WHAT IS SIGNIFICANT—THE WOLLEMI PINE OR THE SOUTHERN RUSHES?[1]

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ABSTRACT

The discovery in 1994 of *Wollemia nobilis*, a new conifer genus and species of Araucariaceae, attracted media and public attention that was probably unprecedented for a botanical discovery. If a plant species may be called charismatic, it is this one: tall, handsome, rare, of a lineage dating from the Jurassic, surviving undiscovered in a mountain gorge. It was front-page news around the world and soon became one of Australia's most publicized species. Scientists shared the enthusiasm, offering research collaboration to investigate its many aspects. *Wollemia* has contributed to understanding of structures in fossil Araucariaceae and conifer-mycorrhizal associations; its survival has added to the picture of long-term regional floristic change. After an extended period of small population size it shows no detectable inter-plant genetic diversity—relevant to the management of rare plant species. Its discovery helped us explain and emphasize to the community the value and nature of biological research and the need for habitat conservation. At the opposite end of the charisma scale are the southern rushes, Australia's relatively inconspicuous Restionaceae and their allies (Centrolepidaceae, Ecdeiocoleaceae, Anarthriaceae). Despite their links with other southern continents and close relationship to the Poaceae, these had been greatly neglected for over 100 years and were largely misclassified generically. Study and fieldwork in recent decades have revealed 61 formerly undescribed species, nearly 40% of the total now distinguished in these families for Australia. DNA sequencing of plastid genes gave surprising results, with evidence that two new plant families should be recognized. New findings are contributing to better understanding of the ancestry of related families and Southern Hemisphere floras. Distinguishing the new rare species allows focus on their conservation needs. Many new species are still being recognized in Australia's flora, among flowering plants and conifers as well as other groups. *Wollemia* and the southern rushes exemplify the significance of these new finds and newly discovered understanding of relationships. In each case the significance of the discoveries is realized only in the context of the knowledge of organisms and their evolution that comes from research in many fields.

Key words: Araucariaceae, Australia, conservation, Restionaceae, Southern Hemisphere floras, *Wollemia*.

WOLLEMIA—A CHARISMATIC SUBJECT FOR RESEARCH

In 1994 my colleagues and I at the National Herbarium of New South Wales in Sydney realized that we had been given a remarkable opportunity—the discovery of a new plant species that would catch public and scientific attention in a truly outstanding way.

David Noble of the New South Wales National Parks and Wildlife Service had found about 40 trees of a previously unknown species, soon to be named *Wollemia nobilis* W. G. Jones, K. D. Hill & J. M. Allen, a new member of the conifer family Araucariaceae (Jones et al., 1995). This rare and highly restricted species had been discovered about 200 km northwest of Sydney, in a deep gorge bounded by sandstone cliffs (McGhee, 1995; Duffy, 1997). Such a site would differ from most of the surrounding area in the constancy of water supply, more equable climate, and especially in being largely protected from wildfire, although one tree showed evidence of fire, followed by resprouting. The trees are mostly emergents overtopping both a dense fern layer and a canopy of closed forest (warm temperate rainforest) of *Doryphora sassafras* Endl. and *Ceratopetalum apetalum* D. Don. Seedlings are present (about 200 juveniles were recorded; Nash, 1997; Offord et al., 1999), but most only produce a few leaves, failing to grow to maturity unless a break occurs in the canopy.

The fossil record of the Araucariaceae has been studied extensively. The family appeared in the late Triassic, with a peak of diversity in the Jurassic and a continued decline since the end of the Cretaceous (Miller, 1977). Some of the earliest Araucariaceae are reported from the Northern Hemisphere, and fossil pollen with *Araucaria*-like features is widespread in both hemispheres in the Jurassic and Cretaceous. Its present survival in the south is thus relictual, rather than implying a Gondwanic origin

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Figure 1. *Wollemia nobilis* in its natural habitat. Photo Jamie Plaza.

