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Under the microscope: plant anatomy and systematics.
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Vicariance, climate change, anatomy and phylogeny of Restionaceae

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Cutler suggested almost 30 years ago that there was convergent evolution between African and Australian Restionaceae in the distinctive culm anatomical features of Restionaceae. This was based on his interpretation of the homologies of the anatomical features, and these are here tested against a 'supertree' phylogeny, based on three separate phylogenies. The first is based on morphology and includes all genera; the other two are based on molecular sequences from the chloroplast genome; one covers the African genera, and the other the Australian genera. This analysis corroborates Cutler's interpretation of convergent evolution between African and Australian Restionaceae. However, it indicates that for the Australian genera, the evolutionary pathway of the culm anatomy is much more complex than originally thought. In the most likely scenario, the ancestral Restionaceae have protective cells derived from the chlorenchyma. These persist in African Restionaceae, but are soon lost in Australian Restionaceae. Pillar cells and sclerenchyma ribs evolve early in the diversification of Australian Restionaceae, but are secondarily lost numerous times. In some of the reduction cases, the result is a very simple culm anatomy, which Cutler had interpreted as a primitively simple culm type, while in other cases it appears as if the functions of the ribs and pillars may have been taken over by a new structure, protective cells developed from epidermal, rather than chlorenchyma, cells. Cutler suggested that this convergent evolution might have been in response to Tertiary climatic deterioration, but this study finds no strong corroborating evidence for this.

ADDITIONAL KEY WORDS:—adaptation – convergent evolution – drought.

CONTENTS

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INTRODUCTION

The evolution of a new structure is a unique, individualistic event. Since evolution is unique, it is difficult to test by replication. However, one situation in which replicated evolution might occur is where two lineages, separated for a sufficiently long time, are subjected to similar environmental changes. Such a situation might be found in paired comparisons of southern African and Australian taxa. These two continents have been physically separated since at least the Late Cretaceous (Hallam, 1994). Since the two continents occupied rather similar latitudinal positions, climatic change during the Tertiary in Africa and Australia was probably similar. Climatic change in Australia is relatively well known (for a review, see Frakes, 1999). The early Tertiary Australian climate, as inferred from foliar physiology, was very humid and very wet. At the end of the Eocene (*c.* 35 Mya) there was a marked cooling of the climate. Based on palaeosols, it appears as if drying was initiated during the Oligocene. Lignite deposits are also consistent with drying during the Oligocene, with dry climates persisting to the present. According to Deacon *et al.* (1992) similar changes occurred in southern Africa. By 3 Mya summer-dry conditions had been established along the south-western coastline of southern Africa, thus establishing a climate very similar to that found in Western Australia. The limited data on the Tertiary floras of the south-western tip of Africa indicate the presence of warm-temperate type forests in the vicinity of Cape Town (Coetzee, 1983; Linder, Meadows & Cowling, 1992). There are, however, no fossils available from the oligotrophic mountains. Hill *et al.* (1999) described the gradual change from subtropical forests in the south-east Australian Miocene to sclerophyllous forests and heathlands, but unfortunately there seems to be a dearth of information for the south-west of Western Australia. Hill *et al.* suggested that the heathlands may have differentiated early in response to the oligotrophic soils, independent of climatic change. A similar scenario might also apply to the fynbos or heathlands of the oligotrophic soils of the south-western tip of southern Africa. Plants with a long history in both areas might therefore be expected to show parallel adaptations to the increasing aridity, and these would be manifested as analogy (if there are detectable morphological differences) or as homoplasy (if such differences are not detectable).

Restionaceae might present such a test case. Almost all of the *c.* 490 species and all 55 genera (Linder, Briggs & Johnson, 1998) are found in either the southwestern tip of Africa, or in the southern, temperate parts of Australia: mostly in south-western West Australia and south-east Australia. There are outliers in Madagascar, Central Africa, New Zealand, Indochina and South America, but these may all have been recently established by dispersal. The family is entirely wind pollinated, the flowers are simple, the plants dioecious, but the fruits are diverse, varying from dehiscent capsules to nuts, from quite unspecialized to wind or ant dispersed. The vegetative structures of the plants are the most striking organs. The leaves are reduced to sheaths, and the culms are the primary photosynthetic organs. Although culm growth is terminated by flowering within a year of the initiation of the culms, they persist as green photosynthetic organs for several years, and as such the plants may be termed evergreen and possibly even as sclerophyllous. Culm anatomy shows several unique features, recognized in the latter half of the 19th century as adaptations to xerophily (Pfitzer, 1870; Haberlandt, 1884; Gilg, 1891). Gilg (1891) provided a survey of the culm anatomy of the family, this was greatly extended by Cutler (1969).

The family is probably ancient. The earliest fossil record of the family is dated to the Palaeocene (Scholtz, 1985; Linder, 1987). However, it is possible that the family is even older, as there has been a single investigation of late Cretaceous–early Tertiary plant fossils from southern Africa, and this reported the presence of Restionaceae. The earliest grass pollens also date to the latest Cretaceous (Linder, 1987), and since grasses are near relatives of Restionaceae (Duvall *et al.*, 1993; Kellogg & Linder, 1995), they should be of similar age. Restionaceae may have originally established its distribution range on the ancient Gondwanan supercontinent (Linder, 1987), or otherwise dispersed across a much narrower proto-Indian Ocean at the end of the Cretaceous or early Tertiary (Raven & Axelrod, 1974; Johnson & Briggs, 1981). Either way it appears likely from the fossil record that from early in the evolution of the family it was represented on both the African and Australian continents. Since the African Restionaceae are monophyletic (Johnson & Briggs, 1981; Linder, 1984; Linder, Briggs & Johnson, 2000) they have probably evolved independently through the climatic changes of the Tertiary.

Cutler (1972) suggested that many of the anatomical similarities between the African and Australian Restionaceae were due to convergence, tracking the Tertiary climatic deterioration. Since then the phylogenetic relationships among the genera have been studied in much detail, using both morphological and molecular techniques. In addition, the generic taxonomy in the family has been much improved (Linder, 1984; Briggs & Johnson, 1998, 1999). It is therefore possible to test the postulate that the African and Australian Restionaceae show convergent adaptations to increasing aridity.

METHODS

Phylogeny

The interpretation of the evolution of the culm anatomy of Restionaceae requires a phylogenetic hypothesis for the family. Ideally such a hypothesis should be based upon a cladogram derived independently from culm anatomical characters, as a phylogeny including these features may be biased by them (Givnish, 1997), and so result in an underestimation of the homoplasy in these characters. However, it may equally be argued that as long as other characters are also used in the estimation of the cladogram, then the dangers of circularity would be reduced (Luckow & Bruneau, 1997). Such arguments are derived from the principle that all data should be used in the estimation of the phylogeny, not just a partition of the data, and by excluding some characters the phylogenetic estimate is weakened (Kluge, 1989).

