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

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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, redesign 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.

INTRODUCTION

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

**DELMITNG 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 infragenetic 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 contain 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 Restionae. 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 assignation 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 charac-
ters (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/Bestimmungsschlussel 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 analy-
sis with the full data set. Essential and differential morpho-
logical 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 spe-
dies 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 diagnos-
ability that is only possible on anatomical attributes is
not optimal.

3. Nomenclatural stability. Genera should be recog-
nized 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 segregated
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 gen-
era 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 mini-
mise 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 morpho-
logical 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 Restionaceae**

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

1. The maximal option is to include the whole sub-
tribe in one genus. This genus would be strongly sup-
ported as being monophyletic by the plastid data (Eldenås
& Linder 2000; Hardy et al. 2008), but would be difficult
to diagnose, as the morphological characters separating
Wildenowieae and Restionaceae 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 Wilde-

### Table 1

<table>
<thead>
<tr>
<th>Character</th>
<th>State 0</th>
<th>State 1</th>
<th>State 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Culms: round or flattened</td>
<td>0</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Culms branching</td>
<td>simple</td>
<td>0</td>
<td>branching</td>
</tr>
<tr>
<td>Membranous sheath shoulders: absent</td>
<td>0</td>
<td>present</td>
<td>1</td>
</tr>
<tr>
<td>Floral bracts: like body</td>
<td>0</td>
<td>with hollow cells</td>
<td>1</td>
</tr>
<tr>
<td>Floral bracts: overtopping flowers</td>
<td>0</td>
<td>shorter than flowers</td>
<td>1</td>
</tr>
<tr>
<td>Floral bracts: chartaceous, cartilaginous or bony</td>
<td>0</td>
<td>membranous</td>
<td>1</td>
</tr>
<tr>
<td>Male spikelets: erect</td>
<td>0</td>
<td>pendulous</td>
<td>1</td>
</tr>
<tr>
<td>Female lateral tepals: as odd tepal</td>
<td>0</td>
<td>conduplicate</td>
<td>1</td>
</tr>
<tr>
<td>Female tepals (texture): papery (flexible, not transparent)</td>
<td>0</td>
<td>winged</td>
<td>1</td>
</tr>
<tr>
<td>Ovary: dehiscent</td>
<td>0</td>
<td>indehiscent</td>
<td>1</td>
</tr>
<tr>
<td>Central ground tissue cavities: none</td>
<td>0</td>
<td>single</td>
<td>1</td>
</tr>
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### Table 2

<table>
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<th>State 1</th>
<th>State 2</th>
</tr>
</thead>
<tbody>
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<td>Willdenowieae</td>
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<td>2</td>
</tr>
<tr>
<td>Sorneria</td>
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<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Plataeae</td>
<td>0</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Elegia</td>
<td>0</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Strabera</td>
<td>0</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Aikialispora</td>
<td>0</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Thunnoborbus</td>
<td>0</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Rhodocoma</td>
<td>0</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Restio subgen. Calopis</td>
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<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Restio subgen. Crasspedolepis</td>
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<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Restio subgen. Eremorestio</td>
<td>0</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Restio subgen. Ischyrolepis</td>
<td>0</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Restio subgen. Locaspis</td>
<td>0</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Restio subgen. Pendulostemon</td>
<td>0</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Restio subgen. Simplicicaulis</td>
<td>0</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Restio subgen. Varinestio</td>
<td>0</td>
<td>1</td>
<td>2</td>
</tr>
</tbody>
</table>
nowiæ—the Restioneæ 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* (Olive 2000) and *Disa* (Byebeier et al. 2007, 2008).

