





# **Cones of conifers**

Morphology, anatomy and functional aspects  
of coniferous reproductive structures

Veit Martin Dörken

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Tel: +49-2228-493  
Fax: +49-3212-1024877

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# 1 Introduction

## 1.1 What are gymnosperms?

There are five large extant groups of seed plants: cycads, *Ginkgo*, conifers, Gnetales and angiosperms (e.g. BOWE et al. 2000; CHAW et al. 2000; SOLTIS et al. 2002; HILTON & BATEMAN 2006; CHRISTENHUSZ et al. 2011; COLE et al. 2017). The first four represent the gymnosperms in total (HILTON & BATEMAN 2006; MATHEWS 2009). Gymnosperms differ from angiosperms, for example by all being woody trees or shrubs, 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 lack of a triploid endosperm.

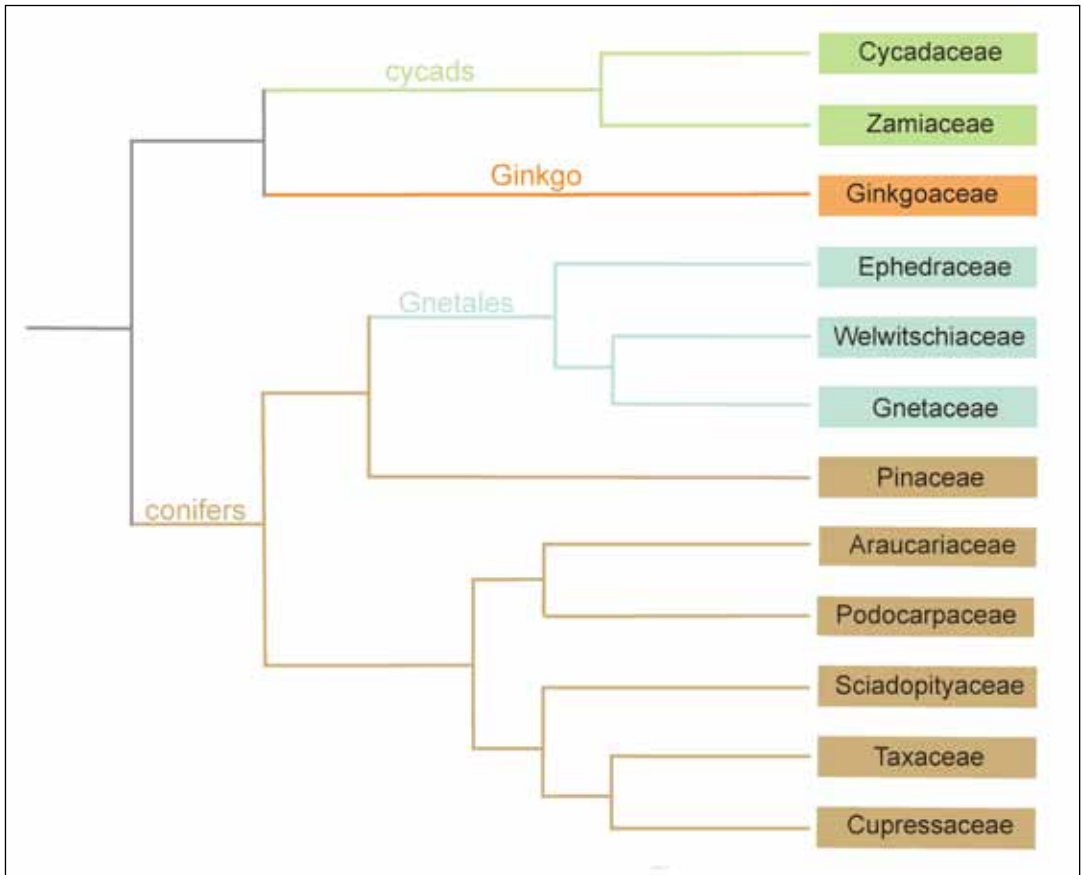
However, even today the systematic relationships within gymnosperms are still controversial and also their relationships to angiosperms, in particular the position of Gnetales (e.g. CHAW et al. 1997, 2000; BOWE et al. 2000; BURLEIGH & MATHEWS 2004; HILTON & BATEMAN 2006; GRAHAM & ILES 2009; MATHEWS 2009; COIRO 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 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).

Among extant seed plants gymnosperms represent the ancestral ones with cycads being the basal-most taxon. Extant gymnosperms are the last reminders of very old lineages with a long evolutionary history. Especially in the Jurassic and Cretaceous, gymnosperms were the dominating group of land plants before they were edged out by the rapidly evolving angiosperms at the end of the Cretaceous/Early Tertiary (GIFFORD & FOSTER 1989; FARJON 2008; TAYLOR et al. 2009). Thus, the species spectrum of gymnosperms and their structural diversity have previously been much higher than is reflected by the recent species spectrum. Compared to the 295.383 extant angiosperms the total number of about 1.079 extant gymnosperms is extremely low. Despite extant gymnosperms being just a small group of seed plants with a low number of species, even today several fundamental gaps in knowledge about their morpho-anatomical structures, their reproductive biology, their origin and their evolutionary pathways still exist. There are three major reasons: (1.) Huge gaps in the fossil record; (2.) Several extant taxa are close to the edge of extinction and are only rarely or not in cultivation, which leads to a strongly limited availability of research material; (3.) Within a genus all species are quite similar to each other showing little variation in their general structure.

The following chapters deal with different structural aspects of coniferous reproductive structures and their evolutionary pathways, but also functional aspects like the pollination process, including pollen release, pollen capture and orientation and withdrawal of pollination drops are treated.





**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).

## 1.2 What are conifers?

Conifers, which comprise 6 extant families and about 629 species (Araucariaceae: 37 species; Cupressaceae: 149 species; Pinaceae: 228 species; Podocarpaceae: 187 species; Sciadopityaceae: 1 species and Taxaceae: 27 species) are the largest group among extant gymnosperms (CHRISTENHUSZ & BYNG 2016). 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 27 cupressaceous genera are monotypic.

The majority of conifers are evergreen trees and rarely shrubs; only few species are decidu-

ous (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).

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 macleayana* (Cupressaceae), *Cupressus vietnamensis* (Cupres-

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saceae), *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. 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, unisexual cones (name conifers! lat. *conus* = cone, *ferre* = carrying); the female (ovulate) cones are called “seed cones”, the male (pollen-bearing) cones “pollen cones”.

## 2 The reproductive structures of conifers

The majority of conifers is monoecious. Seed and pollen cones are developed on the same individual, as is the case e.g. for all Pinaceae (Fig. 2F), Sciadopityaceae and the majority of Cupressaceae (Fig. 2E). Compared to this, the spectrum of strictly dioecious taxa with either functional “male” or “female” individuals is quite low. Dioecy is realized in the majority of Taxaceae (Figs. 2C & D) and Podocarpaceae (Figs. 2A & B) and some Araucariaceae and Cupressaceae. There is a high structural diversity existing among the cones developed in the different groups of extant conifers, which has previously been subject of several fundamental studies published between 1920 and 1950 (e.g. PILGER 1926; HIRMER 1936; PROPACH-GIESELER 1936; DLUHOSCH 1937; FLORIN 1951, 1954) before this topic became more or less dormant. About 40 years later, when scanning electron microscopy technique became popular the topic entered the research focus again and several important SEM studies were carried out (e.g. TAKASO & TOMLINSON 1989a, 1989b; 1990, 1991, 1992; TOMLINSON et al. 1993; JAGEL 2002; FARJON & ORTIZ GARCIA 2003; JAGEL & STÜTZEL 2001a, 2001b, 2003; SCHULZ et al. 2003; SCHULZ & STÜTZEL 2007). Despite all these fundamental studies even today the complex organization and the evolutionary pathways of the coniferous reproductive structures is still not entirely understood. For example the same term is used for structures which are probably not homologous, e.g. the “columella” in callitroid Cupressaceae or the fleshy “aril” in Taxaceae. Thus, it is not surprising that for several frequently used and widely accepted terms, precise definitions can hardly be found and the same term is used for different, non-homologous structures. However, the understanding of gymnosperms reproductive biology is essential to understand the modern seed plants, the angiosperms.

