

Bothalia

A JOURNAL OF BOTANICAL RESEARCH

Vol. 40,1

May 2010

TECHNICAL PUBLICATIONS OF THE SOUTH AFRICAN NATIONAL BIODIVERSITY INSTITUTE PRETORIA

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Volume 40,1

Scientific Editor: G. Germishuizen
Technical Editor: B.A. Momberg



SOUTH AFRICAN

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ISSN 0006 8241

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A generic classification of the Restioneae (Restionaceae), southern Africa

H.P. LINDER* and C.R. HARDY**

Keywords: Africa, generic classification, Restionaceae, Restioneae, taxonomy

ABSTRACT

We propose a new generic classification of the African Restionaceae, tribe Restioneae (subfamily Restionoideae), based on the phylogeny and on extensive morphological data. The phylogeny is based on both plastid sequence data and morphological data. We delimit the genera to be monophyletic, to minimize the nomenclatural changes, and to maximize the ability to diagnose the genera. We recognize eight genera, one of which with nine subgenera, in the tribe. Of the currently accepted genera, only three need changes. We provide descriptions for all genera and subgenera, and include a key to them. In this paper we erect one new genus, *Soroveta*, redelimit *Platycaulos* and *Restio*, and reduce *Calopsis* and *Ischyrolepis* to synonymy under *Restio*. We list the species which we recognize under each genus, make 37 new combinations, propose eight new names, and also describe eight new species that belong in these genera.

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INTRODUCTION

The African Restionaceae (subfam. Restionoideae, ± 350 species) comprise one of the dominant elements of the fynbos vegetation of the Cape Floristic Region (CFR,

Goldblatt 1978) (Taylor 1978; Rebelo *et al.* 2006), and is regarded as one of the most important clades of the larger Cape flora (Linder 2003). Within the African Restionaceae, the tribe Restioneae (Briggs & Linder 2009) includes most species (288), all of which are endemic to sub-Saharan Africa or Madagascar. A user-friendly, maximally informative generic classification of the tribe is thus essential for the effective study of the Cape flora.

The taxonomy of the Restioneae has been investigated several times over the past centuries, using different data sets and different taxonomic concepts. Most of the publications from the 19th and 20th centuries were concerned with describing the many species which were brought to Europe by early collectors: for a summary, see Linder (1985). However, several publications also focused on the generic delimitations. In the 19th century, the morphology of the species was the primary evidence on which the generic delimitation was based, resulting in the classification proposed by Masters (1878; 1897) and used by Pillans (1928). This was based heavily on the gynoecial characters and remained in use until 1984 (Adamson & Salter 1950; Dyer 1976). Citing problems with the Masters classification, Gilg-Benedict (1930) based an alternative classification on the culm anatomical data of her husband, Gilg (1891), but this classification was unfortunately ignored. By 1980 it was evident that there were two major problems with the Masters-Pillans generic classification. Firstly, it did not effectively summarize the new anatomical and palynological data, and so was not natural in a phenetic sense. Secondly, many of the genera were clearly based on plesiomorphic features, and so could not be monophyletic. In 1984, Linder proposed a new generic classification, incorporating a much wider data base than had previously been used—including anatomical (Gilg 1891; Cutler 1969), palynological (Chanda 1966; Chanda & Rowley 1967; Linder & Ferguson 1985), and phytochemical (Harborne & Clifford 1969; Harborne 1979; Harborne *et al.* 1985) data in addition to morphology. He also attempted to define monophyletic genera. However, this classification still contained problems. Firstly, the data sampling was not complete, and the eventual classification proposed was based on the congruence of partial data-set-specific cladograms. Secondly, for

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MS. received: 2009-09-23.

several genera, no explicit morphological or anatomical synapomorphies could be identified, and so these genera could not be justified in a classic Hennigian sense. The first set of problems was in the *Elegia* clade, where *Chondropetalum* lacked synapomorphies. Moline & Linder (2005) solved this problem by combining *Chondropetalum*, *Elegia* and *Dovea*. The next set of problems was in the *Restio* clade. Under *Restio*, Linder noted: 'However, it is still not possible to demonstrate that *Restio*, as delimited here, is monophyletic'. Under *Calopsis*, Linder noted: 'the exact boundary between *Restio* and *Calopsis* is not yet resolved'. These problems remain unresolved.

Recently, Hardy *et al.* (2008) published an almost completely sampled phylogeny of the African Restionaceae (subfam. Restionoideae), expanding the previously published phylogeny for the nested *Elegia* group (Moline & Linder 2005) to include a complete species sampling of the entire tribe Restioneae (Figures 1–5). This study corroborated earlier indications from a much more sparsely sampled phylogeny (Eldenäs & Linder 2000) that several genera were para- or polyphyletic. It also provided the sampling density that enabled a test of the monophyly of all previously recognized genera, as well as the discovery of many new clades, some of which warrant description as new taxa. As such, the objective of this article is to integrate this new information into a revised generic classification of the Restioneae. In order to facilitate the use of the new generic classification, we list the species accepted under each genus and subgenus, and we simultaneously make all necessary new combinations, and formally describe several as yet undescribed species.

DELIMITING GENERA

Theoretical criteria

The criteria for the circumscription and ranking of genera have received little attention and most authors simply indicate that they follow the criteria proposed by Backlund & Bremer (1998). These were expanded by Humphreys & Linder (2009), who argued for larger genera, more consistent with the generic concept used by Bentham & Hooker in *Genera plantarum*. Thus, genera are not necessarily the smallest monophyletic or diagnosable groups. These, they suggest, may be better recognized by formal infrageneric taxa. Our classification that follows represents our attempt to optimize our adherence to the following criteria: 1, monophyly; 2, diagnosability; 3, nomenclatural stability; and 4, informativeness.

1. Monophyly. All genera and subgenera recognized here, were resolved as (potentially) monophyletic (i.e. as clades) by Hardy *et al.* (2008; summarized in Figures 1–5). Monophyletic taxa contain a closed segment of evolutionary history; therefore, such taxa can be expected to have a much greater predictive power than taxa that are not monophyletic. Furthermore, monophyletic taxa are more comparable for evolutionary studies or conservation efforts which seek to account for phylogenetic diversity in addition to species diversity in management decisions.

However, in this context monophyly refers to the 'true' phylogeny. The data collected by phylogeneticists only allow us to estimate this phylogeny. These estimates con-

tain several sources of error, two of which are pertinent to our study. Firstly, different genome partitions may reflect different phylogenetic histories (Doyle 1992; Maddison 1997). Such incongruent phylogenetic histories may result from the transfer of a chloroplast from one species to another during hybridization. In this case, a phylogeny based on the chloroplast plastid genome may not reflect the phylogeny of the nuclear genome. The second error may occur when stochastic variation in DNA base pairs results in the retrieval of clades. In this case, the shared DNA base pairs that lead to the retrieval of a clade are not the result of a common history. An extreme, and possibly quite rare form of this phenomenon results in long branch attraction (Felsenstein 1978). Much more common are nodes with relatively little statistical support.

The phylogenetic inferences of Hardy *et al.* (2008) were based on both parsimony and Bayesian analysis of a moderately large dataset consisting of plastid DNA sequences (± 7.3 Kb) and 150 morphological and anatomical characters for all 292 species and subspecies of the Restioneae. The robustness of these inferences, however, is limited by the inability of Hardy *et al.* (2008) to successfully generate nuclear DNA sequences. As such, the phylogenetic inferences of Hardy *et al.* (2008) were strongly influenced by evolutionary history of the plastid genome which, because of problems associated with phenomena such as introgressive hybridization (e.g. chloroplast capture) or lineage sorting, may not faithfully reflect the organismal phylogeny in all aspects (Doyle 1992; Maddison 1997). Additionally, a plastid-specific bias or imbalance in molecular evolutionary rates across the phylogeny could result in phylogenetic error unchecked by another, unlinked nuclear DNA dataset (e.g. Felsenstein 1978; Doyle 1992). Although the morphological and anatomical data are thought to provide phylogenetic signal under the influence of the nuclear genome and therefore independent of the plastid dataset, the relatively large size of the plastid dataset may have had a disproportionate influence on the resulting phylogenetic inferences. However, because the addition of our morphological data to the plastid data in a combined analysis resulted in increased support (via bootstrap and posterior probabilities) for most clades than did either data set alone (Hardy *et al.* 2008), we are confident that the phylogeny is a good approximation of the species phylogeny.

A second problem with our phylogeny is that several of the deeper nodes from the strict consensus trees have very low bootstrap support. This could mean that these nodes will not be retrieved if a larger dataset were to be generated.

2. Diagnosability. In addition to monophyletic groups, we sought to recognize genera that were diagnosable morphologically. Essential and differential morphological attributes can also be used for the assignment of species to the genera, and to develop a morphological concept of a genus. These characters were sought by using the parsimony options in Mesquite (Maddison & Maddison 2003) to optimize the morphological and anatomical character matrix used in Hardy *et al.* (2008; available at <http://herbarium.millersville.edu/pubs-support.php>) over the complete cladogram from Hardy *et al.* (2008). We defined as diagnostic characters those character states that were optimized to the crown-node (base) of each clade that could be treated as a genus or subgenus, i.e. we ignored variation

within the clade. We then coded these diagnostic characters (Table 1) for the clades into a new matrix (Table 2) and then mapped them onto a summary tree of the clades (Figure 1) using CLADOS (Nixon 1993). Morphological concepts and states were largely as used by Linder (1984), and are explained, illustrated, and fully documented in the interactive key to the species (Linder 2001a) (<http://www.systbot.uzh.ch/Bestimmungsschlüssel/Restionaceae.html>). Species for which molecular data were not available (20 out of 289) were placed on the basis of morphological and anatomical data, by their inclusion in a cladistic analysis with the full data set. Essential and differential morphological and anatomical attributes were extracted from the morphological data set for each postulated clade. Essential attributes are typical (albeit sometimes with exceptions) of each clade, but not unique to it. Differential attributes, often as combinations of characters, are unique to each clade, and can be used to diagnose the clades. Differential attributes can be used to assign previously unstudied species to their appropriate clades.

A second important component of diagnosability is the ability of users to be able to assign species to the right genus without too complex a procedure, ideally even without having to use a hand-lens. Thus diagnosability that is only possible on anatomical attributes is not optimal.

3. Nomenclatural stability. Genera should be recognized at nodes that will minimize nomenclatural changes. Nomenclatural changes fall into three elements. Firstly, minimizing the number of new combinations: these are most common when genera are divided into segregate genera; in these instances the specific epithet stays the same. Secondly, reducing the number of new names that need to be proposed: these are most common when genera are combined, and result when a specific epithet is already occupied; these are much more confusing than new combinations, as the species now has a completely

different name (both genus and species have changed). Thirdly, frequent changes in the combinations: this results when there is a frequent changing of the generic concepts. In some circumstances no new formal names are required, but from the user point of view there are still changes.

A second consideration should be not only to minimize the number of nomenclatural changes required, but also to consider the nomenclatural consequences of future changes in our understanding of the phylogeny. Ideally, genera should be erected at nodes which are likely to remain robust to future additional data, be it new species or new data sources. Theoretically, at least, larger genera should be less sensitive to smaller changes in the phylogenetic hypothesis.

4. Informativeness. Genera should have a morphological and ecological 'coherence', and not consist of mere collections of species that happen to share a plastid genome. This maximizes the number of attributes that we can assign to a genus, and makes the genus concept more useful.

Genera in the Restioneae

With the cladistic and morphological data available for the Restioneae, several generic classifications for the Restioneae are possible. In order to facilitate the discussion here, we refer to the names of clades described later in the paper.

1. The maximal option is to include the whole subtribe in one genus. This genus would be strongly supported as being monophyletic by the plastid data (Eldenäs & Linder 2000; Hardy *et al.* 2008), but would be difficult to diagnose, as the morphological characters separating Willdenowieae and Restioneae are cryptic anatomical and palynological attributes (Linder 1984), and the clade has no diagnostic attributes. The characters listed in Figure 1 as synapomorphies for the clade (the numbers of styles and carpels), should actually be listed under the Willde-

TABLE 1.—Selected generic and subgeneric characters mapped onto trees in Figure 1. Character numbers above branch and state of character below branch

1.	Culms: round or flattened = 0; square or angular = 1.
2.	Culms branching: simple = 0; branching = 1.
3.	Culms: round = 0; compressed = 1.
4.	Sheaths apical half: as lower part = 0; membranous and decaying = 1.
5.	Membranous sheath shoulders: absent = 0; present = 1.
6.	Sheaths: persistent = 0; caducous = 1.
7.	Floral bract apices: like body = 0; with hollow cells = 1.
8.	Floral bracts: overtopping flowers = 0; shorter than flowers = 1.
9.	Floral bracts: chartaceous, cartilaginous or bony = 0; membranous = 1.
10.	Floral bracts transverse pitting: absent = 0; present = 1.
11.	Male spikelets: erect = 0; pendulous = 1.
12.	Anthems at anthesis: exerted from flowers = 0; included in the flowers = 1.
13.	Female tepals (indumentum): glabrous = 0; villous = 1.
14.	Female tepals (texture): papery (flexible, not transparent) = 1; bony or cartilaginous (stiff) = 2.
15.	Female lateral tepals: as odd tepal = 0; conduplicate = 1; winged = 2. [additive].
16.	Number of styles: 1 = 0; 2 = 1; 3 = 2. [additive].
17.	Styles: free or on a stylopodium = 0; fused to form a peg = 1.
18.	Number of ovary locules: 1 = 0; 2 = 1; 3 = 2. [additive].
19.	Ovary: dehiscent = 0; indehiscent = 1.
20.	Central ground tissue cavities: none = 0; single = 1; many = 2. [additive].

TABLE 2.—Matrix-representation of distribution of diagnostic or distinctive characters from Table 1 for proposed genera and subgenera of tribe Restioneae. Polymorphism codes as follows: A = states 0 and 1; B = states 1 and 2; C = states 0 and 2

	1	5	10	15	20
Willdenowieae	0	1	0	0	0
Soroveta	0	1	0	0	0
Platycaulos	0	1	0	0	0
Elegia	0	0	0	0	0
Staberoha	0	0	0	0	0
Askidiosperma	0	0	0	0	0
Thamnochortus	0	0	0	0	0
Rhodocoma	0	0	0	0	0
Restio subgen. Calopsis	1	1	0	0	0
Restio subgen. Craspedolepis	0	1	0	0	0
Restio subgen. Eremorestio	0	1	0	0	0
Restio subgen. Ischyrolepis	0	1	0	0	0
Restio subgen. Locopsis	0	1	0	0	0
Restio subgen. Pendulostemon	0	1	0	0	0
Restio subgen. Restio	0	1	0	0	0
Restio subgen. Simplicaulos	0	0	0	0	0
Restio subgen. Varirestio	0	1	0	0	0

nowieae—the Restioneae have the ancestral condition of three styles and three carpels. The genus would not be exceptionally large (some 300 species), but would be morphologically very heterogeneous. It would require numerous name changes, and would lose on informativeness, as several very distinct genera, such as *Elegia*, *Thamnochortus* and *Staberoha*, would be lost. This broad approach has been followed in several Cape taxa, such as *Erica* (Oliver 2000) and *Disa* (Bytebier *et al.* 2007, 2008).

2. The minimal option is to retain all existing genera that were retrieved as monophyletic (i.e. *Askidiosperma*, *Elegia*, *Ischyrolepis*, *Platycaulos*, *Rhodocoma*, *Staberoha* and *Thamnochortus*), and split the remainder up into the smallest number of genera based on clades with at least 70 % bootstrap support (named in Figures 1–5 as *Restio* subgen. *Calopsis*, *Restio* subgen. *Craspedolepis*, *Restio* subgen. *Eremorestio*, *Restio* subgen. *Locapsis*, *Restio* subgen. *Pendulostemon*, *Restio* subgen. *Restio*, *Restio* subgen. *Simplicaulos*, *Restio* subgen. *Variestio* and *Soroveta*). Note that *Platycaulos* is here somewhat unusual, as this genus receives several species misplaced to *Restio* in the previous classifications. The recognition of more than one genus in the tribe implies that the basal branch leading to *Restio ambiguus* has to be recognized at generic level (as the genus *Soroveta*), as the node excluding this species from the rest of the tribe is very strongly supported. This results in 16 genera, all of which are strongly supported as being monophyletic by the combined plastid DNA and morphological datasets, but not all by the morphological dataset alone. There are great difficulties in diagnosing several of these clades. In some instances no essential or differential characters could be found (e.g. *Restio* subgen. *Variestio*), in others (e.g. *Restio* subgen. *Craspedolepis*, *Restio* subgen. *Eremorestio*, *Restio* subgen. *Locapsis*, *Restio* s.str., *Restio* subgen. *Simplicaulos*) there are essential but no differential characters, i.e. they also occur in other genera albeit relatively rarely. As a result we can have a vague concept of the genus, but cannot key it out. Predictably, these smaller genera are mostly morphologically quite homogeneous. This approach requires more than 70 new combinations, but no new names.

The advantage of this approach is that the monophyly of all genera is strongly supported by the available phylogenetic hypothesis. However, there are two problems. The first is that the generic classification will not be user friendly, as it will be difficult to assign species to the genera, either in the field or in a herbarium. Secondly, there is a very heavy reliance on plastid data in the absence of nuclear DNA data (Doyle 1992). Any mistakes in the phylogeny will result in generic redelimitation.

3. The intermediate option is to retain all existing genera that are not proven to be para- or polyphyletic, and not to start with the assumption that all existing genera that are retrieved as monophyletic have to be retained. In this option, the distinctive and well-supported genera *Askidiosperma*, *Elegia*, *Platycaulos*, *Rhodocoma*, *Soroveta*, *Staberoha* and *Thamnochortus* are retained, and a larger *Restio* s.lat. is assembled. The major advantage of this option is that the two difficult segregates, *Eremorestio* and *Variestio*, will not be recognized as distinct genera. Due to the structure of the phylogeny, in all these solutions, *Ischyrolepis* will need to be included in *Restio* s.lat., together with most species of *Calopsis*, as the nodes embedding

these two genera within *Restio* s.lat. are strongly supported in the combined analysis. In the morphological phylogeny of Linder (1984) *Ischyrolepis* was not included in the *Restio*–*Calopsis* clade, due to its very different pollen morphology. A major insight from the molecular phylogeny is that the pollen data are not phylogenetically conservative, as a result *Ischyrolepis* is found to be nested in the *Restio*–*Calopsis* clade. Three variants of *Restio* s.lat. can be proposed:

3a. Include *Calopsis* s.str., *Craspedolepis*, *Eremorestio*, *Ischyrolepis*, *Locapsis*, *Pendulostemon*, *Restio* s.str., *Simplicaulos* and *Variestio* in one genus. There is weak evidence that this grouping is paraphyletic: in the combined phylogeny, but with no bootstrap support, *Pendulostemon* groups with the *Thamnochortus*–*Rhodocoma* clade, and *Simplicaulos* with *Staberoha*). This large genus is easy to diagnose by exclusion (not *Rhodocoma*, *Thamnochortus*, *Soroveta*, *Platycaulos*, *Elegia* or *Askidiosperma*). It is the most conservative approach, requiring statistically significant evidence to dismantle a genus. The disadvantage of this classification is that there is no evidence for the monophyly of the genus *Restio* s.lat. (but also no evidence that it is not monophyletic). The advantage is that the genus is easy to recognize in the field and herbarium and that it is nomenclaturally conservative (if eventually there is sufficient evidence that to separate *Simplicaulos* and *Pendulostemon* will not require undoing a set of nomenclatural changes). The strongly supported monophyletic units can then be recognized as subgenera of *Restio* s.lat., these should be used for evolutionary investigations.

3b. As above, but retain *Simplicaulos* and *Pendulostemon* as distinct genera on the basis that there is weak evidence linking these to *Staberoha* and *Thamnochortus* respectively. It removes all evidence that *Restio* s.lat. could be paraphyletic, but there is also no evidence that the remaining *Restio* s.lat. is monophyletic. *Pendulostemon* can be readily diagnosed, but *Simplicaulos* lacks differential characters. The most important attribute is the unbranched culms: this is a highly variable character. The advantage is that no genera are recognized for which there is (even poorly supported) evidence for paraphyly. The disadvantages are two-fold: due to the low support values, it remains possible that additional datasets will group the two segregates again with *Restio* s.lat., leading to name changes. Furthermore, one of the two segregate genera cannot be keyed out.

3c. Recognize, in addition to *Simplicaulos* and *Pendulostemon*, also *Craspedolepis*. This leaves the rest of *Restio* s.lat. with positive (albeit weak) evidence of its monophyly, but it adds another genus that is difficult to diagnose. Frustratingly, *Craspedolepis* does have a striking essential character, a band of hollow (concave) cells at the apical margins of the floral bracts, but this is in some species poorly developed, and also occurs in a few species outside the genus. It is thus of little use as a differential character.

We follow here option 3a, which recognizes eight genera in the tribe. The eight strictly monophyletic segregates of *Restio* s.lat. are recognized as subgenera. We hope that this will combine the need for strictly monophyletic taxa for evolutionary analysis (the subgenera),

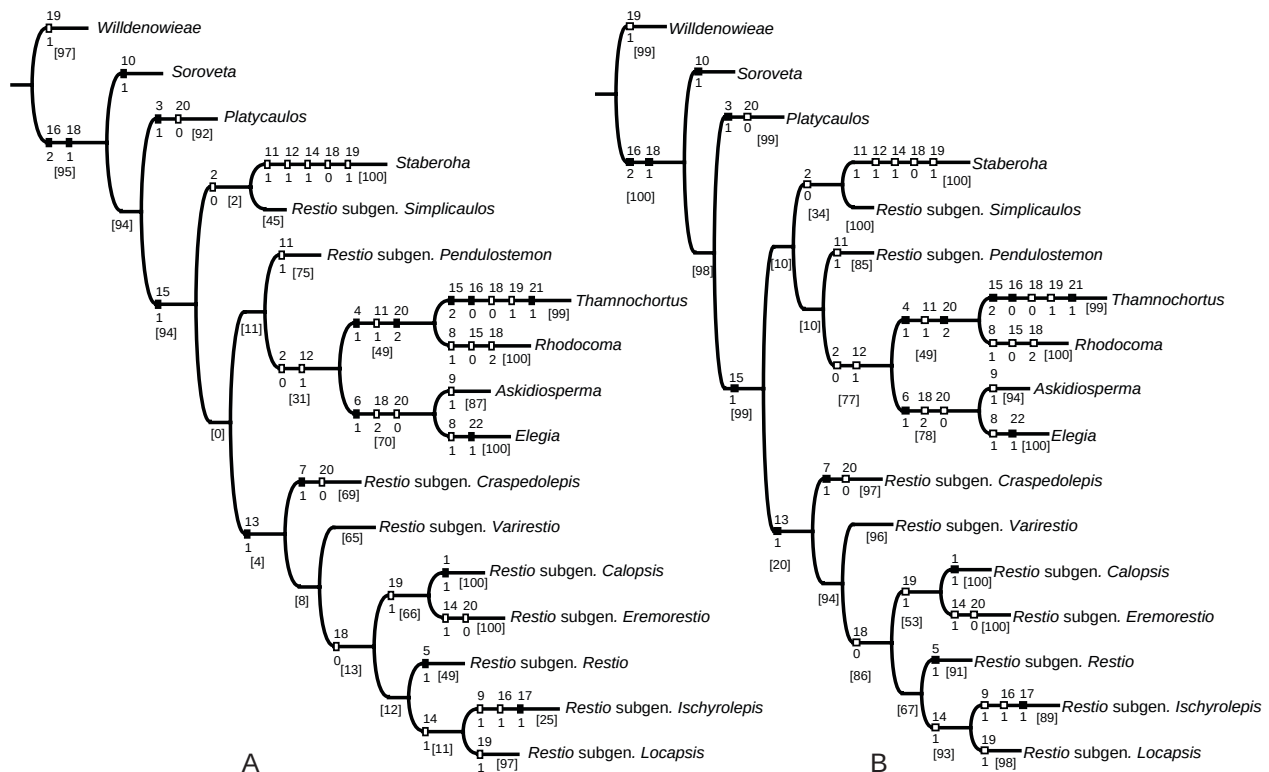


FIGURE 1.—Cladograms summarizing generic and subgeneric relationships in the Restioneae (Hardy *et al.* 2008). A, relationships in the strict consensus tree from the analysis of all 292 species and subspecies. B, relationships in the strict consensus tree from the analysis of 272 species and subspecies omitting 20 species/subspecies for which DNA data were lacking. Bootstrap percentage values (in square brackets) are based on the analysis of Hardy *et al.* (2008). Characters from Tables 1 and 2 are optimized using the *slow* (deltran) options in WinClada: the character number appears above the solid and open squares. The state of the character appears below the solid and open squares. An open square indicates a character that evolved at least twice, whereas a solid square indicates a character that evolved only once.

with easy-to-recognize, nomenclaturally stable genera. It is important, though, that no taxa that are demonstrably para- or polyphyletic be recognized.

TAXONOMY

The full nomenclature and synonymy of the species is not repeated: it was published in 1985, consequently only the accepted species and their place of publica-

tion is given. However, for the new combinations, the basionym and the type is indicated, as required. Again no full synonymy is presented. The complete synonymy, descriptions, illustrations to all species, and an interactive key is available online at <http://www.systbot.uzh.ch/Bestimmungsschlüssel/Restionaceae.html>, or can be bought as a CD from the Bolus Herbarium, University of Cape Town. The species are presented in a 'natural' sequence, partially based on the phylogeny, partially based on their similarity.

Artificial key to genera of Restioneae

- 1a Floral bracts reddish brown, bony, with transverse lacunae 1. *Soroveta*
- 1b Floral bracts pendulous, always without transverse lacunae:
- 2a Male spikelets pendulous:
- 3a Ovary indehiscent; diaspore a nut enclosed in a persistent, papery to cartilaginous, perianth, which may be winged:
- 4a Male spikelets linear-oblong; female flowers with a single style exerted from floral bracts; perianth a firm winged or keeled structure; sheaths decaying in upper half 4. *Thamnochortus*
- 4b Male spikelets ± globose; females with 1–3 styles obscured behind floral bracts; perianth papery, sometimes keeled; sheath apical margins firm, persistent 3. *Staberoha*
- 3b Ovary dehiscent; diaspore a seed:
- 5a Culms branching; female floral bracts taller than flowers, often with longitudinal striations 8.2 *Restio* subgen. *Pendulostemon*
- 5b Culms simple (except for *R. capensis*, where culms have whorled branches); female floral bracts shorter than flowers, never with longitudinal striations 5. *Rhodocoma*
- 2b Male spikelets erect:
- 6a Sheaths falling off, sometimes somewhat tardily so, leaving a distinct dehiscence ring:
- 7a Floral bracts membranous, much taller than flowers; ovary dehiscent or tardily indehiscent 7. *Askidiosperma*
- 7b Floral bracts leathery to bony, rarely taller than flowers, mostly shorter; ovary either dehiscent or indehiscent 6. *Elegia*
- 6b Sheaths persistent:
- 8a Culms laterally compressed (sometimes only at apex); sheaths with stout mucro, both same green colour as culm, usually with woolly scale in sheath axils 2. *Platycaulos*

- 8b Culms round; if laterally compressed then sheaths brown, clearly different from culm, and without woolly scales:
- 9a Female inflorescences of numerous poorly organized spikelets arranged at several nodes; bracts not obscuring flowers; spathes much overtopping groups of spikelets at nodes 6. *Elegia*
- 9b Female inflorescences of one to many well-organized spikelets, either racemously or paniculately organized; bracts mostly obscuring flowers; spathes at most as tall as spikelets (*Restio* s.lat.):
- 10a Culms square or otherwise angular in cross section; plants 1 m or taller; inflorescences large, paniculate, with very numerous spikelets 8.5 *Restio* subgen. *Calopsis*
- 10b Culms round, terete or compressed (flattened) in cross section; plants variable in height, but often less than 1 m; inflorescence rarely very large:
- 11a Style branches two, fused below into persistent styler peg; ovary always dehiscent 8.9 *Restio* subgen. *Ischyrolepis*
- 11b Style branches 1, 2 or 3, never fused into persistent styler peg; ovary either dehiscent or indehiscent:
- 12a Culms simple 8.1 *Restio* subgen. *Simplicaulos*
- 12b Fertile culms branched:
- 13a Floral bracts with upper margin markedly different from bract body, consisting of hollow cells; ovary usually bilocular, dehiscent 8.3 *Restio* subgen. *Craspedolepis*
- 13b Floral bracts without such upper margins; ovary various:
- 14a Female perianth papery, truncate or rounded; ovary indehiscent, unilocular:
- 15a Female floral bracts acuminate, apices somewhat recurved, darker than bract body; sheaths always tightly rolled around culms; nuts triangular, more than 2 mm long 8.6 *Restio* subgen. *Eremorestia*
- 15b Female floral bracts acute, apices erect, same colour as body of bracts; sheaths mostly spreading, sometimes tightly rolled around the culms; nuts various 8.8 *Restio* subgen. *Locapsis*
- 14b Female perianth coriaceous or bony, acute; ovary indehiscent or dehiscent, with 1, 2, or 3 locules:
- 16a Ovary with 1 or 3 locules; sheath awn sometimes as long as sheath; sheaths with poorly developed membranous lobes 8.4 *Restio* subgen. *Variorestia*
- 16b Ovary with 1 or 2, rarely 3 locules; sheath awn shorter than sheath 8.7 *Restio* subgen. *Restio*

Soroveta–*Platycaulos* grade

An expanded *Platycaulos* and the newly erected genus *Soroveta* H.P.Linder & C.R.Hardy, gen. nov., comprise a relatively species-poor grade within the Restioneae that is paraphyletic to the remainder of the Restioneae (Figures 1–5). The monotypic *Soroveta* is rather isolated and does not share any particularly striking morphological characteristics with *Platycaulos*. Perhaps their greatest resemblances lie in their native habitats, where both characteristically grow in areas of impeded drainage or summer rainfall, although the two genera do not co-occur.

1. ***Soroveta*** H.P.Linder & C.R.Hardy, gen. nov., ab aliis generibus tribus Restioneae bracteis floralibus transversaliter foveatis et combinatione vaginorum persistentium cum tepalis uniformibus distinguendum.

TYPE.—*Soroveta ambigua* (Mast.) H.P.Linder & C.R.Hardy.

Plants clumped. *Fertile culms* sparsely branched, round; sheaths persistent, closely convoluted, margins coriaceous, without hyaline shoulders. *Male inflorescence* racemose; spikelets 1–5, erect, several-flowered; spathes persistent, shorter than spikelets; bracts dark brown, with transverse pitting; anthers exserted from flowers. *Female inflorescence* and spikelets similar to males, with 1–5 linear or oblong, acute, 2–8-flowered spikelets; flowers not laterally compressed; tepals chartaceous or cartilaginous, scabrid all over, outer lateral tepals not differentiated from outer odd tepal; staminodes present. *Gynoeceum* with 3 white, feathery styles free to base; ovary bilocular, dehiscent. *Seed* brown, pitted. *Culm anatomy*: epidermal cells single-layered, lateral radial wall straight, unthickened; chlorenchyma two-layered, stomatal cavities with protective cells; parenchymatous layer between chlorenchyma and sclerenchyma of 3–5 cells; central ground tissue with single, central cavity; tannin and silica absent.

Etymology: *Soroveta* (f.): *soror* (Latin: f., III), sister; *vetus* (Latin), ancient; referring to the topological

position of the genus, as the sister to the rest of Restioneae (Figure 2).

Notes: the isolated position of this species was already recognized by Masters (1897) who gave it the very prescient specific epithet. Morphologically, the species shows several unusual features in the male and female inflorescences, notably resembling *Elegia* in the naked female flowers without any lateral (dorsiventral) flattening, but without the caducous sheaths and other attributes typical of that clade. Furthermore, the dark brown floral bracts with transverse pitting are unique in the subfamily. However, there are no obvious synapomorphies for the rest of the Restioneae, consequently the basal position of this species cannot be detected morphologically. In the absence of molecular data, the species would probably have been retained as a highly specialized species of *Restio*.

1.1. ***Soroveta ambigua*** (Mast.) H.P.Linder & C.R.Hardy, comb. nov.

Restio ambiguus Mast. in Flora capensis 7: 96 (1897). Type: Cape, s.loc., Zeyher s.n. (K, holo.!, B!).

2. ***Platycaulos*** H.P.Linder in Bothalia 15: 64 (1984). Type: *Platycaulos compressus* (Rottb.) H.P.Linder.

Plants tufted, tangled or mat-forming. *Fertile culms* branching, more or less compressed, though sometimes only near apex; sheaths persistent, with no abscission line, closely convoluted, usually densely textured and same colour as culms, apical margins narrowly membranous, continuing behind the stout, awl-like awn. *Male inflorescence* racemose or paniculate with up to 20 sessile or stiffly erect, often distichous spikelets; spathes persistent or caducous; male bract with upper margin like body of bract; anthers exserted from flowers. *Female inflorescence* with 1–10 spikelets; spikelets 1–15-flowered, variously shaped; bracts at least as tall as flowers, often much taller, mostly cartilaginous, apical margin like rest of bract; imbricate and obscuring spikelet axis; tepals chartaceous or cartilaginous, glabrous or keels of lateral sepals villous; staminodes present. *Gynoeceum* with 3 white, feathery styles free to base; ovary with 1 or 2 fer-

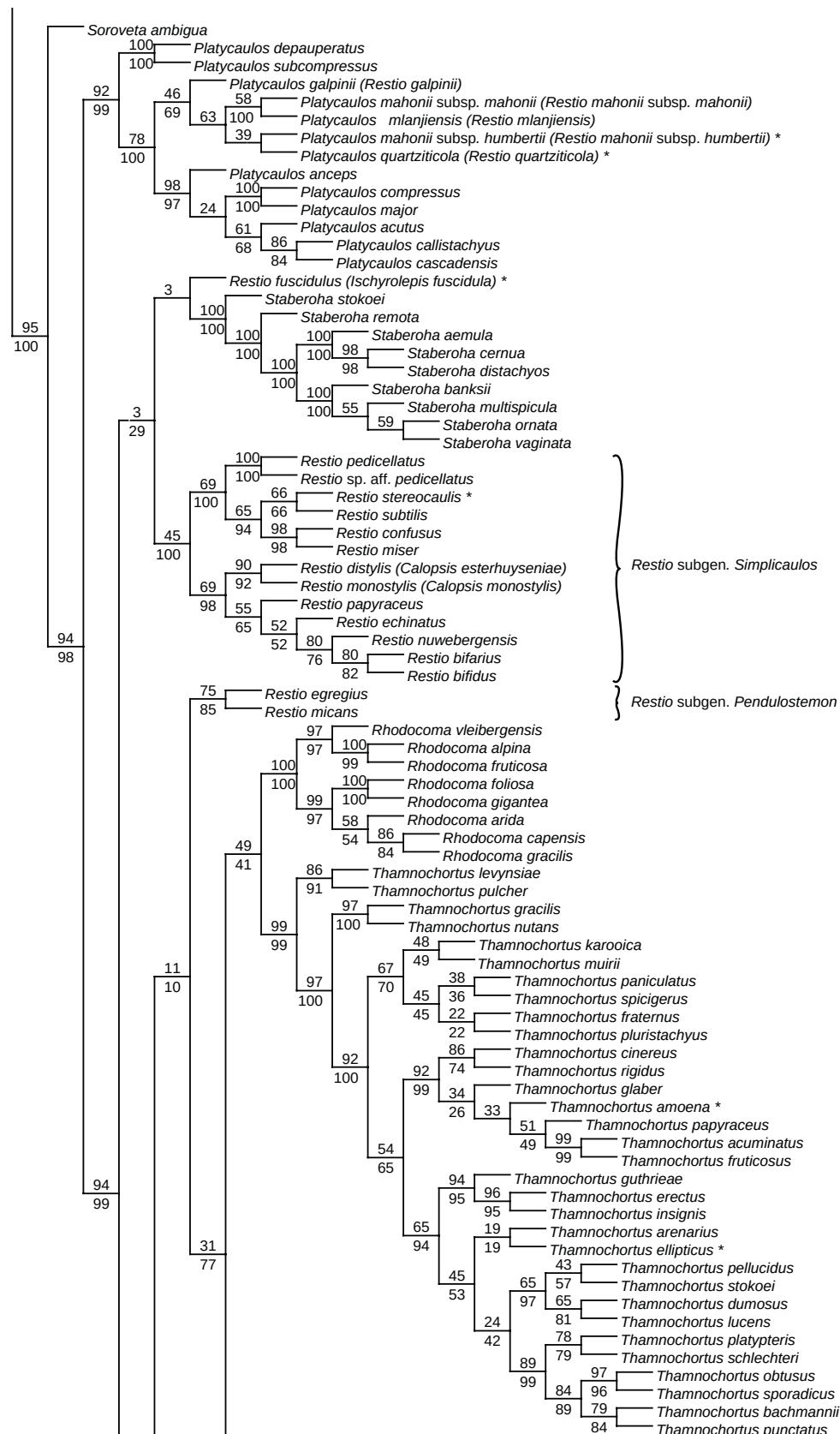


FIGURE 2.—Portion of strict consensus tree of total combined analysis of all species by Hardy *et al.* (2008) containing *Soroveta*, *Platycaulos*, *Staberoha*, *Restio* subgen. *Simplicaulos*, *Restio* subgen. *Pendulostemon*, *Rhodocoma*, and *Thamnochortus*. Names in parentheses are the now synonymous names of Linder (2001a) when different from the ones here proposed. A single species of *Restio* subgen. *Ischyrolepis* (*Restio fuscidulus*) that was missing many data (including all molecular data), was resolved in this tree as sister to *Staberoha*, albeit with 3 % bootstrap support which we do not consider substantial enough to warrant disputing the monophyly of *Restio* subgen. *Ischyrolepis* or the genus *Restio* as circumscribed here. Bootstrap values above branches indicate support based on a 500-replicate bootstrap analysis that included 20 species for which DNA data were lacking (asterisked taxa). Bootstrap values below branches indicate support based on an analysis that excluded these morphology-only taxa. Where no value is given below a branch, it indicates that the clade did not appear in the analysis excluding morphology-only species.

tile, dehiscent locules. *Seed* brown, black, white or tan, with brittle white ornamentation or rarely rugose. *Culm anatomy*: epidermal cells in 1 layer, lateral wall straight, unthickened; parenchymatous layer of 1–4 cells; central ground tissue without cavity; tannin absent or present in epidermis, sclerenchyma or central ground tissue; silica absent.

Etymology: *Platycaulos* (m.): *platys* (Greek), broad, flat; *kaulos* (Greek), stalk; referring to the compressed culms typical of this genus.

Notes: the genus was separated from *Restio* by Linder in 1984, based on a range of morphological, anatomical and palynological attributes. At the time, Linder did not realise that these features were also visible in the tropical species (now included below via new combinations), albeit in a less than obvious fashion. Fortunately, the taxon's namesake attribute, the more or less compressed culms, is also found in the tropical species, therefore the generic name remains appropriate. Almost all species are found in habitats with impeded drainage or summer rainfall.

2.1. ***Platycaulos depauperatus* (Kunth) H.P.Linder** in *Bothalia* 15: 436 (1985).

2.2. ***Platycaulos subcompressus* (Pillans) H.P.Linder** in *Bothalia* 15: 347 (1985).

2.3. ***Platycaulos galpinii* (Pillans) H.P.Linder & C.R. Hardy**, comb. nov.

Restio galpinii Pillans in Transactions of the Royal Society of South Africa 30: 250 (1945). Type: Natal, Underberg, between Cathkin Peak and Giants Castle, *Esterhuysen 8820* (BOL, lecto.! [Linder in *Bothalia* 15: 447 (1985)], K!, NBG!, NY).

2.4a. ***Platycaulos mahonii* (N.E.Br.) H.P.Linder & C.R. Hardy** subsp. ***mahonii***, comb. nov.

Hypolaena mahonii N.E.Br. in Flora of tropical Africa 8: 265 (1901). *Restio mahonii* (N.E.Br.) Pillans: 255 (1945). Type: Malawi, Southern Province, Mt Zomba, *Mahon s.n.* (K, holo.!; B!, BOL!).

2.4b. ***Platycaulos mahonii* (N.E.Br.) H.P.Linder & C.R.Hardy** subsp. ***humbertii* (Cherm.) H.P.Linder & C.R. Hardy**, comb. nov.

Restio madagascariensis Cherm. var. *humbertii* Cherm. in Archives de Botanique, Bulletin Mensuel, Caen 7: 85 (1930). *R. mahonii* (N.E.Br.) Linder subsp. *humbertii* (Cherm.) H.P.Linder: 103 (1986). Type: Madagascar, massif de l'Andohahelo, *Humbert 6147* (P, holo.!; B!, K!, NY).

2.5. ***Platycaulos mlanjensis* (H.P.Linder) H.P.Linder & C.R.Hardy**, comb. nov.

Restio mlanjensis H.P.Linder in Kew Bulletin 50: 623 (1995). Type: Malawi, Mt Mlanje, Sombani, *Verboom, Pauw & Hooks 1* (BOL, holo.!; K!, MAL!, MO!, NSW!, PRE!, S!, SRGH!, WAG!, Z!).

2.6. ***Platycaulos quartziticola* (H.P.Linder) H.P.Linder & C.R.Hardy**, comb. nov.

Restio quartziticola H.P.Linder in Kew Bulletin 41:103 (1986). Type: Zimbabwe, Chimanimani Mts, *Whellan 1252* (K, holo.!; BOL!, BR, LISC, SRGH!).

2.7. ***Platycaulos compressus* (Rottb.) H.P.Linder** in *Bothalia* 15: 436 (1985).

2.8. ***Platycaulos major* (Mast.) H.P.Linder** in *Bothalia* 15: 436 (1985).

2.9. ***Platycaulos anceps* (Mast.) H.P.Linder** in *Bothalia* 15: 436 (1985).

2.10. ***Platycaulos acutus* Esterh.** in Linder in *Bothalia* 15: 434 (1985).

2.11. ***Platycaulos cascadiensis* (Pillans) H.P.Linder** in *Bothalia* 15: 436 (1985).

2.12. ***Platycaulos callistachyus* (Kunth) H.P.Linder** in *Bothalia* 15: 436 (1985).

Staberoha–Elegia clade

Although molecular support for this clade is poor (see also Hardy *et al.* 2008), this clade makes sense morphologically, based largely on its combination of glabrous, conduplicate tepals and, mostly, simple, unbranched culms. Interestingly, the species in the family with pendulous male spikelets (e.g. *Staberoha*, *Thamnochortus*, *Rhodocoma*, *Restio* subgen. *Pendulostemon* H.P.Linder & C.R.Hardy subgen. nov.) all occur in this clade, suggesting that pendulous male spikelets are either plesiomorphic or have evolved repeatedly in parallel within the clade.

Within this clade, the association between *Staberoha* and *Restio* subgen. *Simplicaulos* H.P.Linder & C.R.Hardy subgen. nov. (Figure 2) is weak, and an alternative position is for *Simplicaulos* to be sister to *Elegia*, and for *Staberoha* to occupy an isolated position (Hardy *et al.* 2008). The two taxa may be linked morphologically by their simple culms, but that could be plesiomorphic in the whole clade, with a reversal in *Restio* subgen. *Pendulostemon*. Many species in these two taxa also have large female bracts that completely obscure the female flowers.

Restio subgen. *Pendulostemon*, consisting of just two species, is both phylogenetically and morphologically isolated in the clade. In particular, the branching culms of this genus are unusual for the clade, although species with branching culms also occur occasionally in *Elegia* and *Thamnochortus*.

The *Thamnochortus–Rhodocoma* subclade was previously recognized by Linder (1984). The two genera share pendulous male spikelets (also present in *Staberoha* and *Restio* subgen. *Pendulostemon*), scattered cavities in the central ground tissue, and sheaths of which the upper half is more or less membranous and soon decays. The genera have very different gynoeceia: in *Rhodocoma* the ovaries are dehiscent, and the diaspore is a seed, whereas in *Thamnochortus* the ovaries are unilocular and indehiscent, and the fruit a soft-walled nut, included in an often widely winged, persistent perianth.

The *Elegia–Askidiosperma* subclade also dates back to the morphological phylogeny of Linder (1984), and is recognized by the caducous, or when persistent, poorly structured sheaths, and the inflorescences with numerous partial panicles originating from several nodes along a central axis. Furthermore, the tepals are quite bony, with generally no differentiation between the lateral and odd tepals. The central ground tissue lacks a cavity. *Elegia* is distinguished from *Askidiosperma* by a double-layered culm epidermis, whereas *Askidiosperma* is diagnosed by the very long, membranous bracts, and its more well-defined spikelets.

3. ***Staberoha* Kunth**, Enumeratio plantarum 3: 442 (1841). Lectotype: *Staberoha distachyos* (Rottb.) Kunth.

Plants caespitose or clumped. *Fertile culms* unbranched, round; sheaths persistent, closely or rarely loosely convoluted, margins usually like rest of sheath, rarely nar-

rowly or broadly membranous, but hyaline shoulders never developed. *Male inflorescence* paniculate with 1 to several $\pm$ globose spikelets, pendulous on flattened, flexible pedicels, rarely racemose and erect (*S. stokoei*); bracts much taller than flowers and completely obscuring them; tepals papery, lateral tepals keeled; anthers usually included in flowers at anthesis. *Female inflorescence* racemose with 1–5 linear, oblong, elliptical or ovate, erect spikelets, each with 6–25 flowers and no sterile bracts; female bracts at least twice as long as and obscuring flowers, imbricate. *Female flowers* laterally compressed; tepals mostly chartaceous, glabrous, outer lateral tepals flattened, keeled or winged; staminodes sometimes present. *Gynoecium* with 1–3, white, flattened styles obscured behind bracts at anthesis; style bases usually free or rarely seated on a stylopodium; ovary unilocular, indehiscent. *Fruit* a soft-walled nut dispersed with persistent, often winged, perianth. *Culm anatomy*: epidermal cells in 1 layer, lateral wall usually straight and unthickened, rarely sinuose and thickened; parenchymatous layer of 1–4 cells; central ground tissue rarely solid, usually with scattered cavities or a single, central cavity; tannin usually absent, if present usually restricted to epidermis; silica absent.

Etymology: *Staberoha* (f.): named after H. Staberoh, a medical doctor, pharmacist and experimentalist.

Notes: a very distinctive genus, almost restricted to the Western Cape, where often several species are found co-occurring. The ball-like, pendulous male spikelets and the small female flowers obscured behind the large female bracts allow an easy recognition of the genus. All species are found on well-drained soils, both on deep sandy soils (such as *Staberoha distachyos*) and on rocky slopes (*S. remota*). *S. stokoei* is a remarkable exception to many of the morphological attributes (the male spikelets are erect, and almost identical to the female spikelets), and is a geographically restricted species in the Great Swartberg, where it occupies almost vertical rock ledges on the upper south-facing slopes. It is satisfying to see that it occupies a topological position sister to the rest of the genus, indicating that many of the distinctive attributes of the genus evolved after the origin of the genus. If subdivision of the genus is appropriate, then *S. stokoei* could be regarded as one division, and the rest of the genus the second.

The pollen of this genus is unusual, with a thickened annulus, very similar to the pollen typical of the Poaceae (Linder & Ferguson 1985). Similar pollen is also found in *Restio* subgen. *Ischyrolepis*. In the morphological analysis by Linder (1984) this pollen played an important role in emphasizing the phylogenetically early branching position of *Staberoha*, but the molecular analysis indicates that this curious pollen type most likely evolved twice, independently, in the Restioneae.

3.1. ***Staberoha stokoei*** Pillans in Journal of South African Botany 18: 118 (1952).

3.2. ***Staberoha remota*** Pillans in Transactions of the Royal Society of South Africa 29: 351 (1942).

3.3. ***Staberoha aemula*** (Kunth) Pillans in Transactions of the Royal Society of South Africa 16: 386 (1928).

3.4. ***Staberoha cernua*** (L.f.) Dur. & Schinz, Conspectus florum africae 5: 520 (1894).

3.5. ***Staberoha distachyos*** (Rottb.) Kunth, Enumeratio plantarum 3: 444 (1841).

3.6. ***Staberoha banksii*** Pillans in Transactions of the Royal Society of South Africa 16: 385 (1928).

3.7. ***Staberoha multispicula*** Pillans in Journal of South African Botany 18: 117 (1952).

3.8. ***Staberoha ornata*** Esterh. in Linder in Bothalia 15: 396 (1985).

3.9. ***Staberoha vaginata*** (Thunb.) Pillans in Transactions of the Royal Society of South Africa 16: 384 (1928).

4. ***Thamnochortus*** P.J.Bergius, Descriptiones plantarum ex Capite Bonae Spei 353 (1767). Type: *Thamnochortus fruticosus* P.J.Bergius.

Plants caespitose or with spreading underground rhizomes. *Fertile culms* round and, except in two species, simple; sheaths persistent, closely convoluted, upper half broadly chartaceous and soon becoming lacerated, hyaline shoulders absent. *Male inflorescence* paniculate from one or several nodes, with up to 100 spikelets; spathes persistent; spikelets generally lorate to oblong, pendulous on flexible pedicels; bract margins like body of bract, much taller than and obscuring papery male flowers; anthers included in flowers at anthesis. *Female inflorescence* racemose or somewhat paniculate, with 1–100 erect, many-flowered, lorate to obtriangular spikelets; bracts taller than flowers with only stigmas visible at anthesis. *Female flowers* with glabrous and smooth tepals; outer lateral tepals strongly keeled or widely winged; staminodes usually absent. *Gynoecium* with solitary, white, plumose style; ovary unilocular, indehiscent. *Diaspore* an oblong to completely round, wind-dispersed structure; nut enclosed by persistent perianth. *Culm anatomy*: epidermal cells single-layered, lateral walls usually sinuose and thickened; parenchymatous layer of 1–4 cells; central ground tissue with scattered cavities; tannin present in epidermis, parenchyma, sclerenchyma or central ground tissue; silica mostly absent.

Etymology: *Thamnochortus* (m.): *thamnos* (Greek), bush, shrub; *chortus* (Greek), green herbage, grass, fodder.

Notes: mostly associated with more arid areas, especially in the northwestern Cape, along the coastal plains (*Thamnochortus bachmannii*), Nieuwoudtville (*T. platypteris*), but also typical of the wettest fynbos vegetation (*T. cinereus*). Also noted for the important thatching plants (*T. insignis*). The plants often form extensive stands, and can locally dominate the vegetation. Striking in some species are the widely winged, persistent perianths, making for efficient wind dispersal of the seed.

This genus is very clearly demarcated, and is very readily diagnosed by the slender, pendulous male spikelets, the closely convoluted sheaths with a decaying upper half, the many-flowered, erect female spikelets, and the single plumose style. The closest relative is *Rhodocoma*, with which it shares features of the culm anatomy and pollen structure, as well as the pendulous male spikelets. However, *Thamnochortus* has an indehiscent, unilocular ovary, whereas *Rhodocoma* has a dehiscent, three-locular ovary. In many ways this relationship is similar to that between *Chondropetalum* and *Elegia* s.str., but in the case of *Thamnochortus* there are no morphological intermediates and there is strong

molecular evidence for the reciprocal monophyly of the two genera.

The biogeography and evolution in this genus was investigated by Linder & Mann (1998). It is possible to assign the species to five main groups, not all of which are monophyletic (Figure 2).

a) Basal grade: includes the only two species with branching culms:

- 4.1. **Thamnochortus levynsiae** Pillans in Transactions of the Royal Society of South Africa 16: 364 (1928).
- 4.2. **Thamnochortus pulcher** Pillans in Transactions of the Royal Society of South Africa 29: 350 (1942).
- 4.3. **Thamnochortus nutans** (Thunb.) Pillans in Transactions of the Royal Society of South Africa 16: 365 (1928).
- 4.4. **Thamnochortus gracilis** Mast. in A.DC., Monographiae phanerogamarum 1: 327 (1878).

b) Limestone clade: all species associated with limestones or coastal dunes, except *T. karoocica*:

- 4.5. **Thamnochortus karoocica** H.P.Linder in South African Journal of Botany 56: 450 (1990).
- 4.6. **Thamnochortus muirii** Pillans in Transactions of the Royal Society of South Africa 16: 366 (1928).
- 4.7. **Thamnochortus paniculatus** Mast. in Botanische Jahrbücher 29, Beiblatt 66: 12 (1900b).
- 4.8. **Thamnochortus spicigerus** (Thunb.) Spreng., Systema vegetabilium 1: 187 (1824).
- 4.9. **Thamnochortus fraternus** Pillans in Transactions of the Royal Society of South Africa 16: 370 (1928).
- 4.10. **Thamnochortus pluristachyus** Mast. in Botanische Jahrbücher 29, Beiblatt 66: 12 (1900b).

c) Big bract group: species with large, often silver-coloured female bracts:

- 4.11. **Thamnochortus cinereus** H.P.Linder in Bothalia 15: 473 (1985).
- 4.12. **Thamnochortus rigidus** Esterh. in Linder in Bothalia 15: 477 (1985).
- 4.13. **Thamnochortus glaber** (Mast.) Pillans in Transactions of the Royal Society of South Africa 16: 363 (1928).
- 4.14. **Thamnochortus papyraceus** Pillans in Transactions of the Royal Society of South Africa 29: 350 (1942).
- 4.15. **Thamnochortus amoena** H.P.Linder in South African Journal of Botany 56: 451 (1990).
- 4.16. **Thamnochortus acuminatus** Pillans in Transactions of the Royal Society of South Africa 29: 349 (1942).
- 4.17. **Thamnochortus fruticosus** P.J.Bergius, Descriptiones plantarum ex Capite Bonae Spei 353 (1767).

d) Thatching reed group: plants up to 2 m tall:

- 4.18. **Thamnochortus erectus** (Thunb.) Mast. in Journal of the Linnean Society, Botany 14: 419 (1874).
- 4.19. **Thamnochortus insignis** Mast. in Gardeners' Chronicle, ser. 3, 25: 242 (1899).

e) Typical group: mostly plants < 1 m tall, diaspores often round (as broad as long):

- 4.20. **Thamnochortus guthrieae** Pillans in Transactions of the Royal Society of South Africa 16: 371 (1928).

- 4.21. **Thamnochortus ellipticus** Pillans in Transactions of the Royal Society of South Africa 16: 368 (1928).
- 4.22. **Thamnochortus lucens** (Poir.) H.P.Linder in Bothalia 15: 475 (1985).
- 4.23. **Thamnochortus arenarius** Esterh. in Linder in Bothalia 15: 472 (1985).
- 4.24. **Thamnochortus sporadicus** Pillans in Journal of South African Botany 18: 116 (1952).
- 4.25. **Thamnochortus pellucidus** Pillans in Journal of South African Botany 18: 113 (1952).
- 4.26. **Thamnochortus obtusus** Pillans in Journal of South African Botany 18: 112 (1952).
- 4.27. **Thamnochortus stokoei** Pillans in Transactions of the Royal Society of South Africa 16: 375 (1928).
- 4.28. **Thamnochortus dumosus** Mast. in Botanische Jahrbücher 29, Beiblatt 66: 11 (1900b).
- 4.29. **Thamnochortus platypteris** Kunth in Enumeratio plantarum 3: 429 (1841).
- 4.30. **Thamnochortus schlechteri** Pillans in Transactions of the Royal Society of South Africa 16: 372 (1928).
- 4.31. **Thamnochortus bachmannii** Mast. in Annalen des Kaiserlich-Königlichen Naturhistorischen Hofmuseums, Wien 15: 11 (1900a).
- 4.32. **Thamnochortus punctatus** Pillans in Transactions of the Royal Society of South Africa 16: 376 (1928).

5. **Rhodocoma** Nees in Lindl., A natural system of botany, edn 2: 450 (1836). Type: *Rhodocoma capensis* Nees ex Steud.

Plants caespitose or with straight rhizomes. *Fertile culms* round, unbranched or in *R. capensis* much branched with branches whorled at each node; sheaths persistent, upper half chartaceous and soon decaying, leaving a lacerated remnant; hyaline shoulders absent. *Male inflorescence* racemose from several nodes, each partial inflorescence with several to numerous pendulous spikelets on flexible pedicels; spikelets $\pm$ elliptical; bracts without distinct membranous upper margin; anthers included in flowers at anthesis. *Female inflorescence* similar to male, but partial inflorescences stiffly erect with few to several spikelets; spathes sometimes prominent and membranous or chartaceous; spikelets elliptical to ovate, with 1–5 flowers; bracts shorter than flowers. *Female flowers* not laterally compressed; tepals bony, glabrous and smooth; staminodes present. *Gynoecium* with 3, white to red, feathery styles free to base; ovary 3-locular, dehiscent or rarely falling with seed. *Seed* brown, grey or tan, colliculate or rugose. *Culm anatomy*: epidermal cells 1-layered, lateral walls straight and unthickened or sinuose and thickened; parenchyma of 1–4 rows of cells; central ground tissue with scattered cavities; tannin present in epidermis, parenchyma, sclerenchyma and central ground tissue; silica usually absent, or when present, in parenchyma.

Etymology: *Rhodocoma* (f.): *rhodon* (Greek), rosy; *kome* (Greek), hair of the head; presumably referring to the strikingly red or rosy styles in the type species, *R. capensis*.

Notes: most of the species are found in the southern Cape, where a clear pattern of ecological and geographical replacement is evident. *Rhodocoma fruticosa* is widespread from the Cape to the Drakensberg, and is very common over large areas along the eastern margins of the fynbos.

Superficially the species are similar to *Thamnochortus*, especially because of the pendulous male spikelets and the similar culm and sheath construction. However, they can be separated by the dehiscent female ovaries, by the short bracts in the females, and less confidently by the shorter and more elliptical spikelets.

The evolution in this genus has been investigated twice, first by Linder & Vlok (1991), then by Hardy & Linder (2007).

5.1. *Rhodocoma foliosa* (N.E.Br.) H.P.Linder & C.R.Hardy, comb. nov.

Restio foliosus N.E.Br. in Flora capensis 7: 753 (1900). Type: Garcia's Pass, Galpin 4783 (K, lecto.! [Linder in Bothalia 15: 478 (1985)]; B!, BOL!, K!).

5.2. *Rhodocoma gigantea* (Kunth) H.P.Linder in Bothalia 15: 479 (1985).

5.3. *Rhodocoma capensis* Nees ex Steud., Synopsis plantarum glumacearum 2: 249 (1855).

5.4. *Rhodocoma gracilis* H.P.Linder & Vlok in Plant Systematics and Evolution 175: 156 (1991).

5.5. *Rhodocoma arida* H.P.Linder & Vlok in Plant Systematics and Evolution 175: 158 (1991).

5.6. *Rhodocoma vleibergensis* H.P.Linder, sp. nov., *R. aridae* affinis, sed caespitibus pauciculmis, spiculis femineis longioribus (5–7 mm longis), stomatibus superficiebus notabilis.

TYPE.—Western Cape, 3319 (Worcester): Ceres, Baviaanshoek, Vleiberg, (–BA), 14-10-1994, H.P.Linder 5882 (BOL, holo.; K, Z).

Plants tufted with few 1.0–1.5 m tall culms and with spreading rhizomes. *Fertile culms* unbranched, smooth, olivaceous, apical diam. 1.5–2.5 mm; sheaths closely convoluted, 40–60 mm long, apical margins broadly chartaceous and soon decaying, hyaline shoulders absent, apically acute; mucro penicillate, straight and erect, 4–10 mm long. *Male inflorescence* with up to 500 spikelets, paniculate, 80–300 × 30–50 mm; spathes persistent, chartaceous, upper margins lacerated and largely decayed at anthesis, shorter than spikelets; spikelets pendulous on flexible pedicels longer than spikelets, elliptical, rounded, 4.5–6.5 mm long, 5–7-flowered; bracts shorter than to as tall as flowers, 1.5–2.5 mm long, oblong or ovate, rounded or obtuse, chartaceous. *Male flower* 2.0–2.5 mm long; tepals all same size, cartilaginous, glabrous, outer lateral tepals conduplicate; anthers 1.2–1.4 mm long, included in flowers, pistillode present. *Female inflorescence* with up to 500 spikelets, paniculate, sparsely branching, stiffly erect, 80–200 × 10–30 mm; spathes persistent, chartaceous or membranous, longer than spikelets but not obscuring them; spikelets 1-flowered, with 3–6 sterile bracts shorter than flowers, 2–3 mm long, ovate, rounded or obtuse or acute, chartaceous. *Female flower* 4.5–6.0 mm long; tepals bony, glabrous and smooth, midrib flush with tepal body, apices acute, inner and outer whorls of same length; staminodes present. *Gynoecium*: styles feathery, white, 3, free to base; ovary with 3 dehiscent locules. *Culm anatomy*: epidermal cells single-layered, lateral wall sinuose, thickened, outer wall thickened, colliculate; glabrous, l/w ratio 6 : 4, all the same length; stomatal apparatus superficial, guard cells seated on top of support cells; chlorenchyma of 2 layers of cells, l/w ratio 12 : 8, inner and outer layers somewhat

dissimilar; protective cells reaching to base of chlorenchyma layer; parenchymatous layer of 2 or 3 cells, cells smaller than epidermal cells; sclerenchyma ring of 9–13 layers, without protrusions, cell walls thick; central ground tissue with scattered cavities; tannin present in epidermis, sclerenchyma or central ground tissue; silica sand absent. *Flowering time*: September, seed release in November.

Etymology: Vleiberg, a little known peak in the Swartruggens, from which this new species was first recorded.

Distribution and ecology: endemic to the western margins of the Tanqua Karoo, from the Bonteberg at Touws River, northwards via Baviaansberg, Vleiberg to the Bokkeveld Sneekop. The altitude is from 1 000–1 600 m, the habitat restricted to sandstone- or quartzite-derived soils, where populations are found in well-drained habitats on rocky slopes. The plants are killed by fire, and populations are re-established from seed.

Discussion: this species is morphologically very similar to *Rhodocoma arida*, but with a different 'gestalt', the plants being smaller, tatterier looking, and spreading with a more developed rhizome. The spikelets are generally larger. This applies particularly to the female spikelets. Furthermore, there is a geographical separation, with *R. vleibergensis* found north of the Laingsburg Witteberg, and *R. arida* east of this line. This also determines the proportion of summer rain in the area, with *R. arida* receiving a substantial proportion of its rain in summer, whereas *R. vleibergensis* receives almost no summer rain. Despite the morphological similarity to *R. arida*, the phylogeny of Hardy & Linder (2007) indicates that the species is more closely related to the *R. alpina*–*R. fruticosa* subclade.

Additional collections

WESTERN CAPE.—3319 (Worcester): Ceres, Baviaanshoek, Watervalsberg, between top of track and trig beacon, common on stony soils, (–BA), 14-10-1994, H.P.Linder 5854 (Z, K); Bonteberg, Abrahamshoek, summit ridge on well-drained soils, (–BB), 25-10-2000, H.P.Linder 7103 (Z).

5.7. *Rhodocoma fruticosa* (Thunb.) H.P.Linder in Bothalia 15: 478 (1985).

5.8. *Rhodocoma alpina* H.P.Linder & Vlok in Plant Systematics and Evolution 175: 156 (1991).

6. *Elegia* L., Mantissa plantarum altera 162 (1771). Type: *Elegia juncea* L.

Chondropetalum Rottb.: 11 (1772). Type: *Chondropetalum deustum* Rottb. [= *Elegia deusta* (Rottb.) Kunth], lecto. [Linder 1984].

Dovea Kunth: 457 (1841). Type: *Dovea macrocarpa* Kunth [= *Elegia macrocarpa* (Kunth) Moline & H.P. Linder].

Lamprocaulis Mast. in A.DC.: 349 (1878). Type: *Lamprocaulis grandis* (Kunth) Mast. [= *Elegia grandis* Kunth].

Plants tufted, clumped or mat-forming, often with well-developed, spreading rhizomes. *Fertile culms* mostly unbranched, in some species branched, and in two species branches whorled at each node, mostly round, sometimes ± compressed; sheaths sometimes persistent, but more commonly caducous with distinct abscission line,

when present, most commonly loosely convoluted and same texture over whole structure, rarely upper margins membranous or otherwise different from rest of organ. *Male inflorescence* of several clusters of partial, paniculate inflorescences, each with several to very numerous flowers only poorly organized into spikelets; young partial inflorescences generally hidden behind large spathes, which drop before anthesis; large spathe-like spatheae occasionally present; male bracts usually shorter than perianth, but in appearance similar to tepals. *Male flowers* with undifferentiated, glabrous tepals; anthers included in flowers at anthesis. *Female inflorescence* structurally similar to male inflorescences; each partial inflorescence with 1–many flowers, these poorly organized into spikelets; spathes large, usually persistent, often completely obscuring flowers at anthesis; spikelets often clustered in paniculate partial inflorescences, making them difficult to delimit; bracts mostly shorter than flowers with no differentiation between body and margin, rarely acuminate and/or lacerated on margins. *Female flowers* with undifferentiated, glabrous tepals; staminodes usually present. *Gynoecium* with 2 or 3 mostly feathery styles free to base or more rarely seated on a stylopodium; ovary with 3 usually dehiscent or 1 indehiscent locule. *Nuts* generally triangular, often black, without elaiosomes, perianth sometimes persistent on nuts but never winged; seeds from dehiscent ovaries often brown and smooth. *Culm anatomy*: epidermal cells almost always in 2 layers, lateral wall straight, unthickened; parenchymatous layer of 1–6 cells; central ground tissue solid or with scattered cavities, rarely with a single, central cavity; tannin usually in epidermis and central ground tissue, rarely in parenchyma or sclerenchyma; silica absent.

Etymology: *Elegia* (f.), from the Greek *elegos*, meaning weeping or lament, and this was then used by Plinius in the Latinized form of *Elegia* to refer to a kind of reed.

Notes: this genus contains a remarkably wide range of variation in morphology, previously recognized as four genera. However, this variation does not readily group into reciprocally monophyletic groups, and consequently the whole group is best treated as one large genus, as suggested by Moline & Linder (2005). This larger clade is readily diagnosed by anatomical attributes (epidermis in two layers: Figure 1). The morphological attributes (caducous sheaths; paniculate inflorescences) have numerous exceptions, which makes them more difficult to use.

The genus contains several well-known species, such as *Elegia tectorum*, widely cultivated, previously widely used as a thatching reed; *E. capensis*, widely cultivated, dominant in many areas in regions with some groundwater, where the stoloniferous growth allows the species to take over the vegetation; *E. filacea*, which has an enormous ecological range, and is found in almost all vegetation types.

The species are organized into four clades (Figure 3).

a) *Elegia mucronata* clade, without obvious characters:

6.1. ***Elegia cuspidata* Mast.** in Journal of the Linnean Society, Botany 10: 240 (1868).

6.2. ***Elegia mucronata* (Nees) Kunth**, Enumeratio plantarum 3: 475 (1841).

b) *Chondropetalum* clade: includes most species previously included in *Chondropetalum*. Morphologically this clade is defined by the dehiscent ovaries. However, it also includes *Elegia verreauxii*, which has an indehiscent ovary:

6.3. ***Elegia nuda* (Rottb.) Kunth**, Enumeratio plantarum 3: 462 (1841).

6.4. ***Elegia tectorum* (L.f.) Moline & H.P.Linder** in Systematic Botany 30: 772 (2005).

6.5. ***Elegia elephantina* H.P.Linder**, sp. nov., a *E. tectorum* caespitibus elatioribus (1.0–2.5 m), culmis validioribus (4–6 mm), spiculis maribus maioribus (3.0–3.5 mm diametro), tepalis femineis exterioribus interiores aequantibus recedit.

TYPE.—Western Cape, 3318 (Cape Town): between Hopefield and Koperfontein, 33° 05' 31"S, 18° 34' 36"E, plants up to 2 m tall, forming small populations in hollows among the dunes, (–AB), 22-08-2000, H.P.Linder 7072 (Z, holo.).

Evergreen, tufted plants, 1.0–2.5 m tall. *Rhizome* spreading, unbranched or sparsely branched, culms evenly spaced. *Fertile culms* unbranched, round, smooth, olivaceous, 4–6 mm diam. at base, 1.4–2.5 mm diam. at apex; sheaths caducous, with an abscission line present, loosely convoluted, 30–60 mm long, margins entire, reddish to dark brown with fine tan speckles and tan margins, slightly glossy; sheath mucro penicillate, straight and erect, 6–10 mm long. *Male inflorescence* with more than 100 spikelets, paniculate, 80–500 × 20–30 mm; spathes caducous, taller than spikelets, cartilaginous; spikelets erect on short stiff pedicels, subglobose, 3.0–3.5 mm in diam., 3- or 4-flowered; bracts shorter than flowers, ovate, 1.2–1.7 mm long, acute, margins entire, chartaceous or cartilaginous, bract awn minute or absent. *Male flower* 2.3–2.9 mm long, glabrous; tepals chartaceous or cartilaginous, inner tepals longer than outer tepals, outer lateral tepals conduplicate; anthers included in flowers. *Female inflorescence* with more than 50 spikelets, interrupted, 80–400 × 15–20 mm; spathes longer than spikelets, caducous, bony; spikelets subglobose, 3.2–4.2 mm long, 4- or 5-flowered; bracts all fertile, shorter than flowers, erect, 1.5–2.0 mm long, orbicular (at times wider than tall), rounded or obtuse, cartilaginous (with a sturdy midrib), apical margin like rest of bract, same as body of bract, awn minute or absent. *Female flowers* 2.2–2.8 mm long, tepals bony, glabrous and smooth, midrib raised, margins entire, apices acute, inner and outer whorls equally long; outer lateral tepals conduplicate, odd outer tepal elliptical, inner tepals ovate, 1.8–2.3 mm long; staminodes present. *Gynoecium* with 3 feathery styles, bases free; 3-locular, dehiscent ovary. *Seed* 0.6–0.8 × 0.3–0.5 mm, shape in side view elliptical, shape round in diam. and rectangular in cross section, brown. *Flowering time*: July.

Distribution and ecology: endemic to the west coast of South Africa, from Blouberg to Elands Bay. Local in damp hollows and seepages on well-leached sand below 200 m.

Etymology: this species is known as *olifantsriet* on the west coast. Unfortunately, this name appears to be applied to any very large member of the Restionaceae, thus is not very useful. The name is derived from the Latin for elephant: *elephas*.

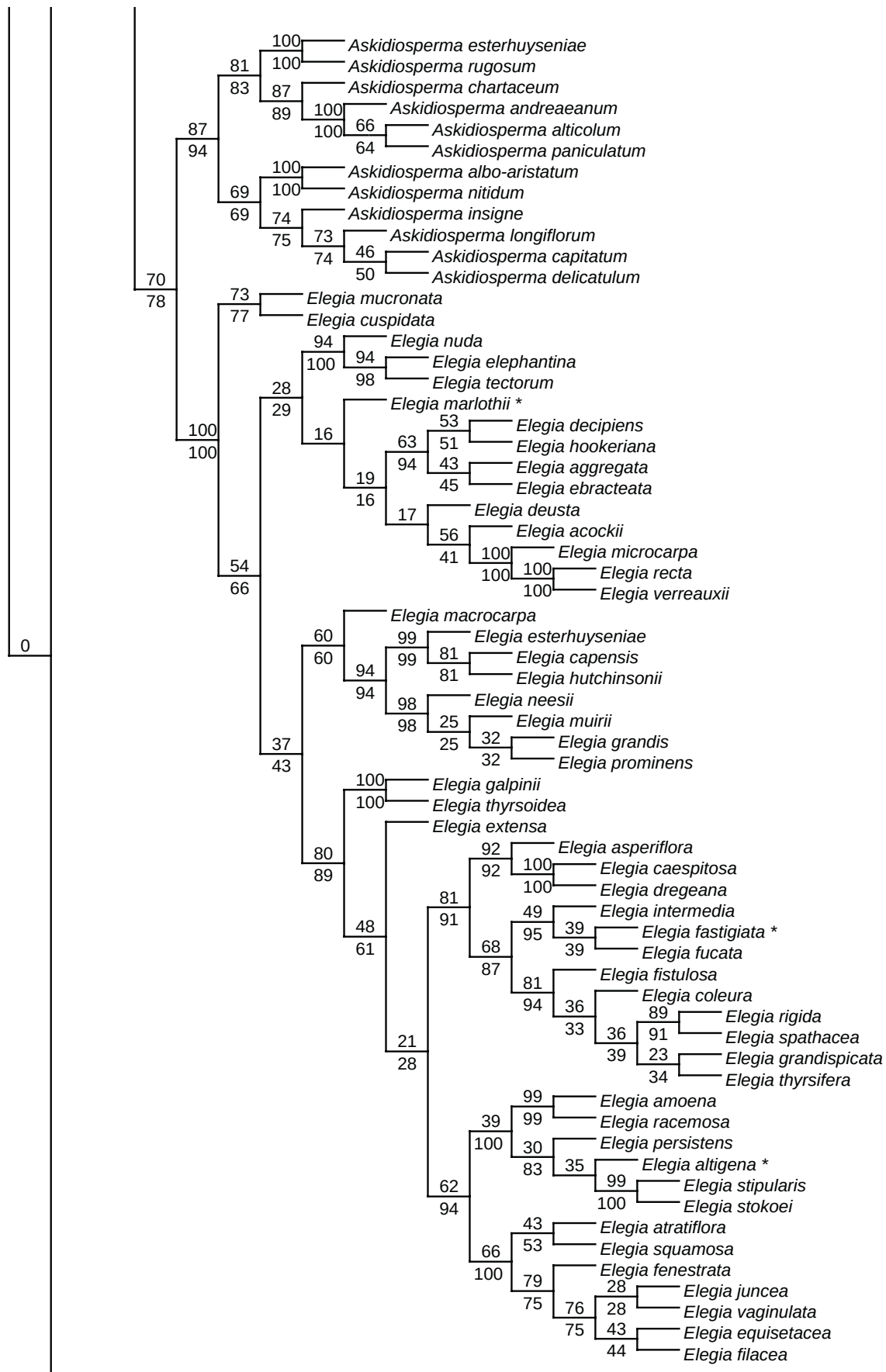


FIGURE 3.—Portion of strict consensus tree of total combined analysis of Hardy *et al.* (2008) containing *Askidiosperma* and *Elegia sensu* Moline & Linder (2005). Bootstrap values above the branches indicate support based on a 500-replicate bootstrap analysis that included 20 species for which DNA data were lacking (asterisked taxa). Bootstrap values below branches indicate support based upon a 500-replicate analysis that included only taxa for which both DNA data and morphology data were available. Where no value is given below a branch, it indicates that the clade did not appear in the analysis excluding morphology-only species.

Discussion: this species is very close to *Elegia tectorum*, from which it primarily differs in being bigger in all dimensions. Furthermore, the inner and outer whorls of the female tepals are the same length, whereas in *E. tectorum* the inner tepals are longer than the outer. Both species co-occur on the west coast at Blouberg, and no intermediate plants have been seen.

- 6.6. *Elegia marlothii* (Pillans) Moline & H.P.Linder in Systematic Botany 30: 772 (2005).
- 6.7. *Elegia hookeriana* (Mast.) Moline & H.P.Linder in Systematic Botany 30: 772 (2005).
- 6.8. *Elegia decipiens* (Esterh.) Moline & H.P.Linder in Systematic Botany 30: 771 (2005).
- 6.9. *Elegia ebracteata* (Kunth) Moline & H.P.Linder in Systematic Botany 30: 771 (2005).
- 6.10. *Elegia aggregata* (Mast.) Moline & H.P.Linder in Systematic Botany 30: 771 (2005).
- 6.11. *Elegia deusta* (Rottb.) Kunth, Enumeratio plantarum 3: 460 (1841).
- 6.12. *Elegia acockii* (Pillans) Moline & H.P.Linder in Systematic Botany 30: 771 (2005).
- 6.13. *Elegia microcarpa* (Kunth) Moline & H.P.Linder in Systematic Botany 30: 772 (2005).
- 6.14. *Elegia recta* (Mast.) Moline & H.P.Linder in Systematic Botany 30: 772 (2005).
- 6.15. *Elegia verreauxii* Mast. in Journal of the Linnean Society, Botany 21: 589 (1885).

c) *Lamprocaulis* clade: includes most species with branching culms, and which have, except for *Elegia macrocarpa*, indehiscent nuts. In several species the sheaths are persistent:

- 6.16. *Elegia macrocarpa* (Kunth) Moline & H.P.Linder in Systematic Botany 30: 772 (2005).
- 6.17. *Elegia capensis* (Burm.f.) Schelpe in Journal of South African Botany 33: 156 (1967).
- 6.18. *Elegia hutchinsonii* Pillans in Transactions of the Royal Society of South Africa 29: 344 (1942).
- 6.19. *Elegia esterhuyseniae* Pillans in Transactions of the Royal Society of South Africa 30: 259 (1945).
- 6.20. *Elegia neesii* Mast. in Journal of the Linnean Society, Botany 10: 246 (1868).
- 6.21. *Elegia muirii* Pillans in Transactions of the Royal Society of South Africa 16: 319 (1928).
- 6.22. *Elegia grandis* (Nees) Kunth, Enumeratio plantarum 3: 475 (1841).
- 6.23. *Elegia prominens* Pillans in Transactions of the Royal Society of South Africa 16: 320 (1928).

d) *Elegia* clade: includes almost all species of the previous genus *Elegia*, characterized by the indehiscent ovaries and usually unbranched culms:

- 6.24. *Elegia galpinii* N.E.Br. in Flora capensis 7: 754 (1900).
- 6.25. *Elegia thyrsioidea* (Mast.) Pillans in Annals of the Bolus Herbarium 3,3: 146 (1922).
- 6.26. *Elegia extensa* Pillans in Transactions of the Royal Society of South Africa 29: 343 (1942).
- 6.27. *Elegia asperiflora* (Nees) Kunth, Enumeratio plantarum 3: 474 (1841).
- 6.28. *Elegia caespitosa* Esterh. in Linder in Bothalia 15: 421 (1985).
- 6.29. *Elegia dregeana* Kunth, Enumeratio plantarum 3: 469 (1841).

- 6.30. *Elegia intermedia* (Steud.) Pillans in Transactions of the Royal Society of South Africa 16: 332 (1928).
- 6.31. *Elegia fastigiata* Mast. in Botanische Jahrbücher 29, Beiblatt 66: 7 (1900b).
- 6.32. *Elegia fucata* Esterh. in Linder in Bothalia 15: 423 (1985).
- 6.33. *Elegia fistulosa* Kunth, Enumeratio plantarum 3: 467 (1841).
- 6.34. *Elegia coleura* Nees ex Mast. in A.DC., Monographiae phanerogamarum 1: 358 (1878).
- 6.35. *Elegia rigida* Mast. in Journal of the Linnean Society, Botany 21: 587 (1885).
- 6.36. *Elegia spathacea* Mast. in Journal of the Linnean Society, Botany 21: 588 (1885).
- 6.37. *Elegia grandispicata* H.P.Linder in Bothalia 15: 424 (1985).
- 6.38. *Elegia thyrsifera* (Rottb.) Pers., Synopsis plantarum 2: 607 (1807).
- 6.39. *Elegia fenestrata* Pillans in Transactions of the Royal Society of South Africa 16: 338 (1928).
- 6.40. *Elegia persistens* Mast. in Botanische Jahrbücher 29 Beiblatt, 66: 8 (1900b).
- 6.41. *Elegia racemosa* (Poir.) Pers., Synopsis plantarum 2: 607 (1807).
- 6.42. *Elegia amoena* Pillans in Transactions of the Royal Society of South Africa 30: 258 (1945).
- 6.43. *Elegia altigena* Pillans in Transactions of the Royal Society of South Africa 30: 257 (1945).
- 6.44. *Elegia equisetacea* Mast. in Journal of the Linnean Society, Botany 21: 583 (1885).
- 6.45. *Elegia filacea* Mast. in Journal of the Linnean Society, Botany 21: 589 (1885).
- 6.46. *Elegia atratiflora* Esterh. in Linder in Bothalia 15: 420 (1985).
- 6.47. *Elegia squamosa* Mast. in Journal of the Linnean Society, Botany 10: 244 (1868).
- 6.48. *Elegia stipularis* Mast. in Journal of the Linnean Society, Botany 21: 587 (1885).
- 6.49. *Elegia stokoei* Pillans in Transactions of the Royal Society of South Africa 29: 345 (1942).
- 6.50. *Elegia juncea* L., Mantissa plantarum altera 297 (1771).
- 6.51. *Elegia vaginulata* Mast. in Journal of the Linnean Society, Botany 21: 586 (1885).

7. *Askidiosperma* Steud., Synopsis plantarum glumacearum 2: 257 (1855). Type: *Askidiosperma capitatum* Steud.

Plants caespitose. *Fertile culms* unbranched, round; sheaths dropping off, with an abscission line present, loosely convoluted or flat and standing free from culm, margins coriaceous, like rest of body, hyaline shoulders absent. *Male inflorescence* with 1 to several partial inflorescences subtended by large spathes; each partial inflorescence with 1 to several, many-flowered spikelets; bracts much taller than flowers, papery or membranous, margins entire or lacerated. *Male flowers* not laterally compressed; tepals glabrous, inner and outer often of different lengths; anthers included in flowers at anthesis. *Female inflorescence*, spikelets and flowers similar to male. *Female flowers* with staminodes. *Gynoeceum*: styles 2 or 3, white, feathery, free to base; ovary 1–3-locular, dehiscent or sometimes dropping with seed. *Seed* silvery or more commonly brown and smooth. *Culm*

anatomy: epidermis with a single layer of cells, lateral walls straight, unthickened; parenchyma of 1–3 layers of cells; central ground tissue solid, rarely with a single, central cavity; tannin usually absent, when present in epidermis, sclerenchyma or (rarely) in central ground tissue; silica usually absent, when present, in parenchyma or sclerenchyma.

Etymology: *Askidiosperma* (n.): from Greek *askion* or *askidion*, which is the diminutive of *askos*, which is a bag, sac, wine skin or hide; and *sperma* (n., Greek), which is a seed. The connection to the genus is unclear.