2. The minimal option is to retain all existing genera that were retrieved as monophyletic (i.e. *Askidosperma*, *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. *Eremoresto*, Restio subgen. *Locapsis*, Restio subgen. *Pendulostemon*, Restio subgen. *Restio*, Restio subgen. *Simplicaulos*, Restio subgen. *Varirestio* 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. *Varirestio*), in others (e.g. Restio subgen. *Craspedolepis*, Restio subgen. *Eremoresto*, 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 *Askidosperma*, *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, *Eremoresto* and *Varirestio* 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*, *Eremoresto*, *Ischyrolepis*, *Locapsis*, *Pendulostemon*, *Restio s.str.*, *Simplicaulos* and *Varirestio* 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 *Askidosperma*). 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),
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 publication 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/Bestimmungsschluessel/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 Restionaceae**

1a Floral bracts reddish brown, bony, with transverse lacunae ............................................................................................................................................. 1. *Soroveta*

1b Floral bracts various, 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*
Bothalia 40.1 (2010)

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 racemose or panicle-like; spikes 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 stylar peg; ovary always dehiscent .................................................................................. 8.9 Restio subgen. Ischvrolepis

11b Style branches 1, 2 or 3, never fused into persistent stylar peg; ovary either dehiscent or indehiscent: 12a Culms simple ............................................................................................ 8.1 Restio subgen. Simplicaus

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. Craspodepis

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. Eremoresi

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. Locapvis

14b Female perianth coriaceous or bony, acute; ovary indehiscent or dehiscent, with 1, 2, or 3 locules: 16a Ovary with 1 or 3 locules; seed awn sometimes as long as sheath; sheaths with poorly developed membraneous lobes .................................................................................................................................... 8.4 Restio subgen. Varriresi

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 alis generibus tribus Restioneae bracteis floribulis transversaliter foveatis et combinatione vaginorum persisten-

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 exerted 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. Gynoecium 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 (L.): 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 synapomorphic features 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 ambigua Mast. in Flora capensis 7: 96 (1897). Type: Capc. s. loc., Zeyher s.n. (K, holo.: B).
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.

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

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). Lectotype: Malawi, Mt Mlanje, Sombani, cv. (BOL, holotype)., comb. nov.

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

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

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


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. Simplicula H.P.Linder & C.R. Hardy subgen. nov. (Figure 2) is weak, and an alternative position is for Simplicula 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 clade 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 disperse 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 clade 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.


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 ± 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. Gynoeceum 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. Calm 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. remotia). 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.

3.4. Staberoha cernua (L.f.) Dur. & Schinz, Conspectus florae africæ 5: 520 (1894).
3.5. Staberoha distachyos (Rottb.) Kunth, Enumeratio plantarum 3: 444 (1841).


Plants caespitose or with spreading underground rhizomes. Fertile culms round and, except in two species, simple; sheaths persistently, 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; stamens persistent; spikelets generally late to late from one or several nodes, with up to 100 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. Gynoeceum with solitary, white, plumose style; ovary unilocular, indehiscent. Diaspore an oblong to completely round, wind-dispersed structure; nut enclosed by persistent perianth. Calm 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. platypetris), but also typical of the wettest fynbos vegetation (T. cinereum). 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 perians, 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:

4.4. Thamnochortus gracilis Mast. in A.D.C., Monographiae phanerogamarum 1: 327 (1878).
4.17. Thamnochortus fruticosus P.J.Bergius, Descriptions plantarum ex Capite Bonae Spei 353 (1767).
4.18. Thamnochortus erectus (Thunb.) Mast. in Journal of the Linnean Society, Botany 14: 419 (1874).
4.28. Thamnochortus dumesus Mast. in Botanische Jahrbücher 29, Beiblatt 66: 11 (1900b).

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 lacereated remnant; hyaline shoulders absent. Male inflorescence racemose from several nodes, each partial inflorescence with several to numerous pendulous spikelets on flexible pedicels; spikelets ± 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. Gymnocium 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 (L.): 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).


