meronectaries (Chesselet *et al.* 2000) (Figure 16Ba) and are morphologically identical, *B. nanus* however, has green nectaries while all other species have yellow nectaries. Nectaries are of taxonomic importance only at a generic level. Bittrich & Struck (1989) interpret lophomorphic nectaries as an advanced condition within the Mesembryanthemaceae while the meronectary is regarded as primitive.

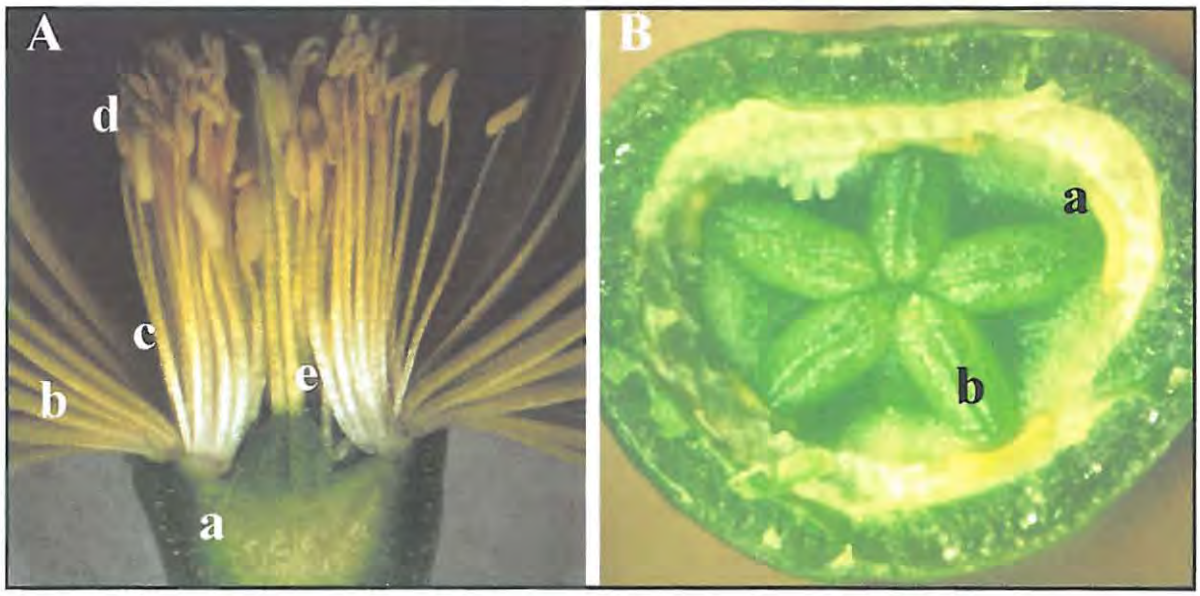

FIGURE 16. —*Bergeranthus* flowers. A. *Bergeranthus scapiger* (*Dold 4262*), longitudinal section of flower showing a = ovary, b = petals, c = stamens, d = anthers, e = stigmata (Ovary 5 mm diameter including hypanthium); B. *B. scapiger* (*Dold 4213*), top of ovary with floral parts removed showing a = nectaries, b = septa (5 mm diameter including hypanthium).

3.1.12. **Fruit:** Loculicidal hygrochastic capsules are considered characteristic of Mesembryanthemaceae (Hartmann 1991a; Croizat 1993). They open repeatedly when moistened and close again on drying. The morphology of the fruit is related to the dispersal mechanism, namely hygroscopic opening of the capsule and subsequent rain mediated ballistic expulsion of the seeds termed ombrohydrochory (Hartmann 1988a, 1991a; Rawe 1975). Four dispersal mechanisms are described by Hartmann (1991a) of which *ejection dispersal* applies to *Bergeranthus* that possesses both the prerequisite covering membrane and closing body. Hartmann (1988a) classifies nine fruit types in the Mesembryanthema based on morphology, and provisionally places *Bergeranthus sensu* Schwantes (1952), including *Rhombophyllum*, in the *Mitrophyllum* group based on similarities of the closing body but suggests that their possession of stout covering membranes is contradictory to the hypothesis. Furthermore, the absence of broad valve wings in *Bergeranthus* noted in this study suggests that a further category is needed. The anatomy of the hygroscopic tissue, closing body and covering membranes of *Bergeranthus* is described by Lockyer (1932).

Some differences in capsule morphology occur between species of *Bergeranthus* (Figure 17) but these should not be solely relied on and should be used in combination with various macro- and micro- morphological characters provided herewith. Capsule morphology is nevertheless an important taxonomic character. The following capsule components were examined:

3.1.13. **Capsule diameter:** The diameter of *Bergeranthus* capsules varies from 6–15 mm. This character is not of taxonomic importance as capsule size varies considerably within species. Fertile capsules, less than half the largest size recorded on the same plant, may develop and produce viable seed. The reason for this not understood.

3.1.14. **Capsule length:** The length of *Bergeranthus* capsules varies from 3–11 mm. Measurements were taken from the first swelling of the pedicel to the valve rims allowing for considerable variation within and between species. This character is of no taxonomic importance.

3.1.15. **Closing body shape:** Previously referred to as the placental tubercle (Huber 1924, Lockyer 1932, Herre 1971), the closing body (Hartmann 1988a) is a large endocarpal protrusion at the distal end of the locule shaped like a sill in longitudinal section, often reaching under the covering membrane into the locule (Figure 19Bb), ± flat on top, pale yellowish–white. The

upper exposed surface of the closing body varies in shape from globose to pyriform and may have a distal nipple-like protrusion[3] that may be divided by a central shallow groove on the upper surface (Figure 18e). The function of the closing body is to block the distal end of the capsule thereby controlling seed dispersal (Figure 19Ba). This character is taxonomically important.

3.1.16. **Covering membrane:** The covering membranes (Hartmann 1988a) (superlocular wings of Lockyer, 1932; cell wings described by Brown, 1921) are large, rigid, semi-transparent sheets covering and closing the top of each locule thereby holding the seeds within (Figure 18d). Hartmann (1988a) broadly describes three main types of covering membrane in the Mesembryanthema and relates them to different forms of expanding tissue. It appears that *Bergeranthus* falls into the group that possess what are described as compound, translucent covering membranes, however they are incorrectly described as vertical but correctly illustrated as horizontal. The distal free margin of the covering membrane of *Bergeranthus*, together with that of the adjoining membrane, may form a deep or shallow "V"-shaped pair that may be incised at the sinus or not, but this character is not of taxonomic importance as it is not consistent. The presence or absence of a covering membrane is a useful character at generic level.

3.1.17. **Expanding sheet:** The hygroscopic expanding tissue responsible for the opening and closing of the fruit comprises an expanding sheet (hygroscopic skin described by Lockyer, 1932) (Figure 18b), attached to the outer lower walls of the valve, and an expanding keel which is an elevated, thickened ridge (Figure 18c). The expanding sheet may be thickened or reduced, narrow or broad, pale yellowish to dark brown, being variable and is therefore not a useful character.

3.1.18. **Expanding keel:** An extension of the expanding sheet, the expanding keel of *Bergeranthus* is termed divergent (Schwantes 1952; Hartmann 1988a). The expanding keel may be short, not exceeding the valve, or exceeding the valve with a long attenuate apex; may be broad or narrow, straight or distally incurved and the outer margin may be serrate or entire. Although colour varies considerably this character is age related.

[3] Closing body morphology has not been described in detail and terminology is therefore limited and no formal convention is available.

Newly formed capsules reveal deep orange or reddish–brown expanding keels that later fade to a dull or semi-transparent yellowish colour. The morphology of the expanding keel is of taxonomic importance (Figure 18c).

3.1.19. **Valve:** The five carpels of the mature fruit split to form five valves that rest over the septa (Figure 18a, 19Aa). These valves are triangular in shape and are not winged. Although slight differences occur in the degree of the distal angle this character is not considered taxonomically useful.

3.1.20. **Valve rim:** the margins of the valves are turned sharply outwards and seen on a closed capsule are termed rims (Hartmann 1991a). The rims allow the entry of water, usually in the form of a raindrop, to enter the capsule and wet the expanding tissue to facilitate opening (Lockyer 1932), and allow for the complete dehydration of the tissue in closing. The degree to which the rims are held outwards (Figure 19Aa) varies greatly even on the same inflorescence and is not taxonomically useful.

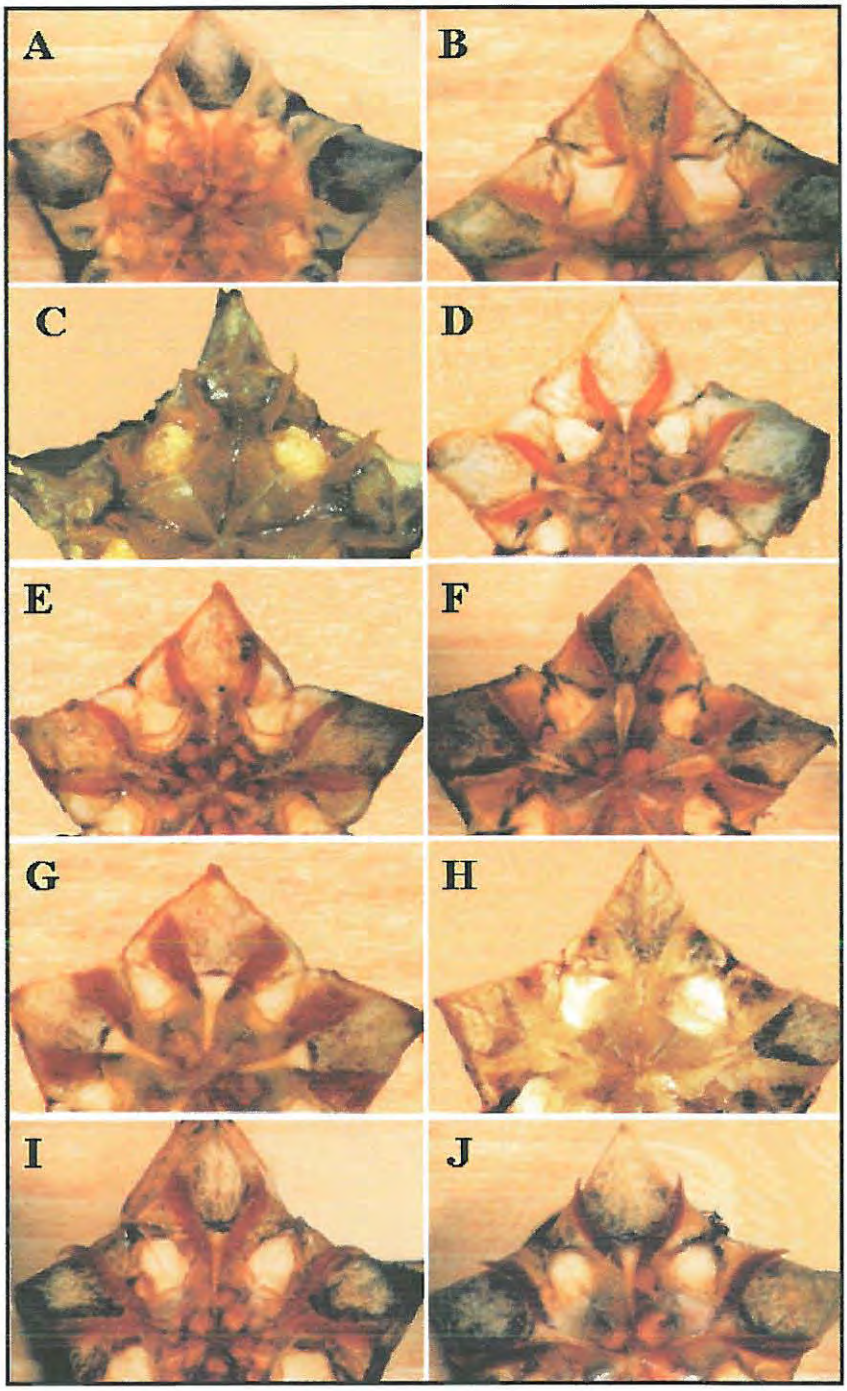

FIGURE 17. —Opened capsules of *Bergeranthus* species. A. *B. addoensis* (*Dold 4324*), 19 mm diameter; B. *B. albomarginatus* (*Dold 4284*), 29 mm diameter; C. *B. artus* (*Dold 4288*), 24 mm diameter; D. *B. concavus* (*Dold 4251*), 19 mm diameter; E. *B. katbergensis* (*Dold 4254*), 16 mm diameter; F. *B. leightoniae* (*Dold 4301*), 26 mm diameter; G. *B. multiceps* (*Dold 4189*), 15 mm diameter; H. *B. nanus* (*Dold 4317*), 8 mm diameter; I. *B. scapiger* (*Dold 4313*), 17 mm diameter; J. *B. vespertinus* (*Dold 4318*), 16.5 mm diameter.

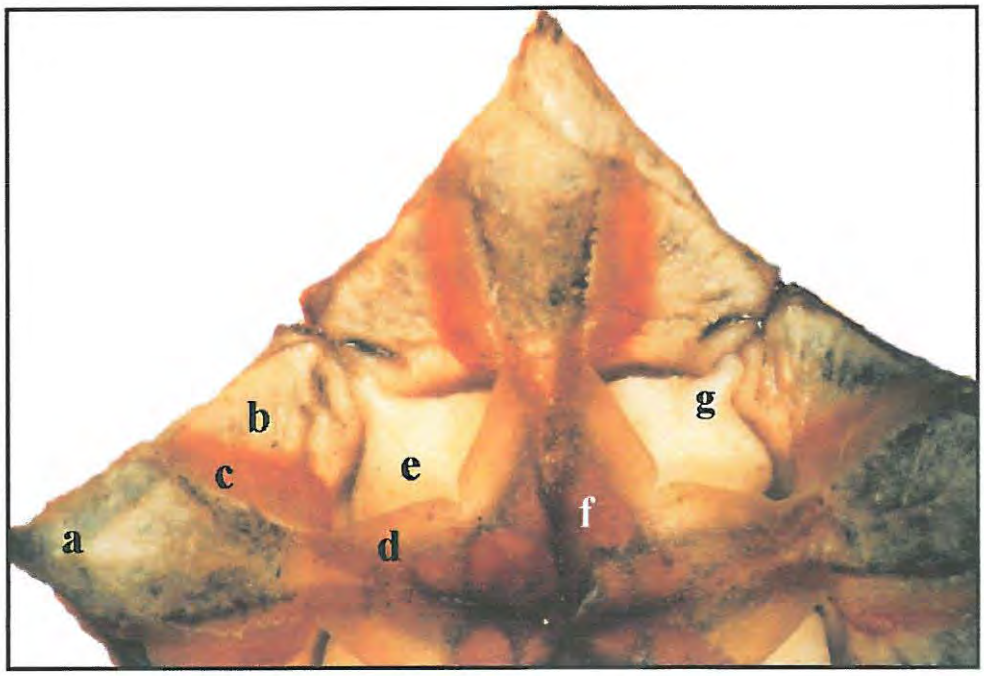

FIGURE 18. —Opened capsule of *B. albomarginatus* (*Dold 4284*), 12 mm radius (a = valve, b = expanding sheet, c = expanding keel, d = covering membrane, e = closing body, f = seeds below transparent covering membrane, g = protruding nipple of closing body).

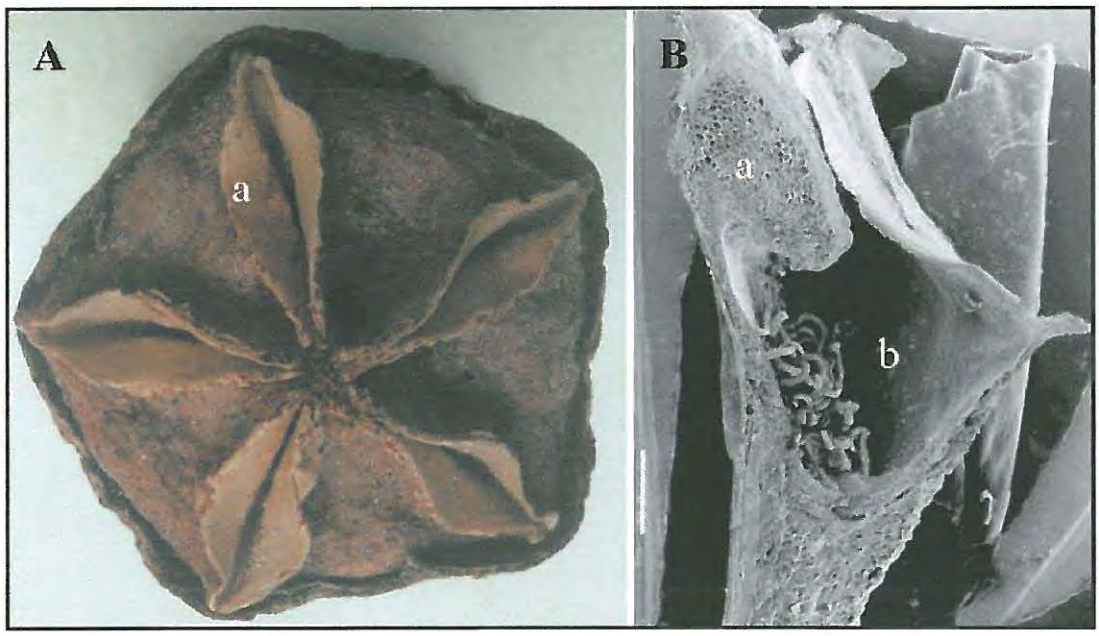

FIGURE 19. —*Bergeranthus* capsules. A. *B. artus* (*Dold 4288*), unopened capsule, 14 mm diameter (a = valve rim); B. *B. scapiger* (*Dold 4328*), scanning electron micrograph of a single locule in longitudinal section, scale bar 1 mm (a = closing body; b = locule).

3.1.21. **Germination:** Seeds germinated from between 27 hours after sowing (*B. vespertinus*) to 144 hours (*B. multiceps*) with the majority germinating between 90 and 114 hours. Germination time is of no taxonomic consequence.

3.1.22. **Seedling morphology:** Dupont (1968), in a detailed study on the ontogeny of seedlings of Mesembryanthemaceae, found that the least succulent species presented the most variation in the course of their development. Conversely, the most succulent species have a reduced phase of ontogenetic development in seedling stages. Ihlenfeldt (1975) concurs with this and notes that in species with maximum adaptation the young plant is identical to the adult through a process of ontogenetic abbreviation. Seedlings showing first true leaves of *Bergeranthus* are identical to parent plants and therefore following Dupont (1968) and Ihleneldt (1975) may be considered to be highly adapted to their environment. All *Bergeranthus* species seedlings grown under comparable conditions (Seedlings of two wild harvested accessions of all 10 species were grown indoors under a permanent 60W bulb in petri-dishes on filter paper.) and examined at 50 days showed very similar morphology within species with the exception of *B. artus* that has its first true leaves noticeably spreading. Differences in morphology of the first true leaf are therefore only of limited taxonomic importance (Figure 20).

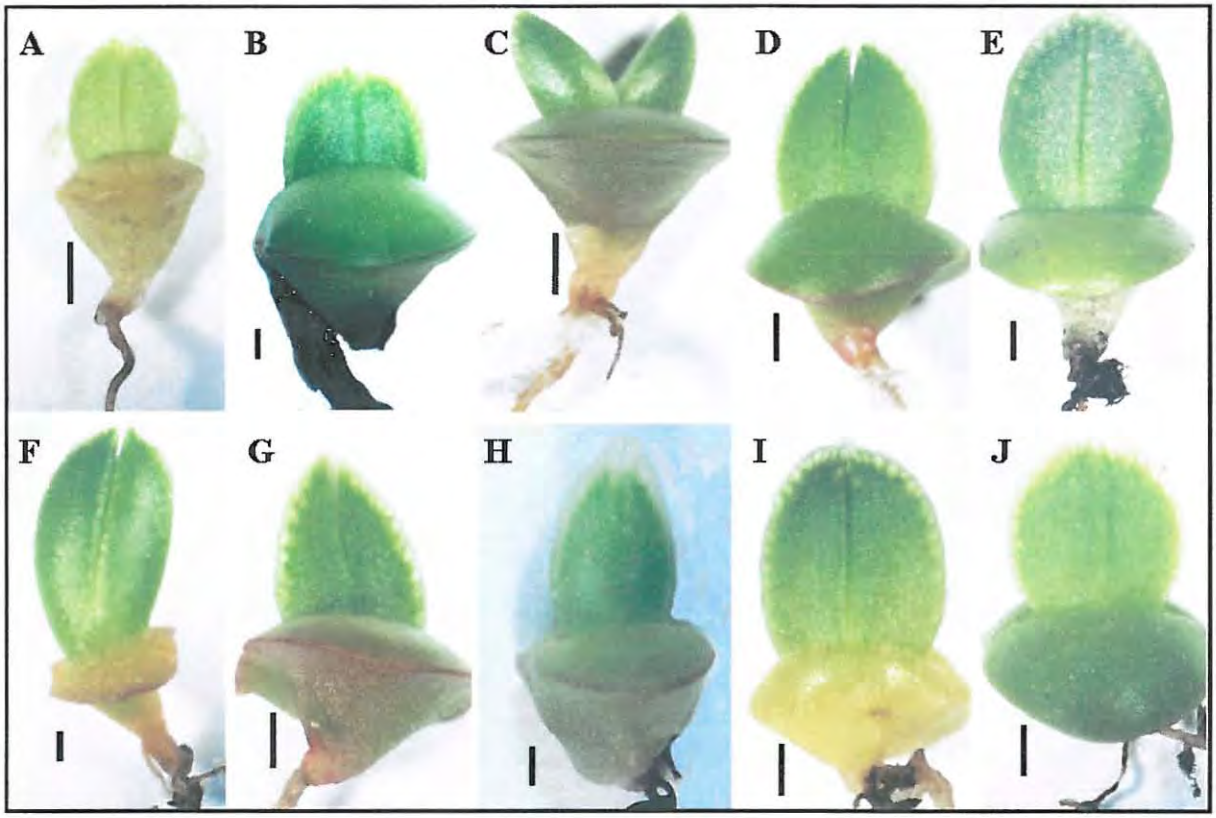

FIGURE 20. —Fifty day-old seedlings of *Bergeranthus* species. A. *B. addoensis* (*Dold 4324*); B. *B. albomarginatus* (*Dold 4287*); C. *B. artus* (*Dold 4288*); D. *B. concavus* (*Dold 4234*); E. *B. katbergensis* (*Dold 4246*); F. *B. leightoniae* (*Dold 4301*); G. *B. multiceps* (*Dold 4197*); H. *B. nanus* (*Dold 4388*); I. *B. scapiger* (*Dold 4231*); J. *B. vespertinus* (*Dold 4294*). Scale bars 4 mm.

3.2. **Micro-morphology**

3.2.1. **Leaf anatomy:** The leaf anatomy of all species of *Bergeranthus*, as well as *Rhombophyllum dolabriforme*, *R. rhomboideum* and *Hereroa granulata* (Table 1), were examined for species and generic comparison. Material for microtome sectioning was dehydrated in alcohol series, embedded in wax and sectioned with a Leitz Wetzler rotary microtome. Sections were immersed in a water bath at 45 °C for 60 seconds before being floated onto slides. Slides were dried at 45 °C for 12 hours, de-waxed with xylol and alcohol series before being stained with safranin for 12 hours. Thereafter the material was dehydrated with alcohol series and stained with Fast-green for 30 seconds, cleared with xylol series, immersed in Clove oil and permanently mounted on slides with Canada Balsam. Slides were examined and photographed with an Olympus BX50 light microscope and camera.

All material examined showed similar anatomical composition and no delimitations between species or genera can be made. Figure 21 represents the leaf anatomy of *Bergeranthus*. Tannin filled idioblast cells and needle-like calcium oxalate raphides are frequent in all three genera and are reportedly common in the Ruschioideae but absent in the Mesembryanthemoideae (Hartmann 1991a).

Landrum (2001) reports the restricted occurrence of wide-band tracheids in the leaves of three families Mesembryanthemaceae, Cactaceae and Portulacaceae. Wide band tracheids (WBTs) have wide secondary walls hypothesized to prevent cell collapse under water stress and are a unique adaptation to severe drought conditions. WBTs in Mesembryanthemaceae were noted only in xylem of leaf secondary and tertiary veins and constitute the majority of lignified cells present in the xylem. The presence of WBTs in *Bergeranthus jamesii*[4], *Bergeranthus* sp., *Hereroa* sp. and *Rhombophyllum dolabriforme* reported by Landrum (2001) suggests that the xeric environment has selected for these cells as a means of withstanding stress.

[4] =*Bergeranthus vespertinus sensu* Dold

TABLE 1. —Voucher specimens examined in study of leaf anatomy.

Taxon	**Voucher specimens**
Bergeranthus addoensis	*Dold 4311*
B. albomarginatus	*Dold 4284*
B. artus	*Dold 4245*
B. concavus	*Dold 4305*
B. katbergensis	*Dold 4239*
B. leightoniae	*Dold 4302*
B. multiceps	*Dold 4195*
B. nanus	*Dold 4271*
B. scapiger	*Dold 4262*
B. vespertinus	*Dold 4334*
Rhombophyllum dolabriforme	*Dold 4397*
R. rhomboideum	*Dold 4399*
Hereroa granulata	*Dold 4405*

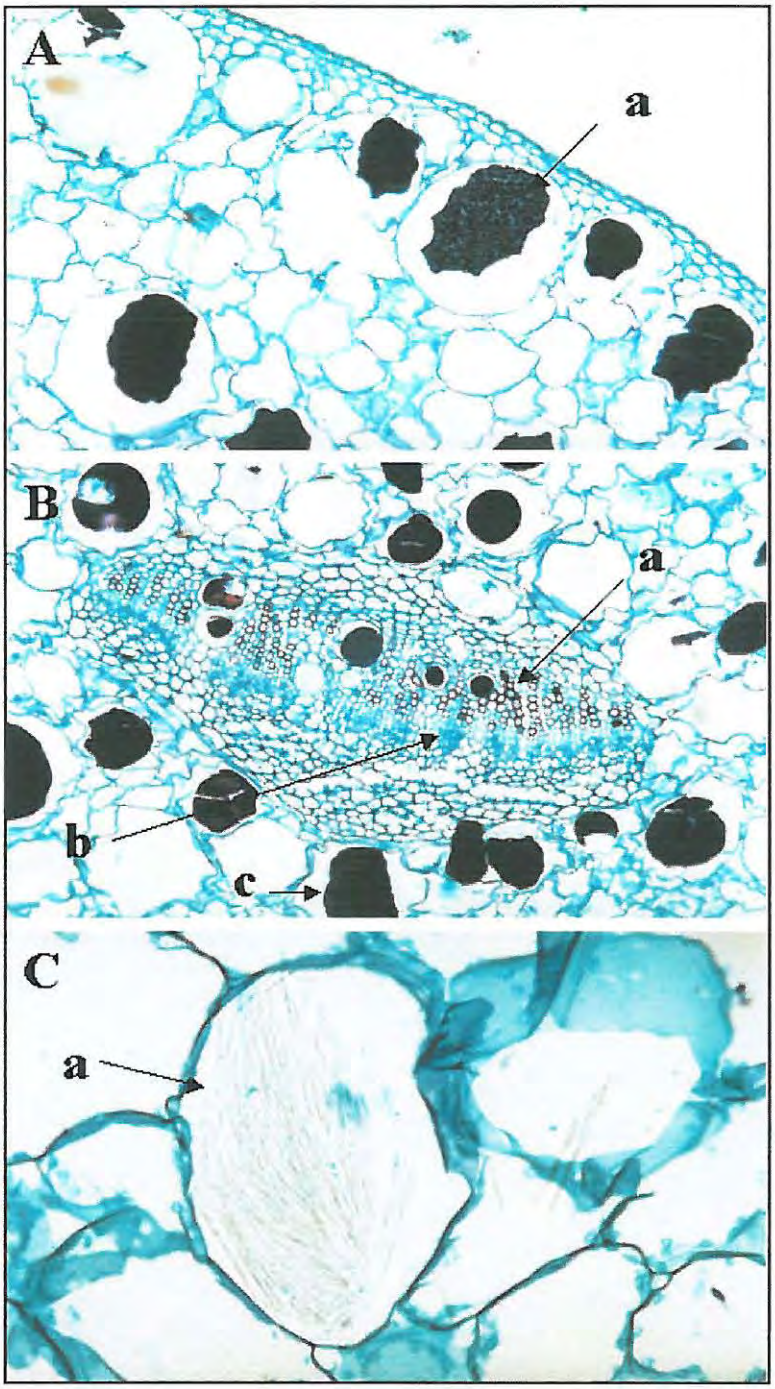

FIGURE 21. —Leaf anatomy of *Bergeranthus*. A. *B. addoensis* (*Dold 4324*), leaf surface, x 20.25 (a = sub-epidermal idioblast cell filled with tannins); B. *B. scapiger* (*Dold 4191*), vascular bundle, x 20.25 (a = xylem, b = phloem, c = idioblast filled with tannins); C. *B. addoensis* (*Dold 4324*), cell containing calcium oxalate raphides, x 202.5 (a = needle-like calcium oxalate raphides).

3.2.2. **Leaf epidermal wax layer:** Hartmann (1979) reports that most homocellular leaf surfaces in the Mesembryanthema[5] are covered by a distinct layer of wax producing a wide variety of fine sculptures that, if air-dried, are comparable. Taxa can therefore be recognized by their wax patterns. All species of *Bergeranthus,* as well as *Rhombophyllum dolabriforme*, *R. rhomboideum* and *Hereroa granulata* (Table 2) were examined in the Rhodes University Electron Microscopy Unit using a JEOL–JSM 840 scanning electron microscope at 12 k. All material was air-dried and sputter coated with gold using a Balzers Union coating unit. It was found that leaf surface wax layers, if critical point dried, were dissolved and examination was not possible.

TABLE 2. —Voucher specimens examined in study of leaf epidermal wax layer characters.

Taxon	**Voucher specimens**
Bergeranthus addoensis	*Dold 4196, 4218*
B. albomarginatus	*Dold 3943, 4284, 4285*
B. artus	*Dold 4245, 4288*
B. concavus	*Dold 4234, 4298*
B. katbergensis	*Dold 4254, 4268*
B. leightoniae	*Dold 4192, 4235*
B. multiceps	*Dold 4186, 4194, 4289*
B. nanus	*Dold 4271, 4317, 4388*
B. scapiger	*Dold 4191, 4193, 4213, 4262*
B. vespertinus	*Dold 4200,4291*
Rhombophyllum dolabriforme	*Dold 4397*
R. rhomboideum	*Dold 4398, 4399*
Hereroa granulata	*Dold 4402,4410*

Leaf surfaces of *Bergeranthus* species have a ± continuous wax layer, with or without cuticular folds, or with various forms of separate, erect wax platelets, with or without long thread-like appendages, or with parallel sulcate formations that are taxonomically useful (Figure 22). Few studies have been undertaken and no information is available for *Bergeranthus* therefore terminology is limited. Terms used in this study are descriptive only.

[5]Hartmann (1988a) refers to the subfamilies Aptenioideae Schwantes and Ruschioideae Schwantes regarded in this study as Mesembryanthemaceae Fenzl following Chesselet *et al.* 1995.

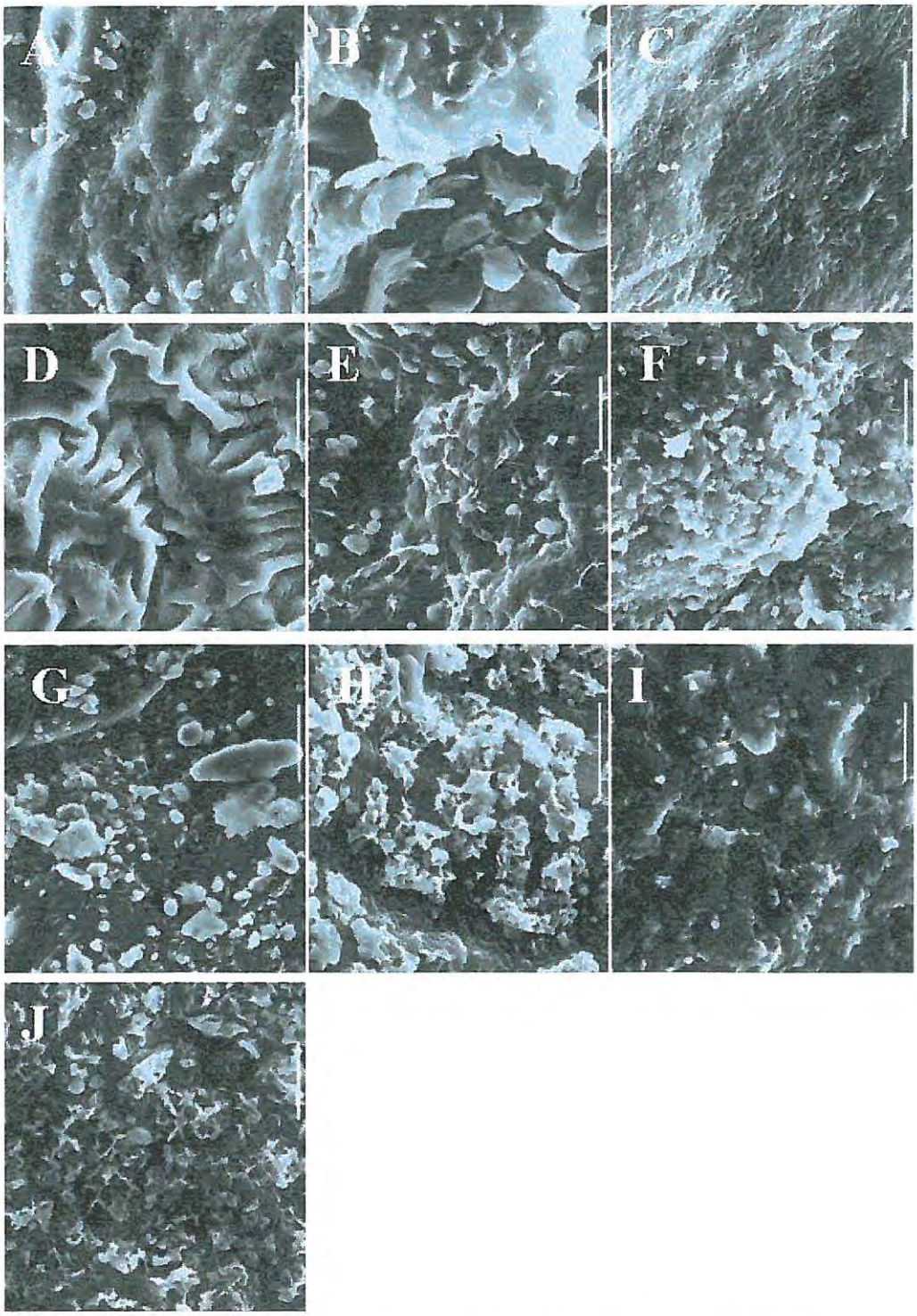

FIGURE 22. —*Bergeranthus* leaf epidermal wax layers. A. *B. addoensis* (*Dold 4196*); B. *B. albomarginatus* (*Dold 3943*); C. *B. artus* (*Dold 4245*); D. *B. concavus* (*Dold 4234*); E. *B. katbergensis* (*Dold 4254*); F. *B. leightoniae* (*Dold 4235*); G. *B. multiceps* (*Dold 4186*); H. *B. nanus* (*Dold 4388*); I. *B. scapiger* (*Dold 4191*); J. *B. vespertinus* (*Dold 4291*). Scale bars 10 μm.

3.2.3. **Anther shape and point of adherence:** Anthers of *Bergeranthus scapiger* (*Dold 4296)* were air-dried and sputter coated with gold using a Balzers Union coating unit and examined with a JEOL–JSM 840 scanning electron microscope at 12 k (Figure 23A). SEM examination showed no additional useful characters. Anthers examined with a hand lens are basally dorsifixed (Figure 16Ad, 23A) and may be ovoid or linear, differing between species and therefore of taxonomic value. The upper surface is concave, yellow and bears copious dry yellow pollen.

3.2.4. **Pollen:** Pollen of all species of *Bergeranthus*, as well as *Rhombophyllum dolabriforme*, *R. rhomboideum* and *Hereroa granulata* (Table 3) was air-dried and sputter coated with gold using a Balzers Union coating unit and examined with a JEOL–JSM 840 scanning electron microscope at 12 k. *Bergeranthus* pollen grains are consistently tricolpate, spinulose–punctate (Figure 23B, see also figure 80), the most widespread type in Mesembryanthema (Hartmann 1991a), and are interpreted by Bittrich & Struck (1989) as a primitive condition. Pollen grains measure 0.015–0.017 x 0.011–0.013 mm. The morphology of pollen is not of taxonomic importance.

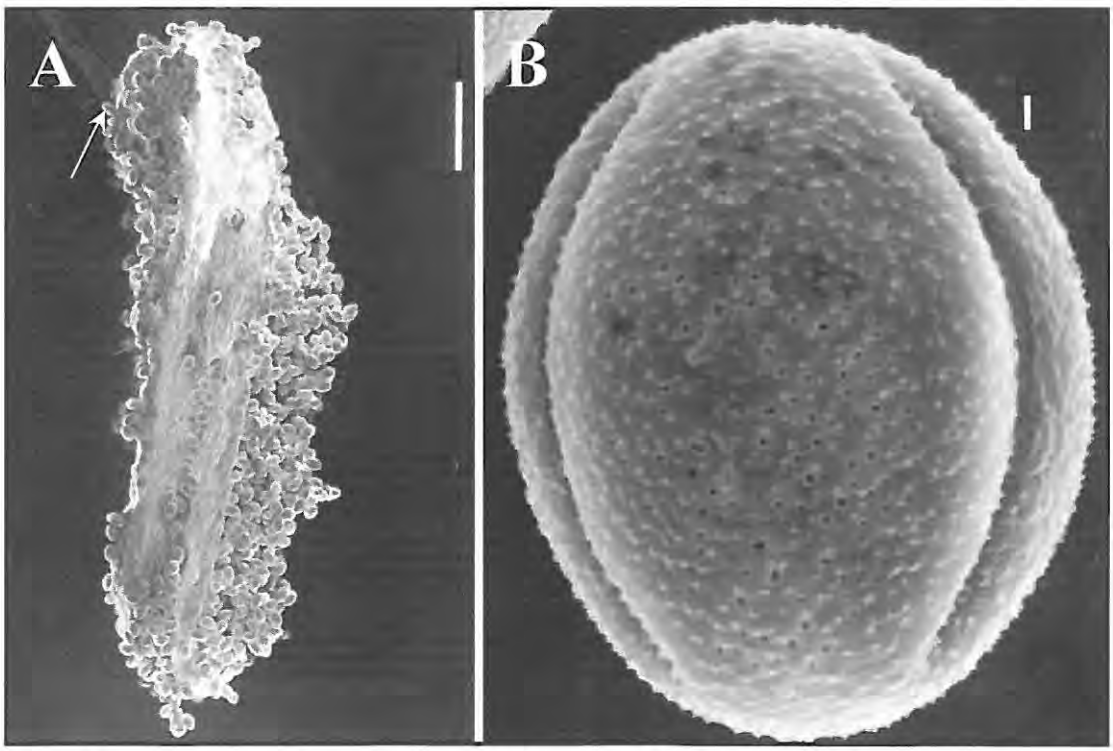

FIGURE 23. —*Bergeranthus scapiger* A. Anther (*Dold 4296*) arrow showing point of attachment to filament; B. Pollen (*Dold 4296*). Scale bars 1 µm.

TABLE 3. —Voucher specimens examined in study of pollen characters.

Taxon	**Voucher specimens**
Bergeranthus addoensis	*Dold 4198*
B. albomarginatus	*Dold 3943*
B. artus	*Dold 4242*
B. concavus	*Dold 4233*
B. katbergensis	*Dold 4236*
B. leightoniae	*Dold 4232*
B. multiceps	*Dold 4188*
B. nanus	*Dold 4271*
B. scapiger	*Dold 4296*
B. vespertinus	*Dold 4190*
Rhombophyllum dolabriforme	*Dold 4397*
R. rhomboideum	*Dold 4401*
Hereroa granulata	*Dold 4410*

3.2.5. **Seed:** Seeds of all species of *Bergeranthus*, as well as *Rhombophyllum dolabriforme*, *R. rhomboideum* and *Hereroa granulata* (Table 4) were air-dried and sputter coated with gold using a Balzers Union coating unit and examined with a JEOL–JSM 840 scanning electron microscope at 12 k. Seeds of *Bergeranthus* as described by Lockyer (1932) are campylotropous. Seeds are ovate with a shortly protruding micropyle, pale brown becoming darker with age and measure 0.8–1.84 x 0.51–1.06 mm. Seed testa sculpture and vesture are considered useful taxonomic characters (Figure 24) and can be smooth or with undulate anticlinal walls that may glabrous or white puberulous (Figure 25). Bittrich & Struck (1989) consider sculptured seeds as a primitive state.

TABLE 4. —Voucher specimens examined in study of seed characters.

Taxon	**Voucher specimens**
Bergeranthus addoensis	*Dold 4272, 4290*
B. albomarginatus	*Dold 3943, 4285*
B. artus	*Dold 4245, 4288*
B. concavus	*Dold 4234, 4251*
B. katbergensis	*Dold 4241, 4244, 4279*
B. leightoniae	*Dold 4232, 4235, 4243, 4258, 4300*
B. multiceps	*Dold 4186, 4215, 4230, 4250, 4256, 4289, 4323*
B. nanus	*Dold 4271, 4317*
B. scapiger	*Dold 4193, 4328*
B. vespertinus	*Dold 4199, 4201, 4200, 4228, 4249, 4260, 4266*
Rhombophyllum dolabriforme	*Dold 4397*
R. rhomboideum	*Dold 4400*
Hereroa granulata	*Dold 4408, 4410*

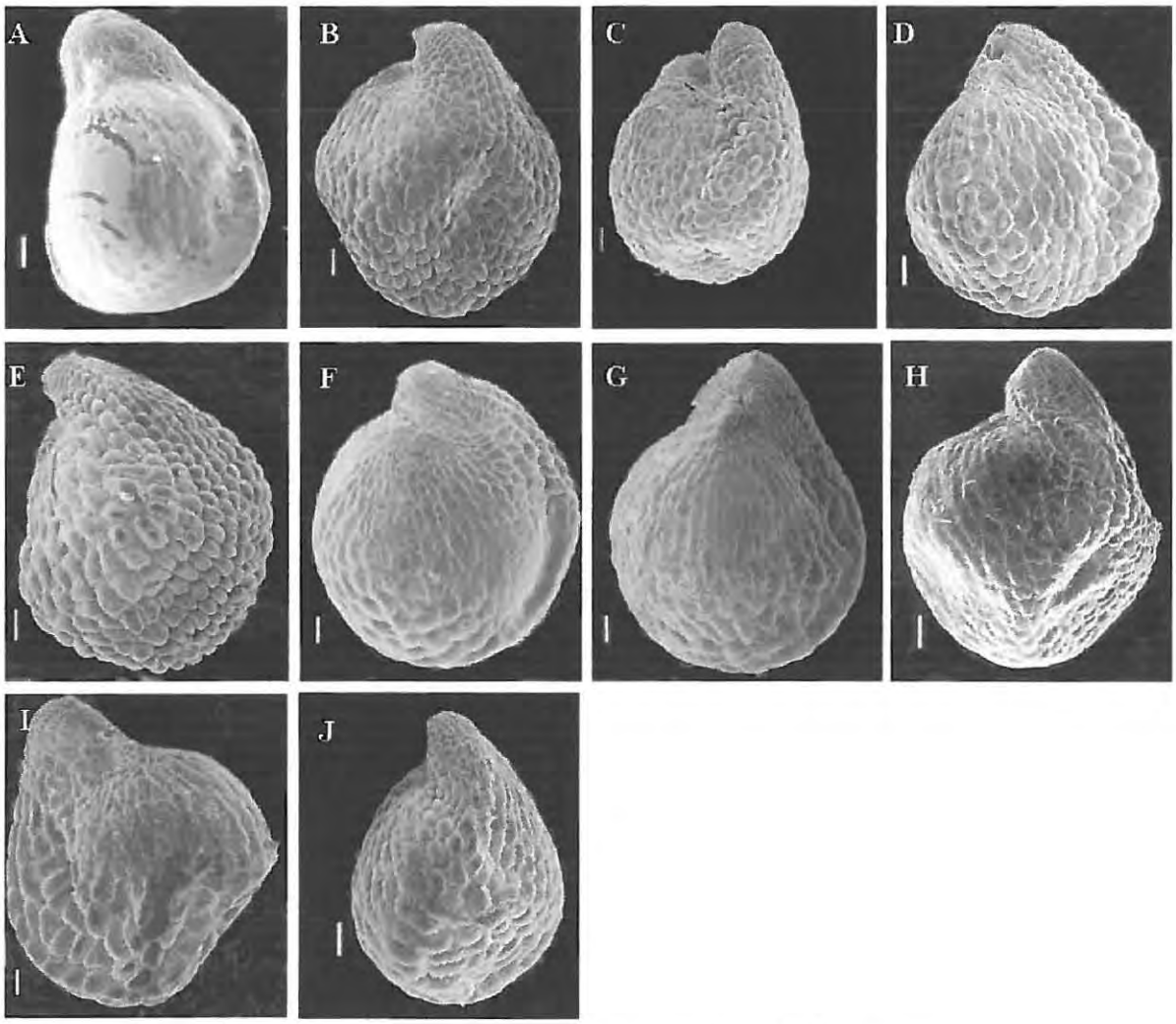

FIGURE 24. —Seeds of *Bergeranthus* species. A. *B. addoensis* (*Dold 4272*); B. *B. albomarginatus Dold 4285*); C. *B. artus* (*Dold 4245*); D. *B. concavus* (*Dold 4234*); E. *B. katbergensis* (*Dold 4241*); F. *B. leightoniae* (*Dold 4300*); G. *B. multiceps* (*Dold 4230*); H. *B. nanus* (*Dold 4271*); I. *B. scapiger* (*Dold 4193*); J. *B. vespertinus* (*Dold 4199*). Scale bars 100 μm.

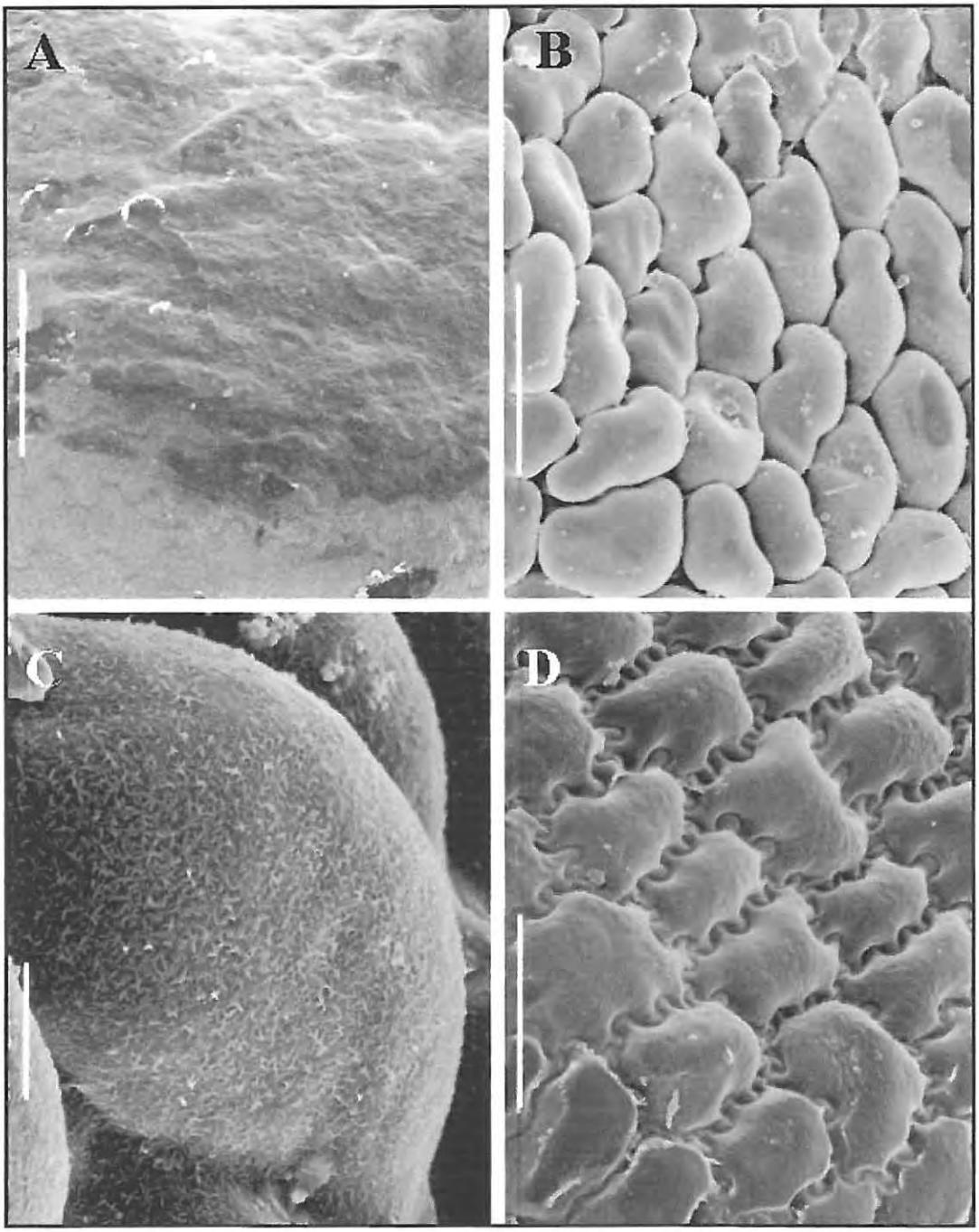

FIGURE 25. —Seed sculpture and vesture of *Bergeranthus* species. A. *B. addoensis* (*Dold 4272*), smooth testa, scale bar 100 µm; B. *B. artus* (*Dold 4245*), testa showing anticlinal walls, scale bar 100 µm; C. *B. artus* (*Dold 4245*), testa showing white pubescence, scale bar 10 µm; D. *B. albomarginatus* (*Dold 3943*), testa showing undulate anticlinal walls, scale bar 100 µm.

TAXONOMY[6]

The previous section elucidated a number of characters that are informative at the species level, which can be used to delimit species or groups of species of *Bergeranthus*. On the basis of the phenetic analysis and these characters, 10 species of *Bergeranthus* can be identified. An emended genus description, species descriptions and a key to species are presented below.

Mesembryanthemaceae Fenzl in Annalen des Wiener Museums der Naturgeschichte 1: 349 (1836), emend. Herre & Volk in Sukkulentenkunde 2: 38 (1948).

Ruschioideae Schwantes in Ihlenfeldt, Schwantes & Straka in Taxon 11: 54 (1962), emend. H.E.K.Hartmann & Bittrich in South African Journal of Botany 57: 74 (1991).

Bergeranthus Schwantes in Zeitschrift für Sukkulentenkunde 2: 179 (1926). Type species *B. scapiger* (Haw.) Schwantes. Etymology Alwin Berger 1871–1931, gardener and horticulturist at La Mortola, Italy, later Berlin and Stuttgart, Germany.

