Patterns of Gondwana plant colonisation and diversification

J. M. ANDERSON,[1,*] H. M. ANDERSON,[1] S. ARCHANGELSKY,[2] M. BAMFORD,[3]
S. CHANDRA,[4] M. DETTMANN,[5] R. HILL,[6] S. MCLOUGHLIN[7] and O. RÖSLER[8]

[1]National Botanical Institute, Private Bag X101, Pretoria 0001, South Africa

[2]Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Casilla de Correo 220,
Sucursal 5, 1405 Buenos Aires, Argentina

[3]Bernard Price Institute for Palæontology, University of the Witwatersrand,
Johannesburg, South Africa

[4]Birbal Sahni Institute of Palæobotany, 53 University Road, Lucknow 226007, India

[5]Department of Botany, University of Queensland, Brisbane, Queensland, Australia

[6]Department of Plant Sciences, University of Tasmania, GPO Box 252-55, Hobart,
Tasmania 7001, Australia

[7]School of Botany, The University of Melbourne, Parkville, Victoria 3052, Australia

[8]Centro Paleontológico de Mafra Universidade do Contestado, Caixa Postal–111,
89.300-000, Mafra, SC, Brasil

ABSTRACT—Charting the broad patterns of vascular plant evolution for Gondwana against
the major global environmental shifts and events is attempted here for the first time. This is
based on the analysis of the major vascular plant-bearing formations of the southern continents
(plus India) correlated against the standard geological time-scale. Australia, followed closely
by South America, are shown to yield by far the most complete sequences of productive
strata. Ten seminal turnover pulses in the unfolding evolutionary picture are identified and
seen to be linked to continental drift, climate change and mass global extinctions. The rise of
vascular plants along the tropical belt, for instance, followed closely after the end-Ordovician
warming and extinction. Equally remarkable is that the Late Devonian extinction may have
caused both the terrestrialisation of the vertebrates and the origin of the true gymnosperms.
The end-Permian extinction, closure of Iapetus, together with warming, appears to have set in
motion an unparalleled, explosive, gymnosperm radiation; whilst the Late Triassic extinction
dramatically curtailed it. It is suggested that the latitudinal diversity gradient clearly recognised
today, where species richness increases towards the tropics, may have been partly reversed
during phases of Hot House climate. Evidence hints at this being particularly so at the heyday
of the gymnosperms in the Late Triassic super-Hot House world. As for the origin of terrestrial,
vascular, plant life, the angiosperms seem closely linked to a phase of marked shift from Ice
House to Hot House.
Insect and tetrapod evolutionary patterns are discussed in the context of the plants providing
the base of the ever-changing ecosystems. Intimate co-evolution is often evident. This isn't
always the case, for example the non-linkage between the dominant, giant, long-necked,
herbivorous sauropod dinosaurs and the dramatic radiation of the flowering plants in the Mid-
Cretaceous. © 1999 Published by Elsevier Science Limited. All rights reserved.

RÉSUMÉ—Pour la première fois, une tentative de reconnaissance des modes principaux de
l'évolution de la plante vasculaire du Gondwana en fonction des variations d'environnements
et des événements globaux majeurs est présentée ici. Elle se fonde sur l'analyse des grandes
formations à plantes vasculaires des continentaux méridionaux (plus l'Inde) corrélées avec les

---

*email: jma@nbipre.nbi.ac.za

niveaux d'étage en fonction de l'échelle standard des temps géologiques. L'Australie, suivie de près par l'Amérique du Sud, montre les séquences de strates productives de loin les plus complètes. Dix épisodes de bouleversement sont identifiés dans l'établissement du tableau de l'évolution et sont liés de façons variées à la dérive des continents, aux changements climatiques et aux extinctions globales en masse. Par exemple, la progression des plantes vasculaires dans la zone tropicale a suivi de près le réchauffement et l'extinction de la fin de l'Ordovicien. Il est également remarquable que l'extinction du Dévonien tardif a pu déclencher à la fois la sortie des eaux des Vertébrés et l'origine des vrais Gymnospermes. L'extinction de la fin du Permien, et la fermeture de l'Océan Iapetus, avec le réchauffement, semble avoir mis en mouvement une expansion explosive, sans parallèle, des Gymnospermes que l'extinction du Trias tardif a stoppée de façon brutale. Il est suggéré que le gradient de diversité en fonction de la latitude, clairement reconnu aujourd'hui, la richesse en nombre d'espèces augmentant vers les tropiques, a pu s'inverser en partie lors des phases de climat à effet de serre. L'apogée des Gymnospermes au Trias tardif sous un climat de super-effet de serre constitue un argument. Comme dans le cas de l'origine des plantes vasculaires terrestres, l'origine des Angiospermes semble étroitement liée à une phase de transition marquée d'un climat glaciaire à un climat chaud.

Les modes d'évolution des Insectes et des Tétrapodes, quoique non reportés, sont discutés dans le contexte des végétaux constituant la base des écosystèmes toujours en réorganisation. Des évolutions intimement mêlées sont souvent évidentes. Ce n'est pas toujours le cas, par exemple l'absence de lien entre les Dinosaures Sauropodes herbivores à long cou dominants et l'expansion extraordinaire des plantes à fleurs au cours du Crétacé moyen. © 1999 Published by Elsevier Science Limited. All rights reserved.

INTRODUCTION

Nature is interlinked and always changing–gradually, but occasionally with precipitate consequences. This paper aims to uncover the broadest patterns of vascular plant evolution, colonisation and diversification on Gondwana (and its later dispersed fragments), and seeks to assess these patterns within the canvas of cause and effect: from continental drift to global climatic shifts and the five main extinction events. Acknowledging the role of plants at the base of the ecosystem, this paper also considers the most general trends observed in insect and tetrapod evolution. A decent balance between observation and hypothesis is sought, in keeping with Darwin's (1861, letter to Henry Fawcett): *"All observation must be for or against some view if it is to be of any service"*.

This account constitutes a synoptic preview primarily of the plant side of the book *'Gondwana Alive: biodiversity and the evolving terrestrial biosphere'*, to be published at the beginning of the next millennium. The book, an integrated, multiauthored project with contributions from numerous specialists, gives the plants, insects and tetrapods (and their changing physical backdrop) equal prominence. Its focus is the Gondwana continents, from the first appearance of vascular plants in the Silurian to the present day. The sixth extinction (Wilson, 1993; Leakey and Lewin, 1996), already occurring today because of the exponential increase in human population, and consequent demands on the environment, is of great and urgent concern. It is hoped that this paper will promote discussion leading to international agreements that will prevent the catastrophe of further wholesale extinction.

ENVIRONMENTAL CHANGE

Continental drift

Plate tectonics and the drifting continents quite evidently play a primary role in the chain of environmental change driving evolution. A cursory scan of the succession of drift maps (adapted from Scotese, 1997b; see also Scotese *et al.*, 1999; Smith, 1999) incorporated into Fig. 1, affords an abundantly clear sense of this motive force. Four broad categories of effect may be considered:

i) climatic change on both the global and regional scale;

ii) territorial proximity or isolation affecting colonisation and diversification;

iii) volcanism (flood basalts, island-arcs) and associated changes in the ratios of atmospheric gases; and

vi) topography of the landscape (fold mountains, plateau uplift, etc.).

Global climatic change

The first order pattern of global climatic shifts may be defined in terms of Hot House and Ice House states (Scotese, 1998; Scotese *et al.*, 1999; Fig. 1). The Ice House intervals are apparently relatively short-lived, whilst the warmer plateaus are of sustained duration. The three marked warming phases of the Phanerozoic are each associated with seminal turning points (the appearance of major new groups) in the evolution of plant life:

i) the end-Ordovician with the origin of life on land;

ii) the Permian with the radiation of the glossopterids and several other gymnosperm orders; and

iii) the Lower to Middle Cretaceous with the rise of the angiosperms.

Global extinction events

The big five mass extinctions (and the sixth, currently in progress) are imprinted clearly on the evolution of plant life. Whether a consequence of continental drift, global climatic change, or of extra-terrestrial impact (asteroids, comets), the causes of these events remain an area of lively debate and are crucial to interpreting the history of evolution. Different causes will bring about different effects (Fig. 1).

GLOBAL PLANT KINGDOMS
Towards greater differentiation

In tracking the changing pattern of the plant kingdoms, adapted largely from Meyen (1987) and Crane (1987), against the succession of drift maps a broad trend towards greater complexity is witnessed. The picture progresses from a single, restricted, tropical, Euramerican kingdom in the Silurian to the traditionally recognised six kingdoms of today.

Terrestrial trilogy

Three distinctive phases in floristic differentiation may be defined: pre-Pangæaic, Pangæaic and post-Pangæaic. From the Silurian to Lower Carboniferous, uniformity persisted with only one cosmopolitan kingdom being recognised. From the Late Carboniferous to Lower Cretaceous (during the Pangæaic phase of Earth history) a trifold zonation is generally recognised: the southern (Gondwanan) and northern (Siberian/Angaran) high latitude kingdoms, separated by the tropical Laurasian Kingdom. Two cycles of increasing provincialisation (Meyen, 1987) characterise this Pangæaic phase, with maxima being reached in the Upper Permian and Lower Cretaceous. During the phase

of continental dispersal from the Upper Cretaceous, a new floristic pattern is forged which reaches maximum differentiation today.

GLOBAL PLANT DIVERSITY TRENDS
The three plant divisions

On Fig. 1, the apparent global diversity trends are plotted separately for the three, successively-evolving, major vascular plant groups–the pteridophytes (psilophytes, lycopods, horsetails and ferns; Fig. 3), gymnosperms (conifers, cycads etc.; Fig. 3) and angiosperms (flowering plants; Fig. 4). This is not only instructive, but obligatory, since the best currently available data sets for each group have been quite differently derived and expressed:

i) The pteridophyte curve expresses the global megafloral species count per geological age as plotted by Niklas *et al.* (1983). The majority of the data analysed were Euramerican (the authors are not aware of any published diversity curve for the pteridophytes at the family level).

ii) The gymnosperm curve traces the global tally of families per geological stage based on seed-bearing fruit–as derived in a recent revised classification of the group by Anderson and Anderson (*in press*).

iii) The angiosperm curve plots the number of first appearances of extant families per age based on fossil pollen (Crane, 1987; after data in Muller, 1981). No systematic attempt has been made to institute additional families based on extinct taxa.

Subdued observed curves

It is necessary to distinguish clearly between 'observed' (as plotted here), 'preserved' and 'existed' diversity (Anderson and Anderson, 1995). There occurs an unknown gap between the observed (sampled, described) record and the preserved (potential) record. Whilst the shape of the observed curves as traced on Fig. 1 may be generally true, their topography is likely to be highly subdued. Were it possible to draft the existed curve, a more pronounced profile would probably be seen, with the peaks far more elevated and the lows more sharply defined. In interpreting these curves, the reader should also be aware that they potentially incorporate biases in sampling (for example, a greater number of systematic studies of Late Permian versus Early Triassic floras).

Diversity heydays

The heydays (diversity peaks) of the three successively dominant plant divisions occurred, apparently, in the Late Carboniferous, Late Triassic and

Pleistocene, respectively. The most intriguing of these peaks is perhaps that of the gymnosperms in the Late Triassic, at the culmination of a period of explosive radiation following the greatest of all extinction events (Anderson and Anderson, *in press*). The end-Permian extinction very nearly terminated gymnosperm history before the group reached its maturity.

GONDWANAN FOSSILIFEROUS STRATA
Resolution of correlations
Plotting and interpreting the evolutionary patterns of terrestrial life depends on many factors. Not least of these is the accuracy of correlation of the fossiliferous beds yielding the raw data. But, as Jim Collinson, Chairman of the Gondwana Subcommission, wrote (May 1998, letter) shortly before the Gondwana-10 Congress: *"the global correlation of late Paleozoic-Mesozoic Gondwana sequences has not been resolved in any detail"*. It was his opinion that the most pressing task of the Subcommission should be the closer resolution of these terrestrial correlations.

The scale employed here in plotting the fossil-bearing beds is generally about 6 to 7 Ma in duration. This is too coarse to debate the true rate of explosive speciation, or to differentiate between geologically instantaneous extinction events and the gradual decline of floras (see Bowring and Martin, 1999).