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 charta­cea 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 whors of same length; stamenoid present. *Gynoe­cum*: 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 Swartruuggen, 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 Sneeukop. 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, tatter 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**


**Type**: *Elegia juncea* L.

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

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

**Lamprocallis** Mast. in A.DC.: 349 (1878). Type: *Lamp­rocallis 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 spathellae occasionally present; male bracts usually shorter than perianth, but in appearance similar to tepals. Male flowers with undifferentiated, glabrous tepals; anthers included 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 inflorescences, making them difficult to delimit; bracts at anthesis; spikelets often clustered in paniculate par­escentences generally hidden behind large spathes, which only poorly organized into spikelets; young partial inflo­rescences, each with several to very numerous flowers only poorly organized into spikelets; large spathes, which drop before anthesis; large spathe-like spathellae occasionally present; male bracts usually shorter than perianth, but in appearance similar to tepals. Male flowers with undifferentiated, glabrous tepals; anthers included 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 acuminated 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 stylodium; 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. Male flower. Male inflorescence: 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:


6.5. Elegia elephantina H.P.Linder, sp. nov., a E. tectoro caespitibus elatioribus (1.0–2.5 m), culmis validioribus (4–6 mm), spiculis maribus maioribus (3.0–3.5 mm diametro), tepalis feminis exterioribus interiores aquantibus 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, holotype). 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 macro 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 cartilaginal, 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 taller), 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 whors 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-loccular, 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.


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:


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


6.34. Elegia coleura Nees ex Mast. in A.DC., Monographiae phanerogamarum 1: 358 (1878).
6.40. Elegia persistens Mast. in Botanische Jahrbücher 29 Beiblatt, 66: 8 (1900b).
6.47. Elegia squamosa Mast. in Journal of the Linnean Society, Botany 10: 244 (1868).
6.50. Elegia juncea L., Mantissa plantarum altera 29 Beiblatt, 66: 8 (1900b).


Plants caespitose. Fertile culms unbranched, round; sheaths drooping 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. Gynoecium: 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 askidon, 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.


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 hasally fused, this fused portion persisting as a peg on the dehisced 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 Simpliciculids. The balance of the evidence places these two segregates into the Staheroha-Elegia clade, but taxonomically they are better kept in the large Restio s.lat.


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

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

Craspedolepis Steud.: 264 (1855). Type: Craspedolepis vertebralis 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 50 laterally compressed flowers; tepals cartilaginous, glabrous or sparsely (rarely densely) villous on keels of lateral sepals; staminodes present. *Gynoeicum* with 1, 2 or 3 feathery styles free to base, fused into a basal peg, or rarely seated on a stylodium; 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 adspectu Restioni, Craspedolepi, Calopsi, Locapsi, Varirestioni et Eremorestioni culmus rotundis, vaginis persistentibus, spiculis maribus et femineis valde similibus differt. *Fruit:* in species with indehiscent ovaries, seed silvery, brown or grey; perianth with up to 50 laterally compressed flowers; tepals cartilaginous, glabrous or keels of lateral sepals villous; staminodes present.

**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 dominant 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. nuevebergenensis* and *R. papyraceus*), that are quite similar to the female spikelets of the possible sister clad *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 conuplicate (*R. subtilis, R. confusus, R. miser*). The third group has thick spikelet-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 in 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 stamnodes 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).

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.


Named for the unusual condition of having two styles.


8.2. Restio subgen. Pendulostemon H.P.Linder & C.R.Hardy, subgen. nov., primo aspectu Restioni, Craspedolepi, Calopsi, Locapsi, Varirestioni, Oecium with 3, white, feathery, free styles; ovary with 2, rarely 3 or 1, fertile locules, dehiscent. Male inflorescence racemose or paniculate, with up to 20 erect, elliptical spikelets; staminodes present. Bracts at least as tall as flowers, imbricate, usually with 3, white, feathery styles free to base:

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 pendant 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 Kraeus in Flora 28: 337 (1845).

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


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 micro. 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 exserted 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 villose on keels of conduplicate tepals, occasionally also on back of outer odd tepal; staminodes present. Gynoeicum with 3, white, feathery styles free to base; ovary usually with 2, rarely 3 or 1, fertile locules, dehiscent. Seed variably 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.) = kruspedon (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, indelhiscent 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-spikeletted, 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:

8.3.5. *Restio praecacus* Mast. in Flora capensis 7: 84 (1897).

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


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.


