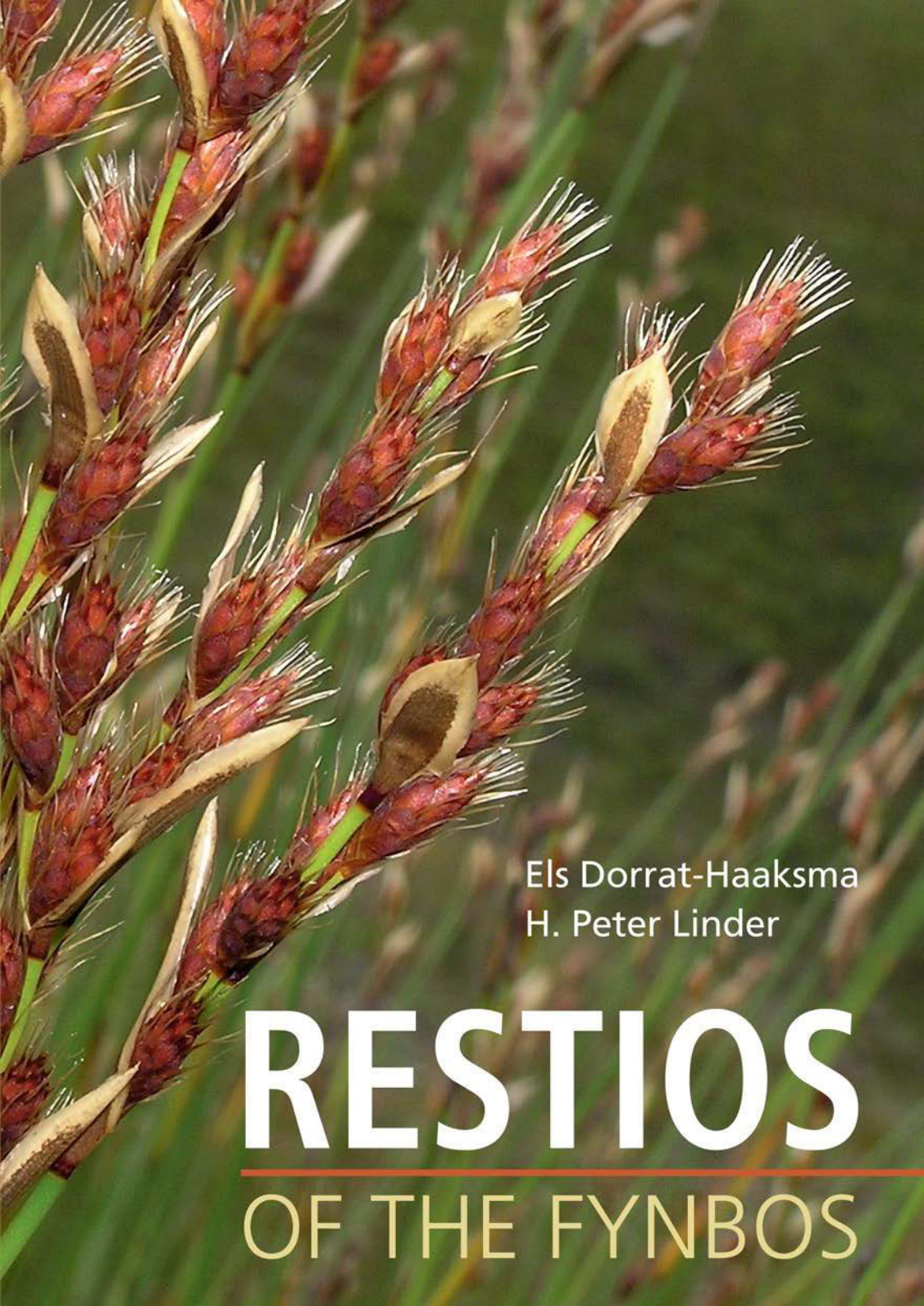

Els Dorrat-Haaksma
H. Peter Linder

RESTIOS
OF THE FYNBOS

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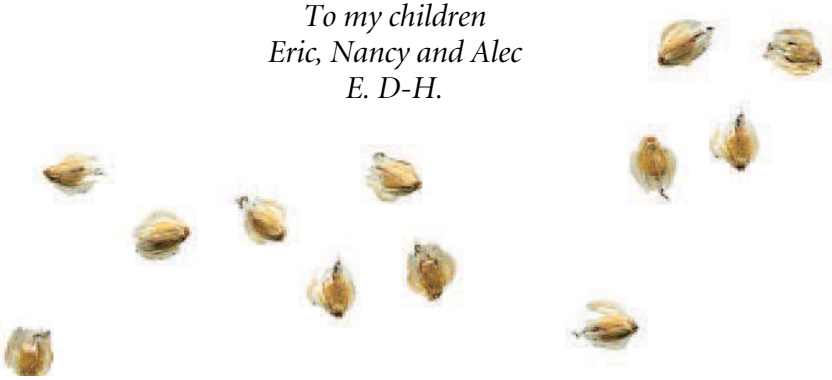
RESTIOS
OF THE FYNBOS

Els Dorrat-Haaksma
H. Peter Linder

To my children
Eric, Nancy and Alec
E. D-H.



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Cover image: *Hypodiscus* sp. (Restionaceae) © Tomáš Hájek & Jana Jersáková

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FOREWORD

I have had the pleasure of tramping through fynbos with innumerable plant lovers. It is such a delight to see what catches their eye, plantwise. Colourful bulbs, flashy proteas and sticky, gaudy ericas invariably attract attention of the 'what's that?' or 'that's this' kind. Seldom, however, am I stopped to gaze at a restio, thumb through its bracts, and admire its graceful culms. But this is changing, thanks to Els and Peter's magnificent guide. Restios demystified.

And so should they be, these quintessential features of fynbos. From the arid sandplains of Namaqualand to the black-soil bogs of misty peaks, wherever there is fynbos, there are restios. Beautiful restios – wind whipped elegias, like a billion caramel cusps, on the damp flats at the Cape of Good Hope; giant cannomois, an elegant border to a soothing stream on a hot summer's day in the Cederberg; stately dekriet, culms glistening with beads of moisture, in the early morning mist of the Agulhas Plain.

So it is with unreserved enthusiasm that I acclaim the re-issue of *Restios of the Fynbos*. As a guide it is perfectly detailed, crisply written and innovatively illustrated (the species are faithfully depicted as three-dimensional scans of actual plants, a novel and appropriate approach for a plant group with such exquisite intricacy of form and function). If you are intrigued but intimidated by restios, buy this book. Very soon you will be keying out your first genus (all 16 are described) and delving further, perhaps matching your specimen to the description of the 119 commonly encountered species are included in the guide.

To Els and Peter: thank you for this gift. Elsie Esterhuysen would have approved!

Richard Cowling
Professor of Botany
