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Cover photo: Torreya californica in its natural habitat in Yosemite National Park, California, USA. © Jeff Bisbee

Some new aspects about the evolution of pollen cones and perisporangiate microsporangiophores in Taxaceae

Abstract

Pollen cones of several Taxaceae (*Cephalotaxus*, *Pseudotaxus*, *Taxus* and *Torreya*) and especially their microsporangiophores were investigated with paraffin technique and SEM. A lot of the investigated pollen cones of *Torreya* and *Cephalotaxus* formed several hyposporangiate microsporangiophores in the distal part of the cone axis instead of the typical terminal perisporangiate one. These hyposporangiate microsporangiophores are always supplied by only one collateral vascular bundle strand. Investigations on the vasculature of the terminal perisporangiate microsporangiophores have shown that they are always supplied with several, mostly 2-4 collateral vascular bundle strands, which enter the cone axis in separate strands. This leads to the idea that the terminal perisporangiate microsporangiophore reflects a radial synangium consisting of several fused hyposporangiate microsporangiophores. Furthermore it could be shown that the lateral perisporangiate microsporangiophores of *Pseudotaxus* and *Taxus* also represent radial synangia consisting of minimum 2 fused hyposporangiate microsporangiophores. The lateral hyposporangiate microsporangiophores of *Torreya* and *Cephalotaxus* are supplied by only a single collateral vascular bundle. Due to the number and the position of microsporangiophores, and also the vasculature within a single pollen cone, *Torreya* is quite similar to the situation within a single lateral pollen cone within the branched *Cephalotaxus* pollen cone represents a strongly reduced *Cephalotaxus* pollen cone or if the branched *Cephalotaxus* pollen cone represents a cluster of several pollen cones.

1 Introduction

Among extant conifers the seed cones are characterized by the bract-/seed-scale-complex, which is, however, strongly modified in the different systematic groups. Thus, seed cones in conifers can be generalized as branched structures fulfilling the definition given for an "inflorescence" in angiosperms (SCHUHMANN 1902; HERZFELD 1914; PILGER 1926; FLORIN 1951, 1954; SCHWEITZER 1963; KRÜSSMANN 1983; FARJON 1984, 2005, 2010; PAGE 1990; STÜTZEL & RÖWEKAMP 1997, 1999; MUNDRY 2000; FARJON & ORTIZ GARCIA 2003; ECKENWALDER 2009; DÖRKEN 2011).

In contrast to this, the situation for the coniferous pollen cones is not as homogenous. Among the different systematic groups of extant conifers, pollen cones have different structures. The majority are unbranched, "flower"-like. Only in a few extant Taxaceae, e.g. in *Cephalotaxus* and *Pseudotaxus* (WILDE 1975; MUNDRY & MUNDRY 2001; DÖRKEN *et al.* 2011), and in Cupressaceae *s. str.* only in *Juniperus drupacea* (e.g. LEMOINE-SEBASTIAN 1967; FARJON 2005; ECKENWALDER 2009), and a few Podocarpaceae like some species of *Podocarpus, Prumnopitys* and *Retrophyllum* (SCHULZ *et. al* 2014) branched pollen cones are formed.

In pollen cones of extant conifers, two different types of microsporangiophores are developed: (1) hyposporangiate (dorsiventral) microsporangiophores, with microsporangia formed only on the abaxial side of the central stalk and an adaxial scutellum (fig 1A); (2) perisporangiate (radial) microsporangiophores, with microsporangia all around the central stalk (fig 1B). The majority of extant conifers are hyposporangiate. Only some extant Taxaceae (-Pseudotaxus



Fig. 1: Microsporangiophores, A: hyposporangiate; B: perisporangiate.

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and *Taxus*) are exclusively perisporangiate. Among other Taxaceae, *Cephalotaxus* and *Torreya* hypo- as well as perisporangiate microsporangiophores are developed within the same cone.

Two contrary major evolutionary concepts about the coniferous microsporangiophores exist. Some authors regard all coniferous microsporangiophores as homologous structures and hyposporangiate (dorsiventral) microsporangiophores are derived from a perisporangiate ancestral condition (e.g. WORDSELL 1901; DUPLER 1919; DLUHOSCH 1937). Other authors (e.g. THOMSON 1940; WILDE 1975; MUNDRY & MUNDRY 2001; DÖRKEN *et al.* 2011), however, suggest perisporangiate microsporangiophores are derived from a radial synangium consisting of several dorsiventral reduced microsporangiophores. However, both scenarios are still discussed controversially.