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:


**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; micro somewhat as long as body of sheath. *Male inflorescences* racemose to paniculate, with up to 10 erect spikelets; spathe often overtopping spikelets; bracts with upper margins sometimes with honeycombed cells; anthers exerted from flowers at anthesis. *Female inflorescence* basically similar to male, but with fewer and larger spikelets; spikelets oblong, elliptical, ovate or ovate, with up to 20 flowers; bracts shorter or longer than flowers, apical margin sometimes with honeycombed cells. *Female flowers* laterally compressed; outer lateral tepals conuplicate, 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* (L.): *var* (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 dehilos** Nees in Linnaea 5: 641 (1830).


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


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 con-duplicate, keels glabrous to sparsely villous; staminodes present. *Gynoeicum* 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* (L.): *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 tetragonum** Thumb., Dissertatione de Restione: 17 (1788).


**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 bristy appearance; flowers laterally compressed; tepals chartaceous, rounded, glabrous or keels of lateral sepals sparsely villous; staminodes present. *Gynoeicum* 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), ropermaker; 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 sub-genus 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 diasporic (soft-walled nuts dispersed in a papery perianth). Such diasporic 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 rounded along 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 Swartruggens Mountains, and *R. rigidus* from the Voetpadsberg near Laingsburg to the Great Swartberg.


8.7. *Restio* subgen. *Restio*

Plants caespitose, clumped, tanged 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 micro. *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 exserted 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 sepalae; staminodes present. *Gynoecium* with 3, white, feathery styles free to base or rarely seated on a styleodium; ovary mostly unilocular, rarely with 2 locules, only in *R. sejunctus* with 3 locules, either dehiscent or indehiscent. *Dupasore* 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.

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


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 hyalina* (Mast.) Pillans: 344 (1928). *Mastersiella hyalina* (Mast.) Gilg-Ben.: 25 (1930). *Calopsis hyalina* (Mast.) H.P.Linder: 467 (1985). Type: Koude River, Schlechter 10464, 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 muco 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.


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).


The name refers to the uniquely villous flower bases.


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


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


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


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


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


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, 34194 (Caledon): Caledon River, 20-06-1978, 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; micro pubescence, straight or 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, or olivaceous, 0.3–0.8 m long, 0.1–0.7 mm diam. at apex; tepals, glabrous or keel sparsely villous (visible only under outer tepals cartilaginous; inner tepals shorter than outer, 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 conuplicate 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 2–3-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; stamnodes present. *Gynoecium*: styles feathery, white, 3, free to base; ovary unilocular, dehiscent. *Seed*: elliptical in side view, triangular in cross section, tan or pink, smooth (shiny). *Culm anatomy*: epidermal cells 1-layered, lateral walls straight and unthickened, outer wall thickened, colliculate, glabrous. 1/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 Kleinriberge 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 underground 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 35352 (BOL); Caledon, Klein River Mtns, nr Hermanus, Rocklands Peak area, in small marsh, on stream banks, (–AD), 03-05-1971, Esterhuysen 35752 (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 31372 (BOL); Caledon, Maanschyn Kop, between Hermanus and Stanford, in small marsh on E slopes, (–AD), 22-02-1968, Esterhuysen 31566 (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 epidemidis culorum unitarum, cum vaginis persistenteribus, spiculisque maribus erectis, ovarique indehiscenti, spiculisque feminine fusiformibus, tepalisque chartaceis rotundatis distinguendam.

**TYPE.—**Restio vimineus Roth.

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 panicle, 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, indehiscent. *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 of 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. r Igoratus*.

**Etymology:** *Locapsis* (L.), an anagarm 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 phylogeneti-
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.


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


This is a limestone species, hence the specific name.


Named for the characteristic white tubercles on the culms.

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


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


Named for Rudolf Marloth.

8.8.9. Restio vimineus Rothb., Descriptions planitarum rariorum 10 (1772).

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

Calopsis adpressus Estehr. in Linder in Bothalia 15: 465 (1985). Type: hills inland from Pearly Beach, Estehr. 32/977 (BOL, holo.); B!, K!, L!, M!, MO!, S!.

