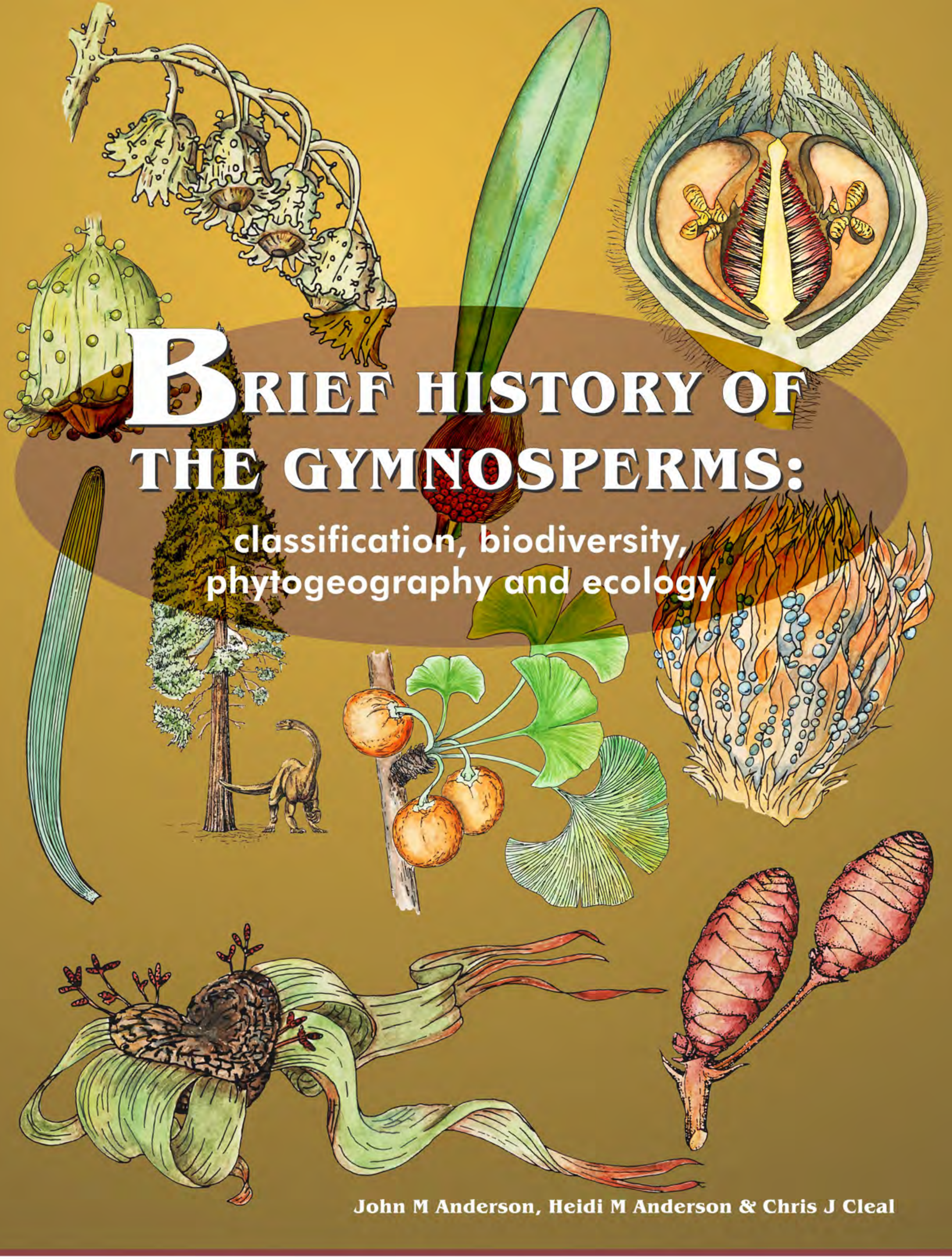

BRIEF HISTORY OF THE GYMNOSPERMS:

classification, biodiversity, phytogeography and ecology

John M Anderson, Heidi M Anderson & Chris J Cleal

STRELITZIA 20

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Brief history of the gymnosperms: classification, biodiversity, phytogeography and ecology

by

John M. Anderson, Heidi M. Anderson & Chris J. Cleal

SOUTH AFRICAN
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SANBI

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2007

STRELITZIA

This series has replaced *Memoirs of the Botanical Survey of South Africa* and *Annals of Kirstenbosch Botanic Gardens* which SANBI inherited from its predecessor organisations.

The plant genus *Strelitzia* occurs naturally in the eastern parts of southern Africa. It comprises three arborescent species, known as wild bananas, and two acaulescent species, known as crane flowers or bird-of-paradise flowers. The logo of the South African National Biodiversity Institute is based on the striking inflorescence of *Strelitzia reginae*, a native of the Eastern Cape and KwaZulu-Natal that has become a garden favourite worldwide. It symbolises the commitment of the Institute to promote the sustainable use, conservation, appreciation and enjoyment of the exceptionally rich biodiversity of South Africa, for the benefit of all people.

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MACROEVOLUTIONARY LIFE CYCLE of the GYMNOSPERMS

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Authors' notes

(1) The manuscript for this volume was essentially completed in 2005, but circumstances have prevailed causing delay of publication until 2007. During this time, a good amount of relevant literature has appeared that could not be incorporated.

(2) For technical reasons, all line drawings in the section *Systematics of the gymnosperms* (pp 92–218) were globally reduced by about 2.75%. Readers should be aware of this in noting the magnifications (or reductions) cited.

CONTENTS TO SYSTEMATICS OF THE GYMNOSPERMS

CLASS
ORDER **GYMNOSPERM CLASSIFICATION**
Family

Diversity

- 10 classes, 37 orders, 84 families
- 21 orders are mono-familial
- a further 6 orders include only 2 families
- *ca* 75% of all orders include < 3 families

FOREWORD

The last few decades have been both inspiring and frustrating with regard to our understanding of living and fossil seed plants and how they are interrelated. On the one hand an extraordinary, and almost overwhelming, amount of new information has accumulated relating to extant seed plants. In particular, a massive amount of effort has been directed to sequencing many different genes in living representatives of the group. But on the other hand a clear understanding of the relationships among these different groups of seed plants continues to remain elusive. In this context, now is perhaps a good moment to pause, take stock, and consider the most appropriate course for future action.

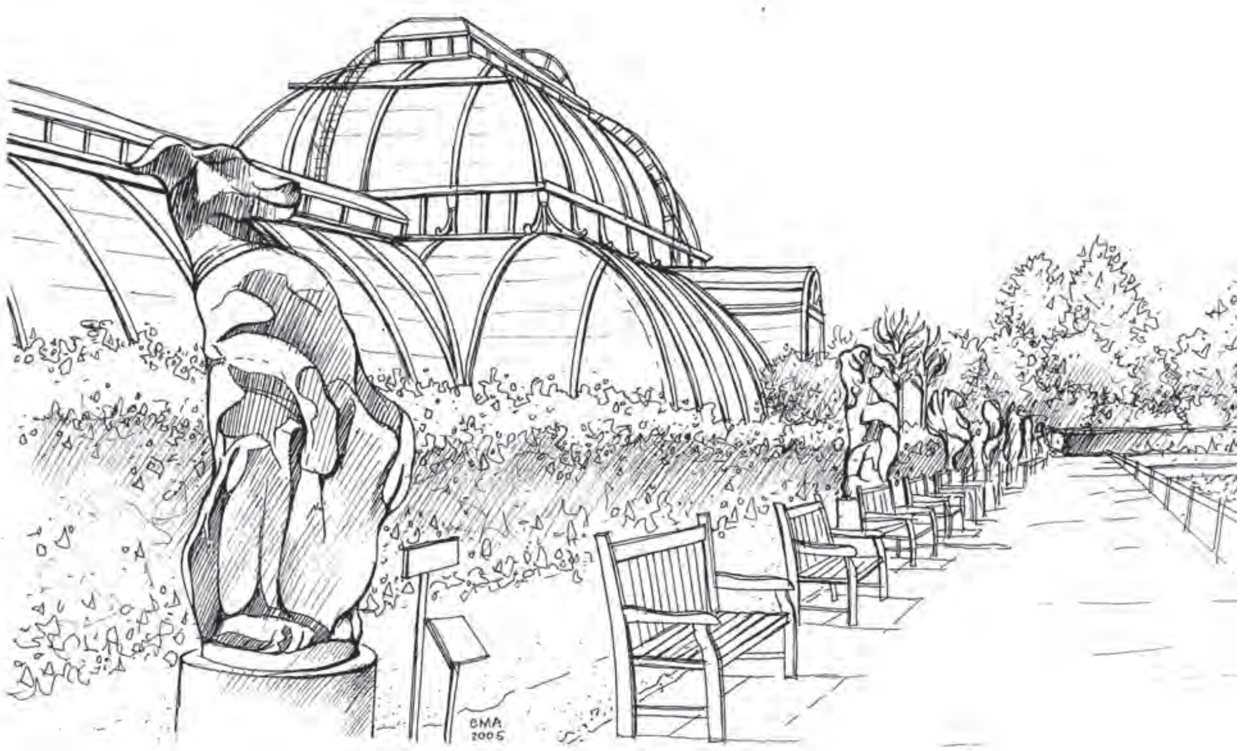
This book contributes to this stocktaking by drawing together much of the scattered literature on the diversity of nonangiosperm seed plants, and integrating this with previous syntheses, using the framework established by Sergei Meyen. And just as Meyen's treatment was a landmark in terms of information on unusual seed plants from Angara, this volume is especially strong on new information from the southern hemisphere. The wonderful results from Permian and Triassic permineralised floras from Antarctica are drawn together, and perhaps most significantly the authors offer an initial view on how the extraordinary diversity of Triassic gymnosperms recognised by John and Heidi Anderson in the Triassic Molteno flora (specifically in their *Heyday of the gymnosperms*) might be accommodated into existing schemes of classification. The aim here is not to develop the last word on the classification of nonangiosperm seed plant diversity, but to provide the synthesis necessary to stimulate further debate and fuel further progress.

No one who reads this book can fail to be impressed by the sheer variety of form—and presumably ecology—among the extinct seed plants of the past. This, in turn, should give us pause to reflect on the extent to which we regard our current very limited sample of living groups, as in any way representative of the total diversity of seed plants that have ever existed. The conclusion is inescapable: cycads, *Ginkgo*, conifers and Gnetales are almost certainly a rather biased, and perhaps misleading sample from which to extrapolate about the patterns and processes of botanical evolution, including the origin of that other key group of seed plants—the angiosperms.

This work is important too for the sweeping synthesis that it provides of changing patterns of plant diversity through time. Understanding these large-scale dynamics of plant evolution is crucial to interpreting how plant evolution links to other ecological and environmental changes through geological time. Interpreting such patterns is fraught with problems but is central to what palaeontologists can contribute to understanding our world. In this book we have a fresh approach and a new foundation on which others can continue to build.

In the coming years the classification of nonangiosperm seed plant diversity, and our understanding of the large-scale evolutionary dynamics of these plants, is certain to continue to change. We will learn more about the fossil plants that we have already recognised, and we will also discover new kinds of plants unlike anything that we have seen before, but in both cases this book will be an essential reference and guide to the bigger picture of seed plant evolution. The specifics of current ideas may not survive but the basic information synthesised here provides a basis for future progress. The authors deserve our thanks for their efforts on our behalf.

Professor Sir Peter Crane FRS
Director
Royal Botanic Gardens, Kew
May 2005



The Royal Botanic Gardens, Kew, London
Sketch by Clara Anderson (6 July 2005) of the Palm House (erected 1844–1848, and thus pre-dating Paxton's Crystal Palace of 1851). The Queen's Beasts—replicas in stone of those designed to stand outside Westminster Abbey at Elizabeth II's coronation in 1953—watch over The Pond to the east.

PREFACES

Through the quirks of our individual histories, the three of us have converged to create this *Brief history.* Heidi and I approach from the perspective primarily of the Triassic floras of Gondwana; and Chris from the Carboniferous coal floras of Laurasia.

As might be expected of all individuals, we each come with our particular idiosyncratic assembly of motives or persuasions. In my case, I come as a strongly left hemisphere-driven scientist who can get deeply engrossed in the finer details of some monospecific, monogeneric, monofamilial order of some otherwise uncertain class of gymnosperm (and feel compelled to append to it some sure measure of its rarity). And I come as an equally passionate right hemisphere devotee of the arts, the general pattern of things, the wonder of things, the sight and sound and kinetics of things. I am pulled always in the two directions: the literal certainty of the solitary cupule, and the broadest holistic sweep. This volume tries to capture both ends of the spectrum.

One might debate quite persuasively the rationale behind including a two-page multi-coloured spindle diagram showing the evolution of the vertebrates in a rather slender volume on the classification and biodiversity of the gymnosperms. To me, though, they are an inseparable part of the whole and this volume would be lacking something from its core without it. And why 10 pages of stratigraphic correlations? Because they have visual appeal, offer a quite unique perspective on our world, and provide a rich scaffolding through which the systematic sinew of the work is woven. Then, on the other hand, there is this formula that defines prominence—the FUDAL rating (6/2/20/-/2=30)—included for Gondwana Triassic families. To me it is no less beautiful than a brightly coloured spindle diagram. It is a diagnostically characteristic minibiography, a passport, of a genus revealing at a glance what we know of the success of the taxon.

This then is a glimpse at my angle on the gymnosperms, the central of the three major groups of vascular plants that have clothed the terrestrial landscape of our world, and that have provided much of the basis for the astonishingly diverse ecosystems that set this world apart. In terms of biodiversity, the gymnosperms seem to have just about run their span. In the landscape of our human history, they remain a prodigious presence.

John M. Anderson
March 2004
Pretoria

In the course of our research on the Triassic Molteno flora we have discovered many exciting ovulate structures new to science. In an effort to relate these to known groups, we have searched the available literature on gymnosperm classification. In this present synthesis we have built on the classification of Sergei Meyen which used the characters of the female ovulate structures. After all our labours it is greatly satisfying to see our classification of the gymnosperms with the inclusion of the new Molteno orders going to press. I feel sure that this will be a most useful reference work for all palaeobotanists and even for botanists seeking a greater understanding of the long geological history of the gymnosperms.

The preparation of this book, like life, has gone through many a twist and turn. In my honours year (1966) at the University of the Witwatersrand, my supervisor, Dr Edna Plumstead, asked me to write an essay on Rudolf Florin's 1963 monograph, *The distribution of conifer and taxad genera in time and space*. The genera were plotted for different eras on world maps. Although Alex du Toit, the eminent South African geologist-palaeontologist, favoured Wegener's theory of 'continental drift' based on the evidence of similar stratigraphic units and fossils across Gondwana continents, in the early 1960s most northern hemisphere geologists still regarded the theory as heresy. Florin, for one, followed the 'land-bridge theory' to explain the world distribution of the conifers. To me, the hypothesis of a Gondwana landmass was a far more plausible theory to explain their distribution, especially for the southern hemisphere genera. In 1970 I attended the Second IUGS Gondwana Congress held in Cape Town and Johannesburg and the new concept of 'sea-floor spreading' was in the fore-front of topics discussed. Dr Plumstead, always a staunch supporter of the ideas of Wegener and Du Toit, could now rejoice that they were at last being recognised and honoured. By that time I had embarked on the collection and study of the Molteno fossil plants. Du Toit (1927) had originally reviewed the Stormberg flora based mainly on collections made during his field work for the stratigraphical study of the Molteno (Beds) Formation—Stormberg Group in the Eastern Cape.

Working together with John Anderson, the study of the Molteno plants has been my lifetime's work. Now in my retirement years I am still trying to close the remaining gaps in our understanding of that flora. Currently I am preparing for the publication of a treatise on the Molteno ferns.

Heidi M. Anderson
August 2004
Pretoria

In my teens, I dreamt of becoming a musician—not a guitar-twanging 'rocker' but a real musician playing real music. As I had no physical talent for playing an instrument or singing, this was perhaps rather unrealistic! However, I was drawn to music (and still am) by the beauty and meaning that exists in pattern. Years later, I became a geologist at Sheffield, under the great teacher Lesley Moore, and then started to study palaeobotany with Bob Wagner. I have sometimes wondered why I followed this route. I had no childhood passion for fossil collecting; nor was I driven by a need to understand the origins of the living world of plants. Looking back now over three decades, I think that it was because I could see patterns in the fossil record—patterns in morphology and patterns in distribution—which revealed the story of a once-living world. These patterns continue to enthral and fascinate me.

Over the years I have met many taxonomists, both palaeontological and biological, and all of the really good ones seem to have the skill of pattern recognition. It equally has to be said that many palaeontologists and biologists (including some very eminent ones) do not. This probably explains the increasing trend towards trying to 'technologise' taxonomy, the most recent flavour of which is computerised cladistics. OK, so you don't have the ability to see pattern in your data, so prepare a data matrix, run it through the 'black box' and out will come the answer. Well, of course it does not work like that; no matter how powerful the analytical tool, you have to understand the patterns in the data before you can understand the results. No matter how much the pattern-blind would wish it, the 'black box' approach can never replace human insight in taxonomy.

This traditional view of taxonomy is always susceptible to the criticism of not being able to replicate analyses, and thus not being 'scientific'. One person's 'feeling' that these genera group together into a family, or those families form an order is thought to be too subjective. However, this is only really true if the criteria for recognising the groups are not clearly defined. If we say exactly what characters cause us to recognise particular taxa, then it surely cannot be regarded as a subjective grouping—or at least it is no more subjective than any other form of taxonomy (cladists, after all, have to choose the characters that they analyse). Such an approach is regarded as self-evident at the ranks of species and genus, but surprisingly not so at higher ranks; orders and higher taxa in particular are rarely defined in any formal sense.

I became aware of this problem some years ago, when I reviewed the distribution of gymnosperm families for the *Fossil Record 2*. I mainly followed the then generally accepted taxonomy, but it worried me that nobody would really say how the higher-ranked taxa were defined. In the present analysis of gymnosperm taxonomy and diversity, we have therefore tackled this problem head-on—we have tried to diagnose the higher taxa. Colleagues may disagree with our proposed definitions, but at least they will know what criteria we are using. Others may wish to propose alternative taxonomic models ('classifications') based on alternative diagnostic criteria, which can then be tested against observed patterns of distributions, and (where available) against molecular DNA evidence. By comparing different classifications, it is hoped that we will move closer to a natural scheme, which will give us a deeper insight into the relationships within this group of plants. It will not come from a 'black box', though, but from human insight into pattern.

The Greeks sought truth in the 'music of the spheres'; maybe we should regard taxonomy as the 'music of the biosphere'. Perhaps J.S. Bach, if he were alive today, would have become a taxonomist!

Chris J. Cleal
May 2004
Cardiff

ABSTRACT

A global synthesis of gymnosperm families, fossil and extant, provides a new and distinctive perspective on the macroevolutionary biodiversity trends within this group through their 375 million-year history. The total diversity recognised here amounts to 84 families in 37 orders and 10 classes, of which 13 families in 4 orders and 4 classes are extant and 71 families in 37 orders and 10 classes are extinct. The 71 extinct families are based on reference whole-plant genera with the focus on ovulate fruit, an approach dictated by the highly varying availability and grade of data on affiliated organs.

The stratigraphic ranges of the 84 gymnosperm families are plotted according to their first and last appearances—at the resolution of the geological stage—in the fossil record. The biodiversity histogram based on these data clearly reveals four broad phases in the history of the gymnosperms: three periods of radiation and extinction from the latest Devonian to latest Cretaceous, followed by an interval of stasis through the Tertiary to present. The 'Secondary Radiation' through the Triassic, following the end-Permian extinction, is clearly the most explosive and leads to the putative diversity heyday of the gymnosperms in the Carnian—with 30 families (23 orders, 10 classes).

A series of 30 full-page colour charts provide the holistic context in which to interpret gymnosperm history. The first group of 10 charts are plotted to matching geological time scales and follow the interdependent histories of the most pertinent physical phenomena (plate tectonics, climate, extinction events) and the major terrestrial biological groups (plants, insects, tetrapods). A second set of 10 charts, again to the same scale, correlates the megaplant-bearing formations globally: it is the floras from these strata that provide the basis for the history outlined here. The third set of 10 charts constitute two pictorial essays, on the phytohistory of the Araucariaceae and on the comparative morphology of the extant gymnosperm families.

In a chapter devoted to the 'macroevolutionary life cycle of the gymnosperms', a systematic coverage of floral kingdoms, biodiversity patterns, insect associations and other fields is traced period by period from the Devonian to Quaternary. Here is included an elaboration of the four major 'phases' (youth, adolescence, maturity, old age) and the lesser 'pulses' punctuating the life cycle.

In a final chapter we touch on gymnosperm biodiversity trends at the microevolutionary (genera and species) level. This is done through documenting the known biodiversity at a selection of some 13 important formations (or localities) scattered globally and through the geological column. Though quite incomplete, the trends witnessed tend to parallel those plotted for macroevolutionary diversity.

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Specifically there are those among our biological and earth-science colleagues, their work by no means restricted to fossil plants, who have joined us by contributing directly to this volume: Tania Dutra, Anamaria Stranz, Thiers Wilberger, Nelsa Cardosa, Claudia Paz and Roberto Iannuzzi (Porto Alegre, Brazil), Oscar Rosler (Mafra, Brazil); Ruben Cuneo (Chubut, Argentina); Thomas Schlüter (Nairobi, Kenya); Johann Neveling (Pretoria, South Africa), Adam Yates and Fernando Abdala (Johannesburg, South Africa); Suresh Bonde (Pune, India), Rakesh Chandra Mehotra (Lucknow, India); Steve Mcloughlin, John Rigby and Mike Pole (Brisbane, Queensland), Keith Holmes (Dorrigo, NSW, Australia); John Isbell (Wisconsin, USA), Greg Retallack (Eugene, Oregon, USA), Sid Ash (Univ. New Mexico, USA), Conrad Labandeira (Smithsonian, Washington, USA); Paul Kenrick (London, England); Han Van Konijnenburg-Van Cittert (Utrecht, Holland); Thomas Stutzel, Marcus Mundry and Iris Mundry (Bochum, Germany), Hans-Jochen Gregor (Augsburg, Germany); David Cantrill (Stockholm, Sweden); Lea Grauvogel-Stamm and Jean-Claude Gall (Strasbourg, France); Valentin Krassilov (Haifa, Israel); Sun Ge (Jilin, China), Zhou Zhiyan (Nanjing, China) and Wang Ziqiang (Tianjin, China). They add a wonderful cosmopolitan flavour to an endeavour embracing all corners of our earth. And they lend a holistic flavour, their interests ranging broadly from insects to plants, from the Devonian to the Present.

Then there are several other colleagues who have provided information of various kinds or who offered critical comment adding breadth and breath to this volume. We wish to thank particularly David Dilcher (Florida, USA), Gar Rothwell (Athens, Ohio, USA), Bill DiMichel (Smithsonian, Washington, USA), Scott Williams and William Parker (Petrified Forest National Park, Arizona, USA); Else Marie Friis (Stockholm, Sweden); Kaj Raunsgaard Pedersen (Univ. of Aarhus, Denmark); Stefan Schmeissner (Kulmbach, near Bayreuth, Germany), Dietrich Mueller-Doblies (Berlin, Germany); Zbynek Simunek (Czech Geological Survey, Prague); Cedric Shute (Natural History Museum, London), Margaret Collinson (Royal Holloway Univ., London) and Barry Thomas (Aberystwyth, Wales).

A book such as this *Brief history* involves considerably more than building the scientific edifice. Over the past two years and more as the science has been assembled, many persons have put in numerous hours, days and months towards the production of the volume. In particular we thank Kopano Dimpe for her major early input into creating the colour graphics and setting the text. Subsequently, the following members of the SANBI Publications Section have moulded and readied the volume for printing: Louisa Liebenberg (overall direction), Daleen Maree (colour graphics, typing, typesetting), Sarie Brink (scanning sketches, typesetting), Emsie du Plessis (copy-editing), Nadine van Wyk (rendering images for cover, colour graphics, typesetting) and Sandra Turck (rendering images for cover, cover design). Natasha Mothapo and Tebogo Mashua, also of SANBI, have made much valued input during the later stages of production.

Warm appreciation goes to Clara Anderson (elder daughter of HMA and JMA), for continuing her tradition of involvement in the production of our fossil volumes. Here she has prepared two captivating pen sketches of historical—and symbolically significant—London buildings, the Palm House (Kew Gardens) and the Natural History Museum.

An essential final touch to any scientific synthesis of this nature is the Foreword. Here we have once again been most fortunate that Prof. Sir Peter Crane FRS, Director of Kew Gardens, London, has jumped to this task. With his intimate research knowledge of the fossil history across the spectrum of seed plants and in his role as Director of one of the world's most famous gardens and botanical research institutes, we can think of no more appropriate person to write this piece.

PERMISSIONS

for pen sketches in the Systematics section

The publishers and/or authors of the following works are gratefully acknowledged for permission to reproduce published pen sketches in this volume. The origin of all relevant sketches is indicated in the text. For full details, see References in this volume.

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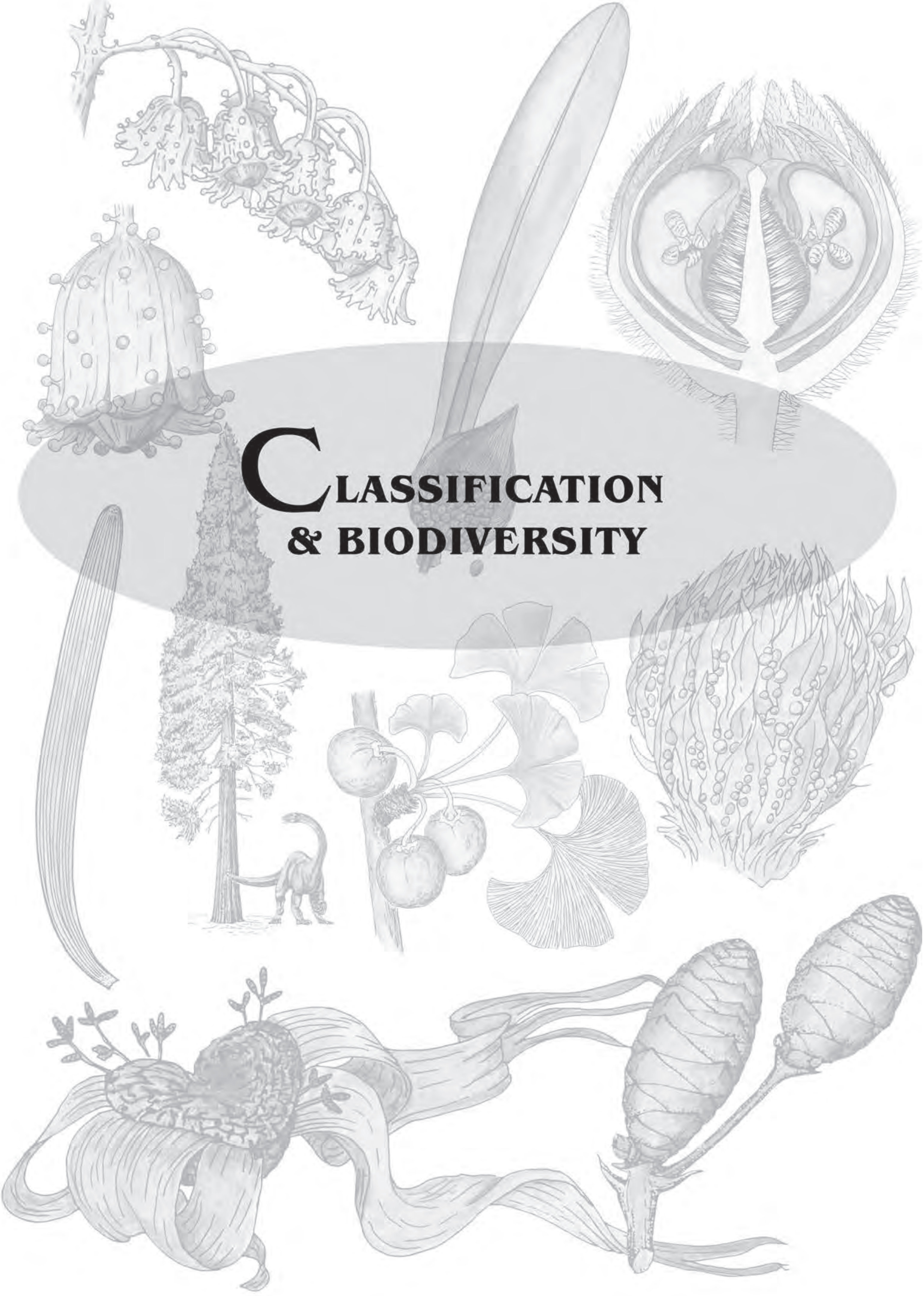
Page (1990): this vol. pp. 134–136, 138, 139, 141–143.
Playford *et al.* (1982): this vol. p. 117.
Raunsgaard-Pedersen *et al.* (1989): this vol. p. 193.
Retallack & Dilcher (1988): this vol. pp. 100, 103.
Rothwell (1988): this vol. p. 113.
Rothwell *et al.* (1989): this vol. p. 99.
Rothwell & Mapes (2001): this vol. p. 123.
Rothwell & Serbet (1994): this vol. p. 201.
Schweitzer (1977): this vol. p. 180.
Serbet & Rothwell (1992): this vol. p. 99.
Stanislavsky (1973): this vol. p. 176.
Stewart & Rothwell (1993): this vol. pp. 98, 99, 101, 102, 104, 111, 115, 124, 125, 142, 148, 197–199.
Taylor (1988): this vol. p. 111.
Taylor *et al.* (1994): this vol. p. 184.
Taylor & Millay (1979): this vol. p. 99.
Taylor & Taylor (1993): this vol. pp. 101, 110, 111, 119, 120, 152, 217.
Townrow (1967): this vol. p. 137.
Van Konijnenburg-Van Cittert (1991): this vol. p. 208.
Verdoorn (1966): this vol. p. 215.
Wang (1999): this vol. p. 105.
Watson (1988): this vol. pp. 118, 119.
Watson & Sincock (1992): this vol. pp. 197, 198.
Weber & Zamudio-Varela (1995): this vol. p. 194.
Yao *et al.* (1997): this vol. p. 140.
Zhou & Zhang (1992): this vol. p. 175.

CLASSIFICATION & BIODIVERSITY



CLASSIFICATION VERSUS PHYLOGENY

Traditional classification and cladistic phylogeny both contribute to our sum of knowledge and understanding of gymnosperm history. Classification bears largely on the diversity of the group, and phylogeny on its evolution. Each has its adherents, yet neither has reached any degree of stability (pp 12–19). Consensus in both disciplines appears some way off.

Why a classification?

Our core concern in this book is biodiversity. In the earlier companion volume, *Heyday of the gymnosperms* (And. & And. 2003), we explored gymnosperm biodiversity from species to class at the apparent Late Triassic gymnosperm heyday as preserved in the Molteno Fm. of the Karoo Basin, South Africa. In the current *Brief history*, our aim is to track gymnosperm diversity globally through the group's 375 my history at higher taxonomic levels: family, order and class. Hence an attempt at a comprehensive traditional hierarchical classification of the gymnosperms, Devonian to present. Cladistic phylogenies, attempting to bring in only the most fully preserved material, cannot achieve this. Only through a consistently defined set of taxa at different ranks, whether genera or classes, can we record biodiversity.

Ovulate structures: The classification is based fundamentally on the ovulate reproductive organs. There are compelling reasons for this: firstly, the deep and pervasive uncertainty of affiliations (p. 94); secondly, the marked imbalance in occurrence of mega- and microsporangiate structures, the latter generally being preserved far less frequently (pp 23, 94); thirdly, at family and higher taxonomic levels, foliage is markedly less diagnostic than reproductive material. Where affiliated foliage or pollen structures have been established, their diagnostic characters lend variable supportive evidence in grouping the ovulate genera. An example is the genus *Fredlindia* (Molteno Fm.), whose foliage affiliate *Halleyoctenis* (pinnae and cuticle features) helps to confirm its early bennettitopsid status (pp 190, 191).

Classification (traditional systematics)

During the quarter century between the first (Harland *et al*. 1967) and second (Benton 1993) editions of *The Fossil Record*, there occurred 'radical changes in gymnosperm taxonomy' (Cleal 1993). The pteridospermopsida (seed ferns) were no longer recognised, for instance, as they were seen to be a polyphyletic 'grade-group'. 'However, trying to find a coherent alternative classification', as Cleal (1993) emphasised, 'is far from easy. In many ways the most useful scheme is that of Meyen (1984, 1987), if only because the taxa are formally named and circumscribed. It has, however, been subjected to severe criticism on a variety of fronts (e.g. Beck 1985; Miller 1985; Rothwell 1985; for a reply, see Meyen 1986), but no alternative formal taxonomy has been proposed.'

In the 1993 edition of *The Fossil Record*, Cleal adopted Meyen's scheme as the core of his own classification, but modified it partly 'to make it compatible' with the cladistic studies of the 1980s.

Cleal's *Fossil Record* classification forms the base for the present work—though it too clearly carries major uncertainties and surely remains far short of a close reflection of the ultimate reality of nature. *The Fossil Record 3*, of another quarter century hence, will undoubtedly reveal further 'radical changes in gymnosperm taxonomy' from those now presented here.

In the half-decade from 1997, a flurry of papers of highly variable scope, perspective and peer acceptance (Melikjan & Bobrov 1997; Zhou Zhiyan 1997; Doweld 1998; Doweld & Reveal 1999, 2001; Bobrov & Melikjan 2000; Rothwell & Mapes 2001; Hernandez-Castillo *et al.* 2001; Doweld 2001) added a considerable number of families, both extinct and extant, to gymnosperm classification. This spell culminated in Doweld (2001) who presented a revised overall classification of the gymnosperms (pp 16, 17), including 10 phyla, 27 classes, 67 orders and 125 families. It is probably fair to reflect that the Doweld classification will meet with criticism similar to the earlier attempts of Meyen (1984, 1987). Indeed, we have found it to include an order of magnitude taxonomic inflation more than we have been working at and have hence largely continued independent of it. The 1997–2001 peak of activity was in effect ongoing in parallel with our preparing the first 1998 draft of this work and the initial phase of expanding it into the present classification.

Our gymnosperm classification, as noted, is firmly founded on that of Cleal (1993). His system is left untouched in certain areas, but is substantially changed or filled out in others, in view, for instance, of the wide range of new Late Triassic Molteno taxa and of the continuing flow of cladistic analyses—including the new input from molecular biology—of the 1990s and early 2000s.

If one's emphasis is strictly cladistic, it is possible to be dismissive of traditional classification as largely subjective. In his criticism of Meyen's (1984, 1987) classification, Rothwell (1985) put it rather strongly, 'In the opinion of this author, such methodology lacks a mechanism for objective hypothesis testing, and the approach invites authoritarian subjectivity.' Avoidance of 'such methodology', though, negates the opportunity for systematic consideration of biodiversity trends through time.

Phylogeny (cladistic analyses)

Cladistics and classification need not be seen as conflicting. Indeed, the construction of phylogenetic trees is complementary to classification (see APG 1998 and APGII 2003 on the angiosperms). They are two necessary disciplines in tracing the history of any group. With comprehensive data, the two would converge as one. Until such hypothetical moment, they stand distinct—phylogeny reflects the history while classification reflects the biodiversity. Elucidation of phylogenetic trees based on the principles of *parsimony* and the recognition of *plesiomorphic* and *apomorphic* characters and taxa (extant and fossil), has made rapid strides over the past two decades. At the root of this is the remarkable parallel development of molecular biology and the cladistic method—molecular characters having proved highly suited for cladistic analysis (e.g. Soltis *et al*. 1992).

Recent attempts at the 'classification' of gymnosperms, whether more traditional (Meyen 1987; Cleal 1993; and later studies) or rigorously cladistic (Crane 1985, 1986, 1988, and later studies) are at considerable variance with one another. Available collections and descriptions of known taxa remain insufficient to yield an unambiguous phylogenetic classification (see pp 18, 19).

Morphological data

Whether portraying the relationships within a group of organisms (in this case the gymnosperms) through hierarchical classification or cladistically generated phylogenetic trees, the basic data set is the same: morphological or molecular.

Extant gymnosperms: Of all the gymnospermous families that have existed, the best known morphologically are, for obvious reasons, the relatively small group of extant taxa—potentially all diagnostic characters for all organs, at all stages of development, are available for study. Even so, a concise, consistent, explicit comparative morphology defining and contrasting the 13 recognised extant families is not yet at hand. The research programme currently under way at the Ruhr-Universität (Bochum, Germany) aims at such a result (see Charts 27–30, pp 62–65) for a four-page colour spread illustrating their work.

Extinct gymnosperms: If we have not yet derived a sufficient synthesis of the comparative morphology of the extant gymnosperm families, how much less is our knowledge of the diagnostic morphology of the extinct families? Of the 71 extinct families recognised and described in this volume, only 44 are putatively known from ovulate, microsporangiate and vegetative remains based on at least some recorded statement of affiliation (Grade 2 or higher, p. 94); of these only 26 are known with all three organs securely affiliated (Grade 4 or higher); and of these there are only 14 with the three organs all known in organic attachment (Tabs 2, 3, pp 6–11).

Cladistic analyses: While the surge of cladistic analyses from the early 1980s (e.g. Hill & Crane 1982; Crane 1985, 1986, 1988; Doyle & Donoghue 1986, 1992, 1993; Doyle *et al*. 1994; Nixon *et al*. 1994; Rothwell & Serbet 1994; Doyle 1996; for more recent works see pp 18, 19, 106, 130–143, 154–159, 172, 210) have certainly firmed up gymnosperm systematics, they equally certainly are no panacea. There remain many alternate and equally plausible phylogenetic trees at all taxonomic levels, genus to class. The cladists are the first to admit this and await the discovery and description of new, well-preserved reproductive fossil material to fill out their analyses (Doyle and Crane pers. comm.).

Sampling: From our collecting history of the Molteno over 35 years, it is amply clear that a significant proportion of reproductive taxa (Tab. 12, p. 23) are both exceedingly infrequent and rare (And. & And. 2003). Projections suggest that a wide array of fruit (representing new genera to new classes) still awaits discovery: the preserved diversity far exceeds the observed diversity. This insight points to the likelihood that intensified collecting globally and throughout the geological column will bring to light genera of ovulate structures (for instance) well in excess of those already known.

Molecular data

Improvement of techniques in DNA isolation and sequencing, and of cloning to amplify selected DNA sequences, has precipitated rapid advances in plant systematics (e.g. Soltis *et al*. 1992; APG 1998; APGII 2003). The earlier research focused particularly on sequencing of chloroplast DNA (cpDNA) and ribosomal RNA (rRNA), but the net continues to widen.

Of interest to us here are the results on the extant gymnosperms: the *ca* 69 genera of conifers, the 11 genera of cycads, the three gnetopsids (*Gnetum, Welwitschia, Ephedra*) and *Ginkgo*. The research of Hamby & Zimmer (1992) incorporating rRNA results on three conifer genera, three cycad genera, the three gnetopsid genera and *Ginkgo*, appears to be the pioneering work in this line. Their results were not unequivocal. The most parsimonious rRNA trees showed the Gnetales—a strongly coherent group—to be the earliest diverging of the extant gymnosperms and the conifers, cycads and *Ginkgo* together to be the sister group of the angiosperms. However, with ‘an insignificant penalty of one step’ in parsimony, a reversed position of the Gnetales and remaining gymnosperms with respect to the angiosperms is found. Within the conifer-cycad-*Ginkgo* clade, the rRNA analyses consistently placed *Ginkgo* as the sister group of the conifers plus cycads.

Paul Kenrick provides a summary in this volume (pp 18, 19) of more recent work. Over 10 years of research since Hamby & Zimmer (1992) has not yet brought clarity to the phylogeny of the extant gymnosperm families.

Combining morphological & molecular data

The total potential data set comprises morphological, cytological, biochemical, ecological and molecular (RNA/DNA) characters, extant and fossil. It is still relatively early days. And whether DNA sequences from plant compression fossils will prove sufficiently and widely enough preserved for the field of molecular palaeobotany to truly emerge remains uncertain.

In their early work combining morphological and molecular (rRNA) data, Doyle *et al*. (1994) set out cladistic experiments to test whether these fields are contradictory or complementary. With regard to the phylogenetic relationships of the extant gymnosperms, they found the Gnetales to be the ‘closest living relatives’ of the angiosperms, but the place of the cycads, conifers and *Ginkgo* was ‘quite unresolved’.

A decade later such discrepancies persist (pp 18, 19).

The Triassic Explosion

We explore the phenomenon of the Triassic Explosion (pp 22–31) at some length since it seemingly generates the climax of the gymnosperm story. Also, however, it offers a focus on the fundamental processes of evolution: does the process vary at the different stages (pp 68–89) in the ‘life cycle’ of a major clade such as the gymnosperms? The evidence would imply this.

Explaining explosive radiation (pp 30, 31): Considering the remarkable effects of explosive radiation and the possible underlying evolutionary processes, it might prove necessary to assess the robustness of cladistics in generating phylogenies for such intervals.

The quest for strict monophyly: In the rapid shift from traditional Linnean classification to the cladistic (phylogenetic) system ‘which invests taxonomy with firm adherence to evolutionary relationships’, there is a ‘quest for strict monophyly of taxa’ (Padian & May 1993). We harbour a suspicion that Hox genes, RNA interference, gene switches and the great array of other recent discoveries in molecular biology may play havoc with this quest, especially during times of explosive evolution such as the Triassic. The fact that an unambiguous solution to gymnosperm phylogeny remains so elusive suggests this to be so.

Equivalence between gymnosperms & angiosperms

Central to the theme of the present work are the concepts of the family, order and class. How morphologically inclusive are the orders, for instance, and what is the morphological distance between them? Some taxonomists will delimit them—as they will other taxa—through seeking *discontinuities* in variation, others through using the criterion of *equivalence* or *comparability* (Stace 1989). How do the orders of extant gymnosperms compare with those of the extant angiosperms: are the Cycadales, Coniferales and Ginkgoales comparable, in scope and morphological distance, to the Poales (grasses), Cyperales and Restionales? No procedure has yet been devised to apply an objective measure to resolving these questions. Perhaps DNA sequencing will provide the tool.

The order, like the family and the class, remains a convenient subjective category that defies definition but has ‘come to have a finite meaning in the minds of most taxonomists’ (Stace 1989).

As in the extant gymnosperms (Tab. 11a, p. 22), the angiosperm orders (or families) range hugely in size: from, say, the Batales with only one family, one genus and two species, to the Sapindales with 16 families and numerous genera and species (Heywood 1993).

THE EXTANT SEED PLANTS

Extant gymnosperms

Global diversity

1998: 4 classes, 6 orders, 14 families, 67 genera, *ca* 800 species.
2005: 4 class, 4 orders, 13 families, 84 genera, 987 species.
For sources see text and Tab. 1a below.

Classification

The extant gymnosperms have been variously classified in recent decades (Tabs 4–10, pp 12–17). At what taxonomic rank should the major groups and subgroups be recognised? Our 1998 tally of taxa above was based largely on Woodland (1991), who quite rightly concluded that the 'final classification of the Pinophyta is yet to be written'. He, in turn, principally followed Cronquist *et al.* (1966), as the most recent, authoritative authors. It is noteworthy that Cronquist (1981, 1988), pre-1998 (see adjacent), was the most widely adopted author on angiosperm systematics and that the classification schemes for the angiosperms and gymnosperms were, therefore, compatible in so far as they were largely derived from the same sources.

As currently perceived, the extant gymnosperms, though considerably less diverse than the angiosperms at species, genus, family and order level are far more diverse at class level. If the extant gymnosperms are but a small relict of their former richness, how rich were they in their heyday and how did this diversity compare with that of the flowering plants today?

The evolutionary record

The gymnosperm zenith (Late Triassic): When was the heyday of the gymnosperms and what was the extent of their biodiversity, at successive ranks, at their peak? This is a central theme of the current monograph. Existing curves (Niklas *et al.* 1983) showing gymnosperm diversity trends at species level reveal massive decline at the close of the Permian, marked radiation to new highs through the Triassic, followed by very slight increase through the Jurassic and steady decline from the mid-Cretaceous. The gymnosperm zenith in these curves—based largely on European and North American sources—shows a gentle rise rather than a marked peak and occurs in the Late Jurassic to Early Cretaceous. Our own research, reflected in this volume and elsewhere (And. & And. 1985, 1995; And. *et al.* 1996), bringing into account Gondwana and particularly Molteno data, suggests a very sharp gymnosperm diversity zenith in the Late Triassic (Fig. 1; Chart 1).

The gymnosperm nadir (earliest Triassic): Where the gymnosperm zenith is recognised here as occurring in the later Triassic, its nadir was reached in the earliest Triassic in the wake of the end-Permian extinction (Chart 1, p. 36).

Extant angiosperms

Global diversity

1998: 2 classes, 83 orders, 383 families, ? gen., 215-000 spp.
2005: 1 class, 45 orders, 457 families, 12-650 gen., 233-885 spp.

The 1998 census figures are from Woodland (1991), based largely on Cronquist (1981, 1988); the 2005 figures as given in Tab. 1b below.

Classification

In our first short draft of this *Brief history* in early 1998 (the year APGI appeared), we wrote:

'A reasonable measure of compatibility exists between authors in recent years in regard to the classification of the flowering plants at family, order and class level. The principal authors represent a wide spread of research institutions: A. Cronquist (New York Botanical Garden, U.S.A.); R. Thorne (Rancho Santa Ana Botanical Garden, U.S.A.); R. Dahlgren (Copenhagen); A. Takhtajan (Botanical Institute of the Academy of Sciences of the U.S.S.R.).'

Then appeared APGI (1998), followed five years later by APGII (2003), reflecting the new and rapidly expanding data from molecular biology. The hard-won consensus reached prior to 1998 was superseded and rendered historical almost overnight. The new insights from DNA and RNA studies have radically changed our knowledge of the phylogeny and classification of the angiosperms.

The evolutionary record

The cone of increasing diversity: In sharp contrast to gymnosperm history, the angiosperm record (Niklas *et al.* 1983; Knoll 1986; Knoll & Niklas 1987) appears to follow the traditional, unbroken pattern of a cone of increasing diversity from their origin to the present day. There appears to have been no break in the curve, even across the Cretaceous-Tertiary boundary.

The angiosperm zenith: The recorded data for the northern hemisphere show a decline in diversity from the mid-Tertiary, reflecting climatic deterioration towards glaciation. It is suggested, however, that subtropical to tropical richness continued to increase through the Tertiary, overshadowing the northern decline (Niklas *et al.* 1983; Knoll 1986; Knoll & Niklas 1987). The angiosperm diversity zenith is generally placed firmly in the present era.

Tab. 1a. Extant gymnosperms

DIVISION **CLASS** **ORDER**	
PINOPHYTA (gymnosperms)	
PINOPSIDA	
PINALES (conifers)	6 families, 69 genera, 623 spp
CYCADOPSIDA	
CYCADALES (cycads)	3 families, 11 genera, 292 spp
GINKGOOPSIDA	
GINKGOALES (ginkgos)	1 family, 1 genus, 1 sp.
GNETOPSIDA	
GNETALES	3 families, 3 genera, 71 spp

***Diversity* (total)**: 4 classes, 4 orders, 13 families, 84 genera, 987 spp.
References: as in this volume (pp 130, 154, 172, 210).

Tab. 1b. Extant angiosperms

DIVISION **CLASS** **ORDER**	
MAGNOLIOPHYTA (angiosperms)	
MAGNOLIOPSIDA (dicotyledons & monocotyledons)	
45 orders	457 families, 12,650 genera, 233,885 spp.

References: Supra-ordinal classification after Woodland 2000 (but Magnoliopsida here taken to include the dicots and monocots, the latter now known—APGI, APGII—to be nested within the former); order & family diversity from APGI (1998) & APGII (2003); genus & species diversity from APGII (after Thorne 1992).

Diversity: 1 class, 45 orders, 457 families, 12,650 genera, 233,885 spp

Tab. 1. The extant seed plants (gymnosperms & angiosperms): comparative classification & diversity

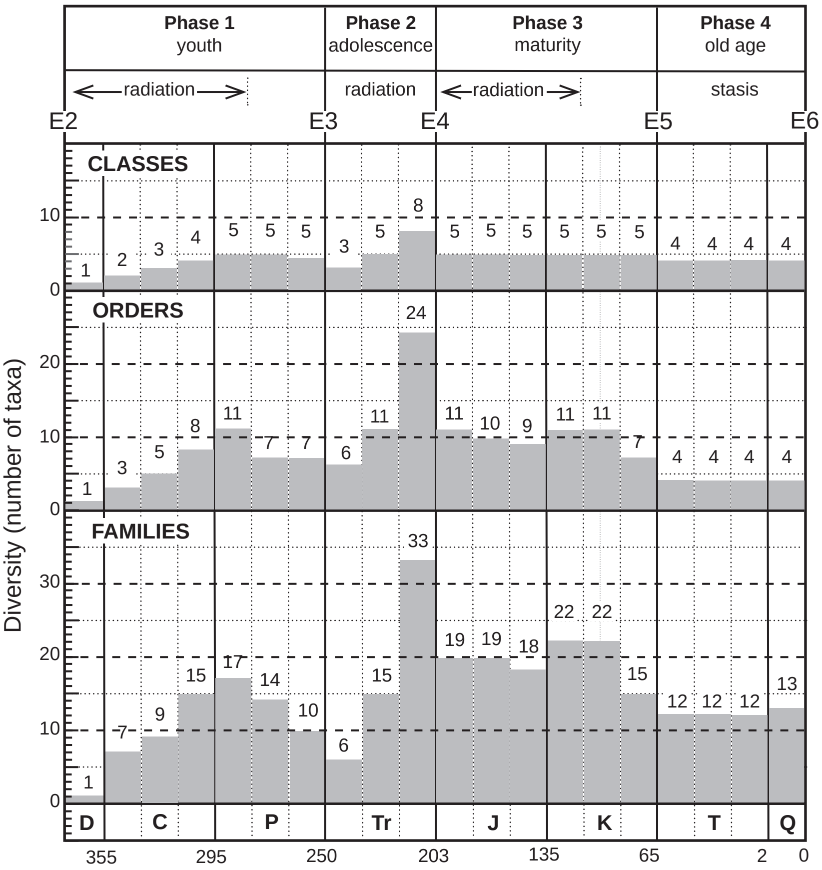


Fig. 1. Macroevolutionary life cycle of the gymnosperms
Showing global biodiversity trends per epoch over the past 375 my (based directly on Charts 3, 4, pp. 38, 39). Four broad phases of evolution, in the wake of four mass global extinctions (E2–E5), are recognized.

Notes on Fig. 1 (& Charts 1–4, pp 36–39)

The range-through method: This method, adopted here for graphing diversity, 'assumes that a family [or other taxon] was present at all time intervals between its first and last appearances ... even if not directly sampled in all intervals' (Labandeira & Sepkoski 1993).

Observed, preserved & existed taxa: The histograms depict the *observed* (published) record only. They reflect only some fraction of the total *preserved* gymnospermous material in the fossil record. And this *preserved* record will be but a fraction of the total taxa that *existed* through time. The measure of divergence—quantity and pattern—between the *observed*, *preserved* and *existed* records remains largely uncertain (see p. 71).

Resolution at level of epoch: There is a discrepancy in the apparent duration of the phases in the gymnosperm cycle depending on whether one plots at the resolution of the geological epoch (as here) or the geologial stage (as on Chart 1). In Fig. 1 the phases coincide with period boundaries, in Chart 1 not always so: the ends of Phase 2 and Phase 3 plotting one stage beyond the Tr/J boundary and one short of the J/K boundary respectively.

EVOLUTIONARY CYCLE OF THE GYMNOSPERMS

(observations based on Fig. 1, Charts 1, 3–6)

Extinction events & evolutionary phases: The broad pattern of gymnosperm evolution is very evidently a manifestation of the four global extinction events punctuating the post-Silurian phase of Phanerozoic history (Fig. 1). The first two extinctions (E2 and E3) promoted major phases of radiation, while the later two (E4 and E5) led to lengthy spells of successively diminished stasis. The first wave of seed plant radiation through the Carboniferous followed the Late Devonian extinction and the Triassic Explosion followed, equally clearly, the end-Permian extinction. The end-Triassic extinction nipped in the bud most of the numerous new starts of the Triassic Explosion, while by the end-Cretaceous event, however, the dominant bennettitopsids and the remnants of the ginkgoopsids had already disappeared through stepwise extinction in competition with the angiosperms.

The random-pruning effect: The effect of the four successive extinction events in the overall evolutionary cycle of the gymnosperms is rather like that of an uncontrolled gardener drastically pruning his bushes at random intervals. The different species will react differently to his treatment according to their seasonal or intrinsic adaptability. Some may respond robustly to the first couple of maulings with a rich spreading crown of new branches, but their vigour will soon be sapped and they will die back, perhaps after a couple of spells of modest reduced display. We might refer to the consequences of randomly timed extinction events in the life of a clade of plants such as the gymnosperms as the *random-pruning effect.*

The Triassic radiation: The *random-pruning effect* of the Late Permian extinction was super-vigorous response of the gymnosperm 'tree' through the Triassic. An explosion of plant life follows the greatest mass extinction known. Three of the four extant gymnosperm classes occurring today—the Pinopsida, Ginkgoopsida and Gnetopsida—underwent major radiation in the later Triassic, as did the Bennettitopsida. The early pinopsids gave rise to the Pinales; the early ginkgoopsids to a diverse array of orders including the Ginkgoales, Umkomasiales and Caytoniales; the ottokariopsids possibly to the bennettitopsids, gnetopsids and axelrodiopsids. A couple of small families, not referable to any of the major classes, also appeared and as quickly disappeared.

The heyday of the gymnosperms: The diversity curve through 375 my of gymnosperm evolution reveals a clear maximum late in the Triassic. A third more families (33) and twice as many orders (24) occur in the Late Triassic as in any other such interval (epoch). The clear diversity peak may partly reflect collecting bias (e.g. in the Molteno), but it seems likely that the picture is broadly real. Collecting has, in support of this, been more intensive in the Carboniferous and Permian, in view of the coal deposits, and the Cretaceous and Tertiary, in view of the angiosperms, over the past two centuries. The Triassic, as far as fossil plants are concerned, has probably been relatively under-collected globally.

The heyday of the gymnosperms evidently occurred in the Late Triassic along with a corresponding explosion of terrestrial animal life. It was during this fecund interval that the dinosaurs, mammals and possibly the flowering plants began their evolutionary paths to dominance.

Tab. 2. Whole-plant families: grading current documentation

CLASS ORDER **Family**	**generic diversity**			**affiliation grade**			**morphology grade**			**anatomy preserved**		
	♀	♂	⬯	♀	♂	⬯	♀	♂	⬯	♀	♂	⬯
LYGINOPTERIDOPSIDA Novák 1961 emend. nov.												
LYGINOPTERIDALES Corsin 1960												
Moresnetiaceae Němejc 1963 emend. nov.	7	-	1	5	-	4	4	-	2	✓	-	-
Genomospermaceae A.G.Long 1975	1	-	1	5	-	4	2	-	3	✓	-	-
Eospermaceae A.G.Long 1975	4	-	-	5	-	-	2	-	-	✓	-	-
Lyginopteridaceae Potonié 1900 emend. nov.	6	1	5	5	3	4	5	5	5	✓	✓	✓
Physostomaceae A.G.Long 1975	1	-	-	5	-	-	2	-	-	✓	-	-
CALAMOPITYALES Němejc 1963												
Calamopityaceae Solms. 1896	3	-	1	5	-	2	3	-	4	✓	-	✓
CALLISTOPHYTALES G.W.Rothwell 1981 emend. nov.												
Callistophytaceae Stidd & J.W.Hall 1970	1	1	1	5	4	4	4	4	4	✓	✓	✓
Emplectopteridaceae R.H.Wagner 1967	1	1	2	5	2	2	2	1	3	-	-	-
PINOPSIDA Burnett 1835												
CORDAITANTHALES S.V.Meyen 1984												
Cordaitanthaceae S.V.Meyen 1984	5	2	1	5	5	5	5	5	5	✓	✓	✓
Rufloriaceae Ledran 1966 emend. S.V.Meyen 1982a	4	2	1	5	3	3	4	4	4	-	-	-
Vojnovskyaceae M.F.Neuberg ex Y.A.Orlov 1963	1	1	1	5	2	3	4	3	4	-	-	-
DICRANOPHYLLALES S.V.Meyen 1984 emend. nov.												
Dicranophyllaceae S.Archang. & Cúneo 1990 emend. nov.	1	1	1	5	5	5	3	3	3	-	-	-
Trichopityaceae S.V.Meyen emend. nov.	1	-	1	5	-	5	2	-	2	-	-	-
FERUGLIOCLADALES Doweld 2001												
Feruglioсladaceae S.Archang. & Cúneo 1987	2	1	3	5	5	5	4	4	4	-	-	-
DORDRECHTITALES And. & And. 2003												
Dordrechtitaceae And. & And. 2003	1	-	-	5	-	-	3	-	-	-	-	-
CHEIROLEPIDIALES And. & And. order nov.												
Cheirolepidiaceae Takht. 1963	1	1	6	5	4	4	3	4	4	-	-	-
PALISSYALES Doweld 2001												
Palissyaceae Florin 1958	3	1	1	5	2	2	3	4	3	-	-	-
VOLTZIALES Andr. 1954												
Thucydiaceae Hern.-Cast., G.W.Rothwell & G.Mapes 2001	1	1	1	5	5	5	3	3	5	-	-	-
Bartheliaceae G.W.Rothwell & G.Mapes 2001	1	1	1	5	5	5	3	3	5	-	-	-
Emporiaceae G.Mapes & G.W.Rothwell 2003	1	1	1	5	5	5	3	3	5	✓	-	-
Utrechtiaceae G.W.Rothwell & G.Mapes 2003	4	4	4	5	5	5	3	1	5	-	-	-
Majonicaceae Clem.-West. 1987	2	1	2	5	5	5	3	2	5	-	-	-
Ullmanniaceae Němejc 1959	1	1	1	5	5	5	2	3	4	-	-	-
Voltziaceae C.A.Arnold 1947	13	6	?	5	5	5	4	4	5	-	-	-
PINALES Dumort. 1829												
Pinaceae Lindl. 1836 extant	**11**	**11**	**11**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**
Podocarpaceae Endl. 1847 extant	**19**	**19**	**19**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**
Araucariaceae Henkel & W.Hochst. 1865 extant	**3**	**3**	**3**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**
Cupressaceae Rich. ex Bartl. 1830 extant	**29**	**29**	**29**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**
Sciadopityaceae Luerss. 1877 extant	**1**	**1**	**1**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**
Taxaceae Gray 1821 extant	**6**	**6**	**6**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**
CYCADOPSIDA Brongn. 1843 emend. nov.												
MEDULLOSALES Corsin 1960												
Potonieaceae T.Halle 1933	1	1	2	5	3	3	3	4	5	✓	✓	✓
Alethopteridaceae Corsin 1960 emend. nov.	2	11	15	5	4	4	3	4	5	✓	✓	✓
Stephanospermaceae Doweld 2001 emend. nov.	1	-	-	5	-	-	3	-	-	✓	-	-
Codonospermaceae Doweld 2001 emend. nov.	1	-	-	5	-	-	2	-	-	✓	-	-
Polylophospermaceae Doweld 2001 emend. nov.	1	-	-	5	-	-	2	-	-	✓	-	-
PHASMATOCYCADALES Doweld 2001												
Phasmatocycadaceae Doweld 2001	5	-	1	5	-	3	2	-	3	-	-	-
GIGANTOPTERIDALES Li & Yao 1983												
Gigantopteridaceae Koidz. 1936	1	1	1	5	5	5	2	3	2	-	-	✓
CYCADALES Dumort. 1829												
Cycadaceae Pers. 1807 extant	**1**	**1**	**1**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**
Stangeriaceae (Pilg.) L.A.S.Johnson 1959 extant	**2**	**2**	**2**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**
Zamiaceae Horan. 1834 extant	**8**	**8**	**8**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**
OTTOKARIOPSIDA And. & And. class nov.												
OTTOKARIALES And. & And. 1985												
Ottokariaceae And. & And. 1985	8	1	3	5	2	5	3	-	3	-	-	-
Rigbyaceae And. & And. 1985	1	1	1	5	4	4	3	2	3	-	-	-
Arberiaceae And. & And. 1985	1	-	1	5	-	3/4	2	-	3	-	-	-
Lidgettoniaceae And. & And. 1985	2	1	1	5	4	4	3	3	3	-	-	-
GINKGOOPSIDA Engl. 1897												
PELTASPERMALES T.N.Taylor 1981												
Peltaspermaceae Thomas 1933	9	4	6	5	3	4	3	3	4	-	-	-
Cardiolepidaceae S.V.Meyen 1977	1	1	2	5	3	3	2	2	3	-	-	-
MATATIELLALES And. & And. 2003												
Matatiellaceae And. & And. 2003	1	-	1	5	-	2	3	-	2	-	-	-
GINKGOALES Goroschankin 1904												
Karkeniaceae Krassilov 1972	1	-	3	5	-	3	3	-	3	-	-	-
Yimaiaceae Z.Zhou 1997	1	-	2	5	-	4	3	-	3	-	-	-
Umaltolepidiaceae Stanisl. 1973 emend. Z.Zhou 1997	2	-	2	5	-	5	3	-	3	-	-	-
Schmeissneriaceae Z.Zhou 1997	1	1	1	5	5	5	3	3	3	-	-	-

CLASS ORDER **Family**		generic diversity			affiliation grade			morphology grade			anatomy preserved		
		♀	♂	⬯	♀	♂	⬯	♀	♂	⬯	♀	♂	⬯
Ginkgoaceae Engl. 1897	extant	**1**	**1**	**1**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**
Avatiaceae And. & And. 2003		1	1	1	5	3	2	3	3	3	-	-	-
LEPTOSTROBALES S.V.Meyen 1987													
Leptostrobaceae S.V.Meyen 1978		3	2	8	5	4	4	3	3	3	-	-	-
HAMSHAWVIALES And. & And. 2003													
Hamshawviaceae And. & And. 2003		1	1	1	5	5	4/5	3	3	3	-	-	-
UMKOMASIALES Doweld 2001													
Umkomasiaceae Petriella 1981		2	1	1	5	4	4	4	4	4	✓	✓	✓
CAYTONIALES Gothan 1932													
Caytoniaceae Kräusel 1926		1	1	1	5	4	4	4	4	4	✓	✓	✓
PETRIELLALES T.N.Taylor *et al.* 1994													
Petriellaceae T.N.Taylor *et al.* 1994		1	-	-	5	-	-	3	-	-	✓	-	-
Kannaskoppiaceae And. & And. 2003		1	1	2	5	5	5	3	3	3	-	-	-
INCERTAE SEDIS (2 classes)													
ALEXIALES And. & And. 2003													
Alexiaceae And. & And. 2003		1	-	-	5	-	-	2	-	-	-	-	-
HLATIMBIALES And. & And. 2003													
Hlatimbiaceae And. & And. 2003		1	-	-	5	-	2	3	-	3	-	-	-
BENNETTITOPSIDA Engl. 1897													
FREDLINDIALES And. & And. 2003													
Fredlindiaceae And. & And. 2003		1	1	1	5	3	3	3	2	4	-	-	-
BENNETTITALES Engl. 1892													
Westerheimiaceae Němejc 1968		1	1	1	5	3	3	3	3	1	-	-	-
Varderkloeftiaceae And. & And. fam. nov.		1	1	1	5	3	3	4	2	3	-	-	-
Laurozamitaceae And. & And. fam. nov.		1	-	1	5	-	3	2	-	4	-	-	-
Sturianthaceae Doweld 2001		1	-	-	5	-	-	3	-	-	-	-	-
Bennetticarpaceae And. & And. fam. nov.		1	1	1	5	3	3	3	2	2	-	-	-
Williamsoniellaceae Nakai 1943		2	2	2	5	5	4	4	4	4	-	-	-
Williamsoniaceae (Carruth. 1870) Nath. 1913		1	1	1	5	3	3	4	4	4	-	-	-
Cycadeoidaceae R.Br. ex G.R.Wieland 1908		2	2	1	5	5	5	4	4	4	✓	✓	✓
PENTOXYLALES Pilg. & Melch. 1954													
Lindthecaceae And. & And. 2003		1	-	1	5	-	3	3	-	3	-	-	-
Pentoxylaceae Pilg. & Melch. 1954		1	1	1	5	3	4	4	4	4	✓	✓	-
GNETOPSIDA Eichler ex Kirpotenko 1884													
FRAXINOPSIALES And. & And. 2003													
Fraxinopsiaceae And. & And. 2003		1	-	2	5	-	4	3	-	4	-	-	-
NATALIGMALES And. & And. 2003													
Nataligmaceae And. & And. 2003		1	-	1	5	-	2	3	-	4	-	-	-
DINOPHYTONALES Krassilov & Ash order nov.													
Dinophytonaceae Krassilov & Ash fam. nov.		1	1	1	5	4	4	3	3	4	-	-	-
DECHELLYIALES Ash order nov.													
Dechellyiaceae Ash fam. nov.		1	1	1	5	3	5	4	2	4	-	-	-
BERNETTIALES Konijn.-Citt. order nov.													
Bernettiaceae Konijn.-Citt. fam. nov.		1	1	1	5	3	3	2	3	3	-	-	-
EOANTHALES Krassilov, And. & And. order nov.													
Eoanthaceae Krassilov, And. & And. fam. nov.		1	-	1	5	-	4	3	-	?	-	-	-
GNETALES Luerss. 1879													
Drewriaceae And. & And. fam. nov.		1	-	1	5	-	5	4	-	4	-	-	-
Ephedraceae Dumort. 1829	extant	**1**	**1**	**1**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**
Gnetaceae Lindl. 1834	extant	**1**	**1**	**1**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**
Welwitschiaceae Markgr. 1926	extant	**1**	**1**	**1**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**
AXELRODIOPSIDA And. & And. class nov.													
AXELRODIALES And. & And. order nov.													
Axelrodiaceae And. & And. fam. nov.		1	1	1	5	5	5	3	3	4	-	-	-
Zamiostrobaceae And. & And. fam. nov.		2	-	-	5	-	-	3	-	-	-	-	-

Global gymnosperm classification: generic diversity; affiliation, morphology, anatomy grades

Total diversity: 84 families, 37 orders, 10 classes; 225 ovulate genera
Extant diversity: 13 families in 4 orders and 4 classes; 84 ovulate genera
Extinct diversity: 71 families in 37 orders and 10 classes; 141 ovulate genera

Affiliations (extinct families)

with all 3 organs attached (grade 5)	14 (of 71) families
with all 3 organs at grade 4 or higher	26 (of 71) families
with all 3 organs at grade 3 or higher	39 (of 71) families
with all 3 organs at grade 2 or higher	44 (of 71) families

Whole-plant families & genera: see Tab. 21, p. 95

Generic diversity
49 of 71 extinct families are monogeneric (ovulate)
10 of 71 ” ” have >3 genera (ovulate)

Affiliation grade (1–5): see p. 73
For extinct taxa, the affiliation (& morphology) grades pertain as a rule (with rare exceptions, e.g. Voltziaceae) to the ‘reference whole-plant genus’ for the family.

Morphology grade (1–5):
1. v. poor: sub-par, insufficient for inclusion in classification
2. poor: only the cone or sporophylls or seeds/pollen moderately known; or the whole assembly available, though still poorly known; leaves—fragments only
3. intermediate: neither poor, nor good; some characters well-preserved and known, others poorly preserved or poorly known; leaves—fragments only, may have cuticle
4. good: cone, sporophylls and seeds/pollen well preserved and well understood (attachment a bonus); leaves—complete and clear as reconstructed, with good cuticle
5. v. good: maximum potential, as for extant taxa; or approaching close to this in fossils; leaves—complete, attached, with cuticle

Anatomy (known or unknown)
Includes coal balls, petrified peat etc.;
no grading attempted

Authors of plant names: see notes on p. 12

Tab. 3. REFERENCE WHOLE-PLANT GENERA

(For explanatory text and usage see p. 12; Tab. 21, p. 95)

	organ	affiliation	Reference stratum			
LYGINOPTERIDOPSIDA Novák 1961 emend. nov.						
LYGINOPTERIDALES Corsin 1960						
MORESNETIACEAE Němejc 1963 emend. nov.						
Elkinsia G.W.Rothwell *et al*. 1989	♀	5	Hampshire Fm.	USA	W. Virginia	D(FAM)
” ” ” ”	⬯	4	”	”	”	”
- - - -	♂	-	-	-	-	-
GENOMOSPERMACEAE A.G.Long 1975						
Genomosperma A.G.Long 1959	♀	5	Inverclyde Gp.	Scotland	Berwickshire	C(TOU)
Lyginorachis A.G.Long 1964b	⬯	4	-	-	-	-
unknown.	♂	-	-	-	-	-
EOSPERMACEAE A.G.Long 1975						
Eosperma Barnard 1959	♀	5	Inverclyde Gp.	Scotland	Berwickshire	C(TOU)
unknown.	⬯	-	-	-	-	-
unknown.	♂	-	-	-	-	-
LYGINOPTERIDACEAE Potonié 1900 emend. nov.						
Lagenostoma Will. 1877	♀	5	Productive Coal Fm.	England	Lankashire	C(BSK)
Lyginopteris Potonié 1897	⬯	4	”	”	”	”
Telangium Benson 1904.	♂	3	”	”	- ”	”
PHYSOSTOMACEAE A.G.Long 1975						
Physostoma Will. 1876	♀	5	Productive Coal Fm.	England	Lankashire	C(BSK)
unknown.	⬯	-	-	-	-	-
unknown.	♂	-	-	-	-	-
CALAMOPITYALES Němejc 1963						
CALAMOPITYACEAE Solms. 1896						
Lyrasperma A.G.Long 1960b	♀	5	Inverclyde Gp.	Scotland	Berwickshire	C(TOU)
Sphenopteridium Schimper 1874.	⬯	2	”	”	”	”
unknown.	♂	-	-	-	-	-
CALLISTOPHYTALES G.W.Rothwell 1981 emend. nov.						
CALLISTOPHYTACEAE Stidd & J.W.Hall 1970						
Callospermarion Eggert & Delevoryas 1960	♀	5	Upper Pennsylvanian	USA	Illinois	C(KAS)
Dicksonites Sterzel 1881	⬯	4	”	”	”	”
Idanothekion Millay & Eggert 1970	♂	4	”	”	”	”
EMPLECTOPTERIDACEAE R.H.Wagner 1967						
Cornucarpus Arber 1914.	♀	5	Tianlongsi Fm.	China	Shanxi	P(WUC)
Gigantonoclea Koidz. 1936.	⬯	2	”	”	”	”
Jiaochengia Wang 1999.	♂	2	”	”	”	”
PINOPSIDA Burnett 1835						
CORDAITANTHALES S.V.Meyen 1984						
CORDAITANTHACEAE S.V.Meyen 1984						
Rothwelliconus Ignatiev & S.V.Meyen 1989.	♀	5	Duquesne Coal	USA	Ohio	C(KAS)
Cordaites Unger 1850	⬯	5	”	- ”	”	”
Florinanthus Ignatiev & S.V.Meyen 1989	♂	5	”	- ”	”	”
RUFLORIACEAE Ledran 1966 emend. S.V.Meyen 1982a						
Suchoviella Ignatiev & S.V.Meyen 1989.	♀	5	Ust’pereborskaya ‘Suite’	Russia	Pechora	P(CAP)
Rufloria S.V.Meyen 1963	⬯	3	”	”	”	”
Pechorostrobus S.V.Meyen 1982b.	♂	3	”	”	”	”
VOJNOVSKYACEAE M.F.Neuberg ex Y.A.Orlov 1963						
Vojnovskya M.F.Neuberg 1955	♀	5	Intinskaya ‘Suite’	Russia	Pechora	P(CAP)
Cordaites Unger 1850	⬯	3	”	”	”	”
Kuznetskia Gorelova & S.V.Meyen in S.V.Meyen 1982.	♂	2	”	”	”	”
DICRANOPHYLLALES S.V.Meyen 1984 emend. nov.						
DICRANOPHYLLACEAE S.Archang. & Cúneo 1990 emend. nov.						
Dicranophyllum Grand’Eury 1877	♀	5	Donnersberg Fm.	Germany	Saar-Nahe Basin	P(SAK)
” ” ”	⬯	5	”	”	”	”
” ” ”	♂	5	”	”	”	”
TRICHOPITYACEAE S.V.Meyen 1987 emend. nov.						
Trichopitys Saporta 1875.	♀	5	Lydiennes Fm.	France	Hèrault	P(ASS)
” ” ”	⬯	5	”	”	”	”
unknown.	♂	-	-	-	-	-
FERUGLIOCLADALES Doweld 2001						
FERUGLIOCLADACEAE S.Archang. & Cúneo 1987						
Ferugliocladus S.Archang. & Cúneo 1987.	♀	5	Arroya Totoral Fm.	Argentina	La Rioja Province	P(ASS)
” ” ” ”	⬯	5	”	”	”	”
” ” ” ”	♂	5	”	”	”	”
DORDRECHTITALES And. & And. 2003						
DORDRECHTITACEAE And. & And. 2003						
Dordrechtites H.M.Anderson 1978	♀	5	Molteno Fm.	S.Africa	Karoo Basin	Tr(CRN)
unknown.	⬯	-	-	-	-	-
unknown.	♂	-	-	-	-	-
CHEIROLEPIDIALES And. & And. order nov.						
CHEIROLEPIDIACEAE Takht. 1963						
Hiermeriella Hörhammer 1933	♀	5	L–U. Deltaic	England	Yorkshire	J(BAJ–BTH)
Pagiophyllum Heer 1881.	⬯	4	”	”	”	”
Classostrobus Alvin, Spicer & Watson 1978	♂	4	”	”	”	”
PALISSYALES Doweld 2001						
PALISSYACEAE Florin 1958						
Stachyotaxus Nath. 1886	♀	5	Höganäs Fm.	Sweden	Scania	Tr(RHT)
” ” ”.	⬯	2	”	”	”	”
” ” ”.	♂	2	”	”	”	”
VOLTZIALES Andr. 1954						
THUCYIDIACEAE Hern.-Cast., G.W.Rothwell & G.Mapes 2001						
Thucydia Hern.-Cast., G.W.Rothwell & G.Mapes 2001	♀	5	Conemaugh Gp.	USA	Ohio	C(KAS)
” ” ” ”	⬯	5	”	”	”	”
” ” ” ”	♂	5	”	”	”	”
BARTHELIACEAE G.W.Rothwell & G.Mapes 2001						
Barthelia G.W.Rothwell & G.Mapes 2001	♀	5	Topeka Limestone Fm.	USA	SE Kansas	C(GZE)
” ” ”	⬯	5	”	”	”	”
” ” ”	♂	5	”	”	”	”

EMPORIACEAE G.Mapes & G.W.Rothwell 2003						
Emporia G.Mapes & G.W.Rothwell 1991	♀	5	Topeka Limestone Fm.	USA	SE Kansas	C(GZE)
” ” ”	⬯	5	”	”	”	”
” ” ”	♂	5	”	”	”	”
UTRECHTIACEAE G.W.Rothwell & G.Mapes 2003						
Otovicia Kerp, Poort, Swinkels & Verwer 1990	♀	5	Rotliegend	Germany	Saar-Nahe Basin	P(ASS)
” ” ”	⬯	5	”	”	”	”
” ” ”	♂	5	”	”	”	”
MAJONICACEAE Clem.-West. 1987						
Majonica Clem.-West. 1987	♀	5	Val Gardena Fm.	Italy	Southern Alps	P(UFI)
” ” ”	⬯	5	”	”	”	”
” ” ”	♂	5	”	”	”	”
ULLMANNIACEAE Němejc 1959						
Ullmannia Göppert 1850	♀	5	Kupferschiefer	Germany	Lower Rhine	P(UFI)
” ” ”	⬯	5	”	”	”	”
” ” ”	♂	5	”	”	”	”
VOLTZIACEAE C.A.Arnold 1947						
Telemachus H.M.Anderson 1978	♀	5	Molteno Fm.	S. Africa	Karoo Basin	Tr(CRN)
Heidiphyllum Retallack 1981	⬯	4	”	”	”	”
Odyssianthus And. & And. 2003	♂	4	”	”	”	”
PINALES Dumort. 1829						
PINACEAE Lindl. 1836						
Pinus L. 1753			**Extant**			
PODOCARPACEAE Endl. 1847						
Podocarpus L.’Hér. ex Pers. 1807			**Extant**			
ARAUCARIACEAE Henkel & W.Hochst. 1865						
Araucaria Juss. 1789			**Extant**			
CUPRESSACEAE Rich. ex Bartl. 1830						
Cupressus L. 1753			**Extant**			
SCIADOPITYACEAE Luerss. 1877						
Sciadopitys Siebold & Zucc. 1842			**Extant**			
TAXACEAE Gray 1821						
Taxus L. 1753			**Extant**			
CYCADOPSIDA Brongn. 1843 emend. nov.						
MEDULLOSALES Corsin 1960						
POTONIEACEAE T.Halle 1933 emend. nov.						
Hexagonocarpus Renault & Zeiller 1890	♀	5	U. Tseishui Fm.	S. China	Guangzhou	C(VIS)
Paripteris Gothan 1941	⬯	3	”	”	”	”
Potoniea Zeiller 1899	♂	3	”	”	”	”
ALETHOPTERIDACEAE Corsin 1960 emend. nov.						
Pachytesta Brongn. 1874	♀	5	Mattoon Fm.	USA	Illinois	C(KAS)
Alethopteris Sternberg 1825	⬯	4	”	”	”	”
Bernaultia G.W.Rothwell & Eggert 1986	♂	4	”	”	”	”
STEPHANOSPERMACEAE Doweld 2001 emend. nov.						
Stephanospermum Brongn. 1874	♀	5	Carbondale Fm.	USA	Illinois	C(MOS)
- -	⬯	-	-	-	-	-
- -	♂	-	-	-	-	-
CODONOSPERMACEAE Doweld 2001 emend. nov.						
Codonospermum Brongn. 1874	♀	5	Grand’Croix	France	Loire Valley	C(KAS)
- -	⬯	-	-	-	-	-
- -	♂	-	-	-	-	-
POLYLOPHOSPERMACEAE Doweld 2001 emend. nov.						
Polylophospermum Brongn. 1874	♀	5	Grand’Croix	France	Loire Valley	C(KAS)
- -	⬯	-	-	-	-	-
- -	♂	-	-	-	-	-
PHASMATOCYCADALES Doweld 2001						
PHASMATOCYCADACEAE Doweld 2001						
Phasmatocycas Mamay 1973	♀	5	Wellington Fm.	USA	Kansas	P(ART)
Taeniopteris Brongn. 1828	⬯	3	”	”	”	”
- -	♂	-	-	-	-	-
GIGANTOPTERIDALES Li & Yao 1983						
GIGANTOPTERIDACEAE Koidz. 1936						
Gigantonomia Li & Yao 1983	♀	5	L. Makou Fm.	S. China	Fujian	P(KUN)
Gigantopteris Schenk 1883	⬯	5	”	”	”	”
Gigantotheca Li & Yao 1983	♂	5	”	”	”	”
CYCADALES Dumort. 1829						
CYCADACEAE Pers. 1807						
Cycas L. 1753			**Extant**			
ZAMIACEAE Horan. 1834						
Zamia L. 1763			**Extant**			
STANGERIACEAE (Pilg.) L.A.S.Johnson 1959						
Stangeria T.Moore 1853			**Extant**			
OTTOKARIOPSIDA And, & And. class nov.						
OTTOKARIALES And. & And. 1985						
OTTOKARIACEAE And. & And. 1985						
Hirsutum Plumstead 1958	♀	5	Middle Ecca	S. Africa	Karoo Basin	P(ART)
Glossopteris Brongn. 1828	⬯	5	”	”	”	”
unknown	♂	-	-	-	-	-
RIGBYACEAE And. & And. 1985						
Rigbya Lacey *et al*. 1975	♀	5	Estcourt Fm.	S. Africa	Karoo Basin	P(WUC)
Belemnopteris Feistm. 1876	⬯	4	”	”	”	”
unnamed	♂	4	”	”	”	”
ARBERIACEAE And. & And. 1985						
Arberia White 1908	♀	5	Middle Ecca	S. Africa	Karoo Basin	P(ART)
Glossopteris Brongn. 1828	⬯	3/4	”	”	”	”
unknown	♂	-	-	-	-	-
LIDGETTONIACEAE And. & And. 1985						
Lidgettonia H.H.Thomas 1958	♀	5	Estcourt Fm.	S. Africa	Karoo Basin	P(WUC)
Glossopteris Brongn. 1828	⬯	4	”	”	”	”
Eretmonia Du Toit 1932	♂	4	”	”	”	”

GINKGOOPSIDA Engl. 1897						
PELTASPERMALES T.N.Taylor 1981						
PELTASPERMACEAE Thomas 1933						
Peltaspermum T.M.Harris 1937	♀	5	Molteno Fm.	S. Africa	Karoo Basin	Tr(CRN)
Lepidopteris Schimp. 1869	⬯	4	”	”	”	”
Antevsia T.M.Harris 1937	♂	3	”	”	”	”
CARDIOLEPIDACEAE S.V.Meyen 1977						
Cardiolepis M.F.Neuburg 1965	♀	5	Scidinsk ‘Suite’	USSR	Pechora Basin	P(WOR)
Phylladoderma Zalessky 1913	⬯	3	”	”	”	”
Permotheca Zalessky 1929	♂	3	”	”	”	”
MATATIELLALES And. & And. 2003						
MATATIELLACEAE And. & And. 2003						
Matatiella And. & And. 2003	♀	5	Molteno Fm.	S. Africa	Karoo Basin	Tr(CRN)
Kurtziana Freng. 1942	⬯	2	”	”	”	”
unknown	♂	-	-	-	-	-
GINKGOALES Goroschankin 1904						
KARKENIACEAE Krassilov 1972						
Karkenia S.Archang. 1965	♀	5	Tico Flora	Argentina	Santa Cruz	K(APT)
Ginkgoites Seward 1919	⬯	3	”	”	”	”
unknown	♂	-	-	-	-	-
YIMAIACEAE Z.Zhou 1997						
Yimaia Z.Zhou & Zhang 1988	♀	5	Yima Fm.	China	Henan Province	J(AAL)
Baiera Braun 1843	⬯	4	”	”	”	”
unknown	♂	-	-	-	-	-
UMALTOLEPIDIACEAE Stanisl. 1973 emend. Z.Zhou 1997						
Toretzia Stanisl. (1971) 1973	♀	5	Novoraisk Fm.	Ukraine	Donetz Basin	Tr(RHT)
” ” ”	⬯	5	”	”	”	”
unknown	♂	-	-	-	-	-
SCHMEISSNERIACEAE Z.Zhou 1997						
Schmeissneria Kirchner & Konijn.-Citt. 1994	♀	5	Lias α	Germany	Bavaria	J(HET)
” ”	⬯	5	”	”	”	”
Stachyopitys Schenk 1867	♂	5	”	”	”	”
GINKGOACEAE Engl. 1897						
Ginkgo L. 1771			**Extant**			
AVATIACEAE And. & And. 2003						
Avatia And. & And. 2003	♀	5	Molteno Fm.	S. Africa	Karoo Basin	Tr(CRN)
Ginkgoites Seward 1919	⬯	2	”	”	”	”
Eosteria And. & And. 2003	♂	3	”	”	”	”
LEPTOSTROBALES S.V.Meyen 1987						
LEPTOSTROBACEAE S.V.Meyen 1978						
Leptostrobus Heer 1876	♀	5	Ravenscar Gp.	England	Yorkshire	J(BAJ–BTH)
Czekanowskia Heer 1876	⬯	4	”	”	”	”
Ixostrobus Raciborski 1891	♂	4	”	”	”	”
HAMSHAWVIALES And. & And. 2003						
HAMSHAWVIACEAE And. & And. 2003						
Hamshawvia And. & And. 2003	♀	5	Molteno Fm.	S. Africa	Karoo Basin	Tr(CRN)
Sphenobaiera Florin 1936	⬯	4/5	”	”	”	”
Stachyopitys Schenk 1867	♂	4	”	”	”	”
UMKOMASIALES Doweld 2001						
UMOMASIACEAE Petriella 1981						
Umkomasia H.H.Thomas 1933	♀	5	Molteno Fm.	S. Africa	Karoo Basin	Tr(CRN)
Dicroidium Gothan 1912	⬯	4	”	”	”	”
Pteruchus H.H.Thomas 1933	♂	4	”	”	”	”
CAYTONIALES Gothan 1932						
CAYTONIACEAE Kräusel 1926						
Caytonia H.H.Thomas 1925	♀	5	L–U. Deltaic	England	Yorkshire	J(BAJ–BTH)
Sagenopteris Presl 1838	⬯	4	”	”	”	”
Caytonanthus T.M.Harris 1937	♂	4	”	”	”	”
PETRIELLALES T.N.Taylor *et al*. 1994						
PETRIELLACEAE T.N.Taylor *et al*. 1994						
Petriellaea T.N.Taylor *et al*. 1994	♀	5	Fremouw Fm.	Antarctica	Transantarctic Mts	Tr(LAD)
unknown	⬯	-	-	-	-	-
unknown	♂	-	-	-	-	-
KANNASKOPPIACEAE And. & And. 2003						
Kannaskoppia And. & And. 2003	♀	5	Molteno Fm.	S. Africa	Karoo Basin	Tr(CRN)
Kannaskoppifolia And. & And. 2003	⬯	5	”	”	”	”
Kannaskoppianthus And. & And. 2003	♂	5	”	”	”	”
CLASS INCERTAE SEDIS						
ALEXIALES And. & And. 2003						
ALEXIACEAE And. & And. 2003						
Alexia And. & And. 2003	♀	5	Molteno Fm.	S. Africa	Karoo Basin	Tr(CRN)
unknown	⬯	-	-	-	-	-
unknown	♂	-	-	-	-	-
CLASS INCERTAE SEDIS						
HLATIMBIALES And. & And. 2003						
HLATIMBIACEAE And. & And. 2003						
Hlatimbia And. & And. 2003	♀	5	Molteno Fm.	S. Africa	Karoo Basin	Tr(CRN)
Batiopteris And. & And. 2003	⬯	2	”	”	”	”
unknown	♂	-	-	-	-	-
BENNETTITOPSIDA Engl. 1897						
FREDLINDIALES And. & And. 2003						
FREDLINDIACEAE And. & And. 2003						
Fredlindia And. & And. 2003	♀	5	Molteno Fm.	S. Africa	Karoo Basin	Tr(CRN)
Halleyoctenis And. & And. 1989	⬯	3	”	”	”	”
Weltrichia Braun 1847	♂	3	”	”	”	”
BENNETTITALES Engl. 1892						
WESTERHEIMIACEAE Němejc 1968						
Westerheimia Krasser 1918	♀	5	Lunz plant beds	Austria	Lunz	Tr(CRN)
Pterophyllum Brongn. 1828	⬯	3	”	”	”	”
Leguminanthus Kräusel & Schaarschmidt 1966	♂	3	”	”	”	”

VARDEKLOEFTIACEAE And. & And. fam. nov.						
Vardekloeftia T.M.Harris 1932b	♀	5	Kap Stewart Fm.	Greenland	E. Greenland	Tr(RHT)
Pterophyllum Brongn. 1828	⬯	3	”	”	”	”
Bennettistemon T.M.Harris 1932b	♂	3	”	”	”	”
LAUROZAMITACEAE And. & And. fam. nov.						
Williamsonia Carruth. 1870	♀	5	Chinle Fm.	USA	New Mexico	Tr(CRN–NOR)
Laurozamites Weber & Zamudio-Varela 1995	⬯	3	”	”	”	”
unknown	♂	-	-	-	-	-
STURIANTHACEAE Doweld 2001						
Sturianthus Kräusel 1950	♀	5	Lunz plant beds	Austria	Lunz	Tr(CRN)
unknown	⬯	-	-	-	-	-
unknown	♂	-	-	-	-	-
BENNETTICARPACEAE And & And. fam. nov.						
Bennetticarpus T.M.Harris 1932b	♀	5	Lunz plant beds	Austria	Lunz	Tr(CRN)
Pterophyllum Brongn. 1828	⬯	3	”	”	”	”
Haitingeria Krasser 1916	♂	3	”	”	”	”
WILLIAMSONIELLACEAE Nakai 1943						
Williamsoniella Carruth. 1870	♀	5	L–M. Deltaic	England	Yorkshire	J(BAJ)
Nilssoniopteris Nath. 1909	⬯	4	”	”	”	”
Williamsoniella Carruth. 1870	♂	5	”	”	”	”
WILLIAMSONIACEAE (Carruth. 1870) Nath. 1913						
Williamsonia Carruth. 1870	♀	5	Wealden	England	Sussex	C(BER)
Ptilophyllum Morris 1840	⬯	3	”	”	”	”
Weltrichia Braun 1847	♂	3	”	”	”	”
CYCADEOIDACEAE R.Br. ex G.R.Wieland 1908						
Cycadeoidea Buckland 1828	♀	5	Black Hills	USA	South Dakota	K(BER)
Zamites Brongn. 1828b	⬯	5	”	”	”	”
Cycadeoidea Buckland 1828	♂	5	”	”	”	”
PENTOXYLALES Pilg. & Melch. 1954						
LINDTHECACEAE And. & And. 2003						
Lindtheca And. & And. 2003	♀	5	Molteno Fm.	S. Africa	Karoo Basin	Tr(CRN)
Taeniopteris Brongn. 1832	⬯	3	”	”	”	”
unknown	♂	-	-	-	-	-
PENTOXYLACEAE Pilg. & Melch. 1954						
Carnoconites Srivastava 1944	♀	5	Rajmahal Hills	India	Rajmahal Hills	K(HAU–APT)
Nipaniophyllum Sahni 1948	⬯	4	”	”	”	”
Sahnia Vishnu-Mitre 1953	♂	3	”	”	”	”
GNETOPSIDA Eichler ex Kirpotenko 1884						
FRAXINOPSIALES And. & And. 2003						
FRAXINOPSIACEAE And. & And. 2003						
Fraxinopsis G.R.Wieland 1929	♀	5	Molteno Fm.	S. Africa	Karoo Basin	Tr(CRN)
Yabeiella S.Oishi 1931	⬯	4	”	”	”	”
unknown	♂	-	-	-	-	-
NATALIGMALES And. & And. 2003						
NATALIGMACEAE And. & And. 2003						
Nataligma And. & And. 2003	♀	5	Molteno Fm.	S. Africa	Karoo Basin	Tr(CRN)
Gontriglossa And. & And. 1989	⬯	2	”	”	”	”
unknown	♂	-	-	-	-	-
DINOPHYTONALES Krassilov & Ash fam. nov.						
DINOPHYTONACEAE Krassilov & Ash fam. nov.						
Dinophyton Ash 1970	♀	5	Chinle Fm.	USA	Arizona/New Mexico	Tr(CRN–NOR)
” ” ”	⬯	4	”	”	”	”
” ” ”	♂	4	”	”	”	”
DECHELLYIALES Ash order nov.						
DECHELLYIACEAE Ash fam. nov.						
Dechellyia Ash 1972	♀	5	Chinle Fm.	USA	NE Arizona	Tr(CRN)
” ” ”	⬯	5	”	”	”	”
Masculostrobus Seward 1911	♂	3	”	”	”	”
BERNETTIALES Konijn.-Citt. order nov.						
BERNETTIACEAE Konijn.-Citt. fam. nov.						
Bernettia Gothan 1914	♀	5	Lias α, Franken	Germany	Bayreuth	J(HET)
Desmiophyllum Lesquereux 1878	⬯	3	”	”	”	”
Piroconites Gothan 1914	♂	3	”	”	”	”
EOANTHALES Krassilov, And. & And. order nov.						
EOANTHACEAE Krassilov, And. & And. fam. nov.						
Eoantha Krassilov 1986	♀	5	Vitim River	Mongolia	Lake Baikal	K(BRM–APT)
Praeherba Krassilov & Bugdaeva 2000	⬯	4	”	”	”	”
unknown	♂	-	-	-	-	-
GNETALES Luerss. 1879						
DREWRIACEAE And. & And. fam. nov.						
Drewria Crane & Upchurch 1987	♀	5	Potomac Gp.	USA	Virginia	K(APT)
” ” ”	⬯	5	”	”	”	”
unknown	♂	-	-	-	-	-
EPHEDRACEAE Dumort. 1829						
Ephedra L. 1753			**Extant**			
GNETACEAE Lindl. 1834						
Gnetum L. 1767			**Extant**			
WELWITSCHIACEAE Markgr. 1926						
Welwitschia Hook.f. 1862			**Extant**			
AXELRODIOPSIDA And. & And. class nov.						
AXELRODIALES And. & And. order nov.						
AXELRODIACEAE And. & And. fam. nov.						
Axelrodia Cornet 1986	♀	5	Trujillo Fm.	USA	NW Texas	Tr(NOR)
Sanmiguelia Brown 1956	⬯	5	”	”	”	”
Synangispadixis Cornet 1986	♂	5	”	”	”	”
ZAMIOSTROBACEAE And. & And. fam. nov.						
Zamiostrobus Endl. 1836	♀	5	Winterpock CM	USA	Virginia	Tr(CRN)
unknown	⬯	-	-	-	-	-
unknown	♂	-	-	-	-	-

GYMNOSPERM CLASSIFICATION 1954–2001

A comparison of seven variously adopted (or rejected) attempts at a supra-generic classification of the gymnosperms over the past 50 years, from Pilger & Melchior (1954) to Doweld (2001), clearly shows the high level of uncertainty and lack of consensus persisting. Though some system of classification is universally sought, the criteria for its construction and its final shape remain elusive.

Pilger & Melchior 1954 (Engler's Syllabus)

Almost two centuries after the coining of the earliest named gymnosperm family—Pinaceae Adans. 1763—appeared the 12th edition (1954) of *Engler, Syllabus der Pflanzenfamilien* (the 11th edition was published in 1936). In it Pilger & Melchior published a particularly complete gymnosperm classification for the time. Of the 29 families covered and briefly described, 18 were extinct—including only the best understood taxa with reproductive material.

Alvin *et al*. 1967 (The Fossil Record)

The first edition of *The Fossil Record* of the Geological Society, London, appeared in 1967. It saw a particularly diverse body of British palaeobotanists, Ken Alvin, Peter Barnard, Tom Harris, Norman Hughes, Richard Wagner and Alan Wesley assembling to compile the section on the gymnosperms. Their classification expressed, at all taxonomic ranks, slightly greater levels of diversity than did Pilger & Melchior (1954), but the overall framework was markedly different.

Meyen 1984, 1987 (Gymnosperm Systematics)

In his *Botanical Review* booklet *Basic features of gymnosperm systematics* (1984), followed soon after by his textbook *Fundamentals of palaeobotany* (1987), Meyen introduced a significantly more inclusive classification of gymnosperms from family level and up, based largely on ovulate organs.

It was profoundly criticised across a broad front by Beck (1985), Miller (1985) and Rothwell (1985) the following year in a subsequent issue of *The Botanical Review*.

Stewart & Rothwell (1993), Taylor & Taylor (1993)

In their palaeobotanical textbooks that appeared in the same year and six years after that of Meyen (1987) (eight years after the deep criticism of his *Basic features*), these authors were clearly reluctant to commit to a comprehensive classification of the gymnosperms from family level. The retreat, for reasons largely relating to the incompleteness of the palaeobotanical record, was not helpful to ourselves (for instance) in our (And. & And. 2003) need for a contextual framework in which to describe the richness and diversity of the Late Triassic Molteno seed plants.

The differences between the two classifications are at least as apparent as the similarities. Significantly each includes only a single class.

Cleal 1993 (The Fossil Record 2)

A quarter century after *The Fossil Record* of 1967, Cleal, in the second edition of this work and concurrent with Stewart & Rothwell (1993) and Taylor & Taylor (1993), took the opposite approach from these works. In essence, he built on the Meyen (1984, 1987) classification, though with significant deviation in detail. The diversity at order and family level is virtually the same, though a third (15) of Cleal's families do not appear in Meyen's work. While the phylogeny expressed in the arrangement of orders into classes is markedly different from Meyen (1984, 1987), the orders employed all appear in the former work.

Doweld 2001 (Prosyllabus Tracheophytorum)

As part of an overall classification of the tracheophytes, Doweld introduces a profoundly revised classification of the gymnosperms. In effect, he introduces at all taxonomic ranks from family to class what approaches a five-fold inflation in diversity over that reflected in Cleal (1993). The diversity levels shift upwards a taxonomic rank (e.g. family-level diversity becomes order-level diversity).

Fluctuating biodiversity

Pilger & Melchior 1954
4 classes, 11 orders, 29 families (11 extant)
- A comprehensive classification from family level.

Alvin et al. *1967*
6 classes, 18 orders, 32 named families (9 extant)
- Families included for only 4 of 18 orders.

Meyen 1984, 1987
3 classes, 19 orders, 41 families (12 extant)
- Most comprehensive classification from family level to date.
- Classification & nomenclature based essentially on ovulate organs.

Stewart & Rothwell 1993
1 class, 13 orders, 25 named families (7 extant)
- Families included for only half of their orders.

Taylor & Taylor 1993
1 class, 19 orders, 18 named families (7 extant)
- Families included for only Bennettitales & Coniferales.

Cleal 1993
5 classes, 16 orders, 45 families (11 extant)
- Return to comprehensive classification from family level.

Doweld 2001
25 classes, 67 orders, 125 families
- Comprehensive classification from family level.
- Expressing highly inflated diversity compared to earlier works.

Notes on classification tables (Tabs 4–10)

*—extant families.
bold type—classes & families.
authorship—prior to Cleal (1993) and Doweld (2001), authorship of supra-generic taxa was not given.

Authors of plant names

(As applied in our various classification tables: Contents, p. v; Tab. 2, pp 6, 7; Tab. 3, pp 8–11)

Earliest author (fossil taxa): It is far from clear-cut establishing the earliest author (and dates) of family, order and class names. In view of this, we outline the steps we have taken. For those families and higher taxa written up by Cleal, Krassilov, Zhou and Van Konijnenburg-Van Cittert, we take the authorships as resolved by them. Beyond these taxa and those established newly in And. & And. (2003) or in this volume, we refer firstly to Doweld (2001), then Cleal (1993) as sources.

Earliest author (extant taxa):--Brummitt (1992) as source for the 13 extant families.

Abbreviations (and initials) of author names: Brummitt & Powell (1992), the generally accepted source for the standard abbreviations of author names, is followed. For more recent authors of fossil taxa not covered, we generally follow their principles for the 'standard forms' of author names, e.g. Konijn.-Citt., Hern.-Cast., Z.Zhou, Y.A.Orlov. For brevity, we make an exception in the case of our own monographs, e.g. And. & And. (1985, 2003), whose standard form would become the unwieldy J.M. Anderson & H.M. Anderson (1985, 2003).

Tab. 4. Pilger & Melchior 1954
‘Engler’s Syllabus der Pflanzenfamilien’

- **DIVISION**
  - **CLASS**
    - ORDER
      - **Family**
        - Subfamily

- **GYMNOSPERMAE** (Archispermae)
  - **CYCADOPSIDA** (Cycadophyta)
    - PTERIDOSPERMAE (Cycadofilices)
      - **Medullosaceae**
      - **Calamopityaceae**
      - **Peltaspermaceae**
      - **Corystospermaceae**
    - CAYTONIALES
      - **Caytoniaceae**
    - CYCADALES
      - **Cycadaceae***
        - Cycadoideae
        - Stangerioideae
        - Bowenioideae
        - Dioonoideae
        - Zamioideae
    - NILSSONIALES
      - **Nilssoniaceae**
    - BENNETTITALES (Cycadeoideales)
      - **Williamsoniaceae**
      - **Wielandiellaceae**
      - **Bennettitaceae (Cycadeoideaceae)**
    - PENTOXYLALES
      - **Pentoxylaceae**
    - GINKGOALES
      - **Ginkgoaceae***
  - **CONIFEROPSIDA (Coniferophyta)**
    - CORDAITALES
      - **Pityaceae**
      - **Cordaitaceae**
      - **Poroxylaceae**
    - CONIFERAE
      - **Lebachiaceae (Walchiaceae)**
      - **Voltziaceae**
      - **Cheirolepidaceae**
      - **Protopinaceae**
      - **Pinaceae***
        - Abietoideae
        - Laricoideae
        - Pinoideae
      - **Taxodiaceae***
      - **Cupressaceae***
        - Cupressoideae
        - Thujoideae
        - Juniperoideae
      - **Podocarpaceae***
        - Pherosphaeroideae
        - Phyllocladoideae
        - Podocarpoideae
      - **Cephalotaxaceae**
      - **Araucariaceae***
  - **TAXOPSIDA (Taxinae)**
    - TAXALES
      - **Taxaceae***
  - **CHLAMYDOSPERMAE (Chlamydospermophyta, Gnetophyta)**
    - GNETALES
      - **Welwitschiaceae***
      - **Ephedraceae***
      - **Gnetaceae***

Diversity
4 classes, 11 orders, 29 families (11 extant)

Tab. 5. Alvin *et al*. 1967
‘The Fossil Record’

- **DIVISION**
  - **CLASS**
    - ORDER
      - **Family**

- GYMNOSPERMOPHYTA
  - **PROGYMNOSPERMOPSIDA**
  - **PTERIDOSPERMOPSIDA**
    - CALAMOPITYALES
    - ARCHAEOPTERIDALES
    - DIPLOPTERIDALES
      - **Diplopteridaceae**
      - **Adiantitaceae**
      - **Cardiopteridaceae**
    - LYGINOPTERIDALES
    - PTERIDOSPERMALES
      - **Diplotmemaceae**
      - **Mariopteridaceae**
      - **Alethopteridaceae**
      - **Protoblechnidaceae**
      - **Callipteridiaceae**
      - **Emplectopteridaceae**
      - **Callipteraceae**
      - **Cyclopteridaceae**
      - **Rachivestitaceae**
      - **Eremopteridaceae**
    - SPHENOSPERMALES
    - TAENIOPTERIDALES
    - GLOSSOPTERIDALES
  - **INCERTAE SEDIS**
    - CORYSTOSPERMALES
    - PELTASPERMALES
    - CAYTONIALES
  - **CONIFEROPSIDA**
    - CORDAITALES
      - **Pityaceae**
      - **Poroxylaceae**
      - **Calamopityaceae**
      - **Cordaitaceae**
    - CONIFERALES
      - **Lebachiaceae**
      - **Voltziaceae**
      - **Cheirolepidiaceae**
      - **Cycadocarpidiaceae**
      - **Palyssiaceae**
      - **Protopinaceae**
      - **Pinaceae***
      - **Araucariaceae***
      - **Taxodiaceae***
      - **Cupressaceae***
      - **Podocarpaceae***
      - **Cephalotaxaceae***
    - TAXALES
    - GINKGOALES
  - **CYCADOPSIDA**
    - CYCADALES
    - BENNETTITALES
    - PENTOXYLALES
  - **GNETOPSIDA**
    - **Ephedraceae***
    - **Gnetaceae***
    - **Welwitschiaceae***

Diversity
6 classes, 18 orders, 32 named families (9 extant)
46 families (assuming at least 1 per order)

Tab. 6. Meyen 1984, 1987
‘Basic features of gymnosperm systematics’

- **DIVISION**
  - **CLASS**
    - ORDER
      - **Family**

- PINOPHYTA (=Gymnospermae)
  - **GINKGOOPSIDA**
    - CALAMOPITYALES
      - **Calamopityaceae**
    - CALLISTOPHYTALES
      - **Callistophytaceae**
    - PELTASPERMALES
      - **Trichopityaceae**
      - **Peltaspermaceae**
      - **Cardiolepidaceae**
      - **Umkomasiaceae (= Corystospermaceae)**
    - GINKGOALES
      - **Ginkgoaceae***
      - **Karkeniaceae**
      - **Pseudotorelliaceae**
    - LEPTOSTROBALES
      - **Leptostrobaceae**
      - **Iraniaceae**
    - CAYTONIALES
      - **Caytoniaceae**
    - GIGANTONOMIALES (=Gigantopteridales)
    - ARBERIALES (=Glossopteridales)
      - **Arberiaceae**
    - PENTOXYLALES
      - **Pentoxylaceae**
    - EPHEDRALES
      - **Ephedraceae***
  - **CYCADOPSIDA**
    - LAGENOSTOMALES (=Lyginopteridales)
      - **Lagenostomaceae**
      - **Buteoxylaceae**
    - TRIGONOCARPALES (=Medullosales)
      - **Trigonocarpaceae**
    - CYCADALES
      - **Beaniaceae**
      - **Cycadaceae* (Cycadeoideaceae)**
      - **Dirhopalostachyaceae**
    - BENNETTITALES (=Cycadeoideales)
      - **Bennettitaceae**
      - **Williamsoniaceae**
    - GNETALES
      - **Gnetaceae***
    - WELWITSCHIALES
      - **Welwitschiaceae***
  - **PINOPSIDA (Coniferopsida)**
    - CORDAITANTHALES
      - **Cordaitanthaceae**
      - **Vojnovskyaceae**
      - **Rufloriaceae**
    - DICRANOPHYLLALES
    - PINALES (=coniferales)
      - **Lebachiaceae**
      - **Buriadiaceae**
      - **Voltziaceae**
      - **Cycadocarpidiaceae**
      - **Cheirolepidiaceae**
      - **Palissyaceae**
      - **Araucariaceae***
      - **Pinaceae***
      - **Taxodiaceae***
      - **Cupressaceae***
      - **Podocarpaceae***
      - **Taxaceae***
      - **Cephalotaxaceae***

Diversity
3 classes, 19 orders, 41 families (12 extant)

- The most complete classification from family level to date; both the classification and nomenclature are based essentially on ovulate organs.
- The system is basically that of Meyen (1984); only the Gigantonomiales and Dicranophyllales (no families included) added in Meyen (1987).

Tab. 7. Stewart & Rothwell 1993
‘Paleobotany and the evolution of plants’

- **CLASS**
  - ORDER
    - **Family**

- **GYMNOSPERMOPSIDA**
  - PTERIDOSPERMALES
    - **Calamopityaceae**
    - **Lyginopteridaceae**
    - **Medullosaceae**
    - **Callistophytaceae**
  - CYCADALES
  - CYCADEOIDALES (BENNETTITALES of some authors)
    - **Williamsoniaceae**
    - **Cycadeoidaceae**
  - CAYTONIALES
    - **Caytoniaceae**
    - **Corystospermaceae**
    - **Peltaspermaceae**
  - GLOSSOPTERIDALES
  - PENTOXYLALES
  - CZEKANOWSKIALES
  - GNETALES
  - GINKGOALES
  - CORDAITALES
    - **Cordaitaceae**
  - VOLTZIALES
    - **Utrechtiaceae**
    - **Emporiaceae**
    - **Majonicaceae**
    - **Voltziaceae**
  - CONIFERALES
    - **Protopinaceae**
    - **Araucariaceae***
    - **Podocarpaceae***
    - **Pinaceae***
    - **Cheirolepidiaceae**
    - **Pararaucariaceae**
    - **Taxodiaceae***
    - **Cupressaceae***
    - **Cephalotaxaceae***
    - **Palissyaceae**
  - TAXALES
    - **Taxaceae***

Diversity
1 class, 13 orders, 25 named families (7 extant)
31 families (assuming at least 1 per order)

Tab. 8. Taylor & Taylor 1993
‘The Biology and Evolution of Fossil Plants’

- **CLASS**
  - **SUBCLASS**
    - ORDER
      - **Family**

- **GYMNOSPERMS** (not given)
  - PTERIDOSPERMOPHYTA (seed ferns)
    - CALAMOPITYALES
    - BUTEOXYLONALES
    - LYGINOPTERIDALES
    - MEDULLOSALES
    - CALLISTOPHYTALES
    - GLOSSOPTERIDALES
  - Mesozoic seed ferns
    - CAYTONIALES
    - CORYSTOSPERMALES
    - PELTASPERMALES
  - CYCADOPHYTES
    - CYCADALES
    - BENNETTITALES
      - **Cycadeoidaceae**
      - **Williamsoniaceae**
  - GINKGOPHYTES
    - GINKGOALES
  - Gymnosperms of obscure affinities
    - CZEKANOWSKIALES
    - VOJNOVSKYALES
    - PENTOXYLALES
    - GIGANTOPTERIDALES
    - GNETALES
  - Extinct group of gymnosperms
    - CORDAITALES
  - Unnamed group
    - CONIFERALES
      - **Utrechtiaceae**
      - **Emporiaceae**
      - **Majonicaceae**
      - **Ullmanniaceae**
      - **Ferngliocladaceae**
      - **Buriadiaceae**
      - **Palissyaceae**
      - **Cheirolepidiaceae**
      - **Podocarpaceae***
      - **Araucariaceae***
      - **Cupressaceae***
      - **Taxodiaceae***
      - **Arctopityaceae**
      - **Pinaceae***
      - **Cephalotaxaceae***
      - **Taxaceae***

Diversity
1 class, 19 orders, 18 named families (7 extant)
35 families (assuming at least 1 per order)

Tab. 9. Cleal 1993
‘The Fossil Record II’

- **CLASS**
  - ORDER
    - **Family**

- **LAGENOSTOMOPSIDA** Cleal 1993
  - LAGENOSTOMALES Seward 1917
    - **Elkinsiaceae** Rothwell *et al.* 1989
    - **Genomospermaceae** Long 1975
    - **Eospermaceae** Long 1975
    - **Lagenostomaceae** Seward 1917
    - **Physostomaceae** Long 1975

- **CLASS UNNAMED**
  - CALAMOPITYALES Taylor 1981
    - **Calamopityaceae** Solms-Laubach 1896
  - CALLISTOPHYTALES Rothwell 1981
    - **Callistophytaceae** Stidd & Hall 1970
  - PELTASPERMALES Němejc 1968
    - **Peltaspermaceae** Thomas ex Harris 1937
    - **Cardiolepidaceae** Meyen 1977
    - **Umkomasiaceae** Meyen 1984
  - LEPTOSTROBALES Meyen 1984
    - **Leptostrobaceae** Meyen 1984
  - ARBERIALES Meyen 1984
    - **Arberiaceae** Meyen 1984
    - **Caytoniaceae** Thomas 1925
  - GIGANTONOMIALES Meyen 1987
    - **Emplectopteridaceae** Wagner 1967

- **CYCADOPSIDA** Barnard & Long 1975
  - TRIGONOCARPALES Seward 1917
    - **Trigonocarpaceae** Seward 1917
    - **Potonieaceae** Halle 1933
  - CYCADALES Engler 1892
    - **Cycadaceae** Persoon 1807*

- **GNETOPSIDA** Engler 1954
  - BENNETTITALES Engler 1892
    - **Bennettitaceae** Engler 1892
  - PENTOXYLALES Pilger & Melchior 1954
    - **Pentoxylaceae** Pilger & Melchior 1954
  - GNETALES Engler 1892
    - **Gnetaceae** Lindley 1834*

- **PINOPSIDA** Meyen 1984
  - CORDAITANTHALES Meyen 1984
    - **Cordaitanthaceae** Meyen 1984
    - **Rufloriaceae** Meyen 1982
    - **Vojnovskyaceae** Meyen 1982
  - DICRANOPHYLLALES Němejc emend. Archangelsky & Cúneo 1990
    - **Dicranophyllaceae** Němejc emend. Archangelsky & Cúneo 1990
    - **Trichopityaceae** Florin emend. Archangelsky & Cúneo 1990
  - PINALES Meyen 1984
    - **Emporiaceae** Mapes & Rothwell 1991
    - **Buriadiaceae** Pant 1977
    - **Utrechtiaceae** Mapes & Rothwell 1991
    - **Ferugliocladaceae** Archangelsky & Cúneo 1987
    - **Majonicaceae** Clement-Westerhof 1987
    - **Ullmanniaceae** Zimmermann 1959
    - **Voltziaceae** Florin 1951
    - **Podocarpaceae** Endlicher 1847*
    - **Palissyaceae** Florin 1958
    - **Araucariaceae** Henkel & Hochstetter 1865*
    - **Pinaceae** Lindley 1836*
    - **Cheirolepidiaceae** Takhtajan 1963
    - **Taxaceae** Gray 1821*
    - **Pararaucariaceae** Stockey 1977
    - **Taxodiaceae** Warming 1890*
    - **Arctopityaceae** Manum & Bose 1989
    - **Sciadopityaceae** Seward 1919*
    - **Cephalotaxaceae** Neger 1907*
    - **Cupressaceae** Bartling 1830*
  - GINKGOALES Engler 1897
    - **Ginkgoaceae** Engler 1897*

Diversity
5 classes, 16 orders, 45 families (11 extant)

Tab. 10.
Doweld 2001 ‘Prosyllabus Tracheophytorum’

- SUPERPHYLUM
  - PHYLUM
    - SUBPHYLUM
      - **CLASS**
        - SUBCLASS
          - ORDER
            - **Family**

- CYCADOPHYTANAE Doweld 2001
  - NOEGGERATHIOPHYTA Zimmerm. 1959
    - **NOEGGERATHIOPSIDA** Krysht. 1934
      - NOEGGERATHIALES Darrah 1939
        - **Noeggerathiaceae** Göpp. ex C.E.I.von Eichwald 1854
      - DISCINITALES Doweld 2001
        - **Discinitaceae** Gao Zhifeng & B.A.Thomas 1994
      - TINGIALES Zimmerm. 1959
        - **Tingiaceae** G.Koidzumi 1938
  - ANEUROPHYTOPHYTA H.Bold 1973
    - ANEUROPHYTOPHYTINA Doweld 2001
      - **RHACOPHYTOPSIDA** T.N.Taylor 1981
        - RHACOPHYTALES Němejc 1963
          - **Rhacophytaceae** G.Radczenko 1963
      - **ANEUROPHYTOPSIDA** Bierhorst ex Takht. 1978
        - ANEUROPHYTALES Bonamo & H.Banks 1967
          - **Aneurophytaceae** A.R.Ananiev 1963
        - PROTOPITYALES Němejc 1963
          - **Protopityaceae** Solms-Laubach 1893
    - ARCHAEOPTERIDOPHYTINA Doweld 2001
      - ARCHAEOPTERIDOPSIDA Takht. 1978
        - ARCHAEOPTERIDALES Zimmerm. 1930
          - **Archaeopteridaceae** Trapl 1926

  - MORESNETIOPHYTA Doweld 2001
    - **MORESNETIOPSIDA** Doweld 2001
      - MORESNETIALES Doweld 2001
        - **Moresnetiaceae** Němejc 1963
        - **Eurystomataceae** A.G.Long 1975
        - **Eospermataceae** A.G.Long 1975
      - PULLARITHECALES Doweld 1998
        - **Pullarithecaceae** Doweld 1998
        - **Calathiopsidaceae** Doweld 2001
        - **Austrocalycaceae** J.C.Vega & S.Archangelsky 2001
        - **Gnetopsidaceae** Doweld 2001
      - TETRASTICHIALES Němejc 1968
        - **Tetrastichiaceae** Němejc 1968
    - **CLASS INCERTAE SEDIS**
      - CALAMOPITYALES Němejc 1963
        - **Calamopityaceae** D.H.Scott 1909

  - LYGINOPTERIDOPHYTA Doweld 2001
    - **LYGINOPTERIDOPSIDA** Novák 1961
      - LYGINOPTERIDALES V.Havlena 1961
        - **Physostomataceae** A.G.Long 1975
        - **Lagenostomataceae** A.G.Long 1975
      - CALLISTOPHYTALES Rothwell 1981
        - **Callistophytaceae** Stidd & J.W.Hall 1970
        - **Cornucarpaceae** Doweld 2001
      - HEXAPTEROSPERMALES Doweld 2001
        - **Hexapterospermaceae** Doweld 2001
        - **Colpospermaceae** Doweld 2001

  - CYCADOPHYTA Bessey 1907
    - **PACHYTESTOPSIDA** Doweld 2001
      - CODONOSPERMALES Doweld 2001
        - **Codonospermaceae** Doweld 2001
      - PACHYTESTALES Doweld 2001
        - **Polylophospermaceae** Doweld 2001
        - **Pachytestaceae** Doweld 2001
        - **Stephanospermaceae** Doweld 2001
    - **PHASMATOCYCADOPSIDA** Doweld 2001
      - GIGANTOPTERIDALES Li Xingxue & Yao Zhaoqi 1983
        - **Emplectopteridaceae** R.H.Wagner 1967
        - **Spermopteridaceae** Doweld 2001
        - **Gigantopteridaceae** Koidzumi 1936
      - PHASMATOCYCADALES Doweld 2001
        - **Phasmatocycadaceae** Doweld 2001
    - **CYCADOPSIDA** Brongn. 1843
      - CYCADIDAE Pax 1894
        - CYCADALES Dumort. 1829
          - **Crossozamiaceae** Doweld 2001
          - **Cycadaceae** Pers. 1807
      - ZAMIIDAE Doweld 2001
        - NILSONIALES Darrah 1960
          - **Nilsoniaceae** Zimmerm. 1959
        - DIOALES Doweld 2001
          - **Dioaceae** Doweld 2001
        - STANGERIALES Doweld 2001
          - **Stangeriaceae** A.Schenk 1880
        - ZAMIALES Burnett 1835
          - **Boweniaceae** D.W.Stevenson 1981
          - **Zamiaceae** Horan. 1834
          - **Encephalartaceae** A.Schenk 1880

  - PELTASPERMOPHYTA Doweld 2001
    - **PELTASPERMOPSIDA** Doweld 2001
      - TRICHOPITYALES Doweld 2001
        - **Trichopityaceae** S.V.Meyen 1987
        - **Psygmophyllaceae** Zalessky 1937
      - PELTASPERMALES T.N.Taylor 1981
        - **Autuniaceae** Doweld 2001
        - **Paltaspermaceae** Pilg. & Melchior 1954
      - SPOROPHYLLITALES Doweld 2001
        - **Sporophyllitaceae** Doweld 2001
        - **Leuthardtiaceae** Doweld 2001
      - UMKOMASIALES Doweld 2001
        - **Umkomasiaceae** Petriella 1981
        - **Angaropeltidaceae** Doweld 2001
    - **ARBERIOPSIDA** Doweld 2001
      - DICRANOPHYLLALES Archangelsky & Cúneo 1990
        - **Dicranophyllaceae** Archangelsky & Cúneo 1990
      - VOJNOVSKYALES M.F.Neuburg ex Emberger 1968
        - **Vojnovskyaceae** M.F.Neuburg 1963
        - **Rufloriaceae** Ledrán ex S.V.Meyen 1987
      - ARBERIALES S.V.Meyen 1984
        - **Arberiaceae** Rigby 1972
    - **CLASS INCERTAE SEDIS**
      - **Schmeissneriaceae** Zhiyan Zhou 2000
    - **DICTYOPTERIDIOPSIDA** Doweld 2001
      - DICTYOPTERIDIALES McLoughlin ex Doweld 2001
        - **Dictyopteridiaceae** Rigby 1978
      - ORDER INCERTAE SEDIS
        - **Breyteniaceae** Doweld 2001
      - RIGBYALES Doweld 2001
        - **Rigbyaceae** J.M.Anderson & H.M.Anderson 1985
      - LIDGETTONIALES Doweld 2001
        - **Lidgettoniaceae** J.M.Anderson & H.M.Anderson 1985
        - **Parthaceae** Doweld 2001
        - **Denkaniaceae** Doweld 2001
    - **PENTOXYLOPSIDA** D.D.Pant ex Doweld 2001
      - PENTOXYLALES Pilg. & Melchior 1954
        - **Pentoxylaceae** Pilg. & Melchior 1954

  - CYCADEOIDEOPHYTA T.N.Taylor 1981
    - **CYCADEOIDEOPSIDA** D.H.Scott 1923
      - CYCADEOIDEALES Berry 1920
        - **Westersheimiaceae** Němejc 1968
        - **Sturianthaceae** Doweld 2001
        - **Williamsoniaceae** (Carruthers) Nathorst 1913
        - **Cycadeoideaceae** R.Br. ex G.R.Wieland 1908
        - **Williamsoniellaceae** Nakai 1943

  - GNETOPHYTA Bessey 1907
    - **GNETOPSIDA** Eichler ex Kirpotenko 1884
      - GNETALES Luerss. 1879
        - **Gnetaceae** Blume 1833
    - **EPHEDROPSIDA** Reveal 1996
      - EPHEDRALES Dumort. 1829
        - **Ephedraceae** Dumort. 1829
    - **WELWITSCHIOPSIDA** Boivin 1956
      - WELWITSCHIALES Reveal 1993
        - **Welwitschiaceae** Caruel 1879

- PINOPHYTA Reveal 1996
  - **CORDAITOPSIDA** Lesquereux 1880
    - CORDAITALES D.H.Scott 1909
      - **Cordaitaceae** Grand'Eury 1877
  - **VOLTZIOPSIDA** Doweld 2001
    - VOLTZIALES Andreánsky 1954
      - **Bartheliaceae** Rothwell & G.Mapes 2001
      - **Otoviciaceae** Doweld 2001
      - **Walchiaceae** (Göpp.) Stur 1875
      - **Thucydiaceae** Hernandez-Castillo, Rothwell & G.Mapes 2001
      - **Majonicaceae** Clement-Westerhof 1987
      - **Voltziaceae** Arnold 1947
      - **Swedenborgiaceae** Zimmerm. 1959
    - ULLMANNIALES Doweld 2001
      - **Ullmanniaceae** Němejc 1959
    - PODOZAMITALES Sze Xingjian & Li Xingxue 1963
      - **Podozamitaceae** Němejc ex Takht. 1956
      - **Aethophyllaceae** Grauvogel-Stamm 1978
    - FERUGLIOCLADALES Doweld 2001
      - **Ferugliocladaceae** Archangelsky & Cúneo 1987
    - ORDER INCERTAE SEDIS
      - **Buriadiaceae** T.N.Taylor & E.L.Taylor 1993
  - **CLASS INCERTAE SEDIS**
    - PALISSYALES Doweld 2001
      - **Palissyaceae** Florin 1958
  - **PINOPSIDA** Burnett 1835
    - **PINIDAE** Cronq., Takht. & Zimmerm. 1966
      - PINALES Dumort. 1829
        - **Pinaceae** Adans. 1763
      - ABIETALES Köhne 1893
        - **Abietaceae** Bercht. & J.Presl 1820
    - **CUPRESSIDAE** Doweld 2001
      - SCIADOPITYALES Reveal 1993
        - **Miroviaceae** M.Bose & Manum 1991
        - **Sciadopityaceae** Luerss. 1877
      - CUNNINGHAMIALES Doweld 2001
        - **Cunninghamiaceae** Sieb. & Zucc. 1842
        - **Taiwaniaceae** Hayata 1932
      - TAXODIALES Heintze 1927
        - **Geinitziaceae** L.Kunzmann 1999
        - **Sequoiaceae** Luerss. 1877
        - **Taxodiaceae** Saporta 1865
        - **Cryptomeriaceae** Goroschankin 1904
      - ATHROTAXIDALES Doweld 2001
        - **Athrotaxidaceae** Doweld 2001
      - CUPRESSALES Bromhead 1838
        - **Cupressaceae** Martynov 1820
        - **Thujopsidaceae** Bessey 1907
        - **Thujaceae** Burnett 1835
        - **Tetraclinaceae** Hayata 1932
        - **Juniperaceae** Bercht. & J.Presl 1820
      - ACTINOSTROBALES Doweld 2001
        - **Libocedraceae** Doweld 2001
        - **Widdringtoniaceae** Doweld 2001
        - **Neocallitropsidaceae** Doweld 2001
        - **Actinostrobaceae** Lotsy 1911
    - **ARAUCARIIDAE** Doweld 2001
      - HIRMERIELLALES Doweld 2001
        - **Hirmeriellaceae** T.M.Harris 1979
      - ARAUCARIALES Goroschankin 1904
        - **Araucariaceae** Henkel & W.Hochst. 1865
  - **PODOCARPOPSIDA** Doweld & Reveal 1999
    - SAXE-GOTHAEALES Doweld & Reveal 1999
      - **Microcachrydaceae** Doweld & Reveal 1999
      - **Saxe-Gothaeaceae** Doweld & Reveal 1999
    - PODOCARPALES Reveal 1992
      - **Acmophylaceae** Melik. & A.Bobr. 1997
      - **Nageiaceae** D.Fu 1992
      - **Phyllocladaceae** Bessey 1907
      - **Prumnopityaceae** A.Bobr. & Melik. 2000
      - **Podocarpaceae** Endl. 1847
      - **Dacrycarpaceae** A.Bobr. & Melik. 2000
      - **Halocarpaceae** A.Bobr. & Melik. 2000
      - **Parasitaxaceae** A.Bobr. & Melik. 2000
    - FALCATIFOLIALES A.Bobr. & Melik. 2000
      - **Falcatifoliaceae** A.Bobr. & Melik. 2000
    - MICROSTROBALES Doweld & Reveal 2001
      - **Microstrobaceae** Doweld & Reveal 2001
  - **TAXOPSIDA** R.Florin ex Doweld & Reveal 1999
    - CEPHALOTAXALES Takht. ex Reveal 1993
      - **Cephalotaxaceae** Neger 1907
    - TAXALES Knobl. 1890
      - **Amentotaxaceae** Kudo & Yamamoto 1931
      - **Taxaceae** S.F.Gray 1821
      - **Torreyaceae** Nakai 1938
  - **GINKGOOPSIDA** Engler 1897
    - UMALTOLEPIDIDAE Doweld 2001
      - KARKENIALES Doweld 2001
        - **Karkeniaceae** Krassilov 1972
        - **Yimaiaceae** Zhiyan Zhou 1997
      - UMALTOLEPIDALES Doweld 2001
        - **Umaltolepidaceae** Zhiyan Zhou 2000
        - **Toretziaceae** F.Stanislawski 1973
    - GINKGOIDAE Pax 1900
      - GINKGOALES Goroschankin 1904
        - **Ginkgoaceae** Engler 1897

- MAGNOLIOPHYTA Cronq., Takht. & Zimmerm. ex Reveal 1996
  - CAYTONIOPHYTINA Doweld 2001
    - **CAYTONIOPSIDA** H.H.Thomas ex Frenguelli 1946
      - CAYTONIALES Gothan 1932
        - **Caytoniaceae** Kräusel 1926
  - LEPTOSTROBOPHYTINA Doweld 2001
    - **LEPTOSTROBOPSIDA** Doweld 2001
      - LEPTOSTROBALES S.V.Meyen 1987
        - **Leptostrobaceae** S.V.Meyen 1978

Diversity

10 phyla, 27 classes, 67 orders, 125 families

What we are seeing in Doweld's classification is, in effect, a quantum-level inflation of taxa over our own scheme: 10 phyla to our 10 classes; 27 classes to our 37 orders; 67 orders to our 84 families.

This emphasises current subjectivity in the recognition of supra-generic taxa. If we are to find concensus on gymnosperm biodiversity, it is clear that the reasons behind such divergent views will need debate and resolution. Is it possible, for instance, to establish some absolute measure based on the genome of extant taxa as a guide to the morphological distance between taxa (extant and extinct): can we systematically cross the genotype-phenotype divide? For literature referred to in the classification above, see Appendix 2.

Authorship (dates): as in Doweld (2001)

GYMNOSPERM PHYLOGENY

Contributor: P. Kenrick

Introduction

The story of gymnosperm evolution is an ancient one, encompassing much of the history of plant life on land. A key element in our understanding of the evolution of the group is the development of a systematic framework. This encompasses issues such as the recognition and circumscription of taxonomic groups and the discovery or development of phylogenetic trees. The taxa that we recognise and name are the things that we talk about when discussing the history of gymnosperms, so the way that we identify and define these is critically important. Knowing how various groups of gymnosperms stand in relation to one another and to other groups of land plants is also a major issue, and this underpins the development of phylogenetic trees. Over the last 20 years, advances on two broad fronts have revolutionised our knowledge of gymnosperm phylogeny. Firstly, there have been theoretical and methodological advances. These are embodied in the cladistic approach to systematics, which deals with the way that we go about recognising taxonomic groups and their relations. Secondly, the use of gene sequencing technology has opened up a vast new source of comparative data for working out the relationships of living species. This facilitates the development of more accurate and detailed phylogenies. Together, these advances afford a much clearer picture of gymnosperm phylogeny than hitherto, and this is providing new perspectives on our understanding of the evolution of the group.

Molecular phylogenies: the big picture

Even though living species represent only a fraction of the known diversity of gymnosperms, knowledge of how these groups are related to one another and to other plants, in particular the angiosperms, can provide valuable insights into several important and topical evolutionary questions. Plants are at the forefront of developments in the application of molecular methods, with more species sampled for a wider range of genes than any other major group of living organisms (Savolainen & Chase 2003; Palmer *et al.* 2004). High-level molecular phylogenies have focused on the relationships between cycads, *Ginkgo*, conifers, Gnetales and angiosperms, but this question has proven remarkably difficult to resolve. Early studies produced conflicting results and on the whole weakly supported phylogenetic trees (see synthesis and summary in Magallon & Sanderson 2002; Rydin *et al.* 2002; Burleigh & Mathews 2004). As more data have accrued and as these have been analysed with more sophisticated model-based methods (baysian, maximum likelihood), the support for a particular phylogenetic hypothesis seems to be building. Recent analyses based on plastid, mitochondrial, and nuclear genes confirm monophyly of gymnosperms and a close relationship between Gnetales and Conifers (Bowe *et al*. 2000; Chaw *et al*. 2000; Soltis *et al.* 2002). This result, dubbed the ‘gne-pine hypothesis’, makes angiosperms the sister group to a clade containing all of the living gymnosperms (crown group gymnosperms). This has interesting implications for the geological history of these two groups. Unequivocal angiosperms have not been recorded in rocks older than the Cretaceous Period, yet putative crown group gymnosperms (e.g., extinct Voltziales, Cordaitales) are known from the Late Carboniferous. The implication here is that notwithstanding the absence of early fossil evidence, the lineage leading to angiosperms must have split from other gymnosperms much earlier than previously thought.

Molecular phylogenies of cycads & conifers

Molecular studies are providing interesting insights into the phylogeny of living gymnosperms in the cycads and the conifers.

Cycadales

Analyses of plastid and nuclear genes resolve the cycads into two well-supported clades, with *Cycas* a distantly related sister group to a clade containing all other living species (Treutelin & Wink 2002; Hill *et al*. 2003; Rai *et al.* 2003). This accords with morphological studies that recognise the distinctiveness of *Cycas* by placing it in the monogeneric higher taxon Cycadaceae or Cycadineae. Also supported is the grouping of *Macrozamia*, *Lepidozamia* and *Encephalartos* (Hill *et al.* 2003). This southern hemisphere Old World clade has also been recognised on the basis of comparative morphology. One interesting consequence of these relationships is that the modern distributions of *Macrozamia* (Australia), *Lepidozamia* (east coast Australia), and *Encephalartos* (Africa) cannot be explained by a simple vicariance model based on the rifting of Gondwana. If the divergence of these genera predated rifting, then their known modern distributions would imply that extinction had occurred in other areas of Gondwana. This is supported by the finding of fossil evidence of cycads related to this grouping from the Cretaceous of South America and Antarctica and possibly as early as the Jurassic of India (Cantrill 2000). Attempts to date the divergence of clades of cycads using a molecular clock approach yield dates that are at odds with the known fossil evidence. Using *rbcL* gene sequences, Treutelin & Wink (2002) dated the deep basal split that gave rise to the Cycadaceae at 50.2 Ma (Late Eocene) (standard deviation ± 21.7 Ma), with a maximum age of 92 Ma (Turonian: Late Cretaceous). Even this maximum age would appear to be an underestimate given the widespread occurrence of crown group cycads in the Late Cretaceous of Gondwana.

Coniferales

Molecular phylogenies support monophyly of conifers with the inclusion of the problematic Taxaceae (Stefanovic *et al*. 1998; Cheng *et al.* 2000; Gugerli *et al.* 2001). The grouping of Taxaceae within conifers is unequivocal, and this refutes earlier ideas that some taxad genera might form separate lineages distinct from conifers *sensu stricto* (e.g. Florin 1951). More controversially, Gnetales have been grouped either within Pinaceae (Bowe *et al.* 2000; Chaw *et al.* 2000) or as sister group to Pinaceae (Soltis *et al.* 2002). Basal clades within conifers include first Pinaceae, which are sister group to all others, and second a clade comprising Araucariaceae and Podocarpaceae (Stefanovic *et al*. 1998; Gugerli *et al.* 2001). This is followed by a clade comprising all other conifers, including *Sciadopitys*. Within this latter grouping, Taxaceae are most closely related to Cephalotaxaceae, and Taxodiaceae are paraphyletic to Cupressaceae (Stefanovic *et al*. 1998; Cheng *et al.* 2000). Based on molecular methods, the divergence of the Cupressaceae/Taxodiaceae clade from other taxads has been estimated at 192 to 230 Ma (Ladinian: mid-Triassic to Pliensbachian: Early Jurassic) (Cheng *et al.* 2000). This is broadly consistent with fossil evidence indicating that Taxodiaceae were well established by the mid-Jurassic. The early departure of the Araucariaceae/Podocarpaceae clade is also consistent with fossil evidence of a Late Permian or Early Triassic origin. More interesting, though, is the basal position of Pinaceae. With the exception of *Pinus*, there is little fossil evidence for living genera prior to the Tertiary. However, fossils showing some of the characteristics of the Pinaceae, such as leaves (*Pityocladus*), seed cone scales (*Schizolepis*) and cones (*Pityostrobus, Pseudoaraucaria*), are present by the mid-Jurassic. Molecular phylogenies would be consistent with a much earlier origin of the group during the Permian Period. If the molecular data are correct, it would seem that the early fossil history of Pinaceae is currently very poorly understood.

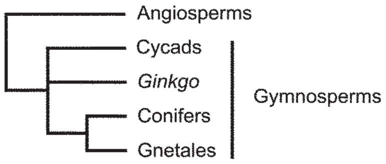


Fig. 2. Summary of relationships among the major groups of seed plants based on living members as deduced from plastid, nuclear, and mitochondrial gene sequences. Gnetales are either sister group to conifers, as depicted, or nested inside conifers within Pinaceae as sister to *Pseudotsuga*. Adapted from the results of Soltis *et al*. 2002.

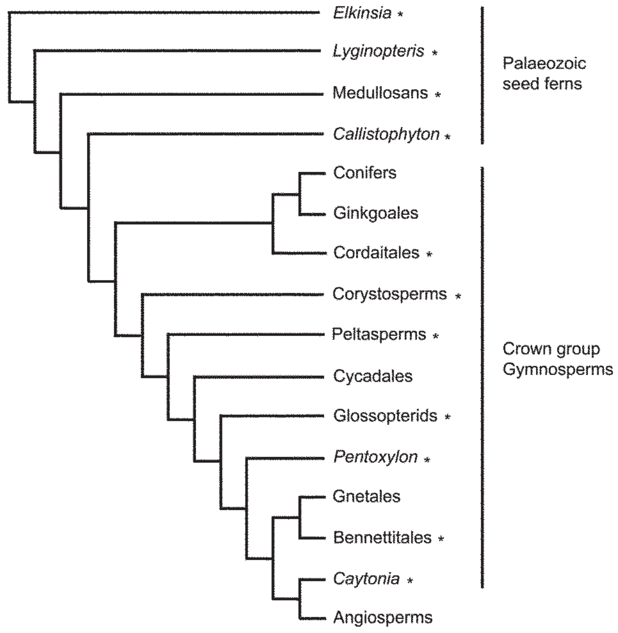


Fig. 3. A representative cladogram of relationships among major groups of living and fossil seed plants based on comparative morphology. Extinct groups are marked "*". Adapted from Doyle (1998).

Morphological phylogenies: the big picture

Comparative morphology still plays an important role in elucidating the evolution of gymnosperms. Much of their diversity is extinct, and in order to capture this information from fossils it is necessary to make use of morphology rather than molecules in phylogenetic analyses. In agreement with molecular analyses, cladistic studies based on comparative morphology show that seed plants (gymnosperms and angiosperms) are a monophyletic group (Crane 1985; Doyle & Donoghue 1986; Rothwell & Serbet 1994). In addition, fossil evidence indicates that the group arose from an assemblage of extinct, predominantly Devonian, antecedents called progymnosperms (Beck & Wight 1988). These were trees or shrubs with conifer-like wood and fern-like reproduction, a combination of features unknown among living species. In addition, the gymnosperm/angiosperm stem group comprises a paraphyletic assemblage of Palaeozoic seed ferns, including extinct groups such as Calamopityales, Hydraspermales, Lyginopteridales, Callistophytales and Medullosales. These results clarify and flesh out stages in the evolution of various aspects of gymnosperm morphology, including stem and leaf architecture and the development of the various tissue systems that make up the seed as well as aspects of their reproductive biology. The seed plant crown group contains by definition all of the living species of gymnosperms and angiosperms as well as many extinct groups such as Cordaitales, Corystospermales, Peltaspermales, Glossopteridales, Pentoxylales, Caytoniales and Bennettitales. Relationships among these groups are still poorly resolved, and several plausible alternative topologies exist (Doyle 1998). In marked contrast to molecular phylogenies, morphological cladistic analyses group living Gnetales with angiosperms. This has been dubbed the 'anthophyte hypothesis'. The anthophyte hypothesis implies a more recent origin of the lineage leading to angiosperms than that implicit in the molecular studies discussed above (Doyle & Donoghue 1993).

Conflict & consensus

In summarising the current status of gymnosperm phylogeny it is easy to forget the absence of methodology and the confused phylogenetic picture that characterised pre-cladistic and pre-molecular studies. Some results that are solidly conventional now were deemed highly controversial or too poorly supported even 20 years ago (Doyle 1998). Major groups such as seed plants and angiosperms are now regarded as well-supported monophyletic groups. Molecular methods have added new data that frequently confirm conclusions reached from comparative morphology, and they also provide much higher resolution of relationships among species in living groups such as conifers and cycads.

Notwithstanding this concordance, there are several areas of uncertainty and disagreement. The relationships among many of the major living and extinct groups of seed plants are still poorly understood. The close relationship between Gnetales and angiosperms predicated on the basis of comparative morphology appears to have been refuted by molecular studies that favour a relationship between Gnetales and conifers (Donoghue & Doyle 2000). Molecular studies indicate that the gymnosperm crown group is monophyletic. However, when one considers the extinct Palaeozoic seed ferns, gymnosperms as a whole must still be regarded as a paraphyletic assemblage. It seems likely that the accumulation of more molecular data combined with a better understanding of the phylogenetic signal contained within will lead to increasingly stable hypotheses of relationship for the living groups. This will provide a framework of constraint within which data from the fossil record can be analysed.

Fossil gymnosperms provide invaluable information on the morphology of plants in the stem groups of major clades. It is the fossils that tell us about the evolution of such key characteristics as stem and leaf architecture and the seed. Fossils also enable us to date the origins of major clades and, importantly, to test independently the calibrated phylogenetic trees that can be derived from molecular phylogenetics. Piecing together extinct gymnosperms to reconstruct conceptual whole organisms and placing them in a phylogenetic context therefore remains an important goal of palaeobotany.

Phylogenetic trees derived either from molecules or morphology often have interesting and surprising implications that can cause us to re-examine the fossil evidence from a new perspective. For example, the results of phylogenetic studies indicate a lengthier history of the conifer family Pinaceae than one would suspect from the known fossil evidence. Within cycads, phylogenies support a relictual interpretation of the distributions of the modern genera *Macrozamia*, *Lepidozamia* and *Encephalartos*, a result that is borne out by a study of the fossil evidence. The close relationship between angiosperms and gymnosperms is confirmed and clarified through phylogenetic work. We know that the history of the flowering plants is intimately bound to that of the gymnosperms, yet paradoxically there is little pre-Cretaceous fossil evidence for this (Crane *et al.* 1995). Even in today's molecular world, the study of fossil plants of Mesozoic and Late Palaeozoic age still has much to offer us in our quest to understand the evolution of gymnosperms.

NOMENCLATURE OF PALAEOZOIC PTERIDOSPERMOUS SUPRA-GENERIC TAXA

Many supra-generic taxa covered in this volume are based on extant plants or, where based on fossil plants, have been relatively recently defined. The nomenclature of these taxa is thus mostly uncontroversial. However, the classification of the Palaeozoic pteridosperms has a much longer history and the nomenclature of the supra-generic taxa is more problematic. This short essay is an attempt to examine these problems and to explain the nomenclature that we have adopted here.

Part of the problem here is that the International Code of Botanical Nomenclature (ICBN—Greuter *et al*. 2000) is more 'relaxed' about the nomenclature of most ranks of supra-generic taxa, especially as far as chronological priority. The main exception is the rank of family, for which chronological priority still applies. The discussion will therefore start with the families of these plants.

Families

We are taking it 'as read' that the families (and higher-order taxa) dealt with in this study are whole-plant taxa, and not morphotaxa as in ICBN Article 1.2. However, some of them clearly started life as morphofamilies, having been subsequently emended so that they now encompass additional or all parts of the plant (or, at least, all parts normally preservable in the fossil record). The ICBN is somewhat ambiguous as to what happens in such circumstances, especially as to what is the date of publication of the family name and who is the author. We have here taken the date and authorship to be based on the first publication of the name, not when it was first applied to a whole-plant family; to do otherwise would be to introduce problems of homonymy. On the other hand, we recognise that the nomenclature could be disrupted by somebody emending one of the earlier-published morphofamilies, whose type can be assigned to a particular whole-plant family, so that it becomes a whole-plant family and takes priority. We have not done this, as it would mean the replacement of some well-established family names; for stability's sake, let us hope that colleagues follow the same philosophy, at least until the ICBN is clarified on this point.

Lyginopteridaceae (Lyginopteridopsida, p. 78)

Doweld (2001) lists nine validly published synonyms for the family which he gives two alternative names—the Lagenostomaceae or Lyginopteridaceae. The name that has probably been most widely used in the literature for this group is the Lyginopteridaceae, but it is not the oldest legitimate name. The earliest published name in Doweld's (2001) list is the Sphenopteridaceae Göppert 1842. However, this was clearly a morphofamily for foliage with lobed pinnules and attached sporangia, and so cannot feasibly be used as a whole-plant family of gymnosperms without emendation. The next oldest name is Pseudopecopteridaceae Lesquereux 1884. Many of the species that were originally included within *Pseudopecopteris* Lesquereux 1880 have foliage that was probably borne on *Lyginopteris* Potonié 1897 or *Heterangium* Corda 1845 stems. Nevertheless, the diagnosis and circumscription given by Lesquereux (1884) clearly show that he intended the family only for foliage.

The next oldest family name listed by Doweld (2001) is the Lyginodendraceae Scott 1900 (not 1909, as given by Doweld). At this time, these plants were envisaged to belong to a plant group that was systematically intermediate between the ferns and gymnosperms, called the 'Cycadofilices'. However, the discovery shortly afterwards (Oliver & Scott 1903) that these stems belonged to fully gymnospermous plants (Oliver & Scott 1903) caused Scott (1908, 1909) to revise the family diagnosis to a form that is virtually identical to how we view it today. Critically, Scott included morphological and anatomical characters of the ovules, pollen-organs, foliage and stems, making it clearly a whole-plant family.

As pointed out by Potonié (1900), however, this name is illegitimate, as it was based on the illegitimate genus name *Lyginodendron* Williamson 1873 non Gourlie 1844 (the latter based the name on cortical impressions of an arborescent lycopsid). Potonié (1900) therefore instigated the 'new' family name Lyginopteridaceae. Doweld (2001) incorrectly attributes the family to Bessey (1907), but Bessey himself clearly states that he is using Potonié's classification. The earliest published legitimate name for this whole-plant family must, therefore, be Lyginopteridaceae Potonié 1900.

In an earlier analysis (Cleal 1993), the family was referred to as the Lagenostomaceae, and incorrectly attributed to Seward (1917). The family was in fact first established by Long (1975), who clearly established it as a morphofamily for ovulate structures. Consequently, not only does it significantly post-date the Lyginopteridaceae, it has a fundamentally different circumscription.

Potonieaceae (Cycadopsida, p. 125)

This name was first established by Halle (1933) as a morphofamily for pollen-organs, but was emended by Remy & Remy (1959) to include details of the foliage. The family has been subsequently further emended to include additional information on the ovules and stem anatomy by Corsin (1960) and Laveine *et al*. (1993), and renamed by them, respectively, as the Rachivestitaceae and Parispermaceae. While the family concepts developed by Corsin (1960) and Laveine *et al*. (1993) are far closer to the family as interpreted here, Halle's (1933) still takes nomenclatural priority.

Alethopteridaceae (Cycadopsida, p. 126)

For the family of plants with *Medullosa* Cotta 1832 and allied stems, Doweld (2001) lists nine synonyms. The oldest name, Neuropteridaceae Göppert 1842, is a morphofamily for foliage, and so cannot be used as a whole-plant family without an emendation. No such emendation has ever been proposed.

The next oldest name is the Medullosaceae Göppert 1865. This was based around anatomically preserved stems and, so again, cannot be taken as a whole-plant family without emendation. In this case, however, there has been a progressive emendation, by Scott (1900) and Potonié (1900) to include details of the foliage, by Scott (1908, 1909) to add details of the ovules, and by Scott (1923) to add details of the pollen-organs. The problem here is that the diagnosis encompasses virtually all of the fossil plants with *Medullosa* stems, which are now generally recognised to represent several families. If the Medullosaceae is to be retained as Scott intended it, as a whole-plant family, which family is it?

This can only be established by determining the type of the family, which by definition is the type of *Medullosa* (ICBN Article 10.6). Unfortunately, the type species is *Medullosa stellata* Cotta 1832 (designated Solms-Laubach 1887) from the Lower Permian of Saxony. It is therefore from towards the end of the known evolutionary history of this order, and where the groupings of taxa are only very imperfectly understood. The evidence of association with other plant remains (e.g. as summarised by Barthel 1976) also does not help us understand the systematic position of this species. All that we can say at present is that the name Medullosaceae Göppert emend. Scott 1923 should be the legitimate name for one of the families of this order, but at present we do not know which one.

The next oldest synonym is the Alethopteridaceae Lesquereux 1884. This was initially just a morphofamily for foliage, but Corsin (1960) subsequently emended the diagnosis to include details of the ovules and pollen-organs, and the general form of the plants. Critically, he stated that the ovules are of the *Pachytesta*-type, and therefore essentially correspond to the family Pachytestaceae Doweld 2001. As this is the family that we have accepted in the present analysis, its correct name must be Alethopteridaceae Lesquereux 1884, albeit emended a little further than in Corsin (1960) to include additional details of the ovule anatomy.

Corsin (1960) also recognised other families for plants that bore *Medullosa*-type stems: Cyclopteridaceae Corsin 1960, Callipteridiaceae Corsin 1960 and Odontopteridaceae Trapl 1926 emend. Corsin 1960. Although these were essentially whole-plant families, the evidence of their reproductive organs was less well-established than with the Alethopteridaceae. Although these families may eventually become more firmly established when evidence of their reproductive structure becomes better known (e.g. see comments by Cleal & Shute 2003), they have not been incorporated in the present study.

Callistophytaceae **(Lyginopteridopsida, p. 96)**

This is one of the most clearly defined and circumscribed Palaeozoic pteridospermous families, but even here there is some uncertainty about the nomenclature. Doweld (2001) records the Poroxylaceae Scott 1923 as an earlier synonym, presumably based on the observation by Rothwell (1975) that its type genus *Poroxylon* Renault 1896 is a 'callistophytacean' and not a cordaitanthalean as originally envisaged. However, Scott (1923) based this family almost entirely on stem anatomy; mention was made of associated ovules and leaves (reported by Grand'Eury 1905) but their details were not included within his concept for the family. The Poroxylaceae may therefore be taken as being a morphofamily for anatomically preserved stems, and whose circumscription is thus fundamentally different from that of the Callistophytaceae. The Callistophytaceae may therefore be allowed to stand as the name for the whole-plant family.

Orders

Unlike families, the use of taxonomic names of the rank of order (and class) does not have to follow simple chronological priority. ICBN Article 16.1 states that such names may be of one of two types: automatically typified names, based on the name of a family but with the termination changes; or descriptive names for taxa with a recognised circumscription.

The Lyginopteridales Corsin 1960 clearly falls into the first category, being typified by the family Lyginopteridaceae. Meyen (1984, 1987) and Cleal (1993) instead used the name Lagenostomales Seward 1917, since their classifications were closely tied to ovule anatomy. However, Seward (1917) had established this taxon purely as a morpho-order for isolated ovules, and Taylor & Taylor (1993) have argued that such a taxonomy for isolated ovules might still have a role in palaeobotanical studies. To avoid confusion, therefore, it seems advisable to use the name Lyginopteridales for this order.

However, the order containing the family Alethopteridaceae is not so straightforward. Most authors have referred to this order as either the Trigonocarpales Seward 1914 or the Medullosales Corsin 1960. The latter name suffers from the same shortcomings as the Lagenostomales (see above) and is probably best rejected for this whole-plant order. The Medullosales as defined by Corsin (1960) is in contrast nearer to a whole-plant taxon such as dealt with in the present study. In one way it may be regarded as an automatically typified name, as the family Medullosaceae remains valid (see earlier), even if we cannot yet fit it into the classification that we are using. It can also be considered to be a descriptive name, as it indicates that it includes the plants with *Medullosa*-type stems. There seems to be no justification, therefore, to create a new, automatically typified order name based on the Alethopteridaceae. Nor is there any reason to replace it with the Pachytestales Doweld 2001, simply because the name Medullosales is not rooted in the generic name of an ovule; at present there is no reason to assume that any plants with *Medullosa* stems do not belong to the Medullosales, nor that the Medullosales includes plants with stems that have an anatomy fundamentally different from that of *Medullosa*.

Classes

The fossil plants discussed in this essay belong to only two classes. The Cycadopsida Brongniart 1843 is based on extant plants, and its nomenclature straightforward, but the second class is more problematic. Cleal (1993) established for it the name Lagenostomopsida, rooting it in the order Lagenostomales as it was there interpreted. As argued above, however, the latter order is probably best called the Lyginopteridales, thus undermining the main argument for the Lagenostomopsida. In the present analysis, we have therefore adopted the existing and automatically typified name Lyginopteridopsida Novák 1961.

THE TRIASSIC EXPLOSION

Towards assessing biodiversity

Explosive radiation in the Triassic

The evolution of terrestrial life (plants, insects, tetrapods) during the Triassic appears to have been as explosive as that of marine life, exemplified by the Burgess Shale (Gould 1989), during the Cambrian. The relatively clean slate following the end-Permian extinction evidently provided unsurpassed opportunities for the adaptive radiation of life on land—as did the slate around the onset of the Cambrian for life in the seas.

Since this volume was originally planned as a section in our *Heyday of the gymnosperms* (And. & And. 2003) on the Late Triassic Molteno Fm., we place some particular focus on the phenomenon of the Triassic Explosion. The investigation with regard to the gymnosperms during this unique phase of Earth history is included here more or less as previously conceived.

We first consider biodiversity at all ranks amongst Triassic plants globally, then take a cursory look through the dramatically expanding science of molecular biology for possible insight into the nature of evolution during such intervals of greatly increased radiation.

Gymnosperm versus angiosperm diversity

During their respective heydays, the gymnosperms appear to have outshone the angiosperms in diversity, at least at higher rank. If the nine classes of Triassic gymnosperm indeed merit recognition as of equivalent rank to the single class of extant angiosperm, then this hypothesis is well founded. Though only 27 orders and 38 families of Triassic gymnosperm are recorded (*observed*) compared to 45 orders and 457 families of extant angiosperms (Tab. 11c adjacent), our statistical projections (And. & And. 1995, 2003; And. *et al*. 1996) suggest that the *preserved* and *existed* gymnosperm tallies at these ranks would at least match those of the angiosperms.

Triassic versus extant gymnosperm diversity

Comparison of gymnosperm diversity at their Late Triassic heyday and their extant nadir reveals a very considerable difference in richness. While the remarkable diversity in the *observed* gymnosperms of the Late Triassic lends perspective to the relict status of the group today, consideration of the taxonomic spectrum of today adds much to our perspective of the *existing* diversity at the heyday (Tab. 11c adjacent).

The *observed* diversity at higher taxonomic levels (classes and orders) in the Molteno Fm., a single geological stratum representing a single simple biome in a restricted region of one country, is far greater than the *existing* gymnosperm diversity globally today. At family level, the figures are roughly equivalent. At generic and specific level, the extant figures far exceed the Molteno figures.

Molteno (observed): 8 classes, 18 orders, 18 families, 20 gen., 51 spp.
Extant (existing): 4 classes, 4 orders, 13 families, 84 gen., 992 spp.

From class down to species, the degree to which the *observed* Molteno diversity represents the *existed* global Carnian diversity shifts dramatically. While the eight Molteno classes might nearly match the Carnian class diversity globally, the 51 Molteno species will be a drop in the ocean compared to the *existing* Carnian species globally.

Relictual nature of extant gymnosperms

Of the 13 extant gymnosperm families, close on 50% (six families) are monogeneric (Tab. 11a adjacent). All 13 families, apparently, saw their diversity heydays in the Early Cretaceous or early to mid-Tertiary (Tab. 11b). After a long and eventful history, the gymnosperms today are clearly a relictual group.

Tab. 11a. Classification of extant gymnosperms; to family with generic & specific diversity

	Diversity	
PINOPSIDA Burnett 1835 (see p. 130)		
PINALES Dumort 1829		
Pinaceae Lindley 1836	11 gen	225 spp
Podocarpaceae Endlicher 1847	19 gen	189 spp
Araucariaceae Henkel & Hochstetter 1865	3 gen	41 spp
Cupressaceae Rich., ex Bartl. 1830	29 gen	133 spp
Sciadopityaceae Luerss. 1877	1 gen	1 sp.
Taxaceae Gray 1821	6 gen	34 spp
CYCADOPSIDA Brongn. 1843 (see p. 154)		
CYCADALES Dumort. 1829		
Cycadaceae Pers. 1807	1 gen	102 spp
Zamiaceae Horan. 1834	8 gen	191 spp
Stangeriaceae (Pilg.) L.A.S.Johnson 1959	2 gen	4 spp
GINKGOOPSIDA Engler 1897 (see p. 172)		
GINKGOALES Goroschankin 1904		
Ginkgoaceae Engler 1897	1 gen	1 sp.
GNETOPSIDA Eichler ex Kirpotenko 1884 (see p. 210)		
GNETALES Luerss.1879		
Ephedraceae Dumort.1829	1 gen	40 spp
Gnetaceae Lindl. 1834	1 gen	30 spp
Welwitschiaceae Markgr. 1926	1 gen	1 sp.
4 classes, 4 orders, 13 families,	84 gen	992 spp

Sources: see pages in this volume as indicated.

Tab. 11b. Heydays of extant gymnosperm families

	Max. radiation (&/or heyday)	Nadir	This vol. general	This vol. family
PINALES				
Pinaceae	Early Cret.	Extant	p.133	p.134
Podocarpaceae	Early Oligoc.	”	p.130	p.136
Araucariaceae	Early Cret.	”	p.57	p.135
Cupressaceae	Early Oligoc.	”	p.130	p.138
Sciadopityaceae	Early Tert.	”	-	p.141
Taxaceae	?	”	-	p.142
CYCADALES				
Cycadaceae	Eocene	”	p.156	p.157
Stangeriaceae	Eocene	”	”	p.158
Zamiaceae	Eocene	”	”	p.159
GINKGOALES				
Ginkgoaceae	Eocene	”	p.172	p.178
GNETALES				
Ephedraceae	Early Cret. (BRM)	”	p.210	p.213
Gnetaceae	?	”	”	p.214
Welwitschiaceae	Early Cret. (BRM)	”	”	p.215

Max. radiation &/or heyday:

- Available information remains sparse and difficult to assess, so all entries in this column could be prefixed by ?.
- Diversity in the extant gymnosperm families overall appear to have peaked during two intervals—in the Early Cretaceous coinciding with the radiation of the angiosperms and again in the Eocene to Early Oligocene.

Sources: see pages in this volume as indicated.

Tab. 11c. Diversity (gymnosperm versus angiosperm)

Gymnosperms (based on ovulate fruit)
Extant: 4 classes, 4 orders, 13 families, 84 genera, 992 spp.
Global Trias.: 9 classes, 27 orders, 38 families, ?58 genera, ? spp.
Molteno (CRN): 8 classes, 18 orders, 18 families, 20 genera, 51 spp.

Angiosperms
Extant: 1 class, 45 orders, 457 families, 12,650 genera, 233,885 spp.

Sources: Tab. 1 (p. 4); Tab. 13 (pp 24, 25)

ovulate genera	TCs	spp.	indivs	classes	pollinate genera	TCs	spp.	indivs	classes
Fanerotheca	26	4	247	GINKGOOPSIDA	*Stachyopitys*	27	6	539	GINKGOOPSIDA
Umkomasia	22	8	503	GINKGOOPSIDA	*Pteruchus*	22	3	425	GINKGOOPSIDA
Telemachus	18	6	311	PINOPSIDA	*Kannaskoppianthus*	12	10	92	GINKGOOPSIDA
Fraxinopsis	18	3	306	GNETOPSIDA	*Rissikianthus*	5	4	79	PINOPSIDA
Dordrechtites	17	3	413	PINOPSIDA	*Antevsia*	5	1	32	GINKGOOPSIDA
Peltaspermum	17	5	257	GINKGOOPSIDA	*Switzianthus*	4	2	54	GINKGOOPSIDA
Rissikistrobus	8	3	85	PINOPSIDA	*Eosteria*	4	2	27	GINKGOOPSIDA
Avatia	6	1	114	GINKGOOPSIDA	*Cycadolepis*	3	1	14	BENNETTITOPSIDA
Hamshawvia	4	4	24	GINKGOOPSIDA	*Weltricha*	2	2	3	BENNETTITOPSIDA
Matatiella	4	4	17	GINKGOOPSIDA	*Lutanthus*	3	3	5	PINOPSIDA
Fredlindia	3	1	16	BENNETTITOPSIDA	*Odyssianthus*	2	1	2	PINOPSIDA
Kannaskoppia	1	1	50	GINKGOOPSIDA	*Androstrobus*	2	2	2	CYCADOPSIDA
Lindtheca	1	1	16	BENNETTITOPSIDA	*Helvetianthus*	1	1	6	PINOPSIDA
Alexia	1	1	6	INCERTAE SEDIS	*Leguminanthus*	1	1	5	BENNETTITOPSIDA
Gypsistrobus	1	1	5	PINOPSIDA	*Fredianthus*	1	1	2	PINOPSIDA
Nataligma	1	1	4	GNETOPSIDA					
Hlatimbia	1	1	2	INCERTAE SEDIS					
Cetifructus	1	1	2	INCERTAE SEDIS					
Hystricia	1	1	1	INCERTAE SEDIS					
Avistrobus	1	1	1	PINOPSIDA					
20 genera		51		8 classes (18 orders)	15 genera		35		4 classes (11 orders)

Tab. 12. Molteno Fm., on the relative rarity of ovulate & pollinate genera

Ovulate & pollinate genera: placed in order of frequency (TCs), then abundance (indivs)
Frequency (TCs): number of TCs (of 100) sampled in Molteno Fm.
Diversity (spp.): number of species described
Abundance (indivs): tally of individuals in curated collection

Reference: And. & And. 2003 (adapted from Tab. 12 (p. 18) & Tab. 15 (p. 21)

Diversity of Late Triassic Molteno gymnosperms

At family, order and class level

In our *Heyday of the gymnosperms* monograph (2003), we aimed to demonstrate the extraordinary morphological range encompassed by the gymnospermous ovulate strobili preserved in the Molteno Fm. The 20 ovulate genera recognised and described were attributed to 18 families in 18 orders spread across as many as eight classes. These represent only the *observed* (collected) taxa. In view of the level of intensive and extensive sampling reached, it has been possible to generate statistical projections of the number of *preserved* orders (based on ovulate structures) in the Molteno. The calculations, imperfect as they necessarily are, hint at Late Triassic gymnospermous diversity at the taxonomic rank of order at least as wide as that of the angiosperms today (And. & And. 1995; Anderson *et al.* 1996).

At family level (though not calculated), we predict a similar result, while at class level (see pp 4, 22), the gymnosperms at their Triassic heyday (eight classes) appear to express considerably greater diversity than do the angiosperms today (one or two classes).

At species level

In a companion monograph (And. & And., in prep.), we explore biodiversity in the Molteno Fm. at the rank of species. We focus particularly on the *Kannaskoppiaceae* (p. 185), a member of the Ginkgoopsida newly described in And. & And. (2003). The reference whole-plant genus appears ideally suited to build a model for the *palaeodeme* (And. & And. 1983, 1989) approach to species delineation. The foliage is diverse (*ca* 10 species), but not too diverse; frequent, 25 of 100 Molteno taphocoenoses (TCs), but not too frequent; common, generally less than 1% of a TC, but never abundant or dominant; and has clearly defined diagnostic features. Very significantly, it is the only Gondwana Triassic gymnosperm whole-plant genus with foliage and both ovulate and microsporangiate structures known in organic connection.

Kannaskoppia/Kannaskoppifolia occurs in all seven primary habitat types recognised in the Molteno Fm. (And. & And. 2003). We interpret the genus as being a herbaceous pioneer that diversified to fill the different ecological niches associated with disturbed or cleared ground in each of the distinctive habitats—riverine forest, sandbank, floodplain and so on. The efficacy of the palaeodeme approach to taxonomy at species level in the framework of the ecozonal pattern of species differentiation can be tested. (It is well established for extant ecosystems or biomes that each species within a genus tends to occupy a distinctive ecozone.)

Through reference to such a model we might hope to develop a naturally based, consistently objective species-level taxonomy in documenting well-sampled fossil floras. The aim is to approximate the species as recognised in extant floras. Compatible data for successive formations might then be generated and meaningful biodiversity trends plotted.

Interim application of the palaeodeme approach along with statistical projections for the Molteno, point to Late Triassic plant (and insect) species diversity matching the levels of richness witnessed today (And. & And. 1995; Anderson *et al.* 1996).

Tab. 13. GLOBAL TRIASSIC OVULATE GENERA: CLASSIFICATION & BIODIVERSITY

DIVISION CLASS ORDER FAMILY Genus (♀ fruit)	Author	Origin of type species	
PINOPHYTA			
PINOPSIDA			
DORDRECHTITALES			
DORDRECHTITACEAE			
Dordrechtites	H.M. Anderson 1978	S.Africa (Molteno Fm.)	L. Trias. (CRN)
CHEIROLEPIDIALES			
CHEIROLEPIDIACEAE			
Cheirolepis	Schimp. 1870	Germany (Bayreuth)	L. Trias. (RHT)
Hirmeriella	Hörnh. 1933	Germany (Franken)	L. Trias. (RHT)
PALISSYALES			
PALISSYACEAE			
Palissya	Endl. 1847	Europe	Trias./Jur.
VOLTZIALES			
VOLTZIACEAE			
Voltziopsis	Potonié 1899	Germany (Coburg)	M. Trias. (NOR)
Voltzia	Brongn. 1828	Europe	• Trias.
Florinostrobus	Delev. & Hope 1987	USA (Pekin Fm.)	L. Trias. (CRN)
Cycadocarpidium	Nath. 1886	Sweden (Scania)	L. Trias. (RHT)
Aetophyllum	Brongn. 1828	France (Vosges)	M. Trias. (ANS)
Telemachus	H.M. Anderson 1978	S. Africa (Molteno Fm.)	L. Trias. (CRN)
Swedenborgia	Nath. 1876	Sweden (Scania)	Jurassic*
Borysthenia	Stanisl. 1976	USSR (Donetz Basin)	L. Trias. (NOR)
Pachylepis	Kräusel 1952	Germany (Württemberg)	L. Trias.
Tricranolepis	Roselt 1958	Germany (Thuringia)	L. Trias.
Schizolepis	Braun 1847	Europe	• Trias.
Glyptolepis	Schimp. 1870	Germany (nr. Coburg)	L. Trias.
INCERTAE SEDIS (1 order)			
INCERTAE SEDIS (1 fam.)			
Gypsistrobus	And. & And. 2003	S. Africa (Molteno Fm.)	L. Trias. (CRN)
Avistrobus	And. & And. 2003	S. Africa (Molteno Fm.)	L. Trias. (CRN)
PINALES			
PINACEAE			
Compsostrobus	Delev. & Hope 1973	USA (N. Carolina)	L. Trias. (CRN/NOR)
PODOCARPACEAE			
Rissikistrobus	And. & And. 2003	S. Africa (Molteno Fm.)	L. Trias. (CRN)
Stalagma	Z.Zhou 1983	China (Hunan)	L. Trias. (RHT)
ARAUCARIACEAE			
Araucarites	C.Presl 1838	Austria (Tirol)	Tertiary*
CUPRESSACEAE			
Parasciadopitys	Yao *et al*. 1997	Antarctica (Fremouw Fm.)	M. Trias. (LAD)
CYCADOPSIDA			
CYCADALES			
CYCADACEAE			
Bjuvia	Florin 1933	Sweden (Bjuv)	L. Trias. (RHT)
Dioonitocarpidium	Lilienstern 1928	Germany (Estenfeld)	L. Trias.
Palaeocycas	Florin 1933	Sweden (Scania)	L. Trias. (RHT)
GINKGOOPSIDA			
PELTASPERMALES			
PELTASPERMACEAE			
Peltaspermum	T.M.Harris 1937	Greenl. (Scoresby Sound)	L. Trias. (RHT)
MATATIELLALES			
MATATIELLACEAE			
Matatiella	And. & And. 2003	S. Africa (Molteno Fm.)	L. Trias. (CRN)
GINKGOALES			
UMALTOLEPIDIACEAE			
Toretzia	Stanisl. (1971) 1973	Ukraine (Novoraisk Fm.)	L. Trias. (RHT)
AVATIACEAE			
Avatia	And. & And. 2003	S. Africa (Molteno Fm.)	L. Trias. (CRN)
LEPTOSTROBALES			
LEPTOSTROBACEAE			
Leptostrobus	Heer 1876	USSR (Siberia)	Jurassic*
Staphidiophora	T.M.Harris 1935	Greenl. (Scoresby Sound)	L. Trias. (RHT)
Irania	Schweitzer 1977	Iran (Alborz Mts.)	L. Trias. (RHT)
HAMSHAWVIALES			
HAMSHAWVIACEAE			
Hamshawvia	And. & And. 2003	S. Africa (Molteno Fm.)	L. Trias. (CRN)
UMKOMASIALES			
UMKOMASIACEAE			
Umkomasia	H.H.Thomas 1933	S. Africa (Molteno Fm.)	L. Trias. (CRN)
Fanerotheca	Freng. 1944c	Argentina (Potrerillos Fm.)	L. Trias. (CRN)
CAYTONIALES			
CAYTONIACEAE			
Caytonia	H.H.Thomas 1925	England (Yorkshire)	Jurassic*
PETRIELLALES			
PETRIELLACEAE			
Petriellaea	T.N.Taylor *et al*. 1994	Antarctica (Fremouw Fm.)	M. Trias. (LAD)
KANNASKOPPIACEAE			
Kannaskoppia	And. & And. 2003	S. Africa (Molteno Fm.)	L. Trias. (CRN)
INCERTAE SEDIS			
INCERTAE SEDIS			
Cetifructus	And. & And. 2003	S. Africa (Molteno Fm.)	L. Trias. (CRN)
INCERTAE (3 classes)			
ALEXIALES			
ALEXIACEAE			
Alexia	And. & And. 2003	S. Africa (Molteno Fm.)	L. Trias. (CRN)

HLATIMBIALES			
HLATIMBIACEAE			
Hlatimbia	And. & And. 2003	S. Africa (Molteno Fm.)	L. Trias. (CRN)
INCERTAE SEDIS			
INCERTAE SEDIS			
Hystricia	And. & And. 2003	S. Africa (Molteno Fm.)	L. Trias. (CRN)
BENNETTITOPSIDA			
FREDLINDIALES			
FREDLINDIACEAE			
Fredlindia	And. & And. 2003	S. Africa (Molteno Fm.)	L. Trias. (CRN)
BENNETTITALES			
WESTERHEIMIACEAE			
Westerheimia	Krasser 1918	Austria (Lunz)	L. Trias. (CRN)
VARDEKLOEFTIACEAE			
Vardekloeftia	T.M.Harris 1932	Greenl. (Scoresby Sound)	L. Trias. (RHT)
LAUROZAMITACEAE			
*Williamsonia**	Carruth. 1870	England (Yorkshire)	Jurassic*
STURIANTHACEAE			
Sturianthus	Kraüsel 1950	Austria (Lunz)	L. Trias. (CRN)
BENNETTICARPACEAE			
Bennetticarpus	T.M.Harris 1932	Greenl. (Scoresby Sound)	L. Trias. (RHT)
WILLIAMSONIELLACEAE			
Wielandiella	Nath. 1910	Sweden (Scania)	L. Trias. (RHT)
PENTOXYLALES			
LINDTHECACEAE			
Lindtheca	And. & And. 2003	S. Africa (Molteno Fm.)	L. Trias. (CRN)
GNETOPSIDA			
FRAXINOPSIALES			
FRAXINOPSIACEAE			
Fraxinopsis	Wieland 1929	Argentina (Potrerrilos Fm.)	L. Trias. (CRN)
NATALIGMALES			
NATALIGMACEAE			
Nataligma	And. & And. 2003	S. Africa (Molteno Fm.)	L. Trias. (CRN)
DINOPHYTONALES			
DINOPHYTONACEAE			
Dinophyton	Ash 1970	USA (south-western)	L. Trias. (CRN/ NOR)
DECHELLYIALES			
DECHELLYIACEAE			
Dechellyia	Ash 1972	USA (NE Arizona)	L. Trias. (CRN)
AXELRODIOPSIDA			
AXELRODIALES			
AXELRODIACEAE			
Axelrodia	Cornet 1986	USA (NW Texas)	L. Trias. (NOR)
ZAMIOSTROBACEAE			
Zamiostrobus	Endl. 1836	England	Cretaceous*
Primaraucaria	Bock 1954	USA (Virginia)	L. Trias. (CRN)

Diversity (total global Triassic)—9 classes (3 unnamed), 27 orders, 38 families, 58 genera
Molteno diversity (taxa in bold)—8 classes, 18 orders, 18 families, 20 genera

Tab. 13. Global Triassic ovulate genera: classification & biodiversity

Classification: extracted and elaborated from the global Devonian–extant classification presented as Tab. 2.

Ovulate genera: the classification is based exclusively on ovulate genera (existing families and orders represented only by other organs in the Triassic are not reflected)

Origin of types: all genera recorded in the Triassic, whether originally based on Triassic or non-Triassic types are included (the 6 non-Triassic types are marked by an *).

Synonyms: genera formally reduced to junior synonymy are excluded.

Diversity of Triassic gymnosperms

(observations based on Tab. 3)

***Observed* global diversity (genera, families, orders):** 58 ovulate genera falling in 38 families and 27 orders are known from Triassic beds globally: an average of only two genera per order. Half of these genera belong to only four orders, the Voltziales, Pinales, Cycadales and Bennettitales. The largest orders are clearly the Voltziales with 12 genera and the Bennettitales with six genera. Most of the remaining orders are monogeneric. And as many as 30 of the 38 families overall are monogeneric. Most of the families are so distinctive as to have been included here in separate orders. The *observed* genera and families evidently represent just isolated spots and twigs on the prodigiously branching gymnosperm phylogenetic 'tree'.

'Preserved' and 'existed' taxa: With the *observed* (recorded) genera and families so disjunctly spread on the gymnosperm 'tree', it is clear that the *preserved* and *existed* taxa must far outnumber them.

***Observed* Molteno diversity (see And. & And. 2003):** As highlighted in Tab. 13 above, the Molteno ovulate genera show particularly high diversity: eight classes, 18 orders, 18 families, 20 genera. The diversity and range of known Molteno genera is far in excess of that from any other formation or country. Statistics for Gondwana countries show that from throughout the Australian Triassic sequence—with many more plant-bearing formations than South Africa (Charts 12, 14)—only 11 ovulate genera have been reported, while from South America, India and Antarctica, only five, nil and two genera, respectively, are known.

Endemism: One third (20 of 58) of the global Triassic ovulate genera occur in the Molteno. Ten of these genera are known only in the Molteno. To what measure does this reflect endemism, the quirks of preservation or simply sampling bias?

Sampling bias: The Molteno has been intensively and extensively sampled (*ca* 30 000 slabs from 100 taphocoenoses). It is an order of magnitude more fully sampled than most productive formations. The obvious conclusion is that a large number of new *preserved* genera remain to be unearthed in other Triassic formations.

Global Triassic ovulate genera: historical overview

An intriguing view emerges of palaeobotanical history and of phytogeography and biodiversity if we trace chronologically the description/institution of Triassic ovulate genera in respect of four possible categories of distortion: chronological, geographical, taxonomic and stratigraphic.

Chronological overview (1828–2005; 177 years)

The history of discovery/description of the ovulate reproductive genera of the Triassic (Tab. 16) has been slow and erratic. The earliest descriptions were those of Brongniart in 1828 (two voltzialean genera). By the close of the 19th Century merely six further genera had been described. Three notable flurries of activity characterised the 20th Century: the first in the late 1920s to mid-1930s (12 new genera) particularly involving Thomas, Florin and Harris; a second in the 1950s (four new genera) a while after the Second World War, involving Kräusel, Bock and Roselt; and a third in the 1970s (eight new genera), involving a new generation of palaeobotanists. The history of Triassic palaeobotany is notably subservient to political history, with each flurry of exploration following with some hiatus, in the wake of major human cataclysms: the First World War, the Second World War and the start of the Cold War.

Geographical bias in collecting & research

The very strong bias (prior to 2000) towards genera being described from Europe is a clear reflection of palaeobotanical history and has no bearing on centres of endemism or diversity. It is abundantly evident that, until recently, Europeans enjoyed an almost total monopoly in the field. All but one of the 22 genera instituted before 1954 were described by Europeans, and of these, only seven derived from localities outside Europe.

In the first 150 years of activity (1828–1977), only two new ovulate genera were described from Gondwana—*Fraxinopsis* from South America (Wieland 1929) and *Umkomasia* from South Africa (Thomas 1933). A further four appeared in the 20 years from 1978 to 1997; and a further 14 since (And. & And. 2003).

USA	6
Arctic (Greenland)	4
Europe	17
Middle East (Iran)	1
USSR (incl. Ukraine)	2
China	1
South America	1
Southern Africa	17
Antarctica	2
Total genera	51

The table excludes the 6 genera recorded in the Triassic, but created for Permian, Jurassic, Cretaceous or Tertiary types.

Source: Tab. 13 (p. 24, 25)

Tab. 14. Geographical bias, genera per region

Taxonomic bias (at class level)

If a *Brief history of gymnosperms* were to have been written in the year 1908, 80 years after Brongniart (1828) described *Voltzia*, the Triassic would have appeared particularly notable, not as the *Heyday of the gymnosperms*, but as a period represented exclusively by Pinopsida. Remarkably, all ovulate Triassic genera (eight in all) described to that date were members of this class.

Over the following quarter century, prior to the outbreak of the Second World War, a further 12 ovulate genera were added, and by then, intriguingly, a further four classes—Bennettitopsida, Cycadopsida, Gnetopsida and Ginkgoopsida—had dramatically filled out the Triassic gymnosperm spectrum.

One can be strongly misled by the available sample—the 'observed' sample. Still today, with 51 genera in 36 families and nine classes, there is every reason to project the 'observed' sample as not at all close to reaching the 'preserved' total.

Stratigraphic occurrence

Highly conspicuous in the pattern of stratigraphic distribution of the type material of the described ovulate genera, is their nearly exclusive origin in the Late Triassic (Carnian–Rhaetic). None of these genera derive from the Early Triassic, only three from the Middle Triassic and the remainder are from the Late Triassic. While it is true that most productive formations cluster higher in the Triassic (Anderson 1981; And. & And. 1983; this volume, Charts 11–20), this is primarily a reflection of the cone of exponentially increasing diversity through the Triassic. Most informative regarding diversity is that around half of the genera remain known only from the formation from which they were originally described.

Future sampling

Considering the historical summary above, and our statistical extrapolations of *preserved* versus *observed* taxa in the Molteno Fm. (Anderson *et al.* 1996; And. & And. 2003), we have predicted that numerous new ovulate genera remain to be discovered in Triassic strata (pp 22–25). Though some localities have been intensively sampled and some formations fairly extensively sampled, collecting overall has gone little beyond the reconnaissance stage overall (Charts 11–20). We have documented this fully for Gondwana Triassic strata (And. & And. 2003), where very few ovulate fruit have been recorded compared to their diversity now known from the Molteno. When the extreme rarity of most genera of reproductive material is considered, it is clear that sampling in general needs to be intensified by an order of magnitude for the still elusive *preserved* (but not yet *observed*) forms to come to light.

	Formations					Stages							
	top	interm.	poor	other	total	IND	OLE	ANS	LAD	CRN	NOR	RHT	total
S America	4	2	5	>7	18	-	-	1	3	4	3	3	14
Africa	1	1	6	-	8	2	-	2	-	3	-	1	8
India	-	-	4	-	4	1	-	2	-	-	1	-	4
Australasia	5	6	12	-	23	5	4	3	5	4	4	3	28
Antarctica	2	4	5	1	12	3	3	2	2	3	3	2	18
N America	5	1	-	-	6	-	-	-	-	4	4	1	9
Europe	4	1	4	-	9	-	-	2	1	1	-	5	9
E Eur–USSR	9	-	1	-	10	1	2	2	3	3	2	4	17
China/SE Asia	9	6	1	1	17	2	2	2	3	3	5	5	22
Total	38	21	38	9	106	14	11	16	17	25	22	24	129

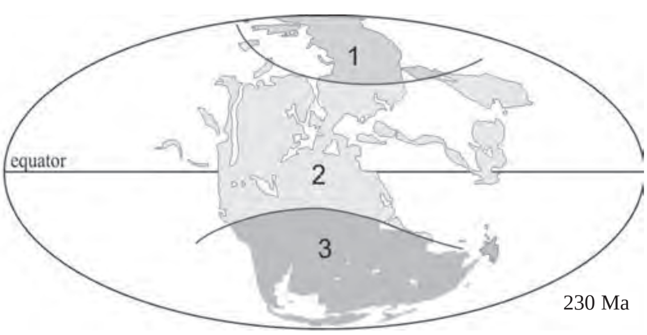
Tab. 15. Productive Triassic Formations

Source: based directly on correlation charts (Charts 11–20)

Formations: includes groups, formations, members, coal measures etc. (as on charts)
- *grades*: top, intermediate, poor (reconnaissance)
- *other*: additional formations as given in subscript on charts

Stages: tally of stages represented for the 7 or 8 columns per chart
- totals for stages and formations differ slightly as some formations span more than one stage, and as subscripts are not considered in counting stages.

Fig. 4. Triassic floral kingdoms



1. Angara (north temperate)
2. Laurasia (tropical)
3. Gondwana (south temperate)

Date	Author	Genus	Family	Class	Origin of type species	Period	Stage
1828	Brongniart	*Voltzia*	Voltziaceae	Pinopsida	Europe –	Trias.	–
”	”	*Aetophyllum*	Voltziaceae	Pinopsida	France (Vosges)	M. Trias.	ANS
1847	Braun	*Schizolepis*	Voltziaceae	Pinopsida	Europe –	L. Trias.	–
”	Endicher	*Palissya*	Palissyaceae	Pinopsida	Europe –	Trias./Jur.	–
1870	Schimper	*Glyptolepis*	Voltziaceae	Pinopsida	Germany (nr. Coburg)	L. Trias.	–
”	”	*Cheirolepis*	Cheirolepidiaceae	Pinopsida	Germany (Bayreuth)	L. Trias.	RHT
1886	Nathorst	*Cycadocarpidium*	Voltziaceae	Pinopsida	Sweden (Scania)	L. Trias.	RHT
1899	Potonié	*Voltziopsis*	Voltziaceae	Pinopsida	Germany (Coburg)	L. Trias.	NOR
1910	Nathorst	*Wielandiella*	Williamsoniellaceae	Bennettitopsida	Sweden (Scania)	L. Trias.	RHT
1918	Krasser	*Westerheimia*	Westerheimiaceae	Bennettitopsida	Austria (Lunz)	L. Trias.	CRN
1928	Lilienstern	*Dioonitocarpidium*	Cycadaceae	Cycadopsida	Germany (Estenfeld)	L. Trias.	–
1929	Wieland	*Fraxinopsis*	Fraxinopsiaceae	Gnetopsida	Argentina (Potrerrilos Fm.)	L. Trias.	CRN
1932	Harris	*Bennetticarpus*	Bennetticarpaceae	Bennettitopsida	Greenl. (Scoresby Sound)	L. Trias.	RHT
”	”	*Vardekloeftia*	Vardekloeftiaceae	Bennettitopsida	Greenl. (Scoresby Sound)	L. Trias.	RHT
1933	Hörnhammer	*Hiermeriella*	Cheirolepidiaceae	Pinopsida	Germany (Franken)	L. Trias.	RHT
”	Florin	*Bjuvia*	Cycadaceae	Cycadopsida	Sweden (Bjuv)	L. Trias.	RHT
”	”	*Palaeocycas*	Cycadaceae	Cycadopsida	Sweden (Scania)	L. Trias.	RHT
”	Thomas	*Umkomasia*	Umkomasiaceae	Ginkgoopsida	S. Africa (Molteno Fm.)	L. Trias.	CRN
1935	Harris	*Staphidiophora*	Leptostrobaceae	Ginkgoopsida	Greenl. (Scoresby Sound)	L. Trias.	RHT
1937	Harris	*Peltaspermum*	Peltaspermaceae	Ginkgoopsida	Greenl. (Scoresby Sound)	L. Trias.	RHT
1944	Frenguelli	*Fanerotheca*	Umkomasiaceae	Ginkgoopsida	Argentina (Potrerillos Fm.)	L. Trias.	CRN
1950	Kräusel	*Sturianthus*	Sturianthaceae	Bennettitopsida	Austria (Lunz)	L. Trias.	CRN
1952	Kräusel	*Pachylepis*	Voltziaceae	Pinopsida	Germany (Württemberg)	L. Trias.	–
1954	Bock	*Primaraucaria*	Zamiostrobaceae	Axelrodiopsida	USA (Virginia)	L. Trias.	CRN
1958	Roselt	*Tricranolepis*	Voltziaceae	Pinopsida	Germany (Thuringia)	L. Trias.	CRN
1970	Ash	*Dinophyton*	Dinophytonaceae	Gnetopsida	USA (south-western)	L. Trias.	CRN/NOR
1971	Stanislavsky	*Toretzia*	Umaltolepidiaceae	Ginkgoopsida	Ukraine (Novoraisk Fm.)	L. Trias.	RHT
1972	Ash	*Dechellyia*	Dechellyiaceae	Gnetopsida	USA (NE Arizona)	L. Trias.	CRN
1973	Delev. & Hope	*Compsostrobus*	Pinaceae	Pinopsida	USA (N Carolina)	L. Trias.	CRN/NOR
1976	Stanislavsky	*Borysthenia*	Voltziaceae	Pinopsida	USSR (Donetz Basin)	L. Trias.	NOR
1977	Schweitzer	*Irania*	Leptostrobaceae	Ginkgoopsida	Iran (Alborz Mts.)	L. Trias.	RHT
1978	Anderson H.M.	*Telemachus*	Voltziaceae	Pinopsida	S. Africa (Molteno Fm.)	L. Trias.	CRN
”	”	*Dordrechtites*	Dordrechtitaceae	Pinopsida	S. Africa (Molteno Fm.)	L. Trias.	CRN
1983	Zhou Zhiyan	*Stalagma*	Podocarpaceae	Pinopsida	China (Hunan)	L. Trias.	RHT
1986	Cornet	*Axelrodia*	Axelrodiaceae	Axelrodiopsida	USA (NW Texas)	L. Trias.	NOR
1987	Delev. & Hope	*Florinostrobus*	Voltziaceae	Pinopsida	USA (Pekin Fm.)	L. Trias.	CRN
1994	Taylor *et al.*	*Petriellaea*	Petriellaceae	Ginkgoopsida	Antarctica (Fremouw Fm.)	M. Trias.	LAD
1997	Yao *et al.*	*Parasciadopitys*	Cupressaceae	Pinopsida	Antarctica (Fremouw Fm.)	M. Trias.	LAD
2003	And. & And.	*Gypsistrobus*	Incertae sedis	Pinopsida	S. Africa (Molteno Fm.)	L. Trias.	CRN
”	”	*Avistrobus*	Incertae sedis	Pinopsida	S. Africa (Molteno Fm.)	L. Trias.	CRN
”	”	*Rissikistrobus*	Podocarpaceae	Pinopsida	S. Africa (Molteno Fm.)	L. Trias.	CRN
”	”	*Matatiella*	Matatiellaceae	Ginkgoopsida	S. Africa (Molteno Fm.)	L. Trias.	CRN
”	”	*Avatia*	Avatiaceae	Ginkgoopsida	S. Africa (Molteno Fm.)	L. Trias.	CRN
”	”	*Hamshawvia*	Hamshawviaceae	Ginkgoopsida	S. Africa (Molteno Fm.)	L. Trias.	CRN
”	”	*Kannaskoppia*	Kannaskoppiaceae	Ginkgoopsida	S. Africa (Molteno Fm.)	L. Trias.	CRN
”	”	*Cetifructus*	Incertae sedis	Incertae sedis	S. Africa (Molteno Fm.)	L. Trias.	CRN
”	”	*Alexia*	Alexiaceae	Incertae sedis	S. Africa (Molteno Fm.)	L. Trias.	CRN
”	”	*Hlatimbia*	Hlatimbiaceae	Incertae sedis	S. Africa (Molteno Fm.)	L. Trias.	CRN
”	”	*Hystricia*	Incertae sedis	Incertae sedis	S. Africa (Molteno Fm.)	L. Trias.	CRN
”	”	*Fredlindia*	Fredlindiaceae	Bennettitopsida	S. Africa (Molteno Fm.)	L. Trias.	CRN
”	”	*Lindtheca*	Lindthecaceae	Bennettitopsida	S. Africa (Molteno Fm.)	L. Trias.	CRN
”	”	*Nataligma*	Nataligmaceae	Gnetopsida	S. Africa (Molteno Fm.)	L. Trias.	CRN
	Diversity	52 genera	36 families	9 classes			

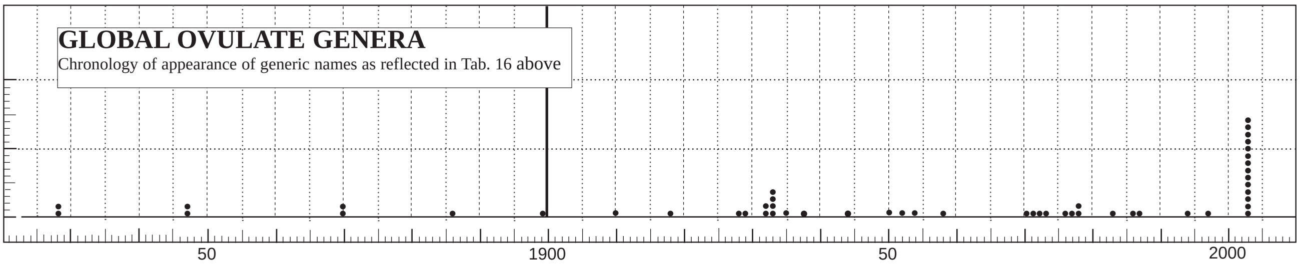
Tab. 16. Global Triassic ovulate genera: chronology of appearance

Diversity: the 36 families include three Incertae sedis
the 9 classes include three Incertae sedis

Chronology: the 52 genera are ordered according to date—1828–2003 (175 years)—of original description. The 6 genera recorded in the Triassic (see Tab. 13), but with type species from younger geological periods, are not included.

Source: Tab. 13 (pp 24, 25)

Fig. 5



Explosive radiation within the six Triassic classes

Evidence of explosive radiation through the Triassic is seen in all six of the (named) gymnospermous classes known to occur in the period (Charts 3, 4, pp 38, 39). The appearance of at least two other supposed (unnamed) classes further portrays the total spread of morphology. We make no attempt here to enter the uncertain field of gymnosperm cladistics.

Pinopsida: origin of extant families

Within the Triassic radiation is seen an explosion of renewed expression in the Pinopsida—particularly in the appearance of the Pinales. Four (possibly five) of the six extant pinalean families are believed to have originated in the Triassic. Aside from these, three further families—Dordrechtitaceae, Cheirolepidaceae and Palissyaceae in three clearly distinct orders—make their first appearance. Of these, the Cheirolepidaceae were destined to be of great significance through the rest of the Mesozoic, being the predominant pinopsid family (Chart 4, p. 41) until the radiation of the angiosperms.

Cycadopsida: hidden radiation

When considering families based exclusively on ovulate organs, the Triassic diversity within this group appears unusually modest. However, through this interval at least, cycadopsid ovulate cones or scales seem to pass virtually without fossil record. In the Late Triassic Molteno Fm., for instance, we record four foliage genera including 18 species (And. & And. 1989, 2003). These four genera are of such diversity (pinnae, venation, cuticle) that in our view they most likely represent four families. Male cycad cones are vanishingly rare in the formation (one genus, two species, two individuals), and ovulate remains entirely absent.

Ginkgoopsida: Triassic flagship

Assessment of the Triassic ginkgoopsids, the most prolific class in the Triassic radiation, hints at an intractable web of evolutionary relationships. When the full morphological spectrum (Fig. 6 opposite) of the different organs, reproductive and vegetative, is accounted for, any unique resolution of a phylogenetic tree would seem especially elusive. The ovulate fruit of *Kannaskoppia* and *Caytonia*, for instance, appear closest within the group, but their foliage is entirely dissimilar other than being reticulate. *Hamshawvia* and *Umkomasia* are very unalike, but their microsporangiate fruit and foliage cuticle suggest a particularly close relationship. Will the discovery of a host of excellently preserved new genera and the firming up of the affiliation of organs throughout bring us closer to a clear ginkgoopsid tree or will that tree show complex networked branching? We are inclined to anticipate the latter.

If the ginkgoopsids as plotted (Chart 4) are indeed a monophyletic group, then the Peltaspermales, the only known order appearing before the Triassic and crossing the P–Tr boundary, will bear the fullest set of plesiomorphic features for the class: e.g. lax spicate ovulate strobili with peltate cupules, glossopterid-like microsporangia, fern-like fronds.

Incertae sedis: glimpsing unknown classes

Between the Ginkgoopsida and the Bennettitopsida (Chart 4), we include two morphologically entirely isolated genera, *Alexia* and *Hlatimbia* from the Molteno Fm., each representing a distinct family, order and (unnamed) class (And. & And. 2003). Each is known only from a few individuals from a single locality. These are seen as the merest fragments of a number of unknown higher plant taxa hinting at communities and habitats rarely represented in fossil deposits.

Bennettitopsida: primary radiation

It is generally agreed (p. 188) that the Bennettitopsida showed far greater diversification during the interval of their initial radiation in the Middle to Late Triassic than through the rest of the Mesozoic.

An interesting aspect to this is that while the diversity (family-level) heyday of the bennettitopsids appears to have been in the Late Triassic (eight families versus no more than three during any epoch within the Jurassic or Cretaceous), their acme with regard to abundance and dominance seems to have stretched unabated through the Jurassic and Early Cretaceous (Charts 5, 6, pp 40, 41).