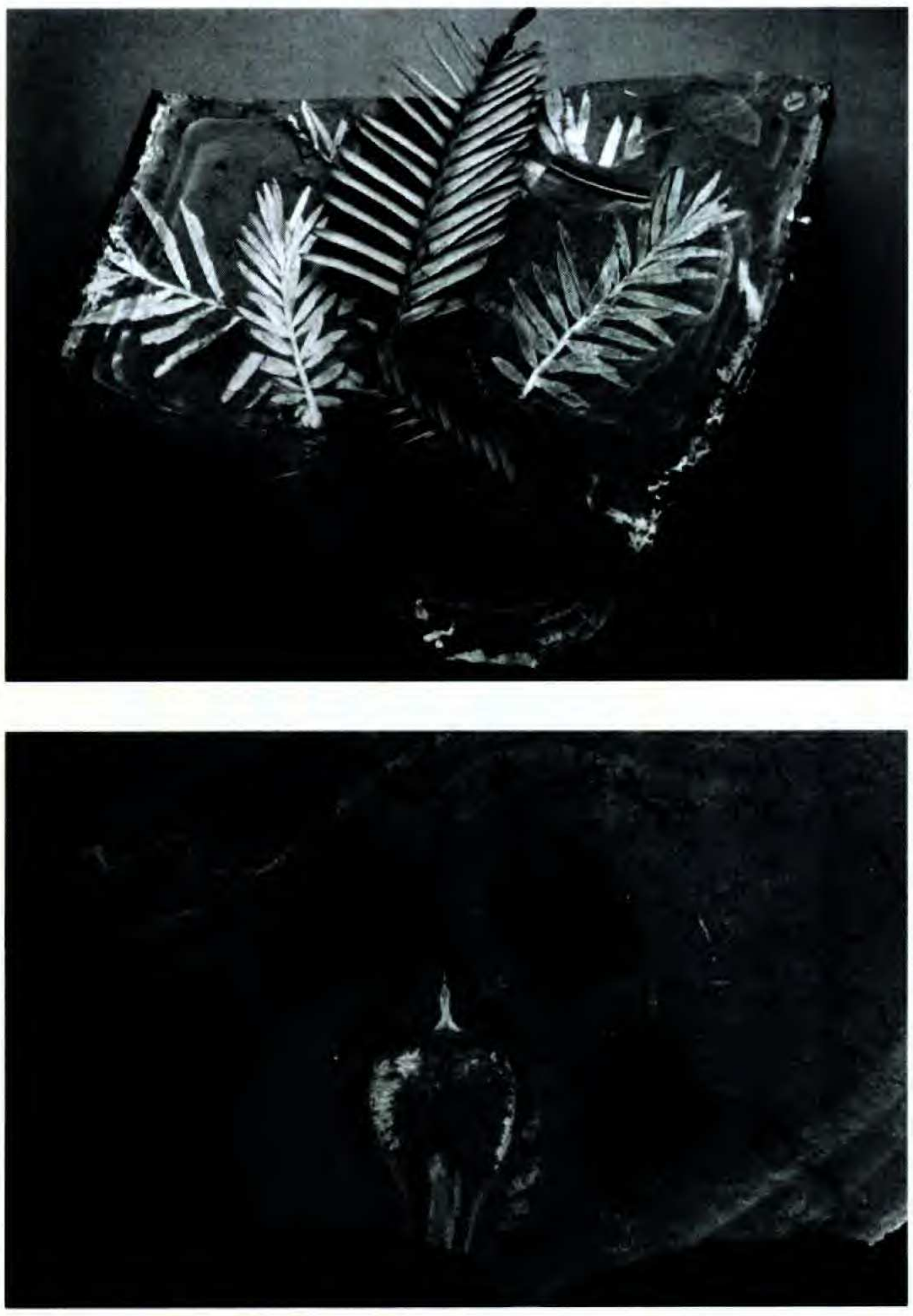


Figure 2. —A (top). Foliage of *Wollemia nobilis* with *Podozamites* (also known as *Agathis jurassica*). This Jurassic fossil conifer is probably not the closest relative of *Wollemia*, but is similar especially to *Wollemia*'s juvenile foliage. —B (bottom). Cone scales of *Wollemia* and of a Jurassic fossil member of the Araucariaceae. Photos J. Plaza.

(Gilmore & Hill, 1997; Setoguchi et al., 1998). Before the discovery of *Wollemia*, the family was known from South America, New Zealand, northeastern Australia, New Guinea, and, in especially rich diversity, in New Caledonia. Two extant genera had been recognized, *Araucaria* and *Agathis*.

The newly discovered *Wollemia* created a sensation. It was handsome, and so large—up to 40 m tall—that it was almost unbelievable that it had been unknown to science until now (Fig. 1). It linked with fossils that connected to ancient groups, back to the Jurassic (Fig. 2), and this in an age when dinosaurs have an unrivalled fascination for adults as well as children. Its habitat, in deep mountain ravines, held an almost sinister appeal.

What followed would not apply to the average newly found species.

A media conference was called to announce the discovery. This brought a response that exceeded our expectations: it was briefly front-page news in the press around the world, with journalists and science writers seeking further information. Television programs and tapes were prepared, featuring its discovery and the subsequent research.

An interagency government committee was set up to develop a conservation plan (Nash, 1997) and to monitor threats and actions affecting its survival. Strict protocols for visits to the habitat were established, especially changing shoes at entry to the site, to avoid bringing in pathogens. Approvals to visit were highly restricted.

