Restionaceae (Poales) in the footsteps of Robert Brown

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Abstract

Barbara G. Briggs (National Herbarium of New South Wales, Mrs Macquaries Road, Sydney 2000, Australia; barbara.briggs@rbgsyd.nsw.gov.au.) 2004. Restionaceae (Poales) in the footsteps of Robert Brown. Telopea *10(2): 499–503.* Brown visited major centres of restiad diversity in Africa at the Cape of Good Hope and in Western Australia at King Georges Sound and Lucky Bay; other taxa were collected in northern and eastern Australia, including Tasmania. He described five genera and 36 species now included in Restionaceae, and four genera and 35 species since excluded from that family. His observation, enlightened by fieldwork, was remarkable and some species he named are now recognised again after decades in confusion or synonymy. Mostly he correctly matched dioecious males and females, but for one species these were placed in different genera. Restionaceae has been much cut down in size since Brown's time. In the *Prodromus*, Restiaceae included what are now Anarthriaceae, Centrolepidaceae, Eriocaulaceae and Xyridaceae, as well as Lyginiaceae if this and Hopkinsiaceae are recognised as separate from Anarthriaceae sens. strict. Currently 145 Australian Restionaceae species are recognised, in 31 genera. The 24 species that Brown included in *Restio* (22 of them then newly described) are now distributed among 11 genera, the majority in *Chordifex*, *Baloskion* and *Hypolaena*, while *Restio* is restricted to African and Madagascan species. Anatomy, palynology and especially DNA sequencing have clarified relationships within Restionaceae and between families of Poales. Molecular data indicate that Centrolepidaceae forms the sister-group to Restionaceae, unless it is embedded in the latter.

Brown's Restiaceae

Among Robert Brown's less publicised achievements was his role in founding an understanding of Australian Restionaceae. At Cape of Good Hope, King Georges Sound and Lucky Bay, Brown visited hot-spots of restiad diversity, collecting 14 species of Restionaceae (and many in closely related families) at King Georges Sound. In northern and eastern Australia, including Tasmania, he saw and collected representatives of genera now recognised but that are not represented in Western Australia or were not collected there (*Dapsilanthus* B.G. Briggs & L.A.S. Johnson, *Baloskion* Raf. and *Empodisma* L.A.S. Johnson & D. Cutler), as well as further species of genera seen in the west, especially of *Lepyrodia* R. Br. and *Sporadanthus* F. Muell.

The family Restionaceae (as Restiaceae) was described by Brown in the *Prodromus* (1810) and was then considerably more inclusive than Restionaceae today. Before Brown's work, only three Australian restiad species, in three genera, had been described, by Labillardière (1806), namely *Restio tetraphyllus*, *Calorophus elongatus* and *Schoenodum tenax*. Labillardière had placed these in the class 'Dioecia triandria', characterised by dioecy and the presence of three stamens. Soon after the *Prodromus*, by the time of Endlicher (1836), the Centrolepidaceae, Eriocaulaceae and Xyridaceae had been excised from Restionaceae. These families, however, remain in Poales as recently recognised (APG 1998, 2003). These excisions left Restionaceae with much the circumscription that it retained until anatomical studies (Cutler 1969) provided the basis for excluding *Ecdeiocolea* F. Muell. and *Anarthria* R. Br. (Cutler & Airy Shaw 1965), and recently DNA data showed *Hopkinsia* W. Fitzg. and *Lyginia* R. Br. to be misplaced in Restionaceae (Briggs & Johnson 2000, Briggs et al. 2000).

Brown described five genera and 36 species now in Restionaceae, and four genera and 35 species since excluded from that family. Like Labillardière, Brown referred some Australian species to *Restio* Rottb., which is now considered to be restricted to Africa and Madagascar (Linder 1985, Linder et al. 1998); indeed classifications of several Restionaceous genera persisted until very recently that treated species on both continents as congeneric.