Plants perennial, compact, branching at base, up to 200 mm across, becoming caespitose with age, developing a fleshy taproot and thick horizontal rhizomes, densely or loosely clump forming, or dying back in the centre of the plant with age, thus forming rings with age; *Leaves* 6–12, ovate to lanceolate, opposite, erect, spreading or decumbent, connate at base, triquetrous with a rounded or sharp keel, sometimes the lower distal keel producing a chin-like protuberance, mucronate, epidermis smooth, stomata almost superficial, dark blue green to yellow green, 11–100 x 4–22 mm; *Flowers* diurnal, opening in the late afternoon or evening or nocturnal, in cymes well above the plants, pedicels and peduncle two-sided to ± winged; *Bracts* lanceolate, leaf-like, sheathing; *Sepals* lanceolate to broadly lanceolate, 6–17 x 2–7 mm, round or indistinctly keeled at distal ends only, smooth or with a small dorsal apiculus (dorsal apiculus) on lower distal keel sometimes extending beyond apex, margins with transparent membranous wings; *Petals* 50–316 in two to three series, linear-lanceolate, 7–26 mm x 1–3 mm, golden yellow, tinged reddish below with age, filamentous staminodes absent; *Stamens* 94–460, in three to four series, white at base turning golden yellow in distal half, in an erect column or a hollow cylindrical arrangement, filaments glabrous or central series basally sparsely white

[6] Abbreviations of authors of plant names follow the recommendations of Brummitt and Powell (1992).

lanulose on inner surface only, *anthers* basally dorsifixed, ovoid or linear, deeply concave, yellow; *Pollen* tricolpate, spinulose–punctate,15–17 x 11–13 µm; *Stigmata* linear, glabrous or basally minutely puberulous–papillate, cohering, later separating and tips curving outwards, exserted slightly beyond or equal to the stamens, translucent pale yellow; *Floral nectaries* 5, free, crescent shaped, rounded, smooth, slightly raised, yellow or green; *Ovary* conical above, upper surface 2–7 mm diameter, placenta parietal; *Fruit* 5-locular, persistent, top flat, rims raised, erect to spreading, base shortly funnel-shaped, covering membranes rigid, flat, covering entire locule, closing body a large endocarpal protrusion shaped like a sill in longitudinal section, often reaching under the covering membranes, ± flat on top, white, becoming yellowish with age, expanding keels short to exserted beyond valve, pale to dark reddish brown, well separated from each other basally, where also a narrow triangle of white, spongy tissue separates the covering membranes, valve wings absent; *Seeds* ovate with shortly protruding micropyle, pale brown becoming darker with age, 0.8–1.84 x 0.51–1.06 mm, seed testa smooth or with undulate anticlinal walls, glabrous or puberulous.

Flowering in spring to early autumn with a peak in November-December. *Habitat*: Fynbos, Grassland, Nama Karoo, Thicket and Savanna Biomes (Low & Rebelo 1996) in the Eastern Cape.

Distinguishing characters: tufted perennials; leaves smooth, glabrous, mucronate; pedicels bracteate; ovary septa conspicuously separated and raised; top of ovary convex; capsule locules deeper than wide; closing bodies large and corky; expanding keels not winged; valve wings absent.

Species 10, Eastern Cape, between Joubertina and Graaff Reinet in the west to Umtata in the east and as far north as Burgersdorp (Figure 26).

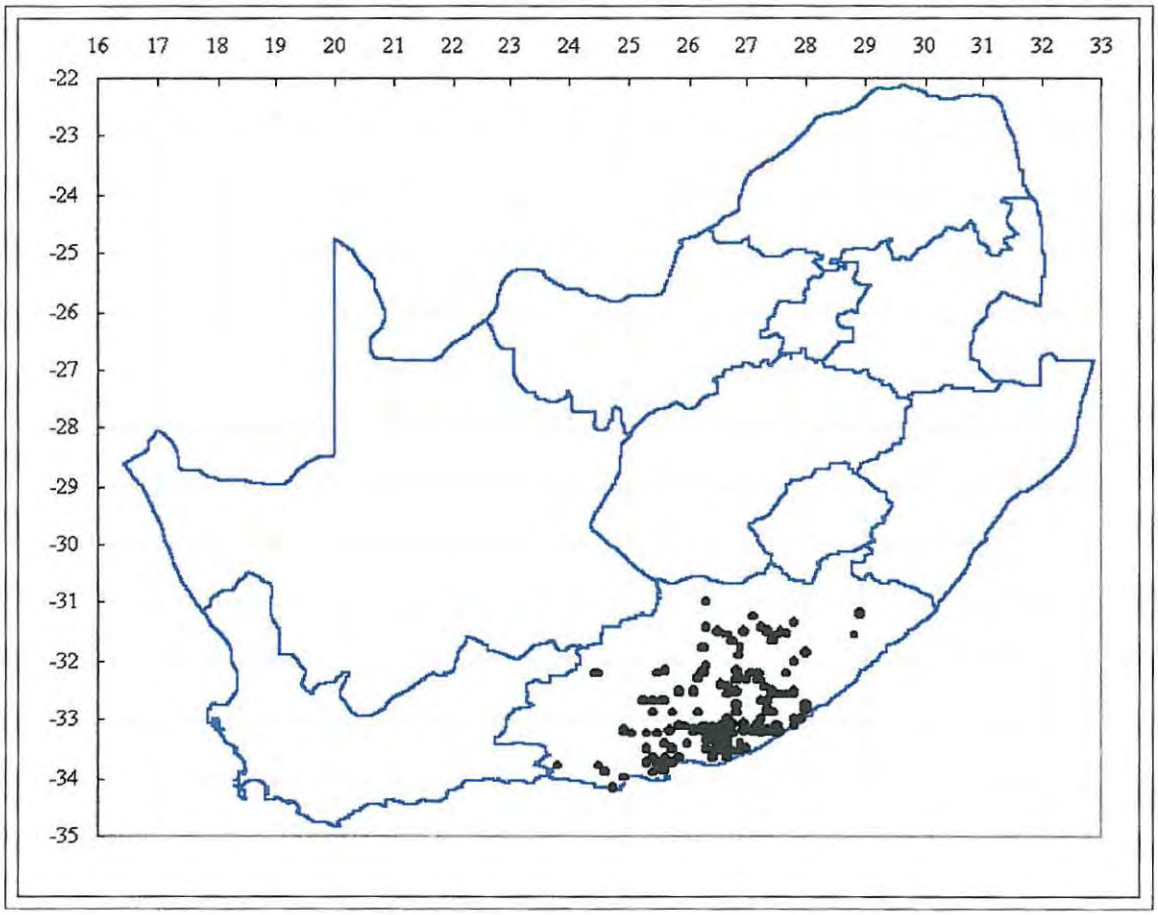

FIGURE 26. —Distribution of *Bergeranthus* species in South Africa.

Key to species of *Bergeranthus*

1a Leaves lanceolate

2a Distal leaf keel chinned to ± dolabriform, 45–101 x 8–20 mm.....*B. scapiger*

2b Distal leaf keel tapering, never chinned, 10–54 x 4–12 mm

3a Associated with thicket, plants in clumps, forming a circular ring when the central plants die off; seed testa not sculptured[7], smooth, glabrous.....*B. addoensis*

3b Associated with open grassland, plants clumped or single, not ring-forming; seed testa always sculptured with undulating anticlinal walls, glabrous or puberulous

4a Flowers nocturnal, sweetly fragrant; stamens arranged in a cylinder; seed testa white puberulous.....*B. artus*

4b Flowers diurnal, not fragrant; stamens arranged in a tightly packed column; seed testa glabrous

5a Leaf keel thickened apically, whitish; leaf wax layer comprising multifaceted raised sculptures arranged in ± parallel rows[8].....*B. nanus*

5b Leaf keel not thickened, concolorous with leaf blade; wax layer sculptures not arranged in parallel rows

6a Flowers opening at ± midday; leaf wax layer with rounded sculptures connected by fine threads.....*B. katbergensis*

6b Flowers opening after 15:30, leaf wax layer sculptures not connected by fine threads

7a Associated with karroid veld, leaves broadest at base; closing bodies of fruit round; expanding sheets much reduced; expanding keels linear, acute, margin serrate, apex attenuate, extended beyond valve.....*B. vespertinus*

7b Associated with open grassland; leaves broadest in middle; closing bodies of fruit triangular; expanding sheets broad, thickened; expanding keels broad, entire, apex broadly acute, not extended beyond valve.....*B. multiceps*

1b Leaves ovate

8a Associated with thicket; leaves blue-green, more than 10 mm wide, keel apically chinned, margins distinctly white.....*B. albomarginatus*

[7] Visible at x 10 magnification.

8b Associated with grassland; leaves not blue-green, less than 10 mm wide, keel not apically chinned, margins not white

9a Occurring below 300 m; leaves pale yellow green, smooth, outer leaves erecto-patent, "D"-shaped in cross section, epidermal wax layer with parallel sulcate ridges without raised wax sculptures; sepals without a dorsal apiculus below the apex; capsule expanding keels linear, entire, acute.....*B. concavus*

9b Occurring above 360 m; leaf dark dull green tinged purple-red, rugose, outer leaves decumbent, broadly "V"- shaped in cross section, epidermal wax layer of raised tightly packed granular particles; sepals with a sharply pointed dorsal apiculus just below the apex; capsule expanding keels broadly triangular with serrate lateral (free) margins.....*B. leightoniae*

[8] Visible only under SEM.

1. ***B. addoensis*** L.Bolus in Notes on Mesembryanthemum and some allied Genera 3: 120 (1938); H.Jacobsen in H.Jacobsen, A.G.J.Herre & O.H.Volk: 86 (1950); H.Jacobsen: 997 (1954); H.Jacobsen: 1187 (1955); D.Court: 36 (1981); C.Hilton-Taylor: 33 (1996); Type: Cape, Addo Bush, October 1937, *F.R.Long s.n.* in NBG 462/33[9] (BOL, holo!).

Plants in loose clumps, forming a mat up to 800 mm across, with the central plants dying off and leaving a ring of younger plants. *Leaves* 6–10(–12), pairs of equal length, lanceolate, acute, mucronate, tapering in proximal half to base, central pair erect, outer pair spreading, blade curving inwards, "D"-shaped in cross section, broadest in middle, dull blue-green, smooth, brittle, (27–)33–37(–42) x (8.0–)9.0–10.0(–10.5) mm, thickest at middle, 6–7 mm; *epidermal wax layer* continuous, unbroken, smooth, with scattered raised, smooth, rounded wax sculptures. *Flower* diurnal, opening at approximately 16:00 and closing towards nightfall; *sepals* broadly lanceolate, acute, (8–)10–12 x 3–4 mm, green with a semi-transparent winged margin, without dorsal apiculus below apex; *petals* (55–)60–81(–96), linear-lanceolate, spreading, (9–)11–12(–14) x 1–2 mm, yellow; *stamens* 130–152(–240), in a solid erect column, basal inner surface of the filaments of the inner series sparsely white lanulose, 5–6 mm in length; *anthers* linear; *stigmata* linear, glabrous; *ovary* upper surface 2.5–3 mm diameter; *nectaries* crescent shaped with blunt, rounded tips, reduced, inconspicuous, smoothly rounded, dry, yellow. *Capsule* 7–8(–10) x 5–7 mm; *closing bodies* triangular, lower half obscured by the covering membrane, sides held below and partially covered by expanding sheet; *covering membranes* shallowly "V"-shaped at distal free margin and incised at the sinus; *expanding sheets* broad, thickened along margin adjacent with closing body; *expanding keels* broad, entire, distally incurved, equal to valve, acute. *Seeds* ovate with short, bluntly protruding micropyles, seed testa smooth, glabrous, pale brown, 0.82–1.08 x 0.55–0.77 mm. Figures 27, 28.

Distribution: *B. addoensis* has been recorded in a narrow latitudinal band from Port Elizabeth to Uitenhage, Kirkwood and as far north as Darlington Dam (Figure 29).

Ecology: *B. addoensis* occurs in Mesic Succulent Thicket (Low & Rebelo #7) around Port Elizabeth and Uitenhage, and Xeric Succulent Thicket (Low & Rebelo #6) north of Kirkwood (Figure 30) between 10 to 400 metres above sea level (Figure 31, 32).

[9] NBG numbers refer to National Botanical Gardens living collection numbers from which herbarium specimens were prepared for BOL. According to Ernst van Jaarsveld (pers. comm. 1999) these plants are no longer alive at NBG Kirstenbosch.

The annual rainfall is 274 to 713 mm with an average of 473.5 mm (Figures 33, 34).
B. addoensis is recorded on five geological formations within its distribution: the Sundays River Formation (green/grey mudstone & sandstone) of the Uitenhage Group, the Kirkwood Formation (red/green mudstone & sandstone) of the Uitenhage Group, the Peninsula Formation (quartzitic sandstone) of the Table Mountain Group, the Blue Water Bay Formation (alluvial sheet gravel and sand) and the Witpoort Formation (quartzitic sandstone and shale) within the Lake Mentz Subgroup of the Witteberg Group (Appendix 3).

Conservation status: As with many succulent groups, the specimen collecting intensity of *Bergeranthus* species is poor due to the difficulties in making good specimens that are time-consuming to process, usually with poor results. Furthermore the lack of work on the genus has resulted in poor identifications of these. The majority of existing specimens were prepared from cultivated material, notably those of Bolus' type sheets, complicating matters further as a result of phenotypic plasticity in response to environmental factors. Lists of 'rare' taxa are often based on herbarium specimen holdings and are more correctly 'rarely collected' than infrequent in their natural habitat. Hilton-Taylor (1996) lists *Bergeranthus addoensis* as insufficiently known (K), i.e. taxa suspected to belong to any of the categories extinct, endangered, vulnerable, rare or indeterminate. In the absence of a formal revision this categorization is based on herbarium specimen holdings. Fieldwork undertaken here has however enabled a more thorough categorisation. *B. addoensis* is restricted to the Uitenhage and Port Elizabeth thicket but is common within its range under no particular threat and therefore does not fit the requirements of the current IUCN categories (http://iucn.org).

Discussion: *B. addoensis* was sent by F.R. Long to Bolus in 1937 and is named in reference to the type locality "Addo bush". Bolus described this species from Long's single living collection. The exact locality is unknown.

B. addoensis has an unusual habit of forming rings when the central clump-forming plants die with age leaving the outer, younger plants in a loose circular formation up to 800 mm in diameter and occurs primarily in an area geologically termed the Algoa Basin characterised by recent deposits of relatively deep, red, lime rich sand clay loams. This is the only species with a smooth, unsculptured seed testa, a unique character for the *Bergeranthus* group (see relationships) and uncommon in the Ruschioideae (Hartmann 1991a).

Hartmann (2002) considers *B. addoensis* to be synonymous with *B. multiceps*.

Vouchers: *Dold 4196, 4272, 4290* (GRA); *Liebenberg 7698* (PRE); *Long s.n.* (NBG).

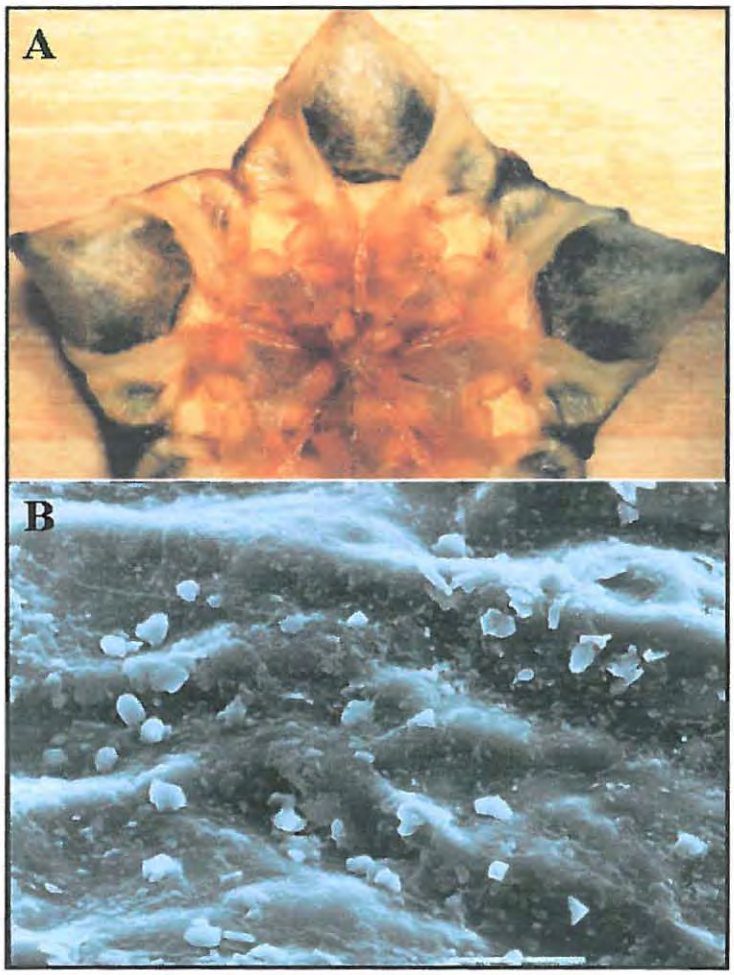

FIGURE 27. —*Bergeranthus addoensis*. A. Capsule (*Dold 4324*), 19 mm diameter; B. Leaf epidermal wax layer (*Dold 4196*), scale bar 10 µm.

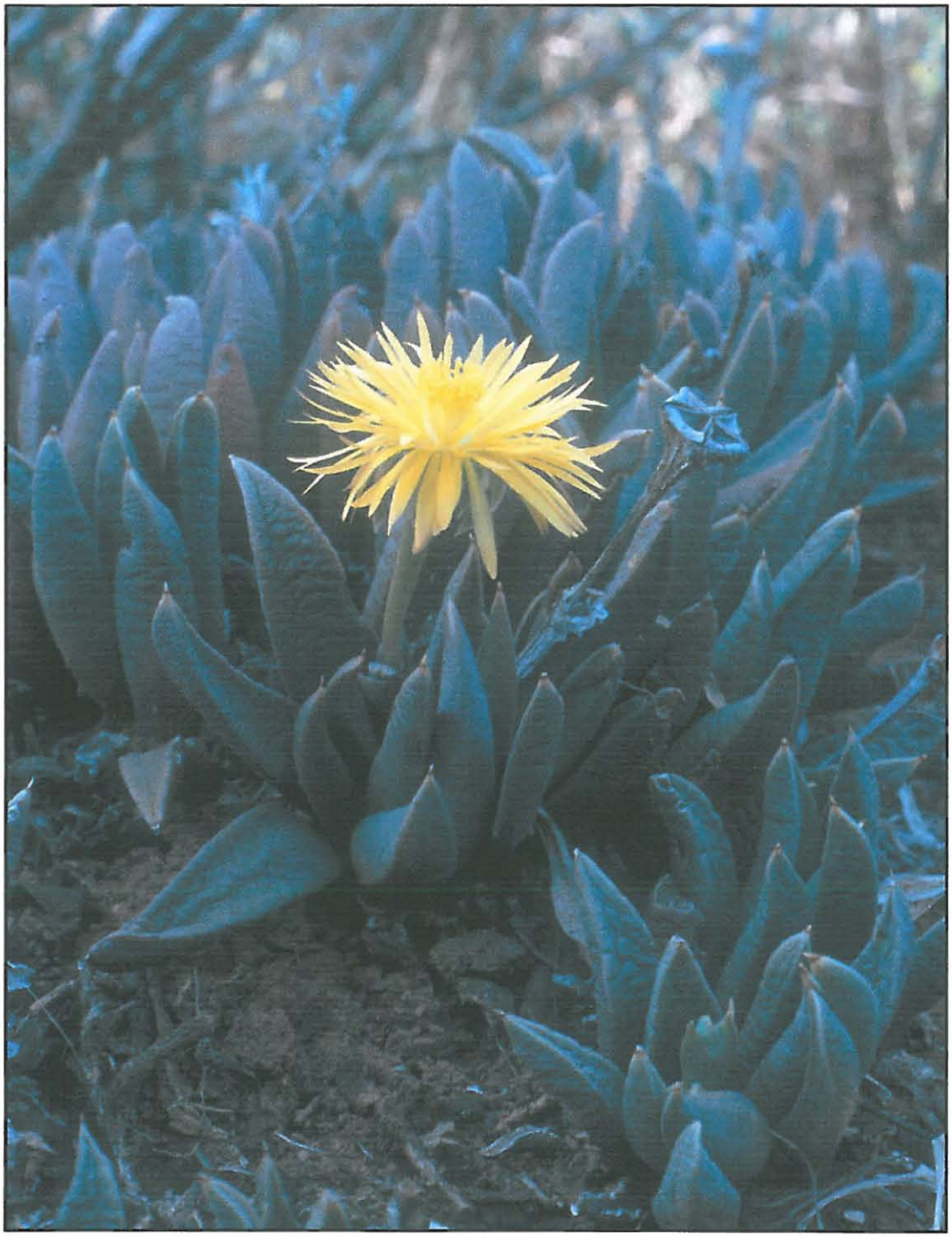

FIGURE 28. —*Bergeranthus addoensis* (*Dold 4290*), Blaaukrantz, Uitenhage.

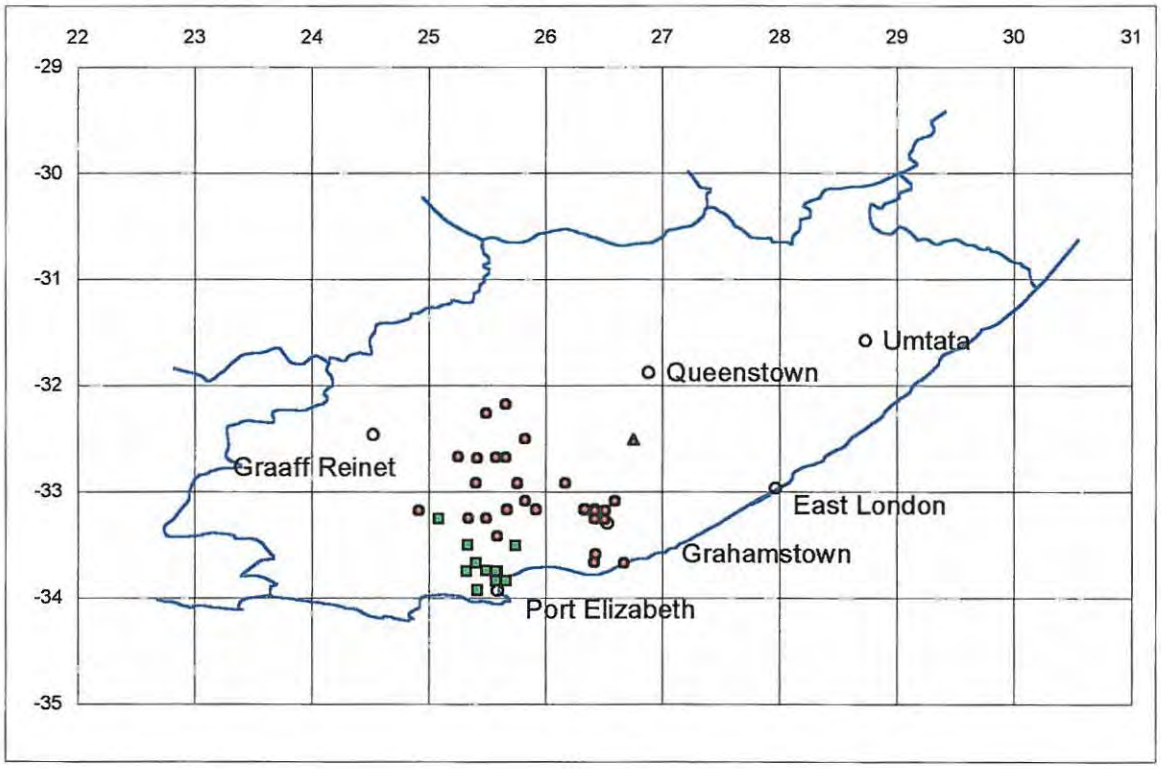

FIGURE 29. —Distribution of *Bergeranthus* species. *B. addoensis* ■ ; *B. albomarginatus* △; *B. vespertinus* ●

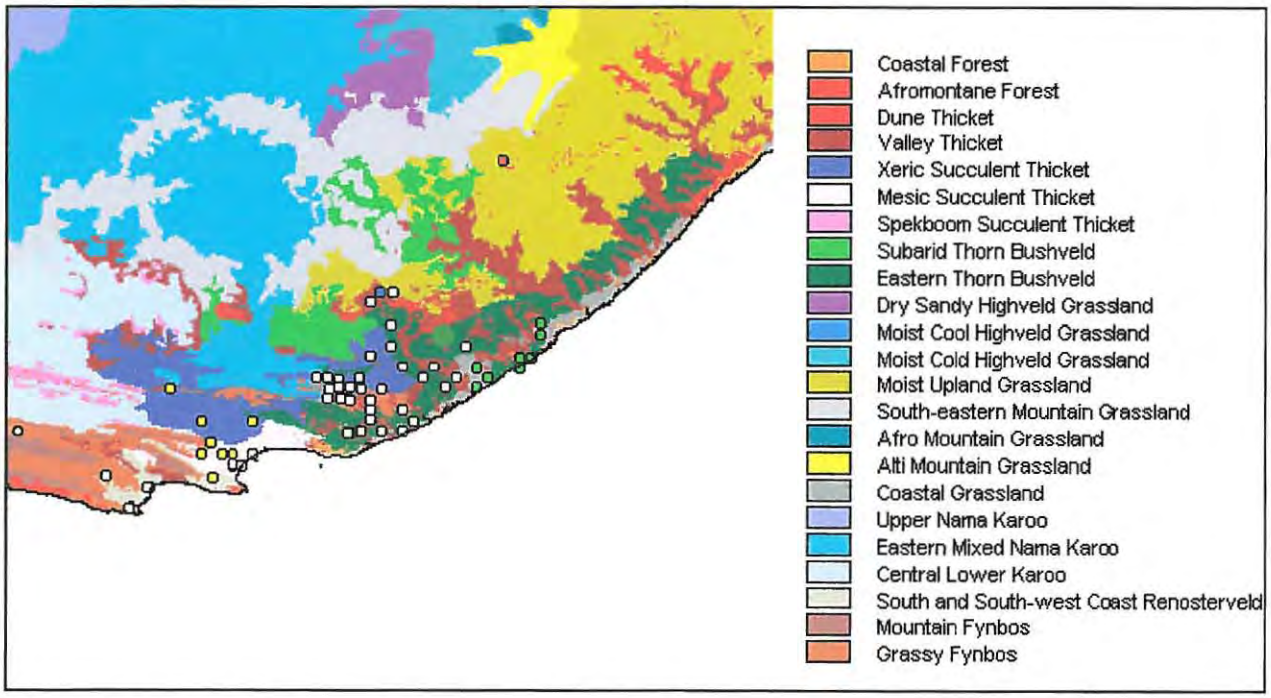

FIGURE 30. —Distribution of *Bergeranthus* species relative to vegetation types (Low & Rebelo 1996). *B. addoensis* □ ; *B. albomarginatus* ■ ; *B. artus* ■ ; *B. concavus* ■ ; *B. multiceps* □

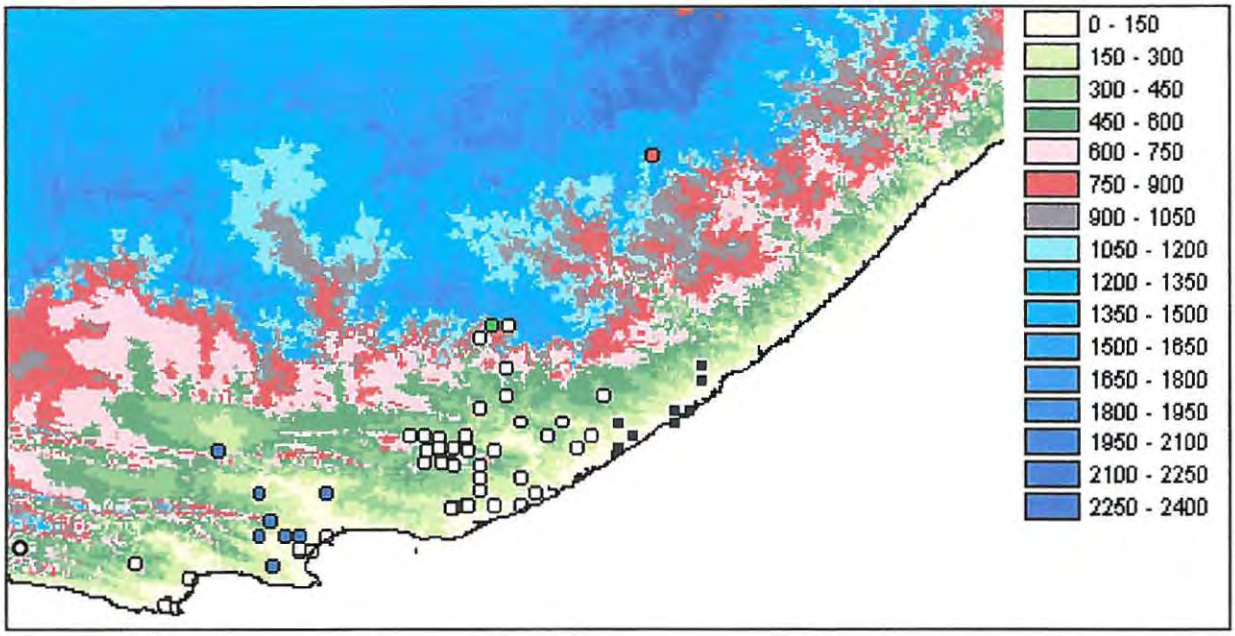

FIGURE 31. —Distribution of *Bergeranthus* species relative to height above sea level (Schulze *et al.*1997). *B. addoensis* ● ; *B. albomarginatus* ■ ; *B. artus* ● ; *B. concavus* ■ ; *B. multiceps* □

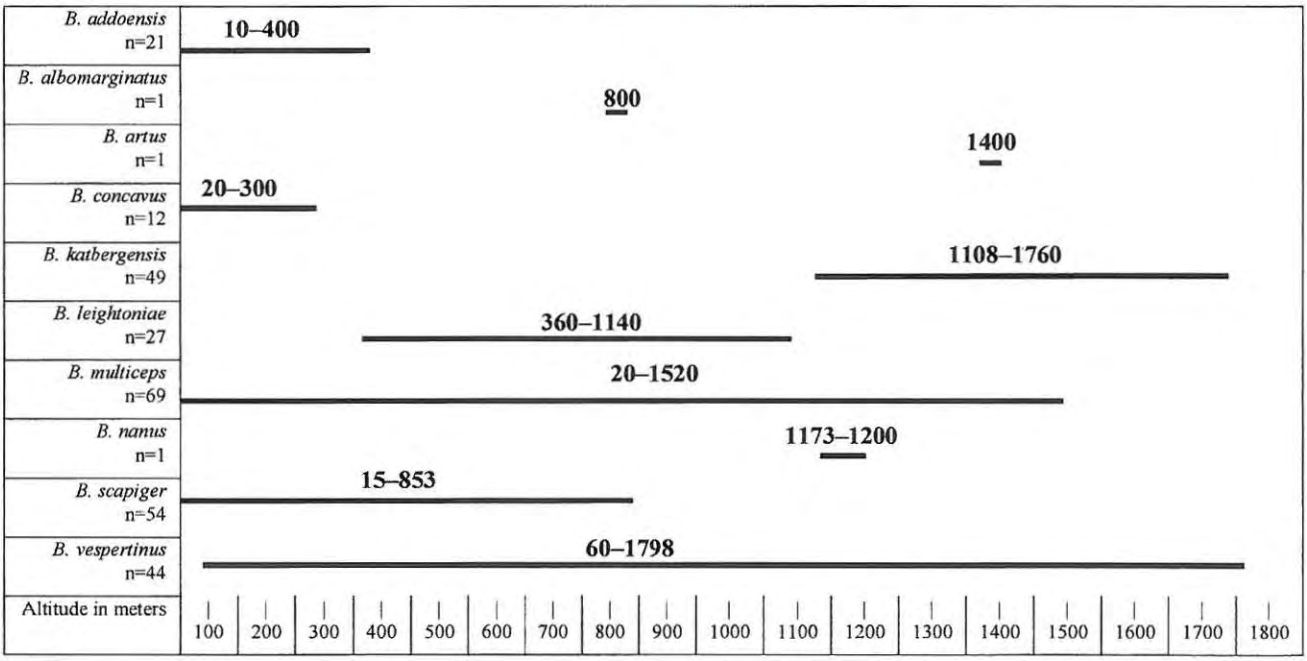

FIGURE 32. —Recorded altitude in meters above sea level of *Bergeranthus* species.

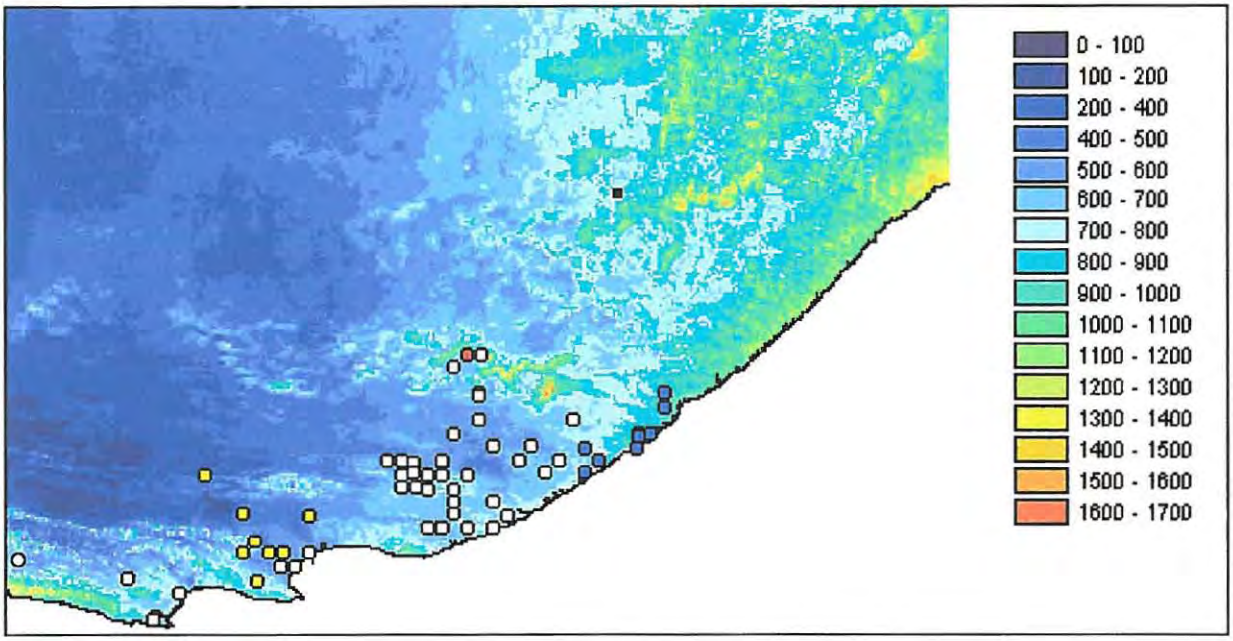

FIGURE 33. —Distribution of *Bergeranthus* species relative to median annual rainfall (Schulze *et al.*1997). *B. addoensis* □ ; *B. albomarginatus* ○ ; *B. artus* ■ ; *B. concavus* ●; *B. multiceps* □

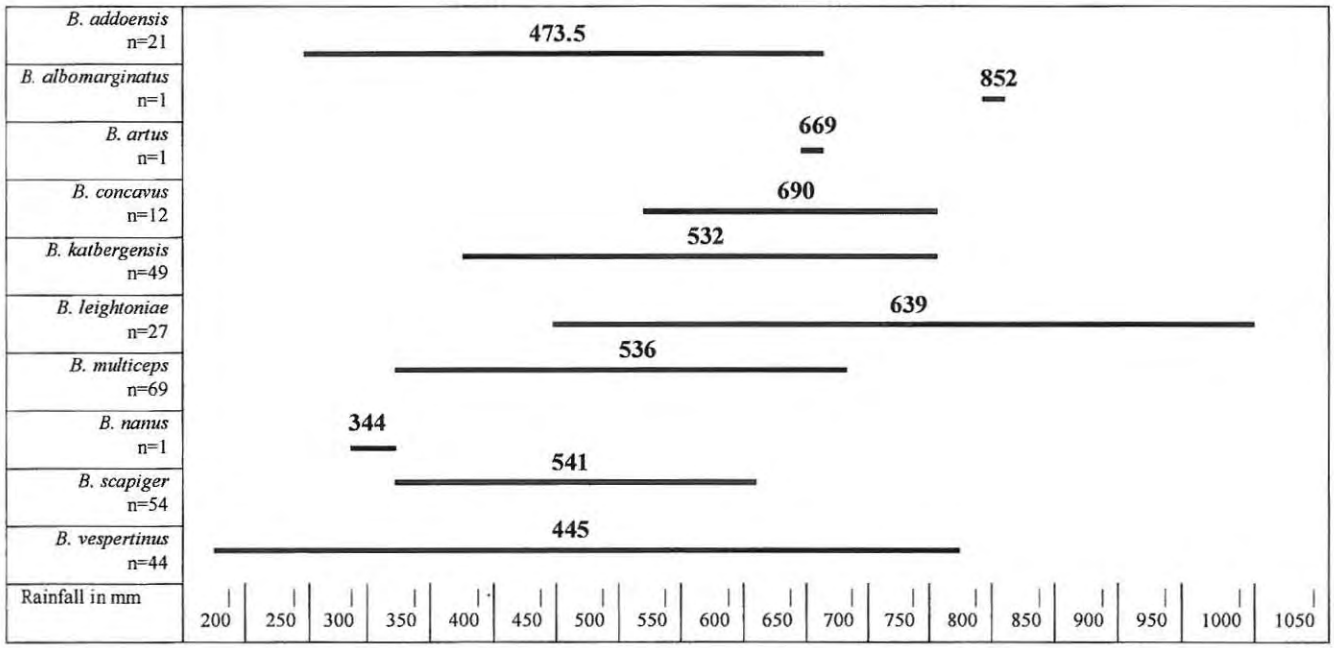

FIGURE 34. —Recorded rainfall in millimetres for *Bergeranthus* species (average given above range).

2. ***B. albomarginatus*** *A.P.Dold* sp. nov.

Bergeranthus albomarginatus *A.P.Dold* sp. nov. *B. scapiger* (Haw.) Schwantes affinis, sed folia breviora ovata dorsale complanataque, venuta marginibus albis distinctis habens.

TYPE.–Eastern Cape, 3226 (Fort Beaufort): Seymour, entrance to Kat River Dam, (–DB), 800 m, 11-09-1999, *Dold 3943* (GRA, holo., BOL, PRE).

Plants single or in loose clumps, up to 120 mm high. *Leaves* 12, pairs of equal length, ovate, acuminate, mucronate, central pair erect, base truncate, outer pair decumbent, blade curving outwards, dorsally flattened, broadest in middle, distal keel somewhat chinned, shiny blue-green with a distinct white margin, smooth, pliable, (34–)37–46(–77) x (13)14–17(–22) mm, thickest above middle, 7–6 mm; *epidermal wax layer* of large raised ± free platelets over entire surface. *Flower* diurnal, opening at approximately 16:00 and closing towards nightfall; *sepals* broadly lanceolate, acute, 10–16 x 5–7 mm, green a with semi-transparent winged margin and without a minute sharply pointed dorsal apiculus just below the apex; *petals* (87–)91–106(–121), linear-lanceolate to oblanceolate, spreading, (12–)16–20(–23) x 2–3 mm, yellow tinged pinkish below at tips; *stamens* 228–312, in a cylindrical arrangement, basal inner surface of the filaments of the inner series sparsely white lanulose, 5–7 mm in length; *anthers* linear; *stigmata* linear, minutely puberulous on basal inner surface; *ovary* upper surface 5–6 mm diameter; *nectaries* crescent shaped with blunt, rounded tips, slightly raised, highest in centre of crest becoming lower towards tips, smooth–rounded, dry, yellow. *Capsule* 11 x 5 mm; *closing bodies* rounded, apex extended into a long round-tipped nipple like appendage; *covering membranes* shallowly "V"-shaped at the distal free margin and incised at the sinus; *expanding sheets* reduced; *expanding keels* broad, straight, margin serrate, equal to valve, apex ± square. *Seeds* ovate with short, bluntly protruding micropyles, seed testa with undulate anticlinal walls, pale brown, 0.91–1.18 x 0.85–0.91 mm. Figures 35, 36.

Distribution: *B. albomarginatus* is only known from a single previously unrecorded locality at the Kat River Dam south of Seymour (Figure 29).

Ecology: *B. albomarginatus* occurs in Valley Thicket (Low & Rebelo #5) in the Kat River Valley south of Seymour (Figure 30) at an altitude of 800 m (Figures 31, 32). The annual

rainfall is 852 mm (Figures 33, 34). *B. albomarginatus* is recorded only on exposed intrusive dolerite sills (Appendix 3).

Conservation status: *B. albomarginatus* is only known from a single locality at the Kat River Dam near Seymour that comprises several small subpopulations within a restricted area confined to exposed dolerite sills. Concerted efforts to find additional localities in the area have been unsuccessful. The recently built Kat River Dam has most likely reduced the population by flooding of the river valley adjacent to the type locality. The IUCN category (www.iucn.org) Vulnerable (VU: B1, B2, C2, D1) is therefore applied to *B. albomarginatus*.

Discussion: *B. albomarginatus* is named with reference to the distinctive white leaf margins. This species is most closely allied to *B. scapiger* by virtue of its morphology and habitat but is differentiated by having ovate dorsally flattened, blue-green leaves with distinct white margins and a pronounced nipple-like protrusion of the outer closing body of the capsule.

Vouchers: *Dold 3943, 4285, 4287* (GRA).

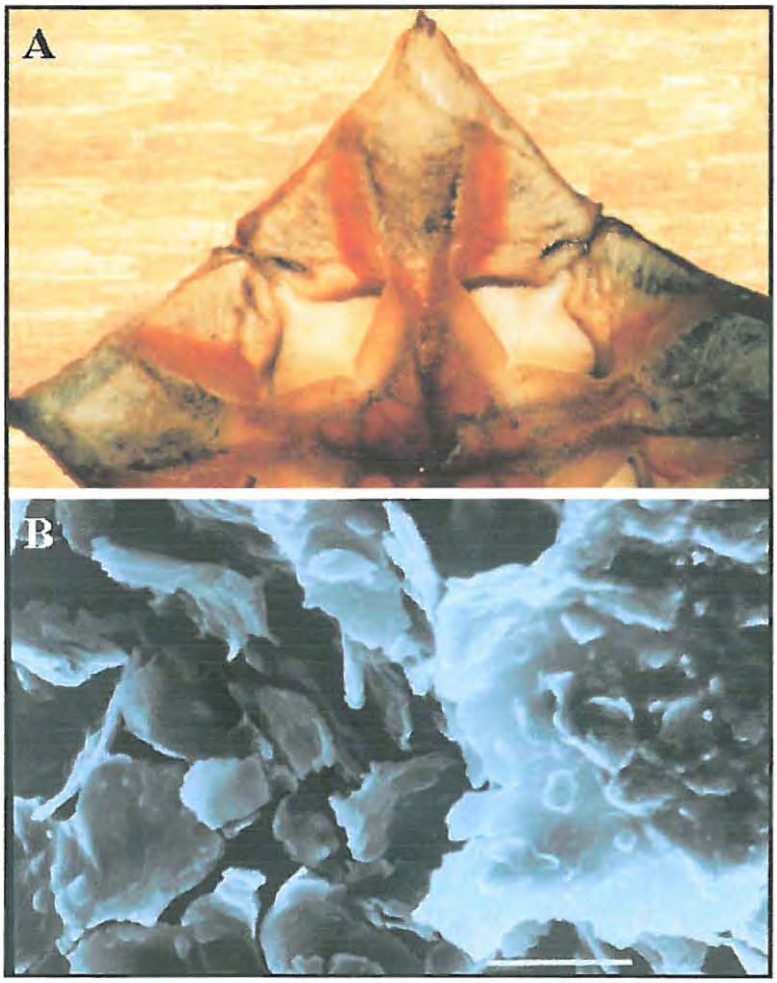

FIGURE 35. —*Bergeranthus albomarginatus*. A. Capsule (*Dold 4284*), 29 mm diameter; B. Leaf epidermal wax layer (*Dold 3943*), scale bar 10 μm.

FIGURE 36. —*Bergeranthus albomarginatus* (*Dold 3943*), Kat River Dam, Seymour.

3. ***B. artus*** L.Bolus in South African Gardening and Country Life 17: 364-365 (1927); L.Bolus: 87, 131 (1928); N.E.Br.: 267 (1928); Pax & K.Hoffmann in Engl. & Harms: 211 (1934); H.Jacobsen in H.Jacobsen, A.G.J.Herre & O.H.Volk: 86 (1950); H.Jacobsen: 997 (1954); Schwantes: 91 (1957); D.Newton & J.Chan:124 (1998); Type: Locality unknown, no date, *N.S. Pillans s.n.* in NBG 470/16 (BOL, holo!).

Plants forming dense clumps becoming cushion-like in older plants, up to 200 mm diameter and up to 120 mm high. *Leaves* 8, pairs of equal length, broadly lanceolate, shortly acute, mucronate, base truncate, central pair erect, outer pair spreading, blade not curving, "D"-shaped in cross section, broadest at base, lime-green to yellow-green, smooth, brittle, (19–)23–25(–34) x (7–)9–10(–12) mm, thickest at base, 4.5–6 mm; *epidermal wax layer* continuous, unbroken, minutely wrinkled, without raised sculpture. *Flower* nocturnal, opening approximately one hour after nightfall and closing at approximately midnight, sweetly fragrant; *sepals* broadly lanceolate, acute, (12–)14–15 x 6–7 mm, green with a semi-transparent winged margin, with or without a minute sharply pointed dorsal apiculus just below the apex; *petals* (184–)207–266(–316), linear-lanceolate, spreading to reflexed, (13–)15–16(–20) x 1.0–1.5 mm, yellow, tinged reddish below; *stamens* 394–460, in an erect cylindrical arrangement, filaments glabrous, (5–)9–12 mm in length; *anthers* linear; *stigmata* linear, basal inner surface sparsely antrorsely puberulous; *ovary* upper surface 5–6(–7) mm diameter; *nectaries* crescent shaped with blunt, rounded tips, slightly raised, highest in the centre of the crest becoming lower towards tips, smooth–rounded, dry, yellow. *Capsule* 15 x 11 mm; *closing bodies* rounded; *covering membranes* with inner margins overlapping; *expanding sheets* reduced; *expanding keels* lanceolate, acute, entire, straight, extended beyond valve. *Seeds* ovate with short, bluntly protruding micropyles, seed testa with undulate anticlinal walls, pale brown, densely white puberulous, 0.93–1.18 x 0.71–0.80 mm. Figures 37, 38, 39.

Distribution: *B. artus* is only known from the Cala Pass (Figure 40).

Ecology: *B. artus* occurs in Southern Tall Grassveld (Acocks #65.) in the Cala Pass (Figure 30) at an altitude of 1 400 m (Figures 31, 32). Southern Tall Grassveld is not differentiated from Moist Upland Grassland (Low & Rebelo #42) by Low & Rebelo (1996). The annual rainfall is 669 mm (Figures 33, 34). *B. artus* is recorded only on an exposed intrusive dolerite sill in the Cala Pass (Appendix 3).

Conservation status: *B. artus* is known from a single locality on the outskirts of Cala with several separated small sub-populations and has not been found elsewhere despite concerted efforts and is therefore afforded the IUCN category (www.iucn.org) Vulnerable (VU: D1, D2).

Newton and Chan (1998) include *B. artus* (most likely incorrectly identified), *B. glenensis* (=*Hereroa glenensis*), *B. jamesii* (=*B. vespertinus*), *B. katbergensis*, and *B. multiceps* in a list of succulent plant species advertised for sale by nurseries worldwide from 1991 to 1994 but without records of export from South Africa. Although species of *Bergeranthus* are easy to grow from seed and stem cuttings, they are not popular amongst growers (pers. comm. S. Hammer[10], 2000) and therefore trade is unlikely to pose a threat to the genus.

Discussion: *B. artus* is named in reference to its cushion-like growth form (artus=densely packed) and is unique in having nocturnal, sweetly fragrant, flowers with stamens in a cylindrical arrangement and a puberulous seed testa.

Dold first collected this plant (*Dold 787*) at Cala in 1995 and, in the absence of matching specimens or an accurate corresponding description, was unable to identify the specimen to species level. Apart from Bolus' type sheet, no herbarium specimens have been seen that resemble her description. After examining the type specimen it has been concluded that the Cala plant is *B. artus*, however this species presents several problems. The fragmentary type specimen includes only a single pair of leaves that bears no resemblance to Bolus' type description. The dimensions given are far greater than any plant in its natural habitat and one can only speculate that the type material had become grossly oversized after having been grown in a pot for twenty years. Beatrice Carter's illustration (Figure 39) of the type material shows sharply margined and keeled leaves with a distinctly flattened upper surface of the blade, which are excessive in length, more closely resembling *B. scapiger* than the Cala plant. The closed capsule shows no valve rims that are so typical of *Bergeranthus*. The opened capsule however agrees with the Cala plant more accurately although the valve apices are shortly acute rather than attenuate as documented in this study. Three exceptional characters of the Cala plant (the cushion like growth—Bolus gives 25 cm across, the nocturnal flowers and the sweet fragrance) match the description of *B. artus*. The type locality is unknown. Bolus (1928) guessed that Pillans collected the plant in the Uitenhage District and Jacobson (1950) guessed Ladismith.

[10] Spheroid Institute, Vista, California

Both localities are indicated as uncertain by means of a question mark in the text. It is suspected that Pillans' plant came from Cala as no other localities have been found. The Selmar Schonland Herbarium archives show that that the Sisters at Cala convent actively collected plant specimens around that time and sent these to herbaria countrywide and it is therefore possible that they may have facilitated the discovery of *B. artus*. Bolus notes that she described the species only 20 years after receiving the specimen from Pillans, dating the collection date to approximately 1907. To our knowledge *Dold 787* is the first collection since Pillans' collection, an interim period of 88 years.

B. artus is the only nocturnal, fragrant-flowering species of *Bergeranthus* and seems to represent a link with the genus *Hereroa* in this respect. This suggested link is supported by the smooth leaf epidermal wax layer common to both *B. artus* and *Hereroa granulata* (see Relationships).

Having not considered this additional material Hartmann (2002) considers *B. artus* to be synonymous with *B. multiceps*. This species is poorly known and it is therefore important to point out that the figure of *B. artus* in Smith *et al.* (1998) is incorrect and is in fact *B. scapiger*.

Fieldwork in the Cala area has revealed that the Xhosa name for *Bergeranthus artus* is *intelezi*, a widespread Xhosa term for a cultural protective charm (Dold & Cocks 2000). The pulped leaves are mixed in a basin of water that is used as a body wash in a ritual cleansing to protect the user from evil spirits and sorcery.

