Wolfgang Frey (Editor)

Syllabus of Plant Families

13th ed.

A. Engler's Syllabus der Pflanzenfamilien

4

Pinopsida (Gymnosperms), Magnoliopsida (Angiosperms) p.p.:

Subclass Magnoliidae [Amborellanae to Magnolianae, Lilianae p.p. (Acorales to Asparagales)]

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Eberhard Fischer Wolfgang Frey	**Pinopsida** (Gymnosperms)
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Eberhard Fischer with contributions of Inge Theisen	Orchidaceae

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Picea orientalis (Pinopsida: Pinaceae), *Amborella trichopoda* (Magnoliopsida: Amborellaceae), *Nymphaea thermarum* (Nymphaeaceae), *Pseudohydrosme gabonensis* (Araceae), *Fritillaria latifolia* (Liliaceae), *Calypso bulbosa* (Orchidaceae).
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Introduction, Pinopsida (Gymnosperms) and **Magnoliopsida** (Angiosperms); Pinopsida (Gymnosperms)

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Magnoliopsida (Angiosperms) p.p.: **Subclass Magnoliidae** [Amborellanae to Magnolianae, Lilianae p.p. (Acorales to Asparagales)]

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Preface

Half a century ago, the 12th edition (vol. 1, 1954) of Adolf Engler´s well-known "Syllabus der Pflanzenfamilien" ("Syllabus of Plant Families"), ed. by H. Melchior and E. Werdermann was published. Later, a revision of the mosses (13th ed., Kapitel V,2 Bryophytina), by K. Walther, followed in 1983.

The 13th edition will be published in five parts, starting in 2009 with **Part 3** "**Bryophytes and seedless Vascular Plants"** and followed in 2012 by **Part 1/1** "**Blue-green Algae, Myxomycetes and Myxomycete-like organisms, Phytoparasitic protists, Heterotrophic Heterokontobionta and Fungi p.p.**" and 2015 by **Part 2/1** "**Eukaryotic Algae [Glaucobionta, Heterokontobionta** p.p. (Cryptophyta, Dinophyta, Haptophyta, Heterokontophyta), **Chlorarachniophyta, Euglenophyta, Chlorophyta, Streptophyta** p.p." (except Rhodobionta). Now **Part 4 "Pinopsida** (Gymnosperms), **Magnoliopsida** (Angiosperms) p.p.: **Subclass Magnoliidae** [Amborellanae to Magnolianae, Lilianae p.p. (Acorales to Asparagales)] is ready.

Numerous molecular analyses led to new insights and a better understanding of the evolution and systematics of the plant groups and fungi. On the other hand, "classical" morphological and taxonomical expertise is in decline, especially for less showy groups of organisms. As also noted in Part 3, "we are convinced that in the 'molecular times' there is an indispensable need to preserve the knowledge of the whole diversity and biology of organisms for the next generations. Otherwise, we will not be able to educate experts in the future who will maintain our knowledge of the full range of the earth's biodiversity":

The present volume provides a basic treatise of the world-wide morphological and molecular diversity of the **Pinopsida** (Gymnosperms) and **Magnoliopsida** (Angiosperms) p.p.: **Subclass Magnoliidae** [Amborellanae to Magnolianae, Lilianae p.p. (Acorales to Asparagales)].

Following the tradition of Engler, and incorporating the latest results from molecular phylogenetics and phylogenomics, the editor and the authors hope to have created an up-to-date overview of families and genera that will serve as reference for a long time.

The authors and the editor are grateful to the publisher, Dr. A. Nägele, for realizing this basic and fundamental systematic treatment, the **Syllabus of Plant Families**.

Berlin, March 2015 W. Frey

Contents

Abbreviations/Symbols

acc.	according to
alp.	alpine, alpine (geo)element
appr.	approximate
arct., Arct.	arctic, arctic (geo)element; Arctic
BP	Before Present
C	Central, central
c.	circa, about, approximately
cf.	confer, compare
circ.-pol.	circumpolar
com.	communication
comb. nov.	combinatio nova
cosmopol.	cosmopolitan
CS	cross-section
cult.	cultivated
diam.	diameter
E	East
e.g.	for example, exempli gratia
esp.	especially
et al.	and others
excl.	excluding
ext.	extending
fam.	family, families
fig., figs	figure, figures
gen.	genus, genera
Hem.	Hemisphere
horticult.	horticulturally
I., Is., i., is.	island, isle; islands, isles
i.e.	that is, id est
inc. sed.	incertae sedis, uncertain systematic position
incl.	including
indigen.	indigenous
intr.	introduced
l.c.	locus cited
lit. cit.	literature cited
loc.	locality, localities
LS	longitudinal section
Ma	million of years ago
max.	maximal, maximally
medit., Medit.	mediterranean, Mediterranean region
min.	minute
mio.	million
mio.y.	million years
morphogen.	morphogenus
mt(s)., Mt(s).	mountain(s)
µm	micrometer
N	North, northern
neotrop., Neotrop.	neotropical, Neotropics, Neotropical region
nom. cons.	nomen conservandum, conserved name

nom. illeg.	nomen illegitimum, illegitimate name
nom. rej.	nomen rejiciendum, rejected name
nom. et orth. cons.	nomen et orthographia conservandum, name and orthography conserved
NE	northeast
NW	northwest
NSW	New South Wales (Australia)
nothosp./nothospp.	nothospecies
occ.	occasional, occasionally
ord.	order, orders
organ gen.	organ genus, organ genera
orig.	originally
palaeotrop., Palaeotrop.	palaeotropical, Palaeotropical region
pantrop.	pantropical, in all tropical areas
p., pp.	page, pages
pers.	personal
phot.	photograph
p.p.	pro parte
predom.	predominant, predominantly
prob.	probably
Prov., prov.	Province, provinces
Qld.	Queensland (Australia)
R!	meiosis
Rep.	Republic
ref.	reference
resp.	respectively
s.	see
S	South, southern
SE	southeast
subclass.	subclasses
subfam.	subfamily
submedit.	submediterranean
superord.	superorder
SW	southwest
s. ab.	see above
s. bl.	see below
s.l.	sensu lato
spec., sp.	species
spp.	species (plural)
s.str.	sensu stricto
subantarct.	subantarctic, subantarctic (geo)element
subfam.	subfamily, subfamilies
subgen., subg.	subgenus, subgenera
subsp.	subspecies
subtrop.	subtropical, Subtropics
SW	southwest
syn.	synonym, synonymous
temp.	temperate, in temperate zones
trop., Trop.	tropical, tropics, Tropic (geo)element, Tropics
TS	transverse section
unpubl.	unpublished
var.	variety

vol.	volume
vs.	versus
W	West, western
warm-temp.	warm-temperate
x	basic chromosome number
y.	year, years
(5)	number of species
±	more or less
∞	numerous
♂	male
♀	female
†	extinct
$\frac{\ast}{\ast}$	in the Northern and Southern Hemisphere
$\underline{\ast}$	in the Northern Hemisphere
$\overline{\ast}$	in the Southern Hemisphere
($\underline{\ast}$)	scattered in the Northern Hemisphere
($\overline{\ast}$)	scattered in the Southern Hemisphere
E N S W	East, North, South, West

1 Introduction

The last two and a half decades provided revolutionary new insights into the phylogeny and diversity of organisms on earth. Especially the gymnosperms and the flowering plants have been in the focus of intensive research studies. The relationships were considerably revised.

The most important insights from recent molecular phylogenies and phylogenomic evidence allow a new understanding of the relationships between and within the taxa of the gymnosperms and angiosperms and are treated in the view of our decade, including morpho-anatomical, molecular and ecological results of the last three decades and bringing them on an up-to date presentation of these plants groups.

The present Part 4 of the 13th edition of "Engler's Syllabus of Plant Families" gives an up-to-date review of the **Pinopsida** (Gymnosperms) and **Magnoliopsida** (Angiosperms) p.p.: **Subclass Magnoliidae** [Amborellanae to Magnolianae, Lilianae p.p. (Acorales to Asparagales)] and the relationships on family and generic level, integrating morphological-anatomical and molecular data. It provides a thorough treatise of Gymnosperms and of part of the Angiosperms. In the Gymnosperms, the extinct diversity is included, and the present treatise is a first synthesis of classical anatomical-morphological characters with modern molecular data combined with the numerous new discoveries of fossils especially from China made during the last ten years.

The Angiosperms are the most diverse group of plants and form nearly 95% of the global vegetation from arctic tundra, resp. subantarctic vegetation formations, to tropical rainforests. There is actually no comprehensive survey covering all families and genera of angiosperms. Engler's Syllabus is an attempt to fill this gap by covering all angiosperms in two volumes arranged according to the most recent phylogenetic system of APG III (2009). In this first volume all families and genera of Magnoliids are described. The monocotyledonous families are covered by the orders Acorales and Alismatales as well as all groups of Liliid orders and families (Petrosaviales, Dioscoreales, Pandanales, Liliales and Asparagales). Especially Asparagales, comprising c. 40% of all extant monocotyledons, include numerous commercially important ornamental plants in Orchidaceae, Alliaceae and Iridaceae. Also, several economically important species are found in genera like *Allium*, *Aloë*, *Asparagus*, *Crocus*, and *Vanill*a. The Orchidaceae are included with a fully revised and modern treatise, thus representing one of the two most species-rich families of plants. The remaining monocotyledonous groups (Arecales, Commelinales, Poales, Zingiberales and Dasypogonales) and the core eudicotyledons will be treated in Part 5.

W. Frey

2 **Pinopsida** (Gymnosperms) and **Magnoliopsida** (Angiosperms)

Pinopsida (Gymnosperms) and **Magnoliopsida** (Angiosperms) are seed plants producing plants with a sporophyte-dominant alternation of generations. The ancient greek word "gymnospermos" (*γυμνόσπερμος*) stands for „naked seeds", αγγείον (angeíon, "receptacle") and *σπέρμα* (spérma, "seed") for angiospermous, seeds within an enclosure. Brongniart (1843) first subdivided the dicotyledons (dicots) in «Angiospermes» and «Gymnospermes». Together with the "Gymnosperms" (Pinopsida) and the Progymnospermopsida the angiosperms are sister to the ferns (Moniliformopses) and form the **Euphyllophytina**.

Extant gymnosperms are trees, shrubs, krummholz (dwarf pine trees) and woody climbers; with only one root parasite, *Parasitaxus usta* (Podocarpaceae). Especially the tree life form is dominant in the boreal zone of the Northern Hemisphere, e.g., conifers in the boreal forest communities with extremely high economic importance. Due to the small landmasses in the Southern Hemisphere extant gymnosperm-dominated forests cover much smaller areas than those of the boreal forests ("taiga"), but are of great significance for floral history and nowadays considered as relicts of tertiary forest communities (temperate rainforests). The extant gymnosperms are clearly monophyletic and sister to the angiosperms (e.g., Ran et al. 2010), comprising c. 1040 spp. in 4 subclass., 8 ord., and 12 fam. (Christenhusz 2011, Cycadales acc. Osborne et al. 2012). But their relationships to fossil gymnospermous taxa remain obscure and incompletely understood. Especially the position of Gnetidae has been problematical and was controversially discussed [e.g. Qiu et al. 1999: embedded in the conifer clade as sister to Pinaceae ("gnepine hypothesis"); Rydin et al. 2002: sisters to all other extant seed plants (cf. Gnetidae)]. The families of modern Pinales appeared in the arid Upper Permian, major diversification in Early Cretaceous; radiation of most genera within the last 25 mio.y.

The **Angiosperms** are the most diverse group of plants, comprising all known life forms from trees to annuals and parasites, and form nearly 95% of the global vegetation from arctic tundra, resp. subantarctic vegetation formations to deserts and tropical rainforests. Their evolutionary dominance is mostly due to the double fertilization and their extraordinary vegetative plasticity and the adaptation to numerous and diverse pollinators. Extant angiosperms comprise c. 250.000–300.000 spp., estimations between 223.000 and 422.125 ; in 2 classes, 18 superord., 68 ord., and 417 fam.

Until 1993 the formal division of angiosperms in dicotyledons and monocotyledons was still undisputed (Kubitzki et al. 1993). An alternative view of relationships among angiosperm groups was that of Huber (e.g., 1991) which ± anticipated the later classifica-

Table 2-1. Synopsis of classification of the Subkingdom **Embryobionta** Cronquist, Takht. & W.Zimm. (excl. Streptophyta p.p., cf. Syllabus Part 2/1).
(Cf. also Syllabus of Plant Families, Part 3, 2009; Table 2-1, p. 6.)