Milton Silverman, who had gone from San Francisco with Ralph Chaney in 1948 to collect the dawn redwood (*Metasequoia glyptostroboides* Hu & W. C. Cheng) in western China, wrote to congratulate us on our efforts and the discovery, which was almost ironic considering how much more accessible our find had been than theirs. The name "Wollemi pine" was coined so that we would not seem too lacking in words in reporting the discovery of a plant that had not yet been botanically named. The intrepid travelers to China had coined "dawn redwood" partly because *Metasequoia glyptostroboides* would not fit across a newspaper column in reporting their collections of that species, which, shortly before, had been discovered and compared with fossil species.

Horticultural research and propagation started immediately, using cuttings and seeds (Fensom & Offord, 1998; Offord et al., 1999). The aims were to learn the propagation requirements, establish a conservation population in cultivation, and eventually to safeguard the species by widespread use in horticulture. As in other Araucariaceae, growth was found to be plagiotropic, with plants raised from cuttings of lateral branches mostly continuing to grow horizontally, whereas those from erect stems continue erect growth. Advertisements for commercial partners in raising large numbers of plants brought many proposals. When a young tree was planted in the Royal Botanic Gardens in Sydney, this was done with ceremony by a senior government member, and the plant was enclosed in a very stout cage.

Offers to collaborate in a diversity of research approaches flowed in, 30 within two weeks of announcing the discovery on the TAXACOM listserver (Brooks, 1997). Studies of genetics, chemical constituents, embryology, and anatomy, as well as associated fungi and insects were soon focused on *Wollemia.* Sequencing of the plastid gene *rbc*L (Gilmore & Hill, 1997) confirmed the distinctness of *Wollemia,* although different analyses using different ranges of other taxa gave sharply contrasting phylogenies for the Araucariaceae. Gilmore and Hill (1997) and Stefanovíc et al. (1998) found *Wollemia* to be sister to *Agathis,* with those two genera forming a clade that is sister to *Araucaria.* By contrast, Setoguchi et al. (1998), using the same sequence data for *Wollemia* but combined with a different range of other conifer taxa, concluded that *Wollemia* diverged before the separation of *Araucaria* and *Agathis.* It is hoped that the study of other genes will resolve this discrepancy.

Comparison of *Wollemia*'s adult and juvenile foliage, stomates, pollen, and cone scales with other living and fossil Araucariaceae (Chambers et al., 1998) helped in the interpretation of fossil Araucariaceae, especially in the structure of the cone scales and seed. Its tree architecture was described as unique (Hill, 1997), differing from previously described structural models and other Araucariaceae. Male and female cones are each terminal on a first-order, short-lived lateral branch, and coppicing is a consistent feature. Leaf anatomy has been studied (Burrows & Bullock, 1999) and so has reproduction (Offord et al., 1999). The pollen was found to be indistinguishable from the fossil pollen form-genus *Dillwinites,* which is recorded in Australia and New Zealand extending back to the late Cretaceous (Macphail et al., 1995; Chambers et al., 1998). The most recent fossil records of this pollen type, from Bass Strait, are about 2 million years old.

An endophytic fungus, *Pestalotiopsis guepinii,* was isolated from *Wollemia* (Strobel et al., 1997) and found to produce taxol, which has anti-cancer properties and is effective in controlling oomycetous fungi. The mycorrhizal associates and susceptibility to common pathogens were studied (B. Summerell, pers. comm.). More than 50 taxa of fungi have been recovered from the trees and their immediate surroundings in a survey that cultured fungi from seeds, leaves, leaf litter, roots, root debris, and soil. Such a number of fungal associates is thought to be typical for a tree species in such an environment, but comparisons are uncertain since few tree species have been examined so comprehensively. Of these 50 fungal taxa, 9 are thought to be undescribed species. Some roots are densely filled with endophytic fungi whereas ectophytic fungi are found in other cases, an unusual condition observed also in other conifers (McGee et al., 1999).

Other studies have focused on *Wollemia* especially because it is so rare and vulnerable (Benson, 1996; Offord, 1996). *Wollemia* was found to be susceptible to some pathogens, including *Phytophthora cinnamomi,* which has been introduced and is spreading in southeast and southwest Australia, confirming the need for strict protocols for site visits. Its population genetics was investigated with studies of allozymes and DNA (Peakall, 1998), and these showed no discernible genetic variation among individuals, although more than 800 loci were evaluated with AFLP fingerprinting. There may be some clonal spread, since plants coppice and some have multiple trunks, but the genetic findings are interpreted as largely the result of extremely low population size over a long time, an extended genetic bottleneck. Preliminary data on *Agathis* and *Araucaria,* while showing some variation, indicate that genetic variability is low in the family as a whole (Peakall, 1998).