The richest strata
The principal vascular palnts on which this paper is based are to be found in different Gondwana continents and basins at different times (Anderson and Anderson, 1985). The most productive strata for the Carboniferous, for instance, outcrop in South America and Australia, whilst southern Africa (apparently under ice for the duration) yields a virtually complete blank for the period. Good Permian floras, on the other hand, are found everywhere in Gondwana, but the fullest sequence through the period is developed in a series of rift valleys in India. Whilst the richest single plant-bearing formation in the Triassic is the Molteno Formation of the Karoo Basin, South Africa, the most complete succession of floras for the period is undoubtedly that found in the series of basins down the active eastern margin of Australia and Tasmania.

EVOLUTIONARY PATTERNS
The Gondwana picture
Whilst the plant kingdoms and diversity trends represent the global picture, the evolutionary

patterns plotted on Fig. 2 are exclusively those for Gondwana. In many ways this picture is significantly different from any expressing the overall global scenario. For instance, the dominant gymnosperm orders-the Ottokariales (*Glossopteris*) and Umkomasiales (*Dicroidium*) (Fig. 3)-that characterise the Gondwana Permian and Triassic, respectively, are virtually endemic to the Gondwana Kingdom.

Turnover pulses
A particularly striking feature of plant history, when viewed at this evolutionary scale is the pattern of episodic turnover pulses followed by recovery and radiation or relative stasis. Ten such seminal moments are recognised, punctuating the flow of Gondwana floral history. Most coincide with the major global extinction events that decimated all of life, plant and animal, terrestrial and marine; whilst others, though global, apparently affected only plant life (pulses 2 and 9, Fig. 2), or were essentially Gondwanan, related to the advance and retreat of the Carboniferous ice sheet (pulses 4 and 5, Fig. 2).

The end-Cretaceous non-event
One of the most interesting of enigmas is why animal life, both marine and terrestrial, was decimated at the end of the Cretaceous, whilst plant life was apparently untouched (Hickey, 1981). The diversity curves of neither the pteridophytes, gymnosperms or angiosperms show any significant response to the extinction event. This may be the only one of the big five (six) extinction events to have been caused by a bolide. Plants, with their very different repertoire of dispersal and hibernation strategies (Knoll, 1984) could perhaps live through the relatively short-term environmental changes initiated by a bolide impact, but not the longer term climatic changes brought about by changing continental configurations.

SILURIAN: terrestrial life appears in the tropics
During the Silurian, Laurasia sat astride the Equator, whilst Gondwana, lying to the south and east of the Iapetus, Rheic and Palæo-Tethys Oceans (Scotese, 1997a), stretched from the southern pole (north Africa/South America) to the Equator (Australia).

The relatively short-lived glacial conditions of the later Ordovician apparently ameliorated rapidly, with the Silurian world thereafter developing under Hot House conditions (Scotese, 1998; Scotese *et al.*, 1999).

The First Extinction

The first of the five main Phanerozoic extinctions may have been the cause or the result of the almost instantaneous shift from Ice House to Hot House at the close of the Ordovician. With 27% of marine invertebrate families (and 57% of genera) lost, in extent it was second only to the end-Permian extinction (Sepkoski, 1986; Sepkoski and Raup, 1986; Erwin, 1993).

The Silurian revolution

True to the concept of environmental change driving evolution, there was a radical turn after the end-Ordovician warming and extinction. In the tropical belt of Laurasia (the Wenlockian of Podolia, Czechoslovakia, England, Ireland and New England), *Cooksonia* is the earliest known vascular (protostelic) plant to establish itself firmly on land (Meyen, 1987). This solitary genus, with slender, repeatedly-forking branches bearing terminal pin-head sporangia, would appear to have formed a low-growing ground cover along the equatorial belt. Its wind-dispersed spores, with their resistant coating, were well adapted for widespread colonisation. Aside from a recent enigmatic record from Bolivia (Morel *et al.*, 1995), the only known Gondwanan occurrences of *Cooksonia* are those from Australia, which, like Laurasia, lay astride the Silurian Equator, but was situated more or less on the far side of the globe. The fossiliferous detritus comes from two areas: the Mudgee Beds of New South Wales and the Mount Daubeny Group near Broken Hill (White, 1986), presumably in the Wenlockian. It should be stressed that the correlation of the Australian Siluro-Devonian strata are as yet insufficiently resolved to verify global phytogeographic interpretations.

By the Ludlovian, two distinctive divergent lineages, the zosterophylls and rhyniophytes, had become established throughout the tropics (White, 1986; Gensel and Andrews, 1987, Hill *et al.*, *in press*). The former gave rise to the lycopods that were to periodically dominate the Gondwana vegetation until the Early Triassic, and the latter gave rise to all other lines of vascular plants, including the horsetails and gymnosperms.

Outside of Australia, in higher latitudes, the Gondwana landscape apparently remained barren of vascular plant life.

DEVONIAN: colonising Gondwana

During the Devonian, near closure between Laurasia and Gondwana occurred due to the marked northward drift of West Gondwana.

Silurian Hot House conditions prevailed through the first half of the Devonian, but a marked cooling dip characterises the latter half of the period and glaciation occurred in parts of South America (Caputo, 1985).

The Second Extinction

With 19% of marine families (and 50% of genera) becoming extinct, this event was similar in proportion to the end-Cretaceous event (Sepkoski, 1986; Sepkoski and Raup, 1986). How sudden was the extinction? Did it occur in a geological instant through a bolide hit or more gradually as a result of the meeting of the supercontinents, sea level fall, and/or climate change?

Global colonisation of plants

In the Hot House world of proto-Pangæa, terrestrial plant life went through a global explosion. The colonisation of Gondwana occurred rapidly through the Devonian, as did the diversification of the pteridophytes, although fossiliferous terrestrial Early Devonian strata are not widely known.

Australia (the Yea Beds in Victoria; White, 1986; Hill *et al.*, *in press*) has one of the most important early land-plant assemblages in the world–the *Baragwanathia* Flora. The flora actually occurs in both the lower (Ludlovian of the Silurian) and upper (?Pragian of the Devonian) horizons at Yea, which are separated by some 30 Ma and 1700 m of Ludlovian siltstone (Garratt, 1978, 1981; Garratt *et al.*, 1984). Both the Late Silurian and Early Devonian floras are very cosmopolitan in character, but the later assemblage is the markedly more species-rich. It includes *Baragwanathia* (Fig. 3), the earliest known genus of herbaceous lycopod (similar to living members of the group), which was derived from the zosterophylls (still present), together with the rhyniophytes and the trimerophytes, which evolved from them and, in turn, gave rise to the progymnosperms.

At the end of the Lower Devonian occurred the second turnover pulse in Gondwanan floral history. The Giant Clubmoss Flora, dominated by a diversity of arborescent lycopods, replaced the *Baragwanathia* Flora (White, 1986; Hill *et al.*, *in press*). Whilst the earlier land plants were all small with no development of secondary wood, the vegetation now became characterised by trees for the first time. This new arborescent vegetation was initially represented by the lycopods, but later in the Devonian they were joined by members of the progymnosperms, including genera such as *Archæopteris* (Anderson *et al.*, 1995; Gess and Hiller, 1995).
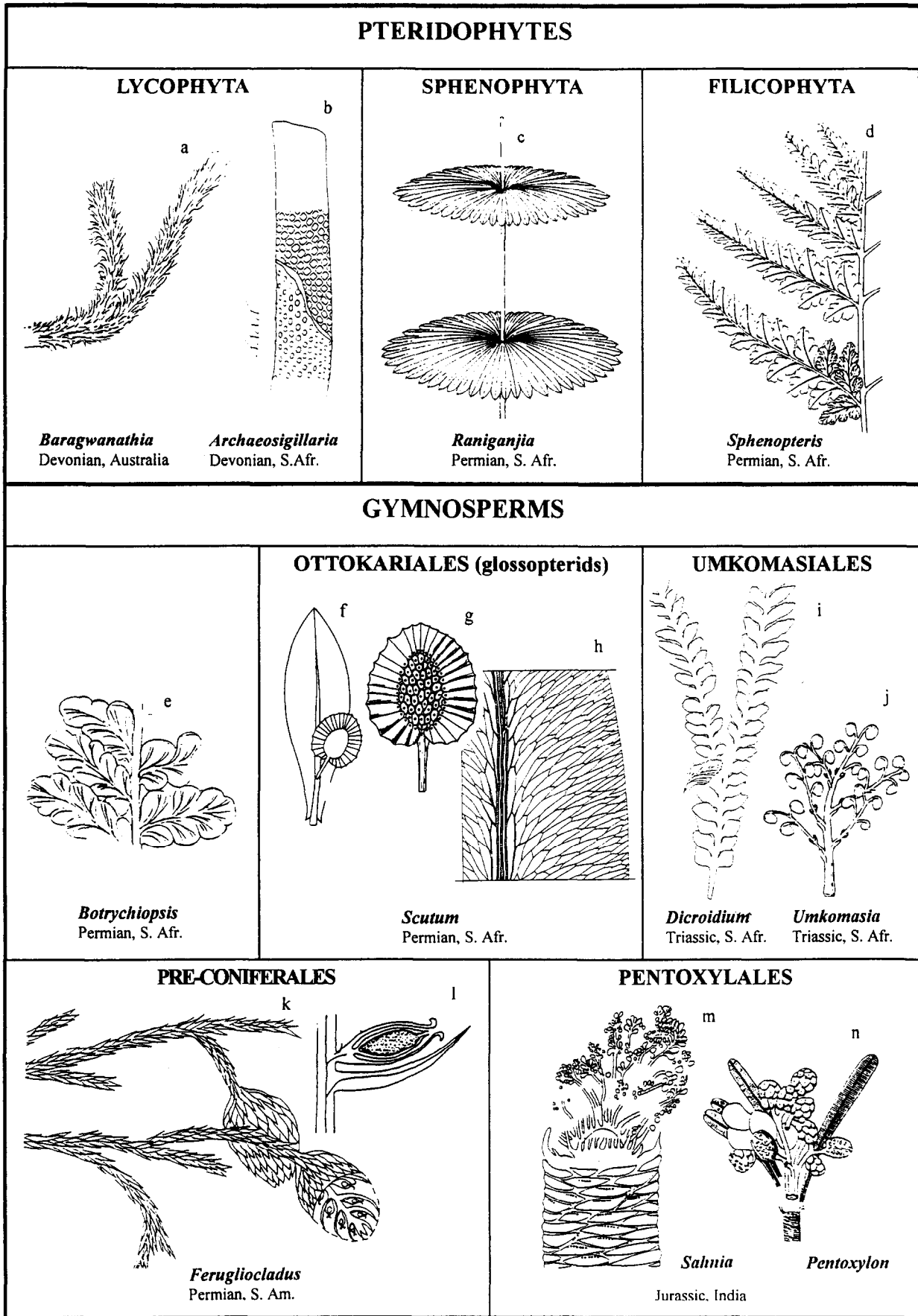
PTERIDOPHYTES

LYCOPHYTA

b

a

Baragwanathia
Devonian, Australia

Archaeosigillaria
Devonian, S.Afr.

SPHENOPHYTA

c

Raniganjia
Permian, S. Afr.

FILICOPHYTA

d

Sphenopteris
Permian, S. Afr.

GYMNOSPERMS

e

Botrychiopsis
Permian, S. Afr.

OTTOKARIALES (glossopterids)

f

g

h

Scutum
Permian, S. Afr.

UMKOMASIALES

i

j

Dicroidium
Triassic, S. Afr.

Umkomasia
Triassic, S. Afr.

PRE-CONIFERALES

k

l

Ferugliocladus
Permian, S. Am.

PENTOXYLALES

m

n

Sahnia

Pentoxylon

Jurassic, India

Figure 3. *A selction af genera representing important Gondwana plant groups. (a) Sketch by H.M. Anderson; (b-h) from Anderson and Anderson (1985); (i-j) from Anderson and Anderson (1983); (k, l) from Archangelsky and Cúneo (1987); (m) from Vishnu-Mittre (1953); (n) from Sahni (1948).*

The Late Devonian (Frasnian-Famennian) extinction apparently had a profound effect on global plant life. It appears to have been the trigger for the rise of the gymnosperms along the equatorial belt.

Amphibian prelude

Fossil evidence defining the transition between osteolepiform fish–the immediate sister group of the land vertebrates–and the earliest amphibian tetrapods, remains sparse (Carroll, 1988, Behrensmeyer *et al.*, 1992, *in prep.*). The first known amphibian fossils (ichthyostegids and anthracosaurians that presumably preyed on aquatic animals and arthropods) are from the uppermost Devonian of East Greenland and Russia. Late Devonian Gondwanan remains are even more sparse, consisting of amphibian footprints and a single jaw from Australia (Warren, *pers. comm.* 1998). All these sites were in the tropical belt. Vascular plants had already colonised the land for some 50 Ma before the tetrapods. It therefore appears that the Late Devonian extinction may have caused not only the origin of true gymnosperms, but also the terrestrialisation of the vertebrates.