Vouchers: *Dold 4242, 4245, 4288* (GRA).

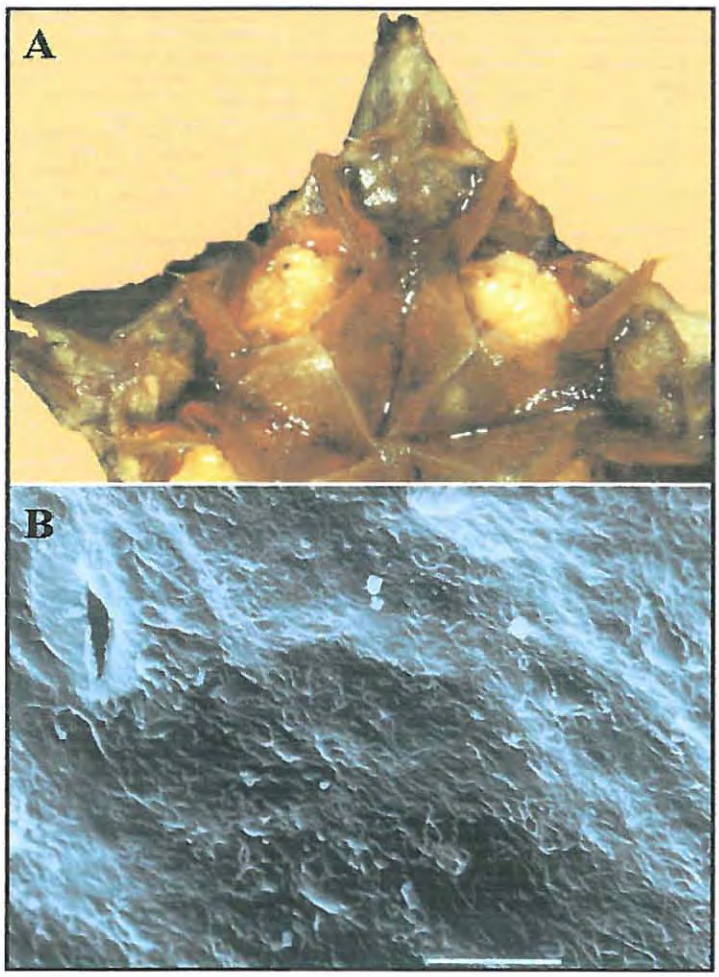

FIGURE 37. —*Bergeranthus artus*. A. Capsule (*Dold 4288*), 24 mm diameter; B. Leaf epidermal wax layer (*Dold 4245*), scale bar 10 µm.

FIGURE 38. —*Bergeranthus artus* (*Dold 4242*), Cala Pass.

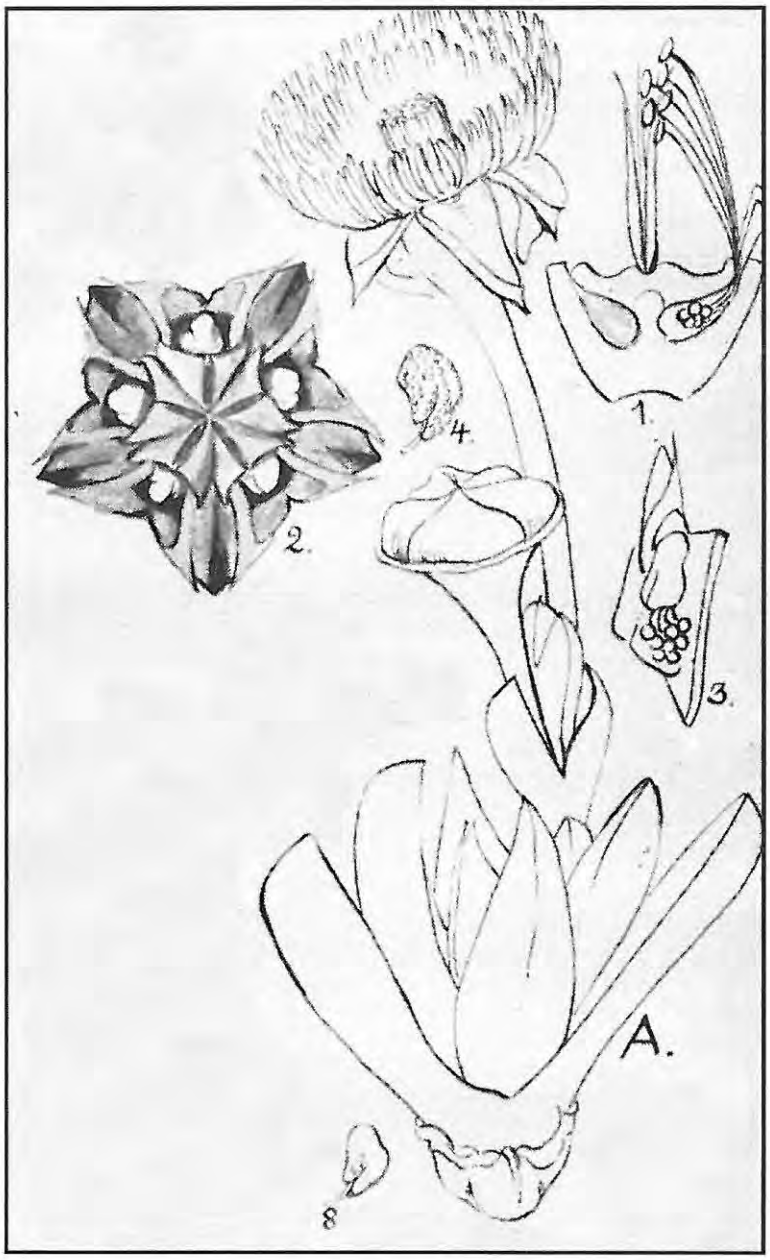

FIGURE 39. —*Bergeranthus artus*, Beatrice Carter's drawing of the type material (Bolus 1928).

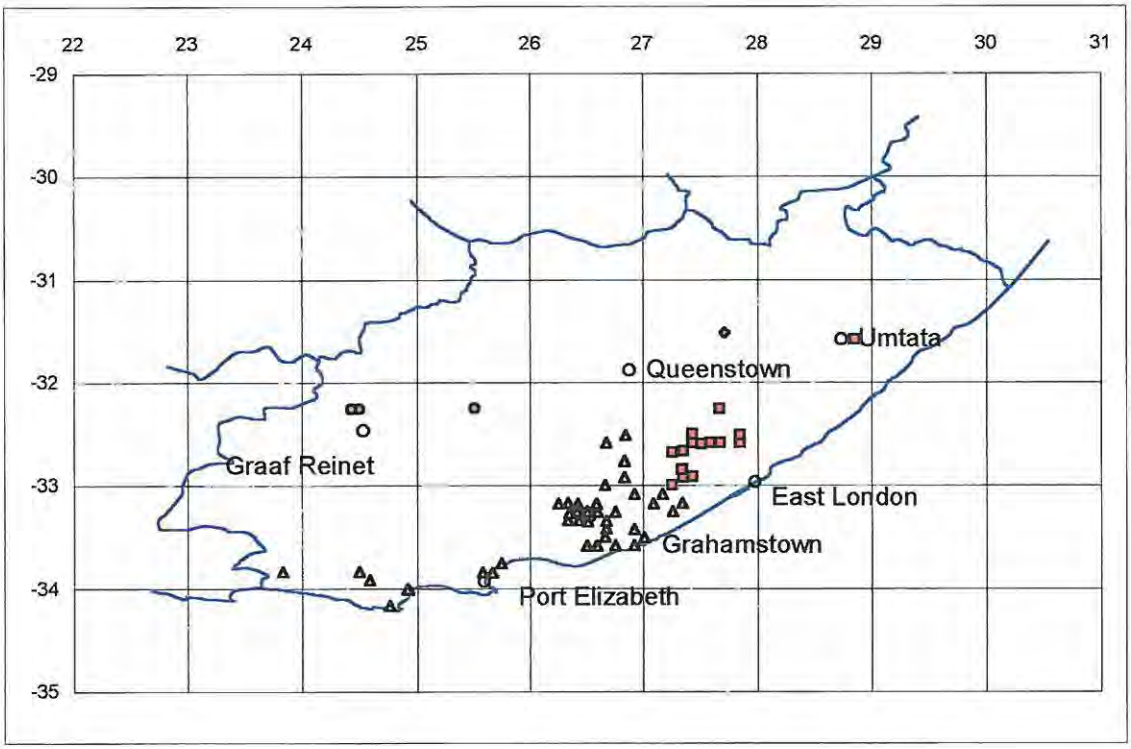

FIGURE 40. —Distribution of *Bergeranthus* species. *B. artus* ○ ; *B. leightoniae* □ ; *B. multiceps* △ ; *B. nanus* ○ .

4. ***B. concavus*** L.Bolus in Notes on Mesembryanthemum and some allied Genera 3: 120 (1938); H.Jacobsen in H.Jacobsen, A.G.J.Herre & O.H.Volk: 86 (1950); H.Jacobsen: 998 (1954); Type: Cape, near East London, July 1935, *A.P.F.Kluth s.n.* in SUG 11048 (BOL, holo!).

Plants single or in loose clumps up to 100 mm across. *Leaves* 8–10, pairs of equal length, ovate, shortly acute, mucronate, tapering in proximal half to the base, central pair erect, outer pair erecto-patent, blade curving outwards, "D"-shaped in cross section, broadest in the middle, yellow-green, smooth, brittle, (24–)27–28(–31) x (7–)10–11(–12) mm, thickest at middle, (4–)5–6(–7) mm, *epidermal wax layer* with parallel sulcate ridges without raised wax sculptures. *Flower* diurnal, opening at approximately 16:00 and closing towards nightfall; *sepals* broadly lanceolate, acute, (7–)9–15 x (3–)4–5(–6) mm, green with a semi-transparent winged margin, without minute sharply pointed dorsal apiculus just below the apex; *petals* (69–)70–76(–88), linear-lanceolate to oblanceolate, spreading, (10–)13–15(–17) x 1–2 mm, yellow, tinged reddish below; *stamens* (130–)179–215(–233), in an erect column, basal inner surface of the filaments of the inner series sparsely white lanulose, (3–)4–5(–7) mm in length; *anthers*

linear; *stigmata* linear, glabrous; *ovary* upper surface 3–4(–5) mm diameter; *nectaries* crescent shaped with blunt, rounded tips, slightly raised, highest in centre of crest becoming lower towards tips, smooth–rounded, dry, yellow. *Capsule* 8–11 x 5–7(–9) mm; *closing bodies* pyriform, apex rounded with a shallow central groove; *covering membranes* shallowly "V"-shaped at distal free margin, not incised at sinus; *expanding sheets* reduced; *expanding keels* linear, acute, entire, distally incurved, short of the valve margin. *Seeds* ovate with short, bluntly protruding micropyles, seed testa with undulate anticlinal walls, pale brown 0.90–1.15 x 0.71–0.76 mm. Figures 41, 42.

Distribution: *B. concavus* has been recorded in a narrow coastal band between Kiwane in the west and Cintsa in the east and only 10 km inland to as far as Chalumna [Tyolomnqa] Police Station (Figure 43).

Ecology: *B. concavus* occurs in Coastal Grassland (Low & Rebelo #48) and open areas within Eastern Thorn Bushveld (Low & Rebelo #16) near East London (Figure 30) at altitudes of 20 to 300 m (Figures 31, 32). The annual rainfall is 544 to 814 mm with an average of 690 mm (Figures 33, 34). *B. concavus* is recorded on calcareous sandstone of the Nanaga Formation within the Algoa Group and sandstone of the Katberg Formation within the Tarkastad Subgroup of the Beaufort Group (Appendix 3).

Conservation status: *B. concavus* is very common within its restricted range. At Kiwane it has been noticed that due to the very loose sandy soil plants are easily kicked over by livestock where they eventually die. Over-stocking of communal farmland is thus a potential threat to this species.

Discussion: Bolus described *B. concavus* from a plant sent to her by A.P.F. Kluth from "near East London" in 1935. The specific name refers to the occasional concave upper leaf surface. *B. concavus* is allied to *B. leightoniae* but the two species are differentiated as follows: *B. concavus* is restricted to bare, exposed sandstone within 10 km of the coast whereas *B. leightoniae* is restricted to exposed dolerite sills in Moist Upland Grassland above 360 m. *B. concavus* has pale yellow-green erect to spreading leaves that are "D"-shaped in cross section and has a unique sulcate leaf epidermal wax formation, the sepals are without a dorsal apiculus and the capsule expanding keels are linear, entire and acute. *B. leightoniae* has dark green, reddish tinged, spreading to decumbent leaves that are "V"-shaped in cross section with an

epidermal wax layer of raised tightly packed granular particles, the sepals are dorsally apiculate and the capsule expanding keels are broadly triangular with serrate lateral (free) margins.

Vouchers: *Dold 4233, 4251, 4352* (GRA).

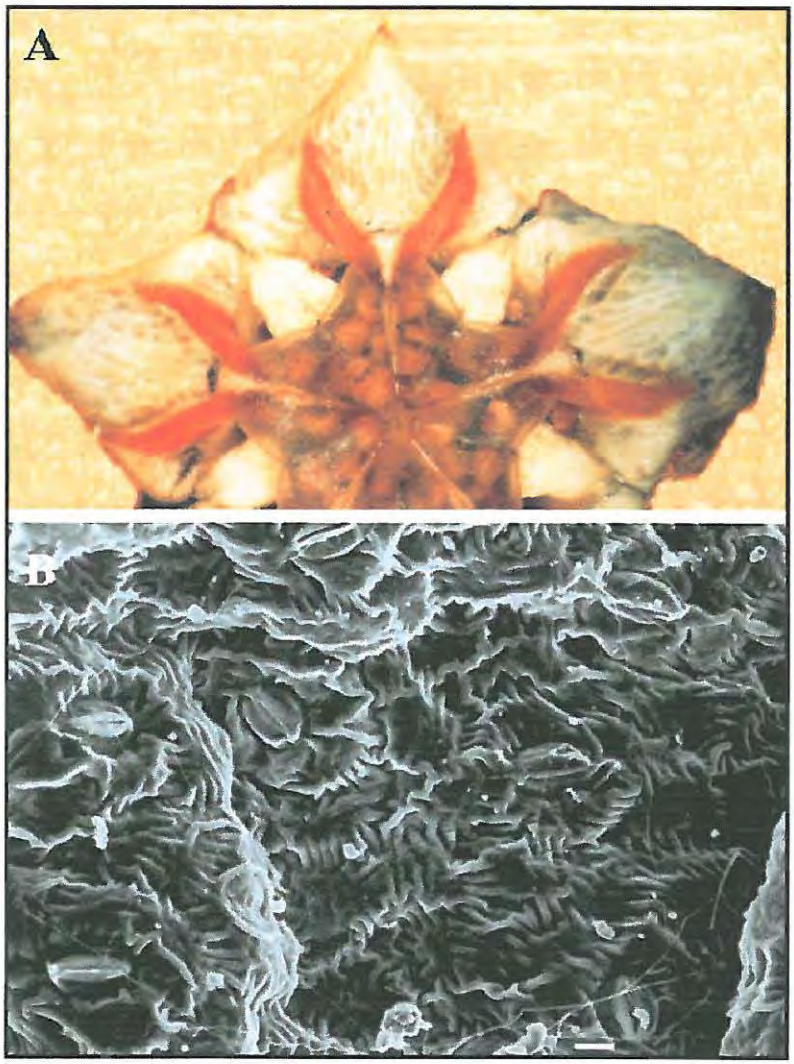

FIGURE 41. —*Bergeranthus concavus*. A. Capsule (*Dold 4251*), 19 mm diameter; B. Leaf epidermal wax layer (*Dold 4234*), scale bar 10 µm.

FIGURE 42. —*Bergeranthus concavus* (*Dold 4237*), Kwelera River Bridge, East London.

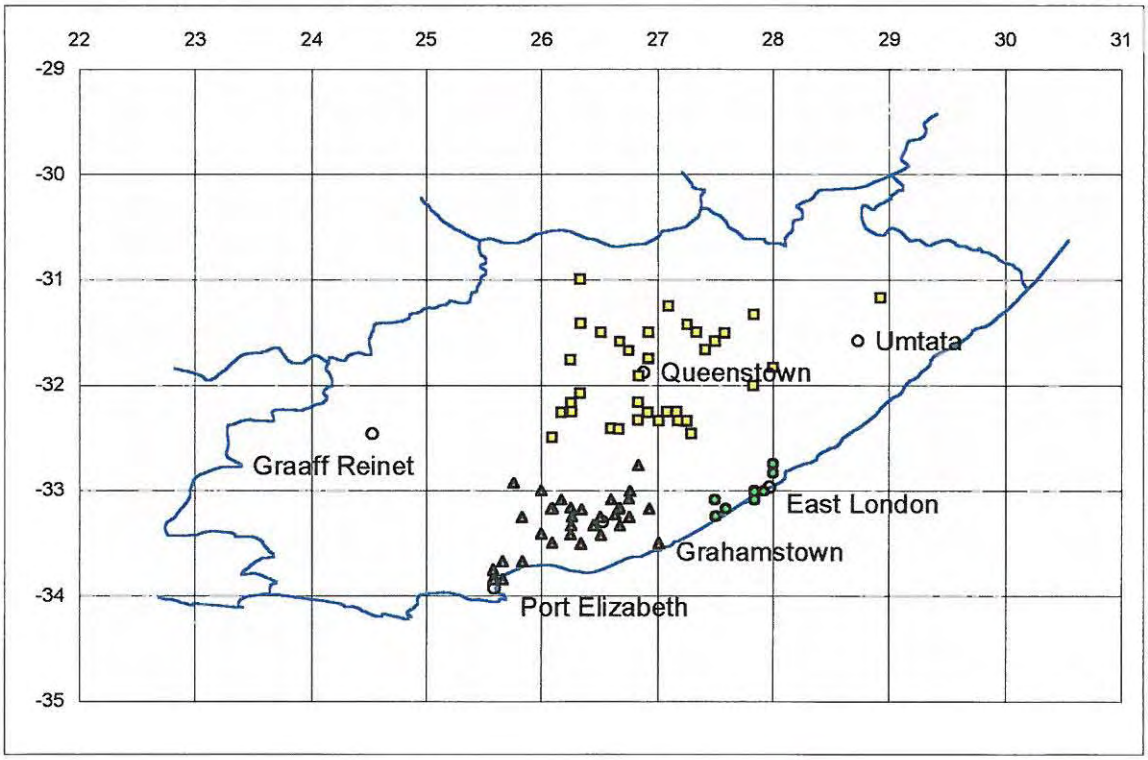

FIGURE 43. —Distribution of *Bergeranthus* species. *B. concavus* ● ; *B. katbergensis* □ ; *B. scapiger* ▲ .

5. ***B. katbergensis*** L.Bolus in Notes on Mesembryanthemum and some allied Genera 3: 233 (1950); H.Jacobsen: 998 (1954); Schwantes: 91 (1957); D.Court: 36 (1981); D.Newton & J.Chan: 124 (1998); C.Hilton-Taylor: 33 (1996); Type: Cape, Katberg Pass, October 1946, *E.E.Esterhuysen 13229* (BOL, holo!).

Plants single or in loose clumps up to 200 mm across in restricted habitats such as rock cracks (see "skeletal habitat" in section on pyhtogeography). *Leaves* (8–)10, pairs of equal length, lanceolate, shortly acute, mucronate, tapering abruptly to base, central pair erect, outer pair erect, blade not curving, "V"-shaped or "D"-shaped in cross section, broadest in middle, yellow green, smooth, brittle, (11–)20–25(–32) x (4–)6– 7(–9) mm, thickest point at the middle, 4–5(–6) mm, *epidermal wax layer* continuous, unbroken, smooth, with scattered raised, smooth, rounded wax sculptures connected by fine threads. *Flower* diurnal, opening at, or shortly after, midday and closing towards nightfall; *sepals* broadly lanceolate, acute, aristate, 7–8(–10) x (2–)3 mm, green with semi-transparent winged margin, without a minute sharply pointed dorsal apiculus just below the apex; *petals* (53–)55–69(–75), linear-lanceolate to oblanceolate, spreading, (10–)12–14(–15) x 1–2 mm, yellow, tinged reddish below; *stamens* (105–)127–146(–160), in an erect column, basal inner surface of the filaments of the inner series sparsely white lanulose, 4–5(–6) mm in length; *anthers* ovate; *stigmata* linear, basal inner surface minutely papillate; *ovary* upper surface 3(–4) mm diameter; *nectaries* crescent shaped with blunt, rounded tips, slightly raised, highest in the centre of the crest becoming lower towards tips, smooth, rounded, dry, yellow. *Capsule* (7–)8–10 x (3–)5–7 mm; *closing bodies* ± pyriform with concave sides, apex rounded with a shallow central groove; *covering membranes* shallowly "V"-shaped at distal free margin, not incised at sinus; *expanding sheets* reduced; *expanding keels* linear, acute, entire, shallowly "C"-shaped, equal to valve. *Seeds* ovate with short, bluntly protruding micropyles, seed testa with undulate anticlinal walls, pale brown 0.93–1.06 x 0.6–0.74 mm. Figures 44, 45.

Distribution: *B. katbergensis* is widespread along the escarpment from Adelaide in the south-west to Shawbury in the east and as far north as Burgersdorp (Figure 43).

Ecology: *B. katbergensis* occurs in Dry Sandy Highveld Grassland (Low & Rebelo #37), Moist Upland Grassland (Low & Rebelo #42) and South-Eastern Mountain Grassland (Low & Rebelo #44) (Figure 46) at altitudes of 1 108 to 1 760 m (Figures 32, 47). The annual rainfall is 398 to 786 mm with an average of 532 mm (Figures 34, 48). *B. katbergensis* is recorded on six

geological formations within its distribution: the Katberg Formation (sandstone) within the Tarkastad Subgroup of the Beaufort Group, the Elliot Formation (sandstone) within the Drakensberg Group, the Molteno Formation (sandstone) of the Drakensberg Group, the Burgersdorp Formation (sandstone) of the Beaufort Group and the Middleton Formation (sandstone) within the Adelaide Subgroup of the Beaufort Group (Appendix 3).

Conservation status: Hilton-Taylor (1996) lists *Bergeranthus katbergensis* as insufficiently known (K), i.e. taxa suspected to belong to any of the categories extinct, endangered, vulnerable, rare or indeterminate. In the absence of a formal revision this categorization is based on herbarium specimen holdings. Fieldwork undertaken here has however enabled a more thorough categorisation. *B. katbergensis* is widespread along the eastern escarpment and very common and therefore does not fit the requirements of the current IUCN categories (http://iucn.org).

Discussion: *B. katbergensis* is named in reference to the type locality, the Katberg Pass in the Fort Beaufort District. Bolus described the species from a cultivated plant sent to her in 1946 by Elsie Esterhuysen and notes that the species was also known from a second collection from Tsomo, made eight years previously by Reynolds. *B. katbergensis* is allied to *B. nanus* but is differentiated from that species by its earlier flower opening time and a distinctive leaf epidermal wax layer of rounded sculptures connected by fine threads. The leaves of *B. katbergensis* are broader than *B. nanus* and the apical keel is not thickened as it is in *B. nanus*.

Hartmann (2002) considers *B. katbergensis* to be synonymous with *B. concavus*.

Vouchers: *Dold 4244, 4254, 4267, 4279, 4392* (GRA).

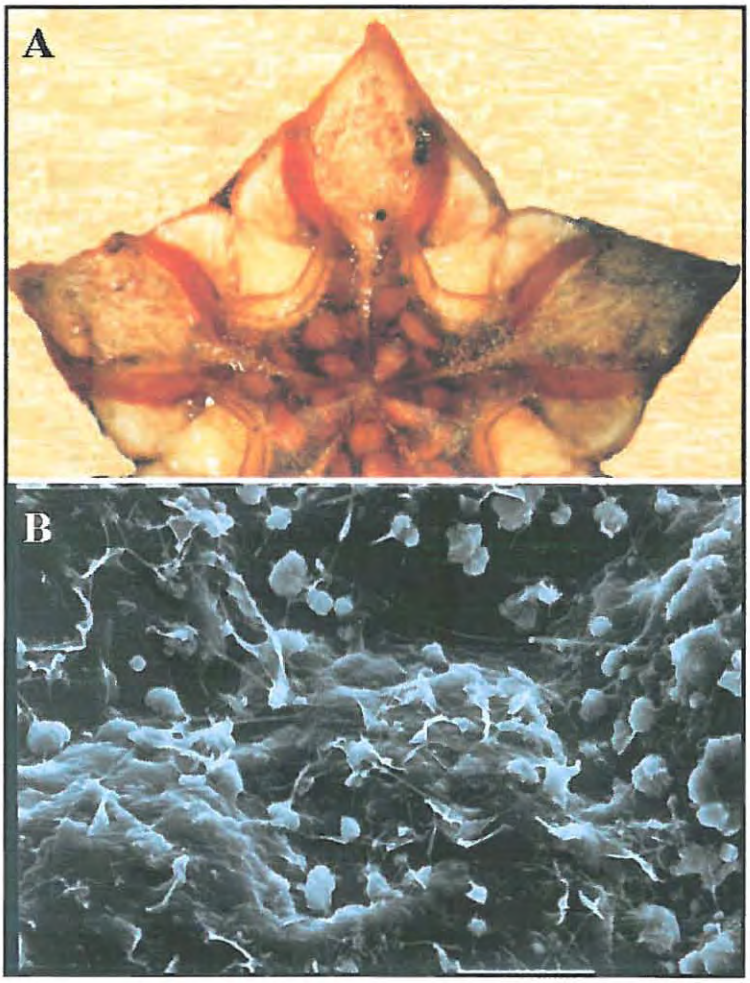

FIGURE 44. —*Bergeranthus katbergensis*. A. Capsule (*Dold 4254*), 16 mm diameter; B. Leaf epidermal wax layer (*Dold 4254*), scale bar 10 µm.

FIGURE 45. —*Bergeranthus katbergensis* (*Dold 4329*), Chilton, Cathcart.

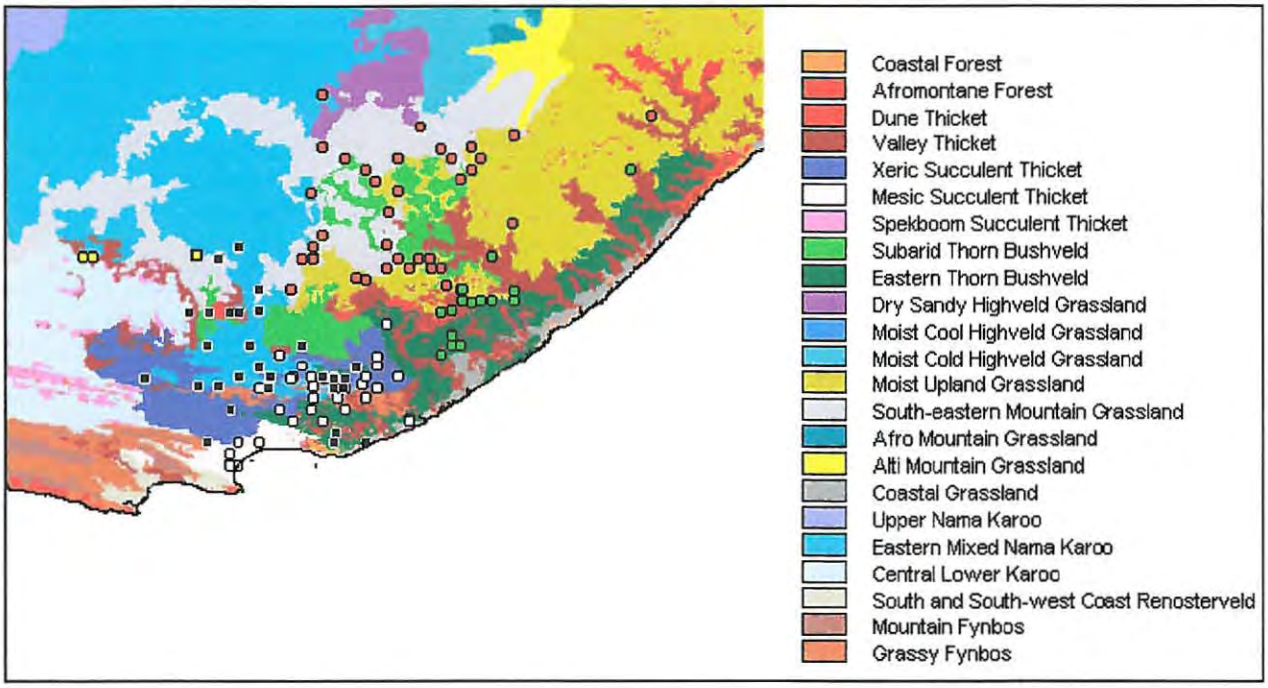

FIGURE 46. —Distribution of *Bergeranthus* species relative to vegetation types (Low & Rebelo 1996). *B. katbergensis* ● ; *B. leightoniae* ■ ; *B. nanus* ■ ; *B. scapiger* □ ; *B. vespertinus* ■

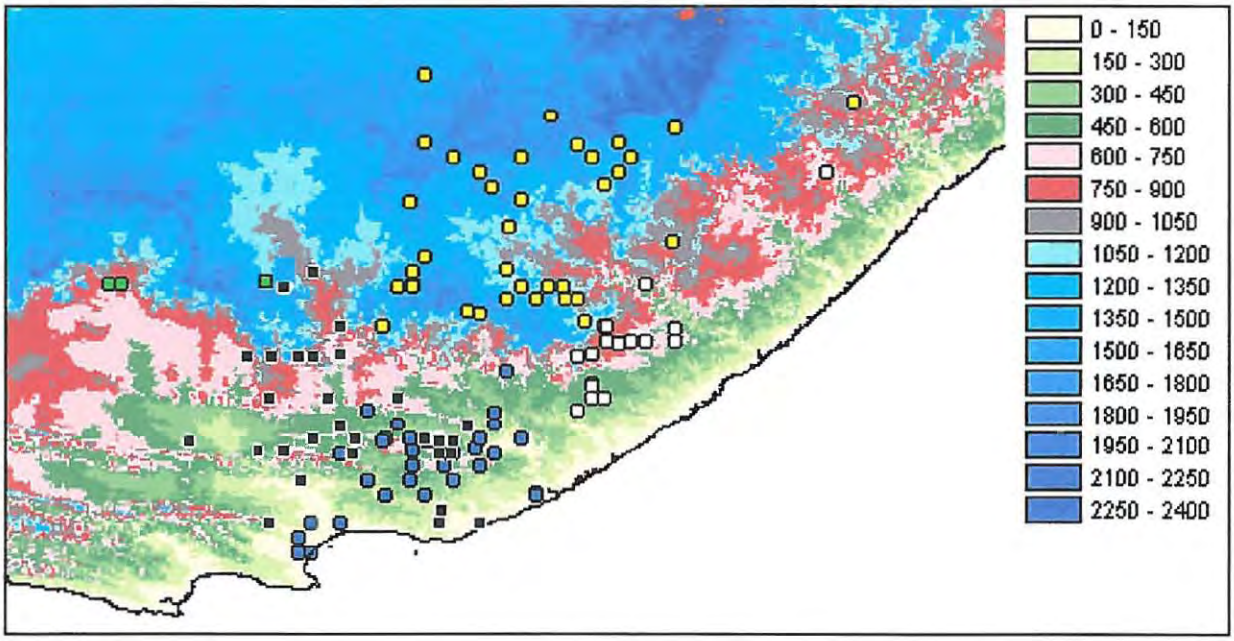

FIGURE 47. —Distribution of *Bergeranthus* species relative to height above sea level (Schulze *et al.*1997). *B. katbergensis* ■ ; *B. leightoniae* □ ; *B. nanus* ■ ; *B. scapiger* ● ; *B. vespertinus* ■

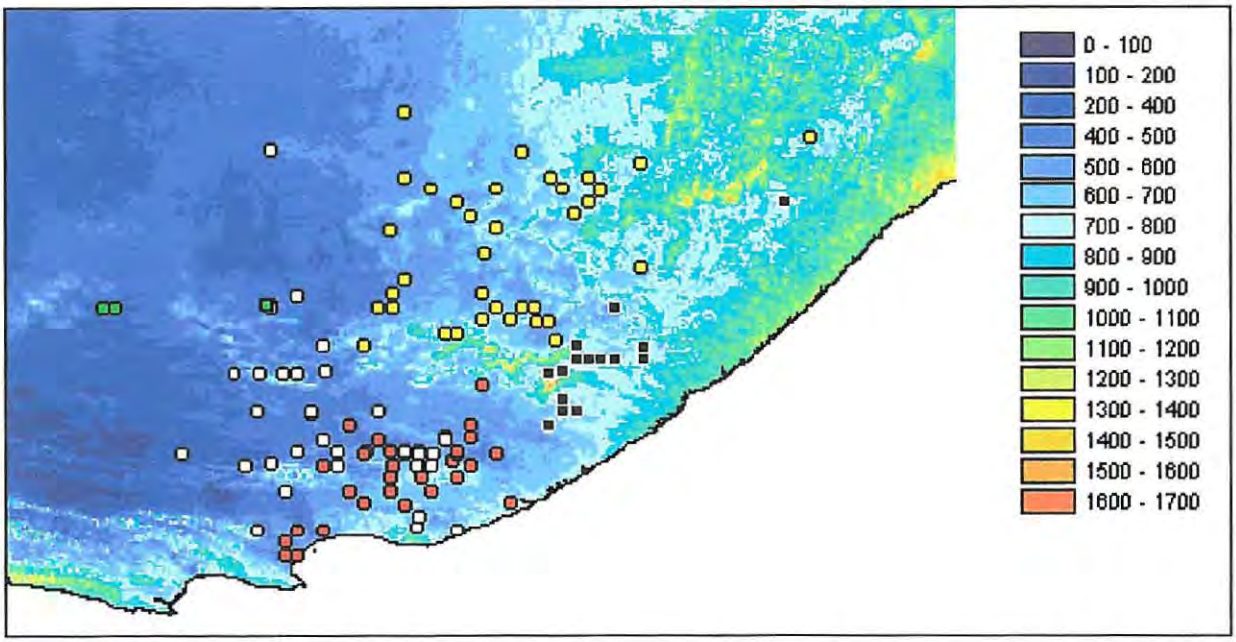

FIGURE 48. —Distribution of *Bergeranthus* species relative to median annual rainfall (Schulze *et al.* 1997). *B. katbergensis* □ ; *B. leightoniae* ■ ; *B. nanus* ■ ; *B. scapiger* ● ; *B. vespertinus* □

6. ***B. leightoniae*** L.Bolus in Notes on Mesembryanthemum and some allied Genera 3: 233 (1950); H.Jacobsen: 998 (1954); Type: Cape, near King William's Town, June 1934, *F.M.Leighton s.n.* in NBG 1537/34 (BOL, holo!).

B. parvus N.E.Br. *ex* A.R.H.Martin & A.R.A.Noel in Flora of Albany and Bathurst: 44 (1960) *nom. nud.*

Plants single, closely dispersed. *Leaves* 8–10, pairs of equal length, ovate, acuminate, mucronate, tapering abruptly to the base or truncate, central pair spreading, outer pair decumbent, blade reflexed, broadly "V"-shaped in cross section, broadest in the middle, dorsally flattened, dull grey-green, apex often tinged reddish, rugose, brittle, (14–)23–30(–44) x (5–)9–10(–11) mm, thickest at the middle, 4–5 mm; *epidermal wax layer* of raised tightly packed granular particles. *Flower* diurnal, opening at approximately 16:00 and closing towards nightfall; *sepals* broadly lanceolate, acute, (10–)11–12(–14) x (3–)4–5 mm, green with semi-transparent winged margins, each with a sharply pointed dorsal apiculus just below the apex; *petals* (50–)65–88(–103), linear to linear-lanceolate, spreading, (7–)10–14(–26) x 1–2 mm, yellow, tinged reddish below; *stamens* (109–)147–174(–216), in an erect column, filaments glabrous, (3–)4–6(–7) mm in length; *anthers* linear; *stigmata* linear, basal inner surface sparsely

puberulous; *ovary* upper surface 3–4(–5) mm diameter; *nectaries* crescent shaped with blunt, rounded tips, slightly raised, highest in the centre of the crest becoming lower towards the tips, smooth, rounded, dry, yellow. *Capsule* 7–8 x 3–6 mm; *closing bodies* pyriform, apex rounded, bilobed; *covering membranes* shallowly "V"-shaped at distal free margin, not incised at sinus; *expanding sheets* broad, extending up to and surrounding the closing body and meeting at the valve sinus; *expanding keels* broad, acute, margin serrate, straight, equal to the valve. *Seeds* ovate with short, bluntly protruding micropyles, seed testa with undulate anticlinal walls, pale brown, 0.81–1.07 x 0.55–0.86 mm. Figures 49, 50.

Distribution: *B. leightoniae* is most common in the King William's Town, Stutterheim and Komgha Districts with a single disjunct population in Umtata (Figure 40). It is likely that this species was once more common in the Transkei region before human settlement.

Ecology: *B. leightoniae* occurs in Moist Upland Grassland (Low & Rebelo #42) (Dohne sourveld – Acocks 44b) between King William's Town and Umtata (Figure 46) at altitudes of 360 to 1 140 m (Figures 32, 47). The annual rainfall is 481 to 1 053 mm with an average of 639 mm (Figures 34, 48). *B. leightoniae* is recorded primarily on exposed intrusive dolerite sills with a single record (Umtata) on grey and brownish-red mudstone and sandstone of the Katberg Formation within the Tarkastad Subgroup of the Beaufort Group (Appendix 3).

Conservation status: Although *B. leightoniae* is restricted by a specific habitat requirement the species is common within its range. It is likely that this species was far more common in the Transkei region in the past but has been severely depleted by overgrazing. Only two populations have been recorded in the region despite an abundance of suitable habitat. At Ndabakazi, near Butterworth, plants were rare and many had been damaged. A large and healthy population in Umtata is within the University of Transkei campus and therefore protected from livestock.

Discussion: *B. leightoniae* is named after Frances Leighton who collected the plant in 1934 at Mgqakwebe just west of King William's Town. The species was described from this cultivated material only. *B. leightoniae* and *B. concavus* are closely allied and the distinguishing features are discussed under the latter species.

N.E. Brown was of the opinion that two specimens, *Dyer 1529* (GRA!) & *Welsh 22* (GRA!) represented a distinct species and in 1933 he noted on the specimens that he intended to publish the name *B. parvus*, however he died in 1934 before he was able to do so. Although Martin &

Noel (1960) listed the species in Flora of Albany and Bathurst on the basis of Brown's determinavit label the name was never formally published.

Hartmann (2002) considers *B. leightoniae* to be synonymous with *B concavus*.

According to Rose and Jacot Guillarmod (1974) *Bergeranthus* sp. (no specimen preserved) is known as *intshawu* in Xhosa and the roots are used to fortify beer in the Transkei region. Recent findings show that roots of several taxa within the Mesembryanthemaceae provide a fermenting mould used in the making of traditional San, Khoekhoe and Xhosa alcoholic beverages (Dold *et al.* 1999). Rose and Jacot Guillarmod (1974) most likely refer to *B. leightoniae* as this is the only species of *Bergeranthus* recorded in the Umtata vicinity where Dr Elizabeth Rose undertook the fieldwork for this study (Dr. E. Rose pers. comm. 1998).

Vouchers: *Dold 4192, 4232, 4243, 4304* (GRA).

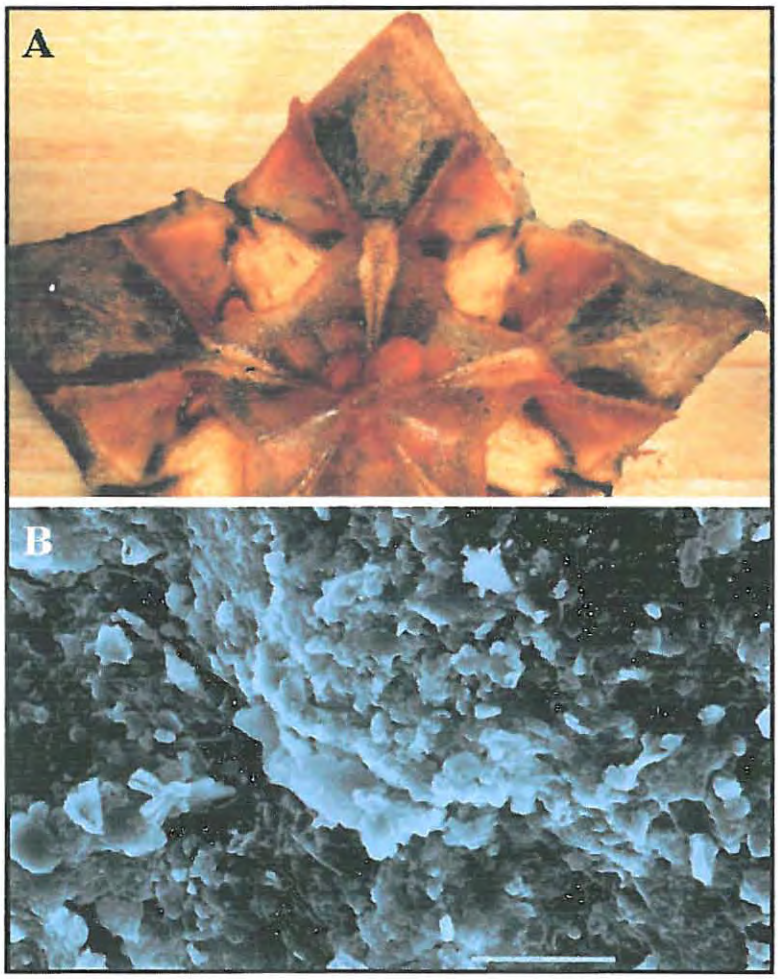

FIGURE 49. —*Bergeranthus leightoniae*. A. Capsule (*Dold 4301*), 26 mm diameter; B. Leaf epidermal wax layer (*Dold 4235*), scale bar 10 μm.

FIGURE 50. —*Bergeranthus leightoniae* (*Dold 4258*), Mgqakwebe, King William's Town.

7. ***B. multiceps*** (Salm-Dyck) Schwantes in Zeitschrift für Sukkulentenkunde 2: 180 (1926); N.E.Br.: 267 (1928); N.E.Br. *et al.*: 121 (1931); H.Jacobsen: 94 (1933); Pax & K.Hoffmann in Engl. & Harms: 211 (1934); H.Jacobsen: 131 (1935); H.Jacobsen in H.Jacobsen, A.G.J.Herre & O.H.Volk: 86 (1950); L.Bolus: 234 (1950); H.Jacobsen: 999 (1954); Schwantes: 90 (1957); A.R.H.Martin & A.R.A.Noel: 44 (1960); A.Batten & H.Bokelman: 67 (1966); D.Newton & J.Chan:124 (1998); N.Urton & D.Page: 70 (1993); H.Vanderplank: 6 (1998); Type: Salm-Dyck *Monogr. Gen Aloe et Mesemb* 3: § 6 f 2 (1854) (GRA, icono!).

Mesembryanthemum multiceps Salm-Dyck in *Monogr. Gen. Aloes Mesemb.* 3: § 6 f 2 (1854); Sond. in Harv. & Sond.: 399 (1862); Sim: 39 (1891); A.Berger: 253 (1908); Schönland: 53 (1919)

M. bibracteatum Ecklon & Zeyher in Enum. pl. afric. austral.: 308 (1837) based on Eckl. & Zeyh. 1980 (G!, B!, MO!) after Sond. in Harv. & Sond.: 399 (1862) (*non* *M. bibracteatum* Haw. Syn. Plant. Succ.: 213, 1812).

Bergeranthus firmus L.Bolus, in Notes on Mesembryanthemum and some allied Genera 3: 121 (1938); H.Jacobsen in H.Jacobsen, A.G.J.Herre & O.H.Volk: 86 (1950); L.Bolus: 234 (1950); Type: Cape, near Swartkops River, July 1931, *L. Bolus s.n.* in NBG 886/31 (BOL, holo!).

Plants single or loosely clump forming up to 130 mm across. *Leaves* (6–)8–10(–12), pairs of equal length, broadly lanceolate, acuminate, mucronate, tapering in the proximal half to the base, central pair erect, outer pair spreading to decumbent, blade curving outwards, "V"-shaped in cross section, broadest in the middle, dark green, apex often tinged reddish, rugose, pliable, (16–)24–45 x (6–)7– 8(–10) mm, thickest at the base, (3–)4–5(–6) mm; *epidermal wax layer* of loosely packed small granular structures interspersed with larger rounded bodies. *Flower* diurnal, opening at approximately 16:00 and closing towards nightfall; *sepals* broadly lanceolate, acute, (6–)8–14(–15) x 3–4(–5) mm, green with semi-transparent winged margins, each with or without a minute sharply pointed dorsal apiculus just below the apex; *petals* (47–)75–90(–117), linear-lanceolate, spreading, (7–)9–15(–16) x 1–2 mm, yellow, tinged reddish below; *stamens* (94–)150–215(–460), in an erect column, basal inner surface of the filaments of the inner series sparsely white lanulose, 3–6(–7) mm in length; *anthers* ovate; *stigmata* linear, glabrous; *ovary* upper surface (2–)3–4(–5) mm diameter; *nectaries* crescent shaped with blunt, rounded tips, slightly raised, highest in the centre of the crest becoming lower towards tips, smooth to rounded, dry, yellow. *Capsule* (6–)7–9(–15) x (3–)4–6(–7) mm; *closing bodies* attenuate-triangular; *covering membranes* shallowly "V"-shaped at distal free margin, not incised at the sinus; *expanding sheets* broad, thickened, the outer margin not reaching the closing body; *expanding keels* broad, entire, straight, short of the valve margin, apex broadly acute. *Seeds* ovate with short, bluntly protruding micropyles, seed testa with undulate anticlinal walls, pale brown, 0.84–1.11 x 0.54–0.76 mm. Figures 2, 51, 52.

Distribution: *B. multiceps* is widespread in the Eastern Cape from Joubertina in the west to the Keiskamma River in the east and as far north as Michell's Pass near Hogsback (Figure 40).

Ecology: *B. multiceps* occurs in Valley Thicket (Low & Rebelo #5) around Grahamstown, Xeric Succulent Thicket (Low & Rebelo #6) north of Grahamstown, Mesic Succulent Thicket (Low & Rebelo #7) around Port Elizabeth, Eastern Thorn Bushveld (Low & Rebelo #16) from Peddie and Alice, Coastal Grassland (Low & Rebelo #48) near Port Alfred, South and South-west Coast Renosterveld (Low & Rebelo #63) near Humansdorp, and Grassy Fynbos (Low & Rebelo #65) around Grahamstown and Humansdorp (Figure 30) at altitudes of 20 to 1 520 m (Figures 31, 32). The annual rainfall is 344 to 741 mm with an average of 536 mm (Figures 33, 34). *B. multiceps* is recorded on 15 geological formations within its distribution: the Balfour Formation (grey mudstone and sandstone) within the Adelaide Subgroup of the Beaufort Group, the Grahamstown Formation (silcrete & kaolinite), the Goudini Formation (brownish weathering quartzitic sandstone) within the Nardouw Formation of the Table Mountain Group, the Middleton Formation (grey & red mudstone) within the Adelaide Subgroup of the Beaufort Group, the Koonap Formation (mudstone & subordinate sandstone) within the Adelaide Subgroup of the Beaufort Group, the Blue Water Bay Formation (alluvial sheet gravel and sand), the Witpoort Formation (quartzite) within the Lake Mentz Subgroup of the Witteberg Group, shale, sandstone and diamictite (not formally placed in a Formation) within the Lake Mentz Subgroup of Witteberg Group, the Weltevrede Formation (shale & quartzite) within the Lake Mentz Subgroup of the Witteberg Group, the Nanaga Formation (calcareous sandstone & sandy limestone) of the Algoa Group, the Boplaas Formation (sandstone) within the Ceres Subgroup of the Bokkeveld Group, the Kommadagga Subgroup (shale, siltstone, sandstone & diamictite) of the Witteberg Group, Dwyka tillite of the Dwyka Group, intermediate and low-level fluvial terrace gravel, and intrusive dolerite sills (Appendix 3).

Conservation status: *B. multiceps* is common within its range.

Discussion: *B. multiceps* (*multus* (L) = many; *kephale* (Gr) = head) refers to its floriferous habit. *B. multiceps* and *B. vespertinus* are closely allied but are distinguished as follows: *B. vespertinus* is associated with karroid veld, the leaves are broadest at the base, the closing body of the fruit is round, the expanding sheet is much reduced, the expanding keel is linear-acute with a serrate margin and the apex is attenuate and extended beyond the valve. *B. multiceps* is associated with open grassland, the leaves are broadest in the middle, the closing body of the fruit is triangular,

the expanding sheet is broad and thickened, the expanding keel is broad and entire and the apex is broadly acute but not extended beyond the valve.

Sonder (1862) placed Haworth's (1812) *Mesembryanthemum bibracteatum* Haw. in synonymy with *M. rostratum* var. *brevibracteatum*, now *Cheiridopsis rostrata* (L.) N.E.Br.

B. multiceps is well known in the Peddie District were it is called *unomgushe*. The roots are eaten as a snack food by children and taste remarkably like unsalted peanut (pers. obs.).

Vouchers: *Dold 4186, 4194, 4219, 4227, 4312* (GRA).

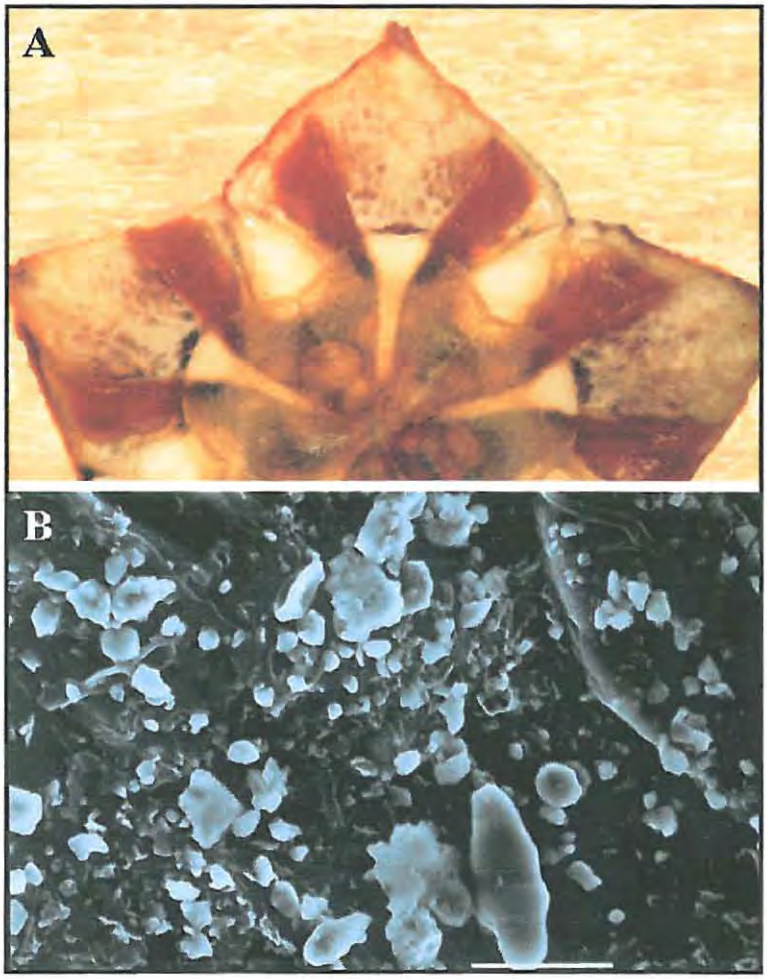

FIGURE 51. —*Bergeranthus multiceps*. A. Capsule (*Dold 4189*), 15 mm diameter; B. Leaf epidermal wax layer (*Dold 4186*), scale bar 10 µm.