Nelson Mandela Metropolitan University
of South Africa

ACKNOWLEDGEMENTS

It is hard to believe that more than 11 years have passed since the Restionaceae were put in the spotlight for the first time in *Restios of the Fynbos*. Over the years I have continued to enjoy my involvement with the Restionaceae and I have been delighted with the opportunity to work on this second edition.

As usual a new book does not arrive without help and co-operation from others, and even a second edition requires renewed assistance, be it sometimes of a different nature. So it is with great pleasure that I wish to express my sincere thanks to all who have helped to bring this book to fruition:

My first words of appreciation go to Peter Linder, my co-author. His extended research on the molecular biology of all species of the Restionaceae was finally published in 2010. It is gratifying to know that this kind of research, bringing interesting taxonomic changes, has not remained hidden in scientific journals but has come alive in this new edition.

The list of 'Sponsorships and donations' would not have featured in this book without the literary and artistic skills of Lucille Krige and Jane Eager. I thank them warmly for helping me in producing a beautiful poster, which beckoned the Cape fynbos-loving public for financial assistance. The spontaneous, heartwarming and generous response to this poster contributed in no small way to the reality of this book.

I am much indebted to Noel McShane and Linda Kay from Creda Communications. It was there where I found the amazing 3-D scanning machine, which was so eminently suitable for producing the restio images, and it was there where the first edition of the book was produced in 2000. And, once again, I have been touched by Noel and Linda's genuine and selfless co-operation – where else can an author work on the manuscript at the company's premises with a specially assigned, skilled DTP operator. No-one else but Clinton Wood would have had the skills and infinite patience to deal with the fiendishly intricate text and detail in the design and layout of the book, with which he was confronted. Thank you all so much! I will really miss the Creda visits once the work is all done.