Was the concentration of attention on *Wollemia* in the media and from scientists justified? This question resonated especially when answering questions about the scientific significance of the find, while in my view the slender silhouettes of other members of the Araucariaceae towered over trees of lesser stature on the skyline of Sydney's Royal Botanic Gardens. That question will be considered after reviewing a contrasting example.

THE SOUTHERN RUSHES

The Restionaceae and allied families in Australia, the southern rushes, are as much in need of charisma as *Wollemia* is blessed with it. The flowers are inconspicuous, with small scarious bracts, glumes, and tepals (Fig. 3) and with the leaves reduced to sheathing scales (Meney & Pate, 1999). They occur exclusively in low-fertility soils and in arid or seasonally waterlogged sites, habitats avoided for agriculture and therefore of low human population and often poor access. In one of the allied families, Centrolepidaceae, the plants are tiny, some species no more than 1 cm tall.

Through such features Restionaceae seem to have brought on themselves extreme botanical neglect over the first half of this century. Before then, the three great early figures of Australian botany had made a good start on their discovery and classification. Robert Brown, naturalist on the first circumnavigation of Australia in 1801–1803 described seven genera and 47 species of Restionaceae that are currently recognized (Brown, 1810). A further 10 species were named by Ferdinand Mueller (1873), whereas George Bentham (1878) recognized 71 species. By the early 1960s, when L. A. S. Johnson and I started our investigations, the number of known species had crept to 86. Around that time also David Cutler of the Royal Botanic Gardens, Kew, made extensive anatomical investigations (Cutler, 1969). It became clear that the generic classification was entirely inadequate (Cutler, 1969, 1972; Johnson & Briggs, 1981; Briggs & Johnson, 1998a) and that many specimens matched no named species.

Clearly this neglected plant group would present a fertile field for new discoveries, but it far exceeded expectations. The discoveries have been both new species and new understanding of relationships, necessitating a radical reclassification.

In recent decades, great swathes of country had become more accessible, especially in the sandplains of Western Australia. Examining the unidentified collections in herbaria revealed many new species; fieldwork brought additional ones. Even the largest of all Australian restiads, with flowering stems over 2 m tall, is among the recently discovered species yet to be formally named. Investigation of supposedly variable species often showed these to be assemblages of several allied species, each with a distinctive distribution and ecological range. The study brought to light 51 new species, mostly from the south of Western Australia. Just when we thought that few additional finds could be expected in Australian Restionaceae, colleagues in Western Australia found a further 10 species (Meney et al., 1996). There was notably little hybridization among the species; the distinctions were sometimes inconspicuous, but they were consistent.

