

Morphology and identification of the world's conifer genera

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Pinus lambertiana,
Yosemite National Park,
California, USA.

1 Introduction to extant gymnosperms

Extant seed plants consists of five major groups: angiosperms, cycads, *Ginkgo*, conifers and Gnetales (BOWE et al. 2000; CHAW et al. 2000; SOLTIS et al. 2002; HILTON & BATEMAN 2006; LEITCH et al. 2001; CHRISTENHUSZ et al. 2011; COLE et al. 2017). The latter four represent the gymnosperms (HILTON & BATEMAN 2006; MATHEWS 2009). Today's gymnosperms can be described as "relict plants" from a group, which previously had a much higher diversity. Gymnosperms were the dominating group of land plants in the Jurassic and Cretaceous, before the rapidly evolving angiosperms began to replace them at the end of the Cretaceous. Even though the extant gymnosperms include only about 800-900 species, they still show a high structural diversity.

Compared to angiosperms, all gymnosperms are woody. Gymnosperms differ from angiosperms by wood that contains in most species only tracheids, absence of angiosperm-like bisexual flowers, freely exposed "naked" ovules, absence of a carpel enveloping the ovules and by the lack of a triploid endosperm.

Despite the small number of extant gymno-

sperms, their systematics are still highly controversial, in particular the position of Gnetales (e.g. CHAW et al. 1997, 2000; BOWE et al. 2000; BURLEIGH & MATHEWS 2004; HILTON & BATEMAN 2006; GRAHAM & ILES 2009; MATHEWS 2009; CORIO et al. 2018). Due to their angiospermous appearance (e.g. flower-like inflorescences and a special kind of double fertilization) the Gnetales are often proposed as the sister group to the angiosperms, forming the so called "Anthophyte-clade" (CHASE et al. 1993; DOYLE 1996, 2006; DONOGHUE 1994). However, based on combined morpho-anatomical and molecular data, several other authors regard a close relationship between Gnetales and angiosperms as unlikely (WINTER et al. 1999; CHAW et al. 1997, 2000; BOWE et al. 2000; FROHLICH & PARKER 2000; SCHMIDT & SCHNEIDER-POETSCH 2002; BURLEIGH & MATHEWS 2004; STÜTZEL & MUNDY 2004), while a close relationship of Gnetales and gymnosperms is suggested (WINTER et al. 1999; FROHLICH & PARKER 2000; BOWE et al. 2000; CHAW et al. 2000; GUGERLI et al. 2001; BURLEIGH & MATHEWS 2004; MUNDY & STÜTZEL 2004; COLE et al. 2017; CORIO

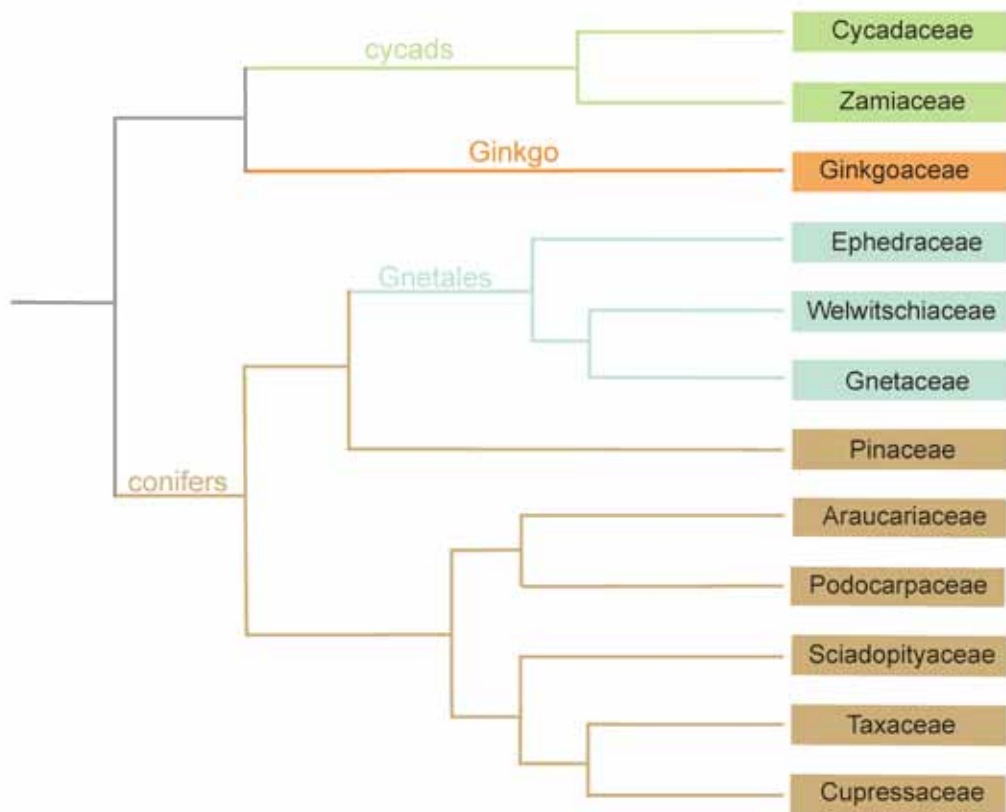


Fig. 1: Possible phylogenetic relationships among extant gymnosperms according to CHAW et al. 2000 and COLE et al. 2017, with Gnetales in the "Gnepine"-topology as sister to Pinaceae (slightly modified).

et al. 2018) and two competing hypotheses exist. In the “Gnepine”-hypothesis (Fig. 1), Gnetales are regarded as sister to Pinaceae (QIU et al. 1999; BOWE et al. 2000; NICKRENT et al. 2000; CHAW et al. 2000; GUGERLI et al. 2001; SOLTIS et al. 2002; BURLEIGH & MATHEWS 2004; COLE et al. 2017), while within the “Gnetifer”-hypothesis Gnetales are regarded as sister to all conifers (CHAW et al. 1997, 2000; BOWE et al. 2000; RYDIN et al. 2002; SOLTIS et al. 2002; SCHMIDT & SCHNEIDER-POETSCH 2002). Other typologies regard the Gnetales as sister to all other extant seed plants as is suggested in the “Gnetales-sister”-hypothesis (HASEBE et al. 1992; ALBERT et al. 1994; SANMIGULLIN et al. 1999; WINTER et al. 1999; FROHLICH & PARKER 2000; RAI et al. 2003; BURLEIGH & MATHEWS 2004).

The **Cycads** are the most primitive group among extant gymnosperms. There are about 300 recent cycad species, which is about one third of the species spectrum of today’s gymnosperms. Today’s cycads are widely accepted to be divided into two families. The Cycadaceae comprise only the genus *Cycas* with about 100 species. All other cycads are placed within the Zamiaceae (STEVENS 2001; HILL et al. 2003; CHAW et al. 2005). Some authors place the genera *Stangeria* and *Bowenia* within an additional family, Stangeriaceae (JONES 1993).

The Cycads are a very old group which can be traced back to the early Permian period (299–270 million years ago) (JONES 1993). It is well

documented in the fossil record (MAMAY 1964, 1969, 1976; DELEVORYAS & HOPE 1976; GAO & THOMAS 1989; SCHWEITZER 2000; HERMSEN et al. 2006; TAYLOR et al. 2009) with a previously much higher number of species and a higher structural diversity (HARRIS 1961; DELEVORYAS & HOPE 1976; STEWART 1983; GAO & THOMAS 1989; SCHWEITZER 2000; HERMSEN et al. 2006; TAYLOR et al. 2009).

Cycads are woody seed plants with large, frond-like pinnate leaves. The tree-like species have a palm-like appearance (Figs. 2, 8, 9). All extant Cycads are terrestrial, except *Zamia pseudoparasitica* from subtropical/tropical parts of Panama, where it is epiphytic on trees, which is uniquely among extant gymnosperms (STEVENSON 1993; CAPUTO et al. 1996; VOVIDES et al. 2003; CALONJE 2009; ZONNEVELD & LINDSTRÖM 2016). The ovules are attached to macrosporophylls (Figs. 8D, 9D), which form either a loose apical leaf rosette (Cycadaceae) (Fig. 8C) or they are arranged in uniaxial, “flower”-like, compact macrosporangiate strobili (Zamiaceae) (Fig. 9C) (STEVENSON 1988, 1990; GIFFORD & FOSTER 1989; JONES 1993; OBERMANN 2003; KUNZE 2008). In contrast, in all cycads the pollen-producing microsporophylls (Fig. 8F, 9F) are arranged in uniaxial, flower-like, compact microsporangiate strobili (Fig. 8E, 9E) (MUNDY & STÜTZEL 2003; DÖRKEN & ROZYNEK 2013). Seeds of Cycads are drupe-like. During maturation, the integument differentiates into two distinct layers, each with a different function. The inner strongly sclerified layer (the sclerotesta) protects the inner embryo and the outer, fleshy, mostly intensively coloured layer (the sarcotesta), attracts animals, which are responsible for seed dispersal.



Fig. 2: *Cycas circinalis*, habitus.

