

# A new subfamilial and tribal classification of Restionaceae (Poales)

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## Abstract

Restionoideae Link, with the newly described Sporadanthoideae and Leptocarpoideae, represent major clades of Restionaceae distinguished by analyses of chloroplast DNA data. These subfamilies are supported by features of morphology, culm anatomy, pollen and phytochemistry. Sporadanthoideae occur in Australia and New Zealand, Leptocarpoideae principally in Australia but with representatives also in New Zealand, New Guinea, Aru Islands, Malesia, Hainan Island and Chile, while Restionoideae are in sub-Saharan Africa and Madagascar. Two tribes, Restioneae Bartl. and Willdenowieae Mast. are recognised within Restionoideae, but their circumscriptions are very different from those of the tribes previously recognised within African Restionaceae. The relationship of Centrolepidaceae to Restionaceae remains unresolved, as sister group or embedded within the latter, but there is some support for Centrolepidaceae embedded within Australian Restionaceae and sister to Leptocarpoideae. This highly distinctive clade may be recognised as subfamily Centrolepidoideae Burnett if included within Restionaceae. Tribe Haplantherae Benth. & Hook. f. has the same circumscription as Restionaceae, as currently recognised, and Restio Rottb. is designated as the lectotype of this tribal name.

## Introduction

Restionaceae have been the subject of much detailed morphological, anatomical and evolutionary study but lack a classification of major infrafamilial groups that is consistent with current phylogenetic inferences. Relevant data have come from morphological studies (Linder 1984, 1985; Meney & Pate 1999; Linder et al. 2000), including anatomical (especially Cutler 1969) and palynological investigations (Chanda 1966, Chanda & Ferguson 1978, Linder & Ferguson 1985). Flavonoid constituents were investigated by Harborne (1979), Harborne et al. (2000) and Williams et al. (1998). Clearer indications of relationships have recently come from DNA-based phylogenetic investigations (Briggs et al. 2000; Linder et al. 2003, 2005; Hardy & Linder 2005, 2007; Linder & Hardy 2005; Moline & Linder 2005; Hardy et al. 2008; Briggs et al. submitted) which also confirmed that Centrolepidaceae was either closely related to Restionaceae or embedded within it.



The phylogenetic hypotheses that are a basis for the suprageneric taxa recognised here are largely inferred from analyses of chloroplast DNA data which have proved more phylogenetically informative than study of the highly reduced vegetative structures and small wind-pollinated flowers. Indeed, homoplasious reduction in floral and vegetative structures has led morphological comparison often to produce erroneous conclusions. For example, the multiple losses of the distinctive and prominent culm anatomical feature of pillar cells in Australian Restionaceae only became apparent when a molecular phylogeny was developed (Briggs et al. 2000). More comprehensive morphological study, combined with DNA data has, however, added resolution to the phylogeny of the African members (Hardy et al. 2008).

When Restionaceae (as Restiaceae) was originally described by Robert Brown (1810) it was much more inclusive than the family now recognised. Diverse genera have been transferred to Anarthriaceae, Centrolepidaceae, Ecdeiocoleaceae, Eriocaulaceae or Xyridaceae. The separation of Anarthriaceae and Ecdeiocoleaceae was initially largely based on differences in their vegetative anatomy (Cutler & Airy Shaw 1965). DNA-based phylogenies (Briggs et al. 2000, Bremer 2002, Chase et al. 2006 and other studies in Columbus et al. 2006, Marchant & Briggs 2007, Briggs et al. in press) show Ecdeiocoleaceae to be more closely allied to Poaceae than to Restionaceae, whereas most DNA data show Anarthriaceae as sister to (Restionaceae plus Centrolepidaceae). While molecular data (Briggs et al. 2000) showed that *Lyginia* and *Hopkinsia* formed a clade with *Anarthria*, the recognition of the separate families Lyginiaceae and Hopkinsiaceae (Briggs & Johnson 2000) was based on the very divergent culm anatomy. However, an enlarged Anarthriaceae, including the three genera, is now generally accepted.