FIGURE 52. —*Bergeranthus multiceps* (*Dold 4189*), Grahamstown commonage.

8. ***B. nanus*** *A.P.Dold* sp. nov.

Bergeranthus nanus *A.P.Dold* sp. nov. *B. katbergensis* L. Bolus affinis, sed carina foliorum apice incrassata, albida, cera foliorum sculpturas multifaciales elevatasque in seriebus parallelis plusminusque facienti.

TYPE.–Eastern Cape, 3224 (Graaff Reinet): Valley of Desolation, lookout point, (–AD), 1 200 m, 23-11-1999, *Dold 4388* (GRA, holo., BOL, PRE).

Plants single or forming loose clumps up to 100 mm across in restricted habitats such as rock cracks. *Leaves* 8, pairs of equal length, lanceolate, shortly acute, mucronate, base truncate, distal keel and apex thickened, whitish, central pair spreading, outer pair spreading, blade curving inwards, "D"-shaped in cross section, broadest at the base, pale green, smooth, brittle, (10–)15–22(–30) x (4–)5–6(–7) mm, thickest at the base ± 5 mm; *epidermal wax layer* of multifaceted

raised sculptures arranged in parallel rows. *Flower* diurnal, opening at approximately 16:00 and closing towards nightfall; *sepals* broadly lanceolate, acute, 6.5–7.0 x 3.0–3.5 mm, green with a semi-transparent winged margin, with or without a minute sharply pointed dorsal apiculus just below the apex; *petals* ± 60, oblanceolate, acute, spreading, 9–10 x 1.0–1.5 mm, yellow; *stamens* 156, in an erect column, basal inner surface of the filaments of the inner series sparsely white lanulose, 3–4 mm in length; *anthers* linear; *stigmata* linear, basal inner surface sparsely puberulous; *ovary* upper surface 2 mm diameter; *nectaries* crescent shaped with blunt, rounded tips, slightly raised, highest in the centre of the crest becoming lower towards the tips, smooth to rounded, dry, green. *Capsule* 6–8 x 5 mm; *closing bodies* broadly triangular; *covering membranes* shallowly "V"-shaped at distal free margin, not incised at sinus; *expanding sheets* reduced; *expanding keels* lanceolate, acute, margin serrate, distally incurved, extended beyond the valve, apex attenuate, incurved. *Seeds* ovate with short, bluntly protruding micropyles, seed testa with undulate anticlinal walls, pale brown, 0.9–0.92 x 0.6–0.62 mm. Figures 53, 54.

Distribution: *B. nanus* is only known from the Valley of Desolation at Graaff Reinet and a single population at Grootvlei south of the Swaershoek Pass (Figure 40).

Ecology: *B. nanus* occurs in the Central Lower Nama Karoo (Low & Rebelo #54) near Graaff Reinet and South-eastern Mountain Grassland (Low & Rebelo #44) between Somerset East and Cradock (Figure 46) at altitudes of 1 200 to 1 173 m (Figures 32, 47). The annual rainfall is 332 to 356 mm with an average of 344 mm (Figures 34, 48). *B. nanus* is recorded only on exposed intrusive dolerite sills (Appendix 3).

Conservation status: *Bergeranthus nanus* is known from two localities 90 km apart, the Valley of Desolation near Graaff Reinet and Groot Vlei farm, 37 km north of Somerset East. Each locality comprises a single scattered population of relatively few plants when compared to other species of *Bergeranthus* whose numbers are usually numerous. The IUCN category (www.iucn.org) Vulnerable (VU: D1, D2) is therefore applied to *B. nanus*. Further fieldwork in the Sneeuwberge and Coetzeesberge mountains will most likely locate additional populations of *B. nanus*.

Discussion: *Bergeranthus nanus* is named in reference to it small size (*nanos* (Gr) = dwarf) and is incorrectly figured in Smith *et al.* (1998) as *B. jamesii*. *B. nanus* is allied to *B. katbergensis* but differs in having an apically thickened whitish leaf keel and a unique epidermal wax layer

comprising multifaceted raised sculptures arranged in ± parallel rows. Furthermore it is a smaller plant with narrower leaves.

Vouchers: *Dold 4271* (GRA); *Hammer 1150* (GRA); *Vlok, 2708* (GRA).

FIGURE 53. —*Bergeranthus nanus*. A. Capsule (*Dold 4317*), 8 mm diameter; B. Leaf epidermal wax layer (*Dold 4388*), scale bar 10 µm.

FIGURE 54. —*Bergeranthus nanus* (*Dold 4271*), Valley of Desolation, Graaff Reinet.

9. ***B. scapiger*** (Haw.) Schwantes in Zeitschrift für Sukkulentenkunde 2: 180 (1926); N.E.Br.: 267 (1928); N.E.Br. *et al.*: 122 (1931); H.Jacobsen: 95 (1933); Pax & K.Hoffmann in Engl. & Harms: 211 (1934); H.Jacobsen: 131 (1935); R.A.Dyer: 97 (1937); H.Jacobsen in H.Jacobsen, A.G.J.Herre & O.H.Volk: 86 (1950); H.Jacobsen: 999 (1954); Schwantes: 91 (1957); A.R.H.Martin & A.R.A.Noel: 44 (1960); E.Gledhill: 113 (1969); A.G.J.Herre: 90 (1971); M.Sajeva & M.Costanzo: 55 (1995); Type: Material grown from seed collected by Bowie in 1820, numbered 305/1821 and 2885/1822, represented by a painting prepared by J. Duncanson, gardener at Kew, numbered 1006/208 (K, icono photo!).

> *Mesembryanthemum scapigerum* Haw. in Phil. Mag. December 1824: 423; DC.: 423 (1828); Salm-Dyck: 3: § 6 f.1 (1854); Sond. in Harv. & Sond.: 399 (1862); A.Berger: 252 (1908); *non M. scapiger* Eckl. & Zeyh.: 309 (1837).

Plants single or in loose clumps, up to 100 mm high. *Leaves* (6–)8–10(–12), pairs of unequal length, lanceolate, mucronate, shortly acute, base truncate, central pair erect, outer pair spreading, blade curving outwards, "V"-shaped or "D"-shaped in cross section, broadest at the base, distal keel chinned, pale yellow-green, smooth, brittle, (45–)60–80(–101) x (8–)11–15(–20) mm, thickest point above the middle (4.5–)6.0–8.0(–10.0) mm; *epidermal wax layer* of smooth slightly raised plates with scattered granular structures. *Flower* diurnal, opening at approximately 16:00 and closing towards nightfall; *sepals* broadly lanceolate, acute, (10–)13–15(–17) x 4–6 mm, green with a semi-transparent winged margin, with or without a minute sharply pointed dorsal apiculus just below the apex; *petals* (90–)96–110(–211), linear-lanceolate, spreading, (10–)14–19 x 1.5–2.0 mm, yellow, tinged reddish below; *stamens* 217–326(–401), in a solid erect column, filaments glabrous, (5–)6–9 mm in length; *anthers* linear; *stigmata* linear, basal inner surface sparsely puberulous; *ovary* upper surface (4–)5(–7) mm diameter; *nectaries* crescent shaped with blunt, rounded tips, slightly raised, highest in the centre of the crest becoming lower towards tips, smooth to rounded, dry, yellow. *Capsule* 9–10(–12) x 5–8(–10) mm; *closing bodies* pyriform, apex rounded with a shallow central groove; *covering membranes* shallowly "V"-shaped at distal free margin and broadly incised at the sinus; *expanding sheets* on the distal half of the keel only, inconspicuous; *expanding keels* lanceolate, margin serrate, distally incurved, extended beyond the valve margin, apex attenuate, incurved. *Seeds* ovate with short, bluntly protruding micropyles, seed testa with undulate anticlinal walls, pale brown, 0.98 x 0.68–0.74 mm. Figures 1, 3, 4, 55, 56.

Distribution: *B. scapiger* occurs from Port Elizabeth in the west to the Kap River Reserve in the east and as far north as Alice (Figure 43).

Ecology: *B. scapiger* occurs in Valley Thicket (Low & Rebelo #5) near Grahamstown, Xeric Succulent Thicket (Low & Rebelo #6) near Fort Beaufort, Mesic Succulent Thicket (Low & Rebelo #7) near Port Elizabeth, and Eastern Thorn Bushveld (Low & Rebelo #16) south of Grahamstown and near Alice (Figure 46) at altitudes of 15 to 853 m (Figures 32, 47). The annual rainfall is 357 to 661 mm with an average of 541 mm (Figures 34, 48). *B. scapiger* is recorded on 10 geological formations within its distribution: the Grahamstown Formation (silcrete & kaolinite), the Collingham/Whitehill/Prince Albert Formation (shale & tuff) of the Ecca Group, the Blue Water Bay Formation (alluvial sheet gravel and sand), the Witpoort Formation (quartzite) within the Lake Mentz Subgroup of the Witteberg Group, the Balfour Formation (grey mudstone, shale & sandstone) within the Adelaide Subgroup of the Beaufort

Group, the Koonap Formation (mudstone & subordinate sandstone) within the Adelaide Subgroup of the Beaufort Group, the Lake Mentz Subgroup (shale, quartzite, sandstone & diamictite) of the Witteberg Group, the Weltevrede Formation (shale & quartzite) within the Lake Mentz Subgroup of the Witteberg Group, the Fort Brown Formation (Rhythmite, subordinate shale and sandstone) of the Ecca Group and Dwyka tillite (Appendix 3).

Conservation status: *B. scapiger* is common within its range. The practice of "bush-clearing" by farmers to open up thicket areas for livestock has had an effect on populations but fortunately this is seldom undertaken anymore.

Discussion: *B. scapiger* is named in reference to the scaped inflorescence. This species is allied to *B. albomarginatus* and differences between the two are discussed under that species. It is unmistakable being the largest species in the genus characterised by its sharply three-angled yellow green leaves.

The iconotype, a painting by J. Duncanson, (Figure 1) was only recently discovered in Kew herbarium by Dr. H. Hartmann (pers. comm. 2001). Duncanson's figure, numbered 1006/208, signed and dated in 1823, is annotated as follows: "*Mesembr. scapiger Haw. in Phil. Mag.*; *Raised from seeds collected by Mr Bowie on rocks on the Cowie River in Albany. 6th Dec. 1829.*" The plant material is numbered *305/1821* and *2885/1822*. No specimen of this material is known to exist but there is little doubt that the painting represents the material seen by Haworth. In his *Third Decade of new Succulent Plants,* Haworth (1824) clearly attributes his description to the plants grown from Bowie's seed. Furthermore he notes " ...these fine plants... as Mr Bowie himself assured me while we were examining them, have almost exactly the face or appearance which they usually assume in their own remote and native land".

Many authors have perpetuated the incorrect specific epithets *scapigerum* and *scapigerus*. It should be noted that Mesembryanthemum is a neuter noun based on *Anthemon* and therefore the correct specific epithet is *scapigerum*. The correct specific epithet for *Bergeranthus*, based on the masculine *anthus* is *scapiger*.

Sonder (1862) placed *Mesembryanthemum scapiger* Eckl. & Zeyh. in synonymy with *M. rhomboideum* Salm-Dyck, now *Rhombophyllum rhomboideum* (Salm-Dyck) Schwantes.

A localised population at Drivers Bush (*Dold 4276*) east of Grahamstown is noteworthy for the plants' atypical diminutive size. It is suggested that this anomaly is a result of veld management whereby the associated thicket has been historically cleared increasing exposure of an already well-established population.

Vouchers: *Cloete 2496* (GRA); *Dold 4193, 4263, 4328, 4252* (GRA).

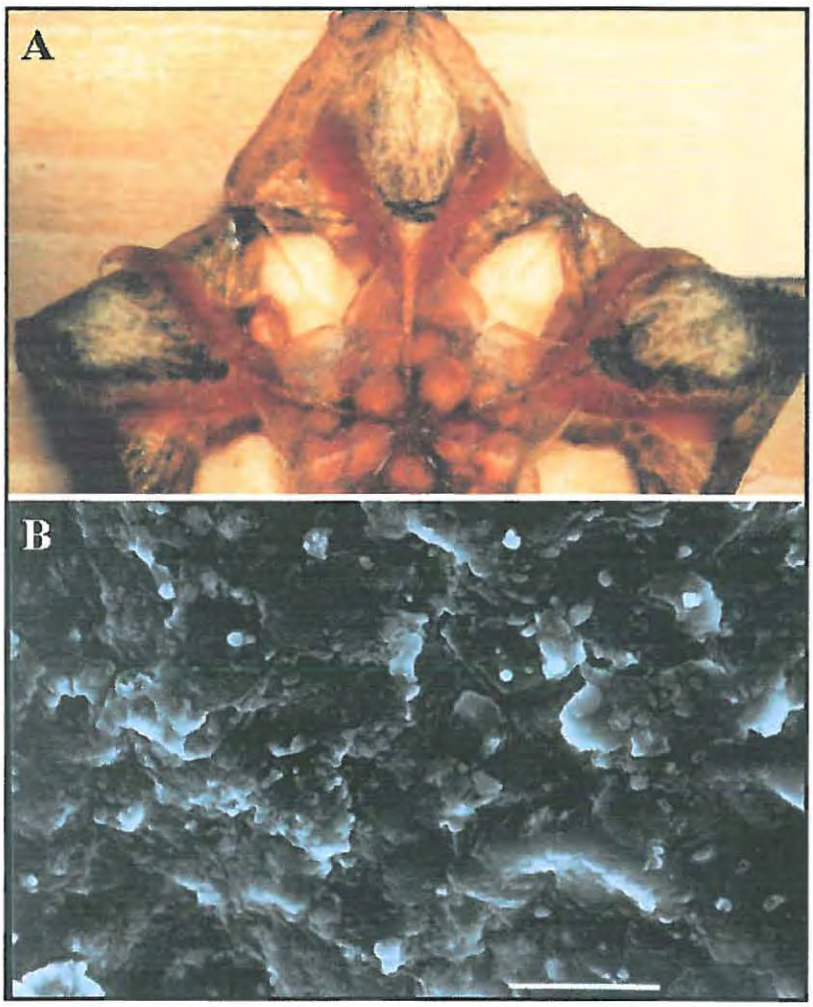

FIGURE 55. —*Bergeranthus scapiger*. A. Capsule (*Dold 4313*), 17 mm diameter; B. Leaf epidermal wax layer (*Dold 4191*), scale bar 10 µm.

FIGURE 56. —*Bergeranthus scapiger* (*Dold 4262*), Bloukrans Reserve, Grahamstown.

10. ***B. vespertinus*** (A.Berger) Schwantes in Zeitschrift für Sukkulentenkunde 2: 180 (1926); N.E.Br.: 267 (1928); H.Jacobsen: 95 (1933); Pax & K.Hoffmann in Engl. & Harms: 211 (1934); H.Jacobsen: 132 (1935); R.A.Dyer: 97 (1937); Fourc.: 7 (1940); H.Jacobsen in H.Jacobsen, A.G.J.Herre & O.H.Volk: 86 (1950); H.Jacobsen: 999 (1954); Schwantes: 90 (1957); A.R.H.Martin & A.R.A.Noel: 44 (1960); Lectotype designated here: *H. Strauss s.n.* BOL 63684 Cape Colony (BOL, lecto!).

Mesembryanthemum vespertinum A.Berger in Mesembrianthemen und Portulacaceen: 253 (1908); A.Berger: 228 (1911).

B. longisepalus L.Bolus in Notes on Mesembrianthemum and some allied Genera 2: 476 (1935); H.Jacobsen in H.Jacobsen, A.G.J.Herre & O.H.Volk: 86 (1950); H.Jacobsen: 998 (1954); Type: Cape, Bushman's River (Alexandria), January 1934, *James s.n.* in NBG 187/35 (BOL, holo!).

B. jamesii L.Bolus in Notes on Mesembryanthemum and some allied Genera 3: 21 (1938); H.Jacobsen in H.Jacobsen, A.G.J.Herre & O.H.Volk: 86 (1950); H.Jacobsen: 998 (1954); D.Newton & J.Chan:124 (1998); Type: Cape, near Halesowen, November 1931, *H.W.James 127* (BOL, holo!).

Plants single or occasionally in loose clumps in restricted habitats. *Leaves* 8–10(–12), pairs of equal or unequal length, lanceolate–attenuate, acute, mucronate, tapering gradually in proximal half to the base or truncate, central pair erect, outer pair spreading, blade curving inwards or outwards, "V"-shaped or "D"-shaped in cross section, broadest at the base, dark green to pale green, rugose, pliable, (20–)24–39(–54) x (4–)5– 6(–8) mm, thickest at the base or below the middle, (2)4–5(–6) mm; *epidermal wax layer* of densely packed multifaceted particles. *Flower* diurnal, opening at approximately 16:00 and closing towards nightfall; *sepals* lanceolate, acute, (6–)7–11(–13) x 3(–5) mm, green with semi-transparent winged margins, without a dorsal apiculus just below the apex; *petals* (52–) 61–78(–90), linear-lanceolate, spreading, (5–)10–15(–18) x 1–2 mm, yellow, most often tinged reddish below; *stamens* 132–188(–213), in an erect column, basal inner surface of the filaments of the inner series sparsely white lanulose, (4–)5–7(–9) mm in length; *anthers* linear; *stigmata* linear, basal inner surface sparsely minutely papillate; *ovary* upper surface 2–3(–4) mm diameter; *nectaries* crescent shaped with blunt, rounded tips, slightly raised, highest in the centre of the crest becoming lower towards tips,

smooth–rounded, dry, yellow. *Capsule* 6–9(–10) x 3–5 mm; *closing bodies* rounded; *covering membranes* shallowly "V"-shaped at distal free margin, not incised at sinus; *expanding sheets* reduced; *expanding keels* linear, acute, margin serrate, shallowly "C"-shaped, apex attenuate, extended beyond the valve margin. *Seeds* ovate with short, bluntly protruding micropyles, testa with undulate anticlinal walls, pale brown, 0.73–0.98 x 0.51–1.38 mm. Figures 57, 58, 59.

Distribution: *B. vespertinus* occurs from Kleinpoort in the west to Fort Brown in the east and as far north as Halesowen near Cradock (Figure 29).

Ecology: *B. vespertinus* occurs in Xeric Succulent Thicket (Low & Rebelo #6) at Kleinpoort, Enon and Fort Brown, Subarid Thorn Bushveld (Low & Rebelo #15) west of Somerset East, Eastern Thorn Bushveld (Low & Rebelo #16) near Alexandria, South Eastern Mountain Grassland (Low & Rebelo #44) south west of Cradock and Somerset East and Eastern Mixed Nama Karoo (Low & Rebelo #52) near Cradock and Riebeek East (Figure 46) at altitudes of 60 to 1 798 m (Figures 32, 47). The annual rainfall is 208 to 827 mm with an average of 445 mm (Figures 34, 48). *B. vespertinus* is recorded on eight geological formations within its distribution: the Boplaas Formation (sandstone) within the Ceres Subgroup of the Bokkeveld Group, the Middleton Formation (mudstone & sandstone) within the Adelaide Subgroup of the Beaufort Group, the Balfour Formation (grey mudstone & sandstone) within the Adelaide Subgroup of the Beaufort Group, the Witpoort Formation (quartzite) within the Lake Mentz Subgroup (shale, quartzite, sandstone & diamictite) of the Witteberg Group, the Dwyka Formation (tillite) of the Ecca Group, the Ripon Formation (sandstone & shale) within the Adelaide Subgroup of the Beaufort Group, the Kommadagga Subgroup (shale, siltstone, sandstone & diamictite) of the Witteberg Group, the Kirkwood Formation (red/green mudstone & sandstone) of the Uitenhage Group (Appendix 3).

Conservation status: *B. vespertinus* is common within its range.

Discussion: *B. vespertinus* refers to the flower opening time (*vesper* (L) = evening). This species is closely allied to *B. multiceps* and is discussed under that species.

Berger did not cite a type specimen but referred to cultivated plants in many gardens at the Riviera, and his own cultivated material in the garden of La Mortola, that were (according to him) erroneously called *B. multiceps*. Annotation on the Strauss specimen at BOL indicates that he grew material sent to him by Berger from La Mortola. Since no type material has been found

at B (Dr Beat Leuenberger pers. comm. 2000), or any other herbarium, the specimen kept as BOL 63684 is chosen as the lectotype here.

Strauss clearly states that his specimen is from cultivated material in Berlin-Dahlem taken from the "original" La Mortola–Berger material. However no part of the label (Figure 59), not even the "det. A. Berger" is written by Berger himself (Dr Beat Leuenberger pers. comm. 2000).

No type locality is known. N.E. Brown (1928: 267) does, however, refer to Somerset East as a reported locality.

B. longisepalus and *B. jamesii* were described by Bolus from cultivated material. Plants have been recollected at both type localities (*Dold 4260 & 4318* respectively) and are considered to be synonymous with *B. vespertinus*.

Bolus noted on the specimen *Lombard s.n.* in SUG10642 (BOL!) that she considered it to represent a distinct species to which she intended to apply the name *B. compressus* but never formalised her opinion. The same applies to the specimen *James 478* (BOL!) to which she intended applying the name *B. ronaldii* in reference to the collector Ronald James. Both of these specimens are regarded as *B. vespertinus* here but are nevertheless recorded as manuscript names.

Hartmann (2002) considers *B. jamesii* to be synonymous with *B. vespertinus*.

Vouchers: *Dold 4228, 4291, 4294, 4303* (GRA).

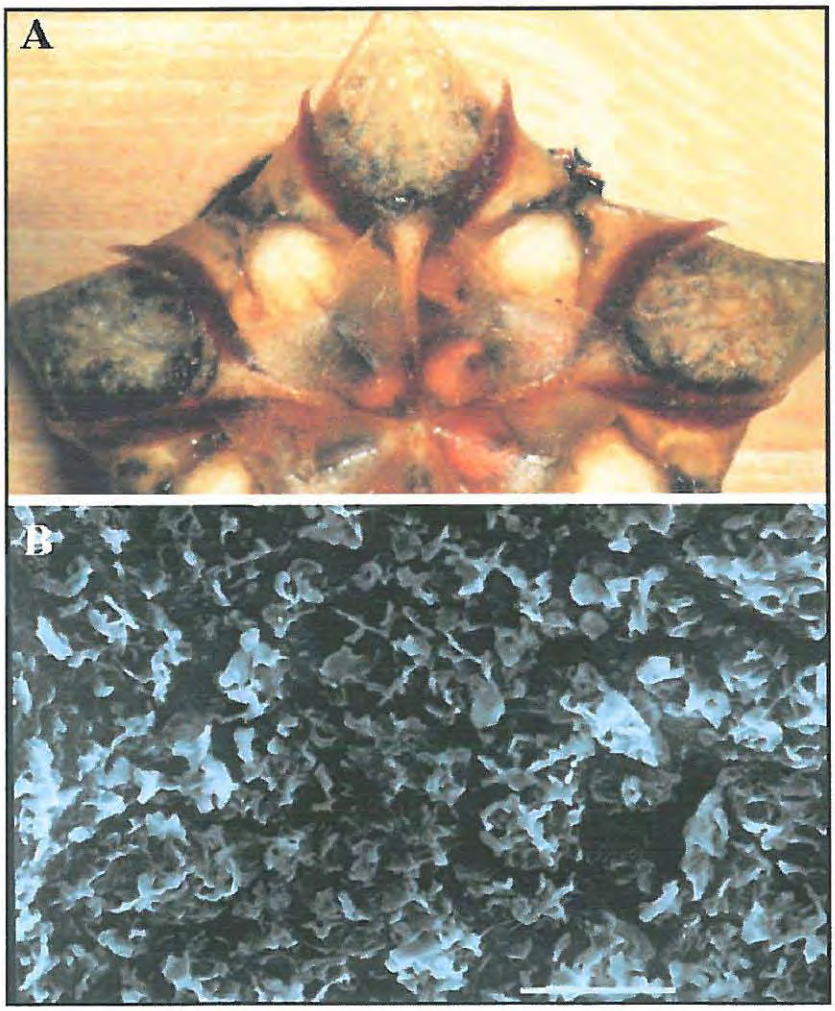

FIGURE 57. —*Bergeranthus vespertinus*. A. Capsule (*Dold 4318*), 16.5 mm diameter; B. Leaf epidermal wax layer (*Dold 4291*), scale bar 10 µm.

FIGURE 58. —*Bergeranthus vespertinus* (*Dold 4212*), Hellspoort, Grahamstown.

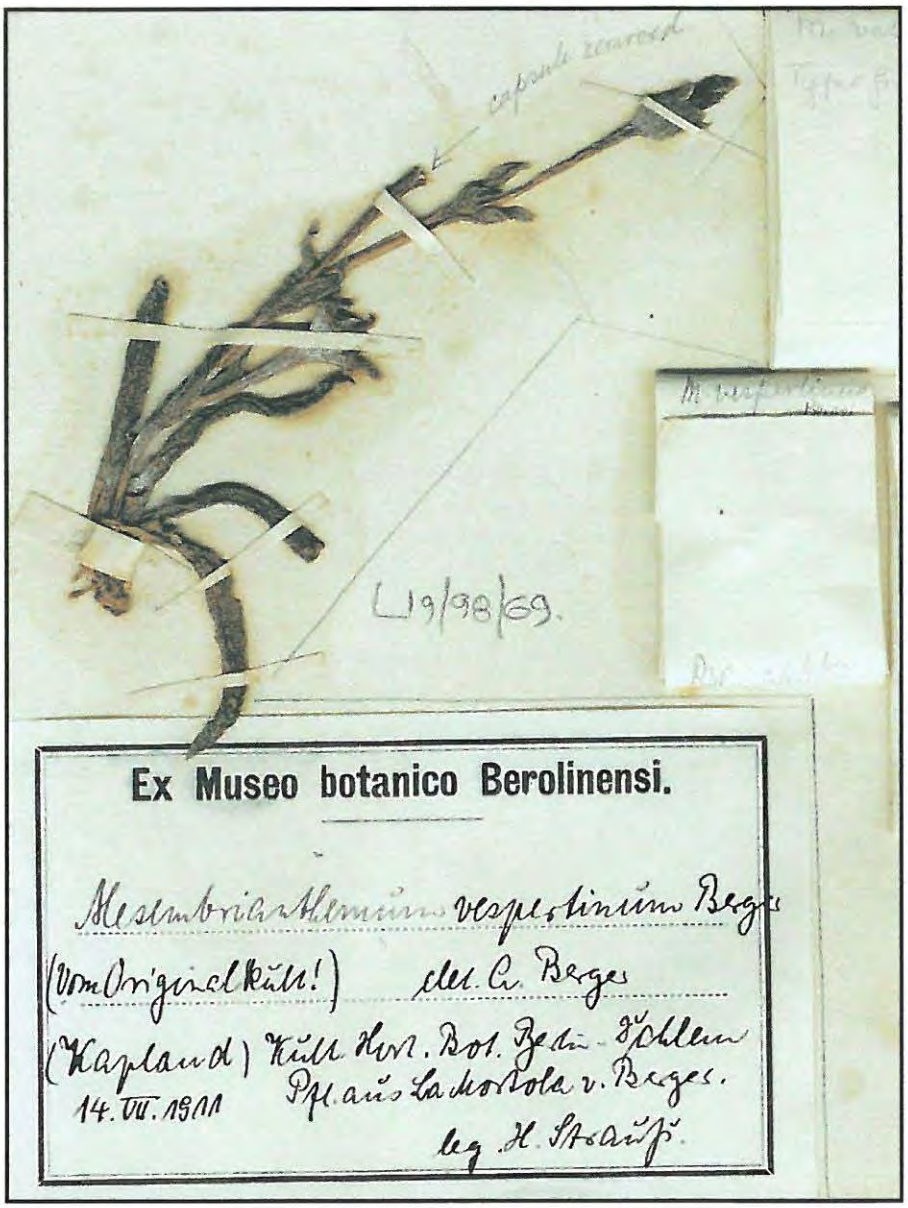

FIGURE 59. —*Bergeranthus vespertinus*, lectotype designated here: *H. Strauss s.n.* BOL 63684 (part of a mixed collection with multiple labels on this sheet).

Excluded Names

Bergeranthus albidus (L.) Schwantes in Zeitschrift für Sukkulentenkunde 2: 180 (1926), based on *Mesembryanthemum albidum* L. = *Machairophyllum albidum* (L.) Schwantes.

Bergeranthus caninus (Haw.) Schwantes in Zeitschrift für Sukkulentenkunde 2: 180 (1926), based on *Mesembryanthemum caninum* Haw. = *Carruanthus ringens* (L.) Boom.

Bergeranthus carinans Schwantes in Zeitschrift für Sukkulentenkunde 2: 180 (1926) based on *Mesembryanthemum carinans* Haw. = *Hereroa carinans* (Haw.) L.Bolus.

Bergeranthus cookii (L.Bolus) Schwantes in Zeitschrift für Sukkulentenkunde 2: 180 (1926), based on *Mesembryanthemum cookii* L.Bolus = *Machairophyllum cookii* (L.Bolus) Schwantes.

Bergeranthus derenbergianus (Dinter) Schwantes in Zeitschrift für Succulentenkunde 2: 180 (1926) based on *Mesembryanthemum derenbergianum* Dinter = *Ebracteola derenbergiana* (Dinter) Dinter & Schwantes.

Bergeranthus glenensis N.E.Br. in Brown, Tischer & Karsten: *Mesembryanthema*: 120 (1930) = *Hereroa glenensis* (N.E.Br.) L.Bolus.

Bergeranthus granulatus (N.E.Br.) Schwantes in Zeitschrift für Sukkulentenkunde 2: 180 (1926), based on *Mesembryanthema granulatum* N.E.Br. = *Hereroa granulata* (N.E.Br.) Dinter & Schwantes.

Bergeranthus ignatius Schwantes (orthographic error in Pax & K.Hoffmann in Engl. & Harms: 211 (1934), based on *Mesembryanthemum ignavum* Schwantes. = *Bergeranthus ignavus* Schwantes.

Bergeranthus ignavus Schwantes in Zeitschrift für Sukkulentenkunde 2: 180 (1926); N.E.Br.: 267 (1928). *nom. nud.*, based on *Mesembryanthemum ignavum* Schwantes.

Bergeranthus montis-moltkei (Dinter) Schwantes in Zeitschrift für Sukkulentenkunde 2: 180

(1926), based on *Mesembryanthemum montis-moltkei* Dinter = *Ebracteola montis-moltkei* (Dinter) Dinter & Schwantes.

Bergeranthus puttkamerianus (Dinter & A.Berger) Schwantes in Zeitschrift für Sukkulentenkunde 2: 180 (1926), based on *Mesembryanthemum puttkammerianum* Dinter & A.Berger = *Hereroa puttkameriana* (Dinter & A.Berger) Dinter & Schwantes.
Dinter & Berger spelled the specific epithet incorrectly assuming the name was of German origin and Schwantes subsequently corrected it in 1926.

Bergeranthus rehneltianus (A.Berger) Schwantes in Zeitschrift für Sukkulentenkunde 2: 180 (1926), based on *Mesembryanthemum rehneltianum* A.Berger = *Hereroa rehneltiana* (A.Berger) Dinter & Schwantes.

Bergeranthus rhomboideus (Salm-Dyck) Schwantes in Zeitschrift für Sukkulentenkunde 2: 180 (1926), based on *Mesembryanthemum rhomboideum* Salm-Dyck = *Rhombophyllum rhomboideum* (Salm-Dyck) Schwantes.

Bergeranthus stenophyllus (L.Bol.) Schwantes *ex* Fourc.: 7 (1940), based on *Mesembryanthemum stenophyllum* L.Bol. = *Ruschia stenophylla* (L.Bol.) L.Bol. (Fourcade listed *B. stenophyllus* in his *Checklist of the flowering plants of the divisions of George, Knysna, Humansdorp & Uniondale* (1940) but as an addendum in the same publication, on the advice of Bolus, renamed the species *Ruschia stenophylla*).

Specimens Examined[11]

(Collector, collection number, species number as referred to in text, herbarium)

Acocks 11880 (7) PRE; *17519* (10) BOL. *Archibald 3805* (1) GRA; *4296* (9) GRA; *5249* (10) GRA; *5744* (9) GRA. *Bayliss 2684* (5) NBG. *Black NBG38856* (4) BOL. *Blenkiron & Grant s.n.* (9) BOL. *Bolus NBG886/31* (10) BOL. *Britten 5120* (9) BOL, GRA; *5135* (10) GRA. *Carter BOL63669* (6) BOL; *NBG38855* (4) BOL; *NBG38858* (4) BOL. *Chan 85* (9) GRA. *Cloete 2496* (9) GRA. *Cubr 28420* (10) B. *Cummings & Weldrick 4* (9) GRA. *Daly & Cherry 997* (9) B, GRA. Daly *& Sole 208* (9) GRA. *Dold 787* (3) GRA; *3943* (2) GRA; *4142* (5) GRA; *4143* (1) GRA; *4186* (7) GRA; *4187* (7) GRA; *4188* (7) GRA; *4189* (7) GRA; *4190* (10) GRA; *4191* (9) GRA; *4192* (6) GRA; *4193* (9) GRA; *4194* (7) GRA; *4195* (7) GRA; *4196* (1) GRA; *4197* (7) GRA; *4198* (1) GRA; *4199* (10) GRA; *4200* (10) GRA; *4201* (10) GRA; *4202* (9) GRA; *4203* (7) GRA; *4204* (9) GRA; *4205* (7) GRA; *4206* (7) GRA; *4207* (1) GRA; *4208* (9) GRA; *4209* (9) GRA; *4210* (9) GRA; *4211* (7) GRA; *4212* (10) GRA; *4213* (9) GRA; *4214* (9) GRA; *4215* (7) GRA; *4216* (7) GRA; *4217* (7) GRA; *4218* (1) GRA; *4219* (7) GRA; *4221* (7) GRA; *4222* (7) GRA; *4223* (7) GRA; *4224* (7) GRA; *4225* (7) GRA; *4226* (7) GRA; *4227* (7) GRA; *4228* (10) GRA; *4229* (10) GRA; *4230* (7) GRA; *4231* (9) GRA; *4232* (6) GRA; *4233* (4) GRA; *4234* (4) GRA; *4235* (6) GRA; *4236* (5) GRA; *4237* (4) GRA; *4238* (6) GRA; *4239* (5) GRA; *4240* (5) GRA; *4241* (5) GRA; *4242* (3) GRA; *4243* (6) GRA; *4244* (5) GRA; *4245* (3) GRA; *4246* (5) GRA; *4247* (5) GRA; *4248* (5) GRA; *4249* (10) GRA; *4250* (7) GRA; *4251* (4) GRA; *4252* (9) GRA; *4253* (7) GRA; *4254* (5) GRA; *4255* (5) GRA; *4256* (7) GRA; *4257* (7) GRA; *4258* (6) GRA; *4259* (9) GRA; *4260* (10) GRA; *4261* (7) GRA; *4262* (9) GRA; *4263* (9) GRA; *4264* (5) GRA; *4265* (6) GRA; *4266* (10) GRA; *4267* (5) GRA; *4268* (5) GRA; *4269* (6) GRA; *4270* (10) GRA; *4271* (8) GRA; *4272* (1) GRA; *4273* (7) GRA; *4274* (10) GRA; *4275* (5) GRA; *4276* (9) GRA; *4277* (5) GRA; *4278* (10) GRA; *4279* (5) GRA; *4280* (5) GRA; *4281* (5) GRA; *4282* (5) GRA; *4283* (5) GRA; *4284* (2) GRA; *4285* (2) GRA; *4286* (5) GRA; *4287* (2) GRA; *4288* (3) GRA; *4289* (7) GRA; *4290* (1) GRA; *4291* (10) GRA; *4292* (9) GRA; *4293* (7) GRA; *4294* (10) GRA; *4295* (9) GRA; *4296* (9) GRA; *4297* (9) GRA; *4298* (4) GRA; *4299* (4) GRA; *4300* (6) GRA; *4301* (6) GRA; *4302* (6) GRA; *4303* (10) GRA; *4304* (6) GRA; *4305* (4) GRA; *4306* (10) GRA; *4307* (7) GRA; *4308* (5) GRA; *4309* (5) GRA; *4310* (7) GRA; *4311* (1) GRA; *4312* (7) GRA; *4313* (9) GRA; *4314* (7) GRA; *4315* (7) GRA; *4316* (9) GRA; *4317* (9) GRA; *4318* (10) GRA; *4319* (7) GRA; *4320* (9) GRA; *4321* (9) GRA; *4322* (10) GRA; *4323* (7)

[11] Localities are provided in Appendix 1.

GRA; *4324* (1) GRA; *4325* (1) GRA; *4326* (10) GRA; *4327* (10) GRA; *4328* (9) GRA; *4329* (5) GRA; *4330* (5) GRA; *4331* (5) GRA; *4332* (5) GRA; *4333* (7) GRA; *4334* (10) GRA; *4335* (5) GRA; *4336* (6) GRA; *4337* (5) GRA; *4338* (6) GRA; *4339* (7) GRA; *4340* (9) GRA; *4341* (5) GRA; *4342* (5) GRA; *4343* (5) GRA; *4344* (10) GRA; *4345* (9) GRA; *4346* (5) GRA; *4352* (4) GRA; *4355* (1) GRA; *4358* (5) GRA; *4359* (5) GRA; *4360* (7) GRA; *4362* (5) GRA; *4370* (5) GRA; *4371* (5) GRA; *4372* (10) GRA; *4375* (6) GRA; *4376* (10) GRA; *4388* (8) GRA; *4389* (10) GRA; *4390* (7) GRA; *4391* (9) GRA; *4392* (5) GRA; *4393* (7) GRA; *Drege 3053* (9) BOL. *Dyer 821* (7) GRA; *1128* (10) GRA; *1529* (10) GRA, PRE. *Ecklon & Zeyher 1980* (7) B, G, MO. *Esterhuysen 13229* (5) BOL. *Feinauer NBG 829/61* (1) NBG. *Flanagan 2230* (6) BOL, GRA; *2591* (6) BOL. *Fourcade 3512* (7) BOL, K. *Galpin 2150* (5) BOL; *5594* (10) GRA. *Gibbs Russell 3092* (&) UFH. *Giffen 355* (7) UFH; *NBG1078/34* (9) BOL; *NBG1705/34* (9) BOL; *NBG63670* (7) BOL. *Gledhill s.n.* (10) BOL. *Graham NBG 2420/15* (9) BOL. *Groen 1050* (9) WAG; *1086* (9) GRA WAG. *Hall 225* (7) NBG; *NBG101/59* (9) BOL. *Hammer 1150* (8) BOL. *Harries NBG2282/33* (10) BOL; *NBG2615/29* (9) BOL. *Holland BOL61242* (10) BOL. *Hosten 109* (9) PEU. *Jacot Guillarmod 9300* (10) GRA. *James 127* (10) BOL; *442* (10) BOL; *478* (10) BOL; *NBG187/35* (10) BOL; *NBG2294/33* (10) BOL; *NBG32080* (1) BOL. *Johnson 1213* (5) GRA. *Kluth NBG11048* (4) BOL; *SUG10670* (4) BOL. *Leighton 2863* (9) BOL; *NBG341/33* (5) BOL; *NBG1557/34* (6) BOL. *Liebenberg 7698* (1) PRE. *Lombard SUG10642* (10) BOL. *Long NBG462/33* (1) BOL. *Luckhoff NBG32078* (7) BOL. *MacOwan 1587* (10) GRA. *Marloth 10874* (7) PRE. *Paterson 105* (1) GRA; *458* (1) GRA, BOL. *Pillans s.n.* (3) BOL. *Potts 1754* (7) BLFU. *Reynolds NBG102/34* (5) BOL. *Rogers 12924* (9) BOL; *12934* (10) BOL. *Schwerdtfeger 20998* (10) B; *21026* (10) B; *21366* (10) B. *Sim 19507* (6) PRE; *19511*(6) PRE; *19522* (5) PRE; *19525* (6) PRE; *19530* (6) PRE; *19539* (7) PRE. *Smythe RUH3915* (7) BOL. *Stayner BOL63671* (9) BOL. *Strauss s.n.* (10) B; *s.n.* (10) BOL; *s.n.* (9) B. *Urton 938* (7) PEU; *1105* (1) PEU. *Van der Merwe 105* (9) BOL. *Van der Walt 356* (10) PRE. *Van Jaarsveld 7918* (7) NBG. *Van Ryneveld NBG1704/34* (6) BOL. *Vlok 2708* (8) BOL. *Welsh 22* (6) GRA. *White s.n.* (9) GRA. *Wisura 2703* (5) NBG. *Zeyher 1089* (7) TCD; *2577* (7) B, G.

PHYTOGEOGRAPHY

The highest frequency of genera of the Mesembryanthemaceae occurs in the arid and semi-arid winter rainfall area on the western part of southern Africa. It is generally accepted that these high genus frequencies reflect the original distribution area of the family. However, contrary to popular assumption, Chesselet *et al.* (2000b) point out that the highest frequencies of genera with "primitive" segmented floral nectaries (such as *Bergeranthus*, *Hereroa* and *Rhombophyllum*) occur in the summer rainfall area and therefore suggest that it is possible that the origin of the Mesembryanthemaceae has lain outside the winter rainfall region. Centres of diversity are not necessarily centres of origin and the source of the family may have been the summer rainfall groups in which less diversification occurred with a greater stability and the absence of the driving force that led to immense diversification known for the more recently evolved winter rainfall groups.

Five centres of diversity are recognized for the Mesembryanthemaceae: the Albany centre, Gariep centre, Karoo centre, Vanrhynsdorp centre and Pofadder centre (Hartmann 1991a). The eastern most, conspicuously isolated, Albany centre comprises 18 genera (the number of endemic genera is unknown) (Chesselet *et al.* 1995, Hartmann 1991a). The Albany centre of endemism, also known as the Albany Hotspot, has been long recognized as an important centre of diversity and endemism (Croizat 1965, Nordenstam 1969, Hartmann 1991a, Cowling & Hilton-Taylor 1994, Cowling *et al.* 1997, Davis & Heywood 1994, Phillipson 1995, Van Wyk & Smith 2001) although its actual geographical limits and estimated number of vascular plant species remain controversial. The Albany Centre comprises a mosaic of diverse floristic and vegetation elements. No less than five of White's (1983) main phytochoria converge on this region, namely, the Cape Region, Karoo-Namib Region, Maputaland (Tongaland)-Pondoland Regional Mosaic, Afro-montane Region and the Kalahari Highveld Regional Transition Zone. In addition almost one third (21 out of 70) of the veld types that Acocks (1953) recognized are represented in the Albany Centre. According to Van Wyk & Smith (2001) the total number of vascular plant species (including infraspecific taxa) in the Albany Centre is ± 4000, 15% of which are endemic or near-endemic and 60.6% of these endemics are succulent taxa.

The genus *Bergeranthus* is endemic to the Eastern Cape province as defined by current political boundaries, however geographically the eastern Cape is an area rich in species and communities that is well known for its complex phytogeography (Gibbs Russell & Robinson 1981, Cowling 1982). Gibbs Russell & Robinson (1981) state that the region is poor in endemic taxa although Van Wyk and Smith (2001) suggest that this is a gross underestimation. Cowling (1982) suggests that the south eastern Cape is one of the richest centres of succulent diversity in South Africa with a strong karroid affinity and that karroid succulent flora was much more widespread and dominant in the south eastern Cape in the past. It is possible that succulent species such as *Bergeranthus*, together with *Platythyra*, *Rhombophyllum*, *Faucaria* and *Orthopterum* are relics of this considerably drier flora (Cowling 1982). These genera are all firmly concentrated in the Albany Centre as demarcated by Van Wyk & Smith (2001), being bounded in the west by the upper reaches of the Sundays and Great Fish River Basins (Graaff Reinet, Middleberg, Sterkstroom, Queenstown), in the east by the Indian Ocean, in the south by the Gamtoos-Groot River Basin and in the north by the Kei River Basin (Figure 60).

Van Jaarsveld (1987) lists *Bergeranthus*, *Faucaria* and *Glottiphyllum* as recently evolved neo-endemic genera resulting from fragmentation of taxa along the borders between climatic zones and floral kingdoms. According to Smith (1991) it appears that although some succulent plants date from the Cretaceous period, extensive radiation in the succulent flora took place during the Oligocene period because open drier habitats became available for colonization. Evolution usually takes place at a faster rate in arid climates (Raven 1983) and Smith (1991) suggests that *Bergeranthus* is therefore most likely a product of recent speciation in the Eastern Cape. This is supported by findings in the current study, i.e. advanced seed dispersal mechanism. Chesselet *et al.* (2000b) however interpret the segmented nectaries (meronectary) of *Bergeranthus* as primitive within the family.

1. Phytogeographical groups:

Four phytogeographical groups of *Bergeranthus* species are immediately evident from species distribution maps (Figures 29, 40, 43). Each group is described and possible reasons for these assemblages are discussed.

1.1. **Escarpment species**: *B. artus*, *B. katbergensis* and *B. nanus* occur above 1 000 m along the Great Escarpment and are strongly associated with open grassland. The average annual rainfall is ± 515 mm and falls predominantly in the summer months in the form of thunderstorms. Populations are restricted to "skeletal" habitats on rock outcrops as are many other species of the genus, however at higher altitudes they are exposed to colder conditions than other species, with frost and/or snow. These three species represent the north western, northern and northeastern extremes of the genus range where they are replaced in their specific habitat niche by *Chasmatophyllum* and *Stomatium* species in the west and northwest, and *Rabiea* and *Mossia* species in the north. The transformation takes place with a noticeable reduction of grass cover. The species comprising this group, unlike any other species, are associated with steep slopes and may therefore be found in almost soil-free rock faces and ridges.

1.2. **Thicket species**: Three species of *Bergeranthus* are associated with the Thicket Biome of more recent tropical origin. Cowling & Holmes (1991) show that Subtropical Thicket (Thicket Biome *sensu* Low and Rebelo 1996) comprises two components, the tree/shrub stratum and the understory/open-habitat species. The endemic flora, including *Bergeranthus*, is overwhelmingly associated with this component (of Karoo-Namib affinity) with the Mesembryanthemaceae being significantly represented here (Cowling & Holmes 1991). *B. addoensis*, *B. albomarginatus* and *B. scapiger* are associated, together with endemic species such as *Orthopterum waltoniae*, with thicket where they contribute to the understory/open-habitat component described by Cowling & Holmes (1991). Although these species are essentially thicket species they are not tolerant of any competition and most often occur on bare ground. This group is generally independent of grassland association and prefers deeper higher nutrient soils to extreme "skeletal" habitats. Altitude ranges from 10 to 853 m with an average annual rainfall of ± 622 mm. *B. addoensis* occurs in the winter maximum rainfall region, *B. scapiger* occurs in winter and spring maximum rainfall regions and

B. albomarginatus occurs in the autumn maximum rainfall region Although the distribution pattern overlaps with the Central Albany species the two groups are clearly defined by habitat requirements. *B. scapiger* and *B. albomarginatus*, perhaps due to protection from the elements and shade offered by the thicket, are the largest plants in the genus. *B. addoensis* has an unusual habit of forming rings when the central clump-forming plants die with age and this species occurs primarily in an area geologically termed the Algoa Basin. The geological formations are recent deposits characterised by relatively deep, red, lime rich sand clay loams (Hartmann 1988b). *B. scapiger* occurs on stony ground in open places between, and along the margins, of bushclumps while *B. albomarginatus* has only been recorded on exposed intrusive dolerite sills, also within dense thicket.

1.3. **Eastern grassland species**: *B. concavus* and *B. leightoniae* represent the eastern most group occurring from between 20 m to 1140 m in altitude with an average annual rainfall of ± 665 mm, being the highest rainfall of the four groups. *B. concavus* occurs in the spring maximum rainfall region and *B. leightoniae* occurs predominantly in the autumn maximum rainfall region. The area of occurrence is mild in both winter and summer as a result of coastal winds. Both species are restricted to extreme "skeletal" habitats, *B. leightoniae* on exposed dolerite sills in Dohne Sourveld and *B. concavus* on exposed sandstone in Coastal Grassland. It is suggested that these two species are closely related but are strongly influenced by the geology and soil as field observations show a clear delimitation as a result. *B. concavus* is restricted to the coastal flats reaching only 10 km inland on very poor recent sandstone-derived soil with *Faucaria subintegra* and *Haworthia cooperi var. leightonii.* Populations of *B. leightoniae* decrease to the east with the increase in rainfall although it is suspected that many have been lost to disturbance and poor veld management in the Transkei region. Unlike the western limits of the genus where habitat is almost immediately colonised by other succulent Mesembryanthemaceae, highly succulent plants do not replace the eastern *Bergeranthus* species due to the increasing rainfall. These margins of exposed rock sheets are colonised by bulbous plants such as *Nerine* species and *Crassula* species. The thin layer of soil also hosts *Selaginella dregei*, a typical sheet rock plant that forms mats around the rock margins.

1.4. **Central Albany species**: *Bergeranthus multiceps* and *B. vespertinus* appear to be closely related and difficult to distinguish, showing a great deal of overlap in a phenetic analysis based on vegetative characters (Figure 8). Furthermore their distributions overlap in the Grahamstown area where they can be found in close proximity and are therefore grouped together here. Altitude ranges from 20 to 1 798 m with an average annual rainfall of ± 490 mm. *B. multiceps* occurs in regions of autumn, winter and spring maximum rainfall while *B. vespertinus* occurs in regions of spring and autumn maximum rainfall. Although locality maps (based on Low & Rebelo, 1996) indicate a wide range of habitats (see taxonomy) for both species it is suggested here that the scale of this map and that of Acocks (1953) is too broad to accurately attribute associations.

Field observations indicate that *B. multiceps* is primarily associated with open grassland around Grahamstown and grassy fynbos to the west as far as Joubertina. Populations often occur in small patches of open grassland on elevated summits surrounded by extensive lower-lying thicket. Grass cover is dense and *B. multiceps* is the only species that tolerates any form of competition within its habitat resulting in it being recorded in a wide range of soil and vegetation types. Dominant grasses include *Themeda triandra*, *Digitaria eriantha* and *Eragrostis curvula*. This habitat is shared with succulent plants such as *Faucaria felina*, *Haworthia cooperi*, *H. gracilis*, *Euphorbia meloformis* and *E. gorgonis*.