There are currently three available estimations of the phylogeny of Restionaceae. The first includes all the genera of the family, as described in Linder *et al.* (1998), and is based on 70 morphological characters (Linder *et al.*, 2000). However, the support at many of the nodes is weak, and the tree topology, especially at the lower, important nodes, is substantially dependent on the anatomical characters. It may therefore be misleading to base the interpretation of the culm anatomy on this cladogram.

The second topology is based on three chloroplast encoded genes: *rbc*L, the *trn*L intron, and *trn*L-*trn*F intergenic spacer (Briggs *et al.*, 2000). This tree includes only the Australian genera, with the African genera represented by a single sequence. In addition, several Australian genera are not included in the analysis. However, most of the nodes are robust, with bootstrap support values of over 60%, and only nodes found in the Jackknife consensus were used. The fact that no morphological characters were used in this analysis makes it more suitable for the analysis of culm anatomical evolution.

The third tree is based on a combined morphological and molecular data set, scored from the non-coding *trn*L-F intron and spacer, situated on the chloroplast genome, and includes only the African genera (Eldenäs & Linder, 2000). The morphological data set includes culm anatomical characters, but the topology of the combined tree follows that of the molecular data set for the basal nodes, while the terminal groupings follow the morphological characters. The single node which is important for the interpretation of the culm anatomy is found by both data sets independently, and is also retrieved by the combined data set. This analysis suggests that *Restio*, *Hypodiscus*, *Anthochortus* and *Hydrophilos* are hopelessly polyphyletic.

None of these trees is ideal, so to interpret the evolution of the anatomical characters, a 'supertree' was constructed, using parts of the trees mentioned above (Fig. 1). The two molecular trees are complementary. The Eldenäs & Linder tree deals with the African Restionaceae, with the non-African Restionaceae used only as outgroup. The molecular tree of Briggs *et al.* (2000) accounts for the Australian Restionaceae, as well as the outgroups of the family. The two trees can therefore be combined without any conflict. The Briggs *et al.* tree does not account for all Australian genera, and the missing genera are inserted in the positions in which they are found in the morphological tree. The African tree is complicated by the evidence of rampant polyphyly in some genera, which complicates the extrapolation from genera to species. Consequently, the genera were used in their current circumscriptions, and the supertree follows the morphological phylogeny for these genera. The polyphyletic genera all fit into anatomically homogeneous clades, consequently any arbitrary resolution of the tree for these nodes would be adequate. It would be pleasing to have a phylogeny that resolves the position of all the genera from a single analysis, and does so with substantial support for each node. However, the purpose of this phylogeny is to evaluate the evolution of the culm anatomical features, and consequently the topology within groups of anatomically homogeneous genera is irrelevant.

Anatomical characters

The anatomical data are based largely on the family-wide survey of Cutler (1969). Additional data for the African Restionaceae were published by Linder (1984), as well as Botha (1982) and Van Greuning & Van der Schijff (1973), while further information on the Australian Restionaceae was presented by Meney, Pate and Dixon (1990). Where data for the newly segregated genera were missing, sections were cut following the methods described by Linder (1984). In addition, the original slides used for the Cutler (1969) paper were re-studied. All original slides investigated for this study are either at the Jodrell Laboratory, Royal Botanic Gardens, Kew, or at the Bolus Herbarium, University of Cape Town. The terminology for the

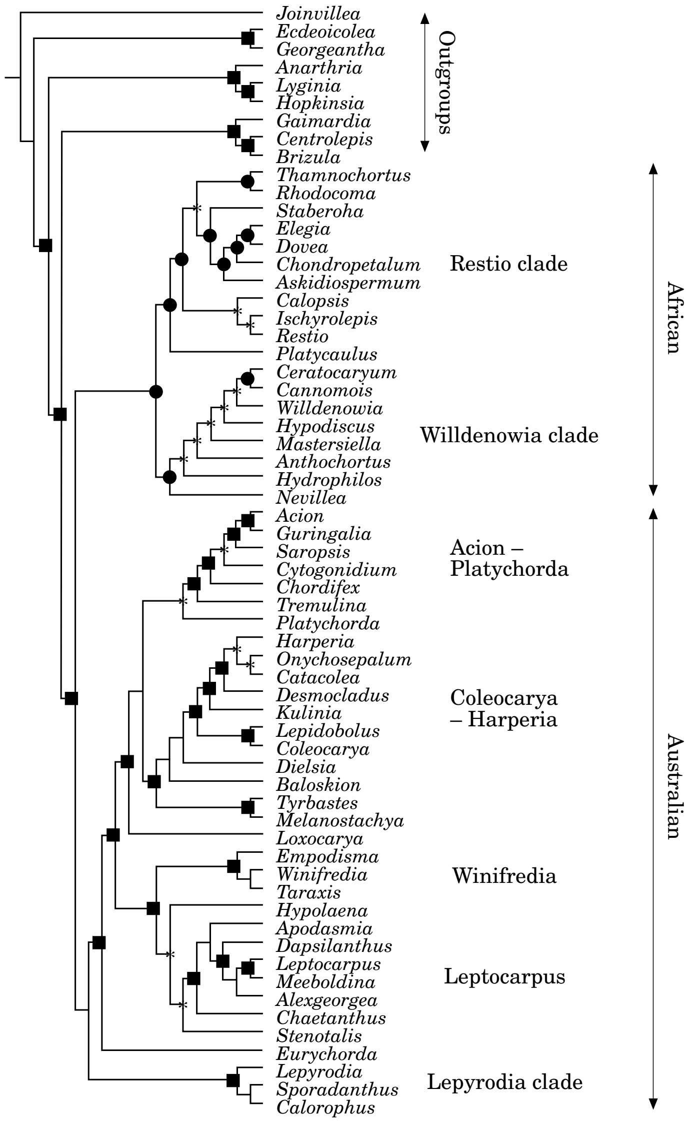
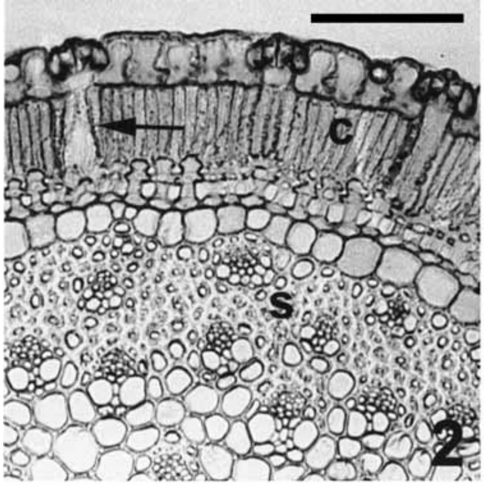