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

Calopsis dura Estehr. in Linder in Bothalia 15: 466 (1985). Type: South Cedarberg suurvlakte, between Kaffirkop and Loskop, Estehr. 32/975 (BOL, holo.); B!, CL!, EF!, GRA!, K!, L!, L!, 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 planitarum glumacearum. 2: 249 (1855). Type: Ischyrolepis subverticillatus Steud. (= Restio subverticillatus (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 micro. Male and female inflorescences basically similar, racemose to paniculate, I 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 obuse to often acuminate and recurved, or extended into a slender awn; anthers exserted 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; ovary with 2, white to red. feathery styles; ovary with 2, white to red. ovary with 2, white to red. ovary with 2, white to red. ovary with 2, white to red. ovary with 2, white to red. ovary with 2, white to red. ovary with 2, white to red.

In hills near Vogelvlei near Elim, Schlechter 10490 (B, lecto.! [Linder in Bothalia 15: 470 (1985)]; BOL!, K!, MO!, NBG!, P!, S!, WAG!, Z!).
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 anomalous** H. P. Linder sp. nov., a *R. feminineus* marginibus vaginarum late membranaceis, tepali superioribus florum linearium 3.0—4.5 mm longis, ovario biloculari statim dignoscenda.

TYPE.—Western Cape, 3419 (Caledon); Pleasants-hoek near Viljoenshof, in a marshy area near *Elegia fistulosa* and *Restio festuceformis*, 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 in florescence* 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.

8.9.2. **Ischyrolepis longiaristata** (Pillans ex H. P. Linder) H. P. Linder & C. R. Hardy, comb. nov.

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 feminineus*, which is also known only from female material, and which forms similar neat little branching tufts. However, *R. anomalous* differs in many details from *R. feminineus*. The sheath margins are broadly membranous (instead of coriaceous or narrowly membranous), the spathes overlap 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. feminineus*, 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.

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.

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.


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

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


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


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 lateritic, probably seasonally waterlogged conditions.


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


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


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


8.9.23. Restio constipatus H.P.Linder, sp. nov., a Restio wittebergensis culmus ramosissimus, a Restio schoenoides spiculis maribus 3–6 mm longis, spathis feminis spiculae aequantibus, seminis argenteis recedit.

Type.—Western Cape, 3319 (Worcester): summit of Matroosberg, among rocks, (-BC), 21-01-2001, H.P.Linder 7139 (Z, holotype; 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, brown, apical margins narrowly membranous, hyaline shoulders absent, apex acute to acuminate; macro pericillate, 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 x 7–25 mm; spathes persistent, as tall as spikelets, coriaceous, rather similar to lower bracts; male spikelets sessile, oblong or elliptical, 7–12 x 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 whors equally long, hyaline or membranous, linear or oblong, outer lateral tepals deliquescent, sparsely villous on keels; anthers 2–3 mm long, exserted 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 x 3–25 mm; spathes equalling spikelets, persistent, coriaceous; spikelets sessile, elliptical, obverse 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. Gynoeceum: styles 2, feathery, white; style bases free but adjacent; ovary dehiscent, bilocular. Seed 1.3–1.5 x 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 Sneeukop 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 tangle. 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 Sneeukop, (-AC), 02-01-1942, Esterhuysen 7567 (BOL); Cedarberg, Middelberg, SW slopes, (-AC), 01-09-1940, Esterhuysen 25246 (BOL); Cold Boekelveld, 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, Sneeukop peaks, on steep upper slopes, SE aspect, (-AA), 02-05-1964, Esterhuysen 30685 (BOL); Worcester, Mosterts Hoek Twins, (-AD), 08-01-1944, Esterhuysen 9832 (BOL); Worcester, Mosters Hoek Twins, S side of summit at base of low rock cap, in solid masses, (-AD), 23-02-1964,
Restio wittebergensis (Esterh.) H.P. Linder & C.R. Hardy, comb. nov.