Bergeranthus vespertinus is associated with karroid elements with little or no grass cover from Grahamstown to the north-west where an increase of succulent species is evident. Open bare patches of ground are preferred although *B. vespertinus* can be found in dense dwarf karroid scrub (Dyer 1937) with *Pentzia incana*, *Felicia filifolia*, *Walafrida geniculata* and *Chrysocoma ciliata* being dominant. The habitat is shared with succulent Mesembryanthemaceae including *Hereroa granulata*, *Glottiphyllum longum*, and *Rhombophyllum dolabriforme*.

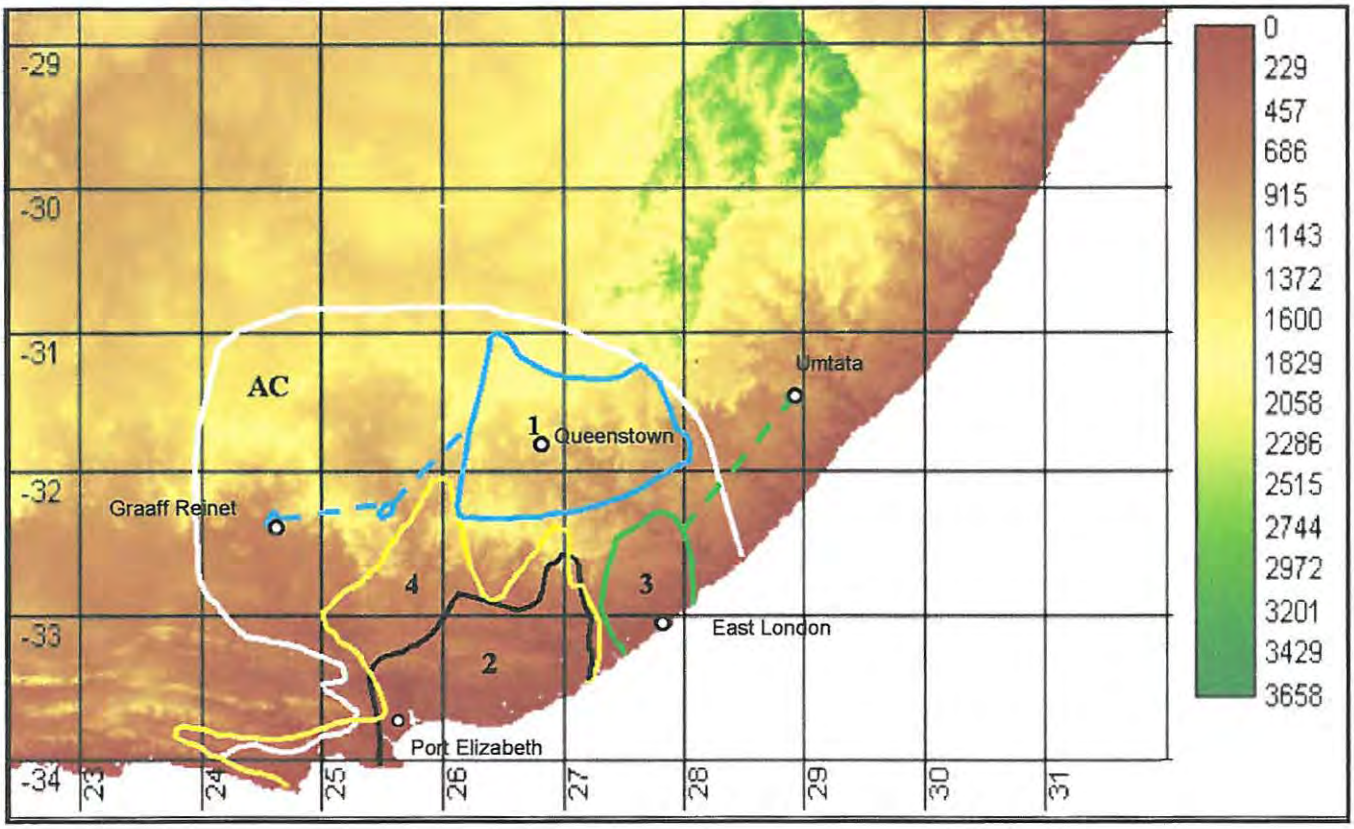

FIGURE 60. —Phytogeographical grouping of *Bergeranthus* species. AC = Albany Centre *sensu* Van Wyk & Smith (2001); 1 = *B. artus/B. katbergensis/B. nanus* "Escarpment" group; 2 = *B. addoensis/B. albomarginatus/ B. scapiger* "Thicket" group; 3 = *B. concavus/B. leightoniae* "Eastern Grassland" group; 4 = *B. multiceps/B. vespertinus* "Central Albany" group. Broken lines connect outlying populations. Legend = altitude.

2. **Discussion**

Bergeranthus species localities plotted on vegetation (Low & Rebelo 1996), geological (S.A. Geological Survey series), altitude and rainfall (Schulze *et al.* 1997)[12] maps have revealed important associations and assemblages within the genus. It is however felt that the scale of these maps are too broad to accurately map species associations and that the concept of "skeletal" habitat should be considered as a superseding factor. The term "skeletal habitat", introduced by Bruce

[12]Digital altitude and rainfall maps of South Africa, Lesotho and Swaziland, developed by Schulze *et al.* (1997), are interpolated from point data obtained from a network of weather recording stations distributed throughout South Africa, to produce continuous digital maps at a resolution of 60 pixels per degree; Specimen localities were plotted using Idrisi 32 GIS image processing system (Eastman 1999).

Bayer (pers. comm. 2000) with regard to *Haworthia*, refers here to the special habitat to which *Bergeranthus* has adapted to overcome competition and enable its own continued existence. This habitat is characterised by poor soil nutrient and low soil moisture holding capacity effectively reducing plant competition, an important requisite for *Bergeranthus*. Furthermore the ability of the habitat to free itself of moisture as quickly as possible after rainfall is important for succulents such as *Bergeranthus*, *Faucaria*, *Hereroa*, *Orthopterum* and *Rhombophyllum* that occur in relatively high rainfall regions. This is achieved in several ways: loose, coarse soil with little or no moisture holding capacity such as the pure sand colonized by *Bergeranthus concavus*; the absence of any vegetation or form of mulch to inhibit the immediate evaporation of moisture; or virtually no soil at all such as the escarpment species that occur on bare rock faces with their roots penetrating cracks and fissures.

This specific habitat adaptation has allowed species of *Bergeranthus* to overcome certain constraints that would otherwise prohibit its occurrence and as a result has enabled what is essentially a Nama-Karoo element to persist in several atypical phytochoria. It is suggested that these neo-endemic taxa may have evolved multiple times and independently from a common ancestor in an isolated discontinuous micro-habitat in response to fragmentation of taxa along the borders between climatic zones and phytochoria. The lack of a long-range dispersal mechanism in the genus contributes to maintaining a localised distribution.

REPRODUCTIVE BIOLOGY

1. **Pollination Biology**

Few data on the pollination of Mesembryanthemaceae are available but the predominance of bright shiny petals suggests insect pollination as the primary mechanism (Hartmann 1991). However Bittrich (1987) reports that many species possess copious dry pollen that suggests wind pollination as well although Chesselet *et al.* (2001) suggest that this requires further investigation. Gess (1996) reports that the general distribution of the Mesembryanthema (Mesembryanthemaceae) coincides markedly with that of the Afrotropical masarines. Furthermore the peak flowering season of the family in the western Cape coincides with the peak flight period of the masarines. Struck (1990) however recorded a wide range of generalist visitors to Mesembryanthemaceae in the Goegab Nature Reserve. The limited available data on pollination of Mesembryanthemaceae (Gess 1996; Gess & Gess 1989; Liede 1989, 1990; Struck 1990; Vogel 1954) is restricted to the arid and semi-arid winter rainfall areas of the western part of southern Africa considered to be the original distribution area for the family (Chesselet *et al.* 1995).

As has been reported for other genera (Hartmann 1991) *Bergeranthus* flowers are protandrous. The stigmata are at first shorter than the stamens but elongate, spread and finally recurve distally with age. As a consequence the flowers have an early male phase and a later female phase of anthesis.

Hartmann (1991) describes four flower types in the Mesembryanthema of which *Bergeranthus* flowers are described as melittophilous. Within this group, characterised by open presentation of large quantities of pollen, hidden nectaries and diurnal opening of bright shiny petals, three sub-divisions are described by means of the arrangement of the stamens. *Bergeranthus* is described as having Large Central Cone flowers and the pollination syndrome is termed Peritribic (Hartmann 1991). The nocturnal, fragrant flower of *B. artus* however has characters described for phalaenophilous flowers (Hartmann 1991). Chesselet *et al.* (2001) discuss the role of floral nectaries in pollination and note the importance of nectar as an attractant to insects.

No data on the pollination of *Bergeranthus* is currently available therefore a preliminary investigation was undertaken.

Two populations of *Bergeranthus multiceps* were visited during November and December 2000 and January 2001 to observe and document their pollination biology. One population (Site 1) comprised seven plants within $8m^2$ of open grassland on Grahamstown aerodrome flats (Represented by *Dold 4186*), the other (Site 2) ± 30 plants over ± 18 m^2 of open grassland at Thomas Baines Nature Reserve (*Dold 4203*). Visits coincided with flower opening times (15:30 to 16:30) on clear, windless, warm days during the peak flowering season. The seasonal flowering period was observed in the field and in 192 collections of cultivated material over three years.

A total of 84 visiting insects were collected using an insect net and a pooper, killed using ethyl acetate, and mounted with pins. Many more insects were observed visiting flowers than were caught due to their quickness (bees and wasps) and the collector's inexperience, however only specimens collected have been included in this investigation. Specimens were identified in the Albany Museum Entomology department by Dr F. W. Gess.

Specimens collected:

Order COLEOPTERA (Beetles)

Family Chrysomelidae

Genus indet.

species indet. A x 4 specimens

Genus indet.

species indet. B x 1 specimen

Family Meloidae (Blister Beetles)

Genus indet.

species indet. A x 2 specimens

Family Scarabaeidae

Subfamily Melolonthinae

Tribe Hopliini (Monkey Beetles)

Genus indet. x 1 specimen

Family indet. x 3 specimens

Order DIPTERA (Flies)

Family Bombyliidae (Bee Flies)

Genus indet. x 3 specimens of 3 unidentified taxa

Family Syrphidae (Hover Flies)

Genus *Metasyrphus corollae* (Fabricius) x 1 specimen

Genus *Ischiodon aegyptius* (Wiedermann) x 1 specimen

Genus indet.

species indet. A x 2 female specimens

Genus indet

species indet. B x 1 specimen

Genus indet

species indet. C x 1 specimen

Family Tachinidae

Genus indet.

species indet. A x 1 specimen

species indet. B x 1 specimen

Order HYMENOPTERA (Bees, Wasps, Ants)

Family Halictidae

Subfamily Halictinae

Tribe Halictini

Genus *Lasioglossum* species A x 1 female specimen

Genus *Lasioglossum* species B x 1 female specimen

Genus *Lasioglossum* species C x 1 female specimen

Genus *Lasioglossum* species D x 1 female specimen

Family Megachilidae

Subfamily Megachilinae

Tribe Megachilini

Genus *Megachile (Eutricharaea) semiflava* (Cockerell) x 1 female specimen

Family Apidae

Subfamily Xylocopinae

Tribe Ceratinini

Genus *Ceratina (Ctenoceratina) pencillata* Friese x 1 female specimen

Tribe Allodapini

Genus *Allodapula variegata* (Smith) x 43 female specimens

Subfamily Apinae

Tribe Anthophorini

Genus *Amegilla punctifrons* (Walker) x 1 female specimen

Genus *Amegilla spilostoma* (Cameron) x 2 female specimens

Order LEPIDOPTERA (Butterflies, moths)

Family Nymphalidae

Genus *Vanessa cardui* (Linnaeus) (Painted lady) x 1 female specimen

Family Lycaenidae

Genus *Freyeria trochylus* (Freyer) (Grass Jewel Blue) x 1 specimen

Family Pieridae

Genus *Pontia helice* (Linneaus) (Meadow White) x 1 specimen

Family Hesperiidae

Genus *Gegenes niso* (Linneaus) (Common Hottentot Skipper) x 2 male specimens

A total of 84 specimens within 14 families and four orders were collected.

It is clear from the range of taxa collected (14 families within four orders) over a relatively short period that *Bergeranthus* attracts generalist visitors by means of its brightly coloured shiny petals.

However 66% of the total flower visitors collected belong to the order Hymenoptera, of which 82% are *Allodapula variegata*. 14% of the total belong to the order Diptera, 14% Coleoptera and 6% Lepidoptera (Figure 61). However not all of these are pollinators. For example, the two species of Meloidae (Blister Beetles) were responsible for eating the entire ovary of the flower and therefore are highly destructive (pers. obs.). Of the Hymenoptera the remaining 18% are the genera *Lasioglossum* (8%), *Amegilla* (6%), *Megachile* (2%), and *Ceratina* (2%) (Figure 62).

Allodapula variegata (Figure 63A, 64B), being the most frequent flower visitor, is most likely to be the primary pollinator of *Bergeranthus multiceps*, and possibly other species of *Bergeranthus*[13]. Field observations attest to this bee being extremely fast, moving from one flower to the next rapidly collecting pollen that is stored on the legs and carried away as a food source (for their progeny) and therefore not available for pollination (Figure 63B, 63C). Scattered pollen has however been observed on almost the entire body that is potentially available for pollination (Figure 64A). This may be attributed to the hasty, seemingly careless, behaviour of the species in the process of harvesting pollen.

Ants were frequently recorded visiting *Bergeranthus* flowers but it is unlikely that they are responsible for pollination as they are reportedly (Rebelo 1987) usually only nectar thieves that

[13] *Allodapula variegata* was seen visiting *B. albomarginatus* but not collected.

seldom make contact with both anthers and stigmata or move between flowers. It is interesting to note that no *Apis* species (honey bees) were collected although they were observed regularly visiting flowers of *Aspalathus spinescens* less than 60 cm away. No explanation can be given for this.

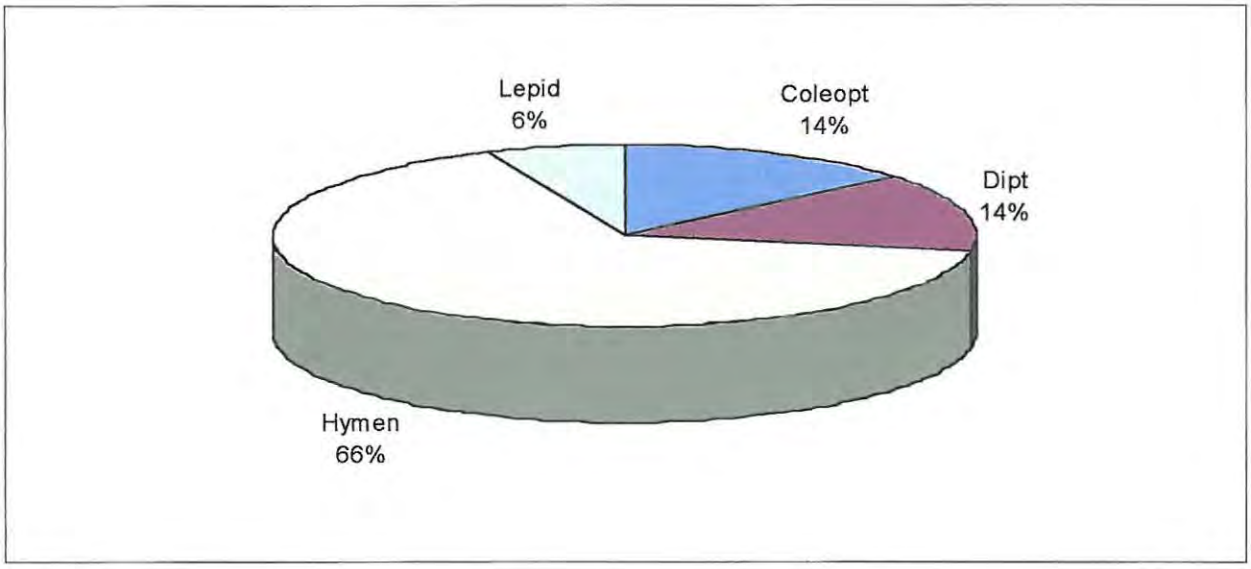

FIGURE 61. —Insect families visiting *Bergeranthus multiceps*. Hymenoptera (Hymen) 66%, Diptera (Dip) 14%, Coleoptera (Coleopt) 14%, Lepidoptera (Lepid) 6%.

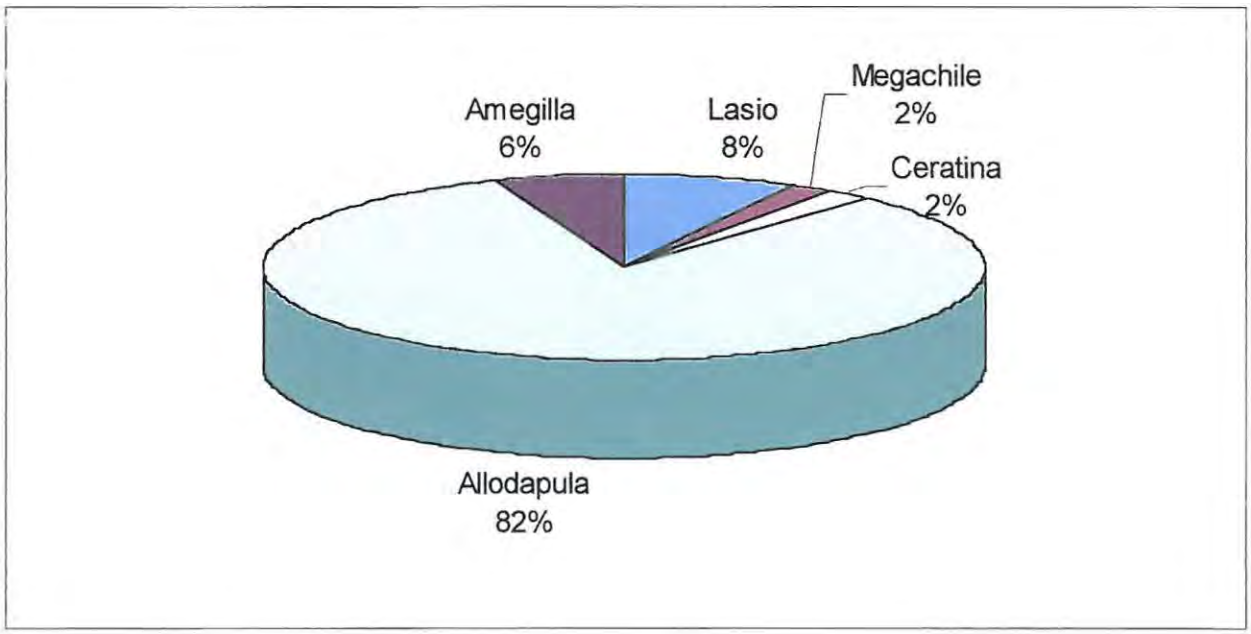

FIGURE 62. —Genera of Hymenoptera visiting *Bergeranthus multiceps*. *Allodapula* 82%, *Lasioglossum* 8%, *Amegilla* 6%, *Megachile* 2%, *Ceratina* 2%.

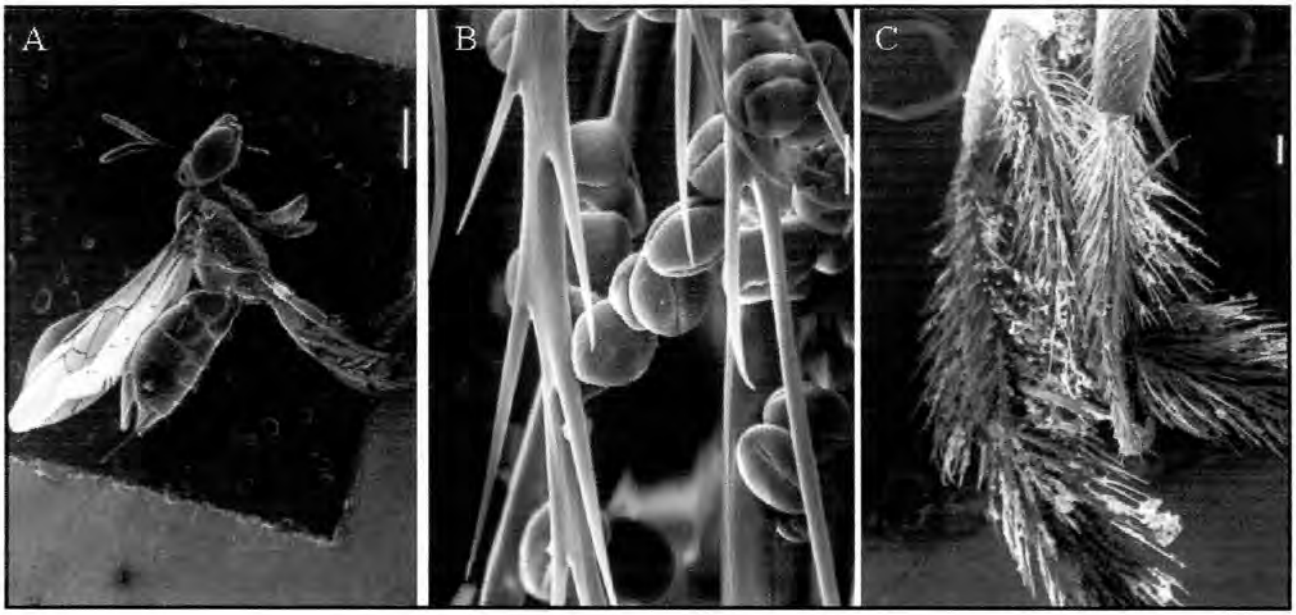

FIGURE 63. —Pollen of *Bergeranthus multiceps* on *Allodapula variegata*. A = *Allodapula variegata* (scale bar 1 mm); B = Pollen on upper hind leg (scale bar 10 μm); C = Pollen collected on hind legs for transportation to nest (scale bar 100 μm).

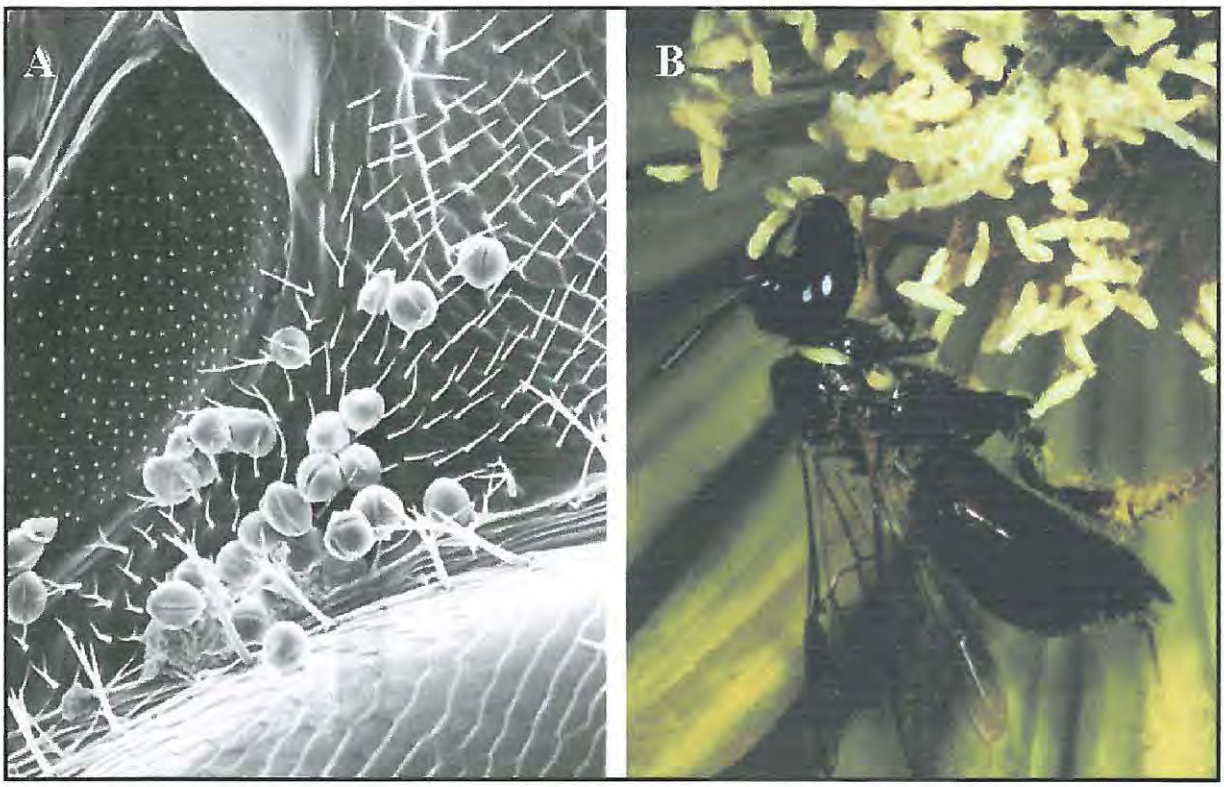

FIGURE 64. —Pollen of *Bergeranthus multiceps* on *Allodapula variegata*. A = Pollen available for pollination on thorax of *Allodapula variegata* (scale bar 10 μm); B–*Allodapula variegata* visiting the flower of *Bergeranthus multiceps*.

According to Rebelo (1987) flower visitation is influenced by:

A. Pollinator needs i.e. nectar and pollen.

Based on the available data it is assumed that the primary attraction is the pollen, which is collected by *Allodapula variegata* as a food source.

B. Floral attraction i.e. colour shape and odour.

Most species of *Bergeranthus* have odourless, brightly coloured, shiny petals that are exposed for part of the day with the exception of *B. artus* that has nocturnal fragrant flowers that are otherwise identical in shape and colour.

C. Physical factors i.e. light intensity, temperature, humidity and wind.

Bergeranthus flowers have clearly adapted to these factors by developing a strict regime of opening and closing daily for a short period of time only under optimum conditions. Repeated

opening and closing of species within the Mesembryanthemaceae is well documented but no explanation for this has been provided.

Bergeranthus has a peak flowering season from November to December and this is closely related to rainfall and temperature. *B. scapiger* flowers later in the summer season (December–January) than the other nine species. Flower opening time for most species is from mid-afternoon (± 15:30) to sundown (± 18:30) although *B. katbergensis* opens at midday and closes long before nightfall, possibly as a result of its high altitude (1 108 to 1 760 m). Diurnal flowers are scentless. An exception to the diurnal flower opening behaviour is that of *B. artus* which is nocturnal. This species opens an hour after nightfall and closes at ± midnight, is strongly scented and therefore is most likely pollinated by nocturnal insects. This behaviour is shared by *Hereroa granulata* and suggests a possible link between the two genera. Flowers repeatedly opening and closing in the afternoon is most likely an adaptation to pollination and this is not uncommon in the Ruschioideae (pers. obs.)

Older flowers, that have already opened a day or several days before, open earlier in the day (up to 30 minutes) than younger, or first time opening flowers. Nevertheless the younger flowers are most sought after by insects that visit the same flower repeatedly without stopping on an older flower at all. This coincides with the pollen gathering activities of potential pollinators and the early male phase of the flower and supports the suggestion that *Allodapula* may be the primary pollen collector. In contrast however, this phenomenon reduces the chances of pollen deposition by the same insect on older flowers.

The opening and closing of *Bergeranthus* flowers of 210 plants (all species except *B. artus* which is nocturnal flowering) grown in pots under natural conditions was monitored over a period of 42 days during peak flowering season and weather conditions were recorded by means of a Davis Weather Monitor (II). Data is presented in Figure 65. Data recorded at a particular time (for all 42 days monitoring) was plotted as a unique symbol. When considering increasing (or decreasing) abiotic data at a particular hour, if points indicate flower non-opening events, then the abiotic factor recorded (at that time) obviously does not affect flower opening/closing events. If, however, as the

abiotic factor increases, a threshold is reached subsequent to which flower opening is triggered, then the abiotic factor recorded at that time is influencing flower opening.

Air temperature and relative humidity (RH) were recorded at two hourly intervals (although only five of these are plotted) during this period to determine their influence on flower-opening events (Figure 65) in addition to which vapour pressure deficit (VPD) (Figure 65) was calculated as follows:

$$VPD = SVP^* \times \frac{RH}{100}$$

(*Saturation Vapour Pressure *sensu* Goff & Gatch 1946)

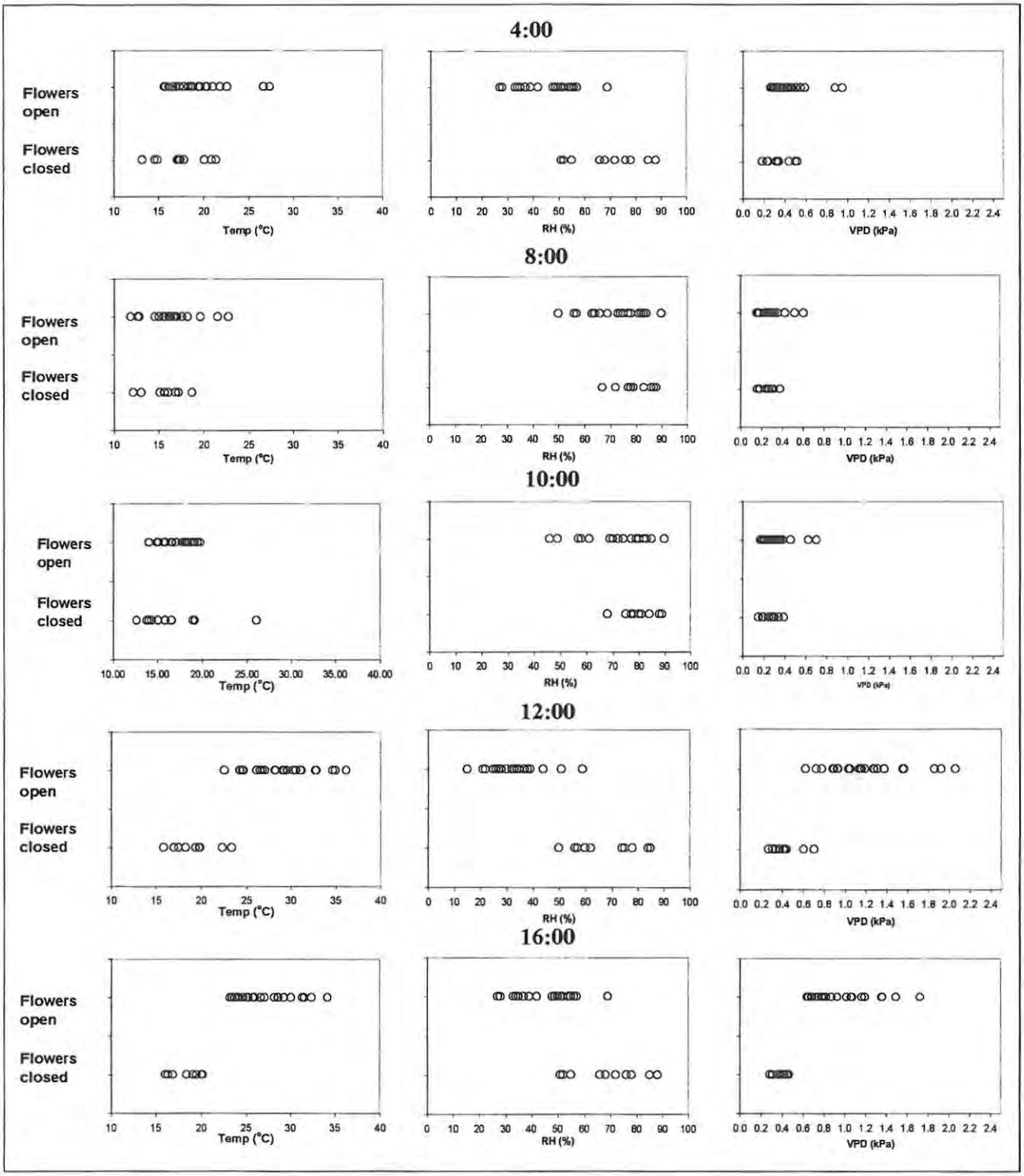

FIGURE 65. —Ambient temperature, relative humidity and vapour pressure deficit recorded at set times (over 42 consecutive days) correlated to *Bergeranthus* flower opening/non-opening events.

It is evident that flower-opening events (recorded at 16:00) are dependant on specific conditions. When considering climatic data recorded at 16:00, flowers only opened if temperatures exceeded 23–24°. Flowers only opened when relative humidity was below 70%, however non-opening events were also recorded for relative humidity ranging from 50% to 70%. This considerable overlap suggests that relative humidity alone was not an important influential condition. When these climatic data were used to calculate vapour pressure deficit it was clear that flowers opened at and above 0.6 kPa.

Although flowers are generally already open at 16:00 conditions prior to this were plotted to determine the triggers of flower opening. It was apparent that specific conditions at 12:00 are already significant in determining flower-opening events but climatic conditions prior to 12:00 do not have an effect. For flowers to open (at approximately 16:00) the VPD at 12:00 must be 0.6 kPa or higher. It can be concluded that flower opening or non-opening events are determined by specific conditions prior to flower opening time.

It is therefore possible to speculate that *Bergeranthus* flowers (with the exception of *B. artus*) remain closed at low ambient temperature and vapour pressure deficit for two reasons. It has been firmly established that pollen fertility is negatively affected through contact with water (pers. comm. S. Hammer, 2000 & pers. obs.) and is thus protected from contact with moisture. Furthermore potential pollinators are inactive at low temperatures and wet conditions. It is not known why *Bergeranthus*, and other species of Ruschioideae, open at mid to late afternoon rather than mid-day when potential pollinators are most active. It is possible that specific pollinators, most active at this time, (*Allodapula*?) are being targeted by means of this behaviour.

2. **Seed dispersal**

Dispersal of seeds within the Mesembryanthemaceae is primarily achieved by water (hydrochory), in the form of rain (ombrohydrochory), the seeds thus only being released at a time most favourable for germination (antitelechory). *Bergeranthus* capsules are woody, persistent and retain viable seeds for several years. Dispersal begins with the hygroscopic opening of the capsule. The expanding keel

(Figure 66b) situated on the valve (Figure 66a) expands due to the absorption of water and lifts the valves, exposing the covering membrane (Figure 66e). This process is adversely affected by low temperatures (Hartmann 1991a). On drying, the expanding keel contracts pulling the valves inwards effectively closing the capsule. This action, first described by Steinbrinck (1883), can be repeated often (hygrochasy). Hartmann (1991) reports that ambient moisture in the air is capable of triggering this process. This can be seen clearly in *Ectotropis* N.E.Br. (pers. obs.). *Bergeranthus* capsules are, however, comparatively robust and require at least heavy mist or prolonged fog to facilitate opening. Once the capsule is open, rain is required to remove the seeds from the deep locule and past the large closing body. Hartmann (1991) presents four dispersal mechanisms in the family, related to the morphological fruit types of which nine are described (Hartmann 1988a).

Bergeranthus, with *Mitrophyllum* type fruit (Hartmann 1988a, interpreted by Ihlenfeldt 1983 as an advanced type), has a dispersal mechanism described as Ejection Dispersal that is correlated with the possession of persistent, resilient covering membranes, closing bodies and sterile funicles (Hartmann 1988a). When the capsule is flooded, a raindrop falling directly on the covering membrane (Figure 66e) will cause the ejection of a jet of water from the locule via the proximal gap between the halves of each covering membrane (Figure 66g). One or more seeds will be carried with this ejection of water over the centre of the capsule and deposited on the opposite side of the locule. The seeds are obstructed from exiting the locule by means of the closing body (Figure 66c). Seed retention by means of closing body (Figure 66c), covering membrane (Figure 66e) and sterile funicles (Figure 66d) extend the period of dispersal and increases the chances of germination under favourable conditions. Ihlenfeldt (1983) interprets simple capsules without covering membranes or closing bodies as primitive and summarises the work of Garside and Lockyer (1930) and Volk (1960) as follows: Seeds from complicated (advanced) capsules are, under the same conditions, ejected twice as far and over an area four times as large as seeds from simple (primitive) capsules.

Experiments using artificial raindrops (Lockyer 1932) have shown that fruits with covering membranes and completely blocked distal openings are the most successful in respect of the distances reached in dispersal. Lockyer (1932) demonstrates this by comparing seed dispersal distances before (1 520 mm) and after (1 170 mm) removing the covering membrane of

Bergeranthus scapiger. Seeds in a capsule without a covering membrane are merely flooded out *en masse* thus curtailing the period of dispersal and chances of successful germination over an extended period (Lockyer 1932). Genera with capsules without covering membranes are therefore the least successful in terms of both seed dispersal distance and extended period of dispersal (Hartmann 1991).

This type of dispersal is described as short distance dispersal by Ihlenfeldt (1983) and is understood as advantages for species with a restricted ecological niche but makes colonization of distant suitable sites difficult. It has long been recognized that adaptation for long-distant dispersal (telechory) is uncommon in arid habitats and that adaptation for dispersal hindrance (antitelechory) is not uncommon (Ellner & Shmida 1981). The currently accepted theory for explaining this phenomenon is that of Zohary (1937) who described it as the 'mother-site' theory whereby plants in arid habitats are restricted by a scarcity of available suitable sites and therefore persist by repeatedly re-establishing themselves in the maternal site. This is supported by the fact that genera such as *Bergeranthus* have a patchy distribution and can be interpreted as an expression of high ecological specialization (Ihlenfeldt 1983). Ellner & Shmida (1981) however offer an alternative theory, i.e. an arid habitat species response to the extremely low benefit of adaptation to long-range dispersal mechanisms.

The role of secondary dispersal by washing and splashing of rain on the ground has not been addressed but field observations show that *Bergeranthus* populations often occur along drainage lines suggesting that this mechanism is significant. The preference of most species to open bare habitats supports this observation.

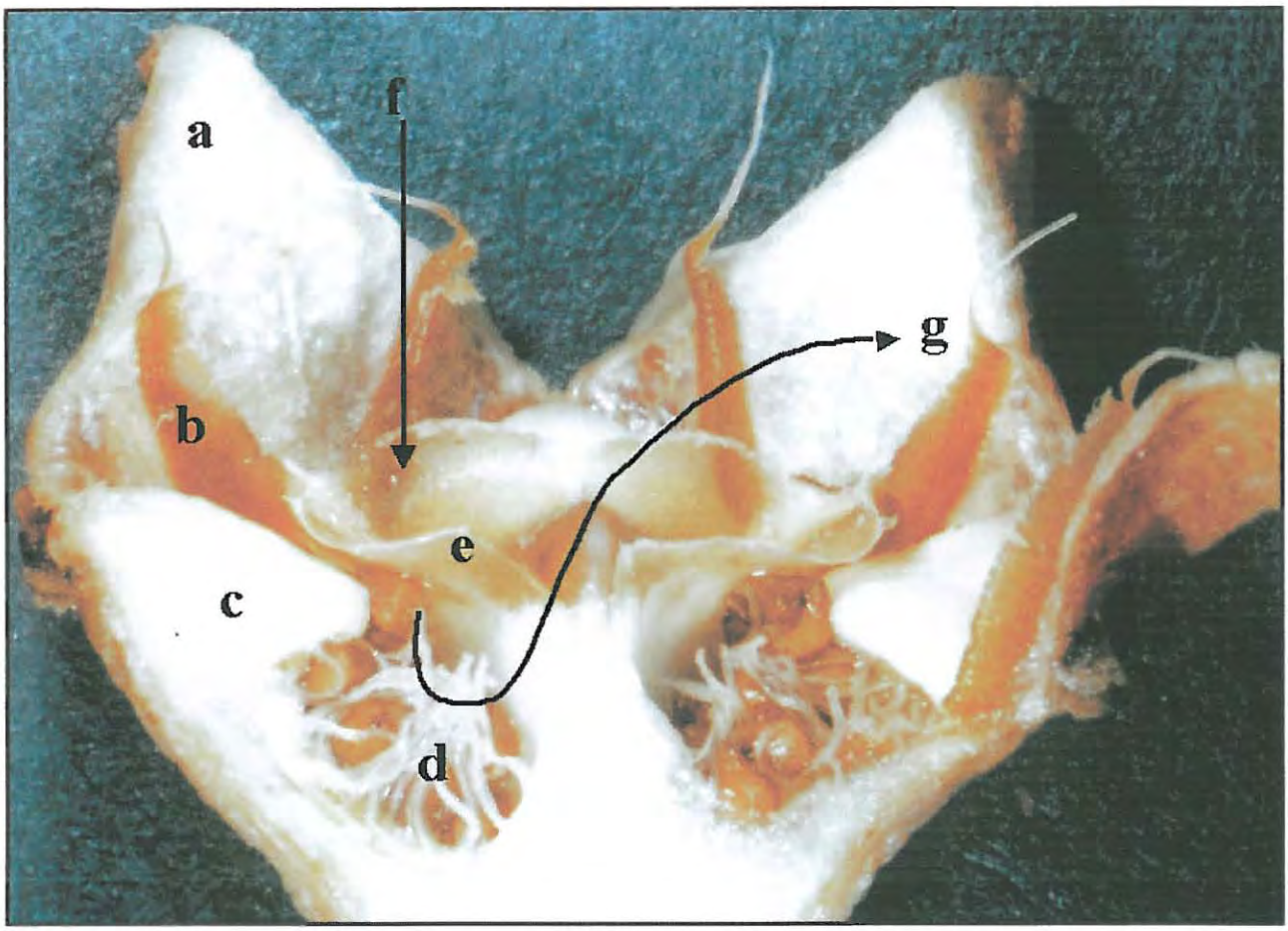

FIGURE 66. —Section of open capsule of *B. albomarginatus* (*Dold 4284*), 12 mm radius (a = valve, b = expanding keel, c = closing body, d = locule with sterile funicles holding seeds, e = covering membrane, f = direction of raindrop impacting on covering membrane, g = Direction of ejection of a jet of water from the locule between the halves of each covering membrane.

RELATIONSHIPS WITH OTHER GENERA

The classification of the Mesembryanthemaceae formulated by Schwantes (1926), subsequently revised and completed by Straka & Ihlenfeldt (1971), represents the latest formally published classification of this family. In the subfamily Ruschioideae a number of monophyletic groups are recognised although relationships and delimitation of genera are still under study. A formal classification is still not available for this large group, which contains ± 1598 species. The system followed here adheres to that of Chesselet *et al.* (2000a) that is based on the work of Hartmann (1988a, 1991a, 1991b, 1993, 1998a). A tribal classification of the family based on characters of the floral nectary is proposed by Chesselet *et al.* (2001).

The genus *Bergeranthus* is currently placed together with *Bijlia*, *Carruanthus*, *Cerochlamys*, *Hereroa*, *Machairophyllum* and *Rhombophyllum* in the Bergeranthus group within the subfamily Ruschioideae of the family Mesembryanthemaceae (Chesselet *et al.* 2000a). This subfamily comprises 12 groups and includes the following synapomorphies: stamens hairy at the base; nectaries lophomorphic; placentation basal or parietal; expanding keels ± restricted to valves; covering membranes often present. The Bergeranthus group is defined by Chesselet *et al.* (2000a) as follows: Plants perennial; Leaves homocellular, xeromorphic, mostly free to base; Flowers mostly in exserted inflorescences with five separate nectaries; Capsules with firm straight, complete covering membranes, closing bodies present of absent, valve wings reduced.

When Schwantes (1926) first described *Bergeranthus*, he also included three subgenera treated as separate genera now: *Carruanthus*, *Hereroa*, and *Rhombophyllum*. Furthermore, he placed species in the genus now considered to belong to *Ebracteola* and *Machairophyllum*[14].

Hartmann (1991a) groups *Bergeranthus* together with *Bijlia*, *Carruanthus*, *Cerochlamys*, *Hereroa*, *Machairophyllum* and *Rhombophyllum* in the Bergeranthus group within the subfamily Ruschioideae but points out that this grouping is a tentative arrangement and that generic delimitations need further study. Hartmann (1998a) delimits the group further into winter and summer rainfall groups where *Bergeranthus* and *Rhombophyllum* form the Bergeranthus–summer rainfall entity.

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[14] Schwantes, G. (in Jacobsen 1954) places *Bergeranthus* in the family Ficoidaceae Juss. emend. Hutchins., subfamily group Mesembryanthema, subfamily Caryotophoroideae – Ruschioideae Schwant., tribe Ruschieae Schwant., subtribe Ruschiinae Schwant..

Smith *et al.* (1998) include *Bergeranthus* in the informal "tufted mesembs" group, based on growth form and leaf characters, together with *Cheiridopsis, Cylindrophyllum, Ebracteola, Hereroa, Khadia, Machairophyllum, Marlothistella, Psammophora, Rabiea, Rhombophyllum* and *Ruschianthus.* However, *Bergeranthus*, *Hereroa* and *Rhombophyllum* are grouped closely within this assemblage and are delimited by means of the presence (*Hereroa*) or absence of raised dots on the leaves, bipartite closing bodies (*Rhombophyllum*) and undivided closing bodies (*Bergeranthus*). Hartmann (1991a) confirms this status and maintains that the three genera form a distinct group but that the generic delimitations need further study.

Hartmann (1998b) notes that *Bergeranthus* develops a broad, undivided sill as a closing body, *Hereroa* possesses a small closing body or none at all, and *Rhombophyllum* has a divided closing body. The current study concurs with these findings although no closing bodies have been seen in the Eastern Cape material of *Hereroa* examined.

Chesselet *et al.* (2000a) provide two keys, one for fruit and flower characters and one for vegetative characters. The former is based on Bolus (1971) and the latter on Hartmann (1991b) (Table 5). A key to 10 fruit types, based on Hartmann (1988a) is also provided. Chesselet *et al.* (2000b) provide a novel diagrammatic representation of relationships among genera of the Mesembryanthemaceae based on floral nectary types also grouping these seven genera. Nevertheless the authors state that the generic groupings follow current concepts and are not absolute.

There is therefore no doubt that *Bergeranthus*, *Hereroa* and *Rhombophyllum* are closely related genera and that their relationships are in need of further study. Furthermore, during the course of fieldwork it became clear that these three genera occur in similar habitats and often in close proximity. The rediscovery of *B. artus*, 88 years after the first collection, necessitates a re-examination of useful characters to separate the three genera as this species in particular presents characters previously attributed to both *Hereroa* and *Bergeranthus* (Single flowered unbranched inflorescence, nocturnal, fragrant flowers). In addition the epidermal wax layer of *Bergeranthus artus* closely resembles that of *Hereroa granulata* (N.E.Br.) Dinter & Schwantes.

The genus *Bergeranthus*, comprises 10 species restricted to the Eastern Cape Province, *Rhombophyllum* comprises five species restricted to the Eastern Cape Province, and *Hereroa* 32 species, which are widespread in South Africa and Namibia. No taxonomic revision has been undertaken for any of these genera since their description in 1926, 1927 (Schwantes 1927) and

1927 (Schwantes 1927) respectively and the synonymy of certain species reveals their past uncertainty.

Key characters used to separate the genera in the past include leaf shape and surface, petaloid staminodes (Bolus 1958), closing bodies (Bolus 1971), rootstock (Herre & Volk 1971), and inflorescence type (Hartmann 1991b). Smith *et al.* (1998) reduce these to leaf surface and closing body. Bolus made an error in 1958 by using staminodes as a character as none of the three genera possess them. This character was excluded in subsequent keys (Bolus 1971; Herre 1971; Hartmann 1991; Smith *et al.* 1998). Previously used characters are synthesised in Table 5.

TABLE 5. —Characters previously used to separate *Bergeranthus*, *Hereroa* and *Rhombophyllum*.

		Bergeranthus	***Hereroa***	***Rhombophyllum***
Bolus (1958)	-Leaves	Triquetrous	Not triquetrous	Not triquetrous
	-Staminodes	Not present	Present	Present
Bolus (1971)	-Leaves	Triquetrous	Not triquetrous, pairs dissimilar	Not triquetrous, pairs dissimilar
	-Closing bodies	Large, undivided	Small, undivided	Bipartite
Herre & Volk (1971)	-Leaves	Dots inconspicuous	Dots prominent	Not noted
	-Closing bodies	Large, 3-sided	Small	Plane
	-Rootstock	Not noted	Woody	Often fleshy
Hartmann (1991b)	-Leaves	± Trigonous	Moderately gibbose	Extensively gibbose
	-Closing bodies	Present, undivided	Single, small or absent	Bipartite, two plates
	-Flowers	Stalked dichasia	± Solitary	± Solitary
Smith *et al.* (1998)	-Leaves	Smooth, inconspicuous dots	Raised dots	Smooth, inconspicuous dots
	-Closing body	Undivided	Not noted	Bipartite

It is therefore necessary to assess previously used characters and to examine living plants of representative species of the three genera towards providing taxonomic characters that will be useful in delimiting the genera, and ultimately providing a key to the genera in the study area. The following living specimens of representative taxa were examined:

1. *Bergeranthus scapiger* (Haw.) Schwantes (Figure 67)
   Mesembryanthemum scapigerum Haw.
Dold 4193, 4202, 4263, 4328, 4252 (GRA).

2. *Bergeranthus artus* L.Bolus (Figure 68)
Dold 4242, 4245, 4288 (GRA)

3. *Hereroa granulata* (N.E.Br.) Dinter & Schwantes[15] (Figure 69)
   Mesembryanthemum granulatum Schwantes
   Mesembryanthemum carinans A.Berger
   Bergeranthus granulatus Schwantes
Dold 4402, 4403, 4404, 4405, 4406, 4407, 4408, 4409, 4410 (GRA).

4. *Rhombophyllum rhomboideum* (Salm-Dyck) Schwantes (Figure 70)
   Mesembryanthemum rhomboideum Salm-Dyck
   Bergeranthus rhomboideus Schwantes
Dold 4398, 4399, 4400, 4401, (GRA).

5. *Rhombophyllum dolabriforme* (L.) Schwantes (Figure 71)
   Mesembryanthemum dolabriforme L.
   Hereroa dolabriformis L.Bol.
Dold 4397 (GRA).

[15] This study included only material collected in the Eastern Cape Province, identified as *H. granulata*, these characters may not apply to species found in Namaqualand and Namibia.

FIGURE 67. —*Bergeranthus scapiger* (*Dold 4262*), Bloukrans Pass.

FIGURE 68. —*Bergeranthus artus* (*Dold 4288*), Cala.

FIGURE 69. —*Hereroa granulata* (*Dold 4403*), Ecca Pass.

FIGURE 70. —*Rhombophyllum rhomboideum* (*Dold 4400*), Coega.

FIGURE 71. —*Rhombophyllum dolabriforme* (no specimen preserved), Carlisle Bridge.

1. CHARACTER ASSESSMENT

Of the 27 characters examined in this study (Table 6), 13 proved useful (highlighted in Table 6) in a key to the three genera and are discussed individually.

TABLE 6. —Characters examined and assessed for taxonomic importance.