Notes: this genus shares with *Elegia* the caducous sheaths, and the tepals which are all the same (outer lateral tepals are not flattened and keeled). The species had been included in *Chondropetalum* by Pillans (1928), but were again separated by Linder (1984), as they differ from *Elegia* by the culms with simple (not doubled-layered) epidermis, and by the floral bracts which are hyaline-membranous and much taller than the flowers, as well as by the phytochemical composition (Harborne *et al.* 1985).

The species are mostly found in the western mountains, rather rarely in the southern mountains of the Western Cape, and are absent from the coastal flats and plains. Species range from seepages over bedrock (*Askidiosperma insigne*) to alluvial soils along streams and on well-drained rocky slopes.

7.1. ***Askidiosperma chartaceum*** (Pillans) H.P.Linder in Bothalia 15: 431 (1985).

7.2. ***Askidiosperma andreaeanum*** (Pillans) H.P.Linder in Bothalia 15: 431 (1985).

7.3. ***Askidiosperma alticolum*** (Esterh.) H.P.Linder in Nordic Journal of Botany 21: 198 (2001b).

7.4. ***Askidiosperma paniculatum*** (Mast.) H.P.Linder in Bothalia 15: 432 (1985).

7.5. ***Askidiosperma esterhuyseniae*** (Pillans) H.P.Linder in Bothalia 15: 432 (1985).

7.6. ***Askidiosperma rugosum*** Esterh. in Linder in Bothalia 15: 432 (1985).

7.7. ***Askidiosperma albo-aristatum*** (Pillans) H.P.Linder in Bothalia 15: 431 (1985).

7.8. ***Askidiosperma nitidum*** (Mast.) H.P.Linder in Bothalia 15: 432 (1985).

7.9. ***Askidiosperma insigne*** (Pillans) H.P.Linder in Bothalia 15: 432 (1985).

7.10. ***Askidiosperma longiflorum*** (Pillans) H.P.Linder in Bothalia 15: 432 (1985).

7.11. ***Askidiosperma capitatum*** Steud., Synopsis plantarum glumacearum. 2: 257 (1855).

7.12. ***Askidiosperma delicatulum*** H.P.Linder in Nordic Journal of Botany 21: 196 (2001b).

Restio clade

This large clade is readily defined by the laterally compressed female flowers, where the keels of the outer lateral tepals are more or less villous. In most species the culms are branching. This clade largely includes most of the segregates of the genus *Restio* sensu Linder (1984) and *Calopsis* sensu Linder (1984), as well as *Ischyrolepis*. Several strongly supported subclades are recognized: *Craspedolepis*, *Calopsis* s.str., *Restio* s.str.,

Locapsis and *Ischyrolepis* which are characterized by different apomorphies and apomorphic tendencies:

***Craspedolepis*:** diagnosed by the bracts with hollow (deeply concave) cells along the upper margin (honeycomb cells), and the plants and spikelets tend to be robust, the ovaries mostly dehiscent, with two locules. In many species the spikelets are relatively massive.

***Calopsis*:** highly paniculate inflorescences with very many small spikelets; culms mostly angular or even square.

***Restio*:** sheaths mostly with large membranous lobes flanking the mucro; the plants and spikelets tend to be small, the ovary mostly unilocular and often indehiscent.

***Locapsis*:** sheaths mostly spreading and without a differentiated apical margin; perianth papery, rounded; diaspore a nut.

***Ischyrolepis*:** ovaries with two styles which are basally fused, this fused portion persisting as a peg on the dehiscent ovary.

Varirestio and *Eremorestio*, however, lack characters, and are recognized in order to retain monophyly.

Morphologically, *Eremorestio* would fit with *Locapsis*, while *Varirestio* could be polymorphic. It remains possible that the apparent monophyly of these two segregates is an artifact of ancient hybridization, and that the plastid phylogeny is not tracking the species phylogeny.

However, the phylogenetic structure within the clade is unclear. There is little molecular support for the groupings, and we cannot postulate good morphological characters for the various molecular clades.

Also included in this clade are *Pendulostemon* and *Simplicaulos*. The balance of the evidence places these two segregates into the *Staberoha*–*Elegia* clade, but taxonomically they are better kept in the large *Restio* s.lat.

8. ***Restio*** Rottb., Descriptiones plantarum rariorum 9 (1772). Type: *Restio triticeus* Rottb. (lecto. McVaugh 1968).

Calopsis Beauv. ex Desv.: 44, t. 3 (1828). Type: *Calopsis paniculata* (Rottb.) Desv. (= *Restio paniculatus* Rottb.).

Ischyrolepis Steud.: 249 (1855). Type: *Ischyrolepis subverticellatus* Steud. (= *Restio subverticellatus* (Steud.) Mast.).

Craspedolepis Steud.: 264 (1855). Type: *Craspedolepis verreauxii* Steud. (= *Restio filiformis* Poir.).

Plants caespitose, clumped, tangled or mat-forming. *Fertile culms* simple or branching, round, or rarely square or compressed; sheaths persistent, closely or loosely convoluted, usually with a narrow membranous margin, often with tall, acute membranous lobes flanking mucro. *Male and female inflorescences* mostly very similar; mostly paniculate, more rarely racemose, with 1 to numerous spikelets; spathes usually persistent;

bracts usually coriaceous, varying from shorter to taller than flowers; anthers exerted from flowers at anthesis. *Female inflorescence* occasionally with fewer spikelets than males; spikelets with up to 30 laterally compressed flowers; tepals chartaceous or cartilaginous, glabrous or sparsely (rarely densely) villous on keels of lateral sepals; staminodes present. *Gynoecium* with 1, 2 or 3 feathery styles free to base, fused into a basal peg, or rarely seated on a stylopodium; ovary 1-, 2- or 3-locular, either dehiscent or indehiscent. *Diaspore* either a seed or a soft-walled nut; seed variously coloured, usually smooth, occasionally colliculate; nut dropped with a persistent papery perianth that is sometimes winged. *Culm anatomy*: epidermal cells 1-layered, lateral walls straight and unthickened or sinuose and thickened; parenchymatous layer of up to 6 cells; central ground tissue either with no cavity, a single central cavity, or with scattered cavities; tannin rarely absent, when present then in the epidermis, sclerenchyma, or central ground tissue; silica either absent, or when present, in chlorenchyma or parenchyma.

Etymology: *Restio* (m., Latin), a ropemaker; it is unclear why Linnaeus referred to restios as such, since they are not to our knowledge useful for the making of ropes, due to the brittle nodes.

The extensive variation in the genus is best expressed in the eight subgenera recognized.

8.1. **Restio** subgen. **Simplicaulos** H.P.Linder & C.R.Hardy, subgen. nov., primo adpectu *Restioni*, *Craspedolepi*, *Calopsi*, *Locapsi*, *Variestioni* et *Eremorestioni* culmis rotundis, vaginis persistentibus, spiculis maribus erectis, staminodiis praesentibus, stylis libris maxime simile, sed a speciebus olim ad subgenera *Calopsem* et *Restionem* ascriptis culmis simplicibus et inflorescentiis maribus et femineis valde similibus differt.

TYPE.—*Restio bifidus* Thunb.

Plants usually tufted. *Fertile culms* mostly unbranched or rarely sparsely branched, round or very rarely compressed (*Restio subtilis*); sheaths persistent, closely or loosely convoluted or rarely flat and standing free from culm (*R. papyraceus*); apical sheath margins narrowly or broadly membranous; hyaline shoulders absent or variously developed. *Male inflorescence* racemose, with 1–20 spikelets, paniculate with pendulous spikelets only in *R. bifarius*; spathes persistent; bracts with upper margin like body of bract, sometimes with hollow cells, obtuse to acuminate and recurved; anthers usually exerted from flowers at anthesis. *Female inflorescence* always racemose with 1–5 variously shaped, 1–40-flowered spikelets; bracts shorter to much longer than flowers, apical margin like rest of bract, membranous or with honeycombed cells, imbricate and obscuring spikelet axis. *Flowers* with outer lateral tepals usually conduplicate, but in three species, undifferentiated; all tepals cartilaginous, glabrous or keels of lateral sepals villous; staminodes present. *Gynoecium* with 1, 2 or 3 white, feathery, free styles; ovary with 1–3 dehiscent or rarely indehiscent locules. *Fruit*: in species with indehiscent ovaries, perianth winged, persistent around ovary, in species with dehiscent ovaries, seed silvery, brown or grey; surface pitted, colliculate or striate. *Culm anatomy*: epi-

dermal cells in 1 layer, lateral wall straight, unthickened or rarely sinuose and thickened; parenchymatous layer of 1–3 cells; central ground tissue solid or rarely with scattered cavities or with single, central cavity; tannin absent or present in epidermis, sclerenchyma or central ground tissue; silica absent.

Etymology: *Simplicaulos* (m.): *simplex* (Latin), simple, unbranched; *caulos* (Greek), stem; referring to the usually unbranched culms in this subgenus.

Notes: many species in this subgenus are associated with impeded drainage, and *Restio miser* and *R. confusus* are often dominants in convex-domed seepages on shale bands and on sandstone. *Restio bifidus* is typical of shallow seepages, and can be dominant over much of the upper plateau of Table Mountain. However, many of the other species are found in well-drained habitats.

There are very distinct morphological groups in this subgenus. The first group has large, almost flat, bracts (*Restio bifarius*, *R. bifidus*, *R. nuwebergensis* and *R. papyraceus*), that are quite similar to the female spikelets of the possible sister clade *Staberoha*. The second group has small button-like spikelets, borne on fine-stemmed tussocky plants, often with only one spikelet per culm, and round female flowers in which the lateral tepals are not conduplicate (*R. subtilis*, *R. confusus*, *R. miser*). The third group has thick spindle-shaped spikelets, and nutlets with a persistent perianth forming a wing (*R. monostylis*, *R. esterhuyseniae*). Finally, *R. echinatus* and *R. pedicellatus* have acuminate bracts.

This subgenus lacks any striking synapomorphies. However, optimization on the phylogeny shows that the subgenus ancestrally had simple culms, and that branched culms evolved only in the *Restio bifarius* group. Even in this group, branching is often absent, and when present, is sparse. The unbranched culms are shared with its possibly nearest relatives, *Elegia* and *Staberoha*, but differentiate the subgenus from the rest of the genus *Restio*. Although it is easy to differentiate subgen. *Simplicaulos* from its putative phylogenetic relatives *Staberoha* or *Elegia* by the persistent sheaths, by staminodes still present in the female spikelets, the (mostly) erect male spikelets and the male flowers aggregated into clear spikelets, these are all plesiomorphic features. It is remarkable how variable the subgenus is regarding previously used generic characters, such as the number of locules and styles and the type of diaspore (nut or seed). Not surprisingly, subgen. *Simplicaulos* contains species previously placed in *Restio sensu* Linder 1985 and *Calopsis sensu* Linder 1985.

Although the clade is strongly supported, its position within the Restioneae is not. The plastid data suggests (weakly) a phylogenetic relationship to *Staberoha* or *Elegia*, but the possibility that it is related to *Restio s.lat.* cannot be rejected, even by plastid data.

8.1.1. **Restio pedicellatus** Mast. in Journal of the Linnean Society, Botany 8: 252 (1865).

8.1.2. **Restio echinatus** Kunth, Enumeratio plantarum 3: 384 (1841).

8.1.3. **Restio stereocaulis** Mast. in Botanische Jahrbücher 29 Beiblatt 66: 1 (1900b).

8.1.4. **Restio subtilis** Nees ex Mast. in Journal of the Linnean Society, Botany 8: 251 (1865).

8.1.5. **Restio confusus** Pillans in Journal of South African Botany 18: 103 (1952).

8.1.6. **Restio miser** Kunth, Enumeratio plantarum 3: 392 (1841).

8.1.7. **Restio distylis** H.P.Linder & C.R.Hardy, nom. nov. pro *Leptocarpus esterhuyseniae* Pillans in Transactions of the Royal Society of South Africa 30: 260 (1945). *Calopsis esterhuyseniae* (Pillans) H.P.Linder: 466 (1985). Type: Mitchell's Pass, Slab Peak, Esterhuysen 6211 (BOL, holo.!, K!), non *Restio esterhuyseniae* Pillans.

Named for the unusual condition of having two styles.

8.1.8. **Restio monostylis** (Pillans) H.P.Linder & C.R.Hardy, comb. nov.

Leptocarpus monostylis Pillans in Journal of South African Botany 18: 108 (1952). *Calopsis monostylis* (Pillans) H.P.Linder: 469 (1985). Type: south slopes of the Langeberg near Riversdale, Esterhuysen 16993 (BOL, holo.!).

8.1.9. **Restio papyraceus** Pillans in Transactions of the Royal Society of South Africa 29: 342 (1942).

8.1.10. **Restio nuwebergensis** Esterh. in Linder in Bothalia 15: 453 (1985).

8.1.11. **Restio bifarius** Mast. in Journal of the Linnean Society, Botany 10: 278 (1868).

8.1.12. **Restio bifidus** Thunb., Phytographische Blätter, Göttingen 1: 7 (1803).

8.2. **Restio** subgen. **Pendulostemon** H.P.Linder & C.R.Hardy, subgen. nov., primo ad spectu *Restioni*, *Craspedolepi*, *Calopsi*, *Locapsi*, *Varirestioni* et *Eremorestioni* culmis rotundis, ramificantibus, vaginis persistentibus, staminodiis praesentibus, stylis libris maxime simile, sed a speciebus olim ad subgenera *Restionem* vel *Calopsem* ascriptis combinatione spiculorum marium pendulorum cum tepalis femineis glabris spiculisque femineis grandibus striis longitudinalibus instructis differt.

TYPE.—*Restio micans* Nees.

Plants tufted or clumped. *Fertile culms* branching, round; sheaths persistent, closely convoluted, margins similar to body of bracts or narrowly membranous. *Male inflorescence* paniculate, with 6–50 pendulous spikelets; bracts ± leathery, overtopping flowers. *Female inflorescences* usually racemose, with up to 20 erect, elliptical or obovate, rounded to acute, several-flowered spikelets; bracts at least as tall as flowers, imbricate, usually with longitudinal striations, margins like body or narrowly membranous. *Female flowers* laterally compressed; tepals bony or cartilaginous, glabrous, outer lateral tepals usually conduplicate and keeled; staminodes present. *Gynoecium* with 3, white, feathery, free styles; ovary with 2 locules, dehiscent. *Seed* silvery or pink, smooth or colliculate. *Culm anatomy*: epidermis single-layered, epidermal lateral cell walls straight, unthickened; parenchyma 1–5-layered; central ground tissue solid or with single, central cavity; tannin found in epidermis or sclerenchyma or central ground tissue; silica absent or present in parenchyma.

Etymology: *Pendulostemon* (m.): *pendulo* (Latin), pendulous; *stemon* (Greek), stamen; referring to the pendulous male spikelets.

Notes: the two species of this subgenus mentioned below were previously included in *Restio* s.str. because of their dehiscent ovaries, laterally flattened flowers and branched culms. Their current position is uncertain, but plastid data weakly indicate a relationship to *Thamnochortus* and *Rhodocoma* (Figure 2) with which they share the pendulous male spikelets. However, a closer relationship to *Restio* s.str. cannot be rejected.

Although the two species had not previously been associated, they share a number of morphological attributes. The plants are rather untidy, erect tussocks with robust, erect, branching culms. The sheaths are coriaceous without a substantial membranous margin. The spikelets, both male and female, are spindle-shaped and relatively large. The male spikelets are pendulous. The only unique feature is the longitudinal striation on the bracts, but this feature is not always easy to observe. *Restio micans* is a rare species on coastal sands, *R. egregius* is more widespread in the wetter mountains of the Western Cape.

8.2.1. **Restio egregius** Hochst. in Krauss in Flora 28: 337 (1845).

8.2.2. **Restio micans** Nees in Linnaea 5: 649 (1830).

8.3. **Restio** subgen. **Craspedolepis** (Steud.) H.P.Linder & C.R.Hardy, stat. nov.

Craspedolepis Steud., Synopsis plantarum glumacearum 2: 264 (1855). Type: *Craspedolepis verreauxii* Steud. (= *Restio filiformis* Poir.).

Plants caespitose to tangled, without spreading rhizomes. *Fertile culms* mostly branching, round or rarely compressed; sheaths persistent, usually closely convoluted, apical margin ± membranous, sometimes with large membranous shoulders flanking mucro. *Male inflorescence* racemose or paniculate, with up to 10 (rarely more) usually erect, mostly elliptical, spikelets (2 spp. with pendulous spikelets); male bract with upper margin usually with honeycombed cells, which eventually decay, taller than flowers; anthers exerted from flowers at anthesis. *Female inflorescence* similar to males, but spikelets are somewhat bigger, mostly elliptical, with up to 40 flowers; female bracts imbricate, shorter to taller than flowers, apical margin with honeycombed cells. *Female flowers*: outer tepals differentiated into conduplicate lateral tepals and a flat odd tepal, rarely glabrous and smooth, usually densely villous on keels of conduplicate tepals, occasionally also on back of outer odd tepal; staminodes present. *Gynoecium* with 3, white, feathery styles free to base; ovary usually with 2, rarely 3 or 1, fertile locules, dehiscent. *Seed* variously coloured, surface smooth or colliculate. *Culm anatomy*: epidermal cells 1-layered, lateral wall straight and unthickened or sinuose and thickened; parenchyma up to 4-layered; central ground tissue usually solid; tannin usually present in epidermis, sclerenchyma and central ground tissue; silica usually absent.

Etymology: *Craspedolepis* (f.): *kraspedon* (Greek), edge, border or fringe; *lepis* (Greek), scale. This name may be interpreted to refer to the upper margin of the floral bracts (scales) which differ from the body of the bract by the honeycombed cells, and are thus bordered.

Notes: this is a very distinctive segregate from *Restio* s.str. The most notable synapomorphy are the hollow

cells (honeycomb cells) that form the upper margins of the floral bracts. This is absent from one species in the subgenus, and similar structures are also found in a few species in two other subgenera. The other characters are more in the nature of 'tendencies': large, elliptical spikelets (where *Restio insignis* and *R. strobilifer* are extreme examples); very hairy tepals, with often all three outer tepals hairy along the keels; almost always with two fertile locules. This contrasts with *Restio s.str.* with its tendency to unilocular, indehiscent or tardily dehiscent ovaries.

The subgenus is widespread especially in the western half of the Cape Floristic Region (CFR), and is almost absent from the eastern parts of the CFR. There is a remarkable range of seed surface ornamentation, from colliculate to smooth. The inflorescence structure is also highly variable, from solitary spikelets, to many-spikeleted, paniculate structures.

The species are organized into several poorly separated subgroups (Figure 4).

a) *Restio fusiformis* group: seed triangular in cross section, either smooth or colliculate. The female spikelets are rather diverse in appearance:

- 8.3.1. ***Restio inveteratus* Esterh.** in Linder in *Bothalia* 15: 450 (1985).
- 8.3.2. ***Restio obscurus* Pillans** in Transactions of the Royal Society of South Africa 29: 341 (1942).
- 8.3.3. ***Restio fusiformis* Pillans** in Journal of South African Botany 18: 104 (1952).
- 8.3.4. ***Restio acockii* Pillans** in Transactions of the Royal Society of South Africa 29: 339 (1942).
- 8.3.5. ***Restio praeacutus* Mast.** in *Flora capensis* 7: 84 (1897).
- 8.3.6. ***Restio rupicola* Esterh.** in Linder in *Bothalia* 15: 459 (1985).

b) *Restio perseverans* group: inner male tepals shorter than the outer; seed triangular in cross section, surface ornamentation smooth:

- 8.3.7. ***Restio perseverans* Esterh.** in Linder in *Bothalia* 15: 457 (1985).

c) *Restio aureolus* group: female flowers only sparsely hairy, seeds planoconvex in cross section, surface ornamentation smooth. This includes *R. occultus*, with numerous few-flowered spikelets in paniculate inflorescences and richly branched plants.

- 8.3.8. ***Restio aureolus* Pillans** in Transactions of the Royal Society of South Africa 30: 246 (1945).
- 8.3.9. ***Restio perplexus* Kunth**, *Enumeratio plantarum* 3: 406 (1841).
- 8.3.10. ***Restio pulvinatus* Esterh.** in Linder in *Bothalia* 15: 457 (1985).
- 8.3.11. ***Restio cymosus* (Mast.) Pillans** in *Annals of the Bolus Herbarium* 3,2: 85 (1921).
- 8.3.12. ***Restio capillaris* Kunth**, *Enumeratio plantarum* 3: 405 (1841).
- 8.3.13. ***Restio patens* Mast.** in *Flora capensis* 7:97 (1897).
- 8.3.14. ***Restio brachiatus* (Mast.) Pillans** in *Annals of the Bolus Herbarium* 3,2: 85 (1921).

- 8.3.15. ***Restio occultus* (Mast.) Pillans** in Transactions of the Royal Society of South Africa 16: 243 (1928).

d) *Restio filiformis* group: seed triangular in cross section, surface ornamentation colliculate. In this group the female spikelets are compact, globose to elliptical, often rather few:

- 8.3.16. ***Restio filiformis* Poir.** in Lam., *Encyclopédie méthodique. Botanique* 6: 173 (1804).
- 8.3.17. ***Restio brunneus* Pillans** in Transactions of the Royal Society of South Africa 16: 250 (1928).
- 8.3.18. ***Restio burchellii* Pillans** in Transactions of the Royal Society of South Africa 29: 340 (1942).
- 8.3.19. ***Restio insignis* Pillans** in Transactions of the Royal Society of South Africa 30: 251 (1945).
- 8.3.20. ***Restio pachystachyus* Kunth**, *Enumeratio plantarum* 3: 399 (1841).
- 8.3.21. ***Restio strobilifer* Kunth**, *Enumeratio plantarum* 3: 398 (1841).
- 8.3.22. ***Restio nodosus* Pillans** in Transactions of the Royal Society of South Africa 30: 252 (1945).
- 8.3.23. ***Restio bifurcus* Nees ex Mast.** in *Journal of the Linnean Society, Botany* 8: 247 (1865).
- 8.3.24. ***Restio bolusii* Pillans** in Transactions of the Royal Society of South Africa 16: 247 (1928).

8.4. ***Restio* subgen. *Varirestio* H.P.Linder & C.R. Hardy**, subgen. nov., primo ad aspectu *Restioni*, *Craspedolepi*, *Calopsi*, *Locapsi* et *Eremorestoni* culmis rotundis, ramificantibus, vaginis persistentibus, spiculis maribus erectis, staminodiis praesentibus, stylis 3, libris, ovario loculis 1 vel 3, dehiscentibus maxime simile, sed vaginis interdum mucronibus pro ratione longis (longioribus quam dimidia pars vaginae) munitis differt et praeterea positio topologica recognitionem subgeneris cogit.

TYPE.—*Restio debilis* Nees.

Plants caespitose. *Fertile culms* branching or rarely simple, round; sheaths persistent, closely to very loosely convoluted; apical margins undifferentiated or forming membranous lobes; mucro sometimes as long as body of sheath. *Male inflorescences* racemose to paniculate, with up to 10 erect spikelets; spathes often overtopping spikelets; bracts with upper margins sometimes with honey-combed cells; anthers exerted from flowers at anthesis. *Female inflorescence* basically similar to male, but with fewer and larger spikelets; spikelets oblong, elliptical, ovate or obovate, with up to 20 flowers; bracts shorter or longer than flowers, apical margin sometimes with honey-combed cells. *Female flowers* laterally compressed; outer lateral tepals conduplicate, outer odd tepal flat, laterals either glabrous or villous; staminodes present. *Gynoecium*: with 3, white, feathery styles, free to base; ovary with 1 or 3 dehiscent locules. *Seed* variously coloured, smooth or colliculate. *Culm anatomy*: epidermal cells 1-layered, lateral wall straight and unthickened or more rarely sinuose and thickened; parenchyma 1- or 2-layered; central ground tissue solid or with a single, central cavity; tannin, when present, found in epidermis, sclerenchyma or central ground tissue; silica absent.

Etymology: *Varirestio* (m.): *vari* (Latin), various, variable; *restio* (Latin), ropemaker; the name reflects the extremely heterogeneous nature of this subgenus.

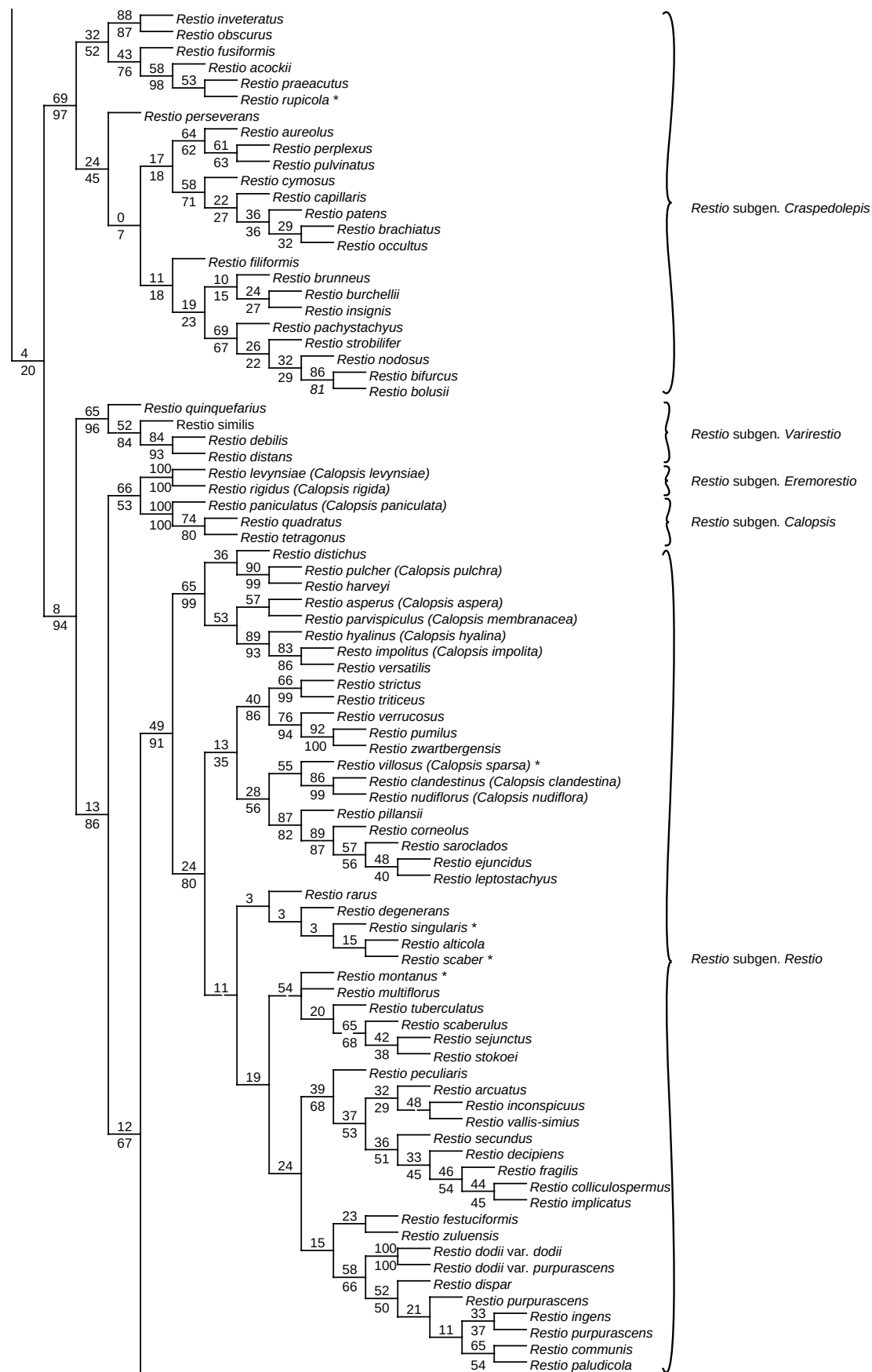


FIGURE 4.—Portion of strict consensus tree of total combined analysis of Hardy *et al.* (2008) containing *Restio* subgen. *Craspedolepis*, *R.* subgen. *Varirestio*, *R.* subgen. *Eremorestio*, *R.* subgen. *Calopsis*, and *R.* subgen. *Restio*. Names in parentheses are the now synonymous names of Linder (2001a) when different from the ones here proposed. Bootstrap values above the branches indicate support based on a 500-replicate bootstrap analysis that included 20 species for which DNA data were lacking (asterisked taxa). Bootstrap values below branches indicate support based upon a 500-replicate analysis that included only taxa for which both DNA data and morphology data were available. Where no value is given below a branch, it indicates that the clade did not appear in the analysis excluding morphology-only species.

Notes: recognition of this subgenus is forced by its topological position, sister to distinctive subgenera such as *Ischyrolepis*, *Locapsis*, *Restio* and *Calopsis*. Its four species appear not to share any unique attributes, and are morphologically very divergent. There is no morphological support for the recognition of this clade. Of the four species, two have three locules and two just one; two species have exceptionally long mucros, the others short mucros. Similarly there is no homogeneity in the anatomy or the seed colour or ornamentation. Nor is there a pattern of variation that would allow the recognition of two diagnosable taxa.

8.4.1. ***Restio quinquefarius*** Nees in *Linnaea* 5: 639 (1830).

8.4.2. ***Restio similis*** Pillans in *Annals of the Bolus Herbarium* 3,2: 82 (1921).

8.4.3. ***Restio debilis*** Nees in *Linnaea* 5: 641 (1830).

8.4.4. ***Restio distans*** Pillans in *Transactions of the Royal Society of South Africa* 30: 247 (1945).

8.5. ***Restio*** subgen. ***Calopsis*** (Beauv. ex Desv.) H.P. Linder & C.R. Hardy, stat. nov.

Calopsis Beauv. ex Desv., *Annales des Sciences Naturelles* 13: 44, t. 3 (1828). Type: *Calopsis paniculata* (Rottb.) Desv. (= *Restio paniculatus* Rottb.).

Large plants with large rhizomes. *Fertile culms* branching, square or at least in upper parts semicircular, always somewhere angular; sheaths persistent, with no abscission line, closely convoluted, apical margins either coriaceous like rest of body, or with large acute hyaline shoulders flanking the penicillate mucro. *Male and female inflorescence* very similar, racemose to paniculate, with very many partial inflorescences terminating apical part of fertile shoot, each with 1 to many elliptical to oblong, many-flowered spikelets. *Male flowers* with anthers exerted at anthesis. *Female spikelets* with up to 14 flowers; bracts shorter than, to as long as, flowers, margins not differentiated; outer lateral tepals conduplicate, keels glabrous to sparsely villous; staminodes present. *Gynoecium* with 3, white, feathery styles, free to base; ovary with 1–3 locules, indehiscent or dehiscent, or sometimes dropping with seed. *Seed* brown and smooth. *Culm anatomy*: epidermal cells single-layered, lateral walls straight and unthickened; parenchymatous layer of 1 or 2 cells; central ground tissue solid or with single, central cavity; tannin present in epidermis, parenchyma, sclerenchyma, or central ground tissue; silica present in parenchyma or central ground tissue.

Etymology: *Calopsis* (f.): *calos* (Greek), beautiful; *opsis* (Greek), aspect; they are quite striking plants, consequently the generic name *Calopsis* (= looking beautiful) is highly appropriate.

Notes: this is a dramatically redefined concept of *Calopsis*, as it excludes the whole genus as currently recognized except the type species, and includes two species formerly placed in *Restio*. However, the three species share a very similar growth form: one can think of them as being huge paniculate inflorescences of which the lower portion is sterile. Segregating them into separate genera was based on an over-reliance on the ovary dehiscence (*Restio* with capsules, *Calopsis* with nuts). Furthermore, in all three

species the culms are more or less angular, and in two of them they are sharply square. All three species are associated with ground water, and *C. paniculata* is a typical streambank species, widespread in the CFR.

8.5.1. ***Restio paniculatus*** Rottb., *Descriptions plantarum rariorum* 10 (1772).

8.5.2. ***Restio quadratus*** Mast. in *Journal of the Linnean Society, Botany* 10: 277 (1868).

8.5.3. ***Restio tetragonus*** Thunb., *Dissertatione de Restione*: 17 (1788).

8.6. ***Restio*** subgen. ***Eremorestio*** H.P. Linder & C.R. Hardy, subgen. nov., *Calopsi* sensu Linder (1984) vaginis persistentibus, antheris exsertis, ovarii unilocularibus indehiscentibus affinis, sed combinatione vaginorum arcte convolutorum, cum nuce triquetra, 2–3 mm longa differt.

TYPE.—*Calopsis rigida* (Mast.) H.P. Linder.

Plants tufted or mat-forming. *Fertile culms* branching, round; sheaths persistent, closely convoluted, upper half more membranous than lower half, soon decaying. *Male inflorescence* racemose or sparsely paniculate with 2–20 ± elliptical spikelets; spathes persistent, sometimes taller than spikelets; bracts acute to acuminate, slightly taller than flowers, apices somewhat darker than bodies; anthers exerted from flowers at anthesis. *Female inflorescence* similar to males, but always racemose and with fewer, somewhat larger spikelets; bracts taller than flowers, bony or cartilaginous, acute to acuminate, apices recurved somewhat from spikelet, giving it a bristly appearance; flowers laterally compressed; tepals chartaceous, rounded, glabrous or keels of lateral sepals sparsely villous; staminodes present. *Gynoecium* with 3, white, feathery styles free to base; ovary unilocular, indehiscent. *Diaspore* a soft-walled nut enclosed in perianth, triangular, 2–3 mm long, perianth not winged. *Culm anatomy*: epidermal cells 1-layered, lateral wall straight, unthickened; parenchymatous layer of 2 or 3 cells; central ground tissue solid; tannin, when present, in epidermis or central ground tissue; silica absent.

Etymology: *Eremorestio* (m.): *Eremia* (Greek), desert; *Restio* (Latin), ropemaker; restios living in arid areas, referring to the habitat of the two species in this genus, occurring along the arid margins of the Cape Floristic Region.

Notes: similar to the situation in *Varirestio*, this subgenus of two species is recognized in order to be able to separate the larger subgenera *Restio* s.str. and *Ischyrolepis*. Contrary to the situation in *Varirestio*, however, there are numerous similarities between the two species. They have similar diaspores (soft-walled nuts dispersed in a papery perianth). Such diaspores defined the genus *Calopsis* sensu Linder 1984. The papery perianth and rather brittle bracts are also typical of this group. Morphologically the genus is very close to *Locapsis*, and it is not clear whether monophyly would be significantly rejected if the two were combined. The morphological distinction between *Eremorestio* and *Locapsis* is not easy, as most of the characteristics of *Eremorestio* are also found in the larger subgen. *Locapsis*. Possibly the best attribute could be that the tips of the floral bracts in the

two species of *Eremorestio* are darker than the bodies of the bracts, and these tips are recurved away from the axis of the spikelet. In *Locapsis* the bract tips are generally the same colour as the body of the bracts, and the tips are closely rolled around the spikelets, resulting in slender spindle-shaped spikelets. However, it is not clear whether this attribute will be a useful, consistent key character.

These two species also occupy a typical *Locapsis* habitat, along the arid fringes of the Cape. They have a disjunct distribution, with *Restio levynsiae* in the Swart-ruggens Mountains, and *R. rigidus* from the Voetpadsberg near Laingsburg to the Great Swartberg.

8.6.1. *Restio levynsiae* (Pillans) H.P.Linder & C.R. Hardy, comb. nov.

Leptocarpus levynsiae Pillans in Transactions of the Royal Society of South Africa 29: 346 (1942). *Calopsis levynsiae* (Pillans) H.P.Linder: 467 (1985). Type: Katbakkies, *Levyns 1845* (BOL, holo.).

8.6.2. *Restio rigidus* (Mast.) H.P.Linder & C.R. Hardy, comb. nov.

Leptocarpus rigida Mast. in Botanische Jahrbücher 29, Beiblatt 66: 10 (1900b). *Calopsis rigida* (Mast.) H.P.Linder: 470 (1985). Type: Koue Bokkeveld, *Schlechter 8882, 8883* (K, lecto.! [Linder in Bothalia 15: 470 (1985)]; BM!, BOL!, BR!, K!, P!, S!, WAG!, Z!).

8.7. *Restio* subgen. *Restio*

Plants caespitose, clumped, tangled or mat-forming. Fertile culms branching (with the sole exception of *R. strictus*), round; sheaths persistent, closely or loosely convoluted, usually with a narrow membranous margin, often with tall, acute, membranous lobes flanking mucro. Male and female inflorescences mostly very similar; mostly paniculate, more rarely racemose, with 1 to numerous spikelets; spathes usually persistent, often overtopping spikelets; bracts varying from shorter to taller than flowers, without honeycombed cells in apical parts; anthers exerted from flowers at anthesis. Female inflorescence occasionally with fewer spikelets than males; spikelets with up to 16 laterally compressed flowers; tepals chartaceous or cartilaginous, glabrous or sparsely (rarely densely) villous on keels of lateral sepals; staminodes present. Gynoecium with 3, white, feathery styles free to base or rarely seated on a stylopodium; ovary mostly unilocular, rarely with 2 locules, only in *R. sejunctus* with 3 locules, either dehiscent or indehiscent. Diaspore either a seed or a soft-walled nut; seed variously coloured, usually smooth, occasionally colliculate; nut dropped with a persistent papery perianth that is sometimes winged. Culm anatomy: epidermal cells 1-layered, lateral walls usually straight and unthickened, occasionally sinuose and thickened; parenchymatous layer of up to 6 cells; central ground tissue either with no cavity, a single central cavity, or with scattered cavities; tannin rarely absent, when present then in the epidermis, sclerenchyma, or central ground tissue; silica either absent, or when present, in chlorenchyma or parenchyma.

Notes: *Restio*, as defined here, is still a very broad subgenus, including species from *Calopsis* and *Restio* sensu Linder 1984. Broadly speaking, it includes the generally more slender members of *Restio s.lat.*, with a tendency towards small spikelets, to unilocular and often indehiscent ovaries, and to more membranous sheaths and bracts. This contrasts to subgen. *Craspedolepis*, which includes the more robust *Restio* species.

Although there are no clearcut synapomorphies for the subgenus, there are a number of attributes which in combination will often lead to a correct identification. Most species in the subgenus have tall membranous lobes flanking the mucro on the sheath. These are also found in many other genera (e.g. subgen. *Ischyrolepis*), but are rare in the other segregates of *Restio s.lat.* In *Restio s.str.* they are optimized as being ancestrally present. As such, this character can be seen as a synapomorphy for the subgenus, although it cannot be used to key out the subgenus, due to the absence of this feature from many species of *Restio*, and its presence in many species in other genera. In most species in the subgenus there is a single functional locule. Furthermore, in most cases this locule is also dehiscent. Typical of the subgenus are rather small spikelets, often with few flowers, rather than the more massive spikelets characteristic of *Craspedolepis*.

Ecologically most species are found along the wetter coastal mountains, where they often form an understorey under other vegetation.

Despite the substantial variation in the subgenus, it is not possible to formally recognize sections, but to facilitate an understanding of the variation in this large taxon, the species are placed into informal groups.

a) *Restio aspera* group: mostly ex-*Calopsis* species, with paniculate inflorescences, rounded tepal apices, tepals sometimes winged, and indehiscent ovaries:

8.7.1. *Restio distichus* Rottb., Descriptiones plantarum rariorum 11 (1772).

8.7.2. *Restio pulcher* (Esterh.) H.P.Linder & C.R. Hardy, comb. nov.

Calopsis pulchra Esterh. in Linder in Bothalia 15: 469 (1985). Type: along road from Elim to Stanford, *Esterhuysen 31255* (BOL, holo.); B!, BOL!, C!, E!, F, GRA!, K!, L, LD, M!, MO!, NBG!, NY, PRE!, RSA, S!, STE!, TCD!, UC, US, W!, WAG!).

8.7.3. *Restio harveyi* Mast. in Journal of the Linnean Society, Botany 8: 253 (1865).

8.7.4. *Restio asperus* (Mast.) H.P.Linder & C.R. Hardy, comb. nov.

Hypolaena aspera Mast. in Journal of the Linnean Society, Botany 10: 264 (1868). *Calorophus asper* (Mast.) Kuntze: 747 (1891). *Leptocarpus asper* (Mast.) Pillans: 345 (1928). *Calopsis aspera* (Mast.) H.P.Linder: 465 (1985). Type: Nieuw Kloof, Houw Hoek, *Burchell 8069* (K, lecto.! [Linder in Bothalia 15: 465 (1985)]; BOL!, K!, P!); Hottentots Holland Mtns, *Ecklon & Zeyher s.n.* (K!); s.loc. *Thom 632* (K!); mountains at Grietjiesgat, *Ecklon & Zeyher s.n.* (K!); Palmiet River, *Ecklon 951* (B!).

8.7.5. *Restio parvispiculus* H.P.Linder & C.R. Hardy, nom. nov.

Hypolaena burchellii Mast. in Journal of the Linnean Society, Botany 10: 268 (1868). *Calorophus burchellii* (Mast.) Kuntze: 747 (1891). *Leptocarpus membranaceus* Pillans: 346 (1928). Type: Nieuw Kloof, Houw Hoek Mtns, *Burchell 8116* (BOL!, K!); Baviaanskloof Mtns, near Genadendal, *Burchell 7894a* (BOL!, K!, P!); 7632 (K, lecto.! [Linder in Bothalia 15: 469 (1985)]; BOL!), non *Restio burchellii* Pillans et *Restio membranaceus* Nees (= *Elegia intermedia* (Steud.) Pillans).

8.7.6. *Restio hyalinus* (Mast.) H.P.Linder & C.R. Hardy, comb. nov.

Hypolaena hyalina Mast. in Botanische Jahrbücher 29, Beiblatt 66: 13 (1900b). *Leptocarpus hyalinus* (Mast.) Pillans: 344 (1928). *Mastersiella hyalina* (Mast.) Gilg-Ben.: 25 (1930). *Calopsis hyalina* (Mast.) H.P.Linder: 467 (1985). Type: Koude River, *Schlechter 10464*,

10465 (K, lecto.! [Linder in Bothalia 15: 467 (1985)]; BOL!, BR!, MEL!, MO!, NBG!, P!, S!, WAG!, Z!).

8.7.7. **Restio impolitus** Kunth, Enumeratio plantarum 3: 404 (1841).

8.7.8. **Restio versatilis** H.P.Linder in Bothalia 15: 463 (1985).

b) *Restio triticeus* group: has dehiscent unilocular ovaries. Two subgroups are recognized, one of which has colliculate seed (rather than the smooth seed typical of the rest of the genus):

8.7.9. **Restio strictus** N.E.Br. in Flora capensis 7: 752 (1900).

8.7.10. **Restio triticeus** Rottb., Descriptiones plantarum rariorum 11 (1772).

8.7.11. **Restio verrucosus** Esterh. in Linder in Bothalia 15: 462 (1985).

8.7.12. **Restio pumilus** Esterh. in Linder in Bothalia 15: 458 (1985).

8.7.13. **Restio zwartbergensis** Pillans in Transactions of the Royal Society of South Africa 16: 229 (1928).

8.7.14. **Restio villosus** H.P.Linder & C.R.Hardy, nom. nov. pro *Calopsis sparsa* Esterh. in Linder in South African Journal of Botany 56: 454 (1990). Type: Caledon Div., Arieskraal, Esterhuysen 32751 (BOL, holo.!, B!, C!, E!, K!, L!, M!, MO!, PRE!, S!, STE!, UPS!), non *Restio sparsus* Mast. (= *Restio strobilifer* Kunth).

The name refers to the uniquely villous flower bases.

8.7.15. **Restio clandestinus** (Esterh.) H.P.Linder & C.R.Hardy, comb. nov.

Calopsis clandestina Esterh. in Linder in Bothalia 15: 465 (1985). Type: mountain above Harold Porter Reserve, Esterhuysen 34146 (BOL, holo.!, B!, C!, E!, F, GRA!, K!, L, M!, MO!, NBG!, NY, PRE, RSA, S!, STE!, TCD!, UC, US, W!, WAG!).

8.7.16. **Restio nudiflorus** (Pillans) H.P.Linder & C.R.Hardy, comb. nov.

Leptocarpus nudiflorus Pillans in Transactions of the Royal Society of South Africa 30: 261 (1945). *Calopsis nudiflora* (Pillans) H.P.Linder: 469 (1985). Type: Somerset Sneeukop, Esterhuysen 8230 (BOL, holo.!, K!).

8.7.17. **Restio pillansii** H.P.Linder in Bothalia 15: 457 (1985).

8.7.18. **Restio corneolus** Esterh. in Linder in Bothalia 15: 443 (1985).

8.7.19. **Restio saroclados** Mast. in A.DC., Monographiae phanerogamarum 1: 291 (1878).

8.7.20. **Restio ejuncidus** Mast. in Botanische Jahrbücher 29, Beiblatt 66: 2 (1900b).

8.7.21. **Restio leptostachyus** Kunth, Enumeratio plantarum 3: 407 (1841).

c) *Restio multiflorus* group: bracts ovate, margins ciliate or shallowly toothed; ovaries with 2(3) locules:

8.7.22. **Restio montanus** Esterh. in Linder in Bothalia 15: 453 (1985).

8.7.23. **Restio multiflorus** Spreng., Systema vegetabilium 1: 187 (1824).

8.7.24. **Restio tuberculatus** Pillans in Annals of the Bolus Herbarium 3,3: 146 (1922).

8.7.25. **Restio scaberulus** N.E.Br. in Flora capensis 7: 751 (1900).

8.7.26. **Restio sejunctus** Mast. in Flora capensis 7: 97 (1897).

8.7.27. **Restio stokoei** Pillans in Transactions of the Royal Society of South Africa 16: 231 (1928).

d) *Restio dodii* group: spathes taller than the spikelets, plants often very fine and tangled, ovaries unilocular and dehiscent:

8.7.28. **Restio rarus** Esterh. in Linder in Bothalia 15: 459 (1985).

8.7.29. **Restio degenerans** Pillans in Transactions of the Royal Society of South Africa 30: 246 (1945).

8.7.30. **Restio singularis** Esterh. in Linder in Bothalia 15: 460 (1985).

8.7.31. **Restio alticola** Pillans in Journal of South African Botany 19: 101 (1952).

8.7.32. **Restio scaber** Mast. in Botanische Jahrbücher 29, Beiblatt 66: 1 (1900b).

8.7.33. **Restio peculiaris** Esterh. in Linder in Bothalia 15: 455 (1985).

8.7.34. **Restio arcuatus** Mast. in A.DC., Monographiae phanerogamarum 1: 247 (1878).

8.7.35. **Restio inconspicuus** Esterh. in Linder in Bothalia 15: 449 (1985).

8.7.36. **Restio vallis-simius** H.P.Linder in Bothalia 15: 462 (1985).

8.7.37. **Restio secundus** (Pillans) H.P.Linder in Bothalia 15: 460 (1985).

8.7.38. **Restio decipiens** (N.E.Br.) H.P.Linder in Bothalia 15: 444 (1985).

8.7.39. **Restio fragilis** Esterh. in Linder in Bothalia 15: 447 (1985).

8.7.40. **Restio colliculospermus** H.P.Linder in Bothalia 15: 443 (1985).

8.7.41. **Restio implicatus** Esterh. in Linder in Bothalia 15: 447 (1985).

8.7.42. **Restio festuciformis** Nees ex Mast. in Journal of the Linnean Society, Botany 8: 248 (1865), as *festucaeformis*.

8.7.43. **Restio zuluensis** H.P.Linder in Bothalia 15: 463 (1985).

8.7.44a. **Restio dodii** Pillans in Annals of the Bolus Herbarium 3,2: 85 (1921) var. **dodii**.

8.7.44b. **Restio dodii** Pillans var. **purpurascens** Pillans in Transactions of the Royal Society of South Africa 16: 252 (1928).

8.7.45. **Restio dispar** Mast. in Journal of the Linnean Society, Botany 8: 246 (1865).

8.7.46. **Restio purpurascens** Nees ex Mast. in Journal of the Linnean Society, Botany 8: 249 (1865).

8.7.47. **Restio ingens** Esterh. in Linder in Bothalia 15: 449 (1985).

8.7.48. **Restio communis** Pillans in Transactions of the Royal Society of South Africa 16: 264 (1928).

8.7.49. **Restio paludicola** H.P.Linder, sp. nov., a *R. communis* spiculis maribus minoribus (8–10 mm longis), paucifloris (1 vel 2) differt.

TYPE.—Western Cape, 3419 (Caledon): Caledon Div., Hermanus Mountain, on rocky banks of a small perennial stream, overlooking coast, growing quite densely in places, 1–2 ft [0.3–0.6 m] tall, ± 1000 ft [300 m], (–AC), 26-08-1973, Esterhuysen 33222 (BOL, holo.).

Plants mat-forming or tangled, stoloniferous. *Fertile culms* sparsely branched, finely to roughly warty, green or olivaceous, 0.3–0.8 m long, 0.1–0.7 mm diam. at apex; sheaths closely convoluted, 10–35 mm long, reddish brown with golden mottling, tuberculate, apical margins truncate, coriaceous, hyaline shoulders up to half as long as sheath, acute; mucro penicillate, straight and erect or recurved, 3–9 mm long. *Male inflorescence* racemose, with 2–10 spikelets, 40–80 mm long; spathes chartaceous, reddish brown with a golden speckling, persistent, taller than spikelets; spikelets sessile, obovate (obtriangular), rounded, 8–10 mm long, 1- or 2-flowered; bracts longer than flowers, 3–6 mm long, linear or oblong, acute, chartaceous, bract with upper margin like body of bract, bract awn minute or absent. *Male flower* 2.0–3.5 mm long; outer tepals cartilaginous; inner tepals shorter than outer, membranous, outer lateral tepals conduplicate or as other tepals, glabrous or keel sparsely villous (visible only under higher magnification); anthers 1.2–1.5 mm long, exserted from flowers; pistillode present. *Female inflorescence* racemose, with 2–10 spikelets, 30–80 mm long; spathes longer than spikelets, persistent, cartilaginous; spikelet sessile, obtriangular, truncate, 9–14 mm long, mostly single-flowered, rarely 2- or 3-flowered; bracts at least as tall as flowers, 5–9 mm long, linear or oblong, acute, chartaceous, awn minute or absent. *Female flower* 3.5–4.0 mm long; tepals cartilaginous, glabrous and smooth or keels of lateral sepals sparsely villous, apices acute, inner and outer whorls same length, 3.5–4.0 mm long; odd outer tepal linear or oblong, inner tepals linear or oblong; staminodes present. *Gynoecium*: styles feathery, white, 3, free to base; ovary unilocular, dehiscent. *Seed* 1.6–1.7 × 0.9–0.95 mm, elliptical in side view, triangular in cross section, tan or pink, smooth (shiny). *Culm anatomy*: epidermal cells 1-layered, lateral walls straight, unthickened, outer wall thickened, colliculate, glabrous, l/w ratio 2.5 : 1.5; stomatal apparatus superficial, guard cells seated on top of support cells; chlorenchyma of 2 layers of cells, l/w ratio 5 : 3, inner and outer layers similar; protective cells reaching to base of chlorenchyma layer; parenchymatous layer of 1 or 2 cells, cells smaller than epidermal cells; sclerenchyma with 4–7 layers of cells, without protrusions; central ground tissue with scattered cavities; tannin found in epidermis, sclerenchyma or central ground tissue; silica sand in chlorenchyma (where protective cells touch parenchyma). *Flowering time*: March or April; seed release in August or September.

Distribution and ecology: restricted to the Kleinrivierberge behind Hermanus, in the Western Cape, where it is found at an altitude of 300–700 m, on Table Mountain Sandstone. The species is restricted to wet habitats, in seepages with *Roridula*, and along stream margins. These are found on the south-facing upper slopes of these low mountains, where they receive ample rain throughout the year. The plants grow into a dense tangled understory under the other vegetation.

Notes: the new species is very close to *Restio communis* from the Cape Peninsula, but it differs in the less robust spikelets, the more slender flowers, and the smaller female bracts. The male spikelets are 8–10 mm long (instead of 15–20 mm), and have only 1 or 2 flowers (instead of 6–12 flowers), and the male flowers are 2.0–3.5 mm long (instead of 3.6–4.0 mm long). There is a single collection

from the Caledon Swartberg, which might be intermediate, or which might constitute yet another segregate.

Etymology: *paluster* (Latin), marshy; *cola* (Latin), dweller in; referring to the habitat of the species in boggy places.

Additional collections

WESTERN CAPE.—3419 (Caledon): Hermanus Mountain, Roridula Stream, forming a dense undergrowth in wet seepages, (–AC), 16-05-1999, H.P.Linder 6933 (Z); Caledon, above Vogelklip Kloof, Hermanus, banks of small open stream, diffuse, amongst shrubs, (–AD), 18-11-1973, Esterhuysen 33352 (BOL); Caledon, Klein River Mtns, nr Hermanus, Rocklands Peak area, in small marsh, on stream banks, (–AD), 03-05-1971, Esterhuysen 32572 (BOL); Caledon, Maanschyn Kop (Rocklands Kop), ± 1 mile [1.6 km] E of summit peak; in small marsh below upper slopes of ridge, (–AD), 08-10-1967, Esterhuysen 31732 (BOL); Caledon, Maanschyn Kop, between Hermanus and Stanford, in small marsh on E slopes, (–AD), 22-02-1968, Esterhuysen 31930a (BOL); Caledon, Swartberg, at base of marsh, on N slope, over ridge, (–AB), 13-03-1976, Esterhuysen 34208 (BOL).

8.8. *Restio* subgen. *Locapsis* H.P.Linder & C.R. Hardy, subgen. nov., a subgeneribus ad *Restio* ascriptis combinatione epidermidis culmorum unistratae, cum vaginis persistentibus, spiculisque maribus erectis, ovario indehiscenti, spiculisque femineis fusiformibus, tepalisque chartaceis rotundatis distinguendum.

TYPE.—*Restio vimineus* Rottb.

Plants mostly tufted, occasionally tending to mat-forming from spreading underground stolons. *Fertile culms* mostly branching, round; sheaths persistent, closely or loosely convoluted or often flat and standing free from culm, margins generally same texture as body of sheath, without membranous upper margin or membranous shoulders. *Male and female inflorescences* similar, racemose or paniculate, with up to 20 erect spikelets; spathes persistent, very rarely overtopping spikelets; bracts concolorous, margins same texture and colour as body of bract, usually cartilaginous, as tall as or somewhat taller than flowers. *Male flowers* with exserted anthers. *Female spikelet* generally narrowly elliptical, with up to 12 flowers, as flowers mature bracts usually diverge, transforming spikelet from slender to bristly. *Female flowers* laterally compressed; female tepals chartaceous and apically rounded, keels of lateral sepals generally ± villous; staminodes present or absent. *Gynoecium* with 3, feathery, white to red styles free to base or seated on a stylopodium; ovary unilocular, indehiscient. *Diaspores* small, soft nuts, perianth persistent and ± enclosing nuts. *Culm anatomy*: epidermal cells in 1 layer, lateral walls straight and unthickened or sinuose and thickened; parenchyma (1)2(3) cells wide; central ground tissue with a single central cavity (this lacking in *R. ramosissimus*) tannin usually absent, when present, in epidermis and central ground tissue; silica usually absent, but present in parenchyma of *R. rigoratus*.

Etymology: *Locapsis* (f.), an anagram of *Calopsis*.

Notes: *Restio* subgen. *Locapsis* contains the largest fragment of *Calopsis* sensu Linder (1984). The genus is readily diagnosed by several attributes. The spreading, concolorous sheaths are not found in all species, but are quite unique in the tribe. The narrow, usually many-flowered female spikelets are also distinctive, especially together with the more-or-less papery, rounded tepals. As such, the genus is easy to delimit against its phylogenetic

cally closest relatives: *Restio* s.str. and *R.* subgen. *Ischyrolepis* (Figure 5). However, it is much more difficult to delimit the genus from *Restio* subgen. *Eremorestio*, and morphologically and ecologically it would be much more satisfying to combine these two genera.

8.8.1. *Restio andreaeanus* (Pillans) H.P.Linder & C.R.Hardy, comb. nov.

Leptocarpus andreaeanus Pillans in Transactions of the Royal Society of South Africa 16: 349 (1928). *Calopsis andreaeana* (Pillans) H.P.Linder: 465 (1985). Type: Willowmore Aasvogelberg, *Andreae* 975 (BOL, holo.; STE!).

8.8.2. *Restio tenuispicatus* H.P.Linder & C.R.Hardy, nom. nov. pro *Hypolaena filiformis* Mast. in Journal of the Linnean Society, Botany 10: 267 (1868). *Calorophus filiformis* (Mast.) Kuntze: 747 (1891). *Calopsis filiformis* (Mast.) H.P.Linder: 467 (1985). Type: Houw Hoek Mtn, *Zeyher* 4349 (K, lecto.! [Linder in Bothalia 15: 467 (1985)]; BOL!, BR!, MEL!, P!); s.loc., *Thom* 1031 (K!), non *Restio filiformis* Poir.

The name refers to the slender culms, also expressed in the specific epithet *filiformis*.

8.8.3. *Restio calcicola* H.P.Linder & C.R.Hardy, nom. nov. pro *Leptocarpus fruticosus* Mast. in Botanische Jahrbücher 29, Beiblatt 66: 9 (1900b). *Calopsis fruticosa* (Mast.) H.P.Linder: 467 (1985). Type: in hills near Ratels River, *Schlechter* 9718 (K, lecto.! [Linder, Bothalia 15: 467 (1985)]; BM!, BR!, MO!, NBG!, P!, S!, WAG!), *Schlechter* 9717 (B!, BM!, BR!, K!, MO!, NBG!, P!, S!, WAG!), non *Restio fruticosus* Thunb. (= *Rhodocoma fruticosa* (Thunb.) H.P.Linder).

This is a limestone species, hence the specific name.

8.8.4. *Restio albotuberculatus* H.P.Linder & C.R.Hardy, nom. nov. pro *Leptocarpus burchellii* Mast. in Journal of the Linnean Society, Botany 10: 222 (1868). *Calopsis burchellii* (Mast.) H.P.Linder: 465 (1985). Type: between Vet River and Krombecks River, *Burchell* 7185 (K, lecto.! [Linder in Bothalia 15: 465 (1985)]; BOL!); foot of Langeberg at Kampsche Berg, *Burchell* 7146 (BOL!, K!); Malgaten River at Wolf Drift, *Burchell* 6101 (BOL!, K!), non *Restio burchellii* Pillans.

Named for the characteristic white tubercles on the culms.

8.8.5. *Restio muirii* (Pillans) H.P.Linder & C.R.Hardy, comb. nov.

Leptocarpus muirii Pillans in Transactions of the Royal Society of South Africa 16: 353 (1928). *Calopsis muirii* (Pillans) H.P.Linder: 469 (1985). Type: north end of Garcia's Pass, *Muir* 3178, 3179 (BOL, holo.).

8.8.6. *Restio ramosissimus* H.P.Linder & C.R.Hardy, nom. nov. pro *Hypolaena gracilis* Nees ex Mast. in Journal of the Linnean Society, Botany 10: 266 (1868). *Calorophus gracilis* (Mast.) Kuntze: 747 (1891). *Leptocarpus gracilis* (Mast.) Pillans: 146 (1922). *Calopsis gracilis* (Mast.) H.P.Linder: 467 (1985). Type: Mui-zenberg, *Zeyher* 4347 (K, lecto.! [Linder in Bothalia 15: 467 (1985)]; MEL!, P!, S!, Z!); near Simonstown, *Zeyher* 1006 (K!); *Wright* 500 (P!), non *Restio gracilis* R.Br.

8.8.7. *Restio rigoratus* (Mast.) H.P.Linder & C.R.Hardy, comb. nov.

Leptocarpus rigoratus Mast. in Botanische Jahrbücher 29, Beiblatt 66: 9 (1900b). *Calopsis rigorata* (Mast.) H.P.Linder: 470 (1985). Type:

in hills near Vogelvlei near Elim, *Schlechter* 10490 (B, lecto.! [Linder in Bothalia 15: 470 (1985)]; BOL!, K!, MO!, NBG!, P!, S!, WAG!, Z!).

8.8.8. *Restio rudolfii* (Pillans) H.P.Linder & C.R.Hardy, nom. nov. pro *Leptocarpus marlothii* Pillans in Transactions of the Royal Society of South Africa 16: 353 (1928). *Calopsis marlothii* (Pillans) H.P. Linder: 467 (1985). Type: Vaalkloof, near Karoopoort, *Marloth* 9102 (BOL, holo.!; B!, K!), non *Restio marlothii* Pillans.

Named for Rudolf Marloth.

8.8.9. *Restio vimineus* Rottb., Descriptiones plantarum rariorum 10 (1772).

8.8.10. *Restio adpressus* (Esterh.) H.P.Linder & C.R.Hardy, comb. nov.

Calopsis adpressa Esterh. in Linder in Bothalia 15: 465 (1985). Type: hills inland from Pearly Beach, *Esterhuysen* 32977 (BOL, holo.!; E!, K!, L, M!, MO!, S!).

8.8.11. *Restio durus* (Esterh.) H.P.Linder & C.R.Hardy, comb. nov.

Calopsis dura Esterh. in Linder in Bothalia 15: 466 (1985). Type: South Cedarberg suurvlaakte, between Kaffirkop and Loskop, *Esterhuysen* 34251 (BOL, holo.!; B!, C!, E!, F, GRA!, K!, L, LD, M!, MO!, NBG!, NY, PRE!, RSA, S!, STE!, TCD!, UC, US, W!, WAG!).

8.9. *Restio* subgen. *Ischyrolepis* (Steud.) H.P.Linder & C.R.Hardy, stat. nov.

Ischyrolepis Steud., Synopsis plantarum glumacearum. 2: 249 (1855). Type: *Ischyrolepis subverticellatus* Steud. (= *Restio subverticellatus* (Steud.) Mast.).

Plants tufted or tangled, often with spreading stolons, but very rarely with rhizomes. Fertile culms usually branching, rarely unbranched or branches whorled at nodes; round or very rarely compressed; sheaths persistent, closely or more rarely loosely convoluted, very rarely standing free from culm; margins coriaceous or membranous, sometimes with tall membranous lobes flanking mucro. Male and female inflorescences basically quite similar, racemose to paniculate, 1 to numerous spikelets, except that females generally have fewer and larger spikelets than males; in some species male spikelets tightly clustered, while females tend to have single spikelets. Male spikelets sometimes linear and curved, bracts obtuse to often acuminate and recurved, or extended into a slender awn; anthers exerted from flowers at anthesis. Female spikelets with up to 40 flowers; bracts shorter to taller than flowers, apically obtuse to often acuminate and recurved, or extended into a fine awn; flowers laterally compressed; tepals chartaceous or cartilaginous; glabrous or keels of lateral sepals more or less villous; staminodes absent. Gynoecium with 2, white to red, feathery styles; style bases fused to form a pillar; ovary with 2(1) locules, dehiscent. Seed translucent or variously coloured, smooth, pitted, colliculate, striate or rarely rugose. Culm anatomy: epidermal cells 1-layered, lateral walls straight and unthickened or sinuose and thickened; parenchymatous layer 1–3 cells deep; central ground tissue solid or with a single, central cavity; tannin absent or present in epidermis, sclerenchyma or central ground tissue; silica absent or present in parenchyma and/or rarely in central ground tissue.

Etymology: *Ischyrolepis* (f.): *Ischyros* (Greek), strong; *lepis* (Greek), scale; presumably this refers to the usually quite tough floral scales which enclose the flowers.



FIGURE 5.—Portion of strict consensus tree of the total combined analysis of Hardy *et al.* (2008) containing *Restio* subgen. *Locapsis* and *R.* subgen. *Ischyrolepis*. A single species of *Restio* subgen. *Ischyrolepis* (*Restio fusciculatus*) that was missing many data (including all molecular data), was resolved in this tree as sister to *Staberoha* (see Figure 1), albeit with 3 % bootstrap support which we do not consider substantial enough to warrant disputing the monophyly of *Restio* subgen. *Ischyrolepis*. Names in parentheses are the now synonymous names of Linder (2001a) when different from the ones here proposed. Bootstrap values above branches indicate support based on a 500-replicate bootstrap analysis that included 20 species for which DNA data were lacking (asterisked taxa). Bootstrap values below branches indicate support based upon a 500-replicate analysis that included only taxa for which both DNA data and morphology data were available. Where no value is given below a branch it indicates that the clade did not appear in the analysis excluding morphology-only species.

Notes: *Restio* subgen. *Ischyrolepis* is readily diagnosed by a basal stylar peg, formed by the fusion of the two style arms. This persists on the ripe ovary, even after the seed has been released, as a distinctive peg. This is unique in the Restioneae. Furthermore, it usually has two styles (compare to the three or one more typically found). The species can look superficially very similar to *Restio s.str.* or *Restio* subgen. *Craspedolepis*. The pollen

type is held in common with *Staberoha*, but the two genera are not phylogenetically closely related, according to the molecular data.

It is particularly common in the more arid parts of the Greater Cape Floristic Region (Born *et al.* 2007), and is replaced along the wetter coastal mountains by the subgenera *Craspedolepis* and *Restio*.

There are a number of groups in this large subgenus, but it is not possible to clearly diagnose them. Furthermore, the subgenus, as currently defined, is so easily diagnosed that there is very little sense recognizing smaller groups at subgeneric level. However, further research may indicate that these subgroups deserve sectional recognition.

a) Female spikelets small and mostly with single flowers; styles often red:

8.9.1. **Restio anomalus** H.P.Linder sp. nov., a *R. femineus* marginibus vaginarum late membranaceis, tepalis interioribus florum feminearum 3.0–4.5 mm longis, ovario biloculari statim dignoscenda.

TYPE.—Western Cape, 3419 (Caledon): Pheasantshoek near Viljoenshof, in a marshy area near *Elegia fistulosa* and *Restio festucaeformis*, and along a small stream (or furrow), in peaty soil and on clayish bank, no male found, (–DA), 15-09-1976, *Esterhuysen* 34374 (BOL, holo.).

Plants compact, tufted, 0.15–0.25 m tall. *Fertile culms* branching, round, solid or with a small central cavity, finely rugulose or finely warty, green or olivaceous, 0.2–0.4 mm diam. at apex; sheaths several, persistent, closely convoluted, 5–13 mm long, acute, margins entire, variable: greenish/olivaceous or tan or light to darker brown, always with brown speckles and tan margins, hyaline shoulders absent; mucro penicillate, straight and erect or recurved, 3–7 mm long. *Female inflorescence* with 2–10 spikelets, interrupted or linear, 5–70 × 3–5 mm; spathes shorter than spikelets, persistent, coriaceous or cartilaginous; spikelet obovate or triangular with fruit sitting at base and tepals flaring apart at top, 4.0–6.5 mm long, with 1 flower, with 0 sterile bracts; bracts shorter than flowers, erect, 2.6–5.0 mm long, oblong, obtuse, cartilaginous, awn minute to less than half as long as bract body. *Flower* with four tepals; tepals 3.0–4.5 mm long, undifferentiated, coriaceous or cartilaginous, glabrous and smooth; margins entire, apices acute; staminodes absent; ovary with 2 locules, dehiscent; style 1, flattened. *Seed* (1.16–)1.27(–1.44) × (0.68–)0.73(–0.8) mm, in side view elliptical, in transverse view round, white, pitted. *Flowering time*: September.

Distribution and ecology: endemic on the Agulhas plains between Elim, Viljoenshof and the Soetanysberg, at an altitude of 50–150 m, on either sandstone or silcretes. The species is locally common on gravelly soils or damp sand, often with impeded drainage.

Notes: this species is known currently only from the female material, and since it can be very common locally, it is presumably apomictic. It is closely related to *Restio femineus*, which is also known only from female material, and which forms similar neat little branching tufts. However, *R. anomalus* differs in many details from *R. femineus*. The sheath margins are broadly membranous (instead of coriaceous or narrowly membranous), the spathes overtop the spikelets (instead of being as tall as the spikelets), the inner and outer tepals are the same length (instead of the inner tepals being shorter than the outer tepals), the inner tepals are 3.0–4.5 mm long, compared to 2.2–2.6 mm in *R. femineus*, and the ovary has

two locules instead of one. In addition, there are numerous small anatomical differences in the culm.

Etymology: *a-* (in Greek composition), not; *normalis* (Greek), normal; abnormal, referring to the absence of male plants.

Additional collections

WESTERN CAPE.—3419 (Caledon): along road from Baardskeerdersbos to Elim; on laterite scrape on hill W of Elim. Locally common on damp sand over laterite, probably seasonally waterlogged conditions. Erect, tuft-like plants, only females seen, (–DA), 03-07-1999, *Linder* 6940 (BOL); Farm 'Brandfontein'; plateau between the sea and Soetanysberg. Table Mountain Sandstone (TMS) with sand overlay. In shallow wet sand on shaved off TMS bedrock, forming small tussocks. No males seen, (–DD), 25-10-1990, *Linder* 5163 (BOL); Hangnes, base of Soetanysberg; in marsh, near windmill, (–DD), 12-04-1978, *Esterhuysen* 34894 (BOL).

8.9.2. **Restio femineus** (Esterh.) H.P.Linder & C.R.Hardy, comb. nov.

Ischyrolepis feminea Esterh. in Linder in Bothalia 15: 404 (1985). Type: Simonstown, near the Four Seasons, W of Betty's Bay, *Esterhuysen* 31662 (BOL, holo.); C!, E!, K!, L!, M!, MO!, NBG!, PRE!, S!, STE!).

8.9.3. **Restio wallichii** Mast. in Journal of the Linnean Society, Botany 8: 234 (1865).

8.9.4. **Restio rivulus** (Esterh.) H.P.Linder & C.R.Hardy, comb. nov.

Ischyrolepis rivula Esterh. in Linder in Bothalia 15: 413 (1985). Type: Wuppertal, Boboskloof, *Esterhuysen* 31912 (BOL, holo.); C!, E!, F!, K!, L!, LD!, M!, MO!, NBG!, PRE!, S!, STE!, TCD!, UC!, US!, W!, WAG!).

8.9.5. **Restio tenuissimus** Kunth in Enumeratio plantarum 3: 394 (1841).

8.9.6. **Restio longiaristatus** (Pillans ex H.P.Linder) H.P.Linder & C.R.Hardy, comb. nov.

Ischyrolepis longiaristata Pillans ex H.P.Linder in Bothalia 15: 407 (1985). Type: Van Rhynsdorp, Driekoppen, Gifberg, *Esterhuysen* 30749 (BOL, holo.); B!, D!, E!, F!, GRA!, K!, L!, LD!, M!, MO!, NBG!, NY!, PRE!, RSA!, S!, STE!, TCD!, UC!, US!, W!, WAG!).

8.9.7. **Restio sabulosus** Pillans in Transactions of the Royal Society of South Africa 16: 285 (1928).

8.9.8. **Restio rottboellioides** Kunth, Enumeratio plantarum 3: 394 (1841).

8.9.9. **Restio paludosus** Pillans in Annals of the Bolus Herbarium 3,3: 142 (1922).

8.9.10. **Restio papillosus** (Esterh.) H.P.Linder & C.R.Hardy, comb. nov.

Ischyrolepis papillosa Esterh. in Linder in Bothalia 15: 410 (1985). Type: Simonstown, Kenilworth Race Course, *Esterhuysen* 30849 (BOL, holo.); B!, C!, E!, F!, GRA!, K!, L!, LD!, M!, MO!, NBG!, NY!, PRE!, RSA!, S!, STE!, TCD!, UC!, US!, W!, WAG!).

8.9.11. **Restio pratensis** (Esterh.) H.P.Linder & C.R.Hardy, comb. nov.

Ischyrolepis pratensis Esterh. in Linder in Bothalia 15: 411 (1985). Type: Cape Town, Paarl Reserve on Paarl Mountain, *Esterhuysen* 31206 (BOL, holo.); C!, E!, F!, K!, L!, M!, MO!, NBG!, S!, STE!, UC!).

8.9.12. **Restio macer** Kunth, Enumeratio plantarum 3: 390 (1841).

8.9.13. **Restio sporadicus** (Esterh.) H.P.Linder & C.R.Hardy, comb. nov.

Ischyrolepis sporadica Esterh. in Linder in Bothalia 15: 413 (1985). Type: Cape Town, Riverlands near Mamre Road, *Esterhuysen* 34656 (BOL, holo.); C!, E!, K!, L!, M!, MO!, S!, STE!).

8.9.14. **Restio pygmaeus** Pillans in Transactions of the Royal Society of South Africa 30: 253 (1945).

8.9.15. **Restio cincinnatus** Mast. in Journal of the Linnean Society, Botany 8: 240 (1865).

8.9.16. **Restio caespitosus** (Esterh.) H.P.Linder & C.R.Hardy, comb. nov.

Ischyrolepis caespitosa Esterh. in Linder in Bothalia 15: 402 (1985). Type: Caledon, Pheasantshoek near Viljoenshof, Esterhuysen 34358 (BOL, holo.; B!, C!, E!, F!, GRA!, K!, L!, LD!, M!, MO!, NBG!, NY!, PRE!, RSA!, S!, STE!, TCD!, UC!, US!, W!, WAG!).

8.9.17. **Restio saxatilis** (Esterh.) H.P.Linder & C.R.Hardy, comb. nov.

Ischyrolepis saxatilis Esterh. in Linder in South African Journal of Botany 56: 456 (1990). Type: Stellenbosch, Dragoon Buttress, Esterhuysen 32360 (BOL, holo.; K!, M!, MO!, S!).

8.9.18. **Restio curviramis** Kunth, Enumeratio plantarum 3: 395 (1841).

8.9.19. **Restio nanus** (Esterh.) H.P.Linder & C.R.Hardy, comb. nov.

Ischyrolepis nana Esterh. in Linder in Bothalia 15: 409 (1985). Type: Worcester, lower Wellington Sneeuwkop, at W base of the shale band, Esterhuysen 32658 (BOL, holo.; C!, E!, K!, L!, M!, MO!, S!, STE!).

8.9.20. **Restio duthieae** Pillans in Transactions of the Royal Society of South Africa 16: 287 (1928).

b) Spikelets larger, usually few, many-flowered:

8.9.21. **Restio marlothii** Pillans in Annals of the Bolus Herbarium 3,2: 83 (1921).

8.9.22. **Restio schoenoides** Kunth, Enumeratio plantarum 3: 391 (1841).

8.9.23. **Restio constipatus** H.P.Linder, sp. nov., a *Restio wittebergensi* culmis ramosis, a *R. schoenoides* spiculis maribus 3–6 mm longis, spathis femineis spicula aequantibus, seminibus argenteis recedit.

TYPE.—Western Cape, 3319 (Worcester): summit of Matroosberg, among rocks, (–BC), 21-01-2001, H.P.Linder 7139 (Z, holo.; BOL, K, MO, NBG).

Plants clumped or tangled, stoloniferous, forming dense cushions among boulders, 0.2–0.5 m tall, or spreading mats on open slopes. *Fertile culms* branching, smooth, green or olivaceous, 0.5–1.5 mm diam. at apex; sheaths closely convoluted, 10–25 mm long, dark brown, apical margins narrowly membranous, hyaline shoulders absent, apex acute to acuminate; mucro penicillate, straight and erect, 2–10 mm long. *Male inflorescence* with 1 spikelet (very rarely, in the Swartberg) or 2–10 spikelets, forming a tight button, 8–25 × 7–25 mm; spathes persistent, as tall as spikelets, coriaceous, rather similar to lower bracts; male spikelets sessile, oblong or elliptical, 7–12 × 3–6 mm, 3–10-flowered; bracts taller than flowers, 5.5–10 mm long, oblong, acuminate, cartilaginous. *Male flower* 4.5–5.0 mm long, both tepal whorls equally long, hyaline or membranous, linear or oblong, outer lateral tepals conduplicate, sparsely villous on keels; anthers 2–3 mm long, exerted from flowers; pistillode absent. *Female inflorescence* with 1 spikelet (rarely, then mostly at western and eastern extremes of range) or 2–10 spikelets, forming a tight button, 10–25 × 3–25 mm; spathes equalling spikelets, persistent, coriaceous; spikelets sessile, elliptical, obtuse or acute, 10–20 mm long, 5–15-flowered, with 4 or 5 sterile bracts; bracts taller than flowers, erect or reflexed, 5.5–10 mm long, oblong, acuminate, cartilaginous, apical margin like rest of bract, same as body of bract, awn less than half

as long as bract body. *Female flower* 5.0–6.5 mm long, tepals cartilaginous, all equally long, outer lateral tepals conduplicate with sparsely villous keels, odd outer and inner tepals oblong; staminodes absent. *Gynoecium*: styles 2, feathery, white; style bases free but adjacent; ovary dehiscent, bilocular. *Seed* 1.3–1.5 × 1 mm, in side view elliptical, in diam. round, silvery, pitted. *Flowering time*: September to December.

Distribution and ecology: widespread on the summits of the inner ranges of the Cape Fold Mountains, from Sneeuwkop in the Cedarberg to Mannetjiesberg in the Kamannassie and Meiringspoortberg in the Groot Swartberg. The species is absent from the lower coastal mountains: the Kogelberg, Kleinriviersberg and the Cape Peninsula. The altitude range is 1 500–2 100 m, all collections are from sandstone habitats. This is a species of rocky summits and exposed ridges. On the Matroosberg, the first author found it growing on shady rock ledges, well protected from fire, and quite cool, but dry. This is consistent with most habitat notes, which indicate cool, dry places, associated with rocks or rocky sites, or ledges. Possibly these are all fire-protected habitats.

Notes: the new species is similar to *Restio wittebergensis*; both species have both male and female spikelets aggregated into button-like heads. However, it differs from *R. wittebergensis* by its branching culms (*R. wittebergensis* has simple culms), and the stoloniferous habit (*R. wittebergensis* is caespitose). The stoloniferous habit and aggregated spikelets suggest a similarity to *R. schoenoides*, but this species is more slender, carpet-forming rather than tangled. There is a wide range of variation within *R. constipatus*, and in its current definition it might include two entities: the typical boulder-habitat (rocky summit) plants from the western part of the range, and more mat-forming plants from the Swartberg, which are very common along the summit ridges of these inland mountains. The differences in growth form are corroborated by a subtle difference in the flower size and a more slender growth form. This needs more, critical, investigation. These collections have in the past been assigned to *R. schoenoides*; however, the latter species is better understood as a summer rainfall species widespread in the Drakensberg and reaching to the Blouberg in the Limpopo Province. The interface between *R. schoenoides* and *R. wittebergensis* remains taxonomically difficult.

Etymology: *constipata* (Latin), crowded together; referring to the male and female spikelets, clustered together in capitate inflorescences. The name does not refer to medicinal use.

Additional collections

WESTERN CAPE.—3219 (Wuppertal): Cedarberg, kloof above Crystal Pool, (–AC), 25-06-1942, Esterhuysen 7897 (BOL); Cedarberg, peak near Sneeuwkop, (–AC), 02-01-1942, Esterhuysen 7567 (BOL); Cedarberg, Middelberg, SW slopes, (–AC), 01-03-1940, Esterhuysen 2524b (BOL); Cold Bokkeveld, Turret Peak, in a cool shady spot above stream, and at base of rock, in colonies, forming patches, (–CC), 15-10-1972, Esterhuysen 33025 (BOL).

3319 (Worcester): Ceres–Tulbagh, Swartgat Peak, Sneeuwkop peaks, on steep upper slopes, SE aspect, (–AA), 02-05-1964, Esterhuysen 30687 (BOL); Worcester, Mosterts Hoek Twins, (–AD), 08-01-1944, Esterhuysen 9832 (BOL); Worcester, Mostert's Hoek Twins, S side of summit at base of low rock cap, in solid masses, (–AD), 23-02-1964,

Esterhuysen 30615 (BOL); Worcester, Ridge Peaks, Waaihoek, summit, 1 800 m, amongst rocks, (–AD), 15-12-1942, *Esterhuysen 8372* (BOL); Ceres, Roodeberg, (–BC), 01-01-1940, *Esterhuysen 1487* (BOL); Worcester–Ceres, Matroosberg, at rocky summit, in shallow soil around base of low rock or along cracks or in stony soil, dense wiry plants, (–BC), 10-10-1962, *Esterhuysen 29728* (BOL); Worcester, Roodeberg, Matroosberg group, on upper rocky slopes, often along step ledges, at the base of rock, dense growth, (–BC), 05-04-1964, *Esterhuysen 30677* (BOL); Worcester, Matroosberg, on upper rocky slopes, along the base of low rock, dense masses, (–BC), 08-04-1980, *Esterhuysen 35419a* (BOL); Ceres, Roodeberg, (–BC), 01-01-1940, *Esterhuysen 1487* (BOL); Worcester, Pulpit Rock Nek, Hex River Mtns, in cracks in rock pavement ledges, (–BC), 09-03-1963, *Esterhuysen 30076* (BOL); Worcester, Upper Wellington Sneekop, N aspect, steep, rocky, well-drained slope, (–CA), 04-10-1964, *Esterhuysen 30779a* (BOL); Worcester, Du Toit's Peak, on rocky upper slopes and summit plateau, in dense masses, (–CA), 21-12-1975, *Esterhuysen 34164* (BOL); Worcester, Du Toit's Peak, on rocky summit and upper rocky slopes and ridges, S aspect, varying in height, (–CA), 01-12-1963, *Esterhuysen 30561* (BOL); Worcester, Du Toit's Peak, (–CA), 26-01-1943, *Esterhuysen 8558* (BOL); Worcester, Witteberg, on rocky slopes near summit, (–CA), 28-02-1965, *Esterhuysen 30957* (BOL); Worcester, Upper Wellington Sneekop, growing against or next to rock, not seen on the smoother slopes, (–CA), 23-01-1972, *Esterhuysen 32798* (BOL); Worcester, Slanghoek Peak, (–CA), 28-12-1975, *Esterhuysen s.n.* (BOL); Worcester, Slanghoek Peak, on shale band on S side, (–CA), 31-12-1972, *Esterhuysen 33070a* (BOL); Worcester, Slanghoek Mtns, ridge S of Grassy Dome, (–CA), 05-06-1966, *Esterhuysen 31556* (BOL); Worcester, Du Toit's Peak, at rocky summit, growing between low rock, (–CA), 25-11-1962, *Esterhuysen 29892* (BOL); Worcester, Witteberg, above Du Toit's Kloof, on summit, growing from between rock and in shallow marshy soil, (–CA), 04-08-1963, *Esterhuysen 30253* (BOL); Worcester, Brandwacht Peak, near summit, growing between rock surfaces or from crevices on W side, growing densely, (–CB), 07-04-1963, *Esterhuysen 30124*; Worcester, Waaihoek Peak, on SSE side of rocky summit, and amongst rocks near summit, common in patches, (–CB), 05-06-1965, *Esterhuysen 31063* (BOL); Kaffir Kop, between Paardekop and Adolph's Kop, Fransch Hoek Pass, Villiersdorp, on sloping sandstone pavement, S aspect, (–CC), 02-11-1969, *Esterhuysen 32309a* (BOL); Caledon, Olifantsberg area near Genadendal, Boscheveld, rocky, summits, (–CD), 02 Jan. 1965, *Esterhuysen 30895* (BOL); Soutrivier, Koo Rd, ± 14 mls [22.4 km] S of Matroosberg Station, in *Protea mellifera* veld, (–DB), 09-02-1964, *Jessop s.n.* (BOL).