We pose the same questions as for each of the other classes. How many genera and families of Triassic bennettitopsids remain *preserved* but not yet collected; and how many *existed*, but were never *preserved*? And, again, for compelling reasons, we imagine the *recorded* material (Tab. 17 below) as being merely the tip of the diversity iceberg: the eight Triassic genera demonstrate a particularly wide spectrum of morphology, each representing a distinct family; most are very restricted in their occurrence, four being known from only one formation, and three of these from only one locality; and lastly there is the limited level of sampling—of over 75 Middle–Late Triassic megaplant-yielding 'formations' (Charts 11–20), only seven (<10%) have thus far yielded bennettitopsid ovulate material.

ovulate genera	← **Formations** →						
	SAf Molteno Fm.	**Aus** Ipswich CM	**Austria** Lunz beds	**Sweden** Scania	**Greenl.** Scoresby Sound	**USA** Chinle Fm.	**Mexico** Santa Clara Fm.
Fredlindia	4(17)	2(5)	-	-	-	-	-
Westerheimia	-	-	1(?c10)	-	-	-	-
Vardekloeftia	-	-	-	-	2(17)	-	-
*Williamsonia**	-	-	-	-	-	3(4)	1(1)
Sturianthus	-	-	1(1)	-	-	-	-
Bennetticarpus	-	-	2(✓)	-	✓	-	-
Wielandiella	-	-	-	✓	6(c10)	-	-
Lindtheca	1(16)	-	-	-	-	-	-

Tab. 17. Bennettitopsida, global Triassic ovulate genera

Genera: 8 Upper Triassic bennettitopsid genera, all but *Wielandiella* restricted to the period, are known. *Williamsonia** from the USA and Mexico should probably be identified as a new genus as it evidently affiliates in both regions with the distinctive and abundant foliage genus *Laurozamites* Weber & Zamudio-Varela (1995).

Families: Each of the 8 genera is considered in this volume to represent a distinct family.

Formations: Though somewhat variable in stratigraphic extent, the 7 columns (from S. Africa to Mexico) each represent a single formation.

Frequency: figure before brackets = number of localities.

Abundance: figure within brackets = number of specimens.
✓ = data not seen (or not given?)

Gnetopsida: primary radiation

With four markedly different orders (each monofamilial and monogeneric) of supposed stem-gnetopsids appearing in the Middle to Late Triassic, the true morphological spectrum of this group is only dimly hinted at. Two of the orders (genera) are known only from the temperate Gondwana Kingdom, and two from the tropical Laurasian Kingdom; and two of these, one from either kingdom, are each known from just a single locality.

Like the bennettitopsids, the class evidently appears in the Triassic explosion and gains greater expression in this period than at any subsequent interval (the mid-Cretaceous Barremian to Aptian being a possible exception).

Axelrodiopsida: possible stem-angiosperms

The two ovulate genera, *Axelrodia* and *Zamiostrobus*, included in this newly named class—each in its own family, but grouped here into a single order, the Axelrodiales—are enigmatic, controversial and known only from the Carnian to Norian of the western Laurasian tropical belt in the USA. Their place in the phylogeny of the gymnosperms (or possibly the stem-angiosperms), and the taxonomic, stratigraphic and geographic extent of the group, remains quite uncertain.

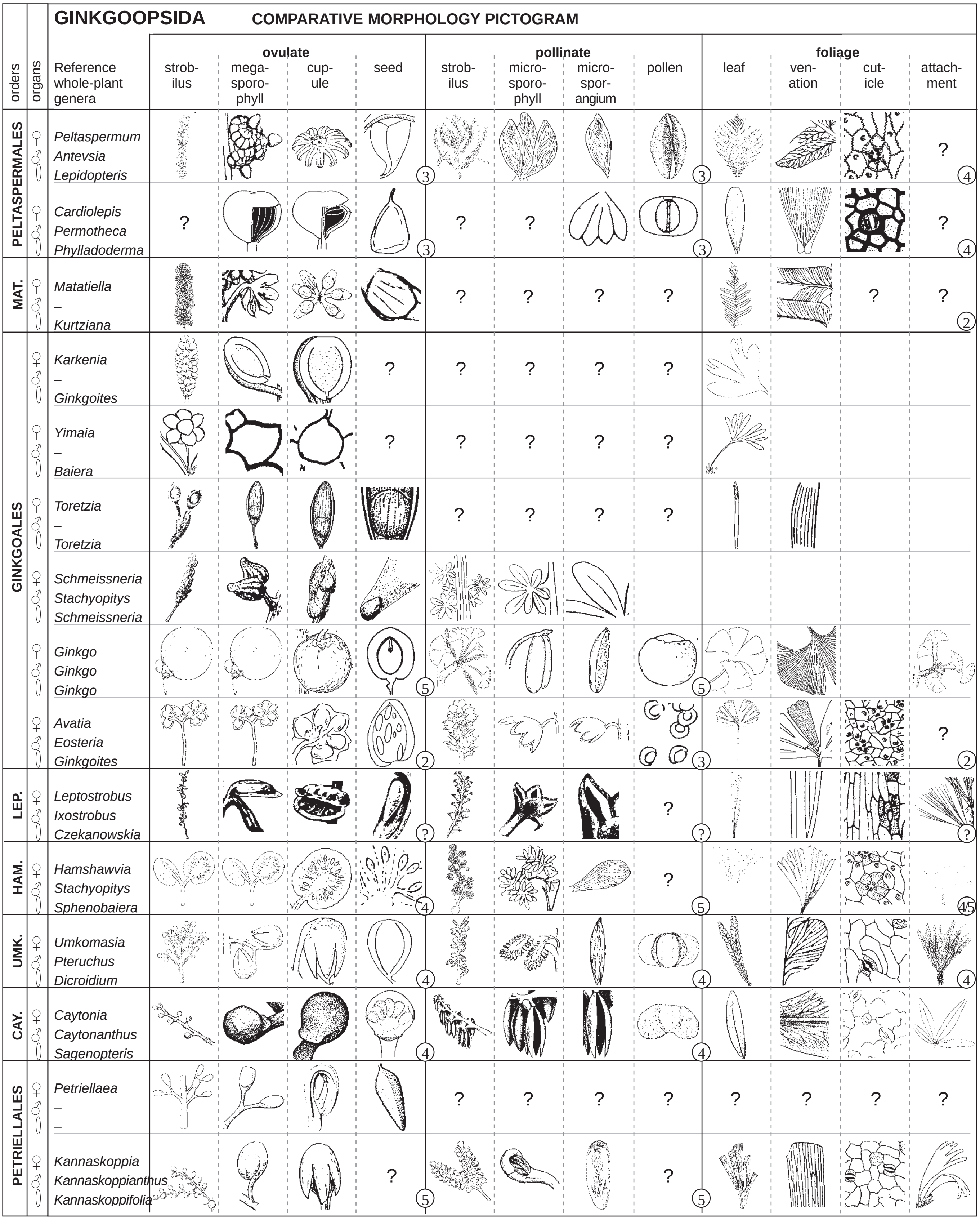


Fig. 6. Ginkgoopsida: comparative morphology pictogram

Diversity: 15 families, 8 orders

Reference whole-plant genera (of the 15 families) See Tab. 3 (pp 8–11) for classified list of the reference genera and 'reference strata'

Comparative morphology

Portrays 12 morphological fields: 4 ovulate, 4 pollinate, 4 foliage

Affiliations

④—affiliation grade (see p. 94 for explanation); grades down right-hand vertical refer to affiliation between foliage and ovulate organ

Explaining explosive radiation

Introduction

A little over 50 years ago, Watson & Crick (*Nature*, 25 April 1953) disclosed the structure of DNA. The ramifications of their discovery continue to grow exponentially and include a plethora of insights concerning the genetic code that might explain explosive radiation. Events such as the Cambrian Explosion of marine life and the Triassic Explosion of terrestrial life no longer seem so inexplicable. Scanning the pages of *New Scientist*, *Science* and *Nature* of the last two or three years provides an extraordinary sense of this new world of molecular biology and of the exotic concepts and vocabulary attending it. A small sample from this rich territory follows.

Hox genes & atavism

Hox genes were first discovered in flies in the 1980s, when geneticists began unravelling the animal genome. This small group of genes was found to control the body plan of the fly, setting out roughly its placement of head, legs, thorax, wings and so on, during early development (Ridley 2003).

Hox genes control (encode) the body plans of embryos of all animals, apparently from the first multicellular animals some 700 my back to fruit flies, elephants and human beings. All mammals have 38 different Hox genes occurring in four clusters which arose from a single ancestral cluster. Experimental tampering with these Hox genes has produced extraordinary results: from mutant mice embryos with therapsid (mammal-like reptile) earbones or with backbones like those of primitive jawless fish to fruit fly embryos with body plans 350 to 400 my out of date, bearing extra pairs of wings. These atavistic mutations reveal a genetic memory and show that this memory can be unlocked (Day 1995).

Are the potentialities of Hox genes given their fullest scope during periods of explosive evolution such as in the seas of the early Cambrian (Burgess Shale)? Are Hox genes confined to animals or do they, or something similar, occur also in plants (see Coen & Meyerowitz 1991)? And if so, can they be invoked to explain the remarkable phase of explosive diversification in Late Triassic terrestrial life, both plant and animal? Do the heyday of the gymnosperms and the origin of the angiosperms find at least partial explanation in Hox genes?

Gene duplication

Ciona intestinalis, the sea squirt, a distant cousin of the vertebrates, was the seventh animal to have its genome sequenced (after the mouse, fruit fly, mosquito, nematode worm, pufferfish and human). *C. intestinalis*, has *ca* 17 000 genes, about half as many as humans, while its genome is about a twentieth the size of ours (with *ca* 160 million letters).

'The creature that gave rise to both sea squirts and vertebrates appeared on the planet during the Cambrian explosion, an orgy of evolutionary experimentation about 550 million years ago. . . . Our extra genes are mostly duplicates of ones that already existed as single copies in *Ciona*. No one was sure when these genes were duplicated but thanks to this study we now know that it probably occurred in an early vertebrate. The extra functions that the duplicated genes can take on may be what allowed vertebrates to become more complex than other animals. "If your genome is big and floppy, maybe you have more flexibility." . . .' (Randerson 2002).

Gene stutters, tandem repeats, junk DNA

DNA sequences called 'tandem repeats' (generally regarded as 'junk DNA') are 'sequences of three or so DNA bases that are repeated over and over again'. Changes in their size within a gene 'can alter the gene's protein, making it work more or less efficiently'. They 'offer a novel mechanism for evolutionary change', such as witnessed in canines rapidly evolving into 100 breeds, with a collie nose transforming into a pug-like one or even a change in the number of toes (Pennisi 2004d).

Gene transfer, gene swapping, mobile genes, transgenes

Horizontal gene transfer, the movement of genes back and forth between species 'is a common phenomenon'. The implications are extremely broad: 'it blurs boundaries between species, making it difficult to determine where organisms fit in the family tree'. Mobile genes 'provide the grist for evolutionary innovations'. One calculation sees gene exchange speeding 'the spread of new traits by a factor of 10 000'. 'We may have to revolutionize' our notion about species (Pennisi 2004b).

Cellular invasions, bacterial invasion, viral invasion

Most profound in this arena are the ancient invasions of prokaryotes by eubacteria more than a billion years ago. These 'endosymbionts developed into organelles such as mitochondria and chloroplasts, thus producing early eukaryotes' (Dyall *et al.* 2004).

Pre-programming

A prime example of pre-programming is found in the Pax-6 gene group that regulates eye development in all vertebrates. Six of the 34 animal phyla—vertebrates, molluscs, insects, flatworms, nemertians (ribbon worms) and a sixth group not yet studied—have eyes. The genes encoding eye development in all five studied phyla are 'astoundingly' similar—they contain a sequence of 130 amino acids (with a 94% match between insects and humans). 'For the Pax-6 gene to have appeared in all phyla having visual systems, it must have been pre-programmed. Eyes were written into life before eyes ever appeared.' They were written into late Pre-Cambrian single-celled life, but only expressed in the six phyla with eyes in the Cambrian explosion (Schroeder 1997).

Chromosome shuffling (out-of-control genome)

The rock hoppers of Queensland provide a highly informative example of the disparity between phenotypic expression and genotypic constitution (Fox 2002). Along the coastal belt of Queensland, from Brisbane to the Cape York Peninsula, occur eight species of rock wallaby. They have overlapping habitat and spatial ranges, they all look identical, yet genetically they are recognised as eight species. Through painstaking DNA studies, the explanation seems to lie with retroviruses thoroughly shuffling the chromosomes of hybrid, yet fertile, individuals (O'Neill *et al.* 1998; O'Neill *et al.* 2001). It has been dubbed the Benny effect: Benny is the unlikely offspring of two distant species, a tall swamp wallaby and a tubby tammar wallaby, and it has a bizarre jumbled chromosome (see De Wit & Anderson 2003).

The O'Neill group claim to have good evidence that the culprit was a group of viruses. What's more, she says, the viruses wrought such profound genetic change that they gave birth to whole new species of rock hoppers—possibly in as little as a few decades. If right, the concept that it takes millions of years through mutation and natural selection to create a new species no longer necessarily holds. Evolutionary biology now includes an out-of-control genome that might do the same job almost overnight.

Retroviruses & recombination

The DNA of complex organisms, both plant and animal, is riddled with the genes of retroviruses that have found their way in through past eras. Once within, they insert copies of themselves into the host's DNA, they appear on other chromosomes, and, through the process called recombination, exchange genes amongst these copies (Fox 2002).

RNA interference (RNAi)

Since the initial description of RNAi by Fire *et al.* (1998) in *Nature*, this field has attracted an overwhelming range of studies. The newly discovered RNA immune system promises to be among the most exciting new areas in biology: in medical therapy where RNAi can be targeted at the cell's biology; and in elucidating evolution where it is now known to be 'one of several mechanisms that silence the expression of specific genes'. To offer a sense of the richness of the field, we note some of the RNAi gene silencing entities: RISC (RNA-Induced Silencing Complex), the catalytic subunit that executes RNAi; dsRNA (double-stranded RNA), involved in triggering RNAi; siRNA (small interfering RNA) and microRNA, induce transcriptional gene silencing; Argonaute 2 is the catalytic engine of mammalian RNAi; Nobox (an 'oocyte-specific homebox gene'), its deficiency disrupts gene expression (Liu *et al*. 2004; Morris *et al*. 2004; Rajkovic *et al*. 2004; Song *et al*. 2004; Van Rij & Andino 2004).

Homing endonuclease genes (HEGs)

'HEGs have found a cunning way of evading the normal rules of heredity, exploiting a loophole to get extra copies of themselves into the next generation. This "selfish gene" behaviour means HEGs are molecular parasites . . .

'In organisms that have paired chromosomes, a gene present on only one chromosome normally gets passed on to exactly half the organism's offspring. Unless, that is, the gene is an HEG. An HEG on one chromosome in a cell can use that cell's repair mechanisms to get itself copied onto the chromosome's partner. If the cell in question is a cell that makes eggs or sperm, this copying means that all the eggs or sperm will contain a copy of the HEG—and so all the offspring get a copy. In this way HEGs can spread through a population very quickly indeed' (Morton 2003).

Fibroblast growth factor (FGF)

'. . . without FGF4 and FGF8, limb development ceased. But when she took a closer look at the underdeveloped paws of her mice, she saw something that couldn't be reconciled with the PZ model. Although the back paws didn't form at all, the front paws did. Thanks to a quirk in the experimental system, the front limb buds produced a transient pulse of FGFs before the genes were knocked out. And this created some very puzzling patterns.

'As predicted by the PZ model, the front paws had normal upper-arm bones. But they also had something the PZ model would rule out: wrist, hand and finger bones, albeit smaller than normal.

'Further analysis of the mutant mice convinced Martin that FGFs have nothing to do with internal clocks, but instead promote cell proliferation. All this fits nicely with Tabin's new model: the limb bud contains precursor cells for all three limb parts, and they proliferate under the influence of growth-promoting FGFs.'

These FGFs are of significance in the field of embryology and specifically around how embryos sprout limbs (Martindale 2003).

Promoters (switches), enhancers (regulatory elements) & transcription factors

Genes are not the static blueprints we use to think they were. They are not immutable, passed on from generation to generation, but play an active part in life, taking environmental cues continuously from conception to death. Most genes have a promoter switch, stretches of DNA up the chromosome from that gene. How they are expressed—where, when and for how long they are switched on or off—is critically affected by the environment, both in gestation and throughout life thereafter.

Consider Hox genes. Like all other genes they are 'switched on or off in different parts of the body at different times'. HoxC8, for instance, is a Hox gene involved in shaping the thorax in all vertebrates, from mice to chickens to pythons. Mice, with seven neck and 13 thoracic vertebrae, and chickens with 14 and seven respectively, are very unlike in this sector of their body plan, yet this rests in relatively minor differences in the promoters attached to their HoxC8 genes. The promoter for both mouse and chicken is a '200-letter paragraph of DNA which differs by just a handful of letters'. Small changes in the promoter can have a profound effect on skeletal structure. No new genes are needed.

Here is a clear mechanism for large evolutionary changes, for explosive radiation following massive environmental disruption (Ridley 2003; Couzin 2004; Hall *et al*. 2004; Mohd-Sarip & Verrijzer 2004; Pennisi 2004c).

The genome's second code

The second code consists of the 'various types of noncoding DNA that control gene expression. It is becoming clear that it's the genome's exquisite control of each gene's activity—and not the genes per se—that matters most.' The 'evolution of genetic diversity' is due more to 'differences in gene regulation' than to the genes themselves. The same genes, after all, appear in widely differing organisms, from jelly fish to mice. Evolutionary innovation lies in the 'variety of types of regulatory DNA'. The genes of chimps and humans are remarkably alike, 'what makes the two species so different' it is suggested, 'lies in where and when these genes are active' (Pennisi 2004c).

Threespine stickleback (rapid parallel evolution at distant locations)

Simple genetic changes in a small stretch of DNA or even a single gene can have profound evolutionary effects. Change in a whole suite of bony characters, from loss of bony plates and pelvic spines to jaw shape, can occur. And this same rapid evolution, through natural selection in similarly changing habitats, can occur in stickleback populations concurrently in widely distant locations, from Japan to California to Iceland. The implications may be far ranging indeed in the context of drifting continents, evolutionary change and biogeography. If the Pitx1 gene 'known to initiate limb formation' is suppressed, for instance, similar effects are seen to result widely across the vertebrate spectrum, from sticklebacks, to mice, to birds. Further, it may be a simple change in the regulation of the gene 'in one part of the anatomy or at one point in development', rather than in the gene itself, driving this evolution (Pennisi 2004a).

Hybridisation

Even the classical debate over hybridisation has recently (see Ananthaswamy 2003) taken on new light. Experiments on the sunflower genus *Helianthus* have shown conclusively that hybridisation can cause an explosion of genetic variation leading to new species 'capable of invading novel ecological niches'. Computer simulations suggest that new species of sunflower can arise from hybrids within 50 to 60 generations, negligible in evolutionary time, and that hybridisation may drive speciation far more rapidly than random mutations.

On the origin of phyla

In his book of the above title, Valentine (2004) sets out to explore (and explain) the origin of the highest taxonomic groups (phyla) of metazoans. Towards the close of the book he brings in the genome and causal mechanism. Cameron (2004), in a review of *On the origin of phyla*, toys with 'gene regulation networks' and 'Cis-regulatory interactions that operate at the genome level' and might explain the appearance of 'entire organ systems or embryonic germ layers, features that distinguish higher taxa'.

Is it still too early to seek to explain the causes of the origin of phyla? No, suggest both Cameron and Valentine.

HOLISTIC OVERVIEW: SILURIAN to PRESENT

Chart 1 Macroevolutionary life cycle of the gymnosperms
Chart 2 Earth physiology
Charts 3 & 4 Global gymnosperms: family range chart
Charts 5 & 6 Global gymnosperm macroevolution
Charts 7 & 8 Global insect macroevolution
Charts 9 & 10 Global tetrapod macroevolution
Charts 11–20 Megafloral correlations
Charts 21–24 Araucariaceae: phytohistory of a family
Charts 25 & 26 Epiphytes on *Araucaria angustifolia*
Charts 27–30 Extant gymnosperm families: comparative morphology

Geological time scale

Charts 1–20 on the pages that follow are all set to the same scale to facilitate direct comparison of the different histories plotted. They are based on the two latest Geological Time Scales (Remane *et al*. 2000; Gradstein & Ogg 2004) formalised by the International Commission on Stratigraphy (ICS) under the parent body, the International Union of Geological Sciences (IUGS).

The scale, from the Silurian to Neogene, as drafted here is a compromise, with the relative duration of the periods based on the earlier ICS scale of 2000 and the absolute ages on the later scale of 2004. The duality arises through our charts having been originally drafted prior to the publication of the revised scale.

This latest ICS scale is of the greatest significance. It is the first fully revised geological time scale to appear in 15 years and it is the first for which absolute ages are given for all 91 stage boundaries from the start of the Cambrian to the present (Whitfield 2004).

Duration of periods

Major changes with regard to the ages and duration of some geological periods in particular have been effected in the years separating the two time scales. Most significant from our perspective are the Jurassic and Cretaceous, the former losing 14 my in length, the latter gaining 11 my:

ICS 2000—Jurassic (203–135 Ma), 68 my duration.
ICS 2004—Jurassic (200–146 Ma), 54 my duration.

ICS 2000—Cretaceous (135–65 Ma), 70 my duration.
ICS 2004—Cretaceous (146–65.5 Ma), 81 my duration.

Other periods, Silurian to Neogene, have been far less affected and more or less retain their previously held duration.

Duration of stages

For convenience, we have plotted the stages within each period as of equal duration. This might no longer be well advised with ages available for all boundaries and the stages now understood to be of such unequal length. Consider, for instance, the Cretaceous with stage durations ranging from the Santonian (of 2.3 my) to the Albian (12.4 my) and Aptian (13.0 my); or the Triassic ranging from the Induan (of 1.3 my) to the Carnian (11.5 my) and Norian (12.9 my).

Stage abbreviations

We follow the system of three-letter abbreviations adopted in *The Fossil Record 2* (1993). For stages not in *FR 2*, e.g. P (Wuchiaping) through to Tr (Olenekian), the abbreviations are our own, following the principles of that work.

Cenozoic (Paleogene plus Neogene) epochs

The seven epochs of the Cenozoic are of highly unequal duration and the 20 stages overall cannot be plotted at our scale. Instead we apply the traditional Early (E), Middle (M) and Late (L) subdivisions of the epochs as plotting intervals. We deviate (for convenience) from ICS (2004) in adopting only two subdivisions for the Paleocene instead of three and only one for the Pliocene instead of two. The Pleistocene and Holocene, covering only the last 1.81 my, are each plotted to match the earlier subdivisions of the Cenozoic.

INTRODUCTORY NOTES TO THE *HOLISTIC OVERVIEW*

To readily evaluate the relationship between the continuously changing global environment—continental drift, climatic shifts, atmospheric oxygen levels—and the macroevolutionary picture of the terrestrial plants, insects and tetrapods, the five two-page spreads plotting these patterns (Charts 1–10) are set to the same scale against standard geological time (p. 33). The 10-page megafloral correlation section (Charts 11–20), providing the framework for tracking our knowledge of global plant evolution, is again set to the same scale. Then follow two pictorial essays (Charts 21–30), the first a history and epiphytes of a select extant family, the Araucariaceae, the second a comparative morphology of the extant gymnosperm families.

Macroevolutionary life cycle of the gymnosperms (Chart 1)

Core to this chart is the macroevolutionary diversity histogram of the gymnosperms, reflecting directly the family-range data as plotted on Charts 3 & 4. Four phases—youth, adolescence, maturity, old age—in the macroevolutionary 'life cycle' of the gymnosperms are recognised. These are seen in the context of the shifting continents (and plant kingdoms) and the six major global extinction events.

Earth physiology (Chart 2)

This graphic is complementary to Chart 1. Major trends in four primary features of Earth physiology—temperature, precipitation, atmospheric oxygen, organic carbon-isotopes—are tracked through geological time. These graphs remain particularly fluid—hence our plotting alternative schemes at least in the case of mean global temperature.

Global gymnosperms: family range chart (Charts 3 & 4)

The 84 gymnosperm families (in 37 orders and 10 classes) are plotted following the range-through method (Labandeira & Sepkoski 1993) as simple lineages from first to last occurrences in the fossil record. No attempt is made to show relative abundance or absolute biodiversity (of genera or species). Biodiversity at family, order and class levels per geological epoch and stage is recorded to the right of the spread; this provides the direct basis for plotting the histograms on p. 5 and Chart 1.

Global gymnosperm macroevolution (Charts 5 & 6)

Two charts have been compiled: the first based exclusively on Gondwanan floras, the second exclusively on Laurasian floras. Each shows the three major groups of vascular plants, the pteridophytes (spore-bearing plants), gymnosperms (cone-bearing plants) and angiosperms (flower-bearing plants). Aside from the flowering plants, the spindles are generally (not always) plotted at the resolution of the order.

While the broad pattern of plant evolution for the southern and northern continents/kingdoms is similar, there are marked differences. Most conspicuous is in the Carboniferous, where floras flourished luxuriantly in the largely tropical latitudes of Laurasia, but were absent or marginal due to the continental icecap covering much of Gondwana.

Global insect macroevolution (Charts 7 & 8)

The known geological ranges of the 43 orders of extinct and living insects (plus three 'orders' of para-insects) are plotted—showing changes in family diversity through time. Though there already exists a remarkable database, the insect fossil record remains relatively sparse. It is particularly evident that the hypothetical extension following cladistics of the order-ranges back beyond the known fossil record (body fossils) suggests far higher levels of early diversity than is directly observed. Striking is that the primary radiation of each major (superordinal) clade in the later Palaeozoic, Devonian to Carboniferous, remains phantom.

Global tetrapod macroevolution (Charts 9 & 10)

This double-page spread on the tetrapods complements those on the plants and the insects. The three groups together constitute (as far as the fossil record elucidates) the essence of past terrestrial ecosystems. We are particularly interested here in the co-macroevolutionary patterns evident or suggestive at the resolution plotted. These patterns are briefly outlined in the text for each geological period in the chapter on the *Macroevolutionary life cycle of the gymnosperms* (pp 67–89).

Megafloral correlations (Charts 11–20)

Reliability of correlations

Reliable correlations are clearly of central importance in tracing the evolutionary history of the gymnosperms (or any other group), yet the reality persists that many terrestrial formations cannot be well dated with respect to the standard marine 'stages'. Diversity histograms based on first and last appearances of taxa at 'stage' resolution will markedly improve as correlations improve. Establishing the absolute ages (radiometric dating) of significantly more fossiliferous horizons will corroborate attempts at correlations based on fossil assemblages alone—as will improved ties to the framework of magnetic reversals.

Pen sketches & systematic text (provenance)

As far as possible, we record 'locality' and 'formation' of origin of each generic or specific taxon illustrated or mentioned in the systematic text—and, with obvious space constraints, include the 'formation' in the correlation charts. Provenance in time and space are integral to any lucid history. To achieve this more fully, the set of correlation charts would need to be doubled in extent.

Flagship formations & lagerstätte

We emphasise through colour coding the highly variable richness (quality and quantity) of the fossiliferous strata; and of current levels of sampling and publication of the preserved floras.

Recorded opposite are a selection of lagerstätte (e.g. Hamilton quarries, Topeka Limestone Fm., Kansas, USA; Gzhelian, Late Carboniferous) and flagship formations (e.g. Molteno Fm., Karoo Basin, South Africa; Carnian, Late Triassic). Modes of preservation could be usefully built into correlations, but are not attempted here. Again, key examples are included opposite (e.g. the silicified peats of the Fremouw Fm., Transantarctic Mountains, Antarctica; Middle Triassic).

Araucariaceae: phytohistory of a family (Charts 21–26)

Of the 13 extant gymnosperm families, the Araucariaceae are probably the most completely known in regard to their geological history. Four phases of that history are tracked here: their emergence in the Triassic; their expansion to global prominence in the Late Jurassic to Early Cretaceous; their retreat into Gondwana in the face of the angiosperm radiation in the Late Cretaceous to Early Tertiary; and their further migration to southern latitudes in the Neogene to Recent.

As an addendum emphasising community and diversity, a two-page spread documenting the astonishing richness of epiphytes on *Araucaria angustifolia* in the plateau forests of Rio Grande do Sul, Brazil, follows.

Extant gymnosperm families: comparative morphology (Charts 27–30)

In this pictorial comparative morphology of the living gymnosperm families, the homology of organs is stressed. Rigorous work along such lines is fundamental to interpreting morphology in extinct families and in constructing any robust classification or phylogeny. These four pages reflect the current state of research of the Bochum team in Germany (pp v, xiv): the programme is ongoing; the families are not yet equally covered, and the Stangeriaceae (cycads) not yet represented at all.

Megaplant-bearing formations: towards a database

A database of productive formations would be of indispensible value in compiling a second edition of the history of the gymnosperms. Here we anticipate such a database for the group by listing a selection of the most significant formations from the Late Devonian to Tertiary. The selection generally takes in two formations per geological period and is reasonably scattered across Laurasia and Gondwana. We suggest a number of sub-heads, emphasising location, age, environment, significance, flora and fauna. Cross-reference within this volume, mostly to those families with reference whole-plant genera from the relevant formations, is given.

Lower Regatta Point to Monpeelyata (Chart 14, p. 49)
Location: Tasmania, Australia.
Age: Tertiary (Early Eocene to Early Miocene).
Environment: Southern temperate, terrestrial.
Significance: The richest and fullest sequence globally for tracking southern pinalean history through the middle 35 my interval of the Tertiary.
Flora: Diverse mixed conifer and angiosperm assemblages.
Fauna: None found in association with the plant assemblages.
This volume: Araucariaceae (pp 58, 59).
References: Stephen McLoughlin (2005 pers. comm.).

Fort Union Fm. (Chart 17, p. 52)
Location: Western Interior, USA.
Age: Early Tertiary (Palaeocene).
Environment: Fluvial (including overbank) and paludal, limited lacustrine.
Significance: The fullest sequence globally through the first 12 my following the K–T boundary.
Flora: Deciduous dicots dominant, especially swamp species.
Fauna: Teleost fish, crocodylians, mammals; insects depauperate.
This volume: Tertiary insect associations (p. 86).
References: Conrad Labandeira (2005 pers. comm.)

Crato M., Santana Fm., Araripe Gp. (Chart 11, p. 46)
Location: NE Brazil.
Age: Mid. Cret. (APT–ALB), *ca* 110–114 Ma.
Environment: Small inland basin, lacustrine.
Significance: Important record of early angiosperms; major occurrence of early Welwitschiaceae hinting at a mid-Cretaceous gnetalean radiation.
Flora: Gnetales, ferns, coniferous shoots, early angiosperms.
Fauna: Diverse excellently preserved, articulated insects; beautifully preserved fish known globally.
This volume: Welwitschiaceae (p. 215).
References: Dilcher (2004 pers. comm.), Dilcher *et al.* (2004).

'Jianshangou Bed', basal Yixian Fm. (Chart 20, p. 55)
Location: Western Liaoning, NE China.
Age: Early Cret. (? BRM), 125 Ma (but see Sun Ge *et al*. 2002).
Environment: Terrestrial, volcano-sedimentary sequence.
Significance: Source of arguably the earliest known angiosperm flower, *Archaefructus*; many fertile and sterile specimens suggesting the families Ephedraceae and Welwitschiaceae and a mid Cretaceous gnetalean radiation.
Flora: Diverse, conifer dominated, with early angiosperms.
Fauna: Includes theropod dinosaurs, primitive birds, mammals.
This volume: Ephedraceae (p. 213), Welwitschiaceae (p. 215).
References: Sun Ge *et al*. (2001), Dilcher (2004 pers. comm.).

Ravenscar Gp., Yorkshire Jurassic (Chart 18, p. 53)
Location: Cleveland Basin, near Scarborough, N. Yorkshire, UK.
Age: Mid. Jur. (AAL, BAJ, BTH).
Environment: Subtropical, deltaic.
Significance: Most diverse-known mid-Jurassic flora globally; much of the early work on the Bennettitales and Caytoniales was done here.
Flora: Mostly dominated by bennettitaleans, conifers and ferns.
Fauna: Virtually nil in plant beds; associated beds with some trace fossils.
This volume: Caytoniaceae (p. 183), Williamsoniellaceae (p. 197).
References: Van Konijnenburg-Van Cittert & Morgans (1999), Cleal *et al*. (2001).

Lias α (Chart 18, p. 53)
Location: Bavaria, Germany, Europe.
Age: earliest Jurassic (HET).
Environment: Deltaic plain, terrestrial, occasional marine influence.
Significance: With rich new gymnospermous (reproductive) material, mainly ginkgoales and gnetopsids, showing a minor radiation after the end-Triassic.
Flora: Ferns, conifers & ginkgophytes common; Gnetales (*Bernettia*), Bennettitales, cycads, Caytoniales uncommon.
Fauna: Many insects; some shark eggs.
This volume: Schmeissneriaceae (p. 177), Bernettiales (p. 208).
References: Van Konijnenburg-Van Cittert (2005 pers. files)

Molteno Fm. (Chart 12, p. 47)
Location: Karoo Basin, South Africa.
Age: Late Trias. (CRN).
Environment: Intracontinental floodplain, braided rivers.
Significance: Richest known Triassic flora globally; showing clear evidence of the heyday of the gymnosperms coincident with the origin of mammals and dinosaurs.
Flora: Diverse, gymnosperm-dominated (*Dicroidium*, *Heidiphyllum*).
Fauna: Diverse insects (Coleoptera, Hemiptera, Blattodea dominant).
This volume: e.g. Fredlindiaceae (p. 190), Lindthecaceae (p. 200).
References: And. & And. (1983, 1989, 2003).

Upper Fremouw Fm. (Chart 15, p. 50)
Location: Fremouw Peak, Transantarctic Mts., Antarctica.
Age: Mid. Trias. (LAD).
Environment: Foreland floodplain, between orogenic belt and craton.
Significance: The only known silicified peat deposits in the Gondwana Triassic; show clear anatomical details of a rich flora within the Triassic radiation.
Flora: Diverse, *Dicroidium* dominated.
Fauna: Terrestrial vertebrates (*Cynognathus* fauna)
This volume: Petriellaceae (p. 184).
References: Taylor & Taylor (1989), Hammer (1989).

Ust'pereborskaya Suite (Chart 19, p. 54)
Location: Arkhangelsk Region, northern Russia.
Age: Perm. (KUN–WUC).
Environment: Warm temp., mixed marine and deltaic.
Significance: The best documented warm-temperate flora for the Permian, especially important for the Peltaspermaceae and Vojnovskiaceae.
Flora: Mainly ferns and gymnosperms, with rare bryophytes, lycophytes and sphenophytes.
Fauna: Virtually nothing in plant beds; associated beds with marine brachiopods.
This volume: Vojnovskiaceae (p. 113).
References: Meyen (1983).

Vryheid Fm., Middle Ecca Gp. (Chart 12, p. 47)
Location: northern Karoo Basin, South Africa.
Age: Early Perm. (ART).
Environment: Deltaic coal swamps fringing inland sea.
Significance: Source of the earliest described attached glossopterid fruits; shows a rich diversity in this gymnospermous class.
Flora: Medium diversity; glossopterid & lycopod dominated.
Fauna: Very limited; insects, pelecypods, conchostraca, fish scales.
This volume: Ottokariaceae (p. 162), Arberiaceae (p. 164).
References: And. & And. (1985).

Topeka Limestone Fm., Hartford Limestone (Chart 17, p. 52)
Location: SE Kansas, USA (with the Hamilton quarries lagerstätten).
Age: latest Carb. (GZE).
Environment: forested estuarine with marine tidal influence.
Significance: Includes a diverse well-preserved early Voltzialean dominated flora, with highly important attached reproductive and vegetative material.
Flora: Diverse conifer-dominated (five coniferophyte species).
Fauna: Richly diverse, from terrestrial reptiles to marine inverts.
This volume: Bartheliaceae (p. 123), Emporiaceae (p. 124).
References: Mapes & Rothwell (1984, 1988, 1991, 2003), Rothwell & Mapes (2001).

Tseishui Fm. (Chart 20, p. 55)
Location: Guangzhou, South China.
Age: Early Carb. (VIS).
Environment: Alternating shallow marine and deltaic.
Significance: Includes the earliest putative member of the Cycadopsida.
Flora: Medullosales dominant; arborescent lycophytes; ferns, sphenophytes rare.
Fauna: Fusulinids, corals, brachiopods, conodonts.
This volume: Potonieaceae (p. 147).
References: Laveine *et al*. (1993b).

Hampshire Fm. (Chart 17, p. 52)
Location: Near Elkins, West Virginia, USA.
Age: latest Dev. (FAM).
Environment: Tropical, deltaic.
Significance: Records the earliest known occurrence of the gymnosperms.
Flora: Arborescent-lycophyte-dominated pteridophytic associations.
Fauna: Sparse; phyllocarid crustacea.
This volume: Moresnetiaceae (p. 98).
References: Scheckler (1986a,b).

Chart 1. MACROEVOLUTIONARY LIFE CYCLE OF THE GYMNOSPERMS

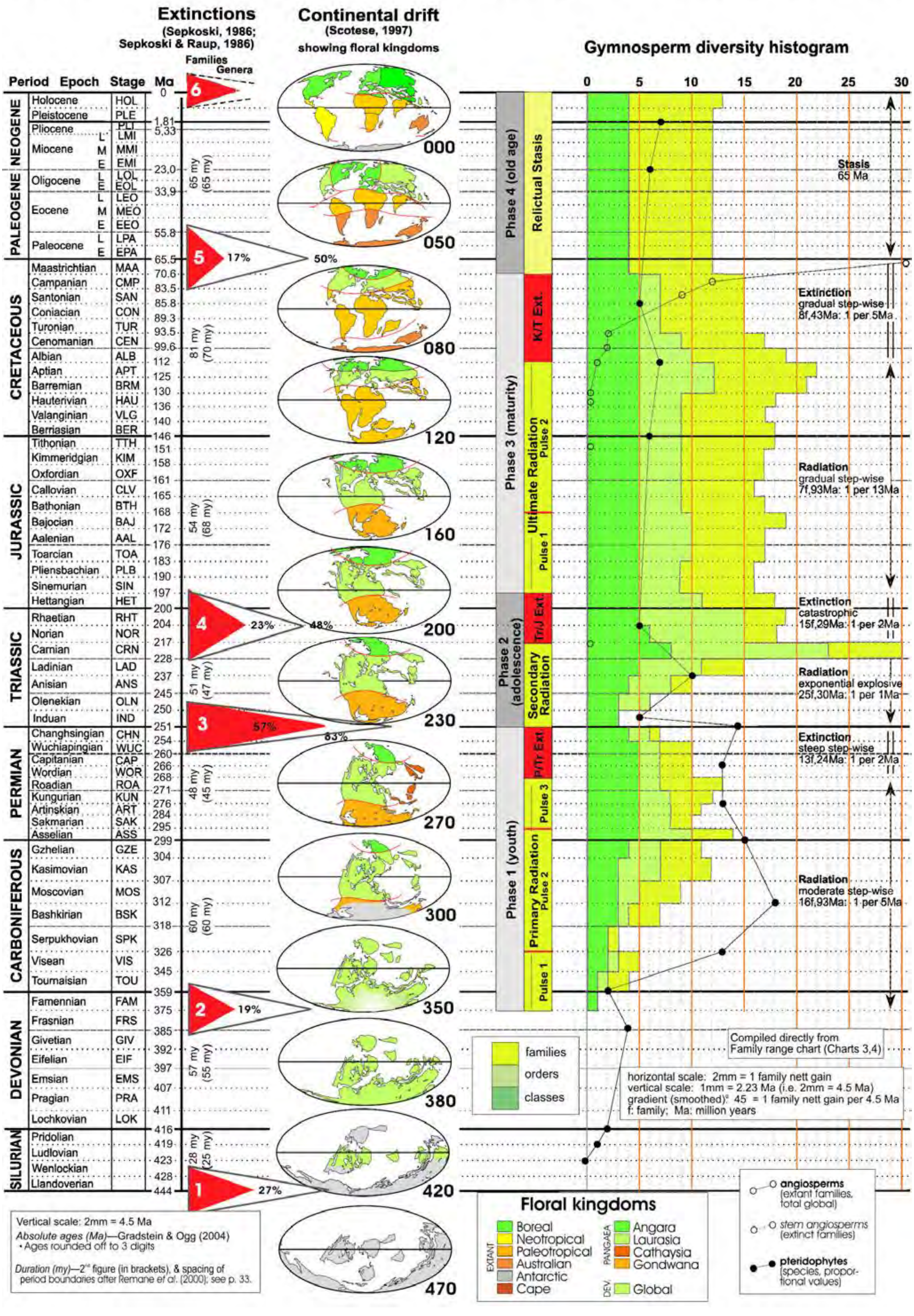
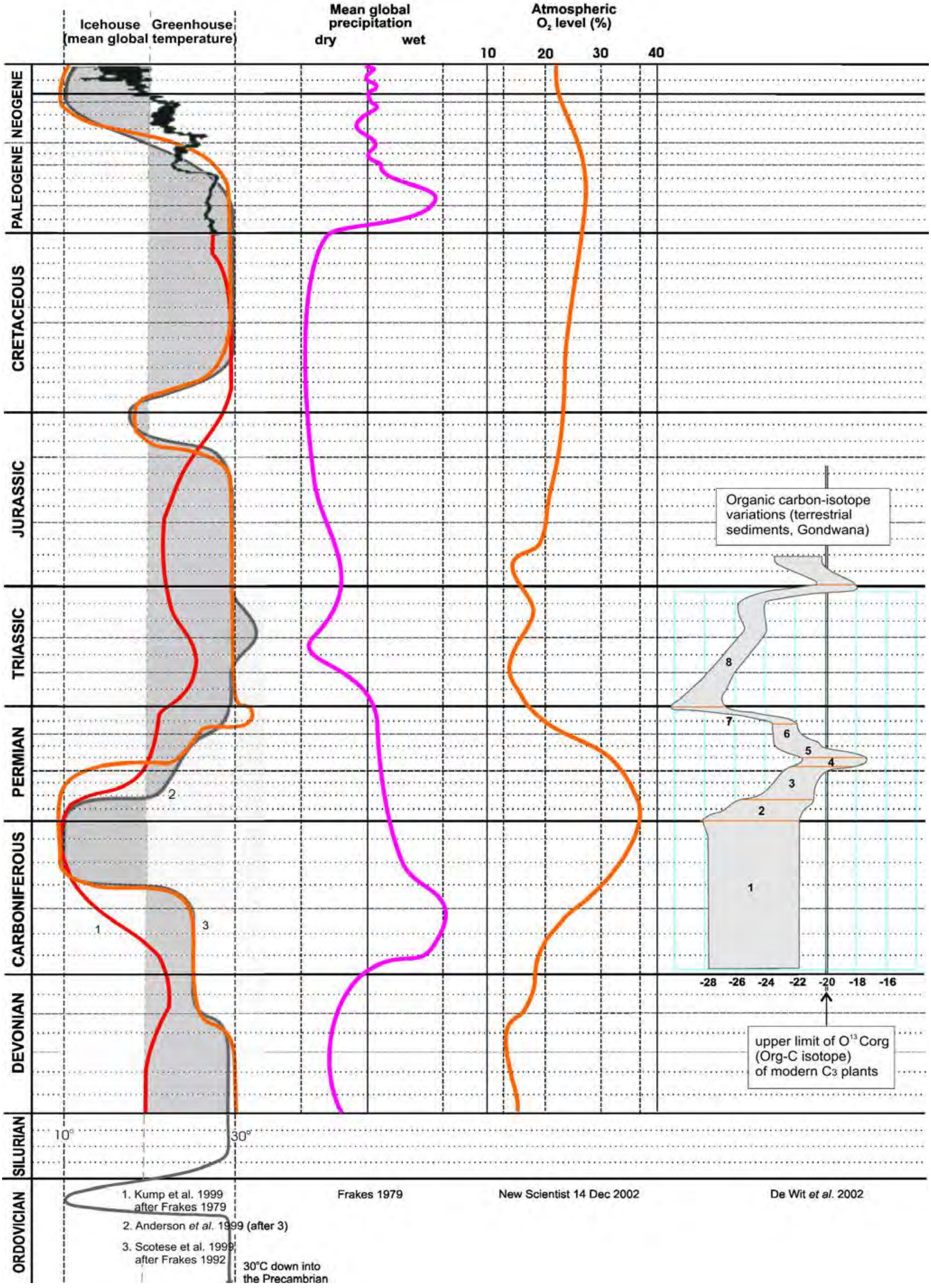


Chart 2. EARTH PHYSIOLOGY



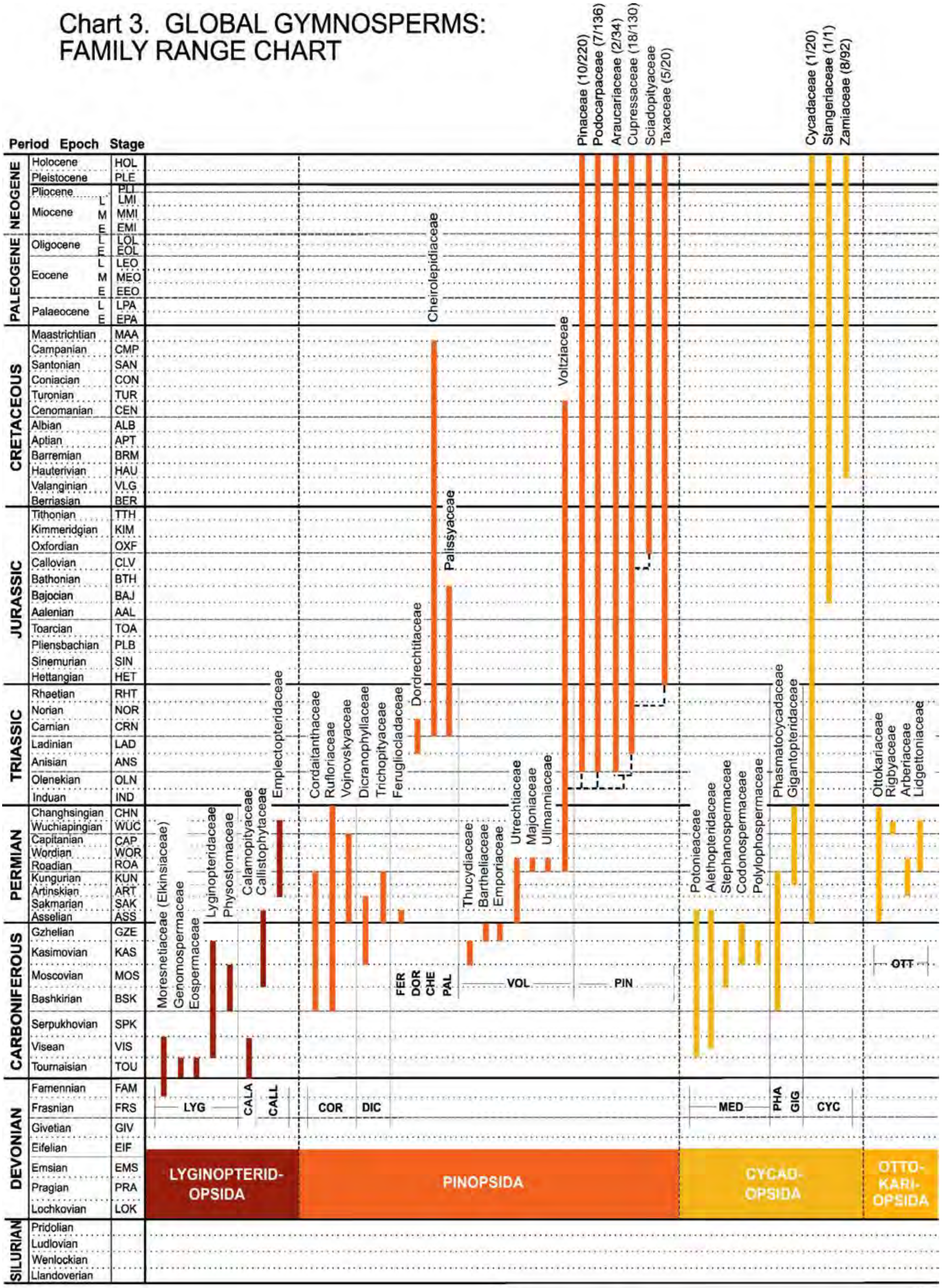


Chart 3. GLOBAL GYMNOSPERMS: FAMILY RANGE CHART

10 CLASSES (opsida)
37 ORDERS (ales)
84 FAMILIES (aceae)

Notes

1) ***Range bottoms & tops***: are generally placed at stage boundaries; exceptions highlight specific 'observed' step-wise originations

2) ***Order-spindles (Charts 5, 6) & family-range discrepancies***: occasionally occur (e.g. Voltziales), since the earliest representatives of an order may include foliage or pollen cones, but no ovuliferous cones, and are thus not included in any family

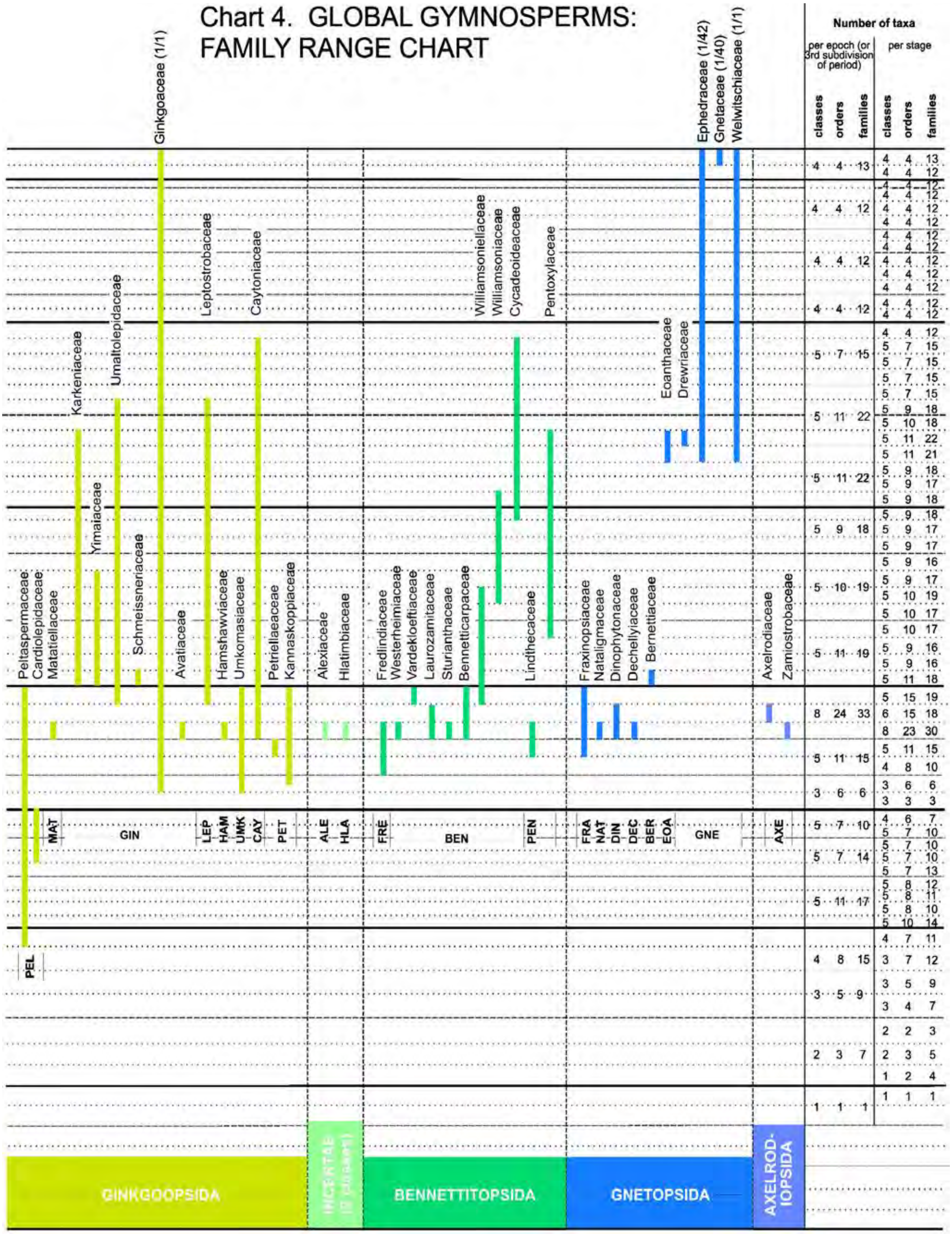
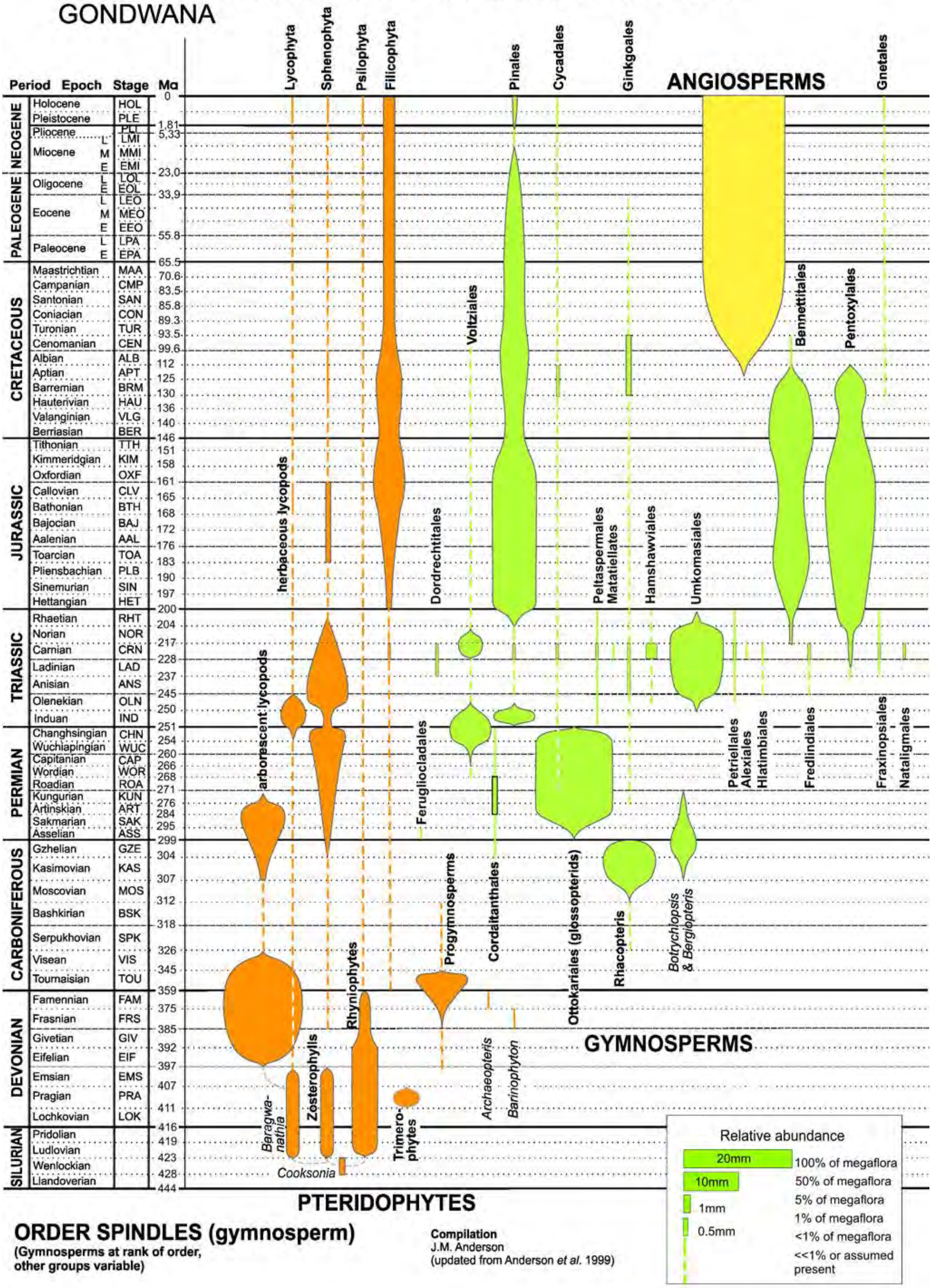


Chart 4. GLOBAL GYMNOSPERMS: FAMILY RANGE CHART

Notes (cont.)

3) ***Range-through method***—applies to all taxa (families, orders, classes) (see p. 5)

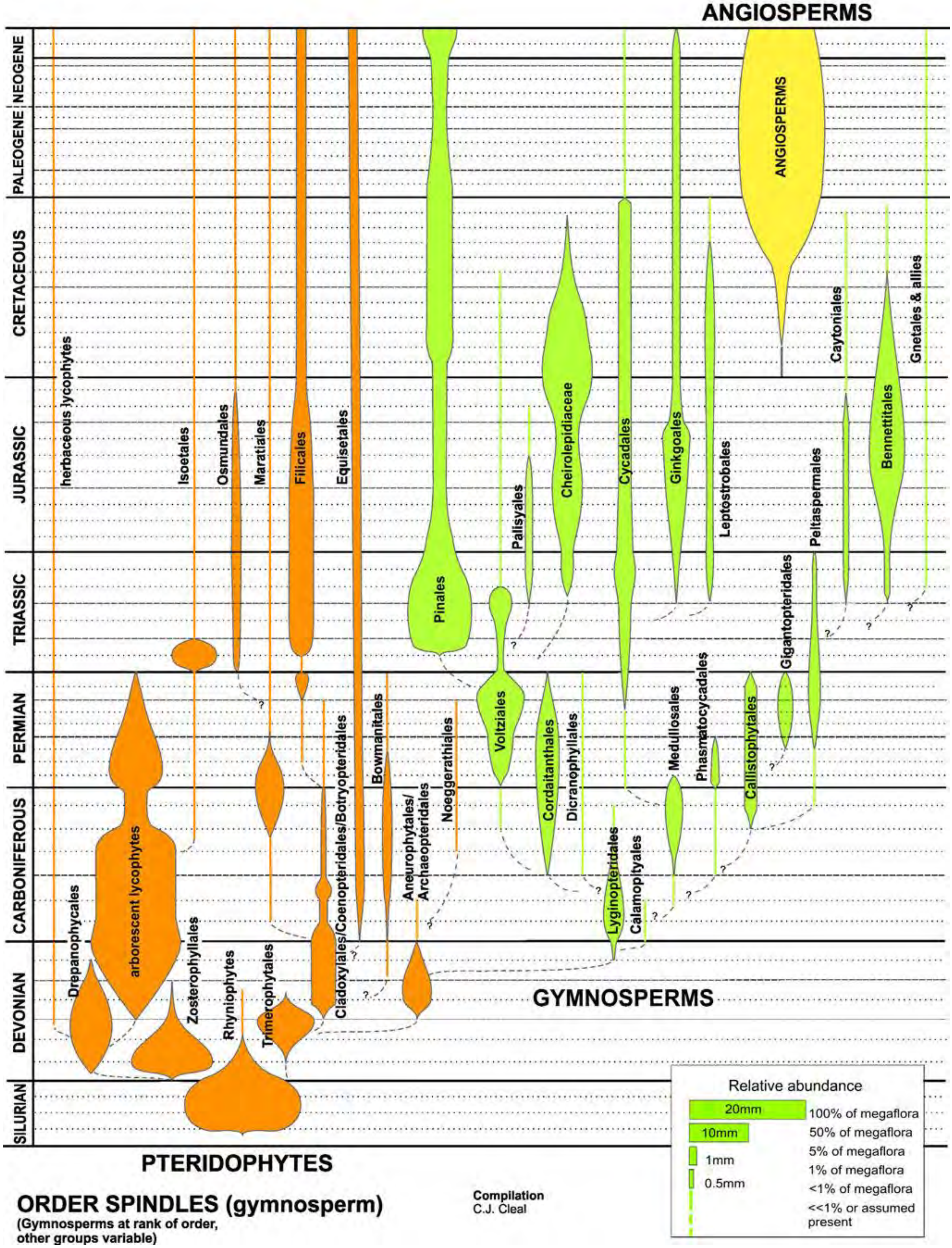
Chart 5. GLOBAL GYMNOSPERM MACROEVOLUTION: GONDWANA



ORDER SPINDLES (gymnosperm)
(Gymnosperms at rank of order, other groups variable)

Compilation
J.M. Anderson
(updated from Anderson *et al.* 1999)

Chart 6. GLOBAL GYMNOSPERM MACROEVOLUTION: LAURASIA



ORDER SPINDLES (gymnosperm)

(Gymnosperms at rank of order, other groups variable)

Compilation
C.J. Cleal

Chart 7. GLOBAL INSECT MACROEVOLUTION

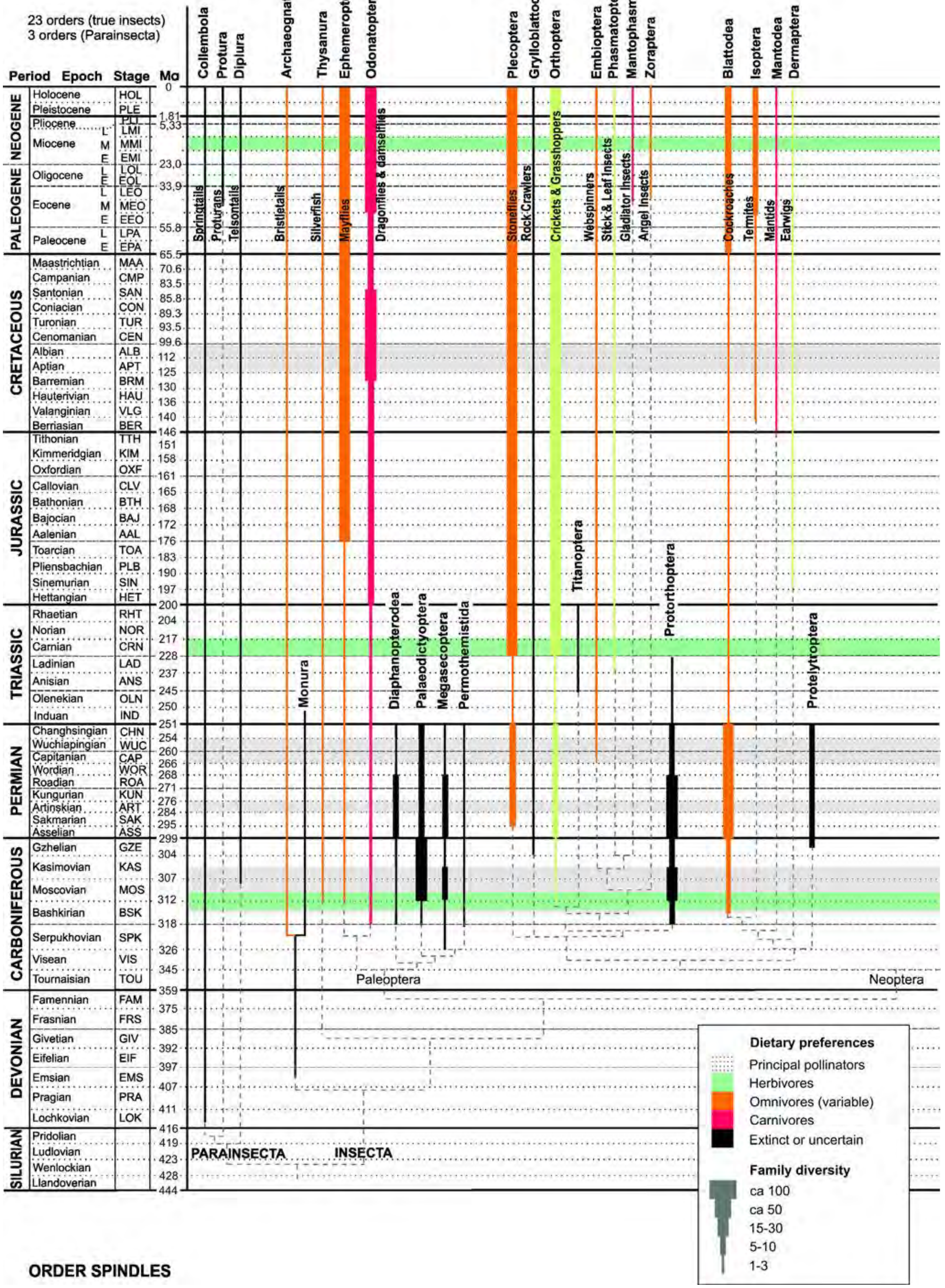
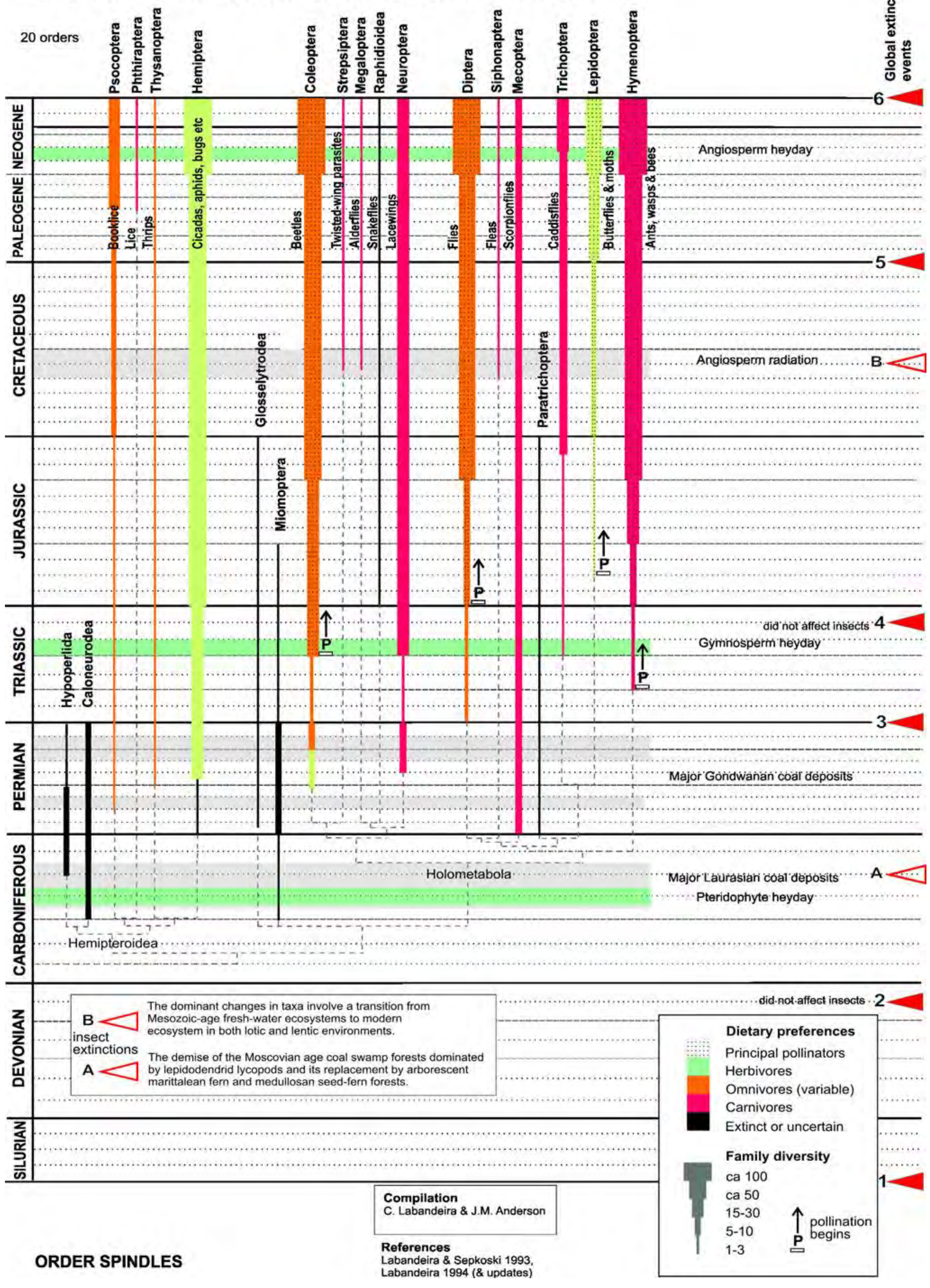


Chart 8. GLOBAL INSECT MACROEVOLUTION



The dominant changes in taxa involve a transition from Mesozoic-age fresh-water ecosystems to modern ecosystem in both lotic and lentic environments.

The demise of the Moscovian age coal swamp forests dominated by lepidodendrid lycopods and its replacement by arborescent marittalean fern and medullosan seed-fern forests.

Dietary preferences
- ▨ Principal pollinators
- 🟩 Herbivores
- 🟧 Omnivores (variable)
- 🟥 Carnivores
- ⬛ Extinct or uncertain

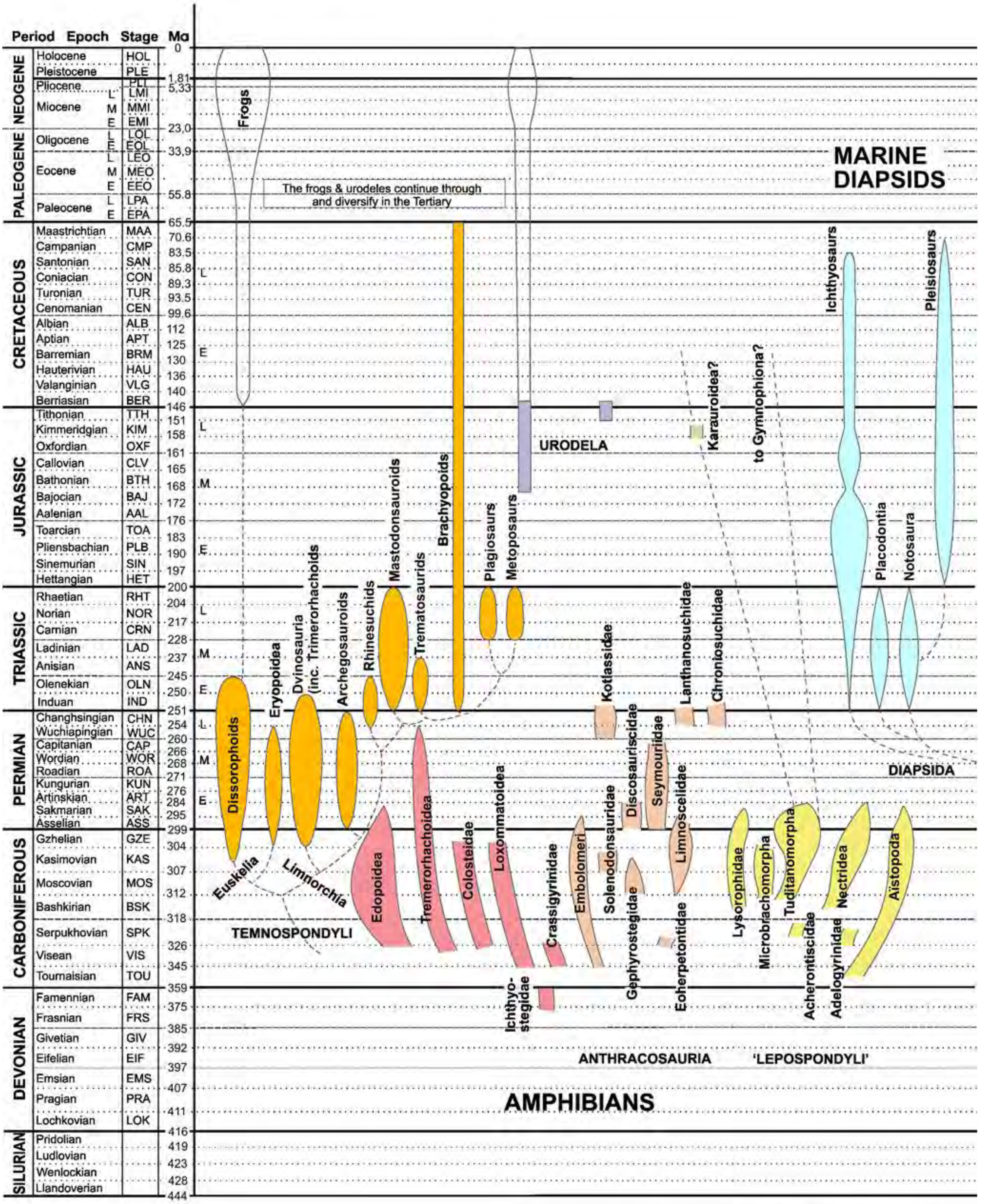
Family diversity
- ca 100
- ca 50
- 15-30
- 5-10
- 1-3

↑ P pollination begins

Compilation
C. Labandeira & J.M. Anderson

References
Labandeira & Sepkoski 1993,
Labandeira 1994 (& updates)

Chart 9. GLOBAL TETRAPOD MACROEVOLUTION: Amphibians, marine diapsids

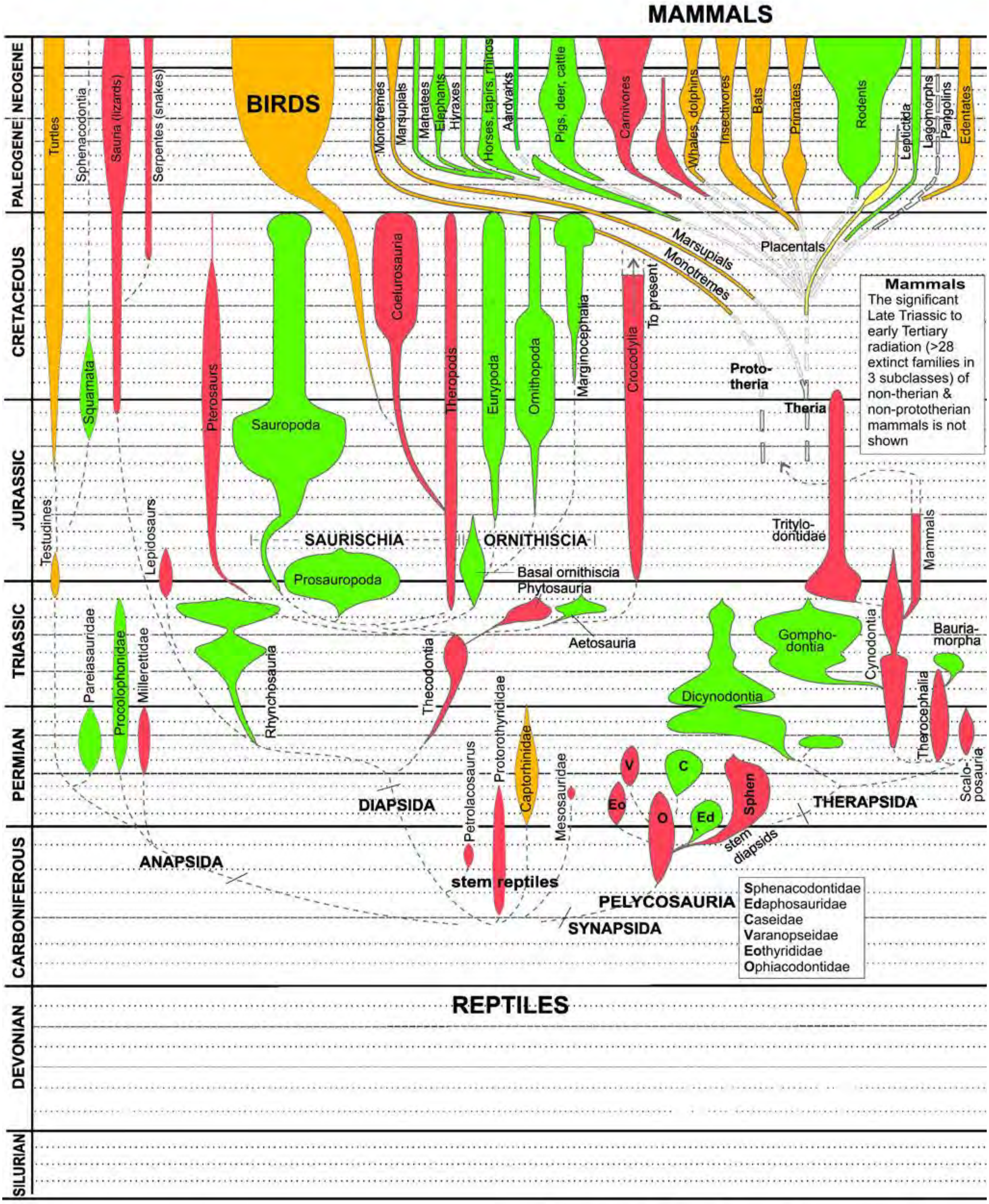


ORDER SPINDLES

Adapted partly from:
Carroll (1988)

Contributors
Adam Yates
Johann Neveling
Fernando Abdala
John Anderson

Chart 10. GLOBAL TETRAPOD MACROEVOLUTION: Reptiles, birds, mammals



Mammals
The significant Late Triassic to early Tertiary radiation (>28 extinct families in 3 subclasses) of non-therian & non-prototherian mammals is not shown

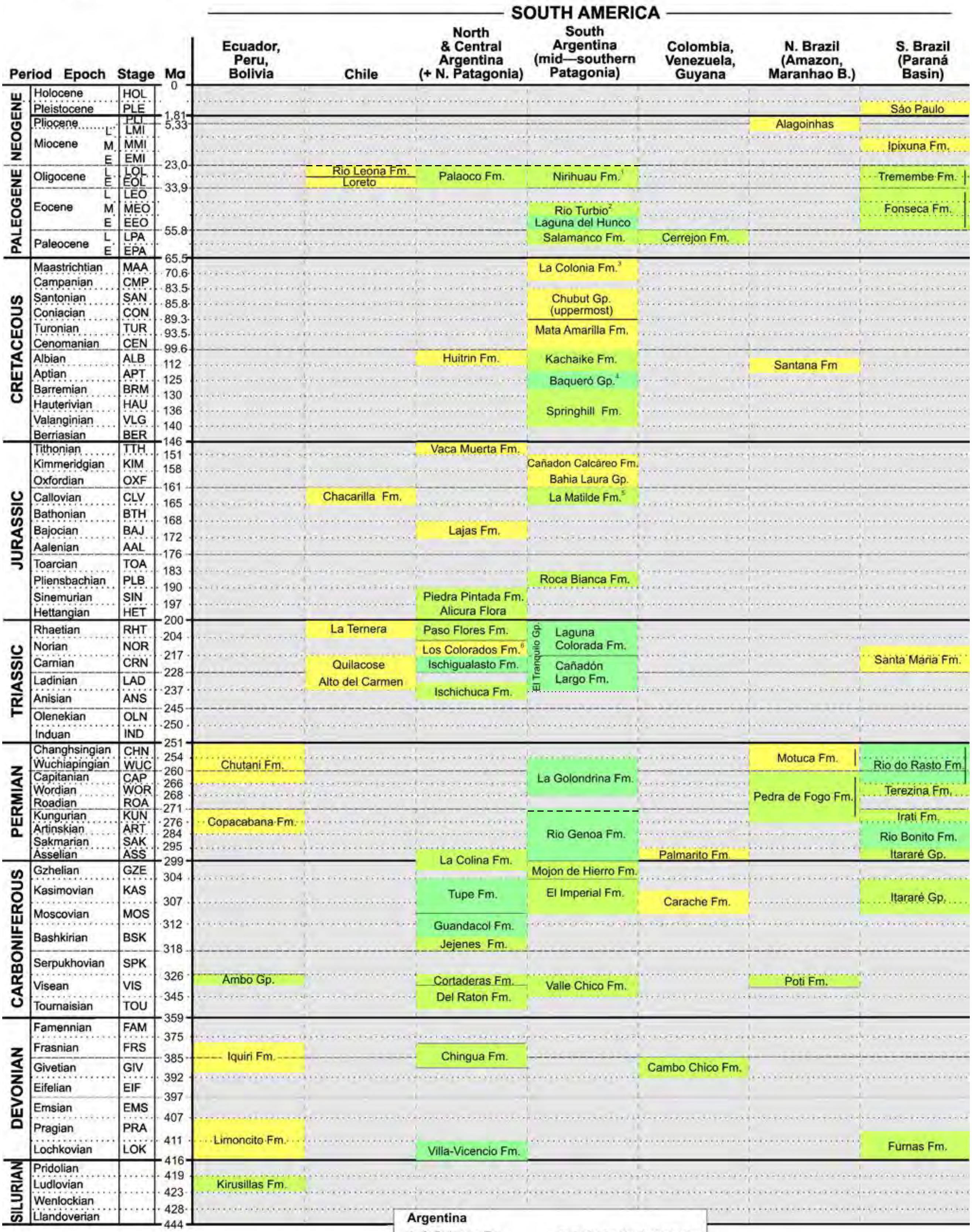
Sphenacodontidae
Edaphosauridae
Caseidae
Varanopseidae
Eothyrididae
Ophiacodontidae

ORDER SPINDLES

Contributors
Adam Yates
Johann Neveling
Fernando Abdala
John Anderson

References
Sereno 1997, dinosaurs (Jur-Cret)
Benton 2005 in prep (general)
Carrol 1988 (Carb-Perm)
Anderson 1999, mammals

Chart 11. MEGAFLORAL CORRELATIONS



Megafloras

🟩 top (quality/studied)
intermediate
🟨 poor (quality/understudied)

Gp: Group
Fm: Formation
M: Member

Only those strata including megafloras are plotted; marine, vertebrate-bearing & barren strata are excluded.

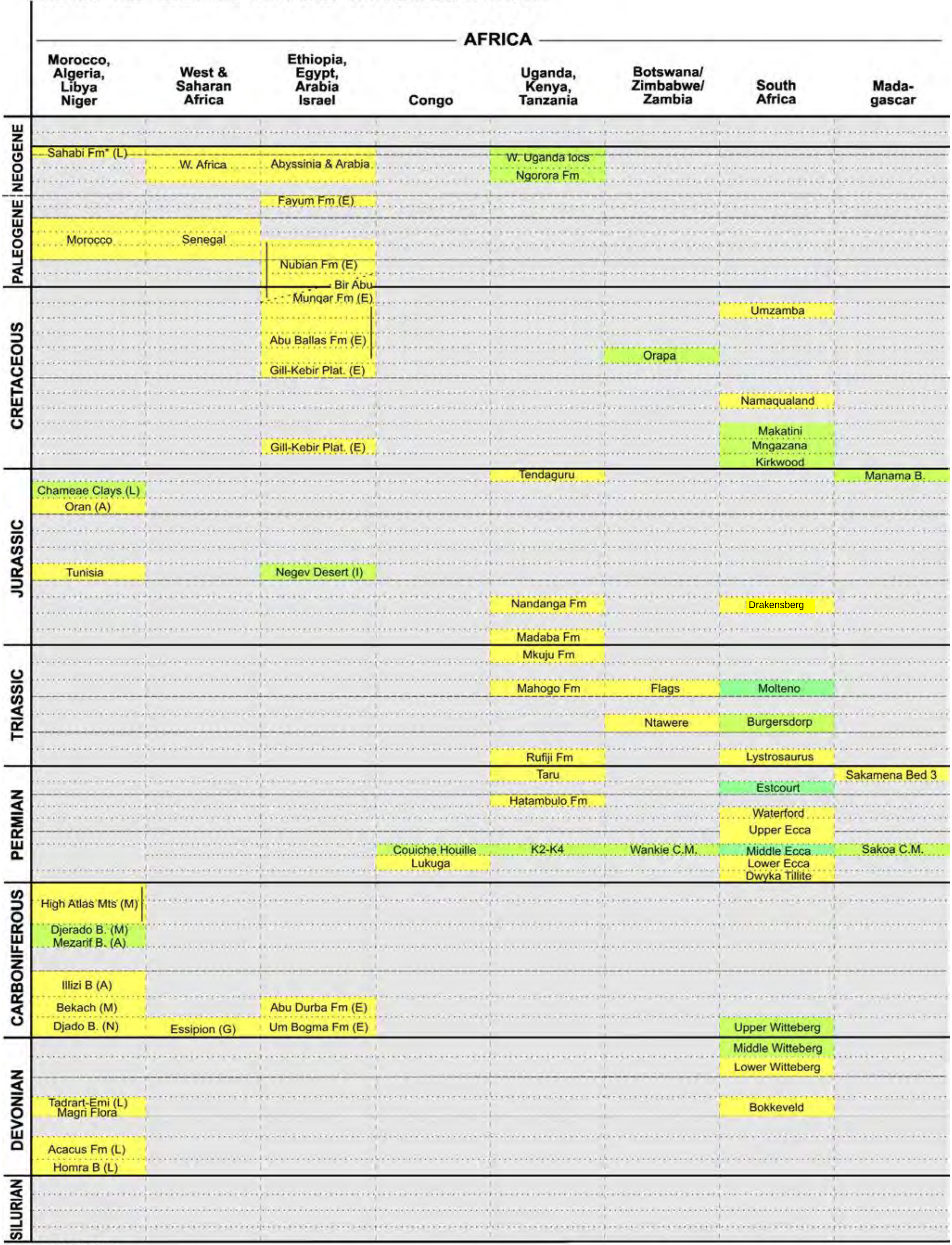
Argentina

1. & Palaoco Fm.
2. & Rio Pichileufa Flora
3. & Paso del Sapo Fm.
   Los Alamitos Fm.
   Lefipan Fm.
4. Includes top to bottom
   Punta del Barco Fm.
   Bajo Tigre Fm.
   Anfiteatro Ticó Fm.
5. & Cañadón Asfalto Fm.
6. & other mid-Late Trias. Fms
   Sorocayense Gp.
   (Barreal & other fms)
   Uspallata Gp.
   (Potrerillos, Cacheuta & other fms)

Contributors

Roberto Iannuzzi (general)
Oscar Rösler (general)
Ruben Cuneo (Argentina)
Conrad Labandeira (S Argentina, Tert)

Chart 12. MEGAFLORAL CORRELATIONS



AFRICA

	Morocco, Algeria, Libya Niger	West & Saharan Africa	Ethiopia, Egypt, Arabia Israel	Congo	Uganda, Kenya, Tanzania	Botswana/ Zimbabwe/ Zambia	South Africa	Mada-gascar
NEOGENE	Sahabi Fm* (L)	W. Africa	Abyssinia & Arabia		W. Uganda locs Ngorora Fm			
PALEOGENE	Morocco	Senegal	Fayum Fm (E) Nubian Fm (E) Bir Abu Munqar Fm (E)					
CRETACEOUS			Abu Ballas Fm (E) Gill-Kebir Plat. (E) Gill-Kebir Plat. (E)			Orapa	Umzamba Namaqualand Makatini Mngazana Kirkwood	
JURASSIC	Chameae Clays (L) Oran (A) Tunisia		Negev Desert (I)		Tendaguru Nandanga Fm Madaba Fm		Drakensberg	Manama B.
TRIASSIC					Mkuju Fm Mahogo Fm Rufiji Fm	Flags Ntawere	Molteno Burgersdorp Lystrosaurus	
PERMIAN				Couiche Houille Lukuga	Taru Hatambulo Fm K2-K4	Wankie C.M.	Estcourt Waterford Upper Ecca Middle Ecca Lower Ecca Dwyka Tillite	Sakamena Bed 3 Sakoa C.M.
CARBONIFEROUS	High Atlas Mts (M) Djerado B. (M) Mezarif B. (A) Illizi B (A) Bekach (M) Djado B. (N)	Essipion (G)	Abu Durba Fm (E) Um Bogma Fm (E)				Upper Witteberg	
DEVONIAN	Tadrart-Emi (L) Magri Flora Acacus Fm (L) Homra B (L)						Middle Witteberg Lower Witteberg Bokkeveld	
SILURIAN								

*& Omo Gp

Megafloras

🟩 top (quality/studied)
intermediate
🟨 poor (quality/understudied)

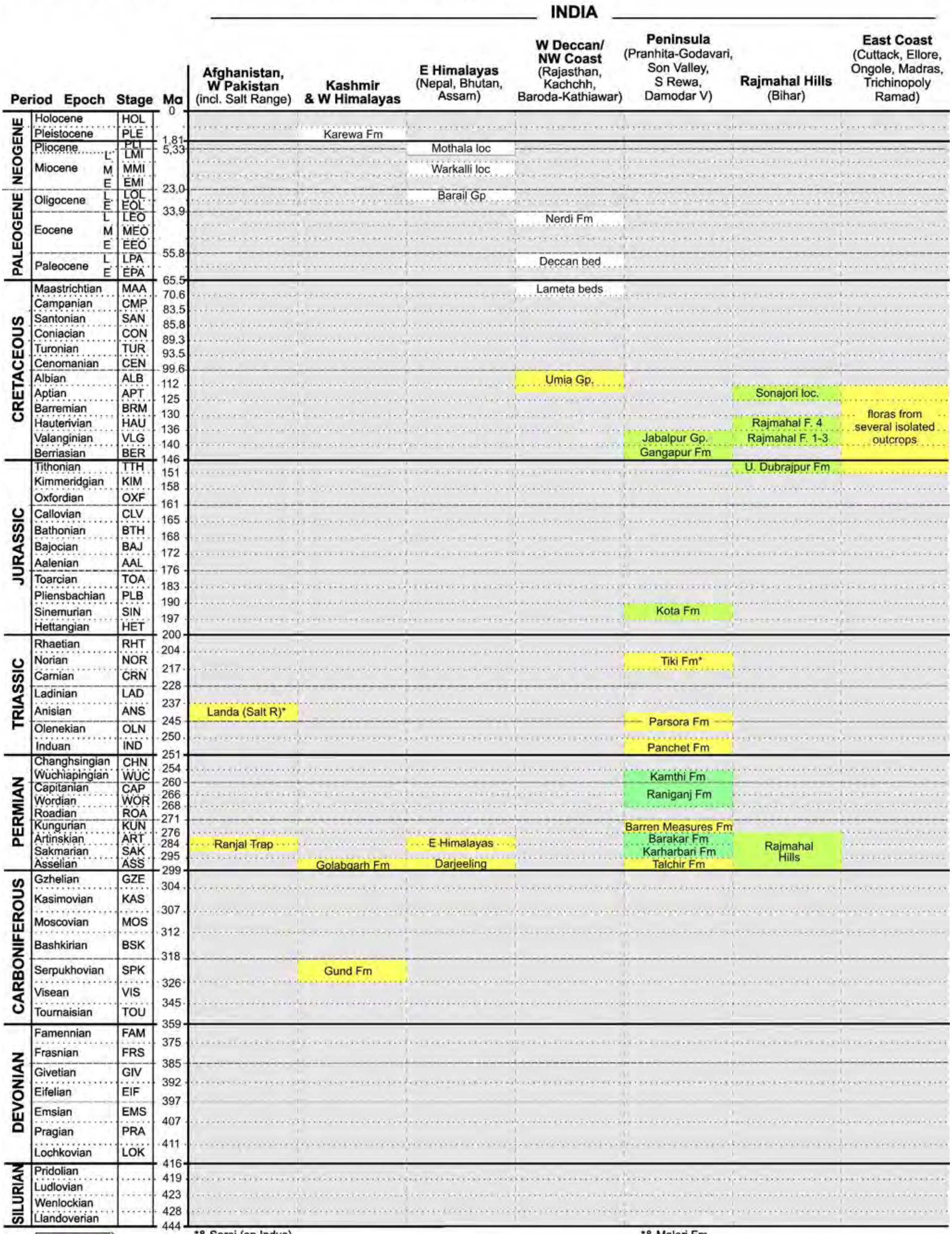
Gp: Group
Fm: Formation
M: Member

Only those strata including megafloras are plotted; marine, vertebrate-bearing & barren strata are excluded.

References (selected)
Anderson 1981: Permo-Trias, Southern Africa
Anderson et al. 1999: South Africa, general
Archangelsky 1989 (in Taylor & Taylor): Sil-Carb, N.Africa
Edwards 1989 (in Taylor & Taylor): Sil-Carb, N. Africa

Contributors
Chris Cleal (N & W Africa, Dev-mid Cret)
Hans-Jochen Gregor (Laurasian Africa, general)
Thomas Schlueter (E.Africa, Perm-Tert)
John Anderson (Gondwanan Africa, general)

Chart 13. MEGAFLORAL CORRELATIONS



INDIA

Period	Epoch		Stage	Ma	Afghanistan, W Pakistan (incl. Salt Range)	Kashmir & W Himalayas	E Himalayas (Nepal, Bhutan, Assam)	W Deccan/ NW Coast (Rajasthan, Kachchh, Baroda-Kathiawar)	Peninsula (Pranhita-Godavari, Son Valley, S Rewa, Damodar V)	Rajmahal Hills (Bihar)	East Coast (Cuttack, Ellore, Ongole, Madras, Trichinopoly Ramad)
NEOGENE	Holocene		HOL	0							
	Pleistocene		PLE	1.81		Karewa Fm					
	Pliocene		PLI	5.33			Mothala loc				
	Miocene	L	LMI								
		M	MMI				Warkalli loc				
		E	EMI								
PALEOGENE	Oligocene	L	LOL	23.0			Barail Gp				
		E	EOL								
	Eocene	L	LEO	33.9				Nerdi Fm			
		M	MEO								
		E	EEO								
	Paleocene	L	LPA	55.8				Deccan bed			
		E	EPA								
CRETACEOUS			Maastrichtian MAA	65.5				Lameta beds			
			Campanian CMP	70.6							
			Santonian SAN	83.5							
			Coniacian CON	85.8							
			Turonian TUR	89.3							
			Cenomanian CEN	93.5							
			Albian ALB	99.6				Umia Gp.			
			Aptian APT	112						Sonajori loc.	floras from several isolated outcrops
			Barremian BRM	125							
			Hauterivian HAU	130						Rajmahal F. 4	
			Valanginian VLG	136					Jabalpur Gp.	Rajmahal F. 1-3	
			Berriasian BER	140					Gangapur Fm		
JURASSIC			Tithonian TTH	146						U. Dubrajpur Fm	
			Kimmeridgian KIM	151							
			Oxfordian OXF	158							
			Callovian CLV	161							
			Bathonian BTH	165							
			Bajocian BAJ	168							
			Aalenian AAL	172							
			Toarcian TOA	176							
			Pliensbachian PLB	183					Kota Fm		
			Sinemurian SIN	190							
			Hettangian HET	197							
TRIASSIC			Rhaetian RHT	200							
			Norian NOR	204					Tiki Fm*		
			Carnian CRN	217							
			Ladinian LAD	228							
			Anisian ANS	237	Landa (Salt R)*				Parsora Fm		
			Olenekian OLN	245							
			Induan IND	250					Panchet Fm		
PERMIAN			Changhsingian CHN	251							
			Wuchiapingian WUC	254					Kamthi Fm		
			Capitanian CAP	260					Raniganj Fm		
			Wordian WOR	266							
			Roadian ROA	268							
			Kungurian KUN	271					Barren Measures Fm		
			Artinskian ART	276	Ranjal Trap		E Himalayas		Barakar Fm	Rajmahal Hills	
			Sakmarian SAK	284					Karharbari Fm		
			Asselian ASS	295		Golabgarh Fm	Darjeeling		Talchir Fm		
CARBONIFEROUS			Gzhelian GZE	299							
			Kasimovian KAS	304							
			Moscovian MOS	307							
			Bashkirian BSK	312							
			Serpukhovian SPK	318		Gund Fm					
			Visean VIS	326							
			Tournaisian TOU	345							
DEVONIAN			Famennian FAM	359							
			Frasnian FRS	375							
			Givetian GIV	385							
			Eifelian EIF	392							
			Emsian EMS	397							
			Pragian PRA	407							
			Lochkovian LOK	411							
SILURIAN			Pridolian	416							
			Ludlovian	419							
			Wenlockian	423							
			Llandoverian	428							
				444	*& Sarai (on Indus)				*& Maleri Fm		

Megafloras
top (quality/studied)
intermediate
poor (quality/understudied)

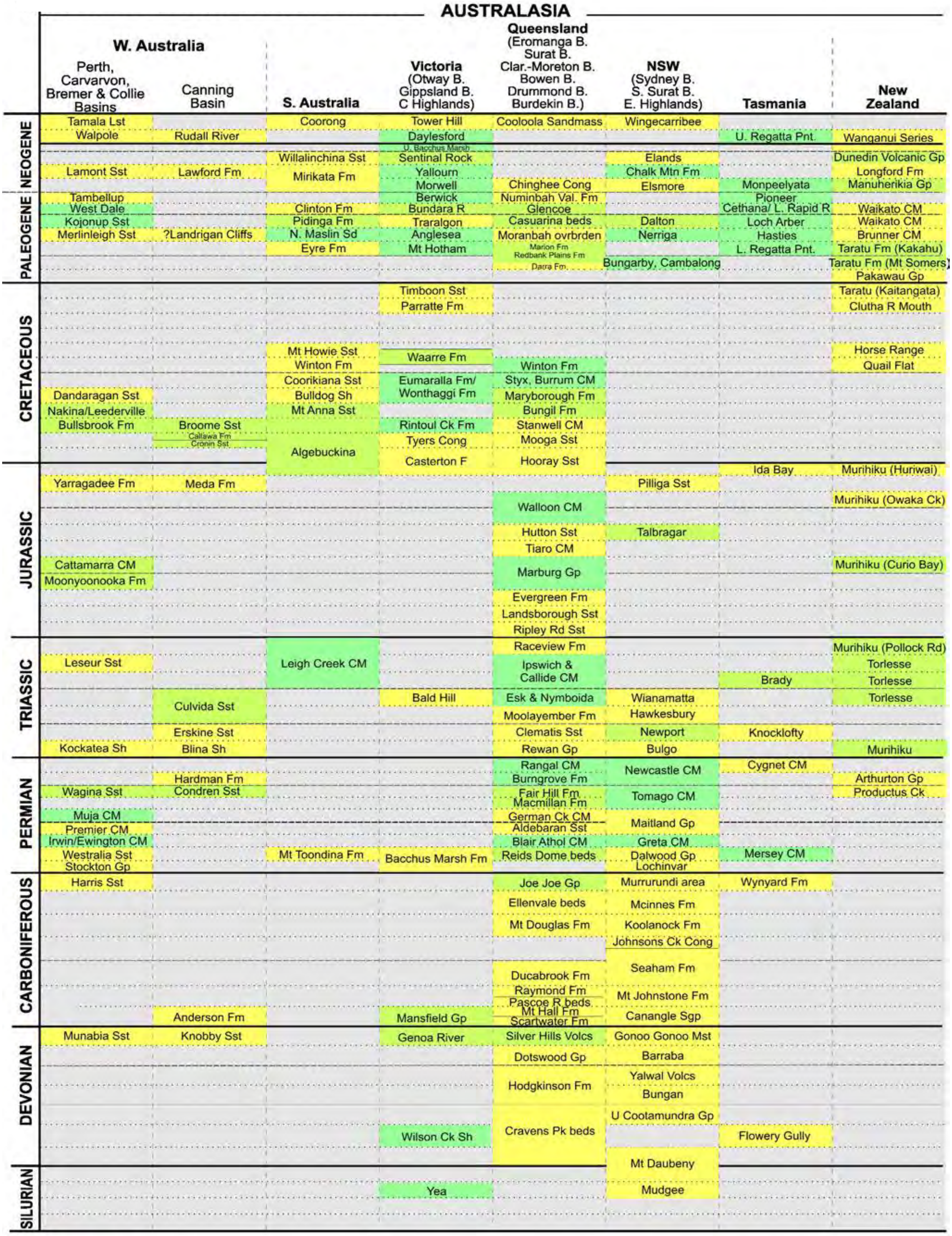
Gp: Group
Fm: Formation
M: Member

Only those strata including megafloras are plotted; marine, vertebrate-bearing & barren strata are excluded.

References
Anderson 1981: Perm-Trias (general)
Bose, Taylor & Taylor 1989: Perm-L Cret (general)
Chandra in Anderson et al. 1999: Perm (Godavari etc)
Banerji (in prep. 2005): Jur-Cret (Rajmahal Hills)

Contributors
John Anderson (general)
Chris Cleal (general)
Suresh Bonde
Rakesh Mehotra

Chart 14. MEGAFLORAL CORRELATIONS



AUSTRALASIA

	W. Australia: Perth, Carvarvon, Bremer & Collie Basins	W. Australia: Canning Basin	S. Australia	Victoria (Otway B. Gippsland B. C Highlands)	Queensland (Eromanga B. Surat B. Clar.-Moreton B. Bowen B. Drummond B. Burdekin B.)	NSW (Sydney B. S. Surat B. E. Highlands)	Tasmania	New Zealand
NEOGENE	Tamala Lst		Coorong	Tower Hill	Cooloola Sandmass	Wingecarribee		
	Walpole	Rudall River		Daylesford			U. Regatta Pnt.	Wanganui Series
				U. Bacchus Marsh				
			Willalinchina Sst	Sentinal Rock		Elands		Dunedin Volcanic Gp
	Lamont Sst	Lawford Fm	Mirikata Fm	Yallourn		Chalk Mtn Fm		Longford Fm
				Morwell	Chinghee Cong	Elsmore	Monpeelyata	Manuherikia Gp
PALEOGENE	Tambellup			Berwick	Numinbah Val. Fm		Pioneer	
	West Dale		Clinton Fm	Bundara R	Glencoe		Cethana/ L. Rapid R	Waikato CM
	Kojonup Sst		Pidinga Fm	Traralgon	Casuarina beds	Dalton	Loch Arber	Waikato CM
	Merlinleigh Sst	?Landrigan Cliffs	N. Maslin Sd	Anglesea	Moranbah ovrbrden	Nerriga	Hasties	Brunner CM
			Eyre Fm	Mt Hotham	Marion Fm Redbank Plains Fm		L. Regatta Pnt.	Taratu Fm (Kakahu)
					Darra Fm.	Bungarby, Cambalong		Taratu Fm (Mt Somers)
								Pakawau Gp
CRETACEOUS				Timboon Sst				Taratu (Kaitangata)
				Parratte Fm				Clutha R Mouth
			Mt Howie Sst	Waarre Fm				Horse Range
			Winton Fm		Winton Fm			Quail Flat
			Coorikiana Sst	Eumaralla Fm/ Wonthaggi Fm	Styx, Burrum CM			
	Dandaragan Sst		Bulldog Sh		Maryborough Fm			
	Nakina/Leederville		Mt Anna Sst		Bungil Fm			
	Bullsbrook Fm	Broome Sst		Rintoul Ck Fm	Stanwell CM			
		Callawa Fm Cronin Sst	Algebuckina	Tyers Cong	Mooga Sst			
				Casterton F	Hooray Sst			
JURASSIC							Ida Bay	Murihiku (Huriwai)
	Yarragadee Fm	Meda Fm				Pilliga Sst		
								Murihiku (Owaka Ck)
					Walloon CM			
					Hutton Sst	Talbragar		
					Tiaro CM			
	Cattamarra CM				Marburg Gp			Murihiku (Curio Bay)
	Moonyoonooka Fm							
					Evergreen Fm			
					Landsborough Sst			
					Ripley Rd Sst			
TRIASSIC					Raceview Fm			Murihiku (Pollock Rd)
	Leseur Sst		Leigh Creek CM		Ipswich & Callide CM			Torlesse
							Brady	Torlesse
		Culvida Sst		Bald Hill	Esk & Nymboida	Wianamatta		Torlesse
					Moolayember Fm	Hawkesbury		
		Erskine Sst			Clematis Sst	Newport	Knocklofty	
	Kockatea Sh	Blina Sh			Rewan Gp	Bulgo		Murihiku
PERMIAN					Rangal CM	Newcastle CM	Cygnet CM	
		Hardman Fm			Burngrove Fm			Arthurton Gp
	Wagina Sst	Condren Sst			Fair Hill Fm	Tomago CM		Productus Ck
					Macmillan Fm			
	Muja CM				German Ck CM	Maitland Gp		
	Premier CM				Aldebaran Sst			
	Irwin/Ewington CM				Blair Athol CM	Greta CM		
	Westralia Sst		Mt Toondina Fm	Bacchus Marsh Fm	Reids Dome beds	Dalwood Gp	Mersey CM	
	Stockton Gp					Lochinvar		
CARBONIFEROUS	Harris Sst				Joe Joe Gp	Murrurundi area	Wynyard Fm	
					Ellenvale beds	Mcinnes Fm		
					Mt Douglas Fm	Koolanock Fm		
						Johnsons Ck Cong		
						Seaham Fm		
					Ducabrook Fm			
					Raymond Fm	Mt Johnstone Fm		
					Pascoe R beds			
					Mt Hall Fm			
		Anderson Fm		Mansfield Gp	Scartwater Fm	Canangle Sgp		
DEVONIAN	Munabia Sst	Knobby Sst		Genoa River	Silver Hills Volcs	Gonoo Gonoo Mst		
					Dotswood Gp	Barraba		
						Yalwal Volcs		
					Hodgkinson Fm			
						Bungan		
						U Cootamundra Gp		
					Cravens Pk beds			
				Wilson Ck Sh			Flowery Gully	
						Mt Daubeny		
SILURIAN				Yea		Mudgee		

Megafloras

top (quality/studied)
intermediate
poor (quality/understudied)

Gp: Group
Fm: Formation
M: Member

Only those strata including megafloras are plotted; marine, vertebrate-bearing & barren strata are excluded.

References

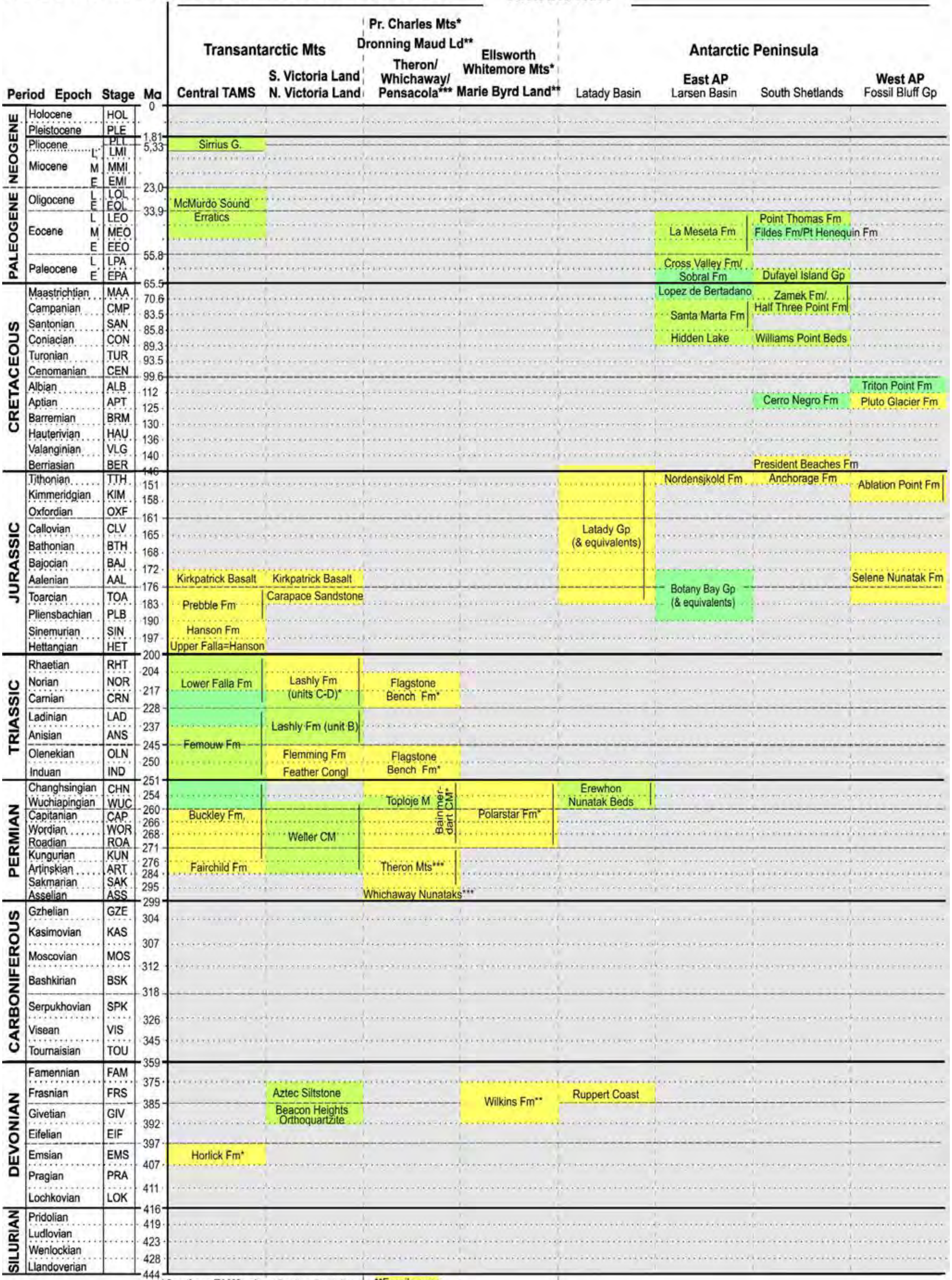
McLoughlin in Anderson et al.1999: general
McLoughlin in prep. 2005: Jurassic-M.Cret. floras

Contributors

Steve McLoughlin (Aus, general)
John Rigby (Aus, Permo-Triassic)
Mike Pole (NZ, general)

Chart 15. MEGAFLORAL CORRELATIONS

ANTARCTICA



***Southern TAMS:** *also* Mt *Glossopteris* Fm (Ohio Range), equiv. to Buckley & top of Fairchild Fm; Queen Maud Fm, equiv. in part to Buckley & upper Mt *Glossopteris* Fm

*Section Peak Fm (in N. Victoria Land)

**Fossilryggen (Wuch.–Roadian)

**Milorgfjella (Kung.–Asselian)

(see top of columns for key to asterisks)

Contributors

David Cantrill (general)

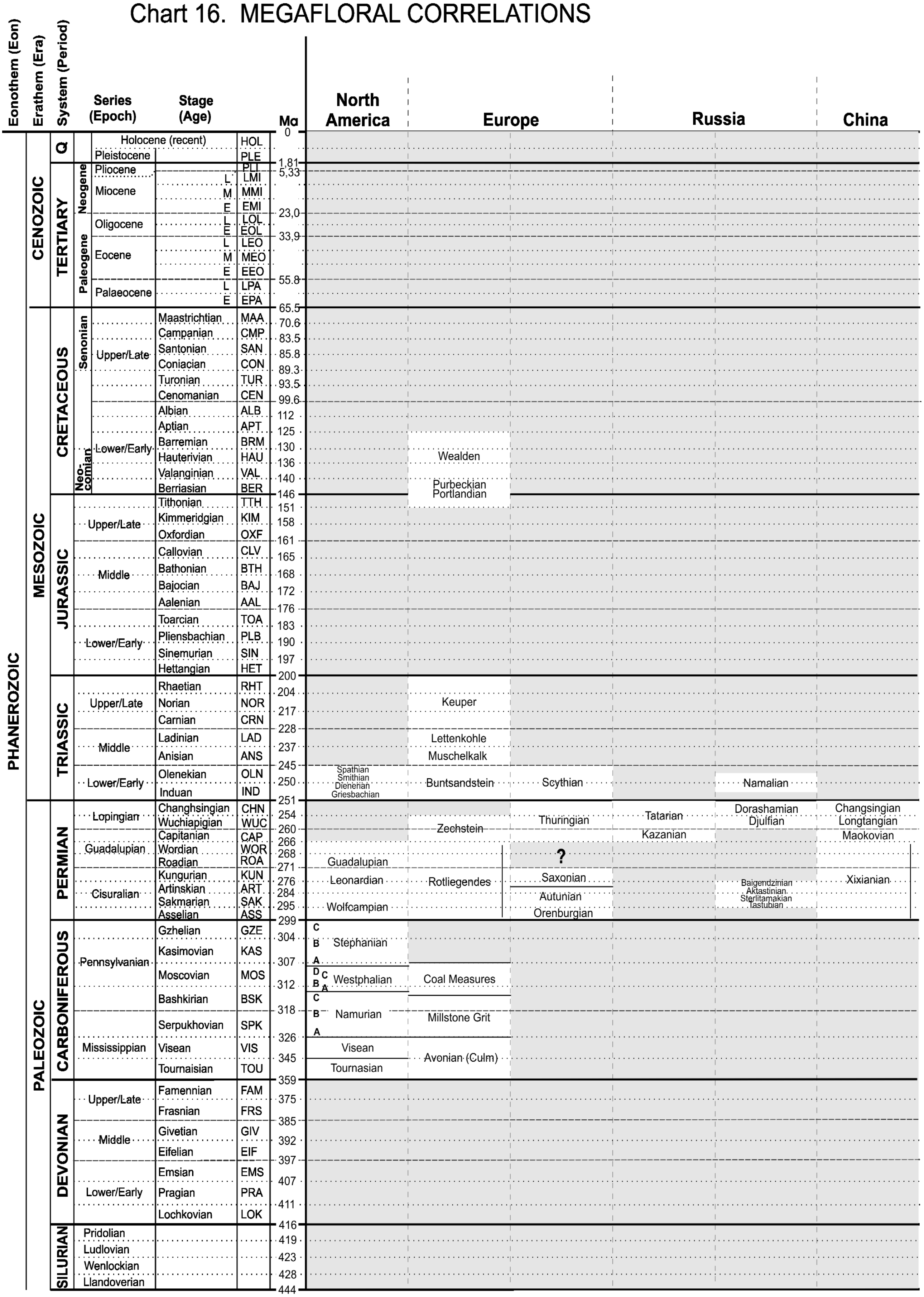
John Isbell (Perm, Transantarctic Mts & Victoria Land)

References

Bose, Taylor & Taylor 1989: Perm.-L.Cret.

Taylor & Taylor 1989: Perm. & Trias.

Chart 16. MEGAFLORAL CORRELATIONS



Eonothem (Eon)	Erathem (Era)	System (Period)		Series (Epoch)	Stage (Age)		Ma	North America	Europe		Russia		China
PHANEROZOIC	CENOZOIC	Q		Holocene (recent)		HOL	0						
				Pleistocene		PLE	1.81						
		TERTIARY	Neogene	Pliocene		PLI	5,33						
				Miocene	L	LMI							
					M	MMI							
					E	EMI	23,0						
			Paleogene	Oligocene	L	LOL							
					E	EOL	33,9						
				Eocene	L	LEO							
					M	MEO							
					E	EEO	55.8						
				Palaeocene	L	LPA							
					E	EPA	65.5						
	MESOZOIC	CRETACEOUS	Senonian	Upper/Late	Maastrichtian	MAA	70.6						
					Campanian	CMP	83.5						
					Santonian	SAN	85.8						
					Coniacian	CON	89.3						
					Turonian	TUR	93.5						
					Cenomanian	CEN	99.6						
				Lower/Early	Albian	ALB	112						
					Aptian	APT	125						
					Barremian	BRM	130						
			Neo-comian		Hauterivian	HAU	136		Wealden				
					Valanginian	VAL	140						
					Berriasian	BER	146		Purbeckian Portlandian				
		JURASSIC		Upper/Late	Tithonian	TTH	151						
					Kimmeridgian	KIM	158						
					Oxfordian	OXF	161						
				Middle	Callovian	CLV	165						
					Bathonian	BTH	168						
					Bajocian	BAJ	172						
					Aalenian	AAL	176						
				Lower/Early	Toarcian	TOA	183						
					Pliensbachian	PLB	190						
					Sinemurian	SIN	197						
					Hettangian	HET	200						
		TRIASSIC		Upper/Late	Rhaetian	RHT	204		Keuper				
					Norian	NOR	217						
					Carnian	CRN	228						
				Middle	Ladinian	LAD	237		Lettenkohle				
					Anisian	ANS	245		Muschelkalk				
				Lower/Early	Olenekian	OLN	250	Spathian Smithian Dienerian Griesbachian	Buntsandstein	Scythian		Namalian	
					Induan	IND	251						
	PALEOZOIC	PERMIAN		Lopingian	Changhsingian	CHN	254			Thuringian	Tatarian	Dorashamian	Changsingian
					Wuchiapigian	WUC	260		Zechstein			Djulfian	Longtangian
				Guadalupian	Capitanian	CAP	266				Kazanian		Maokovian
					Wordian	WOR	268			?			
					Roadian	ROA	271	Guadalupian					
				Cisuralian	Kungurian	KUN	276	Leonardian	Rotliegendes	Saxonian		Baigendzinian	Xixianian
					Artinskian	ART	284			Autunian		Aktastinian	
					Sakmarian	SAK	295	Wolfcampian				Sterlitamakian	
					Asselian	ASS	299			Orenburgian		Tastubian	
		CARBONIFEROUS		Pennsylvanian	Gzhelian	GZE	304	C					
					Kasimovian	KAS	307	B Stephanian A					
					Moscovian	MOS	312	D C B A Westphalian	Coal Measures				
					Bashkirian	BSK	318	C					
				Mississippian	Serpukhovian	SPK	326	B Namurian A	Millstone Grit				
					Visean	VIS	345	Visean	Avonian (Culm)				
					Tournaisian	TOU	359	Tournasian					
		DEVONIAN		Upper/Late	Famennian	FAM	375						
					Frasnian	FRS	385						
				Middle	Givetian	GIV	392						
					Eifelian	EIF	397						
				Lower/Early	Emsian	EMS	407						
					Pragian	PRA	411						
					Lochkovian	LOK	416						
		SILURIAN		Pridolian			419						
				Ludlovian			423						
				Wenlockian			428						
				Llandoverian			444						

References

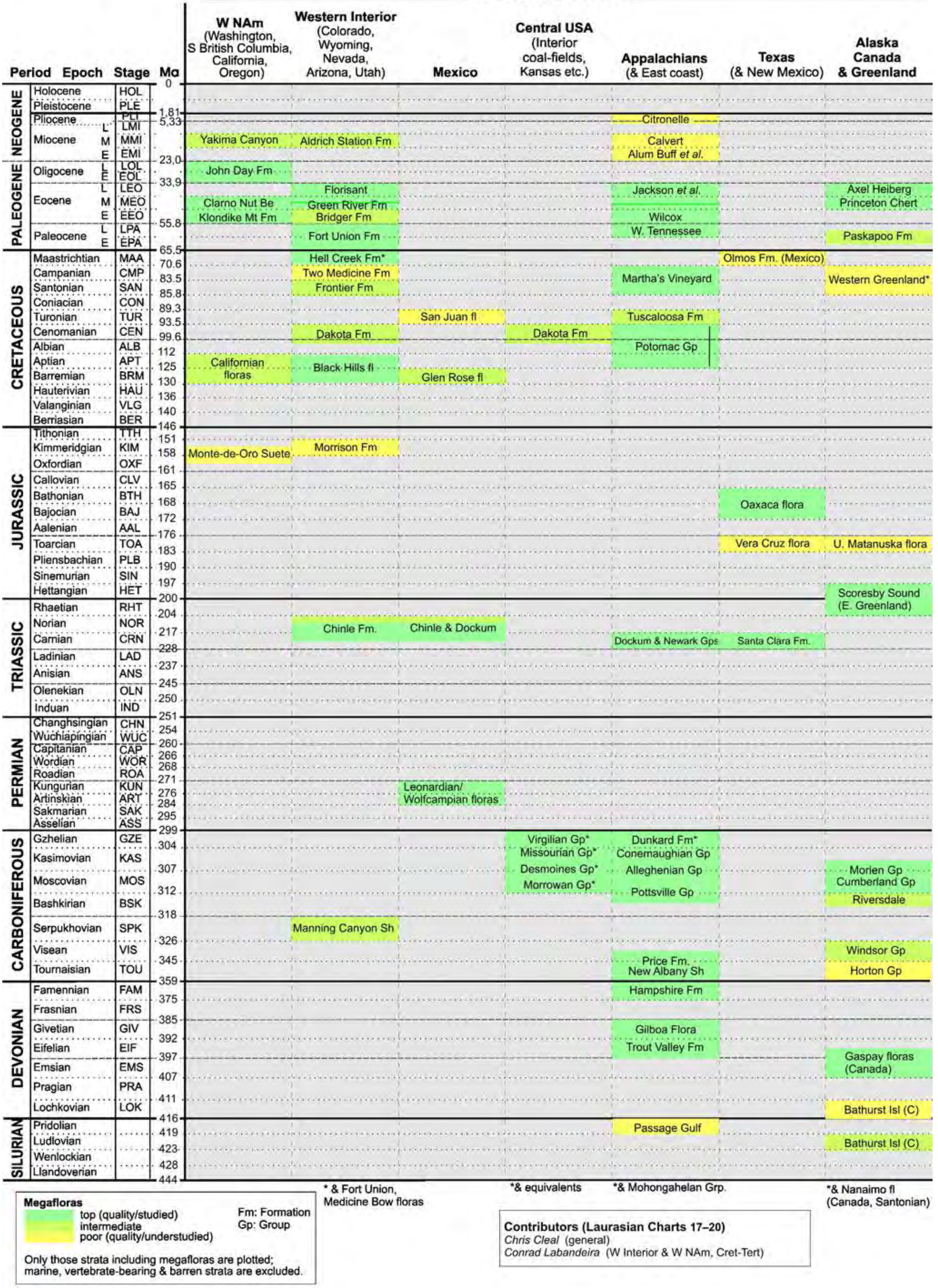
IUGS 2000: "International Time Scale"; International standards

Elsevier 1998: "Geological Time Table"; commonly used alternate standards

LAURASIAN STANDARDS

Chart 17. MEGAFLORAL CORRELATIONS

NORTH AMERICA



Period	Epoch		Stage	Ma	W NAm (Washington, S British Columbia, California, Oregon)	Western Interior (Colorado, Wyoming, Nevada, Arizona, Utah)	Mexico	Central USA (Interior coal-fields, Kansas etc.)	Appalachians (& East coast)	Texas (& New Mexico)	Alaska Canada & Greenland
NEOGENE	Holocene		HOL	0							
	Pleistocene		PLE								
	Pliocene		PLI	1.81					Citronelle		
	Miocene	L	LMI	5.33							
		M	MMI		Yakima Canyon	Aldrich Station Fm			Calvert		
		E	EMI						Alum Buff *et al.*		
PALEOGENE	Oligocene	L	LOL	23.0	John Day Fm						
		E	EOL								
	Eocene	L	LEO	33.9		Florisant			Jackson *et al.*		Axel Heiberg
		M	MEO		Clarno Nut Be	Green River Fm					Princeton Chert
		E	EEO		Klondike Mt Fm	Bridger Fm			Wilcox		
	Paleocene	L	LPA	55.8					W. Tennessee		
		E	EPA			Fort Union Fm					Paskapoo Fm
CRETACEOUS	Maastrichtian		MAA	65.5		Hell Creek Fm*				Olmos Fm. (Mexico)	
	Campanian		CMP	70.6		Two Medicine Fm			Martha's Vineyard		Western Greenland*
	Santonian		SAN	83.5		Frontier Fm					
	Coniacian		CON	85.8							
	Turonian		TUR	89.3			San Juan fl		Tuscaloosa Fm		
	Cenomanian		CEN	93.5		Dakota Fm		Dakota Fm			
	Albian		ALB	99.6					Potomac Gp		
	Aptian		APT	112	Californian floras	Black Hills fl					
	Barremian		BRM	125			Glen Rose fl				
	Hauterivian		HAU	130							
	Valanginian		VLG	136							
	Berriasian		BER	140							
JURASSIC	Tithonian		TTH	146							
	Kimmeridgian		KIM	151	Monte-de-Oro Suete	Morrison Fm					
	Oxfordian		OXF	158							
	Callovian		CLV	161							
	Bathonian		BTH	165						Oaxaca flora	
	Bajocian		BAJ	168							
	Aalenian		AAL	172							
	Toarcian		TOA	176						Vera Cruz flora	U. Matanuska flora
	Pliensbachian		PLB	183							
	Sinemurian		SIN	190							
	Hettangian		HET	197							Scoresby Sound (E. Greenland)
TRIASSIC	Rhaetian		RHT	200							
	Norian		NOR	204		Chinle Fm.	Chinle & Dockum				
	Carnian		CRN	217					Dockum & Newark Gps	Santa Clara Fm.	
	Ladinian		LAD	228							
	Anisian		ANS	237							
	Olenekian		OLN	245							
	Induan		IND	250							
PERMIAN	Changhsingian		CHN	251							
	Wuchiapingian		WUC	254							
	Capitanian		CAP	260							
	Wordian		WOR	266							
	Roadian		ROA	268							
	Kungurian		KUN	271			Leonardian/ Wolfcampian floras				
	Artinskian		ART	276							
	Sakmarian		SAK	284							
	Asselian		ASS	295							
CARBONIFEROUS	Gzhelian		GZE	299				Virgilian Gp*	Dunkard Fm*		
	Kasimovian		KAS	304				Missourian Gp*	Conemaughian Gp		
	Moscovian		MOS	307				Desmoines Gp* Morrowan Gp*	Alleghenian Gp		Morien Gp Cumberland Gp
	Bashkirian		BSK	312					Pottsville Gp		Riversdale
	Serpukhovian		SPK	318		Manning Canyon Sh					
	Visean		VIS	326							Windsor Gp
	Tournaisian		TOU	345					Price Fm. New Albany Sh		Horton Gp
DEVONIAN	Famennian		FAM	359					Hampshire Fm		
	Frasnian		FRS	375							
	Givetian		GIV	385					Gilboa Flora		
	Eifelian		EIF	392					Trout Valley Fm		
	Emsian		EMS	397							Gaspay floras (Canada)
	Pragian		PRA	407							
	Lochkovian		LOK	411							Bathurst Isl (C)
SILURIAN	Pridolian			416					Passage Gulf		
	Ludlovian			419							Bathurst Isl (C)
	Wenlockian			423							
	Llandoverian			428							
				444							
						* & Fort Union, Medicine Bow floras		*& equivalents	*& Mohongahelan Grp.		*& Nanaimo fl (Canada, Santonian)

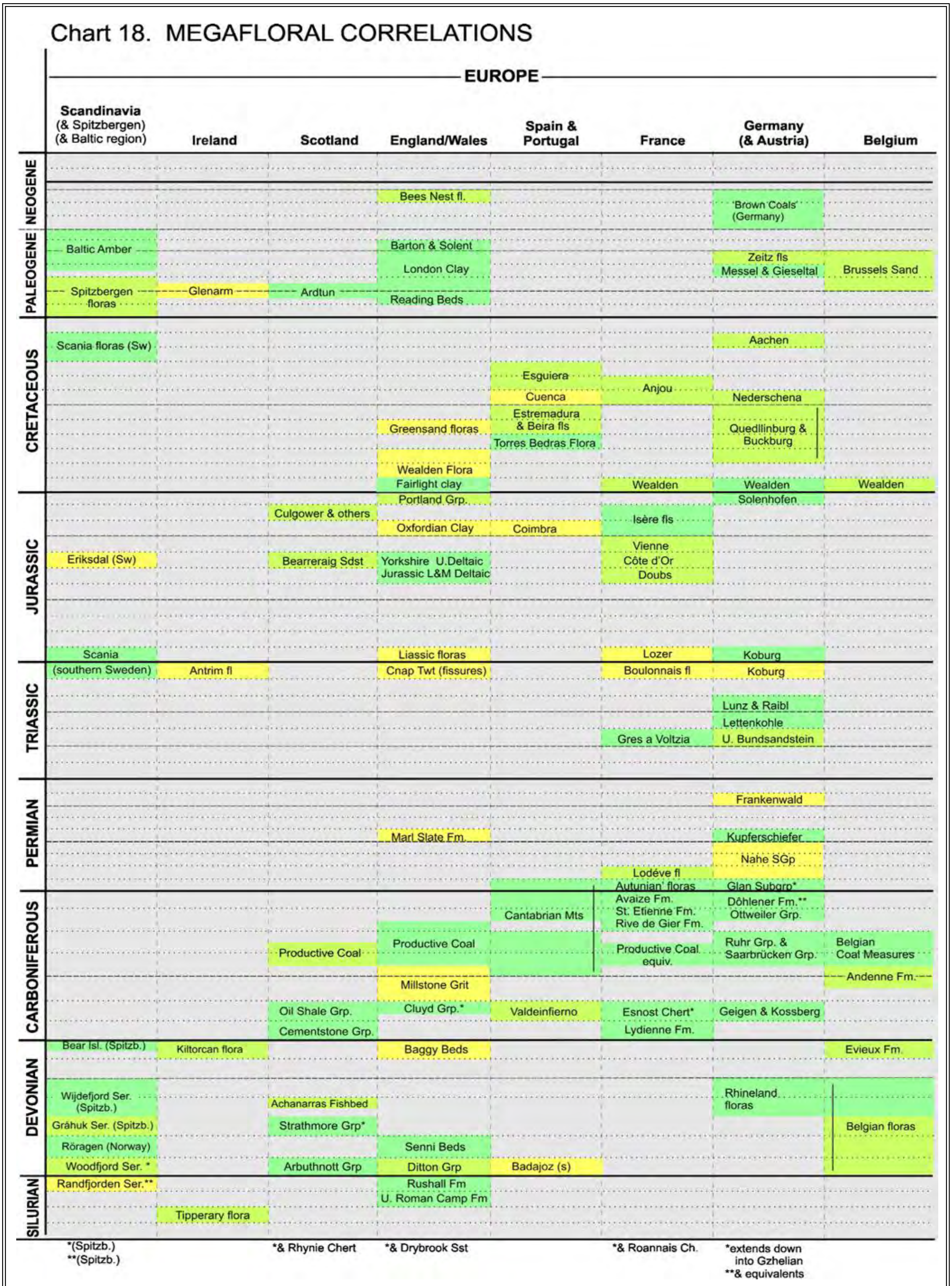
Megafloras
🟩 top (quality/studied)
intermediate
🟨 poor (quality/understudied)

Fm: Formation
Gp: Group

Only those strata including megafloras are plotted; marine, vertebrate-bearing & barren strata are excluded.

Contributors (Laurasian Charts 17–20)
Chris Cleal (general)
Conrad Labandeira (W Interior & W NAm, Cret-Tert)

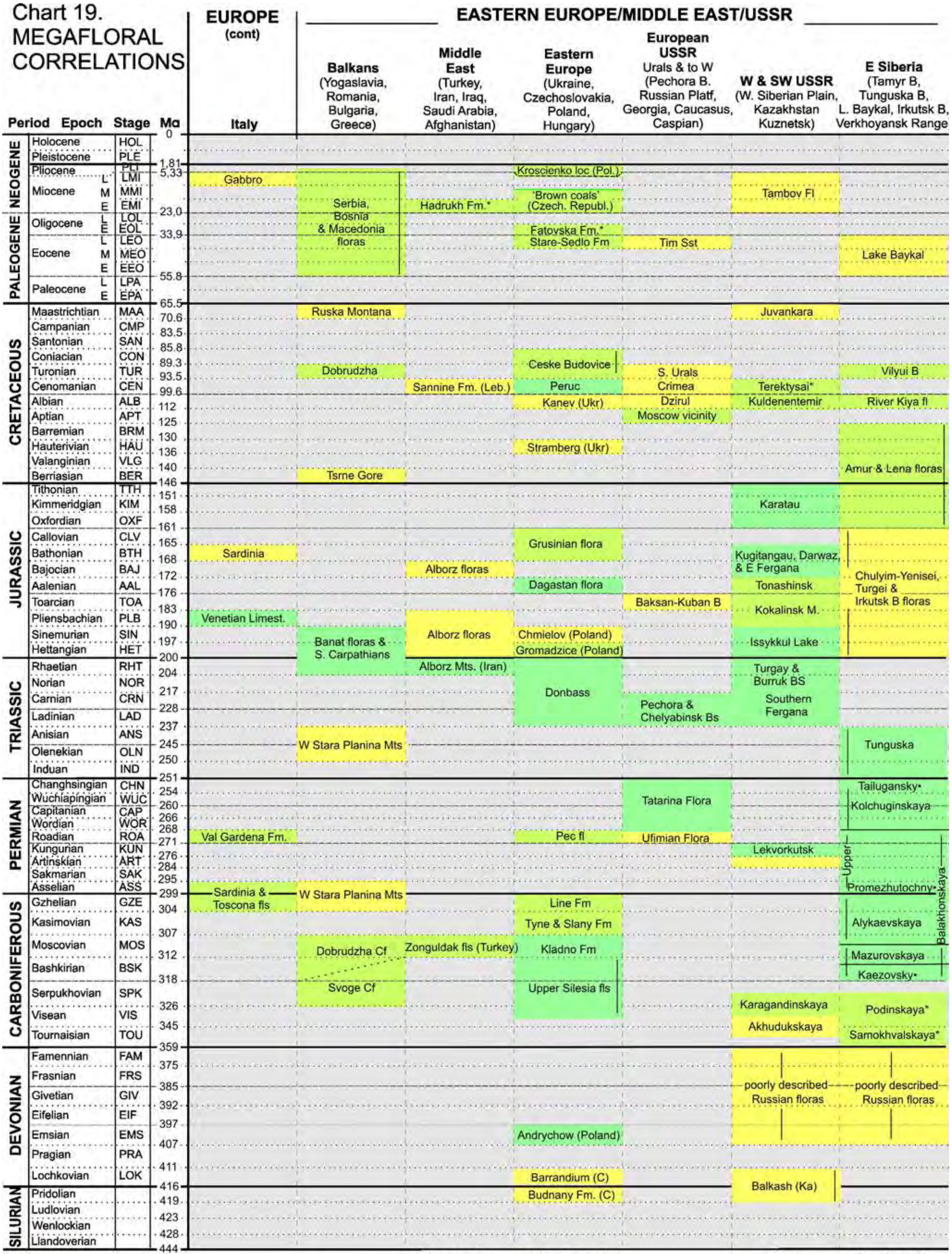
Chart 18. MEGAFLORAL CORRELATIONS



EUROPE

	Scandinavia (& Spitzbergen) (& Baltic region)	Ireland	Scotland	England/Wales	Spain & Portugal	France	Germany (& Austria)	Belgium
NEOGENE				Bees Nest fl.			'Brown Coals' (Germany)	
PALEOGENE	Baltic Amber Spitzbergen floras	Glenarm	Ardtun	Barton & Solent London Clay Reading Beds			Zeitz fls Messel & Gieseltal	Brussels Sand
CRETACEOUS	Scania floras (Sw)			Greensand floras Wealden Flora Fairlight clay	Esguiera Cuenca Estremadura & Beira fls Torres Bedras Flora	Anjou Wealden	Aachen Nederschena Quedlinburg & Buckburg Wealden	Wealden
JURASSIC	Eriksdal (Sw) Scania		Culgower & others Bearreraig Sdst	Portland Grp. Oxfordian Clay Yorkshire U.Deltaic Jurassic L&M Deltaic Liassic floras	Coimbra	Isère fls Vienne Côte d'Or Doubs Lozer	Solenhofen Koburg	
TRIASSIC	(southern Sweden)	Antrim fl		Cnap Twt (fissures)		Boulonnais fl Gres a Voltzia	Koburg Lunz & Raibl Lettenkohle U. Bundsandstein	
PERMIAN				Marl Slate Fm.		Lodéve fl 'Autunian' floras	Frankenwald Kupferschiefer Nahe SGp Glan Subgrp*	
CARBONIFEROUS			Productive Coal Oil Shale Grp. Cementstone Grp.	Productive Coal Millstone Grit Cluyd Grp.*	Cantabrian Mts Valdeinfierno	Avaize Fm. St. Etienne Fm. Rive de Gier Fm. Productive Coal equiv. Esnost Chert* Lydienne Fm.	Dôhlener Fm.** Ottweiler Grp. Ruhr Grp. & Saarbrücken Grp. Geigen & Kossberg	Belgian Coal Measures Andenne Fm.
DEVONIAN	Bear Isl. (Spitzb.) Wijdefjord Ser. (Spitzb.) Gråhuk Ser. (Spitzb.) Röragen (Norway) Woodfjord Ser. *	Kiltorcan flora	Achanarras Fishbed Strathmore Grp* Arbuthnott Grp	Baggy Beds Senni Beds Ditton Grp	Badajoz (s)		Rhineland floras	Evieux Fm. Belgian floras
SILURIAN	Randfjorden Ser.**	Tipperary flora		Rushall Fm U. Roman Camp Fm				
	*(Spitzb.) **(Spitzb.)		*& Rhynie Chert	*& Drybrook Sst		*& Roannais Ch.	*extends down into Gzhelian **& equivalents	

Chart 19. MEGAFLORAL CORRELATIONS



Period	Epoch	Stage		Ma	EUROPE (cont)	EASTERN EUROPE/MIDDLE EAST/USSR					
					Italy	**Balkans** (Yogaslavia, Romania, Bulgaria, Greece)	**Middle East** (Turkey, Iran, Iraq, Saudi Arabia, Afghanistan)	**Eastern Europe** (Ukraine, Czechoslovakia, Poland, Hungary)	**European USSR** Urals & to W (Pechora B. Russian Platf, Georgia, Caucasus, Caspian)	**W & SW USSR** (W. Siberian Plain, Kazakhstan Kuznetsk)	**E Siberia** (Tamyr B, Tunguska B, L. Baykal, Irkutsk B, Verkhoyansk Range
NEOGENE	Holocene	Holocene	HOL	0							
	Pleistocene	Pleistocene	PLE								
	Pliocene	Pliocene	PLI	1,81				Kroscienko loc (Pol.)			
	Miocene L		LMI	5,33	Gabbro	Serbia, Bosnia & Macedonia floras				Tambov Fl	
	Miocene M		MMI					'Brown coals' (Czech. Republ.)			
	Miocene E		EMI				Hadrukh Fm.*				
PALEOGENE	Oligocene L		LOL	23,0							
	Oligocene E		EOL					Fatovska Fm.*			
	Eocene L		LEO	33,9				Stare-Sedlo Fm	Tim Sst		Lake Baykal
	Eocene M		MEO								
	Eocene E		EEO								
	Paleocene L		LPA	55.8							
	Paleocene E		EPA								
CRETACEOUS		Maastrichtian	MAA	65.5		Ruska Montana				Juvankara	
		Campanian	CMP	70.6							
		Santonian	SAN	83.5							
		Coniacian	CON	85.8				Ceske Budovice			
		Turonian	TUR	89.3		Dobrudzha			S. Urals		Vilyui B
		Cenomanian	CEN	93.5			Sannine Fm. (Leb.)	Peruc	Crimea	Terektysai*	
		Albian	ALB	99.6				Kanev (Ukr)	Dzirul	Kuldenentemir	River Kiya fl
		Aptian	APT	112					Moscow vicinity		
		Barremian	BRM	125							Amur & Lena floras
		Hauterivian	HAU	130				Stramberg (Ukr)			
		Valanginian	VLG	136							
		Berriasian	BER	140		Tsrne Gore					
JURASSIC		Tithonian	TTH	146						Karatau	
		Kimmeridgian	KIM	151							
		Oxfordian	OXF	158							
		Callovian	CLV	161				Grusinian flora			Chulyim-Yenisei, Turgei & Irkutsk B floras
		Bathonian	BTH	165	Sardinia					Kugitangau, Darwaz, & E Fergana	
		Bajocian	BAJ	168			Alborz floras				
		Aalenian	AAL	172				Dagastan flora		Tonashinsk	
		Toarcian	TOA	176					Baksan-Kuban B	Kokalinsk M.	
		Pliensbachian	PLB	183	Venetian Limest.		Alborz floras				
		Sinemurian	SIN	190		Banat floras & S. Carpathians		Chmielov (Poland)		Issykkul Lake	
		Hettangian	HET	197				Gromadzice (Poland)			
TRIASSIC		Rhaetian	RHT	200			Alborz Mts. (Iran)	Donbass		Turgay & Burruk BS	
		Norian	NOR	204							
		Carnian	CRN	217					Pechora & Chelyabinsk Bs	Southern Fergana	
		Ladinian	LAD	228							
		Anisian	ANS	237		W Stara Planina Mts					Tunguska
		Olenekian	OLN	245							
		Induan	IND	250							
PERMIAN		Changhsingian	CHN	251					Tatarina Flora		Tailugansky•
		Wuchiapingian	WUC	254							Kolchuginskaya
		Capitanian	CAP	260							
		Wordian	WOR	266							
		Roadian	ROA	268	Val Gardena Fm.			Pec fl	Ufimian Flora		
		Kungurian	KUN	271						Lekvorkutsk	
		Artinskian	ART	276							Upper
		Sakmarian	SAK	284							
		Asselian	ASS	295	Sardinia & Toscona fls	W Stara Planina Mts					Promezhutochny•
CARBONIFEROUS		Gzhelian	GZE	299				Line Fm			
		Kasimovian	KAS	304				Tyne & Slany Fm			Alykaevskaya Balakhonskaya
		Moscovian	MOS	307		Dobrudzha Cf	Zonguldak fls (Turkey)	Kladno Fm			
		Bashkirian	BSK	312							Mazurovskaya Kaezovsky•
		Serpukhovian	SPK	318		Svoge Cf		Upper Silesia fls			
		Visean	VIS	326						Karagandinskaya	Podinskaya*
		Tournaisian	TOU	345						Akhudukskaya	Samokhvalskaya*
DEVONIAN		Famennian	FAM	359						poorly described Russian floras	poorly described Russian floras
		Frasnian	FRS	375							
		Givetian	GIV	385							
		Eifelian	EIF	392							
		Emsian	EMS	397				Andrychow (Poland)			
		Pragian	PRA	407							
		Lochkovian	LOK	411				Barrandium (C)		Balkash (Ka)	
SILURIAN		Pridolian		416				Budnany Fm. (C)			
		Ludlovian		419							
		Wenlockian		423							
		Llandoverian		428							
				444							
							*(Saudi Arabia)	*& Serafimova Fm.; Kuclin Fl		*& Tsaran	*& equivalents

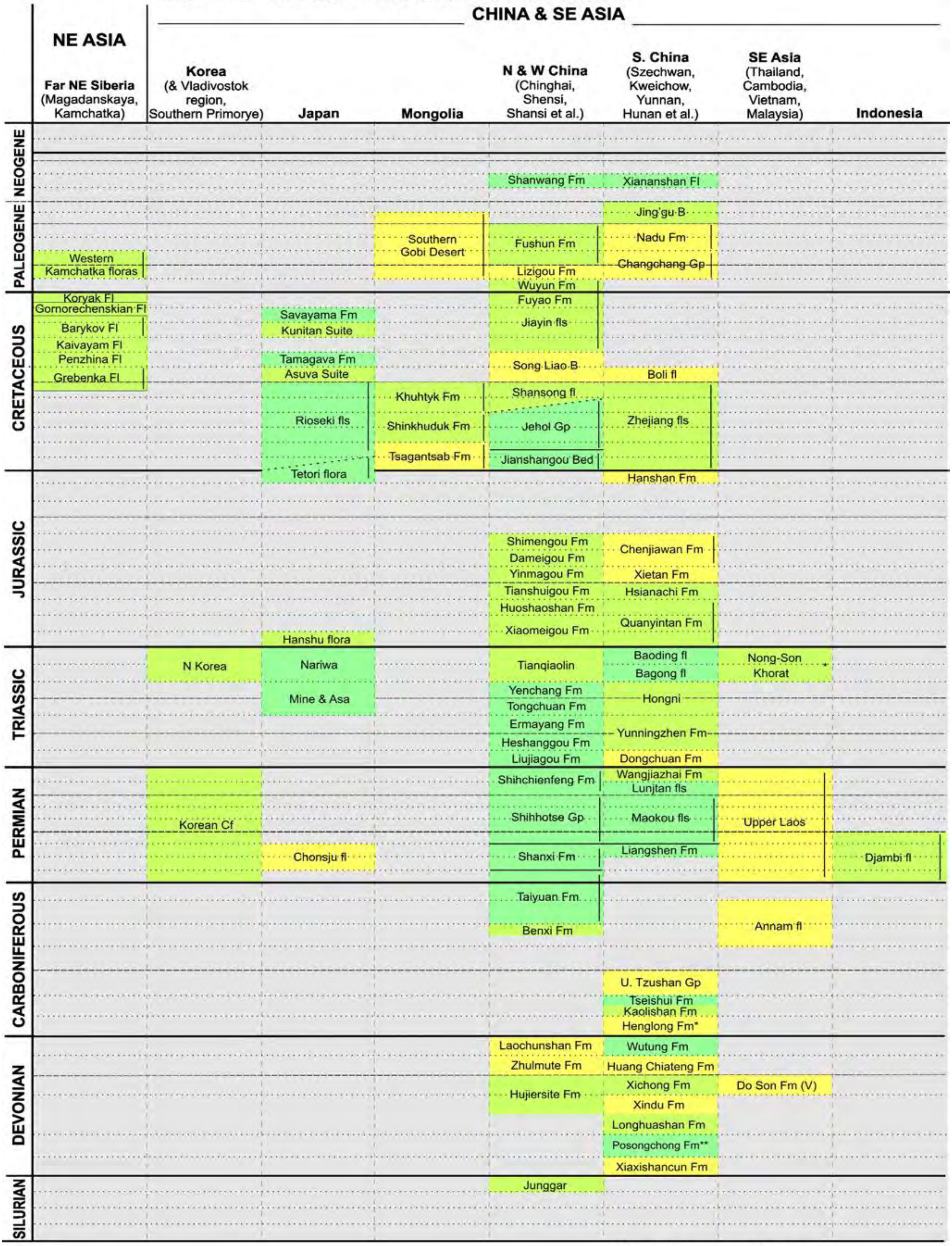
Megafloras

🟩 top (quality/studied)
intermediate
🟨 poor (quality/understudied)

Fm: Formation
Gp: Group

Only those strata including megafloras are plotted; marine, vertebrate-bearing & barren strata are excluded.

Chart 20. MEGAFLORAL CORRELATIONS



*& equivalents
**& Pingyien Fm.

*& Hongay (Vietnam)

Chart 21. ARACAUCARIACEAE: PHYTOHISTORY OF A FAMILY

Of the four extant orders of gymnosperm (Pinales, Cycadales, Ginkgoales and Gnetales),
the history of the Pinales is by far the most comprehensively known; and of the six extant families of Pinales,
that of the Araucariaceae surely ranks as the best known.

Tania Dutra, Anamaria Stranz, Thiérs P. Wilberger
UNISINOS, Rio Grande do Sul, SE Brazil

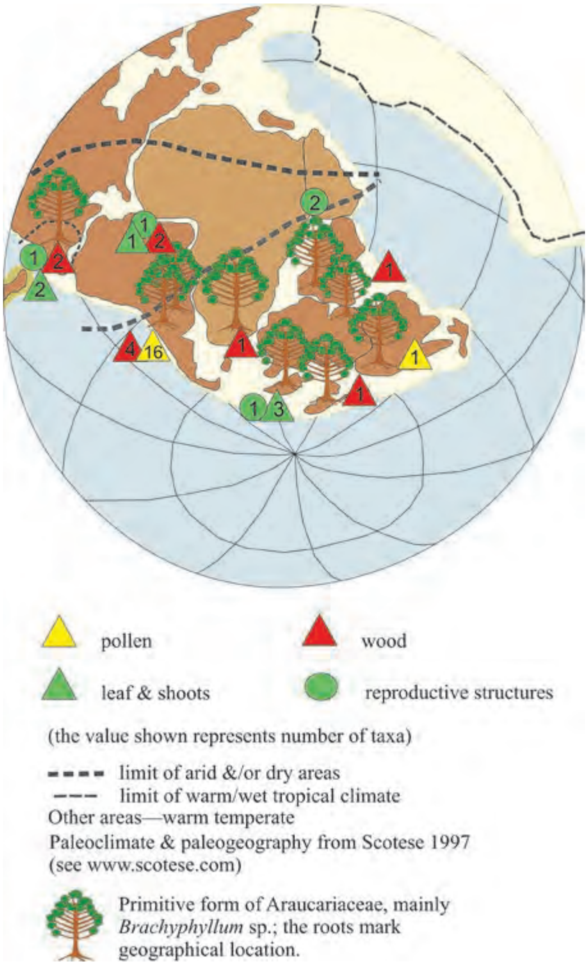
For references and for further data on the fossil record in boxes see Appendix 1 (pp 268–277)

1. LATE TRIASSIC

The Late Triassic marks the earliest appearance of forms that can be clearly related to the Araucariaceae family. Although most available fossils show morphological characteristics also found in the Podocarpaceae, Taxaceae and Cheirolepidiaceae, some reproductive structures confirm assignment to the family.

The fossils are found in places located between medium and high latitudes (40–60° S) of the Gondwana landmasses and in the southwestern part of Laurasia. The climatic parameters indicate that they grew near or within the arid belts but in zones where active tectonism produced altitudinal gradients and seasonal wet conditions.

Most of the deposits represent fluvial systems (mainly braided) where the Araucariaceae occupied the uplands and higher areas.



Araucarioxylon, Caturrita Fm., Parana Basin, Late Triassic (Rhaetic), Rio Grande do Sul, Brazil, trunk *ca* 1.5 by 0.7 m. **Photo**: Tania Dutra.

LEAF, SHOOT, CONES, SCALES
Leaf, shoot: *Brachyphyllum*, *Pagiophyllum*.
Cones, scales: *Araucarites.*

***USA** (Late Trias.)*—Smith Clark Quarry, Pennsylvania; Chinle Fm., Arizona.
***Brazil** (Late Trias.)*—Caturrita Fm., Parana Basin, Norian/Rhaetian.
***India** (Mid. Trias.)*—Parsora Fm., South Rewa, Anisian.
***New Zealand** (Late Trias.)*—Canterbury, Southland, Rhaetian.
***Antarctica** (Late Trias.)*—W Ant. Pen., Carnian/Norian.

WOOD
Wood: *Araucarioxylon*, *Kaokoxylon*.

***USA** (Late Trias.)*—Pennsylvania; Chinle Fm., Arizona, Norian.
***N. Chile** (Late Trias.)*—La Ternera Fm., Norian.
***Brazil** (Late Trias.)*—Caturrita Fm., Parana Basin, Norian/Rhaetian.
***Argentina** (Mid–Late Trias.)*—Água de La Zorra, Mendoza; Barreal, Paramillo, Ischigualasto & Potrerillos Fms., Ladinian–Norian.
***South Africa** (Mid.–Late Trias.)*—Beaufort Gp. & Elliot Fm.
***Antarctica** (Late Trias.)*—Amery Gp., E Ant., Norian.

POLLEN
Pollen: *Araucariacites*, *Inaperturopollinites*, *Callialasporites*.

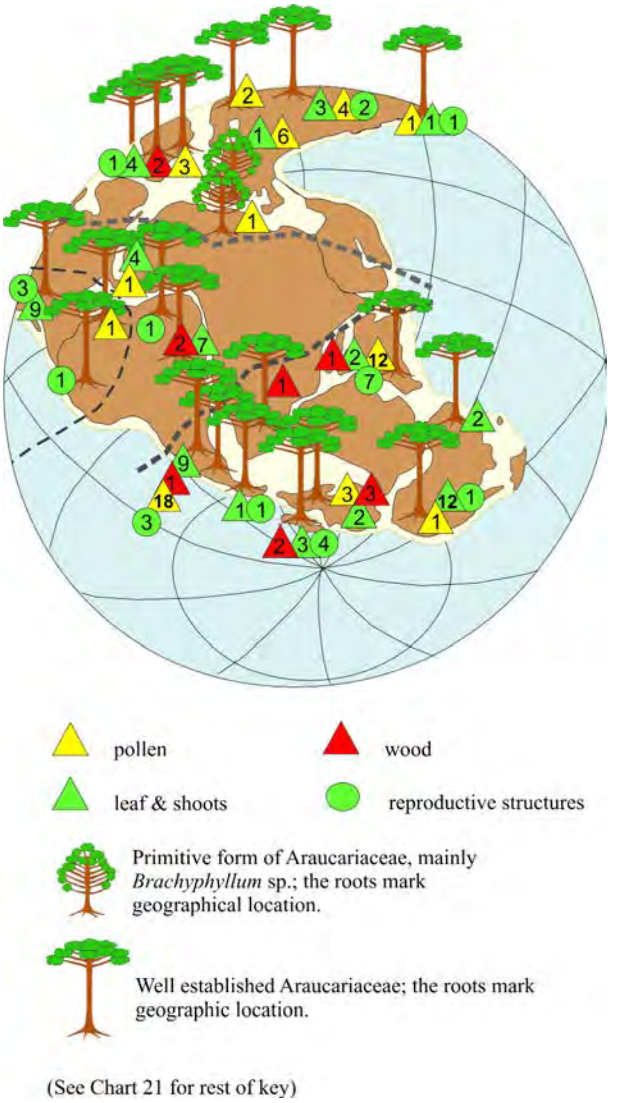
***Argentina** (Late Trias.)*—Cacheuta, Carrizal, Chihuido, Comallo, Ischichuca, Ischigualasto, Las Cabras, Paramillo, Paso Flores & Santa Clara de Arriba Fms., Carnian–Rhaetian.
***Australia** (Early Trias.)*—Clematis Sdst., Queensland, Olenekian.

cf. *Araucariacites australis*
Photo: Silvia Césari

Brachyphyllum sp., Faxinal do Soturno, Brazil, Caturrita Fm., Late Triassic (Ladinian).
Photo: Thiérs Wilberger

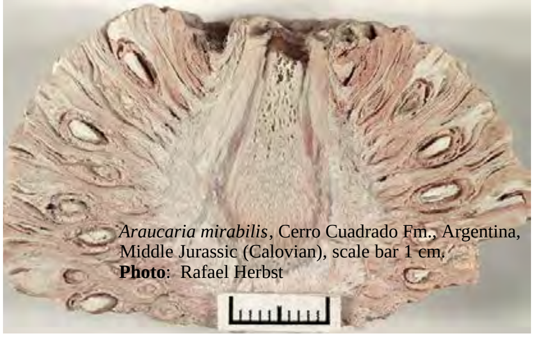
Chart 22.

2. JURASSIC–MIDDLE CRETACEOUS



During this interval the Araucariaceae spread and colonise nearly the entire world; with forms of *Araucaria* sect. *Bunya* and *Eutacta* being confirmed by the morphological characters of reproductive structures. The continuous landmasses and mild climates favoured this spread, resulting in the family occurring from the highest latitudes of Gondwana (where it is more frequent) to mid latitudes in the northern hemisphere. Mapping the fossil record shows clearly that the Araucariaceae are found in both dry and wet areas of the tropical and warm temperate climatic belts and are linked to near-shore environments under the influence of oceanic conditions. In South America, they are absent from the region that corresponds to southern Brazil and northern Argentina (dominated by desertic aeolian sediments), but are common in Patagonia. For the first time they appear in areas of northeast Brazil, Colombia and Guiana. Their greatest diversity and abundance is in India, Australia, Antarctic Peninsula and Patagonia, where they are represented by both macrofossils (with reproductive structures) and microfossils.

The fossils are associated with fluvial, lacustrine (macrofossils) and deltaic (microfossils) deposits, where the volcanic influence is clearer than in the Late Triassic.



Araucaria mirabilis, Cerro Cuadrado Fm., Argentina, Middle Jurassic (Calovian), scale bar 1 cm.
Photo: Rafael Herbst

LEAF, SHOOT, CONES, SCALES
Leaf, shoot: *Brachyphyllum, Pagiophyllum, Desmiophyllum*.
Cones, scales: *Araucarites, Ontheodendron, Dammarites, Araucariostrobus, Palissya, Pararaucaria, Nothopehuen*.
Whole-plant: *Araucaria, Agathis.*

USA *(Early Cret.)*—Potomac beds, Albian.
Portugal *(Early Cret.)*—Almargem Basin.
Spain *(Early Cret.)*—Montsec, Lérida.
England *(Jur.)*—Yorkshire.
NE Russia *(mid. Cret.)*—Krivorechanskaya Fm.
East Asia, Russia & China *(Early Cret.)*—Suchan Basin.

Colombia *(Early Cret.)*—?
Brazil *(Early Cret.)*—Santana Fm., Araripe Basin, Ceará; Areado Fm., Minas Gerais.
Argentina *(Early Jur.)*—Pedra Pintada Fm., NW Patagonia.
(Mid. Jur.)—Cañadon Asfalto Fm., Chubut Basin; Lotena Fm., Neuquen Basin; La Matilde Fm., Santa Cruz.
(Jur.)—Santa Cruz Basin; Cerro Quadrado.
(Early Cret.)—Baqueró Gp., Santa Cruz; Springhill Fm., Santa Cruz.

Israel *(Late Jur.)*—Kidod Fm., Dead Sea

India *(Early Jur.)*—Hartala Fm., Madhya Pradesh.
(Late Jur.)—Rajmahal Hills, Bihar, Jabalpur Stage; Bansa, Rajmahal, Umia, Kota & Jabalpur Stage.

Australia *(Jur.)*—Talbragar Fish Beds, NSW.
(Early Cret.)—Gippsland Basin, SE Aus; Eromanga Basin, Queensland.
(Early Cret.)—Otway Basin, Koonwarra, Victoria; Regatta Point, Tasmania.
(mid. Cret.)—Winton Fm., Queensland.
(mid. Cret.)—Perth & Canning Basins, SW Aus., Turonian.
New Zealand *(Cret.)*—Shag Point Fm.; Waikawa & Mokoia, N Isl.
(Early Cret.)—Wairarapa, N Isl., Albanian.
(mid. Jur.)—Mokoia, Southland, S Isl.

Antarctica *(Early Cret.)*—Fossil Bluff Gp., Alexander Isl., Ant. Pen.; Cerro Negro Fm., Byers Gp., Ant. Pen.

WOOD
Wood: *Agathoxylon, Araucarioxylon, Dadoxylon.*

France *(Late Jur.)*—'Sables de Glos' Fm., Paris, Jura & Subalpine Basin.
(mid. Cret.)—Clarente-Maritime, SW France, Cenomanian.
Chile *(Early Jur.)*—Quebrada del Pobre Fm.
Brazil *(Early Cret.)*—Japoatá Fm., Malhada dos Bois, Sergipe.
(Late Jur.)—Sergi Fm., Bahia & Sergipe.
Argentina *(Mid Jur.)*—La Matilde Fm., Santa Cruz Basin.
South Africa *(Early Jur.)*—Clarens Fm., Karoo Basin.
India *(Early Cret.)*—Sriperumbudur Fm., Tamil Nadu, S Ind.
(Mid Jur.)—Kota Fm., Bansa.
New Zealand *(Cret.)*—Shag Point Fm., Waikawa, N Isl.
(Mid. Jur.)—Mataura, Southland, Callovian.
Antarctica *(Early Cret.)*—Cerro Negro Fm., Byers Peninsula, Ant. Pen.; Byers Gp., Byers Peninsula & Williams Point, Ant. Pen.

POLLEN
Pollen: *Araucariacites, Inaperturopollenites, Callialasporites.*

West Europe *(Late Jur.)*—Kimmeridgian.
France *(Mid Cret.)*—Charentes, Albian-Cenomanian.
East Asia, Russia & China *(Early Cret.)*—Suchan & Suifun Basins.

Guiana *(Early Cret.)*—?
Argentina *(Mid Jur.)*—Lotena/Lajas Fms., Nequen Basin.
(Mid–Late Jur.)—Cura Niyen, Neuquen Basin; Grupo Cuyo, Neuquen Basin;
(Early Cret.)—Albornoz Fm., San Jorge Basin; Agrio Fm., Neuquen Basin; Punta Del Barco Fm., Baqueró Gp.

Israel *(Late Jur.)*—Kidod Fm., Dead Sea.
Israel &Jordan *(Early Cret.)*—amber with pollen.
Egypt *(Late Jur.)*—Abu Ballas Fm.

India *(Late Jur.)*—Madhya Pradesh (Jabalpur Stage).
(Early Cret.)—Raniganj Basin, W Bengal; Bhuj Series, Ghuneri, Kutch District.
Antarctica *(Early Cret.)*—Gustav Gp., James Ross Isl., Ant. Pen.

Chart 23.

3. LATE CRETACEOUS–PALEOGENE

(See Charts 21 & 22 for rest of key)

LEAF, SHOOT, CONES, SCALES
Araucaria, Agathis, Pseudoaraucaria, Dammara, Araucarioides.

Japan *(Late Cret.)*—Upper Yezo Gp., Hokkaido.
Germany *(Late Eoc.)*—Stavé Sedlo Fm.

Chile *(Late Cret.)*—Dorotea Fm., Cerro Guido.
Argentina *(Late Paleoc.)*—La Huitrera Fm., Austral Basin; Curanilahue, Patagonia.
(Late Eoc.)—Rio las Minas Fm., Austral Basin.
(Paleoc.–Eoc.)—Nirihuau, Rio Negro.

Australia *(Late Cret.)*—Pakawau Basin, S Aus.
(Late Cret.)—Maryborough Fm., NE Aus.
(Paleoc.)—SE Aus & S Aus.
(Early Oligoc.)—Cethana & Little Rapid River, Tasmania.
(?Oligoc.)—Bacchus Marsh, Victoria.
(Late Oligoc.–Early Mioc.)—Berwick Quarry, Victoria.
(Oligoc.–Mioc.)—Yallourn & Morwell, Victoria; Monpeelyata, Tasmania.
(Early Eoc.)—Regatta Point Flora, W Tasmania.
(Mid. Eoc.)—West Dale, W Aus; Maslin Bay, S Aus; Lefroy/Cowan paleo-drainages, W Aus.
(Mid.–Late Eoc.)—Hasties, NE Tasmania.
(Eoc.)—Victoria; SE & S Tasmania.
New Zealand *(Late Cret.)*—Kaipara District, eastern Otago, Shag Point & Pakawaw, Nelson Island.
(Paleoc.)—Taratu Fm., S Isl.
(Eoc.)—S Isl.

Circum-Antarctica *(Paleoc.)*—Kerguelen Isl.
Antarctica *(Late Cret.)*—Lopez de Bertodano Fm., Cape Lamb, Vega Isl., Ant. Pen.
(Paleoc.–Eoc.)—Point Hennequin Gr., King George Isl., Ant. Pen.
(Eoc.)—Minna Bluff, McMurdo Sound.
(Eoc.)—La Meseta Fm., Seymour Isl., Ant. Pen.

WOOD
Araucarioxylon, Dadoxylon, Dammara.

Chile *(Late Cret.)*—Pichasca, N Chile.
Antarctica *(Eoc.)*—Fildes Fm., Barton Pen., King George Isl., Ant. Pen.
New Zealand *(Late Cret.)*—Amuri Bluff, Marlborough; Shag Point.

Thanks to the diversification of the angiosperms and to the changing geography and climate that marks the end of the Mesozoic, the Araucariaceae retreat in areal distribution and adapt to life at higher altitudes. Some forms become isolated in the newly formed continents (the exception being the unbroken stretch of land from South America to Australia). The warm climatic conditions that mark the Upper Paleocene-Eocene along with the domination of flowering plants in tropical lands, further causes their concentration in high latitudes of the southern hemisphere. Except for records in Germany and Japan, they virtually disappear from the northern hemisphere.

These processes had a deep influence on the evolution of the group and to the differention into their modern genera and sections. The preserved material can now be more securely assigned to the genera *Agathis*, *Wollemia* (exclusive throughout the interval to the eastern sector of Gondwana) and to the four modern sections of *Araucaria*. *Araucaria* (sect. *Eutacta* and *Columbea*) was more cosmopolitan, found during the Eocene from Australia to South America and through the Antarctic continent. A distinctive feature of the modern distribution of this genus, is that sect. *Eutacta* is exclusive to Australasia and sect. *Columbea* to South America (the latter being the only forms associated with more microthermic conditions). According to Dettmann (1989), the forests of this sector of Gondwana in the Late Cretaceous (with Podocarpaceae, Proteaceae, Myrtaceae, Winteraceae and other taxa) can be identified as the original modern subtropical rainforest of the southern hemisphere.

The minor proportion of pollen grains in fossil assemblages and the associated lithologies (indicating fluvial and deltaic/estuarine deposits) attest to their affinity for higher ground near ocean margins subject to tectonic and volcanic activity.


Araucaria angustifolia, Santa Catarina, Brazil.
Photo: Tania Dutra

POLLEN
Araucariacites, Dilwynites.

Germany *(Eoc.)*—Saxony.
Czech Republic *(Eoc.)*—Staré Sedlo Fm.

Columbia *(Paleoc.)*—Cordillera Central.
Chile *(Eoc.–Recent)*—no further info.
Argentina *(Early Paleoc.)*—Pedro Luro Fm., Los Colorados Basin, C & W Arg.
(Paleoc.)—Chubut Basin, Danian.
(Eoc.)—Rio Turbio Fm., Santa Cruz; Neuquén & Chubut Basins, C& W Arg.
(Oligoc.)—San Julian Fm., Austral Basin.
(Latest Oligoc.–early Mioc.)—Rio Foyel Fm., Nirihuau Basin, NW Patagon.

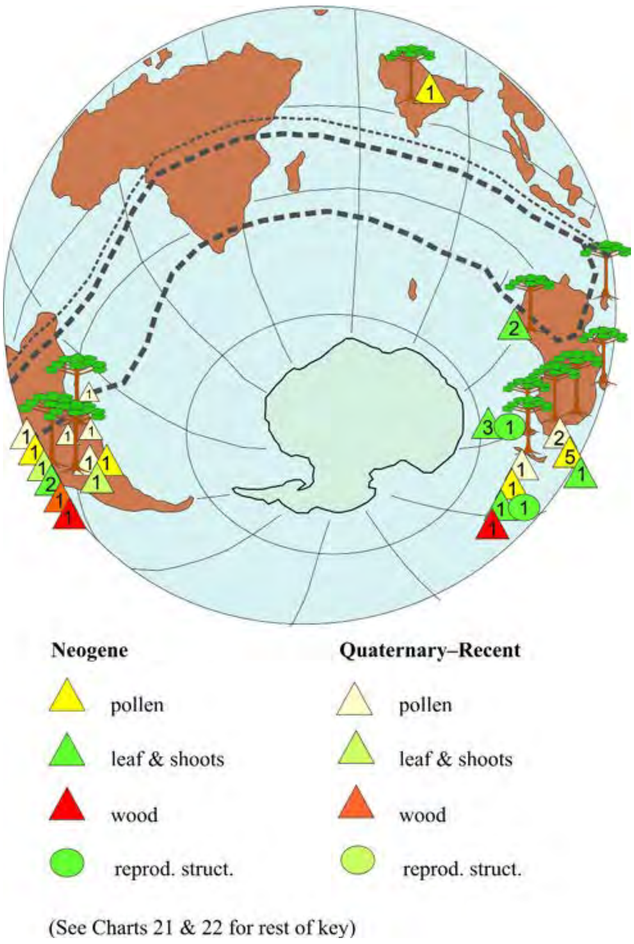
India *(Early Eoc.)*—Kopili Fm.
(Olig.–Mioc.)—Bengal Fm., Indian Ocean.

Australia *(Eoc.)*—Napperby, C Aus; Yaamba Basin, NE Aus; Ulgnamba Lignite, Hale River Basin; E & C Aus.
(Paleoc.)—E & C Aus.
(Mid. Oligoc.)—SE Aus.
(Late Oligoc.)—Tasmania.
New Zealand *(Eoc.)*—Middle Waipara, S Isl.
(Late Cret.)—Maastrichtian.

Antarctica *(Paleoc.)*—King George Isl., Seymour Isl., Ant. Pen.

Chart 24.

4. NEOGENE—RECENT



The gradual covering of the Antarctic Continent by ice and the dry intervals corresponding to the icehouse periods of the Oligocene-Miocene and Miocene-Pliocene boundaries and the Quaternary glaciations have a profound effect on the Araucariaceae, and give rise to the distribution pattern very like that of today. The exceptions are their continued presence in India (pollen only) and Western Australia during the Neogene. Subsequently they became exclusive to the southern hemisphere and tropical areas of Australasia.

Their migration to low latitudes in the Eastern sector (disappearing from Tasmania) and extinction in latitudes below 40°S in South America are the most distinctive character of the group during the last 20 million years.

Since the start of the Holocene, with climatic amelioration, the family has gradually re-conquered its ancestral niches confirming a preference for high areas, with poor, acid soils (volcanic or calcareous) and wet oceanic climates—as established since the radiation of the flowering plants in the Late Cretaceous. The palynological spectrum of the Quaternary shows that the grasslands, a heritage of the dry and cold Miocene and Pliocene, became their preferred associated biome—with the characteristic scenery following the recolonisation of disturbed landscapes.

LEAF, SHOOT, CONES, SCALES
Leaf: *Agathis*, *Araucaria*.
Whole-plant: *Araucaria*.

Chile *(Olig.–Mioc.)*—Lonquimay sedimentary sequence.
(Olig.–Recent)—Central Chile.
(Mioc.)—Navidad Fm., Matanzas.
Argentina *(Olig.–Mioc.)*—Pico Quemado Fm., Rio Negro Basin.
Australia *(Early Mioc.)*—Latrobe Valley, SE Aus.
(Eoc.–Oligoc.)—West Dale, Perth, SWAus.
(Late Mioc.)—S. Aus.
(Olig.–Mioc.)—Little Rapid River, NW Tasmania.
(Olig.–Plioc.)—NE Tasmania.
New Zealand *(Early Mioc.)*—Manuherikia Gp.

WOOD
Wood: *Araucarioxylon*, *Agathoxylon*.

Chile *(Oligoc.–Pleistoc., Recent)*—Central Chile.
New Zealand *(Late Tert.)*—Roxburgh, Central Otago.

POLLEN
Pollen: *Araucariacites*, *Dilwynites*.

Brazil *(Pleistoc., Recent)*—C & S Brazil.
Chile *(Oligoc.–Pleistoc., Recent)*—C Chile.
Argentina *(Late Mioc.)*—Parana Fm., Santa Fé.
(Oligoc.)—San Julian Fm., Austral Basin.
(Latest Oligoc.–Early Mioc.)—Rio Foyel Fm., Nirihuan Basin, NWPatag.
India *(Mioc.)*—Dafla Fm., Bhalukpong-Bomdila, W Kameng District, Arunachal Pradesh.
(Oligoc.–Mioc.)—Bengal Fan, Indian Ocean.
Australia *(Mid Oligoc.)*—SE Aus.
(Mioc.)—New South Wales.
(Pleistoc.)—Western Plains, Victoria.
(Pleistoc.–Recent)—E Aus.
(Plioc.)—Bass Strait.
(Late Oligoc.)—Tasmania.
(Mioc.–Pleistoc.)—W. Tasmania.

Araucaria angustifolia, Rio Grande do Sul, Brazil.
Photo: Tania Dutra

Chart 25.

EPIPHYTES ON *ARAUCARIA ANGUSTIFOLIA*
South Eastern Brazil

Thiérs P. Wilberger, Nelsa Cardoso, Claudia P. Paz & Anamaria Stranz
UNISINOS, Rio Grande do Sul, Brazil

Biodiversity: 5 major plant groups, 45 families, 85 genera, >103 species

LICHENS		
LECANORALES		
Usneacea	*Usnea*	*barbata* Web.
		quadriculata
Ramalinaceae	*Ramalina*	
Parmeliaceae	*Parmelia*	
	Elaphoglossum	sp.
LIVERWORTS		Classification: Crandall-Stotler & Stotler (2000)
METZGERIALES		
Metzgeriaceae Klinggr.	*Metzgeria* Raddi	
LEPICOLEALES		
Trichocoleaceae Nakai	*Tricholea* Dum.	
JUNGERMANNIALES		
Geocalycaceae Klinggr.	*Lophocolea* (Dum.) Dum.	
Lepidoziaceae Limpr.	*Bazzania* S.F. Gray	
Plagiochilaceae (Jorg.) K. Müll.	*Plagiochila* (Dum.) Dum.	
PORELLALES		
Bryopteridaceae R. Stotl.	*Bryopteris* (Nees) Lindenb.	
Lejeuneaceae Cas.-Gil	*Anoplolejeunea* (Spruce) Schiffn.	
	Frullanoides Raddi	
	Lejeunea Libert	
	Leucolejeunea Evans	
	Omphalanthus Lindenb. & Nees	
	Taxilejeunea (Spruce) Schiffn.	
Porellaceae Cavers	*Porella* L.	
RADULALES		
Radulaceae (Dum.) K. Müll.	*Radula* Dum.	
MOSSES		Classification: Buck & Goffinet (2000)
POLYTRICHALES		
Polytrichaceae Schwaegr. in Willd.	*Atrichum* P.-Beauv.	
GRIMMIALES		
Ptychomitriaceae Schimp.	*Ptychomitrium* Furnr.	
DICRANALES		
Dicranaceae Schimp.	*Bryohumbertia* P. de la Varde & Thér.	
	Campylopus Brid.	
	Holomitrium Brid.	
	Sclerodontium Schwaegr.	
Leucobryaceae Schimp.	*Leucobryum* Hampe.	
POTTIALES		
Pottiaceae Schimp.	*Leptodontium* (C.Müll.) Hampe ex Lindb.	
	Tortella (Lindb.) Limpr.	
ORTHOTRICHALES		
Orthotrichaceae Arnott.	*Macrocoma* (C.Müll.) Grout	
	Macromitrium Brid.	
	Scholotheimia Brid.	
	Zygodon Hook. & Tayl.	
HEDWIGIALES		
Hedwigiaceae Schimp.	*Braunia* B.S.G.	
BRYALES		
Bryaceae Schwaegr. in Willd.	*Bryum* Hedw.	
RHYZOGONIALES		
Rhizogoniaceae Broth.	*Pyrrhobryum.* Mitt.	
Racopilaceae Kindb.	*Racopilum* P. Beauv	
HOOKERIALES		
Adelotheciaceae Buck	*Adelothecium* Mitt.	
Pilotrichaceae Kindb.	*Callicostela* (C.Müll.) Mitt. (Buck)	
	Lepidopilum (Brid.) Brid. (Buck)	
Hypopterygiaceae Mitt.	*Hypopterygium* Brid.	
	Lopidium Hook. F. & Wils.	

Metzgeria dichotoma

Bryopteris sp.

Frullania sp.

all watercolours:
Claudia P. Paz

Araucaria angustifolia

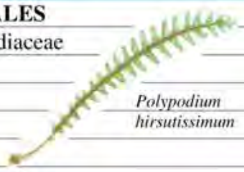
sketch:
Anamaria Stranz

Chart 26.

HYPNALES		
Brachytheciaceae G. Roth	*Rhynchostegium* B.S.G.	
Rigodiaceae Crum (Buck & Vitt.; Crum)	*Rigodium* Kunze ex Schaegr.	
Thuidiaceae Schimp.	*Cyrto-hypnum* Hampe & Lor. (Buck & Crum)	
	Thuidium B.S.G.	
Fabroniaceae Schimp.	*Fabronia* Raddi	
Meteoriaceae Kindb.	*Aerobryopsis* Fleisch.	
	Meteoridium (C.Müll.) (Manuel, Buck)	
	Papillaria (C.Müll.) C.Müll.	
	Pilotrichella (C.Müll.) Besch.	
	Squamidium (C.Müll.) Broth.	
	Zelometeorium Manuel (Manuel)	
Entodontaceae Kindb.	*Entodon* C.Müll.	
Hypnaceae Schimp.	*Chryso-hypnum* Hampe (Buck)	
	Hypnum Hedw.	
	Isopterygium Mitt.	
	Mittenothamnium Henn.	
Sematophyllaceae Broth.	*Sematophyllum* Mitt.	
Cryphaeaceae Schimp.	*Schoenobryum* Dozy & Molk.	
Prionodontaceae Broth.	*Prionodon* C.Müll.	
Leucodontaceae Schimp.	*Leucodon* Schwaegr.	
Pterobryaceae Kindb.	*Pterobryom* Hornsch.	
Phyllogoniaceae Kindb.	*Phyllogonium* Brid.	
Neckeraceae Schimp.	*Neckera* Hedw.	
	Neckeropsis Reichardt	
	Porotrichum (Brid.) Hampe	
Leptodontaceae Schimp. (Buck)	*Forsstroemia* Lindb.	
FERNS		
PTERIDALES		
Polypodiaceae	*Polypodium*	*hirsutissimum* Raddi.
		pectinatiforme Lindm.
		lanceolatum L.
		filicula Hlf.
	Microgramma	
Vittariaceae	*Vittaria*	*lineata* (L.) Sm.
FLOWERING PLANTS		
MICROSPERMAE		
Orchidaceae Kunth	*Bulbophyllum* Thouars	*glutinosum* (Barb. Rodr.) Cogn.
		regnellii Rchb. f.
	Capanemia Barb. Rodr.	*superflua* (Rchb. f.) Garay
	Dryadella Luer	*zebrina* (Porsch) Luer
	Epidendrum L.	*caldense* Barb. Rodr.
	Eurystyles Wawra	*cotyledon* Wawra
	Isabelia Barb. Rodr.	*pulchella* (Kraenzl.) Senghas & Teusch.
	Maxillaria Ruiz & Pav.	*cogniauxiana* W. Hoehne
		picta Hook.
	Octomeria R. Br.	*ochroleuca* Barb. Rodr.
	Oncidium Sw.	*bifolium* Sims
		concolor Hook.
		gravesianum Rolfe
		hookeri Rolfe
		loefgrenii Cogn.
		longicornu Mutel
		longipes Lind.
		macronix Rchb. f.
	Phymatidium Lindl.	*paranaense* A. Samp.
	Pleurothallis R. Br.	*grobyi* Bateman ex Lindl.
		linearifolia Cogn.
		saundersiana Rchb. f.
	Sophronitis Lindl.	*coccinea* (Lindl.) Rchb. f.
Bromeliaceae fam.	*Aechmea* Ruiz & Pav.	*recurvata*
	Tillandsia L.	*stricta* Sol. ex Sims
		usneoides (L.) L.
		geminiflora Brongn.
	Vriesea Lindl.	*plathynema* Gaudich.
CACTALES		
Cactaceae	*Ripshalis*	*pulcherrima* Loefgren
		penduliflora N.E.Brown


Araucaria angustifolia

photo: Tania Dutra


Polypodium hirsutissimum

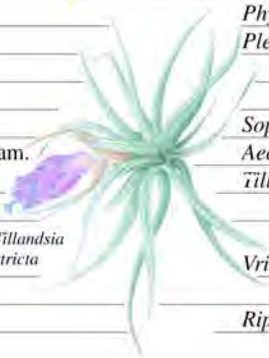

Oncidium longicornu


Maxillaria picta


Pleurothallis grobyi


Sophronites coccinea

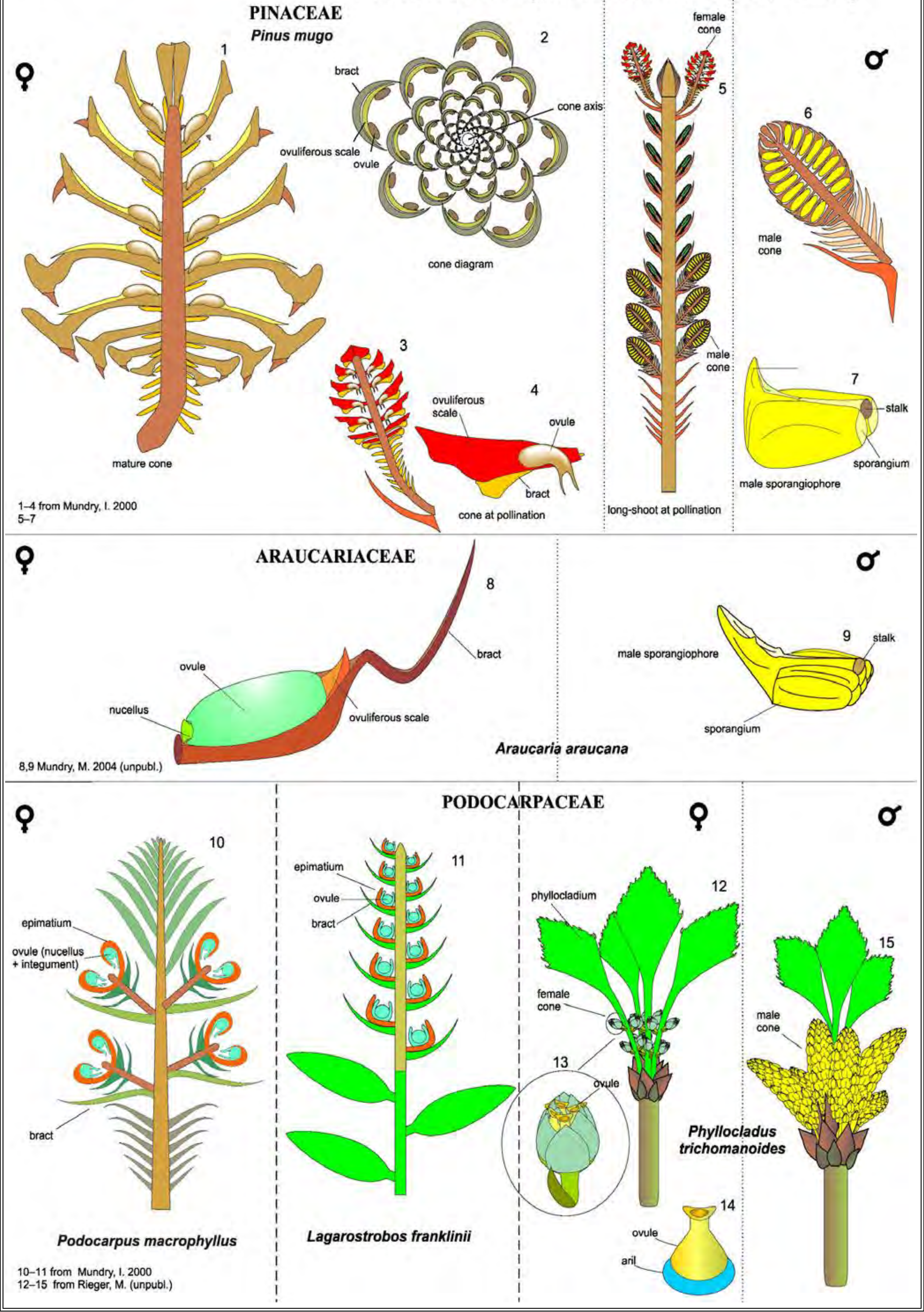

Oncidium longipes


Tillandsia stricta


Vriesea plathynema

Chart 27. EXTANT GYMNOSPERM FAMILIES: COMPARATIVE MORPHOLOGY

Marcus & Iris Mundry, Thomas Stützel, Bochum, Germany



1–4 from Mundry, I. 2000
5–7

8,9 Mundry, M. 2004 (unpubl.)

10–11 from Mundry, I. 2000
12–15 from Rieger, M. (unpubl.)

Chart 28.

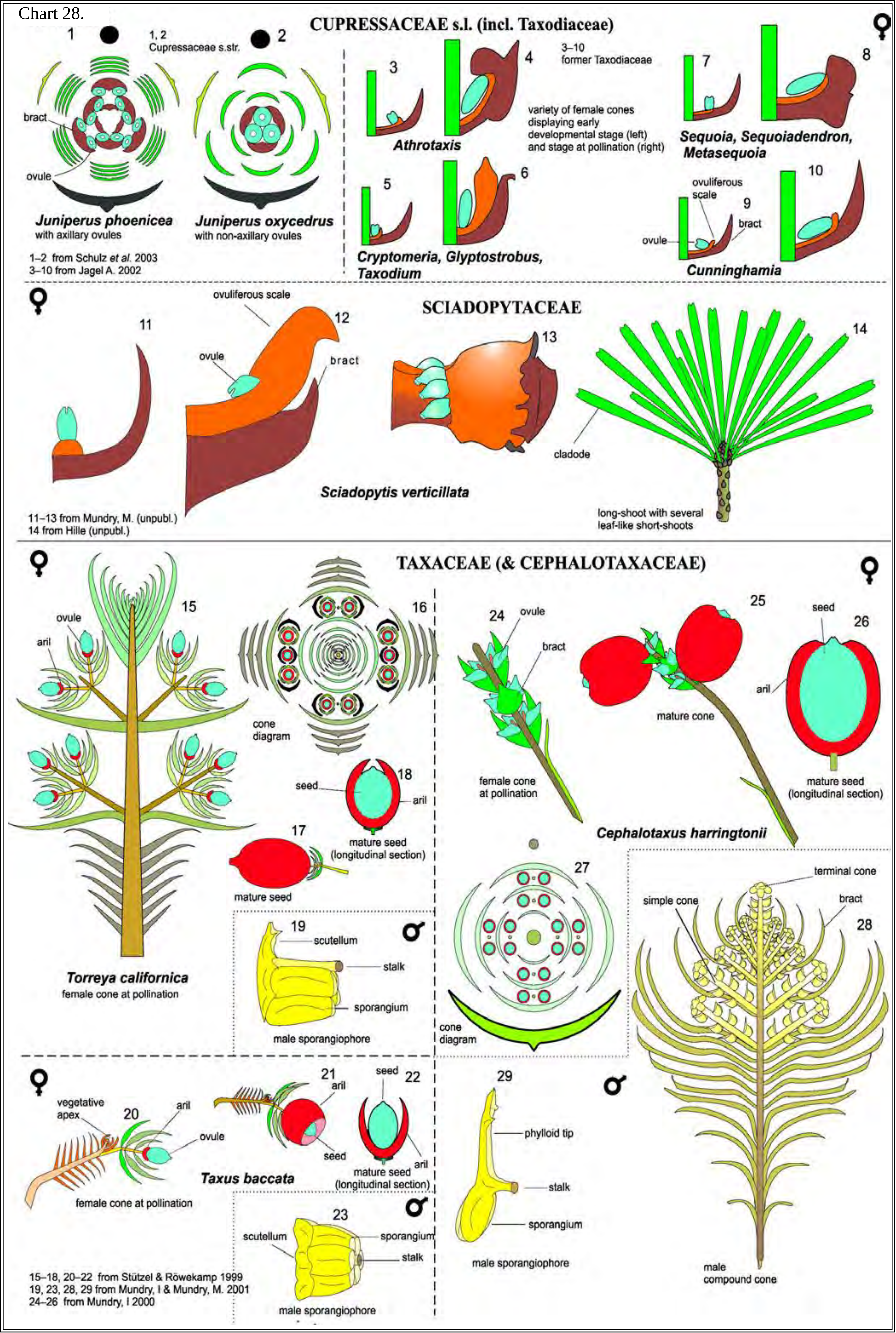
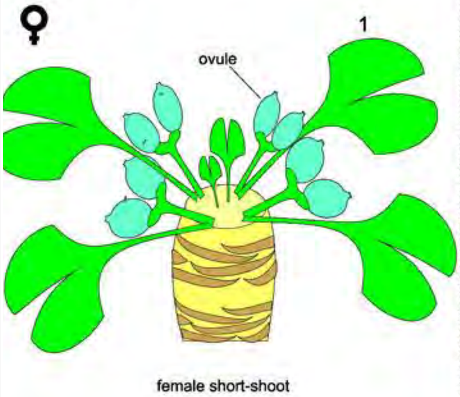

CUPRESSACEAE s.l. (incl. Taxodiaceae)
1
2
1, 2
Cupressaceae s.str.
bract
ovule
Juniperus phoenicea
with axillary ovules
Juniperus oxycedrus
with non-axillary ovules
1–2 from Schulz et al. 2003
3–10 from Jagel A. 2002
3
4
3–10
former Taxodiaceae
Athrotaxis
variety of female cones
displaying early
developmental stage (left)
and stage at pollination (right)
7
8
Sequoia, Sequoiadendron,
Metasequoia
5
6
Cryptomeria, Glyptostrobus,
Taxodium
ovuliferous
scale
9
bract
ovule
10
Cunninghamia
SCIADOPYTACEAE
11
ovuliferous scale
12
ovule
bract
13
14
cladode
Sciadopytis verticillata
11–13 from Mundry, M. (unpubl.)
14 from Hille (unpubl.)
long-shoot with several
leaf-like short-shoots
TAXACEAE (& CEPHALOTAXACEAE)
ovule
aril
15
16
cone
diagram
seed
18
aril
17
mature seed
(longitudinal section)
mature seed
Torreya californica
female cone at pollination
19
scutellum
stalk
sporangium
male sporangiophore
24
ovule
bract
female cone
at pollination
25
mature cone
seed
26
aril
mature seed
(longitudinal section)
Cephalotaxus harringtonii
27
cone
diagram
terminal cone
simple cone
bract
28
male
compound cone
vegetative
apex
20
aril
ovule
female cone at pollination
21
aril
seed
seed
22
Taxus baccata
aril
mature seed
(longitudinal section)
23
scutellum
sporangium
stalk
male sporangiophore
29
phylloid tip
stalk
sporangium
male sporangiophore
15–18, 20–22 from Stützel & Röwekamp 1999
19, 23, 28, 29 from Mundry, I & Mundry, M. 2001
24–26 from Mundry, I 2000

Chart 29.

GINKGOACEAE

♀



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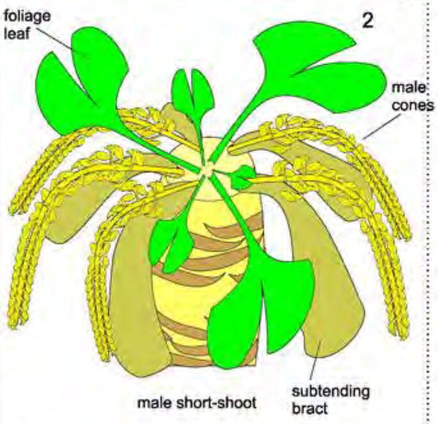
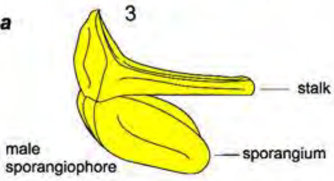
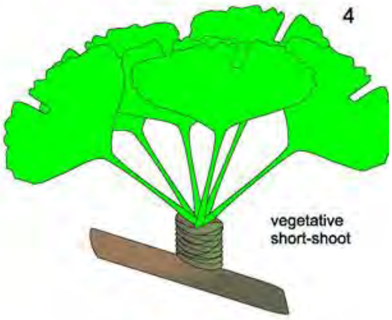
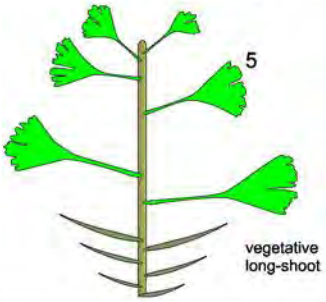






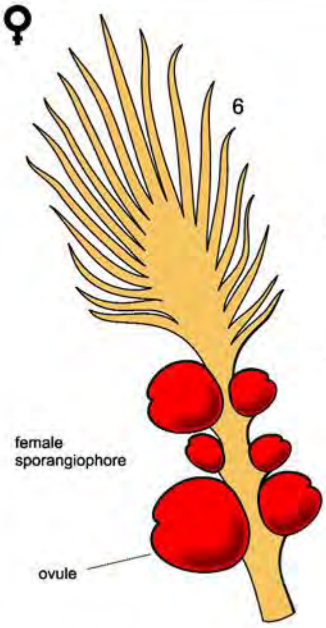


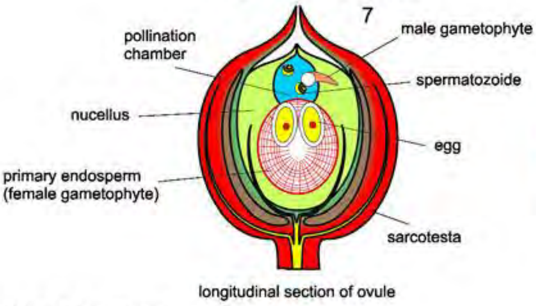
Ginkgo biloba

1 from Mundry, I. 2000
2 from Mundry, M. (unpubl.)
3 from Mundry, M. & Stützel 2004
4, 5 from Hille (unpubl.)

CYCADACEAE

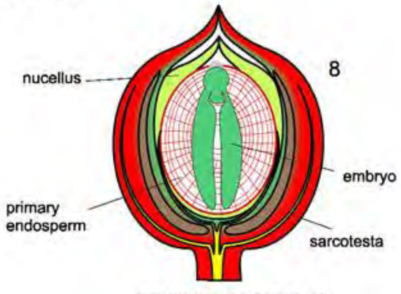
♀





longitudinal section of ovule

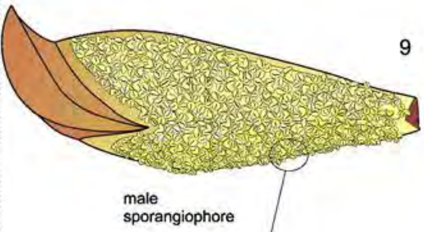
Cycas revoluta

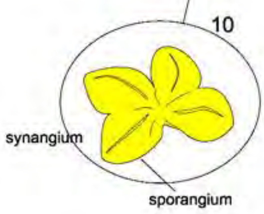


longitudinal section of seed

♂

Cycas

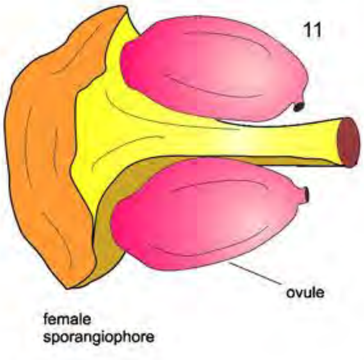




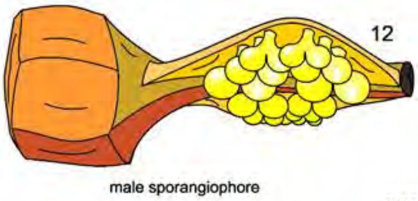
6–8 from Stützel (unpubl.)
9,10 from Mundry, M. (unpubl.)

