

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)]



Borntraeger



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Eberhard Fischer
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Pinopsida (Gymnosperms)

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

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, Liliae 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, Lillianae 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, Lillianae 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	IX
1 Introduction	1
2 Pinopsida (Gymnosperms) and Magnoliopsida (Angiosperms)	2
3 Pinopsida (Gymnosperms, Gymnospermopsida, Gymnospermae)	6
Characterization and relationships	6
Synopsis of classification of the Spermatophytes	11
Systematic arrangement of taxa of the Pinopsida (Gymnosperms)	13
Pinopsida (Gymnosperms)	13
“Pteridospermatidae”	14
Cycadidae	22
Ginkgoidae	38
Gnetidae	47
Pinidae	55
4 Magnoliopsida p.p. (Angiosperms, Angiospermae)	111
Magnoliopsida	113
Characterization and relationships	113
Synopsis of classification of the Magnoliopsida	125
Systematic arrangement of taxa	131
Magnoliopsida	131
Magnoliidae	131
Amborellanae	131
Amborellales	131
Nymphaeanae	133
Nymphaeales	133
Austrobaileyanae	140
Austrobaileyales	140
Magnolianae	144
Chloranthales	144
Canellales	145
Piperales	148
Laurales	159
Magnoliales	174
Lilianae	200
Acorales	201
Alismatales	203
Petrosaviales	240
Dioscoreales	241
Pandanales	252

Liliales	263
Asparagales	283
5 Taxonomic novelties	466
Sources of Illustrations	467
Index to Taxa	468

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, <i>exempli gratia</i>
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, <i>id est</i>
inc. sed.	<i>incertae sedis</i> , 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., <i>Medit.</i>	mediterranean, Mediterranean region
min.	minute
mio.	million
mio.y.	million years
morphogen.	morphogenus
mt(s), <i>Mt(s)</i> .	mountain(s)
µm	micrometer
N	North, northern
neotrop., <i>Neotrop.</i>	neotropical, Neotropics, Neotropical region
nom. cons.	<i>nomen conservandum</i> , 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
\pm	more or less
∞	numerous
$\text{\textcircled{M}}$	male
$\text{\textcircled{F}}$	female
\dagger	extinct
$\overset{*}{*}$	in the Northern and Southern Hemisphere
$\overset{*}{*}$	in the Northern Hemisphere
$\underset{*}{*}$	in the Southern Hemisphere
$(\overset{*}{*})$	scattered in the Northern Hemisphere
$(\underset{*}{*})$	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, Liliae 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 *Vanilla*. 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 Kenrick & 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 (†), Lycopsidea 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, Ginkgoideae 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., Lillianae 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., Dilleniae 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 impetus 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! \rightarrow 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

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 (\rightarrow testa, seed coat, with funiculus, chalaza and micropyle)], $\infty-1$ on leaf-like (*Cycas*) or reduced, simple megasporophylls or ovules $\infty-1$, often included in cones or cone-like structures (Pinidae), or rarely exposed (e.g., *Cycas*, *Ginkgo*). R! of the megaspore mother cell (embryo sac mother cell) \rightarrow 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).

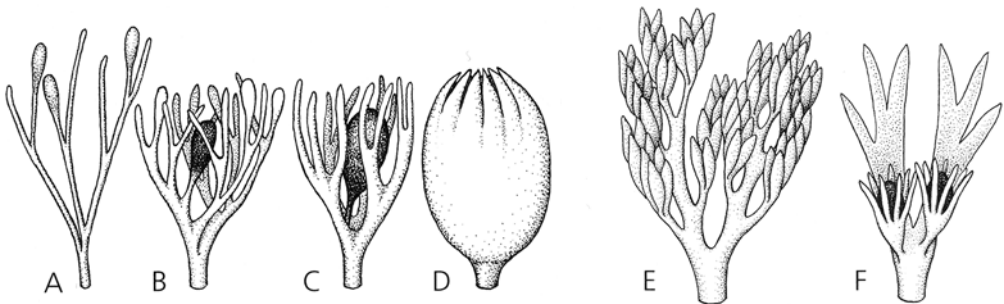


Fig. 3-1. Evolution of ovuliferous structures (ovules). A–D. After the telome concept a nucellus (dark) with a sterile cover (integument) (white, dotted) developed partly of a vegetative, partly of a sporangia bearing branched telome system. E–F. The Neosynangial hypothesis postulates "the ovule as a 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: *Armoiraciphyton chateau-pannese* 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 occurred 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 *Shanxiioxylon* as sister to a clade of *Cordaioxylon*, *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 stage. 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