In contrast to the quite heterogenous pollen cone structure in Taxaceae (branched vs. unbranched; perisporangiate vs. hyposporangiate), the situation among nearly all other conifers is quite homogenous, and mostly one type of pollen cones is developed: unbranched, hyposporangiate and without a terminal microsporangiophore. Thus, suggesting evolutionary scenarios about the coniferous pollen cones and their microsporangiophores is quite difficult. We found pollen cones and microsporangiophores in different Taxaceae showing several types of anomalies, which were also included in our investigations. Our morpho-anatomical investigations should help towards a better understanding of the evolution of the taxaceous pollen cones and especially their microsporangiophores.

2 Material & Methods

2.1 Material

Typical and anomalous pollen cones of *Torreya californica* TORR. were collected in the Botanic Garden of the Ruhr-University Bochum, Germany. *Pseudotaxus chienii* (W.C.CHENG) W.C.CHENG was collected in the private living collection of HUBERTUS NIMSCH, Bollschweil, St. Ulrich, Germany where the specimens are cultivated as potted plants in a temperate house. *Cephalotaxus harringtonii* (KNIGHT ex J.FORBES) K. KOCH was collected in a private garden in Verbania, Italy, in the Botanic Garden of the Ruhr-University Bochum (Germany), and on the Isle of Mainau (Konstanz, Germany). Pollen cones of *Taxus baccata* L. were collected from several trees growing on the campus of the University of Konstanz (Germany). From each taxon material we collected from several individuals, and within an individual also from different branches within the crown.

2.2 Methods

Freshly collected material was photographed and then fixed in FAA (100 ml FAA = 90 ml 70% ethanol + 5 ml acetic acid 96% + 5 ml formaldehyde solution 37%) before being stored in 70% ethanol. The cone anatomy was studied from sections using the classical paraffin technique and subsequent astrablue/safranin staining (GERLACH 1984). For SEM-analysis the FAA-material was dehydrated in formaldehyde dimethyl acetal (FDA) for at least 24 hours (GERSTBERGER & LEINS 1978) and critical point dried. Sputter coating was done with a sputter coater SCD 50 BAL-TEC (BALZERS). The specimens were examined with an AURIGA ZEISS TM. Macrophotography was accomplished using a digital camera (CANON POWERSHOT IS2) and microphotography with a digital microscope (KEYENCE VHX 500F) equipped with a high-precision VH mounting stand with X-Y stage and bright field illumination (KEYENCE VH-S5).

2.3 Special terms

Most authors regard the microsporangia bearing structure in conifers as "microsporophylls". We avoid using the term "sporophyll" or "microsporophyll" for the microsporangia bearing structure. Otherwise we would introduce *a priori* a homology that is applied to it. Thus we are calling them microsporangiophores. The green, adaxial scale-like structure in hyposporangiate microsporangiophores will be termed a scutellum, and not "phylloid rest" as is frequently done. "Inflorescence"-like pollen cones consisting of several lateral cones, each of them inserted in the axil of a bract, are called branched.

3 Results

3.1 Anomalous hyposporangiate microsporangiophores

3.1.1 Pseudotaxus chienii (W.C.CHENG) W.C.CHENG

Pollen cones of *Pseudotaxus chienii* are inserted at the lower side of the branches (figs 2A, C, D). Typical pollen cones are branched and consist of exclusively perisporangiate microsporangiophores,

each inserted in the axil of a scale-like bract (figs 2B, E, F), that cover the microsporangiophores before anthesis (figs 2A, B, E). In distal parts of the pollen cones bracts are sometimes lacking. In all, 19% of the 300 investigated pollen cones differed from the majority which have perisporangiate microsporangiophores, by having some hyposporangiate ones with a different number of abaxial microsporangia (2–4) and a green phyllom-like scutellum developed (fig. 3). Within some perisporangiate microsporangiophores a central green column-like structure is developed (fig. 4).