CARBONIFEROUS: competing with ice

During the Early Carboniferous, the Rheic Ocean, now narrowed to a seaway, still separated Euramerica from Gondwana. By the Late Carboniferous, the northern and southern landmasses were suturing along the Appalachian Mountains, Gondwana rotated clockwise and 'Australia' shifted southwards from tropical to temperate latitudes through at least 20°.

Ice House Gondwana

The dip in global temperatures, starting in the Mid-Devonian and progressing ever deeper towards the Ice House of the Upper Carboniferous, no doubt relates closely to the coupling of the northern and southern continents to form Pangæa with the radical rerouting of ocean currents.

In Fig. 1, the Gondwana icecap is depicted as centred earlier in the period on southern 'Africa' and southeastern 'South America'; and spreading through the Carboniferous to eventually cover much of the supercontinent (see Scotese, 1997a). By the Late Carboniferous only the northern belt of 'Africa', the northern and western rims of South America, and the eastern periphery of Australia are shown as remaining exposed (for further details see Scotese *et al.,* 1999; Smith, 1999). It must be emphasised that many details of the history of

the growth and retreat of the Gondwana icecap remain to be resolved.

Plant life around the icesheet

The second of the mass global extinctions, in conjunction with the spreading mega-icecap, precipitated wholesale change in the terrestrial biosphere.

Whilst life flourished along the tropical belt of Laurasia–with the giant lycopod and horsetail forests contributing to extensive lowland coal deposits–that in Gondwana led a more marginal existence.

Two entirely different, successive floras characterised the harsh landscape fringing the Gondwana icecap during the Early and Late Carboniferous. Between these two floras there is a relative blank in Gondwana (to be clarified by improved correlations), with the inclement conditions (at least in eastern 'Australia') exacerbated by major volcanic activity. It is in eastern 'Australia' and parts of 'South America' that evidence must be sought. In the Early Carboniferous a "struggling Giant Clubmoss [lycopod] Flora" which "never reached luxuriance" (White, 1986; see also Sessarego and Césari, 1989) represents the final phase of the Devonian floras. By the Late Carboniferous an impoverished, low diversity, *Nothorhacopteris-Botrychiopsis* (seed fern) Flora had taken hold under the extreme climatic conditions (Morris, 1975; Retallack, 1980; Archangelsky *et al.*, 1987; Azcuy *et al.*, 1987; Hill *et al., in press*).

The icecap caused the decimation of the pteridophytes and the rise of the gymnosperms which were to dominate for 200 Ma till the Mid-Cretaceous.

Insect record of the Gondwanan Late Carboniferous

Whilst the true insects make their earliest recorded appearance in remarkable diversity (9 orders with 79 families reported in Carpenter, 1992) in the tropical vegetation of the Laurasian Late Carboniferous, their occurrence in contemporaneous strata in Gondwana remains relatively meagre (Schlüter, 1990). Several specimens have been recorded from the Malanzan and Bajo de Veliz Formations of South America (e.g. Pinto and Ornellas, 1978a, b; Riek and Kukalová-Peck, 1984). Only a few scattered specimens are known from elsewhere in Gondwana, and most of these are from formations of disputed age–possibly Lower Permian.

Amphibian/reptilian evidence in Australia

Recent discoveries of Lower Carboniferous tetrapods in Australia (still situated in more or less

tropical latitudes) indicate that the stem taxa of the temnospondyl and lepospondyl amphibians, and of the earliest amniote reptileans, colonised Gondwana early and were all closely related to the Laurasian taxa (Carroll, *in prep.*; Warren, *pers. comm.* 1998). None seem to have ventured further south, however, towards the spreading Gondwana icecap. No later Carboniferous tetrapod fossils have been found anywhere in the Southern Hemisphere continents. The spreading ice and inclement conditions may have driven the amphibians and reptiles from their Australian stronghold by the latter half of the period. Tetrapod diversification continued apace through the Carboniferous along the tropical belt, and by the end of the period the first clear vertebrate herbivores, still few in number, had appeared (Tiffney, 1992).

PERMIAN: the glossopterid empire

The Late Permian, at around 250 Ma, represented the climax of collision between Gondwana and Laurasia. The Iapetus Ocean between the two continental plates drained during the Permian, resulting in a global sea level drop (Scotese, 1997a).

The Gondwana ice sheet melted and global warming continued throughout the Permian to reach, according to some (e.g. Scotese, 1998), a peak at the Permo-Triassic boundary. Figure 1 shows the alternative view that this peak was reached in the Middle to Late Triassic (de Wit, *pers comm.* 1998; Turner, 1999).

Glossopterid radiation

With the retreat of the supracontinental ice sheet and warming climates, the glossopterids colonised and radiated throughout Gondwana, reaching peak diversity in the Late Permian. The widespread coal-forming forests covering the floodplains of Gondwana in both the Early (Artinskian) and later (Kazanian) Permian were heavily dominated by *Glossopteris*. There is an enormous amount of literature on this order of plants, whose fruit are found attached to the foliage or reduced scale leaves (e.g. Rigby, 1978; Rösler, 1978; Chandra and Surange, 1979; Anderson and Anderson, 1985; White, 1986; McLoughlin, 1990a, b; Pigg and Trivett, 1994). But there is still heated controversy concerning virtually all issues surrounding the group: classification, reproductive morphology, diversity, phytogeography and nomenclature. Some authors recognise numerous species based largely on the leaves, whilst others are more conservative, seeing far fewer species based on the female fruit. Either way, a pattern of generic

ubiquity and species endemism when considering the reproductive organs is perhaps less open to dispute.

Of great significance, aside from the glossopterids, was the origin of the Voltziales–probably from the Cordaitanthales–and their rise to dominance in the latest Permian. They are one of the few plant groups that survived the end-Permian extinction and it is from them that true conifers apparently evolved in the Early Triassic (Taylor and Taylor, 1993; Anderson and Anderson, *in press*). Amongst the pteridophytes, the arborescent lycopods dominated many Gondwanan wetland assemblages early in the Permian (particularly in western Gondwana), as did a diversity of sphenophytes later in the period.

Hemiptera (bugs, etc.) co-evolving with *Glossopteris*

Along with the spread of the new glossopterid-dominated, post-Ice House vegetation, the insects flourished across Gondwana. By the Late Permian, the faunas–known particularly from South Africa (Estcourt Formation) and eastern Australia (Belmont locality)–were well-established and diversified with over 200 species recorded in 21 orders (Anderson and Anderson, 1993). The Hemiptera are generally dominant in both numbers and diversity, comprising nearly half the total number of known species. They rose to such prominence in Gondwana in co-evolution with the glossopterids. The Coleoptera (beetles) and Blattodea (cockroaches) (the other major herbivorous groups by the later Triassic) were still only minor elements in the faunas.

Therapsids (mammal-like reptiles) and herbivory

Whilst the history of tetrapod-vertebrate evolution through the first half of the Permian is still preserved almost exclusively within the tropical Laurasian Kingdom, the focus shifts strongly to Gondwana, and particularly the fossiliferous Karoo Basin of South Africa, through the latter half of the period (Anderson and Cruickshank, 1978). Vertebrate herbivory came to maturity with the therapsids during the Permian. The first fully-established terrestrial ecosystems involving plant-vertebrate-insect interaction are the hallmark of the Permian (Tiffney, 1992). The co-radiation of the glossopterids, Hemiptera and therapsids (most importantly the dinocephalia and dicynodonts) in Gondwana reflect this event most fully (Anderson and Anderson, 1993).

The Third Extinction

The end-Permian extinction was by far the most cataclysmic, with 57% of marine families (and

83% of genera) destroyed. The debate continues as to its cause. Evidence does suggest a rapid event: a bolide rather than global warming (Erwin, 1993; Erwin, 1999; Bowring and Martin, 1999). However, features traditionally associated with bolide impact (widespread shocked quartz, microspherules and Ir anomalies) have not been readily forthcoming and a multicausal and multiphase extinction may have occurred (Stanley and Yang, 1994; Erwin, 1995).

TRIASSIC: the gymnosperm heyday

Pangæa settled again in the earliest Triassic with the continental shelves flooding globally. Northward drift continued, over the 43 Ma duration of the period, through a significant range of latitude.

Hot House conditions prevailed through the Triassic, possibly reaching record super-Hot House proportions in the mid to later stages of the period (de Wit, *pers comm*. 1998; Turner, 1999). A clear peak in biodiversity apparently coincided with this putative peak of global solar-energy uptake. Hot House conditions continued throughout the Mesozoic, apart from a relatively brief mini-Ice House occurrence at the Jurassic-Cretaceous boundary.

The Triassic explosion

The evidence suggests that the radiation of terrestrial life in the wake of the end-Permian extinction was of record proportions; prompting the hypothesis that the greater the extinction the greater the radiation (Anderson and Anderson, *in press*). By the Late Triassic, the gymnosperm heyday was in place and there is reason to suggest, in marked contradiction to traditional belief, that it might have surpassed the angiosperm heyday of today in richness – at least at order and class, if not species, level (*ibid.*).

In the depositional basins at least, *Dicroidium* (Fig. 3) dominated both woodland and forest through most of the Triassic and across the Gondwana Kingdom. It was during the Triassic that the conifers appeared and radiated (Bamford and Corbett, 1994; Yao *et al.*, 1997; Bamford, *in press*). By the close of the period, six of the eight extant families were already in place. Most prominent, particularly in the Lower Triassic of Gondwana, as evidenced largely by silicified wood, were the Podocarpaceæ and Araucariaceæ. Along an exponentially growing diversity curve there appeared (with *Dicroidium* and the conifers) numerous new families in over ten new orders of gymnospermous plants. Amongst these were the Bennettitales and Pentoxylales (Fig. 3) that emerged later in the

period and were important through the Jurassic and earlier Cretaceous (Anderson and Anderson, *in press*; Hill *et al.*, *in press*; McLoughlin and Tosolini, *in prep.*).

Though there is no evidence yet from Gondwana, and though not generally accepted (see Taylor and Taylor, 1993), rare inflorescences, pollen and foliage from the Late Triassic tropics of North America provide an indication of the earliest appearance of the angiosperms as one expression of the post-Permian explosion.

The demise of the Gondwana lycophytes and sphenophytes, at least in playing a prominent role as widespread dominants in wetland floras occurred through the Triassic. Interestingly, during both the Permian and Triassic, these two groups appear to have been mutually exclusive in this regard. The lycophytes appeared first during the phase of recovery in each period, and were followed by the sphenophytes. Ferns, though rarely dominating communities, evolved to marked diversity by the Late Triassic.

Coleoptera radiation

Insect life radiated explosively along with the plants through the Triassic. This is shown by the large collections from the Molteno Formation. (Anderson *et al.*, 1998). A remarkable tally of 335 insect species (in 117 genera and 18 orders) have been identified from 43 sites. Since the great majority of these species (*ca* 90%) appear in only one assemblage, and many others in only two or three, it is clear that numerous species remain undiscovered. Statistical extrapolations suggest 7740 species being preserved in the Molteno Formation (Anderson and Anderson, 1995; Anderson *et al.*, 1996). Whilst Coleoptera were still insignificant in Permian faunas, they now constitute around half the total faunal diversity–a pattern not unlike today. Hemiptera and Odonata (dragonflies) were the next most diverse forms, whilst Blattodea are preserved most abundantly.

The origin of dinosaurs and mammals

Shadowing the explosive radiation of plants and insects in the Triassic occurred a similarly rich diversification of tetrapods (Anderson and Anderson, 1993). At the outset of the period, elements of the low diversity *Lystrosaurus* Zone assemblage could be traced across Gondwana (and into Asia). By the close of the Triassic, both the dinosaurs and mammals had made their earliest appearance (Benton, 1993; Forster, 1999). Of particular importance is the Ischigualasto Formation, Ischigualasto Basin, northern Argentina,

which has yielded the most primitive known dinosaurs from Gondwana (Sereno, 1997).

The Fourth Extinction

The Late Triassic extinction (with 23% of marine families and 48% of genera being erased) was approximately at the same level as those of the Late Devonian and end-Cretaceous. Evidence suggests it was a double event (Benton, 1993), with the first crisis at the Carnian-Norian boundary (220 Ma) and the second at the Triassic-Jurassic boundary (208 Ma).