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


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


8.9.37. Restio elsiae H.P. Linder, sp. nov., R. ocreatae affinis, sed culmis simplicibus, spiculis femineis ellipticos vel ovatis, semenibus longioribus (2,2-2,8 mm) notabilis. TYPE. Western Cape, Cape of Good Hope, 3319 (Worcester): Waaihoek Mtns, between Zebrasberg and Mt Superior, alt. 1,600 m, (AD), 17-03-2002, H.P. Linder 7460 (Z, holotype; B, BL, K, MO, NBG, NSW, PRE).

Plants tufted, 0,16-0,45 m tall, without spreading rhi­zones 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; micro hair-like, straight and erect or recurved or twisted, 3-8 mm long. Male flowers long, ovary with a single style, fruits 3-5 mm long. Male inflorescence racemose or globose, 15,35 x 9,20 mm wide, with 2-10 spikeltes; spiketals persistent, at least as tall as spikeltes, coriaceous or carti­laginous; spikeltes erect, elliptical, 7-13 x 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, exserted 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, aphan 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; stamnodes absent. **Gynoeceum**: styles 2, feathery, style bases fused to form a pillar; ovary dehiscent, bilocular. Seed (2.24–2.47(-2.76) x (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 virgineus, and the two species alternate on the stony slopes between Zebra Berg and Mt Superior. The plants appear to be killed by fire, regenerating from seed.

**Notes**: Restio elsiiae 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. elsiiae* 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, Fonteintjesberg, 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 30243 (BOL); Worcester, Fonteintjesberg, above Pulpit Rock Neck, rocky plateau, N and S aspects and steep slope, (CB), 16-12-1963, Esterhuysen 30588 (BOL); Ceres, Buffelskorke Peak, leading into Wieds, shale band, SW aspect, (AD), 08-10-1956, Esterhuysen 25617 (BOL); Ceres, Milner Peak, Hex River Mtns, rocky W slopes, (AD), 11-11-1960, Esterhuysen 26060 (BOL); Worcester, Waahloek Peak, upper rocky slopes, abundant in patches of almost pure stands, dense, scratchy tufts, stems unbranched, (AD), 11-02-1964, Esterhuysen 30612 (BOL); Worcester, Buffelskorke Peak and Buffelskorke Twins, rocky places, (AD), 19-09-1965, Esterhuysen 31183 (BOL).

8.9.38. **Restio cedarbergensis H.P. Linder**, sp. nov., a *R. ocreata* culmis gracilibus, bracteis maribus brevioribus (3.5–5.0 mm longis), floribus maribus brevioribus (2.5–3.0 mm longis), spiculis semifereae brevioribus (5–11 mm longis), floribus spiculis semifereae 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 x 6–12 mm; spathes persistent, at most as tall as spikelets, cartilaginous, acuminate; spikelets pendulous on flexible pedicels, linear or ovate, acute, 6–12 x 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, exserted from flowers; pistillode absent. **Female inflorescence** with up to 5 spikelets, sparsely paniculate, 5–35 x 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; stamnodes absent. **Gynoeceum**: styles 2, feathery, bases fused to form a pillar; ovary dehiscent, bilocular. Seed 1.7–2 x 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 Sneeukop, 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, between Sandfontein Peak and huysen 27213 (BOL); S Cedarberg, Dwarsrivierberg, rocky slope, (-CA), 01 Apr. 1956, Esterhuysen 25548 (BOL); S Cedarberg, on E spur of Houndverbrand 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).


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


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).


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


8.9.49. Restio parthenocarpos 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 ramificantibus, basi stylorum pubescenti recedit.

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

Plants tufted, compact, 0.25-0.4 m tall, without spreading rhizomes or stolons, all plants female. Fertile culms sparsely branched, round, smooth, oliveaceous, 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, macro 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, con­uplicate with keels densely villous; 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 Suurvlakte 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 750-100 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 parthenocarpos 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. cederbergensis. 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: parthenocarpos (Greek), producing seed or fruit without fertilization; the specific epithet is a noun in apposition.

Additional collection


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


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 Bolus 4234, 4235 (BOL, K!, MO, NBG, !).

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


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

ACKNOWLEDGEMENTS

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