3321 (Ladismith): Ladismith, Toverkop, Swartberg, on upper slopes, (–AC), 02-09-1973, *Esterhuysen 33231* (BOL); Ladismith, Toverkop, Swartberg, on ledges and rocky places, N or roughly N aspect, common in patches, (–AC), 30-03-1964, *Esterhuysen 30671* (BOL); Ladismith, from Toverkop to Seven Weeks Poort Berg, common on upper rocky slopes, (–AC), 30-03-1959, *Esterhuysen 28269* (BOL); Prince Albert, Seven Weeks Poort Mtns, (–AD), 01-12-1928, *Stokoe s.n.* (BOL); Ladismith, Swartberg, Kouveldberg, (–AD), 30-03-1964, *Esterhuysen 30666a* (BOL); Ladismith, Seven Weeks Poort Berg to Toverkop, Swartberg, very common on upper slopes forming dense stands or pure communities in places, in stony, rocky places, on ledges, 1.0–1.5 ft [0.3–0.5 m] tall, (–AD), 27-03-1964, *Esterhuysen 30656* (BOL); Ladismith, Seven Weeks Poort Berg, common on upper slopes, N north side and summit, (–AD), 01-04-1975, *Esterhuysen 33798* (BOL); Calitzdorp, Gamka Reserve, Snygans-Baakens Kop area, at base of small cliff, S aspect, below hilltop, and between rock on top of cliff, (–BC), 22-05-1975, *Esterhuysen 33834* (BOL).

3322 (Oudtshoorn): Prince Albert, Swartberg, (–AC), 01-10-1949, *Stokoe in SAM74945* (BOL); Prince Albert, Swartberg, (–AC), 01-10-1949, *Stokoe in SAM74944* (BOL); Prince Albert, Tierberg area, Swartberg, N slopes, (–AD), 01-06-1962, *Esterhuysen 29549* (BOL); Oudtshoorn, Meiringspoortberg, on S slopes near summit and on N side on small vlakte, (–BC), 09-04-1966, *Esterhuysen 31494* (BOL); Uniondale, Mannetjiesberg, S slopes, (–DB), 05-11-1941, *Esterhuysen 6403* (BOL).

8.9.24. *Restio virgeus* Mast. in *Botanische Jahrbücher* 29, Beiblatt 66: 4 (1900b).

8.9.25. *Restio curvibracteatus* (Esterh.) H.P.Linder & C.R.Hardy, comb. nov.

Ischyrolepis curvibracteata Esterh. in Linder in *Bothalia* 15: 403 (1985). Type: Worcester, Du Toit's Peak, *Esterhuysen 29894* (BOL, holo.: B!, C!, E!, F!, K!, L!, M!, MO!, S!, STE!, UC!).

8.9.26. *Restio wittebergensis* (Esterh.) H.P.Linder & C.R.Hardy, comb. nov.

Ischyrolepis wittebergensis Esterh. in Linder in *Bothalia* 15: 417 (1985). Type: Montagu, upper rocky S slopes of Witteberge, *Esterhuysen 30479* (BOL, holo.: C!, E!, F!, K!, L!, LD!, M!, MO!, NBG!, S!, STE!, UC!, WAG!).

8.9.27. *Restio setiger* Kunth, Enumeratio plantarum 3: 385 (1841).

8.9.28. *Restio vilis* Kunth, Enumeratio plantarum 3: 389 (1841).

8.9.29. *Restio coactilis* Mast. in *Botanische Jahrbücher* 29, Beiblatt 66: 3 (1900b).

8.9.30. *Restio karooicus* (Esterh.) H.P.Linder & C.R.Hardy, comb. nov.

Ischyrolepis karooica Esterh. in Linder in *Bothalia* 15: 406 (1985). Type: Worcester, Karooport, on mountain slopes above the poort, *Esterhuysen 30458* (BOL, holo.: BM!, C!, E!, F!, GRA!, K!, L!, LD!, M!, MO!, NBG!, NY!, PRE!, RSA!, S!, STE!, TCD!, UC!, US!, W!, WAG!).

8.9.31. *Restio hystrix* Mast. in *Journal of the Linnean Society, Botany* 10: 276 (1868).

8.9.32. *Restio esterhuyseniae* Pillans in *Transactions of the Royal Society of South Africa* 30: 248 (1945).

8.9.33. *Restio gossypinus* Mast. in *Botanische Jahrbücher* 29, Beiblatt 66: 3 (1900b).

8.9.34. *Restio affinis* (Esterh.) H.P.Linder & C.R.Hardy, comb. nov.

Ischyrolepis affinis Esterh. in Linder in *Bothalia* 15: 401 (1985). Type: Montagu, Langeberg, Kruispad Ridge between Goedgeloof Peak and Protea Valley, *Esterhuysen 35612* (BOL, holo.: B!, C!, E!, F!, K!, L!, LD!, M!, MO!, NBG!, PRE!, S!, STE!, TCD!, UC!, US!, W!, WAG!).

8.9.35. *Restio ocreatus* Kunth, Enumeratio plantarum 3: 385 (1841).

8.9.36. *Restio fraternus* Kunth, Enumeratio plantarum 3: 386 (1841).

8.9.37. *Restio elsiae* H.P.Linder, sp. nov., *R. ocreatae* affinis, sed culmis simplicibus, spiculis femineis ellipticis vel ovatis, seminibus longioribus (2.2–2.8 mm) notabilis.

TYPE.—Western Cape, 3319 (Worcester): Waaihoek Mtns, between Zebasberg and Mt Superior, alt. 1 600 m, (–AD), 17-03-2002, *H.P.Linder 7460* (Z, holo.: B, BOL, K, MO, NBG, NSW, PRE).

Plants tufted, 0.16–0.45 m tall, without spreading rhizomes or stolons. *Fertile culms* unbranched, round, solid or with a small central cavity, smooth, olivaceous, 1.2–2.0 mm diam. at apex; sheaths several, persistent, loosely convoluted, 18–36 mm long, orange to reddish brown, apical margins narrowly to broadly membranous, acute to acuminate, hyaline shoulders continuing behind mucro; mucro hair-like, straight and erect or recurved or twisted, 3–8 mm long. *Male inflorescence* racemose or globose, 15–35 × 9–20 mm wide, with 2–10 spikelets; spathes persistent, at least as tall as spikelets, coriaceous or cartilaginous; spikelets erect, elliptical, 7–13 × 2.8–4 mm, 10–40-flowered; bracts longer than flowers, 5–11 mm long, widely oblong, acuminate, coriaceous, bract with upper margin membranous, awn recurved, acuminate, at least half as long as the bract body. *Male flower* 4.5–6.0 mm long; tepals equally long, oblong to elliptical, outer tepals more rigid than inner tepals, outer lateral tepals conduplicate and sparsely to densely villous on keels; anthers 1.8–

3.0 mm long, exerted from flowers; pistillode absent. *Female inflorescence* with 1 spikelet; spathes up to as long as spikelet, persistent, coriaceous or cartilaginous; spikelet elliptical or ovate, 14–23 mm long, 10–30-flowered; bracts longer than flowers, reflexed, 8–14 mm long, ovate, acute or acuminate, coriaceous, awn up to as long as bract body. *Female flower* 5–7 mm long, tepals cartilaginous; outer lateral tepals conduplicate, villous along keels, 5–7 mm long; odd outer tepal oblong or ovate, 5–7 mm long; inner tepals ovate, 4.0–6.5 mm long; staminodes absent. *Gynoecium*: styles 2, feathery, style bases fused to form a pillar; ovary dehiscent, bilocular. *Seed* (2.24–)2.47(–2.76) × (1.3–)1.43(–1.53) mm, in side view elliptical, diam. round, silvery or white (and shiny), pitted. *Flowering time*: January and February; seed release in March and April.

Distribution and ecology: endemic in the Hex River Mountains between Worcester and Ceres, where it is locally very common between 1 600–2 100 m. It is found on stony, well-drained mountain slopes. It appears to occupy the same habitat as *Restio virgeus*, and the two species alternate on the stony slopes between Zebasberg and Mt Superior. The plants appear to be killed by fire, regenerating from seed.

Notes: *Restio elsieae* species is a high-altitude segregate from *R. ocreata*. It differs by the simple, stout culms, and smaller growth form. The single female spikelet with recurved bracts and the unbranched culms are similar to *R. curvibracteatus*, but *R. elsieae* can immediately be recognized by the flat, spreading sheaths.

Etymology: the species is named for Elsie E. Esterhuysen, the foremost collector from the Cape mountains, who made Restionaceae her speciality. She collected actively from 1930 to 1990, and contributed more to our knowledge of the Cape flora than any other collector. Her meticulous collections, assembled to reflect the distribution range and morphological variability of each species, are currently housed at the Bolus Herbarium, but duplicates of her collections are widely distributed.

Additional collections

WESTERN CAPE.—3319 (Worcester): Brandwacht Peak, rocky slopes SW-S aspect, below beacon and at base of summit cap, clumps, forming dense pure stands in places, erect, stiffly rounded, seed shed, (–CB), 07-04-1963, *Esterhuysen* 30123 (BOL); Worcester, Fonteintjiesberg, rocky places on E slopes of ridge below plateau, local, stiff habit, dense rounded clumps, stems pointing in all directions, (–CB), 20-10-1963, *Esterhuysen* 30423 (BOL); Worcester, Fonteintjiesberg, above Pulpit Rock Nek, rocky plateau, N and S aspects and steep slope, (–CB), 16-12-1963, *Esterhuysen* 30588 (BOL); Ceres, Buffelshoek Peak, leading into Witels, shale band, SW aspect, (–AD), 08-10-1956, *Esterhuysen* 26361 (BOL); Ceres, Milner Peak, Hex River Mtns, rocky W slopes, (–AD), 11-11-1960, *Esterhuysen* 28606 (BOL); Worcester, Waaihoek Peak, upper rocky slopes, abundant in patches of almost pure stands, dense, scratchy tufts, stems unbranched, (–AD), 11-02-1964, *Esterhuysen* 30612 (BOL); Worcester, Buffelshoek Peak and Buffelshoek Twins, rocky places, (–AD), 19-09-1965, *Esterhuysen* 31183 (BOL).

8.9.38. *Restio cedarbergensis* H.P.Linder, sp. nov., a *R. ocreatae* culmis gracilioribus, bracteis maribus brevioribus (3.5–5.0 mm longis), floribus maribus brevioribus (2.5–3.0 mm longis), spiculis femineis brevioribus (5–11 mm longis), floribus spiculis femineis paucibus (3–8 floribus), seminibus laevibus differt.

TYPE.—Western Cape, 3219 (Wuppertal): Central Cedarberg, Gabriel's Pass directly above De Rif, 1 300 m, (–AC), 30-09-2000, *H.P.Linder* 7090 (Z, holo.; BOL, K, MO, NBG, PRE).

Plants tufted, 0.3–0.6 m tall, without spreading rhizomes or stolons. *Fertile culms* branching, round, smooth to roughly warty, green or olivaceous, slender, 0.2–0.5 mm diam. at apex; sheaths loosely convoluted or flat and standing free from culm, 8–20 mm long, golden brown to yellow, acuminate, apical margins narrowly membranous, hyaline shoulders absent; mucro absent or awl- or needle-shaped, straight and erect, 0.5–3.0 mm long. *Male inflorescence* with 6–20 spikelets, racemose or paniculate, 20–55 × 6–12 mm; spathes persistent, at most as tall as spikelets, cartilaginous, acuminate; spikelets pendulous on flexible pedicels, linear or ovate, acute, 6–12 × 2–3 mm, 4–15-flowered; bracts equalling flowers, 3.5–5.0 mm long, ovate, acuminate, cartilaginous, awn minute or at least less than half as long as bract body, acuminate recurved apices give spikelet a bristly appearance. *Male flowers* 2.5–3.0 mm long; tepals all equally long, linear to oblong; outer tepals cartilaginous, laterals conduplicate and sparsely villous on keels; inner tepals chartaceous; anthers 1.5–2.0 mm long, exerted from flowers; pistillode absent. *Female inflorescence* with up to 5 spikelets, sparsely paniculate, 5–35 × 4–8 mm; spathes up to as long as spikelets, persistent, cartilaginous; spikelets sessile, elliptical or obovate, rounded, obtuse or acute, 5–11 mm long, 3–8-flowered; bracts 4.5–6.0 mm long, ovate, apiculate, bony or coriaceous, awn less than half as long as bract body. *Female flower* 3.0–4.5 mm long; tepals all equally long, 2.5–4.5 mm long, ovate, acute, bony or coriaceous, outer lateral tepals conduplicate with densely villous keels; staminodes absent. *Gynoecium*: styles 2, feathery, bases fused to form a pillar; ovary dehiscent, bilocular. *Seed* 1.7–2 × 1.1–1.3 mm, side view oblong (but distinctly bulged at one end), cross section triangular (with corners very rounded), grey (often with brown mottling), smooth. *Flowering time*: April.

Distribution and ecology: this new species is restricted to the southern Cedarberg and the northern Bokkeveld, and has been collected from Bloukop, north of the Bokkeveld Sneeuokop, to Gabriel's Pass in the central Cedarberg. In this region, *Restio cedarbergensis* is found from 900–1 500 m, on well-drained soils, often described as rocky. Several collections are from shale bands, and the first author has seen the species grow next to renosterveld, where sandstone meets shale, as well as on typical dry TMS soils. The species appears to prefer hot, dry, well-drained localities. Plants appear to be killed by fire, regenerating from seed.

Notes: *Restio cedarbergensis* was previously included under *R. ocreatus*, but it differs by the slender culms, and much smaller spikelets. On Gabriel's Pass the two species co-occur, without intermediates. The new species has finer culms and smaller spikelets, and forms lower, more tangled plants, whereas *R. ocreatus* is much stouter, with larger spikelets. Curiously, the molecular phylogeny does not indicate the relationship to *R. ocreatus*, but suggests a relationship to the *R. sieberi* group, which appears to be unlikely on the basis of the morphological data.

Etymology: the name indicates the distribution range of the species, from the Cedarberg.

Additional collections

WESTERN CAPE.—3219 (Wuppertal): Cedarberg, Wolfberg-Tafelberg area, in rocky places, common (–AC), 28-12-1962, *Esterhuysen 30008* (BOL); S Cedarberg, (–AC), 01-04-1947, *Stokoe 9570* (BOL); S Cedarberg, Dwarsrivierberg, rocky slope, (–CA), 01 Apr. 1956, *Esterhuysen 25548* (BOL); S Cedarberg, on E spur of Hondverbrand Ridge, sandy vlakte [flats], (–CB), 21-04-1946, *Esterhuysen 12719* (BOL); S Cedarberg, Sandfontein Peak, between rocks, (–CB), 05-04-1947, *Esterhuysen 13871* (BOL); S Cedarberg, Sandfontein Peak, on rocky sandy W slopes, frequent, (–CB), 20-04-1957, *Esterhuysen 27213* (BOL); S Cedarberg, between Sandfontein Peak and Gideon's Kop, on lower stony W slopes, (–CB), 18-04-1965, *Esterhuysen 31024* (BOL); N Cold Bokkeveld, Bloukop, on shale band slopes, locally very common, not seen along rocky sandstone ridge, (–CB), 07-07-1968, *Esterhuysen 31971* (BOL).

8.9.39. ***Restio fuscicululus* Pillans** in Transactions of the Royal Society of South Africa 30: 249 (1945).

8.9.40. ***Restio aridus* Pillans** in Annals of the Bolus Herbarium 3,2: 84 (1921).

8.9.41. ***Restio capensis* (L.) H.P.Linder & C.R.Hardy**, comb. nov.

Schoenus capensis L., *Amoenitates* 4: 264 (1755). *Restio dichotomus* L.: 735 (1767), nom. illeg. *Thamnochortus dichotomus* (L.) Spreng.: 187 (1824), nom. illeg. *Ischyrolepis capensis* (L.) Linder: 402 (1985). Type: Cape, s.loc., in *Herb. Linn.* 1164.3 (LINN holo.).

8.9.42. ***Restio eleocharis* Mast.** in Journal of the Linnean Society, Botany 8: 238 (1865).

8.9.43. ***Restio leptoclados* Mast.** in Journal of the Linnean Society, Botany 8 (1865).

8.9.44. ***Restio subverticellatus* (Steud.) Mast.** in Journal of the Linnean Society, Botany 8: 227 (1865)

8.9.45. ***Restio triflora* Rottb.**, *Descriptiones plantarum rariorum* 10 (1772).

8.9.46. ***Restio helenae* Mast.** in Journal of the Linnean Society, Botany 8: 233 (1865)

8.9.47. ***Restio sieberi* Kunth**, *Enumeratio plantarum* 3: 387 (1841).

8.9.48. ***Restio monanthos* Mast.** in Journal of the Linnean Society, Botany 8: 238 (1865).

8.9.49. ***Restio parthenocarpus* H.P. Linder** sp. nov., a *R. sieberi* spiculis femineis floribus 2 vel 3, bracteis femineis acutis, stylis roseis, a *R. monanthos* spiculis femineis 10–15 mm longis, bracteis femineis 10–13 mm longis, tepalis 5.0–5.5 mm longis, ab ambabus culmis parce ramicantibus, basi styli pubescenti recedit.

TYPE.—Western Cape, 3219 (Wuppertal): Northern Bokkeveld at start of pass to Suurvlaakte, (–CA), 13-09-2002, *H.P.Linder 7509* (Z, holo.; BOL, K, MO, NBG, NSW, PRE).

Plants tufted, compact, 0.25–0.4 m tall, without spreading rhizomes or stolons, all plants female. *Fertile culms* sparsely branched, round, smooth, olivaceous, finely warty or finely rugulose, 0.7–0.9 mm diam. at apex; sheaths several, persistent, closely convoluted, brown, acute, 13–20 mm long, hyaline shoulders absent, mucro awl- or needle-shaped, straight and erect, 3–8 mm long. *Female inflorescence* with up to 5 spikelets, racemose or spicate, 10–35 × 3–10 mm; spathes like floral bracts, persistent, coriaceous; spikelets sessile, oblong, elliptical or ovate, rounded to acute, 10–15 mm long, 2–3-flowered; bracts overtopping

flowers, ovate, 10–13 mm long, acute, coriaceous or cartilaginous, imbricate and obscuring spikelet axis; bract awn less than half as long as bract body. *Female flower* 5–6 mm long; tepals coriaceous or chartaceous, apices acute to acuminate; outer lateral tepals 5.0–5.5 mm long, conduplicate with keels densely villous; odd outer tepal ovate, 4.0–4.5 mm long; inner tepals shorter than outer, ovate, 3 mm long; staminodes absent; styles 2, feathery, pink or red, with villous bases fused to form a pillar; ovary dehiscent, bilocular. *Seed* 1.9–2.1 × 1.2–1.3 mm, in side view oblong, in cross section round or elliptical, silvery, pitted. *Flowering time:* September and October.

Distribution and ecology: this new, apparently apomictic species is known from only two localities in the Cold Bokkeveld, from the Suurvlaakte at the northern end of the Cold Bokkeveld, and from the summit of the Skurweberg Pass at the southern end of the Cold Bokkeveld. The two locations are at 750–1 100 m, on sandstone, in deep sand over groundwater. Both locations showed some disturbance; the Skurweberg Pass population showed substantial disturbance.

Notes: the affinities of *Restio parthenocarpus* are not clear, but it may be related to *Restio sieberi* and *R. monanthos* by the seed surface morphology, seed shape, and general spikelet construction. It may also be of hybrid origin. The molecular phylogeny indicates an affinity to *R. sieberi*, *R. monanthos* and *R. cedarbergensis*. It differs from all species to which it might be assigned by numerous minor characters. The complex of variation associated with *R. sieberi* has not been critically explored, and this possibly apomictic species appears to be well embedded within this variation.

Etymology: *parthenocarpus* (Greek), producing seed or fruit without fertilization; the specific epithet is a noun in apposition.

Additional collection

WESTERN CAPE.—3319 (Worcester): Agterwitsenberg Pass at dam on pass summit, (–AB), 14-09-2002, *Linder, Hardy & Moline 7523* (BOL, E, K, MO, NBG, NSW, PRE, Z).

8.9.50. ***Restio nubigenus* (Esterh.) H.P.Linder & C.R.Hardy**, comb. nov.

Ischyrolepis nubigena Esterh. in Linder in *Bothalia* 15: 409 (1985). Type: Worcester, Matroosberg, *Esterhuysen 27780* (BOL, holo.; E!, K!, L!, M!, MO!, S!, STE!).

8.9.51. ***Restio gaudichaudianus* Kunth**, *Enumeratio plantarum* 3: 387 (1841).

8.9.52. ***Restio luxurians* (Pillans) H.P.Linder**, comb. et stat. nov.

Restio gaudichaudianus Kunth var. *luxurians* Pillans in Transactions of the Royal Society of South Africa 16: 280 (1928). Type: Glen Leith, foot of the Lange Berge (?), *Muir 3078* (BOL, lecto.; [Linder in *Bothalia* 15: 405 (1985)]; K!); Worcester, Hex River Mountains, *Bolus 4234*, *4235* (BOL!, K!); *Bolus 15949*, *15950* (BOL!); *Wilde Paarde Berg* (?), *Stokoe* in *BOL17665* (BOL!); Montagu, Langeberge at Montagu, *Marloth 3118*, *3119* (BOL!); *Page* in *BOL16540* (BOL!); *Mitchell* in *BOL16626* (BOL!); Ladismith, Zwarteberge, *Marloth 3170* (BOL!); Willowmore, Aasvogelberg, *Andreae 940* (BOL!); s.loc., Zwartwaterpoort, *Burchell 3409* (BOL!, K!).

Notes: since this form can always and readily be distinguished from *Restio gaudichaudianus*, it is best recognized at specific level.

8.9.53. **Restio venustus** Kunth, Enumeratio plantarum 3: 388 (1841).

Notes: although the spikelet structure is very similar to the hyper-variable (and probably too broadly defined) species *Restio sieberi*, the plants can always be distinguished by growth form, by the woolly prophylls, and by the stouter culms and somewhat larger spikelets. Ecologically it is also distinct, and is always associated with large rocks, or even more commonly with passages through the sandstone bedrock, where it often forms large monospecific stands. These habitats are presumably more shaded and colder than the typically sunny open habitat of the numerous forms of *R. sieberi*.

8.9.54. **Restio laniger** Kunth, Enumeratio plantarum 3: 386 (1841).

8.9.55. **Restio distractus** Mast., Flora capensis 7: 70 (1897).

8.9.56. **Restio unispicatus** (H.P.Linder) H.P.Linder & C.R.Hardy, comb. nov.

Ischyrolepis unispicata H.P.Linder in Bothalia 15: 415 (1985). Type: Wuppertal, Northern Cold Bokkeveld, Vredelus at E base of Schoongezicht Peak, Esterhuysen 29670 (BOL, holo.!; C!, E!, K!, L!, M!, MO!, S!).

ACKNOWLEDGEMENTS

This study was funded by the Swiss Science Foundation grant SNF 31-66594-01, and the field work was supported by the Claraz Foundation and National Geographic Society Grant 7289-02. CapeNature provided collecting permission. We particularly want to thank Philip Moline (field work, collaboration on the *Elegia* complex), the Bolus Herbarium and Terry Trinder-Smith for handling our collections in Cape Town. Peter Goldblatt, Barbara Briggs and Nick Helme are thanked for critical input into the paper, and Peter Wilson and Otto Leistner for checking the Latin.

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 hyalinus (Mast.) H.P.Linder & C.R.Hardy, 21
 hystrix Mast., 28
 implicatus Esterh., 22
 impolitus Kunth, 22
 inconspicuus Esterh., 22

Restio *Rottb.*, (cont.)

- ingens* *Esterh.*, 22
insignis *Pillans*, 18
inveteratus *Esterh.*, 18
karooicus (*Esterh.*) *H.P.Linder & C.R.Hardy*, 28
laniger *Kunth*, 31
leptoclados *Mast.*, 30
leptostachyus *Kunth*, 22
levynsiae (*Pillans*) *H.P.Linder & C.R.Hardy*, 21
longiaristatus (*Pillans ex H.P.Linder*) *H.P.Linder & C.R.Hardy*, 26
luxurians (*Pillans*) *H.P.Linder*, 30
macer *Kunth*, 26
madagascariensis *Cherm. var. humbertii* *Cherm.*, 8
mahonii (N.E.Br.) *Linder* subsp. *humbertii* (*Cherm.*) *H.P.Linder*, 8
mahonii (N.E.Br.) *Pillans*, 8
marlothii *Pillans*, 27
micans *Nees*, 17
miser *Kunth*, 17
mlanjiensis *H.P.Linder*, 8
monanthos *Mast.*, 30
monostylis (*Pillans*) *H.P.Linder & C.R.Hardy*, 17
montanus *Esterh.*, 22
muirii (*Pillans*) *H.P.Linder & C.R.Hardy*, 24
multiflorus *Spreng.*, 22
nanus (*Esterh.*) *H.P.Linder & C.R.Hardy*, 27
nodosus *Pillans*, 18
nubigenus (*Esterh.*) *H.P.Linder & C.R.Hardy*, 30
nudiflorus (*Pillans*) *H.P.Linder & C.R.Hardy*, 22
nuwebergensis *Esterh.*, 17
obscurus *Pillans*, 18
occultus (*Mast.*) *Pillans*, 18
ocreatus *Kunth*, 28
pachystachyus *Kunth*, 18
paludicola *H.P.Linder*, 22
paludosus *Pillans*, 26
paniculatus *Rottb.*, 20
papillosus (*Esterh.*) *H.P.Linder & C.R.Hardy*, 26
papyraceus *Pillans*, 17
parthenocarpos *H.P. Linder*, 30
parvispiculus *H.P.Linder & C.R.Hardy*, 21
patens *Mast.*, 18
peculiaris *Esterh.*, 22
pedicellatus *Mast.*, 16
perplexus *Kunth*, 18
perseverans *Esterh.*, 18
pillansii *H.P.Linder*, 22
praeacutus *Mast.*, 18
pratensis (*Esterh.*) *H.P.Linder & C.R.Hardy*, 26
pulcher (*Esterh.*) *H.P.Linder & C.R.Hardy*, 21
pulvinatus *Esterh.*, 18
pumilus *Esterh.*, 22
purpurascens *Nees ex Mast.*, 22
pygmaeus *Pillans*, 26
quadratus *Mast.*, 20
quartziticola *H.P.Linder*, 8
quinquefarius *Nees*, 20
ramosissimus *H.P.Linder & C.R.Hardy*, 24
rarus *Esterh.*, 22
rigidus (*Mast.*) *H.P.Linder & C.R.Hardy*, 21
rigoratus (*Mast.*) *H.P.Linder & C.R.Hardy*, 24
rivulus (*Esterh.*) *H.P.Linder & C.R.Hardy*, 26
rottboellioides *Kunth*, 26
rudolfii (*Pillans*) *H.P.Linder & C.R.Hardy*, 24
rupicola *Esterh.*, 18
sabulosus *Pillans*, 26
saroclados *Mast. in A.DC.*, 22
saxatilis (*Esterh.*) *H.P.Linder & C.R.Hardy*, 27
scaber *Mast.*, 22
scaberulus *N.E.Br.*, 22
schoenoides *Kunth*, 27
secundus (*Pillans*) *H.P.Linder*, 22
sejunctus *Mast.*, 22
setiger *Kunth*, 28
sieberi *Kunth*, 30
similis *Pillans*, 20
singularis *Esterh.*, 22
sporadicus (*Esterh.*) *H.P.Linder & C.R.Hardy*, 26
stereocaulis *Mast.*, 16
stokoei *Pillans*, 22
strictus *N.E.Br.*, 22
strobilifer *Kunth*, 18
subgen. *Calopsis* (*Beauv. ex Desv.*) *H.P.Linder & C.R.Hardy*, 20
subgen. *Craspedolepis* (*Steud.*) *H.P.Linder & C.R.Hardy*, 17
subgen. *Eremorestio* *H.P.Linder & C.R.Hardy*, 20
subgen. *Ischyrolepis* (*Steud.*) *H.P.Linder & C.R.Hardy*, 24
subgen. *Locapsis* *H.P.Linder & C.R.Hardy*, 23
subgen. *Pendulostemon* *H.P.Linder & C.R.Hardy*, 17
subgen. *Restio*, 21
subgen. *Simplicaulos* *H.P.Linder & C.R.Hardy*, 16
subgen. *Varirestio* *H.P.Linder & C.R.Hardy*, 18
subtilis *Nees ex Mast.*, 17
subverticellatus (*Steud.*) *Mast.*, 30
tenuispicatus *H.P.Linder & C.R.Hardy*, 24
tenuissimus *Kunth*, 26
tetragonus *Thunb.*, 20
triflora *Rottb.*, 30
triticeus *Rottb.*, 22
tuberculatus *Pillans*, 22
unispicatus (*H.P.Linder*) *H.P.Linder & C.R.Hardy*, 31
vallis-simius *H.P.Linder*, 22
venustulus *Kunth*, 31
verrucosus *Esterh.*, 22
versatilis *H.P.Linder*, 22
vilis *Kunth*, 28
villosus *H.P.Linder & C.R.Hardy*, 22
vimineus *Rottb.*, 24
virgeus *Mast.*, 28
wallichii *Mast.*, 26
wittebergensis (*Esterh.*) *H.P.Linder & C.R.Hardy*, 28
zuluensis *H.P.Linder*, 22
zwartbergensis *Pillans*, 22
Rhodocoma *Nees*, 10
alpina *H.P.Linder & Vlok*, 11
arida *H.P.Linder & Vlok*, 11
capensis *Nees ex Steud.*, 11
foliosa (N.E.Br.) *H.P.Linder & C.R.Hardy*, 11
fruticosa (*Thunb.*) *H.P.Linder*, 11
gigantea (*Kunth*) *H.P.Linder*, 11
gracilis *H.P.Linder & Vlok*, 11
vleibergensis *H.P.Linder*, 11
Schoenus capensis *L.*, 30
Soroveta *H.P.Linder & C.R.Hardy*, 6
ambigua (*Mast.*) *H.P.Linder & C.R.Hardy*, 6
Staberoha *Kunth*, 8
aemula (*Kunth*) *Pillans*, 9
banksii *Pillans*, 9
cernua (*L.f.*) *Dur. & Schinz*, 9
distachyos (*Rottb.*) *Kunth*, 9
multispicula *Pillans*, 9
ornata *Esterh.*, 9
remota *Pillans*, 9
stokoei *Pillans*, 9
vaginata (*Thunb.*) *Pillans*, 9
Thamnochortus *P.J.Bergius*, 9
acuminatus *Pillans*, 10
amoena *H.P.Linder*, 10
arenarius *Esterh.*, 10
bachmannii *Mast.*, 10
cinereus *H.P.Linder*, 10
dichtomus (*L.*) *Spreng.*, 30
dumosus *Mast.*, 10
ellipticus *Pillans*, 10
erectus (*Thunb.*) *Mast.*, 10
fraternus *Pillans*, 10
fruticosus *P.J.Bergius*, 10
glaber (*Mast.*) *Pillans*, 10
gracilis *Mast.*, 10
guthrieae *Pillans*, 10
insignis *Mast.*, 10
karooica *H.P.Linder*, 10
levynsiae *Pillans*, 10
lucens (*Poir.*) *H.P.Linder*, 10
muirii *Pillans*, 10
nutans (*Thunb.*) *Pillans*, 10
obtusius *Pillans*, 10
paniculatus *Mast.*, 10
papyraceus *Pillans*, 10
pellucidus *Pillans*, 10
platypteris *Kunth*, 10
pluristachyus *Mast.*, 10

Thamnochortus *P.J.Bergius* (cont.)

pulcher *Pillans*, 10
punctatus *Pillans*, 10
rigidus *Esterh.*, 10

schlechteri *Pillans*, 10
spicigerus (*Thunb.*) *Spreng.*, 10
sporadicus *Pillans*, 10
stokoei *Pillans*, 10

New synonyms and a new name in Asteraceae: Senecioneae from the southern African winter rainfall region

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Keywords: Aluka website, Asteraceae, *Othonna*, *Senecio*, southern Africa, taxonomy

ABSTRACT

A review of the genera *Othonna* and *Senecio* undertaken for the forthcoming *Greater Cape plants 2: Namaqualand-southern Namib and western Karoo* (Manning in prep.) led to a re-examination of the taxonomic status of several species. This was facilitated by the recent availability of high-resolution digital images on the Aluka website (www.aluka.org) of the Drège isotypes in the Paris Herbarium that formed the basis of many species described by De Candolle in his *Prodromus systematis naturalis regni vegetabilis*. These images made it possible to identify several names whose application had remained uncertain until now. Each case is briefly discussed, with citation of additional relevant herbarium specimens. The following species are reduced to synonymy: *O. incisa* Harv. is included in *O. rosea* Harv.; *O. spektakelensis* Compton and *O. zeyheri* Sond. ex Harv. are included in *O. retrorsa* DC.; *S. maydae* Merxm. is included in *S. albopunctatus* Bolus, which is now considered to include forms with radiate and discoid capitula; *S. cakilefolius* DC. is included in *O. arenarius* Thunb.; *S. pearsonii* Hutch. is included in *O. asperulus* DC.; *S. parvifolius* DC. is included in *S. carroensis* DC.; *S. eriobasis* DC. is included in *S. erosus* L.f.; and *S. lobelioides* DC. is included in *S. flavus* (Decne.) Sch.Bip. The name *S. panduratus* (Thunb.) Less. is identified as a synonym of *S. erosus* L.f. and plants that are currently known under this name should be called *S. robertiifolius* DC. The confusion in the application of the names *O. perfoliata* (L.f.) Jacq. and *O. filicaulis* Jacq. is examined. *O. perfoliata* is lectotypified against a specimen in the Linnaean Herbarium (LINN) with radiate capitula. The name *O. filicaulis* correctly applies to a radiate species and is treated as a synonym of *O. perfoliata*. The vegetatively similar taxon with disciform capitula that is currently known as *O. filicaulis* should be known as *O. undulosa* (DC.) J.C.Manning & Goldblatt, comb. nov. The new name *O. daucifolia* J.C.Manning & Goldblatt is provided to replace the later homonym *O. abrotanifolia* (Harv.) Druce.

INTRODUCTION

The South African species of *Othonna* L. and *Senecio* L. were last revised at a regional level by Harvey (1865). Since then, the summer rainfall species from KwaZulu-Natal have been studied intensively by Hilliard (1977) but many species in the southern African winter rainfall region remain poorly understood. The recent availability of high-resolution digital images of type material of many African taxa (www.aluka.org), especially the Paris isotype material of the Drège collections that formed the basis of a number of De Candolle's (1838) species, has made it possible to identify several taxa that were never seen by Harvey (1865) and whose identity has remained uncertain. During the preparation of a review of the tribe Senecioneae (Manning in prep.), various nomenclatural and taxonomic issues were encountered that can now be addressed. The application of some of these names and other taxonomic and nomenclatural issues arising during the study are dealt with here.

The digital images, or virtual herbaria, available online through Aluka and other sites such as the Herbarium of the Linnean Society of London (www.linnean-online.org) are often adequate for providing confirmation of the identity of names where the gross morphology of the taxa in question is diagnostic but they cannot replace microscopic examination of actual material for critical features. We have, therefore, avoided making any taxonomic inferences in instances where the identity of the digital image depends on examination of such micro-characters. In addition,

digital images have only been accepted as genuine type material where it is absolutely clear that this is the case from the collecting number and locality details on the sheets in question.

OTHONNA

1. The shrublet with dissected leaves and radiate capitula from the southwestern Cape currently known as *Euryops abrotanifolius* (L.) DC. (1838) is based on *Othonna abrotanifolia* L. (1753). The same epithet was also used for *Doria abrotanifolia* Harv. (1865), a species with disciform capitula from Namaqualand, which was later transferred to *Othonna* as *O. abrotanifolia* (Harv.) Druce (1917). Although aware of the existence of Linnaeus' combination, Druce (1917) did not consider it an impediment to his transfer of the epithet and it escaped the notice of later authors, who continued to treat the species under this name (e.g. Welman 2006). However, the existence of Linnaeus' earlier name renders Druce's combination an illegitimate homonym (McNeil *et al.* 2006: Art. 53.1), and the Namaqualand species therefore requires a new name, which we provide here, alluding to the unusually finely dissected leaves.

***Othonna daucifolia* J.C.Manning & Goldblatt, nom. nov. pro *Othonna abrotanifolia* (Harv.) Druce: 638 (1917), non *Othonna abrotanifolia* L. (1753) [= *Euryops abrotanifolius* (L.) DC.]. *Doria abrotanifolia* Harv.: 324 (1865). Type: South Africa [Northern Cape], Springbokfontein [Springbok], without date, *Whitehead s.n.* TCD0003161 (TCD, holo.—Aluka image!, website accessed 20-03-09).**

2. The application of the names currently used for the two species *Othonna filicaulis* Jacq. and *O. perfoliata* Jacq. (e.g. Goldblatt & Manning 2000) is highly confused

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MS. received: 2009-03-31.

(Table 1). These vegetatively similar, deciduous geophytes from the Western Cape are tuberous perennials producing slender, often scandent, annual stems bearing perfoliate or amplexicaul leaves and terminating in pedunculate capitula. Their remarkable vegetative similarity led Rowley (1994: 174) to treat both radiate and disciform plants in a single, variable species under the name *O. filicaulis*. He may be correct, but until the situation is fully investigated we continue to treat them as distinct.

Othonna perfoliata is distinguished from *O. filicaulis* by its generally fewer phyllaries (8–10 vs 10–12) and radiate marginal florets, although in some collections the rays are reduced and rather small. The marginal florets in *O. filicaulis*, in contrast, are filiform and rayless, with the truncate corolla less than half as long as the style. All fruiting material of *O. perfoliata* that we have seen has the mature pappus in the marginal florets 5–8 mm long and $\pm$ as long as the cypselae or only slightly longer, whereas in *O. filicaulis* the pappus often elongates greatly, reaching 10–20 mm long, therefore 2–4 times as long as the cypselae at maturity. *O. filicaulis* as currently understood (e.g. Goldblatt & Manning 2000) is widespread in the southern African winter rainfall region, mainly on sandy, often coastal flats, from southern Namibia as far east as Uniondale, whereas *O. perfoliata* is essentially restricted to montane habitats in the southwestern Cape, where it occurs on rocky slopes between the Bokkeveld Mountains and Caledon (Goldblatt & Manning 2000).

The epithet *perfoliata* was first used in this context by Linnaeus f. (1782) in the combination *Cineraria perfoliata* L.f., based on material collected at the Cape of Good Hope by Thunberg. There are no sheets under this name in the Linnaean Herbarium at Stockholm (S) but the Herbarium of the Linnean Society (LINN) contains two sheets labelled as such, one of them a radiate plant (LINN1000.32) and the other one evidently disciform (LINN1000.33). The protologue, unfortunately, makes no mention of the condition of the capitula but the description of the leaves as ovate-cordate and of the peduncles as elongated, with a solitary capitulum [*foliis ovatis cordatis amplexicaulis, pedunculis unifloris elongatis*] matches the radiate-flowered specimen more closely than the disciform one, in which the leaves are lanceolate-undulate and the inflorescence sparsely branched. It is in the sense of a radiate taxon that Jacquin (1797) illustrated and described the species, citing *C. perfoliata* L.f. under the name *Othonna perfoliata*, which therefore constitutes the new combination *O. perfoliata* (L.f.) Jacq.

Thunberg, however, understood the taxon in the opposite way when he established the genus *Doria* Thunb. (1800a) for various Senecioneae with disciform capitula and transferred the name to that genus as *Doria perfoliata* (L.f.) Thunb. (1800b). This interpretation evidently

stems from the duplicate material in his possession, as the Thunberg Herbarium (UPS-THUNB) contains a single, disciform plant (UPS-THUNB19833) under the name *Doria perfoliata*. The name was subsequently used in this sense as applying to the disciform taxon by both De Candolle (1838) and Harvey (1865) (although the latter mistakenly attributed the basionym to Lamarck). As a result of this, De Candolle (1838) described the new species *O. amplexifolia* DC. for the conspicuously radiate taxon, based on material collected by Drège, citing Jacquin's illustration and interpretation of *O. perfoliata* in the protologue to his *O. amplexifolia*, but explicitly excluding the Linnaean basionym *Cineraria perfoliata* in keeping with his application of this name to the disciform taxon (as *Doria perfoliata* (L.f.) Thunb.). The name was subsequently transferred to *Othonna* as *O. perfoliata* (L.f.) Sch.Bip. (1844) but this combination is in any event preoccupied by *Othonna perfoliata* (L.f.) Jacq. (1797), making it a later homonym and thus illegitimate (McNeil *et al.* 2006: Art. 53).

At the time that he figured the radiate taxon under the name *Othonna perfoliata*, Jacquin (1797) described a second, similar taxon under the name *O. filicaulis* Jacq. This species was distinguished from *O. perfoliata* by the narrower, lanceolate-undulate leaves and by the smaller, linear rays. The ligulate condition of the marginal florets is clearly described and is also illustrated in a detail of a marginal floret but the rays are not evident in the drawing of the whole plant, which thus appears to be disciform. Both De Candolle (1838) and Harvey (1865) treated the species as circumscribed by Jacquin although neither knew it from actual material. The name later became associated with the disciform species, presumably because Jacquin's painting of the whole plant appeared to represent a disciform individual, and it is this application that is current (e.g. Goldblatt & Manning 2000). This transfer in the application of the name *O. filicaulis* to the disciform taxon appears to date to the *Flora of the Cape Peninsula* (Adamson & Salter 1950), in which the name *O. filicaulis* is explicitly applied to the disciform species with filiform, truncate marginal corollas 'previously misidentified as *O. perfoliata*' (Adamson & Salter 1950: 820). In any event, the protologue of *O. filicaulis* makes it quite clear that the name is properly applied to a radiate plant.

Examination of available herbarium specimens of *Othonna perfoliata* shows that the species exhibits a wide range of leaf shapes, ranging from suborbicular and plane (typical *O. perfoliata*) to lanceolate and undulate (typical *O. filicaulis*). The ray florets also vary from well-developed and oblong to smaller and narrow. We therefore conclude that *O. filicaulis* is conspecific with *O. perfoliata* and place the name in synonymy under it.

TABLE 1.—Application of epithets in *Othonna filicaulis-perfoliata* group

Epithet	Application					
	Linnaeus f. (1782)	Jacquin (1797)	Thunberg (1800)	De Candolle (1838)	Harvey (1865)	Adamson & Salter (1950) <i>et seq.</i>
<i>perfoliata</i> (1782)	not stated	radiate	disciform	disciform	disciform	radiate
<i>filicaulis</i> (1797)		radiate	—	radiate	radiate	disciform
<i>amplexifolia</i> (1838)				radiate	radiate	—
<i>undulosa</i> (1838)				disciform	disciform	—

This leaves the disciform species, currently identified as *Othonna flicaulis*, without a name. *Doria undulosa* DC. (1838) was described for a collection with straggling stems bearing cordate-lanceolate, undulate leaves and disciform capitula with short, truncate marginal corollas that was gathered in the Hex River Mountains by Drège. The species was imperfectly known to Harvey (1865) but our examination of the isotype material at Paris convinces us that it falls within the range of variation of the taxon that is currently incorrectly called *O. flicaulis*. The name *D. undulosa* is therefore available for the disciform taxon and the new combination required in *Othonna* is made here.

***Othonna perfoliata* (L.f.) Jacq.**, *Plantarum rariorum horti caesarei schoenbrunnensis* 2: 61, t. 240 (1797). *Cineraria perfoliata* L.f.: 375 (1782 '1781'). *Doria perfoliata* (L.f.) Thunb.: 155 (1800b). *Othonna perfoliata* (L.f.) Sch.Bip.: 769 (1844), illegit. superfl. name. Type: South Africa, without locality or date, *Thunberg s.n.* (LINN1000.32, lecto., here designated—Linnean image!, website accessed 20-03-09).

O. flicaulis Jacq.: 62, t. 241 (1797), not of Adamson & Salter (1950) and later authors [= *Othonna undulosa* (DC.) J.C.Manning & Goldblatt], syn. nov. Type: illustration in Jacq.: t. 241 (1797), lecto., here designated: original material unknown.

O. amplexifolia DC.: 480 (1838), syn. nov. Type: South Africa, [Western Cape], Paarl, [31 August 1827], Drège [6063] (G-DC, holo.—microfiche!; K, P—Aluka images!, website accessed 20-03-09).

Representative additional specimens examined

NORTHERN CAPE.—3119 (Calvinia): Oorlogskloof Nature Reserve, (—AC), 6 June 1995, Pretorius 245 (NBG).

WESTERN CAPE.—3118 (Vanrhynsdorp): Matsikamma, (—DB), 12 July 1974, Thompson 2054 (NBG). 3219 (Wuppertal): Cedarberg, Gonnafontein, (—CB), 23 May 2000, Pond 77 (NBG). 3319 (Worcester): Rawsonville, (—CA), 28 July 1962, Walters 659 (NBG); Voetpadsberg, (—DA), 8 June 1985, Van Wyk 2373 (NBG). 3419 (Caledon): Panorama, (—CB), 4 July 1976, Neethling s.n. (NBG).

***Othonna undulosa* (DC.) J.C.Manning & Goldblatt**, comb. nov. *Doria undulosa* DC.: 472 (1838). Type: South Africa, [Western Cape], Hexriviersberg, [Hex River Mountains, 3 June 1820], Drège [289] (G-DC, holo.—microfiche!; P—Aluka image!, website accessed 20-03-09).

O. flicaulis sensu auct., non Jacq. [= *O. perfoliata* (L.f.) Jacq.].

Representative additional specimens examined

NORTHERN CAPE.—2917 (Springbok): bottom of Wildepaardehoek Pass, (—DC), 24 August 1976, Van Jaarsveld 1399 (NBG). 3018 (Kamiesberg): Studer's Pass, (—AC), 30 August 1975, Oliver 5952 (NBG).

WESTERN CAPE.—3218 (Velddrif): Rocher Pan Reserve, (—CB), 25 July 1981, Le Roux & Van Rooyen 6 (NBG). 3319 (Worcester): Karoo Garden veld, (—CB), Perry 165 (NBG). 3420 (Bredasdorp): Zoetendalsvlei Vallei turnoff from Bredasorp—Agulhas road, (—CA), 6 July 1995, Paterson-Jones 433 (NBG).

3. *Othonna lingua* L.f. (1782) was based on a collection made by Thunberg at the Cape of Good Hope. The name of the taxon has been incorrectly rendered as *O. lingua* (Less.) Sch.Bip. (1844) based on the name *Doria lingua* Less. (1832) but reference to Lessing (1832: 89) reveals that he did not in fact publish this name. It first appears as *D. lingua* in De Candolle (1838: 471), where it is mistakenly attributed to Lessing as being based on the basionym *Othonna lingua* Jacq. What Lessing (1832) actu-

ally published was the combination *Doria digitata* (L.) Less., based on *Othonna digitata* L., for a similar taxon with toothed leaves, followed by a list of names that he regarded as conspecific with it. Among them was *Othonna lingua* sensu Jacquin (1797). Jacquin (1797) was in any event also not the author of the name since he cited the *Systema vegetabilium* of 1784 (edition 14, Murray 1784), which in turn refers the name to Linnaeus fil. (1782). This is in fact the first appearance of the name, which is thus correctly attributed to Linnaeus f. as *O. lingua* L.f.

There is no material under the name *Othonna lingua* in either LINN or S but there is a specimen under this name in the Thunberg herbarium (UPS-THUNB20882), which therefore represents the type. This specimen was cited by Harvey (1865: 342) under *O. tuberosa* Thunb. (itself an illegitimate, superfluous name for *O. bulbosa* L.), who followed De Candolle (1838: 471) in retaining the name [*Doria lingua* (Jacq.) Less.] as applied to a quite different taxon with disciform capitula. We have examined the specimen of *Doria lingua* in the Thunberg herbarium and find no reason to disagree with Harvey (1865) that it represents *O. bulbosa* L. The name *O. lingua* L.f. should therefore be treated as a synonym of *O. bulbosa* L. and we make the necessary nomenclatural correction below.

The incorrect application of the name *Othonna lingua* by De Candolle (1838) and Harvey (1865) arose from an initial misunderstanding by Jacquin (1797), whose illustration and description apply to an erect-stemmed, tuberous geophyte with petiolate radical leaves, lanceolate cauline leaves, and disciform capitula.

Linnaeus f. (1782) did not mention the condition of the marginal florets in the protologue of *Othonna lingua* but neither did he mention the florets in any but one of the remaining 14 species enumerated by him in *Othonna*. Since all of these are in fact radiate, this is strong circumstantial evidence that he had a radiate taxon in mind when describing *O. lingua*. There is also no indication as to whether the epithet refers to the shape of the leaves or to the presence of rays but the description of the leaves as ovate-lanceolate and semi-amplexicaul suggests that it more probably alludes to the latter. In any event, the Thunberg collection, which is evidently the type, fixes the application of the name. We accordingly place *O. lingua* in synonymy under *O. bulbosa*.

***Othonna bulbosa* L.**, *Species plantarum*: 1309 (1753). Type: illustration in Breyne: t. 66 (1674–1678).

O. lingua L.f.: 387 (1782 '1781'), syn. nov.; Jacq.: 60 (1797), name only, excl. description and figure; Thunb.: 718 (1823); Sch.Bip.: 769 (1844) [as '(Less.) Sch.Bip.']. *Doria lingua* (L.f.) DC.: 471 (1838). Type: South Africa, without precise locality, UPS-THUNB20882 (UPS-THUNB, presumed holo.—microfiche!).

O. bulbosa Thunb.: 720 (1823), illegit. superfl. name. Type: as for *O. bulbosa* L.

4. *Othonna lingua* is a species with radiate capitula and is, according to our interpretation of the type, conspecific with *O. bulbosa* (see discussion above). It is, therefore, necessary to consider the identity of the disciform species to which this name has been applied in many herbaria. The collections under this name represent a tuberous geophyte with disciform capitula and ± erect, annual stems bearing variously oblanceolate to ovate leaves, the

lowermost leaves $\pm$ tapering to the base and $\pm$ truncate or sessile, and the upper leaves mostly auriculate.

We have examined herbarium material filed under the name *O. lingua* and are able to distinguish two sets of populations. One represents a western, coastal species occurring from Namaqualand to the Olifants River, mostly with fleshy, oblanceolate leaves with conspicuously revolute margins, capitula in which the phyllaries are connate in the basal third, and disc cypselae with short, caducous pappus bristles 1–3 mm long. A second series of plants with $\pm$ plane leaves occurs inland, from the Cedarberg eastwards to Port Elizabeth, and is distinguished by the phyllaries connate for $\pm$ half their length or more, and most strikingly by the disc cypselae entirely lacking a pappus (very rarely with one or two short bristles on the outer disc florets in some collections from the Little Karoo).

Only two species of *Othonna* are known in which the disc florets lack a pappus and both were described by De Candolle (1838). *O. gymnodiscus* (DC.) Sch.Bip. was based on a plant collected by Ecklon near Port Elizabeth, and *O. semicalva* (DC.) Sch.Bip. on a collection made by Drège in the Olifant's River Valley. The two taxa were distinguished primarily by differences in leaf shape (respectively oblong-ovate and auriculate vs linear-lanceolate and sessile). Both taxa were known to De Candolle (1838) from the type specimens only. Collections made since then have filled in the distribution between the type localities and also suggest that the purported differences between them in leaf shape and size of capitula are not significant. Leaves in herbarium material range from narrowly lanceolate to obovate, with the leaf base narrowed or $\pm$ auriculate, and the phyllaries vary from 6–10 mm long, sometimes even on the same plant depending on their stage of development. Our examination of type material of both names leads us to conclude that they represent forms of a single species, for which we choose the name *O. gymnodiscus* as being most appropriate. The name *O. semicalva* is accordingly reduced to synonymy.

The second series of populations from the west coast with pappus bristles present in the disc florets appears to represent an undescribed species but further study is required to assess this.

***Othonna gymnodiscus* (DC.) Sch.Bip.**, *Compositae Kraussiana*: 769 (1844). *Doria gymnodiscus* DC.: 473 (1838). Type: South Africa, [Eastern Cape], near Port Elizabeth, without date, Ecklon & Zeyher (G-DC, holo.–microfiche!; S–digital image!).

O. semicalva (DC.) Sch.Bip.: 769 (1844), syn. nov. *Doria semicalva* DC.: 473 (1838). Type: South Africa, [Western Cape], Langevalley ad Olifantsrivier, [Rhinoosterfontein, 15 July 1830], Drège [2878] (G-DC, holo.–microfiche!; P–Aluka image!, website accessed 20-03-09).

O. lingua sensu Goldblatt & Manning (2000), non L.f. [= *O. bulbosa* L.].

Selected additional specimens examined

WESTERN CAPE.—3218 (Clanwilliam): Pakhuis Pass, (–BB), 7 July 1984, Taylor 10985 (NBG). 3219 (Wuppertal): Swartrug-gens, Knolfontein Farm, (–DC), 7 August 2007, Jardine & Jardine 699 (NBG). 3318 (Cape Town): Malmesbury, Katzenberg, (–DA), 26 June 1976, Andrag & Boucher 5 (NBG); McGregor, Farm Vrolikheid, (–DD), 1971 without month, Jooste 88 (NBG). 3319 (Worcester): Rawsonville, (–CA), 28 July 1962, Walters 652 (NBG); Karoo Garden,

(–CB), 12 July 1948, Compton 20525 (NBG); Karoo Garden, (–CB), 30 June 1958, Willems 47 (NBG); Karoo Garden, (–CB), 18 August 1976, Bayer 184 (NBG); Worcester Veld Reserve, (–CB), 13 August 1986, Midgley & Bosenberg 50 (NBG). 3321 (Ladismith): Calitzdorp, Sandberg, (–DA), 24 July 1953, Compton 24101 (NBG). 3322 (Oudtshoorn): Robinson Pass, (–CC), 30 July 1947, Compton 19620 (NBG).

5. Only three species of *Othonna* are known with purple or magenta rays, all of them tuberous geophytes from Namaqualand. They are distinguished essentially by the shape of the leaves, specifically the degree of lobing. At the time that Harvey (1865) established *O. incisa* Harv. and *O. rosea* Harv. as species distinct from *O. cakilefolia* DC., he knew all three taxa from just a single collection each. With further collecting it appears that *O. incisa* and *O. rosea* represent extreme forms that grade into one another. Plants from the Richtersveld southwards to Springbok have leaves that are entire, sparsely denticulate or dentate (typical *O. rosea*), whereas those from the Kamiesberg southwards to Nuwerus have sharply pinnatifid leaves (typical *O. incisa*). The difference in lobing appears to be one of degree and not of kind. The phyllaries in *O. rosea* were described by Harvey (1865) as ‘semiconcrete’ and those of *O. incisa* as ‘connate’. In the material of *O. rosea* that we have examined, the phyllaries range from basally connate to joined up to halfway, and a similar variation is evident in the material of *O. incisa* (Hall 4932), in which the degree of fusion ranges from one quarter to two thirds of the length of the phyllaries. Although the cypselae of *O. rosea* were described as glabrous, this observation was based on immature fruits, and in such cases the hairs are usually not readily seen. More recent collections of plants with entire leaves (e.g. Hall 575 NBG) develop pubescent achenes. In our opinion, *O. rosea* and *O. incisa* represent extreme forms of a single species and should be treated as one. The name *O. rosea* is chosen as being the more descriptive.

Collections of *Othonna cakilefolia* that we have examined have leaves very deeply dissected into narrow, $\pm$ obtuse lobes, thus differing significantly from the lacerate-pinnatifid forms of *O. rosea*, which always have distinctly apiculate lobes.

***Othonna rosea* Harv.** in Harv. & Sond., *Flora capensis* 3: 341 (1865). Type: South Africa, [Northern Cape, Springbok], Modderfontein, without date, Whitehead s.n. (TCD, holo.–Aluka image!, website accessed 20-03-09).

O. incisa Harv.: 341 (1865), syn. nov. *Othonna cakilefolia* var. *latifolia* DC.: 482 (1838). Type: South Africa, [Western Cape, Nuwerus], between Uitkomst and Geelbeksraal, without date [August 1830], Drège (Doc. 95.2) (G-DC, holo.–microfiche!; P–Aluka image!, website accessed 25-11-09).

Additional specimens examined

NORTHERN CAPE.—2817 (Vioolsdrif): hills east of Perdewater, (–CA), 11 July 1997, Bruyns 7268 (NBG). 2917 (Springbok): Harrasberg, (–AD), 16 July 1995, Bruyns 6344 (BOL); Anenous Pass, (–BA), 30 May 1954, Hall 910 (NBG); west of Bulletrap on road to Waalheuwel, (–BC), 12 May 2005, Harrower 1500 (NBG); 5 miles [8 km], north of Grootmis, (–CA), 20 August 1952, Hall 575 (NBG); Komaggas, (–CD), 5 July 1991, Bruyns 4614 (BOL); Spektakel Pass, (–DB), 15 May 2003, Manning 2923 (NBG); 10 km west of foot of Spektakel Pass, (–DA), 4 July 1987, Bruyns 2705 (NBG); Messelpad, (–DC), 23 July 1948, R.H. Compton 20672 (NBG); Kourkammaberg, (–DC), 11 July 1987, Bruyns 3876 (BOL). 3017 (Hondeklipbaai): Riethuis, (–AB), 11 July 1989, Bruyns 3860 (BOL). 3018 (Kamiesberg): west slopes of Rusbospoort on Farm Damsland, (–AC), 23 April 1982, Hall 4932 (NBG); Andriesskloof, (–CB), 24 August 1991, Bruyns 4750 (BOL); Knersvlakte, Bruinberg, (–DC), 10 September 1992, Bruyns 5322 (BOL).

6. *Othonna retrorsa* DC. is an easily recognizable, cushion-forming perennial with a many-headed caudex producing rosettes of very distinctive, leathery, reticulate-veined leaves. These are oblanceolate with cartilaginous margins bearing few to many pale, patent or retrorse denticles. The leaves are persistent at the base and their dried remains accumulate around the short stems, gradually decaying into a fibrous mass. One or more, sparsely branched flowering stems are produced from each rosette. The species was described by De Candolle (1838) from material collected in the Kamiesberg by Drège. Plants from further north, around Springbok, were later treated by Compton (1953) as the separate species *O. spektakelensis*. Differences between the two taxa are slight and are centred on the relatively broader leaves and more northerly distribution of *O. spektakelensis*. Other listed differences include the average number of phyllaries and ray florets but these are inconsistent even within the type material. The taxon was subsequently treated as merely a variety of *O. retrorsa* (Rowley 1990). A collection with smaller, narrower leaves made by Drège at an unlocalized site in Namaqualand was described as var. *linearifolia* DC. (1838). Material matching the description has subsequently been collected from Ezelskop near Leliefontein in the Kamiesberg (*Le Roux & Ramsey* 760 NBG) and from near Kamieskroon (*Hall s.n.* NBG462/52 NBG). These plants were growing in cracks in exposed granite sheets, which is consistent with their more compact and dwarf habit. This habitat struck Compton (1953) as significantly different from that of *O. retrorsa*, which he knew from rocky slopes in somewhat deeper soils, but subsequent collections of typical *O. retrorsa* have been made from bare rock cracks and sandy depressions on granite (*Oliver* 5965 NBG) and the variation in growth form is evidently purely ecological. The salient differences between the three varieties are given in Rowley (1994). Additional collections (*Le Roux* 3391 NBG) of *O. retrorsa* from Ezelsfontein, the type locality of *O. spektakelensis*, have the relatively narrow leaves of the type variety and there seems to be nothing to be gained by continuing to distinguish varieties in the species. Indeed, cultivated plants of var. *retrorsa* and var. *spektakelensis* illustrated by Rowley (1994: 192) are vegetatively indistinguishable.

Another similar species, *Othonna zeyheri* Sond. ex Harv., was based on *Zeyher* 996 collected near Kliprand at the southeastern end of the Kamiesberg. The status of this taxon in relation to *O. retrorsa* was questioned by Harvey himself (1865), and Rowley (1994) later tentatively included it in *O. retrorsa* var. *spektakelensis*. Compton (1953), however, was convinced that it was a good species, equating it with Hall's collection from near Kamieskroon mentioned above. Examination of the ample isotype material shows that this taxon matches typical *O. retrorsa* and cannot be retained at any level.

***Othonna retrorsa* DC.**, *Prodromus compositae* 6: 479 (1838). Type: South Africa, [Northern Cape], Kasparskloof, 19 August 1839, *Drège* 2726 (G-DC, holo.–microfiche!; P–Aluka image!, website accessed 25-11-09).

O. retrorsa var. *linearifolia* DC.: 479 (1838), syn. nov. Type: South Africa, Namaqualand without precise locality, *Drège* (G-DC, holo.–microfiche!).

O. zeyheri Sond. ex Harv.: 339 (1865), syn. nov. Type: South Africa, [Western Cape, Kliprand], between Lieslap and Hofkraal, 1846 without month, *Zeyher* 996 (S, holo.; BOL!, BM–Aluka image!, website accessed 25-11-09, P, SAM!).

O. spektakelensis Compton: 118 (1953), syn. nov. *O. retrorsa* var. *spektakelensis* (Compton) G.D.Rowley: 282 (1990). Type: South Africa, [Northern Cape], Ezelsfontein, between Springbok and Spektakel Pass, 8 September 1950, *H. Hall* 141 (NBG, holo.).

Additional specimens examined

NORTHERN CAPE.—2917 (Springbok): Eselsfontein, between Springbok and Spektakel, (–DA), 21 August 1953, *Hall* NBG771/49 (NBG); Farm Ezelsfontein, between Tierhoek and Sandhoogte, (–DA), 3 September 1985, *Le Roux* 3391 (NBG); Spektakel Mountain, (–DA), 26 September 1974, *Goldblatt* 2805 (NBG); Komaggas, Koufonteinberg, (–CD), October 1933, *Herre* 2929 (NBG). 3017 (Hondeklipbaai): Grootvlei, (–BB), 26 August 1954, *Barker* 8413 (NBG); Kamieskroon, (–BB), July 1952 [fruiting], *Hall* NBG462/52 (NBG); 10 miles [16 km] south of Kamieskroon, (–BB), 7 September 1945, *Compton* 17304 (NBG). 3018 (Kamiesberg): west side of Eselkop Mountain, (–AC), 13 October 1981, *Le Roux & Ramsey* 760 (NBG); Kamiesberg, Farm Welkom, (–AC), 31 August 1975, *Oliver* 5965 (NBG); Boplaas Farm, near top of Studer's Pass, (–AC), 30 August 2004, *Helme* 3258 (NBG).

7. *Cacalia rigida* Thunb. is a thorny shrublet with obovate, sparsely denticulate leaves and shortly pedunculate, disciform capitula (Thunberg 1823). The species was transferred to *Kleinia* by De Candolle (1838) on the basis of the description alone, with the result that the taxon was redescribed by him in the same publication under the name *Doria spinescens* DC. from a collection of Drège's from the Sneeuberg. In a reversal of the situation, Harvey (1865), who had access to the Thunberg herbarium but not to the Drège specimen, was nevertheless confident that they represented the same species and therefore transferred Thunberg's name to *Doria*, placing De Candolle's name in synonymy under it. We have been able to examine both relevant types for the first time and confirm Harvey in his decision. Schultz (1944), who included *Doria* in *Othonna*, later transferred *D. spinescens* to *Othonna* under the new name *O. rhamnoides* Sch.Bip. as De Candolle's epithet was preoccupied in the genus. Thunberg's *Cacalia rigida* is actually the earliest name for the taxon but this epithet is also preoccupied in *Othonna*, and Schultz's new name is thus the correct name for the species in *Othonna*. The species, which is rarely collected, has been overlooked in southern African checklists for the family under any of its available names (Welman 2006). We provide the complete nomenclature here.

***Othonna rhamnoides* Sch.Bip.**, *Compositae Kraus-sianae*: 769 (1944) [replacement name for *Doria spinescens* DC.: 470 (1838), non *Othonna spinescens* DC.: 332 (1838)]. Type: South Africa, [Eastern Cape], Sneeuberg, [September 1829], *Drège* [619] (G-DC, holo.–microfiche!; K–Aluka image!, website accessed 25-11-09).

Doria rigida (Thunb.) Harv.: 322 (1865), non *Othonna rigida* DC.: 476 (1838) [= *Othonna amplexicaulis* Thunb.]. *Cacalia rigida* Thunb.: 624 (1823). *Kleinia rigida* (Thunb.) DC.: 338 (1838). Type: South Africa, without precise locality or date, *UPS-THUNB18765* (UPS-THUNB, holo.–microfiche!).

SENECIO

8. *Senecio albopunctatus* Bolus (1887) was described from a single gathering of several plants collected in Namaqualand at Klipfontein, west of Steinkopf on the old Steinkopf–Port Nolloth railway. *S. albopunctatus*

is a subshrub with terminal tufts of pinnatifid leaves, the lobes tipped with characteristic pale thickenings or calli that give the species its name, and solitary, radiate capitula on long peduncles. The plant was described as glabrous but careful examination of the type material shows the leaves and peduncles to be scantily clad in minute, sessile glands. No similar plants with radiate capitula have been collected since then but several collections have been made of plants that are vegetatively identical to *S. albopunctatus* but differ from it in having discoid capitula. The first of these collections was made in 1935 by R.H. Compton at Klipfontein hill, west of Steinkopf (Compton 5442 NBG), at the type locality of *S. albopunctatus*. It was identified tentatively by Compton as *S. albopunctatus* following careful comparison with the type, with the comment that apart from the slightly less indurated leaflet tips, he could find no significant differences between the two species and that he, therefore, interpreted his material as a rayless variant of *S. albopunctatus*. Since then several additional collections of this rayless form have been made in the Richtersveld, all of them agreeing exactly with Bolus's and Compton's original gatherings and also proving very good matches with the type of *S. albopunctatus*, apart from the clear absence of rays.

The occurrence of both discoid and radiate forms in a single species is rare in *Senecio* but not unknown. Among species from the Cape Floristic Region (CFR) it has been recorded in *S. agapetes* C.Jeffrey and *S. crispus* Thunb. (Goldblatt & Manning 2000), and in several species from KwaZulu-Natal, including *S. conrathii* N.E.Br., *S. hypochoerideus* DC., *S. polyodon* DC. and *S. poseidonis* Hilliard & B.L.Burt (Hilliard 1977). Such species are scattered throughout the genus. In most instances one of the forms is dominant, with the other rare or occasional, but in a few species both forms are common. A strikingly similar example is provided by *S. erosus* L.f., in which both radiate and discoid plants have been collected near Mooresburg (Helme 2131 [discoid] and Helme 2339 [radiate] NBG) in this otherwise entirely radiate species. We have no hesitation, therefore, in following Compton in treating both discoid and radiate forms as a single species.

However, it is now clear that the discoid material of *Senecio albopunctatus* from the Richtersveld is indistinguishable from *S. maydae* Merxm. (1960), which was based on several collections from the Huib Hoch Plateau and adjacent hills in southern Namibia (Dinter 1932). Of particular significance is the presence of unusual, sessile glands on the leaves, peduncles and phyllaries that render the surface of the plant sticky, evidenced in some specimens by a conspicuous load of adhering sand grains. The name *S. maydae* is accordingly placed in synonymy under *S. albopunctatus*.

***Senecio albopunctatus* Bolus** in Botanical Journal of the Linnean Society 24: 177 (1887). Type: South Africa, [Northern Cape], Namaqualand minor [Namaqualand], Klipfontein, September 1883, Bolus 423 (BOL, holo.!; K, P—Aluka images!, website accessed 25-11-09, SAM!).

S. maydae Merxm.: 608 (1960) [replacement name for *S. longipedunculatus* Dinter: 93 (1932)], syn. nov. Syntypes: Namibia, [Lüderitz], Garub, Tigerberg, 17 October 1922, Dinter 4107 (WIND, SAM!); Namibia, Buchberge [Boegoeburg], 28 June 1929, Dinter 6464 (NBG!, PRE, SAM!, WIND).

Additional specimens examined

NORTHERN CAPE.—2816 (Oranjemund): Richtersveld, Helskloof area northeast of Khubus, (—BD), 29 August 1977, Oliver, Tölken & Venter 348 (NBG); Vandersterrersberg, (—AC), 30 July 1933, Van der Walt 296 (NBG). 2817 (Vioolsdrif): Kodaspiek, (—AA), 2 September 1977, Oliver, Tölken & Venter 450 (NBG); south of Van Zylsrus, (—CB), 4 September 1977, Thompson & Le Roux 324 (NBG). 2917 (Steinkopf): Klipfontein koppie, (—BA), 29 August 1935, Compton 5442 (NBG).

9. Among the 20 annual species of *Senecio* recognized by Harvey (1865), are five with mauve or purple ray florets. Two of these species are well known: *S. elegans* L. is essentially a species of sand dunes along the western and southern Cape coast, from Saldanha in Western Cape to Port Alfred in Eastern Cape, whereas *S. arenarius* Thunb. is widely distributed on sandy and gravelly flats and in washes along the west coast and interior, from central Namibia through much of the western half of South Africa as far south as Agulhas in Western Cape (Goldblatt & Manning 2000). Both are ± glandular-pubescent herbs, extremely variable in leaf form [polymorphous is how they are described by Harvey (1865)] but readily separable by their different involucre: ± cylindrical and with a few subulate bracteoles in *S. arenarius*; ± campanulate and closely enveloped at the base by several imbricating, lanceolate, black-tipped bracteoles in *S. elegans*. The remaining three species in the group were known to Harvey from the type specimen or description alone and they remain poorly known today.

One of them, *Senecio cakilefolius* DC., was based on a collection made by Drège at Silverfontein, southeast of Springbok. This material was not seen by Harvey (1865), who relied entirely on De Candolle's (1838) description. The species was distinguished from *S. arenarius* by its glabrous stem and leaves, and supposedly larger capitula but examination of the type collection confirms that the plants are actually sparsely but quite evidently glandular-pubescent and the capitula are no larger than commonly encountered in *S. arenarius*. The name has subsequently been applied rather indiscriminately to any *arenarius*-like plants with less than the usual pubescence. Subglabrous or thinly pubescent plants of the *cakilefolius* type are common between Springbok and Kamiesberg but also occur further south near Clanwilliam and through the Tanqua River Basin to Whitehill, whereas more densely pubescent plants of the *arenarius* type are widespread. With a full range of material from Namaqualand and the West Coast now available, it is clear that there are any number of intermediate conditions from almost glabrous plants to those with sparsely glandular-pubescent stems and leaves to densely glandular-pubescent plants. The size of the capitula also varies greatly and independently of the vestiture. Populations from Namaqualand and the Bokkeveld Plateau have slightly larger capitula with phyllaries 5–7 mm long compared with those from the Cold Bokkeveld and Little Karoo, in which the phyllaries are 4–6 mm long, but this small size difference is not correlated with other differences, and is not uncommonly encountered in other species in the genus. With the ample collections now at our disposal, it appears to us that the concepts of *S. arenarius* and *S. cakilefolius* represent the extremes of a continuous range of variation and we thus treat them as a single species.

Senecio arenarius Thunb., *Prodromus plantarum capensium*: 158 (1800b). Type: South Africa, without precise locality or date, *Thunberg UPS-THUNB19545* (UPS-THUNB, holo.–microfiche!).

S. cakilefolius DC.: 408 (1838), syn. nov. Type: South Africa, [Northern Cape], Silverfontein [Silwerfontein, September 1830], *Drège* [2816] (G-DC, holo.–microfiche!; P–Aluka image!, website accessed 25-11-09).

10. *Senecio pearsonii* Hutch. (1917) was based on a collection from the Kamiesberg and diagnosed against *S. hypochoerideus* DC., from which it was distinguished by its more finely serrate leaves and striate-papillate, as opposed to uniformly pubescent, achenes. Actually, the achenes of *S. hypochoerideus*, like those of most species of *Senecio*, are striate-hispid (Hilliard 1977). Examination of the type of *S. pearsonii* confirms Hutchinson's opinion of the Kamiesberg material in respect of *S. hypochoerideus* but shows his species to be a perfect match for the closely allied *S. asperulus* DC. This species differs primarily from *S. hypochoerideus* in its narrower leaves 2–10 mm wide, with more finely serrate margins with simple teeth vs broader, doubly-serrate leaves 10–40 mm wide in *S. hypochoerideus* (Hilliard 1977). At the time of Hilliard's (1977) treatment of the genus in Natal, *S. asperulus* was known from the escarpment of the Eastern Cape northwards along the Drakensberg into the Highveld but recent collections have extended its range westwards through the Nieuweveld Mountains and along the western escarpment as far as the Hantamsberg. The inclusion of *S. pearsonii* in *S. asperulus* is a natural extension of the range along the western escarpment to the Kamiesberg.

Senecio asperulus DC., *Prodromus systematis naturalis regni vegetabilis* 6: 386 (1838). Type: South Africa, [Eastern Cape], Albany, *Ecklon* [83] (G-DC, lecto., here designated–microfiche!; P–Aluka image!, website accessed 25-11-09).

S. pearsonii Hutch. in Pearson & Hutchinson: 398 (1917), syn. nov. Type: South Africa, [Northern Cape], Khamiesberg [Kamiesberg], southwest of Leliefontein, 16 January 1911, *Pearson* 6310 (K, holo.–Aluka image!, website accessed 25-11-09).

Additional specimens (Greater CFR) examined

NORTHERN CAPE.—3119 (Calvinia): Hantamsberg, Van Rhynshoek Farm, (–BD), 18 August 1976, *M.F. Thompson* 2349 (NBG); 10 October 1983, *M. Thomas* 41a (NBG). 3220 (Sutherland): Sutherland, (–BC), 8 July 1968, *F. Stayner* s.n. NBG87.402 (NBG). 3221 (Merweville): Nuweveldberge, Bok se Plaas, (–BA), 26 February 1986, *Moffett & Steensma* 4017 (NBG).

11. *Senecio carroensis* DC. (1838) was based on a collection made by Drège along the southern margin of the Great Karoo at Kendo [Kendouslaagte] between Klaarstroom and Willowmore. The species is a slender, laxly branched shrublet with deeply incised, almost bipinnatisect leaves, the lobes narrow and deeply toothed. The sparsely woolly or subglabrous branches are characteristically yellowish striate when young, often flushed purple when older. The radiate, yellow capitula are in lax corymbs, with glabrous phyllaries. Ample material of the taxon has now been collected from the drier mountains of the Little Karoo westwards to Karooport and thence northwards through the Cold Bokkeveld and Swarttruggens as far as the Bokkeveld Mountains. This material displays significant variation

in the shape and size of the leaf lobes, a feature that was already evident to De Candolle. Although mostly narrowly oblong or linear and 2–7 mm long, the lobes in some collections are much reduced, almost quadrate, and 1–2 mm long. These plants are an exact match for *Senecio parvifolius* DC., another of Drège's collections, from the Kamiesberg in Namaqualand, and which was distinguished from *S. carroensis* essentially by its smaller leaf lobes. Further collections from the Kamiesberg confirm the general constancy of this leaf character among the Namaqualand plants but also include plants in which the leaf lobes are longer and narrower and thus indistinguishable from more xeromorphic forms of *S. carroensis*. With this larger range of material now available, we conclude that these two species represent extreme leaf forms in a single species.

Senecio carroensis DC., *Prodromus systematis naturalis regni vegetabilis* 6: 396 (1838). Type: South Africa, [Eastern Cape], Carro [Willowmore], Kendo, [22 June 1829], *Drège* [5910] (G-DC, holo.–microfiche!; K, P–Aluka images!, website accessed 25-11-09).

S. parvifolius DC.: 396 (1838), syn. nov. Type: South Africa, [Northern Cape], Kamiesberg, Modderfontein, [4 November 1830], *Drège* [2820] (G-DC, holo.–microfiche!; K, P–Aluka images!, website accessed 25-11-09, SAM!).

Additional specimens examined

NORTHERN CAPE.—2917 (Springbok): Brakdam, (–BC), 24 July 1941, *Compton* 11085 (NBG). 3018 (Kamiesberg): Kamiesberg, Farm Welkom, (–AC), 16 October 1954, *Esterhuysen* 23680 (NBG); koppie east of Rooiberg, (–AC), 14 October 1981, *Le Roux & Ramsey* 791 (NBG); between Garies and Leliefontein, (–AC), November 1939, *Esterhuysen* 1399 (NBG). 3118 (Vanrhynsdorp): Gifberg, (–DC), 2 September 1948, *Compton* 20777 (NBG); Nardouw, (–DC), 6 September 1951, *Compton* 22833 (NBG). 3119 (Calvinia): Oorlogskloof Nature Reserve, (–AC), 19 September 1996, *Pretorius* 353 (NBG); 20 September 2000, *Pretorius* 508 (NBG); top of Botterkloof Pass, (–CD), 24 August 1950, *B. Maguire* 188 (NBG).

WESTERN CAPE.—3219 (Wuppertal): Cedarberg, Matjiesrivier Reserve, (–CB), 4 October 1997, *Lechmere-Oertel* 749 (NBG); Swarttruggens, Knolfontein, (–DC), 15 September 2006, *Jardine & Jardine* 448 (NBG). 3319 (Worcester): Karooport, (–BA), 28 September 1951, *Compton* 22932 (NBG). 3320 (Montagu): Laingsburg, Wittebergskloof, (–BC), 16 July 1923, *Compton* 2502 (NBG); eastern end of Anysberg, (–DA), 6 October 1982, *Van Zyl* 3372 (NBG); Touwsberg, (–DB), 17 September 1993, *Snijman* 1336 (NBG); 7 October 1993, *McDonald* 2442 (NBG). 3321 (Merweville): Ladismith, Seweweekspoort, (–AD), 13 September 1938, *Compton* 7877 (NBG).

12. Among the taxa with yellow, radiate capitula that were included in Harvey's (1865) *Sinuosi* are two species characterized by a short, vertical rhizome closely covered by imbricating leaves, with the base of the petioles expanded and encircling the rhizome. The investing leaf bases form an almost bulb-like structure, with their inner faces densely covered with woolly hairs that also run up along the margin of the sheath and onto the petiole for a short distance. These woolly rhizomes set these two species apart from others in the group but the difference between them is not clear. *Senecio eriobasis* DC. (1838), based on a collection from Worcester, was distinguished from *S. erosus* L.f. (1782) by its glabrous vs scabro-pubescent leaves and involucre. Like many other species of *Senecio*, *S. erosus* is extremely variable in the degree of development of the vestiture, varying from sparsely to densely pubescent, with no clear distinction between the two conditions. More significantly, however, examination of the type of *S. eriobasis* shows

the leaves and peduncles to be distinctly pubescent and quite indistinguishable from those of *S. erosus*, and there is no doubt that Goldblatt & Manning (2000) were correct in their conclusion that the two could not be separated. We accordingly formally include *S. eriobasis* in the synonymy of *S. erosus*. The species is distributed from Namaqualand to the southern Cape.

Examination of the type of *Doria incisa* Thunb., treated as a synonym of *Senecio erosus* by Harvey (1865), confirms that it has radiate capitula, despite its initial placement in *Doria*, and that it cannot be distinguished from *S. erosus*. Harvey (1865) also included in *S. erosus* the species described by Thunberg (1823) as *Cineraria pandurata* Thunb. (later transferred to *Senecio* as *S. panduratus* (Thunb.) Less.), but he explicitly excluded De Candolle's (1838) application of the name. De Candolle (1838) based his interpretation of *S. panduratus* on several specimens in G-DC. These represent a taxon very similar to *S. erosus* in leaf and inflorescence but differing from it in the rootstock, which is a $\pm$ horizontal rhizome bearing a lax tuft of leaves that are not strongly widened at the base and lacking the distinctive woolly vestiture in the axils and along the base of the petiole that is such a striking feature of *S. erosus*. Harvey (1865) considered that De Candolle's plants represented *S. hastatus* but this is not the case (see below under *S. robertiifolius*).

There are two specimens labelled *Cineraria pandurata* in UPS-THUNB. One of them, a complete plant with the diagnostic erect, villous rhizome of *Senecio erosus*, is also labelled *Doria incisa* and constitutes the type of that name. The second specimen, securely identified by the locality data as the type of *Cineraria pandurata*, comprises just an inflorescence and a single, unattached basal leaf. This incomplete specimen, in our opinion, might equally be assigned either to *S. erosus* or to the taxon that is currently known under the name *S. panduratus* but Thunberg's (1823) application of the name is quite clear. His phrase '*caulis erectus, striatus, villosus*' is essentially identical to his description of the stem of *Doria incisa* as '*caulis ... flexuoso-erectus, simplex, teres, striatus, pubescens*' and clearly indicates *S. erosus*. We thus have no hesitation in following Harvey (1865) in treating *S. panduratus* as a synonym of *S. erosus*.

Although mostly radiate, occasional plants have discoid capitula, sometimes with both forms in the same population (e.g. *Helme* 2131, 2339 NBG).

***Senecio erosus* L.f.**, Supplementarum plantarum: 370 (1782 '1781'). Type: South Africa, without locality or date, *Thunberg* 446 (LINN996.72, holo.—Linnean Society of London image!, website accessed 25-11-09).