Leaf	**Flower**	**Rootstock**	**Inflorescence**	**Fruit**	**Seed**
Leaf apex mucronate or not.	Filament vesture.	Rootstock shape.	Inflorescence branching or not.	Capsule locule depth and shape in cross-section.	Seed size shape and testa sculpture.
Leaf shape.	Ovary surface shape.		Pedicel length.	Closing body presence or absence and shape.	
Leaf surface.	Floral nectary size and shape.			Covering membrane size.	
Leaf wax layer.					
Central leaf pairs equal in length or not.	Ovary septa raised or not.			Expanding keel winged or not.	
Leaf keel shape.	Anther shape and point of adherence.			Valve wings presence or absence.	
Leaf cross-section shape.	Calyx lobe winged, apiculate or mucronate.				
Leaf margin.	Flowering time of day.				
	Pollen.				
	Scent.				
	Stigma shape & vesture				

1.1. **Capsule locule** depth and shape in longitudinal section: All three genera have five locules, although occasionally a four loculed capsule occurs in *Bergeranthus* (pers. obs.). The locules of *Bergeranthus* are always as deep, or deeper, than they are wide (Figure 72A) resulting in a deeply cupped locule whereas those of both *Hereroa* (Figure 73B) and *Rhombophyllum* (Figure 72B, 73A) are always wider than they are deep resulting in a shallow saucer-shaped locule.

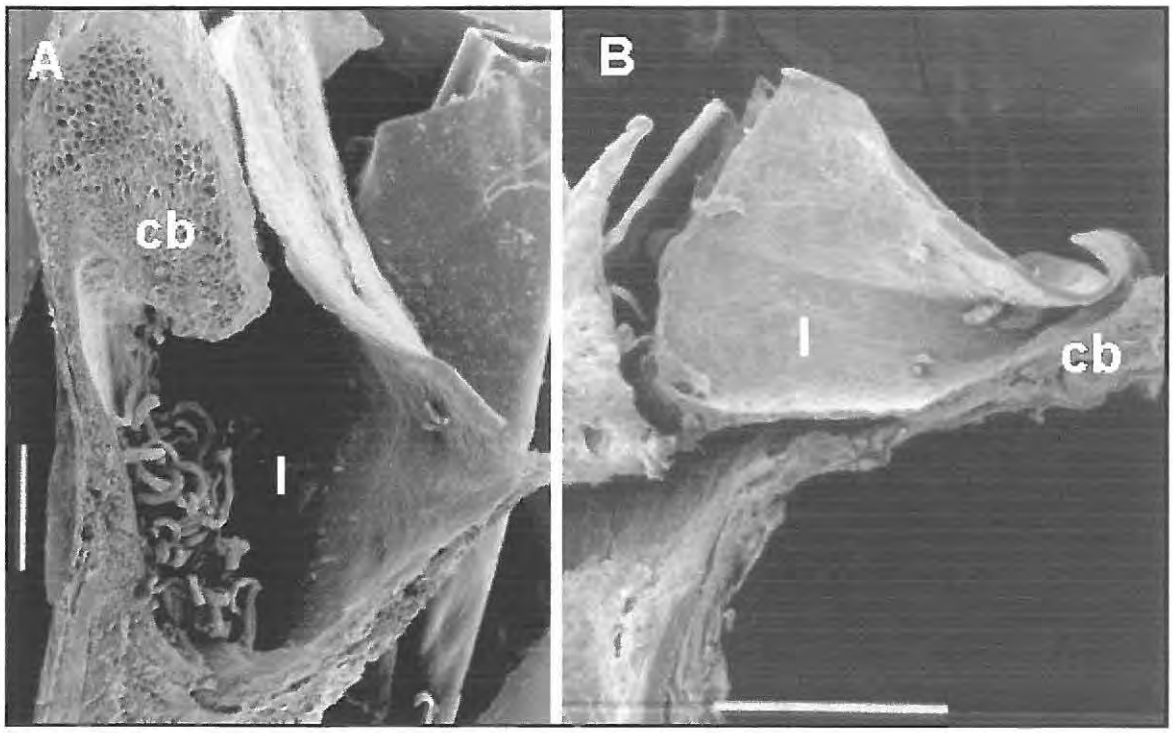

FIGURE 72. —Scanning electron micrographs of longitudinal sections of capsules: A. *Bergeranthus scapiger* (*Dold 4328*); B. *Rhombophyllum dolabriforme* (*Dold 4397*). Scale bars 1 mm (cb = closing body, l = locule).

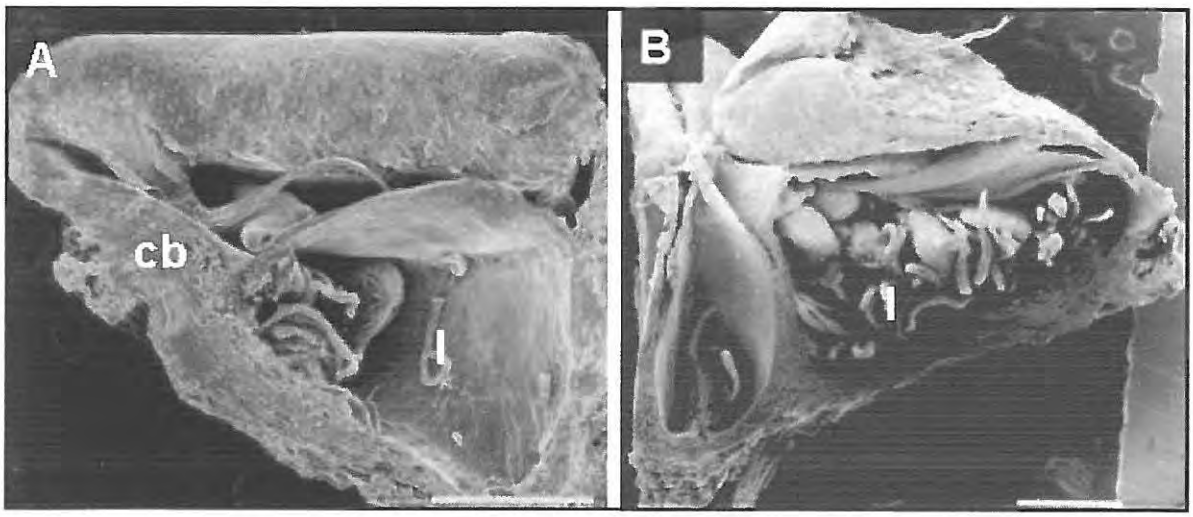

FIGURE 73. —Scanning electron micrographs of longitudinal sections of capsules: A. *Rhombophyllum rhomboideum* (*Dold 4398*); B. *Hereroa granulata*, (*Dold 4402*). Scale bars 1 mm (cb = closing body, l = locule).

1.2. **Closing body** presence or absence and shape: The closing body at the distal end of the locule has also been called a tubercle (Lockyer 1932). The closing body of *Bergeranthus* is a large corky body with a lower lip protruding from the distal end of the locule severely impeding seed dispersal so that some seeds are retained until the capsule disintegrates, as long as a year after developing (Figures 72A, 74A). *Rhombophyllum* has a greatly reduced divided closing body that is merely the raised outer floor of the capsule (Figures 72B, 73A, 74B, 74C). Consequently seeds are dispersed easily and the capsule disintegrates soon afterwards. *Hereroa* has no closing body and relies on numerous sterile funicles to retain seeds (Figures 73B, 74D). The seeds disperse easily and the capsule disintegrates quickly, the pedicel is however strongly persistent. The findings of this study concur with those of Hartmann (1998b) although Hartmann has recorded small closing bodies in some species of *Hereroa* but does not provide specimen data or localities for these. Hartmann (1991a) suggests that *Hereroa*, being so poorly known, may comprise more than one genus. It is possible that the material studied here could provide a useful character (i.e. the absence of a closing body) in future studies on *Hereroa.*

1.3. **Covering membrane**: The term covering membrane is taken from Hartmann (1988a) and is equivalent to the superlocular wings of Lockyer (1932) and the cell wings described by Brown (1921). The covering membranes of both *Bergeranthus* (Figure 74A) and *Rhombophyllum* (Figure 74B, 74C) are a pair of large semi-transparent sheets covering the top of the locule and holding the seeds within. The covering membrane of *Hereroa* covers only the proximal half of the locule while the distal half is uncovered and seeds are partially exposed (Figure 74D). The absence of covering membranes has been interpreted as a primitive feature for Mesembryanthemaceae (Schwantes 1952, Ihlenfeldt 1960, Hartmann 1988a) although it is unclear if reduced covering membranes are also primitive.

1.4. **Capsule expanding keel** winged or not: The expanding keel consists of hygroscopic cells facilitating the repeated opening and closing of the loculicidal hygrochastic capsules that is a characteristic of the Mesembryanthemaceae (Hartmann 1988a). These are distinct and sometimes winged in some genera or reduced and without wings in others. The expanding keel of *Bergeranthus* is not winged (Figure 74A) while those of *Rhombophyllum* (Figure 74B, 74C) and *Hereroa* (Figure 74D) are fimbriate winged with an attenuate apex. The function of a fimbriate wing is unclear (Hartmann 1988a).

1.5. **Capsule valve wing** presence or absence: Bittrich (1986) includes the presence of valve wings among the three apomorphic characters of the Mesembryanthema (i.e. the Aptenioideae

and the Ruschioideae). Hartmann (1988a) states that it is probable that the possession of valve wings represents a primitive state in the Aptenioideae and the Ruschioideae and that they can be used as taxonomically useful characters. The function of the valve wings remains uncertain (Hartmann 1988a). Valve wings are absent in *Bergeranthus* whereas the valves of *Rhombophyllum* (Figure 74B, 74C) and *Hereroa* (Figure 74D) have transparent wings of various dimensions.

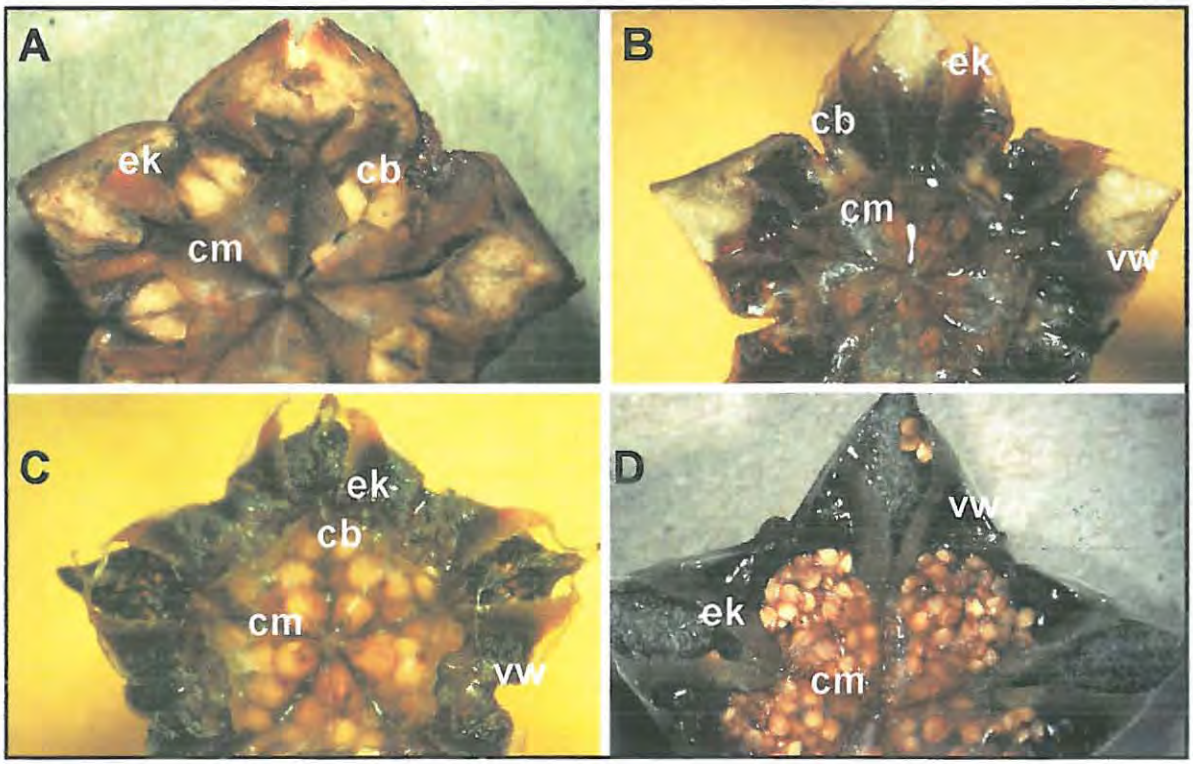

FIGURE 74. —Open capsules: A. *Bergeranthus scapiger* (*Dold 4328*), 21 mm diam.; B. *Rhombophyllum rhomboideum* (*Dold 4398*), 10 mm diam.; C. *Rhombophyllum dolabriforme* (*Dold 4397*), 12 mm diam.; D. *Hereroa granulata* (*Dold 4402*), 18 mm diam. (cl = closing body, cm = covering membrane, ek = expanding keel, vw = valve wing).

1.6. **Filament vesture**: Chesselet *et al.* (2000a) incorrectly describe the filaments of *Bergeranthus* species as exclusively epapillate. The central filaments of *Bergeranthus* and *Rhombophyllum* are glabrous, papillate or sparsely clothed with long white hairs (Figure 75A) while those of *Hereroa* are densely white pilose (Figure 75B).

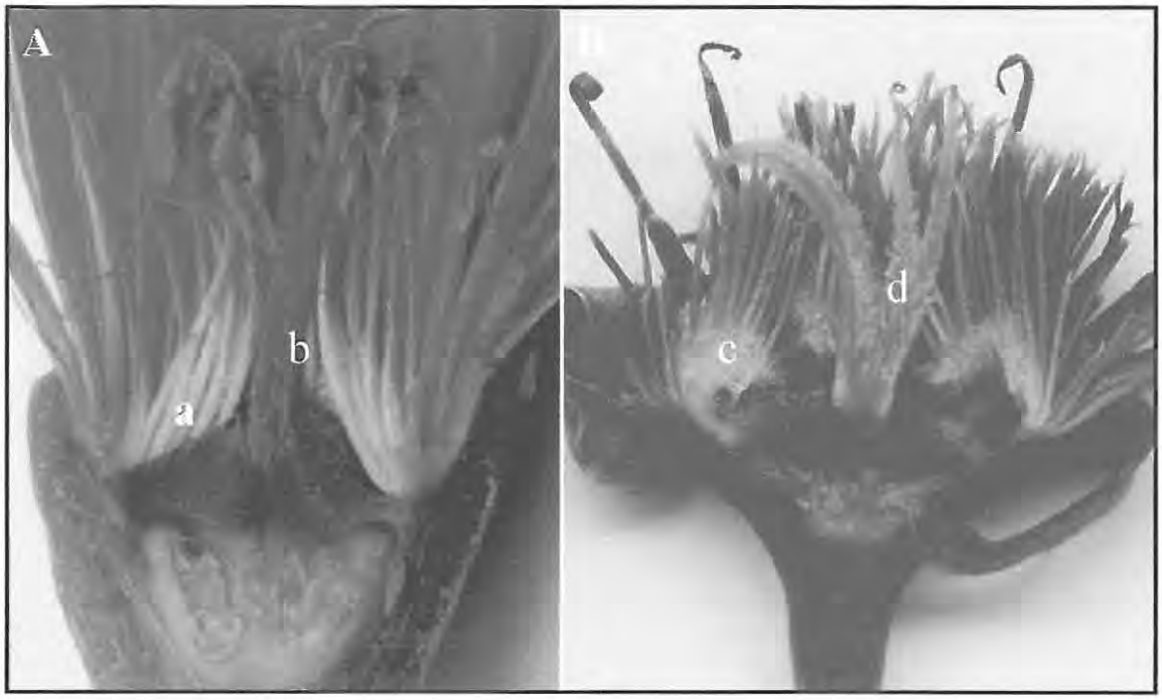

FIGURE 75. —Filament and stigma vesture: A. *Bergeranthus scapiger* (*Dold 4296*) x 10, B. *Hereroa granulata* (*Dold 4410*) x .4.5 (a=sparsely haired filaments, b=papillate stigmata, c=densely pilose filaments, d=densely pilose stigmata).

1.7. **Ovary upper surface** shape: The upper surface of the ovary of *Bergeranthus* is distinctly raised (Figure 76A, 76B) while that of *Hereroa* is cupped (Figure 76C) and that of *Rhombophyllum* is ± flat (Figure 76D).

1.8. **Floral nectary** size and shape: Chesselet *et al.* (2000a) incorrectly describe the nectary of *Bergeranthus* as a crenate ring, however Chesselet *et al.* (2000b) report that *Bergeranthus* and *Rhombophyllum* have lophomorphic meronectaries and that *Hereroa* has some species with lophomorphic meronectaries and others with lophomorphic holonectaries. The findings of this study agree with this although no Eastern Cape material of *Hereroa* has shown holonectaries thereby supporting Hartmann's (1991a) suggestion that *Hereroa* may comprise more than one genus. Chesselet *et al.* (2000b) interpret segmented nectaries (meronectary) as primitive within the family and state that they occur predominantly in summer rainfall species. The nectaries of *Bergeranthus* (Figure 76A, 76B) and *Rhombophyllum* (Figure 76D) are small, crescent shaped, yellow and not raised whereas those of *Hereroa* are large, raised, yellow, toothed crescents (Figure 76C).

1.9. **Ovary septa** raised or not: The septa of *Bergeranthus* are raised and distinctly separated by means of a groove down the center (Figure 76A, 76B) whereas those of *Rhombophyllum* (Figure 76D) and *Hereroa* (Figure 76C) are inconspicuous. The septa show characters that later become important in the fruit, e.g. the raised septa become raised valve margins ("rims" *sensu* Hartmann 1991a).

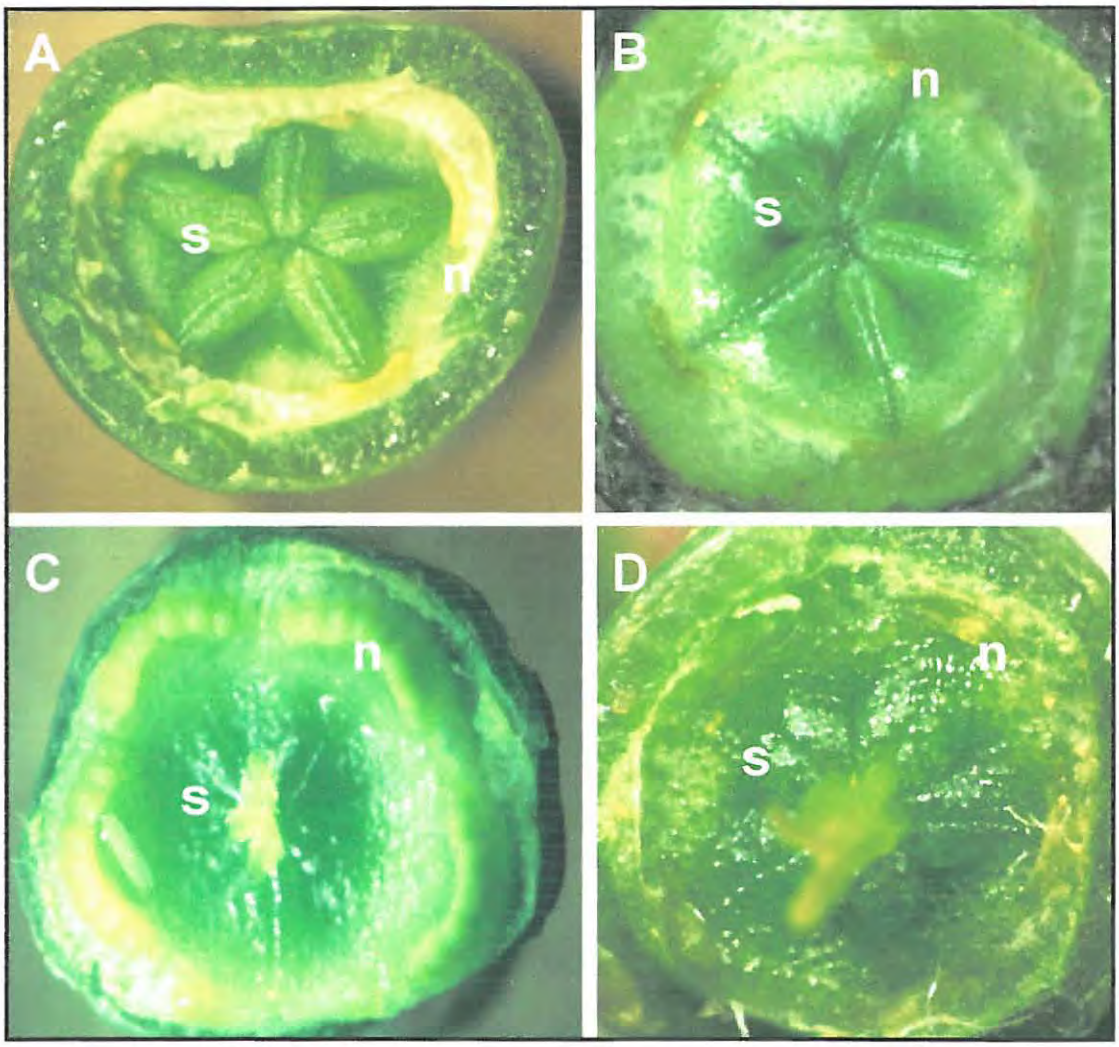

FIGURE 76. —Top of ovary with floral parts removed: A. *Bergeranthus scapiger* (*Dold 4252*), 5 mm diam.; B. *Bergeranthus artus* (*Dold 4245*), 6 mm diam.; C. *Hereroa granulata* (*Dold 4410*), 6 mm diam.; D. *Rhombophyllum dolabriforme* (*Dold 4397*), 4 mm diam. (n = floral nectaries, s = septa).

1.10. **Inflorescence** branching or not: Dehn (1990) reports that *Bergeranthus*, *Hereroa* and *Rhombophyllum* represent a group with reduced dichasia that often consist of only three flowers.

This study concurs that *Bergeranthus* and *Rhombophyllum* have a branched inflorescence, however all specimens of *Hereroa* examined produced an unbranched inflorescence.

1.11. **Leaf apex** mucronate or not: The leaf apex of *Bergeranthus* is mucronate while *Hereroa* and *Rhombophyllum* are not.

1.12. **Leaf shape**: All species of *Bergeranthus* have ± triquetrous leaves. *Hereroa* has terete or semi-terete leaves, described by Chesselet (2000a) *et al.* as finger-like, while *Rhombophyllum* has a rhomboid, dolabriform or sickle-shaped leaf with a prominent gibbosity on the lower distal keel.

1.13. **Leaf surface** under light microscope: *Bergeranthus* has a smooth leaf surface (Figure 77A) while *Hereroa* (Figure 77D) and *Rhombophyllum* (Figure 77B, 77C) have raised dots or pustules on the leaf surface.

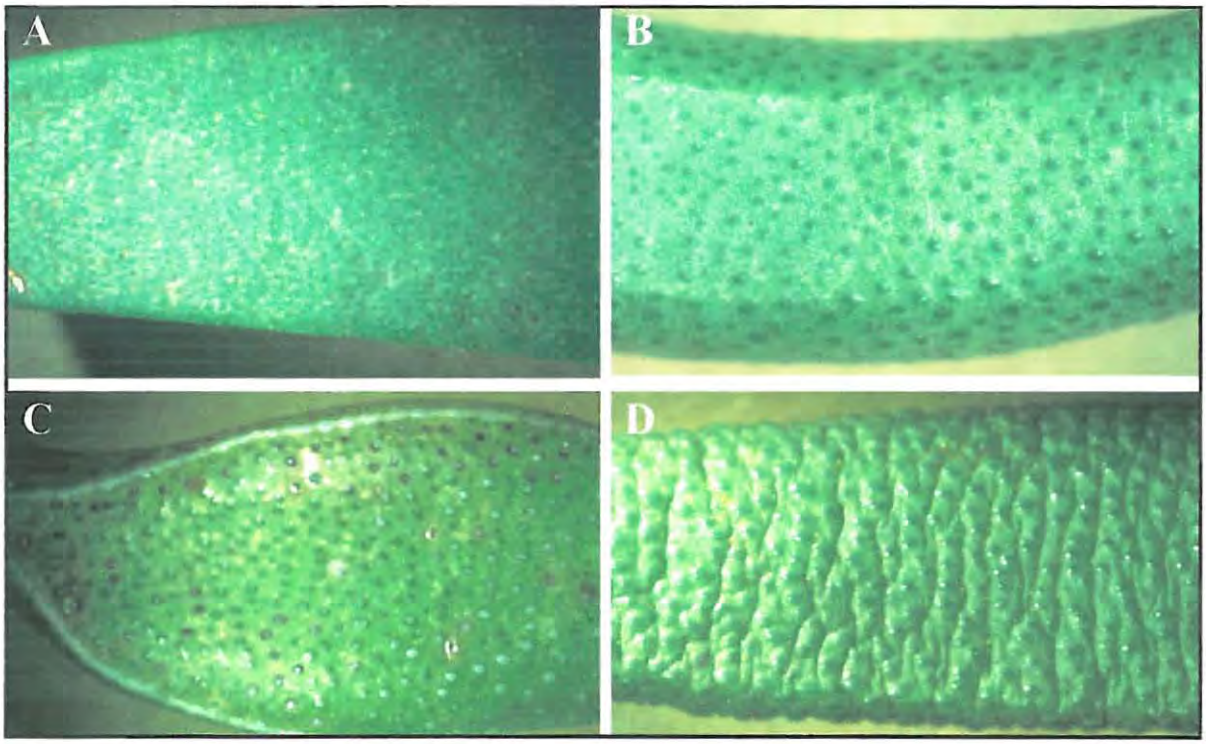

FIGURE 77. —Leaf surface. A. *Bergeranthus scapiger* (*Dold 4252*), 9 mm width; B. *Rhombophyllum dolabriforme* (*Dold 4397*), 4 mm width; C. *Rhombophyllum rhomboideum* (*Dold 4399*), 11 mm width; D. *Hereroa granulata* (*Dold 4410*), 6 mm width.

Of these 13 characters, nine have not been previously used (covering membrane, expanding keel, filament vesture, top of ovary, leaf apex, locule, nectary, ovary septa, valve wing). The remaining 14 characters that did not prove useful were discarded (anther shape and point of adherence; calyx lobe winged or dorsally apiculate; central leaf pairs of equal length or not; flowering time of day; leaf keel shape; leaf cross–section shape; leaf surface wax layer under electron microscope; leaf margin shape; pedicel length; pollen; rootstock shape; scent of flower; seed size, shape and testa sculpture; stigma shape and vesture) but are clarified briefly below:

1.14. **Anther** shape and point of adherence: The anthers of *Bergeranthus* are linear to ovate in shape with a deeply concave upper surface and are basally dorsifixed. *Hereroa* has dorsifixed, linear anthers with a deep narrow groove down the upper surface. The anthers of *Rhombophyllum* are ovate to elliptic, deeply concave and basifixed.

1.15. **Calyx lobe**: Calyx lobes are lanceolate to ovate, acute with transparently winged margins in all three genera. *Hereroa* and *Rhombophyllum* calyx lobes have an acute dorsal apiculus, which is reduced to a blunt gibbosity in *R. dolabriforme*. *Bergeranthus* calyx lobes can be dorsally apiculate or not.

1.16. **Central leaf pairs** of equal length or not: the central leaf pair of *Hereroa* and *Rhombophyllum* are unequal in length, one leaf being slightly longer with its apex curving inwards to cradle the shorter leaf. *Bergeranthus* shares this characteristic, although inconsistently, in some species.

1.17. **Flowering time** of day: *Rhombophyllum* has diurnal flowers and *Hereroa* has nocturnal flowers. A single species of *Bergeranthus* (*B. artus*) has nocturnal flowers while the remaining nine species are diurnal.

1.18. **Leaf keel**: *Hereroa* and *Rhombophyllum* leaves are not keeled. All species of *Bergeranthus* with the exception of *B. artus* are at least distally keeled.

1.19. **Leaf cross–section**: *Hereroa* leaves are "D"-shaped in cross-section. *Rhombophyllum rhomboideum* has a "D"-shaped leaf in cross section while *R. dolabriforme* is "O" shaped.

Bergeranthus can be "D"-shaped or "V"-shaped. Leaves were sectioned midway between base and apex.

1.20. **Leaf epidermal wax layer**: Leaves of *Bergeranthus*, *Hereroa* and *Rhombophyllum* (Table 2) were examined in the Rhodes University Electron Microscopy Unit using a JEOL–JSM 840 scanning electron microscope at 12 k. All material was air-dried and sputter coated with gold using a Balzers Union coating unit. Leaf surfaces were examined at a magnification of x 2000 under electron microscope at the central upper surface of each leaf. Most species of *Bergeranthus* and both species of *Rhombophyllum* have fine sculptures of the platelet type (Hartmann 1991a) while *Hereroa* has an unusual smooth surface with fine thread-like particles scattered horizontally (Figure 78). *Bergeranthus artus* has a smooth wax layer remarkably like that of *Hereroa* (see Taxonomy, Figure 37B). Consequently it is suggested here that *B. artus* is a possible link between these genera. This is supported by further shared characters, i.e. nocturnal flowering and sweetly scented flowers.

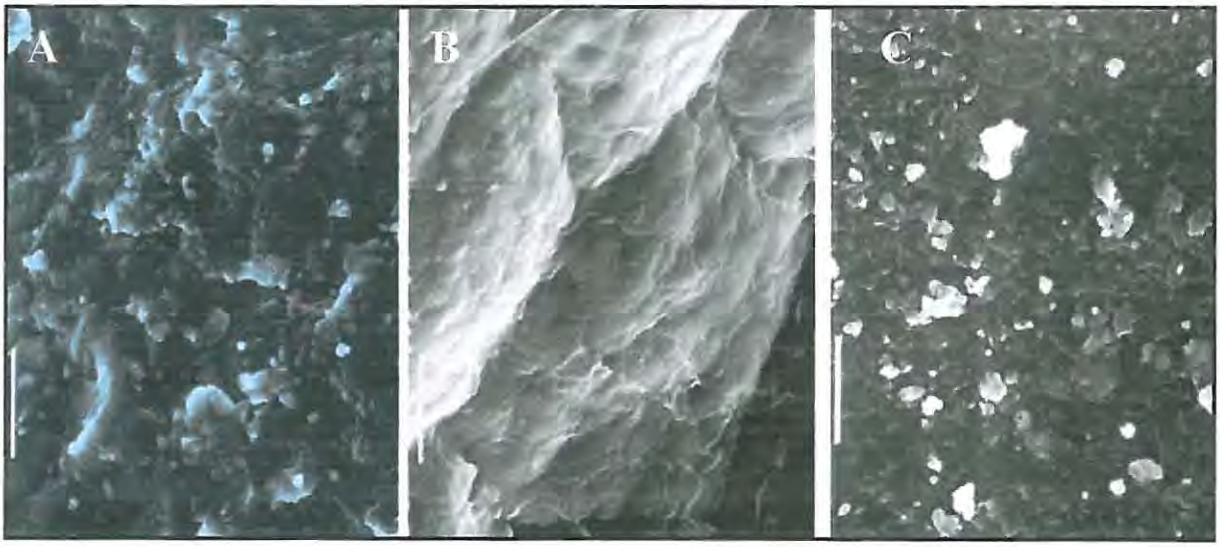

FIGURE 78. —Scanning electron micrographs of leaf epidermal wax layers. A. *Bergeranthus scapiger* (*Dold 4328*); B. *Hereroa granulata* (*Dold 4408*); C. *Rhombophyllum rhomboideum* (*Dold 4400*). Scale bars 10 μm.

1.21. **Leaf margin**: *Hereroa granulata* and *Rhombophyllum dolabriforme* have rounded, indistinct leaf margins. *Rhombophyllum rhomboideum* and all species of *Bergeranthus* have a distinct, sharp-edged leaf margin.

1.22. **Pedicel length**: Pedicel length varies from 5 mm to 180 mm within genera and species and appears to be influenced by the degree of exposure to shade and direct sunlight.

1.23. **Rootstock**: All three genera produce a thickened woody rootstock with a prominent taproot and copious fibrous lateral roots. *Bergeranthus* alone develops a flattened horizontal rhizomatous taproot that gives rise to new vegetative growth. Older, well-developed plants' roots become densely and tightly intertwined (Figure 79).

1.24. **Pollen**: All three genera have tricolpate pollen grains ± 15 x 12 µm. *Bergeranthus* and *Rhombophyllum* have a punctate microspinulose tectum. *Hereroa* has an imperforate (complete) tectum with pronounced pyramidal shaped ornamentation (Figure 80).

1.25. **Flower scent**: *Hereroa granulata* and *Bergeranthus artus* have fragrant flowers, *Rhombophyllum* and *Bergeranthus*, with the exception of *B. artus*, are not fragrant.

1.26. **Seed**: Seeds of all three genera are ± ovoid with a pronounced micropyle (Figure 81). Seeds of most species have a sculptured testa characterised by undulate anticlinal walls (Figure 82) with the exception of *B. addoensis* that has a smooth testa (See morphological character assessment – figure 25A). *B. artus* is the only species with a puberulous vesture on the seed testa that is a useful character at species level (Figure 82A).

1.27. **Stigma shape and vesture**: *Bergeranthus* has linear, erect stigmata that become swollen tipped (± club-like) with age. The inner basal surfaces of the stigmata are puberulous, with minute white threads, or papillate. *Hereroa granulata* has linear or swollen tipped stigmata that are densely white-pilose on the basal inner surfaces. *Rhombophyllum rhomboideum* has linear, glabrous stigmata while *Rhombophyllum dolabriforme* has puberulous or papillate stigmata. Hartmann (1991a) reports that most genera within the Ruschioideae possess papillae on the stigmata but their function is unknown. The presence of long white hairs on the base of the stigmata of *Hereroa* appears to have been overlooked by Hartmann (1991a).

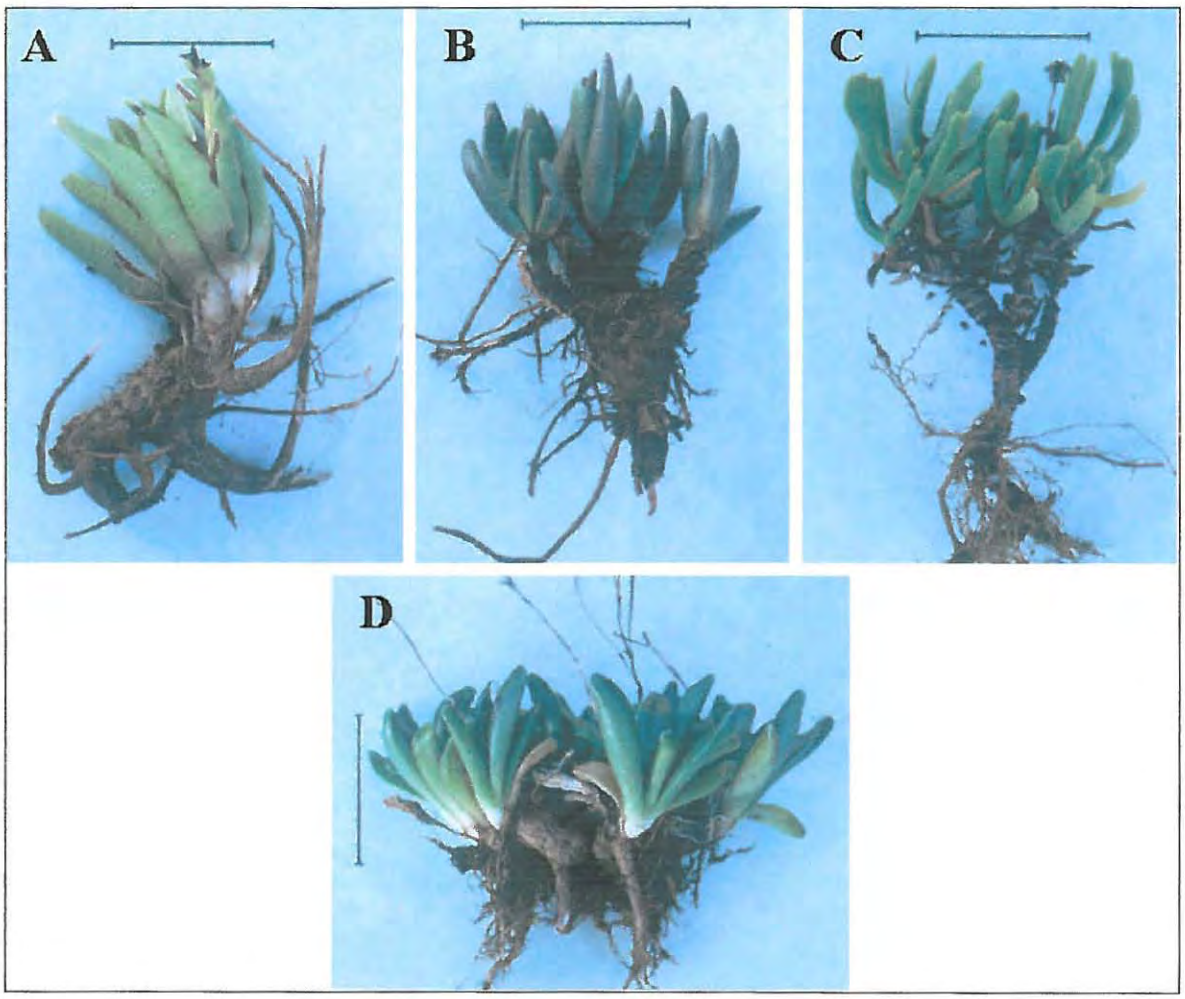

FIGURE 79. —Rootstock. A. *Bergeranthus scapiger* (*Dold 4202*); B. *Hereroa granulata* (*Dold 4403*); C. *Rhombophylum dolabriforme* (*Dold 4398*); D. *Rhombophyllum rhomboideum* (*Dold 4397*). Scale bars 100 mm.

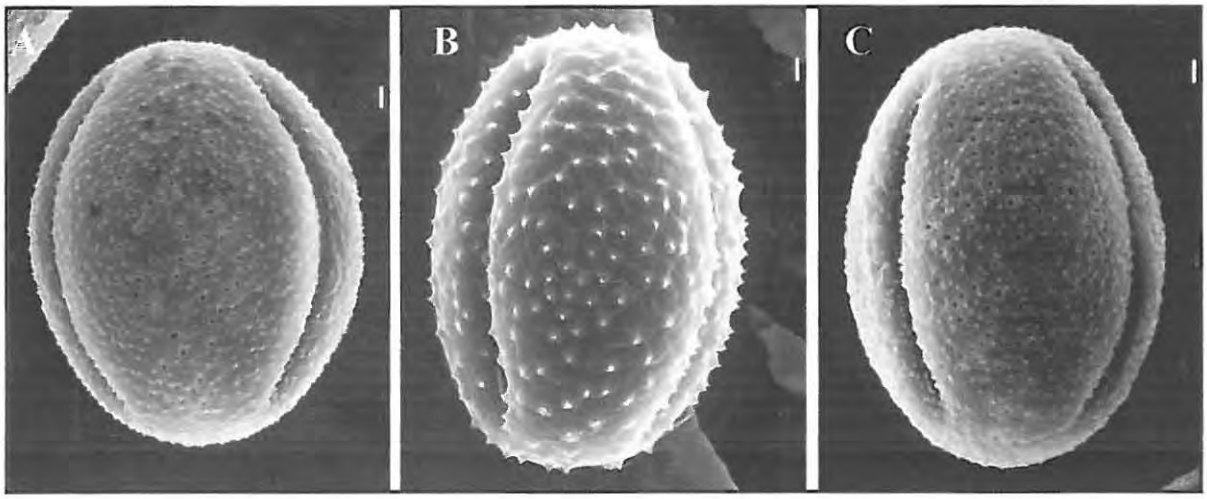

FIGURE 80. —Scanning electron micrographs of pollen. A. *Bergeranthus scapiger* (*Dold 4296*); B. *Hereroa granulata* (*Dold 4410*); C. *Rhombophyllum rhomboideum* (*Dold 4401*). Scale bars 1 μm.

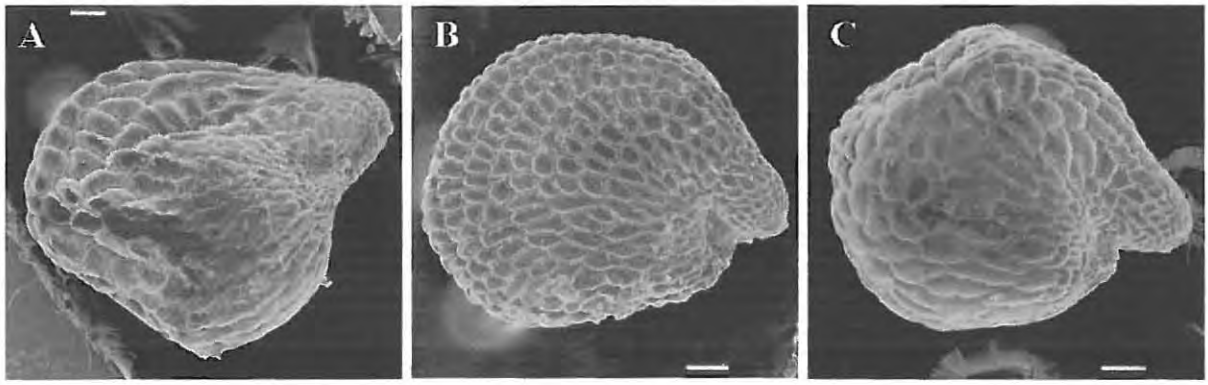

FIGURE 81. —Scanning electron micrographs of seeds. A. *Bergeranthus scapiger* (*Dold 4328*); B. *Hereroa granulata* (*Dold 4408*); C. *Rhombophyllum rhomboideum* (*Dold 4400*). Scale bars 100 μm.

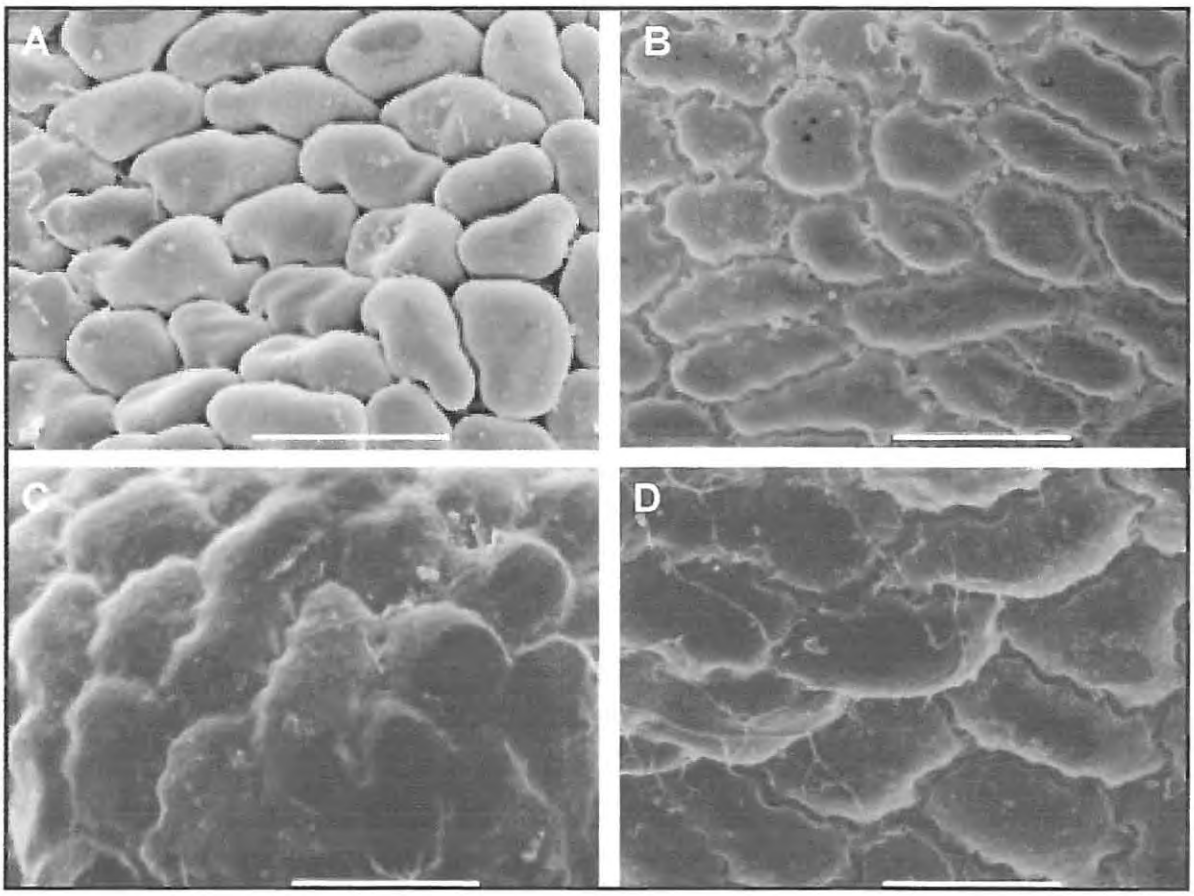

FIGURE 82. —Scanning electron micrographs of seed testa. A. *Bergeranthus artus* (*Dold 4288*); B. *Hereroa granulata* (*Dold 4408*); C. *Rhombophyllum rhomboideum* (*Dold 4400*); *Bergeranthus scapiger* (*Dold 4328*). Scale bars 100 µm.

A key to the three genera, based on Eastern Cape material is provided using the 13 characters examined in this study:

2. KEY TO *Bergeranthus*, *Hereroa* AND *Rhombophyllum* OF THE EASTERN CAPE PROVINCE

1a Leaf surface smooth; apices awned; ovary septa conspicuously separated and raised; top of ovary convex; locules deeper than wide; closing bodies large and corky; expanding keels not winged; valve wings absent.....***Bergeranthus***

1b Leaf surface white-dotted or pustulate; apices without awns; ovary septa inconspicuous and flat; top of ovary cupped or flat; locules wider than deep; closing bodies absent or reduced and bi-partite; expanding keels fimbriate winged; valve wings present

2a Leaf ± rounded (terete); inflorescence not branched, short-lived; nectaries large, raised, toothed; filaments densely pilose at base; top of ovary deeply cupped; closing bodies absent; covering membrane only partially covering locule.....***Hereroa*** (only Eastern Cape species)

2b Leaf rhomboid, dolabriform or sickle-shaped with a prominent gibbosity on the lower distal keel; inflorescence branching, persistent (as in *Bergeranthus*); nectaries minute (similar to *Bergeranthus*) inconspicuous, not raised; filaments sparsely pilose at base; top of ovary flat; closing bodies small, bi-partite; covering membrane completely covering locule.....***Rhombophyllum***

3. PHYLOGENETIC ANALYSIS

A phylogenetic analysis of all 10 species of *Bergeranthus*, both species of *Rhombophyllum* and a single species of *Hereroa* (*H. granulata*) was undertaken to support species and generic delimitation, which, as has already been noted, have been unclear since their description. The rediscovery of *Bergeranthus artus* has complicated matters further due to its strong similarity to *Hereroa granulata*.

The analysis, based on 26 morphological characters and two phenological characters (Table 7) of *Bergeranthus*, *Hereroa* and *Rhombophyllum*, with *Rhombophyllum* as the outgroup, used a Heuristic search using PAUP (version 4.0b8). This search found a single most parsimonious tree (58 steps long, ci 0.672, ri 0.683). Bootstrap support was calculated from 1 000 replicates. Figure 83 shows this single tree.

It is clear from the analysis that the monophyly *Bergeranthus* is strongly supported with 91% bootstrap support (Figure 83). Supporting characters are the large flattened rootstock, smooth leaf surface and apical leaf mucro, raised ovary septum, deep capsule locule with large a closing body and the absence of a marginal wing on the expanding keel (represented by the closed circle on figure 83). *Hereroa* and *Rhombophyllum dolabriforme* are supported with 89% bootstrap support suggesting that *Rhombophyllum* may not be monophyletic. Within *Bergeranthus*, species relationships are poorly supported (< 50%) and some characters are homoplasic. Therefore little emphasis can be placed on any application of the phylogeny. However, based on these data, the following can be said about the species relationships.

Bergeranthus multiceps and *B. leightoniae* are both characterised by decumbent outer leaves (character 23, also found in *Rhombophyllum rhomboideum*).

The group ((*B. multiceps* and *B. leightoniae*) *B. addoensis*) is supported by the capsule expanding sheet being broad and thickened (character 27, also found in *Hereroa granulata*).

The above *Bergeranthus* species together with *B. katbergensis* and *B. concavus* share the feature of the capsule expanding keel being equal in length to the valve (character 25). However this feature is also found in the basal species, *B. albomarginatus*.

Bergeranthus artus shares several characters with *Hereroa granulata* (nocturnal flower, unbranched inflorescence, large raised nectaries, deeply cupped ovary, flower scent, smooth epidermal wax layer – represented by the square on figure 83) but remains in *Bergeranthus* as it

also has the genus-specific features mentioned above. Of these six characters shared with *Hereroa*, all but two are floral characters suggesting that *B. artus* may have independently responded to a similar pollination syndrome to that of *Hereroa*. As has already been discussed in the taxonomy and reproductive biology sections this is the only species of *Bergeranthus* that has a scented nocturnal flower that is so prevalent in the genus *Hereroa*. Although Bolus hesitated to describe *B. artus* for 20 years (from a single cultivated plant) she made no mention of its unusual characteristics that are shared with *Hereroa*. Although there are no confirmed data it is likely that the flowers of *Bergeranthus artus* and *Hereroa granulata* attract nocturnal pollinators such as moths.

B. nanus is placed basal to *B. artus* and the previously mentioned *Bergeranthus* species, and these taxa together share the feature of having central leaf pairs being equal in length (character 3), although this character is polymorphic in some of these species. However, the basal group (*B. albomarginatus* and *B. scapiger*) consistently have unequal central leaf pairs.

B. vespertinus is placed below *B. nanus* and the other taxa and all these taxa are characterised by the leaf apex being without a "chin" (character 9).

TABLE 7. —Characters and data set used in phylogenetic analysis.