#### **Centrolepidaceae Endl. (1836) or Centrolepidoideae Burnett (1835)**

Centrolepidaceae have long been considered to be closely related to Restionaceae or a derivative of it (Dahlgren et al. 1985, Linder & Rudall 1993, Kellogg & Linder 1995, Linder et al. 2000) and together they form a robustly supported monophyletic group in chloroplast DNA studies of Poales (Briggs et al. 2000, Bremer 2002, Briggs et al. in press). Similarities in embryology have been especially noted (Hamann 1962, 1975, Prakash 1969, Rudall and Linder 1988, Linder & Rudall 1993), as well as the similarity of Centrolepidaceae plants to Restionaceae seedlings (Linder & Caddick 2001). Restionaceae, as in many other Poales, show a relatively fast rate of nucleotide substitution and long branches in molecular phylograms, but Centrolepidaceae have exceptionally long branches. Although the currently available plastid DNA sequence data (Briggs et al. in press) suggest that Centrolepidaceae is embedded in Restionaceae, as sister to Leptocarpoideae, the alternative arrangement as sister to Restionaceae cannot yet be convincingly rejected (Fig. 1).

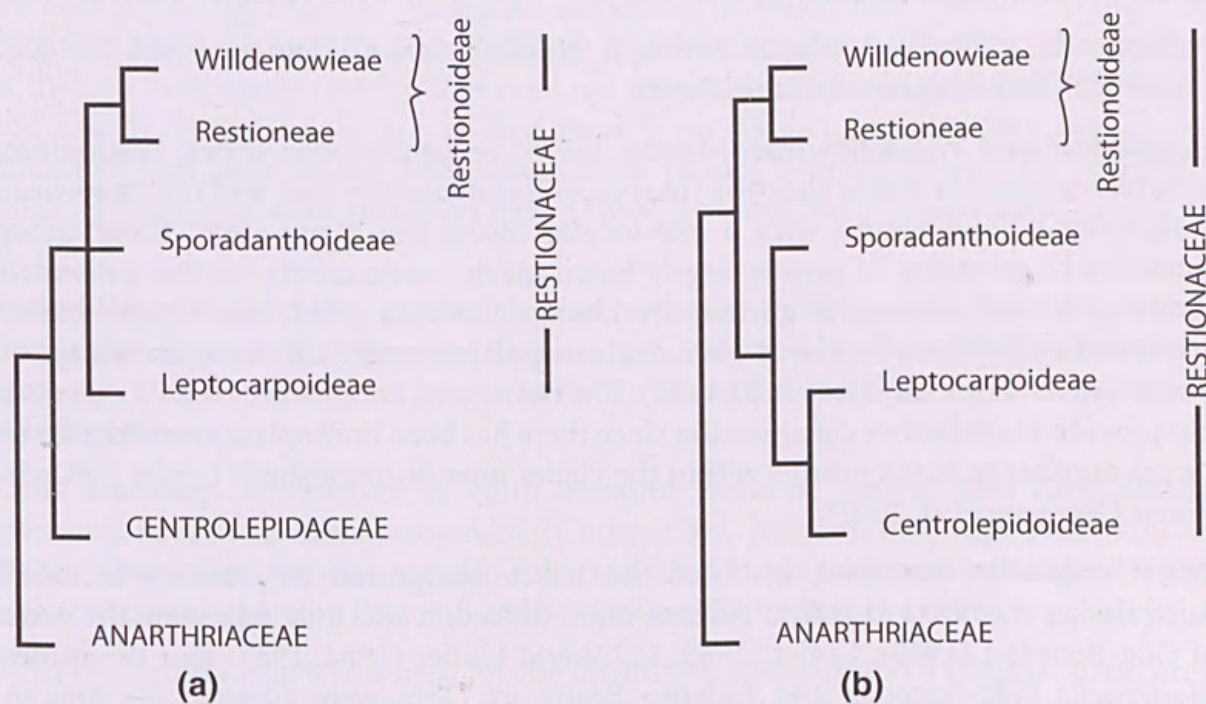
If a position embedded within Restionaceae is accepted, this clade would be known as subfamily Centrolepidoideae Burnett (1835, page 416), see also Reveal (2007). Centrolepidoideae differ conspicuously from other Restionaceae in their diminutive size, sometimes annual habit, unreduced leaves, lack of perianth, and in the floral structures which have been regarded as pseudanthia of male flowers reduced to a single stamen and female flowers to a single carpel (Hamann 1962, 1975; Cooke 1998) but could also be highly modified flowers (Sokoloff et al. submitted). The pollen of Australian Restionaceae have been described as 'centrolepidoid' (Chanda 1966, Chanda & Rowley 1967, Ladd 1977, Chanda & Ferguson 1979, Johnson & Briggs 1981) but Linder and Ferguson (1985) drew attention to important features of Centrolepidaceae