### 2.1 The general structure of coniferous seed cones

In all extant conifers the ovuliferous structures are aggregated in compact unisexual structures, so-called “seed cones”, which have an enormous structural diversity throughout the different

groups. They strongly vary in size and shape and also in the number of cone scales and ovules (KRÜSSMANN 1983; ECKENWALDER 2009; FARJON 2005, 2010; DÖRKEN & NIMSCH 2019). The majority of coniferous seed cones is characterized by the presence of the so called “bract/seed scale complex”. The bract scale represents a leaf, carrying an axillary ovuliferous short shoot (= seed scale). Thus, coniferous seed cones represent strongly condensed and compact inflorescences (SCHUHMAN 1902; HERZFELD 1914; SCHWEITZER 1963; SPORNE 1965; STEWART & ROTHWELL 1993; ESCAPA et al. 2008; WILLIAMS 2009; BATEMAN et al. 2011; ROTHWELL et al. 2011; RUDALL et al. 2011; SPENCER et al. 2015; DÖRKEN & RUDALL 2018, 2019). The number of bract/seed scale complexes per seed cone varies strongly between the different conifers, with only a single one in some Podocarpaceae to several hundred in some Pinaceae and Araucariaceae. However, only in Pinaceae (Figs. 3, 17, 18) and Sciadopityaceae (Fig. 31), bract and seed scale are visible as two distinct types of scales even at maturity (SCHUHMAN 1902; HERZFELD 1914; PILGER 1926; FLORIN 1951, 1954; SCHWEITZER 1963; FARJON 1984, 2005; STÜTZEL & RÖWEKAMP 1997, 1999b; MUNDRY 2000; FARJON & ORTIZ GARCIA 2003; ECKENWALDER 2009). In all other conifers the bract/seed scale complex got strongly modified, so that finally the cones consist of only one type of uniformly shaped cone scale (PAGE 1990; TAKASO & TOMLINSON 1992; GADEK et al. 2000; JAGEL & STÜTZEL 2001b, 2003; JAGEL 2002; SCHULZ 2006; SCHULZ & STÜTZEL 2007). The identity of which is still controversial: Are these scales representing just the bract scale, while the seed scales are more or less reduced to their ovules as is suggested for several Cupressaceae or are bract and seed scale congenitally fused to each other to form a common cone scale as is suggested for Araucariaceae? In this case, the question arises which portions within such a fusion product is formed by the bract and which part by the seed scale. In *Cryptomeria*, *Glyptostrobus* and *Taxodium* (taxodioid Cupressaceae) only one type of cone scale is formed. However, in all three genera teeth-like structures are formed below the ovules. These teeth are fused basally to the cone scale. Distally they are free and significantly exceed the cone scale in length. The

identity of these teeth is controversial: Do they belong to the seed scale? Do they represent the tips of macrosporophylls? Do they possibly represent a row of sterile ovules helping to seal the maturing cone? Thus, all these open questions show that the structure and the branching pattern within the coniferous seed cones are still not finally solved. In this context, teratological seed cones showing anomalous developmental sequences with successive processes that usually occur simultaneously, or such cones showing different kinds of proliferations are helpful in solving some of these open questions, which cannot be answered from wild-type material (compare DÖRKEN & RUDALL 2018).

### 2.1.1 The fertile zones within coniferous seed cones

In the different coniferous groups, the number of bract/seed scale complexes varies strongly from one or two, for example within some Podocarps (Figs. 27; 28; 29) up to several hundred in numerous Araucariaceae (KRÜSSMANN 1983; ECKENWALDER 2009; FARJON 2010; DÖRKEN & NIMSCH 2019). Particularly in seed cones with a high number of bract/seed complexes, the basal and distal ones are usually sterile. The fertile zone is located in the middle of the cone, as in all Pinaceae, Sciadopityaceae and early-divergent Cupressaceae (including the subfamilies Cunninghamioideae, Athrotaxoideae, Taiwanoideae, Sequoioideae and Taxodioideae) and also some Podocarpaceae, including *Lagarostrobos* (Figs. 29A-C), *Microcachrys* and *Microstrobos* (DÖRKEN & NIMSCH 2019). In basal-most parts of these seed cones, several transitional leaves are developed which represent intermediate stages between trophophylls and the basal-most cone scales (JAGEL & DÖRKEN 2014; DÖRKEN & NIMSCH 2019). Towards the apex of the seed cone, the bract/seed complexes are sterile, strongly reduced in size and often not entirely separated from the cone axis.

However, within seed cones of Cupressaceae s. str., which includes the two subfamilies Cupressoideae and Callitroideae, there is a distinct evolutionary tendency to reduce such sterile terminal elements and to shift the fertile zone into distal-most parts of the cone (Fig. 4). In numerous primitive cupressoid Cupressaceae, including for example *Calocedrus* (Figs. 5E & F), *Platycladus* (Fig. 5A), *Thuja* (Fig. 47A) and

*Chamaecyparis* (Figs. 5B-D), a distinct sterile terminal piece still occurs, which consists of one or two sterile pairs of cone scales, which is/are not entirely separated from the cone axis and is/are still fused to it (JAGEL 2002; JAGEL & DÖRKEN 2015a). However, in modern cupressoid Cupressaceae, for example in the genera *Tetraclinis*, most *Cupressus*-species (Fig. 4D) and *Juniperus* (Fig. 4E & F) (JAGEL & STÜTZEL 2001a, 2003; SCHULZ et al. 2003; JAGEL & DÖRKEN 2015a) such a sterile terminal piece is usually absent and all distal cone scales are fertile. This feature is also realized throughout all callitroid Cupressaceae (Fig. 6) (JAGEL 2002; JAGEL & DÖRKEN 2015b; DÖRKEN & JAGEL 2017; DÖRKEN & NIMSCH 2019). In *Juniperus* and *Tetraclinis*, the reduction of sterile terminal elements is so strongly advanced that even non-axillary or terminal ovules occur (Fig. 4F) (JAGEL & STÜTZEL 2003; SCHULZ et al. 2003; JAGEL & DÖRKEN 2015a). The shift of the fertile zone into distal-most parts as in modern-most cupressoid and all callitroid Cupressaceae, seems advantageous in the pollination process. It allows a free exposure of pollination drops and an apically dense arrangement of ovules in more or less the same plane, which favors the fusion of pollination drops of neighbouring ovules into a common larger one (Figs. 53A-D). Both increase the success in pollen capture (DÖRKEN & JAGEL 2014). In this case, the reductions of sterile terminal elements in cupressaceous seed cones are assumed to be important improvements in the pollination process. Reduced seed cone biomass may play a subordinate role in that respect.

In seed cones of numerous modern Cupressaceae s. str., the reduction of sterile terminal elements is so marked that often only the apex of the cone axis remains visible as a more or less distinct central spine (Fig. 6). In particular, within callitroid Cupressaceae (Figs. 6B-F), it is a very prominent feature (SAHNI & SINGH 1931; DOYLE 1934; DALLIMORE & JACKSON 1966; KRÜSSMANN 1983; ECKENWALDER 2009; FARJON 2005, 2010; JAGEL & DÖRKEN 2015b; DÖRKEN & JAGEL 2017; DÖRKEN & NIMSCH 2019) and therefore often referred to and given the term "columella" (DOYLE 1934; KRÜSSMANN 1983; JAGEL 2002; ECKENWALDER 2009; FARJON 2005, 2010; JAGEL & DÖRKEN 2015b). However, previously this term was not defined precisely enough so that even the three central, apical lobes in *Fitzroya* seed cones (Fig. 6F) were frequently described as a columella, de-

spite their highly controversial identity. They were described previously as resin glands (JACKSON 1946; KRÜSSMANN 1955; DEN OUDEN & BOOM 1965; DALLIMORE & JACKSON 1966; FARJON 2010) or even as naked nucelli (SAHNI & SINGH 1931). However, ontogenetic and morpho-anatomical studies (JAGEL 2002; JAGEL & DÖRKEN 2015a; DÖRKEN & JAGEL 2017) have shown that they represent a distal, strongly reduced whorl of sterile cone scales, and the term *columella* being inappropriate. DÖRKEN & JAGEL (2017) therefore suggested that the term *columella* should be only used for seed cone apices that exclusively represent the elongated tip of the cone axis, given that it does not reach the periphery of the seed cone and does not take part in its formation. However, according to this new definition, the *columella* is no longer a feature restricted exclusively to callitroid Cupressaceae, but occurring also in this respect in some cupressoid Cupressaceae, including *Cupressus* (Fig. 6A) and *Thujaopsis* (DÖRKEN & JAGEL 2017).

### 2.1.2 Homologies within coniferous cone scale complexes

Only within seed cones of Pinaceae (Figs. 3; 17; 18) and Sciadopityaceae (Fig. 31), bract and seed scales are still visible as two distinct structures even at maturity (FLORIN, 1951; DALLIMORE & JACKSON 1966; KRÜSSMANN 1983; TAKASO & TOMLINSON 1991; MUNDY, 2000; FARJON 2010; DÖRKEN & NIMSCH 2019). In other extant conifers, including Araucariaceae (Fig. 24) and Cupressaceae (Figs. 5; 6; 7; 38; 40C-F), the bract/seed scale complex became strongly modified so that seed cones consist of only one type of cone scale (PAGE 1990; GADEK et al. 2000; JAGEL & STÜTZEL 2001a, b; SCHULZ & STÜTZEL 2007; DÖRKEN 2011; JAGEL & DÖRKEN 2014, 2015a, b; DÖRKEN et al. 2017b; DÖRKEN & RUDALL 2019). However, these cone scales are of different origin to the previous type and are therefore not homologous throughout the conifers.