The **Ginkgos** consist of only one extant monogeneric family (Ginkgoaceae). Its single genus *Ginkgo* is monotypic, with *G. biloba* as the only living member of this group (DEL TREDICI 2004). However, in the fossil record several further Ginkgoalean taxa were found, showing that this group was much more diverse with a higher structural and species diversity and a wider distribution, as was also the case for the genus *Ginkgo* (e. g. ZHIYAN 1991; TU et al. 2003; KVACEK et al. 2005; ZHIYAN & XIANGWU 2006; WANG et al. 2007; WU et al. 2007; ZHOU et al. 2007; TAYLOR et al. 2009; QUAN et al. 2010).

The extant *G. biloba* is a large dioecious tree with distinct long shoot-short shoot differentiation and characteristic fan-shaped, foliar leaves (Figs. 3, 10A) with open dichotomous venation (Fig. 10B). The reproductive structures of both

genders are axillary on short shoots. Ovules are terminal on long-stalked microsporangiophores (Fig. 10C). The pollen-producing structures are arranged in uniaxial, compact, pendulous, catkin-like structures (Fig. 10E). The microsporangiophores are hyposporangiate, each with two, abaxial yellow microsporangia (MUNDY & STÜTZEL 2004b; DÖRKEN 2014) (Fig. 10E, F). Seeds of *Ginkgo* and cycads are very similar to each other. As with cycads the integument differentiates into an inner strongly woody sclerotesta and an outer fleshy, yellow sarcotesta, so that mature seeds are also drupe-like (Figs. 10 C, D).

The **Conifers** comprise about 500-600 extant species and represent the largest group among extant gymnosperms. The species spectrum of the coniferous genera varies strongly, for example genera like *Pinus* (Pinaceae) and *Podocarpus* (Podocarpaceae) comprises about 100 species, while for example 17 of the 28 cupressaceous genera are monotypic.

The majority of conifers are evergreen trees and rarely shrubs; only few species are deciduous (DALLIMORE & JACKSON 1966; KRÜSSMANN 1955, 1983; FRANKIS 1988; FARJON 2005, 2010a, b; ECKENWALDER 2009). All extant conifers are terrestrial, except the New Caledonian *Parasitaxus* (Podocarpaceae), which is the only parasitic gymnosperm existing today. It grows on shoots and roots of *Falcatifolium taxoides* (Podocarpaceae) (WOLTZ et al. 1994; MUSELMANN & PRESS 1995; STOCKEY et al. 1995; SINCLAIR et al. 2002; FIELD & BRODRIBB 2005; SEYFULLAH et al. 2017; NIMSCH 2018).

The foliage of today's conifers is either needle-leaved or scale-leaved. In scale-leaved species, the juvenile trees are always needle-leaved before shifting to the mature scale leaf type. A few species, for example *Callitris macroleayana* (Cupressaceae), *Cupressus vietnamsis* (Cupressaceae), *Juniperus phoenicea* (Cupressaceae) or *Halocarpus bidwillii* (Podocarpaceae) are characterized by a distinct leaf dimorphism, with needle and scale leaves occurring on the same tree, even at adult stages. Needle leaves of most species are quite rigid and show an acuminate tip, which can be classified into two groups: 1. Acuminate, but not pungent for example *Cryptomeria* (Cupressaceae) or *Pinus* (Pinaceae); 2. Strongly pungent for example *Araucaria araucana* (Araucariaceae), *Araucaria angustifolia* (Araucariaceae), *Juniperus drupacea* (Cupressaceae), *Picea polita* (Pinaceae) or *Torreya nucifera* (Taxaceae). In contrast, the needle leaves of for example *Glyp-*

ostrobus, *Metasequoia* and *Taxodium* (Cupressaceae) or *Larix* (Pinaceae) are flexible. In the evergreen genus *Phyllocladus* (KENG 1963a, b, 1973, 1974 1977, 1978) and the genus *Sciadopitys* (e.g. CARRIÈRE 1868; DICKSON 1866; ENGELMANN 1868; MOHL 1871a, b; STRASBURGER 1872; SCHNEIDER 1913; TROLL 1937; ROTH 1962; TETZLAF 2004; HILLE 2002, 2008; DÖRKEN & STÜTZEL 2011) the foliage is replaced by complex, green phylloclades (*Phyllocladus*) or cladodes (*Sciadopitys*).

The reproductive structures of both genders are arranged in compact cones (name conifers! lat. *conus* = cone, *ferre* = carrying). The female cones are called "seed cones", the male ones "pollen cones". Although conifers show a high structural diversity in their vegetative and reproductive parts, the bract/seed scale complex in seed cones (Fig. 4C) is, however, a common feature of all (COULTER & CHAMBERLAIN 1917; PILGER 1926; FLORIN 1951, 1954; SCHWEITZER 1963; WILDE 1975; STÜTZEL & RÖWEKAMP 1999b). Within a bract/seed scale complex the bract scale represents a bract (= leaf). In the axil of the bract scale the seed scale (= ovuliferous short shoot) is inserted. Thus, seed cones are always polyaxial, compound structures, homologous with an angiospermous inflorescence (e.g. SCHUHMAN 1902; HERZFELD 1914; SPORNE 1965; STEWART & ROTHWELL 1993; ESCAPA et al. 2008; TAYLOR et al. 2009; BATEMAN et al. 2011; ROTHWELL et al. 2011; RUDALL et al. 2011; SPENCER et al. 2015; DÖRKEN & RUDALL 2018). The number of bract/

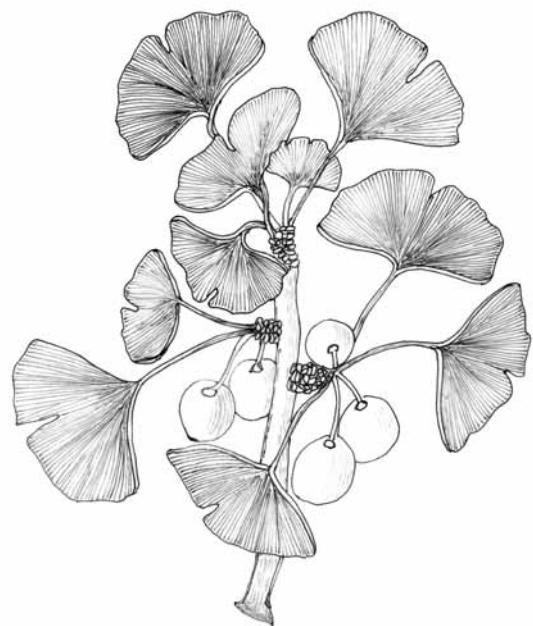


Fig. 3: *Ginkgo biloba*, fertile shoot.

seed scale complexes per seed cone varies intergenerically, but also interspecifically (e.g. *Pinus*, Pinaceae). In several Podocarpaceae, the number of bract/seed scale complexes per seed cone is very low, in some species reduced to a single complex. In contrast, seed cones of several Araucariaceae (e.g. *Araucaria*) consist of several hundred bract/seed scale complexes. However, only among species of Pinaceae and Sciadopityaceae are both types of cone scale developed as two distinct structures, which are still visible even in mature cones (TAKASO & TOMLINSON 1991; MUNDY 2000; DÖRKEN & RUDALL 2018). In other conifer families the bract/seed scale complex is strongly modified and reduced so that in seed cones of most conifers just a single type of cone scale is developed (DÖRKEN 2012; DÖRKEN & RUDALL 2018), which is, however, of different origin and therefore not homologous among all taxa. In Araucariaceae, the bract and seed scale are entirely fused to form a common cone scale, in which the upper tissue represents the seed scale, and the lower tissue the bract scale (e.g. COULTER & CHAMBERLAIN 1917; ECKENWALDER 2009; FARJON 2010a, b). In Cupressaceae s. str., the seed scales are reduced to their ovules and the visible cone scale exclusively represents the bract scale (PAGE 1990; FARJON 2007, 2010a, b; DÖRKEN 2012 a, b; GROTH et al. 2011; JAGEL & DÖRKEN 2014, 2015a, b; DÖRKEN & JAGEL 2017; DÖRKEN & RUDALL 2018). In the majority of conifers, mature seed cones are strongly woody, with thickened and lignified cone scales.