Figure 1. ‘Supertree’ for the Restionaceae, compiled from three separate trees: a complete morphology-based tree for all Restionaceae genera, a molecular tree for the Australian genera, and a combined molecular and morphological tree for the African genera. The informal groups referred to in the text are indicated on the tree. Nodes based on the Briggs *et al.* (2000) phylogeny are marked with squares, those based on the Eldenäs & Linder (2000) phylogeny with dots, and those based on the morphological (Linder *et al.*, 2000) phylogeny with stars. Unmarked nodes are effectively random resolutions, sometimes based on molecular trees with poor bootstrap support, sometimes based on morphological indications.

anatomical characters follows Cutler (1969). This terminology is consistent with that used by Gilg (1891) almost a century earlier. The primary homology (De Pinna, 1991) interpretations follow Cutler. There have to date been no attempts to test these homology interpretations ontogenetically, although such a test could be interesting.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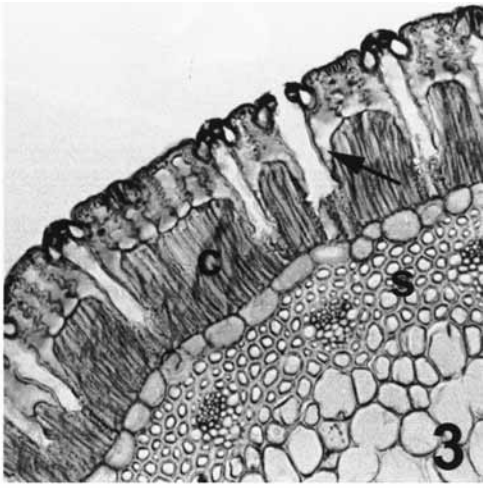
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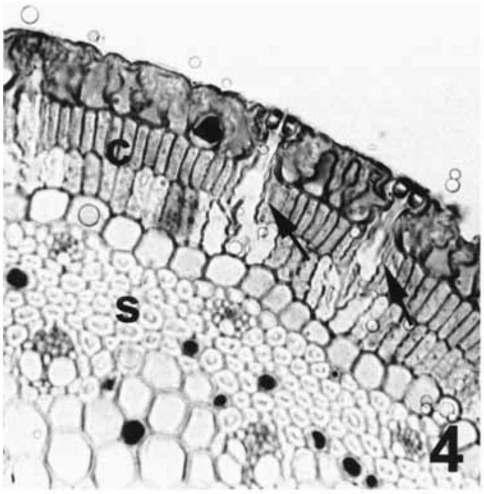
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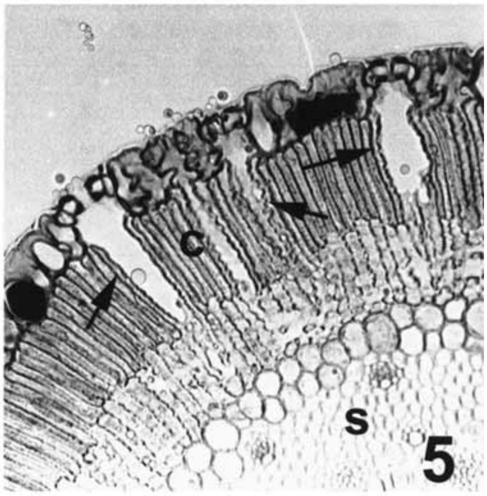
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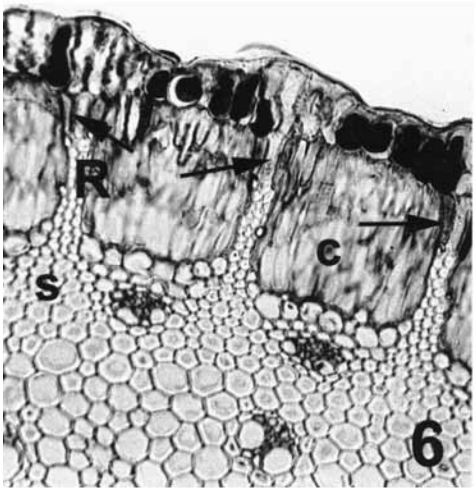
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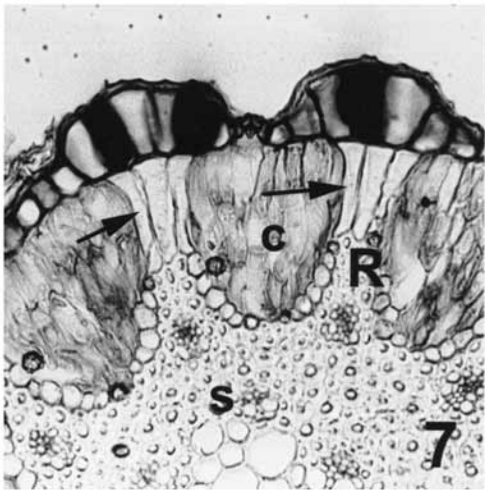
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Mapping of the characters was done in MacClade vs. 3 (Maddison & Maddison, 1993). Optimizations were mapped using ACCTRAN, DELTRAN optimizations are discussed individually below.

In order to trace the evolution of analogous features, these have been grouped together. These groupings have been based on the position and structure of the cells within the culms. The three groups recognized can be considered as three multistate cladistic characters:

(1) Protective cells (four states: absent, epidermally derived, specialized collenchyma derived and undifferentiated collenchyma derived), which flank the substomatal cavities, and have suberized walls. These form a basket around the substomatal cavity (Figs 2–5).
(2) Ribs (three states: absent, false and true) which project outwards from the sclerenchyma sheath. The ribs are continuous with the sheath, and may in some cases reach the epidermis, but frequently penetrate only some distance into the chlorenchyma (Figs 6, 7).
(3) Pillar cells (three states: absent, false and true), which connect the apices of the ribs with the epidermal cells (Figs 6, 7).

Functional interpretation

No experimental work has been done to substantiate the functional interpretations of these anatomical features. From the first publications on the culm anatomy of Restionaceae these features have been interpreted as xerophytic adaptations (Pfitzer, 1870; Gilg, 1891), but these have all been 'just so' stories, arguing that structures are 'obviously' adapted for a particular function. This is clearly a dubious procedure, but as still no experimental work has been done, this tradition will be followed here. Curiously, the original terminology for the various structures in Restionaceae culm anatomy was completely functional. Gilg described cells as being either 'Schutzzellen' (protective cells) or 'Stützzellen' (support cells) and noted instances where the same cells function as both.

RESULTS AND DISCUSSION

Protective cells

Cutler (1969) recognized three types of protective cells. In the most distinctive type, the substomatal basket is formed by the epidermal cells flanking the stomata.