For example within Araucariaceae (Figs. 24E-F) the bract and seed scales are fused and form a common cone scale, with the lower side formed by bract scale tissue and the upper one by seed scale tissue (COULTER & CHAMBERLAIN 1917; JAGEL & DÖRKEN 2014; DÖRKEN & RUDALL 2019). However, compared to Araucariaceae, in Cupressaceae the situation is more complex. In the cupressaceous subfamilies Taiwanioidae and

Sequoioidae (Figs. 7C & D) no vegetative parts of the seed scale are visible, either at pollination time or at maturity, and ovules are always non-axillary and developed in basal parts on the upper surface of the cone scale. Thus, it seems that the basal, adaxial part of the cone scale up to the point where ovules are inserted is formed by the seed scale, which is adnate or congenitally fused to the bract scale (JAGEL 2002; SCHULZ & STÜTZEL 2007; DÖRKEN 2011; JAGEL & DÖRKEN 2014). However, within the cupressaceous subfamily Cunninghamioidae, there are 2-3 adaxial teeth-like bulges in basal parts of the cone scale (Figs. 7A & B). Each of these bulges carries an ovule, a situation that is comparable to Sciadopityaceae, but unlike Taiwanioidae and Sequoioidae. Within Cunninghamioidae these bulges are only visible in earliest ontogenetic stages and are assumed to be vegetative parts of the seed scale which are fused in a recaulescent way to the bract scale (JAGEL 2002; SCHULZ & STÜTZEL 2007; JAGEL & DÖRKEN 2014). Within the cupressaceous subfamily Taxodioidae, that includes the genera *Cryptomeria* (Figs. 8A-D), *Glyptostrobus* (Fig. 8E) and *Taxodium* (Fig. 8F), teeth-like structures are also developed below the ovules. However, unlike Cunninghamioidae, ovules are always inserted in an axillary position and the number of ovules and teeth seems not to be correlated (TAKASO & TOMLINSON 1990; JAGEL 2002; SCHULZ & STÜTZEL 2007; JAGEL & DÖRKEN 2014; DÖRKEN & RUDALL 2018). Additionally, the teeth are also visible at maturity, significantly exceed the cone scales (Figs. 8 A, B, E, F) and help to close the maturing seed cone (KRÜSSMANN 1983; JAGEL 2002; ECKENWALDER 2009; FARJON 2010; JAGEL & DÖRKEN 2014; DÖRKEN & RUDALL 2018). However, more importantly, within Taxodioidae the teeth below the ovules are always developed later than the ovules (TAKASO & TOMLINSON 1990; JAGEL 2002; JAGEL & DÖRKEN 2014; DÖRKEN & RUDALL 2018). DÖRKEN & RUDALL (2018) who investigated teratological seed cones of *Glyptostrobus*, with anomalous vegetative proliferated teeth, could clearly show that within the axil of the cone scale two axillary shoots are inserted. Thus, the cone scale complex of Taxodioidae consists of a bract, which forms the visible cone scale that is carrying two descending axillary accessory shoots (= seed scales). The one that is distant from the cone scale is developed first. It is fertile and always strongly reduced, so that only its ovules remain,

usually without any visible vegetative parts of the seed scale. The second lowest seed scale, which is inserted in the axil of the cone scale, is developed later. It is sterile and forms the teeth (DÖRKEN & RUDALL 2018). This explains the axillary position of ovules in Taxodioideae, which is unlike to all other early-divergent Cupressaceae (including the subfamilies Cunninghamioideae, Athrotaxoideae, Taiwanoideae, Sequoioideae and Taxodioideae) (DÖRKEN & RUDALL 2018). Within these cupressaceous subfamilies ovules are non-axillary and inserted on the adaxial surface of the cone scale (JAGEL 2002; JAGEL & DÖRKEN 2015a, b; DÖRKEN et al. 2017b). Thus, Cunninghamioideae and Taxodioideae differ significantly from each other. In Cunninghamioideae there is just one fertile seed scale per cone scale complex, which's vegetative parts are visible as adaxial, ovule carrying teeth in basal parts of the cone scale (SCHULZ & STÜTZEL 2007; JAGEL & DÖRKEN 2014).

Within sequoioid, cupressoid and callitroid Cupressaceae the number of ovuliferous rows and the total number of ovules per cone scale as well is markedly increased compared to the rest of the Cupressaceae and all other conifers as well. In some *Cupressus* (Figs. 7E & F) and *Callitris* species there are up to four ovuliferous rows per cone scale (DÖRKEN 2011; DÖRKEN & JAGEL 2014, 2017; JAGEL & DÖRKEN 2015a, b). The rows are developed in a centrifugally developmental sequence, so that the one which is most distant from the cone scale is developed first (JAGEL 2002; DÖRKEN 2011; DÖRKEN & JAGEL 2014, 2017; JAGEL & DÖRKEN 2015a, b). Each row is supposed to represent a strongly reduced ovuliferous short shoot (= seed scale) being reduced entirely to the ovules. Thus, these cone scale complexes consist of a bract which forms the visible cone scale and carries several axillary descending ovuliferous short shoots, which are, however, being reduced entirely to their ovules (JAGEL 2002; DÖRKEN 2011; DÖRKEN & JAGEL 2014, 2017; JAGEL & DÖRKEN 2015a, b). This is a simple, but very efficient way to increase the total number of ovules per seed cone, in this case without the need to form larger cones and without high investments in the seed cone biomass, as it would be needed when only one (Araucariaceae) or two (Pinaceae) ovules per cone scale occur. The small seed size, typical for most Cupressaceae, is also advantageous in this respect.

To summarize, in conifers showing only one type of cone scale, the scale is not a homologous structure throughout. It can represent either an aggregation of the bract and seed scale with different degrees of fusion or it represents just the bract scale, with the seed scale being reduced entirely to its ovules.

### 2.1.3 Conclusions

Coniferous seed cones are strongly reduced and compact inflorescences throughout the entire group. Most coniferous seed cones are characterized by the presence of the so-called bract/seed scale complex, with the bract scale representing a leaf, which carries an axillary fertile short shoot – the seed scale. Only in Pinaceae and Sciadopyaceae both types of cone scales are visible as two distinct structures even at maturity. In numerous conifers only one type of cone scale is developed, which, however, is not homologous throughout the different groups. In Araucariaceae and most of the early divergent Cupressaceae bract and seed scale are congenitally fused and form a common cone scale. However, in Cupressaceae s. str. (subfamilies Cupressoideae and Callitroideae) the seed scale is reduced entirely to its ovules and the visible cone scale is represented exclusively by the bract scale.

In numerous sequoioid, cupressoid and callitroid Cupressaceae several ovuliferous rows are formed in a centrifugally developmental sequence per cone scale complex. Each row is assumed to represent a fertile, descending accessory shoot being reduced entirely to its ovules. This leads to a distinctly increased number of ovules per cone scale and represents an efficient way to increase the total number of ovules per seed cone without the need of increasing the overall cone size and without significantly increased investments into seed cone biomass. In this respect, also the small size of mature seeds is of relevance.

In numerous conifers, the basal- and distal-most cone scales are sterile and only those in the middle of the cone are fertile. However, within Cupressaceae there is a strong tendency to shift the fertile zone into apical parts of the seed cone and to reduce sterile distal elements, so that in several modern-most cupressoid and all callitroid Cupressaceae only the apex of the cone axis remains visible as a distinct spine-like columnella and all apical cone scales are fertile. Thus,

in several Cupressoideae and all Callitroideae ovules are in an apically dense arrangement in more or less the same plane. This arrangement allows a free exposure of pollination drops to the ambient airflow. Furthermore it favors the fusion of pollination drops of neighbouring ovules into a common larger one, which is advantageous in the pollination process, in particular in respect to pollen capture. These important improvements in the pollination process seem to be more relevant, than a reduced seed cone biomass, which is assumed to play a subordinate role in that respect.

## 2.2 The general structure of coniferous pollen cones

Compared to seed cones, for pollen cones, their ontogeny and morphogenesis as well as their evolution are significantly less well investigated. This seems mainly caused by the limited availability of research material, which is only available for a very short seasonal period. Mature pollen cones dry out and are abscised or disintegrate. Additionally, pollen cones of all conifers are non-woody structures. Thus, it is not astonishing that they are less well documented in the fossil record, compared to the seed cones, which are all more or less woody. Another problem is that decisive developmental steps already take place long before any visible external signs. A major problem for suggesting the evolutionary pathway for the coniferous pollen cones is that within a genus they are more or less uniformly shaped, and have the same basic structure.

In most extant conifers, they are uniaxial, simple "flower"-like structures with lateral, non-axillary hyposporangiate microsporangiophores (Figs. 9A-C; 22A-C; 25B, C, F; 30D & E; 41; 42) (e.g. KRÜSSMANN 1955, 1983; DALLIMORE & JACKSON 1966; GIFFORD & FOSTER 1989; ECKENWALDER 2009; FARJON 2010). Compound, polyaxial, "inflorescence"-like pollen cones are and only developed with some Podocarpaceae (Figs. 2B; 30A-C), Taxaceae (Fig. 37) and *Sciadopitys* (Fig. 32). The structural diversity among Taxaceae with either simple, uniaxial e.g. *Taxus* (Figs. 36A & B) and *Torreya* (Figs. 36D-F) or compound, polyaxial pollen cones e.g. *Cephalotaxus* (Figs. 37D-F) and *Pseudotaxus* (Figs. 37A-C) and the occurrence of two types of microsporangiophores (hyposporangiate and perisporangiate) is unique among ex-

tant conifers (e.g. WORDSELL 1901; DUPLER 1919; DLUHOSCH 1937; THOMSON 1940; NOZERAN 1955; WILDE 1975; MUNDRY & MUNDRY 2001; SCHULZ et al. 2014; DÖRKEN & NIMSCH 2016).

The hyposporangiate type (Figs. 9A-C) consists of a central stalk, a phylloid-like scutellum, which is species-specifically developed either adaxial or has a peltate-like shape. Microsporangia are developed exclusively adaxial at the stalk. The hyposporangiate microsporangiophores of all conifers are supplied by a single collateral vascular bundle strand, with xylem towards adaxial and phloem towards abaxial. A bundle sheath surrounding the vascular bundle strand and a cambium separating xylem and phloem is absent. The perisporangiate type of microsporangiophores (Figs. 9D-F) has a radial structure, with a peltate scutellum and microsporangia inserted all around the stalk. The perisporangiate microsporangiophore is always supplied with several (2-4) collateral vascular bundle strands (Fig. 9), which leave the concentric stem bundle of the pollen cone axis in separate strands. A bundle sheath and a cambium separating xylem and phloem is also not developed.