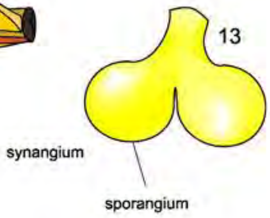
ZAMIACEAE

♀



♂

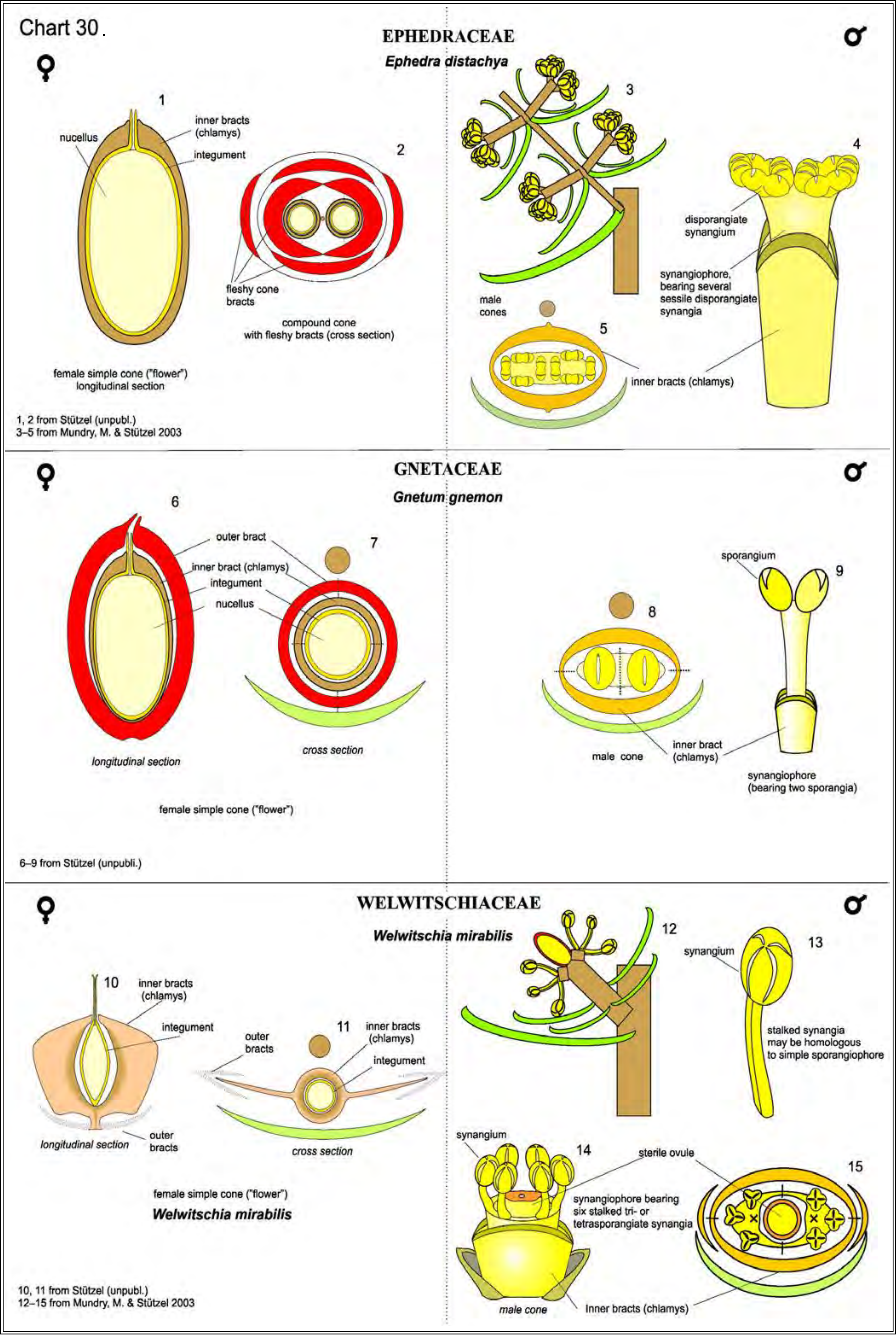




Zamia amblyphyllidia

11 from Mundry, M. (unpubl.)
12, 13 from Mundry, M. & Stützel 2003.

Chart 30.

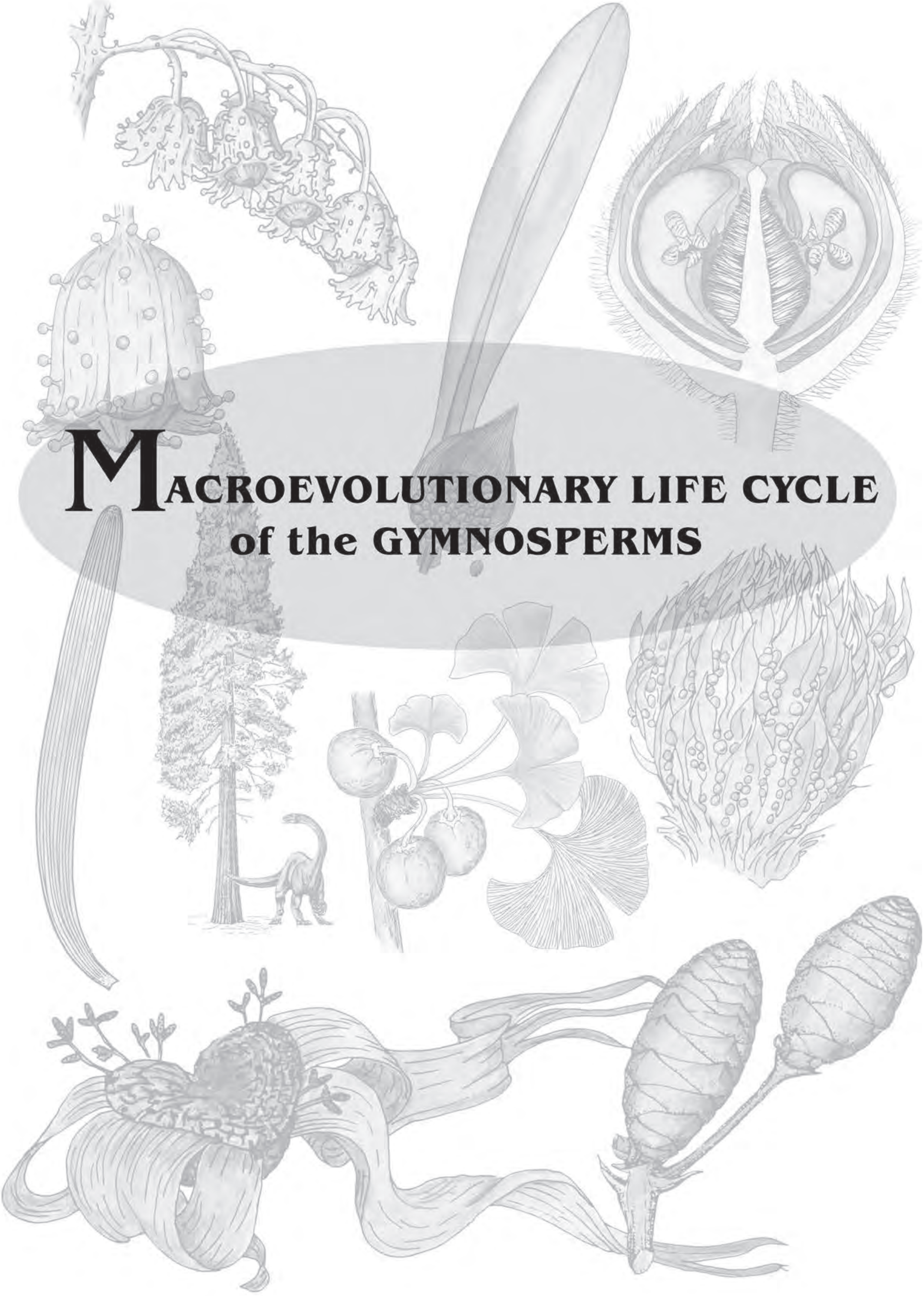


1, 2 from Stützel (unpubl.)
3–5 from Mundry, M. & Stützel 2003

6–9 from Stützel (unpubli.)

10, 11 from Stützel (unpubl.)
12–15 from Mundry, M. & Stützel 2003

MACROEVOLUTIONARY LIFE CYCLE of the GYMNOSPERMS



FROM EMERGENCE TO OLD AGE

To employ a phrase such as the 'macroevolutionary life cycle' (definition of terms on p. 70) to encapsulate the history of the gymnosperms from their emergence in the Late Devonian, through their long span of dominance, to their decline and apparent relict status today, might presuppose firstly that the division is in genuine old age and cannot rebound in renewed genetic (biodiversity) vigour. It could, of course, be that in a new phase of explosive radiation—following the 'Sixth Extinction' (Chart 1, p. 36) that has decimated global diversity to say 10%—we could conceivably see the emergence of new classes of gymnosperm from the remnant gene pool. A new and vigorous phase of gymnosperm evolution could ensue. This seems unlikely given the very evident relict status of a high proportion of the extant gymnosperms (pp 130, 155, 172, 210). More likely would be that the next radiation of higher vascular plants would arise from the angiosperms.

Secondly there is the question of adopting anthropocentric terminology. Should we speak of a life cycle of the Division Pinophyta (gymnosperms) in the way that we speak of the life cycle of an individual human or of a human civilisation or empire? Does a major plant clade (or even a species) go through a comparable life cycle? Does it go through conception (mutation, recombination, origin), gestation (silent evolution of stem group), birth (emergence of crown group), infancy (diversification), youth (primary radiation), adolescence (secondary radiation), maturity (stasis), old age (relictual status, senescence) and death (extinction) in the way a human does? Not exactly, but there are obvious parallels as suggested by the words included in parentheses. Even if these parallels are not strictly biologically equivalent, we find the life-cycle metaphor vivid and clear and therefore useful.

Alternate terms to replace 'life cycle' might be span, history, period, era, aeon, epoch, but these are also all loaded with specific meanings, particularly geological, and therefore hardly more appropriate in our context.

Format for chronological coverage

Through this chapter, we outline the life cycle of gymnosperms period by period. The history is followed under a standard set of headings.

Plate tectonics and global physiology: See Charts 1, 2 (pp 36, 37) for a sequence of 13 thumbnail reconstructions showing the pattern of drifting continents through the Phanerozoic and for a set of temperature, precipitation and atmospheric oxygen graphs. The changing physical environment provides the context in which the gymnosperms evolved. The terrestrial plants are an integral part of that changing environment—part effect and part cause.

Floral kingdoms: See Chart 1 (p. 36). On the Phanerozoic reconstructions noted above are portrayed the evolving plant kingdoms from a single global flora in the Devonian and Early Carboniferous to the present spread of six kingdoms.

Megafloral occurrences, key sequences: See Charts 11–20 (pp 46–55) for a set of 10 correlation charts showing the principal mega-plant-bearing formations continent by continent. A summary of the extent (quantity) and quality of megafloral deposits ('formations') representing each floral kingdom provides a sense of the relative robustness of the 'brief history' for the period in question.

Biodiversity & macroevolutionary patterns: See Chart 1 (p. 36) for gymnosperm megafloral diversity histogram including demarcation into cycles of radiation and extinction. With biodiversity at the core of our study, this section is treated particularly extensively and systematically.

Insect associations: See Charts 7, 8 (pp 42, 43) for range chart of the 43 orders of extant and extinct orders of insect, plus three 'orders' of para-insects. Here Conrad Labandeira (contributor) outlines the known history of plant-insect interactions, a relatively young and fast expanding field of exploration.

Tetrapod co-macroevolutionary patterns: See Charts 9, 10 (pp 44, 45) for spindle diagrams providing an overview of tetrapod macroevolution. Here we relate very succinctly the most prominent tetrapod characteristics (e.g. radiations, extinctions) of the period and any evident parallels at this resolution with the plant macroevolution patterns.

Phases in the gymnosperm cycle

We recognise four phases in the macroevolutionary cycle of the gymnosperms: three cycles of radiation and extinction followed by a protracted period of stasis (Chart 1, p. 36).

Phase 1, youth

(Late Palaeozoic megacycle): D(FAM)–P(CHN); 124 my
Primary Radiation, followed by P/Tr Extinction.

The youthful phase of radiation is divided into three distinctive pulses, each characterised by the radiation of a new class, or classes, of gymnosperm (the Lyginopteridopsida, Pinopsida plus Cycadopsida, and Ottokariopsida respectively), followed by an extinction event.

Phase 2, adolescence

(Triassic explosion): Tr(IND)–J(HET); 54 my
Secondary Radiation, followed by Tr/J Extinction.

This adolescent phase of radiation is characterised by a single explosive exponential growth of gymnospermous biodiversity to record heights, followed by the largest of all gymnosperm extinctions.

Phase 3, maturity

(Mesozoic megacycle): J(SIN)–K(CMP); 126 my
Ultimate Radiation, followed by K/T Extinction.

The mature phase of radiation sees two stepwise pulses to greater diversity, the latter more vigorous than the former, separated by an extinction event in the mid-Jurassic, and followed by the longest of all gymnosperm extinctions.

Phase 4, old age

(Cenozoic equilibrium): K(MAA)–Q(HOL); 71 my
Relictual Stasis, followed by Sixth Extinction.

After the explosive radiation of the angiosperms and the K/T Extinction, the gymnosperms settle into a protracted interval of stasis, seemingly with no further potential for macro-morphological innovation.

Overview of gymnosperm macroevolution

Devonian: Emergence in wake of Second Extinction

Tectonics: Laurasia astride equator, Gondwana drifts N.
Climate: Hothouse world, Late Dev. dip of 5ºC.
Floral Kingdoms: Single Global Kingdom,
Pangaea (from N mid-latitude to S polar).
Biodiversity: Emergence of first gymnosperm family.
1 family—originations 1, extinctions 0, nett gain 1.
Emergence—D(FAM).
Late Dev. Extinction (endFRS)—initiates gymnosperm evolution.
Max diversity—FAM, 1 family global.
Insects: Emergence and 'silent' radiation of insects.
Tetrapods: Emergence of amphibians along equatorial belt.

Carboniferous: Primary radiation

Tectonics: Pangaea unites, then drifts N.
Climate: Slide into icehouse world.
Floral Kingdoms: Earliest zonation into distinct kingdoms,
Angara (N cold-temp.), Amerosinia (tropical), Gondwana (S cold-temp.).
Biodiversity: Pulses 1 & 2 of Primary Radiation.
20 families—originations 19, extinctions 12, nett gain 7.
Radiation—D(FAM)–P(ASS), 80 my, moderate stepwise.
Global extinctions—nil.
Max diversity—KAS, 12 families global.
Insects: Explosive primary radiation; expansion of herbivory.
Tetrapods: Primary radiations of amphibians and reptiles.

Permian: End of the Palaeozoic

Tectonics: Pangaea sutures, swivels E, drifts N.
Climate: From icehouse to hothouse, O_2 drops steeply.
Floral Kingdoms: Four distinctive kingdoms, Angara (N temperate),
Euramerica (W tropical), Cathaysia (E tropical), Gondwana (S temperate).
Biodiversity: Third pulse of Primary Radiation.
23 families—originations 15, extinctions 20, nett loss 5.
Radiation—P(SAK–ROA), 27 my, steep stepwise.
P/Tr Extinction—P(endROA–endCHN), 17 my, steep stepwise, nett loss 10 families.
Max diversity—ASS, 14 families global.
Insects: Appearance of extant orders; herbivory goes global.
Tetrapods: Herbivory reaches maturity along with glossopterids.

Triassic: Heyday of gymnosperm biodiversity

Tectonics: Pangaea united, swivels anticlockwise.
Climate: Hothouse world, precipitation & O_2 levels well below today.
Floral Kingdoms: Three distinctive kingdoms,
Angara (N temperate), Laurasia (tropical), Gondwana (S temperate).
Biodiversity: Secondary radiation to heyday of gymnosperms.
36 families—originations 33, extinctions 23, nett gain 10.
Radiation—Tr(IND–CRN), 34 my, exponential explosive.
Tr/J Extinction—Tr(endCRN)–J(endHET), catastrophic, nett loss 14 families.
Max diversity—S temp., CRN, 30 families global.
Insects: Emergence of pollinating orders.
Tetrapods: Emergence of mammals and dinosaurs.

Jurassic: A decimated maturity

Tectonics: Fragmentation of Pangaea, clockwise swivel.
Climate: Continuing icehouse, precipitation declines, O_2 rises.
Floral Kingdoms: Three kingdoms weakly emphasised,
Angara (N high-lat.), Laurasia (trop.), Gondwana (S high-lat.).
Biodiversity: Ultimate Radiation.
23 families—originations 9, extinctions 5, nett gain 4.
Radiation—J(SIN)–K(APT), 85 my, gradual stepwise.
Global extinctions—nil.
Max diversity—BAJ, 19 families global.
Insects: Expansion of pollinators, decline in richness.
Tetrapods: Radiation and dominance of herbivorous dinosaurs.

Cretaceous: Ancillary peak of diversity

Tectonics: Pangaean fragmentation and drift.
Climate: Hothouse, low precipitation, O_2 increases.
Floral Kingdoms: New configuration into four kingdoms,
Boreal (N polar), Laurasia (N mid-lat.), Palaeotropical, Australian (S polar).
Biodiversity: Ancillary radiation with rise of angiosperms.
23 families—originations 5, extinctions 11, nett loss 6.
Radiation—K(VAL–APT), 28 my, gradual stepwise.
K/T Extinction—K(endAPT–endCMP), 41 my, gradual stepwise, nett loss 10 families.
Max diversity—APT, 22 families global.
Insects: Continued radiation of pollinators with rise of angiosperms.
Tetrapods: Continued dominance of herbivorous dinosaurs.

Tertiary: Stasis

Tectonics: Continental drift towards extant configuration.
Climate: Decline into icehouse, precipitation peaks and drops, O_2 reduces.
Floral Kingdoms: Four kingdoms; Boreal (N temp. to polar),
Laurasia (N trop. to temp.), Paleotrop., Australian (S temp. to polar).
Biodiversity: Stasis throughout Tertiary.
12 families—originations 0, extinctions 0, nett change 0.
Radiation—nil.
Global extinctions—nil.
Max diversity—all stages at 12 families global.
Insects: Expanding radiation of herbivores and pollinators.
Tetrapods: Radiation of mammals and birds.

Quaternary: relicts of a 375 my cycle

Tectonics: Extant configuration.
Climate: Icehouse World.
Floral Kingdoms: Maximum differentiation into six kingdoms,
Boreal, Neotropical, Paleotropical, Australian, Cape, Antarctic.
Biodiversity: Stasis continues.
13 families—originations 1, extinctions 0, nett gain 1.
Radiation—nil.
Sixth Extinction—not yet reflected at family level.
Max diversity—HOL, 13 families global.
Insects: Into the Sixth Extinction.
Tetrapods: Into the Sixth Extinction.

TERMS, CONCEPTS & LAWS

To describe and interpret the richly eventful macroevolutionary history of the gymnosperms, a growing lexicon of terms, concepts, principles and laws—as in any field—is inevitable. Acknowledgement is given where terminology is adopted from previous authors; elsewhere the usage is adapted to fit our particular purpose, or the terms are newly coined.

Macroevolution & microevolution

Macroevolution
'Large-scale evolution, entailing major alterations in anatomy or other biological traits, sometimes accompanied by adaptive radiation' (Wilson 1992).

'Evolution above the species level' (Stanley 1979).

Evolution at family level or above—our emphasis in this volume.

Microevolution
'Evolutionary change of minor degree, such as increase in size or body part, usually controlled by a relatively small number of genes' (Wilson 1992).

Evolutionary change within the species (Stanley 1979).

Macroevolutionary life cycle

The history of a major clade (the Division Pinophyta or gymnosperms in the case of this volume) from origin to extinction; the cycle includes a series of phases and may not necessarily be complete.

Intervals within the macroevolutionary life cycle

Phase (of the macroevolutionary life cycle): a major and particularly clearly defined interval—at the scale of one or two geological periods—within the history of the gymnosperms; the four phases recognised here coincide closely (not exactly) with the Carboniferous plus Permian, the Triassic, the Jurassic plus Cretaceous, and the Tertiary plus Quaternary respectively.

Pulse (of radiation & extinction): a clear yet relatively minor cycle of radiation and extinction—at around the scale of a geological epoch—within one of the phases or major cycles of radiation; the three pulses of primary gymnosperm radiation within Phase 1, for instance, coincide closely (not exactly) with the Early Carboniferous, Late Carboniferous and Early Permian respectively.

Relictual Stasis: a prolonged interval—at the scale of a geological period—during which there occurs no macroevolutionary recovery; the single phase recognised here that coincides with the Tertiary plus Quaternary.

Turnover

Turnover: the displacement from dominance of one major clade of organism (e.g. division, class or order of plant) by another through environmental change (circumstantial) or competition.

Concurrent turnover: occurs primarily through competitive displacement involving extinction, severe biodiversity loss or marginalisation to peripheral territory; e.g. the angiosperm-gymnosperm turnover in the mid-Cretaceous.

Delayed turnover: occurs primarily through environment change involving mass extinction and catastrophic niche vacation; e.g. the glossopterid-Umkomasiales (plus several other new orders) turnover at the end-Permian.

Co-macroevolutionary patterns

Here we consider, in particular, interactions between plants, insects and/or tetrapod vertebrates. While the term co-evolution has achieved a precise meaning essentially at the microevolutionary level, we are unaware of any such exclusive sense attached to *co-macroevolution*. We refer generally to the degree of coincidence (or lack thereof) of patterns of evolution (such as reflected in spindle diagrams) at family level or above. The more nearly these patterns coincide, the closer the interdependent evolutionary fortunes of the groups may be. The parallel patterns may also be circumstantial (see text on turnovers above), as might occur where large-scale environmental change (as caused by asteroid impacts, for instance) has similar effect on the different groups of organism.

Concordant co-macroevolutionary turnover—where turnover between major clades is more or less parallel.

Discordant co-macroevolutionary turnover—where turnover between major clades is markedly nonparallel.

Plant/tetrapod empires
The concept is an adaptation of the tetrapod empires introduced for the Laurasian Permo-Triassic in Anderson & Cruickshank (1978). It is not applied throughout in our *History* but only where particularly clear-cut based on current syntheses—e.g. the *Glossopterid/Therapsid* Empire in the Gondwana Permian and the *Dicroidium/Diademodontoid* Empire in the Gondwana Triassic. While a plant province is essentially defined as a spatial entity (though it obviously has duration), a plant/tetrapod Empire is a spatial/temporal entity. Like an empire in the context of human civilisation, a plant/tetrapod empire goes through a life cycle—emerging, expanding, attaining peak vigour and dominance, declining and dying. The scope of an Empire varies, but generally such as those noted above, extends supercontinentally at its acme and endures through a geological period.

Diversity histogram

***Concurrent patterns** (between families, orders and classes)*—the patterns refer to the histograms of any two taxonomic ranks through successive geological stages during a phase or pulse of radiation or extinction.

Divergent (during a phase of radiation): where the adjacent histograms diverge through time, e.g. the families and orders through Pulse 2 of the Primary Radiation in the Carboniferous.

Convergent (during a phase of extinction): where the adjacent histograms converge through time, e.g. the families and orders through the P/Tr and Tr/J extinctions.

Parallel (during phases of radiation or extinction): where the adjacent histograms run parallel through time, e.g. the families and orders through the Cretaceous and Tertiary.

Global extinction events

The six global extinction events are profoundly linked to the history of the gymnosperms. The four phases in the macroevolutionary cycle of the group are defined by the extinction events.

First Extinction (end Ordovician): sparks the origin of the pteridophytes and the colonisation of the tropical belt.

Second Extinction (Late Devonian): sparks the origin of the gymnosperms along the tropical belt.

Third Extinction (end Permian): terminates Phase 1 (Youth), and sparks the Secondary Radiation in the macroevolutionary life cycle of the gymnosperms.

Fourth Extinction (Late Triassic): terminates Phase 2 (Adolescence) and sparks the Ultimate Radiation in the history of the gymnosperms.

Fifth Extinction (end Cretaceous): terminates Phase 3 (Maturity) and initiates the interval of old age.

Sixth Extinction (Present): threatens to bring about the final demise of the gymnosperms or its further decimation.

Radiation (at the macroevolutionary level)

In this volume we are concerned only with diversification at the macroevolutionary level. The phases of radiation are characterised according to the following four criteria:

Sequence
Primary: the initial radiation of the Late Palaeozoic.
Secondary: the intermediate radiation of the Early Mesozoic.
Tertiary: the final radiation of the Middle to Late Mesozoic.

Rate (families nett gain per stage)
Explosive: 5 or more families nett gain per stage;
gradient (mean) as plotted on diversity histogram: >>45º
e.g. Secondary Radiation (Tr): 25 fam. in 34 my (*ca* 1 in 1 my)

Stepwise: 2–3 families nett gain per stage;
gradient (mean) as plotted on diversity histogram: *ca* 45º
e.g. Primary Radiation, Pulse 2 (C/P): 11 fam. in 31 my (1 in 3 my)

Gradual: 1 family nett gain per 2–3 stages;
gradient (mean) as plotted on diversity histogram: <<45º
e.g. Ultimate Radiation, Pulse 2 (J/K): 5 fam. in 56 my (1 in 10 my)

Magnitude (families nett gain per pulse)
Major: >20 families nett gain (e.g. Tr Radiation)
Moderate: *ca* 10 families nett gain (e.g. C/P Radiation, Pulse 2)
Minor: <5 families nett gain (e.g. C/P Radiation, Pulse 3)

Duration
Long: e.g. Ultimate Radiation (85 my)
Interim: e.g. Primary Radiation, Pulses 1 plus 2 (49 my)
Short: e.g. Secondary Radiation (34 my)

Extinction (at the macroevolutionary level)

As for radiation, we are concerned here with extinction at the macroevolutionary level.

Rate (families nett loss per stage)
Catastrophic: 5 or more families nett loss per stage
Stepwise: 2–3 families nett loss per stage
Gradual: 1 family nett loss per 1–3 stages

Random-pruning effect (see p. 5)

Biodiversity

(first three definitions adapted from And. & And. 2003)

Observed: The actual tally of taxa of a particular rank (e.g. family, order, class) collected from a particular geological interval (e.g. stage, epoch, period).

Preserved: The projected tally of a particular rank representing the full potential sample (assuming theoretically absolute comprehensive sampling of all preserved floras) from a particular geological interval.

Existed: The projected tally of taxa of a particular rank representing the full set of floras that actually inhabited the various habitats within the basins of deposition representing a particular geological interval.

Range-through method: This method, adopted here for graphing diversity (Fig. 5), 'assumes that a family was present at all time intervals between its first and last appearances ... even if not directly sampled in all intervals' (Labandeira & Sepkoski 1993).

Originations: the number of families, orders or classes 'observed' to appear in a geological stage (or epoch) for the first time in the fossil record.

Nett gain: the number of originations less the number of extinctions within a phase or pulse of radiation.

Extinctions: the number of families, orders or classes 'observed'—at the resolution of the geological stage (or epoch or period)—to disappear from the fossil record.

Nett loss: the number of extinctions less the number of originations within a phase or pulse of extinction.

Observations based on gymnosperms

Innovative phases: During the youthful, adolescent and early maturity phases—the innovative, seminal phases—in the macroevolutionary cycle of a major clade (e.g. the gymnosperms), the lower taxonomic ranks (e.g. families) diversify faster than the higher ranks (e.g. orders).

Conservative phases: During the later maturity and old-age phase—the conservative to sterile phases—in the macroevolutionary cycle of a major clade (e.g. the gymnosperms), the relative levels of diversity between successive taxonomic ranks (e.g. families and orders) tend to remain constant, they run parallel; the number of families per order remains constant; the morphological plasticity of the families has run its course.

Laws of biodiversity

In establishing the laws of diversity, it might be that we should distinguish between the extant world and earlier geological epochs of the Phanerozoic world, or at least between icehouse and hothouse phases of geological time.

The Extant world
Wilson (1992), in his classic, *The diversity of life*, stressed four laws of biodiversity, the first three relating largely to solar energy.

Latitudinal Diversity Gradient—It is an '*indisputable general feature of life that biodiversity rises towards the tropics.*'

Rapoport's Rule—'*The ranges of individual species shrink steadily the closer you come to the equator*.' It also holds that '*the altitudinal range of species*' contracts '*along the sides of mountains*' towards the equator.

Energy-Stability-Area Theory (ESA)—'*The more solar energy, the greater the diversity; the more stable the climate, both from season to season and from year to year, the greater the diversity*; *… the larger the area, the greater the diversity.*'

The Theory of Island Biogeography—'*The number of species living on an island increases*' with increasing area. '*Increasing the area of an island tenfold doubles the number of species.*'

The Phanerozoic world
The laws outlined by Wilson hold generally for the extant world, but it appears debatable to what degree they apply during earlier geological periods (Anderson 1999). How, for instance, does the Energy-Stability-Area Theory (ESA) hold up during the later Palaeozoic and earlier Mesozoic world of Pangaea? Flowing from the current study of the gymnosperms, we offer the following hypotheses or amendments to the laws of biodiversity.

Extinction-diversity Law—*In the early phases in the evolution of a major clade (gymnosperms), extinction stimulates diversity, and the greater that extinction the greater the subsequent radiation of new diversity.*

Latitudinal Diversity Gradient (amendment)—*In an icehouse world, biodiversity rises towards the equator; in a hothouse world, biodiversity rises towards middle latitudes*.

DEVONIAN:
Emergence in wake of Second Extinction

Plate tectonics & global physiology

Proto-Pangaea

During the Devonian, Laurasia sat more or less static astride the equator, much as it had through the Silurian. Gondwana swivelled clockwise, with 'Australia' moving south from its former equatorial position and 'Africa/South America' moving north to form near closure with Laurasia.

Hothouse world

The hothouse conditions of the Silurian prevailed through the lower two-thirds of the Devonian; then followed a decisive dip of perhaps 5ºC (global average)—initiating the slide into icehouse conditions of the later Carboniferous. Glaciation appeared in parts of South America.

Concomitant with the Late Devonian dip in temperatures, it appears that similarly decisive rises in mean global precipitation and atmospheric oxygen levels (from *ca* 13% to 18%) occurred.

Floral kingdoms

Global: The gymnosperms emerge along the equatorial belt of a global pteridophyte kingdom.

Megafloral occurrences, key sequences

The only reconstructed seed-plant from the Devonian (*Elkinsia*) is found at the Famennian Elkins locality in the Appalachians, USA (Rothwell *et al*. 1989). However, cupulate ovules and fragments of foliage from similar plants are also known from several contemporaneous floras in Europe (e.g. the Baggy Fm. in SW England).

Biodiversity & macroevolutionary patterns

Family-level diversity

Upper: total 1; originations 1; extinctions 0; nett gain 1

Second Extinction (Late Devonian)

The great significance—from our perspective—of the Late Devonian extinction is that it appears to have ignited the radiation of the gymnosperms (and the amphibians). The earliest family of gymnosperms (see below), appears directly after the extinction.

Emergence of the first gymnosperm family

From the diverse world of Devonian pteridophytes emerged the Moresnetiaceae (Elkinsiaceae) towards the close of the Devonian (Famennian). The family is confined to Euramerica and the earliest species, *Elkinsia polymorpha,* to the Hampshire Fm., West Virginia, USA. If this were indeed the only family of gymnosperm in existence at the time and the group is monophyletic, then it bore within it the genetic potential to radiate explosively to yield the extraordinary gymnosperm 'tree' that was to follow and the angiosperm 'tree' that arose from that.

Morphological innovations

The key reproductive innovation during the Devonian was the surrounding of the megasporangium (or nucellus) by a protective sheaf of telomes to form an integument. Unlike later gymnosperms, however, the integument does not entirely encase the nucellus, which is exposed at the distal end. Pollen capture was facilitated by a tubular prolongation of the nucellus (lagenostome or salpinx), in which a central column of tissue sealed the nucellus after pollination has occurred. This distinctive strategy is known as hydrasperman reproduction (Rothwell 1986). Early gymnosperm foliage consists of large compound leaves ('fronds') characterised by a basal dichotomy of the main rachis.

Insect & other arthropod associations [Contributor: C.C. Labandeira]

Emergence & 'silent' radiation of the insects

The Rhynie Chert (Scotland), in the Emsian of the later Early Devonian has yielded the earliest recognised insect (Archaeognatha). By this stage, the pteridophytes, some 25 my after their earliest appearance, were well into the first pulse of their primary radiation. It is evident that the apterygote insects as well as myriapods and arachnids arose within the pteridophytic ecosystems of the Euramerican equatorial belt (Chart 1, p. 36)—and that they predate the gymnosperms.

The pterygote insects, embracing almost all remaining extinct and extant orders, very possibly arose (Charts 7, 8, pp 42, 43) along with gymnosperms and amphibians in the Late Devonian (Famennian) in the wake of the Second Extinction. It must be emphasised that this remains hypothesis in much the same way that the primary ('silent') radiation of the insects in the Early Carboniferous is based on cladistic studies in the absence of body fossils.

The earliest evidence

Given the relatively limited extent of Devonian floras in terms of taxonomic diversity, growth forms and range of tissues available for arthropod consumption, there is a surprising amount of evidence for arthropod associations. There is a limited body-fossil record of terrestrial arthropods, consisting of centipedes, millipedes, mites, spiders and related arachnids, and rare insects. However, the record of plant damage indicates several significant associations in the absence of such important substrates as leaves, seeds and wood which only appeared in a limited way toward the close of the period (Gensel & Edwards 2001).

The earliest evidence for any type of association in a terrestrial ecosystem is from spore-bearing coprolites produced by unknown arthropods during the latest Silurian (Pridoli) and Early Devonian (Kevan *et al.* 1975; Edwards *et al.* 1995; Hotton *et al.* 1996; Habgood 2004). Evidently some of these coprolites have mono- or nearly monospecific assemblages of spores indicating targeting of plant sporangia, although the nutritional advantages of such a food resource have been doubted (Habgood 2004). In addition to consumption of spores and sporangia, other tissues were ingested such as surface and cortical tissues of *Psilophyton* stems (Banks 1981) and the deeper fluid tissues of trimerophyte and rhyniophyte stems (Banks & Colthart 1993), the former probably by mandibulate and the latter by piercing-and-sucking arthropods. These surface lesions and deeper penetrations exhibit response tissue similar to that induced by extant microarthropods (Labandeira & Phillips 1996a). In addition to spore consumption, external feeding, and piercing-and-sucking, a forth major trophic strategy is evident, namely boring, but into lignified tissues of the massive basidiomycete fungus *Prototaxites*, similar in structure to the wood of plants (Hotton *et al.* 1996). Two known examples, one from the Early Devonian and the other from the Late Devonian, displaying different patterns of boring, remain undescribed.

Tetrapod co-macroevolutionary patterns

Emergence of the amphibians

As noted above, the emergence of both the gymnosperms (the first of the seed plants) and the amphibians (the first of the tetrapod vertebrates)—both along the equatorial belt—were evidently catalysed by the Second Extinction. It is the first of many examples of the close concordance at macroevolutionary resolution of the history of the gymnosperms and of the tetrapods.

CARBONIFEROUS: Primary Radiation

Plate tectonics & global physiology

Pangaea united

Gondwana continued, through the Carboniferous, its marked clockwise swivel that had characterised the Devonian. Its eastern end ('Australia') moved southwards through the mid-latitudes during the Early Carboniferous and into high southern latitudes by the end of the period. And its western sector ('Africa/South America') moved strongly northwards with just a narrow seaway separating the southern continent from Euramerica in the Lower Carboniferous, to full closure and suturing along the Appalachian Mountains in the later half of the period. After closure, Laurasia was propelled northwards across the equator.

Slide into icehouse world

Through the Carboniferous, there occurs a profound shift from hothouse world to icehouse world—with a supposed drop of some 15ºC (global average). This drop in global temperatures, deepening progressively from the later Devonian to later Carboniferous, is no doubt coupled to the formation of Pangaea and the 'radical rerouting of ocean currents' (Anderson *et al*. 1999).

The Gondwana Carboniferous icecap is understood to have centred earlier in the period on southeastern 'South America' and southern 'Africa', and to have spread subsequently to cover the greater part of the former southern supercontinent. Only the outer rim remained exposed.

Rainfall is taken to have swung to an all-time high in the Early Carboniferous and to have dipped again to more normal proportions by the end of the period (Frakes 1979). Atmospheric oxygen levels, on the other hand, are thought to have risen steeply throughout the period to record highs of *ca* 37% by the start of the Permian (Chart 2, p. 37).

Floral kingdoms: earliest zonation into distinct kingdoms

Angara (north cold temperate): Gymnosperms all but absent in the Tournaisian and Viséan. Pteridospermous gymnosperms of uncertain affinity dominant in the Serpukhovian and early Bashkirian. Cordaitanthales appear in the Bashkirian and become dominant in the Kasimovian.

Amerosinia (tropical): Lyginopteridales and Calamopityales dominant in the Tournaisian to Serpukhovian. Lyginopteridales, Medullosales and Cordaitanthales dominant in the Bashkirian to Gzhelian.

Gondwana (south cold temperate and austral): Gymnosperms all but absent through most of Carboniferous except for some pteridosperms of uncertain affinity in the Kasimovian.

Megafloral occurrences, key sequences

Amerosinia: The most complete evidence of Viséan and Tournaisian vegetation is to be found in Britain, France, Germany and the Appalachians. These tend to fall into two categories. (1) Adpression sites, normally associated with fluvio-lacustrine sequences, such as those in Britain (Oil Shales, Clwyd Group at Teilia and Drybrook Sandstone), Germany and the Appalachians (Price Fm.), which provide details of morphology and distribution (Vakhrameev *et al*. 1978; Cleal & Thomas 1995). (2) Petrifaction sites, normally associated with volcanigenic, shallow marine or lagoonal sequences, such as those in Scotland (Inverclyde Group, Oil Shales), France and the Appalachians (New Albany Shales) (Scott *et al.* 1984; Cleal & Thomas 1995). Dating of those sites in marine or fluvio-lacustrine settings is often well established as they are associated with biostratigraphically sensitive faunas. Volcanigenic or lagoonal settings present greater difficulties, although palynology normally has allowed dating to be achieved.

Serpukhovian and Bashkirian floras are generally poorly represented here, the best being in Central Europe (Upper Silesia) and Belgium (Stockmans & Willière 1953; Purkyňova 1970). However, dating of these floras is well established based on associated marine intervals with biostratigraphically diagnostic faunas.

Late Bashkirian and Moscovian (Westphalian in the European chronostratigraphy) floras are widely distributed and intensively studied. Adpression floras are widely occurring across the Variscan Foreland from Bulgaria in the east to the Canadian Maritimes, and from the upland intramontane basins in France, Germany, Czech Republic and Romania (Vakhrameev *et al*. 1978). Most important are the floras from the Canadian Maritimes, Yorkshire, Saar-Lorraine and Central Bohemia, which yield well-preserved cuticles. There are also adpression floras over large areas of the Appalachians (from Alabama to Pennsylvania) and the Central Interior Coalfield of the USA, although these have been remarkably little studied (Pfefferkorn & Gillespie 1980; Blake *et al.* 2002). Other areas of note are the parallic sequences in Ukraine, which provide macrofloral horizons interbedded with limestones allowing correlations with the marine-based chronostratigraphy.

Petrifaction floras in these tropical deposits are mainly in the coal-balls that occur in coals formed in marine-influenced parallic settings. The historically most important is the late Bashkirian Halifax Hard/Union Seam in northern England (Galtier 1997). However, there are also numerous other coal-ball horizons through the Moscovian in the Appalachian Basin (Phillips 1980).

Kasimovian and Gzhelian sequences occur mainly in the intramontane basins of France and Germany, and parallic settings in the Ukraine and the Appalachians (Darrah 1969; Vakhrameev *et al.* 1978). The latter are particularly important because of the well-preserved coal-ball floras (Phillips 1980).

Finally of note are a number of extra-basinal floras mainly from North America, which contrast sharply with the lowland vegetation encountered in most other sites. Of particular note are the Manning Canyon Shale flora in Utah (Serpukhovian) and the Hamilton Quarry flora in Kansas (Tidwell 1967; Mapes & Mapes 1988).

Cathaysia: Chinese Carboniferous floras are reviewed by Wu in Li *et al.* (1995). Mississippian floras are restricted to South China, where they are widely occurring although relatively little studied. Pennsylvanian floras in contrast are restricted to North China. Late Moscovian floras known as the Benxi Flora are widespread but particularly well known in the Shanxi and Liaoning provinces. Shanxi also has the best developed Taiyuan Fm. floras of Kasimovian-Gzhelian age.

Angara: Carboniferous floras are widespread in Angara, although as many are in geographically isolated areas they have not been intensively studied. The most important are the Mississippian floras of the Minusa Basin and the Pennsylvanian floras of Kuznetsk, both in southern Siberia (Meyen 1982).

Gondwana: 'Whilst life flourished along the tropical belt of Laurasia ... that in Gondwana led a more marginal existence' (Anderson *et al.* 1999). With the continental icecap covering much of Gondwana, it is only around its fringes that megafloras—impoverished at that—are to be sought. The principal sequences are those in Argentina and eastern Australia (Queensland and NSW).

Biodiversity patterns

Family-level diversity (Charts 3, 4; pp 38, 39)
Late: total 16; originations 7; extinctions 7; nett gain 0
Mid: total 9; originations 6; extinctions 1; nett gain 5
Early: total 7; originations 6; extinctions 4; nett gain 2
Overall: total 20; originations 19; extinctions 12; nett gain 7

Pulses 1 & 2 of Primary Radiation D(FAM)–P(ASS)
Rate: moderate stepwise
Magnitude (families): originations 26; extinctions 16, nett gain 10
Duration: 9 stages (80 my)
Family/order concordance: concordant divergent
Order/class concordance: concordant divergent
Causes: sparked by the end-Devonian extinction
Insect co-evolution: explosive primary radiation of insects
Tetrapod co-evolution: primary radiation of amphibians and reptiles
Gymnosperm history: pteridophyte/gymnosperm turnover; comparative displacement, apparently akin to the mid-Cretaceous gymnosperm/angiosperm turnover. As regards originations, the primary radiation (first and second pulses) approaches the scale of the Triassic (Secondary) Radiation, but as regards nett family gain, it is only half the size.

Primary radiation of the gymnosperms

The primary radiation of the gymnosperms occurs stepwise from the latest Devonian (Famennian), through the Carboniferous, and into the earliest Permian (Asselian)—an interval of *ca* 80 my (Chart 1). It originates with a single family (one order, one class) and reaches a maximum in the Asselian with 17 families (10 orders, five classes). The family, order and class patterns of radiation are concordant/convergent.

Within the Tournaisian, the earliest stage of the Carboniferous, appear three new families, all representing the Lyginopteridopsida. Before the close of the period (in the Gzhelian), 11 families in seven orders and four classes are in evidence. The Lyginopteridales, the ancestral order, however, appear to have become extinct by the end of the Kasimovian.

During the Mississippian Subperiod (TOU–SPK), the moderate stepwise radiation of the gymnosperm families occurred mainly in the palaeotropics (six families appear); there is little evidence of gymnosperms in higher latitudes of either the northern or southern hemispheres. However, as was inevitable with such a phase of innovative evolution, some of these families were not long-lived and by the end of the Serpukhovian there were only three known gymnosperm families still in existence. As in the Devonian, the Lyginopteridales were dominant, together with the less diverse Calamopityales; by the end of the Viséan, the Medullosales had also appeared (the Trigonocarpaceae in the western palaeotropics, the Potonieaceae in the eastern palaeotropics) but it was some time before they developed any significant diversity.

Response to global climatic cooling, Bashkirian to Moscovian

The start of the Bashkirian saw the slide into a time of ice-house conditions, with a marked increase in global vegetational provincialism. This coincided with a moderate macroevolutionary explosion among the gymnosperms, with five families appearing at the time. This was mainly in the palaeotropics, in both lowland (Physostomaceae, Cordaitanthaceae) and upland (Phasmatocycadaceae, and voltzialean conifers of uncertain family attribution) vegetation. Another two families appeared in the palaeotropics during the late Moscovian (Callistophytaceae, Stephanospermaceae). Species biodiversity patterns in the palaeotropics varied considerably during the Bashkirian and Moscovian, with micro-evolutionary explosions occurring in the basal, early and late Bashkirian, coinciding with the initiation and rapid expansion of wetland habitats here. Extinction rates remained more or less static for much of this time, until the late Moscovian (early Westphalian D), when there was a significant drop in species numbers.

The much colder climate was generally not favourable to gymnosperms in higher latitudes. Virtually none are known from the southern high and middle latitudes. In northern middle latitudes (there was no land at high latitudes at this time), the Rufloriaceae appear in the early Bashkirian, associated with pteridosperms of uncertain family attribution.

Response to climate change in the Kasimovian & Gzhelian

The start of the Kasimovian saw major global environmental change. The wetlands in tropical Euramerica contracted dramatically in response to topographic changes caused by Variscan tectonics, but at the same time similar habitats were appearing in the eastern palaeotropics, in northern China. This also coincided with a marked global warming and interglacial. Surprisingly, however, this is marked by only a moderate macroevolutionary change in the gymnosperms, with only one extinction (Physostomaceae) and four originations (Dicranophyllaceae, Thucydiaceae, Codonospermaceae, Polylophospermaceae) occurring at the family rank.

This process continued in the Gzhelian, with the virtual disappearance of the western palaeotropical wetlands, and their replacement by drier habitats. This is marked by another moderate macroevolutionary explosion, with the appearance of the conifer families Bartheliaceae and Emporiaceae and of the Peltaspermaceae.

Morphological innovations

As well as being marked by taxonomic diversification, the Carboniferous was a time of marked morphological innovation in gymnosperms. The Calamopityales and the early Lyginopteridales retain the primitive hydrasperman reproduction, but the Viséan also sees the appearance of ovules with a micropyle as in modern gymnosperms (the apparent failure of the Calamopityales to develop this improved style of reproduction may explain why they became extinct in the Viséan).

In the most primitive gymnosperms, the ovules were borne in clusters within a protective cupule, which in turn was attached to a leaf. In the Medullosales, the number of ovules per cupule was reduced to one, the cupule becoming in effect an outer integument. In the Peltaspermales, which appear towards the end of Carboniferous, the ovules are attached to peltate discs, sometimes found arranged in groups along an axis, thus resembling a strobilus ('cone'). In the Pinopsida, however, ovules became arranged in more tightly organised strobili, which included sterile protective bracts. In some cases, the strobili were arranged singly, but in the Cordaitanthaceae and the Voltziales they were clustered into compound fertile structures.

There was also a great diversity in pollen-organs. In the primitive gymnosperms, they were simply clusters of pollen-sacs, sometimes loose, sometimes fused together. Some Medullosales also have relatively simple synangial structures, whereas others (e.g. Potonieaceae) developed complex clusters of synangia, to form intricate male reproductive organs. In the Pinopsida, the pollen-sacs were, like the ovules, borne in strobili. Pollen varied greatly from the relatively simple trilete pre-pollen in the Lyginopteridales, that superficially resembles pteridophytic spores, to the large monolete pre-pollen of the Medullosales, to the saccate pollen of some Cordaitanthaceae.

Most early gymnosperms (pteridosperms) had large, frond-like leaves. Mostly, they had pinnules with a simple midvein and dichotomous lateral veins. In the Medullosales, reticulate veining appears, but of an architecture with only one order of meshes and no freely-ending veinlets. The Pennsylvanian Subperiod also saw the appearance of other foliage types among gymnosperms, most notably the large, strap-like leaves of the Cordaitanthales) and the microphyllous leaves of the Voltziales.

Early gymnosperms were mainly trees or small woody plants. However, the Pennsylvanian Subperiod saw the appearance of the lianescent habit, initially among the Lyginopteridales but later (Kasimovian) also among the Medullosales. This can be seen as a response to the development of dense tropical forests at this time, increasing competitive pressure on plants for light collection.

Tropical Coal Forests

The Coal Forests overall (west to east) peak generally during the Moscovian: the Euramerican forests peak in the early Moscovian, then dip slightly as Variscan tectonic activity starts to kick in; during the Late Moscovian, they expand eastwards into China.

Pteridophyte heyday

Considering species diversity (Niklas *et al.* 1983), the pteridophyte heyday plots in the Late Carboniferous at the Bashkirian-Moscovian boundary (Chart 1, p. 1–36; Chart 6, p. 41)—during Pulse 2 within the Primary Radiation of the gymnosperms. This appears to coincide very closely with the peak occurrence of tropical forests (and coal deposits) in Euramerica.

Insect associations [Contributor: C.C. Labandeira]

Explosive primary radiation of the insects

Just as the early pteridophyte ecosystems appear to have spawned the emergence of the apterygote insects, and other major terrestrial arthropod clades, so the early gymnosperm ecosystems spawned the primary radiation of the insects. Considering Charts 7, 8 (pp 42, 43), which reflect current knowledge of body fossils, plant-insect associational evidence and cladistic phylogenetic extrapolation, this primary diversification of the insects is an event that parallels very closely that of the primary radiation of the gymnosperms.

The expansion of herbivory

During the Pennsylvanian, there is extensive evidence for the expansion of herbivory, at least in equatorial Euramerica (Scott & Taylor 1983; Chaloner *et al*. 1999), illustrated by several documented associations from the Calhoun Coal (Labandeira & Phillips 1996a, 1996b, 2002), representing an important coal-swamp community from the Late Pennsylvanian (Kasimovian). Two component communities, consisting predominantly of herbivores, but also detritivores, are documented on *Psaronius* fern and *Medullosa* seed-fern plant hosts. These include pith borers, wood borers, external foliage feeders, gallers, piercer-and-suckers and sporangiovores on *Psaronius*. There also is evidence for the targeting of *Medullosa* prepollen (*Florinites*) by pollinivorous insects, indicating perhaps the beginning of pollination-type syndromes. Evidently herbivores were targeting a wide variety of vascular plant tissues in these coal-swamp floras during the Late Pennsylvanian, for example the occurrence of the gall *Pteridoscaphichnus* solely on *Psaronius chasei* indicates that only a particular organ (rhachis) and tissue (inner parenchyma) was targeted within this host species (Labandeira & Phillips 2002).

Additional documentation, mostly records of individual plant-insect or mite associations, originate from several localities of the Euramerican Middle Pennsylvanian based on a variety of evidence (Labandeira 1998a). The most obvious interaction is external foliage feeding on various seed-fern pinnules (Müller 1982; Scott & Taylor 1983), but also other types of foliage (Ameron & Boersma 1971; Castro 1997). The earliest occurrence of this type of folivory is considerably earlier, from the Late Mississippian of eastern Australia (Iannuzzi & Labandeira pers. observation). In addition, galls have been described from sphenopsid fructifications (Van Ameron 1973). Both pollen in the guts of paleodictyopterid insect nymphs (Kukalová-Peck 1991) and the consumption of sporangia indicated by permineralised coprolites (Meyen 1984; Rothwell & Scott 1988) provide evidence for the targeting of reproductive tissues. Minute borings by mites in woody tissues as well as much larger galleries by insects in pith parenchyma are known for several arborescent plant species (Rothwell & Scott 1983; Labandeira *et al.* 1997; Labandeira & Phillips 2002). Piercing-and-sucking of parenchymatic tissues in a fern petiole (Scott & Taylor 1983) and seed predation on *Samaropsis* seeds (Sharov 1973) have been attributed to paleodictyopterid insects with stylate mouthparts (Labandeira 1997).

Some of the earliest indirect evidence for primitive insect pollination is during the mid-Carboniferous. For example, in the case of Late Mississippian to Early Pennsylvanian lyginopterid seed ferns, there is structural evidence indicating an association with insects, based on conspicuous, outwardly directed capitate glands on pecopterid and sphenopterid leaves of *Lyginopteris* and importantly the anatomically associated *Lagenostoma* cupules (Oliver & Scott 1904). Like medullosan and other seed-fern clades, *Lagenostoma* had a pollination drop mechanism which presumably sequestered aerial blankets of wind-dispersed pollen through the flooding of an erect tubular micropyle by sticky fluids that were secreted by ovular tissues (Rothwell 1977). However, there are indications in Mesozoic gymnospermous taxa that pollinivorous insects may have vectored distant pollen to conspecific ovular structures (Labandeira 2000), and such a mechanism is suggested in *Lagenostoma*—if the cupulate capitate glands are interpreted as rewards (‘extrafloral’ nectaries) that provide secretions imbibed by frequenting insects. In addition to this potential interaction, lyginopterid stems occasionally are riddled with mite borings (Tomescu *et al.* 2001).

Tetrapod co-macroevolutionary patterns

Primary radiations of the amphibians & reptiles

The emergence and primary radiation of the amphibians (Chart 9, p. 44) coincides almost exactly with the emergence and the first and second pulses of the primary radiation of the gymnosperms (Chart 1, p. 36). An abrupt C/P extinction (end-Asselian) breaks the radiation of both. Equally striking is the primary stepwise emergence and radiation of the stem reptiles, and of the pelycosaurs that follow, which coincide closely with the second and third pulses of the primary gymnosperm radiation.

PERMIAN:
End of the Palaeozoic

Plate tectonics & global physiology

Pangaea united

With the continuing northward drift of Gondwana, the suture with Laurasia is finally complete. The collision gives rise to the Variscan and Appalachian Mountains in Europe and North America, and causes major environmental changes in the western palaeotropics. Many shelves and seas are progressively drained through the period. However, the eastern Palaeotropics are hardly touched by these changes and tropical wetland habitats persist for much of the Permian. During this time, the united Pangaea swivels anticlockwise, and continues to be propelled northwards, such that by the P/Tr boundary, the equator bisected the united Pangaea along the juncture between the two former supercontinents.

From icehouse world to hothouse world

The start of the Permian Period sees a reversion to icehouse conditions, with glaciation appearing in parts of Gondwana. However, this was relatively short-lived, and the remainder of the period saw an increase of about 20ºC in global temperatures.

Mean global precipitation is thought to have declined moderately during the Permian to around today's pattern, while atmospheric oxygen levels dropped steeply through some 20% to around 17% (5% below current levels).

Floral kingdoms: four distinctive kingdoms are recognised

Angara (north temperate): Peltaspermales and Cordaitanthales dominant.

Euramerica (western tropical): Voltziales dominant.

Cathaysia (eastern tropical): Gigantopteridales, Phasmatocycadales, Callistophytales dominant.

Gondwana (south temperate): Ottokariales (glossopterids) dominant. Throughout the Gondwana Kingdom and virtually throughout the Permian, the glossopterids are overwhelmingly dominant in abundance and diversity.

Megafloral occurrences, key sequences

Correlation uncertainty: In the absence of good absolute dates or interfingering marine beds, it is notoriously difficult correlating terrestrial plant or vertebrate-bearing formations (particularly of Gondwana) with the richly fossiliferous, marine Permian standard stages of Laurasia.

Euramerica: Permian floras are sporadic and generally of low diversity in Euramerica. The main exceptions are the Asselian floras of the Autun and Saar-Lorraine areas in France and Germany (Kerp & Fichter 1985), the Artinskian-Kungurian floras in Texas (Read & Mamay 1964), and the Roadian floras in the Kupferschiefer of Germany and the Marl Slate in England (Schweitzer 1986).

Cathaysia: In contrast, Permian floras are widespread in the Far East palaeotropical areas (reviewed by Shen in Li *et al*. 1995). The best documented are those of Shanxi in North China from the Shanxi Fm., Shihhotse Group and Shihchienfeng Fm., which range through much of the Permian. In South China, the lowest Permian is mainly in marine facies with few floras, but between the Artinskian and Wuchiapingian there are diverse and well preserved floras (Liangshen, Maokou and Lungtan Formations). There are also Permian floras in Japan, Korea, Laos and Indonesia, but these have not been studied to the same extent.

Angara: Permian floras are widespread across much of Siberia and have been reviewed by Meyen (1982). Although there is no land in the northern polar regions, parts of Primorye were at high latitudes and yield what can be termed a Boreal Flora. However, the best documented Angaran floras are from Kuznetsk and Tunguska in southern Siberia, which range throughout much of the Permian, and which were then in middle latitudes (e.g. Gorelova *et al*. 1973). Of particular importance is the Korvunchanskaya Fm. in Tunguska, which yields floras of apparently Mesozoic aspect in beds that are independently dated as latest Permian in age.

Further west, in the Fore-Urals area, there are floras that appear to be intermediate in character between the classic Angaran vegetation and the more temperate vegetation of Sub-Angara. The best documented of these are the Tatarina Floras from the Pechora Basin that are Wordian to possibly Changhsingian in age (Meyen 1983; Gomankov & Meyen 1986).

Further west and south again are the Sub-Angara Floras, which include elements of both Angaran and Euramerican vegetation. They occur widely in Kazakhstan, the Middle East and northern China (Meyen 1982).

Gondwana: In marked contrast to the Carboniferous, megafloras—often associated with coal deposits—are well developed throughout Gondwana. The key sequences are those in the Parana Basin (South Brazil), the Karoo Basin (South Africa), a network of rift valleys in Peninsula India, the Bowen and Sydney basins (of Queensland and NSW respectively), and the Central Transantarctic Mountains (Antarctica). Glossopterid floras dominate throughout.

P/Tr boundary: The best opportunity for assessing gymnosperm fortunes across the P/Tr boundary in Gondwana are in the Bowen Basin (Queensland) and the Sydney Basin (New South Wales) down the eastern seaboard of Australia, and in Laurasia in the Tunguska Basin of Eastern Siberia and the remarkably continuous sequences of both North and South China. The scarcity of Late Permian and Early Triassic megaplant-bearing strata across Laurasia is quite remarkable! They are indeed virtually absent in North America and Europe.

Biodiversity & macroevolutionary patterns

Family-level diversity

Late: total 10; originations 1; extinctions 7; nett loss 6
Middle: total 14; originations 5; extinctions 5; nett gain 0
Early: total 17; originations 9; extinctions 8; nett gain 1
Overall: total 23; originations 15; extinctions 20; nett loss 5

Early Permian (end-Asselian) Extinction

Rate: catastrophic
Magnitude (families): extinctions 4; nett loss 4
Duration: 0 my (instantaneous at our resolution)
Family/order concordance: concordant, extinctions 2
Order/class concordance: discordant, no loss at class level
Causes: global warming and flooding of shelves and low country, associated with the meltdown of the continental Gondwana icecap
Insect co-macroevolution: no order-level extinctions
Tetrapod co-macroevolution: major dislocations and turnovers evident
Gymnosperm history: extinctions occur amongst Lyginopteridopsida (1 family), Pinopsida (1 family), and the Cycadopsida (2 families, 1 order)

Third Pulse of Primary Radiation P(SAK–ROA)

Rate: steep stepwise
Magnitude (families): originations 7; extinctions 4; nett gain 3
Duration: 4 stages (27 my)
Family/order concordance: stepwise discordant (families increase, orders in decline)
Order/class concordance: discordant (classes stable at 5)
Causes: recovery after end-Asselian extinction; colonisation and radiation in Gondwana after meltdown of Carboniferous mega-icecap
Insect co-macroevolution: origination or rise to prominence of several major extant orders
Tetrapod co-macroevolution: primary radiation of herbivorous reptiles
Gymnosperm history: largely an effect of the development of four distinctive floral kingdoms across Pangaea: with the appearance of three new families of derived Voltzialean pinopsids in Eurasia, the Gigantopteridaceae in Cathaysia; and two new families of Ottokariopsida in Gondwana

P/Tr Extinction P(endROA–endCHN)

Rate: steep stepwise

*Magnitude (*families): extinctions 12; nett loss 10

Duration: 4 stages (17 my)

Family/order concordance: parallel-convergent, merging at 3 families and 3 orders at end-Changhsingian

Order/class concordance: parallel-convergent, merging at 3 orders and 3 classes at end-Changhsingian

Causes: excessive rapid global warming and concurrent decrease in atmospheric O_2 levels

Insect co-macroevolution: most profound turnover in insect history

Tetrapod co-macroevolution: profound turnover in major groups of amphibians and reptiles

Gymnosperm history: extinction of profound severity, with 2 classes (Lyginopteridopsida and Ottokariopida) disappearing altogether, and the remaining 3 classes (Pinopsida, Cycadopsida and Ginkgopsida) being decimated with only 1 family observed to survive in each

Continued Late Palaeozoic radiation

Family level diversity (per stage) ranges quite widely from a high of 14 (Asselian) to a low of seven (Changhsingian), with a significant number of appearances and terminations throughout the period.

Palaeotropics; change to hothouse conditions

In the western palaeotropics, some refugial wetland communities were still present at the start of the Permian but they disappeared by the end of the Asselian as the entire area suffered aridification. Through most of the rest of the Permian, these western areas favoured mainly low diversity assemblages of voltzialean conifers, probably similar to the vegetation growing in the tropical uplands during the Pennsylvanian. During the Permian, these voltzialean conifers underwent a minor macroevolutionary radiation.

Wetland plant communities continued to flourish in the eastern palaeotropics, where initially they were similar to the vegetation seen in the western palaeotropical wetlands in the Pennsylvanian, and included a number of the same gymnosperm families. However, towards the end of the Asselian these typically Pennsylvanian gymnosperm families became extinct, and through the rest of the Permian new families started to appear (Emplectopteridaceae, Gigantopteridaceae), or proliferate (Phasmatocycadaceae), giving the Cathaysian Floras a distinctive composition. It is quite possible that at least some of these families would have also flourished in the western palaeotropics if the wetlands there had not dried out. Significantly, plants that closely resemble these Cathaysian gymnosperms appear briefly in North America during the Middle Permian, in habitats that are clearly not wetlands, although no evidence of their reproductive structures is preserved to confirm that they truly are the same families as the Cathaysian plants.

Northern middle & high latitudes; change to hothouse conditions

There was a significant increase in plant productivity during this time in the northern middle and high latitudes, with considerable production of coal-forming peat. There was also a significant increase in latitudinal provincialism in northern hemisphere vegetation. In the high and northern-middle latitudes, the forests were dominated by the Cordaitanthales, with some examples of Peltaspermales and rare conifers (?Voltziales). Moving south, however, the Peltaspermales become more abundant, especially in the Tatarina Floras of Pechora (Gomankov & Meyen 1986). Further south again, in the southern-middle latitudes, the Kazakhstanian forests, conifers become abundant (Meyen 1997). Despite the abundance and species diversity in these northern middle and high latitudes, however, there is little evidence currently available of any significant macroevolutionary change taking place.

Southern middle & high latitudes; change to hothouse conditions

Permian vegetation in Gondwana is characterised by large areas of glossopterid (Ottokariales) forest. The most widely found fossils of these trees are of the foliage, and these represent a relatively small number of leaf architectures. However, evidence of reproductive structures has shown that several distinct families were in fact present, and that the glossopterids had undergone a moderate gradual macroevolutionary radiation during the Period.

The appearance of the glossopterid forests is conventionally taken to mark the start of the Permian Period in Gondwana, although there is little independent evidence to support this. The earliest glossopterids may in fact be Gzhelian in age (Wagner 1980), and the appearance of glossopterid fossils is probably an index to the retreat of the glacial ice from a particular area and not when it occurred. Nevertheless, glossopterid forests seem to have become remarkably widespread across Gondwana by the Sakmarian, even at very high palaeolatitudes, suggesting that there was little or no ice cover at the south pole for most of the Permian. In many areas, these forests generated thick coal-forming peat that is now of major economic importance. As in the northern middle and high latitudes, the peat was mainly the product of woody trees, which were slow-growing relative to the arborescent lycophytes of the Carboniferous palaeotropical forests. However, together with the northern hemisphere forests they will have covered a much larger area than those of the Carboniferous palaeotropics and will have represented a significant carbon-sink.

Morphological innovations

Despite the taxonomic radiation that took place during the Permian, there were remarkably few morphological innovations; it would seem that most of the morphological motifs for organs had already evolved by the end of the Carboniferous.

The range of ovulate structures remained essentially similar to that seen in the Carboniferous. The Emplectopteridaceae had them attached singly to vegetative fronds. More typical, however, was for the ovules to be borne in clusters (polysperms), which were directly attached to fertile leaves (glossopterids) or formed into loose strobilate structures (Peltaspermales).

In the Pinopsida, these fertile clusters were becoming more compact and more like individual strobili.

Although some compound fronds similar to those found in the Carboniferous Lyginopteridales and Medullosales occur, gymnosperm leaves were generally smaller in the Permian, often consisting of undivided leaves. Venation was sometimes dichotomous or pinnate, but there was an increased prevalence of anastomosed veining. The Emplectopteridaceae were the first family to develop veining with several orders of anastomosis, but the norm continued to be leaves with only one order of meshing (e.g. glossopterids).

End-Permian Extinction

At the end-Permian Extinction a profound disjunction occurs, with the early pinopsids (Laurasian) and the glossopterids (Gondwanan) disappearing from the record. With only three families in three classes, the Voltziaceae (Pinopsida), the Cycadaceae (Cycadopsida) and the Peltaspermaceae (Ginkgoopsida) known to survive the boundary, it is remarkable how close the seed-bearing plants came to permanent oblivion at this greatest of extinction events.

Gymnosperms in the Permian-Triassic extinction-recovery process

[Contributor: Wang Ziqiang]

The Permian-Triassic (P/Tr) boundary extinction was part of a long-term, full collapse-recovery cycle in both marine and terrestrial ecosystems, spanning about 30 my (Visscher *et al*. 1996; Hallam & Wignall 1997; Looy *et al*. 1999). In terrestrial ecosystems, the process had its beginning in the Stephanian, with the rapid dieback of the Carboniferous forests that coincided with the onset of an interval of global warming. This was followed by a diachronous Permian gymnosperm radiation (i.e. the so-called Palaeophytic-Mesophytic Transition).

At least two large-scale, abrupt biotic crises occurred towards the end of the Permian. The first occurred during the Capitanian, but this had relatively little effect on gymnosperms compared with other coeval land biotas (e.g. vertebrates and insects). There was a drop in diversity among the ancient Carboniferous gymnosperms (Erwin 1994), but conifers, peltasperms and cycads flourished in the Northern Hemisphere, and glossopterids in the Southern Hemisphere. In North China, there was a wide diversity of peltasperm foliage morphology (e.g. *Neuropteridium, Callipteris, Comia, Supaia, Lepidopteris, Protoblechnum*); and the cycads comprise *Primocycas, Cladotaeniopteris, Pterophyllum,* and *Nilssonia,* which may all represent natural taxa at generic or family level (Wang &

Zhang 1998). Among the conifers found in North China, many also occur in the Upper Permian Zechstein in Europe, suggesting their high diversity.

However, the end-Changhsingian (end-Permian) mass extinction, generally regarded as the most profound global biotic crisis in Earth history, had a much more dramatic impact on terrestrial vegetation. It was closely accompanied by a series of other biogenic events: a global fungal event (Visscher *et al*. 1996), a global biotic dead-zone above the P/Tr boundary (Looy *et al*. 2001), and a coal gap representing *ca* 10 my. It also coincided with a negative δ13C spike indicating extreme warming in global climate (Wang *et al*. 1994; De Wit *et al*. 2002) and the Siberia Trap volcanism (Renne & Basu 1991; Retallack *et al*. 1996).

Many Permian gymnosperm groups failed to extend into the Triassic Period, including the 'ancient' pteridosperms, cordaites, gigantopterids and glossopterids, while many other groups suffered a reduced diversity and richness. On the other hand, some Permian conifers, peltasperms, and cycads did apparently survive the event in the Northern Hemisphere. For instance, Schweitzer (1996) has shown that the seed-scale complex of the Zechstein conifer *Pseudovoltzia* is essentially the same as that of the Early Triassic *Voltzia*. In North China, many large peltate discs of *Peltaspermum* occur in the Lower Triassic in association with *Pleuromeia*, an index fossil unique to the Lower Triassic (Wang & Wang 1989). Significantly, these taxa all had large seeds enclosed by a thick, strongly sclerified or lignified seed-coat (Schweitzer 1963; Wang 2000), which may have enhanced their ability to survive periods of severe environmental conditions and perhaps to survive long-distance transportation. Also, many other Early Triassic gymnosperms had leaves very similar to the Permian glossopterids (e.g. *Neoglossopteris*—Wang 1996, pl. 2), and whether this was due to convergence or vestigial relicts of Permian gymnosperms is difficult to say.

Insect associations [Contributor: C.C. Labandeira]

Appearance of the major extant orders of insect

A third pulse in the primary radiation of the insects coincides closely with the third pulse in the primary radiation of the gymnosperms. The Late Palaeozoic history of the insects runs, as might be anticipated, parallel with that of the gymnosperms. Of particular significance in this Permian pulse is the earliest diversification of several prime extant orders: the herbivorous Orthoptera (crickets, grasshoppers), Hemiptera (cicadas, aphids etc.) and Coleoptera (beetles); the carnivorous Neuroptera (lacewings) and carrion-feeding Mecoptera (scorpionflies).

Herbivory goes global

During Early Permian (Artinskian) times, there is evidence for significant insect herbivory that evolved outside the earlier Pennsylvanian equatorial coal swamps of Euramerica. These studies mostly originate from mesic riparian floras. One study from a gigantopterid-dominated flora from north-central Texas (Beck & Labandeira 1998), shows that total values for the surface area of insect-mediated damage and leaf-attack frequency were at levels about half that from modern tropical floras. An interesting feature is the preferential targeting of particular plant hosts (gigantopterids) for consumption by insects, and the relative paucity of consumption of other host taxa (cycadophytes, sphenophytes)—a conclusion borne out in a mid-Permian gigantopterid flora from China (Glasspool *et al.* 2004). Studies from the Late Permian of the Karoo Basin in South Africa (Plumstead 1963; Zavada & Mentis 1992) and other Gondwanan localities (Srivastava 1987; Guerra-Sommer 1995; Holmes 1995) indicate similar resource use for geographically disparate glossopterid-dominated floras. Recently, several examinations of the gut contents of insects from Eurasia have revealed an extensive syndrome of pollinivory by several clades of mid-Permian (Kungurian) insects, including hypoperlids, grylloblattodeans, and psocopterans, indicating that particular gymnospermous taxa, such as cordaites, gnetaleans, glossopterids, and others were being used as food sources (Rasnitsyn & Krassilov 1996; Krassilov & Rasnitsyn 1997).

Less is known for Late Permian plant-insect interactions, other than emerging evidence that glossopterid-dominated floras were similarly targeted by external foliage feeders and also acted as substrates for oviposition by dragonflies. With the possible exception of wood borings (Zavada & Mentis 1992; Weaver *et al.* 1997), curiously there is little evidence for endophytic use of plant tissues throughout the Permian, such as those found in the Late Pennsylvanian of equatorial Euramerica and the Late Triassic of the high-latitude Karoo Basin of Gondwanaland.

Tetrapod co-macroevolutionary patterns

Tetrapod herbivory comes to maturity

A recurring pattern revealed in the macroevolution of the reptilean tetrapods (Chart 10, p. 45) is that in each successive major clade—stem reptiles, pelycosaurs, therapsids, thecodonts/dinosaurs—the pioneers are small carnivorous (or insectivorous) forms. In their subsequent primary radiations appear the herbivores that become dominant in numbers and biomass. It is in the Permian that this pattern becomes clearly and repetitively evident. Here we witness the first explosive appearance of the herbivorous (and omnivorous) reptilean tetrapods: the captorhinids (primitive stem reptiles) and the edaphosaurids and caseids (pelycosaurs), in the Early to mid-Permian; and the procolophonids, pareiasaurs (anapsids) and the dicynodonts (therapsids), in the mid- to Late Permian.

Through the first half of the Permian, the history of tetrapod vertebrate evolution is still found preserved almost exclusively within the tropical Laurasian Kingdom. The focus then shifts strongly through the upper half of the period to Gondwana, and particularly the richly fossiliferous Karoo Basin of South Africa (Anderson & Cruickshank 1978). And it is in the glossopterid-dominated southern temperate kingdom that vertebrate herbivory is seen to come to maturity within the therapsids (mammal-like reptiles). Further, the first fully established terrestrial ecosystems originated in the co-radiation of the plants (glossopterids), insects (hemipterids) and tetrapods (therapsids) as reflected in Gondwana (Tiffney 1992; And. & And. 1993; Anderson *et al*. 1999).

TRIASSIC:
Heyday of gymnosperm biodiversity

Plate tectonics & global physiology

Pangaea swivels anticlockwise

The united supercontinent continues swivelling anticlockwise through into the mid- to Late Triassic when it extends from the North to the South Poles. Thereafter, through the later Triassic into the Early Jurassic, Pangaea drifts northwards, with Angara now straddling the North Pole, and Gondwana well north of the South Pole. Rift valleys pre-empting the break-up of Pangaea—such as that between the eastern seaboard of the 'USA' and 'North Africa'—appear in the Late Triassic.

Hothouse world

The Triassic sees the start of an enduring 185 Ma hothouse world lasting (with a possible lapse at the J/K boundary) throughout the Mesozoic. Details for the Triassic vary, depending on whose graph one follows (Chart 2, p. 37): with a record super-hothouse peak, for instance, occurring just prior to the P/Tr boundary (Frakes 1992, Scotese *et al*. 1999), or astride the Carnian in the Late Triassic (Anderson *et al*. 1999). This becomes highly significant when considering phytogeographic aspects of the gymnosperm diversity curve and heyday (see below).

Both precipitation and atmospheric oxygen levels are judged to have dipped to levels significantly below extant figures during the Triassic. If the Earth-physiology curves (Chart 2) are a reasonable reflection of reality, then the world in which we witness the Triassic explosion in biological innovation—with temperatures at an all-time high and precipitation and oxygen levels nearing Phanerozoic lows—was distinctly unfamiliar with respect to today.

Floral kingdoms: three distinctive kingdoms recognised

Angara (north temperate): Characterised by Leptostrobales, *Sphenobaiera*, Caytoniales (exclusive to Angara); Bennettitales absent.

Laurasia (tropical): Pinopsida dominant; Caytoniales absent.

Gondwana (south temperate): Umkomasiales (*Dicroidium* foliage) dominant. Like the glossopterids in the Permian, so the Umkomasiales were overwhelmingly dominant, in abundance and diversity, in the Gondwana Triassic.

Megafloral occurrences, key sequences

Angara: Well-preserved floras (if not too thoroughly known) appear to occur throughout the Triassic.

Laurasia: While the Lower Triassic is essentially barren throughout Euramerica, the Middle and Upper Triassic are well represented through a scatter of horizons: from the excellently sampled Gres à Voltzia (Anisian, France) to the well known Chinle and Newark floras (Carnian, USA), to the Rhaetian floras of Scoresby Sound (Greenland) and Scania (Sweden). Further east in Laurasia, a full sequence of good floras is recorded throughout the Triassic in China and through the latter half of the period in Japan.

Gondwana: As in Euramerica, the occurrence and quality of megafloras in Gondwana improves markedly up through the Triassic. The most complete sequence of floras through the period is certainly that in eastern Australia; the richest and most fully sampled of floras is that of the Molteno Fm. (Carnian) of South Africa; and the most celebrated petrified floras those of the Trans-antarctic Mountains (Ladinian/Carnian).

Considering sampling bias

Though the Molteno (Carnian) has been extensively (localities) and intensively (specimens) collected to an unusual degree, and has yielded record diversity, sampling bias seems unlikely to prove the explanation for the marked Triassic 'heyday'. The Triassic globally, if anything, is relatively poorly represented by floras and (with exceptions) these have been under-studied (see correlation Charts 11–20, pp 46–55). In contrast, the Carboniferous Coal Measures of Laurasia are extensive and have been intensively studied. The Permian Coal Measures across Gondwana are likewise prolific and have gained particular attention. While the Jurassic is not over-abundantly fossiliferous (megafloras), certain floras—Scania in Sweden (lowest Jurassic), the Yorkshire Jurassic floras (mid-Jurassic) and others—have become especially famous for the focus of research devoted to them. Cretaceous floras are also unusually well known in view of the search for angiosperm origins, their history at the K/T boundary, and their subsequent radiation. Lastly, because of their relevance to understanding extant floras and mammal diversification, the Tertiary floras have likewise received particular attention.

Late Triassic correlation (resolving the Tr/J Extinction)

As for the P/Tr boundary, the correlation of terrestrial beds through the Late Triassic and Early Jurassic remains insecure: any discussion of the sequence of events characterising this interval has to be considered in this light. The critical strata are those of the Norian and Rhaetian (or more broadly from the Carnian through to the Hettangian).

Biodiversity patterns

Family-level diversity

Late: total 33; originations 20; extinctions 22; nett loss 2
Middle: total 15; originations 8; extinctions 1; nett gain 7
Early: total 6; originations 3; extinctions 0; nett gain 3
Overall: total 36; originations 33; extinctions 23; nett gain 10

Secondary Radiation, Tr(IND–CRN)

Rate: exponential explosive
Magnitude (families): originations 28; extinctions 1; nett gain 27
Duration: 5 stages (34 my)
Family/order concordance: concordant divergent
Order/class concordance: concordant divergent
Cause: massive niche vacation after P/Tr Extinction
Insect co-macroevolution: emergence of pollinating insect orders
Tetrapod co-macroevolution: explosive radiation, closely parallels gymnosperm radiation; therapsid (mammal-like reptile)-dinosaur turnover
Gymnosperm history: of the three phases of gymnosperm radiation, that of the Triassic is by far the most dramatic: it is the most explosive, the greatest in magnitude, and of relatively short duration.

Tr/J Extinction, Tr(endCRN)–J(endHET)

Rate: catastrophic reverse-exponential
Magnitude (families): extinctions 24; nett loss 14
Duration: 3 stages (20 my)
Family/order concordance: concordant parallel
Order/class concordance: concordant convergent
Causes: successive bolide impacts
Insect co-macroevolution: no macroevolutionary evidence of extinction; post-Permian radiation continues
Tetrapod co-macroevolution: therapsid (mammal-like reptile)-dinosaur turnover continues
Gymnosperm history: the Tr/J Extinction (nett loss 15 families) has the greatest magnitude of the three such events pruning gymnosperm lineages; it far exceeds that of the P/Tr Extinction (nett loss 10 families).

Explosive radiation

Whereas the Carboniferous radiation of the gymnosperms occurred essentially along the Laurasian tropical belt, that of the Triassic appears to have been more notably emphasised in the temperate latitudes of Gondwana.

From nadir to heyday

Following current sampling and taxonomic understanding, the Triassic is highly distinctive as regards gymnosperm biodiversity at family, order and class rank. It witnesses both the nadir (3 families in the Induan, after the end Permian Extinction) and the heyday (30 families in the Carnian) of gymnosperm diversity.

In the 34 my from the Induan to the Carnian, it shows an explosive radiation of new taxa at these higher ranks far outstripping anything else in gymnosperm history. The initial radiation of the gymnosperms by comparison, from a single family in the Famennian (latest Devonian) to 14 families in the Asselian (earliest Permian), covers an interval of 80 my.

This Triassic diversification includes the initial radiation of the Pinales (with four of the six extant families appearing), the greatest spread within the ginkgoopsids (10 new families), the initial radiation within the bennettiopsids (eight new families) and the gnetopsids (four new families) and the axelrodiopsids (two new families).

If we plot the diversity at epoch rather than stage resolution (dividing the systems for convenience and consistency into three roughly equal, lower, middle and upper divisions), then the biodiversity peak in the Triassic shows up even more dramatically (Fig. 1, p. 5).

Pruning the heyday

Equally dramatic is the number of family-level terminations that occur within the Late Triassic. These amount to no less than 22 losses from the Carnian to Rhaetian. Numerous families and many orders of gymnosperm had no sooner appeared in the Triassic radiation than they were eliminated again in the Late Triassic Extinction(s). Over a similar interval in the Late Permian (end-Roadian to end-Changhsingian), there are in contrast only 10 family-level losses—and this through the most cataclysmic of the five global extinction events.

Microevolutionary explosion (species diversity)

In view of the comprehensive sampling (27 000 catalogued slabs) from 100 taphocoenoses, the Molteno Fm. (Carnian, Karoo Basin, South Africa) has provided the opportunity to explore the question of species level diversity—observed, preserved and existed—at the acme of the explosive radiation of biodiversity in the Triassic. A full taxonomic overview of the Molteno vegetative taxa (bryophyte, pteridophyte and gymnosperm) reveals an observed tally of 206 species. This is the tip of the iceberg when considering the preserved (statistically calculated at 667 species) and existed (conservatively estimated at 2 000 species) tallies. From these studies we suggested that species-level floral diversity at the gymnosperm heyday may have been akin to that of today (And. & And. 1995, 2003; And. *et al.* 1996). Roughly one half of the total species diversity was gymnospermous.

Laws of biodiversity

These laws (pp 70, 71) explain biodiversity patterns in the extant icehouse world with marked climatic and vegetation zonation from poles to equator, but do they hold for the Mesozoic hothouse world (And. *et al*. 1999; And. & And. 2003)? Although more robust analysis of existing data—levels of sampling, reliability of correlations, taxonomic consistency, biomes and habitats—is required, current assessment of the known Late Triassic floras suggests otherwise. It appears that diversity at middle latitudes (e.g. Molteno Fm. of South Africa), was greater than that within the tropics (e.g. Chinle, Newark and Dockum formations of the USA). Solar energy may well have been excessive at low latitude under hothouse conditions, while optimal at mid-latitudes.

The greater the extinction, the greater the radiation

A further law of biodiversity is added: evidence suggests (And. *et al*. 1999; And. & And. 2003) that 'the greater the extinction, the greater the radiation'. This is borne out by the gymnosperms. Their explosive radiation to their heyday follows the end-Permian Extinction, generally agreed to be the greatest of all extinction events. If at species level, the gymnosperms reached a richness akin to the angiosperms today; at class and order level they evidently reached a peak of diversity of significantly greater proportion.

Gymnosperm biodiversity at their heyday

For expanded discussion of the Triassic Explosion, see pp 22–31.

Angiosperms: 1. The carpel

Origin of the stem-angiosperms

Theories relating to angiosperm origins abound, yet the solution remains elusive. The rise of cladistics—embracing morphological characters (extant and fossil) and, more recently, molecular characters—has added greatly to the rigour of the debate, but has not resolved the enigma (see, for instance, Doyle & Donoghue 1993; Doyle *et al*. 1994; Doyle 1996, 1998a, 1998b, 1999, 2001; Angiosperm Phylogeny Group, 1998, 2003; Friis *et al.* 1999, 2000). From our perspective, the most compelling hypothesis to date is that of Stuessy (2004), referred to as the transitional-combinational theory. He suggests three fundamental transitions—the serial acquisition of the three definitive angiosperm characters—as the 'angiosperms evolved slowly from seed ferns in the Jurassic beginning first with the carpel, followed later by double fertilization, and lastly by the appearance of flowers.' Stuessy looks to the well-known 'seed ferns', in particular the Corystomales (our Umkomasiales) and the Caytoniales of the Triassic and Jurassic, as the known fossils with structures that emulate carpels.

Recently, in And. & And. (2003), we described a new 'seed-fern' whole-plant genus and family, *Kannaskoppia/Kannaskoppifolia* (Kannaskoppiaceae, p. 185 this volume), reminiscent of *Caytonia* (Caytoniaceae, p. 183 this volume), which adds to the early Mesozoic group from which the angiosperm carpel may have derived. The first appearance of the Caytoniaceae is perhaps as early as the Carnian, while that of the Kannaskoppiaceae is still earlier, by some 20 my, in the mid-Olenekian—both well down in the Triassic. We suggested in the 2003 work (see also Anderson 1999) that the stem-angiosperms (as did the stem-mammals) evolved within the Triassic explosion of diversity, and reiterate that view here.

Insect associations [Contributor: C.C. Labandeira]

Appearance of the major pollinator orders

One of the most momentous, long-enduring consequences of the gymnospermous explosion in the Triassic is the first appearance or significant diversification of the major pollinator orders. The Coleoptera (beetles) radiate to great diversity, at least in Gondwana, in the Late Triassic; the Diptera (flies) first appear in significant numbers; the Trichoptera (caddisflies), sister group to the Lepidoptera (moths and butterflies), appear for the first time in the fossil record; as do the Hymenoptera (wasps, ants and bees). Considering the disappearances in the P/Tr Extinction and the new appearances in the Triassic, the spectrum of orders in this period takes on, for the first time, a modern appearance.

Peak richness and diversity

Four principal areas—SW United States, Western Europe, Eastern Australia and South Africa—have provided insights into the extent by insects of plant-host use following the devastating end-Permian mass extinction. In all instances both the plant hosts and the insect herbivores represent taxa different from those occurring during the Pennsylvanian and Permian, although the associations (boring, galling, piercing-and-sucking, external foliage feeding, palynivory) remained the same. The only exception is leaf mining, which first appears during the early Late Triassic of South Africa (Scott *et al.* 2004), but may have an earlier origin in the Middle Triassic of Kazakhstan (Zherikhin 2002). Of the four areas, the Late Triassic (Carnian) has provided the most diverse and abundant evidence for plant-insect associations, supplemented by data from Arizona, USA (Walker 1938; Ash 1997, 1999, 2000; Creber & Ash 2004), Western Europe (Kelber 1988; Grauvogel-Stamm & Kelber 1996), and eastern Australia (Tillyard 1922; Rozefelds & Sobbe 1987; Holmes 1995). Collectively these late mid-Triassic (Anisian) to early Late Triassic (Carnian) biotas provide evidence for significant external feeding on leaves, borings in conifer wood, galls on a variety of gymnosperms, leaf-mining on *Heidiphyllum* leaves, and a variety of hosts for dragonfly oviposition.

Most spectacular is the material from the Molteno Fm. of the Karoo Basin of South Africa. From an exceptionally diverse assemblage of pteridophyte and gymnospermous plant hosts, a modern-aspect suite of plant-insect associations was developed on a variety of tissues. Many of these associations are specific to particular plant-host species, and presumably were targeting particular tissues. Among leaf miners, which probably represent the activity of beetles, at least four leaf-mine types are known, based on patterns of frass structure, size and geometry of the mines, and terminal chamber development. Several plant hosts are documented for Molteno leaf miners, most notably the broad-leaved conifer *Heidiphyllum* (And. & And. 1989; Scott *et al*. 2004), representing most of the major clades of seed plants, as well as two species of ferns. Like leaf miners, gallers also had host specific associations, especially on the peltasperm *Dicroidium.* Piercing-and-sucking evidence is present as scale-insect impressions on leaves, and minute punctures are evident on various plant species. Additionally, piercing-and-sucking and mandibulate insects were involved in seed predation. External consumption of the margins of leaves, as well as hole-feeding, skeletonisation and surface abrasion is diverse, and in several instances constitute repeated, stereotyped damage patterns on particular hosts. More than one type of seed predation is also present. Lastly, a diversity of ovipositional damage is present, mostly attributable to damselfly emplacement of eggs in plant tissues such as midribs or medially located pseudoveins on leaves. In summary, Molteno plant-insect associations overall are as rich and diverse as any similarly examined angiosperm-dominated flora in the fossil record.

Tetrapod co-macroevolution

Turnover from the mammal-like reptiles to the dinosaurs

The T/J extinction interval, so profound in gymnosperm history, is reflected closely in the tumultuous history of the tetrapods through the same time span. The interval begins with the catastrophic decline of the mammal-like reptiles and the concordant explosive primary radiation of the dinosaurs. It continues through the 20 my span with successive extinctions and originations of dinosaurian and thecodont-derived groups. The catastrophic extinction of the prosauropods—the first group of outsized herbivorous dinosaurs—in the Sinemurian, is its culmination.

JURASSIC:
A decimated maturity

Plate tectonics & global physiology

Pangaea fractures

Fragmentation of Pangaea (Chart 1, p. 36) is initiated in the earliest Jurassic (pre-empted by rift-valley development in the Late Triassic). Associated with this occurred major flood basalts at various stages through the Jurassic and Cretaceous. This, in turn, undoubtedly had a major effect on the macroevolution of the dinosaurs, but apparently far less so on that of the gymnosperms.

A renewed clockwise swivel of the supercontinent occurs; and most evident later in the period occurs the separation of Gondwana from Euramerica and of eastern Gondwana from western Gondwana.

Continuing hothouse world

Hothouse conditions attained in the Triassic continued through the Jurassic—with a possible dip to semi-icehouse conditions at the J/K boundary (Chart 2, p. 37).

Global precipitation declined steadily through the Jurassic to a Phanerozoic low which was to persist through the Early Cretaceous, while oxygen levels, after an Early Jurassic low, rose to *ca* 23% (akin to today).

Floral kingdoms: three kingdoms recognised

In the wake of Fourth Extinction and in the Jurassic hothouse world, the distinction into floral kingdoms, in contrast to the Permian and Triassic, is relatively weakly emphasised.

Angara (northern high-latitude): Abundant Ginkgoopsida, especially Leptostrobales; Bennettitales rare except in Late Jurassic; Cheirolepidiales rare as macrofossils in the Early and Middle Jurassic (though pollen is sometimes abundant), but become more abundant in the Late Jurassic.

Laurasia (tropical): Abundant Bennettitales, Cycadales, Ginkgoales (Ginkgoaceae), Pinales (Pinaceae, Taxodiaceae) and Cheirolepidiales; Leptostrobales and Peltaspermales are present but on the whole uncommon.

Gondwana (southern high-latitude): Characterised by the dominance of the Pentoxylales (absent in Laurasia).

Megafloral occurrences, key sequences

Angara: In contrast to Laurasia and Gondwana, the Jurassic of Angara appears particularly well represented through the period, especially in 'W & SW USSR' (the western Siberian Plain, Kazakhstan and Kuznetsk).

Laurasia: In the eastern sector of Laurasia, a succession of intermediate quality megafloras (in discreet formations through the Lower and most of the Middle Jurassic) occurs in northern China and to a lesser extent in southern China. The high quality Tetori Early of Japan is considered to cross the J/K boundary.

In the Euramerican sector, Scoresby Sound (E. Greenland) and Scania (southern Sweden) in the lowest Jurassic, Yorkshire floras in the mid-Jurassic, and the Isêre floras (France) and Solenhofen (Germany) through the Late Jurassic, are the top quality megafloras.

Gondwana: The southern continents are relatively poorly represented in the Jurassic. The fullest sequence is certainly that in Queensland, with the best floras in the Marburg Gp. (Toarcian to Aalenian) and the Walloon Coal Measures (Callovian to Oxfordian).

Biodiversity & macroevolutionary patterns

Family-level diversity

Late: total 18; originations 2; extinctions 0; nett gain 2
Mid: total 19; originations 2; extinctions 3; nett loss 1
Early: total 19; originations 5; extinctions 2; nett gain 3
Overall: total 23; originations 9; extinctions 5; nett gain 4

Ultimate Radiation: J(SIN)–K(APT)

Rate: gradual stepwise
Magnitude (families): originations 10; nett gain 7
Duration: 15 stages (85 my)
Family/order concordance: concordant parallel-divergent
Order/class concordance: discordant
Cause: niche vacation through Tr/J Extinction
Insect co-macroevolution: continued radiation of pollinating insect orders
Tetrapod co-macroevolution: continued radiation of herbivorous dinosaurs
Gymnosperm history: of the three gymnosperm radiations, this is the last, the most gradual and the longest enduring, but in magnitude it is only a little greater than that of the lower half of the Permian.

K/T Extinction: K(endAPT–endCMP)

Rate: gradual stepwise
Magnitude (families): extinctions 10; nett loss 10
Duration: 6 stages (41 my)
Family/order concordance: concordant parallel
Order/class concordance: discordant convergent
Cause: competitive displacement through angiosperm radiation
Insect co-macroevolution: no apparent influence on insect macroevolution
Tetrapod co-macroevolution: concordant decline of certain herbivorous dinosaur clades
Gymnosperm history: this last occurring extinction event in the macroevolutionary life cycle of the gymnosperms is remarkable for the closely parallel nature of the decline of families and orders. With a duration of 41 my, this is the longest-running of the three gymnosperm extinction events. The end-Cretaceous Extinction (end Maastrichtian) remarkably sees no family extinctions—the 10 terminations having occurred stepwise from the end Aptian to end Campanian.

Into maturity

In regard to overall family-level (gymnosperm) diversity, the figures for the Jurassic are fairly steady, fluctuating between 16 and 19 families throughout. Overall, there is a nett gain of four families (nine originations and five extinctions). The principal originations are amongst the Pinales (Sciadopityaceae and Taxaceae), Ginkgoales (Karkeniaceae, Yimaiaceae and Schmeissneriaceae) and the Bennettitopsida (Williamsoniaceae, Cycadeoidaceae and Pentoxylaceae). Indeed, the Bennettitopsida underwent a secondary, moderate and stepwise radiation during the Jurassic, becoming the most dominant (abundant) group during this interval—at least in Gondwana.

Biodiversity gradient towards mid-latitudes

Do we observe the same diversity increase towards mid-latitudes in the Jurassic hothouse world as is apparent in the Late Triassic? Are the middle Jurassic floras of Angara (Kugitangau, Darwaz and E Fergana of the USSR) and Gondwana (Marburg Gp. and Walloon CM of Queensland) more diverse than those of Laurasia (Yorkshire in the west, or various formations of northern China to the east)? As far we are aware, no attempt has been made to test such a hypothesis, but good floras are available for study and the analysis could be most revealing.

Across the J/K boundary

There is an unbroken transition at the J/K boundary, with no recorded macroevolutionary extinctions or originations.

Angiosperms: 2. Double fertilisation

Evolution of the stem-angiosperms

Double fertilisation is the second of the three defining characters of the angiosperms. In the transitional-combinational theory of flowering-plant origins (Stuessy 2004), this complex adaptation is considered to have evolved gradually over a considerable interval, presumably throughout the Jurassic. The fossil record does not reflect anything of this evolutionary breakthrough.

Flowers, the third critical development defining angiosperms, are first reportedly seen in *Archaefructus* in the new basal angiosperm family Archaefructaceae (Sun Ge *et al*. 1998, Sun Ge *et al*. 2001, Sun Ge *et al*. 2002). While this critical fossil from the lower part of the Yixian Fm. (i.e. Jianshangou Bed or Fm.) of northeast China was formally placed in the latest Jurassic (Tithonian, 146–151 Ma), the strata are now thought to be more probably Early Cretaceous (Barremian, 125–130 Ma) in age (Dilcher 2004, pers. comm.).

Insect associations [Contributor: C.C. Labandeira]

Expansion of pollinators

The most compelling characteristic of insect evolution through the Jurassic concerns the major pollinator orders. Though they appeared earlier in the Triassic and Permian, respectively, the Hymenoptera (wasps, ants and bees) and the Diptera (flies) undergo primary, major, stepwise family-level radiations through the period. The Lepidoptera (moths and butterflies) appear in the early Jurassic, but radiate only in the Cretaceous; the Coleoptera (beetles) continue their Triassic radiation throughout the Mesozoic and beyond. This highly significant phase in insect history occurred prior to the emergence and radiation of the angiosperms and is ecologically linked to an intensive radiation of parasitoid life-habits in mid-level clades of the Diptera and Hymenoptera (Labandeira 2002b). It is intimately linked in many instances with the major prevailing gymnospermous orders: the Pinales, Cheirolepidiaceae, Cycadales, Ginkgoales, Caytoniales, Bennettitales and Pentoxylales. Pollination, so crucial in angiosperm history and ecology, is a strategy forged in the diversifying world of the gymnosperms.

Possible decline in richness

Of all the geologic periods examined from the Late Carboniferous to the Recent, the Jurassic is the least known in terms of plant-insect associations. This is attributable partly to poorly preserved plant fossils and minimal study in much of the world. No comprehensive study of plant-insect interactions exists for any Jurassic flora, and the possibility that the Jurassic represents a depauperate level of associational diversity cannot be ruled out (Scott *et al.* 2004). However, there are glimpses into specific associations that may represent a continuation into the Northern Hemisphere of the later Triassic elevated level of associations that was pronounced especially in southern Gondwana. Examples of Jurassic plant-insect associations are few in number and highly scattered throughout the period and across the continents but represent the broad spectrum of all functional feeding groups (Labandeira 1998d). With regard to external foliage feeding, there is very limited evidence for insect consumption. Examples include plant damage on cycadophyte foliage (Scott & Paterson 1984), and gut contents from grasshoppers of the Middle to Late Jurassic at Karatau, Kazakhstan, have provided an alternative approach for establishing herbivory of foliage (Rasnitsyn & Krassilov 2000). Similarly, there are few examples of boring into wood, such as the conifer *Protocupressinoxylon* from the Middle Jurassic of northern China (Zhou & Zhang 1989), and the enigmatic gymnosperm *Hermanophyton* from the western USA (Tidwell & Ash 1990). Galling is equally limited; one of the few examples is *Wonnacottia* galls on a bennettitalean leaf (Alvin *et al.* 1967). The single demonstrable case of leaf mining is from the Jurassic-Cretaceous boundary interval of northern Queensland, Australia, where lepidopteran-like serpentine leaf mines are recorded from corystosperm leaves assigned to *Pachypteris* (Rozefelds 1988), presaging the greater diversity on mid-Cretaceous angiosperms (Kozlov 1988; Labandeira *et al.* 1994). These single cases paint a picture of limited host-plant use but the probability is of more widespread diversity of herbivore associations, provided sufficiently diverse floras are examined comprehensively.

Significant contributions toward understanding the interrelationships of Jurassic seed plants and orthopteroid and especially holometabolous insects have been made by examining insect gut contents and mouthpart structure, as well as the reproductive biology and strobilar damage patterns of presumably coexisting plants. The intestines of prophalangopsid grasshoppers (Orthoptera) and sawflies (Hymenoptera) at Karatau have demonstrated the presence of pollinivory on a variety of gymnosperms by mandibulate insects (Krassilov *et al.* 1997). Similarly, surface fluid-feeding insects bearing long proboscides, such as nemestrinid and apiocerid flies (Mostovsky 1998; Ren 1998), exhibit nonpiercing, elongate mouthpart structure for probing into deep, tubular structures for consumption of nutritionally rewarding fluids (Labandeira 2005). In addition, the head and proboscis base of a few Jurassic and Early Cretaceous fly specimens display monospecific clumps of cheirolepidaceous pollen, indicating a pollination mutualism analogous to similar extant angiosperms and holometabolous insects (Labandeira 2005).

Tetrapod co-macroevolutionary patterns

Radiation & dominance of the herbivorous dinosaurs

Herbivorous dinosaurs dominated the Jurassic landscape. Major stepwise to explosive radiations within the Sauropoda and Ornithiscia are a marked feature of the Middle Jurassic—and follow with some delay the catastrophic extinctions of the Prosauropoda and early ornithiscian lineages in the Early Jurassic. The scale and abruptness of these changes is not reflected in the gymnosperms. Where the outpouring of sheet lavas evidently played a major role in dinosaur macroevolution, there appears no such effect on plant evolution. Through their eventful 162 my history, the dinosaurs show particular susceptibility—radiation or extinction—to major environmental disruption.

CRETACEOUS:
Ancillary peak of diversity

Plate tectonics & global physiology

Pangaean fragmentation and drift

Through the 80 my span of the Cretaceous, fragmentation accelerates and continental drift becomes a primary factor in biogeography. By the close of the period, the continents of today's world are readily recognised and are well separated. Africa remained central, not far from its extant position, while the surrounding landmasses drifted essentially radially outwards.

Hothouse world

Following the possible dip in temperature at the J/K boundary, the hothouse conditions of the Mesozoic persisted through to the end of the Cretaceous.

Paired with the elevated global temperatures was an enduring record low in the Phanerozoic precipitation pattern. Interestingly and possibly of notable significance, is the fact that both the heyday and ancillary peaks of gymnosperm diversity occur at times of maximum heat paired with minimal precipitation globally—an observation which appears counter-intuitive with the present world as our model.

The atmospheric oxygen graph, as plotted, shows a steady increase throughout the 80 my period from 23ºC to *ca* 27ºC, i.e. from 1 to 5 degrees in excess of present levels.

Floral kingdoms

In the post-Pangaea hothouse world, a very different configuration of kingdoms unfolds—a transition from the Pangaean to the extant pattern.

Boreal (northern polar latitudes): In the Early Cretaceous, Leptostrobales and ginkgooids remain abundant, but are progressively replaced during the Late Cretaceous by angiosperms; Cycadales, Bennettitales and Pinales locally abundant; Cupressaceae (subfam. Taxodioideae) also abundant.

Laurasia (northern mid-latitudes): Bennettitales, Cycadales, Caytoniales, Cheirolepidiales and Taxodioideae abundant, many with xeromorphic characters; Leptostrobales and ginkgooids rare in Early Cretaceous, becoming extinct in Late Cretaceous.

Palaeotropical: Megafloral record very poor, but palynology indicates abundant Cheirolepidiales.

Australian (southern polar latitudes): Again, it is the Pentoxylales that characterise the kingdom (to the mid-Cretaceous). From the mid-Cretaceous the distinction is less clear.

Megafloral occurrences, key sequences

Gondwana: Cretaceous floras are not abundant in Gondwana. The best Early Cretaceous pre-angiosperm floras are those of southern Argentina (Springhill and Baquero formations), the eastern coastline basins of South Africa (Kirkwood, Mngazana and Makatini formations), the Rajmahal Hills of India (Rajmahal and Sonajori localities), a series of basins in S. Australia, Victoria and Queensland (including several formations), and of the Antarctic Peninsula (Cerro Negro and Triton formations).

Late Cretaceous angiosperm floras of note are still fewer in number. They include occurrences in southern Argentina (Chubut Basin), Botswana (Orapa Diamond Pipe), Victoria and Queensland (Waarre and Winton formations), and again in the Antarctica Peninsula (various formations).

Non-Gondwana & the Early angiosperms: The best non-Gondwana Cretaceous sequences are widely scattered through the northern continents and are most often best known and documented through the quest for the early angiosperms. Cretaceous flowers of Euramerica, many carbonised and preserving remarkable morphological detail, derive mainly from the early Cretaceous (BRM) Torres Bedras Flora of Iberia, the mid-Cretaceous (APT-CEN) Potomac Gp. of the eastern USA, and the later Cretaceous (SAN-CMP) Scania floras of Sweden. The gymnospermous content in these important floras is documented in a spread of references including Watson (1977), Upchurch & Doyle (1981), Vakhrameev (1988) and Srinivasana & Friis (1989).

The earliest reputed angiosperms are those from the excellent Early Cretaceous sequence of China (see box on p. 83).

Floras astride the K/T boundary

Interestingly, there are very few megafloral sequences known to span the K/T boundary. In Gondwana such successions are encountered only in New Zealand (poorly known floras of Taratu and the Pakawan Gp.) and the Antarctic Peninsula (far better floras of the Larsen Basin and Shetland Islands), both along the southern active margin of the supercontinent. In Laurasia, there are again only two relevant successions, the first in the western interior of the USA (good floras from the Hell Creek Fm. and equivalents overlain by the Fort Union Fm.), the second in northern China (the lesser known floras of the Fuyao & Wuyun formations).

What do these floras reveal of gymnosperm fortunes crossing from the Maastrichtian into the lower Palaeocene? Mike Pole (pers. comm., e-mail 9 March 2001, writes for instance, 'The Late Cretaceous floras of New Zealand are characterised by a mixture of angiosperms and conifers—including the Podocarpaceae and a general abundance of Araucariaceae. Some conifer genera crossed the K/T boundary, but perhaps the biggest change is the drop in importance of the Araucariaceae between the Cretaceous and the Palaeocene. This change need not have occurred at the boundary.'

Biodiversity patterns

Family-level diversity

Late: total 15; originations 0; extinctions 3; nett loss 3
Mid: total 23; originations 1; extinctions 7; nett loss 6
Early: total 23; originations 4; extinctions 1; nett gain 3
Overall: total 23; originations 5; extinctions 11; nett loss 6

Gymnosperm-angiosperm concurrent turnover

Gymnosperm diversity patterns through the Cretaceous are intriguing and closely coupled to the rise and radiation of the angiosperms. There occurs a gradual increase from 18 families (nine orders) in the Berriasian to a maximun of 22 families (11 orders) in the Aptian, followed by a progressive decline to 12 families (four orders) in the Maastrichtian. The rise in fortunes of the gymnosperms through the early to mid-Cretaceous—to an ancillary peak of diversity second only to that in the Late Triassic—coincides with the (initially gradual) emergence of the angiosperms. Thereafter occurs the dramatic radiation to dominance of the angiosperms from the end-Aptian to the Turonian with the concurrent decline of the gymnosperms (with a loss of seven families through this interval). From the start of the Albian to the end of the Maastrichtian, as recorded by Crane (1987), there occurs an exponential increase in the presence (total global) of extant angiosperm families from one to over 30 (Chart 1, p. 36). Through the same 46 my interval, the observed family-level diversity of gymnosperms declines stepwise from 22 to 12 (10 families nett loss), and at order-level diversity, in almost exact parallel, from 12 to four (eight orders nett loss).

Biodiversity hotspot latitudes in the mid-Cretaceous

As for the Triassic and Jurassic periods, we ask the question for the Cretaceous: in which latitudinal belt do we find the highest biodiversity? Does biodiversity increase towards the equator as in the icehouse world of today, or does it increase towards middle latitudes as hypothesised for the hothouse world of the Triassic? Again, as far as we are aware, this question has not been seriously addressed. One might focus on mid-Cretaceous floras, from the Aptian to Turonian, avoiding the semi-icehouse dip early in the Cretaceous and a possible dip in temperatures towards the close of the period (Chart 2, p. 37). To address this issue, a series of well-preserved, well-studied floras are at hand: the best perhaps being for Angara (Peruc flora of Eastern Europe); for western Laurasia (the Potomac Gp. of the USA) and for eastern Laurasia (the Rioseki to Tamagava floras of Japan); and for Gondwana (the Santana Fm. of Brazil, a number of floras from Victoria and Queensland, and the Cerro Negro and Triton Point floras of the Antarctic Peninsula).

Fifth Extinction (end Cretaceous)

On the basis of current *observation* (not necessarily the reality of *preservation* or *existence*), the end-Cretaceous Extinction had no notable effect on the gymnosperms at family level. The conifers, cycads and ginkgos negotiated the crisis unscathed. The bennettitopsids (with the three surviving families, Williamsoniaceae, Cycadeoidaceae and Pentoxylaceae) appear to have succumbed stepwise through the Cretaceous. The most broad-spectrum losses as *observed* were in the mid-Cretaceous: with the Karkeniaceae (Ginkgoopsida), Pentoxylaceae (Bennettitopsida), and Eoanthaceae and Drewriaceae (Gnetopsida) disappearing at the end Aptian, and the Voltziaceae (Pinopsida), with the Umaltolepidaceae and Leptostrobaceae (Ginkgoopsida), at the end Cenomanian.

Angiosperms: 3. The flower

Basal angiosperms

If the evolution of the carpel occurred within the Triassic explosion, and of double fertilisation gradually through the Jurassic, then the third of the critical angiosperm features, the flower, arose in the early Cretaceous (see text on the earliest supposed flower *Archaefructus* in the box on p. 83). According to Stuessy (2004), it was this appearance of the flower that enabled the angiosperms to radiate explosively in the mid-Cretaceous—in co-evolutionary synergy with the pollinating insects.

The initial radiation of the crown angiosperms in the mid-Cretaceous is partly reminiscent of that of the pteridophytes in the wake of the First Extinction at the end-Ordovician and of the gymnosperms in the wake of the Second Extinction in the Late Devonian. While the first two major plant groups (the spore- and cone-bearing clades) were evidently the effect of extinction events, the dramatic rise of the third major group (flower-bearing) was the cause of extinction—that of the gymnosperms, from their phase of 'maturity' into that of their 'old age'. This mid-Cretaceous gymnosperm-angiosperm turnover has a striking parallel with that of the pteridophyte-gymnosperm turnover through the Carboniferous and Permian. The angiosperm rise occurs within (is part of) a clear pulse of general gymnosperm radiation in much the same way that the gymnosperms arise as an expression of the major pteridophyte radiation (Chart 1, p. 36).

Insect associations [Contributor: C.C. Labandeira]

Continued radiation of the pollinators

In macroevolutionary terms, the radiation of the Coleoptera, Diptera and Hymenoptera, so significant in the Jurassic, continues stepwise throughout the Cretaceous. The Lepidoptera diversify for the first time, but not to a major degree. Remarkable is that the pattern of diversification (all orders just mentioned) continues essentially unchanged through the mid-Cretaceous gymnosperm/angiosperm turnover.

Enter the angiosperms

The most important event for the development of plant-insect associations during the Cretaceous was the appearance of angiosperms at the beginning of the period and their subsequent diversification. The evolution of floral types had distinct implications for the expansion of pollinating insects, including the modification of mouthparts into elongated, lapping, siphoning and sponging proboscides, which represented a profound set of innovations (Crepet & Friis 1987; Labandeira 1997). This resulted in mutualisms, some of which probably were coevolved between genetically outcrossing plants and their obligate insect pollinators that were able to derive nectar, pollen, resin, and other rewards by providing an essential service. An example is an advanced bee with leg pollen baskets (corbiculae) in mid-Cretaceous amber of New Jersey, USA (Michener & Grimaldi 1988). Although pollinivory extends to the late Paleozoic (Labandeira 1998a; Rasnitsyn & Krassilov 1996), and is documented from Cretaceous sawflies feeding on gymnosperms (Krassilov & Rasnitsyn 1983) and other insects (Labandeira 2000), it becomes more diverse and an obligate relationship for many insects and plant taxa during the Cretaceous (Willemstein 1987; Crepet & Nixon 1998). Nevertheless, pollination is only one of the major associations during the Cretaceous that expanded its scope on plant hosts. Exceeding substantially that of the Jurassic are numerous examples of exophytic and endophytic consumption of a wide variety of vascular plants (Crepet 1974; Stevenson 1992; Labandeira *et al.* 1994, 2002a; Labandeira 1998b), such as specialised associations between hispine leaf beetles and their ginger-family plant hosts (Wilf *et al.* 2000). A detritivorous association documented by Chin & Gill (1996) involves the processing of conifer-rich dinosaur dung by scarab beetles.

One important association documented predominately on gymnospermous plants is borings on various woody tissue and pith in bennettitaleans, pentoxylaleans and coniferaleans. For bennettitaleans such as Cycadeoideaceae from the Early Cretaceous of the USA, Poland, Japan and possibly India, there is an apparently widespread syndrome of borings into the male reproductive tissues that consist of tunnels, galleries and entry or exit holes (Reymanówna 1960; Crepet 1974). A Late Cretaceous pentoxylalean is known from Japan with a beetle larva preserved *in situ* within a chamber adjacent to ovules (Nishida & Hayashi 1996). For conifers, cambium borings resembling the gallery-and-tunnel network of bark beetles are known from the Berriasian of England (Jarzembowski 1990); pinaceous cones from China have damage similar to the activity of extant *Conophthorous* beetles (Falder *et al.* 1998). Also, termite borings with diagnostic frass are known from conifers and bennettitaleans (Rohr *et al.* 1984; Labandeira pers. observ.). Like borings, leaf mines have a relatively rich occurrence throughout the Cretaceous, but are best documented for the latest Early Cretaceous (Albian) Dakota Fm. from the central USA where several leaf mine types are documented for basal lepidopteran clades (Labandeira *et al.* 1994). In addition, leaf mines from somewhat younger deposits are recorded on a ginkgophyte leaf from Lebanon (Krassilov & Bacchia 2000), and a variety of basal angiosperm groups from Kazakhstan (Kozlov 1988). Later Late Cretaceous occurrences are known from the Campanian Ripley Fm. (Stevenson 1992) of the southeastern USA and especially the late Maastrichtian Hell Creek Fm. of North Dakota (Labandeira *et al.* 2002a, 2002b). Almost all of these leaf mine occurrences exhibit high levels of plant host specificity and frequently are monophagous on a single species and tissue type. In addition, the floras exhibiting leaf-mined hosts also present evidence for galls, although the plant host specificities and insect affinities are less clear. There is also some evidence for the presence of seed predators on palms (Genise 1995) and other plant hosts. Evidence for external foliage feeding is diverse and occurs in all major floras (Stevenson 1992; Lang 1996; Labandeira *et al.* 2002b) and includes gymnospermous taxa. Piercing-and-sucking is relatively rare (Watson 1977). Significantly, at the terminal Cretaceous event, there was a severe decline in insect herbivore associations in terms of intensity, retaining all types of generalised associations but severely reducing the diversity of host-specialised associations into the Paleocene. Recovery to latest Maastrichtian levels did not occur until the Paleocene-Eocene boundary, about 10 my later, at least for western North America (Labandeira *et al.* 2002a, 2002b).

Tetrapod co-macroevolutionary patterns

Continued dominance of the herbivorous dinosaurs

Herbivorous dinosaurs, as in the Jurassic, continued to dominate the landscape throughout the Cretaceous (Chart 10, p. 45). And, as in the Jurassic, there occurs major turnover between clades around the middle of the 80 my interval. Both the gigantic long-necked, long-tailed Neosauropoda and the lumbering arched Eurypoda had attained static 'maturity' by the start of the Cretaceous. It was between the Ornithopoda and the Marginocephalia that the major turnover occurred.

Coincident gymnosperm-angiosperm and dinosaur turnovers

A comparison of macroevolutionary patterns between the herbivorous dinosaurs (Chart 10, p. 45) and the seed plants (Charts 5, 6, pp 40, 41) shows broad co-evolutionary trends that are strongly suggestive: the stable, mature pinalean clade supports the neosaurapod and eurypod dinosaurian clades, while the ornithopod-marginocephalian turnover coincides closely with the bennettitopsid/cheirolepidiaceaen-angiosperm turnover. As throughout the history of terrestrial life, the tetrapod vertebrates (at around order and class rank) closely track the overall pattern of vascular-plant evolution.

TERTIARY:
Stasis

Plate tectonics & Earth physiology

Continental drift towards extant configuration

Drift continues radially outward from Africa throughout the 63 Ma of the Tertiary—to reach approximately the extant configuration of the continents. Exceptional in rate of drift were Australasia, from far south still close to Antarctica to near its current location reaching the equator, and India, from alongside Africa to its present position thrusting into Asia. Of great significance biogeographically is the successive closure between South America and North America, between India and central Asia, and between Australasia and southeastern Asia at intervals through the period.

Decline into icehouse world

After a 260 my cycle, the Tertiary sees a decline from hothouse to icehouse very like that witnessed in the Carboniferous. The obvious difference is that through the Tertiary we are able to plot the nature of the curve with far greater resolution.

Global precipitation likewise follows a similar pattern to that of the Carboniferous: with a marked peak to record levels in the lower part of the period followed by a reversion to median conditions. Atmospheric oxygen reduces gradually to current levels of 22%.

Floral kingdoms

Boreal (northern temperate to polar): Ginkgoales, Pinaceae and Taxodioideae the characteristic gymnosperms.

Laurasia (northern tropical to temperate): Angiosperms dominant; Taxodioideae and some Pinaceae the only significant gymnosperms; Gnetales rare, from pollen records.

Paleotropical: Angiosperms dominant; Araucariaceae and Podocarpaceae occasional; Ginkgoales, Cycadales and Gnetales rare.

Australian (southern temperate to polar): Podocarpaceae, Araucariaceae and Cycadales the most typical gymnosperms.

Megafloral occurrences, key sequences

In view of their relevance to understanding the origins of extant floras and their great significance in the radiation of the mammals, Tertiary floras have been the object of obvious attention. In Gondwana, the most comprehensive, well-preserved floral sequences are certainly those of Australia (particularly Victoria and Tasmania). In Euramerica, well-known, well-preserved floras are known—different basins—for all stages from the Early Paleocene to the Late Miocene. From the eastern half of Laurasia, the Tertiary floras are not as well known, although the full period is covered in one region or another. The Middle Miocene (Shangwang Fm. and Xianshan Flora) is particularly notable.

Biodiversity patterns

Family-level diversity

Upper: total 12; originations 0; extinctions 0; nett 0
Middle: total 12; originations 0; extinctions 0; nett 0
Lower: total 12; originations 0; extinctions 0; nett 0
Overall: total 12; originations 0; extinctions 0; nett 0

Relictual stasis

Rate: stasis
Magnitude (families): originations 1; extinctions 0; nett gain 1
Duration: 14 ‘stages’ (70.6 my from K(endCMP)–Q(HOL))
Family/order concordance: parallel (unequal)
Order/class concordance: parallel (equal)
Cause: old age in wake of K/T Extinction
Insect co-evolution (now with the angiosperms): expanding radiation of herbivorous and pollinator clades
Tetrapod co-evolution (now with the angiosperms): radiation of mammals and birds
Gymnosperm history: having evolved through three major radiation-extinction cycles, the gymnosperms appear to have exhausted their potential for macroevolutionary innovation.

The macroevolutionary history of the gymnosperms through the Tertiary is uncompromisingly monotonous. Most notable in the wake of the K/T event is the appearance of the subfamily Cupressoideae (Pinales). Beyond that, for some 64 my from the Early Palaeocene to the end-Pliocene, the pattern of 12 families (four orders, four classes)—six Pinales, three Cycadales, one Ginkgoales, two Gnetales—persisted unchanged. No further appearances or terminations are witnessed.

Continued competitive displacement

As the angiosperm radiation and colonisation gained momentum, the gymnosperms were evidently outcompeted. This is clearly seen in the extant world where the most extensive pinopsid populations are often found marginalised in cool temperate latitudes or at higher altitude in mountainous terrain (pp 130–133). This is remarkable considering the abundance of the pinopsids throughout the hothouse world of the Mesozoic (Charts 5, 6, pp 40, 41).

Angiosperm heyday

During which stage of the Tertiary (or Quaternary) did the angiosperms reach their heyday of biodiversity? Did the heydays at family level (macroevolution) and species level (microevolution) necessarily coincide? To what extent does consideration of mammalian radiation and of the dating of diversity heydays at family-level in selected orders (e.g. Perissodactyla, Artiodactyla and elephants, Tab. 18) provide reliable insight?

Insect associations [Contributor: C.C. Labandeira]

Expanding radiation of herbivores and pollinators

Through the early half of the Tertiary (Early Palaeocene to Late Eocene) the stepwise radiation, especially of herbivorous and pollinator clades, continues. Thereafter, through some 12 my from the later Eocene to the start of the Miocene, an explosive phase of radiation across the full spectrum of herbivorous insects—Coleoptera, Diptera, Lepidoptera and Hymenoptera—occurs. This is followed by apparent stasis through to the present. It would be significant to determine to what extent this momentous change was directly related to macro- or microevolutionary shift within the angiosperms (flowering plants), or to an increase in the occurrence of insect fossil deposits (such as amber). What is clear, is that the gymnosperms, in stasis throughout this interval, play hardly any role in the event.

Angiosperm & insect radiation

Whereas the primary radiation of the herbivore and palynivore insect orders was a co-evolutionary effect of gymnosperm radiation, their accelerated radiation through the Tertiary ranged from loose associational to tight co-evolutionary relationships with the radiating angiosperms.

Extinction and recovery

A major consequence of the end-Cretaceous event was the severe diminution of plant-insect associations, partly a legacy of depauperate Paleocene floras in warm-to-cool temperate latitudes of the Western Interior of North America (Labandeira *et al.* 2002b), and probably elsewhere. The diversity of plant-insect associations accordingly is very low in Paleocene floras, of the Western Interior, and do not recover to latest Cretaceous levels until the Paleocene-Eocene boundary, with the onset of the Early Cenozoic Thermal Maximum (ECTM) about 9 my later (Wilf & Labandeira 1999; Wilf *et al.* 2001). During the global ECTM interval, ranging from latest Paleocene to early middle Eocene and including a few pulses of exceptionally warm temperatures, there was a transformation of warm-temperate floras into vegetation with a subtropical character, and a concomitant shift in insect herbivory patterns emphasising higher levels and greater diversity, especially of endophytic types. There was a widening partitioning through this interval toward two herbivore strategies: a highly defended strategy of typically evergreen plant taxa, rich in antiherbivore defences, and an accommodationist strategy of deciduous taxa with high levels of insect-mediated damage. Plant-host taxa involved in these two different approaches towards dealing with herbivory exist today on many of the descendant clades of species that occurred during the ECTM.

In addition to early evidence of extant antiherbivore strategies, several studies indicate that associations between extant low-rank clades of insects and plants are indeed old. For conifers, three studied associations are between larches (*Larix*) and *Dendroctonus* bark beetles (Labandeira *et al*. 2001), which extend to the middle Eocene of the Canadian Arctic, as well as two types of cecidomyiid galls on cupressaceous taxa (Labandeira 2002a). One association is between a middle Miocene species of *Taxodium* from Idaho, USA, and a gall virtually indistinguishable from extant *Taxodiomyia cupressiananassa* on extant twigs of *T. distichum* (Lewis 1985). The other is the cone gall *Sequoiomyia kraeuseli*, with entombed larvae, on the late Miocene *Sequoia langsdorfi* from Germany (Möhn 1960; Gagné 1968). Similarly, angiosperm leaf-mining associations extend to the Miocene (Berger 1949; Opler 1973) or older (Hickey & Hodges 1975), a situation paralleled in the fossil record of galls (Mädler 1936; Waggoner & Poteet 1996), wood-borers (Süss & Müller-Stoll 1980; Guo 1991), seed predators (Collinson 1990; Mikulás *et al.* 1998) and nectarivores (Pemberton 1992). Additionally, there is an abundant record of diverse types of external foliage feeding (Stephenson & Scott 1992; Labandeira 1998c; Lang 1996) including all types of margin and hole feeding, skeletonisation and other types such as bud-feeding and surface abrasion. Piercing-and-sucking is rarely documented although there is an abundance of oviposition, principally by damselflies (Hellmund & Hellmund 1996). In addition to the fossil record, many molecularly based studies of plant clades and their insect herbivores indicate origins throughout the Cenozoic, although the specific mechanisms are quite variable and include parallel cladogenesis, sequential evolution, escape-and-radiate co-evolution and diffuse 'co-evolution' (Labandeira 2002a). Classic examples of such associations are figs and fig wasps (Machado *et al.* 2000), yuccas and yucca moths (Pellmyr *et al*. 1996) and *Tetraopes* longhorn beetles and their milkweed hosts (Farrell & Mitter 1998), the latter two which originated during the mid-Cenozoic based on rates of gene change and calibration to important fossil occurrences.

Two major events during the Cenozoic dramatically affected the course of plant-insect associations. The first was the origin of the grassland biome, which offered plant-host resources for a variety of herbivore feeding guilds on grasses (Ross 1970; Whitcomb *et al.* 1987). The second was the origin of the modern desert biome, which similarly offered opportunity for colonisation of xeric vegetation by intricately bound herbivores and pollinators (Holland & Fleming 2001). Throughout the Cenozoic plant-insect associations of modern clades were well established, although some host shifts are indicated (Labandeira 1998c).

Tetrapod co-macroevolutionary patterns

Radiation of the mammals & birds

This event represents the clearest and best-known instance of the explosive radiation of one major group of animals (the mammals) following the catastrophic extinction of another (the dinosaurs). It is the surest example of concurrent turnover though niche vacation.

Mammal order	**Biodiversity heyday**	
Rodentia (squirrels, beavers, rats, mice)	extant??	0 Ma
Carnivora (cats, dogs)	Pleistocene	1 Ma
Marsupials (numbats, koalas, kangaroos)	Pleistocene	1 Ma
Primates (lemurs, monkeys, apes, humans)	Late Pliocene	2 Ma
Edentates (armadillos, sloths)	mid Pliocene	3 Ma
Artiodactyla (deer, bovids, giraffes)	Early Pliocene	5 Ma
Proboscidea (elephants), global *ca* 200 spp	mid Miocene	15 Ma
Artiodactyla (pigs, hippos, camels)	Late Oligocene	25 Ma
Perissodactyla (horses, tapirs, rhinoceroses)	mid Oligocene	28 Ma

Tab. 18. Mammals: shifting biodiversity heydays of the orders

Orders: includes a selection of 8 of the 18 mammal orders

Biodiversity heyday: expressed at family-level

- a clear pattern of successive biodiversity heydays for the different mammal orders from the mid Oligocene to present is evident.

Source: compiled from phylogenies in Halstead (1978).

QUATERNARY: Relicts of a 375 my cycle

Plate tectonics & Earth physiology

Extant configuration

The 1.81 my span of the Quaternary has seen the tectonic plates continue their relative movements much as in the later Tertiary. The orogenic belts continue to rise through subduction (the Andes) or impact (the Himalayas). The earthquake/volcanogenic belts continue ceaselessly to promote environmental change at all scales affecting the local to global biota.

Icehouse world

The world in which hominids have evolved from their relatively recent australopithecine past, via a succession of *Homo* species to their current super-dominance globally, has seen the repeatedly shifting pattern of glacials and interglacials within an icehouse world. Through this same interval, in contrast, mean global precipitation and atmospheric oxygen levels (22%) have seemingly remained relatively constant (Chart 2, p. 37).

Floral kingdoms

Boreal (northern temperate to polar)
Neotropical (New World tropical to south temperate)
Paleotropical (Old World tropical)
Australian (Australasian tropical to south temperate)
Cape (southern temperate)
Antarctic (polar)

Megafloral occurrences, key sequences

Megafloral deposits of the last 1.81 my

Apparently there are few, if any, megafloral deposits of consequence representing the Quaternary of Laurasia (Charts 17–20, pp 52–55). Knowledge of the interval is based seemingly entirely on palynological studies. Knowledge of Gondwanan floras of this age is confined very largely to Australia (Chart 14, p. 49), where most of the assemblages are either poorly preserved or of a reconnaissance nature.

Biodiversity patterns

Family-level diversity

Total 13; originations 1; extinctions 0; nett gain 1

Relictual Stasis: K(MAA)–Q(HOL)

The Holocene represents a special case in recording megafloral biodiversity patterns: *observed*, *preserved* and *existed* diversity figures, markedly different for all earlier time intervals, are now essentially equal, through the opportunity for comprehensive sampling. In view of this, the Holocene (with the three additional gnetalean families, Ephedraceae, Gnetaceae and Welwitschiaceae) is excluded from the following synopsis.

Gymnosperm relicts

The Pleistocene record offers hardly perceptible shift from the unchanging Tertiary picture of the Pinales (with six families), Cycadales (three families), Ginkgoales (one family) and Gnetales (two families). This pattern persists through into our extant world, aside from the additional presence of the single gnetalean family, Gnetaceae, represented by a single genus. The order Gnetales overall appear to enjoy virtually no megafloral fossil record (apart from that in the Early Cretaceous, Barremian/Aptian) and offer a sobering reminder of the sparse nature of this record. They emphasise the gulf between *observed* diversity, *preserved* diversity, and *existed* diversity. They are the relicts of a very long and very silent history—assuming the identification of the Fraxinopsiaceae, Nataligmaceae, Dinophytonaceae and Dechelyiaceae of the Late Triassic as gnetopsids is correct. After the early Mesozoic flurry, and aside from the Eoanthaceae and gnetalean material of the mid-Cretaceous, the gnetopsids (megafossil record) disappeared with hardly a trace for 200 my.

Angiosperms: Decimation, extinction

Having radiated for 130 million years to their current prodigious diversity of near 250 000 species in 457 families and 45 orders (p. 3), the flowering plants are now in severe decline—if not yet so evident in regard to taxonomic diversity, then certainly in terms of habitat destruction (see Anderson 1999 for summary), mostly over the past 500 years since the ages of human exploration, scientific revolution, then industrialisation were set in motion.

Of the 18 biodiversity hotspots defined globally prior to the turn of the millennium (2000 AD), an estimated 70% or more of the total combined area has been destroyed—replaced largely by farmland and human habitation. An unimaginable 90% of the richest of all hotspots, the belt of tropical montane (Andean) forest including the headwaters of the Amazon, has been erased. The tropical forests globally, already reduced to less than 50% of their former extent, are disappearing at a rate of 1.5% to 2% annually through cutting or burning at the hands of humans.

Should the present extinction of the angiosperms come to resemble that of the gymnosperms towards the close of the Triassic, then given the chance to recover, how might their further history unfold?

Insect associations [Contributor: C.C. Labandeira]

Into the Sixth Extinction

The close relationship between plants and insects in a world such as ours catapulting ever deeper into the sixth global extinction event, is of the greatest significance. We note here just one area of concern involving gymnosperms. Only in the past decade or two have we learned that cycads are pollinated by insects, not wind. In central and northern America 'many species of the cycad family Zamiaceae are imperilled. It has been demonstrated that all of these endangered species are pollinated by host-specific weevils which presently appear in low populations, and not throughout the entire range of their dependent plant hosts.' The lack of recruitment to diminishing populations of Zamiaceae will in time lead to mutual extinction—including any other associates in the component community.

Tetrapod co-macroevolutionary patterns

Into the Sixth Extinction

The escalating Sixth Extinction is an event of the last 100 000 years or so—a geological instant. Uniquely, it is being caused by the runaway population explosion and global colonisation of one particular species of omnivorous mammal (*Homo sapiens*) at the expense of all other animals and their habitat. Unlike the K/T Extinction, where the dinosaurs succumbed but the gymnosperms continued through unscathed and the angiosperms continued their Cretaceous radiation, the tetrapods and both groups of seed plants are now threatened by concurrent catastrophic extinction.

Tab. 19. Extant gymnosperms: classification, biodiversity, phytogeography

DIVISION
CLASS
ORDER
FAMILY

	diversity	climatic zone	occurrence	biome (habitat)
PINOPHYTA				
PINOPSIDA				
PINALES (conifers)				
Pinaceae	11 gen., 225 spp	temperate*	N Hemisph.*	monotypic forest*
Podocarpaceae	19 gen., 189 spp	trop. to sub-trop.*	S Hemisph.*	montane forest*
Araucariaceae	3 gen., 41 spp	trop. to sub-trop.	S Hemisph. (excl Afr)	montane forest*
Cupressaceae	29 gen., 133 spp	cool to warm-temp.*	global	montane forest*
Sciadopityaceae	1 gen., 1 sp.	cool-temp.	Japan	montane forest*
Taxaceae	6 gen., 34 spp	cool-temp. to sub-trop.	N Hemisph.* (I New Caled.)	valley forest*
CYCADOPSIDA				
CYCADALES				
Cycadaceae	1 gen., 102 spp	trop. to warm-temp.	E Afr., Asia, Males., Aus, Polyn.	various
Stangeriaceae	2 gen., 4 spp	trop. to sub-trop.	S Afr., NE Aus	coastal
Zamiaceae	8 gen., 191 spp	trop. to warm-temp.	Amer., Afr., Aus	woodl.–forest*
GINKGOOPSIDA				
GINKGOALES				
Ginkgoaceae	1 gen., 1 spp	temp.	China	uncertain
GNETOPSIDA				
GNETALES				
Gnetaceae	1 gen., 30 spp	pantrop.	SE Asia, W Afr., E & C SAm	lowland forest*
Welwitschiaceae	1 gen., 1 sp.	S sub-trop.	Namibia, Angola	coastal desert
Ephedraceae	1 gen., 35-45 spp	N & S sub-trop.	Americas, Eurasia	arid

13 families, 84 genera, 987 spp

* mostly

Classification & diversity: see pp 130, 154, 210
Other sources: Jones 2002—Cycadopsida
Kubitzki 1990—other

Tab. 20. Extant floral kingdoms: biodiversity at family level

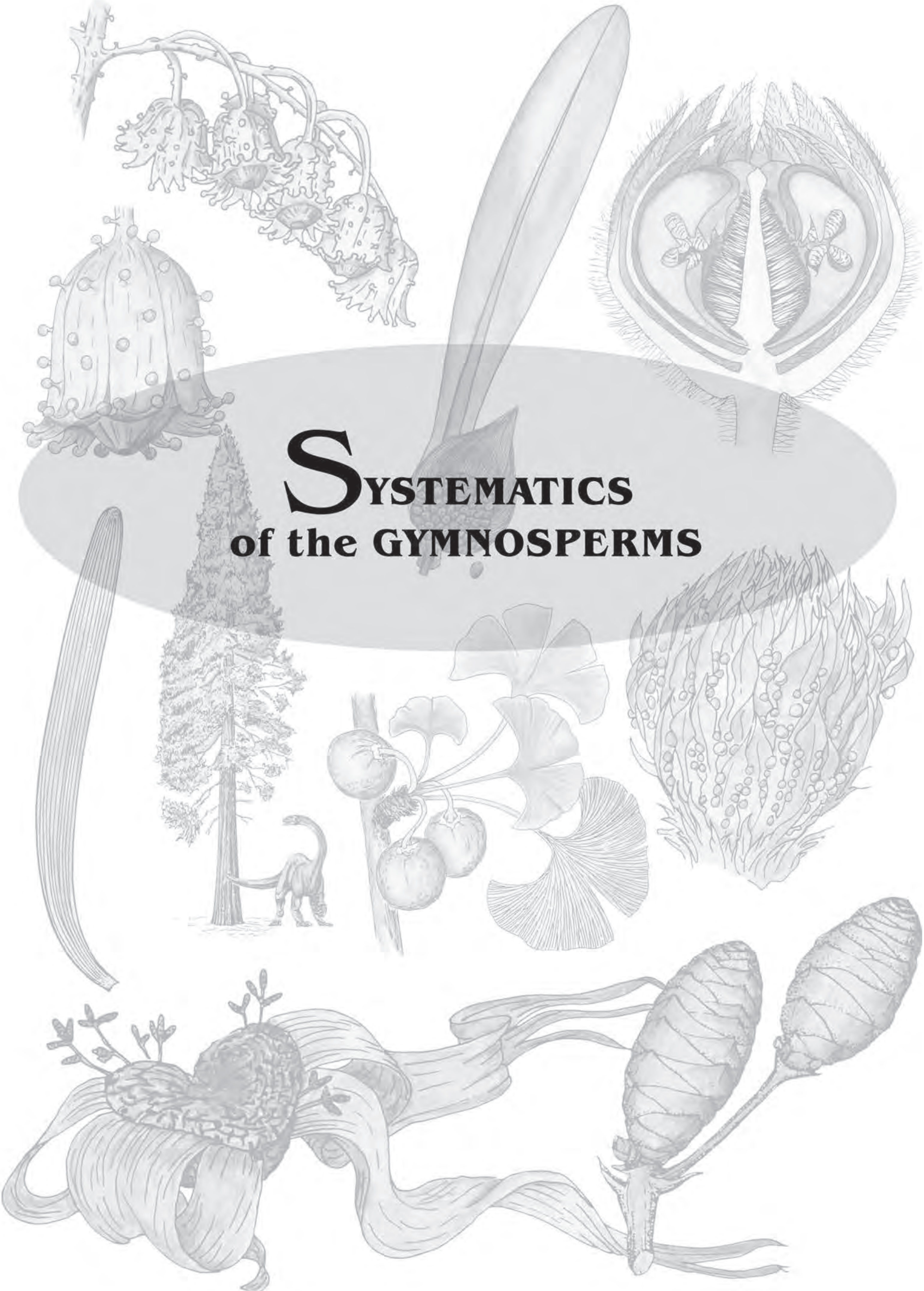
Plant kingdoms (global)	**Plant diversity (angiosperms)**	**Gymnosperms (typical families or orders)**
Holarctic (Boreal)	202 families	Pinaceae, Taxaceae, Cupressaceae, Ephedraceae
Neotropical	223 families	Araucariaceae, Cupressaceae, Zamiaceae, Gnetaceae, Ephedraceae
Paleotropical	342 families	Podocarpaceae, Cupressaceae, Cycadales, Gnetales
Australian	177 families	Podocarpaceae, Araucariaceae, Cycadaceae, Stangeriaceae, Zamiaceae
Cape	150 families	Podocarpaceae, Cupressaceae
Antarctic & Patagonian	?	Podocarpaceae, Araucariaceae, Cupressaceae

Plant kingdoms: The six broadly recognised plant kingdoms of the world.

Plant biodiversity: The number of angiosperm families per plant kingdom (based on Heywood 1978); figures seem not available for all vascular plants, or for diversity at generic or specific level. How would ‘existed’ family-level diversity for the gymnosperms have compared from the Late Devonian to recent times?

Gymnosperms (typical families or orders): Listed are the more characteristic families of the six kingdoms. Marked differences are evident.

SYSTEMATICS of the GYMNOSPERMS



FORMAT OF SYSTEMATICS SECTION

Layout & style

The format originates with that followed in *The Fossil Record 2* (Cleal in Benton 1993), but is expanded extensively in line with our purpose to sketch a 'brief history' of the gymnosperms involving aspects of their classification, phylogeny, phytogeography, ecology and primarily their *biodiversity*. We have aimed to follow a consistent treatment for each of the eight named classes, 37 orders and 84 families included. Some variation and deviation does occur and where pertinent is discussed below.

Classes

Each of our eight named classes (aside from the Axelrodiopsida) is introduced in a two-page spread (four pages for the Pinopsida, the largest of the classes), including family range chart, diagnosis and other introductory text, classification table and a schematic pictorial phylogeny based on ovulate organs. For the Pinopsida, a parallel microsporangiate phylogeny is added.

Family range chart: Here we show the stratigraphic range, based on 'first' and 'last' known occurrences as given in the systematic text, for each of the families recognised in the class. This is extracted directly from the *Global gymnosperms: family range chart* (Charts 3, 4, pp 38, 39; further explanatory notes on p. 34), which covers all 84 families described.

Diagnosis & other introductory text: Aside from the diagnosis (see below for approach), we include remarks on such issues as nomenclature, classification and phylogeny. Then follows a list of the orders recognised in the current volume.

Classification table: This is an extract from the *Global gymnosperm classification* (Tab. 2, pp 6, 7) showing generic diversity, affiliation and morphology grades, and presence/absence of preserved anatomy.

Pictorial phylogeny: Through a pictogram showing the ovulate organs (more specifically the megasporophylls in most cases) of the 'reference-whole-plant genera', the purpose is to suggest the most evident phylogenetic links between those families currently recognised within the class. The phylogeny does not reflect any rigorous attempt at cladistic analysis.

Orders

The four extant orders (Pinales, Cycadales, Ginkgoales and Gnetales) are likewise introduced through a two- or four-page spread. Emphasis is placed on their classification, phytogeography, biodiversity and ecology—the themes traced through this volume.

A good proportion of the extinct orders (21 of 33) are monofamilial, and in these cases the order plus family appear on the same page. This holds generally also for the first family in more diverse orders.

Families

In most cases, each family is given a full-page treatment. A few particularly diverse families, such as the Cordaitanthaceae (p. 110), Cheirolepidiaceae (p. 118) and Voltziaceae (p. 127) of the Pinopsida, are given two- or even three-page coverage. On the other hand, a few poorly known families, such as the Genomospermaceae and Eospermaceae (p. 102), are allotted just a single column each.

Sequence

We have aimed to treat the families within each order in the sequence they appear in the *Gymnosperm classification* (p. v) and range chart (Charts 3, 4, pp 38, 39). In only two cases (Lyginopteridaceae, pp 100, 101, and Podocarpaceae, pp 136, 137), we deviate from the format so as to keep the full cover of sketches and text of important families adjacent to another.

Nomenclature

Following the lead of Meyen (1984, 1986, 1987), we aim to base names of all ranks (family, order, class) on genera of ovulate fruit (for certain exceptions, see pp 20, 21 this volume): the rationale being that the classification is based exclusively on these organs. In adopting this procedure there is some clash, especially at family level, with the rules and recommendations of the Code of Botanical Nomenclature (ICBN). There are such pervasive problems in palaeobotany relating to the affiliation of dispersed organs, not explicitly or sufficiently accounted for by the Code, however, that this is felt justified. We would strongly recommend further amendments to the Code acknowledging fully the peculiarly palaeobotanical problems and encourage a uniform, more biologically based nomenclatural system for fossil material.

Diagnosis (classes, orders, families)

The diagnoses are based in most cases exclusively on the ovulate organs. They aim generally at giving the most succinct morphological account of the taxon such as to include all forms considered to fall within the group and to exclude all other known forms. They are a statement of comparison between the families within an order or between the orders within a class, not full descriptions of the taxon. Microscopic anatomical details are not considered, except indirectly where they have confirmed basic morphological structure such as in the Bennettitales.

Emendations: While the diagnoses of many taxa are effectively emended to varying degree, we append the term 'emend. nov.' where relevant only to taxa contributed by Cleal.

Family diagnoses are treated somewhat variably as follows:

Extant families (by Mundry et al.)
Included here are the 13 extant families (six pinopsid, three cycadopsid, one ginkgoopsid, and three gnetopsid). For these the diagnosis covers ovulate, polliniferous and foliage organs.

Laurasian Palaeozoic families (by Cleal)
Included here are all eight lyginopteridopsid families, the earliest five pinopsid families, and the seven extinct cycadopsid families. The general approach to diagnoses is that the ovulate organ is given primary focus, while the polliniferous organs, foliage and sometimes stems are given lesser focus.

Ginkgoales (by Zhou Zhiyan), gnetopsids (by Krassilov et al. or Konijn.-Citt.)
For the four ginkgoalean families authored by Zhou, the focus is exclusively on the ovulate organs, for the three gnetopsid families it is more inclusive.

All other taxa (by Anderson & Anderson)
For all families written up by two of us (J.M.A. & H.M.A.), based either on Molteno Fm. or other material, the diagnosis considers exclusively the ovulate organs.

Female & male
We employ these terms purely as a shorthand convenience for subheadings, being aware that there may be valid objections to such usage. Technically 'the sporophyte does not have a gender, only the gametophyte phase of the life cycle is male or female (or both)' (Gar Rothwell, pers. comm. Sept. 2004).

Range

First and last appearances of families are documented in the manner of Cleal (1993) in *The Fossil Record 2*. We quote his entries largely unchanged for those taxa not diverging from his 1993 concept and whose known range remains the same. The *Global gymnosperm* range chart is based on these data and follows the *range-through* method, which assumes the family to have occurred throughout the interval bracketed by the first and last appearances (see also Fig. 1, p. 5).

Reference whole-plant genus & stratum

The best understood ovulate genus with its affiliated organs is nominated as reference around which the taxonomic concept of a particular family is based. It has the same function as a 'reference palaeodeme' in forming the concept of a species or a reference species in forming the concept of a genus (And. & And. 1985, 1989, 2003). That stratigraphic unit (ideally a formation) or locality from which the genus is best documented, is nominated as the reference stratum and will usually be the primary source of data on the affiliation of organs. For further on affiliation grades and symbols, see overpage (p. 94), and on *whole-plant genera*, see p. 95. The *whole-plant* name pairs the ovulate fruit and foliage, where available, acknowledging the central roles of these different organs in forming the concept of the plant: in classification/phylogeny and prominence respectively.

Prominence (colonisation success)

Discussion embraces the whole family, but since most extinct families (49 of 71, see Tab. 2) are monogeneric, details of prominence (diversity, ubiquity, frequency, abundance and longevity) are mostly those only of the reference *whole-plant* genus through its known geographic and stratigraphic range. Statistics are based on leaves, since they are almost invariably far more widely encountered than the reproductive structures. For full account, see overpage (p. 95).

Ecology

Entries here will refer in general to the reference whole-plant genus in the reference stratum—where it is best known.
Habit: A simple statement of plant form.
Habitat: A concise statement of known preferred habitat.

Other genera

Included are those additional genera (‘natural’ or ‘organ’), aside from the ‘reference whole-plant genus’, considered to represent the family. Only genera in current use are noted; synonyms are excluded. The intention is to record the known diversity at generic level within the family (see Tab. 2, pp 6, 7).

A remarkable 49 of 71 of all extinct families are monogeneric (considering ovulate organs only). Only 10 extinct families include more than three ovulate genera; the Voltziaceae (p. 127), with 13 ovulate genera, is the most diverse of the extinct families.

Remarks

There is no attempt here to be fully consistent with regard to subheadings or focus on any particular topic.

Classification & phylogeny: Given the current reality of unresolved classification and phylogeny within the gymnosperms, it is often appropriate, however briefly, to comment on the reasons behind the classification adopted, and on any perceived phylogenetic relationships (e.g. the Late Palaeozoic pinopsids Trichopityaceae, p. 115, or *Thucydia* and *Barthelia*, pp 122, 123).

Nomenclature: We comment especially where we have veered from our standard procedure of naming supra-generic taxa after genera of ovulate fruit (e.g. the lyginopteridopsid Moresnetiaceae, p. 98, and the cycadopsid Gigantopteridales, p. 152). To emphasise the nomenclatural uncertainties (many around taxa first described and named in the early days of palaeobotany in the 19th Century) particularly relating to the Laurasian Late Palaeozoic taxa, Cleal has prepared a dedicated discussion (pp 20, 21).

Morphology: Here we offer occasional comment on issues of notable interest, e.g. the ‘remarkably large ... spherical head’ reaching the size of a grapefruit of the ovulate *Bennetticarpus* (p. 196), or the grape-sized *Vardekloeftia* (p. 193)—both expressions of the adaptive radiation of the Late Triassic bennettitaleans.

Taphonomy: This is only occasionally touched on (though it relates strongly to affiliations), e.g. *Dordrechtitales* (p. 117), frequent and abundant in the Late Triassic Molteno Fm., yet with no polliniferous or foliage affiliates known.

Affiliations: In that this topic is particularly key to our approach, we offer comment on a more or less regular basis, e.g. the Gondwana Triassic Fraxinopsiaceae (p. 204), with the ovulate organ being frequent and common, yet with the polliniferous organ remaining entirely unknown.

References

The most recent, most comprehensive references are cited, and the fields of information noted.

Illustrations (pen-sketches)

Comparative study: We complement the family treatments with the clearest line drawings readily available (sources indicated). Sketches add a dimension that text alone cannot capture. They enable the reader at a glance to visualise similarities and differences between taxa, firstly of the ovulate organs, generally of the set of affiliated organs. An impression is quickly gained of the group of families included in an order or of the orders within a class. The emphasis is on interpretive reconstructions of reproductive structures and their affiliated foliage.

Reference whole-plant genus & stratum: Ideally, for each family, the selection of sketches would be exclusively of material from the reference whole-plant genus and reference stratum (e.g. family Umkomasiaceae, whole-plant genus *Umkomasia/Dicroidium*, Molteno Fm., p. 182; or family Utrechtiaceae, whole-plant genus *Otovicia*, Rotliegend, p. 125). This is far from always possible, with the most explicit, available reconstructions often being generalised or of material of unspecified provenance (e.g. family Cycadeoidaceae, p. 199).

Scope & sequence: A fully comparative set of R4 or R5 (see below) sketches at consistent scale should optimally be presented for each family. The idea is to include reconstructions following a standard arrangement down the right column of the page—first the ovulate material (general to specific), then the polliniferous organs (again general to specific) followed by foliage and habit of plant, if available.

Cuticle: In view of their undoubted diagnostic value at generic and family level, cuticle drawings have been included where readily accessible. Uniform treatment would clearly be a goal of any future editions of this work. Details of other microscopic anatomy are beyond the scope of this work.

Captions: We aim, as far as possible (based on the references cited), to consistently record binomial, scale, reconstruction grade, locality, formation and age (to stage) of the specimens figured. All are critical to an optimal presentation. Formation and ‘stage’ are central to tracking temporal distributions and hence biodiversity per stage.

Sources & permissions: Due credit (Permissions on p x.) is given to original authorship, but this is not always feasible where illustrations have gone through one or more generations of redrafting.

Reconstruction grades (as introduced in And. & And. 1989, 2003 for the Molteno Fm.): All pen sketches of fossil plants are interpretive to some degree. All reflect the subjective view of the artist and/or author. In order to reflect the intentions of the author, a series of reconstruction grades (R1–R5) is applied. Where feasible, the grade of each sketch is indicated.

R1: no intended reconstruction; based on a single specimen.

R2: minor intended reconstruction; correcting and cleaning unnecessary or ambiguous noise (minor irregularities, distortions, breaks in detail) due to imperfections of preservation or incomplete preparation; based on a single specimen.

R3: intermediate reconstruction; completing or adding missing parts of the organ; based primarily on a single specimen but other members of the home palaeodeme may be consulted.

R4: extensive reconstruction (composite for palaeodeme); full organ or assembly of organs, reconstructed from a number of specimens from a single fossil population from a single TC.

R5: extensive reconstruction (composite for formation); as in R4 but based on a number of specimens from sister palaeodemes.
Only for the Molteno Fm. material can we consistently note the grade; for most other sketches, the grade is an approximation based on the incomplete information in the sources cited.

AFFILIATED ORGANS

Towards whole-plant genera and families

It is clear that a consistent strategy towards establishing the affiliation of organs is essential in researching the true (natural) diversity at species and genus level in the flora of any geological formation. A similar strategy is no less critical as a foundation towards seeking natural diversity at family and order level of a division of plants globally—the gymnosperms—through their Phanerozoic history.

A good many organs (ovulate, polliniferous, foliage) in palaeobotanical collections occur alone with no known affiliates, a remarkable few are found in organic attachment, for the remainder the reality settles somewhere in between. Some system for grading reliability of affiliations must be introduced. That adopted here was established by ourselves for studying plant diversity in the Late Triassic Molteno and other South African Permo-Triassic formations (And. & And. 1985, 1989, 2003). The system ranges from Grade 1 (marginal likelihood of affiliation) to Grade 4 (virtually exclusive likelihood of affiliation) to Grade 5 (certain affiliation through attachment).

Criteria for affiliations (elaborated after And. & And. 1985, p. 85)

Judgements concerning affiliations are based on an array of observations. Reliability will depend on the following criteria (the abbreviations used throughout this volume are those given in brackets):

Organic attachment (Org.att.)—Organs that are found in direct organic connection constitute the only irrefutable case for conspecific/congeneric status (e.g. Cordaitanthaceae, p. 110; Kannaskoppiaceae, p. 185).

Cuticle correspondence (Cut.cor.)—It is reasonably established that the cuticles of different organs of the same species (or genera) display like characteristics (e.g. Fraxinopsiaceae, p. 204; Dinophytonaceae, p. 206).

Morphological/Anatomical correspondence (Mor.cor./Anat.cor.)—In certain instances, diagnostic macroscopic features, such as ornamentation, blistering and texture, or microscopic features are seen in conspecific/congeneric organs (e.g. Peltaspermaceae, p.-168; Nataligmaceae, p. 205).

Pollen correspondence (Pol.cor.)—A special case of morphological correspondence is where *in situ* pollen of the same kind is found both in the nucellar beak or pollen chamber of the ovules and in the microsporangia of the pollen organs (e.g. Emporiaceae, p. 124; Utrechtiaceae, p. 125).

Kindred reinforcement (Kin.rein.)—Well authenticated organ affiliations for other genera in the family or order offer a secure foundation for proposing linkage (e.g. Vardekloeftiaceae, p. 193; Lindthecaceae, p. 200).

Mutual occurrence, presence or absence (Mut.occ.)—Where different dispersed organs occur in the same assemblage, the possibility exists that they derive from the same parent species (e.g. Caytoniaceae, p. 183; Fredlindiaceae, p. 190). The likelihood of affiliation will increase with:

- *coupling frequency*—the number of assemblages in which the mutual occurrence is repeated;
- *mutual abundance*—the mutual dominance or rarity of the organs in question;
- *process of elimination*—the preoccupation of organs in other established affiliations;
- *bedding-plane bonds*—the extent to which the organs are confined to particular bedding planes;
- *assemblage paucity*—the lowering of diversity levels;
- *assemblage autochthony*—the degree to which the assemblage represents a single, local plant association.

Reliability grades (after And. & And. 1985, p. 85)

The evidence for linking organs ranges from marginal to certain. At the lower end of the range the evidence will be slim, yet suggestive, or alternate options might be more or less equally likely, while at the upper end of the range clear organic attachment certifies linkage.

Grade 1, *marginal* —Marginal likelihood of affiliation:
mutual occurrence (weak).

Grade 2, *poor* —Most feasible affiliation (alternatives
may be competitive):
mutual occurrence (uncertain).

Grade 3, *fair* —Probable affiliation (alternatives weak):
mutual occurrence (fairly clear),
usually some supportive data.

Grade 4, *good* —Virtually exclusive likelihood of affiliation:
mutual occurrence (particularly clear),
cuticle correspondence and/or
kindred reinforcement
and/or possible organic attachment.

Grade 5, *certain* —Certain affiliation:
organic attachment undoubted.

Reference whole-plant genera

Each whole-plant genus selected as ‘reference’ is graded as follows for the Umkomasiaceae (p. 182): *Umkomasia*(4)*Dicroidium*(4)*Pteruchus*(4). The sequence in recording the organs is ovulate strobilus, foliage and microsporangiate strobilus. In this particular case, the circle is closed by grading the *Pteruchus-Umkomasia* affiliation as 4, i.e. the final bracketed number grades the male to female affiliation.

Relative paucity of reproductive organs

Particularly relevant to the discussion of affiliations is the differing frequency (localities) and abundance (individuals) of preservation of the different plant organs. Foliage, almost invariably, is far more frequent and abundant than the reproductive organs (see tables in And. & And. 2003 for the Molteno). And in the latter, the ovulate organs are generally more frequent and abundant than the microsporangiate organs (see Tab. 12, p. 23, this volume). Inevitably, the variable filtering effect of taphonomy on the different organs renders the search for affiliations uncertain and incomplete.

Extreme rarity of organic attachment: For only 14 of the 71 extinct families (Tab. 2, pp 6, 7) are the ovulate strobili, microsporangiate strobili and foliage found in organic attachment. Most often such attachment is nevertheless imperfect in that all three organs are not found simultaneously attached in any particular specimen. The foliage is most likely to be the element linking the three (e.g. Kannaskoppiaceae, p. 185).

PROMINENCE (colonisation success)

In that 'affiliations' and 'prominence' are so integral to our treatment of families, we repeat the outline of these concepts largely unchanged from And. & And. (2003) in reference to the Gondwana Triassic.

Colonising the Gondwana Triassic (GT)

The terms *prominence* and *success* are applied in our Gondwana work synonymously. The *prominence* of a genus in the *Gondwana Triassic Empire* refers to its relative consequence and is measured as the sum of the five attributes—Frequency, Ubiquity, Diversity, Abundance and Longevity (FUDAL).

Vegetative organs

Considering the far wider occurrence of vegetative versus reproductive organs and the uncertainties concerning the affiliation of organs, the FUDAL rating system is based exclusively on the former. While the measure of prominence based on foliage fossils alone may be imperfect, the formula provides a good approximation of the success of the relevant whole-plant genus.

Attributes of success (Gondwana Triassic)

Frequency (F): measure of repetitiveness of occurrence.
The number of subregions (degree squares), of the 85 across Gondwana yielding Triassic megaplants, in which the genus has been recorded. The tally is derived directly from the distribution maps published in the Molteno monograph series (And. & And. 1983, 1989, 2003).

Ubiquity (U): measure of general range of occurrence.
The number of superregions (continents), of the five making up Gondwana, from which the genus has been recorded.

Diversity (D): measure of speciation, radiation, variability.
The number of species recognised in the genus for the Gondwana Triassic (as documented in And. & And. 2003).

Abundance (A): measure of quantity.
The norm of the abundance figures for the genus in those assemblages (only those judged to largely represent the local flora) in which it occurs. The data are based exclusively on Molteno assemblages since clear abundance figures are rarely available for other formations.

Longevity (L): measure of duration of the lineage.
The duration in number of international standard ammonite biozones between first and last recorded appearances—as plotted on the stratigraphic figures in And. & And. (2003). Longevity will probably prove more effectively measured in millions of years, but this was not attempted as our GT stratigraphic base for plotting generic occurrence still shows only the ammonite biozones (And. & And. 1983, 1989, 2003).

FUDAL fingerprints

The FUDAL fingerprint or formula for each genus is clearly distinctive and, along with 'geostrat' (geographic-stratigraphic) occurrence, it tells a great deal about the kind of parent plant being considered. *Dejerseya* (7/2/1/11/2), p. 186 in And. & And. (2003) and *Kannaskoppifolia* (23/3/10/-/26), p. 185 this volume, for instance, could hardly be more different in terms of colonisation, diversification and autecology. *Dejerseya*, interpreted as a shrub to small tree that appeared (apparently) only late in the Triassic, is very infrequent yet common where it occurs and, though morphologically variable, never appears to have had the time to diversify. *Kannaskoppifolia*, seen as a herbaceous pioneer, appeared early in the Triassic and colonised widely through Gondwana during the rest of the period, becoming frequent (though always rare) and well diversified.

For the foliage genus *Kannaskoppifolia*, as example (see more fully on p. 185), the FUDAL rating for the Gondwana Triassic is 23/3/10/-/26: frequency (F) is 23 degree squares, ubiquity (U) is 3 continents, diversity (D) is 10 species, abundance (A) is <1%, and longevity (L) is 26 my.

Tab. 21. WHOLE-PLANT GENERA

The whole-plant genus is central to our systematic treatment of gymnosperm families. It is critical, therefore, to clarify our usage of the concept (see definitions below). In a sense, the only genuine whole-plant genera are extant genera; all others are to lesser or greater extent incompletely known—from those with both ovulate and microsporangiate reproductive organs and foliage well known and in organic attachment (e.g. Kannaskoppiaceae), to those represented only by dispersed seeds from a single locality (e.g. Polylophospermaceae).

A selection of seven reference whole-plant genera, largely from the Molteno Fm. (being most consistently sampled regarding affiliated organs), is listed to demonstrate the range of the concept.

If whole-plant families were to be based strictly on whole-plant genera at least as fully based as *Kannaskoppia/Kannaskoppifolia* (Kannaskoppiaceae), we would be left with very few such families. And there would be no opportunity to trace family diversity through the Phanerozoic.

Kannaskoppiaceae (p.185)
Reference whole-plant genus: *Kannaskoppia/Kannaskoppifolia*;
Molteno Fm., South Africa.
Organs known: ovulate & microsporangiate strobili, foliage;
sure organic attachment, grade 5 affiliation
Geostrat. occurrence (foliage): Gondwana Triassic, Tr(SPA–RHT);
Chile, Argentina, South Africa, eastern Australia, New Zealand

Caytoniaceae (p. 183)
Reference whole-plant genus: *Caytonia/Sagenopteris*;
L–U. Deltaic, Yorkshire, England
Organs known: ovulate & microsporangiate strobili, foliage;
secure grade 4 affiliation
Geostrat. occurrence (general): Laurasia Mesozoic, Tr(CRN)–K(CMP);
from Greenland through Europe to the USSR

Fraxinopsiaceae (p. 204)
Reference whole-plant genus: *Fraxinopsis/Yabeiella*
Molteno Fm., South Africa
Organs known: dispersed winged seeds; foliage;
secure grade 4 affiliation
Geostrat. occurrence (foliage): Gondwana Triassic, Tr(LAD–RHT);
Chile, Argentina, South Africa, eastern Australia, New Zealand

Fredlindiaceae (p. 190)
Reference whole-plant genus: *Fredlindia/Halleyoctenis*
Molteno Fm., South Africa
Organs known: ovulate & microsporangiate strobili, foliage;
intermediate grade 3 affiliation
Geostrat. occurrence (foliage): Gondwana Triassic, Tr(ANS–CRN);
South Africa, Australia

Hlatimbiaceae (p. 187)
Reference whole-plant genus: *Hlatimbia/Batiopteris*
Molteno Fm., South Africa
Organs known: ovulate strobili, foliage;
insecure grade 2 affiliation
Geostrat. occurrence (foliage): Gondwana Triassic, Tr(LAD–CRN);
Argentina, South Africa, Tasmania

Dordrechtitaceae (p. 117)
Reference whole-plant genus: *Dordrechtites*
Molteno Fm., South Africa
Organs known: ovulate cones only (no affiliated organs)
Geostrat. occurrence: Gondwana Triassic, Tr(LAD–CRN);
Argentina, South Africa, Queensland, NSW

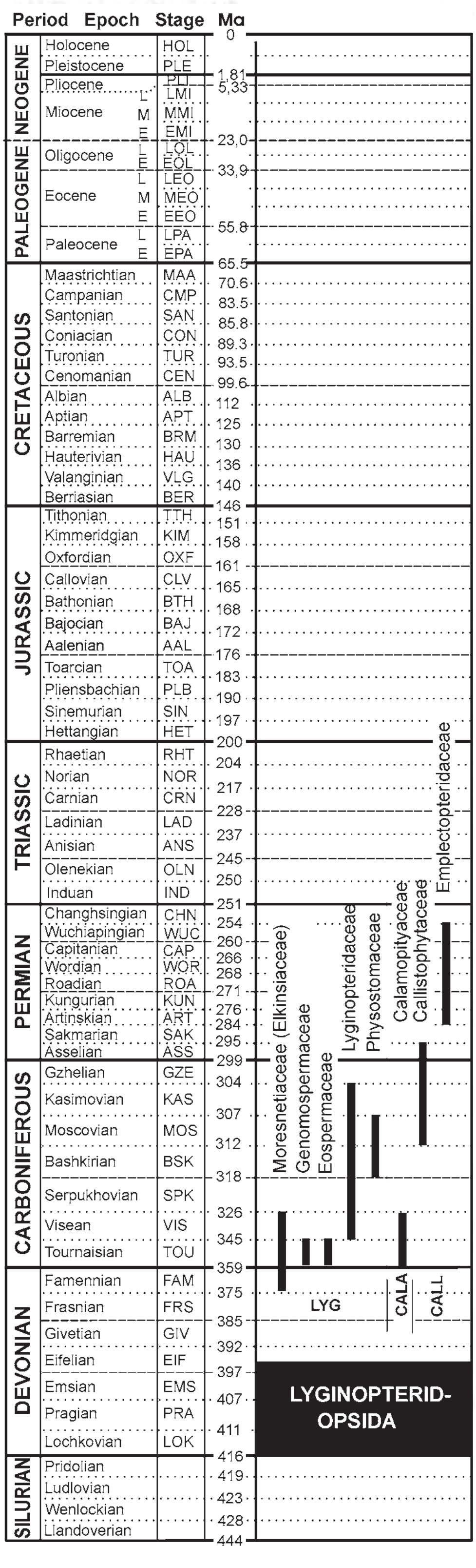
Polylophospermaceae (p. 150)
Reference whole-plant genus: *Polylophospermum*
Grand'croix, France
Organs known: dispersed ovules only (no affiliated organs)
Geostrat. occurrence: Euramerica Carboniferous, C(KAS);
from a single locality in France only

Whole-plant genus: A fossil-plant genus considered 'natural' that includes one or more organ-genera. For the Molteno Fm. (And. & And. 2003, p. 396), the term was applied only after comprehensive and systematic analysis of affiliations for the gymnosperms had been made. For the gymnosperms globally, the term cannot be as strictly adopted—the assessment of the affiliation of organs having been inconsistently applied in past research.

Whole-plant family: An extinct (fossil-plant) family considered 'natural' and based on a reference whole-plant genus'.

Whole-plant order: An extinct (fossil-plant) family considered 'natural' and based on a reference whole-plant family'.

Fig. 7. LYGINOPTERIDOPSIDA: FAMILY RANGE CHART



Class **LYGINOPTERIDOPSIDA** Novák 1961 emend. nov.

Diagnosis: Gymnospermous plants bearing ovules with a flask-shaped pollen chamber terminated by an elongate neck (salpinx/lagenostome/nucellar-beak) and that are supplied by a single vascular system.

Foliage: Frond-like with proximal dichotomy of primary rachis.

Remarks

Emended diagnosis: Cleal (1993) interpreted this as a monotypic class and thus gave no diagnosis. However, it is now evident that the Lyginopteridales share a number of key characters with the Calamopityales and Callistophytales, and that the latter two orders may also be incorporated within the class, which thus requires a new diagnosis.

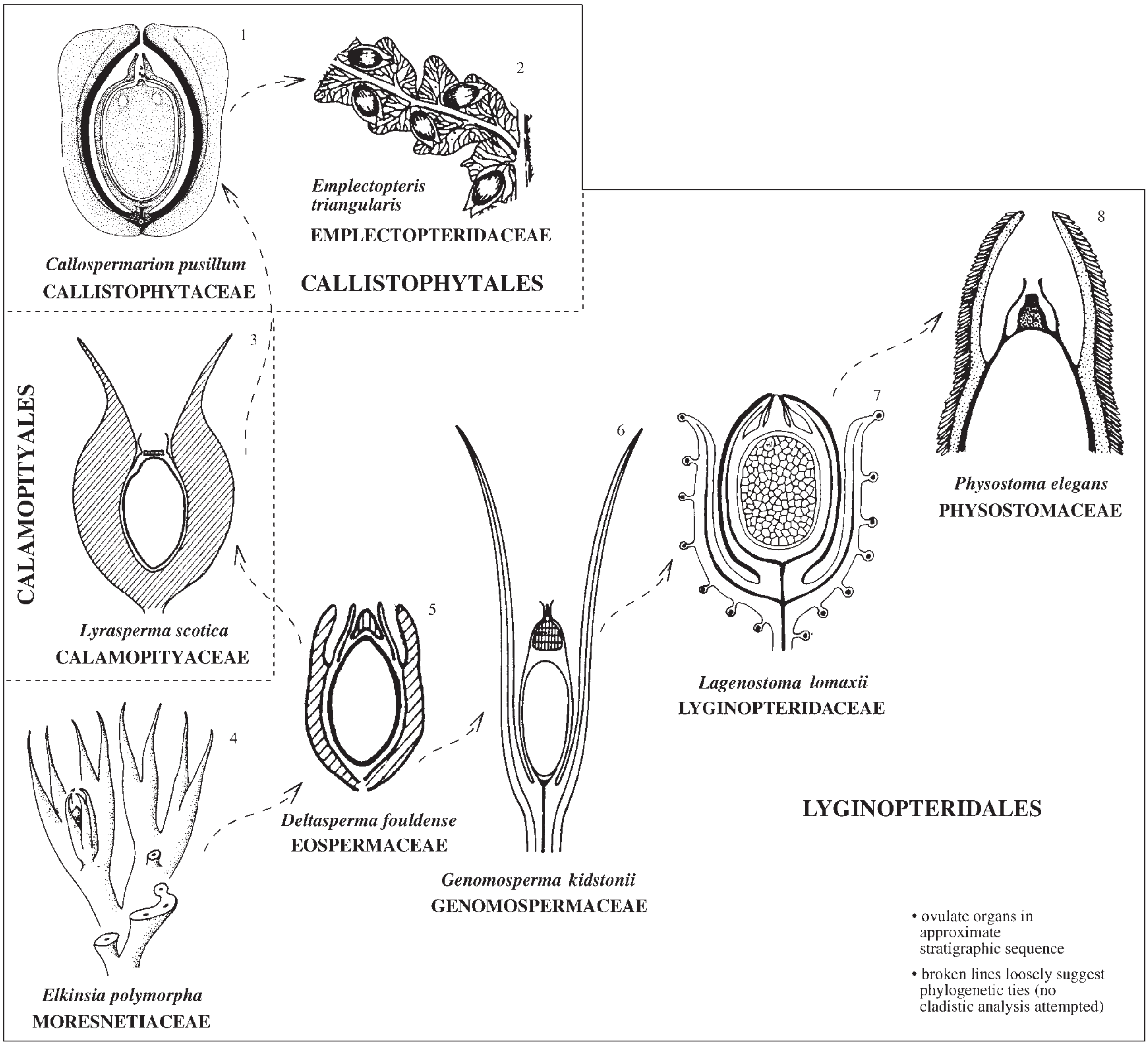
Classification: Doweld (2001) assigned this class to its own phylum, but we have adopted a more traditional approach and kept the taxonomic division of these plants to lower ranks. Doweld also separated the hydrasperman pteridosperms with preovules (i.e. the nucellus is not fully enclosed by an integument) into their own division (Moresnetiophyta Doweld). However, we do not regard this as warranted in view of the underlying similarities of these plants, especially of their ovules and foliage.

Orders: Includes the three orders Lyginopteridales, Calamopityales and Callistophytales.

Tab. 22. LYGINOPTERIDOPSIDA

CLASS ORDER Family	generic diversity			affiliation grade			morphology grade			anatomy preserved		
	♀	♂	⬯	♀	♂	⬯	♀	♂	⬯	♀	♂	⬯
LYGINOPTERIDOPSIDA Novák 1961 emend. nov.												
LYGINOPTERIDALES Corsin 1960												
Moresnetiaceae Němejc 1963 emend. nov.	7	-	1	5	-	4	4	-	2	✓	-	-
Genomospermaceae A.G.Long 1975	1	-	1	5	-	4	2	-	3	✓	-	-
Eospermaceae A.G.Long 1975	4	-	-	5	-	-	2	-	-	✓	-	-
Lyginopteridaceae Potonié 1900 emend. nov.	6	1	5	5	3	4	5	5	5	✓	✓	✓
Physostomaceae A.G.Long 1975	1	-	-	5	-	-	2	-	-	✓	-	-
CALAMOPITYALES Němejc 1963												
Calamopityaceae Solms. 1896	3	-	1	5	-	2	3	-	4	✓	-	✓
CALLISTOPHYTALES G.W.Rothwell 1981 emend. nov.												
Callistophytaceae Stidd & J.W.Hall 1970	1	1	1	5	4	4	4	4	4	✓	✓	✓
Emplectopteridaceae R.H.Wagner 1967	1	1	2	5	2	2	2	1	3	-	-	-

Fig. 8. LYGINOPTERIDOPSIDA: SIMPLIFIED PHYLOGENY (OVULATE ORGANS)



Order **LYGINOPTERIDALES** Corsin 1960

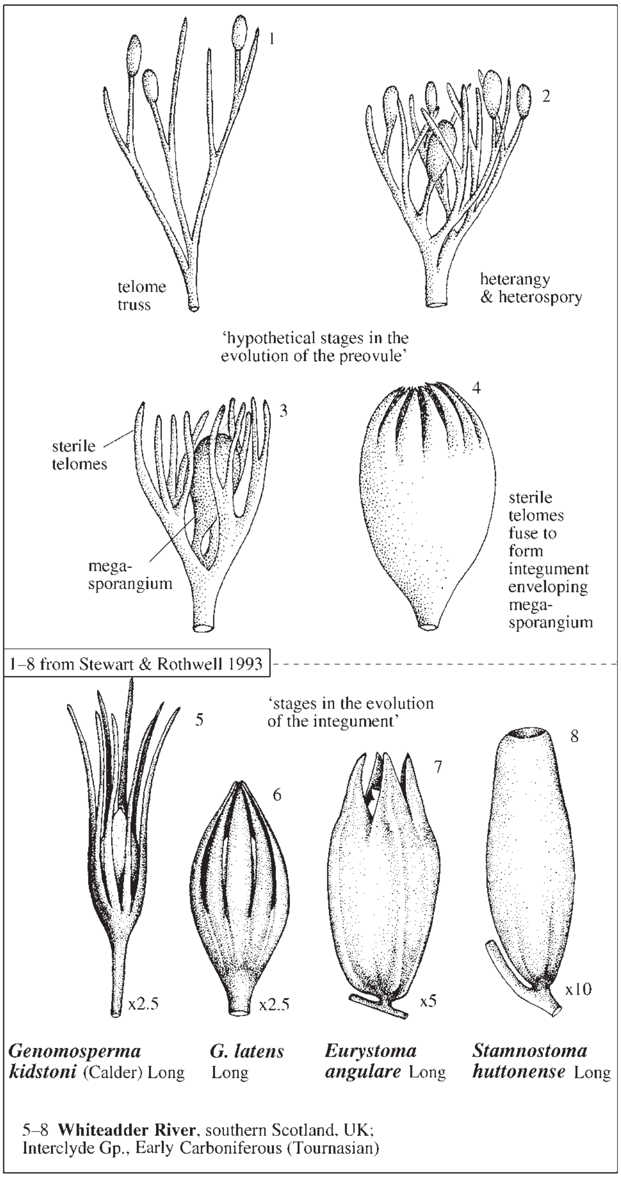
Diagnosis: Lyginopteridopsid plants with ovules in which the vascular tissue is only in inner portion of integument, none in nucellus; ovules borne in uniovular or multiovular cupules; lagenostome closed after pollination by cellular plug or column.

Male: Pollen organs compound, consisting of clusters of usually elongate pollen sacs; prepollen trilete or monolete.
Foliage: Fronds bi- to quadripartite.
Stem: Protostelic or eustelic.

Remarks
Taxonomy/diversity: This order essentially corresponds to the group of Palaeozoic pteridosperms with hydrasperman ovules (Serbet & Rothwell 1995). There are records of lyginopteridalean foliage and reproductive organs from the topmost Carboniferous of Euramerica (Mamay 1992) but it is unclear to which family they belong. The discovery that the Early Carboniferous foliage morphogenera *Rhacopteris* Schimper 1869 and *Spathulopteris* Kidston 1923 are lyginopteridalean (Galtier *et al*. 1998) indicates that there is far greater diversity among the early members of the order than indicated in the following classification.

Nomenclature: For discussion on the controversial nature of the nomenclature surrounding Palaeozoic pteridosperms, see text on pp 20, 21.

Families: Includes the five families Moresnetiaceae, Genomospermaceae, Eospermaceae, Lyginopteridaceae and Physostomaceae.



1–8 from Stewart & Rothwell 1993

Genomosperma kidstoni (Calder) Long ***G. latens*** Long ***Eurystoma angulare*** Long ***Stamnostoma huttonense*** Long

5–8 **Whiteadder River**, southern Scotland, UK;
Interclyde Gp., Early Carboniferous (Tournasian)

Family **MORESNETIACEAE** Němejc 1963 emend. nov.

Diagnosis: Lyginopteridalean plants with radiospermic ovules borne in multiovular cupules; distal part of nucellus exposed and forms a wide lagenostome with a prominent conical to flask-shaped central plug; integument adnate to nucellus only in proximal part of ovule.

Range: Euramerica, D(FAM)–C(VIS)
First: *Elkinsia polymorpha* Rothwell *et al*. 1989, Hampshire Fm., West Virginia, USA.
Last: *Calathospermum scoticum* Walton 1949, Loch Humphrey Burn, Scotland. This is based on anatomically preserved material. Adpression multiovular cupules of similar type known from the slightly younger Oil Shale Gp., Lothian Region, Scotland (Andrews 1940).

Reference whole-plant genus & stratum—Hampshire Fm.
Elkinsia Rothwell *et al*. 1989 (including ovules, foliage and anatomically preserved stems); 1 TC, 1 sp., abundant (100s of indivs).

Stratum: Hampshire Fm. (FAM), near Elkins, West Virginia, USA (Rothwell *et al*. 1989; Serbert & Rothwell 1992).
Affiliations: Stems and foliage Grade 5 (Org.att.); reproductive organs with rest of plant Grade 4 (Mut.occ.).

Prominence (colonisation success)—Euramerica Late Dev.–Early Carb.
Frequency/ubiquity: Fossils unequivocally known only from one locality, but was probably originally widespread, at least in Euramerica.
Diversity: 1 species.
Abundance: Reportedly abundant within its only known locality but no absolute data are available.
Longevity: Known only from a single stratigraphic level, but probably lived for *ca* 50 my.

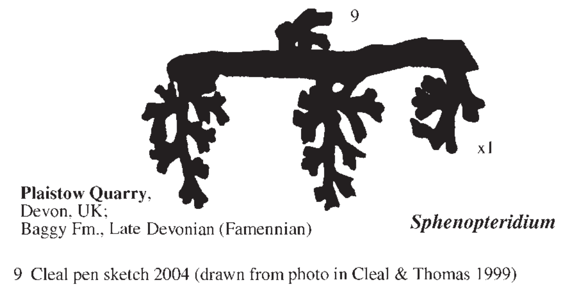
Ecology
Habit: Small woody plant about 1 m high.
Habitat: Found in deltaic strata and may have originated from riparian habitats.

Other genera
Female (cupulate structures): *Calathospermum* Walton 1940, *Moresnetia* Stockmans 1946, *Stamnostoma* Long 1960a, *Archaeosperma* Pettitt & Beck 1968, *Kerryia* Rothwell & Wight 1989, *Pullaritheca* Rothwell & Wight 1989.
Isolated ovules: *Salpingostoma* Gordon 1941, *Hydrasperma* Long 1961b; from two or three of the above cupulate structures.

Remarks
Nomenclature: This family was referred to by Cleal (1993) as the Elkinsiaceae, following Rothwell *et al*. (1989) but, as indicated by Doweld (2001), this name was not validly published as no diagnosis was ever given. Moresnetiaceae Němejc (1963) takes priority, although its diagnosis is in need of emendation to make it coincident with the concept that Rothwell *et al*. clearly had for this taxon.

Other genera: The family includes most of the primitive lyginopteridalean pteridosperms with hydrasperman ovules. Another small woody plant similar to *Elkinsia* was the *Calathospermum fimbriatum*-bearing plant from the Oxroad Bay flora, southern Scotland (TOU) (Retallack & Dilcher 1988). This favoured well-drained habitats associated with volcanic activity. In contrast, the *Stamnostoma*-bearing plant (TOU) which, based on ovule anatomy, was also elkinsiacean, was a substantial tree growing in well-drained alluvial terraces associated with lagoons (Retallack & Dilcher 1988). The reconstructed plant *Diplopteridium holdenii* Lele & Walton 1962 (Rowe 1988) from the upper Viséan might also belong to this family, but details of the ovules were not preserved.

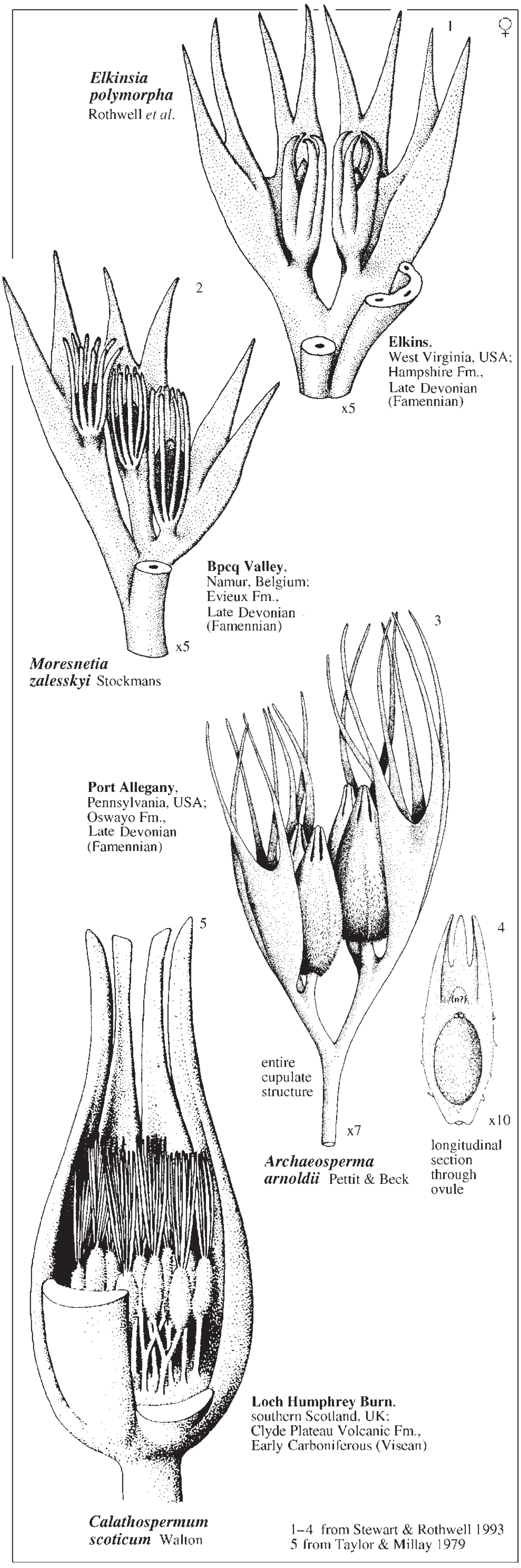
References
Rothwell (1982), Rothwell & Scheckler (1988): General.
Rothwell et al. (1989), Serbet & Rothwell (1992): Reconstruction of *Elkinsia* plant.



Plaistow Quarry, Devon, UK;
Baggy Fm., Late Devonian (Famennian)

Sphenopteridium

9 Cleal pen sketch 2004 (drawn from photo in Cleal & Thomas 1999)



Elkinsia polymorpha Rothwell *et al.*

Elkins,
West Virginia, USA;
Hampshire Fm.,
Late Devonian
(Famennian)

Bpcq Valley,
Namur, Belgium;
Evieux Fm.,
Late Devonian
(Famennian)

Moresnetia zalesskyi Stockmans

Port Allegany,
Pennsylvania, USA;
Oswayo Fm.,
Late Devonian
(Famennian)

entire cupulate structure

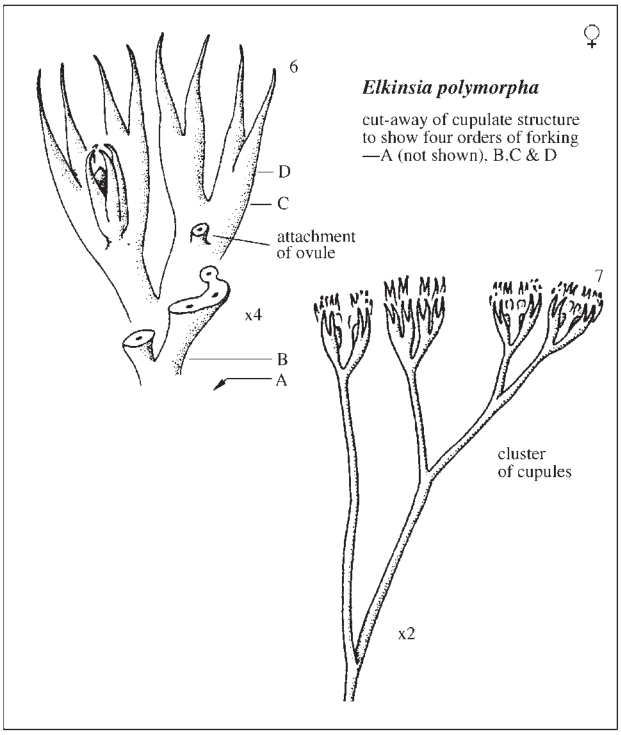
longitudinal section through ovule

Archaeosperma arnoldii Pettit & Beck

Loch Humphrey Burn,
southern Scotland, UK;
Clyde Plateau Volcanic Fm.,
Early Carboniferous (Visean)

Calathospermum scoticum Walton

1–4 from Stewart & Rothwell 1993
5 from Taylor & Millay 1979

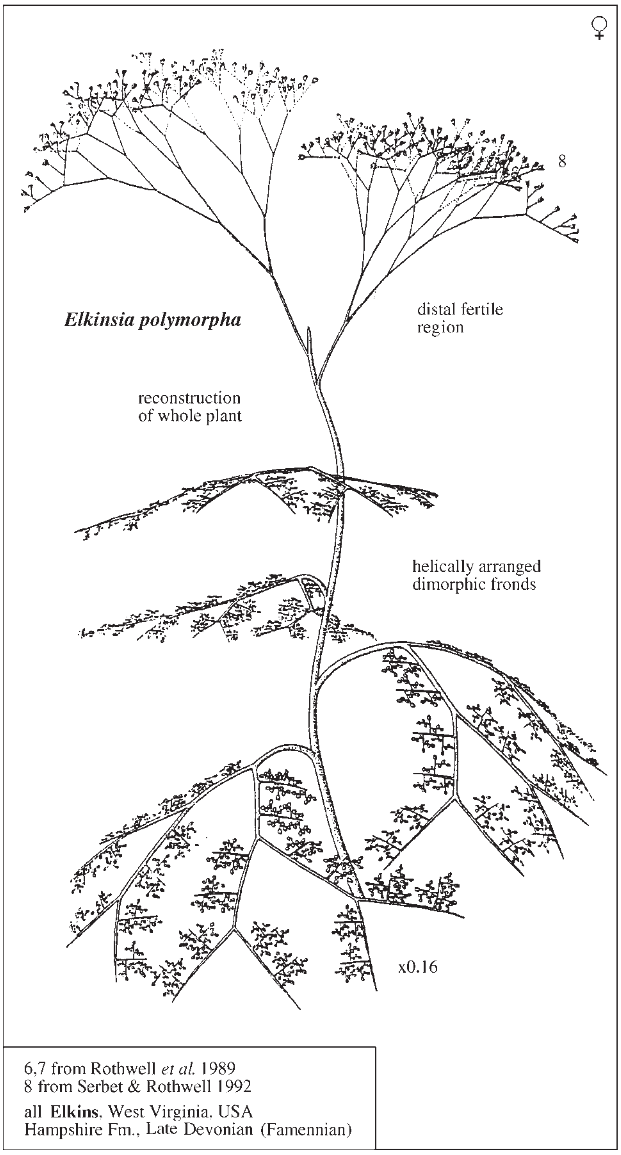


Elkinsia polymorpha

cut-away of cupulate structure to show four orders of forking —A (not shown), B,C & D

attachment of ovule

cluster of cupules



Elkinsia polymorpha

distal fertile region

reconstruction of whole plant

helically arranged dimorphic fronds

6,7 from Rothwell *et al.* 1989
8 from Serbet & Rothwell 1992
all **Elkins**, West Virginia, USA
Hampshire Fm., Late Devonian (Famennian)

Family **LYGINOPTERIDACEAE** Potonié 1900 emend. nov.

Diagnosis: Lyginopteridalean plants with radiospermic ovules bearing well-developed micropyle, noncupulate or borne in multi- or uniovular cupules; distal part of nucellus forms a broad, flask-shaped lagenostome with an obconical central plug; integument adnate with nucellus except near pollen chamber.

Range: Euramerica and Cathaysia, C(VIS–KAS); northern Gondwana (MOS)
First: *Sphaerostoma ovale* Benson 1914, Pettycur Limestone, southern Scotland, UK.
Last: *Gnetopsis elliptica* Renault & Zeiller 1884, Rive de Gier Fm., Grand'Croix, France (Galtier 1991). There are records of foliage probably of the Lyginopteridaceae from slightly younger strata (e.g. *Eusphenopteris rotundiloba* Němejc 1937). The records from the middle Permian of China (e.g. Shen 1995) need to be verified.

Reference whole-plant genus & stratum—Productive Coal Fm.
Female: *Lagenostoma* Williamson 1877; 6 TCs, 2 spp, rare.
Male: *Telangium* Benson 1904; 1 TC, 1 sp., rare.
Foliage/stem: *Lyginopteris* Potonié 1897; 3 TCs, 3 spp, abundant (up to 48% biomass in some coals).
Stem: *Lyginopteris oldhamia* (Binney) Potonié 1897.

Stratum: First Coal, lower Productive Coal Fm. (not Millstone Grit as stated by Retallack & Dilcher 1988), Lancashire, UK, C(BSK).
Affiliations: For the foliage, stems and ovules, Grade 4 (Anat.cor., Mut. occ.) (Retallack & Dilcher 1988); the affiliation of the pollen organs is Grade 3 (Mut.occ., Kin.rein.).

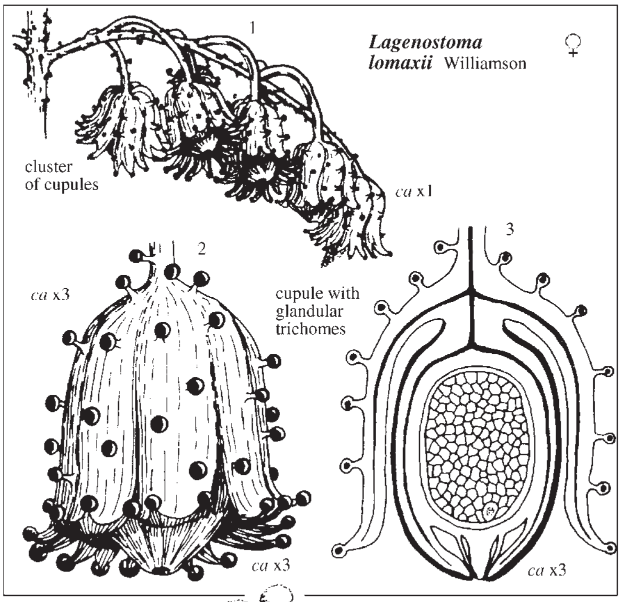
Prominence (colonisation success)—Euramerica Carboniferous
Frequency/ubiquity: *Lyginopteris* foliage is widespread in western palaeotropical floras, especially in late Viséan to upper Bashkirian. Records from the eastern palaeotropical floras (Cathaysia) are doubtful.
Diversity: 14 species (based on foliage of *Lyginopteris*).
Abundance: In late Bashkirian floras it is consistently occurring but usually at <1% of the adpression macrofloras (e.g. Davies 1929). Locally, however, it can comprise up to 38% of coal ball floras (Phillips 1981).
Longevity: *ca* 40 my.

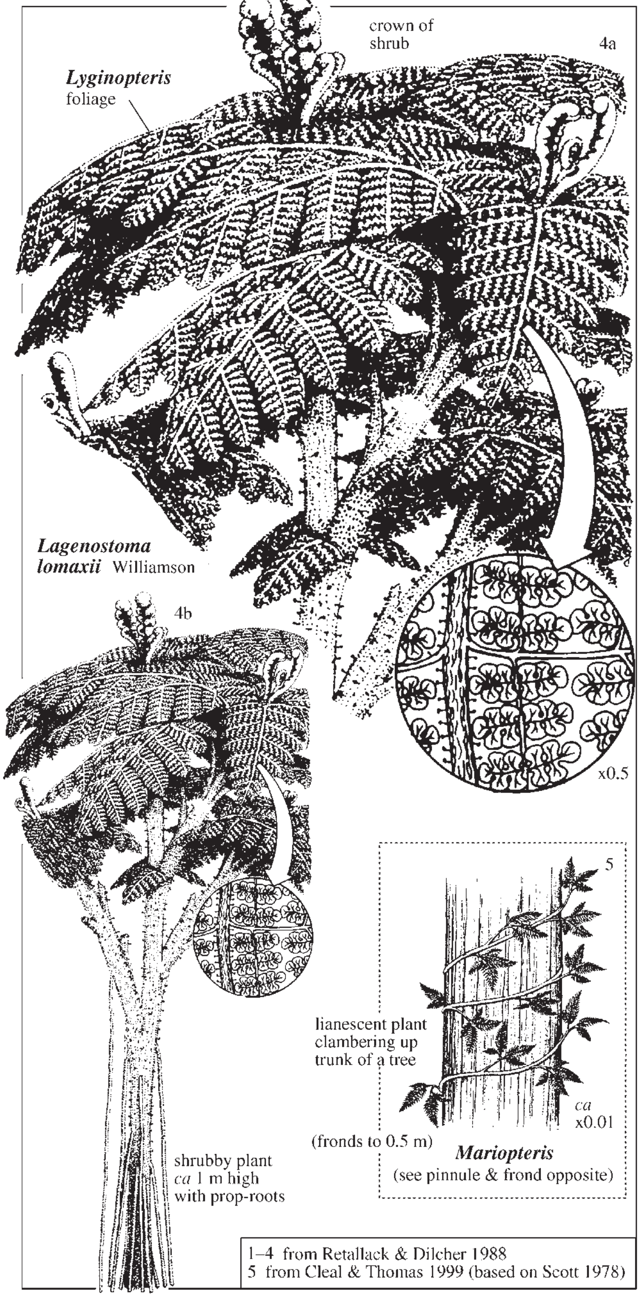
Ecology
Habit: Semi-self-supporting shrub with a tangle of prop roots (Retallack & Dilcher 1988; Speck 1994), perhaps with a liana-like habit (Tomescu *et al.* 2001).
Habitat: It is best-known from lowland coastal and peat-forming habitats, although it can occur in more inland habitats (e.g. Appalachians).