3.2 Hyposporangiate microsporangiophores in the distal part of the cone axis instead of the typical terminal perisporangiate microsporangiophores

3.2.1 Torreya californica TORR.

Pollen cones of *Torreya californica* are located mostly at the lower side of a branch, although some can also be developed on the upper side, but not terminal at the shoot axis. Typical shaped pollen cones consist of several spirally arranged lateral hyposporangiate microsporangiophores, each of them bearing 2-5 microsporangia and a terminal perisporangiate microsporangiophore with 2-8 microsporangia. The microsporangia developed at the perisporangiate terminal microsporangiophore have the same dimensions as these of the lateral hyposporangiate ones (fig. 5). The terminal perisporangiate microsporangiophore is supplied with a varying number of collateral vascular bundle strands. In the investigated material 2 (figs 6 A-C), 3 and 4 (figs 6 D-F) collateral vascular bundles are developed within the central stalk of the microsporangiophore. The bundle strands do not fuse. They enter the cone axis in separate strands. In 38% of the 300 investigated pollen cones a terminal perisporangiate microsporangiophore was absent. Here 2 (figs 7 A & B), 3 (figs 7 C & D) or 4 (figs 7 E & F) hyposporangiate microsporangiophores are arranged in distal parts of the cone axis in the position where usually the terminal perisporangiate microsporangiophore is located. The dimensions of these anomalous distal hyposporangiate microsporangiophores together conform to the dimensions and the number of microsporangia in typical perisporangiate microsporangiophores (fig. 5). Each of the hyposporangiate microsporangiophores is supplied with a single collateral vascular bundle (fig. 8).

3.2.2 Cephalotaxus harringtonii (KNIGHT ex J. FORBES) K.KOCH

Pollen cones of *Cephalotaxus* are developed mostly on the lower side of a branch, and are inserted in the axil of a typical needle-leaf. The pollen cones are branched and consist of 6-11 lateral units (cones), each inserted in the axil of a small scale-like bract. Within the branched cone bud scales for the lateral cones are lacking. Each cone consists of several lateral spirally hyposporangiate microsporangiophores carrying between 2–4 microsporangia. In most cases the cone axis terminates with a perisporangiate microsporangiate microsporangiate microsporangiophore with a varying number of microsporangia (figs 9 A–E). Microsporangia in both, the peri- and in the hyposporangiate microsporangiophores 2–3 collateral vascular bundle strands are developed, which do not fuse when entering the stem bundle of the cone axis (fig. 9F). In 37% of the 300 investigated pollen cones, instead of the typical terminal perisporangiate microsporangiophores are developed in the distal part of the cone axis, each supplied with a single collateral vascular bundle strand (fig. 10F). Taking the size and also the number of microsporangia of all anomalous distal hyposporangiate microsporangiate microsporangia for the number of microsporangia of all anomalous distal hyposporangiate microsporangiate microsporangia for the associated within a perisporangiate microsporangia for the dimensions and also to the number of microsporangia of all anomalous distal hyposporangiate microsporangiate microsporangiate microsporangiate microsporangia for the number of microsporangia of all anomalous distal hyposporangiate microsporangiate microsporangia developed in th

3.3 Vasculature in lateral microsporangiophores

The results of the morpho-anatomical studies on the vasculature within the lateral microsporangiophores show significant differences between the hypo- and the perisporangiate type. The lateral hyposporangiate microsporangiophores of *Torreya californica* (fig. 11A) and *Cephalotaxus harringtonii* (fig. 11B) are always supplied by a single collateral vascular bundle strand. Within the vascular bundle, xylem is pointing towards the adaxial scutellum, the phloem towards the abaxial microsporangia. The lateral perisporangiate microsporangiophores of *Pseudotaxus chienii* (fig. 11C) and *Taxus baccata* (figs 11D–E) are mostly supplied with 2 collateral vascular bundle strands, as is also the case for anomalous hyposporangiate microsporangiophore found in *Taxus baccata* (fig. 11F). Especially in *Taxus baccata* it can be clearly observed that the xylem parts of both bundle strands are orientated towards the centre of the stalk so that they are facing each other. The phloem parts are pointing towards the microsporangia.

3.4. Proliferated pollen cones

On a *c*. 30 year old specimen of *Cephalotaxus harringtonii* growing on the Isle of Mainau (Konstanz, Germany), several pollen cones were found showing proliferation in different intensities (fig. 12). In all proliferated pollen cones a terminal pollen cone is absent and the apical meristem is still active and develops a well expanding shoot axis (figs 12A, B, D). The basal part of this shoot axis is surrounded by persisting bud scales. The outer bud scales are all sterile (figs 12C, F). Several of the inner bud scales are fertile and carry a pollen cone in their axil (figs 12C, E, F). If the internodes developed between the inner bud scales are small, the pollen cones remain densely packed closely to each other in the basal part (figs 12A, B, C), as is also the case for typical shaped pollen cones. In some of the proliferated pollen cones the internodes between the inner bud scales are strongly expanded and the inner bud scales are arranged spirally and distantly from each other on the shoot axis (figs 12D, E, F). In distal parts of the shoot, typical shaped needle leaves are developed (fig. 12A, B, D). Such proliferated pollen cones were not found in the investigated individuals of *Torreya californica, Taxus baccata* and *Pseudotaxus chienii*.