Division	**Marchantiophyta** Stotler & Crand.-Stotl. (Hepaticae, Liverworts)
Division	**Bryophyta** Schimp. (Musci, Mosses)
Division	**Anthocerotophyta** Rothm. ex Stotler & Crand.-Stotl. (Hornworts)
Superdivision	**Polysporangiomorpha** Kenrick & P.R.Crane
	“Protracheophytes” sensu Kenrick & P.R.Crane (Rhyniophyta H.P.Banks p.p.)
Class	Horneophytopsida Kenric k & P.R.Crane
Division	**Tracheophyta** Sinnott ex Cavalier-Smith sensu Kenrick & P.R.Crane (Vascular plants)
Subdivision	**Rhyniophytina** H.P.Banks sensu Kenrick & P.R.Crane (†)
Class	Rhyniopsida Kenrick & P.R.Crane
Subdivision	**Lycophytina** Kenrick & P.R.Crane (Club mosses)
Classes	Zosterophyllopsida Bierhorst (†), Lycopsida D.H.Scott
Subdivision	**Euphyllophytina** Kenrick & P.R.Crane
	“Trimerophytina” H.P.Banks sensu Kenrick & P.R.Crane (†)
Superclass	**Moniliformopses** Kenrick & P.R.Crane (Horsetails, Ferns)
Classes	“Cladoxylopsida” Pic.Serm. (†), Psilotopsida D.H.Scott, Equisetopsida C.Agardh, Marattiopsida Doweld; Polypodiopsida Cronquist, Takht. & W.Zimm.
Superclass	**Radiatopses** Kenrick & P.R.Crane (Spermatophytes, Seed plants)
Class	**Progymnospermopsida** C.B.Beck (†)
Class	**Pinopsida** Burnett (Gymnosperms)
Subclasses	“Pteridospermatidae” (†), Cycadidae Pax, Ginkgoidae Engl., Gnetidae Pax, Pinidae Cronquist, Takht. & W. Zimm.
Class	**Magnoliopsida** Brogn. (Angiosperms)
Subclass	**Magnoliidae** Novák ex Takht.
Superorders	Amborellanae M.W.Chase & Reveal, Nymphaeanae Thorne ex Reveal, Austrobaileyanae Doweld ex M.W.Chase & Reveal Magnolianae Takht., Lilianae Takht. (Monocots), Ceratophyllanae Takht. ex Reveal & Doweld
Subclass	**Rosidae** Takht. (Eudicots)
Superorders	Ranunculanae Takht. ex Reveal, Proteanae Takht., Trochodendranae Takht. ex Reveal, Buxanae Takht. ex Reveal & Doweld, Myrothamnanae Takht., Dillenianae Takht. ex Doweld, Saxifraganae Reveal, Rosanae Takht., Berberidopsanae Thorne & Reveal, Santalanae Thorne ex Reveal, Caryophyllanae Takht., Asteranae Takht.

tion based on molecular data (e.g., Chase et al. 1993). Huber proposed a basal division in angiosperms between a "First principal group" comprising magnoliid families, the monocotyledons and the Centrospermae, and a "Second principal group" with the rest of the dicotyledons and stated that basal dicotyledonous angiosperms like the magnoliid families are closer related to the monocotyledons than to the rest of the dicotyledons. With molecular data, esp. DNA sequences as a potential source of phylogenetically informative characters, new imput was brought into systematics. Chase et al. (1993) provided a first set of nearly 500 taxa which revealed also a split between Magnoliales, Laurales, the so-called "**palaeoherbs**" and the monocots on one side and the modern eudicots with ranunculids, hamamelids, caryophyllids, Rosidae and Asteridae on the other side. Subsequent analyses (e.g., APG III 2009) changed this image slightly but the split between the monosulcate primitive dicots + the monocots and the tricolpate (or with a derived condition) eudicots is still confirmed. (Cf. Chapter 4: "Recent history of angiosperm classification and molecular phylogeny".)

The sudden appearance and the subsequent dramatic rise of the angiosperms in the Upper Cretaceous and Early Tertiary have caused much debate. The relationships of angiosperms to the gymnosperms are still a mystery, and it is until now unclear which seed plant fossils belong to the stem-group angiosperms. (Cf. Chapter 4 "Fossil history and evolution").

Actually no comprehensive survey covering all families and genera of angiosperms is available as the ambitious work of Kubitzki (ref. cited) is still not complete. Engler's Syllabus intends to be the first comprehensive survey covering all angiosperms in two volumes and arranged according to the most recent phylogenetic system of APG III (2009).

Table 2-1 gives an overview of the classification of the Subkingdom **Embryobionta** with **Pinopsida** and **Magnoliopsida**.

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3

Pinopsida Burnett (Gymnosperms, Gymnospermopsida, Gymnospermae)

Characterization and relationships

Seed plants, Gymnosperms. Greek word “gymnospermos” (*γυμνόσπερμος*) = „naked seeds“. With a sporophyte-dominant alternation of generations. Ovules exposed on the surface of megasporophylls (Cycadidae), a pair of ovules on the end of a short stalk (Ginkgoidae), erect ovule enclosed in an integument (Gnetidae), or modified axillary short shoots with bract scales and seed scales, resp. bract-scale complexes (Pinidae, resp. Cupressaceae). Trees, shrubs, krummholz (dwarf pine trees), woody climbers and one root parasite, *Parasitaxus usta* (Podocarpaceae); often with slow growing rates. Secondary xylem pycnoxylic or manoxylic, with secondary thickening; with tracheids, rarely with vessels (Gnetidae). Leaves simple, pinnate, rarely bipinnate or multipinnate (Cycadidae); fan-shaped, petiolate (Ginkgoidae), strap-shaped (*Welwitschia*), broadly elliptic (Gnetales) or scale-like (Ephedrales); variable, needle-or scale-like or rarely broad (Pinidae). Basic venation dichotomous, extant derived.

Reproductive organs mostly unisexual, naked or with 1–2 pairs of bracts (Gnetidae). Heterosporous (microspores/pollen grains and megaspores/embryo sac cells). Microsporophylls (stamens) often in cones. Microsporophylls with stalked or sessile microsporangia (pollen sacs) or simply scale-like; very rarely peltate, with ∞–2 (rarely 1) microsporangia. Microsporangia with an exothecium, rarely with endothecium. R! → 4 microspores (pollen grains), often with air-bladders, dispersed mostly by air, rarely by insects (some extant cycads and gnetophytes). Megasporophylls loosely composed, in simple cones (= ♀ flowers), or in composed ♀ cones (“inflorescences”) (conifers). Ovules [megasporangium = nucellus + embryo

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Characterization, presentation of relationships, distribution patterns, and enumeration of taxa of the Gymnosperms are mainly based on the fundamental works of Kramer & Green (1990), Farjon (2005a, b; 2010) and Farjon & Filer (2013), and for fossil taxa on Anderson et al. (2007) and Taylor et al. (2009). Based on these two latter treatments, a classification is presented here that combines all major sources of information, supplemented by the authors own experience and observations. The systematics of fossil groups, however, is still tentative. All these works imply a great source of information. Especially parts of the description of extant families and genera, the distributional patterns and the forest communities are adopted for this compilatory work of extinct and extant gymnosperms from the publications cited above. The base for the classification of extant gymnosperms is Christenhusz et al. (2011).

sac mother cell/embryo sac (♀ gametophyte) + unitegmic integument (→ testa, seed coat, with funiculus, chalaza and micropyle)], ∞–1 on leaf-like (*Cycas*) or reduced, simple megasporophylls or ovules ∞–1, often included in cones or cone-like structures (Pinidae) , or rarely exposed (e.g., *Cycas*, *Gingko*). R! of the megaspore mother cell (embryo sac mother cell) → 4 megaspores (embryo sac cells). Development of ♀ gametophyte mostly by 1 megaspore (monosporic), rarely by 4 megaspores (*Gnetum*, *Welwitschia*). Gametophytes reduced (♀ with reduced archegonia, ♂ 4– to more-celled). Spermatozoids rarely motile (*Ginkgo*, Cycadidae; zoidiogamy), in Pinidae and Gnetidae (no flagella, fertilization by a pollen tube). Between pollination and seed maturity often slow rates of growth and long periods.

Seeds with primary endosperm (=nutritive tissue) (haploid tissue of the ♀ gametophyte), at maturity often enclosed by fused cone scales or in *Juniperus* fleshy ("berries").

Evolution of seeds (Fig.3-1). Seeds are considered the end member of a development from homospory over various types of heterospory (Pettitt 1970, Taylor et al. 2009). Seeds consist of an indehiscent megasporangium (s. ab.) surrounded by 1 or 2 integuments. An explanation of the integument evolution is either the telome concept ("Elementarprozesse" Zimmermann 1930, 1952, 1959) where the ultimate axes of a branched axial system, called telomes, are reduced and become sterile, thus surrounding a single (mega)sporangium, figured by Andrews (1961). Other theories are the "Synangial hypothesis", which interprets the integument of seed plants as homologous to a cluster of sporangia (Benson 1904) and the "Neosynangial hypothesis" which postulates that "the ovule as a transformation of a stalked sporangium cluster that involves the sterilization of the peripheral sporangia to form a ring of free integumentary lobes surrounding single central megasporangium" (Kenrick & Crane 1997, p. 292). Many of the earliest seeds are surrounded by a cupule prob. originating by fusion of second-order branches. The cupule may have the function to protect the ovules and seeds, or was a structure to attract pollinators (Taylor et al. 2009).

The earliest known seed is *Runcaria heinzelinii* F.Stockmans, Middle Devonian (Middle Givetian), Belgium. It has a 4-parted cup-shaped cupule at base (Gerienne et al. 2004) and the 16-lobed integument is twisted in a helical pattern. The ovulate structure of *Runcaria* F.Stockmans has been defined as a proto-ovule by Gerienne & Meyer-Berthaud (2007).

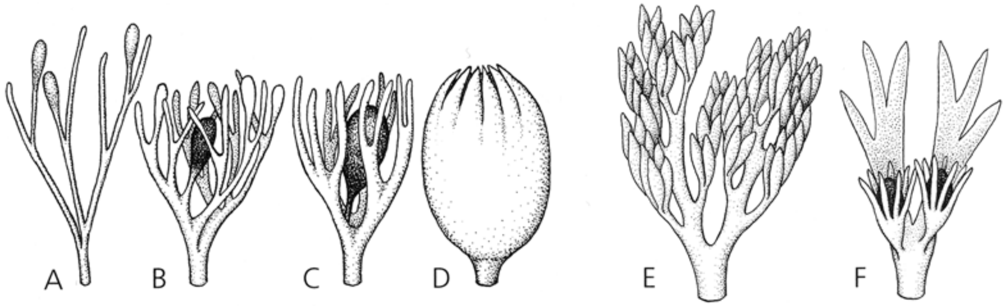

Fig. 3-1. Evolution of ovuliferous structures (ovules). A–D. After the telome concept a nucellus (dark) with a sterile cover (integument) (white, dotted) developed partly of a vegetative, partly of a sporangia bearing branched telome system. **E–F.** The Neosynangial hypothesis postulates "the ovule as a transformation of a stalked sporangium cluster that involves the sterilization of the peripheral sporangia to form a ring of free integumentary lobes surrounding single central megasporangium" (Kenrick & Crane 1997, p. 292). Without scales. (A–D after Andrews, E–F after Kenrick & Crane 1997. Adopted from Strasburger, 35. Aufl., 2002, Fig. 11-289, p. 862).

Polyembryony is common, but only few fully developed seeds contain more than 1 embryo.

Few species are polyploid, e.g., *Sequoia* 6x, *Fitzroya* 4x, no allopolyploid taxa are known. Oldest known extant non-clonal gymnosperm taxa, *Pinus longaeva* 4800 y., *Fitzroya cupressoides* 3600 y.

Extant gymnosperms are dominant trees in the boreal zone of the Northern Hemisphere, e.g., conifers in the boreal forest communities, and in temp. regions of the Southern Hemisphere. Of high economic importance.

Fossil history and evolution of gymnosperms. Extant gymnosperms are clearly monophyletic (Christenhusz et al. 2011) and sister taxon to the angiosperms (Chaw et al. 1997, 2000; Ran et al. 2010). But their relationships to fossil gymnospermous taxa remain obscure and incompletely understood. Gymnospermous plants appeared already in the Palaeozoic. The Pteridosperms ("Pteridospermatidae") are considered to be the first unequivocal gymnospermous taxa. Earliest woody plant: *Armoricaphyton chateau-pannense* Strullu-Derrien & al. (classis incertae sedis) (Strullu-Derrien et al. 2014). Cladistic analysis of seed plants (Crane 1985) reveal that Lyginopteridales are prob. sister group to all other seed plants. Nixon et al. (1994) found *Caytonia* as a sister taxon to the Glossopteridales. Pteridosperms occured with their highest diversity in the Palaeozoic but existed until Mesozoic. The Cordaitales are considered as a modern gymnosperm group and Florin (1951) suggested that they were the ancestors of all other modern gymnosperms. Recent phylogenetic analysis (Hilton & Bateman 2006) resolved *Shanxioxylon* as sister to a clade of *Cordaixylon*, *Pennsylvanioxylon* and *Mesoxylon*. This clade is sister to a Conifer group incl. Palaeozoic, Mesozoic and several modern conifers.

Voltziales have historically been referred as transition between Cordaitales and the modern conifers. The phylogenetic analyses of Hernandez-Castillo et al. (2003) and Rothwell et al. (2005) resolved the Cordaitales and Vojnovskyales as basal to the Voltziales, which form a clade with the early conifers. They are also crucial for the understanding of seed cone morphology and evolution of modern conifers. The seed cones, e.g., of *Pinus* consist of helically arranged seed scales, and each of the scales is associated with a bract scale adnate to the abaxial basal region (Foster & Gifford 1974). Each seed scale bears a pair of inverted ovules on the adaxial side, where the micropyle is oriented towards the base of the scale. As the seed scale is subtended by a bract scale, the seed cone is a compound strobilus homologous to an inflorescence, while the pollen cone is a simple strobilus, i.e., a short shoot with microsporophylls (flower). Florin (1944) suggested that the ovuliferous (seed) scale with axillary position to a bract scale is phylogenetically a modified and highly condensed fertile ovule-bearing short shoot and its present appearance is the result of fusion and specialisation of the sterile and fertile components of such an ancestral structure (Foster & Gifford 1974). The Voltziales contain such possible ancestors (Florin 1944). In *Utrechtia* (= *Lebachia*) the seed cone consists of a series of helically arranged bifid bracts which developed short, uniovulate, radial leafy shoots in their axils. Usually only one scale-like leaf was fertile, the remaining being sterile, the fertile appendage or megasporophyll was situated near base or middle of the dwarf shoot, bearing a single ovule (Florin 1944, Fig. 3-2). The reproductive structures of *Ernestiodendron* were similar but differed in the larger number of ovuliferous appendages. Florin (1944) named this type of fertile shoot as "seed-scale-complex" and argued that this compound type of megasporangiate strobilus represented the ancestral stade. In *Pseudovoltzia*, each axillary seed-scale complex was composed of a short axis bearing 5 sterile scales and 2–3 stalked megasporophylls, each with an inverted ovule. In the Triassic *Voltzia* the 5 sterile scales are basally fused to form a flat sterile component, and the 3 megasporophylls are adnate to the inner surface of these united scales for most of their length (Florin 1944, Foster & Gifford 1974). Fig. 3-2.