Other genera
Ovulate cupules: *Gnetopsis* Renault & Zeiller 1884, *Sphaerostoma* Benson 1914.
Isolated ovules: *Conostoma* Williamson 1877.
Male: *Telangiopsis* Eggert & Taylor 1971, *Feraxotheca* Millay & Taylor 1977.
Foliage: *Diplothmema* Stur 1877, *Mariopteris* Zeiller 1879, *Eusphenopteris* Simson-Scharold 1934, *Pseudomariopteris* Danzé-Corsin 1953.
Stems: *Heterangium* Corda 1845, *Schopfistriatum* Andrews 1945, *Microspermopteris* Baxter 1949.

Remarks
Taxonomy: This may be regarded as the archetypal pteridosperm family, as it includes the first 'fern-like' species for which ovules were shown to be almost certainly attached (Oliver & Scott 1904). In addition to the Reference whole-plant mentioned above, other part reconstructions have been proposed based on the correlation between the stem *Heterangium* and foliage *Eusphenopteris* (Shadle & Stidd 1975), and the stem *Schopfistriatum* and foliage *Mariopteris* Stidd & Phillips 1973). In neither case are anatomical details of the reproductive organs known, although the stem anatomy clearly points to them being lyginopteridacean. Both foliage morphogenera occur commonly in Westphalian floras.

References
Patteisky (1957), Boersma (1972), Van Amerom (1975): Foliage.
Taylor & Millay (1981): Pollen organs.
Galtier (1988): General.
Retallack & Dilcher (1988), Speck (1994), Tomescu et al. (2001): Reconstructions





1–4 from Retallack & Dilcher 1988
5 from Cleal & Thomas 1999 (based on Scott 1978)

1–4 **Shore, Littleborough**, Lancashire, UK; Upper Foot Coal, Pennine Coal Measure GP., Late Carboniferous (Bashkirian)

5 **Yorkshire Coalfield**, UK; Pennine Coal Measures Gp., Late Carboniferous (Moscovian)

Family **PHYSOSTOMACEAE** A.G.Long 1975

Diagnosis: Lyginopteridalean plants with radiospermic ovules bearing well-developed micropyle, not borne in cupules; distal part of nucellus forms a short, narrow lagenostome with a small central plug; integument adnate to nucellus in proximal half of ovule.

Range: Euramerica, C(BSK–MOS)
First: *Physostoma elegans* Williamson 1875, Upper Foot Seam, lower Productive Coal Fm., Lancashire, UK (BSK) (Oliver 1909).
Last: *Physostoma calcaratum* Leisman 1964, Cabaniss Subgroup, Kansas, USA (Leisman 1964). Cleal (1993) mentioned the record of a *Physostoma* ovule from the Viséan (Gordon 1910). However, this was based on poorly preserved material and is well outside of the normal stratigraphic range of the genus.

Reference whole-plant genus & stratum—Upper Foot Seam
Female: *Physostoma* Williamson 1877; 9 TCs, 2 spp, rare.
Foliage: Unknown.
Male: Unknown.

Stratum: As for ‘First’ above.
Affiliations: Nil.

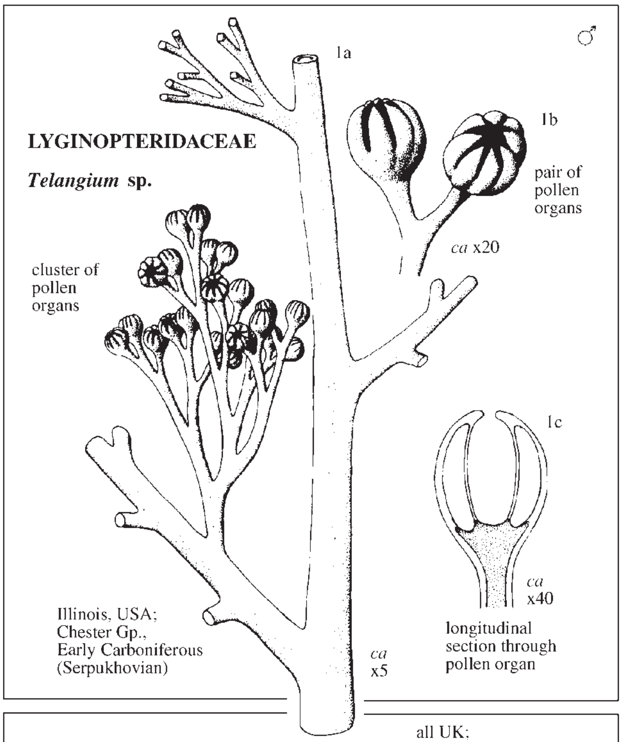
Prominence (colonisation success)—Euramerica Late Carboniferous
Frequency/ubiquity: *Physostoma* ovules are widespread (13 TCs) in the coal-ball floras of Europe and North America.
Diversity: 5 species (based on ovules).
Abundance: Never abundant (at best ‘rare’, <0.1%), but no absolute data are available.
Longevity: *ca* 0.5 my or less.

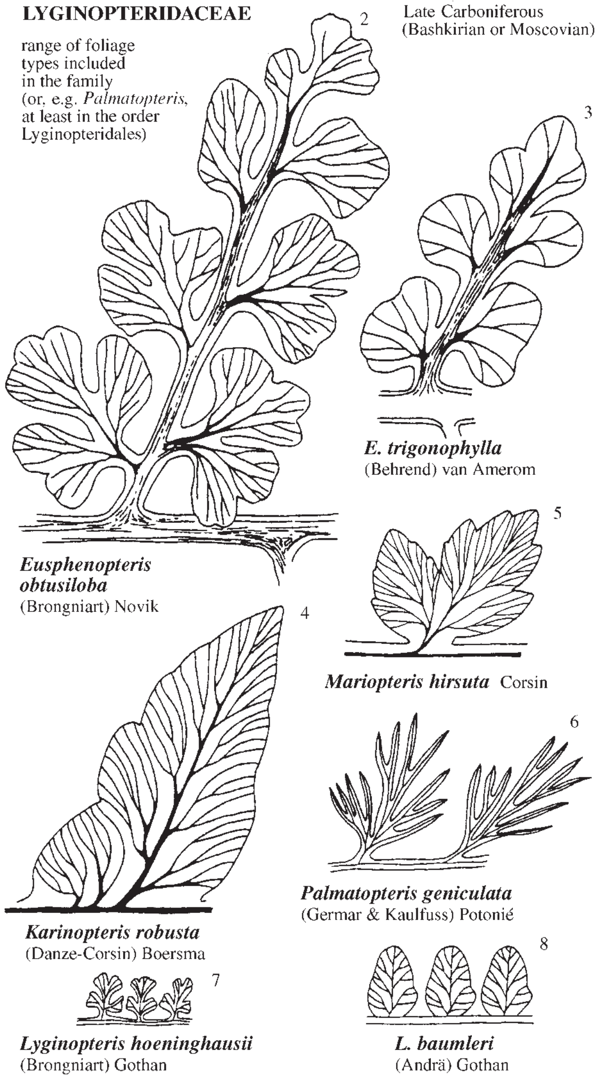
Ecology
Habit: No direct evidence, but from related families it is likely to have been a lianescent plant or small shrub.
Habitat: Lowland coastal, especially areas marginal to peat-forming habitats.

Other genera—nil.

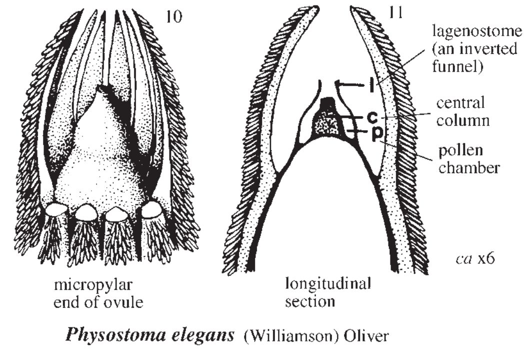
Remarks
Taxonomy: This is a poorly understood family known only from the isolated ovules *Physostoma*. In some ways it is analogous to the Genomospermaceae, except that the ovules have a micropyle. However, more needs to be found out about the plants that bore these ovules before their relationship can be properly established.

References
There are no recent reviews of this group.



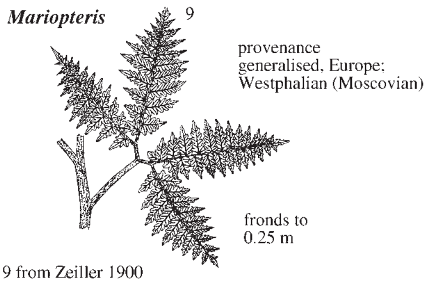


1 from Taylor & Taylor 1993 (from Millay & Taylor 1979)
2–8 from Cleal & Thomas 1994



Lancashire, UK;
Upper Foot Coal, Pennine Coal Measure Gp.,
Late Carboniferous (Bashkirian)

10,11 from Stewart & Rothwell 1993
(10 redrawn from Niklas 1981, 11 redrawn from Andrews 1963)



9 from Zeiller 1900

Family **GENOMOSPERMACEAE** A.G.Long 1975

Diagnosis: Lyginopteridalean plants with radiospermic ovules; hydrasperman, not borne in cupules; distal part of nucellus forms a short, narrow lagenostome with a small central plug; integument completely free from nucellus.

Range: Euramerica, C(TOU)
First & Last: *Genomosperma kidstonii* Long 1959 and *G. latens* Long 1959, Inverclyde Gp. (Cementstone Gp.), Borders Region, southern Scotland, UK (Long 1959).

Reference whole-plant genus & stratum—Inverclyde Gp.
Female: *Genomosperma* Long 1959; 6 TCs, 2 spp, rare.
Foliage: *Lyginorachis* Long 1964b; 6 TCs, 1 sp., 8 indivs.
Male: Unknown.
Stem: *Rhetinangium* Gordon 1912; 2 TCs, 1 sp., 2 indivs.

Stratum: As for 'First & Last' above.
Affiliations: Grade 4 (Anat.cor., Mut.occ.) (Long 1964b).

Prominence (colonisation success)—Euramerica Early Carboniferous
Frequency/ubiquity: Known only from 7 TCs in a small area of SE Scotland (Berwickshire).
Diversity: 2 species (based on ovules).
Abundance: Rare, but no absolute figures available.
Longevity: <1 my; all known specimens from about the same stratigraphic level.

Ecology
Habit: No direct evidence, but may have been small trees.
Habitat: Fossils found in lacustrine deposits, so the plant probably lived by the lake margins, or possibly on the banks of rivers that fed the lake.

Other genera—nil.

Remarks
Taxonomy: This is a poorly understood family known only from the isolated ovules *Genomosperma*. Long (1959) believed that they were not borne in cupules but this is highly speculative. Doweld (2001) synonymised this family with the Moresnetiaceae, but we retain them as separate in view of the differences in the central column of the pollen chamber.

Reference
Long (1959): Ovules.

Family **EOSPERMACEAE** A.G.Long 1975

Diagnosis: Lyginopteridalean plants with platyspermic ovules; hydrasperman, not borne in multiovular cupules; distal part of nucellus forms a tapered lagenostome with an obconical central plug; integument adnate to nucellus below lagenostome.

Range: Euramerica, C(TOU)
First & Last: *Eosperma edromense* Long 1966, *Deltasperma fouldense* Long 1961a, *Eccroustosperma langtonense* Long 1961b and *Camptosperma berniciense* Long 1961a, Inverclyde Gp. (Cementstone Gp.), southern Scotland, UK.

Reference whole-plant genus & stratum—Inverclyde Gp.
Female: *Eosperma* Barnard 1959; 2 TCs, 2 spp, >200 indivs.
Foliage: Unknown.
Male: Unknown.

Stratum: As for 'First & Last' above.
Affiliations: Nil.

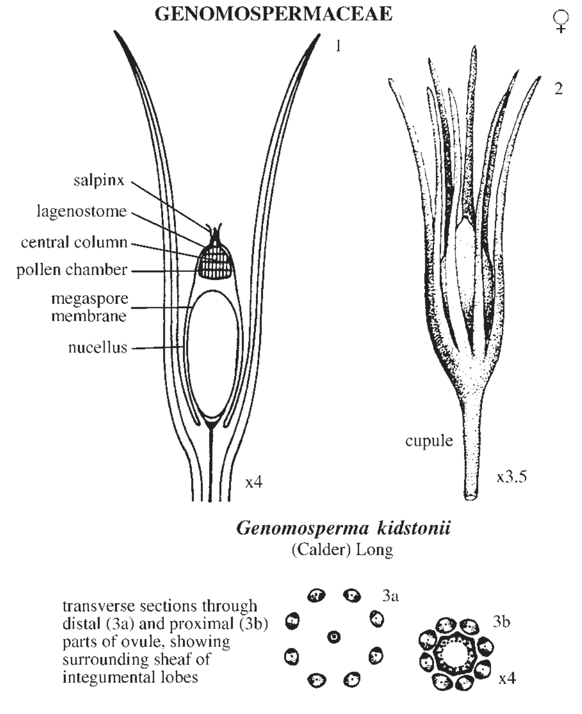
Prominence (colonisation success)—Euramerica Early Carboniferous
Frequency/ubiquity: Known from several TCs in SE Scotland (Berwickshire).
Diversity: 5 species (based on ovules).
Abundance: Never abundant but absolute figures not available.
Longevity: <1 my; known only from a single stratigraphic level.

Ecology
Habit: As for *Genomosperma*.
Habitat: As for *Genomosperma*.

Other genera
Isolated ovules: *Camptosperma* Long 1961a, *Deltasperma* Long 1961a, *Eccroustosperma* Long 1961b.

Remarks
Taxonomy: Like the Genomospermaceae, this is a poorly understood family known only from isolated ovules. Long (1961a, 1961b, 1966) believed at they were not borne in cupules but this is highly speculative.

References
Long (1961a, 1961b, 1966): Ovules.

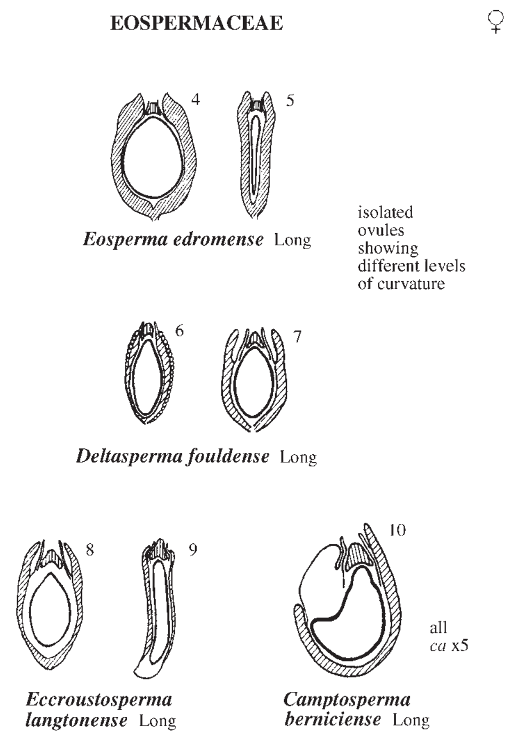


Genomosperma kidstonii
(Calder) Long

transverse sections through distal (3a) and proximal (3b) parts of ovule, showing surrounding sheaf of integumental lobes

1 from Stewart & Rothwell 1993
2–3 from Long 1959

all **Whiteadder River**, southern Scotland, UK;
Inverclyde Gp. (Cementstone Gp.),
Early Carboniferous (Tournasian)



Eosperma edromense Long

isolated ovules showing different levels of curvature

Deltasperma fouldense Long

Eccroustosperma langtonense Long

Camptosperma berniciense Long

4–10 from Cleal & Thomas 1995 (based on Long 1961, 1966)

all **Whiteadder River**, southern Scotland, UK;
Inverclyde Gp. (Cementstone Gp.),
Early Carboniferous (Tournasian)

Order **CALAMOPITYALES** Němejc 1963

Diagnosis: Lyginopteridopsid plants with ovules of varying symmetry, controlled by 2, 3, 4 or 6 vascular bundles extending through integument, and nucellus adnate to integument except near ovule apex; vascular tissue in ovule only in inner portion of integument, none in nucellus; ovules borne in multiovular cupules; lagenostome closed after pollination by cellular plug or column.

Male: Prepollen trilete.
Foliage: Fronds bi- to quadripartite.
Stem: Protostelic or eustelic.

Family: Includes the single family Calamopityaceae.

Family **CALAMOPITYACEAE** Solms 1896

Diagnosis: As for the Calamopityales.

Range: Euramerica, C(TOU–VIS)
First: *Calamopitys americana* Scott & Jeffrey 1914, *C. foerstii* Read 1936a, *Stenomyleon muratum* Read 1936a, *Diichnia kentukiensis* Read 1936b and *Bostonia perpelxa* Stein & Beck 1978, Falling Run Member, New Albany Shales, Kentucky, USA (see also Read 1937).
Last: *Kalymma* sp., Middle Visean, Loch Humphrey Burn, Scotland, UK (Bateman & Cleal 1995). Cleal (1993) gave a rather longer stratigraphic range for this family, based on the assumption that *Spathulopteris* fronds were calamopityacean. However, this is now known not to be the case (Galtier *et al*. 1998).

Reference whole-plant genus & stratum—Inverclyde Gp.
Female: *Lyrasperma* Long 1960b (possibly borne in *Alcicornopteris* Kidston 1887 cupules); mostly from loose blocks so number of TCs cannot be estimated, 1 sp., rare (46 indivs reported).
Male: Unknown.
Foliage: *Sphenopteridium* Schimper 1874 (known as *Kalymma* Unger 1856 when anatomically preserved); 6 TCs, 1 sp., abundant.
Stem: *Stenomyelon* Kidston in Scott 1909; 4 TCs, 2 spp, rare.

Stratum: Inverclyde Gp. (TOU), Foulden, SE Scotland, UK.
Affiliations: For the foliage and stems, Grade 5 (Org.att.) (Long 1964; see also Galtier 1981); for ovules to rest of plant, Grade 2 (Mut.occ.).

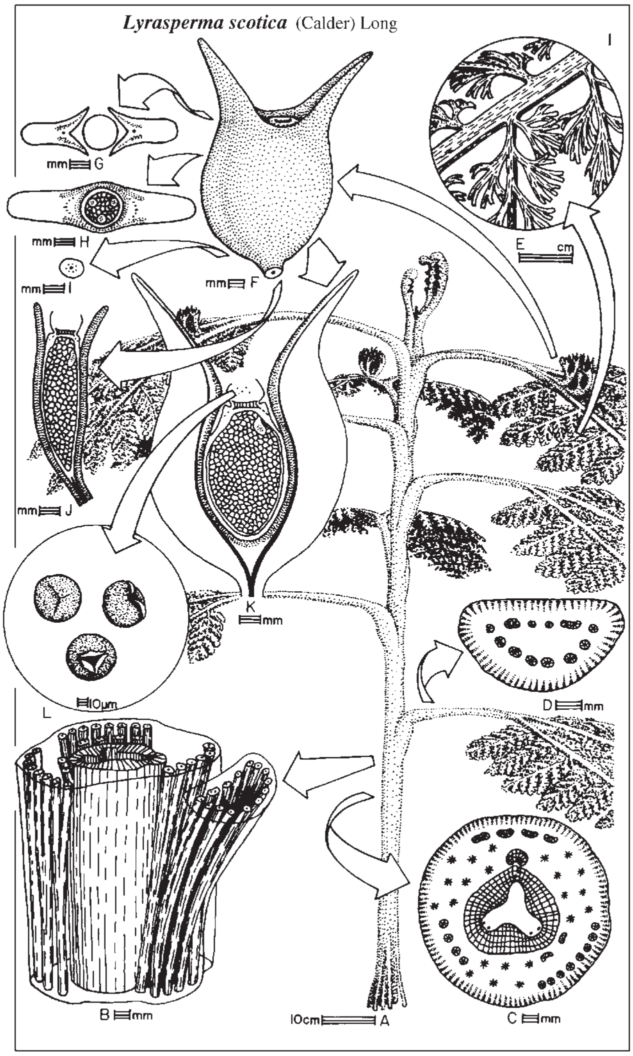
Prominence (colonisation success)—Euramerica Early Carboniferous
Frequency/ubiquity: Foliage and anatomically preserved stems are widespread in the Tournaisian of Europe and North America; to date, none are reported from Cathaysia.
Diversity: 8 species (based on ovulate structures associated with calamopityalean stems), although this is probably a significant underestimate of the original diversity.
Abundance: Usually abundant but no absolute data are available.
Longevity: *ca* 25 my.

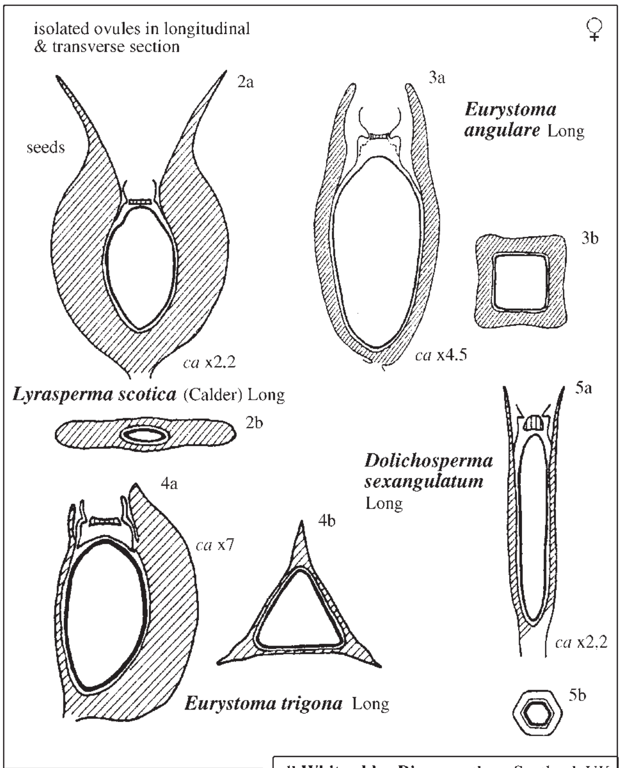
Ecology
Habit: Woody monoaxial plant about 1.5 m high (Retallack & Dilcher 1988).
Habitat: Mainly lowland coastal habitats.

Other genera
Ovulate organs: *Eurystoma* Long 1960b (cupules & ovules), *Dolichosperma* Long 1961b (isolated ovules only).
Stems: *Calamopitys* Unger 1854.

Remarks
Classification: Cleal (1993) followed Meyen (1987) and assigned this family to an unnamed class that otherwise included mainly Mesozoic pteridosperms. However, a re-examination of the evidence clearly points to these plants being most closely related to the Lyginopteridales, especially in view of the hydrasperman ovules, the bipartite fronds and the trilete prepollen. It is in fact arguable that the Calamopityaceae are merely a family within the Lyginopteridales, but we have here retained the traditional view of separating it as an order, but within the Lyginopteridopsida.

References
Long (1960): Ovules.
Galtier (1981): Foliage anatomy.
Retallack & Dilcher (1988): Reconstruction.
Galtier & Beck (1995): Stems.





1 from Retallack & Dilcher 1988
2–5 from Cleal & Thomas 1995

all **Whiteadder River**, southern Scotland, UK, Interclyde Gp., Early Carboniferous (Tournasian)

Order **CALLISTOPHYTALES** G.W.Rothwell 1981 emend. nov.

Diagnosis: Lyginopteridopsid plants with bilaterally symmetrical ovules, and with nucellus free from integument except in the basal one-fifth of the ovule; ovules noncupulate, borne on abaxial surface of unmodified pinnules; nucellar beak lacks a cellular plug or column.

Male: Pollen-bearing organs consisting of clusters of 2–8 basally fused sporangia.

Remarks
Emended diagnosis: The diagnosis has been modified so as to incorporate the Emplectopteridaceae.

Families: Includes the two families Callistophytaceae and Emplectopteridaceae.

Family **CALLISTOPHYTACEAE** Stidd & J.W.Hall 1970

Diagnosis: Callistophytalean plants with ovule enclosed by integument except for the micropyle; ovules attached medially to lateral veins.

Male: Pollen-bearing organs, consisting of 6–8 sporangia, attached to abaxial surface of unmodified pinnules; prepollen monosaccate of the *Vesicaspora*-type.
Foliage: Fronds bipartite, each branch tripinnately divided.
Stems: Eustelic with secretory system composed of spherical cavities lined with epithelium.

Range: Euramerica, C(MOS)–P(ASS)
First: *Dicksonites plueckenetii* (Sternberg) Sterzel 1881, middle Westphalian D of western Europe and the Canadian Maritimes (e.g. Cleal 1978, 1984; Zodrow & Cleal 1985).
Last: *Dicksonites beyrichii* (Weiss) Doubinger 1956, Lower Rotliegend, Saarland, Germany (Kerp & Fichter 1985).

Reference whole-plant genus & stratum—Upper Pennsylvanian
Female: *Callospermarion* Eggert & Delavoryas 1960; 1 TC, 1 sp., rare.
Male: *Idanothekion* Millay & Eggert 1970; 1 TC, 1 sp., v. rare.
Foliage: *Dicksonites* Sterzel 1881; 1 TC, 1 sp., abundant.
Stem: *Callistophyton* Delavoryas & Morgan 1954; 1 TC, 1 sp., abundant.

Stratum: Upper Pennsylvanian (KAS), Berryville locality, Illinois, USA.
Affiliations: Grade 4 (Anat.cor., Mut.occ.) (Stidd & Hall 1970; Rothwell 1975, 1980, 1981).

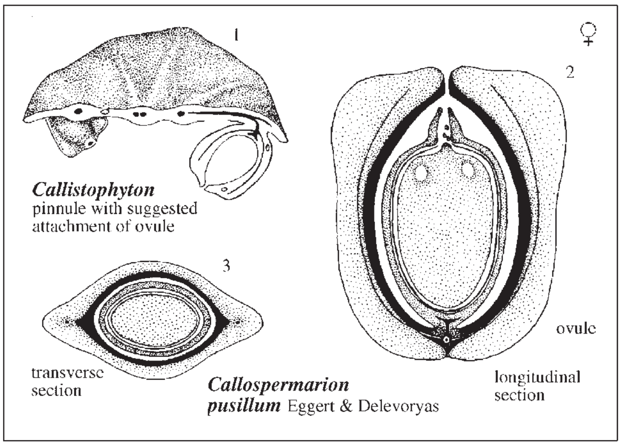
Prominence (colonisation success)—Euramerica, Late Carb.–Early Perm.
Frequency/ubiquity: *Dicksonites* foliage is widespread in western palaeotropical floras between the late Moscovian and Asselian.
Diversity: 4 species based on foliage (Guthörl 1952; Doubinger 1956).
Abundance: In late Moscovian floras, it is consistently occurring in adpression floras, at Radstock for instance forming 6% of the assemblage (Procter 1994). In Kasimovian coal-ball floras, *Callistophyton* stems can form 2–5% of the flora by volume (Phillips 1981).
Longevity: *ca* 15–20 my.

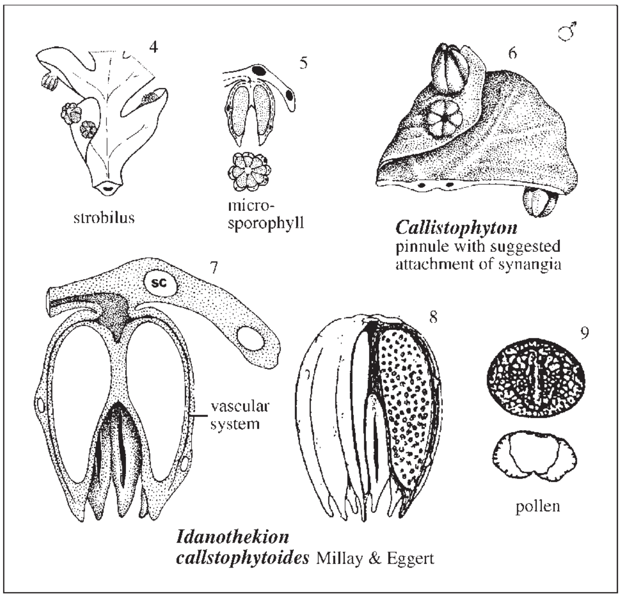
Ecology
Habit: Shrubby plant with a scrambling habit.
Habitat: Moist, somewhat shady understorey habitats, especially on disturbed ground (Retallack & Dilcher 1988).

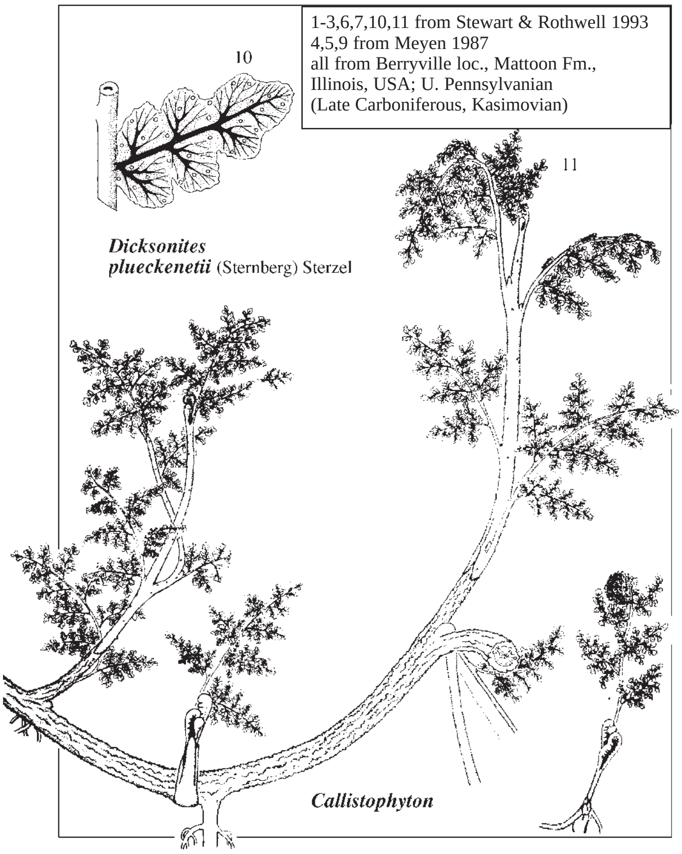
Other genera—nil.

Remarks
Classification: This is one of the best-documented families of pteridosperm, largely due to the work of Rothwell (1975, 1980, 1981). Cleal (1993) classified it with the peltaspermaleans and ‘glossopterids’, mainly following Meyen (1987), but a re-examination of the evidence now indicates that it is most closely related to the lyginopteridaleans (see also Doweld 2001). The reproductive strategy, especially the postpollination closure of the pollen chamber, is rather more sophisticated than in the lyginopteridaleans (Serbet & Rothwell 1994). However, the presence of a nucellar beak in the ovules (probably homologous to the lagenostome/salpinx of the Lyginopteridales), and the proximal dichotomy of the fronds (Galtier & Béthoux 2002), both indicate that the two orders are related.

References
Rothwell (1975, 1980, 1981): Stem and reproductive anatomy.
Retallack & Dilcher (1988): Reconstruction.
Galtier & Béthoux (2002): Foliage.






1-3,6,7,10,11 from Stewart & Rothwell 1993
4,5,9 from Meyen 1987
all from Berryville loc., Mattoon Fm., Illinois, USA; U. Pennsylvanian
(Late Carboniferous, Kasimovian)

Family EMPLECTOPTERIDACEAE R.H.Wagner 1967

Diagnosis: Callistophytalean plants with ovules attached to basal part of first lateral veins of pinnules.

Male: Pollen-bearing organs, consisting of 2–8 sporangia, attached to filiform microsporophylls.

Foliage: Fronds large, nonbipartite up to tripinnate, evolving towards simple coherent leaves by progressive fusion of pinnules and pinnae; pinnules in the pinnately divided fronds broadly based, confluent, somewhat asymmetric, with anastomosed or free veins arising from the midvein; intercalated pinnules on rachides of the penultimate order.

Range: Cathaysia, P(ART–WUC)

First: *Emplectopteris triangularis* Halle 1927, upper Shanxi Fm. (ART), Taiyuan Coalfield, Shanxi, northern China (Halle 1932).

Last: *Gigantonoclea taiyuanensis* (Asama) Li in ‘Gu & Zhi’ 1974, upper Tianlongsi Fm. (WUC), Taiyuan Coalfield, Shanxi, northern China (Asama 1962).

Reference whole-plant genus & stratum—Tianlongsi Fm.

Female: *Cornucarpus* Arber 1914; ? TCs, 3 spp, rare.

Male: *Jiaochengia* Wang 1999; 1 TC, 1 sp., rare.

Foliage: *Gigantonoclea* Koidzumi 1936; 10 TCs, 4 spp, abundant.

Stem: Unknown.

Stratum: Top of Tianlongsi Fm. (WUC), Huoshan section, Jiaocheng district, central Shanxi, northern China.

Affiliations: Foliage and male organs, Grade 3 (Mut.occ.) (Wang 1999); female organs and rest, Grade 2 (Kin.rein.) (Halle 1932; Wang 1999).

Prominence (colonisation success)—Cathaysia Permian

Frequency/ubiquity: *Gigantonoclea* foliage is a characteristic and widespread component of Permian floras of the one palaeocontinent Cathaysia (Glasspool *et al*. 2004).

Diversity: 31 species based on foliage (Shen 1995).

Abundance: Foliage of this family is normally abundant but there are no absolute data.

Longevity: *ca* 30 my.

Ecology

Habit: Shrubby plant with a scrambling or upright habit.

Habitat: Highly varied, from arid to moist or even aquatic conditions (Wang 1999).

Other genera

Foliage: *Emplectopteris* Halle 1927.

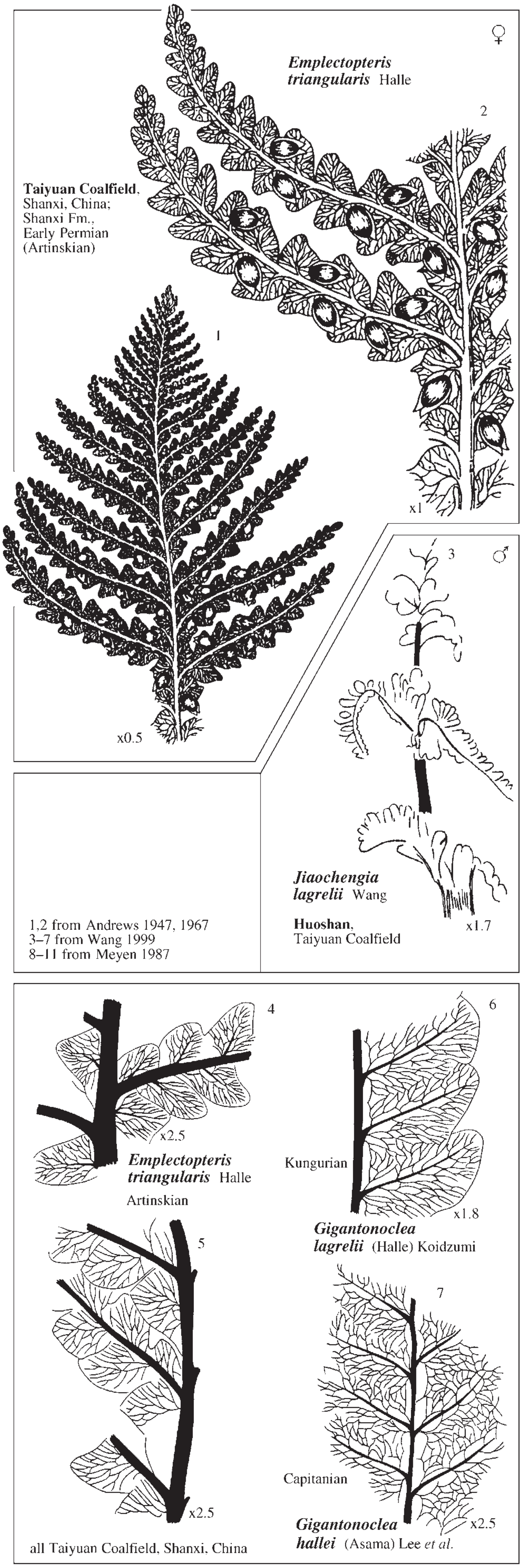
Remarks

Classification: Cleal (1993) interpreted this family very widely, to incorporate most if not all of the gigantopteroid plants in the Permian Cathaysian floras. However, Wang (1999) and Glasspool *et al*. (2004) have shown that such a circumscription is too wide. True *Gigantopteris* leaves have a complex venation pattern, and appear to be restricted to South China; these are assigned to the Gigantopteridaceae, within the Cycadopsida. Leaves with a less complex venation, and which occur in both South and North China, correspond to the *Emplectopteris* Series of Asama (1962), and are referred to here as the Emplectopteridaceae. Wang (1999) suggested that this family is most closely allied to the Callistophytaceae, and this view has been adopted here.

Fossil leaves resembling *Gigantonoclea* (e.g. Mamay 1986, 1988, 1989; Mamay *et al*. 1988) are widespread in the Permian of North America. However, the better known ‘gigantopterids’ from North America may be peltasperms, based on evidence of venation and associated reproductive structures (W.A. DiMichele, pers. comm., 2004).

Reference

Wang (1999): Foliage, pollen organs, distribution.



1,2 from Andrews 1947, 1967
3–7 from Wang 1999
8–11 from Meyen 1987

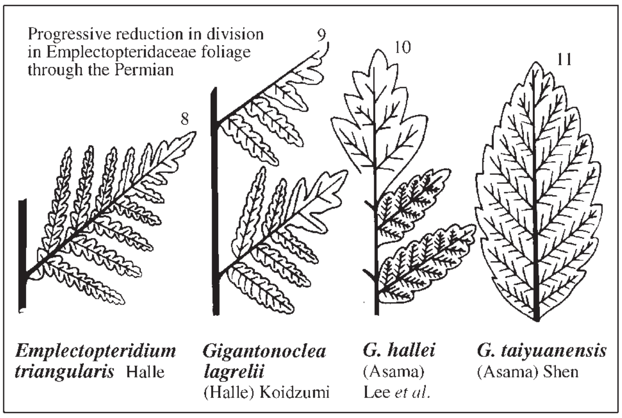
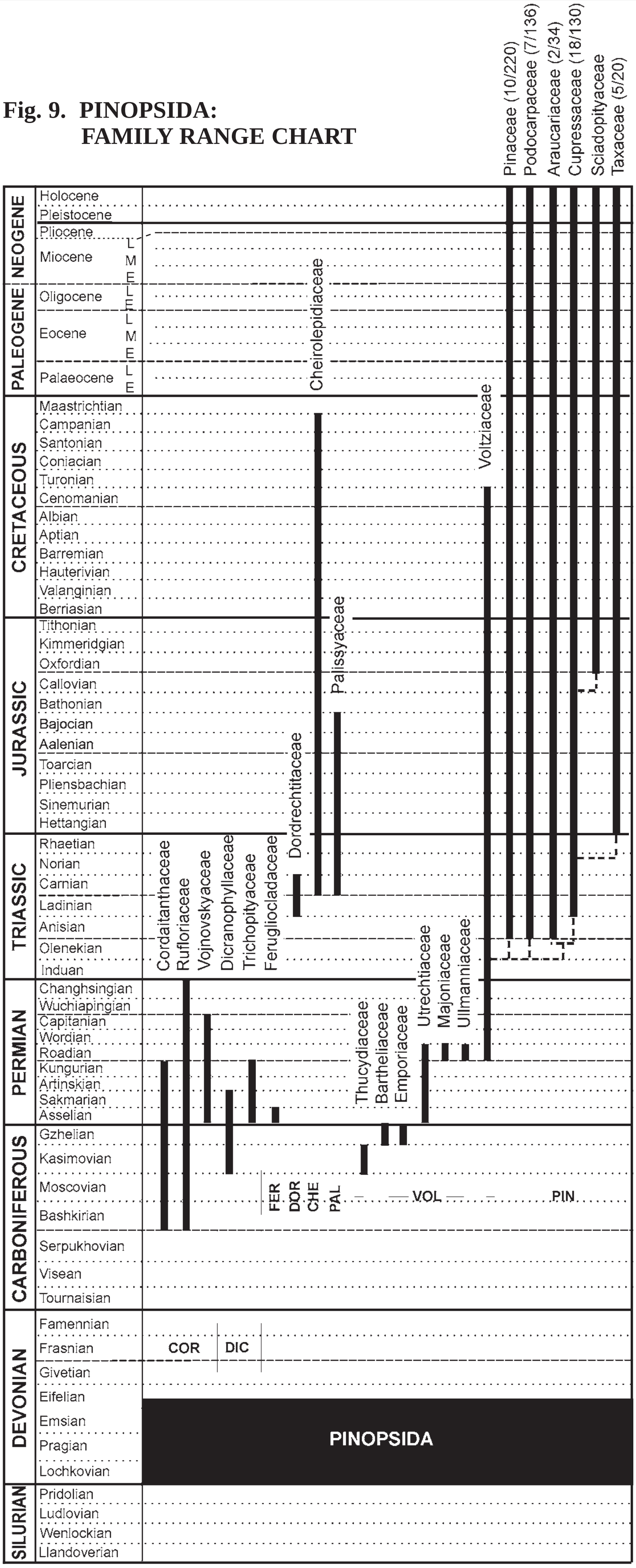


Fig. 9. PINOPSIDA:
FAMILY RANGE CHART



Class **PINOPSIDA** Burnett 1835

Diagnosis: Gymnospermous plants with megasporophylls consisting of bract/scale complexes in which the fertile scales—from compound radially symmetrical to simple bilaterally symmetrical—occur free to almost fully fused in the axils of sterile bracts.

Male: Cones compact, unisexual, helical, smaller and morphologically more conservative than ovulate cones, with simple microsporophyll units comprising scale and 2 to several microsporangia; pollen unisulcate, disaccate to nonsaccate.
Foliage: Helical, scale-like to linear, with a single midvein to several parallel and forking veins.

Classification

The classification is founded on that of Cleal (1993) who followed Meyen (1987) except that he included the Ginkgoales and gave an expanded treatment of the Palaeozoic conifers. Some further changes are made here to account for new insights from the Molteno and other sources: (a) the Ginkgoales are again excluded to conform with more recent cladistic analyses (see Hamby & Zimmer 1992 and later references in Kenrick, this volume, pp 18, 19); (b) the orders Ferugliocladales, Cheirolepidiales, Palissyales and Voltziales are split off from the Pinales, trimming the latter to more definable proportions; and (c) the new Molteno order Dordrechtitales is added.

Cladistics (phylogeny)
Molecular & morphological data: For a review of recent works on the phylogeny of both extinct and extant gymnosperms, see Kenrick (this volume, pp 18, 19).

Macrodiversity

Over the five years from 1997 to 2001 several authors, culminating in Doweld (Melikjan & Bobrov 1997; Doweld & Reveal 1999, 2001; Bobrov & Melikjan 2000; Doweld 2001), kindled an extraordinary inflation of higher taxa within the extant Pinopsida. In effect there occurred a six-fold increase of taxa at family level, a 15-fold increase at order level and a three-fold increase at class level, over the more traditional view as reflected in our own classification.

Doweld (2001)—extant taxa
Pinophyta: 1 phylum, 3 classes, 15 orders, 35 families

This volume—extant taxa
Pinopsida: 1 class, 1 order, 6 families

Were Doweld's classification of the extant 'conifers' adopted, the diversity histogram and macroevolutionary life cycle of the gymnosperms (Chart 1, p. 36) would appear entirely different. From the perspective of the 'observed' biodiversity alone, it would seem evident that the gymnosperm heyday were in the present day and not in the Late Triassic as here concluded. Of course, in the present, the *observed, preserved* and *existed* diversity (p. 71) converge to near equity, while they diverge greatly in all previous periods.

Orders: Includes the seven stem-orders Cordaitanthales, Dicranophyllales, Ferugliocladales, Dordrechtitales, Cheirolepidiales, Palissyales and Voltziales, and the single crown-order Pinales.

Tab. 23. PINOPSIDA

CLASS ORDER **Family**	**generic diversity**			**affiliation grade**			**morphology grade**			**anatomy preserved**		
	♀	♂	⬯	♀	♂	⬯	♀	♂	⬯	♀	♂	⬯
PINOPSIDA Burnett 1835												
CORDAITANTHALES S.V.Meyen 1984												
Cordaitanthaceae S.V.Meyen 1984	5	2	1	5	5	5	5	5	5	✓	✓	✓
Rufloriaceae Ledran 1966 emend. S.V.Meyen 1982a	4	2	1	5	3	3	4	4	4	-	-	-
Vojnovskyaceae M.F.Neuberg ex Y.A.Orlov 1963	1	1	1	5	2	3	4	3	4	-	-	-
DICRANOPHYLLALES S.V.Meyen 1984 emend. nov.												
Dicranophyllaceae S.Archang. & Cúneo 1990 emend. nov.	1	1	1	5	5	5	3	3	3	-	-	-
Trichopityaceae S.V.Meyen emend. nov.	1	-	1	5	-	5	2	-	2	-	-	-
FERUGLIOCLADALES Doweld 2001												
Ferugliocladaceae S.Archang. & Cúneo 1987	2	1	3	5	5	5	4	4	4	-	-	-
DORDRECHTITALES And. & And. 2003												
Dordrechtitaceae And. & And. 2003	1	-	-	5	-	-	3	-	-	-	-	-
CHEIROLEPIDIALES And. & And. order nov.												
Cheirolepidiaceae Takht. 1963	1	1	6	5	4	4	3	4	4	-	-	-
PALISSYALES Doweld 2001												
Palissyaceae Florin 1958	3	1	1	5	2	2	3	4	3	-	-	-
VOLTZIALES Andr. 1954												
Thucydiaceae Hern.-Cast., G.W.Rothwell & G.Mapes 2001	1	1	1	5	5	5	3	3	5	-	-	-
Bartheliaceae G.W.Rothwell & G.Mapes 2001	1	1	1	5	5	5	3	3	5	-	-	-
Emporiaceae G.Mapes & G.W.Rothwell 2003	1	1	1	5	5	5	3	3	5	✓	-	-
Utrechtiaceae G.W.Rothwell & G.Mapes 2003	4	4	4	5	5	5	3	1	5	-	-	-
Majonicaceae Clem.-West. 1987	2	1	2	5	5	5	3	2	5	-	-	-
Ullmanniaceae Němejc 1959	1	1	1	5	5	5	2	3	4	-	-	-
Voltziaceae C.A.Arnold 1947	13	6	?	5	5	5	4	4	5	-	-	-
PINALES Dumort. 1829												
Pinaceae Lindl. 1836 extant	**11**	**11**	**11**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**
Podocarpaceae Endl. 1847 extant	**19**	**19**	**19**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**
Araucariaceae Henkel & W.Hochst. 1865 extant	**3**	**3**	**3**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**
Cupressaceae Rich. ex Barkl. 1830 extant	**29**	**29**	**29**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**
Sciadopityaceae Luerss. 1877 extant	**1**	**1**	**1**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**
Taxaceae Gray 1821 extant	**6**	**6**	**6**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**

Fig. 10. PINOPSIDA: SIMPLIFIED PHYLOGENY (MEGASPOROPHYLLS)

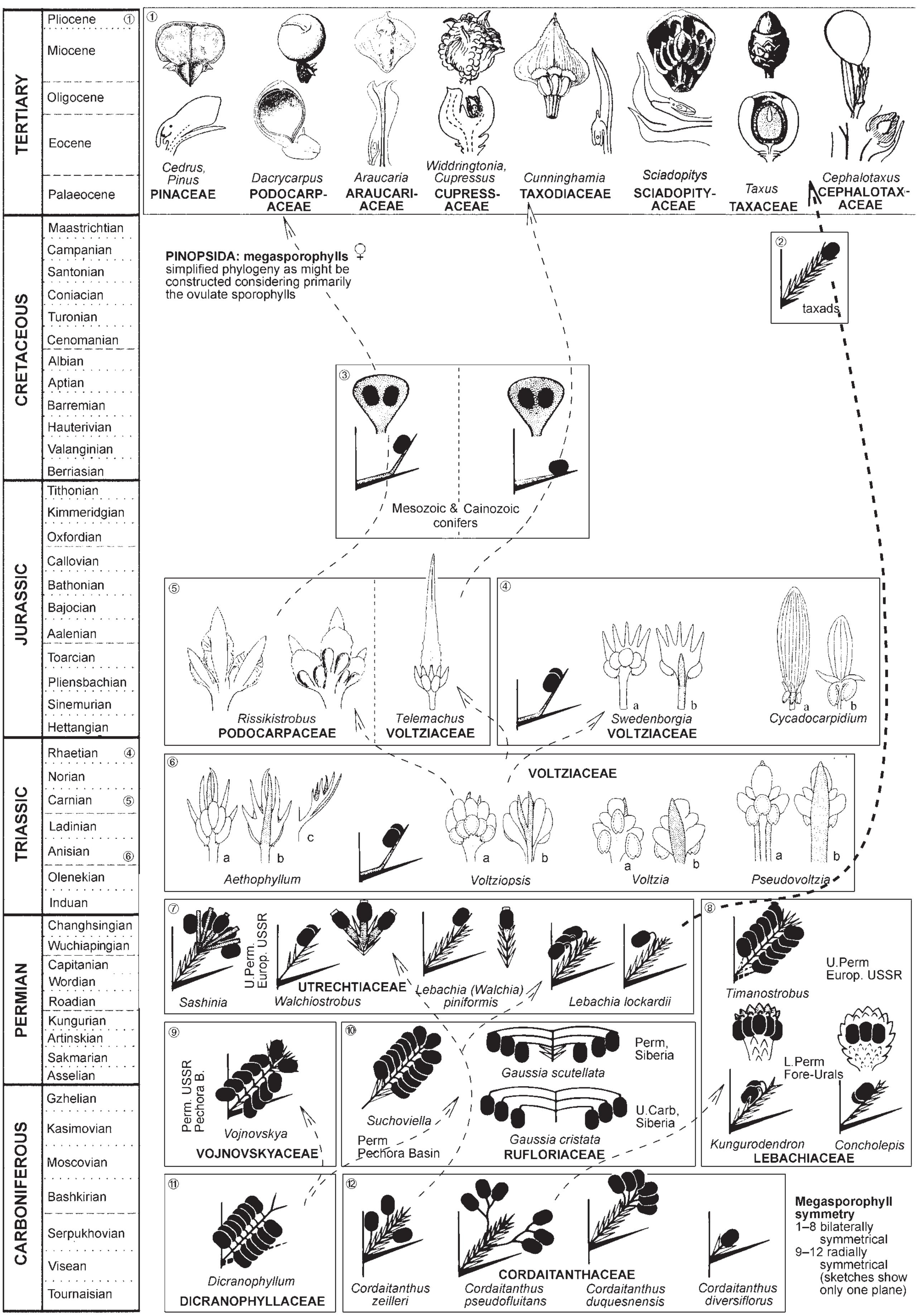
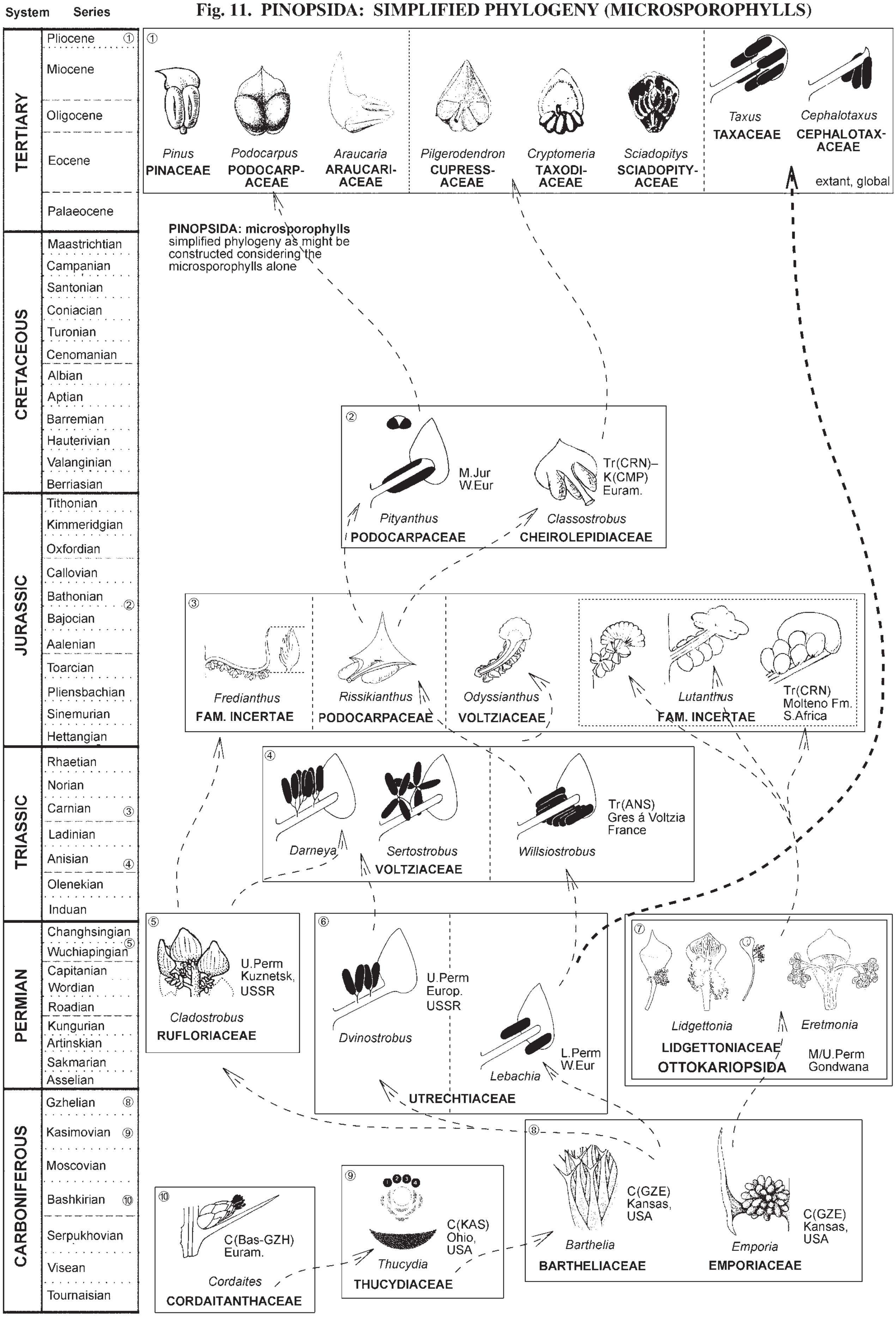


Fig. 11. PINOPSIDA: SIMPLIFIED PHYLOGENY (MICROSPOROPHYLLS)



Order **CORDAITANTHALES** S.V.Meyen 1984

Diagnosis: Pinopsid plants with reproductive organs borne in unisexual strobili consisting of helically arranged scales, which can be sterile or bear terminal clusters of ovules or of pollen sacs; ovules platyspermic.

Male: Pollen monosaccate.
Foliage: Leaves large, strap-like; veins parallel.

Remarks
Diagnosis & phylogeny: The above diagnosis is based on information in Meyen (1982, 1987, 1988), Rothwell (1988) and Trivett & Rothwell (1991). Early studies tended to indicate that the Cordaitanthales may have been ancestral to the Pinopsida, but the current consensus seems to be that they were a sister group to the primitive pinopsids.

Families: Includes the three families Cordaitanthaceae, Rufloriaceae and Vojnovskyaceae.

Family **CORDAITANTHACEAE** S.V.Meyen 1984

Diagnosis: Cordaitanthalean plants with strobili arranged in compound fertile structures (polysperms), consisting of two paired ranks of strobili on either side of the axis, the polysperm thus having an apparent decussate arrangement. Each strobilus was axillary to a slender bract; ovules borne erect on the fertile scales, with the integument partly free from nucellus.

Male: Male strobili similar to female strobili; pollen organs produced monosaccate pollen or prepollen.
Foliage: Leaves hypostomatic or amphihypostomatic; stomata on lower surface in distinct rows but not in stomatiferous furrows.
Stem: Trees or shrubs, with eustelic stems often with septate pith.

Range: Euramerica, C(BSK–GZE); Cathaysia, C(KAS)–P(KUN)
First: *Cordaitanthus pitcairniae* (Lindley & Hutton) Feistmantel 1876, Assise de Chokier, Belgium (Stockmans & Willière 1961).
Last: *Cordaitanthus rigidus* Shen 1995, Dahuangou Fm., Longshou Mountains, NW China. There are also Chinese records of foliage from as high as the Changhsingian Stage in South China, but they are not supported by reproductive structures.

Reference whole-plant genus & stratum—Duquesne Coal
Female: *Rothwelliconus* Ignatiev & Meyen 1989; 1 TC, 1 sp., rare.
Male: *Florinanthus* Ignatiev & Meyen 1989 (containing *Florinites* Schopf *et al*. 1944 pollen); 1 TC, 1 sp., rare.
Foliage: *Cordaites* Unger 1850; 1 TC, 1 sp., abundant.
Stem: *Cordaixylon* Grand'Eury 1877; 1 TC, 1 sp., moderately abundant.
Roots: *Amyelon* Williamson 1874.

Stratum: Duquesne Coal, Steubenville, Ohio, USA (KAS).
Affiliations: Grade 5 (Rothwell 1982; Rothwell & Warner 1984; Trivett & Rothwell 1991).

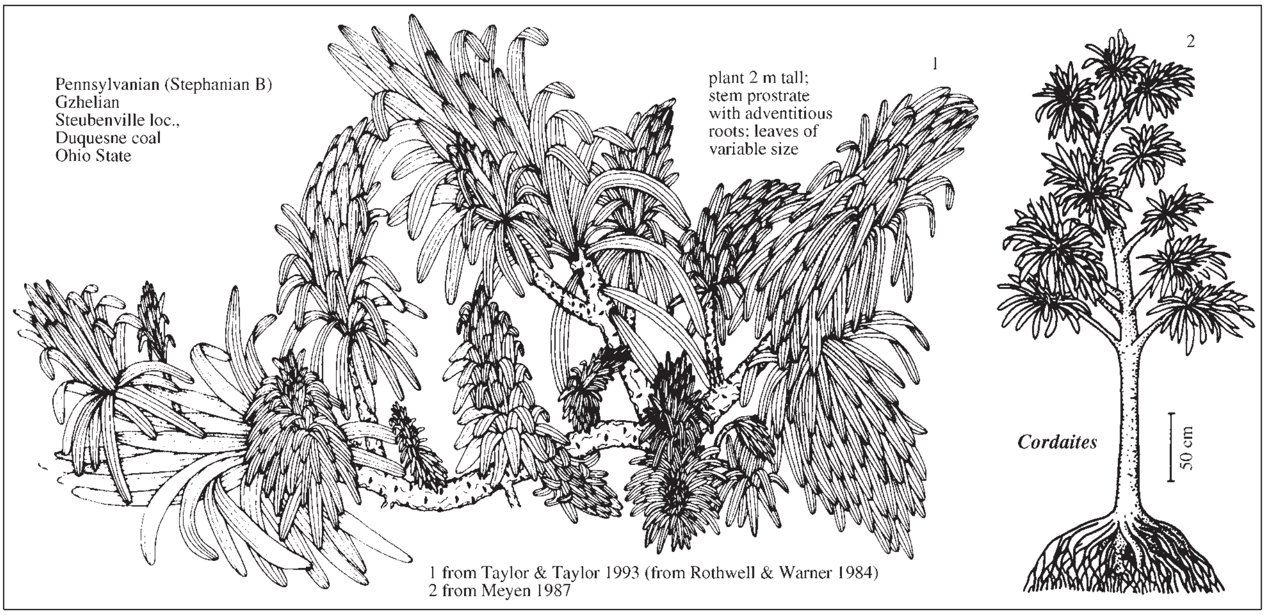
Prominence (colonisation success)—palaeotropics Carb. to Perm.
Frequency/ubiquity: Throughout palaeotropical areas during Late Carboniferous, mainly restricted to eastern palaeotropics (Cathaysian floras) in Permian.
Diversity: 4 species currently accepted (based on foliage morphology)—probably many more if epidermal characters are taken into account; as many as 128 foliage species have been created (named); the true diversity probably falls somewhere between these two figures.
Abundance: Variable abundance in adpression floras; Davies (1929) reports *Cordaites* representing between <1% to nearly 45% of adpression floras in South Wales. In the middle Moscovian, *Cordaites* represents less than 1% of floras in Germany (Drägert 1964) and 1–>25% in northern England (although restricted to certain facies—Scott 1977, 1978, 1979), while in the late Moscovian Radstock Flora it represents about 4% of the flora (Procter 1994). In coal ball floras, *Cordaites* remains are usually rare, indicating that they were uncommon in the freshwater palaeotropical wetlands. However, there are exceptions where they can represent over 70% of the coal ball plant debris, which were probably formed in coastal mangrove-like communities (Raymond & Phillips 1983).
Longevity: *ca* 50 my.

Ecology
Habit: Semi-self-supporting woody shrub (Rothwell & Warner 1984). Other cordaites have been reconstructed as monoaxial trees with prop roots (Cridland 1964).
Habitat: Wide-ranging, including upland extra-basinal (Falcon-Lang & Bashforth 2003), lowland levee (Ledran 1966), and mangrove habitats (Raymond & Phillips 1983).

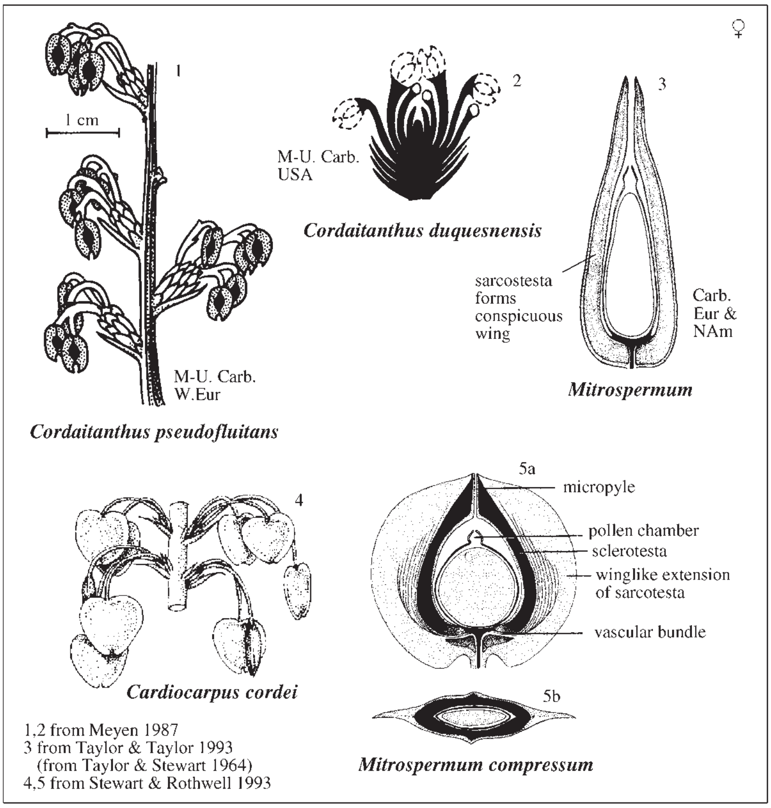
Other genera
Female cones: *Cordaianthus* Grand'Eury 1877, *Grandeuryconus* Ignatiev & Meyen 1989, *Procordaiconus* Ignatiev & Meyen 1989, *Renaulticonus* Ignatiev & Meyen 1989.
Male cones: *Lesqueranthus* Ignatiev & Meyen 1989.
Uncertain gender: *Cordaianthus* Grand'Eury 1877, *Gothania* Hirmer 1933.
Stems: *Cordaicladus* Grand'Eury 1877, *Mesoxylon* Scott & Maslen 1910.

Remarks
Systematics: This family has become particularly well known through the work on coal ball petrifactions (summarised by Rothwell 1988; Trivett & Rothwell 1991). The systematics of the cones have been revised by Ignatiev & Meyen (1989). The foliage, which represents the most widely found macrofossils, presents particular difficulties because of the limited number of taxonomically useful morphological characters available. A preliminary study on foliar epidermal anatomy (Ledran 1966) indicated that there was a far greater biodiversity than suggested by gross morphology alone, or even by the reproductive structures, and this is being confirmed by detailed investigations by Šimůnek (2000).

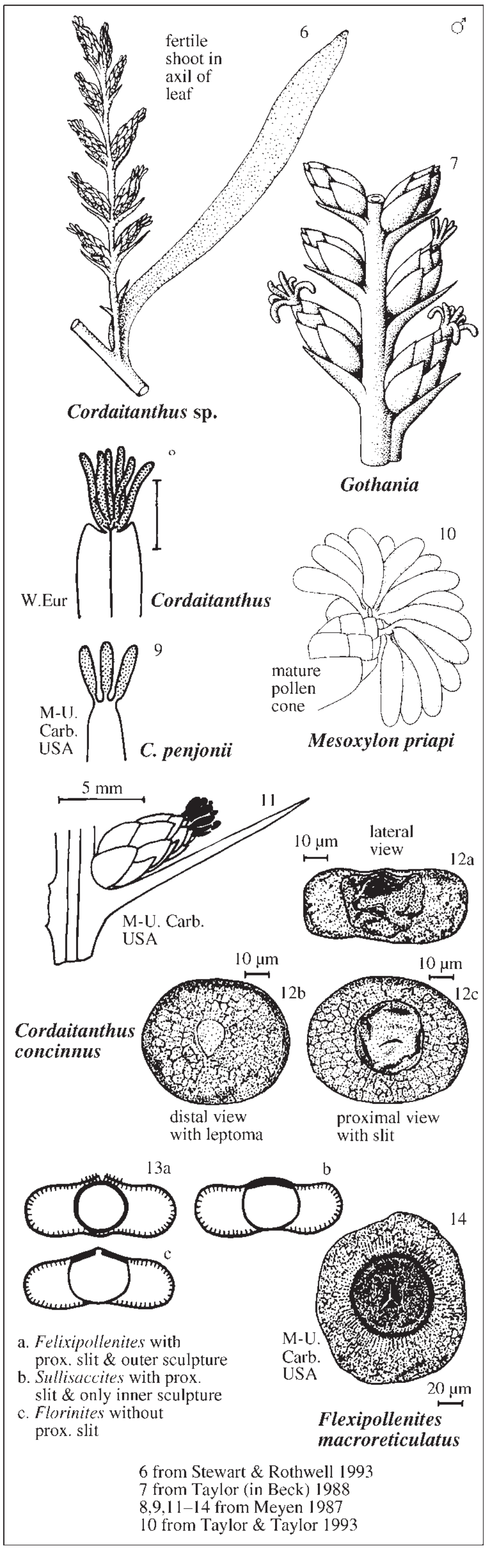
References
Ledran (1966), Šimůnek (2000): Foliage.
Meyen (1984), Rothwell (1988), Trivett & Rothwell (1991), Wang Shijun et al. (2003): General.
Ignatiev & Meyen (1989): Cones.
Hilton et al. (2003): Ovules.



1 from Taylor & Taylor 1993 (from Rothwell & Warner 1984)
2 from Meyen 1987

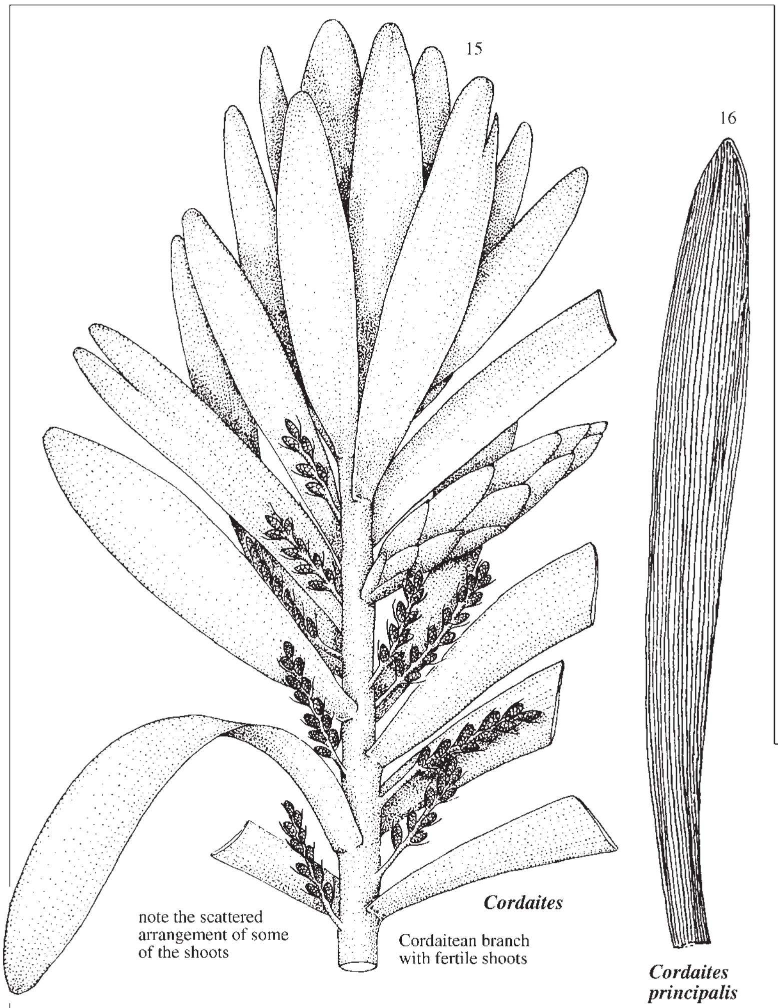


1,2 from Meyen 1987
3 from Taylor & Taylor 1993
(from Taylor & Stewart 1964)
4,5 from Stewart & Rothwell 1993

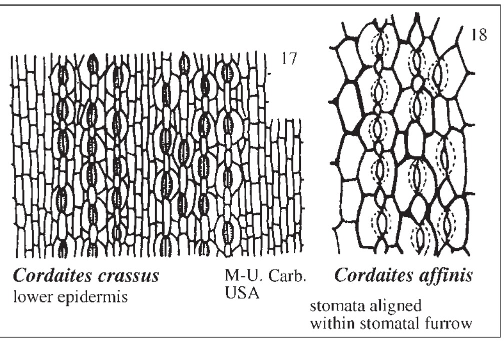


a. *Felixipollenites* with
prox. slit & outer sculpture
b. *Sullisaccites* with prox.
slit & only inner sculpture
c. *Florinites* without
prox. slit

6 from Stewart & Rothwell 1993
7 from Taylor (in Beck) 1988
8,9,11–14 from Meyen 1987
10 from Taylor & Taylor 1993



15,16 from Stewart & Rothwell 1993 (redrawn from Grand'Eury 1877)
17 from Meyen 1987
18 from Stewart & Rothwell 1993



Family **RUFLORIACEAE** Ledran 1966 emend. S.V.Meyen 1982a

Diagnosis: Cordaitanthalean plants with simple strobili, not grouped into compound polysperms; ovules borne erect, with integument partly free from nucellus.

Male: Male strobili similar to female strobili; pollen quasi-monosaccate.
Foliage: Leaves hypostomatic; stomata in distinct furrows between veins.
Stem: Trees or shrubs, with eustelic stems.

Range: Angara, C(BSK)–P(CHN)
First: *Krylovia sibirica* Chachlov 1939, Alykaevsk 'Horizon', Mostochki Gully, Staraya Balakhonka Village, Kuznetsk, Russia (Ignatiev 2001). *Rufloria* Meyen 1963 foliage ranges down as far as the Kaezovsky 'Horizon' (BSK—Gorelova *et al.* 1973) but is not accompanied by reproductive structures.
Last: *Suchoviella synensis* Ignatiev & Meyen 1989, Ust'pereborskaya 'Suite', Bol'shaya Synya River, Pechora, Russia. *Rufloria* Meyen 1963 foliage ranges up to the Tailugansky 'Horizon' (CHN—Gorelova *et al.* 1973) in the Kuznetsk but is not accompanied by reproductive structures.

Reference whole-plant genus & stratum—Ust'pereborskaya 'suite'
Female: *Suchoviella* Ignatiev & Meyen 1989; 1 TC, 1 sp., rare.
Male: *Pechorostrobus* Meyen 1982b; 1 TC, 1 sp., rare.
Foliage: *Rufloria* Meyen 1963; 1 TC, 1 sp., abundant.

Stratum: Ust'pereborskaya 'Suite', Bol'shaya Synya River, Pechora, Russia (CAP).
Affiliations: Grade 3 (Mut.occ.) (Meyen 1988; Ignatiev & Meyen 1989).

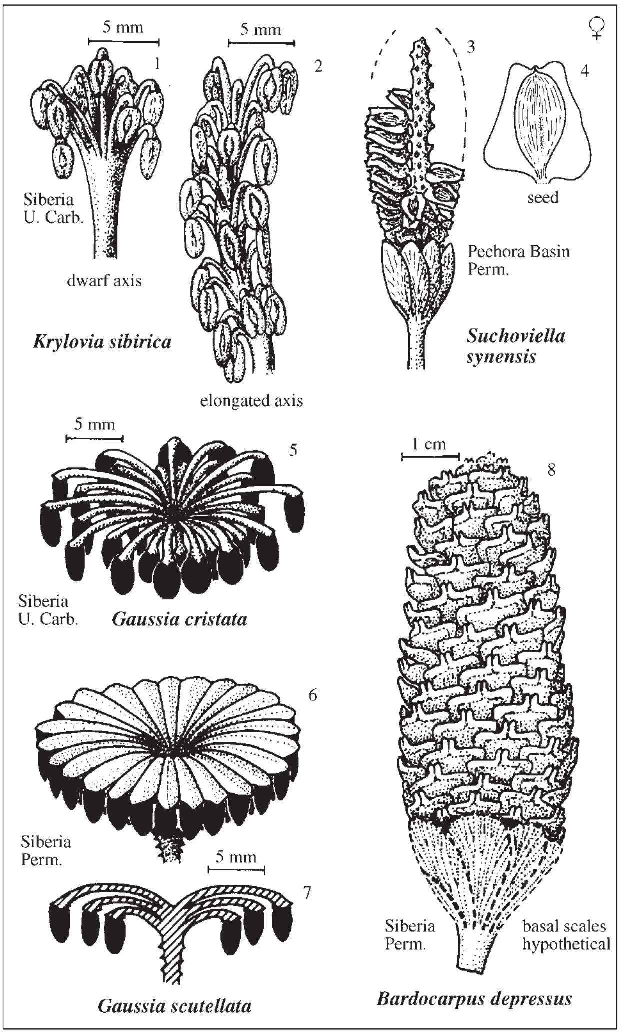
Prominence (colonisation success)—Angara Carb. to Perm.
Frequency/ubiquity: Based on foliage, the Rufloriaceae was widespread and abundant in Late Carboniferous and Permian floras of Angara and Subangara.
Diversity: 51 spp known (based on foliage).
Abundance: Abundant, details not recorded.
Longevity: At least 40 my, maybe up to 65 my if most or all *Rufloria* foliage belongs to the family.

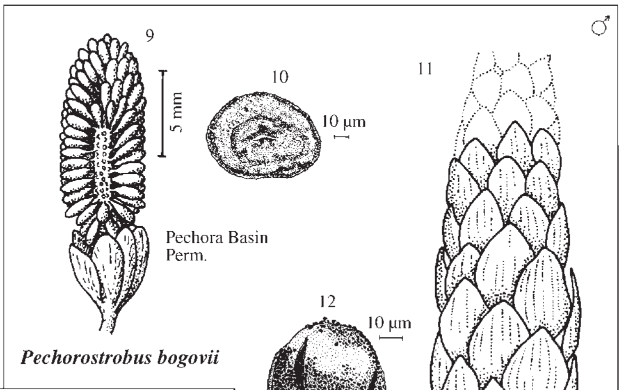
Ecology
Habit: ? Trees or shrubs.
Habitat: Probably riparian and lakeside habitats.

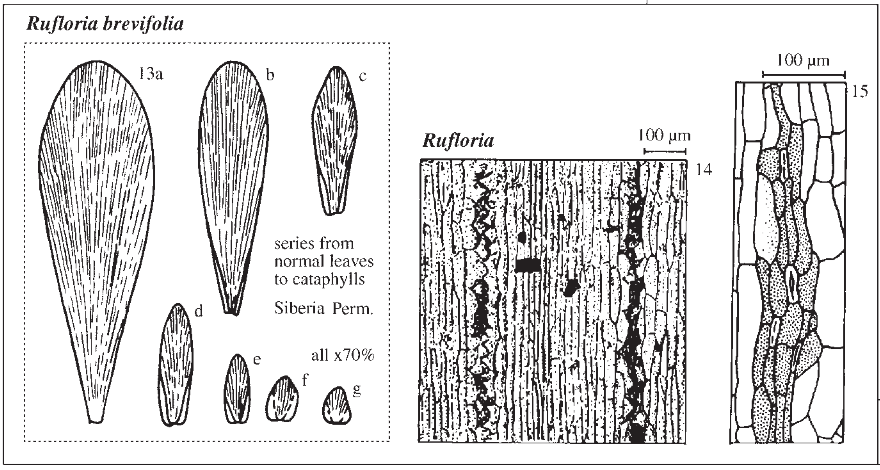
Other genera
Female (cones): *Gaussia* Neuburg 1934, *Bardocarpus* Zalessky 1937, *Krylovia* Chachlov 1939.
Male (cones): *Cladostrobus* Zalessky 1918.

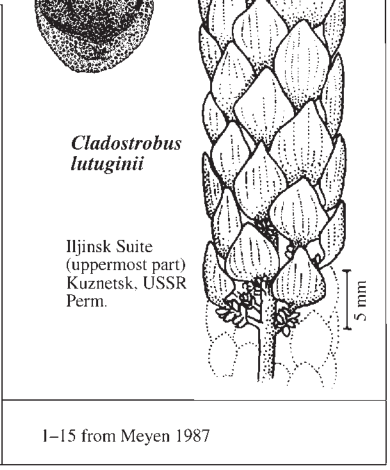
Remarks
Systematics: The systematics of this family have been investigated mainly by Meyen (summarised by Meyen 1982, 1987, 1988). The reconstructions that he proposed were mostly based on the co-occurrence of dispersed organs, although it is often supported by cuticular evidence (see comments by Rothwell 1988).

References
Meyen (1982, 1984, 1987, 1988): General.
Ignatiev & Meyen (1989): Cones.









1–15 from Meyen 1987

Family **VOJNOVSKYACEAE** M.F.Neuburg ex Y.A.Orlov 1963

Diagnosis: Cordaitanthalean plants with ovulate strobili attached to axis between leafy bracts, and grouped loosely into spirally arranged compound polysperms; ovules reflexed on the seed-scale.

Male: Male strobili differ from female strobili, the pollen organs being borne on the margin of a palmately lobed structure, but it is unknown if they were parts of compound structures; pollen quasi-monosaccate.
Foliage: Leaves hypostomatic; stomata not in regular files.
Stem: Trees or shrubs, with eustelic stems often with septate pith.

Range: Angara, P(ASS–CAP)
First: *Vojnovskya usjatensis* Gorelova in Gorelova *et al*. (1973), Promezhutochny ‘Horizon’, Kemerov Region, Kuznetsk, Russia. Foliage that may belong to this family occurs as early as the C(BSK) in the same region but cannot be corroborated with fertile structures.
Last: *Kuznetskia planiscula* Meyen 1982, Tailungansky ‘Horizon’, Borehole 11733, Chusovitinsky profile, Kuznetsk, Russia.

Reference whole-plant genus & stratum—Intinskaya ‘Suite’
Female: *Vojnovskya* Neuberg 1955; ? TCs; 1 sp., rare.
Male: *Kuznetskia* Gorelova & Meyen in Meyen 1982; ? TCs, 1 sp., rare.
Foliage: *‘Cordaites’*; ? TCs; 1 sp., abundant.

Stratum: Intinskaya ‘Suite’, Khalmeryu, Pechora, Russia P(CAP).
Affiliations: Female cones and foliage, Grade 3 (Mut.occ.) (Meyen 1982); male cones with the others, Grade 2.

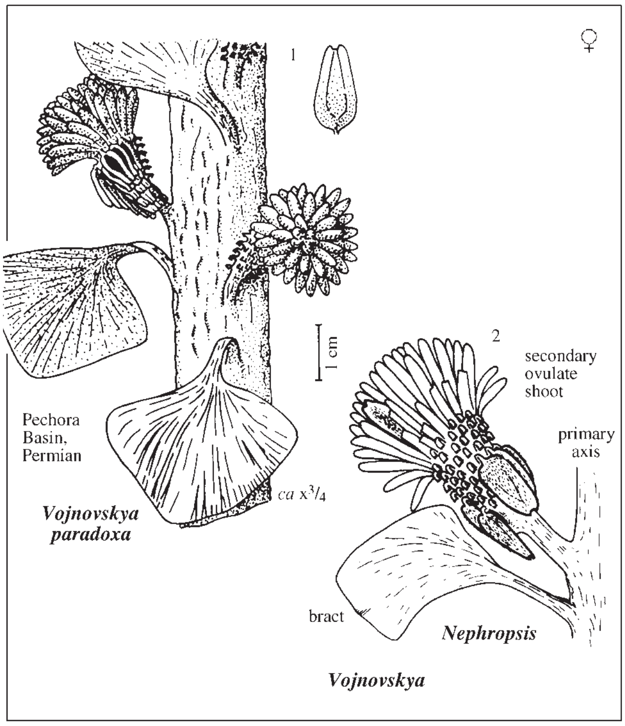
Prominence (colonisation success)—Angara Permian
Frequency/ubiquity: Widespread and (if the foliage is a reliable guide) abundant in Permian floras of Angara and Subangara.
Diversity: 5 spp based on ovulate structures, but almost certainly more diverse.
Abundance: Details not available.
Longevity: At least 40 my, possibly longer if the Carboniferous foliage can be attributed to the family.

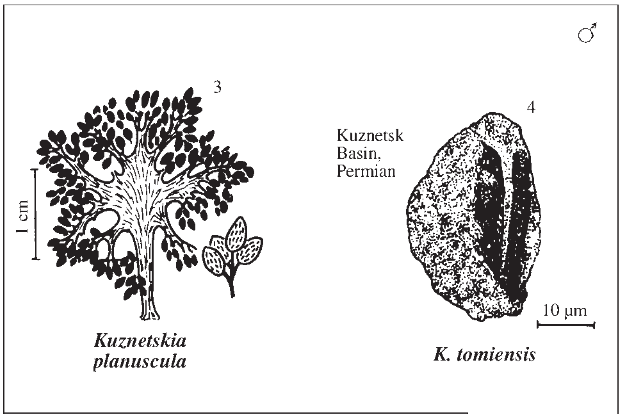
Ecology
Habit: ? Trees or shrubs.
Habitat: Probably riparian and lakeside habitats.

Other genera—nil.

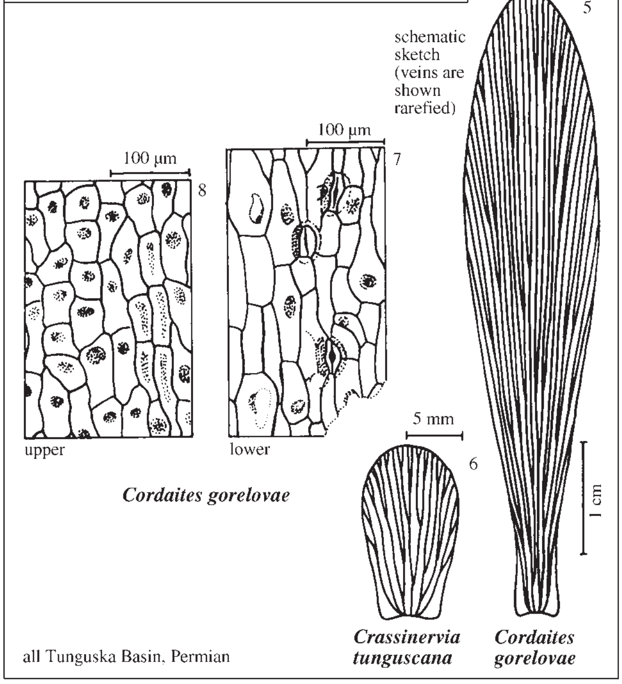
Remarks
Systematics/phytogeography: This, the least well-known of the Cordaitanthales families, appears to be exclusively Angaran. Rothwell *et al.* (1996) argued that *Sergeia*, from Upper Carboniferous marine shales in Texas, belonged to the Vojnovskyaceae. Based on the traditionally accepted interpretation of the Vojnovskyaceae, *Sergeia* differs in that the cones are not borne in compound polysperms and are axillary to their basal bract, and the ovules are not reflexed on the scales. This latter character of the Vojnovskyaceae has been queried by Rothwell & Mapes (2001) as being due to taphonomic distortion in the holotype. However, until the matter has been investigated more fully, we find it difficult to accept that *Sergeia* is evidence that this family occurs outside of Angaran floras.

References
Meyen (1982, 1984, 1987, 1988): General.





1,3–8 from Meyen 1987
2 from Rothwell (in Beck) 1988 (redrawn from Meyen 1982)
all Angara flora, former USSR, L–U. Perm.



Order **DICRANOPHYLLALES** S.V.Meyen 1984 emend. nov.

Diagnosis: Pinopsid plants with ovulate strobili borne axillary to a bract or leaf; ovules platyspermic, borne on pinnate sporophylls.

Male: Pollen organs formed into loose cones; pollen monosaccate.
Foliage: Leaves elongate-linear, helically disposed, with a single longitudinal vein.

Remarks
Systematics: Many of the taxa traditionally included within the Dicranophyllales are incompletely known and Rothwell & Mapes (2001) have queried whether it represents a valid taxonomic concept. However, we have retained it, using essentially the diagnosis given by Archangelsky & Cúneo (1990) except that we have included the observation that the ovulate sporophylls are pinnate, as this seems to be the critical character that separates it from the Cordaitanthales. We recognise, however, that future work on these plants may require this interpretation to be revised. Archangelsky & Cúneo (1990) placed *Polyspermophyllum* from the Permian of western Gondwana (Argentina) in this order, but it differs in that the ovules are borne terminally on fertile leaves, rather than on sporophylls arranged singly or in helical cones that are axially positioned with respect to leaves.

Families: Includes the two families Dicranophyllaceae and Trichopityaceae.

Family **DICRANOPHYLLACEAE** S.Archang. & Cúneo 1990 emend. nov.

Diagnosis: Dicranophyllalean plants with ovulate sporophylls arranged in cones (strobili), and with ovules borne apically on pinnate arms.

Foliage: Leaves fork once or twice; cuticle hypostomatic, with stomata in two furrows near the leaf margin.
Stem: With prominent leaf cushions.

Range: Euramerica, C(KAS)–P(SAK)
First: *Dicranophyllum gallicum* Grand'Eury 1877, Commentry, France. Foliage that may belong to this family occurs as early as the C(BSK) (e.g. Belgium—Stockmans & Willière 1953) but cannot be corroborated with fertile structures.
Last: *Dicranophyllum hallei* Remy & Remy 1959, Rotterode Fm., Gasberg Quarry, SW-Saale Basin, Thüringia, Germany (Barthel & Noll 1999).

Reference whole-plant genus & stratum—Saar-Nahe Basin
Female/male/foliage: *Dicranophyllum* Grand'Eury 1877; 2 TCs; 1 sp., abundant.

Stratum: Winnweiler, Saar-Nahe Basin, Germany; Donnersberg Fm.; L. Perm. (SAK).
Affiliations: Grade 5 (Org.att.); more or less complete plants being found (Barthel & Noll 1999).

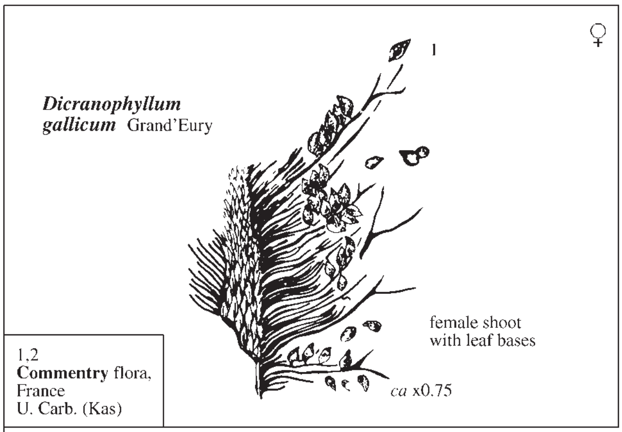
Prominence (colonisation success)—Euramerica Carb. to Perm.
Frequency/ubiquity: Limited distribution in the Stephanian and Early Permian of Europe.
Diversity: 18 spp based on foliage, but only 2 spp have known reproductive structures.
Abundance: Usually rare, but no absolute data available.
Longevity: *ca* 25 my.

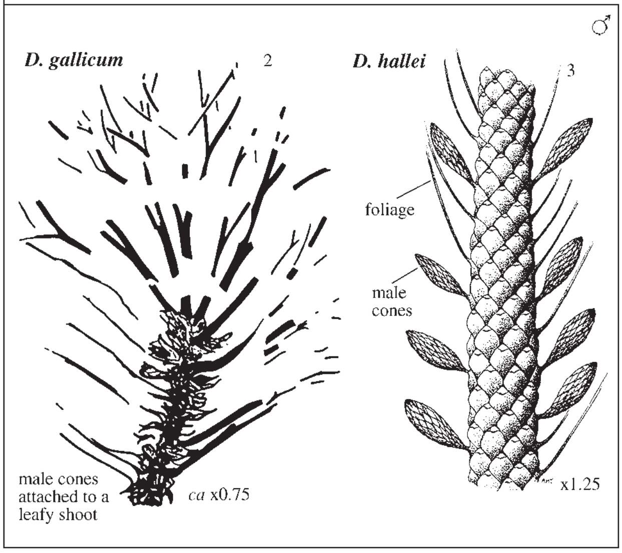
Other genera—nil.

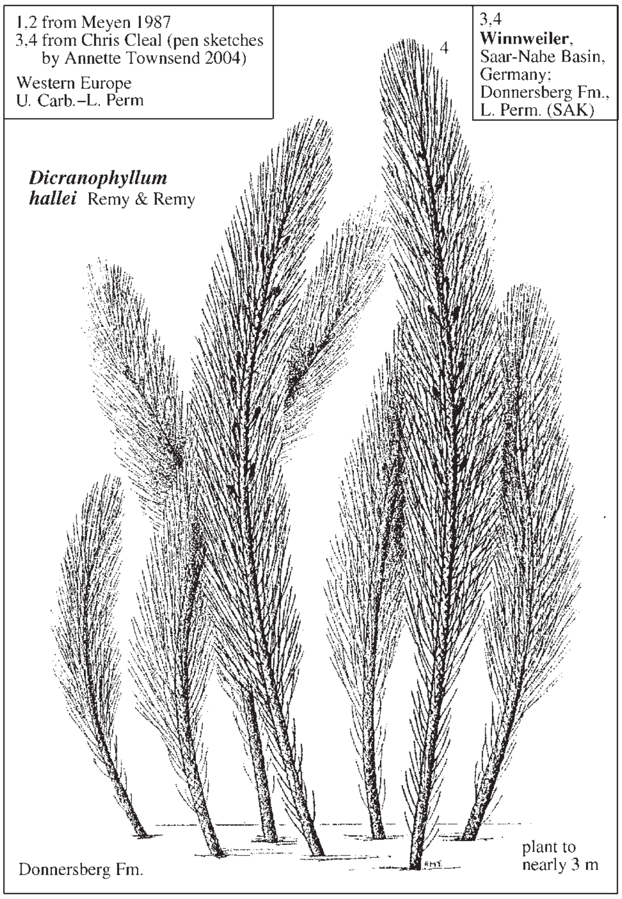
Ecology
Habit: Unbranched woody plants, perhaps 2 m high.
Habitat: Probably riparian and lakeside habitats.

Remarks
Systematics: Much of our understanding of the habit of this plant is based on the remarkable discoveries of almost complete plants, including roots, reported by Barthel & Noll (1999). Full details of the anatomy of the cones are still not completely resolved but, critically, Rothwell & Mapes (2001) reported that the ovules were pinnately arranged on the sporophylls. The interpretation of this family by Meyen (1987) depended heavily on the foliage, in particular the presence of abaxial stomatiferous furrows. Consequently, he included several genera from Permian Angaran floras (*Entsovia* Meyen 1969, *Slivkovia* Meyen 1969), but without associated evidence of reproductive structures.

References
Barthel & Noll (1999): Whole plant.
Rothwell & Mapes (2001): General.






1,2 from Meyen 1987
3,4 from Chris Cleal (pen sketches by Annette Townsend 2004)
Western Europe
U. Carb.–L. Perm

Family **TRICHOPITYACEAE** S.V.Meyen 1987 emend. nov.

Diagnosis: Dicranophyllalean plants with ovulate sporophylls attached singly to the leaf axil; ovules borne subapically on pinnate arms of sporophylls.

Foliage: Leaves fork twice or three times.
Stem: With no leaf cushions.

Range: Euramerica and Subangara, P(ASS–KUN)
First: *Trichopitys heteromorpha* Saporta 1875, Lydiennes Fm., Hérault, France (Florin 1949). Meyen (1987) included *Dichophyllum moorei* Ellias ex Andrews 1941 (C–KAS) in this family but this is based only on foliage.
Last: *Biarmopteris pulchra* Zalessky 1933b and *Mauerites gracilis* Zalessky 1933b, Sylva River, Middle Fore-Urals, Russia (Meyen 1982, 1988).

Reference whole-plant genus & stratum—Lydiennes Fm.
Female/foliage/stem: *Trichopitys* Saporta 1875; 1 TC, 1 sp., v. rare.
Male: Unknown.

Stratum: Lydiennes Fm. (ASS), Hèrault, France (Florin 1949).
Affiliations: Grade 5 (Org.att.) (Florin 1949); rest of the plant unknown.

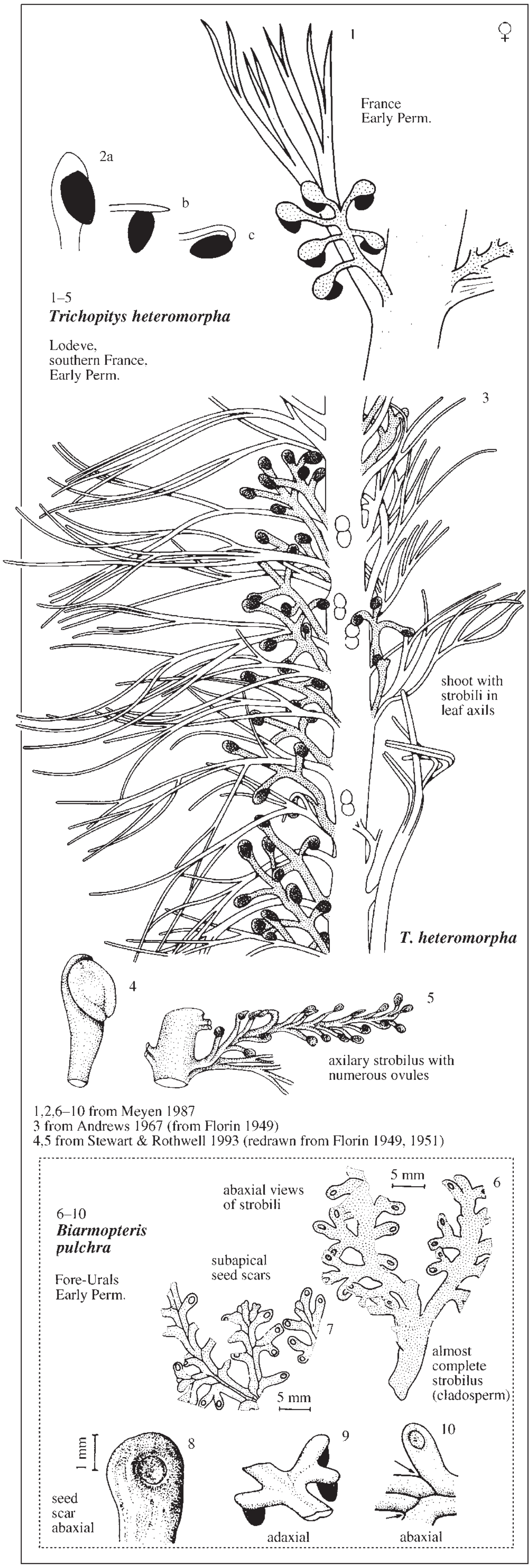
Prominence (colonisation success)—Laurasia Permian
Frequency/ubiquity: Rare in the Early Permian of Europe and Subangara.
Diversity: 2 or possibly 3 spp.
Abundance: Very rare.
Longevity: *ca* 25 my.

Ecology
Habit: ? Small tree.
Habitat: Unknown.

Other genera—nil.

Remarks
Classification: This family has been variously assigned to the Ginkgoales (Florin 1949; Zhou 1997) and the Peltaspermales (Meyen 1982, 1987, 1988). However, we have followed Archangelsky & Cúneo (1990) and included it within the Dicranophyllales because of the pinnate structure of the ovulate sporophylls. Meyen (1987) gave particular emphasis to the subapical attachment of the ovules, but we see no major obstacle to deriving this arrangement from the apical arrangement seen in the Dicranophyllaceae. The important fact is that both have sporophylls with pinnately arranged ovules.

Reference
Archangelsky & Cúneo(1990): General.



1,2,6–10 from Meyen 1987
3 from Andrews 1967 (from Florin 1949)
4,5 from Stewart & Rothwell 1993 (redrawn from Florin 1949, 1951)

Order **FERUGLIOCLADALES** Doweld 2001

Diagnosis: Pinopsid plants bearing ovate cones with helically arranged megasporophyll units comprising a single, large, triangular, free bract, and single, sessile, orthotropous, fully enclosed ovules.

Families: Includes the single family Ferugliocladaceae.

Family **FERUGLIOCLADACEAE** S.Archang. & Cúneo 1987

Diagnosis: As for the order Feruglioclаdales.

Range: P(ASS)
First & Last: *Ferugliocladus riojanum* Archangelsky & Cúneo 1987, *F. patagonicus* (Feruglio 1951) Archangelsky & Cúneo 1987 and *Ugartecladus genoensis* Archangelsky & Cúneo 1987, Rio Genoa Group, Central Patagonian Basin, Argentina.

Reference whole-plant genus & stratum—Arroya Totoral Fm.
Female/foliage/male: *Ferugliocladus* Archangelsky & Cúneo 1987; several TCs, 2 spp, *ca* 25–30%.

Stratum: Arroya Totoral Fm., La Rioja Province, Argentina.
Affiliations: Female(5)foliage(5)male; Grade 5 (Org.att.).

Prominence (colonisation success)–Gondwana Permian
Frequency/ubiquity: Several localities in Argentina.
Diversity: 2 genera (3 species) of whole-plants.
Abundance: 10–40% of glossopterid floras.
Longevity: <1 my.

Ecology
Habit: Unspecified.
Habitat: Plants mesophyllous to hygro-mesophyllous, temperate humid climate, swampy (coals) environments close to water table, varied ecological range from extensive plains with meandering rivers in proximity of the sea to smaller basins 'flanked by hills in a continental mountain system'.

Other genera
Ovulate cone: *Ugartecladus* Archangelsky & Cúneo 1987.
Dispersed seeds: *Eucerospermum* Feruglio 1946.
Vegetative shoots: *Paranocladus* Florin 1940, *Brasilocladus* Bernardes de Oliveira & Yoshida 1981; these two genera at least in part.

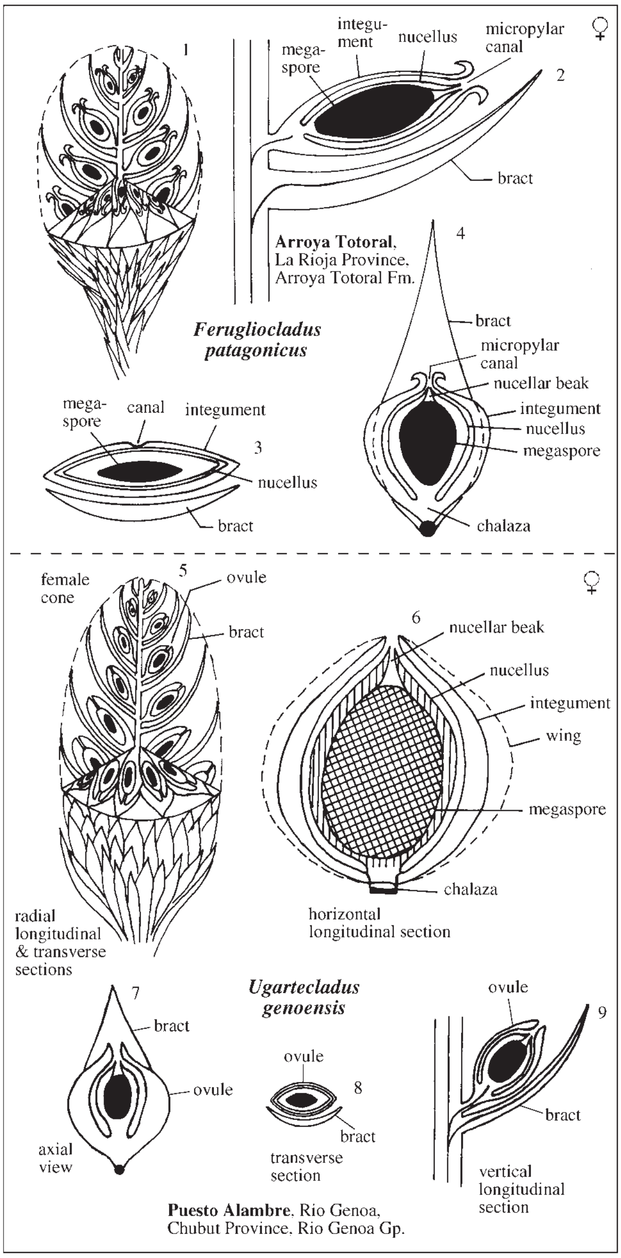
Remarks

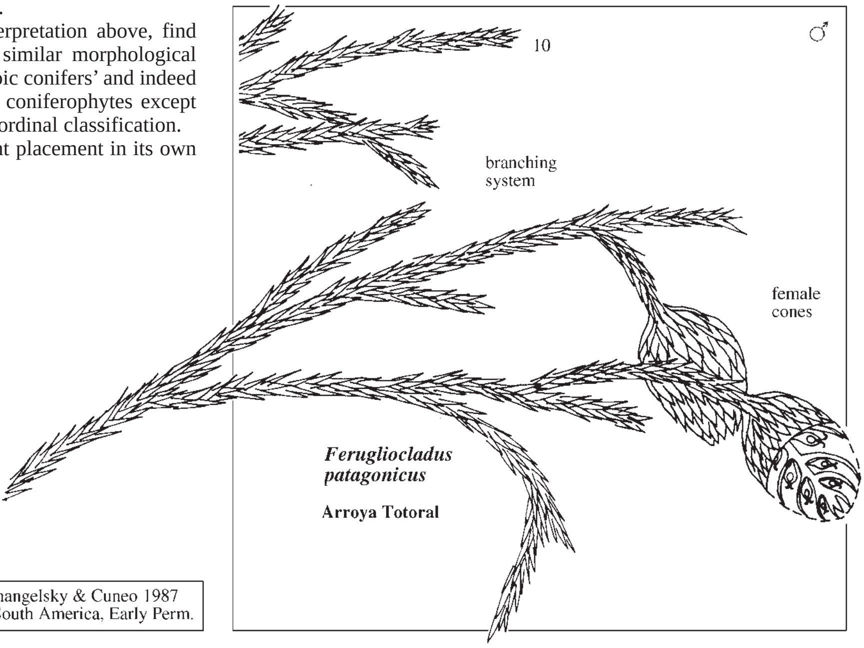
Rothwell & Mapes (2001) and Hernandez-Castillo *et al.* (2001) concur with Archangelsky & Cúneo 1987 that *Ferugliocladaceae* (and *Ugartecladus)* bear ovulate cones with a 'simpler structure' than 'all other Palaeozoic conifers'. They interpret, however, that the stalked erect ovules—which are radial, not bilateral—are 'ovuliferous dwarf shoots that consist of only a stem with one dwarf ovule'. To them, the cone is a 'compound shoot system' with 'simple dwarf shoots ... borne in the axil of a bract on the cone axis'. Critical to their interpretation is the 'recognition by Harris (1976) that shoots (not leaves or sporophylls) are borne in the axils of foliar structures (i.e. bracts) of seed plants'.

Rothwell & Mapes (2001), based on their interpretation above, find the *Ferugliocladaceae* to have a 'fundamentally similar morphological organisation' to all other 'ovulate cones of Palaeozoic conifers' and indeed 'the ovulate fructifications of all other Palaeozoic coniferophytes except *Polyspermophyllum'*. They make no suggestion of ordinal classification.

We feel the family sufficiently unique to warrant placement in its own order.

Reference
Archangelsky & Cúneo (1987): General.





1–10 from Archangelsky & Cuneo 1987
all Argentina, South America, Early Perm.

Order **DORDRECHTITALES** And. & And. 2003

Diagnosis: Putative pinopsids bearing elongate cones of numerous subopposite, subdecussate fascicles of 3(?4) T-shaped ovuliferous scales (bracts absent or fully fused) attached to short pedicels.

Families: Includes the single family Dordrechtitaceae.

Family **DORDRECHTITACEAE** And. & And. 2003

Diagnosis: As for the order Dordrechtitales.

Range: Tr(LAD–CRN)
First: *Dordrechtites dikeressa* Rigby 1982; Moolayember Fm., Bowen Basin, Queensland.
Last: *Dordrechtites elongatus* H.M.Anderson 1978 (female); Molteno Fm.

Reference genera & stratum: Molteno Fm.
Female: *Dordrechtites* H.M.Anderson 1978; 17 TCs, 3 spp, >400 indivs.
Male: Unknown.
Foliage: Unknown.

Stratum: Molteno Fm., Karoo Basin, S. Africa, Tr(CRN).
Affiliations: Unknown.

Prominence (colonisation success)—Gondwana Triassic

Since the affiliate for *Dordrechtites* is unknown, the prominence of the plant remains obscure. The data recorded below are based, therefore, on the ovulate structures in contrast to the foliage following our standard approach.

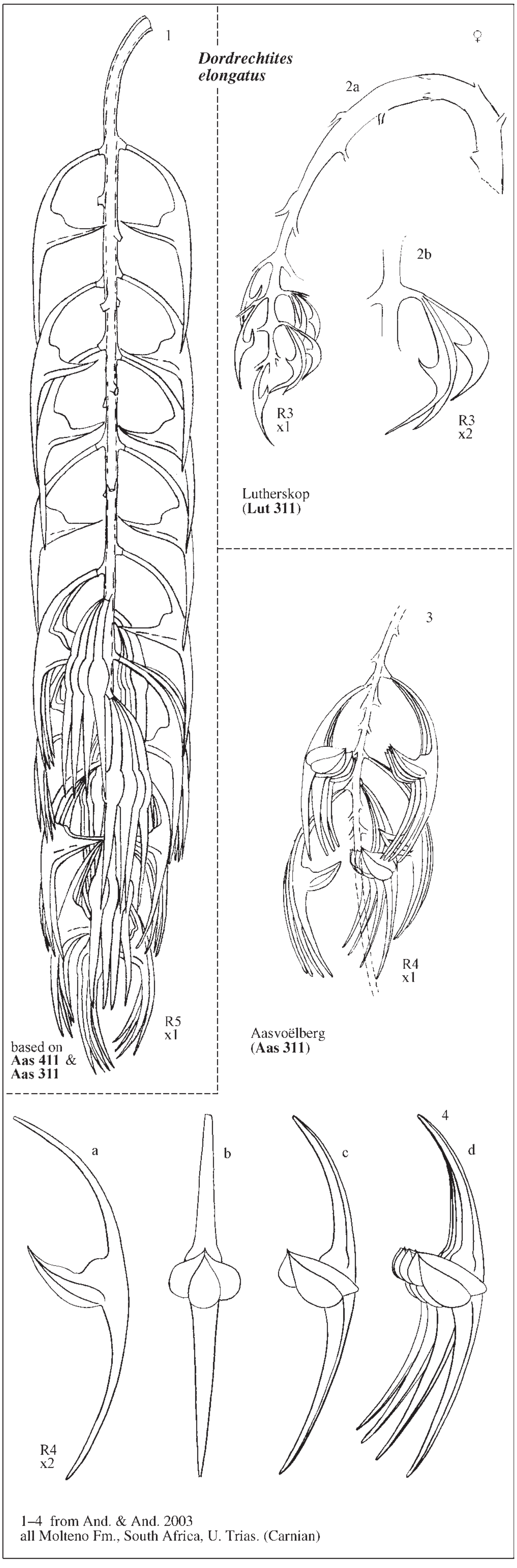
Frequency: 10 of 84 Gondw. degree squares.
Ubiquity: 3 of 5 Gondw. continents.
Diversity: 4 species in Gondw. Trias.
Abundance: Very rare to common in 17 Molteno TCs.
Longevity: *ca* 13 my.

Ecology
Habit: Presumably a tree (with wind- and water-dispersed seeds).
Habitat: Extensive inland floodplain.

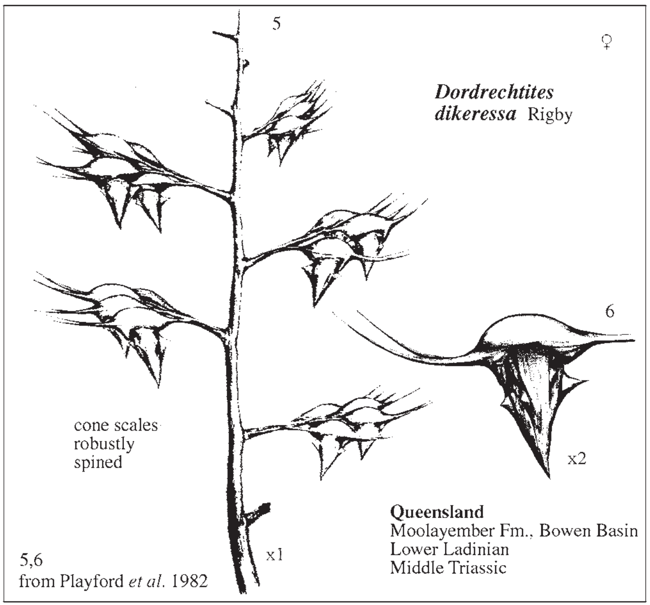
Other genera—nil.

Remarks
Taphonomy: *Dordrechtites* (represented almost exclusively by its dispersed scales) is remarkable in that it is both frequent and common in the Molteno, yet there remains no clue as to its foliage or male affiliates. The most likely solution is that *Dordrechtites* is an allochthonous element in the TCs in which it is found: having blown or washed in from more distant communities. This is supported by the extreme rarity of intact or partially intact strobili.

Reference
And. & And. (2003): General.



1–4 from And. & And. 2003
all Molteno Fm., South Africa, U. Trias. (Carnian)



Queensland
Moolayember Fm., Bowen Basin
Lower Ladinian
Middle Triassic

5,6
from Playford *et al.* 1982

Order **CHEIROLEPIDIALES** And. & And. nov.

Diagnosis: Putative pinopsids bearing elliptical cones with megasporophyll units comprising large free bracts; ovuliferous scales complex, with 6–10 lobes and usually 2 ovules apparently enclosed in cutinised sacs.

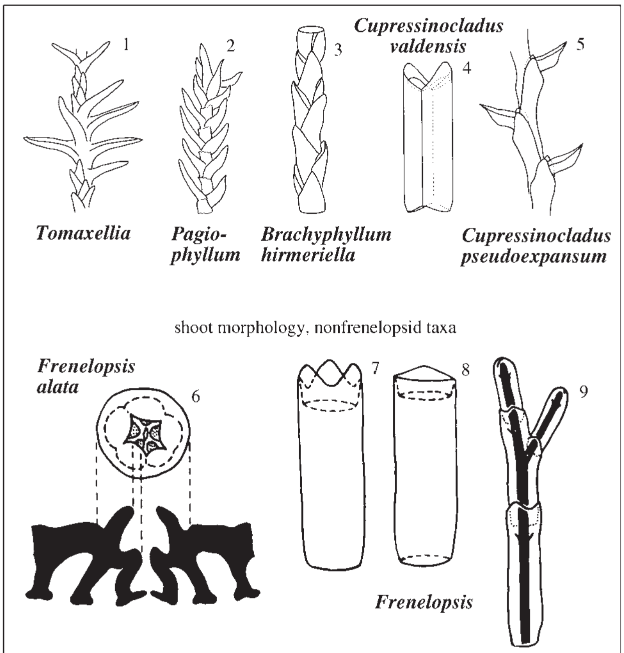
Remarks

Earlier suggestions of affinity with the Taxodiaceae, Cupressaceae or Araucariaceae were based principally on foliage. The position of the family remains perplexing, as highlighted for instance by Krassilov (1982, p. 143)—'with their unique pollen grains and ovuliferous structures they apparently stand apart from true conifers'; and by Watson (1988, p. 435)—'the phylogenetic relationships of this amazing family seem impossible to determine at this juncture ......'. Doweld (2001) includes his new order Hirmeriellales (our Cheirolepidiales, see below) along with the order Araucariales Goroschankin (1904) in a new subclass Araucariidae—but without giving his reasons for suggesting the link.

Nomenclatural comment

Doweld (2001) employs the family Hirmeriellaceae T.M.Harris 1979 and order Hirmeriellales Doweld 2001 for the Cheiropidiaceae and Cheirolepidiales respectively. His reason for the shift is unclear and we prefer to retain the use of the earlier and more traditional Cheirolepidiaceae.

Families: Includes the single family Cheirolepidiaceae.



1–5 from Watson 1988 (redrawn from Alvin 1982, Watson 1982)
6–9 from Meyen 1987

Family **CHEIROLEPIDIACEAE** Takht. 1963

Diagnosis: As for order Cheirolepidiales.

Range: Tr(CRN?)–K(CMP?)
First: ??*Brachyphyllum hegewaldia* Ash (1973) and *Pagiophyllum* spp, Chinle Fm., Arizona, USA (Watson 1988).
Last: ??*Frenelopsis hoheneggeri* (Ettingshausen) Carpentier 1937; Sainte Baume, France.

Reference whole-plant genus & stratum—Yorkshire Jurassic
Female: *Hirmeriella* Hörhammer 1933; 2 TCs, 2 spp, *ca* 7 indivs.
Male: *Classostrobus* Alvin, Spicer & Watson 1978; 1 TC, 1 sp., 2 indivs.
Foliage: *Pagiophyllum* Heer 1881; many TCs, 6 spp, numerous indivs.

Stratum: Yorkshire Jurassic (L-U. Deltaic), J(BAJ–BTH).
Affiliations: *Hirmeriella*(4)*Classostrobus*(4)*Pagiophyllum*, Grade 4 (Mut.occ., Cut.cor., Mor.cor.).

Prominence (colonisation success)—Global Mesozoic
Frequency/ubiquity: The Cheirolepidiaceae, ranging from the Late Triassic to Late Cretaceous, are the most dominant pinopsids through the Jurassic and Lower Cretaceous, as well as being the most dominant gymnospermous family of any class through the greater part of the 160–165 my dinosaurian era (Chart 10, p. 45).

Watson (1988) writes that the Cheirolepidiaceae were an 'important Mesozoic conifer family of a diversity probably unparalleled in any other conifer family, extinct or living. It is now obvious that members of this family displayed a quite remarkable range of morphology, habit and habitat, the full extent of which may not yet be fully recognised'. Stewart & Rothwell (1993) note specifically that remains of the family constituted a predominant part of the Yorkshire Jurassic sites, indicating that they were an important part of the coniferous forests of the period.

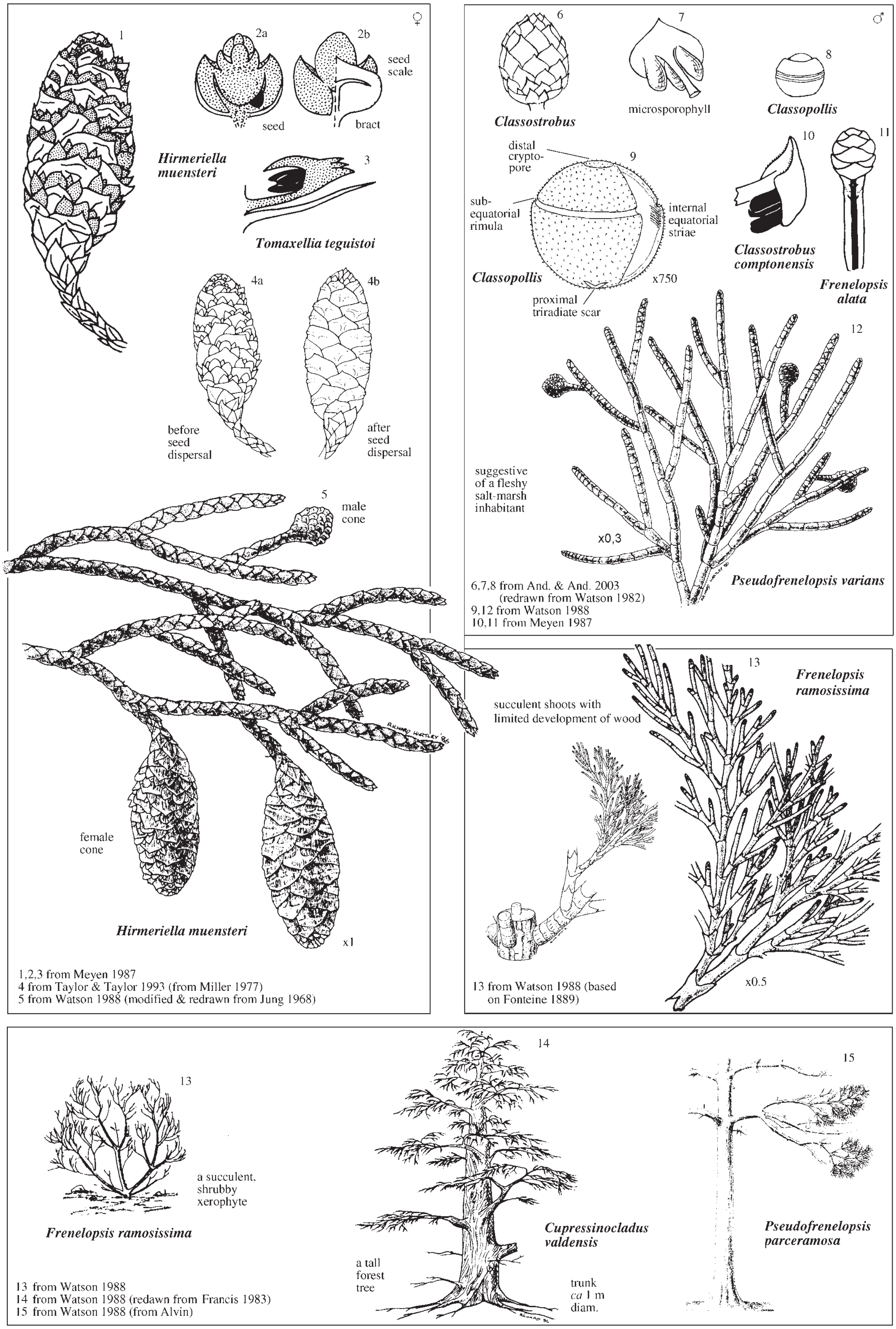
Diversity: 7 genera, 22 species; after Watson (1988) who provided a list of well-authenticated taxa based on vegetative shoots.
Abundance: Dominant through Jurassic and Cretaceous.
Longevity: *ca* 158 my.

Ecology—Global Mesozoic
Habit: Species range widely from succulent, shrubby xerophytes to tall forest trees (tfs 10–12 opposite) (Watson 1988; Stewart & Rothwell 1993).
Habitat: 'enjoyed conspicuous success in the Mesozoic at least in tropical and subtropical climes, inhabiting many of the niches now dominated by angiosperms' (Watson 1988).

Other genera
Vegetative shoots: *Brachyphyllum* Brongniart 1828, *Frenelopsis* Schenk 1869, *Pseudofrenelopsis* Nathorst 1893, *Cupressinocladus* Seward 1919, *Tomaxellia* Archangelsky 1963.

Remarks
Morphology: The pollen *Classopollis* is unique to and unites the family. 'To date', as Watson (1988) puts it, 'the single most reliable character on which to base assignment to this family is possession of the distinctive and unusual pollen genus *Classopollis* Pflug. Indeed, it is beginning to look as though it may be the only reliable character, and one of considerable evolutionary significance. The possession of *Classopollis* bearing male cones, together with whatever female mechanism was involved, may be the only unifying feature of phylogenetic significance.' The female cones are complex and poorly understood.

References
Watson (1988), Rothwell & Stewart (1993): General.
Cleal (1993): 'First & last'.



1,2,3 from Meyen 1987
4 from Taylor & Taylor 1993 (from Miller 1977)
5 from Watson 1988 (modified & redrawn from Jung 1968)

6,7,8 from And. & And. 2003
(redrawn from Watson 1982)
9,12 from Watson 1988
10,11 from Meyen 1987

13 from Watson 1988 (based on Fonteine 1889)

13 from Watson 1988
14 from Watson 1988 (redawn from Francis 1983)
15 from Watson 1988 (from Alvin)

Order **PALISSYALES** Doweld 2001

Diagnosis: Putative pinopsids bearing lax strobili with helically arranged megasporophyll units comprising a single (?) free, lanceolate, leafy bract, and stalked ovuliferous scales with 1–5 pairs of opposite, erect ovules partly enclosed by an aril.

Remarks
Classification: Placement of this small family of three genera is far from settled (Stewart & Rothwell 1993; Taylor & Taylor 1993): Florin (1951, 1958) saw the family as probably distinct from any living conifers and possibly evolving from *Ernestiodendron* (Utrechtiaceae); Schweitzer (1963) envisaged a reduction series leading to the extant *Cephalotaxus* (Cephalotaxaceae), the partially enclosed ovules within an asymmetrical aril being particularly suggestive; *Dacrydium* of the Podocarpaceae has also been envisaged as a possible derivative; Delevoryas & Hope (1981) noted similarities with the putative ginkgophyte *Trichopitys*. The family cannot usefully be included in any of the other pinopsid orders.

Doweld (2001) placed the family in his newly erected order Palissyales and class Incertae sedis. We adopt the order, but not the elevated status of class.

Families: Includes the single family Palissyaceae.

Family **PALISSYACEAE** Florin 1958

Diagnosis: As for order Palissyales.

Range: Tr(CRN)–J(BAJ)
First: *Stachyotaxus lipoldii* (Stur) Kräusel 1952, Lettenkohle, Lunz, Austria; and *S. sahnii* Kräusel 1952, Lettenkohle, Neuewelt, Switzerland (Cleal 1993).
Last: *Palissya* sp., Saltwick Fm., North Yorkshire, England, UK (Hill & Van Konijnenburg-Van Cittert 1973). 'This material has not been described in detail, but is reported to include a female cone' (Cleal 1993).

Reference whole-plant genus & stratum—Höganäs Fm.
Female/male/foliage: *Stachyotaxus* Nathorst 1886; 1 TC, 1 sp., very rare (no absolute data available).
Stratum: Shales associated with coals in Höganäs Fm., Scania, Sweden (RHT).
Affiliations: Grade 2 (Mut.occ.).

Prominence (colonisation success)—Euramerica Late Trias.–M. Jur.
Frequency/ubiquity: Only reliably recorded from central Europe (Alps), Scandinavia (southern Sweden, Denmark), Greenland and North America (N. Carolina). Records from the southern hemisphere (especially India, New Zealand and South America) need to be verified.
Diversity: 14 spp.
Abundance: Rare, but no absolute data available.
Longevity: *ca* 60 my.

Ecology
Habit: Only isolated shoots and cones are known, but they are assumed to originate from trees.

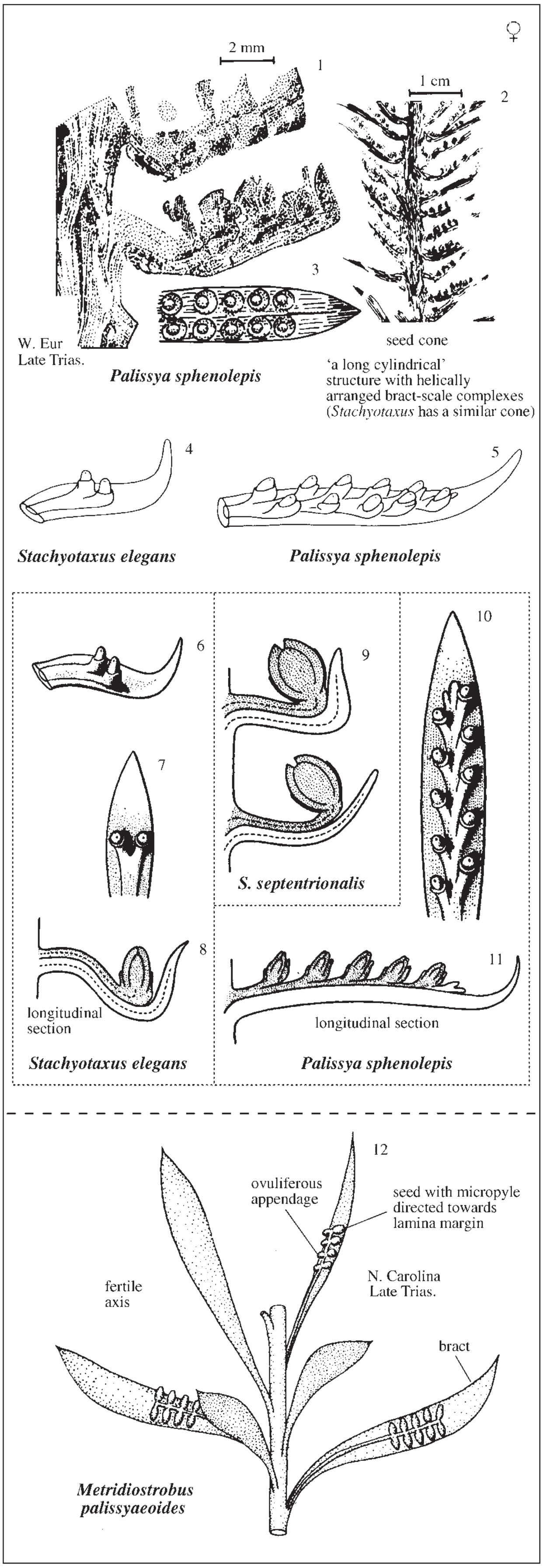
Habitat: Mainly lowland, possibly adjacent to lakes.

Other genera
Shoots with ovulate cones: *Palyssia* Endlicher 1847, *Metridiostrobus* Delevoryas & Hope 1981.

Remarks
Nomenclature: 'The validity of this family has recently been questioned (Meyen 1984; Miller 1985) but, in the absence of any formal taxonomic changes, the traditional concept has been maintained' (Cleal 1993).

Permian origins & extant derivatives: Stewart & Rothwell (1993), reflecting the views of earlier investigators (Florin 1951, 1958; Schweitzer 1963), write: 'They envisage the origin of the Palissyaceae bract-scale complex from genera of the Permian *Ernestiodendron* type where the secondary shoot bears several spirally arranged erect ovules. By reduction and planation an ovuliferous scale in the axil of a bract similar to *Palissya* would be produced. By further reduction *Stachyotaxus* would evolve into the bract-scale complex characterized by *Cephalotaxus* with its highly reduced ovuliferous scale that bears a pair of erect ovules.'

References
Cleal (1993): 'First & last'.
Stewart & Rothwell (1993), Taylor & Taylor (1993): Classification.



1–3 from Meyen 1987
4,5,12 from Taylor & Taylor 1993 (from Delevoryas & Hope 1981)
6–11 from Florin 1951

Order **VOLTZIALES** Andr. 1954

Diagnosis: Pinopsid plants bearing cones with megasporophyll units comprising single (unlobed) sterile bracts, more or less free to the base, and ovuliferous scales almost invariably multilobed and multiovulate.

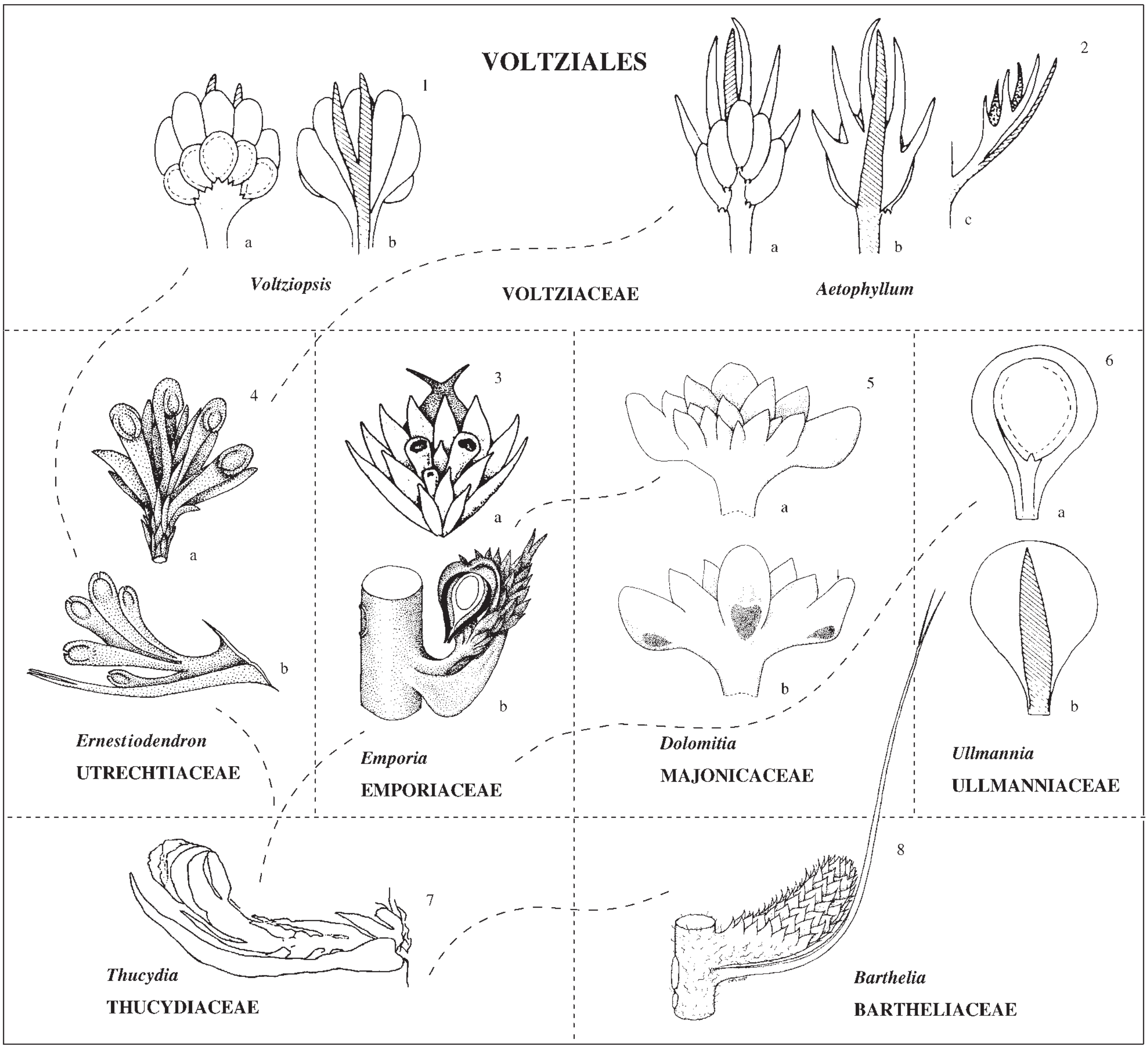
Remarks

It is essentially in the sense of Stewart & Rothwell (1993) that we conceive the Voltziales—as a group 'transitional' between the Cordaitales and Pinales. This is by no means a universal viewpoint and it remains uncertain whether the families included constitute a natural monophyletic group. Taylor & Taylor (1993), for instance, make no attempt to distinguish orders within the conifers, fossil or extant.

Doweld (2001) elevates the Voltziales to the rank of class and includes within it five orders and 12 families (Tab. 10, p. 17). As noted earlier (p. 106), we do not follow the inflated status of many of the taxa as proposed by Doweld. In this light, we do not adopt the class Voltziopsida. Doweld's Ferugliocladales is accepted as a distinct order here; his Ullmanniales and the Podozamitales are included within the Voltziales; the Buriadiaceae (order Incertae sedis) are excluded following Singh *et al.* (2003) who show that the previously described 'attached seeds' of this family are vegetative and that the reproductive structures of *Buriadia* remain unknown.

Families: Includes the seven families Thucydiaceae, Bartheliaceae, Emporiaceae, Utrechtiaceae, Majonicaeae, Ullmanniaceae and Voltziaceae.

Fig. 12. VOLTZIALES: SIMPLIFIED PHYLOGENY (MEGASPOROPHYLLS)



Family **THUCYDIACEAE** Hern.-Cast., G.W.Rothwell & G.Mapes 2001

Diagnosis: Voltzialean plants with ovulate pre-cones comprising a compound cone-like zone of axillary dwarf shoots between proximal and distal 'vegetative zones'; ovuliferous dwarf shoots bilateral, with a zone of several sterile scales subtending a fan of 3 or 4 uniovulate sporophylls; ovules inverted.

Range: Euramerica, C(KAS)
First & Last: *Thucydia mahoningensis* Hernandez-Castillo *et al.* 2001, terrestrial black shale between Mahoning coal and Brush Creek marine silty unit, Conemaugh Gp., Late Pennsylvanian (Stephanian A), abandoned strip mine (7-11 Coal Company), near East Liverpool, Columbiana County, Ohio, USA.

Reference whole-plant genus & stratum—Conemaugh Gp.
Ovulate organs: *Thucydia* Hernandez-Castillo *et al.* 2001; 1 TC, 1 sp., 22 compound ovulate zones.
Pollen cones: *Thucydia*; 1 TC, 1 sp., 1 compound pollen cone.
Foliage: *Thucydia*; 1 TC, 1 sp., 342 vegetative shoots.
Stratum: As above.
Affiliations: Grade 5 (Org.att., Mut.occ., Mor.cor.).

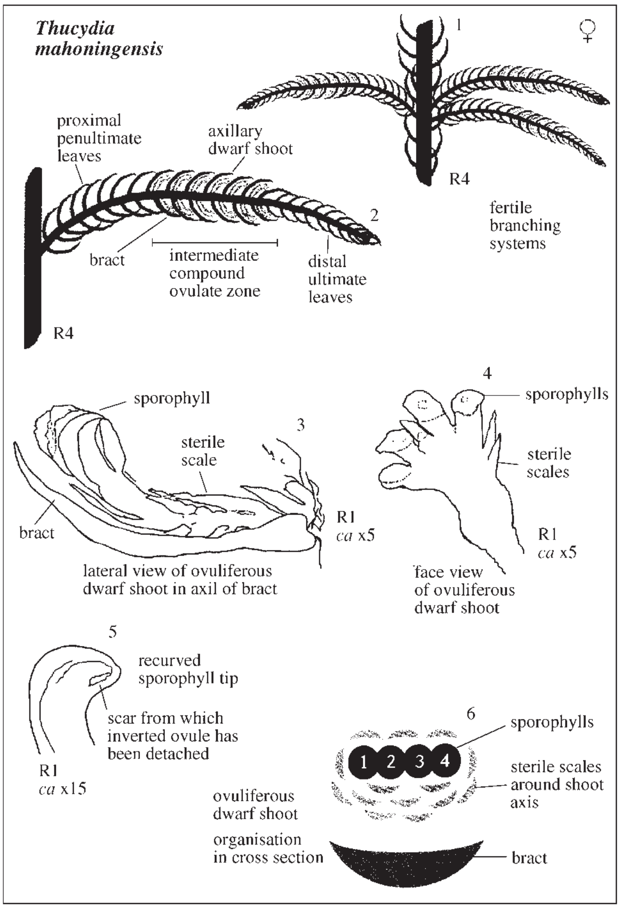
Prominence (colonisation success)—Euramerica Carboniferous
Frequency/ubiquity: Known from 1 TC only.
Diversity: 1 species.
Abundance: Abundant.
Longevity: Known from only the single stratigraphic level.

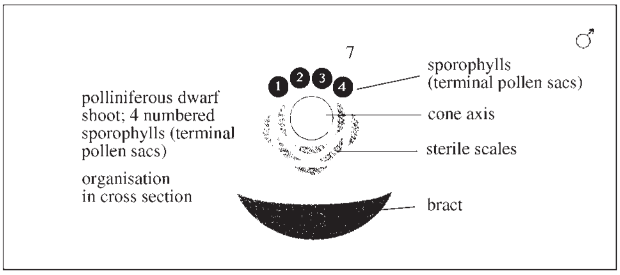
Ecology
Habit: Small trees, with dense wood and lateral branches with at least three orders of branching.
Habitat: Forested basinal slopes (of the Euramerican equatorial tropics).

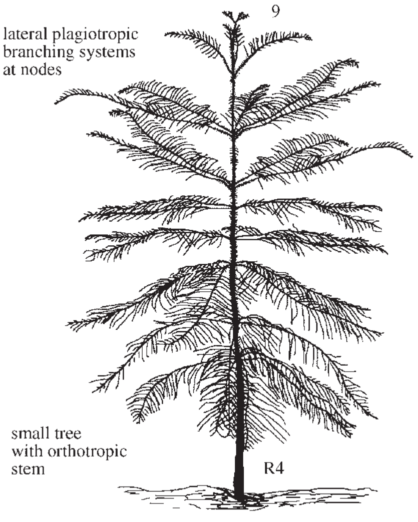
Other genera—nil.

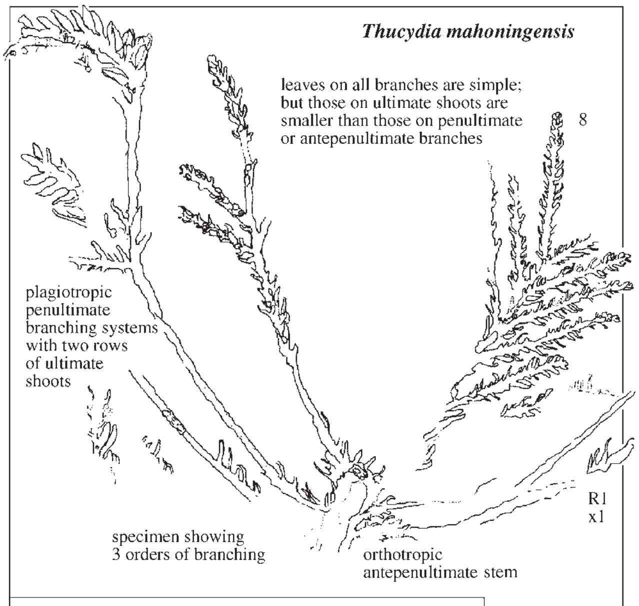
Remarks
Classification & phylogeny: *Thucydia*, according to Hernandez-Castillo *et al.* (2001), 'is the only conifer with ovuliferous fertile zones, compound pollen cones, and dissimilar stomatal distributions on vegetative and fertile leaves'. It is through this 'novel combination of features' that they characterise their new family Thucydiaceae. In the 'confused state of primitive conifer taxonomy', *Thucydia* is recognised by them as providing a 'benchmark for developing sound taxonomic concepts' for identifying Walchian species (conifers of the earliest Late Carboniferous to Permian found largely in the Euramerican equatorial tropics), and more broadly, 'for resolving phylogenetic relationships among fossil and living conifers'.

References
Hernandez-Castillo et al. (2001, 2003): General.









all abandoned strip mine, near **East Liverpool**, Ohio, USA
Conemaugh Gp., Late Carboniferous (Kasimovian)
1,2,9 from Hernandez-Castillo *et al.* 2003
3–8 from Hernandez-Castillo *et al.* 2001

Family **BARTHELIACEAE** G.W.Rothwell & G.Mapes 2001

Diagnosis: Voltzialean plants with ovulate pre-cones comprising a 'compound cone-like fertile zone of axillary dwarf shoots' extending into a distal 'vegetative zone'; ovuliferous 'dwarf shoots' radial, with 'numerous sterile scales', and in the 'axils of helically' arranged bracts with forked-tips; ovules 'apparently erect', 'borne on narrow sporophylls' (adapted from Rothwell & Mapes 2001).

Range: Euramerica, C(GZE)
First & Last: *Barthelia furcata* Rothwell & Mapes 2001, Hamilton quarries, Hartford Limestone, Topeka Limestone Fm., Shawnee Gp., Late Pennsylvanian, southeastern Kansas, USA.

Reference whole-plant genus & stratum—Hartford Limestone
Ovulate organs: *Barthelia* Rothwell & Mapes 2001; 1 TC, 1 sp., 6 ovulate fructifications.
Pollen cones: *Barthelia*; 1 TC, 1 sp., 3 pollen cones.
Foliage: *Barthelia*; 1 TC, 1 sp., *ca* 66 vegetative indivs.
Stratum: Topeka Limestone Fm., Kansas, USA, C(GZE).
Affiliations: Grade 5 (Org.att., Mut.occ., Mor.cor., Cut.cor.).

Prominence (colonisation success)—Euramerica Carboniferous
Frequency/ubiquity: Known from 1 TC only.
Diversity: 1 species.
Abundance: Co-dominant.
Longevity: Known from only the single stratigraphic level.

Ecology
Habit: Coniferophyte plant with irregular branching.
Habitat: Richly diverse, conifer-dominated (five coniferophyte species), forested, estuarine environment with marine tidal influence.

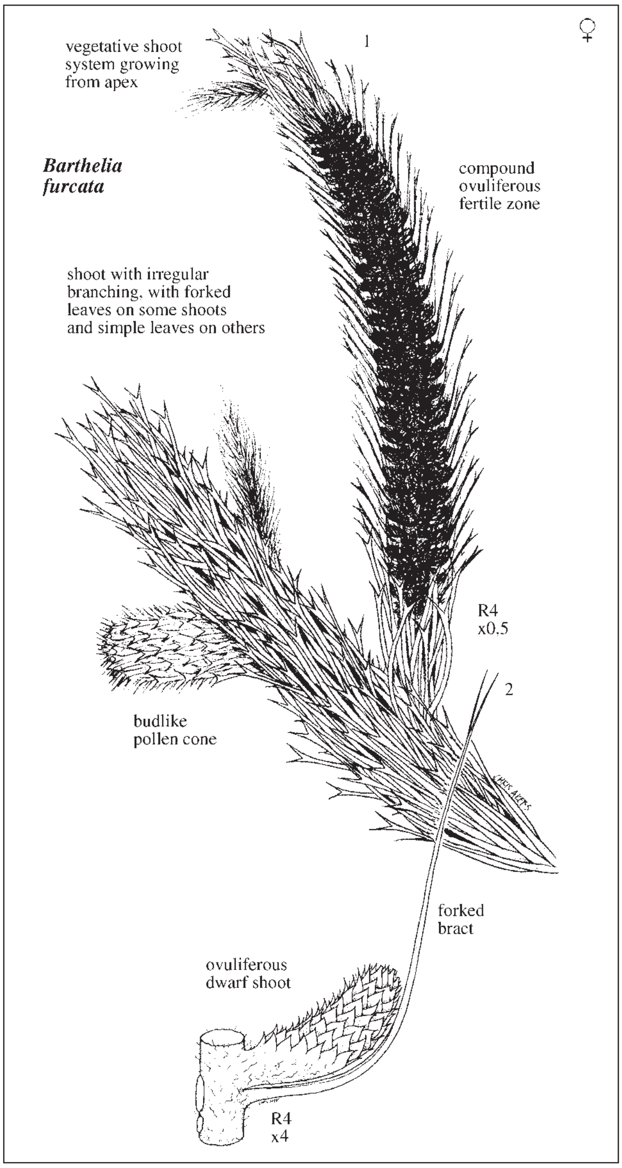
Other genera—nil.

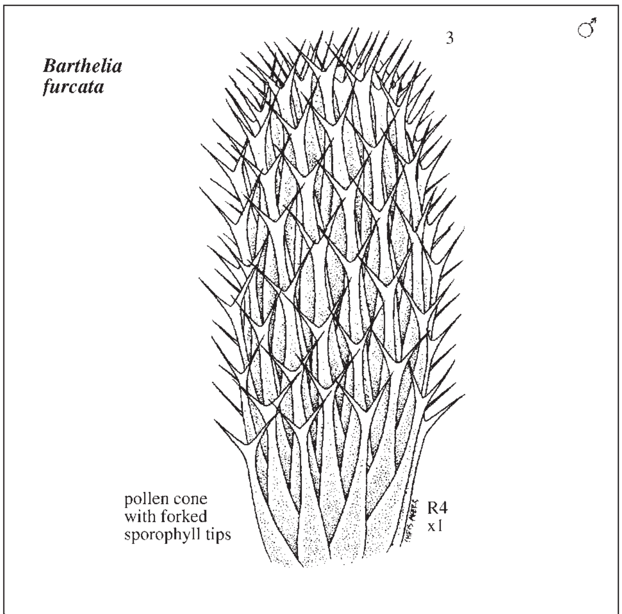
Remarks
Classifications & phylogeny: The study of *Barthelia* (Rothwell & Mapes 2001) from the richly diverse Hamilton Quarry lagerstätte—yielding everything from marine and nonmarine invertebrates to insects and tetrapods from amphibians to reptiles, aside from the superbly preserved flora—'is part of a broader program to reinvestigate previously described primitive conifers and other coniferophytes, to re-evaluate and more precisely define morphological characters of these plants and to describe new species of Paleozoic coniferophytes, with the ultimate goal of resolving the phylogenetic relationships of conifers'.

This programme, with many papers by Rothwell, Mapes and their colleagues on the Hamilton and other floras, was initiated over two decades ago (see Rothwell 1982). One especially significant observation made by Rothwell & Mapes (2001) concerning Paleozoic coniferophytes is that the 'numerous' morphological characters 'intergrade considerably', such that the wide diversity of taxa previously described and currently being revealed 'are not nearly as well understood as popularly believed'. Any coherent systematic framework based on 'incompletely known, isolated coniferophytic organs' is clearly 'extremely challenging'. They conclude that it is still uncertain 'whether coniferophytes form a clade, or whether they represent a grade of plants with parallel evolution of the coniferophytic syndrome of characters'.

Barthelia furcata emerges as one of a very few thoroughly known whole-plant (with a full set of affiliated organs) coniferophyte species. The syndrome of reproductive and vegetative characters is sufficiently unique to warrant its placement in a distinct family. Yet with coniferophyte phylogeny still so unresolved, Rothwell & Mapes (2001) felt they could not assign their new family to any particular order.

Reference
Rothwell & Mapes (2001): General.





all **Hamilton Quarry**, southeastern Kansas, USA
Hartford Limestone, Topeka Limestone Fm.,
Shawnee Gp., Late Carboniferous (Gzhelian)

1–3 from Rothwell & Mapes 2001

Family **EMPORIACEAE** G.Mapes & G.W.Rothwell 2003

Diagnosis: Voltzialean plants with compact ovulate cones bearing bilateral bract-scale complexes; sterile bracts free from dwarf shoots, with forked tip; ovuliferous dwarf shoots with 15–30 sterile scales and 1 or 2 (rarely 3–5) narrow, cylindrical fertile scales; ovules one per fertile scale, apical, inverted (adapted from Mapes & Rothwell 1984, 1991, 2003).

Range: C(GZE)
First & Last: *Emporia lockardii* (Mapes & Rothwell 1984) Mapes & Rothwell 2003; Hamilton quarries, Hartford Limestone, Topeka Limestone Fm., Shawnee Gp., Late Pennsylvanian, southeastern Kansas, USA.

Reference whole-plant genus & stratum—Topeka Limestone Fm.
Ovulate cones: *Emporia* Mapes & Rothwell 1991; 1 TC, 1 sp., 15 whole & partial permineralised cones, numerous compressed cones.
Pollen cones: *Emporia*; 1 TC, 1 sp., abundant.
Foliage: *Emporia*, 1 TC, 1 sp., abundant.

Stratum: Hamilton lagerstätte Topeka Limestone Fm., Kansas, USA, Pennsylvanian (Stephanian B/C), C(GZE).
Affiliations: Grade 5 *Empora*(5)*Emporia*(5)*Emporia*. (Org.att., Mut.occ., Mor.cor., Pol.cor.).

Prominence (colonisation success*)*—Euramerica Carboniferous
Frequency/ubiquity: Known from 1 TC only.
Diversity: 1 species.
Abundance: Co-dominant.
Longevity: Known from only the single stratigraphic level.

Ecology
Habit: 'Small eustelic coniferous trees with orthotropic stem' (Mapes & Rothwell 2003).
Habitat: Richly diverse, conifer-dominated, forested, estuarine environment with marine tidal influence; five coniferophyte species are recognised in this flora, a second being *Barthelia furcata* (Rothwell & Mapes 2001) in the family Bartheliaceae (p. 123).

Other genera—nil.

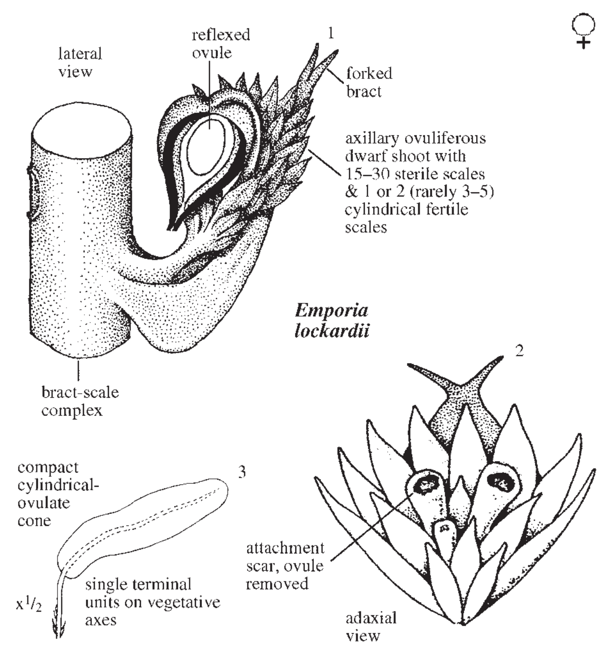
Remarks
Affiliations: The question of affiliations amongst the rich assemblage of coniferous ovulate cones, pollen cones and foliage from the Hamilton quarries lagerstätte is not given clear focus in the references cited. Mapes & Rothwell (1998), for instance, note that the pollen cones are abundant and well-preserved, but that considerable ontogenetic variation renders 'reliable separation' into species difficult. Though five coniferophyte species are recognised in the lagerstätte according to Rothwell & Mapes (2001), an explicit overview of these taxa is not yet at hand. For both ovulate and pollen cones of *Emporia*, vegetative axes are known with vegetative leaves showing a 'gradual transition' to 'sporophyll morphology'.

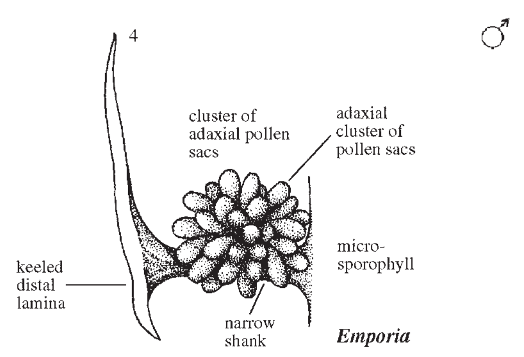
Topeka Limestone Fm.: For further detail on the Hamilton quarries lagerstätte, see under family Bartheliaceae (p. 123).

Taxonomy: Mapes & Rothwell (1991) created this family to include cones that 'bear ovules at the tip of distinct sporophylls' and have a 'larger number of ancestral characters than any other family of primitive conifers'. With the recognition of the families Thucydiaceae (p. 122) and Bartheliaceae (p. 123) by Hernandez-Castillo *et al.* (2001) and Rothwell & Mapes (2001), respectively, this status no longer fully holds.

Nomenclatural validation: Doweld (2001), in his classification of the gymnosperms, recorded the name Emporiaceae as *nom. invalid.*, and introduced the new family name Otoviciaceae to replace it. Mapes & Rothwell (2003) provided 'validation' for their 1991 names Emporiaceae, *Emporia* and *Emporia lockardi*—due to 'nomenclatural inadequacies' in their original publication. *Emporia lockardii* is based 'on fossil specimens originally assigned to the illegitimate Lebachia Florin as *L. lockardii* Mapes & G.W.Rothwell'.

References
Mapes & Rothwell (1984): Ovulate cones.
Mapes & Rothwell (1991): Original creation of genus & family.
Stewart & Rothwell (1993): General.
Mapes & Rothwell (1998): Pollen cones.
Mapes & Rothwell (2003): Nomenclature (validation).





pollen cones: cylindrical-elongated, with herbaceous axis;
pollen: monosaccate monolete prepollen (*Potonieisporites*);
often also found in pollen chamber and micropyle of ovules.

1,4 from Stewart & Rothwell 1993 (based on Mapes & Rothwell 1998)
2 from Mapes & Rothwell 1991
3 J.M. Anderson sketch 2004 (based on Mapes & Rothwell 1984)

Family **UTRECHTIACEAE** G.W.Rothwell & G.Mapes 2003

Diagnosis: Voltzialean plants with compact ovulate cones bearing bilateral bract-scale complexes; sterile bracts free, simple or forked; ovuliferous dwarf shoots with 10–30 sterile scales and one or more broad, flattened fertile scales; ovules one per fertile scale, laterally attached, inverted (adapted from Clement-Westerhof 1988; Mapes & Rothwell 1991).

Range: P(ASS–ROA)
First: *Utrechtia floriniformis* Rothwell & Mapes 2003, Sudetengau (Ottendorf bei Braunau), Oberrotliegendes, Germany.
Last: *Ortiseia leonardii* Florin 1964, Val Gardena Fm., Dolomites and Vicentinian Alps, Italy (Clement-Westerhof 1984).

Reference whole-plant genus & stratum—Rotliegend
Ovulate & pollen cones/foliage: *Otovicia* Kerp *et al*. 1990; ?TCs, 1 sp., numerous. Within the confusing plethora of taxa and names in this family, *Otovicia* emerges as a clearly conceived 'natural genus' for reference.

Stratum: Rotliegend, Saar-Nahe Basin, Germany, Permian (ASS).
Affiliations: *Otovicia*(5)foliage(5)male; Grade 5 (Org.att., Mut.occ., Pol.cor.).

Prominence (colonisation success)—Laurasia Permian
Frequency/ubiquity: Many localities, primarily Europe.
Diversity: 4 'natural genera' as recorded in Clement-Westerhof (1988).
Abundance: A dominant element in many floras.
Longevity: *ca* 30 my.

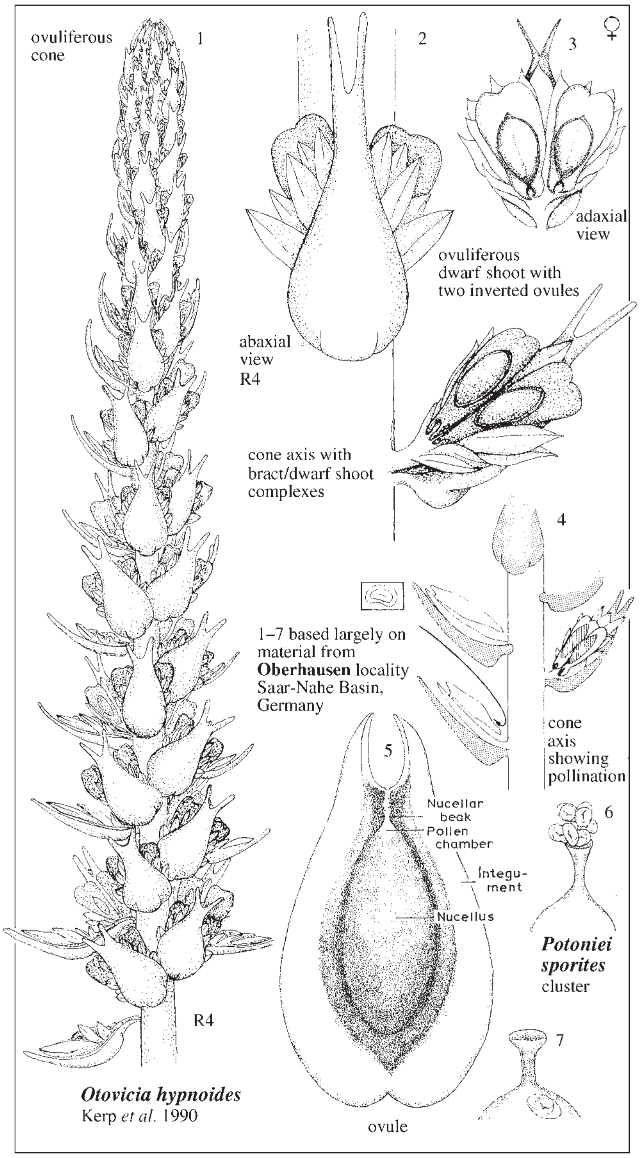
Ecology
Habit: Coniferous trees with orthotropic stems.
Habitat: Tropical, hinterland to deltaic and littoral floodplains.

Other genera
Cones &/or foliage: *Walchia* Sternberg 1825, *Ernestiodendron* Florin 1934, *Lebachia* Florin 1938, *Walchianthus* Florin 1940, *Walchiostrobus* Florin 1940, *Culmitzschia* Ullrich 1964 emend Clement-Westerhof 1984, *Ortiseia* Florin 1964, *Moyliostrobus* Miller & Brown 1973, *Utrechtia* (Mapes & Rothwell 1991) Rothwell & Mapes 2003.

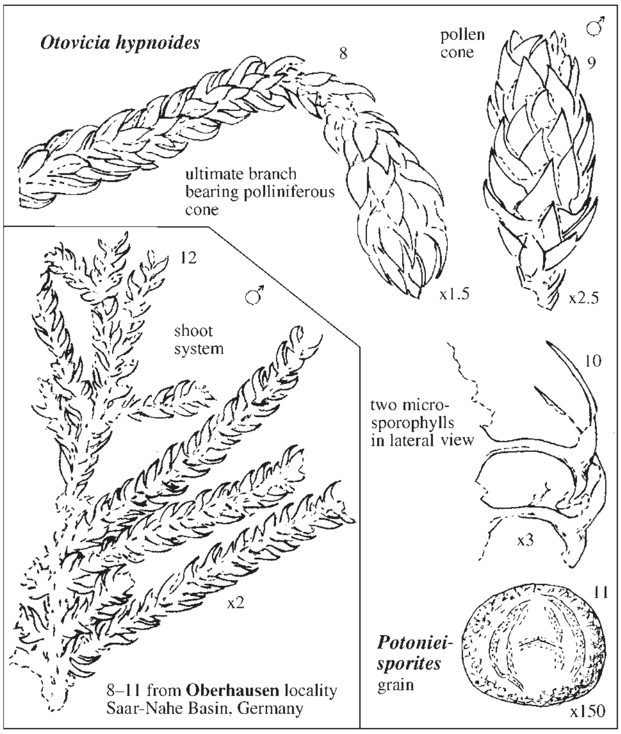
Remarks
Classification: 'This family is approximately equivalent to the Walchiaceae *sensu* Clement-Westerhof (1984) and Kerp *et al*. (1990). However, Mapes & Rothwell (1991) gave the family a more rigorous definition based mainly on ovulate cone structure, necessitating a change of name' (Cleal 1993).

Nomenclatural validation: Due to irregularities in the original naming of *Utrechtia floriniformis* in their new family Utrechtiaceae (Mapes & Rothwell 1991)—based on specimens previously included in *Lebachia piniformis*—Rothwell & Mapes (2003) published a special note validating the nomenclatural status of this species, genus and family. Doweld (2001) considered the name Utrechtiaceae *nom. invalid.* and employed the old name Walchiaceae (Goeppert 1865) Stur 1875.

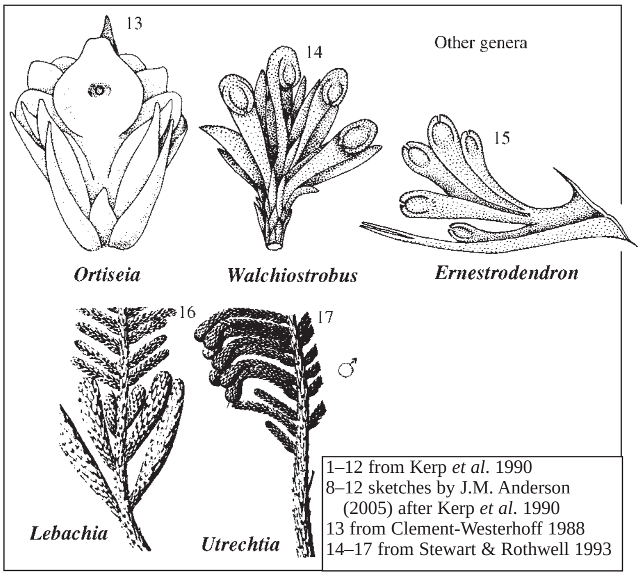
References
Clement-Westerhof (1984, 1988): Classification, other genera.
Kerp et al. (1990): *Otovicia*.
Mapes & Rothwell (1991), Rothwell & Mapes (2003): General.
Cleal (1993): Range, classification.



Otovicia hypnoides
Kerp *et al.* 1990



8–11 from **Oberhausen** locality Saar-Nahe Basin, Germany



1–12 from Kerp *et al*. 1990
8–12 sketches by J.M. Anderson (2005) after Kerp *et al*. 1990
13 from Clement-Westerhoff 1988
14–17 from Stewart & Rothwell 1993

Family **MAJONICACEAE** Clem.-West. 1987

Diagnosis: Voltzialean plants with compact ovulate cones bearing bilateral bract-scale complexes; sterile bracts free or partially fused with dwarf shoots, simple; ovuliferous dwarf shoots with 1–15 sterile scales and 2 or 3 variously shaped, flattened fertile scales; ovules one per fertile scale, laterally attached, inverted (adapted from Clement-Westerhof 1988).

Range: P(ROA)
First & Last: *Majonica alpina* Clement-Westerhof 1987 and *Dolomitia cittertiae* Clement-Westerhof 1987, Val Gardena Fm., Dolomites and Vicentinian Alps, Southern Alps, Italy.

Reference whole-plant genus & stratum—Val Gardena Fm.
Ovulate cone: *Majonica* Clement-Westerhof 1987; 3 TCs, 1 sp., numerous.
Pollen cone: *Majonica*; 1 TC, 1 sp., ?1 indiv.
Foliage: *Majonica*; 3 TCs, 1 sp., numerous.

Stratum: As for 'Range' above.
Affiliations: Female(5)foliage(5)male; Grades 3 to 5 (Org.att., Mut.occ., Cut.cor.).

Prominence (colonisation success)—Euramerica Late Permian
Frequency/ubiquity: Confined to the Alpine region.
Diversity: 2 genera, 2 species (Clement-Westerhof 1987).
Abundance: Numerous.
Longevity: *ca* 3 my.

Ecology
Habit: Most likely trees, but size unknown.
Habitat: Tropical, alluvial-plain hinterland from the sea.

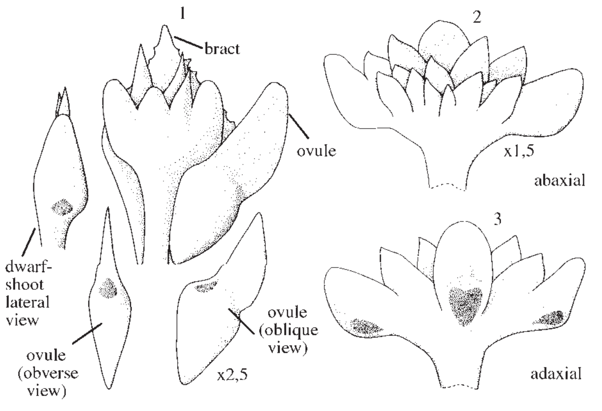
Other genera
Foliage & ovuliferous dwarf shoots: *Dolomitia* Clement-Westerhof 1987.

Remarks
Classification: We conceive this family differently to Clement-Westerhof (1987) and Cleal (1993) in transferring *Pseudovoltzia* to the Voltziaceae. The family thus includes only the two genera *Majonica* and *Dolomitia*.

Clement-Westerhof (1988) writes 'It is here considered that Majonicaceae differ from most known extinct and extant conifers in one distinct aspect: the fertile scales and consequently the ovules are not arranged in one plane (with the exception of *Pseudovoltzia sjerpii*)'.

Doweld (2001) includes the Majonicaceae within his concept of the order Voltziales.

References
Clement-Westerhof (1984, 1987, 1988): General.



Majonica alpina

reconstruction of
bract, ovuliferous
dwarf-shoot,
and ovule

Dolomitia cittertiae

reconstruction of
ovuliferous dwarf-
shoot

1–3 from Clement-Westerhof 1988
all Val Gardena Fm., Dolomites
& Vicentinian Alps, Italy

Family **ULLMANNIACEAE** Němejc 1959

Diagnosis: Voltzialean plants with compact ovulate cones bearing bilateral bract-scale complexes; sterile bracts free, simple; ovuliferous dwarf shoots reduced to a single, simple, orbicular fertile scale; ovules one per scale, laterally attached, inverted (adapted from Clement-Westerhof 1988).

Range: P(ROA)
First & Last: *Ullmannia bronnii* Göppert 1850 and *U. frumentaria* Göppert 1850; Kupferschiefer, Lower Rhine, Germany (Schweitzer 1963); and Marl Slate, Cumbria and Durham, UK (Stoneley 1958). (From Cleal 1993.)

Reference whole-plant genus & stratum—Kupferschiefer
Ovulate cone: *Ullmannia* Göppert 1850; TCs/spp/abundance uncertain.
Pollen cone: *Ullmannia*; TCs/spp/abundance uncertain.
Foliage: *Ullmannia*; 12 TCs, 2 spp, v. abundant.

Stratum: Kupferschiefer, Lower Rhine, Germany, P(ROA).
Affiliations: female(5)foliage(5)male; Grade 5 (Org.att.).

Prominence (colonisation success)—Euramerica Late Permian
Frequency/ubiquity: Confined to Germany and England.
Diversity: 1 genus, 2 species (Clement-Westerhof 1988).
Abundance: Numerous.
Longevity: *ca* 3 my.

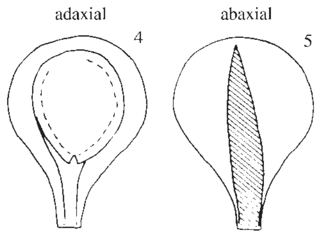
Ecology
Habit: Presumably trees.
Habitat: Tropical, lowland wetland and coastal habitats.

Other genera—nil.

Remarks
Classification & scope: Our treatment of the family follows Cleal (1993), who wrote 'The natural status of this family has still to be confirmed (Clement-Westerhof 1988). *Ullmannia* Göppert 1850, has also been reported from older (SAK?) and slightly younger (KAZ) Angaran assemblages (summarized by Vakhrameev *et al*. 1978), but their relationship to the European species (and thus to the family) is unclear.'

Doweld (2001) erected a new order Ullmanniales for this rather unique monogeneric family, but we see it as falling reasonably within our concept of the Voltziales.

References
Clement-Westerhof (1988): General.
Cleal (1993): Range, classification.



Ullmannia

4,5 from And. & And. 1989

Family **VOLTZIACEAE** C.A.Arnold 1947

Diagnosis: Voltzialean plants with compact ovulate cones bearing bilateral bract-scale complexes; sterile bracts generally fused to axis of scale, free beyond (fully free in *Pseudovoltzia*), and generally unforked towards tip (forked only in *Voltziopsis*); ovuliferous scales mostly 1-, 3- or 5-lobed; ovules 1–5, inverted.

Range: Global, P(ROA)–K(CEN)
First: *Pseudovoltzia sjerpii* Clement-Westerhof 1987, Val Gardena Fm., Dolomites and Vicentinian Alps, Italy. Also *Pseudovoltzia liebeana* (Geinitz) Florin 1927, Kupferschiefer, Lower Rhine, Germany; and Marl Slate, Cumbria and Durham, England, UK.
Last: *Protodammara speciosa* Hollick & Jeffrey 1909 and *Dectylolepis cryptomerioides* Hollick & Jeffery 1909, Raritan Fm., Staten Island, USA.

Reference whole-plant genus & stratum—Molteno Fm.
Ovulate cone: *Telemachus* H.M.Anderson 1978; 18 TCs, 6 spp, 311 indivs.
Pollen cone: *Odyssianthus* And. & And. 2003; 1 TC, 1 sp., 2 indivs.
Foliage: *Heidiphyllum* Retallack 1981; 62 TCs, 1 sp., >70%.

Stratum: Molteno Fm., Karoo Basin, S. Africa, Tr(CRN).
Affiliations: *Telemachus*(4)*Heidiphyllum*(4)*Odyssianthus*, Grade 4 (Mor.cor., Mut.occ., Kin.reinf.).

Prominence (colonisation success)—Gondwana Triassic (GT)
Heidiphyllum (foliage): Widespread in all Gondwana continents.

FUDAL rating: 26/5/3/95/18 = 47; the 2nd most prominent gymnospermous foliage genus in the GT.
Frequency: High, 26 of 84 Gondw. degree squares.
Ubiquity: High, 5 of 5 Gondw. continents.
Diversity: Low, 3 species in GT.
Abundance: Abundant (often monodominant), 95% norm in Molteno TCs.
Longevity: Moderate, 18 my through Triassic.

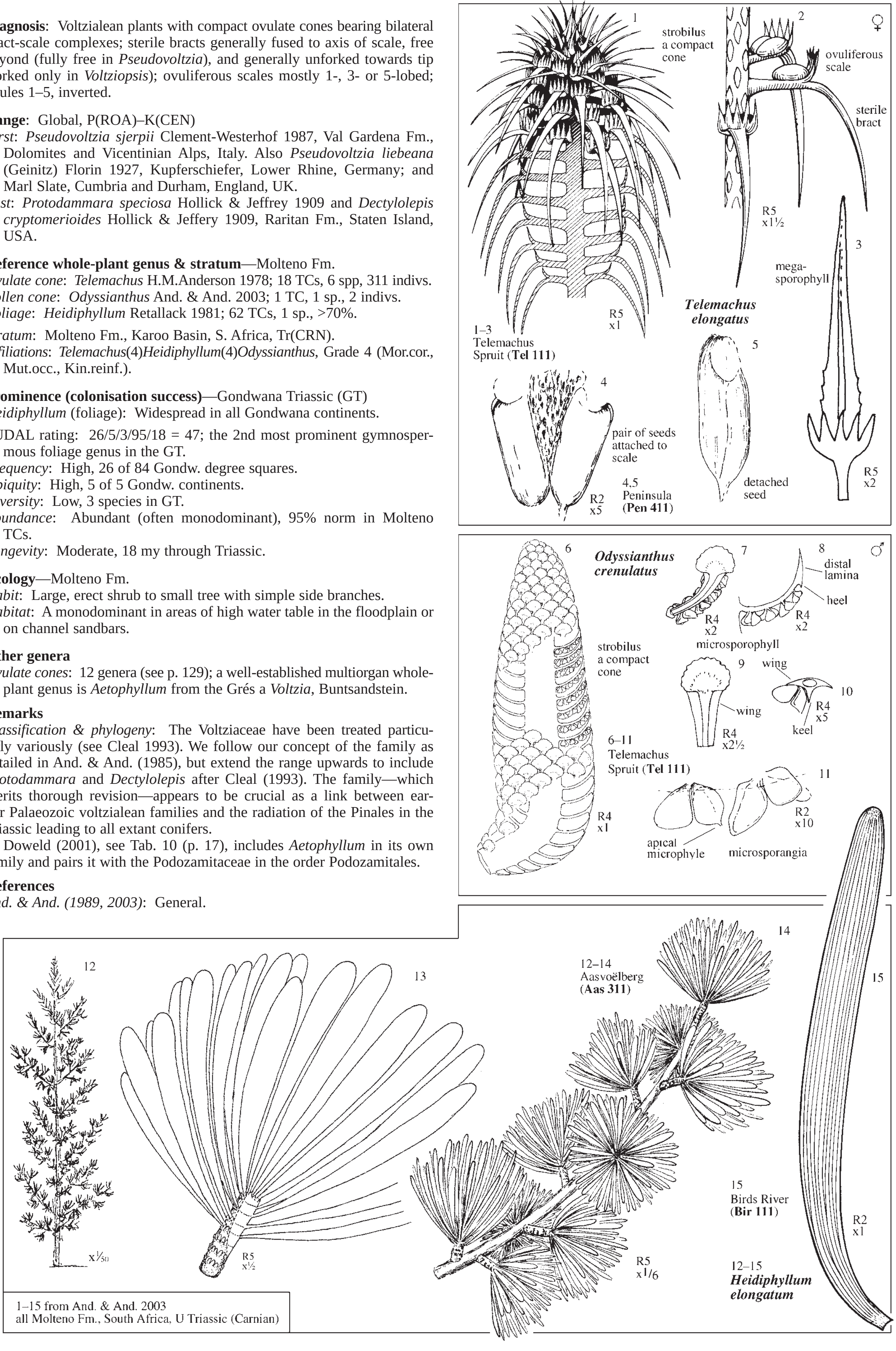
Ecology—Molteno Fm.
Habit: Large, erect shrub to small tree with simple side branches.
Habitat: A monodominant in areas of high water table in the floodplain or on channel sandbars.

Other genera
Ovulate cones: 12 genera (see p. 129); a well-established multiorgan whole-plant genus is *Aetophyllum* from the Grés a *Voltzia*, Buntsandstein.

Remarks
Classification & phylogeny: The Voltziaceae have been treated particularly variously (see Cleal 1993). We follow our concept of the family as detailed in And. & And. (1985), but extend the range upwards to include *Protodammara* and *Dectylolepis* after Cleal (1993). The family—which merits thorough revision—appears to be crucial as a link between earlier Palaeozoic voltzialean families and the radiation of the Pinales in the Triassic leading to all extant conifers.

Doweld (2001), see Tab. 10 (p. 17), includes *Aetophyllum* in its own family and pairs it with the Podozamitaceae in the order Podozamitales.

References
And. & And. (1989, 2003): General.



1–15 from And. & And. 2003
all Molteno Fm., South Africa, U Triassic (Carnian)

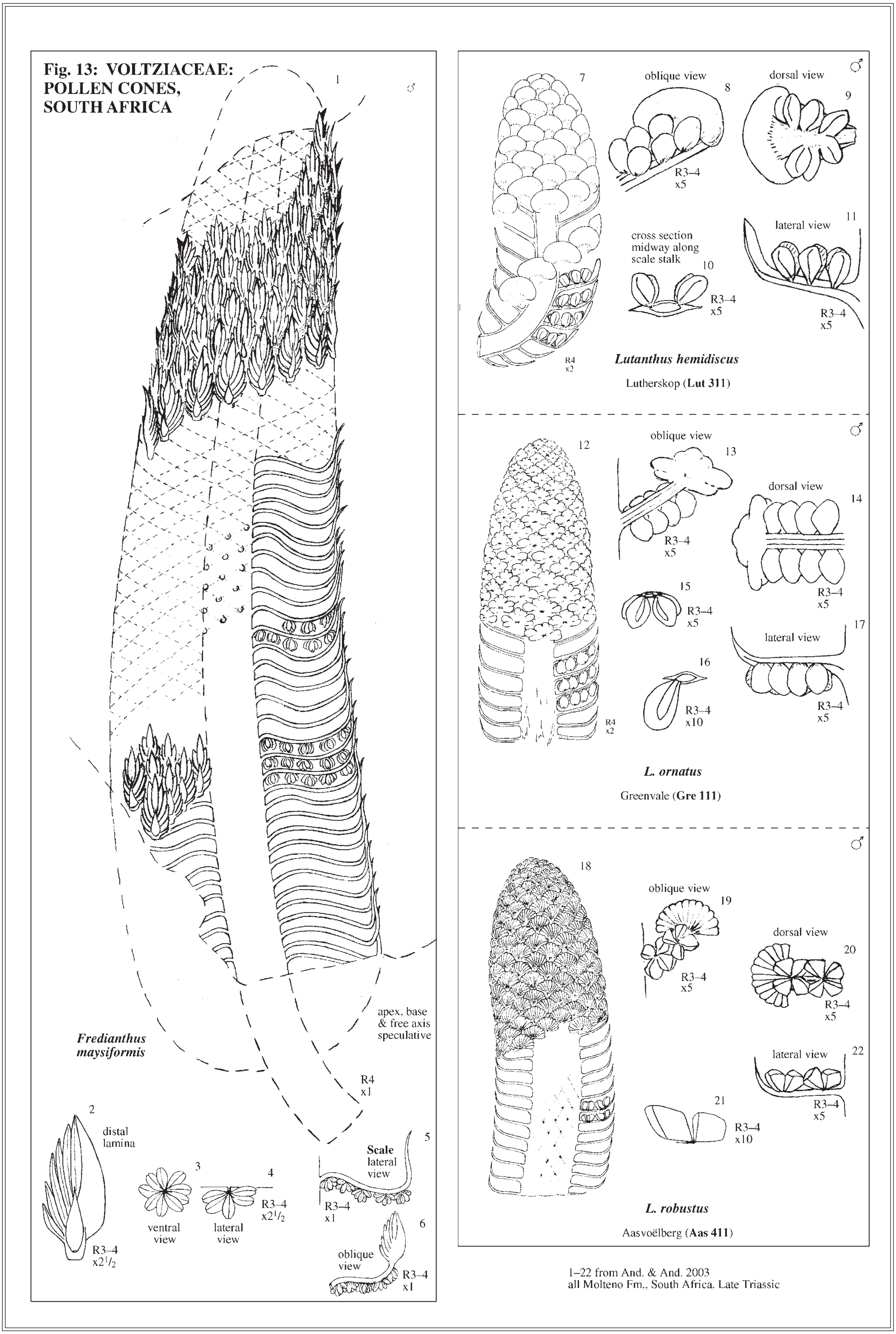


Fig. 13: VOLTZIACEAE: POLLEN CONES, SOUTH AFRICA

1–22 from And. & And. 2003
all Molteno Fm., South Africa, Late Triassic

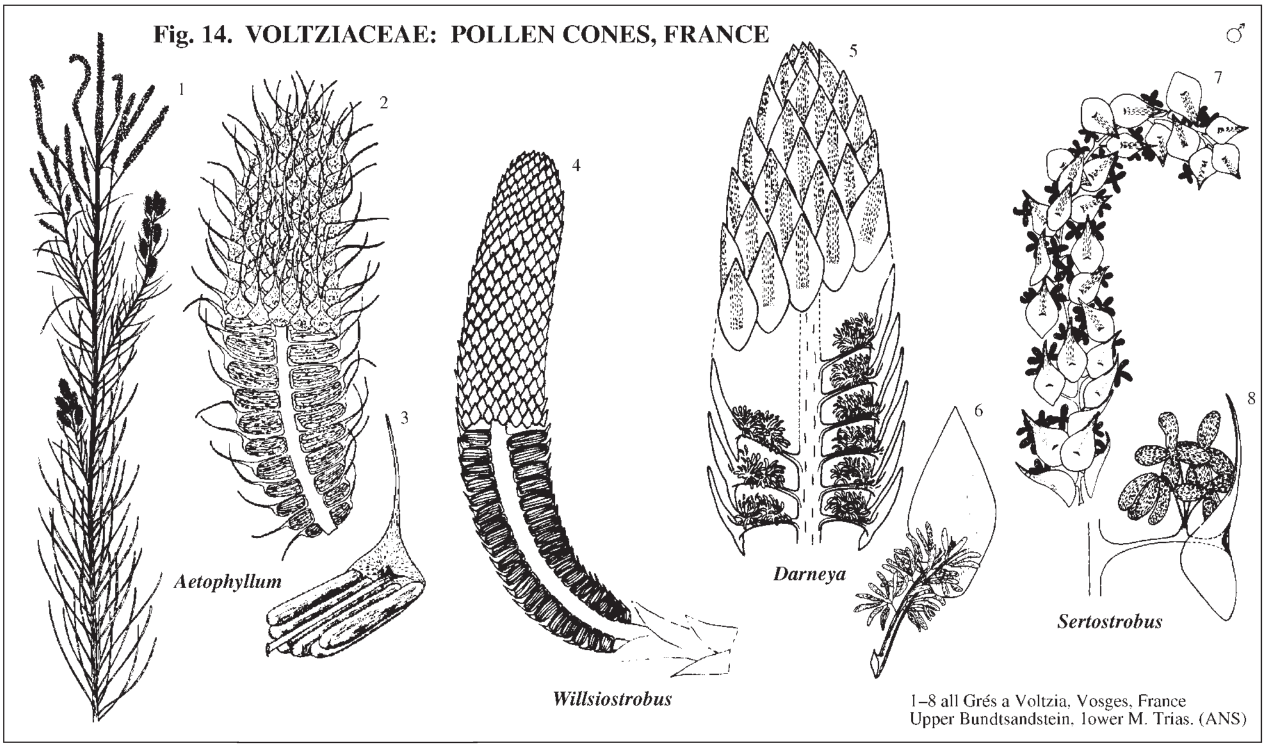


Fig. 14. VOLTZIACEAE: POLLEN CONES, FRANCE

1–8 all Grés a Voltzia, Vosges, France
Upper Bundtsandstein, lower M. Trias. (ANS)

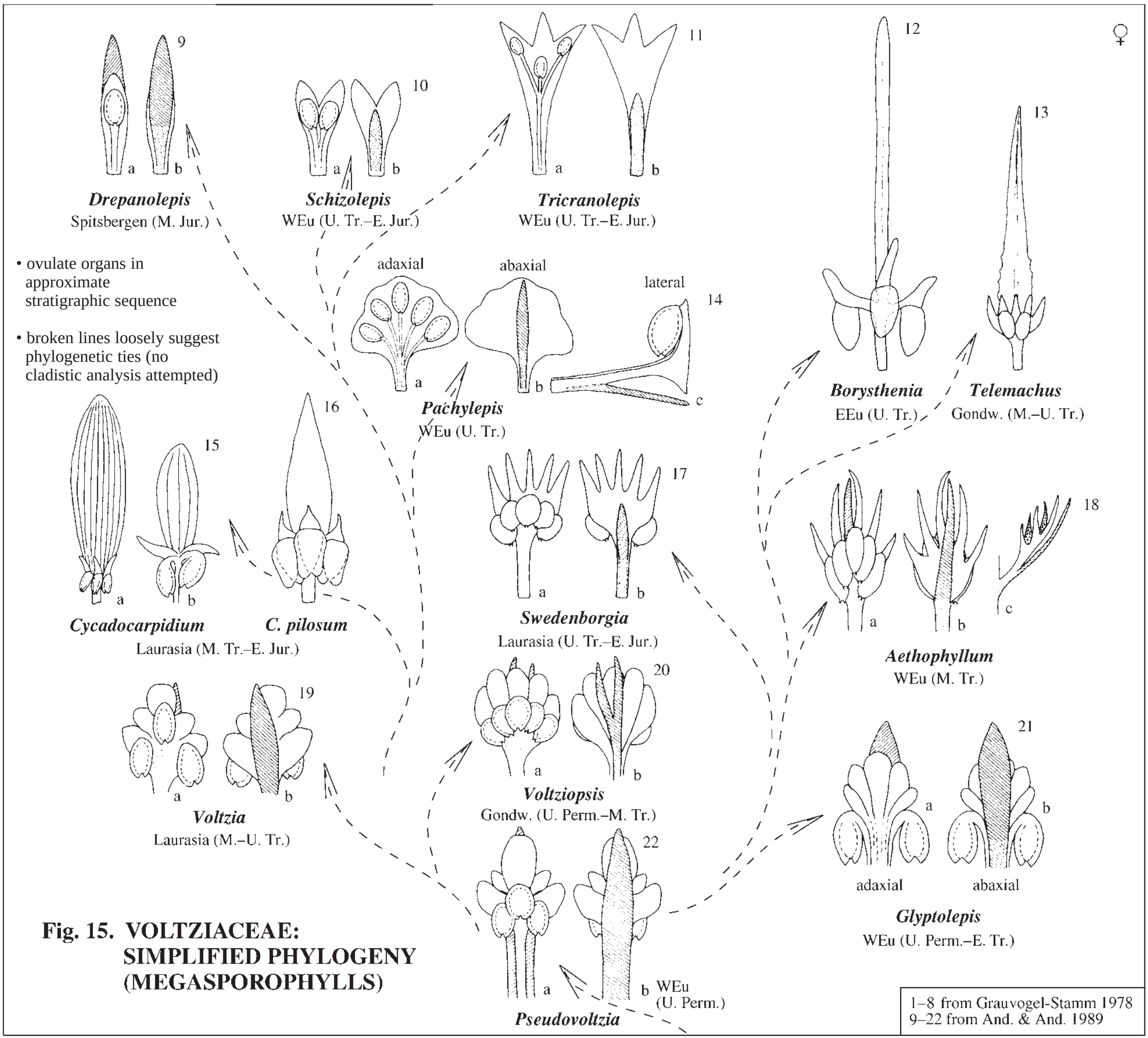


Fig. 15. VOLTZIACEAE: SIMPLIFIED PHYLOGENY (MEGASPOROPHYLLS)

- ovulate organs in approximate stratigraphic sequence
- broken lines loosely suggest phylogenetic ties (no cladistic analysis attempted)

1–8 from Grauvogel-Stamm 1978
9–22 from And. & And. 1989

Order **PINALES** Dumort. 1829

Contributors: M. Mundry, I. Mundry & T. Stützel

Diagnosis: Pinopsid plants bearing compact ovuliferous cones, or drupe-like fruit, with megasporophyll units comprising single (unlobed) sterile bracts more or less fused throughout but for a free tip; ovuliferous scales almost invariably unlobed and with 1 to several ovules.

Classification & phylogeny (within Pinales)

The following classification of the genera and families mainly follows Farjon (2001) but for two major modifications. The first is the fusion of the Taxaceae and Cephalotaxaceae, as molecular data strongly support a close relationship of these families. They are combined by male and female reproductive structure (*Amentotaxus*, for instance, has recently been transferred to the Taxaceae *s.str.*). The other modification is the fusion of Phyllocladaceae and Podocarpaceae, although they differ in some morphological details (e.g. leaves). The relationships of the remaining families are clear. In most morphological analyses, Sciadopytaceae are closely related to Cupressaceae *s.l.*, but recent molecular studies place them at the base of a Cupressaceae *s.l.*/Taxaceae *s.l.* clade. The Araucariaceae and the Podocarpaceae also seem to be sister groups, sharing the character of one ovule/cone bract. In the study of Quinn *et. al.* (2002), the Pinaceae are basal to all the other Pinales families.

Origins (fossil evidence)

Fossil evidence (Yao *et al*. 1997) suggests that all modern conifer families were well established by the Jurassic, with the Podocarpaceae, Araucariaceae, Pinaceae and Taxodiaceae known to first appear in the Triassic. The first appearance of the Cupressaceae *s.str.* is taken as lowest Tertiary (Danian), as in Cleal (1993).

Families: Includes the six families Pinaceae, Podocarpaceae, Araucariaceae, Cupressaceae (includes former Taxodiaceae), Sciadopityaceae and Taxaceae (includes former Cephalotaxaceae).

Tab. 24. EXTANT CONIFERS: CLASSIFICATION & BIODIVERSITY

[Contributors: Mundry, Mundry & Stützel]

ORDER
Family
Subfamily
Genus

PINALES (6 fam, 69 gen, 623 spp)
PINACEAE (11 gen, 225 spp)
Pinoideae
Pinus (ca 109 spp), *Picea* (34 spp), *Cathaya* (1 sp.), *Larix* (11 spp), *Pseudotsuga* (4 spp)
Abietoideae* (maybe paraphyletic)
Cedrus (4 spp), *Abies* (48 spp), *Pseudolarix* (1 sp.), *Keteleeria* (3 spp), *Nothotsuga* (1 sp.), *Tsuga* (9 spp)

PODOCARPACEAE (19 gen, 189 spp)
Podocarpoideae
Saxegothaea (1 sp.), *Prumnopitys* (9 spp), *Sundacarpus* (1 sp.), *Retrophyllum* (5 spp), *Nageia* (6 spp), *Afrocarpus* (6 spp), *Podocarpus* (107 spp), *Parasitaxus* (1 sp.), *Acmopyle* (2 spp), *Dacrycarpus* (9 spp), *Falcatifolium* (6 spp), *Dacrydium* (21 spp), *Halocarpus* (3 spp), *Lepidothamnus* (3 spp), *Lagarostrobus* (1 sp.),
Microcachrys (1 sp.), *Microstrobus* (2 spp), *Manoao* (1 sp.)
Phyllocladoideae
Phyllocladus (4 spp)

ARAUCARIACEAE (3 gen, 41 spp)
Agathis (21 spp), *Araucaria* (19 spp), *Wollemia* (1 sp.)

CUPRESSACEAE incl. Taxodiaceae (29 gen, 133 spp)
Taxodioideae
Athrotaxis (3 spp), *Cunninghamia* (2 spp), *Taiwania* (1 sp.), *Cryptomeria* (1 sp.), *Sequoiadendron* (1 sp.), *Sequoia* (1 sp.), *Metasequoia* (1 sp.), *Glyptostrobus* (1 sp.), *Taxodium* (2 spp).
Cupressoideae
Neocallitropsis (1 sp.), *Callistris* (15 spp), *Actinostrobus* (3 spp), *Widdringtonia* (4 spp), *Tetraclinis* (1 sp.), *Platycladus* (1 sp.), *Microbiota* (1 sp.), *Thuja* (5 spp), *Pilgerodendron* (1 sp.), *Austrocedrus* (1 sp.), *Libocedrus* (5 spp), *Papuacedrus* (1 sp.), *Calocedrus* (3 spp), *Fokienia* (1 sp.), *Fitzroya* (1 sp.), *Diselma* (1 sp.), *Thujopsis* (1 sp.), *Chamaecyparis* (6 spp), *Cupressus* (15 spp), (*Xanthocyparis*, 2 spp probably better treated as members of *Cupressus*), *Juniperus* (53 spp).

SCIADOPITYACEAE (1 gen, 1 sp.)
Sciadopitys (1 sp.)