In contrast with the polyaxial, inflorescence-like seed cones, pollen cones are mostly uniaxial, simple, flower-like structures. In a few species, polyaxial, compound pollen cones are formed, bearing either flower-like elongated lateral subunits carrying several microsporangia (e.g. *Cephalotaxus*, Taxaceae and most species of *Podocarpus*, Podocarpaceae) or single flower-like microsporangiphores are inserted in the axil of each bract (e.g. *Pseudotaxus*, Taxaceae). The pollen cones consist of a varying number of microsporangia (= pollen sacs) bearing structures (microsporangiphores) that are either decussate, helical or whorled (ECKENWALDER 2009; FARJON 2010a, b; SCHULZ et al. 2014; DÖRKEN & NIMSCH 2015, 2017; DÖRKEN 2017; DÖRKEN et al. 2017b). Two types of microsporangiphores exist among extant conifers. The hyposporangiate, dorsiventral microsporangiphore (Fig. 4A) is the most common type, consisting of a central stalk, an adaxial terminal scutellum and abaxial microsporangia. The sec-

ond perisporangiate type is radial (Fig. 4B), with microsporangia arranged all around the central stalk (ECKENWALDER 2009; FARJON 2010a, b; SCHULZ et al. 2014; DÖRKEN & NIMSCH 2015). The perisporangiate type is rare and occurs only in some Taxaceae (e.g. *Cephalotaxus*, *Torreya* and *Pseudotaxus*). The structure (polyaxial vs. uniaxial), type of microsporangiphore (hyposporangiate vs. perisporangiate), their arrangement at the cone axis (decussate, helical or whorled) and the number of microsporangia per microsporangiphore, are important diagnostic features for species identification. Additionally, the size and surface structure and in particular the presence or absence of air bladders on the pollen grains are also important in this respect.

The majority of coniferous seeds are dispersed by wind, bearing winged seeds at maturity. However, the seed wing is not a homologous structure among all taxa. For example in Cupressaceae it is formed by the ovuliferous integument, while in Pinaceae it is formed by the upper seed scale tissue. In taxa with animal-dispersed seeds, different types of fleshy structure attract potential dispersers. In *Juniperus* (Cupressaceae), maturing cone scales become fleshy and form the characteristic *Juniperus* berry-like seed cone (Fig. 119C, D; 121D, 123C, D) (adaptation to bird dispersal). Among Taxaceae, the seeds are also partly or entirely surrounded by fleshy structures. Seeds of *Taxus* and *Pseudotaxus* are surrounded by a fleshy aril, which is not fused to the seeds. Seeds of *Cephalotaxus* are surrounded by a fleshy sarcotesta, formed by outer layers of the integument. Among several Podocarpaceae the cone axis, including the inserted leaves, becomes strongly swollen, so that finally a fleshy and mostly conspicuously coloured structure (the receptaculum) is formed (Fig. 4D), while the seeds of most podocarpaceous taxa become entirely enveloped by the seed scale which also becomes swollen and forms a fleshy seed coat (the epimatium) (Fig. 4D).

The **Gnetales** are a diverse group of only three extant monogeneric families (Welwitschiaceae Figs. 5 & 13, Ephedraceae, Figs. 6, 11, Gnetaceae Figs. 7 & 12), with Ephedraceae as sister to Gnetaceae and Welwitschiaceae (DOYLE 1996; PRICE 1996; CHAW et al. 2000; COLE et al. 2017). Each of these families is characterized by a unique morphology distinguishing all three distinctly from each other (GIFFORD & FOSTER 1989).

Welwitschia is characterized by its unique

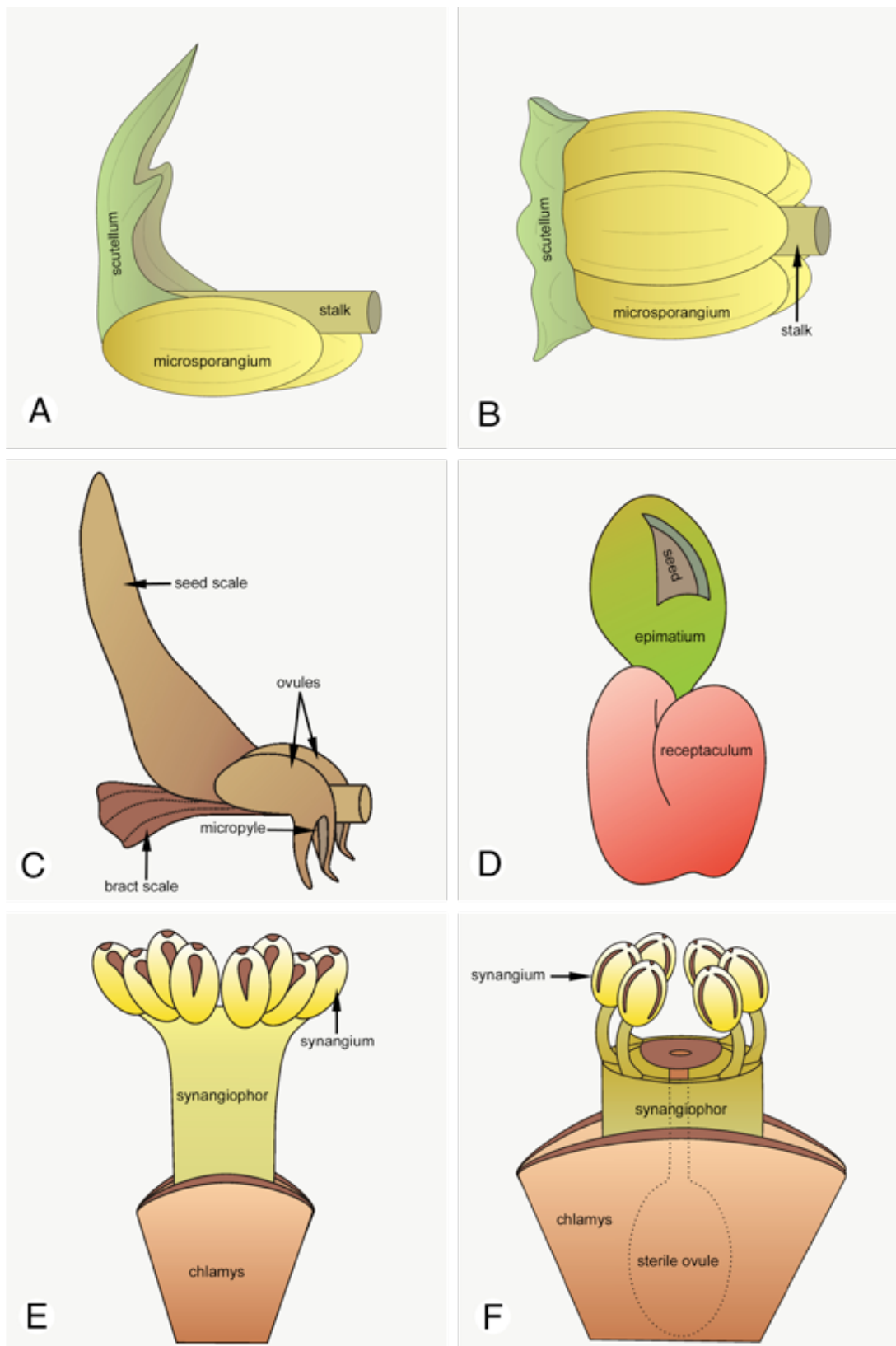


Fig. 4: Explanations of the used morphological terms; **A & B:** Coniferous microsporangiophores in lateral view; **A:** Hyposporangiate; **B:** Perisporangiate; **C:** Bract/seed scale complex of *Pinus* (Pinaceae); **D:** Mature *Podocarpus* (Podocarpaceae) seed with fleshy epimatium (= seed scale) and fleshy receptaculum (= peduncle and inserted leaves); **E & F:** Male reproductive structures of Gnetales with distinct chlamys; **E:** *Ephedra* (Ephedraceae); **F:** *Welwitschia* (Welwitschiaceae).



Fig. 5: *Welwitschia mirabilis* ssp. *mirabilis*, habit.

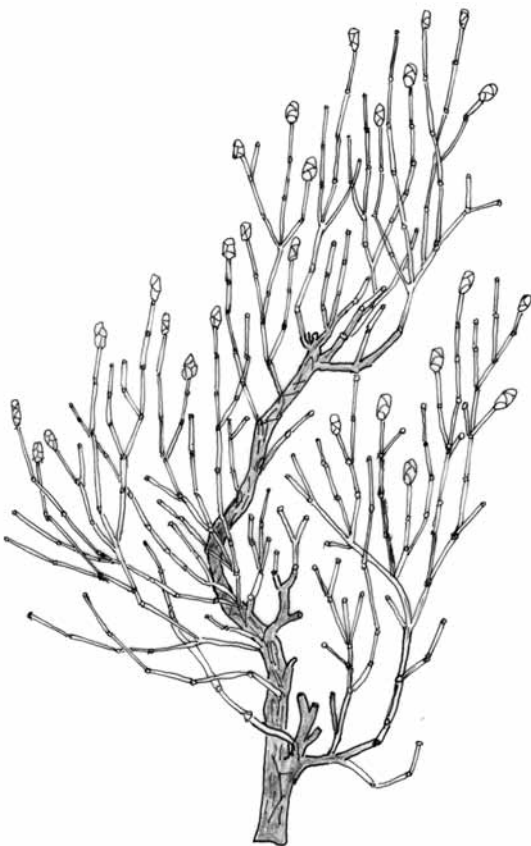


Fig. 6: *Ephedra andina*, fertile shoot.