Most species of Restionaceae are dioecious and difficulties in matching male and female collections have been noted since these were first studied botanically. Mostly Brown correctly matched the male and female plants of the dioecious species, although for *Meeboldina scariosa* (R. Br.) B.G. Briggs & L.A.S. Johnson he placed males in *Restio* (as *R. microstachys* R. Br.) but the corresponding females in *Leptocarpus* R. Br. (as *L. scariosus* R. Br.). Observant field studies prevented more such misplacements. One of the first Australian Restionaceae described, *Schoenodum tenax* Labill., was recognised by Brown as based on material of two collections and these were referred by him to two genera, *Leptocarpus* (female specimen) and *Lyginia* R. Br. (male), now placed in separate families. Since the males and females of both of these genera are remarkably dissimilar, such a mixture of collections is understandable. The male specimen however cannot have come from Tasmania but, as with several other Labillardière specimens attributed to 'van Diemens Land' (Nelson 1974), must have been collected in Western Australia.

At one further point some confusion was generated since Brown named two taxa as '*Restio laxus*' i.e. *Restio* species 3 and 12, now *Chordifex laxus* (R. Br.) B.G. Briggs & L.A.S. Johnson and *Meeboldina laxus* (R. Br.) B.G. Briggs (Briggs 2001).

Brown saw in the field all except one of the 39 species he recognised; his regular annotation '*v.v.*' showing the importance he placed on field study. The one exception was *Leptocarpus ramosus* R. Br. [now *Dapsilanthus ramosus* (R. Br.) B.G. Briggs & L.A.S. Johnson based on a specimen collected by Banks and Solander at the Endeavour River. Brown's observation was remarkable and species he named, such as *Chordifex monocephalus* (R. Br.) B.G. Briggs (*Restio monocephalus* R. Br., synonym *Acion monocephalum* (R. Br.) B.G. Briggs & L.A.S. Johnson), are now recognised after many decades in confusion or synonymy (Morris 1991; Briggs & Johnson 2004). Similarly, *Lyginia imberbis* R. Br. is now recognised after long confusion with *L. barbata* R. Br. The above-ground structures of these *Lyginia* species show some differences but the most reliable characters are in the clumped habit of the former, with culms crowded on the short rhizomes, in contrast to the large patches of sparsely scattered culms connected by elongated rhizomes in *L. barbata*. These differences were clear to the astute field observer but not apparent in specimens that lacked underground parts. Not surprisingly, since he lacked field observation or habit notes, Bentham (1878) synonymised these species.

Brown's observations

The quality and amazing thoroughness of his observations may be seen in the features Brown used to characterize the Restiaceae. '[The] lenticular embryo being placed at the extremity of the seed opposite to the umbilicus' and 'from Juncaceae it also differs in the order of suppression of its stamina, which when reduced to three are opposite to the inner laciniæ of the perianthium' and the 'simple and unilocular antherae'. Brown was justly notable for endorsing the 'natural system' of Jussieu (1789) and departing from the Linnaean System of plant classification based on the number of reproductive parts in the flowers (Mabberley 1985). Where his classification of Restionaceae was unsatisfactory it was because vestiges remained of classification based on the numbers of floral parts. It is now clear that there has been homoplasious loss of floral parts in

many clades and this has obscured relationships (Briggs & Johnson 1999). The small, wind-pollinated flowers do not show great diversity and leaves reduced to sheaths are general throughout the family. Until a wider range of data became available, a satisfactory classification was scarcely possible. *Restio* sens. lat., as Brown recognised it, was polyphyletic but his *Lepyrodia* (now *Lepyrodia* with *Sporadanthus*) and *Leptocarpus* (now *Leptocarpus* with *Apodasmia* B.G. Briggs & L.A.S. Johnson, *Dapsilanthus* B.G. Briggs & L.A.S. Johnson and *Meeboldina* Suess.) correspond reasonably well with clades that are supported by DNA and other data.

In Restionaceae, as in Proteaceae and Myrtaceae, Brown contributed greatly to knowledge of notable Southern Hemisphere families. He commented on the similarities of the South African and southern Australian floras, as well as the proportion of monocotyledons in the floras of different continents and the absence of certain groups from Australia's flora. Unlike Joseph Hooker (1855) who followed him to Australia almost 40 years later, Brown does not appear to have pondered greatly the questions posed by the distribution of these families on separated land masses. In this he was a scientist of his time, decades before evolution opened the way to understanding speciation and diversification, and even longer before plate tectonics gave a new interpretation of the post-Gondwanic Southern Hemisphere.