Cineraria incisa (Thunb.) Willd.: 2074 (1803). *Doria incisa* Thunb.: 156 (1800b). Type: South Africa, without precise locality or date, *Thunberg* UPS-THUNB19830 (UPS-THUNB, holo.—microfiche!).

S. panduratus (Thunb.) Less.: 392 (1832). *Cineraria pandurata* Thunb.: 672 (1823). Type: South Africa, [Western Cape], Kamtoos [Gamtoos] River, December without year, *Thunberg* UPS-THUNB19934 (UPS-THUNB, holo.—microfiche!).

S. eriobasis DC.: 388 (1838), syn. nov. Type: South Africa, [Western Cape], Worcester, without date, *Ecklon* [1901] (G-DC, holo.—microfiche; P—Aluka image!, website accessed 25-11-09).

Selected additional specimens examined

NORTHERN CAPE.—3017 (Hondeklipbaai): Kamieskroon, (—BB), 29 August 1937, *Compton* 6799 (NBG); Grootvlei, (—BB), 7 September 1945, *Compton* 17284 (NBG); Darter's Grave, (—BD), 2 September 1951, *Maguire* 970 (NBG). 3018 (Kamiesberg): Welkom, near Garies, (—AB), 16 October 1954, *Esterhuysen* 23666 (BOL) [discoid capitula]. 3119 (Calvinia): top of Vanrhyn's Pass, (—AC), 1 October 1947, *Taylor* 2864 (NBG); west of Nieuwoudtville on road to Vanrhyn's Pass, (—AC), 23 August 1950, *Barker* 6453, *Middlemost* 1603 (NBG); Nieuwoudtville Reserve, (—AC), 8 September 1983, *Perry & Snijman* 2333 (NBG); Oorlogskloof Nature Reserve, (—AC), 19 September 1995, *Pretorius* 298 (NBG); Karigabosch Fountain, (—DD), 20 August 1975, *Thompson* 2468 (NBG); Kareehout River, south of Perdekloof, (—DD), 21 August 1975, *Thompson* 2520 (NBG). 3220 (Sutherland): 11 km east of Sutherland, (—BD), 22 September 1985, *Moffett* 3774 (NBG). 3319 (Worcester): Tweedside, (—AB), 25 September 1932, *Compton* 4000 (NBG).

WESTERN CAPE.—3118 (Vanrhynsdorp): Nardouw, (—DC), 6 September 1951, *Johnson* 242 (NBG). 3217 (Vredenburg): Vredenburg, Trekossenkraal, (—DD), 28 September 2002, *Boucher* 6992 (NBG). 3218 (Clanwilliam): near Clanwilliam, (—BB), 20 July 1941, *Compton* 10996 (NBG). 3219 (Wuppertal): Pakhuis, (—AA), 18 September 1937, *Compton* 6951 (NBG); 13 September 1947, *Barker* 4693 (NBG); Nieuwoudt's Pass, (—AC), 3 September 1982, *Le Maître* 322 (NBG); Matjiesrivier, (—AD), September 1943, *Wagener* 183 (NBG); Kromrivier Farm, (—CA), 15 September 1984, *Taylor* 11050 (NBG); Gonnafontein Farm, (—CB), 2 September 2000, *Pond* 125 (NBG); Swarttruggens, Knollfontein, (—DC), 15 September 2006, *Jardine & Jardine* 452 (NBG). 3318 (Cape Town): Mooresburg, (—BA), [discoid capitula], 31 August 2001, *Helme* 2131 (NBG); 12 September 2001, *Helme* 2339 (NBG); Stellenbosch, (—DD), 13 September 1989, *Buys* 30 (NBG). 3319 (Worcester): Worcester, (—CB), 23 August 1976, *Bayer* 202 (NBG); near Rusbos, (—CC), 29 August 1979, *Hugo* 1824 (NBG). 3320 (Montagu): Bantams, (—BA), 27 October 1941, *Compton* 12216 (NBG). 3321 (Ladismith): Gamka Mountain Nature Reserve, (—CB), 15 August 1983, *Cattell* 291 (NBG). 3322 (Oudtshoorn): George, (—AC), September 1932, *Fourcade* 4709 (BOL). 3418 (Simon's Town): Cape of Good Hope Nature Reserve, (—AD), 17 September 19709, *Taylor* 7792 (NBG); Greyton Nature Reserve, (—BA), 19 September 1980, *Rycroft* 3365 (NBG). 3420 (Bredasdorp): De Hoop, (—AD), 14 September 1979, *Burgers* 2242 (NBG). 3421 (Riversdale): Reisiesbaan Siding, (—AB), 6 August 1983, *Bohnen* 8231 (NBG). 3424 (Humansdorp): Kromme River, Company's Drift, (—BA), September 1922, *Fourcade* 2318 (BOL).

13. The name *Senecio panduratus* (Thunb.) Less. was misapplied by De Candolle (1838) to plants that resemble *S. hastatus* L. in general appearance but which are distinct from it in their sparsely branched corymbs with much larger capitula. Both *S. hastatus* and *S. panduratus* sensu DC. have a short, $\pm$ horizontal rhizome, and radical leaves with long petioles and inciso-pinnatifid blades, and the stems and leaves are thinly or densely pubescent with a mix of short, glandular hairs and longer eglandular hairs. True *S. hastatus* is characterized by few- to well-branched corymbs of up to 20, relatively small, cylindrical capitula, 9–12 $\times$ 5–7 mm, with 12–14 phyllaries. It is widely distributed in moister situations from Ceres in the southwestern Cape eastwards to Lesotho and the Free State (Hilliard 1977; Goldblatt & Manning 2000). The taxon currently known under the name *S. panduratus*, in contrast, has sparsely branched corymbs of (1–)3–10, larger, campanulate capitula, 10–12 $\times$ 8–12 mm, with 20–24 phyllaries. It has a more restricted distribution in the interior southwestern Cape, in more arid environments. The name *S. hastatus* is in fact a synonym of *S. erosus* (see above) and the plant currently known under that name thus requires a new name. Examination of the type of *S. robertiifolius* DC. (1838), a poorly known taxon based on a collection made in the Kamiesberg, confirms that it precisely matches the plants currently identified as *S. hastatus* and this name is therefore available for use.

Senecio robertiifolius DC., *Prodromus systematis naturalis regni vegetabilis* 6: 384 (1838). Type: South Africa, [Northern Cape], Camiesberg [Kamiesberg], Modderfontein, [4 November 1830], Drège [5901] (G-DC, holo.-microfiche!; P-Aluka image!, website accessed 25-11-09).

S. panduratus sensu DC., non (Thunb.) Less.

Additional specimens examined

NORTHERN CAPE.—2917 (Springbok): Steinkopf, Besondermeid, (–BC), 27 September 1933, Herre s.n. (NBG). 3017 (Hondeklipbaai): Kamieskroon, (–BB), 29 August 1937, Compton 6810 (NBG). 3018 (Kamiesberg): Welkom, near Garies, (–AB), 16 October 1954, Esterhuysen 23683 (BOL). 3119 (Calvinia): Nieuwoudtville Reserve, (–AC), 7 September 1983, Perry & Snijman 2297 (NBG); Oorlogskloof Nature Reserve, (–AC), 28 September 2000, Pretorius 538 (NBG); Zoetwater, west of Calvinia, (–BC), 24 September 1952, Maguire 1933 (NBG); Akkerendam Nature Reserve, (–BD), 6 August 1993, Jooste 1 (NBG); behind Hantam, Farm Saaihoek, (–BD), 7 September 2002, Rosch 124 (NBG). 3220 (Sutherland): 11 km east of Sutherland, (–BD), 22 September 1985, Moffett 3772 (NBG); Komsberg, Farm Klein Jakhals Valley, (–DA), 6 September 1986, Cloete & Haselau 237 (NBG).

WESTERN CAPE.—3219 (Wuppertal): Pakhuis, (–AA), 29 September 1940, Compton 9559 (NBG). 3318 (Cape Town): Riebeeck-Kasteel, (–BD), 14 September 1941, Compton 11723 (NBG). 3319 (Worcester): Tweedside, (–AB), 25 September 1932, Compton 4011 (NBG); Whitehill, (–BA), 17 September 1945, Compton 17398 (NBG); Whitehill Ridge, (–BA), 20 September 1943, Compton 14900 (NBG); Bonteberg, (–BD), 20 September 1931, Compton 3780 (NBG); Rabiesberg, (–DA), 26 September 1935, Compton 5835 (NBG). 3321 (Ladismith): west of Seweweekspoortberg, (–AD), 3 February 1992, Oliver 9998 (NBG); Klein Swartberg, east of Kouveldberg, (–AD), 23 December 2006, Helme 4370 (NBG). 3322 (Oudtshoorn): Kamanassie, Mannetjiesberg, (–DB), 1 February 1941, Compton 10563 (NBG).

14. *Senecio lobelioides* DC. (1838) was based on material collected by Drège on the Farm Silverfontein, midway between Springbok and Kamieskroon. It was not seen by Harvey (1865), who merely repeated De Candolle's description. Examination of isotype material at Paris confirms that it is readily recognized among the other annual species by being completely glabrous, and with characteristic leaves, the lower conspicuously petiolate with ovate-reniform blades, and the upper sessile and cordate-amplexicaul. Although becoming progressively smaller towards the end of the branches, the upper leaves retain their distinctive shape, giving the inflorescences a rather leafy character. Another distinctive feature of the species is the narrowly cylindrical capitula, which are obscurely radiate with very short rays barely exceeding the involucre. Drège's material of *S. lobelioides*, however, is indistinguishable from collections at SAM that have been identified as *Senecio flavus* (Decne.) Sch.Bip. subsp. *flavus* by both Merxmüller (1967) and later, in 1988, by Aaron Lister (now Department of Botany and Plant Pathology, Oregon State University). Although we have not been able to examine type material of *S. flavus*, the protologue (Decaisne 1834), as well as the description and accompanying illustration in Boulos & Hind (2002), give us no reason to doubt this opinion and we accordingly treat *S. lobelioides* as a synonym of *S. flavus*.

Senecio flavus (Decne.) Sch.Bip. in Webb. & Berth., *Histoire naturelle des Îles Canaries* 2: 319, t. 107 (1845). *Crassocephalum flavum* Decne.: 265 (1834). Type: Arabia [Egypt], Sinai, without date or collector (P). Illus.: Boulos & Hind: 264 (2002).

S. lobelioides DC.: 382 (1838), syn. nov. Type: South Africa, [Northern Cape], Silverfontein [Silverfontein], [31 August 1830], Drège [2730] (G-DC, holo.-microfiche!; P-Aluka image!, website accessed 25-9-09).

Additional specimens examined

NAMIBIA.—2426 (Maltahohe): Bullsport, (–AB), July 1947, R.G. Strey 2175 (NBG).

NORTHERN CAPE.—3120 (Williston): Wolwe Rivier, (–CA), 26 July 1941, R.H. Compton 11144 (NBG).

15. The replacement name *Senecio odontophyllus* C.Jeffrey (1992) that was published for the Indian species until then known under the illegitimate later homonym *S. linifolius* (DC.) C.B. Clarke, was applied in error by Goldblatt & Manning (2000) to the Eastern Cape species that is correctly known as *S. linifolius* L.

Senecio linifolius L., *Systema naturae* 2: 1215 (1759). *Senecio odontophyllus* sensu Goldblatt & Manning (2000) [non C.Jeffrey: 95 (1992) (= *Senecio linifolius* (DC.) C.B. Clarke: 202 (1876)].

ACKNOWLEDGEMENTS

We thank Anne-Lise Fourie of the Mary Gunn Library, SANBI for making the G-DC microfiche available to us for study, Mary Stiffler of Missouri Botanical Garden for assistance with older literature, and Dr Arne Anderberg and Dr Johannes Lundberg for arranging for a digital image of the S isotype of *Doria gymnodiscus*. Two anonymous referees provided valuable insights and comments, for which we are most grateful.

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New taxa of *Babiana* (Iridaceae: Crocoideae) from coastal Western Cape, South Africa

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Keywords: *Babiana* Ker Gawl., Iridaceae, southern Africa, systematics, winter rainfall region

ABSTRACT

Discovery of populations south of Elandsbaai of a small-flowered plant closely allied to *Babiana ringens* led to a critical re-evaluation of this sunbird-pollinated Western Cape species. We conclude that these populations represent a new species, *B. avicularis*, recognized by long, arching, subterete leaves, and flowers with the lower part of the perianth tube sigmoid and ± 4 mm long, a dorsal tepal 15–18 mm long, pale green lower tepals directed forward, and a style dividing below the bases of the anthers. In addition, the southern coastal populations of *B. ringens* merit recognition as a separate subsp. *australis*, recognized by the smaller flower, filaments not reaching the apex of the dorsal tepal and the style dividing at or below the bases of the anthers. Field work along the Western Cape coast also resulted in the discovery of a new species, *B. teretifolia*, allied to the distinctive *B. brachystachys* but differing from that species in the linear, spreading, twisted tepals, filaments 12 mm long, white anthers 5.5–6.0 mm long, and the style dividing opposite the anther tips, with branches ± 5 mm long and notched at the tips.

INTRODUCTION

The southern African and largely winter rainfall genus *Babiana* Ker Gawl. was recently revised (Goldblatt & Manning 2007a), at which time 88 species were recognized, but novelties have continued to be added. Just a year later, two new species were described (Goldblatt *et al.* 2008), both found while the revision was in press. In the spring of 2008, two more novelties came to our attention. Neither species was to our knowledge represented in any herbarium but a careful search revealed that one of them, the red-flowered *B. avicularis*, had been collected twice before but had been identified as *B. ringens* (L.) Ker Gawl., largely because of the red flower and unusual sterile main stem. We found *B. avicularis* in strandveld south of Elandsbaai but earlier records are from the Olifants River Mountains north of Clanwilliam and near Leipoldville. Although resembling *B. ringens* in its sterile main stem axis with flowers carried on branches borne close to ground level, *B. avicularis* differs in the long, subterete, arching leaves and smaller flowers with *inter alia* the lower part of the perianth tube sigmoid and only ± 4 mm long, dorsal tepal 15–18 mm long, and style dividing below the bases of the anthers. The discovery of this species prompted us to review the variation in *B. ringens* and closely allied *B. hirsuta* and we conclude that the southern populations of the former merit recognition as a separate subspecies that we name subsp. *australis*. This taxon has smaller flowers than subsp. *ringens*, with a dorsal tepal only 18–30 mm long vs 25–45(–50) mm in subsp. *ringens*, filaments not reaching the apex of the dorsal tepal and, like *B. avicularis*, a style dividing below the bases of the anthers.

The second new species, *Babiana teretifolia*, from sandveld on the farms Kommandokraal and Skilpadvlei,

northwest of Vredendal in southern Namaqualand, is allied to *B. brachystachys* (Baker) G.J.Lewis, a species centred in coastal Namaqualand but extending south to Lambert's Bay in Western Cape, the latter a range extension for the species. Both *B. brachystachys* and *B. teretifolia* have $\pm$ terete leaves with 5 or 6 narrow longitudinal grooves, the main and lateral spikes decumbent and usually held at ground level, and flowers with an elongate perianth tube exceeding 60 mm. *B. teretifolia* is distinctive in its linear, channelled, slightly twisted tepals 26–30 mm long, spreading at right angles to the tube, with the dorsal tepal barely differing from the others in size, shape and orientation. In addition, *B. teretifolia* has filaments exerted ± 9.5 mm, white anthers 5.5–6.0 mm long, and longer style branches ± 5 mm long compared with filaments exerted up to 3 mm, anthers 4–5 mm long, usually mauve to violet, and style branches ± 2.5 mm long in *B. brachystachys*. With the two new species described here, *Babiana* now comprises 92 species.

1. *Babiana avicularis* Goldblatt & J.C.Manning, sp. nov.

Plantae ad 120 mm altae foliis exclusis, axe principali sterili velutino, ramis ad basem productis, foliis 6–8 linearibus ad 300×2 –3 mm arcuatis laevigatis, spicis horizontalibus subsecundis usitate 8–12-floris, bracteis minute scabridis viridibus apicibus brunneis mucronatis, bractea externa 14–22 mm longa interiora fere ad basim divisa, floribus zygomorphis rubro-carneis in fauce flavis tepalis inferioribus pallide viridibus in medio atroviridioribus, tubo perianthii compresso-infundibuliformi parte inferiori cylindrico ± 4 mm longo, parte superiori 12–17 mm longa, tepalis inaequalibus dorsale 15–18 mm longo, filamentis 25–32 mm longis, antheris 3.5–5.0 mm longis atrovioleaceis ovario laevigato, stylo infra basim antherarum diviso, ramis 4–5 mm longis.

TYPE.—Western Cape, 3218 (Clanwilliam): coast south of Elands Bay, ± 30 km north of Rocher Pan, sandy flats, (–AD), 11 September 2008, Goldblatt & Porter 13109 (NBG, holo.; K, MO, PRE, S, iso.).

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Plants up to 120 mm high, excluding leaves, with main axis suberect and sterile, usually with two decumbent, fertile branches borne close to ground level, minutely velvety on aerial axes. *Leaves* 6–8, linear, up to 300 × 2–3 mm, firm but arching toward ground, ± oval in cross section and closely plicate, usually with 2 or 3 folds on each surface, glabrous. *Fertile spike* horizontal, subsecund with flowers in two ranks, mostly 8–12-flowered; bracts minutely scabrid, green with dry brown apices, outer bracts 14–22 mm long, bearing a prominent mucro, inner ± half as long as outer, divided almost to base and diverging distally, joined by transparent tissue at ovary level. *Flowers* zygomorphic, facing spike apex, predominantly reddish pink, paler in throat, lower part of tube yellow, lower five tepals with pale green limbs sometimes fading to pink near tips, darker green in midline, unscented; perianth tube compressed-funnel-shaped, lower part ± 4 mm long, cylindric, sigmoid distally then abruptly expanded into flared upper part 12–17 mm long; tepals unequal, outer whorl prominently mucronate, dorsal 15–18 × 2.5–3.5 mm, ascending, channelled below with margins curving inward and enclosing filaments and style for most of their length, expanded to 3 mm wide and recurved in upper 5 mm, lower three tepals united with upper laterals for ± 4 mm in prominent lip, free parts directed forward, lower and upper laterals ± 8 × 1.5 mm, lower median 3–7 × 1–2 mm. *Stamens* unilateral; filaments straight, suberect, 25–32 mm long, enclosed below by dorsal tepal, exserted ± 16 mm and reaching apex of dorsal tepal; anthers 3.5–5.0 mm long, purple. *Ovary* smooth; style dividing shortly below base of anthers, style branches 4–5 mm long, recurved. *Capsules* barrel-shaped, ± 11 × 8.5 mm, showing outline of seeds. *Mature seeds* not known. *Flowering time*: mid-August to late September. Figure 1A–D.

Distribution and ecology: restricted to the West Coast and near interior of Western Cape (Figure 2). Just four populations of *Babiana avicularis* are known: two are from sandy flats between Elands Bay and Rocher Pan, a short distance inland from the densely vegetated coastal dunes adjacent to the beach; a third is from the Olifants River Valley north of Clanwilliam, also on sandy ground; and the fourth, the earliest record, is from coastal fynbos close to Leipoldtville. The four records fall within three quarter-degree squares of latitude and longitude.

Diagnosis and relationships: flowers of *Babiana avicularis* resemble those of the other two predominantly red-flowered species of the genus, *B. hirsuta* (Lam.) Goldblatt & J.C.Manning (= *B. thunbergii* Ker Gawl.), and *B. ringens*, except that they are almost half the size (Figure 1). Like *B. ringens*, the main axis is sterile and we infer that, as in *B. ringens*, it serves as a perch for birds taking nectar from the flowers (Anderson *et al.* 2005) but the flowers differ from that species in some important respects apart from their smaller size (Table 1). Flowers of *B. ringens* subsp. *ringens* have a perianth tube 28–40 mm long, a dorsal tepal 25–45(–50) mm long, enlarged lower lateral tepals ± 20 mm long, and the upper tepals are recurved (Figure 1H). In addition, the filaments are 37–70 mm long, the anthers 5.0–7.5 mm long, and the style divides opposite the upper half of the anthers or shortly beyond their tips. Subsp. *australis* has slightly smaller flowers with the dorsal tepal 18–30 mm long and filaments 24–34 mm long. In contrast, flowers of *B. avicularis* have a tube 16–21 mm long, a dorsal tepal 15–18 mm long, and all three lower tepals pale green and directed forward. In both species, as well as in *B. hirsuta*, the margins of the dorsal tepal curve together and loosely enclose the filaments and style, and only the distal third or quarter is expanded and slightly recurved. The filaments of *B. avicularis* are 25–32 mm long, the anthers 3.5–5.0 mm long and the style divides below the bases of the anthers. The leaves of *B. ringens* are lanceolate to sublinear but firm to rigid in texture with almost pungent tips, in contrast to the longer, linear, fairly soft-textured leaves of *B. avicularis* that arch outward gracefully.

The flowers of *Babiana avicularis* resemble those of *B. hirsuta* more closely than *B. ringens* in their proportions but in *B. hirsuta* the upper and lower lateral tepals are recurved distally and extended outward, and the lowermost tepal is substantially larger than the lower laterals (Figure 1E–G), the reverse of the situation in *B. avicularis*. The lower tepals of *B. avicularis* are pale green, sometimes pink at the tips, lanceolate and directed forward and the perianth tube has one feature not found in its two allies: it is slightly constricted at the apex of the short, narrow cylindrical part and forms an S-shaped bend before expanding into the flared upper part of the tube.

The floral bracts of *Babiana avicularis* are notable in two respects: they are rust-tipped and prominently

TABLE 1.—Comparison of important taxonomic features of *Babiana avicularis*, *B. ringens* and *B. hirsuta*. Data were taken from new collections and well-pressed herbarium specimens

Character	<i>B. avicularis</i>	<i>B. ringens</i> subsp. <i>ringens</i>	<i>B. ringens</i> subsp. <i>australis</i>	<i>B. hirsuta</i>
Leaf shape	linear, fairly soft, arching	lanceolate to linear, firm to rigid, pungent	lanceolate to linear, firm to rigid, pungent	lanceolate to oval in section
Perianth tube length (mm)				
upper part	12–17	12–15	12–15	15–22
lower part	± 4	16–25	15–20	18–22
Dorsal tepal length (mm)	15–18	25–45(–50)	18–30	18–24
Outer bract length (mm)	14–22	25–50	18–30	22–40
Filament length (mm)	25–32, exserted ± 16	37–70, exserted 22–50	24–34, exserted 15–22	30–36, exserted 18–20
Anther length (mm)	3.5–5.0	5.0–7.5	4.0–5.5	± 6–7
Point of style division	below base of anthers	(middle to) upper third of anthers or above anthers	at or below base of anthers	base to middle third of anthers
Style branch length (mm)	4–5	4–5	2–4	± 4
Orientation of				
upper lateral tepals	directed forward	recurved	recurved	directed forward
lower lateral tepals	directed forward	recurved	recurved	recurved

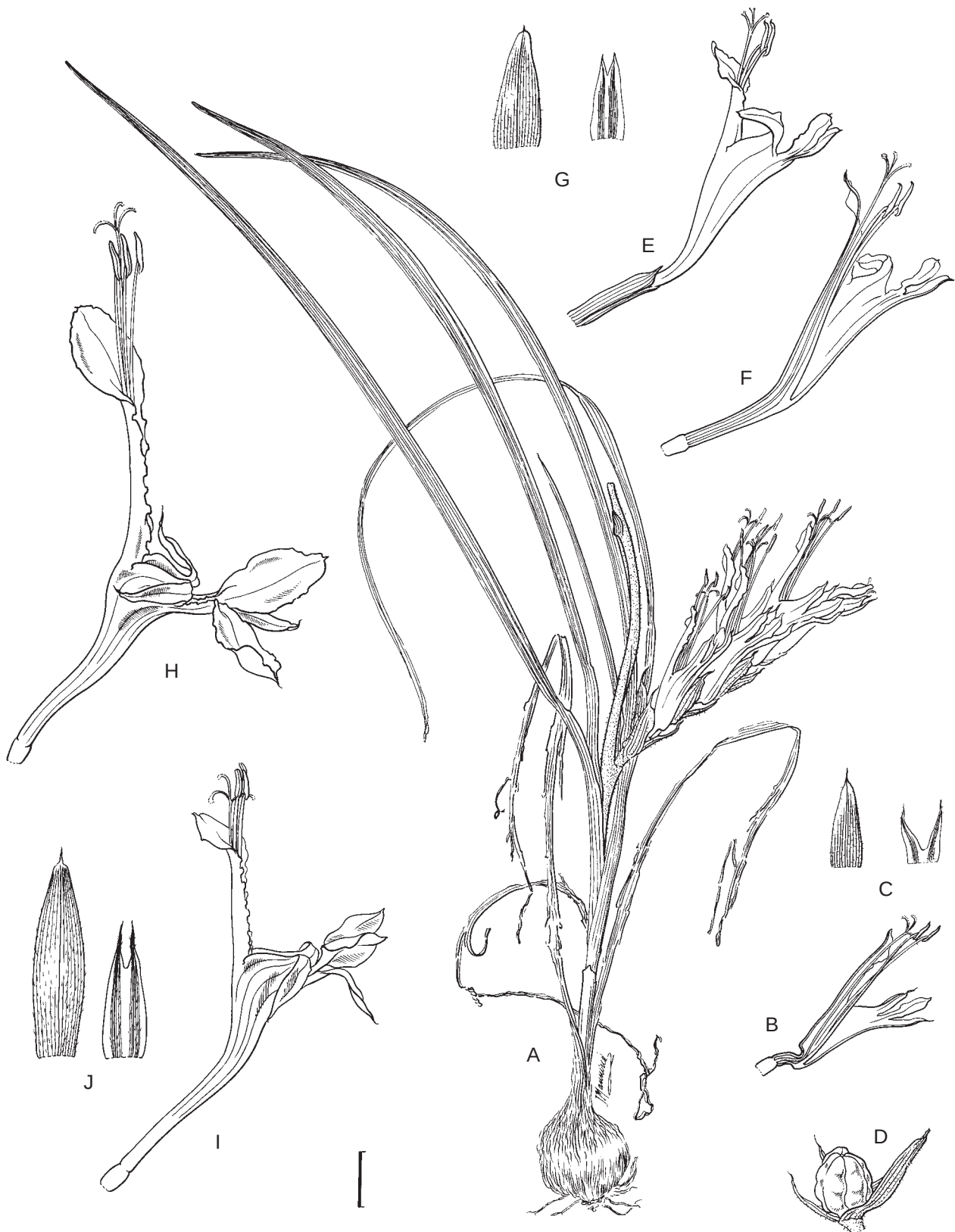


FIGURE 1.—A–D, *Babiana avicularis*, Goldblatt & Porter 13109 (NBG); E–G, *B. hirsuta*, Goldblatt & Porter 13110; H, *B. ringens* subsp. *ringens*, found at Atlantis, Schnitzler & Manning 13 (NBG); I, J, *Babiana ringens* subsp. *australis*, De Waal s.n. (NBG). A, whole plant; B, half-flower; C, outer (left) and inner (right) bracts; D, capsule; E, flower, side view; F, half-flower; G, outer (left) and inner (right) bracts; H, flower; I, flower; J, outer (left) and inner (right) bracts. Scale bar: 10 mm. Artist: John Manning.

mucronate, and the shorter inner bracts are divided for about three-quarters of their length, with the two halves strongly divergent, whereas in both *B. hirsuta* and *B. ringens*, the inner bracts are divided in the

upper third to half and do not notably diverge. The two coastal populations of *B. avicularis* are sympatric and co-blooming with *B. hirsuta* but we found no sign of hybrids at either site.

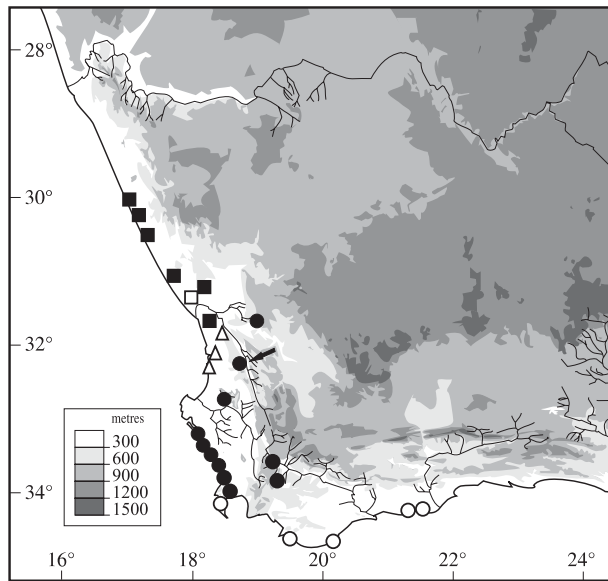


FIGURE 2.—Known distribution of *Babiana avicularis*, $\triangle$; *B. brachystachys*, $\blacksquare$; *B. ringens* subsp. *ringens*, $\bullet$ (Graafwater populations arrowed); *B. ringens* subsp. *australis*, $\circ$; and *B. teretifolia*, $\square$.

We assume from the floral morphology that, like its two relatives, *Babiana avicularis* is adapted for pollination by sunbirds. Flowers produce $3.8\text{--}5.0\ \mu\text{l}$ of nectar of relatively low sugar concentration ($24\% \pm 1.6\%$ sucrose equivalents; $n = 5$). Flowers of *B. hirsuta* produce up to $30\ \mu\text{l}$ of nectar of $\pm 25\%$ sucrose equivalents and in *B. ringens* up to $28\ \mu\text{l}$ nectar has been recorded of $\pm 23\%$ sucrose equivalents (Goldblatt *et al.* 1999; Goldblatt & Manning 2007b). The nectar in *B. avicularis* is therefore similar in sucrose concentration but far less in quantity to that offered by *B. hirsuta* and *B. ringens*, a reflection of the smaller size of the flower and much shorter perianth tube. If *B. avicularis* proves to be pollinated by sunbirds, it will be among the smallest-flowered species of the Iridaceae with this pollination system.

Additional specimens examined

WESTERN CAPE.—3218 (Clanwilliam): 19 km north of Clanwilliam, sand dunes, (–BB), 23 August 1974, Nordenstam & Lundgren 1505 (MO, NBG, S); west coast south of Elands Bay, ± 30 km north of Rocher Pan, sandy flats, (–AD), 24 September 2008, Goldblatt & Porter 13161 (MO, NBG, PRE); 2.5 miles [3.5 km] SW of Leipoldville, coastal fynbos on white sand, ± 400 ft [640 m], (–AB), 23 August 1958, Acocks 19677 (K, PRE).

2. *Babiana ringens* subsp. *australis* Goldblatt & J.C.Manning, subsp. nov.

Plantae ad 120 mm altae, spicis 2–4-floris; bractea externa 18–30 mm longa, tubo perianthii 27–35 mm longo, tepalis inaequalibus tepalo dorsali 18–30 mm longo, filamentis 24–34 mm longis, antheris 4.0–5.5 mm longis, stylo infra basim antherarum diviso, ramis 2–4 mm longis.

TYPE.—Western Cape, 3419 (Caledon): Bredasdorp, Frikkiesbaai, (–CB), 24 August 1946, Compton 18185 (NBG).

Like *Babiana ringens* in general aspect, subsp. *australis* has a sterile stem up to 120 mm long and spikes with 2–4 smaller flowers. Flowers with tepals oriented as

in subsp. *ringens*; perianth tube 27–35 mm long, slender lower part 15–20 mm long and upper wider part 12–15 mm long; dorsal tepal 18–30 mm long, upper lateral and lower median tepals narrowly lanceolate, 20–25 mm long, attenuate and mucronate, lower lateral tepals clawed with ovate blade, $22\text{--}25 \times 7.5$ mm. Stamens unilateral; filaments 24–34 mm long, exerted 15–22 mm, not reaching apex of dorsal tepal; anthers 4.0–5.5 mm long, reaching or sometimes exceeding apex of dorsal tepal. Style dividing at or 1–2 mm below base of anthers; style branches 2–4 mm long. Capsules and seeds unknown. Flowering time: mid-July to late August. Figure 1I, J.

Distribution and ecology: *Babiana ringens* subsp. *australis* extends along the southern coast of Western Cape, from Albertinia in the east to the Agulhas Peninsula, with outlying populations in the southern Cape Peninsula south of Scarborough (Figure 2). Plants occur in sandy ground in coastal fynbos and are often more prominent after fire.

Diagnosis: subsp. *australis* stands out among the numerous collections of *Babiana ringens*, a fairly common coastal and near-interior species that is especially frequent in the western half of Western Cape, extending from Albertinia to the Cape Peninsula and north to Lambert's Bay, in its generally smaller size, 2–4-flowered spike and markedly smaller flowers, with tube 27–35 mm long, and smaller tepals, the dorsal 18–30 mm long (Tables 1; 2). In comparison, subsp. *ringens* has spikes of (3–)6–10 flowers, a perianth tube 28–40 mm long, and a dorsal tepal 25–45(–50) mm long. In keeping with the longer perianth tube, the filaments are 37–70 mm long, and the anthers are 5.0–7.5 mm long vs filaments 24–34 mm long and anthers 4.0–5.5 mm long in subsp. *australis*. The style of subsp. *australis* divides at or below the base of the anthers and the style branches are relatively short, 2–4 mm, compared with a style usually dividing beyond the anther tips (rarely opposite the middle of the anthers) in subsp. *ringens* and the style branches are 4–5 mm long. Both subspecies occur on the Cape Peninsula, with subsp. *australis* recorded from Scarborough in the southwestern Peninsula and subsp. *ringens* north of Fish Hoek; therefore, as far as we can determine, their ranges abut but do not overlap.

Two northern populations of *Babiana ringens* from the immediate vicinity of Graafwater (Goldblatt 3628 MO; Schlechter 8518 MO) (Figure 2) have unusually small flowers for the subspecies (Table 2), with a perianth tube 31–40 mm long and a dorsal tepal ± 25 mm long, but unlike subsp. *australis* they have anthers 5.0–5.5 mm long, a style dividing opposite the middle to upper third of the anthers, and style branches 4–5 mm long. These populations occur close to others with larger flowers, typical of subsp. *ringens*, and may represent a local race or even introgressed hybrids with *B. avicularis*.

Additional specimens examined

WESTERN CAPE.—3418 (Simonstown): Cape Peninsula, Schusterskraal, after fire, (–AB), 10 October 1945, Barker 3885 (NBG); Scarborough, Red Hill trail, (–AB), 4 August 2009, De Waal s.n. (NBG); 3421 (Riversdale): 2 km west of Dekriet, west of Albertinia, (–AB), 26 July 1979, Bohnen 6101 (NBG); 10 km west of Albertinia, (–AB), 22 September 1949, Sidey 1762 (MO); Stilbaai, Groot Jongensfontein, (–AD), 23 August 1978, Bohnen 3968 (NBG); Victoriasdale, sandy slopes of Brandkop, 600 ft [190 m], (–AC), 6 September 1975,

Oliver 5996 (NBG); Albertinia commonage, next to graveyard, sandy hillside, (–BA), 20 August 1971, Thomas s.n. (NBG92938).

3. ***Babiana teretifolia* Goldblatt & J.C.Manning**, sp. nov.

Plantae acaulescentes ad 300 mm altae foliis inclusis, cormo 25–30 mm diam., foliis subteretibus $\pm 2 \times 1.3$ –1.6 mm diam., anguste 3-sulcatis, spica decumbenti congesta subsecunda spica principali ad 10-flora, bracteis viridibus apicibus atrobrunneis acuto-attenuatis, 18–25 mm longis, bractea interiora ad apicem 3–4 mm furcata, tubo perianthii cylindrico elongato 65–70 mm longo pauciter curvato, tepalis subaequalibus linearibus torsivis patentibus tepalo dorsali $\pm 30 \times 4$ mm aliis $\pm 26 \times 2.5$ mm, filamentis ± 12 mm longis ± 9.5 mm exsertis, antheris 5.5–6.0 mm longis albis, stylo ad apices antherarum vel ultra diviso, ramis ± 5 mm longis ad apicem bifurcatis.

TYPE.—Western Cape, 3118 (Vanrhynsdorp): southern Namaqualand, Farm Kommandokraal, NW of Vredendal, (–AC), 10 September 2008, Goldblatt & Porter 13101 (NBG, holo.; MO, iso.).

Plants acaulescent, up to 300 mm high including leaves; corm deeply seated, up to 200 mm below ground, globose, 25–30 mm diam., outer tunics dry and brown, extending upward with dry remains of leaf sheaths in collar around stem base; stem usually 1- or 2-branched at ground level, glabrous or sparsely pubescent. *Leaves* ± 8 , $\pm$ oval to round in section, $\pm 2 \times 1.3$ –1.6 mm, narrowly 2-grooved on wider surfaces, 1-grooved on narrow surfaces, margins sparsely hairy proximally. *Spike* decumbent, crowded, secund with flowers ± 1.5 mm apart in 2 ranks, main spike with up to 10 flowers, branches usually with fewer flowers; bracts 18–25 mm long, acute-attenuate, green below and rust-coloured at tips, inner $\pm$ as long as outer, forked apically for 3–4 mm. *Flowers* zygomorphic, predominantly pink, beige toward bases of tepals; lower 3 tepals with narrow diamond-shaped markings in lower midline, red in throat; perianth tube cylindric, slender, 65–70 mm long, hollow, slightly curved; tepals narrowly linear and twisted, spreading with dorsal one held slightly apart from upper lateral, dorsal $\pm 30 \times 4$ mm, upper lateral and lower tepals $\pm 26 \times 2.5$ mm, tepals $\pm$ uniformly pink outside, tube translucent, light purple distally, fading to beige proximally. *Stamens* unilateral; filaments ± 12 mm long, inserted ± 2.5 mm below mouth of tube, therefore exserted ± 9.5 mm; anthers 5.5–6.0 mm long, white, pollen white. *Ovary* smooth; style arching over stamens, dividing at or shortly beyond anther tips,

branches ± 5 mm long, notched apically. *Capsules* and *seeds* unknown. *Flowering time*: September. Figure 3.

Distribution: known from a single extended population on the farms Kommandokraal and Skilpadvlei in southern Namaqualand, in deep sand in coastal sandveld (Figure 2).

Diagnosis and relationships: *Babiana teretifolia* superficially appears to be merely a variant of *B. brachystachys*, a species centred in coastal Namaqualand and extending south to Lambert's Bay in Western Cape, in its subterete leaves and crowded, decumbent spikes of extremely long-tubed flowers (Lewis 1959). The flowers themselves are, however, different in several respects, especially in the remarkably narrow, spreading and twisted tepals and the dorsal tepal hardly differentiated from the remaining five. The tepals are linear, $\pm$ channelled, and twisted with the dorsal tepal $\pm 30 \times 4$ mm and the remaining tepals $\pm 26 \times 2.5$ mm, whereas typical *B. brachystachys* has oblong-lanceolate, $\pm$ plane tepals, the dorsal tepal 20–24 $\times$ 6–8 mm and the lower three tepals 15–18 $\times$ 4–6 mm (e.g. the type, Mader s.n. K; Goldblatt & Manning 9997 K, MO, NBG). These differences are combined with striking differences in the stamens: in *B. teretifolia* the filaments are ± 12 mm long and exserted ± 9.5 mm from the tube and the anthers are 5.5–6.0 mm long and white, as is the pollen. Populations of *B. brachystachys* have filaments 4–5 mm long, exserted 1–3 mm, and anthers 4–5 mm long and are usually pale violet to purple when fresh, as is the pollen (anthers in a population north of Lambert's Bay discovered in September 2009, Goldblatt & Porter 13321 MO, NBG, have white anthers and pollen). In addition, the style of *B. teretifolia* divides opposite the anther tips so that the style branches, ± 5 mm long, arch above the anthers and can readily be seen to be notched at the tips. In *B. brachystachys*, the style divides opposite the upper third of the anthers and the style branches are only ± 2.5 mm long. Added to the floral differences are the sparsely hairy leaf sheaths and flowers spaced ± 1.5 mm apart, in contrast with the woolly leaf sheaths and flowers set 3–6 mm apart in most populations of *B. brachystachys*. The extraordinarily long, linear twisted tepals, compared to the more conventional oblong-lanceolate tepals of *B. brachystachys*, mark *B. teretifolia* as a derived, geographic segregate of its already highly specialized sister species.

Babiana teretifolia, like *B. brachystachys*, has the stereotypical adaptations for pollination by the long-

TABLE 2.—Comparison of important taxonomic features of population sets of *Babiana ringens*

Character	Population sets		
	Graafwater vicinity	Central	Southern
Outer floral bract length (mm)	30–40	25–50	18–30
Perianth tube length (mm)			
lower part	16–25	17–25	15–20
upper part	± 15	12–15	12–15
Dorsal tepal length (mm)	± 25	36–45(–50)	18–30
Filament length (mm)	37–40, exserted 22–25	55–70, exserted 35–50	24–34, exserted 15–22
Anther length (mm)	5.0–5.5	6.0–7.5	4.0–5.5
Style branch length (mm)	4–5	4–5	2–4
Point of division of style	middle to upper third of anthers	upper third of anthers or above	at or below anther bases

Population sets: Graafwater vicinity. Central: central Cape Peninsula (Fish Hoek) to Lambert's Bay; Worcester District, Clanwilliam to Botterkloof. Southern: Cape Peninsula (Scarborough) to Albertinia (Figure 2).



FIGURE 3.—*Babiana teretifolia*, Goldblatt & Porter 13101 (NBG). A, whole plant; B, flower, front view; C, half- flower; D, outer (left) and inner (right) bracts. Scale bar: 10 mm. Artist: John Manning.

proboscis fly, *Moegistorhynchus longirostris* (Manning & Goldblatt 1997; Goldblatt & Manning 2000), viz. beige-pink tepals marked with red towards the base, and an elongate perianth tube. Other species in the guild of species adapted for pollination by *Moegistorhynchus* that co-occur with *B. teretifolia*, include *Geissorhiza exscapa* (Thunb.) Ker Gawl., *Pelargonium appendiculatum* (L.f.) Willd., and (flowering slightly later in the season) *Lapeirousia anceps* (L.f.) Ker Gawl. and *L. fabricii* (D.Delaroche) Ker Gawl. We did record *Moegistorhynchus longirostris* visiting one member of the guild, *G. exscapa* in September 2009, but saw no visitors to *B. teretifolia* during three days in the field in the same month in 2008, perhaps due either to cool, windy weather that is less than ideal for fly activity.

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Notes on African plants

VARIOUS AUTHORS

ARECACEAE

LIVISTONA CHINENSIS, A FIRST RECORD OF A NATURALIZED PALM IN SOUTH AFRICA

Seven genera of the Arecaceae occur in southern Africa and southern tropical Africa, comprising 18 indigenous species (Table 1) (Glen 2000; Leistner 2005). Of these, only six palm species are indigenous to South Africa, probably due to prevailing climatic conditions that are unfavourable for tropical taxa, and it is therefore not surprising that no non-indigenous member of the Arecaceae has previously been regarded as naturalized or invasive in southern Africa (Henderson 2006).

The aim of this paper is to report on the first palm to have become semi-naturalized in South Africa, namely *Livistona chinensis* (Jacq.) R.Br. ex Mart. This palm is also considered as naturalized in some parts of the United States of America (Butts 1959; Oppenheimer 2003) and Mauritius (Mauder *et al.* 2002). The palm was introduced to South Africa as an ornamental during the early 1900s and has hitherto been widely planted throughout the eastern coastal regions of South Africa due to its availability, vigour and hardiness (Esterhuysen *et al.* 2001).

Although one of the most commonly cultivated ornamental palms in the world (Dowe 2009), *Livistona chinensis* is now 'Vulnerable' in its indigenous Japan, Taiwan and China (Hainan Island), where it occurs mostly in coastal forests on various soils, often in sand, sometimes in dense monospecific colonies, or isolated groups or individuals, up to 100 m in altitude. The species was first described as *Latania chinensis* (Jacquin 1801), from plants cultivated in Mauritius and brought to Schoenbrunn Gardens, Vienna in 1788. The species name was taken from that used for the palm in Mauritius, '*Latanier de la Chine*'. Bretschneider (1898) provided some evidence to suggest that the naturalist and traveller

Pierre Poivre was responsible for introducing the palm, during the mid-1700s, to Mauritius where it became naturalized. The common name, Chinese fan palm, came into use very early (Jacquin 1801) and was based on the Latin name as well as subsequent knowledge of its distribution in eastern Asia (Yoshida *et al.* 2000). In South Africa it is also known as the Chinese fountain palm. An extensive search in southern African herbaria for *Livistona chinensis* revealed only two voucher specimens, both of garden origin, which were made by H.F. Glen on 23 March 1991 at Vaalwater, Limpopo, and by J.C. Scheepers in April 1992 in Pretoria, Gauteng.

Arecaceae (alt. Palmae), subfamily Coryphoideae, tribe Trachycarpeae, subtribe Livistoninae (Dransfield *et al.* 2008).

***Livistona chinensis* (Jacq.) R.Br. ex Mart.**, Historia Naturalis Palmarum 3,7: 240 (1838). *Latania chinensis* Jacq.: t. 11, fig. 1 (1801). *Saribus chinensis* (Jacq.) Blume: 49 (1838). *Livistona sinensis* Griff.: 131 (1845), ortho. var. Type: without locality and collector [lecto., illustration in Jacquin: tab. 11, fig. 1 (1801), designated by Moore (1979)].

Latania borbonica auct. non Lam.: 427 (1792).

Livistona mauritiana Wall. ex Mart.: 240 (1838), nomen.

Chamaerops biroo Siebold: 11 (1830). Type: Japan, Siebold s.n. [L, lecto., designated by Dowe (2009)].

Livistona olivaeformis (Hassk.) Mart.: 319 (1850); Miquel: 59 (1855); Miquel: 13 (1868). *Saribus olivaeformis* Hassk.: 176 (1842). *Latania olivaeformis* (Hassk.) Devansaye: 34 (1875), nom. illeg. Type: Indonesia, cultivation, Bogor Botanic Gardens, 'nel viale presso la chiesta', May 1878, Beccari s.n. [FI, lecto., sheets 1131, 1131-B & 1131-C, designated by Dowe (2009)].

Livistona subglobosa (Hassk.) Mart.: 319 (1850); Miquel: 59 (1855); Miquel: 13 (1868); Nakai: 224 (1935). *Saribus subglobosus* Hassk.: 177 (1842); Hassk.: 65 (1844). *Livistona chinensis* var. *subglobosa* (Hassk.) Becc.: 16 (1921). Type: Indonesia, cultivation, Bogor Botanic Gardens, May 1878, Beccari s.n. [FI, lecto., sheets 1133 & 1133-B, designated by Dowe (2009)].

Livistona japonica Nakai ex Masam. (as *Livistonina japonica*): 50 (1929); Masamune & Suzuki: 73 (1933). Type: not designated.

Diagnostic characters: monoecious hermaphroditic tree, single trunk up to 15 m tall, enveloped by dry leaf sheaths, dense crown of numerous divided, palmate and pendulous pale green leaves, up to 1.8 m long, prominent undivided central area and numerous deeply bifid segments, tips pendulous. Petioles armed with stout prickles. Flowers sessile, pale yellow, carried in clusters of up to seven, borne in 5–7 inflorescences up to 1 m or more long, of several branches along a single main rachis, each 2 or 3 times divided into rachillae; bracts

TABLE 1.—Palm genera and no. species per genus occurring naturally in southern Africa and southern tropical Africa respectively and in totality

Genera	Species per genus		Total
	Southern Africa*	Southern tropical Africa**	
<i>Borassus</i>	1	1	1
<i>Calamus</i>	0	1	1
<i>Eremospatha</i>	0	3	3
<i>Hyphaene</i>	2	5	5
<i>Jubaeopsis</i>	1	0	1
<i>Phoenix</i>	1	1	1
<i>Raphia</i>	1	6	6
Total: 7	6	17	18
<i>Livistona</i> †	1	0	1
Total: 8	7	17	19

* Glen (2003); ** Leistner (2005); † alien.



FIGURE 1.—*Livistona chinensis*. A, habit; B, trunk showing dry leaf sheaths and prickles on petioles; C, base of stem; D, leaf. Photographs: H. de Wet.

brown tomentose. Fruit ellipsoid to subglobose or pyriform, $15\text{--}26 \times 9\text{--}18$ mm; bright green to bluish green, china-blue-grey with age, in dense clusters. *Flowering time*: December to February. Figure 1.

Distribution and habitat: *Livistona chinensis* has become semi-naturalized in swamp forest in the subtropical coastal region of KwaZulu-Natal. Current, confirmed populations include three localities in the Empangeni-Richards Bay area, with sight records for the Durban area (Figure 2). In Zululand it occurs in forest dominated by the trees *Bridelia micrantha*, *Phoenix reclinata*, *Syzygium cordatum* and *Voacanga thouarsii*,

and an understorey dominated by the ferns *Microsorium scolopendria* and *Nephrolepis biserrata*.

Studies by Siebert (2009) could not confirm any natural distribution vectors, but found that the masses of seed produced by these palms end up in garden dumping sites during autumn. Naturalized populations are only associated with garden refuse in swamp forest patches, as the prevailing microclimate here, which is predominantly warm and moist, is probably most suitable for germination. Siebert (2009) has reported that in these favourable habitats, single individuals reach maturity over time, but in turn these successful individuals produce masses of

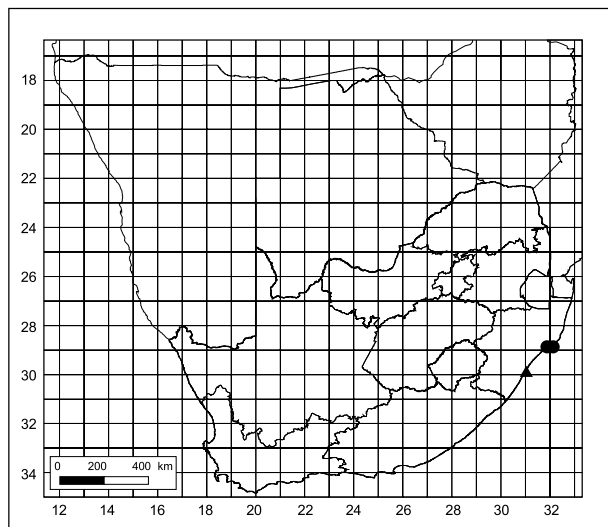


FIGURE 2.—Naturalized distribution of *Livistona chinensis* in South Africa. Voucher records, ●; sight record, ▲.

seed that lead to mass seedling establishment through gravitational dispersal. Although this only leads to localized, controllable invasions, it should serve as a warning sign, and calls for an urgent action to assess the invasive status and potential of cultivated palms in South Africa.

Voucher specimens

KWAZULU-NATAL.—2831 (Nkandla): KwaDlangezwa, swamp forest along Umhlatuze River, (–DD), Siebert 2456 (NH, PRE, ZULU); Ngwelezana, swamp forest along Umhlatuze River, (–DD), Siebert 3188 (ZULU). 2832 (Mtubatuba): Richards Bay, swamp forest along Thulazihleka Pan, (–CC), Siebert 3499 (ZULU).

LIMPOPO.—2427 (Vaalwater): cultivated, Waterberg, (–BB), Glen 2628 (PRE).

GAUTENG.—2528 (Pretoria): garden, Menlo Park, (–DB), Sheepers s.n. (PRE).

ACKNOWLEDGEMENTS

Ms Lesley Henderson, Agricultural Research Council, commented on an earlier version of the manuscript. Mr Barry Long, Durban Botanic Gardens, confirmed the identity of the palm. Dr Hugh Glen, South African National Biodiversity Institute (SANBI), confirmed the occurrence of naturalized individuals of the palm in Durban. Ms Hester Steyn, National Herbarium, SANBI, is thanked for the production of the distribution map.

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MS. received: 2009-04-14.

ASPHODELACEAE

OCCURRENCE OF *HAWORTHIA BOLUSII* VAR. *BLACKBEARDIANA* IN THE FREE STATE, SOUTH AFRICA

The genus *Haworthia* Duval, which consists of $\pm$ 85 species and 200 taxa, is endemic to southern Africa (Bayer *et al.* 1999). It occurs predominantly in the Western and Eastern Cape Provinces, with outliers extending into Namibia and Mozambique (see Smith & Van Wyk 1991 for a distribution map of the genus).

To date, the climatically severe grasslands of the Free State have been known to harbour only a single species of *Haworthia*, viz. *H. venosa* (Lam.) Haw. subsp. *tessellata* (Haw.) M.B.Bayer (Scott 1985: xxvii; Smith *et al.* 2000). However, the occurrence of a second species of *Haworthia*, *H. bolusii* Baker var. *blackbeardiana* (V.Poelln.) M.B.Bayer, has been suggested for the Free State, but confirmation of this has thus far remained elusive (Bayer 1999: 45). In a comprehensive interpretation of the *H. cooperi* Baker and *H. bolusii* var. *blackbeardiana* complexes, Bayer (2002) concentrated his discussion on their Eastern Cape distribution ranges. *Haworthia bolusii* var. *blackbeardiana* is a miniature (the size of a golf ball), rosulate plant with flattish, incurved leaves that are adorned with hair-like marginal spines.

Haworthia bolusii var. *blackbeardiana* was recently found in the Rouxville District, Free State at the following locality:

FREE STATE.—3027 (Zastron): Brandwacht 190, Rouxville, vegetative plant, 1 640 m, S 30° 30' 11.3" E 27° 03' 26.0", (–AC), 23-05-2008, P.C. Zietsman 4410 (NMB).

This locality falls within the vegetation unit Besemkaree Koppies Shrubland (Gh 4) of the Grassland Biome (Mucina & Rutherford 2006).

The plants were found on the western slope of a *koppie* (hill). Most of them grow tucked away in cracks between the dolorite rocks and are well protected from direct sunlight during the early morning and late afternoon. They are fully exposed for most of the day (Figure 3).

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MS. received: 2009-03-25.



FIGURE 3.—*Haworthia bolusii* Baker var. *blackbeardiana* in its natural habitat near Rouxville in the Free State. Photograph: P.C. Zietsman.

ASPHODELACEAE

INCLUSION OF THE GENUS *JODRELLIA* IN *BULBINE* (ASPHODELOIDEAE)

The genus *Jodrellia* Baijnath was described to accommodate three white-flowered species from tropical Africa, two of which were formerly included in *Bulbine* Wolf (Baijnath 1978). These species were separated from *Bulbine* based on a combination of characters, namely radiate roots, inflorescences shorter than the leaves, a white perianth with three- to five-nerved outer tepals, and obscure stigmatic papillae (Baijnath 1978). These characters, with the exception of the three- to five-nerved outer tepals, are also found in species of *Bulbine* and other genera of the Asphodelaceae, thus reducing their significance as generic characters. Radiate roots, which are situated on a small vertical rhizome in *Jodrellia* (Baijnath 1978), occur sporadically in other genera of the Asphodelaceae, notably *Trachyandra* Kunth, and are not unique to *Jodrellia*. The underground parts of *Bulbine* species are variable but normally either tuberous or a horizontal rhizome. White flowers, as are found in *Jodrellia*, occur in forms of *Bulbine frutescens* (L.) Willd. (which some authors regard as a separate species, i.e. *B. triebneri* Dinter; Van Jaarsveld 2001; Klopper *et al.* 2008; Klopper & Smith 2009), while some forms of *B. abyssinica* A.Rich. have inflorescences that are shorter than the leaves. The outer tepals in *Bulbine* species are narrower than the inner ones, whereas the reverse is found in *Jodrellia*. The outer tepals are wider than the inner ones and accessory venation has developed, possibly as a result of the wider lamina. The obscure stigmatic papillae of *Jodrellia*, although shorter and fewer, are similar to those of *Bulbine*. Both genera share the hairy filaments, which is the most striking feature of the genus *Bulbine* and is unique to these two genera within the Asphodelaceae.

Molecular sequence data from chloroplast (*rbcL*, *matK* and *ndhF*) and nuclear (ITS) markers confirm the close relationship between the two genera, indicating that *Jodrellia* is embedded within *Bulbine* with strong support in both the analysis of chloroplast and nuclear regions (Devey *et al.* 2006). The genus *Bulbine* is thus paraphyletic without the inclusion of *Jodrellia*, and Devey *et al.* (2006) have no hesitation in recommending the transfer of *Jodrellia* to *Bulbine*. This is necessary in order to preserve the monophyly of the genus. Species of *Jodrellia* should thus be viewed as representing a small, specialized lineage within *Bulbine* rather than as a genus distinct from it. This interpretation is supported by the weak morphological differences between the two, essentially the development of accessory veins in the outer tepals in *Jodrellia*. The necessary nomenclatural changes are presented below.

***Bulbine* Wolf**, Genera plantarum: 84 (1776). Type species: *B. frutescens* (L.) Willd. *Jodrellia* Baijnath: 574

(1978), syn. nov. Type species: *Jodrellia macrocarpa* Baijnath.

***Bulbine fistulosa* Chiov.** in Annali di Botanica (Roma) 9: 143 (1911). *Jodrellia fistulosa* (Chiov.) Baijnath: 576 (1978). Type: Ethiopia, Chioyenda 557 (FI, holo.).

***Bulbine macrocarpa* (Baijnath) Boatwr. & J.C.Manning**, comb. nov. *Jodrellia macrocarpa* Baijnath in Kew Bulletin 32: 574 (1978). Type: Kenya, Gillett 13141 (K, holo.).

***Bulbine migiurtina* Chiov.** in Lavori eseguiti presso il Reale Istituto Botanico di Catania 1: 5 (1928). *Jodrellia migiurtina* (Chiov.) Baijnath: 577 (1978). Type: Somaliland, Puccioni & Stefanini 777 [860] (FI, holo.).

ACKNOWLEDGEMENTS

This work formed part of a Post-Doctoral Fellowship of the first author at the Compton Herbarium and the University of Cape Town. The Parker family from the Elandsberg Nature Reserve is kindly thanked for generously providing funding for the Fellowship.

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 MS. received: 2009-03-09.

IRIDACEAE

REAPPRAISAL OF *IXIA MACULATA* WITH *I. CALENDULACEA* SP. NOV., AND AN EARLIER NAME FOR *I. LUTEA*

A serendipitous discovery of two varieties of *Ixia maculata* L., *I. maculata* var. *fusco-citrina* (Desf. ex DC.) G.J.Lewis and *I. maculata* var. *intermedia* G.J. Lewis, growing and flowering in close proximity in

September 2007, led us to review the taxonomy of the species, which was treated by Lewis (1962) and De Vos (1999) as comprising three varieties. *Ixia maculata* is a member of section *Ixia* of the genus, which is endemic to

the winter rainfall zone of southern Africa and comprises over 70 species at the latest count (Goldblatt & Manning 2008a, b). Section *Ixia* includes 19 species with brightly coloured flowers with a narrow, subfiliform perianth tube, non-decurrent filaments inserted at or close to the top of the tube, and conduplicate style branches (Lewis 1962). Most species of the section have flowers with contrasting dark central marks, now believed to represent beetle marks, and indications are that most species are pollinated by hopliine beetles (Scarabaeidae: Hopliini) (Goldblatt *et al.* 2000).

Ixia maculata sensu G.J.Lewis stands out in sect. *Ixia* in its bright orange or yellow perianth with a dark central eye, dry and crinkly floral bracts that are usually partly or entirely brown, basally to completely united filaments, and the style dividing opposite or above the base of the anthers. These features are shared in the section only with *I. curta* Ker Gawl., which differs from *I. maculata* in its strongly dark-cuspidate bracts and its corms. The corms of *I. maculata* were described by Lewis (1962) as typically having submembranous or rarely fibrous tunics and producing stolons from the base, whereas corms of *I. curta* have persistent, fibrous, netted tunics, and cormlets, when present, are borne at the base of the corm, which is the more common condition in *Ixia*. Only *I. dubia* Vent., *I. lutea* Eckl. and *I. polystachya* L. of sect. *Ixia* also have yellow or orange flowers, but none have corms producing stolons, and all three have free filaments and a style usually dividing below the level of the anthers, except in *I. polystachya* var. *lutea*, which may prove to be a separate species. *Ixia lutea* and *I. polystachya* more often have white or pink flowers and *I. dubia*, which is the taxon most often confused with *I. maculata*, has pale, translucent floral bracts, sometimes suffused with pink. All these species share a range in Western Cape, and were once common from Cape Town northward to the Olifants River.

Lewis (1962) and De Vos (1999) distinguished three taxa within *Ixia maculata* primarily using features of the floral bracts, degree of filament union, and perianth tube length but a degree of overlap in these characters led to segregation of the known populations as varieties, rather than as distinct species. Our observations show that the nature of the stolons, corm tunics, colour of the filaments, and the shape and markings of the tepals are equally, if not

more important in distinguishing populations (Table 2). Some of these features are correlated with ecological differences and have convinced us that the present taxonomy does not adequately represent the biology of the *I. maculata* complex. We present a revised taxonomy in which we recognize var. *intermedia* as a separate species, *I. calendulacea*. Whereas vars. *maculata* and *fusco-citrina* have yellow filaments, and tepals with a concave base to which the dark brown or black pigmentation is restricted, *I. calendulacea* has dark brown filaments (drying violet), and the tepals are plane, thus lacking a concave base, and the brown to dull red centre is edged with a halo of translucent red. In addition, populations of *I. calendulacea* grow in deep, well-drained sandy soils, whereas typical *I. maculata* grows in sandy or granitic habitats that are always waterlogged in the growing season.

The differences between *Ixia maculata* var. *maculata* and var. *fusco-citrina* remain more or less as described by Lewis (1962) but the two taxa are insufficiently resolved. We note the potential taxonomic significance of the short stolons bearing up to three small cormlets that are produced in var. *maculata* and the long stolons of var. *fusco-citrina* which bear a single cormlet but additional field work is needed to assess the status of these two taxa.

***Ixia calendulacea* Goldblatt & J.C.Manning, sp. nov.**

I. maculata var. *intermedia* G.J.Lewis in Journal of South African Botany 27: 142 (1962). Type: Western Cape, 3218 (Clanwilliam): Redelinghuys, 29 September 1943, W.F. Barker 2591 (NBG, holo.).

Plantae 200–500 mm altae usitate eramosae, cormo depresso-globoso 12–16 mm diam. tunicis fibrosis sobolis horizontalibus ± 1.5 mm diam., ad 120 mm longis praedito, foliis usitate 4–6 raro 3, usitate (8–)12–20 mm latis lanceolatis saepe supra torsivis, spica flexuosa usitate 5–8-flora, bracteis siccis albo-transparentibus infra brunneis supra, bractea externa ± 8 mm longa $\pm$ truncata vel biloba cuspi brevi centrali, interna ad apicem furcata in dua cuspidibus attenuata 2 mm longa, floribus vadosis cupulatis calendulaceis centro brunneo vel rubro ± 15 mm diam., usitate margini rubro-translucenti, tubo perianthii 5–8(–10) mm longo cylindrico, tepalis subequalibus ascendentibus pauciter imbricatis (18–)22–25 $\times$ 12–14 mm, externis ± 2 mm

TABLE 2.—Characteristics of *Ixia calendulacea* compared with those of *I. maculata* var. *maculata* and var. *fusco-citrina*. Because there is doubt about the status of cultivated plants referred in herbaria to var. *fusco-citrina*, we have not included measurements from these specimens. Observations for taxonomically important features are taken only from well-preserved specimens, bearing in mind that floral features may shrink up to 20 % of original size, depending on the care with which specimens are prepared. We did not use Lewis's (1962) or De Vos's (1999) measures for any taxa because we apply some names in different ways

Character	<i>I. maculata</i> var. <i>maculata</i>	<i>I. maculata</i> var. <i>fusco-citrina</i>	<i>I. calendulacea</i> (= <i>I. maculata</i> var. <i>intermedia</i>)
Stolons	short, with multiple small cormlets	long, with single cormlet	long, single cormlet
Corm tunics	papery-membranous	papery-membranous	fibrous
Perianth tube length (mm)	5–8	10–13	6–8
Outer tepals (mm)	15–22 $\times$ 8–12	21–27(–30) $\times$ 7–14	15–30 $\times$ 9–12
Perianth colour	orange or yellow, centre brown often with star mark	pale yellow, solid dark brown-black centre	orange, brown eye edged red
Stamens			
filaments (mm)	2.5–5.5; united 1–3	3.5–5.0; united 1.0–1.5	± 4 –6; united 0.5–6.0
anthers (mm)	8–11	9–11	8–10
Style branch length (mm)	3.5–4.0	2.5–4.0	± 4
No. flowers per spike	5–10	8–15	5–8
Outer bract length (mm) and colour	8–15; entirely brown or lower half pale	8–13; brown, lower half pale	7–12; brown, lower half pale

lterior quam internis, filamentis $\pm$ 4 mm longis connatis in pars dimidio vel omnino raro liberis atrobrunneis, antheris 9–11 mm longis, stylo inter basem et inferiori tertio antherarum diviso, ramis 3–4 mm longis.

TYPE.—Western Cape, 3318 (Cape Town): granite-topped hill east of Langebaan, in deep sand, (–AA), 19 September 2008, Goldblatt & Porter 13152 (NBG, holo., K, MO, PRE, iso.).

Plants 200–500 mm high; corm depressed-globose, 12–16 mm diam., outer tunics fibrous with fibres mostly oriented vertically, sometimes accumulating, producing long horizontal stolons up to 120 mm long, $\pm$ 1.5 mm diam., each bearing a terminal cormlet 8–9 mm diam.; stem usually unbranched, robust plants often with a node in upper third bearing a short branch or dry, attenuate scale, sheathing only at base and often curved back against stem. *Leaves* (3)4–6, lowermost largest, decreasing in size above, uppermost $\pm$ entirely sheathing, $\frac{2}{3}$ to $\frac{3}{4}$ as long as stem, lanceolate, lowermost mostly (8–)12–20 mm wide, often twisted in one or two rotations. *Spike* flexuose, mostly 5–8-flowered; bracts dry, white-translucent below, brown in upper half or third, outer bract $\pm$ truncate or bilobed with a short central tooth, (6–)8–12 mm long, becoming $\pm$ lacerate, inner $\pm$ as long as outer, forked in upper 2 mm into attenuate cusps. *Flowers* shallowly cupped when fully open, orange with brown or dull red central marking, 15–20 mm diam., usually with translucent reddish halo; perianth tube cylindric, 5–8(–10) mm long, $\pm$ 2 mm diam. in lower part, expanded in upper 1 mm; tepals subequal, ascending and overlapping slightly when fully open, (18–)22–30 $\times$ 11–15 mm, outer $\pm$ 2 mm wider than inner. *Stamens* with filaments 3–4 mm long, united in lower half or entirely (rarely $\pm$ free), dark red-brown (often drying violet but ultimately losing colour); anthers ascending, 9–11 mm long, yellow. *Style* dividing between base and lower third of anthers, branches (3–)4 mm long. *Capsules* and *seeds* unknown. Figure 4A–F.

Distribution and biology: largely a coastal species, *Ixia calendulacea* has a scattered distribution along the Western Cape Coast and near interior, from the Cape Peninsula and Saldanha Bay northwards to the Namaqualand coastal plain, as far north as the Groen River (Figure 5). Plants occur in sandy habitats, usually deep sands but also in areas of limestone substrate. Plants are most often associated with strandveld and sandveld vegetation but inland populations in the Olifants River Valley and the hills west of Piketberg, occur on stony sandstone slopes and flats in dry fynbos. When treated by Lewis (1962) and De Vos (1999) as *I. maculata* var. *intermedia*, its range was known from Saldanha to the Olifants River Valley. Later collections, notably Reid 1291 from Namaqualand, near Kotzesrus, and from the Western Cape west coast northwest of Vredendal, Goldblatt & Manning 12876 (not in bloom but with the characteristic long stolons and relatively broad leaves of *I. calendulacea*), document the presence of the species north of the Olifants River. A very recent collection from a remnant patch of Cape Flats Sand Fynbos in the southeastern suburbs of Cape Town, Dorse sub Manning 3231, is the first record of the species from the Cape Peninsula. There is no indication that this population, which has flowers with a large, translucent red centre and dark filaments connate to the tip, is not native to the Peninsula (Dorse pers. comm.). The population, which occurs in a military area inaccess-

sible to the public, is heavily infested with alien acacias, and flowered after a fire, six months earlier, burned off the canopy and woody undergrowth.

Observation of flowering plants from the type locality near Langebaan (Goldblatt & Porter 13152) confirm that *Ixia calendulacea* is visited by small brown hopliine beetles. These insects become covered in pollen as they crawl across the open perianth and readily transfer pollen as they fly from one open flower to another. This is consistent with what is known about pollination in several other species of section *Ixia* (Goldblatt *et al.* 2000).

Diagnosis and relationships: *Ixia calendulacea* is recognized by the relatively large, bright orange flower with a brown to dull red central eye with a translucent red halo, and brown filaments that are partly to entirely united, rarely $\pm$ free (Figure 4A, C, D). Plants have fairly large corms, 12–16 mm diam., with fibrous tunics and bearing long, flattened stolons up to 120 mm long (Figure 4B). They typically have four to six basal leaves with lanceolate blades twisted in the upper half. As in *I. maculata*, the bracts are dry, firm and crinkled and brown at least in the upper part and the style divides above the base of the anthers. When compared directly with living *I. maculata*, the differences between the two come into sharp focus (Figure 4; Table 2). *Ixia maculata* has a particularly crowded spike, and the flower, viewed from the side, shows that the tepals form a shallow cup in the proximal third (the brown part of the tepals), whereas the distal, orange or yellow portions spread horizontally (Figure 4I, J). The tepals are $\pm$ narrowly oblong-ovate with nearly parallel sides, $\pm$ 22 $\times$ 9 mm, do not overlap, and are tapered below so that the cup is narrowly windowed. In the southern form of the species the windows together with orange margins of the cupped portion of the tepals provides the star-like pattern in the brown cup. In typical *I. maculata* (as defined by Lewis 1962) the stolons are short and somewhat twisted and bear more than one (up to three) small cormlets (Figure 4H) and these contrast markedly with the long, flattened stolons of *I. calendulacea* (Figure 4B). Plants corresponding to var. *fusco-citrina* have similar long, flattened stolons and this feature may prove to be an important distinction between that and var. *maculata*. Unfortunately, too few collections have corms well enough preserved to allow examination of the stolons; indeed many collections lack corms altogether. As we noted above, *I. calendulacea* and *I. maculata* sometimes grow in close proximity but in different habitats, the latter always in seasonally wet sites. Their ranges, however, overlap very little (Figure 5), *I. maculata* being restricted to the southwestern Cape between Paarl and the western end of the Piketberg, whereas *I. calendulacea* extends from Langebaan and Porterville to central Namaqualand. An annotation on a collection from near Leipoldville (De Wet 00903) indicates a diploid chromosome number of $2n = 42$, which suggests the species may be polyploid (Goldblatt & Manning in prep.). Basic chromosome number in *Ixia* is $x = 10$ (Goldblatt & Takei 1997). The count is unpublished.

A collection from near Porterville, Goldblatt 2745, is somewhat unusual in having narrow leaves (resembling those of *Ixia maculata*) but the flowers have united filaments and pale bracts, 9–10 mm long, with only the tips turning brown, thus corresponding with *I. calendulacea*. We regard this collection as best referred to the latter and it constitutes the southernmost record of the species.



FIGURE 4.—*Ixia calendulacea*: A, flowering stem; B, corm; C, two flowers; D, half-flower; E, outer (left) and inner (right) bracts; F, details of stamens and style. *Ixia maculata*: G, flowering stem; H, corm; I, flower; J, half-flower; K, outer (left) and inner (right) bracts; L, detail of stamens and style. Scale bar: A–E, G–K, 10 mm; F, L, 2 mm. Artist: John Manning.

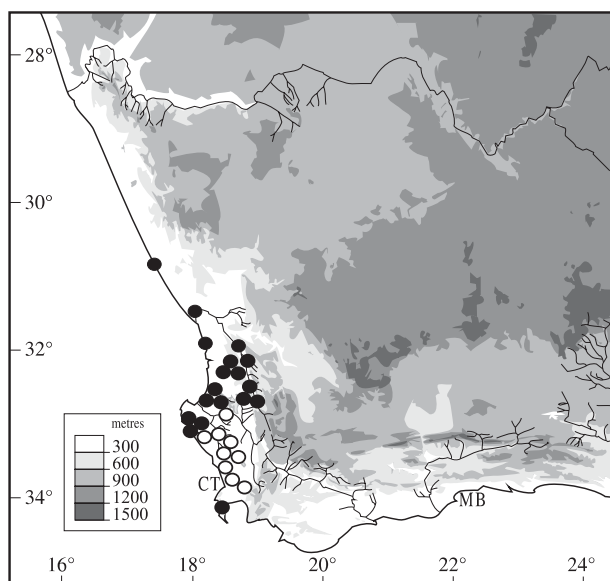


FIGURE 5.—Known distribution of *Ixia calendulacea*, ○; and *I. maculata* including var. *fusco-citrina*, ●.

Key distinctions between *Ixia calendulacea* and *I. maculata*

- 1a Tepals forming concave cup in central dark zone and spreading horizontally in distal part; tepals mostly 15–25 × 8–12 mm, not or hardly overlapping one another toward base; central eye 6–12 mm diam., dark brown, often with star-shaped mark within; filaments yellow; stolons either long, up to 100 mm long, bearing a single terminal cormlet or short, up to 20 mm long, usually more than one cormlet, each up to 3 mm diam. *I. maculata*
- 1b Tepals when fully open forming shallow cup and curved uniformly from base to apex; tepals mostly 16–28 × 9–14 mm, the inner obviously overlapping the outer in lower half; central eye of perianth ± 15 mm diam., glossy brown with pale reddish halo or dull, translucent red; filaments dark red-brown (violet when dry); stolons extending horizontally for up to 120 mm and bearing single terminal cormlet 7–9 mm diam. *I. calendulacea*

Representative specimens

NORTHERN CAPE.—3017 (Hondekliapaai): Farm Hardekoppie NW of Kotzesrus, (–DC), 29 September 1987, Reid 1291 (PRE).

WESTERN CAPE.—3118 (Vanrhynsdorp): Farm Graafwater, W of Koekenaap, (–AC), August 2007 (sterile), Goldblatt & Manning 12876 (NBG); Nardouw, (–DC/DD), 22 September 1937, Barker 272 (NBG). 3217 (Vredenburg): Witteklip rocks, Vredenburg, (–DD), 18 September 1980, Goldblatt 5845 (MO). 3218 (Clanwilliam): Lambert's Bay road at Leipoldville turnoff, (–BA), 8 October 1965, De Wet 00903 (PRE); Farm Sandberg, sandy slope burned two years ago, (–BC), 27 September 1995, Goldblatt & Manning 10324 (MO, NBG); Farm Nooitgedacht, N of Vredenburg, (–CC), 9 October 1985, De Vos 2624 (PRE); Piketberg, Farm Weltevrede, sandy slope, (–DA), 19 September 2007, Goldblatt & Manning 13011 (MO); sandveld between Porterville and Piekieners Kloof Pass, (–DD), 24 September 1974, Goldblatt 2745 (MO, NBG, PRE); 'Posberg Reserve' (ex Darling Flower Show), (?–AA), 19 September 1986, De Vos 2665 (NBG). 3418 (Simonstown): Cape Town, Youngsfield Military Base, (–BA), 13 October 2009, Dorse sub Manning 3231 (NBG).

AN EARLIER NAME FOR *IXIA LUTEA*

While examining the protologues of synonyms of *Ixia maculata* listed by Lewis (1962) in order to determine if any might apply to *I. calendulacea*, we found that *I. abbreviata* Houtt. (1780) (Figure 6) was misplaced in

the synonymy of this species. The type, an illustration (Figure 7), shows an *Ixia*-like plant with large flowers in which the style divides below the level of the anthers. The description, remarkably detailed for the time, emphasizes the short style, noting that this feature distinguishes the plant from most other species [of *Ixia*-like plants]. Houttuyn (1780) described the flowers as arising from transparent sheaths (i.e. bracts), sulphur yellow with a bluish central eye, anthers longer than the filaments and with a perianth tube almost half an inch long.

(35) *Ixia* die getrost Bloemen heeft, met zeer korte Stylen. XXXV. a. Abbreviata. Kortstyl.
De korthed van den Styl onderscheidt deeze PLAAT LXXXVIII. van Fig. 3.
(34) *Ixia Umbellâ bifida* Racemosa. BURM. Prodr. 2.
(35) *Ixia Floribus Racemosis, Pistillo brevissim o.* HOUTT.
C 5
II. DEEL. XII. STUK.

42 DRIEMANNIG LELIE

V. van de meeste anderen. Haar Bladen zyn L. niaal-Lancetvormig, bekleedende om laag de Stengel, die een Voet lang is, rond en dun, op 't end een Trosje hebbende van zes Zwaavelgele Bloemen, taamelyk groot. Zy komen voort uit Vliezige doorschynende tweekleppige Scheedjes, wier kortste of kleinste Lip twee lange punten heeft. Dunne Steeltjes van een half Duim langte, draagen deeze Bloemen, die byna een Duim lang zyn, bestaande uit zes ovaalachtige, fyn geaderde Blaadjes. De Meelknopjes, taamelyk dik, langer dan de Draadjes, Liniaal of oyerel even breed, komen uit den Stool der Bloem, die wat blaauwachtig is, voort; naby den oirsprong der drie Stempels, welke langwerpig, dik en omgekromd, naauwlyks eenigen Styl hebben, zittende op den bodem van de Bloem. Ik hebze ook die blaauw zyn van Kleur.

XXXVI. *Ixia Campanulata, Klokbloemige.* (36) *Ixia* met getrost Bloemen, die Klokvormig zyn, en Grasachtige Bladen.

De figuur der Bloemen, welke naar die der Klokjes gelyken, onderscheidt deeze zo zeer van de voorgaande niet, als de langte van den Styl, waar van de lange dunne Stempels boven de Meelknopjes zig verheffen. De Bladen zyn Gras.

(36) *Ixia Floribus Racemosis, Campaniformibus, Fol. Gramineis.* HOUTT.

FIGURE 6.—Protologue of *Ixia abbreviata* Houtt.: 41, 42 (1780). Translated by J.P. Roux: (35) *Ixia* with flowers in bunches and with short styles / The short style separates this [species] from most others. The leaves are linear-lanceolate and form a sheath around the stem, which is one foot long, round and slender, and bears at the tip a single group of six, reasonably large, sulphur-yellow flowers. They [the flowers] arise from membranous, transparent, two-valved sheaths [bracts], of which the lip of the shortest or smallest has two long points. Slender stalks [tubes] half an inch long bear the flowers, which are nearly one inch long and consist of six elliptic, finely veined tepals. The relatively thick, linear or parallel-sided anthers are longer than the stamens and originate from the base of the flower [mouth of the tube], which is bluish, and near the origin of the three stigmas [style branches], which are elongated, thick and recurved. The blue style is almost absent and seated at the base of the flower.

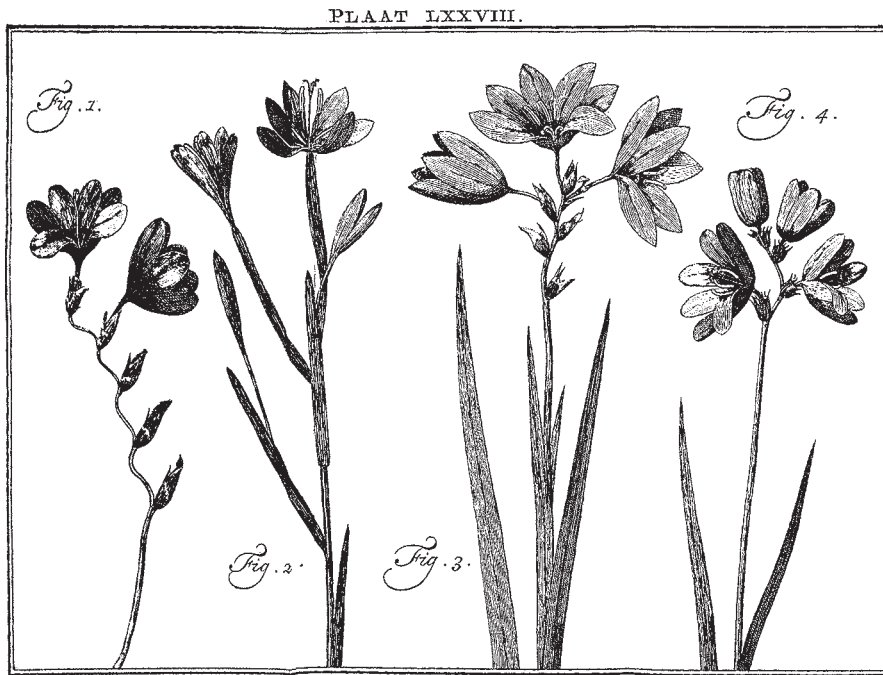


FIGURE 7.—Original illustration of *Ixia abbreviata*. Plate 78, fig. 3 (Houttuyn 1780).

There are few yellow-flowered species of *Ixia* section *Ixia* and the one that matches the description best is the plant currently called *I. lutea*. *Ixia polystachya* L. sometimes has pale yellow flowers, but typically has anthers shorter than, to as long as the filaments (rarely longer). Yellow-flowered *I. curta* and *I. maculata* have a very dark central eye, a style dividing above the anther base and brown rather than translucent floral bracts. Lastly, *I. dubia* Vent. has a small central dark eye and deep yellow to orange flowers usually red on the outside, and does not accord with Houttuyn's plant.

***Ixia abbreviata* Houtt.**, *Natuurlijke historie* 12: 41, t. 78 f. 3 (1780). Type: South Africa, without precise locality or collector, illustration in Houttuyn (1780).

I. lutea Eckl.: 24 (1827), syn. nov. Type: South Africa, without precise locality, cultivated in Cape Town, *Ecklon s.n.* (S, holo.).

We provisionally follow De Vos (1999) in recognizing a second variety of the species, providing the new combination for what she called var. *ovata* (Andrews) B.Nord.