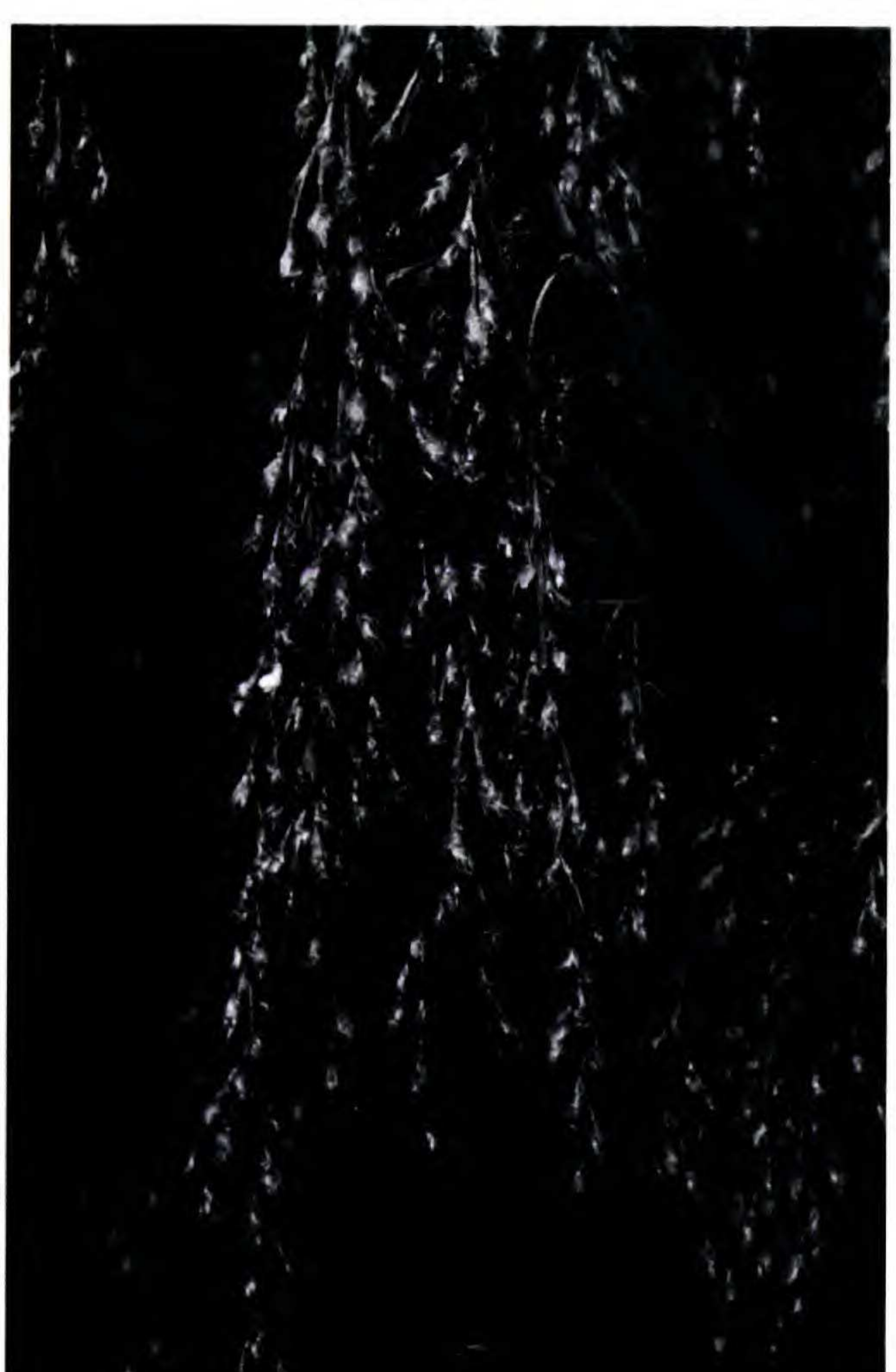
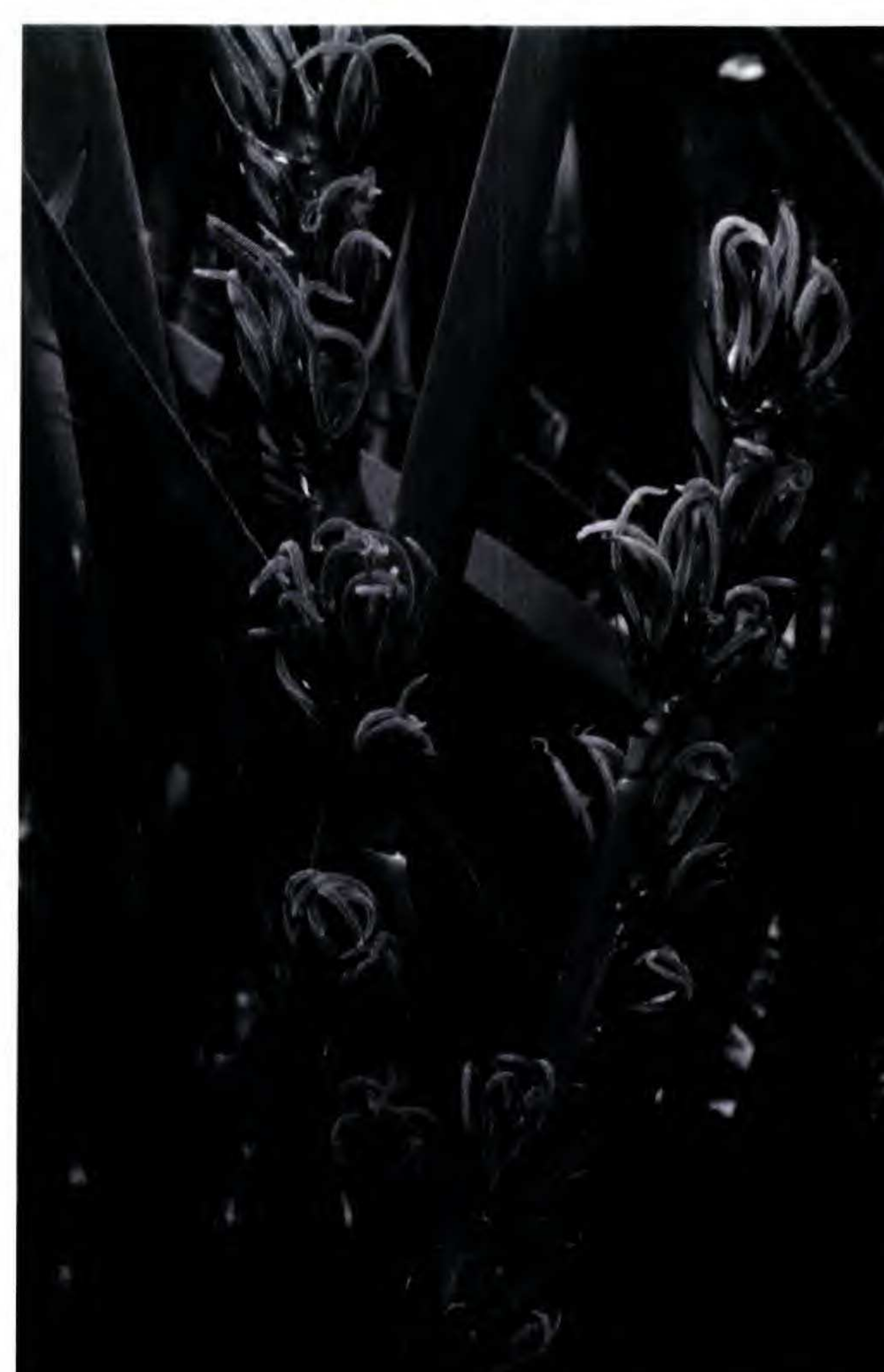
Restionaceae show an exceptionally high proportion of newly recognized species, but it is estimated that about 15% of Australia's flowering plants are still to be discovered (A. Orchard, pers. comm.), in addition to many now distinguished but awaiting publication.