Restionaceae today

Now 145 Australian species are recognised (including 21 not yet formally named) in 31 genera (Briggs & Johnson 1999, 2004). Many of those described after Brown's time are from heathlands and shrublands north of Perth and elsewhere in the semi-arid inland of Western Australia, not traversed by botanical collectors till long after his visit. The 24 species that he included in *Restio* sens. lat. (22 of them then newly described) are now distributed among 11 genera, the majority in *Chordifex* B.G. Briggs & L.A.S. Johnson, *Baloskion* Raf. and *Hypolaena* R. Br., while *Restio* is restricted to African and Madagascan species.

DNA sequencing, anatomy, seed morphology, palynology, embryology and phytochemistry are clarifying relationships within Restionaceae and between families of Poales (Cutler 1969; Linder & Ferguson 1985, Rudall & Linder 1988, Briggs & Johnson 1998; Williams et al. 1998, Meney & Pate 1999; Briggs et al. 2000; Linder et al. 2000; Eldenäs & Linder 2000). The genera removed from Restionaceae in recent decades to form the families Ecdeiocoleaceae and Anarthriaceae were distinguished initially on their striking anatomical differences from Restionaceae (Cutler & Airy Shaw 1965). *Lyginia* and *Hopkinsia* WoFitzg., more recently removed from Restionaceae, form a clade with Anarthriaceae but show equally notable anatomical differences from *Anarthria* (Briggs & Johnson 2000).

Within Restionaceae, seed surface patterns are very varied and useful in characterising genera. At a finer level of relationship, seed ornamentation differs markedly among species of *Chordifex*; all have raised patterns of lines of cells but, in *C. chaunocoleus* (F.Muell.) B.G. Briggs & L.A.S. Johnson and the newly described species *C. sinuosus* B.G. Briggs & L.A.S. Johnson and *C. reseminans* B.G. Briggs & L.A.S. Johnson, these form very pronounced ridges (Briggs & Johnson 2004). Differences in seed surfaces were also the initial clue to distinguishing three new species (yet to be formally named) among specimens previously included in *Lepyrodia scariosa* R. Br.

An unresolved question remains under investigation: the status of the Centrolepidaceae. These have highly reduced floral structures; for instance the inflorescences are pseudanthia of several male flowers, each reduced to a single stamen (lacking tepals), and female flowers, each consisting of only a single carpel (Cooke 1998). Some are perennial cushion plants of subalpine or high-latitude

habitats, but others are tiny annual plants of seasonally moist sites. Despite the many apomorphic differences from Restionaceae, including differences in anatomy (Cutler 1969) and pollen (Linder & Ferguson 1985), DNA data from several genes show Centrolepidaceae and Restionaceae forming a robustly supported clade, a relationship also indicated by similarities in embryology. The question remains: are the Centrolepidaceae sister to Restionaceae or a specialized neotenous derivative embedded in the latter? Analyses of sequences of different genes have given conflicting results. Briggs et al. (2000) found that *rbc*L data did not separate Centrolepidaceae (represented by *Centrolepis* Labill.) from Restionaceae, and Bremer (2002) obtained a similar result when data from *atp*B were added. Neyland (2002) found a surprising association of *Centrolepis* with *Ecdeiocolea* F.Muell., based on nuclear DNA (26S rDNA), although various recent studies of chloroplast DNA have placed *Ecdeiocolea* in the Poaceae clade, rather than among the closest allies of Restionaceae. Michelangeli et al. (2003) placed Centrolepidaceae (represented by *Aphelia* R. Br.) as sister to Restionaceae on the basis of *rbc*L, *atp*A and morphology). Further data on a wider range of taxa, from *mat*K and *trn*L–*trn*F chloroplast DNA (Marchant & Briggs, in preparation) may, however, still be insufficient to corroborate a position as sister to Restionaceae. Brown's outstanding insight is exemplified in his recognition of the affinities of these plants and inclusion of representatives of the Centrolepidaceae, and other families now in modern Poales, within his Restiaceae.

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