Due to their high structural diversity, Taxaceae seem to be a good starting point for investigations leading to new insights into structure and evolution of coniferous pollen cones, in particular, to answer the question whether the simple, uniaxial structure developed within the majority of extant conifers might be derived from an ancestral compound, polyaxial one. Additionally the origin and the identity of the microsporangiophores, are still controversial and two major conflicting evolutionary concepts exist: (1.) All coniferous microsporangiophores are homologous structures; the hyposporangiate (dorsiventral) type is derived from a perisporangiate (radial) ancestral condition (e.g. WORDSELL 1901; DUPLER 1919; DLUHOSCH 1937); (2.) The perisporangiate type is derived from a radial syngonium consisting of several dorsiventral reduced and fused microsporangiophores (e.g. THOMSON 1940; WILDE 1975; MUNDRY & MUNDRY 2001; DÖRKEN et al. 2011; DÖRKEN & NIMSCH 2016). The coniferous microsporangiophores are widely accepted as pollen producing leaves in the sense of a microsporophyll. However, the axillary position of the perisporangiate microsporangiophores in *Pseudotaxus* definitively excludes this and points towards a much more complex identity of this structure (MUNDRY & MUNDRY 2001; DÖRKEN

et al. 2011). Thus, detailed morpho-anatomical studies on Taxaceae are needed which are then correlated with data from other coniferous groups as one of the best ways to get new insights into the overall structure and the evolutionary pathway of coniferous pollen cones. As shown in the brief discussion above huge gaps in our knowledge of staminate reproductive structures of conifers still exist today.

### 2.2.1 Correlation between the number of pollen cones per tree, microsporangiophores per pollen cone and microsporangia per microsporangiophore

Within extant conifers, the number of the traits above varies strongly (PAGE 1990; MUNDRY 2000; FARJON 2005, 2010; ECKENWALDER 2009; SCHULZ et al. 2014; DÖRKEN et al. 2017a). However, their quantity appears to be distinctly correlated and different strategies are realized to produce high amounts of pollen per tree.

Due to the fact that nearly all conifers, except the majority of Gnetales, are wind-pollinated (NIKLAS 1982, 1984; OWENS et al. 1998; SCHWENDEMANN et al. 2007; DÖRKEN & JAGEL 2014) the amount of pollen that is needed for a successful pollination is much higher compared to insect-pollinated taxa (FRIEDMAN & BARRETT 2009; MANGLA & TANDON 2014), because the anemophily syndrome excludes a precise deposition of pollen only on the female receptive structures. In consequence, enormous amounts of pollen get lost, unlike the condition within insect-pollinated taxa (MANGLA & TANDON 2014). Within conifers two major strategies are realized to achieve a maximum in pollen production per tree: (1.) If the pollen cones are small with only a low number of microsporangiophores which have a low number of microsporangia, the total number of pollen cones per tree is high (common case within conifers); (2.) If the pollen cones are large with a high number of microsporangiophores which have a high number of microsporangia, the total number of pollen cones per tree is low, as in all Araucariaceae and a few Pinaceae (SCHULZ et al. 2014; DÖRKEN & NIMSCH 2015a). In most cases the certain same strategy is realized throughout the entire family (SCHULZ et al. 2014; DÖRKEN 2019a). For example, in Arau-

cariaceae the number of pollen cones per tree is significantly less compared to other conifers. However, here the pollen cones are large with several hundred microsporangiophores (Figs. 25A, D, E), each with up to 20 or even more microsporangia (Figs. 25B, C, F), which is the highest number within extant conifers (FARJON 2005, 2010; ECKENWALDER 2009; SCHULZ et al. 2014; DÖRKEN & RUDALL 2019). Compared to Araucariaceae, in nearly all other conifers the total number of pollen cones per tree is significantly higher. However, their pollen cones are quite small and contain a significantly lower number of microsporangiophores, each carrying a markedly lower number of microsporangia, for example just two per microsporangiophore in Pinaceae (Figs. 22A-C), Podocarpaceae (Fig. 30D), Sciadopityaceae (Fig. 32E) and some early-divergent Cupressaceae (COULTER & CHAMBERLAIN 1917; SPORNE 1965; MUNDRY 2000; FARJON 2010; DÖRKEN & NIMSCH 2015a; DÖRKEN 2017).

However, within the pinaceous taxa *Cedrus* (Figs. 21C; 46A) and *Cathaya* (Fig. 21A) the number of pollen cones per tree is significantly lower compared to all other Pinaceae, but they are much bigger in size and comprise a high number of microsporangiophores per pollen cone, in both cases over one hundred (DÖRKEN & NIMSCH 2015a). The number of microsporangia per microsporangiophore is, however, not increased, still being two as is the typical family trait (DÖRKEN & NIMSCH 2015a). In this case a maximum in pollen production per tree is achieved not by increasing the number of pollen cones or microsporangia but by increasing the pollen cone size and the number of inserted microsporangiophores.

Within *Juniperus* (cupressoid Cupressaceae) it is assumed that the formation of pollen cones in distal clusters, as in *Juniperus drupacea* (Fig. 12), led to a strongly reduced total number of pollen cones and in consequence to a reduced total amount of pollen produced per tree. In contrast to Pinaceae, in *Juniperus drupacea* the reduction of the pollen cone number per tree is not compensated by larger pollen cones, but by higher number of microsporangia per microsporangiophore, which are developed in up to three abaxial rows. Within all other *Juniperus* species the pollen cone size is more or less similar to a single pollen cone within the *Juniperus drupacea* pollen cone cluster. However, their pollen cones are inserted either axillary (*Juniperus* Section *Ju-*



*niperus*) or terminal (*Juniperus* Section *Sabina*) on lateral shoots. In contrast to the *Juniperus drupacea* pollen cone clusters they are developed in a high quantity, with microsporangia inserted on the microsporangioophores mostly in only a single abaxial row (ECKENWALDER 2009; FARJON 2010; DÖRKEN 2019a). Thus, within *Juniperus* two strategies are realized to increase pollen production: (1.) Low number of pollen cones per tree, but an increased number of microsporangia per microsporangioophore (e.g. *Juniperus drupacea*); (2.) High number of pollen cones per tree, without increased number of microsporangia per microsporangioophore (majority of all other *Juniperus* species).

However, at present, there is still a huge lack of statistical data about the total number of pollen cones, microsporangioophores, microsporangia, and in particular the total amount of pollen produced per tree, which would be needed to get further insights into the correlations existing between these traits.

### 2.2.2 Branching pattern in coniferous pollen cones

The coniferous pollen cones are genus-specifically either simple uniaxial (Figs. 21; 22A & B; 25A, D, E) or compound polyaxial (Figs. 2B & D; 30A-C; 32; 37) (LEMOINE-SEBASTIAN 1967; WILDE 1975; PAGE 1990; MUNDRY & MUNDRY 2001; DÖRKEN et al. 2011; SCHULZ et al. 2014; DÖRKEN & NIMSCH 2016; DÖRKEN & RUDALL 2019; DÖRKEN 2019a, b). Among extant conifers compound inflorescence-like pollen cones are rare and are only developed within some Taxaceae (Fig. 37), Podocarpaceae (Figs. 2B; 30A-C) and Sciadopityaceae (Fig. 32) (WILDE 1975; MUNDRY & MUNDRY 2001; DÖRKEN et al. 2011; SCHULZ et al. 2014; DÖRKEN & NIMSCH 2016; DÖRKEN 2019a). The dimensions of the subunits within these polyaxial pollen cones show genus-specific enormous variations, but they can be classified into two major groups: (1.) Open and loose; each axillary subunit represents a pollen cone with an elongated cone axis carrying several microsporangioophores, including examples like *Cephalotaxus* (Taxaceae) (Figs. 37D-F) and *Podocarpus* (Podocarpaceae) (Figs. 2B; 30A-C); (2.) Dense and compact-globose; each subunit is strongly reduced to a single axillary, short-stalked perisporangiate microsporangioophore, including examples like *Pseudotaxus* (Taxaceae) (Figs.

37A-C). Within both types the shoot apex of the inflorescence is exhausted entirely while forming either a terminal pollen cone (*Cephalotaxus*, *Sciadopitys* and *Podocarpus*) or a single perisporangiate microsporangioophore (*Pseudotaxus*). This clearly distinguishes these compound structures from inflorescence-like apical pollen cone clusters like those found in a few Cupressaceae, including *Cunninghamia* (Cunninghamioideae) (Figs. 43A-C), *Taiwania* (Taiwanioidae) (Figs. 43D-F) and *Juniperus drupacea* (*Juniperus* Section *Caryocedrus*, Cupressoideae) (Fig. 12) (KRÜSSMANN 1983; ECKENWALDER 2009; FARJON 2010, SCHULZ et al. 2014). Within such apical pollen cone clusters, the shoot apex is not exhausted by a terminal pollen cone and remains visible as a terminal bulge (DÖRKEN 2019a). However, to distinguish between a polyaxial, compound structure, in the sense of a true inflorescence and an apical pollen cone cluster, consisting of “just” densely arranged simple pollen cones, is often difficult. These difficulties are demonstrated best within the monotypic *Juniperus* Section *Caryocedrus*, which is sister to *Juniperus* Section *Juniperus* (MAO et al. 2010; ADAMS et al. 2013). At first glance, the distal pollen cone clusters of *Juniperus drupacea* appear quite similar to the inflorescences of *Cephalotaxus* (Figs. 37D-E). This impression is supported by the fact that in *Juniperus drupacea* the shoot apex does not proliferate in the next season, and the pollen cones and the distal-most parts of the shoot axis dry out after pollen release. This is unlike pollen cone clusters of other conifers, including *Cunninghamia* (Fig. 43C), which usually proliferate in the next season (SCHULZ et al. 2014; DÖRKEN 2019a). The absence of a terminal pollen cone/microsporangioophore distinguishes such pollen cone clusters distinctly from the polyaxial inflorescences as developed within *Cephalotaxus* (Figs. 37D-E), *Pseudotaxus* (Figs. 37A-C), *Sciadopitys* (Fig. 32) and *Podocarpus* (Fig. 2A; 30A-C) (MUNDRY 2000; MUNDRY & MUNDRY 2001; DÖRKEN et al. 2011; DÖRKEN & NIMSCH 2016).