Figures 2–7. Anatomical features of Restionaceae. Scale bar in Fig. 2 = 100 μm relevant for all figures. Abbreviations: s = sclerenchyma ring; c = chlorenchyma, R = sclerenchyma ribs. Fig. 2. *Lepyrodia scariosa* R.Br., *Coveny* 6315, arrow indicating undifferentiated protective cells, derived from chlorenchyma cells. Fig. 3. *Harperia lateriflora* W.Fitzg., *Briggs* 6674, arrow indicating protective cells derived from epidermal cells. Fig. 4. *Ischyrolepis curvibracteata* Esterhuysen, *Esterhuysen* 31556, arrow indicating specialized protective cells derived from chlorenchyma cells. Fig. 5. *Staberoha stokoei* Pillans, *Esterhuysen 31495*, arrow indicating specialized protective cells derived from chlorenchyma cells. Fig. 6. *Willdenowia incurvata* (Thunb.) Linder, *Esterhuysen 11682*, arrow indicating false pillar cells (derived from chlorenchyma) seated on ribs alternating with the vascular bundles. Fig. 7. *Hypolaena fastigiata* R.Br., *Coveny 6032*, arrow indicating true pillar cells (derived from the parenchyma ring) seated on ribs opposite the vascular bundles.

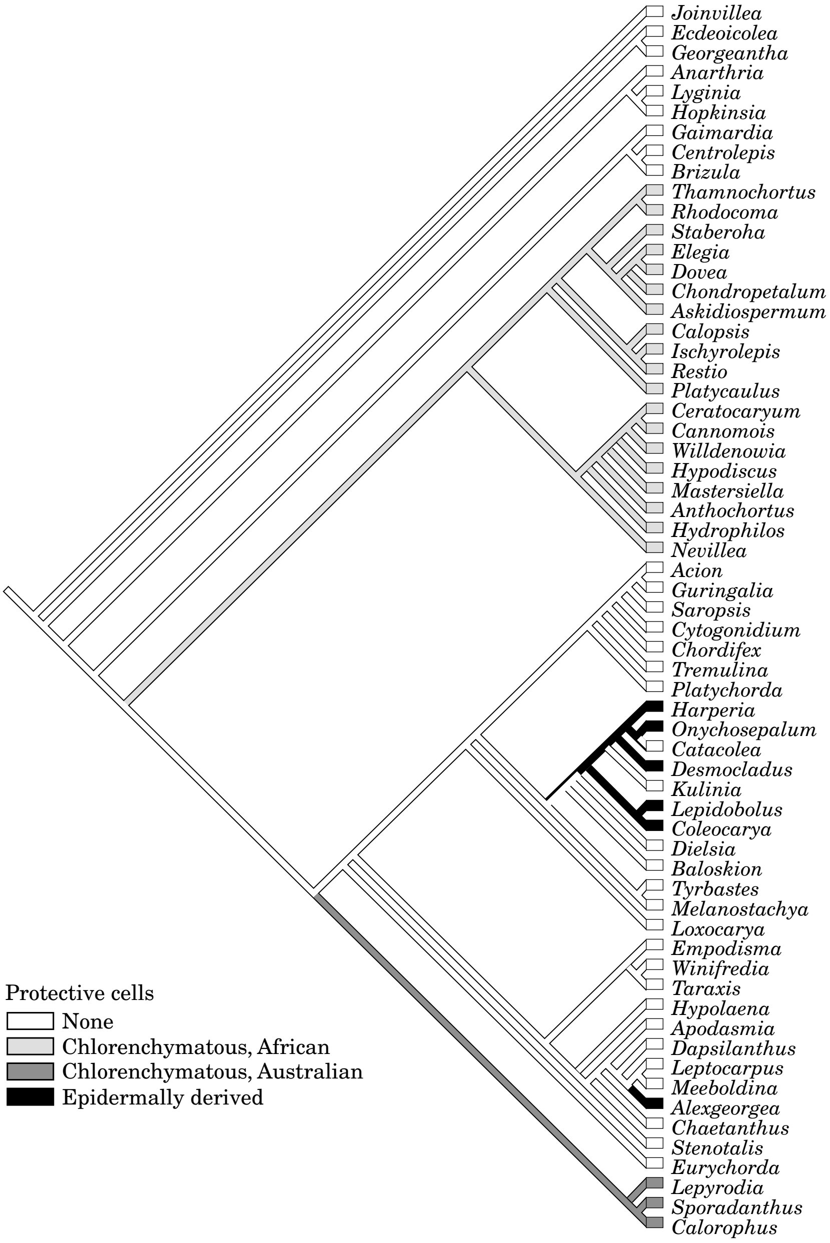

Figure 8. ACCTRAN optimization of the protective cells on the supertree.

These cells are elongated inwards, with their inner walls forming the basket. According to the phylogeny based on molecular data these evolved twice and were lost twice, if we assume losses of structures to be more likely than gains (ACCTRAN optimization, see Fig. 8). These two gains are in the *Coleocarya–Harperia* clade and in *Alexgeorgia*. With DELTRAN optimizations, which assume gains are more likely than losses, there are three gains and one loss. If we wish to argue that these cell types could have evolved only once (Dollo parsimony), then we will have to accept 14 separate losses, not a parsimonious interpretation. It seems more likely that these peculiar cells evolved at least twice in the Australian Restionaceae.

The other two types of protective cells are modified chlorenchyma cells. In the African genera the protective cells form a single layer around the cavity, and are bone-shaped: narrower in the middle, with the ends thickened. The three Australian genera have a much simpler type of protective cell, which occurs in larger numbers in the surrounds of the substomatal cavities. Cutler (1969) did not regard these as primary homologues, but later (1972) implied that they were. Optimization on the cladogram (Fig. 8) indicates that if the two types were indeed primary homologues, then the number of origins of protective cells remain ambiguous: DELTRAN would suggest two origins and no losses (thus not secondary homologues, in the sense of De Pinna (1991)), while ACCTRAN (Fig. 8) suggests one gain followed by a loss, thus indicating that they are secondary homologues. The cladogram for the whole family based on morphological evidence (Linder *et al.*, 2000) places the Australian genera with protective cells (*Lepyrodia, Sporadanthus, Calorophus*) in a paraphyletic sequence basal to the African genera, thus forcing the optimization of a common origin of protective cells, with their subsequent loss in the more 'derived' Australian genera.

There is substantial variation in the form of the protective cells in the African genera, but this is hardly surprising, considering that this is a group of over 300 species, all of which have protective cells.

The function of the protective cells remains obscure. Gilg (1891) presumed that they slowed down the rate of water loss from the chlorenchyma. The protective cell walls facing the substomatal cavity are cutinized, consequently moisture has to pass between the cells to reach the substomatal cavity from the chlorenchyma. In the upper half of the substomatal cavity, directly below the stomata, there are no openings between the protective cells. However, at the base of the cavity, above the parenchyma sheath, there are slits between the protective cells, and presumably these constitute the pathway for gas exchange (Gilg, 1891; Cutler, 1972).