***Ixia abbreviata* var. *ovata* (Andrews) Goldblatt & J.C.Manning**, comb. nov. *Ixia capitata* var. *ovata* Andrews, *The botanist's repository* 1: t. 23 (1798). *I. lutea* var. *ovata* (Andrews) B.Nord.: 284 (1972). Type: South Africa, without precise locality or collector, illustration in Andrews: t. 23 (1798).

ACKNOWLEDGEMENTS

We thank the curators of the following herbaria, BOL, K, MO, NBG, PRE, and SAM (acronyms following Holmgren *et al.* 1990) for permitting access to their collections or for the loan of material for extended study. Field work was supported by grants 7799-05 and 8248-07 from the National Geographic Society (United States). Collecting permits were provided by the Nature Conservation authorities of Western Cape. We thank Lendon Porter for his assistance and companionship in the field,

Koos Roux for his translation of Houttuyn's text, and Michelle Smith for assistance in preparing the images.

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MS. received 2009-06-29.

LAMIACEAE

REDISCOVERY IN SOUTH AFRICA OF THE NEGLECTED AFRICAN VEGETABLE *PLECTRANTHUS ESCULENTUS*

Plectranthus esculentus N.E.Br. was rediscovered in habitat during 2005, in rocky grassland on a hillside at Inanda, inland of Durban (Figure 8). Herbarium records reveal that this species has not been encountered in the wild by botanists in southern Africa for over 30 years, with several records reflecting collections from cultivation sites made predominantly during the early decades of the 20th century (e.g. *Van Warmelo* TRV3617 PRE; *Gerstner* 5436 PRE). Subsequent popularity of this crop in South Africa has evidently waned considerably, although limited use in Mpumalanga is reported to persist (*Allemann* 2002).

The rediscovery in South Africa of this taxon has significant implications for the strengthening of efforts to reintroduce, for household food security, a neglected African vegetable which is well adapted to areas of low agricultural potential. Only one other South African genotype (from Limpopo Province) is presently known, and is represented in the holdings of the Agricultural Research Council (ARC) at the Roodeplaat Vegetable and Ornamental Plant Institute (*J. Allemann* pers. comm.

2007). The current find at Inanda is of particular importance as the formation of tubers has been observed at latitude $> 29.5^{\circ}\text{S}$ (*Crouch* 1237 NH) (Figure 9), somewhat beyond the range (15°N – 28°S) determined for this species as a crop (*Allemann & Hammes* 2006). As such, this collection may represent a photoperiodic ecotype of agronomic consequence. *Plectranthus esculentus* is characterized by finger-like edible tubers (Figure 10) and bright yellow flowers (*Pooley* 1998) presented in short pseudoracemes during spring, usually after the leaves have been shed (*Codd* 1985). This geophyte produces several lax stems which trail amongst grasses and root at the nodes, thereafter seasonally producing stem tubers (*Allemann et al.* 2003). Plants at the Inanda site were found to not regenerate well from aerial parts, a characteristic earlier documented by *Burkill* (1995). This feature is shared with tuberous forms of *P. hadiensis* (*Forssk.*) *Schweinf. ex Spreng.* var. *hadiensis* which occur in grassland, the stems of which do not strike as well as those of genus members found in more mesic habitats. Success with striking of cuttings may relate to the timing of tuber initiation, which appears to retard aerial growth (*J. Allemann* pers. comm. 2008).



FIGURE 8.—*Plectranthus esculentus* in habitat, Inanda, KwaZulu-Natal. Photograph: N. Crouch.

The vegetation in which plants may be encountered at Inanda is referred to as KwaZulu-Natal Sandstone Sourveld (SVs 5) by *Rutherford et al.* (2006) who describe it as ‘short, species-rich grassland with scattered low shrubs and geoxyllic suffrutices’. The underlying geology is Ordovician Natal Group sandstones. This vegetation type is considered Endangered, with only 0.2 % statutorily conserved and some 68 % already transformed (*Rutherford et al.* 2006). The habitat of *Plectranthus esculentus* here comprises shallow soil amongst rocks, on the edge of, and above steep cliffs and escarpment edges at an altitude of ± 700 m. Small aggregations of fewer than ten individuals occur at scattered points on dry, northerly aspects over a distance of ± 500 m. The dominant grass amongst which this *Plectranthus* species grows is *Aristida junciformis* subsp. *junciformis*, which although a typical element in KwaZulu-Natal Sandstone Sourveld, also proliferates in response to overgrazing and overburning. Other associates include *Acalypha glandulifolia*, *Gymnosporia woodii*, *Pentanisia prunelloides*, *Phymaspermum pinnatifidum*, *Plectranthus hadiensis* var. *hadiensis*, *Tetraselago natalensis* and *Thunbergia atriplicifolia*. The site is neither suitable for, nor gives indication of prior cultivation by earlier inhabitants; accordingly the plant appears here to be native rather than naturalized. Similarly, Angolan subpopulations have been observed ‘in [a] perfectly wild state’ (*Good & Taylor* 1931) and in Zimbabwe within *Julbernardia* and *Brachystegia* woodland (*Wild et al.* 1972).

Elsewhere in South Africa, particularly in the vicinity of Nelspruit and Barberton, annotated herbarium specimen labels (e.g. *Lavranos* 4681 PRE; *Repton* 647 PRE; *Thorncroft* 353 NH) indicate its natural occurrence. *Wood* (1896) noted that the species ‘[*Plectranthus esculentus*, or *umbondwe*] is cultivated [around Durban]

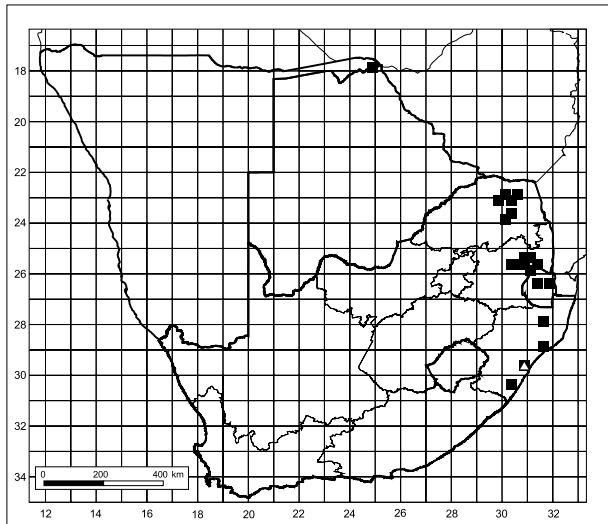


FIGURE 9.—Reported geographical distribution of *Plectranthus esculentus* in FSA region based on specimens at BOL, NBG, NH, NU, PRE and SAM, ■, extant subpopulation at Inanda, △.

by the natives, who use the tuber as a vegetable. I have not seen it in a wild state, but a closely allied species (*P. floribundus*, N.E.B.) is occasionally met with'. Gerstner (1938) similarly claimed that amongst the Zulus, *P. esculentus* is not found wild but that it had been planted 'since ancient times'. Forester Tustin of Ngome Forest in KwaZulu-Natal, in correspondence with his superiors during 1923 noted that 'I really do not know if the plant is indigenous to this part, or if it was previously brought here. It is chiefly found growing in old lands' (Tustin s.n. PRE39880). According to oral Zulu tradition, *P. esculentus* (as *umhlaza*) and *Colocasia esculenta* (L.) Schott (as *amadumbi*) were brought south of the Umfolozi River by a chief called Langa. He entered what was later to become Zululand from the direction of Swaziland, some ten generations before Tshaka (Webb & Wright 2001). Accordingly, *P. esculentus* may have been introduced to the region in the mid- to late 16th century.

Based on his field observations, Wood (1896) evidently considered *Plectranthus esculentus* distinct from *P. floribundus* N.E.Br., a taxon described from an Inanda collection of his. Accordingly, it is likely that the Zulus at Inanda were at that time cultivating at least one morphologically distinct landrace of *P. esculentus*. Fox & Norwood Young (1982) recorded that cultivation of different varieties was once commonplace in the Msinga District on the middle Thugela. Such local diversity may further be inferred from the variety of isiZulu names for this species—no fewer than sixteen are documented (Wood 1896; Bryant 1908; Gerstner 1938; Fox & Norwood Young 1982; Allemann 2002). After 15 years of ethnobotanical experience, the first author is yet to encounter this edible lamiate in cultivation; as elsewhere (Burkill 1995), this starch-rich and otherwise nutritious crop (Allemann & Hammes 2003) has been displaced by less labour-intensive and sometimes higher-yielding introductions. These include *Ipomoea batatas* (L.) Lam. (sweet potato) and maize (*Zea mays* L.) from the New World, and the Old World *Colocasia esculenta* (taro, *idumbe*) from Asia. By the late 19th and early 20th centuries, these crop species were well established amongst

the Zulus (Wood 1896; Bryant 1908). During the last century, cultivation of the New World starch crop *Solanum tuberosum* L. (potato) has further marginalized *Plectranthus esculentus*. As *P. esculentus* has been co-dispersed synanthropically, its natural distribution is imprecisely known, although this may at one time have extended from Senegal in Equatorial Africa broadly southwards to coastal KwaZulu-Natal (Codd 1975; Burkill 1995). The original site of domestication and dispersal is uncertain, with various authors proposing West (Purseglove 1976), Central (Portères 1962), South-central or East (Greenway 1944) Africa. It has reasonably been surmised that domestication occurred independently in different regions across its wide range (Shaw 1976). Whereas several centres of cultivation are known from various Central African countries, e.g. Nyanga terraces in eastern Zimbabwe (Sutton 1984), some user groups eat only wild-sourced material, and then just as a supplement or famine food (Burkill 1995). This may reflect social stigmas which have led to preferences for exotic crops (Kyesmu 1994).

Plectranthus esculentus and *P. floribundus* were described synchronously by Brown (1894) who distinguished them on account of the latter species bearing taller, more erect stems, and closely sessile leaves with



FIGURE 10.—Stem tuber cluster of a *Plectranthus esculentus* plant sourced from Inanda, KwaZulu-Natal. Photograph: N. Crouch.

broader, rounded bases, more prominent reticulation and a rougher surface. Good & Taylor (1931) subsequently placed *P. floribundus* in synonymy under *Coleus esculentus* (N.E.Br.) G.Tayl., so allowing for a circumscription that accommodates the wide diversity of cultivars known, as well as natural variation across its range. Subsequent workers on African Lamiaceae have accepted this broader species concept (Codd 1975, 1985; Van Jaarsveld 2006).

Rutherford *et al.* (2006) observed that most of the remaining areas of KwaZulu-Natal Sandstone Sourveld are subjected to grazing pressures and fire frequencies that are not conducive to the recruitment of seedlings. This is evident at the Inanda site where the leafless shoots of plants have, for three consecutive years, been burned off by intentional fires set during the winter months. This has resulted in non-flowering and a lack of seed set. The grassland in which *Plectranthus esculentus* occurs, still retains a fair diversity of forbs and geophytes, particularly in the rockiest parts. However, without respite from these impacts and encroaching urban sprawl, the trend over time will be towards increased degradation and loss of species diversity. *P. esculentus* is a rare species within its habitat, and is therefore likely to become even more so in future. In view of the above, further collections from the last-known South African locality of *P. esculentus* should be genebanked as a matter of urgency, if residual germplasm diversity is to be conserved.

Specimen examined

KWAZULU-NATAL.—2930 (Pietermaritzburg): Inanda, in grassland along rocky ridge, 715 m, S 29° 36' 19.18"; E 30° 49' 34.01" (–DB), 08-04-2009, Crouch 1237 (NH).

ACKNOWLEDGEMENTS

Dr J. Allemann of the Department of Soil, Crop and Climate Sciences at the University of the Free State is thanked for helpful discussions; Mr R. Edwards for growing the original gathering made by D. Styles; Ms H. Steyn and Ms E. Fouché for preparing the map; the Curators of BOL, NBG, NH, NU, PRE and SAM for use of their specimens; the staff of the Mary Gunn Library and Dr E. Retief of PRE for facilitating access to literature, and the Data Section of the National Herbarium for providing PRECIS data.

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MS. received: 2009-06-18.

PTERIDOPHYTA

NEW DISTRIBUTION RECORDS AND NOTEWORTHY COLLECTIONS OF PTERIDOPHYTES IN KWAZULU-NATAL

Rediscovery of Didymoglossum erosum

During a field trip to Ngoye Forest in Zululand in early April 2009, a colony of *Didymoglossum erosum* (Willd.) Beentje (syn. *Trichomanes erosum* Willd.) was encountered on a dry vertical rock face in deep shade. This small, easily overlooked, filmy fern (Figure 11) had not been gathered in the FSA region since John Medley Wood (1907, 1908) initially collected material from Ngoye in 1887.

Didymoglossum erosum (Hymenophyllaceae) is easily distinguished from most other filmy ferns by the simple fronds. The only other species in southern Africa with simple fronds is *D. reptans* (Sw.) C.Presl (syn. *Trichomanes reptans* Sw.) from which it differs by being variably pinnatifid and having sori that do not protrude from the lamina but are rather winged by it. Furthermore, they lack marginal hairs, and possess a false marginal vein (Burrows 1990). The most recent literature considers *D. erosum* as a single taxon (Beentje 2008; Roux 2009), whereas historically, distinction has been made between *Trichomanes erosum* var. *erosum* and *T. erosum* var. *aerugineum* (Bosch) C.Chr. ex Bonap. (Schelpe 1970; Burrows 1990; Roux 2001). This was based on morphological differences, reinforced by habitat preferences (Schelpe 1970; Burrows 1990). *Didymoglossum erosum* is a rare fern that occurs from the eastern highlands of Zimbabwe through eastern and central Africa (Figure 12) and into western Africa to Sierra Leone and Guinea, as well as Madagascar and the small islands of Annobon, Bioko, Pemba, Príncipe, Réunion and São Tomé (Burrows 1990; Roux 2009). In South Africa this fern is only known from the Ngoye Forest Reserve (specimens earlier ascribed to *Trichomanes erosum* var. *aerugineum*, Schelpe & Anthony 1986), where it has eluded re-collection, despite ongoing botanical survey work (Huntley 1965).

In recent years, links in the pteridophyte flora of Ngoye and the rainforests of eastern Zimbabwe have also been highlighted: *Christella buehneri* (Schelpe) J.P.Roux and *Christella hispidula* (Decne.) Holttum have recently been collected from Ngoye (Burrows & Burrows 2001), both of which are also known from the forests of southeastern Zimbabwe, as is *Asplenium blastophorum* Hieron. (Burrows 1990).

*Specimens examined**Didymoglossum erosum*

KWAZULU-NATAL.—2831 (Nkandla): Ngoye Forest Reserve, ± 800 m northwest of Zululand Birding Route prefabricated accommodation, in valley below, colony growing in deep shade on dry vertical rock face in view of a perennial stream 15 m distant. Growing in close proximity to, but separate from colonies of both *Didymoglossum reptans* and *Crepidomanes melanotrichum*, 280 m, (–DC), 01-04-2009, N. Crouch 1231 (NH, PRE); Ngoye Forest, (–DC), 23-03-1907, J. Medley Wood 11947 (BOL; NBG; NH; PRE); Ngoye, (–DC), 26-03-1907, J. Medley Wood 11948 (K).

New distribution record for Amauropelta oppositifomis

Amauropelta oppositifomis (C.Chr.) Holttum [Thelypteridaceae, syn. *Thelypteris oppositifomis* (C.Chr.) Ching] is a rare fern found along fast-flowing mountain streams in high altitude grassland in full sun or light shade of evergreen forest margins. It has tufted fronds that are narrowly elliptic in outline and 2-pinnatifid, with the basal pinnae gradually decreasing in size. The pinnae are opposite and the pinnae lobes acute, with the basal pair of veins not meeting below the sinus. It is easily confused with *A. bergiana* (Schltdl.) Holttum [syn. *T. bergiana* (Schltdl.) Ching], but is distinguished from this species by the presence of small golden to red glands and the lack of hooked hairs on the lower surface of the frond (Burrows 1990). Within southern



FIGURE 11.—Detached fronds of *Didymoglossum erosum*, Ngoye Forest Reserve. Photograph: N. Crouch.

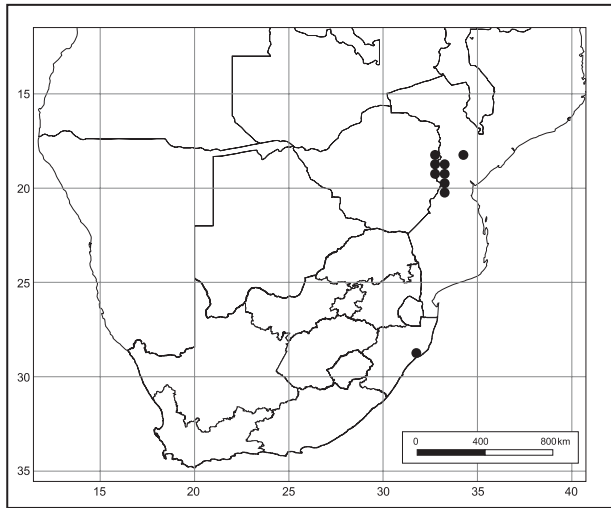


FIGURE 12.—Distribution of *Didymoglossum erosum*, adapted from Burrows (1990), ●.

and Central Africa it has been collected at Die Berg in Mpumalanga, South Africa, Nyanga Mountain in Zimbabwe, and the Zomba Plateau in Malawi. It occurs further into eastern, central and western Africa as far north as Ethiopia, Sudan, the DRC and Nigeria, and is also present on Madagascar (Burrows 1990; Roux 2001, 2009). The current record extends its distribution into the southern Drakensberg range from Mpumalanga by 500 km and is a first record for KwaZulu-Natal (Figure 13).

Specimen examined

KWAZULU-NATAL.—2929 (Underberg): Cobham Forest Reserve, 200 m northwest of Pinnacle Rock, growing on side of sinkhole in montane grassland, 2 000 m, (–CB), 19-10-2008, *N. Crouch* 1241 (PRE).

First record of *Amauropelta bergiana* var. *calva* in South Africa

Amauropelta bergiana (Schltdl.) Holttum is a fairly commonly encountered fern in deeply shaded forests associated with mountainous regions receiving high rainfall. It grows along permanent or seasonally moist streambanks, riverine scrub and earthbanks in forests (Burrows 1990; Roux 2001). *Amauropelta bergiana* var. *bergiana* occurs throughout the Afrotropical regions of southern and eastern Africa, from the Cape Peninsula, through Central Africa to Ethiopia, as well as on Bioko, Madagascar and Réunion (Burrows 1990; Roux 2001, 2009). Two other varieties of *A. bergiana* were described by Holttum (1974): *A. bergiana* var. *calva* Holttum occurs in West Africa, the Comoro Islands and Réunion; while *A. bergiana* var. *tristanensis* Holttum is confined to the islands of Gough, Inaccessible and Tristan da Cunha (Roux 2009).

Amauropelta bergiana is a rather large fern with tufted, deeply 2-pinnatifid fronds of up to 1 m long. The basal pinnae gradually decrease in size with a pair of very small, vestigial pinnae usually present. Basal veins of the pinnae do not unite below the sinus between each lobe. The typical variety of this species is characterized by the presence of hooked hairs on the abaxial surface of the pinnae, and very small indusia. It can easily be

confused with *A. knysnaensis* (N.C. Anthony & Schelpe) Parris (endemic to the Knysna area); this latter species possesses larger indusia set with minute stalked glands, and lacks the characteristic hooked hairs of *A. bergiana* var. *bergiana*. Another close relative is *A. oppositifolius*, which is distinguished by the absence of hooked hairs and the presence of small golden to red glands on the lower surface of the frond (Burrows 1990).

On a recent trip to the Umtamvuna Nature Reserve in southern KwaZulu-Natal, a plant was found that matched the description of *A. bergiana*. However, on closer inspection, it was found that the hairs on the abaxial surface were not hooked. Furthermore, the plant lacked glands on either indusia or lamina surfaces, so eliminating the two aforementioned related species. This represents the first record of *A. bergiana* var. *calva* in South Africa (Figure 13). This Umtamvuna taxon has previously only been recorded on mainland Africa from Cameroon, and as far south as Réunion in the Indian Ocean (Roux 2009). It is characterized by the presence of straight hairs on the rachis, costae and costules and the absence of hairs on the abaxial surface of the lamina between the veins. It is without hooked hairs (Holttum 1974).

Specimen examined

KWAZULU-NATAL.—3130 (Port Edward): Umtamvuna Nature Reserve, growing at the base of a waterfall tumbling into the Bololo River, 225 m, (–AA), 15-03-2009, *N. Crouch* 1228 (PRE).

ACKNOWLEDGEMENTS

Ms Sharon Louw and Mr Richard Nxele of Ezimvelo-KZN Wildlife are thanked for kindly facilitating field work; Dr Hugh Glen for the Latin translation; Mr John Burrows for giving permission to use distribution maps of these species from his book *Southern African ferns and fern allies* (1990); Ms Hester Steyn, National Herbarium, SANBI, Pretoria, for producing updated distribution maps.

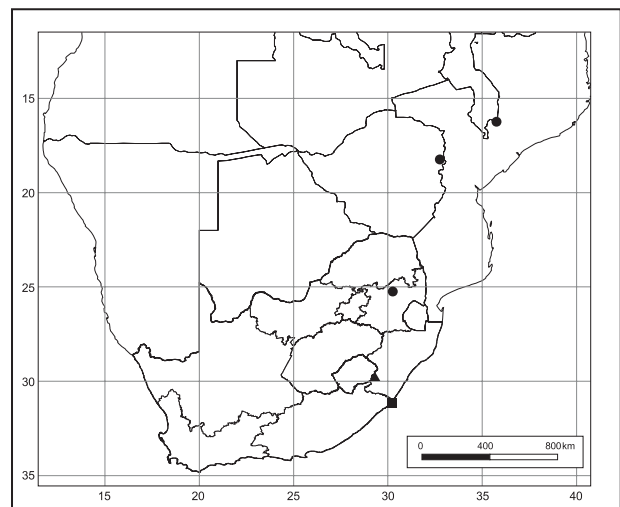


FIGURE 13.—Distribution of *Amauropelta oppositifolius*, adapted from Burrows (1990), ●; new locality in KwaZulu-Natal, ▲. Distribution of *A. bergiana* var. *calva* in the FSA region, ■.

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MS. received: 2009-06-25.

RUBIACEAE

FIRST RECORD OF *GEOPHILA* IN SOUTHERN AFRICA

Geophila D.Don, a small herbaceous genus of forest floor perennials, has previously not been recorded from the *Flora of southern Africa* (FSA) region (Leistner 2005), the closest known locality being in eastern Zimbabwe (Govaerts *et al.* 2009). The genus comprises more than 20 species from both the Old and New World (Mabberley 2008; Govaerts *et al.* 2009), with only three taxa reported in the *Flora zambesiaca* (FZ) region (Verdcourt 1989).

In July of 2008, red-fruited plants of *Geophila* were encountered in shade alongside the road traversing Ngoye Forest in Zululand (Figure 14). This low-growing herb occupied the poorly developed field layer community of climax forest (Huntley 1965) in vegetation classified recently as Scarp Forest (FOz5) (Rutherford *et al.* 2006). Material was grown on to flowering in Everton near Durban and a voucher specimen prepared. A return trip to Ngoye Forest in late May 2009 enabled the gathering of fruiting material from the colony, which occupies an area of ± 12 m². Comparison with literature revealed this collection to be *Geophila repens* (L.) I.M. Johnston, a pantropical herb of evergreen forest floors, widespread in both the Old and New World (Verdcourt 1989). The nearest known locality of this species lies some 940 km north of Ngoye Forest in Zimbabwe's Chirinda Forest (Drummond & Mapaire 1994), a medium altitude rainforest (Müller 1999) within the Chimanimani-Nyanga Centre (CIC) of Endemism (Van Wyk & Smith 2001). These *Geophila repens* records represent a significant range extension, and they also serve to confirm the close floristic relationship of the rainforests of eastern Zimbabwe with Ngoye Forest—as part of the Maputaland-Pondoland Region of Floristic Endemism, approximating the Tongaland-Pondoland Regional Mosaic of White (1983) (Müller 1999). Various pteridophytes (Burrows & Burrows 2001), lianes (*Urera trinervis*), shrubs (*Pseuderanthemum subviscosum*) and grasses (*Olyra latifolia*) exhibit similar disjunctions. The distributions of certain fauna such as the butterfly *Euriphene achlys* further reflect this pattern (Swanepoel 1953). Whereas some such taxa remain regionally localized within Ngoye Forest (Klopper & Crouch 2010), a number extend their range southwards

to Pondoland (Huntley 1965; Van Wyk & Smith 2001). The *Geophila* species occurring nearest to Ngoye Forest is *Geophila obvallata* (Schumacher) F.Didr., which was recorded from the Maputo region of Mozambique (Verdcourt 1989), somewhat closer than Chirinda Forest. This species is associated with a much broader range of habitats than *G. repens*, which is restricted to evergreen forest. *Geophila repens* is distinguished from *G. obvallata* by its bright red or orange rather than black, purple or blue berries. Furthermore, the inflorescences of *G. repens* are usually 1-flowered in our region and without an involucre, whereas those of *G. obvallata* are always several-flowered and subtended by a distinct involucre comprising separate bracts. The style of *G. repens* is between 3.5–7.0 mm long vs not more than 1 mm in *G. obvallata* (Verdcourt 1989).

The full synonymy for *Geophila repens*, with species description and illustration, is provided by Verdcourt (1989).

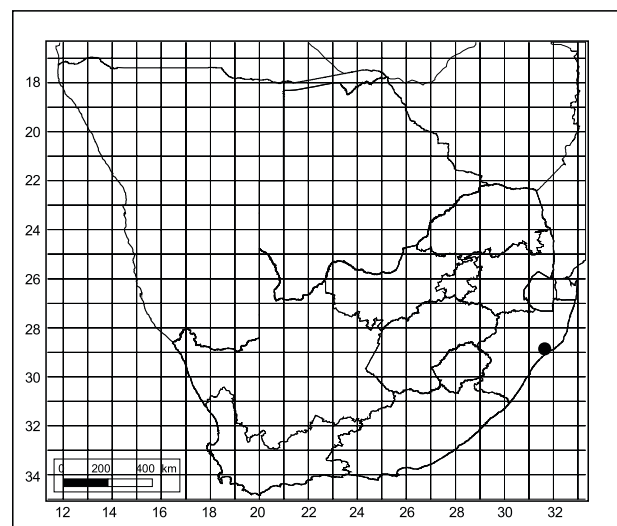


FIGURE 14.—Distribution of *Geophila repens* in the FSA region, ●.

Specimens examined

KWAZULU-NATAL.—2831 (Nkandla): Ngoye Forest Reserve, $\pm$ 3 km west of gauge weir in forest, on northern roadside verge in shade, 440 m, grown on to flowering in Everton, (–DC), 20-05-2009, R. Edwards 1 (PRE), fruiting, 24-05-2009, R. Edwards 2 (PRE).

ACKNOWLEDGEMENTS

Mr D. Styles is thanked for helpful discussions regarding the identity of the discovery; Mrs H. Snyman, SANBI, for preparing the map; and the staff of the Mary Gunn Library, SANBI, for facilitating access to literature. This note is dedicated to the late Mr Ian Garland who for many years recognized the uniqueness of Ngoye Forest and surrounds, and actively supported its botanical exploration.

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MS. received: 2009-05-26.

PTERIDOPHYTA

NOTES ON SOME NATURALIZED FERNS OF THE EASTERN CAPE AND KWAZULU-NATAL

BLECHNACEAE

Doodia caudata

There has been some confusion as to the exact identity of the *Doodia* species (Figure 15A) naturalized in KwaZulu-Natal, South Africa. Specimens from Pietermaritzburg collected in the mid-20th century were first identified as *Doodia media* R.Br. by Prof. E. Schelpe. Subsequently, Burrows (1990) referred this taxon to *Doodia caudata* (Cav.) R.Br., and more recently it has been assigned to *Doodia squarrosa* Colenso (Roux 2001, 2009). The fact that no single identification key to all *Doodia* species exists has confounded attempts to verify the identity of the South African naturalized species. There are separate keys available to the New Zealand (Parris 1972) and Australian (Parris 1998) taxa of *Doodia*. However, *D. caudata* is an Australian entity (Parris 1980, 1998), whereas *D. squarrosa* is confined to northern New Zealand (Parris 1972). Although *D. caudata* was initially considered to occur also in New Zealand (Parris 1972), plants so associated with this name were described subsequently as a New Zealand endemic, *Doodia mollis* Parris (Parris 1980). Accordingly, the two available keys are not definitive in respect of resolving *D. squarrosa* and *D. caudata*.

There is a high level of morphological variation in most species of *Doodia*; accordingly *D. caudata* and

D. squarrosa are apparently often confused in herbaria. Both have pinnate dimorphic fronds with discrete to confluent sori, and pinnae that are auriculate or stalked to partly adnate in the middle and adnate to decurrent in the upper part of the frond (Parris 1972, 1998). The fronds of *D. caudata* are 57–460 mm long with the longest pinnae 2–110 $\times$ 1–4 mm (Parris 1998), whereas the fronds of *D. squarrosa* are of similar maximum length, 140–450 mm long, but with the longest pinnae only 15–60 $\times$ 1–2 mm (Parris 1972). Frond and pinnae length are not always useful distinguishing characters especially since they are frequently environmentally influenced.

South African material was compared to the lectotype of *Doodia squarrosa* (Colenso 9/83, frond second from right, K) and a high resolution image of the holotype of *D. caudata* (L.Née s.n. MA). It was found to match the material for *D. caudata* more closely. During subsequent correspondence with Dr B. Parris, she confirmed the identity of the South African material as *D. caudata*, the most variable species in the genus and the one that has become the most widely naturalized. According to Parris (pers. comm.) the South African material approaches *D. media* R.Br. var. *moorei* Baker in having rather longer fertile pinnae than the typical form; this aforementioned variety intergrades with the typical form in Australia and



FIGURE 15.—A, *Doodia caudata*, habit; B, *Phlebodium aureum*, habit. Photographs: N.R. Crouch.

cannot be upheld. It has consequently been placed in synonymy under *D. caudata* (Parris 1998).

Accordingly, the *Doodia* species that has escaped from cultivation in KwaZulu-Natal is *D. caudata*, the small rasp fern.

***Doodia caudata* (Cav.) R.Br.** in Prodrumus florum Novae-Hollandiae: 151 (1810); Burrows: 338 (1990). Type: Nova Hollandia [Australia], *L.Née s.n.* (MA, hol.).

D. squarrosa sensu Roux: 153 (2001) et sensu Roux: 105 (2009), non Colenso: 382 (1881).

For a complete list of synonyms see Parris (1998).

Rhizome erect, up to 0.1 m tall, to short- or long-creeping; rhizome scales brown. **Fronds** markedly dimorphic; stipe slender, short, dark towards base and without tubercles. **Fertile lamina** generally more erect and scabrous, longer and broader than sterile ones, 57–460 × 5–180 mm, with a long apical segment ($\frac{1}{3}$ – $\frac{1}{6}$ – $\frac{1}{9}$ of lamina length, 1-pinnate; pinnae more distant and narrower than sterile ones, simple, oblong to linear-lanceolate, margins sharply toothed, more than 2 pairs of pinnae stalked in basal third of lamina, stalked to partly adnate to decurrent in middle third, partly adnate to decurrent in distal third, longest pinnae 2–110 × 1–4 mm, rachis and pinna midvein without tubercles. **Sterile lamina** decumbent, 1-pinnate, pinnae simple, oblong, apices rounded, margins toothed. Venation with some anastomoses forming areoles on either side of costa. **Sori** in 1 (rarely partial second) row on each side of costa, 0.8–10 (or more) × 0.8–1.5 mm, often laterally confluent when mature, confluent across costa, nearer to midvein than margin; indusium linear, entire to repand, opening towards the costa (Andrews 1990; Parris 1998).

Doodia caudata is a native of Australia where it occurs in eastern South Australia, eastern Queensland, New South Wales, southern Victoria, northern Tasmania

and Lord Howe Island (Parris 1998). It has naturalized in KwaZulu-Natal, South Africa (Burrows 1990; Roux 2001, 2009), California (USA), as well as the Azores, Madeira and in Sri Lanka (Burrows 1990; Parris 1998). It can locally be found growing exposed or in deep shade on seasonally moist earthbanks, roadside cuttings and forest margins (Crouch 1994; Roux 2001).

An attempt has been made to trace the original source of the *Doodia* material imported into South Africa. Since the South African material most closely resembles the form described as *D. media* var. *moorei* which was collected from the Richmond River north of Sydney in New South Wales, the most likely source would be what is today known as the Royal Botanic Garden of New South Wales, Australia (B.S. Parris pers. comm.). Reports of the Natal Botanic Gardens in Durban from a century ago, reveal that its Curator, J.M. Wood was regularly exchanging plant material with the Botanic Gardens in Sydney, and from the accession register of 'Overseas and Tropical African specimens ex Wood Herbarium. Vol. I' it is apparent that J.H. Maiden of the Sydney Gardens provided Wood with plants of *D. caudata* for cultivation. A voucher (*J.M. Wood 5766 NH*) at the KwaZulu-Natal Herbarium indicates that this species was first grown in the Natal Botanic Gardens (Durban Botanic Gardens) prior to the mid-1890s. Notably, this particular specimen was correctly named *D. caudata* and has not been subject to re-determinations, likely due to its placement in the cultivated section of the NH collection. As Wood also exchanged live material with the Pietermaritzburg Botanic Garden at that time, plants from the Durban facility may have been transferred to the Pietermaritzburg Garden, from where they escaped.

Although *Doodia caudata* is locally common across the mistbelt zone of Pietermaritzburg (Figure 16), from Sunnyside to Ferncliffe (1 000 m), this species has apparently not naturalized elsewhere in the Midlands,

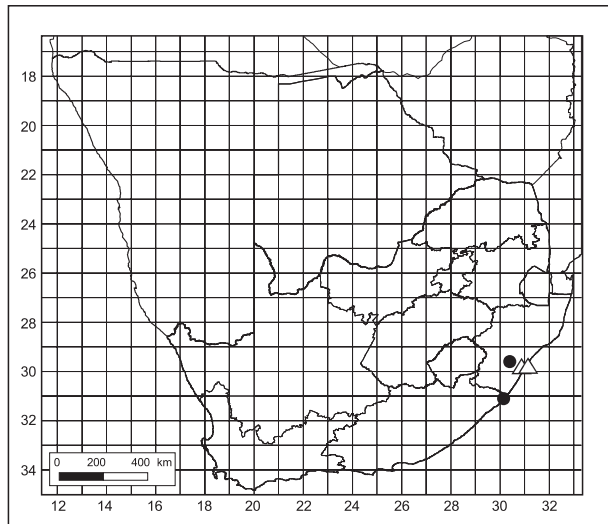


FIGURE 16.—Distribution in FSA region of *Doodia caudata*, ●; and *Phlebodium aureum*, △.

besides Howick (Crouch 1994)—this since its documented escape from cultivation over half a century ago. It was somewhat surprising then to encounter this taxon growing in a remote site near the Transkei coast under different climatic conditions, indicating that it may now be an emerging weed. This record extends the previous distribution range southwards some 170 km (Figure 16).

Specimens examined

KWAZULU-NATAL.—2930 (Pietermaritzburg): Sunnyside, Pietermaritzburg, (–CB), 01-03-1953, A. Dohse & L. Lindahl 102 (NH); Maritzburg District, 4000 ft [1 200 m], (–CB), 16-08-1956, ACS 10 (NU); Ferncliffe Nature Reserve, Pietermaritzburg, 1 000 m, (–CB), 23-02-1992, N.R. Crouch 561 (NU); Ferncliffe Nature Reserve, earth bank adjacent to parking area, 1 000 m, (–CB), 30-04-2007, N.R. Crouch 1153 (PRE); KwaZulu-Natal National Botanical Garden, growing alongside path on banks, in indigenous forest section on far side of river in garden, (–CB), 03-09-2008, N.R. Crouch 1172 (PRE); opposite 11 Tanner Rd, Wembley, Pietermaritzburg, colony on earth bank, (–CB), 06-01-2008, N.R. Crouch 1145 (NH). 2931 (Stanger): Natal Botanic Garden, in cultivation, (–CC), J.M. Wood 5766 (NH).

EASTERN CAPE.—3130 (Port Edward): Lukabeni stream junction with Mtentu River, 30 m upstream of high tide mark, small colony growing on earthbank in coastal forest, 4 m, (–AA), 04-01-2008, N.R. Crouch 1143 (NH).

POLYPODIACEAE

Phlebodium aureum

Phlebodium aureum (L.) J.Sm. (Figure 15B) is commonly cultivated in South Africa and has escaped from cultivation in the vicinity of Durban, KwaZulu-Natal and Port St Johns in the Eastern Cape (Burrows 1990). It has also been reported to have become naturalized in Zimbabwe (Roux 2009). This fern species was documented in cultivation in the Durban Botanic Gardens in 1941 (C. Kent 16 NH), and to have started escaping in the immediate vicinity of the gardens by 1968 (R.G. Strey 8071 NH). It has more recently been collected in Kloof some 25 km distant, and has been sighted and photographed growing on a decaying log in remnant indigenous riverine scrub, at Inanda to the north of the metropol (Figure 16).

The golden polypody or golden serpent fern is so named because of the golden scales on its creeping rhizome. Its arching to pendent fronds are deeply lobed (Nauman 1993) and very similar to those of *Microsorium scolopendria* (Burm.f.) Copel. It is distinguished from this indigenous fern by the venation of the lamina (fewer included veinlets), its very dense tomentum of golden scales clothing the rhizome, the close spacing of the pinnatifid segments and the sori which are not sunken into the lamina (Schelpe & Anthony 1986). It has been reported to grow epiphytically in moist evergreen riverine forests and forest margins (Roux 2001, as *Polypodium aureum* L.), and is also found in Durban growing as a lithophyte in more exposed situations, and on building ledges in a manner reminiscent of *Pteris vittata* L.

Phlebodium aureum is native to Central America from Florida and Georgia in the USA, through Mexico to Brazil in South America and the West Indies (Burrows 1990; Nauman 1993; Roux 2001). Plants are reportedly intolerant of heavy frosts which would account for limited naturalization of *P. aureum* along the warm eastern seaboard. Additionally, although usually evergreen, plants may be briefly deciduous during periods of drought stress, so allowing them to invade relatively dry areas such as man-made structures. Although it is recognized as a garden escape, no herbarium specimens documenting it as a truly naturalized species could be traced for South Africa; this report with associated voucher corrects this insufficiency.

***Phlebodium aureum* (L.) J.Sm.** in Journal of Botany 4: 59 (1842). *Polypodium aureum* L.: 1087 (1753). Type: *Herb. Linn. No. 1251.10* (LINN, lecto.), designated by Proctor (1977: 334).

Rhizome creeping, $\pm$ 8–15(–30) mm diam., densely scaled; rhizome scales reddish to golden, long attenuate, 10–20 mm. **Fronds** bright green or glaucous, arching to pendent, 0.3–1.3 m; stipe 150–500 mm, smooth, with a few scales near base; lamina deeply pinnatifid, 300–800 $\times$ 100–500 mm, glabrous, terminal segment conform; pinnae up to 35, lanceolate to elliptic, or linear-lanceolate to linear, 60–200 $\times$ 10–40 mm, margins entire, occasionally undulate. **Sori** in a single line on each side of costae, occasionally a 2nd row present, terminal or at a plexus of included veinlets; exindusiate (Nauman 1993).

Specimens examined

KWAZULU-NATAL.—2930 (Pietermaritzburg): Krantzklouf Nature Reserve, Kloof, at eastern end of reserve, immediately above The Splash, growing as a lithophyte adjacent to Molweni River in full sun, 218 m, (–DD), 28-04-2009, N.R. Crouch 1243 (PRE); Kloof, opposite Maytime Centre on ledge of pedestrian bridge across the M13 highway on eastbound carriageway, 450 m, (–DD), 27-04-2009, N.R. Crouch 1244 (PRE). 2931 (Stanger): Durban Botanic Gardens, (–CC), 06-1941, C. Kent 16 (NH); Natal Herbarium garden, epiphyte on *Raphia*, (–CC), 03-03-1968, Strey 8071 (NH).

WOODSIACEAE

Diplazium esculentum

Diplazium esculentum (Retz.) Sw., the vegetable fern (Figure 17), is a widespread native from both tropical and temperate eastern and southeastern Asia, where it



FIGURE 17.—*Diplazium esculentum*, habit. Photograph: N.R. Crouch.

is commonly cultivated and/or harvested for its young fronds which are used as a vegetable (Kato 1993; Mertz 1999; Roux 2001). It has become naturalized in South Africa and Zimbabwe (Roux 2009), as well as in Florida, Louisiana and Hawaii (USA) (Kato 1993; Smithsonian Institution 2009) and Australia (Jones 1998). It grows mostly in disturbed areas, exposed or in partial shade but always in wet sites such as streambanks (Roux 2001), where it forms large clonal colonies due to prolific root budding. Sporing in South Africa is evidently rare; close examination of large colonies at Kirstenbosch (Cape Town), Pietermaritzburg and Durban surrounds over several years has revealed only three plants bearing sori. *Diplazium esculentum* has an erect rhizome that can become rather trunk-like (up to 1 m tall) in older plants, for which feature it is grown as an ornamental. It is distinguished by its broad, arcuate 2-pinnate fronds of up to 2 m long, with veins that unite along the costae below the sinuses. The scales on the stipe bases and rhizomes have black margins and forked teeth (Hoshizaki & Moran 2001; Olsen & Olsen 2007).

Until recently, invasion by *Diplazium esculentum* was known only from several sites in the greater Durban region, where it seems to have escaped from gardens and established along watercourses. Once colonies are established, erosive flooding events disperse root buds and plantlets which establish downstream. More recently, the vegetable fern has been found naturalized both in Pietermaritzburg and in Zululand (Figure 18), indicating that it is an emerging alien invader. Urgent attention should be directed towards its eradication.

***Diplazium esculentum* (Retz.) Sw.** in Journal für die Botanik 1801,2: 312 (1803). *Hemionitis esculenta* Retz.: 38 (1791). Type: 'Habitat in India orientali', J.G. König s.n. (LD, holo.).

For a complete list of synonyms see Roux (2009).

Rhizome erect, often forming a slender black trunk 0.3(–1) m tall; scaled at apex, rhizome scales $\pm$ 10 mm

long, dark brown, margins finely toothed, apex long-acuminate; forms clonal colonies by vegetative increase from root buds. **Fronds** 1–2 $\times$ 0.5–1 m, erect to arching; stipe black and scaly at base, paler above; lamina 2- to 3-pinnate, 0.5–1.5 $\times$ 0.5–1 m, dark green; pinnules variable in size, $\pm$ 50–80 $\times$ 15–25 mm, subsessile, margins very shallowly lobed, lobes toothed, basal lobes longer than the rest, glabrous abaxially; veins simple or forked, lowest 3–5 pairs of adjacent vein groups anastomosing. **Sori** spreading along most veins; indusium thin, dark brown, margins becoming uneven with age (Jones 1998).

Specimens examined

KWAZULU-NATAL.—2930 (Pietermaritzburg): KwaZulu-Natal National Botanical Garden, naturalized in sandbank in seasonally flooded river running through the garden, highly disturbed site, (–CB), 03-09-2008, N.R. Crouch 1173 (PRE); Krantzklouf Nature Reserve, Kloof, colony growing in semi-shade to full sun immediately above The Splash on the lower Molweni River, 215 m, (–DD), 28-04-2009, N.R. Crouch 1242 (PRE); Pinetown, Sarnia, along banks of Umbilo River, plants form large stands on streambank, (–DD), 24-06-2001, J.P. Roux 3137 (NBG); Durban, on banks of Umhlatuzana River as it passes next to Old Mill, adjacent to Coedmore Road, Yellowwood Park, 40 m, (–DD), 12-05-2009, N.R. Crouch 1245 (NH, PRE). 2831 (Nkandla): footslope of Ongoye Mountains, rocky area among homesteads, (–DC), 2006, N.F. Magagula 1 (ZULU).

ACKNOWLEDGEMENTS

We would like to thank Dr Barbara Parris of the Fern Research Foundation, New Zealand, for valuable discussions and input regarding the identity of *Doodia* in South Africa; Keeper of the Herbarium, Royal Botanic Gardens, Kew, for granting access to the type specimen of *D. squarrosa*; Ms Olwen Grace, Kew, for facilitation; the Curators of NBG, NH, NU and PRE for use of specimens; Ms H. Snyman and Ms E. Fouché of PRE for producing the distribution maps. Dr Stefan Siebert is thanked for providing specimen data for the Zululand collection of *D. esculentum*.

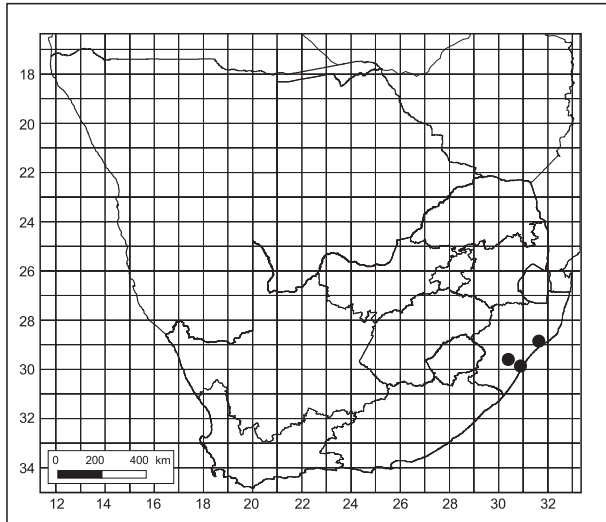


FIGURE 18.—Distribution in FSA region of *Diplazium esculentum*, ●.

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MS. received: 2009-06-03.

HYACINTHACEAE

DRIMIA COOPERI IN KWAZULU-NATAL, AND THE ETHNOMEDICINAL TRADE

Drimia cooperi (Baker) Baker is currently regarded as being restricted to the Eastern Cape Province (Jessop 1977; Manning & Goldblatt 2006). Within this province, Jessop (1977) recorded it from only the Stutterheim and Butterworth Districts, but more recent collections (Bester 1529 NH) extend its known range northwards to Maclear (Figure 19).

Following the appearance of bulbs of an unknown member of the Hyacinthaceae in late 2004 in the Warwick Triangle medicinal market in Durban, plants purchased were grown on to flowering and subsequently identified as *D. cooperi*. This collection of market-traded material (N.R. Crouch 1038 NH) was sold under the isZulu name *umahlukoloza*, and noted by the trader to have been harvested in the Eastern Cape, although further details on the locality were not forthcoming.

The bulbs of this species are distinguished from other Hyacinthaceae in trade on the basis of a combination of characters: their medium size (± 50 mm diameter), flesh-pink to salmon-orange colour, and loosely arranged scales (Figure 20A). The bulb scales are not thickly succulent and brittle, but rather of a tough fibrous yet semi-succulent nature. Among other Hyacinthaceae in trade in KwaZulu-Natal, the fibrous character of the bulb best approximates that of *Drimia altissima* (L.f.) Ker Gawl., although the tough scales are tightly packed in this latter species. Notably, the vernacular name *umahlukoloza* is also applied in Durban to *D. altissima* (N.R. Crouch 792 NH). We have since observed *D. cooperi* in the Warwick Triangle market on two further occasions during infrequent visits, suggesting that this taxon is more numerous and possibly more widely distributed than indicated by herbarium vouchers. Its Red List assessment, based

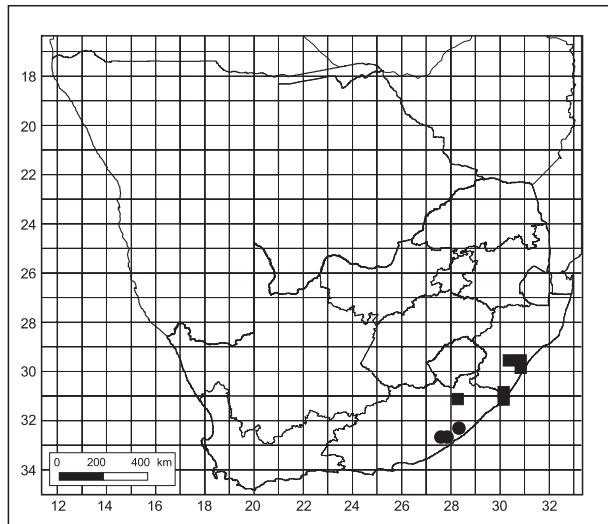


FIGURE 19.—Known distribution of *Drimia cooperi*, according to Jessop (1977), ●, with additional localities, ■, following a reassessment of herbarium materials.

on 2001 IUCN Red List criteria, is currently VU A2ad; C2a(i) (Williams & Crouch 2009). The rationale for this Vulnerable assessment is that the species is estimated to have experienced a decline of more than 30 % during the last 30 years, attributed to land transformation and medicinal plant harvesting. The extant subpopulations are fragmented and suspected to occur in fewer than 10 locations. Furthermore, the population size is estimated to be less than 10 000 mature individuals, and the number of mature individuals that have been recorded in a subpopulation is less than 100 (Williams & Crouch 2009).

In flower, *Drimia cooperi* produces inflorescences up to 600 mm tall, with flowers presented on pedicels no longer than 4 mm (Figure 20B). The perianths are shorter than 6 mm long. Plants bear 2–4 sublinear leaves, each up to 270 mm long and 13 mm broad. The species was considered by Jessop (1977) to occupy rather an isolated position in the genus, although it shows similarities in floral characteristics to *D. anomala* (Baker), another species with its primary distribution in the Eastern Cape, though typically in more arid situations. *Drimia anomala* is separated by its rigid, terete leaves, which are usually produced singly each season (Dyer 1951) and its shorter bracts up to 1 mm long, and longer pedicels, up to 13 mm (Jessop 1977). Although *D. delagoensis* (Baker) Jessop is keyed out by Jessop alongside *D. cooperi*, their distribution ranges do not overlap. *D. delagoensis* possesses predominantly epigeal bulbs of an olive-green and silvery brown colour, the scales of which are somewhat more succulent, and brittle rather than fibrous. The leaves are narrower too, thicker, and strongly channelled on the dorsal surface.

Subsequent examination of herbarium specimens at NH has revealed a flowering voucher (W.J. Lawson 584 NH) documenting the presence of *Drimia cooperi* in KwaZulu-Natal for more than half a century. Jessop, in revising *Drimia* and allied genera, evidently did not utilize NH collections and accordingly missed the significant collection by Lawson. Further NH accessions misidentified as *Urginea kniphofioides* Baker are here assigned to *D. cooperi*. Subsequent to Lawson's

gathering, an imperfect collection was made (E.J. Moll 1869 PRE) during August 1965 on the fringes of what was then the Oribi aerodrome in Pietermaritzburg. As only plants in bud were found and collected by Moll, this would account for reticence on the part of Jessop to identify this specimen as *D. cooperi*, thereby reflecting a significant range extension for the species.

A recent field trip (October 2008) to Pietermaritzburg surrounds to revisit the perimeter of Oribi Airport has revealed that this species is still to be found in grassland bordering the cordoned off area. The species is also extant within the Hesketh Conservation Area adjacent to the old Roy Hesketh racetrack in Hayfields, a 65 hectare site of grassland and savanna that since 1995 has been afforded some protection by the local municipality. At both sites, plants grow in shallow clay soils overlying Lower Ecca Shale in vegetation corresponding to Ngongoni Veld (Svs 4) (Rutherford *et al.* 2006). The hypogeal bulbs develop a 20–30 mm long neck that protrudes above the soil surface. Residual fibrous leaf bases persist to provide the bulb apex with protection from flames, and necks were observed to be intact following veld fires that occurred approximately one month prior to the site visits. Although flowering was observed on these occasions, the extent to which fire stimulates this process is presently unknown. The linear leaves of *D. cooperi* are partly synanthous, with a single inflorescence produced per bulb, and within a single subpopulation at Oribi in Pietermaritzburg, two floral colour forms are evident: tepal segments are either cream-coloured with green central stripes, or salmon-brown with brown stripes. Geophytes associated with *D. cooperi* at Oribi include *Cyrtanthus breviflorus* and *C. contractus* (Amaryllidaceae), *Ledebouria ovatifolia*, *Albuca virens*, and *Schizocarpus nervosus* (Hyacinthaceae). At the Hesketh site, *Albuca* sp. cf. *pachychlamys* Baker grows alongside *D. cooperi*. Small bulb clumps of up to six plants occur, indicating limited vegetative reproductive capacity.

Additional records from the Umtamvuna Nature Reserve in southern KwaZulu-Natal document the occurrence of *Drimia cooperi* in the intervening part of its range (Figure 19), and show that it occurs within at least this formally protected area.

Our investigation has revealed that plants growing in Pietermaritzburg, and those reputedly harvested in the Eastern Cape, differ in several respects from the ones described by Jessop (1977). Whereas Jessop (1977) described the bulb scales as more or less firmly arranged, we observed the scales to be loosely attached (Figure 20A), although we do not dismiss the possibility that this is turgor-related. Such is their looseness that *Drimia cooperi* bulbs readily disintegrate if cut tangentially in the course of preparing herbarium specimens. This phenomenon would account for the scale-depleted bulb specimen (H.G. Flanagan 1302 PRE), essentially the central core, that seemingly informed Jessop of bulb shape and dimensions. Given the difficulty of pressing these organs, most sheets of this species lack well-preserved bulbs. The largest field bulb measured 80 × 75 mm (excl. neck), as opposed to the length range of 25–50 mm recorded earlier (Jessop 1977). Such non-representative herbarium bulb vouchers and associated artifactual information (Baker 1897) were earlier noted by



FIGURE 20.—*Drimia cooperi*, N.R. Crouch 1180 (NH): A, bulb; B, median portion of inflorescence. Photographs: N.R. Crouch.

Dyer (1942) for *D. delagoensis*. As indicated above, the scales of *D. cooperi* were uniformly dark salmon-orange or flesh-coloured, rather than 'more or less white' as indicated by Jessop—a likely artifact of the preservation process. Perianth segments in the field were observed to spread, as anticipated by Jessop (1977), with margins distinctly rolled under (Figure 20B). The stability of this margin character has not been ascertained. Consideration of the holotype of *Urginea echinostachya* Baker has revealed this to be conspecific with *D. cooperi* rather than with *D. macrocentra* (Baker) Jessop as concluded by Jessop (1977). The type of *Urginea echinostachya* is of a plant with a peduncle substantially less stout at the base (± 4.5 mm diameter) than that of *D. macrocentra* (± 25 mm diameter). The raceme of the *U. echinostachya* type is less dense and the flowers have shorter perianths.

***Drimia cooperi* (Baker) Baker** in *Flora capensis* 6: 443 (1897). *Ornithogalum cooperi* Baker: 284 (1873). Type: Cape [Eastern Cape], 'ad oram orientalis', Barber s.n. (TCD, lecto., designated by Jessop: 287 (1977); –K, photo!).

Urginea echinostachya Baker (1897), syn. nov. Type: Natal [KwaZulu-Natal], Inanda, J.M. Wood 276 (K, holo.!; NH, iso.!).

Additional specimens examined

KWAZULU-NATAL.—2930 (Pietermaritzburg): Oribi, Pietermaritzburg, (–CB), 25-09-1957, W.J. Lawson 584 (NH); Oribi aerodrome, Pietermaritzburg, grassland, 730 m, (–CB), 17-08-1965, E.J. Moll 1869 (PRE); Hesketh Conservation Area, top of Hayfields, Pietermaritzburg.

To west of old Hesketh racing track, 700 m, S 29° 36' 59.68", E 30° 25' 30.73", (–CB), 12-10-2008, N.R. Crouch 1179 (NH); grassland adjacent to Oribi Airport alongside railway line near Oribi Village, Pietermaritzburg, 710 m, S 29° 38' 36.64", E 30° 24' 7.57", (–CB), 12-10-2008, N.R. Crouch 1180 (NH); Inanda, (–DB), October, J.M. Wood 276 (NH); New Germany, mountain ridge, along M19, ± 700 m from Otto Volek Drive towards Blair Atholl, 300 m, (–DD), 17-09-1998, Y. Singh 402 (NH). 3030 (Port Shepstone): Umtamvuna Forestry Reserve, grassveld, (–CC), 22-09-1966, R.G. Strey 6967 (NH). 3130 (Port Edward): Umtamvuna Nature Reserve, Pont Outpost, grassland, (–AA), 11-09-1983, A. Abbott 1313 (NH), 300 m, (–AA), 01-09-1994, A. Abbott 6268 (NH, PRE); Umtamvuna Nature Reserve, Clearwater, grassland, 240 m, (–AA), 14-08-1985, A. Abbott 2704 (NH). Without locality: purchased at Warwick Triangle medicinal plant market, Durban, 01-12-2004, N.R. Crouch 1038 (NH); 23-01-2008, V.J. Brueton 33 (J).

EASTERN CAPE.—3128 (Umtata): Maclear, Farm Sunny Slopes, 1 300 m, S 31° 6' 54", E 28° 24' 29", (–AB), 06-11-93, S.P. Bester 1529 (NH). 3227 (Stutterheim): near Komgha, grassy hills, 605 m, (–DB), December 1892, H.G. Flanagan 1302 (PRE).

ACKNOWLEDGEMENTS

The Curators of BOL, GRA, J, NBG, NH, NU, PRE and SAM kindly facilitated use of their collections. The staff of the Mary Gunn Library facilitated access to literature, and Dr H.F. Glen is thanked for helpful discussions.

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PASSIFLORACEAE

FIRST DESCRIPTION OF FEMALE FLOWERS OF THE DIOECIOUS *ADENIA FRUTICOSA* SUBSP. *TRIFOLIOLATA*

The genus *Adenia* Forssk., with ± 100 Old World species, occurs particularly in tropical and subtropical regions of Africa, Madagascar, Southeast Asia, Malaysia and northern Australia (Feuillet & MacDougal 2007). A significant number of the African taxa are also associated with very arid regions (e.g. Somalia and Namibia) (see Van Wyk & Smith 2001: 157, 158 on the Afro-arid corridor that links northern Namibia to the Horn of Africa). Ten species occur in southern Africa; most are dioecious, with monoecy or polygamy rare (Archer 2000; Feuillet & MacDougal 2007).

Subsequent to publication of the typical subspecies of *Adenia fruticosa* Burt Davy, sect. *Microblepharis* (Wight & Arn.) Engl. (Burt Davy 1926), based only on male material, Liebenberg (1939) described the female flowers. The revision of South African adenias by him accommodated a broad concept for *A. fruticosa*, upheld until two further subspecies were distinguished by De Wilde (1971). For the delimitation of *A. fruticosa* Burt Davy subsp. *simplicifolia* De Wilde, herbarium material of both male and female flowers were available to its author. However, this was not the case for *A. fruticosa* Burt Davy subsp. *trifoliolata* De Wilde, for which female flowers and fruit were reportedly not seen. De Wilde (1971), nevertheless distinguished this KwaZulu-Natal endemic based on vegetative and male floral characters, and provided a key to this end, which was later reproduced (De Wilde 1976) in slightly modified form. Information on fruits was additionally documented for the *Flora of southern Africa* account (De Wilde 1976), but not of female flowers, which were unavailable at the time. We have been unable to trace the existence of any historical vouchers representing female flowers.

During a field trip to Ulundi in Zululand in August 2008, both male and female plants of this narrowly distributed KwaZulu-Natal endemic were encountered in full and synchronous bloom; as is usual with woody dioecious taxa, female plants were far less prevalent than males in the subpopulation. A female voucher and further male herbarium specimens were gathered, enabling illus-

tration (Figure 21) and completion of the description for *Adenia fruticosa* subsp. *trifoliolata*, including an amplified circumscription of the male element. Female floral characters (Table 3) confirm the distinctions recognized by De Wilde (1971), for flowers of subsp. *trifoliolata* open substantially wider than those of other subspecies, based in part on their somewhat longer sepals. Newly acquired data have enabled the construction of a key for female plants of the three allopatric subspecies, all of which occur within the FSA region (Figure 22). *Adenia fruticosa* subsp. *simplicifolia* occurs also in southern and eastern Zimbabwe and neighbouring Mozambique (De Wilde 1971, 2002). The subspecific epithets of two of the three taxa are misnomers: subsp. *simplicifolia* is not always simple-leaved, and subsp. *trifoliolata* may be 5-foliolate. Accordingly, leaf characters are not deemed particularly useful when identifying material.

Field observations have revealed that flowering of both male and female plants of subsp. *trifoliolata* extends, intermittently, from August to December, with fruiting occurring from September onwards.

Key for ♂ plants (from De Wilde 1976)

- 1a Leaves 3–5-foliolate; petiolule of leaflets 2–5(–7) mm; anthers ± 3.0 mm subsp. *fruticosa*
- 1b Leaves simple or 3(or 4)-foliolate; leaflets sessile; anthers 4.0–5.5 mm:
- 2a Hypanthium broadly cup-shaped, ± 5-saccate, corona hairs 0.5–1.0 mm; disc-glands foliolate subsp. *simplicifolia*
- 2b Hypanthium cup-shaped, tapering, not saccate; corona hairs up to 0.5 mm, or partly absent; disc-glands absent subsp. *trifoliolata*

Key for ♀ plants

- 1a Flowers opening to 12–14 mm; stipe 1.5 mm ... subsp. *trifoliolata*
- 1b Flowers opening to 6–7 mm; stipe up to 1 mm:
- 2a Leaves 3–5-foliolate; petiolule of leaflets 2–5(–7) mm; disc-glands absent; staminodes 3–4 mm subsp. *fruticosa*
- 2b Leaves simple or 3-foliolate; leaflets sessile; disc-glands 0.2–0.5 mm; staminodes 2–2.5 mm subsp. *simplicifolia*



FIGURE 21.—*Adenia fruticosa* subsp. *trifoliolata*. A, habit; B, leaf; C, ♂ flower (large form); D, ♂ flower (small form); E, ♂ half-flower diagram; F, petal: reduced lamina with awn; G, connective of ♂ flower (arrowed); H, ♀ inflorescence with leaves; I, ♀ inflorescence structure; J, ♀ flower; K, ♀ half-flower diagram; L, ovule; M, mature fruit. Scale bars: A, M, 10 mm; B–E, H–J, 5 mm; F, G, 2 mm; K, 1 mm; L, 0.2 mm. Artist: Angela Beaumont.

TABLE 3.—Morphological comparison of female flowers of *Adenia fruticosa* subspecies

Character	subsp. <i>fruticosa</i> (De Wilde 1976)	subsp. <i>simplicifolia</i> (De Wilde 1976)	subsp. <i>trifoliolata</i>
Stipe length (mm)	0.5–1.0	0.5–0.75	1.5
Flower opening to (mm)	7	6	12–14
Sepal length (mm)	5–7	5–6	6.0–8.5
Petal length (mm)	3–4	3–4	3–4
Staminode length (mm)	3–4	2.0–2.5	2.25
Staminodes connate for (mm)	1–2	1	1.8
Corona hair length (mm)	0.2	0.5	0.35
Disc glands (mm)	absent	0.2–0.5	0.3
Pistil length (mm)	6.5–8.0	5.0–6.5	8
Gynophore length (mm)	2–3	1.5–2	2
Ovary (mm)	3–4 × 3.0–3.5	1.5–3 × 1.5–2.5	3.75 × 3
Styles connate for (mm)	0.7	0.5–0.7	1
Style arms (mm)	0.5–0.7	0.5–1.0	0.5–1.0
Stigma diameter (mm)	± 1	± 1.5	± 1.6

The following descriptions and general notes for floral characters have been based on Ulundi material.

Description of female flowers

Stipe 1.5 mm long, shorter than in male flowers, articulation not clear; bract at base of stipe heart-shaped with tiny gland at base of lamina, 1 mm long; bracteoles 2, at apex of stipe, triangular, 0.5 mm long. *Hypanthium* cup-shaped, base broadly cuneate to rounded, 2.5–3.0 mm from top of stipe to bases of sepals, 2.8–3.8 mm wide. *Sepals* 5, arrangement quincuncial; innermost 2 sepals oblong, 7.5–8.0 × 2.5–3.0 mm, midvein and immediate parallel, secondary, lateral veins somewhat thicker than rest of lamina, altogether forming a triangular thickened middle region, broadest at sepal base or sinus, narrowest at sepal apex, lamina without ornamentation except at region level with and immediately adjacent to apex of corona bearing some minute fimbriate processes; margins slightly erose or sinuous, or entire basally, erose distally; apex acute, with pronounced beak-like, recurved extension; outermost 3 sepals oblong to slightly oblong-elliptic, 6.0–8.5 × 2.5–3.0 mm, midvein thicker than lateral and immediate parallel, secondary, lateral veins, midvein and immediate secondary veins altogether less thickened than in inner sepals, lamina without ornamentation except at region level with and immediately adjacent to apex of corona bearing some minute fimbriate processes, margins entire basally, slightly sinuous to entire distally. *Disc-glands* minute, 0.3 mm wide, at bases of sepals, level with base of fused part of gynophore-staminode structure. *Petals* 5, shorter than sepals, inserted in sinuses of sepals, linear-lanceolate, 4.5–5.0 × 0.5–0.8 mm, 1–3-nerved; margins entire basally, erose to slightly sinuous distally; base truncate; apex acuminate. *Androecium* of 5 staminodes, bases fused into a tube around gynophore, free parts of staminodes 2.25 mm long; bases broad, 2 mm wide; apex minute with tiny, incurved tip representing vestigial anther. *Corona* comprising ring of 5 vertical connectives, each one between base of petal and inter-staminodal part of androecial column, connectives 0.5 mm long, 0.5 mm wide, (when viewed from above), edges fimbriate. *Gynoecium*: pistil 8 mm long from base of free gynophore to top of stigmatic arms; gynophore 3 mm long from base of fused part with androecial col-

umn to base of ovary, free part of gynophore 1.5 mm long; ovary 3.5 mm from base of gynophore to bases of styles, 3 mm diam.; placentation parietal, placentas 3; ovules usually 6 per ovary, 2 per placenta, 0.5 mm long, anatropous, with prominent ridge along length and beak-like apex, funiculus somewhat expanded; styles 3, connate for 0.5 mm, stylar arms 0.7–1.0 mm long, each stylar arm split in 2; stigmas 3, vertical (i.e. parallel with long axis of flower), each connecting the two split stylar arms of each of 3 styles, 1.50 × 1.75 mm, surface papillose, edges lacinate-papillose. *Fruit* subglobose to broadly turbinate, 16.5 × 15 mm, with persistent remnants of perianth. *Seeds* (immature) with pitted testa and swollen funiculus next to base of seed. Figure 21H–M.

Description of male flowers

Hypanthium base to articulation, 1–3 mm long. *Pedicel* 2–7 mm long, 1 or 2 buds along pedicel, buds each with bract and bracteoles, bracts of buds minute, 1.0–1.8 mm long, leaf-like; bracteoles of buds 2, 1 mm long, triangular margins irregular, articulation between base of hypanthium and pedicel distinct; fused portion of bases of sepal lobes cup-shaped in outline, base broadly cuneate to rounded, 2.5–3.5 mm deep (i.e. from point of divergence of sepal lobes to apex of hypanthium), 4.2–6.5 mm wide. *Sepals* quincuncial arrangement, inner 2 sepals oblong, 9.0–12.8 × 3.0–4.8 mm, midveins prominently thickened into a broad-based triangle, narrowing towards apex, margins entire or minutely wavy basally, minutely erose to unevenly serrate distally, apex acute to rounded, tip incurved, beak-like with fimbriae; outer 3 sepals oblong, 10–13 mm × 3.0–4.8 mm, midveins slightly thickened, margins entire to very slightly sinuous throughout, apex acute to rounded. *Petals* usually 5, shorter than sepals, inserted in sinuses of sepal lobes, development variable, linear-lanceolate, 5.0–8.8 × 0.7–2.3 mm; margins slightly serrate to entire basally, erose to unevenly serrate distally; tips acuminate; lamina sometimes partly reduced with awn-like extension of midvein, or lamina absent and petal represented by awn-like structure alone. *Stamens* 5, opposite sepal lobes; filaments broadly triangular, 2.5–4.5 × 0.5–1.0 mm, anther attachment sub-basal; anthers oblong, 3.0–5.0 × 0.5–1.8 mm, bi-theate, dehiscence introrse, pollen yellow. *Corona* connecting bases of petals to bases of filaments,

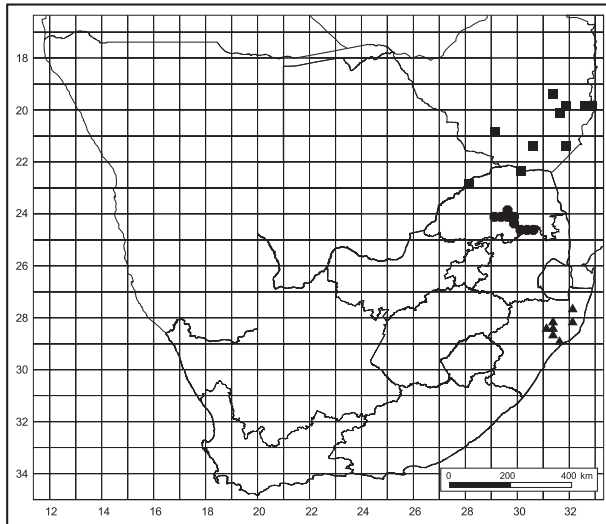


FIGURE 22.—Known distribution of *Adenia fruticosa* based on specimens at NH, NU and PRE and those cited by De Wilde (1971): subsp. *fruticosa*, ●; subsp. *trifoliolata*, ▲; subsp. *simplicifolia*, ■.

outermost (visible) tips of connectives of corona up to 0.5 mm wide, minutely fimbriate, some fimbriae also arising from the inner surfaces of the sepals immediately adjacent to, and level with the tips of the corona arms; pistillode vestigial, up to 1 mm long. Figure 21A–G.

Male flowers produced synchronously on single plants were dimorphic in respect of overall flower size (Figure 21C, D) and variable petal development as described currently. De Wilde (1971) noted that considerable infraspecific variation in both the size of flowers, and their components, is known for *Adenia*. Whereas Liebenberg (1939) related various abnormalities and variations in the flowers of several South African genus members, he did not document male flower dimorphism in *Adenia fruticosa*.

Specimens examined

KWAZULU-NATAL.—2831 (Nkandla): Ondini Historic Reserve, Ulundi, male plant, 513 m, S 28° 18.765', E 31° 27.407', (–AD), 17-08-2008, J. van Vuuren 1 (NH); Ondini Historic Reserve, Ulundi, female plant, 515 m, S 28° 18.783', E 31° 27.402', (–AD), 17-08-2008, J. van Vuuren 2 (NH).

ACKNOWLEDGEMENTS

James van Vuuren of Ulundi kindly brought the existence of a subpopulation of *Adenia fruticosa* subsp. *trifoliolata* to our attention. He subsequently collected voucher material of both sexes, and made observations on the phenology. The use in part of PRECIS data is gratefully acknowledged, kindly supported by Mrs H. Snyman. The staff of the Mary Gunn Library at the National Herbarium in Pretoria generously assisted with sourcing literature.

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MS. received: 2009-06-05.

PTERIDOPHYTA

CHEILANTHES PERRIERI J.P.ROUX, NOM. NOV. (PTERIDACEAE), CORRECTING A NOMENCLATURAL ERROR

In the *Synopsis of the Lycopodiophyta and Pteridophyta of Africa, Madagascar and neighbouring islands* (Roux 2009), I proposed a new combination—*Cheilanthes lanceolata* (Bonap.) J.P.Roux, and a new name *Cheilanthes perrieri* J.P.Roux. Both these names are based on *Notholaena lanceolata* Bonap. and therefore on the same type. According to the Code (McNeill et al. 2006: Art. 34.2) both these names are not validly published.

To correct this oversight and to validate the new name in *Cheilanthes*, it is here proposed anew.

***Cheilanthes perrieri* J.P.Roux**, nom. nov. for *Notholaena lanceolata* Bonap., non *Cheilanthes lanceolata* C.Ch. (1913: 334).

Notholaena lanceolata Bonap. in Notes Ptéridologiques 5: 65, 66 (10 Dec. 1917). Type: Madagascar. 'Région floristique de l'Ouest. Bassin de Monjoky, Menomatz. Grès du trias; bois secs. Septembre 1911', H. Perrier de la Bâthie 7886 (P00466499, holo.).

N. *madagascariensis* Bonap.: 66–68 (10 Dec. 1917). Type: Madagascar. 'Région floristique de l'Ouest. Cime du mont Ambatomainty ou Ambatomahay; sur la Sofia. Rochers dénudés et très secs. Gneiss. Août 1905', H. Perrier de la Bâthie 7727 (P00466500, holo.; P00466464, P00466463!, iso.).

N. lanceolata Bonap. var. *madagascariensis* (Bonap.) Tardieu: 135 (May 1958).

Acrostichum squamosum sensu Hook.: 411 (Apr. 1868), p.p.

Cheilanthes lanceolata (Bonap.) J.P.Roux: 183 (17 Mar. 2009), nom. non rite public. (McNeill *et al.* 2006: Art. 34.2).

Cheilanthes perrieri J.P.Roux: 184 (17 Mar. 2009), nom. non rite public. (McNeill *et al.* 2006: Art. 34.2).

ACKNOWLEDGEMENT

My thanks to Katherine Challis, IPNI Editor, for pointing this blunder out to me.

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MS. received: 2009-08-20.

PTERIDOPHYTA

RANGE EXTENSION RECORDS FROM THE SOUTHERN DRakensBERG, EASTERN CAPE, SOUTH AFRICA

The southern-most parts of the Drakensberg Mountains extend into the central to northern areas of the Eastern Cape Province. Most of the botanical exploration of this region is concentrated along the main roads. Up until 1993, a mere 1 900 specimens were collected in the area (Bester 1998). It is therefore not surprising that botanical surveys of this area will lead to new distribution records.

A study with its primary aim to obtain a basic knowledge on the vegetation of the Maclear-Elliot districts was conducted in the early 1990s (Bester 1998). During this study the area was properly surveyed and more than 3 600 specimens collected. These include new distribution records for *Elaphoglossum spathulatum* (Bory) T.Moore var. *spathulatum* (Dryopteridaceae) and *Isoetes transvaalensis* Jermy & Schelpe (Isoetaceae) in the area, which are reported here.

Elaphoglossum spathulatum is distinguished from other *Elaphoglossum* species in the region by its small, strongly dimorphic fronds that are covered with pale brown scales on both surfaces. The spatulate lamina of the sterile fronds is 11–45 × 4–9 mm, whereas the fertile lamina is 6–23 × 6–9 mm. Another distinguishing feature is that the fertile fronds are folded along the midrib (Burrows 1990).

This fern has a restricted habitat preference and grows mostly on moss-covered boulders adjacent to fast-flowing mountain streams in deeply shaded evergreen forests. Because of effective vegetative reproduction by the creeping rhizomes, it can become locally abundant, forming mats over suitable rocks. It has a rather wide distribution from the KwaZulu-Natal Drakensberg to as far north as Tanzania and the Democratic Republic of the Congo, as well as Réunion, Madagascar and tropical America (Jacobsen 1983; Burrows 1990; Roux 2001, 2009). Until now it has not been formally recorded for the Eastern

Cape and the collection in the Ugie area represents the southern-most record for this species (Figure 23).

EASTERN CAPE.—3128 (Umtata): Farm Wildebeest. ± 20 km W of Ugie, edge of small stream, (–AA), Bester 2591 (NH, PRE!, PRU!).

Isoetes species (quillworts) are notoriously difficult to recognize in the field, because of their grass- or sedge-like appearance, and they are similarly problematic to distinguish from one another. Spore ornamentation is very useful in identifying quillworts, but a good microscope is needed. The spores of *I. transvaalensis* are black when wet and almost smooth, but can be variably tuberculate. Another distinguishing character, which is also hard to see, is the fan-shaped ligule above the sporangia at the base of the leaf (Burrows 1990).

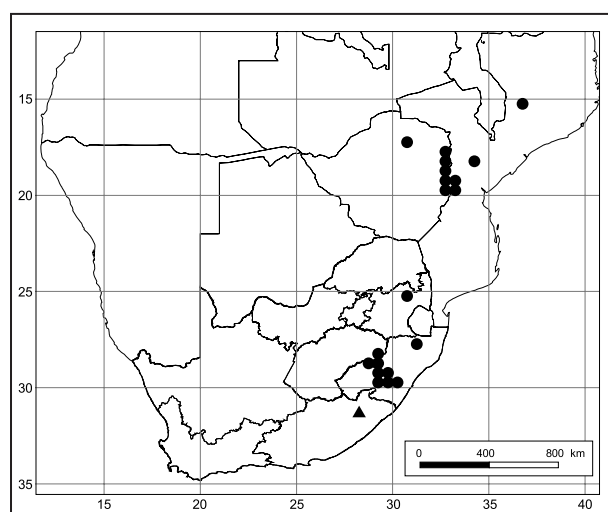


FIGURE 23.—Distribution of *Elaphoglossum spathulatum* var. *spathulatum* in southern Africa, adapted from Burrows (1990), with kind permission of the author, ●; new locality in the Eastern Cape, ▲.

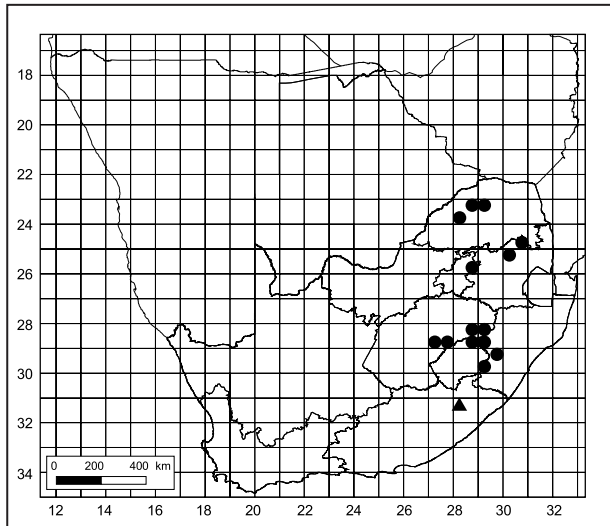


FIGURE 24.—Distribution of *Isoetes transvaalensis*, based on specimens at PRE, NBG and BOL, and cited in Burrows (1990), used with kind permission of the author, ●; new record in the Eastern Cape, ▲.

Isoetes transvaalensis grows submerged in shallow pools that dry out in winter (April–October). It is generally found on Clarens sandstone in mid-high altitude montane grassland. The species is rather widely distributed in South Africa, occurring from the Limpopo Province and Mpumalanga to the eastern Free State and southwestern KwaZulu-Natal, as well as in Lesotho (Schelpe & Anthony 1986; Burrows 1990; Roux 2001, 2009). The collection reported here from the Ugie area is the southern-most record for this species and the first for the Eastern Cape (Figure 24).

EASTERN CAPE.—3128 (Umtata): Gatberg, Farm Odairn, ± 21 km SW from Ugie, (–AC), Bester 2430 (PRU!).

ACKNOWLEDGEMENTS

Mr John Burrows is thanked for giving permission to use the distribution maps of these species from his book *Southern African ferns and fern allies* (1990); Ms Hester Steyn, National Herbarium, SANBI, Pretoria, for producing the distribution maps; Ms Magda Nel, H.G.W.J. Schweickerdt Herbarium, University of Pretoria, for providing access to the relevant specimens held at PRU.

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MS. received: 2009-04-08.

FABACEAE

PEARSONIA MBABANENSIS, AN OVERLOOKED SYNONYM OF *P. SESSILIFOLIA* SUBSP. *MARGINATA* (TRIBE CROTALARIEAE)

During the databasing of the Fabaceae collection at the Compton Herbarium, the type of *Pearsonia mbabanensis* Compton [holotype: Dlamini s.n. (NBG)] was brought to my attention. This species was described by Compton (1967) during his botanical survey of Swaziland. Polhill (1974) was clearly unaware of the description of *Pearsonia mbabanensis* in his revision of the genus *Pearsonia* Dümmer, but cited a Compton specimen of this species (Compton 25203) under *P. sessilifolia* (Harv.) Dümmer subsp. *marginata* (Schinz) Polhill. Recent checklists of the southern African flora also make no mention of *P. mbabanensis* (Arnold & De Wet 1993; Retief & Herman 1997; Nkonki 2003; Germishuizen 2006; Klopper *et al.* 2006). *P. sessilifolia* is an extremely variable species which currently includes four subspecies (Polhill 1974). Seven out of the nine species that Compton (1976) listed in his treatment of *Pearsonia* for the *Flora of Swaziland* have since been reduced to the synonymy of the subspecies of *P. sessilifolia* (Polhill 1974). *P. mbabanensis* represents another such case as it clearly falls within the current circumscription of *P.*

sessilifolia subsp. *marginata*. The synonymy is formalized below:

***Pearsonia sessilifolia* (Harv.) Dümmer subsp. *marginata* (Schinz) Polhill** in Kew Bulletin 29: 402 (1974). *Lotononis marginata* Schinz: 31 (1899). Type: South Africa, [Mpumalanga], near Barberton, Galpin 960 (Z, holo.–photo.!, BOL!, PRE!, K, NH–photo.!).

P. mbabanensis Compton: 296 (1967); Compton: 251 (1976), syn. nov. Type: Swaziland, Mbabane Dist., near Poliniane River, Dlamini s.n. (NBG, holo.!).

ACKNOWLEDGEMENTS

This work forms part of a Post-Doctoral Fellowship at the Compton Herbarium and the University of Cape Town. The Parker family (Elandsberg Nature Reserve) is gratefully acknowledged for providing funding for the Fellowship. Mrs Marilyn Constable is thanked for bringing the type of *Pearsonia mbabanensis* to my attention.

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MS. received: 2009-09-17.