The new view of Australian Restionaceae did not stop at species. When this study began, 29 Australian species were named within the genus *Restio*, but it became clear that *Restio* was a member of a group of genera limited to Africa and Madagascar (Cutler, 1972; Johnson & Briggs, 1981; Linder, 1985, 1991; Briggs & Johnson, 1999). Therefore, new genera were required, or old synonyms taken into use, to accommodate all the Australian species hitherto included there (Briggs & Johnson, 1998a, b).

Moreover, Restionaceae showed a pattern similar to that in Proteaceae, Fabaceae, Ericaceae, and Poaceae in their post-Gondwanic floristic richness. The history of climates, migrations, and survivals has left different traces on the African and Australian continents, so that Africa has large numbers of species in relatively few genera, but Australia has a diversity of groups appropriate for recognition as genera. This pattern has shown even when the same botanist studied groups in both continents, rather than being an artifact of different generic concepts (Peter Weston, pers. comm.; Nigel Barker, pers. comm.), although it is not apparent when Proteaceae of the Cape Region are compared with only the southwest of Western Australia (Cowling & Lamont, 1998). Our case led to the description of the rather alarming number of 16 new genera of non-African Restionaceae (Briggs & Johnson, 1998a).

Morphological cladistics (Linder et al., 2000) and DNA data both indicate that an early division within Restionaceae is between the African clade and the Australasian clade (though the DNA data give only weak support). This would be consistent with an ancient Gondwanic connection. By contrast, the single species in South America, *Apodasmia chilensis* (Gay) B. G. Briggs & L. A. S. Johnson, is extremely similar to the New Zealand *A. similis* (Edgar) B. G. Briggs & L. A. S. Johnson, indicating long-distance dispersal. Moreover, *Apodasmia* (recently segregated from *Leptocarpus;* Briggs & Johnson, 1998a) includes foredune coastal species and is the only notably salt-tolerant genus of the family; it is singularly well suited to establish successfully after dispersal.



Sequencing of plastid DNA was done in parallel with morphological studies and gave a further unexpected result, evidence that two new plant families should be recognized (Briggs et al., 2000). *Hopkinsia* and *Lyginia* are small genera, of two and three species, respectively (one species of each genus undescribed). Their inclusion in Restionaceae had never been questioned, even when they were the subject of detailed anatomical investigations (Gilg, 1890; Cutler, 1969). But two sets of DNA sequence data (from *rbc*L, and from the *trn*L intron with the *trn*L-*trn*F spacer) are consistent in grouping them (each with 100% jackknife support) with *Anarthria* (Fig. 4) rather than with Restionaceae. That grouping is shown in a jackknife consensus tree from analysis of the total sequence from these DNA regions and is further supported by the presence of two distinctive indels (one insertion and one deletion) in the *trn*L intron (Fig. 4).

Although further investigations are needed and proceeding, it appears that the *Anarthria* clade (*Anarthria, Hopkinsia, Lyginia*) is not the sister group to Restionaceae. That position appears to be held by Centrolepidaceae. Such close affinities, or even inclusion of Centrolepidaceae within Restionaceae, have been suggested on morphological and embryological grounds (Hamann, 1962, 1975; Kellogg & Linder, 1995; Linder et al., 2000) and now have some support (although not robust) from analyses of DNA data (Fig. 4; Briggs et al., 2000). It has been suggested that Centrolepidaceae are neotenous, with mature plants showing some similarities to seedlings of related families, although their inflorescences are very different.