The position of Gnetidae has been problematical and was controversially discussed. Qiu et al. (1999) suggested that they are embedded in the conifer clade as sister to Pinaceae ("gnepine hypothesis"). Other authors, e.g., Rydin et al. (2002) considered them to be sisters to all other extant seed plants

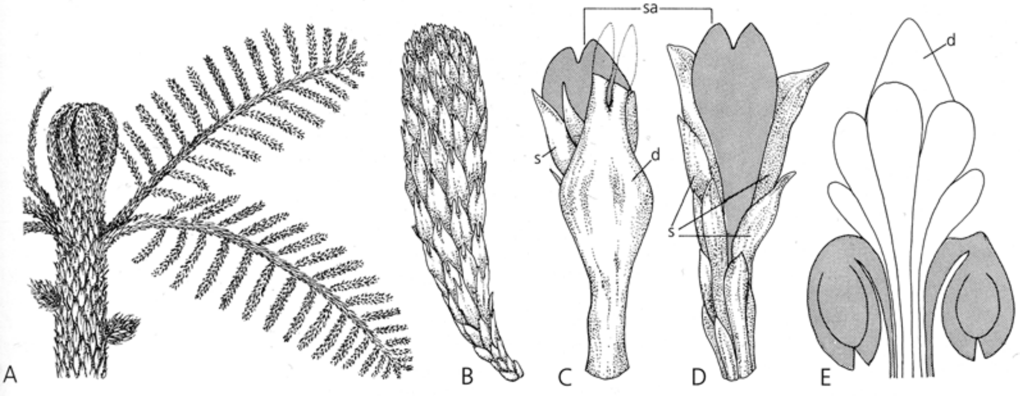

Fig. 3-2. Voltziales. A–D. *Utrechtia piniformis* (Lower Permian/Rotliegendes). **A.** Apex of shoot; main axis with bifid leaves (c. 0.25x). **B.** Erect ♀ cone with bifid bract scales (c. 0.4x). **C–D.** ♀ flower, back and front side; bract scale (bract = subtending leaf, d), sterile scales(s) and flattened atropous ovules (sa) with biparted integument (c. 4x). **E.** *Glyptolepis longibracteata* (Lower Triassic). ♀ flower with bract scale (d), sterile scales and anatropous ovules (schematic, 1.6x). (d bract scale, s sterile scale, sa atropous ovule). After Florin. (Adopted from Strasburger, 35. Aufl., 2002, Fig. 11-207, p.789).

(cf. Gnetidae). The families of modern conifers appear about the same time in Mesozoic, except for Taxaceae (Taylor et al. 2009) (cf. ord. Cordaitales and Voltziales).

For the most recent classification on extant gymnosperms see Christenhusz et al. (2011). The "Evolution and biogeography of Gymnosperms" is dealt with in the review article of Wang & Ran (2014; "Phylogenetic relationships at different taxonomic levels, patterns of species diversification, roles of vicariance and dispersal in development of intercontinental disjunctions, modes of molecular evolution in different genomes and lineages, mechanisms underlying the formation of large nuclear genomes and pathways for dispersal of gymnosperms.")

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Synopsis of classification of the Spermatophytes (incl. subclasses, orders and families of Pinopsida)

Author's names: Fossil genera acc. Index Nominum Genericum (ING), extant genera and species acc. Tropicos (www.tropicos.org), partly after Brummit, R.K. & Powell, C.E. 2011: Authors of Plant Names. – Roy. Bot. Gardens, Kew.

Classification

Superclass **Radiatopses** Kenrick & P.R.Crane (Spermatophytes, Seed plants)
Class **Progymnospermopsida** C.B.Beck (†) (Cf. Syllabus of Plant Families, Part 3, 2009.)
Class **Pinopsida** Burnett (Gymnosperms)
  Subclass "**Pteridospermatidae**" (†)
    Order **Buteoxylonales** P.D.W.Barnard & A.G.Long
    Order **Calamopityales** Němejc
      Calamopityaceae Solms
    Order **Callistophytales** G.W.Rothwell
      Angaranthaceae Naugolnykh, **Callistophytaceae** B.M.Stidd & J.W.Hall, **Emplectopteridaceae** R.H.Wagner
    Order **Glossopteridales** D.D.Pant
      Glossopteridaceae D.D.Pant
    Taxa of uncertain affinities with Glossopteriales
      Nystroemiaceae J.Wang & H.W.Pfefferkorn
    Order **Lyginopteridales** Gothan & W.Zimm.
      Lyginopteridaceae Potonié
  Subclass **Cycadidae** Pax
    Order **Bennettitales** Engl. (†)
      Cycadeoideaceae R.Br. ex G.R.Wieland, **Fredlindiaceae** J.M.Anderson & H.M.Anderson, **Laurozamitaceae** J.M.Anderson & H.M.Anderson, **Sturianthaceae** Doweld, **Vardekloeftiaceae** J.M.Anderson &H.M. Anderson, **Westerheimiaceae** Němejc, **Williamsoniaceae** (Carruth.) Nathorst, **Williamsoniellaceae** Nakai
    Order **Cycadales** Pers. ex Bercht. & J.Presl
      Cycadaceae Pers., **Zamiaceae** Horan.
    Order **Gigantopteridales** X.Li & Z.Q.Yao (†)
      Gigantopteridaceae Koidzumi
    Order **Medullosales** Corsin (†)
      Medullosaceae O.Weber & J.T.Sterzel

Order **Pentoxylales** Sahni (†)
Lindthecaceae J.M.Anderson & H.M.Anderson, **Pentoxylaceae** Pilg. & Melch.
Subclass **Ginkgoidae** Engl.
Order **Caytoniales** Gothan (†)
Caytoniaceae Kräusel
Order **Corystospermales** H.H.Thomas (†)
Corystospermataceae H.H.Thomas
Order **Czekanowskiales** D.D.Pant (†)
Iraniaceae Schweitzer, **Leptostrobaceae** S.V.Meyen
Order **Ginkgoales** Gorozh.
Ginkgoaceae Engl.
(†) **Karkeniaceae** Krassilov, **Schmeissneriaceae** Z.Zhou, **Umaltolepidiaceae** Stanislawskij, **Yimaiaceae** Z.Zhou
Order **Hamshawviales** J.M.Anderson & H.M.Anderson (†)
Hamshawviaceae J.M.Anderson & H.M.Anderson
Order **Matatiellales** J.M.Anderson & H.M.Anderson (†)
Matatiellaceae J.M.Anderson & H.M.Anderson
Order **Peltaspermales** T.N.Taylor (†)
Cardiolepidiaceae S.V.Meyen, **Peltaspermaceae** H.H.Thomas
Order **Petriellales** T.N.Taylor, del Fueyo & E.L.Taylor (†)
Kannaskoppiaceae J.M.Anderson & H.M.Anderson, **Petriellaeaceae** T.N.Taylor, del Fueyo & E.L.Taylor
Subclass **Gnetidae** Pax
Order **Welwitschiales** Skottsb. ex Reveal
Welwitschiaceae Caruel
Order **Gnetales** Blume
Gnetaceae Blume
Order **Ephedrales** Dumort.
Ephedraceae Dumort.
Subclass **Pinidae** Cronquist, Takht. & W.Zimm.
Order **Cordaitales** Grand'Eury (†)
Cordaitaceae Grand'Eury, **Vojnovskyaceae** M.F.Neuburg
Order **Voltziales** Andr. (†)
Bartheliaceae G.W.Rothwell & G.Mapes, **Buriadiaceae** D.D.Pant & Nautiyal, **Emporiaceae** G.Mapes & G.W.Rothwell, **Feругliocladaceae** S.Archangelsky & R.Cunéo, **Majonicaceae** Clem.-West., **Thucydiaceae** G.R.Hernandez-Castillo, G.W.Rothwell & G.Mapes, **Ullmanniaceae** Němejc, **Utrechtiaceae** G.Mapes & G.R.Rothwell, **Voltziaceae** C.A.Arnold
Taxa of uncertain affinities to Voltziales
Order **Dordrechtitales** J.M.Anderson & H.M.Anderson (†)
Dordrechtitaceae J.M.Anderson & H.M.Anderson
Order **Pinales** Gorozh.
Pinaceae Spreng. ex F.Rudolphi

Order **Araucariales** Gorozh.
Araucariaceae Henkel & W.Hochst.
Podocarpaceae Endl. (incl. Phyllocladaceae Bessey)
Order **Cupressales** Link
Cheirolepidiaceae Takht. (†), **Cupressaceae** Gray, **Geinitziaceae** Kunzmann (†), **Palissyaceae** Florin (†), **Sciadopityaceae** Luerss., **Taxaceae** Gray
Taxa of uncertain position within gymnosperms (†)
Order **Alexiales** J.M.Anderson & H.M.Anderson
Alexiaceae J.M.Anderson & H.M.Anderson
Dirhopalostachyaceae Krassilov
Order **Hermanophytales** Tidwell & Ash
Order **Hlatimbiales** J.M.Anderson & H.M.Anderson
Hlatimbiaceae J.M.Anderson & H.M.Anderson
Class **Magnoliopsida** Brogn. (Angiosperms)
Subclass **Magnoliidae** Novák ex Takht.
Subclass **Rosidae** Takht. (Eudicots)

Systematic arrangement of taxa of the Pinopsida (Gymnosperms)

Species numbers are provisional. Reliable taxonomic concepts until January 2015. Author abbreviations acc. to Brummit, R.K. & Powell, C.E. 2011: Authors of Plant Names. – Roy. Bot. Gardens, Kew and Tropicos (www.tropicos.org).

Class **Pinopsida** Burnett (Gymnosperms)

Extant Pinopsida classification after Christenhusz et al. (2011). Extinct groups after Anderson et al. (2007) and Taylor et al. (2009)

Cf. also other classifications and treatises, e.g., Bierhorst 1971, Bobrov & Melikian 2006, Strasburger 2008.

Nowadays the extant gymnosperms are thought to be monophyletic and sister to the angiosperms (Chaw et al. 1997, 2000; Ran et al. 2010). Relationships of extant gymnosperms to fossil gymnosperms remain obscure and incompletely understood.

Extant gymnosperms c. 1041 spp. Cycadidae: 1 ord., 2 fam., 10 gen. (325); Ginkgoidae: 1 ord., 1 fam., 1 gen. (1); Gnetidae: 3 ord., 3 fam., 3 gen. (c. 72); Pinidae: 3 ord., 6 fam., 70 gen. (c. 615) (Christenhusz 2011, Cycadales acc. Osborne et al. 2012).

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Strasburger (A. Bresinsky, C. Körner, J.W. Kadereit, G. Neuhaus, U. Sonnewald) 2008: Lehrbuch der Botanik, 36. Aufl. – Spektrum, Akad. Verlag, Heidelberg.

1. Subclass "**Pteridospermatidae**" Seed ferns (†)

Extinct group of seed plants exhibiting leaf features of ferns and generative features of gymnosperms. Small trees, shrubs or possibly vines/woody climbers with helically arranged large fern-like fronds. Vascular arrangement from simple protosteles to eusteles. Wood usually of parenchyma and thin-walled tracheids giving a spongy manoxylic appearance. Pollen-bearing structures and seeds borne on leaves. Pollen organs usually aggregated into clusters, sometimes microsporangia synangiate. Seeds large and solitary or small and borne in multiovulate cupules. Fig. 3-3.

Pteridosperms were first characterized by Oliver & Scott (1904) based on the fossil connection of *Lyginopteris oldhamia* (Binney) Potonié and *Lagenostoma lomaxii* W.C.Williamson The Lyginopteridales prob. evolved from Late Devonian progymnosperms (Aneurophytales, Rothwell & Erwin 1987, Fischer 2009). Cladistic analysis of seed plants (Crane 1985) revealed that Lyginopteridales are prob. sister group to all other seed plants. Nixon et al. (1994) found *Caytonia* as a sister taxon to the Glossopteridales. Anderson et al. (2007) placed Glossopteridales as new class **Ottokariopsida** J.M.Anderson & H.M.Anderson with the only ord. **Ottokariales** J.M.Anderson & H.M.Anderson close to Cycadidae and *Caytonia* into Gingkoidae. We follow Anderson et al. (2007) in assigning ord. Gigantopteridales, Medullosales and Pentoxylales to Cycadidae and Caytoniales, Corystospermales, Czekanowskiales, Peltaspermales and Petriellales to Gingkoidae.

1. Order **Buteoxylonales** P.D.W.Barnard & A.G.Long

Stems protostelic with manoxylic secondary xylem containing high, narrow vascular rays. Petiolar vascular bundle trilobed or T-shaped in cross-section. Pollen- or ovulate organs unknown. Buteoxylonales are the least understood Palaeozoic seed ferns (Taylor et al. 2009) and the discovery of pollen- and seed-organs may reveal a different systematic position.

Buteoxylon P.D.W.Barnard & A.G.Long (1). Permineralized stem fragment with petioles attached to the stem in a helical pattern of 2/5 phyllotaxy. Stems and petioles contain a sparganum outer cortex. - *B. gordonianum* P.D.W.Barnard & A.G.Long, Upper Devonian, Ireland to Upper Tournaisian Calciferous Sandstone Series, Scotland. – ***Triradioxylon*** P.D.W.Barnard & A.G.Long (1). Stem with small trilobed protostele. Petioles in a 1/3 phyllotaxy. - *T. primaevum* P.D.W.Barnard & A.G.Long, Lower Carboniferous, Scotland.

2. Order **Calamopityales** Němejc

Fam. **Calamopityaceae** Solms Mainly characterized by manoxylic wood and an unsual thick cortex. Pollen and seed organs unknown. Missisippian; Europe, N America.

Kalymma Unger Morphotaxon for petioles, that bifurcates near base with petiolar vascular bundles arranged in a C-shape above (Long 1964, Barnard & Long 1975, Matten & Trimble 1978, Braun & Wilde 2002). The seed *Lyrasperma scotica* (Calder) A.G.Long was suggested by Long (1964) to be borne on *Stenemyelon* stems. Important contributions by Stein & Beck (1978), Beck & Stein (1987) and Decombeix et al. (2006).