PTERIDOPHYTA

THE CORRECT AUTHOR CITATION FOR *CHEILANTHES MARLOTHII* (SINOPTERIDACEAE)

Since Schelpe (1969) transferred *Notholaena marlothii* Hieron. to *Cheilanthes*, authors have consistently given the authority for this species as *Cheilanthes marlothii* (Hieron.) Schelpe (Jacobsen 1983; Burrows 1990; Roux 2001, 2006, 2009). Although listed by Christensen (1917), the earlier combination made by Domin in 1915 has been overlooked. The correct citation for this species native to Angola, Namibia and South Africa is therefore *Cheilanthes marlothii* (Hieron.) Domin in *Bibliotheca Botanica* 20,85,2: 133 (Jan. 1915).

A further combination relevant to southern African ferns was made in the same publication—*Cheilanthes buehneri* (Baker) Domin [*Bibliotheca Botanica* 20,85,2: 133 (Jan. 1915)], based on *Notholaena buehneri* Baker. This taxon, however, is generally treated as *Cheilanthes inaequalis* (Kunze) Mett. var. *buehneri* (Baker) Schelpe (Schelpe 1967).

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MS. received: 2009-11-25.

SCROPHULARIACEAE

TWO NEW SPECIES OF LIMOSELLEAE FROM WESTERN SOUTH AFRICA: *TRIEENIA OCCULTA* AND *ZALUZIANSKYA REGALIS*

The tribe Manuleeae Benth. is a common and characteristic element of the Cape flora, and has been comprehensively revised by Hilliard (1994). Since then the circumscription of the tribe has been substantially expanded to include both the tribe Selagineae Horan. (Kornhall *et al.* 2001) and the genus *Limosella* L. (Kornhall & Bremer 2004). The group, now known as tribe Limoselleae Dumort. and comprising ± 635 species in 29 genera, remains almost entirely southern African in distribution.

Here we describe a new species each of *Trieenia* and *Zaluzianskya* from recent collections in the Western and Northern Cape. We searched BOL, NBG and SAM (herbarium acronyms after Holmgren *et al.* 1990), the main herbaria with good representation of collections of Cape species, for additional records of the two new species, with little success. This is not surprising as these herbaria were all consulted by Hilliard for her revision of the group (Hilliard 1994). The single additional collection of *Z. regalis* that we located at NBG (Oliver 9609)

was at that time in the Stellenbosch Herbarium (STE), which amalgamated with NBG in 1996, and was not consulted by Hilliard.

1. *Trienia* Hilliard is a small genus of nine species endemic to the mountains of the Cape Floristic Region (CFR). Seven of the known species are local endemics of the Cedarberg and adjacent Cold Bokkeveld Mountains, where they are often sympatric, with just two species found south of this: *T. longipedicellata* Hilliard, endemic in the Du Toitskloof and Hottentots Holland Mountains; and *T. glutinosa* (Schltr.) Hilliard, which is widely distributed throughout the mountains of the southwestern and southern Cape as far east as the Kouga and Great Winterhoek Mountains. The genus is readily recognized by the bushy habit, broad, deeply toothed leaves, bracts usually adnate to the base of the pedicel only, and the small, trumpet-shaped, white or mauve flowers marked with an orange patch running from the base of the posterior (posticous) lip down the back of the tube (Hilliard 1994). All of the species are restricted to deeply shaded rock overhangs or caves at high altitude in sandstone. They are generally poorly represented in herbaria, leading Hilliard (1994) to observe that 'much more field work is needed before the distribution patterns are fully established and the total number of species known'.

Cape Town residents Ivor and Cora Jardine have spent several years carefully and thoroughly documenting the flora around their weekend cottage in the Swartruggens Mountains, a relatively poorly collected portion of the CFR on the arid eastern fringe of the Cold Bokkeveld. Their activities have already produced a new species of *Hesperantha* (Iridaceae) (Goldblatt & Manning 2007) and here we describe another of their collections, a new species of *Trienia*, named for the uncharacteristically included anthers (Latin *occultus*, hidden). In all other species thus far known, at least the anterior (anticous) pair of stamens is exserted, although the posterior pair may be either exserted or shortly included (Hilliard 1994).

***Trienia occulta* J.C.Manning & Goldblatt, sp. nov.**

Herba perennis vel suffruticosa mollis base lignosa, caulibus foliosis sed scaposis infra racemos, densiter glanduloso-puberulis pilis patentibus 0.1–0.2 mm longis, foliis petiolatis ovatis 10–20(–30) × 5–15(–20) mm profunde laceratis vel grosse dentatis paribus 2–4(–6) dentorum munitis, glanduloso-puberulis, pilis patentibus 0.1–0.2 mm longis, floribus 3–7 subsecundis, pedicellis 3–7 mm longis, bracteis inferioribus ovatis vel subfoliaceis, superioribus linearo-lanceolatis 2–5 × 0.8–2.0(–5.0) mm, glanduloso-puberulis ad basem pedicellis adnatis, corolla alba lobis malvinis vel caeruleis vividis, floribus subroseis ubi siccis, tubo infundibuliformi 6–7 mm longo, lobis ovatis ad subrotundis ± 1.0–1.5 mm longis, staminibus 4 inclusis, anthera attingentibus 1.5–2.0 mm infra orem tubi, stylo incluso ± 4 mm longo, parum ultra antheras attingenti, in summo ± 1 mm stigmatico, capsulis ampulliformibus 4–5 × 2.0–2.5 mm.

TYPE.—Western Cape, 3219 (Wuppertal): Swartruggens, Farm Knolfontein, 60 km NE of Ceres, 1 252 m, deep overhang/cave in rock, (–DC), 3 December 2008, I. & C. Jardine 1031 (NBG, holo.; MO, iso.).

Short-lived perennial herb or soft shrublet up to 450 mm high, well branched from woody base; stems decumbent or diffuse, up to 2 mm diam. at base; leafy but scapose below racemes, densely glandular-puberulous with patent hairs 0.1–0.2 mm long. *Leaves* opposite but uppermost alternate, petiolate; blade ovate, 10–20(–30) × 5–15(–20) mm, thin-textured and bright green, deeply lacerate or coarsely toothed, with 2–4(–6) pairs of teeth, occasionally 1 or more primary lobes with smaller secondary tooth (sometimes only on proximal margin), both surfaces glandular-puberulous with patent hairs 0.1–0.2 mm long, base tapering into petiole 4–10 mm long, shorter than blade. *Flowers* (1–)3–7, subsecund in very lax racemes terminating all branchlets, sometimes 1–few smaller secondary racemes developing to produce an open panicle; pedicels becoming shorter acropetally, 3–7 mm long; lowermost bracts ovate or almost leaflike with one pair of teeth but upper bracts linear-lanceolate, 2–5 × 0.8–2.0(–5.0) mm, glandular-puberulous as in leaves, adnate to base of pedicel only. *Calyx* obscurely bilabiate, tube 0.5–1.0 mm long, lobes lanceolate, 2.0–2.5 × 0.5–0.8 mm, enlarging in fruit, glandular-puberulous as in leaves, posterior lip split almost to base, anterior lip split ± halfway. *Corolla* white with mauve or bright blue lobes but whole flower drying pinkish; tube funnel-shaped, 6–7 mm long, cylindric in lower ± 4 mm and ± 1 mm diam., abruptly expanded above and ± 2 mm diam. at mouth, thinly glandular-puberulous outside, limb ± 3 mm diam., base of posterior lip thinly bearded with clavate hairs, sometimes extending around mouth of tube below all lobes, lobes ovate to subrotund, posterior lobes ± 1 × 1 mm, anterior lobe ± 1.5 × 1.5 mm. *Stamens* 4, inserted ± midway up tube, included, anthers reaching 1.5–2.0 mm below mouth of tube; filaments glabrous, 0.7–0.8 mm long, posterior filaments shortly decurrent; anthers ± 0.4 mm long. *Style* included, ± 3 mm long, reaching slightly beyond anthers; stigma ligulate with marginal papillae, ± 1 mm long. *Capsules* flask-shaped, 4–5 × 2.0–2.5 mm, thinly glandular-puberulous. *Seeds* up to 20 in each locule, ± 0.3 × 0.4 × 0.2 mm, irregularly wrinkled in longitudinal bands, pale watery yellow. *Flowering time*: December to January. Figures 25; 26.

Distribution and ecology: thus far known from several rock overhangs on the Farm Knolfontein in the Swartruggens Mountains northeast of Ceres (Figure 27). Plants grow in shallow sandy loam, their roots wedged in cracks in the rock, in deeply shaded situations under overhangs or shallow caves. They appear to be restricted to situations that are permanently shaded, favouring east-facing situations where they are sheltered from the afternoon sun. The plants are very brittle and exude a resinous smell when touched. They are browsed by hyraxes.

Diagnosis and relationships: *Trienia occulta* is distinguished by its very lax racemes (sometimes developed into weak panicles) of funnel-shaped flowers, the tube 6–7 mm long, with both pairs of anthers included in the lower three-fourths of the tube. Most species of *Trienia* have densely racemose or capitate inflorescences, and the very lax racemes of *T. occulta* suggest a relationship with *T. frigida* Hilliard, a poorly known species from the Cold Bokkeveld, and *T. schlechteri* (Hiern.) Hilliard, from there and the Cedarberg. The flowers in both of these species, however, are very much smaller. The corolla tube in *T. schlechteri* measures only 2–3 mm



FIGURE 25.—*Trieenia occulta*, I. & C. Jardine 1031 (NBG). Flowering stems showing racemose inflorescence.

long (therefore half the size of *T. occulta*), and both pairs of stamens are exserted; the tube in *T. frigida* is ± 4.5 mm long, the anterior pair of stamens is exserted, and the posterior pair is included, with the filaments decurrent almost to the base of the tube.

Of the two, *Trieenia occulta* is most likely to be confused with *T. frigida*, which also has the lower bracts $\pm$ leaf-like (always linear and less than 1 mm broad in *T. schlechteri*) but this species, although known only from a single, fruiting specimen collected at Elandskloof in the Cold Bokkeveld, is immediately distinguished by its glandular-pilose stems and leaves, with hairs up to 1.0–1.5 mm long (Hilliard 1994), and very much shorter pedicels, 0.75–2.0 mm long, with the bract adnate to both the pedicel and base of the calyx. In contrast, the stems and leaves in *T. occulta* are glandular-puberulous with very short hairs up to 0.2 mm long, and the pedicels measure 3–7 mm long. Pedicels of similar length are known only in the aptly named *T. longipedicellata* from the Du Toitskloof and Hottentots Holland Mountains but this species has very leafy racemes of smaller flowers with the tube 3–4 mm long.

We are unable to distinguish an orange patch below the posterior lip in *Trieenia occulta* (also not mentioned in the colour notes on the type collection), evidently characteristic of the genus (Hilliard 1994). This is seldom mentioned on the collecting labels of the other species that we have examined and is thus evidently easily overlooked or may actually be lacking in this species.

Other specimens seen

WESTERN CAPE.—3219 (Wuppertal): Swartruggens, Farm Knolfontein, 60 km NE of Ceres, 1 241 m, (–DC), 13 January 2008, I. & C. Jardine 1067 (E, MO, NBG); 15 January 2008, I. & C. Jardine 1079 (E, NBG).

2. *Zaluzianskya* F.W.Schmidt (including *Reyemia* Hilliard) (Archibald *et al.* 2005) is one of the larger genera in the tribe, comprising ± 60 species of mainly southern African annual and perennial herbs. It is distinguished by its spikes of long-tubed flowers with the corolla only slightly inflated at the apex, bracts adnate to the plicate, strongly ribbed calyx, filaments decurrent to the base of the tube to form a channel enclosing the style, and $\pm$ beaked capsule with pale beige or mauve seeds with colliculate testa. The genus is currently divided into four sections (Hilliard 1994), primarily on the basis of flower colour, shape of the corolla lobes, and on the time of anthesis. Section *Zaluzianskya* subsect. *Zalusianskya* is distinguished by its mainly diurnal flowers with moderately-sized calyx and mostly retuse or bifid corolla lobes, often coloured pink or mauve. It comprises 15 species of annual herbs distributed primarily across the drier western and central parts of South Africa.

One of the most distinctive species in subsection *Zalusianskya* is *Z. violacea* Schltr., diagnosed by an unusual vestiture on the stems, comprising short, retrorse, eglandular hairs (often mixed with tiny patent glands), and by its relatively long corolla tubes, 10–25 mm long, covered with delicate, acute, eglandular hairs (Hilliard 1994). Populations of plants from dolerite-derived clay flats west of Calvinia with the retrorsely-haired stems of *Z. violacea* have larger, strikingly patterned flowers with unusually long perianth tubes, well outside the normal dimensions of the species. The colouring and dimensions of these larger-flowered plants are discordant with nearby populations of *Z. violacea* and, combined with the difference in ecology, suggest that they represent a distinct species that we describe here as *Z. regalis* for its showy, magenta flowers (Latin *regalis*, regal).

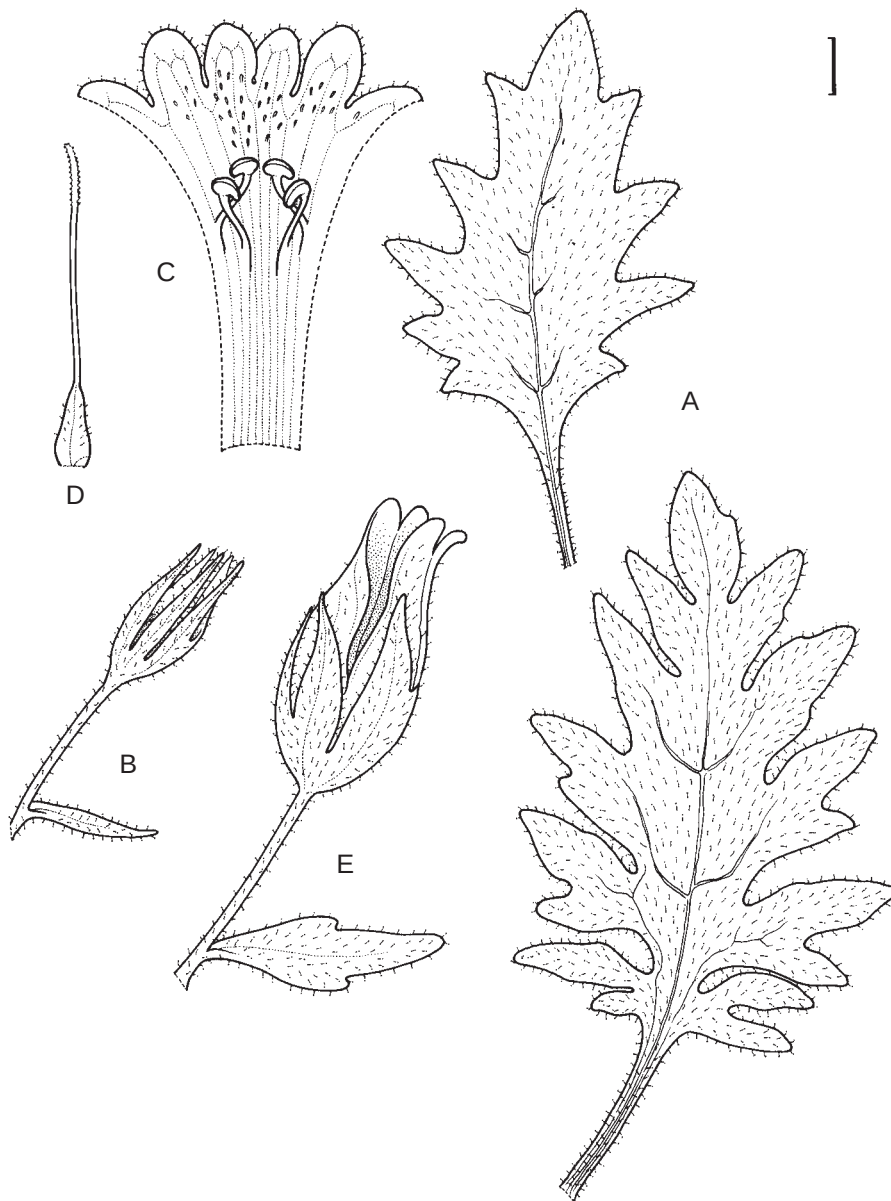


FIGURE 26.—*Trieenia occulta*, I. & C. Jardine 1031 (NBG). A, leaves showing variation; B, calyx with narrow bract adnate to base of pedicel; C, corolla opened out, showing included stamens—two central lobes comprise posterior lip; D, ovary and style; E, capsule from lowermost flower with leaf-like bract. Scale bar: A, 20 mm; B–E, 10 mm. Artist: John Manning.

***Zaluzianskya regalis* J.C.Manning & Goldblatt,**
sp. nov.

Haec species quoad caulem pilis retrorsis eglandulosis cum glandulis parvis patentibus intermixtis vestitum et tubum corollae sat longum pilis mollibus acutis pubescentem ad *Z. violaceam* proxime accedit, sed ab ea tubo corollae longiore (35–40 mm contra 10–25 mm longo), limbo majore (15–18 mm contra 7–12 mm diam.), stylo 30–35 mm (contra 11–18 mm) longo et lobulis perianthii atrocarnis ad magenteis (contra malvinis vel flavis) differt.

TYPE.—3119 (Calvinia): ± 10 km southeast of Nieuwoudtville on Calvinia road, in damp dolerite, (–AC), 21 September 2001, J. Manning 2642 (NBG, holo.; E, MO, iso.).

Annual herb, 70–100 mm high; primary stem erect, soon branching from base; branches ascending or decumbent, mostly simple, pubescent with retrose, acute hairs up to 0.3 mm long, mixed with minute, gland-tipped hairs, distantly leafy, mostly with only 1 pair above cotyledons. Leaf blade ovate, tapering below and petiolate, mostly

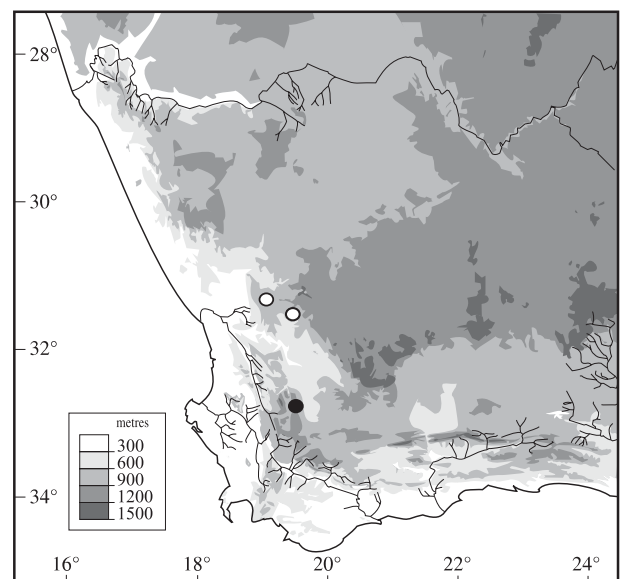


FIGURE 27.—Known distribution of *Trieenia occulta*, ●; *Zaluzianskya regalis*, ○.

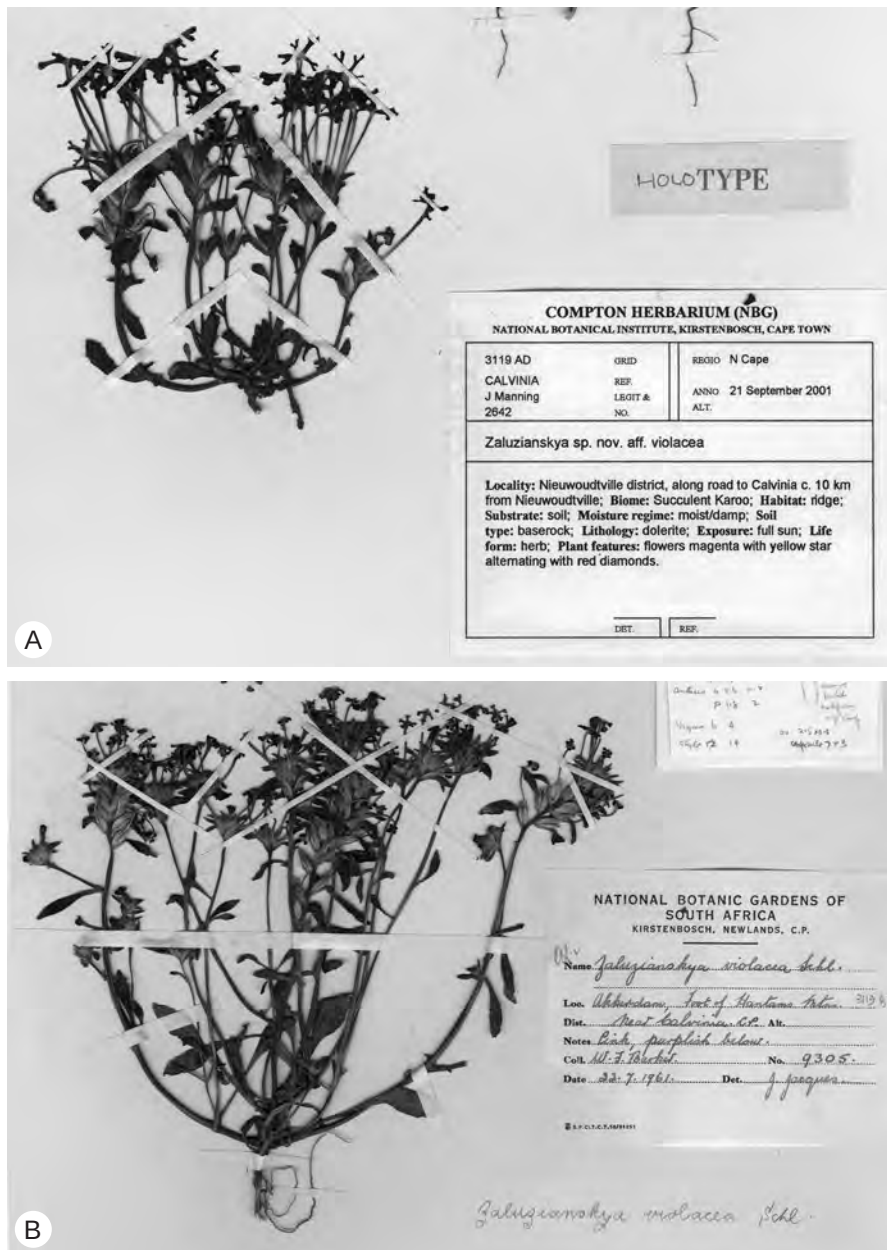


FIGURE 28.—A, *Zaluzianskya regalis*, Manning 2642 (NBG); B, *Z. violacea*, Barker 9305 (NBG).

10–15 × 5–8 mm, obscurely dentate, both surfaces shortly pubescent with acute hairs mixed with minute, gland-tipped hairs. Flowers 4–10, at first crowded in heads but elongating into short spikes in fruit, diurnal; bracts adnate to calyx for 4–5 mm, elliptic to ovate in distal part, contracted into broad, membranous shaft, lowermost 13–14 × 2–6 mm, shortly pubescent on both surfaces, more densely on proximal half, hairs patent or ± retrorse, sometimes longer on margins and then up to 1 mm long. Calyx 7–8 mm long, lobes 2–3 mm long, densely pubescent with delicate, acute hairs up to 0.8 mm long, mixed with minute, gland-tipped hairs. Corolla tube cylindrical, 35–40 mm long, densely pubescent with delicate, acute hairs mixed with minute gland-tipped hairs up to 0.8 mm long; limb 15–18 mm diam., actinomorphic, lobes Y-shaped, 6–8 × 5–7 mm, minutely glandular-haired posteriorly, deep pink to magenta with deep yellow star-shaped patch around mouth, rays extending shortly up sinuses and enclosing dark red diamond-shaped blotch extending halfway or almost entirely up shaft, mouth encircled by sparse, stiff, acute

hairs. Stamens usually 4 or anterior pair aborted, posterior pair included, anthers ± 2 mm long, anterior pair exerted, anthers 0.1–0.2 mm long. Ovary ± 5 mm long, with small, rounded nectariferous gland, ± 0.4 mm long; style 30–35 mm long; stigma included, ± 4 mm long. Capsules 8–9 × 3–4 mm. Seeds obscurely angled, angles narrowly winged, ± 0.8 × 0.5 mm, pale yellow. Flowering time: late August to late September. Figures 28A; 29A; 30A.

Distribution and ecology: known so far from two populations west of Calvinia (Figure 27). Plants are locally common on seasonally damp clay flats derived from dolerite rock.

Diagnosis and relationships: arguably the most brilliantly flowered member of the genus, *Zaluzianskya regalis* is an annual herb with retrorsely-haired stems and relatively large, dark pink to deep magenta flowers marked in the mouth with a yellow star surrounded by conspicuous red diamonds. The perianth tube is 35–40 mm long and covered in long, soft, acute hairs mixed

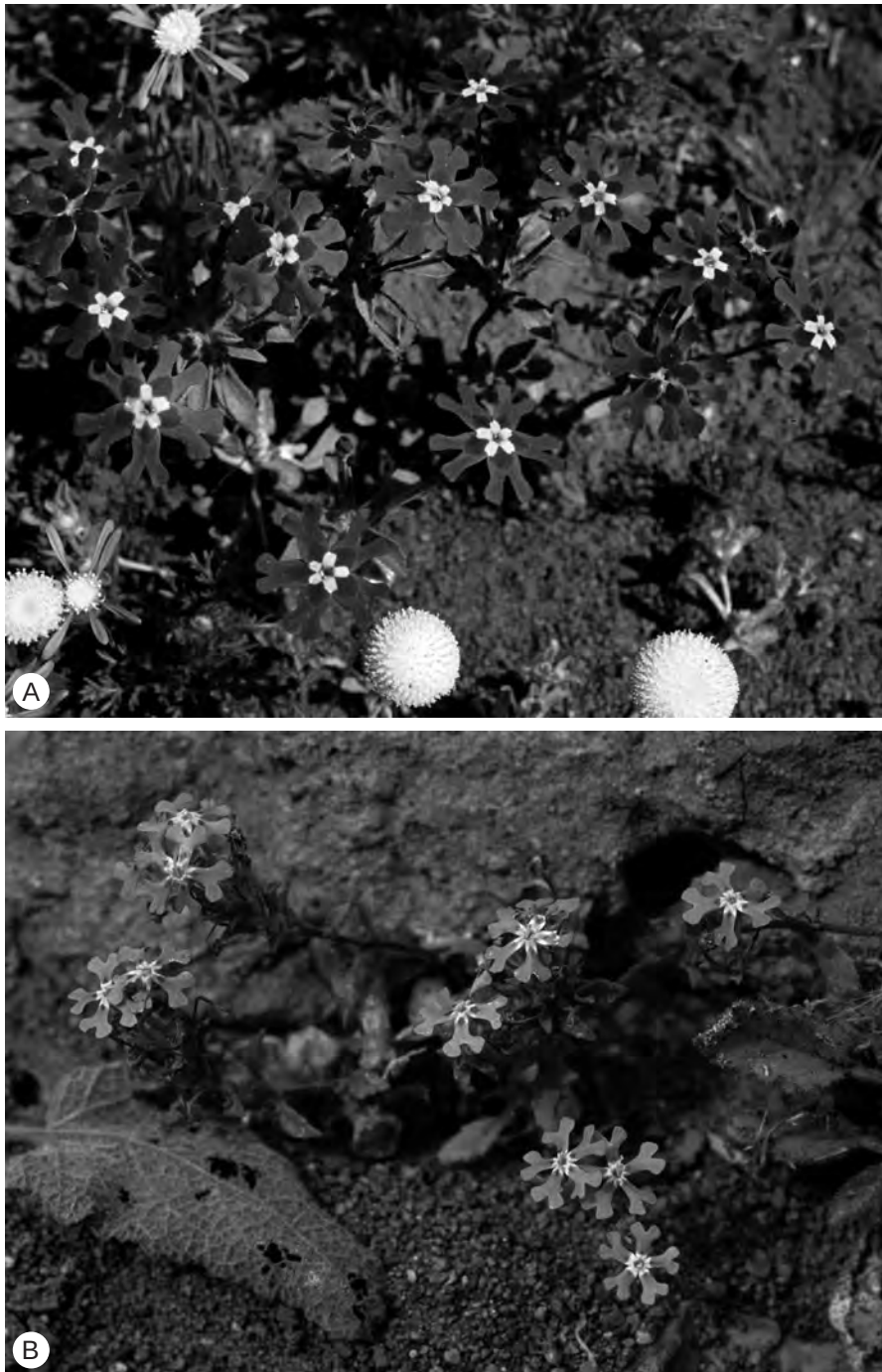


FIGURE 29.—A, *Zaluzianskya regalis*, Manning 2642 (NBG); B, *Z. violacea*. Photographer: John Manning.

with minute, gland-tipped hairs, and both pairs of stamens are usually developed.

The retrorse hairs on the stem of *Zaluzianskya regalis* are diagnostic of a small group of closely allied species in subsection *Zaluzianskya* centred on the Roggeveld and Hantam Plateau (Hilliard 1994). *Z. regalis* is distinguished in the alliance by having the largest and brightest flowers, with a corolla tube 30–40 mm long, limb 15–18 mm in diameter, and style 30–35 mm long. The dark pink or magenta limb is boldly marked with a star-shaped yellow patch around the mouth, the rays bifid and extending shortly up the sinuses to enclose a conspicuous dark red diamond- or spade-shaped patch that covers most of the shaft of each corolla lobe (Figure 30A). Both *Z. pilosissima* and *Z. violacea* have smaller, pink or pale

mauve flowers with inconspicuous red flecks around the yellow eye (Figures 28B; 29B; 30B; Manning & Goldblatt 1997) (occasional pale yellow-flowered plants with a darker eye have also been recorded in *Z. violacea*). The corolla tube in both species is 10–25 mm long, the limb 7–12 mm in diameter, and the style 9–18 mm long.

Zaluzianskya pilosissima is distinguished from *Z. violacea* by its more densely pubescent bracts, and flowers in which only the posterior two stamens are developed (both pairs are usually present in *Z. violacea*). It is distributed across the Upper Karoo from Middelpos and Sutherland on the Roggeveld Escarpment eastwards to Carnarvon and Fraserburg, whereas *Z. violacea* ranges slightly to the north and west, from the Knersvlakte across the Hantam and Roggeveld Plateaus as far south as Middelpos.

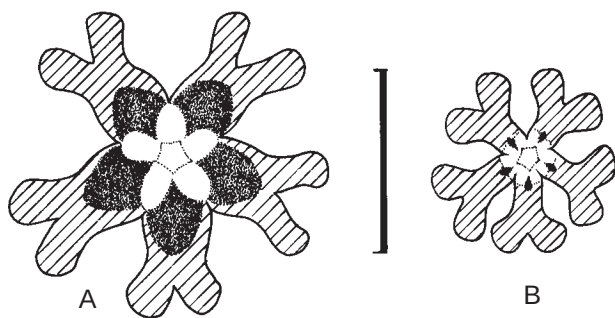


FIGURE 30.—Perianth patterning. A, *Zaluzianskya regalis*. B, *Z. violacea*. Scale bar: 10 mm. Artist: John Manning.

Zaluzianskya regalis appears to be restricted to seasonally moist, heavy clay soils derived from dolerite, in contrast to the lighter clays or loamy soils favoured by *Z. pilosissima* and *Z. violacea*. Similar edaphic segregation between sister species on doleritic clays and on Karoo shales has been documented in several other genera on the Hantam-Bokkeveld (Manning & Goldblatt 2004).

Other specimen seen

NORTHERN CAPE.—3119 (Calvinia): Klein Platberg to Wilgenbos, SW of town, (–DA), 31 August 1990, E.G.H. Oliver 9609 (NBG).

ACKNOWLEDGEMENTS

Michelle Smith kindly prepared the electronic figures. Material was collected under permits from Northern Cape Nature Conservation and CapeNature.

BORAGINACEAE

NOMENCLATURAL NOTES ON *ECHIMUM FRUTICOSUM* VAR. *MAJOR* AND VAR. *MINOR*

Echium fruticosum var. *major*

Echium fruticosum L. was first described in *Species plantarum* (Linnaeus 1753). Jacquin (1797: t. 34) provided an illustration and lengthy description of a plant identified by him as *Echium fruticosum*. Ker Gawler (1815) called into question Jacquin's application of the name, stating that, they '... certainly have some doubt whether that of Jacquin, admitted for a synonym ... is of the same species. There the inflorescence terminates each branch in a simple continuous scattered axillary upright spike...' Similarly, Sims (1816), spurred on by Ker Gawler's comment, noted the considerable difference between the two contrasted entities mentioned above and delegated Jacquin's figure to his new variety *E. fruticosum* var. *major*. An examination of the Jacquin plate reveals what is currently known as *Lobostemon argenteus* (P.J.Bergius) H.Buek—diagnosed in part as distinctly separate from *L. fruticosus* by possessing an inflorescence that represents a pseudo-spike as opposed to a cyme. Original Jacquin material exists in the Naturhistorisches Museum, Vienna (W). The specimens W0007532 and W0007531 cannot be considered for typification because, although the former was collected by Banks and is accompanied by '*Echium fruticosum*' in Jacquin's hand in the left hand corner of the sheet and

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MS. received: 2009-06-05.

the latter is a Scholl collection, also with '*Echium fruticosum*' in Jacquin's hand, both specimens represent what is currently known as *L. fruticosus* (L.) H.Buek and in no way resemble the plate, especially so in the absence of a spike-like inflorescence.

Jacquin based many new names on specimens collected from plants cultivated in botanical gardens such as Schönbrunn (D'Arcy 1970; Buys & Nordenstam 2007). That a cultivated plant was at hand is most probably evidenced by the illustration of a rooted plant. There is a Boos specimen at W (W0018220) which might be considered to be part of the original material. Franz Boos (1753–1832) called twice at the Cape, once while accompanying the official Austrian expedition to Mauritius, arriving in May 1786 and remaining there for nine months before proceeding to Mauritius in February 1787 (Neilreich 1855), and again on his return to Europe during the summer of January 1788, to arrive back in Vienna in July (Garside 1942; Gunn & Codd 1981). Specimen W0018220 is *L. argenteus*, but is accompanied by only '*Echium*' in Jacquin's hand in the left hand corner of the sheet, and on the accompanying label, 'Hb. Jacq. Cap. B. Sp. Boos' is written in an unidentified hand. On the reverse, too, 'Cap. B. Sp. Boos' is written in an unidentified hand. In the absence of a specific epithet in Jacquin's

hand on the specimen, we are of the opinion that there is no concrete evidence that this specimen is directly associated with Jacquin's concept of '*fruticosum*', although it is apparent from the extensive description, that Jacquin did have a specimen at hand. We therefore view Jacquin's illustration as a lectotype, thus placing *E. fruticosum* var. *major* in synonymy with what is currently known as *Lobostemon argenteus* (P.J.Bergius) H.Buek (Buys 2000).

Lehmann (1818) independently also recognizes a variety (*B*) *major*, identifying it with Thunberg's concept of *Echium fruticosum* L. (Thunberg 1794). The sheet in the Thunberg herbarium marked *E. fruticosum* by Thunberg (UPS-THUNB4098) consists of two different specimens. To the right is mounted what is currently known as *Lobostemon fruticosus*, to the left, a specimen corresponding to Lehmann's var. *major*. Typification of this illegitimate later homonym, by a specimen in MEL places it in synonymy with *L. montanus* H.Buek (Buys & Nordenstam 2009).

***Lobostemon argenteus* (P.J.Bergius) H.Buek**, in *Linnaea* 11: 133 (1837).

Echium fruticosum L. var. (*α*) *major* Sims: no. 1772 (1816). Lecto., here designated: [icon in] Jacquin, *Plantarum rariorum horti caesarei Schoenbrunnensis descriptiones et icones*, plate 34 (1797) non *Echium fruticosum* L. var. *major* Lehm. in *Plantae e familia Asperifoliarum nuciferae*: 421 (1818).

Echium fruticosum var. *minor*

Sims (1816) cites Ker Gawler's *The botanical register*: t. 39 (1815) under *Echium fruticosum* L. var. *minor*. The reference to t. 39 is an error for it represents *Ipomoea* L. and it is t. 36 instead that depicts a *Lobostemon*. Sims (1816) also alludes to being aware of a collection in the Banksian Herbarium made from a plant cultivated by Philip Miller in 1759 in the Chelsea garden. In BM there is a sheet with 'Hort Chels' in an unidentified hand on the reverse. The sheet has an undated watermark 'GR' included in it, a reference to George Rex (King George). This is likely a reference to George III who was on the throne from 1760–1820. The paper was presumably produced during that period which puts the specimen in the right time frame, but the specimen is not considered to be original material due to the absence of unswerving evidence that it is directly associated with Sims' concept of *E. fruticosum* var. *minor*. In the light of Sims' original material consisting of a specimen and the illustration, we view *The botanical register* plate as lectotype. This typification places *E. fruticosum* var. *minor* in synonymy with what is currently known as *Lobostemon fruticosus* (Buys 2000).

***Lobostemon fruticosus* (L.) H.Buek**, in *Linnaea* 11: 134 (1837).

Echium fruticosum L. var. (*β*) *minor* Sims: t. 1772 (1816). Lecto., here designated: [icon in] Ker Gawler, *The botanical register*: t. 39 (1815).

ACKNOWLEDGEMENTS

We thank the curators of the herbaria at the Natural History Museum, Vienna (W) and The Natural History Museum, London (BM) for allowing access to the mentioned specimens. Thanks in particular to Anton Igersheim (W) and John Hunn (BM) for assistance. Our appreciation also to Dick Brummitt for commenting on an earlier draft.

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MS. received: 2009-09-04.

ASPHODELACEAE: ALOOIDEAE

REINSTATEMENT OF *ALOE SPECTABILIS*

Aloe spectabilis Reynolds (1937) was described from material that was collected from KwaZulu-Natal, the eastern-most province of South Africa. Previously, material of this species was erroneously considered to represent a form of *A. ferox* Mill. (Berger 1908: 310, 311), a

predominantly southern and eastern Cape species (see Van Wyk & Smith 2003: 56 for a distribution map of *A. ferox*). *Aloe spectabilis*, in contrast, has its present-day centre of distribution around Bushman's River Valley near Weenen, along the Mooi River near Muden and

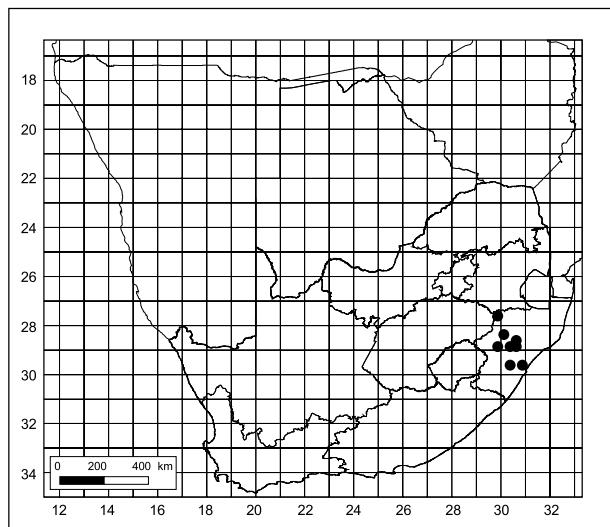


FIGURE 31.—Distribution of *Aloe spectabilis*, based on specimens at PRE.

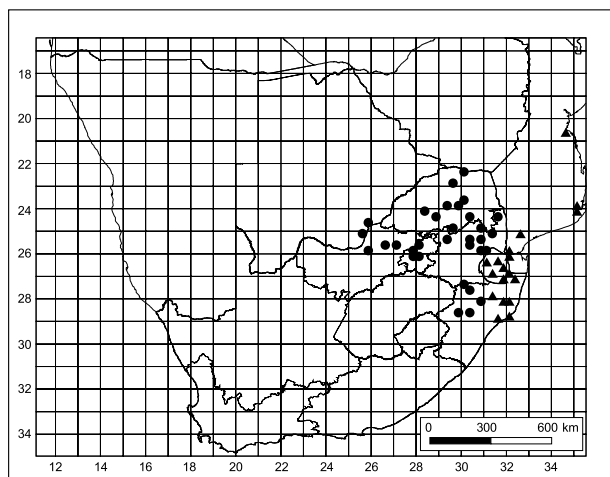


FIGURE 32.—Distribution of *Aloe marlothii* subsp. *marlothii*, ●; and *A. marlothii* subsp. *orientalis*, ▲, adapted from Glen & Hardy (2000).

Keats Drift, and in the Tugela [Thukela] River Valley between Mpofana and Pomeroy on the Greytown–Dundee Road in KwaZulu-Natal (Figure 31).

Further north in Zululand this species seems to grade into *Aloe marlothii* A. Berger, which is its closest relative. However, *A. marlothii* is typically an element of southern Africa's northcentral and northeastern savannas, with subsp. *marlothii* widely distributed in KwaZulu-Natal, western Swaziland, Mpumalanga, Limpopo, Gauteng, North-West and the eastern border of Botswana, while *A. marlothii* subsp. *orientalis* Glen & D.S. Hardy has a more easterly distribution in northern KwaZulu-Natal, Swaziland and into Mozambique (Glen & Hardy 2000) (Figure 32).

Overall, plants of *Aloe marlothii* tend to be more robust than *A. spectabilis* in general appearance. *Aloe spectabilis* is a single-stemmed, tree-like aloe up to 5 m high (Figure 33). It is distinguished by its tall, unbranched stem and much-branched inflorescences with very dark brown to almost black peduncles and

between 10 and 14, erect to slightly spreading, rather truncate racemes. Furthermore, it differs from *A. marlothii* in having almost erect racemes that are shorter and broader, with flowers more evenly distributed around the axis. The apices of the inner perianth segments are a dull to deep glossy black and the exerted portion of the filaments is orange in *A. spectabilis*, whereas both are a light to deep purple in *A. marlothii* (Reynolds 1937, 1950; Jeppe 1969; Bornman & Hardy 1972) (Table 4).

Given superficial similarities between *Aloe spectabilis* and *A. marlothii*, some previous authors considered the two species to be conspecific (Glen & Hardy 2000; Van Wyk & Smith 2003). Others have more recently suggested that *A. spectabilis* represents a good species (Smith & Van Wyk 2008), and warrants reinstatement. This is done here.

***Aloe spectabilis* Reynolds** in *Journal of South African Botany* 3: 129 (1937). Type: South Africa, [KwaZulu-Natal], 2830 (Dundee): Tugela [Thukela] Valley, between Greytown and Helpmekaar, (–CB), Reynolds 2033 (PRE!, holo.; BOL, iso.).

A. ferox auct., sensu A. Berger, non Mill.: 310 (1908).



FIGURE 33.—*Aloe spectabilis* in the Tugela [Thukela] River Valley. Photograph: G.F. Smith.

TABLE 4.—Differences between *Aloe spectabilis* and *A. marlothii*

Character	<i>A. spectabilis</i>	<i>A. marlothii</i>
Raceme		
orientation	suberect	oblique to horizontal
dimensions	± 250 × 90–100 mm	300–500 × 50–60 mm
number	10 to 14	20 to 30
Peduncle colour	dark brown to almost black	green to reddish brown
Flower disposition	evenly distributed around axis	secund
Apex of inner perianth segments	dull to deep glossy black	light to deep purple
Exserted portion of filaments	orange	light to deep purple

A. ferox auct., sensu A.Berger, non Mill. var. *xanthostachys* A.Berger: 310 (1908). Type: South Africa, [KwaZulu-Natal], Lady-smith, *Marloth 4157* (B).

Specimens examined

KWAZULU-NATAL.—2729 (Volksrust): valley at Igogo, ± 32 km from Newcastle, (–DB), 1970-07-22, *Floquet PRE38541* (PRE). 2829 (Harrismith): Weenen Dist., Blaauwkrantz Valley near Weenen, (–DD), 1944-08-11, *Acocks 10526* (PRE). 2830 (Dundee): Meduna, (–AC), 1915-07-16, *Keeling 110* (PRE); Dundee Dist., Biggarsberg, near Waschbank, (–AC), 1935-06-02, *Reynolds 1394* (PRE); Weenen Dist., in Muden Valley, ± 18 miles [± 11.2 km] NW of Greytown, Mooi River Valley, (–CD), 1936-07-28, *Reynolds 2031* (PRE); Kranskop Dist., Inadi River Valley leading into Tugela River Valley, (–DA), 1943-05-12, *Dyer 4383* (PRE); Estcourt Dist., near Keat's Drift in the Mooi River Valley, (–DC), 1936-07-28, *Reynolds 2034* (PRE). 2930 (Pietermaritzburg): Lion's River Dist., Zwartkop Location, (–CB), 1964-09-30, *Moll 1125* (PRE); Ndwedwe Dist., 3 miles [± 1.9 km] W of Ndwedwe, (–DB), 1966-07-13, *Moll 3287A* (PRE).

ACKNOWLEDGEMENTS

The authors would like to thank Ms Hester Steyn, National Herbarium, South African National Biodiversity Institute, Pretoria, for producing the distribution map; and an anonymous referee for suggesting improvements to the manuscript.

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MS. received: 2009-08-27.

ASPHODELACEAE: ALOOIDEAE

ALOE NEILCROUCHII, A NEW ROBUST LEPTALOE FROM KWAZULU-NATAL, SOUTH AFRICA

To facilitate the identification of species of *Aloe* L. (Asphodelaceae: Alooideae), formal infrageneric groupings, mostly based on growth form, have been proposed for the genus (Berger 1908; Reynolds 1950). Two of these, *Aloe* sect. *Graminialoe* Reynolds and *A. sect. Leptoaloe* A.Berger, include the grass-like aloes (Van Wyk & Smith 2004; Craib 2005). The former consists of species that are truly very small in stature with their leaves closely resembling blades of grass, whereas the latter includes plants that are considerably more robust, with leaves that are much broader and flatter.

The appropriate Afrikaans common names, *slank- or skraalaalwyne* (English: slender aloes) are widely applied to leptoaloe species, as opposed to *grasaalwyne* (English: grass aloes) which is reserved for the true grass aloes (Laubscher 1973). Although it has been proposed that these two groups should be combined under the old-

est name, *A. sect. Leptoaloe* (Glen & Hardy 2000) to include all the grass-like aloes, keeping them separate considerably assists with conceptualizing the gross morphology of their constituent species. Only a few of the species of *Aloe* described from Africa after 2000 belong to the graminoid and leptoaloid groups [see for example Smith (2003) on *A. craibii* Gideon F.Sm. and Van Jaarsveld & Van Wyk (2006) on *A. chalissii* Van Jaarsv. & A.E.van Wyk]; their comparatively small stature make them difficult to locate in their often grassy habitats (Smith 2005). Grass aloes and leptoaloes are absent from the Arabian Peninsula, the Mascarene Islands off the east coast of Africa, and Madagascar.

The species described here, *Aloe neilcrouchii* Klopper & Gideon F.Sm., belongs to *A. sect. Leptoaloe* and represents the largest and most robust species known in this group.



FIGURE 34.—*Aloe neilcrouchii*, Crouch & Johnson 1247 (PRE). A, plant, $\times 0.33$; B, inflorescence, $\times 0.66$; C, tuberculate leaf surface, $\times 1$; D, leaf margin, $\times 1$; E, fruit capsule, $\times 1$; F, seeds, $\times 1$. Artist: G. Condy.

Aloe neilcrouchii R.R.Klopper & Gideon F.Sm., sp. nov., *A. boylei* Baker affinis sed caulibus longis, prostratis, aphyllis, e basi ramificantibus vel ramos laterales secus longitudinem caulem emetentibus; foliis brevioribus latoribusque, elongato-deltatis, dense maculis albis, tuberculatis in superficiebus ambabus punctatis, inflorescentiisque altioribus differt.

TYPE.—KwaZulu-Natal, 2930 (Durban): Midlands, near Karkloof, (–AD), 2009-01-14, N.R. Crouch & I. Johnson 1247 (PRE, holo.; NH, iso.).

Grass aloe. Stem up to 950 × 90 mm, decumbent to erect, branched mainly from base, forming robust offshoots along its length, without persistent dried leaves. Leaves deciduous, densely rosulate, erectly spreading, green, with numerous elongated, white, somewhat tuberculate spots on both surfaces, deltoid to ovate-lanceolate, up to 430 mm long, up to 135 mm wide at base; margin narrow, cartilaginous, whitish, with small whitish, deltoid, irregularly spaced teeth, 1–2 mm long, 2–5 mm apart; leaf exudate clear, drying clear, not bitter. Inflorescence 1 per rosette, 0.6–0.8 m high, erect, simple. Peduncle laterally compressed below, terete above, up to 25 mm wide at base, ± 10–15 mm diam. above, bright green; sterile bracts, ± 9, ovate-lanceolate, acuminate, 30–50 mm long, 15–20 mm wide at base, pale whitish with pinkish tinge, thin, subscarios, many-nerved. Raceme capitate, ± 120 × 100 mm, erect, dense; buds erect to erectly spreading, flowers spreading to nodding when open. Floral bracts lanceolate-acuminate, subamplexicaul, ± 30 × 7 mm, pale whitish, thin, subscarios to almost fleshy, many-nerved. Pedicels 30–45 mm long, pale yellowish to salmon-pink. Flowers: perianth salmon-pink, green-tipped, ± 45 mm long, 10–13 mm across ovary, slightly narrowed above ovary to 8–10 mm, slightly constricted to ± 7 mm just before flared mouth, cylindric-trigonal; outer segments free almost to base, tips spreading. Stamens with very pale greenish yellow, flattened filaments, not or only slightly exerted. Ovary ± 10 × 3–4 mm, light green; style very pale yellowish green, exerted to ± 5 mm. Fruit an oblong capsule, bright green to yellowish green, up to 40–45 × ± 22 mm. Seeds angular, black, 3 × 2 mm, with semi-transparent, light brownish wing, ± 1 mm wide. Flowering time: December to February. Chromosome number: unknown. Figure 34.

Habitat: *Aloe neilcrouchii* grows on southeast-facing slopes of rocky grassland in Drakensberg Foothill Moist Grassland and in vulnerable Ngongoni Veld (Mucina & Rutherford 2006). At the type locality, it was found in association with *Agapanthus campanulatus*, *Alepidea*

cordifolia, *Blechnum inflexum*, *Senecio oxyriifolius* and *Merwillia plumbea*.

Distribution: the species is known from only two localities, in the vicinity of the Karkloof and near New Hanover in the KwaZulu-Natal Midlands (Figure 35).

Etymology: the species is named for Prof. Neil R. Crouch of the Ethnobotany Unit of the South African National Biodiversity Institute, based at the KwaZulu-Natal Herbarium, who brought the specimens to our attention. Over the past several years Neil has added considerably to our knowledge of succulents, particularly aloes, and their uses. His first name is combined with his surname in the specific epithet to prevent confusion with *Aloe croucheri* Hook.f., the basionym of *Gasteria croucheri* (Hook.f.) Baker (Klopper et al. 2006).

Diagnostic characters: *Aloe neilcrouchii* belongs to *A. sect. Leptoaloe* and represents the largest of the known species of this group. Its closest affinity appears to be *A. boylei* Baker, especially *A. boylei* subsp. *major* Hilliard & Burt. However, it differs from that species by its long, sprawling, leafless stems that branch from the base or form offshoots along its length, its shorter but broader, elongated-deltoid leaves that are copiously covered with white tuberculate spots on both surfaces and its taller inflorescences (Table 5).

Conservation status: before both populations are properly assessed, it is not possible to assign a Red List status to this new taxon. However, the authors are convinced that *Aloe neilcrouchii* is a species of conservation concern. The area surrounding the type locality has been transformed extensively by plantation forestry. As a result, the grassland habitat between the two known localities has been mostly destroyed. The New Hanover population is in threat of being destroyed by expanding sugar cane plantations.

Notes: there were no plants of *Aloe boylei* in the vicinity of the two populations. In fact, no other grass aloes were encountered at these sites. Old leaves of *A. neilcrouchii* are destroyed by fire. However, prevalent fire intensity in the undisturbed habitats appears to be low enough not to destroy the plants themselves. It seems that fire promotes branching of young stems, and possibly offshoots along older stems. Honey bees (*Apis mellifera scutellata* Lepelletier) were observed visiting the flowers and collecting pollen, but no other potential pollinators, such as sunbirds, were noticed. General seed set seems to be fairly good. Plants of various sizes were observed, although small seedlings are difficult to detect amongst the tall grass.

TABLE 5.—Differences between *Aloe neilcrouchii* and *A. boylei*

	<i>A. neilcrouchii</i>	<i>A. boylei</i>
Stem	Up to 0.95 m long, 90 mm diam. Branched from base and above, forming offshoots along length.	Up to 0.2 m long, 60 mm diam. Simple or with offshoot from ground level.
Leaves	Rosulate, erectly spreading, deltoid to ovate-lanceolate, up to 430 mm long, up to 135 mm wide at base.	Rosulate, erect, lanceolate-ensiform, 500–600 mm long, 60–90 mm wide at base.
Leaf markings	Both surfaces with numerous, white, somewhat tuberculate spots.	Upper surface usually without spots; lower surface copiously white-spotted near base.
Inflorescence	0.6–0.8 m high.	0.4–0.6 m high.
Flowers	± 45 mm long.	± 40 mm long.

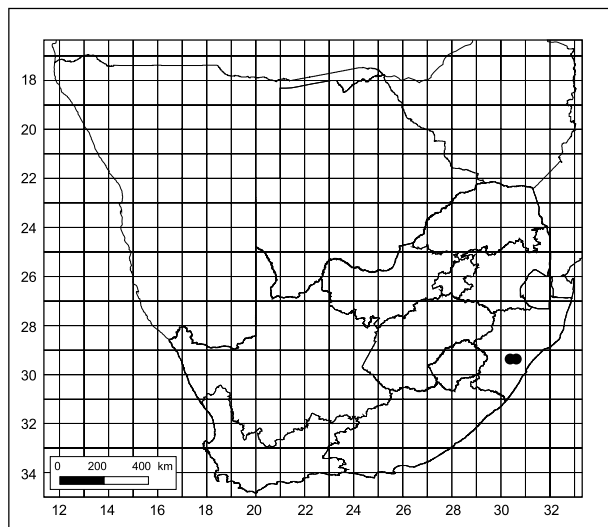


FIGURE 35.—Known distribution of *Aloe neilcrouchii*.

Additional specimen examined

KWAZULU-NATAL.—2930 (Durban): between New Hanover and Dalton, (–BC), 2010-01-05, *N.R. Crouch, G.F. Smith & I. Johnson* 1260 (PRE).

ACKNOWLEDGEMENTS

The authors would like to thank the following people: Ms Isabel Johnson, KwaZulu-Natal National Botanical Garden, South African National Biodiversity Institute (SANBI), for providing transport, and facilitating access to the site; Ms Hester Steyn, National Herbarium, SANBI, Pretoria, for producing the distribution map; Dr Otto Leistner for providing the Latin diagnosis; Ms Gill Condy, SANBI, Pretoria, for the line drawing; two referees for suggesting improvements to the manuscript.

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MS. received: 2009-09-17.

BRUNIACEAE

NEW SPECIES OF *THAMNEA* AND *BRUNIA* FROM WESTERN CAPE, SOUTH AFRICA

The Bruniaceae is one of the 33 ‘Cape floral clades’ (Linder 2003) mainly distributed in the Western Cape, South Africa. Since the revision published by Pillans (1947), much work has been done to understand the intergeneric relationships and biology of the family (Claßen-Bockhoff, in press). Based on molecular and morphological data, a new classification has been proposed accepting six of the formerly 12 genera (Claßen-Bockhoff *et al.* in press). With the two newly described species in the present paper, there are currently 79 species in the family.

Thamnea matroosbergensis A.V.Hall, sp. nov.

Fruticulus humilis usque ad 0.3 m altus; foliis 0.8–1.0(–1.2) mm longis spiraliter insertis ellipticis sessilibus, pagina laterali paulo discoidea pagina abaxiali profunde carinata castanea. Inflorescentia flore solitario sessili ad apicem ramorum principalium vel in ramis lateralibus. Flores bracteis 6–10 usque ad 2 mm longis; sepalis liberis 1.7–2.1 mm longis; petalis $\pm$ 25 mm longis, albidis,

limbis late obovatis obtusis patentibus; staminibus 1.5–2.1 mm longis, antheris 0.9 mm longis; nectario annulari viridi 0.1 mm alto; ovario uniloculari, placenta libera centrali, ovulis 4–8 pendulis; stylo superne contracto; fructu 1.8 mm longo, ellipsoideo, castaneo, tholo umbonato longo terminanti.

TYPE.—Western Cape, 3319 (Worcester): Worcester Dist.; SE slopes of Matroosberg, (–BC), 5000–6000' [1 520–1 830 m], 18 November 1962, *Esterhuysen* 29877 (BOL, holo.). Figure 36.

Sprawling shrublets, up to 0.3 m high; no coppice shoots or lignotuber recorded; distal branching dense to diffuse, main lateral branches spreading rather widely from main axis, fairly evenly dispersed along it; leaves obscuring more densely branched stems; young stems ridged, glabrous, older stems almost smooth. Leaves spirally arranged, elliptic, 0.8–1.0(–1.2) mm long, sessile with attachment $\pm$ $\frac{1}{3}$ of leaf’s area (Figure 37A), from side



FIGURE 36.—Holotype of *Thamnea matroosbergensis*, Esterhuysen 29877 (BOL).

rather discoid with base curving abruptly into stem, abaxial surface strongly keeled (Figure 37B), flat or slightly channelled between keel and leaf margin, surfaces glossy brown, glabrous; margins hyaline; stipules absent; stomata on abaxial side only (Figure 37A, B). *Bud leaf colleter* incurved, broadly triangular-acute (Figure 37B), semiterete, 0.1 mm long, dark brown, lost from older leaves. *Inflorescence*: flowers solitary (Figure 38A), sessile at ends of main branches, some on 1–22 mm long side branches no different from leafy vegetative stems, terminal flower opening from before to later than those on side branches; old receptacles and bracts not persistent. *Involucral bracts* 6–10, up to 2 mm long, lower leaf-like but with a rapid transition distally to wider laminae, upper ovate, obtuse but with a dark apiculus, rather hard-textured, distally shortly ciliate. *Floral receptacle* ± 0.2 mm long, glabrous, finely ribbed, transition to calyx with a slight indentation (Figure 37C). *Sepals* free, lanceolate, 1.7–2.1 mm long, acute, imbricate, keeled, terminating in a hyaline to brown tip, distally ciliate. *Petals* ± 2.5 mm long, white, weakly clawed; limb broadly obovate obtuse, spreading; 2 narrow ridges along the prominent midrib near base of adaxial surface. *Stamens* 1.5–2.1 mm long; anthers 0.9 mm long (Figure 37C), distally lunate; pollen 3-colporate (Figure 37E). *Flower scent* not recorded. *Nectarostomata* present around upper edge of ovary (Figure 37D). *Ovary* $2/3$ infe-

rior, 1-locular with free central axile placenta bearing 4–8 pendulous ovules at apex; style 0.6–0.9 times as long as sepals, tapering; stigma capitate (Figure 37C). *Fruit* ellipsoid, 1.8 mm long, distal end with short umbonate dome, red-brown, shallowly sulcate, glabrous; style-base persistent, broadly convex. *Flowering time*: November to April.

Diagnostic features: *Thamnea matroosbergensis* is similar to *T. thesioides* Dummer and *T. uniflora* (L.) Sol. ex Brongn., both belonging to different subclades within the genus (Quint & Claßen-Bockhoff 2006). It differs from *T. thesioides* in having a longer style (1.3–1.6 mm long vs 0.7 mm long in *T. thesioides*); stamens almost as long as the sepals; a style of almost double the length (1.3–1.6 mm vs 0.7 mm in *T. thesioides*) and a convex dome at the fruit apex. It differs from *T. uniflora* in having longer sepals (1.7–2.1 mm vs 1.2–1.4 mm in *T. uniflora*); a semi-inferior instead of an inferior ovary and in lacking a hairy fruit with a nectary rim on its top. The material is clearly distinct enough to warrant recognition at species level, although the extremely small size of the main organs will require careful analysis for identification. It is remarkably constant in the three collections from the site except that one shoot is taller and more diffuse, but in other respects they are identical.

Distribution and ecology: *Thamnea matroosbergensis* has seldom been collected and is known from a single area, the steep, rocky southeast-facing slopes of the Matroosberg in the Hex River Mountains, from 1 500 to 1 800 m (Figure 39). This site lies 35 km east from the locality of *T. thesioides* in the Ceres area, but is at a rather higher altitude.

Additional material examined

WESTERN CAPE.—3319 (Worcester): Matroosberg, amongst boulders, S side of 'Coat of Arms' Rock, $\pm 6000'$ [1 830 m], 19-01-1959, Esterhuysen 28150 (BOL); ibid., rocks on SE slope, 5000–6000' [1 520–1 830 m], 7-04-1959, Esterhuysen 27710 (BOL).

Brunia compacta A.V.Hall, sp. nov.

Frutex patens usque ad ± 0.5 m altus basiramifer, ramificatio distali densa; foliis 2.7–3.2 mm longis, usque ad 4.8 mm longis in circulis rapide crescentibus, lanceolatis acutis, sessilibus, abrupte ex caulibus crescentibus; abaxialiter villosis minus adaxialiter. Inflorescentia floribus in capitulis densis terminalibus, 3–4 mm latis, racemosis; axe principali per anthesin non crescendi, axibus ulterioribus novis sympodialibus. Flores bractea 0.6–0.8 mm longa, arcte appressa, ovata, dense villosa; bracteo-lis dense villosis; receptaculis florum 0.6–0.8 mm longis; sepalis ± 1.1 mm longis, anguste deltoideis acuminatis, abaxialiter villosis, dense ciliatis; corolla alba, petalis liberis 0.6–1.2 mm longis, ellipticis, abaxialiter villosis; staminibus ± 0.8 mm longis, distaliter incurvatis; ovario semi-infero, ± 0.7 mm longo, biloculari, utroque loculo ovulo unico pendulo; nectario absenti; stylis duobus 0.9–1.3 mm longis, leviter connatis, distaliter recurvatis.

TYPE.—Western Cape, 3219 (Clanwilliam): Ceres Dist., Gideon's Kop, S Cederberg, Sandfontein area, (–CB), 4500–5000' [1 370–1 520 m], 25 Oct. 1966, Esterhuysen 31628 (BOL, holo.). Figure 40.

Shrubs spreading, up to 0.5 m high, branched at base. *Lignotubers* unknown but can produce fast-growing cop-

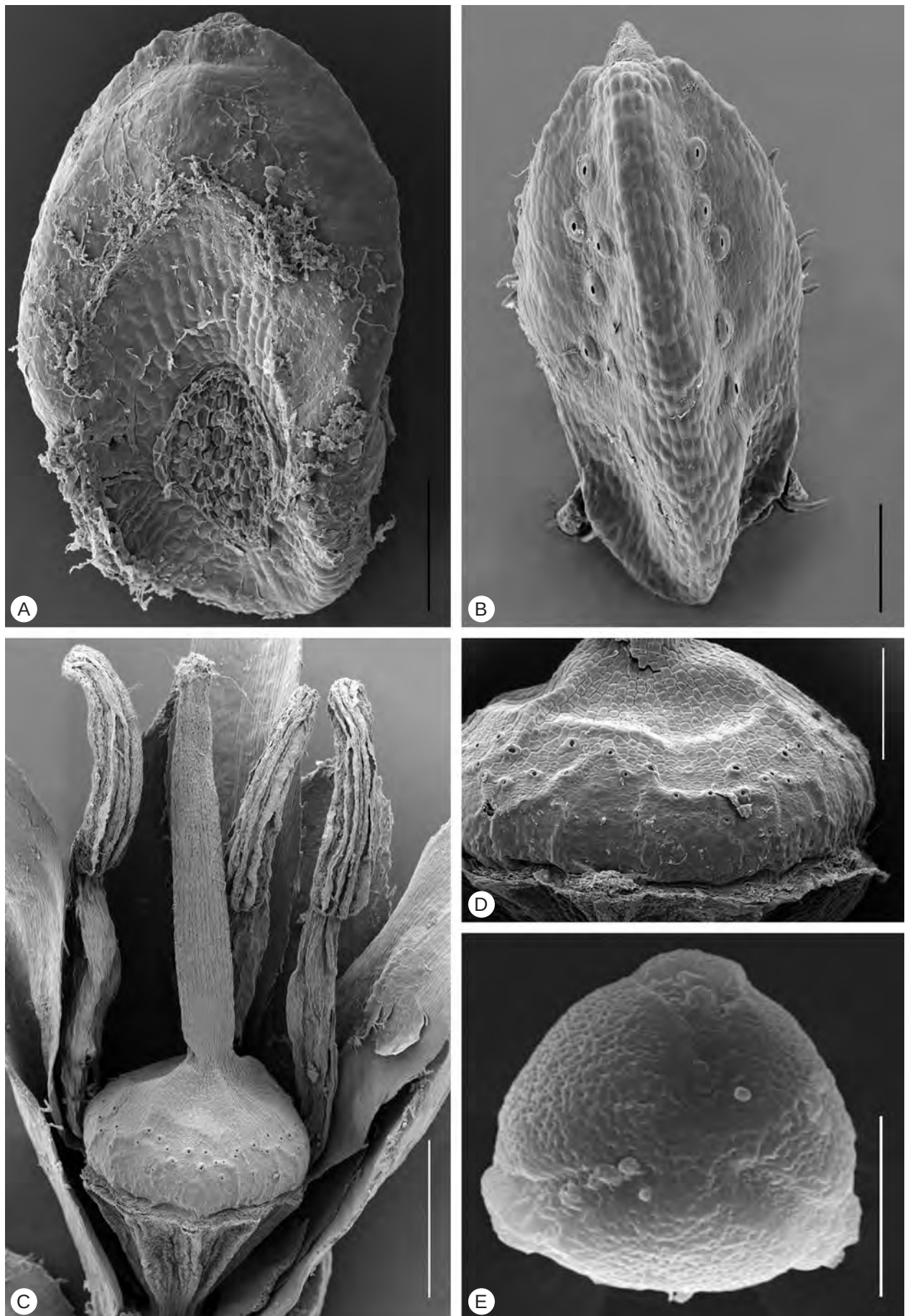


FIGURE 37.—*Thamnea matroosbergensis*. A, B, leaf: A, adaxial side; B, abaxial side. C, side-view into an artificially opened flower; D, nectarostomata at upper flanks of ovary; E, 3-colporate pollen grain. Scale bars: A, B, D, 200 μm ; C, 500 μm ; E, 10 μm .

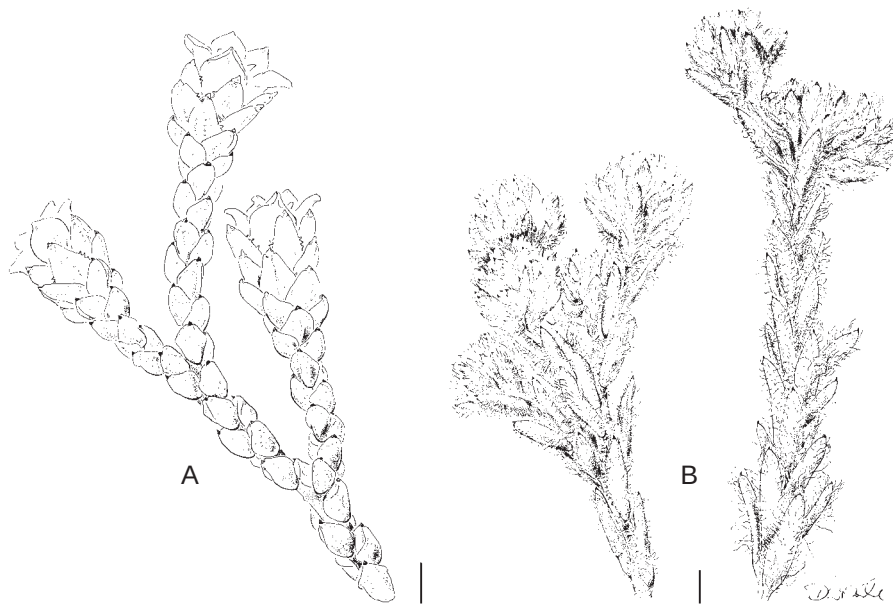


FIGURE 38.—Flowering branchlets. A, *Thamnea matroosbergensis*; B, *Brunia compacta*. Scale bars: 1 mm. Artist: D. Franke, Mainz).

pice shoots. *Distal branching* dense, lateral branches close to main axis, somewhat clustered at nodal zones with fewer branches in between. *Young stems* usually hidden by leaves, lacking decurrent ridges, tomentose distally, with older shoots pale brown when dried; old leafless stems dark grey-brown, smooth, with scattered leaf scars; stipules absent. *Leaves* lanceolate (Figure 41A, B), 2.7–3.2 mm long, up to 4.8 mm in fast-growing coppice shoots, acute, sessile, appearing abruptly from stem, lamina from side basally appressed to stem then gradually curving slightly away, increasingly so throughout its length; adaxial surface slightly concave and basally keeled, abaxial surface smoothly rounded, abaxially villous (Figure 41B), adaxially less so (Figure 41A), older leaves glabrescent, in coppice shoots more densely villous; stomata only on adaxial surface (Figure 41C). *Bud leaf colleter* as a brown, erect papilla 0.2 mm long, soon broadening slightly and

darkening to form a black deltoid apiculus shrinking to a minute patch in older leaves. *Inflorescence* with 6–10 flowers in terminal, dense clusters (Figure 38B), 3–4 mm wide, main axis not continuing growth during anthesis,

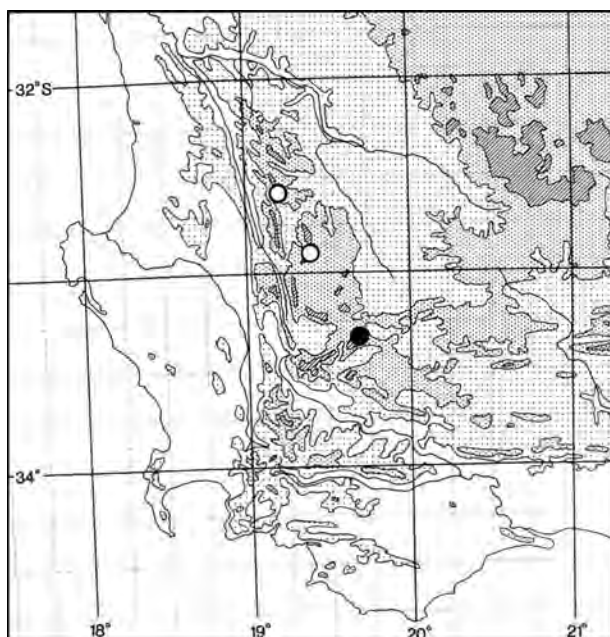


FIGURE 39.—Known distribution of *Thamnea matroosbergensis*, ●; and *Brunia compacta*, ○.



FIGURE 40.—Holotype of *Brunia compacta*, Esterhuysen 31628 (BOL).

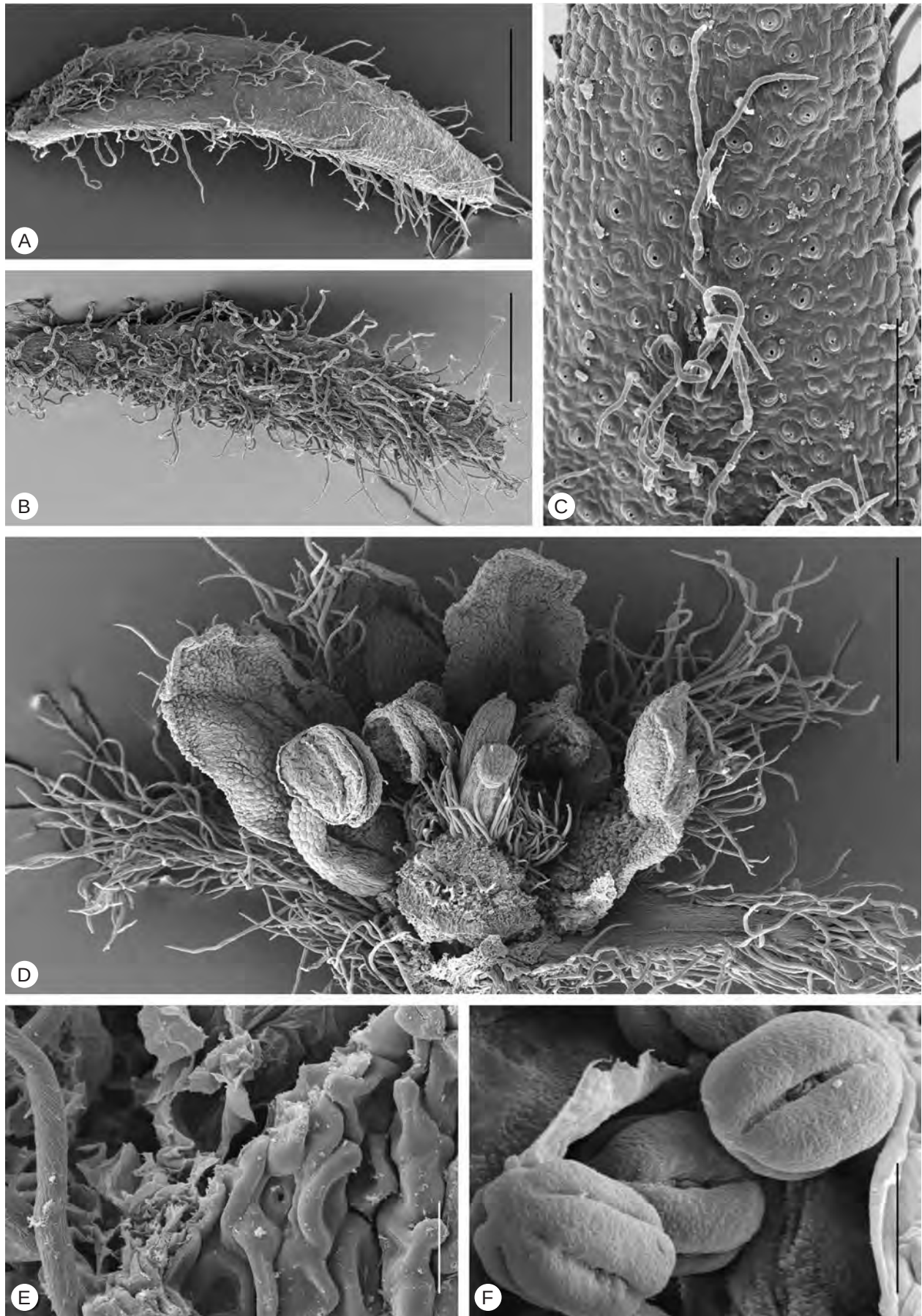


FIGURE 41.—*Brunia compacta*. A, B, leaf: A, adaxial side; B, abaxial side. C, stomata on adaxial leaf side; D, side-view into an artificially opened flower; E, single nectarostomata (centre) at upper edge of ovary seen in D (lower centre); F, (4)5-colporate pollen grains. Scale bars: A, B, D, 500 μ m; C, 200 μ m; E, 20 μ m; F, 10 μ m.

further branching sympodial with one new dominant shoot, old inflorescence peduncles persistent as bracteate, villous structures among older branches. *Bract* subtending each flower closely appressed, ovate, 0.6–0.8 mm long, midrib not visible, densely villous, with a black apiculus; bracteoles 2, oblanceolate, navicular, black-tipped, densely villous. *Floral receptacle* 0.6–0.8 mm long, with transition to calyx lacking a constriction. *Calyx* tube vestigial, segments narrowly deltoid, ± 1.1 mm long, acuminate, separated by a broadly obtuse gap, abaxially villous, densely ciliate, lacking a midrib, hyaline with minute dark apiculus. *Corolla* white, petals free from stamens, elliptic, 0.6–1.2 mm long, erect to spreading, abaxially villous, adaxial surface with a thick cushion-like swelling lying against top of ovary. *Stamens* ± 0.8 mm long, distally incurved; anthers 0.2 mm long, lobes parted and slightly divergent below; pollen (4)5-colporate (Figure 41F). *Ovary* half-inferior, ± 0.7 mm long, top villous with single nectarostomata (Figure 41D, E); locules 2, wall between complete at anthesis, each bearing a pendulous ovule on one of two placentas in each loculus; styles 0.9–1.3 mm long, slightly adnate, distally curved to point terminal stigmas into a lateral position. *Fruit* with enlarged receptacle and shrivelled flower parts attached; seed ovoid, 1.3×0.8 mm, brown, transversely wrinkled, lacking an elaiosome. *Flowering time*: January, April, May, August and October.

Diagnostic features: *Brunia compacta* differs from *B. sacculata* (Kirchner ex Pillans) Class.-Bockh. & E.G.H. Oliv. in having hairs on the adaxial leaf side, from *B. microphylla* Thunb. in having larger leaves (2.4–2.8 mm instead of 1.2–2.4 mm in *B. microphylla*) and from *B. squalida* E.Mey. ex Sond. in having distally recurved instead of erect styles. With the second group it shares the very short petals (shorter than 1.5 mm) appearing in all species so far included in this group. Herein, *B. compacta* is very similar to *B. bullata* (Schltr.) Class.-Bockh. & E.G.H.Oliv. differing in having 6–10 instead of only 1(–3) flowers per inflorescence. Though the relationships are not clear, the species is preliminarily grouped under *Brunia* subgen. *Mniothamnea*.

The species varies within the collections in having fast-growing coppice shoots among the normal ones, as in *Esterhuysen 32160* (BOL). These have longer and more densely villous leaves, and less profuse branching.

Distribution and ecology: *Brunia compacta* has been collected in the southern Cedarberg and Cold Bokkeveld Mountains, north of Ceres, at altitudes from 1 200 to 1 500 m (Figure 39). At one of its localities it is recorded as not common but widespread in the area (Apollo Peak, southern Cedarberg: *Esterhuysen 32160*). The shrubs occur among rocks, large boulders and cliffs on upper slopes. After fires the species reproduces from seedlings.

Note: this new species was at first recorded as one belonging in the genus *Raspalia* Brongn., but according to the new classification of the family (Claßen-Bockhoff *et al.* in press), it must be placed in the genus *Brunia* Lam. under which *Raspalia* is being placed in synonymy based on molecular analyses (Quint & Claßen-Bockhoff 2006).

Additional material examined

WESTERN CAPE.—3219 (Clanwilliam): Clanwilliam, Apollo Peak, S Cederberg, on S side at base of massive rock or cliffs, 4000–5000' [1 520 m], (–CA), 17-05-1969, *Esterhuysen 32160* (BOL); Clanwilliam, Kaffirkop [Kafferskop], suurvlaakte, S Cederberg, amongst boulders on upper slopes, (–CA), 17-04-1976, *Esterhuysen 34250* (BOL); Ceres, central peak of Schurweberg above 'Excelsior' N of Bokkeveld Tafelberg, amongst rocks on SW side of rocky summit, 4800' (?) [1 460 m], (–CD), 15-08-1971, *Esterhuysen 32619* (BOL); Ceres, Schurweberg Peak (between Bokkeveld Sneeuweg and Bokkeveld Tafelberg) amongst rocks, 4500' [1 370 m], (–CD), 1-01-1962, *Esterhuysen 29432* (BOL).

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- MS. received: 2008-10-16.

PTERIDOPHYTA: POLYPODIACEAE

THE STATUS OF $\times$ *PLEOPODIUM* IN AFRICA

A widespread central and southern African taxon almost intermediate between *Pleopeltis macrocarpa* (Bory ex Willd.) Kaulf and *Pleopeltis polypodioides* (L.) E.G. Andrews & Windham subsp. *ecklonii* (Kunze) J.P.Roux was shown convincingly by Anthony & Schelpe (1985) to arise from the hybridization of these two polypods. As at that time, *Pleopeltis polypodioides* subsp. *ecklonii* was referred to the genus *Polypodium* L., these authors necessarily established the hybrid genus $\times$ *Pleopodium* Schelpe & N.C.Anthony to accommodate their putative hybrid, $\times$ *Pleopodium simianum* Schelpe & N.C.Anthony. Roux

(2001) estimated that ± 10 such $\times$ *Pleopodium* taxa are known from the neotropics, with only one recorded for Africa (Roux 2009). We have been able to trace only five validly published $\times$ *Pleopodium* taxa worldwide (Anthony & Schelpe 1985; Mickel & Beitel 1987).

Following the transfer in Windham (1993) of the typical (neotropical) subspecies of *Polypodium polypodioides* (L.) Watt to *Pleopeltis* Humb. & Bonpl. ex Willd., Roux (2009) provided a new combination for the African subsp. *ecklonii*. Despite recognizing both puta-

tive parents of the southern African hybrid as belonging to *Pleopeltis*, Roux (2009) nevertheless retained it in $\times$ *Pleopodium*. This note corrects this oversight and accordingly provides a necessary new combination.

The Code (Art. H.10.1) requires a nothospecies to have a type (McNeill *et al.* 2006), as designated by Anthony & Schelpe (1985). However, nothogeneric names are condensed hybrid formulae (Art. H.6.1) defined by parentage and do not have a type (McNeill *et al.* 2006). Accordingly, although the first nothospecies described (Anthony & Schelpe 1985) represents a hybrid between two species of *Pleopeltis*, the nothogenus $\times$ *Pleopodium* remains a valid name applicable to (condensed formula) hybrids between *Pleopeltis* and *Polypodium*.

As the Code (Art. H.5.2) requires that the correct rank of a nothotaxon is the lower of the postulated parental ranks where these differ (McNeill *et al.* 2006), we must necessarily recognize the African hybrid at nothosub-specific rank. So to use nothospecific rank for a hybrid between *Pleopeltis macrocarpa* and *Polypodium polypodioides* subsp. *ecklonii* is incorrect. $\times$ *Pleopodium simianum* is the correct name for all hybrids between *Pleopeltis macrocarpa* and *Polypodium polypodioides*. It would appear that there is as yet no validly published name for the hybrid *Pleopeltis macrocarpa $\times$ *Polypodium polypodioides* subsp. *ecklonii* or for that matter *Pleopeltis macrocarpa $\times$ *Pleopeltis polypodioides* subsp. *ecklonii*. We note that Schelpe & Anthony's name is validly published apart from being at a rank not in accordance with the aforementioned article of the Code. This, and the inclusion by Roux (2009) of both putative parents in the same genus, makes the new combination necessary.**

Whereas Anthony & Schelpe (1985) identified the first valid publication of the name *Polypodium lanceolatum* var. *sinuatum* in Sim (1892), they seemingly overlooked the earlier publication of Sim (1891), *Handbook of the ferns of Kaffraria*. Subsequent workers (Burrows 1990; Roux 2001; Roux 2009) have accepted the interpretation of Anthony & Schelpe (1985). Although there was no explicit citation of a voucher in the protologue (Sim 1891) for *Polypodium lanceolatum* var. *sinuatum*, only one specimen implicitly mentioned by Sim from the correct location and time exists. We therefore nominate it as lectotype. There is a second Sim specimen from Perie (Sim TRV445C in PRE) but this is dated 1891 and as we cannot be certain that it existed before the protologue was published it cannot be designated a type. We have been unable to trace Sim material from the adjacent Evelyn Valley (Eastern Cape), mentioned by Sim (1891).