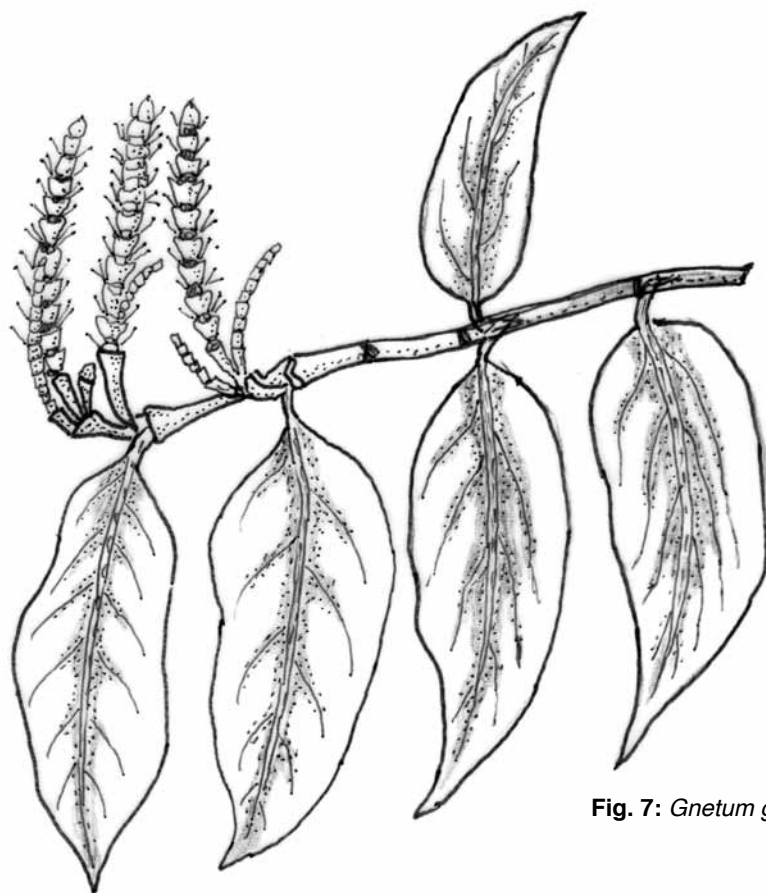


Fig. 7: *Gnetum gnemon*, fertile shoot.

foliage. Subsequent to the cotyledons, only one pair of decussate, parallel-veined, band-like leaves is developed, showing intercalary growth. Thus, new laminar surface is developed in basal parts of the leaf, while the distal parts dry out (SYKES 1911; COULTER & CHAMBERLAIN 1917; GIFFORD & FOSTER 1989; KUBITZKI 1990; DÖRKEN & STEINECKE 2013).

Ephedra-species are either shrubs or climbers that are characterized by their strongly reduced foliage. The decussate leaves are reduced to membranous scales, which no longer participate in photosynthesis, which is restricted to green shoot axes (e.g. THOMPSON 1912; FEUSTEL 1921; VOTH 1934; CUTLER 1939; INAMDAR & BHATT 1971; FOSTER 1972; KUBITZKI 1990; PRICE 1996; FREITAG & MAIER-STOLTE 2003; ICKERT-BOND & WOJCIECHOWSKI 2004).

Gnetum is characterized by large-sized, foli-

ar leaves showing a distinct reticulate venation, which is unique among extant gymnosperms and provides an angiospermous appearance (COULTER & CHAMBERLAIN 1917; GIFFORD & FOSTER 1989; KUBITZKI 1990).

Despite the high structural diversity between the three families, there are also common features, in particular within the reproductive structures, uniting all as a distinct group which is clearly distinguishable from the other gymnosperms. The male and female reproductive structures are arranged within polyaxial, though strongly reduced, compound strobili, which are characterized by the presence of the chlamys, a perianth-like structure made up of two or four fused leaves enveloping the inner reproductive structures within each "flower/inflorescence" (Figs. 4E, F) (SYKES 1911; KUBITZKI 1990; STÜTZEL & MUNDY 2001; MUNDY & STÜTZEL 2004a).

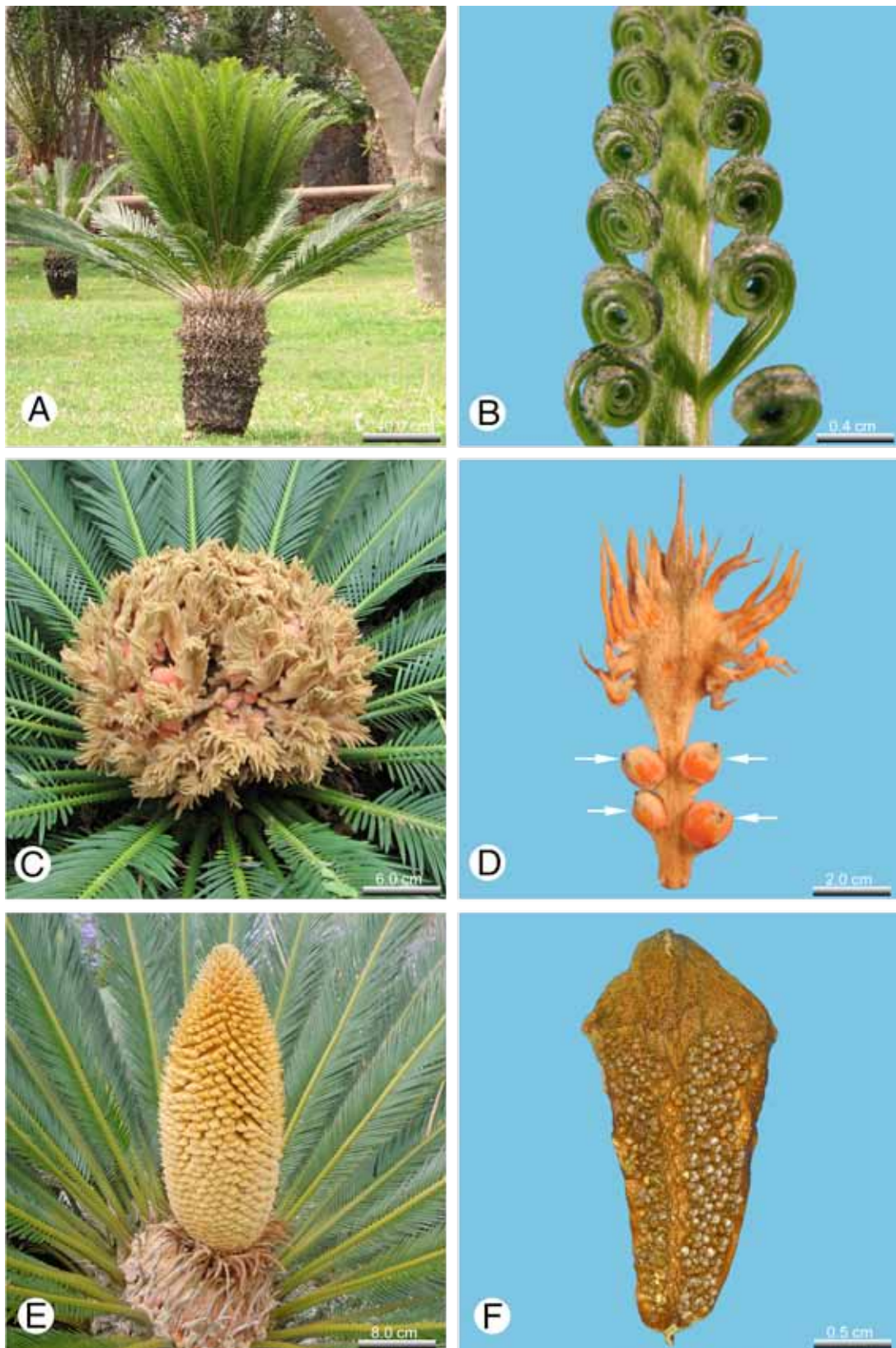


Fig. 8: *Cycas* (Cycadaceae, Cycadales); **A:** Habit (*C. revoluta*); **B:** Young leaves frond-like rolled up (*C. revoluta*); **C:** Macrosporophylls and trophophylls alternating at the shoot axis (*C. revoluta*); **D:** Macrosporophyll with ovules in the position of basal leaflets (arrows) (*C. revoluta*); **E:** Microsporophylls in compact erect strobili (*C. revoluta*); **F:** Abaxial side of a microsporophyll with several synangia; microsporangia already opened (*C. circinalis*).