4 Discussion

The systematic relationships within Taxaceae are still controversial. Morpho-anatomical studies of vegetative structures e.g. leaves have shown that *Taxus* + *Pseudotaxus* and *Cephalotaxus* + *Torreya* each form a closely related complex (e.g. GHIMIRE & HEO 2014). The close relationship of *Pseudotaxus* + *Taxus* is also proved by molecular data. Here it could be shown that the *Pseudotaxus*-*Taxus-Austrotaxus*-complex (Taxeae) represents the sister clade of the *Torreya-Amentotaxus*-complex (Torreyeae), however, *Cephalotaxus* is placed basal to all other Taxad genera (e.g. CHENG *et al.* 2000). Apart from this, the evolutionary pathway of taxaceous pollen cones and their microsporangiophores are still controversial. Features such as branched vs. unbranched cones and perisporangiate vs. hyposporangiate microsporangiophores are of great interest within this discussion. The results gained in this study seem to be quite helpful to deliver new insights in the evolution of taxaceous pollen cones and their microsporangiophores.

The terminal position of the perisporangiate microsporangiophore in Cephalotaxus and Torreya clearly indicates that the microsporangia bearing structure cannot represent just a simple peltate microsporophyll, because a leaf is always developed lateral at the apex and can therefore never be inserted terminal. However, it should be considered that leaves can be shifted by subsequent growing processes out of their original positions into a secondary ones. Within the investigated anomalous pollen cones of Torreya and Cephalotaxus, several circle-like arranged hyposporangiate microsporangiophores (figs 7, 8, 10) were formed in the distal part of the cone axis instead of the usual single perisporangiate microsporangiophore (figs 5, 6, 9). If these anomalous distal hyposporangiate microsporangiophores were to fuse, a radial structure would be formed. Its position, the size dimensions and the number of microsporangia would correspond to a typical terminal perisporangiate microsporangiophore. Depending on the number of fused hyposporangiate microsporangiophores the number of microsporangia within the perisporangiate microsporangiophores varies greatly. During the formation of perisporangiate microsporangiophores the scutellum gets nearly completely reduced. However, within Torreya and Pseudotaxus, some perisporangiate microsporangiophores were found still showing a conspicuous green central column-like structure (fig. 4). It seems that this represents rudiments of the scutella of the fused hyposporangiate microsporangiophores as it might also be the case that the green central region developed within typical shaped microsporangiophores (fig. 2F).

Taking these anomalies together, they support the idea that the perisporangiate type of microsporangiophores represents a radial synangium consisting of several fused hyposporangiate microsporangiophores as was suggested earlier by e.g. THOMSON (1940), NOZERAN (1955), MUNDRY & MUNDRY (2001), DÖRKEN *et al.* (2011) and SCHULZ *et al.* (2014). When regarding the perisporangiate microsporangiophores within Taxaceae as a radial synangium consisting of several fused hyposporangiate microsporangiophores, it seems that they are developed exclusively terminally at the cone axis due to a lack of space in this region. This would mean, if the apex of the cone axis is small in diameter, the distal hyposporangiate microsporangiophores would fuse to a radial structure, and if the diameter of the apex is unusually broad the microsporangiophores in the distal part would not fuse, as can be observed in several pollen cones of *Torreya* and *Cephalotaxus* (figs 7, 8, 10). This could explain why within these taxa the perisporangiate type of microsporangiophores is exclusively formed

terminally at the cone axis. This idea is supported by the fact that the number of vascular bundle strands developed within the central stalk of the terminal perisporangiate microsporangiophore varies between 2 and 4. Each vascular bundle strand belongs to one of the microsporangiophores that are involved in forming the perisporangiate structure.