The digital age presents great competition to the publication of real books, so I feel particularly grateful to Pippa Parker and the publishing department at Random House Struik for the trust they have put in us by accepting the book into their publishing programme.

The pleasant collaboration with the editor, Helen de Villiers, has been most rewarding and I would like to thank her and designer Gillian Black for their expertise in handling this challenging book.

I am sure everyone will be delighted with the poetic and enthusiastic descriptions of the restios in the Foreword written by Richard Cowling. Thank you so much, Richard, for your wonderful words.

Thank you both, Ruth and Carly from Cape Nature, for granting me a permit for collecting Restio plants for new illustrations, and James Cooper for so enthusiastically helping me to find a seemingly lost species at Kenilworth Nature Reserve. Ivor and Cora Jardine gave assistance with collecting a special restio species to be scanned in as illustration; their willing help was much appreciated. Other friends who helped are Leslie van der Merwe, Audrey Reid, Richard Eastwick, Jaap Hendriks, Solveig Bosch and Valerie Sandilands.

Last, but not least, I wish to thank most sincerely Ian Dorrat, my best friend of many years, for his moral support, wise council and spontaneous help on numerous occasions in matters concerning the fund-raising campaign to bring this second edition to fruition. Thank you, Ian, for all you did.

Els Dorrat-Haaksma

Restio tetragonus, x 0.5

Elegia capensis

SPONSORSHIPS AND DONATIONS

Els Dorrat-Haaksma and H. Peter Linder would like to thank most sincerely the following people and associations for their financial contributions:

Ant Smith
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The Friends of Cape Good Hope Nature Reserve, in memory of the late Joanna Sharland