The effect of the extinction on land was of profound proportions. The gymnosperm radiation, reaching a maximum of 26 families, including several new orders, by the Carnian (Anderson and Anderson, *in press*) was cut short. Where the Third Extinction had initiated the radiation, the Fourth Extinction ended it. Had the extinction not hit, it is possible that the gymnosperm radiation would have endured (as did the angiosperms later) through the Jurassic to yield extraordinary unexpressed riches. The effect of the extinction on tetrapod evolution was equally dramatic. The rhynchosaurs, basal archosaurs and the therapsids disappeared, allowing the dinosaurs, which had only just emerged, to develop dramatically (Benton, 1993).

JURASSIC:
volcanism, conifers and bennettitaleans

With the fragmentation of Gondwana occurred the intrusion of dolerites and extrusion of sheet lavas on an unprecidented scale. Their geographic focus shifted across Gondwana through the Jurassic and into the Lower Cretaceous (see Hawkesworth *et al.*, 1999). Plotting these lava floods spatially and temporally in relation to the palæogeographic trends of the major plant (conifers, Bennettitales, Pentoxylales) and tetrapod (dinosaurs) groups through the Mid-Mesozoic should reveal interesting patterns.

The Jurassic was mainly a Hot House world. The semi-Ice House conditions at the close of the Jurassic and persisting into the Early Cretaceous (Francis and Frakes, 1993; Francis, 1994) appears to have had a profound affect on the dinosaurs, but far less so the plants. This disassociation between the evolution of the plants and dinosaurs was a conspicuous pattern throughout the Jurassic and Cretaceous.

After the Fourth Extinction

While the vertebrate record indicates substantial diversification, the plant record is more equivocal. A surge in plant diversification after an extinction

has not yet been documented for the Jurassic in terms comparable to that for the radiation of gymnosperms following the end-Permian extinction. However, this may in part be due to a lack of studies on Gondwanan Jurassic floras. A review of the disparate Gondwanan palæobotanical literature suggests that a series of botanical novelties did arise amongst pteridophytes and gymnosperms during the Jurassic. Most notable is the rise and diversification amongst cheirolepidiacean conifers, Caytoniales and a series of seed-fern groups of obscure affinities (e.g. pachypterids, palissyoids, *Komlopteris*, *Ticoa*, *Archangelskya*) at that time.

Acme of conifers and bennettites

The Jurassic was clearly the peak of conifer dominance with respect to biomass, if not diversification (at least not at family level). The suite of six extant families that had originated in the Triassic persisted and were augumented by only one minor new family, the Sciadopityaceæ (Anderson and Anderson, *in press*). The two other dominant gymnospermous orders of the period, the Bennettitales (global) and Pentoxylales (endemic to Gondwana), had also appeared in the Triassic and continued through the Jurassic. The bennettites show a dramatic diversification of frond architecture in the Jurassic (Herbst, 1966; Herbst and Troncoso, 1996; McLoughlin and Tosolini, *in prep.*), resulting in their assignment to several foliage genera. Unfortunately, reproductive structures have been too infrequently preserved to assess whether the diversity in foliage types is matched by reproductive novelty.

The pteridophytes, dominant in both biomass and diversity through most of the later Palæozoic, now played a distinctly more subserviant role. The one line that did flourish was the ferns, with their heyday expressed in the Late Jurassic and Early Cretaceous, seemingly in response to the onset and close of the mini-Ice House spanning the period boundary. The plethora of dispersed microspore taxa in Jurassic palynomorph assemblages suggests that the macrofossil record probably underestimates the diversity and ecological significance of ferns during this period.

Enigmatic dearth of insects

Whether through a lack of preservation or real scarcity, insects remain virtually unknown in Gondwana Jurassic strata (Schlüter, 1990). Certainly, the desert landscape and extensive flood basalts will account for this in areas such as South Africa and Antarctica, but not the absence in the many plant-bearing Jurassic strata of Australia. With 11 orders

ANGIOSPERMS

This diagram shows four key angiosperm (flowering plant) families, which, together, demonstrate the principles of island biogeography on the largest scale (see Wilson, 1993): colonisation and diversification on the spreading Gondwana continental fragments. These are outlined here in order of their first appearance in the geological record (Dettmann, *in prep.*; Hill, *in press*; see also Heywood, 1993).

Winteraceae
Time of origin: Aptian/Albanian (or earlier)
Centre of origin: north Africa/Brazil Rift (tropical forest)
Heyday: Late Cretaceous to Palaeogene
Extant distribution: typical Gondwana distribution, excluding Africa
Extant diversity: 7-8 genera (60-120 species)

Proteaceae
Time of origin: Late Cenomanian
Centrae of origin: north Africa/Brazil Rfit (tropical forest)
Heyday: *i)* Campanian-Eocene (Australasia)
    ii) Neogene-Recent (southern Africa, southwest Australia)
Extant distribution: Gondwana, spreading into southeast Asia and southern North America
Extant diversity: *ca* 75 genera (1600 species)
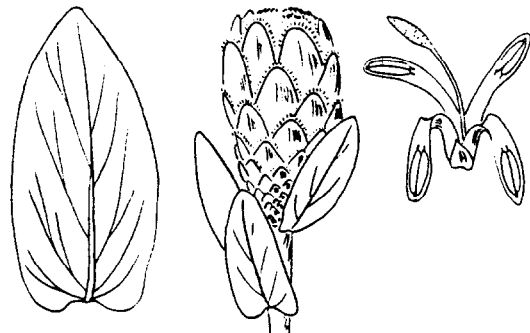
Nothofagaceae
Time of origin: Late Cretaceous (Campanian)
Centre of origin: Antarctic Peninsula/Patagonia
Heyday: *i)* as for time and centre of origin
    ii) Late Eocene (southern Australasia/New Zealand)
Extant distribution: South America and Australasia (into New Guinea)
Extant diversity: 1 gensus (*ca* 50 species)
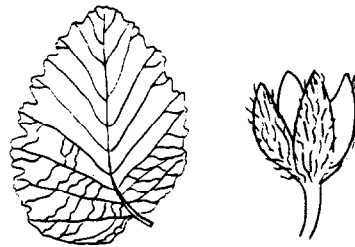
Asteraceae
Time of origin: ?Eocene (Orange River), Oligocene (90°E Ridge)
Centre of origin: Orange River/90°E Ridge/Patagonia
Heyday: Recent (following explosive radiation and world-wide occurrence by the Miocene; through evolving optimal dispersal mechanisms)
Extant distribution: world-wide
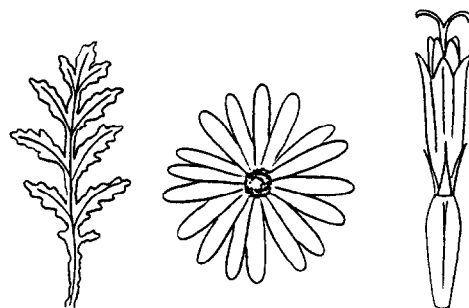Extant diversity: *ca* 1100 genera (25,000 species)

Figure 4. Towards patterns of angiosperm radiation and continental dispersal from the Mid-Cretaceous to present. Sketches by H.M. Anderson.

and 120 families reported in Carpenter (1992), no such dearth is reflected in the Laurasian Jurassic.

The 'first dinosaur empire'

Cursory perusal of a recent, calibrated phylogeny of the dinosaurs (Sereno, 1997) shows a clear, broad division into two historical phases: the first from the Late Triassic to the Late Jurassic; the second persisting through phases will be loosely called the 'first' and 'second dinosaur empires'.

The 'first dinosaur empire' is characterised by continual innovation and renewal of the origin and extinction of families and higher taxonomic lineages. A massive turnover phase, coinciding temporally with the cooling curve in the Late Jurassic, brought this empire to a close. The hyperdynamics of dinosaur evolution through this interval reflects the pattern of fragmentation of Pangæa, but contrasts remarkably with the more cosmopolitan signature of the world's flora (Meyen, 1987).

CRETACEOUS: of flowers and pollination

With fragmentation largely complete, the dispersal of the Gondwana continents to widely separated positions occurred through the Cretaceous. This coincided broadly with the radiation of the angiosperms (Fig. 4). As the isolation of the island continents increased, so the exponential growth in angiosperm diversity occurred.

Climatic trends through the Cretaceous were the reverse to those in the Jurassic. A Hot House world persisted after the initial warming from the brief semi-Ice House trough at the Jurassic-Cretaceous boundary (Scotese, 1998).

Origin and radiation of the angiosperms

An intriguing reversal in patterns between plants and tetrapods characterised the Cretaceous. The 9th, and perhaps most incisive, of the plant turnover pulses divides the period into an earlier half, with a continuation of the Jurassic floral patterns (Menendez, 1966, 1969; Anderson and Anderson, 1985; Archangelsky, 1996; Banerji, *in prep.*; Hill *et al., in press*; McLoughlin and Tosolini, *in prep.*), and a latter half, constituting the radiation of the angiosperms. The earliest undisputed angiosperm pollen is probably that found in Israel and Britain, but a tropical (African-South American) centre of origin has been inferred (Crane, 1987). Angiosperms then steadily diversified and extended their range to higher latitudes throughout the remainder of the Cretaceous (Crane, 1987; Drinnan and Crane, 1989, Hill *et al., in press*). Cretaceous angiosperm radiation may have occurred in two

pulses: an Early Cretaceous differentiation and diversification of monocots and magnoliids; and a subsequent (Albian-Cenomanian) origin and expansion of hammamelid dicots. By Cenomanian times angiosperms constitute about 50% of some assemblages in high latitude eastern Australian localities (McLoughlin *et al.*, 1995).

The dramatic radiation of the angiosperms is perplexing in that it is in no way associated with a sudden extinction event, nor does it seem to touch the broad pattern of dinosaur or insect evolution in any significant way.

Co-evolution of insects and angiosperms?

It has long been supposed that the radiation of the angiosperms fueled the extraordinary diversification of the insects (Gould, 1996). However, the family level record of insect diversity shows no signature of the great Aptian-Cenomanian angiosperm radiation. A more or less continuous exponential diversification of insects at the rank of family can, in fact, be traced from the Early Triassic to the present time (Labandeira and Sepkoski, 1993). They also found that 65-88% of modern insect mouthpart classes had already appeared by the Middle Jurassic. The insect orders most closely associated with pollination–the Coleoptera, Diptera, Lepidoptera and Hymenoptera–all arose in the Permian or Triassic and underwent major initial radiation in the Triassic and Jurassic (Crepet and Friis, 1987; Labandeira and Sepkoski, 1993; Labandeira *et al.*, 1994).

In marked contrast to the Jurassic, three richly fossiliferous lake deposits reveal the character of Gondwana Cretaceous insect life. Three continents are represented: the Santana Formation of Brazil (Lower Cretaceous), the Koonwarra Lake fauna of Victoria, southeast Australia (Lower Cretaceous) and the crater facies capping the Orapa diamond pipe of Botswana (Mid-Cretaceous).

The 'second dinosaur empire'

The 'second dinosaur empire', in contrast to the first, is characterised by an essential stability; with far fewer extinctions and innovations at the family or higher level (Sereno, 1997). One definite phase of extinctions (amongst the herbivorous ornithischians, however, is seen in the later Aptian and Albian (*ibid.*). This coincides with the demise, in Gondwana, of the conifers, bennettitaleans and pentoxylaleans, and the radiation of the angiosperms. Interestingly, the several family lineages of sauropodomorph Saurischia were unscathed throughout these changes, suggesting that they were generalist browsers.

The Fifth Extinction

The effects of the Fifth Extinction have been briefly discussed under the section 'Evolutionary patterns'. Whilst the dinosaurs died out, apparently in a geological instant (Gould, 1996; Sereno, 1997), plant evolution, whether seen from a biodiversity or biomass perspective, shows no evident shift in pattern, at least in Gondwana.

CENOZOIC: towards the angiosperm heyday

Three features of continental drift characterise the Cenozoic and each clearly and contrastingly drives the evolutionary patterns and diversification on the Gondwana continents. Continuing separation of the continental fragments leads to ever greater isolation and independent evolution of endemic biota; the progressive closure of South America with North America and of India/Australia with Eurasia initiates reorientation of oceanic currents, the slide towards glaciation at the poles, and the shifting mosaic of forest, woodland and grassland biomes, as well as the mixing of northern and southern faunas and floras; the further northward swing of India and Australia through considerable latitudinal space causes regional climatic shifts and adaptive radiation on these continents.