pollen such as the granular rather than columellate interstitium, lack of endexine and differences in the aperture and scrobiculi. *Centrolepis* (c. 26 spp., Cooke 1998), *Gaimardia* (4 spp.) and *Aphelia* (6 spp.) occur in southern temperate regions and mountains of the tropics: in Australia, south-east Asia, Pacific Islands and southern South America.

### Major clades of Restionaceae

In addition to Centrolepidoideae, if included in Restionaceae, three major clades are now distinguished and here recognised as subfamilies: Sporadanthoideae and Leptocarpoideae are here newly described, along with Restionoideae (subdivided into two tribes, Restioneae and Willdenowieae). Relationships among the subfamilies are still not robustly resolved (Briggs et al. in press) but there is support for a clade of (Sporadanthoideae + Leptocarpoideae + Centrolepidoideae), with these either forming a trichotomy or grouped as (Sporadanthoideae (Leptocarpoideae + Centrolepidoideae)) (Fig. 1a). Thus the primarily Australian clade forms a sister group to the African Restionoideae. This topology is not supported by parsimony analyses of *trnK* and *trnL-F* data (Fig. 1b), but evidence from slowly evolving genes and from Bayesian or maximum likelihood analyses are considered more reliable in investigating ancient relationships (Jiang et al. 2008) than parsimony results from fast-evolving genes. The latter are more subject to artifacts arising from long-branch attraction.



**Fig. 1.** Alternative positions of the centrolepid clade: (a) sister to Restionaceae (family Centrolepidaceae), as found from parsimony analysis of *trnK* or *trnL-F*; (b) embedded in Restionaceae (subfamily Centrolepidoideae) and sister to Leptocarpoideae, as found from *rbcL* data or from Bayesian analysis of *trnK* or *trnL-F* (Briggs et al. in press).



### Previous subfamily and tribal nomenclature and classifications

The earliest valid use of names at subfamily and tribal rank based on *Restio* (Reveal 2007) are Restionoideae Link, Handbuch 1: 134. Jan-Aug 1829, and at tribal rank Restioneae Bartl., Ord. Nat. Pl.: 36. Sep 1830. These names are adopted here, as is Willdenowieae (Willdenovieae) Masters in A. DC., Monogr. Phan. 1: 314. Jun 1878. The circumscription of these taxa is, however, very different from when these names were first applied. In Bartling's treatment, Restioneae equates to the whole of Restionaceae (excluding Centrolepidaceae) as here recognised (examples from all major clades being included), whereas the two other subfamilies consisted of genera now placed in Centrolepidaceae, Anarthriaceae and Eriocaulaceae.

**Haplantherae and Diplantherae.** Bentham and Hooker (1883) divided Restionaceae, as then circumscribed, into two tribes: Haplantherae with one anther locus and Diplantherae with two anther loculi. This classification was also used by Gilg-Benedict (1930) and these tribes were subsequently referred to as Restioneae and Anarthrieae (Hamann 1964). The latter tribe consisted of *Ecdeiocola* F. Muell., *Anarthria* R.Br. and *Lyginia* R.Br. Subsequently *Ecdeiocola* and *Anarthria* were excluded from Restionaceae with the description of Ecdeiocolaceae and Anarthriaceae by Cutler and Shaw (1965). As mentioned above (Briggs et al. 2000), DNA data later showed that *Ecdeiocola* is more closely allied to Poaceae than to Restionaceae and that *Lyginia*, *Hopkinsia* and *Anarthria* form a clade that is sister to (Restionaceae + Centrolepidaceae). So all members of Diplantherae are now excluded from Restionaceae.