The Botanical Society of South Africa

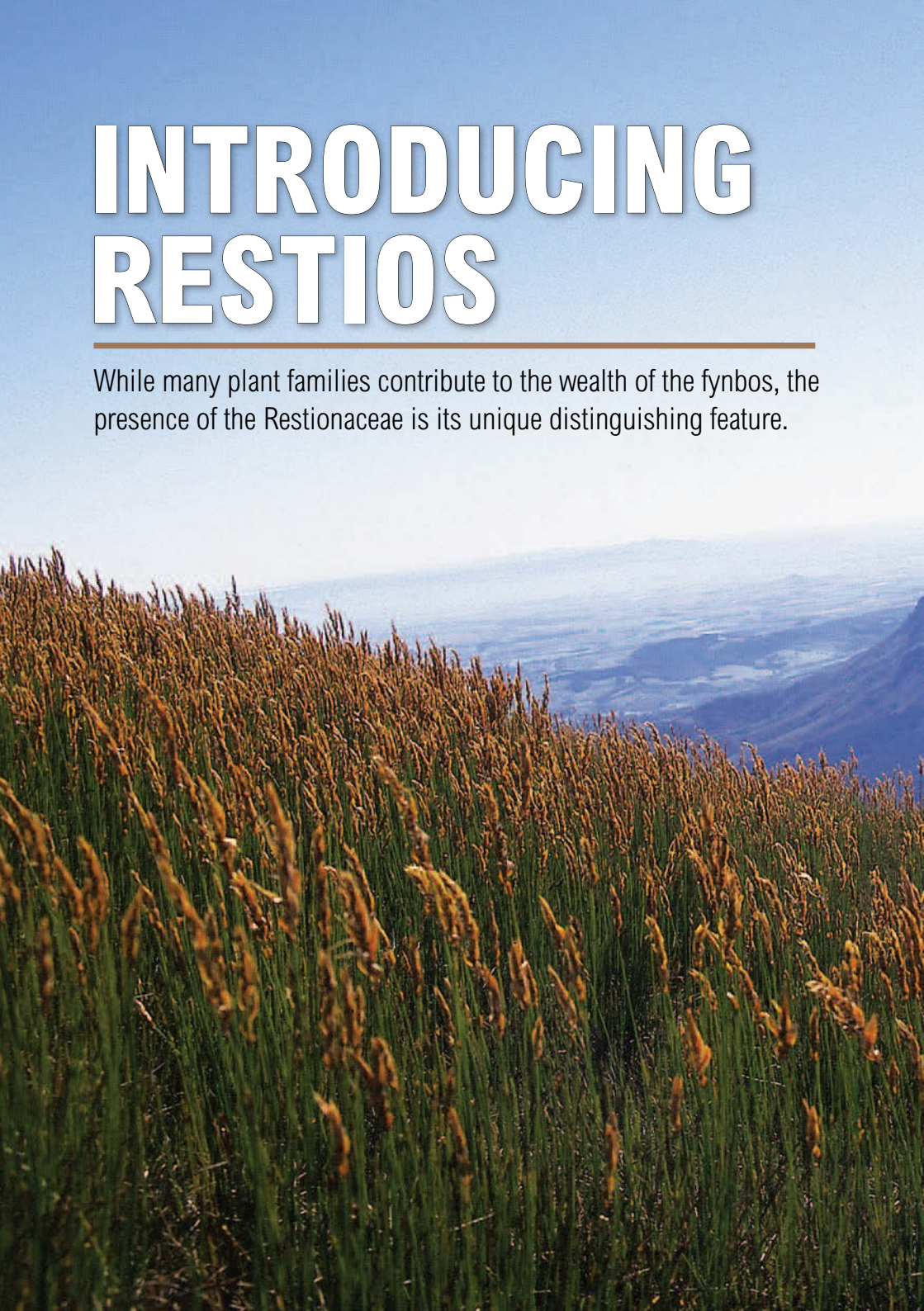
The Friends of Silvermine Nature Area

The Mountain Club of South Africa (Cape Town branch)

The Cape Town Section of the Mountain Club of South Africa has sponsored this book as part of achieving one of its six objectives, namely, to promote interest and research into mountain environments.

INTRODUCING RESTIOS

While many plant families contribute to the wealth of the fynbos, the presence of the Restionaceae is its unique distinguishing feature.



BIOGEOGRAPHY

The Restionaceae or, as they are commonly called, the restios, are a family of perennial, evergreen, grass-like plants. They range from 10 cm to 3 m in height and often have a tufted growth form. The plants have erect, green, photosynthetic stems, with leaves that are reduced to leaf sheaths. The flowers are very small and are contained in spikelets, which in turn make up the flower heads or inflorescences.

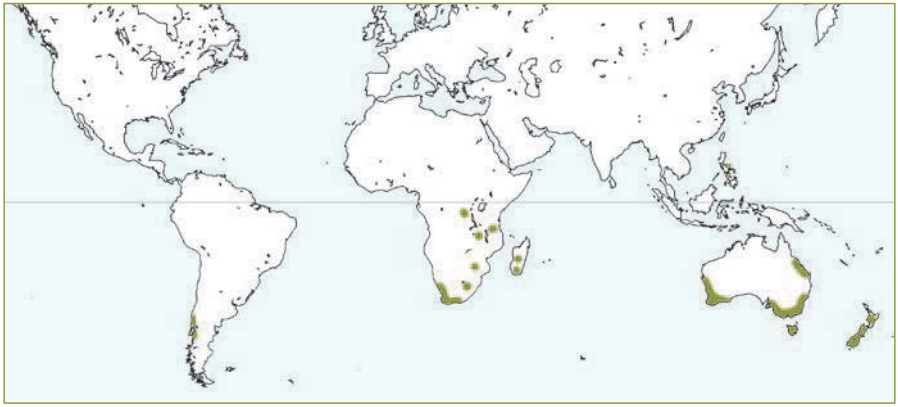
The family is dioecious, i.e. the male and female flowers are borne on separate plants, and are wind pollinated. The fruit is a nut or capsule.

The Restionaceae family is a typical 'southern' or 'austral' plant family. It is found on all the southern continents, with ±357 species in Africa, ±150 species in Australia, four species in New Zealand, a single species in South America and a single species widespread in South East Asia.

However, only in the Cape Floristic Region of South Africa do the Restionaceae dominate the vegetation over large areas. With so many species and such ecological dominance, the family is obviously of great importance, and this leads to an interest in its biology, ecology and origins.