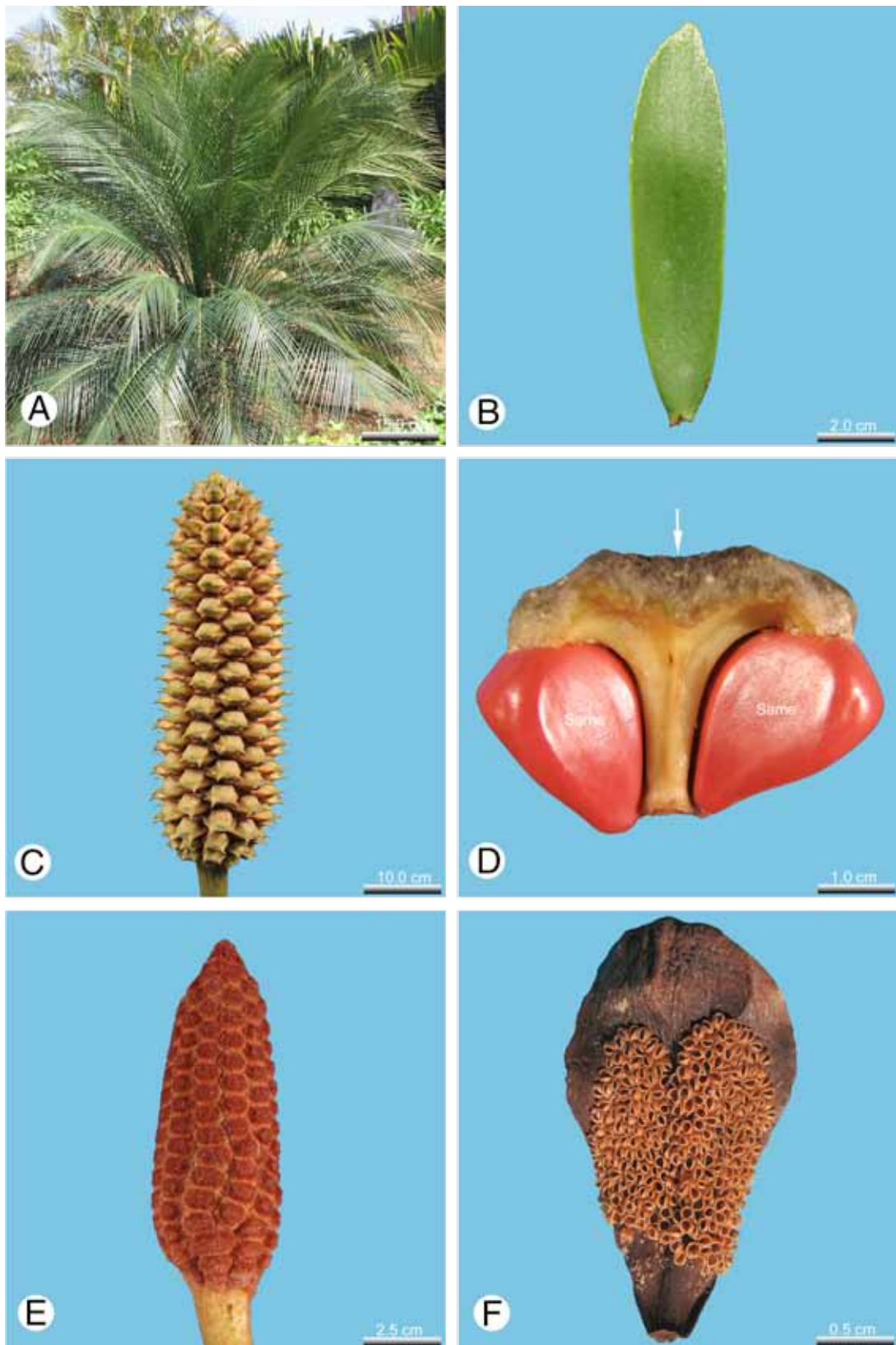


Fig. 9: Zamiaceae (Cycadales); **A:** Habit (*Macrozamia communis*); **B:** Leaflets without midrib (*Zamia amblyphyllidia*); **C:** Macrosporophylls in compact, erect strobili (*Ceratozamia robusta*); **D:** Detail macrosporophyll; lamina flattened; each macrosporophyll with two seeds (*Zamia amblyphyllidia*); **E:** Microsporophylls in compact, erect strobili (*Zamia amblyphyllidia*); **F:** Microsporophyll with several abaxial synangia (*Macrozamia communis*).

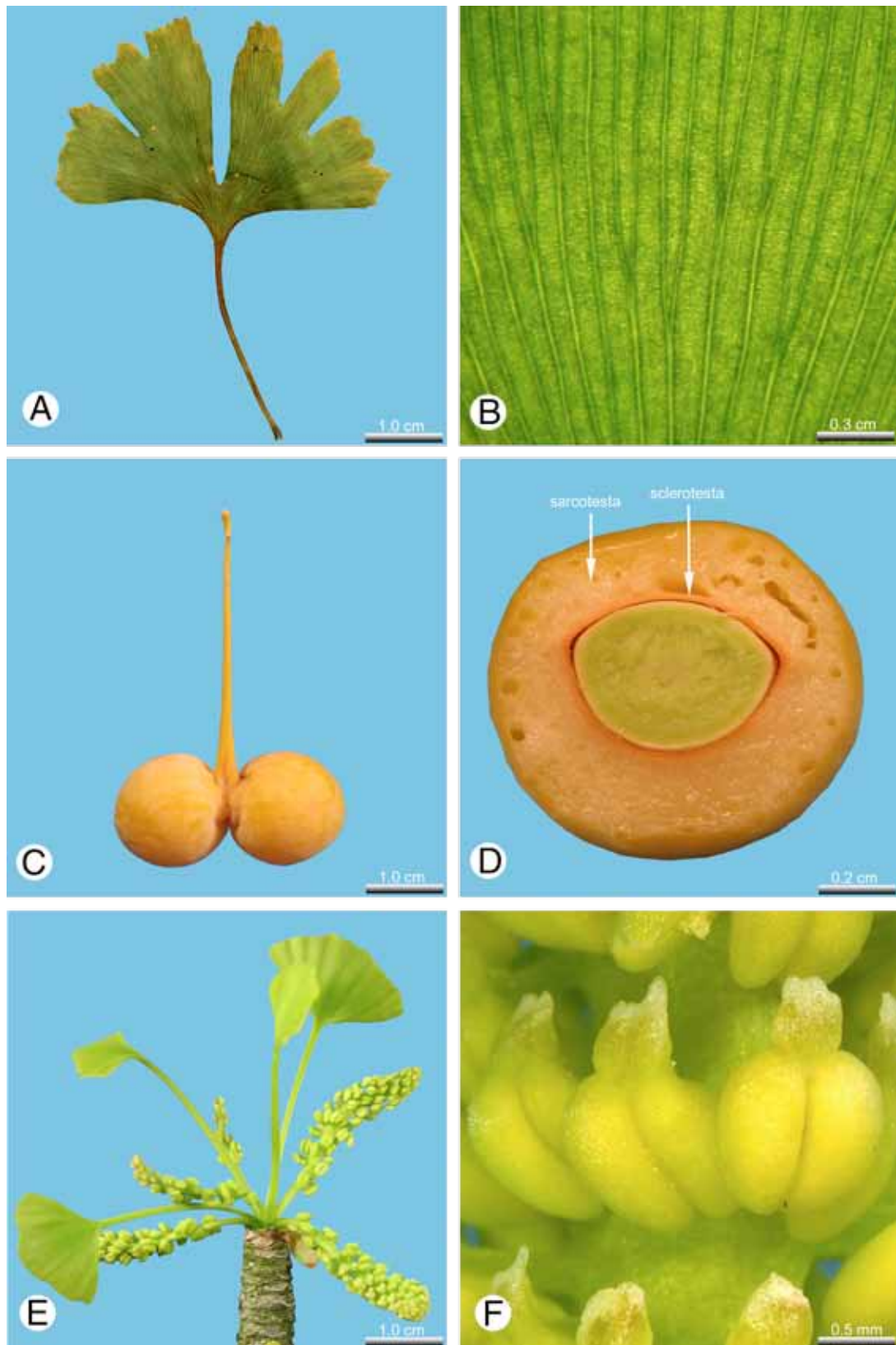


Fig. 10: *Ginkgo biloba* (Ginkgoaceae, Ginkgoales); **A:** Fan-shaped leaf; **B:** Detail dichotomous venation; **C:** Macrosporangium long-stalked; seeds terminal; **D:** Mature seed (cross section) with fleshy sarcotesta and woody sclerotesta; **E:** Microsporangia in compact, catkin-like structures; **F:** Hypo-epigynous microsporangia, each with two, abaxial, yellow microsporangia.