Since Haplantherae has a circumscription equivalent to that of family Restionaceae, as the latter is now recognised, it is appropriate that it be typified by the same type. We therefore designate a lectotype.

Restionaceae tribe Haplantherae Benth. & Hook.f., *Genera Plantarum* vol. 3: 1028. Lectotype (here designated) *Restio* Rottb.

**Restioideae and Willdenowieae.** Masters (1878) recognised two tribes, Restioideae, with two or three (or one by abortion) ovary loculi and capsular fruit, and Willdenowieae (originally Willdenovieae) with a one-locular ovary and a nut fruit. These tribes formalised a grouping of genera largely based on the same criteria as that presented (without formal naming of groups) by Lindley (1836, p. 386), but which Lindley attributed to Nees von Esenbeck. Nees made important contributions to knowledge of Restionaceae (especially Nees 1830, 1846). The character of number of ovary loculi does not provide a satisfactory classification since there has been homoplasious reduction in carpel number in many groups within the clades now distinguished (Linder 1992a,b; Ronse Decraene et al. 2002).

When originally described, both of the tribes recognised by Masters included Australasian members as well as African ones. Indeed, it was only following the work of Gilg-Benedict (1930), Cutler (1969, 1972) and Linder (1984, 1985) that the names *Mastersiella* Gilg-Benedict and *Calopsis* Beauv. ex Desv. were adopted for African members, in contrast to the Australian *Hypolaena* R.Br. and *Leptocarpus* (Labill.) R.Br. More recently, the Australian taxa formerly included in *Restio* were separated from the African genus *Restio* (Briggs & Johnson 1998a, b), so that each of the genera now recognized can be assigned to the African clade or to one of the largely Australasian clades and subfamilies. This fulfils the prediction of Cutler (1972) that, when revised, no genus would be common to Australia and Africa. Our circumscription of tribes



also shows no agreement with the classification of the African members by Pillans (1928), who included in Restionoideae only *Restio* and *Chondropetalum* (the latter now included in *Elegia*), placing all other genera in Willdenowieae.

### Characters distinguishing subfamilies and tribes

**Morphology.** As a result of highly reduced structures and numerous homoplasious changes, neither external vegetative nor floral morphology offer features that we find useful in characterising the subfamilies, apart from Centrolepidoideae. Features are mostly not unique to a subfamily or are absent from some members of the subfamily, often by loss of the feature. For example, spikelet structure is widely found but in Sporadanthoideae the inflorescence is not always organised into spikelets: *Lepyrodia* and *Sporadanthus* lack spikelet structure, possibly having lost this feature, whereas *Calorophus* shows spikelet structure in both male and female inflorescences. However, lack of spikelet structure is not unique to Sporadanthoideae since, in Restionoideae, *Elegia* and males of *Willdenowia* do not have flowers aggregated into distinct spikelets.

Tribe Willdenowieae differs from Restioneae in that the pericarp is usually heavily lignified and the floral pedicel sometimes becomes thickened and functions as an elaiosome, and the gynoeceum has two styles. Ronse Decraene et al. (2001) found a concordant pattern of loss of the anterior carpel and displacement of the remaining carpels throughout Willdenowieae, indicating that these aspects of floral development were synapomorphic. Linder (1992b) also found a single pattern of carpel development in the tribe, as well as a single origin of the hard, woody nutlet.

**Pollen morphology.** Pollen grains of the Sporadanthoideae and Leptocarpoideae are both of the type termed Australian restionoid (as 'Australian restioid') (Linder & Ferguson 1985), whereas the Restionoideae have African restionoid pollen. Thus pollen of the two Australasian subfamilies does not show the tectum raised around the large and usually irregular aperture, so that there is no distinct annulus; also there is no thickened foot layer. In the Restionoideae the tectum is raised around the relatively small aperture and some members have a thickened foot layer (Linder 1984, Linder et al. 1998).

**Embryology.** Proliferating antipodals were reported in Restioneae but were absent from those Sporadanthoideae and Leptocarpoideae studied (Rudall & Linder 1988). However, only a minority of genera have been sampled and there are no reports for Willdenowieae.