The distribution range over all the southern continents has led to suggestions that the family is ancient, dating to the end of the Cretaceous period, more than 60 million years ago, when the southern continents were still in close proximity to each other, forming the supercontinent Gondwana – a hypothesis supported by fossil pollen records from southern Africa.

Global distribution of the Restionaceae



Areas coloured green indicate distribution of the Restionaceae

FYNBOS

Fynbos is the dominant vegetation in the Cape Floristic Region. The word comes from the Dutch *fijn bosch* which describes the narrow-leaved bushes characterizing much of this vegetation. However, fynbos also supports broad-leaved bushes, for example, members of the Proteaceae family. The ±8 000 fynbos species can be divided into several groups, according to their growth form. One of these is the restioid group, including the family Restionaceae. While any of the other groups can be absent from a particular habitat, the presence of the Restionaceae family is the unique distinguishing component of fynbos.

The hypothesis is that at this time the family would have been widespread on all the southern continents, and when the continents became separated, each drifted off with its own complement of Restionaceae. However, another possibility is that the family crossed the Pacific Ocean only recently (in the last 30 million years), leading to the establishment of the single South American species, *Apodasmia chilensis.* This species is closely related to a species in New Zealand, which is found under very similar ecological conditions, strengthening this hypothesis.

The distribution of the Restionaceae in Africa is very uneven. There is a single species in Madagascar, which is also found in the Democratic Republic of the Congo, Tanzania and Malawi. Another species is found on the Chimanimani Mountains of eastern Zimbabwe.

In South Africa there are four species in the KwaZulu-Natal Drakensberg, one of which is also found in the Northern Province and Mpumalanga. But the vast majority of the species are found in the fynbos of the Cape Floristic Region, especially on the hard sandstone mountains of the southwestern and southern Cape.

The distribution of individual species varies from being widespread, like *Ischyrolepis sieberi,* which ranges from the Richtersveld to Port Elizabeth, to being restricted to a single mountain peak, such as the narrowly endemic species *Hypodiscus montanus* from Misty Point behind Swellendam.

The greatest richness in species is found in the Kogelberg mountains, where over one third of all Restionaceae species are found. Moving away from the Kogelberg, the species richness drops off, until one reaches the peripheries of the Cape Floristic Region, where there are rather few species. This distribution pattern is typical for most elements of the Cape Flora, and is seen in the *Ericas,* Proteaceae, (Orchidaceae (*Disas)*, and numerous other groups.

ECOLOGY

Restios can be found in virtually all habitats of the fynbos, from sandy plains to mountain summits and from very dry places to seasonally wet or permanent marshes. In many areas the Restionaceae make up the most dominant component of the fynbos vegetation to the extent that they are regarded as the 'loyal supporting cast' to the other more colourful flowering families such as Ericaceae, Proteaceae and Iridaceae.

However, they cannot be found as annuals or in aquatic habitats and are also absent from the forest understorey. *Restio subverticulatus* and *Restio fourcadei* are often found along the margins of the forests or in the light shade of scrub forest alongside streams, but avoid the deep shade of the forest.

Restionaceae are excellent indicators of the ecology of an area, and if the list of Restionaceae for a particular spot is known, it is possible to predict the climate and soil moisture conditions.

Mountain fynbos in the Slanghoek Mountains with *Elegia amoena*

Seasonally inundated flats at Cape Point, with *Elegia cuspidata* and *Elegia filacea* forming extensive monospecific stands

Elegia microcarpa in coastal dune vegetation at De Hoop. Coastal sand restios typically spread by underground rhizomes that form mats

Seepage vegetation on Table Mountain, with hummocks of *Anthochortus crinalis*

Sandy plains in the Slanghoek mountains with large stands of *Elegia spathacea*

A seepage on the Hexberg, Bokkeveld mountains, with *Elegia grandispicata* fringing the wet centre of the seepage

An ice-encased restio on Groot Winterhoek near Tulbagh

BIOLOGY

The Restionaceae have a rich biology. Although this will be discussed under a number of different headings, the biological processes are all integrated to make a functional plant that successfully traps pollen of the right type, sets seed, which is effectively dispersed, and germinates successfully to grow into an adult plant. The interactions with the physical environment and with the animals and other plants that share their habitat provide yet another interesting aspect of the biology of the Restionaceae.