It appears also likely that the protective cells can function to mechanically prop up the epidermis in those species in which the protective cells reach the parenchyma (Gilg, 1891). In this sense they would be functionally comparable to pillar cells. This is somewhat corroborated in the African Restionaceae. In the *Willdenowia* clade, where ribs and pillar cells are found, protective cells are short and do not reach the parenchyma sheath. In the *Restio* clade, which lacks ribs and pillar cells, the protective cells either reach the parenchyma sheath, or very nearly do so. Protective cells and ribs are mutually exclusive in the Australian Restionaceae. There is only one genus with epidermally derived protective cells and ribs: that is the generally anomalous *Alexgeorgea* (Meney *et al.*, 1990).

Ribs

Ribs are outgrowths from the sclerenchyma ring. When poorly developed, they appear as small bumps along the outer margins of the ring, but when well developed reach like long buttresses to the epidermis. When they reach the epidermis, they form striations on the culm surface, which are readily visible with some magnification.

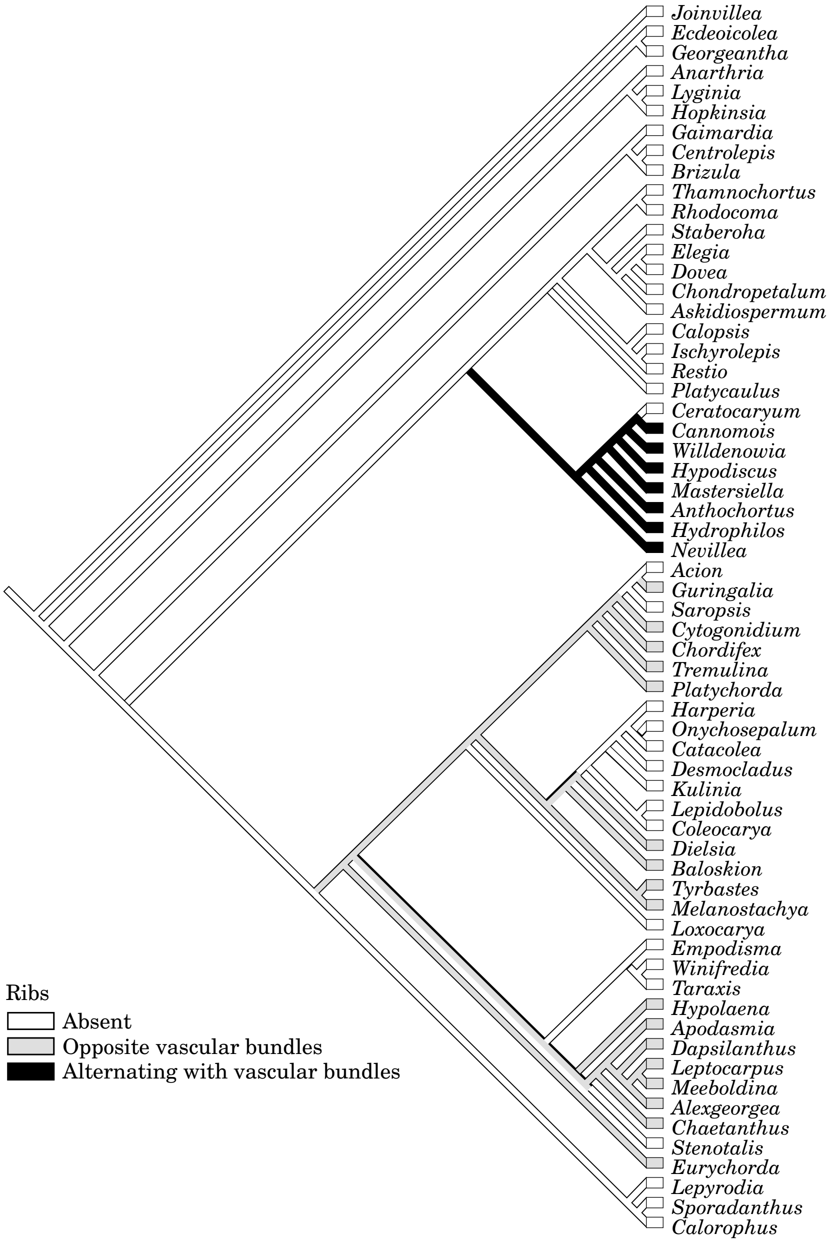

Figure 9. ACCTRAN optimization of ribs on the supertree.

As Cutler (1969, 1972) recognized, there are two different types of ribs, depending on their position relative to the vascular bundles.

In the African genera, the ribs alternate with the vascular bundles. These appear to have evolved only once, but have been lost in *Ceratocaryum* (Fig. 9). The degree of development of the ribs in this clade is highly variable (see Linder, 1984), and

Cutler suggested that the generic limits may need adjustment to reduce the intrageneric variability of this structure. Preliminary molecular results suggest that the generic limits are indeed incorrect, but the new alignments suggested do not improve the fit of this character.

Ribs in the Australian genera develop opposite the vascular bundles, and could be interpreted to be outgrowths of the sclerenchyma caps on the vascular bundles. The evolution of this structure is much more confused in the Australian genera than the African. It has either been gained once and lost six times (ACCTRAN optimization, see Fig. 9), or gained five times. There is no way to distinguish between these two options. If gained only once, then it is almost basal in the Australian Restionaceae. Ribs clearly evolved independently in Africa and Australia. Even if they were structurally identical, a single origin in the common ancestor of the Restionaceae, with subsequent losses in the *Restio* and *Lepyrodia* lineages would be one step longer than two separate origins.

There have been several proposed functions for this structure, but as at least some of these functions also involve the pillar cells, these are best discussed together.

Pillar cells

Pillar cells connect the apex of the ribs to the epidermis, they are elongated and somewhat lignified, and are not photosynthetic. There appear to be two types of pillar cells. The common form of pillar cells is found in numerous genera of Australian Restionaceae, and are clearly derived from the parenchyma sheath. In transverse sections it is evident that the parenchyma sheath flanks the sclerenchyma ring and pillars, and at the apices of the ribs the parenchyma cells are enlarged to form the pillar cells. In the African genera *Hypodiscus* and *Willdenowia* the pillar cells appear to be modified chlorenchyma cells (Cutler, 1969), these are called 'False pillar cells'. The sclerenchyma ribs penetrate through the parenchyma sheath, thus there are no parenchyma cells flanking the sclerenchyma ribs.

False pillar cells are found only in the African Restionaceae. It is currently not possible to determine how often they have evolved, as the phylogenetic relationships within the *Willdenowia* clade, in which all species with false pillar cells occur, have not been resolved (Eldenäs and Linder, 2000). On current taxonomy, false pillar cells have evolved at least twice in African Restionaceae (Linder, 1984), or once with secondary loss (ACCTRAN optimization, see Fig. 10). False pillar cells occur in two genera: *Hypodiscus* contains two species with pillar cells, while only three species of *Willdenowia* have pillar cells.