TAXACEAE incl. Cephalotaxaceae (6 gen, 34 spp)
Taxoideae
Pseudotaxus (1 sp.), *Taxus* (10 spp), *Torreya* (5 spp), *Austrotaxus* (1 sp.), *Amentotaxus* (6 spp)
Cephalotaxoideae
Cephalotaxus (11 spp)

References

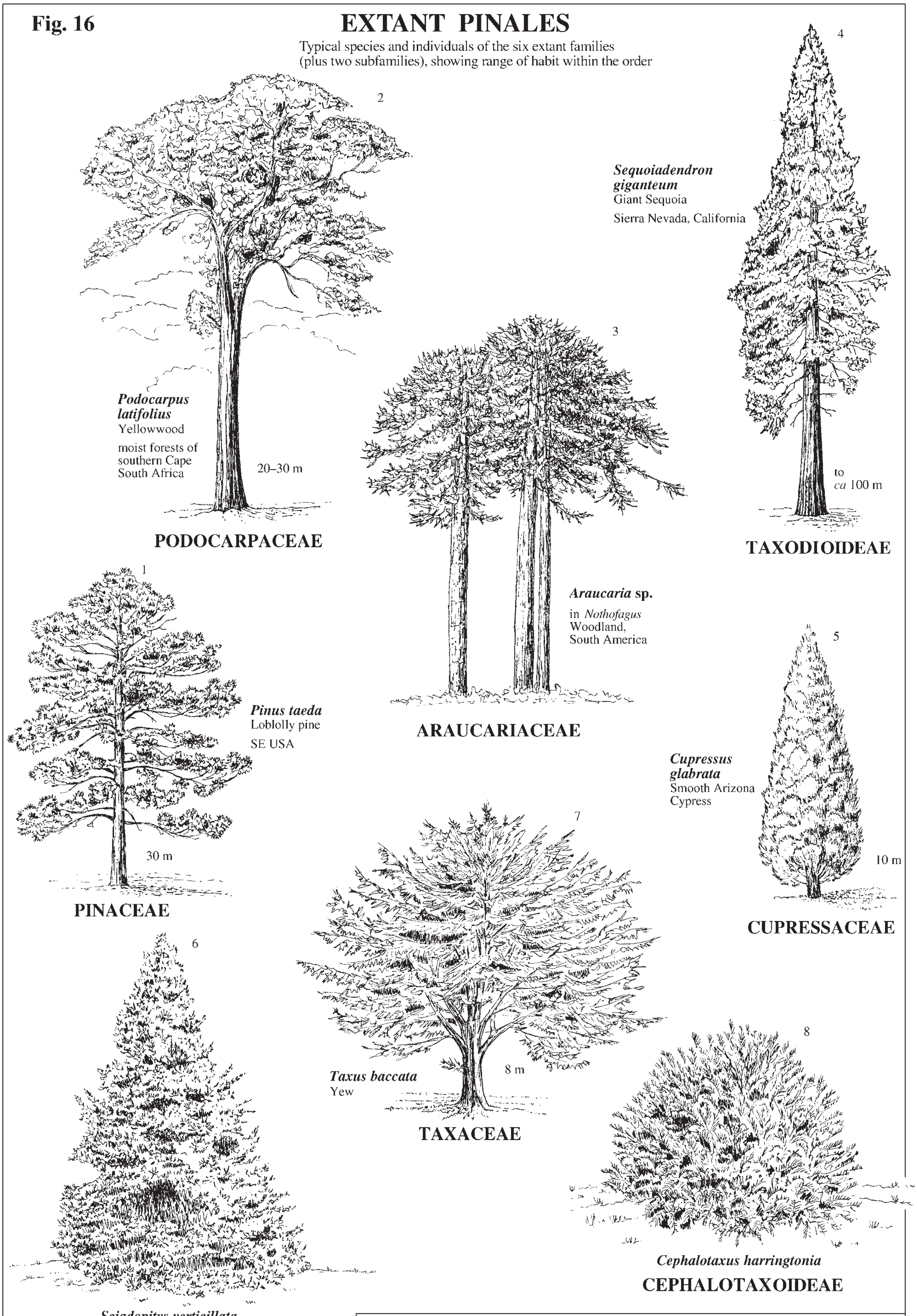
Quinn, Price & Gadek 2002: Phylogeny

Relict status of extant conifers

Most species in all families of extant conifers, including the Pinaceae, are ‘more or less rare endemics, very often with a relict distribution’. ‘Not a few’, in the wild, are ‘restricted to a few score or less individuals’. Several species have become known to science only recently, ‘most notably in China’, simply because the small isolated populations had not yet been discovered. Many such species are known from the fossil record to have been ‘much more common and widespread’ in the Tertiary. Many were reduced to rarity during the Pleistocene ice age, and several still earlier. Though humankind has been involved in deforestation for millennia, especially around the Mediterranean and in SE China, their very great impact came after the decline of the conifers. How many rare, relict conifer species have been lost to human pressure (agriculture, cities), we simply cannot know—but considering the ‘remnants of populations as exist today of *Abies* in the Mediterranean and *Abies, Cathaya* and *Pseudotsuga* in China’, the number of such extinctions are surely ‘not a few’. The 550–600 conifer species still extant, are but a ‘remnant of a plant world from a distant past’ (Farjon 1990).

Fig. 16 EXTANT PINALES

Typical species and individuals of the six extant families (plus two subfamilies), showing range of habit within the order



1–8 all H.M. Anderson sketches 2004 (1 after Brockman 1986; 2 after Palmer 1972; 3 after White 1990; 4,5 after A. Mitchel 1974; 6,8 after van Gelderen & van Hoey Smith 1986; 7 after J. Mitchell 1982)

PINALES AND THE FOREST DOMAINS OF THE WORLD

Forest occurs at virtually all latitudes, aside from the polar regions of tundra and ice, and in all climatic belts, aside from desert and semidesert.

We discuss briefly the role of the conifers in those three of the six natural forest domains in which they are most prevalent (adapted from J. Page 1984).

Coniferous forest

The Pinales (conifers) dominate 'unchallenged in the coldest and most forbidding regions' north of *ca* 55ºN. The most northerly of all conifers, the larches (*Larix*, Pinaceae), occur in eastern Siberia to near 70ºN. These hardy trees are among the few species able 'to stand picket along the frigid, empty tundra'. They are able to survive in extreme cold since, 'unlike most evergreens they shed all their needles each year just before winter, thus reducing moisture loss and minimising' damage caused 'by high wind and heavy snow'. 'Larches at the tree line in the taiga grow much more slowly than other conifers'—with up to 60 growth rings per inch, a rate one tenth that of conifers in the southern United States (J. Page 1984).

These coniferous forests exist on the poorest of soils left in the wake of the Pleistocene Ice Age. And they contribute further to the impoverishment: evergreen needles are acid, decompose slowly, and form a layer of black, acid humus, leading to barren forest floors with no undergrowth.

Temperate mixed forest

From around 55º in the north and southward as far as Mexico and Florida, the Mediterranean belt and Canton city in China, occurs the belt of temperate mixed forest across the Northern Hemisphere. Some 2 500 species of broad-leaved, deciduous trees are encountered in this belt. Along its northern reaches willows, poplars and birches appear scattered through the coniferous forests; further south the forest becomes dominated by 'such trees as oak, hickory, beech and maple'. Most familiar amongst the evergreens are the pines, firs, hemlock, spruce and cedar (Pinaceae), cypress and junipers (Cupressaceae) and the redwoods (Taxodiaceae). These conifers, of far deeper origins than the deciduous angiospermous trees, 'still hold the records for size and longevity'.

Temperate moist forest (not considered)

Dry forest

In the dry forests of the world (e.g. California, Mediterranean and widespread across the Gondwanan Southern Hemisphere), coniferous evergreens are far from being the only evergreens. Much more common in the Southern Hemisphere are the broad-leaved sclerophyllous ('hard-leaved') evergreens. Eucalyptus trees, accounting for 75% of Australia's forest, are a prime example. In the regions of Mediterranean climate, with typically warm, wet winters, the sclerophylls bear small, leathery leaves that retain their moisture through the long, dry summers.

Tropical deciduous forest (not considered)

Tropical rain forest (not considered)

Phytogeographic highlights of extant Pinales

Here follows an impressionistic selection of highlights, mostly Gondwanan, aimed at giving a sense of the character and spread of conifers in the present time frame.

Canada: The Pinaceae make up the bulk of the boreal northern coniferous forest. *Abies balsamea*, the balsam fir 'is an important component of the Canadian boreal forest' (Woodland 2000).

California: Two of the most spectacular tree species on Earth (former family Taxodiaceae) occur in this Mediterranean state: *Sequoia sempervirens* (coastal redwood of SW Oregon and coastal N California), reaching over 115 m, is the tallest tree on Earth; *Sequoiadendron giganteum* (giant sequoia, Sierra Nevada), reaches *ca* 100 m and has greater girth, and with estimates of over 4-000 years in age, includes perhaps, after the bristlecone pine, the oldest trees on Earth (Woodland 2000).

Nevada: *Pinus longaeva* (Pinaceae), the bristle-cone pine of the American southwest, has generally been regarded 'the oldest living organism in the world', dating to *ca* 5-000 years (Woodland 2000).

India: Only one species, *Nageia wallichiana* (Podocarpaceae), occurs on the subcontinent of India. Like *Podocarpus*, it is an extremely tall tree (Woodland 2000; C.N. Page 1990).

Japan: The family Sciadopityaceae, including the single genus and species *Sciadopitys verticillata* (umbrella pine), is endemic to the cool temperate mountains of central and southern Japan (C.N. Page 1990).

Australia: A fairly rich diversity of conifers (four families, 14 genera, 44 species) are indigenous to Australia: Podocarpaceae (seven genera, 16 species), Araucariaceae (three genera, six species), Cupressaceae (three genera, 20 species), former Taxodiaceae (one genus, two species) (Morley & Toelken 1983; K.D. Hill 1998).

Wollemia nobilis (Araucariaceae), the Wollemia pine, was discovered very recently and described only in 1995. It occurs in a remote area in the Blue Mountains less than 200 km from Sydney (Woodland 2000).

New Caledonia: With five species of *Agathis* and 13 species of *Araucaria*, this isolated island is the biodiversity hotspot of the family Araucariaceae (Woodland 2000). Indeed, both extant genera of the family have their greatest species concentration here (C.N. Page 1990).

New Zealand: Like Australia, New Zealand is home to a diverse indigenous conifer flora (three families, five genera, 19 species): Podocarpaceae (three genera, 16 species), Araucariaceae (one genus, one species), Cupressaceae (one genus, two species). Interestingly, all 19 species are endemic (Allan 1961).

When Europeans settled these islands some 150 years ago, various Podocarpaceae species (e.g. *Dacrydium cupressinum* and *Halocarpus biformis*) 'formed extensive stands in the lowland, mixed hardwood forest' (Woodland 2000).

South Africa: Two genera of conifer, *Podocarpus* (Podocarpaceae, four species) and *Widdringtonia* (Cupressaceae, three species), occur indigenously in the country. The former is found primarily in montane and coastal forests, the latter is exclusively montane, with two species confined to limited areas in the Cape Fold Belt (Leistner 1966; Marsh 1966).

Southern South America: The family Podocarpaceae has an interesting Gondwanan distribution: while most of the 17 genera show a SE Asian-Australasian centre of endemism, three of them—*Lepidothamnus, Prumnopitys* and *Retrophyllum*—demonstrate links across to southern South America, the first two from New Zealand, the latter from New Caledonia-Fiji. A fourth genus in the family, '*Saxegothaea* is confined to far southern South America' (C.N. Page 1990).

Araucaria (Araucariaceae), phytogeographically reminiscent of the Podocarpaceae, shows a New Caledonia via southern Pacific-Antarctic link to South America (the pattern is shared also by 'such arborescent angiosperms as *Nothofagus* (Nothofagaceae)') (C.N. Page 1990).

The Patagonian cypress (Cupressaceae), with wood similar to that of the Californian redwood and living nearly as long, 'is the monarch of the southern Andes mountains' (J. Page 1984).

EXTANT OCCURRENCE OF THE PINACEAE

(notable aspects of biodiversity, ecology & phytogeography)

Pinaceae floristic regions (adapted from Farjon 1990)

At species level (213 species), the Pinaceae is the largest family of extant conifers; at generic level (11 genera) it is the third largest, after the Cupressaceae (20 genera) and Podocarpaceae (17 genera). The family is 'virtually restricted to the Northern Hemisphere', where 'many species are important dominant or co-dominant components of coniferous forests. Especially in northern latitudes, a few species form extensive forests dominated in the climax stage by a single taxon. Together they are the major woody components of the Northern coniferous forest biome', which 'stretches as a broad belt across the northern parts of Eurasia and North America' (Farjon 1990).

1. Mediterranean-Black Sea region: 'Characterised by Mediterranean Pines and relict populations of *Abies*, *Cedrus* and *Picea*', the region is 'distantly linked with the Himalayas' through species of the latter two genera. These 'Mediterranean vicarians are relict species' of restricted occurrence. They 'may have stretched along the mountain chains north of Tethys Sea in the Palaeogene'.

2. Central European region: The region supports 'at present only a few remnant species (in *Abies, Larix, Picea* and *Pinus*) of a once extremely rich but during the Pleistocene greatly impoverished gymnosperm flora'.

3. Boreal region (from northern Scotland, through Scandinavia, Russia and Siberia to the Lena River): Across this vast region 'only *Abies*', *Larix*, *Picea* and *Pinus* are present, each with a single species except for *Pinus* with two species.

4. Eastern-Asian region: Region 3 grades into Region 4 'through a change in species and, closer to the coast, the addition of some more species and in Japan of two genera: *Pseudotsuga* and *Tsuga*'.

5. Sino-Himalayan region: This region constitutes the biodiversity hotspot of the extant Pinaceae. All 11 genera of the family are represented, four of these—*Cathaya, Keteleeria, Nothotsuga* and *Pseudolarix*—are endemic to the region, and the two large genera *Abies* and *Picea* are more diverse here than anywhere else. (This richness is found also in other gymnosperms.)

6. NW North American region: Region 6 in North America is the counterpart of Region 4 in Eurasia. 'Except on the coasts, the number of species is very limited in the greater part of each'. *Abies, Larix, Picea* and *Pinus* are the only genera present.

7. California-Central America region: Second only to the Sino-Himalayan region in Pinaceae diversity, this region is at much the same latitude and on the opposite side of the Pacific. It also has a 'great concentration of species', but fewer genera—*Abies, Larix, Picea, Pinus, Pseudotsuga* and *Tsuga*—than Region 5. *Abies* and *Pinus* make up a high proportion of the total pinaceaen richness, and the latter has its diversity hotspot in California and Mexico.

8. NE North American region: The counterpart of Region 3 in Eurasia, the American northeast is poor in diversity (with likewise only the genera *Abies, Larix, Picea* and *Pinus* and few species), though members of the family dominate the coniferous forests.

9. SE USA-Caribbean region: This subtropical to warm-temperate region includes only a few species of *Pinus* and some scattered populations of *Tsuga canadaenses* in N Georgia and N Alabama.

Southern Hemisphere

Though many Pinaceae species grow extremely well in the Southern Hemisphere, none are native south of the equator.

Pinaceae: aspects of their fossil history

Late Triassic origins: *Compsostrobus neotericus* Delevoryas & Hope (1973) and *Millerostrobus pekinensis* Taylor *et al.* (1987) from the Carnian, Pekin Fm., North Carolina, USA, were recorded as the first appearance of the family by Cleal (1993). *Compsostrobus* was originally placed by Delevoryas & Hope (1973) in a separate family, the Compsostrobaceae, but most authors now include it in the Pinaceae. *Millerostrobus* is a pollen cone with features indicative of both the Pinaceae and the Podocarpaceae, but Taylor *et al.* (1987) favoured placement in the former.

Middle Jurassic maturity: The family was well established by the Middle Jurassic as evidenced (Harris 1979) by *Schizolepis* (seed cones and scales) and *Pityocladus* (leafy shoots). Ratzel *et al.* (2001), however, claim that the earliest 'unequivocal evidence for the family does not appear until the Cretaceous' and that the 'Pinaceae may be the most recently derived conifer family'. Fossils are well known from the late Mesozoic and Tertiary.

Early Cretaceous radiation: Explosive evolutionary radiation of the Pinaceae, along with that of the angiosperms, is recorded in the Early Cretaceous. Pinaceous elements—with the diversity mostly chronicled by ovuliferous cones of the extinct genera *Pityostrobus*, *Pseudaraucaria* and *Obirastrobus*—become common components of terrestrial plant communities. Deposits yielding such cones are encountered in a circumpolar belt from North America through Europe and Russia, to eastern Asia (Ratzel *et al.* 2001) (see also Miller 1976a; Falder *et al.* 1988; Ohsawa *et al.* 1992; Smith & Stockey 2001).

Affiliations in fossil Pinaceae: 'Unfortunately, at only a few localities are there pinaceous vegetative organs associated with the fossil ovulate cones. None of these have been found in attachment; nor have taxa been reconstructed as whole plants. Unless such material can be recovered, all that we have are cone characters' (Smith & Stockey 2001).

Origins of extant Pinaceae genera: 'Most modern pinaceous genera' according to Miller (1997) 'probably did not originate until the Tertiary' and most appear to have evolved by the Oligocene. The earliest described *Pinus* species (*P. belgica*) is from the Early Cretaceous of Belgium.

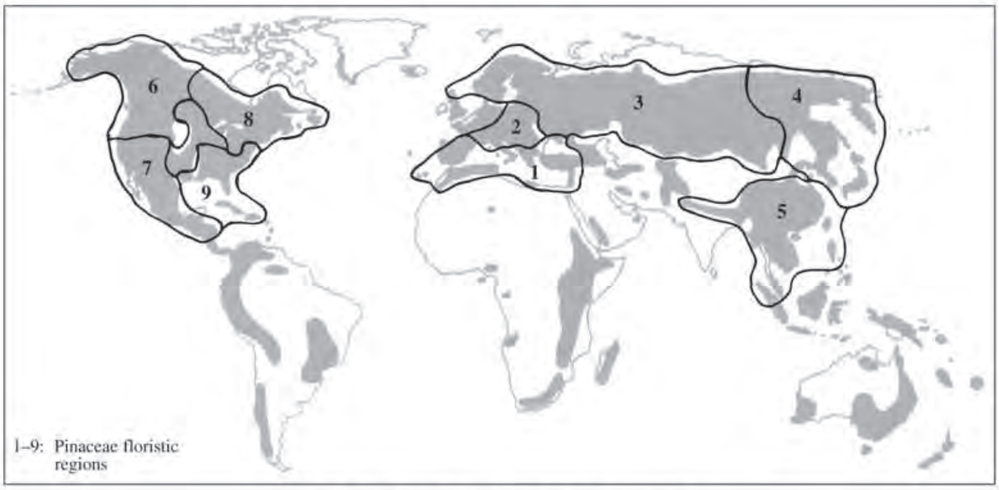


Fig. 17. Extant Pinales: global occurrence

Base map: adapted from Woodland 2000 (after Farjon 1998)
Pinaceae floristic regions: adapted from Farjon 1990

Family **PINACEAE** Lindl. 1836

Contributors: M. Mundry, I. Mundry & T. Stützel

Diagnosis

Plants: Monoecious.

Ovulate cones: Compound; cone bracts spirally arranged, flattened, tongue-shaped, free from scale, with a single vascular strand; ovuliferous scales flattened; ovules 2, inverted, proximal, fused to ovuliferous scale, with a single vascular strand dividing up to 20 times, micropyle laterally directed; seeds typically winged, rarely unwinged (e.g. *Pinus pinea*), wing descended from ovuliferous scale.

Pollen cones: Simple, sometimes clustered on short shoots originating from a common bud; sporangiophores several, hyposporangiate, always with 2 sporangia; pollen mostly with two distinct air-bladders.

Leaves: Simple, arranged either along long-shoots (persistent), or on long- and short-shoots (deciduous or persistent), or only on short-shoots (persistent); with two vascular strands surrounded by a common bundle sheath.

Range: Global, T(ANS)–Rec.
First: See *Compsostrobus*, p. 133.

Prominence (colonisation success)—extant
Frequency/ubiquity/abundance: See pp 130–133.
Diversity: 11 genera, *ca* 225 species; the most species-rich of the extant pinalean families (Farjon 2001); mainly Northern Hemisphere; a dominant component of mountain and boreal evergreen coniferous forests throughout the hemisphere (Florin 1963). In spite of the abundance of certain species, 'the majority ... are more or less rare endemics, very often with a relict distribution' (Farjon 2001).

Ecology

Habit: Trees usually of moderate to large size, less often shrubs, mostly monopodial when young, but become more irregular with age in most genera, mostly fast-growing, sometimes reaching considerable age, deciduous or evergreen, monoecious (C.N. Page 1990).

Habitat: Mostly temperate, 'extending into high northerly latitudes', many form 'extensive monotypic stands over large, north-temperate areas', less often form 'mixed evergreen or evergreen-broad leaved forests', mostly on poor, acidic, wet or rocky substrate (C.N. Page 1990).

Remarks

Classification of extant genera: Although the monophyly of the Pinaceae is always accepted, a convincing systematic classification within the family is still lacking. Recent molecular studies give strong support for the sister genera (Wang *et al*. 2000; Liston *et al*. 2003). In most such studies one group (Pinoideae) is strongly supported to be monophyletic: included are the sister genera *Pinus*/*Picea*/*Cathaya* and *Pseudotsuga*/*Larix*. The remaining group coincides with the sometimes accepted Abietoideae, but the position of *Cedrus* in molecular studies, basal to all other Pinaceae genera, makes the group paraphyletic.

Phylogeny within extant gymnosperms: A few recent molecular studies show the Pinaceae as sister to the Gnetales (Chaw *et al*. 2000; Gugerli *et al*. 2001), but others (Bowe *et al*. 2000) find the Gnetales basal to the Pinales or to all other gymnosperms (Schmidt & Schneider-Poetsch 2002). Morphological data also negate a close relationship of the Gnetales and Pinaceae. Quinn *et al*. (2002) place the Pinaceae as sister to all other Pinales families, but Gnetales were not included in this study.

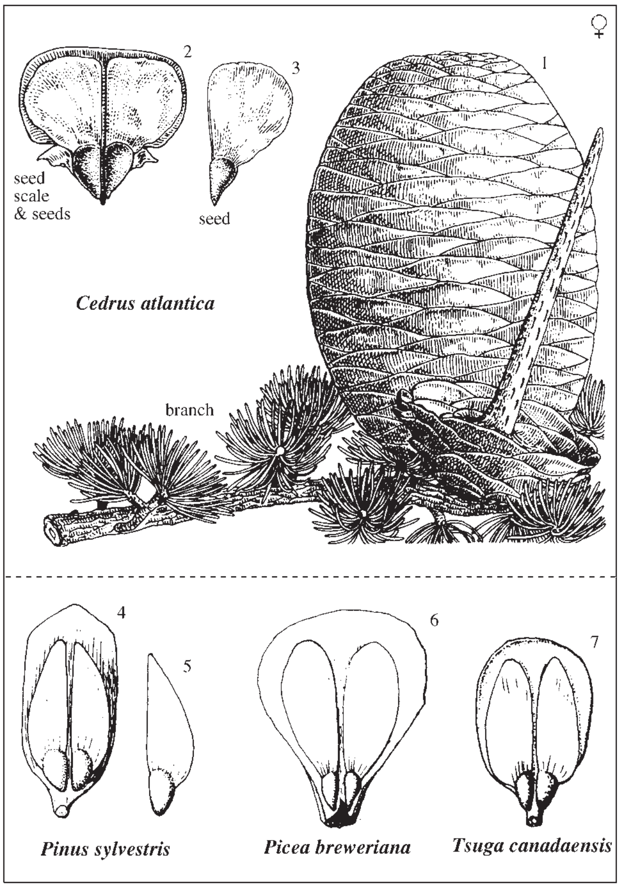
Morphology: The initiation of the ovuliferous scale is quite similar within this group (e.g. Owens 1969; Owens & Molder 1974; Owens *et al*. 1981; Mundry 2000). In the axil of the cone bracts arises a large primordium. Two inverted ovules are always initiated at the lateral margin of these primordia. The distal part of the primordium is differentiated from the ovuliferous scale and the ovules are congenitally fused with it. The typical bisaccate pollen is lost at least twice, and in *Tsuga* pollen-tube fertilisation is evolved.

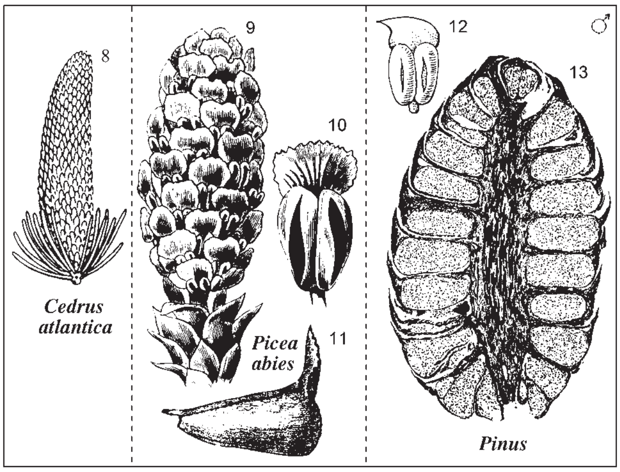
Phytogeography: See p. 133.

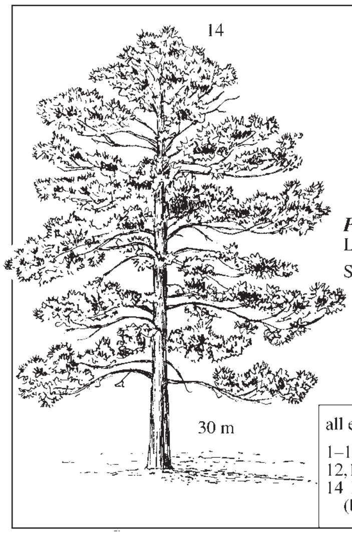
Fossil history: See p. 133.

References

C.N. Page (1990): Habit, habitat.
Ratzel et al. (2001), Smith & Stockey (2001): Fossil record.







all extant
1–11 from C.N. Page (in Kubitzki) 1990
12,13 from Foster & Gifford 1974
14 H.M. Anderson pen sketch 2004
(based on Brockman 1986)

Family **ARAUCARIACEAE** Henkel & W.Hochst. 1865

Contributors: M. Mundry, I. Mundry & T. Stützel

Diagnosis

Plants: Dioecious or monoecious.

Ovulate cones: Compound; cone bracts almost completely fused to scale, large and woody; ovuliferous scale highly reduced, flattened; ovule usually single, large, inverted, free or fused to ovuliferous scale/bract complex.

Pollen cones: Very large, sporangiophores numerous; sporangia 4–20, initiated in two rows; pollen-tube fertilisation (Owens *et al*. 1995a, 1995b), pollen without air-bladders.

Leaves: Scale-like or laminar, with parallel venation originating from basal dichotomies.

Range: Tr(ANS)–Rec.

First: *Araucarites parsorensis* Lele (1955) and *A. indica* Lele (1962); Parsora Fm., South Rewa, India. These specimens are isolated cone scales.

Prominence (colonisation success)—extant

Frequency/ubiquity/abundance: See pp 130–133.

Diversity: 3 genera, *ca* 41 species; disjunct distribution in the Southern Hemisphere concentrated in Malaysia and Australasia but with 2 species in South America. Recently was added the monotypic genus *Wollemia*, discovered in a Canyon in New South Wales, Australia. Five species of *Agathis* and 13 species of *Araucaria* are endemic to New Caledonia (Farjon 2001).

Ecology

Habit: Moderate to extremely large trees, strongly monopodial, some become 'irregularly broad-crowned with age', mostly fast-growing, can reach considerable age, evergreen, monoecious or dioecious (C.N. Page 1990).

Habitat: *Agathis* mostly tropical or subtropical, mostly scattered individuals or as small groves in dense rainforest, crowns typically 'conspicuous canopy emergents'; *Araucaria* tropical to temperate, small groves (localised pure populations), more mesic temperate habitats on tropical mountain flanks', 'restricted to mountain ridges, crests, river margins, and shorelines' in New Caledonia (C.N. Page 1990).

Remarks

Classification & phylogeny: In former morphological studies, this family was regarded either as a quite distinct group or as related to the Pinaceae. Recent molecular studies of different genes give strong support for the Araucariaceae being closely related to the Podocarpaceae (Quinn *et al*. 2002).

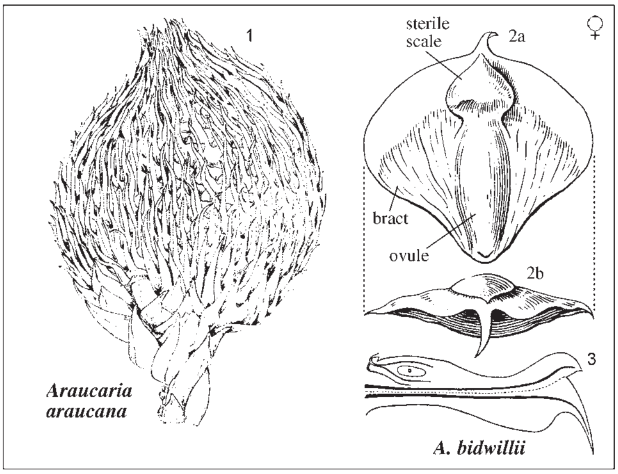
The genus *Wollemia* appears to be the oldest lineage within this family and sister to an *Araucaria*/*Agathis*-clade (see Quinn & Price 2003).

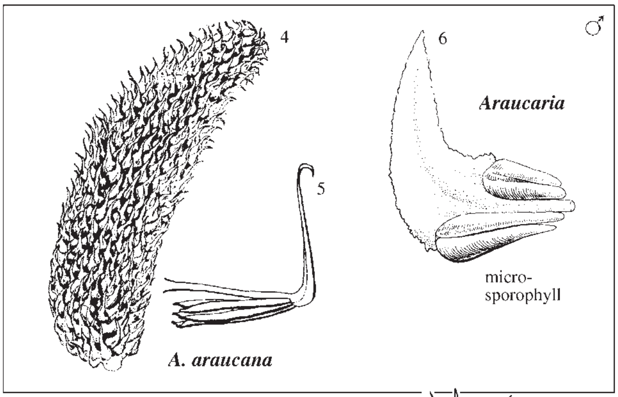
Intervening: Distinctive since the Jurassic, when the family probably reached its zenith with as much sectional diversity as today.

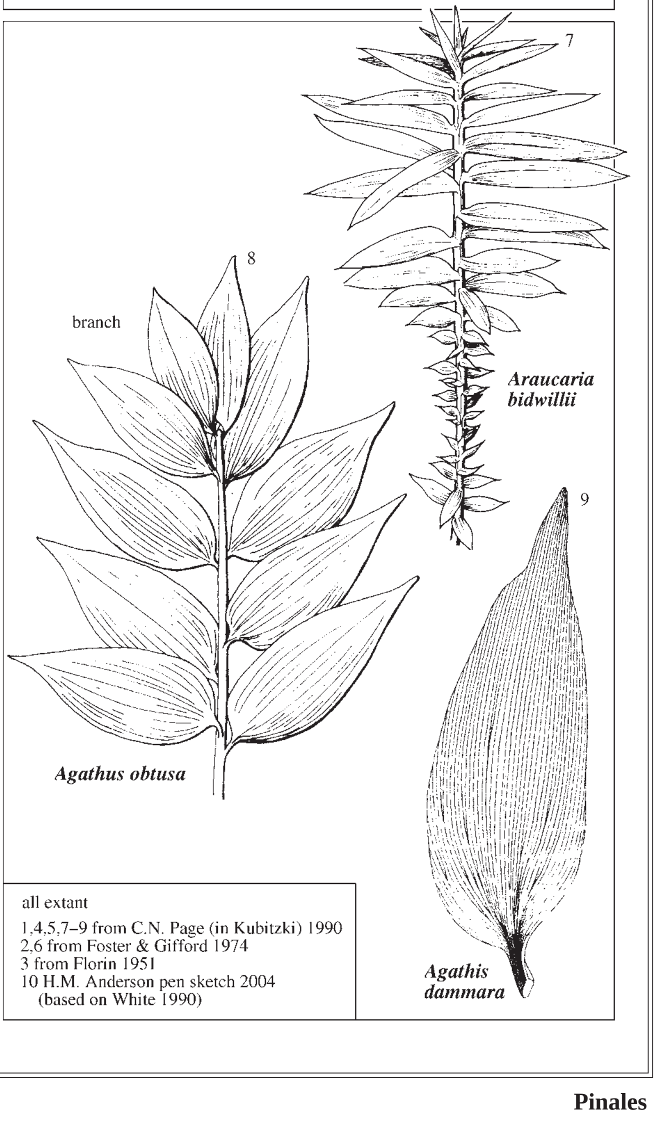
Phytohistory: See Dutra *et al*., Charts 21–24, pp 56–59.

Reference

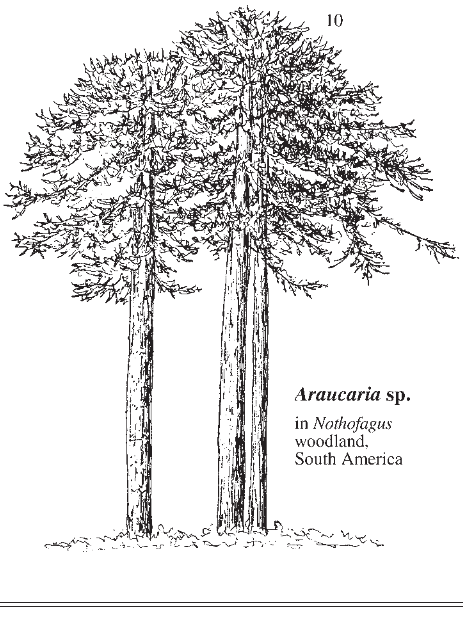
C.N. Page (1990): Ecology.







all extant
1,4,5,7–9 from C.N. Page (in Kubitzki) 1990
2,6 from Foster & Gifford 1974
3 from Florin 1951
10 H.M. Anderson pen sketch 2004
(based on White 1990)



***Araucaria* sp.**
in *Nothofagus*
woodland,
South America

Family **PODOCARPACEAE** Endl. 1847

Contributors: M. Mundry, I. Mundry & T. Stützel

Diagnosis

Plants: Mostly dioecious, rarely monoecious.

Ovulate cones: Compound, small, greenish, herbaceous, spiral or decussate phyllotaxis, ovules many to few; each subtended by a bract, inserted at a small primordium which later forms the epimatium, erect (*Microstrobus*, *Phyllocladus*) or ± inverted by the epimatium; epimatium a one-sided outgrowth which covers the mature ovule (except in *Microstrobus* and *Phyllocladus*); mature seeds mostly not enclosed in the cone, often large, associated with fleshy parts (epimatium, peduncle or cupule), often colourful (zoochorous; birds, mammals such as bats).

Pollen cones: Simple (often clustered, catkin-like); male sporangiophores simple, hyposporangiate, with two sporangia; pollen with two, three or one ring-like air-bladders (except *Saxegothaea* without air-bladders).

Leaves: Mostly simple needles, with one median or with multiple vascular bundles that originate from basal bifurcations; in *Phyllocladus* the leaves are reduced and scale-like, with assimilative phylloclades (leaf-like shoots).

Range: Global, Tr(ANS)–Rec.

First: *Rissikia eskensis* And. & And. 1989, Bryden Fm., Clarence-Moreton Basin, Australia (And. & And. 1989). The earliest well-documented cones are *Rissikistrobus* (3 spp) and *Rissikianthus* (4 spp) ovulate and pollen cones respectively, occurring with the well-affiliated foliage *Rissikia media* (Tenison-Woods 1883) Townrow 1967, Molteno Fm., S. Africa (And. & And. 2003). See p. 137 opposite.

Stalagma samara Zhou 1983, Yangbaichong Fm., Shaqiao, Hunan, China (Taylor & Taylor 1993; Li Xingxue *et al.* 1995).

Prominence (colonisation success)—extant

Frequency/ubiquity/abundance: See pp 130–133.

Diversity: According to Farjon (2001) (but he places the genus *Phyllocladus* in the Phyllocladaceae): 19 genera, *ca* 185 species; mostly tropical to subtropical montane, mostly southern hemisphere. One species of *Acmopyle* is endemic to New Caledonia; 2 species of *Dacrycarpus* to New Guinea; 3 species of *Dacrydium* to New Guinea; the genus *Halocarpus* to New Zealand; *Manoao* (1 species separated from *Lagarostrobos*) to New Zealand; the monotypic genus *Microcachrys* to Tasmania; and *Parasitaxus*, the only parasitic conifer known, is endemic to New Caledonia.

Ecology

Habit: Shrubs or trees from small to very large in size, mostly monopodial, slow- or fast-growing, can reach considerable age, evergreen, dioecious or rarely monoecious (C.N. Page 1990).

Habitat: Fully tropical to warm or occasionally cool-temperate, mostly plants of mesic forests, usually as scattered individuals in broad-leaf vegetation, less often as localised pure communities, mostly midmontane (C.N. Page 1990).

Remarks

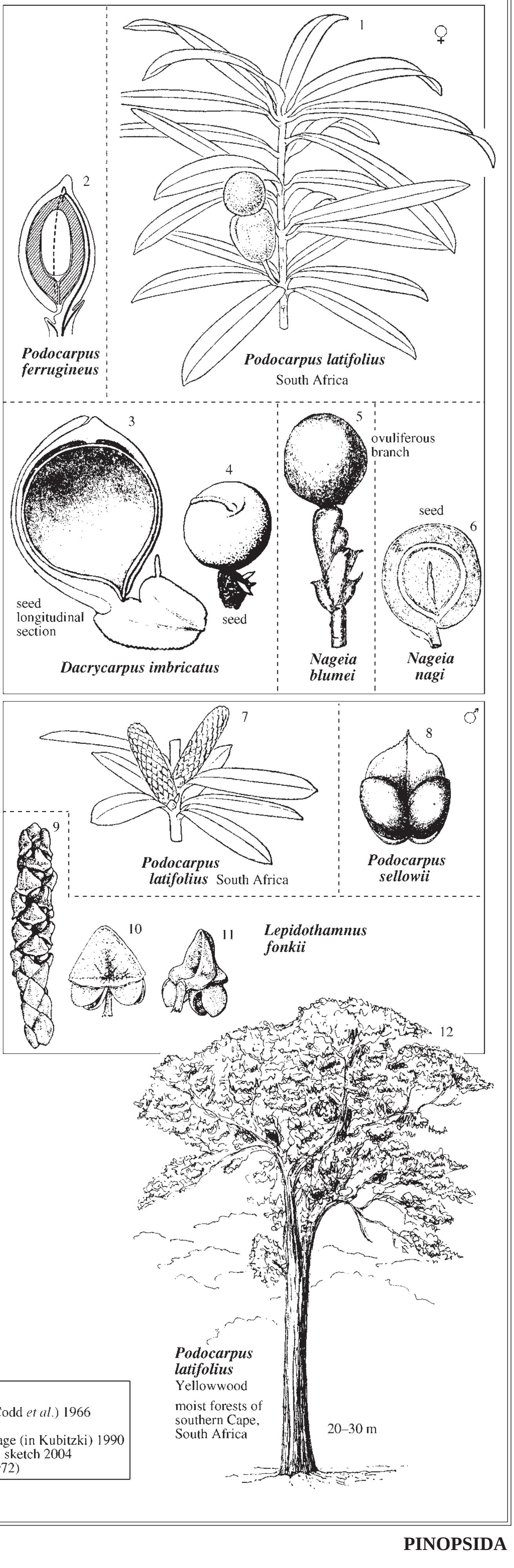
Rank of Phyllocladus: Traditionally, *Phyllocladus* has been classified within the Podocarpaceae. Keng (1973) separated the genus into a distinct family, the Phyllocladaceae, but recent molecular analyses (e.g. Quinn *et al*. 2002) show that *Phyllocladus* is basal to or within the Podocarpaceae, which are sister to the Araucariaceae.

Morphology: Wilde (1944) and Tomlinson (1992) differentiated the Podocarpaceae into genera with terminal cones and genera with lateral cones; but Restemeyer (2002) shows that all genera follow the same branching pattern.

The epimatium is the classical structure of the Podocarpaceae, yet the interpretation of the structure remains open. The most common view finds the epimatium/seed-scale complex to be a reduced fertile dwarf-shoot (Chamberlain 1935; Wilde 1944; Beck 1988; De Laubenfels 1992). Tomlinson (1992) postulated that the function of the epimatium is to produce an inverted ovule and is therefore a new structure in the Podocarpaceae. Page (1990) termed it a 'false aril'.

Reference

C.N. Page (1990): Ecology.



all extant
1,7 from Leistner (in Codd *et al.*) 1966
2 from Florin 1951
3–6,8–11 from C.N. Page (in Kubitzki) 1990
12 H.M. Anderson pen sketch 2004
(based on Palmer 1972)

Genus ***Rissikistrobus*** And. & And. 2003

Diagnosis: Podocarpaceous plants with linear ovulate cones bearing bract/scale complexes of 1–3 lobes with a pair of adaxial ovules on each lobe.

Range: Gondwana, Tr(ANS–NOR)
First: *Rissikia eskensis* And. & And. 1989; Bryden Fm., Ipswich/Esk, Clarence-Moreton Basin, Queensland, late Anisian, Middle Triassic (And. & And. 1989).
Last: *Rissikia media* (Tennison-Woods 1883) Townrow 1967a; Tiki Fm., Giar, Son River, S. Rewa/Tiki Subregion, India; Norian, Late Triassic (And. & And. 1989).

Reference whole-plant genus & stratum—Molteno Fm.
Ovulate cones: *Rissikistrobus* And. & And. 2003; 7 TCs, 3 spp, 85 indivs.
Pollen cones: *Rissikianthus* And. & And. 2003; 5 TCs, 4 spp, 79 indivs.
Foliage: *Rissikia* Townrow 1967; 21 TCs, 2 spp, <1%–38%.

Stratum: Molteno Fm., Karoo Basin, S. Africa, Tr (CRN).
Affiliations: *Rissikistrobus(4)Rissikia(4)Rissikianthus*, Grade 4 (Kin.reinf., Mut.occ.).

Prominence (colonisation success)—Gondwana Triassic (GT)
Rissikia (foliage): Widespread throughout Gondwana.

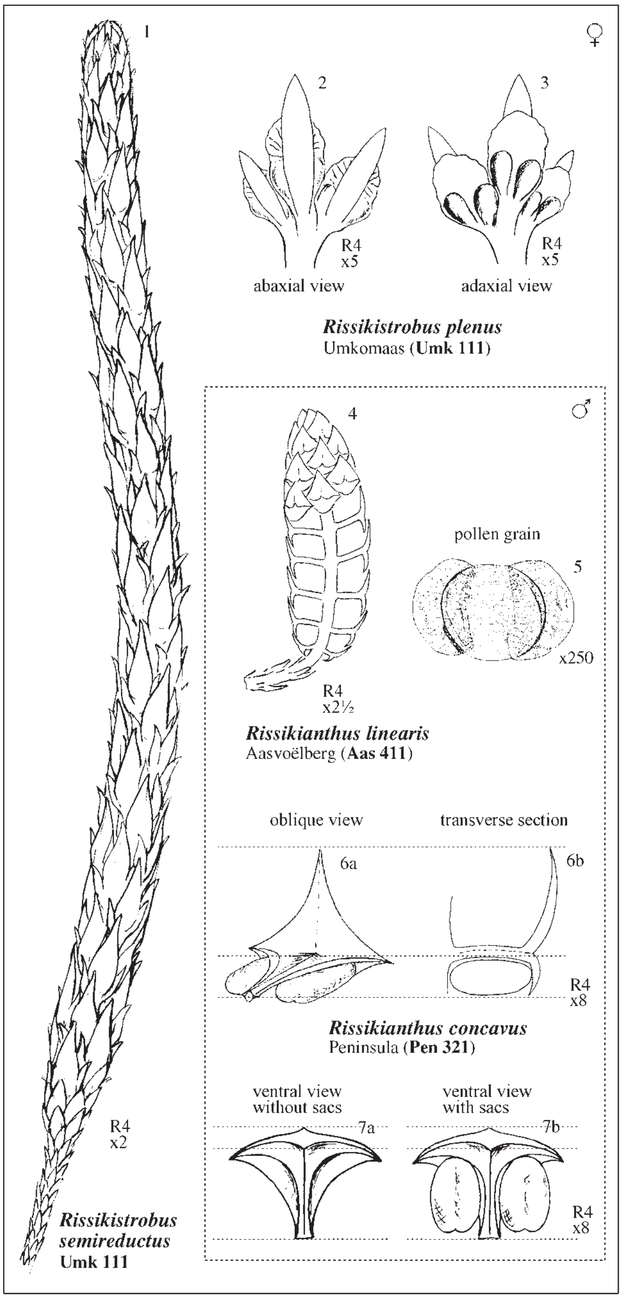
FUDAL rating: 17/5/2/1/14 = 39; the 11th most prominent gymnospermous foliage genus in the GT.
Frequency: High, 17 of 84 Gondw. degree squares.
Ubiquity: V. high, 5 of 5 Gondw. continents.
Diversity: V. low, 2 species in GT.
Abundance: Rare, 1% norm in Molteno TCs.
Longevity: High, 14 my through Triassic.

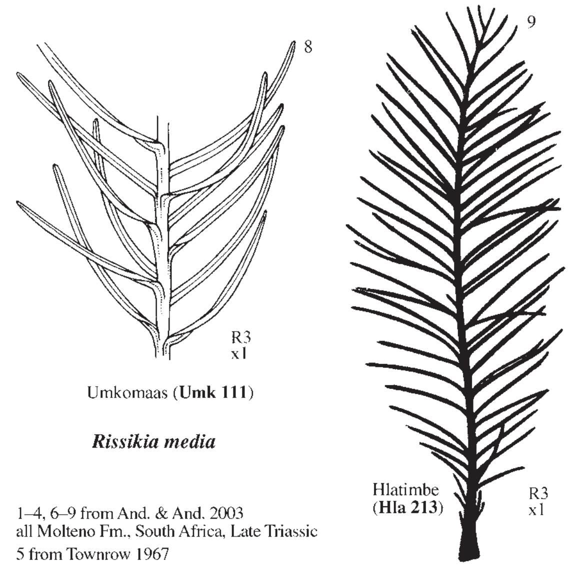
Ecology—Molteno Fm.
Habit: Probably a large tree.
Habitat: *Dicroidium* riparian forest or *Dicroidium* open woodland, occasionally forming monodominant wetland stands.

Other genera—unknown.

Remarks
Classification: The *Rissikistrobus/Rissikia* plant shows characteristics of both the Pinaceae and Podocarpaceae. In And. & And. (2003), we wrote 'Considerable published debate has been devoted to which of the two families is represented by this widespread Gondwana Triassic genus. The debate is not settled and we have wavered this way and that, settling, for now, with no great confidence on the Podocarpaceae'.

References
And. & And. (1989): Foliage.
And. & And. (2003): Ovulate and pollen cones, affiliations, general.





1–4, 6–9 from And. & And. 2003
all Molteno Fm., South Africa, Late Triassic
5 from Townrow 1967

Family **CUPRESSACEAE** Rich. ex Bartl. 1830 *s.l.* (inclusive Taxodiaceae)

Contributors: M. Mundry, I. Mundry & T. Stützel

Diagnosis

Plants: Monoecious, rarely dioecious.

Ovulate cones: Compound; cone bracts spirally or decussately arranged, rarely in trimerous whorls, mainly fused to scale; ovuliferous scales variable, from prominent with several teeth to completely reduced; ovules 1–30, arranged in 1–4 rows, erect or inverted; seeds winged or unwinged.

Pollen cones: Sporangia 1–8 per sporangiophore; pollen without air-bladders.

Leaves: Needle- or scale-like, with one median vascular bundle.

Former Taxodiaceae

Ovulate cones: Cone bracts spirally or decussately (*Metasequoia*) arranged; ovuliferous scales variable; ovules 1 (*Taiwania*) to 13 (*Sequoiadendron*), arising on adaxial side of cone bract, arranged in single or triple rows (*Sequoiadendron*), erect or inverted.

Pollen cones: Sporangiophores spirally arranged.

Leaves: Usually with spiral phyllotaxis (exception *Metasequoia*); sometimes showing shoot-dimorphism, with spirally or decussately needled long-shoots (persistent) and distichous-needled short-shoots (entire short-shoot deciduous).

Cupressaceae s.str.

Ovulate cones: Cone bracts decussate or in trimerous whorls, ovuliferous scales completely reduced; ovules 1–30, axillary, single- to multirowed; seeds winged (formed by seed coat) or unwinged.

Pollen cones: Sporangiophores decussate.

Leaves: Decussate or in whorls of three or four.

Range: Tr(LAD)–Rec.

First: *Parasciadopitys aequata* Yao *et al.*1997; Mt Falla, Queen Alexander Range, Antarctica (covered fully overpage, p. 140).

Prominence (colonisation success)—extant

Frequency/ubiquity/abundance: See pp 130–133.

Diversity: 29 genera, 135 species, including Taxodiaceae (8 genera, 13 species), worldwide distribution (Farjon 2001).

Ecology

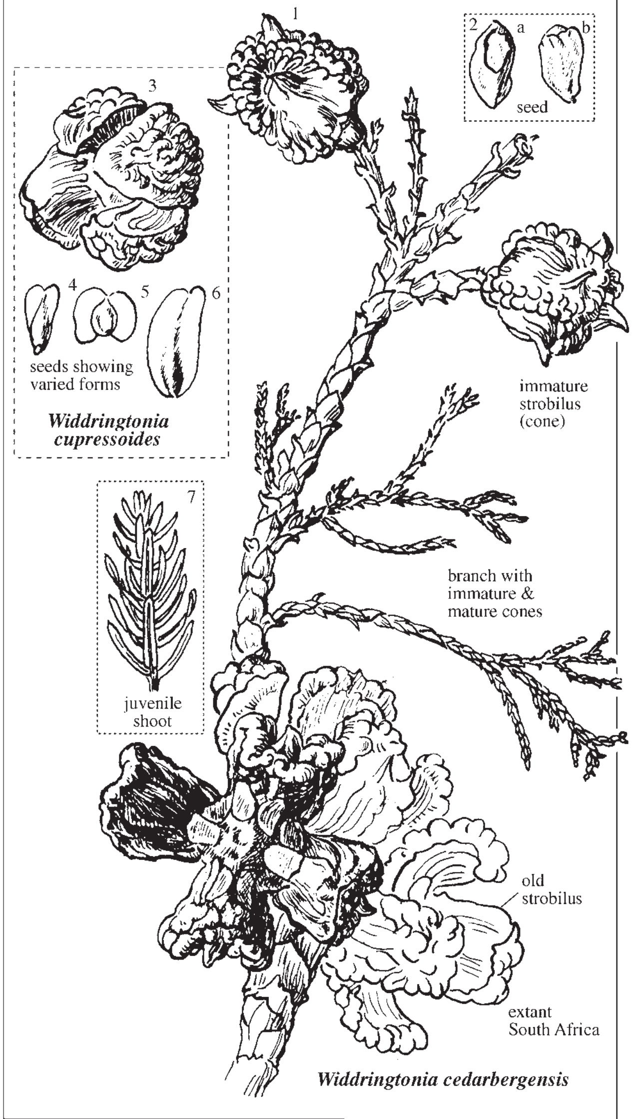
Habit (former Taxodiaceae): Trees of large to extremely large size, monopodial, mostly fast growing, reaching 'very considerable age', evergreen or 'annually deciduous', monoecious (C.N. Page 1990).

Habitat (former Taxodiaceae): Mostly warm-temperate, with narrow 'highly discontinuous' ranges, often in mountain-flank vegetation with highly 'reliable rainfall and enhanced air humidity', mostly on rich, moist soil (where most other conifer species are absent), mostly in local groves in 'mixed evergreen or evergreen-broad leaved vegetation' (C.N. Page 1990).

Habit (Cupressaceae *s.str.*): From dwarf shrubs to tall trees, monoecious or dioecious.

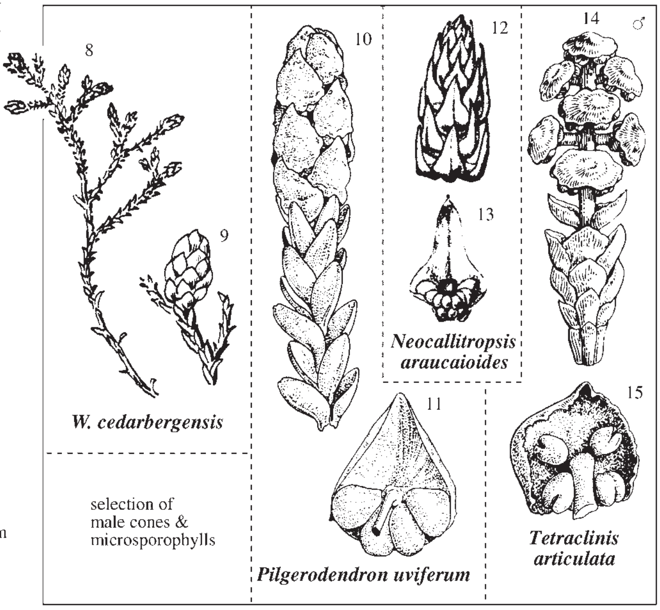
Habitat (Cupressaceae *s.str.*): Mostly cool to warm-temperate; many genera strictly mesic, with species mostly favouring high rainfall and humidity, mostly mountain flanks, less often riverside to boggy valley bottoms; mostly in dense monospecific stands; several species in various genera form tall forest dominants.

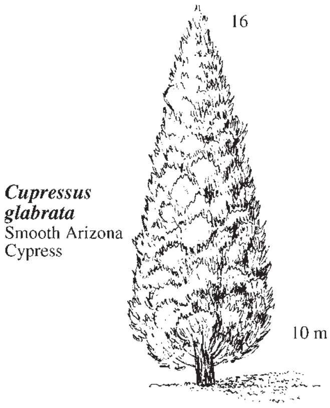
1–16 Former Cupressaceae ♀



all extant

1–9 from Marsh (in Codd *et al.*) 1966
10–15 from C.N. Page (in Kubitzki) 1990
16 H.M. Anderson pen sketch 2004
(based on A. Mitchell 1974)





Remarks

Phylogeny: In the past this family was split into two families, but recent molecular (Brunsfeld *et al*. 1994; Gadek *et al*. 2000; Quinn *et al*. 2002) and morphological (Hart 1987; Jagel & Stützel 2001) analyses show the former Taxodiaceae to be a paraphyletic group basal to the Cupressaceae *s.str.* In most morphological studies, the Taxodiaceae are directly linked with the Sciadopityaceae, but Quinn *et al.* (2002) placed them basal to a Cupressaceae *s.l.*/Taxaceae *s.l.* clade.

Morphology: Bract and ovuliferous scale morphology is quite variable within this group. In some genera of the former Taxodiaceae, the ovuliferous scale is virtually reduced (*Sequoia*, *Metasequoia*, and *Sequoiadendron* (Farjon & Ortiz Garcia 2003; Takaso & Tomlinson 1992); in other genera, ovuliferous appendages arise later (Jagel 2002) or simultaneous with (Farjon & Ortiz Garcia 2003) the ovule; and in the Cupressaceae *s.str.*, the ovules arise axillary to the cone bracts with no indication of an ovuliferous scale (Schulz *et al*. 2003). In some genera of the Cupressaceae *s.str.*, some ovules are not axillary (Jagel & Stützel 2001, *Microbiota*; Jagel & Stützel 2003, *Tetraclinis*; Schulz *et al*. 2003, *Juniperus*), but terminal at the cone axis.

Fossil history

Jurassic: Previous to the discovery of *Parasciadopitys*, the first appearance was taken as *Elatides thomasii* Harris (1979) from the Middle Jurassic (BAJ) of Yorkshire, England (Cleal 1993).

Ovulate cones from the Jurassic and Cretaceous show features of different present-day genera in combinations precluding assignment to any of them (Miller 1988).

Paskapoo Fm. (Paleocene), Alberta, Canada: A particularly notable occurrence is that from floodplain deposits of the Munce's Hill and Gao Mine localities, central Alberta, Canada, in the Paskapoo Fm., mid-Paleocene. 'Compression/impression' fossils of *Metasequoia*-like taxodiaceous conifers 'are preserved in upright growth positions'. Also found were numerous seeds, a few that were 'buried while germinating', and over 500 seedlings of various ages—including some with 'axillary branches that show varying sizes and numbers of opposite leaves arranged in a single plane' (Falder *et al*. 1999).

A large collection of 10 147 compression specimens ('1 upright trunk, 2 536 vegetative shoots, 123 shoots bearing pollen cones, 2 373 ovulate cones, 3 263 seeds, and 1 850 seedlings in a broad range of developmental stages') from the contemporaneous Munce's Hill and Gao Mine localities form the basis of a new species, *Metasequoia faxii*, described by Stockey *et al.* (2001). This dominant element in the deposits has to be one of the most comprehensively known of fossil species.

Tertiary abundance: Conifer remains of the former Taxodiaceae are 'among the most abundant of Tertiary plant fossils' (Stockey *et al*. 2001, after Florin 1963). Further, it is the genus *Metasequoia* that is now known 'as one of the most abundant taxodioid conifers' of the Northern Hemisphere Tertiary.

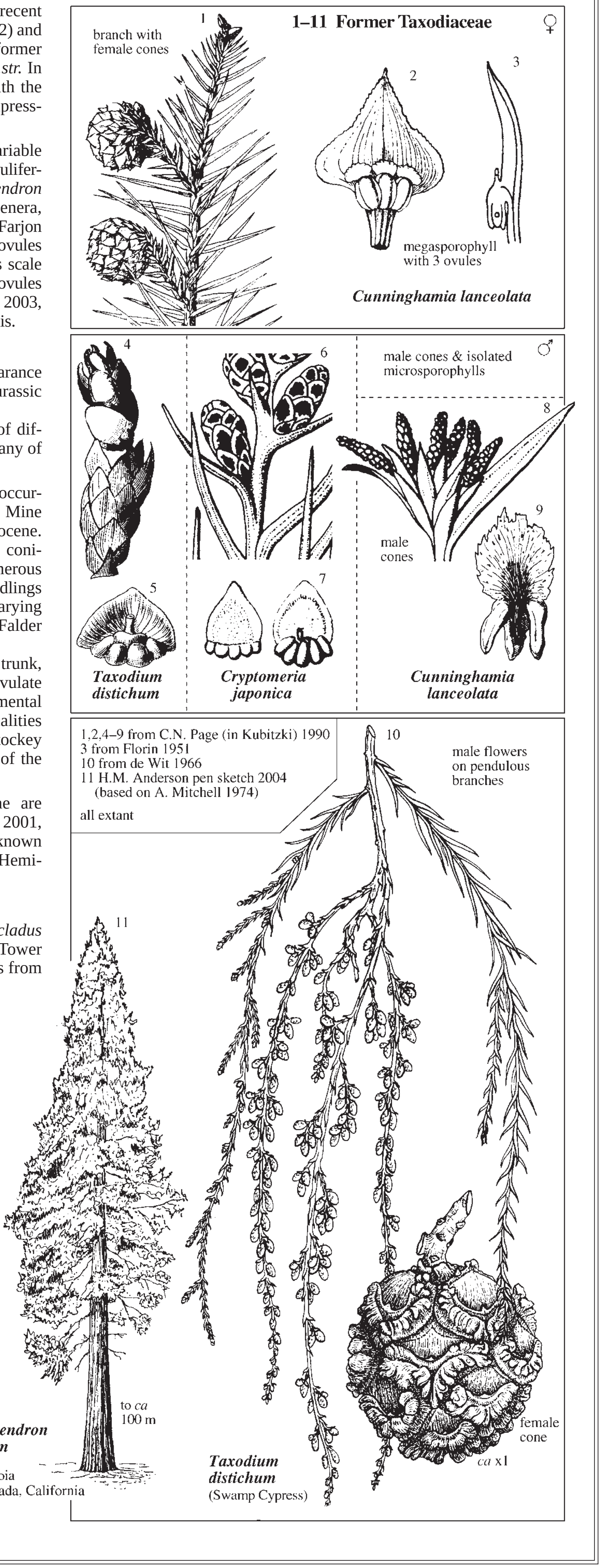
Cupressaceae *s.str.*

The first definite appearance of Cupressaceae *s.str.* is *Cupressinocladus interruptus* (Newbury) Schweitzer 1974; Volcanic Tuff, Smoky Tower T(Danian)–Rec., Alberta, Canada (Christophel 1976). Earlier records from the Jurassic and Cretaceous are based on wood (Miller 1988).

References

C.N. Page (1990): Habit, habitat.
Falder et al. (1999), Stockey et al. (2001): Fossil history.

1–11 Former Taxodiaceae



1,2,4–9 from C.N. Page (in Kubitzki) 1990
3 from Florin 1951
10 from de Wit 1966
11 H.M. Anderson pen sketch 2004
(based on A. Mitchell 1974)
all extant

Genus ***Parasciadopitys*** Z-Q.Yao, T.N.Taylor & E.L.Taylor 1997

Diagnosis: Cupressaceous plants with ovulate cones bearing spirally arranged bracts fused for a quarter to three quarters of their length to the scale; ovuliferous scales prominent, 5-toothed; ovules 5, in a single row, inverted, narrowly winged.

Range: Gondwana, Tr(LAD)
First & last: *Parasciadopitys aequata* Yao *et al*. 1997; Fremouw site, Fremouw Peak, Queen Alexandra Range, Transantarctic Mountains; Fremouw Fm., Beacon Supergroup.

Reference whole-plant genus & stratum—Fremouw Fm.
Ovulate cones: *Parasciadopitys* Yao *et al*. 1997: 1 TC, 1 sp., 2 indivs.
Pollen cones: Unknown.
Foliage: Unknown.

Stratum: As for 'Range' above.
Affiliations: Nil.

Prominence (colonisation success)—Gondwana Triassic (GT)
Frequency/ubiquity: *Parasciadopitys* remains known from a single site only.
Diversity: 1 species.
Abundance: 2 ovulate cones.
Longevity: <1 my.

Ecology—Fremouw Fm.
Habit: Unknown.
Habitat: Periphery of peat swamp.

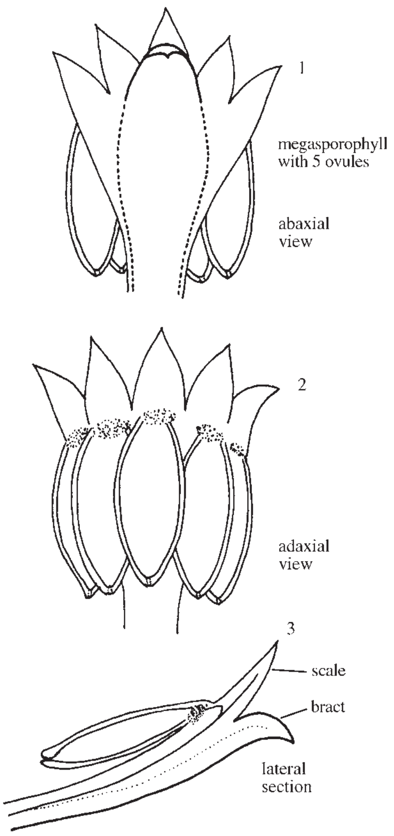
Other genera—nil.

Remarks
Material: *Parasciadopitys* is based on two nearly intact permineralised seed cones from the famed silicified peat deposit ('rafted peat clasts' in a paleostream channel), near Fremouw Peak, Transantarctic Mts (Yao *et al.* 1997).

Classification/phylogeny: Following an extensive comparative analysis of *Parasciadopitys* and a range of Late Permian to Late Cretaceous (and extant) ovulate cones, Yao *et al*. (1997) conclude that their new genus is the oldest known representative of the former family Taxodiaceae (now included in the family Cupressaceae).

Reference
Yao et al. (1997): General.

TAXODIACEAE



Parasciadopitys aequata

all **Fremouw Peak**, Transantarctic Mts.
Fremouw Fm., Middle Triassic
1–3 from Yao, Taylor & Taylor 1997

Family **SCIADOPITYACEAE** Luerss. 1877

Contributors: M. Mundry, I. Mundry & T. Stützel

Diagnosis

Plants: Monoecious

Ovulate cones: Compound; cone bracts spirally arranged, fused to ovuliferous scale for two thirds of length, with a single vascular strand; ovuliferous scales prominent, toothed at the distal end, with two traces from base, each dividing several times to supply ovules and teeth (Takaso & Tomlinson 1991); ovules 5–9, inverted; seeds with wings originating from integument.

Pollen cones: Simple, forming ellipsoid cluster at the end of long-shoots; sporangiophores simple, hyposporangiate, with two sporangia, and with prominent adaxial phylloid tip; pollen without air-bladders.

Leaves: Scale-like, on long-shoots; cladodes assimilative, in axils of scale-like leaves, consisting of two 'leaves' fused to shoot-axis and with two vascular bundles each surrounded by its own bundle sheath.

Range: J(OXF)–Rec.

First: *Sciadopitys macrophylla* (Florin) Manum (1987), *S. lagerheimii* (Johansson) Manum (1987) and *Sciadopitys*-like cone scales, Ramsa Fm., Andøya, Norway (Bose 1955, Manum 1987).

Prominence (colonisation success)—extant

Frequency/Ubiquity/Abundance: See pp 130–133.

Diversity: Monotypic genus (*Sciadopitys verticillata*) endemic to mountains of central and southern Japan.

Ecology

Habit: Long-lived, monoecious, evergreen 'strongly monopodial trees with narrowly pyramidal crowns ... often emerging above the surrounding forest canopy' (C.N. Page 1990).

Habitat: Thinly scattered, montane, at moderate altitude, confined to rich moist soils, cloud-wrapped mountain flanks; in cool-temperate, mixed evergreen-deciduous forest; scattered individuals or 'more often as gregarious or small monospecific stands' (C.N. Page 1990).

Remarks

Classification & phylogeny: *Sciadopitys* has long been included in the former Taxodiaceae, but differs in having unique false leaf whorls (compound of two leaves plus short-shoot (Roth 1962)) and many other features of seedling morphology, wood anatomy, female cones etc. (C.N. Page 1990). Although the close relationship of Cupressaceae *s.l.* (including former Taxodiaceae) and Sciadopityaceae is mostly accepted in morphological studies, some molecular studies place Sciadopityaceae basal to a Cupressaceae *s.l.* plus Taxaceae *s.l.* clade (Quinn *et al*. 2002).

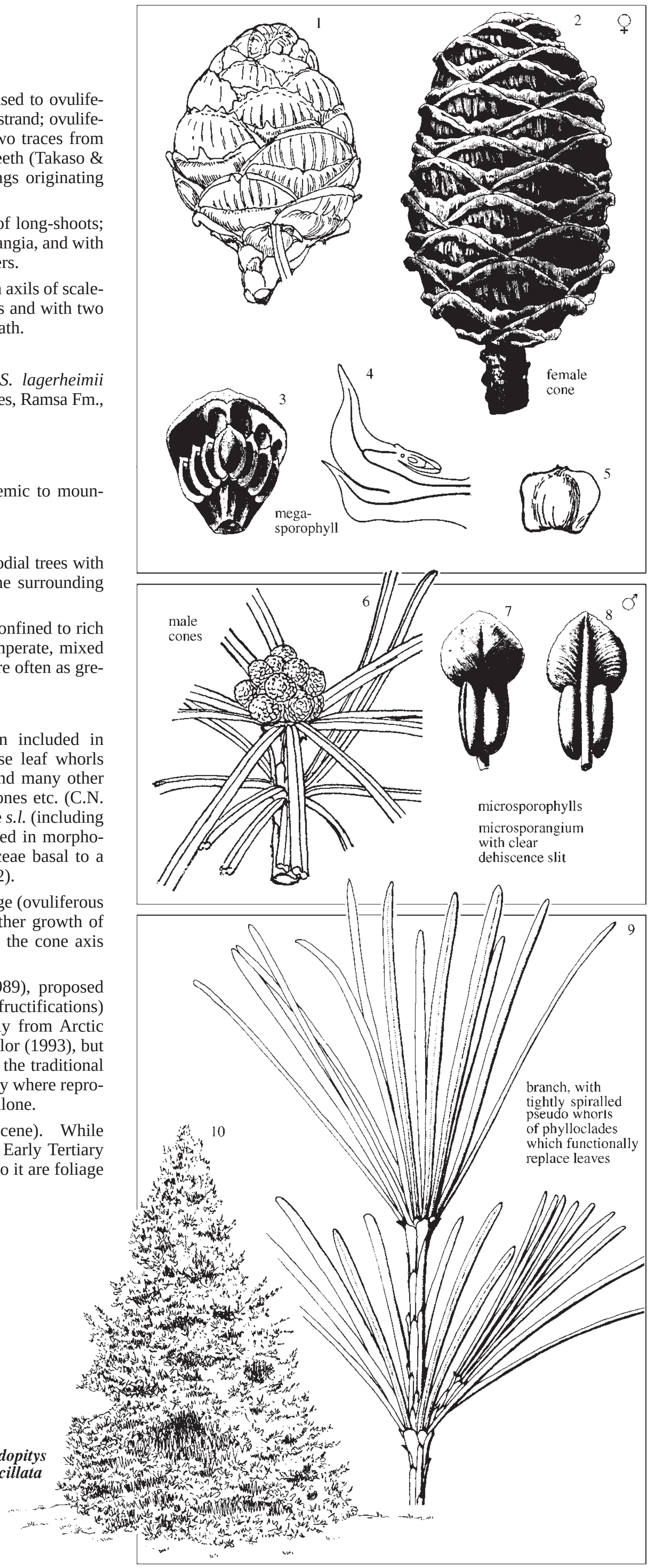
Morphology: The ovules of *Sciadopitys* arise on a small bulge (ovuliferous scale)—they are erect at first, not inverted, but during further growth of the ovuliferous scale, the ovules become inverted towards the cone axis (Takaso & Tomlinson 1991).

Arctopityaceae: The Arctopityaceae Manum & Bose (1989), proposed for a variety of characteristic leafy shoots (with no known fructifications) ranging from the Late Jurassic to Late Cretaceous, mainly from Arctic regions, were maintained by Cleal (1993) and Taylor & Taylor (1993), but are included here in the Sciadopityaceae as was previously the traditional option. We follow a strict policy of recognising families only where reproductive material is at hand, and not on vegetative material alone.

Intervening: Earliest Tertiary (Danian) to present (Holocene). While there is good palynological evidence for the family in the Early Tertiary (Manum & Bose 1988), virtually all macrofossils assigned to it are foliage fragments (Cleal 1993).

Reference

C.N. Page (1990): General.



all *Sciadopitys verticillata*, Japan, extant

1,5,6 from Dallimore & Jackson 1966
2,3,7,8,9 from C.N. Page (in Kubitzki) 1990
4 from Florin 1951
10 H.M. Anderson pen sketch 2004 (see p.131)

Family **TAXACEAE** Gray 1821

Contributors: M. Mundry, I. Mundry & T. Stützel

Diagnosis

Plants: Dioecious.

Ovulate cones: Compound, greenish, herbaceous, rarely condensed to form compact multiovulate cones, sometimes reduced to a single ovule; scales mostly decussate; ovules erect, terminal on lateral shoots, mostly with basal foliage leaves or bracts; mature seeds with aril (fleshy, ± congenitally fused with seed).

Pollen cones: From compound (with a terminal simple cone) to simple; sporangiophores simple, hyposporangiate, or complex, perisporangiate (see remarks); pollen without air-bladders.

Leaves: Simple, spirally or decussately arranged; with a single median vascular bundle.

Range: J(HET)–Rec.

First: *Palaeotaxus rediviva* Nathorst (1908); upper Coal Bed, Skrombergia Colliery, Scania, Sweden (Florin 1958).

Prominence (colonisation success)—extant

Frequency/Ubiquity/Abundance: see pp 130–133.

Diversity: *ca* 6 genera, *ca* 34 species; mainly Northern Hemisphere; with two monotypic genera, *Austrotaxus spicata* endemic to New Caledonia and *Pseudotaxus chienii* endemic to southern China.

Ecology

Habit: Understorey shrubs or small trees, much-branched, slow-growing, often long-lived, evergreen, generally dioecious.

Habitat: Cool-temperate to subtropical; populations of most species 'particularly small & local', almost all species with 'discontinuous pattern of sites within sheltered forest-vegetation'; most species 'in groves in valley-bottom sites' with deep leaf litter and free of 'severe summer desiccation'; *Austrotaxus* only in mountain cloud forest; *Pseudotaxus* 'only on permanently wet-rock substrates'.

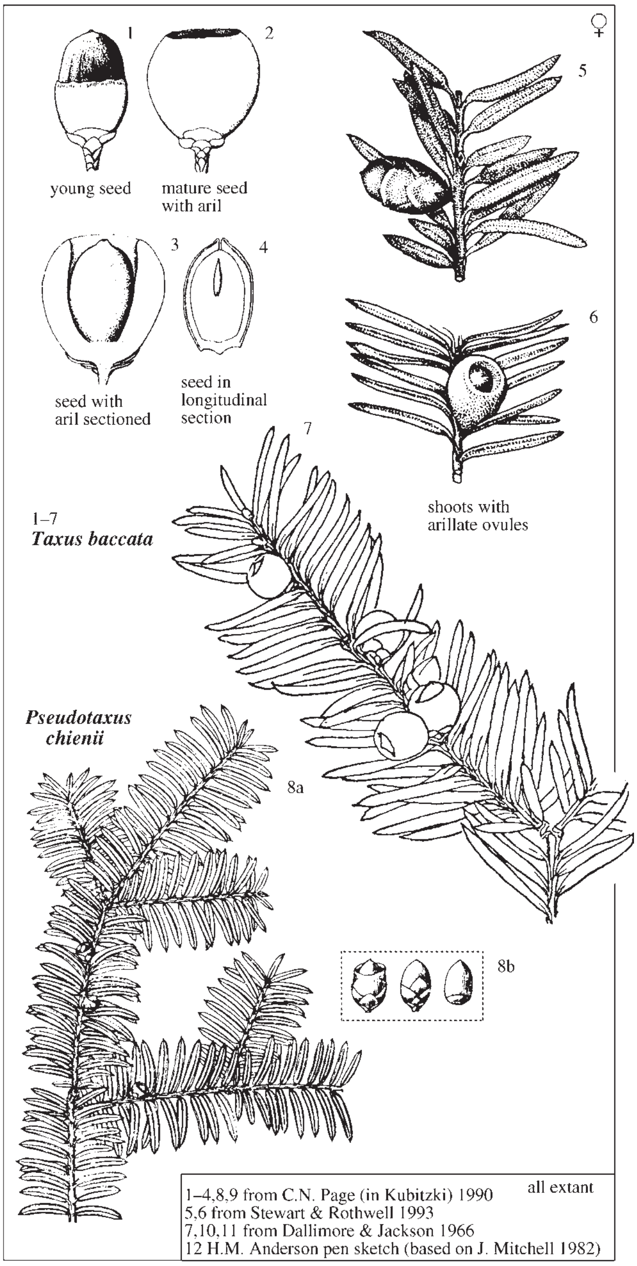
Remarks

Origins: The earliest fossil representatives from the Early Jurassic (*Palaeotaxus*) are almost identical to extant forms (Taylor & Taylor 1993).

Classification & phylogeny: Taxaceae taxonomy has been debated at all ranks from order to species. Pilger (1926) separated *Cephalotaxus* and *Amentotaxus* from Taxaceae and established the Cephalotaxaceae. Florin (1948) and Singh (1961) considered the Cephalotaxaceae monotypic and associated with the classical conifers, while Florin created a new order (Taxales) for the Taxaceae. Current cladistic analyses of molecular data group both families in the Pinales (Chaw *et al*. 1993; Cheng *et al*. 2000; Quinn *et al*. 2002; Price 2003).

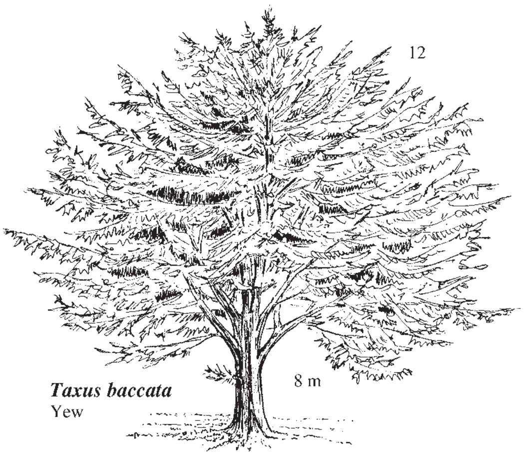
The recent analyses of Quinn *et al*. (2002) give strong support for the *Cephalotaxus* being basal to the Taxaceae *s.str.* and the two together being sister to the Cupressaceae *s.l.*

C.N. Page (1990) writes concerning the Cephalotaxaceae and Taxaceae, 'Indeed obscurity is probably the only aspect of the generic and family affinities of these undoubtedly ancient plants about which we can be totally sure.' He found the affinity between the two families to be 'considerably uncertain' as was the 'possible relationship, if any, of either family to the

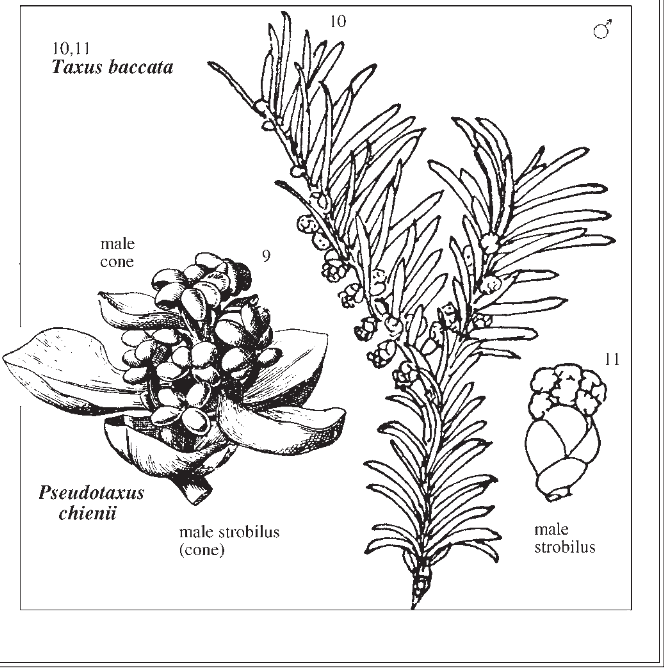


all extant

1–4,8,9 from C.N. Page (in Kubitzki) 1990
5,6 from Stewart & Rothwell 1993
7,10,11 from Dallimore & Jackson 1966
12 H.M. Anderson pen sketch (based on J. Mitchell 1982)



Taxus baccata
Yew



rest of the conifers'; and continued, 'two alternative family treatments are to group *Amentotaxus* and *Cephalotaxus* as two monogeneric families, or to group both together with the remainder of the taxads into the single family Taxaceae'. He quotes Keng (1963, 1969) as finding a possible link from *Amentotaxus* through *Phyllocladus* to the Podocarpaceae.

Morphological analyses of the extant conifers show the Cephalotaxaceae and Taxaceae to be most closely related and for this clade to be the sister group to a clade including the Araucariaceae, Sciadopityaceae, Taxodiaceae and Cupressaceae (Hart 1987). In the cladograms of Doyle (1996), the Cephalotaxaceae-Taxaceae clade is shown as the sister group to the Taxodiaceae alone (see Chart 3, p. 38).

Intervening: Middle Jurassic (BTH)–Holocene. 'Foliage regarded as typical of this family occurs reasonably commonly in the fossil record, but records of fructifications are equivocal' (Cleal 1993).

Morphology: The fleshy layer around the seed of *Cephalotaxus* is often described as the sarcotesta. Only Lotsy (1911) and Melikajan & Bobrov (1997) regard it as an aril. Mundry (2000) shows a transition series between the aril of *Taxus*, *Torreya* and the fleshy layer of *Cephalotaxus* as a congenitally fused aril. The branching pattern of the female reproductive structures of *Taxus* and *Torreya* are interpreted either as compound cones (Stützel & Röwekamp 1999) or as reduced cones. The uncommon perisporangiate *Taxus* sporangiophore is presumably derived from the hyposporangiate *Cephalotaxus* sporangiophore and represents a reduced lateral simple cone (Wilde 1975; Mundry & Mundry 2001).

Genus ***Cephalotaxus*** Siebold & Zucc. ex Endl.

In that the genus *Cephalotaxus* has until recently been included in its own monogenetic family, we discuss aspects of its fossil record and ecology below and provide a set of pen sketches as for each of the recognised Pinales families.

Range: J(BAJ?)–Rec.
First: ?*Elatocladus zamioides* (Leckenby) Seward 1919; foliage only; Cloughton Fm., North Yorkshire, England, UK (Harris 1979).

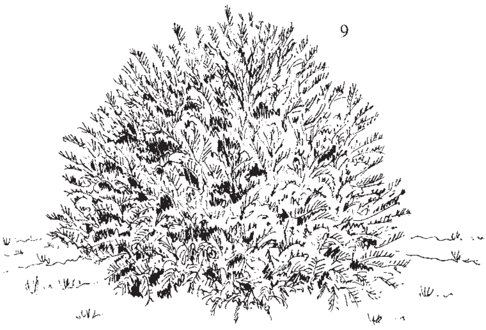
Ecology
Diversity: 1 genus, 6 species; eastern Himalayas to Japan.

Habit: Woody shrubs or slender trees, slow-growing, evergreen.

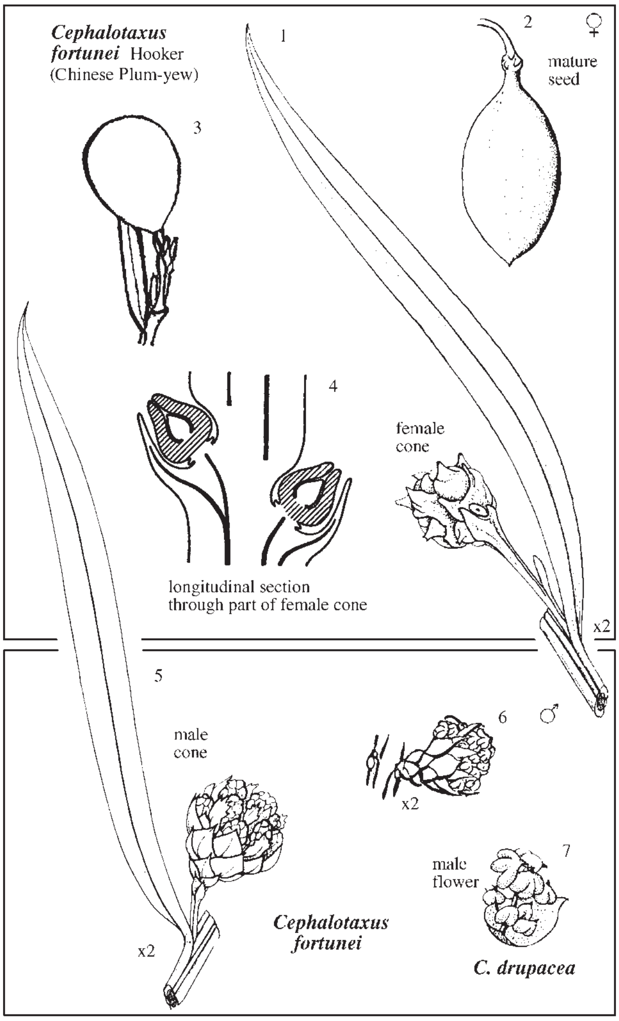
Habitat: Mostly warm to cool-temperate, 'all species inhabit damp, valley bottom sites', mainly riverine on 'mountain flanks and in mountain valleys, at moderate altitude'.

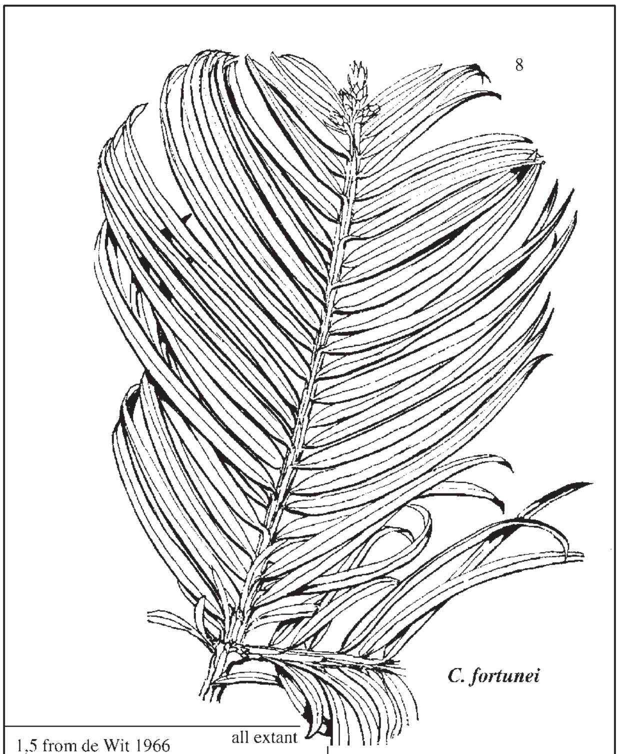
References

C.N. Page (1990), Woodland (2000): Habit, habitat.



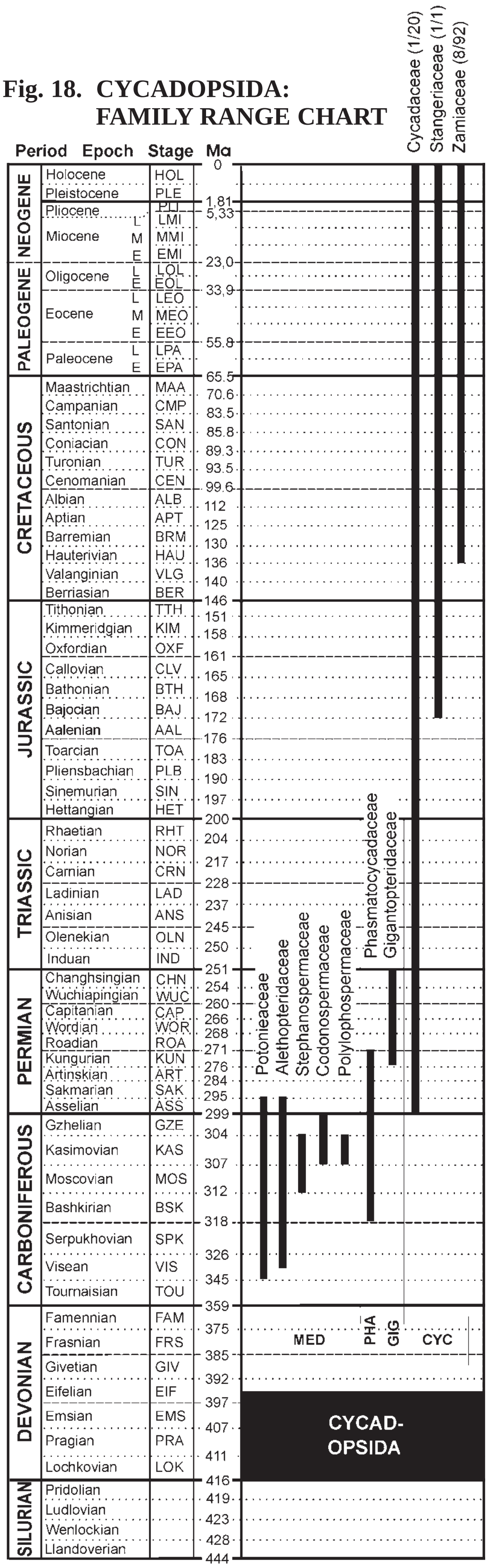
Cephalotaxus harringtonia





1,5 from de Wit 1966
2,7 from C.N. Page (in Kubitzki) 1990
3,6,8 from Dallimore & Jackson 1966
4 from Florin 1951
9 H.M. Anderson pen sketch (based on van Gelderen & van Hoey Smith 1986)

Fig. 18. CYCADOPSIDA: FAMILY RANGE CHART



Class **CYCADOPSIDA** Brongn. 1843 emend. nov.

Diagnosis: Gymnospermous plants bearing ovules in which a nucellar-beak is absent or very rudimentary, and that are supplied by a double vascular system, one to the outer integument, the other to the inner integument or nucellus.

Foliage: Fronds simple, or with or without proximal dichotomy of primary rachis.

Remarks

Classification: Barnard & Long (1975) included all megaphyllous gymnospermous plants within this class, but Meyen (1987) restricted it to the Medullosales and Cycadales. We have essentially followed Meyen in our classification, although we have also added the Phasmatocycadales and Gigantopteridales (essentially following Doweld 2001). Crane (1985) noted that the Cycadales and Medullosales have ovules with a double vascular system, a feature known in no other gymnosperm. Whether it also occurred in the Phasmatocycadales and Gigantopteridales is unknown.

Orders: Includes the three extinct orders Medullosales, Phasmatocycadales and Gigantopteridales, and the single extant order Cycadales.

CLASS ORDER Family — Tab. 25. CYCADOPSIDA		generic diversity			affiliation grade			morphology grade			anatomy preserved	
	♀	♂	⬯	♀	♂	⬯	♀	♂	⬯	♀	♂	⬯
CYCADOPSIDA Brongn. 1843 emend. nov.												
MEDULLOSALES Corsin 1960												
Potonieaceae T.Halle 1933	1	1	2	5	3	3	3	4	5	✓	✓	✓
Alethopteridaceae Corsin 1960 emend. nov.	2	11	15	5	4	4	3	4	5	✓	✓	✓
Stephanospermaceae Doweld 2001 emend. nov.	1	-	-	5	-	-	3	-	-	✓	-	-
Codonospermaceae Doweld 2001 emend. nov.	1	-	-	5	-	-	2	-	-	✓	-	-
Polylophospermaceae Doweld 2001 emend. nov.	1	-	-	5	-	-	2	-	-	✓	-	-
PHASMATOCYCADALES Doweld 2001												
Phasmatocycadaceae Doweld 2001	5	-	1	5	-	3	2	-	3	-	-	-
GIGANTOPTERIDALES Li & Yao 1983												
Gigantopteridaceae Koidz. 1936	1	1	1	5	5	5	2	3	2	-	-	✓
CYCADALES Dumort. 1829												
Cycadaceae Pers. 1807 extant	**1**	**1**	**1**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**
Stangeriaceae (Pilg.) L.A.S.Johnson 1959 extant	**2**	**2**	**2**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**
Zamiaceae Horan. 1834. extant	**8**	**8**	**8**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**

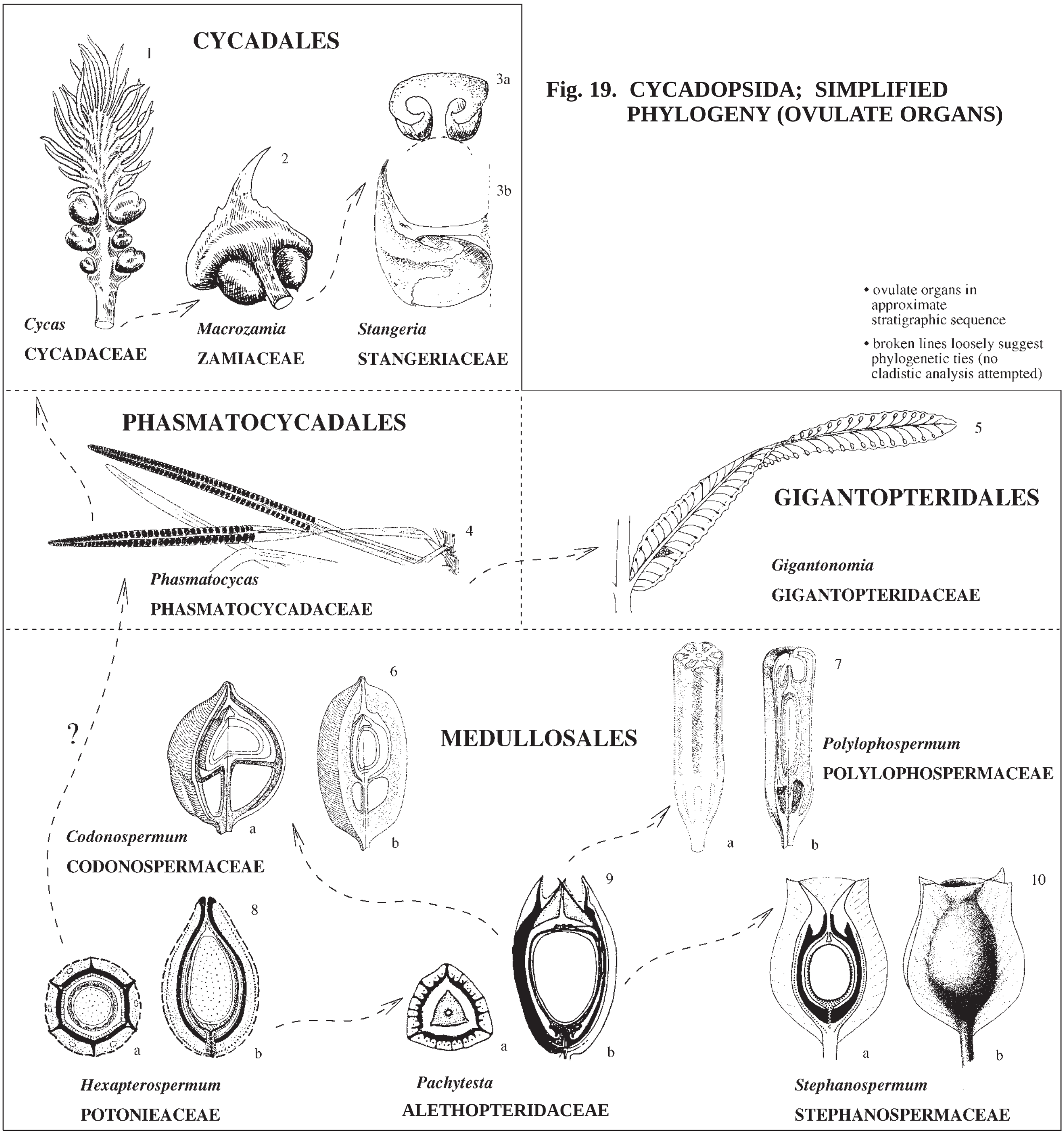


Fig. 19. CYCADOPSIDA; SIMPLIFIED PHYLOGENY (OVULATE ORGANS)

- ovulate organs in approximate stratigraphic sequence
- broken lines loosely suggest phylogenetic ties (no cladistic analysis attempted)

Order **MEDULLOSALES** Corsin 1960

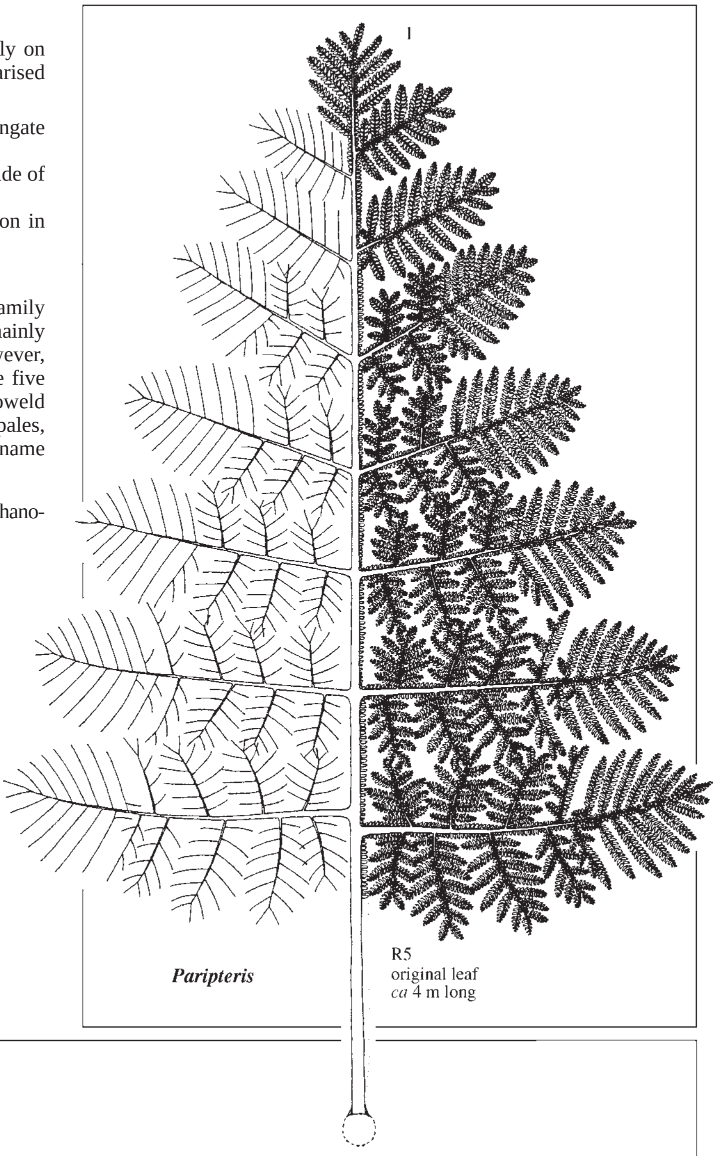
Diagnosis: Cycadopsid plants with radiospermic ovules borne singly on fronds or in loose clusters on dichotomously branched axes; vascularised nucellus free from the integument.

Male: Pollen organs compound, consisting of clusters of usually elongate pollen sacs.
Foliage: Fronds mainly compound; leaf traces arise from the same side of stem as the frond they supply.
Stem: Stele dissected, superficially resembling a polystelic condition in transverse-section.

Remarks
Classification: Cleal & Shute (2003) have recently revised the family classification of this order based on a combination of reproductive (mainly ovulate) and vegetative characters, and recognised four families. However, to remain internally consistent, in the present analysis we recognise five families based essentially on ovule anatomy (broadly following Doweld 2001). The latter analysis referred to this order as the Trigonocarpales, following Meyen (1986). However, we have here reverted to the name Medullosales, which has been more widely used in the literature.

Families: Includes the five families Potonieaceae, Alethopteridaceae, Stephanospermaceae, Codonospermaceae and Polylophospermaceae.

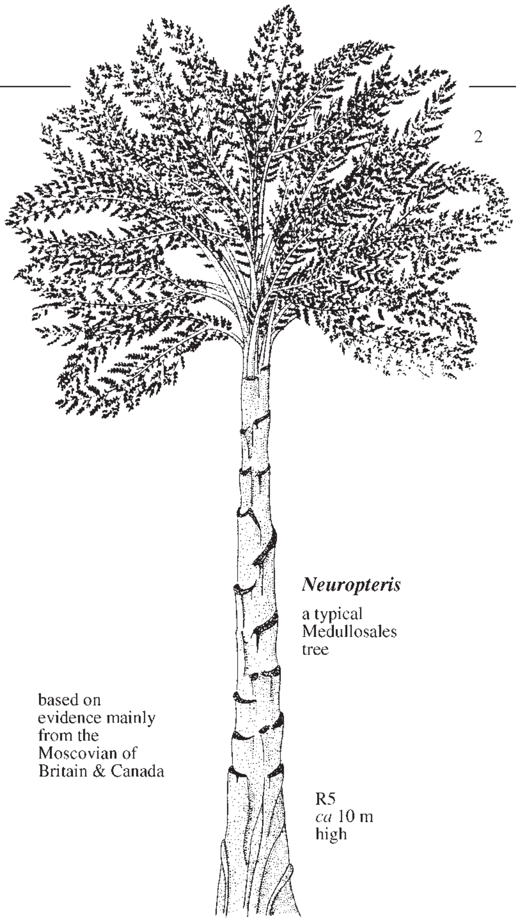
1



Paripteris

R5
original leaf
ca 4 m long

2



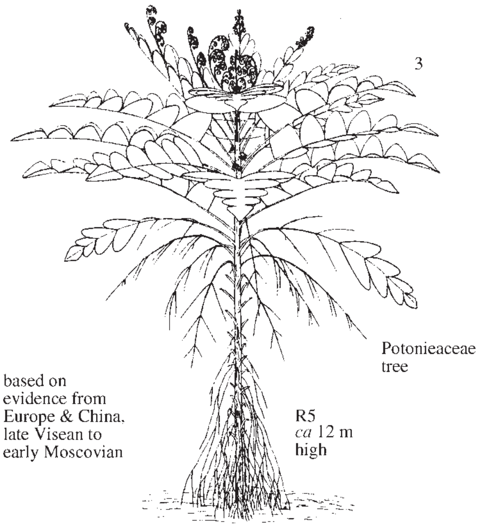
Neuropteris

a typical
Medullosales
tree

based on
evidence mainly
from the
Moscovian of
Britain & Canada

R5
ca 10 m
high

3



Potonieaceae
tree

based on
evidence from
Europe & China,
late Visean to
early Moscovian

R5
ca 12 m
high

all figures generalised, based
on data from many localities

1,3 from Laveine *et al.* 1993
2 from Cleal & Shute 1995

Family **POTONIEACEAE** T.Halle 1933 emend. nov.

Diagnosis: Medullosalean plants bearing large ovules with six longitudinal ribs; nucellus vascularised by a series of discrete vascular bundles.

Male: Pollen organs compound, branching (‘potonieaphores’), with bell-shaped sporangial clusters at end of each axis; sporangial clusters consist of numerous groups of usually four elongate sporangia, the groups arranged in four or five concentric rings; prepollen trilete.
Foliage: Fronds pseudopinnate *sensu* Laveine (1997), i.e. with no proximal dichotomy of the tri- or quadripinnate frond; pinnules attached to all orders of rachis and readily abscised.
Stem: Stele partly dissected.

Range: Euramerica, C(BSK)–P(ASS); Cathaysia, C(VIS–MOS); also possibly in Angara (MOS)
First: *Paripteris gigantea* (Sternberg) Gothan 1941, *Potoniea* sp., upper Tseishui Fm., Guangzhou, South China (Laveine *et al*. 1993).
Last: *Linopteris gangamopteroides* (De Stefani) Wagner in Wagner & Breimer 1958, Surmoulin and Millery Fm., Autun, France (Bouroz & Doubinger 1977).

Reference whole-plant genus & stratum—upper Tseishui Fm.
Female: *Hexagonocarpus* Renault in Renault & Zeiller 1890/ *Hexapterospermum* Brongniart 1874; ?2 TCs, 1 sp., v. rare.
Male: *Potoniea* Zeiller 1899; 2 TCs, 1 sp., abundant.
Foliage: *Paripteris* Gothan 1941; 2 TCs, 1 sp., v. abundant.
Stem: *Sutcliffia* Scott 1906; 2 TCs, 1 sp., abundant.

Stratum: Upper Tseishui Fm., Guangzhou, South China (VIS).
Affiliations: *Sutcliffia/Paripteris gigantea* (Sternberg) Gothan 1941, Grade 3 (Kin.rein.) (Stidd *et al*. 1975). *Paripteris gigantea* (Sternberg) Gothan 1941/*Potoniea* sp., Grade 5 (Org.att.) (Laveine *et al*. 1993). *Paripteris gigantea* (Sternberg) Gothan 1941/*Hexagonocarpus* sp., Grade 3 (Mut.occ.) (Laveine *et al*. 1993).

Prominence (colonisation success)—Cathaysia/Euramerica Carb.
Frequency/Ubiquity: *Paripteris* is widespread throughout the palaeotropics and also possibly in northern temperate palaeolatitudes. It occurs in three continents: Euramerica, Cathaysia and Angara (the latter based on records of *Neuropteris dichotoma* Neuberg 1921, *N. siberiana* Zalessky 1933b, *N. pulchra* Neuberg 1948 and *N. izylensis* (Tchirkova) Neuberg 1948; see Laveine *et al*. (1993).

Diversity: 16 spp in Euramerica and Angara, probably more in Cathaysia (based on foliage); Cleal & Shute (1995) give five ‘good’ species from Europe, and these probably also occur in North America. There are a further four species from Angara (Neuberg 1948); Chinese records (e.g. Wu 1995) indicate greater biodiversity in China, but the systematics of these fossils have not been properly worked out.

Abundance: In the Two Feet Nine Seam in the South Wales Coalfield, *Paripteris* foliage represents 1.3% of the assemblage (Davies 1929). In the middle Moscovian of northern Germany, Drägert (1964) reported *Paripteris* to be about 9% of the flora.

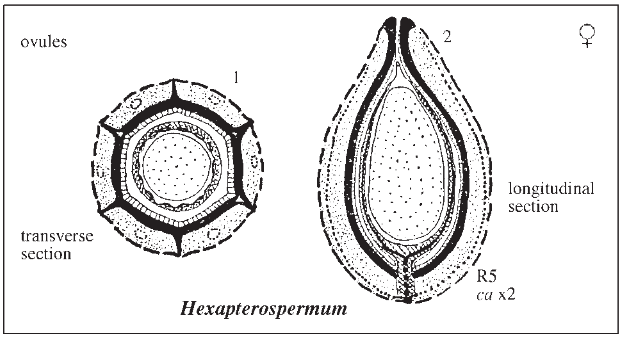
Longevity: Long-lived (*ca* 25 my, possibly longer if some of the Cathaysian records are verified).

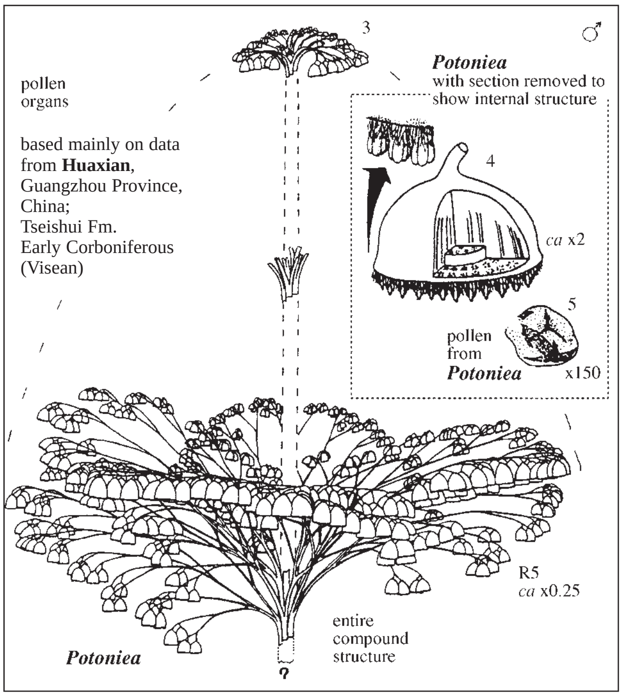
Ecology
Habit: Small to medium monoaxial trees.
Habitat: Clastic substrate levee vegetation.

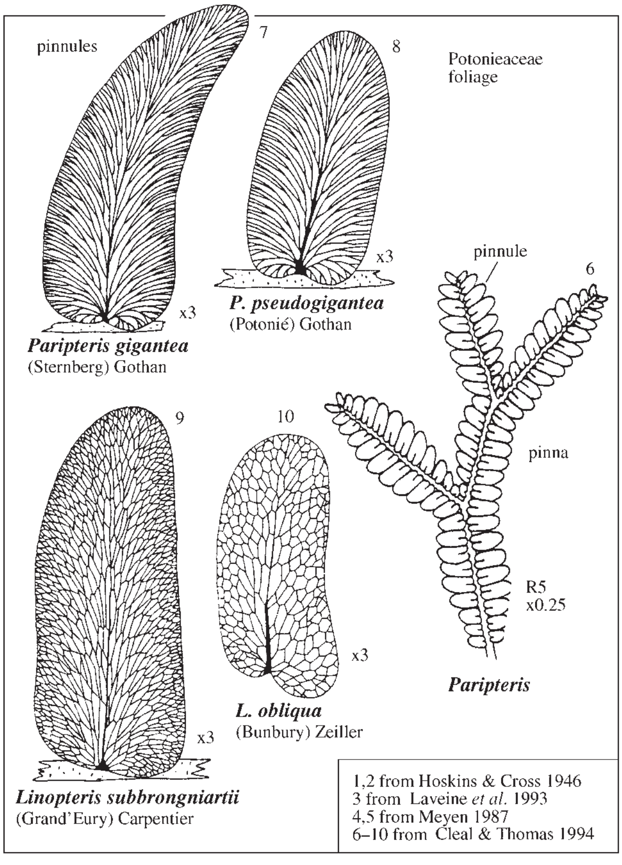
Other genera
Foliage: *Linopteris* Presl in Sternberg 1838.

Remarks
Classification: Doweld (2001) placed this family (referred to as the Hexapterospermaceae) within the Lagenostomopsida, apparently based on the type of pollen produced. However, ovule and stem anatomies all seem to support the traditional view that these plants are most related to the Trigonocarpaceae. Also, no member of the Lagenostomopsida is known to have had foliage with reticulate veins, whereas it occurs commonly in the Trigonocarpaceae.

References
Taylor (1966): Ovules.
Laveine et al. (1993): General.







1,2 from Hoskins & Cross 1946
3 from Laveine *et al*. 1993
4,5 from Meyen 1987
6–10 from Cleal & Thomas 1994

Family **ALETHOPTERIDACEAE** Corsin 1960 emend. nov.

Diagnosis: Medullosalean plants bearing large ovules, attached singly and directly to fronds, and with three longitudinal ribs; nucellus vascularised by a series of discrete vascular bundles.

Male: Prepollen monolete.
Foliage: Fronds bifurcate, semipinnate or bifurcate pinnate *sensu* Laveine (1997).
Stem: Stele highly dissected.

Range: Euramerica, C(VIS–GZE); Cathaysia, C(KAS)–P(ASS)
First: *'Neuropteris' antecedens* Stur 1875 and *Holcospermum ellipsoideum* (Göppert) Walton 1931, Teilia Fm., Clwyd, Wales, UK (Walton 1931).
Last: *Odontopteris subcrenulata* (Rost) Zeiller 1888, Lower Shihhotse Fm., Shanxi, China (Halle 1927). There are records of this species from higher strata within both North and South China (e.g. Shen 1995), but they have not been fully documented in the literature.

Reference whole-plant genus & stratum—Mattoon Fm.
Female: *Pachytesta* Brongniart 1874; 3 TCs, 3 spp, rare.
Male: *Bernaultia* Rothwell & Eggert 1986; 3 TCs, 1 sp., rare.
Foliage: *Alethopteris* Sternberg 1825; 3 TCs, ?2 spp, v. abundant.
Stem: *Medullosa* Cotta 1832; 3 TCs, 3 spp, abundant.

Stratum: Mattoon Fm. (KAS), Illinois, USA.
Affiliations: *Medullosa noei* Steidtmann 1937/*Alethopteris zeilleri* Ragot ex Jongmans 1960/ *Bernaultia formosa* (Schopf) Rothwell & Eggert 1986/ *Pachytesta* sp., Grade 4 (Anat.cor., Mut.occ.); there are other suggested affiliations, but this is the best documented (Ramanujam *et al*. 1974; Basinger *et al*. 1974).

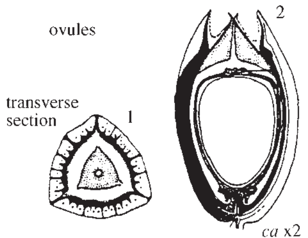
Prominence (colonisation success)—Euramerica Carb. to Early Perm.
Frequency/Ubiquity: *Alethopteris* (foliage) is widespread in western palaeotropical floras, especially in late Moscovian and Kasimovian. Also possibly in the eastern palaeotropical floras (Cathaysia).
Diversity: 128 spp known (based on foliage). We estimate 34 'good' *Alethopteris* species for Euramerica based on records in recent literature (Buisine 1961; Wagner, 1968; Purkynová 1970; Josten 1983). The species in the Cathaysian floras have yet to be fully documented.
Abundance: Late Bashkirian and early Moscovian floras, consistently occurring, usually at <1% (e.g. Davies 1929); middle Moscovian floras of northern Germany, 8% (Drägert 1964), and in the late Radstock Flora, 30% (Procter 1994); Kasimovian floras, such as those of central France, 2–13% (Doubinger *et al.* 1995).
Longevity: Long-lived (35 my, possibly longer if some of the Cathaysian records are verified).

Ecology
Habit: Mainly small to medium monoaxial trees.
Habitat: Clastic substrate levee vegetation. In Kasimovian, it also occurred on peaty substrates.

Other genera
Female (ovules): *Rhynchosperma* Taylor & Eggert 1967.
Male (pollen organs): *Whittleseya* Newberry 1853, *Codonotheca* Sellards 1903, *Boulaya* Carpentier 1913, *Aulacotheca* Halle 1933, *Dolerotheca* Halle 1933, *Schopfitheca* Delevoryas 1964, *Rhetinotheca* Leisman & Peters 1970, *Halletheca* Taylor 1971, *Sullitheca* Stidd *et al.* 1977, *Stewartiotheca* Eggert & Rothwell 1979.
Foliage: *Lonchopteris* Brongniart 1828, *Neuropteris* Brongniart 1828, *Odontopteris* Brongniart 1828, *Callipteridium* Weiss 1870, *Neurodontopteris* Potonié 1893, *Neurocallipteris* Sterzel 1895, *Lonchopteridium* Gothan in Potonié 1909, *Margaritopteris* Gothan 1913, *Reticulopteris* Gothan 1941, *Neuralethopteris* Cremer ex Laveine 1967, *Laveineopteris* Cleal *et al*. 1990, *Macroneuropteris* Cleal *et al*. 1990, *Barthelopteris* Zodrow & Cleal 1993, *Cardioneuropteris* Goganova *et al*. 1993.

Remarks
Classification: Doweld (2001) included the Protoblechnidaceae Wagner 1967 within this family, presumably based on the fact that the former includes '*Alethopteris' norinii* Halle. As pointed out by Wagner (1967), this species is only superficially similar to true *Alethopteris*. However, it is also far from clear that the other taxa included within the Protoblechnidaceae form a natural systematic group, and so the family has not been included within the present analysis.

References
Delevoryas (1955): Stems.
Taylor (1965): Ovules.
Wagner (1968), Zodrow & Cleal (1998): Foliage.
Stidd (1981): General.
Drinnan & Crane (1994): Pollen organs.



Pachytesta

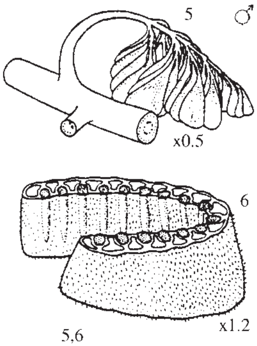
♀ 1,2 generalised provinance

1,2 from Stewart & Rothwell 1993
3–9 from Meyen 1987
10 from Cleal & Shute 1991
11–14 from Cleal & Thomas 1994
all Laurasia, Carb.–Perm.

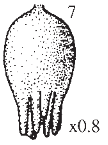
pollen & pollen organs of Trigonocarpaceae ♂

Halletheca reticulata Taylor
Berryville, Illinois
Mattoon Fm. (KAS)

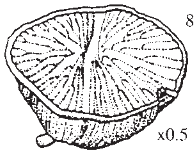
Aulacotheca iowensis Eggert & Kryder
Redfield, Iowa
Cherokee Gp. (MOS)



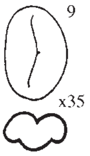
5,6 ***Parasporotheca leismanii*** Dennis & Eggert
Calhoun, Illinois
Mattoon Fm. (KAS)



Sullitheca dactylifera Stiff *et al.*
Cayuga, Indiana
Staunton Fm. (MOS)

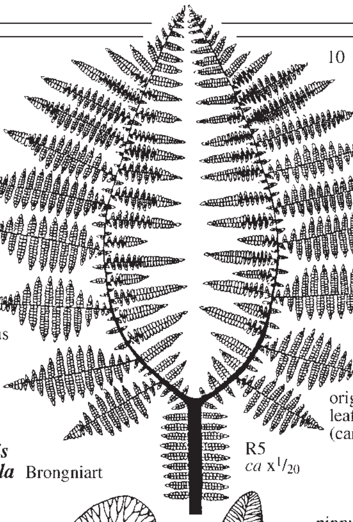


Bernayultia formosa (Schopf) Rothwell & Eggert
Berryville & **Calhoun**, Illinois
Mattoon Fm. (KAS)



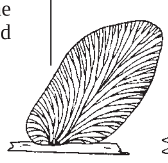
Monoletes pollen
generalised provinance

foliage of Trigonocarpaceae

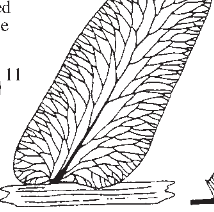


Clay Cross, Derbyshire, UK: Middle Coal Measures, Late Carboniferous (Moscovian)
Neuropteris heterophylla Brongniart

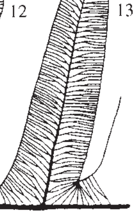
11–14 generalised provinance
pinnules all x2



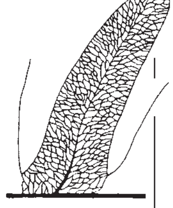
Neuropteris ovata Hoffmann



Reticulopteris muensteri (Eichwald) Gothan



Alethopteris lonchitica Sternberg



Lonchopteris petitii Buisine

Family **STEPHANOSPERMACEAE** Doweld 2001 emend. nov.

Diagnosis: Medullosalean plants bearing large ovules, borne in clusters on dichotomously branched axes, radially symmetrical, usually with three major ribs alternating with three minor ribs (minor ribs sometimes inconspicuous); nucellus vascularised by continuous sheaf of tracheids.

Male: Prepollen monolete (as found in micropyle).

Range: Euramerica, C(MOS–KAS)
First: *Stephanospermum elongatum* Hall 1954, Rock Island Coal (MOS), USA (further locality details not recorded; Phillips 1980).
Last: *Stephanospermum akenioides* Brongniart 1874 and *S. caryoides* Oliver 1904, Grand'Croix (KAS), St Étienne, France (Doubinger *et al*. 1995).

Reference whole-plant genus & stratum—Carbondale Fm.
Female: *Stephanospermum* Brongniart 1874; many TCs, 1 sp., >193 indivs.
Male: Unknown.
Foliage: Unknown.
Stem: Unknown.

Stratum: Carbondale Fm., Mazon Creek, Illinois, USA, C(MOS).
Affiliations: Nil.

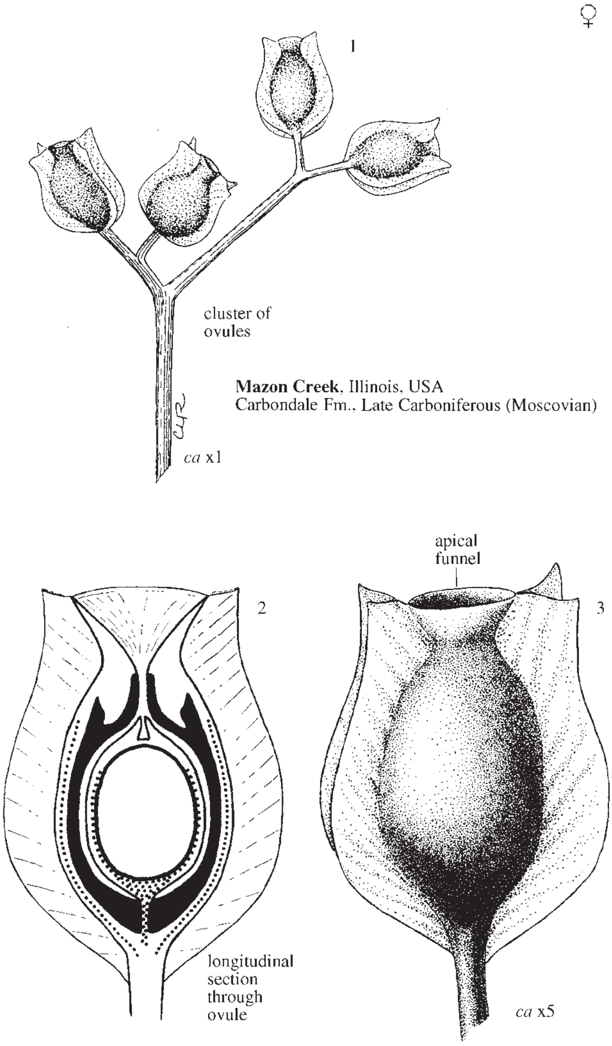
Prominence (colonisation success)—Euramerica Carboniferous
Frequency/Ubiquity: Widespread in late Westphalian and Stephanian anatomically preserved floras of Euramerica.
Diversity: 7 spp known (based on ovules).
Abundance: As the foliage produced by the *Stephanospermum*-bearing plant is unknown, this cannot be determined in any meaningful way at present.
Longevity: *ca* 5–10 my.

Ecology
Habit: Probably medium-sized monoaxial trees.
Habitat: Marginal areas between peat and clastic substrates.

Other genera—nil.

Remarks
Anatomy: Doweld (2001) established this family based on the ovules known as *Stephanospermum* Brongniart 1874. Although the underlying anatomy and presence of monolete prepollen in the pollen chamber clearly indicate that they are medullosalean, they differ from alethopteridacean ovules in a number of key respects. Most significant is that they were borne in clusters on branching axes, rather than directly on the fronds, and the nucellar vascular system consisted of a sheaf of tracheids (Drinnan *et al*. 1990; Serbet & Rothwell 1995). This latter feature was not mentioned by Doweld (2001) and so the family diagnosis has been modified here. Doweld also regarded the crown-like structure surrounding the micropyle as being significant, but as pointed out by Drinnan *et al*. (1990), this is not present in all species. There is no evidence of the rest of the plant that bore these ovules.

References
Leisman & Roth (1963), Drinnan et al. (1990), Serbet & Rothwell (1995): Ovules.



Mazon Creek, Illinois, USA
Carbondale Fm., Late Carboniferous (Moscovian)

Stephanospermum konopeonus
(Langford) Drinnan *et al.*

1–3 from Drinnan *et al.* 1990

Family **CODONOSPERMACEAE** Doweld 2001 emend. nov.

Diagnosis: Medullosalean plants bearing large ovules with 6 to 9 (usually 8) longitudinal ribs; nucellus vascularised by a series of discrete vascular bundles; large cavity occupies the proximal part of the ovule.

Male: Prepollen monolete (as found in micropyle).

Range: Euramerica, C(KAS–GZE)
First: *Codonospermum anomalum* Brongniart 1874 and *C. olivaeforme* Renault in Renault & Zeiller 1888, Grand-Croix C(KAS), St Étienne, France (Combourieu & Galtier 1985).
Last: *Codonospermum decangulosum* Renault in Renault & Zeiller 1888, *C. laevicostatum* Renault in Renault & Zeiller 1888, *C. majus* Renault in Renault & Zeiller 1888, *C. minus* Grand'Eury 1877, *C. oblongum* Renault in Renault & Zeiller 1888 and *C. olivaeforme* Renault in Renault & Zeiller 1888, Commentry C(GZE), France (Renault & Zeiller 1888).

Reference whole-plant genus & stratum—Grand-Croix
Female: *Codonospermum* Brongniart 1874; 1 TC, 2 spp, *ca* 10 ovules.
Male: Unknown.
Foliage: Unknown.
Stem: Unknown.

Stratum: As for '*First*' above.
Affiliations: Nil.

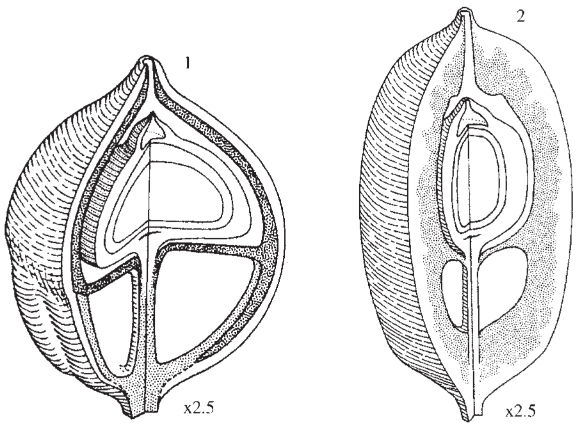
Prominence (colonisation success)—Euramerica Carboniferous
Frequency/Ubiquity: Known only from the Loire region of France.
Diversity: 7 spp known (based on ovules).
Abundance: Rare.
Longevity: *ca* 5–10 my.

Ecology
Habit: Unknown.
Habitat: Probably upland wetlands.

Other genera—nil.

Remarks
Anatomy: Doweld (2001) established this family for the distinctive Stephanian ovules with a basal cavity, the latter having been interpreted as a possible floatation structure. Doweld tentatively suggested a link with *Dolerophyllum* Saporta 1878 foliage, which would tend to undermine the assignment of these seeds to the Medullosales. However, the general anatomy of the ovules and the presence of monolete prepollen in the micropyle of *Codonospermum* Brongniart 1874 (Combourieu & Galtier 1985) appear to support its medullosalean affinities. We have emended the diagnosis to include the details of the vascularisation of the nucellus, not mentioned by Doweld.

Reference
Combourieu & Galtier (1985): Ovules.



Codonospermum anomalum Brongniart

Codonospermum olivaeforme Renault

Grand-Croix, Loire region, France
Late Carboniferous (Kasimovian)

1,2 from Combourieu & Galtier 1985

Family **POLYLOPHOSPERMACEAE** Doweld 2001 emend. nov.

Diagnosis: Medullosalean plants bearing elongate ovules with 5 to 7 (usually 6) major longitudinal ribs, alternating with 6 smaller ribs; nucellus vascularised by a series of discrete vascular bundles; prominent sclerotesta prolonged at each end of the ovule to form a basal extension, and an apical chamber surrounding a long micropylar beak.

Male: Prepollen monolete (as found in micropyle).

Range: Euramerica, C(KAS)
First & Last: *Polylophospermum stephanense* Brongniart 1874, Grand-Croix (KAS), St Étienne, France (Combourieu & Galtier 1985).

Reference whole-plant genus & stratum—Grand-Croix
Female: *Polylophospermum* Brongniart 1874; 1 TC, 1 sp., *ca* 7 ovules.
Male: Unknown.
Foliage & stem: Unknown.

Stratum: As for '*First & Last*' above.
Affiliations: Nil.

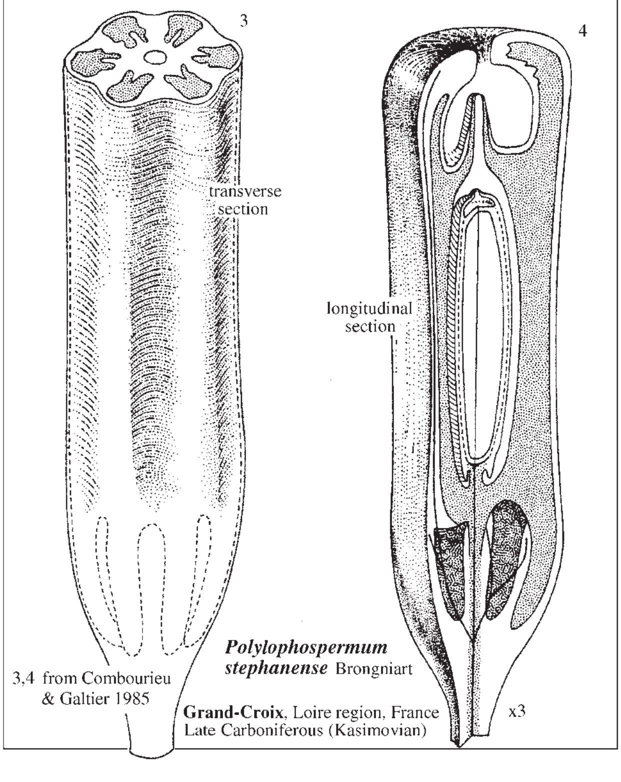
Prominence (colonisation success)—Euramerica Carboniferous
Frequency/Ubiquity: Known only from the Loire region of France.
Diversity: 1 sp. known (based on ovules).
Abundance: Rare.
Longevity: Known only from one stratigraphical level.

Ecology
Habit: Unknown.
Habitat: As for Codonospermaceae (adjacent).

Other genera—nil.

Remarks
Anatomy: Doweld (2001) established this family for the distinctive Stephanian ovules with 'bimicropylar' apical structure. However, he incorrectly stated that the ovules had a basal cavity similar to the Codonospermaceae, which they did not. He also did not incorporate the details of the sclerotesta described by Combourieu & Galtier (1985). We have therefore emended the diagnosis to take these factors into account. The general anatomy of the ovules (Oliver 1907) and the presence of monolete prepollen in the micropyle of *Polylophospermum* (Combourieu & Galtier 1985) support its medullosalean affinities. There is no evidence of the rest of the plant that bore these ovules.

Reference
Combourieu & Galtier (1985): Ovules.



3,4 from Combourieu & Galtier 1985

Polylophospermum stephanense Brongniart

Grand-Croix, Loire region, France
Late Carboniferous (Kasimovian)

Order **PHASMATOCYCADALES** Doweld 2001

Diagnosis: Cycadopsid plants with platyspermic ovules borne abaxially in two rows on either side of the axis of unmodified leaves (megasporophylls); two vascularised membranes enclosing the megaspore.

Foliage: Entire taeniopteroid.

Families: Includes the single family Phasmatocycadaceae.

Family **PHASMATOCYCADACEAE** Doweld 2001

Diagnosis: As for Phasmatocycadales.

Range: Euramerica, C(BSK)–P(KUN)
First: *Lesleya cheimarosa* Leary & Pfefferkorn 1977, Cedar Valley Limestone Fm. C(BSK), western Illinois, USA (Leary 1990).
Last: ?*Phasmatocycas* sp., Vale Fm. P(KUN), Haskell County, Texas, USA (Mamay 1976).

Reference whole-plant genus & stratum—Wellington Fm.
Female: *Phasmatocycas* Mamay 1973; 1 TC, 1 sp., v. rare.
Male: Unknown.
Foliage: *Taeniopteris* Brongniart 1828; 4 TCs, 1 sp. medium abundance.
Stem: Unknown.

Stratum: Elmo Limestone Member, Wellington Fm. P(ART), near Elmo, Kansas, USA (Mamay 1976).
Affiliations: Grade 3 (Mor.cor., Mut.occ.).

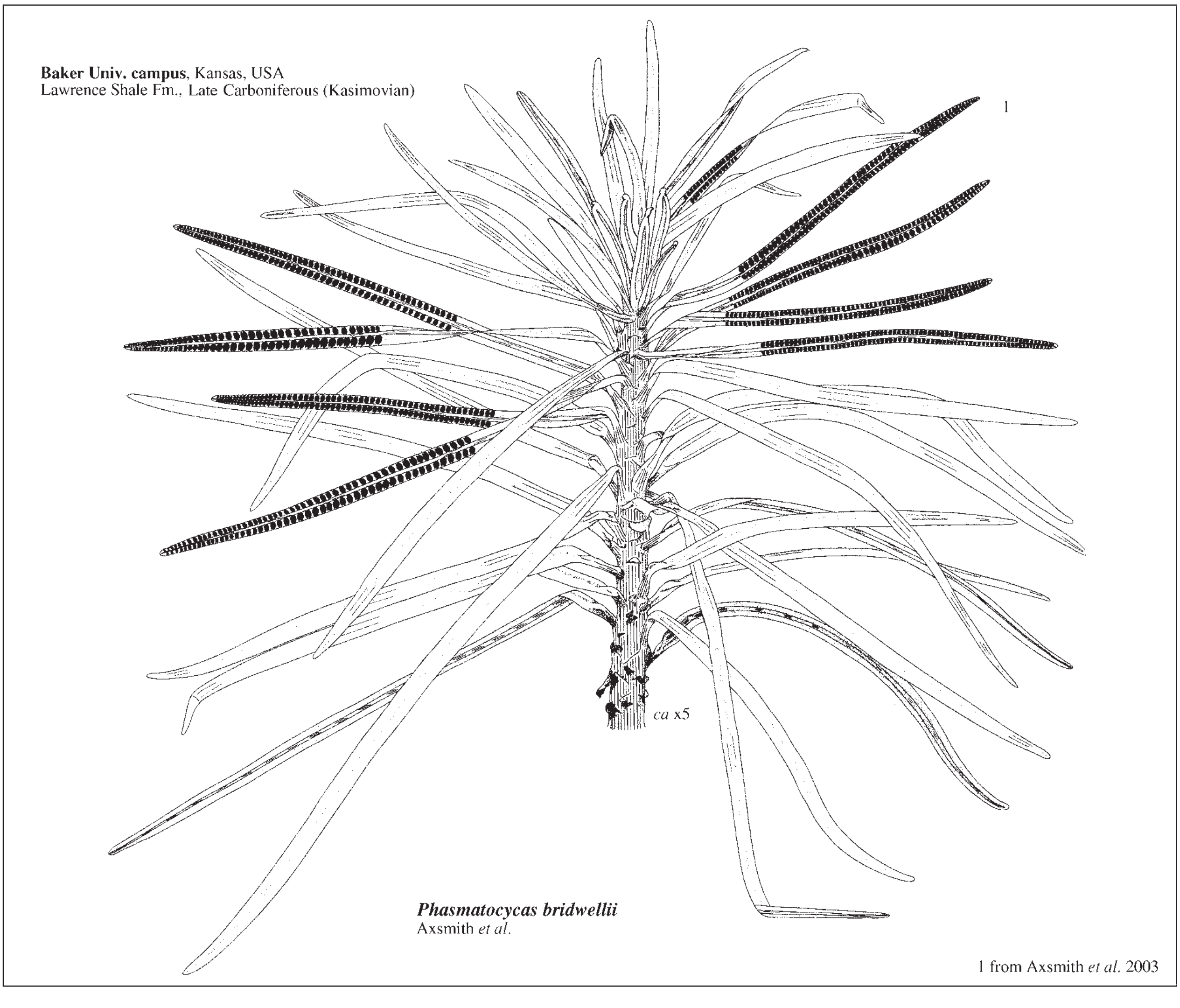
Prominence (colonisation success)—Euramerica Permian
Frequency/Ubiquity: Unequivocal evidence of this plant is only from North America.
Diversity: Only 2 spp unequivocally belong here; similar taeniopterid foliage is more widespread in both North America and Europe, but it is impossible to be sure if it belongs to *Phasmatocycas*, one of the other genera in this family, or even to a different family.
Abundance: Not recorded.
Longevity: Has a range of *ca* 45 my, based on North American occurrence.

Ecology
Habit: Unknown.
Habitat: Dry tropical, both basinal and extra-basinal.

Other genera
Female: *Lesleya* Lesquereux 1880, *Spermopteris* Cridland & Morris 1960, *Archaeocycas* Mamay 1973, *Sobernheimia* Kerp 1983.

Remarks
Phylogeny: Mamay (1976) suggested that these plants were evolutionary precursors of the cycadaleans, and that the *Cycas* megasporophyll was derived from fertile leaves such as *Phasmatocycas*. Axsmith *et al.* (2003) have subsequently shown that at least some of the evidence for this relationship is doubtful. Doweld (2001) separated them from the Cycadales at the rank of order, although still recognising their likely phylogenetic relationship, and this view we have accepted here. Doweld (2001) also separated off *Spermopteris* into a separate family, which he placed within the Gigantopteridales. However, Axsmith *et al.* (2003) showed that the apparent differences between *Spermopteris* and *Phasmatocycas* are due to preservation and that they are in fact the same genus.

References
Mamay (1976), Axsmith et al. (2003): General.



Order **GIGANTOPTERIDALES** X.Li & Z-Q.Yao 1983

Diagnosis: Cycadopsid plants with platyspermic ovules borne abaxially near leaf margin of unmodified leaves.

Male: Microsporangia (?synangia) attached to abaxial surface of unmodified leaves; in compact rows along lateral veins in their lower part.
Foliage: Fronds entire taeniopteriod to three-times pinnate; veins reticulate.

Remarks
Nomenclature: Meyen (1987) argued that the name of the order should not be based on the foliage morphogenus *Gigantopteris* as the latter might also occur in other orders, notably the Peltaspermales. However, it now seems likely that all gigantopterid leaves belong to the same order, if not family, and so the original name proposed by Li & Yao (1983) may be retained.

Phylogeny: The systematic position of the Gigantopteridales is far from clear due to the limited available evidence on the reproductive structures, but we have decided essentially to follow Doweld (2001) and regard it as most closely allied with the Phasmatocycadales, and thus belonging to the Cycadopsida.

Families: Includes the single family Gigantopteridaceae.

Family **GIGANTOPTERIDACEAE** Koidz. 1936

Diagnosis: As for Gigantopteridales.

Range: South Cathaysia, P(KUN–CHN)
First: *Gigantonomia fukiensis* (Yabe & Oishi) Li & Yao 1983, *Gigantotheca paradox* Li & Yao 1983, lower Maokou Fm., Fujian, southern China P(KUN).
Last: '*Gigantonoclea*' *guizhouensis* 'Gu & Zhi' 1974, Dalong Fm., western Guizhou, southern China P(CHN) (based on similarity in foliage).

Reference whole-plant genus & stratum—Lower Maokou Fm.
Female: *Gigantonomia* Li & Yao 1983; 1 TC, 1 sp., 1 indiv.
Male: *Gigantotheca* Li & Yao 1983; 1 TC, 1 sp., 1 indiv.
Foliage: *Gigantopteris* Schenk 1883; many TCs, 3 spp, abundant.
Stem: Unknown.

Stratum: Lower Maokou Fm. P(KUN), Fujian, southern China (Li & Yao 1983).
Affiliations: Grade 5 (Org.att., Mor.cor., Mut.occ.).

Prominence (colonisation success)—South Cathaysia Permian
Frequency/Ubiquity: *Gigantopteris* foliage is a characteristic and widespread element in the Permian floras of part of one palaeocontinent (South Cathaysia).
Diversity: 2 or 3 spp (based on foliage) were recognised by Glasspool *et al.* (2004).
Abundance: No available data in individual floras.
Longevity: *ca* 25 my.

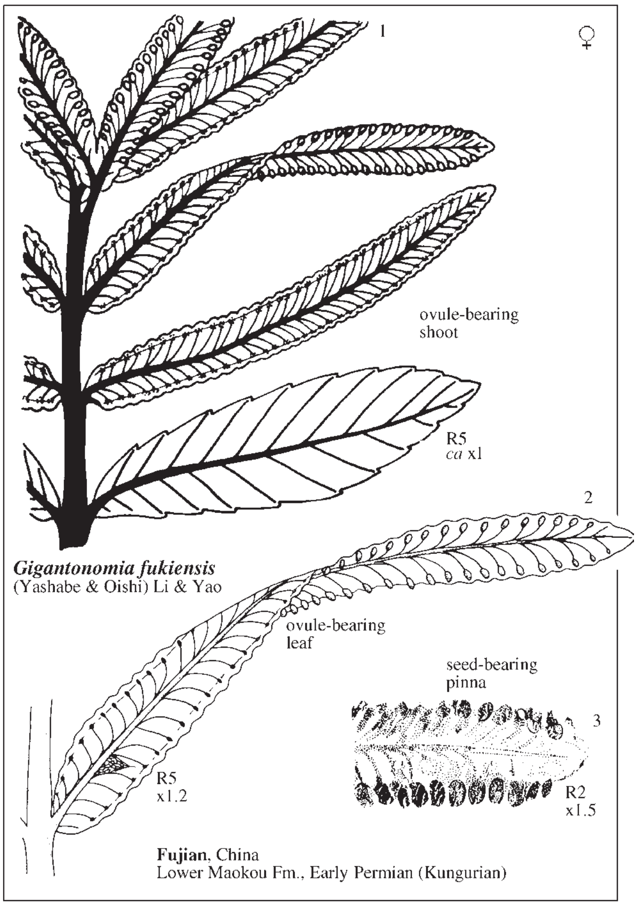
Ecology
Habit: Shrub of scrambling or upright habit.
Habitat: Understorey in tropical forests or possibly aquatic conditions.

Other genera—nil.

Remarks
Taxonomic concept: Despite the abundance of gigantopteroid foliage in southern China, this is a poorly understood family. The concept used here is centred around the studies of Li & Yao (1983), who linked the foliage and ovulate and pollen organs mentioned above. We have also included foliage from the Upper Permian of southern China that has been assigned to *Gigantopteris*, but we recognise that this is highly speculative. Wang (1999) has argued that true *Gigantonoclea* is unknown from southern China (see also Glasspool *et al.* 2004).

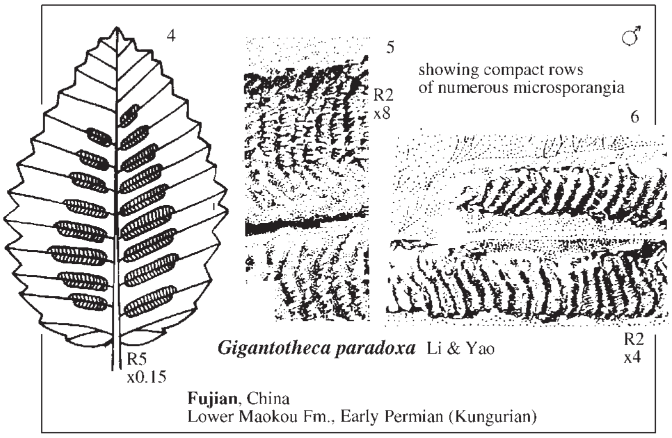
The frequent reports of Gigantopteridaceae from the Permian of North America refer to sterile leaves, which superficially resemble the foliage of the Emplectopteridaceae; true *Gigantopteris* appears to be absent (Mamay *et al.* 1988).

References
Li & Yao (1983): General.
Glasspool et al. (2004): Foliage.



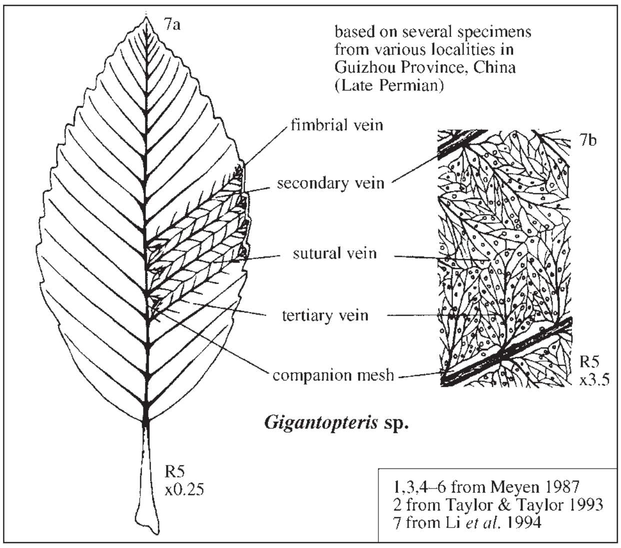
Gigantonomia fukiensis
(Yashabe & Oishi) Li & Yao

Fujian, China
Lower Maokou Fm., Early Permian (Kungurian)



Gigantotheca paradoxa Li & Yao

Fujian, China
Lower Maokou Fm., Early Permian (Kungurian)



based on several specimens from various localities in Guizhou Province, China (Late Permian)

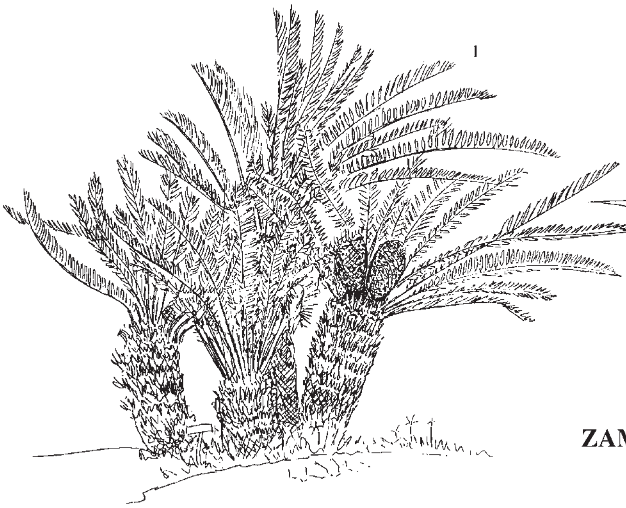
***Gigantopteris* sp.**

1,3,4–6 from Meyen 1987
2 from Taylor & Taylor 1993
7 from Li *et al.* 1994

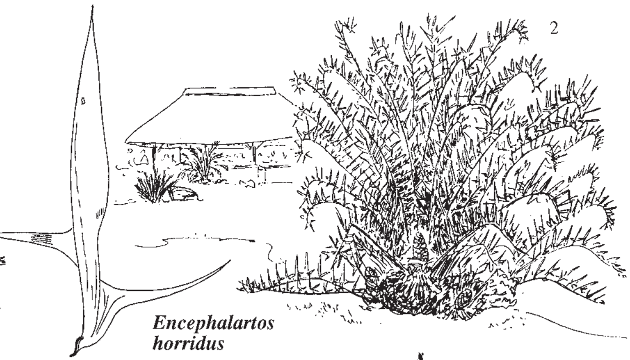
Fig. 20

EXTANT CYCADALES

A selection of *Encephalartos* species from South Africa,
showing range of habit within the genus



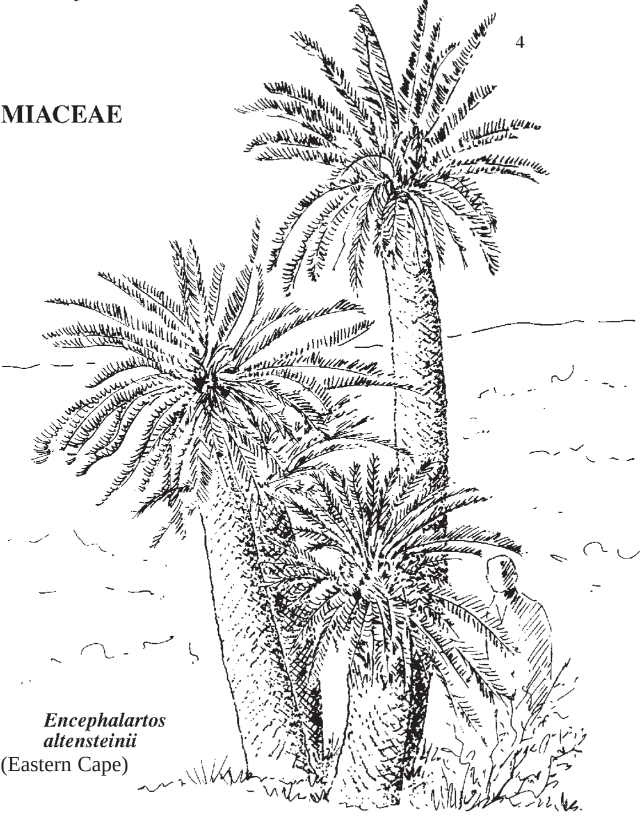
Encephalartos altensteinii
(Pretoria National Botanical Garden)



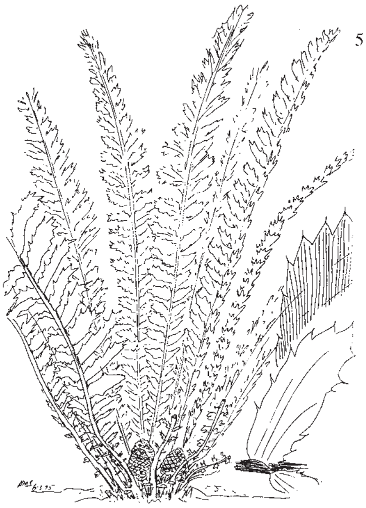
Encephalartos horridus

ZAMIACEAE

Encephalartos lebomboensis



Encephalartos altensteinii
(Eastern Cape)



Encephalartos ferox

Encephalartos villosus

1–6 all H.M. Anderson sketches 1997, 2004
(1–3,5,6 from nature; 4 after Dyer 1965)

Order **CYCADALES** Dumort. 1829

Diagnosis [Contributors: M. Mundry, I. Mundry & T. Stützel]: Cycadopsid plants with radiospermic or platyspermic ovules borne in lax or compact cones; nucellus fused to the integument except in the most apical part.

Male: Pollen organs borne in compact cones.
Foliage: Frond simple to once- or twice-pinnate; leaf traces arise from the opposite side of the stem from the frond they supply.
Stem: Mostly pith and cortex, with a small central cylinder of wood.

Remarks
Morphology: For graphic portrayal of aspects of comparative morphology, see Chart 29 (p. 64).

Phylogeny: For text on gymnosperm phylogeny, including the Cycadales, see pp 18, 19.

Families: Includes the three extant families Cycadaceae, Stangeriaceae and Zamiaceae.

Tab. 26. Extant Cycadales: classification, diversity, habitat

CYCADALES (3 fam, 11 gen, 292 spp)
CYCADACEAE (1 gen, 102 spp)
Cycas (102 spp)—east coast Africa, Madagascar, Asia (India to Japan), Malesia, Australia, Polynesia;
various forest types, woodland, savannah.

STANGERIACEAE (2 gen, 4 spp)
Stangeria (1 sp.)—east coast South Africa & Mozambique;
coastal grassland & forest.
Bowenia (3 spp)—northeastern Australia;
near coast, open spaces in rainforest & eucalypt forest.

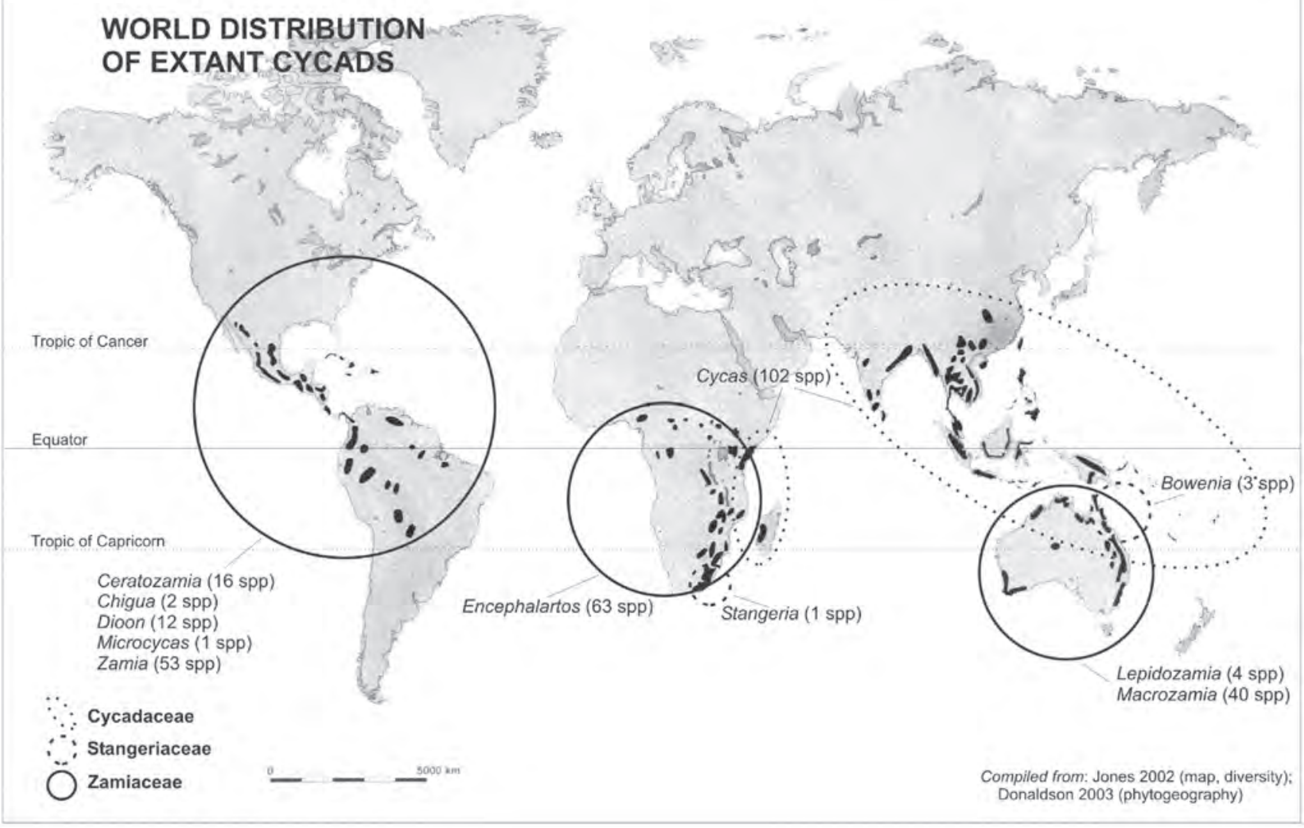
ZAMIACEAE (8 gen, 191 spp)
Dioon (12 spp)—central America (Mexico & Honduras);
limestone cliffs to dense tropical forests, sea level to >3000 m.
Encephalartos (63 spp)—central & southern Africa;
open grassland to forest, sea level to > 1800 m.
Macrozamia (40 spp)—warm-temperate to sub-tropical Australia; mostly poor siliceous soils, sclerophyll forests & woodlands;
1 sp. in arid ranges of central Australia.
Lepidozamia (2 spp)—east coast Australia;
wet sclerophyll forest or near rainforest.
Ceratozamia (16 spp)—Central America (Mexico to Belize);
dense tropical rainforest to open woodland, often on calcareous soils, to *ca* 3500 m.
Microcycas (1 sp.)—Cuba (Pinar del Rio Province);
woodlands of sierra foothills. *Zamia* (53 spp)—West Indies, Florida, Georgia, Mexico to Brazil; coastal sand dunes to tropical forests, often on calcareous soils.
Chigua (2 spp)—Colombia;
primary rainforest.

ORDER
SUBORDER
FAMILY
SUBFAMILY
TRIBE
SUBTRIBE
Genus

	extant species	
	1990	2002
CYCADALES		
CYCADINEAE		
CYCADACEAE		
Cycas	20	102
ZAMIINEAE		
STANGERIACEAE		
STANGERIOIDEAE		
Stangeria	1	1
BOWENIOIDEAE		
Bowenia	2	3
ZAMIACEAE		
ENCEPHALARTOIDEAE		
DIOOEAE		
Dioon	10	12
ENCEPHALARTEAE		
ENCEPHALARTINAE		
Encephalartos	35	63
MACROZAMIINAE		
Macrozamia	14	40
Lepidozamia	2	2
ZAMIOIDEAE		
CERATOZAMIEAE		
Ceratozamia	10	16
ZAMIEAE		
MICRICYCADINAE		
Microcycas	1	1
ZAMIINAE		
Zamia	30–40	53
Chigua	2	2
	123	**292**

References (tables)
Jones (2002): diversity (in 2002), general
Johnson & Wilson (1990): diversity (in 1990), occurrence, habitat
Stevenson (1990, 1992): classification (cladistics)

Fig. 21



Biodiversity (3 fams, 11 gen., 292 spp)
Increased levels of taxonomic study in the extant cycads over the past decade offer a remarkable insight as to how much we have yet to learn of biodiversity levels generally. While Johnson & Wilson (1990) recorded only 123 species, Jones (2002) details 292 species (Tab. 26 opposite), over double the number. Jones (2002) estimates that the final number will probably settle around 320 species. The number of cycad genera, in contrast, has remained stable at 11 over this same interval.

Centres of diversity (Donaldson 2003)
Centres of cycad diversity differ significantly at family, genus and species level. (Species numbers quoted below are those given by Donaldson; we make no attempt to adjust them to tally with Jones 2002.)

Family level: Of the three diversity centres (Fig. 21), southern Africa, Australia and the tropical New World—all three families occur only in southern Africa and Australia. The New World and southeastern Asia are each represented by one family only.

Generic level: At generic level, it is the New World—with the five genera *Ceratozamia, Chigua, Dioon, Microcycas* and *Zamia*—that shows the greatest diversity. Australia with four genera, *Cycas, Bowenia, Lepidozamia* and *Macrozamia*, is second richest at this level. Africa is third with the three genera *Cycas*, *Stangeria* and *Encephalartos*, while Asia is fourth with only the single genus *Cycas*.

Species level: Cycad diversity at the rank of species is far more evenly distributed. Wide evolutionary radiation is seen in six of the 11 genera—*Cycas* (20 spp), *Encephalartos* (35 spp), *Macrozamia* (14 spp), *Zamia* (30–40 spp), *Ceratozamia* (10 spp) and *Dioon* (10 spp)—with Australia, Asia, Africa and the New World each having over 60 species. Australia, South Africa, Mexico, China and Vietnam, together with 70% of all cycad species, stand out as the richest centres of diversity.

Ecology (Donaldson 2003)
Cycad-animal interactions: Research of the past few decades has increasingly revealed the extent to which cycads have evolved symbiotic interactions with a rich diversity of other organisms—'nitrogen fixing cyanobacteria, arbuscular mycorrhizae, bird and mammal dispersal agents, various insect pollinators'—and, no doubt, a good many more, including fungi and bacteria. A similarly rich set of nonsymbiotic interactions, including other insect groups, occurs. 'Many of the known interactions are specific to one or a few cycad species and have influenced the evolution of unique chemical, morphological, and behavioural attributes.'

Relict status: While the 1997 IUCN Red List of Threatened Plants included '12.5% of the world's vascular plants' in one or other of the threatened categories, 'a staggering 82% of the world's cycads were listed as threatened'. The 123 species (297 species and subspecies) are suffering a major extinction crisis. Some species are 'almost certainly dying out naturally', but human activities are the major factor in extinction. 'Many species exist as relatively small isolated populations—within the dynamic context of ongoing evolution and extinction'. Some of these are small relict species; others are emerging species from isolated populations. The situation varies from region to region.

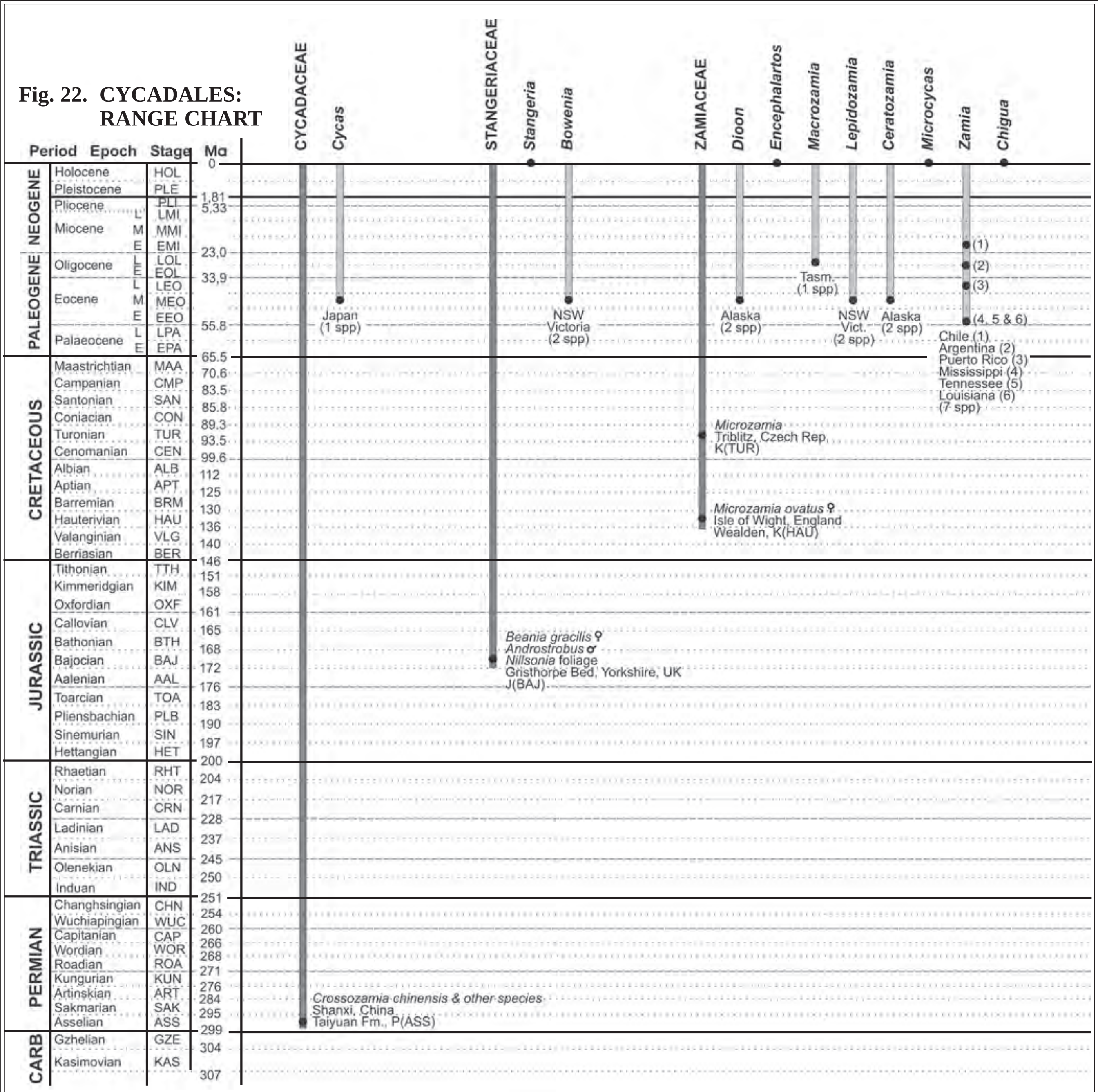
Sub-Saharan Africa & adjacent islands (2 fams, 2 gen., 69 spp & subspp): Most species localised; 45 taxa (species and subspecies) occur in only one country.

Australia (3 fams, 4 gen., 76 spp & subspp): Has a rich cycad diversity; many species occur in restricted areas, while others are represented by large healthy populations.

South-East Asia (1 fam., 1 gen., *ca* 63 spp): Abundance and diversity far from uniform; 14 species (*ca* 25%) are widespread (in more than one country), but the remainder have restricted occurrence.

New World (1 fam., 5 gen., 89 spp): Four of the genera are endemic (or nearly so) to a single country (e.g. *Microcycas* to Cuba, *Chigua* to Columbia); many species have restricted distributions; generally populations within species are small and disjunct, often with <1 000 individuals.

Fig. 22. CYCADALES: RANGE CHART



On the fossil record of the Cycadales (families & genera)
Extant genera: The fossil record of the 11 extant genera of cycads would appear to be extremely sparse. The 'first' and only known fossil occurrence of *Cycas*, *Bowenia*, *Dioon*, *Lepidozamia* and *Ceratozamia* is recorded in each case from the Eocene (stage not noted in Jones 2002). *Macrozamia* is recorded only from the Oligocene. *Zamia* is the most widely (geographically and stratigraphically) known: from the early and late Eocene, the Oligocene and the early Miocene from various sites in South America, central America and the USA. *Stangeria*, *Encephalartos* and *Microcycas* apparently have no fossil record.

Extinct genera: The earliest occurrences noted for the three families are those recorded in our systematic text (under 'first') for the relevant family. We make no attempt to plot all the intervening records (aside from the Turonian occurrence of *Microzamia*, a better record than that from the Hauterivian).

Sources (for fossil record)
Families: for 'first' occurrences see our text (pp 157–159)
Extant genera: Jones 2002

Family **CYCADACEAE** Pers. 1807

Diagnosis [Contributors: M. Mundry, I. Mundry & T. Stützel]: Cycadalean plants with platyspermic seeds borne in lax cones without a central axis; megasporophylls leafy, bearing two or more pairs of marginal ovules.

Male cones: Simple, compact with central axis, arising at apices not bearing leaves; sporangiophores with two flanks each bearing 4 or more abaxial sporangiate synangia.

Foliage: Leaves arranged spirally, with trophophylls alternating in series with scale-like cataphylls and fertile megasporophylls; leaflets with a single distinct median vein.

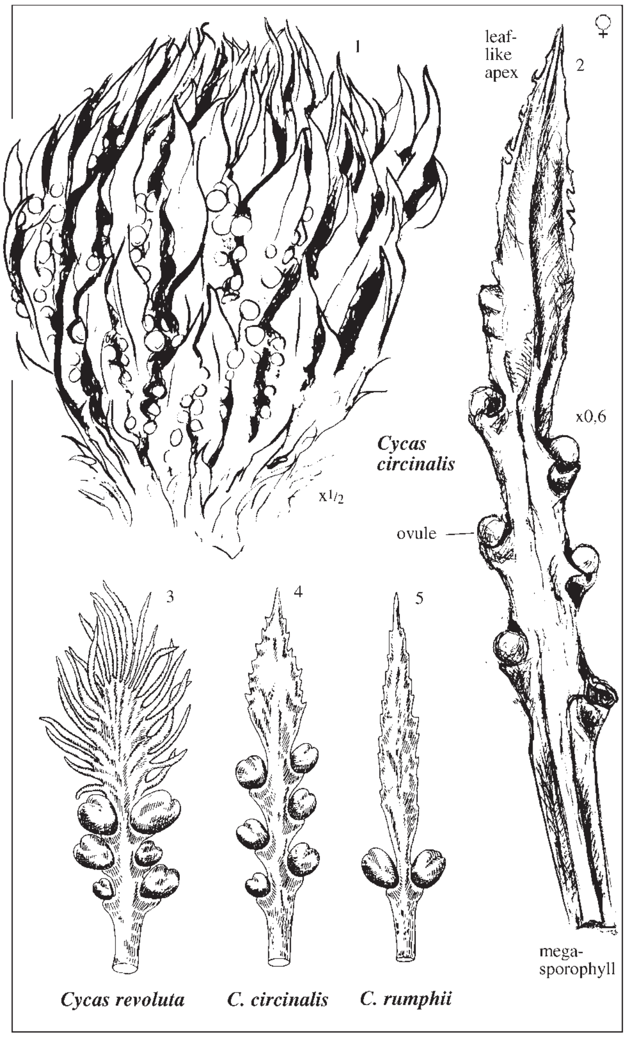
Range: P(ASS)–Rec.
First: *Crossozamia chinensis* (Zhu & Du) Gao & Thomas 1989, *C. minor* Gao & Thomas 1989, *C. spadicia* Gao & Thomas 1989, *C. cucullata* (Halle) Gao & Thomas 1989, *Tianbaolinia circinalis* Gao & Thomas 1989, *Yuania chinensis* Zhu & Du 1981 and *Taeniopteris taiyuanensis* Halle 1927, Taiyuan Fm. (ASS), Shanxi, China (Gao & Thomas 1989). The stratigraphically older fossils such as *Lesleya*, *Phasmatocycas*, *Archaeocycas* and *Sobernheimia*, previously assigned to the Cycadaceae, are here assigned to a separate family, the Phasmatocycadaceae (Phasmatocycadales) (Cleal 1993).
Last: Extant.

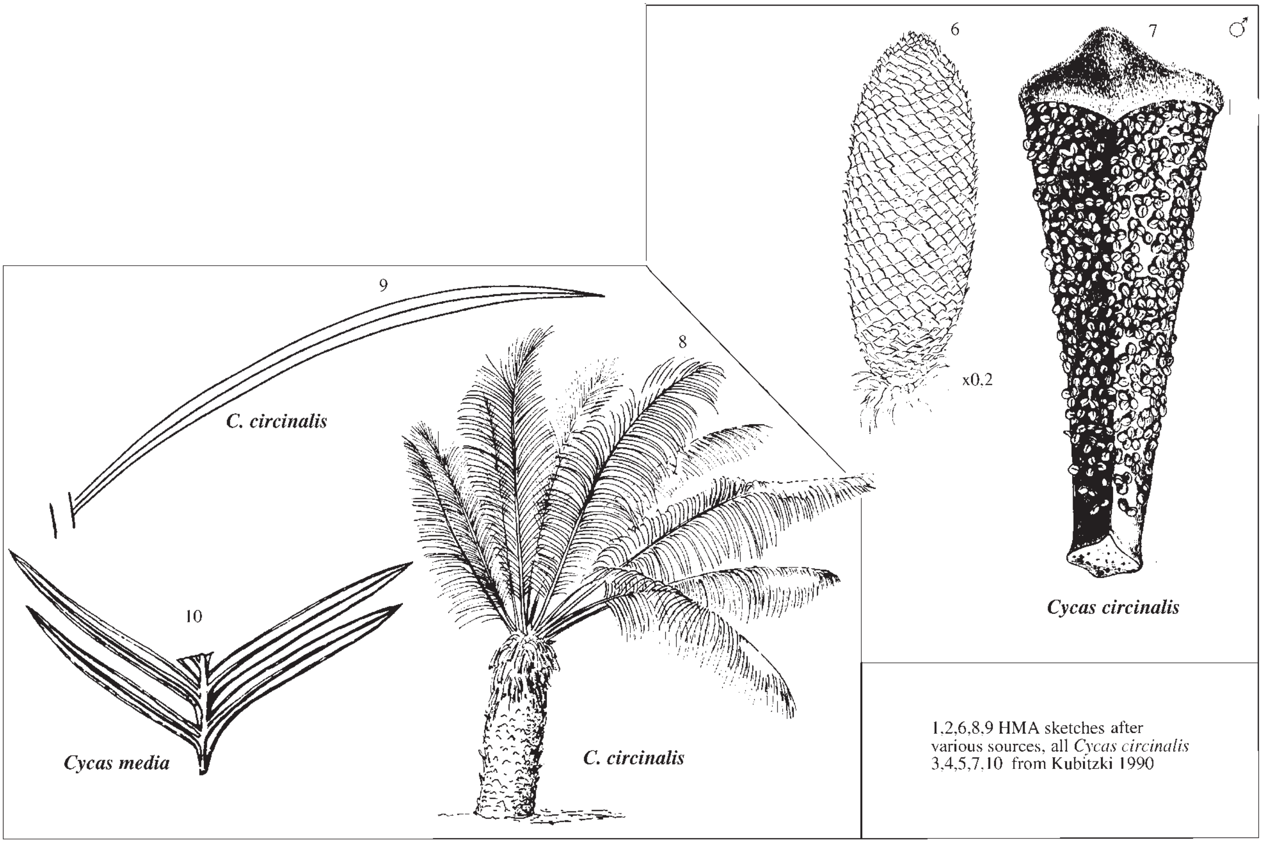
Prominence (colonisation success)—full family, extant
Frequency/Ubiquity: Tropical to warm-temperate, widespread through E Africa, W Madagascar, India, SE Asia, Malesia, N to NE Australia, and Polynesia.
Diversity: 1 genus (*Cycas*), 102 species.
Abundance: See Fig. 21 (p. 155) & accompanying text.
Longevity: See Fig. 22 (p. 156).

Ecology
Habit: Palm-like, usually with tall trunks.
Habitat: Widely variable; forest, woodland and savanna.

Remarks
Family distinctiveness: The unique female sporophylls and the leaflets with a single median vein readily distinguish this family.

References
Johnson & Wilson (in Kubitzki) (1990): Habit, habitat.
Stevenson (1992): Classification.
Cleal (1993): Range.
Jones (2002): General.





1,2,6,8,9 HMA sketches after various sources, all *Cycas circinalis*
3,4,5,7,10 from Kubitzki 1990

Family **STANGERIACEAE** (Pilg.) L.A.S.Johnson 1959

Diagnosis [Contributors: M. Mundry, I. Mundry & T. Stützel]: Cycadalean plants with radiospermic seeds borne in compact cones with a central axis; megasporophylls woody, peltate, bearing a single pair of lateral ovules.

Foliage: Leaflets either taenopteroid or with many parallel veins.

Range: J(BAJ)–Rec.
First: *Beania gracilis* Carruthers 1869, Gristhorpe Bed, Middle Deltaic, Yorkshire, UK. Harris (1964) gives a good description of these cones and associated leaves (*Nilssonia*) and pollen cones (*Androstrobus*). On the basis of the *Nilssonia* foliage which is taenopteroid like the modern *Stangeria* we place *Beania* in this family.

Last: Extant.

Prominence (colonisation success)—full family, extant
Frequency/Ubiquity: *Stangeria* (1 species), South Africa, eastern coastal; *Bowenia* (3 species), Australia, northeastern coastal.
Diversity: 2 genera, 4 species.
Abundance: See Fig. 21 (p. 155) and accompanying text.
Longevity: See Fig. 22 (p. 156).

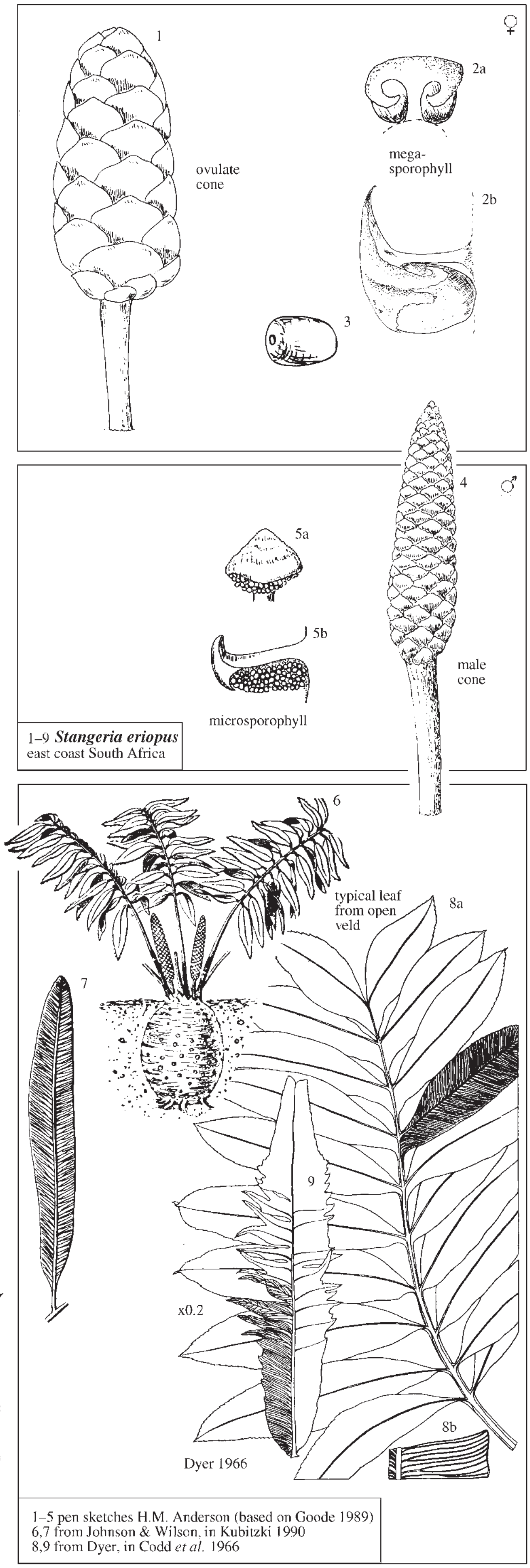
Ecology
Habit: *Stangeria*—perennial, fern-like, herb, with subterranean, tuberous (up to 10 cm diam.), branched or unbranched stems (Dyer 1966); *Bowenia*—palm-like foliage head, naked subterranean stem.

Habitat: *Stangeria*—eastern coastal grassland and forest; *Bowenia*—subtropical, near coast, open spaces in rainforest and eucalypt forest.

Remarks
Family affinities: The two genera are readily distinguished based on their unique leaves, each being unlike the typical pinnate leaves of the other two families. *Bowenia* has bipinnate leaves while *Stangeria* has pinnate leaves with taeniopteroid venation.

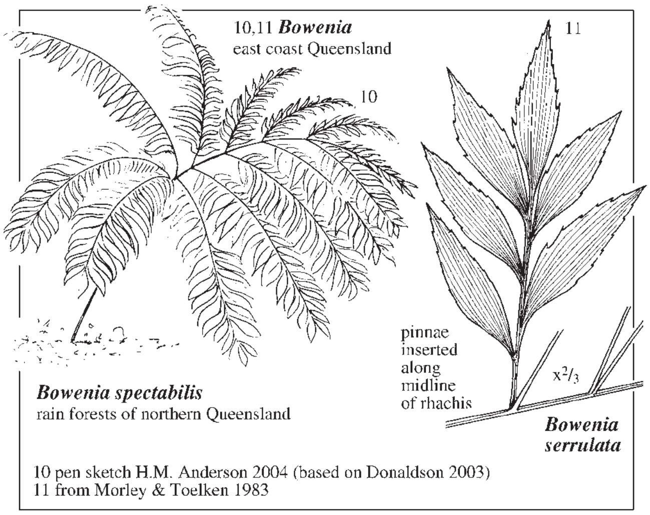
Cladistics: The classification followed here is based on the cladistic analysis of extant cycads undertaken by Stevenson (1990, 1992).

References
Johnson & Wilson (in Kubitzki) (1990): Habit, habitat.
Stevenson (1992): Classification.
Jones (2002): General.



1–9 ***Stangeria eriopus***
east coast South Africa

1–5 pen sketches H.M. Anderson (based on Goode 1989)
6,7 from Johnson & Wilson, in Kubitzki 1990
8,9 from Dyer, in Codd *et al.* 1966



10,11 ***Bowenia***
east coast Queensland

Bowenia spectabilis
rain forests of northern Queensland

Bowenia serrulata

10 pen sketch H.M. Anderson 2004 (based on Donaldson 2003)
11 from Morley & Toelken 1983

Family **ZAMIACEAE** Horan. 1834

Diagnosis [Contributors: M. Mundry, I. Mundry & T. Stützel]: Cycadalean plants with radiospermic seeds borne in compact cones with a central axis; megasporophylls woody, peltate, bearing a single pair of lateral ovules.

Male cones: Simple; sporangiophores peltate, with two lateral lobes each bearing several abaxial, di- to tetrasporangiate, shortly stalked synangia.

Foliage: Leaflets with many, generally parallel, veins.

Range: K(HAU)–Rec.
First: *Microzamia (Cycadeostrobus) ovatus* (Carruthers 1867) Kvacek 1997, Brook Point, Isle of Wight, England, Wealden. Better *Microzamia* cones are described by Kvacek (1997) from Trziblitz, Czech Republic, Cretaceous (TUR).

Last: Extant.

Prominence (colonisation success)—full family, extant
Frequency/Ubiquity: Tropical to warm-temperate; widespread through central and northern South America, central and southern Africa and Australia.
Diversity: 8 genera (*Lepidozamia, Macrozamia, Encephalartos, Dioon, Ceratozamia, Zamia, Chingua, Microcycas*), 191 species.
Abundance: See Fig. 21 (p. 155) and accompanying text.
Longevity: See Fig. 22 (p. 156).

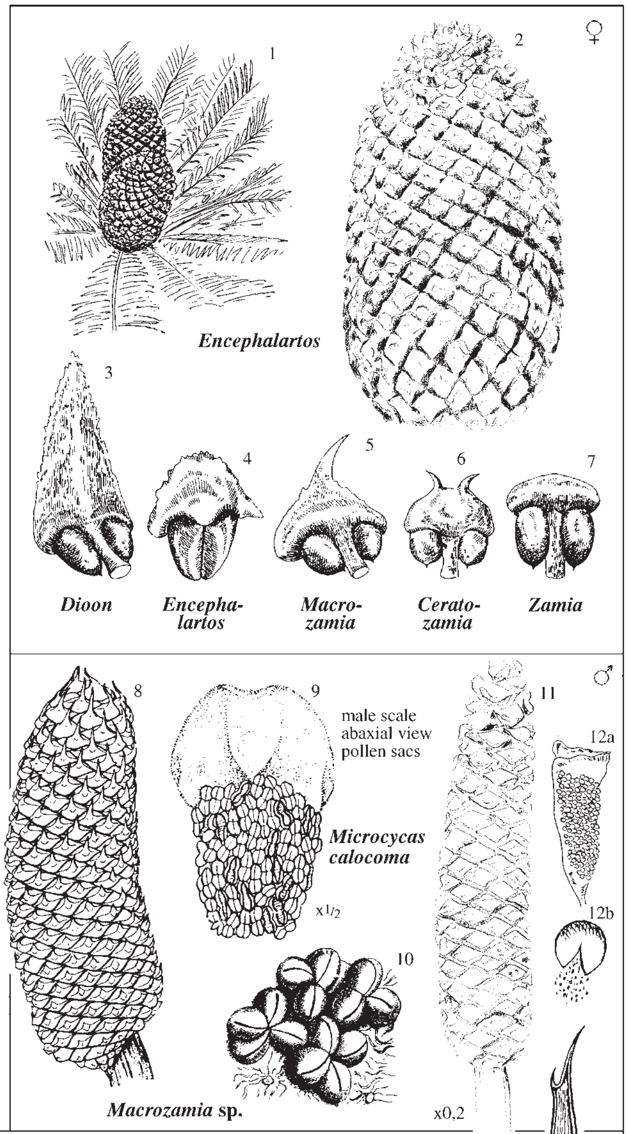
Ecology
Habit: Palm-like, stem subterranean to tall aerial.

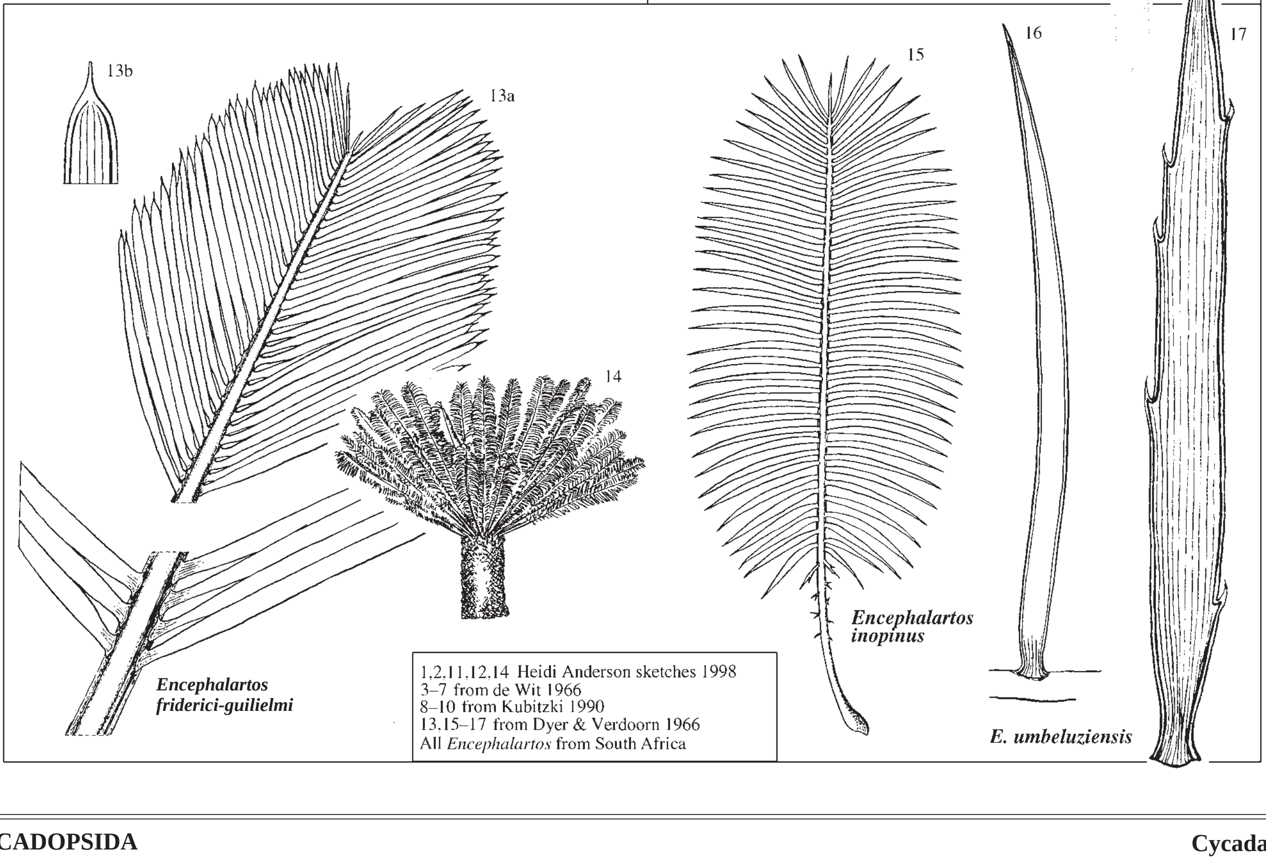
Habitat: Highly variable, from sea level to 3 500 m, from coastal sand dunes to rocky limestone cliffs, from open grassland to woodland to dense tropical rainforest, and to the arid ranges of central Australia.

Remarks
Family affinities: As currently understood, the family includes four tribes, two of which each include two subtribes (Stevenson 1992; Jones 2002)—the genera are readily distinguished and mostly have widely separated distributions.

Morphology [Contributors: M. Mundry, I. Mundry & T. Stützel]: In contrast to the female sporangiophores, the male sporangiophores are usually regarded to be nonpinnate. Morphogenetic studies in *Zamia amblyphyllidia* show their early developmental patterns to be quite similar to those of pinnate leaves (Mundry 2003). It is possible, therefore, to assume that the male sporangiophores, in accordance with the female sporangiophores, originate from a pinnate structure.

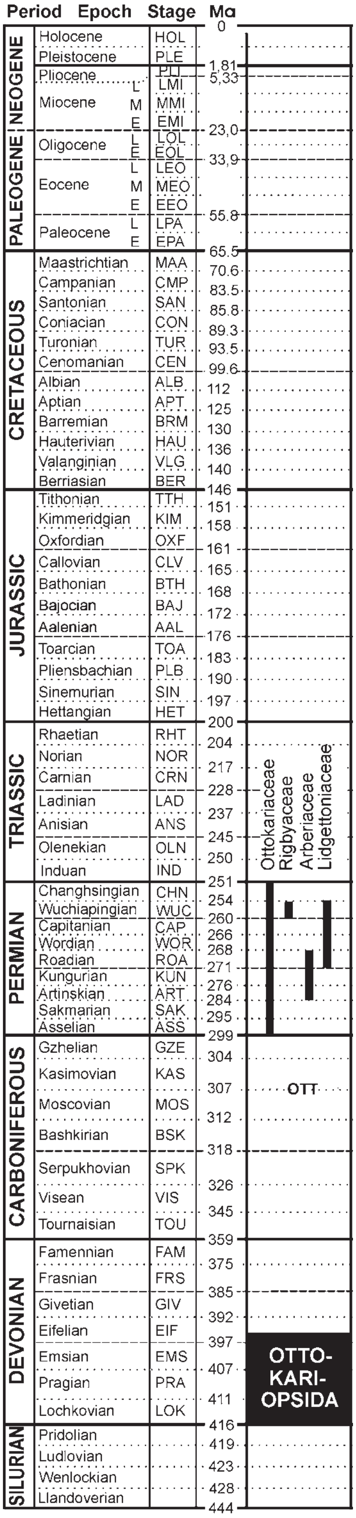
References
Johnson & Wilson (in Kubitzki) (1990): Habit, habitat.
Stevenson (1992): Classification.
Jones (2002): General.





1,2,11,12,14 Heidi Anderson sketches 1998
3–7 from de Wit 1966
8–10 from Kubitzki 1990
13,15–17 from Dyer & Verdoorn 1966
All *Encephalartos* from South Africa

Fig. 23. OTTOKARIOPSIDA: FAMILY RANGE CHART



Class **OTTOKARIOPSIDA** And. & And. nov.

Diagnosis: Gymnospermous plants with megasporophylls consisting of bract/scale complexes in which the fertile scales (megasporangia) are variously palmate multiovulate structures found attached to the midrib of sterile bracts ranging from unmodified glossopterid leaves to highly reduced glossopterid 'scale' leaves.

Classification & nomenclature

Cleal (1993) included all glossopterids in the single order Arberiales Meyen (1984) and family Arberiaceae Meyen (1984), and placed the group in an unnamed class along with several other orders of 'Mesozoic pteridosperms' (e.g. Peltaspermales and Leptostrobales). The glossopterids are of such morphological scope and apparent phylogenetic significance that they are here considered to warrant independent class status.

Meyen (1982, 1984) introduced the order Arberiales in preference to Glossopteridales to conform with his global approach—in reviewing fossil-gymnosperm systematics—towards basing classification and nomenclature on female fructifications. In the prodromus of South African megafloras And. & And. (1985) adopted Meyen's approach, but introduced the order Ottokariales to replace the Arberiales since the genus *Ottokaria* Zeiller (1902) has priority over *Arberia* White (1908) (hence, likewise the reasoning for the class Ottokariopsida).

Phylogeny (cladistic analyses)

In his recent cladistic review of seed plant phylogeny, Doyle (1996) stressed the apparent significance of the glossopterids: 'Trees with glossopterids at the base of the glossophytes suggest the possibility that Gnetales, *Caytonia*, angiosperms, Bennettitales, and *Pentoxylon* were derived from the radiation of glossopterids in the Permian of Gondwana'. This would embrace the noncladistic views, for instance, of Retallack & Dilcher (1981) that the angiosperms derived from the glossopterids, and of Schopf (1976) that the Gnetales were of similar stock. White (1986), in her *Greening of Gondwana*, entertained in a pictorial phylogenetic tree the possibility that virtually all lines of Mesozoic seed plants, including the angiosperms and even the cycads and southern conifers, could have evolved from one or other group of the glossopterids.

For a current synopsis of gymnosperm phylogeny including the glossopterids, see pp 18, 19.

Orders: Includes the single order Ottokariales.

Order **OTTOKARIALES** And. & And. 1985

Classification

In spite of the great apparent significance of the glossopterids in the phylogeny of the gymnosperms, there exists no thorough systematic overview of the ovulate fruit. We follow, here, the systematics of And. & And. (1985), in which a full taxonomic review of South African glossopterids was given, including a comprehensive summary and reassessment of all Gondwana glossopterid genera (63 in total) erected to that date. Four distinctive families were recognised. It should be noted that Steve McLoughlin (Brisbane, Australia) and Rose Adendorff (Grahamstown, South Africa) are working on a Gondwana-wide revision of the reproductive organs of this group (pers. comm.). They anticipate their taxonomic changes being more at the genus level than at the family and order levels.

Prominence & biodiversity

The glossopterids were the overwhelmingly dominant plant group, especially amongst the gymnosperms, throughout the Gondwana Permian. Numerous species of foliage and a great many of the affiliated fruit have been described.

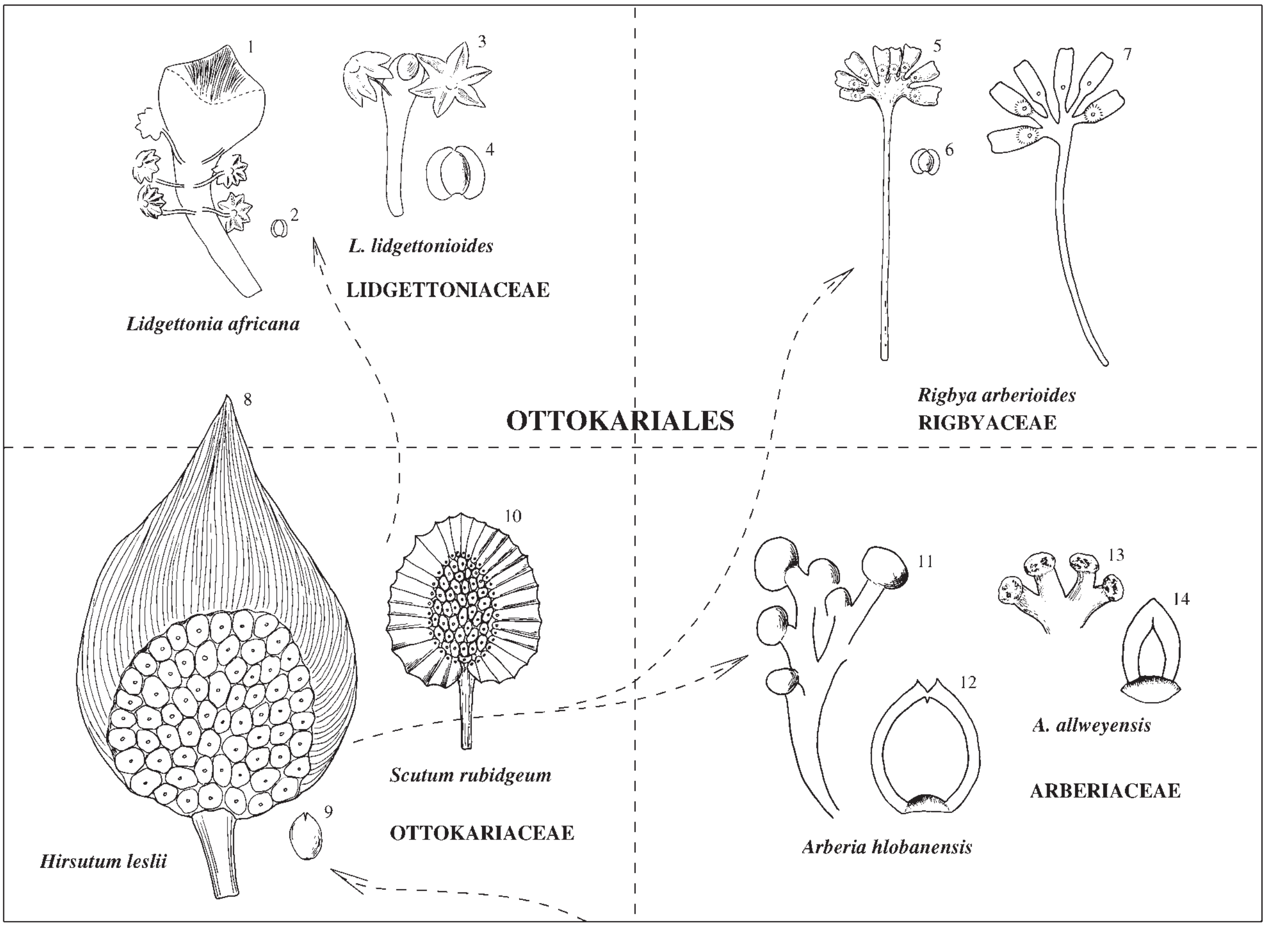
Ranges: Correlations of terrestrial Permian strata around Gondwana in relation to the international marine standards remain controversial. Dating of first and last appearances have been adopted from the general reviews in And. & And. (1970) and J.M. Anderson (1973, 1980). For the last three families in this order the ranges as documented are based exclusively on South African material as revised in And. & And. (1985). Fruit from all three families, though rare, occur widespread around Gondwana from roughly equivalent strata.