**Culm anatomy.** Differences in culm anatomy between African and Australasian members have long been recognised (Cutler 1969, Johnson & Briggs 1981, Linder 2000). Anatomical features are also reported for African members by Linder (1984) and Australian genera by Pate and Delfs (1999) and Meney et al. (1999).

Most of the following terms used for the distinctive anatomical cell types or structures were defined by Cutler (1969) who clearly recognised their taxonomic significance and pointed out differences between those Australian and African taxa that were at that time considered to be congeneric.

*Protective cells:* modified cells of the chlorenchyma with slightly to moderately thickened lignified walls surrounding a substomatal cavity forming a tube extending all or part way through the chlorenchyma. These occur in Restionoideae and Sporadanthoideae,



being absent from Leptocarpoideae. Analogous protection of the substomatal cavity in members of the *Desmocladus* group and *Alexgeorgea* within Leptocarpoideae is by elongated and thick-walled epidermal cells. Using a broader definition of protective cells, Linder (2000) regarded epidermally-derived protective cells and chlorenchyma-derived protective cells as an example of convergence.

*Pillar cells*: elongate, palisade-like cells of the parenchyma sheath, usually with moderately thickened (lignified) walls, radiating from the sclerenchyma sheath to the epidermis, dividing the chlorenchyma into longitudinal bands. Since they arise from the parenchyma sheath, pillar cells are not homologous with 'false pillar cells'. Pillar cells are restricted to Leptocarpoideae, and are present in *Eurychorda*, sister group to the rest of that subfamily, as well as in ten other leptocarpoid genera. However, there appear to have been homoplasious losses of this feature in at least four leptocarpoid clades (Briggs et al. 2000).

'False pillar cells' (Linder 1984, 2000) are lignified cells of the chlorenchyma that extend outwards from ridges of the sclerenchyma in some species. These are unique to the Willdenowieae, but are found only in a small minority of the species and genera.

*Girders*: sclerenchyma ridges opposite the outer vascular bundles, extending from the sclerenchyma sheath all or part-way through the chlorenchyma. These occur in Leptocarpoideae, although in only a few genera; they were designated as 'ribs opposite vascular bundles' by Linder (2000).

*Ribs*: sclerenchyma ridges alternating with the outer vascular bundles, extending from the sclerenchyma sheath all or part-way through the chlorenchyma (Cutler 1969, p. 327). They are a feature of most Willdenowieae.

*Silica bodies*: sphaeroidal-nodular bodies or granular sand may be present, especially in the parenchyma sheath (between the chlorenchyma and the sclerenchyma cylinder) or in the outer layer of the sclerenchyma. Silica bodies are absent from Anarthriaceae (Cutler 1969, Prychid et al. 2004). Such inclusions are widespread in the commelinid families, so presumably their loss is a synapomorphy of that family. Within Restionaceae, silica bodies are found in members of all subfamilies and tribes but are reported as absent from some genera, especially in the Restioneae (*Elegia*, *Staberoha*, *Rhodocoma*).

**Phytochemistry.** The subfamilies show significant differences in the flavonoid constituents of their culms (Harborne 1979, Williams et al. 1998, Harborne 2000, Harborne et al. 2000). Myricetin is reported only in Sporadanthoideae (present in *Lepyrodia* and *Sporadanthus*, although absent from *Calorophus*). Leptocarpoideae are characterised by flavones, commonly luteolin and hypolaetin, as well as sulphated flavonoid derivatives. Restionoideae show flavonols, commonly derivatives of myricetin and its methyl ethers larycitrin and syringetin, and also proanthocyanidins.

### Description of subfamilies of Restionaceae

#### **Sporadanthoideae** B.G.Briggs & H.P.Linder, **subfam. nov.**

A Restionoideis et Leptocarpoideis combinatione characterum sequentium distinguenda: chlorenchyma continua, cellulis columnaribus nullis; parietes cellularum cavitates substomatales cingentes incrassati; flores in spiculis aggregati vel singulatim in inflorescentia portati; apertura pollinis ampla, irregularis, stratum fundum crassum deficiens.