The swing over some 50 Ma from Hot House conditions in the Eocene to Ice House conditions today is most reminiscent of the Carboniferous. In both instances, changing continental configuration led to the rerouting of oceanic currents and extensive polar glaciation. Significantly, it appears to be only during these two Ice House peaks of the Late Carboniferous and the Plio-Pleistocene that tropical forests spread along the equatorial belt. During the Hot House world of the Late Permian and Triassic, for instance, the latitudinal diversity gradient may well have been partially reversed, with the most luxuriant and diverse vegetation occurring in belts of middle latitude (Anderson and Anderson, *in press*) in Gondwana and Angara (the Permian Cathaysian flora may have been a diverse, wet, tropical flora, incorporating liana-like and mangrove-like elements—possibly more diverse than the Permian Gondwana or Angara floras). It would seem reasonable to assume an optimum window in the temperature/energy spectrum for maximum biodiversity, and that optimum is now along the tropical belt.

After the Fifth Extinction

The terrestrial world offered entirely new evolutionary challenges during the first few million years after the extinction of the dinosaurs. The mammals inherited a unique environment in which to radiate: whilst the tetrapods had been more or less wiped out, the environment was rich in plant and insect life (Knoll, 1984, 1986; Tiffney, 1992; Labandeira and Sepkoski, 1993).

Co-evolution of grassland and herbivorous tetrapods

Grassland pastures were perhaps the most significant innovation of the Cenozoic. As far as the authors know they were an entirely new vegetation type which allowed new tetrapod vertebrates to evolve. The earliest fossil evidence of grasses (pollen and leaf cuticles) appears in the Eocene at around 50 Ma (Muller, 1981; White, 1986; Gibbs Russell *et al.*, 1991; Macphail and Hill, *in press*). Grazing herbivores with high-crowned teeth adapted to chewing grass—abrasive with silica bodies in the epidermis also appear in the Eocene. By the Oligocene grasslands had become a widepsread vegetation type (*ibid.*). Grass features especially striking in their co-evolution with herbivorous tetrapods are the lack of repellant chemicals found in many other families and the intercalary meristems facilitating growth in spite of repeated grazing. With their much reduced florets and uniform wind-blown pollen (not even distinguishable to subfamily), the grasses are not intimately linked to the insects.

The phytogeography of grasses is intriguing. The subfamilies and tribes are distributed globally in broad climatic bands, the extant genera by continent. Perhaps they had already diversified to supra-generic level well before the continents became widely separated by oceans prior to their first fossil evidence.

The second absorbing feature of Cenozoic angiosperm history is the exponential trajectory of the diversity curve. Where the gymnosperms from the end-Devonian have undergone a very interupted and varied evolutionary story, the angiosperm picture, at least from the Early Cretaceous, has been one of uniform taxonomic radiation, albeit with different orders of angiosperms undergoing radiations at different times (Niklas *et al.*, 1983; Crane, 1987). The dispersal of the Gondwana continents must have accentuated this pattern.

A multitude of insect specialists

The exponential diversification of insects paralleled that of the flowering plants through the Cenozoic. At species level, at least, there is evidence for a high degree of co-evolution in this dual radiation of plant and insect (Labandeira and Sepkoski, 1993).

The Mammalian Empire

The dinosaurs left an ecological void after the end-Cretaceous extinction, reminiscent of that back in the Devonian, which was filled by land mammals. The mammals, insignificant since their earliest tentative beginnings in the Late Triassic, filled the vacuum with brilliant innovative success. Their diversification through the Cenozoic far exceeds that of any tetrapod group in earlier periods (*ibid.*), and parallels that traced by the plants and insects on the dispersing continental plates.

EXTANT: the angiosperm heyday

On contemplating continental drift through the Phanerozoic, it is evident that the number of continental fragments and their degree of scatter is greater today than at anytime earlier in this 540 Ma span. It might be argued, alternatively, that separation was greatest in the Late Cretaceous or Palæogene when South and North America were still divided, before India and Australia collided with Asia, and while Antarctica still supported a vascular flora. Clearly, though, the theoretical maximum has by no means been approached. It would prove an intriguing exercise, in terms of the established principles of island biogeography, to determine the optimum pattern of fragmentation and dispersal of the landmasses for maximum taxonomic diversity.

On the grand scale of things, we are still living in the Ice House world of the Pleistocene (Scotese, 1998). But, with the uncontrolled emission of diverse pollutant gasses, there may be a precipitate return to Hot House conditions, resulting in a chain reaction of biospheric changes.

The diversity of extant life

"With the help of other systematists", Wilson (1993) *"recently estimated the number of known species of organisms, including all plants, animals, and microorganisms, to be 1.4 million"*. His estimates put the insects, with 751,000 species, at a little over half the total known diversity. The higher plants come in second with 248,400 described species and the tetrapod vertebrates way down with 14,500 species. But the biodiversity audit is hopelessly incomplete, claimed Wilson (1993), and estimated that *"the grand total for all life falls somewhere between 10 and 100 million species."*

The latitudinal diversity gradient

A latitudinal gradient in species richness is convincingly demonstrated by Wilson (1993) as a true general principle of biology. That diversity generally increases towards the tropics is an undisputable pattern in the present world. Terrestrial biodiversity is concentrated in the tropical rain forests: *ca* 68% of the known 250,000 vascular plants occur in the tropics and subtropics, especially rain forests; 30% of the world's 9000 bird species occur in the Amazon Basin; insect faunas are immensely rich in the tropical forests. Estimates suggest that more than half the species of organisms alive today occur in tropical rain forests, although they occupy only 6% of the Earth's land surface.

However, evidence does tend to suggest that during the putative Late Triassic Hot House peak, for instance, the diversity gradient was reversed: the flora and insect fauna of the Molteno Formation (South Africa), at mid- to high latitudes in Gondwana, appears to have been significantly richer than that of tropical Euramerica (Anderson *et al.*, 1998).

An insect cornucopia

Comprising over half the known living species of organism on earth the insects have clearly won the biodiversity stakes–for multicellular organisms at least (Wilson, 1993). They have been considerably understudied and their proportionate lead in richness is estimated to be still far higher: at least 10:1 over the vascular plants, for instance. What is the secret of their success? Whilst at family level it has been established that there was little co-evolution between angiosperms and insects (Labandeira and Sepkoski, 1993), at species level the evidence suggests the reverse. Numerous cases of intricate symbiosis have been recorded between insect and plant taxa (Crepet and Friis, 1987).

The hominids

For most of the last five million years the hominids have been evolving on the African Savannah. Their phylogenetic tree appears to have radiated in response to the continued cooling trend through the Pliocene and Pleistocene, along with the parallel shift from woodland to grassland (Leakey and Lewin, 1996). The degree of diversity reached within the family remains a matter of debate, but sometime within the last quarter million years, the single species *Homo sapiens* emerged. And this species, with the unique ability to adapt and control the environment is causing the sixth global extinction (Wilson, 1993; Leakey and Lewin, 1996).

This startling event has occurred due to three waves of colonisation over the past 100,000 years–

an instant in geological time. The first wave of extinction (from 100,000-30,000 yr BP) occurred when anatomically modern *H. sapiens* spread from Africa across Eurasia; the second (from 30,000-1,000 yr BP) when the species expanded to the Pacific, Australasia and the Americas; and the third (from 1500-2000 AD) when technologically-advanced Europeans spread globally (Attenborough, 1987; Wilson, 1993; Leakey and Lewin, 1996). The third wave continues uncontrollably along an exponential curve of destruction with the exploding human population.

Will we pool our knowledge, resources and inclination in time to curb this sixth extinction before it reaches and exceeds the proportions of the earlier five events?

ACKNOWLEDGEMENTS

REFERENCES

Almond, J.E., Evans, F.J., Long, J.A., Anderson, M.E., 1998. Fish palæontology of the Cape Supergroup (U.Ordovician – L. Carboniferous), South Africa. Interim report for SACS Task Group for Biostratigraphy.

Anderson, H.M., Hiller, N., Gess, R.W., 1995 *Archæopteris* (Progymnospermopsida) from the Devonian of southern Africa. Botanical Journal Linnean Society 117, 305-320.

Anderson, J.M., 1981. World Permo-Triassic correlations: their biostratigraphic basis. In: Cresswell, M.M., Vella, P. (Eds.), Gondwana Five, Proceedings of the Fifth International Gondwana Symposium, Wellington, New Zealand, 1980. A.A. Balkema, Rotterdam, pp. 3-10.

Anderson, J.M., Anderson, H.M., 1983. Palæoflora of southern Africa: Molteno Formation (Triassic), Vol. 1: Part 1, Introduction, Part 2, *Dicroidium*. A.A. Balkema, Rotterdam, 227p.

Anderson, J.M., Anderson, H.M., 1985. Palæoflora of southern Africa: *Prodromus* of South African megafloras, Devonian to Lower Cretaceous, A.A. Balkema, Rotterdam, 423p.

Anderson, J.M., Anderson, H.M., 1993. Terrestrial flora and fauna of the Gondwana Triassic. Part 2-Co-evolution. In: Lucas, S.G., Morales, M. (Eds.), The Nonmarine Triassic. New Mexico Museum Natural History Science Bulletin 3, 13-25.

Anderson, J.M., Anderson, H.M., 1995. The Molteno Formation: window onto Late Triassic floral diversity. In: Pant, D.D. (Ed.), Proceedings of the international conference on global environment and diversification of plants through geological time. Society of Indian Plant Taxonomists. Allahabad, India, pp. 27-40.

Anderson, J.M., Anderson, H.M., in press. The gymnosperm heyday: as seen through the Molteno window. Strelitzia.

Anderson, J.M., Anderson, H.M., Cruickshank, A.R I., 1998. Late Triassic ecosystems of the Molteno/Lower Elliot biome of Southern Africa. Palæontology 41 (3), 387-421.

Anderson, J.M., Anderson, H.M., Fatti, L.P., Sichel, H., 1996. The Triassic explosion (?): a statistical model for extrapolating biodiversity based on the terrestrial Molteno Formation. Palæobiology 22 (3), 318-328.

Anderson, J.M., Cruickshank, A.R.I., 1978. The biostratigraphy of the Permian and Triassic. Part 5. A review of the classification and distribution of Permo-Triassic tetrapods. Palæontologia Africana 21, 15-44.

Andreis, R.R., Archangelsky, S., González, C.R., Gamundi, O.L., Sabattini, N., 1987. In: Archangelsky, S. (Ed.), El Sistema Carbonifero en la Republica Argentina. Academia Nacional de Ciencias, Cordoba, pp. 169-196.

Archangelsky, S., 1965a. Tafofloras Paleozoicas y eomeso-zoicas de Argentina. Boletín Sociedad Argentina Botanica 10 (4), 247-291.

Archangelsky, S., 1965b. Fossil Ginkgoales from the Tico Flora, Santa Cruz Prov., Argentina. Bulletin British Museum (Natural History), Geology 10 (5), 121-137.

Archangelsky, S. (Ed.), 1970. Fundamentos de Paleobotanica. La Plata Natural History Museum.

Archangelsky, S., 1981. *Fedekurtzia*, a new Carboniferous frond from Gondwanaland and its fructification. American Journal Botany 68 (8), 1130-1138.

Archangelsky, S., 1989. Plant distribution in Gondwana during the Late Paleozoic. In: Taylor, T.N., Taylor, E.L. (Eds.), Antarctic paleobiology, its role in the reconstruction of Gondwana. Springer-Verlag, New York, pp. 102-117.

Archangelsky, S., 1996. The Jurassic and Cretaceous vegetation of the Patagonian Province. In: Akhmetiev, M.A., Doludenko, M.P. (Eds.), Memorial Conference dedicated to Vsevolod Andreevich Vakhrameev, 1996. Russian Academy of Sciences, pp. 8-9.

Archangelsky, S., Azcuy, C.L., González, C.R., Sabattini, N., 1987. Paleontologia, bioestratigrafia y paleoecologia de las cuencas Paganzo, Calingasta-Uspallata y Rio Blanco. In: Archangelsky, S. (Ed.), El Sistema Carbonifero en la Republica Argentina. Academia Nacional de Ciencias, Cordoba, pp. 133-151.

Archangelsky, S., Cúneo, R., 1987. Feruglocladaceæ, a new conifer family from the Permian of Gondwana. Review Palæobotany Palynology 51, 3-30.

Arrondo, O.G., Petriella, B., 1980. Alicura, nueva localidad plantifera Liassic de la Provincia de Neuquén, Argentina. Ameghiniana 17, 200-215.

Attenborough, D. (Ed.), 1987. The First Eden: the Mediterranean world and man. Collins, London, 240p.

Azcuy, C.L., Andreis, R.R., Cuerda, A., Hünicken, M.A., Pensa, M.V., Valencio, D.A., Vilasy, J.F., 1987. In: Archangelsky, S. (Ed.), El Sistema Carbonifero en la Republica Argentina. Academia Nacional de Ciencias, Cordoba, pp. 41-99.