		H. granulata	*R. rhomboideum*	*R. dolabriforme*	*B. addoensis*	*B. albomarginatus*	*B. artus*	*B. concavus*	*B. katbergensis*	*B. leightoniae*	*B. multiceps*	*B. nanus*	*B. scapiger*	*B. vespertinus*
1	Rootstock: 0=woody tap & dense lateral, 1=Large woody tap, laterally flattened & rhizomatous	0	0	0	1	1	1	1	1	1	1	1	1	1
2	Leaf shape: 0=linear, 1=ovate, 2=lanceolate	0	1	0	2	1	2	1	2	1	2	2	2	2
3	Central leaf pairs: 0=unequal length & shape, 1=equal length & shape	0	0	0	0&1	0	1	1	0&1	1	1	1	0	0
4	Leaf cross-section mid length: 0=semi terete, 1=D-shaped, 2=triquetrous, 3=terete below "hatchet"	0	1	3	2	2	1	2	2	2	2	2	2	2
5	Leaf surface: 0=pustulate, 1=smooth, 2=white dotted	0	0	0	1	1	1	1	2	1	1	1	1	1
6	Leaf margins: 0=rounded, 1=sharply distinct	0	1	0	1	1	1	1	1	1	1	1	1	1
7	Leaf keel: 0=not keeled, 1=keeled	0	0	0	1	1	0	1	1	1	1	1	1	1
8	Leaf apex lateral flattening: 0=flattened, 1=not flattened	0	1	0	1	1	1	1	1	1	1	1	1	1
9	Leaf apex: 0=not chinned, 1= chinned 2=bi-lobed	1	1	2	0	1	0	0	0	0	0	0	1	0
10	Leaf mucro/awn: 0=absent, 1=present	0	0	0	1	1	1	1	1	1	1	1	1	1
11	Flowering time: 0=nocturnal, 1-late afternoon	0	1	1	1	1	0	1	1	1	1	1	1	1
12	Inflorescence: 0=unbranched, 1=branched	0	1	1	1	1	0	1	1	1	1	1	1	1
13	Nectary: 0=large raised structure, 1= minute, inconspicuous or obselete	0	1	1	1	1	0	1	1	1	1	1	1	1
14	Septa: 0=insignificant, not raised, 1=clearly demarcated & raised	0	0	0	1	1	1	1	1	1	1	1	1	1
15	Ovary: 0=deeply cupped, 1=flattened, 2=convex & raised well above base of filaments, 3=deeply cupped but raised in centre	0	1	1	2	2	3	2	2	2	2	2	2	2
16	Scent: 0=strong lemon smell, 1=no scent	0	1	1	1	1	0	1	1	1	1	1	1	1
17	Capsule locules in cross-section: 0=shallow cup, walls almost horizontal, 1=deep cup, walls almost vertical	0	0	0	1	1	1	1	1	1	1	1	1	1
18	Closing bodies shape: 0=no closing body, seeds held by funicles, 1=insignificant raised bipartite transparent bulge, 2=large pear shaped corky body	0	1	1	2	2	2	2	2	2	2	2	2	2
19	Expanding keel: 0=broadly fimbriate winged, 1=not winged	0	0	0	1	1	1	1	1	1	1	1	1	1
20	Leaf waxes: 0=sculptured, 1=smooth	1	0	0	0	0	1	0	0	0	0	0	0	0
21	Sepals: 0=dorsally apiculate, 1=not apiculate	0	0	0	1	1	0&1	1	1	0	0&1	0&1	0&1	1
22	Filament vesture: 0=densely pilose, 1=sparesly pilose, 2=glabrous	0	1	1	1	1	2	1	1	2	1	1	2	1
23	Outer leaves: 0=erect, 1=decumbent	0	1	0	0	0	0	0	0	1	1	0	0	0
25	Expanding keel: 0=equal to valve, 1=exserted beyond valve	1	1	1	0	0	1	0	0	0	0	1	1	1
26	Expanding keel margin: 0=entire, 1=serrate	1	1	1	0	1	0	0	0	1	0	1	1	1
27	Expanding sheet: 0=broad & thickened, 1=reduced	0	1	1	0	1	1	1	1	0	0	1	1	1
28	Leaf broadest: 0=at base, 1=at mid length, 2=at distal end	1	2	1	1	1	0	1	1	1	0	0	0	0

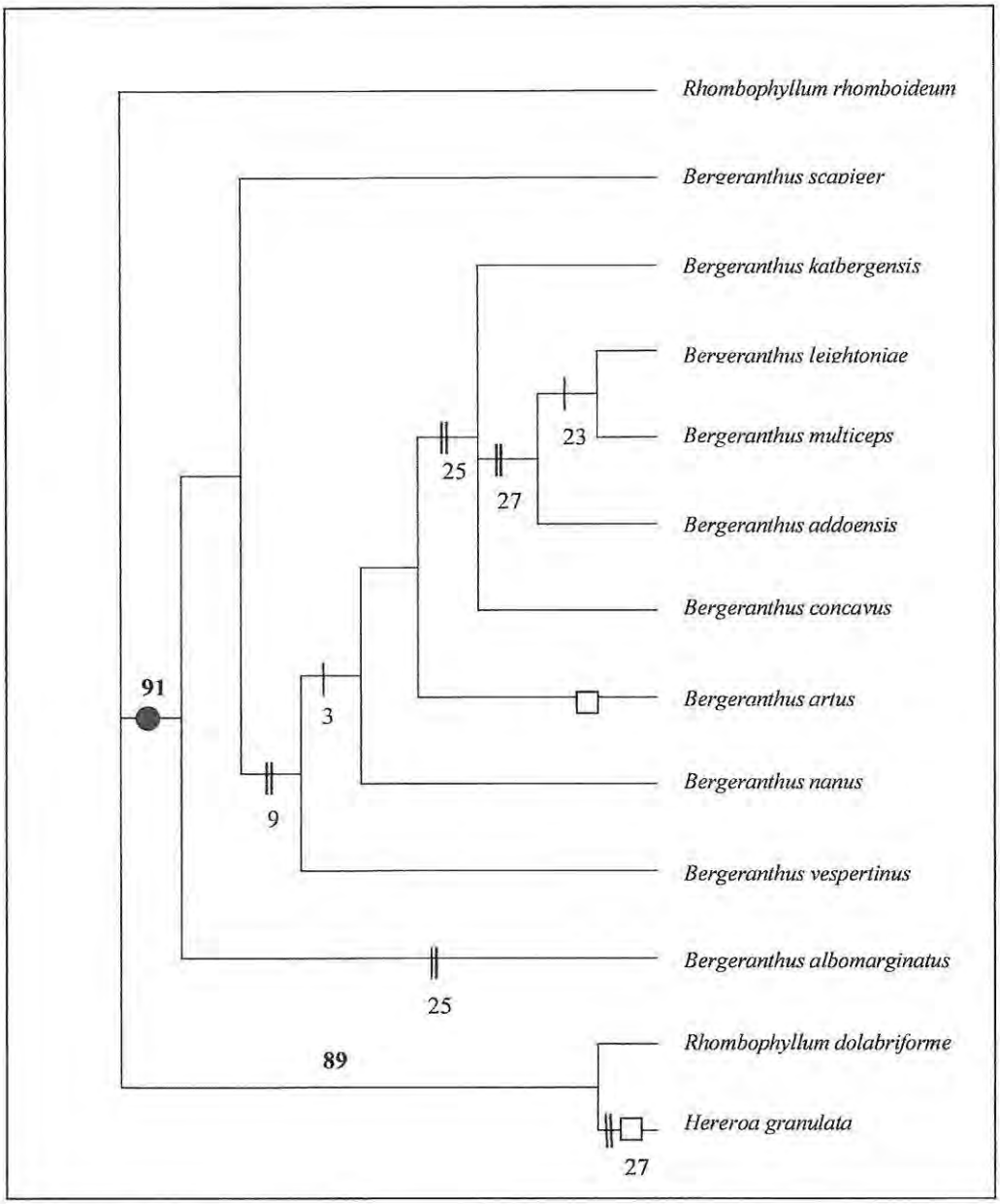

FIGURE 83. —Single most parsimonious tree (Bootstrap support 1000, ci 0.627, ri 0.683) found by heuristic search. Numbers above branches are bootstrap support values; numbers below branches refer to characters (Table 7). Single bars are synapomorphies; double bars are parallel gains; closed circle indicates characters specific to *Bergeranthus* (see text); square indicates characters shared by *Bergeranthus artus* and *Hereroa granulata* (see text).

4. PHYTOGEOGRAPHY REVISITED

When considering phytogeographical groups of *Bergeranthus* (based on edaphic and biotic factors alone) in relation to the results of the phylogenetic analysis (based on 26 morphological and two phenological characters) (Figure 83) it is clear that there is little apparent correlation between phytogeography and phylogeny (Figure 84). This finding however supports the interpretation, discussed in the section on phytogeography, that taxa have evolved independently into narrow micro-habitat requirements termed "skeletal habitats" in this revision.

Bergeranthus species (345 specimens) localities plotted on vegetation, geological, altitude and rainfall maps have revealed important associations and assemblages within the genus. It is however felt that the scale of these maps are too broad to accurately map species associations and that the concept of "skeletal" habitat should be considered as a superseding factor in the distribution of the species (see section on Phytogeography for details).

It is suggested that these neo-endemic taxa may have evolved multiple times and independently from a common ancestor in an isolated discontinuous micro-habitat in response to fragmentation of taxa along the borders between climatic zones and phytochoria. The lack of a long-range dispersal mechanism in the genus contributes to maintaining a localised distribution.

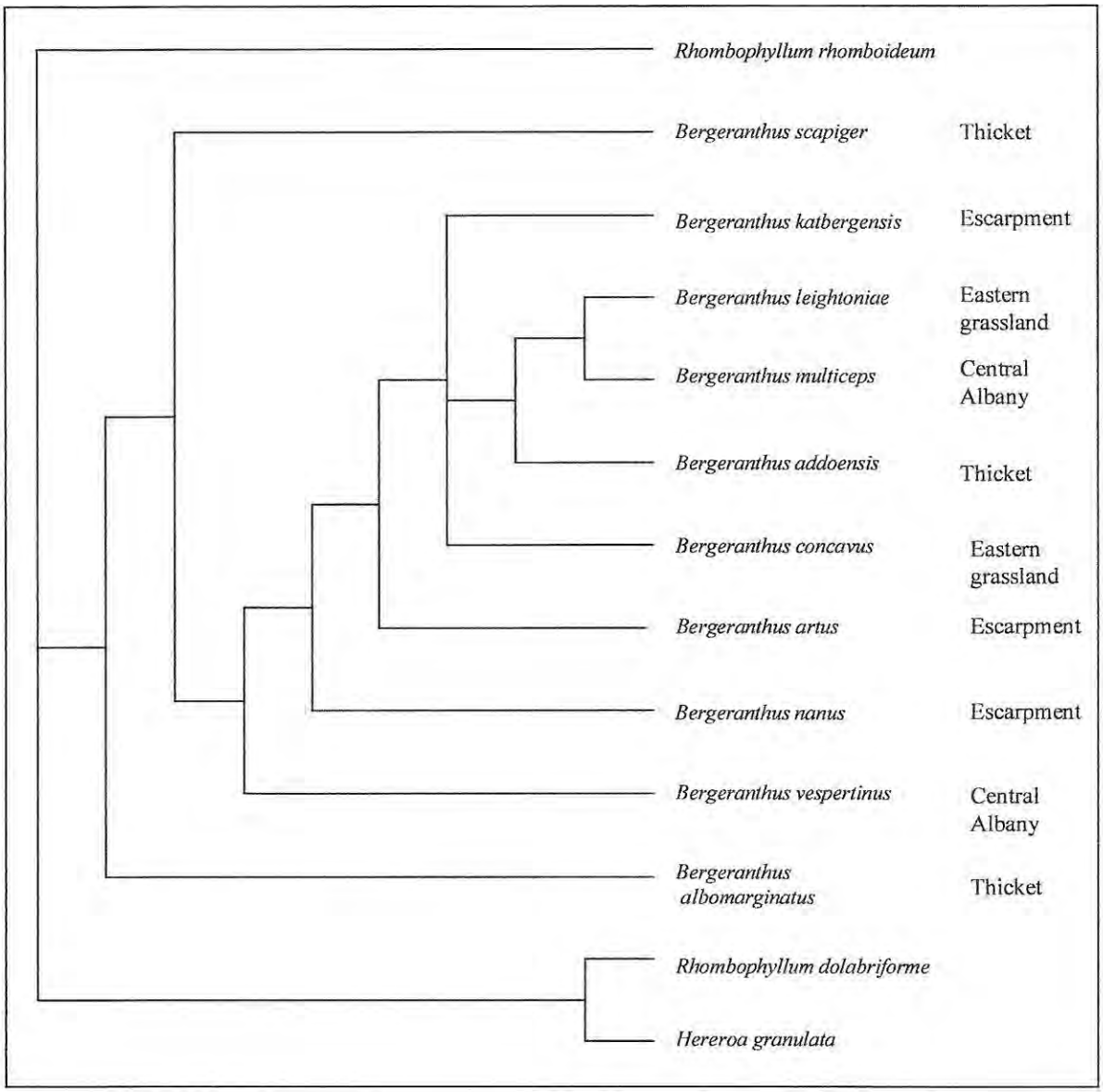

FIGURE 84. —Phylogenetic analysis correlated to phytogeographical groups.

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APPENDIX 1. Herbarium specimens examined with locality data, listed alphabetically for each species:

(Collector, collection number, herbarium acronym, date, locality, grid reference, altitude (where known).

B. addoensis

Archibald, E.E.A. 3805 (GRA); 8/10/1951; Korhaan Vlakte, Addo National Park; 33°30'30"S 25°45'00"E; 100 m.

Dold, T. 4143 (GRA); 7/2000; Kwa-Nobuhle, Uitenhage, thicket on western outskirts of township; 33°25'00"S 25°45'30"E; 100 m.

Dold, T. 4196 (GRA); 1999; Bridgemead (Parson's Vlei), Port Elizabeth. Open grassy fynbos amongst sandstone rock outcrop; 33°55'40"S 25°25'30"E; 200 m.

Dold, T. 4198 (GRA); 1999; Bridgemead, Port Elizabeth west, localised along rock outcrop in open fynbos; 33°55'40"S 25°25'30"E; 200 m.

Dold, T. 4207 (GRA); 1999; Coega flats, open rocky scrub veld below and south of Coega Kop. Limestone outcrop with *Aloe humilis* and *Rhombophyllum rhomboideum*; 33°45'0"S 25°35'40"E; 50 m.

Dold, T. 4218 (GRA); 1999; Uitenhage, Glen Stuart farm, 4 km north of Uitenhage; 33°40'30"S 25°25'00"E; 500 m.

Dold, T. 4272 (GRA); 1999; Addo National Park, lower Korhaan Vlakte around Caesar's dam on flat bare ground between scrub and scattered bushclumps, densely clump to cushion forming. red Hutton soil; 33°30'30"S 25°45'00"E; 100 m.

Dold, T. 4290 (GRA); 1999; Blaaukrantz farm, 15 km due south of Kirkwood on R75 to Uitenhage on the bank of the Bezuidenhouts river; 33°30'15"S 25°20'30"E; 200 m.

Dold, T. 4311 (GRA); 1999; Sondagsrivierpoort, south of Lake Mentz [Darlington Dam]; 33°15'15"S 25°5'15"E; 250 m.

Dold, T. 4324 (GRA); 2000; Uitenhage municipal tar depot just before Zwartkops River bridge on townside of road to Humansdorp; 33°45'15"S 25°20'00"E; 250 m.

Dold, T. 4325 (GRA); 2000; Arizona farm, roadside, road from Uitenhage to Cockscomb State Forest, due north of Uitenhage, 5 km west of R75 on road to Adolph's Kraal; 33°35'10"S 25°25'0"E; 250 m.

Dold, T. 4355 (GRA); 1999; Motherwell, Uitenhage, Coega junction; 33° 45'S 25° 35'E; 100 m.

Feinauer, G.M. *s.n.* in NBG 829/61 (NBG); 12/1969; Amsterdamhoek, Port Elizabeth; 33°50'30"S 25°40'00"E; 50 m.

James, R. *s.n.* in NBG32080 (BOL); 08/1939; Addo (exact locality unknown); 33°30'30"S 25°45'00"E; ± 200 m.

Liebenberg, L.C.C. 7698 (BOL, PRE); 27/011966; Caesar's Dam, Addo Elephant National Park; 33°30'30"S 25°45'00"E; 100 m.

Long, F.R. *s.n.* in NBG462/33 (BOL); 1937; Addo Bush, Uitenhage (exact locality unknown) ± 200 m

Paterson, F. 458 (BOL, GRA); 10/1911; Redhouse, Port Elizabeth; 33°50'30"S 25°35'00"E; 100 m.

Paterson, T.V. 105 (GRA); 07/1908; Redhouse; 33°50'30"S 25°35'00"E; 100 m.

Urton, N.R. 1105 (PEU); 2/11/1991; Redhouse; 33°50'30"S 25°35'00"E; 100 m.

B. albomarginatus

Dold, T. 3943 (GRA); 09/1999; Seymour, Kat River Dam; 32°30'50"S 26°45'5"E; 800 m.

Dold, T. 4284 (GRA); 1999; 4 km south of Seymour on Fort Beaufort road roadside on smooth flat rock slabs between succulent thicket, uncommon; 32°30'50"S 26°45'5"E; 800 m.

Dold, T. 4285 (GRA); 1999; Entrance to Kat River Dam reserve, south of Seymour on flat rock slabs, common but localized; 32°30'50"S 26°45'5"E; 800 m.

Dold, T. 4287 (GRA); 1999; 4 km south of Seymour on Fort Beaufort road, roadside on smooth flat rock slabs between succulent thicket clumps, uncommon; 32°30'50"S 26°45'5"E; 800 m.

B. artus

Dold, T. 787 (GRA); 1995; Cala Pass; 31°30' 52"S 27° 42' 31"E; 1 300 m.

Dold, T. 4242 (GRA); 1999; 0.5 km north-east of Cala on road to Elliot; 31°30' 52"S 27° 42' 31"E; 1 300 m.

Dold, T. 4245 (GRA); 1999; Bottom of Cala pass on large dolerite sheet outcrops with succulent flora and invasive *Euyrops* sp., uncommon, very localised; 31°30' 52"S 27° 42' 31"E; 1 300 m.

Dold, T. 4288 (GRA); 18/08/1999; Cala pass on large dolerite sheet outcrops; 31°30'52"S 27° 42' 31"E; 1 300 m.

Pillans, N.S. *s.n.* in NBG470/16 (BOL); Cape Province, south eastern region (Locality unknown).

B. concavus

Black, A.J. *s.n.* NBG38856 (BOL); 04/1931; (Locality unknown).

Carter, B. *s.n.* NBG38855 (BOL); 28/12/1930; Shelley Beach, East London; 33° 00'30"S 27° 50'25"E; ± 50 m.

Carter, B. *s.n.* NBG38858 (BOL); 01/1931; Shelly Beach, East London; 33° 00'30"S 27° 50'25"E. <50 m.

Dold, T. 4233 (GRA); 1999; Leach's Bay on southern East London coastline. Rocky outcrop 500 m from the sea in open flat grassland, common but localised, clump forming on edges of flat rocks; 32° 00'30"S 27° 50'25"E; 25 m.

Dold, T. 4234 (GRA); 1999; Potters Pass, West Bank, East London. Uncommon on rocky outcrop, clump forming on edges of flat rocks; 32° 00'50"S 27° 50'35"E; 25 m.

Dold, T. 4237 (GRA); 1999; Kwelera river slopes near the bridge on N2, gentle slopes with large flat rock outcrops, restricted to edges of the flat rock patches, very localised; 32° 45'00"S 28° 00'30"E; 150 m.

Dold, T. 4251 (GRA); 1999; East London, 40 km south west of E.L. on E.L.- Port Alfred coastal road, 5 km south of Kaysers beach turn-off; localised clumps in poor sandy soil; 33° 10'30'00"S 27° 35'00"E; 50 m.

Dold, T. 4298 (GRA); 1999; East London, Cintsa East Coast Resort, flat, bare sandstone outcrop on grassy hillside; 32° 45'00"S 28° 00'30"E; 60 m.

Dold, T. 4299 (GRA); 1999; Kiwane Resort, Tyolomnqa [Chalumna], flat bare sandstone outcrop on grassy hillside; 33° 15'00"S 27° 30'30"E; <50 m.

Dold, T. 4305 (GRA); 1999; Dyam Dyam village, Kiwane, north of Hamburg on exposed sandstone sheet, 3 km from shoreline; 33° 15'00"S 27° 30'30"E; <50 m.

Dold 4352 (GRA); 2000; Chalumna Police station, rocks above bridge; 33° 05'30"S 27° 30'05"E; 100 m.

Kluth, A.P.F. *s.n.* in NBG11048 (BOL); 1937; East London (exact locality unknown).

Kluth, A.P.F. *s.n.* in SUG10670 (BOL); no date; East London (exact locality unknown).

B. katbergensis

Bayliss, R.D. 2684 (NBG); 12/1969; Table Mountain, Clarke's Siding, Dordrecht; 31°15'10"S 27°5'30"E; 1 700 m.

Dold, T. 4142 (GRA); 07/2000; De Beers pas, Tarkastad; 32°15'50"S 26°10'5"E; 1 600 m.

Dold, T. 4236 (GRA); 1999; Cathcart, 1 km south of town on Stutterheim road on grassy sandy rock outcrop; 32°15'30"S 27°10'00"E; 1 200 m.

Dold, T. 4239 (GRA); 1999; 5 km south-west of Cathcart on road to Fort Beaufort; 32°15'30"S 27°5'00"E; 1 200 m.

Dold, T. 4240 (GRA); 1999; Chilton farm, 500 m from turnoff to Cathcart off Fort Beaufort-Seymour road, on east side of road on northern bank of Klipplaatrivier; 32°15'50"S 26°55'00"E; 1 400 m.

Dold, T. 4241 (GRA); 1999; Three Crowns farm on McKay's Neck, 30 km north east of Queenstown; 32°45'00"S 27°5'10"E; 1 500 m.

Dold, T. 4244 (GRA); 1999; Tina Falls village, near Shawbury, Qumbu district. Small population on overgrazed isolated peak, exposed sheet rock outcrop, uncommon, localised. No other plants found in the adjacent peaks and mountains; 31°10'30"S 28°55'40"; 1 200 m.

Dold, T. 4246 (GRA); 1999; Dordrecht, Clarks Siding, Table hill, common in grassland along rock outcrops and ridges; 31°15'10"S 27°5'30"E; 1 700 m.

Dold, T. 4247 (GRA); 1999; Indwe, 10 km west of Indwe on Dordrecht road. Fairly common in scattered clumps or singly in open dry grassland; 31°25'45"S 27°15'40"E; 1 500 m.

Dold, T. 4248 (GRA); 1999; Ida, 5 km east of Ida on Indwe – Elliot road, near Tsomo river bridge; Occasional small clumps or singly in grassland; 21°25'00"S 27°30'30"E; 1 400 m.

Dold, T. 4254 (GRA); 1999; Fort Beaufort, summit of Katberg pass, localised on grassy crest of east facing cliffs; 32°25'00"S 26°35'50"E; 1 600 m.

Dold, T. 4255 (GRA); 29/05/1999; Cathcart, Old Thomas River siding, north-east facing slope, 20 m from River bank in 1 m vertical rock face; 32°27'47"S 27°17'40"E; 1 200 m.

Dold, T. 4264 (GRA); 1999; Queenstown, south-facing lower slopes of Longhill above Toptown suburb. Open rocky grassland, growing tightly between exposed flat rock strata, uncommon; 31°55'00"S 26°50'35"E; 1 200 m.

Dold, T. 4267 (GRA); 1999; Tsomo, 2 km west of town at Tsomo mission, steep, rocky, east facing slope with *Euphorbia clavaroides* & *Haworthia cooperi*. Common but localized between exposed rock strata and at summit on flat rocks; 32°00'30"S 27°50'00"E; 1 100 m.

Dold, T. 4268 (GRA); 1999; Sterkstroom, 15 km east of town at Penhoek siding, south facing rocky scree slope, common, growing between densely populated *Hereoa granulata* and *Lachenalia karooica* at margin of grassland and exposed rock sheets; 31°30'5"S 26°30'40"E; 1 500 m.

Dold, T. 4275 (GRA); 1999; Bergfontein farm, 20 km north of Tarkastad on Sterkstroom road, common on steep east facing grassy slope; 31°45'50"S 26°15'5"E; 1 500 m.

Dold, T. 4277 (GRA); 1999; Buffelskloof farm, Doornkloof district, 45 km north of Adelaide in the Baviaansrivierberge. Occasional, localized on steep rocky north-west facing slope in rock strata outcrop; 32°30'00"S 26°05'30"E; 1 400 m.

Dold, T. 4279 (GRA); 1999; 20 km north-east of Queenstown on Dordrecht road, south-east facing rocky slope of Bonkolo Nek. Flat red rock boulders with dense *Aloe ferox*; 31°45'00"S 26°55'15"E; 1 250 m.

Dold, T. 4280 (GRA); 1999; Emnxe, 30 km south west of Cala on Indwe road, north-east facing slope on dry sandstone outcrop; 31°30'20"S 27°35'00"E; 1 500 m.

Dold, T. 4281 (GRA); 1999; Summit of Nico Malan Pass on Seymour-Queenstown road. Sandstone outcrop in open grassland; 32°25'15"S 26°40'00"E; 1 500 m.

Dold, T. 4282 (GRA); 1999; Three Crowns farm on McKay's Neck, 30 km north-east of Queenstown. Sandstone escarpment; 32°45'00"S 27°5'10"E; 1 500 m.

Dold, T. 4283 (GRA); 1999; Stokwe's basin, between Cala and Lady Frere. Open grassland on sandstone flats; 31°35'10"S 27°30'00"E; 1 260 m.

Dold, T. 4286 (GRA); 1999; Welgeluk farm, 20 km south of Indwe on Lady Frere road, low sandstone outcrop in open grassy flat plain; 31°30'00"S 27°20'20"E; 1 500 m.

Dold, T. 4308 (GRA); 1999; St Albans Mission, Egossa, 20 km south of Engcobo. Very localized but common on sandstone outcrop on east facing slope about halfway to the summit; 31°50'00"S 28°0'30"E; 1 200 m.

Dold, T. 4309 (GRA); 1999; Cloverdale farm, between Hogsback and Cathcart just after turn-off to Fort Beaufort. Localised and uncommon on sandstone outcrop; 32°20'20"S 27°00'45"E; 1 300 m.

Dold, T. 4329 (GRA); 2000; Chilton farm, junction at turn-off from Seymour-Queenstown road to Cathcart. Sandstone outcrop on roadside, open grassland. Occasional; 32°15'50"S 26°55'00"E; 1 400 m.

Dold, T. 4330 (GRA); 2000; Surbiton Station, 12 km south of Cathcart on flat sandstone sheet in open grassland. Occasional; 32°20'40"S 27°15'00"E; 1200 m.

Dold, T. 4331 (GRA); 2000; Ellington farm, dolerite domes on roadside 10 km south of Cathcart on road to Stutterheim. Succulent-rich grassy hillside. Uncommon. *Hereroa granulata* also present; 32°20'30"S 27°10'40"E; 1200 m.

Dold, T. 4332 (GRA); 2000; Elima-Soga, between Lubisi dam and Lady Frere. Uncommon on sandstone ridge overlooking Zingqwene settlement; 31°40'00"S 27°25'00"E; 1 500 m.

Dold, T. 4335 (GRA); 2000; Mount Shepstone, summit, 28 km north west of Queenstown; 31°40'40"S 26°45'05"E; 1 997 m.

Dold, T. 4337 (GRA); 2000; Thomas River siding, Cathcart; 32°20'30"S 27°15'20"E; 1 200 m.

Dold, T. 4341 (GRA); 2000; 10 km south-east of Tarkastad, Stanford Park farm, roadside at junction to Haslop Hills, flat exposed sandstone plate; 32°05'00"S 26°20'00"E; 1 350 m.

Dold, T. 4342 (GRA); 2000; Volstruisnek, Wheatlands farm, 22 km south east of Tarkastad. roadside on steep sandstone hill; 32°10'20"S 26°15'30"E; 1 500 m.

Dold, T. 4343 (GRA); 2000; Swallowkrantz farm, 40 km south-east of Tarkastad, flat sandstone domes; 32°15'30"S 26°15'50"E; 1 500 m.

Dold, T. 4346 (GRA); 1999; Spring Valley farm, 30 km south-east of Tarkastad, steep sandstone slopes; 32°15'10"S 26°15'30"E; 1 600 m.

Dold, T. 4358 (GRA); 10/11/2000; Cathcart, Sam Meyer Dam; 32°15'30"S 27°10'00"E; 1 200 m.

Dold, T. 4359 (GRA); 10/11/2000; Cathcart – Sam Meyer Dam; 32°15'30"S 27°10'00"E; 1 200 m.

Dold, T. 4362 (GRA); 25/11/2000; Andriesberg Mountain, north of Queenstown, open rocky grassland; 31°40'00"S 26°45'00"E; 830 m.

Dold, T. 4370 (GRA); 30/12/2000; Lana farm, south-east of Burgersdorp. Flat exposed sandstone rock sheets; 26°40' 00"S 31°10' 00"E; 1 750 m.

Dold, T. 4371 (GRA); 25/12/2000; Bankies, south of Dordrecht; 26°55'30"S 31°30'00"E; 1 600 m.

Dold, T. 4392 (GRA); 02/2001; Goedehoop farm, south of Molteno; 31°34'00"S 26°11'00"E; 1 730 m.

Esterhuysen, E. 13229 (BOL); 10/1946; Top of Katberg Pass, Stockenstroom District; 32°25'00"S 26°35'50"E; 1 600 m.

Galpin, E.E. 2150 (BOL); 01/1914; Lower slopes of Longhill, Queenstown; 31°55'00"S 26°50'35"E; 1 200 m.

Johnson, S.M. 1213 (GRA); 14/4/1955; Rockford Bridge, Cathcart; 32°15'00"S 27°10'00"E; 1 200 m.

Leighton, F.M. *s.n.* in NBG341/33 (BOL); Elliot; 31°20'00"S 27°50'20"E; 1 500 m.

Reynolds *s.n.* in NBG102/34 (BOL); 1955; Tsomo, Transkei. 32°00'30"S 27°50'00"E; 1 100 m.

Sim, T.R. 19522 (PRE); 1899; Thomas River, Cathcart; 32°20'30"S 27°15'20"E; 1 200 m.
Wisura, W. 2703 (NBG); 06/1973; Katbergpass, Fort Beaufort; 32°25'00"S 26°35'50"E; 1 600 m.

B. leightoniae

Carter, B. O. *s.n.* in BOL63669 (BOL); 1940; Between King William's Town and East London; 3327CD/327BB (exact locality unknown).

Dold, T. 4192 (GRA); 1999; University of Transkei campus, west side of Umtata, localised, densely clump/mound forming in disturbed grassland; 31°35'5"S 28°45'30"E; 800 m.

Dold, T. 4232 (GRA); 1999; Stutterheim, 4 km out of town on N6 to East London, turn-off to Frankfort then 2 km on gravel road to Gasela village. Clump forming on edges of flat rock outcrops, common but very localised; 32°35'40"S 27°30'30"E; 800 m.

Dold, T. 4235 (GRA); 1999; Komgha, Moordenaars Kop farm on upper Kei River, densely clump forming on edges of flat rocks but very localised; 32°30'50"S 27°50'50"E; 600 m.

Dold, T. 4238 (GRA); 1999; Thamara, King William's Town, rocky outcrop in open grassland, plants single or in small groups but not clump forming, size variable with degree of shade from grass clumps; 33° 00'00"S 27°15'00"E; 550 m.

Dold, T. 4243 (GRA); 1999; University of Transkei campus, Umtata. Disturbed grassland on slight rocky outcrop, clump forming small clusters, uncommon and extremely localised; 31°35'5"S 28°45'30"E; 800 m.

Dold, T. 4258 (GRA); 1999; Mgqakwebe, type locality for *B. leightoniae*, just out of King William's Town on road to Dimbaza, flat open rocky grassland, large population on fringes of flat dolerite plate, plentiful singly or in small clumps; 32°50'45'00"S 27°20'15"E; 450 m.

Dold, T. 4265 (GRA); 1999; Acton Caba, crossing over Kei river between Tsomo and Bolo, rocky loose gravel in dry scrub, flat, level ground; 32°15'15"S 27°40'00"E; 650 m.

Dold, T. 4269 (GRA); 1999; Stutterheim, turnoff from Kei Road road to Frankfort at Indakana railway crossing. Exposed flat dolerite sheet rock, common but localised on rock sheets; 32°35'05"S 27°25'40"E; 800 m.

Dold, T. 4300 (GRA); 1999; Campagna experimental farm, Dohne Research Station, Stutterheim, Dohne sourveld; 32°30'00"S 27°25'40"E; 900 m.

Dold, T. 4301 (GRA); 1999; 10 km south of Stutterheim on road to King William's Town at junction to Amabele, Happy Vale farm. Dohne sourveld; 32°40'00"S 27°20'40"E; 800 m.

Dold, T 4302 (GRA); 1999; Wriggleswade Dam, Wauldby farm, between Stutterheim & Komgha. Flat exposed dolerite rock outcrop in Dohne sourveld; 32°35'10"S 27°35'00"E; 800 m.

Dold, T. 4304 (GRA); 1999; Toleni Head, roadside ± 5 km north of Ndbakazi on Nqamakwe road. Flat dolerite sill in shallow soil, localized, uncommon; 32°20'00"S 28°00'00"E; 900 m.

Dold, T. 4336 (GRA); 2000; 9 km from Komgha road at Kubusie Drift near Police Station on banks of Kubusie river; 32°35'05"S 27°40'20"E; 700 m.

Dold, T. 4338 (GRA); 2000; King William's Town, south end of golf course below and south of reservoir; 32°55'10'S 27°20'45"E; 450 m.

Dold, T. 4375 (GRA); 2000; King William's Town golf course. Hill above and eastwards of course. Open patches between scattered bushclumps on exposed rock slabs; 32°55'00"S 27°25'30"E; 450 m.

Flanagan, H.G. 2230 (BOL, GRA); 11/1893. Grassy Valleys near Komgha; 32°35'00"S 27°50'45"E; 600 m.

Flanagan, H.G. 2591 (BOL); 03/1898; Mordenaar's Kop, Komgha; 32°30'50"S 27°50'50"E; 600 m.

Leighton, F.M. *s.n.* in NBG1557/34 (BOL); 06/1934; Near King William's Town; 32°50'30"S 27°20'30"E; 450 m.

Sim, T.R. 19507 (PRE); 1895; Dohne, Stutterheim; 32°30'15"S 27°25'30"E; 900 m.

Sim, T.R. 19511 (PRE); 1895; Dohne, Stutterheim; 32°30'15"S 27°25'30"E; 900 m.

Sim, T.R. 19525 (PRE); 1888; Perie [Pirie], King William's Town; 32°40'30"S 27°15'10"E; 500 m.

Sim, T.R. 19530 (PRE); 1888; King William's Town (exact locality unknown).

Van Ryneveld *s.n.* in NBG1704/34 (BOL); no date; King William's Town; 32°50'30"S 27°20'30"E; 450 m.

Welsh, Miss. 22 (GRA); 10/1926; King William's Town; 32°50'30"S 27°20'30"E; 450 m.

B. multiceps

Acocks, J.P.H. 11880 (PRE); 10/1945; Keiskamma river valley, Line Drift; 33°5'00"S 27°10'5"E; 250 m.

Dold, T. 4186 (GRA); 1999; Grahamstown commonage north, Mayfield farm. Single scattered plants in hard baked soil, open grassveld; 33°15'5"S 26°30'10"E; 600 m.

Dold, T. 4187 (GRA); 1999; Table farm, Cradock road, 15 km west of Grahamstown. Dry karroid veld, uncommon in scattered clumps; 33°15'00"S 26°25'00"E; 600 m.

Dold, T. 4188 (GRA); 1999; Grahamstown commonage, north, Mayfield farm. Single scattered plants in hard baked soil, open grassveld; 33°15'5"S 26°30'10"E; 600 m.

Dold, T. 4189 (GRA); 1999; Grahamstown commonage north, Mayfield farm. Single scattered plants in hard baked soil, open grassveld; 33°15'5"S 26°30'10"E; 600 m.

Dold, T. 4194 (GRA); 1999; Redhouse, occasional, localised in dense bush clumps along Swartkops River bank; 33°50'10"S 25°35'00"E; 75 m.

Dold, T. 4195 (GRA); 1999; Riebeeck East, Palmietfontein farm – growing between *Faucaria gratiae* on quartz rock outcrop; Occasional, singly or small looses clumps; 33°10'15"S 26°15'5"E; 710 m.

Dold, T. 4197 (GRA); 1999; Rabbit's Bush, open rocky ridge at escarpment overlooking Blaaukrantz river valley, top of Rabbit's bush. Occasional in cracks and fissures in sandstone rock outcrop; 33°20'40"S 26° 40'30"E; 840 m.

Dold, T. 4205 (GRA); 1999; Roundhill, Oribi Reserve, Bathurst, north boundary in open grassveld near dam. Occasional, single, not forming clumps; 33°25'30"S 26°55'00"E; 370 m.

Dold, T. 4206 (GRA); 1999; Grahamstown commonage–north. Single scattered plants in hard baked soil, open grassveld; 33°15'5"S 26°30'10"E; 650 m.

Dold, T. 4211 (GRA); 1999; Belmont Valley turn-off from Grahamstown–Port Alfred road. Disturbed grassy, rocky patch on roadside next to farm school. Uncommon, plants singly in a small population; 33°15'15"S 26°35'50"E; 565 m.

Dold, T. 4215 (GRA); 1999; Nutwood farm, on roadside of N2 towards Peddie, just before Collingham towers. Open stony grassveld. Uncommon single plants; 33°15'15"S 26°35'50"E; 840 m.

Dold, T. 4216 (GRA); 1999; Table farm, Cradock road, about 12 km west of Grahamstown in open karroid veld, uncommon single scattered plants; 33°10'50"S 26°25'15"E; 640 m.

Dold, T. 4217 (GRA); 1999; Helspoort, dry *Chrysocoma/Felicia* veld, localised, solitary or small, clump forming; 33°10'10"S 26°20'10"E; 670 m.

Dold, T. 4219 (GRA); 1999; Gwabeni Village, Breakfast Vlei, Peddie District (previously called Springvale farm). Open grassveld with scattered bushclumps; 33°5'00"S 26°55'30"E; 530 m.

Dold, T. 4221 (GRA); 1999; Pony club, north-west Grahamstown, between Municipal dumps and pony club in rocky *Pteronia/Relhania/Chrysocoma* dominated veld. Occasional, scattered, solitary or loosely clumped; 33°15'20"S 26°30'00"E, 630 m.

Dold, T. 4222 (GRA); 1999; Tharfield farm, Port Alfred, uncommon and localised along rock outcrop in open rangeland, growing tightly between rock cracks; 33°30'30"S 27°00'30"E; 170m.

Dold, T. 4223 (GRA); 1999; Grahamstown commonage north, Mayfield farm, open grassland. Occasional scattered plants; 33°15'5"S 26°30'10"E; 640 m.

Dold, T. 4224 (GRA); 1999; Grahamstown Commonage, open grassveld along N2 to Peddie, opposite Wylie's Dairy (Gletwyn farm), Grahamstown east. Scattered, occasional single plants in hard baked soil. Recently burnt; 33°15'15"S 26°35'50"E; 640 m.

Dold, T. 4225 (GRA); 1999; Turn-off main Grahamstown-Port Alfred road to Belmont Valley, just before Manley Flats. Grassy slopes below farm school; 33°15'15"S 26°35'50"E; 570 m.

Dold, T. 4226 (GRA); 1999; Turn-off main Grahamstown-Port Alfred road to Belmont Valley, just before Manley Flats. Grassy slopes below farm school; 33°15'15"S 26°35'50"E; 570 m.

Dold, T. 4227 (GRA); 1999; Southwell. Rock outcrop in open grassland at turnoff to Bathurst. Common between rocks in sandy soil, single plants or in groups but not clump forming; 33°30'00"S 26°40'00"E; 295 m.

Dold, T. 4230 (GRA); 1999; Grahamstown commonage north, open rocky grassland, uncommon; 33°15'5"S 26°30'10"E; 640 m.

Dold, T. 4250 (GRA); 1999; Jeffrey's Bay, rock outcrop near off-ramp from N2 into town, common; 34°00'15"S 24°55'00"E; 95 m.

Dold, T. 4253 (GRA); 1999; Brakfontein farm, 10 km south of Grahamstown on Southwell road, grassveld between dense bushclumps, uncommon, clump forming; 33°20'45"S 26°30'40"E; 300 m.

Dold, T. 4256 (GRA); 1999; Keiskamma River Bridge, Mount Vale, north of Hamburg. Highest point above bridge, rocky grassland. Single scattered plants; 33°10'10"S 27°20'25"E; 200 m.

Dold, T. 4257 (GRA); 1999; Keiskamma River Valley - Line Drift, top of hillside overlooking bridge before descent. Occasional in rocky grassland with scattered bushclumps. Single or loose clumps; 33°5'00"S 27°10'5"E; 250 m.

Dold, T. 4261 (GRA); 1999; Kleinemonde district, Cuylerville Church at junction from Seafield to Trappe's Valley. Open rocky grassland. Unusual in very loose sand, only 2 km from the coast. Not very common and localised around flat dolerite outcrop. Single scattered plants; 33°35'00"S 26°55'00"E; 50 m.

Dold, T. 4273 (GRA); 1999; Olifantshoek pass, summit, north of Paterson on road to Cookhouse, uncommon on east facing grassy slope between rocks. Single scattered plants; 33°15'45"S 25°55'00"E; 650 m.

Dold, T. 4289 (GRA); 1999; Tuku village, 20 km east of Peddie, Hamburg. Open grassland; 33°15'0"S 27°15'20"E; 150 m.

Dold, T. 4293 (GRA); 1999; Melville Park farm, 20 km west of Grahamstown on N2 to Port Elizabeth, open grassland with scattered bushclumps. Single plant found, uncommon; 33°20'15"S 26°20'15"E; 350 m.

Dold, T. 4307 (GRA); 1999; Ecca Wildflower Reserve, uncommon in rocky Dwyka tillite outcrop at lower (north) end of reserve along old Queen's road, very near to *B. scapiger* populations; 33'10'50"S 29°35'15"E; 528 m.

Dold, T. 4310 (GRA); 1999; Michell's Pass, between Hogsabck and Seymour. Glenholm farm, 12 km west of Hogsback on road to Seymour. Uncommon on edge of sandstone cliffs, south facing; 32°30'45"S 26°50'30"S; 850 m.

Dold, T. 4312 (GRA); 2000; Uitvlught farm on the road to Groothoek, north of Humansdorp. Stony ground in dense grassy fynbos, about 0.5 m high, on gentle north facing slope on the south bank of the Hol river. Uncommon, localised; 33°55'00"S 24°35'20"E; 400 m.

Dold, T. 4314 (GRA); 2000; Jameson Dam, Cold Springs, west of Grahamstown, rare in rocky grassland on quartz ridge top with scattered bushclumps; 33°15'45"S 26°25'30"E; 700 m.

Dold, T. 4315 (GRA); 2000; Fir Glen farm, below microwave tower on Highlands road, 4 km east of Atherstone station. Sandstone/quartz outcrop on flat, open ground. Single plant, uncommon; 33°15'50"S 26°20'40"E; 700 m.

Dold, T. 4319. (GRA); 2000; Harvestvale farm, between Bushman's River Mouth and Alexandria. Common in fairly dense thicket on red clay soils, scattered single plants, with *Ceropegia bowkeri*; 33°35'20"S 26°30'00"E; 150 m.

Dold, T. 4323 (GRA); 2000; Mount Pleasant farm, south of Stoneshill on hillside just west and above main road. 10 m from Trig Beacon; 33°15'40"S 26°30'30"E; 316 m.

Dold, T. 4333 (GRA); 2000; Coombsvale farm, at Coombs turnoff from Grahamstown road to Peddie. Open grassland on flat rocks. 100 m from *B. scapiger*; 33°15'15"S 26°45'15"E; 550 m.

Dold, T. 4339 (GRA); 2000; Tweni Village (Klipfontein farm), Masakhane, 15 km south of Alice. Rare; 32°55'15"S 26°50'00"E; 500 m.

Dold 4360 (GRA); 2000; St Francis Bay, Osbos farm, between St Francis Bay & Humansdorp. Open grassland, locally common; 34°10'00"S 24°45'40"E; 50 m.

Dold 4390 (GRA); 2000; Table Hill farm west of Grahamstown on Cradock road – rare, dwarfed plants in karroid scrub; 33°15'00"S 26°25'10"E; 600 m.

Dold 4393 (GRA); 01/2001; Barville Park, Southwell. Open grassland along quartz rock outcrop – with *Brachystelma schizoglossoides*; 33°35'15"S 26°35'40"E; 100 m.

Dyer, R.A. 821 (GRA); 1926; Eight miles along Cradock road, Grahamstown; 33°15'00"S 26°25'10"E; 600 m.

Dyer, R.A. 1529 (PRE); 05/1928; Albany, "*Selago* experimental plot", Mr Jolly's farm (Locality - Jolly's farm - not known).

Ecklon & Zeyher 1980 (B, G, MO); no date; *Cap de Bonne Espérance* (exact locality not known).

Fourcade, H.G. 3512. Uitvlught, on road from Humansdorp to Groothoek. 12/1927. K & (BOL); 33°55'00"S 24°35'20"E. 400 m.

Gibbs Russell, G.E. 3092 (UFH); 18/11/1976; Fort Hare University farm, Fort Beaufort; 33°45'45"S 26°50'00"E; 800 m.

Giffen, M.H. 355 (UFH); 17/02/1935; Tyumie River, Fort Hare, Alice; 33°45'45"S 26°50'00"E; 600 m.

Giffen, M.H. *s.n.* in BOL63670 (UFH); no date; Sandile's Kop, between Alice and Fort Hare; 33°45'45"S 26°50'00"E; 600 m.

Hall, H. 225 (NBG); 11/1950; North of Grahamstown (exact locality not known).

Luckhoff, C. *s.n.* in NBG32078 (BOL); 09/1930; Fort Armstrong, near Fort Beaufort; 32°35'00"S 26°40'30"E; 550 m.

Marloth, R. 10874 (PRE); 11/192; Grahamstown, Koonap Hotel; 33°00'00"S 26°40'00"E; 750m.

Potts, G. 1754 (BLFU); 12/1914; Alice; 33°45'45"S 26°50'00"E; 600 m.

Sim, T.R. 19539 (PRE); 1895; Peddie; 33°10'30"S 27°5'15"E; 300 m.

Smythe, L. *s.n.* in RUH3915 (BOL); 08/1946; Between Bathurst and Manley Flats; 33°25'00"S 26°40'30"E; 250 m.

Urton, N.R. 938 (PEU); 5/10/1987; Bluewater Bay, Port Elizabeth; 33°50'30"S 25°40'00"E; 50 m.

Van Jaarsveld, E.J. 7918 (NBG); 1986; Jeffreys Bay; 34°00'30"S 24°55'30"E; Altitude not known.

Zeyher, C. 1089 (TCD); Date not known; Between Zwartkops & Zondagsrivier, Uitenhage; 33°45'00"S 25°45'00"E; Altitude not known.

Zeyher C.L. 2577 (B, G); 1847; *P.B. Spei*; (exact locality unknown).

B. nanus

Dold, T. 4271 (GRA); 1999; Graaff Reinet. Valley of Desolation, upper viewpoint, flat rocky grassland, uncommon on exposed rock outcrop between rocks; 32°15'25"S 24°25'50"E; 1 390 m.

Dold, T. 4317 (GRA); 2000; Grootvlei farm, road between Somerset East and Cradock over Swaershoek mountains, ± 30 km from Cradock. Uncommon on sandstone step, low grassy slope overlooking Klein Vis Rivier. Loose, well drained sandy soil; 32°15'00"S 25°30'30"E; 1 250 m.

Dold, T. 4388 (GRA); 2000; Grootvlei farm, road between Somerset East and Cradock over Swaershoek mountains, ± 30 km from Cradock. Uncommon on sandstone step, low grassy slope overlooking Klein Vis Rivier. Loose, well drained sandy soil; 32°15'00"S 25°30'30"E; 1 250 m.

Hammer, S. 1150 *ex hort.*, no specimen preserved; Valley of Desolation, Graaff Reinet. Point above valley of Desolation in crevices of shale rubble; 32°15'25"S 24°25'50"E; 1 390 m.

Vlok, J. 2708 *ex hort.*, no specimen preserved; Valley of Desolation, Graaff Reinet.. 32°15'25"S 24°25'50"E; 1 390 m.

B. scapiger

Archibald, E.E.A. 4296 (GRA); 02/04/1952; Zoetvlei farm, north of Sandflats [Paterson]; 33°25'00"S 26°00'00"E; 300 m.

Archibald, E.E.A. 5744 (GRA); 4/10/1955; Bushman's River Poort [Alexandria], top of hills, Witteberg quartzite; 33°30'30"S 26°20'30"E; 300 m.

Blenkiron, M.E & Grant, A. *s.n.* in NBG2266/26 (BOL); 1933; Sandile's Kop, Grahamstown. [exact locality unknown, possibly an error for Makana's kop?].

Britten, L. 5120 (GRA); 09/10/1924; Grahamstown, common on rock ledges; 33°25'35"S 26°30'30"E; 600 m.

Britten, L.L. 5120 (BOL); 1933; Grahamstown; 33°25'35"S 26°30'30"E; 600 m.

Chan, J. 85 (GRA); 31/03/1992; Grahamstown, Ecca Reserve, Valley Bushveld; 33°13'40"S 26°38'5"E; 520 m.

Cloete, E. 2496 (GRA); 12/2/1994; Kap River Reserve, Port Alfred; 33°30'00"S 27°00'30"E; 130 m.

Cummings, E. & Weldrick, S. 4 (GRA); 20/07/1990; Monument Hill, Grahamstown; 33°25'35"S 26°30'30"E; 600 m.

Daly & Cherry 997 (B, GRA); 08/1908; Hill at back of Botanic Gardens, Grahamstown 33°25'35"S 26°30'30"E; 600 m.

Daly, M.F. & Sole, M.I. 208 (GRA); 06/1902; Near Grahamstown; 33°25'35"S 26°30'30"E; 600 m.

Dold, T. 1999; 57 (GRA); 03/03/1992; Somerset Heights, Grahamstown; 33°25'35"S 26°30'30"E; 600 m.

Dold, T. 4191 (GRA); 1999; Kaffirdrift, Lower Fish River, open grassland, somewhat clump forming, occasional; 33°20'00"S 27°00'00"E; 280 m.

Dold, T. 4193 (GRA); 1999; Willowfontein farm, (Mr Pohl) on road from Riebeeck East to Carlisle Bridge on steep north facing rocky slope in dense thicket, clump forming, somewhat spreading. Common but localised; 33°05'50"S 26°10'00"E; 850 m.

Dold, T. 4202 (GRA); 1999; Gowie's Kloof, Grahamstown north, common, clump forming in thick thorn-scrub; 33°15'30"S 26°30'15"E; 650 m.

Dold, T. 4204 (GRA); 1999; Lowestof farm, Double Drift Reserve on Fish River. Uncommon in dry baked soil, in 0.5 m high karroid scrub; 33°5'00"S 26°45'15"E; 450 m.

Dold, T. 4208 (GRA); 1999; Riebeeck East, hill above town, common, clump forming, in *Euphorbia polygona* scrub and *Passerina* slopes; 33°10'20"S 26°5'50"E; 700 m.

Dold, T. 4209 (GRA); 1999; Ecca Wildflower Reserve. Karroid veld at south end of reserve near Bain's plinth; 33°10'50"S 26°35'15"E; 528 m.

Dold, T. 4210 (GRA); 1999; Signal Kop farm, Riebeeck East, open heavily grazed rangeland, occasional scattered plants; 33°5'15"26°10'5"E; 482 m.

Dold, T. 4213 (GRA); 1999; Top of Pluto's Vale, open grassveld, clump forming, occasional; 33°10'40"S 26°40'00"E; 340 m.