Type genus: *Sporadanthus* F.Muell. Type: *Sporadanthus traversii* (F.Muell.) F.Muell. ex Kirk.

Flowers aggregated or not aggregated into spikelets; pollen with the tectum not raised around the large (8–25  $\mu\text{m}$ ) and usually irregular aperture and lacking a thickened foot layer (Australian restionoid type); proliferating antipodal cells in embryo sac lacking (so far as known); protective cells lining substomatal cavities present; chlorenchyma not interrupted by pillar cells or ‘false pillar cells’ or sclerenchyma girders or ribs; silica bodies or granular silica often present in epidermis and sometimes in ground tissue and parenchyma sheath; the flavonols myricetin and quercetin often present, flavones and protoanthocyanidins mostly absent.

A subfamily of three genera and about 31 species (including some not formally named), occurring in Australia and New Zealand. Sporadanthoideae equates with the *Lepyrodia* group of Briggs and Johnson (1999) and Briggs et al. (2000), but with the combined *Lepyrodia* and *Calorophus* groups of Johnson and Briggs (1981). The three genera recognized in the Sporadanthoideae, *Lepyrodia* R.Br. (species: 13 described, about 9 undescribed), *Sporadanthus* F.Muell. (7 described, 1 undescribed), and *Calorophus* Labill. (2 spp.), did not form a monophyletic group in a morphological cladistic study (Linder et al. 2000) but the clade is supported in most DNA analyses (Marchant & Briggs unpublished data).

**Leptocarpoideae** B.G.Briggs & H.P.Linder, **subfam. nov.**

A Restionoideis et Sporadanthoideis combinatione characterum sequentium distinguenda: chlorenchyma continua vel cellulis columnaribus vel costis schlerenchymatis interrupta; parietes cellularum cavitates substomatales cingentes non incrassati; flores in spiculis aggregati; apertura pollinis ampla, irregularis, stratum fundum crassum deficiens.

Type: *Leptocarpus* R.Br. (nom. cons.). Type (type. cons.): *L. tenax* (Labill.) R.Br.<sup>1</sup>

Flowers in spikelets; pollen lacking a thickened foot layer and the tectum not raised around the large (8–25  $\mu\text{m}$ ) and usually irregular aperture (Australian restionoid type); protective cells absent; pillar cells in the chlorenchyma present or absent; sclerenchyma girders mostly absent but when present opposite vascular bundles; ‘false pillar cells’ and sclerenchyma ribs absent; silica bodies often present in parenchyma sheath and epidermis; flavones luteolin and hypolaetin often present, flavonols and protoanthocyanidins mostly absent.

A subfamily with 28 genera currently recognised and about 117 species (including some not formally named), occurring in Australia, New Zealand, New Guinea, Aru Islands, Malesia, Hainan Island and Chile. Leptocarpoideae equates to the *Leptocarpus* group of Johnson and Briggs (1981) but to the combined *Winifredia*, *Desmocladus*, *Loxocarya* and *Leptocarpus* groups of Briggs and Johnson (1998a, 1999), together with

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<sup>1</sup> The proposal of this new conserved type (Briggs 2001, 2005) was recommended by the Committee for Spermatophyta (Brummitt 2005: p. 1096), endorsed by the General Committee (Barrie 2006: p. 800) and approved at the XVII International Botanical Congress (McNeill et al. 2005) but unfortunately the listing of the conserved type in the International Code of Botanical Nomenclature (Vienna Code) (McNeill et al. 2006: p. 270) was not changed to incorporate this decision. This oversight should be corrected in the next issue of the Code.



*Alexgeorgea* which was ungrouped. It also corresponds to the combined *Desmocladus*, *Loxocarya* and *Leptocarpus* clades of Linder et al. (2000) derived from morphological cladistic study.

The Leptocarpoideae are discussed by Briggs and Johnson (1999) and Meney and Pate (1999). The *Desmocladus* and *Leptocarpus* groups based on morphology of Briggs and Johnson (1998a, 1999) and Linder et al. (2000) are supported by DNA data but the *Loxocarya* group is paraphyletic and these groups do not adequately represent the main clades within Leptocarpoideae. Especially, the position of *Eurychorda* as sister-group to the remainder of Leptocarpoideae was not expected from morphological studies. The status of several genera is under review following results from analyses of DNA data.