Baldoni, A.M,. 1980. Tafoflora Jurasica de la zona de Picun Leufu, Provincia del Neuquén. Ameghiniana 17, 243-254.

Bamford, M.K., 1990. The angiosperm palæoflora from the Orapa pipe, Botswana. Unpublished Ph.D. Thesis, University of the Witwatersrand, Johannesburg.

Bamford, M.K., in press. Fossil woods from the South African Karoo. Palæontologia Africana.

Bamford, M.K., Corbett, I.B., 1994. Fossil wood of Cretaceous age from the Namaqualand continental shelf, South Africa. Palæontologia Africana 31B, 83-95.

Banerji, J., 1991. Upper Gondwana megafloral succession of Rajmahal Basin, India. In: Gondwana IX, Vol. I. Geological Survey of India Publication, pp. 269-282.

Behrensmeyer, A.K., Damuth, J.K., di Michelle, W.A., Potts, R., Sues, H.D., Wing, S.L. (Eds.), 1992. Terrestrial ecosystems through time. Evolutionary paleoecology of terrestrial plants and animals. University Chicago Press, Chicago, 568p.

Benton, M.J., 1993. Late Triassic extinctions and the origin of the dinosaurs. Science 260, 769-770.

Berry, C.M., 1994. First record of the Devonian lycophyte *Leclercqia* from South America. Geological Magazine 131, 269–272.

Bose, M.N., Taylor, E.L., Taylor, M.N., 1989. Gondwana floras of India and Antarctica – a survey and appraisal. In: Taylor, T.N., Taylor, E.L. (Eds.), Antarctic paleobiology, its role in the reconstruction of Gondwana. Springer-Verlag, New York, pp. 118–147.

Bowring, S.A., Martin, M.W., 1999. High precision U-Pb geochronology, the tempo of evolution and the record from Gondwana. Journal African Earth Sciences 28, 187–201.

Cantrill, D.J., 1997. The pteridophyte *Ashicaulis livingstonensis* (Osmundaceæ) from the Upper Cretaceous of Williams Point, Livingston Island, Antarctica. New Zealand Journal Geology Geophysics 40, 315–323.

Cantrill, D.J., Nichols, G.J., 1996. Taxonomy and palæoecology of Early Cretaceous (Late Albian) angiosperm leaves from Alexander Island, Antarctica. Review Palæobotany Palynology 92, 1–28.

Caputo, M.V., 1985. Late Devonian glaciation in South America. Palæogeography, Palæoclimatology, Palæoecology 51, 291–317.

Carpenter, F.M., 1992. Superclass Hexapoda. In: Kaesler, R.L., Brosins, E., Keim, J., Priesner, J. (Eds.), Treatise on Invertebrate Paleontology. Geological Society of America and the University of Kansas, Boulder, Colorado and Lawrence, Kansas.

Chandra, S., Surange, K.R., 1979. Revision of the Indian species of *Glossopteris*. Birbal Sahni Institute of Palæobotany, Lucknow, India. Monograph No. 2, 291p.

Collinson, J.W., Isbell, J.L., Elliot, D.A., Miller, M.F., Miller, J.M.G., 1994. Permian-Triassic Transantarctic basin. In: Veevers, J.J., Powell, C. McA., (Eds.), Permian-Triassic Pangean Basins and Foldbelts along the Panthalassan Margin of Gondwanaland. Geological Society America, Memoir 184, 173–222.

Carroll, R.L. (Ed.), 1988. Vertebrate palæontology and evolution. Freeman and Co., New York, 698p.

Crane, P.R., 1987. Vegetational consequences of the angiosperm diversification. In: Friis, E.M., Chaloner, W.G., Crane, P.R. (Eds.), The origins of angiosperms and their biological consequences. Cambridge University Press, Cambridge, pp. 107–144.

Crepet, W.L., Friis, E.M., 1987. The evolution of insect pollination in angiosperms. In: Friis, E.M., Chaloner, W.G., Crane, P.R. (Eds.), The origins of angiosperms and their biological consequences. Cambridge University Press, Cambridge, pp. 181–201.

De Wit, M.J., Booth, P., Brönn, P., Shone, R., 1998. Cape Fold Belt field trip: 450 million years of stress and strain along the edge of Gondwana. Gondwana-10 (Cape Town, 1998).

Douglas, J.G., 1969. The Mesozoic floras of Victoria, parts 1 and 2. Geological Survey Victoria, Memoir 28, 1–310.

Drinnan, A.N., Crane, P.R., 1989. Cretaceous paleobotany and its bearing on the biogeography of austral angiosperms. In: Taylor, T.N., Taylor, E.L. (Eds.), Antarctic paleobiology, its role in the reconstruction of Gondwana. Springer-Verlag, New York, pp. 118–147.

Duarte, L., Japiassú, A.M.S., 1971. Vegetais Meso e Cenozóicos do Brasil. Anais Academia Brasileira Ciências 43 (suppl.), 433–443.

Edwards, D., 1989. Silurian-Devonian paleobotany: problems, progress, and potential. In: Taylor, T.N., Taylor, E.L. (Eds.), Antarctic paleobiology, its role in the reconstruction of Gondwana. Springer-Verlag, New York, pp. 89–101.

Erwin, D.H. (Ed.), 1993. The Great Paleozoic Crisis. Columbia University Press, New York, 327p.

Erwin, D.H., 1995. The end-Permian mass extinction. In: Scholle, P.A., Peryt, T.M., Ulmer-Scholle, (Eds.), The Permian of northern Pangæa: paleogeography, paleoclimates, stratigraphy. Springer-Verlag, Berlin, pp. 20–34.

Erwin, D.H., 1999. Biospheric perturbations during Gondwanan times: from the Neoproterozoic-Cambrian radiation to the end-Permian crisis. Journal African Earth Sciences 28, 115–127.

Forster, C.A., 1999. Gondwanan dinosaur evolution and biogeographic analysis. Journal African Earth Sciences 28, 169–185.

Francis, J.E., 1986. Growth rings in Cretaceous and Tertiary wood from Antarctica and their palæoclimatic implications. Palæontology 29, 665–684.

Francis, J.E., 1994. Palæoclimates of Pangæa – geological evidence. Canadian Society Petroleum Geologists Memoir 17, 265–274.

Francis, J.E., Frakes, L.A., 1993. Cretaceous climates. Sedimentolgy Review 1, 17–30.

Francis, J.E., Hill, R.S., 1996. Fossil plants from the Pliocene Sirius Group, Transantarctic Mountains: evidence for climate from growth rings and fossil leaves. Palaios 11, 389–396.

Gamundi, O.L., Azcuy, C.L., Cuerda, A., Valencio, D.A., Vilas, J.F., 1987. Cuencas Rio Blanco y Calingasta-Uspallata. In: Archangelsky, S. (Ed.), El Sistema Carbonifero en la Republica Argentina. Academia Nacional de Ciencias, Cordoba, pp. 101–132.

Garratt, J.M., 1978. New evidence for a Silurian (Ludlow) age for the earliest *Baragwanathia* flora. Alcheringa 2, 217–224.

Garratt, J.M., 1981. The earliest vascular land plant: comment on the age of the oldest *Baragwanathia* flora. Lethaia 14, 8.

Garratt, J.M., Tims, J.D., Rickards, R.B., Chambers, T.C., Douglas, J.G. 1984. The appearance of *Baragwanathia* (Lycophytina) in the Silurian. Botanical Journal Linnean Society 89, 355–358.

Gensel, P.G., Andrews, H.N., 1987. The evolution of early land plants. American Scientist 75, 478–489.

Gess, R.W., Hiller, N., 1995. A preliminary catalogue of fossil algal, plant, arthropod and fish remains from a Late Devonian black shale near Grahamstown, South Africa. Annals Cape Provincial Museums (Natural History) 19 (5), 225–304.

Gibbs Russell, G.E., Watson, L., Koekemoer, M., Smook, L., Barker, N.P., Anderson, H.M., Dallwitz, M.J., 1991. Grasses of southern Africa. Memoir, Botanical Survey South Africa 58, 437p.

Gould, S.G. (Ed.), 1996. Dinosaur in a haystack. Penguin Books, London, 480p.

Gutiérrez, R., Archangelsky, S., 1997. *Haplostigma baldisii* sp. nov. (lycophyta) del Devónico de la Precordillera de San Juan, Argentina. Ameghiniana 34, 275–282.

Hawkesworth, C., Kelley, S., Turner, S., le Roex, A., Storey, B., 1999. Mantle processes during Gondwana break-up and dispersal. Journal African Earth Sciences 28, 239–261.

Hayes, P., 1996. The Coniacian-Santonian (Late Cretaceous) flora of the Hidden Lake Formation, James Ross Basin, Antarctic Peninsula. Abstracts of the International Organisation of Palæobotany Conference 5, Santa Barbara. p.41.

Herbst, R., 1966. Revision de la flora Liassica de Piedra Pintada, Provincia de Neuquén, Argentina. Revista Museo Plata N.S. 5, 27–53.

Herbst, R., Troncoso, A., 1996. La tafoflora de Juan de Morales del Jurásico Medio (Formación Chacarilla), Región de Tarapacá, Chile. Revista Geologica Chile 23, 3–15.

Heywood, V.H. (Ed.), 1993. Flowering plants of the world, updated edition. Oxford University Press, New York, 336p.

Hickey, L.J., 1981. Land plant evidence compatible with gradual, not catastrophic, change at the end of the Cretaceous. Nature 292, 529–531.

Hill, R.S., Truswell, E.M., McLoughlin, S., Dettmann, M.E., in press. The evolution of the Australian flora: fossil evidence. In: Orchard, A.E. (Ed.), Flora of Australia. Australian Government Publishing Service, Canberra.

Knoll, A.H., 1984. Patterns of extinction in the fossil record of vascular plants. In: Nitecki, M. (Ed.), Extinctions. University Chigago Press, USA, pp. 21–68.

Knoll, A.H., 1986. Patterns of change in plant communities through geological time. In: Diamond, J., Case, T.J. (Eds.), Community Ecology. Harper and Row, New York, 665p.

Labandeira, C.C., Dilcher, D.L., Davis, D.R., Wagner, D.L., 1994. Ninety-seven million years of angiosperm-insect association: paleobiological insights into the meaning of co-evolution. Proceedings, National Academy Sciences, USA 91, 12,278–12,282.

Labandeira, C.C., Sepkoski Jr, J.J., 1993. Insect diversity in the fossil record: myth and reality. Science 261, 310–315.

Leakey, R., Lewin, R., 1996. The Sixth Extinction, biodiversity and its survival. Phoenix, London, 271p.

Macphail, M.K., Hill, R.S., in press. Palæobotany of the poaceæ. In: Orchard, A.E. (Ed.), Flora of Australia. Australian Government Publishing Service, Canberra.

McLoughlin, S., 1990a. Some Permian glossopterid fructifications and leaves from the Bowen Basin, Queensland, Australia. Review Palæobotany Palynology 62, 11–40.

McLoughlin, S., 1990b. Late Permian glossopterid fructifications from the Bowen and Sydney Basins, eastern Australia. Geobios 23 (3), 283–297.

McLoughlin, S., Drinnan, A.N., Rozefelds, A.C., 1995. A Cenomanian flora from the Winton Formation, Eromanga Basin, Queensland, Australia. Memoirs Queensland Museum 38 (1), 273–313.

McLoughlin, S., Long, J.A., 1994. New records of Devonian plants from Southern Victoria Land, Antarctica. Geological Magazine 131 (1), 81–90.

Menéndez, C.A., 1966. Fossil Bennettitales from the Ticó flora, Santa Cruz Province, Argentina. Bulletin British Museum Natural History 12 (1), 1–42.

Menéndez, C.A., 1969. Die fossilen Floren Südamerikas. In: Fittkau, E.J., et al. (Eds.), Biogeography and Ecology in South America Vol. 2. W. Junk Publishers, The Hague, pp. 519–561.

Meyen, S.V., 1987. Fundamentals of palæobotany. Chapman and Hall, London, 432p.

Morel, E., Edwards, D., Rodriguez, M.I., 1995. The first record of *Cooksonia* from South America in Silurian rocks of Bolivia. Geological Magazine 132, 449–452.

Morris, N., 1975. The *Rhacopteris* Flora in New South Wales. In: Campbell, K.S.W. (Ed.), Papers from the Third Gondwana Symposium, Canberra, Australia, 1973. Australian National University Press, Canberra, pp. 99–108.