Bostonia W.E.Stein & C.B.Beck (1). Stems with parenchymatous ground-tissue with nests of sclerotic cells and multiple segments of primary xylem surrounded by secondary vascular tissue. Phyllotaxis helical, regular. Petioles of the *Kalymma*-type, but with 3-ribbed medial petiole bundle. - *B. perplexa* W.E.Stein & C.B.Beck, Early Mississippian (Lower Carboniferous), New Albany Shale. – ***Calamopitys*** Unger (c. 5–10). Erect tree-or shrub-like habit or lianescent. Slender stems, usually 2–3 cm in diam., vascular arrangement protostelic to eustelic; xylem mesarch; secondary phloem of alternating bands of parenchyma and sieve cells. Leaves large, bipartite with naked petioles. Upper Tournaisian-Mississipian. – ***Chapelia*** C.B.Beck & R.E.Bailey (1). Petiole just below branching point in the frond. Vascular sytem of a 4-lobed protostele with mesarch xylem, surrounded by manoxylic secondary xylem. - *C. campbellii* C.B.Beck & R.E.Bailey, Lower Mississippian, N America. – ***Diichnia*** C.B.Read (2). Stem with pentagonal eustele of 5 mesarch primary xylem bundles. Leaves helically arranged. Early Mississippian, N America. – ***Faironia*** Decombeix, Galtier & Meyer-Berthaut (1). Stem with broad eustele; wood dense, with multifascicular leaf traces and *Kalymma*-type petioles. - *F. difasciculata* Decombeix, Galtier & Meyer-Berthaut, Tournaisian, France. – ***Galtiera*** C.B.Beck & W.E.Stein (1). Stem with primary xylem in cross-section a 3-ribbed protostele. Leaf bases of the *Kalymma*-type. Cortex with a large number of sclerotic clusters. - *G. bostonensis* C.B.Beck & W.E.Stein, Early Mississipppian, New Albany Shale. – ***Stenomyelon*** Kidston (4–5). Stem with solid protostele dissected into nearly equal thirds by thin plates of parenchyma. Petioles attached in a 2/5 phyllotaxy, unique pattern of petiolar bundle development. Adventitious roots present. Calciferous Sandstone series, Lower Carboniferous; England. – ***Triichnia*** Galtier & C.B.Beck (2). Stem with eustelic primary vascular system of a nearly contiguous ring of primary mesarch bundles around a wide parenchymatous pith. Petioles of the *Kalymma*-type. Tournaisian, France.

3. Order **Callistophytales** G.W.Rothwell

Plants with eustelic stems that produce pinnately compound fronds with axillary buds or branches at each node. Pollen organs synangiate, borne on pinnules of the frond; pollen grains small and saccate. Seeds flattened (platyspermic), attached on abaxial side of reduced pinnules; nucellus and integument free except at chalaza. Middle-Upper Pennsylvanian to Lower Permian (Stidd & Hall 1970a, b; Rothwell 1975, 1976, 1981; Hilton et al. 2002; Naugolnyk 2012).

Fam. **Angaranthaceae** Naugolnykh Leaves compound pinnate; pinnules triangular, entire to deeply dissected. ♂ reproductive organs with reduced leaf lamina, lateral extensions bearing last order fertile segments with lax cluster of microsporangia. ♀ reproductive organs with reduced pinnae bearing winged ovules of the *Angarocarpus*-type. Middle Carboniferous Siberia, N Kazakhstan.

Angaranthus Naugolnykh (1). ♂ reproductive organs: fertile pinnae with clusters of fusiform microsporangia. - *A. victorii* Naugolnyk, Middle Carboniferous, Siberia. – ***Angaridium*** M.D.Zalessky (5). Sterile pinnules. Middle Carboniferous, Siberia. – ***Angarocarpus*** G.P.Radczenko (1). Seeds. - *A. ungensis* (M.D.Zalessky) G.P.Radczenko, Middle Carboniferous, Siberia. – ***Gondwanotheca*** M.F.Neuburg (1) (incl. *Paragondwanidium* S.V.Meyen). ♀ reproductive seed-bearing organ. - *G. sibirica* M.F.Neuburg, Middle Carboniferous, Siberia.

Fam. **Callistophytaceae** B.M. Stidd & J.W. Hall

Callistophyton Delevoryas & Morgan (1–3) (incl. organ gen. *Callospermarion* D.A.Eggert & Delevoryas, *Dicksonites* Sterzel, *Idanothekion* M.A.Millay & D.A.Eggert, *Vesicaspora* M.P.Schemel). Ovules (*Callospermarion*) scattered on abaxial surface of leaves, with single integument free from nucellus except at chalaza. Stem with eustelic primary vasculature; secondary xylem well developed. Foliage (*Dicksonites*) with bipartite fronds, each branch tripinnately divided. Microsporangiate organs (*Idanothekion*): radially symmetrical synangia arising abaxially on pinnules, each synangium of 6–8 sporangia. Pollen described as *Vesicaspora*. Middle and Upper Pennsylvanian; Europe, N America; Lower Permian; Brazil, China.

Fam. **Emplectopteridaceae** R.H.Wagner Leaves pinnate, bipinnate or simple. Pollen organs a complex of filiform microsporophylls each bearing 2–8 sporangia, described as *Jiaochengia* (Wang 1999) (see also Gigantopteridales). ♀ organs described as *Cornucarpus* Archer. Ovules bilateral and attached to lower surface of fronds. Sometimes included in Gigantopteridales (s. bl.).

Emplectopteris Halle (1–2). Foliage. Lower Permian, China.

4. Order **Glossopteridales** D.D.Pant (incl. Ottokariopsida J.M.Anderson & H.M.Anderson, Ottokariales J.M.Anderson & H.M.Anderson)

Glossopterids dominated the flora of the supercontinent Gondwana during the Permian (Rigby 1978, White 1990) and the discovery of structurally preserved megasphorophylls bearing seeds revealed Glossopterids to belong to the seed ferns (Gould & Delevoryas 1977, Nishida et al. 2007).

Fam. **Glossopteridaceae** D.D.Pant (incl. Ottokariaceae J.M.Anderson & H.M.Anderson, Rigbyaceae J.M.Anderson & H.M.Anderson, Arberiaceae J.M.Anderson & H.M.Anderson, Lidgettoniaceae J.M.Anderson & H.M.Anderson) Numerous species only weakly defined and based on foliage impressions. Only 3 genera known with leaves and associated micro- and megasporophylls (Crane 1985).

Flagellated sperms in *Glossopteris* from the Late Permian of Qld., Australia, first known example for Zooidogamy (Nishida et al. 2004).

Glossopteris Brongn. (c. 150–200) (incl. organ gen. *Eretmontia* Du Toit, *Glossotheca* K.R.Surange & H.K.Maheshwari, *Hirsutum* Plumstead, *Arberiella* D.D.Pant & D.D.Nautiyal). Orig. described as leaf morphogenus. Leaves simple, with midribs and well developed reticulate venation. Microsporangia described as *Eretmontia* or *Glossotheca*, bearing clusters of the pollen sac organ gen. *Arberiella*. Ovule-bearing structures adnate to leaf surface, either a leaf-homologue (megasporophyll) or a modified axis. Permian to Triassic, Gondwanan. - Early Permian *Glossopteris* flora from India (Tewari et al. 2012). – ***Lidgettonia*** H.H.Thomas (c. 5–10) (incl. organ gen. *Eretmontia*, *Arberiella*, *Protohaploxypinus* S.R.Samoilovitch). Sterile leaves with adnate megasporophyll, bearing c. 8 fertile cupules on slender stalks adnate to leaf lamina. Each cupule an expanded disc bearing ovules on lower surface. Microsporophylls described as *Eretmontia*, pollen sac as *Arberiella*, pollen as *Protohaploxypinus*. Upper Permian, S Africa. – ***Lonchiphyllum*** P.E.Ryberg & E.L.Taylor *L. aplospermum* P.E.Ryberg & E.L.Taylor Megasporophyll, Upper Permian, Antarctica (Ryberg & Taylor 2013). – ***Ottokaria*** Zeiller (c. 20) (incl. organ gen. *Pterygospermum* D.D.Pant & D.D.Nautiyal, *Platycardia* D.D.Pant & D.D.Nautiyal, *Protohaploxypinus*). Megasporophylls adnate to upper leaf surface, expanded distally to form a spoon-shaped head with sterile marginal lobes bearing ovules on the concave side. Ovules described as *Pterygospermum* and *Platycardia*, pollen as *Protohaploxypinus*. Permian, Gondwana.

Leaf morphotaxa. ***Belemnopteris*** O.Feistmantel Similar to *Glossopteris* or *Gangamopteris* but leaf sagittate at base. Permian. – ***Gangamopteris*** F.McCoy Well defined midrib absent. Lower Permian. – ***Rhabdotaenia*** D.D.Pant Nonanastomosing lateral veins present. Permian – ***Palaeovittaria*** O.Feistmantel Permian. – ***Surangephyllum*** S.Chandra & K.J.Singh Permian. **Pollen structure.** ***Squamella*** M.E.White *S. australis* M.E.White considered by White (1978) as the pollen cone of *Glossopteris linearis* F.McCoy; Late Permian, Australia. **Ovulate structures.** ***Arberia*** D.White Branching structure bearing at least 4 uniovulate cupules. Upper Permian, Antarctica. – ***Cometia*** S.McLoughlin Flattened, simple organ with 2 lobes. Late Permian. – ***Denkania*** K.R.Surange & S.Chandra C. 6 seed-bearing cupules attached to long pedicels borne on midrib of a *Glossopteris* scale leaf. Permian, India. – ***Dictyopteridium*** O.Feistmantel ex R.Zeiller Flattened organ with a receptacle bearing seeds or seed-scars on surface. Permian. – ***Gladiopomum*** Adendorff, McLoughlin & Bamford Ovulate organs with receptacle and wing-like structure, with spine at distal end of receptacle. Early Permian. – ***Homevaleia*** Nishida & al. Megasporophyll with attached seeds on short stalks. Seeds orthotropous, integument 2-layered, with sarco- and sclerotesta. – ***Plumsteadia*** J.F.Rigby Similar to *Gladiopomum* but lacking the distal spine; receptacle more elongated. Early Permian. – ***Rigbya*** W.S.Lacey, D.E.van Dijk & K.D.Gordon-Gray Similar to *Cometia,* bearing 5–9 lobes. – ***Scutum*** E.Plumstead Megasporophyll with cupules. Bract-like structures orig. interpreted as pollen-bearing. Pant (1987) questions this observation. – ***Squamella*** M.E.White Cones with aggregations of “scale fronds” bearing sporangia or seeds. Acc. to White (1978) close to *Lidgettonia*. Late Permian, Australia.

Taxa of uncertain affinities with Glossopteridales
The recently described Nystroemiaceae (Wang & Pfefferkorn 2010) show some plesiomorphic characters of early seed plants, while leaves and branches exhibit apomorphic characters of broad-leaved gymnosperms. The authors argue for a position as sister group to Glossopteridales.
Fam. **Nystroemiaceae** J.Wang & H.W.Pfefferkorn Main axis furcate, with pinnate lateral branches bearing numerous small bicornute ovules at their tips. Long and short shoots present. Vegetative leaves with long petiole and broad lamina showing reticulate venation; lamina cordate or tapering at base. Ovuliferous leaves arising in leaf-axils; ovuliferous organs attached in leaf axil or crowded on a node.

Nystroemia Halle (incl. organ gen. *Chiropteris* J.G.Kurr) (2). *N. pectiniformis* Halle, *N. shouyangensis* J.Wang & H.W.Pfefferkorn Leaves described as *Chiropteris reniformis* Kawaski. Middle-Late Permian, China.

5. Order **Lyginopteridales** Gothan & W.Zimm.

Stems narrow and prob. often climbing. Pollen organs of clusters of sporangia. Pollen trilete, prob. wind-dispersed. Cupulate seeds with pollen-receiving structures and pollen chamber. Fig. 3-3.A–G.

Lyginopterid seed ferns are prob. a polyphyletic and heterogeneous group.

Fam. **Lyginopteridaceae** Potonié (incl. Physostomaceae A.G.Long, Genomostomaceae A.G.Long, Eospermaceae A.G.Long).

Lyginopteris Potonié (c. 20) [incl. organ gen. *Sphenopteris* (Brongn.) Sternberg, *Lyginorachis* Brongn., *Crossotheca* Zeiler, *Telangium* Benson, *Calymmatotheca* Benson, *Lagenostoma* W.C.Williamson, *Lagenospermum* Nathorst, *Hydrosperma* A.G.Long]. Small stems of possibly vine-like habit, not self-supporting (Speck 1994); vascular organisation eustelic with bifacial cambium. Wood with large tracheids and multiseriate, oval bordered pits on radial walls. Leaves of *L. oldhamia* (Binney) Potonié prob. *Sphenopteris hoeninghausii* Brogn.; petioles with V- or W-shaped bundle (*Lyginorachis* A.G.Long). Microsporangiate organs prob. *Crossotheca* sp. (= *Feraxotheca* M.A.Millay & T.N.Taylor) or *Telangium scottii* Benson (Benson 1904) with bilaterally symmetrical synangia. Ovules (*Lagenostoma lomaxii* W.C.Williamson) borne terminally on distal part of leaves in pedicellate cupules (*Calymmatotheca*), with single integument fused with nucellus except near micropyle. Seeds (*Lagenospermum*, *Hydrosperma)* ellipsoidal. ♀ gametophyte of *Lagenostoma ovoides* W.C.Williamson and *Hydrosperma tenuis* A.G.Long cellular with archegonia (Long 1944, Matten et al. 1984). Upper Carboniferous; Europe, N America.