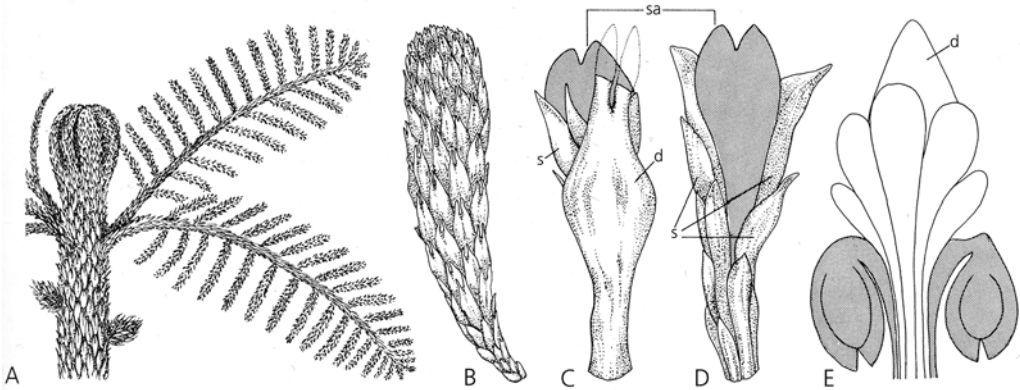


Fig. 3-2. Voltziales. A–D. *Utrechia piniformis* (Lower Permian/Rotliegendes). **A.** Apex of shoot; main axis with bifid leaves (c. 0.25x). **B.** Erect ♀ cone with bifid bract scales (c. 0.4x). **C–D.** ♀ flower, back and front side; bract scale (bract = subtending leaf, d), sterile scales (s) and flattened atropous ovules (sa) with bipartite 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, **Fredliniaceae** J.M.Anderson &

H.M.Anderson, **Laurozamiaceae** J.M.Anderson & H.M.Anderson,

Sturianthaceae Doweld, **Vardekloeftiaceae** J.M.Anderson & H.M. Ander-

son, **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** Sahní (†)
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, **Ferugliocladaceae** S.Archangelsky & R.Cunéo, **Majonicaceae** Clem.-West., **Thucydiaceae** G.R.Hernandez-Castillo, G.W.Rothwell & G.Mapes, **Ullmanniaceae** Němejč, **Utrechtiaceae** G.Mapes & G.R.Rothwell, **Voltziaceae** C.A.Arnold

Taxa of uncertain affinities to Voltziales

Order **Dordrechtiales** 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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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 Ginkgoideae. We follow Anderson et al. (2007) in assigning ord. Gigantopteridales, Medullosales and Pentoxylales to Cycadidae and Caytoniales, Corytospermales, Czekanowskiales, Peltaspermales and Petriellales to Ginkgoideae.

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 sparganium 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 protosteles. Petioles in a 1/3 phyllotaxy. - *T. primaevum* P.D.W.Barnard & A.G.Long, Lower Carboniferous, Scotland.

2. Order Calamopityales Nĕmejċ

Fam. **Calamopityaceae** Solms Mainly characterized by manoxylic wood and an unusual thick cortex. Pollen and seed organs unknown. Mississippian; 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 *Stenomyelon* 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-Mississippian. - **Chapelia** C.B.Beck & R.E.Bailey (1). Petiole just below branching point in the frond. Vascular system 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 Mississippian, 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.Zalesky (5). Sterile pinnules. Middle Carboniferous, Siberia. - *Angarocarpus* G.P.Radczenko (1). Seeds. - *A. ungensis* (M.D.Zalesky) 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 megasporophylls 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. Microsporphylls described as *Eretmontia*, pollen sac as *Arberiella*, pollen as *Protohaploxypinus*. Upper Permian, S Africa. - ***Lonchiphllum*** 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.