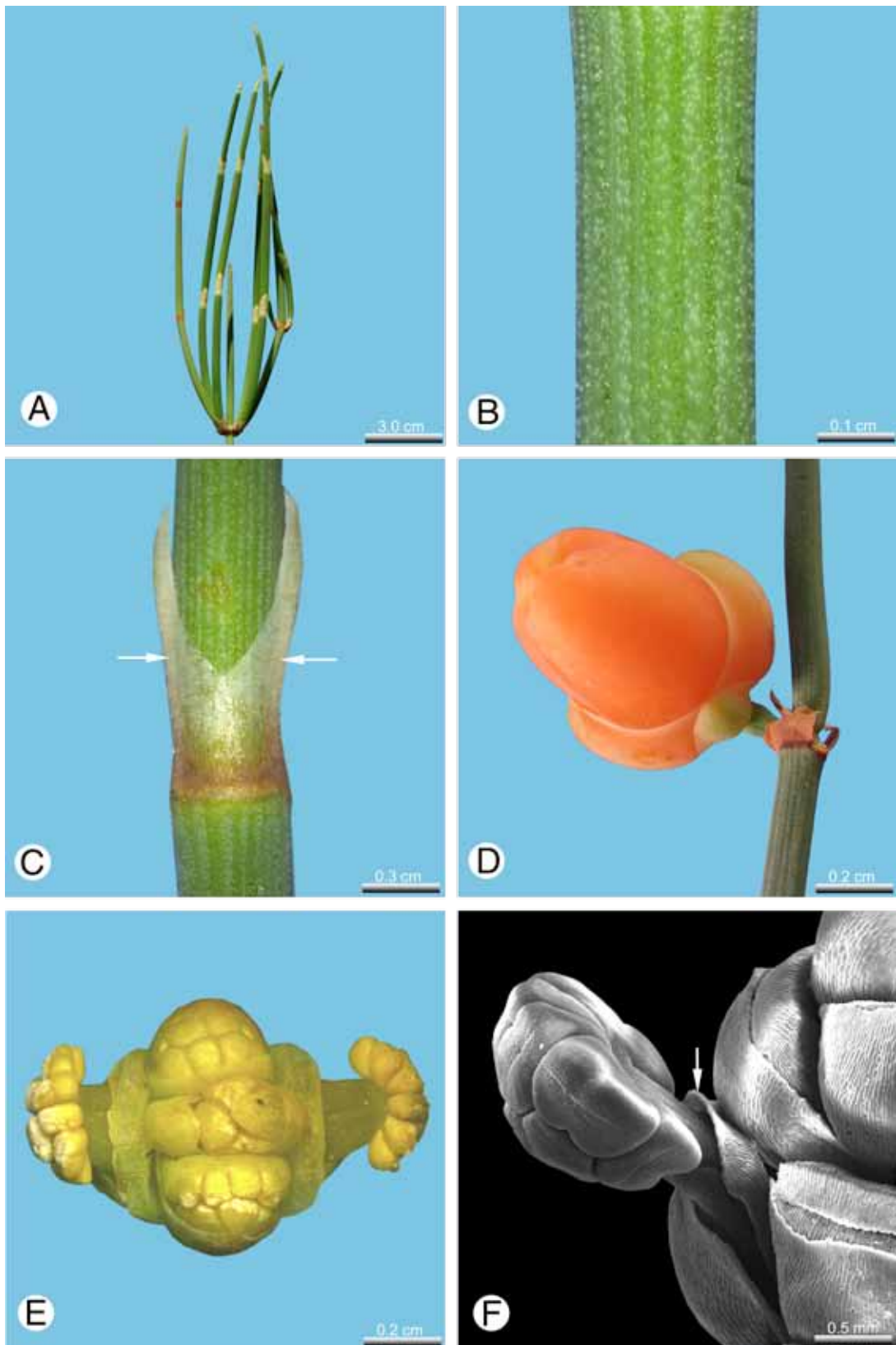


Fig. 11: Ephedraceae (Gnetales); **A:** Shoot system (*Ephedra distachya*); **B:** Detail of the green shoot axis with several stomata, visible as whitish dots (*Ephedra distachya*); **C:** Each node with two strongly reduced, membranous scale leaves (arrows) (*Ephedra distachya*); **D:** Mature seed surrounded by fleshy, red leaves (*Ephedra distachya*); **E:** Male strobilus (*Ephedra distachya*); **F:** Detail of a single male “flower”; synangiophor with basal chlamys (arrow) (*Ephedra distachya*).

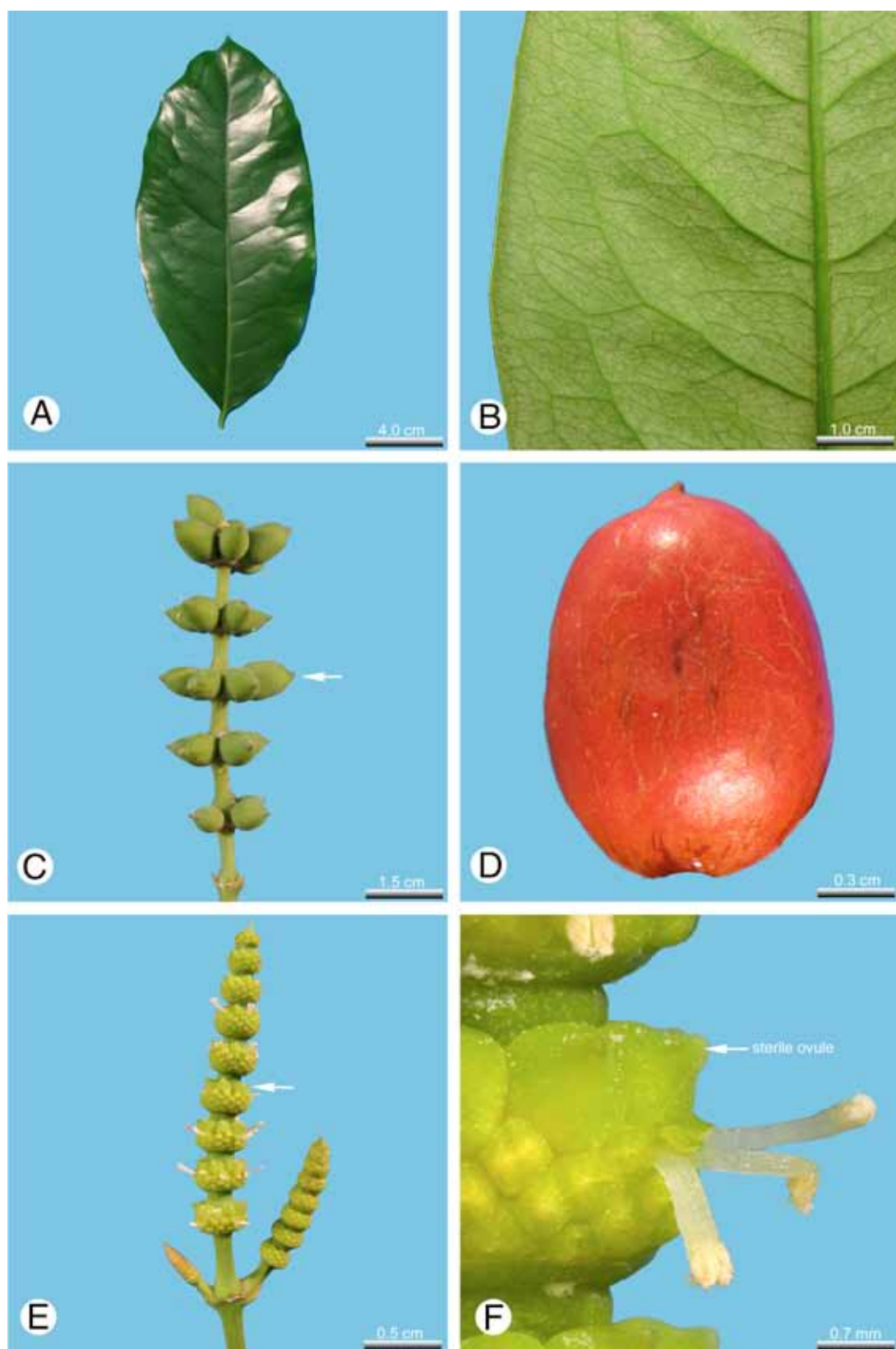


Fig. 12: Gnetaceae (Gnetales); **A:** Foliar leaf with reticulate venation (*Gnetum gnemon*); **B:** Detail reticulate venation (*Gnetum gnemon*); **C:** Female inflorescence, ovules arranged in whorls (*Gnetum gnemon*); **D:** Mature seed, the two bracteoles forming a fleshy, red seed coat (*Gnetum gnemon*); **E & F:** Male inflorescence (*Gnetum gnemon*); **E:** Male flowers in whorls, above each male whorl a whorl of sterile ovules (arrow); **F:** Detail taken from **E**.