Morphotaxa of Lyginopteridaceae. Vegetative remains. Numerous vegetative remains are assigned to Lyginopteridaceae, but they can usually not be connected to reproductive remains. – ***Eristophyton*** Lacey (2). Similar to *Pitys*. Mississipian, Scotland. – ***Heterangium*** Corda (c. 5–10). Stem similar to *Lyginopteris*, associated with pinnules of the *Sphenopteris*-type from Carboniferous, ext. possibly to Permian. – ***Kerryoxylon*** L.C.Matten, W.R.Tanner & W.S.Lacey (1). Outer cortex of sparganum-type. Petioles similar to *Lyginorachis* Brongn. Uppermost Devonian, Ireland. – ***Microspermopteris*** R.W.Baxter (3–5). Stems similar to *Heterangium*, differing in protoxylem architecture and pinnate fronds. Petioles in a 2/5 phyllotaxy. Pennsylvanian; N America, Germany. – ***Pitys*** H.T.M.Witham (c. 5). Large forest trees. Center of stem with parenchymatous pith and up to 50 mesarch primary xylem strands. Possibly *Lyginorachis papilio* Kidston represents the petiole of *Pitys* and *Tristichia ovensii* Bar-

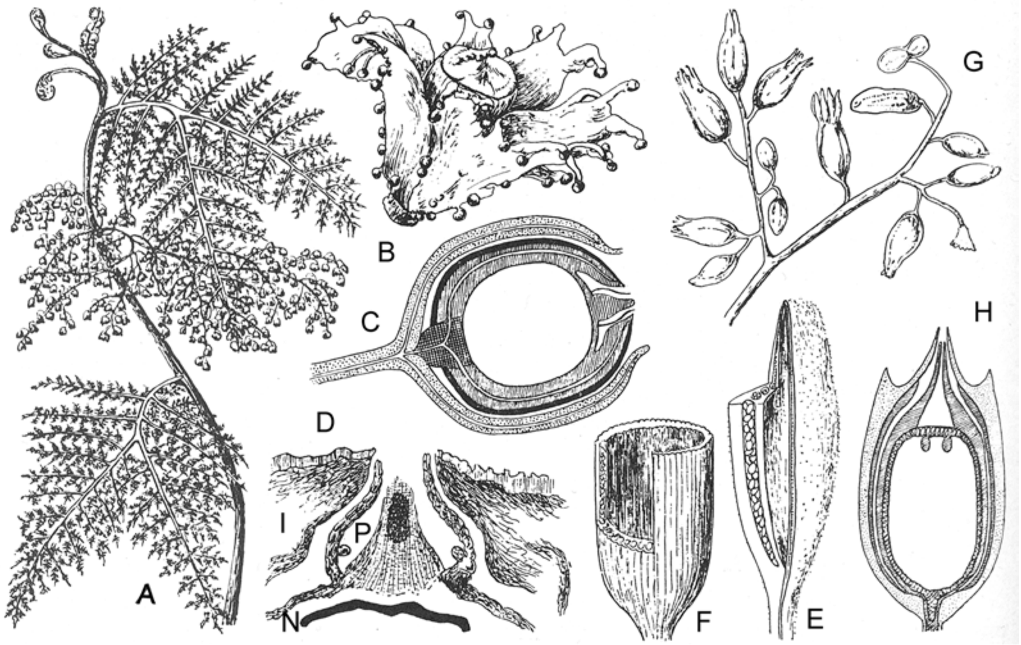

Fig. 3-3. Pteridospermatidae, Lyginopteridales (A–G). Cycadidae, Medullosales (H). A–D. *Lyginopteris oldhami.* A. Habit (*Sphenopteris hoeninghausi*). B. Seed (*Lagenostoma*) with cupule. C. Seed with cupule (*Lagenostoma lomaxi*), LS (c. 6x). D. LS through the top of an ovule with integument (I), nucellus (N), pollen chamber (P). **E.** *Aulacotheca.* Microsporophyll, partly cut open. **F.** *Whittleseya.* Microsporophyll, partly, LS. **G.** *Lagenostoma sinclairi.* Sporophyll with seeds, enclosed in cupule. **H.** *Stephanospermum akenioides.* Seed with pollen chamber, LS. Without scale. After Arber, Brongiart, Halle, Oliver, Potonié, Scott. (Adopted from the 12th ed. of 'Syllabus der Pflanzenfamilien' 1954, **I**, p. 316, Fig. 125).

nard & A.G.Long the ovule-bearing axis (Long 1963). – ***Rhetinangium*** Gordon (1). Stem with a mixed protostele and clusters of tracheids surrounded by thin-walled parenchyma and secretory cells. Mississipian; N America, Scotland. – ***Schopfistriatum*** H.N.Andrews (1). Stem similar to *Heterangium*. Middle Pennsylvanian, N America. – ***Stanwoodia*** Galtier & D.H..Scott (1). Stem ressembling *Eristophyton*. Mississipian. – ***Tetrastichia*** Gordon (1). Stem with cruciform protostele. Leaves decussate. Mississipian, Scotland. Affinities of *Tetrastichia* are unclear and the genus is provisionally placed in Lyginopteridaceae (Taylor et al. 2009). – ***Tristichia*** A.G.Long (2). Stem with triangular protostele. Petioles large and arranged in a 1/3 phyllotaxy. Uppermost Devonian to Mississipian. – ***Trivena*** M.T.Dunn, G.W.Rothwell & G.Mapes (1). Permineralized stem. Carboniferous, Upper Mississipian; N America.

Seeds and cupules. Numerous cupules with ovules and seeds of Lyginopteridaceae with pollen-chamber and lagenostome are known. – ***Calathospermum*** J.Walton Cupule with c. 70 stalked ovules. Possibly a younger developmental stage of *Salpingostoma*. Mississpian, Scotland. – ***Conostoma*** W.C.Williamson Pennsylvanian; Europe, N America. – ***Coronostoma*** F.E.Neely Late Pennsylvanian. – ***Gnetopsis*** Renault & Zeiller Multiovulate cupules, each cupule with 2–4 seeds. Micropylar region with hair-covered extensions. Cupule structure (Galtier 2013). Lower Mississipian. – ***Megatheca*** H.N.Andrews Cupule lacking seeds. Mississpian, Scotland. – ***Physostoma*** W.C.Williamson Radiospermic ovule borne in cupules. Middle Pennsylvanian, N America. Assigned by Anderson et al.

(2007) to fam. **Physostomaceae** A.G.Long – ***Salpingostoma*** Gordon Lower Carboniferous, East Lothian; Scotland. – ***Sphaerostoma*** M.Benson Integument divided into 3 parts, with outer layer as sarcotesta and middle layer as sclerotesta, nucellus and integument fused. Associated with stems of *Heterangium* Corda. Mississipian, Scotland. – ***Tyliosperma*** S.H.Mamay Integument divided at distal end into 7 apical lobes. Seed developing in a fleshy cupule. Middle Pennsylvanian.

Taxa of uncertain affinities within Lyginopteridales
Elkinsia G.W.Rothwell, S.E.Scheckler & H.W.Gillespie (1). Lax aggregations of cupules on cruciately forked branching system. Cupules singly or in pairs; ovules with integument consisting of 4–5 lobes fused at basal region. Late Devonian (Famenian), N America. *E. polymorpha* G.W.Rothwell, S.E.Scheckler & H.W.Gillespie, Late Devonian (Famenian), N America. – ***Moresnetia*** F.Stockmans (1). Cupules similar to *Elkinsia*, each cupule with up to 4 ovules, each ovule with free integumentary lobes. Late Devonian (Famennian), Belgium. *Elkinsia* and *Moresnetia* are considered by Anderson et al. (2007) as members of a separate fam. **Moresnetiaceae** Němejc in ord. Lyginopteridales. The following fossil seeds prob. belong to Lyginopteridales. - ***Archaeosperma*** *arnoldii* J.M.Pettitt & C.B.Beck 2 cupules in terminal position on a furcate branch system. Upper Devonian, N America. – ***Coumiasperma*** J.Galtier & N.Rohe Tip of nucellus of solid parenchyma lacking a pollen chamber. Carboniferous, Middle Tournaisian; France. – ***Eurystoma*** A.G.Long, Lower Carboniferous, Scotland. – ***Genomosperma*** *kidstonii* (Calder) A.G.Long Integument of 8–11 free lobes. Considered by Anderson et al. (2007) to represent fam. **Genomospermaceae** A.G.Long, Lower Carboniferous, Scotland. – ***Menaisperma*** J.M.Pettitt & W.S.Lacey Integument attached to nucellus only at chalaza. Carboniferous, Upper Visean; England. – ***Xenotheca*** *devonica* E.A.N.Arber & R.H.Goode, Upper Devonian, England.

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2. Subclass **Cycadidae** Pax

1. Order **Bennettitales** Engl. (†)

Stems short and stout, pachycaulous, to slender and richly branched, eustelic, with large medulla; branching bifurcate. Leaves simple (*Nilssoniopteris*) or pinnate, with parallel or occ. dichotomous veins in the pinnae, reticulate in *Dictyozamites*. Leaves of *Pterophyllum filicoides* Brogn. (Carnian, Upper Triassic) displaying circinnate venation (Pott & Krings 2007), thus resembling extant Cycads. Microsporophylls and ovules aggregated into flower-like heads, usually surrounded by a "perianth" of bracts (except *Vardekloeftia*). "Flowers" unisexual (monosporangiate) or bisexual (bisporangiate). Microsporophylls in whorls, either pinnately branched and involute, or undivided and leaf-like flattened. Pollen sacs with exothecium and fused to a synangium. Pollen monosulcate "boat-shaped" (Zavialova et al. 2009). Ovules orthotropous, unitegmic, joined to nucellus only at chalaza; the integument distally prolonged into a micropylar tube. Ovules crowded into heads and not subtended by any other organ, separated by sterile interseminal scales prob. homologous with ovules. Upper Triassic to Upper Cretaceous. Fig. 3-4.

Phylogenetic analyses (e.g., Nixon et al. 1994) resolved Bennettitales in a clade with Gnetales and angiosperms. This may, however, be due to the fact that many fossils are anatomically preserved and include both vegetative and reproductive features thus providing numerous characters (Taylor et al. 2009). There is evidence that at least some Bennettitales had close associations with insects. Harris (1969) suggested that the resin-containing "synangia" on the bracts of the pollen cone *Weltrichia* represented an attractans for insect pollinators. Crane (1986) suggested that Bennettitales perhaps did possess a double integument, the outer integument being homologous to the cupule of genera like *Vardekloeftia*. Characters of bennettitalean plants and anthophyte hypothesis are discussed in Rothwell et al. (2009). Extinction of Bennettitales [NSW, Australia; *Ptilophyllum muelleri* (Ettingsh.) LcLoughlin & al.], cf. McLoughlin et al. (2011). Recognition of families within Bennettitales is far from resolved. Traditionally only 2 fam. (Cycadeoidaceae, Williamsoniaceae) are recognized (Watson & Sincock 1992). We agree with Anderson et al. (2007) that the morphological diversity warrants the recognition of 8 families.

Fam. **Cycadeoideaceae** R.Br. ex G.R.Wieland Cones bisexual, borne on short lateral branches or peduncles, not ext. beyond level of the trunk surface (Delevoryas 1968).

Cycadoidella Y.Ogura (1). Ovules orbicular in transverse section. - *C. japonica* Y.Ogura, Upper Cretaceous, Japan. – ***Cycadeoidea*** W.Buckland ex Lindl. & W.Hutton (c. 30–50). Trunks cylindrical to columnar or globose, with a crown of helically arranged leaves. Flowers bisporangiate (bisexual) on short pedicels in leaf axils. Perianth of helically arranged outer bracts surrounding c. 20 microsporophylls. Ovules angular to starshaped in transverse section. Upper Jurassic to Lower Cretaceous. The type of *C. etrusca* Capellini & Solms was discovered in an Etruscan grave apparently placed as a burial object (Capellini & Solms-Laubach 1890). – ***Monanthesia*** G.W.Wieland ex Delevoryas (1). "Flowers" borne on long slender peduncles in the axils of almost every leaf; receptacle conical. - *M. magnifica* Delevoryas, Upper Cretaceous, New Mexico.

Fam. **Fredlindiaceae** J.M.Anderson & H.M.Anderson Bilaterally symmetrical "gynoecia" attached in whorls, without differentiation into ovules and scales.

Fredlindia J.M.Anderson & H.M.Anderson (1). Leaves pinnate (*Halleyoctenis* J.M.Anderson & H.M.Anderson). Elongate axis bearing bilaterally symmetrical fleshy structures (described as "gynoecia") in a series of whorls. Each of these structures consists of a thickened lamina bearing ovuliferous units prob. to be considered as ovules. - *F. fontifructus* J.M.Anderson & H.M.Anderson, Upper Triassic, Molteno Formation; S Africa. Assigned by Anderson & Anderson (2003) to ord. **Fredlindiales** J.M.Anderson & H.M.Anderson.

Fam. **Laurozamitaceae** J.M.Anderson & H.M.Anderson Flowers unisexual, attachment unknown. "Gynoecia" discoid without differentiation into ovules and scales, surrounded by a "perianth" of c. 10 large bracts.

Laurozamites Weber & Zamudio-Varela (2) (incl. *Williamsonia* W.Carruthers p.p.). Upper Triassic, Chinle Formation, Mexico. Acc. to Anderson et al. (2007), the family appears to be intermediate between Fredlindiaceae and typical Bennettitales.

Fam. **Sturianthaceae** Doweld Unisexual flowers on slender pedicels attached helically to form a cone, without differentiation into ovules and scales, surrounded by a "perianth" of 25–30 small bracts.

Sturianthus Kräusel (1) (incl. *Sturiella* Kräusel). Late Triassic (Carnian), Austria.

Fam. **Vardekloeftiaceae** J.M.Anderson & H.M.Anderson Flowers unisexual, "gynoecia" small, spherical, with differentiation into ovulate and sterile scales; "perianth" lacking.

Vardekloeftia T.M.Harris (incl. organ gen. *Pterophyllum* Brongn.) (1). Spherical ovulate heads; each head composed of flattened, bilaterally symmetrical ovules separated by numerous interseminal scales. Ovules few (<20) and large with outer cutinized layer (cupule). Often associated with leaves of the organ gen. *Pterophyllum*. - *V. sulcata* T.M.Harris, Rhaetic, Greenland.

Pollen morphogenus. *Bennettistemon* T.M.Harris Lanceolate microsporophyll, entire surface covered with pollen sacs. Upper Triassic.

Fam. **Westerheimiaceae** Němejc Flowers unisexual, attached pinnately to a pedicel to form a lax cone, "gynoecia" elliptical, without differentiation into ovules and scales, without a "perianth" of bracts.