It could be shown that the lateral perisporangiate microsporangiophores in *Taxus baccata* (figs 11D–F) and *Pseudotaxus chienii* (fig. 11C) are mostly supplied with two vascular bundle strands. Within the central stalk of the microsporangiophores the xylem parts are facing each other, while the phloem parts are pointing towards the microsporangia. This fact is a strong argument supporting the idea that the lateral perisporangiate microsporangiophores in both taxa are also representing radial synangia consisting in this case of 2 fused microsporangia. It seems that the former hyposporangiate microsporangiophores were fused with their adaxial sides, where the scutella were developed. This would explain why the xylem parts of both strands are facing each other. The lateral hyposporangiate microsporangiophores of *Torreya californica* (fig 11A) and *Cephalotaxus harringtonii* (fig 11B) are supplied by a single collateral bundle strand with xylem pointing towards the scutellum and phloem pointing towards the microsporangia. If two hyposporangiate microsporangiophores were to fuse along their adaxial sides an arrangement of xylem and phloem would occur as is developed within the stalk of *Pseudotaxus chienii* and *Taxus baccata*.

Different evolutionary scenarios exist about the pollen cones in Taxaceae. In one of the latest scenarios (e.g. MUNDRY & MUNDRY 2001; DÖRKEN et al. 2011; SCHULZ et al. 2014) the unbranched pollen cones of e.g. Taxus and Torreya are regarded as derived from an ancestral branched pollen cone similar to these developed in extant Cephalotaxus. In this transitional line pollen cones of Pseudotaxus are derived from a *Cephalotaxus*-like ancestor by the reduction of all lateral hyposporangiate microsporangiophores and also the lateral cone axes. If the bracts within the Pseudotaxus pollen cones become reduced the Taxus pollen cone would be formed. By the reduction of adaxial microsporangia within the lateral perisporangiate microsporangiophores of Taxus, the Torreya pollen cone is formed (fig. 13A). In this scenario the lateral hyposporangiate microsporangiophores in Torreya are homologous to lateral strongly reduced perisporangiate microsporangiophore of Pseudotaxus and Taxus. Thus, pollen cones of Torreya might reflect the most derived ones within Taxaceae. In this case the pollen cones of Pseudotaxus (figs 1B & F) with partly reduced bracts would represent an intermediary stage. The pollen cones of Taxus differ from Pseudotaxus only in lacking bracts. Within this scenario the perisporangiate microsporangiophores of Pseudotaxus, Taxus and the terminal synangium of Cephalotaxus would be homologous and the perisporangiate microsporangiophores of Pseudotaxus and Taxus would comply with an entire, however, strongly reduced lateral unit within the branched Cephalotaxus pollen cone. It seems that in *Pseudotaxus* and *Taxus* the cone axis is so strongly reduced that only some cells remain, which can no longer be recognised as shoot tissue. Such a strong reduction of shoot axis is nothing unusual in conifers and can also be found in vegetative parts e.g. in cladodes of Sciadopitys verticillata, Sciadopityaceae (DÖRKEN & STÜTZEL 2011a, b). Thus, the evolutionary scenario for taxaceous pollen cones as described above can demonstrate quite well how sporophyll-like perisporangiate microsporangiophores can be developed by the reduction of lateral cones. This idea is supported by two further facts:

1. The number of perisporangiate microsporangiophores in *Pseudotaxus* and *Taxus* corresponds quite well with the number of lateral units within the branched *Cephalotaxus* pollen cones.

2. The pollen cones of *Pseudotaxus* and *Taxus* are exclusively perisporangiate. As it could be shown the perisporangiate microsporangiophores developed in *Cephalotaxus* and *Torreya* represent radial synangia resulting from a fusion of hyposporangiate microsporangiophores, which can only take place when the apex of the cone axis is so small that in earliest ontogenetic stages the primordia of the microsporangiophores get in contact and fuse to each other.

Regarding the perisporangiate mircosporangiophores in *Pseudotaxus* and *Taxus* as complying with an entire lateral cone than it is not astonishing, that here exclusively perisporangiate microsporangiophores are developed, due to lateral cones axis that are reduced to some cells that can no longer be recognized as such ones. Thus, microsporangiophores developed at such a strongly reduced lateral cone axis have to fuse consequently to a radial synangium due to the reduced apex.

That the lateral hyposporangiate microsporangiophores in *Torreya* might be derived from a perisporangiate ancestor is supported by the anomalous hyposporangiate microsporangiophores found in

Pseudotaxus (figs 3, 4) which are quite similar to these of *Torreya*. For the anomalous hyposporangiate *Pseudotaxus* microsporangiophores it could be shown that the adaxial scutellum is formed by the reduction of one or more adaxial microsporangia which became sterile and scale-like.