The optimization of pillar cells in Australia is not simple. With ACCTRAN there are three gains and three losses of pillar cells (Fig. 10), while with DELTRAN there are six gains and no losses. If we wish to map the structure to achieve a single gain (Dollo parsimony), we would have to postulate six losses: three more than the minimum number. This is therefore a possible scenario, where ribs and pillar cells both evolved near the base of the Australian Restionaceae, but have been lost independently several times.

The ribs and pillars have been proposed to perform several functions:

(1) Pfitzer (1870) suggested that the ribs plus pillar cells divide up the chlorenchyma into chambers, thus preventing desiccation damage from spreading all around

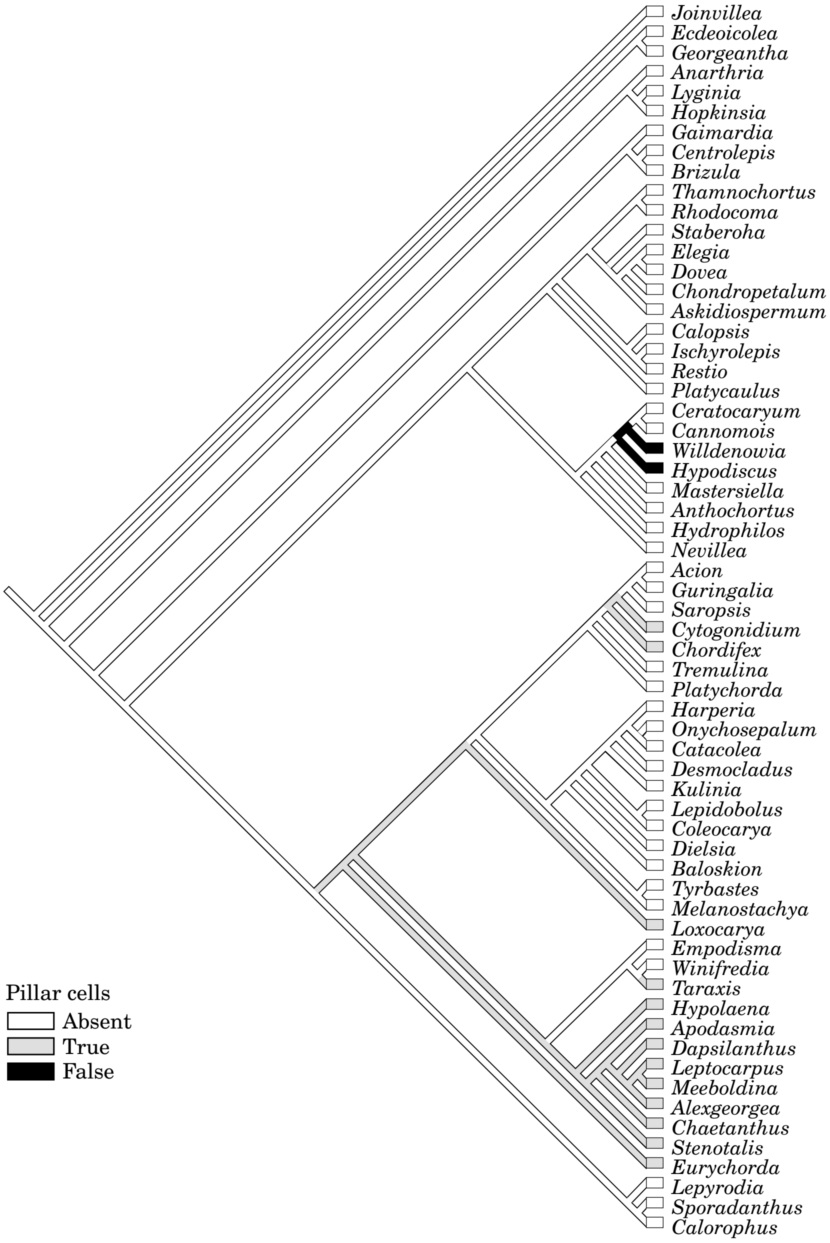

Figure 10. ACCTRAN optimization of pillar cells on the supertree.

the culm. This is similar to arguments that the structures prevent infection from spreading too (e.g. Cutler, 1972). However, I have never seen linear streaks of damage such as would be expected if cell damage were contained between the rows of pillar cells, and so doubt that they perform this function.

(2) Gilg (1891) argued that the pillar cells prevent the chlorenchyma from imploding during very arid periods. The structure would keep the epidermis away from

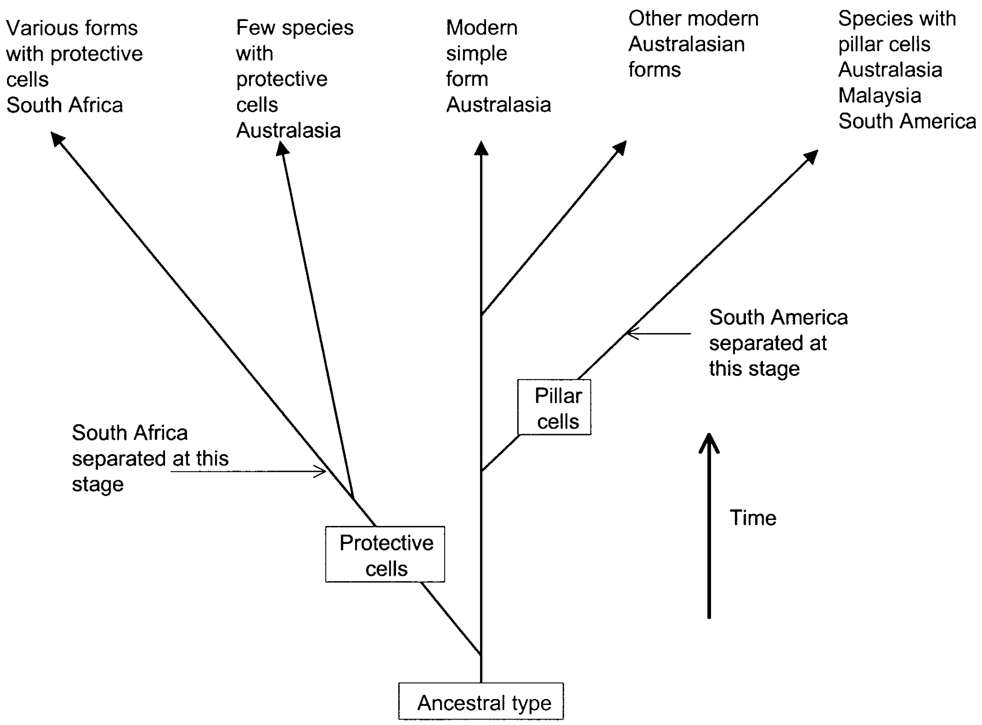

Figure 11. Cutler's scenario for Restionaceae, modified from Cutler (1972).

the sclerenchyma ring. Linder (1991) compiled the available data on the water relationships of the African Restionaceae: during summer the negative pressure in the culms, as measured by Solander Bomb, descends to −40 bars (Moll & Sommerville, 1985; Van der Heyden & Lewis, 1989). Presumably the plants can only survive these immense negative pressures due to their mechanical design.