Families: Includes the four families Ottokariaceae, Rigbyaceae, Arberiaceae and Lidgettoniaceae.

CLASS ORDER **Family** — **Tab. 27. OTTOKARIOPSIDA**	**generic diversity**			**affiliation grade**			**morphology grade**			**anatomy preserved**		
	♀	♂	⬯	♀	♂	⬯	♀	♂	⬯	♀	♂	⬯
OTTOKARIOPSIDA And. & And. class nov.												
OTTOKARIALES And. & And. 1985												
Ottokariaceae And. & And. 1985	8	1	3	5	2	5	3	-	3	-	-	-
Rigbyaceae And. & And. 1985	1	1	1	5	4	4	3	2	3	-	-	-
Arberiaceae And. & And. 1985	1	-	1	5	-	3/4	2	-	3	-	-	-
Lidgettoniaceae And. & And. 1985	2	1	1	5	4	4	3	3	3	-	-	-

Fig. 24. OTTOKARIOPSIDA: SIMPLIFIED PHYLOGENY (OVULATE ORGANS)

- ovulate organs in approximate stratigraphic sequence
- broken lines loosely suggest phylogenetic ties (no cladistic analysis attempted)



Family **OTTOKARIACEAE** And. & And. 1985

Diagnosis: Ottokarialean plants with single, continuously winged, capitulate multiovuliferous megasporophylls (fertile scales) attached to the midrib of unmodified glossopterid leaves (sterile bracts).

Range: Gondwana, P(ASS–CHN)
First: Glossopterid foliage from the Dwyka Fm., Karoo Basin, South Africa and equivalent glacial deposits (e.g. Talchir Fm., India; Itararre Fm., Brazil) of the lowermost Permian (ASS) around Gondwana (And. & And. 1985).
Last: Glossopterid foliage from Bed 3, Sakamena Grp. Malagasy and equivalent deposits (e.g. Coal Cliff, Narabeen Grp, Sydney Basin) of the uppermost Permian (CHN) around Gondwana (And. & And. 1970). This foliage could represent one or more of the other glossopterid families but is placed here, the largest of the families, for convenience. The youngest ovulate fruit appear to be species of *Plumsteadia* Rigby 1962, *Estcourtia* And. & And. 1985, *Venustostrobus*, Chandra & Surange 1977, *Austroglossa* Holmes 1974 and *Senotheca* Banerjee 1969, from Late Permian strata (CAP–CHN) around Gondwana (And. & And. 1985).

Reference whole-plant genus & stratum—Middle Ecca (Vryheid Fm.)
Female: *Hirsutum* Plumstead 1958; 3 TCs, 3 spp, 125 indivs.
Male: Unknown.
Foliage: *Glossopteris* Brongniart 1828; 4 TCs, 3 spp, 25–50%.

Stratum: Middle Ecca (Vryheid Fm.), South Africa, P(ART).
Affiliation: *Hirsutum*(5)*Glossopteris*, Grade 5 (Org.att., Mut.occ.).

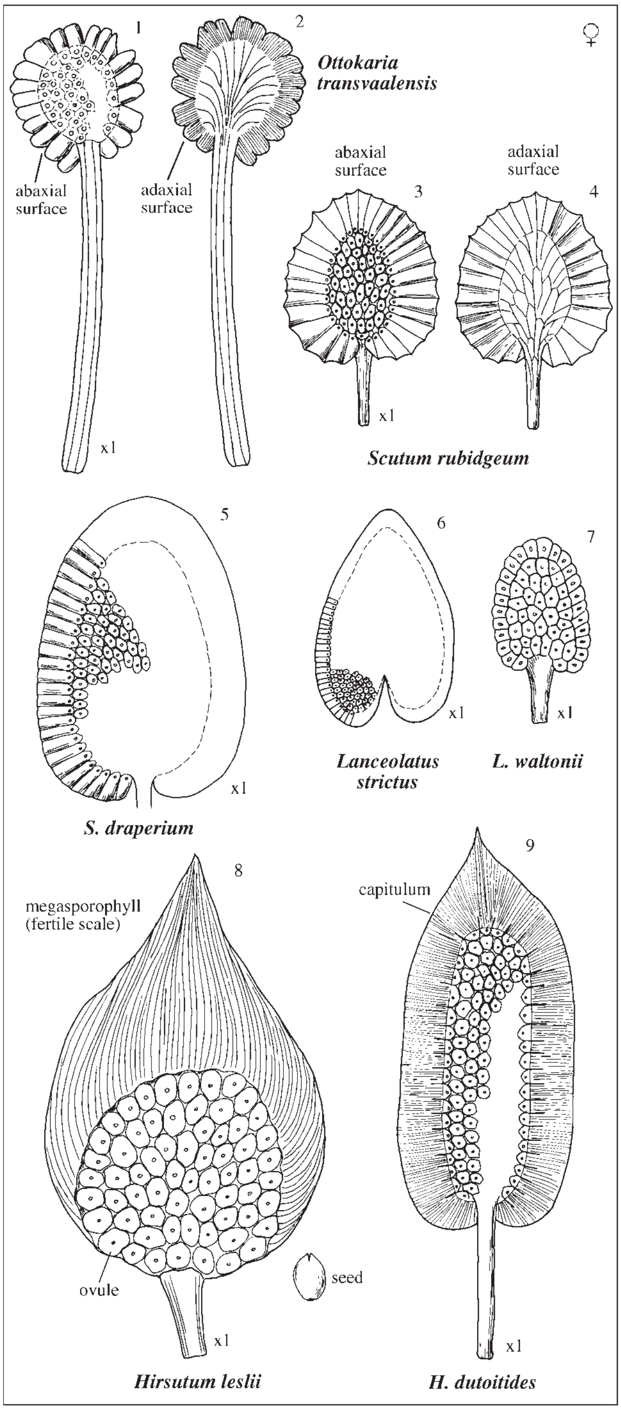
Prominence (colonisation success)—Gondwana Permian
Frequency/Ubiquity: The most frequently occurring family across all Gondwana continents through the Permian.
Diversity: Numerous species.
Abundance: Ovulate organs rare, polliniferous fruit enigmatically unknown or unsure, foliage dominant.
Longevity: *ca* 50 my (more or less throughout the Gondwana Perm.).

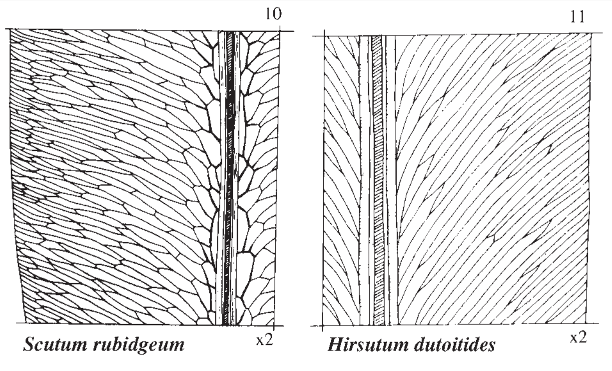
Ecology—Karoo Basin
Habit: Trees in mixed glossopterid forest and woodland.
Habitat: Deposits largely associated with deltaic coal swamps fringing the inland Karoo Sea.

Other genera
Female: *Ottokaria* Zeiller 1902, *Lanceolatus* Plumstead 1952, *Scutum* Plumstead 1952, *Plumsteadia* Rigby 1962, *Senotheca* Banerjee 1969, *Austroglossa* Holmes 1974, *Venustostrobus* Chandra & Surange 1977, *Estcourtia* And. & And. 1985.
Male: *Dictyopteridium* Feistmantel 1880.
Foliage: *Gangamopteris McCoy* 1875, *Palaeovittaria* Feistmantel 1876.

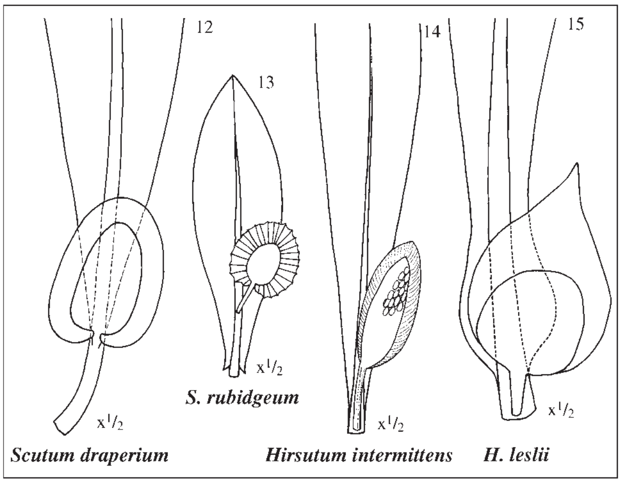
Remarks
Affinities: If we recognise *Ottokaria* as representing the primitive (plesiomorphic) form of the glossopterid 'polysperm' (Meyen 1987 term), the trends witnessed within the Ottokariaceae are either towards the fusing and elaboration of the capitulum wing (*Scutum, Hirsutum*), or the reduction and disappearance of the wing (*Plumsteadia, Lanceolatus*).

Reference
And. & And. (1985): General.





1–15 from And. & And. 1985
1–7,9–14 Vereeniging (**Ver 3**, Leeukuil Quarries), Vryheid Fm.
8,15 Hammanskraal (**Ham 111**), Vryheid Fm. equiv.
all Karoo Basin, South Africa, Perm.



Family **RIGBYACEAE** And. & And. 1985

Diagnosis: Ottokarialean plants with single deeply cleft, palmate, multi-ovuliferous megasporophylls (fertile scales) of unknown attachment.

Range: Gondwana, P(WUC)
First & Last: *Rigbya arberioides* Lacey *et al.* 1975, with affiliated polliniferous fruit and foliage, Estcourt Fm., Karoo Basin (And. & And. 1985).

Reference whole-plant genus & stratum—Estcourt Fm.
Female: *Rigbya* Lacey *et al.* 1975; 4 TCs, 1 sp., 40 indivs.
Male: Unnamed (see And. & And. 1985); 3 TCs, 1 sp., 77 indivs.
Foliage: *Belemnopteris* Feistmantel 1876; 9 TCs, 1 sp., 10–20%.

Stratum: Estcourt Fm., South Africa, P(WUC)
Affiliation: *Rigbya*(4)male(4)*Belemnopteris*(4), Grade 4 (Mut.occ., Kin.rein.).

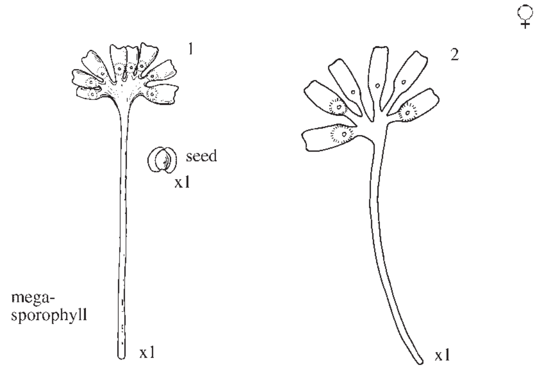
Prominence (colonisation success)—Gondwana Permian
Frequency/Ubiquity: Female, SAf, Ant, Aus; foliage SAf, Ind, Ant, Aus.
Diversity: 2 species (female) across Gondwana.
Abundance (Estcourt Fm.): Female in 4 of 25 TCs, relatively common in one of these; foliage in 9 of 25 TCs, often common, co-dominant in one TC.
Longevity: *ca* 5 my.

Ecology—Karoo Basin
Habit: Trees in mixed glossopterid woodland.
Habitat: Inland deltaic system fringing the extensive Karoo Basin floodplain.

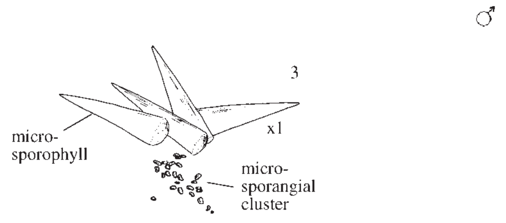
Other genera—nil.

Remarks
Affinities: The *Rigbya* 'polysperm' (Meyen 1987 term) can be readily derived from that of *Ottokaria* by reduction of the ovuliferous capitulum centre and development of the radial outer ring of winged ovules.

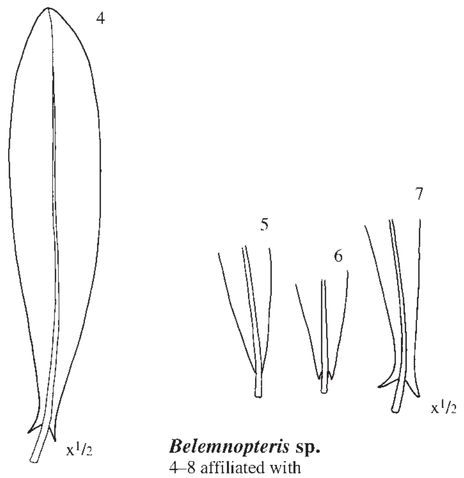
Reference
And. & And. (1985): General.



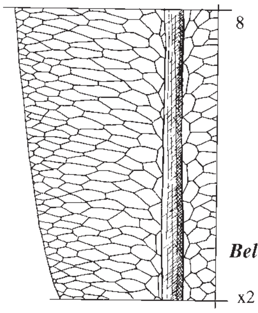
Rigbya arberioides



unnamed



***Belemnopteris* sp.**
4–8 affiliated with
R. arberioides at
Mooi River (**Moo 211**)



***Belemnopteris* sp.**

1–8 from And. & And. 1985

all Mooi River (**Moo 211**)
Estcourt Fm.,
Karoo Basin, South Africa, Perm.

Family **ARBERIACEAE** And. & And. 1985

Diagnosis: Ottokarialean plants with single bifurcate, pinnate, multiovuliferous megasporophylls (fertile scales) of unknown attachment.

Range: Gondwana, P(ART–ROA)
First: *Arberia hlobanensis* And. & And. 1985, *A. madagascariensis* (Appert 1977) And. & And. 1985 and *A. leeukuilensis* And. & And. 1985, with affiliated foliage, Middle Ecca, Karoo Basin, South Africa (And. & And. 1985).
Last: *Arberia cedaraensis* And. & And. 1985 and *A. allweyensis* And. & And. 1985, with affiliated foliage, Upper Ecca, Karoo Basin, South Africa (And. & And. 1985).

Reference whole-plant genus & stratum—Middle Ecca (Vryheid Fm.)
Female: *Arberia* White 1908; 4 TCs, 3 spp, 7 indivs.
Male: Unknown
Foliage: *Glossopteris* Brongniart 1828; 4 TCs, 3 spp, 20–40%

Stratum: Middle Ecca (Vryheid Fm.), South Africa, P(ART)
Affiliation: *Arberia*(3/4)*Glossopteris*, Grade 3/4 (Mut.occ).

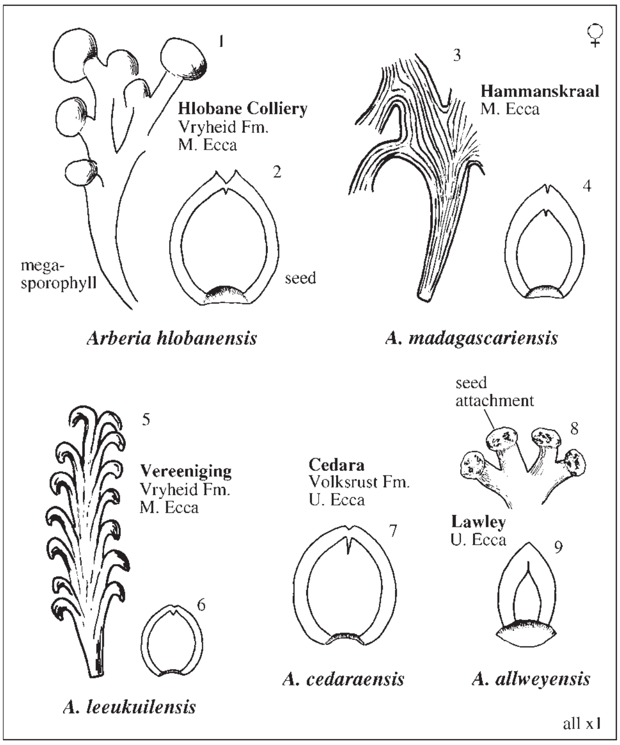
Prominence (colonisation success)—Gondwana Permian
Frequency/Ubiquity: Female, Early to Middle Perm., SAm, SAf, Mal, Ind, Aus; foliage, widespread Gondwana.
Diversity: 5 species (female) across Gondwana.
Abundance: Female extremely rare, seeds fairly common, leaf a dominant component in South Africa (M–U Ecca Gp.).
Longevity: *ca* 15 my.

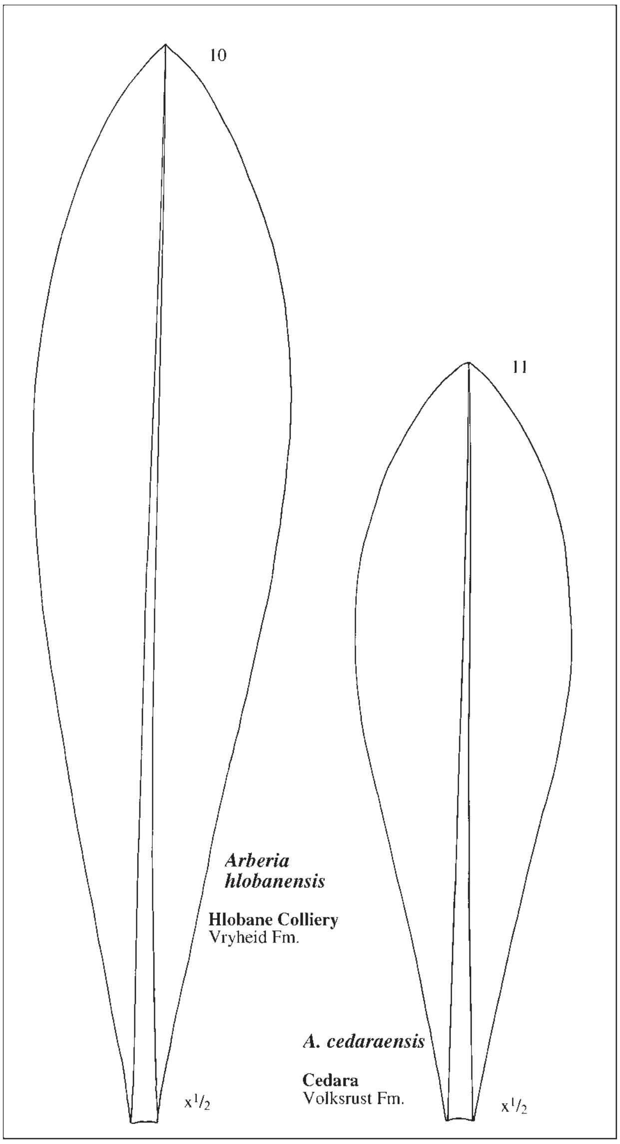
Ecology—Karoo Basin
Habit: Trees in mixed glossopterid forest and woodland.
Habitat: Deltaic coal swamps fringing the inland Karoo Sea.

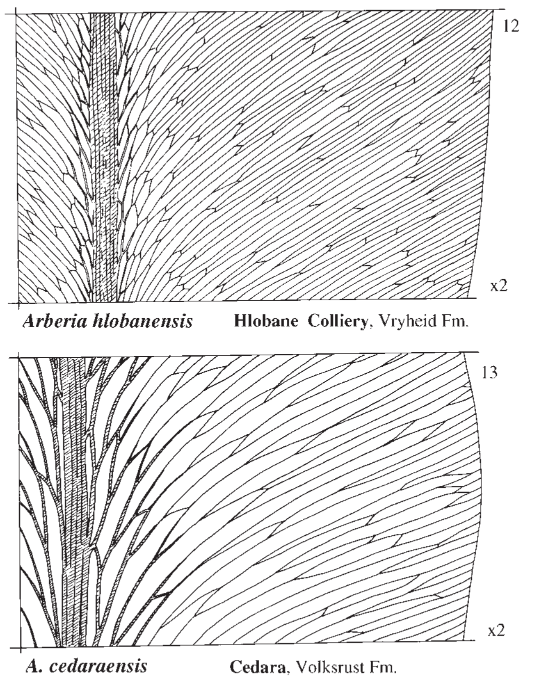
Other genera—nil.

Remarks
Affinities: The *Rigbya* 'polysperm' can be readily derived from that of *Ottokaria* by reduction of the ovuliferous capitulum centre and development of the radial outer ring of winged ovules.

Reference
And. & And. (1985): General.







1–13 from And. & And. 1985
all Karoo Basin, South Africa, Early–U. Ecca Grp., Early–M. Perm.

Family **LIDGETTONIACEAE** And. & And. 1985

Diagnosis: Ottokarialean plants with a bank of 1 to 4 pairs of lobed singly to multiovuliferous cupules (fertile scales) attached to the midline of glossopterid 'scale' leaves (sterile bracts).

Range: Gondwana, P(ROA–WUC)
First: *Lidgettonia lawleyensis* And. & And. 1985, with affiliated male fruit and foliage, Upper Ecca, Karoo Basin, South African (And. & And. 1985).
Last: *Lidgettonia africana* Thomas 1958, *L. mooiriverensis* And. & And. 1985, *L. inhluzanensis* And. & And. 1985, *L. lidgettonioides* (Lacey *et al.* 1975) And. & And. 1985 and *L. elegans* (Lacey *et al.* 1975) And. & And. 1985, with affiliated male fruit and foliage, Estcourt Fm., Karoo Basin, South Africa (And. & And. 1985).

Reference whole-plant genus & stratum—Estcourt Fm.
Female: *Lidgettonia* Thomas 1958; 11 TCs, 5 spp, 400 indivs.
Male: *Eretmonia* Du Toit 1932; 11 TCs, 4 spp, 130 indivs.
Foliage: *Glossopteris* Brongniart 1828; 23 TCs, 5 spp, 80–90%.

Stratum: Estcourt Fm., S. Africa, P(WUC).
Affiliation: *Lidgettonia*(4)*Eretmonia*(4)*Glossopteris*(4), Grade 4 (Mut.occ., Kin.rein., Mor.cor.).

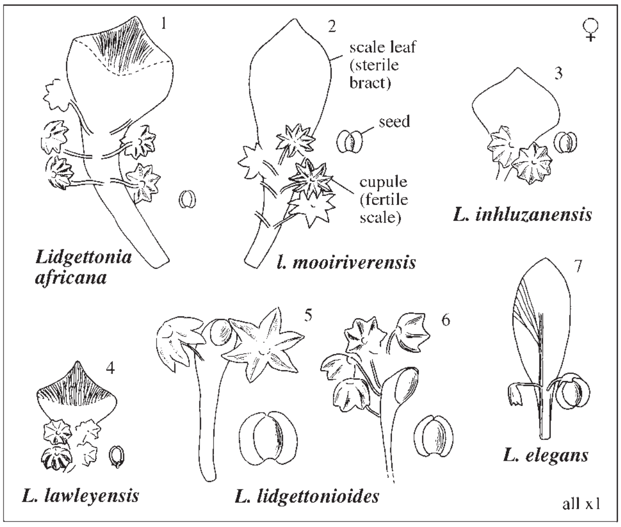
Prominence (colonisation success)—Gondwana Permian
Frequency/Ubiquity: Female, SAf, Ind, Aus; male (including dispersed microsporangia), SAf (and elsewhere in Africa south of Sahara), Ind, Ant, Aus; foliage widespread Gondwana.
Diversity: 9 species (based on ovulate organ) across Gondwana.
Abundance: *Lidgettonia* and affiliates are the most dominant (and diverse) taxon in the Estcourt Fm.
Longevity: *ca* 15–20 my.

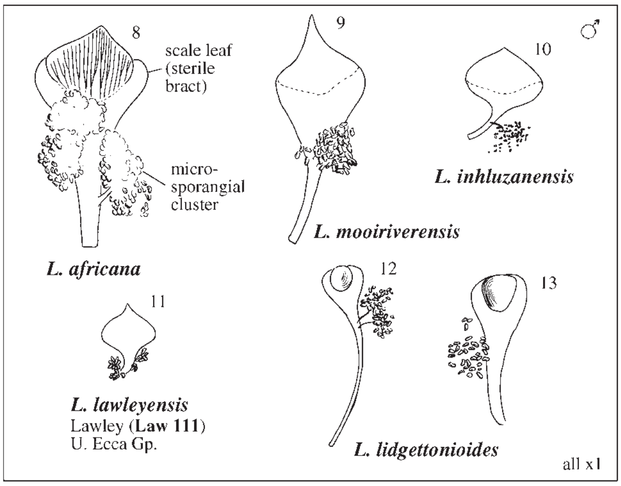
Ecology—Karoo Basin
Habit: Trees in mixed glossopterid woodland.
Habitat: Inland deltaic system fringing the extensive Karoo Basin floodplain.

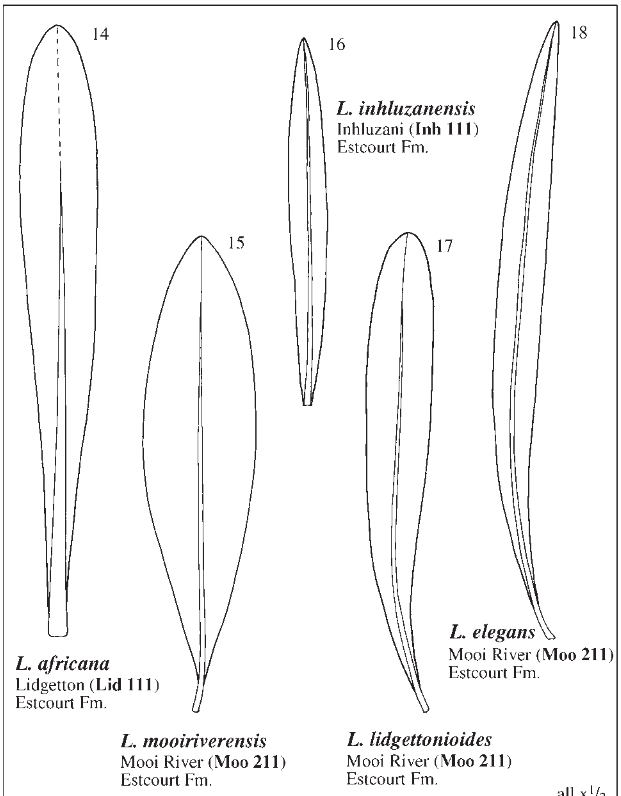
Other genera
Female: *Denkania* Surange & Chandra 1973.
Male (microsporangium): *Arberiella* Pant & Nautiyal 1960.

Remarks
Affinities: The *Lidgettonia* 'polysperm' is somewhat further removed from other glossopterid genera. *Rigbya arberioides* can, however, again be taken as a prototype: the truncate, elliptical ovuliferous scales in *Rigbya* become palmate to campanulate, lobed ovuliferous scales in *Lidgettonia*; the free stalk in *Rigbya* becomes adnately attached to the midline of the scale-leaf in *Lidgettonia*; the palmately lobed capitulum becomes a bank of 1 to 4 pairs of opposite to subopposite ovuliferous scales.

Reference
And. & And. (1985): General.







1–22 from And. & And. 1985
all Karoo Basin, South Africa, Perm.

Locality & Fm. for each species as indicated for 11, 14–18.

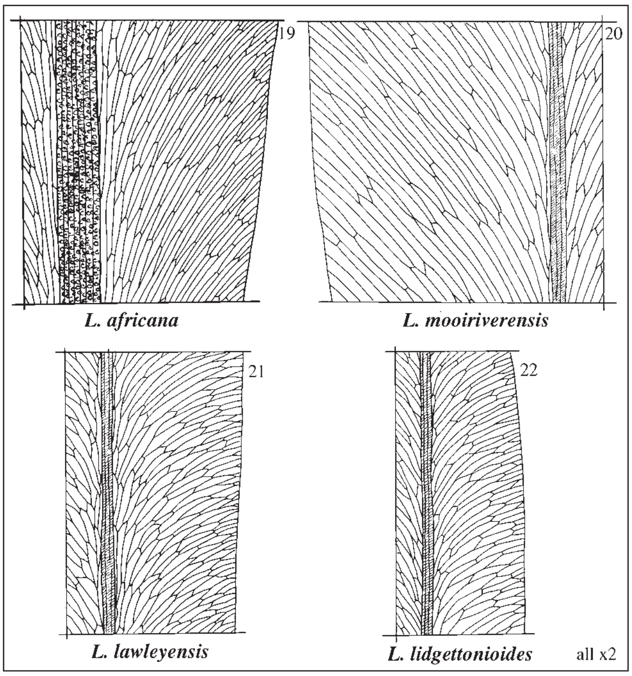
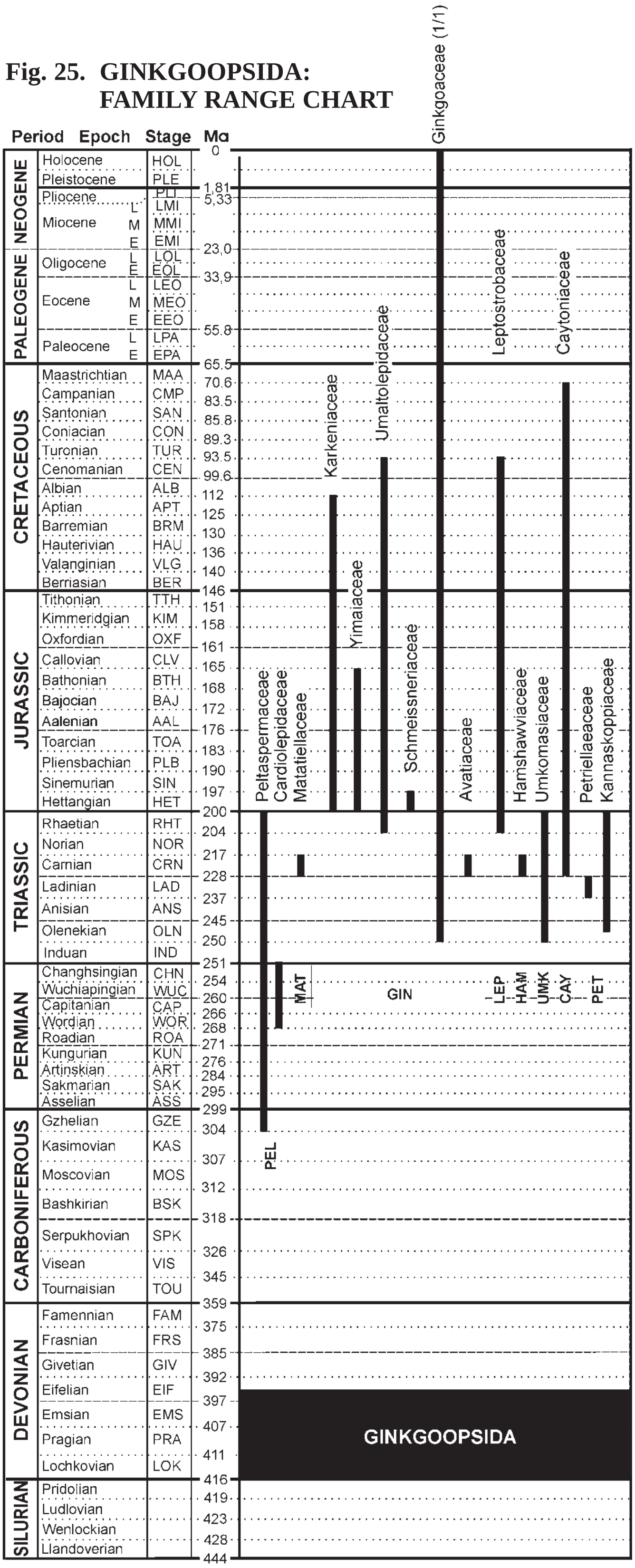


Fig. 25. GINKGOOPSIDA: FAMILY RANGE CHART



Class **GINKGOOPSIDA** Engl. 1897

Diagnosis: Gymnospermous plants with lax strobili, generally spicate, from radially to bilaterally symmetrical, less often reduced to a forked structure with a single pair of opposite cupules; seeds relatively few, mostly platyspermic.

Male: Strobili of comparable size to those of the ovulate structures, morphologically generally less derived; microsporophylls simple to compound, with microsporangia aggregated into synangia.

Foliage: Widely diverse, fern-like to *Ginkgo*-like; venation from simple parallel to strongly anastomosing; attachment (where known) clustered terminally or on short-shoots.

Remarks

Classification: Meyen (1987) grouped the Mesozoic pteridosperms, including the Ginkgoales, together with the glossopterids and referred to them as the Ginkgoopsida. Acknowledging the more traditional view that the ginkgos cluster rather with the conifers—supported by the earlier cladistic analyses of Crane (1985) and Doyle & Donoghue (1989)—Cleal (1993) followed Meyen (1987) but for this uncertainly placed group. Cleal classified the pteridosperm/glossopterid complex in an unnamed class.

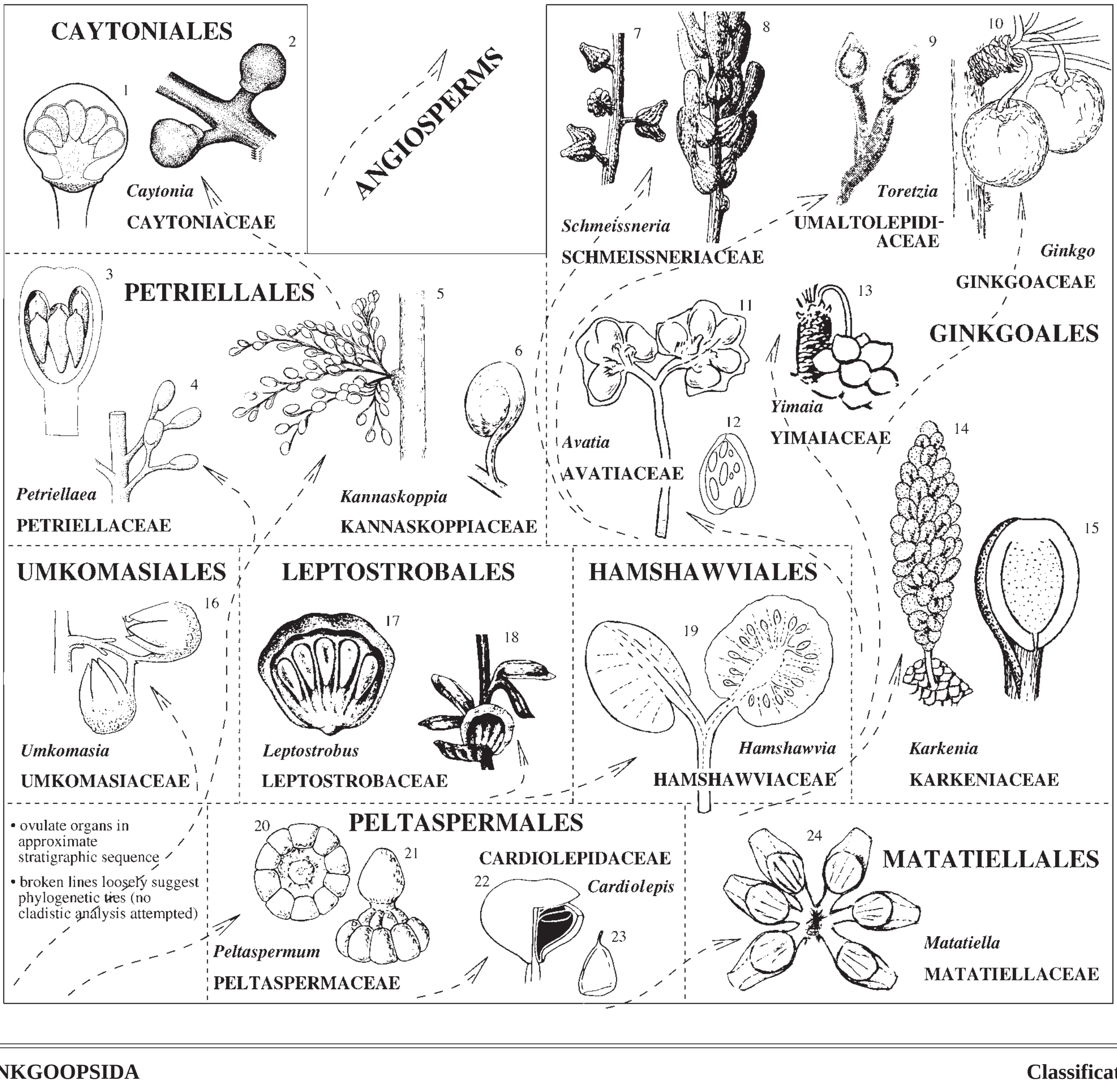
Our Ginkgoopsida is largely the unnamed class of Cleal (1993), but excludes the glossopterids (Ottokariopsida), re-includes the ginkgos (Ginkgoales) and adds the Matatiellales, Hamshawviales and Petriellales, based on Molteno and Gondwana Triassic taxa.

Phylogeny: For a current review of gymnosperm phylogeny including *Ginkgo* and several of the longer-known taxa included here under the Ginkgoopsida, see pp 18, 19. In marked conflict with our grouping of families and orders is, for instance, the cladogram adapted by Kenrick from Doyle (1998). This shows the 'Ginkgoales', 'Corystosperms' (our 'Umkomasiales'), 'Peltasperms', and '*Caytonia*' in widely different places on the gymnosperm tree.

Orders: Includes the eight orders Peltaspermales, Matatiellales, Ginkgoales, Leptostrobales, Hamshawviales, Umkomasiales, Caytoniales and Petriellales.

CLASS ORDER Family — **Tab. 28. GINKGOOPSIDA**	generic diversity ♀	♂	0	affiliation grade ♀	♂	0	morphology grade ♀	♂	0	anatomy preserved ♀	♂	0
GINKGOOPSIDA Engl. 1897												
PELTASPERMALES T.N.Taylor 1981												
Peltaspermaceae Thomas 1933	9	4	6	5	3	4	3	3	4	-	-	-
Cardiolepidaceae S.V.Meyen 1977	1	1	2	5	3	3	2	2	3	-	-	-
MATATIELLALES And. & And. 2003												
Matatiellaceae And. & And. 2003	1	-	1	5	-	2	3	-	2	-	-	-
GINKGOALES Goroschankin 1904												
Karkeniaceae Krassilov 1972	1	-	3	5	-	3	3	-	3	-	-	-
Yimaiaceae Z.Zhou 1997	1	-	2	5	-	4	3	-	3	-	-	-
Umaltolepidiaceae Stanisl. 1973 emend. Z.Zhou 1997	2	-	2	5	-	5	3	-	3	-	-	-
Schmeissneriaceae Z.Zhou 1997	1	1	1	5	5	5	3	3	3	-	-	-
Ginkgoaceae Engl. 1897 extant	**1**	**1**	**1**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**
Avatiaceae And. & And. 2003	1	1	1	5	3	2	3	3	3	-	-	-
LEPTOSTROBALES S.V.Meyen 1987												
Leptostrobaceae S.V.Meyen 1978	3	2	8	5	4	4	3	3	3	-	-	-
HAMSHAWVIALES And. & And. 2003												
Hamshawviaceae And. & And. 2003	1	1	1	5	5	4/5	3	3	3	-	-	-
UMKOMASIALES Doweld 2001												
Umkomasiaceae Petriella 1981	2	1	1	5	4	4	4	4	4	✓	✓	✓
CAYTONIALES Gothan 1932												
Caytoniaceae Kräusel 1926	1	1	1	5	4	4	4	4	4	✓	✓	✓
PETRIELLALES T.N.Taylor *et al.* 1994												
Petriellaceae T.N.Taylor *et al.* 1994	1	-	-	5	-	-	3	-	-	✓	-	-
Kannaskoppiaceae And. & And. 2003	1	1	2	5	5	5	3	3	3	-	-	-

Fig. 26. GINKGOOPSIDA: SIMPLIFIED PHYLOGENY (OVULATE ORGANS)

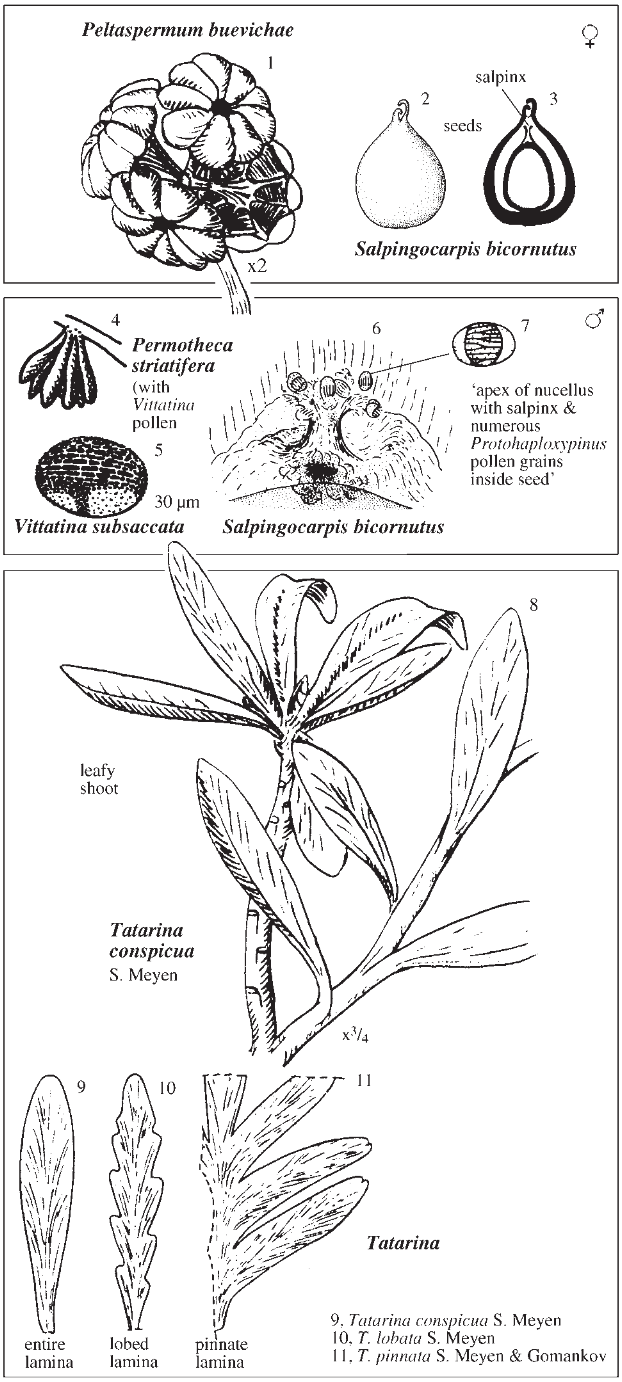


Order **PELTASPERMALES** T.N.Taylor 1981

Diagnosis: Ginkgoopsid plants with relatively compact spicate strobili bearing spirally arranged megasporophylls comprising 1 to 5 peltate, multiovuliferous cupules.

Remarks
Classification: With their peltate cupules, the Peltaspermales are clearly distinct from the other ginkgoopsids. The Matatiellaceae, with multiovulate heads borne in racemose strobili, appear most closely related.

Families: Includes the two families Peltaspermaceae and Cardiolepidaceae.



Family **PELTASPERMACEAE** Thomas 1933

Diagnosis: Peltaspermalean plants with open peltate cupules and well exposed seeds.

Range: C(GZE)–Tr(RHT)
First: *Autunia conferta* (Sternberg) Kerp and *Lodevia nicklesii* (Zeiller) Haubold & Kerp 1988, Faisceau de Beaubrun, St Étienne, France.
Last: *Peltaspermum ottonis* (Göppert) Poort & Kerp 1990, Mine Fm., Scania, Sweden.

Reference whole-plant genus & stratum—Molteno Fm.
Female: *Peltaspermum* T.M.Harris 1937; 17 TCs, 4 spp, 257 indivs.
Male: *Antevsia* T.M.Harris 1937; 5 TCs, 1 spp, 32 indivs.
Foliage: *Lepidopteris* Schimper 1869; 30 TCs, 2 spp, 1%.

Affiliations: *Peltaspermum*(4)*Lepidopteris*(3)*Antevsia*(3), Grades 3 & 4 (Kin.rein., Mut.occ., Mor.cor.).

Prominence (colonisation success)—Gondwana Triassic (GT)
Lepidopteris (foliage): Widespread in four Gondwana continents; South America, southern Africa, India and Australasia.

FUDAL rating: 19/4/5/1/21 = 50; *Lepidopteris* was the 8th most prominent gymnospermous foliage genus in the GT.
Frequency: High, 19 of 84 Gondw. degree squares.
Ubiquity: High, 4 of 5 Gondw. continents.
Diversity: Moderate, 5 species in GT.
Abundance: Rare, 1% norm in Molteno TCs.
Longevity: High, 21 my through Triassic.

Ecology—Molteno Fm.
Habit: Woody, much-branched, spreading shrub.
Habitat: Ubiquitous as an undershrub in *Dicroidium* riparian forest, less frequent (5 of 10 TCs) in closed woodland of the lake margin.

Other genera
Whole-plant 'natural' genera: *Autunia* Krasser 1919 emend. Kerp 1988, *Peltaspermopsis* Gomankov in Gomankov & Meyen 1986 emend. Poort & Kerp 1990, *Meyenopteris* Poort & Kerp 1990.
Ovulate organs: *Tinsleya* Mamay 1966, *Sandrewia* Mamay 1975, *Stiphorus* Meyen in Gomankov & Meyen 1986, *Lopadangium* Zhao in Zhao *et al*. emend. Gomankov & Meyen 1986, *Autuniopsis* Poort & Kerp 1990.
Foliage-(with associated peltoid discs of Peltaspermaceae type): *Compsopteris* Zalessky 1934, *Tatarina* Meyen 1969, *Vittaephyllum* Dobruskina 1975.

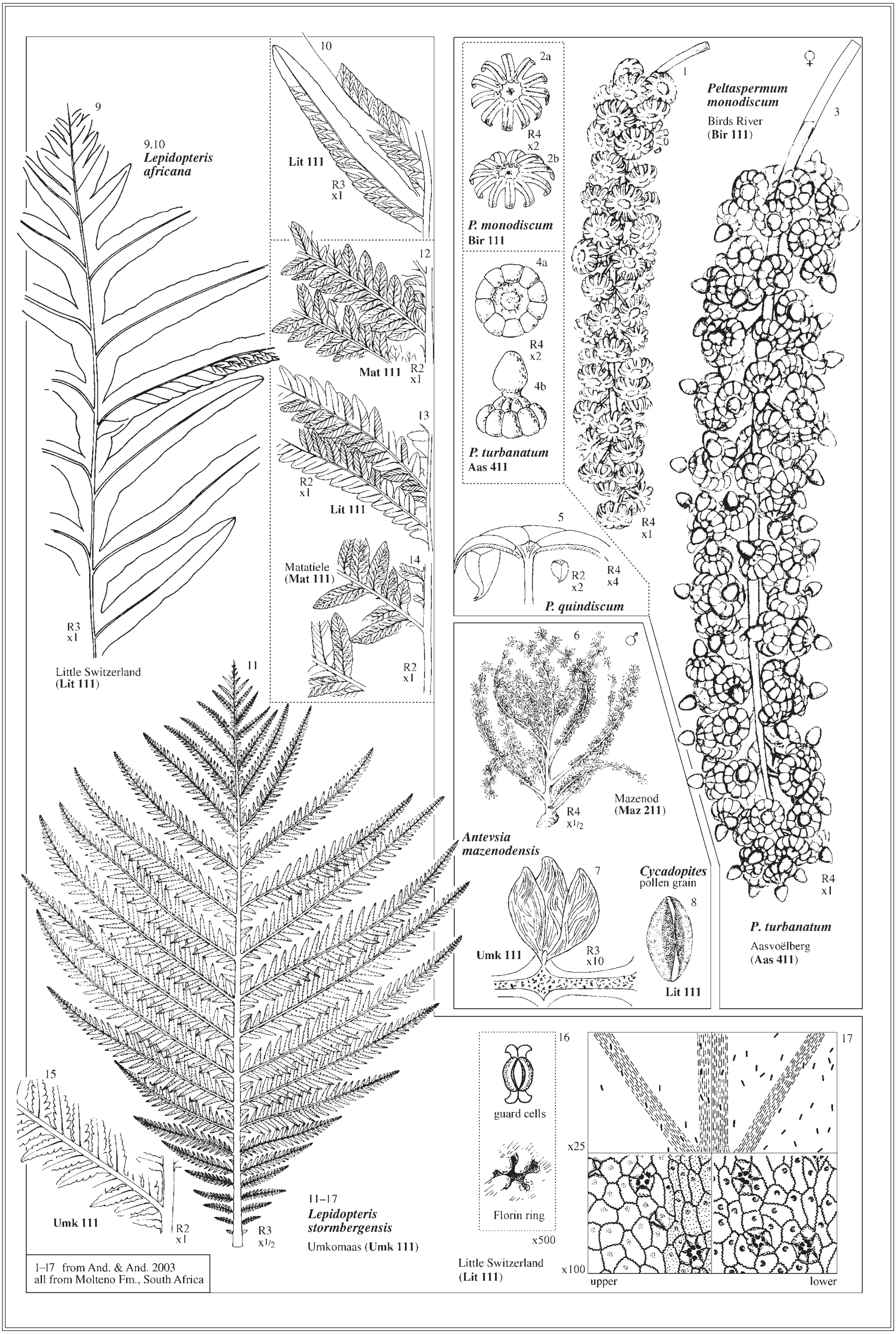
Remarks
Systematics: The treatment of this family is that of Cleal (1993), who followed the interpretation of Kerp & Haubold (1988).

Prominence: Though the foliage genus *Lepidopteris* is Pangaean and not confined to the Triassic, the data recorded under 'Prominence' above are only those for the Gondwana Triassic for which a clear synthesis is available (And. & And. 1989, 2003).

References
And. & And. (1989): Foliage.
And. & And. (2003): Female, male, foliage.

1,8–11 H.M. Anderson sketches after Meyen 1982, 1988, Gomankov & Meyen 1986
2–6 from Meyen 1988 (partly from Gomankov & Meyen 1986)
7 from Meyen 1987

1–11 assembly of '*Tatarina* and allied plants' from the *Tatarina* flora (western Angara, former USSR, 'uppermost Permian')
1,5,8 from **Aristovo** locality (N. of Eur USSR), Malaya Severnaya Dvina R., Vyatski horizon, Upper Tatarian substage



1–17 from And. & And. 2003
all from Molteno Fm., South Africa

Family **CARDIOLEPIDACEAE** S.V.Meyen 1977

Diagnosis: Peltaspermalean plants with closed peltate cupules and virtually encapsulated seeds.

Range: P(WOR–WUC)
First: ?*Phylladoderma chalyshevii* Fefilova & Smoller ex Meyen 1983, Lekvorkutsk 'Suite', Pechora Coalfield, former USSR. This record is of foliage fragments with cuticles preserved. Better documented are the fructifications *Nucicarpus piniformis* Neuburg 1965, and *Cardiolepis piniformis* Neuburg 1965, Scidinsk 'Suite' (WOR), Pechora Coalfield, former USSR (Meyen 1983, 1988).
Last: *Phylladoderma tatarica* Meyen 1986, and *Doliostomia krassilovii* Meyen 1986, Titov, Russian Platform, former USSR (Gomankov & Meyen 1986). (These data on '*First*' and '*Last*' are taken verbatim from Cleal 1993.)

Reference whole-plant genus & stratum—Scidinsk 'Suite'
Female: *Cardiolepis* Neuburg 1965 (ovulate capsules); with *Nucicarpus* Neuburg 1965 (ovules); 1 TC, 1 sp., rare.
Male: (The ovules have saccate pollen similar to that found in the pollen organs *Permotheca* Zalessky 1909 and which is usually linked with *Cardiolepis* (e.g. Meyen 1982a, 1987), but such pollen-organs have yet to be reported from the reference stratum for this family.)
Foliage: *Phylladoderma* Zalessky 1913; many TCs (total number not recorded), 2 spp, abundant (no absolute data available).

Stratum: Scidinsk 'Suite', Pechora Basin, Fore-Urals, Russian Federation (WOR).
Affiliations: Grade 3 (Mut.occ.).

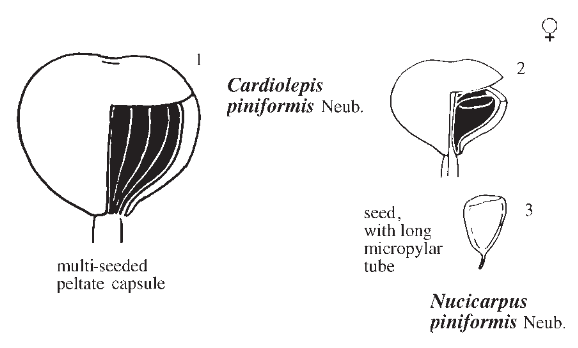
Prominence (colonisation success)—Subangara Middle–Late Permian
Frequency/Ubiquity: Known only from the northern-temperate Pechora Basin of Subangara.
Diversity: 4 spp (based on foliage).
Abundance: Foliage is reasonably abundant, especially as evidenced by dispersed cuticles (Meyen 1983), but no absolute data available.
Longevity: *ca* 15 my.

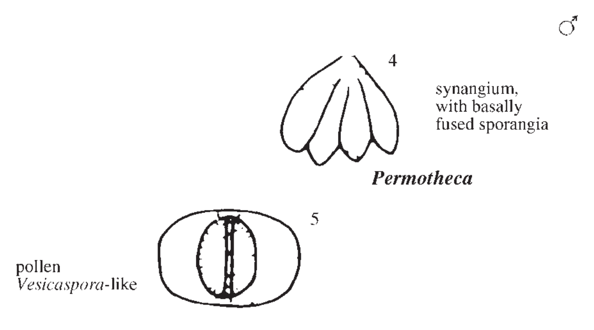
Ecology
Habit: Unknown.
Habitat: Unknown.

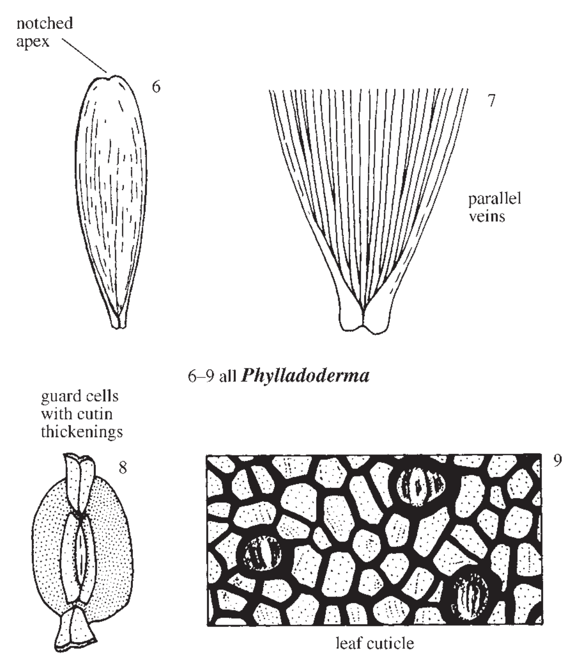
Other genera
Foliage: *Doliostomia* Meyen in Gomankov & Meyen 1986.

Remarks
Classification: The treatment essentially follows Meyen (1982a, 1984, 1987). Subsequent work was being undertaken by Meyen and H.G. Smoller, but has never been published (see comments in Meyen 1982a, p. 40).

References
Meyen (1983, 1984, 1988), Gomankov & Meyen (1986): General.
Cleal (1993): First & last.







1–9 all from Meyen 1987 (6 redrawn by H.M. Anderson)
all Angara flora, Pechora Province, former USSR, U. Permian

Order **MATATIELLALES** And. & And. 2003

Diagnosis: Ginkgoopsid plants with relatively compact spicate strobili bearing spirally arranged megasporophylls with single palmate, multiovuliferous cupules.

Families: Includes the single family Matatiellaceae.

Family **MATATIELLACEAE** And. & And. 2003

Diagnosis: As for the order Matatiellales

Range: Gondwana, Tr(CRN)
First & Last: *Matatiella rosetta* And. &. And. 2003 and three other species (see adjacent), Molteno Fm., South Africa. Since the affiliation with *Kurtziana* is insufficiently established and since the circumscription of the foliage genus remains uncertain, the range of this family is based solely on the ovulate fruit.

Reference whole-plant genus & stratum—Molteno Fm.
Female: *Matatiella* And. & And. 2003; 4 TCs, 4 spp, 17 indivs.
Male: Unknown.
Foliage: *Kurtziana* Frenguelli 1942; 13 TCs, 16 spp, <1%.

Stratum: Molteno Fm., Karoo Basin, South Africa, Tr (CRN).
Affiliations: *Matatiella*(2)*Kurtziana*, Grade 2 (Mut.occ.).

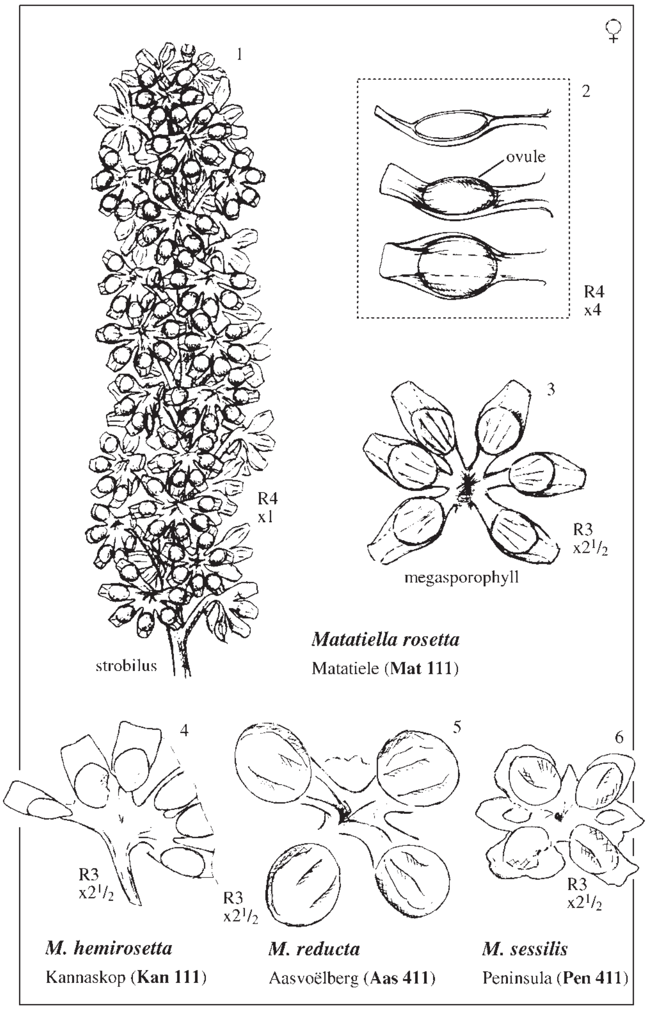
Prominence (colonisation success)—Gondwana Triassic (GT)
Kurtziana (foliage): Recorded from Argentina and South Africa.
FUDAL rating: 6/2/20/–/2 = 30; the 12th most prominent gymnospermous foliage genus in the GT.
Frequency: Low, 6 of 84 Gondw. degree squares.
Ubiquity: Low, 2 of 5 Gondw. continents.
Diversity: V. high, 20 species in GT.
Abundance: V. rare, <1% norm in Molteno TCs.
Longevity: V. low, 2 my through Triassic.

Ecology—Molteno Fm.
Habit: Possibly a small spreading tree.
Habitat: On the periphery of *Heidiphyllum* thicket.

Other genera—nil.

Remarks
Affiliation: Though the affiliation of ovulate strobilus and foliage is no better than Grade 2, we record for 'prominence' above the statistical data for the foliage genus *Kurtziana*.

Reference
And. & And. (2003): Female, male, foliage.

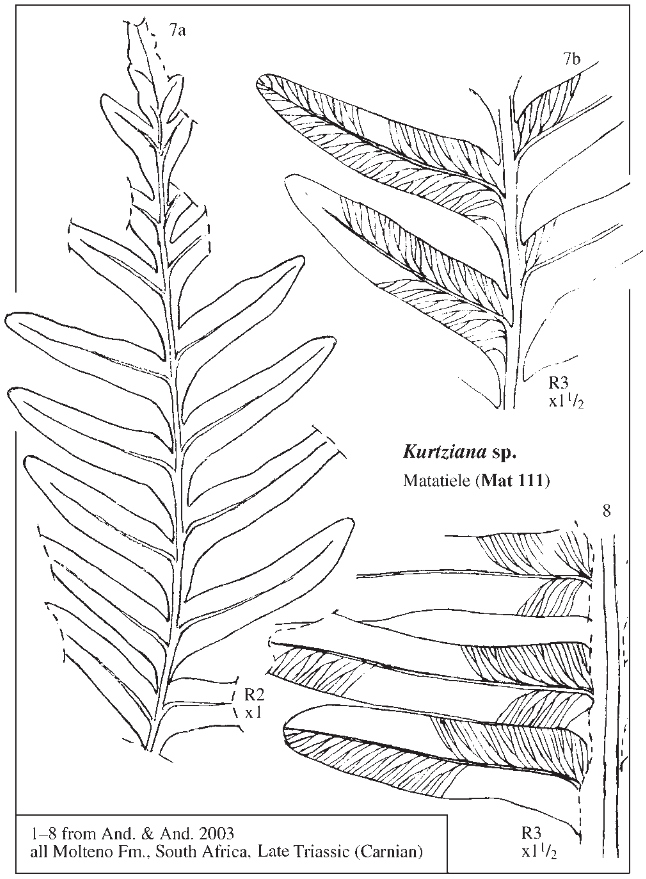


Matatiella rosetta
Matatiele (**Mat 111**)

M. hemirosetta
Kannaskop (**Kan 111**)

M. reducta
Aasvoëlberg (**Aas 411**)

M. sessilis
Peninsula (**Pen 411**)



***Kurtziana* sp.**
Matatiele (**Mat 111**)

1–8 from And. & And. 2003
all Molteno Fm., South Africa, Late Triassic (Carnian)

Order **GINKGOALES** Gorozh. 1904

Diagnosis: Ginkgoopsid plants with short-shoots bearing fascicles of leaves and reproductive organs; ovulate strobili lax to compact spicate with many megasporophylls to reduced paired or single ovulate heads; megasporophylls mostly uniovulate, rarely to pentaovulate.

Foliage: Fan-shaped, multiply bifidly lobed to linear; venation parallel, dichotomising repeatedly throughout to rarely only near base, never anastomosing.

Phylogeny (historical, pre-1998)
Molecular data (rRNA): The relatively recent ribosomal RNA analyses of Hamby & Zimmer (1992) show the extant conifers and cycads together to form a monophyletic group, and that they are more closely related to one another than either is to *Ginkgo*.

Morphological data: The phylogenetic placement of the ginkgos emerges as quite uncertain. Early morphologically based cladistic analyses (Crane 1985; Donoghue & Doyle 1989) placed *Ginkgo* and the conifers in a monophyletic group that excluded the cycads—in conflict with the rRNA work of Hamby & Zimmer (1992). Analyses of more recent complete (extant plus fossil) data sets (Doyle & Donoghue 1992; Doyle *et al.* 1994) suggested that the ginkgos may be more closely associated with the Permian-Triassic seed-fern *Peltaspermum* than with the conifers (cf. Meyen 1984).

Phylogeny (current) [Contributors: M. Mundry, I. Mundry & T. Stützel]
The phylogenetic position of the Ginkgoales is quite uncertain. In morphological analyses they are often placed sistered to the coniferophytes (Doyle & Donoghue 1996), but in molecular analyses the results are equivocal. Although mainly focussed on the systematic position of Gnetales, the position of *Ginkgo biloba* in molecular studies varies between a close relationship to conifers or to cycads (Hasebe *et al*. 1992; Bowe *et al*. 2000; Chaw *et al*. 2000; Frohlich & Parker 2000; Rydin *et al*. 2002; Schmidt & Schneider-Poetsch 2002). See also pp 18, 19.

Morphology
See notes for *Ginkgo* (Ginkgoaceae), p. 178.

Families: Includes the six families Karkeniaceae, Yimaiaceae, Umaltolepidiaceae, Schmeissneriaceae, Avatiaceae and Ginkgoaceae.

Tab. 29. Extinct & extant Ginkgoales: classification adapted and elaborated from Zhou 1997

ORDER
Family
genus

GINKGOALES
Karkeniaceae Krassilov 1972
Karkenia Archangelsky 1965; Tico Flora, Argentina, K(APT)
(leaves: *Ginkgoites*, *Sphenobaiera*, and *Eretmophyllum* types)
Yimaiaceae Zhou 1997
Yimaia Zhou & Zhang 1992 (Yima Fm., China, J(AAL).
(leaves: mainly of *Baiera* type)
Umaltolepidiaceae Zhou 1997
Umaltolepis Krassilov (1970) 1972; (Late Jur.–Early Cret., Siberia)
(leaves: *Pseudotorellia* type)
Toretzia Stanislavsky (1971) 1973; Novoraisk Fm., Ukraine, Tr(RHT)
Schmeissneriaceae Zhou 1997
Schmeissneria Kirchner & Van Konijnenburg-Van Cittert 1994; Lias α, Bavaria, J(HET)
(pollen organ: believed to be of the *Stachyopitys* type)
Avatiaceae And. & And. 2003
Avatia And. & And. 2003 (Molteno Fm., South Africa, Tr(CRN).
(pollen organ: *Eosteria*, Grade 2–3 affiliation)
(leaves: *Ginkgoites*, Grade 2 affiliation)
Ginkgoaceae Engler 1897
Ginkgo L. 1771
Grenana Samylina 1990 (Jur., Middle Asia)
(leaves: *Sphenobaiera* or *Baiera* types)

The classification by Zhou (1997), on which our treatment is based, follows a full systematic review and phylogenetic analysis of Mesozoic ovulate, microsporangiate and foliage genera considered to be ginkgoalean (*Trichopitys* from the Permian is used as his outgroup). The framework like our own, is structured exclusively around the ovulate genera. All of his families, aside from the Schmeissneriaceae, are adopted by Doweld (2001) (see Tab. 10, pp 16, 17) and mostly raised to order level.

Our classification differs from Zhou (1997) only slightly, in excluding the Trichopityaceae, here placed in the Pinopsida (p. 115), and including the Avatiaceae (p. 179).

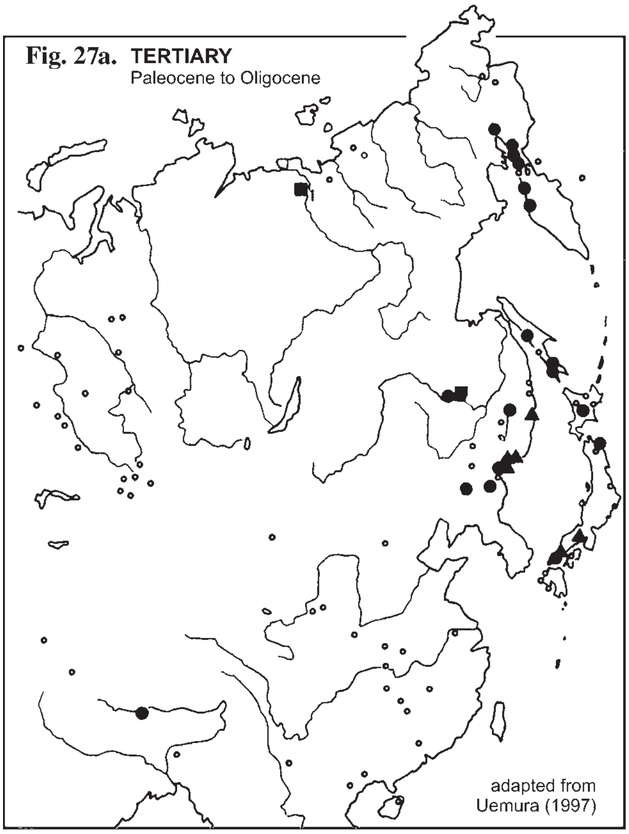


Fig. 27a. TERTIARY
Paleocene to Oligocene

adapted from Uemura (1997)

Paleogene occurrence of *Ginkgo* in eastern Eurasia

- ○ plant megafossil localities without *Ginkgo* remains
- ▲ Oligocene (33,7–23,5 Ma)......................6 localities
- ● Eocene (53–33,7 Ma).............................18 localities
- ■ Paleocene (65–53 Ma)............................2 localities

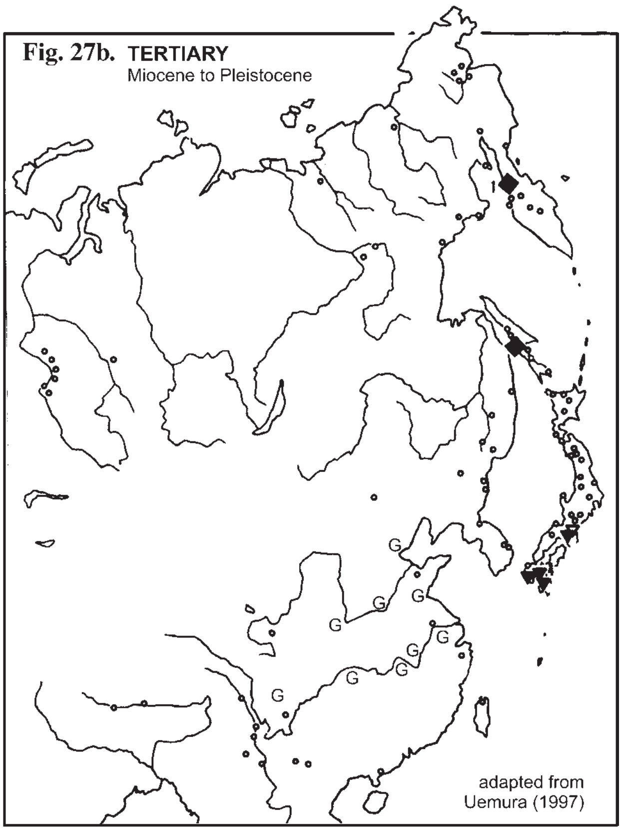


Fig. 27b. TERTIARY
Miocene to Pleistocene

adapted from Uemura (1997)

Neogene & Quaternary occurrence of *Ginkgo* in eastern Eurasia

- ○ plant megafossil localities without *Ginkgo* remains
- ▽ Pleistocene (1,75 Ma).......................1 locality
- ▼ Pliocene (5,3–1,75 Ma).....................4 localities
- ◆ Miocene (23,5–5,3 Ma).....................2 localities
- G Extant tree >1 000 years old

Post-Cretaceous retreat of *Ginkgo*

Tertiary floras in eastern Asia are numerous both stratigraphically and geographically (Figs 27a, 27b above), so it is possible to gain an impression of the drift towards relict status of the genus *Ginkgo*.

Tertiary to Quaternary occurrence (*Ginkgo* foliage)

According to Uemura (1997), as plotted in the maps above, fossil records of the genus *Ginkgo* (the records are exclusively of leaf remains) occur throughout the Tertiary to Recent—though most frequently (18 localities) during the Eocene and least frequently (one locality) in the Quaternary.

Dispersed pollen grains: It is significant to note that while dispersed pollen is of great value in tracing the history of many plant groups, it fails in the case of *Ginkgo* due to difficulty in distinguishing it from certain cycadophytes (Uemura 1997).

Extant wild occurrence (He *et al.* 1997)

It remains quite uncertain whether there still exist any true 'wild' specimens of *Ginkgo*. There appears no sure way of establishing whether apparently naturally occurring individuals are cultivated, escaped (with seeds spread by animals), or indeed original (wild). Even the 'most' probable wild population located in the West Tienmushan mountains may, in view of the lack of genetic variation in 40 sampled trees, be the 'progeny of plants cultivated at nearby temples by monks'. When the long history of *Ginkgo* cultivation is considered—and the literature on the subject is extensive—the problem becomes clearly evident.

Many very old ginkgos occur in China, with 100 or so known to be older than 1 000 years, and are protected by the government. Particularly old trees include: one over 3 500 years in Baoyacun village, Hunan province; another over 3 000 years (dating back to the Shang dynasty), in Dinlinsi Temple, Shandong province; a third at over 2 000 years in Longuangtai, Shaanxi province; and a fourth also over 2 000 years in Tancheng county, Shandong province. The 'old trees are almost always located near temples or inside sites of historical interest and scenic beauty'.

Cultural history of Ginkgo biloba *in Japan*: As Hori & Hori (1997) point out, the Japanese people of today are surrounded by many trees of *Ginkgo biloba*, they enjoy the nuts, and they employ the shape of the leaves in their logos; but how old is the oldest *G. biloba* in Japan and is it native to the country? After an extensive exploration of available sources—archaeological excavations, legends, dictionaries, books, arts and crafts—Hori & Hori conclude that the earliest evidence of *G. biloba* in Japan goes back to the 1300s.

Family **KARKENIACEAE** Krassilov 1972

Contributor: Zhou Zhiyan

Diagnosis: Ginkgoalean plants with unforked, pedunculate ovulate strobili bearing up to 100 small, densely packed, pedicellate, orthotropous, inverted ovules.

Range: Global, J(HET)–K(APT)
First: *Karkenia hauptmannii* Kirchner & Van Konijnenburg-Van Cittert 1994; Lias α, Pechgraben, Germany.
Last: *Karkenia incurva* Archangelsky 1965; Tico Flora, Bacqueró Gp., Santa Cruz, Argentina.

Reference whole-plant genus & stratum—Tico Flora
Female: *Karkenia* Archangelsky 1965 [*K. incurva*]; 1 TC, 1 sp., >60 indivs.
Male: Unknown.
Foliage: *Ginkgoites* Seward 1919 [*G. tigriensis* Archangelsky 1965, 1 TC (Grade 3 affl.), 1 sp., >78 indivs.] [*Sphenobaiera* Florin 1936, (Grade 5 affl.), 4 spp, Jurassic, Laurasia; *Baierella* Potonie 1933, (Grade 3), 1 TC, Early Cret. Mongolia.]
Stratum: As for '*Last*' above.
Affiliations: *Ginkgoites* dwarf shoots and roots closely associated with *K. incurva*. [*Sphenobaiera* type leaves attached to short-shoots with *K. hauptmannii* (Kirchner & Van Konijnenburg-Van Cittert 1994) and closely associated with three other species of ovulate organs in the Jurassic of Laurasia (Krassilov 1972; Schweitzer & Kirchner 1995; Zhou *et al*. 2002)].

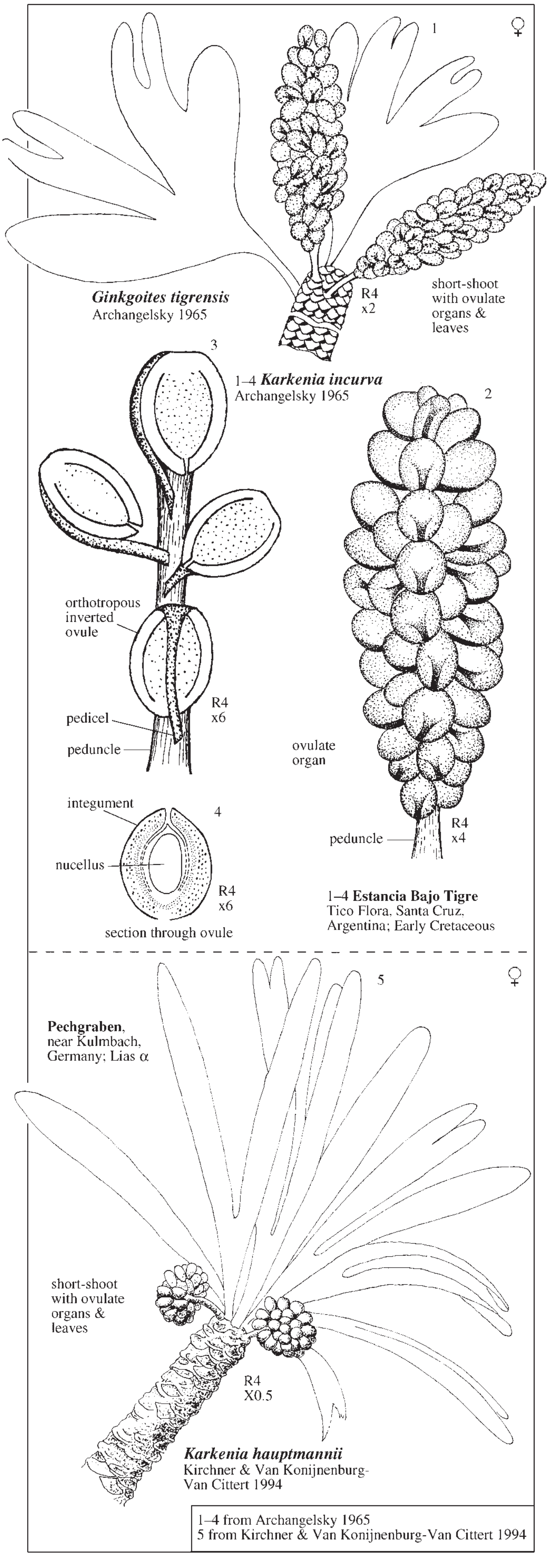
Prominence (colonisation success)— Global Jurassic-Cretaceous
Frequency/Ubiquity: Most in Early Jur. to Early Cret. of Laurasia; 1 record from Early Cret. of Gondwana. Ovulate organs known from Early Jur. of Germany (2 localities) and Iran (1 locality), M. Jur., Late Jur. of E. Asia, and Early Cret. of Mongolia and Argentina (1 locality each); affiliated *Sphenobaiera* widely spread globally from Permian to Early Cret. and *Ginkgoites* from Early Tr. to Neogene; *Baierella* restricted to Asia (Late Jur. to Early Cret.) (Zhou & Wu in prep.).
Diversity: Ovulate organs 6 spp (5 in Laurasia, 1 in Gondwana); affiliated foliage *Sphenobaiera* 4 spp, *Ginkgoites* 1 sp., *Baierella* 1 sp.
Karkenia incurva Archangelsky 1965, Early Cret., Santa Cruz, Argentina;
K. hauptmannii Kirchner & Van Konijnenburg-Van Cittert 1994, Lias α, Pechgraben, Germany;
K. cylindrica Schweitzer & Kirchner 1995, Early Jur., Elburs, Iran;
K. henanensis Zhou *et al*. 2002, M. Jur., Henan, China;
K. asiatica Krassilov 1972, Late Jur., Bureja, Siberia;
K. mongolica Krassilov 1982, Early Cret., Mongolia.
Abundance: Ovulate organs very abundant in the *Ginkgoites tigriensis* bed of the Baqueró Gp., Argentina (Archangelsky 1965), but usually rare (e.g. only <0.05% in Yima Fm., China and 10 indivs. found in Bureja); isolated seeds occasionally occurring in groups (as caddis fly cases) (Krassilov & Sukatsheva 1979); affiliated vegetative leaves abundant.
Longevity: *ca* 90 my.

Ecology
Habit: Possibly a deciduous tree.
Habitat: A mesic element.

Other genera
Pollen: *Entylissa* and *Ginkgocycadophytus* found within the ovules.

Remarks
Classification/affiliations: Krassilov (1972) also referred *Eretmophyllum* type leaves and *Carpolithes* type seeds to Karkeniaceae, but neither have been found associated with *Karkenia*. Zhou (2003) mentioned that leaves associated with (or occasionally connected with) *Karkenia* changed from the Jurassic *Sphenobaiera* type (incomplete leaf without a petiole) to the petiolate *Ginkgoites* (or *Baierella*) type in the Cretaceous. Del Fueyo & Archangelsky (2001) suggest that the ancestor of *Karkenia* might belong to the Dicranophyllales.

References
Archangelsky (1965): Diagnosis.
Krassilov (1972): General.
Kirchner & Van Konijnenburg-Van Cittert (1994): *K. hauptmannii.*
Zhou et al. (2002): Other information.



1–4 from Archangelsky 1965
5 from Kirchner & Van Konijnenburg-Van Cittert 1994

Family **YIMAIACEAE** Z.Zhou 1997

Contributor: Zhou Zhiyan

Diagnosis: Ginkgoalean plants with unforked, pedunculate ovulate strobili with up to eight or nine terminal, contiguous, sessile, orthotropous, recurved (when mature) ovules.

Range: Laurasia, J(?HET–BTH)
First: ?*Baiera muensteriana* (Presl in Sternberg 1833) Heer 1876 (young ovulate organs); basal Liassic (Hettangian), Franconia, Germany (Kirchner 1992).
Last: *Baiera gracilis* Bunbury 1851 [= *B. furcata* (L. & H. 1837) Braun 1843 (Harris & Millington 1974)] (ovulate organs) recorded from the Upper Deltaic (Bathonian), Scalby, Yorkshire, England (Black 1929; Harris & Millington 1974).

Reference whole-plant genus & stratum—Yima Fm.
Female: *Yimaia* Zhou & Zhang 1988 [*Y. recurva* Zhou & Zhang 1988; whole-plant—*Y. hallei* (Sze 1933) Zhou & Zhang 1992]; 1 TC, 1 sp., >54 indivs.
Male: Unknown.
Foliage: *Baiera* Braun 1843, emend. Florin 1936, partly *Ginkgoites* Seward 1919; *Baiera hallei* Sze 1933; 2 TCs (9 TCs in North China), estimated at >5%.

Stratum: Yima Fm., Henan Province, China, J(?AAL).
Affiliations: Grade 4; besides close association, cuticles of leaves are similar to those of collars and peduncles of ovulate organs; and lysigenous resin bodies are present in leaves, bud scales and the fleshy layer of ovule integument. (Recurrent associations of leaves and similar ovulate organs are also recorded from Europe (Black 1929; Kirchner 1992).)

Prominence (colonisation success)— Laurasia Jurassic

Frequency/Ubiquity: Ovulate organs from the M. Jur. of China and England (1 locality each) and possibly the Lias of Germany (1 locality); affiliated foliage leaves, *Baiera hallei*, more than 9 localities from the M. Jur. of North China, *B. gracilis/furcata* complex and *B. muensteriana* recorded from many localities of the Early Jur. to the Early Cret. in Laurasia (Dijkstra 1971); possibly affiliated seeds *Allicospermum xystum*, *A. baiereanum* and *A. ginkgoideum* >5 localities (Harris 1935; Tralau 1966).

Diversity: *Yimaia* type ovulate organs >3 spp; similar dispersed ovules (seeds) >3 spp; leaves >4 spp in Laurasia (Zhou *et al*. in press).

Abundance: Ovulate organs rare, estimated at <0.1%; vegetative leaves >5% in Yima Fm. In Yorkshire, England, a large number of isolated seeds found in two localities of the Upper Daltaic, but ovulate organs extremely rare (only from Scalby); leaves of *B. gracilis/furcata* complex very common (27 localities) in both the Lower and Upper parts of the Daltaic Group (Bajocian to Bathonian) (Black 1929; Harris & Millington 1974). In Germany, *B. muensteriana* abundant (known from 12 localities); *Yimaia*-like young ovulate organs (and detached seeds) extremely rare (found only from one locality) (Kirchner 1992).

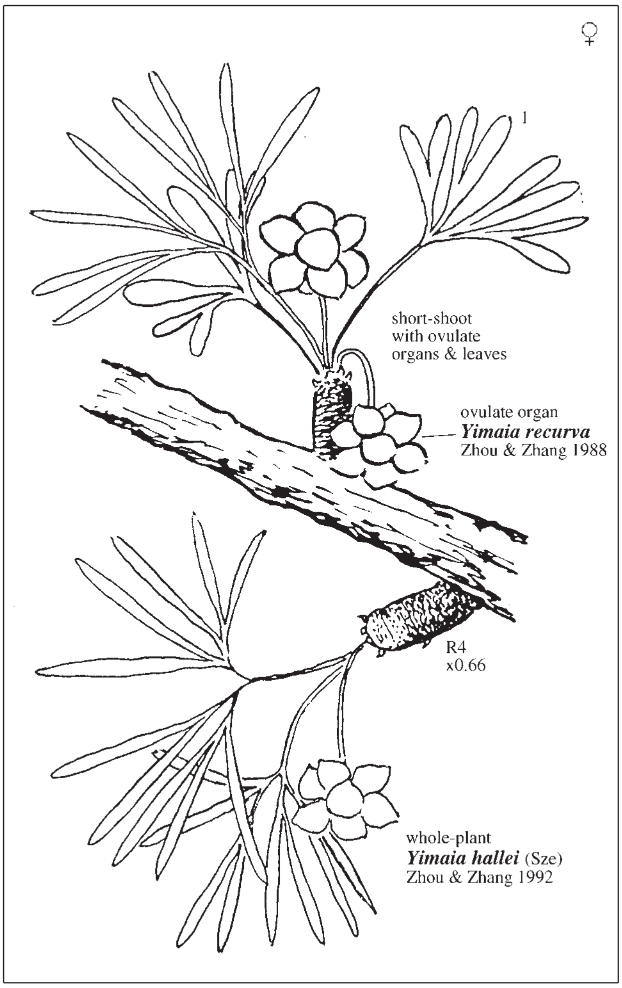
Longevity: ? 30–35 my.

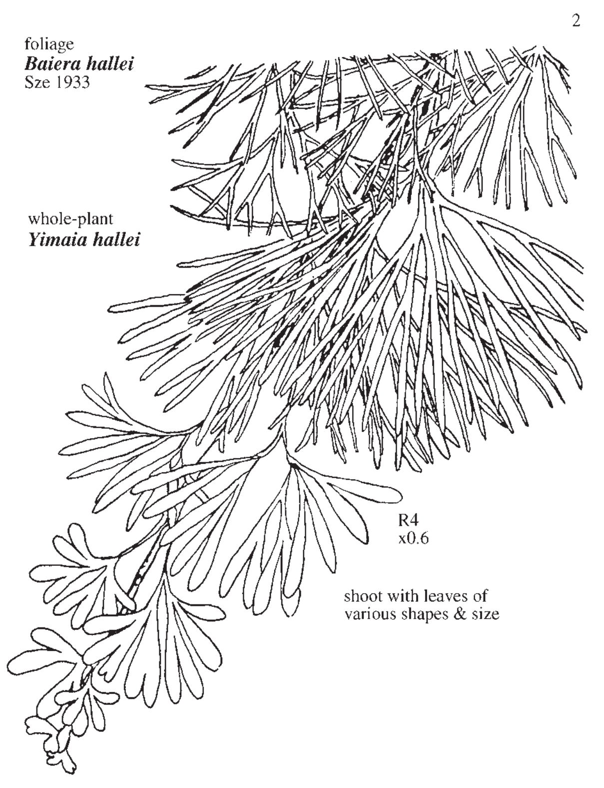
Ecology
Habit: Possibly a *Ginkgo*-like deciduous tree.
Habitat: Usually occurring in coal-bearing strata suggesting a mesic climatic condition.

Other genera
Dispersed seeds: *Allicospermum* Harris 1935, *pro parte*.
Vegetative leaves: *Baiera* Braun 1843, emend. Florin 1936, *pro parte*, in most cases, *Ginkgoites* Seward 1919, *pro parte*.
Shoots: *Ginkgoitocladus* Krassilov 1972, *pro parte*.
Pollen: *Ginkgocycadophytus* type.

Remarks
Classification/affiliations: Zhou & Zhang (1992) referred *Yimaia* to the Ginkgoales based on the general morphological resemblance of the ovulate organs, associated vegetative leaves, long- and short-shoots, bud scales and pollen grains to *Ginkgo biloba*. The ovulate organs differ from those of *G. biloba* in the absence of a collar and in having large numbers of sometimes recurved ovules. Cladistic analysis (Zhou 1997) shows that *Yimaia* may be sister to the Umaltolepidiaceae (p. 176), rather than being in the direct Ginkgoaceae lineage as initially suggested.

References
Zhou & Zhang (1992): General, ovulate organs, foliage.
Zhou (1997): Classification.





1,2 from Zhou & Zhang 1992
North Opencast Mine, City of Yima,
Yima Fm., Henan, China

Family **UMALTOLEPIDIACEAE** Stanisl. 1973 emend. Z.Zhou 1997

Contributor: Zhou Zhiyan

Diagnosis: Ginkgoalean plants with reduced, pedunculate fertile shoots each bearing a single, terminal inverted ovule attached or adnate to the abaxial side of a bract; bracts sessile, elongate, entire, sometimes divided into two lobes (*sensu* Zhou 1991, 1997).

Range: Laurasia, Tr(RHT)–K(CEN?)
First: *Toretzia angustifolia* Stanislavsky (1971) 1973; Novoraisk Fm. (Rhaetian), Donetz Basin, Ukraine.
Last: *Umaltolepis rarinervis* Krassilov 1972; Urgalsk Fm., Early Cret. (? Barremian), Bureja Basin, former USSR. Possible is *Pseudotorellia postuma* Samylina 1988 (foliage); Arkagalinsk Fm., Late Cret. (Cenomanian), Kolyma Basin, Northeast Asia, former USSR.

Reference whole-plant genus & stratum—Novoraisk Fm.
Female/foliage/long--& short-shoots: *Toretzia* Stanislavsky (1971) 1973 [whole-plant—*T. angustifolia* Stanislavsky 1973]; 1 TC, 2 spp, >6 indivs.
Male: Unknown.

Stratum: As for '*First*' above.

Affiliations: *Toretzia angustifolia* Stanislavsky: female/foliage/long- & short-shoots (Grade 5, organic connection); *T. longifolia* Stanislavsky 1973, only leafy shoots.

Prominence (colonisation success)—Laurasia Mesozoic
Frequency/Ubiquity: *Toretzia* (including whole plants) known only from the Late Tr. (Rhaetian) of Ukraine (1 locality), with a doubtful occurrence (1 locality) in the Early Cret. of Northeast China (Cao 1992); *Umaltolepis* recorded from Early Jur. (Lias) of Iran, Late Jur. of Bureja Basin, Siberia (2 localities), Early Cret. of Bureja Basin, North and Northeast China (1 locality each) (Krassilov 1972; Wang 1984; Chen *et al*. 1988; Schweitzer & Kirchner 1995); affiliated foliage *Pseudotorellia* Florin 1936 widely distributed, recorded from many localities of Late Tr. to Late Cret. in Laurasia (Florin 1936; Vachrameev & Doludenko 1961; Lundblad 1968; Krassilov 1972; Harris & Millington 1974; Wang 1984; Chen *et al*. 1988; Samylina 1988; Schweitzer & Kirchner 1995; Zhou in prep.; Zhou & Wu in prep.).

Diversity: *Toretzia* 2 spp; *Umaltolepis* 4 spp; *Pseudotorellia* >20 spp (Florin 1936; Vachrameev & Doludenko 1961; Lundblad 1968; Krassilov 1972; Harris & Millington 1974; Schweitzer & Kirchner 1995; Zhou in prep.).

Abundance: *Toretzia* very rare; *Umaltolepis* in Bureya >30 indivs., but in most cases only few indivs. *Pseudotorellia* very common in Laurasia.

Longevity: *ca* 110 my.

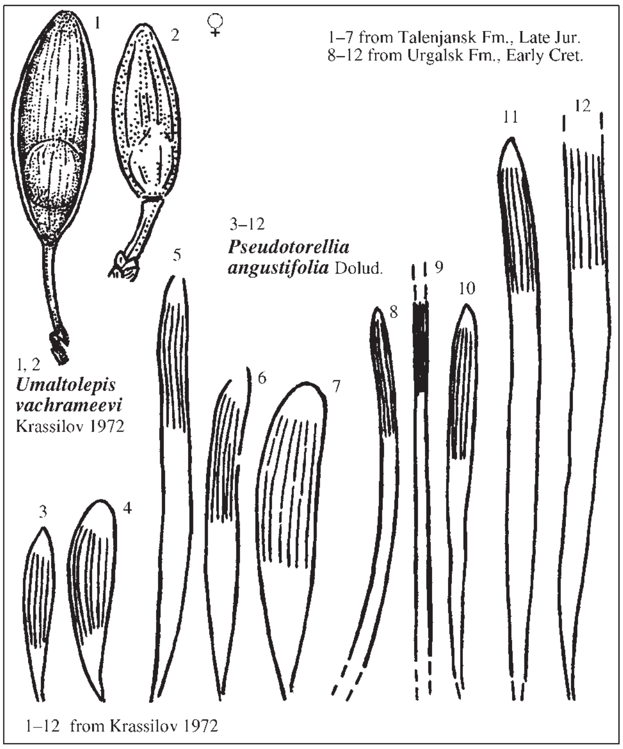
Ecology
Habit: Possibly deciduous dioecious trees.
Habitat: Possibly in mesic environmental conditions.

Other genera
Ovulate organs: *Umaltolepis* Krassilov (1970) 1972, type species *U. vachrameevii* Krassilov 1972, from the Talenjansk Fm., Umaltinsk and Azanovsk, Bureja Basin, previous USSR.; Late Jurassic.
Foliage: *Pseudotorellia* Florin 1936, type species *P. nordenskjoeldii* (Nathorst 1897) Florin 1936, from the Wealden, Spitzbergen.

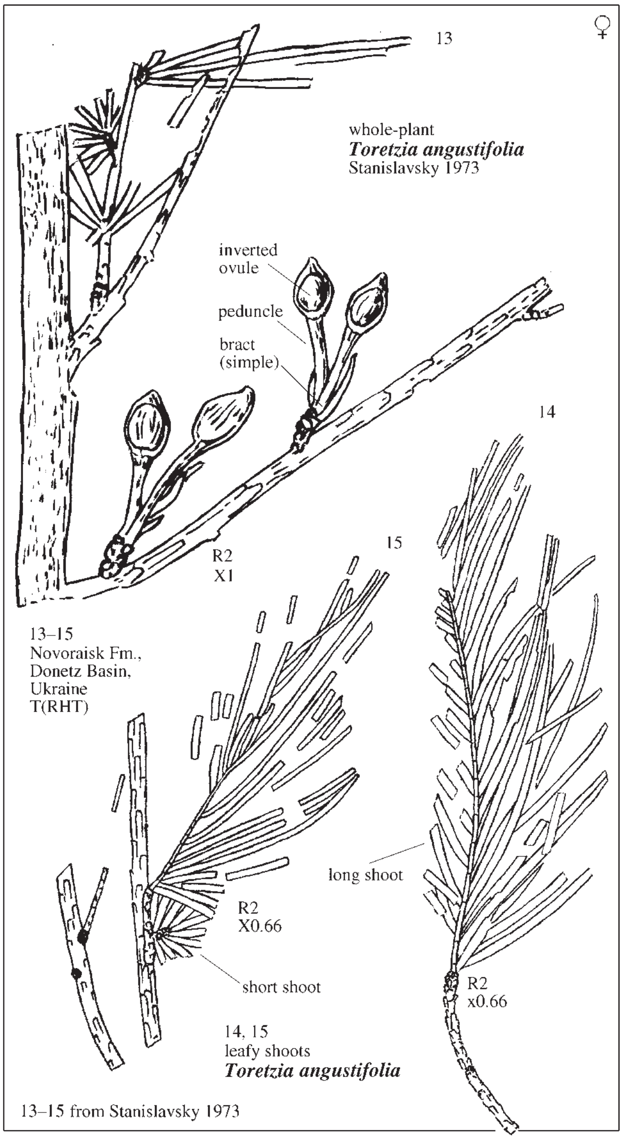
Remarks
Affiliation: Krassilov (1972) also linked the supposed seeds *Burejospermum* and pollen of the *Entylissa* type with *Umaltolepis*, but no organic attachment was found.

Classification: Krassilov (1972) erected the family Pseudotorelliaceae for *Umaltolepis* and associated foliage *Pseudotorellia*. Stanislavsky (1973) elected to replace the family name by Umaltolepidiaceae based on the ovulate organs rather than the vegetative organs. At the same time he proposed the name Toretziaceae for the Rhaetian plant *Toretzia* founded on the basis of ovulate organs/foliage/long- and short-shoots. Zhou (1991, 1997) merged the two families in the Umaltolepidiaceae based on their common apomorphies: reduced ovulate organs (without pedicel and with only one ovule) and sessile foliage.

References
Krassilov (1972): *Umaltolepis*.
Stanislavsky (1973): *Toretzia*.
Zhou (1991, 1997): Classification, other.



1–12 from Krassilov 1972



13–15 from Stanislavsky 1973

Family **SCHMEISSNERIACEAE** Z.Zhou 1997

Contributor: Zhou Zhiyan

Diagnosis: Ginkgoalean plants with lax, pedunculate, ovulate strobili comprising a main axis with a number of sessile or pedicellate cupules (collars); ovules 1 per cupule, winged when mature.

Range: Laurasia, J(HET)

First & Last: *Schmeissneria microstachys* (Presl 1833), Lias α, Reundorf near Bamberg, Bavaria, Germany (Kirchner & Van Konijnenburg-Van Cittert 1994). (*Stachyopitys* type pollen organs are known from M. Tr. to Early Jur. in Pangea.)

Reference whole-plant genus & stratum—Lias α

Female/foliage/long- & short-shoots: *Schmeissneria* Kirchner & Van Konijnenburg-Van Cittert 1994; >8 TCs, 1 sp., many indivs.

Male: *Stachyopitys* Schenk 1867; 9 TCs, 1 sp., many indivs; pollen of the *Monosulcites/Cycodopitys*-type.

Stratum: As for '*First & Last*' above.

Affiliations: Organic connection between female organs and leafy shoots (Grade 5); more recently, *Stachyopitys preslii* has been found attached to short-shoots with *Schmeissneria* leaves (Grade 5).

Prominence (colonisation success)—Laurasia Early Jurassic

Frequency/Ubiquity: Ovulate organs (and leafy shoots) only from Early Jur. Germany (8 localities); detached ovulate organs have also been recorded from the Lower Liassic of Odrowaz, Poland (see Wcislo-Luraniec 1992); affiliated male organs from Early Jur. Germany (6 localities), but similar organs found from M. Tr. to Early Jur. globally, especially in Gondwana (many localities) (And. & And. 2003).

Diversity: *Schmeissneria* 1 sp. in Laurasia only; *Stachyopitys*-type male organs 1 sp. attached to *Schmeissneria* in Germany (numerous species, however, through Pangea, And. & And. 2003).

Abundance: Relatively common.

Longevity: *ca* 3 my.

Ecology

Habit: Probably a shrub (or small tree) with long- and short-shoots; the latter bearing the leaves and fructifications.

Habitat: These plants must have grown in the proximity of fresh water as at least 10% of the *Schmeissneria* leaves have imprints of dragonfly eggs on them (Van Konijnenburg-Van Cittert & Schmeissner 1999).

Other genera—nil.

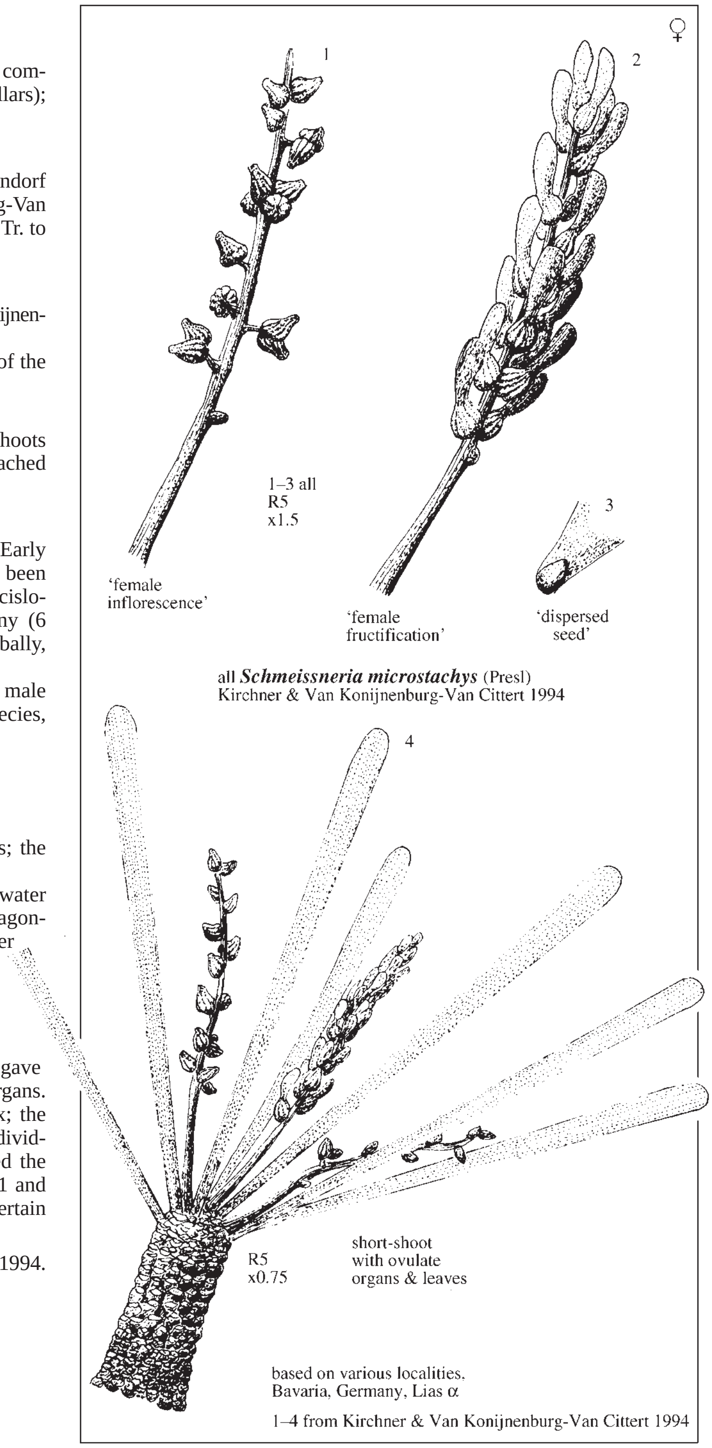
Remarks

Vegetative organs: Kirchner & Van Konijnenburg-Van Cittert (1994) gave no special names for the leaves and shoots that bear the ovulate organs. The leaves are slender, slightly cuneiform and with an obtuse apex; the veins are parallel, more than two in the basal part of leaf, and dividing in the lower third of the lamina. The original authors compared the leaves with *Glossophyllum* Kräusel 1943, *Eretmoglossa* Barale 1981 and *Pseudotorellia* Florin 1936, but found them to differ from each in certain respects.

Affiliations: *Schmeissneria* Kirchner & Van Konijenburg-Van Cittert 1994.

References

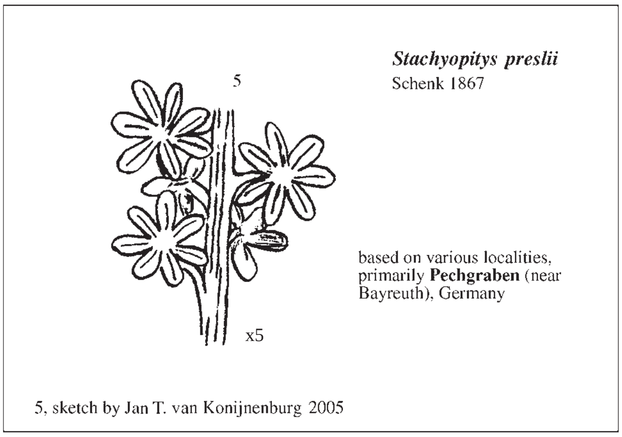
Wcislo-Luraniec (1992): Female.
Kirchner & Van Konijnenburg-Van Cittert (1994): General.
Van Konijnenburg-Van Cittert (pers. comm. 2005): General.



all ***Schmeissneria microstachys*** (Presl)
Kirchner & Van Konijnenburg-Van Cittert 1994

based on various localities.
Bavaria, Germany, Lias α

1–4 from Kirchner & Van Konijnenburg-Van Cittert 1994



Stachyopitys preslii
Schenk 1867

based on various localities,
primarily **Pechgraben** (near
Bayreuth), Germany

5, sketch by Jan T. van Konijnenburg 2005

Family **GINKGOACEAE** Engl. 1897

Diagnosis [Contributors: M. Mundry, I. Mundry & T. Stützel]
Ovulate organ: Once, rarely more times, bifurcate, in the axils of short-shoot leaves or scales; ovules single, orthotropous, one per tip of fork; the base of the ovule develops a green, somewhat fleshy collar before anthesis, the outer layer of the single integument becoming thick, fleshy and yellow at maturity; usually only one of two ovules matures.

Male cones: Simple, rarely compound, catkin-like, in the axil of short-shoot leaves; sporophylls with two pollen sacs; pollen without air-bladders.

Leaves: Fan-shaped, those of long-shoots with a deep median slit, which is less prominent or lacking in short-shoot leaves; venation strictly dichotomous.

Range: Tr(OLN)–Rec.
First: The oldest putative vegetative leaves are *Ginkgoites* sp. recorded from the Spathian (U. Olenekian), Sydney Basin, Australia (And. & And. 2003, p. 199); oldest putative isolated seeds are *Allicospermum xystum* Harris 1935, Scoresby Sound, Greenland, *Thumatopteris* Zone (earliest Liassic); oldest authenticated ovulate organs are *Ginkgo yimaensis* Zhou & Zhang 1989, M. Jur. (Aalenian), Yima Fm., Henan, China.

Last: Extant.

Prominence (colonisation success)—extant
Frequency/Ubiquity/abundance: See p. 173.
Diversity: A single monotypic genus (*Ginkgo biloba*); temperate, China.

Ecology
Habit: Large to massive trees reaching 30 m and up to 9 m in girth, monopodial or often with a once-forked trunk, deciduous, dioecious, long-lived.

Habitat: Poorly known, 'it is thought it may still occur in mesic habitats in remote mountain valleys, as small populations in mixed conifer-broad-leaf forests' (C.N. Page 1990, but see p. 173).

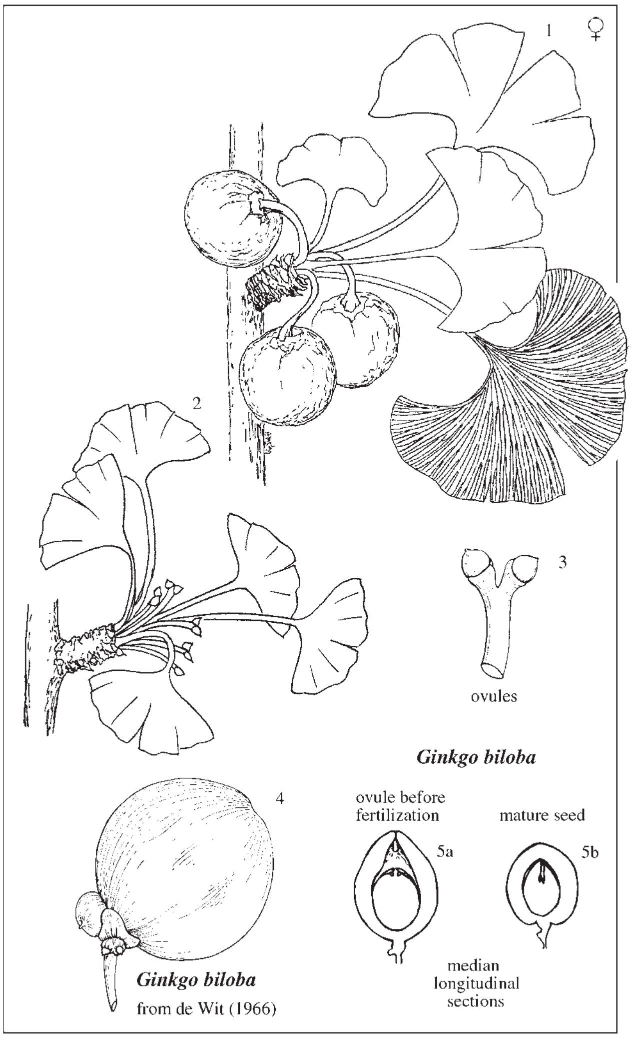
Remarks
Pollination: Wind-pollinated.

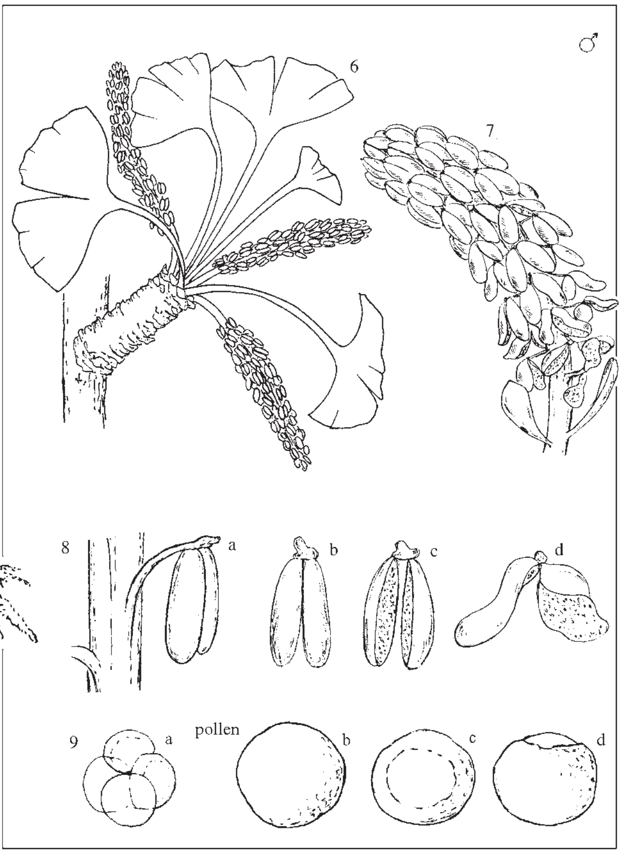
Dispersal: Colour and texture of the mature drupe-like seeds suggest dispersal by animals; observations from natural populations are lacking, however.

Morphology [Contributors: M. Mundry, I. Mundry & T. Stützel]: Leaf-like structures with a marginal ovule near the distal slit, or in its place, have been described and illustrated (e.g. Goebel 1932, p. 1746). It is unclear whether they are positioned in the axil of leaves like the normal ovule-bearing organ, or whether they are normal leaves with marginal ovules. The fleshy collar at the base of the ovule develops later than the ovule, it therefore being problematic to regard it as a sporophyll. Long-shoot leaves, in particular, may be very variable in shape, from nearly entire to bilobed (the typical form in long-shoots) to multifid. Much of the variation in the fossil record could, therefore, be interpreted as intraspecific variability.

Other genera
Ovulate organ & leaves: *Grenana* Samylina 1990, type species *G. angrenica*, M. Jur., Angren, Uzbekistan (Zhou 1997).

Reference
C.N. Page (1990): Habit, habitat, pollination, dispersal.





10

Ginkgo biloba

1,2,6 H.M. Anderson sketches 1999
3,4 from de Wit (1966)
5a,b J.M. Anderson sketches
7–9 from And. & And. 2003
10 H.M. Anderson sketch 2004 (after Mitchell 1974)

Family **AVATIACEAE** And. & And. 2003

Diagnosis: Ginkgoalean plants with once-forked ovulate strobili bearing a pair of pedunculate, bilaterally symmetrical, palmate, multiovulate megasporophylls consisting of several lobes each bearing a flattened winged seed.

Range: Gondwana, Tr(CRN)
First & Last: *Avatia bifurcata* And. & And. 2003, Molteno Fm., South Africa. Since the affiliation with the foliage *Ginkgoites* is insufficiently established, the range of this family is based solely on the ovulate fruit which remains known only from the Molteno Fm. *Ginkgo*-like foliage is common and widespread in the Gondwana Triassic (see under 'Prominence' below), ranging from the L. Newport Fm., Sydney Basin, Australia (SPA) to the Molteno Fm. (CRN).

Reference whole-plant genus & stratum—Molteno Fm.
Female: *Avatia* And. & And. 2003; 6 TCs, 1 spp, >110 indivs.
Male: *Eosteria* And. & And. 2003; 4 TCs, 2 spp, 27 indivs.
Foliage: *Ginkgoites* Seward 1919; 19 TCs, 6 spp, <1%.

Stratum: Molteno Fm., Karoo Basin, South Africa, Tr(CRN).
Affiliations: *Avatia*(2)*Ginkgoites*(3)*Eosteria*(2), Grades 2 & 3 (Mor.cor., Kin.rein., Mut.occ.).

Prominence (colonisation success)—Gondwana Triassic (GT)
Ginkgoites (foliage): Recorded from Argentina, South Africa, Peninsula India, Australia and New Zealand.
FUDAL rating: 21/4/9/–/17 = 51; the 7th most prominent gymnospermous foliage genus in the GT.
Frequency: High, 21 of 84 Gondw. degree squares.
Ubiquity: High, 4 of 5 Gondw. continents.
Diversity: High, 9 species in GT.
Abundance: Rare, <1% norm in Molteno TCs.
Longevity: High, 17 my through Triassic.

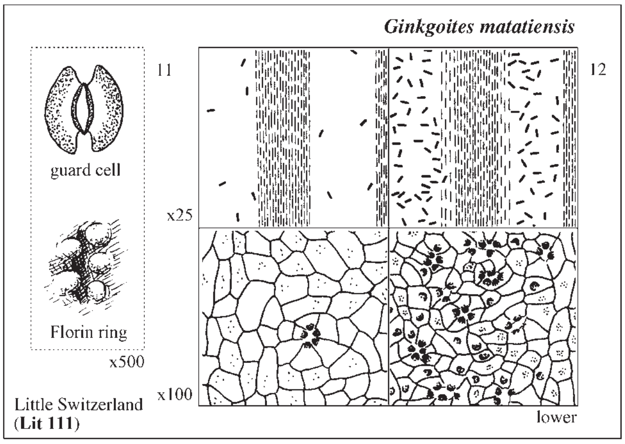
Ecology—Molteno Fm.
Habit: Probably a tall deciduous tree.
Habitat: A scattered element in riparian forest and woodland of the Molteno Floodplain Biome.

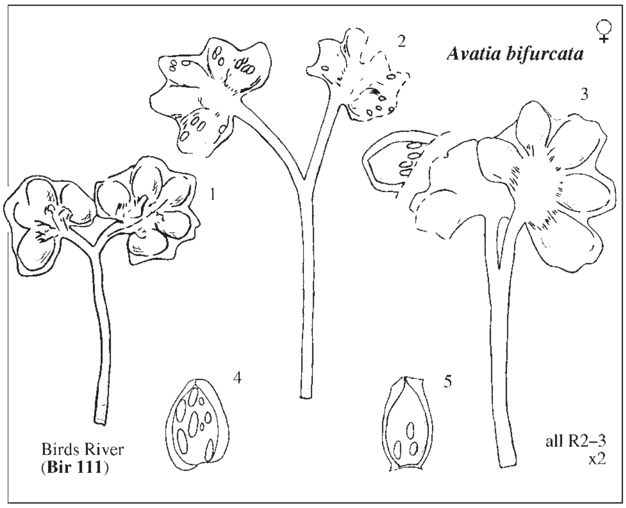
Other genera—nil.

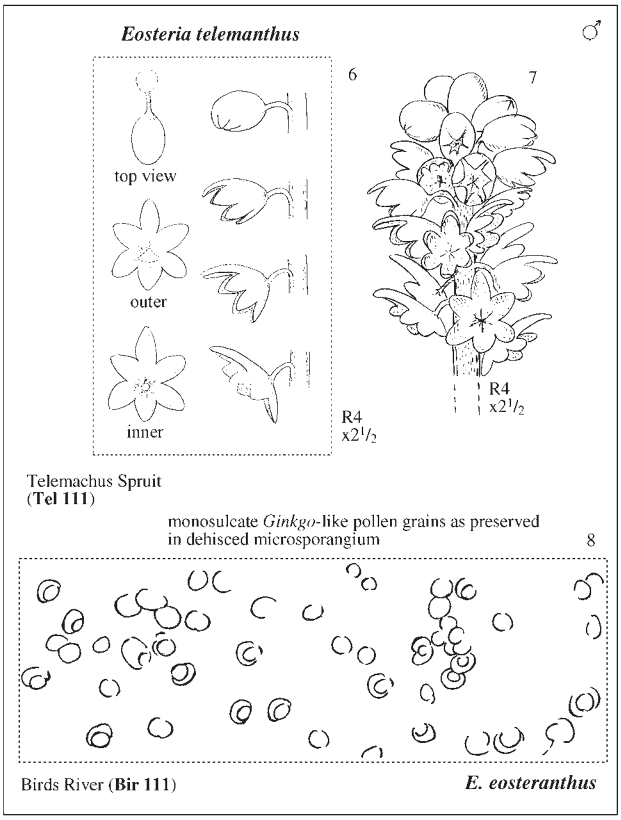
Remarks
Classification: The true relationship between the extant *Ginkgo* and the many species of fossil *Ginkgo* and *Ginkgoites* recorded globally from the Permian onwards has long been an enigma (Tralau 1968; Harris & Millington 1974; Zhou 1997), and remains so. Ovulate organs resembling those of *G. biloba* have been recorded from: M. Jur. of Henan (Zhou & Zhang 1989); Early Cret. of Liaoning, China (*G. apodes* Zheng & Zhou 2004) (Zhou & Zheng 2003); and Paleocene of North Dakota, United States (*G. adiantoides*, Crane *et al.* 1990) (Zhou pers. comm. 2004). Various other ovulate genera (Zhou 1991, 1997; Del Fueyo & Archangelsky 2001) have been affiliated with fossil *Ginkgo*-like leaves. *Avatia* is another such case.

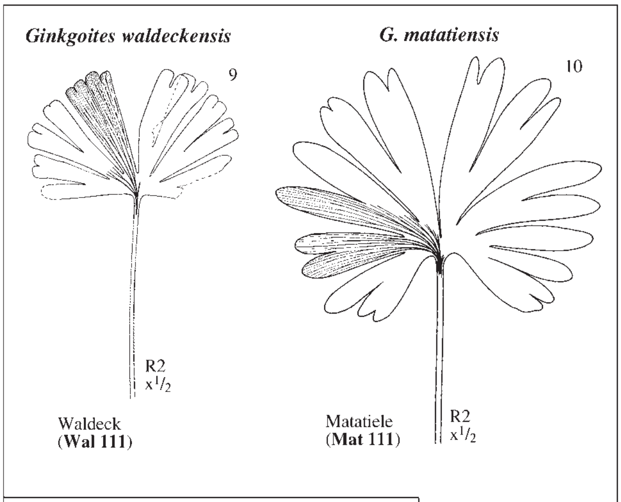
It is beyond the scope of our present task to attempt to resolve the *Ginkgo* (*Ginkgoites*) impasse globally. In considering 'Prominence' above, we confine ourselves to consideration of the Gondwana Triassic *Ginkgo*-like foliage and deal with the full set as if representing a single natural genus—with *Avatia* as the ovulate affiliate. Rather than introduce a new order for the Gondwana taxon (And. & And. 2003), we placed it in a new family included along with the Ginkgoaceae in the order Ginkgoales.

References
And. & And. (1989): Foliage.
And. & And. (2003): Female, male, foliage.









1–12 from And. & And. 2003
all Molteno Fm., South Africa, Late Triassic (Carnian)

Order **LEPTOSTROBALES** S.V.Meyen 1987

Diagnosis: Ginkgoopsid plants with relatively lax spicate strobili bearing spirally arranged megasporophylls comprising (before dehiscence) a closed pair of palmate 2–5-ovulate heads.

Families: Includes the single family Leptostrobaceae.

Family **LEPTOSTROBACEAE** S.V.Meyen 1978

Diagnosis: As for the order Leptostrobales.

Range: Tr(RHT)–K(CEN?)
First: *Leptostrobus longus* Harris 1935, Scoresby Sound, Greenland; and *Irania hermaphroditica* Schweitzer 1977, Iran (Cleal 1993).
Last: ?*Czekanowskia* ex group *rigida* Heer 1876 and *Phoenicopsis steenstrupii* Seward, Koèvunjsker Fm., Anadyr River and Arkagalinsker and Armanjsker Formations, Kolyma River, eastern Siberia, former USSR (Vakhrameev 1966; Samylina 1973). These records are based on adpressions of foliage. The youngest fructifications are of *Leptostrobus laxiflorus* Heer 1876, Ilinureksker Fm. (BER), Tyl River, eastern Siberia, former USSR (Vakhrameev in Vakhrameev *et al*. 1978). (These data on 'Range' have been taken verbatim from Cleal 1993.)

Reference whole-plant genus & stratum—Ravenscar Gp.
Female: *Leptostrobus* Heer 1876; 6 TCs, 1 sp., 'hundreds of capsules'.
Male: *Ixostrobus* Raciborski 1891; 3 TCs, 1 sp., 11 indivs.
Foliage: *Czekanowskia* Heer 1876; 10 TCs, 8 spp, only locally abundant.

Stratum: Plant beds within Ravenscar Gp. (mainly Saltwick and Cloughton Fms.), Yorkshire, UK (BAJ–BTH).
Affiliations: Grade 4 (Cut.cor., Mut.occ.).

Prominence (colonisation success)—Euramerica Late Trias.–M. Jur.
Frequency/ubiquity: During the Triassic Period, the family was widespread, but most common in palaeoequatorial areas (especially North America and Europe). During the Early and Middle Jurassic it disappeared from southern temperate palaeolatitudes, but becomes widespread albeit never very abundant in palaeoequatorial latitudes (North America, Europe, Central Asia, China), and very abundant in northern temperate and high palaeolatitudes (Siberia, northern Canada). During the Late Jurassic and Early Cretaceous it progressively declined in palaeoequatorial latitudes, eventually becoming restricted to Siberia.
Diversity: 40 spp (based on foliage).
Abundance: Rare, never abundant except in northern temperate and high palaeolatitudes.
Longevity: *ca* 110 my.

Ecology
Habit: Unknown.
Habitat: Mainly lowland, riparian and lakeside vegetation.

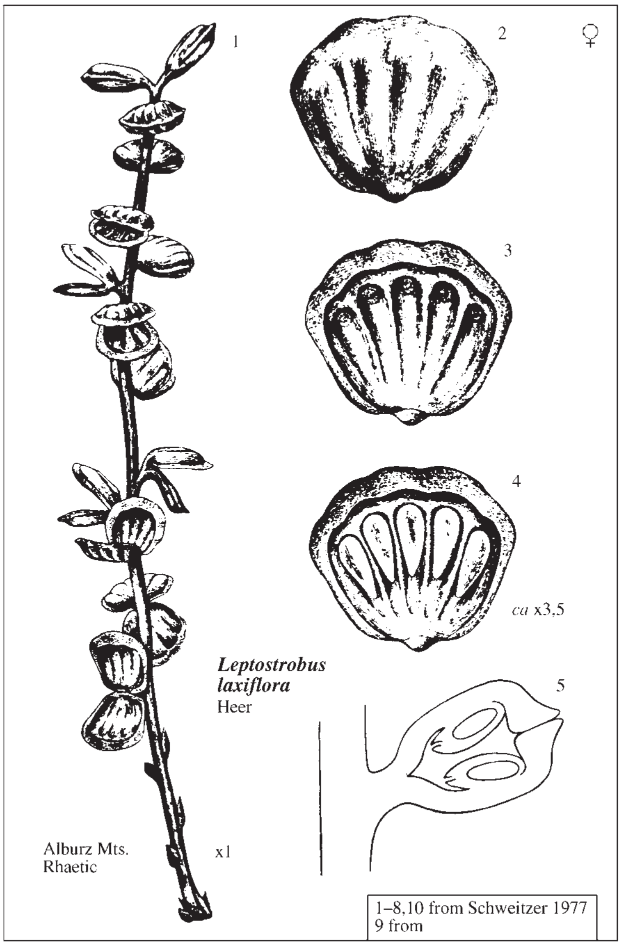
Other genera
Ovulate organs: *Staphidiophora* Harris 1935.
Ovulate plus pollen organs: *Irania* Schweitzer 1977.
Foliage: *Solenites* Lindley & Hutton 1834, *Phoenicopsis* Heer 1876, *Hartzia* Harris 1935, *Arctobaiera* Florin 1936, *Culgoweria* Florin 1936, *Stenophyllum* Florin 1936, *Winwardia* Florin 1936.

Remarks

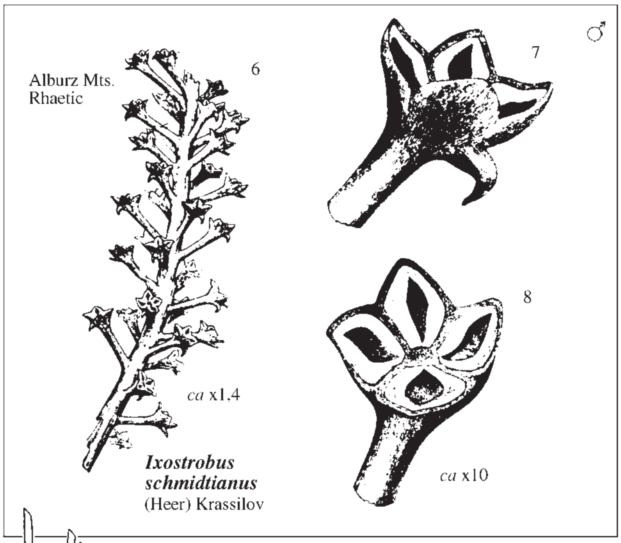
Classification/phylogeny: The family has also been referred to as the Czekanowskiaceae. Its position in gymnosperm phylogeny is far from settled, having been variously placed close to the Ginkgoaceae, Peltaspermales and Callistophytales (Meyen 1984, 1987; Crane 1985; Cleal 1993). We nest it within our Ginkgoopsida, finding it closest to the Hamshawviales in both foliage and ovulate features.

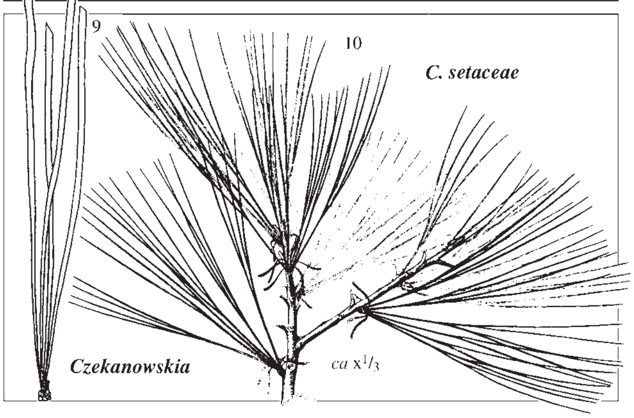
Schweitzer (1977) referred his new 'hermaphrodite flower' *Irania hermaphroditica* from the Rhaetic of the Alburz Mts, N Iran, to a new order Iraniales in the class Czekanowskiopsida. We have chosen to include *Irania*, on the basis of its spike of bi-valved ovulate capsules, with *Leptostrobus* in the Leptostrobaceae—perhaps too conservatively.

References
Harris (1951): Affiliations.
Harris & Miller in Harris et al. (1974): Female, affiliations.
Cleal (1993): First & Last.



1–8,10 from Schweitzer 1977
9 from





Order **HAMSHAWVIALES** And. & And. 2003

Diagnosis: Ginkgoopsid plants with (?short) shoots bearing fascicles of reduced once-forked strobili bearing a pair of megasporophylls comprising single, flattened, (?)fleshy, multiovulate heads with *ca* 8–20 seeds.

Families: Includes the single family Hamshawviaceae.

Family **HAMSHAWVIACEAE** And. & And. 2003

Diagnosis: As for the order Hamshawviales.

Range: Gondwana, Tr(OLN–RHT)
First: *?Sphenobaiera* sp., Narrabeen Grp., Sydney Basin, Australia.
Last: *Sphenobaiera steinmannii* (Sol. & Stein. 1899) And. & And. 1989, Copiapo region, Chile; and *?S. schenkii* (Feistmantel 1889) And. & And. 1989, El Puquen Fm., Los Vilos region, Chile (And. & And. 1989).

Reference whole-plant genus & stratum—Molteno Fm.
Female: *Hamshawvia* And. & And. 2003; 4 TCs, 4 spp, 24 indivs.
Foliage: *Sphenobaiera* Florin 1936; 43 TCs, 9 spp, 30%.
Male: *Stachyopitys* Schenk 1867; 27 TCs, 6 spp, 539 indivs.
Stratum: Molteno Fm., Karoo Basin, S. Africa, Tr(CRN).
Affiliations: *Hamshawvia*(4/5)*Sphenobaiera*(5)*Stachyopitys*(4), Grades 4 to 5 (Org.att., Mut.occ., Kin.rein., Cut.cor.).

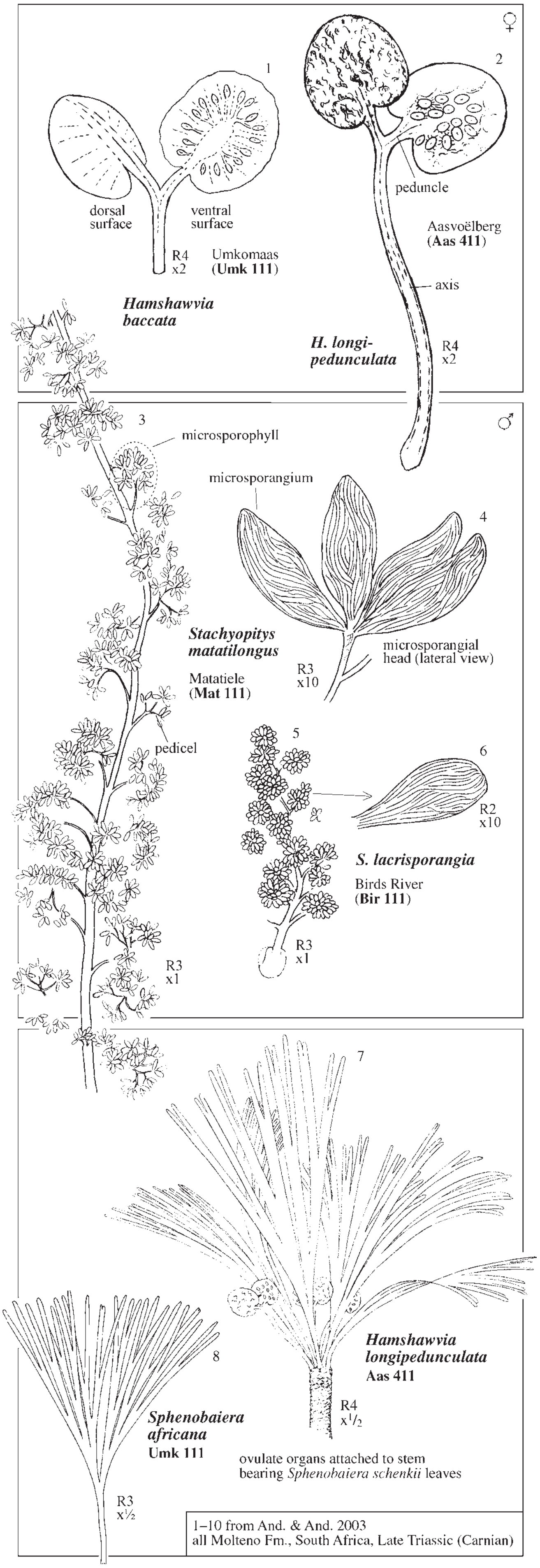
Prominence (colonisation success)—Gondwana Triassic (GT)
Sphenobaiera (foliage): Widespread in all Gondwana continents.
FUDAL rating: 26/5/12/30/26 = 99; the third most prominent gymnospermous foliage genus in the GT.
Frequency: High, 26 of 84 Gondw. degree squares.
Ubiquity: V. high, 5 of 5 Gondw. continents.
Diversity: High, 12 spp in Gondw. Trias.
Abundance: Abundant/co-dominant, 30% in preferred Molteno habitats.
Longevity: V. high, 26 my through Triassic.

Ecology—Molteno Fm.
Habit: Woody shrubs to large trees.
Habitat: *Sphenobaiera* is a mono-dominant or co-dominant in lake-deposit TCs; it is relatively rare elsewhere.

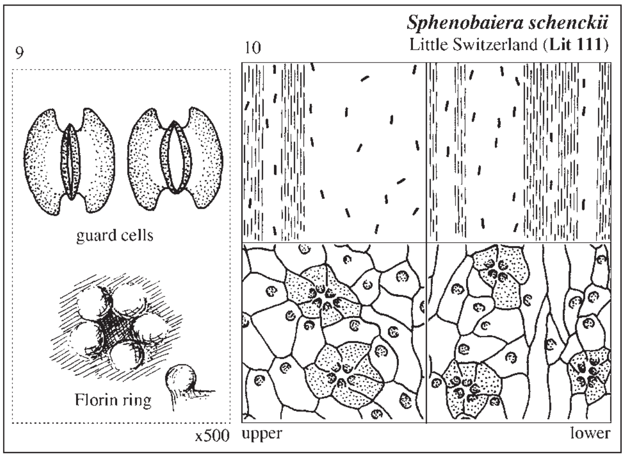
Other genera—nil.

Remarks
Phytogeography: The ovulate fruit *Hamshawvia* is known only from Nymboida, New South Wales (Ladinian) and the Molteno Fm. Although *Sphenobaiera* foliage occurs globally from the Permian to Early Cretaceous, we confine our concept of this family to the Gondwana Triassic.

References
And. & And. (2003): Female, male, foliage.
And. & And. (1989): Foliage.



1–10 from And. & And. 2003
all Molteno Fm., South Africa, Late Triassic (Carnian)



Order **UMKOMASIALES** Doweld 2001

Diagnosis: Ginkgoopsid plants with lax paniculate strobili bearing spirally to laminately borne megasporophylls comprising 1 to 7 pairs of opposite to subopposite, reflexed, uniovulate, almost closed cupules.

Remarks
Classification: On the basis of the ovulate strobili, particularly their cupules, the Umkomasiales appear closest to the Caytoniales and Petriellales. The polliniferous strobili, however, are far more like those of the Hamshawviales (*Stachyopitys*) and Peltaspermales (*Antevsia*), while the foliage has features in common with several other ginkgoopsid taxa, but least of all the Caytoniales-Petriellales group. It is hardly feasible not to recognise an independent order.

Families: Includes the single family Umkomasiaceae.

Family **UMKOMASIACEAE** Petriella 1981

Range: Gondwana, Tr(OLN–RHT)
First: *Dicroidium zuberi* (Szajnocha 1888) Archangelsky 1968, Banks Wall Fm., Sydney Basin, Australia (And. & And. 1983).
Last: *Dicroidium zuberi* and *D. odontopteroides* (Morris 1845) Gothan 1912 forma *odontopteroides* And. & And. 1983, El Puquen Fm., Los Vilos region, Chile; and *D. zuberi*, Copiapo region, Chile (And. & And. 1983).

Reference whole-plant genus & stratum—Molteno Fm.
Female: *Umkomasia* Thomas 1933; 22 TCs, 8 spp, 503 indivs.
Male: *Pteruchus* Thomas 1933; 22 TCs, 3 spp, 431 indivs.
Foliage: *Dicroidium* Gothan 1912; 75 TCs, 21 spp, 90%.

Stratum: Molteno Fm., S. Africa, Tr(CRN).
Affiliations: *Umkomasia*(4)*Dicroidium*(4)*Pteruchus*(4), Grade 4 (Mut.occ., Cut.cor., Kin.rein.).

Prominence (colonisation success)—Gondwana Triassic (GT)
Dicroidium (foliage): Widespread in all Gondwana continents.

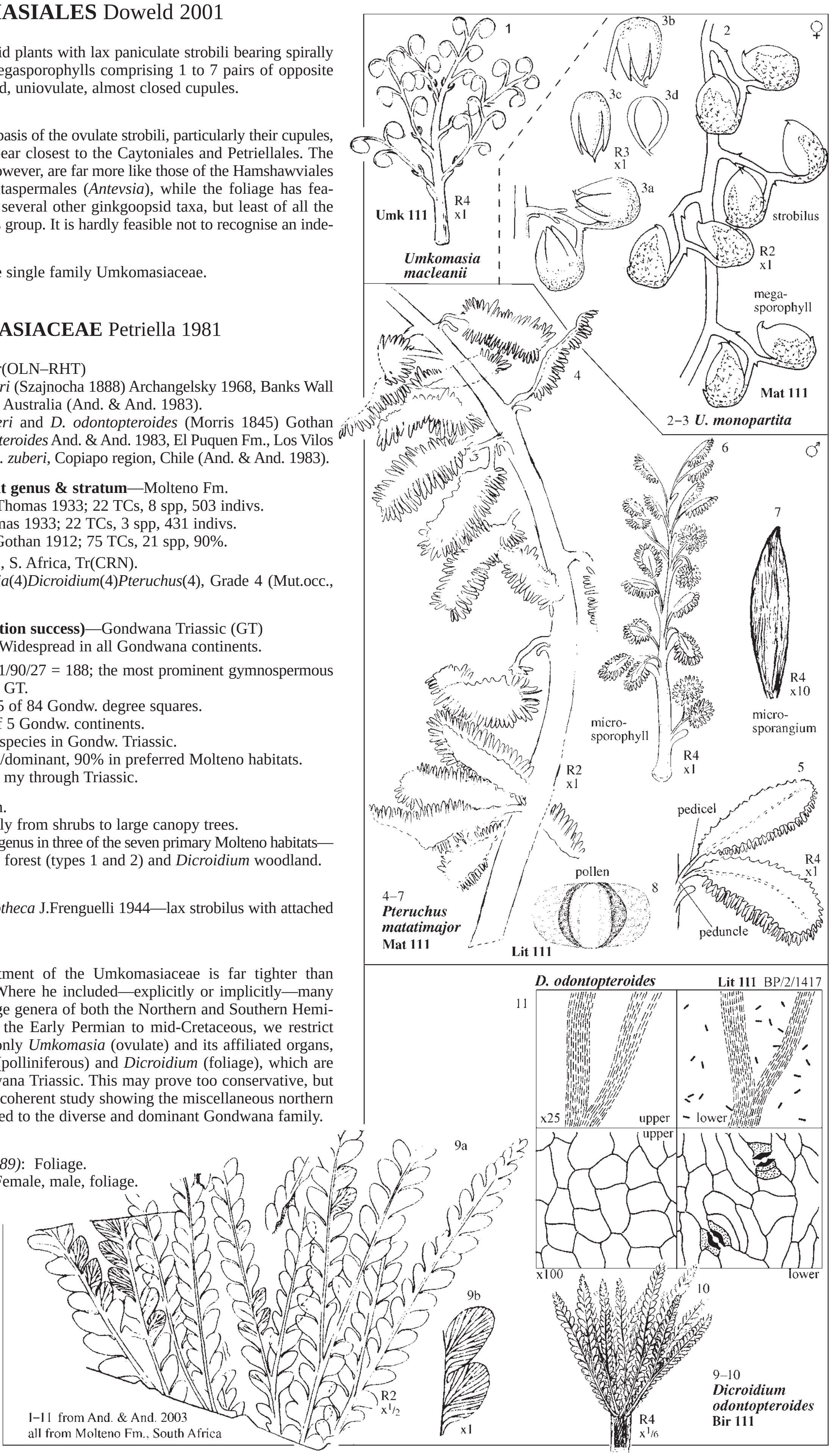
FUDAL rating: 45/5/21/90/27 = 188; the most prominent gymnospermous foliage genus in the GT.
Frequency: V. high, 45 of 84 Gondw. degree squares.
Ubiquity: V. high, 5 of 5 Gondw. continents.
Diversity: V. high, 21 species in Gondw. Triassic.
Abundance: Abundant/dominant, 90% in preferred Molteno habitats.
Longevity: V. high, 27 my through Triassic.

Ecology—Molteno Fm.
Habit: Woody, probably from shrubs to large canopy trees.
Habitat: The dominant genus in three of the seven primary Molteno habitats—*Dicroidium* riparian forest (types 1 and 2) and *Dicroidium* woodland.

Other genera
Ovulate organ: *Fanerotheca* J.Frenguelli 1944—lax strobilus with attached *Feruglioa* seeds.

Remarks
Systematics: Our treatment of the Umkomasiaceae is far tighter than that of Cleal (1993). Where he included—explicitly or implicitly—many reproductive and foliage genera of both the Northern and Southern Hemispheres, ranging from the Early Permian to mid-Cretaceous, we restrict the family to include only *Umkomasia* (ovulate) and its affiliated organs, essentially *Pteruchus* (polliniferous) and *Dicroidium* (foliage), which are confined to the Gondwana Triassic. This may prove too conservative, but there exists no serious coherent study showing the miscellaneous northern taxa to be closely related to the diverse and dominant Gondwana family.

References
And. & And. (1983, 1989): Foliage.
And. & And. (2003): Female, male, foliage.



1–11 from And. & And. 2003
all from Molteno Fm., South Africa

Order **CAYTONIALES** Gothan 1932

Diagnosis: Ginkgoopsid plants with lax laminate strobili bearing several opposite to subopposite pairs of megasporophylls consisting of single, bilaterally symmetrical, reflexed cupules fully enclosing 6 to >30 ovules.

Remarks
Classification: Whether the Caytoniales and Petriellales are considered two orders or one depends on the relative weight given the ovulate organs and the other organs in assessing phylogenetic relationship. Their ovulate strobili suggest close similarity, while their polliniferous strobili and foliage point to a distant relationship.

Families: Includes the single family Caytoniaceae.

Family **CAYTONIACEAE** Kräusel 1926

Range: Tr(CRN)–K(CMP?)
First: *Caytonanthus koehii* Harris 1932, *Amphorispermum ellipticum* Harris 1932, *A. rotundum* Harris 1932, *A. major* Harris 1932, and *Sagenopteris hallei* Harris 1932, Scoresby Sound (RHT), Greenland (Harris, 1932a,b). It should be noted that the typically caytoniacean foliage, *Sagenopteris* sp., has been reported from Raibl, Austria, Tr(CRN) (Stur 1885), although this requires further authentication, we take it in this volume as the 'first' appearance of the family.

Last: *??Sagenopteris variabilis* Velenovsky, Barykovsker Fm., Ugol'naja Basin, eastern Siberia, former USSR (Vakhrameev 1966). This record is based on adpressions of foliage. The youngest fructifications are *Caytonia nathorstii* (Thomas) Harris 1940, Scalby Fm. (BTH), North Yorkshire, England, UK (Harris 1964; Cleal 1993) and *Caytonanthus* (with *in situ* pollen), lowermost Cret. (?Ber) of Tyrma River, Amur Province (Krassilov pers. comm. 2005).

Reference whole-plant genus & stratum—Yorkshire Jurassic
Female: *Caytonia* Thomas 1925; 15–20 TCs, 3 spp, many indivs.
Male: *Caytonanthus* Harris 1937; 2 TCs, 3 spp, several indivs.
Foliage: *Sagenopteris* Presl 1838; 11 TCs, 2 spp, many indivs.
Stratum: Yorkshire Jurassic (L–U. Deltaic), England, J(BAJ–BTH).
Affiliations: *Caytonia*(4)*Sagenopteris*(4)*Caytonanthus*, Grade 4 (Mut.occ., Pol.cor.)

Prominence (colonisation success)—Laurasia Mesozoic
Frequency/ubiquity: The ovulate organ *Caytonia* is now known as a widespread element of the lower half of the Jurassic of Eurasia: Yorkshire (9 localities, M. Jurassic, Bajocian to Bathonian); Greenland (2 localities, basal Liassic, Hettangian); Poland (1 locality, U. Liassic); Sardinia and the USSR. Foliage identified as *Sagenopteris* has been reported from the Late Triassic to Late Cretaceous.

Diversity: No recent taxonomic revision of the *Caytonia* plant has been attempted, so any real sense of specific diversity is very difficult to gather. Five named species of the genus *Caytonia* appear to stand currently.

Abundance: Explicit abundance and frequency data on fossil taxa are rarely given and this holds true also for the *Caytonia* plant. In the Yorkshire sites where it is best known, Harris (1964) writes that it is 'by no means common'.

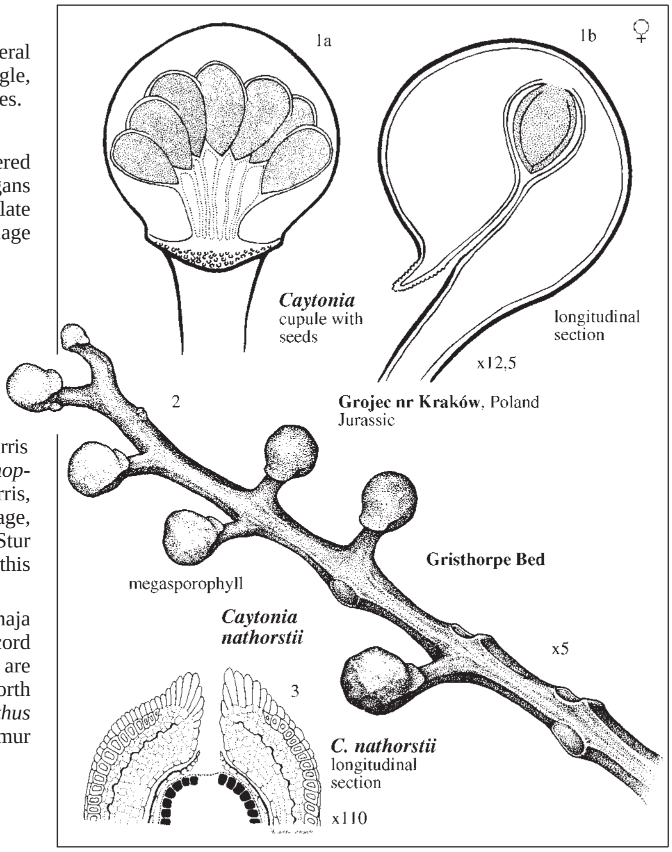
Longevity: *ca* 157 my.

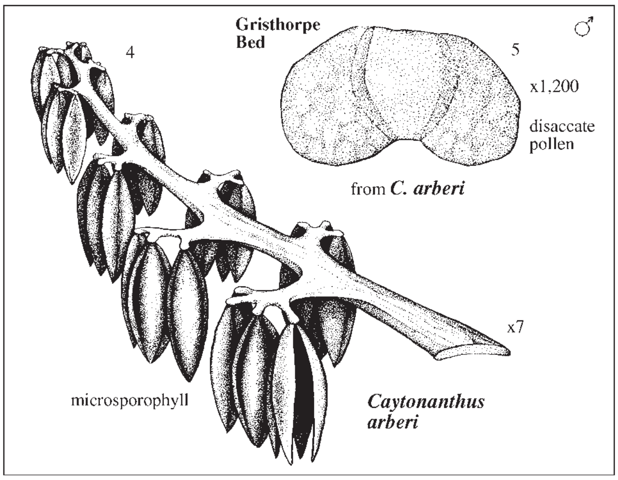
Ecology—Yorkshire Jurassic
Habit: A woody shrub or tree (Crane 1985).
Habitat: Deltaic.

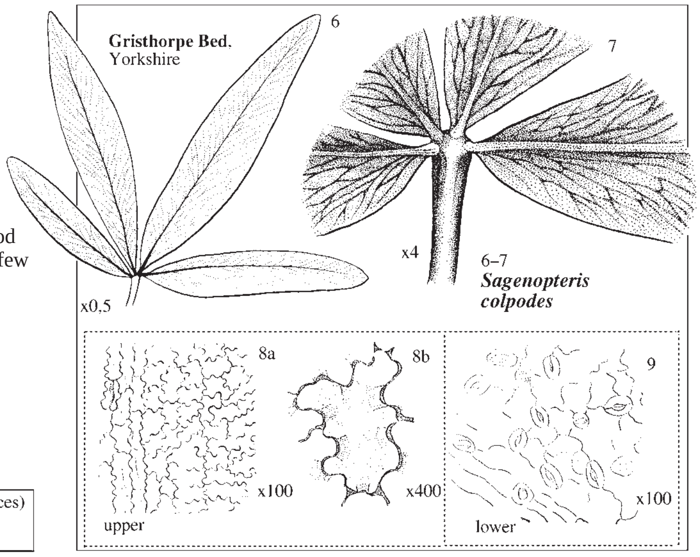
Other genera
Seed: *Amphorispermum* Harris 1932.

Remarks
Affiliations: With the firmly established affiliations between its various organs and the well-preserved compression material from a good number of localities, the *Caytonia* plant has long been one of the few sound taxa in phylogenetic analyses of the gymnosperms.

References
Harris 1964: Yorkshire Jurassic.
Crane 1985: General, habit, text figures.
Cleal 1993: 'First & Last'.







1–7 from Crane 1985 (based on, or redrawn, from various sources)
8–9 from Harris 1964
mostly from Yorkshire Jurassic (1 from Polish Jurassic)

Order **PETRIELLALES** T.N.Taylor, G.M.Del Fueyo & E.L.Taylor 1994

Diagnosis: Ginkgoopsid plants with bulbous short-shoots bearing fascicles of lax, laminate, once-forked strobili with each axis bearing several alternate to subopposite pairs of megasporophylls consisting of single bilaterally symmetrical, reflexed cupules fully enclosing up to 5 ovules.

Remarks

The diagnosis is based on an unsatisfactory conflation of the two genera *Petriellaea* and *Kannaskoppia*, consisting of petrified and impression/compression material respectively. Considering the ovulate organs alone, the Petriellales are very close to the Caytoniales, but the microsporangiate strobili and foliage are entirely dissimilar, indicating the recognition of separate orders.

Families: Includes the two families Petriellaceae and Kannaskoppiaceae.

Family **PETRIELLACEAE** T.N.Taylor, G.M.Del Fueyo & E.L.Taylor 1994

Diagnosis: Petriellalean plants with megasporophylls consisting of a forked pair of multiovulate cupules.

Range: Gondwana, Tr(LAD)
First & Last: *Petriellaea triangulata* Taylor *et al.* 1994; Fremouw site, Fremouw Peak, Queen Alexandra Range, Transantarctic Mountains, Fremouw Fm., Beacon Supergroup.

Reference whole-plant genus & stratum—Fremouw Fm.
Female: *Petriellaea* Taylor *et al.* 1994; 1 TC, 1 sp., numerous cupules.
Male: Unknown.
Foliage: Unknown.

Stratum: Fremouw Fm., Antarctica, Tr(LAD).
Affiliations: Nil.

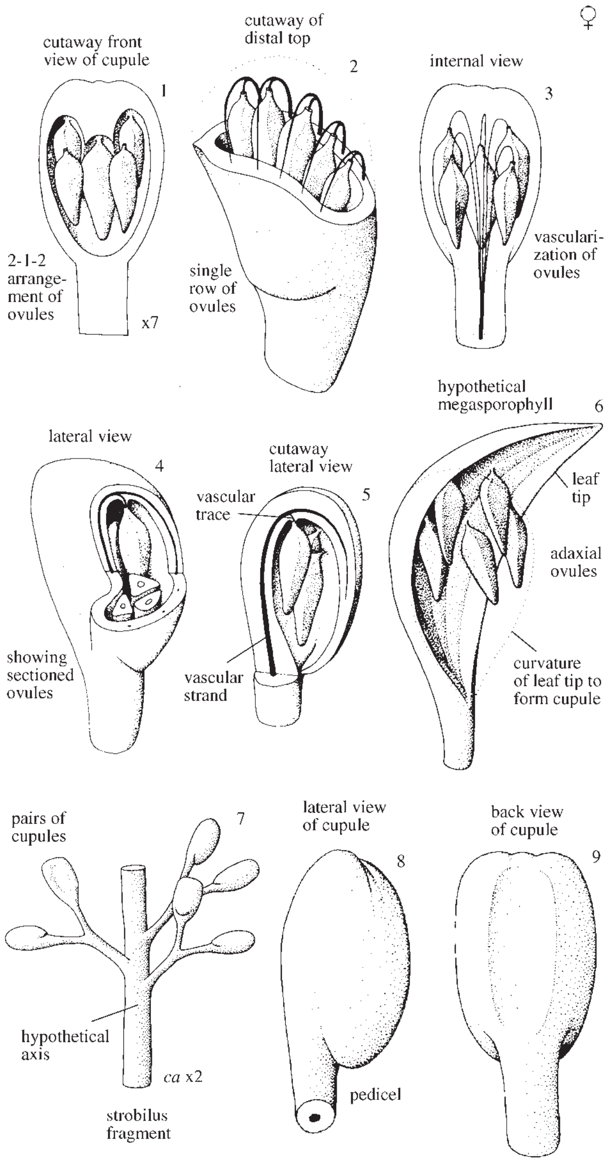
Prominence (colonisation success)—Gondwana Triassic
Frequency/ubiquity: *Petriellaea* remains known from a single site only.
Diversity: 1 species.
Abundance: Numerous cupules.
Longevity: <1 my.

Ecology
Habit: Unknown.
Habitat: Periphery of peat swamp.

Other genera—nil.

Remarks
Classification: The reconstruction of the strobilus fragment (tf 7) of *Petriellaea* is based on the interpretation of serial acetate peels of silicified peat samples, and is acknowledged to be uncertain (Taylor *et al*. 1994; Edie Taylor pers. comm. 1996). Our interpretation of the photos of the peels in Taylor *et al.* (1994) is that they might equally indicate megasporophyll morphology identical to that known for *Kannaskoppia* (p. 185), i.e. with rows of unpaired rather than paired cupules. Without further study this question remains unresolved and the genera are treated as distinct and as representing separate families within the order Petriellales.

Reference
Taylor et al. (1994): General.



Petriellaea triangulata

1–9 from Taylor *et al.* 1994
all Fremouw Fm., Antarctica

Family **KANNASKOPPIACEAE** And. & And. 2003

Diagnosis: Petriellalean plants with megasporophylls consisting of single, bilaterally symmetrical, reflexed cupules fully enclosing a (?)single ovule.

Range: Gondwana, Tr(OLN–RHT)
First: *Kannaskoppifolia* sp., Sydney Basin, New South Wales (And. & And. 2003).
Last: *Kannaskoppifolia* spp, Chile, New Zealand (And. & And. 2003).

Reference whole-plant genus & stratum—Molteno Fm.
Female: *Kannaskoppia* And. & And. 2003; 1 TC, 1 spp, 50 indivs.
Male: *Kannaskoppianthus* And. & And. 2003; 12 TCs, 4 spp, 92 indivs.
Foliage: *Kannaskoppifolia* And. & And. 2003; 25 TCs, 10 spp, <1%.

Stratum: Molteno Fm., Karoo Basin, S. Africa, Tr(CRN).
Affiliations: *Kannaskoppia*(5)*Kannaskoppifolia*(5)*Kannaskoppianthus*, Grade 5 (Org.att., Mut.occ., Mor.cor., Kin.rein.).

Prominence (colonisation success)—Gondwana Triassic (GT)
Kannaskoppifolia (foliage): Recorded in Chile, Argentina, South Africa, eastern Australia and New Zealand.

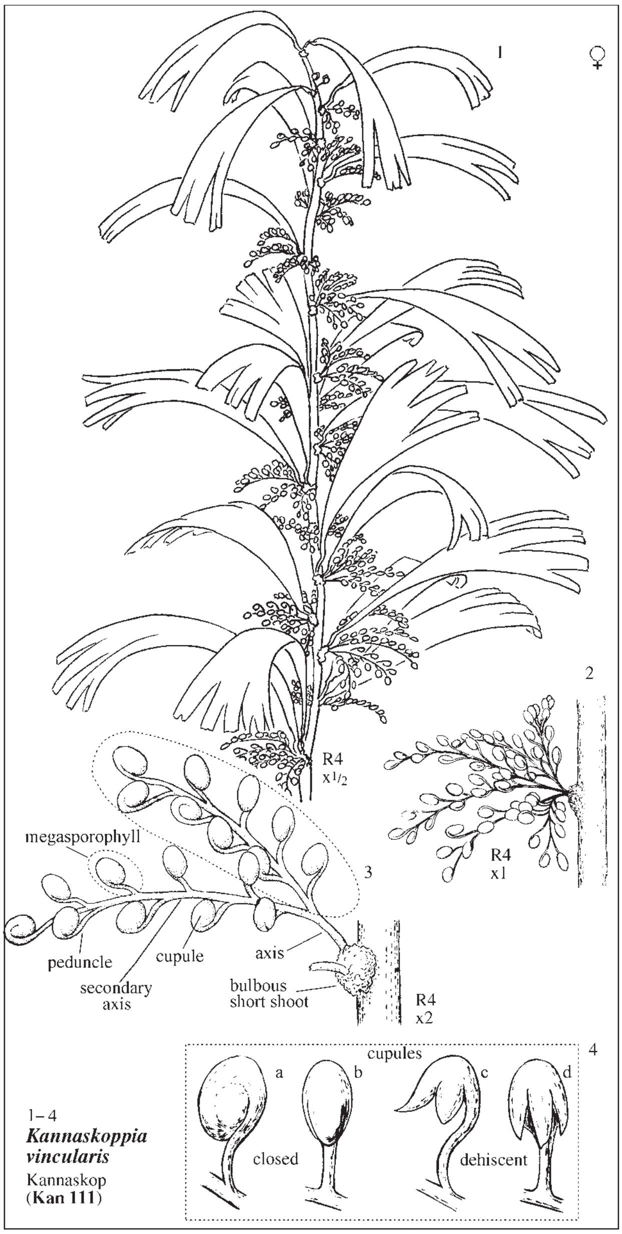
FUDAL rating: 23/3/10/–/26 = 62; the 5th most prominent gymnospermous foliage genus in the GT.
Frequency: High, 23 of 84 Gondw. degree squares.
Ubiquity: Moderate, 3 of 5 Gondw. continents.
Diversity: High, 10 species.
Abundance: Rare, <1% norm in Molteno TCs.
Longevity: High, 26 my through Triassic.

Ecology—Molteno Fm.
Habit: Herbaceous pioneers, from erect shrublets to climbers.
Habitat: Occupies a wide range of habitats, but principally *Dicroidium* riparian forest, *Heidiphyllum* thicket and fern meadows of riverine sandbanks and floodplain wetlands.

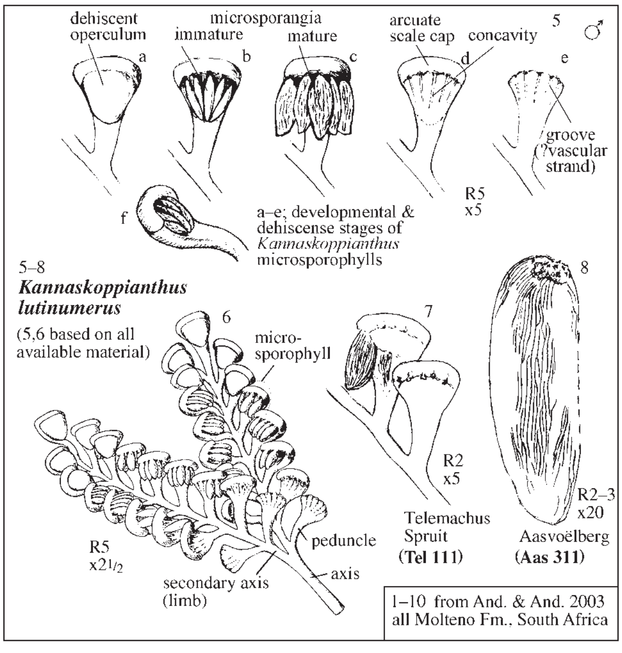
Other genera
Foliage: *Rhochipteris* Herbst *et al*. 2001.

Remarks
Comparison: *Kannaskoppia*/*Kannaskoppifolia* is preserved as impressions and compressions providing an excellent idea of the general morphology (including cuticle) of the plant, but with no anatomical detail known. *Petriellaea* (ovulate material only), in the family *Petriellaceae*, occurs in a permineralised peat deposit providing fine anatomical detail, but the general morphology is poorly understood. It is possible that the two plants will prove to be one and the same, but this cannot be demonstrated at present.

Reference
And. & And. (2003): General.



1–4
Kannaskoppia vincularis
Kannaskop
(**Kan 111**)

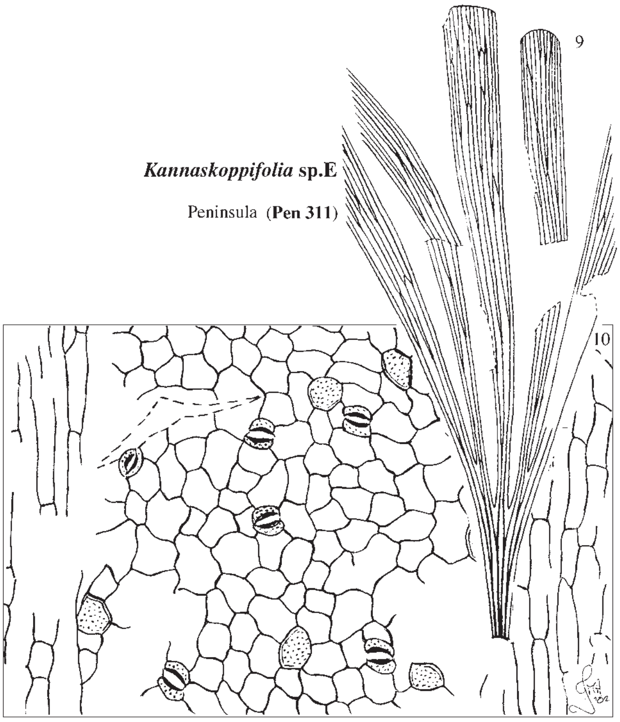


5–8
Kannaskoppianthus lutinumerus
(5,6 based on all available material)

Telemachus Spruit
(**Tel 111**)

Aasvoëlberg
(**Aas 311**)

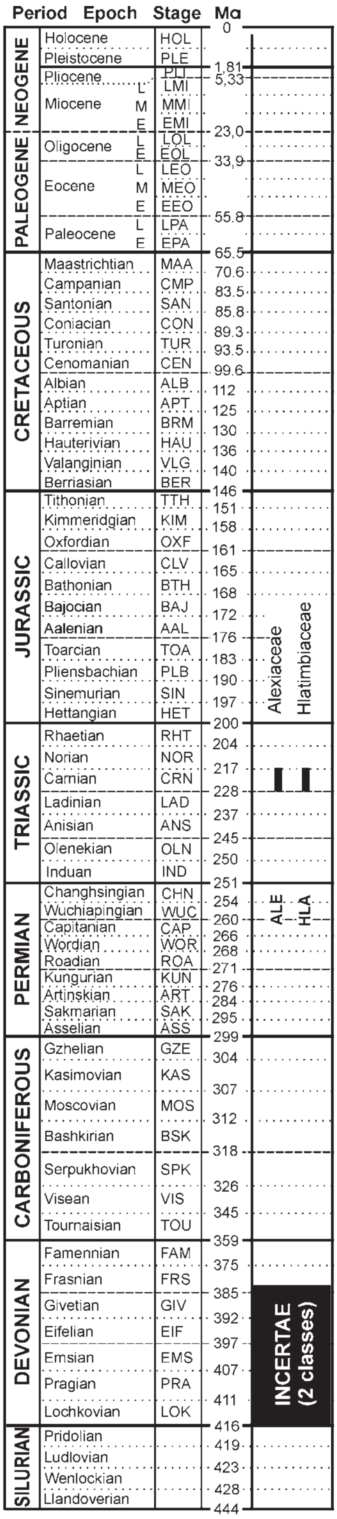
1–10 from And. & And. 2003
all Molteno Fm., South Africa



***Kannaskoppifolia* sp.E**
Peninsula (**Pen 311**)

Kannaskoppifolia vincularis lower **Lit 111** x100

Fig. 28. INCERTAE SEDIS: FAMILY RANGE CHART



Tab. 30. INCERTAE SEDIS

CLASS ORDER Family	generic diversity			affiliation grade			morphology grade			anatomy preserved		
	♀	♂	⬯	♀	♂	⬯	♀	♂	⬯	♀	♂	⬯
INCERTAE SEDIS (2 classes)												
ALEXIALES And. & And. 2003												
Alexiaceae And. & And. 2003	1	-	-	5	-	-	2	-	-	-	-	-
HLATIMBIALES And. & And. 2003												
Hlatimbiaceae And. & And. 2003	1	-	-	5	-	2	3	-	3	-	-	-

Class **INCERTAE SEDIS**

Orders: Includes the single order Alexiales.

Order **ALEXIALES** And. & And. 2003

Diagnosis: Putative gymnosperms bearing linear strobili with numerous subopposite to alternate, simple, small, pitcher-shaped cupules completely enclosing a (?)single ovule.

Classification & phylogeny

Like a high proportion of the Molteno Fm. megasporangiate strobili, *Alexia* appears unlike any other gymnospermous genus, fossil or extant. It appears to be the sole known representative of a distinct order and class. ‘It is possible, though very unlikely, that *Alexia* is a fern belonging to a new advanced order with elaborately developed, pitcher-shaped indusia and fully modified/reduced fertile fronds; with the indusia attached directly to the midrib. Maceration has revealed no spores or ovules to resolve this question. It is not impossible, on the other hand, that we are dealing with some stem-angiosperm. Is the ovary fully enclosed? Are the ovules bitegmic? What of the presence of endosperm? And what of double fertilization?’ (And. & And. 2003).

Families: Includes the single family Alexiaceae.

Family **ALEXIACEAE** And. & And. 2003

Diagnosis: As for Alexiales above.

Range: Gondwana, Tr(CRN)
First & Last: *Alexia urceolus* And. & And. 2003; Molteno Fm., S. Africa.

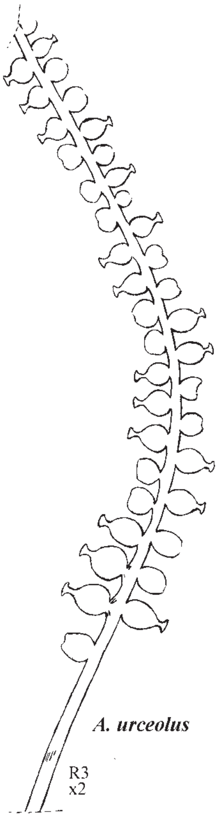
Reference genera & stratum—Molteno Fm.
Female: *Alexia* And. & And. 2003; 1 TC, 1 sp., vanishingly rare.
Male: Unknown.
Foliage: Unknown.

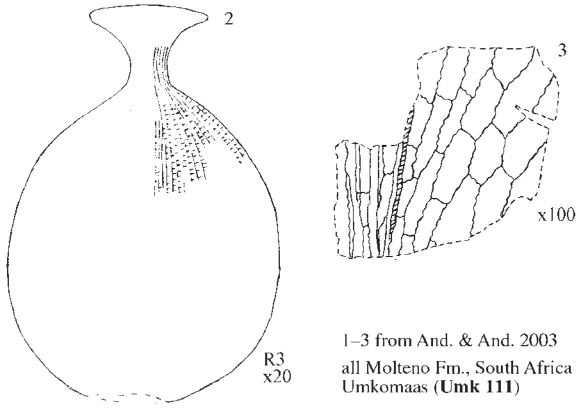
Stratum: Molteno Fm., Karoo Basin, S. Africa, Late Triassic (CRN).
Affiliations: Nil.

Prominence (colonisation success)—Gondwana Triassic (GT)
With no foliage affiliate proposed for *Alexia*, the plant remains obscure, but it may be assumed that it was an extremely rare and probably endemic element.

Ecology
Habit/habitat: Unknown.

Reference
And. & And. (2003): General.





1–3 from And. & And. 2003
all Molteno Fm., South Africa
Umkomaas (**Umk 111**)

Class **INCERTAE SEDIS**

Orders: Includes the single order Hlatimbiales.

Order **HLATIMBIALES** And. & And. 2003

Diagnosis: Putative gymnosperms bearing large, lax, planar, paniculate strobili with several alternate, linear megasporophylls consisting of numerous, alternate, pedicellate, bivalved cupules (ovules unknown).

Classification & phylogeny: At first glance, *Hlatimbia* gives the impression of being a rather bizarre form of fertile fern found, but the bivalved (?ovuliferous) cupules and the absence of sori place the genus clearly in the gymnosperms. It is unlike any other known ovuliferous structure, though, and surely represents a new order and possibly a new class of plants.

Families: Includes the single family Hlatimbiaceae.

Family **HLATIMBIACEAE** And. & And. 2003

Diagnosis: As for the order Hlatimbiales.

Range: Gondwana, Tr(CRN)
First & Last: *Hlatimbia tommacleanii* And. & And. 2003, Molteno Fm. Since the affiliation with the foliage *Batiopteris* is insufficiently established, the range of this family is based solely on the ovulate fruit.

Reference whole-plant genus & stratum—Molteno Fm.
Female: *Hlatimbia* And. & And. 2003; 1 TC, 1 spp, 2 indivs.
Male: Unknown.
Foliage: *Batiopteris* And. & And. 2003; 10 TCs, 5 spp, <1% indivs.

Stratum: Molteno Fm., Karoo Basin, S. Africa, Late Triassic (CRN).
Affiliations: *Hlatimbia*(2)*Batiopteris*, Grade 2 (Mut.occ.)

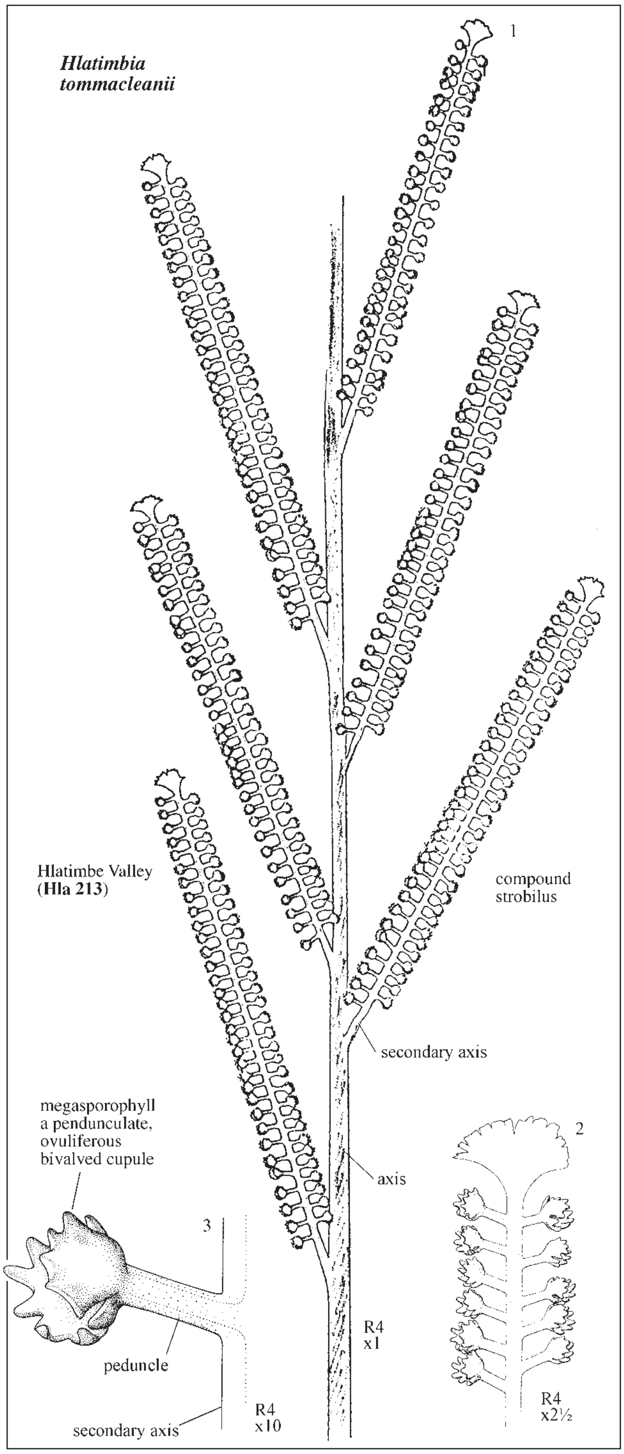
Prominence (colonisation success)—Gondwana Triassic (GT)
Batiopteris (foliage): Recorded in northern Argentina, South Africa and Tasmania.

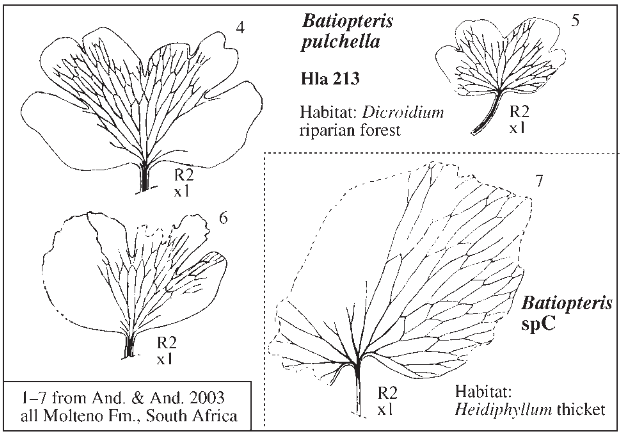
FUDAL rating 7/3/7/–/2 = 19; the 18th most prominent gymnospermous foliage genus in the GT.
Frequency: Low, 7 of 84 Gondw. degree squares.
Ubiquity: Moderate, 3 of 5 Gondw. continents.
Diversity: Moderate, 7 species in GT.
Abundance: V. rare, <1% norm in Molteno TCs.
Longevity: V. low, 2 my through Triassic.

Ecology
Habit: Interpreted as twiners and scramblers.
Habitat: A range of forested and woodland habitats.

Other genera—nil.

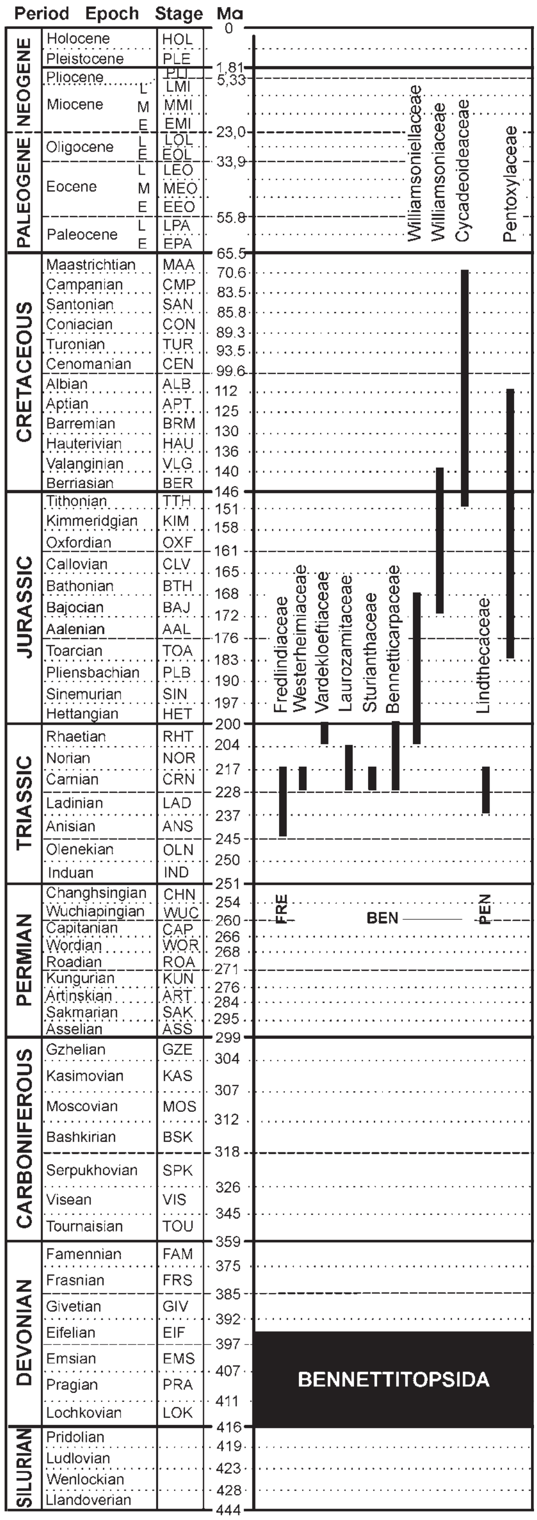
Reference
And. & And. (2003): General, foliage.





1–7 from And. & And. 2003
all Molteno Fm., South Africa

Fig. 29. BENNETTITOPSIDA: FAMILY RANGE CHART



Class **BENNETTITOPSIDA** Engl. 1897

Diagnosis: Gymnospermous plants with compact multiovulate 'gynoecia' composed of a honeycomb-like aggregate of ovuliferous and (in some families) sterile cells.

Classification

Reflecting the cladistic analyses of Crane (1985) and Doyle & Donoghue (1986), Cleal (1993) recognised a class Gnetopsida including the three orders Bennettitales, Pentoxylales and Gnetales, each including a single family. Within the context of the origins of these clades in the Triassic radiation, we see far greater diversity at all ranks: the Bennettitopsida and Gnetopsida are taken as distinct classes, including three orders (11 families) and seven orders (10 families) respectively.

Families: The recognition of families within the Bennettitopsida, more particularly the Bennettitales, is far from resolved. Traditionally only two families have been accepted, the Cycadeoidaceae and the Williamsoniaceae (Crane 1988; Watson & Sincock 1992). We agree, however, with Watson & Sincock (1992) that the great diversity of form within the Bennettitales warrants the recognition of more families—we suggest eight, as described here.

Phylogeny (cladistics)

In the classic earlier works on gymnosperm cladistics (Crane 1985, 1986, 1988; Doyle & Donoghue 1986), an uneasy consensus was reached that a Bennettitales-*Pentoxylon*-Gnetales clade could be recognised as the sister group of the angiosperms—the whole being referred to as the 'anthophytes'. Within the 'anthophytes', the Bennettitales and *Pentoxylon* were generally seen as sister taxa.

Far greater ambiguity emerged in subsequent phylogenetic analyses of the next decade, particularly with the entry of new researchers in the field (Doyle & Donoghue 1992, 1993; Nixon *et al*. 1994; Rothwell & Serbet 1994; Doyle 1996). Considering a series of representative, most parsimonious cladograms, the Bennettitales were variously seen, for instance, as the sister group of the Gnetales (Doyle & Donoghue 1992); of the angiosperms plus Gnetales (Rothwell & Serbet 1994); of *Caytonia* plus the angiosperms (Doyle 1996); or even as nested within the Gnetales (Nixon *et al.* 1994). *Pentoxylon* plots out equally ambiguously: as sister group, for instance, of the Bennettitales plus Gnetales (Doyle & Donoghue 1992); of the Bennettitales, angiosperms plus Gnetales (Rothwell & Serbet 1994); of a whole *Cordaitales*-*Ginkgo*-conifers-Gnetales-Bennettitales-angiosperm clade (Nixon *et al*. 1994); or even of the glossopterids (Doyle 1996).

The ambiguity persists. As Kenrick (pp 18, 19, this volume) states in his current review of the subject, relationships amongst the better and longer established orders of extinct gymnosperms (e.g. Cordaitales, Corystospermales, Peltaspermales, Glossopteridales, Pentoxylales, Caytoniales, Bennettitales) 'are still poorly resolved, and several plausible alternative topologies exist (Doyle 1998)'. The cladogram illustrated by Kenrick (p. 19) shows the Bennettitales and Gnetales as sister orders, with this combined clade as sister to *Caytonia* plus the angiosperms—and *Pentoxylon* as sister to a clade comprising all four. Our classification, after consideration of the new (And. & And. 2003) families, Fredlindiaceae and Lindthecaceae, from the Late Triassic Molteno Fm., differs from this cladogram in one major regard: the Pentoxylales and Bennettitales are considered sister orders within a class Bennettitopsida, taking us back, largely, to the classic works of the middle to late 1980s.

Biodiversity

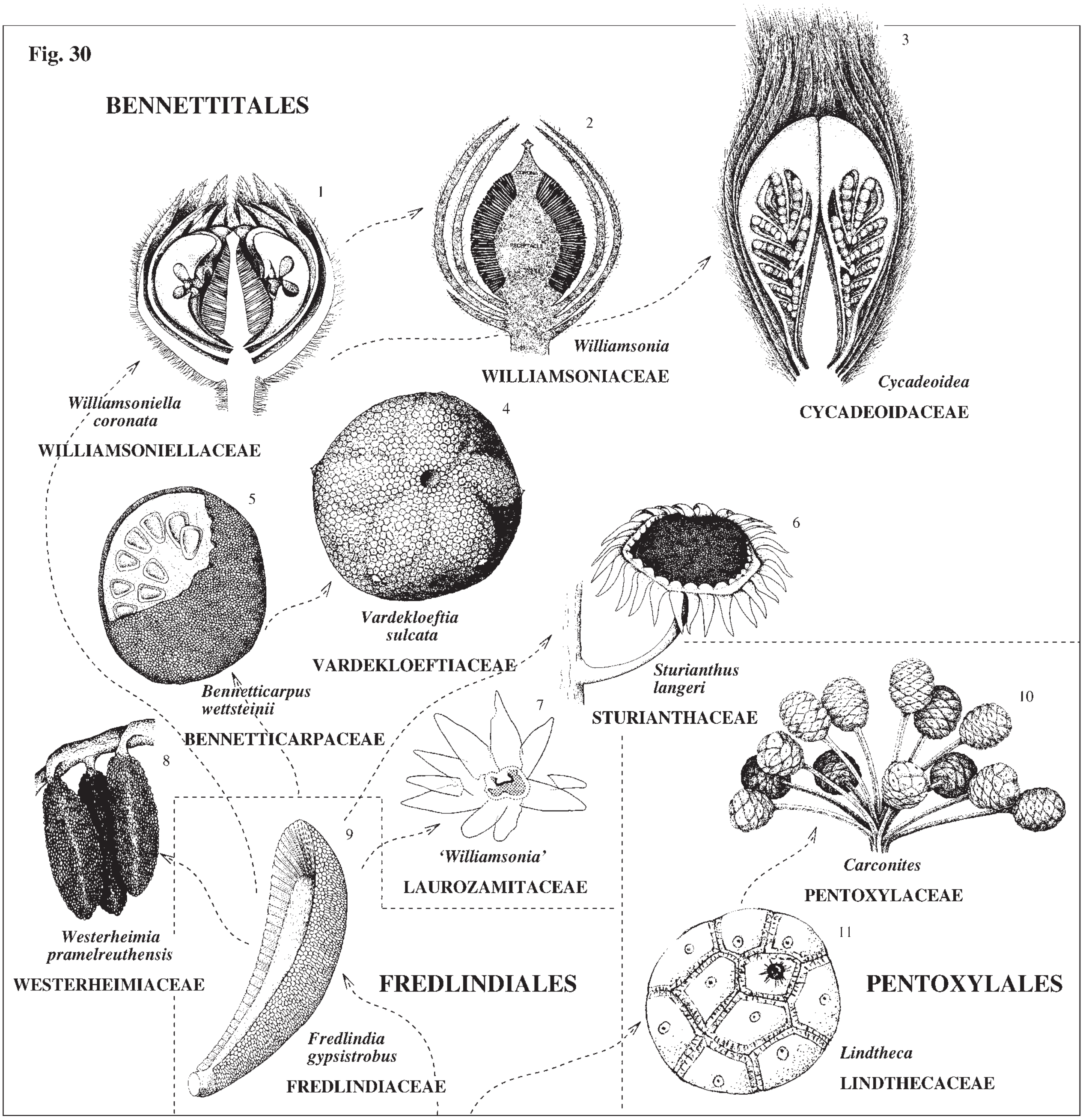
From the wide morphological range displayed by the eight known Late Triassic bennettitopsid ovulate genera and from their pattern of rarity and endemism (Tab. 17, p. 28), it seems likely that concerted collecting will reveal many more genera from this early phase of the radiation of the clade. It is generally recognised that the group was significantly more diverse at generic level during this initial Late-Triassic flush of their evolution than at any later time during the Jurassic or Cretaceous (e.g. Crane 1986; Watson & Sincock 1992; Kimura & Van Konijnenburg-Van Cittert pers. comm. 1995). This substantiates the emerging picture of unique gymnosperm diversity in the Late Triassic.

References: And. & And. 1989, 2003; Harris 1932b, 1969; Ash 1968, 1975; Crane 1985, 1986, 1988; Doyle & Donoghue 1986, 1992, 1993; Dobruskina 1988, 1998; Pedersen, Crane & Friis 1989; Watson & Sincock 1992; Stewart & Rothwell 1993; Taylor & Taylor 1993; Nixon *et al.* 1994; Rothwell & Serbet 1994; Weber & Zamudio-Varela 1995; Doyle 1996, 1998.

Orders: Includes the three orders Fredlindiales, Bennettitales and Pentoxylales.

CLASS ORDER Family — Tab. 31. BENNETTITOPSIDA	generic diversity			affiliation grade			morphology grade			anatomy preserved		
	♀	♂	0	♀	♂	0	♀	♂	0	♀	♂	0
BENNETTITOPSIDA Engl. 1897												
FREDLINDIALES And. & And. 2003												
Fredlindiaceae And. & And. 2003	1	1	1	5	3	3	3	2	4	-	-	-
BENNETTITALES Engl. 1892												
Westerheimiaceae Němejc 1968	1	1	1	5	3	3	3	3	1	-	-	-
Varderkloeftiaceae And. & And. fam. nov.	1	1	1	5	3	3	4	2	3	-	-	-
Laurozamitaceae And. & And. fam. nov.	1	-	1	5	-	3	2	-	4	-	-	-
Sturianthaceae Doweld 2001	1	-	-	5	-	-	3	-	-	-	-	-
Bennetticarpaceae And. & And. fam. nov.	1	1	1	5	3	3	3	2	2	-	-	-
Williamsoniellaceae Nakai 1943	2	2	2	5	5	4	4	4	4	-	-	-
Williamsoniaceae (Carruth. 1870) Nath. 1913	1	1	1	5	3	3	4	4	4	-	-	-
Cycadeoidaceae R.Br. ex G.R.Wieland 1908	2	2	1	5	5	5	4	4	4	✓	✓	✓
PENTOXYLALES Pilg. & Melch.1954												
Lindthecaceae And. & And. 2003	1	-	1	5	-	3	3	-	3	-	-	-
Pentoxylaceae Pilg. & Melch. 1954	1	1	1	5	3	4	4	4	4	✓	✓	-

Fig. 30



Order **FREDLINDIALES** And. & And. 2003

Diagnosis: Bennettitopsid plants with bilaterally symmetrical 'gynoecia', attached in whorls, and without differentiation into sterile cells (interseminal scales) and ovuliferous 'cells' (ovules).

Classification & phylogeny

Fredlindia, with its putative foliage affiliate *Halleyoctenis*, is clearly bennettitopsid in morphology. Including it within the order Bennettitales, though, would necessitate significantly expanding the diagnosis of that well known clade. Hence the erection (And. & And. 2003) of the new order within the class Bennettitopsida. Aside from the strikingly distinctive ovulate fruit, the foliage cuticle with anomocytic stomata and straight cell walls, sets this taxon apart (but see *Laurozamitaceae*).

Families: Includes the single family Fredlindiaceae.

Family **FREDLINDIACEAE** And. & And. 2003

Diagnosis: As for the order Fredlindiales.

Range: Gondwana, Tr(ANS–CRN)
First: *Halleyoctenis multilineata* (Shirley 1897) And. & And. 1989; Bryden Fm., Clarence-Moreton Basin, Queensland, Anisian (foliage only, And. & And. 1989).
Last: *Fredlindia fontifructus* And. & And. 2003; Molteno Fm., South Africa, Carnian.

Reference whole-plant genus & stratum—Molteno Fm.
Female: *Fredlindia* And. & And. 2003; 4 TCs, 1 sp., 17 indivs.
Male: *Weltrichia* Braun 1847; 2 TCs, 2 spp, 3 indivs.
Cycadolepis Saporta 1873; 3 TCs, 1 sp., 14 indivs.
Foliage: *Halleyoctenis* And. & And. 1989; 10 TCs, 2 spp, 2%.

Stratum: Molteno Fm., S. Africa, Late Triassic (Carnian).
Affiliations: *Fredlindia*(3)*Halleyoctenis*(3)*Weltrichia/Cycadolepis*, Grade 3 (Mut.occ., Kin. rein.).

Prominence (colonisation success)—Gondwana Triassic (GT)
Halleyoctenis (foliage): Recorded in South Africa (Karoo Basin) and Australia (Clarence-Moreton Basin).

FUDAL rating: 7/2/3/2/9 = 23; the 14th most prominent gymnospermous foliage genus in the GT.
Frequency: Low, 7 of 84 Gondw. degree squares.
Ubiquity: Low, 2 of 5 Gondw. continents.
Diversity: Low, 3 species in Gondw. Trias.
Abundance: Moderate, 2% norm in Molteno TCs.
Longevity: Moderate, 9 my through Triassic.

Ecology—Molteno Fm.
Habit: All three species interpreted as slender, somewhat cycad-like plants.
Habitat: Scattered through open woodland of the Molteno floodplain.

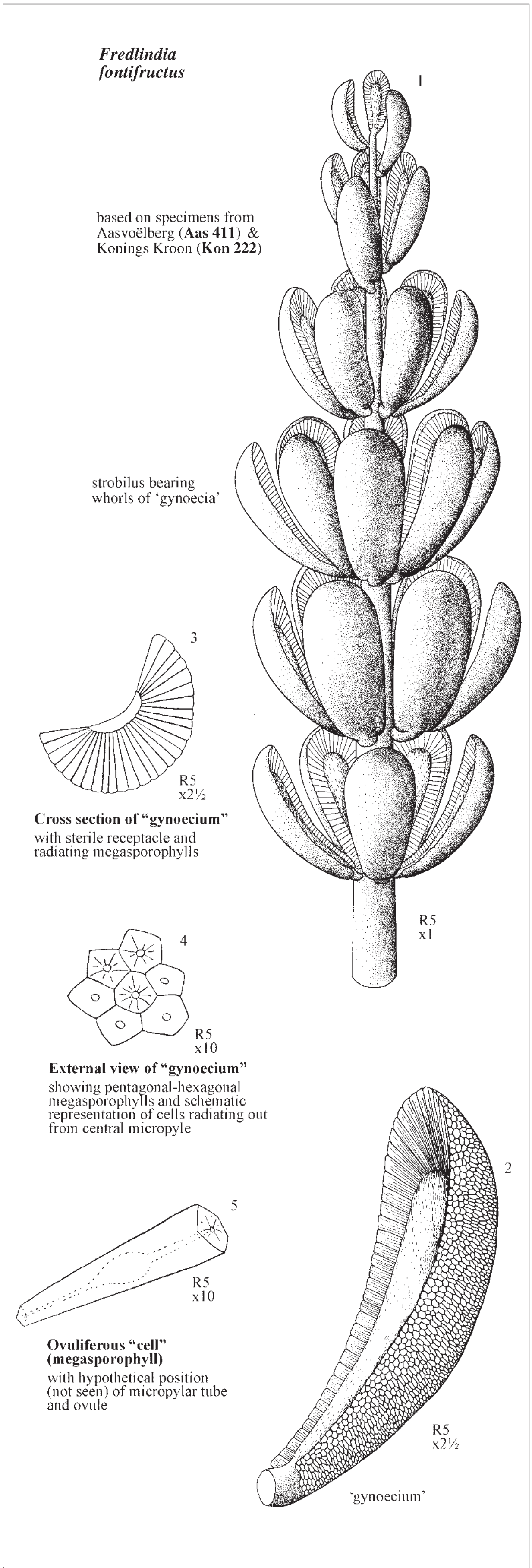
Other genera—nil.

Remarks

Foliage affiliation: *Halleyoctenis*, from 10 of 100 TCs in the Molteno Fm., is clearly the most 'probable' affiliate of *Fredlindia* (And. & And. 2003). Fragments or isolated gynoecia of *Fredlindia* occur in four (only three recorded in And. & And. 2003) Molteno TCs, each of which yields *Halleyoctenis*. In the Clarence-Moreton Basin, Queensland, the only other place in the GT where *Halleyoctenis* is known, the two genera co-occur in two TCs. Supporting the co-occurrence evidence for affiliation is that both *Halleyoctenis* (pinnae, cuticles) and *Fredlindia* (gynoecia, megasporophylls) display obviously bennettitalean features.