Despite the evidence that *Hopkinsia, Lyginia,* and *Anarthria* form a clade, they share no synapomorphies of morphology, anatomy, flavonoids, pollen, or seeds, except for features that are either plesiomorphic within the Poales or widespread in the order. Similarly, studying these genera in light of the DNA data showed that those features that they have in common with Restionaceae are plesiomorphies, although each has distinctive autapomorphies. *Hopkinsia* has a reduced carpel number and succulent indehiscent fruits. *Lyginia* shows a distinctive arrangement of thick- and thin-walled cells interspersed in the chlorenchyma, sloping stomates, fused stamen filaments, and highly distinctive seeds ornamented by minute pits and spines. *Anarthria* lacks a sclerenchyma cylinder in the culms and has unreduced, ensiform leaves and also large chromosomes (Briggs, 1966). Such chromosomes are, in general, associated with large genomes, an apomorphic feature (Bennetzen & Kellogg, 1997; Bennett & Leitch, 2000). Without some morphological basis there appears to be no case for enlarging Anarthriaceae or describing a single new family for *Hopkinsia* and *Lyginia*. The most logical course is the recognition of "Hopkinsiaceae" and "Lyginiaceae," and these new families are being described (Briggs & Johnson, in press).

The families mentioned above, Restionaceae, Centrolepidaceae, Anarthriaceae, "Hopkinsiaceae," "Lyginiaceae," together with the Ecdeiocoleaceae, Joinvilleaceae, and Flagellariaceae, appear to be the closest relatives of the Poaceae (Dahlgren et al., 1985; Chase et al., 1993; Duvall et al., 1993; Briggs et al., 2000). These are all families with primarily Southern Hemisphere distribution. Especially notable is their high concentration in the southwest of the Australian continent: six of the eight families occur in that region and four are limited to it. Together with nine other families they constitute the Poales as recognized by the Angiosperm Phylogeny Group (APG, 1998). Three of the other families are primarily in the Southern Hemisphere (Hydatellaceae, placed here but with little evidence, Prioniaceae, and Thurniaceae), while six are distributed in both hemispheres (Cyperaceae, Eriocaulaceae, Juncaceae, Sparganiaceae, Typhaceae, and Xyridaceae). The concentration of allied families in the south has led to the suggestion that the Poaceae itself had a southern origin (Doyle et al., 1992), although these distributions could also be relictual, as with the Araucariaceae.

What Is Significant?

The examples considered above are two ends of a spectrum. In *Wollemia nobilis* we have a single new species and genus in a recognized plant family, but an exceptionally charismatic and interesting find. In Restionaceae and its allies we have some 60 new species, many new genera, and two new

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Figure 3. Australian Restionaceae and Anarthriaceae. —A (top left). *Lepidobolus preissianus*, male (left) and female spikelets, each ca. 1.5 cm long. —B (top right). *Baloskion tetraphyllum* subsp. *meiostachyum*, female, spikelets ca. 5 mm long. —C (bottom left). *Meeboldina scariosa*, male, spikelets ca. 4 mm long; photo B. Fuhrer. —D (bottom right). *Anarthria scabra*, female, with prominent stigmas; linear leaves ca. 6 mm wide; photo B. Fuhrer.