It has been shown that the inflorescence-like pollen cone cluster of *Juniperus drupacea* is probably derived from an ancestral condition as it is still represented in all taxa of *Juniperus* Section *Juniperus*, with uniaxial, axillary pollen cones usually developed in lower parts on lateral shoots (Fig. 12A) (DÖRKEN 2019a). Beginning with this condition only few steps are needed to form the

*Juniperus drupacea* pollen cone cluster, including a shift of the fertile zone into distal-most parts on the shoot axis (Fig. 12B) and a profound reduction of the distal internodes and the bracts (Fig. 12C) (DÖRKEN 2019a). This novel interpretation is very surprising insofar as *Juniperus drupacea* is the earliest-divergent taxon within this genus (ADAMS & DEMEKE 1993; DÖRKEN 2019a). Thus, it could be expected that the species would still reflect the primitive condition of this genus and not derived ones. The selection pathways leading to the formation of pollen cone clusters in *Juniperus drupacea*, however, still remain open to question. Possible advantages within the pollination process, including a better exposure of the pollen cones to the wind, might be one of the driving forces. Within *Juniperus drupacea* as part of forming the pollen cone clusters, a decrease in the total number of pollen cones and the total amount of pollen produced per tree is assumed. In this case the arrangement of pollen cones in distal clusters represents a distinct trade-off, which strongly influences the ratio between the total number of pollen cones and the total amount of pollen produced per tree. However, the strongly increased number of microsporangia per microsporangium may compensate for the reduced total number of pollen cones and pollen per tree (DÖRKEN 2019a). Depending on these results it is assumed that within *Juniperus* the simple, uniaxial pollen cone structure reflects the primitive condition.

However, within other conifers, including Taxaceae, the evolutionary pathway of staminate reproductive structures seems to be completely inverse to that. Within Taxaceae the simple, uniaxial pollen cone structure is regarded as being derived from an ancestral compound, polyaxial inflorescence. Different evolutionary concepts (Fig. 13) are suggested, that can explain the simple, flower-like structure of *Taxus* and *Torreya* as derived from a compound polyaxial *Cephalotaxus*-like inflorescence. Within the first evolutionary concept (Fig. 13A) the *Torreya* pollen cone is regarded as the final link of the following transitional series: *Cephalotaxus* → *Pseudotaxus* → *Taxus* → *Torreya* (MUNDRY & MUNDRY 2001; DÖRKEN et al. 2011; DÖRKEN & NIMSCH 2016).

Within the *Cephalotaxus* inflorescence each subunit (= lateral pollen cone) is inserted in the axil of a bract and consists of several lateral hyposporangiate microsporangia and a termi-

nal perisporangiate one. The *Pseudotaxus* pollen cone – a compact inflorescence that comprises several perisporangiate microsporangia, each lateral microsporangium is inserted in the axil of a bract – is assumed to be derived from a loose *Cephalotaxus*-like ancestral condition by reductions of all lateral hyposporangiate microsporangia and profound shortening of the cone axis, so that finally each lateral subunit within the *Cephalotaxus* inflorescence is reduced to the single, terminal perisporangiate microsporangium. A simple reduction of the bracts leads to a pollen cone structure typical for *Taxus* – a compact cone with non-axillary, perisporangiate microsporangia. When the adaxial microsporangia within the lateral perisporangiate microsporangia of *Taxus* get reduced the *Torreya* pollen cone is formed – a uniaxial pollen cone consisting of several lateral hyposporangiate microsporangia and a terminal perisporangiate one. In this case, the perisporangiate microsporangia of *Pseudotaxus* and *Taxus* are homologous to a lateral subunit within the *Cephalotaxus* inflorescence, which became reduced to the terminal perisporangiate microsporangium. This evolutionary concept is supported by the fact that the number of perisporangiate microsporangia in *Pseudotaxus* and *Taxus* corresponds perfectly to the number of subunits within the *Cephalotaxus* inflorescence (DÖRKEN & NIMSCH 2016).

However, the number of lateral, hyposporangiate microsporangia within *Torreya* pollen cones significantly exceeds the number of perisporangiate microsporangia within *Pseudotaxus* and *Taxus* (ECKENWALDER 2009; FARJON 2010; DÖRKEN & NIMSCH 2016). This might argue against a derivation of *Torreya* from an ancestral *Taxus*-like condition. Thus, a second scenario could be suggested with two different evolutionary lineages leading independently from each other towards a uniaxial pollen cone structure (Fig. 13B). Both lineages start with a compound, polyaxial pollen cone structure: (1.) *Cephalotaxus* → *Pseudotaxus* → *Taxus*; (2.) *Cephalotaxus* → *Torreya*. Also, as part of this concept, the simple, uniaxial pollen cone structure of *Taxus* and *Torreya* is assumed to be derived from an ancestral compound *Cephalotaxus*-like structure as was suggested by MUNDRY & MUNDRY (2001) and DÖRKEN et al. (2011). However, with this scenario, the simple *Torreya* pollen cone structure is

regarded as derived without transitional stages from a *Cephalotaxus*-like inflorescence, by reducing all lateral subunits so that finally only the terminal one remains. This is the shortest and at first glance the easiest way to evolve the simple *Torreya* pollen cone structure (WILDE 1975). However, *Torreya* pollen cones and subunits within the *Cephalotaxus* inflorescences show distinct differences, including a different size and shape of their primordia and differences in the orientation of microsporangia. These differences strongly argue against a homology of the *Torreya* pollen cone and the terminal subunit within the *Cephalotaxus* inflorescence. According to MUNDY & MUNDY (2001) the primordia of the entire *Cephalotaxus* inflorescence are broad and dome-shaped, while the primordia of its subunits, however, quite small. If *Torreya* pollen cones and the terminal subunit of *Cephalotaxus* inflorescence are homologous, for both a small apex would be expected. However, *Torreya* pollen cones have broad primordia. Their dimensions are similar to the primordia of the entire compound *Cephalotaxus* inflorescence, but also to those of *Taxus* pollen cones. The broad primordium in *Taxus* can be explained by a derivation of the simple *Taxus* pollen cone structure from a *Cephalotaxus*-like ancestral condition. The broad primordium in *Torreya* is explained best by regarding *Torreya* pollen cones as derived from an ancestral *Taxus*-like condition, by a simple reduction of adaxial microsporangia (MUNDY & MUNDY 2001; DÖRKEN et al. 2011; DÖRKEN & NIMSCH 2016). This scenario is strongly supported by the fact that the perisporangiate microsporangioophores of *Taxus* and the hyposporangiate microsporangioophores of *Torreya* are located parallel to the stalk of the microsporangioophore, while in *Cephalotaxus*, they spread vertically from the stalk at more or less a right angle (MUNDY & MUNDY 2001). Summarizing this, it seems most likely that *Torreya* pollen cones and the terminal subunit within *Cephalotaxus* inflorescences are not homologous structures as suggested by WILDE (1975), and the evolutionary pathway *Cephalotaxus* → *Pseudotaxus* → *Taxus* → *Torreya* as suggested by MUNDY & MUNDY (2001), DÖRKEN et al. (2011) and DÖRKEN & NIMSCH (2016) seems to be the most likely one.

In summary, it seems that within conifers, different evolutionary pathways of male reproductive structures were realized – in Taxaceae from compound, polyaxial inflorescences to simple,

uniaxial pollen cones, in Cupressaceae from simple, uniaxial, pollen cones to inflorescence-like, apical pollen cone clusters.

If the simple, uniaxial pollen cone structure of other coniferous taxa e.g. Pinaceae, Cupressaceae or Araucariaceae could be also derived from a former compound, polyaxial inflorescence as is assumed for Taxaceae remains, however, still an open question (DÖRKEN 2017; DÖRKEN & STÜTZEL 2019).

### 2.2.3 The origin of perisporangiate microsporangioophores

Among extant conifers two types of microsporangioophores exist (Fig. 9). The hyposporangiate, dorsiventral type (Figs. 9A-C) is the most common one. It consists of a central stalk, abaxial microsporangia and a distal phylloid-like scutellum (e.g. PILGER 1926; DALLIMORE & JACKSON 1966; KRÜSSMANN 1955, 1983; PAGE 1990; ECKENWALDER 2009; FARJON 2005, 2010; DÖRKEN 2017). The perisporangiate, radial type (Figs. 9D-F) is rare and can be found only among extant Taxaceae. It consists of several microsporangia which are arranged all around the central stalk (WILDE 1975; MUNDY & MUNDY 2001; DÖRKEN et al. 2011; SCHULZ et al. 2014; DÖRKEN & NIMSCH 2016). Within a pollen cone usually only one type of microsporangioophore is developed (Figs. 9B-C; 22A & B; 30A, B, D, E) (PILGER 1926; DALLIMORE & JACKSON 1966; KRÜSSMANN 1955, 1983; PAGE 1990; ECKENWALDER 2009; FARJON 2005, 2010; DÖRKEN 2017). In this respect pollen cones of *Cephalotaxus* (Figs. 37E & F) and *Torreya* (Figs. 10; 36E & F) are remarkable because they comprise both types of microsporangioophores within the same cone, the lateral ones are hyposporangiate, the terminal one is perisporangiate (MUNDY 2000; MUNDY & MUNDY 2001; DÖRKEN et al. 2011; DÖRKEN & NIMSCH 2016).