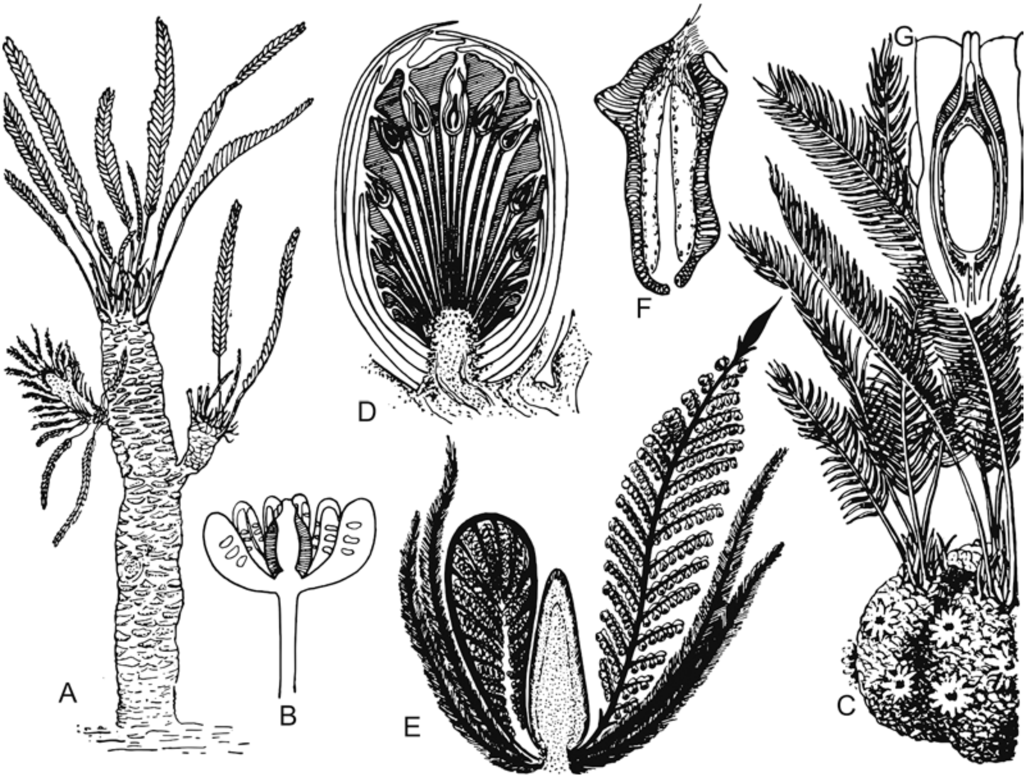

Fig. 3-4. Bennettitales. A. *Williamsonia sewardiana.* Jurassic. Habit (height of stem, c. 2 m). Reconstruction. **B.** *Williamsoniella coronata.* Jurassic. Cone with micro- and megasporophylls. **C–G.** *Cycadeoidea* spp. Upper Jurassic to Lower Cretaceous. C. *C.* sp. Pachycaulous stem with leaves and flower buds (reconstruction, reduced in size). D. *C. gibbsoniana.* Lower Cretaceous. LS. ♀ cone with perianth, interseminal scales, and stalked seeds. E–G. *C. dacotensis.* E. Cone, LS, ♂ stage. F. Synangium, LS. G. Ovule, LS. Without scale. (After Hirmer, Sahni, Scott, Thomas, Wieland. Adopted from the 12th ed. of 'Syllabus der Pflanzenfamilien' 1954, **I**, p. 322. Fig. 129).

Leguminanthus Kräusel & Schaarschmidt Detached microsporophyll. - *L. siliquosus* Kräusel & Schaarschmidt, Upper Triassic, Switzerland. – ***Westerheimia*** F.Krasser - *W. pramelreuthensis* F.Krasser, Upper Triassic, Switzerland.

Fam. **Williamsoniaceae** (W.Carruthers) Nathorst Plants with slender branching stems and stalked reproductive organs borne among the leaf bases on the trunks. Divaricate growth habit (Pott & McLoughlin 2014). Leaves widely separated along the stems. Cones usually monosporangiate, unisexual. Plants monoicous or dioicous.

Williamsonia W.Carruthers (c. 10) (incl. organ gen. *Bucklandia* Brogn. nom. cons. prop., *Cycadolepis* Saporta, *Ptilophyllum* J.Morris, *Weltrichia* C.F.W.Braun). Trees up to 2 m tall. Receptacle conical or hemispherical, bearing ovules and interseminal scales. Ovules orbicular in transverse section. - *W. sewardiana* Sahni attached with *B. indica*-stems and *P. cf. cutchense*-leaves, *W. gigas* (Lindl. & Hutton) W.Carruthers (ovulate flowers) with *B. gigas* Seward (stem), *Weltrichia sol* T.M.Harris (microsporangiate flowers) and *B. gigas* Seward (stem with leaf) (Harris 1969), *W.*

hildae T.M.Harris (ovulate flowers) with *B. pustulosa* T.M.Harris (stem), *Weltrichia whitbiensis* Nathorst (microsporangiate flowers), *P. pectinoides* (Phillips) Morris (leaf) and *C. hypene* T.M.Harris (perianth bracts) (Crane 1985). Jurassic; England, India.

Fam. **Williamsoniellaceae** Nakai (incl. Nilssoniaceae T.Kimura & S.Sekido) Flowers bisexual.

Wielandiella Nathorst (incl. organ gen. *Anomozamites* W.P.Schimper, *Hydropterangium* Halle). Microsporangiate flowers described as *H. marsileoides* Halle, leaves as *A. minor* (Brogn.) Nathorst (Harris 1932). - *W. angustifolia* Nathorst, monosporangiate flowers. Rhaetic of Sweden. – ***Williamsoniella*** H.H.Thomas (incl. organ gen. *Nilssoniopteris* Nathorst). Bisporangiate cone with whorl of wedge-shaped pinnate microsporophylls surrounding a reduced receptacle bearing interseminal scales and seeds. - *W. coronata* H.H.Thomas (bisexual ovulate flowers attached with *Nilssoniopteris vittata* (Brogn.) Florin (Harris 1969). *Nilssoniopteris binggouensis* Na, Sun, Dilcher et al., Lower Cretaceous, NE China. Easternmost occurrences of this predom. Eurasian organ genus. (Na et al. 2014).

Taxa of uncertain position within Bennettitales

The following leaf genera belong to Bennettitales but can not be assigned with certitude: ***Coreanophyllum*** T.Kimura & B.-K.Kim Leaves with double pinnation. Upper Triassic, Korea. – ***Cycadolepis*** Saporta Scale-like leaves. Lower Cretaceous, Argentina. – ***Deltolepis*** T.M.Harris Scale-like leaves (cataphylls). - *D. crepidota* Harris, Jurassic (Bajocian), England. – ***Dictyozamites*** Seward Veins reticulate, anastomosing. Cretaceous; India, Argentina. – ***Otozamites*** C.F.W.Braun Pinnate leaves. Jurassic to Upper Cretaceous; England, Japan. – ***Pseudocycas*** Nathorst Leaves. Lower Jurassic, Sweden.

Pollen organs. Upper Triassic bennettitalean reproductive structures (Krasser 1916, 1917; Kräusel & Schaarschmidt 1966): ***Haitingeria*** Kräusel Microsporophylls. *H. krasseri* Kräusel, Upper Triassic, Switzerland. – ***Leuthardia*** Kräusel & F.Schaarschmidt Detached microsporophyll. *L. ovalis* Kräusel, Upper Triassic, Switzerland. – ***Parmelreuthia*** F.Krasser Planar pinnate structure with naked axis bearing stalked synangia each containing 20 pollen sacs. Upper Triassic; Europe (Switzerland), N America. **Ovulate organs.** ***Bennetticarpus*** T.M.Harris Reproductive features distinctly bennettitalean but insufficiently preserved to be assigned to a family or genus. Anderson et al. (2007) placed it in a family of its own **Bennetticarpaceae** J.M.Anderson & H.M.Anderson.

2. Order **Cycadales** Pers. ex Bercht. & J.Presl

Perennial, woody plants. Dioecious. Pachycaulous, relative slow-growing, ± of palm- or fern like habit. Stem usually (apparently) unbranched, subterranean (± tuberous) or aerial (up to 17 m); pith starch-containing. Secondary xylem manoxylic; without vessels. Mucilaginous canals in all parts of the plants. Stem with a crown of leaves (megaphylls), large or scale-like (between 3 m and 5 cm), helically arranged, with apical growth, simply pinnate, bipinnate (*Bowenia*) or multipinnate (e.g., *Cycas multipinnata*). Venation dichotomously branched, unbranched in *Cycas*. Cuticula thick. Stomata sunken, superficial in *Zamia*. Micro- and megasporophylls helically arranged, in ♂ and ♀ flowers (strobili) (not in ♀ plants of *Cycas*) (♀ up to 70 cm), terminal or in *Macrozamia* and *Encephalartos* lateral. Microsporophylls scale-like or peltate, with ∞ small microsporangia (pollen sacs) on the abaxial leaf surface, in groups (sori) of 3–5; 5–1000 microsporangia per microsporophyll. Microspores with 1 spermatogenous cell and 3 further cells. The spermatogenous cell divides in 2 large multiflagellate, motile spermatozoids, the largest known ones in plant and animal kingdom (up to

400 µm) (*Microcycas* with 8–11 spermatogenous cells and up to 22 spermatozoids). Megasporophylls simple, except in *Cycas*, thickened end with 2 (rarely 3 or more) sessile unitegmic ovules. *Cycas* with leaf-like megasporophylls, with 8–2 ovules, marginally inserted. Wind- or beetle-pollinated (*Zamia*, *Encephalartos*, *Cycas revoluta*). Female thrips (Melanthripidae) pollinated *Cycadopites* R.P.Wodehouse (fossilated in Early Cretaceous amber of Spain) (Peňalver et al. 2012). Cycad volatiles (eucalyptol and 2-methoxy-3-(1-methylethyl)-pyrazine may form, together with cone thermogenesis, part of the attraction system for beetles in *Encephalartos villosus* Lem. (Suinyuy et al. 2012). Cf. also Wallenius et al. 2012: *Macrozamia communis* L.A.S. Johnson Overview of cycad pollination cf. Terry et al. (2012). Zoidiogamy (fertilization by spermatozoids). Long time span between pollination and fertilization, up to 6 months. ♀ gametophyte with 2–6(–10) archegonia (*Microcycas* up to 100), each with 2 neck canal cells, a vanishing venter canal nucleus and a large egg cell (up to 6 mm). 2 cotyledons (3–6 in *Microcycas*). Time span between fertilization and seed maturation c. 3 years. Seeds large, outer layer of the 2(3)-layered testa usually fleshy and coloured (sarcotesta), inner developed as a sclerotesta. Seeds often shed with immature embryos; dispersal by animals (zoochory). Arbuscular mycorrhizal fungi (AMF) in Cycads, cf. Hernández Reyes et al. (2012).

Chromosome numbers: 2n = 16–28. *Stangeria, Ceratozamia* 2n = 16; *Bowenia*, *Dioon, Encephalartos*, *Lepidozamia*, *Macrozamia* 2n = 18; *Cycas* 2n = 22; *Microcycas* 2n = 26; *Zamia* 2n = 16, 17–20, 22–28.

♀ flowers mostly with determinate growth; after seed maturation overtopped by a ramification (also in ♂ flowers). In *Cycas*, ♀ flowers continuing vegetative growth. "Coralloid" roots in many species present, partly with *Nostoc*, *Calothrix*, and *Anabaena*, fixing atmospheric nitrogen. Chemical compounds: poisonous glycosids, e.g., cycasin and macrozamin. Economic use: Stems and seeds used as starch source; horticulturally cultivated. Threatened by habitat destruction and collection. Often highly toxic; neurotoxins, carcinogenic compounds.

Today restricted to trop. and subtrop. regions. Living fossils. Terricolous, rarely epiphytic (*Zamia pseudoparasitica* J.Yates). Extant 2 fam., 10 gen. (332). Fig. 3-5.

Fossil history and evolution. Numerous leaves of presumed Cycadales have been described fom Palaeozoic or Mesozoic as impression-compression fossils, e.g., *Mesodescolea* Archangelsky, *Nilssonia* T.M.Harris, *Kurtziana* Frenguelli (Taylor et al. 2009), *Baikalophyllum* E.V.Bugdaeva in V.A.Krassilov and *Rehezamites* S.Q.Wu from Cretaceous strata of Liaoning, Inner Mongolia (Pott et al. 2012). Anatomically preserved wood, with affinity to the wood of *Cycas* (*Shuichengoxylon tianii* S.-J.Wang, X.-Y. He & L.-Y.Shao), is known from the Lopingian Formation (Late Permian) Guizhou Prov., China (Wang et al. 2011). Structurally preserved specimens are *Cycadinorachis* B.D.Sharma from Lower Cretaceous of India and *Cretocycas* M.Nishida, A.Yoshida & H.Nishida from Upper Cretaceous of Japan. *Restrepophyllum chiguoides* Passalia & al. is known from the Aptian Anfiteatro de Ticó Formation, Santa Cruz, Argentinia and shows palaeophytographic evidence for a S American origin of *Zamia* (Passalia et al. 2010). Preserved stems are *Lyssoxylon grigsbyi* Daugherty from Upper Triassic, orig. described as member of Williamsoniaceae, but anatomical studies showed affinities to Cycadales (Gould 1971). Another fossil silicified stem is *Michelillloa waltonii* S.Archangelsky & D.W.Brett from Upper Triassic of Argentina (Archangelsky & Brett 1963). *Chamorgia dijolii* Ash (Ash 1985) is a large stem of c. 30 cm in diam. from Chinle Formation, Upper Triassic N America. It closely resembles extant cycads, however, there is no close relation to any Cycadalean taxon. *Brunoa santarossensis* A.E.Artabe, A.B.Zamuner & D.W.Stevenson and *Worsdellia bonettiae* A.E.Artabe, A.B.Zamuner & D.W.Stevenson from Late Cretaceous of Argentina are polyxylic and assigned to subfam. **Encephalartoideae** of fam. **Zamiaceae** and closely related to extant *Encephalartos* (Artabe et al. 2004). *Nilssonio-*

cladus T.Kimura & S.Sekido is a morphogenus for long slender shoots with attached helically arranged short shoots bearing leaves from Jurassic to Early Lower and Upper Cretaceous of Japan and the Arctic. *Phasmatocycas* S.H.Mamay was erected for compressed megasporophylls from Lower Permian of N America (Mamay 1973). Anderson et al. (2007) assign it to an ord. of its own **Phasmtocycadales** Doweld with fam. **Phasmatocycadaceae** Doweld. *Sobernheimia* J.H.F.Kerp from Lower Permian (Autunian), Germany is similar to *Phasmatocycas*. In *Archaeocycas* S.H.Mamay from Early Permian, the ovules are prob. borne in opposite pairs along the stalk of the megasporophyll. Other Permian megasporophylls are *Crossozamia* Pomel (Zhu & Du1981) and *Primocycas chinensis* J.Zhu & X.Du (Zhu & Du 1981) from China. *Lasiostrobus* T.N.Taylor from Upper Pennsylvanian, N America is an unusual pollen cone with pollen grains bearing 3–8 subequatorial sacci, a feature unknown from extant cycads (Taylor & Millay 1977). *Antarcticycas* E.L.Smoot, T.N.Taylor & T.Delevoryas with *A. schopfii* E.L.Smoot & al. from Middle Triassic of Antarctica is known in sufficient detail that most of the plant can be reconstructed. The detached leaves are included in the organ gen. *Yelchophyllum* Hermsen & al. (Hermsen et al. 2006; 2007a, b; 2009), the pollen cones are *Delemaya spinulosa* S.D.Klavins & al. (Klavins et al. 2003). *Anarcticycas* prob. grew from a subterranean stem. *Leptocycas gracilis* Delevoryas & Hope (Delevoryas & Hope 1971) from Upper Triassic of N America was a tree-like cycad of 1.5 m. The leaves are pinnately compound and belong to the organ gen. *Pseudoctenis* A.C.Seward. *Bjuvia simplex* Florin from Late Triassic was a tree bearing leaves of *Taeniopteris gigantea* Florin (Florin