Morris, L.N., 1985. The floral succession in eastern Australia. In: Diaz, C.M. (Ed.), The Carboniferous Geology of the World. 2. Australia, Indian subcontinent, South Africa, South America and North America. Instituto geológico y Minero de España, pp. 118–123.

Muller, J., 1981. Fossil pollen records of extant angiosperms. The Botanical Review 47, 1–142.

Müller-Stoll, W.R., Madel, E., 1962. Fossil woods of Monimiaceæ and Euphorbiaceæ from the Upper Cretaceous Umzamba beds of East Pondoland, CP. Transactions Geological Society South Africa 62, 93–104.

Niklas, K.J., Tiffney, B.H., Knoll, A.H., 1983. Patterns in vascular land plant diversification. Nature 303, 614–616.

Petriella, B., Arrondo, O.G., 1984. La tafoflorula Liasica de la estancia la Juanita, Provincia de Santa Cruz, Argentina. Ameghiniana 21, 35–41.

Pigg, K.B., Trivett, M.L., 1994. Evolution of the glossopterid gymnosperms from Permian Gondwana. Journal Plant Research 107, 461–477.

Pinto, I.D., Ornellas, L.P., 1978a. Upper Carboniferous insects from Argentina. 1. Familia Diaphanopteridæ (Megasecopteroidea). Pesquisas, Universidad Federal Rio Grande Sul 10, 77–86.

Pinto, I.D., Ornellas, L.P., 1978b. Carboniferous insects (Protorthoptera and Paraplecoptera) from the Gondwana (South America, Africa and Asia). Pesquisas, Universidad Federal Rio Grande Sul 11, 305–321.

Ragonese, A.M., 1977. *Nothofagoxylon menendezii*, Leño petrificado del Terciario de General Roca, Rio Negro, Argentina. Ameghiniana 14, 75–86.

Rajanikanth, A., 1996. Palæobotany of Mesozoic Gondwana sediments of Pranhita-Godavari. In: Gondwana IX, Vol. I. Geological Survey of India Publication, pp. 425–438.

Retallack, G.J., 1980. Late Carboniferous to Middle Triassic megafossil floras from the Sydney Basin. In: A guide to the Sydney Basin. Bulletin Geological Survey New South Wales 26, 385–430.

Riek, E.F., Kukalová-Peck, J., 1984. A new interpretation of dragonfly wing venation based on early Upper Carboniferous fossils from Argentina (Insecta: Odonatoidea) and basic character states in pterygote wings. Canadian Journal Zoology 62, 1150–1166.

Rigby, J.F., 1978. Permian glossopterid and other cycadopsid fructifications from Queensland. Geological Survey Queensland Publication 367, Palæontological Paper 41, 1–21.

Romero, E.J., 1978. Paleoecologia y paleofitogeografia de las tafofloras del Cenofitico de Argentina y areas vecinas. Ameghiniana 15, 209–227.

Romero, E.J., Archangelsky, S., 1986. Early Cretaceous angiosperm leaves from southern South America. American Association Advancement Science 234, 1580–1582.

Rösler, O., 1978. The Brazilian eogondwanic floral succession. Bol. IG, University of São Paulo, Brasil 9, 85–90.

Roy Chowdhury, M.K. *et al.*, 1975. Triassic floral succession in Gondwana of Peninsula India. In: Campbell, K.S.W. (Ed.), Papers from the Third Gondwana Symposium, Canberra, Australia, 1973. Australian National University Press, Canberra, pp. 149–158.

Sahni, B., 1948. The Pentoxyleæ: a new group of Jurassic gymnosperms from the Rajmahal Hills of India. Botanical Gazette 110, 47–80.

Schlüter, T., 1990. Fossil insect localities in Gondwanaland. Entomologia Generalis 15 (1), 61–76.

Scotese, C.R., 1997a. Paleogeographic Atlas, Paleomap Project (Report 90-0497). University of Texas at Arlington, Arlington, Texas, USA.

Scotese, C.R., 1997b. Continental drift, Edition 7, The Paleomap Project.

Scotese, C.R., 1998. Gondwana's climate changes. Journal African Earth Sciences 27 (1A), 172–173.

Scotese, C.R., Boucot, A.J., Mckerrow, W.S., 1999. Gondwanan palæogeography and palæoclimatology. Journal African Earth Sciences 28, 99–114.

Sepkoski Jr, J.J., 1986. Phanerozoic overview of mass extinction. In: Raup, D.M., Jablonski, D. (Eds.), Patterns and Processes in the History of Life. Springer-Verlag, Berlin, pp. 277–295.

Sepkoski Jr, J. J., Raup, D.M., 1986. Periodicity in marine extinction events. In: Elliot, D.K. (Ed.), Dynamics of Extinction. John Wiley, New York, pp. 3–36.

Sereno, P.C., 1997. The origin and evolution of dinosaurs. Annual Review Earth Planetary Science 25, 435–489.

Sessarego, H.L., Césari, S.N., 1989. An Early Carboniferous flora from Argentina. Biostratigraphic implications. Review Palæobatany Palynology 57, 247–264.

Smith, A., 1999. Gondwana: its shape, size and position from Cambrian to Triassic times. Journal African Earth Sciences 28, 71–97.

Srivastava, R., 1991. A catalogue of fossil plants from India. Part 4. Cenozoic (Tertiary) megagossils. Special Publication Birbal Sahni Institute Palæobotany, Lucknow.

Stanley, S.M., Yang, X., 1994. A double mass extinction at the end of the Paleozoic Era. Science 266, 1340–1344.

Sukh-Dev, 1988. Floristic zones in the Mesozoic formations and their relative age. Palæobotanist 36, 162–167.

Surange, K.R., 1975. Indian Lower Gondwana Floras: a review. In: Campbell, K.S.W. (Ed.), Papers from the Third Gondwana Symposium, Canberra, Australia, 1973. Australian National University Press, Canberra, pp. 135–147.

Taylor, T.N., Taylor, E.L., 1989. Structurally preserved Permian and Triassic floras from Antarctica. In: Taylor, T.N., Taylor, E.L. (Eds.), Antarctic paleobiology, its role in the reconstruction of Gondwana. Springer-Verlag, New York, pp. 149–163.

Taylor, T.N., Taylor, E.L., 1993. The biology and evolution of fossil plants. New Jersey, USA, Prentice Hall, 982p.

Tiffney, B.H., 1992. The role of vertebrate herbivory in the evolution of land plants. In: Venkatachala, B.S., Dilcher, D.L., Maheshwari, H.K. (Eds.), Essays in evolutionary plant biology. The Palæobotanist 421, 87–97.

Turner, B., 1999. Tectonostratigraphical development of the Upper Karoo foreland basin: orogenic unloading versus thermally-induced Gondwana rifting. Journal African Earth Sciences 28, 215–238.

Vishnu-Mittre, 1953. A male flower of the Pentoxyleæ with remarks on the structure of the female cones of the group. The Palæobotanist 2, 75–84.

White, M.E., 1972. Plant fossils from the Drummond Basin, Queensland. Bureau Mineral Resources, Geology Geophysics, Australia, Bulletin 132, 73–78.

White, M.E., 1986. The greening of Gondwana. Reed Books, NSW, Australia, 256p.

Wilson, E.O., 1993. The diversity of life. Penguin Books, London, 406p.

Yao, X., Taylor, T.N., Taylor, E.L., 1997. A taxodiaceous seed cone from the Triassic of Antarctica. American Journal Botany 84 (3), 343–354.

APPENDIX
GONDWANA FORMATIONS YIELDING THE PRINCIPAL VASCULAR PLANTS

The productive vascular plant horizons plotted on Fig. 2 in abbreviated form are spelled out here. Only the richest or best sampled and researched formations (occasionally localities) for each continent are listed. The broad evolutionary picture of Gondwana floras derives largely from these strata. It is obviously not within the scope of this work to attempt an exhaustive census. The references cited for each continent are the most comprehensive or most recent at hand. It is stressed that the correlation of terrestrial Gondwana strata against the standard international stages generally remains uncertain. The placement of formations on Fig. 2 must be understood in this light. Only where the source reference gives an indefinite age, spreading beyond a single stage, is the uncertainty noted (in brackets).

South America
Lying along the active southwestern convergent margin of Gondwana, South America comes second to Australia (its counterpart along the southeastern flank of the supercontinent) in yielding a reasonably full sequence of fossil floras through the post-Ordovician Phanerozoic. The principal breaks occur in the Devonian, where no reasonably good vascular plants are known, and the lower half of the Triassic. An alternate Permian sequence to that of the Paraná Basin, Brazil, occurs in Patagonia, south Argentina, where most of the Permian occurs in two sequences: La Golondrina Formation, Santa Cruz Province, (Late Permian) and the Rio Genoa Group, Chubut Province (Early Permian).

Cenozoic
S.Paulo: Sáo Paulo State, Brazil
Alag: Alagoinhas, Bahia State, Brazil
Pala: Palaoco Formation, Neuquén, Central Argentina
Ipix: Ipixuna Formation, Irituia, Paraná, Brazil (Miocene)
R. Leo: Rio Leona Formation, southernmost South America (Oligocene)
Loret: Loreto, Chile (Oligocene)
Turb: Rio Turbio Formation, Santa Cruz Province, south Argentina (Eocene)
Lagun: Laguna del Hunco, Chubut Province, south Argentina (Eocene)
Salam: Salamanco Formation, Chubut Province, south Argentina (Palæocene)

Cretaceous
Chub: Several formations, Chubut Basin, south Argentina (Cenomanian–Maastrichtian)
Huit: Huitrin Formation, Neuquén Basin, Central Argentina (Aptian–Albian)
Baqu: Baqueró Formation (Ticó Flora), Santa Cruz Province, south Argentina
Spring: Springhill Formation, Santa Cruz Province, south Argentina; Magallanes Basin, south Chile

Jurassic
Vaca: Vaca Muerta Formation, Neuquén Basin, Central Argentina (Upper Kimmeridgian–Berriasian)
Chaca: Chacarilla Formation, Chile (Callovian?)
Matil: La Matilde Formation, Santa Cruz Province, south Argentina, (includes the world-renowned *Araucaria* Petrified Forest)
Laja: Lajas Formation, Neuquén, central Argentina
Lauro: Bahio Lauro Group, Santa Cruz, (?Upper Lias)
Roca: Roca Bianca Formation, Santa Cruz Province, south Argentina
Pi Pi: Piedra Pintada Formation, Neuquén, central Argentina (?Sinemurian)
Alic: Alicura flora, Neuquén, central Argentina

Triassic
Tranq: El Tranquilo Formation, Santa Cruz Province, south Argentina
Isch: Ischigualasto Formation, Ischigualasto Basin, north Argentina

Cach: Cacheuta and Potrerillos Formations, Cacheuta Basin, north Argentina

Cabr: Las Cabras Formation, Cacheuta Basin, north Argentina

Permian (Paraná Basin, Brazil)
Ras (L.-U.): Lower–Upper Rio Do Rasto Formation (Taphoflora E)
Terez: Terezina Formation (Taphoflora D)
R. Bon: Rio Bonito Formation (Taphoflora B and C)
Itar: Itararé Formation (Taphoflora A)

Carboniferous
Colin: La Colina Formation, La Rioja Province, north Argentina (latest Carboniferous)
Tupe: Tupe Formation, La Rioja Province, north Argentina (Upper Carboniferous)
Guan: Guandacol Formation, La Rioja and San Juan Province, northwest Argentina (Carboniferous)
Jejen: Jejenes Formation, San Jaun Province, west Argentina (early Upper Carboniferous)
Parac: Paracas, Peru (earliest Upper Carboniferous)
Poti: Poti Formation, Teresina Flora, Piaui State, Brazil
Raton: EL Raton, San Juan Province, west Argentina (Lower Carboniferous)

Devonian
Chig: Chigua Formation, San Juan Province, west Argentina (Givetian-Frasnian)
C Chi: Cambo Chico Formation, Sierra de Perijá, Venezuela

Silurian
Kiru: Kirusillas Formation, Bolivia

References: Anderson and Anderson, 1983 (Triassic); Andreis *et al.*, 1987 (Carboniferous); Archangelsky, 1965a, b, 1970, 1981, 1989, 1996, (Devonian–Cretaceous); Archangelsky *et al.*, 1987 (Carboniferous); Arrondo and Petriella, 1980 (Jurassic); Azcuy *et al.*, 1987 (Carboniferous); Baldoni, 1980 (Jurassic); Berry, 1994 (Devonian); Duarte and Japiassú, 1971 (Cenozoic); Gamundi *et al.*, 1987 (Carboniferous); Gutiérrez and Archangelsky, 1997 (Devonian); Herbst, 1966 (Jurassic); Herbst and Troncoso, 1996 (Jurassic); Menendez, 1966, 1969 (Carboniferous, Cretaceous); Morel *et al.*, 1995 (Silurian); Petriella and Arrondo, 1984 (Jurassic); Ragonese, 1977 (Cenozoic); Romero, 1978 (Cenozoic); Romero and Archangelsky, 1986 (Cretaceous); Rösler, 1978 (Permian); Sessarego and Césari, 1989 (Carboniferous).