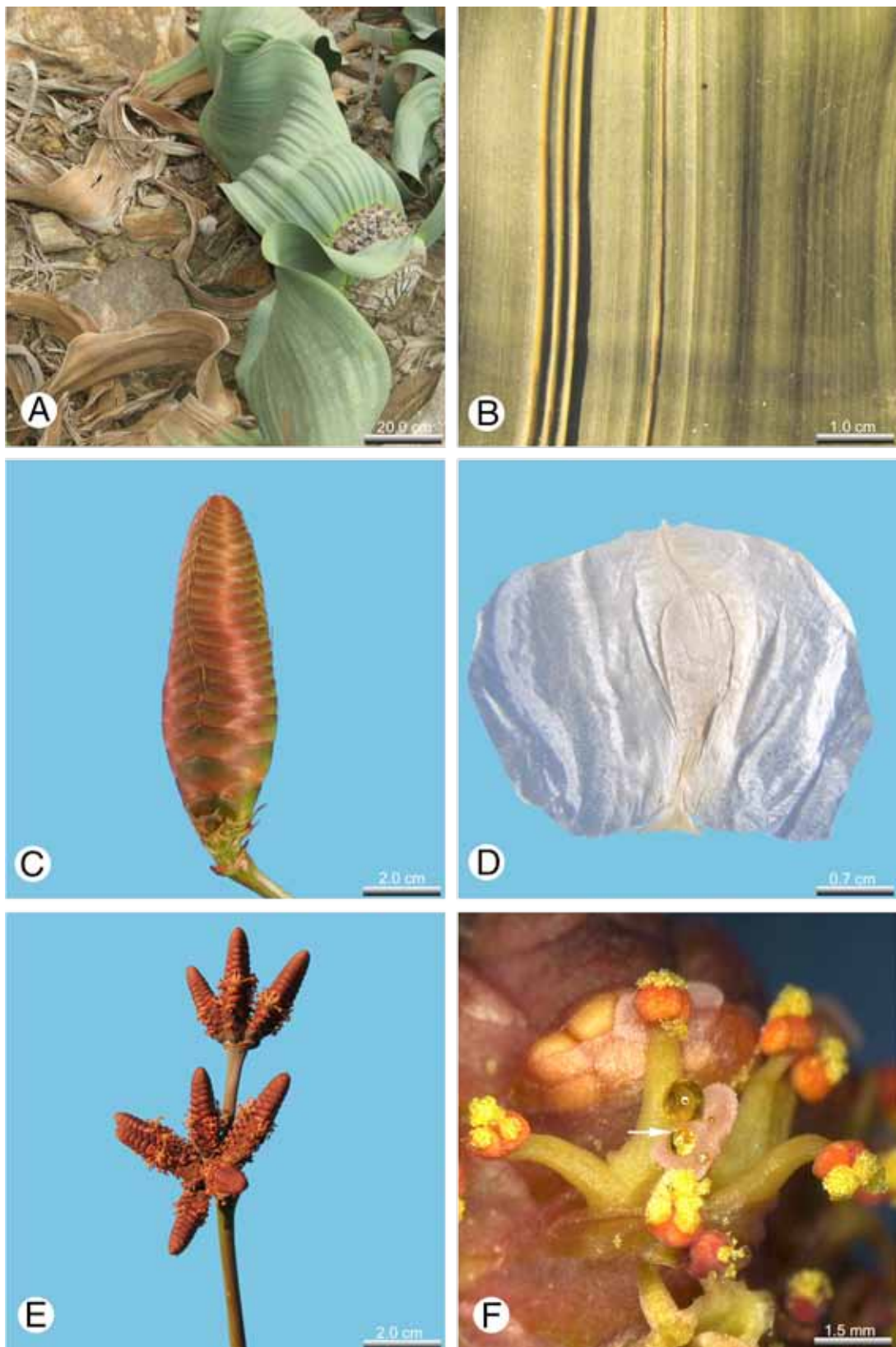


Fig. 13: *Welwitschia mirabilis* ssp. *mirabilis* (Welwitschiaceae, Gnetales); **A:** Habit; **B:** Detail parallel leaf venation; **C:** Female strobilus; **D:** Mature seed; seed wing formed by the chlamys; **E & F:** Male reproductive structures; **E:** Habit male strobili; **F:** Detail of a male inflorescence with a central, sterile ovule, which still produces a pollination drop (arrow).

2 Conifer systematics

In particular within conifers, as the largest group of extant gymnosperms, several, extensive systematic changes have been made in the last years. These comprise several fundamental new combinations including splitting and merging at all systematic levels – families, genera and species as well. According to these changes only 6 coniferous families (Araucariaceae, Cupressaceae, Pinaceae, Podocarpaceae, Sciadopityaceae and Taxaceae) remain today (QUINN et al. 2002; CHRISTENHUSZ et al. 2011). The most significant changes within the coniferous family concept affected the Taxodiaceae, Phyllocladaceae and Cephalotaxaceae.

As a part of this reordering the former **Taxodiaceae** were merged into the Cupressaceae (KUSUMI 2000; GADEK et al. 2000; QUINN 2002; SCHULZ & STÜTZEL 2007; YANG et al. 2012; JAGEL & DÖRKEN 2014; COLE et al. 2017). The genus *Sciadopitys*, formerly placed in the monogeneric subfamily Sciadopityoideae within Taxodiaceae (e.g. PILGER 1926), was separated from the Taxodiaceae to form the new, distinct, monogeneric family Sciadopityaceae. According to molecular family trees the new Sciadopityaceae is separated from the Cupressaceae by the Taxaceae (STEFANOVIC 1998; QUINN et al. 2002; RAI et al. 2008; CHRISTENHUSZ et al. 2011; LESLIE et al. 2012; YANG et al. 2012; COLE et al. 2017).

According to the results gained in several morpho-anatomical and molecular based cladistic analyses, but also in studies on their embryogeny it is widely accepted today that the small monogeneric family of **Phyllocladaceae** was merged into the large Podocarpaceae-family (QUINN 1986, 1987; HART 1987; CHAW et al. 1995; KELCH 1996, 1997; HILL 1998; GADEK 2002; CHRISTENHUSZ et al. 2011; KNOFF et al. 2011; CONTRERAS 2016). The unique phylloclade formations replacing the photosynthetic foliage and an aril surrounding more than half of the seeds are characteristic traits developed among all extant *Phyllocladus*-species and can be regarded as autapomorphies (HILL 1998). In KNOFF et al. (2011) the genus *Phyllocladus* is placed with *Halocarpus*, *Lagarostrobos*, *Manoao* and *Prumnopitys* within the “Prumnoid-Clade”.

The systematic range of the monogeneric **Cephalotaxaceae** is still controversial. On the one hand it is regarded as a distinct family, on the other hand it is suggested that it be merged into the Taxaceae (compare e.g. STÜTZEL & RÖWEKAMP 1999a; FARJON, 1998, 2001, 2010; MUNDY 1999; MUNDY & MUNDY 2001;

STEVENS 2001; GADEK et al. 2002; ECKENWALDER 2009; RAN & WANG 2010; CHRISTENHUSZ et al. 2011; LU et al. 2014; CONTRERAS 2016).

In addition to that changes were also made within the coniferous genus concept, which mainly affected the genera *Fokienia* (Cupressaceae), *Microbiota* (Cupressaceae), *Tsuga* (Pinaceae), *Podocarpus* (Podocarpaceae) and *Xanthocyparis* (Cupressaceae).

Among **Pinaceae** *Tsuga longibracteata* was separated from *Tsuga* depending on some distinct morphological differences (e.g. a non-serate leaf margin, amphistomatic foliage, erect seed cones and bisaccate pollen grains) and placed in the new genus *Nothotsuga*. *Nothotsuga* and *Tsuga* represent sister groups and are said to be closely related (WANG et al. 2000). In addition, the systematic position of taxa placed within the section *Hesperopeuce* is still controversial. These taxa show several features distinguishing them distinctly from the other *Tsuga*-species (e.g. dense and irregularly arranged radial foliage; amphistomatic distribution of stomata; large sized, more or less erect seed cones with unusually large bract scales and pubescent seed scales; bisaccate pollen grains leading to another pollination mechanism than those occurring in the other *Tsuga*-species with non-saccate pollen grains). These features could justify a placement into a distinct genus *Hesperopeuce* (PAGE 1988, 1990).

Among **Cupressaceae**, *Thuja orientalis* was separated from *Thuja* and returned to the genus *Platycladus* which SPACH had proposed in 1847. In addition, JAGEL & DÖRKEN (2015a) showed that *Microbiota* represents an alpine dwarf form of *Platycladus*. Thus, *Microbiota decussata* was renamed *Platycladus decussata* (KOM.) JAGEL & DÖRKEN and merged into *Platycladus* (JAGEL & DÖRKEN 2015a). A further merging is suggested for the very closely related cupressaceous genera *Fokienia* and *Chamaecyparis*. Morpho-anatomical and morphogenetic studies clearly show that among these two genera no fundamental structural differences exist either in their vegetative or in their reproductive structures (JAGEL & STÜTZEL 2001; JAGEL & DÖRKEN 2015a). Due to the absence of distinct differences clearly separating *Fokienia* from *Chamaecyparis*, *Fokienia hodginsii* was renamed and merged into the genus *Chamaecyparis* as *Chamaecyparis hodginsii* (DUNN) RUSHFORTH (RUSHFORTH 2007). Morpho-anatomical and also morphogenetic

investigations on reproductive structures of *Xanthocyparis* clearly showed that both *Xanthocyparis*-species represent true *Cupressus*-species. The small seed cones and the low number of ovules can be regarded as falling in the range of variation occurring among *Cupressus*, and the genus *Xanthocyparis* can no longer be justified (JAGEL & STÜTZEL 2001; JAGEL 2002; SILBA 2005; RUSHFORTH 2007; JAGEL & DÖRKEN 2015; DÖRKEN et al. 2017a; DÖRKEN & NIMSCH 2017). With the merging of *Xanthocyparis* into *Cupressus*, the supposed intergeneric hybrid \times *Cupressocyparis*/ \times *Cuprocypris* is also obsolete, because taxa of \times *Cupressocyparis*/ \times *Cuprocypris* are just interspecific hybrids of different *Cupressus*-species

(JAGEL & STÜTZEL 2001; JAGEL 2002; JAGEL & DÖRKEN 2015; DÖRKEN et al. 2017a).