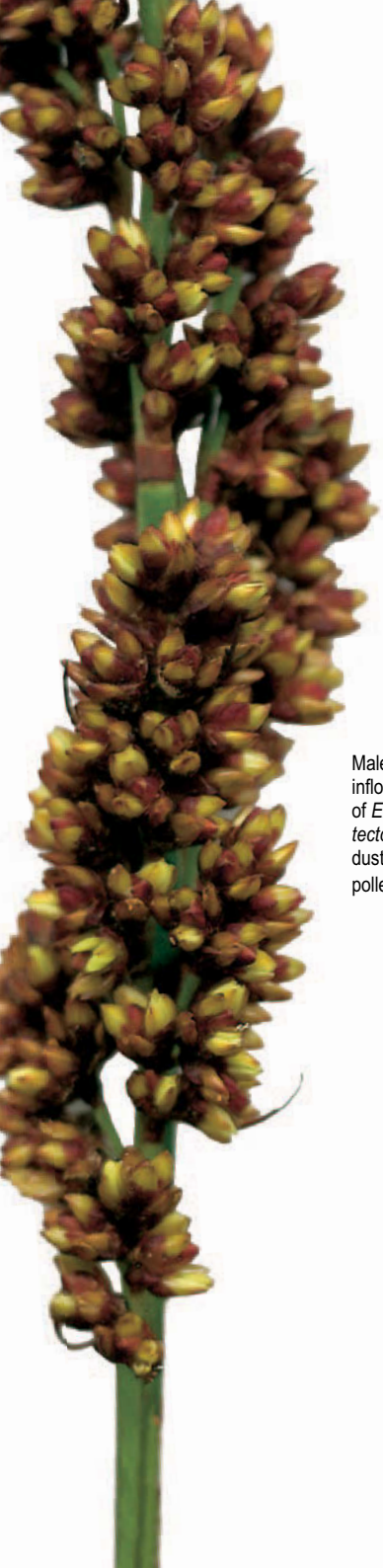
POLLINATION

All Restionaceae are wind pollinated, and although this means that there are no interesting visible interactions between pollinators and the flowers, the way in which the flowers and inflorescences are adapted for wind pollination is particularly fascinating.

Restionaceae are dioecious, i.e. male and female flowers are borne on separate plants. This may function primarily in preventing the plants from fertilizing themselves, but at the same time has led to morphological specialization of the different roles of male and female flowers.

A variety of restio flowers

The flowers are very small and inconspicuous. The petals and sepals are dull brown, sometimes transparent and scale-like. This suggests that their main function is to protect the anthers and ovary. There are no nectaries. The flowers are aggregated into small spikelets, which in turn make up the inflorescences. Although the role of the spikelets, as such, for wind pollination is not quite clear, the numbers of spikelets per inflorescence will certainly affect pollination.



Male inflorescence of *Elegia tectorum*, dusted with pollen, x 5

Male flowers, to be efficient at wind pollination, have to produce large amounts of pollen, which have to be shed into the wind. The large pollen production is achieved by numerous flowers with three anthers each, rather than few flowers with many anthers. In addition, the anthers are quite large and, when ripe, bright yellow and very visible. Most species have anthers on long filaments protruding from the bracts and exposing the anthers outside the spikelet to the airflow.

Male spikelets of *Hypodiscus willdenowia*

As usual, there are exceptions, and in the *Elegia* genus, the ripe anthers open inside the petals. However, the petals open to release the pollen.

The pollen also has to be modified for efficient transport by air. The most important feature is that the pollen is not sticky (unlike that of insect-pollinated plants), thus ensuring that it is dispersed like dust in the wind. In addition, the grains are round and smooth, which appears to improve their aerodynamic characteristics.

Electron microscope scan of pollen of *Hypodiscus striatus* with the typically rounded aperture, x 1 000

Female flowers show some spectacular adaptations to wind pollination. These are evident in the construction of the inflorescences and in the shape of the styles, both designed to maximize the ability of the flowers to trap pollen.