The coniferous microsporangioophore is widely accepted as a pollen producing leaf in the sense of a microsporophyll (e.g. LOTSY 1911; COULTER & CHAMBERLAIN 1917; KRÜSSMANN 1955, 1983; SPORNE 1965; DALLIMORE & JACKSON 1966; MIROV 1967; LIU 1971; FARJON 1984, 2005, 2010; PAGE 1990; ECKENWALDER 2009; WILLIAMS 2009). However, the axillary position of the peltate leaf-like, perisporangiate microsporangioophores in *Pseudotaxus* excludes a priori a leaf character for this structure. Additionally, the ontogeny of

perisporangiate microsporangiophores and peltate leaves differs strongly (MUNDRY & MUNDRY 2001). The characteristic developmental steps occurring in the formation of peltate leaves, including meristem incorporation, meristem fusion and the formation of a meristematic cross zone (TROLL 1932; FRANCK 1976; DÖRKEN & PARSONS 2018), are absent in coniferous perisporangiate microsporangiophores (MUNDRY & MUNDRY 2001). Thus, two conflicting theories about the origin of the coniferous microsporangiophores exist: (1.) All coniferous microsporangiophores are homologous structures, and the hyposporangiate type is derived from an ancestral perisporangiate condition (e.g. WORDSELL 1901; DUPLER 1919; DLUHOSCH 1937). (2.) The perisporangiate type represents a radial synangium, consisting of several dorsiventral reduced microsporangiophores (e.g. THOMSON 1940; WILDE 1975; MUNDRY & MUNDRY 2001, DÖRKEN et al. 2011; DÖRKEN & NIMSCH 2016).

In morpho-anatomical investigations on the apical pollen cone structure of *Cephalotaxus* and *Torreya*, several hyposporangiate microsporangiophores were found instead of the “typical” terminal perisporangiate one (Figs. 10 C-E), in *Torreya* in 38% and in *Cephalotaxus* in 37% of the investigated cones (DÖRKEN & NIMSCH 2016). It was clearly shown that the presence or absence of a terminal perisporangiate microsporangiophore is strictly correlated with the diameter of the pollen cone apex. If the apex is small, the primordia of apical hyposporangiate microsporangiophores come into contact and subsequently fuse to form a radial synangium – the perisporangiate microsporangiophore. However, if the pollen cone apex is broad, the primordia of the microsporangiophores are widely separated, which prevents their fusion. Thus, instead of a terminal perisporangiate microsporangiophore several distal hyposporangiate ones are developed. In this case the apex of the cone axis is not exhausted and remains visible even in mature cones. Thus, it is not surprising that the perisporangiate microsporangiophores in *Cephalotaxus* and *Torreya* are always developed terminal at the cone axis (DÖRKEN & NIMSCH 2016).

The interpretation of perisporangiate microsporangiophores as radial synangia is strongly supported by the differences in the vasculature between hypo- and perisporangiate microsporangiophores. The hyposporangiate ones are always

supplied with a single collateral, vascular bundle strand, with xylem located towards the adaxial and phloem towards the abaxial side. However, in the stalk of the perisporangiate ones, 2 to 4 ring-like arranged, collateral vascular bundle strands are developed, which leave the cone axis in separate strands (Fig. 9F). Their xylem poles are pointing towards the center of the stalk. Each of these vascular bundles can be understood as belonging to one of the hyposporangiate microsporangiophores, which are involved in forming the radial synangium (DÖRKEN & NIMSCH 2016).

The idea that the taxaceous perisporangiate microsporangiophores represent radial synangia, is strongly supported by the fact, that within some of the investigated perisporangiate microsporangiophores of *Pseudotaxus* a central “columella”-like structure was found (Figs. 11C-E), which represents the apical meristem of a strongly reduced lateral shoot axis, which is not exhausted, as is the usual case. It remains visible as the central “columella” even at maturity. This lateral shoot axis usually carries two or rarely three hyposporangiate microsporangiophores. As a result of the strongly reduction of the shoot axis, the primordia of these hyposporangiate microsporangiophores come into contact and subsequently fuse to form a radial synangium – the perisporangiate microsporangiophore (DÖRKEN & NIMSCH 2016).

This novel interpretation of the origin of perisporangiate microsporangiophores supports the idea that the perisporangiate lateral microsporangiophores in cones of *Pseudotaxus* and *Taxus* correspond to an entire lateral, but, strongly reduced subunit of the *Cephalotaxus* inflorescence. In *Pseudotaxus* and *Taxus* the axis of the lateral subunits became profoundly reduced, so that the primordia of all hyposporangiate microsporangiophores always get in contact and fuse subsequently (DÖRKEN & NIMSCH 2016). This would explain why the number of perisporangiate microsporangiophores in *Taxus* and *Pseudotaxus* is identical to the number of subunits in the *Cephalotaxus* inflorescence and why these perisporangiate microsporangiophores are always supplied with several vascular bundle strands (DÖRKEN & NIMSCH 2016).

In summary, among extant conifers, only one basic type of microsporangiophores exists – the dorsiventral, hyposporangiate one. The radial, perisporangiate type does not reflect a second basic microsporangiophore type, but is a fusion

product of several hyposporangiate microsporangiophores.

## 2.2.4 The identity of coniferous microsporangiophores

Since it has been shown that there is just one basic type of microsporangiophores – the hyposporangiate one, the question about its identity arises. Its non-axillary position and the single collateral vascular bundle strand, strongly point towards a pollen-producing leaf, homologous to a microsporophyll and comparable to sporophylls developed within cycads or higher ferns (SCHULZ et al. 2014). However, microsporophylls of cycads (Fig. 14) differ from those of conifers by representing strongly reduced pinnate leaves with a broad and plain stalk (Figs. 14D-F), which is carrying the microsporangia in abaxial soral clusters (Figs. 14D-F), a feature that can be also found at the fertile fronds of higher ferns (JONES 1993; MUNDY & STÜTZEL 2003; SCHULZ et al. 2014). Thus, it seems that at least for some conifers, in particular conifers with hyposporangiate microsporangiophores with exclusively abaxial microsporangia, the stalk of the microsporangiophores can be interpreted as homologous to sporophylls as they are developed within cycads and higher ferns (SCHULZ et al. 2014).

This leads to the question about the homology of the different parts within the dorsiventral coniferous microsporangiophore and the cycad microsporophyll. At first glance, it seems that within the coniferous microsporangiophore the scutellum corresponds to the lamina, and the stalk to the petiole. However, such homologies are difficult to justify and should be avoided for several reasons, particularly, because sharp borders between scutellum and stalk do not exist (Fig. 16C). Additionally, the size and shape of the distal scutellum vary not only species-specifically, but also even within a single cone (Figs. 15A & C; 41C & D) (SCHULZ et al. 2014; DÖRKEN 2017; DÖRKEN et al. 2017a). Thus, within a microsporangiophore the exact portions of the scutellum and the stalk are difficult to define, as is also the case for the exact border between the stalk and the scutellum. Particularly, in microsporangiophores developed in distal parts of the pollen cones (Figs. 15A & C; 41C & D), the scutellum is strongly reduced or can be entirely lacking (Fig. 15), so that frequently only stalked microsporangia are devel-

oped (Fig. 15) (SCHULZ et al. 2014; DÖRKEN 2017; DÖRKEN et al. 2017a). This clearly indicates that the microsporangia are formed by the stalk of the microsporangiophore and not by the scutellum (SCHULZ et al. 2014; DÖRKEN 2017; DÖRKEN et al. 2017a). This is supported by the fact that the sporogenous tissue gets developed within the earliest ontogenetic stages of the microsporangiophore, even before the scutellum gets differentiated (MUNDY 2000; SCHULZ et al. 2014; DÖRKEN et al. 2017a).

The final position and orientation of the microsporangia vary between species and cones. They are strongly influenced by significant differences existing in spatial and temporal growth patterns occurring in the development of the microsporangiophores (Fig. 16) (MUNDY 2000; SCHULZ et al. 2014; DÖRKEN 2017). Additionally, the size and shape of the distal scutellum has a strong impact on the position and orientation of the microsporangia (MUNDY 2000; SCHULZ et al. 2014; DÖRKEN & NIMSCH 2015b; DÖRKEN 2017). An exclusively adaxial scutellum (Figs. 16A-C) allows microsporangia to be developed even in distal-most parts on the stalk, which can lead to the wrong impression that the scutellum and microsporangia are fused. However, within the investigated pollen cones no evidence was found supporting the idea that the scutellum is responsible for the formation of microsporangia as suggested previously by DLUHOSCH (1937). A peltate-shaped scutellum (Figs. 16D-F), however, enormously obstructs the growth direction of the microsporangia, and prevents from forming of microsporangia in distal-most parts on the stalk. Consequently the scutellum and the microsporangia are developed distantly and microsporangia are attached to the stalk in lower parts towards the pollen cone axis (MUNDY 2000; SCHULZ et al. 2014).