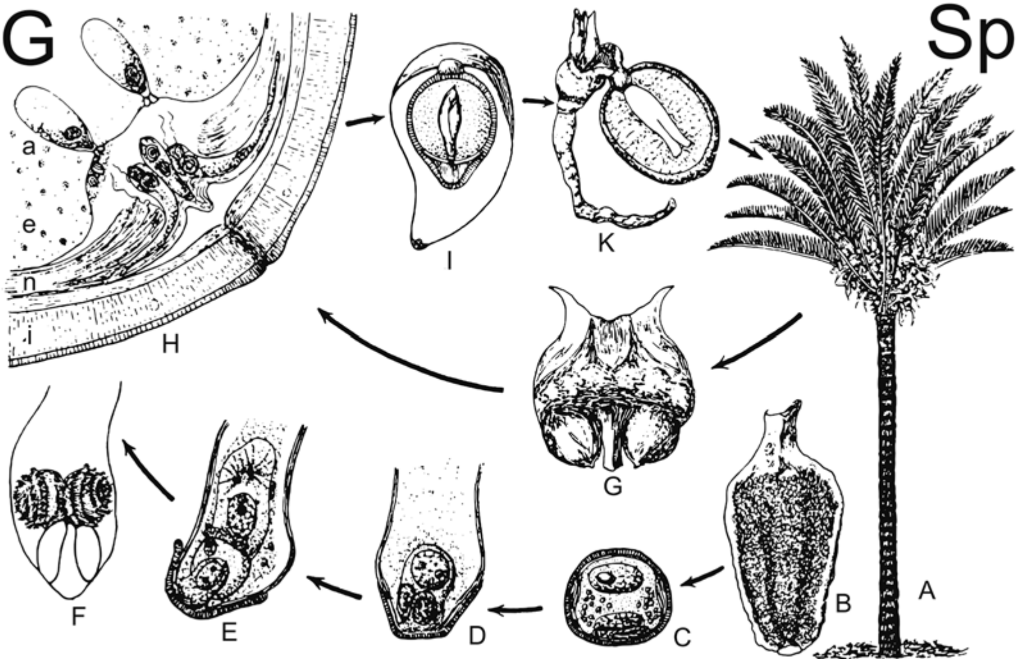

Fig. 3-5. Cycadales. Cycadaceae. A–K. Alternation of generations. A. *Cycas media.* Habit. **B.** *Encephalartos altensteinii*. Microsporophyll. **C–E**. *Dioon edule*. Development of microspore (pollen grain). **F.** *Zamia floribunda*. Development of spermatozoids. **G.** *Ceratozamia mexicana.* Megasporophyll. **H–I.** *Cycas revoluta.* H. Apex of an ovule with integument (i), nucellus (n) and pollen chamber, embryo sac (e) with prothallium and archegonia (a). I. Seed, LS. **K.** *C. thouarsii.* Germination. G gametophyte. Sp sporophyte. Without scale. (After Chamberlain, F.v.Mueller, Miyake & Schuster. Adopted from the 12th ed. of 'Syllabus der Pflanzenfamilien' 1954, **I**, p. 319, Fig. 130).


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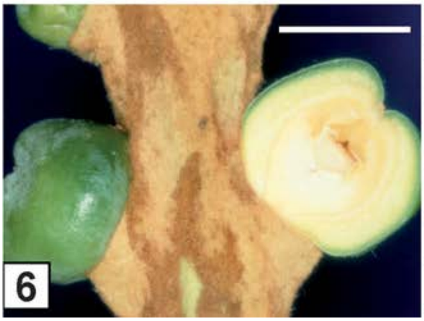
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8

1933). The megasporophylls were arranged in a terminal crown resembling that of *Cycas*. *Androstrobus* W.P.Schimper, known from Triassic to Cretaceous, is a morphogenus for small cylindrical pollen cones (Harris 1941, Thomas & Harris 1960, Van Konijnenburg-Van Crittert 1968). Ovulate cones of this plant are called *Beania* Carruthers (Harris 1964, Schweitzer et al. 2000). Another morphogenus from Upper Triassic is *Cycadospadix* W.Schimper. **Cycadaceae.** *Cycas fushunensis* Su, Quan & Liu; Eocene of NE China, partial frond containing about 15 leaflets; casting doubt on the hypothesis of the late Miocene differentiation of modern cycads (Su et al. 2014).

Most morphological phylogenetic analyses suggest that Cycadales have their origin among Palaeozoic seed ferns with the Medullosales as ancestors. Crane (1985), Nixon et al. (1994) and Doyle (2006) proposed that the Medullosales are sister to all seed plants except the Lyginopteridales. A developmental analysis of the ♂ sporophylls of the extant *Zamia amblyphyllidia* D.W.Stevenson (Mundry & Stützel 2003) also suggests that cycads evolved from a pinnate, pteridospermous ancestor with radial synangial groups. Medullosales and Gigantopteridales are included here in subclass Cycadidae following Anderson et al. (2007).

Fam. **Cycadaceae** Pers. Plants of palm-like habit. Stems closed with old leaf-bases. Leaves simply pinnate, multipinnate in *Cycas multipinnata* C.J. Chen & S.Y.Yang, Yunnan (China), N Vietman; *C. debaoensis* Y.C.Zhong & C.J. Chen, Guangxi, Yunnan (China). Pinnules (pinnate leaflets) with 1 single midrib and no lateral veins. Megasporophylls helically arranged, with pinnatifid, pectinate or toothed lamina, not forming a determinate cone; central axis mostly continuing vegetative growth. 8–2 ovules, obliquely marginally inserted. 1 gen. (107). Alternation of generations cf. Figs 3-5–3-6. Spp. numbers acc. Osborne et al. (2012).

Cycas L. (107). Characters of family. Madagascar to Malesia, Japan, Australia and Polynesia. With the most primitive character of the Cycadales (cf., e.g., megasporophylls). Forests, woodlands and savannas. - *C. revoluta* Thunb. Native to S Japan. One of the most widely cultivated cycads in warm temp. and subtrop. regions, or in glasshouses in colder areas. Wind- and insect pollinated (Kono & Tobe 2007).

Fam. **Zamiaceae** Horan. Plants palm-like, sometimes small; or stem subterranean (*Bowenia, Stangeria*). Leaves simply pinnate, bipinnate in *Bowenia*. Pinnules (pinnate leaflets) without or with a midrib (*Stangeria*). Micro- and megasporophylls in determinate cones. Megasporophylls scale-like or peltate, apex thickened and laterally expanded; with 2 (rarely 3 or more) inward-facing ovules. 9 gen. (227), trop. and subtrop. Africa, Australia and America. Classification cf. Zgurski et al. (2008). Fig. 3-7.

Bowenia Hook. ex Hook.f. (2), NE Australia (Qld.). Stem subterranean, producing 1 to many bipinnate leaves and cone-bearing branches. Pinnules without a midrib, with numerous ± parallel longitudinal veins. Trop. rainforest. - *B. serrulata* (W. Bull) Chamb., *B. spectabilis* Hook. ex Hook. f. – ***Ceratozamia*** Brongn. (27), C America (most species endemic to Mexico, few species in Guatemala, Honduras and Belize). Subterranean or short aerial stem, with persistent leaf bases and cataphylls. Sporophyll apices 2-horned. Trop. rainforest to open woodland, to c. 3500 m; species with extremely limited ranges; on calcareous soil. - *C. mexi-*

Fig. 3-6. Cycadales. Cycadaceae. 1–4. *Cycas revoluta*. 1. ♀ strobilus. 2–3. Megasporophylls with ovules. 4 ♂ strobilus with microsporangia. **5–8.** *C. circinnalis*. 5. Megasporophyll with ovules. 6–8. Details of ovule showing archegonia and nucellus. (Orig.; 1, 4–6 phot. W. Barthlott; 2–3, 7–8 phot. W. Rauh; 1–8 courtesy WB) (Scale bar 1, 4: 10 cm; 2–3: 5 cm; 5–6: 1 cm; 7: 5 mm; 8: 1 mm).

cana Brongn., cold-tolerant, trop. lowland to dry mountainous cloud forests; Sierra Madre Mts. of Mexico. – ***Dioon*** Lindl. (14), C America (Mexico, Honduras). Stem with persistent leaf bases. Sporophyll apices truncate to acuminate. Megasporophyll apices flattened, upturned, overlapping. Prob. the most primitive genus within Cycadales (sporophylls "leaf-like"). From rocky limestone cliffs to trop. forest habitats. Beginning of Tertiary: distribution from C America to N Alaska. – Molecular phylogenetic relationships, cf. Gonzáles et al. (2008). *Dioon* may be a remnant of a lineage related to *Dioonopsis* Horiuchi & Kimura, Eocene of N America and Japan. 2 majour groups (Edule clade and Spinulosum clade, Moynihan et al. 2012). – ***Encephalartos*** Lehm. (65), C and S Africa. Stem subterranean or aerial, with persistent leaf bases. ♀ cones, up to 50 cm long. Sporophyll apices truncate. Beetle-pollinated (cantharophily). Open grassland to forest. Previously used as sago (stems). - *E. caffer* (Thunb.) Lehm., S Africa, first Cape cycads to be declared endangered species. – ***Lepidozamia*** Regel (2), trop. coastal region E Australia (Qld.) (rain forest), N NSW (wet sclerophyll forest). Stem tall, with persistent leaf bases. Cataphylls present. Sporophyll apices tomentose, not spiniferous. - *L. peroffskyana* Regel, ♀ cones up to 70 cm long; *L. hopei* (W. Hill) Regel (tallest living cycad, 17.5 m). – ***Macrozamia*** Miq. (41), Australia; majority of species in E Australia (Qld., NSW), (1), Northern Territory, (3) S Western Australia. Stem subterranean or aerial, with persistent leaf bases. Sporophyll apices glabrous, spiniferous. Cones stalked. Warm-temp. and subtrop. Australia; margin of rain forests, sclerophyll forests and woodlands. - *M. communis* L.A.S. Johnson, most commonly occurring cycad in NSW. *M. miquelii* (F.Muell.) A.DC., grove forming plants with short-range dispersal (Hall & Walter 2013). – ***Microcycas*** (Miq.) A.DC. (1). *M. calocoma* (Miq.) A.DC. Sierra del Rosario, W Cuba. Tall aerial stem, up to 10 m. Leaves bases and cataphylls persistent. Sporophylls valvately-arranged, not horned, with 2 round apical projections. Egg cells 500–600 µm in diam., largest in plant kingdom; spermatozoids 300(–500) µm. C. 600 plants, critically endangered. Woodland species. – ***Stangeria*** T.Moore (1). *S. eriopus* (Kunze) Baill. Of fern-like appearance. Stem subterranean, "carrot-like". Pinnules with a definite midrib and venation (dichotomously branched veins). Sporophylls imbricate, in cones. E coast S Africa, S Mozambique. – ***Zamia*** L. (incl. *Chigua* D.W.Stev.) (3, incl. *Z. nana* A.Lindstr., Calonje, D.W.Stev. & al.). Pinnules with midrib, with irregularly dichotomously branched lateral veins, rainforest, Columbia; (73), N, C and S America (south to N Bolivia). Northern border in Georgia and Florida (*Z. integrifolia* L.f.), Mexico, C America, the West Indies, to Bolivia [*Z. boliviana* (Brongn.) A.DC.], Brazil and N Chile. Stem subterranean or short aerial usual without persistent leaf bases. Stipules present. Pinnules without midrib, with ± parallel longitudinal veins. ♀ cones up to 45 cm. Insect-pollinated. Sporophylls valvately-arranged, apices truncate. Dispersal of seeds possibly through birds and rodents. Rain forest, savannas, coastal dunes, semideserts; 0–2500 m, calcicolous. - *Z. pseudoparasitica* J.Yates, epiphytic. Phylogeography of *Zamia paucijuga* Wieland (Nolasco-Soto et al. 2014).

Fig. 3-7. Cycadales. Zamiaceae. 1–2. *Stangeria paradoxa*. 1. ♂ plant with ♂ strobili. Habit. 2. Details of ♂ strobilus. **3.** *Encephalartus horridus*. ♂ strobilus. **4–6.** *Zamia parasitica*. 4. ♀ (left) and ♂ strobilus (right). 5. ♂ plant. Habit. 6. Megasporophyll with ovules. **7.** *Ceratozamia mexicana*. Microsporophyll. **8.** *Macrozamia communis*. Megasporophylls showing ovules. (Orig.; 1–2, 4 phot. W. Barthlott; 3, 5 W. Lobin; 6–8 W. Rauh; 1–2, 4, 6–8 courtesy WB; 3, 5 courtesy WL) (Scale bar 1, 3, 5: 10 cm; 2, 4, 6–8: 1 cm).