Dold, T. 4214 (GRA); 1999; Bushman's River Poort, roadside on Salem side before descent. Low grassy scrub; 33°30'20"S 26°20'30"E; 250 m.

Dold, T. 4231 (GRA); 1999; Lower Caxton farm, 2 km from Coombs turn-off on Kaffirdrift road on steep forested slope just above the Kap river bridge; 33°20'00"S 26°27'00"E; 260 m.

Dold, T. 4252 (GRA); 1999; Rietrivier farm, 5 km east of Annsvilla, Zuurberg, rocky open grassland on top of ridge; 33°15'15"S 25°50'00"E; 600 m.

Dold, T. 4259 (GRA); 1999; Bushmans River Poort, Alexandria, top of poort on northern side at highest point on roadside, rocky outcrop with fynbos elements, together with *Corpuscularia* sp., quartzitic sandy soil. Clump forming; 33°30'20"S 26°20'30"E; 250 m.

Dold, T. 4262 (GRA); 1999; Bloukrans pass, steep east facing slope. Small clearing in otherwise dense succulent thicket, rocky, sandy soil. Occasional but localised. Clump forming; 33°20'15"S 26°40'30"E; 300 m.

Dold, T. 4263 (GRA); 1999; Zoetvlei farm, 4 km north of Paterson on R32. Quartzite outcrop on west and east side of road. Common, localized in sandy soil between rocks, loosely clump forming; 33°25'00"S 26°00'00"E; 444 m.

Dold, T. 4276 (GRA); 1999; Drivers Bush (East), 30 km east of Grahamstown on N2, roadside between flat quartz outcrops. Uncommon, single plants scattered in almost pure quartzitic sand. Found with *Corpuscularia* sp.; 33°15'15"S 26°45'30"E; 550 m.

Dold, T. 4292 (GRA); 1999; Turn-off N2 to Hope Fountain, 30 km west of Grahamstown. Common on east facing slope between quartz boulders, grassland with succulents, scattered bushclumps; 33°25'20"S 26°15'00"E; 450 m.

Dold, T. 4295 (GRA); 1999; Thornkloof farm, 20 km west of Grahamstown on road to Riebeeck east. Large population between and underneath woody shrubs, localised; 33°15'5"S 26°15'45"E; 550 m.

Dold, T. 4296 (GRA); 1999; Quetu, west bank of Kap River, north facing slopes, clump forming; 33°30'15"S 27°0'40"E; 50 m.

Dold, T. 4297 (GRA); 1999; Lower Edendale farm, south of Fort Beaufort. Rocky east-facing slope, loosely clump forming, uncommon; 32° 55' 00"S 26° 40'00"E; 600 m.

Dold, T. 4313 (GRA); 2000; Woodbury farm, on N2 near the Bushman's River bridge, quartz outcrop/ridge. Very uncommon, probably grazed by sheep; 33°30'5"S 26°5'35"E; 250 m.

Dold, T. 4316 (GRA); 2000; Highlands station opposite farm church/railway bridge. Sandstone/quartz outcrop on west facing dry slope with *Euphorbia polygona*. Uncommon; 33°20'00"S 26°15'20"E; 600 m.

Dold, T. 4320 (GRA); 2000; Coega Kop summit, with *Orthopterum coegana*; 33°45'15"S 25°35'15"E; 145 m.

Dold, T. 4321 (GRA); 2000; Drivers Bush; 33°15'15"S 26°45'30"E 550 m.

Dold, T. 4328 (GRA); 2000; Fort Brown, Munster farm, between Fort Brown and Committees Drift, rocky open patch in valley bush, localized (just north of Glen Melville dam.); 33°10'0"S 26°40'30"E; 250 m.

Dold, T. 4340 (GRA); 2000; Southern slopes of Kentucky Kop, NW section of Andries Vosloo Kudu Reserve. Very common, clump forming in thicket; 33°5'10"S 26°35'45"E; 400 m.

Dold, T. 4345 (GRA); 2000; Swartwaterspoort, Riebeeck East, east facing rocky, grassy slope with *Faucaria nemorosa*. Uncommon; 33°10'45"S 26°5'00"E; 700 m.

Dold, T. 4391 (GRA); 2001; Double Drift Reserve. Top of Adams Krans at viewpoint; 33°5'00"S 26°45'15"E; 450 m.

Drege, I.L. 3053 (BOL); 10/1912; Aloes [Port Elizabeth]; 33°50'00"S25°35'30"S; 50 m.

Giffen, M.H. *s.n.* in NBG1078/34. (BOL) 1935; Alice; 32°45'30"S 26°50'00"S; 600 m.

Giffen, M.H. *s.n.* in NBG1705/34. (BOL) 1937; Between Alice and Fort Hare (exact locality unknown).

Graham, Miss. *s.n.* in NBG 2420/15 (BOL); Grahamstown; 33°25'35"S 26°30'30"E; 600 m.

Groen, B. 1050 (WAG); Palmietfontein farm, Riebeeck East; 33°10'00"S 26°15'00"E; 700 m.

Groen, B. 1086 (WAG); Mar kman Industrial site, Port Elizabeth; 33°45'30"S 25°35'30"E; 100 m.

Hall, H. *s.n.* in NBG 101/59 (NBG); 12/1969; Grahamstown; 33°25'35"S 26°30'30"E; 600 m.

Harries *s.n.* in NBG2615/29 (BOL); 1935; Sundays River; 33°40'30"S 25°50'15"E; 50 m.

Hosten, L. 109 (PEU); 18/07/1978; Bluewater Bay, Port Elizabeth; 33°50'30"S 25°40'00"E; 50 m.

Leighton, F.M. 2863 (BOL); 01/1947; Trumpeter's Drift between Grahamstown and Peddie; 33°10'40"S 26°55'35"E; 150 m.

Rogers, B. 12924 (BOL); 11/1907; *In aridis prope* Middleton *in dit.* Somerset East; 32°55'40"S 25°45'50"E; 650 m.

Stayner, F. *s.n.* in BOL63671 (BOL); 08/1959; 27 miles from Port Elizabeth on Addo road; 33°40'30"S 25°40'00"E; 100 m.

Strauss, H. *s.n.* (B); 13/7/1911; Kapland; Strauss pressed this in 1911 but it was a cultivated plant from La Mortola garden in 1909; (exact locality unknown).

Van der Merwe, N.J.B. 105. (BOL); 06/1935; Bonnievale, south western region [Swartkops, Port Elizabeth]; 33°50'30"S 25°35'35"E; 50 m.

White, G. *s.n.* (GRA); no date; Brak Kloof farm, Grahamstown; 33°110'50"S 26°20'35"E; 650 m.

B. vespertinus

Acocks, J.H.P. 17519 (BOL); 10/1953; Somerset East; 32°40'40"S 25°35'00"E; 750m.

Archibald, E.E.A. 5249 (GRA); 22/09/1953; Coerney River Valley, Zuurberg, Alexandria District; 33°10'20"S 25°40'30"E; 200 m.

Bolus, L. *s.n.* in NBG886/31 (BOL); 07/1931; Cape, near Zwartkops River (exact locality unknown).

Britten, L. 5135 (GRA); 10/1921; 6 km from Grahamstown on Cradock road; 33°15'15"S 26°25'15"E; 550 m.

Cubr 28420 (B); (Locality unknown, ex hort.).

Dold, T. 4190 (GRA); 1999; Ecca Wildflower Reserve, south end near Bain's plinth in dry karroid rocky grassland with scattered dense bushclumps. Occasional and localised, singly or loosely clumped; 33°10'50"S 35°15'00"E; 528 m.

Dold, T. 4199 (GRA); 1999; Middelton farm, ± 20 km south of Cookhouse on R32 to Port Elizabeth. Uncommon in dry sandy soils in karroid scrub. Single scattered plants; 32°55'15"S 25°45'50"E; 750 m.

Dold, T. 4200 (GRA); 1999; Daggaboersnek, pass between Cookhouse and Cradock, common on steep rocky slope with karroid scrub/grassland; plants single, scattered; 32°30'15"S 25°50'00"E; 1100 m.

Dold, T. 4201 (GRA); 1999; Kariega Park, Alexandria, open rocky grassland, with *Apodolirion amayanum.* Uncommon, scattered, not clumped; 33°35'10"S 26°35'00"E; 150 m.

Dold, T. 4203 (GRA); 1999; Howieson's Poort, Grahamstown; 33°20'5"S 26°25'50"E; 400 m.

Dold, T. 4212 (GRA); 1999; Helspoort, Grahamstown district. Open karroid veld, *Pteronia/Chrysocoma* etc, scattered occasional plants; 33°10'10"S 26°20'10"E; 670 m.

Dold, T. 4228 (GRA); 1999; Rare in open rocky grassland. Hillside on road between Bosfontein and Olievenfontein farms on the boundary between Kirkwood and Somerset East magisterial districts; 33° 15'00"S 25° 30'00"E; 690 m.

Dold, T. 4249 (GRA); 1999; Patryshoogte, near Eastpoort station, north of Cookhouse; 32°40'00"S 25°50'30"E; 750 m.

Dold, T. 4260 (GRA); 1999; 4 km south west from Ghio (*Ncio*) marsh, 2 km on roadside to Port Alfred-Alexandria road. Dry, rocky north facing slope, uncommon, bare open places together with *Euphorbia silenifolia & E. squarrosa.* Single or paired clumps, large woody root-stock, flesh reddish; 33°35'25"S 26°30'15"E; 150 m.

Dold, T. 4266 (GRA); 1999; Klein Vis Rivier bridge, 2 km west of Somerset East on road to Graaff Reinet; Open stony flat grassveld, common but localized together with *Haworthia cooperi,* scattered under *Selago* herbaceous scrub; 32°40'50"S 25°25'20"E; 850 m.

Dold, T. 4270 (GRA); 1999; Somerset East, 29 km from R63 (to Graaff Reinet) to Waterford. Low grassy stony east facing slope on Rietfontein farm; Uncommon on exposed rock strata; 32°55'10"S 25°25'00"E; 700 m.

Dold, T. 4274 (GRA); 1999; Grootbruintjieshoogte pass, on R63, 25 km west of Somerset East. Open dry rocky grassland, occasional but localized; 32°40'10"S 25°15'40"E; 950 m.

Dold, T. 4278 (GRA); 1999; Krans Drift farm, 15 km due west of Fort Brown, open karroid rocky grassland, north facing slope; 33°10'00"S 26°25'30"E; 550 m.

Dold, T. 4291 (GRA); 1999; Springs municipal nature reserve, 10 km north of Uitenhage on R75 to Jansenville. Very uncommon on rocky south-east facing ridge, single plants in bare red soil between quartz rocks and big clumps of *Euphorbia polygona*; 33°40'30"S 25°25'00"E; 200 m.

Dold, T. 4294 (GRA); 1999; Witpoort farm, 4 km south of Kommadagga. Localised population on flat, grassy "table" top; 33°10'5"S 25°55'30"E; 650 m.

Dold, T. 4229 (GRA); 1999; Charlegrove farm, north of Kasouga, open rocky grassland, growing with *Haworthia venusta*; 33°35'15"S 26°35'40"E; 160 m.

Dold, T. 4303 (GRA); 1999; Verdun farm, west of Kommadagga, south-east facing rocky slope, between cracks of dolerite rock, uncommon; 33°10'00"S 25°55'00"E; 550 m.

Dold, T. 4306 (GRA); 1999; Brakloof farm, 20 km west of Grahamstown on Cradock road. Open rocky summit on grassy hillsides, uncommon; 33°10'20"S 26°20'40"E; 600 m.

Dold, T. 4318 (GRA); 2000; Brandhoek farm, at southern foot of Maraiskloof pass, 15 km south of Cradock on road to Somerset East over Swaershoek mountains. Uncommon on sandstone steps on steep south facing slope in grassveld; 32°15'40"S 25°30'00"E; 1 350 m.

Dold, T. 4322 (GRA); 2000; Lower slopes of Zuurberg south west of De Plaat farmhouse near boundary with Kabouga; 33°15'5"S 25°20'45"E; 800 m.

Dold, T. 4326 (GRA); 2000; Bosfontein farm, north of Uitenhage on rocky, quartz summit above stock car racing track. Very uncommon, in red soils, bare patches between exposed rock sheets; 33°40'30"S 25°25'00"E; 150 m.

Dold, T. 4327 (GRA); 2000; Hopefield farm, between Kirkwood and Slagboom/Addo National Park entrance. Uncommon in flat, grassy patch between dense bushclumps; 33°25'10"S 25°35'50"E; 150 m.

Dold, T. 4334 (GRA); 2000; Burntkraal farm in SADF property between aerodrome and Hounslow farm. Open grassland on flat rock outcrop. Uncommon; 33°10'50"S 26°25'30"E; 550 m.

Dold, T. 4344 (GRA); 2000; Arundel farm, Kaga, Bedford District; 32°55'10"S 26°10'20"E; 600 m.

Dold 4372 (GRA); 07/01/2001; Kleinpoort, Steytlerville, with *Brachystelma cummingii*; 33°10'50"S 24°55'00"E; 694 m.

Dold. 4376 (GRA); 2001; Harvestvale farm between Bushman's River Mouth and Alexandria. Common in fairly dense thicket on red clay soils, scattered single plants, with *Ceropegia bowkeri*; 33°35'20"S 26°30'0"E; 200 m.

Dold. 4389 (GRA); 2001; Helspoort, Grahamstown, open karroid scrub/grassland; 33°10'10"S 26°20'10"E; 670 m.

Dyer, R.A. 1128 (GRA); 12/1927; Botha's Hill, Grahamstown; 33°10'45"S 26°30'55"E; 600 m.

Galpin, E.E. 5594 (GRA); 10/1899; Calmshoek, Dryplains (Locality unknown).

Gledhill, E.E. *s.n.* (BOL); 15/6/1931; Grassy bank above station road, Alexandria; 33°40'00"S 26°25'00"E; 150 m.

Harries *s.n.* in NBG2282/33 (BOL); 1933; Somerset East (Locality unknown).

Holland, F.H. *s.n.* in BOL61242 (BOL); 01/1932; Bushman's River; 33°40'25"S 26°40'00"E; 50 m.

Jacot Guillarmod, A.J.G. 9300 (GRA); 13/11/1983; Grahamstown industrial site; 33°15'40"S 26°30'00"E; 600 m.

James, H.W. 127 (BOL); 11/1931; Hillsides near Halesowen, Cradock District; 32'10'50"S 25'40'10"E; 1 000 m.

James, H.W. 442 (BOL); no date; Fort Brown Mountain; 33°5'35"S 26°35'30"E; 350 m.

James, H.W. *s.n.* in NBG187/35 (BOL); Bushman's River, Alexandria; 33°40'25"S 26°40'00"E; 100 m.

James, H.W. *s.n.* in NBG2294/33 (BOL); 10/1933; Daggaboer mountain top; 32°30'15"S 25°50'00"E; 1 100 m.

James, R. 478 (BOL); 11/1932; *In ditione* Cradock, Zwagershoek [Swaershoek pas]; 32°15'00"S 25°30'30"E; 1 200 m.

Lombard, E. *s.n.* in SUG10642 (BOL); no date; Between Mortimer and Cradock; (exact locality unknown).

MacOwan, P. 1587 (GRA); 1870; Boschberg, Somerset East; 32°40'30"S 25°35'00"E; 1 000 m.

Rogers, F.A. 12934 (BOL); 12/1907; *In aridus-prope* Middleton; 32°55'40"S 25°45'50"E; 650 m.

Schwerdtfeger 20998 (B); no date; (ex hort., locality unknown).

Schwerdtfeger 21026 (B); no date; (ex hort., locality unknown).

Schwerdtfeger 21366 (B); no date; (ex hort., locality unknown).

Strauss, H. *s.n.* in BOL63684 (BOL); 14/07/1911; (ex hort., La Mortola garden, locality unknown).

Strauss, H. *s.n.* (B); 14/7/1911; Kapland; (ex hort., La Mortola garden, locality unknown).

Van Der Walt, P.T. 356 (PRE); 9/1968; Somerset East, the Twin [mountain peak east of Bosberg]; 32°40'40"S 25°40'10"E; 900 m.

Specimen number	Dold 4259	Dold4263	Dold4231	Dold4214	Dold4210
Species abbreviation	scap	scap	scap	scap	scap
Living collection number	BRP0rt91	Zoetvl96	Kdrift61	BRport35	Komada29
APPENDIX 2: Vegetative Characters					
1. No. of leaves	8	10	8	8	12
2. Leaf pairs: :0 = equal length, :1 = unequal length	1	1	1	1	1
3. Unopened leaf pairs :1 = central unopened pair with one cradling the other :2 = central unopened pair of equal size and position	1	1	1	1	1
4. Leaf shape :1 = oblanceolate, :2 = lanceolate, :3 = ovate, :4 = broadly ovate, :5 = linear-lanceolate, :6 = broadly lanceolate	6	2	2	6	2
5. Cenral pair of leaves :0 = erect, :1 = spreading, :2 = declinate, :3 = recurved	0	0	0	0	0
6. Outermost pair of leaves :0 = erect, :1 = spreading, :2 = decumbent, :3 = recurved	1	1	1	1	1
7. Leaf curving :0 = inwards (falcate), :1 = curving outwards, :2 = not curving :3 = curving outwards and back "S" shaped, :4 = reflexed	1	1	1	1	1
8. Colour :0 = dark green, :1 = pale yellow-green, :2 = yellow green, :3 = blue green, :4 = grey green, :5 = lime green, :6 = pale whitish green	1	1	1	1	1
9. Surface :0 = matt, :1 = glossy	0	0	0	0	0
10. Surface :0 = waxy, :1 = with a bloom, :2 = smooth, :3 = rugose	0	0	0	0	0
11. Surface :0 = turgid (swollen from fullness), :1 = rugose (wrinkled) :2 = defined raised dots, :3 = smooth/unmarked, :4 = noticeable darker green-black flecks (not raised), :5 = noticeable maroon flecks (not raised)	3	3	3	3	3
12. Texture :0 = succulent, :1 = fleshy, :2 = leathery	0	0	0	0	0
13. Leaf pliability :0 = brittle, :1 = pliable	0	0	0	0	0
14. Length (average of 4 leaves in mm)	60	68	101	88	58
15. Broadest part : 0 =base, : 1 = middle, : 2 = above middle	0	0	0	0	0
16. Broadest part (average of 4 leaves in mm)	20	20	13	12	8
17. Cross-section height at thickest part (mm)	10	9	8	9	6
18. Cross-section thickest :0 = at base of leaf, :1 = at middle of leaf, :2 = above middle of leaf	2	2	2	2	2
19. Margins :1 = inconspicous, :2 = thickened/cartilaginous, :3 = dense concentration of epidermal cells	1	1	1	1	1
20. Margin angle :0 = acute, :1 = rounded	0	0	0	0	0
21. Margin color :0 = whitish, :1 = darker green than leaf, :2 = same as leaf, :3 = reddish	0	0	3	0	0
22. Keel :0 = entire length, :1 = distal half only	1	1	1	1	1
23. Keel angle :0 = acute, :1 = rounded	0	0	1	0	0
24. Keel texture :0 = inconspicous, :1 = cartilaginous/thickened	1	1	1	1	0
25. Distal end :0 = chinned, :1 = not chinned	0	0	0	0	1
26. Apices :0 = acuminate, :1 = shortly acute, :2 = obtuse, :3 = acute (drawn out)	1	1	1	1	1
27. Apices :0 = inwardly hooked, :1 = outwardly hooked, :2 = straight (not hooked)	0	0	0	2	2
28. Apices :0 = mucronate, :1 = not mucronate or aristate, :2 = aristate	0	0	0	1	1
29. Cross-section :0 = flattened dorsally (top to bottom) :1 = triangular/V-shaped, :2 = D-shaped, :3 = broadly/shallowly D-shaped	1	1	2	2	2
30. Cental tissue :1 = Conspicous central vascular. bundle :2 = No conspicous central vasc. bundle	1	1	1	1	1
31. Upper surface :0 = flat, :1 = concave, :2 = convex, :3 = broadly V-shaped	1	1	0	0	0
32. Leaf base :0 = truncate, :1 = tapering abruptly, :2 = tapering gradually	1	1	1	0	0
33. Leaf tips :1 = tinged reddish, :2 = not tinged reddish	2	2	2	2	2
34. Lower basal leaf surface :0 = pustulate, :1 = not pustulate	1	1	1	1	1
35. At least older leaves :0 = turning white, :1 = not turning white	1	1	1	1	1
36. Most leaves :0 = with a lateral twist on its own axis :1= without a lateral twist on its own axis	1	1	1	1	1

	Dold4204 scap Dbdrif21	Dold4296 scap Kaprv134	Dold4292 scap Hopef130	Dold4186 scap Grahams1	Dold4226 scap Belmnt52	Dold4252 scap Annsvl83	Dold4191 scap Kfdrift6	Dold4209 scap Eccapa27	Dold4313 scap Woodb156	Dold4316 scap Highl159
1	6	12	9	12	8	8	8	6	6	8
2	1	1	0	1	1	1	1	1	1	1
3	1	1	1	1	1	1	1	1	1	1
4	2	6	2	2	2	2	2	2	2	2
5	0	0	0	0	0	0	0	0	0	0
6	1	1	1	1	1	1	1	1	1	1
7	0	1	1	1	1	1	1	1	1	1
8	1	1	1	1	1	1	1	1	1	1
9	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0	0
11	3	3	3	3	3	3	3	3	3	3
12	0	0	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	0	0
14	65.5	53	60.5	60	70	58	50	80	36	60
15	0	0	0	0	0	0	0	0	0	0
16	8.2	14.7	12.5	13	11	9	9.7	8.2	9	11.5
17	6.5	8	10	8	8	6	6	5.5	4.6	6
18	2	2	2	2	2	2	2	2	2	2
19	1	1	1	1	1	1	1	1	1	1
20	0	0	0	0	0	0	0	0	0	0
21	0	0	0	0	0	0	0	0	0	0
22	1	1	1	1	1	1	1	1	1	1
23	1	0	1	0	0	0	0	1	0	0
24	0	0	0	0	0	0	0	0	0	0
25	0	0	0	0	0	0	0	0	0	0
26	1	1	1	1	1	1	1	1	1	1
27	0	0	0	0	0	0	0	0	0	0
28	1	1	1	0	0	0	0	0	0	0
29	2	1	2	2	1	2	2	2	2	2
30	1	1	1	1	1	1	1	1	1	1
31	0	2	2	2	1	0	0	2	0	0
32	0	0	0	0	0	0	0	0	0	0
33	2	2	2	2	2	2	2	2	2	2
34	1	1	1	1	1	1	1	1	1	1
35	1	1	1	1	1	1	1	1	1	1
36	1	1	1	1	1	1	1	1	1	1

	Dold4297 scap Ftbeu135	Dold4213 scap Plutos34	Dold4316 scap Highl159	Dold4202 scap Gowies18	Dold4295 scap Thorn133	Dold4276 scap Drive113	Dold4193 scap Willoft8	Dold4310 katbgsis Hogsb151	Dold4277 katbgsis Wintb114	Dold4254 katbgsis Katbeg86
1	8	8	8	12	8	8	9	8	8	12
2	1	1	1	0	1	1	1	0	0	1
3	1	1	1	1	1	1	1	2	1	1
4	2	2	2	2	2	2	2	6	2	6
5	0	0	0	0	0	0	0	0	0	0
6	1	1	1	1	1	1	1	1	1	1
7	2	1	1	1	1	0	1	1	1	1
8	1	1	1	1	1	1	1	0	2	2
9	0	0	0	0	0	0	0	1	1	1
10	0	0	0	0	0	0	0	2	2	2
11	3	3	3	3	3	3	3	4	2	2
12	0	0	0	0	0	0	0	1	0	0
13	0	0	0	0	0	0	0	1	1	0
14	45	76	61	81	47	28.5	76	19	32	25
15	0	0	0	0	0	1	0	1	1	1
16	7.5	10	13.5	15	12	8	12	7	5	9
17	5	6	7	9	7	4	6.5	5	5	6
18	2	2	2	2	2	2	2	1	1	2
19	1	1	1	1	1	1	1	2	3	3
20	0	0	0	0	0	1	0	0	0	1
21	0	0	0	0	0	0	0	0	0	0
22	1	1	1	1	1	1	1	0	0	0
23	1	0	0	0	0	1	0	0	0	0
24	0	0	0	0	0	0	0	1	0	1
25	0	0	0	0	0	0	0	1	1	1
26	1	1	1	1	1	1	1	0	1	1
27	0	2	0	0	0	0	0	0	0	0
28	0	0	0	0	0	0	0	2	2	2
29	2	1	2	1	2	1	2	1	1	1
30	1	1	1	1	1	1	1	1	2	1
31	0	0	2	1	0	2	0	3	3	0
32	0	0	0	0	0	1	0	2	1	1
33	2	2	2	2	2	2	2	2	2	2
34	1	1	1	1	1	1	1	1	0	0
35	1	1	1	1	1	1	1	0	1	0
36	1	1	1	1	1	1	1	1	1	1

	Dold4246 katbgsis Dordre76	Dold4280 katbgsis Emmx117	Dold4286 katbgsis Indwe123	Dold4279 katbgsis Qtown116	Dold4236 katbgsis Cathca66	Dold4248 katbgsis Idatow78	Dold4244 katbgsis Shawbu74	Dold4239 katbgsis Cathca69	Dold4309 katbgsis Cathc150	Dold4283 katbgsis Stokw120
1	12	10	10	8	10	12	8	10	0	10
2	1	1	0	0	0	0	0	0	0	0
3	1	1	1	1	2	1	2	2	1	1
4	6	6	6	2	6	2	6	2	2	2
5	0	0	0	0	0	0	0	0	0	0
6	0	0	0	0	1	0	1	0	0	0
7	2	2	2	2	2	2	2	2	2	2
8	2	2	2	2	2	2	2	2	2	2
9	1	1	1	1	1	1	1	1	1	1
10	2	2	2	2	2	2	2	2	2	2
11	2	2	2	4	4	4	4	4	4	4
12	0	0	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	0	0
14	22	18	19	25	32	25	20	22	25	20
15	1	1	1	1	1	1	1	1	1	1
16	6	8.5	7	6	8	7	9	8	6	6
17	4	4	4	5	5	4	5	5	5	4
18	2	2	2	2	2	1	2	2	2	2
19	3	3	3	3	3	3	3	3	3	3
20	1	1	1	1	1	1	1	1	1	1
21	0	0	0	0	0	0	0	0	0	0
22	1	1	1	0	1	1	1	1	1	1
23	0	0	0	0	1	1	1	1	1	1
24	1	1	1	0	0	0	0	0	0	0
25	1	1	1	1	1	1	1	1	1	1
26	1	1	1	1	1	1	1	1	1	1
27	0	0	0	0	0	0	0	0	0	0
28	2	2	2	2	2	2	2	2	2	2
29	1	1	1	1	2	1	2	2	1	2
30	1	1	1	2	2	1	2	2	2	2
31	0	0	2	0	0	2	1	0	1	1
32	1	1	1	1	1	1	1	1	1	1
33	2	2	2	2	2	2	2	2	2	2
34	0	0	0	1	1	1	1	1	1	1
35	0	0	0	0	0	0	0	0	0	0
36	1	1	1	1	1	1	1	1	1	1

	Dold4247 katbgsis Inndwe77	Dold4275 katbgsis Tarka110	Dold4268 katbgsis Sterk103	Dold4240 katbgsis Chilton70	Dold4264 katbgsis Quetwn98	Dold4267 katbgsis Tsomo102	Dold4281 katbgsis Nicom118	Dold4282 katbgsis Makay119	Dold4277 katberg Wnter114	Dold4308 katbgsis Stalb149
1	8	10	10	8	10	10	10	10	10	10
2	0	0	0	0	0	0	0	0	0	0
3	1	2	2	2	1	2	2	2	2	2
4	2	2	2	2	2	2	2	2	2	2
5	0	0	0	0	0	0	0	0	0	0
6	0	0	0	0	0	0	0	0	0	0
7	2	2	2	2	2	2	2	2	2	2
8	2	2	2	2	2	2	2	2	2	2
9	1	1	1	1	1	1	1	1	0	1
10	2	2	2	2	2	2	2	2	2	2
11	4	4	4	4	4	4	4	4	4	4
12	0	0	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	0	0
14	20	25	26	11	22	22	20	16	24	24
15	1	1	1	1	1	1	1	1	1	1
16	6	6	7	4	6	7	5	5	8	6
17	4	4	5	4	4	4	4	4	4	4
18	2	1	2	2	2	1	1	1	0	1
19	3	3	3	3	1	3	3	1	3	3
20	1	1	1	1	1	1	1	1	1	1
21	0	0	0	0	0	0	0	0	0	0
22	1	1	1	1	1	1	1	1	0	1
23	1	1	1	1	1	1	1	1	1	1
24	0	0	0	0	0	0	0	0	0	0
25	1	1	1	1	1	1	1	1	1	1
26	1	1	1	1	1	1	1	1	1	1
27	0	0	0	0	0	0	0	0	0	0
28	2	2	2	2	2	2	2	2	2	2
29	2	1	2	1	1	2	1	1	1	2
30	2	2	2	2	2	1	2	2	2	1
31	2	0	0	0	2	0	0	0	0	0
32	1	1	1	1	1	1	1	1	2	1
33	2	2	2	2	2	2	2	2	2	2
34	1	1	1	1	1	1	1	1	0	1
35	0	0	0	0	0	0	0	0	1	0
36	1	1	1	1	1	1	1	1	1	1

	Dold4238 leighton Tamara68	Dold4258 leighton Kingwm90	Dold4232 leighton Stutte62	Dold4235 leighton Komgha65	Dold4269 leighton Stutt104	Dold4192 leighton Unitrac7	Dold4243 leighton Unitra73	Dold4302 leighton Wrigg140	Dold4300 leighton Campg138	Dold4304 leighton Ndaba142
1	10	8	12	12	12	12	10	8	10	8
2	0	0	0	0	0	0	0	0	0	0
3	2	2	2	2	2	2	2	2	2	2
4	4	3	4	4	4	4	6	3	3	3
5	1	1	1	1	1	1	1	0	0	1
6	2	2	2	2	2	2	2	2	2	2
7	4	4	4	4	4	4	4	4	4	4
8	4	4	4	4	4	4	4	4	4	4
9	1	1	1	1	1	1	1	1	1	1
10	2	2	2	2	2	2	2	2	2	2
11	5	5	5	5	5	5	5	4	4	4
12	0	0	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	0	0
14	23	25	26	26	26	26	44	24	26	14
15	1	1	1	1	1	1	1	1	1	1
16	10	8	10	10	10	10	9	7	10	5
17	5	4	5	5	5	5	5	5	5	4
18	1	1	1	1	1	1	1	1	1	1
19	1	1	1	1	1	1	1	1	1	1
20	1	1	1	1	1	1	1	1	1	1
21	0	1	1	1	1	1	1	2	0	1
22	1	1	1	1	1	1	1	1	1	1
23	1	1	1	1	1	1	1	1	1	1
24	0	0	0	0	0	0	0	0	0	0
25	1	1	1	1	1	1	1	1	1	1
26	0	0	0	0	0	0	1	0	0	1
27	0	0	0	0	0	0	0	0	0	0
28	2	2	2	2	2	2	2	2	2	2
29	0	0	0	0	0	0	2	2	3	2
30	2	2	2	2	2	2	2	2	2	2
31	2	0	2	2	2	2	1	0	2	0
32	1	2	0	0	0	0	2	2	0	0
33	2	1	1	1	1	1	1	1	2	2
34	1	1	1	1	1	1	1	1	1	1
35	1	1	1	1	1	1	1	1	1	1
36	1	1	1	1	1	1	1	1	1	1

	Dold4301 leighton Amabe139	Dold4265 leighton Actonc99	Dold4284 albomarg Seymr121	Dold4285 albomarg Seymr122	Dold4288 artus Cala125	Dold4245 artus Calat75	Dold4234 concav Potter64	Dold4237 concav Kweler67	Dold4233 concav Leachb63	Dold4298 concav Cints136
1	10	12	12	12	8	8	10	10	10	10
2	0	0	0	0	0	0	0	0	0	0
3	2	2	1	1	2	2	2	2	2	2
4	6	3	4	4	6	6	3	3	3	3
5	1	1	0	0	0	0	0	0	0	0
6	2	2	2	2	1	1	1	1	1	1
7	4	4	1	1	2	2	1	1	1	1
8	4	4	3	3	5	5	2	2	2	2
9	1	1	1	1	0	0	0	0	0	0
10	2	2	2	2	3	3	0	0	0	0
11	4	4	4	4	4	4	4	4	4	4
12	0	0	1	1	0	0	0	0	0	0
13	0	0	1	1	0	0	0	0	0	0
14	22	30	37	46	23	23	27	24	33.5	32
15	1	1	1	1	0	0	1	1	1	1
16	11	9	15	22	10	10	11	10	11	11
17	4	4	7	6	6	6	7	6	5	5
18	1	1	2	2	0	0	1	1	1	1
19	1	1	2	2	3	3	1	1	1	1
20	1	1	0	0	1	1	1	1	1	1
21	0	0	0	0	1	1	2	2	0	0
22	1	1	1	1	1	1	0	1	1	1
23	1	1	0	0	1	1	1	1	1	1
24	0	0	1	1	0	0	0	0	0	0
25	1	1	0	0	1	1	1	1	1	1
26	0	0	0	0	1	1	1	1	1	1
27	0	0	0	0	2	2	2	2	2	2
28	2	2	0	0	0	0	2	2	2	2
29	0	1	0	0	2	2	1	2	2	2
30	2	2	1	1	1	1	2	2	2	2
31	3	1	1	1	0	0	1	1	1	1
32	0	2	0	0	0	0	2	2	2	2
33	2	2	2	2	1	1	2	2	2	2
34	1	1	1	1	1	1	1	1	1	1
35	1	1	1	1	1	1	1	1	1	1
36	1	1	1	1	1	1	1	1	1	1

	Dold4251 concav Kayser82	Dold4305 concav Dyamd143	Dold4199 concav tyolo137	Dold4207 addo Coega155	Dold4311 addo Mentz152	Dold4198 addo Bridge13	Dold4290 addo Kirkw127	Dold4272 addo Addoa107	Dold4324 addo4324 Uiten172	Dold4253 multiceps Brakfn85
1	8	8	8	10	10	6	6	6	12	8
2	0	0	0	0	0	0	0	0	0	1
3	2	2	2	1	1	2	2	2	2	2
4	2	3	3	2	2	2	2	2	2	5
5	0	0	0	0	1	1	1	0	0	0
6	1	1	1	1	1	1	1	1	1	1
7	1	1	1	0	0	0	0	0	0	1
8	2	2	2	3	3	3	3	3	3	0
9	0	0	0	1	1	1	1	1	1	0
10	0	0	0	1	1	1	1	1	1	3
11	4	4	4	4	4	4	4	4	4	4
12	0	0	0	0	0	0	0	0	0	2
13	0	0	0	0	0	0	0	0	0	1
14	28	31.5	27	37.5	33	42	33.5	37.5	27.2	35
15	1	1	1	1	0	1	1	1	1	1
16	7	9	11	9	9	10	10	10	8	6
17	4	6	5	6	6	7	6	7	6	4
18	1	1	1	1	1	1	1	1	1	0
19	1	1	1	1	1	1	1	1	1	1
20	1	1	1	1	1	1	1	0	0	0
21	0	0	0	2	1	2	2	2	2	2
22	1	1	1	1	1	1	1	1	1	1
23	1	1	1	1	1	1	1	1	1	1
24	0	0	0	0	0	0	0	0	0	0
25	1	1	1	1	1	1	1	1	1	1
26	1	1	1	3	3	3	3	3	3	3
27	2	2	2	2	2	2	2	2	2	1
28	2	2	2	0	0	0	0	0	0	2
29	2	2	2	2	2	2	2	2	2	3
30	2	2	2	1	1	2	2	2	2	2
31	0	2	2	0	2	2	2	0	0	0
32	2	2	2	2	1	2	2	2	2	2
33	2	2	2	2	2	2	2	2	2	1
34	1	1	1	1	1	1	1	1	1	0
35	1	1	1	1	1	1	1	1	1	1
36	1	1	1	0	0	0	0	0	0	1

	Dold4223 multiceps Mayfld48	Dold4315 multiceps Micro158	Dold4224 multiceps Commn50	Dold4288 multiceps TukuB126	Dold4249 multiceps Cookhs80	Dold4230 multiceps Common60	Dold4219 multiceps Gwaben43	Dold4314 multiceps Jamsn157	Dold4189 multiceps Mayfild4	Dold4195 multiceps Palmit10
1	12	8	10	10	12	8	12	9	12	6
2	1	1	0	0	0	0	0	0	0	0
3	2	2	2	2	2	2	2	2	2	2
4	5	6	2	2	2	6	2	2	2	2
5	0	0	0	0	0	0	0	0	0	0
6	1	3	3	0	1	3	1	1	1	3
7	1	1	1	1	1	1	1	1	1	1
8	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0
10	3	3	3	3	3	3	3	3	3	3
11	4	4	4	4	4	4	4	4	4	4
12	2	2	2	2	2	2	2	2	2	2
13	1	1	1	1	1	1	1	1	1	1
14	43	34	34.5	32	31	25	45	27	36	30
15	1	1	1	1	1	1	1	1	1	1
16	7	10	8	6	6	9	8	7	7	8
17	4	4	4	4	4	4	4	4	4	4
18	0	0	0	0	0	0	0	0	0	0
19	1	1	1	3	3	3	3	3	1	3
20	0	0	0	0	0	0	0	0	0	0
21	2	2	2	0	0	0	0	0	2	0
22	1	1	1	1	1	1	0	0	0	0
23	0	1	1	1	1	1	1	1	1	1
24	0	0	0	0	0	0	1	1	0	1
25	1	1	1	1	1	1	1	1	1	1
26	3	0	0	0	0	0	0	0	0	0
27	1	0	0	0	0	0	0	0	0	0
28	2	2	2	2	2	2	2	2	2	2
29	1	1	1	1	1	1	1	1	1	1
30	2	2	2	2	2	2	2	2	2	2
31	1	2	3	2	0	3	0	3	0	0
32	2	2	2	2	2	2	2	2	2	2
33	1	2	1	1	1	1	0	2	1	1
34	0	0	0	0	0	0	0	0	0	0
35	1	1	1	1	1	1	1	1	1	1
36	1	1	1	1	1	1	1	1	1	1

	Dold4312 multiceps Uitvg154	Dold4261 multiceps Kleind93	Dold4257 multiceps Linedt89	Dold4215 multiceps Nutwod36	Dold4256 multiceps Keiska88	Dold4197 multiceps Rabbit12	Dold4225 multiceps Belmnt51	Dold4188 multiceps Grahams3	Dold4221 multiceps Graham45	Dold4194 multiceps Redhose9
1	8	8	8	8	8	12	10	10	8	10
2	0	0	0	0	0	0	1	0	0	0
3	2	2	2	2	2	2	2	2	2	2
4	2	2	2	2	2	2	5	2	2	2
5	0	0	0	0	0	0	0	0	0	0
6	3	3	1	3	1	1	3	1	1	3
7	1	1	1	1	1	1	1	1	1	1
8	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0
10	3	3	3	3	3	3	3	3	3	3
11	4	4	4	4	4	4	4	4	4	4
12	2	2	2	2	2	2	2	2	2	2
13	1	1	1	1	1	1	1	1	1	1
14	32	25	37	34	29	49	44	25	40	45
15	1	1	1	1	1	1	1	1	1	1
16	9	9	9	7	6	7	7	6	8	10
17	4	5	4	3	3	4	3	3	3	5
18	0	0	0	0	0	0	0	0	0	0
19	1	3	2	1	3	1	1	1	3	1
20	0	0	0	0	0	0	0	0	0	0
21	0	0	0	2	0	0	0	0	0	0
22	1	0	0	0	0	0	0	0	0	0
23	1	1	1	1	1	1	1	1	1	1
24	0	1	1	0	0	0	0	0	0	0
25	1	1	1	1	1	1	1	1	1	1
26	0	0	0	0	0	0	3	0	0	0
27	0	0	0	0	0	0	0	0	0	0
28	2	2	2	2	2	2	2	2	2	2
29	1	1	1	1	1	1	2	1	1	1
30	1	2	1	2	2	2	2	2	2	2
31	1	2	0	0	2	1	0	0	0	0
32	2	2	2	2	2	2	2	2	2	2
33	2	1	1	1	1	2	1	1	1	2
34	0	0	0	0	0	0	0	0	0	0
35	1	1	1	1	1	1	1	1	1	1
36	1	1	1	1	1	1	1	1	1	1

	Dold4194 multiceps Oribir23	Dold4273 multiceps Olifn108	Dold4222 multiceps Tharfi46	Dold4250 multiceps Jefbay81	Dold4323 multiceps Stone171	Dold4187 multiceps Tablefm2	Dold4216 multiceps Tablef37	Dold4270 vesper Somst105	Dold4278 vesper Krans115	Dold4294 vesper Witpt132
1	10	8	10	8	8	12	12	8	10	10
2	0	0	0	0	0	0	0	1	1	1
3	2	2	2	2	2	2	2	2	2	2
4	2	2	2	2	2	2	2	5	5	5
5	0	0	0	0	0	0	0	1	1	1
6	1	3	1	1	3	3	3	1	1	1
7	1	1	1	1	1	2	2	1	1	1
8	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	1	1	1
10	3	3	3	3	2	3	3	3	3	3
11	4	4	4	4	3	4	4	2	2	2
12	2	2	0	2	2	2	2	2	2	2
13	1	1	1	1	1	1	1	1	1	1
14	30	37.5	35	34.5	28	21	16	39	34	48
15	1	1	1	1	0	1	1	0	0	0
16	6	8	8	9	9	7	7	6	7	6
17	4	5	5	4	6	5	4	4	4	4
18	0	0	0	0	0	2	2	0	0	0
19	3	1	3	1	1	1	1	1	1	1
20	0	0	0	0	0	0	0	0	0	0
21	0	2	0	0	2	2	2	2	2	2
22	1	1	1	1	1	1	1	0	0	0
23	1	1	1	1	1	1	1	1	1	1
24	0	0	0	0	0	0	0	0	0	0
25	1	1	1	1	1	1	1	1	1	1
26	0	0	1	0	1	0	0	3	3	3
27	1	0	0	0	0	0	0	0	0	0
28	2	2	2	2	2	2	2	2	2	2
29	1	1	2	1	2	1	1	2	2	2
30	2	2	2	2	2	2	2	2	2	2
31	0	0	0	0	0	2	2	0	1	1
32	2	2	2	2	0	2	2	0	0	0
33	2	2	2	1	2	2	2	2	2	2
34	0	0	0	0	1	0	0	0	0	0
35	1	1	1	1	1	1	1	1	1	1
36	1	1	1	1	1	1	1	1	1	1

	Dold4228 vesper Oliven54	Dold4322 vesper Zuurb170	Dold4325 vesper Uiten173	Dold4326 vesper Uiten174	Dold4327 vesper Enonn175	Dold4303 vesper Verdu141	Dold4199 vesper Cookhs14	Dold4317 vesp Swaar164	Dold4200 vesp Daggab15	Dold4306 vesp Brakl144
1	8	10	10	10	8	10	8	8	10	10
2	1	0	0	0	1	1	0	0	0	0
3	2	2	2	2	2	1	2	2	2	2
4	5	5	5	5	5	5	5	5	5	5
5	1	1	1	0	0	0	0	0	0	0
6	1	1	1	1	1	0	1	0	3	3
7	1	1	1	0	0	0	1	0	1	1
8	0	4	0	0	0	0	0	6	0	0
9	1	0	0	1	0	0	1	1	0	0
10	3	3	3	3	3	1	2	2	3	3
11	3	4	4	3	3	3	2	2	4	4
12	2	2	2	2	2	1	1	0	2	2
13	1	1	1	1	1	1	1	1	1	1
14	37	54	40	30	22	24	35	20	39	39
15	0	0	0	0	0	0	0	0	1	1
16	6	7	6	6	4	5	5	5	6	4
17	4	6	4	5	2	3	5	4	4	3
18	0	1	1	0	0	0	0	1	0	0
19	1	1	1	1	1	1	1	1	1	1
20	1	1	1	1	0	1	1	0	1	0
21	2	2	2	2	2	2	2	2	2	2
22	1	1	1	1	1	1	1	1	1	0
23	1	1	1	0	1	1	1	0	1	1
24	0	0	0	1	1	0	0	1	0	0
25	1	1	1	1	1	1	1	1	1	1
26	3	3	3	3	3	1	3	1	3	3
27	0	2	2	0	0	0	0	0	0	0
28	2	2	0	2	0	2	2	0	2	2
29	2	2	2	1	1	2	1	1	2	1
30	2	2	2	2	2	2	2	1	2	2
31	2	2	2	0	0	1	2	2	0	0
32	0	0	0	0	0	0	0	0	2	2
33	2	2	2	1	2	2	2	2	2	2
34	1	1	1	1	1	1	1	1	0	0
35	1	1	1	1	1	1	1	1	1	1
36	1	1	1	1	1	1	1	1	1	1

	Dold4274 vesp Somst109	Dold4266 vesp Klein100	Dold4212 vesp Helspt31	Dold4260 vesp Ghioma92	Dold4299 vesp Charlg57	Dold4203 vesp Howies19	Dold4201 vesp Karieg16	Dold4190 vesp Eccapas5	Dold4318 vesp Swaar165	Dold4344 vesp Kaga195	Dold4388 nanus Desol106
1	8	10	12	8	8	10	8	10	8	12	8
2	1	0	1	0	0	0	0	0	0	0	0
3	2	2	2	2	2	2	2	2	2	2	2
4	5	5	5	5	2	2	5	5	5	5	5
5	1	0	0	0	0	0	0	0	0	0	1
6	1	1	1	3	1	1	1	1	0	0	1
7	1	1	1	1	1	1	1	1	0	0	1
8	0	0	0	0	0	0	0	0	6	6	6
9	1	0	0	0	0	0	0	0	1	0	1
10	3	3	3	3	3	3	3	3	2	3	2
11	2	4	4	4	4	4	4	4	2	2	0
12	2	2	2	2	2	2	2	2	0	2	0
13	1	1	1	1	1	1	1	1	1	1	0
14	37	44	45	40	44	35	48.5	50	30	29	24
15	0	1	1	1	1	1	0	0	0	0	0
16	5	6	7	6	6	8	7	7	6	5	6
17	3	4	5	4	4	6	4	4	4	3	5
18	0	0	0	0	0	0	0	0	1	1	0
19	1	1	1	1	1	1	1	1	1	1	3
20	0	0	1	0	0	0	0	0	0	0	1
21	2	2	2	2	0	2	0	2	2	2	1
22	0	0	1	0	0	1	1	0	1	0	1
23	1	1	1	1	1	1	1	0	0	0	1
24	0	0	0	0	0	0	0	0	1	0	0
25	1	1	1	1	1	1	1	1	1	1	1
26	3	3	3	3	3	1	3	3	3	3	1
27	0	0	0	0	0	0	0	0	0	0	2
28	2	2	2	2	2	2	2	2	0	0	0
29	2	1	2	2	1	1	2	1	4	4	2
30	2	2	2	2	2	2	2	2	1	1	2
31	0	0	0	3	1	2	2	0	0	0	2
32	0	2	2	2	2	2	1	1	0	0	0
33	2	1	2	1	1	2	2	2	2	2	2
34	0	0	0	0	0	0	0	0	0	0	1
35	1	1	1	1	1	1	1	1	1	1	1
36	1	1	1	1	1	1	1	1	1	1	1

APPENDIX 3: Geology and lithology of *Bergeranthus* species localities

Species	Formation	Sub-group	Group	Lithology
B. albomarginatus	-	-	-	Exposed intrusive dolerite sills
B. artus	-	-	-	Exposed intrusive dolerite sills
B. leightoniae	-	-	-	Exposed intrusive dolerite sills
B. nanus	-	-	-	Exposed intrusive dolerite sills
B. concavus	Nanaga	-	Algoa	Calcareous sandstone
	Katberg	Tarkastad	Beaufort	Sandstone
B. katbergensis	Katberg	Tarkastad	Beaufort	Sandstone
	Elliot	-	Drakensberg	Sandstone
	Molteno	-	Drakensberg	Sandstone
	Middleton	Adelaide	Beaufort	Sandstone
	Katberg	Tarkastad	Beaufort	Brownish-red mudstone & sandstone
B. addoensis	Sundays River	-	Uitenhage	Grey/green mudstone & sandstone
	Kirkwood	-	Uitenhage	Red/green mudstone & sandstone
	Peninsula	-	Table Mountain	Quartzitic sandstone
	Blue Water Bay	-	-	Alluvial sheet gravel and sand
	Witpoort	Lake Mentz	Witteberg	Quartzitic sandstone & shale
B. multiceps	Balfour	Adelaide	Beaufort	Grey mudstone and sandstone
	Grahamstown	-	-	Silcrete & kaolinite

	Goudini	Nardouw	Table Mountain	Brownish weathering quartzitic sandstone
	Middleton	Adelaide	Beaufort	Grey & red mudstone
	Koonap	Adelaide	Beaufort	Mudstone & subordinate sandstone
	Blue Water Bay	-	-	Alluvial sheet gravel & sand
	Witpoort	Lake Mentz	Witteberg	Quartzite
	-	Lake Mentz	Witteberg	Shale, sandstone & diamictite
	Weltevrede	Lake Mentz	Witteberg	Shale & quartzite
	Nanaga	-	Algoa	Calcareous sandstone & sandy limestone
	Boplaas	Ceres	Bokkeveld	Sandstone
	-	Kommadagga	Witteberg	Shale siltstone, sandstone & diamictite
	-	Dwyka	Ecca	Tillite
	-	-	-	Intermediate & low-level fluvial terrace gravel
	-	-	-	Intrusive dolerite sill
B. scapiger	Grahamstown	-	-	Silcrete & kaolinite
	Collingham/Whitehill/Prince Albert	-	Ecca	Shale & tuff
	Witpoort	Lake Mentz	Witteberg	Brownish-weathering quartzitic sandstone
	Blue Water Bay	-	-	Alluvial sheet

				gravel & sand
	Balfour	Adelaide	Beaufort	Grey Mudstone, shale & sandstone
	Koonap	Adelaide	Beaufort	Mudstone & subordinate sandstone
	-	Lake Mentz	Witteberg	Shale, quartzite, sandstone & diamictite
	Weltevrede	Lake Mentz	Witteberg	Shale & quartzite
	Fort Brown	-	Ecca	Rhythmite, subordinate shale & sandstone
	-	Dwyka	Ecca	Tillite
B. vespertinus	Boplaas	Ceres	Bokkeveld	Sandstone
	Middleton	Adelaide	Beaufort	Grey & red mudstone & sandstone
	Balfour	Adelaide	Beaufort	Grey Mudstone, shale & sandstone
	Witpoort	Lake Mentz	Witteberg	Shale, quartzite, sandstone & diamictite
		Dwyka	Ecca	Tillite
	Rippon	Adelaide	Beaufort	Sandstone & shale
	-	Kommadagga	Witteberg	Shale, siltstone, sandstone & diamictite
	Kirkwood		Uitenhage	Red/green mudstone & sandstone