Since it is now known that the stalk is responsible for the formation of microsporangia (DÖRKEN et al. 2017a), at first glance the scutellum is seemingly functionless. However it has been shown that it still serves different important functions, including covering and protecting maturing microsporangia until pollen release (DÖRKEN & NIMSCH 2015a, b), and it also plays a role in the pollen release process (MUNDY 2000; DÖRKEN & NIMSCH 2015a, b; DÖRKEN 2017, 2019b).

## 2.2.5 Conclusions

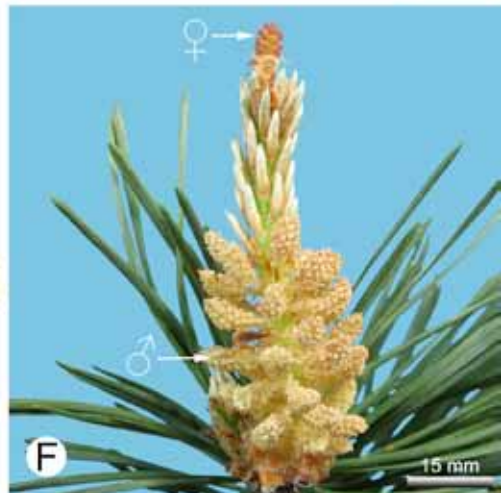
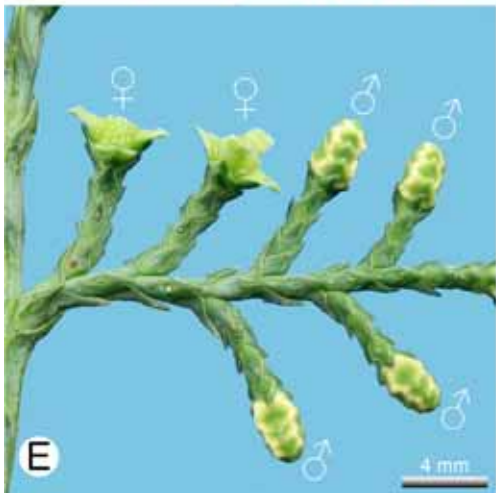
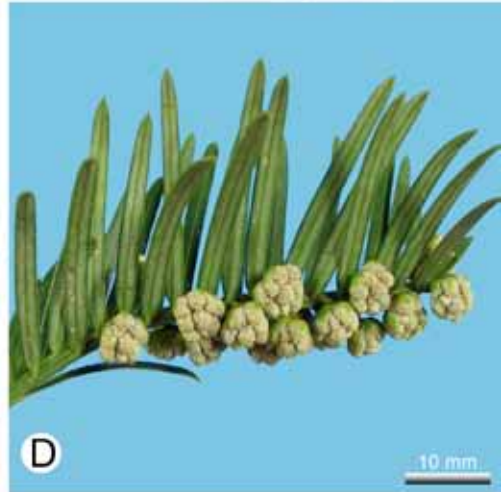
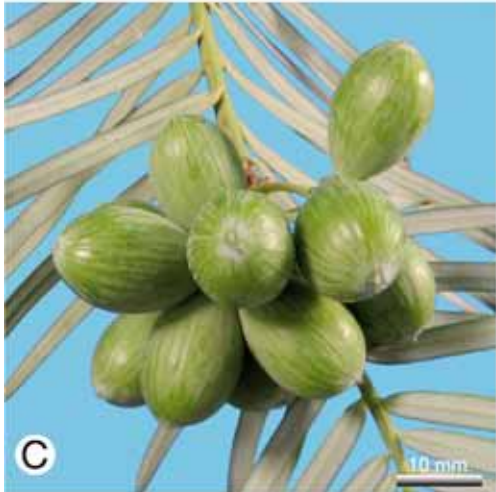
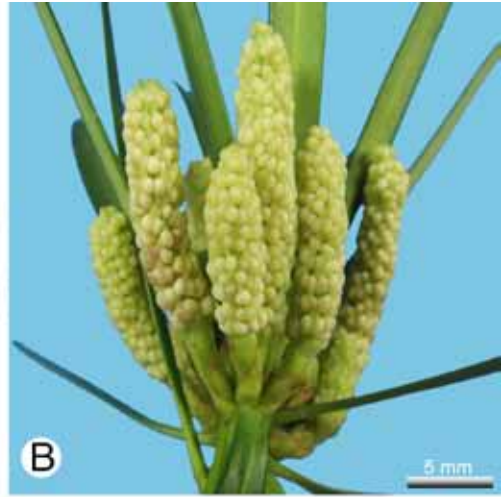
The majority of coniferous pollen cones are uniaxial, simple, “flower-”like structures, polyaxial, compound, “inflorescence-”like ones are rare. Concerning the overall structure of coniferous pollen cones, two major evolutionary trends were found: (1.) Beginning with an ancestral compound inflorescence towards a derived simple, flower-like structure, as is suggested for Taxaceae. Whether such an evolutionary scenario is also realized in other coniferous groups is still open. (2.) Beginning with simple, axillary pollen cones towards distal pollen cone clusters, as is the case in some Cupressaceae. The formation of such pollen cone clusters might be advantageous within the pollination process.

There is a distinct correlation between the number of pollen cones per tree, the number of microsporangiophores per pollen cone and the number of microsporangia per microsporangiophore. A low number of pollen cones per tree leads to the formation of large pollen cones with a high number of multisporangiate microsporangiophores. A high quantity of pollen cones per tree is accompanied by small pollen cones with a distinctly lower number of microsporangiophores

and microsporangia per microsporangiophore. In both cases a high amount of pollen is produced per tree. However, there is still a huge lack of statistical data about these correlations mentioned, which would be needed to get further insights into the correlations existing between these traits.

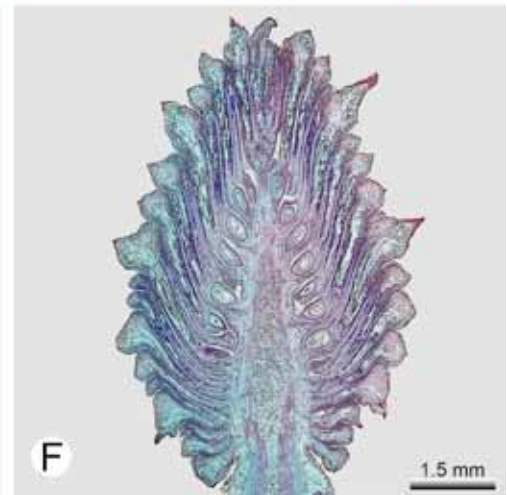
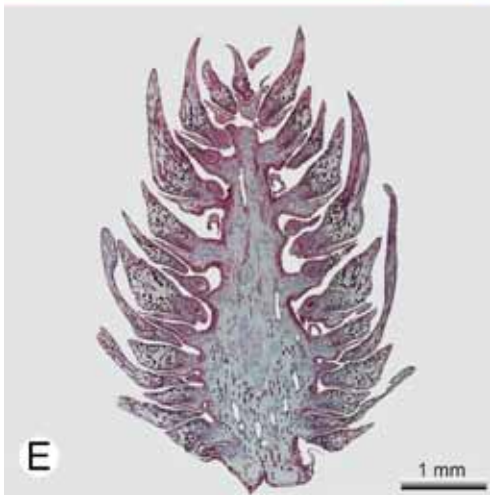
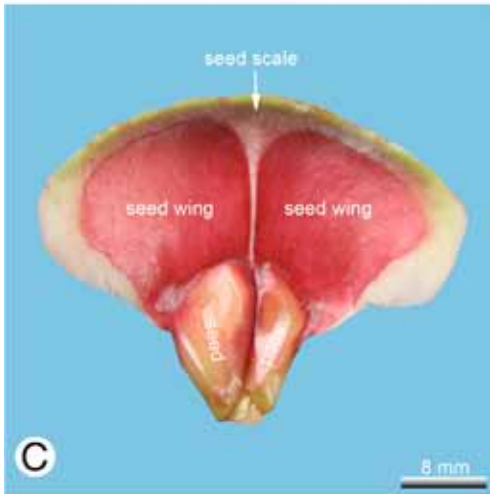
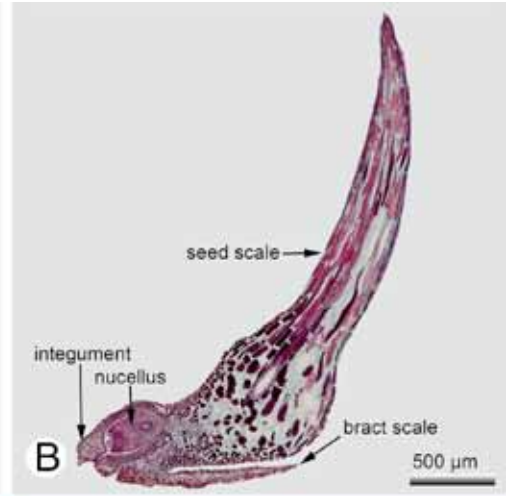
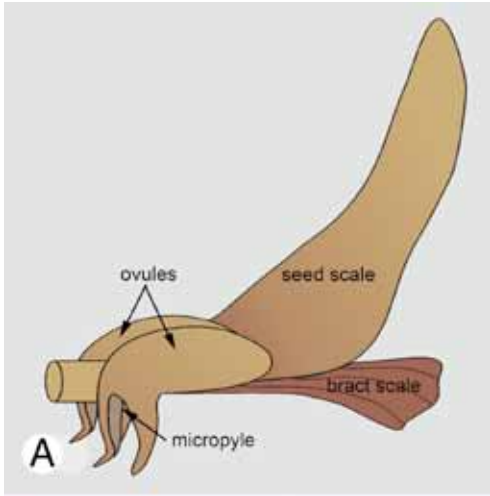
There is just one basic type of microsporangiophore – the hyposporangiate one. The perisporangiate type represents a radial synangium, consisting of several fused hyposporangiate microsporangiophores. The stalk of the microsporangiophore is responsible for the formation of microsporangia and not the scutellum. The insertion and orientation of microsporangia on the stalk of the microsporangiophore is strongly influenced by the size and shape of the terminal scutellum. An exclusively adaxial scutellum allows the formation of microsporangia even in distal-most parts of the stalk, which is obstructed by a peltate scutellum. The dorsiventral, hyposporangiate microsporangiophore or at least its central, microsporangia-bearing stalk, seems to be homologous to a fertile leaf, in the sense of a microsporophyll comparable to the sporophylls among cycads and higher ferns.