The styles, as in the grasses, are usually feathery and, in most species, are exposed outside the spikelets, where they are well positioned to filter the pollen out of the air. They are found in a variety of beautiful colours, from white to pink or red or even maroon. Some species have quite substantial, stiff styles.

Female spikelets of *Restio quinquefarius*

In the genera *Staberoha* and *Elegia,* the bracts and spathes are much enlarged and completely enclose the flowers and even whole spikelets. In these plants the bracts and spathes presumably act as air scoops, which funnel the wind past the styles, or cause local eddies resulting in the pollen dropping down onto the styles. These mechanisms are amazingly efficient, as very little 'foreign' pollen has been observed on the styles of such genera. The plants appear to trap only their own pollen, excluding the pollen from other species and the general debris that is found in the air.

More detailed information on flowers, spikelets and inflorescences can be found in the morphology section (pp. 40–55).

Spathes of *Elegia* sp. enclosing the spikelets

Stout styles of *Ceratocaryum argenteum* partially hidden by the big spathes

DISPERSAL

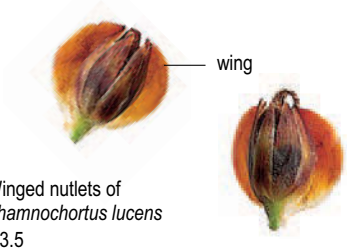
Seeds from a variety of restio species

Restionaceae have a remarkable diversity of seed dispersal mechanisms, and these are intricately linked to the construction of the flowers. In the simplest, and presumably the most primitive method, the ovary of the flower produces two or three small seeds, and the fruit is a capsule. When the seeds are ripe, the capsule splits open and the seeds are released. The seeds are generally of similar shape, more or less elliptical, and 1–2 mm long. However, there is great variation in the ornamentation of the seed surfaces, from completely smooth and shiny, to pitted, ridged or otherwise modified.

This ornamentation can best be seen under a magnification of x 10 or more. The purpose of the ornamentation is obscure, but a clue may be found when looking for the seed on the sand around the base of the plant: it is almost invisible. The seed is the same size as grains of sand, and the texture and shape mimics such grains. So this is possibly a means of camouflage. How the seeds are dispersed from the parent plant is not quite clear, as there are no obvious dispersal agents.

Seeds
x 5

In those species in which only a single seed is formed in each ovary, the fruit is a nut or nutlet, and a diversity of dispersal mechanisms has developed. In these cases the seed stays inside the nut, and often the petals and sepals persist around the nut, aiding its dispersal. For many small-nutted species, no obvious additional dispersal mechanisms exist. However, in some species of *Staberoha* and *Calopsis* and in all species of *Thamnochortus*, the lateral sepals are deeply keeled, forming a wing around the nut, thus producing a wind-dispersed fruit. This is clearly evident in *Thamnochortus*, where the winged nutlet can be seen blowing along in the wind.



Winged nutlets of *Thamnochortus lucens*
x 3.5

The most interesting dispersal mechanism is found in species of *Willdenowia, Hypodiscus, Mastersiella, Ceratocaryum* and *Cannomois,* where the nuts are evidently dispersed by ants. These nuts are much larger than those of the other genera, up to 10 mm long. The walls are very hard, distinctly woody and brown to black in colour. The persistent petals and sepals are papery, often much smaller than the nut, forming a small skirt around the base of the nut. As the nut ripens, the base of the stalk becomes swollen and fleshy, and contains oils which are apparently very attractive to ants. This structure is called an elaiosome and stays attached to the nut. Once the nuts have dropped to the ground, ants carry them away underground and feast on the elaiosomes. This interesting dispersal mechanism protects the seed from predators like mice, as well as from fire.

A few species in this group of genera make very large nuts, ±11 mm in diameter, but have no elaiosomes to attract ants. However, the seedlings of these plants all erupt from several centimetres below the soil, so something buries the nuts. Currently, suspicion falls on mice that might hoard the nuts but then fail to find their buried stores, or are themselves killed before they can retrieve them.

In general, plants involved in this kind of dispersal mechanism make few spikelets, each one carrying only one big nut. So there appears to be a close link between the dispersal mechanism, nut size, the architecture of the spikelets and the inflorescences of the plants.