Roux (2009) cites as syntypes of *Polypodium lanceolatum* var. *sinuatum* some of the specimens mentioned in Sim (1892). However, as none of them were cited by Sim (1891), these are not available for selection (Code Artt. 9.2, 9.9, 9.10, 9.11 and 9.17; McNeill *et al.* 2006). We have, however, traced a specimen that was available, and necessarily overturn Roux's citations.

***Pleopeltis* $\times$ *simiana* (Schelpe & N.C. Anthony)
N.R. Crouch & Kloppe subsp. *simiana*, comb. nov.**

$\times$ *Pleopodium simianum* Schelpe & N.C. Anthony in Bothalia 15: 557 (1985). Type: South Africa, [KwaZulu-Natal], Lions River District, Everglades, 15-10-1964, Moll 1263 (BOL, holo.!, PRE, iso.!).

Polypodium lanceolatum L. var. *sinuatum* Sim: 51 (1891). *Pleopeltis macrocarpa* (Bory ex Willd.) Kaulf. forma *sinuata* (Sim) Schelpe: 96 (1969). Type: Eastern Cape, 3227 (Stutterheim): Perie, 4000 ft [1 220 m], (–CB), 12-1890, Sim TRV447C (PRE, lecto.!, designated here).

This paper does not make any combination for the hybrid *Pleopeltis macrocarpa* $\times$ *P. polypodioides* subsp. *polypodioides*, because no such hybrid from the neotropics is known to us. Should it exist or be made artificially, it would need to be named as a second nothosubspecies of *Pleopeltis* $\times$ *simiana*. We note though that actual hybrids between *Pleopeltis s.str.* and *Polypodium s.str.* ($\times$ *Pleopodium*) are of increasingly doubtful existence, based on recent treatments of neotropical polypods (Windham 1993; Hooper 1995; Salino 2009).

ACKNOWLEDGEMENT

We thank Dr John McNeill of the Royal Ontario Museum and Royal Botanic Gardens, Edinburgh for providing valuable nomenclatural insights.

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MS. received: 2009-10-07.

Pollen and reproductive morphology of *Rhigiophyllum* and *Siphocodon* (Campanulaceae): two unique genera of the fynbos vegetation of South Africa

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Keywords: Campanulaceae, Campanuloideae, Cape flora, carpels, floral evolution, fynbos, pollen, Rhigiophylleae, seed pockets, tribus nov., Wahlenbergioideae

ABSTRACT

Pollen grains of *Rhigiophyllum squarrosum* Hochst., *Siphocodon spartioides* Turcz. and *S. debilis* Schltr., are flattened and triangular with pores at the angles. This morphology is radically different from known pollen of the Campanulaceae s.str.: the Campanulaceae are treated here as a family separate from the Lobeliaceae, Cyphiaceae, Nemacladaceae, Pentaphragmataceae and Sphegnocleaceae (Lammers 1992). As traditionally conceived, the Campanulaceae is very heterogeneous and, in many classifications, these families were treated as subfamilies of a much-enlarged Campanulaceae. The consistently different floral morphology, biochemistry and pollen structure of the Lobeliaceae favours the recognition of this predominantly tropical group as a separate family.

The pollen grains of these species are described in comparison with other members of the Campanulaceae. Based on surface characteristics of their pollen grains, we conclude that they represent an early offshoot of the wahlenbergioid lineage in southern Africa. We suggest that this unique pollen may also be the result of a highly selective regime in the fynbos, associated with specialized pollinators, and base-poor soils, in addition to possible adaptations for ant dispersal and fire. *Rhigiophyllum* Hochst. and *Siphocodon* Turcz. are also unique in having free carpel-like structures within the ovary. These shrink to form seed pockets around the seeds and disperse as units when the capsule matures. Data from molecular studies support the contention that these taxa form a sister group to all other wahlenbergioids and that this should be formally recognized in a classification system. We treat *Rhigiophyllum* and *Siphocodon* within the Campanulaceae: Wahlenbergioideae, as a separate tribe, the **Rhigiophylleae** tribus nov., the species of which are distinguishable from other wahlenbergioids by unique angulaperturate pollen, epipetalous stamens, free carpel-like structures and seed pockets.

INTRODUCTION

During the course of a palynological re-investigation of the Campanulaceae¹ s.str., a number of pollen samples were obtained from material in the herbarium of the Royal Botanic Garden Edinburgh and sent to the third author for scanning electron micrograph imaging (SEM). Subsequently, samples representing *Rhigiophyllum squarrosum* Hochst. and *Siphocodon spartioides* Turcz., were found to have flattened, angular (triangular) pollen grains with pores at the angles. This morphology is radically different from all known pollen of the Campanulaceae, although it was reported for both genera in the landmark paper (in Russian) by Avetisian in 1967, which we had inadvertently overlooked. Initially, we suspected that the samples were contaminated, possibly due to alien pollen on the stigmas of the herbarium material. However, an examination of material at the Compton Herbarium at Kirstenbosch by the second author using light microscopy, confirmed that both of these species indeed had radically different pollen morphology. A third species, *S. debilis* Schltr., was also examined by the second author and found to have pollen similar to its congener but was not included in the SEM analyses.

This report describes the pollen shape and surface features of the exine of the two principal species and genera involved. We also discuss other features of these two genera such as floral morphology and the unique seed pockets, particularly with respect to their possible ecological significance. Finally, we discuss the systematic usefulness of these findings for a revised classification of the wahlenbergioid genera and describe a new tribe, the Rhigiophylleae, to accommodate *Rhigiophyllum* and *Siphocodon*.

MATERIALS AND METHODS

Pollen (Table 1) was examined with a JEOL model 880 scanning electron microscope after cleaning with acetolysis (Erdtman 1960) and made electrically conductive with gold/palladium (Chisoe & Skvarla 1996). For the light microscope (LM) examination, pollen of the respective species was removed from alcohol-preserved flowers. The pollen was placed on a microscope slide in a drop of water and examined. The gynoecium of *Rhigiophyllum* was exposed by a longitudinal free-hand section through the hypanthium wall and the removal of tissue with forceps.

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MS. received: 2009-03-30.

¹ The Campanulaceae is treated here as a family separate from the Lobeliaceae, Cyphiaceae, Nemacladaceae, Pentaphragmataceae and Sphegnocleaceae (Lammers 1992). As traditionally conceived, the Campanulaceae is very heterogeneous and, in many classifications, these families were treated as subfamilies of a much-enlarged Campanulaceae. The consistently different floral morphology, biochemistry and pollen structure of the Lobeliaceae favours the recognition of this predominantly tropical group as a separate family. Welman (2000) treats the Campanulaceae separately from Lobeliaceae, within which she included the genus *Cyphia* P.J.Bergius.

TABLE 1.—Species of Campanulaceae and Lobeliaceae for which pollen samples were examined in this study

Species	Collector/No.	Herbarium
<i>Burmeistera vulgaris</i> E.Wimm.	R. Lent 526	Bebb
<i>Campanumoea javanica</i> Blume	A. Henry 9634	RBGE
<i>Codonopsis convolvulacea</i> Kurz	Chungtien-Liang-Dali Expedition 648	RBGE
<i>Craterocapsa montana</i> (A.DC.) Hilliard & B.L.Burt	O.Hilliard & B.L. Burt 13221	RBGE
<i>Cyclocodon lancifolius</i> (Roxb.) Kurz	Collector unknown 1563	RBGE
<i>Jasione montana</i> L.	F.J. Hermann 4405	Bebb
<i>Leptocodon gracilis</i> (Hook.f.) Lem.	Sinclair & Long 4980	RBGE
<i>Merciera brevifolia</i> A.DC.	Schlechter 7211	RBGE
<i>Microcodon hispidulus</i> (L.f.) Sond.	Collector unknown 1993	RBGE
<i>Prismatocarpus fruticosus</i> (L.) L'Hér.	C.M. van Wyk 3420	RBGE
<i>Rhigiophyllum squarrosum</i> Hochst.	Schlechter 9616	RBGE
<i>Roella prostrata</i> E.Mey. ex A.DC.	R. Dümmer 938	RBGE
<i>Siphocodon spartioides</i> Turcz.	E. Esterhuysen 35770	RBGE
<i>Wahlenbergia marginata</i> (Thunb. ex Murray) A.DC.	J. & C. Taylor 16613	Bebb

RBGE, Royal Botanic Garden, Edinburgh.

Brief history of original description of *Rhigiophyllum* and *Siphocodon*

Hochstetter (1842) established the genus *Rhigiophyllum* for the sole species *R. squarrosum*, which was first collected near Elim, Bredasdorp. *Siphocodon* was established a decade later by Turczaninow (1852) for *S. spartioides*, based on collections from Klein Houwhoek, east of Grabouw, and from Swartberg, Caledon. Forty-five years later, Schlechter (1897) described a second species, *Siphocodon debilis* from Elim.

Ecology, distribution and morphology

Rhigiophyllum squarrosum and both species of *Siphocodon* occur on nutrient-poor soils associated with sandstone slopes of the southwestern Cape and are typical, but highly localized, fynbos plants. *Rhigiophyllum* occurs from Akkedisberg, northeast of Stanford to Napier and Bredasdorp, whereas *S. spartioides* occurs from Sir Lowry's Pass near Somerset West to the Langeberg in Riversdale and *S. debilis* occurs from the Hottentots Holland Mountains near Stellenbosch to Bredasdorp and inland to Riviersonderend (Figure 1).

Rhigiophyllum squarrosum is a rigid, sparsely branched subshrub, $\pm$ 0.30–0.45 m tall with the habit of species of *Roella* L. Its broadly ovate, coriaceous leaves are imbricate, squarrose, entire and in four ranks. Lanceolate bract-like leaves subtend the azure-violet flowers, which are aggregated in a terminal head. The corolla is elongated and consists of a long narrow tube terminated by five spreading obtuse lobes. The style is filiform, exserted, and terminates into three short stigmatic lobes (Figure 2A, B).

The two species of *Siphocodon* are radically different in appearance from *Rhigiophyllum*. They are glabrous, wiry subshrubs (*S. spartioides* is 0.3–0.6 m tall, *S. debilis* somewhat smaller) with sparse, minute, scale-like, appressed leaves. The flowers are solitary, terminal and axillary, mostly towards the apices of the stems in a loose, few-flowered inflorescence. The flowers of *Siphocodon spartioides* are bluish purple, whereas those of *S. debilis* are violet or whitish with pinkish brown honey-guides on the corolla tube. The corolla is narrowly tubular-campanulate with five spreading obtuse

lobes incised to about one-third the length of the tube. The style is filiform, included and terminates into three short stigmatic lobes in *S. spartioides*, whereas in *S. debilis* the stigma is capitate (Figure 2C–E).

On closer inspection of the corolla and capsule of both genera, a number of common features are found. For example, both have rather long, tubular corollas with the stamens adnate via the filaments to the corolla tube, the latter feature being unique among the Campanulaceae. The stamens of *Rhigiophyllum squarrosum*, which are almost exserted, are attached below the apex of the corolla tube but the filaments are decurrent nearly to the base. In *Siphocodon debilis*, the stamens are included and are attached at the middle of the corolla tube, whereas in *S. spartioides*, they are attached in the upper part of the tube.

The capsule dehiscence is by means of a plug in *Rhigiophyllum* (Figure 3C) or circumscissile by means of an operculum in *Siphocodon* (Figure 3E). In both genera, these structures comprise the upper part of the ovary and the style, surrounded by the persistent corolla. In *Rhigiophyllum*, the line of dehiscence is above the calyx lobes and the seeds (within seed pockets) are dispersed through a narrow hole, whereas in *Siphocodon* it is below, so that, when the operculum detaches, the remaining lower

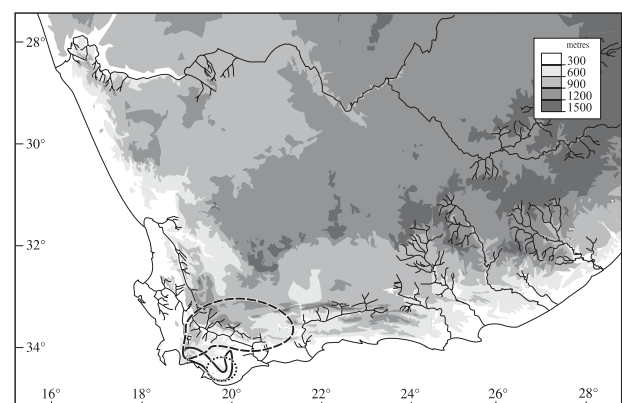


FIGURE 1.—Known distribution of *Rhigiophyllum squarrosum* (dotted line); *Siphocodon spartioides* (solid line) and *S. debilis* (dashed line).

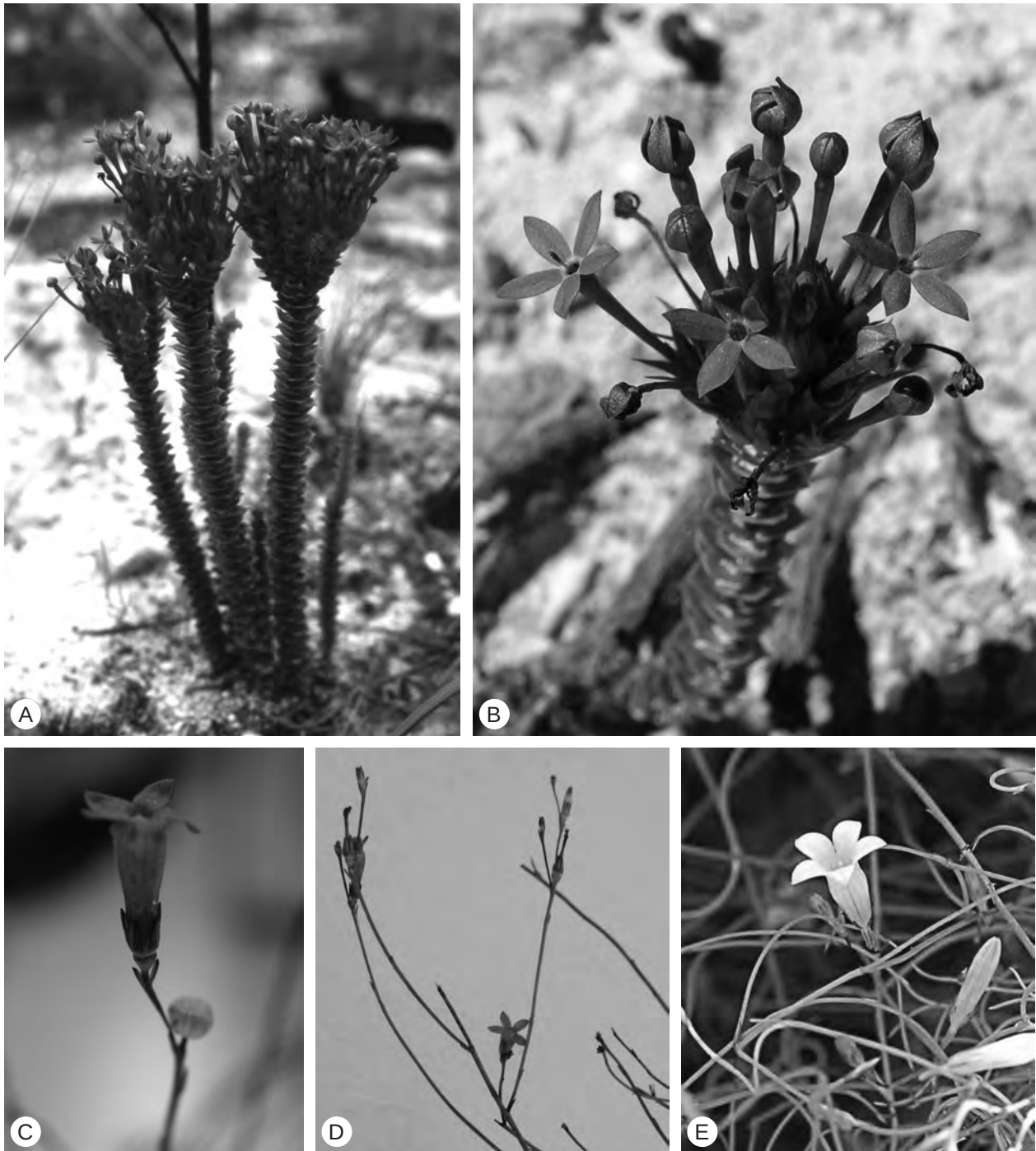


FIGURE 2.—A, B, *Rhigiophyllum squarrosum*: A, habit; B, details of inflorescence. C, D, *Siphocodon spartioides*: C, details of flower and remains of capsule; D, slender wiry stems. *S. debilis*: E, details of flower showing honey-guides and the twisted, entwined stems. Photographs: A, W.M.M. Eddie; B–E, C.N. Cupido.

part of the capsule is a neat, open, cup-like structure. In *Rhigiophyllum*, the remainder of the capsule easily detaches from the pedicel and disperses, probably with some seeds remaining inside. Since the line of dehiscence in the capsule of *Rhigiophyllum* is above the calyx lobes, it resembles that of *Roella* and therefore differs in positional homology from the mechanism in *Siphocodon*.

Unlike other wahlenbergioids, these two genera have (2)3 free carpel-like structures within the inferior ovary, each of which has two to several pendulous ovules attached near the top (Figure 4B7). It is difficult to decide if the seed pockets separate from the wall of the infe-

rior ovary of adult flowers or if they are formations *sui generis* (proliferations of the placentae) (Erbar & Leins pers. comm.)*. Some ovules appear to abort before maturity leaving just one or two seeds per structure (Figure

* Profs Claudia Erbar and Peter Leins conducted a preliminary investigation of the ovary of *Rhigiophyllum* from material supplied by the second author. They report that the inferior ovary develops as in all other cases [of Campanulaceae] due to an intercalary growth in the floral axis and that the seed pocket is a special form of an endocarp. The epidermis (and eventually a few cells of deeper layers) of the ovary locules separates from the wall of the inferior ovary to form the seed pockets. A complete ontogenetical study (including histology and SEM-investigation) is planned and the results will be published in due course.

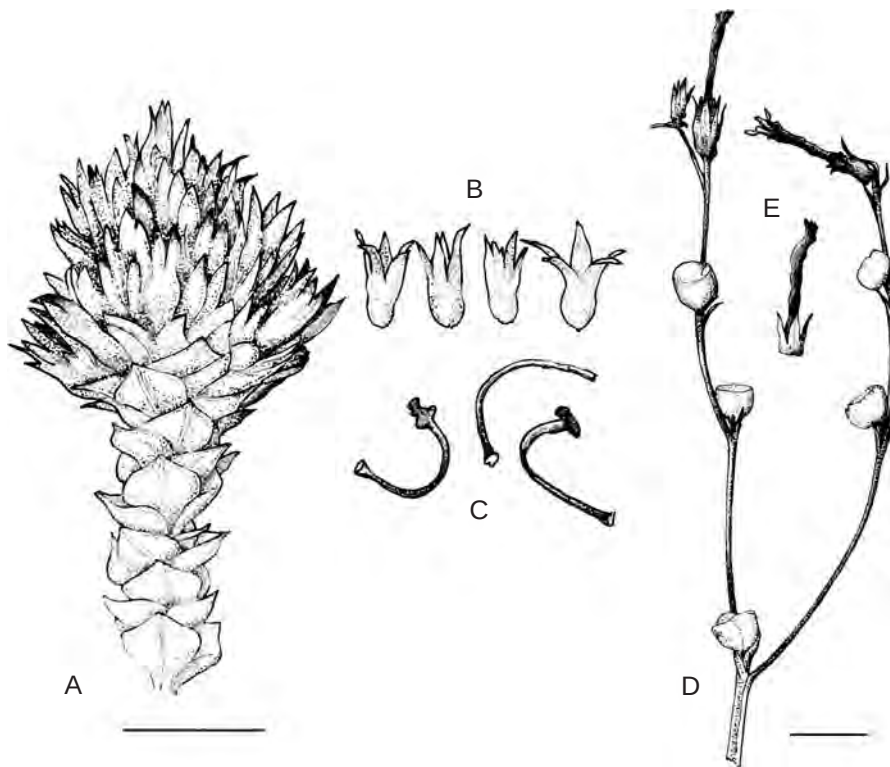


FIGURE 3.—A–C, *Rhigiophyllum squarrosum*, Cupido s.n.: A, fruiting head showing aggregation of mature capsules; B, individual mature capsules removed from head and showing spreading calyx lobes; C, withered corollas enclosing styles with attached plug (ovary top). D, E, *Siphocodon spartioides*, Eddie 1017: D, branched stem showing remains of dehiscent capsules; E, corolla enclosing style and attached to upper calyx and calyx lobes (circumscissile lid or operculum). Scale bars: A–C, 10 mm; D, E, 10 mm. Artist: W.M.M. Eddie.

4E11). The walls of these carpel-like structures shrink to enclose the seed at maturity, forming a carunculated pocket (Figure 4D10), which is released entire from the mature capsule. This structure was apparently overlooked by Botting Hemsley in *Hooker's Icones plantarum* (1897) where he described the ovary simply as: 'Ovarium 3-loculare, loculis pluriovulatis, ovulis pendulis'. In Sonder (1865: 596), this seed pocket is apparently misidentified as a 'very loose, rugose testa'. The protuberances on the surface of the seed pocket are more round and regular. There are also slight differences in seed shape. *Siphocodon* seeds are slightly diamond-shaped in comparison with the oval seeds of *Rhigiophyllum*. In both genera the seeds have a strong electrostatic charge and 'jump' to about 0.1 m when manually extracted from the pockets. The function of the seed pocket is unknown, but it may perform a role in dispersal, for example by ants. The seeds of these three taxa are large and few in number and this may be correlated with the establishment of the seedling in nutrient-poor environments (Eddie & Cupido 2001). The shiny testa of the seed would suggest that dormancy and nutrient release by fire may be important components in their ecology. Shiny testae are a feature of many annual species of the Campanulaceae where seed dormancy is the norm (Eddie 1997).

Description of pollen grains of *Rhigiophyllum squarrosum* and *Siphocodon spartioides*

Figures 5 and 6 show the radical differences in pollen morphology between *Rhigiophyllum squarrosum* and *Siphocodon spartioides* and other wahlenbergioid genera such as *Wahlenbergia* Schrad. ex Roth, *Craterocapsa* Hilliard & B.L.Burt, *Prismatocarpus* L'Hér., *Roella*, *Merciera* A.DC. and *Microcodon* A.DC. and between platycodonoid genera such as *Leptocodon* (Hook.f.) Lem.,

Campanumoea Blume, *Cyclocodon* Griff. ex Hook.f. & Thomson and *Codonopsis* subgen. *Pseudocodonopsis* Kom.

Pollen grains disperse as monads and they are superficially like *Alnus* Miller/*Betula* L./*Corylus* L. (Betulaceae) or *Rhamnus* L. (Rhamnaceae), but very unlike the pollen of *Pentaphragma* Wall. ex G.Don (Pentaphragmataceae), which was formerly considered to be close to the Campanulaceae, and which has trilobate pollen with the pores between the lobes (Dunbar 1978, 1979, 1981). Their shape in polar view is reminiscent of species of *Acarpha* Griseb. (Calyceraceae) (De Vore *et al.* 2007) or species of *Lopezia* Cav. (Onagraceae) (third author). They are angular (triangular and obtuse or straight to slightly convex) in polar view; non-angular (elliptic and obtuse) in equatorial view; trizonoporate (rarely tetrazonoporate) (stephanoporate of Faegri & Iversen 1975) in equatorial zone; pori circular, situated at the angles (angulaperturate) and non-vestibulate; large, $\pm 50 \mu\text{m}$ diameter (*R. squarrosum*, Figure 5A) or $\pm 40 \mu\text{m}$ diameter (*Siphocodon spartioides*, Figure 5B); sculpturing is verrucate in *S. spartioides*, or psilate in *R. squarrosum*.

Palynological investigations of the Campanulaceae

Studies of the pollen of the Campanulaceae are extensive and the family is comparatively well known palynologically, but there are gaps in our knowledge of the wahlenbergioid taxa of the southern hemisphere, and of many endemic campanuloid taxa of central Asia. A brief, if diverse, survey of Campanulaceae pollen was provided by Erdtman (1952), followed by a similar survey of 21 genera by Chapman (1967). Avetisyan (1967) provided a firm foundation for a systematic re-appraisal of the family using palynological characters, but the most thorough examination of the family using scanning electron microscopy was conducted by Dunbar (1973a–c,

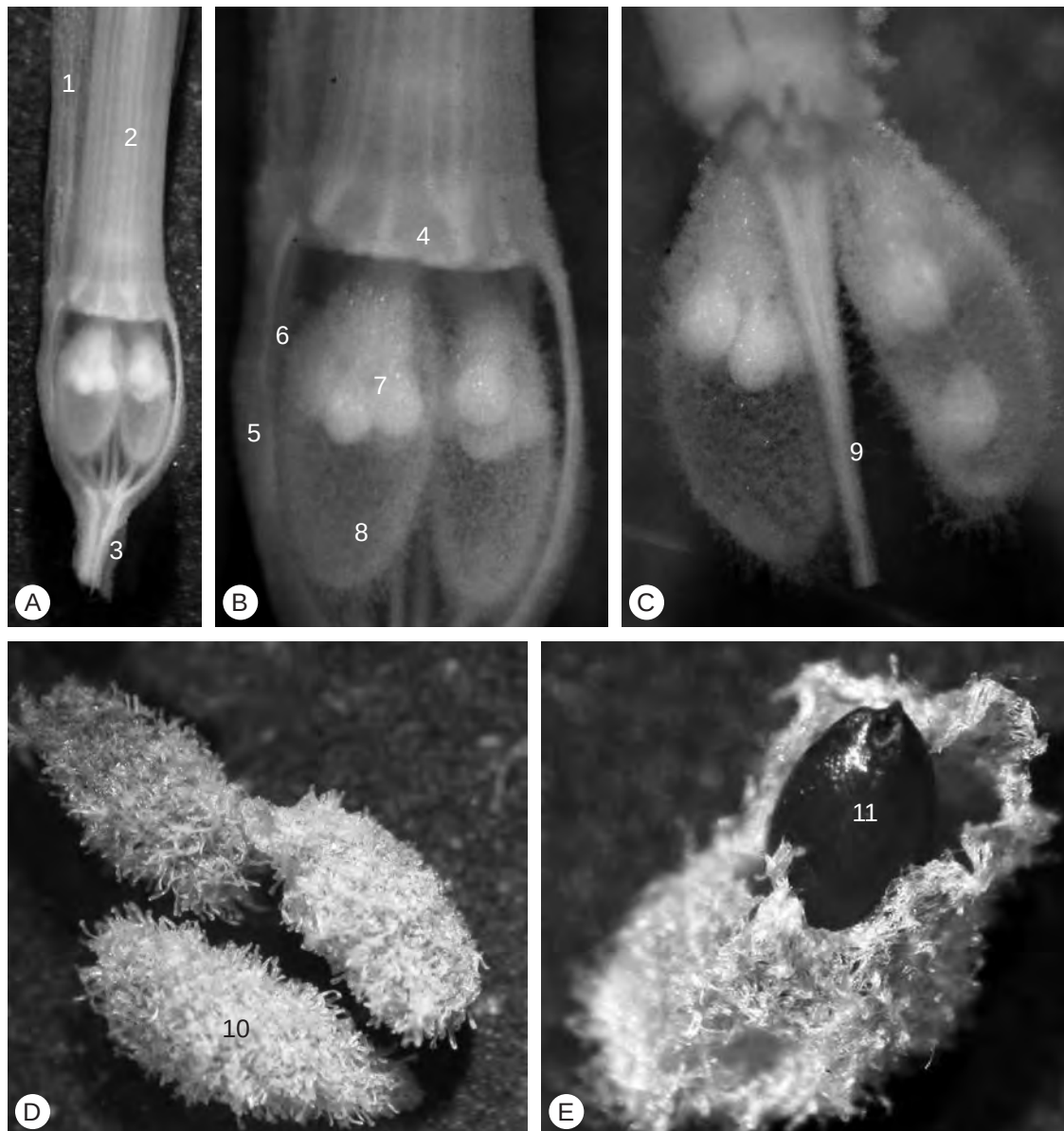


FIGURE 4.—LM photographs of *Rhigiophyllum squarrosum*. A, gynoecium and corolla showing: A1, calyx lobes; A2, corolla; A3, peduncle. B, detail of gynoecium showing: B4, corolla; B5, calyx lobe; B6, ovary wall; B8, separate carpel-like structures; enclosing B7, pendulous ovules. C9, central veins of ovary; D10, carunculated seed pockets formed by shrinking carpel-like structures; E11, seed pocket showing a mature seed. Photographer: C.N.Cupido.

1975a, b, 1978, 1979, 1981, 1984), who also studied ontogeny, and by Dunbar & Wallentinus (1976) using phenetic methods. The pollen of the Campanulaceae can be divided into two broad groups as follows:

1. The platycodonoid taxa of Asia and Africa (e.g. *Platycodon* A.DC., *Cyananthus* Wall. ex Benth., *Codonopsis* Wall., *Cyclocodon*, *Campanumoea*, and *Canarina* L.) have pollen that is either 6–10-colpate, 3-colporate, or 5- or 6-colporate (Figure 6). They have in common an oblate-spheroidal shape, a relatively high number of colpi and an exine sculpturing that consists of spinules, verruca-like spinules, or verrucae, between which are small pits of uniform diameter, or a reticulum in low relief with very small lumina. The ectexine structure consists of a tectum perforated by mostly narrow channels, medium to high bacula that are closely adpressed in some species, and a reduced or absent foot layer. The endexine is almost undivided.

2. The campanuloid and wahlenbergioid taxa have pollen that is 3- or 4-porate, 6-porate, or 12-porate (Figure 5). The porate taxa are mostly zontotreme or rarely pantoporate. The pantoporate condition is approached in those species that have an increased number of pores and where the position of the pores becomes irregular and not strictly zontotreme. The shape of the pollen is spheroidal or oblate-spheroidal, rarely suboblate or prolate-spheroidal. The exine sculpture consists of spinules of different number, shape and size. Between the spinules there are ridges, protrusions or a low-relief reticulum, finger-like structures, or ridges with the top end bent upwards (Dunbar 1975a). The ectexine structure (and sculpture) varies from simple to complex. Complex ectexine consists of a surface covered by spinules, distinctly divided basally, short ridges/protrusions between spinules, a sponge-like tectum, stubble-like bacula continuous with an undivided foot layer, and connections to the tectum may be thin. Less complex ectexine con-

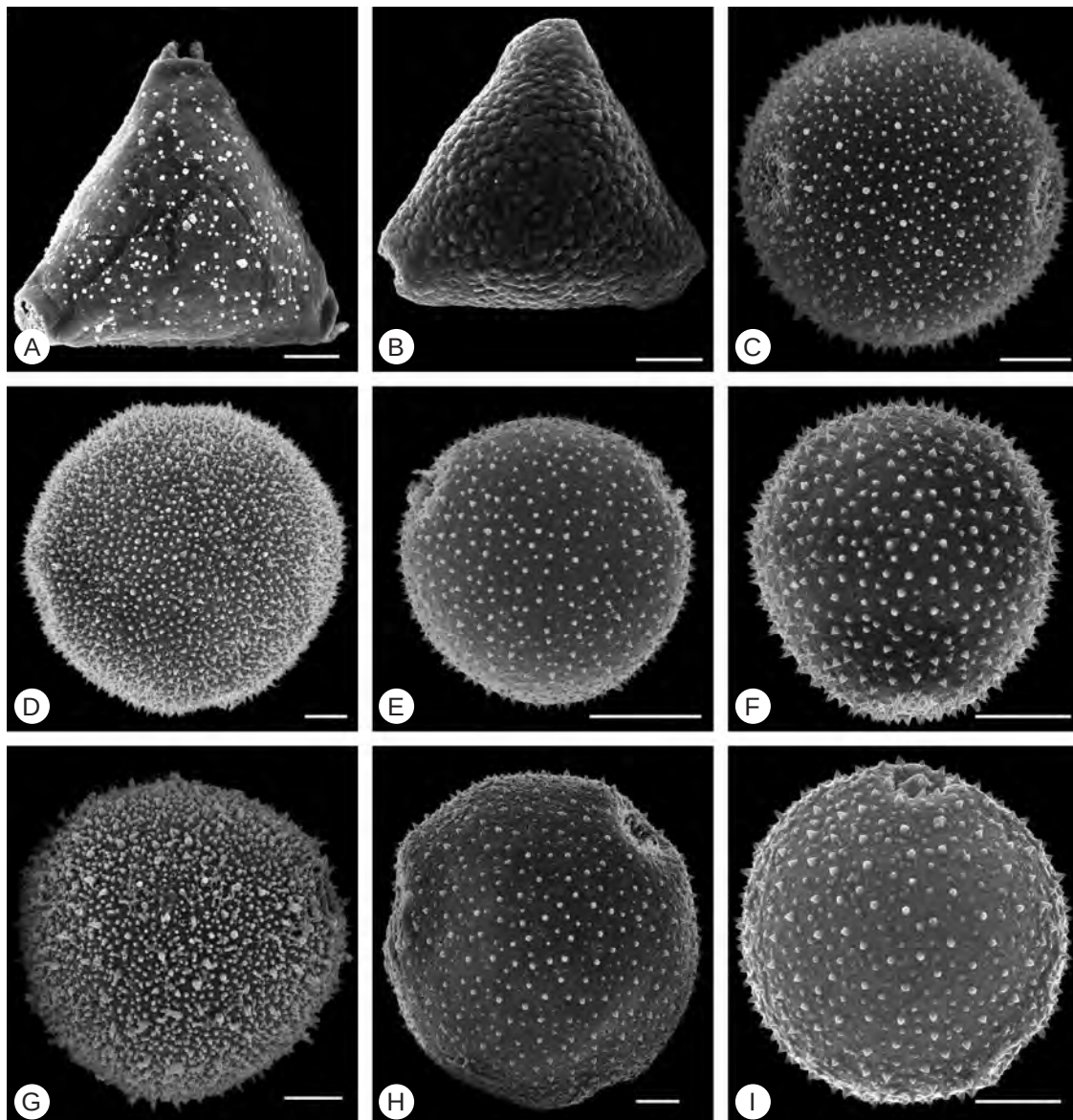


FIGURE 5.—SEM micrographs of pollen of wahlenbergioid genera of Campanulaceae plus *Jasione* (all polar view except C). A, *Rhigiophyllum squarrosum* Hochst.; B, *Siphocodon spartioides* Turcz.; C, *Prismatocarpus fruticosus* (L.) L'Hér. (equatorial view); D, *Wahlenbergia marginata* (Thunb. ex Murray) A.DC.; E, *Craterocapsa montana* (A.DC.) Hilliard & B.L.Burt; F, *Microcodon hispidulus* (L.f.) Sond.; G, *Roella prostrata* E.Mey. ex A.DC.; H, *Merciera brevifolia* A.DC.; I, *Jasione montana* L. Scale bars: A–C, E–G, 10 μ m; D, H, I, 5 μ m. SEM micrographs by J.J. Skvarla.

sists of a surface covered by spinules, which, in some species, divide basally, together with protrusions, low-relief reticula, a thin, distinctly outlined tectum perforated by channels, high bacula that are continuous with the tectum and an undivided foot layer. Simple ectexine consists of a surface covered by discrete spinules, less distinctly divided than the complex type, and low protrusions. The uniformly outlined tectum is perforated by narrow channels and has the same thickness as the undivided foot layer. The bacula are medium/high, and are continuous with the tectum and foot layer. The endexine, which varies in thickness, is lamellated, except in the simple ectexine type.

Knowledge of pollen morphology in the wahlenbergioid genera is patchy and mostly concentrated on the genus *Wahlenbergia* (Thulin 1974; Dunbar 1975a, b), although a detailed study of the pollen of *Hetero-*

chaenia A.DC. was undertaken by Badré *et al.* (1972), and by Straka & Simon (1969). Wahlenbergioid genera such as *Prismatocarpus*, *Roella*, and *Wahlenbergia* are all in Dunbar's Group 1, i.e. pollen grains that are mostly radially symmetrical, isopolar, zontotreme, 3–5-porate, spheroidal and tectate. Spinules are evenly distributed over the non-apertural surface of the pollen grains. These three genera did not show any particular clustering with each other with respect to the other taxa (Dunbar 1975a, b). Apparently Von Brehmer (1915) considered the pollen morphology to be of no value as a taxonomic character in *Wahlenbergia*. However, Erdtman (1952) placed *Wahlenbergia*, *Roella* and *Prismatocarpus* in a group of genera with (2)3–(5)-porate, suboblate to oblate spheroidal pollen with spinuliferous sexine, which is thinner than the nexine. Avetisian (1967) studied five species of *Wahlenbergia* (including *W. hederacea* (L.) Rchb.), seven species of *Lightfo-*

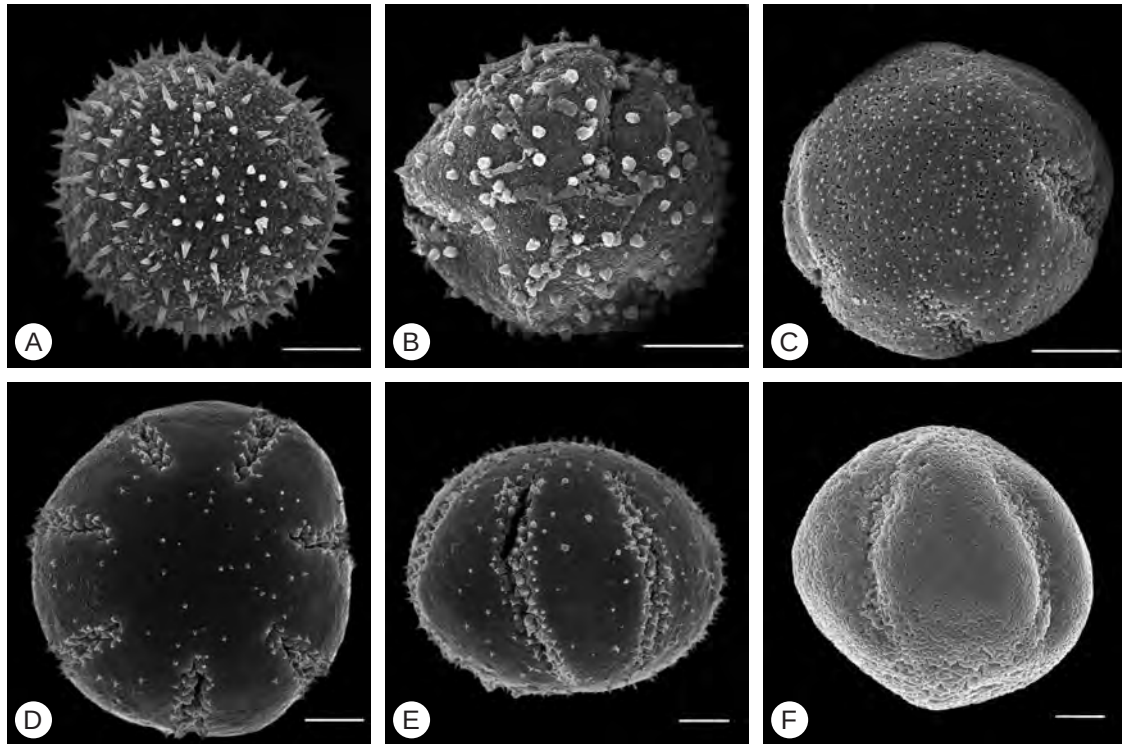


FIGURE 6.—A–F, SEM micrographs of pollen of platycodonoid genera of Campanulaceae and Lobeliaceae (all polar view except E and F): A, *Codonopsis* (subgen. *Pseudocodonopsis* Kom.) *convolvulacea* Kurz.; B, *Cyclocodon lancifolius* (Roxb.) Kurz.; C, *Campanumoea javanica* Blume; D, E, *Leptocodon gracilis* (Hook.f.) Lem.; F, *Burmeistera vulgaris* E.Wimm. (Lobeliaceae). Scale bars: A–C, 10 μ m; D–F, 5 μ m. SEM micrographs by J.J. Skvarla.

tia L'Hér. nom. illeg. and *Cephalostigma* A.DC., and claimed to be able to differentiate between these three taxa. Straka & Simon (1969) distinguished two types of wahlenbergioid pollen in the Madagascan flora. The *Cephalostigma*-type is characteristic of *C. hirsutum* Edgew. and is 4–6-pantoporate, whereas the *Wahlenbergia*-type, which is 3-zonoporate is characteristic of *W. perrieri* Thulin and *W. madagascariensis* A.DC., in addition to the Mascarene endemic genera *Berenice* Tul. and *Heterochaenia* (Thulin 1975).

The species studied by Thulin (1975) and formerly placed in *Cephalostigma* included: *Wahlenbergia erecta* (Roth ex Schult.) Tuyn; *W. flexuosa* (Hook.f. & Thomson) Thulin; *W. hirsuta* (Edgew.) Tuyn; *W. hookeri* (C.B.Clarke) Tuyn; *W. ramosissima* (Hemsl.) Thulin; and *W. perrottettii* (A.DC.) Thulin. He concluded that *Wahlenbergia*, *Cephalostigma* and *Lightfootia* could not be distinguished on pollen characters, although *W. hirsuta* has an increased numbers of pores that could be of taxonomic value. According to Thulin, with increasing number of pores, the position of the pores becomes irregular and not strictly zonotreme. Several differences in spinule size and density exist between different groups of the genus *Wahlenbergia*. For example, the *W. undulata* (L.f.) A.DC. group has longer spinules than other groups, and the area of the exine between the spinules in the *W. undulata* and *W. madagascariensis* groups is distinctly granular or with short ridges. Thulin (1974) also reported that the pollen of *Namacodon* Thulin disperses in tetrads, unlike the pollen grains of all other taxa in the family, which disperse as monads—tetrads have been recorded in *Legousia falcata* (Ten.) Fritsch ex Janch. (first author, unpublished data).

Molecular studies

Recent molecular studies using *trnL*-F and ITS gene sequences (Cupido 2008) and combined chloroplast DNA datasets (*rbcL*, *atpB* and *matK*) (Haberle *et al.* 2009) have shown quite conclusively that the strongest molecular affinities of *Rhigiophyllum* are with the two species of *Siphocodon* (Figures 7; 8). *Merciera*, *Roella* and *Prismatocarpus* form a well-supported clade, but the relationships within this clade are largely unresolved. *Merciera* however, forms a weakly supported subclade. *Roella*, *Prismatocarpus* and *Wahlenbergia* were also found to be paraphyletic, the latter massively so. *Theilera* E.Phillips was found to be closest to several species of *Wahlenbergia*, all of which were formerly treated as *Lightfootia*, and in a clade comprising *Craterocapsa* and *Wahlenbergia procumbens* (L.f.) A.DC., *W. huttonii* (Sond.) Thulin, and *W. stellarioides* Cham.

Another surprising result of the molecular studies has shown that *Rhigiophyllum* and *Siphocodon* form a sister group to all the other southern hemisphere wahlenbergioids, including taxa from the Mascarene Islands and St Helena (Haberle *et al.* 2009). This has profound implications, for it suggests that this split in lineages was a very ancient one. Previous molecular studies (Eddie *et al.* 2003) using ITS nrDNA found a clear dichotomy between the colpate/colporate platycodonoid taxa and the porate wahlenbergioid and campanuloid taxa. This major split in the Campanulaceae is hypothesized to be a consequence of the isolation engendered by tectonic activity in a fragmenting Early Tertiary Gondwana (Eddie *et al.* 2003). Subsequent evolution of these two lineages was independent, with the bulk of the platycodonoid taxa remaining in the southern hemisphere.

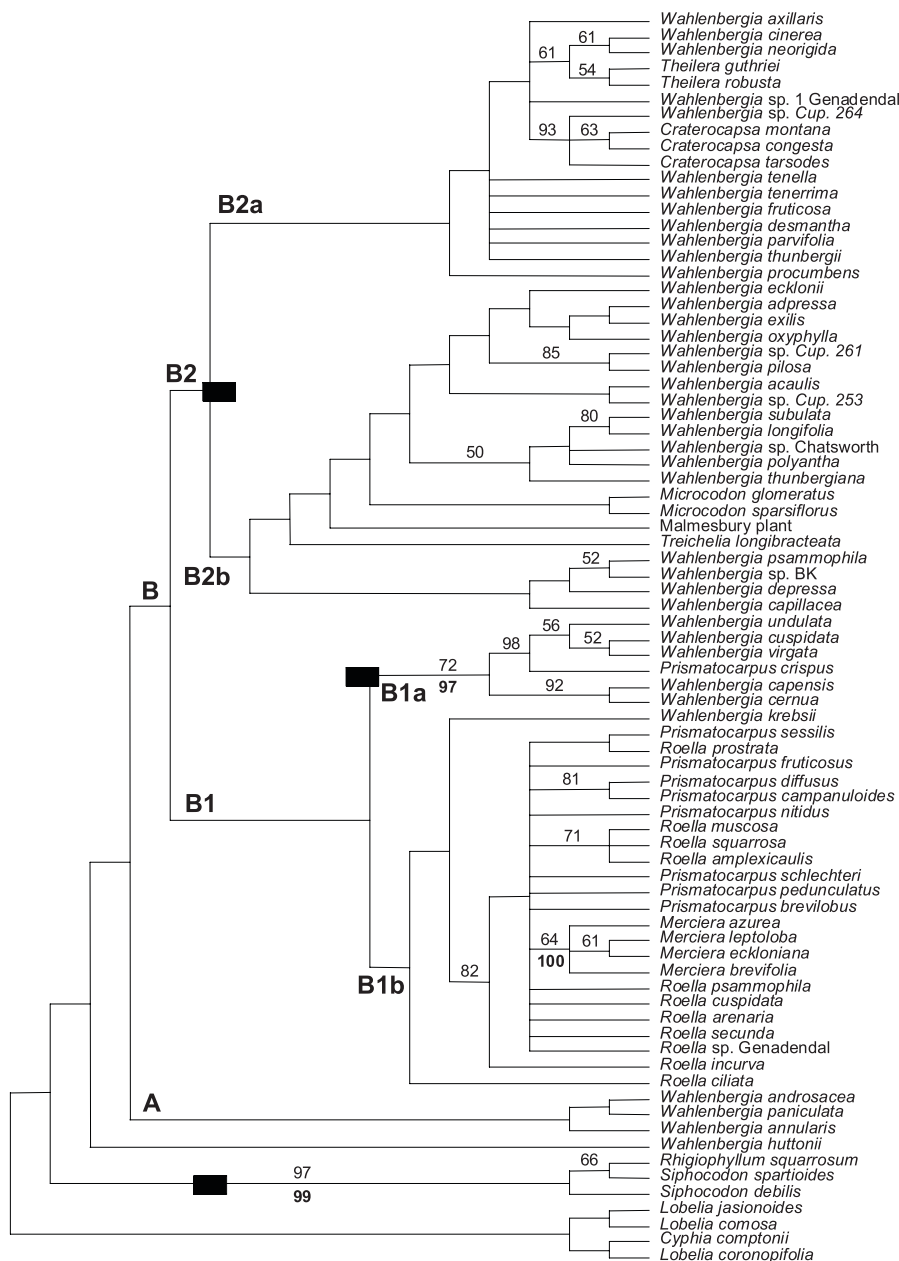


FIGURE 7.—Strict consensus of 165 equally parsimonious trees (length = 859, CI = 0.511, RI = 0.739) found after heuristic search of the ITS data set for 75 taxa of the South African Campanulaceae and four Lobeliaceae/Cyphiaceae (outgroup). Bootstrap values $\geq 50\%$ indicated above branches. Numbers below branches indicate posterior probability values expressed as percentages (from Cupido 2008). ■, clades common to all analyses.

donoids in eastern Asia, the wahlenbergioids in Africa, and the campanuloids differentiating primarily in northern Africa and the evolving Mediterranean region.

DISCUSSION AND CONCLUSIONS

Pollen morphology of Rhigiophyllum and Siphocodon

The triangular pollen of *Rhigiophyllum* and *Siphocodon* is so unlike the known pollen of the Campanulaceae that it throws their relationship with that family into question. Kolakovsky (1987: 1573) excluded both genera from the Campanulaceae, yet, from molecular data (Eddie *et al.* 2002; Haberle *et al.* 2009) and their possession of porate pollen, it would appear that these genera are correctly placed close to typical wahlenbergioid, porate taxa. From a biogeographical viewpoint, one would favour a relationship with the wahlenbergioid taxa so characteristic of southern Africa, and with which they have traditionally been associated. The surface sculpturing of the

pollen is more simplified, lacks the dense spinuliferous condition, and recalls the surface features of the pollen found in the platycodonoid genera. This suggests that these two genera may represent an older lineage of the Campanulaceae in southern Africa that is somewhat intermediate between platycodonoids and wahlenbergioids, or it may be that the pollen morphology is convergent with that of the platycodonoids (perhaps the result of paedomorphosis and/or neoteny). However, some porate pollen in the Campanulaceae is simpler in structure than the dense spinuliferous type. Avetisyan (1967) suggested that tropical colpate/colporate pollen is the most primitive type within the Campanulaceae, whereas porate pollen from temperate zones, including pantoporate pollen, is considered an advanced type (Van Campo 1966; Muller 1970; Punt 1976). Dunbar's (1984) results agree partially with this view with respect to complex exine. Perhaps the unique triangular pollen represents a highly specialized adaptation either to conditions pertaining to their pollinators or to some, yet unknown, biological component

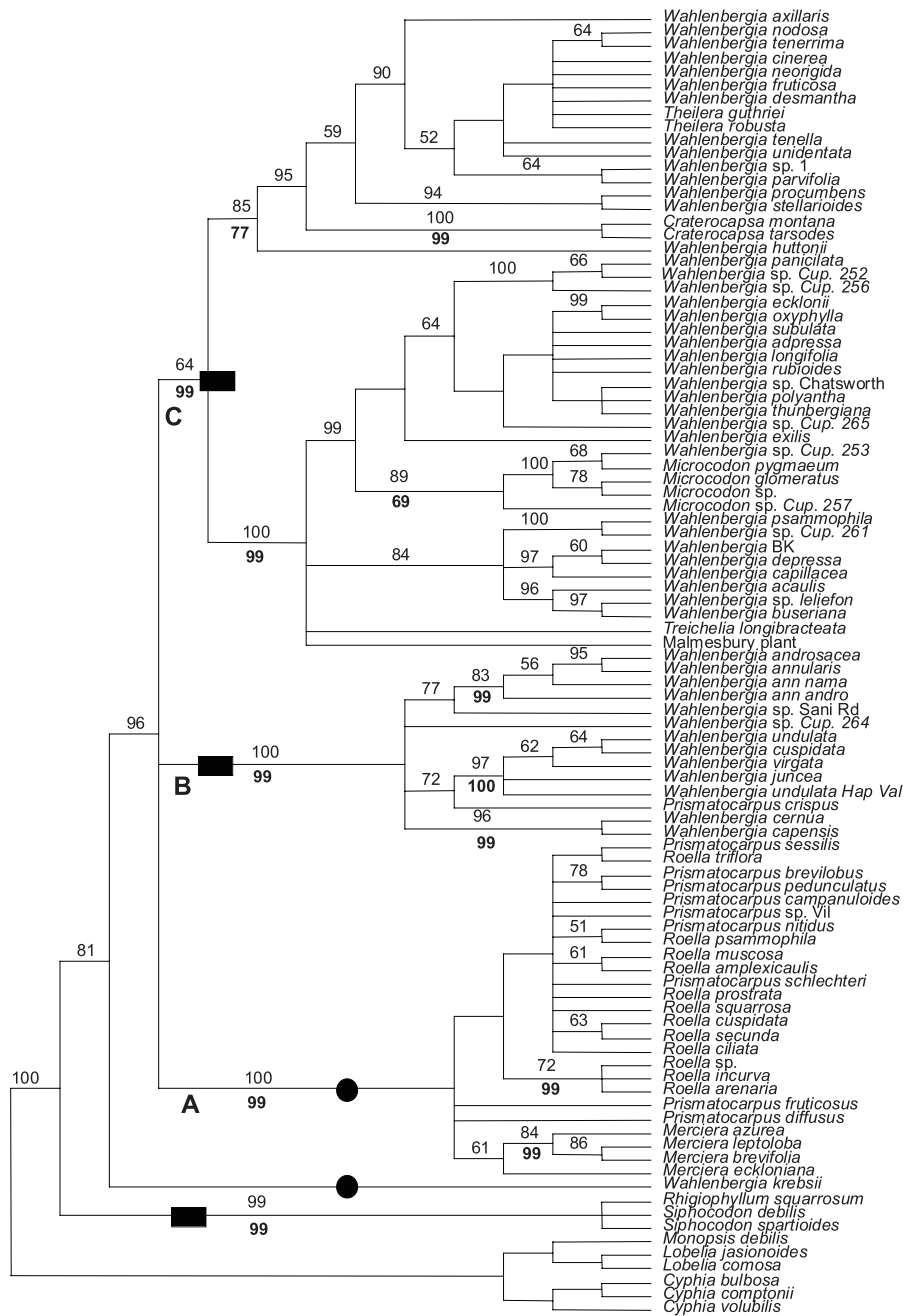


FIGURE 8.—Strict consensus of 415 equally parsimonious trees (length = 945, CI = 0.684, RI = 0.872) found after heuristic search of the *trnL-F* data set for 90 taxa of the South African Campanulaceae and six Lobeliaceae/Cyphiaceae (outgroup). Bootstrap values $\geq 50\%$ indicated above branches. Numbers below branches indicate posterior probability values expressed as percentages (from Cupido 2008). ■, clades common to all analyses; ●, clades common between *trnL-F* and the combined analysis.

of the fynbos vegetation. This explanation seems highly plausible, but no other members of the Campanulaceae have this type of pollen, so the functional significance of the triangular pollen remains unresolved.

General morphology and ecology of the fynbos wahlenbergioids

Rhigiophyllum and *Siphocodon* share a number of morphological features with other fynbos taxa such as *Merciera*, *Theilera*, *Roella*, *Pristmatocarpus* and many fynbos species of the group formerly included in the illegitimate genus *Lightfootia*. They all show radical departures in a whole suite of morphological characters from the temperate Campanulaceae *bauplan*, although most can loosely be described as ericoid. All are dwarf undershrubs or shrublets, somewhat rigid or wiry, and frequently with ericoid leaves in fascicles (e.g. *Merciera* and *Theilera*), or imbricate, as in *Rhigiophyllum*.

Many of them have long tubular flowers (*Merciera*, *Theilera*, *Rhigiophyllum*, and *Siphocodon*) and indehiscent capsules (*Merciera*) or at least an unusual capsule dehiscence mechanism (*Pristmatocarpus*, *Roella*, *Rhigiophyllum*, and *Siphocodon*). Several of these genera (e.g. *Merciera*, *Theilera*, and *Pristmatocarpus*, subgen. *Afrotrachelium* Adamson) even show a remarkable, if superficial, resemblance to the Lobeliaceae and Stylidiaceae, and the flowers of *Rhigiophyllum* look similar to those of *Calyceia* Cav. (Calyceaceae). The flowers are either solitary and more or less sessile (*Roella*, *Pristmatocarpus*, *Theilera* and *Merciera*), in loose terminal inflorescences (*Pristmatocarpus*, *Siphocodon*), or rarely in dense heads (*Rhigiophyllum*). These features suggest a general convergence in morphologies that may correlate with similar ecologies. However, as shown by the molecular studies, these subgroups are not part of the same phylogenetic sublineages and their similarities are probably superficial. They may be best considered as parallel ecotypes.

Rhigiophyllum is so dissimilar morphologically from both species of *Siphocodon* that, on first inspection, a close relationship between these two genera is not obvious. Furthermore, *Siphocodon spartioides* is very unlike *S. debilis*, yet, the infrageneric disparity in morphology between *Siphocodon spartioides* and *S. debilis* offers a possible clue to the evolutionary history of all three taxa, in addition to that of the fynbos wahlenbergioids in general. This disparity suggests that divergent selection pressure has been intense, driving three closely related species towards radically different morphologies. A similar situation is seen in the two species of *Musschia* Dumort. (Campanulaceae) on Madeira (Eddie *et al.* 2003).

The evolutionary divergence of *Rhigiophyllum* and *Siphocodon* probably occurred early, in concert with the progressive aridity of the Cape Region (Cupido 2008). From the similarity of their floral morphology with other fynbos plants, we can infer that these taxa have highly specialized pollination syndromes, probably with long-proboscid flies (including horse flies, tangle-wing flies and bee flies) as the principal pollen vectors (Goldblatt *et al.* 1995). However, until further studies are completed, we simply do not know what adaptive advantages, if any, are conferred by the unique pollen morphology, and ontogenetic studies are required to determine the significance of the triangular shape before and after tetrad formation.

It is clear that these three species display a highly integrated complex of adaptations to the fynbos vegetation and that nuances in ecological requirements probably account for the differences between them, but the functional aspects of these adaptations remain unclear. This argument applies also to all the other wahlenbergioid genera in the fynbos, and therefore the merging of genera such as *Theilera* and the illegitimate *Lightfootia* in *Wahlenbergia* is surely premature (Lammers 1995; Goldblatt & Manning 2000), although Lammers (2007: 382) acknowledged that some species, currently included in *Wahlenbergia*, could be given separate generic recognition. From this perspective, the recognition of *Rhigiophyllum* and *Siphocodon* should be upheld.

From the pollen studies, and the work of Dunbar, it would appear that there are more similarities between the pollen of the Campanulaceae and the Cyphiaceae s.lat. than the Lobeliaceae. The unique stylar morphology of the Cyphiaceae suggests that this family may be the most ancient lineage of Campanulales in Africa and possibly derived from ancestors, which, themselves, eventually diversified in Australia as the Goodeniaceae and Stylidiaceae. This hypothesis requires further investigation. The Cyphiaceae have unicellular stylar hairs, which resemble those of the Campanulaceae more than those of Lobeliaceae (Leins & Erbar 2005), and it would be interesting to survey this character as well as secondary pollen presentation mechanisms in all South African genera of the Campanulales.

The major dichotomy between the pollen of the platycodonoids (represented in Africa and the Canary Islands by the relict *Canarina*) and the wahlenbergioids/campanuloids, suggests that this split is an ancient one (Eddie *et al.* 2003) dating from the early Tertiary. Yet, we do not know what the ancestral morphology of these

ancient African progenitors was like, but from them the wahlenbergioids diversified into several morphological types such as herbs or shrubs. Perhaps the Mascarene genera such as *Nesocodon* Thulin and *Heterochaenia*, both of which recall the platycodonoids in their floral morphology, most resemble the ancient forms. In southern Africa, the onset of aridity, beginning in the Oligocene, probably is the ultimate cause of evolutionary diversification within the wahlenbergioids, with additional factors such as geographic and ecological isolation (especially soil types and pollinators). Shrubby types such as *Roella* are particularly associated with the Mediterranean climate of the Cape region, whereas herbaceous, rosette types such as *Craterocapsa* would appear to be restricted to areas with a greater moisture regime. The relictual disjunct distribution of *Craterocapsa* from eastern South Africa to the Chimanimani Mountains of Zimbabwe may be highly significant.

Taxonomic implications

One can of course attempt to analyse it, to fit it into this system of thought or that, but by its very nature it is bound to cause a diversion in the neatly-fitted jigsaw. In the end the diversion becomes the deviation that wrecks the system. No wonder those who create systems fear it like the devil.

Neil Gunn 1956 (*The Atom of Delight*)

Since their original discovery and description, *Rhigiophyllum* and *Siphocodon* were classified by all southern African workers as being close to other wahlenbergioid genera. We now know that the two genera are more divergent from all other wahlenbergioid taxa than was previously thought, yet, from molecular analyses, they are obviously still part of that nexus of southern African Campanulaceae. However, they represent a sister lineage separate from other South African taxa, which suggests that they are an old, albeit highly adapted group (≥ 28 million years, Cupido 2008). The current classification of South African wahlenbergioids is not adequate for the recognition of these taxa and should therefore be modified accordingly.

Kolakovsky (1987, 1994) recognized four subfamilies within the Campanulaceae based largely on the nature of carpel dehiscence and the presence or absence of an axicorn: Prismaticocarpoideae Kolak.; Canarinoideae Kolak.; Wahlenbergioideae (Endl.) Kolak.; and Campanuloideae. In this treatment, the South African genera were divided between his Prismaticocarpoideae (*Craterocapsa*, *Namacodon*, *Prismatocarpus*, *Roella* and *Treichelia* Vatke) and his Wahlenbergioideae (*Heterochaenia*, *Microcodon*, *Theilera* and *Wahlenbergia*, plus a number of typically platycodonoid and campanuloid genera).

Takhtajan (1997) also divided the Campanulaceae into four subfamilies: (Cyananthoideae *nom. inval.*? ; Ostrowskioideae (Fed.) Takht.; Canarinoideae Kolak.; and Campanuloideae, giving great weight to the type of pollen grains. He subdivided the Campanuloideae into about thirteen tribes, including four South African tribes: the Wahlenbergieae (*Wahlenbergia*, *Berenice*, *Theilera*, *Gunillaea* Thulin, *Nesocodon*, *Heterochaenia*, and *Microcodon*); Prismatocarpeae (*Prismatocarpus*, *Namacodon*, *Roella*, *Craterocapsa*, and *Treichelia*); Siphocodoneae (*Siphocodon* and *Rhigiophyllum*); and Merciereae (*Merciera*). The

problem with both of these systems is that there are too many tribes, that each tribe is almost the equivalent of a genus, and that it is difficult to get a perspective of the major lineages within the subfamilies. Kolakovsky's system places far too much emphasis on the axicorn, which is probably more useful in delimiting campanuloid taxa. Takhtajan's treatment of the South African genera comes closest to our thinking but the number and boundaries of his tribes may have to be revised.

Sonder (1865) included the four tribes Lobelieae, Campanuleae, Cyphieae and Goodenovieae in the Campanulaceae. He subsequently divided the Campanuleae into three subtribes: Wahlenbergieae (capsule opening at the apex; ovules many); Merciereae (stamens free; ovary one-celled, with an incomplete septum; 4 basal ovules); and Siphocodae (stamens epipetalous; ovary 3-celled, each cell with 2 ovules). Note that Sonder used the same suffix '-eae' for his subtribal names instead of '-inae'. He considered *Rhigiophyllum* to be a 'doubtful genus' and we think he simply tagged it on at the end of his account of the Campanuleae immediately after *Siphocodon*. He probably never intended to include it in his 'Siphocodae' but there is some ambiguity to his account (p. 597) and it would have been clearer if he had placed it sequentially after *Roella*. *Rhigiophyllum* is certainly very distinct from *Siphocodon* and, if he had meant to include it in his Siphocodae, he would surely not have considered it to be of doubtful status. Takhtajan (1997) placed these two genera in his tribe Siphocodoneae Takht., which he recognized along with 12 other tribes in his subfamily Campanuloideae. As far as we can determine, Takhtajan's Siphocodoneae was not formally validated. Was Takhtajan swayed by Sonder's rather ambiguous account? Lammers (2007: 671) lists the Siphocodoninae Sond. as a subtribe of the Wahlenbergieae Endl.

It would be tempting, given the highly divergent pollen morphology, to give subfamily status to *Rhigiophyllum* and *Siphocodon*. However, there are a number of other taxa that are also somewhat anomalous and do not fit comfortably into either the Wahlenbergioideae or the Campanuloideae, e.g. *Wahlenbergia hederacea*, *Feeria* Buser, *Jasione* L., *Musschia* and *Campanula* L. sect. *Pterophyllum* Damboldt. *Wahlenbergia hederacea*, which is a unique component of western European Atlantic regions, is remote from all other wahlenbergioids. *Feeria* is closer in its morphology to the wahlenbergioids, whereas *Jasione* is closer to the campanuloids (Eddie *et al.* 2003; Eddie unpubl.). Molecular studies also support the closer association between *Jasione* and the campanuloids (Cosner *et al.* 2004). These taxa probably stem from ancestral taxa common to both groups, what Eddie *et al.* (2003) referred to as 'transitional groups'. In the world of classification, there are always taxa that do not fit neatly into man-made schemes. Given the uniqueness of *Rhigiophyllum* and *Siphocodon*, we hereby include them in a new tribe of the Campanulaceae as follows:

Rhigiophylleae Eddie & Cupido, tribus nov. Type: *Rhigiophyllum* Hochst.

Siphocodoninae Sond. in Harv. & Sond., Flora capensis 3: 531 (1865) (as 'Siphocodae'). *Siphocodoneae* Takht.: 409 (1997).

Fruticuli habitu et affinitate *Roellae* vel *Prismatocarpi*, a quibus praecipue pollinis granis applanatis et triangularibus, uno poro in quoque angulo praeditis, differunt; corolla longe tubulosa, staminibus inclusis, ad tubi medium vel infra corollae orem insertis; structuris membranaceis liberis intra ovarium carpella simulantibus, in tempore maturitatis se contrahentibus, seminum marsupia rugosa vel carunculata formantibus et semina continentibus dispersis; capsula dehiscente aut obturamento supra calycis lobos amoto (*Rhigiophyllum*) aut operculo infra calycis lobos circumscissili (*Siphocodon*).

Shrubs with the appearance of, and affinity with, *Roella* or *Prismatocarpus*, principally differing from them by pollen grains that are flattened horizontally and triangular, with one pore at each angle; with corolla long-tubular, with stamens included and inserted at the middle of the tube or below the mouth of the corolla; with free membranous structures within the ovary resembling carpels, shrinking at maturity, forming rugose or carunculated seed pockets and dispersed containing the seeds; with the capsule dehiscing either by removal of a plug above the calyx lobes (*Rhigiophyllum*) or by a circumscissile operculum below the calyx lobes (*Siphocodon*).

This also necessitates that we clarify the placement of this new tribe within a suggested overall classification system of the Campanulaceae. To date, the reclassification of the Campanulaceae is still fluid and a presentation of a new system is inappropriate in this paper. However, we recommend the recognition of three subfamilies within the Campanulaceae to embrace the platycodonoids, wahlenbergioids and campanuloids, based principally on pollen morphology, but also supported by biogeography. Thus, the tribe Rhigiophylleae would be included in subfamily Wahlenbergioideae Kolak. (1987)—including Prismatocarpoideae Kolak. (1987), comprising *Wahlenbergia*, *Prismatocarpus* and allied genera possessing spherical or triangular, porate pollen and capsule dehiscence that is predominantly apical by valves. Their distribution primarily in the southern hemisphere, extending marginally into the northern hemisphere in Eurasia but poorly represented in South America.

This study has shown that what at first sight appears as novel, morphological divergences are integrated with many other features of a plant's morphology, ecology and evolution, and that no single aspect can ultimately be divorced from the plant as a whole. Because these unique plants are so finely tuned to their unique environment, they are highly vulnerable to disturbance, habitat degradation and climate change. We still know very little about them but we hope that their protection is assured and that further studies of such intriguing plants will be forthcoming.

ACKNOWLEDGEMENTS

We thank the Regius Keeper and the librarians of the Royal Botanic Garden, Edinburgh, for access to the herbarium collections and for their help in locating numerous obscure references. We are indebted to Prof. R.K. Jansen and the University of Texas at Austin for funding that enabled us to collect many of the taxa in the field, and for facilities available to W.M.M. Eddie during the tenure of a NSF postdoctoral scholarship. The

Curator of the Compton Herbarium is also thanked for facilities during the course of this study and the Western Cape Nature Conservation Board for granting permission to collect plants. Thanks also to W.F. Chisoe of the Samuel Roberts Noble Electron Microscopy Laboratory, University of Oklahoma, for meticulous help with pollen preparation and use of the scanning electron microscope. Ian Hedge (Royal Botanic Garden, Edinburgh), Dr Martin Ingrouille (University of London) and Assoc. Prof. Tom Lammers (University of Wisconsin, Oshkosh) commented on an earlier draft and made many helpful suggestions for improvement. In particular we are grateful to Tom for helping to extract us from the nomenclatural quagmire of the Campanulaceae. Philip Oswald and Dr Ted Oliver kindly corrected and greatly improved our initial attempt at the Latin diagnosis, for which Peter Bostock's software program TRANSLAT proved extremely helpful. We are also grateful to Dr Geoffrey Harper (Royal Botanic Garden, Edinburgh) for his excellent translations of Kolakovsky's papers from the Russian. We would also like to thank Profs Claudia Erbar and Peter Leins (University of Heidelberg) for their very informative and helpful comments and for elucidating the nature of the seed pockets.

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Floristic composition of wetlands of the South African section of the Maloti-Drakensberg Transfrontier Park

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Keywords: altitude, Drakensberg, grasslands, mires, soil wetness, wetlands

ABSTRACT

A survey was conducted on the wetlands in the South African section of the Maloti-Drakensberg Transfrontier Park (MDTP), along altitudinal gradients from the foothills to the summit plateau in six different catchments. Environmental indices of soil wetness, texture and organic contents of the soil were determined to relate wetland community types to their environment. Thirty-six plant communities were recognized with a total of 56 subcommunities. These communities fall into five different categories: 1, the high-altitude fens and seepages are a loose grouping of distinct vegetation types from the summit plateau and just below; 2, hygrophilous grasslands are the marginal areas of the wetlands that are temporarily wet and dominated by grasses, most of which are common outside wetlands; 3, shrubby wetlands are in most cases hygrophilous grasslands that have been invaded by shrubby species due to disturbance; 4, mixed sedge/land are the largest grouping and are dominated by sedges or grass species that are specifically adapted to wet conditions; 5, low-altitude sedge and reedlands are vegetation types that occur only marginally in the Maloti-Drakensberg area and are dominated by *Carex acutiformis* and *Phragmites australis*. The most important variables that explain the variation in wetland vegetation are altitude and soil wetness.

INTRODUCTION

The Maloti-Drakensberg area is one of the major mountain catchment areas in southern Africa, supplying a significant amount of fresh water to South Africa's major industrial and agricultural areas through the Lesotho Highlands Water Project scheme (Sandwith & Pfothenhauer 2002). It is one of the main centres of biodiversity in South Africa (Drakensberg Alpine Centre), containing many different grassland, shrubland, savanna and forest habitats (Van Wyk & Smith 2001). The wetlands at the summit plateau, often incorrectly referred to as bogs (ombrotrophic mires) have been extensively studied (Jacot Guillarmod 1962, 1963; Van Zinderen Bakker & Werger 1974; Grobbelaar & Stegman 1987; Backeus & Grab 1995; Schwabe 1995). These wetlands are interesting in their own right, but there have been few studies on wetlands across the entire altitudinal gradient from the foothills of the Drakensberg to the summit (Dely *et al.* 1999). The abundant rainfall and the strong gradients in climate and geomorphological setting, across altitude and latitude in this region have resulted in a diverse array of wetland habitats, which was first recognized by Dely *et al.* (1999). To a large extent, however, wetlands are concentrated on the summit plateau and the lower altitudes due to the steepness of the intermediate slopes, and Hill (1996) described two wetland communities in the Cathedral Peak area, one for lower altitudes and one for higher altitudes. In the national vegetation classification by Mucina & Rutherford (2006), two important wetland types were recognized as being

characteristic of the Maloti-Drakensberg region, namely the Drakensberg Wetlands and the Lesotho Mires (from the summit plateau).

Considering the importance of the water resources in the Maloti-Drakensberg region for the South African economy, it should have priority in conservation planning. Therefore it is necessary to have a more detailed overview of all aspects (vegetation, biodiversity, soils) of aquatic habitats including wetlands in the Drakensberg region. Existing research on the wetland vegetation of the Maloti-Drakensberg has been either of localized individual wetlands (Guthrie 1996) or, if broad-scale (Dely *et al.* 1999; Mucina & Rutherford 2006), limited in detail. This research addresses this deficit by providing a detailed analysis of wetland vegetation in the Maloti-Drakensberg at a macro-scale.

There has been a shift in the focus of biological conservation from the conservation of single species and their habitats toward conservation of the interactive ecological networks on which species and even human communities and industries depend (Ostfeld *et al.* 1997). The Maloti-Drakensberg Transfrontier Park (MDTP) (Sandwith & Pfothenhauer 2002) provides just such an opportunity to adopt a holistic conservation approach for the MDTP area on the eastern border between Lesotho and South Africa. Within the MDTP, wetlands were singled out as a landscape feature that conservation planning should focus on, given the significance of the area for water resources. An inventory of wetland habitats as defined by the RAMSAR convention but excluding rivers (Ewart-Smith *et al.* 2006) in the MDTP area should, therefore, at least include a description of the vegetation types and the physical environment of those wetlands to elicit the relationships between vegetation distribution patterns, altitude, edaphic factors and the inundation regime. When the relationships between vegetation patterns, edaphic factors and ecosystem functioning are understood, vegetation patterns can be used to assess the integrity and conservation status of a wetland site.

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MS. received: 2009-02-24.

Vegetation in itself is worthy of conservation since vegetation represents a large component of the biodiversity in a wetland, but wetland vegetation also provides a good descriptor of the habitat for many animals and other components of biodiversity that are part of a wetland ecosystem. Furthermore, since plants are immobile and have to cope with year-round stresses and variability in climate and hydrological regime, they also provide excellent information regarding the factors that play an important role in structuring the wetland. For this reason, a survey of wetland vegetation provides valuable information for conservation planning (Gopal *et al.* 2001).

Two important determinants of wetland vegetation structure and composition are local climate and hydrological regime (Mitsch & Gosselink 1986; Kotze & O'Connor 2000). Altitude, in the context of the MDTP area, is a suitable surrogate measure for climate (Barry & Van Wie 1974), and represents an indirect gradient (*sensu* Austin *et al.* 1984), the influence of which is through temperature and rainfall (Woodward 1988; Körner 2007). Temperature, for example, influences the distribution of C_3 and C_4 grasses in South Africa and Lesotho (Vogel *et al.* 1978). The hydrological regime of a wetland is complex and multidimensional, encompassing a variety of different factors, throughflows and outflows and such variables as the duration and timing of soil saturation and flooding. However, for practical purposes the hydrological regime can be described using various classification systems, with the hydro-geomorphic approach of Brinson (1993) being one of the most widely and successfully applied.

Although most wetlands in the MDTP are located in a wilderness area (several nature reserves and the Ukhahlamba World Heritage Site) there are several threats to the wetlands in the area, in particular, overgrazing by livestock and resulting erosion (Nüsser & Grab 2002).

In this paper, we aim to describe the plant communities found in wetlands across the Maloti-Drakensberg Transfrontier Park, along altitudinal transects from the

lowest foothills to the summit plateau. These vegetation units will be described together with environmental information such as soil type, wetness and altitudinal zone.

METHODS

Wetlands were sampled extensively along altitudinal transects in six major catchments across the entire Maloti-Drakensberg Transfrontier Park Project area (Figure 1). These transects, chosen to represent an equal spread of wetlands across the mountain range, are located within the catchments of the following rivers: the Bell River flowing through the town of Rhodes in the Eastern Cape, the Wildebeest River near Ugie in the Eastern Cape, the Tswereka River near Cedarville on the border between the Eastern Cape and KwaZulu-Natal, the Umkomazi River in Lotheni Nature Reserve in KwaZulu-Natal, the Mlamboja River near Cathedral Peak in KwaZulu-Natal and the Klerkspruit River in the Golden Gate area in the Free State. Within these catchments, all altitudes between 1 200 and 3 000 m were examined for wetlands on a 1:10 000 topographic map (e.g. by looking at the relationship between drainage lines and surrounding slopes) and inventoried in the field. An attempt was made to visit all areas in the field where wetlands were to be expected from the inspection of the maps, in order to obtain a representative sample of wetland vegetation types in each transect. Wetland type (or hydrogeomorphic unit) was identified according to the classification scheme of Ewart-Smith *et al.* (2006) and the habitat was described on the basis of several environmental variables, such as soil texture, soil depth and hydroperiod (time of saturation of the soil, see Kotze *et al.* 1996).

Individual wetlands were subdivided into their hydro-geomorphic units (*sensu* Ewart-Smith *et al.* 2006) and further subdivided into as many distinct vegetation types as could be recognized on a single field visit to the wetland that took place between January and March 2006. These vegetation types were sampled in representa-

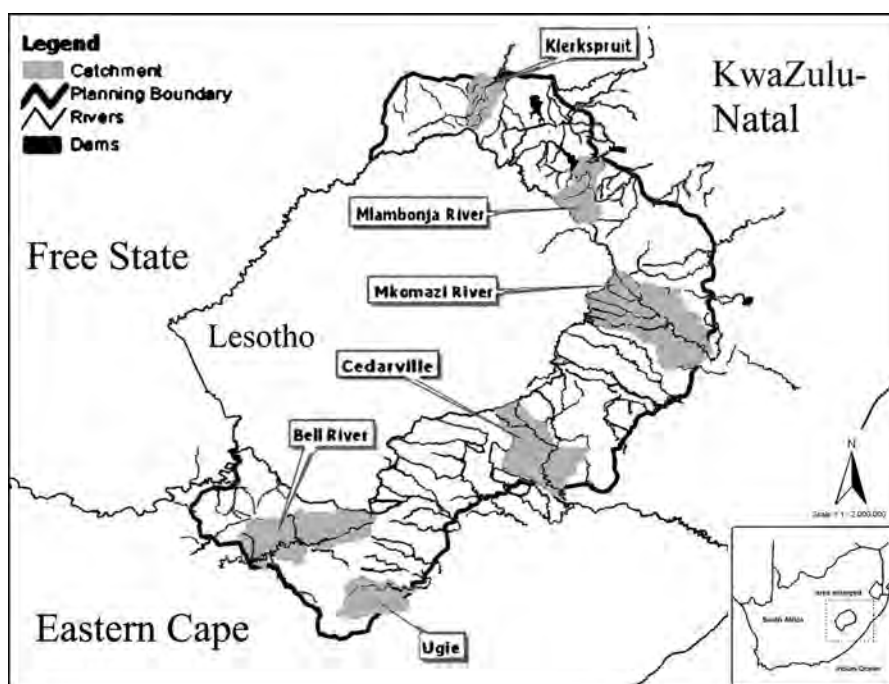


FIGURE 1.—Outline of study area with six catchments in which data on wetlands was collected.

TABLE 1.—Indices used for estimation of soil variables in field

Wetness index	
1	No wetland
2	Temporary wetness; mottles present below 20 cm
3	Temporary / seasonal wetness
4	Seasonal wetness; mottles present at the surface, some gleying
5	Semi-permanent wetness
6	Permanent wetness, peaty or gleyed soil
Texture index	
1	Gravel / grit
2	Sand
3	Loamy sand
4	Sandy loam / silt / silty loam
5	Loam
6	Clay loam / peat
7	Loamy clay
8	Clay
Organic material index	
1	Mineral soil
2	Humic, black or dark brown soils
3	Organic soil, no minerals present

tive relevés (3 × 3 m) according to the Braun-Blanquet method (Westhoff & Van der Maarel 1978), and a cover-abundance value was recorded for each species present. Some environmental variables were assessed at a plot level, such as soil depth (measured with a soil auger), soil texture (the field method, described by Ball 1986) and hydroperiod (as described by Kotze *et al.* 1996). Indices were developed for soil variables based on ranked classes (Table 1). The total number of vegetation relevés was 262 (Appendices A–C), and these relevés were distributed over more than 5 000 ha of wetlands. Areas that did not have an extensive period of saturation according to the hydroperiod assessment, were excluded from the study.

The vegetation samples were classified using TWINSpan (Hill 1979), based on cover-abundance values for each species. After the TWINSpan analysis, the classification was refined and data clusters were re-arranged by manual tabulation, as recommended by Feoli & Orloci (1985).

The relationship between identified wetland community types and environmental variables that varied on a large-scale (i.e. altitude) or locally (i.e. soil wetness, texture and humic indices) in the study area was examined using canonical variate analysis (CVA). CVA, akin to linear discriminant function analysis, is an ordination method that separates groups (classes from an *a priori* classification) along axes that are linear combinations of explanatory environmental variables, thus relating the distribution of communities to the environmental variables that best explain their distribution (Manly 1994).

Twenty-one of the identified community types, each represented by a minimum of four relevés to ensure an adequate sample size to estimate within and between community variability, were included in the CVA, which was undertaken using SPSS 13.0 for Windows (SPSS Inc., Chicago, IL, USA). This was followed by projection of community centroids and environmental variables in a low-dimensional biplot using software from the Canoco 4.5 package (ter Braak & Šmilauer 1997).

RESULTS

Thirty-six wetland communities were identified and a number of these were further subdivided into subcommunities based on the presence or absence of a co-dominant species or small differences in the list of diagnostic species, resulting in a total of 56 distinct plant communities. Tables 2 to 6 present a summary of these communities and subcommunities. In the descriptions below, communities are referred to by their name and number, whereas subcommunities are referred to by their number and dominant species.

The 36 communities have been divided into five major groups which have various components of their vegetation and their habitat in common, according to the refined TWINSpan survey. These groups are: high-altitude fen and seepage communities, hygrophilous grasslands, shrubby wetland communities, mixed sedgeland, and low-altitude sedge and reedlands; all taxa recorded in the Appendices occur in the herb layer, with the exception of *Leucosidea sericea* which occurs in the shrub layer.

A large proportion of the communities are concentrated at lower altitudes, with 50 % of the communities more or less restricted to altitudes lower than 2 000 m. The following provides a brief description of communities, with an emphasis on those communities which are unique to the MDTP.