Genera currently recognised: *Alexgeorgea* (3 species), *Apodasmia* B.G.Briggs & L.A.S.Johnson (3 described, 1 undescribed), *Baloskion* Raf. (8), *Catacolea* B.G.Briggs & L.A.S.Johnson (1), *Chaetanthus* R.Br. (3), *Chordifex* B.G.Briggs & L.A.S.Johnson (within which the previously described genera *Acion*, *Guringalia* and *Saropsis* [Briggs & Johnson 1998a] have been synonymised [Briggs & Johnson 2004]) (20), *Coleocarya* S.T.Blake (1), *Cytogonidium* B.G.Briggs & L.A.S.Johnson (1), *Dapsilanthus* B.G.Briggs & L.A.S.Johnson (4), *Desmocladus* Nees (15), *Dielsia* Gilg (1), *Empodisma* L.A.S.Johnson & D.F.Cutler (2), *Eurychorda* B.G.Briggs & L.A.S.Johnson (1), *Harperia* W.Fitzg. (4), *Hypolaena* R.Br. (8), *Kulinia* B.G.Briggs & L.A.S.Johnson (1), *Lepidobolus* Nees (6 described, 3 or 4 undescribed), *Leptocarpus* R.Br. (2 described, 1 undescribed), *Loxocarya* R.Br. (5), *Meeboldina* Suess. (5 described, 6 undescribed), *Melanostachya* B.G.Briggs & L.A.S.Johnson (1), *Onychosepalum* Steud. (3), *Platychora* B.G.Briggs & L.A.S.Johnson (2), *Stenotalis* B.G.Briggs & L.A.S.Johnson (1), *Taraxis* B.G.Briggs & L.A.S.Johnson (1), *Tremulina* B.G.Briggs & L.A.S.Johnson (2), *Tyrbastes* B.G.Briggs & L.A.S.Johnson (1), *Winifredia* L.A.S.Johnson & B.G.Briggs (1).

Within Leptocarpoideae, pillar cells appear to be a pleisiomorphous character (Briggs et al. 2000), being present in eleven genera including *Eurychorda* which appears in molecular phylogenetic trees as sister to the remainder of the subfamily. The loss of pillar cells is, however, a homoplasy shown in the *Desmocladus* group (absent throughout), *Winifredia* group (pillars present in *Taraxis*; absent in *Empodisma* and *Winifredia*) and *Loxocarya* group (present in *Alexgeorgea*, western Australian *Chordifex*, *Dielsia*, *Eurychorda* and *Loxocarya*; absent in *Baloskion*, eastern Australian *Chordifex* (Briggs & Johnson 2004), *Cytogonidium*, *Dielsia*, *Melanostachya*, *Tremulina*, *Platychora* and *Tyrbastes*). They are present throughout the *Leptocarpus* group.

### Restionoideae Bartl.

Type: *Restio* Rottb. (nom. cons.) Lectotype: *Restio triticeus* Rottb. (McVaugh 1968).

Flowers mostly in spikelets; pollen with the tectum raised around the relatively small (4–10 µm) aperture and some members with thickened foot layer (African restionoid type); embryo-sac often with proliferating antipodals; protective cells present lining substomatal cavities; pillar cells absent; sclerenchyma ribs sometimes present, alternating with outer vascular bundles; 'false pillar cells' sometimes present; silica bodies often present in the parenchyma sheath or the outer layer of the sclerenchyma cylinder; proanthocyanidins mostly present; glycosides of myricetin, larycetin and syringetin sometimes present.

A subfamily of about 350 species, occurring in sub-Saharan Africa and Madagascar, with principal diversity in the Cape Floristic Region of South Africa. Restionoideae



comprises the African clade of Restionaceae, postulated to be a monophyletic group by Johnson and Briggs (1981) on the basis of morphological and anatomical features. Subsequently, morphological (Linder et al. 2000) and DNA studies (Eldenäs & Linder 2000, Linder et al. 2003, Briggs et al. in press) have corroborated its monophyly. Its morphology and members are described and discussed by Linder (1984; 1985; 1991a, b). Genera currently recognised are listed under the tribes.