Male affiliation: The male affiliate of *Fredlindia* and *Halleyoctenis* remains ambiguous (And. & And. 2003). Three presumed-male genera, *Cycadolepis*, *Weltrichia* and *Leguminanthus* (tfs 1–8, p. 191 opposite), co-occur at the Molteno Fm. Konings Kroon (Kon 222) locality with both the ovulate and foliage genera. Any, or all three, of the male genera could be the affiliates: in And. & And. 2003, we favoured *C. rexiplumea* and *W. regalis*, but *L. leopardus* is perhaps equally likely. Consideration of the Williamsoniellaceae (p. 197) and Cycadeoidaceae (p. 199) hermaphrodite flowers, suggests that the three Kon 222 organs might combine into one microsporangiate 'flower'—with *Leguminanthus* (reminiscent of the later Mesozoic microsporophylls) occurring in a whorl within or around the *Weltrichia* cup and enclosed within a 'perianth' of many *Cycadolepis* bracts.

References
And. & And. (1989, 2003): General.


Fredlindia fontifructus

based on specimens from Aasvoëlberg (**Aas 411**) & Konings Kroon (**Kon 222**)

strobilus bearing whorls of 'gynoecia'

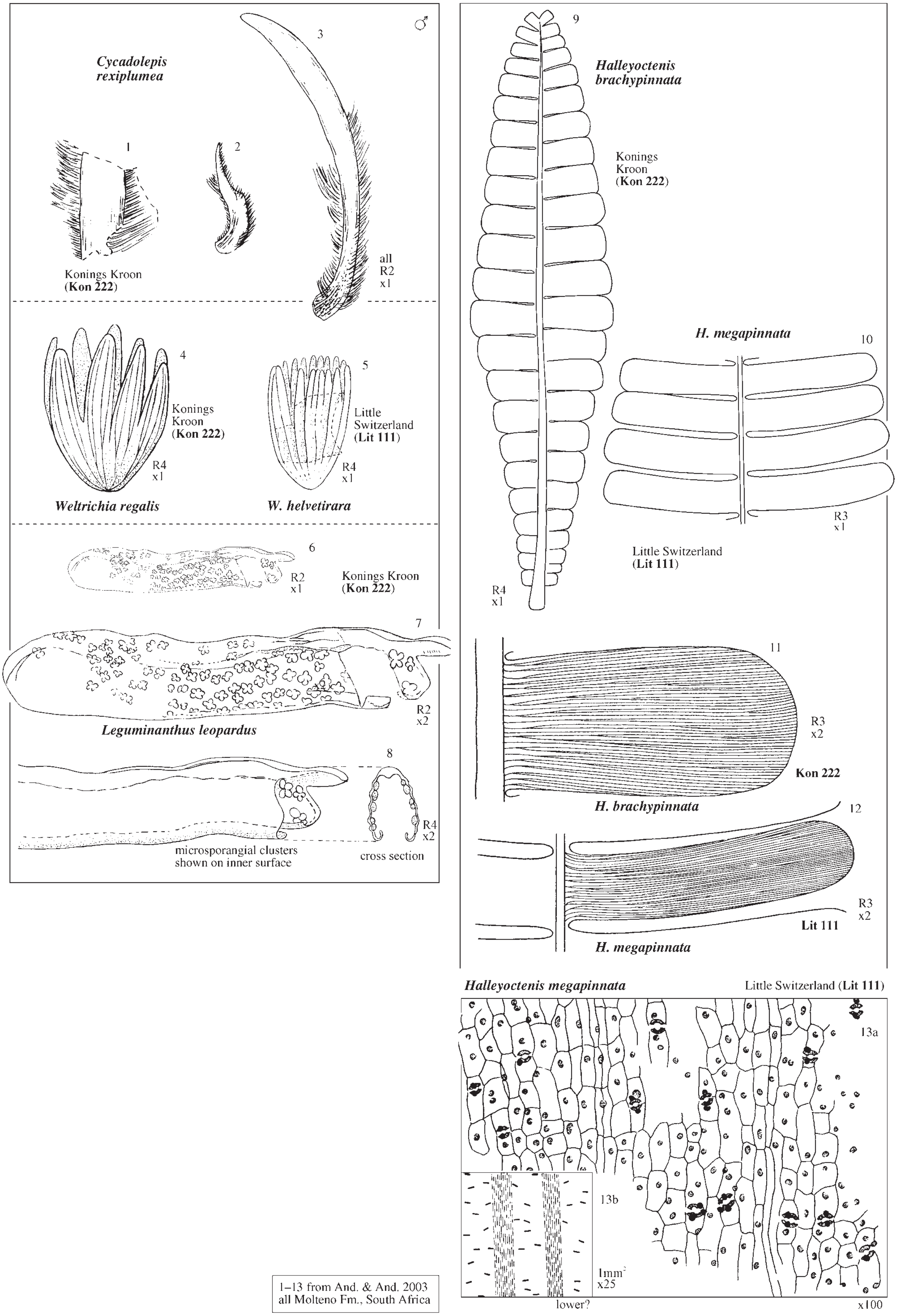
Cross section of "gynoecium" with sterile receptacle and radiating megasporophylls

External view of "gynoecium" showing pentagonal-hexagonal megasporophylls and schematic representation of cells radiating out from central micropyle

Ovuliferous "cell" (megasporophyll) with hypothetical position (not seen) of micropylar tube and ovule

'gynoecium'

1–5 from And. & And. 2003
all Molteno Fm., South Africa



1–13 from And. & And. 2003
all Molteno Fm., South Africa

Order **BENNETTITALES** Engl. 1892

Diagnosis: Bennettitopsid plants with radially symmetrical ‘gynoecia’, attached individually or spirally on lax cones, and with or without clear differentiation into numerous sterile and ovuliferous cells.

Remarks
Prominence: The Bennettitales are prominent and widespread globally from the Late Triassic to the mid-Cretaceous (and extend more rarely to near the end Cretaceous). Though bennettitalean foliage is often abundant in the Late Triassic (e.g. USA, Mexico), the ovulate structures, as is clearly evident in Tab. 17 (p. 28), are infrequent and rare in this interval.

Late Triassic Endemism: As currently known, the bennettitalean ovulate genera of this interval indicate a high degree of endemism: the six non-Gondwana genera are each restricted to a narrow region of occurrence.

Families: Includes the eight families Westerheimiaceae, Vardekloeftiaceae, Laurozamitaceae, Sturianthaceae, Bennetticarpaceae, Williamsoniellaceae, Williamsoniaceae and Cycadeoidaceae.

Family **WESTERHEIMIACEAE** Němejc 1968

Diagnosis: Bennettitalean plants with unisexual ‘flowers’ on stocky pedicels attached pinnately to form a lax cone; ‘gynoecia’ elliptical, without apparent external differentiation into ovulate and interseminal scales; without a ‘perianth’ of bracts?

Range: Euramerica, Tr(CRN)
First & Last: *Westerheimia pramelreuthensis* Krasser 1918; Lunz, Austria, Carnian.

Reference whole-plant genus & stratum—Lunz plant beds
Female: *Westerheimia* Krasser 1918; 1 TC, 1 sp., *ca* 10 indivs.
Male: *Leguminanthus* Kräusel & Schaarschmidt 1966; ? TCs, 1 sp., 22 indivs.
Foliage: *Pterophyllum* Brongniart 1828; ? TCs, 2 spp, 50%.

Stratum: Lunz plant beds, Austria, Late Triassic (Carnian).
Affiliations: *Westerheimia*(3)*Pterophyllum*(3)*Leguminanthus*, Grade 3 (Mut.occ., Kin.rein.)

Prominence (colonisation success)—Europe Late Triassic
Frequency/ubiquity: *Westerheimia* known from a single area in Europe.
Diversity: 1 species (of ovulate organ).
Abundance: *ca* 10 individuals from a single ‘locality’.
Longevity: <1 my.

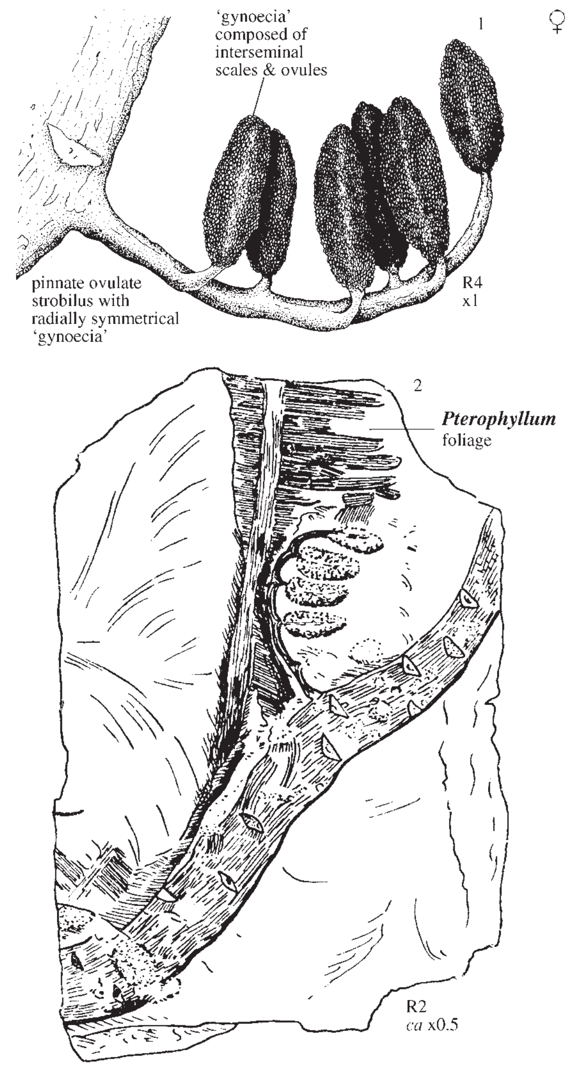
Ecology
Habit: Unknown.
Habitat: Deltaic/estuarine, subtropical latitudes.

Other genera—nil.

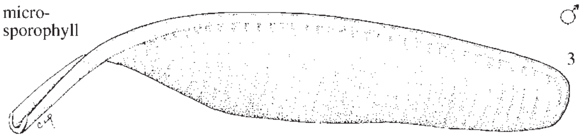
Remarks
Morphology: Crane (1988) notes that the ovulate reproductive structures consist of ‘typical bennettitalean “gynoecia” composed of interseminal scales and ovules’, but that there is no evidence that they were ‘subtended by a “perianth” or microsporophylls’. He adds that one of the specimens (tf. 2 adjacent) ‘clearly shows that *Westerheimia* was borne laterally on a vegetative axis’, though ‘it is unclear whether *Westerheimia* is a branch with several lateral branches, a branch with several megasporophylls, or a single megasporophyll with the “gynoecia” borne on lateral pinnae’.

Affiliations: For consideration of affiliations, see notes (p. 195) on the Lunz flora under Sturianthaceae and the table (Tab. 17, p. 28) of known bennettitopsid ovulate genera, with frequency and abundance, for the global Late Triassic. Three genera of ovulate organ (*Westerheimia*, *Sturianthus*, *Bennetticarpus*), three of pollen organ (*Leguminanthus*, *Haitingeria*, *Cycadolepis*) and three of foliage (*Pterophyllum*, *Anomozamites*, *Nilssonia*) are recorded in the Lunz flora. *Westerheimia*, *Leguminanthus* and *Pterophyllum* are clearly the most common of the three organs respectively. Short of further information, we consider these three genera the most likely affiliates. (It should be noted that Crane 1988 refers to *Cycadolepis wettsteinii* bracts as forming the ‘perianth’ of *Bennetticarpus wettsteinii*.) Although *Pterophyllum*, the dominant foliage genus at Lunz (50% of the flora), occurs associated with *Westerheimia* on the slab figured adjacent (tf. 2), it is not attached, and there is no confirmation of affiliation. (See also under ‘Affiliations’ for Bennetticarpaceae, p. 196.)

References
Crane (1986, 1988): Morphology.
Dobruskina (1988, 1998), And. & And. (2003): Lunz flora.

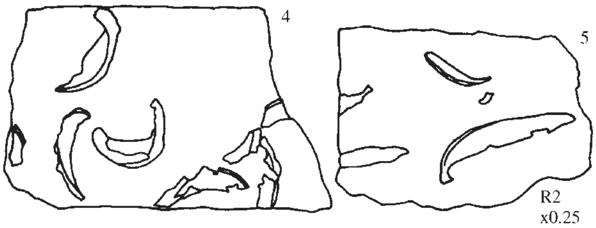


Westerheimia pramelreuthensis



Leguminanthus siliquosus
(Leuthardt) Kräusel & Schaarschmidt

pollen sacs: ellipsoidal, overlapping, in numerous rows on inner (adaxial) surface of the lamina



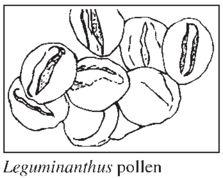
2 fossiliferous slabs showing scatter & size variation of microsporophylls

pollen: monosulcate, ellipsoidal, 14–20 µm long

cuticle: with numerous bennettitalean stomata

1 from Crane 1988 (based on Kräusel 1949)
2 from Gothan & Weyland 1973
3–5 from Crane 1986
6 J.M. Anderson sketch
from Kräusel & Schaarschmidt 1966

all **Lunz,** Austria;
Late Triassic (Carnian)



Leguminanthus pollen
Neuewelt bei Basel

Family **VARDEKLOEFTIACEAE** And. & And. nov.

Diagnosis: Bennettitalean plants with unisexual ‘flowers’ on gracile pedicels (attachment unknown); ‘gynoecia’ small, spherical, with clear external differentiation into very few (typically 5) ovulate and numerous interseminal scales; without a ‘perianth’ of bracts.

Range: Euramerica, Tr(RHT)
First & Last: *Vardekloeftia sulcata* Harris 1932b; Kap Stewart Fm., Scoresby Sound, Greenland, Rhaetic.

Reference whole-plant genus & stratum—Kap Stewart Fm.
Female: *Vardekloeftia* Harris 1932b; 2 TCs, 1 sp., 17 indivs.
Male: *Bennettistemon* Harris 1932b; 1 TC, 2 spp, ?rarity.
Foliage: *Pterophyllum* Brongniart 1828; 1 TC, 9 spp, ?abundance.

Stratum: Kap Stewart Fm., East Greenland, Late Triassic (Rhaetic).
Affiliations: *Vardekloeftia*(3)*Pterophyllum*(3)*Bennettistemon*(3), Grade 3 (Mut.occ., Cut.cor., Kin.rein).

Prominence (colonisation success)—Euramerica Late Triassic
Frequency/ubiquity: Based on the ovulate organ alone, *Vardekloeftia* is confined to a single region of Euramerica.
Diversity: 1 species (of ovulate organ).
Abundance: 17 isolated ‘gynoecia’ or fragments of ‘gynoecia’ and *ca* 35 dispersed seeds from 2 localities.
Longevity: <1 my.

Ecology
Habit: Unknown.
Habitat: Low-lying, midlatitude.

Other genera—nil.

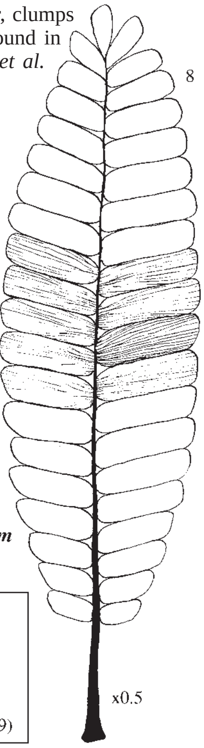
Remarks
Family recognition: In the view of Watson & Sincock (1992), the cladistic analyses of Crane (1986, 1988) showed *Vardekloeftia* to be sufficiently distinctive to warrant placing in a new family. They never, however, formalised such a family, nor has any author since.

Morphology: These small, grape-sized fruit would have contrasted strongly with the other Late Triassic members of the order, the lemon- to grapefruit-sized *Bennetticarpus* (p. 196). Important, also, for ‘distinguishing *Vardekloeftia* from other bennettitalean reproductive structures’, according to Pedersen *et al*. (1989), are the ‘small stalk scars’.

Affiliations: Based on the mutual occurrence of *Vardekloeftia sulcata* and *Pterophyllum kochi*, particularly the localised abundance of both in a part of the Vardekløft *Stachyotaxus* bed, Harris (1932b) first proposed the affiliation of these organs. He also recorded the cuticular correspondence, notably the cuticularised stomatal thickenings, between the female organs and foliage.

Both the pollen organs *Bennettistemon amblum* and *B. ovatum* likewise occur in association with *Vardekloeftia*. Moreover, clumps of pollen very like that from these species are found in the micropyles of *Vardekloeftia* seeds (Pedersen *et al.* 1989).

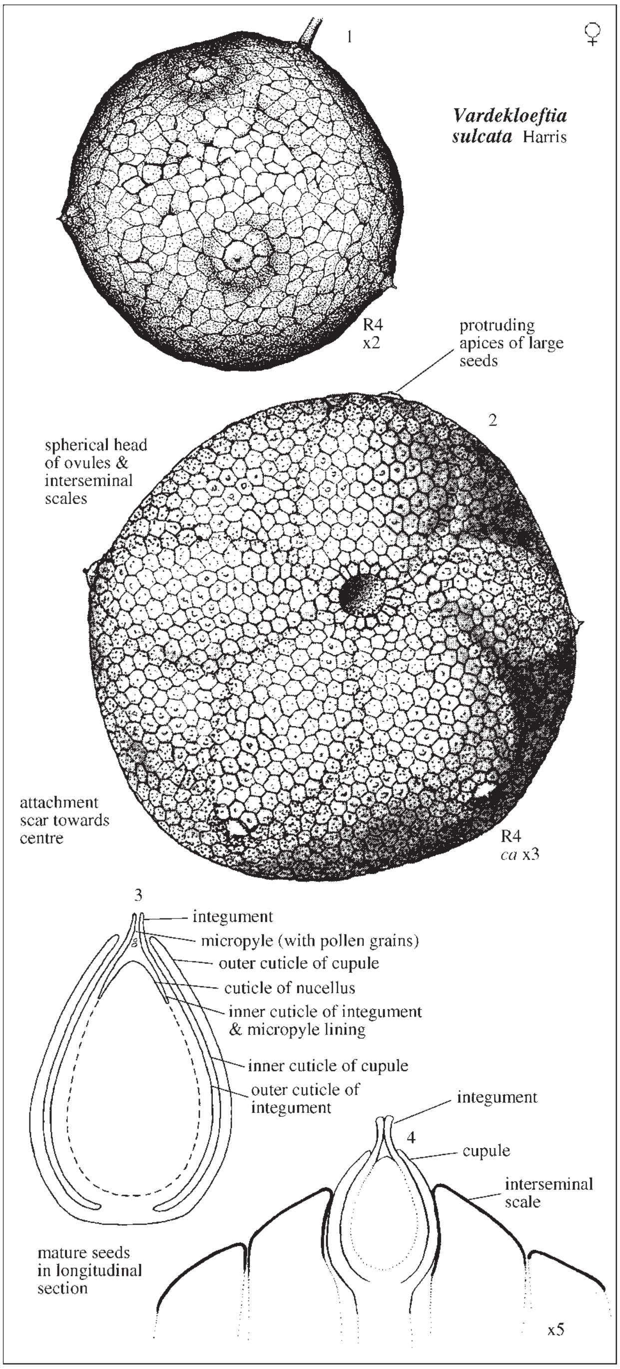
References
Crane (1985, 1988): Phylogeny.
Crane (1986): Pollen organs.
Pedersen et al. (1989): General, affiliations.



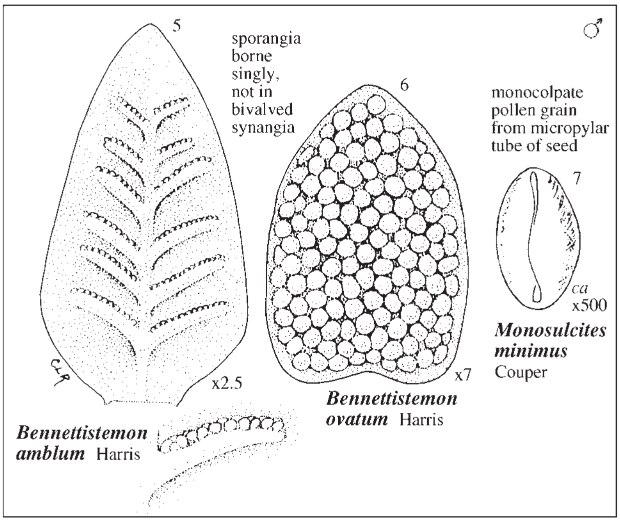
Pterophyllum kochii

all **Astartekløft or Vardekløft**,
Hurry Inlet, Scoresby Sound, East Greenland;
Kap Stewart Fm., Late Triassic (Rhaetic)

1,4,8 from Crane 1985 (all based on Harris 1932b)
2,3 from Raunsgaard Pedersen *et al.* 1989
5,6 from Crane 1986
7 J.M. Anderson sketch (based on Pedersen *et al.* 1989)



Vardekloeftia sulcata Harris



Bennettistemon amblum Harris

Bennettistemon ovatum Harris

Monosulcites minimus Couper

Family **LAUROZAMITACEAE** And. & And. nov.

Diagnosis: Bennettitalean plants with unisexual 'flowers' (attachment unknown); 'gynoecia' discoid without apparent external differentiation into ovulate and interseminal scales, and encircled by a 'perianth' of *ca* 10 large bracts.

Range: Euramerica, Tr(CRN–NOR)
First & Last: *Williamsonia nizhonia* Ash 1968; Chinle Fm., USGS locality 10061, Fort Wingate, New Mexico, USA, and *Laurozamites powelli* (Fontaine 1890) Weber & Zamudio-Varela 1995, many localities, Utah to N. Carolina, USA, Chinle Fm., Dockum Gp., and Newark Gp. (Upper Carnian–Lower Norian); *Laurozamites fragilis* (Newberry 1876) Weber & Zamudio-Varela 1995; and other *Laurozamites* species, Santa Clara Fm., Sonora, Mexico, Carnian (–Norian?).

Reference whole-plant genus & stratum—Chinle Fm.
Female: *Williamsonia* Carruthers 1870; 1 TC, 1 sp., 1 indiv.
Male: Unknown.
Foliage: *Laurozamites* Weber & Zamudio-Varela 1995; 13 TCs, 2 spp, many indivs.

Stratum: Chinle Fm., New Mexico, USA, Tr(CRN–NOR).
Affiliations: *Williamsonia*(3)*Laurozamites*, Grade 3 (Mut.occ., Anat.cor., Cut.cor.).

Prominence (colonisation success)—North America Late Triassic
Foliage: *Laurozamites* would appear to be the most prominent (frequency, abundance, diversity) foliage genus of the Carnian to Norian in Mexico and the USA. Apart from longevity (where we account for foliage), we refer below solely to the ovulate organ *Williamsonia*.

Frequency/ubiquity: 1 individual from 1 locality, Chinle Fm., USA; and 1 individual from 1 locality, Santa Clara Fm., Sonora, Mexico.
Diversity: 1 or 2 spp.
Abundance: 2 indivs.
Longevity: *ca* 20–25 my.

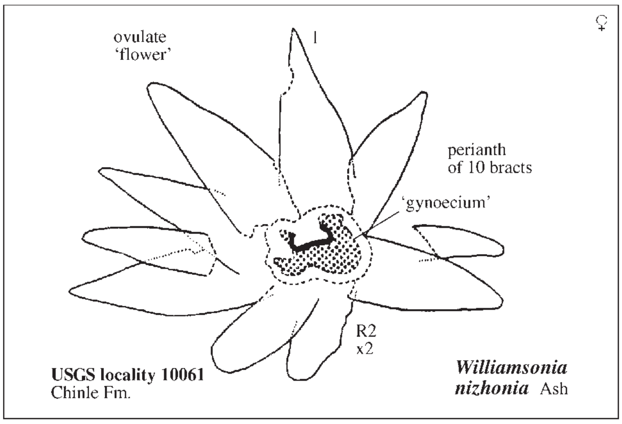
Ecology
Habit: Unknown.
Habitat: Delta or fluvial floodplain, tropical.

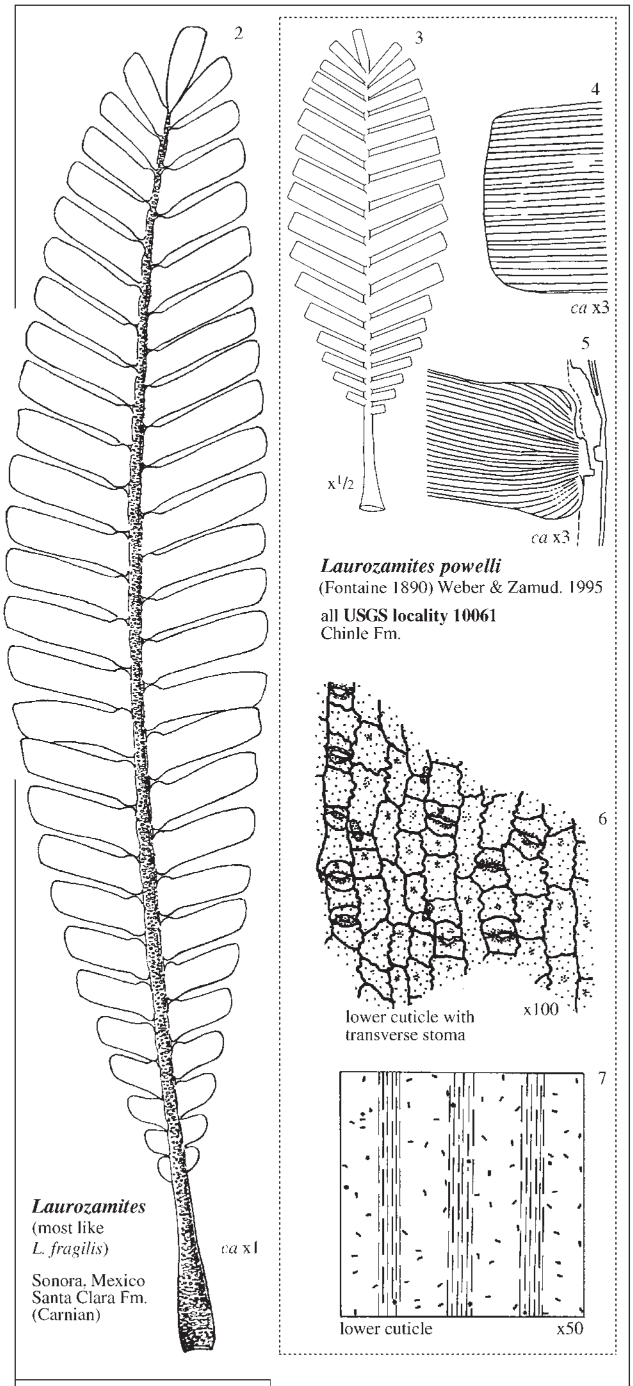
Other genera—nil.

Remarks
Family recognition: The foliage genus *Laurozamites*, with regard to frond and pinna morphology as well as cuticle, appears to be a perfect intermediate between *Halleyoctenis* (Fredlindiaceae) and the typical bennettitalean foliage genera such as *Zamites*, *Pterophyllum* and *Ptilophyllum* (And. & And. 2003). To place this distinctive and abundant North American Late Triassic genus (with its supposed '*Williamsonia*' affiliate) in any other bennettitalean family would seem unjustified. We create a new family named after the foliage (as an exception to our standard policy of naming families only after ovulate organs), rather than create a new generic name for the still poorly known ovulate affiliate (*Williamsonia nizhonia*) and institute a new family name based on that genus.

Affiliations: At Fort Wingate, the cuticle of *Laurozamites* and the ovulate 'flower' are similar. (A second bennettitalean leaf, *Nilssoniopteris* sp. A (Ash 1968), does occur at the site.) Weber & Zamudio-Varela (1995) report recurrent association of *Laurozamites*, the most common element of the Late Triassic (Carnian) Santa Clara Fm. of Sonora, Mexico—and one of the most common leaves (from 35 localities) in the Carnian to Lower Norian formations of the Late Triassic in the USA (Ash 1975; And. & And. 2003)—with both ovulate (*Williamsonia*) and microsporangiate (*Weltrichia*) structures.

References
Ash (1968, 1975): General, USA.
Weber & Zamudio-Varela (1995): Foliage, affiliation, Mexico.





1,3–7 all **USGS plant locality 10061**, near Fort Wingate, west-central New Mexico; Lower Red Member, lower Chinle Fm., Upper Triassic (Carnian)

2 from Sonora, Mexico
Santa Clara Fm., Upper Triassic (Carnian)

1 from Ash 1968
2 from Weber & Zamud. 1995
3–7 from Ash 1975

Family **STURIANTHACEAE** Doweld 2001

Diagnosis: Bennettitalean plants with unisexual ‘flowers’ on slender pedicels attached (?)spirally to form a lax cone; ‘gynoecia’ discoid, without apparent external differentiation into ovulate and interseminal scales, and encircled by a ‘perianth’ of 25–30 small bracts.

Range: Euramerica, Tr(CRN)
First & Last: *Sturianthus langeri* (Kräusel 1948) Kräusel 1950; Lunz, Austria.

Reference whole-plant genus & stratum—Lunz plant beds
Female: *Sturianthus* Kräusel 1950; 1 TC, 1 sp., 1 indiv.
Male: Unknown.
Foliage: Unknown.

Stratum: Lunz plant beds, Austria, Late Triassic (Carnian).
Affiliations: See under ‘Remarks’.

Prominence (colonisation success)—Europe Late Triassic
Frequency/ubiquity: *Sturianthus* is known only from the single area in Europe.
Diversity: 1 species (of ovulate organ).
Abundance: A single individual from a single locality.
Longevity: <1 my.

Ecology
Habit: Unknown.
Habitat: Deltaic/estuarine, subtropical latitudes.

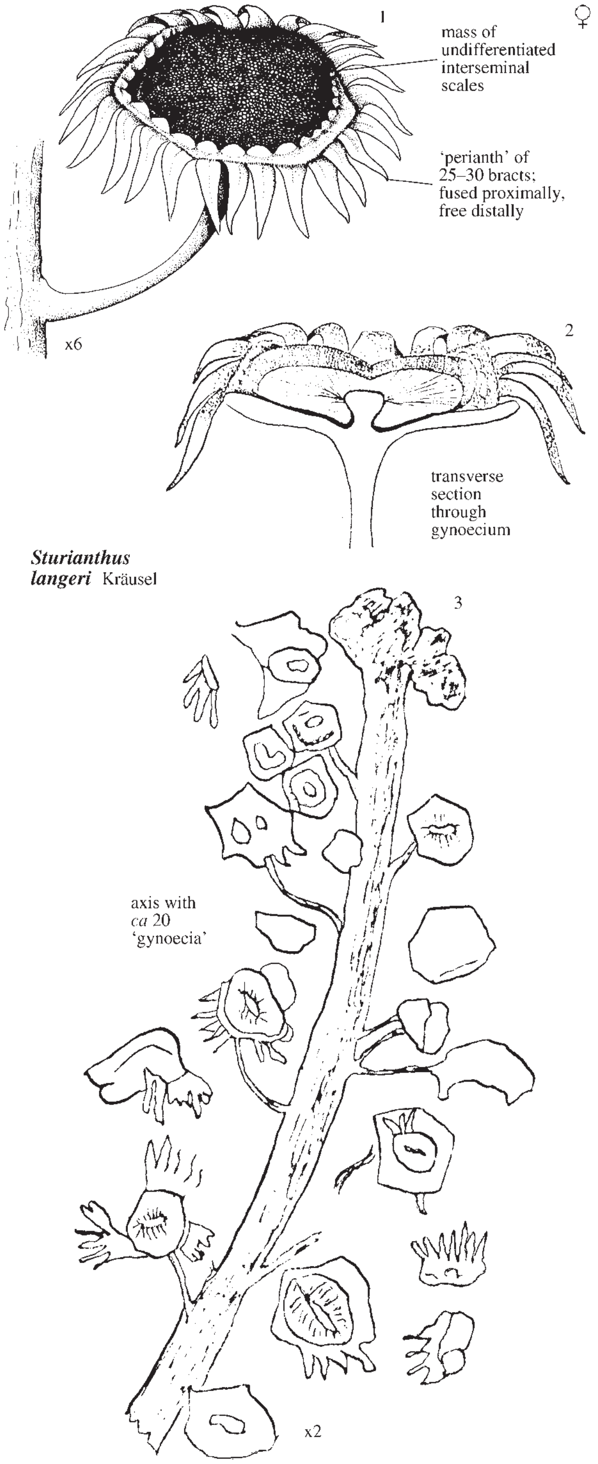
Other genera
Female: *Sturiella* Kräusel 1948 (synonym of *Sturianthus*).

Remarks
Morphology: Crane (1988) interprets these structures as unisexual and, in the absence of any pollen having been isolated, disagrees with Kräusel (1949) who viewed a bulge on some of the ‘perianth’ bracts as being pollen sacs.

Affiliations: The plant beds of Lunz, with several TCs over a couple of kilometres, occur in a coal mining area 100 km SW of Vienna, Austria. The coal-bearing strata are part of a limestone sequence—with marine invertebrates providing a Carnian age—in the northern foothills of the Alps (And. & And. 2003).

Comprising *ca* 53% of the overall flora from these Lunz plant-beds, the Bennettitales are dominant in both abundance and diversity. The order is represented by three genera and four species of foliage (*Pterophyllum longifolium* at 50%, *Pterophyllum* sp. B., *Anomozamites* sp. and *Nilssonia sturi* each at <1%), three genera of ovulate fruit (*Sturianthus*, *Westerheimia* and *Bennetticarpus*), and three genera of pollen organ (*Cycadolepis*, *Haitingeria* and *Leguminanthus*) (Dobruskina 1988, 1998; And. & And. 2003). However, there exists no thorough documentation of abundance of taxa per site for the Lunz collections and it is therefore difficult to establish the most likely affiliations between these diverse organs confidently. For *Westerheimia* (p. 192) and *Bennetticarpus* (p. 196), the other two ovulate genera from Lunz, though not for *Sturianthus*, microsporangiate and foliage affiliates (Grade 3) have nevertheless been suggested.

References
Crane (1988): Morphology.
Dobruskina (1988, 1998), And. & And. (2003, p. 342): Lunz flora.



Sturianthus langeri Kräusel

1 from Crane 1988 (based on Kräusel 1948)
2,3 from Kräusel 1948

all **Lunz**, Austria; Late Triassic (Carnian)

Family **BENNETTICARPACEAE** And. & And. nov.

Diagnosis: Bennettitalean plants with unisexual 'flowers' (pedicels and attachment unknown); 'gynoecia' large, spherical, with many (25–30) seeds but no apparent or sharp external differentiation into ovulate and interseminal scales, and with a 'perianth' of *Cycadolepis* bracts.

Range: Euramerica, Tr(CRN–RHT)
First: *Bennetticarpus wettsteinii* Krasser (Kräusel 1949); Lunz and Schrambach, Austria, Carnian.
Last: *Bennetticarpus crossospermus* Harris 1932b; Scoresby Sound, East Greenland, Rhaetic.

Reference whole-plant genus & stratum—Lunz plant beds
Female: *Bennetticarpus* Harris 1932b; ? TCs, 2 spp, ? indivs.
Cycadolepis Saporta 1873; ? TCs, 1 sp., ? indivs.
Male: *Haitingeria* Krasser 1916; ? TCs, 1 sp., ? indivs.
Foliage: *Pterophyllum* Adolphe Brongniart 1828; ? TCs, 2 spp, 50%.

Stratum: Lunz plant beds, Austria, Late Triassic (Carnian).
Affiliations: *Bennetticarpus*(3)*Pterophyllum*(3)*Haitingeria*(3), Grade 3 (Mut.occ.).

Prominence (colonisation success)—Euramerica Late Triassic
Foliage: In the absence of any general review of the supposed affiliate *Pterophyllum*, we refer here solely to the ovulate organ *Benneticarpus*.

Frequency/ubiquity: ? TCs from two areas in Euramerica, East Greenland and Austria.
Diversity: 2 species.
Abundance: Unspecified.
Longevity: *ca* 28 my.

Ecology
Habit: Unknown.
Habitat: Deltaic/estuarine, subtropical latitudes.

Other genera—nil.

Remarks
Morphology: *Bennetticarpus wettsteinii* is a remarkably large ovulate structure consisting of a 'spherical head typically 6–7 cm' in diameter, 'but ranging from' 3.5 cm to as much as 13 cm across (Crane 1988). A fruit ranging from the size of a lemon to that of a grapefruit can be visualised. It is presumed to have had a leathery outer surface and to have been fleshy within.

Affiliations: Crane (1988) suggested that the male affiliate of *B. wettsteinii* may have been the 'microsporangiate "flowers" ... composed of *Haitingeria krasseri* microsporophylls' found associated with it at the Lunz locality. No further elaboration was offered.

Bennetticarpus is the third of the Lunz flora ovulate genera (see *Westerheimia*, p. 192; and *Sturianthus*, p. 195). The pollen organ at Lunz affiliated to *Westerheimia* appears most likely to be *Leguminanthus*; and if *Haitingeria* does indeed affiliate with *Bennetticarpus*, then no further fertile pollen organ remains for affiliation with *Sturianthus*.

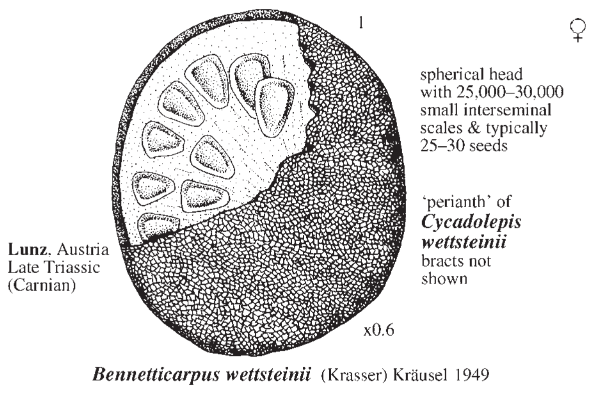
There is apparently some evidence of *B. crossospermus* and *Pterophyllum ptilum* being affiliated at Scoresby Sound (Harris 1932b; Crane 1985). (See also under 'Affiliations' for Westerheimiaceae, p. 192.)

Family classification: The extraordinary Late Triassic ovulate genus *Bennetticarpus*, with its large ovulate head and 'perianth' of bracts (but unknown attachment) is not readily placed in any other family of this period and appears to warrant recognition of a new family.

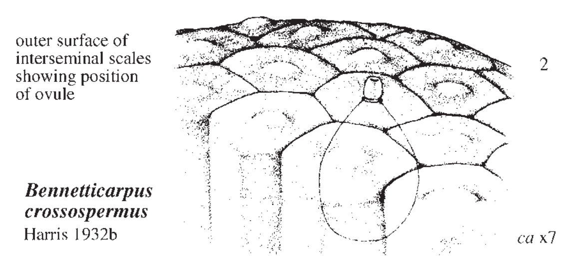
In his original definition of the form-genus *Bennetticarpus* (based on Scoresby Sound, East Greenland, Rhaetic material), Harris (1932b) wrote 'This designation is intended for all gynoecia which show definitely Bennettitalean characters, but which are not fully enough known either to be included in or definitely separated from the existing genera'. Following this lead, Watson & Sincock (1992), for instance, describe three new species of *Bennetticarpus* from the English Wealden (lowest Cretaceous, Berriasian).

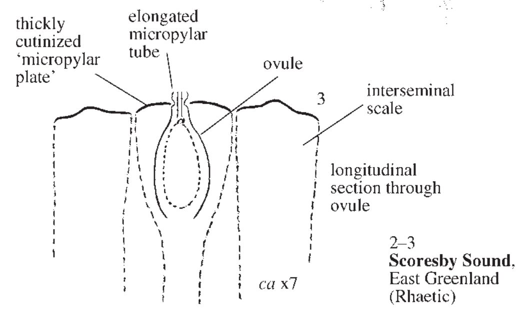
Aware of the nomenclatural (and taxonomic) pitfalls, but in the global context of the present work, we institute the family name Bennetticarpaceae to include only the Carnian to Rhaetic species of the genus noted under 'Range' above and illustrated adjacent. Though our intention, as elsewhere, is to seek natural taxa at all ranks as far as the very variable quality and quantity of the material allows, we remain obviously unsure whether *B. crossospermus* and *B. wettsteinii* do indeed belong to the same natural genus, and whether all Jurassic species should be excluded.

References
Crane (1986, 1988): Morphology.
Dobruskina (1988, 1998), And. & And. (2003): Lunz flora.

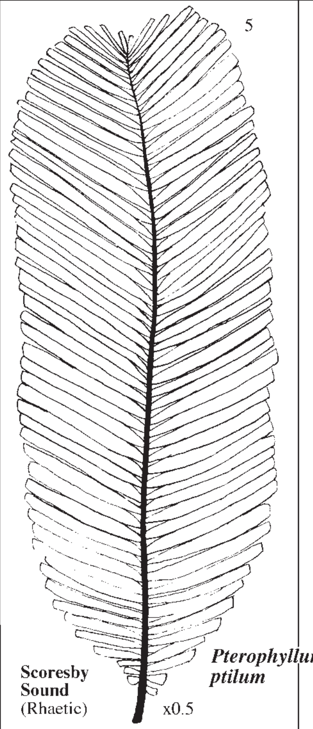


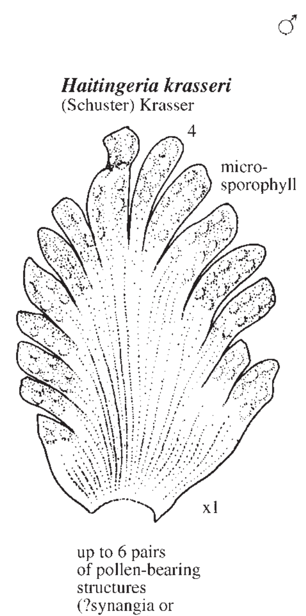
Bennetticarpus wettsteinii (Krasser) Kräusel 1949





2–3
Scoresby Sound,
East Greenland
(Rhaetic)





Lunz
(Carnian)

1,4 from **Lunz**, Austria; Upper Triassic (Carnian)
2,3,5 from **Scoresby Sound**, East Greenland; Late Triassic (Rhaetic)

1 from Crane 1988 (based on Kräusel 1949)
2,3,5 from Crane 1985 (based on Harris 1926, 1932b)
4 from Crane 1986 (based on Harris 1932b)

Family **WILLIAMSONIELLACEAE** Nakai 1943

Diagnosis: Bennettitalean plants with exposed hermaphrodite 'flowers' borne individually on slender branches in the axils of leaves or branches.

Range: Euramerica, Tr(RHT)–J(BAJ)
First: *Wielandiella angustifolia* Nathorst 1910; Scania, Sweden and Scoresby Sound, East Greenland, Rhaetic.
Last: *Williamsoniella coronata* Thomas 1915; Lower and Middle Deltaic (Bajocian), Yorkshire, UK (Harris 1969).

Reference whole-plant genus & stratum—Yorkshire Jurassic
Female/male: *Williamsoniella* Carruthers 1870; 3 TCs, 1 sp., >20 indivs.
Foliage: *Nilssoniopteris* Nathorst 1909; many TCs & indivs, 3 spp.

Stratum: Yorkshire Jurassic (L–M. Deltaic), England, J(BAJ).
Affiliations: *Williamsoniella*(4)*Nilssoniopteris*, Grade 4 (Mut.occ., Cut.cor., Mor.cor.).

Prominence (colonisation success)—Euramerica Late Trias.–Middle Jur.
Foliage: In the absence of any Euramerica-wide synthesis of the genera *Anomozamites* and *Nilssoniopteris*, we refer here exclusively to the hermaphrodite 'flowers'.

Frequency/ubiquity: Aside from the occurrences in Greenland, Sweden and Yorkshire, it is hardly possible (from the literature cited) to gain an assessment of frequency, ubiquity, diversity or abundance.
Diversity: See above.
Abundance: See above.
Longevity: *ca* 36 my.

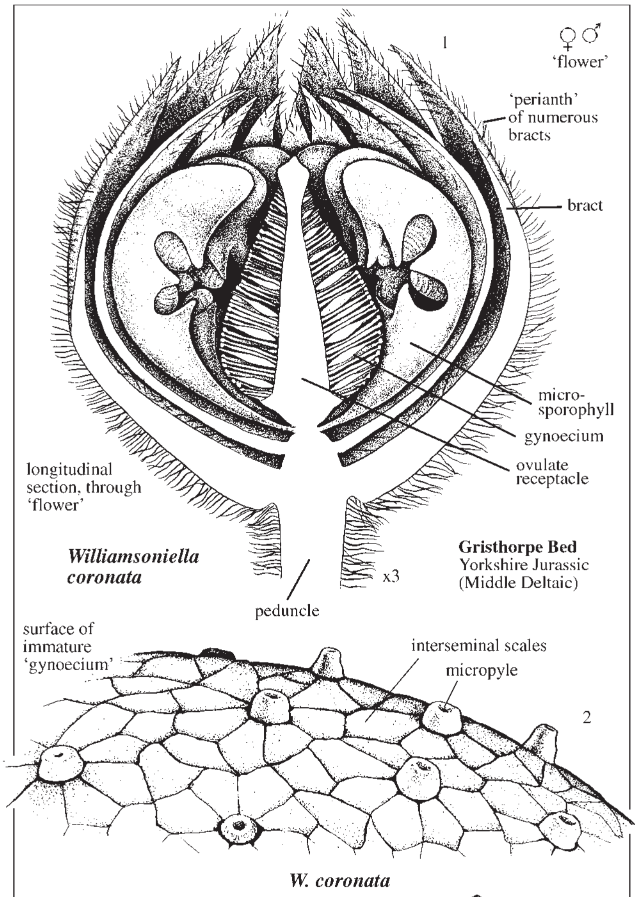
Ecology
Habit: Zimmerman (1959), based on Thomas (1915), regarded this taxon as a shrubby plant. Harris (1969) states, 'there is nothing to suggest whether it belongs to a shrub or a tree'.
Habitat: Deltaic (Yorkshire Jurassic) (Harris 1961, 1969).

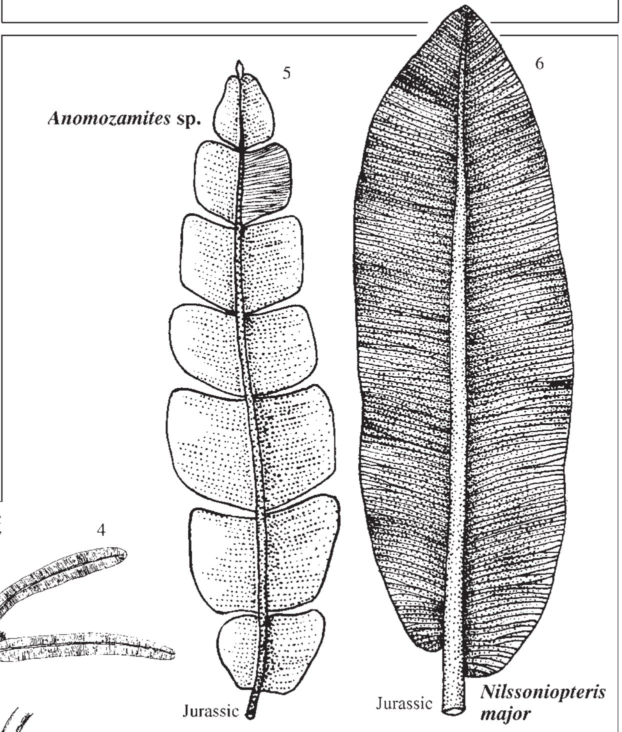
Other genera
Female/male: *Wielandiella* Nathorst 1910.
Foliage: *Anomozamites* Schimper 1870.

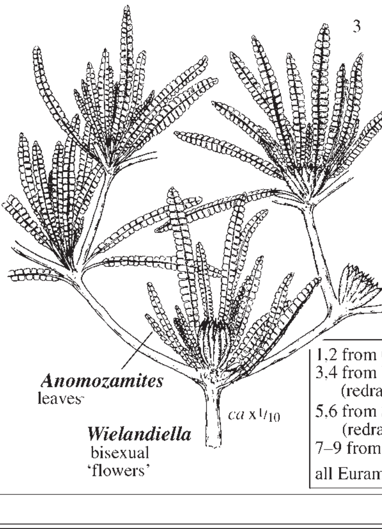
Remarks
Affiliations: Thomas (1915), based on association, stomatal structure, leaf bases and stem scars, made a good case for *Williamsoniella coronata* belonging to a plant with a forked stem, bearing the leaves *Nilssoniopteris* (*Taeniopteris*) *vittata*. His reconstruction has been variously refigured and we include here a recent version by Watson & Sincock (1992).

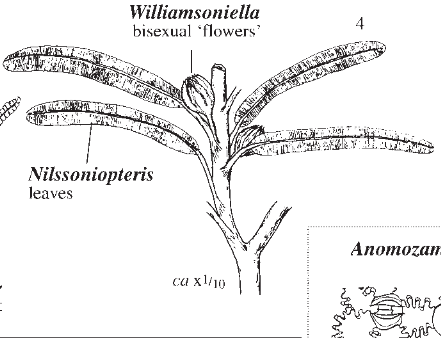
Family classification: The genera *Wielandiella* Nathorst 1910 and *Williamsoniella* Thomas 1915 remain unsatisfactorily resolved taxonomically and nomenclaturally. Watson & Sincock (1992) consider the two genera probably synonymous (but see Crane 1985 who records *Wielandiella* as unisexual). They note that Thomas (1915) based *Williamsoniella* on 'much more complete flowers with intact gynoecia and androecia', that he discussed the similarity with *Wielandiella*, but that the matter is still unsettled. We use the later name *Williamsoniella* (hence the family Williamsoniellaceae), in line with common usage (see also Harris 1932b, 1969), rather than *Wielandiella*.

References
Harris (1961, 1969): Yorkshire Jurassic.
Crane (1985): Phylogeny, reconstruction of 'flower'.
Watson & Sincock (1992): General.
Stewart & Rothwell (1993): General.

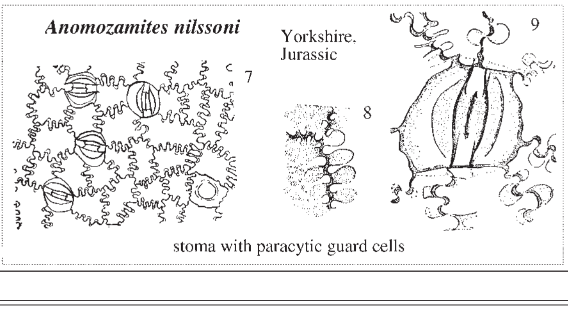








1,2 from Crane 1985 (based on Harris 1944, 1969)
3,4 from Watson & Sincock 1992
(redrawn from Thomas 1915)
5,6 from Stewart & Rothwell 1993
(redrawn from Harris 1932b, 1969)
7–9 from Harris 1969
all Euramerica, Triassic-Jurassic



Family **WILLIAMSONIACEAE** (Carruth. 1870) Nath. 1913

Diagnosis: Bennettitalean plants with unisexual 'flowers' borne on short, stout pedicels, attached individually to branched stems; 'gynoecia' spherical to oval, with clear differentiation into stalked ovules and interseminal scales, and enclosed within a 'perianth' of *Cycadolepis* bracts.

Range: Euramerica, J(BAJ)–C(BER)
First: *Williamsonia gigas* (Lindley & Hutton) Carruthers 1870; Yorkshire Jurassic (Lower Deltaic), Bajocian (Harris 1969).
Last: *Williamsonia cynthiae* Watson & Sincock 1992 and other species; English Wealden, Berriasian (Watson & Sincock 1992).

Reference whole-plant genus & stratum—English Wealden
Female: *Williamsonia* Carruthers 1870; 2 TCs, 4 spp, 25 indivs.
Male: *Weltrichia* Braun 1847; 1 TC, 1 sp., 1 indiv.
Foliage: *Ptilophyllum* Morris 1840; ? 2 TCs, 5 spp, 22 indivs.
Wood: *Bucklandia* Presl 1825; ? TCs, 2 spp, *ca* 10 indivs.

Stratum: Fairlight Clays, Ashdown Beds, E. Sussex, UK., C(BER).
Affiliations: *Williamsonia*(3)*Weltrichia*(3)*Ptilophyllum*(3)*Bucklandia*, Grade 3 (Mut.occ., Mor.cor.).

Prominence (colonisation success)—Global, Middle Jur.–earliest Cret.
Foliage: In the absence of any global synthesis, we refer here exclusively to the ovulate organ *Williamsonia*.

Frequency/ubiquity: Widespread through Laurasia & Gondwana.
Diversity: Numerous species described (revision due).
Abundance: Common.
Longevity: *ca* 32 my.

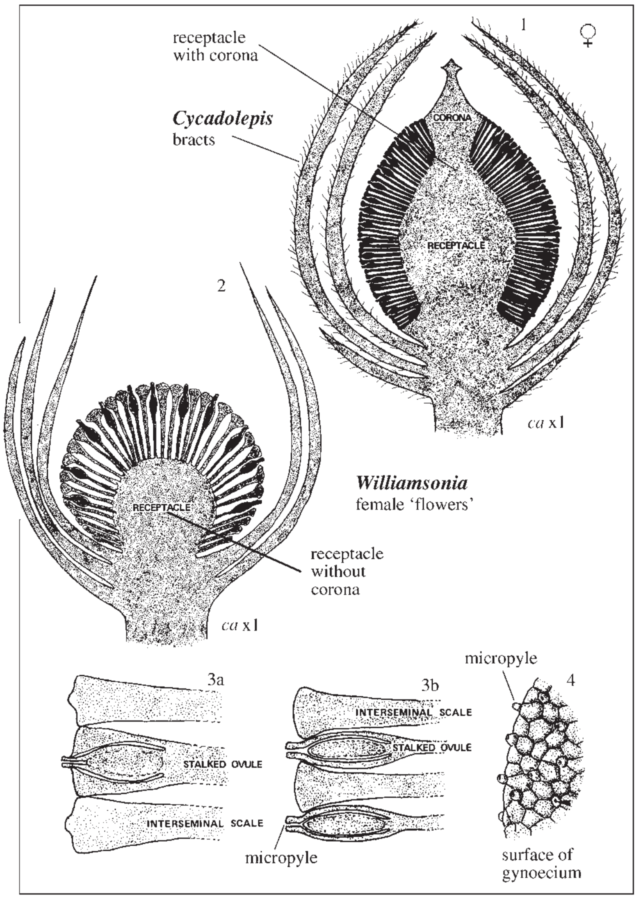
Ecology
Habit: Harris (1969) regarded the taxon as consisting of large trees occurring as dominants in a mixed forest with conifers and ginkgos.
Habitat: Deltaic (Yorkshire Jurassic), coastal plain (English Wealden), and many other low-lying basinal environments.

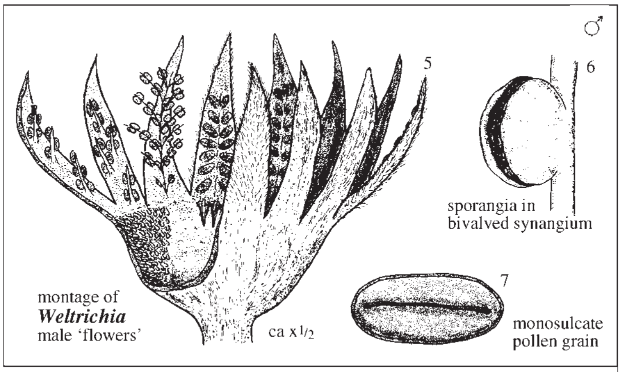
Other genera
Bracts: *Cycadolepis* Saporta 1875.

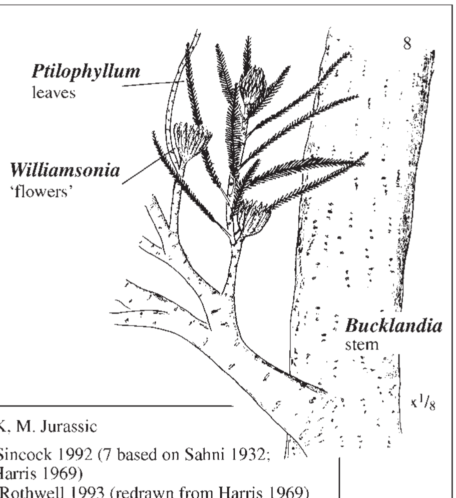
Remarks
Affiliations: Harris (1969), based on associations (and the attachment of a bud to a stem), affiliates the female flower *Williamsonia leckenbyi* with the foliage *Ptilophyllum pectin* and the stems *Bucklandia pustulosa*.

Family classification: Harris (1932b, 1969), in his works on the Scoresby Sound (East Greenland) and Yorkshire Jurassic floras, referred well-characterised female flowers to *Williamsonia* and hermaphrodite flowers to *Williamsoniella* (see also Watson & Sincock 1992). These genera are the basis of the two younger Bennettitalean families, Williamsoniaceae and Williamsoniellaceae—with exposed reproductive structures and slender branched stems—as recognised in our work.

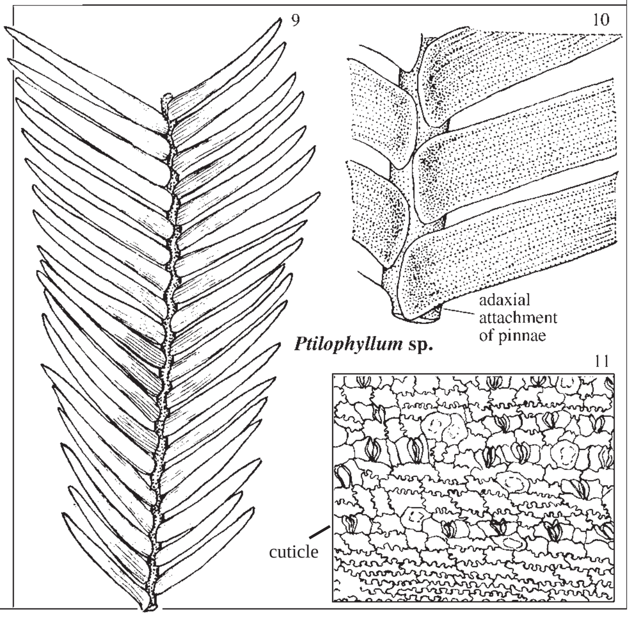
References
Harris (1969): Yorkshire Jurassic, habit.
Watson & Sincock (1992): English Wealden, general.
Stewart & Rothwell (1993): General.







mainly Yorkshire, UK, M. Jurassic
1–8 from Watson & Sincock 1992 (7 based on Sahni 1932; 8 redrawn from Harris 1969)
9,10 from Stewart & Rothwell 1993 (redrawn from Harris 1969)
11 J.M. Anderson sketch 2004 (based on Watson & Sincock 1992)



Family **CYCADEOIDACEAE** R.Br. ex Wieland 1908

Diagnosis: Bennettitalean plants with hermaphrodite 'flowers' embedded within close pack of persistent leaf bases on massive, often squat, sparsely branched trunks.

Range: Euramerica, J(TTH?)–K(CMP)
First: Cycadeoid stems; Freezeout Hills, Wyoming, USA, Upper Jurassic (Andrews 1967).
Last: *Monanthesia magnifica* Wieland ex Delevoryas 1959 (includes fructifications); Mesaverde Fm., New Mexico, USA (Cleal 1993).

Reference whole-plant genus & stratum—Black Hills
Stem/female/male: *Cycadeoidea* Buckland 1828; ? TCs, ? spp, many.
Foliage: *Zamites* Brongniart 1828b; ? TCs, 2 spp, numerous.

Stratum: Black Hills, South Dakota, USA, Early Cretaceous (BER).
Affiliations: *Cycadeoidea*(5)*Zamites*, Grade 5 (Org.att.).

Prominence (colonisation success)—Euramerica Late Jur–Late Cret.
Frequency/ubiquity: Widespread in Euramerica (& India?).
Diversity: Many species of 'flower' described (revision due).
Abundance: Abundant.
Longevity: *ca* 80 my.

Ecology
Habit: Long-lived plants with massive, mostly globose (also stout cylindrical up to >2 m diam.), rarely branched trunks.
Habitat: More stable 'upland' areas of coastal plains and other basins.

Other genera
Female/male/stem: *Monanthesia* Wieland 1934 ex Delevoryas 1959.

Remarks
Intervening: *Cycadeoidea* stems with fructifications are especially common in the Northern Hemisphere in the early Cretaceous (BER). Bennettitalean foliage occurs commonly from the Late Triassic to Late Cretaceous and, thereafter, meagre records have been reported in the Tertiary (Stewart & Rothwell 1993). However, without cuticles the distinction between the foliage of the Bennettitales and Cycadales cannot always be readily made and so we have opted to record first and last appearances based on fertile material alone.

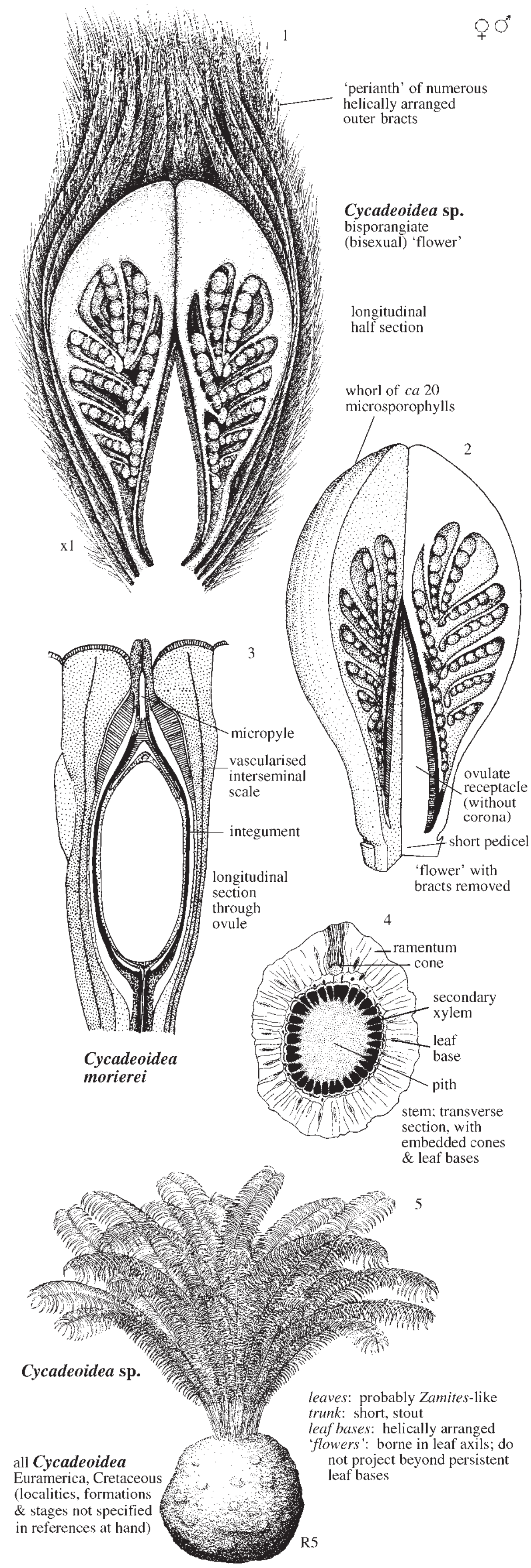
Affiliations: Numerous specimens of *Cycadeoidea*, the best-known genus of the family, have been collected from the USA, Mexico, Europe (and apparently India). Most of these have evidently come from the famous Black Hills locality, South Dakota, Early Cretaceous (BER). According to Taylor & Taylor (1993), the genus *Cycadeoidea* is 'known principally from silicified trunks' with the reproductive organs, consisting invariably of bisporangiate (bisexual) cones ('flowers'), 'embedded in the trunk among the leaf bases'. They observe further that 'no mature leaves have ever been found attached to the trunks, although immature foliage of *Zamites* has been discovered attached to a *Cycadeoidea* stem'.

Family classification (Jurassic–Cretaceous genera): The later, essentially Jurassic and Cretaceous, genera of the order Bennettitales are traditionally grouped into two loosely defined families, the Williamsoniaceae and Cycadeoidaceae (Crane 1985; Watson & Sincock 1992; Stewart & Rothwell 1993; Taylor & Taylor 1993). Crane (1985), however, concludes from his cladistic analysis of the better known ovulate 'flower' genera (*Williamsoniella*, *Wielandiella*, *Williamsonia*, *Monanthesia*, *Cycadeoidea*) and species of the order, that the two families do not form monophyletic groups.

Watson & Sincock (1992) note that a few authors (e.g. Sporne 1965) recognise three families for this group of genera, while others (e.g. Harris 1969; Bernard & Miller 1976) avoid the use of families. Their own view is that the 'great diversity' of form within these genera 'probably warrants the recognition of at least three families'. While supporting the greater-diversity option in this volume, and recognising the three families Williamsoniellaceae, Williamsoniaceae and Cycadeoidaceae, we feel that a global synthesis of the material is needed with far greater focus on localities and affiliations of organs, on abundance and habitat, and on age (to stage) before any consensus on families is likely to emerge.

Rothwell & Stockey (2002), based on 'excellently preserved specimens from Western Canada and elsewhere', record sufficient contrasting characters to confirm the clear distinction between the Cycadeoidaceae and Williamsoniaceae. They offer no comment on the familial placement of *Williamsoniella* (or *Wielandiella*).

References
Crane (1985): Morphology, phylogeny.
Watson & Sincock (1992), Stewart & Rothwell (1993), Taylor & Taylor (1993): General.



1 from Crane 1985 (based on Wieland 1906 & Crepet 1974)
2–5 from Stewart & Rothwell 1993 (2,4 from Crepet 1974; 3 redrawn from Seward 1917; 5 redrawn from Delevoryas 1971)

Order **PENTOXYLALES** Pilg. & Melch. 1954

Diagnosis: Bennettitopsid plants with more or less spherical, radially symmetrical ‘gynoecia’, attached (or putatively attached) in terminal fascicles, and with relatively few undifferentiated ovuliferous cells.

Families: Includes the two families Lindthecaceae and Pentoxylaceae.

Family **LINDTHECACEAE** And. & And. 2003

Diagnosis: Pentoxylalean plants with ‘gynoecia’ enclosed within a quilted sheath and with multiovulate megasporophyll cells.

Range: Gondwana, Tr(LAD–CRN)
First: *Taeniopteris homerifolius* And. & And. 1989; Wianamatta Grp., Sydney Basin, Australia (And. & And. 1989).
Last: *Lindtheca hackysackia* And. & And. 2003; Molteno Fm., S. Africa.

Reference whole-plant genus & stratum—Molteno Fm.
Female: *Lindtheca* And. & And. 2003; 1 TC, 1 sp., 16 indivs.
Male: Unknown.
Foliage: *Taeniopteris* Adolphe Brongniart 1832; 38 TCs, 8 spp, 2%.

Stratum: Molteno Fm., Karoo Basin, S. Africa, Late Triassic (CRN).
Affiliations: *Lindtheca*(3)*Taeniopteris homerifolius,* Grade 3 (Kin.rein., Mut.occ.).

Prominence (colonisation success)—Gondwana Triassic (GT)
Taeniopteris (foliage): Widespread in all Gondwana continents.

FUDAL rating: 32/5/10/2/20 = 69; the 4th most prominent gymnospermous foliage genus in the GT.
Frequency: High, 32 of 84 Gondw. degree squares.
Ubiquity: V. high, 5 of 5 Gondw. continents.
Diversity: High, 10 species in GT.
Abundance: Moderate, 2% norm in Molteno TCs.
Longevity: High, 20 my through Triassic.

Ecology—Molteno Fm.
Habit: Interpreted as ranging from woody shrubs to small trees.
Habitat: Occurred as scattered elements in forested and woodland habitats of the Molteno Floodplain Biome.

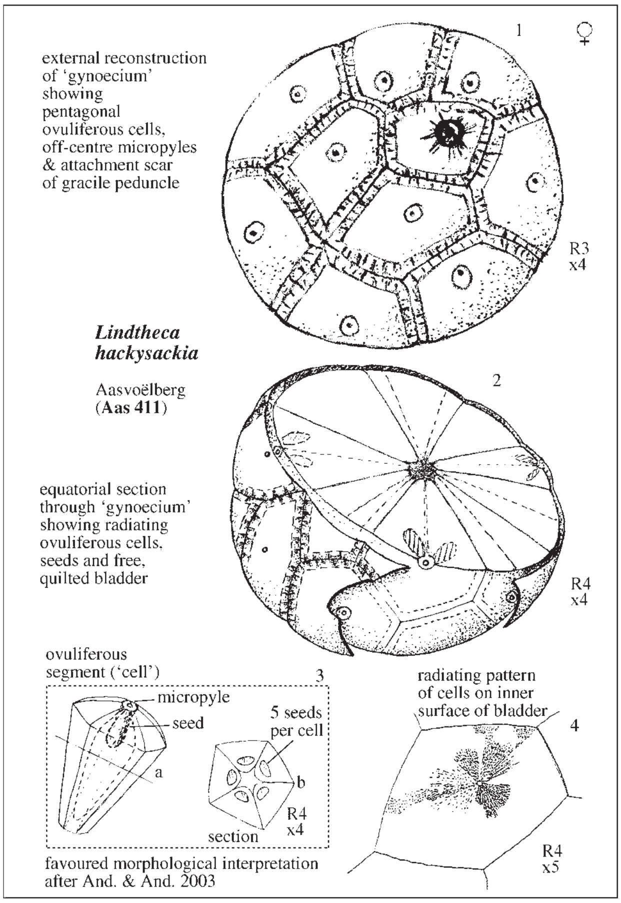
Other genera—nil.

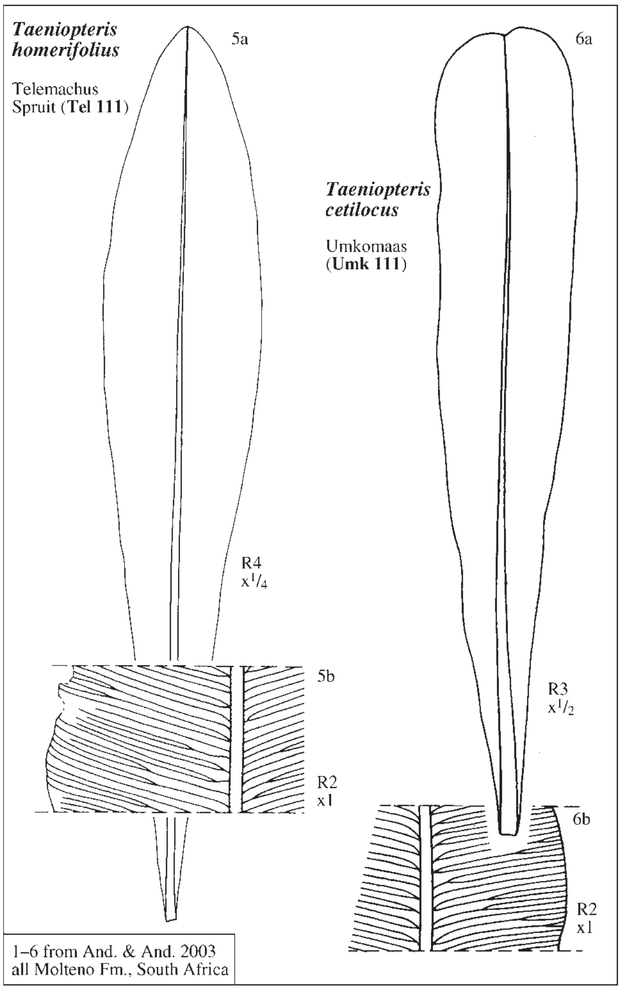
Remarks
Foliage: *Taeniopteris* is a diverse and common genus in the Gondwana Triassic occurring from the Spathian (later Olenekian) to Norian. The species are difficult to circumscribe and quite possibly represent different gymnosperm orders or even classes. Also, they are found widespread, both geographically and stratigraphically, beyond the GT. The ovulate organ *Lindtheca*, in marked contrast, remains known only from a single species (*L. hackysackiensis*) from a single locality (Aasvoëlberg, Aas 411) in the Molteno.

Affiliations: Although *Taeniopteris* is such a prominent element of GT palaeofloras, the Grade 3 affiliation of the particular species *T. homerifolius* with *Lindtheca* at the single Molteno locality remains the only such association recorded for the entire kingdom (*Dicroidium* Empire).

Stem: *Rhexoxylon*, a typical stem genus of Late Triassic Gondwana deposits, has often been considered as part of the *Dicroidium* plant. It has, however, much in common with *Pentoxylon* (Stewart & Rothwell 1993) and may well prove to affiliate rather with *Lindtheca/Taeniopteris*.

References
And. & And. (1989): Foliage.
And. & And. (2003): Ovulate organ, foliage.





1–6 from And. & And. 2003
all Molteno Fm., South Africa

Family **PENTOXYLACEAE** Pilg. & Melch. 1954

Diagnosis: Pentoxylalean plants with ‘gynoecia’ apparently lacking a quilted sheath and with uniovulate megasporophyll cells.

Range: Gondwana, J(TOA)–K(APT)
First: *Taeniopteris spatulata* McClelland 1850 and *Carnoconites* sp.; Talbragar Fish Beds, New South Wales (Cleal 1993).
Last: *Pentoxylon sahnii* Srivastava 1944, *Nipanioxylon guptai* Srivastava 1944, *Nipaniophyllum raoi* Sahni 1948, *Carnoconites compactum* Srivastava 1944, *C. rajmahalensis* (Wieland) Bose *et al.* 1984, and *Sahnia nipaniensis* Vishnu-Mittre 1953; Rajmahal Fm., Bihar, India (Cleal 1993, Banerji 2005, in prep.).

Reference whole-plant genus & stratum—Rajmahal Hills
Female: *Carnoconites* Srivastava 1944; 4 TCs, 2 spp, common.
Male: *Sahnia* Vishnu-Mittre 1953; 1 TC, 1 sp., rare.
Foliage: *Nipaniophyllum* Sahni 1948; 2 TCs, 2 spp, dominant.
Stem (long shoot): *Pentoxylon* Srivastava 1944; 2 TCs, 1 sp., common.

Stratum: Rajmahal Hills, India, Early Cretaceous (HAU–APT).
Affiliations: *Carnoconites*(4)*Nipaniophyllum*(4)*Pentoxylon*(3)*Sahnia*, Grades 3 & 4 (Mut.occ., Anat.cor.).

Prominence (colonisation success)—Gondwana Early Jur.–Early Cret.
Frequency/ubiquity: The Pentoxylaceae, previously considered to be rather restricted, are emerging as a particularly prominent (widespread and abundant) group in Gondwana from the Early Jurassic to Early Cretaceous. Like the dominant glossopterids in the Permian and the Umkomasiales (*Dicroidium)* in the Triassic, the Pentoxylales in the Early Jurassic to Early Cretaceous appear to be confined—or very nearly so—to Gondwana. The ovulate cone *Carnoconites* is now known from the late Early Jurassic Talbragar Fish Beds of New South Wales; the Early Cretaceous of the Rajmahal Hills, India; the latest Jurassic to earliest Cretaceous of the Waikato Heads, North Island, New Zealand; and the Early Cretaceous of Victoria, Australia.

Diversity: Many species of the various organs described (Gondwana-wide revision due).

Abundance: The abundance, from many localities, of species of *Nipaniophyllum* (in India) or of *Taeniopteris*—assumed at least in part to affiliate with *Carnoconites*—attests to the important role of the Pentoxylaceae in the fossil floras of a good number of formations.

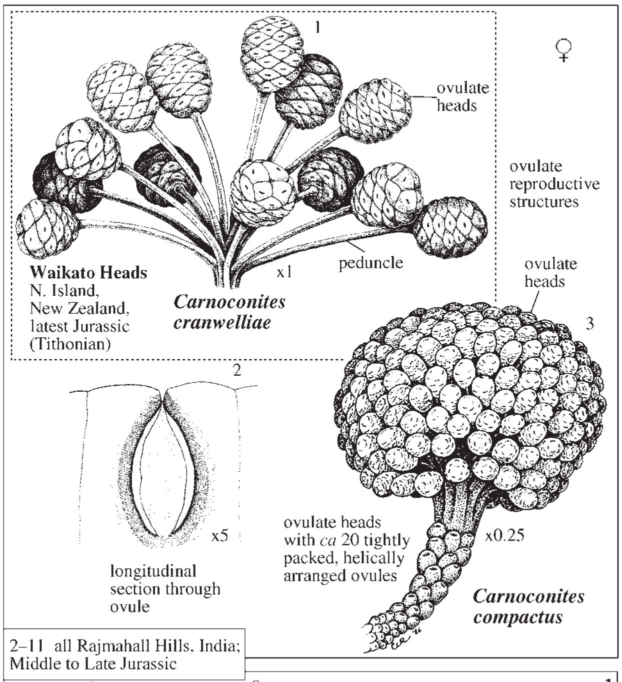
Longevity: *ca* 70 my.

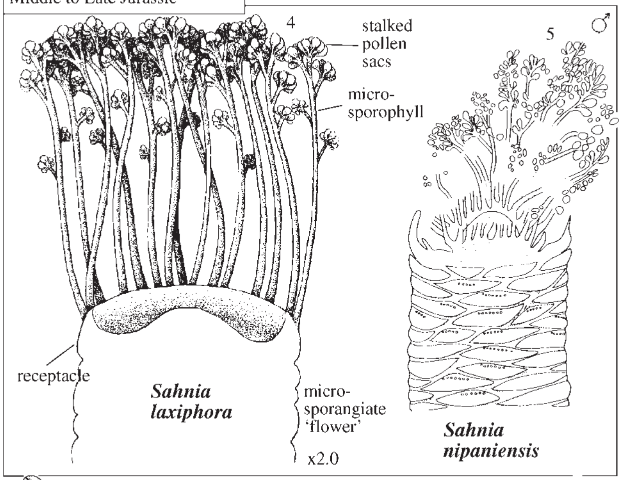
Ecology
Habit: Thicket-forming, branching shrubs (Bose *et al*. 1985).
Habitat: Woodland and forest surrounding a variety of freshwater lakes.

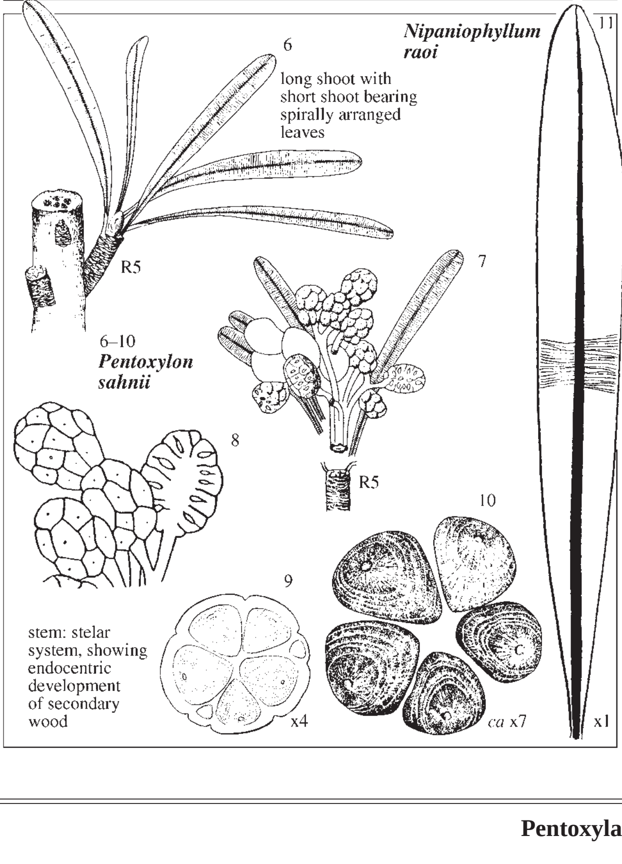
Other genera
Foliage: *Taeniopteris* Adolphe Brongniart 1832?
Stem: *Nipanioxylon* Srivastava 1944.

Remarks
Affiliations: The pentoxylaceaen plant is amongst the best known of the extinct gymnospermous families with regard to the assembly of affiliated organs. Though not known in organic connection, the various organs of the plant—*Carnoconites* (ovulate cones), *Sahnia* (microsporangiate organs), monocolpate pollen, *Pentoxylon* (stems), *Taeniopteris* and *Nipaniophyllum* (foliage)—have been confidently grouped by many authors (references as above for ‘Range’) on the basis of repeated association and anatomical detail.

References
Sahni (1948): Reconstruction of *Pentoxylon* plant (excluding pollen organs).
Harris (1962, 1983), Rao (1974), White (1981, 1986), Crane (1985, 1988), Drinnan & Chambers (1985), Stewart & Rothwell (1993): General.
Bose et al. (1985), Banerji (2005, in prep.): Rajmahal Hills.

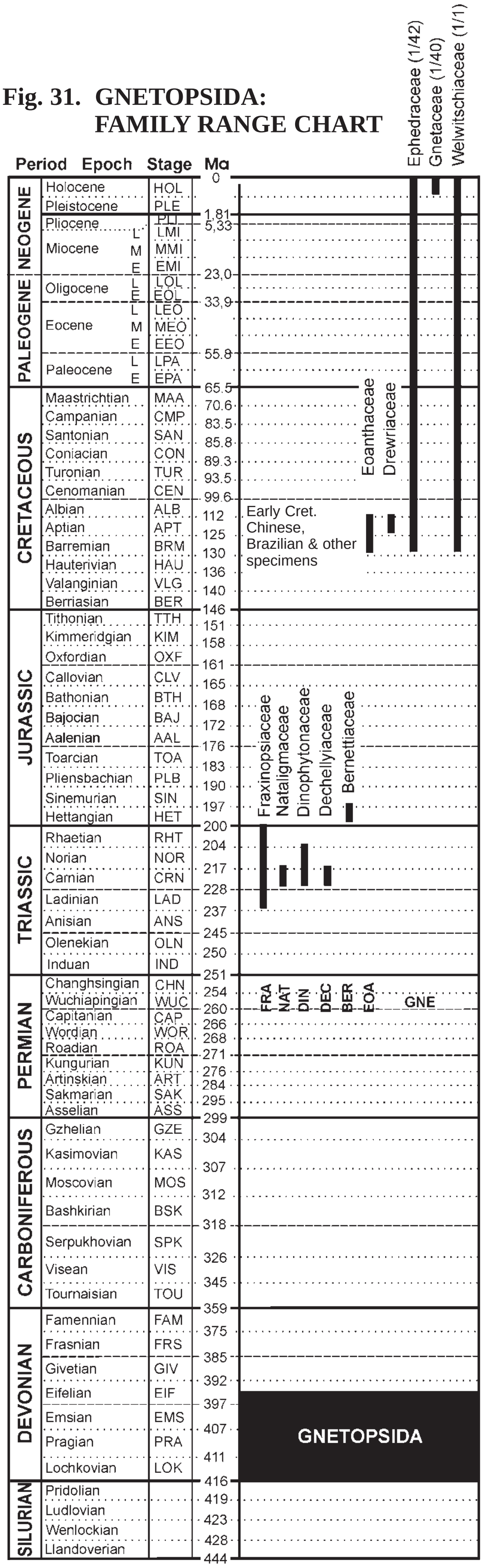






1,2,4,9,11 from Crane 1985 (1 based on Harris 1962; 9 based on Sahni 1948; 4 based on Vishnu-Mittre 1953)
3 from Crane 1988 (redrawn from Bose, Pal & Harris 1985)
5,6,7,10 from Andrews 1967 (5 from Vishnu-Mittre 1953; 6,7,10 from Sahni 1948)
8 from Rothwell & Serbet 1994

Fig. 31. GNETOPSIDA: FAMILY RANGE CHART



Class **GNETOPSIDA** Eichler ex Kirpotenko 1884

Diagnosis: Gymnospermous plants with ovulate strobili composed of megasporophylls arranged in opposite and decussate ranks or whorls.

Remarks

Classification & phylogeny: In Cleal 1993, the Gnetopsida are given a particularly wide circumscription, taking in the Bennettitopsida, (including Pentoxylales) and Gnetopsida, here taken as two separate classes.

We recognise the Gnetopsida to include the crown-group Gnetales, with the three extant families plus Drewriaceae (Cretaceous); and a morphologically very diverse assembly of six orders, each including a single family, putatively considered stem-gnetopsids. Three of the families—Dechellyiaceae, Bernettiaceae and Eoanthaceae—are included in the stem-group largely on the basis of their ephedroid pollen; the remaining three—Dinophytonaceae, Nataligmaceae and Fraxinopsiaceae—on an assortment of partly shared characters such as whorled inflorescences, elaborately winged seeds, opposite and decussate foliage, reticulate venation, and epidermal cells with strongly sinuous walls.

Stem-group diversity (Late Triassic): It is possible, perhaps likely, that some of the earlier stem-gnetopsid families (and orders) should be placed in unique classes—still further increasing diversity at higher ranks in the Late Triassic gymnosperms. Considering the wide morphological range covered, and that the orders are each represented by a single family and genus only—in one case possibly two genera—it might be anticipated that a great diversity of forms remain to be unearthed.

Crown-group emergence (Early Cretaceous): Coinciding with the Early Cretaceous radiation of the angiosperms, appears to have occurred a parallel radiation of crown-group gnetopsids. This is seen in earliest Barremian to Early Aptian beds (*ca* 130–110 Ma) globally as recorded in a flurry of papers in recent years on new megaplant finds.

Eastern USA: Potomac Gp., Aptian–Albian (Rydin *et al*. 2004, 2005).

Portugal: Calvaria Member, Figueira da Foz Fm., Aptian–early Albian (Friis & Pedersen 1996, Rydin *et al*. 2004).

Transbaikalia, Russia: Baisa locality, Lake Baikal area, Zazinskaya Fm., Late Hauterivian–Barremian (Krassilov & Bugdaeva 1999, 2000); see p. 244, this volume.

W. Liaoning, NE China: Jianshangou Bed, Lower Yixian Fm., Barremian–Aptian boundary (Sun Ge *et al*. 1998, 2001, 2002; Shun-qing Wu 2003); see p. 245, this volume.

N. Brazil: Crato Member, Santana Fm., Aptian–Albian boundary (Dilcher *et al*. 2004, Dilcher pers. comm. 2004).

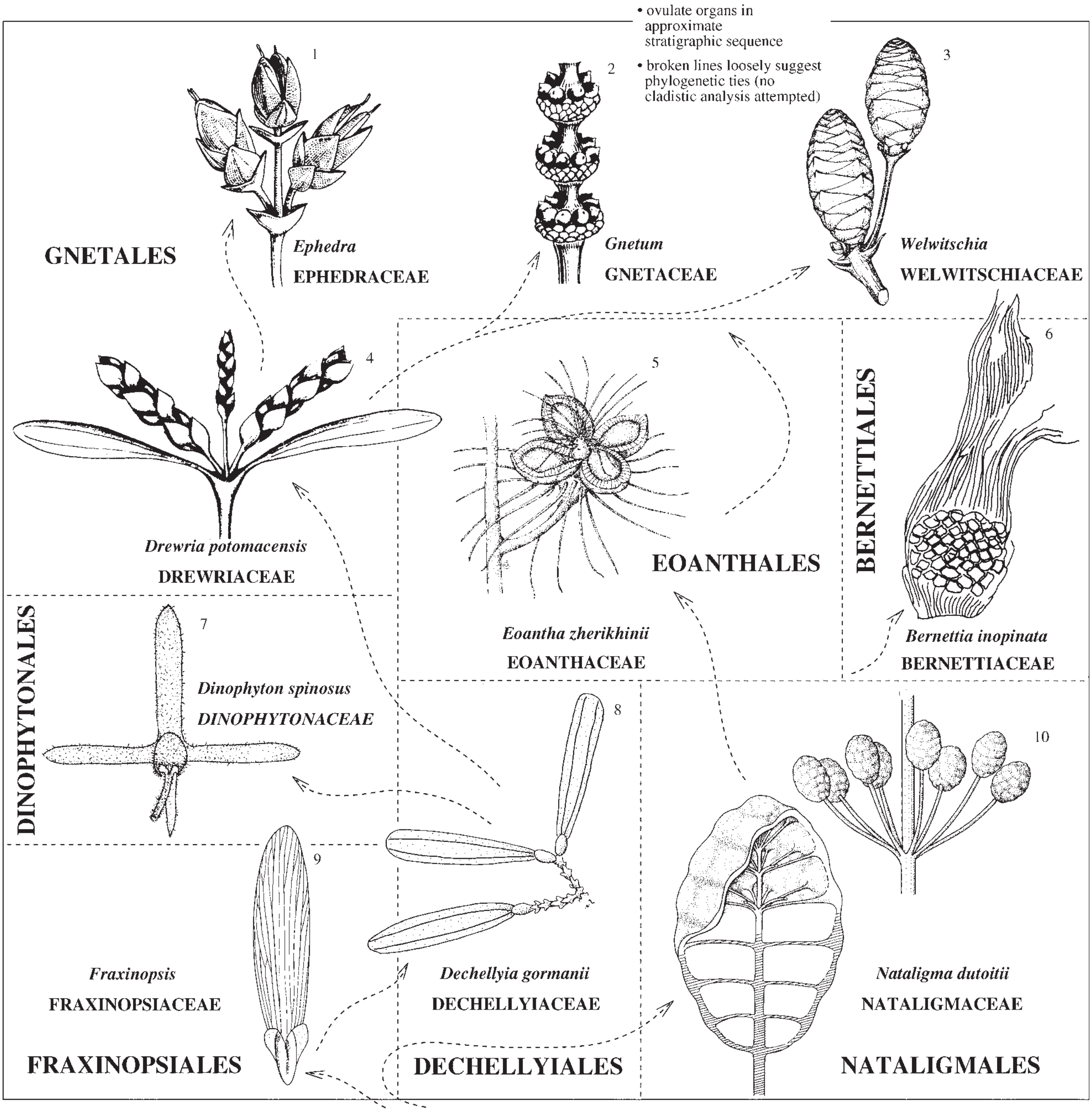
Makhtesh Ramon, Israel: Hatira Fm., Lower Aptian (Krassilov *et al*. 2004).

Victoria, Australia: Gippsland Basin, Koonwarra Fossil Bed, Lower Aptian (Krassilov *et al*. 1998).

Orders: Includes the six putative stem-gnetopsid orders Fraxinopsiales, Nataligmales, Dinophytonales, Dechellyiales, Bernettiales and Eoanthales, and the single crown-order Gnetales.

CLASS ORDER Family — **Tab. 32. GNETOPSIDA**	generic diversity ♀	♂	⬯	affiliation grade ♀	♂	⬯	morphology grade ♀	♂	⬯	anatomy preserved ♀	♂	⬯
GNETOPSIDA Eichler ex Kirpotenko 1884												
FRAXINOPSIALES And. & And. 2003												
Fraxinopsiaceae And. & And. 2003	1	-	2	5	-	4	3	-	4	-	-	-
NATALIGMALES And. & And. 2003												
Nataligmaceae And. & And. 2003	1	-	1	5	-	2	3	-	4	-	-	-
DINOPHYTONALES Krassilov & Ash order nov.												
Dinophytonaceae Krassilov & Ash fam. nov.	1	1	1	5	4	4	3	3	4	-	-	-
DECHELLYIALES Ash order nov.												
Dechellyiaceae Ash fam. nov.	1	1	1	5	3	5	4	2	4	-	-	-
BERNETTIALES Konijn.-Citt. order nov.												
Bernettiaceae Konijn.-Citt. fam. nov.	1	1	1	5	3	3	2	3	3	-	-	-
EOANTHALES Krassilov, And. & And. order nov.												
Eoanthaceae Krassilov, And. & And. fam. nov.	1	-	1	5	-	4	3	-	?	-	-	-
GNETALES Luerss. 1879												
Drewriaceae And. & And. fam. nov.	1	-	1	5	-	5	4	-	4	-	-	-
Ephedraceae Dumort. 1829 extant	**1**	**1**	**1**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**
Gnetaceae Lindl. 1834 extant	**1**	**1**	**1**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**
Welwitschiaceae Markgr. 1926 extant	**1**	**1**	**1**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**

Fig. 32. GNETOPSIDA: SIMPLIFIED PHYLOGENY (OVULATE ORGANS)



Order **FRAXINOPSIALES** And. & And. 2003

Diagnosis: Putative stem-gnetopsids (strobilus unknown) with megasporophylls comprising longitudinally grooved, oval seeds proximal to a pronounced elongate wing or bract with 7 to 16 parallel, forking and occasionally anastomosing veins.

Remarks
Gnetopsid radiation: In a review of our monograph on the gymnospermous foliage of the Molteno (And. & And. 1989), Retallack (1990) made the suggestion that the Fraxinopsiales (and Nataligmales, opposite) may represent early gnetopsids: 'The most exciting discovery to me is the cuticular unity of the leaves *Yabeiella*, *Gontriglossa* (formerly *Glossopteris*) and *Jungites* (formerly *Taeniopteris*). Furthermore, *Gontriglossa* has truly verticillate leaf insertion, quite unlike the compact short-shoots of *Glossopteris*. Also illustrated are intriguing scales around the ovules of *Fraxinopsis*, the likely winged fruit of *Yabeiella*. These finds together with recent work by Bruce Cornet on Late Triassic fructifications from Texas, stimulated me to speculate that we might be seeing a great Late Triassic adaptive radiation of gnetaleans'.

Family: Includes the single family Fraxinopsiaceae.

Family **FRAXINOPSIACEAE** And. & And. 2003

Diagnosis: As for the order Fraxinopsiales.

Range: Gondwana, Tr(LAD–RHT)
First: *Yabeiella brackebuschiana* (Kurtz 1921) Oishi 1931, Esk Fm., Clarence-Moreton Basin, Queensland (And. & And. 1989).
Last: *?Yabeiella brackebuschiana*, Woogaroo Fm., Brisbane Region, Queensland (And. & And. 1989). The ovulate organ *Fraxinopsis* has a more restricted known distribution, being confined to the Carnian.

Reference whole-plant genus & stratum—Molteno Fm.
Female: *Fraxinopsis* Wieland 1929; 18 TCs, 3 spp, 306 indivs.
Male: Unknown.
Foliage: *Yabeiella* Oishi 1931; 29 TCs, 2 spp, <1%.
Stratum: Molteno Fm., Karoo Basin, S. Africa, Tr(CRN).
Affiliations: *Fraxinopsis*(4)*Yabeiella*, Grade 4 (Cut.cor., Mut.occ.).

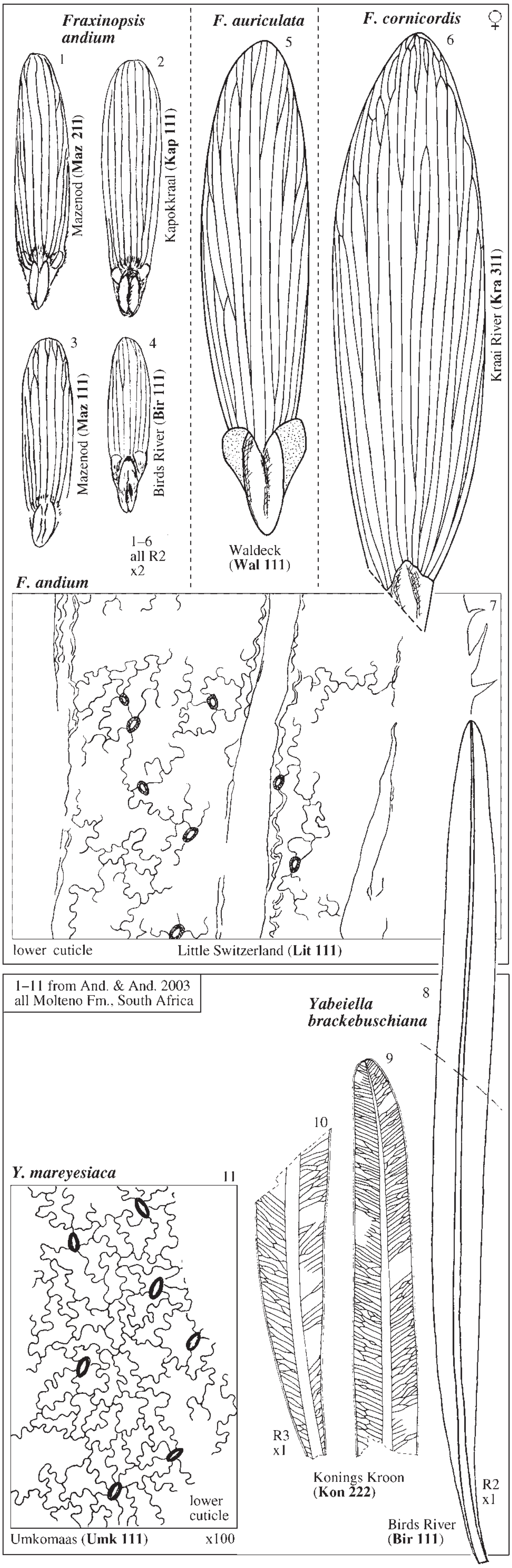
Prominence (colonisation success)—Gondwana Triassic (GT)
Yabeiella (foliage): Recorded in Chile, Argentina, South Africa, eastern Australia and New Zealand.
FUDAL rating: 21/3/2/–/17 = 43; *Yabeiella* was the 10th most prominent gymnospermous foliage genus in the GT.
Frequency: High, 21 of 84 Gondw. degree squares.
Ubiquity: Moderate, 3 of 5 Gondw. continents.
Diversity: V. low, 2 species in GT.
Abundance: Rare, <1% norm in Molteno TCs.
Longevity: High, 17 my through Triassic.

Ecology—Molteno Fm.
Habit: Medium-sized tree.
Habitat: Ubiquitous in *Dicroidium* riparian forest and closed woodland of the lake margin; far less frequent in open woodland (10 of 31 TCs).

Other genera
Foliage: *Yungites* And. & And. 1989.

Remarks
Affiliations: The Fraxinopsiaceae reflect the broad pattern in the Molteno Fm. (and the fossil record generally), of gymnospermous pollen organs being 'less diverse, less frequent and less abundant than the female strobili' (And. & And. 2003, p. 17, see also this volume, Tab. 12, p. 23). While *Yabeiella* is the tenth most prominent gymnospermous foliage genus through the GT and the ovulate organ *Fraxinopsis* (with undoubted Grade 4 affiliation) is a frequent and common element, there remains no hint anywhere of the pollen organ. It remains to be discovered.

References
And. & And. (1989): Foliage.
And. & And. (2003): Female, foliage.



1–11 from And. & And. 2003
all Molteno Fm., South Africa

Order **NATALIGMALES** And. & And. 2003

Diagnosis: Putative stem gnetopsids with a compound strobilus (inflorescence) comprising whorls of 8 pedicellate cones, each in turn consisting of a series of megasporophyll whorls.

Remarks
Classification & phylogeny: As with a good many other Molteno Fm. genera, *Nataligma* is unlike any other plant known, fossil or living, and evidently represents a distinct plant group of at least order status. In the pronounced whorled character of its fruiting structure, the apparent relationship is with the sphenophytes, but for varied reasons, including the most possible foliage affiliate (only Grade 2), we feel the more likely placement is in the gymnosperms (And. & And. 2003).

Amongst the gymnosperms, the only groups of which we are aware that bear (in some families) whorled fruiting structures are the gnetopsids and bennettitopsids. The small individual cones of *Nataligma*, though, are certainly unlike anything within these two groups. The clusters of small compact cones on long pedicels in *Carnoconites cranwelliae* (Pentoxylales) are somewhat reminiscent of *Nataligma*, but there is no hint of whorling in the cluster or in the individual ovulate heads.

The Nataligmales are included here alongside the Fraxinopsiales primarily on the basis of the cuticular similarities (and reticulate venation) between their foliage affiliates (Grade 4 in the latter, only Grade 2 in the former).

Families: Includes the single family Nataligmaceae.

Family **NATALIGMACEAE** And. & And. 2003

Diagnosis: As for the order Nataligmales.

Range: Gondwana, Tr(CRN)
First & Last: *Nataligma dutoitii* And. & And. 2003, Molteno Fm., Karoo Basin, S. Africa (see comment under remarks).

Reference whole-plant genus & stratum—Molteno Fm.
Female: *Nataligma* And. & And. 2003; 1 TC, 1 sp., 4 indivs.
Foliage: *Gontriglossa* And. & And. 1989; 8 TCs, 1 sp., 1%.
Male: Unknown.
Stratum: As for 'First & Last' above.
Affiliations: *Nataligma*(2)*Gontriglossa*, Grade 2 (Mut.occ., Mor.cor.).

Prominence (colonisation success)—Gondwana Triassic (GT)
Gontriglossa (foliage): Recorded from Argentina, South Africa, India, eastern Australia and Tasmania.
FUDAL rating: 10/4/1/1/19 = 25; *Gontriglossa* was the 13th most prominent gymnospermous foliage genus in the GT.
Frequency: Moderate, 10 of 84 Gondw. degree squares.
Ubiquity: High, 4 of 5 Gondw. continents.
Diversity: V. low, 1 species in GT.
Abundance: Rare, 1% norm in Molteno TCs.
Longevity: High, 19 my through Triassic.

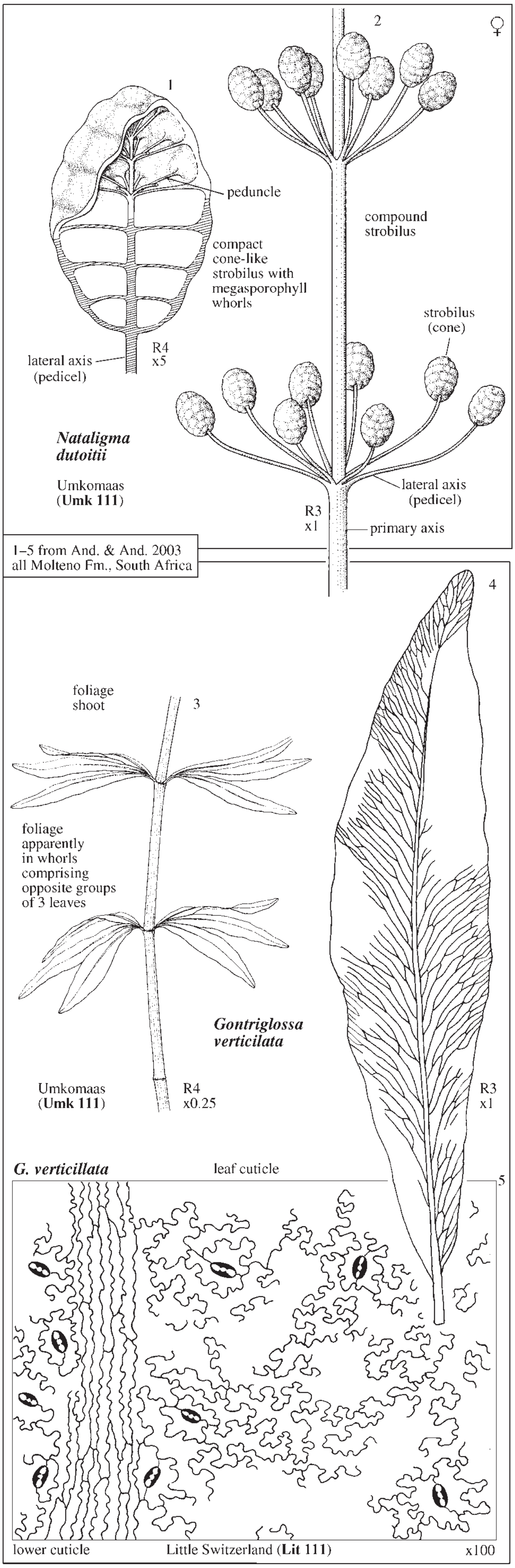
Ecology—Molteno Fm.
Habit: Possibly a slender herbaceous pioneer.
Habitat: Frequent in the *Dicroidium* riparian forest (6 of 10 TCs); also found in fern/horsetail meadows (wetlands).

Other genera—nil.

Remarks
Affiliations: The Nataligmaceae offer another instance (see Fraxinopsiaceae adjacent) where there remains no hint of the pollen-organ affiliate.

Stratigraphic range: Since the affiliation with the foliage *Gontriglossa verticillata* (Thomas 1958) And. & And. 1989 is insufficiently established, the range of this family is based solely on the ovulate fruit. The earliest occurrence of *G. verticillata* is in the Wianamatta Grp., Sydney Basin, Australia Tr(LAD) and the latest in the Molteno Fm. (And. & And. 1989).

References
And. & And. (1989): Foliage.
And. & And. (2003): Female, foliage.



1–5 from And. & And. 2003
all Molteno Fm., South Africa

Order **DINOPHYTONALES** Krassilov & Ash nov.

Contributors: V.A. Krassilov & S.R. Ash

Diagnosis: Putative stem-gnetopsids with an ovulate organ comprising a spherical cupule with four free tips, pedicellate on leafy shoots, attached to a robust four-lobed bracteate perianth persisting as a propeller at ?Krassilov fruit; ovules solitary, erect, with a free 3-faceted nucellus.

Male: Pollen organ a whorl of cupulate sporangiophores attached to a miniature four-lobed bracteate perianth; pollen grains bisaccate to bilobed monosaccate.
Foliage shoot: Heteroblastic, with helical to pinnate arrangement of scaly to linear, occasionally forked, hairy leaves.

Remarks
Dinophyton is important as a morphological link between pteridosperms (frond-like shoots, mono/bisaccate pollen, trigonocarp-like structure of ovule) and gnetophytes (verticillate perianths, cupulate sporangiophores, four-lobed ovulate cupules, stachyospermic position of ovule).

Families: Includes the single family Dinophytonaceae.

Family **DINOPHYTONACEAE** Krassilov & Ash nov.

Diagnosis: As for order Dinophytonales.

Range: Euramerica, Tr(CRN–NOR)
First & Last: *Dinophyton spinosus* Ash 1970; Chinle Fm. (Arizona, New Mexico), Dockum Gp. (Texas), New Oxford and Stockton Fms (Pennsylvania) and Pekin Fm. (North Carolina) of the Newark Supergroup; Late Triassic (Carnian to Norian). The specimens in the Stockton and Pekin Fms in the eastern USA and in the basal beds of the Chinle at a location in central Arizona lack trichomes and may represent a new species.

Reference whole-plant genus & stratum—Chinle Fm. (& coeval fms)
Female: *Dinophyton* Ash 1970; 10 TCs, 1 sp., numerous.
Male: 'pollen organ of *Dinophyton*' (Krassilov & Ash 1988); 1 sp., numerous fragments among the *Dinophyton* debris from the type locality.
Foliage: *Dinophyton* Ash 1970; as for ovulate organ.

Stratum: As for 'Range' above.
Affiliation: *Dinophyton*(4)foliage(4)male(4), Grade 4 (Mut.occ., Cut.cor.)

Prominence (colonisation success)—W. Euramerica Late Triassic
Frequency/ubiquity: *Dinophyton* (foliage and ovulate organ) is known from 10 localities scattered across a discontinuous 700 mile west-to-east belt from E.C. Arizona, through New Mexico into W.C. Texas (Ash 1970), and from three localities scattered along the eastern seaboard of the USA from Pennsylvania to North Carolina (Cornet 1977, Gensel 1986, Axsmith & Kroehler 1989).
Diversity: 1 species (possibly a second species that lacks trichomes).
Abundance: Both the foliage shoots and the 'pinwheels' (ovulate appendages) are amongst the 'more common plant fossils' found in the Chinle Fm. and Dockum Gp. (Ash 1970), but are rarely found in the Newark Supergroup in the eastern USA.
Longevity: *ca* 24 my.

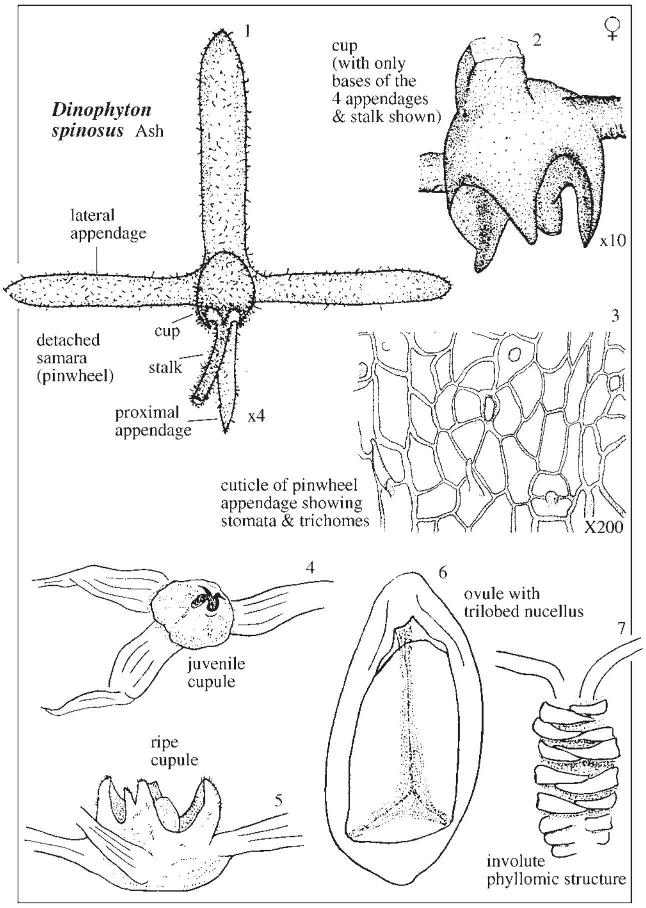
Ecology
Habit: Presumably arboreal, with wind-dispersed samaras; scleromorphic, growing on water-logged soil.
Habitat: The genus dominated a number of fossil localities and was especially abundant in the paper coals—possibly indicating a swampy habitat—of Arizona (Krassilov & Ash 1988).

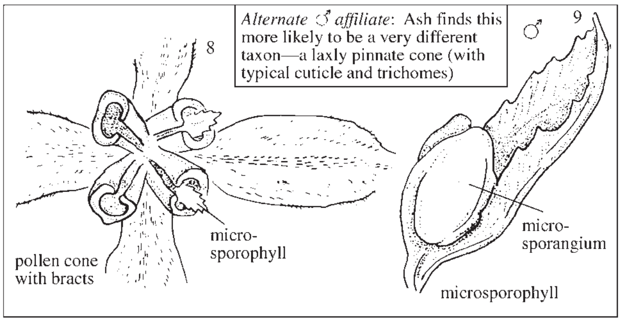
Other genera—nil.

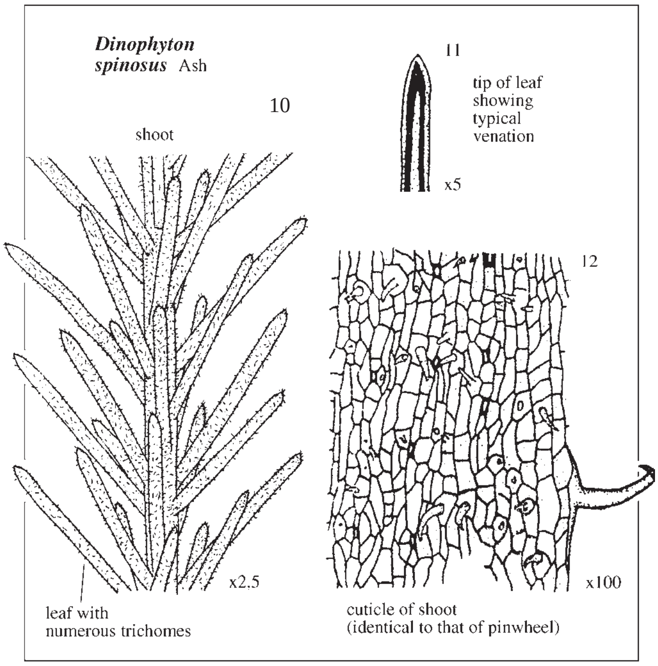
Remarks
Affiliation: Specimens of paper coals from the Chinle of Arizona (? locality), when bulk-macerated (Krassilov & Ash 1988), yielded abundant plant compressions: mostly leafy shoots and detached samaras ('pinwheels') of *Dinophyton*, followed by dispersed sporangiophores (containing bisaccate pollen—*Alisporites*). The leaves, samaras and dispersed sporangia have strikingly similar cuticle, with characteristic pubescence. (The conifer *Brachyphyllum* also occurred.)

Classification/phylogeny: Krassilov (1997) sees *Dinophyton* as phylogenetically significant in combining gnetalean (e.g. decussate perianth bracts in both 'seed organs' and 'pollen cones') and 'pteridosperm' (e.g. structure of the ovule) features. (See also above.)

References
Ash (1970), Krassilov & Ash (1988): General.
Krassilov (1997): Classification/phylogeny.




Alternate ♂ affiliate: Ash finds this more likely to be a very different taxon—a laxly pinnate cone (with typical cuticle and trichomes)



1–12 from 10 localities, Texas, New Mexico & Arizona, USA
Chinle Fm., Dockum Gp., Late Triassic (Carnian & Norian)

1–3,10–12 from Ash 1970
4–9 from Krassilov 1997 (after Krassilov & Ash 1988)

Order **DECHELLYIALES** Ash nov.

Contributor: S.R. Ash

Diagnosis: Putative stem gnetopsids with megasporophylls comprising a smooth oval seed proximal to a pronounced elongate wing or bract with parallel veins; megasporophylls generally attached in decussate pairs to lax strobilus.

Remarks

Classification/phylogeny: The winged seeds of *Dechellyia* from the USA and *Fraxinopsis* from Gondwana are superficially alike, but their foliage is entirely different, the former with parallel veins as in conifers, the latter with variously anastomosing side veins and a pronounced midrib. The affiliation of foliage and seeds is firmly established in both cases, but while the attachment in *Dechellyia* is known, it has not been established for the *Fraxinopsis/Yabeiella* plant. On the other hand, the cuticle of both *Fraxinopsis* and *Yabeiella* is known and very characteristic, but that of *Dechellyia* remains unknown. While it is tempting on the basis of the winged seeds alone to suggest a relationship at the order or even family level, this seems unlikely in view of the fundamentally different foliage.

Doyle (1996) found *Dechellyia*, along with *Piroconites* (Bernettiaceae) to be a probable stem relative of the modern Gnetales. Crane (1988) found *Dechellyia*, with 'decussate phyllotaxy', details of the seed wing and of the leaf venation, and characteristic pollen, to be gnetalean, but the 'leaf-like' microsporophylls and the winged seeds as difficult to interpret in gnetalean terms.

Family: Includes the single family Dechellyiaceae.

Family **DECHELLYIACEAE** Ash nov.

Diagnosis: As for the order Dechellyiales.

Range: Euramerica, Tr(CRN)

First & Last: *Dechellyia gormanii* Ash 1972 (shoots with attached foliage and winged seeds), together with the affiliated (Grade 3) microsporophyll *Masculostrobus clathratus* Ash 1972 with *in situ* pollen grains—*Ephedra chinleana* (Daugherty 1941) Scott 1960; Chinle Fm., Arizona, USA, Late Triassic (Carnian).

Reference whole-plant genus & stratum—Chinle Fm.

Female/foliage: *Dechellyia* Ash 1972; 2 TCs, 1 sp., abundant at type TC.

Male: *Masculostrobus* Seward 1911; 1 TC, 1 sp., >4 indivs. *Ephedra* (*in situ* pollen).

Stratum: Chinle Fm. (Monitor Butte M.), NE Arizona and New Mexico, USA, Late Triassic (Carnian).

Affiliation: Female and foliage, Grade 5 (Org.att.); *Dechellyia*(3)*Masculostrobus*, Grade 3 (Mut.occ.).

Prominence (colonisation success)—W. Euramerica Late Triassic

Frequency/ubiquity: Known from two localities.

Diversity: 1 species.

Abundance: Both the foliage and the reproductive structures (female and male) occur very commonly in the Canyon de Chelly TC (less so in the second TC, Fort Wingate, Ash 1989) and considering the delicate attachment of seed and leaves, the plants must have grown close at hand.

Longevity: <1 my.

Ecology

Habit: Possibly a small bushy tree.

Habitat: Floodplain, tropical.

Other genera—nil.

Remarks

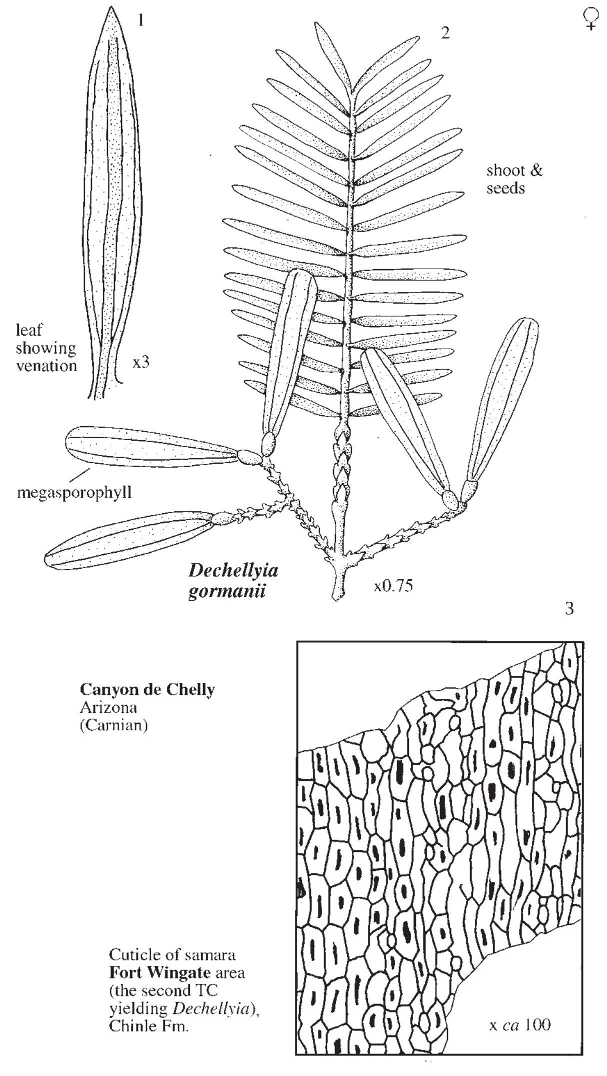
Affiliation: The material derives primarily from the type locality, Canyon de Chelly. Aside from the above-mentioned forms, the locality includes only the leafy shoot and cone of *Selaginella anasazia* Ash 1972 and the remains of other plants too poorly preserved and fragmentary to describe. The affiliation of *Dechellyia* and the male cones (with *Ephedra* pollen) is therefore reasonably well established (Grade 3).

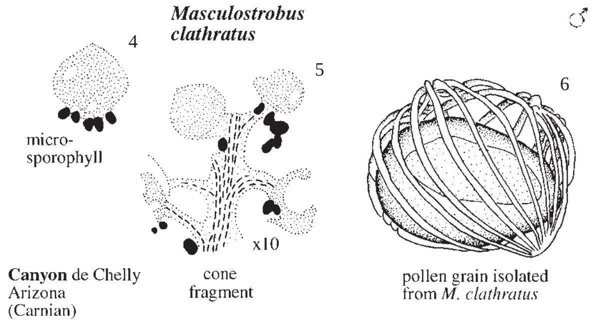
References

Ash (1972, 1989): General.

Crane (1988): Morphology, phylogeny.

Doyle (1996): Phylogeny.





Arizona, USA; Chinle Fm., Late Triassic
1,2,4–6 from Crane 1988 (redrawn from Ash 1972)
3, sketch by Ash

Order **BERNETTIALES** Konijn.-Citt. nov.

Contributor: J.H.A. Van Konijnenburg-Van Cittert

Diagnosis: Putative stem gnetopsids with 'gynoecia' comprising a planar aggregate ('megasporophylls') of many ovuliferous cells apparently always adhering to a large leafy bract with a crescent-shaped base and numerous longitudinal, parallel, sometimes forking, and apically converging veins.

Male: Microsporophylls sometimes attached to a similar bract but usually not; adaxial side of 'microsporophylls' almost completely covered with three-locular synangia containing ephedroid pollen.
Foliage: Associated leaves long, with a crescent-shaped base and numerous parallel veins, sometimes forking but without cross-veins, probably attached in pairs on the stem.

Remarks

Gnetopsids and bennettitopsids are mostly considered sister groups in gymnosperm phylogeny (e.g. Crane 1985; pp 18, 19, this volume). On the assumption that the *Bernettia/Piroconites* affiliation is correct, this plant appears to show features of both classes (e.g. the gnetalean synangia and pollen, and the bennettitalean 'gynoecia'). *Bernettia* bracts with gynoecia have been found in a strobilus and appear to be arranged in pairs. Van Konijnenburg-Van Cittert (1992) gave a description of *Piroconites* with *in situ* pollen and the subtending bract *Chlamydolepis*, and suggested gnetalean affinities. Doyle (1996) favoured a hypothesis where *Piroconites/Bernettia* fall on a lineage from the glossopterids to the modern Gnetales, as might also be the case for *Dechellyia* (p. 207). Crane (1996) also suggested a putative gnetalean affinity.

Family: Includes the single family Bernettiaceae.

Family **BERNETTIACEAE** Konijn.-Citt. nov.

Diagnosis: as for the order Bernettiales.

Range: Euramerica, J(HET)
First & Last: *Bernettia inopinata* Gothan 1914 (ovulate organ), with the affiliated organs *Piroconites kuespertii* Gothan 1914 and *P. froschii* (Schuster 1911) Gothan 1914 (microsporophylls), *Chlamydolepis lautneri* (Boersma 1985) Van Konijnenburg-Van Cittert 1992 (bract subtending both the ovulate and pollen organs), *Desmiophyllum gothanii* Florin 1936 (foliage, sometimes attached, probably in pairs, to a stem). Early Liassic, Franken, area around Bayreuth (11 localities between Kulmbach and Neurenberg), Germany.

Reference whole-plant genus & stratum—early Liassic of Franken
Female: *Bernettia* Gothan 1914; 8 TCs, 1 sp., >100 indivs.
Male: *Piroconites* Gothan 1914; 8 TCs, 1 or 2 spp, >100 indivs. *Ephedripites*-type pollen
Bract: *Chlamydolepis* Van Konijnenburg-Van Cittert 1992; 4 TCs, 1 sp., >20 indivs.
Foliage: *Desmiophyllum* Lesquereux 1878; 11 TCs, 1 sp., >100 indivs.

Stratum: As for 'First & Last' above.
Affiliation: *Bernettia*(3)*Desmiophyllum*(3)*Piroconites*, Grade 3 (Mut.occ., Mor.cor., Cut.cor.).

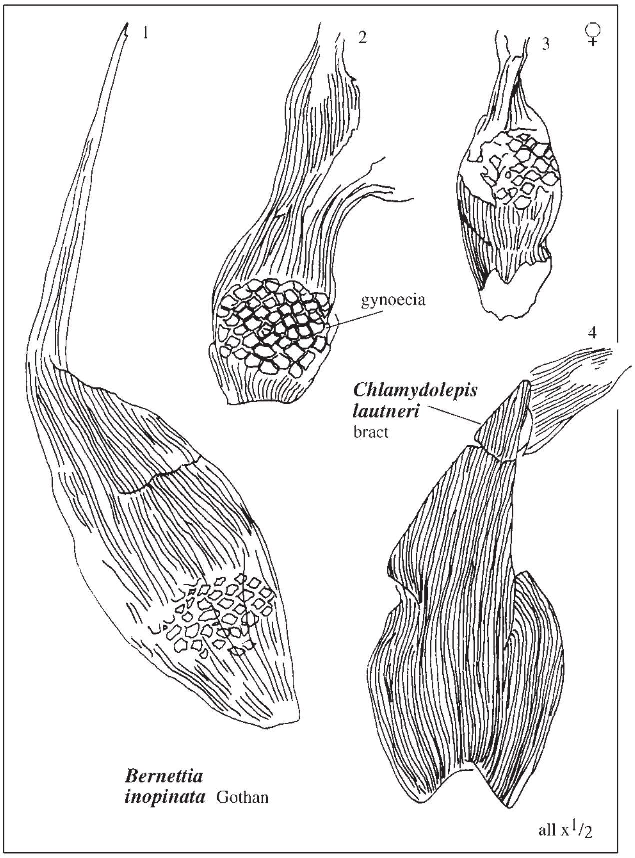
Prominence (colonisation success)—Europe, Early Jurassic
Frequency/ubiquity: Reproductive material from 8 TCs in Franken area.
Diversity: 1 (or 2) species.
Abundance: Fairly common.
Longevity: *ca* 3 my.

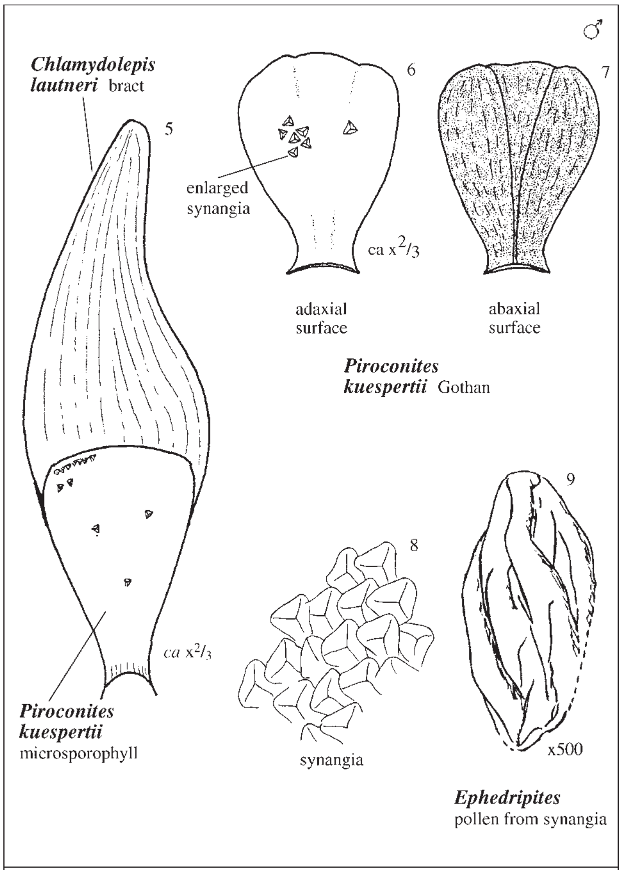
Ecology
Habit: Probably a shrub (or small tree); stem *ca* 20 mm diam.; leaves up to >500 mm; *Bernettia* megasporophylls in tight strobilus up to *ca* 300 mm long.
Habitat: Most specimens occur in small clay lenses in sand deposits, representing fluviatile beds; the plants probably grew in a lowland area near small rivers or streams.

Other genera—nil.

Remarks
Phylogeny: The trilocular synangia yielding *Ephedripites* pollen strongly suggest gnetopsid affinities; this is supported by the arrangement of leaves, and possibly the megasporophyll complexes in pairs.

References
Gothan (1914), Boersma (1985), Kirchner (1992): Male, female.
Florin (1936): Foliage.
Crane (1985, 1996), Doyle (1996): Phylogeny.
Van Konijnenburg-Van Cittert (1992): General, male.





specimens from 4 localities
(**Lautner, Schnabelwaid, Pechgraben & Grossbellhofen**)
all near Bayreuth, Franken, Germany; Jurassic, Early Liassic (Hettangian)

1–4 from Kirchner 1992 (? Schweitzer)
5–7 from van Konijnenburg-van Cittert 1991
8,9 J.M. Anderson sketches 1998 (drawn after Van Konijnenburg-Van Cittert 1992)

Order **EOANTHALES** Krassilov, And. & And. nov.

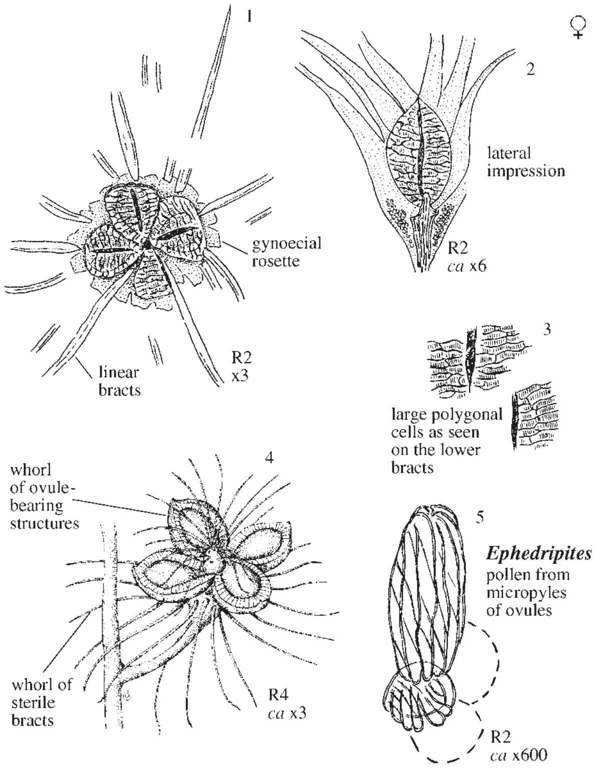
Contributor: V.A. Krassilov

Diagnosis: Putative stem gnetopsids with gynoecia comprising a stalked, radially symmetrical, four-lobed cupule subtended by a perianth of free or partly coalescent, linear bracts; floral axis protruding over the gynoecium, terminating in a tuft of linear bracts, variously reduced; ovules one per gynoecial lobe, orthotropous, with a thick megaspore membrane; nucellus shortly beaked, with a broad pollen chamber harbouring costate pollen grains.

Remarks

Eoantha was the first recorded Mesozoic ovulate structure related to gnetophytes. Its structure was interpreted (Krassilov 1986, 1987) as homologous to a single fertile node of a gnetalean spike with linear bracts subtending two pairs of bracteolate ovules. A tuft of bracts on the protruding floral axis was considered a vestige of a consecutive floral node. Although the mode of pollination, with pollen grains entering the pollen chamber, was definitely gymnospermous, the flower-like structure of the gynoecium and perianth warranted a proangiospermous interpretation of the fossil.

Family: Includes the single family Eoanthaceae.



Eoantha zherikhinii Krassilov

all **Baisa** locality, Vitim River, Lake Baikal area (Transbaikalia)
Early Cretaceous (Barremian–Aptian)

1–5 from Krassilov 1986
4 Gill Condy sketch 2005 (drawn from Krassilov rough 2005)

Family **EOANTHACEAE** Krassilov, And. & And. nov.

Diagnosis: As for the order Eoanthales.

Range: Laurasia, K(BRM–APT)
First & Last: *Eoantha zherikhinii* Krassilov 1986 (ovulate structure with pollen grains in the pollen chamber), Krassilov & Bugdaeva 2000 (ovulate structure attached to a slender axis, with affiliated leaves *Praeherba spathulata*); another species *Eoantha ornata* (Krassilov & Bugdaeva 1999); Baisian Assemblage, Vitim River, Lake Baikal area (Transbaikalia), Russia, Early Cretaceous.

Reference whole-plant genus & stratum—Vitim, Lake Baikal area
Female: *Eoantha* Krassilov 1986; 1 TC, 2 spp, 5 indivs.
Male: unknown
Pollen grains: *Ephedripites* sp., found in the pollen chamber.
Foliage: *Praeherba* Krassilov & Bugdaeva 2000, 1 TC, 1 sp., 2 indivs.

Stratum: As for 'First & Last' above.
Affiliations: *Eoantha*(4)*Praeherba*, Grade 4 (?Org.att., Mut.occ., Mor.cor.).

Prominence (colonisation success)—E. Laurasia, Early Cretaceous
Frequency/ubiquity: Known from a single locality.
Diversity: 2 species.
Abundance: Rare; each of the species based on two to several compression specimens with counterparts (Baisa locality on the Vitim River at the mouth of Sololy Creek, Transbaikalia, Russia).
Longevity: <1 my.

Ecology
Habit: Apparently herbaceous with graminoid leaves and flower-like ovulate structures on slender axis.
Habitat: Preserved in paper shales and marls of Baisa locality with a lacustrine fauna, terrestrial insects and a plant assemblage containing several pro-angiospermous species.

Other genera—nil.

Remarks
Affiliation: The leaves *Praeherba spathulata* Krassilov & Bugdaeva 2000 are found in close association with *Eoantha zherikhinii*; similar vascular elements are macerated from axes with leaves and ovulate cupules (Krassilov & Bugdaeva 2000). *Ephedripites* pollen is found in the pollen chamber (Krassilov 1986).

Classification: Gnetophytic affinities are indicated by the structure of the verticillate bracteate perianth and bracteolate cupules, as well as by the erect ovules and *Ephedripites*-type pollen grains. Yet the flower-like structure of the ovulate organ, cutinised megaspore membrane and the affiliated graminoid leaves justify separation from the Gnetales at the ordinal level.

References
Krassilov (1986, 1987, 1997): General.
Krassilov & Bugdaeva (1999, 2000): General.

Order **GNETALES** Luerss. 1879

Diagnosis: Crown gnetopsids with ‘flowers’ comprising a system of opposite and decussate bracteoles axillary to a primary bract (adapted from Crane 1985).

Classification

The three genera of extant Gnetales have been variously classified: Cleal (1993) had a single order with only one family, the Gnetaceae; Martens (1971) and Kubitzki (1990) had a single order with three families; Crane (1988), Taylor & Taylor (1993) and Stewart & Rothwell (1993) all had a single order with three genera not placed in families; Woodland (1991, 2000) had a unique subdivision and class with three subclasses and three families. Doweld (2001), took the taxonomic inflation a step further in recognising the group as a phylum with three classes, three orders and three families. Clearly no consensus exists. We follow Martens (1971) and Kubitzki (1990) with a single order and three families.

Phylogeny (pre-1998)

To give a deeper sense of continuing uncertainty of the place of the Gnetales in gymnosperm phylogeny, we briefly trace the history of cladistic analyses involving the group since the mid-1980s.

Cladograms generated over the decade from 1985 reveal conflicting results. Crane (1985), for instance, found the Gnetales (*Gnetum*, *Welwitschia* and *Ephedra*) to be the sister group to the angiosperms, while Nixon *et al.* (1994) found the angiosperms to be nested within the gnetopsids, with *Ephedra* being the sister group to the angiosperms plus *Welwitschia* and *Gnetum*. Nixon *et. al.* (1994) concluded that ‘the question of whether the gnetopsids form a monophyletic group or are paraphyletic relative to the angiosperms (or to the angiosperms plus Bennettitales) remains a question that deserves much more attention’.

In Doyle & Donoghue (1992, 1993), the Gnetales plotted out as the sister group of the Bennettitales, which together formed the sister group of *Pentoxylon* and all three were the sister group of the angiosperms. All together formed the anthophytes.

Doyle (1996) specifically addressed the Nixon *et al.* (1994) hypothesis that the angiosperms were nested within the Gnetales, finding it weakly supported. On both morphological and molecular evidence he showed the Gnetales to be a monophyletic group, on a line quite distinct from the angiosperms. His plots show the gnetopsids plus Bennettitales to be the sister group of the angiosperms plus *Caytonia*.

Molecular-data-(rRNA): The rRNA data of Hamby & Zimmer (1992) indicate that the extant Gnetales are a monophyletic group and that they are the closest living relatives of the angiosperms. At genetic level, *Welwitschia* and *Gnetum* are found to be more closely related to one another than either is to *Ephedra.*

Morphological data: Phylogenetic trees detailing the Gnetales based on morphological and molecular data prove to be complementary (Doyle & Donoghue 1992, 1993; Doyle *et al.* 1994). This holds also for the relationships between the three extant gnetalean genera. The cautious conclusion of Nixon *et al*. (1994) that the Gnetales are paraphyletic, with the angiosperms nested within them, is not supported by the two most recent analyses of Doyle (1996). The most parsimonious trees of Doyle (1996) show the Gnetales to be most closely related to the Bennettitales and Pentoxylales and that these, together with the angiosperms and *Caytonia*, may be linked with the glossopterids, making up a clade called the glossophytes.

Phylogeny (current) [Contributors: M. Mundry, I. Mundry & T. Stützel]

In contrast to the above, recent molecular data reject a close relationship between Gnetales and angiosperms, although an alternative well-supported topology is still lacking. Sometimes the Gnetales are placed as sister to the conifers (Winter *et al*. 1999; Bowe *et al*. 2000; Chaw *et al*. 2000; Frohlich & Parker 2000; Schmidt & Schneider-Poetsch 2002), or even sistered to the Pinaceae (making conifers a paraphyletic group; Chaw *et al*. 2000; Gugerli *et al*. 2001) and in other studies they are placed as sister to all other gymnosperms (Rydin *et al*. 2002; Schmidt & Schneider-Poetsch 2002).

Because of the striking differences between the three genera of the Gnetales, they are often regarded as belonging to three monogeneric families. In contrast to this, molecular data indicate *Welwitschia* and *Gnetum* as sistered (Gnetaceae) with a basal family Ephedraceae (Price 1996).

Morphology [Contributors: M. Mundry, I. Mundry & T. Stützel]

Interpretation of the male synangiophore of the Gnetales, especially that of *Welwitschia mirabilis*, has aroused much controversy (reviewed by Hufford 1996). In recent years, the structure has been mostly regarded as a compound of two fused decussate male sporangiophores with adaxial synangia (therefore often termed pinnate or compound), as the synangiophore originates from two distinct primordia in decussate position (Martens 1971; Hufford 1996). As the primordia of the synangiophore in *Welwitschia mirabilis* exhibit some similarities to an apex, an alternative interpretation regards each half of the synangiophore as one reduced lateral male cone, each with three simple sporangiophores and one terminal synangium (Mundry & Stützel 2004a).

In the past, the inner bracts were often described as an outer integument and homologised with the outer integument of the angiosperms, but Endress (1996) points out that this is unlikely as the initiation of the inner pair of bracts and the outer integument of the angiosperms is different (acropetal in Gnetales and basipetal in angiosperms).

Crown & stem groups

Doyle & Donoghue (1993) considered the extant genera *Ephedra, Gnetum* and *Welwitschia* together with the Early Cretaceous genera *Eoantha* and *Drewria* to form the crown-group of the Gnetales (the Gnetopsida in this volume), while the Late Triassic and Early Jurassic forms were considered the stem-gnetaleans. (See further on p. 202.)

The palynological record

The palynological record of the gnetopsids, as summarised in Crane (1988), is apparently far more complete than the macrofossil record. *Ephedra* and *Welwitschia* yield striate-ribbed (‘ephedroid’) pollen of the *Equisetosporites* type (tf 9, p. 213; tf 9, p. 215). Such pollen is recorded from as early as the Middle Permian in North America, but is particularly abundant in the low to middle paleolatitude floras of northern Gondwana and southern Laurasia during the mid-Cretaceous (BRM-CEN). *Gnetum*, on the other hand yields spinulose inaperturate grains of the *Elaterosporites* type (tf 10, p. 214), which Crane (1988) notes to be probably the more specialised form within the class. A variety of such grains also characterise these mid-Cretaceous floras.

Extant diversity

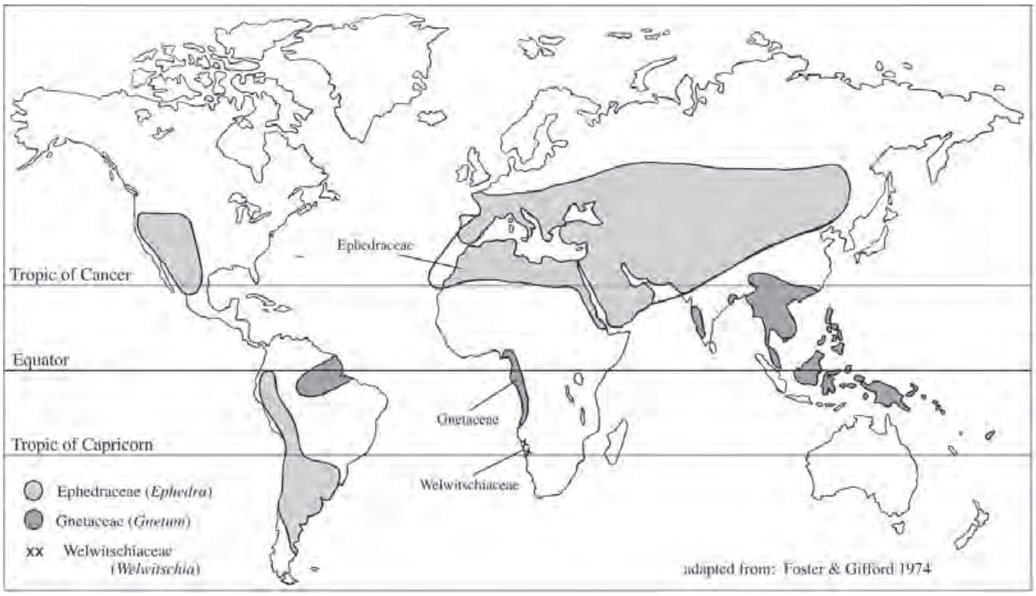
GNETOPSIDA

GNETALES	*extant diversity*
Ephedraceae	1 genus, 35–45 spp
Gnetaceae	1 genus, 30 spp
Welwitschiaceae	1 genus, 1 sp.
Total	3 genera, 71 spp

Families: Includes the single extinct family Drewriaceae and the three extant families Ephedraceae, Gnetaceae and Welwitschiaceae.

References

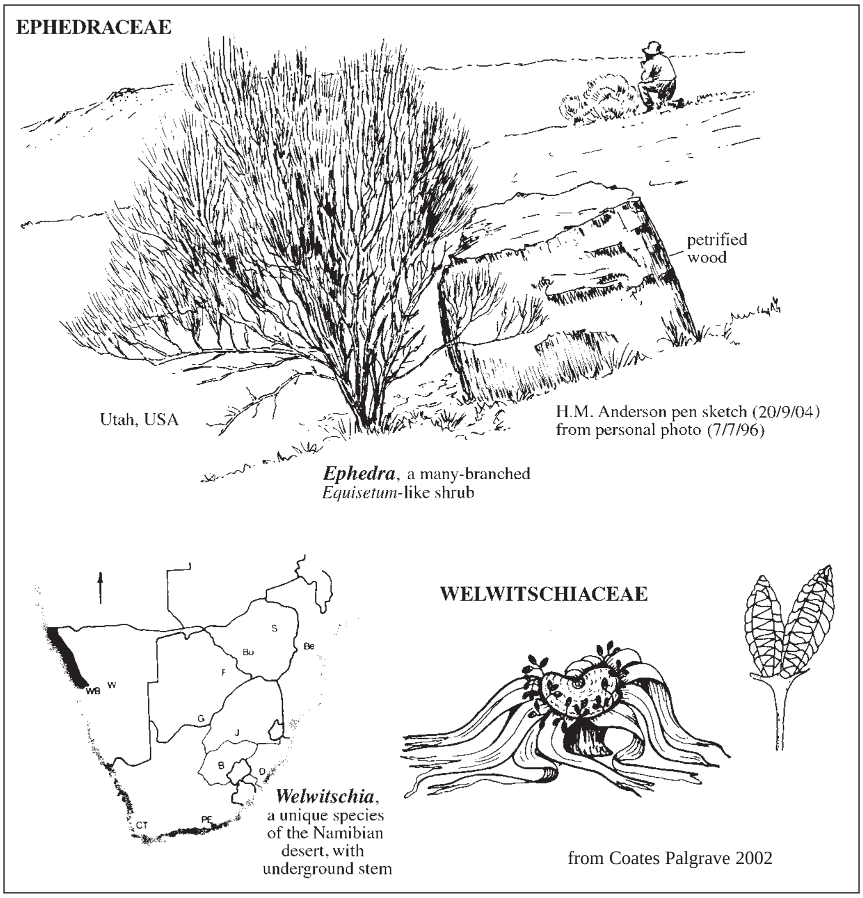
Crane (1985) (& later authors): Phylogeny (pre-1998).
Crane (1988): Palynology.
Kubitzki (1990) (& others): Classification.
Doyle & Donoghue (1993): Crown and stem groups.



adapted from: Foster & Gifford 1974

Fig. 33. EXTANT GNETALES, GLOBAL OCCURRENCE

Phytogeography of a relict class: The three monogeneric families show an intriguing mutually exclusive occurrence. This is the kind of distribution one might expect for three species within a global genus, or for three genera within a cosmopolitan family, but hardly for the only three surviving genera representing three morphologically distant families in a relict class. Tracing the phytohistory of these three families (as for the Araucariaceae—see Charts 21–24, pp. 56–59) would be of particular interest.



H.M. Anderson pen sketch (20/9/04) from personal photo (7/7/96)

from Coates Palgrave 2002

Fig. 34. *EPHEDRA* & *WELWITSCHIA*, RELICTS OF THE GNETOPSIDA

Relicts: Two of the three surviving genera of the 235 my old class.

Family **DREWRIACEAE** And. & And. nov.

Diagnosis: Gnetalean plants bearing spicate strobili with *ca* 4–6 pairs of apparently decussate primary bracts, each subtending an ovulate flower (adapted from Crane & Upchurch 1987).

Range: Euramerica, K(APT)
First & Last: *Drewria potomacensis* Crane & Upchurch 1987; Drewrys Bluff, Potomac Gp. (Zone 1), Virginia, USA, Early Cretaceous (Aptian).

Reference whole-plant genus & stratum—Potomac Gp.
Female/foliage: *Drewria* Crane & Upchurch 1987; 1 TC, 1 sp., >100 indivs.
Male: Unknown.

Stratum: As for 'First & Last' above.
Affiliation: Female(5)foliage, Grade 5 (Org.att., Mut.occ.)

Prominence (colonisation success)—W. Euramerica, Early Cretaceous
Frequency/ubiquity: Known from a single locality.
Diversity: 1 species
Abundance: *D. potomacensis*, fern fronds and angiosperms (5 species) are the commonest fossils at Drewrys Bluff, the single locality from which the genus is known.
Longevity: <1 my.

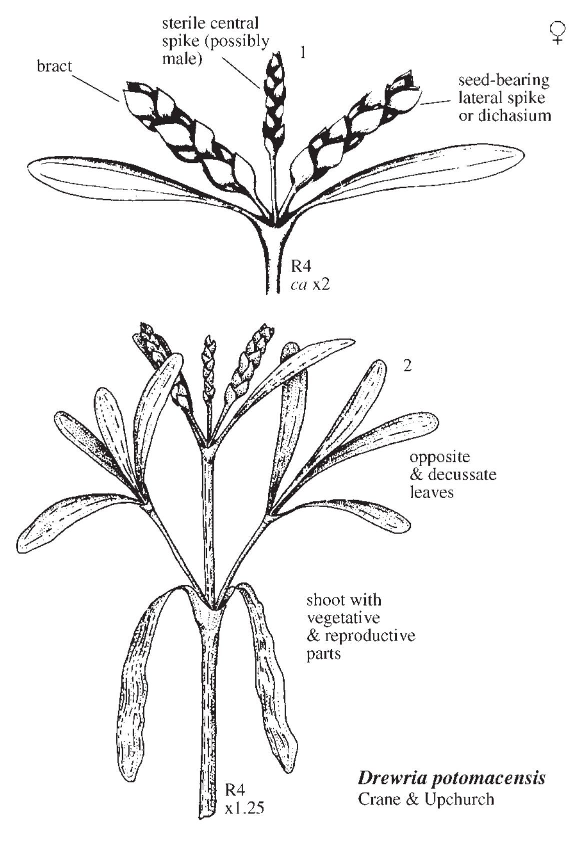
Ecology
Habit: Herbaceous or shrubby.
Habitat: Apparently an important component of the early successional streamside vegetation of mesic environments.

Other genera—nil.

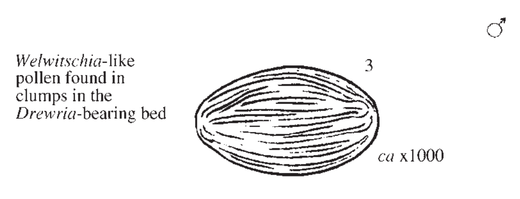
Remarks
Gnetalean characteristics: *Drewria* appears similar enough to the three extant gnetopsid genera, and particularly *Welwitschia*, to be included in the order Gnetales. The characters of *Drewria* that, according to Crane & Upchurch (1987), suggest a gnetalean relationship include: opposite bracts surrounding the seeds; network of subepidermal foliar fibres; distinctive leaf venation (very like that in *Welwitschia* cotyledons); opposite and decussate leaves, with swollen nodes; dichasial arrangement of reproductive spikes; and the affiliated polyplicate pollen (like that of *Welwitschia*).

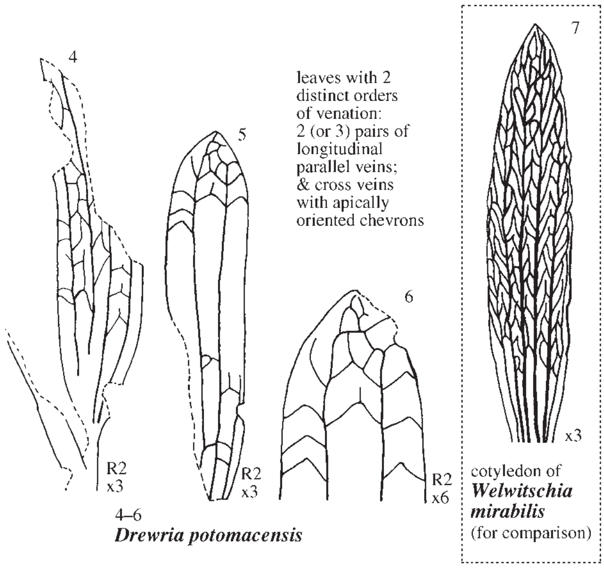
Affiliation: All material derives from a 40 mm-thick bed of micaceous grey clay at Drewrys Bluff. It includes stems with attached leaves and reproductive structures. Masses of *Welwitschia*-type pollen were found in association with the megafossils.

Reference(s)
Crane & Upchurch 1987: General.
Crane 1988: Classification/affiliation.



Drewria potomacensis
Crane & Upchurch





4–6
Drewria potomacensis

cotyledon of ***Welwitschia mirabilis*** (for comparison)

all **Drewrys Bluff**, Virginia, USA
Potomac Gp. (Zone 1), Early Cretaceous (Aptian)

1,4–7 from Crane & Upchurch 1987 (7 redrawn from Rodin 1953)
2 from Crane 1988 (based on Crane & Upchurch 1987)
3 J.M. Anderson sketch (based on Crane & Upchurch 1987)

Family **EPHEDRACEAE** Dumort. 1829

Diagnosis [Contributors: M. Mundry, I. Mundry & T. Stützel]
Plants: Dioecious, sometimes monoecious.

Ovulate cones: Compound; bracteoles decussate, usually in 3 pairs, mostly fleshy, forming 'baccate' cones or winged, with only the terminal pair being fertile and each subtending a single ovule surrounded by a pair of fused bracts forming a stony layer during maturation (simple cone or 'flower'); occasionally a whorl of three simple axillary cones ('flower') occurs (Yang Yong 2001).

Male cones: Cones simple, each male flower derived from two reduced male shoots (see Gnetales, 'Morphology', Chart 30, p. 65), several, lateral, each with one synangiophore bearing several sessile or shortly stalked disporangiate synangia; synangiophore sheathed by two fused median bracts until pollination; pollen without air-bladders.

Leaves: Scale-like, reduced; shoot axis assimilative.

Range: K(BRM)–Rec.
First: Undescribed fertile and sterile material from the 'Jianshangou Bed', basal Yixian Fm., NE China (Sun Ge *et al*. 2001; Dilcher 2004, pers. comm.) (see p. 35), K(BRM).
Last: Extant.

Prominence (colonisation success)—extant
Frequency/ubiquity/abundance: See pp 210, 211.
Diversity: 1 genus (*Ephedra*), *ca* 35–45 species; arid subtropics of Eurasia (*ca* 40 spp), N. America (*ca* 14 spp), and S. America (13 spp); no more than 5–7 species co-occur in any one region.

Ecology
Habit: Mostly many-branched, erect or prostrate equisetum-like shrubs, some climbers (hanging or scandent), one species up to a small tree.

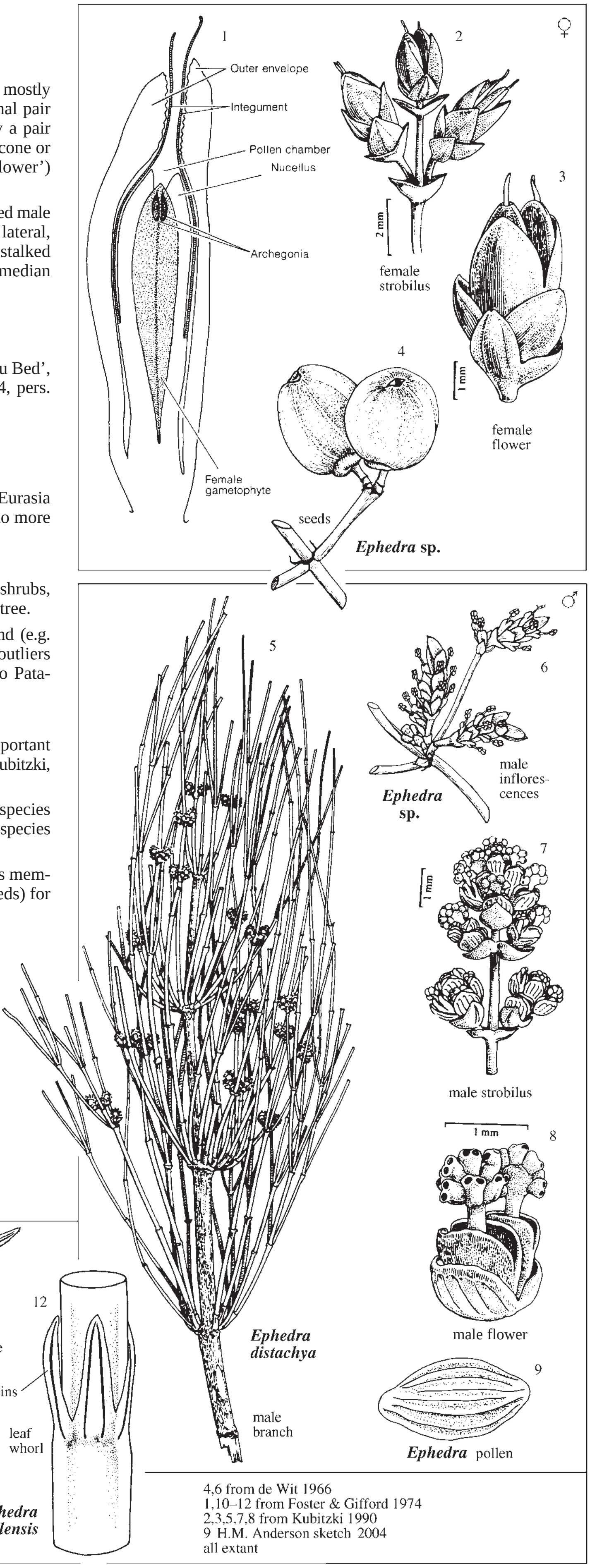
Habitat: Xerophytic, heliophilous, partly cold-resistant; from lowland (e.g. Arabian Gulf and much of lowland Argentina) to montane (e.g. outliers in the Tibesti Mts of the Sahara, to the Andes from Ecuador to Patagonia).

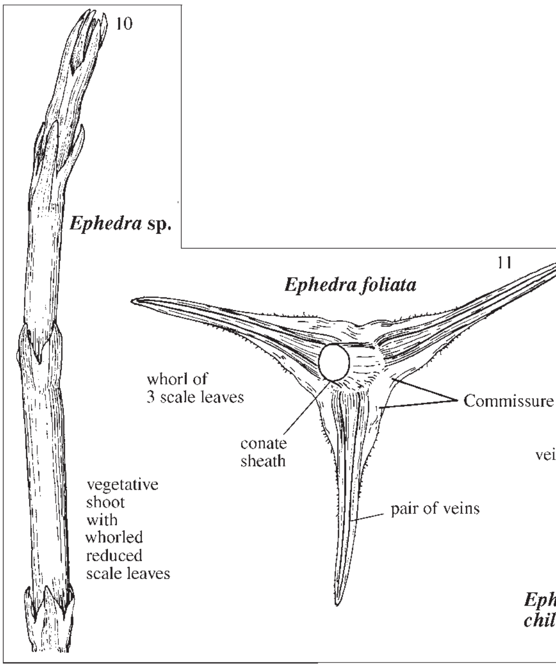
Remarks
Pleistocene: Pollen studies show *Ephedra* to have 'formed an important element of the Eurasian periglacial cold steppes of the Pleistocene' (Kubitzki, 1990).

Pollination: Most species anemophilous (wind-pollinated), some species insect-pollinated (mainly Diptera), with the attractant in at least one species being a 'nectarial exudate'.

Dispersal: Two adaptations occur—from bracts of fruiting strobilus membranous with keeled wings, to a pseudoberry (with two enclosed seeds) for bird dispersal.

References
Kubitzki (1990): Prominence, ecology, remarks.





4,6 from de Wit 1966
1,10–12 from Foster & Gifford 1974
2,3,5,7,8 from Kubitzki 1990
9 H.M. Anderson sketch 2004
all extant

Family **GNETACEAE** Lindl. 1834

Diagnosis [Contributors: M. Mundry, I. Mundry & T. Stützel]

Ovulate cones: Compound, with several ring-like collars (fused cone bracts), each subtending a cone axis with radial arrangement of 5–7 simple cones (‘flower’); simple cones composed of two outer fleshy bracts (transverse position), two inner bracts (median position), and one terminal ovule.

Male cones: Compound, with sterile ovules; in the axils of each ring-like collar arise several series of simple male cones and an apical ring of sterile ovules; simple male cones composed of one synangiophore usually bearing two sporangia sheathed by two fused median bracts until pollination; pollen without air-bladders.

Leaves: Laminar with reticulate venation.

Range: Recent
First: Without a known megafossil record.
Last: Extant.

Prominence (colonisation success)—extant
Frequency/ubiquity/abundance: See pp 210, 211.
Diversity: 1 genus (*Gnetum*), *ca* 30 species; pantropical, mainly lowland, southeast Asia (*ca* 21 spp), West Africa (2 spp), eastern and tropical South America (*ca* 7 spp).

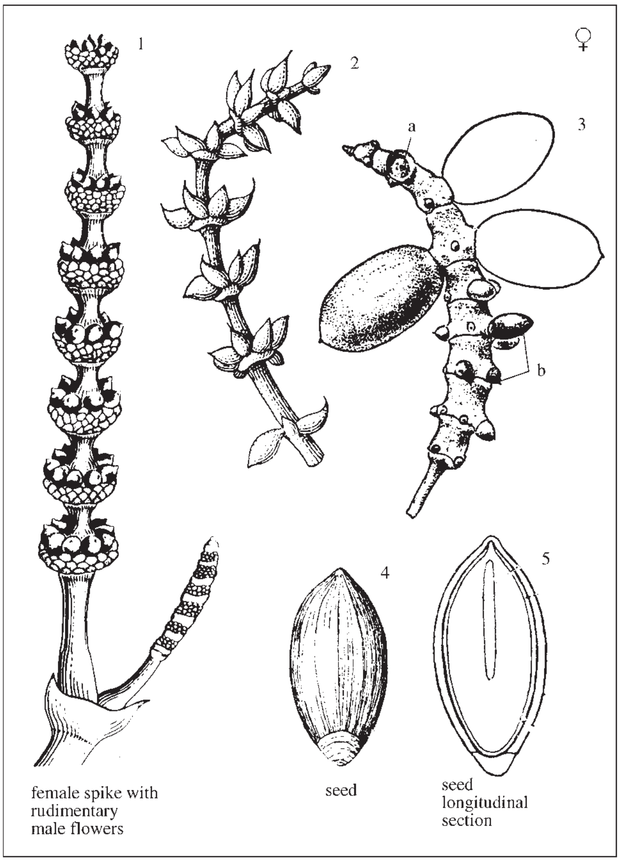
Ecology
Habit: Mostly climbers with twining stems, some shrubs, rarely trees.
Habitat: Lowland forests, riverine forests, occasionally cloud forests up to 2 000 m in SE Asia (several species straddle the Wallace line); restricted to humid forests in W Africa; lowland forests, forest margins and savanna in the Americas.

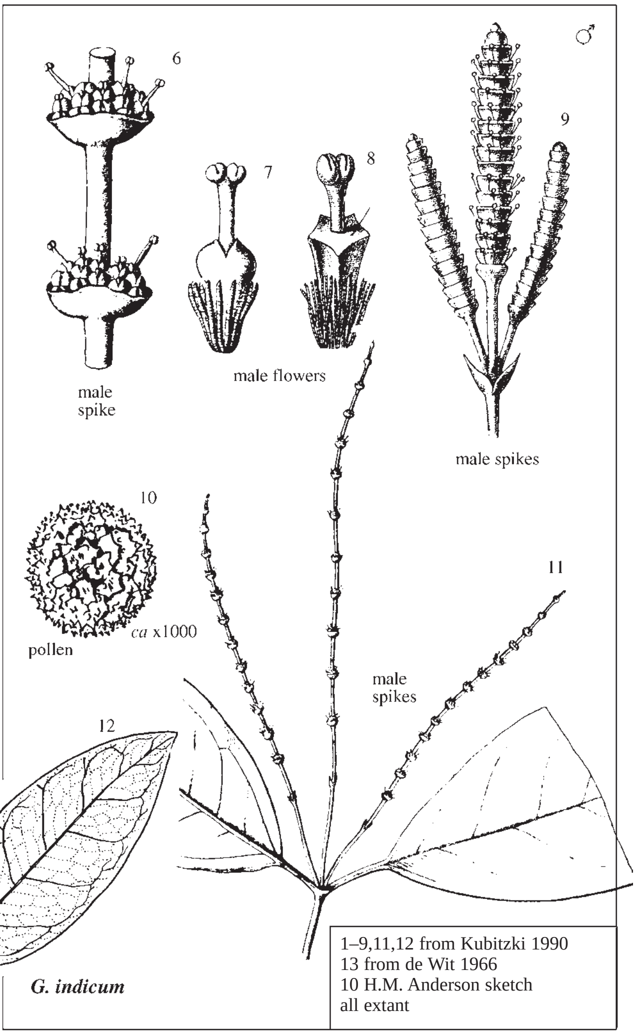
Remarks
Species: Kubitzki (1990) records that the American and African species are regarded as more closely related to each other than to the Asian species.

Pollination: Uncertain, often presumed to be by wind, but possibly by insects—indications being the sweetish odour produced by male flowers, and a rich sugary pollination droplet by female flowers.

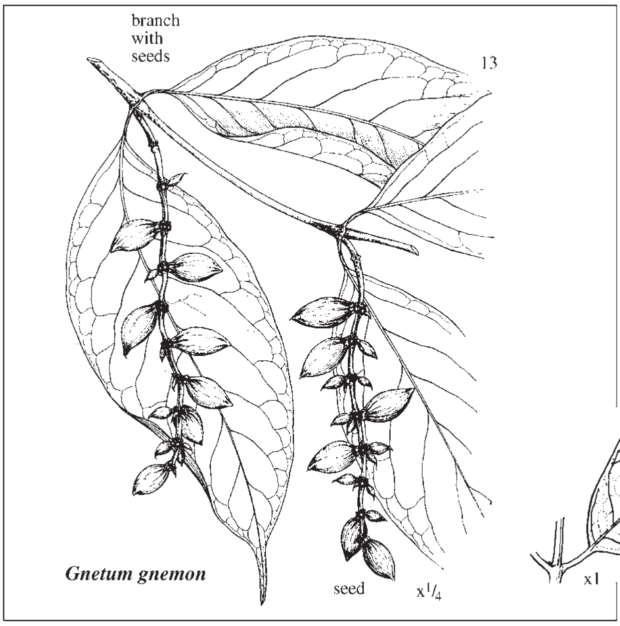
Dispersal: Outer envelope of seed fleshy and vividly coloured (red, pink or yellow) at maturity, attracting a diversity of seed dispersers—toucans and white-faced monkeys in the New World, larger birds and civets in SE Asia; one liana species of the Amazonian riverine forests has a dirty-grey fruit dispersed by a catfish species; another riverine species has large, corky fruit and is possibly water-dispersed.

Reference
Kubitzki (1990): Prominence, ecology, remarks.





1–9,11,12 from Kubitzki 1990
13 from de Wit 1966
10 H.M. Anderson sketch
all extant



Family **WELWITSCHIACEAE** Markgr. 1926

Diagnosis [Contributors: M. Mundry, I. Mundry & T. Stützel]

Ovulate cones: Dense strobili with *ca* 50 pairs of decussate bracteoles each subtending a simple cone (‘flower’); ovules terminal on simple cone, surrounded by two fused inner bracts and sometimes two transverse outer bracts; seeds with two prominent wings formed by the inner pair (chlamys) of bracts.

Male cones: Similar to female cones, dense with *ca* 30 pairs of decussate bracteoles each subtending a simple cone (flower, derived from a compound cone, see Gnetales ‘Morphology’, Chart 30, p. 65); simple cones terminal, with a sterile ovule surrounded by a synangiophore with 6 stalked synangia; both structures basal with two pairs of bracts, the inner pair (chlamys) sheathe the ovule and synangiophore until pollination; synangia tri- or tetrasporangiate; pollen without air-bladders.

Foliage: Plants with only two large, elongate leaves, persistent throughout the entire lengthy lifespan, deeply dissected.

Range: K(BRM)–Rec.
First: Undescribed fertile and sterile material from the ‘Jianshangou Bed’, basal Yixian Fm., NE China (Sun Ge *et al*. 2001; Dilcher 2004, pers. comm.) (see p. 35), K(BRM).
Last: Extant.

Prominence (colonisation success)—extant
Frequency/ubiquity: See pp 210, 211.
Diversity: A single monotypic genus (*Welwitschia mirabilis*); coastal desert of Namibia and Angola.
Abundance: Very localised, rare.

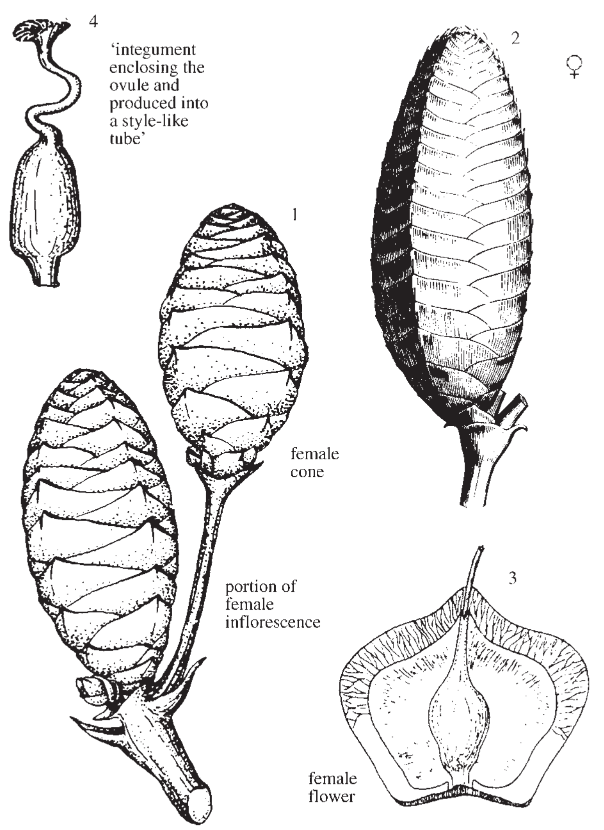
Ecology
Habit: Unique dwarf woody stem (up to 1 m diam.), with two large, prostrate leaves. *Welwitschia*, Coates Palgrave (2002) writes, is ‘a dwarf but massive tree driven underground by the rigours of the desert climate; the largest specimens have a stem 1.5 m in diameter rising 2 m above the ground, with 2 to 3 m below the ground before the very large tap-root starts’.
Habitat: Restricted to a narrow coastal strip; water uptake, aside from through roots, possibly from dew and coastal fog through the large amphistomatic leaves; occurring in gravelly soils along dry water-courses in desert regions, even surviving in the deep, loose sand of the desert itself.

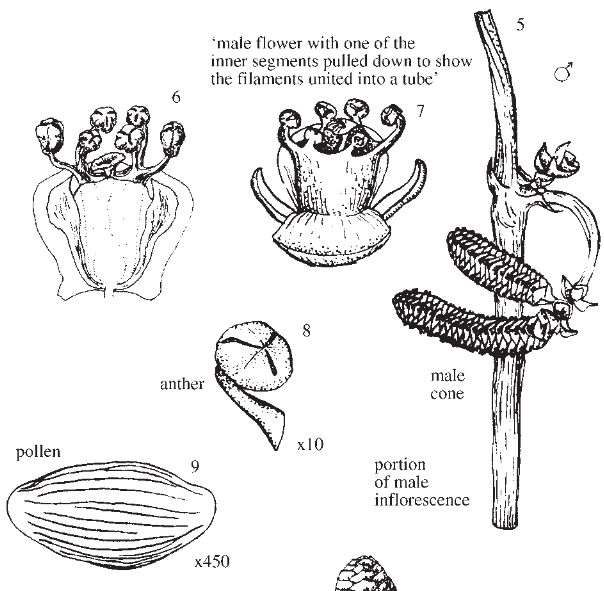
Remarks
Pollination: Apparently anemophilous (wind-pollinated), possibly ambophilous; various insects, including Hymenoptera and mosquitoes, have been observed visiting the flowers in search of liquid—‘pollination droplets appear at the apex of the tubillus both in female and in male flowers’ (Kubitzki 1990).

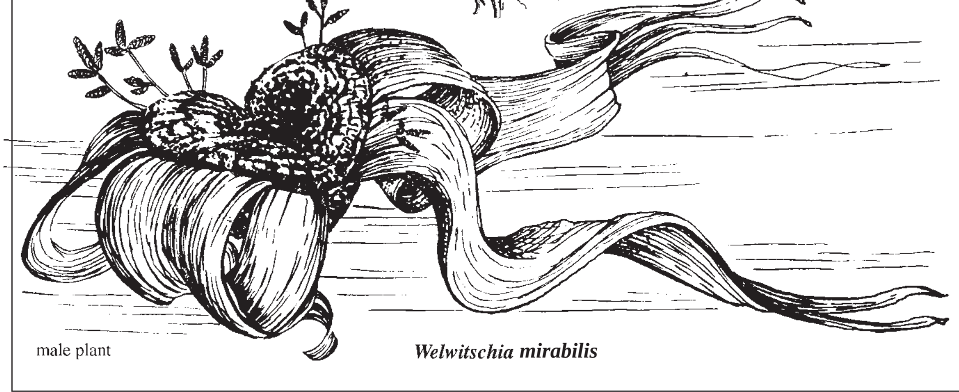
Lifespan: These are some of the oldest plants on Earth, with average specimens being dated by the C-14 method at 500 to 600 years, and large old individuals estimated at over 2 000 years (Coates Palgrave 2002).

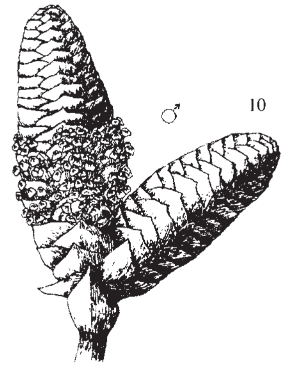
Dispersal: Mature seeds winged, wind-disseminated.

References
Kubitzki (1990): Prominence, remarks.
Coates Palgrave (2002): Habit, habitat, longevity.







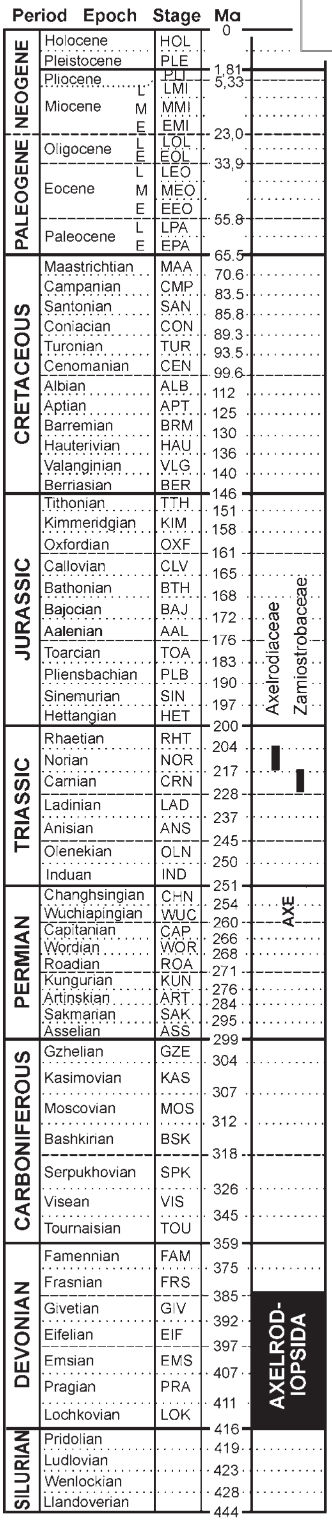


Welwitschia mirabilis

1,4,5,7,8,12 from Verdoorn 1966
3,6,9,11 from Kubitzki 1990
9, J.M. Anderson sketch
all extant

CLASS ORDER Family	Tab. 33. AXELRODIOPSIDA	generic diversity			affiliation grade			morphology grade			anatomy preserved		
		♀	♂	⬯	♀	♂	⬯	♀	♂	⬯	♀	♂	⬯
AXELRODIOPSIDA And. & And. class nov.													
AXELRODIALES And. & And. order nov.													
Axelrodiaceae And. & And. fam. nov.		1	1	1	5	5	5	3	3	4	-	-	-
Zamiostrobaceae And. & And. fam. nov.		2	-	-	5	-	-	3	-	-	-	-	-

Fig. 35. AXELRODIOPSIDA: FAMILY RANGE CHART



Class **AXELRODIOPSIDA** And. & And. nov.

Diagnosis: Putative gymnospermous plants with unisexual, radially symmetrical ‘flowers’ comprising an aggregate of several to many carpel-like megasporophyll units with stigma-like apices.

Remarks
Classification: Cleal (1993) made no attempt to classify the group of taxa included here, nor are we aware of any other attempt to do so formally. The class Axelrodiopsida is introduced here to house this enigmatic complex of material from the Late Triassic of the eastern USA. The axelrodiopsids may point to an early radiation of stem-angiosperms in the Late Triassic or may be further evidence of the rich diversity of gymnosperms at this interval (see further discussion below). We include the enigmatic group here, not because we strongly favour the gymnosperm option, or accept without reservation the reconstructions refigured here adjacent and overpage, but to give it further exposure in the hope of a resolution to the problem.

Order: Includes the single order Axelrodiales.

Order **AXELRODIALES** And. & And. nov.

Diagnosis: As for the class Axelrodiopsida.

Families: Includes the two families Axelrodiaceae and Zamiostrobaceae.

Family **AXELRODIACEAE** And. & And. nov.

Diagnosis: Axelrodialean plants with ‘flowers’ comprising relatively few megasporophyll units individually surrounded by a perianth-like structure of 8 or 9 bracts.

Range: Euramerica, Tr(NOR)
First & Last: *Axelrodia burgeri* Cornet 1986 (ovulate organ), *Nemececkigone fabaforma* Cornet 1986 (dispersed seeds), *Synangispadixis tidwellii* Cornet 1986 (pollen organ) and *Sanmiguelia lewisii* Brown 1956 (foliage), Upper Trujillo Fm., Dockum Gp., NW Texas, USA; and *S. lewisii*, Dolores Fm., SW Colorado. Zone of *Sanmiguelia*, Late Triassic, Upper Norian (Ash 1976, 1987; Cornet 1986).

Reference whole-plant genus & stratum—Trujillo Fm. (& equivs.)
Female: *Axelrodia* Cornet 1986; 1 TC, 1 sp., common.
Seeds: *Nemececkigone* Cornet 1986; 1 TC, 1 sp., 10 indivs.
Male: *Synangispadixis* Cornet 1986; 1 TC, 1 sp., 7 indivs.
Foliage: *Sanmiguelia* Brown 1956; several TCs, 1 sp., common.

Stratum: As for ‘Range’ above.
Affiliation: *Axelrodia*(5)*Sanmiguelia*(5)*Synangispadixis*, Grade 5 (Org.att., Mut.occ.).

Prominence (colonisation success)—W. Euramerica, Late Triassic
Frequency/ubiquity: The foliage *Sanmiguelia* is known from several localities of approximately equivalent age from SW Colorado to NW Texas.
Diversity: 1 species.
Abundance: *Sanmiguelia* appears to have been a not uncommon plant of the Upper Norian of the USA.
Longevity: *ca* 5–10 my.

Ecology
Habit: Herbaceous plants (up to *ca* 600 mm) with underground rhizomes.
Habitat: Lake margin. Based on ‘an *in-situ* vegetative colony of S. *lewisii* ... with organic remains preserved’, Cornet (1986) felt that the *Axelrodia/Sanmiguelia* plant ‘may have been a common waterside element in the tropical floodplain flora of the Late Triassic Dockum Group.’

Other genera—nil.

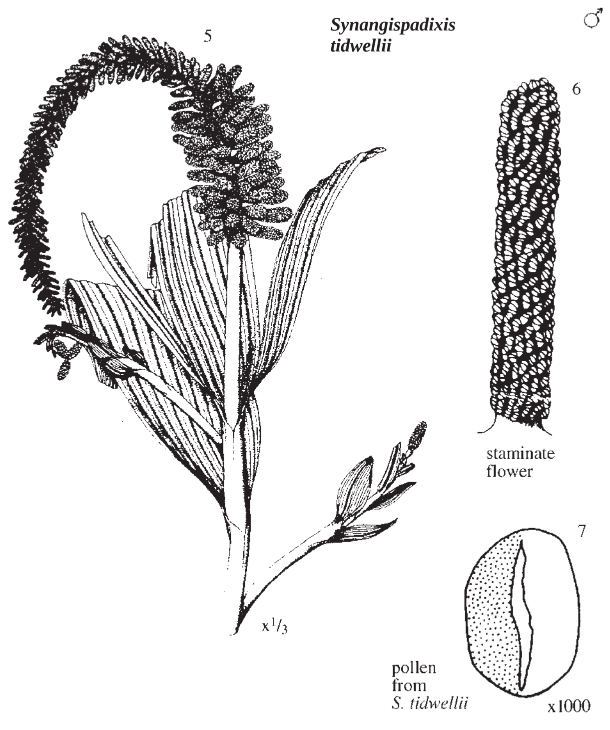
Remarks

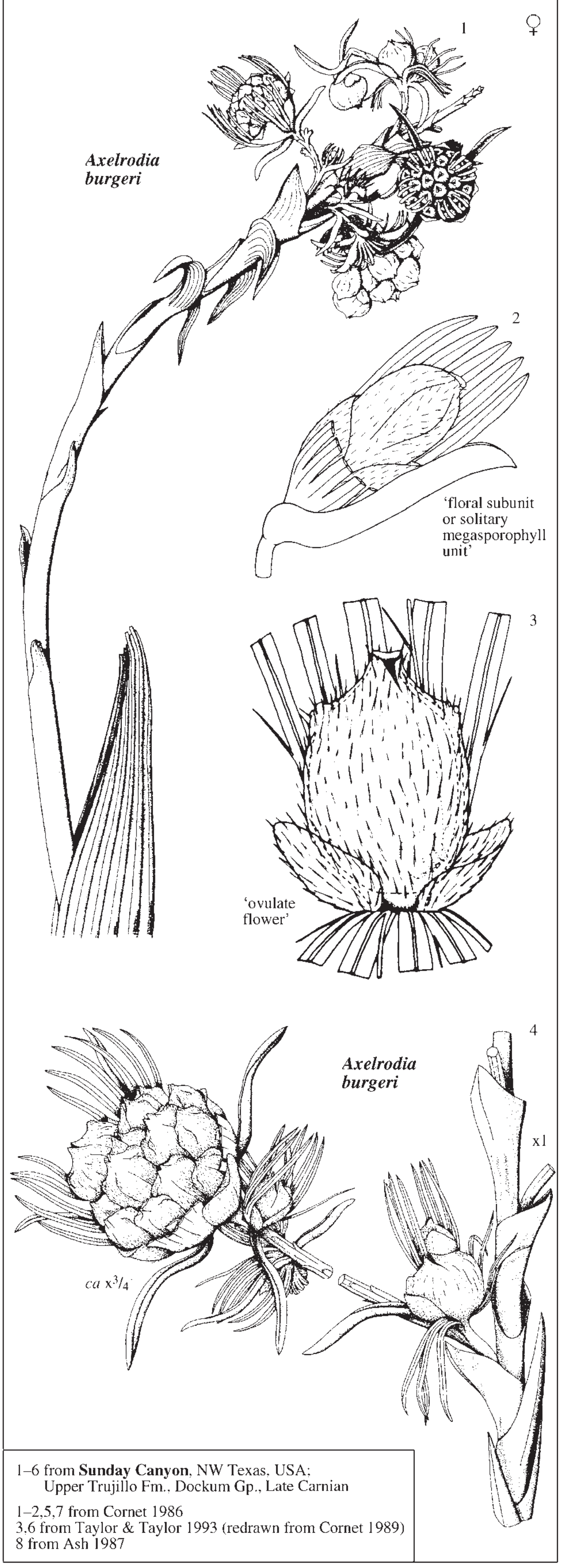
Classification: When Brown (1956) initially described *Sanmiguelia lewisii* from the Late Triassic Dolores Fm. of Colorado, he suggested a possible relationship with the Palmae. The phylogenetic position of *Sanmiguelia* has since raised much controversy—being compared to monocotyledons, cycads and even arthrophytes—and continues to do so. After detailed attempts at reconstruction of the reproductive structures, Cornet (1986) concluded that his material could best be interpreted as representing a line of primitive angiosperms near the evolutionary branch between monocotyledons and dicotyledons. Others who have seen the material cast some doubt on Cornet's reconstructions and interpretations (e.g. Dilcher, Doyle, pers. comm.). Taylor & Taylor (1993), while not dismissing the evidence, advised caution in regarding this suite of fossils as early angiosperms until further data are at hand. Stewart & Rothwell (1993) also let the case rest on whether the *Axelrodia/Sanmiguelia* plant is a primitive angiosperm or a complex gymnosperm.

Affiliation: From a single locality in Sunday Canyon (Upper Trujillo Fm.) representing the margin of an interdistributary lake deposit, Cornet (1986) discovered 'an entire vegetative colony of *Sanmiguelia* ... in growth position that yielded unusually well-preserved leaves, stems, roots, wood, reproductive axes, seeds, and pollen'. Both male and female reproductive axes included specimens suggesting organic connection with *Sanmiguelia* foliage.

References

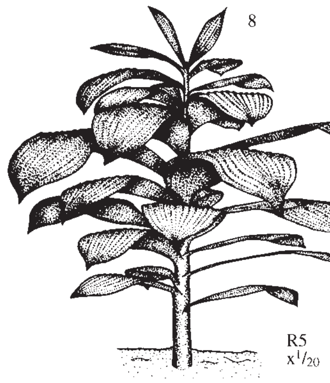
Ash (1976, 1987), Cornet (1986, 1989): General.
Stewart & Rothwell (1993), Taylor & Taylor (1993): Classification.





1–6 from **Sunday Canyon**, NW Texas, USA;
Upper Trujillo Fm., Dockum Gp., Late Carnian

1–2,5,7 from Cornet 1986
3,6 from Taylor & Taylor 1993 (redrawn from Cornet 1989)
8 from Ash 1987



Sanmiguelia lewisii

based largely on material from near **Placerville**,
Colorado Plateau (locality 5), USA;
upper Chinle Fm. and equivalents, Norian, Triassic

Family **ZAMIOSTROBACEAE** And. & And. nov.

Diagnosis: Axelrodialean plants with ‘flowers’ comprising many megasporophyll units individually surrounded by a simplified perianth-like structure of bracts or without such a structure.

Range: Euramerica; Tr(CRN)
First & Last: *Zamiostrobus virginiensis* Fontaine 1883 (or *Primaraucaria wielandii* Bock 1954), Winterpock coal measures, L–M Carnian, Richmond Basin, Virginia, USA (Cornet 1986).

Reference whole-plant genus & stratum—Winterpock coal measures
Female: *Zamiostrobus* Endlicher 1836; ?TCs, ?3 spp, 200 indivs.
Male: Unknown.
Foliage: Unknown.

Stratum: As for ‘Range’ above.
Affiliations: nil.

Prominence (colonisation success)—W. Euramerica, Late Triassic
Frequency/ubiquity: Ovulate organs known from only the single area in the USA.
Diversity: ? 3 spp, (see tfs 1–3 adjacent).
Abundance: According to Cornet (1986), Bock (1969) ‘reported finding about 200 specimens’ of these reproductive structures ‘and indicated that they were a common element in the Winterpock coal flora, where they were associated with *Podozamites tenuistriatus*, large *Macrotaeniopteris*, *Eoginkgoites* leaves, large fern fronds and giant *Equisetites* stems’.
Longevity: <1 my.

Ecology
Habit: Unspecified.
Habitat: Lowland coal-swamp (Cornet 1986).

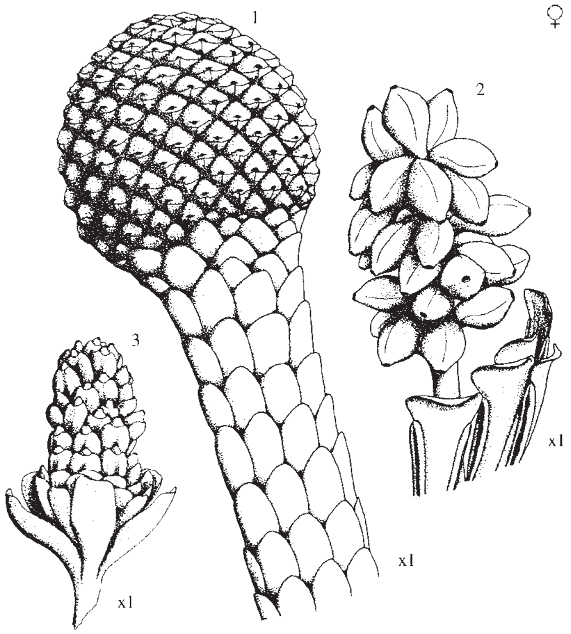
Other genera
Ovulate organ: *Primaraucaria* Bock 1954.

Remarks
Classification: Cornet (1986) felt that amongst the many Bock specimens, which he variously describes as ‘Magnolia-like reproductive axes’ or resembling ‘giant magnolian fruit’, were at least three different types of reproductive structures. In Cornet’s view, both generic names *Zamiostrobus* and *Primaraucaria* would probably hold after revision of the material. He felt, further, that there was a ‘fundamental relationship’ underlying the ‘superficial differences’ between these Virginia cones and his *Axelrodia* material from Texas. In the absence of further study, we take the Bock specimens to represent a separate family.

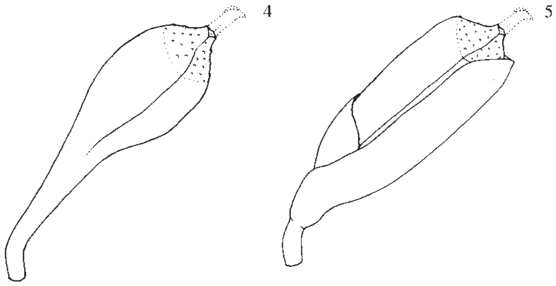
Nomenclature: There is clearly a nomenclatural problem that arises in using the generic name *Zamiostrobus* Endlicher 1836 as the basis for the new family *Zamiostrobaceae*. The generic name was originally introduced in the combination *Zamiostrobus macrocephala* (Lindley & Hutton 1834) Endlicher 1836 for *Zamia macrophylla* Lindley & Hutton 1834, a ?coniferalean cone from the Cretaceous of England (Andrews 1970). *Primaraucaria* Bock 1954 is hardly better as the nomenclatural basis for this new family. It was introduced for the species *P. wielandii* Bock 1954 to include leafy shoots and seed cones thought to represent the conifer family Araucariaceae.

We apply the name Zamiostrobaceae here to include the Cornet (1986) material illustrated adjacent, but recognise that a new name will be appropriate when this seemingly significant material is revised and fully described.

References
Cornet (1986): General.



1–3 ‘***Zamiostrobus virginiensis*** Fontaine 1883
(or ***Primaraucaria wielandii*** Bock 1954 sensu lato)’
‘three different types of fruiting heads and
reproductive structures illustrated by Bock (1969)
under *P. wielandii*’ (Cornet 1986)



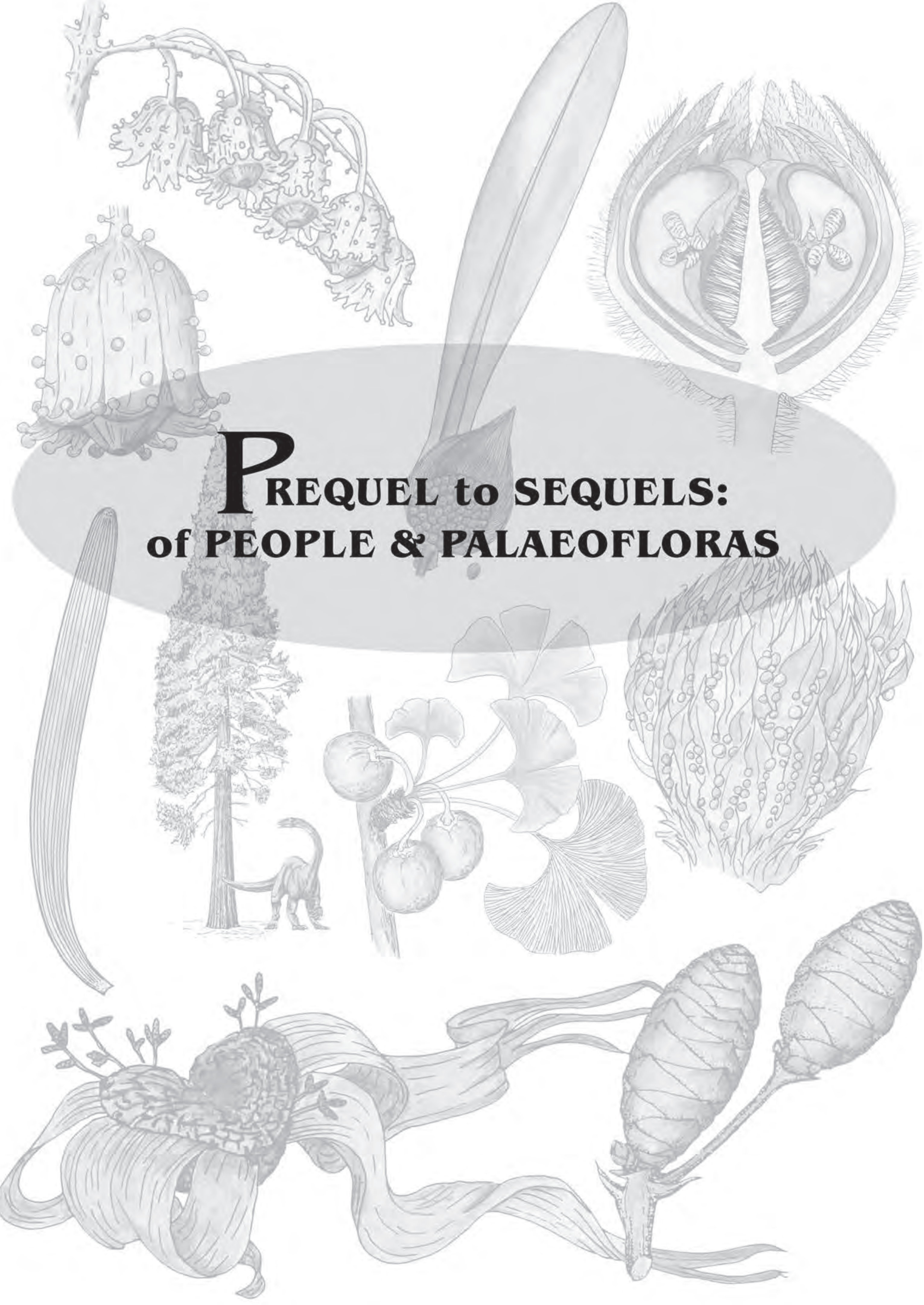
‘***Primaraucaria***’ Type B
‘one of many aggregate
megasporophylls’

‘***Primaraucaria***’ Type A
‘one of many aggregate
megasporophyll subunits’

1–5 **Winterpock** coal measures, Richmond Basin, Virginia, USA;
L–M Carnian, Triassic

all from Cornet 1986

PREQUEL to SEQUELS: of PEOPLE & PALAEOFLORAS



PREQUEL to SEQUELS: OF PEOPLE & PALAEOFLORAS

> '*I heartily beg that what I have here done may be read with candour; and that the defects I have been guilty of upon this difficult subject may be not so much reprehended as kindly supplied and investigated by new endeavours of my readers.*'—**Sir Isaac Newton** (1642–1727), Trinity College, Cambridge, 8 May 1686; from the preface to his *Philosophiae naturalis principia mathematica*.