(3) Haberlandt (1884) interpreted the whole central structure of the Restionaceae culm as mechanical strengthening, and this would include the ribs. This is a very possible explanation, as it would account for the frequent occurrence of short ribs which do not reach the epidermis. These could not possibly function to isolate plates of chlorenchyma, or to hold up the epidermis, but must surely simply provide mechanical strength to the culm.

EVOLUTION AND CLIMATE

Anatomical evolution

Cutler (1972) attempted to decipher the evolution of Restionaceae based only on anatomical data. His interpretation was based on the assumption that the simplest anatomical form was ancestral, and that the development of more complex anatomical forms faithfully reflected the phylogeny of the family. His model (Fig. 11) postulated

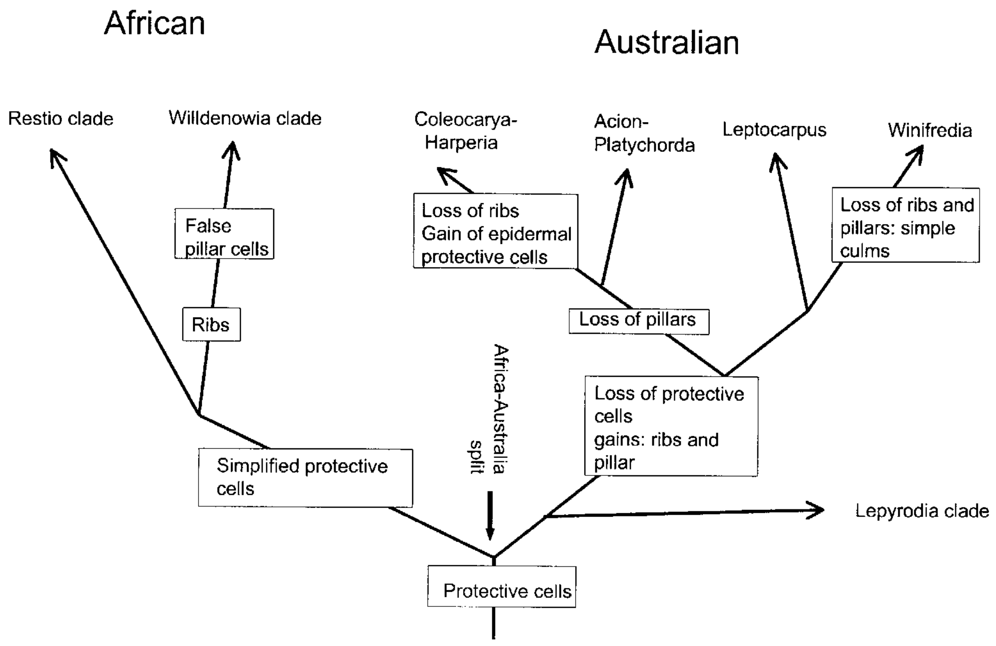

Figure 12. Simplified phylogeny indicating anatomical evolution in Restionaceae.

a simple ancestral form, without protective cells, ribs or pillar cells. The first evolutionary split then separated a lineage characterized by protective cells, and this lineage is the only one found in Africa, while only a few species of the lineage are still found in Australia. The bulk of the Australian genera were then derived from this simple group, with pillar cells and ribs evolving in one subdivision of this group. Even though Cutler explicitly allowed for the possibility that secondary simplification might have happened, he had no evidence to this effect, since at that stage the phylogeny was based entirely on the culm anatomical characters. In effect he used Dollo parsimony with the anatomical characters to reconstruct the phylogeny of the Restionaceae.

With the availability of an independent phylogeny, it is possible to re-evaluate the anatomical evolution in Restionaceae, and not surprisingly, the results show a more complex picture (Fig. 12). The most likely (if simplified) scenario is that the ancestral Restionaceae species lacked pillar cells and ribs, but had protective cells. The optimization of the protective cells on the supertree, if the cells in the *Lepyrodia* clade and the African Restionaceae are homologous, is ambiguous. However, the evidence from morphological phylogeny, combined with a preference for minimizing the number of gains of complex structures, argues for the primitive presence of protective cells, and their subsequent loss in the main radiation of the Australian Restionaceae. This interpretation also receives support from the diversity of protective cell form in the *Lepyrodia* clade, which suggests that this character might be labile in this clade.

The anatomical specialization within the African Restionaceae is simple. The basal split in African Restionaceae, strongly supported by molecular data (Eldenäs and Linder, 2000) is also consistent with culm anatomical data. The *Restio* lineage retains the basic African Restionaceae culm organization, with its specialized protective cells. Within this lineage various other culm anatomical specializations are found: a double epidermis in the *Elegia* clade, cavities in the central ground tissue in the *Thamnochortus* clade (Linder, 1984), but these specializations are not mirrored in the Australian Restionaceae. By contrast, the *Willdenowia* clade is characterized by sclerenchyma ribs, analogous to the ribs in the Australian Restionaceae. In addition, in two genera false pillar cells occur.

The patterns of specialization in the Australian Restionaceae are much more difficult to interpret, since the patterns of gains and losses of ribs, pillar cells and epidermally derived protective cells are too complex to lead to any unambiguous optimizations for the presence of ribs and pillars at the basal nodes of the Australian Restionaceae.

The implication of a single origin of protective cells would be that the Australian genera with simple anatomy (lacking protective cells, ribs and pillar cells: *Empodisma* and *Winifredia*) are not primitively simple, but the result of secondary loss of the protective cells. These 'simple' culm genera are not basal on the phylogeny, but the possibility that their simple anatomy could be a retained plesiomorphic feature cannot be ruled out by the phylogeny. Cutler's (1972) reconstruction suggested that 'Modern simple forms' of Australasian Restionaceae may be primitively simple, and this may indeed apply to *Empodisma* and *Winifredia*, but only if parallel gains of ribs and pillar cells are preferred to parallel losses of these structures. Even with this assumption, however, the character optimizations still imply that the simple culms of *Acion, Saropsis, Catacolea, Kulinia* and *Loxocarya* are the result of secondary simplification.