Southern Africa
The floral history of Africa south of the Sahara is told essentially through South African material. By far the best preserved, sampled and studied vascular plant sequences are from this country. Even so, the fossiliferous succession is far from complete, with the Silurian, Lower Devonian and Carboniferous apparently unrepresented and the Jurassic to Holocene (with the exception of the Lower Cretaceous), very poorly covered. The Permo-Triassic sequence of the Great Karoo Basin is most productive, the richest single formation by a wide margin being the Upper Triassic Molteno.

Cretaceous
Umza: Umzamba Beds, East Pondoland, Cape Province (Upper Cretaceous)
Orapa: Orapa Diamond Mine, north central Botswana
Nama: Namaqualand (continental shelf and onshore) (Aptian–Albian)
Maka: Makatini Formation, Zululand
Mnga: Mngazana Formation, Transkei
Kirk: Kirkwood Formation, Algoa Basin

Jurassic
Drak: Drakensberg Group, central Karoo Basin

Triassic
Molt: Molteno Formation, Karoo Basin
Burg: Burgersdorp Formation, Beaufort Group, central Karoo Basin
Lyst: *Lystrosaurus* Zone, Beaufort Group, northeast Karoo Basin

Permian
Estc: Estcourt Formation, Beaufort Group, northeast Karoo Basin
Wate: Waterford Formation, uppermost Ecca Group, south Karoo Basin
U. Ecc: Upper Ecca Group (Volksrust Formation), northeast Karoo Basin
M. Ecc: Middle Ecca Group (Vryheid Formation), northeast Karoo Basin
L. Ecc: Lower Ecca Group (Pietermaritzburg Formation), northeast Karoo Basin
Dwyk: Dwyka Tillite, northeast Karoo Basin

Devonian
Wit (L.-U.): Lower–Upper Witteberg Group, Cape Supergroup
Bokk: Bokkeveld Group, Cape Supergroup

References: Almond *et al.*, 1998; Anderson and Anderson, 1995 (Devonian); Anderson and Anderson, 1985 (Devonian–Lower Cretaceous); Bamford, 1990 (Cretaceous); Bamford and Corbett, 1994 (Cretaceous); Gess and Hiller, 1995 (Devonian); Müller-Stoll and Madel, 1962 (Cretaceous).

India
Peninsula India–the Indian Craton–was one of twelve or so major Precambrian 'building blocks' welded together to form Gondwana in the Late Palæozoic (de Wit *et al.*, 1998). The particularly important sequence of Permian floras in India were

preserved in the system of faulted rifts considered to have formed in the craton in response to the 'impact' tectonics along the distant southern margin of Gondwana. The second important sequence of floras is that of the later Jurassic and earlier Cretaceous deposits formed during break-up of the supercontinent. The ages and sequencing of the Triassic formations are particularly uncertain. These have been placed as in Anderson and Anderson (1983).

Cenozoic
Karew: Karewa Formation, Jammu and Kashmir Provinces
Moth: Mothala locality, Kutch, Siwalik, Himalayan foothills
Wark: Warkalli locality, Kerala, Siwalik (Miocene)
Bara: Barail Group, Assam (Oligocene)
Nerdi: Nerdi Formation, Gujarat; and Jaintia Group, Meghalayn
Decc: Deccan intertrappean bed, Madhya Pradesh (Palæocene)

Cretaceous (Rajmahal Hills, Bihar)
Lamet: Intertrappean Lameta beds, Madhya Pradesh
Sona: Sonajori locality, Rajmahal Formation
Raj 4: 4th intertrappean bed, Rajmahal Formation
Raj 1–3: 1st – 3rd intertrappean beds, Rajmahal Formation

Jurassic
Dubr: Dubrajpur Formation, Rajmahal Hills, Bihar
Kota: Kota, Pranhita-Godavari Basin

Triassic
Tiki: Tiki Formation, south Rewa Basin
Pars: Parsora Formation, south Rewa Basin
Panc: Panchet Formation, Raniganj Coalfield, Damodar Basin

Permian (various basins of Peninsula India)
Kamt: Kamthi Formation
Rani: Raniganj Formation
Barr: Barren Measures Formation
Bara: Barakar Formation
Karh: Karharbari Formation
Talc: Talchir Formation

References: Banerji, 1991, *in prep.* (Upper Jurassic–Lower Cretaceous); Bose *et al.*, 1989 (Permian–Lower Cretaceous); Chandra, *in prep.* (Permian–Lower Cretaceous); Rajanikanth, 1996 (Triassic–Lower Cretaceous); Roy Chowdhury *et al.*, 1975 (Triassic); Srivastava, 1991 (Cenozoic); Sukh-Dev, 1988 (Triassic–Cretaceous); Surange, 1975 (Permian).

Antarctica
Though the dedicated study of Antarctic fossil floras is hardly four decades old and the outcrops are restricted, our knowledge of these floras is growing rapidly. The older succession is most akin to that in South Africa, Australia and India, the younger to that of South America, but the potential for sampling is probably not quite on a par.

Cenozoic
Siri: Sirius Group, Central Transantarctic Mountains
Mese: La Meseta Formation, Seymour Island (Upper Eocene–Lower Oligocene)
Cross: Cross Valley and Sobral Fms, Seymour Island (Palæocene)

Cretaceous (south Shetland Islands, Antarctic Peninsula)
Lopez: Lopez de Bertodano Formation, Seymour Island (Campanian–Maastrichtian)
Naze: Lachman Crags and The Naze, James Ross Island
Hidd: Hidden Lake Formation, James Ross B., Antarctic Peninsula (Coniacian–Santonian)
Will: Williams Point Beds, Livingston Island (Cenomanian–Campanian)
Trit: Triton Point Member, Neptune Glacier Formation, Alexander Island
Livi: Livingstone Island (Byers Formation??) (Barremian–Aptian)

Jurassic
Hope: Mount Flora Formation, Hope Bay (Lower–Middle Jurassic)

Triassic (Transantarctic Mountains)
McKe: McKelvey Member (Upper Flagstone Bench Formation), Prince Charles Mountains
Fall: Lower Falla Formation, Beardmore Glacier
Frem: Fremouw Formation, Beardmore Glacier
Lash: Lashly Formation (lower), south Victoria Land
Ritch: Ritchie Member (Lower Flagstone Bench Formation), Prince Charles Mountains (Scythian)

Permian (Transantarctic Mountains)
Buck: Buckley Formation, central Transantarctic Mountains
U. Pol: Upper Polarstar Formation, Ellsworth Mountains
Bain: Bainmedart C.M., Prince Charles Mountains
Takr: Takrouna Formation, north Victoria Land

Devonian
Rupp: Ruppert Coast metavolcanics, Marie Bryd Land (Upper Devonian)
Beac: Beacon Heights Orthoquartzite (and overlying Aztec Siltstone), Taylor Group, south Victoria Land

References: Bose *et al.*, 1989 (Permian–Lower Cretaceous); Cantrill, 1997 (Upper Cretaceous); Cantrill and Nichols, 1996 (Lower Cretaceous); Collinson *et al.*, 1994 (Permian–Triassic); Edwards, 1989 (Devonian); Francis, 1986 (Cretaceous–Cenozoic); Francis and Hill,

1996 (Cenozoic); Hayes, 1996 (Upper Cretaceous); McLoughlin and Long, 1994 (Devonian); Taylor and Taylor, 1989 (Permian–Triassic).

Australia
Australia, and essentially the eastern seaboard of the continent (the active Tasman orogenic margin of eastern Gondwana), provides the most complete sequence of fossiliferous beds outlining the evolution of vascular plants (megafloras) in Gondwana. It rates a little ahead of South America in this regard. The most significant gap in the Australian megafloral sequence is that through the Coniacian to Maastrichtian of the Late Cretaceous, for which outcrops remain unknown.

Cenozoic
U. Reg: Upper Regatta Point locality, Tasmania
U.B.M: Upper Beds overlying Bacchus Marsh Coal, Madingley Pit, Victoria
Dayl: Daylesford and Malmsbury localites, Victoria
Yall: Yallourn Coal Mines, Latrobe Valley, Victoria
Monp: Monpeelyata and Pioneer localities, Tasmania
Morw: Morwell Coal Mine, Latrobe Valley, Victoria
Ceth: Cethana and 4 other localities, Tasmania
Hast: Hasties and Loch Aber localities, Tasmania, plus several other localities near Adelaide, Melbourne, Canberra and Perth
L. Reg: Lower Regatta Point and 3 other localities, Tasmania
Bung: Lake Bungarby and Cambalong Creek (southeast corner of New South Wales)

Cretaceous
Waar: Waarre Formation, Otway Basin, Victoria (borecores)
Wint: Winton Formation, Eromanga Basin, central Queensland
Otw A–D: floral zones A–D of Douglas (1969), Otway and Gippsland Basins, Victoria
Hoor: Hooray Sandstone, Eromanga Basin, Queensland, New South Wales, South Australia, Nothern Territory (Late Jurassic–Early Cretaceous)

Jurassic
Ida: Ida Bay and Lune River localities, Tasmania
Yarr: Yarragadee Formation, Perth Basin, Western Australia
Wall: Walloon C.M., Clarence-Moreton Basin, Queensland
Talb: Talbragar Fish Beds, lowest Purlawaugh Formation, Surat Basin, Queensland
Tiar: Tiaro C.M., Maryborough Basin, Queensland
Brig: Brighton Beds and Marburg Subgroup, Bundamba Group, Clarence-Moreton Basin, Queensland
Ever: Evergreen Formation, Surat Basin, Queensland

Land: Landsborough, Myrtle Creek, and Precipice Sandstones, Queensland

Triassic
Aber: Aberdare and Raceview Formations, Clarence-Moreton Basin, Queensland
Leigh: Leigh Creek C.M., South Australia (Carnian–Rhætian)
Ipsw: Ipswich Group, Clarence-Moreton Basin
Esk: Esk Formation and Nymboida C.M., Clarence-Moreton Basin
Mool: Moolayember Formation, Bowen Basin, Queensland (Anisian–Ladinian)
Newp: Newport Formation, Narrabeen Group, south Sydney Basin
Bulg: Bulgo, Bald Hill and Garie Formations, Narrabeen Group, south Sydney Basin
Rewan: Rewan Group, Bowen Basin, Queensland

Permian (Sydney Basin)
IIIa(1-3): Illawarra and Tomago C.M.
Mait: Maitland and upper Shoalhaven Groups
Gret: Greta C.M.
Dalw: Dalwood and lower Shoalhaven Groups
Loch: Lochinvar Formation and Clyde C.M.

Carboniferous (Sydney Basin)
Seah: Seaham Formation
Pate: Paterson Volcanics
Mt. Jo.: Mount Johnstone and McInnes Formations (age uncertain, 332–295 Ma; Late Namurian and Westphalian)
Gilm: Gilmore Volcanic Group
Wall: Wallaringa/Flagstaff Formations, Star of Hope/Ducabrook/Mount Rankin Formations
Scar: Scarwater/Mount Hall/Telemon/Raymond Formations, Drummond Basin, Queensland

Devonian
Silv: Silver Hills Volcanics, Drummond Basin, Queensland
Barr: Barraba locality, New South Wales
Yalw: Yalwal Volcanics, southern New South Wales
Bung: Bungan Head locality, New South Wales
U. Yea: upper sections at Yea locality, Victoria

Silurian
L. Yea: lower sections at Yea locality, Victoria
Mudg: Mudgee locality, New South Wales

References: Douglas, 1969 (Lower–Middle Cretaceous); Garratt, 1978, 1981 (Silurian–Devonian); Garratt *et al.*, 1984 (Silurian–Devonian); Hill, *in prep.* (Cenozoic); Hill *et al.*, *in press* (Silurian–Pleistocene); Morris, 1975, 1985 (Carboniferous); McLoughlin and Tosolini, *in prep.* (Jurassic–Middle Cretaceous); Retallack, 1980 (Carboniferous–Triassic); White, 1972, 1986 (Silurian–Holocene).