Prequel

Like the gymnosperms themselves, this volume has evolved. It began as a chapter intended for inclusion in our volume on the gymnospermous fruit of the Molteno—*Heyday of the gymnosperms*: *classification and biodiversity of the Molteno fructifications* (And. & And. 2003). The *Heyday*, in its first bound draft of mid-1998 (then just half the thickness of its final published form) for display at the *10th International Gondwana Symposium* in Cape Town, included a 50-page chapter on the global classification and diversity of the gymnosperms. Sometime in 2002, to hasten completion of the *Heyday* for publication, we elected to detach the global chapter. It has since, incrementally, been expanded into this 280-page volume and prepared for publication as an independent work. The title, *A brief history of the gymnosperms*, we feel pairs well with its sister work, its prequel.

People, places, plants and palaeofloras

This concluding chapter is intended as a form of addendum to our prefaces, in essence it is an expanded preface. As such, it frees us from the rigours and constraints of pure science standing alone; it gives us the freedom to explore at the interface between our humanity and our profession. Through it we weave four main themes: people, places, plants and palaeofloras; and through each in turn may be woven further strands. Formations and localities are the chapters and the pages of our palaeobotanical story; the various ranks of taxa are our sentences, phrases and words; the specimens are our alphabet. We are the historians unscrambling the codes and clues.

People: Co-authors, contributors, select biologist forebears and a further handful of towering characters in the arts and sciences of the past half-millennium who helped craft our civilisation, are the human strands woven through our tapestry. As a species we are as rich and as diverse as any palaeoflora. It is for us, infinitely complex, born of those early mammals that evolved in the womb of the gymnospermous forests and woodlands of geological time, to read and interpret our own deep history.

Places: Sketches of 22 localities, representing significant moments in our gymnosperm story from the earliest Carboniferous to the earliest Tertiary, are spread chronologically through the chapter. As a selection of sites, from mountainside to riverside and roadside, from quarry to coalmine, ranging across all the continents, they lend authenticity to our story. These sites—and thousands more—are our clay tablets, our Rosetta Stones (p. 223). They are the true pages of this *Brief history*.

Plants: Species and genera, and their diversity at our fossil sites, are the core focus in this chapter—whereas in the body of the work it is their grouping into families, orders and classes, and biodiversity at those levels, that concern us. Here we touch on microdiversity; through the previous chapters we focused on macrodiversity.

Palaeofloras: The assemblages of plants from particular places (taphocoenoses) and from particular formations (palaeofloras) are the final theme uniting the whole. How close to an accurate reflection of the preserved biodiversity shifts have we as a fraternity of palaeobotanists come so far? We suspect, as for any centuries-old Renaissance fresco awaiting renovation, that there are many layers obscuring our view that still have to be peeled back.

'On the shoulders of giants'

(Newton, 1676, in a letter to Hooke)

Science, no less than art or business or politics, is a deeply personal pursuit. It is absorbing to peruse the confessions of three of our greatest biological predecessors who graced successive centuries with their fundamental insights. Extreme science with extreme stakes evokes extreme emotions. Consider the following fragments in which aspects of our fragile humanity are laid bare.

Carolus Linnaeus (1707–1778), who gave us the binomial system and the classification of living things.

'*The King of England* [George III] *has established a very large garden* [Kew] *containing every obtainable plant, and beside each plant is a wooden label bearing its generic and specific name according to my system. The King of France did the same, more than two years ago, at the Trianon near Versailles*.' (29 Oct. 1774, letter to his pupil Thunberg).

Linnaeus, beloved by his pupils, recorded alarming flights of self-congratulation: of his *Species plantarum* (1753) he writes: '*The greatest achievement in the realm of science*'; of his *Systema naturae* (1735): '*A masterpiece that no one can read too often or admire too much*'; and of his *Clavis medicinae duplex:* '*The fairest jewel in medicine*'. He summarised his total achievement in no less sure terms: '*I have fundamentally reorganised the whole field of natural history, raising it to the height it has now attained.*'

Rigidly orthodox, Linnaeus held insistently that all species were created separately at the beginning and that none had gone extinct since Creation.

Charles Darwin (1809–1882), who published *The origin of species* (1859) and *The descent of man* (1871), establishing the theory of evolution through natural selection. He first aimed at the church (studying in Edinburgh), then medicine (studying in Cambridge), but settled as a gentleman scientist at Down House outside London.

In his later life, Darwin lamented (see his autobiography, edited by his granddaughter, 1958) the extent to which that part of his brain concerned with the '*higher tastes*' appeared to have atrophied: '….*my mind has changed during the last twenty or thirty years. Up to the age of thirty, or beyond it, poetry of many kinds ... gave me great pleasure, and even as a schoolboy I took intense delight in Shakespeare, especially his historical plays ... But now for many years I cannot endure to read a line of poetry: I have tried lately to read Shakespeare, and found it so intolerably dull that it nauseated me.*'

He had also lost any taste for pictures or music—he had in earlier days spent much time admiring the paintings in the National Gallery in London, and listening to the choristers in King's College Chapel, Cambridge—and felt that his mind had '… *become a kind of machine for grinding general laws out of large collections of facts*'.

Edward O. Wilson (b. 1929), who breathed vibrant life into the concept of biodiversity—popularised in *The diversity of life* (1992)—at present gaining prime currency around our vulnerable world. An artist with words, Wilson writes in his autobiography (*Naturalist*, 1994): '*I have been … a happy man in a terrible century*.'

Elsewhere in the latter volume, Wilson makes this singular admission: '*Without a trace of irony I can say that I have been blessed with brilliant enemies. They made me suffer … but I owe them a great debt, because they redoubled my energies and drove me in new directions. We need such people in our creative lives. … James Dewey Watson, the codiscoverer of the structure of DNA, served as one such adverse hero for me. When he was a young man, in the 1950s and 1960s, I found him the most unpleasant human being I had ever met*.'

Wilson and Watson, just one year apart in age, both gained positions at Harvard in the Department of Biology in the mid-1950s. They apparently had their offices on the same corridor, and spoke to one another directly no more than half a dozen times in 12 years. There was a hint of ethnic cleansing in these 'molecular wars': with Watson brutally pushing his molecular biology to the desired exclusion of traditional biology, Wilson's biology.

MICRODIVERSITY: SPECIES & GENERA
Diversity at the microevolutionary level

Here are included the available **microevolutionary** (genera and below) biodiversity data for the 13 formations covered in this preliminary chapter. The figures are not truly comparative in view of a range of inconsistencies persisting in the derivation of the data: extensiveness (localities) and intensiveness (specimens) of sampling, levels of study, taxonomic approach, focus on affiliation of organs. Even so, the pattern of changing biodiversity that emerges up through the column reflects remarkably closely that of the **macroevolutionary** (families and above) biodiversity pattern (see Chart 1, p. 36).

Considerable further work is needed here and a ten-fold increase in the number of formations covered would no doubt prove very revealing.

							Biodiversity							
							Formation				**Locality (TC)**			
Period	**Epoch**	**Fm.**	**Locality**	**Country**	**Stage**	**Ma**	**Total flora**		**Gymnos**		**Total flora**		**Gymnos**	
							spp	**gen.**	**spp**	**gen.**	**spp**	**gen.**	**spp**	**gen.**
Into the Tert.		K/T	Bug Creek	USA		**65,5**	/	/	/	/	/	/	/	/
Cret.	Early	Jianshangou	Huangbanjigou	China	BRM	128	88	56	65	41	.	.	.	.
Cret.	Early	Zazinskaya	Baisa	Russia	APT	125	-	-	-	-	40	30	37	27
Juras.	Middle	Claughton	Cayton Bay	Yorkshire	CLV	164	169	59	117	35	81	38	54	21
Juras.	Middle	Yima	N. Opencast	China	AAL	174	70	>34	39	>23	.	.	.	.
Juras.	Early	Lias a	Pechgraben	Germany	HET	199	55	40	30	25	45	35	25	20
Trias.	Late	/	Potrerrilos	Argentina	/	/	/	/	/	/	/	/	/	/
Trias.	Late	Chinle Fm.	Petrified Forest	W. USA	CRN	216	72	49	54	33	.	.	.	.
Trias.	Late	Molteno Fm.	Umkomaas	S. Africa	CRN	223	205	57	143	38	75	37	29	18
Trias.	Middle	Nymboida	Nymboida Q	NSW	LAD	237	103	46	48	15	-	-	-	-
Trias.	early Mid.	Grès à Voltzia	Adamswiller	France	ANS	244	28	20	17	11	.	.	.	.
Into the Trias.	/	P/Tr	Graphite Peak	Antarct.	/	**251**	/	/	/	/	/	/	/	/
Perm.	Late	Estcourt	Lidgetton	S. Africa	WUC	257	24	14	16	9	5	5	2	2
Perm.	Early	M. Ecca	Vereeniging	S. Africa	ART	280	45	26	34	17	32	27	26	21
Carb.	Late	L. Productive	Shore	England	MOS	310	39	26	10	5	-	-	-	-
Carb.	Early	Inverclyde	Whiteadder	Scotland	TOU	350	24	18	16	11	-	-	-	-

Explanatory notes

Formations: The selection of formations aims at a reasonably even spread across geological time through well-studied megafloras worked on in some measure by the contributors to this book.

Localities: These are the localities illustrated through this chapter; in most cases they are the richest in the formation they represent; ideally the biodiversity should exclusively reflect a single taphocoenosis (TC), but is mostly a composite of two of more TCs.

Age (Ma): The age given is generally an estimate for midway through the formation.

Biodiversity: Four columns are given, two (‘total flora’ and ‘gymnosperms’) for the formations and two for the listed localities. Blanks remain where the biodiversity is either unavailable (-) or we have not attempted to source it (.), or it is not relevant (/).

CO-AUTHORS
Further to our prefaces

John M. Anderson (SANBI, Pretoria, South Africa)

Steps along the trail of human history

On my 60th birthday (28 June 2003) at Chateau Beduer overlooking the Lot Valley cutting into the Central Massif in France, I first saw a copy of Heidi's and my *Heyday of the gymnosperms*. It had come off the press a week or two earlier in Pretoria.

I rather enjoyed the symbolism not just of timing but also of place. Less than a half-hour drive upstream of our Renaissance chateau, lies the town of Figeac. It was here that Jean-Francois Champollion (1790–1832), Egyptologist and decipherer of hieroglyphics (1822), lived. The Rosetta Stone, discovered in 1799 by members of Napoleon's expedition to Egypt in the NW Nile Delta, is a polished basalt slab with chiselled inscriptions in three different texts: Egyptian hieroglyphics, demonic (a simplified Egyptian script appearing *ca* 650 BC), and Greek. Champollion acquired a copy of the slab and succeeded in unravelling the hieroglyphics. With this breakthrough he revealed in greatly enhanced relief the world of one of the earliest of human civilisations.

And a half-hour drive downstream of Beduer lies the remarkable Peche-Merle Cave (interconnected series of chambers). In this and many other caverns and shelters in adjacent limestone valleys—most notably that of the Dordogne—occur some of the best galleries opening a window onto the lives of our prehistoric, Upper-Palaeolithic (*ca* 40 000–10 000 BP), *Homo sapiens* ancestors. On the walls of these grottoes, Cro-Magnon left his paintings and engravings, in effect their 'hieroglyphics'.

Back through time from our earliest civilisations, to our Paleolithic forebears, to the Late Triassic forests and woodlands in which the earliest mammals emerged. These are all decisive steps in our story and it is to different parts of the world that we go to bring to life that story. Yes, I enjoyed toying with the symbolism there in the dissected midlands of France.

And along our individual human history

Evolution has played an unkind trick on us bemused humans, giving us an outsized brain and the capacity for boundless imaginative thought, yet a paltry lifespan that barely enables us to get started in some chosen field. This affects us quite differently across the professional spectrum: from mathematicians who tease out their grand new formulae in their twenties and can enjoy their fruits for the next few decades, to us biologists and palaeontologists who more often proceed in reverse. It takes us a few decades to gather our data and then we race against life's clock to describe it all, synthesise it and extract some meaning from it.

This reverse pattern has certainly held generally true, in variations, in the study of Triassic floras in our generation. It has been Heidi's and my experience in our work on the Molteno Fm. (pp 234, 235). It has been much the same for Sid Ash working on the Late Triassic Chinle floras of the U.S.A. (pp 236, 237), for Inna Dobruskina on the Russian floras, for Lea Grauvogel-Stamm on her Buntsandstein floras of France (p. 232), for Keith Holmes on his Nymboida flora of New South Wales (p. 233), and perhaps also for Tom and Edith Taylor and colleagues on their Fremouw floras of the Antarctic Middle Triassic.

Of course, most of us do not chart a simple track through our professional life, we usually start with some suspect early programming and influences, we head off on all manner of tangents, we become overloaded with other tasks, and we play out our often tumultuous personal lives concurrently.

On prefaces

The five extracts from prefaces—from the pens of **Sir Isaac Newton** (1686), **Sir Francis Bacon** (1620), **Samuel Johnson** (1755), **Nicolaus Copernicus** (1543) and **Sir Walter Raleigh** (1614)—have been selected to add a further thread to this chapter. They are all derived from the *Harvard Classics* volume of *Famous Prefaces* (Elliot 1969, first published 1909 and having reached its 62nd printing by 1969).

In the 'Introductory note', the editor writes: '*No part of a book is so intimate as the Preface. Here, after the long labor of the work is over, the author descends from his platform, and speaks with his reader as man to man, disclosing his hopes and fears, seeking sympathy for his difficulties, offering defence or defiance, according to his temper, against the criticisms which he anticipates.*'

Heidi M. Anderson (Dorrigo, New South Wales)

Heidi retired in April 2002 from the National Botanical Institute, Pretoria, shortly before the completion of the Molteno *Heyday* manuscript and its publication in June 2003. She now lives in Dorrigo, New South Wales (married to Keith Holmes, see p. 233), just a short walk from a fine expanse of UNESCO World Heritage rain forest on the Great Dividing Range. And she commutes to South Africa once or twice a year to put in time towards rounding off our Molteno Palaeoflora monograph series. With the gymnosperms done (essentially), it is now the turn of the pteridophytes. During these African sojourns, Heidi has continued with her input into the *Brief history*.

Heidi honed her skill at rapid impressionistic pen sketches of landscapes while driving to and through the Molteno: with the road winding into the distance between the flat-topped sandstone koppies (hills) of the Karoo. Speed was clearly a prerequisite, forging the distinctive style that enlivens these pages.

Like a painting or a gallery of paintings, like the *Brief history* itself, this chapter has evolved and grown. A core stimulus has been Heidi's locality sketches. Originally these included just a couple of Molteno Fm. localities; then the Nymboida (Middle Triassic) site was added; followed by the three early-angiosperm Chinese sites and the Triassic, Tr/J boundary and K/T boundary sections in Argentina, the USA and Antarctica respectively; then the Jurassic sites in Germany (Pechgraben) and China (Yima Mine) were added; and then the three British sites (Whiteadder, Shore Mine and Cayton Bay), along with the Russian site at Baisa; and then it was imperative to add two Permian sites (Vereeniging and Lidgetton, South Africa) and an Early Triassic site (Adamswiller, France), followed lastly by the Late Triassic Petrified Forest in the western USA.

No less than these pen sketches being key thumbprints of Heidi's, so too is compulsively adding and evolving a signature of my own. Each addition required twisting Heidi's arm further (mostly from halfway around the world). Each time she tried resisting, then consented. It has taken some persuasion to get Heidi to acknowledge the appeal of a whole assembly of her own sketches.

And as the number of localities grew, so the number of captions had to grow with them and they needed to be filled out to offer a hint of the story of gymnosperm biodiversity at the lesser ranks of genus and species (the microevolutionary level). So the Roman-numeral pages (as they originally were) proliferated and so this chapter has expanded, become independent, and been shifted from the start of the book to the end of the book.

We could go on indefinitely to provide a fully representative trail through gymnosperm time, but sadly we must put a stop to this. There lies another sequel.

Kannaskoppia And. & And. 2003
A diverse and relatively common genus through the Gondwana Triassic. It may well prove of significance in the search for angiosperm origins (p. 80) and in developing a sound approach to species-level taxonomy in palaeobotany (p. 23).

Chris J. Cleal (Natural History Museum, Cardiff)

Back in early 1998 Chris Cleal prepared a review of our original chapter on gymnosperm classification; and has subsequently joined us as a full co-author on the current volume. Considering that he had contributed the chapter on the gymnosperms in *The Fossil Record* 2 (Benton 1993), and with his research focus on Laurasian Palaeozoic floras, Chris was ideally placed to complement our focus on Gondwana floras.

During a week together at the Natural History Museum in Cardiff, Wales in July 2003, Chris and I plotted the scope of our expanded volume. What was more or less feasible, who would do what, whom else among our colleagues should we aim at enlisting? At the very English pub across the road we conjured up the *Brief history* title—obviously borrowing from Stephen Hawking's *A brief history of time* (1988) and perhaps less obviously from Bill Bryson's *A short history of nearly everything* (2003) which was piled high in all the English bookshops at the time. It was Chris's idea and it did not take long to grow on me. If 'time' and if 'nearly everything' can have a brief or short history, then why not the gymnosperms?

> '*Those who have taken upon them to lay down the law as a thing already searched out and understood, whether they have spoken in simple assurance or professional affectation, have therein done philosophy and the sciences great injury. For as they have been successful in inducing belief, so they have been effective in quenching and stopping inquiry; and have done more harm by spoiling and putting an end to other men's efforts than good by their own.*'—**Sir Francis Bacon**, London, 1620; from the preface to *Novum organum*, the work in which he first significantly formulated the inductive method in science.

Wales to Waterberg

The growth of our *Brief history* from a 50-page chapter to a 300-page book began (largely) with a week in Cardiff, Wales and ended (largely) with a week in the Waterberg, to the north of Gauteng, South Africa—a two-year spell from July 2003 to June 2005. There is, again, obvious symbolism in this: Wales and the Waterberg represent two peak moments in biological history.

Wales: Southern Wales, Cardiff in particular, owes much to its coal-mining history. The coal forests of Euramerica peaked in the Late Carboniferous (Moscovian) around 310 Ma at virtually the moment of crossover from pteridophyte to gymnosperm dominance (Chart 1, p. 36; pp 73–75).

The South Wales Coalfield lay very close to the then equator and a third of the way along the dense tropical rainforest belt running west to east across Pangaea. This was the first tropical rainforest ecosystem in Earth history (Thomas & Cleal 1993; Cleal & Thomas 1994). It was a prime moment in the history of gymnosperms, which were destined to dominate the plant world until the rise to dominance of the angiosperms some 200 my later.

Waterberg: This 'Prequel to sequel' chapter was inflated by a further 12 pages in a time-share chalet in the Waterberg Game Park. If Wales represents gymnosperm abundance and diversity in the earliest rainforests, then the Waterberg represents the origin of higher organisms and extant diversity.

The Waterberg Supergroup dates from 1-900 to 1-700 Ma. It was deposited in a series of terrestrial basins in the Kaapvaal Craton, with up to 5-000 m of 'rust'-pigmented sediments, largely red sandstones and conglomerates. Two profoundly significant (and surely related) events occurred globally at around 1.8 billion years ago, midway through the accumulation of the beds: the first major boost to substantial oxygen levels in the atmosphere occurred, and the first eukaryotes (higher organisms with membranes enclosing their cellular nuclei and DNA) appeared. The red-rusted sandstones are witness to these events (De Wit & Anderson 2003).

Sitting on the veranda of the chalet writing of past biodiversity seems appropriate when looking out at the richness of the unsullied landscape before one. The stretch of Waterberg scarp and plateau just 200 m distant are clad in a wilderness of closed woodland that will include within a square km some 64 species of indigenous trees, 180 species of birds, 45 of butterflies and over 33 of medium to large mammals.

The epitomal co-author

In the creation of this volume over the past two years, Chris and I have exchanged 555 e-mails (38 in 2003, 355 in 2004, 162 in 2005) between Cardiff and Pretoria. They have been of a rather distinctive genre: mostly my queries and Chris's answers to those queries. The replies have been invariably fast, often seemingly impossibly so (in view of the considerable assembly of factual data included), always concise and to the point. And an inseparable characteristic of the genre (from the Chris angle) has been the thin scatter of crisp English humour filtering through (selection below). Chris has indeed been the epitomal co-author!

2 Oct 2003: 'With luck and a following wind, I should get the Lagenostomopsida and Cycadopsida sections to you today or tomorrow.'

25 Nov 2003: 'I am still digging myself out from under a pile of papers and e-mails after my visit to Sofia. It was nice to be away from things for a couple of weeks, but you don't half cop it when you return.'

17 Feb 2004: 'Back to Siberia.' [literally and figuratively]

1 April 2004: 'Spring lasted a day! It is raining today. But it was nice whilst it lasted.'

8 June 2004: 'As I think that I said before, he who nags first tends to get the results.'

11 June 2004: 'I am now going to get a quick cup of tea, and then will proceed to answer your questions.'

5 July 2004: 'A minor delay this morning (a meeting of the Museum's Intellectual Development Group—normally a wonderful way to gradually wake up on a Monday morning, but not when you have things to do!).'

13 July 2004: 'OK, the Lagenostomopsida sheets have just arrived by fax. As have 90 pages of page-proofs for another paper, plus a grant application to review from Prague. So, please excuse me momentarily whilst I scream. Aaaaagh!'

14 July 2004: 'I think that everything is under control here—but only just!'

5 Aug 2004: 'I had to go to hospital about a damaged finger. Nothing serious—just a snapped ligament in my left middle finger, which I did on holiday. Luckily, I am a two-finger typist, so it doesn't affect work!'

23 Sept 2004: 'Sorry, no reply yesterday. Had a hospital appointment about a damaged finger (snapped ligament—an inconvenient but totally painless injury that gets lots of lovely sympathy from the ladies!).'

2 Dec 2004: 'I don't know about laughing? I was fit to pull out the little hair that I have left after this morning's little session! But I think that this one is important though, if only because the Yanks could use it as a stick to beat us with.'

6 Jan 2005: 'I am not going anywhere exotic until June.'

18 Jan 2005: 'Now for the bad news. I am in London at meetings tomorrow and Thursday.'

21 Jan 2005: 'Just received the fax. Now there's a challenge!! [and after a considerable assembly of facts] That will have to be it. I leave in 15 minutes. A good day's work!'

18 March 2005: 'Spam has gone, so now for some science!!'

22 March 2005: 'Next week, being Easter week, will be a bit of a mess.'

11 April 2005: 'The meeting is Thursday–Saturday this week. So, don't expect too much from me this week. Panic is starting to set in!'

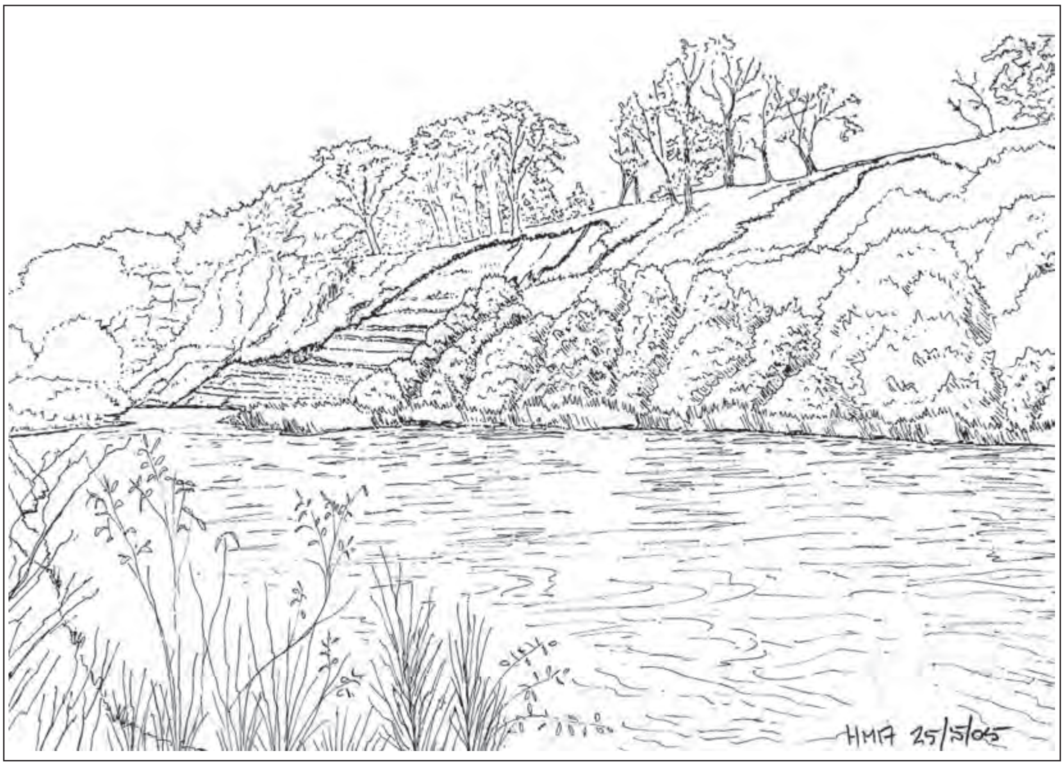
6 May 2005: 'Ah! That is me trying to be just too clever, and confusing myself! The Vakhrameev book I am really referring to is 1991.'

18 May 2005: 'This is a bit of a puzzler.'

26 May 2005: 'I am in the middle of moving our departmental library from its old "temporary" location (i.e. for the last 15 years!) to its new room in the basement.'

10 June 2005: 'Well, a weekend is due shortly, and a rest from shifting books! I am pretty well finished on that job anyway … I certainly feel fitter—the scales tell me I am nearly half a stone lighter since I started the move.'

CARBONIFEROUS (Early, *ca* 350 Ma)
Scotland, Berwickshire



Whiteadder River, Berwickshire, SE Scotland.
Inverclyde Gp., Tournasian, *ca* 350 Ma.
Gymnosperm history: Into the first pulse of their Primary Radiation.

Sketch by HMA (25 May 2005), after photo by Chris Cleal (1982).

Whiteadder River: The site consists of a *ca* 14-km length of the Whiteadder River, between Paxton and Preston, and lies 8–22 km east of Berwick-upon-Tweed, Berwickshire, SE Scotland.
Inverclyde Gp. (was Cementstone Gp.), C (TOU).

Historical: Early work on the site includes studies by H.T.M. Witham in the early 19th century and R. Kidston in the early 20th century; however, the most significant progress was made during the 1960s and 1970s by Albert Long.

Significance: Long showed that the site yielded a greater diversity of early gymnosperms than anywhere else in the world; Whiteadder is a Site of Special Scientific Interest, and part of a proposed World Geosite for these early gymnosperms.

Gymnosperms
Genomospermaceae (*Genomosperma*).
Eospermaceae (*Eosperma, Deltasperma, Eccroustosperma, Camptosperma*).
Moresnetiaceae (*Stamnostoma, Salpingostoma, Calathaspermum*).
Calamopityaceae (*Lyrasperma, Eurystoma, Dolichosperma*).
Nearly all the records are based on isolated ovules and ovulate organs.

References
Scott *et al.* (1984), Cleal & Thomas (1995).

Contributor: Chris Cleal.

Inverclyde Gp.

Localities: Seven reasonably well-documented TCs at similar but not necessarily identical stratigraphic levels; exposure other than along the rivers is poor and the exact stratigraphical relationship between the localities has not been worked out in detail; however, loose blocks of fossiliferous deposits can be found along many of the rivers and along the shoreline of the Borders Region of Scotland; total extent *ca* 250 sq km, though access to bedrock is limited over most of the area.

Edrom exposure (shown in sketch): The plant horizon in the river bed below the small cliff is, by far, the most diverse TC for the Inverclyde Gp. flora; the other TCs along the Whiteadder River have yielded only subsets of this Edrom flora.

Abundance
Genomosperma, Stamnostoma & *Lyrasperma*, abundant (>90 specimens);
Eurystoma, Deltasperma & *Camptosperma,* common (25–35 specimens);
Other genera: relatively uncommon (<20 specimens).

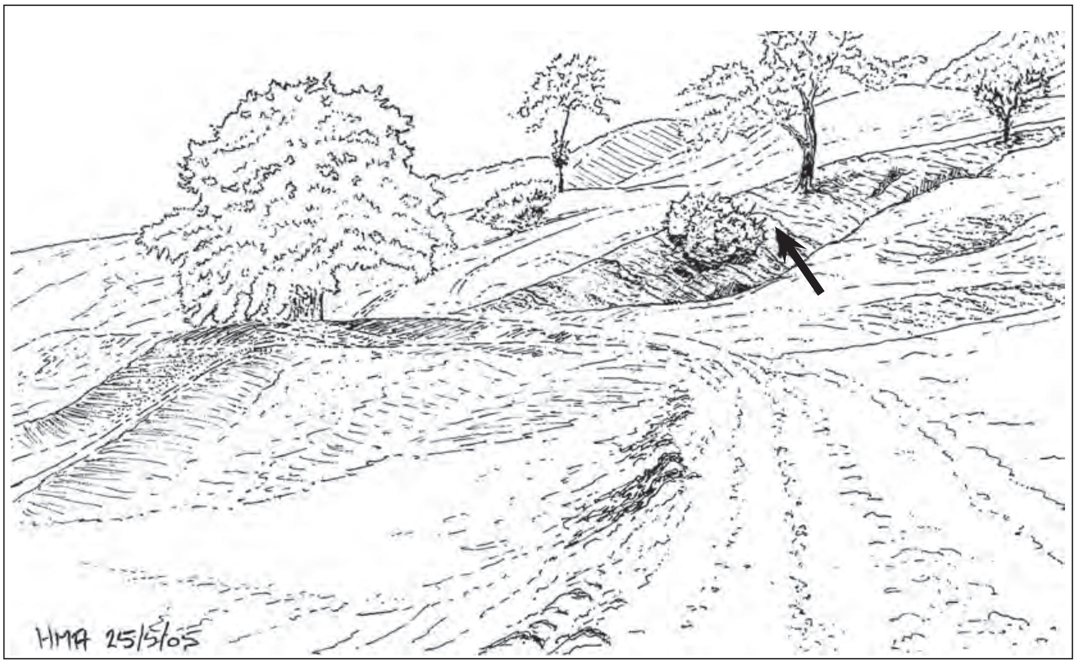
These abundance figures are derived from the number of specimens described in Long's various papers. The material was apparently all very fragmentary, with the individual ovules remaining most intact. There occur also abundant bits of stem and leaf, but these are so broken up (though still yielding anatomical detail) that they are difficult to identify.

Environment: Lagoonal deposits; tropical, very close to the equator.

Biodiversity ('natural' taxa): 24 spp (18 gen.)
Non-gymnosperms: 8 spp (7 gen.).
- Bryophyta (liverworts, mosses): Nil.
- Filicophyta (ferns): 5 spp (4 gen.).
- Lycophyta (lycopods): 3 spp (3 gen.).
- Sphenophytra (horsetails): Nil.

Gymnosperms: 16 spp (11 gen.).

CARBONIFEROUS (Late, *ca* 310 Ma)
England, Lancashire



Shore Mine, Lancashire, NW England.
Lower Productive Coal Fm., Moscovian, *ca* 310 Ma.
Gymnosperm history: Into the second pulse of their Primary Radiation.

Sketch by HMA (25 May 2005), after photo by Chris Cleal (1980).

Shore Mine:

A disused mine near Littleborough, 5 km NE of Rochdale, Lancashire, NW England.
Lower Productive Coal Fm., C(MOS).

Historical: Most of the early collecting was done by a commercial collector and dealer, James Lomax, who seems to have come to an arrangement with the mine owner. He sold prepared thin sections of the coal balls from here extensively to the academic community, including W.C. Williamson and D.H. Scott (Howell 2005). It was these 'gentlemen', who did none of their own collecting, who published most of the early papers on the material during the late 19th and early 20th centuries.

Significance: Regarded as the most diverse of the classic coal-ball localities; yielded most of the anatomically preserved gymnosperms.

Gymnosperms
Lyginopteridaceae *(Lagenostoma/Lyginopteris/Telangium, Conostoma*).
Physostomaceae (*Physostoma*).
Potonieaceae (*Hexapterospermum/Sutcliffia*).
Alethopteridaceae (*Pachytesta/Medullosa/Alethopteris*).
Cordaitanthaceae (*Cordaites/Gothania/Mesoxylon*).

Abundance
Lyginopteris (48% of flora), *Cordaites* (5–16%), *Medullosa* (2%).
Sutcliffia (rare): little other abundance data is available; all figures are estimates of plant biomass from thin sections. This is an essentially autochthonous deposit and inevitably roots comprise about a third of the debris, stems and foliage most of the remaining two-thirds; ovules and pollen grains are normally rare.

References
Phillips *et al.* (1985), Galtier (1997), Howell (2005).

Contributor: Chris Cleal.

Lower Productive Coal Fm.

Localities: Virtually all of the British coal balls come from the same coal, known variously as the Upper Foot, Union and Halifax Hard Seams, depending on where they occur. This coal occurs along a narrow strip 45 km long and *ca* 5 km wide in Lancashire (*ca* 225 sq km), and a small area near Halifax, Yorkshire (*ca* 25 sq km). The coal balls were all from underground pits, all now closed. Until about 15 years ago, there were opportunities to collect from old spoil tips, but these have all now been landscaped.

Environment: Peat-substrate wetlands; tropical, very close to the equator.

Biodiversity ('natural' taxa): 39 spp (26 gen.)
Non-gymnosperms: 29 spp (21 gen.).
  Bryophyta (liverworts, mosses): Nil.
  Filicophyta (ferns): 16 spp (12 gen.).
  Lycophyta (lycopods): 8 spp (6 gen.).
  Sphenophyta (horsetails): 5 spp (3 gen.).
Gymnosperms: 10 spp (5 gen.).

Source: These biodiversity data are not specifically for Shore, but for the Upper Foot Seam as given by Galtier (1997); they probably reflect Shore, generally regarded as the most diverse locality for this flora, reasonably well. There are evidently no gymnosperms known from elsewhere in the formation that are not at Shore.

PERMIAN (Early, *ca* 280 Ma)
South Africa, N. Karoo Basin

Leeukuil quarries, Vereeniging, South Africa.
Middle Ecca (Vryheid Fm.), Artinskian, *ca* 280 Ma.
Gymnosperm history: Into the 3rd pulse of their Primary Radiation.

Sketch by HMA (June 2005), after photo by S.F. le Roux (1948).

Vereeniging (Leeukuil quarries)

The Leeukuil quarries lie on the northern bank of the Vaal River, 10 km SW of the centre of the coal-mining town of Vereeniging, and *ca* 60 km S of Johannesburg, South Africa.
Middle Ecca (Vryheid Fm.), Ecca Gp., Karoo Supergroup.

Historical: George William Stow (1822–1882) discovered the coalfields in the northern Orange Free State and adjoining Transvaal in 1878, and is the first person on record to have collected fossil plants from the Ecca Gp. (at Vereeniging in 1878). Thomas Nicolas Leslie (1858–1942) followed, collecting from several Vereeniging sites from *ca* 1892–1904.

Significance: The great palaeobotanical importance of the Leeukuil quarries was revealed by Edna Plumstead in her series of five renowned papers (1952–1962) in which she described a diversity of glossopterid fruit, several taxa of which were found—for the first time—attached to *Glossopteris* leaves. The discoveries were those of Stephanus Francois le Roux, initially a local cabinetmaker and, after obtaining a university degree, a science teacher. He collected regularly from the area, primarily the Leeukuil quarries, from 1941–1974.

Gymnosperms: 26 spp (21 gen.)
Cordaitanthales: *Noeggerathiopsis* (2 spp).
Coniferales: *Walkomiella* (1 sp.), *Cyparissidium* (1 sp.).
Ottokariales: *Palaeovittaria* (1 sp.), *Ottokaria* (3 spp), *Scutum* (3 spp), *Hirsutum* (1 sp.), *Lanceolatus* (3 spp), *Arberia* (1 sp.).
Ginkgoales: *Sphenobaiera* (1 sp.), *Metreophyllum* (1 sp.), *Ginkgophyllum* (3 spp), *Flabellofolium* (2 spp).
Incertae: *Taeniopteris* (1 sp.), *Botrychiopsis* (1 sp.).

Abundance: Aside from the Lycophyta (*Cyclodendron* 25%), the glossopterids heavily dominate the flora in both abundance and diversity. The first five of the Ottokariales genera listed (all Ottokariaceae), and nearly all their species, are found attached to distinctive *Glossopteris* leaf species; whereas *Arberia* (Arberiaceae) is found in clear affiliation with another recognisable form of *Glossopteris*.

Reference: And. & And. (1985).

Contributors: John Anderson & Heidi Anderson.

Middle Ecca (Vryheid Fm.)

Localities: 5 TCs, 5 localities (1 km diam.), 5 superlocalities (10 km). The localities occur along a broad front some 400 × 150 km in extent around the northern margin of the Karoo Basin. Other localities have been sampled in the region, but not systematically, and there is no doubt the potential to put many more localities on the map. The important Vereeniging superlocality includes 10 sampled localities, but the assemblages are not well recorded. The flora recorded here from Vereeniging is that from the Leeukuil quarries and combines a number of TCs.

Environment: The Middle Ecca attains its fullest development of 425 m in the 'Vryheid area where it comprises a clear regressive cycle'—from delta front to delta with coal swamps (yielding the extensive coal deposits of South Africa) to delta front. The formation wedges out southwards into the continental sea of the Great Karoo Basin.

Age: Early Permian (Artinskian).

Biodiversity

Middle Ecca (Vryheid Fm.) (all localities): 45 spp (26 gen.)
Max. spp per TC: 30 spp.
Average spp per TC: 13 spp.
Non-gymnosperms: 11 spp (9 gen.).
  Bryophyta (liverworts, mosses): 1 sp. (1 gen.).
  Filicophyta (ferns): 4 spp (3 gen.).
  Lycophyta (lycopods): 3 spp (3 gen.).
  Sphenophyta (horsetails): 3 spp (2 gen.).
Gymnosperms: 34 spp (17 gen.).
  Cordaitanthales: 2 spp (1 gen.).
  Coniferales: 3 spp (3 gen.).
  Ottokariales: 19 spp (7 gen.).
  Ginkgoales: 8 spp (4 gen.).
  Incertae: 2 spp (2 gen.).

Vereeniging (Leeukuil quarries): 32 spp (27 gen.)
Non-gymnosperms: 6 spp (6 gen.).
  Bryophyta (liverworts, mosses): Nil.
  Filicophyta (ferns): 3 spp (3 gen.).
  Lycophyta (lycopods): 2 spp (2 gen.).
  Sphenophyta (horsetails): 1 sp. (1 gen.).
Gymnosperms: 26 spp (21 gen.).

Taxonomy: See comment for Estcourt Fm. opposite.

PERMIAN (Late, *ca* 257 Ma)
South Africa, KwaZulu-Natal

Lidgetton, KwaZulu-Natal, South Africa.
Estcourt Fm., Beaufort Gp., Wuchiapingian, *ca* 257 Ma.
Gymnosperm history: In decline towards the P/Tr Extinction.

Sketch by HMA (June 2005), after photo by HMA (26 June 1969).

Figures left to right, top to bottom:
A.O.D. Mogg, Mr Plumstead,
unknown, Anthony Tankard,
Dr Edna Plumstead, local farmer.

Lidgetton

The Lidgetton locality lies in the southern sector of the plant-bearing Estcourt Fm. outcrop, and *ca* 35 km NW of Pietermaritzburg in KwaZulu-Natal, South Africa.
Estcourt Fm., Beaufort Gp., Karoo Supergroup.

Historical: Dr A.O.D. Mogg discovered the Lidgetton site in 1927, though it seems that the earliest collection of any Estcourt Fm. plants (locality unknown) was made by Peter Cormack Sutherland (1822–1900) in *ca* 1854.

Significance: Of the 21 Estcourt Fm. localities (25 TCs) fully documented in And. & And. (1985), we have selected Lidgetton to illustrate here, not because of the abundance or diversity of material, but because it lends its name to one of the most important glossopterid genera (*Lidgettonia)* of the South African Late Permian and to one of the four glossopterid families (Lidgettoniaceae) Gondwana-wide.

Gymnosperms: 2 spp (2 gen.)
Ottokariales: *Lidgettonia africana*, Ottokariaceae/*Glossopteris* (1 sp.).

Abundance: This low-diversity assemblage is dominated by two species, the sphenophyte *Phyllotheca australis* (50%) and the glossopterid *Lidgettonia africana* (48%). The *Lidgettonia* whole-plant is well established through good collections of all of its organs that might be expected to occur in such a deposit—foliage, scale leaves, pollen organs, pollen, ovulate organs and seeds.

Plant associations
The TC is considered to represent two clear associations:
Lidgettonia africana—very low-diversity forest or woodland, with *Lidgettonia* heavily monodominant, of the river banks (levees) and other elevated ground.
Phyllotheca australis—dense monospecific sphenophyte stands (bamboo-like) associated with interdistributary pans and swamps.

Reference: And. & And. (1985).

Contributors: John Anderson & Heidi Anderson.

Estcourt Fm.

Localities: 25 TCs, 21 localities (1 km diam.), 13 superlocalities (10 km).
The localities occur along a sinuous N–S outcrop stretching some 200 km (and 20 km across) from Harrismith to Pietermaritzburg in the province of KwaZulu-Natal, South Africa. The strata are riddled by dolerite dykes and sills, making it difficult to place the sites in stratigraphic sequence.

Environment: The Escourt Fm., in this NE sector of the Karoo Basin, comprises primarily deltaic deposits (rich in plants and to a lesser extent insects), whereas the coeval deposits in the basin to the S and SW consist of floodplain deposits (rich in tetrapod fossils).

Age: Late Permian (Wuchiapingian).

Biodiversity

Estcourt Fm. (all localities): 24 spp (14 gen.)
Max. spp per TC: 16 spp.
Average spp per TC: 8 spp.
Non-gymnosperms: 8 spp (6 gen.).
  Bryophyta (liverworts, mosses): 1 sp. (1 gen.).
  Filicophyta (ferns): 1 sp. (1 gen.).
  Lycophyta (lycopods): Nil.
  Sphenophyta (horsetails): 6 spp (4 gen.).
Gymnosperms: 16 spp (9 gen.).
  Cordaitanthales: 1 sp. (1 gen.).
  Coniferophyta: 1 sp. (1 gen.).
  Ottokariopsida (glossopterids): 12 spp (5 gen.).
  Incertae: 2 spp (2 gen.).

Lidgetton: 5 spp (5 gen.)
Non-gymnosperms: 3 spp (3 gen.).
  Bryophyta (mosses): 1 sp. (1 gen.).
  Filicophyta (ferns): 1 sp. (1 gen.).
  Sphenophyta (horsetails): 1 sp. (1 gen.).
  Gymnosperms: 2 spp (2 gen.).
  Ottokariopsida (glossopterids): 2 spp (2 gen.).

Taxonomy: The diversity figures represent ‘natural’ (whole-plant) species and genera after a comprehensive attempt at establishing affiliations has been made, i.e. there is no inflation of diversity based on separate organs.

GLOBAL INSECT MACROEVOLUTION
Contributor to Charts 7 & 8 (pp 42, 43)

Conrad Labandeira (National Museum of Natural History, Smithsonian, Washington, USA)

Conrad is approaching midway in a five- to six-year study of plant/insect associations as preserved in the Late Triassic Molteno Fm. His first visit was in January 2002. For around six weeks per year (on two to three separate trips to Pretoria) he can be found bent over the microscope recording every recognisable leaf, fruit or seed specimen—along with any insect damage—as preserved on the upper and lower surface of some 30 000 slabs from 100 Molteno taphocoenoses. This is part of a global study aimed at tracking the evolution of the interdependent plant-insect story over 425 my from the mid-Silurian to the present. This is the preserve that Conrad has staked out and he is surely an alpha fish in the territory. A brief history of the gymnosperms can hardly be fully told without the insect perspective. Their stories are invisibly linked—and this story in brief outline (as currently known) is told period by geological period in the chapter entitled 'Macroevolutionary life cycle of the gymnosperms'.

For 12 concentrated hours each day, Conrad builds up his database. He knows well the size of the project he has set himself and he knows the brevity of three-score years and ten, and he knows how much time he has spent 'dry-walling' in the States to fund his way through studies. Conrad is a man in a hurry—seven days a week when here in South Africa—yet in the hours of free time, he switches readily to relax mode and finds it great fun sporting with words (adjacent).

Conrad's words

During Conrad's sojourns here in South Africa, I reserve a special place headed 'Conrad's words' at the foot of each page in my daily diary. Conrad is a great conversationalist and a master with words. Whether writing a strictly scientific paper on fossil insects or tossing words light-heartedly back and forth in the car in transit somewhere, he shows equally easy mastery. Here are some of the words I have jotted down—nothing earth shattering but wonderful in the context of repartee.

Lollygagging: taking things in a very relaxed fashion.

Tres amigos: The rather splendid and variously eccentric three Russian (Moscovite) paleoentomologists, Alex Rasnitsyn, Alexandr Ponomorenko and Yuri Popov, who had a week or so earlier been here in Pretoria at the 3rd International Paleoentomological Conference (Feb 2005).

Back to normalcy: Quoting Warren G. Harding, a former President of the USA; in our case, getting back to the 12-hour-a-day routine of research and books after the flurry of hosting 65 overseas delegates at the fossil insect conference just noted (Feb 2005).

Chauncy Gardener: Another reference to a US President, in this case a fictional film character played by the inimitable Peter Sellers. Chauncy was an illiterate gardener who, through a succession of quirky, upwardly mobile steps, finally found himself occupying the oval office.

A gaggle of luminaries: A smallish gathering of palaeontologists for example.

A clique of intimates: Quoting Donald Rumsveld, US Secretary of Defence; a variation of the above, but generally referring to top-ranking politicians.

Factoid: Something uttered as if it were fact but cannot be proved.

Dumpsters: Those who remove builders' debris every second day or so; this is a regular topic since there is only too evidently no such profession established in South Africa.

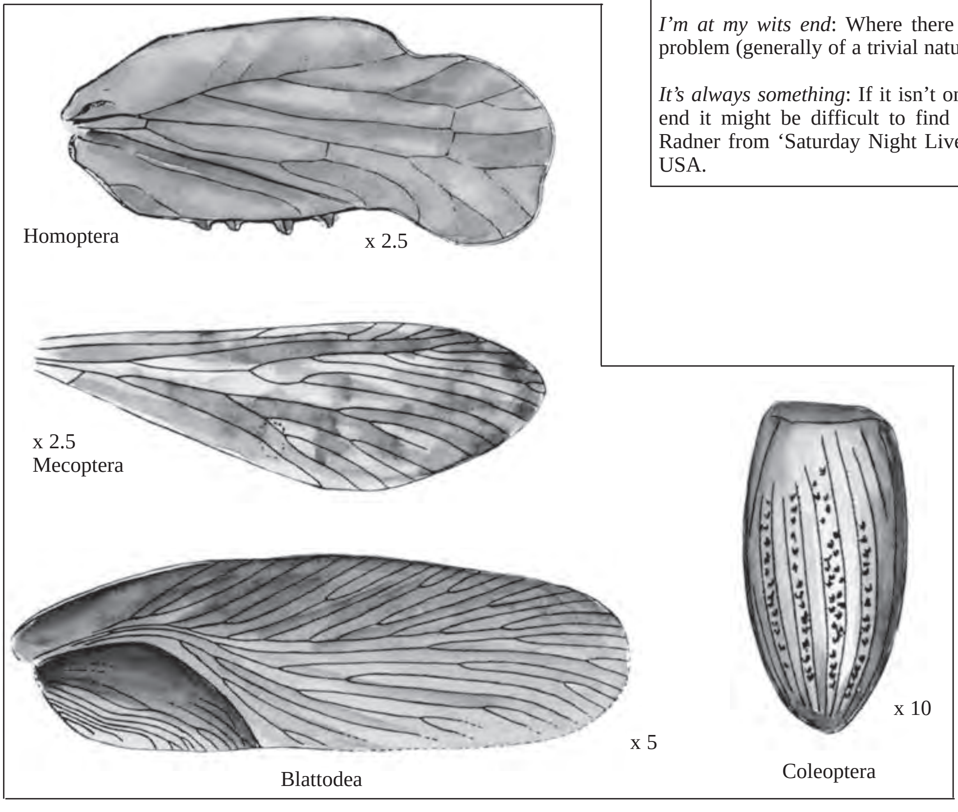
Comestibles and consumables: Would include, for instance, one's sandwiches, apple and banana brought along for lunchtime.

Appertinences and accoutrement: Refer generally to non-consumable belongings carried with one for the day's activities; best when spoken with a beautifully modulated French accent.

I'm at my wits end: Where there is no apparent solution to a recurrent problem (generally of a trivial nature).

It's always something: If it isn't one thing then it's another, so that in the end it might be difficult to find space for *lollygagging*; quoting Gilda Radner from 'Saturday Night Live'—a late-hour comedy show from the USA.

Molteno Fm. Late Triassic Insects



GLOBAL TETRAPOD MACROEVOLUTION
Contributors to Charts 9 & 10 (pp 44, 45)

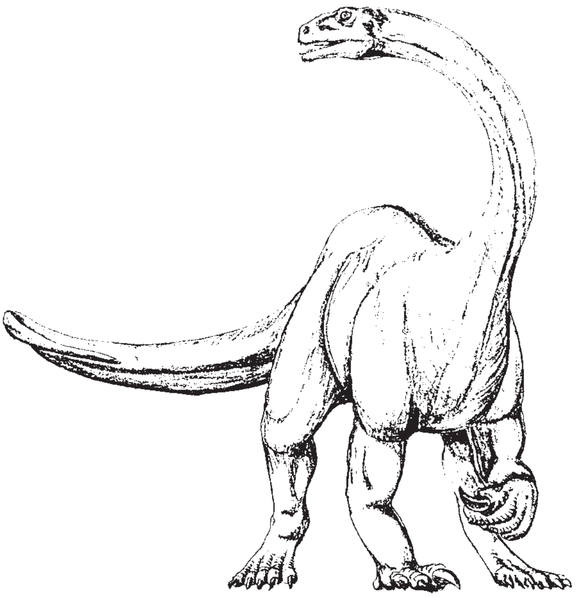
Adam Yates and Fernando Abdala (Johannesburg) and Johann Neveling (Pretoria), all of Gauteng Province, South Africa, have contributed significantly to updating the two tetrapod vertebrate charts (pp 44, 45)—in particular the dinosaur, therapsid and temnospondyl amphibian clades.

The sense that the evolution of science as seen through the histories of individual scientists and scientific schools emerges as a phylogenetic tree analogous to that of, say, the tetrapod vertebrates, is amply evidenced by the brief biographies below:

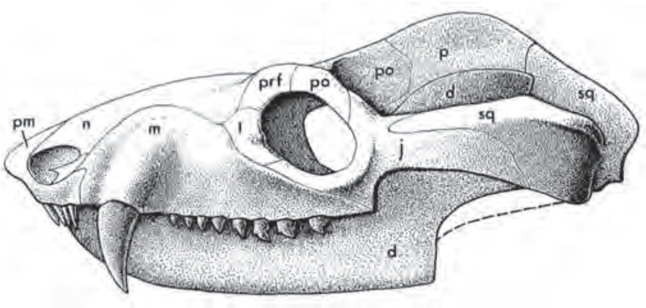
Adam Yates (BPI, Univ. of the Witwatersrand, Johannesburg): Ph.D. Melbourne, under Anne Warren. Post-doc, three yrs, Bristol University, UK, on sauropod dinosaurs under Mike Benton. Since 2003, first a post-doc, currently as lecturer at BPI, working on the sauropod and prosauropod dinosaurs of the Karoo and elsewhere.

Johann Neveling (Council for Geoscience, Pretoria): Ph.D. Wits (2003), under Bruce Rubidge and John Hancox, on the vertebrate biostratigraphy of Early to mid-Triassic strata in the Karoo Basin. At the CGS since 1995, with a focus on the biostratigraphy and sedimentology of Late Triassic vertebrate beds across the end-Permian Extinction, Karoo.

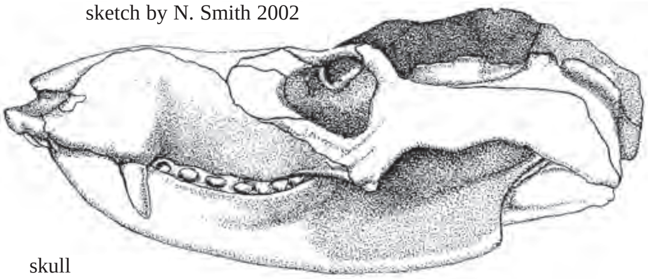
Fernando Abdala (BPI, Univ. of the Witwatersrand, Johannesburg): Ph.D. (1996) Universidad Nacional de Tucuman (Argentina), under Dr Jaime E. Powell, on chiniquodontoid cynodonts from South America. Moved in 1997 as post-doc to Brazil, Pontifica Universidade Catolica do Rio Grande do Sul, Porto Alegre, studying Brazilian cynodonts and Triassic faunas under Martha Richter. Since 2002 at BPI studying South African cynodonts and therocephalians.



sketch by N. Smith 2002



Chiniquodon, Brazilian Triassic cynodont.
from: Romer (1969) [Fernando Abdala]

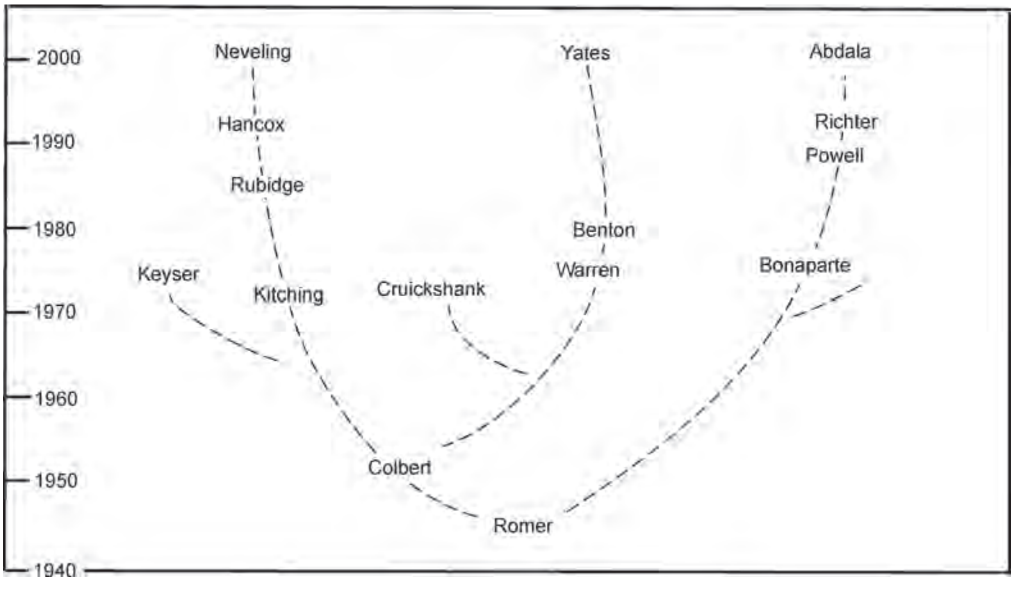


skull
ca 13 cm long

Abdala, Neveling & Welman 2005 (in press)

Langbergia modisei Abdala, Neveling & Welman 2005 (in press): A new genus and species of gomphodont trirachodont cynodont from the lowermost subzone (A) of the *Cynognathus* Assemblage Zone, Karoo Basin, South Africa; Upper Olenekian/Spathian, Early–Middle Triassic.

A (70 yrs, 1940–2010) phylogeny of tetrapod researchers



ON PHYLOGENY & MORPHOLOGY
Contributors to 'Gymnosperm phylogeny' (pp 18, 19) & Charts 27–30 (pp 62–65)

Phylogeny, cladistics (pp 18, 19)

Early in our planning of the expanded *Brief history*, we considered inviting some colleagues to undertake a cladistic analysis of the set of families covered in the book. We were advised that this would amount to a major piece of research requiring a serious time commitment: anything less would be premature and invite counterproductive criticism. In its stead, Paul Kenrick agreed to prepare a two-page summary on the current status of morphological and molecular phylogeny within the extant and fossil gymnosperms.

Paul Kenrick is a palaeobotanist at the Natural History Museum, London. Prior to this he has held research posts at several other institutes in Europe and the USA, including the Swedish Museum of Natural History, Stockholm, and the Field Museum, Chicago. His main research interests include the origins and early evolution of the land flora and the systematics of ferns and fern allies. His work in these areas was recognised by the award of the Bicentennial Medal of the Linnean Society of London in 1999 and the Henry Gleason Award of The New York Botanical Garden in 1998. He is the author of a book on land plant origins published in 1997 and one on fossil plants published in 2004.

> '*When I took the first survey of my undertaking, I found our speech copious without order, and energetic without rule: wherever I turned my view, there was perplexity to be disentangled and confusion to be regulated.*'—**Samuel Johnson**, London, 1755; from the preface to his *English Dictionary*.

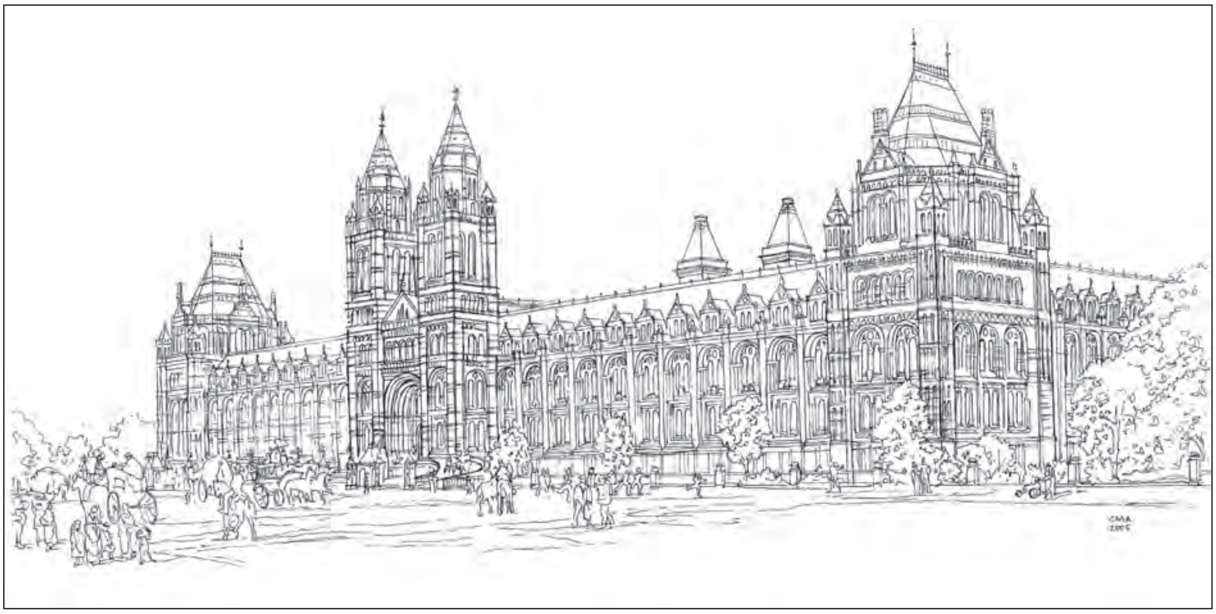
Comparative morphology (Charts 27–30)

At a particularly late stage (August 2004), a few months before the planned completion of our manuscript, the opportunity arose to bring in a significant piece on the comparative morphology of the extant gymnosperm families. This could not be missed. Sound interpretation of morphology in palaeobotany is fundamental to robust taxonomy and ultimately the generation of well-supported phylogenetic trees. Remarkably, research dedicated to unravelling the complex reproductive and vegetative structures (involving embryology, ontogeny, homology) of the living gymnosperms remains in its relative infancy. The team from Bochum (see below) is at the forefront. A set of the team's superbly crafted CorelDraw graphics portraying comparative diagnostic features of selected genera is included here as Charts 27–30 (pp 62–65). Some of the figures were especially prepared for our *Brief history*; most have been published (in black-and-white) over the past few years. This four-page spread is essentially a preview of their work in progress. They anticipate completing over the next few years a full comparative morphology, in this same vein, of key genera covering all 13 extant gymnosperm families.

Thomas Stützel, Marcus Mundry & Iris Mundry

Prof. Dr Thomas Stützel previously worked on the morphology and systematics of monocots, in particular the Eriocaulaceae, but shifted to the gymnosperms around nine years ago. He is now leader of the dynamic Plant Systematics and Evolution Group at the University in Bochum, Germany, is currently Dean of the Faculty of Science, and is Head of the associated Botanical Garden.

The origin of the gymnosperm-morphology-phylogeny working group under Thomas can be dated to 1996 when Iris Mundry initiated her studies on the ovulate cone of the living conifers for her Ph.D. thesis (*Morphological and morphogenetic studies in the evolution of the gymnosperms*, published 2000). The team has since grown to include some eight persons. Marcus Mundry—who in effect shares a scientific-researcher post with Iris—is a master at creating (CorelDraw) graphic imagery. He delivered a fine presentation at the International Botanical Conference (Gymnosperm Symposium), Vienna, July 2005, with animations showing the ontogenetic development of the ovulate cones of the extant conifers.



The Natural History Museum, Bloomsbury, London

Sketch by Clara Anderson (August 2005), after watercolour (1876) by the architect Alfred Waterhouse, showing his final neo-Romanesque design for the museum.

Sir Richard Owen (1804–1892), discoverer of the dinosaurs, was the first director of the Museum.

INTO THE TRIASSIC (P/Tr, 251 Ma)
Antarctica, Central Transantarctic Mts

Fremouw Fm. (Triassic, beds 4–8)
Lower Fremouw (4–6), Upper Fremouw (7, 8)

8. *Neocalamites carrerei, Dicroidium odontopteroides*.

7. *Dicroidium zuberi*.

6. Fauna—amphibian
   Austrobrachyops jenseni.

5. *Voltziopsis africana*.

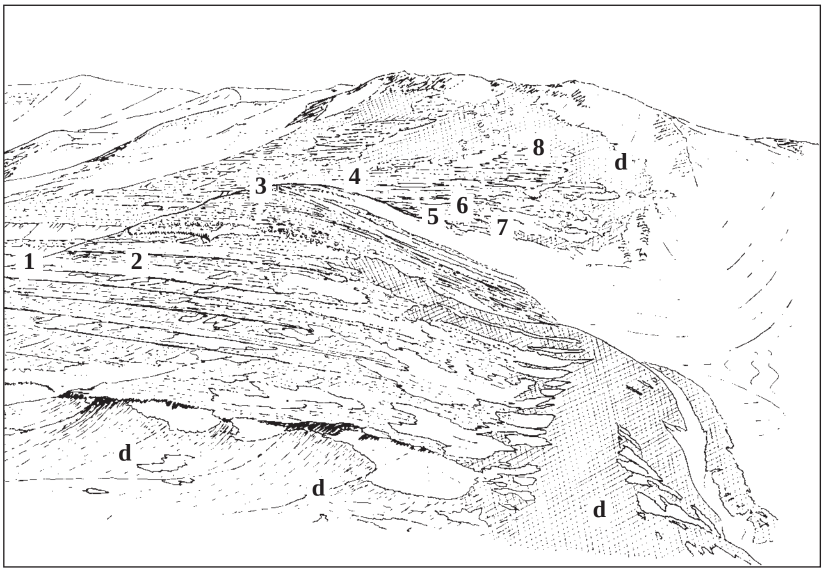
4. Fauna—reptilians
   Lystrosaurus murrayi, Thrinaxodon liorhinus.

3. **Permo-Triassic boundary (bed 3)**

Buckley Fm. (Permian, beds 1–2)

2. *Squamella australis / Glossopteris angustifolia*.
   Plumsteadia jenseni / Glossopteris browniana.
   Dictyopteridium walkomi / Glossopteris decipiens.

1. *Cometia biloba, Glossopteris indica*.



Graphite Peak, Central Transantarctic Mountains.
Buckley Fm. (Permian) to **Fremouw Fm.** (Triassic).
Gymnosperm history: Major turnover across the P/Tr boundary.

Sketch by HMA (June 2005), after photo by Greg Retallack (12 Dec. 1995).

Notes on Graphite Peak section

Listed for each bed is a selection of species only, either plant (all gymnosperm other than *Neocalamites*) or tetrapod.

Scale: *ca* 550 m (stratigraphic) from the lower dolerite (bottom left) to the upper dolerite (above bed 1).

Dolerite dykes & sills (prominent in the section): Indicated by d.

Plant assemblages: These are generally of low diversity, but with abundant leaves per bedding plane; as yet there is not a relative abundance of data at hand; the reproductive/vegetative pairings shown for the glossopterid taxa of bed 2, are based on organic connection (*Dictyopteridium, Plumsteadia*) or bedding plane associations; it is notable in this section that *Dicroidium*-yielding assemblages first appear only in the Upper Fremouw Fm.

Gregory J. Retallack (Dept of Geological Sciences, Univ. of Oregon)

For unflagging originality, energy, productivity and global sweep, Greg has to be very hard to beat. His fluid flow of hypotheses, bound to generate a degree of controversy, are invariably couched with precision and clarity. The unique style of his superb 3-dimensional stratigraphic-habitat-soil profile sketches render his books and papers instantly recognisable. With Sid Ash (see p. 236) back in 1984, Greg accompanied Heidi and me on our first and our only complete circuit of the Molteno outcrop stretching in a belt around Lesotho at the heart of the Great Karoo Basin, South Africa. This venture clearly was some kind of expression of Greg's being in our midst.

Greg Retallack is a fifth-generation Australian, but has now lived in Eugene, Oregon, almost as long as his first 26 years in Australia. His 1978 Ph.D. thesis from the University of New England in Australia compared Triassic plants from Australia and New Zealand. That same year he began a post-doc working on Cretaceous early angiosperms with David Dilcher at Indiana University in Bloomington. With appointment to the University of Oregon in 1981 he turned his interests to the long fossil record of soils (paleopedology), with major field programmes studying Neogene ape evolution in Kenya, Cenozoic climate change in North America, the Cretaceous–Tertiary boundary in Montana, the Permian–Triassic boundary in Antarctica and early land plant evolution in Pennsylvania.

References: Retallack (2001a, b).

Contributor: Greg Retallack (see also p. 247).

Gymnosperms and the global extinctions

Elsewhere in this volume (pp 5, 36, 70–89), we have stressed the central role the global extinction events have played in the history of the gymnosperms. Here, with Greg's Antarctic P/Tr section, we stress further this fundamental relationship. At this largest of all Phanerozoic extinctions, there is a profound gymnosperm turnover: in the Gondwana continents from the glossopterid-dominated Permian floras to the *Dicroidium*-dominated Triassic floras. (See Greg's Montana K/T section, p. 247, for a contrasting picture.)

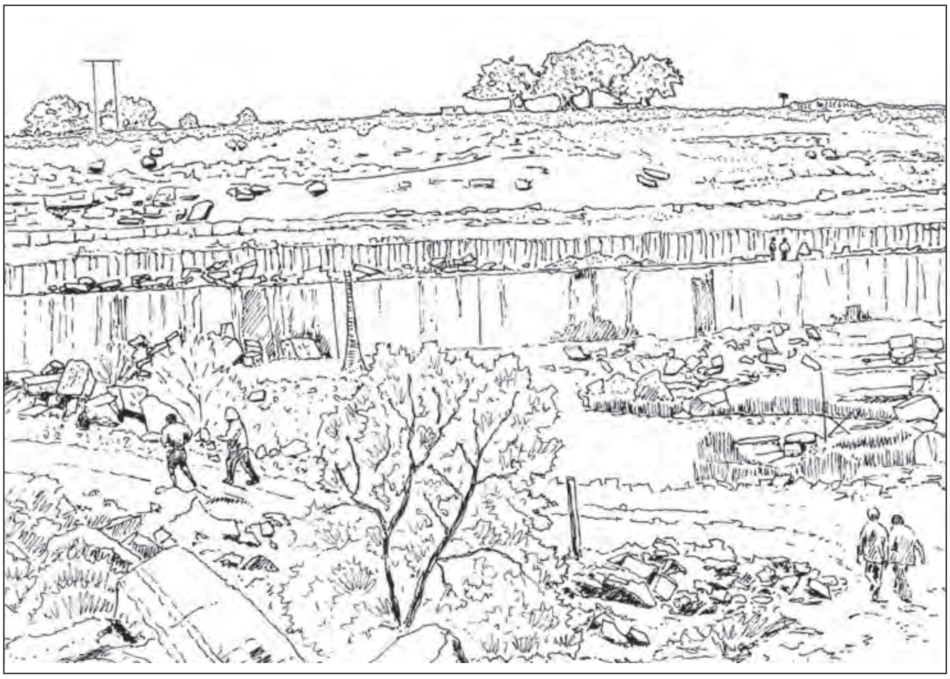
> *'Therefore I would not have it unknown to your holiness, that the only thing that induced me to look for another way of reckoning the movements of the heavenly bodies was that I knew that mathematicians by no means agree in their investigations thereof.'*—**Nicolaus Copernicus**, 1543; from his dedication to Pope Paul III of the *Revolutions of the heavenly bodies*.

Wang Ziqiang (Tianjin Institute of Geology, Tianjin, China)

North China appears to have the most continuous sequence globally of prolific megaplant-bearing strata through the Permian, across the Permo–Triassic boundary, and through the Triassic (Chart 20, p. 55). In view of this, Chris approached his good colleague Wang Ziqiang to prepare a short piece on gymnosperm fortunes across the end-Permian extinction (p. 78) as seen from the Chinese perspective.

Wang Ziqiang, now 68, has in the past 10 years concentrated on writing research papers on the plants—collected by him—of the Permo–Triassic redbed sequences of North China. These have been published in international (see also Zhou Zhiyan: 241) rather than Chinese journals. Through this work, he has become interested in the terminal-Permian mass extinction, the rarely studied Late Permian gymnosperms and in plant phylogeny.

TRIASSIC (early Middle, *ca* 245–243 Ma)
France, Strasbourg district



Adamswiller Quarry, 55 km NW of Strasbourg, NE France.
Grés a Voltzia, Upper Buntsandstein, early Anisian (*ca* 245–243 Ma).
Gymnosperm history: In the early stages of the post-P/Tr recovery.

Sketch by HMA (24 June 2005), after photo by HMA (26 Aug 1980).

Figures left to right:
John M. Anderson,
Louis Grauvogel,
Lea Grauvogel-Stamm,
Jeanne Doubinger.

Grés a Voltzia, Upper Buntsandstein

Localities: 33 localities, over an area 70 km N-S and 50 km W-E; the majority (26 localities, including Adamswiller) over a narrow belt of outcrop 30 km N-S, 50–60 km NW of Strasbourg, France.

Historical: The Grés a Voltzia is the emblematic stone of NE France and was used to build the famous Strasbourg Cathedral. Since 1935, Louis Grauvogel (died 1987), Lea's father, who had a metallurgy firm (forging and stamping), had collected fossils from the 33 localities noted above. Jean-Claude Gall had collaborated with him since 1961 and Lea since 1966. Grauvogel was a passionate polymath, dextrous at the piano, and a naturalist to the core. His collecting of primitive extant butterflies (Hepialidae), led to his search for their ancestors in the Grés a Voltzia.

Significance: The palaeobiocoenoses of the Grés a Voltzia—perhaps better than anywhere else globally—illustrate the earliest stages of the progressive recovery of the biosphere after its dramatic decimation at the end-Permian.

Environment: The 20-m thick deltaic beds of the Grés a Voltzia, deposited at the western margin of the extensive Germanic basin, constitute the transition between the Bundsandstein sandstones of fluviatile origin and the carbonate rocks of the Muschelkalk sea.

Fauna
Aquatic: *ca* 70 spp; jellyfish, annelids, lingulids, bivalves, limulids, insect larvae, fish (diverse bony groups, eggs of cartilaginous forms).
Terrestrial: Amphibians (stegocephalid, disarticulated bones), reptiles (rhynchosaurid, footprints only); arthropods diverse, with scorpions, mygalomorph spiders, diplopod myriapods and numerous insects.
Insects: >200 spp, 15 orders; dominated in abundance by Blattodea (41%) and diversity by Coleoptera (*ca* 40 spp), followed by Hemiptera (38 spp), Diptera (13 spp) and Orthoptera (11 spp).
Marine incursions: Rare marine organisms associated with incursions; foraminifera (2 gen.), bivalves (2 gen.), gastropods (2 gen.).

References
Gall (1971), Grauvogel-Stamm (1978), Gall *et al.* (1998), Marchal-Papier (1998), Gall & Grauvogel-Stamm (1999).

Biodiversity (megaplants)
Grés a Voltzia (all localities): *ca* 28 spp (20 gen.)
Non-gymnosperms: 11 spp (9 gen.).
Gymnosperms: 17 spp (11 gen.).

Non-gymnosperms: 11 spp (9 gen.)
Bryophyta (mosses, liverworts): Nil.
Lycophyta (lycopods): 3 spp (3 gen.), rare.
- *Bustia* (1 sp., isolated sporophylls).
- *Annalepis* (1 sp., 2 indivs).
- *Pleuromeia* (1 sp., extremely rare).

Sphenophyta (horsetails): 3 spp (2 gen.).
- *Equisetites/Equisetostachys* (1 sp.).
- *Schizoneura* (1 sp.)/*Echinostachys* (2 spp).

Filicophyta (ferns): 5 spp (4 gen.).
- *Anomopteris* (1 sp., most common fern).
- *Neuropteridium* (2 spp)/*Crematopteris* (1 sp.).
- *Cladophlebis* (1 sp.).
- cf. *Tongchuanophyllum* (1 sp.).

Gymnosperms: 17 spp (11 gen.)
Pinopsida: Dominant in the flora, abundant, diverse.
- Voltziales: *ca* 10 spp (4 gen.).
  - *Voltzia foliage* (>1 sp.).
  - *Aethophyllum* (1 sp.)/*Willsiostrobus.*
  - *Pelourdea* (1 sp.)/*Willsiostrobus.*
  - *Albertia* (1 sp.).
  - Male cones: *Willsiostrobus* (5 spp), *Darneya* (3 spp), *Sertostrobus* (1 sp.).
  - Ovulate cones: *Voltzia* (?spp), *Cycadocarpidium* (1 sp.).

Cycadopsida: 1 sp. (1 gen.), extremely rare.
- cf. *Pseudoctenis* (1 sp., 1 fragm.).

Bennettitopsida: 2 spp (2 gen.), extremely rare.
- *Otozamites* (1 sp., 1 indiv.).
- cf. *Nilssonia* (1 sp., 1 indiv.).

Ginkgoopsida: 1 sp. (1 gen.), very rare.
- Ginkgoales.
  - *Sphenobaiera* (1 sp., seedlings from 1 TC).

Undescribed: *ca* 3 spp (3 gen.).

Contributors: Lea Grauvogel-Stamm, Jean-Claude Gall.

TRIASSIC (mid-Middle, *ca* 237 Ma)
Australia, New South Wales

Nymboida Reserve Quarry, NE New South Wales.
Nymboida Coal Measures, Anisian/Ladinian boundary (*ca* 237 Ma).
Gymnosperm history: Well into their post-P/Tr radiation.

Figure with geology pick:
Keith Holmes.

Sketch by HMA (Sept 2004), after photo by HMA (May 2000).

Nymboida Coal Measures, Basin Creek Fm.

Localities: The megaflora listed opposite derives from two localities (Nymboida Coalmine Quarry and Nymboida Reserve Quarry) 5.3 km apart near the village of Nymboida, 300 km S of Brisbane in NE NSW, Australia. The Nymboida Coal Measures occur in the small (*ca* 20 × 10 km) Nymboida Sub-basin, to the SW of the far larger Middle to Late Triassic (into Jurassic) Clarence-Moreton Basin.

Sampling: In that the collecting has been done almost entirely from blocks blasted from the quarry faces, it is not possible to distinguish discrete taphocoenoses (assemblages) or palaeodemes (populations). The flora represents a single composite assemblage.

Historical: De Jersey (1958) was the first to mention Nymboida megafloras, McElroy (1963) the first to describe the Basin Creek Fm. and Nymboida Coal Measures, and Retallack (1977) the first to publish an initial plant list. Keith Holmes has collected from the two quarries from the late 1960s to the present. The quarries have been operated as brickpits over a period of 40 years throughout these visits.

Significance: This is the richest and most diverse megaflora known from the Middle Triassic (*ca* 237 Ma, Retallack *et al.* 1993) of Gondwana. The two quarries are the most actively and continuously collected plant localities in Australia. Nymboida ideally represents the Triassic radiation between the Grés a Voltzia and Molteno Fm.

Environment: The sequences 'at both quarries represent overbank flooding by a large meandering river onto an alluvial floodplain with open stagnant lakes and permanent swampland' (Holmes 2000).

Fauna: Nil.

References: Holmes (2000, 2001, 2003), Holmes & Anderson (2005a,b).

Contributors: Keith Holmes, Heidi Anderson.

Biodiversity (megaplants)

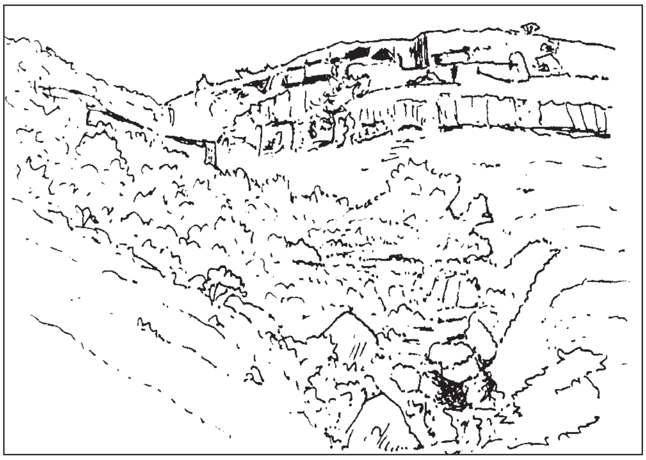
Nymboida (all localities): *ca* 103 spp (46 gen.)
Non-gymnosperms: 55 spp (31 gen.).
Gymnosperms: 48 spp (15 gen.).

Non-gymnosperms: 55 spp (31 gen.).
Bryophyta (mosses, liverworts): 3 spp (2 gen.).
Lycophyta (lycopods): Nil.
Sphenophyta (horsetails): 7 spp (7 gen.).
Filicophyta (ferns): 18 spp (10 gen.).
    Fern-like foliage: 27 spp (12 gen.).

Gymnosperms: 48 spp (15 gen.).
Pinopsida (4 spp, 2 gen.).
    *Voltziales: *Heidiphyllum* (2 spp, r-c).
    *Pinales: *Rissikia* (2 spp, o)/*Rissikianthus* (1 sp., r).
Cycadopsida (7 spp, 1 gen.).
    *Cycadales: *Pseudoctenis* (*ca* 7 spp, r-o).
Ginkgoopsida (26 spp, 6 gen.).
    Dicroidium (7 spp, r-c)/*Umkomasia* (3 spp, r)/*Pteruchus*(2 spp, r).
    Lepidopteris (4 spp, r-c)/*Peltaspermum* (2 spp, r)/*Antevsia* (1 sp., r).
    Kurtziana (2 spp, o), *Rochipteris* (6 spp, r).
    **Ginkgoites* (5 spp, r-o).
    **Sphenobaiera* (2 spp, r)/*Hamshawvia* (1 sp., r)/S*tachyopitys* (2 spp, r).
Bennettitopsida (6 spp, 3 gen.).
    **Halleyoctenis* (1 sp., r), *Taeniopteris* (4 spp, r), *Nilssonia* (1 sp., o).
Gnetopsida (4 spp, 2 gen.).
    **Yabeiella* (1 sp., r)/*Fraxinopsis* (1 sp., r), *Gontriglossa* (3 spp, o).
Incertae (1 sp., 1 gen.).
    Walkomiopteris (1 sp., r).

Abundance scale: r = rare, o = occasional, c = common.
Affiliations: Indicated by oblique stroke as far as possible.
Diversity: The gymnosperm diversity total reflects whole-plant taxa. As those genera marked by an asterisk have not yet been formally described, the number of species listed for them is an estimate.

TRIASSIC (Late, *ca* 223 Ma)
South Africa, Karoo Basin



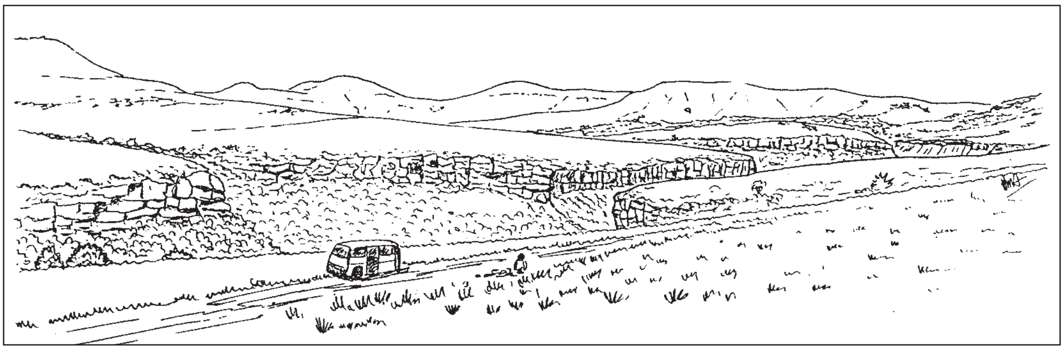
Molteno Fm. plant localities

Molteno Fm., Carnian, *ca* 223 Ma.
Selection of five localities, Karoo Basin, South Africa.
Gymnosperm history: At the heyday of gymnosperm biodiversity.

Sketches by HMA (1998–2005), after photos by HMA (1980–2000).

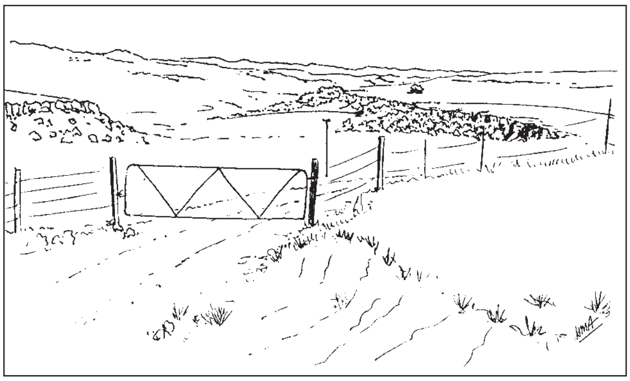
Umkomaas (Umk 111)

Habitat: *Dicroidium* riparian forest (immature).
Dominants: *Dicroidium* (69%), *Sphenobaiera* (5%), *Heidiphyllum* (7%), horsetails (2%), ferns (1%).
Biodiversity: Vegetative total: 75 spp (37 gen.).
Non-gymnosperms: 46 spp (19 gen.).
Gymnosperms: 29 spp (18 gen.).



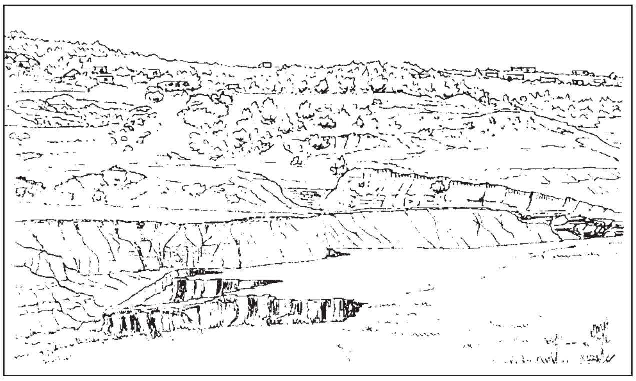
Peninsula (Pen 411)

Habitat: *Heidiphyllum* thicket.
Dominants: *Dicroidium* (13 indivs), *Sphenobaiera* (nil), *Heidiphyllum* (94%), horsetails (2%), ferns (3%).
Biodiversity: Vegetative total: 11 spp (10 gen.).
Non-gymnosperms: 6 spp (6 gen.).
Gymnosperms: 5 spp (4 gen.).



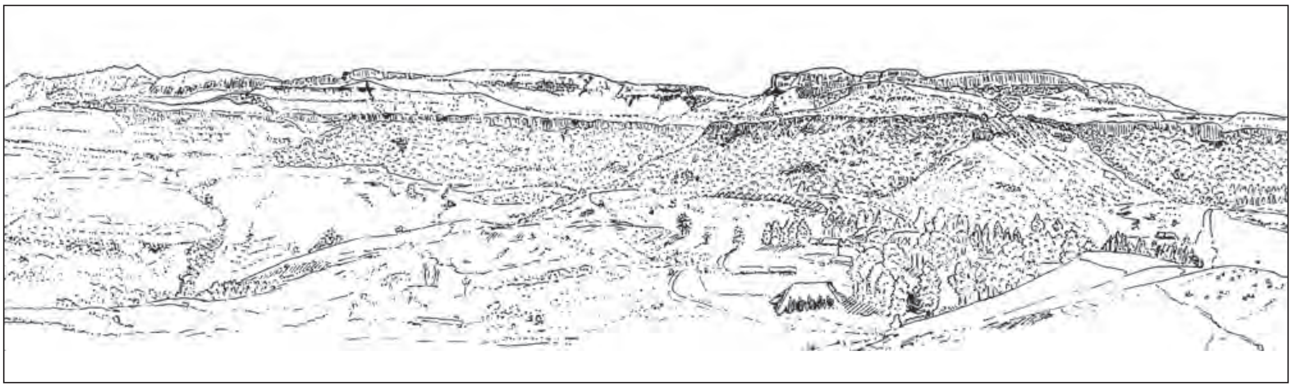
Waldeck (Wal 111)

Habitat: *Sphenobaiera* closed woodland.
Dominants: *Dicroidium* (92%), *Sphenobaiera* (3%), *Heidiphyllum* (nil), horsetails (nil), ferns (nil).
Biodiversity: Vegetative total: 11 spp (8 gen.).
Non-gymnosperms: Nil.
Gymnosperms: 11 spp (8 gen.).



Mazenod (Maz 211)

Habitat: *Dicroidium* riparian forest (mature).
Dominants: *Dicroidium* (64%), *Sphenobaiera* (1%), *Heidiphyllum* (32%), horsetails (7 indivs), ferns (4 indivs).
Biodiversity: Vegetative total: 19 spp (13 gen.).
Non-gymnosperms: 4 spp (4 gen.).
Gymnosperms: 15 spp (9 gen.).



Little Switzerland (Lit 111)

Habitat: *Dicroidium* riparian forest (immature).
Dominants: *Dicroidium* (50%), *Sphenobaiera* (1%), *Heidiphyllum* (23%), horsetails (10 indivs), ferns (10 indivs).
Biodiversity: Vegetative total: 38 spp (25 gen.).
Non-gymnosperms: 32 spp (19 gen.).
Gymnosperms: 6 spp (6 gen.).

Molteno Fm., vegetation, observed diversity

	spp	TCs	abundance
BRYOPHYTA			
5 genera	19	28	very to extremely rare
LYCOPHYTA			
2 genera	6	7	very to extremely rare
SPHENOPHYTA			
5 genera	21	60	very rare to monodominant
FILICOPHYTA			
18 genera	46	56	extremely rare to sparse
PINOPHYTA			
PINOPSIDA			
Heidiphyllum	2	62	monodominant
Clariphyllum	1	3	very rare
Rissikia	2	21	sparse
Pagiophyllum	1	1	extremely rare
CYCADOPSIDA			
Pseudoctenis	9	21	sparse
Jeanjacquesia	3	3	very rare
Ctenis	2	2	very rare
Moltenia	4	5	very rare
GINKGOOPSIDA			
Lepidopteris	2	30	sparse
Scytophyllum	1	1	extremely rare
Kurtziana	16	13	rare
Dejerseya	1	5	abundant
Ginkgoites	6	19	rare
Paraginkgo	1	2	very rare
Sphenobaiera	9	43	monodominant
Dicroidium	19	75	monodominant
Kannaskoppifolia	10	26	rare
INCERTAE SEDIS			
Batiopteris	5	10	rare
Saportaea	1	1	extremely rare
Linguifolium	1	9	sparse
BENNETTITOPSIDA			
Halleyoctenis	3	10	common
Taeniopteris	8	38	common
GNETOPSIDA			
Gontriglossa	1	8	sparse
Graciliglossa	1	1	very rare
Cetiglossa	1	1	extremely rare
Yabciella	2	29	sparse
Jungites	2	1	very rare
Totals: 57 gen., 205 spp, 100 TCs			

Molteno Fm.: **Biodiversity**, from various perspectives

Vegetative diversity, whole flora (observed)
Total diversity: 205 spp (57 gen.).
Non-gymnosperms: 92 spp (30 gen.).
Gymnosperms: 113 spp (27 gen.).

Gymnosperm diversity (observed)

Ovulate organs:	8 classes,	18 orders,	18 fams,	20 gen.,	51 spp.
Pollen organs:	4 classes,	11 orders,	13 fams,	15 gen.,	35 spp.
Foliage:	8 classes,	17 orders,	24 fams,	27 gen.,	113 spp.
Whole-plant:	10 classes,	23 orders,	32 fams,	38 gen.,	143 spp.

Notes on whole-plant taxa
See And. & And. (2003, pp 20, 21).

Vegetative diversity, whole flora (observed, per TC)
Minimum (per TC): 1 sp. (1 gen.), as in several TCs.
Maximum (per TC): 75 spp (37 gen.), as in Umk 111 Dic 2 spp.
Average (per TC).
Total vegetative: 9.2 spp (6.81 gen.).
Non-gymnosperm: 2.65 spp (2.49 gen.).
Gymnosperm: 6.44 spp (4.34 gen.).

Observed, preserved & existed diversity
Observed (vegetative): 206 spp.
Preserved (vegetative): 876 spp.
Existed (whole-plant): *ca* 2 000 spp.

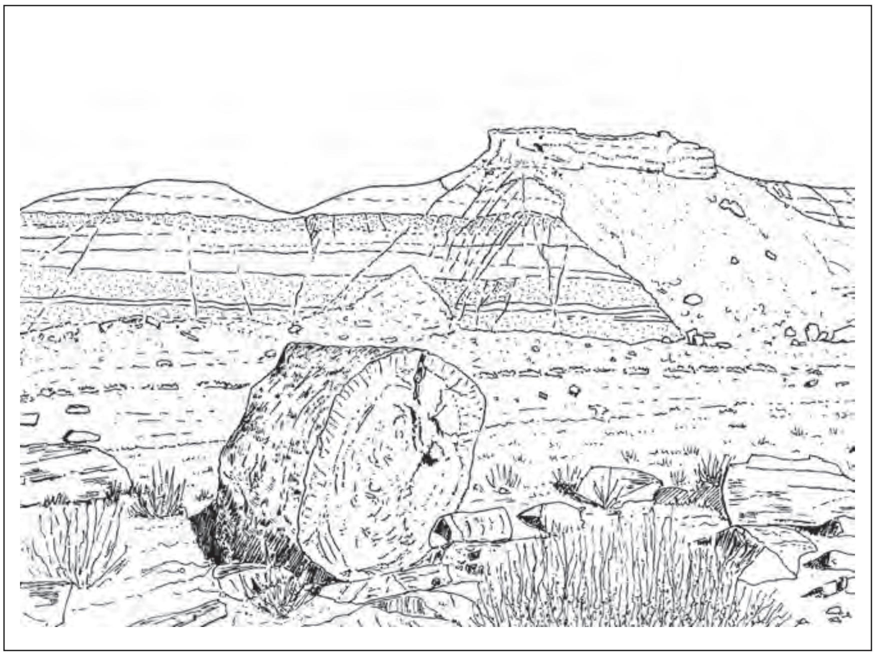
Vegetative species (full flora):	206 observed,	667 preserved.
Ovulate orders (gymnosperms):	16 observed,	84 preserved.
Insect species (full fauna):	335 observed,	7 740 preserved.

Notes on observed, preserved, existed diversity
See And. & And. (2003, pp 20–25).

References: And. & And. (1989, 2003).

Contributors: John Anderson & Heidi Anderson.

TRIASSIC (Late, *ca* 222–210 Ma)
United States of America



Petrified Forest National Park, east-central Arizona, USA.
Petrified Forest Member, Chinle Fm., Late Carnian, *ca* 220 Ma.
Gymnosperm history: At the heyday of gymnosperm biodiversity.

Sketch by HMA (28 June 2005), after photo by NPS/T. Scott Williams.

Araucarioxylon arizonicum, section of petrified trunk in foreground.
Outcrops: The full sequence, from trunks in foreground to purple, red and white mudstones of hill-scape, falls in the Lower Part of the PFM.

Sidney Ash (New Mexico, USA)

Sid was one of the last to join us in this evolving *Brief history*: through a somewhat vexed e-mail that arrived on 5 May 2005 (05/05/05): '*I never did hear back from you after I agreed in January to work with Krassilov on part of your new book. … What has happened*?' He was also the first, with Greg Retallack (who did his early palaeobotanical and paleosol work in Australia and New Zealand and has since settled at the University of Oregon, Eugene, USA), to join Heidi and me on the debut—and only—circum-field-excursion of the *ca* 400 × 200 km trapezoidal outcrop of the Molteno Fm. This was in the late southern summer (March) of 1984 when Sid was here with his family in South Africa on sabbatical (October 1983 to May/June 1984).

Val Krassilov has published, with Sid, on aspects of the Chinle Fm. gnetopsids, so it was natural that Sid should contribute to the write-up of the relevant families and orders for the current work. Thus it was that Val and I tried to reach Sid in December (2004) and both inexplicably failed. It is only through e-mails that compiling a book of the nature of our *Brief history* can be seriously contemplated, but they are not yet foolproof.

Sid & the Chinle

Sid has been collecting the Late Triassic floras of the USA since 1963, originally working for the US Geological Survey, subsequently while teaching at Weber State University, Ogden, Utah, until his retirement (1997). His Ph.D. thesis under Tom Harris ('*what an experience*') at Reading University, UK (1964–1966) concerns the Chinle flora.

Now an adjunct professor in the Dept of Earth and Planetary Sciences, University of New Mexico, he conducts his research from his home laboratory and has no '*plans to quit anytime soon because I keep finding new undescribed fossils*'. So Sid has been working for 43 years now on the Chinle and coeval Late Triassic floras of the USA—120 published papers, three in press, five in preparation—and can visualise many more. (His dedication to this task was recognised earlier this year through a special award from the US National Park Service.) A professional lifespan is barely sufficient to sample and describe the flora of a widely outcropping, richly fossiliferous formation. This is a common refrain.

Biodiversity of the Late Triassic floras of the USA

The Late Triassic floras of the USA fall into two natural geographic groups: western floras (Chinle Fm. and Dockum Gp) which are by far the best known; and the eastern floras (Newark Supergroup), most of which have not been studied in half a century except by Bock (who unfortunately brought little clarity).

There are also clear stratigraphic differences between the floras. In the Chinle Fm. there occur two distinctive floral zones: a much more diverse (Carnian) and better preserved flora in the lower 'bentonitic lithogenic sequence' (lower part of Chinle and equivalents); and the far less diverse (Norian), poorly preserved flora in the upper 'red bed lithogenic sequence' (upper part of Chinle and equivalents). This latter flora includes only five identifiable species (in 5 genera), *Neocalamites* sp., the three conifers *Pelourdea poloensis* (tf 2), *Brachyphyllum* sp. and *Araucarioxylon* sp., and the enigmatic *Sanmiguelia lewesii* (tf 3).

Western floras: Paleolatitude *ca* 4–10°N, Chinle Fm. & coeval strata.
Total diversity: 72 spp (49 gen.).
Non-gymnosperms: 18 spp (16 gen.).
Gymnosperms: 54 spp (33 gen.).
Localities: 45 TCs.

Eastern floras: Paleolatitude *ca* 3°S–15°N, Newark Supergroup.
Diversity: Estimated 70 spp (54 gen.).
Localities: 23 TCs.

Total Late Triassic floras (USA)
Diversity: Estimated 107 spp (76 gen.).
Localities: 68 TCs.

The combined diversity reflected here is based on a rough estimate that there is a *ca* 50% overlap of taxa (generic and specific) between the western and eastern floras. This requires clarification.

Contributor: Sidney Ash.

Western floras (Chinle & coeval strata)

Environment: Primarily a floodplain.
Biodiversity: 72 spp, 49 gen.

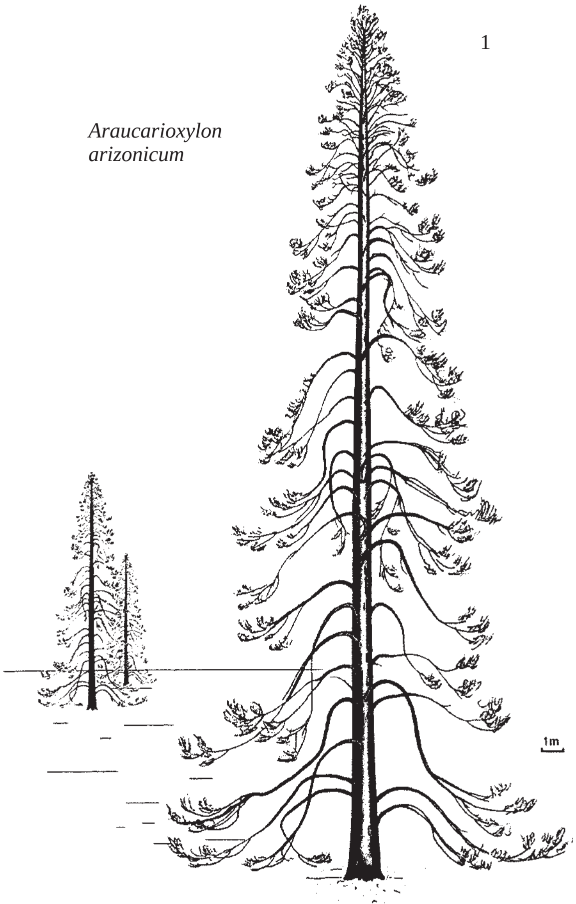
Pteridophytes (18 spp, 16 gen.).
Bryophyta: Nil.
Lycophyta: *Selaginella* (1 sp., rare), *Chinlea* (1 sp., rare).
Sphenophyta: *Equisetites* (1 sp., common)/*Equicalastrobus* (1 sp., common), *Neocalamites* (1 sp., common), *Schizoneura* (1 sp., rare).
Filicophyta: *Cameronoptris* (1 sp., rare), *Cladophlebis* (3 spp, common), *Clathropteris* (1 sp., common), *Coniopteris* 1 sp., rare), *Cynepteris* (1 sp., rare), *Hopetedia* (1 sp., rare), *Itopsidema* (1 sp., rare), *Phlebopteris* (1 sp., common), *Sphenopteris* (1 sp., rare), *Todites* (1 sp., common), *Wingatea* (1 sp., common).

Gymnosperms (54 spp, 33 gen.)
Pinopsida (30 spp, 11 gen.).
  Voltziales: Nil.
  Pinales: *Araucarioxylon* (1 sp., dominant throughout western Triassic)/ *Araucariorhiza* (1 sp., rare), *Araucarites* (1 sp., rare), *Pagiophyllum* 15 spp, rare)/*Masculostrobus* (1 sp., rare)/ *Alostrobus* (1 sp., rare), *Creberstrobus* (1 sp., rare), *Brachyphyllum* (2 spp, rare), *Pelourdea* (1 sp., common), *Pityoidolepis* (1 sp., rare), *Podozamites* (1 sp., rare), *Protocupressinoxylon* (1 sp., rare), *Samaropsis* (5 spp, rare), *Woodworthia* (1 sp., rare).
Cycadopsida (8 spp, 8 gen.).
  Cycadales: *Macrotaeniopteris, Aricycas, Charmorgia, Cycadospadix, Lyssoxylon, Palaeocycas, Nilssonia, Pseudoctenis* (1 sp. each, rare).
Ginkgoopsida (2 spp, 2 gen.).
  Ginkgoales: *Sphenobaiera, Czekanowskia* (1 sp. each, rare).
Bennettitopsida (6 spp, 5 gen.).
  Bennettitales: *Zamites* (2 spp, 1 dominant)/*Williamsonia* (2 spp, rare), *Eoginkgoites* (1 sp., common), *Nilssoniopteris* (1 sp., common), *Otozamites* (1 sp., rare), *Pterophyllum* (1 sp., rare).
Gnetopsida (4 spp, 3 gen.).
  Dinophytonales: *Dinophyton* (2 spp, 1 dominant throughout western Triassic, all organs known, except pollen).
  Dechellyiales: *Dechellyia* (1 sp., dominant at one locality, otherwise rare)/*Masculostrobus* (1 sp., common at 1 locality).
Incertae (4 spp, 4 gen.).
  Pramelreuthia (2 spp, common), *Chibinia* (1 sp., rare), *Sanmiguelia* (1 sp., common)/*Archaestrobilus* (1 sp., rare)/ *Axelrodia* (1 sp., rare)/*Nemececkigone* (1 sp., rare)/ *Synangispadixis* (1 sp., rare), *Creberstrobus* (1 sp., rare), *Schilderia* (1 sp., common).

Affiliations: Very few links (marked by an oblique stroke) between organs have been established; it is quite uncertain, for instance, which foliage affiliates with *Araucarioxylon*, or with the *Samaropsis* seeds.

Diversity: The richness of *Pagiophyllum* (15 spp) and *Samaropsis* (5 spp) appears sound.

Undescribed/unnamed taxa: Several oddities remain to be described.

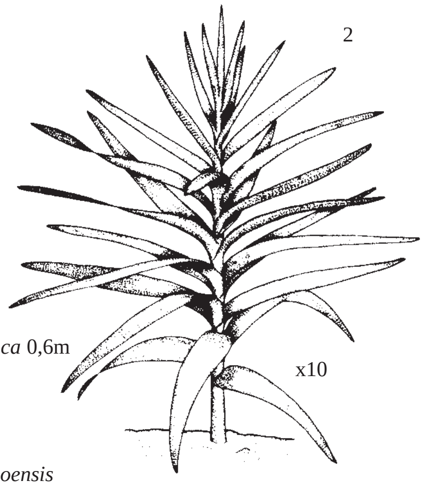


Petrified Forest
National Park (PFNP)
Chinle Fm.
from Ash & Creber 2000

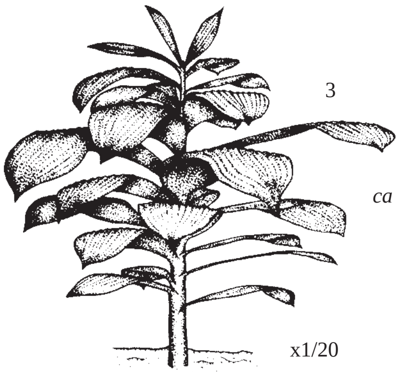
Western faunas (Chinle Fm. & coeval strata)

Compiled by: Sid Ash & William Parker, palaeontologist at PFNP.
Fish remains (bones): 11 spp, 11 gen., rare, diverse.
Fish scales & eggs: Rare, not diverse (unnamed).
Amphibians: 4 spp, 4 gen., dominant, not diverse.
Reptiles: 64 spp, 64 gen., common to dominant, diverse.
Insects (body fossils): Rare, diverse (none described).
Insect-damaged leaves: Rare, diverse (not named).
Insect-damaged wood: Common, diverse (5 spp, 4 gen., many still unnamed).
Clams: 13 spp, 2 gen., common, diverse.
Crayfish: 1 sp., 1 gen., rare, not diverse.
Horseshoe crab: 1 sp., 1 gen., rare, diverse.

Reconstructions from the Late Triassic (Norian) red bed flora of the Colorado Plateau. Ash (1987) referred to this distinctive flora (with 5 species) as the Zone of *Sanmiguelia*.



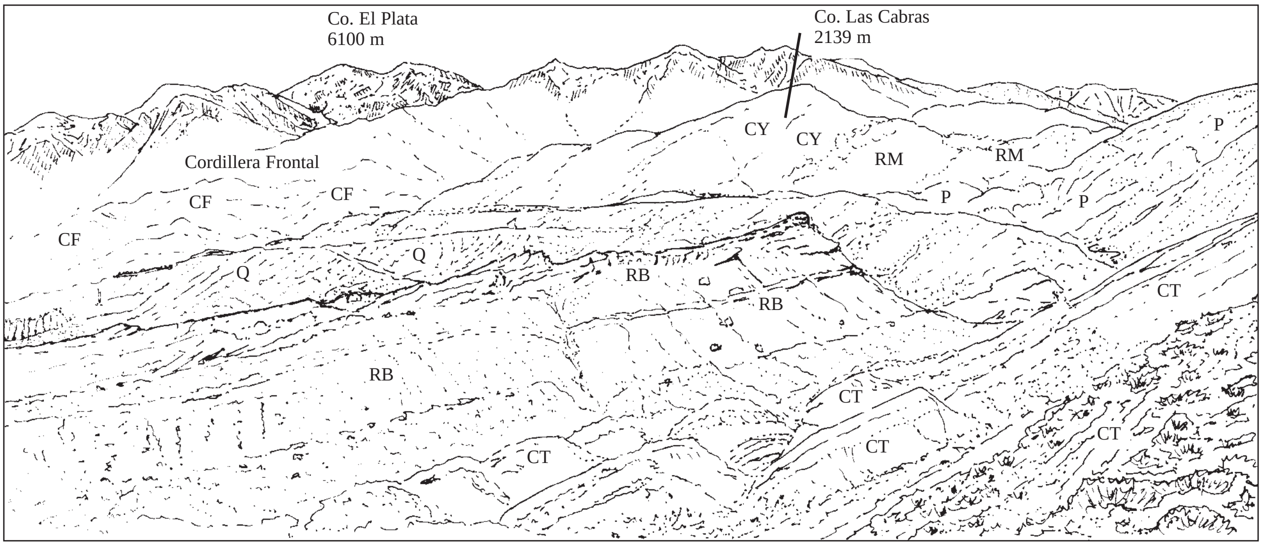
Coniferophyta
Pelourdea poleoensis
Big Indian Wash, SE Utah
Upper Chinle Fm. (Siltstone Member)



Sanmiguelia lewisii
Placerville, SW Colorado
Dolores Fm. (Middle Member)

1,2 from Ash 1987
(2 after Tidwell)

TRIASSIC (Middle–Late)
Argentina, Mendoza



Potrerillos, Mendoza, NW Argentina.
Rio Mendoza to Rio Blanco Fms, Anisian–Carnian, *ca* 245–217 Ma.
Gymnosperm history: Up through the explosive Triassic Radiation.

Sketch by HMA (March 2005), after photo by Ana Maria Zavattieri & Daniel Rosales in Stipanicic & Marsicano (2002).

Cacheuta Basin

QUAT.		Quaternary sediments (Q)		
				angular disconformity
TRIASSIC	? Carnian Carnian Carnian	Rio Blanco Fm. (RB) Cacheuta Fm. (CT) Potrerillos Fm. (P)	Uspallata Gp.	
				angular disconformity
	Anis/Ladin Anisian	Cerro de Las Cabras Fm. * Rio Mendoza Fm. (RM)		
				disconformity
CARB.		Choiyo Gp. (CY) Carboniferous beds (CF)		

* missing in this particular section

Cacheuta Basin

Sampling: Variable from *ca* 10 localities (?assemblages).

Preservation: Fair to good (no cuticular work published).

Publications: Some 30 papers, from Geinitz (1876), have included descriptive accounts or comment on this important megaplant sequence. A recent synthesis is, however, urgently necessary. The situation regarding the localities, assemblages and associations is particularly unclear.

Lithology: The lithology, thicknesses and positions of plant horizons recorded below refer to the type section at Potrerillos village.

Associations: It is not possible to extract a synthesis on associations, but it is clear that various *Dicroidium* taxa form a common component of the floras.

Cacheuta Fm.

Lithology: Argillaceous; claystones, siltstones, carbonaceous shale (150 m); intercalations of fine to medium sandstones & tuffaceous beds. Plants in lower section.

Diversity: *ca* 10 spp described or recorded.

Potrerillos Fm.

Lithology: Greenish grey, fine to conglomeratic quartzose tuffaceous sandstones; intercalations of grey & white tuff (430 m). Plants in thin bituminous shales & carbonaceous siltstones.

Diversity: *ca* 40 spp described or recorded.

Las Cabras Fm.

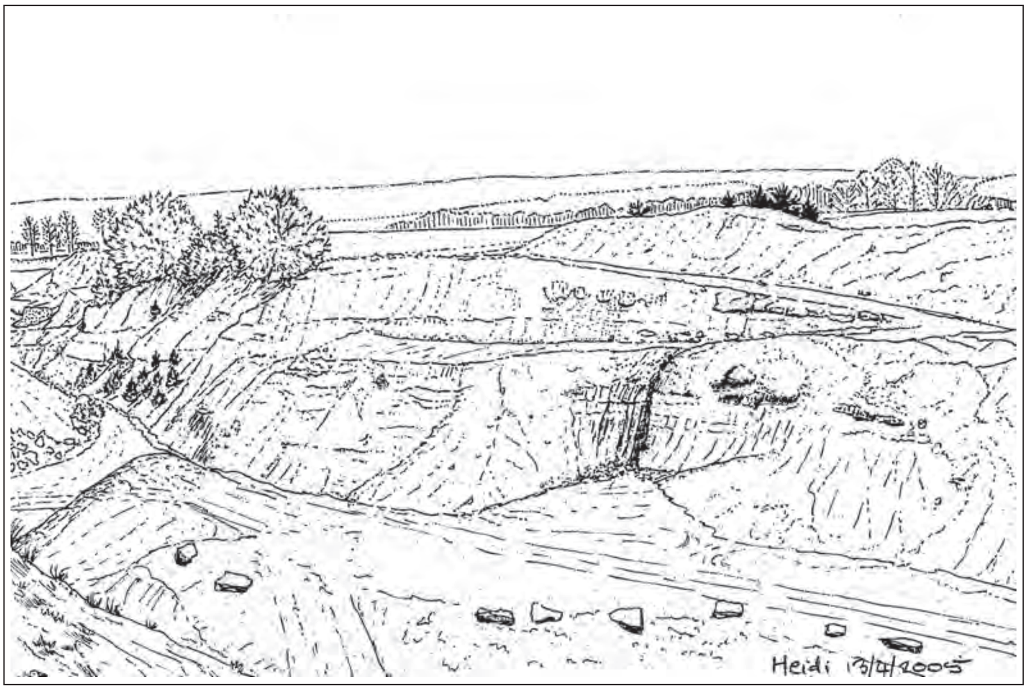
Lithology: Conglomerates, sandstones, siltstones, abundant tuffaceous intercalations (550 m); greenish grey below becoming red in upper part. Plants in subbituminous intercalations in upper part.

Diversity: *ca* 20 spp described or recorded.

Reference: Adapted from And. & And. (1985) (no update attempted).

Contributors: John Anderson & Heidi Anderson.

JURASSIC (Early, *ca* 199 Ma)
Germany, Franken



Pechgraben, near Bayreuth, Franken, Germany.
Lias a, early Liassic, Hettangian, *ca* 199 Ma.
Gymnosperm history: In the wake of the Tr/J Extinction.

Sketch by HMA (13 April 2005), after photo by Stefan Schmeissner (25 March 2005).

Pechgraben (Kufner quarry), a small village in the hills *ca* 12 km NE of Bayreuth, Germany.

Historical: Palaeobotanical collecting began in the Lias 'a' beds of the Bayreuth region around 1840 and has since been intermittent. Early collectors include Graf von Muenster (*ca* 1840), A. Schenk (1850s), Gruembel (*ca* 1890) and Gothan (*ca* 1900–1920). After World War II the group from Munich, Proff. Jung, Weber and Kirchner, worked there. Since 1990, mainly amateurs, Hauptmann, Schmeissner (who found the Pechgraben locality), Deutz and others, have been active.

Geographical: The Lias 'a' plant localities of the region extend *ca* 90 km north to south and *ca* 50 km west to east.

Localities: These are almost always quarries mined for sandstone (with the fossils usually occurring in clay lenses), and they disappear with time. At least 30 such localities have been collected since *ca* 1840. The old 19th century pits are not well described and none exist any more. At present some 10 quarries are visited several times a year.

Environment: Freshwater assemblages, deposited mainly in small ponds (clay lenses), near major streams (sandstones) and probably near shore (transgressions)—a broad delta plain, terrestrial with occasional marine influence (flooding).

Han van Konijnenburg-Van Cittert: Longer term, Han has focused her research on the fossil floras of Mesozoic strata in various areas across Europe (Yorkshire, Germany, Italy), mainly on ferns and gymnosperms. She currently teaches as a part-time professor at Leiden University, Holland, with a general interest in pre-Quaternary palaeobotany, and is also employed one day a week at the National History Museum (Leiden), where her research is on the Early Permian flora of Jambi, Indonesia, and the Late Cretaceous flora from the type area of the Maastrichtian in the south of Holland. She is, moreover, a guest scientist at the Laboratory of Palaeobotany and Palynology, University of Utrecht, where her research field ranges from the Permian/Triassic boundary to the Early Cretaceous.

Biodiversity

No comprehensive survey exists of the overall fossil flora of the Lias 'a' of the region but the diversity is estimated at *ca* 55 species (40 genera). The Pechgraben Kufner quarry in particular has yielded *ca* 45 species (35 genera). Around 50–60% of the taxa, both regionally and locally, would be gymnosperms.

Flora (Lias 'a')
Non-gymnosperms: Lycophytes (*Annalepis*) extremely rare; horsetails rare; ferns common.
Gymnosperms: Conifers common; ginkgophytes common; seed ferns (e.g. *Sagenopteris* and *Pachypteris*, with fructifications); cycads, Bennettitales and Gnetales neither common nor rare.
Bernettiaceae affiliations: *Bernettia* ovulate organ, *Piroconites* pollen organ, *Chlamydolepis* bract, *Desmiophyllum* foliage—in most localities in Bavaria where the family has been found, these four affiliated taxa occur in the same taphocoenosis.
Palynoassemblages: With diverse pollen (conifers dominate) and spores; some brackish algae and shallow marine phytoplankton during the transgressions.

Fauna (Lias 'a')
Insects many and diverse (both larger and smaller species), including dragonfly wings and dragonfly eggs on leaves.

Mr Stefan Schmeissner, after whom the Ginkgoalean genus *Schmeissneria* and the family Schmeissneriaceae (p. 177) are named, is a teacher in the town of Kulmbach not far from Bayreuth. The biodiversity estimates for the Pechgraben quarry in particular and for the Bayreuth region in general (see above) are his, as is the photo—taken specially—from which Heidi drew the pen sketch.

Contributors: Han van Konijnenburg-Van Cittert & Stefan Schmeissner.

JURASSIC (Middle, *ca* 174 Ma)
China, Henan Province

North Opencast Mine, City of Yima, Henan, China.
Yima Fm., Middle Jurassic (?Aalenian, *ca* 174 Ma).
Gymnosperm history: Maturity between Tr heyday and rise of angiosperms.

Sketch by HMA (April 2005), after photo by Zhou Zhiyan (1994).

North Opencast Mine (Yima Mine Company)

Yima City, *ca* 55 km west of Luoyang (a famous old city), W Henan Province, China.

Historical: Zhang Bole and members of his family who were working at Yima have collected numerous well-preserved specimens since the early 1980s. Many palaeobotanists have collected in the mine and a considerable number of works on the fossil plants have been published.

Significance: Plans are in progress to keep the Opencast Mine as a Permanent Geosite by the Ministry of National Land and Resources of China. A museum will be constructed to protect the whole Opencast Mine with all the mining machines and the railways, besides the outcrops of rock and coal seams. There will be a special exhibition with a large glass case to preserve the *Ginkgo*-bearing bed in the mine.

Gymnosperms: 39 spp (>23 gen.)
Ginkgoales (most dominant): >10 spp (>7 gen.).
  Ginkgoaceae (*Ginkgo/Ginkgoites* several spp).
  Yimaiaceae (*Yimaia/Baiera* 1 sp.).
  Karkeniaceae (*Karkenia/Sphenobaiera* 1 sp.).
  Umaltolepidaceae (*Umaltolepis/Pseudotorellia* 1 sp.).
  Possible Ginkgoales *(Leptotoma, Rhaphidopteris* 3 spp).
Czekanowskiales (2nd most dominant order): 7 or 8 spp (6 gen.).
  Phoenicopsis, Czekanowskia, Arctobaiera, *Tianshia,*
  Leptostrobus, Vittifoliolum, Ixostrobus (all 1 sp.).
Conifers common: 7 spp (6 gen.).
  Taxodiaceae (*Sewardiodendron* 1 sp.).
  Family(s)? (*Lindleycladus* 1 sp. common, is *Podozamites*-like).
  Taxaceae? (*Storgaardia* 1 sp., *Elatocladus* 1 sp.).
  Pinaceae? (*Schizolepis* 1 or 2 spp, *Pityospermum* 1 sp.).
Nilssoniales common (*Nilssonia* 1 sp.).
Bennettitales sparse (*Nilssoniopteris* 1 sp.).
Caytoniales sparse (*Sagenopteris* 1 sp.).
Incertae (*Tharrisia* 1 sp., foliage ?10 spp, fructifications several spp).

Yima Fm.

Localities: The Yima coalfield is about 28 × 5 km in extent. Collecting has been confined to the mining area: nearly all the fossils have come from the North Opencast Mine, only a few from two other coal pits of the coalfield, and none from the scattered outcrops of the formation. Only the lower part of the Yima Fm. is well exposed in the North Opencast Mine. Collecting is done mostly from waste rock.

Environment: The Yima Fm. represents roughly two cycles of sedimentation from river deposits at the base, to delta-marsh, to lake deposits above.

Fauna
Bed 7 (at the very base): Bivalves (*Unio, Margaritifera*), fish scales.
Bed 1 (black mudstone of lake deposits): Insect wings, fish scales and faeces, bivalves, gastropods.

Biodiversity (megaplants)

Total flora, all sites, all horizons: *ca* 70 spp (>34 gen.).
Non-gymnosperms (North Opencast Mine): >12 spp (7 gen.).
  Bryophyta (liverworts, mosses): 2 or 3 spp (1 gen.).
  Lycophyta (lycopods): Nil.
  Sphenophyta (horsetails): 3 or 4 spp (2 gen.).
  Filicophyta (ferns): >6 spp (4 gen.).
Gymnosperms (North Opencast Mine): 39 spp (>23 gen.).

References
Zeng *et al*. (1995), Zhou & Zhang (1995, 1998, 2000).

Contributor (pp 240, 241): Zhou Zhiyan.

Zhou Zhiyan: Now 73 years, and continuing his research full time, Zhou has worked at the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, since 1954. With 19 palaeobotanists (not counting palynologists), some elderly and attending only part time, the institute must rank as the most numerate in our field anywhere.

Zhou's main research interests are Mesozoic gymnosperms, especially Ginkgoales, and mostly from Laurasia. On the personal front, he participates in Taijijuan (Taiji meaning the supreme ultimate in Chinese), a system of physical exercise for attaining bodily or mental control and well-being, as well as for self-defence.

Mr Zhang Bole (Zhou's collaborator): Together with his parents, Zhang discovered both *Ginkgo yimaensis* and *Yimaia hallei*. He was a geologist in a coal geology team at Yima, and is now in Qingdao as a 'geotechnical' engineer.

North Opencast Mine: Beds as marked on sketch opposite.

Bed 1: *Nilssoniopteris.*
Bed 2: Coal (3–4 m thick).
Bed 3: *Ginkgo* bed: *G. yimaensis, Sewardiodendron, Cupressoxylon*:
Some 50 specimens of *G. yimaensis* initially described and 'quite a number of ovulate organs collected subsequently by other persons including some foreign palaeobotanists; only leaves are found attached to short-shoots, never ovulate organs; there is no sign of the pollen organ'.
Bed 4: Coal (*ca* 1 m thick).
Beds 5 & 6: Includes all taxa listed opposite except those found in Beds 1 & 3.
A total of 54 specimens of *Yimaia hallei* were recorded in 1992 (very few discovered since); it occurs abundantly in Bed 5, sporadically in the upper part of Bed 6; though leaves of *Baiera hallei* are common in both beds, none are found connected with ovulate organs; good specimens of putative male organs of *Yimaia*, with *in situ* 'boat-shaped' pollen, are still to be studied.
Bed 7: White sandstone with a thin dark shale at its base; only *Czekanowskia* and *Pseudotorellia* found in the dark shale and *Coniopteris* in the basal part of the sandstone.
Bed 8: Coal seam up to 28 m thick.

Zhou's 50 years in Chinese palaeobotany

My question to Zhou was how the Mao Tse-tung era from the founding of the People's Republic of China in 1949, to the Cultural Revolution instigated in 1966 and the Chairman's death in 1976, affected or moulded his life as a palaeobotanist? Zhou responded as follows:

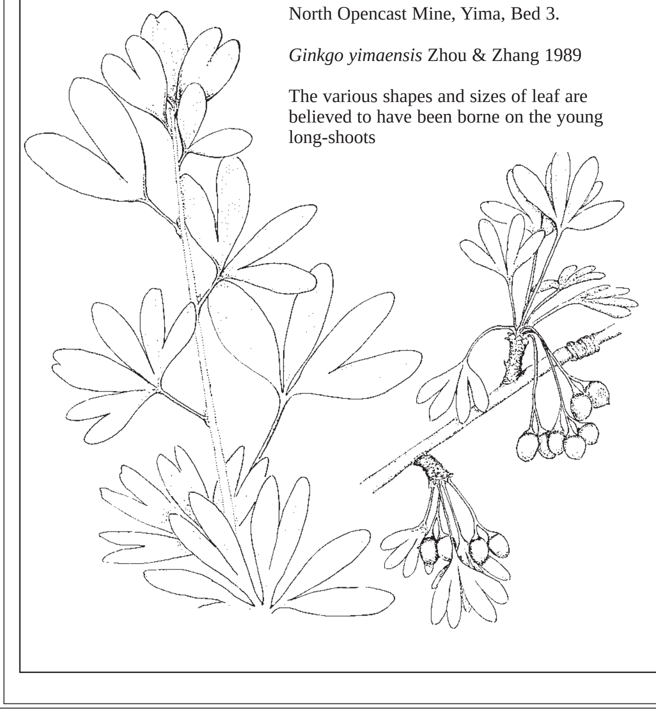
'My career in palaeobotany started in 1954 when I graduated from the Nanjing University and was fortuitously recruited to the newly established Institute of Palaeontology, Academia Sinica, which was set up with a few palaeontologists from different geological institutions. I worked as an assistant in the palaeontology and palynology research group lead by **H.C. Sze**. He had a Europe-oriented background, having studied in Berlin for a doctorate under the supervision of **W. Gothan** and also worked shortly with **T.G. Halle** in Stockholm. At that time, China was not open to the world. Although we had a fine library and quite a number of new issues of professional periodicals, there were few academic and personal exchanges with colleagues and specialists from western countries.

'Palaeontologists were working chiefly on biostratigraphy, serving the needs of geological exploration and regional surveying towards economic reconstruction. Few works were done on the morphology, anatomy, taxonomy, ecology and biology of fossil plants using new methods and techniques. Sometimes, palaeobotanists were even appointed as leaders in charge of geological prospecting parties for coal and other mineral resources. In the late sixties, I also joined the coal exploration surveying parties in Jiangxi, Hunan and Guangdong Provinces to determine the geological age and correlation of the Mesozoic coal-bearing strata using my palaeobotanical knowledge.

'In 1980, Academia Sinica sent me to England to study with **Tom Harris** and **Bill Chaloner** for two years. Not only did I learn modern methods and techniques from them, but also new insights into the fossil material. Under their influence, I started to work on the detailed structure and anatomy of fossil plants, and aimed at gaining biological and ecological information from them.

'It is evident that there are no national boundaries in the natural sciences. Collaboration between scientists from different countries and areas is indispensable and urgently needed, particularly when topics of a global scale are dealt with as in the biological and earth sciences. As members in such collaborations, we inevitably learn from one another, especially advanced thoughts and methods in scientific pursuits, as well as the sharing of information and achievements.

'Scientific achievements belong to and should bring benefit to the whole of mankind.'

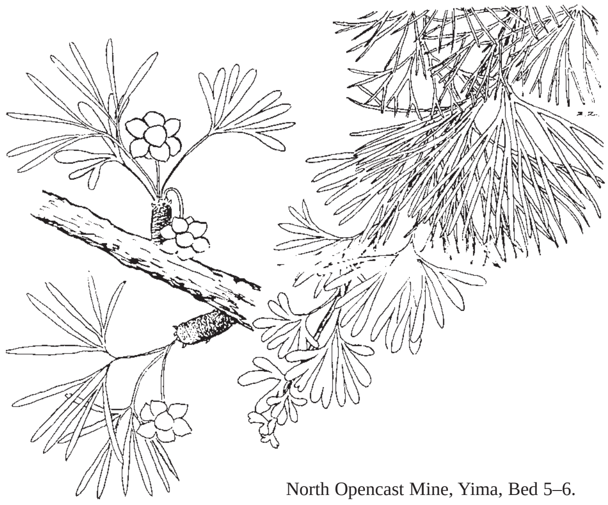


North Opencast Mine, Yima, Bed 3.

Ginkgo yimaensis Zhou & Zhang 1989

The various shapes and sizes of leaf are believed to have been borne on the young long-shoots

from Zhou & Zhang 1992



North Opencast Mine, Yima, Bed 5–6.

"foliage leaves of various shapes and sizes, reconstructed as we believe they may have been borne on a newly sprung long shoot."

Yimaia hallei (Sze) Zhou & Zhang 1992

JURASSIC (Middle, *ca* 164 Ma)
England, Yorkshire

Cayton Bay, Yorkshire, England.
Claughton Fm., Ravenscar Gp., Callovian, *ca* 164 Ma.
Gymnosperm history: Jurassic maturity before the rise of angiosperms.

Sketch by HMA (25 May 2005), after photo by Chris Cleal (1994).

Cayton Bay: Lies on the Yorkshire coast 5 km SE of Scarborough; the fossil plant exposures are in the foreshore.
Gristhorpe Member (Bed), Claughton Fm., Ravenscar Gp.

Historical: Most significant contributions by A.C. Seward and H.H. Thomas (late 19th and early 20th centuries) and T.H. Harris (mid-20th century).

Significance: The site has yielded the most diverse gymnosperm assemblage from the classic Middle Jurassic flora of Yorkshire. It gives its name to *Caytonia* and the Caytoniaceae, contender as sister to the angiosperms. It is a Site of Special Scientific Interest and a proposed World Geosite.

Gymnosperms: Most evident are
Caytoniaceae (*Caytonia/Caytonanthus/Sagenopteris*).
Cycadales (*Androstrobus/Beania/Nilssonia, Pseudoctenis, Stenopteris*).
Williamsoniaceae (*Williamsonia/Weltrichia/Ptilophyllum*).
Williamsoniellaceae (*Williamsoniella/Nilssoniopteris*).
Cycadeoidaceae (*Conites/Zamites*).
Ginkgoaceae (*Ginkgo/Eretmophyllum*).
Leptostrobaceae (*Leptostrobus/Czekanowskia*).
Cheirolepidiaceae (*Brachyphyllum, Pagiophyllum*).
Araucariaceae (*Araucaria*).
Taxodiaceae (*Elatides*).

Abundance
Nilssoniopteris, Nilssonia, Ptilophyllum & *Elatides* abundant;
Caytonia, Ginkgo, Eretmophyllum, Czekanowskia & *Brachyphllum* common; all other genera rare.

References
Van Konijnenburg-Van Cittert & Morgans (1999), Cleal *et al*. (2001).

Yorkshire Jurassic

Localities: 12 ‘sites’ are well known; these include 97 TCs, based on Tom Harris’s manuscript notebooks, as listed in Cleal *et al.* (2001); most sites occur along a 25-km length of the Yorkshire coast, though some are inland up to 45 km due east; total extent of deposit *ca* 1 200 sq km, the vast majority of which is covered by superficial deposits.

Environment: Cayton Bay was a vegetated delta plain, as were most of the other Yorkshire sites: northern mid-latitudes (35–40ºN).

Age: Middle Jurassic (Bajocian to Bathonian).

Biodiversity

Cayton Bay: 81 spp (38 gen.)
Non-gymnosperms: 27 spp (17 gen.).
    Bryophyta (liverworts, mosses): 3 spp (1 gen.).
    Filicophyta (ferns): 21 spp (14 gen.).
    Lycophyta (lycopods): 1 sp. (1 gen.).
    Sphenophyta (horsetails): 2 spp (1 gen.).
Gymnosperms: 54 spp (21 gen.).

Yorkshire Jurassic (all localities): 169 spp (59 gen.)
(includes L, M & U Deltaic, Bajocian & Bathonian)
Non-gymnosperms: 52 spp (24 gen.).
    Bryophyta (liverworts, mosses): 4 spp (1 gen.).
    Filicophyta (ferns): 39 spp (19 gen.).
    Lycophyta (lycopods): 1 sp. (1 gen.).
    Sphenophyta (horsetails): 8 spp (3 gen.).
Gymnosperms: 117 spp (35 gen.).

Taxonomy: The diversity figures represent ‘natural’ species and genera as far as that is reasonably possible.

Contributor: Chris Cleal.

CORRELATION CHARTS (Charts 11–20, pp 46–55)
Contributors to the Gondwana continents

Scaffolding

The stratigraphic framework from the Silurian to the present underscores this plant history. Our story of the gymnosperms is told at the resolution of the geological stage—*ca* 5 million-year time slices—and in the set of 10 correlation charts; the megaplant-bearing formations are placed largely at this resolution. For these charts to be current and reliable, colleagues with a close knowledge of the horizons in their regions have been approached to contribute. Particularly for the Gondwana continents, with more dispersed and less accessible literature, this has been vital. We are greatly indebted to the following colleagues for their willing participation.

South America

Roberto Iannuzzi: Palaeobotanist at Universidade Federal do Rio Grande do Sul (UFRGS), Porto Alegre, SE Brazil. He is currently working on the Permian glossopterid floras of the Parana Basin, and with Conrad Labandeira (p. 228), on plant-insect interactions encountered in the region. With Tánia Dutra and others, he organised the *X1 Reuniáo de Paleobotânicos and Palinólogos* (Nov. 2004) held at Gramado up on the superb *Araucaria*-forested, Basaltic (Early Cretaceous) Plateau north of Porto Alegre.

Oscar Rösler: Founder of the Cenpaleo Museum, Mafra, Santa Catarina Province, SE Brazil. He has been a leading figure in the study of Brazilian Palaeozoic floras since the 1960s and is currently initiating the drive to establish a Gondwana Alive Corridor—'The Parana-Pantanal Corridor'—from the richly diverse rainforest of the Atlantic Forest Region to the unique lowland Pantanal matogrossense at the very centre of South America.

Ruben Cuneo: Director of the Museo Egidio Feruglio, Trelew, Chubut, Argentina. He completed a post-doc in the USA under Tom Taylor and is currently working on the Permian and Triassic megafloras of southern South America. He was the organising chairperson of the 7th Organisation of Palaeobotany (IOP) meeting in Chubut, Argentina (2007), and with M.A. Gandolfo of the symposium on 'Southern Hemisphere Paleofloras and their relationships with mass extinction events' (though in the end he could not attend) at the XV11 International Botanical Congress, Vienna (IBC, 17–23 July 2005).

Africa

Thomas Schlüter: Programme Specialist in Earth Sciences, UNESCO, Nairobi Office, Kenya. He is effectively the UNESCO geologist for Africa and has a particular interest in geosites and geoheritage, and also in paleoentomology. He recently (2004) published a book on the geology of Africa, following a standard layout for each country.

Hans-Jochen Gregor: Around the middle of 2002, Hans-Jochen had a 'strange lucky day': 'I was on the way … looking for gravel, plants and bones, as I did many times working as a geologist in the Bavarian molasses. Two brownish bands looked out of the gravel, giving a sign that two tusks were nearly falling out of the wall of a sand pit.' By 20 December 2004, the first nearly complete fossil elephant (*Archaeobelodon* cf. *filholi*) yet to be found in Germany was ready to move to its new home in the Naturemuseum, Augsburg. Old 'Backlegs' (as dubbed in our correspondence) had tusks like shovels, rather than rounded in section, and consisted of most of the skull, the mandible and 50% of the skeleton, but had lost his forelegs. As a palaeobotanist with a focus on Laurasian Tertiary floras, this was indeed a special find.

India

Suresh Bonde: Research scientist at the Agharkar Research Institute, Pune, India. He has worked on the palaeo-biodiversity of the Deccan Intertrappean beds of India for the last 30 years. His focus is on fossil angiosperms, especially palms and other monocotyledons. He attended the XV11 IBC, Vienna, July 2005, with Rakesh Mehrotra (below), where together they updated our Maastrichtian to Pleistocene correlations for India.

Rakesh Chandra Mehrotra: Research scientist for the past 25 years at the Birbal Sahni Institute of Palaeobotany, Lucknow, India, who has published more than 50 research papers on the Tertiary megafloras of India. He presented a talk at the XV11 IBC meeting in Vienna (see above) on the floras of the subcontinent as preserved across the K/T boundary.

Australasia

Stephen Mcloughlin: Completed his Ph.D. (1990) on Permian floras of the Bowen Basin, eastern Australia and has published over 50 papers on southern hemisphere fossil floras of Devonian to Neogene age, particularly focusing on Late Permian and Early Cretaceous floras of Australia and Antarctica. He has also worked on the biogeography of extant austral plants including *Nothofagus* and *Wollemia*. Since 2003 he has been a lecturer in sedimentology at the School of Natural Research Sciences, Queensland University of Technology, Brisbane.

John Rigby: Has a record of palaeobotanical research extending back to 1961 and has published around 100 articles, with a primary research focus on the systematics of macrofossils from the Gondwana Permian *Glossopteris* flora. He was employed for over two decades to undertake palynological and palaeobotanical research in the Geological Survey of Queensland. Since official retirement he continues to do active research on Permian floras in the School of Natural Sciences, Queensland University of Technology.

Mike Pole: Over the past 20 years has moved from the Dept of Geology, University of Otago, to Plant Sciences, University of Tasmania, to the Botany Dept, University of Queensland, and currently lectures (exclusively to American students) at the Centre for Marine Studies at this university. His interests are primarily in the prehistory of New Zealand, and the ecology of the higher taxonomic groups of plants. 'I make a point of seeing real vegetation, with my latest trip taking in the coniferous rainforests of the Olympic Peninsula, Washington, and the Cedars of Lebanon.'

Antarctica

David Cantrill: Of all palaeobotanists, it appears true to say that David has spent the greatest accumulated time in Antarctica: two years spread over seven expeditions. This has included an unusually wide spread of destinations, taking in the Prince Charles Mountains, Alexander Island, South Shetland Islands, the James Ross-Seymour Island region and the Beardmore Glacier in the Transantarctic Mountains. These trips were completed largely during his 10 years (1992–2002) with the British Antarctic Survey (BAS) in Cambridge. His major research thrust in the continent has been on Cretaceous fossil floras, and his general interest in the role that Antarctica played in the development of the southern hemisphere vegetation.

David was born (1962), raised and educated in Melbourne, Australia, moved to Cambridge, England, in 1992 and has been at the Swedish Museum of Natural History (Naturhistoriska riksmuseet), Stockholm, as a Senior Research Scientist, palaeobotany, since 2002.

John Isbell: A sedimentologist and stratigrapher at the University of Wisconsin-Milwaukee. He has worked extensively on Palaeozoic and early Mesozoic sequences in the Transantarctic Mountains.

CRETACEOUS (Early, *ca* 130 Ma)
Russia, Lake Baikal area

Valentin Krassilov

1985–1989: Head of Paleobotany Laboratory and Evolutionary Dept, Institute of Biology and Soil Science, Vladivostok.
1989–1993: Director of Nature Conservation Institute, Moscow.
1994–present: Head of Paleobotany Laboratory, Paleontological Institute, Moscow.
2001–present: Professor of Paleobotany and Paleoecology, Institute of Evolution, University of Haifa, Israel.
Research focus: Paleofloristics of Permian/Triassic boundary; Mesozoic and Paleogene of former USSR, Mongolia and the Middle East; morphology and systematics of bryophytes, ferns, gymnosperms, proangiosperms and early angiosperms; Devonian thalloid plants; paleoecology, ecosystem evolution and implications for analysis of human personality, the ***egosystem*** (Krassilov 1995).

Val Krassilov: some taxonomic viewpoints

The 3rd Paleoentomological Congress (7–11 February 2005) was held in Pretoria, South Africa. Val Krassilov was one of a broadly cosmopolitan assembly of around 65 delegates (only three were from South Africa) to attend. And he was one of around 30 delegates to participate in the post-conference tour to the scenic Late Permian to Early Jurassic sections of the Natal Drakensberg region.

Spacious buses on conference excursions often provide the ideal venue for scientific discourse. Through the less compelling grassland plateau (underlain by the Early to Middle Permian of the northern Karoo Basin) on the return trip to Johannesburg, Val paged through the draft of the taxonomic section of the *Brief history*. Some of his viewpoints jotted down concerning our gymnosperm classification, follow. These clearly emphasise the pervasive scope for debate and disagreement at the higher ranks within the gymnosperms (see classification tables ranging from 1954 to 2001, pp 13–17, for a further sharp focus on this continuing truth).

Cordaitanthales: 'Some palaeobotanists in Russia, me included, feel that *Vojnovskya-Gaussia* are fairly different from *Cordaites*, constituting an order Vojnovskyales Neuberg with simple strobili. Therefore Vojnovskyaceae and Rufloriaceae fall into Vojnovskyales.'

Pinales: 'The differences between the Taxaceae and the rest of the conifers may be of the same rank as between the Pinales and Voltziales. Maybe Taxales Florin should be restored?'

Medullosales: 'Do you think that Codonospermaceae and Polylophospermaceae, as emended by you, really deserve familial rank or can they be included in the Medullosaceae?'

Phasmatocycadales: 'I think that *Phasmatocycas-Archaeocycas* has little in common with Cycadales. They probably are related to emplectopterids as a poorly studied group of the latter, the more so that a similar plant (forget the name) was described by Dilcher *et al.* from the emplectopterid assemblage of China.'

Gigantopteridales: 'There is a problem with the Gigantopteridales because both *Gigantonomia* and *Gigantotheca* seem to belong to the Marattiales, ferns in fact. This has to be mentioned. As for *Gigantopteris* foliage, it is often confused with *Gigantonoclea*: both are sometimes found in the same locality and the differences may be preservational. I would suggest the order be marked as doubtful.'

Ginkgoopsida: 'Again, the Ginkgoopsida does not seem natural to me. The orders Peltaspermales, Matatiellales, Leptostrobales, Hamshawviales, Umkomasiales, Caytoniales and Petriellales seem closely related. On the other hand, a large gap divides them from the Ginkgoales, and they seem closer to such cycadopsids as ottokariopsids.'

Acknowledgment: Prof. Krassilov is supported by the Russian Foundation of Basic Research.

Baisa, Lake Baikal area, Upper Vitim Basin, Transbaikalia, Russia.
Zazinskaya Fm., Late Hauterivian-Barremian, *ca* 130 Ma.
Gymnosperm history: Near the peak of their final radiation.

Sketch by HMA (April 2005), after photo by Val Krassilov.

Baisa Brook: Left bank of Vitim River, *ca* 400 km north of Chita City, Lake Baikal area, Transbaikalia, Russia.
Environment: Rich lacustrine fauna; ostracods, aquatic insect larvae, fish; allochthonous remains of land plants and insects.

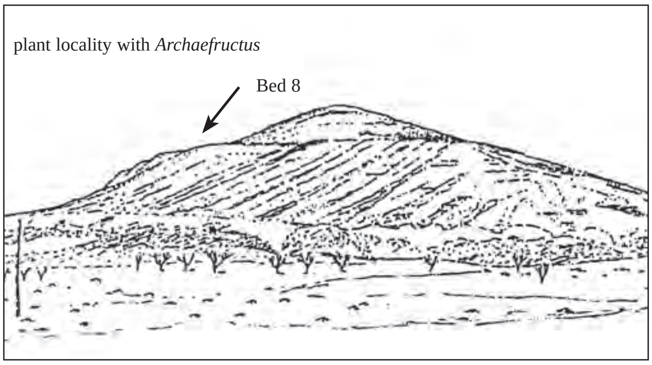
Zazinskaya Fm., a sequence of conglomerates, black shales, sandstone/siltstone/marl cyclothems.
Age: Late Hauterivian-Barremian, based on ostracods (Scablo & Lyamina 1986); Aptian? based on palynology (Vakhrameev & Kotova 1977).

Historical: Fossil plants discovered in the course of paleoentomological collecting headed by V. Zherikhin (Paleontological Institute, Moscow), in the early 1970s, and first described in Vakhrameev & Kotova (1977). Subsequent collecting by Bugdaeva and Krassilov (Institute of Biology and Soil Science, Vladivostok), summarised in Krassilov & Bugdaeva (1999, 2000).

Biodiversity (megaflora): Baisa locality (other localities in the formation are far less important).
Total flora: *ca* 40 spp (30 gen.).
Non-gymnosperms: 2 spp (2 gen.).
Horsetails (1 sp.), ferns (1 sp., rare).
Gymnosperms: 37 spp (27 gen.).
Pinales (17 spp): *Podozamites, Elatides, Pseudolarix*.
Ginkgoales (4 spp), Leptostrobales (3 spp).
Bennettitales (3 spp), *Nilssoniopteris*, *Otozamites*.
Gnetophytic proangiosperms (10 spp), including *Eoantha* (Eoanthales) recorded also from coeval localities in Mongolia and China.
Putative angiosperms: 1 sp. (1 gen.).
Represented by a dubious leaf *Dicotylophyllum,* and by *Clavatipollenites* pollen grains.

Contributor: Val Krassilov.

CRETACEOUS (Early, *ca* 125 Ma)
China, W. Liaoning



East Hill of Huangbanjigou, W Liaoning, NE China.
Jianshangou Bed, Lower Yixian Fm., Barremian-Aptian boundary, *ca* 125 Ma.
Gymnosperm history: In the early phase of the angiosperm radiation.

Sketch by HMA (March 2005), after photo by Sun Ge.

Sun Ge (Jilin University, NE China)
Archaefructus liaoningensis Sun, Dilcher, Zheng & Zhou was described by Sun and his colleagues in *Science* in 1998, and is considered to be the world's earliest flower. The find was acclaimed one of the 'ten Top News on basic research in China in 1998,' and has achieved almost iconic status. In 2001, Sun was invited to establish a new Research Centre of Palaeontology at Jilin University in NE China, prior to which he had been Deputy Director at the Nanjing Institute for five years. Sun was the prime mover of the especially pleasant and opportune International Conference of Diversification and Evolution of Terrestrial Plants in Geological Time (ICTPG), in Nanjing in 1995. He was as superbly attentive to us all in Nanjing and later at his sites in the field (NE China) as he is at ferreting out early angiosperms from the later Mesozoic strata of his home country.

Disputed age of *Archaefructus*
Like much else surrounding *Archaefructus*, its age remains in dispute. Though Sun holds to a Late Jurassic age (e-mail 5 July 2005), established on the basis of the associated fossils in the Yixian Fm., most early-angiosperm researchers (e.g. Dilcher and Pedersen, pers. comm. 2005) accept the Barremian-Aptian boundary date (*ca* 125 Ma) based on absolute dating (Chang *et al*. 2003, Friis *et al*. 2003, Friis *et al*. 2005). We follow this younger date here.

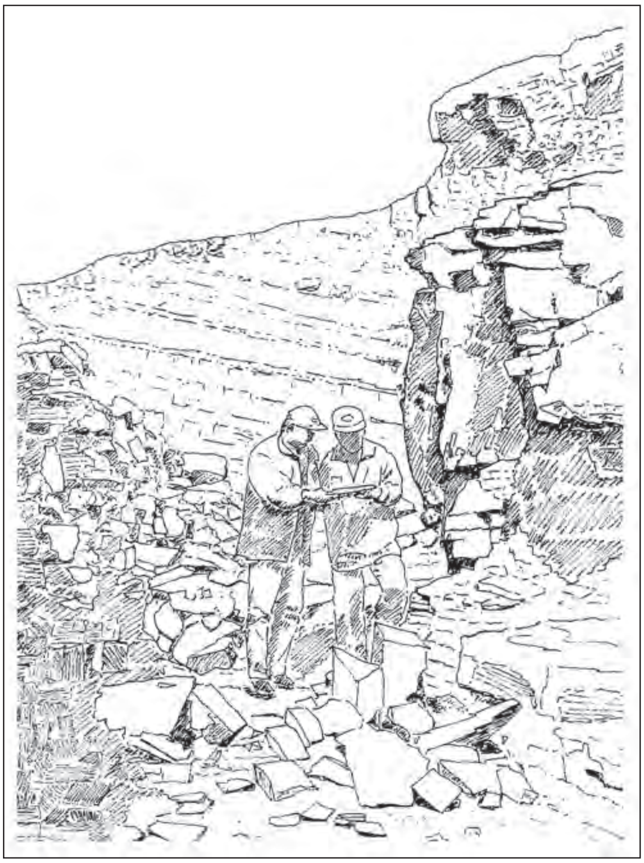
Jianshangou Fm. (W. Liaoning) Biodiversity megaflora)
(Sun *et al*. 2001, pp 165–167)

Total flora: 88 spp (56 gen.).
Non-gymnosperms: 18 spp (13 gen.).
Gymnosperms: 65 spp (41 gen.).
Angiosperms: 5 spp (2 gen.).

Non-gymnosperms: 18 spp (13 gen.).
Bryophyta: 4 spp (3 gen.).
Lycophyta: 1 sp. (1 gen.).
Sphenophyta: 3 spp (1 gen.).
Filicophyta: 10 spp (8 gen.).

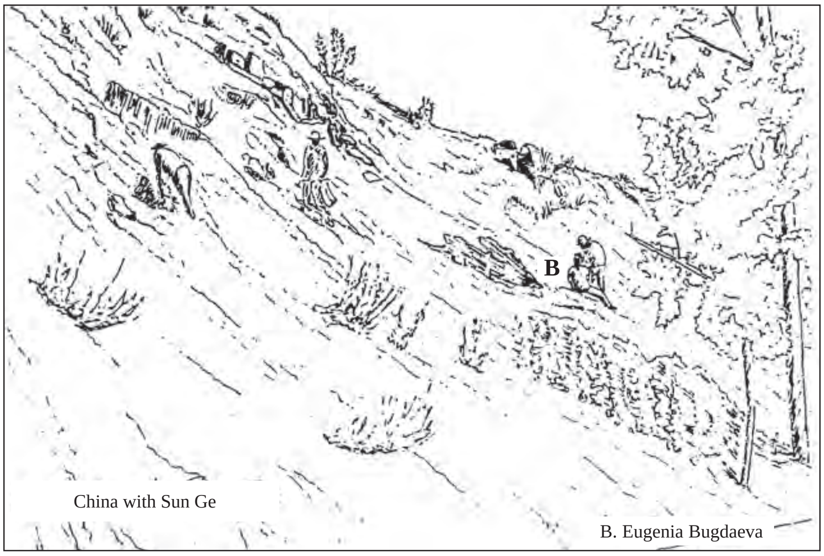
Gymnosperms: 65 spp (41 gen.).
Coniferales: 32 spp (19 gen.); dominant, 36.4%.
Pteridosperms: 1 sp. (1 gen.).
Czekanowskiales: 7 spp (4 gen.); uncommon.
Ginkgoales 4 spp (3 gen.); uncommon.
Bennettitales: 8 spp (7 gen.).
Gnetales: 4 spp (2 gen.); 14.3% (with Bennettitales).
Incertae: 9 spp (5 gen.).

Angiosperms (early): 5 spp (2 gen.); 3.4%.



Sun Ge (right) and Mr Chuntian Li (C.T. Li) collecting from the **Huangbanjigou** locality (see top left) yielding *Archaefructus liaoningensis*, the world's earliest reputed flower.

Sketch by HMA (March 2005), after photo by Wang X.F. (June 1999).



Chengzihe of Jixi City, near Muling R., E Heilongjiang Prov., NE China.
Chengzihe Fm., Late Hauterivian–early Barremian (based on intercalated marine beds with dinoflagelates); the formation yields rare early angiosperms (*ca* 8% of flora; 8 spp in 5 gen. identified) (Sun & Dilcher 2002).

Sketch by HMA (2004), after photo by John Anderson (Sept. 1995).

References: Sun *et al*. (2001), Sun & Dilcher (2002).

Contributor: Sun Ge

ARAUCARIACEAE: PHYTOHISTORY
Contributors to Charts 21–26 (pp 56–61)

Tánia Dutra, Anamaria Stranz, Thiers P. Wilberger & Nelsa Cardosa; Porto Alegre, Brazil.

Paging through the excursion guide following the *XI Reuniáo de paleobotânicos e Palinógos* (RPP), November 2004, I was irresistibly drawn to an article by Tánia Dutra on the global history of the Araucariaceae. Both the presentation and the science of it were fascinating and appealing. We were travelling by bus across the Early Cretaceous Basaltic Plateau inland of Porto Alerge, southern Brazil—a wonderful dissected landscape clothed in the richness of the *Araucaria angustifolia* and Atlantic forests.

Within a few moments I had moved in alongside Tánia Dutra a seat or two further up the bus: ‘I have a proposal, Tánia. It would be splendid to include an updated version of your *Araucaria* chapter in our *Brief history of the gymnosperms*. Your beloved Araucariaceae have surely the best-known history of the 13 extant families of gymnosperm. They will add a great touch to our volume. We could call it *A brief history of the Araucariaceae*.’ She jumped at the suggestion and she, Anamaria, Thiers and Nelsa (the latter three also on the bus and guiding the tour) have put in a mighty effort on it since—right through the 2004/2005 festive season.

Tánia Dutra: D.Sc., Universidade Federal do Rio Grande do Sul (UFRGS), Porto Alegre, RS, Brazil 1997. She has since been Professor in the Postgraduate Program in Geology, Universidade do Vale do Rio dos Sinos (UNISINOS), Sao Leopoldo, RS, Brazil, and also palaeobotanist, devoted to Mesozoic and Tertiary fossil floras (macrofossils) from Brazil and the Antarctic Peninsula, with special interest in the paleogeographic and paleoclimatic events controlling the ancient and modern distribution of floras (phytogeography), mainly those composed of conifers (Araucariaceae and Podocarpaceae) and other gymnosperms.

Thiers P. Wilberger: Biology student, UNISINOS; doing palaeobotany (Mesozoic and Tertiary floras of Brazil and the Antarctic Peninsula) under Tánia Dutra. He has an extraordinary knowledge of the extant flora of the Atlantic Rainforest and its epiphytes, with a particular love for orchids. Another passion is for developing ‘ecological gardens’ (indigenous plants), doing work for the City Council of Macae, Rio de Janeiro.

Anamaria Stranz: Graduate in biological sciences, UNISINOS (2003) and researcher in Laboratory of the History of Life and Earth (LaViGea), UNISINOS (since 2000). Research interests—phytogeography, evolution of gymnosperms, Geographic Information Systems (GIS) and their use in the mapping of forest areas.

Nelsa Cardosa: Graduate in biological sciences, UNISINOS (1999); M.Sc. in management and diversity of forest life, UNISINOS (2002). Currently doing Ph.D. in palaeontology, UFRGS (2003–2007). Research interests—reproductive biology, morphology, taxonomy, cryptogamic and phanerogamic systematics, palaeobotany.

Claudia P. Paz: Undergraduate in biological sciences, UNISINOS, with Fellow scholarship from CNPq (Brazilian Scientific Research Council). Currently working in Laboratory of Restoration Ecology, UNISINOS. Research interests—theoretical and applied ecology, biological conservation, botany, mycology.

Conversations across the Atlantic

Writing books is not all hard labour; and writing books with many contributors from around the world can involve delightfully human moments. Here are a few extracts from six months of e-mails between Tánia Dutra and me (JMA) from November 2004 to May 2005:

Tánia, 16 Nov. 04: ‘We are all with great nostalgia of those good times together. The people are now relax and prepared to the next RPP ...’

JMA, 22 Nov. 04: ‘Abundant thanks from this side of the wide Atlantic. Your Australian/Antarctic English is charming.’

Tánia, 22 Nov. 04: ‘Your letter and the messages make all very happy, thank you very much for so kindly words. … We do not forget our mission with the *Araucaria* … It is a goal for us (besides the honour), so we take it with great responsibility.’

JMA, 29 Nov. 04: ‘And I am calm in the knowledge that you (with your lovely Antarctic English) and Anamaria (drinking her *Ilex* tea) and Thiers (amidst his orchids and bromeliads) are enjoying constructing your 4-page Araucariaceae piece.’

Tánia, 6 Dec. 04: ‘Your plans are what the people and the nature of the world need and since now I am a soldier in the fight of the Gondwana Alive.’

JMA, 7 Dec. 04: ‘I take it that Anamaria has told you by now how she so subtly twisted my arm into adding the extra 2 pages … On the priceless epiphytic flora clothing … *Araucaria*.’

Tánia, 21 Dec. 04: ‘You are a really poet, talking about the *Brief history*. Be happy, we are working in the architecture of this four ?6 pages.’

JMA, 22 Dec. 04: ‘And you are the dearest writer in littoral Gondwana English.’

Tánia, 5 Jan. 05: ‘We are working intensively in the chapter … You give to us a hard working … With care and nostalgy.’

Tánia, 7 Jan. 05: ‘We will try to accomplish your plans and dates ... A little before the ‘Seventh Extinction’ of three poor Brazilian students …’

JMA, 10 Jan. 05:‘ “Seventh Extinction!” Please take all possible precautions to avoid this extinction.’

Tánia, 18 Jan. 05: ‘The material is nearly ready for to send to you … ’

JMA, 20 Jan. 05: ‘Your Araucariaceae are like a hologram: I and a world of others will go on a deep time eco-tour in and around these forests.’

Tánia, 21 Feb. 05: ‘So, I am ready for your queries and asking for very lucky days for you during this last moments involved with the book ….’

JMA, 4 Mar. 05: ‘Hoping this does not add too heavily to the great load in a new university year.’

Tánia, 16 Mar. 05: ‘The work is splendid, handsome! Thanks for made so beautiful diagramation of our dispersed informations. WE LOVE IT!’

JMA, 29 Mar. 05: ‘Good dear Tánia, … so we have plenty of time to perfect your treasured pieces on the Araucs.’

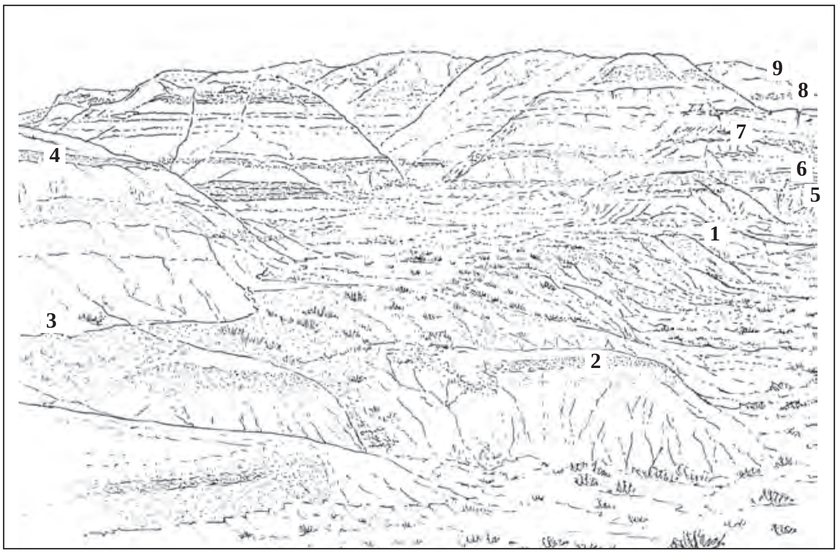
Tánia, 30 Mar. 05: ‘Thanks to God you are there. We are plenty of pleasure! To stay without your delicate and beautiful messages would be a disgrace.’

JMA, 5 May 05: ‘The biographical bit you dropped in about your “astral map” is perfectly charming. So the planets were holding your strings from the very start and making quite sure you could never rest up from your hard labours.’

Tánia, 6 May 05: ‘I would be delighted if I could dominate the Shakespeare idiom a little more, for to be so kind and reward your beautiful words.’

INTO THE TERTIARY (K/T, 65.5 Ma)
USA, E Montana

9. W coals: with angiosperms *Cercidiphyllum genetri* & *Platanus raynoldsii*; & gymnosperms *Glyptostrobus europaeus* (dominant) & *Cupressiinocladus interruptus.*
8. X coals: with stumps & foliage of *Glyptostrobus europaeus.*
7. Y coals.
6. Upper Z coal.
5. Lower Z coal; & trench for study of K/T boundary with weak iridium anomaly, & fern-spike from palynological study.
4. Upper Z coal atop Big Bugger Paleochannel.
3. Base of Big Bugger Paleochannel with alligator (*Leidyosuchus sternbergi*), champsosaurus (*Champsosaurus natator*) and turtle (*Compsemys viata*), as well as Paleocene plants—*Cercidiphyllum genetrix*, '*Populus*' *nebrascensis*, and *Wardiaphyllum daturaefolium* (all angiosperms). (The Bug Creek Anthills locality 200 m west of here is also at the base of the Big Bugger Paleochannel complex and includes a mix of latest Cretaceous and earliest Paleocene mammal teeth.)
2. Late Cretaceous old-growth lowland forest paleosol (Ottsko pedotype along strike from type profile).
1. Highest dinosaur—frill of *Triceratops horridus*.



N of Bug Creek, S of Fort Peck, E Montana, USA
Hell Creek Fm., Late Cretaceous (Maastrichtian), overlain by **Tullock Fm.**, Early Paleocene (Danian).
Gymnosperm history: Across the K/T boundary into relictual stasis.

Sketch by HMA (March 2005), after photo by Greg Retallack in Retallack (1997).

Contributor: Greg Retallack (see also p. 231).

Notes on Bug Creek section
(Retallack e-mail, 1 Sept. 2005)

K/T boundary: 3. This 'is an erosional contact, where the Big Bugger paleochannel has eroded several metres down into the Cretaceous'.
5. 'The K/T boundary almost coincides with the formation here. The formation boundary is at the base of the Z coal, and the K/T boundary is about 10 cm above the base of this 15 cm thick coal here as indicated by the fern spike.'

Fort Union Gp.: The Tullock Fm. forms the lower part of the Fort Union Gp. in this section, 'The U.S. Stratigraphic Code also accepts a Fort Union Fm. in places where it is thin'.

Megafloras across the K/T boundary: The Bug Creek and other sections in the US Western Interior (see Charts 17–20, pp 52–55), apparently offer the best opportunity through Laurasia to study the fortunes of megafloras from the Maastrichtian into the Paleocene.

Reference: Retallack (1997).

Biota across the K/T boundary, Montana
The ***Fort Union Fm.*** (Paleocene) consists of mostly fluvial (including overbank) and paludal deposits, mixed with limited lacustrine deposits, and is dominated by deciduous dicots, especially swamp species (e.g. cupressaceous and platanoid taxa) and a vertebrate fauna of teleost fish, crocodylians, early placental mammals such as condylarths and pantotheres, and a depauperate insect fauna). By comparison, the subjacent ***Hell Creek Fm.*** (Late Cretaceous, Maastrichtian) has a richer biota (including dinosaurs and much more evidence for herbivorous insects), warmer climates, and a more warm-temperate vegetation. (Conrad Labandeira, e-mail 11 April 2005).

Anticipated sequels (updates)
Though aiming at a complete evolutionary history of the gymnosperms, this volume is neither complete nor from certain perspectives is it strictly an evolutionary history. It will still be many years before something approximating a definitive history will be written.

We are fully aware that we will have missed a number of established families, or of genera warranting independent family status. This is inevitable—short of involving a far wider spectrum of contributing authors. We have finally had to draw the line, otherwise this volume might never have reached the press.

Also, we have chosen not to get involved in any rigorous cladistical phylogenetic studies. Many such studies have been attempted in recent years and have not as yet achieved any consistent results. We have elected rather to devote our energies to a comparative assembly of available systematic data. Future volumes will certainly embrace phylogenies at different taxonomic levels. The evolution of this *Brief history* is far from run.

A series of sequels (revisions, updates) is anticipated. Aside from bringing in previously known but overlooked families and newly discovered families, there are several other interlinking themes to perfect. We need to bring in successively improved correlation charts that tie ever-closer with the systematic text and pen sketches. The interdependent histories of the plants, insects and vertebrates need likewise to be fleshed out. And there is the increasingly resolved global physiology—temperature, rainfall, atmospheric composition, carbon isotopes—to be tied in. Holistic synthesis!

Optimal will be maintaining a database (online) of gymnospermous families and their reference whole-plant genera; and publishing a revised edition (including phylogenies) of this *Brief history* at perhaps five-year intervals. Concepts of classification and phylogeny will no doubt firm up during these intervals, leading ultimately to far greater levels of consensus among researchers. Any update should incorporate a closer consensus also regarding the use of terms, taxa and names. Histograms depicting biodiversity trends will become progressively more reliable.

It might have been most productive to aim at involving many more colleagues globally from the start of this project—each on those families with which they are most familiar—but, as more generally happens in science, this volume evolved as circumstances arose and insight grew.

Following Sir Walter Raleigh back in 1614, on endeavouring to write a history of the world, we appeal to the gentler nature of our colleagues in assessing and using this work. And we call on all our colleagues to join us in the anticipated sequels.

John M. Anderson (11 July 2005, Pretoria)

> *'I do therefore forbear to style my readers gentle, courteous, and friendly, thereby to beg their good opinions, or to promise a second and third volume (which I also intend) if the first receive grace and good acceptance.'*—**Sir Walter Raleigh**, London, 1614; from the preface to his '*History of the world*'.

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APPENDIX 1

ARAUCARIACEAE: PHYTOHISTORY OF THE FAMILY

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This appendix consisting of boxes of fossil data and a list of references accompanies the article of the same title (Charts 21–24, pp. 56–59) by Tánia Dutra and colleagues. The fossil data as presented here add to those in the main article and form the basis for the generation of the phytographic reconstructions. The data and references are not fully comprehensive (the literature is vast) and though a convincing history is derived, this might best be seen as an interim approximation in a succession of drafts, each more closely approaching the reality of Araucarian history.

UPPER TRIASSIC

LEAF, SHOOT, SEED SCALE, CONE

Araucarites dinossaurica Bock
  Carnian/Norian, Smith Clark Quarry, Penn., USA (6 %)
Brachyphyllum-Pagiophyllum complex
  Norian, Chinle Fm., Arizona, USA
Brachyphyllum hegewaldia Ash (Araucariaceae?)
  Norian, Chinle Fm., Arizona, USA
Araucarites parsorensis Lele 1955
Araucarites indica Lele 1962
  Anisian, Parsora Fm., South Rewa, India
Araucarites cutchensis Feistmantel 1876
  Late Triassic (Rhaetic?), cone scale, Canterbury, Southland, New Zealand
Brachyphyllum–Pagiophyllum complex
  Norian/Rhaetian, Parana Basin, Caturrita Fm., Brazil
Pagiophyllum Heer (Araucariaceae?)
  Carnian/Norian, West Antarctic Peninsula

WOOD

Araucarioxylon dinossaurica
  Late Triassic, Pennsylvania, USA (6% of the flora)
Araucarioxylon arizonicum Daugherty 1941
  Norian, Chinle Fm., Arizona, USA
Araucarioxylon Kraus. emend. Mahesh.
  Carnian/Norian, Água de La Zorra, Mendoza, Argentina
  Norian/Rhaetian, Parana Basin, Caturrita Fm., Brazil, (100% of the fossil occurrence)
  Carnian/Norian, Ischigualasto Fm., Argentina
  Mid–Late Triassic, Beaufort Gp., Elliot Fm., South Africa
  Norian, Amery Group, East Antarctica
Araucarioxylon protoaraucana Brea
  Ladinian/Anisian/Norian, Barreal/Paramillo/Ischigualasto/Potrerillos Fms, Argentina (10%)
Araucarioxylon semibiseriatum
  Late Triassic (Norian?), La Ternera Fm., N Chile
Kaokoxylon zalessky (Sahni) Maheshwari (Araucariaceae?)

POLLEN

Araucariacites Cookson 1947
  Early Triassic, Clematis Sandstone, Queensland, Australia
Araucariacites australis Cookson 1947
  Carnian, Las Cabras Fm., Mendoza Province, Argentina
  Norian/Rhaetian, Paramillo/Chihuido Fm., Argentina
Araucariacites*. *pergranulatus Volkheimer
  Carnian, Ischichuca Fm., Argentina
  Carnian, Comallo Fm., Argentina
  Norian, Santa Clara de Arriba Fm., Argentina
  Norian, Cacheuta Fm., Mendoza, Argentina
  Rhetic, Paso Flores Fm., Argentina
  Norian/Rhaetian, Paramillo/Chihuido Fm., Argentina
Araucariacites* sp.** cf. ***A. pergranulatus
  Carnian, Ischichuca Fm., La Rioja Province, Argentina
Araucariacites fissus Reiser & Williams
  Carnian, Comallo Fm., Argentina
  Carnian/Norian, Carrizal Fm., Argentina
  Norian, Cacheuta Fm., Mendoza, Argentina
  Norian, Paramillo/Chihuido Fms, Argentina
  Norian, Ischigualasto Fm., Argentina
  Rhaetic, Paso Flores Fm., Argentina
Inaperturopollenites Reid & de Jersey
Callialasporites
  Norian/Rhaetian, Paramillo/Chihuido Fm., Argentina

JURASSIC–MIDDLE CRETACEOUS

LEAF, SHOOT, SEED SCALE, CONE

Brachyphyllum–Pagiophyllum–Desmiophyllum
Jurassic, Assemblage Zone, Hartala Fm., Madhya Pradesh, E India
Araucarites bindrabunensis Vishnu-Mitre 1954
Late Jurassic (Jabalpur Stage), cone/seed scale, Rajmahal Hills Mountains, Bihar, India
Araucarites latifolius Feistmantel 1882
Late Jurassic (Jabalpur Stage) leaf, Bansa, India
Araucarites macropteris Feistmantel 1887
Late Jurassic (Rajmahal, Kota & Jabalpur Stage), seed scales, Bansa, India
Araucarites nipaniensis
Late Jurassic, female cone, Rajmahal Series, India
Ontheodendrom florini Sahni & Rao 1933
Late Jurassic (Jabalpur Stage), cone, Bansa, India
Araucarites cutchensis Feistmantel 1876
Late Jurassic (Umia, Kota & Jabalpur Stage), seed scales, Bansa, India
Mid-Jurassic, cone scale, Mokoia, Southland, New Zealand
Brachyphyllum lorchii Raab, Horow. & Conway 1986
Late Jurassic, Kidod Fm., Dead Sea, Israel
Araucarites Cookson 1947
Late Jurassic (Jabalpur Stage), seed scales, Bansa, India
Araucarites anadyrensis Krysht.
Araucarites male & female cone
Pagiophyllum triangulare Prynada
Mid-Cretaceous, shoot/leaf, Krivorechanskaya Fm., NE Russia
Pagiophyllum maculosum Kendall
Jurassic, shoot, male cone, North Yorkshire, England
Araucarites phillipsii Carruters (sect. *Eutacta*)
Jurassic, seed scales, female cone & cuticle, Yorkshire, England
Brachyphyllum mamillare Kendall 1949
Jurassic, foliage, Yorkshire, England
Agathis jurassica (ex *Podozamites lanceolatus*) White 1981
Jurassic, leaf twig & cone, Talbragar Fish Beds, NSW, Australia (*Wollemia* from Araucariaceae or Podocarpaceae)
Brachyphyllum aff. ***expansum*** (Sternb.) Sew.
Early Cretaceous, Suchan Basin, East Asia, Russia & China
Araucarites pedreranus Barale 1989
Early Cretaceous, Spain
Dammarites coriacea Barale 1992
Early Cretaceous, male microsporophylls, Montsec, Lérida, Spain
Brachyphyllum obesum Heer 1881
Early Cretaceous, Almargem Basin, Portugal
Araucaria obtusifolia Font 1889
Araucaria zamioides Font 1889
Araucaria podocarpoides Font 1889
Early Cretaceous (Albian), Potomac beds, USA
Araucariostrobus creutzbergii Huertas 1970
Araucariostrobus camargoi Huertas 1970
Early Cretaceous, male cone, Colombia
Brachyphyllum obesum Heer 1881
Early Cretaceous (Albian), Foliage, Santana Fm., Araripe Basin, NE Brazil
Early Cretaceous, shoot, Areado Fm., Minas Gerais, Brazil (10%)
Brachyphyllum castilhoi Duarte 1985
Early Cretaceous, shoots/leaf, Santana Fm., NE Brazil
Brachyphyllum insigne Heer 1876
Early Cretaceous, Santana Fm., Araripe Basin, Ceará, Brazil
Araucaria cartellei Duarte 1993
Early Cretaceous, leaf, Santana Fm., Araripe Basin, NE Brazil (10%)
Araucarites vulcanoi Duarte 1989
Early Cretaceous, seed scales, Santana Fm., Ceará, Brazil (10%)
Araucaria buchanani Hector 1886
Araucaria carinaria Hector 1886
Agathis lanceolatus Hector 1886
Cretaceous, Shag Point, New Zealand
Araucaria lanceolatus Cantrill
Early Cretaceous, Otway Basin, Victoria, Australia
Araucaria acutifoliatus Cantrill
Early Cretaceous, Gippsland Basin, SE Australia
Early Cretaceous, foliage, Otway Basin, Victoria, Australia
Araucaria sp.
Early Cretaceous, shoots, Eromanga Basin, Queensland, Australia
Araucaria seorsum Cantrill (sect. *Columbea*)
Early Cretaceous, foliage, Otway Basin, Victoria, Australia
Araucaria carinatus Cantrill (sect. *Eutacta*)
Early Cretaceous, foliage, Otway Basin, Victoria, Australia
Araucaria falcatus Cantrill (sect. *Eutacta*)
Early Cretaceous, foliage, Otway Basin, Victoria, Australia
Araucaria sp. cf. ***A. heterophylla*** (Salisb.) Franco (sect. *Eutacta*)
Early Cretaceous, foliage, Koonwarra, Victoria, Australia
Araucaria otwayensis Cantrill (sect. *Eutacta*)
Early Cretaceous, foliage, Otway Basin, Victoria, Australia
Araucaria readiae (R.S.Hill & Bigwood) emend. R.S.Hill
Early Cretaceous, foliage, Regatta Point, Tasmania, Australia
Araucarites sp. Mildenhall & Johnston 1971
Early Cretaceous (Albian), megastrobilus, Wairarapa, North Island, New Zealand
Agathis victoriensis Cantrill 1992
Early Cretaceous, foliage, Otway Basin, Victoria, Australia
Araucarites grandis Walkom
Cretaceous, seed scales, Waikawa, North Island, New Zealand
Palissya bartrumi
Cretaceous, cones, Waikawa, North Island, New Zealand
Araucarites cutchensis Feistmantel 1876
Mid-Jurassic (Callovian), seed scales, Mokoia, North Island, New Zealand
Araucaria sp. cf. ***A. mesozoica*** Walkom
Mid-Cretaceous, foliage, Winton Fm., Queensland, Australia
Podozamites taenioides Cantrill (= *Araucarioides*)
Early Cretaceous, foliage, Otway Basin, Victoria, Australia
Araucaria sp.
Turonian, shoots, Perth & Canning Basins, SW Australia
Araucarites Cookson 1947
Mid-Jurassic, seed scales, Cañadon Asfalto Fm., Chubut Basin, Argentina (40º S)
Mid-Jurassic (Bajocian-Callovian), Lotena Fm., Neuquen Basin, N Patagonia, Argentina
Araucarites phillipsii Carruters
Early Jurassic, leaf, Pedra Pintada Fm., NW Patagonia, Argentina (60% of the assemblage)
Brachyphyllum ramosum
Mid-Jurassic (Callovian), foliage, Lotena Fm., Neuquen Basin, Patagonia, Argentina
Araucarites santaecrucis Calder 1953
Mid-Jurassic, twigs & leaf, La Matilde Fm., Santa Cruz, Argentina
Araucaria mirabilis Spegazzini (sect. *Bunya*)
Jurassic, seed scale/female cone, Santa Cruz Basin, Argentina
Pararaucaria patagonica
Jurassic, seed scale, Cerro Quadrado, Santa Cruz, Argentina
Araucaria grandifolia Feruglio 1951
Early Cretaceous, leaf/shoot, Baqueró Group, Santa Cruz, Argentina
Araucarites minumus Arch. 1966
Araucarites baqueroensis Arch. 1966
Early Cretaceous, seed scale, Baqueró Group, Santa Cruz, Argentina
Nothopehuen brevis Del Fueyo 1991
Early Cretaceous, leaf/cuticle/male cone, Baqueró Group, Argentina
Brachyphyllum irregulare
Early Cretaceous, shoot with cone, Baqueró Fm., Santa Cruz, Argentina
Brachyphyllum Lindley & Hutton ex Brongniart
Early Cretaceous, leaf/cuticle, Springhill Fm., Santa Cruz, Argentina
Araucaria alexandrensis Cantrill & Falcon-Lang 2001
Araucaria chambersii Cantrill & Falcon-Lang 2001
Early Cretaceous, leaf/shoot, Fossil Bluff Group, Antarctic Peninsula
Araucarites wollemiaformis Cantrill & Falcon-Lang 2001
Araucarites citadelbastionensis Cantrill & Falcon-Lang 2001
Early Cretaceous, Fossil Bluff Group, Alexander Island, Antarctica
Araucarites cf. ***baqueroensis***
Early Cretaceous, Cerro Negro Fm., Byers Group, Antarctic Peninsula

JURASSIC–MIDDLE CRETACEOUS (cont.)

WOOD

Hausmannia–Ptilophyllum–Araucarioxylon
Mid-Jurassic, Kota Fm., Bansa, India
***Agathoxylon* sp.** Bamford 1998
Early Jurassic (Upper Karoo), Clarens Fm., South Africa
Mid-Upper Jurassic (Bathonian/Callovian/Oxfordian), Paris, Jura and Subalpine Basin, France (38–51%)
Late Jurassic, Sergi Fm., Bahia and Sergipe, Brazil
Mid-Cretaceous (Cenomanian), Charente-Maritime, SW France
Agathoxylon liguaensis Torres & Philippe 2002
Early Jurassic, Quebrada del Pobre Fm., Chile
Araucarioxylon australe Crié 1889
Mid-Jurassic (Callovian), Mataura, Southland, New Zealand
Dadoxylon australae
Mid-Jurassic, Waikawa, North Island, New Zealand
***Araucarioxylon* sp.**
Mid-Jurassic, La Matilde Fm., Santa Cruz Basin, Argentina
Early Cretaceous, Cerro Negro Fm., Byers Peninsula, Antarctic Peninsula
Araucarioxylon arayaii
Early Cretaceous, Byers Group, Byers Peninsula, Antarctic Peninsula
Araucarioxylon floresii
Early Cretaceous, Byers Group, Williams Point, Antarctic Peninsula
Araucarioxylon mosurense Jeyasingh & Kumarasamy 1995
Early Cretaceous, Sriperumbudur Fm., Tamil Nadu, S India
Dadoxylon benderi Mussa 1959
Early Cretaceous, Japoatã Fm., Sergipe, Brazil

POLLEN

Araucariacites singhii Saxena 1993
Late Jurassic (Jabalpur Stage), Madhya Pradesh, Central India
Early Cretaceous, Bhuj Series, Ghuneri, Kutch District, India
Araucariacites australis Cookson 1947
Late Jurassic, Kidod Fm., Dead Sea, Israel
Late Jurassic (Kimmeridgian), West Europe
Early Cretaceous, Raniganj Gondwana Basin, W Bengal, India (10–12%)
Mid-Cretaceous, Charentes, France
Mid-Jurassic, Lotena/ Lajas Fms, Neuquen Basin, Argentina
Mid-Late Jurassic, Neuquen Basin, Argentina (5–10%)
Early Cretaceous, Albornoz Fm., San Jorge Basin, Argentina
Early Cretaceous, Neuquen Basin, Argentina
Early Cretaceous, Agrio Fm., Neuquen Basin, Argentina
Early Cretaceous, Punta Del Barco Fm., Baqueró Group, Argentina
Early Cretaceous, Gustav Group, James Ross Island, Antarctic Peninsula
Araucariacites fissus Reiser & Williams
Mid-Late Jurassic, Neuquen Basin, Argentina (5%)
Early Cretaceous, Raniganj Gondwana Basin, W Bengal, India (10–12%)
Araucariacites pergranulatus Volkheimer1964
Mid-Late Jurassic, Cura Niyeu, Neuquen Basin, Argentina
***Araucariacites* sp.**
Late Jurassic, Abu Ballas Fm., Southern Egypt
Mid-Jurassic, Grupo Cuyo, Neuquen Basin, Argentina (10–40%)
Early Cretaceous, Guiana
Early Cretaceous, amber & pollen, Jordan & Israel
Early Cretaceous, Suchan Basin, East Asia, Russia and China
Inaperturopollenites Reid & de Jersey
Mid-Jurassic, Grupo Cuyo, Neuquen Basin, Argentina (10–40%)
Mid-Jurassic, Lotena/Lajas Fms, Neuquen Basin, Argentina
Mid-Cretaceous (Albian-Cenomanian), Charentes, France (8%)
Inaperturopollenites limbatus Balme 1957
Early Cretaceous, Baqueró Group, Santa Cruz, Argentina
Early Cretaceous, Suifun & Suchan Basin, Russia
Mid-Cretaceous, Charentes, France, Albian-Cenomanian (8%)
Inaperturopollenites microgranulatus Volkheimer 1972
Early Cretaceous, Albornoz Fm., San Jorge Basin, Argentina
Inaperturopollenites turbatus Balme 1957
Early Cretaceous, Neuquen Basin, Argentina
Callialasporites trilobatus (Balme) Dev 1961
Late Jurassic, Kidod Fm., Dead Sea, Israel
Late Jurassic, Kimmeridgian, Raniganj, West Europe
Early Cretaceous, Gondwana Basin, W Bengal, India (10–12%)
Early Cretaceous, Albornoz Fm., San Jorge Basin, Argentina
Early Cretaceous, Gustav Group, James Ross Island, Antarctic Peninsula
Callialasporites dampieri (Balme) Dev 1961
Late Jurassic, Kimmeridgian, West Europe
Early Cretaceous, Raniganj Gondwana Basin, W Bengal, India (10–12%)
Early Cretaceous, Neuquen Basin, Argentina
Early Cretaceous, Gustav Group, James Ross Island, Antarctic Peninsula
Callialasporites turbatus
Late Jurassic, Kimmeridgian, West Europe
***Araucariacites* sp.**
Araucariacites cooksoniis Singh, Srivastava & Roy 1964
Araucariacites ghuneriensiss Singh, Srivastava & Roy 1964
Callialasporites monoalasporos Dev 1961
Callialasporites reticulatus Ramanujan & Srisal 1974
Callialasporites triletes Singh, Srivastava & Roy 1964
Early Cretaceous, Raniganj Gondwana Basin, W Bengal, India (10–12%)
Callialasporites segmentatus (Balme) Srivastava 1963
Early Cretaceous, Raniganj Gondwana Basin, W Bengal, India (10–12%)
Early Cretaceous, Albornoz Fm., San Jorge Basin, Argentina
Early Cretaceous, Neuquen Basin, Argentina
***Dilwynites* sp.** (*Wollemia*?)
Mid-Cretaceous, S & N Australia

Appendix 1

LATE CRETACEOUS–PALEOGENE

LEAF, SHOOT, SEED SCALE, CONE

Araucaria nihongii Stockey, Nishida & Nishida 1992 (*Eutacta-Intermedia* sect.)
Late Cretaceous, female cones & ovuliferous scales, Upper Yezo Group, Hokkaido, Japan
Agathis? sp.
Late Cretaceous, leaf, Pakawau Basin, South Australia
Araucaria haastii Ettingshausen 1887 (sect. *Intermedia*)
Late Cretaceous, leaves, cuticle, Shag Point, New Zealand
Araucaria desmondii Pole
Late Cretaceous, foliage, E Otago, New Zealand
Araucaria danai Ettingshausen 1887
Late Cretaceous, leaves, Shag Point, New Zealand
Araucaria taieriensis Pole
Late Cretaceous, foliage, E Otago, New Zealand
Dammara oweni Ettingshausen 1887
Late Cretaceous, leaves, cone, cone scale, Shag Point & Otago, New Zealand
Dammara uninervis Ettingshausen 1887
Late Cretaceous, leaves, cone scale, Shag Point, New Zealand
Dammara mantelli Ettingshausen 1887
Late Cretaceous, leaves, Pakawaw, Nelson Island, New Zealand
Araucarioides falcata Pole
Late Cretaceous, foliage, E Otago, Australia
Araucarioides taenioides (Cantrill) Pole
Late Cretaceous, foliage, E Otago, New Zealand
Indet. ovulate cone
Late Cretaceous, Maryborough Fm., NE Australia (20%)
Agathis marshalli
Late Cretaceous, leaf, Kaipara District, New Zealand
***Agathis*? sp.**
Late Cretaceous, seeds, scales, leaf, Dorotea Fm., Cerro Guido, Chile
Pseudoaraucaria valentini (Kurtz ex Hün.) Menéndez
Late Cretaceous, Dorotea Fm., Cerro Guido, Chile
Araucaria antarctica Césari, Marenssi, Santillana 2001
Late Cretaceous, cone, leaves, shoots (conifer-dominated flora), Informal Unit K3, Lopez de Bertodano Fm., Cape Lamb, Vega Island, Antarctic Peninsula (10%)
***Araucaria* sp.** (*Columbea* sect.)
Paleocene, Kerguelen Island
***Araucaria* spp** (Pole 1998)
Early-mid-Paleocene, Mt Sommers, New Zealand
Araucaria lignitici Cookson & Duigan 1951
Paleocene, leaf & cuticle (sect. *Eutacta*), SE Australia
***Agathis* sp.** & ***Araucaria* sp.**
Paleocene, foliage, South Australia
Araucaria balcombensis Selling (sect. *Columbea*)
Paleocene, leaf, Australia
Indet. cone scales
Late Paleocene, La Huitrera Fm., Austral Basin, Argentina
Araucaria araucoensis Engelh.
Leaf & shoots, Curanilahue, Patagonia, Argentina
Araucaria imponens Dusén 1908
Paleocene, leaf/seeds (sect. *Columbea*), Antarctic Peninsula
Araucaria* sp. cf. *Araucaria nathorsti Dusén 1907 (sect. *Columbea*)
Paleocene–Eocene, Ñirihuau, Rio Negro, Argentina
Paleocene–Eocene, Point Hennequin Gr., King George Isl., Antarctic Peninsula
***Agathis*?**
Paleocene–Eocene, Point Hennequin Gr., King George Isl., Antarctic Peninsula
***Araucaria* sp.** (sect. *Eutacta*)
Paleocene–Eocene, Point Hennequin Gr., King George Isl., Antarctic Peninsula (5%)
Araucarioides linearis (Bigwood & Hill) emend. Hill & Bigwood 1987
Araucarioides sinuosa Bigwood & Hill 1985
Early Eocene, foliage, Regatta Point, Tasmania, Australia
***Araucaria* sp.**
Eocene, leaf, Minna Bluff, McMurdo Sound, Antarctica
Araucaria nathorsti Dusén 1907
Eocene, leaf (sect. *Columbea*), La Meseta Fm., Seymour Island, Antarctic Peninsula (16%)
Agathis intermedia Chapman & Crespin
Eocene, leaf, Victoria, Australia
Araucaria derwentensis Selling
Eocene, leaf, SE & S Tasmania, Australia
***Araucaria* sp.** (sect. *Eutacta*)
Eocene, cuticle, South Island, New Zealand (7.7%)
Araucaria readiae Hill & Bigwood 1987 (sect. *Eutacta*)
Early Eocene, leaf & cuticle, Regatta Point Flora, W Tasmania, Australia
***Agathis* sp.**
Mid-Eocene, foliage, Maslin Bay, South Australia
Mid-Eocene, foliage, Lefroy/Cowan paleodrainages, Western Australia
Agathis kendrickii Hill & Merrifield 1993
Mid-Eocene, foliage, West Dale, Western Australia
Araucaria balcombensis Selling
Eocene, leaf, Victoria, Australia
***Araucaria* sp.**
Late Eocene, leaf, Germany
Araucaria hastiensis Hill & Bigwood 1987 (sect. *Columbea*)
Mid-Late Eocene, leaf & cuticle, Hasties, NE Tasmania, Australia
Araucaria annulata Pole 1992 (sect. *Columbea*)
Mid-Late Eocene, foliage, Hasties, Tasmania, Australia
Araucaria nathorsti Dusén 1907
Upper Eocene, leaf (sect. *Columbea*), Rio las Minas Fm., Austral Basin, Argentina
Agathis tasmanica Hill & Bigwood 1987
Early Oligocene, foliage, Little Rapid River, Tasmania, Australia
Agathis parwanensis Cookson & Duigan 1951
?Oligocene, foliage, Bacchus marsh, Victoria, Australia
Agathis (3 spp) Carpenter 1991
Early Oligocene, foliage, cone, Cethana, Tasmania, Australia
***Araucaria* sp. 1** Carpenter 1991
Early Oligocene, foliage, cone, Cethana, Tasmania, Australia
Araucaria fimbriatus Hill 1990
Early Oligocene, foliage, Little Rapid River, Tasmania, Australia
Agathis berwickensis Pole, Hill, Green & Macphail
Late Oligocene–Early Miocene, foliage, Berwick Quarry, Victoria, Australia
aff. ***Araucaria* sp.** Blackburn 1985
Oligocene–Miocene, foliage, Morwell, Victoria, Australia
Agathis yallounensis Cookson & Duigan 1951
Oligocene–Miocene, foliage, Yallourn & Morwell, Victoria, Australia
Araucaria lignitici (Cookson & Duigan) emend. Hill 1990 (sect. *Eutacta*)
Oligocene–Miocene, foliage, Yallourn & Morwell, Victoria, Australia
Araucaria prominens (Hill & Bigwood) emend. Hill 1990 (sect. *Eutacta*)
Oligocene–Miocene, foliage, Monpeelyata, Tasmania
Araucaria planus Hill 1990 (sect. *Eutacta)*
Oligocene–Miocene, foliage, Monpeelyata, Tasmania

LATE CRETACEOUS–PALEOGENE (cont.)

WOOD

Araucarioxylon pichasquensis Torres & Rallo 1981
  Late Cretaceous, Pichasca, N of Chile (25%)
***Dadoxylon* sp.** (?)
  Eocene, Fildes Fm., Barton Pen., King George Island, Antarctic Peninsula
Dadoxylon ettingshauseni Edwards 1926
  Late Cretaceous, Shag Point, New Zealand
Dammara oweni Ettingshausen 1887
  Late Cretaceous, Shag Point, New Zealand
Dadoxylon novae-zeelandiae Edwards 1926
  Late Cretaceous, Amuri Bluff, Marlborough, New Zealand

POLLEN

***Dilwynites* sp.** (*Wollemia*?)
  Late Cretaceous (Maastrichtian), New Zealand
Araucariacites Cookson 1947
  Paleocene, Cordillera Central, Colombia
Araucariacites australis Cookson 1947
  Early Eocene, Kopili Fm., India
  Early Paleocene, Pedro Luro Fm. Los Colorados Basin, C & W Argentina (35–40º S)
  Paleocene (Danian), Chubut Basin, Argentina
  Eocene, Neuquén & Chubut Basins, C & W Argentina (35–40º S) & Chile
  Eocene, Rio Turbio Fm. Santa Cruz, Argentina
  Eocene, Middle Waipara, South Island, New Zealand
  Eocene, Yaamba Basin, NE Australia
  Eocene, Napperby, Central Australia (3%)
  Eocene, Ulgnamba Lignite, Hale River Basin, Australia (1.7%)
  Paleocene, King George Island, Antarctic Peninsula
Araucariacites europaeus
  Eocene, Staré Sedlo Fm, Czech Republic & Saxony, Germany
***Dilwynites* sp.** (*Wollemia*?)
  Paleocene, Seymour Island, Antarctic Peninsula
  Paleocene, E & Central Australia
  Eocene, E & Central Australia
Araucariacites Cookson 1947
  Mid-Oligocene, SE Australia
  Oligocene–Pleistocene–Recent, Central Chile
Araucariacites australis Cookson 1947
  Oligocene–Miocene, Bengal Fan, Indian Ocean, India
  Oligocene, San Julian Fm., Austral Basin, Argentina (9%)
  Upper Oligocene, Tasmania, Australia
  Latest Oligocene–Early Miocene, Rio Foyel Fm., Nirihuau Basin, NW Patagonia, Argentina

NEOGENE–RECENT

LEAF, SHOOT, SEED SCALE, CONE

***Agathis* sp.**
Early Miocene, leaf, Latrobe Valley, SE Australia
Agathis kendrickii Hill & Merrifield 1991
Eocene–Oligocene, leaf/cuticle, West Dale, Perth, SW Australia (4%)
Agathis tasmanica Hill & Bigwood 1987
Oligocene–Miocene, leaf/cuticle, Little Rapid River, NW Tasmania, Australia
***Araucaria* sp.** Pole 1992 (sect. *Eutacta*)
Early Miocene, leaf, shoots, cone scales and male cone?, Manuherikia Group, New Zealand
Late Miocene, leaf, South Australia
Oligocene–Miocene–Pliocene, leaf, NE Tasmania, Australia
***Araucaria* sp.**
Oligocene–Miocene, Lonquimay sedimentary sequence, Chile
Oligocene–Pleistocene–Recent, leaf, Central Chile
Miocene, Navidad Fm., Matanzas, Chile (1.5%)
Araucaria nathorsti Dusén 1907 (sect. *Columbea*)
Oligocene–Miocene, leaf, Pico Quemado Fm., Rio Negro Basin, Argentina

WOOD

***Araucarioxylon* sp.**
Oligocene, Pleistocene & Recent, Central Chile
Agathoxylon australe Evans (= *Agathis australis*)
Late Tertiary, Roxburgh, Central Otago, New Zealand

POLLEN

Araucariacites Cookson 1947
Early Miocene, Latrobe Valley, SE Australia (*Agathis*)
Miocene, Dafla Fm., Bhalukpong–Bomdila, W Kameng District, Arunachal Pradesh, India
Late Miocene, Parana Fm., Santa Fé, Argentina
Pleistocene–Recent, Central Chile
Araucariacites australis Cookson 1947
Miocene, NSW, SE Australia (1.5%)
Pliocene–Pleistocene, W Tasmania, Australia (1.5%)
Pleistocene, Western Plains, Victoria, SE Australia (2%)
***Dilwynites* sp.** (*Wollemia*?)
Pliocene, Bass Strait, Australia
***Araucariacites* sp.**
Pleistocene–Recent, C & S Brazil (wet & warm periods) (5%)
Pleistocene–Recent, E Australia

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Appendix 1

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APPENDIX 2

REFERENCES TO DOWELD (2001) CLASSIFICATION

The references given here are those relevant to the Doweld (2001) classification of the gymnosperms (pp. 16, 17). Most are given fully, some in abbreviated form: in both cases as they appear in Doweld's *Prosyllabus Tracheophytorum*. The only changes made are such as to comply in general with the *Strelitzia* format.

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