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3. Order **Gigantopteridales** X.Li & Z.Q.Yao (Gigantonomiales S.V.Meyen) (†)

Leaves diverse, many of them resembling extant angiosperms, usually large; venation dichotomizing, anastomosing, reticulate or pinnate. Leaf shape unknown in most forms. Synangiate structures on lower leaf surface. Pollen unknown. Seeds borne on both sides of leaf-midrib. Permian to Permo-Triassic. Systematic assignment questionable. Meyen (1984) suggested affinities with Callistophytales, Caytoniales, or Ginkgoales. Anderson et al. (2007) placed it in the class Cycadopsida.

Fam. **Gigantopteridaceae** Koidzumi Extinct family, dominating in the Cathaysian flora of Sino-Malaya (*Gigantopteris* flora). Carboniferous and Permian to Permo-Triassic (Koidzumi 1936, Wang 1999).

Cathaysiopteris Mamay Furcate and pinnately compound leaves up to 20 cm long, margin sinuous, with pinnate venation. Permian; N America, Asia. – ***Delnortea*** *abbottiae* Mamay & al. Permineralized foliage with simple, petiolate oblong-elliptical leaves with entire to crenulated margins, venation pinnate. Lower Permian, N America. – ***Gigantopteris*** H.Yabe Leaves up to 50 cm long, with pinnate venation and entire margin. Permian, China, N America. – ***Gigantopteridium*** Koidzumi Leaves amphistomatic, stomata surrounded by papillate subsidiary cells. Middle Permian, China. – ***Gigantonoclea*** Koidzumi (4). Stems described as *Aculeovinea yunguiensis* H.Q.Li & D.W.Taylor (Li & Taylor 1998), exhibiting a sparganum cortex. Leaves similar to *Gigantopteris*, fronds dimorphic, suggesting a possible water plant. Seeds on either side of midvein, borne on abaxial surface described as *Gigantonomia* X.Li & Z.Yao. Synangiate pollen structures are called *Gigantotheca* X.Li & Z.Yao and *Jiaochengia* Wang Zi-Qiang (Wang 1999). Permian; China, N America. – ***Gothanopteris*** Koidzumi Foliage. Carboniferous (Stephanian), Sumatera. – ***Palaeogoniopteris*** Koidzumi Foliage, Carboniferous (Stephanian), Sumatera. – ***Vasovinea*** H.Q.Li & D.W.Taylor *V. tianii* H.Q.Li & D.W.Taylor, permineralized axis from Upper Permian, China. Stem with compound hooks, trichomes and prickles suggesting a climbing plant. *Vasovinea* is reconstructed as bearing *Gigantopteris*-leaves (Li & Taylor 1999). – ***Zeilleropteris*** Mamay Leaves furcate, venation with up to 4 orders. Permian; N America, Asia.

4. Order **Medullosales** Corsin (†)

Largest seed ferns. Stem anatomy characterized by several segments of vascular tissue surrounded by secondary xylem. Leaf traces with terete strands produced by more than one cauline protoxylem sympodium. Fig. 3-3.H.

Fam. **Medullosaceae** O.Weber & J.T.Sterzel (incl. Alethopteridaceae Corsin, Potonieaceae T.Halle, Stephanospermaceae Doweld, Codonospermaceae Doweld, Polylophospermaceae Doweld) Stems with 2 or more vascular segments but polystely prob. only a modification of the eustelic arrangement. Stele considered as a series of sympodia which constitute a single stele.

Colpoxylon D.H.Scott (1). Similar to *Medullosa*, but stem lacking vascular strands in the pith. Permian, France. – ***Medullosa*** Cotta (15). Stem with 1 to many segments of vascular tissue. Climbing growth habit (Wilson & Fischer 2011). Lower Namurian A (uppermost Mississipian) to Permian; Europe, N America. – ***Quaestora*** G.Mapes & G.W.Rothwell (1). Exarch protostele and bifacial cambium with secondary xylem and secondary phloem. - *Q.*

amplecta G.Mapes & G.W.Rothwell (Mapes & Rothwell 1980), Upper Missisippian, Arkansas. – ***Sutcliffia*** D.H.Scott (1). Stem with large, central vascular segment from which other vascular segments. Differs from *Medullosa* by the presence of leaf traces appearing as miniature vascular segments, lacking secondary xylem. Permian; Europe, N America.

Leaf genera. Large and pinnately organized with bifurcation of primary rhachis. ***Alethopteris*** Sternberg – ***Neuropteris*** (Brongn.) Sternberg Earliest occurrence in the Culm sequences (Tournaisean-Visean). – ***Odontopteris*** (Brongn.) Sternberg **Petiole genus.** ***Myeloxylon*** Brongn. With large number of scatterd bundles. Earliest records from Namurian A (middle Mississipian), Belgium (Taylor et al. 2009). **Seed genera**. Large seeds linked to vegetative parts on the base of association evidence. ***Hexapterospermum*** Brongn. Seeds with 6 longitudinal ribs, with flattened base and tapered apex. Middle Pennsylvanian; Europe, N America. – ***Pachytesta*** Brongn. Seeds large (>1cm long), radially symmetric, with ribbed sclerotesta; nucellus free from integument except at chalaza. Pennsylvanian-Lower Permian; Europe, China. – ***Rhynchosperma*** T.N.Taylor & D.A.Eggert Integument 3-layered. Mississipian, N America. – ***Stephanospermum*** Brongn. Seeds 1 cm, with apical integumentary crown encircling an elongated micropylar canal; sclerotesta not ornamented externally; sarcotesta between integumentary crown and beak. Pennsylvanian; Europe, N America. – ***Trigonocarpus*** Kidston (Hoskins & Cross 1946, Taylor 1965), large (up to 11 cm) and radiospermic. Each ovule with single integument, divided into sarcotesta, sclerotesta and endotesta; integument and nucellus free except at chalaza. Middle Pennsylvanian. **Pollen organs.** Large, with up to several cm in diam., synangiate, from simply and solitary to compound forms, borne as pairs. ***Aulacotheca*** Halle Pollen organ with stalked synangia. Lower Pennsylvanian. – ***Bernaultia*** G.W.Rothwell & D.A.Eggert Established for *Dolerotheca* specimens that consist of 4 synangial units united together. Pennsylvanian. – ***Dolerotheca*** Halle Large, complex and compound synangiate pollen organs, called a campanulum. External morphology and internal organisation not known in detail. Pennsylvanian. – ***Halletheca*** T.N.Taylor Pyriform synangium of 5 sporangia. Middle to Late Pennsylvanian. – ***Murielatheca*** Serbet, T.N.Taylor & E.L.Taylor Synangium composed of 10–12 thin-walled elongated sporangia containing *Monoletes* pollen. Serbet et al. (2006) suggested that *M. delicata* Serbet, T.N.Taylor & E.L.Taylor was borne on *Medullosa anglica* D.H.Scott stems. Middle Pennsylvanian, N America. – ***Potoniea*** Zeiller Campanulum bell-shaped, c. 1 cm in diam., composed of numerous elongated sporangia embedded in a parenchyma. Pennsylvanian; Europe, N America. – ***Rhetinotheca*** G.A.Leisman & J.S.Peters Central fibrous area surrounded by 4 sporangia. Middle Pennsylvanian. – ***Schopfitheca*** T.Delevoryas Stalked, clavate pollen organ, with 5–6 lobes around rim, surface covered with dense hairs. Pennsylvanian. – ***Stewartiotheca*** D.A.Eggert & G.W.Rothwell Campanulate synangium c. 1 cm in diam. Similar to *Bernaultia*. Late Pennsylvanian. – ***Sullitheca*** B.M.Stidd, G.A.Leisman & T.L.Phillips Large pollen organ (2.5 cm), with 40 elongated sporangia. Pennsylvanian. – ***Whittleseya*** White A ring of fused sporangia around a central hollow. Lower Pennsylvanian.

The majority of pollen organs produced *Monoletes* T.van der Hammen (= *Schopfipollenites* Potonié & G.O.W.Kremp) pollen. Occ., the pollen [*Parasporites* J.M.Schopf, Dennis & Eggert (Schopf et al.1978) has a pair of small sacs.

5. Order **Pentoxylales** Sahni (†)

Small order. While Taylor et al. (2009) placed it as a group with uncertain affinities, Nixon et al. (1994) suggested it as a sister to *Cordaites* and the extant conifers close to Peltaspermales and other seed ferns. In the analysis of Crane (1985), *Pentoxylon* is resolved as sister to Bennettitales. Anderson et al. (2007) assigned it to their class **Bennettitopsida** Engl.

Fam. **Lindthecaceae** J.M.Anderson & H.M.Anderson "Gynoecia" enclosed within a quilted sheath; megasporophylls multiovulate.

Lindtheca J.M.Anderson & H.M.Anderson (1). *L. hackysackia* J.M.Anderson & H.M.Anderson, Molteno Formation, Gondwana Triassic, S Africa. Leaves described as *Taeniopteris homerifolius* J.M.Anderson & H.M.Anderson.

Fam. **Pentoxylaceae** Pilg. & Melch. Small trees with strap-shaped leaves and long and short shoots. Leaf cushions borne on smaller branches. Ovulate elliptical heads and branching microsporophylls arranged in a whorl on a rim subtending a terminal dome-like structure (Crane 1985, Nixon et al. 1994). "Gynoecia" lacking a quilted sheath, megasporophylls uniovulate.

Pentoxylon B.P.Srivastava (incl. organ gen. *Carnoconites* B.P.Srivastava, *Nipaniophyllum* Sahni, *Taeniopteris* Brongn., *Sahnia* Vishnu-Mittre). Stems (*Pentoxylon*) differentiated into long and short shoots. Secondary xylem pycnoxylic with uniseriate rays lacking axial parenchyma. Leaves (*Nipaniophyllum*, *Taeniopteris*) strap-shaped. Microsporophylls (*Sahnia*) in a whorl or low helix, with 10–20 stalked unilocular sporangia. Ovulate heads (*Carnoconites* B.P.Srivastava) terminally on short shoots, with sessile, orthotropous ovules helically arranged into compact ovoid (e.g., *C. compactum* B.P.Srivastava, *C. cranwelliae* T.M.Harris) or elongated heads (*C. laxum* T.M.Harris); each head of c. 20 ovules, with 2 integuments free from nucellus except at chalaza. Jurassic, India. - *Donponoxylon* Tidwell, Britt & Wright (2), taxon of uncertain position, related to *Pentoxylon*; Middle to Late Jurassic of Australia and New Zealand (Tidwell et al. 2013).

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3. Subclass **Ginkgoidae** Engl.

Trees or shrubs. Leaves diverse, fern-like to fan-shaped (*Ginkgo*). ♀ strobili lax, usually spicate, radially to bilaterally symmetrical, sometimes reduced to a furcate structure with a single pair of opposite cupules. Microsporophylls simple to compound; microsporangia aggregated to synangia.

Meyen (1987) included here all Mesozoic pteridosperms together with the glossopterids. We follow Anderson et al. (2007) in their circumscription, incl. Ginkgoales, Peltaspermales, Matatiellales, Czekanowskiales, Hamshawviales, Corystospermales, Caytoniales and Petriellales. This classification is in contrast to Doyle (1998) where Ginkgoales, Corystosperms, Peltasperms and Caytonia appear in different places in the gymnosperm tree.

1. Order **Caytoniales** Gothan (†)

Orig. considered by Thomas (1925) as a new group of angiosperms. The cupule is linked with the carpel of angiosperms (Doyle 1978, 1996, 2006).

Fam. **Caytoniaceae** Kräusel Leaves (*Sagenopteris* Trevisan) palmately compound, composed of 3–5 leaflets. Microsporophylls (*Caytonanthus* T.M.Harris) pinnate. Pollen described as *Vitreisporites* G.Leschik Megasporophylls (*Caytonia*) pinnate, bearing lateral cupules on short stalks, at maturity the cupules prob. fleshy and berry-like. Ovules flattened, with 1 integument free from nucellus except at chalaza; micropylar slit narrow. Upper Triassic to Upper Cretaceous.

Caytonia H.H.Thomas (incl. organ gen. *Sagenopteris* Presl, *Caytonanthus* T.M.Harris, *Vitreisporites* G.Leschik). 3 species known from megasporophylls, microsporophylls and leaves (Crane 1985): *C. sewardi* H.H.Thomas (leaf *S. colpodes* T.M.Harris, microsporophyll *C. oncodes* T.M.Harris), Middle Jurassic, England; *C. nathorstii* H.H.Thomas [leaf *S. phillipsii* Sternberg, microsporophyll *C. arberi* (H.H.Thomas) T.M.Harris], Triassic; *C. thomasii* T.M.Harris (leaf *S. nilssoniana* (Brogn.) Ward, microsporophyll *C. kochii* T.M.Harris), Upper to Lower Jurassic, Greenland.

Other leaf- or ovule-morphogenera. *Ktalenia* Archangelsky Isolated cupules associated with *Ruflorinia*. Lower Cretaceous (Aptian), Argentina. – ***Ruflorinia*** Archangelsky Bi- or tripinnate leaves Lower Cretaceous (Aptian), Argentina.

2. Order **Corystospermales** H.H.Thomas (incl. Umkomasiales Doweld) (†)

Small to large woody shrubs and trees. Leaves pinnate with open dichotomous venation. Cupules helmet-shaped, uniovulate, on a branching system. Triassic to Lower Jurassic (ext. to Cretaceous). Mainly Gondwanan, some fossils also known from Europe.

Fam. **Corystospermataceae** H.H.Thomas (incl. Umkomasiaceae Petriella) Woody plants. Stems sometimes with polystelic arrangement, prob. only a modification of a basic eustele. Leaf rhachis forked with simple or bipinnate arrangement. Microsporophylls (*Pteruchus*) irregularly branched, with groups of pendulous pollen sacs on expanded distal laminae. Megasporophylls dorsiventrally arranged and branched in single plane: main axis with ir-