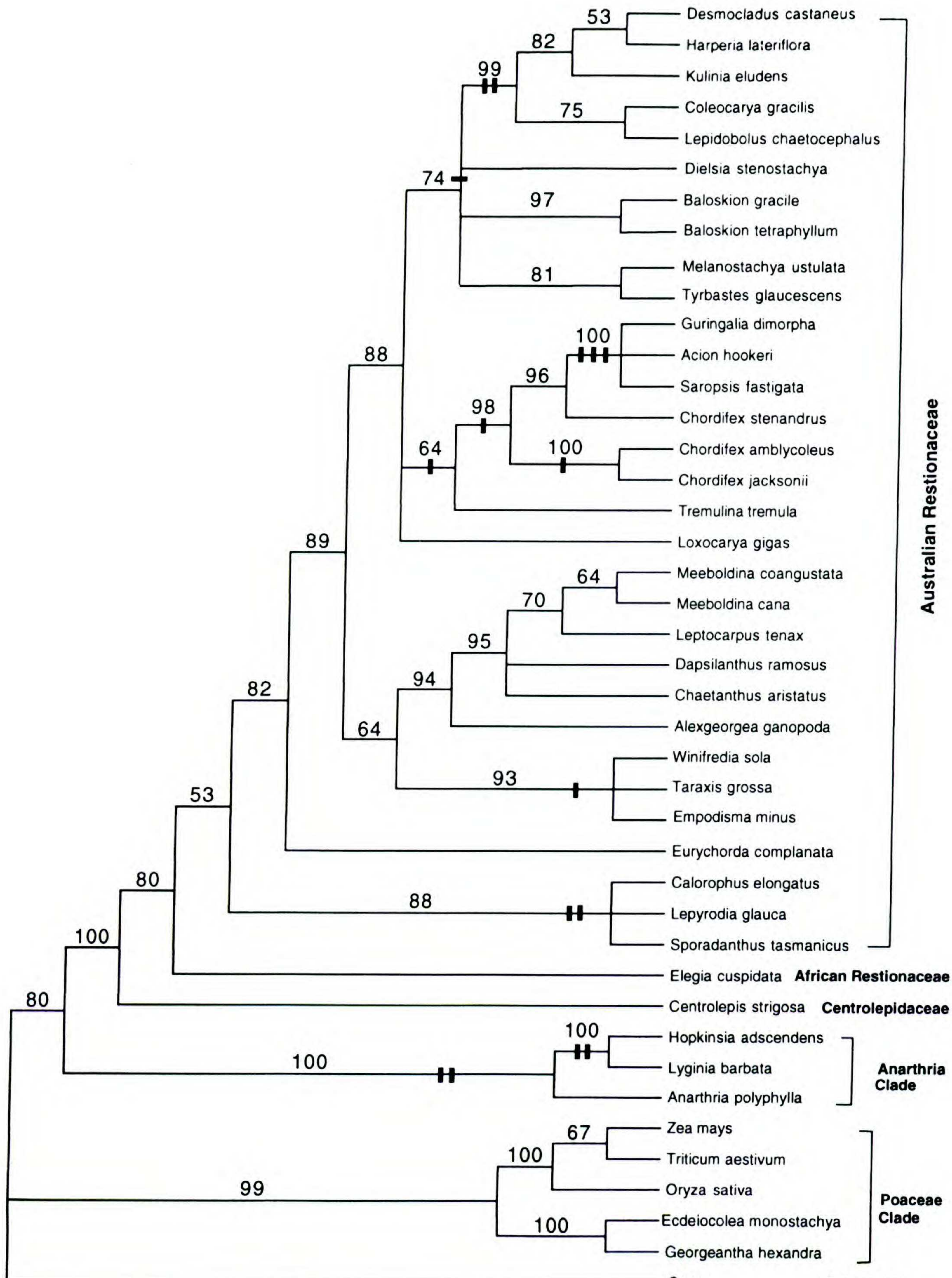

Figure 4. Jackknife consensus tree for Restionaceae and allied families from parsimony analysis of chloroplast DNA data. Numbers indicate jackknife support for individual nodes. Cross-bars indicate unique (non-homoplasious) indels, in the *trn*L intron or *trn*L-*trn*F spacer, that are synapomorphies for clades.

plant families. Neither of these examples is typical of the situation in the Australian flowering plants.

Wollemia created unprecedented public, media, and scientific interest. It raised public enthusiasm, awareness, and knowledge of environmental and biodiversity conservation issues. Its importance and rarity make it a wonderful example in education programs and political contexts. It has emphasized to the community the need for habitat conservation in species survival and given a focus for programs to explain the nature of biological research. To investigate its significance and conservation there has been research in systematics and evolutionary relationships, palaeontology, ecology, genetics, plant pathology, mycology, and plant propagation; this has helped to publicize the role of all these disciplines (Hill, 1996). School groups, government members, and the general community are enthusiastic about seeing the plants, so it has raised the profile of our botanic gardens and of their scientific and educational programs; it has also been a major profile-raiser for the New South Wales National Parks and Wildlife Service. *Wollemia* has contributed to understanding of structures in fossil Araucariaceae and conifer-mycorrhizal associations; its survival has added to the picture of long-term regional floristic change, perhaps even a step in the regional replacement of coniferous vegetation by flowering plants. After an extended period of small population size, it shows no discernible inter-plant genetic diversity.

Our other example, Restionaceae and allies, was probably the most neglected of all substantial Australian flowering plant groups and so was the richest site remaining for new discoveries. Distinguishing the many new rare species permits a focus to be developed on their conservation needs. Better knowledge of relationships within the Restionaceae clarifies an instance of the distinction between the intercontinental links that date from at least Gondwanic times and those that may represent relatively recent long-distance dispersal. In addition to greater understanding of Southern Hemisphere floras, there is improved understanding of relationships among the families of the Poales, with the recognition of the *Anarthria* clade and further demonstration (Fig. 4) of the closeness of Ecdeiocoleaceae to Poaceae, in agreement with Doyle et al. (1992).

Both examples are significant, but in each case the significance of the discoveries is only fully realized in the context of knowledge of organisms and their evolution that has been established by research in many fields. The history and antiquity of the Araucariaceae make *Wollemia* so notable. Similarly, relationship to the Poaceae adds to the relevance of findings in the Restionaceae. The historical biogeography of world floras, especially those of the Southern Hemisphere, provides a context for discoveries in both these groups; findings in these groups, in turn, clarify aspects of the development of these floras.

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