### Description of tribes within Restionoideae

Two tribes are recognised within Restionoideae, corresponding to the major clades apparent in most analyses of DNA data (Linder et al. 2003, Hardy et al. 2008, Briggs et al. in press). That the genera now placed in Willdenowieae formed a clade was also apparent from analyses of morphological data (Linder 1984, 1991b; Linder et al. 2000). Linder (1991b) observed that the *Willdenowia* clade is strongly supported by several unique morphological synapomorphies derived from a wide range of organs. The Restioneae, however, were not recognised as a clade (including *Staberoha* and *Ischyrolepis*) until molecular data were available.

**Restioneae** Bartl., Ord. Nat. Pl.: 36. Sep 1830.

Restioideae Mast. In A. & C. de Candolle, Monograph Phanerogamarum vol. 1: 218–398. 1878

All carpels fertile or variously reduced, styles 3, 2 or 1; fruits soft-walled nuts or capsules; young seed coat tanniniferous; pollen aperture various; sclerenchyma ribs absent; false pillar cells absent; chlorenchyma cells radially elongated; silica bodies often present in the parenchyma sheath but absent from the sclerenchyma.

Linder (1992b) found homoplasy in the patterns of carpel loss in the tribe, in contrast to the single pattern shown in the Willdenowieae. There was also evidence of multiple origins of unligified nutlets in Restioneae. The evolution and ecology of members of the Restioneae have been investigated by Linder and Mann (1988), Linder and Hardy (2005), Hardy and Linder (2005), Linder et al. (2005) and Moline and Linder (2005).

A tribe of about 300 species, including many as yet undescribed species, Restioneae comprises the *Thamnochortus*, *Restio* and *Elegia* clades of Linder (1984). Genera currently recognised in Restioneae: *Askidosperma* Steud. (12), *Calopsis* Beauv. (23), *Elegia* L. (51, within which the previously recognised genera *Chondropetalum* Rottb. and *Dovea* Kunth have been synonymised [Moline & Linder 2005]), *Ischyrolepis* Steud. (c. 48), *Platycaulos* H.P. Linder (c. 8), *Restio* Rottb. (c. 93), *Rhodocoma* Nees (7), *Staberoha* Kunth (c. 9), *Thamnochortus* Berg. (33).

Analyses of chloroplast DNA data and morphology (Eldenäs & Linder 2000, Hardy et al. 2008) show that *Restio* and *Calopsis* are polyphyletic and changes to the generic classification are expected (Linder & Hardy in prep.).

**Willdenowieae** Masters in A. DC., Monogr. Phan. 1: 314. Jun 1878 (*Willdenovieae*).

Type: *Willdenowia* Thunb. Lectotype: *W. striata* Thunb. (Linder 1984: p. 67)

Mostly with a single functional carpel, and with carpels 2 and 3 fused; styles 2; young seed coat not tanniniferous; fruits mostly large woody nuts, often on fleshy pedicels; pollen aperture with foot layer scarcely thickened, border region  $\pm$  sharply raised



forming a very regular ring (aperture type 2b of Linder 1984); sclerenchyma ribs alternating with the outer vascular bundles mostly present; false pillar cells present or absent; chlorenchyma cells often radially short and squat; silica bodies usually present in the sclerenchyma.

A tribe of about 50 species, Willdenowieae equates to the *Ceratocaryum*–*Willdenowia* clade of Linder (1984) and many of the taxa are myrmecorous (Linder 1991a). Genera currently recognised in the Willdenowieae: *Anthochortus* Nees (15), *Cannomois* Beauv. ex Desv. (6), *Ceratocaryum* Nees (6), *Hypodiscus* Nees (15), *Hydrophilus* HPLinder (1), *Mastersiella* Gilg-Ben. (13), *Nevillea* Esterh. & H.P.Linder (2), *Willdenowia* Thunb. (12).

Molecular-based phylogenetic work (Eldenäs & Linder 2000, Hardy et al. 2008) suggests that a number of the genera are not monophyletic.

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