High-altitude fen and seepage communities

These are typical wetland communities of high altitudes, where precipitation is high, and where the headwaters of most streams are located (Table 2; Appendix A). Most of these communities only occur above 2 000 m and typically occur in slope or valleyhead seepages, which are the most common wetland systems at these altitudes. Peat is sometimes present (rarely on the South African side, more common in Lesotho) and many of these wetlands are affected by natural erosion. Usually they are dominated by forbs and C₃ grasses and only a few are dominated by sedges. Sedges are common in the permanently and seasonally wet parts of the wetlands, but many communities can also extend into the temporary zone of the wetland. Some of the most common wetland communities in this group are *Haplocarpha nervosa* Subcommunity (1c), together with the *Kniphofia caulescens* Subcommunity (2a), the *Scirpus ficinioides* Community (4), the *Merxmuellera macowanii* Community (5), and the *Gunnera perpensa* Subcommunity (8b).

Hygrophilous grasslands

These communities occur mostly in temporarily wet parts of wetlands towards the periphery and have floristic similarity with the surrounding non-wetland vegetation. They are found at all altitudes but mostly in floodplains or at the edge of valleyhead or slope seepages. They are generally dominated by C₄ grasses (Subcommunity 9a is dominated by *Festuca caprina*, a C₃ grass), in most cases grass species that would also be found outside wetlands. The most common wetland communities of this type (Table 3; Appendix B) are dominated either by *Themeda triandra* (Community 9), *Aristida junciformis* (Community 11), *Eragrostis plana* or *E. planiculmis* (Community 12), and, in the northern part of the Drakensberg, by *Hyparrhenia dregeana* (Community 13).

Shrubby wetlands

Although wetlands with woody plants are not usually encountered in the Drakensberg, there were a few cases where wetlands were found dominated by woody species, such as *Leucosidea sericea*, suggesting some form of disturbance. Some of the other shrubby wetland types are unusual communities that have been encountered only occasionally. Only a few shrubs can be regarded as typical wetland species, such as *Mentha longifolia*. Riparian species not usually associated with wetlands such as *Cliffortia linearifolia* are found occasionally. Few vegetation plots were located in this group of communities and an overview of the types of shrubby wetlands in the area is presented in Table 4; Appendix B.

Mixed sedgeland

These are the most common seasonal and permanent wetland communities in the MDTP area, with a mixture

of various sedges and grasses. The dominant species are mostly sedges, but there are various species of grass that appear to be adapted to wetland conditions. Most of these communities are dominated by a single grass or sedge species. The communities occur mostly in seasonally or permanently wet areas on a loamy soil at low and intermediate altitudes (below 2 300 m). The most common wetland communities in this group (Table 5) are the *Fuirena pubescens* Mixed sedgeland Subcommunity (21b), the *Andropogon appendiculatus* Mixed sedgeland Community (24) and the *Leersia hexandra*–*Eleocharis dregeana* wetland Community (32). Another very common community is the *Miscanthus capensis* grassland Community (26), a tall grass that often occurs in a temporarily flooded setting. As a consequence of its species composition, the *Miscanthus capensis* Community fits better with the mixed sedgelands than with the hygrophilous grasslands, even though it is dominated by a grass species. The same applies to communities dominated by *Leersia hexandra* or *Arundinella nepalensis*.

TABLE 2.—High-altitude fens and seepages in MDTP area

Community no.	Community name	Subcommunity	Dominants	No. relevés	Wetland type	Soil type	Wetness	Altitude zone (m)	Transects
1	High altitude dicot lawns	1a	<i>Koeleria capensis</i> , <i>Poa binata</i> , <i>Merxmuellera disticha</i> , <i>Scirpus falsus</i> , many co-dominants	10	valleyhead seepages	loam, clay or peat	temporary to permanent	2 500–2 900	Bell River and Umkomazi River
		1b	<i>Juncus dregeanus</i> , <i>Athrixia fontana</i> , <i>Restio sejunctus</i> , many co-dominants	4	valleyhead seepages	peat or humic sand over sheet-rock	seasonal or permanent	2 500	Bell River
		1c	<i>Haplocarpha nervosa</i> , <i>Cotula hispida</i> , <i>Ranunculus meyeri</i> , many co-dominants	10	valleyhead seepages	loam, clay or peat	temporary to permanent	1 900–2 600	Bell River and Ongeluknek
2	<i>Kniphofia</i> or <i>Carex</i> seepages	2a	<i>Kniphofia caulescens</i>	3	valleyhead seepages	clay loam	semi-permanent	2 300–2 600	Bell River and Umkomazi River
		2b	<i>Carex cognata</i>	3	valleyhead seepages	clay loam or peat	seasonal or permanent	1 600–2 600	Cedarville, Umkomazi River and Bell River
3	<i>Kyllinga</i> depressions	3	<i>Kyllinga pulchella</i>	2	bedrock pools or other depressions	organic material and loam, shallow	seasonal or permanent	2 300–2 500	Bell River and Klerkspruit
4	<i>Scirpus</i> seepages	4	<i>Scirpus ficinioides</i>	6	various seepages	silty or sandy loam	temporary to permanent	1 800–2 400	Bell River, Mlambonja River, Umkomazi River and Klerkspruit
5	<i>Merxmuellera</i> wetlands	5	<i>Merxmuellera macowanii</i>	7	valleyhead seepages	humic loam	temporary or seasonal	2 000–2 500	Bell River, Mlambonja River, Umkomazi River and Klerkspruit
6	Broad-leaved seepages	6	<i>Alepidea amatymbica</i> , <i>Peucedanum thodei</i> , <i>Senecio inornatus</i>	2	various seepages	humic loam	temporary	2 300	Umkomazi River
7	<i>Carpha filifolia</i> wetlands	7a	<i>Carpha filifolia</i>	2	various seepages	sand or peat	semi-permanent	2 300–2 400	Ugie and Umkomazi River
		7b	<i>Carpha filifolia</i> , <i>Isolepis pellocolea</i> and <i>Ranunculus baurii</i>	2	various seepages	clay loam	semi-permanent	2 300–2 400	Ugie and Umkomazi River
8	<i>Gunnera perperna</i> wetlands	8a	<i>Kniphofia northiae</i> with many co-dominants	1	slope seepage	humic clay	permanent	2 200	Ugie
		8b	<i>Gunnera perperna</i> with many co-dominants	7	various seepages and oxbow in floodplain	loam or clay loam	very broad, sometimes also outside wetlands	1 700–2 300	Bell River, Ugie, Umkomazi River and Klerkspruit

TABLE 3.—Hygrophilous grasslands in MDTP area

Community no.	Community name	Subcommunity	Dominants	No. relevés	Wetland type	Soil type	Wetness	Alt. zone (m)	Transects
9	Hygrophilous grasslands with <i>Themeda</i>	9a	<i>Festuca caprina</i>	5	various seepages	loam or clay loam	temporary to seasonal	1 600–2 600	Bell River, Umkomazi River and Klerkspruit
		9b	<i>Aristida monticola</i>	1	slope seepage	loam	temporary	2 300	Klerkspruit
		9c	<i>Themeda triandra</i> , <i>Harpochloa falx</i> and <i>Festuca caprina</i>	21	floodplains and seepages	loam	temporary to seasonal	1 400–2 600	across all transects
		9d	<i>Microchloa caffra</i> and <i>Eragrostis racemosa</i>	2	footslope seepages	sandy loam	temporary to seasonal	1 900–2 200	Bell River and Klerkspruit
10	Hygrophilous grasslands with <i>Eragrostis chloromelas</i>	10a	<i>Pennisetum sphecelatum</i> , <i>Eragrostis chloromelas</i>	6	valleyhead or foot-slope seepages	loam or clay loam	temporary	1 800–1 900	Bell River
		10b	<i>Fingerhuthia sesleriiformis</i>	2	valleyhead seepage	?	?	1 600–2 500	Bell River and Umkomazi River
		10c	<i>Catalepis gracilis</i>	4	various seepages	various loamy substrates	temporary to seasonal	1 800–2 600	Bell River and Klerkspruit
11	Hygrophilous grasslands with <i>Aristida junciformis</i>	11a	<i>Stiburus alopecuroides</i>	2	valleyhead or foot-slope seepages	loam or sandy loam	temporary	1 900–2 400	Bell River and Ugie
		11b	<i>Aristida junciformis</i> , <i>Helichrysum aureo-nitens</i>	10	various	various loamy and sandy substrates	temporary to seasonal	1 300–2 100	Ugie, Cedarville, Umkomazi River and Klerkspruit
12	<i>Eragrostis plana</i> / <i>Eragrostis planiculmis</i> grasslands	12a	<i>Eragrostis plana</i> , <i>Sporobolus africanus</i>	7	floodplains, pans and footslope seepages	various types of loam	temporary to seasonal	1 300–1 800	Bell River, Cedarville and Mlambonja River
		12b	<i>Eragrostis planiculmis</i>	6	floodplains and seepages	clay loam	seasonal	1 400–2 100	Cedarville, Mlambonja River and Klerkspruit
13	<i>Hyparrhenia dregeana</i> grasslands	13	<i>Hyparrhenia dregeana</i>	5	valleyhead seepages and floodplain	various types of loam	temporary to seasonal	1 600–2 400	Klerkspruit, Cedarville and Umkomazi River
14	Grasslands with disturbance species	14	<i>Imperata cylindrica</i> , <i>Paspalum dilatatum</i>	2	floodplain and footslope seepage	sandy loam	temporary to seasonal	1 300–1 400	Mlambonja River

Reed and sedgeland

These communities typically occur at low altitudes within the study area (lower than 2 000 m), with a dominance of some very widespread wetland species such as *Phragmites australis* and *Carex acutiformis*, occurring in permanently wet situations. These communities, except for the one dominated by *Carex acutiformis*, occur only marginally in the study area while being widespread across the mesic parts of the central plateau of the South African interior [Mucina & Rutherford 2006; N. Collins, Free State Dept of Economic Development, Tourism and Environmental Affairs (DTEEA) pers. comm.]. The wetlands dominated by *Persicaria* species represent disturbed patches within reedlands. Table 6; Appendix C indicates the different types of reed and sedgeland found in the study area.

Community–environment relations

A Canonical Variate Analysis (CVA) of the 21 wetland communities with four or more representative relevés in the study area reveals two significant ($P < 0.001$) orthogonal canonical functions that explained 90 % of the distribution of these communities along the examined envi-

ronmental gradients (Table 7). Altitude is closely related to the first ($r = 0.964$), and wetness index to the second ($r = 0.991$) CVA function with the former axis accounting for almost twice as much variability as the latter (59.5 % vs 30.5 %). Soil texture and humic indices are not strongly correlated with any of the main environmental gradients of altitude and wetness.

Wetland communities are widely distributed along the altitude gradient (Figure 2), ranging in altitude from just over 1 400 m to more than 2 400 m ('high altitude dicot lawns') (Figure 3a). Most of the communities at low altitudes are dominated by grasses or sedges, and whereas there are still grass and sedge-dominated communities at high altitudes, communities dominated by bulbous monocots and dicots become more prominent. The soil wetness coenocline is independent of the altitudinal distribution of wetlands (Figure 2), with most communities located on temporary to semi-permanently wet soils (wetness index 2–5) (Figure 3b). The communities on the drier end of the spectrum tend to be dominated by grasses, whereas most of the communities on the wetter end of the spectrum, are dominated by sedges. Some exceptions are the *Phragmites australis* Community (36), the *Kniphofia caulescens* Subcommunity(2a) and the *Kniphofia lineari-*

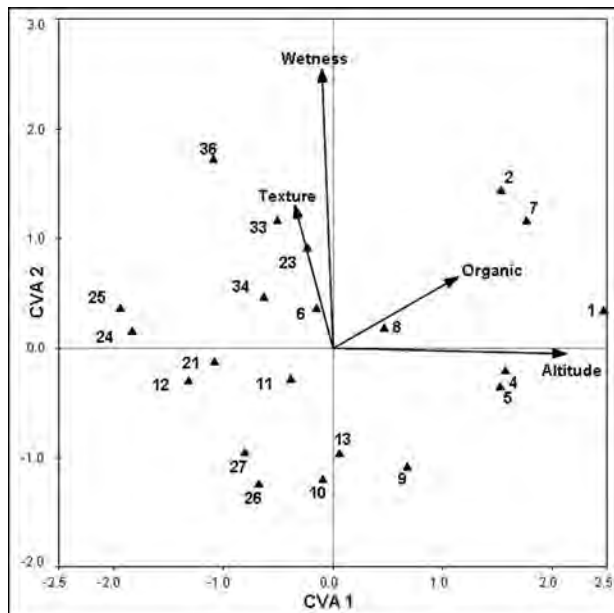


FIGURE 2.—Canonical variate analysis (CVA) plot of MDTP wetland community centroids and direction of maximum variation in environmental variables (see Table 7 for details of environmental variables and Tables 2–6 for a description of community types).

folia Community (33), which occur in the permanently wet areas of a wetland. An overview of the occurrence of the various community types across the spectrum of altitude and hydroperiod is presented in Table 8.

DISCUSSION

Most of the vegetation types that have been described above are easily differentiated on the basis of their dominant species. In wetland communities it is very common for just one or two species to dominate the entire vegetation community (Boutin & Keddy 1993; Cronk & Fennessy 2002). However, when two communities are dominated by different species but the overall species composition is similar, they have been retained as a single community since it is possibly a matter of stochastic factors as to which species starts to dominate (e.g. which species arrived first). It is assumed that most of the communities that occur at low altitudes within the study area are actually widespread in other parts of the Grassland Biome and in some cases this can be confirmed (Mucina & Rutherford 2006; N. Collins, DTEEA Bloemfontein, pers. comm.).

The most important environmental gradients impacting on wetlands in the MDTP area are altitude and wetness. Wetlands are most common at low altitudes (below 2 500 m) and at high altitudes (2 800 m and higher) and there is a clear dichotomy between them in the vegetation classification, as has been described by Hill (1996) and Mucina & Rutherford (2006). The Eastern Cape portion of the MDTP has slightly more wetlands at intermediate altitudes but the dichotomy between high- and low- altitude wetlands remains in place, and some of the typical 'high-altitude communities' descend to altitudes of $\pm 1\,700$ m (*Gunnera perpensa* communities). Being the southernmost extension of the Drakensberg, this could also be due to the latitudinal effect on vegeta-

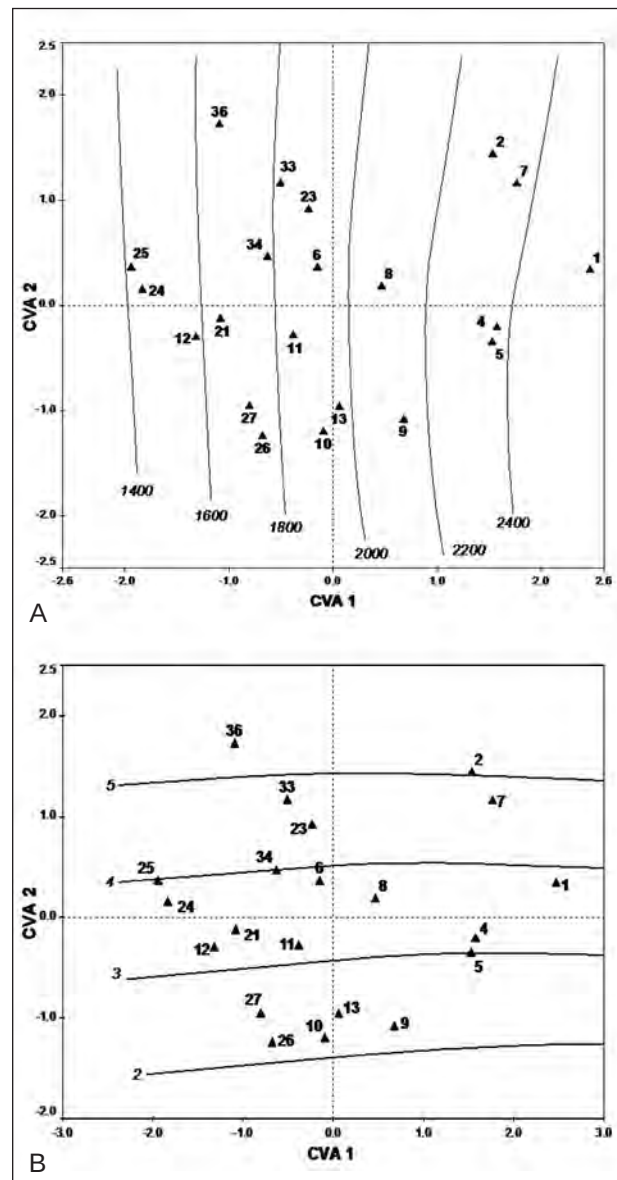


FIGURE 3.—Centroids for MDTP wetland communities in relation to trends (fitted by locally weighted smoothing) in A, altitude (m); and B, wetness index (ranked scale) across the canonical variate analysis (CVA) plot (Figure 2). Numbers refer to Community types in Tables 2–6.

tion patterns, with more frost present at lower altitudes in the southern extensions of the MDTP area (Hilliard & Burt 1987). Some of the high-altitude wetland communities, such as the *Kyllinga pulchella* depression Community (3) and *Carpha filifolia* Community (7), were not encountered very often during this study.

The high-altitude communities in the MDTP have the highest conservation value of the communities described, since most are endemic to this high-lying 'island' in the South African landscape. Studies of the mires in Lesotho (Jacot Guillarmod 1962, 1963; Van Zinderen Bakker & Werger 1974; Backeus 1988; Backeus & Grab 1995) show that these vegetation types (Communities 1 to 8) are more diverse in composition than described in the present study, and some communities, for example those dominated by *Merxmuellera macowanii*, also occur widely in the mountainous areas of Lesotho. There is a steep rain-

TABLE 4.—Shrubby wetlands in MDTP area

Community no.	Community name	Subcommunity	Dominants	No. relevés	Wetland type	Soil type	Wetness	Alt. zone (m)	Transects
15	<i>Mentha longifolia</i> wetlands	15a	<i>Mentha longifolia</i>	1	valleyhead seepage	silty clay	seasonal	2 200	Klerkspruit
		15b	<i>Mentha aquatica</i> , <i>Senecio inornatus</i>	2	valleyhead seepage or valley bottom	clay or clay loam	permanent	1 300–1 400	Ugie and Umkomazi River
16	Sheetrock wetland with <i>Crassula dependens</i>	16	<i>Crassula dependens</i> , <i>Cyperus schlechteri</i> , <i>Aristida junciformis</i>	1	bedrock pool	gravel and grit	seasonal	2 000	Umkomazi River
17	<i>Leucosidea sericea</i> wetlands	17	<i>Leucosidea sericea</i>	2	valleyhead or foot-slope seepage	clay loam or loam	temporary to seasonal	1 400–2 100	Klerkspruit and Umkomazi River
18	<i>Helichrysium splendidum</i> encroachment	18	<i>Helichrysium splendidum</i> encroachment	1	footslope seepage	humic loam	temporary	2 200	Bell River
19	<i>Cliffortia</i> wetlands	19	<i>Cliffortia linearifolia</i> , <i>Helichrysium umbraculigerum</i>	1	footslope seepage	loam	temporary	1 400	Umkomazi River
20	<i>Artemisia</i> wetlands	20	<i>Artemisia afra</i>	2	floodplains and footslope seepage	loam	temporary	1 500–1 700	Ugie and Umkomazi River

TABLE 5.—Mixed sedgeland in MDTP area

Community no.	Community name	Subcommunity	Dominants	No. relevés	Wetland type	Soil type	Wetness	Alt. zone (m)	Transects
21	Mixed sedgeland with <i>Fuirena pubescens</i>	21a	<i>Scleria welwitschii</i>	5	valleyhead seepages, valley bottom and isolated pan	loam, sandy loam or sandy clay	temporary to seasonal	1 300–2 000	Ugie, Umkomazi River and Cedarville
		21b	<i>Fuirena pubescens</i>	7	valleyhead and footslope seepages	sandy clay or sandy loam	temporary to seasonal	1 300–2 300	all except Klerkspruit
22	Mixed sedgeland with <i>Pycnus macranthus</i>	22a	<i>Pycnus macranthus</i>	2	depressions and footslope seepages	loam	seasonal	1 400–2 000	Cedarville and Mlambonja River
		22b	<i>Cyperus denudatus</i>	1	pan	humic clay	permanent	2 100	Klerkspruit
23	Mixed sedgeland with <i>Kyllinga pauciflora</i>	23	<i>Pennisetum thunbergii</i> , <i>Kyllinga pauciflora</i>	8	seepages, valley bottoms or floodplains	clay loam or peat	seasonal to permanent	1 400–2 300	Cedarville, Umkomazi River, Klerkspruit and Bell River
24	Mixed sedgeland with <i>Andropogon appendiculatus</i>	24	<i>Andropogon appendiculatus</i> , <i>Fimbristylis complanata</i>	9	seepages and floodplain	sandy clay or loam	temporary to permanent	1 300–1 800	Ugie, Umkomazi River and Bell River
25	<i>Arundinella</i> grasslands	25a	<i>Ludwigia palustris</i>	1	footslope seepage	loam	seasonal	1 400	Mlambonja River
		25b	<i>Arundinella nepalensis</i>	8	valley bottom wetlands, floodplains and seepages	loam or clay	temporary to permanent	1 300–1 700	Klerkspruit, Ugie, Mlambonja River and Umkomazi River
26	<i>Miscanthus</i> grasslands	26	<i>Miscanthus capensis</i>	16	floodplains, valley-head and footslope seepages	various types of loam	temporary	1 400–2 200	in all transects except Cedarville
27	<i>Cyperus marginatus</i> sedgeland	27	<i>Cyperus marginatus</i>	4	footslope seepages and floodplains	loam, loamy sand or clay silt	temporary to seasonal	1 500–1 900	Bell River, Umkomazi River and Klerkspruit
28	<i>Eleocharis limosa</i> wetlands	28	<i>Eleocharis limosa</i>	2	isolated pans and floodplains	humic clay	semi-permanent to permanent	1 700–2 100	Klerkspruit
29	<i>Cyperus fastigiatus</i> wetlands	29	<i>Cyperus fastigiatus</i>	3	floodplains	sand, clay or clay loam	seasonal to permanent	1 600	Cedarville
30	<i>Typha capensis</i> wetlands	30	<i>Typha capensis</i>	3	floodplains or isolated pans	clay or clay loam	semi-permanent to permanent	1 600–2 000	Klerkspruit and Cedarville
31	<i>Schoenoplectus decipiens</i> wetlands	31	<i>Schoenoplectus decipiens</i>	3	floodplains or valleyhead seepages	clay or clay loam	seasonal to permanent	1 600–1 800	Cedarville and Bell River
32	<i>Leersia hexandra</i> / <i>Eleocharis</i> wetlands	32a	<i>Leersia hexandra</i> , <i>Hemarthra altissima</i>	12	isolated pans and floodplains	clay or clayey soils	seasonal to permanent	1 300–2 100	Cedarville, Ugie and Klerkspruit
		32b	<i>Eleocharis dregeana</i> , <i>Leersia hexandra</i>	12	floodplains, isolated pans and seepages	loam, clay loam or clay	seasonal to permanent	1 400–2 600	all except Ugie

TABLE 6.—Reed and sedgelands in MDTP area

Community no.	Community name	Subcommunity	Dominants	No. relevés	Wetland type	Soil type	Wetness	Alt. zone (m)	Transects
33	<i>Kniphofia linearifolia</i> wetlands	33	<i>Kniphofia linearifolia</i>	3	valleyhead or footslope seepages	loam or clay loam	temporary to semi-permanent	1 400–1 600	Umkomazi River
34	<i>Carex acutiformis</i> wetlands	34a	<i>Carex acutiformis</i> , <i>Miscanthus capensis</i>	5	floodplains or footslope seepages	clay or loam	temporary to seasonal	1 400–1 900	Bell River and Umkomazi River
		34b	<i>Carex acutiformis</i>	10	floodplains, valley bottom wetlands, and seepages	loam, clay or clay loam	temporary to permanent	1 600–2 300	Bell River, Ugie, Cedarville and Klerkspruit
35	<i>Persicaria</i> wetlands	35a	<i>Persicaria decipiens</i>	1	valleyhead seepage	clay loam	permanent	2 000	Cedarville
		35b	<i>Persicaria lapathifolia</i>	1	floodplain	?	permanent	1 600	Cedarville
36	<i>Phragmites australis</i> wetlands	36a	<i>Phragmites australis</i> , <i>Carex acutiformis</i>	3	floodplains or footslope seepages	loam, peat or clay loam	semi-permanent to permanent	1 400–1 500	Mlambonja River and Umkomazi River
		36b	<i>Phragmites australis</i>	3	floodplains	clay loam or clay	semi-permanent to permanent	1 700	Ugie and Klerkspruit

fall gradient from the escarpment area in the KwaZulu-Natal Drakensberg towards inland Lesotho, with the actual escarpment being the wettest (Schulze 1997).

The foothills of the MDTP area have numerous wetlands, which may otherwise be quite uncommon in areas such as KwaZulu-Natal or Eastern Cape, where the deeply dissected landscape precludes the development of extensive wetlands. Most of the vegetation communities in the wetlands of the foothills are, however, more widely distributed, especially in areas such as the eastern Free State or the KwaZulu-Natal midlands (pers. obs.). Many of the communities described in the present study can also be expected in the mesic grassland areas of KwaZulu-Natal and Eastern Cape, and the higher-lying areas of eastern Free State and Mpumalanga.

Regarding the influence of soil wetness on wetland composition and structure, the typical pattern is that the temporary wetlands are dominated by grasses and the seasonal and permanent wetlands are dominated by sedges and other monocots. High altitudes are, however, depauperate in sedge species and a mix of other taxa occupy the niches of seasonal to permanent wetlands, such as *Kniphofia caulescens* and *Haplocarpha nervosa*. Other studies have found these herb-rich communities in permanently flooded soils at high altitudes (Backeus 1988; Backeus & Grab 1995). It seems that wetness has a major impact on the distribution of functional types in these communities (Sieben *et al.* 2009), whereas in the current study, altitude (a variable closely linked to many factors that directly influence plant growth and survival) explains more variation of the wetland vegetation composition.

At all altitudes, erosion is a severe threat to these wetlands. Due to the location on a scarp, there is already a

significant proportion of natural erosion and this can only be exacerbated by overgrazing. The process of overgrazing has been described in detail for the high-altitude mires of Lesotho (Jacot Guillarmod 1968; Nüsser & Grab 2002); however, it certainly also applies to the South African portion of the MDTP. At altitudes lower than 2 000 m, in particular, there are many wetlands that are badly degraded as a result of overgrazing, which is not surprising given the extensive permanent human settlement in this region. Many wetlands at the foothills of the MDTP have steep erosion gullies and the overall health of these wetlands is lower than those at higher altitudes (Kotze *et al.* 2006). This presents one of the biggest conservation challenges in the MDTP area.

An overview of wetland types as it is presented in this paper is particularly important for conservation planning. The high-altitude wetlands are unique to the moun-

TABLE 7.—Results of canonical variate analysis (CVA) of environmental differences among 21 wetland community types in Maloti-Drakensberg Transfrontier Park

	Canonical function			
	1	2	3	4
Eigenvalue	1.458	0.747	0.134	0.110
% of variance	59.5	30.5	5.5	4.5
Cumulative %	59.5	90.0	95.5	100.0
Canonical correlation	0.770	0.654	0.344	0.315
P-value*	<0.001	<0.001	0.106	0.215
Correlation with environmental variables				
Altitude	0.964	-0.023	-0.208	0.166
Wetness	-0.040	0.991	0.091	-0.094
Organic	0.393	0.224	0.880	-0.143
Texture	-0.115	0.430	0.207	0.871

* Wilks' Lambda test of significance of canonical function.

TABLE 8.—Number of relevés of community types in all altitudinal and wetness zones

Community type	Altitudinal zone					Total	Hydroperiod		
	1 000–1 400 m	1 400–1 800 m	1 800–2 200 m	2 200–2 600 m	2 600–3 200 m		Temporary	Seasonal	Permanent
1			1	12	11	24	9	6	8
2		1		3	2	6		2	4
3				2		2		1	1
4			2	3	1	6	2	2	1
5			3	4		7	3	4	
6				2		2	2		
7				4		4		1	3
8		1	4	3		8	3	2	3
High-altitude fens and seepages	0	2	10	33	14	59	19	18	20
9	1	6	5	12	5	29	23	4	
10		1	8	1	2	12	8	2	
11	1	5	5	1		12	4	7	
12	1	10	2			13	4	9	
13		2	1	2		5	4	1	
14	1	1				2		2	
Hygrophilous grasslands	4	25	21	16	7	73	43	25	0
15	1	1		1		3		1	2
16			1			1		1	
17		1	1			2	1	1	
18			1			1	1		
19		1				1	1		
20		2				2	2		
Shrubby wetlands	1	5	3	1	0	10	5	3	2
21	4	5	2	1		12	2	6	1
22		1	2			3		2	1
23		3	4	1		8		6	2
24	6	1	2			9	2	4	2
25	3	6				9	2	4	3
26		8	7	1		16	12	4	
27		2	2			4	3	1	
28		1	1			2			2
29		3				3		1	2
30		2	1			3			3
31		1	2			3		2	1
32	1	12	8	2	1	24		13	11
Mixed sedgeland	14	45	31	5	1	96	21	43	28
33		3				3	1	1	1
34		4	8	1		13	2	5	6
35		1	1			2			2
36		6				6			6
Reed and sedgeland	0	14	9	1	0	24	3	6	15

tains of the Drakensberg and Lesotho (where they occur more extensively). Lesotho has a high proportion of the community types 1 to 8 as described in this study, therefore the wetlands of Lesotho need to be an integral component of any conservation planning undertaken for the region. However, the wetlands in Lesotho face particular problems of overgrazing and the grazing regime is very difficult to regulate (Nüsser & Grab 2002). From a South African perspective, it is interesting to note that a considerable number of large wetlands have been found in the Eastern Cape portion of the MDTP area. Some of these wetlands contain vegetation types that seem to be largely

confined to this area, such as Subcommunities 1b, 1c and 10a. This part of the MDTP area certainly deserves more official protection, to ensure conservation of the structural integrity, composition, diversity and functionality of the wetland communities.

ACKNOWLEDGEMENTS

This study was carried out as part of an assessment of the wetlands in the Maloti-Drakensberg Transfrontier Park planning area. We would like to thank Richard Lechmere-Oertel, of the Maloti-Drakensberg Transfrontier Project, for co-ordinating the project and for making wetlands a priority in conservation planning within the area. Many thanks to Prof. Kate Gordon-Gray who helped with the identification of many grass and sedge species, and to the many people who have joined us in the field to collect the data: Doug McCulloch, Samantha Adey, Craig Cowden, Dean Ricketts, Eric Qonya and many more.

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Appendix A.—Phytosociological table of Communities 1–8 (High-altitude fen and seepage communities) (cont.)

Community Subcommunity	1			2			3	4				5				6	7			8																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																				
	1a	1b	1c	2a	2b	2009		2073	2166	2011	2115	2222	2031	2262	2067		2076	2078	2095	2112	2152	2000	2068	2097	2113	2173	2175	2261	2164	2169	2016	2165	2014	2167	2013	2017	2019	2025	2080	2163	2172	2254																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																														
Relevé no.	2004	2008	2012	2138	2157	2158	2159	2160	2161	2162	2001	2002	2003	2069	2005	2006	2072	2074	2075	2231	2232	2233	2234	2250	2009	2073	2166	2011	2115	2222	2031	2262	2067	2076	2078	2095	2112	2152	2000	2068	2097	2113	2173	2175	2261	2164	2169	2016	2165	2014	2167	2013	2017	2019	2025	2080	2163	2172	2254																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																													
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Afrotysonia gluchidiata 2172(a), 2173(+), Andropogon amethystinus 2112(b), 2114(m), Berkheya macrocephala 2003(b), 2017(1), Berkheya purpurea 2004(+), 2080(+), Bulbostylis humilis 2016(1), 2031(a), Carex sp. 2095(r), 2175(1), Conyza pinnata 2112(b), 2173(1), Crassula natalensis 2013(+), 2157(r), Crassula pepioides 2001(1), 2004(r), Crassula tuberosa 2001(+), 2005(r), Cyperus schlechteri 2001(m), 2014(+), Epilobium tetragonum 2250(r), 2254(1), Eragrostis planiculmis 2067(3), 2175(a), Geranium robustum 2004(1), 2113(b), Geranium schlechteri 2097(+), 2166(+), Helichrysum adenocarpum 2159(+), 2162(1), Helichrysum aureonitens 2001(r), 2003(1), Helichrysum longifolium 2012(1), 2262(+), Isolepis costata 2113(m), 2222(3), Isolepis sp. 2072(r), 2097(r), Juncus exsertus subsp. lesuiticus 2231(+), 2232(r), Limosella inflata 2008(+), 2075(+), Limosella vesiculosa 2069(b), 2074(1), Merxmüllera sp. 2158(m), 2161(m), Miscanthus capensis 2067(a), 2097(+), Myosotis atropalustris 2013(1), 2017(r), Passerina montana 2001(+), 2012(r), Pennisetum thunbergii 2025(1), 2175(m), Pentaschistis setifolia 2157(b), 2169(a), Phragmites australis 2019(+), 2202(3), Sebaea natalensis 2001(1), 2004(+), Senecio natalicola 2001(+), 2160(m), Sporobolus africanus 2008(+), 2031(1), Stiburus alopecuroides 2014(+), 2095(1), Taraxacum officinale 2012(1), 2074(+), Arctotis arctotoides 2009(+), Aristida junciformis subsp. galpinii 2004(+), Aristida junciformis subsp. junciformis 2097(+), Aristida sp. 2080(+), Ascolepis capensis 2017(1), Aster erucifolius 2001(1), Berkheya speciosa 2112(b), Bronus catharticus 2067(+), Bulbostylis schoenoides 2014(b), Bulbostylis sp. 2095(1), Carex austro-africana 2175(b), Carex monotropa 2001(+), Carex subinflata 2009(1), Cliffortia linearifolia 2097(+), Commelina africana 2031(1), Conyza albida 2019(1), Cotula socialis 2001(1), Crassula dependens 2031(+), Crassula setulosa 2095(+), Cymbopogon dieterlenii 2097(1), Cynoglossum hispidum 2112(m), Cyperus congestus 2019(1), Cyperus marginatus 2067(1), Cyperus sp. 2031(+), Denekia capensis 2009(r), Diascia barbaeae 2157(r), Digitaria longiflora 2031(1), Dimorphotheca caulescens 2162(b), Disa crassicornis 2003(1), Disa fragrans 2004(r), Drimia sp. 2001(r), Epilobium salignum 2025(1), Eragrostis chloronelas 2067(+), Eragrostis curvula 2112(+), Eragrostis sp. 2072(r), Erodium cicutarium 2262(+), Eucomis autumnalis 2097(+), Eumorphia prostrata 2001(1), Euphorbia epicyparissias 2097(3), Felicia wrightii 2004(r), Festuca costata 2112(1), Festuca sp. 2003(+), Ficinia cinnamomea 2163(1), Furena pubescens 2016(m), Galium capense 2080(1), Galium spurium subsp. africanum 2097(+), Geranium pulchrum 2164(3), Geranium sp. 2019(1), Geranium wakkerboomianum 2097(+), Gnaphalium limicola 2001(m), Gnida sp. 2004(+), Helichrysum cephaloides 2004(+), Helichrysum cooperi 2097(1), Helichrysum flanaganii 2012(+), Helichrysum griseolanatum 2001(1), Helichrysum mundtii 2025(1), Helichrysum nudifolium 2175(+), Helichrysum sp. 2162(1), Hesperantha baurii 2095(1), Heteropogon contortus 2080(1), Hibiscus trionum 2019(r), Hypochaeris radicata 2233(r), Ipomoea crassipes 2031(a), Jamesbrittenia pristisepala 2031(+), Juncus exsertus 2250(+), Juncus punctatus 2250(a), Kniphofia linearifolia 2097(+), Kniphofia triangularis 2113(r), Kyllinga pauciflora 2017(r), Leonotis ocyimifolia 2097(+), Lepochloa fusca 2031(r), Lessertia perennans 2097(+), Leucosidea sericea 2164(a), Limosella africana 2078(+), Lobelia galpinii 2069(1), Lobelia preslii 2157(r), Merxmüllera stereophylla 2152(b), Merxmüllera stricta 2003(1), Microchloa caffra 2031(a), Mohria rigida 2095(+), Monopsis decipiens 2113(+), Monsonia angustifolia 2031(+), Monsonia brevirostrata 2112(+), Moraea sp. 2002(r), Myosotis arvensis 2164(+), Oenothera rosea 2019(r), Ornithogalum paludosum 2160(m), Papaver aculeatum 2009(1), Pentaschistis airoides 2095(1), Pentaschistis aurea subsp. pilosistigma 2004(+), Pentaschistis oreodoxa 2004(b), Pentaschistis praecox 2069(r), Persicaria decipiens 2025(r), Plectranthus grallatus 2097(1), Psammotropha mucronata 2004(+), Pycreus nitidus 2095(+), Rubus rigidus 2113(1), Rumex acetosella 2113(r), Satyrium longicauda 2004(r), Scabiosa columbiana 2004(1), Schizochilus flexuosus 2167(r), Schoenoxiphium bracteatum 2014(1), Schoenoxiphium rufum 2004(1), Sebaea sp. 2012(+), Senecio cathartensis 2016(1), Senecio napifolius 2097(a), Senecio rhomboideus 2031(+), Senecio sp. 2162(b), Senecio tanacetopsis 2001(1), Setaria pumila 2019(+), Sium repandum 2250(1), Solanum sp. 2112(1), Stachys rugosa 2004(+), Tetrachne dregei 2067(b), Tetraria cuspidata 2001(a), Thesium sp. 2004(1), Ursinia alpina 2161(+), Ursinia nana 2095(+), Urtica urens 2076(r), Urtica livida 2069(1), Verbena bonariensis 2019(1), Wahlenbergia krebbsii 2113(+), Xerophyta viscosa 2152(m), Zaluzianskya microstemon 2004(+).

[illegible]

Appendix B: Phytosociological table Communities 9–20 (Hygrophilous grasslands and shrubby wetland communities) (cont.)

[illegible]

-s1 : shrub layer.

[illegible]

[illegible]

Wetland craft plants in KwaZulu-Natal: an ecological review of harvesting impacts and implications for sustainable utilization

C.H. TRAYNOR*†, D.C. KOTZE** and S.G. McKEAN***

Keywords: basketry, cutting disturbance, management, sustainable utilization, wise use of wetland

ABSTRACT

In South Africa, wetland plants have been used for centuries and they continue to be harvested for subsistence and commercial purposes. Fibres for crafts are collected by cutting the aboveground parts. KwaZulu-Natal is one of the major basket-producing regions in southern Africa and at least twenty-two species of wetland plants are harvested for crafts. A literature review of the harvested species revealed that the impacts of cutting have only been extensively investigated for *Phragmites australis* (Cav.) Steud. and *Juncus kraussii* Hochst. The review suggested that, where plants display strong seasonal aboveground productivity patterns, cutting should take place after shoot senescence and before new shoot emergence to minimize damage to plants. Cutting in the short term could increase the density of green stems. However, in the long term in *Phragmites australis*, it may deplete the rhizome reserves and reduce the density of useable (longer and thicker) culms. The opportunity for sustainable harvests was investigated by considering the geographic distribution, whether species are habitat specific or not, and local population sizes of the craft plants. *Juncus kraussii* is of the greatest conservation concern. Ecologically sustainable wetland plant harvesting could contribute to the wise use of wetlands, an approach promoted nationally and internationally.

INTRODUCTION

Wetlands in South Africa are defined by the National Water Act (No. 36 of 1998) as 'land which is transitional between terrestrial and aquatic systems where the water table is usually at or near the surface, or the land is periodically covered with shallow water, and which land in normal circumstances supports or would support vegetation typically adapted to life in saturated soil' (RSA 1998). Wetlands are valued as a habitat for rare flora and fauna, as part of a mosaic of ecosystems that maintain global diversity, for their provision of wetland products, for their functional values (Denny 1994; Dixon 2002; Dixon & Wood 2003), and as sinks for greenhouse gases (Brix *et al.* 2001).

Wetlands in the northern hemisphere, have a long history of use which has been relatively well documented (Smart *et al.* 1986; Van Wirdum 1993; Kiviat & Hamilton 2001). In Europe, many wetlands have been managed for centuries and the plant and animal communities are dependent upon this management (Haslam *et al.* 1998). Particular types of wetlands such as reedbeds are managed socio-economically for the reeds and sedges which are used commercially for thatching materials and also for nature conservation purposes (Hawke & José 1996). The long history of wetland utilization combined with an academic tradition of research concerning ecology and the impacts of use, mean that many wetland systems in temperate regions are relatively well understood and management is strongly influenced by science (Hawke & José 1996; English Nature 2006).

In Africa, the history of human disturbance and its effects upon ecosystems including wetlands is poorly understood (Macdonald 1989; Maclean *et al.* 2003). However, many African people 'depend *inter alia* upon wetlands for food, water, medicine, shelter, energy and waste disposal-wastewater treatment' (Denny 2001: 22). African wetlands provide a range of services and goods, particularly to local people (Terer *et al.* 2004; Bernard & Moetapele 2005; Cooper *et al.* 2006). However, wetlands have tended to be taken for granted (Denny 1994), and regarded as wastelands and are therefore not formally protected (Dovie 2003; Mmopelwa 2006). Some African wetlands have been modified (Richards 1995; Thenya 2001; Schuyt 2005) and in the past it was government policy to promote the drainage of wetlands for agriculture (Denny & Turyatunga 1992; Gichuki *et al.* 2001). Overexploitation and unsustainable use threaten many wetlands (Diop *et al.* 1999; Dixon 2002; Uluocha & Okeke 2004). Documented ecological and environmental knowledge of African wetlands is fragmentary; some systems have been investigated intensively but large areas of wetlands remain unrecorded. Furthermore, due to northern-driven global environmental activities, information tends to be within Europe and America rather than Africa itself (Denny 2001).

In South Africa, recovered artefacts show that wetland plants have been used for centuries; sedges were used during the Holocene Stone Age (Manhire *et al.* 1985), reeds by the Khoi San bushmen (Bassani 2000) and sedge mats to roof houses by the Khoi Khoi herders (Cunningham & Terry 2006). Use of wetland plants by the Bantu population has also been recorded, particularly for the Xhosa (Kepe 2003), the Tembe-Tonga (Pooley 1980; Liengme 1981; Cunningham & Gwala 1986) and the Zulu (Bryant 1949; Grossert 1978; Jones 2001). Wetland plants continue to be harvested in South Africa both for subsistence and commercial purposes (Cunningham 1987; Kepe 2003; Shackleton & Shackleton 2004). In some African countries excessive reed

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MS. received: 2007-12-19.

cutting has resulted in local scarcity (Kgathi *et al.* 2005) and wetland degradation (Green *et al.* 2002). In South Africa, plant harvesting has been reported as a threat to grasslands (Cowling & Hilton-Taylor 1994). Within South Africa, investigations into the implications of utilization with regard to management and sustainability have tended to be species specific (McKean 2003) or site specific (Tarr *et al.* 2004; Dahlberg 2005). These investigations provide extremely useful information, but a broader understanding of species utilized, the impacts of use and implications for management is lacking for wetland habitats.

The aim of this paper is to consider wetland plants used for craftwork and to review the ecological impacts of utilization on these species. The province of KwaZulu-Natal in South Africa was selected as a case study area as it is one of the three major basket-producing areas in southern Africa (Cunningham & Terry 2006). During plant harvesting for crafts, the leaves and stems of wetland plants are typically removed by cutting. Therefore this paper will focus on the effects of cutting disturbance upon plants with reference to relevant aspects of physiology, biology and ecology. The effects of harvesting upon plant populations and the wetland habitat will also be elucidated. Finally, the implications of the review for the management of South African wetlands will be discussed with an emphasis on the ecological sustainability of these ecosystems.

METHODS

The main species of plants utilized for crafts within South Africa were determined from literature (Grossert 1978; Pooley 1980; Liengme 1981; Cunningham 1985, 1987; Cunningham & Gwala 1986; Heinsohn 1990, 1991; Heinsohn & Cunningham 1991; Moffett 1997; Christiansen 2000; Hennesey & Koopman 2000; Cunningham 2001; Krüger & Verster 2001; Simpson & Inglis 2001; Kepe 2003; Van Wyk & Gericke 2003; Tarr *et al.* 2004; Cunningham & Terry 2006; Traynor & Kotze 2007b; Kotze & Traynor in prep.).

Plants were classified using the wetland indicator status system of Reed (1988). This system assigns wetland plants to categories based upon their level of occurrence in wetlands (Table 1). This was carried out with reference to published work (Gordon-Gray 1995; Kotze & O'Connor 2000; Glen *et al.* in prep.) and examination of the habitat descriptions of specimens in the University of KwaZulu-Natal Herbarium. The current study focused upon obligate wetland species.

The names of the selected species were used in a literature search, the following general terms were also searched; craft plants, basketry, grasswork, wetland, reedbed, rush, sedge used in combination with management, cutting, harvesting, and Africa. The species names were searched using the Royal Botanic Gardens, Kew Electronic Plant Information Centre (<http://www.kew.org/epic/>). The ISI database at <http://wok.mimas.ac.uk> and Google 'scholar' (<http://scholar.google.com/>) databases were searched for manuscript references using the terms listed above.

The distribution of species within KwaZulu-Natal (KZN) was determined using records from the University of KwaZulu-Natal Herbarium (Pietermaritzburg Campus) and from the PRECIS species database of the South African National Biodiversity Institute (SANBI), Pretoria. The locality references were assigned to 1:50 000 map series and their distribution plotted.

RESULTS

Wetland species used in KwaZulu-Natal

The literature search of species used for crafts revealed 27 plants, 13 of these were obligate wetland species, and eight facultative wetland species (Table 2).

The species used belong to four plant families, Cyperaceae, Poaceae, Junceae and Typhaceae. Within South Africa, species within other plant families do provide a source of fibres for basketry, the most important of which are: *Hyphaene coriacea* and *Phoenix reclinata* of the Arecaceae family (Moll 1972; Cunningham 1988; Van Wyk & Gericke 2003), and the forest climber, *Flagellaria guineensis* of the Flagellariaceae family (Cawe & Ntloko 1997). However, these species are not classified as obligate or facultative wetland species and were, therefore, excluded from the current study.

The obligate and facultative wetland species listed in Table 2 provide plant fibres with characteristics suitable for crafts. These include tough fibres that can be twisted and bent without breaking; resilient fibres that can be dried and stored but that can also re-absorb moisture and retain flexibility for weaving; and sufficient length, so fewer 'ends' are produced during weaving; silica crystals or chemicals that reduce insect attack (Letšela *et al.* 2003; Cunningham & Terry 2006).

Individual plant response to harvesting

Plant physiology is an important factor that determines a plant's response to defoliation. The harvesting

TABLE 1.—Classification of plants according to occurrence in wetlands, based on US Fish and Wildlife Service Indicator Categories (Reed 1988)

Wetland indicator classification	Habitat and occurrence
Obligate wetland species	Almost always grow in wetlands (> 99 % occurrence)
Facultative wetland species	Usually grow in wetlands (67–99 % occurrence) but are occasionally found in non-wetland areas
Facultative species	Equally likely to grow in wetland and non-wetland areas (34–66 % occurrence)
Facultative dryland species	Usually grow in non-wetland areas but sometimes grow in wetlands (1–34 % occurrence)
Dryland species	Almost always grow in drylands (< 1 % occurrence in wetland areas)

of leaves can be considered a low-impact harvesting activity, but the opportunity for sustainable harvesting is partially dependent upon plant physiology. Characteristics such as a rapid growth rate and asexual reproduction (clonal resprouters) produce high opportunities for sustainable harvesting (Cunningham 2001). Published information relating to the impacts of cutting was generally limited to the grass *Phragmites australis* (Cav.) Steud. and the rush *Juncus kraussii* Hochst. Therefore, these species are used to illustrate the relationship between plant physiology and response to cutting.

Phragmites australis, which is one of the most widely distributed plants on earth (Soetaert *et al.* 2004), is a rhizomatous and perennial grass, with annual shoots. In undisturbed reedbeds, the perennial rhizome produces shoots in spring, which grow in summer and die in autumn producing litter which can persist for several years (Schmidt *et al.* 2005). *Phragmites* is a long-lived clonal species, it colonizes by vegetative growth of aboveground runners and belowground rhizomes (Mau-champ *et al.* 2001). It can form dense, monospecific stands. The rhizomes have important storage functions, which largely determine the stability, survival capacity

and spread of the stand (Chapin *et al.* in Graneli *et al.* 1992; Karunaratne *et al.* 2004). Rhizome biomass and rhizome standing stocks of nonstructural carbohydrates and mineral nutrients have been shown to decrease early in the growing season and to increase later in the year. This seasonal pattern is attributed to mobilization of rhizome carbohydrate and mineral nutrient stores to support spring shoot growth, that takes place before any foliar structure has developed. Once the foliar structure has been established, basipetal transport of nonstructural carbohydrates and mineral nutrients occurs immediately (Graneli *et al.* 1992). The rhizomes can persist for several years, and Asaeda *et al.* (2006a) reported a clear variation between rhizome age-class in seasonal belowground resource translocation patterns; in late summer and autumn, translocation from shoots to rhizomes was concentrated in young rhizomes and older rhizomes shrank in size due to metabolic loss. In *P. australis*, the increase in aboveground biomass is a combination of new production, regenerated production and dissimilatory processes (Soetaert *et al.* 2004). The carbon budget for total reed growth was estimated to be 78–80 % photosynthesis, 17–19 % remobilization from rhizomes, and 3 % resorption of carbon from leaves. Half of all assimilates were transported belowground (Soetaert *et al.* 2004). In late summer and autumn and again in late winter and spring, the rhizomes produce buds from which shoots develop (Haslam 1969). The number and size of buds may be dependent upon the size and amount of newly formed rhizomes, which themselves may be affected by the reserves available (Mook & Van der Toorn 1982). The basal diameter of the bud is an important property, as once it is known early in the season, it can be used to predict the length and weight of the reed (Van der Toorn & Mook 1982). *Phragmites australis* stands are extremely productive communities and figures for peak aboveground biomass lie between 587–2 659 g DW m⁻² (Soetaert *et al.* 2004; Bedford & Powell 2005); belowground biomass values are larger with typical values between 2 806–3 346 g DW m⁻² (Soetaert *et al.* 2004). In natural reed stands, the dead leaves and stems accumulate at the end of the growing season. Stands are detritus-based ecosystems with litter accumulation and eventual drying out of the reedbed (Cowie *et al.* 1992; Bedford & Powell 2005).

Harvesting impacts vary according to the frequency and intensity of harvesting; frequent and/or intense harvesting of the vegetative parts, such as leaves, will deplete the carbohydrate reserves or disrupt water and nutrient flows (Cunningham 2001). In terms of management, the rationale behind cutting the aboveground parts of *Phragmites australis* is that it will retard subsequent growth and development of the stand because reserves produced during that season are exported from the system (Asaeda *et al.* 2003). Cutting also decreases oxygen transport to the root zone, which inhibits shoot regrowth (Weisner & Graneli 1989). Continuous nutrient removal could theoretically result in nutrient limitation. However Schröder (1987 cited in Ostendorp 1995) argued that harvesting dead aboveground material was beneficial because it limited the build-up of organic matter that could lead to oxygen depletion within the water body. Schmidt *et al.* (2005) suggested that cutting may reduce the natural silting-up process in *P. australis* reedbeds and therefore slow vegetation succession to scrub and woodland.

TABLE 2.—Wetland plant species used for craft in South Africa and their wetland indicator status

Scientific name	Family	Wetland indicator status
<i>Aristida junciformis</i> Trin. & Rupr.	Poaceae	F
<i>Digitaria eriantha</i> Steud.	Poaceae	FD
<i>Eragrostis plana</i> Nees	Poaceae	F
<i>Festuca costata</i> Nees	Poaceae	FD
<i>Miscanthus capensis</i> (Nees) Andersson	Poaceae	F
<i>M. junceus</i> (Stapf) Pilg.	Poaceae	FW
<i>Merxmüllera macowanii</i> (Stapf) Conert	Poaceae	F
<i>Phragmites australis</i> (Cav.) Steud.	Poaceae	OW
<i>P. mauritanicus</i> Kunth	Poaceae	FW
<i>Sporobolus africanus</i> (Poir.) Robyns & Tournay	Poaceae	F
<i>Cladium mariscus</i> (L.) Pohl	Cyperaceae	OW
<i>Cyperus esculentus</i> L.	Cyperaceae	FD
<i>C. fastigiatus</i> Rottb.	Cyperaceae	OW
<i>C. latifolius</i> Poir.	Cyperaceae	OW
<i>C. marginatus</i> Thunb.	Cyperaceae	OW
<i>C. natalensis</i> Hochst.	Cyperaceae	F
<i>C. papyrus</i> L.	Cyperaceae	OW
<i>C. sexangularis</i> Nees	Cyperaceae	FW
<i>C. solidus</i> Kunth	Cyperaceae	OW
(<i>Mariscus solidus</i> (Kunth) Vorster)		
<i>C. textilis</i> Thunb.	Cyperaceae	OW
<i>Schoenoplectus brachyceras</i> (A. Rich.) Lye*	Cyperaceae	OW
<i>S. scirpoides</i> (Schr.) J.Browning†	Cyperaceae	OW
<i>Juncus kraussii</i> Hochst.	Juncaceae	OW
<i>J. punctatorius</i> L.f.	Juncaceae	OW
<i>Hyphaene coriacea</i> Gaertn.	Arecaceae	F
<i>Phoenix reclinata</i> Jacq.	Arecaceae	F
<i>Typha capensis</i> (Rohrb.) N.E.Br.	Typhaceae	OW

* *Schoenoplectus brachyceras* was previously known as *Scirpus corymbosus* (Smith 1966). † *Schoenoplectus scirpoides* was previously known as *Scirpus litoralis* (Schr.) Palla. Reclassification of *Scirpus litoralis* identified two distinct species *Schoenoplectus scirpoides* and *S. subulatus* (Vahl) Klye. F, facultative; FD, facultative dryland; FW facultative wetland; OW, obligate wetland.

The harvesting time of *Phragmites australis* strongly affects regrowth (Karunaratne *et al.* 2004). In the United Kingdom, in mixed species stands, a summer cut is used to suppress the dominant, taller species and so promote plant species diversity and benefits to wildlife (Hawke & José 1996). The competitiveness of *P. australis* is reduced through removing the photosynthesizing parts and so the rhizome is deprived of energy. Summer cutting reduces shading, decreases competition for nutrients and creates space for other plant species to grow. Summer cutting is generally not used for commercial reedbeds but is commonly used for nature conservation purposes (Hawke & José 1996). Karunaratne *et al.* (2004) reported that summer cutting of *P. australis* decreased shoot height, increased leaf production and reduced the stem diameter and storage accumulation capacity of older rhizomes.

Asaeda *et al.* (2006b) compared cutting in Japan and its effect upon *Phragmites australis* growth in the subsequent year. They investigated two time periods: when shoot growth was rapid and rhizome reserve storage was near the seasonal minimum (June) against slower shoot growth and recharging rhizomes (July). They observed that cutting when shoot growth was rapid and rhizome reserve storage levels low, significantly reduced the aboveground biomass and it also reduced annual resource allocation compared to uncut stands. However, cutting when shoot growth was slower had less impact (Asaeda *et al.* 2006b). Karunaratne *et al.* (2004) also found that cutting when rhizomes were at their lowest storage level had the greatest effect on suppressing subsequent *P. australis* growth. They stated that the rhizome storage level at the time of cutting determines the response of shoots and rhizomes to disturbance. In these studies, the rhizome reserves were at their lowest 7–10 weeks after shoot emergence. Therefore, the timing of spring shoot formation can be used to determine the least appropriate disturbance time—the exact timing would depend upon local conditions.

Winter cutting in the United Kingdom removed dead stems, thus reducing litter-producing build-up and hence succession. It also promoted a better reed quality in terms of producing tall, wide-diameter, dense stems. Winter cutting favours *Phragmites australis* dominance, reduces plant species diversity (Wheeler & Giller 1982a, b), increases ground level temperature fluctuations and radiation, and may benefit wildlife by sustaining the habitat (Hawke & José 1996). Annual cutting removes the overwintering microhabitat for most invertebrates and can therefore be an efficient control method for insect pests of *P. australis*. However, certain species of reed-dwelling moths may not survive annual cutting (Hawke & José 1996). Biennial cutting allows reedbeds to 'rest', it provides uncut reeds for reed-dwelling wildlife, and enables biennial and perennial herbs to flower and set seed (Hawke & José 1996). Cowie *et al.* (1992) surveyed commercial reedbeds that had been regularly cut for twenty years in the United Kingdom. They reported that plant species richness and diversity were significantly greater and reed density was double that of uncut sites. In French Mediterranean reedbeds, Mauchamp (1998 cited in Poulin & Lefebvre 2002) reported that cut reedbeds had a higher density of green stems than uncut reedbeds (238±

45 vs 137± 12, $P = 0.02$); additionally, above a green reed density of 200 stems m⁻² species richness declined. Van der Toorn & Mook (1982) stated that regardless of the cause of injury to *P. australis* (e.g. cutting, burning or frost damage) the most important factor determining the plant's response is whether the apical meristem of the shoot is killed. They found if treatments were applied before new shoots emerged, damage was minimal. However, killing of the shoot-growing point during harvesting resulted in replacement by several thinner shoots.

In South Africa, the effects of harvesting *Phragmites australis* were investigated in the Thembe Elephant Park, KZN. Reed harvesting typically occurred in winter (April to September) after the flowering period and once the reeds were mature (Cunningham 1985). Reed diameter was positively correlated with time since harvest, such that uncut reedbeds had a significantly larger diameter than cut reeds, which may indicate a larger rootstock and improved shoot production (Tarr *et al.* 2004). The long-term effects of winter cutting were investigated at Hluhluwe-Umfolozi Park in KZN where McKean (2001) compared annual cutting, biennial cutting and control treatments. He found that harvested treatments had higher total shoot densities than the control (uncut) treatment. As such, cutting appeared to stimulate new growth, a finding in agreement with Van der Toorn & Mook (1982). However, harvesting altered the reed size structure over time, and annual and biennial harvested areas showed reduced density of useable culms (length > 2.5 m and diameter > 10 mm) compared to uncut areas (McKean 2001).

Experimental cutting trials with perennial grass species in South Africa showed that regular cutting altered species composition through a shift in competitive hierarchy (Fynn *et al.* 2005b). Experiments demonstrated that summer mowing tended to decrease the abundance of taller species such as *Aristida junciformis* and increase the abundance of smaller species such as *Themeda triandra*. Annual mowing during the dormant period favoured medium to tall grass species such as *Aristida junciformis* (Fynn *et al.* 2005a).

The rush *Juncus kraussii* is a perennial, rhizomatous herb. In Australia, Congdon & McComb (1980) reported a lack of seasonality in standing crop as culms were produced in every month and reached their maximum length in two to five months. The highest nitrogen and phosphorus concentrations occurred several months before the peak standing crop, which was during the warm season. Nutrients may be translocated to rhizomes on senescence of the culms, which occurs throughout the year (Congdon & McComb 1980).

Juncus kraussii has similar morphology and occupies comparable positions in marshes as *J. gerardii* in Europe and *J. roemerianus* in the United States of America (Congdon & McComb 1980). In the warmer parts of the USA, the standing crop of *J. roemerianus* was reported to be seasonally constant (Williams & Murdoch 1972; Giurgevich & Dunn 1982). In South Africa, Heinsohn (1990) reported that during the rhizome lifetime of *J. kraussii* there is continuous culm production. An experimental field study indicated that annual and biennial cut treatments stimulated the growth of individual culms

(McKean 2002). In the related species *J. roemarianus*, primary net productivity increased by 21–48 % in the year following harvesting in the USA (De la Cruz & Hackney cited in Özsesmi 2003). However, other studies in South Africa have suggested that in the long term, annual cutting resulted in a reduction in yield and plant vigour (Heinsohn 1991).

In KZN, cutting of *Juncus kraussii* within many protected areas is permitted from May each year. During April to July, the useable material as a percentage of total live material is the greatest (Heinsohn 1991). Culms are harvested through plucking or cutting with a sickle. Plucking has been observed in the north of KZN at Kosi Bay and may be possible due to the longer, more robust culms in this area (Taylor 1996). Plucking is regarded as the traditional method of harvesting *J. kraussii* but this method may damage the underground rhizomes (Heinsohn 1990). The sickle-cut method has been criticised for being wasteful as only 25 % of the cut culms are selected (Heinsohn 1990) and the unselected stems may be discarded and form a thick mat of litter, which impedes new growth by blocking sunlight reaching new shoots. *Juncus kraussii* rush harvesters tend to favour removal of all stems as it allows the new culms to grow uniformly (Christiansen 2000).

All wetland plant species harvested for crafts have a perennial life cycle. The morphology differs between families: the Juncaceae and Typhaceae are herbs, the Poaceae are graminoids and the Cyperaceae are grass-like herbs. Many of the species are rhizomatous such as *Cyperus papyrus*, *C. textilis*, *C. sexangularis*, *Schoenoplectus brachyceras*, *S. scirpioides*, *Aristida junciformis* and *Phragmites mauritianus*. Although the response of plants to cutting is likely to be species specific, morphological characteristics are an important factor influencing responses (Li *et al.* 2004). Thus, shared characteristics may increase the likelihood of similar responses.

Investigations of the response of plants to harvesting have largely been undertaken for only two plant species

that are used for craft production in South Africa, namely *Juncus kraussii* and *Phragmites australis*. An important question to address is: how applicable are the findings of these studies to other species that are harvested for craft production? Given that all of the other species, together with *J. kraussii* and *P. australis*, are vigorously growing rhizomatous perennials, in a general sense they are all likely to respond in a similar way. However, some differences are likely to be exhibited given that there is considerable morphological diversity amongst the species. In an attempt to account for this diversity, the species can be grouped according to shared morphological characteristics, and these groups of species will probably respond in a similar way to harvesting, although this requires further investigation. From Table 3 it can be seen that whereas some taxa, such as *Phragmites* and *Schoenoplectus*, are confined to one particular morphology, other taxa, notably *Cyperus*, have a diverse range of morphological characteristics.

Harvested plant populations: abundance, distribution and landscape level factors

The response of a species to cutting disturbance at the population level is determined by factors such as geographic distribution, whether species are habitat specific or not, and local population sizes. Species with a wide geographic distribution are not habitat specific and large local population sizes have a high potential for sustainable harvests (Cunningham 2001). Some of the landscape scale factors that influence a plant's population response to cutting disturbance are shown in Table 4. Species with a restricted geographic distribution that are habitat specific and with small local population sizes, have a low potential for sustainable harvesting. *Cyperus papyrus*, *C. textilis* and *Juncus kraussii* all have a restricted geographic distribution within KZN (Figure 1). However, they also all have large local populations at specific sites which increase their opportunity for sustainable harvests. Most of the wetland plant species are habitat specific as they tend to occur along rivers and streams, in pools,

TABLE 3.—Obligate wetland species used for craft production in KwaZulu-Natal, grouped according to shared morphological characteristics. All species listed are rhizomatous and perennial

Morphological characteristic	<i>Miscanthus junceus</i>	<i>Cyperus latifolium</i>	<i>Typha capensis</i>	<i>Phragmites australis</i>	<i>P. mauritianus</i>	<i>Cyperus papyrus</i>	<i>C. sexangularis</i>	<i>C. textilis</i>	<i>C. marginatus</i>	<i>Schoenoplectus brachyceras</i>	<i>S. scirpioides</i>	<i>Juncus kraussii</i>	<i>J. punctatorius</i>
Leaves													
basal, terete	x												
basal, with blades		x	x										
terete													x
several sheathing full length of each tall culm, with blades				x	x								
single sheathing lower portion of each terete photosynthetic culm													x
reduced to small bracts						x	x	x	x	x	x	x	
Culms													
terete, photosynthetic						x	x	x	x	x	x	x	x
with very many terminal photosynthetic prophylls						x							
with many terminal photosynthetic leaf-like bracts							x	x					

swamps and dams. *Schoenoplectus scirpoides* and *J. kraussii* display more specific habitat requirements. *Schoenoplectus scirpoides* occurs mainly in estuarine areas and *Juncus kraussii* is most abundant in intertidal mudflats. Although *J. kraussii* can grow in freshwater conditions, it may be out-competed, and it is more competitive in saline environments where it can form monodominant stands (Heinsohn 1991).

Implications of the findings

Most research concerning the biology and physiology of *Phragmites australis* was conducted in northern temperate regions (e.g. Mook & Van der Torn 1982; Karunaratne *et al.* 2004; Soetaert *et al.* 2004). The applicability of these findings to populations in South Africa needs to be considered. Experiments have suggested that *P. australis* displays differentiation of genotypes adapted to local geographical conditions, and that latitude can affect growth dynamics and biomass allocation patterns (Bastlovà *et al.* 2004). High phenotypic variation in morphology and life-history traits have also been reported (Clevering & Lissner 1999; Clevering *et al.* 2001). Although *P. australis* from different locations displays different growth rates in experimental cultures (Daniels 1991), the build-up of reserves in the rhizomes is a 'strongly determined mechanism' (Muachamp *et al.* 2001: 161).

In South Africa, as in the northern temperate regions, *Phragmites australis* shows a well-defined growing season in spring and summer with a pronounced senescence of aboveground parts in autumn/winter. Thus, the general trends in plant growth and resource mobilization outlined for the temperate regions are probably highly applicable to South Africa. Studies suggest that to maintain plant vigour, cutting should take place when rhizome storage levels are high and when shoot growth rates are slow. Cutting should not take place when new shoots are emerging, and should not remove the apical meristem, as this can lead to replacement by several smaller shoots. Therefore, cutting in autumn/winter is recommended. In fact, in South Africa, the timing of harvesting of *P. australis* occurs after flowering, once the shoots and leaves have begun to senesce. This timing is acceptable because the main uses in South Africa are for walls, screens (Van Wyk & Gericke 2003) and thatching (Cunningham 1985) as the stems do not have to be very flexible because they are not woven. The split stems can be used in basketry (Van Wyk & Gericke 2003), but this has not been widely reported in South Africa. Thus, in terms of the timing of cutting, current harvesting practices are in general agreement with recommendations from the published literature.

In contrast to *Phragmites australis*, the shoots and leaves of species used for weaving and basketry such as *Aristida junciformis*, *Eragrostis plana*, *Festuca costata*

TABLE 4.—Landscape scale factors which influence response to cutting of wetland species used for crafts

Species	Geographic distribution within KZN*	Wetland system**	Habitat specificity**	Local abundance	Conservation information**
<i>Miscanthus junceus</i>	Limited to northern KZN, Midlands, coast	RPL	Riverbanks and vleis		I
<i>Phragmites australis</i>	Widespread	RPL	Along edge of rivers, shallow water, margins of pools, swamps	Common or locally dominant (in riverbeds)	IC
<i>P. mauritanus</i>	Widespread	RPL	Along edge of rivers, shallow water, margins of pools, swamps, and dams	Common or locally dominant (in riverbeds)	I
<i>Cyperus latifolius</i>	Widespread	RP	Along edge of rivers and streams, freshwater swamps, wet depressions in grasslands	Locally common at specific sites	I
<i>C. marginatus</i>	Limited to Uplands and Midlands	P	Common along stream banks, usually rooted in shallow water, often among rocks; sometimes border isolated small pools	Can form locally extensive stands.	I
<i>C. papyrus</i>	Restricted to coast and Maputaland	RPL	Along edge of rivers, seasonal pools, swamps	Can form extensive stands at river mouths and floodplains	I
<i>C. sexangularis</i>	Widespread	R	Along edge of streams or rivers, often in water		I, En
<i>C. textilis</i>	Restricted to coast and Midlands	RP	Wet, marshy areas along coast, in shallow water along rivers/streams, marsh/vlei, brackish water	Locally common at specific sites	N
<i>Schoenoplectus brachyceras</i>	Limited to Uplands and Midlands	RL	Along edge of rivers, around edge of lakes and dams		I
<i>S. scirpoides</i>	Restricted to coast and Maputaland	PE	Coastal marshy areas, saline pools		I
<i>Juncus kraussii</i>	Restricted to coast and Maputaland	PE	Intertidal mud flats	Locally common at specific sites	I, NT
<i>J. punctorius</i>	Limited	RP	Along edge of rivers, wet, marshy areas around pools, swamps		I
<i>Typha capensis</i>	Wide	RPL	Gregarious, along edge of rivers, around edge of lake, in marsh or vlei areas, ditches, dams		I

*SANBI PRECIS Database and herbarium records. ** Source: Glen *et al.* in prep. R, riverine; P, palustrine; L, lacustrine; E, estuarine; I, indigenous; C, cosmopolitan; En, endemic to southern Africa; N, naturalized; NT, not threatened.

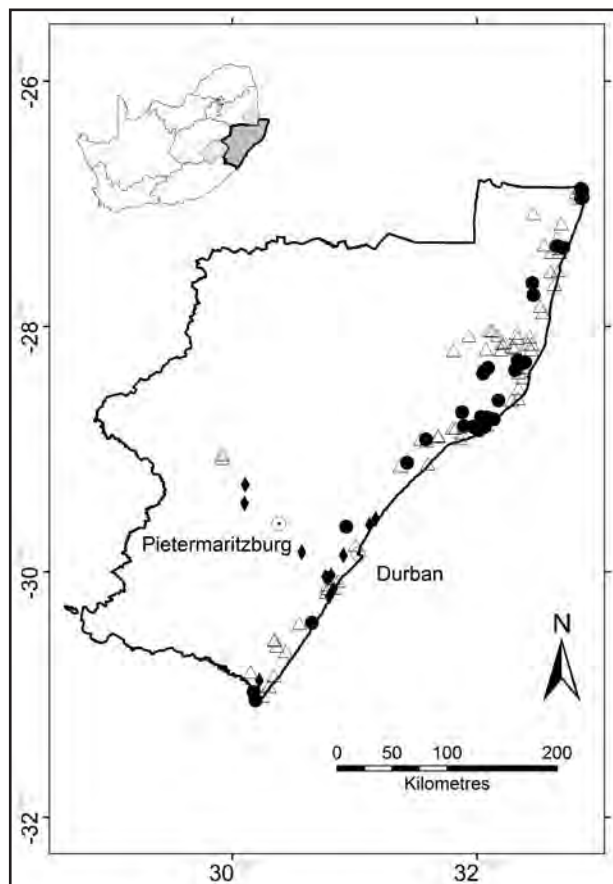


FIGURE 1.—Geographic distribution of *Cyperus papyrus*, ●; *Cyperus textilis*, ◆; and *Juncus kraussii*, △, in KwaZulu-Natal.

and *Sporobolus africanus*, must retain their flexibility. Therefore, the availability of these species is restricted to the spring and summer seasons (Cunningham & Terry 2006) as they are harvested before senescence in autumn/winter. Although their response to cutting disturbance has not been widely researched, the sharing of some key plant physiological traits suggests that these species may display a response similar to that documented for *P. australis*. Studies on *Glyceria maxima*, a perennial, rhizomatous aquatic species that belongs to the Poaceae family, showed that the amount of non-structural carbohydrates stored in rhizomes in autumn, has a strong relationship with the number of large-diameter shoots produced the following spring (Sundblad 1990).

Species within the Juncaceae may show a strong seasonality in growth at high latitudes but limited seasonality at lower latitudes where less extreme winter conditions exist (Congdon & McComb 1980). In *Juncus kraussii*, the main growth period is during the warm season. However, new culms are produced throughout the year in Australia (Congdon & McComb 1980), and South Africa (Heinsohn 1991). Thus, in South Africa, culms suitable for weaving and basketry are available during the entire year (Cunningham & Terry 2006). In terms of obtaining useable fibres for basketry and weaving, the timing of harvesting for the Juncaceae is less restrictive than for the Poaceae. Heinsohn (1991) investigated the timing of *J. kraussii* harvesting in South Africa, recommending that the period between April and July was best to obtain fibres for crafts, as the percentage of useable material

(long, green, non-flowering culms with limited signs of senescence) in relation to total live material, was greatest during this period. *Juncus kraussii* culms produced at any time of year, display an initial rapid growth, followed by a stationary phase with slow growth rate and slow senescence rate, and then finally a negative growth rate and increased senescence (Heinsohn 1991). The patterns of mineral nutrient and non-structural carbohydrate storage and movement between rhizomes and aboveground parts are unlikely to display seasonal trends as there is no single flush of growth. Rather, storage should be specific to the developmental stage of a particular plant. Thus, the timing of cutting disturbance, if it aims to maximize plant vigour, rhizome storage levels and culm diameter, will be determined by the developmental stage of the plant. As individual plant developmental stages vary throughout the year, no specific time of the year can be recommended for cutting from an ecological perspective. Investigations into the standing crop of *J. kraussii* in South Africa show that the amount of dead material peaks during August and September (Heinsohn 1991). Therefore, ecologically, this may be the most appropriate time for cutting disturbance.

The frequency of cutting has an impact on plant growth, and in the short term, cutting of *Phragmites australis* and species of *Juncus* may stimulate aboveground production (e.g. Cowie *et al.* 1992; McKean 2002). However, in *P. australis*, cutting in the long term may reduce the number of longer-length and large-diameter culms (McKean 2001; Tarr *et al.* 2004). Unfortunately, investigations of the long-term impacts of cutting upon species such as *J. kraussii* are limited. Crafters seek longer-length culms as it means there are fewer 'ends' produced in items. Additionally, culm length determines the width of sleeping mats, so long culms produce wide mats. Large-diameter culms have advantages over thin diameter culms in crafts, as it reduces the time required to construct items such as mats, as fewer culms are required. Furthermore, large culms are easier to handle. To obtain culms with these characteristics, biennial cutting has been suggested for both *P. australis* (Tarr *et al.* 2004) and *J. kraussii* (Heinsohn 1991; McKean 2002). Limited information exists concerning the other species harvested for crafts, but the precautionary principle and the above recommendations could be applied until further information is available.

From a resource management and conservation perspective, species with restricted distributions are important, especially if demand for their fibres is high. The results from this study suggest that *Juncus kraussii* and *Schoenoplectus scirpoides* are particularly important because of their restricted distribution and specific habitat requirements. Within KZN, demand for *J. kraussii* is extremely high. Although many species can be used to make sleeping mats, *J. kraussii* is the only species that is culturally acceptable for the production of bridal sleeping mats (Hennessy & Koopman 2000). Crafters have travelled up to 200 km to obtain supplies (Traynor 2008) and it was one of only two craft species where trade in unprocessed fibres away from the source was recorded (Cunningham 1985). Field studies within KZN have suggested that demand is greater than supply (Traynor & Kotze 2007b). Cultivation programmes have been established in KZN to meet the demand from crafts-

men (Traynor & Kotze 2007a). Information concerning *S. scirpoides* is limited, but this species does not have the same strong cultural associations as *J. kraussii* and it is used to produce fewer types of craft items (Kotze & Traynor in prep.). Thus, from a resource management perspective, *J. kraussii* is of primary importance.

For conservation purposes, it has been recommended that reedbeds are cut so that a mosaic of different-aged cut and uncut stands are produced within the landscape. These recommendations are applicable to South Africa. In fact, in many communal areas, wetland harvesting takes place on an *ad hoc* basis and individuals often walk to sites and harvest one bundle of fibres. Thus, cutting is often on a micro-landscape scale with small recently cut patches interspersed with regenerating patches and uncut patches. In some of KZN's nature reserves, the harvesting of *Juncus kraussii* is managed on a rotational basis (C. Beattie, Umlalazi, pers. comm.; S. Kyle, Kosi Bay, pers. comm.). Approaches such as these should be maintained as they are beneficial from a conservation perspective.

Wetland plant harvesting that is ecologically sustainable can contribute towards the wise use of wetlands. This requires maintenance of wetland ecological character and is achieved through the implementation of ecosystem approaches within the context of sustainable development (Ramsar 2006). The wise use concept is being globally promoted by international organizations such as Ramsar and Wetlands International. Within South Africa, local organizations such as Working for Wetlands and the Mondi Wetlands Project are developing wise use programmes for wetlands. These initiatives aim to support local livelihoods and increase economic empowerment of communities living near wetlands. Wetland plant crafting activities, if appropriately managed, could play an important role in such endeavours. Furthermore, support for harvesting and crafting may assist to enhance the perceived value of wetlands in their natural state and thereby reduce the pressure to convert the wetlands for alternative uses such as agriculture.

ACKNOWLEDGEMENTS

The following organizations are kindly thanked for their support for the 'Wise use of wetlands through craft production' project: WWF-SA, the Anglo American Chairman's Fund and the Wildlife and Environment Society of South Africa (WESSA). The South African National Biodiversity Institute is thanked for the use of data from the National Herbarium, Pretoria (PRE) Computerised Information System (PRECIS); wetland plant species distribution data. Christina Potgieter and Prudence Magwaza (Herbarium, University of KwaZulu-Natal, Pietermaritzburg Campus) are thanked for access to plant specimens and their kind assistance and Ruth Howison (Cartographic Unit, Discipline of Geography, University of KwaZulu-Natal, Pietermaritzburg Campus) for production of the figures. The staff at WESSA, Howick are thanked for all their support and assistance during the project. Scotty Kyle and Callum Beattie are thanked for discussions and the anonymous referees for their valuable comments.

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OBITUARY

SANTIAGO CASTROVIEJO BOLIBAR (1946–2009)

With the untimely passing of the doyen of plant systematics on the Iberian Peninsula, Dr Santiago Castroviejo Bolibar (Figure 1), shortly after his 63rd birthday, on 30 September 2009, the global plant taxonomic fraternity lost one of its staunchest supporters and contributors. He was a mild-mannered and humble person who easily and readily shared his considerable expertise in matters of a taxonomic nature with his colleagues. He worked well beyond the borders of his native Spain and participated widely in a wide range of international botanical initiatives.

Santiago was born on 7 August 1946 and spent his childhood in Tirán, Moaña (Pontevedra). After completing his secondary schooling, he entered the Universidad Complutense, Madrid, where he eventually graduated with a doctoral thesis entitled 'Flora y Cartografía de la Península del Morraza en Pontevedra' under the tutelage of Prof. Francisco Bellot Rodríguez. He always had a strong interest in systematics and was one of a rare breed of biodiversity specialists who understood the value of, and strongly supported, descriptive taxonomy in a biosystematics framework. During his professional botanical career, Santiago held various scientific and administrative positions, among others as director of the Real Jardín Botánico, Madrid, from 1984 to 1994.

His taxonomic interests and background led naturally to a significant involvement in the *Flora iberica* project of which he was a major architect. This project brought the by then outdated *Prodromus florum hispanicae* into the 20th century, and is indeed what Santiago will be best remembered for. This model hard copy and web-based project benefitted greatly from his international experience and is today regarded as one of the leading sources of primary taxonomic information on a significant component of the Iberian flora. Significantly, Santiago did not simply rely on others to produce treatments for the *Flora iberica* project, he also conducted taxonomic research himself, including a treatment of, for example, the Crassulaceae of the region.

He was very much aware of the importance of international collaboration with a global reach and actively pursued the establishment of professional links with a range of colleagues and institutions from abroad. This awareness and his commitment to the *Flora iberica* project gave rise to a strong involvement in the Species Plantarum Programme—Flora of the World (SPPFW), where he served on the Steering Committee since the revival of the programme in the early 1990s. The SPPFW benefitted greatly from his considerable expertise in developing electronic and web-based taxonomic products, such as identification and mapping tools. In 2005, Santiago was also elected to the Council of the International Association for Plant Taxonomy (IAPT), where he served until shortly before his death.

In spite of his considerable administrative duties in the various appointments he held in Spain, he retained a lifelong passion for field work and collecting herbarium specimens. Field trips were as far as possible linked to attending international botanical meetings. These gave him an opportunity to further satisfy his curiosity on a range of botanical interests that covered not only taxonomy and systematics, but extended into biogeography, ecology and conservation science. Santiago undertook two collecting trips to South Africa, the first coinciding with the hosting of the 3rd SPPFW Steering Committee meeting from 10 to 12 February 1999 (Smith 1999) at the Kirstenbosch Research Centre of the South African National Biodiversity Institute (SANBI) in Cape Town. The second trip followed after he attended the first-ever Africa-hosted Council Meeting of the IAPT, which was held at the National Herbarium of SANBI in Pretoria on 12 January 2008. On these two trips, Santiago collected 726 accessions of mainly Asteraceae, Ericaceae, Fabaceae, and Restionaceae. The specimens are deposited in the Herbarium of the Real Jardín Botánico, Madrid (MA), which is the main preserved plant collection in Spain.



FIGURE 1.—Santiago Castroviejo processing collected material gathered around Ladysmith during a field trip to South Africa in 1999. Photographer: A. Prunell.

Santiago finally succumbed to cancer of the mouth following a two-year battle with the disease. We join his numerous colleagues and collaborators in mourning his passing. His untimely death leaves a void that will be felt well beyond his native Spain.

ACKNOWLEDGEMENT

Dr Paco Pando, a former colleague of Dr Santiago Castroviejo, is thanked for useful comments on a draft of this paper.

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Abstracted, indexed or listed in • AETFAT Index • AGRICOLA • AGRIS • BIOSIS: *Biological Abstracts/RRM* • CABS • CABACCESS • CAB ABSTRACTS • ISI: *Current Contents*, *Scisearch*, *Research Alert* • *Kew Record of Taxonomic Literature* • *Taxon*: reviews and notices.

ISSN 006 8241

© Published by and obtainable from: South African National Biodiversity Institute, Private Bag X101, Pretoria 0001, South Africa.
Tel. (012) 843-5000. Fax (012) 804-3211. e-mail: bookshop@sanbi.org website: www.sanbi.org. Typesetting and page layout: E. Fouché.
Printing: Seriti Printing (Pty) Ltd, P.O. Box 24829, Gezina, 0031 Pretoria.