It is certainly much more tempting to prefer parallel losses to gains of complex structures. Under this optimization ribs and pillar cells evolved once very early in the diversification of the Australian Restionaceae (Fig. 12), and may have replaced the chlorenchyma derived protective cells, which are interpreted as primitive in the Restionaceae. This is also the interpretation preferred by Briggs *et al.* (2000). Although ribs and pillar cells are lost numerous times, in the largest clade lacking them, the *Coleocarya–Harperia* clade, they may have been replaced by epidermis-derived protective cells. Cutler derived the *Coleocarya–Harperia* clade (his "Other modern Australasian forms") from the simple forms, which removes the need for a secondary loss of the anatomical ribs. However, the molecular phylogeny suggests instead that these are derived by simplification by the anatomically more complex segregates of *Restio* s.l.: *Baloskion, Dielsia, Melanostachya.*

In summary, the following cases of convergence can be made:

(1) Protective cells may have been present in the common ancestor, as suggested by Cutler (1972), or less likely, evolved independently in both the African and the basal Australasian genera.
(2) The evolution of epidermally derived protective cells is convergent with the persistence and elaboration of the chlorenchyma-derived protective cells in the African Restionaceae.
(3) Ribs evolved independently in Africa and Australia, as is evident both from the optimizations on the molecular phylogeny, and as can be inferred from the positional homological arguments.
(4) Pillar cells evolved independently in Africa and Australia, and as with ribs this is supported by both topological and positional homological arguments.
(5) Within Australia pillars evolved at least twice. As with ribs, the basal optimizations

are ambiguous as to whether pillars were present early in the evolution of the Australian Restionaceae, or whether they evolved numerous times independently.

The selective regime and adaptation

It is tempting to search for an explanation for this remarkable convergence in the culm anatomies of the African and Australian Restionaceae. There is no obvious developmental constraint that might have resulted in the independent evolution of ribs, pillar cells and protective cells. Such a constraint has been suggested to operate in the reduction of the number of fertile locules in Restionaceae, from three to one (Linder, 1991, 1992a, b). In this case, any change from the primitive situation of three locules is likely to be a reduction, and consequently it may not be necessary to invoke a selective advantage for the reduction in the number of locules. However, such constrained evolution should result in parallel evolution, where similar final forms evolve independently from the same initial structure. The anatomical changes described above show convergent evolution, where similar final forms evolve from different initial organs.

The anatomical convergences must therefore be adaptations to similar selective regimes, or to similar changes in the selective regime, to which these plants were exposed (Baum & Larson, 1991). Cutler (1972) proposed a plausible scenario. He suggested that the anatomically unspecialized, basal form of the family occurred in semi-aquatic habitats in the late Cretaceous, “when the climate in the southern hemisphere land mass was less extreme than in present-day Cape Province or Australia. . .”. With the aridification of the climate during the Tertiary species evolved that could cope with seasonally dry conditions. In South Africa only these forms survived, while in Australia some of the simple forms persisted in the arid environments. We are now in a position to evaluate this broad generalization.

We do not have direct evidence of the habitats of the original Restionaceae, and the only fossils available are pollen grains, summarized by Hochuli (1979) and Linder (1987). These give no indication as to the habitat of the species. Since all relatives of Restionaceae are wind-pollinated, it is most likely that the first Restionaceae were also wind-pollinated, and this would suggest that they grew in open and not forested habitats (Whitehead, 1969, 1983). Open habitats may be found in marshes, in subalpine habitats, on the arid fringes of woodland, or in heathlands on oligotrophic soils. Consequently we do not know whether they occurred in semi-aquatic habitats, other habitats are equally possible. A comparison with the habitats of extant species does not help, since most larger groups contain species from marshes as well as seasonally or even permanently dry habitats. Attempts to optimize habitat conditions to the basal nodes of the tree results in an ambiguous optimization.

It appears likely that the ancestral Restionaceae had protective cells. Protective cells are generally thought to function in reducing the transpiration rate; they might also serve as structural elements protecting the chlorenchyma from collapse during long dry periods. This suggests that the ancestral Restionaceae were already growing in habitats which were at least seasonally dry. These could have been in heathlands on oligotrophic, sandy, well-drained soils. Such soils are common both in the kwongan of south-western West Australia, and in the hard sandstone mountains of the south-western tip of South Africa. Indeed, Restionaceae are still found in these higher rainfall areas in the Knysna (South Africa), in Tasmania and New Zealand.

These areas have short dry seasons, and these may well approximate the Tertiary habitats.

Subsequent evolution of pillar cells and ribs clearly happened in parallel between Africa and Australia, and these could well be adaptations either to deteriorating climates, or to range expansions from wetter to drier habitats. If the suggestion above that Restionaceae first diversified in heathlands on oligotrophic soils is correct, then the climatic deterioration during the Neogene would provide change in selective regime which happened both in Africa and Australia, without requiring the Restionaceae in these areas to change their habitats. This argument would be strengthened by demonstrating the current utility of ribs and pillar cells in withstanding drought (Baum & Larson, 1991).

This simple picture is confounded by a number of observations. Among the African Restionaceae, species with ribs co-occur with species without ribs, and indeed, the species found in the most arid environments is *Ischyrolepis sieberi* (Kunth) H.P. Linder, which lacks ribs, while *Hypodiscus striatus* (Kunth) Masters, which is almost as widespread and as common on the arid fringes of the Cape Fynbos vegetation, has well developed ribs. There is clearly a need of comparative studies to evaluate these features, and also to take into account other possible parameters, general culm morphology, rooting strategies, etc., that could impact the stresses to which the culms might be exposed. The potential confounding effects of 'hidden' variables in studies of adaptation have long been recognized (Clutton-Brock & Harvey, 1979; Gould & Lewontin, 1979).

The situation in the Australian Restionaceae is more complex, with several losses of ribs and pillar cells postulated. In the *Coleocarya-Harperia* clade ribs and pillar cells have been lost and possibly replaced by epidermally derived protective cells. Maybe there are several different ways in which the same degree of drought tolerance can be achieved. Ribs and pillar cells might provide mechanical support for the epidermis, and prevent the chlorenchyma from collapsing, but they cannot slow down transpiration. Protective cells probably slow down transpiration, and might also provide a mechanical function. This might be a good problem to address with comparative studies to investigate the reaction of the different anatomical structures to desiccation.

There are some striking differences between the African and Australian Restionaceae. The anatomical evolution in the African Restionaceae is relatively simple, with little need to postulate homoplasy. By contrast, anatomical evolution in the Australian Restionaceae has been confounded by much homoplasy and numerous losses of previously gained structures. This suggests that the Australian environment in which Restionaceae are found is more complex, or that the environmental history has been more complex. It would be interesting to explore the comparative effects of fires in Africa and Australia, in particular their role in removing forest overstorey and so creating habitats more suitable for Restionaceae.

A further test of the Cutler hypothesis would be to date the evolution of these structures: the Cutler hypothesis would predict that they date to the climatic deterioration of the Oligocene.

There has almost certainly been convergent evolution in the culm anatomical structures between Restionaceae lineages separated in Africa and Australia: this is supported both by anatomical homologies and by optimization on the molecular phylogeny. However, the evolutionary pathway of these structures is more complex than originally anticipated. This does not refute the hypothesis that much of the anatomical structure may have evolved in response to Tertiary climatic deterioration. Indeed, all the results above are consistent with that hypothesis, but none of the results provide really strong corroborating evidence. This would need to be found either in functional studies, or in molecular clock approaches.

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