Depending on morpho-anatomical and molecular phylogenetic data the most extensive systematic changes were made within the **Podocarpaceae**, in particular within the genus *Podocarpus*. Several new genera *Afrocarpus*, *Halocarpus*, *Manoao*, *Nageia*, *Retrophyllum* and *Sundacarpus* were split off the former large genus *Podocarpus*. This splitting led finally to much more complex intergeneric relationships within Podocarpaceae (e.g. BUCHHOLZ & GRAY 1948; DE LAUBENFELS 1985; PAGE 1988, 1990; CHAW et al. 1995; MOLLOY 1995; KELCH 1997, 1998; BOBROV & MELIKJAN 1998; KNOPF 2011; KNOPF et al. 2011; LITTLE et al. 2013).



Pinus canariensis, natural site in lava fields, ca. 1800 m above sea level, Mount Teide, Tenerife, Canary Island, Spain.



Pinus cembra (center of the image) and *Larix decidua*, natural site in the southern Alps, Haute-Nendaz, Wallis, Switzerland.



Abies pinsapo, Parque National de las Nieves, Andalusia, Spain.



Araucaria columnaris, natural coastal forest, Lagoon, New Caledonia. © B. Suprin.



Pilgerodendron uviferum, Esquel - El Bolson, Argentina.



Neocallitropsis pancheri, Plaine des Lacs, New Caledonia. © B. Suprin



Juniperus communis, natural site on Jurassic limestone, Swabian Jura, Germany.



Retrophyllum minor, natural site at the margin of a slow-moving river, Chutes de la Madeleine, New Caledonia.
© B. Suprin.

3 The coniferous genera

The dichotomous identification key presented here is based on genera and does not key to species level. For a better handling, in particular also outdoor in the field, only diagnostic characteristics are included which are easily recognizable with the naked eye or a magnifying glass. Thus, diagnostic micromorphological and anatomical features, which are only recognizable by microscopy, are excluded.

3.1 Spectrum of coniferous genera

The identification key includes all 68 coniferous genera (see list below). The successful determination to genus is essential for subsequent successful species identification. In particular, the large coniferous genera are often divided into several sections which are not keyed here. However, the morpho-anatomical traits of the 3 *Juniperus* sections (Cupressaceae) differ so strongly from each other, which justifies a special treatment. Thus, all 3 *Juniperus* sections are described below.

Araucariaceae HENKEL & W. HOCHST

Agathis SALISB., *Araucaria* JUSS., *Wollemia* W.G. JONES, K.D. HILL et J.M. ALLEN

Cupressaceae GRAY (incl. Taxodiaceae)

Actinostrobus MIQ., *Athrotaxis* D. DON, *Austrocedrus* FLORIN et BOUTELJE, *Callitris* VENT., *Calocedrus* KURZ, *Chamaecyparis* SPACH (incl. *Fokienia* A. HENRY & H.H. THOMAS), *Cryptomeria* D. DON, *Cunninghamia* R. BR., *Cupressus* L. (incl. *Xanthocyparis* FARJON et HIEP), *Diselma* HOOK. f., *Fitzroya* LINDL., *Glyptostrobus* ENDL., *Juniperus* L. sect. *Caryocedrus* ENDL., *Juniperus* L. sect. *Juniperus*, *Juniperus* L. sect. *Sabina* SPACH, *Libocedrus* ENDL., *Metasequoia* HU et W.C. CHENG, *Neocallitropsis* FLORIN, *Papuacedrus* H.L. LI, *Pilgerodendron* FLORIN, *Platycladus* SPACH (incl. *Microbiota* KOM.), *Sequoia* ENDL., *Sequoiadendron* J. BUCHHOLZ, *Taiwania* HAYATA, *Taxodium* RICH., *Tetraclinis* MAST., *Thuja* L., *Thujopsis* SIEBOLD & ZUCC., *Widdringtonia* ENDL.

Pinaceae SPRENG. ex F. RUDOLPHI

Abies MILL., *Cathaya* CHUN et KUANG, *Cedrus* TREW, *Keteleeria* CARRIÈRE, *Larix* MILL., *Nothotsuga* HU ex N. C. PAGE, *Picea* A. DIETR., *Pinus* L., *Pseudolarix* GORDON, *Pseudotsuga* CARRIÈRE,

Tsuga CARRIÈRE

Podocarpaceae ENDL. (incl.

Phyllocladaceae)

Acropyle PILG., *Afrocarpus* (J. BUCHHOLZ & N.C. GRAY) C.N. PAGE, *Dacrycarpus* (J.J. BENNETT) DE LAUB., *Dacrydium* SOL. ex G. FORST., *Falcatifolium* DE LAUB., *Halocarpus* QUINN, *Lagarostrobos* QUINN, *Lepidothamnus* PHIL., *Manao* MOLLOY, *Microcachrys* HOOK f., *Microstrobos* J. GARDEN & L.A.S. JOHNSON, *Nageia* GAERTN., *Parasitaxus* DE LAUB., *Phyllocladus* RICH. ex MIRB., *Podocarpus* L'HÉR. ex PERS., *Prumnopitys* PHIL., *Retrophyllum* C.N. PAGE, *Saxegothaea* LINDL., *Sundacarpus* (J. BUCHHOLZ & N.C. GRAY) C.N. PAGE

Sciadopityaceae LUERSS.

Sciadopitys SIEBOLD & ZUCC.

Taxaceae GRAY (incl. Cephalotaxaceae)

Amentotaxus PILG., *Austrotaxus* R.H. COMPTON, *Cephalotaxus* SIEBOLD & ZUCC., *Pseudotaxus* W.C. CHENG, *Taxus* L., *Torreya* ARN.

3.2 Key to the genera

I. Key to the major gymnospermous groups

1. Evergreen woody plants with frond-like pinnate leaves; the tree-like species with a palm-like shape
Cycads
 - Plants different in shape **2**
- 2(1). Deciduous large trees with distinct long shoot-short shoot differentiation, leaves fan-shaped with a distinct open dichotomous venation **Ginkgo**
 - Plants different in shape **3**
- 3(2). Either shrubs or climbers with strongly reduced, membranous, decussate, rudimentary scale leaves, or plants with only one pair of decussate, parallel-veined, band-like leaves and a flat topped stem; or evergreen trees or climbers with decussate, broad leaved foliage with distinct reticulate venation . . . **Gnetales**
 - Trees and shrubs; evergreen, few deciduous; with green needle or scale leaves, sometimes with leaf dimorphism; seed cones woody, with bract-seed scale complex; some species with fleshy seed cones . . **Conifers**

II. Key to the coniferous families

1. Seed cones with distinct bract-seed scale complex **2**
 - Seed cones without distinct bract-seed scale complex. **3**
- 2(1). Seed scale always with 2 seeds; seeds mostly winged, rarely unwinged; seed wing originated from seed scale tissue **Pinaceae**
 - Seed scale with 4-8 (-12) seeds; seeds flat with 2 narrow, lateral wings; seed wing formed by the integument **Sciadopityaceae**
- 3(1). Cone scale with 1 seed. **4**
 - Cone scale with more than 1 seed **6**
- 4(3). Seed cones woody, fleshy structures absent; numerous, helical cone scales; disintegrating at maturity; seeds only exceptionally winged; seed and cone scale fused to each other **Araucariaceae**
 - Seed cone or seed with fleshy structures **5**
- 5(4). Seed with fleshy aril or sarcotesta; peduncle and bracts not fleshy **Taxaceae**
 - Seeds with fleshy or membranous coat (epimatium); peduncle and inserted bract often strongly swollen, forming a fleshy “foot” below the seed (receptaculum) **Podocarpaceae**
- 6(3). Cone scales of the seed cones either helical, whorled or decussate; mature seed cones woody, exceptionally fleshy; seeds mostly winged, seed wing formed by the integument. **Cupressaceae**

III. Key to the coniferous genera

A. Key – Pinaceae

1. Deciduous **2**
 - Evergreen **3**
- 2(1). Mature seed cone disintegrating; pollen cones clustered distally at short shoots, not terminal; short shoots after pollen cone formation not dying **Pseudolarix**
 - Seed cones not disintegrating, remaining on the trees for years; pollen cones terminating a short shoot, which then dies **Larix**
- 3(1). Shoot system with distinct long shoot-short shoot differentiation **4**
 - Shoot system without distinct long shoot-short shoot differentiation **5**
- 4(3). Short shoot with either 1, 2, 3, (4-) 5 (-8) needle leaves **Pinus**
 - Short shoots with significantly more leaves than above **Cedrus**
- 5(3). Pollen cones erect, over 100 microsporangioophores **Cathaya**
 - Pollen cones pendulous, significantly less microsporangioophores **6**
- 6(5). Seed cones erect, disintegrating at maturity **Abies**
 - Seed cones mostly not erect, but when erect not disintegrating at maturity **7**