**Fig. 2:** Gender distribution in conifers; **A-D:** Dioecy; “female” and “male” reproductive structures occurring on different individuals; **E & F:** Monoecy; “female” and “male” reproductive structures occurring on the same individual; **A & B:** *Podocarpus macrophyllus* (Podocarpaceae); **A:** Fertile branch of a “female” individual with mature seed cones; **B:** Fertile branch of a “male” individual with mature pollen cones; **C & D:** *Cephalotaxus harringtonii* (Taxaceae); **C:** Fertile branch of a “female” individual with mature seed cones; **D:** Fertile branch of a “male” individual with mature pollen cones; **E:** *Cupressus torulosa* (Cupressaceae); fertile branch with pollen and seed cones developed on the same branch; **F:** *Pinus sylvestris* (Pinaceae); cones of both genders develop on the same long shoot; a seed cones in a distal position, the pollen cones in a dense basal cluster.

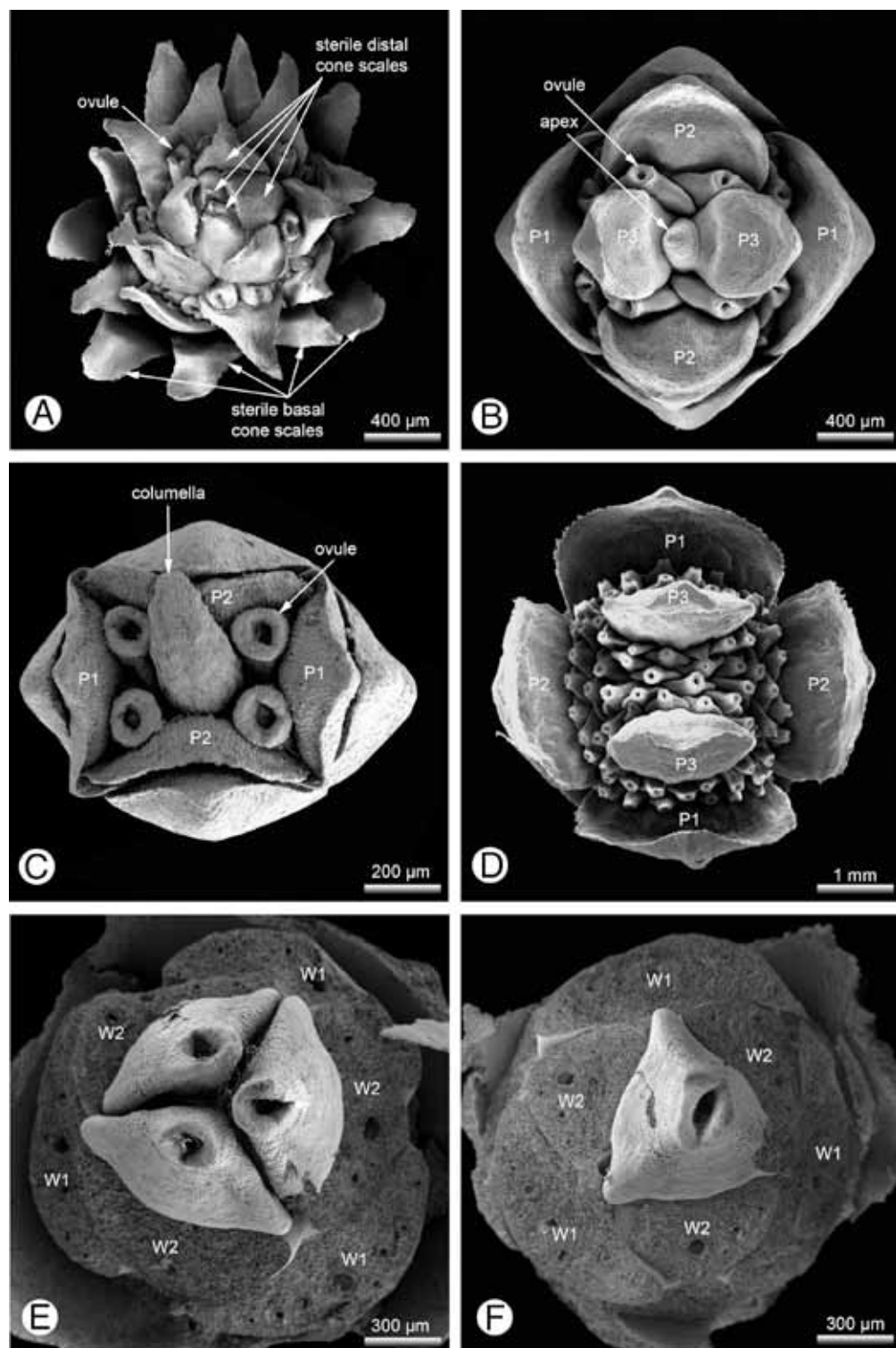


**Fig. 3:** The coniferous bract/seed scale complex; the majority of coniferous seed cones is characterized by the presence of a distinct bract seed scale complex, which however got markedly modified in the different coniferous groups; only in Pinaceae and Sciadopityaceae both are visible as two distinct structures even within mature cones; the bract scale represents a leaf that is carrying an axillary, however, markedly reduced and modified, fertile short shoot (= seed scale); **A:** Schematic drawing of a bract/seed scale complex of *Pinus* (Pinaceae); **B:** *Pinus sylvestris*; longitudinal section of a bract/seed scale complex, shortly after pollination; **C & D:** A single bract/seed scale complex of *Abies alba* (Pinaceae); **C:** Adaxial view; **D:** Abaxial view; **E & F:** Longitudinal section of an entire seed cone of *Pinus sylvestris* in two different ontogenetic stages; **E:** At pollination time; the cone scales are markedly spreading from the cone axis; **F:** After pollination; the cone closes by an excessive growth of the seed scale, that finally markedly exceeds the bract scale.





**Fig. 4:** The distribution of the fertile zone in cupressaceous seed cones; **A-F:** Different types of seed cones at pollination time; **A:** *Taxodium distichum* var. *distichum* (Taxodiaceae) (SEM-image); only the cone scales in the middle of the seed cone are fertile, the basal and distal ones are sterile; **B:** *Chamaecyparis lawsoniana* (Cupressaceae) (SEM-image); the distal pair of cone scale (pair 3) is sterile; it is not entirely separated from the cone axis; these sterile cone scales and the apex of the cone axis form the so-called "sterile terminal piece"; **C:** *Diselma archeri* (Callitricaceae) (SEM-image); all sterile terminal elements, except the apex of the cone axis, entirely reduced; the apex of the cone axis forms a central spine-like structure, the so-called "columella"; **D:** *Cupressus arizonica* (Cupressaceae) (SEM-image); all sterile terminal elements entirely reduced; **E & F:** *Juniperus drupacea* (Cupressaceae) (SEM-images); **E:** All sterile elements reduced; each cone scale bears one ovule; **F:** Non-axillary ovule in a terminal position on the cone axis (P1 = cone scale of pair 1; P2 = cone scale of pair 2; P3 = cone scale of pair 3; W1 = cone scale of whorl 1; W2 = cone scale of whorl 2).



**Fig. 5:** The occurrence of distal sterile elements in seed cones of cupressoid Cupressaceae; within seed cones of several Cupressoideae sterile elements can be found, in most cases consisting of one or rarely two distal pairs of sterile cone scales which are usually not entirely separated from the cone axis and form the so-called “sterile terminal piece”, which is of different shape in the different taxa; **A:** *Platycladus orientalis* (Cupressoideae); mature seed cone; the two sterile terminal cone scales and the apex of the cone axis still visible as two distinct structures; **B-D:** *Chamaecyparis lawsoniana* (Cupressoideae); mature seed cone; the sterile terminal piece is formed by a distal pair of cone scales and the apex of the cone axis, in most cases both are visible as two separate structures, however, they can fuse to a common shield-like structure; **C:** Longitudinal section of a seed cone at pollination time; **D:** Cross section of the distal part showing two sterile, decussate cone scales and the central cone axis; **E & F:** *Calocedrus decurrens* (Cupressoideae); **E:** Mature seed cone; usually a distal pair of sterile cone scales and the cone axis are so markedly fused, that finally a two-dimensional flattened, shield-like terminal piece is formed; **F:** Anomalous shaped terminal piece, showing the central cone axis and two, not entirely separated sterile cone scales.