However, two of the largest barriers in regarding the hyposporangiate pollen cones of *Torreya* as being derived from a Taxus-like ancestor is the different number of microsporangiophores between both taxa, and more importantly the number of vascular bundles supplying the microsporangiophores. The number of lateral hyposporangiate microsporangiophores within Torreya significantly exceeds the number of perisporangiate microsporangiophores in *Pseudotaxus* and *Taxus* and also the number of the lateral units (cones) within the branched Cephalotaxus pollen cone. Furthermore the lateral hyposporangiate microsporangiophores in Torreya are always supplied by only a single vascular bundle strand as is also the case for the lateral hyposporangiate microsporangiophores in Cephalotaxus. Within both taxa the orientation of xylem and phloem within the bundle strand is exactly the same. Thus, it would be very unlikely that the hyposporangiate *Torreya* microsporangiophore is derived from a radial synangium as developed within *Pseudotaxus* and *Taxus*. This incongruity is strongly conflicting with the evolutionary scenario described above and leads to another hypothesis about the evolution of taxaceous pollen cones. Pollen cones of Torreya could be regarded as being derived directly from a branched Cephalotaxus-like ancestor. The pollen cones of Torreya show great similarities with a lateral unit within the branched Cephalotaxus pollen cone, especially in respect to the number, the position and the vasculature within the microsporangiophores. Thus, a single pollen cone of Torreya fits significantly better to a complete lateral unit within the branched Cephalotaxus pollen cone than to a single Pseudotaxus and Taxus pollen cone. Within such an evolutionary scenario the pollen cones of Pseudotaxus and Taxus do not represent intermediate forms between Cephalotaxus and Torreya (fig. 13B). Thus it might be possible that within taxaceous pollen cones two lineages have evolved independently from each other:

(1) Cephalotaxus \rightarrow Torreya;

(2) Cephalotaxus \rightarrow Pseudotaxus \rightarrow Taxus.

In this case pollen cones of *Torreya* and *Taxus* would reflect the most derived cones within each lineage. However, the situation could be also completely different from that. Pollen cones of Torreya might also reflect the most primitive condition. If the inner bud scales that are developed at the stalk of the Torreya pollen cone would become fertile and carry an axillary pollen cone, a structure similar to the Cephalotaxus pollen cone is formed. In this case the Cephalotaxus pollen cone could represent a cluster of Torreya-like pollen cones (fig. 13C). This idea is supported by the anomalous proliferated pollen cones found in Cephalotxus harringtonii (fig. 12). Here it could be clearly shown that the pollen cones are inserted in the axil of the inner bud scales. In typical Cephalotaxus pollen cones the cone axis is terminated by a pollen cone and the apex is completely consumed and a further development of the cone is excluded. If the terminal pollen cone is absent the apex can continue growing and forming a typical shaped shoot axis with bud scales in the basal and green needle leaves in the distal part. If the internodes between the inner bud scales become expanded the pollen cones are also arranged distantly from each other at the shoot axis (figs 12D, F). Thus the branching pattern in typical shaped Cephalotaxus pollen cones corresponds exactly to the phyllotaxis of the inner bud scales. Thus it would be not so unlikely that the branched pollen cone of *Cephalotaxus* represents a cluster of several *Torreya* like pollen cones. The number of lateral units within a Cephalotaxus pollen cone is corresponding to the number of fertile inner bud scales. In this scenario the pollen cones of Pseudotaxus and Taxus can be derived from a *Cephalotaxus*-like ancestor in the way as described in the first scenario above (fig. 13A). In this case pollen cones of Taxus reflect the most derived condition. Unfortunately pollen cones of Austrotaxus and Amentotaxus were not available for this study. However, there is an urgent need to investigate the pollen cones of these taxa to see how they fit in the evolutionary scenarios as described above.

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Fig. 2: Pseudotaxus chienii, typical shaped pollen cones.

A: Young cones at the shoot axis. B: Longitudinal section of a young cone; the exclusively perisporangiate microsporangiophores are covered by bud scales and bracts. C: Ripe pollen cones. D: Detail of C. E: Pollen cone shortly before anthesis; bracts within the cone still cover the microsporangiophores. F: Detail of a ripe pollen cone; the bracts are spreading distantly out of the cone.



Fig. 3: *Pseudotaxus chienii*, anomalous shaped microsporangiophores. Instead of typical perisporangiate microsporangiohores several hyposporangiate microsporangiophores showing a distinct adaxial scutellum are formed (arrow).



Fig. 4: *Pseudotaxus chienii*. Anomalous shaped microsporangiophores with a central, green column-like structure (arrow).



Fig. 5: Torreya californica.

Top view of typical shaped pollen cones with a perisporangiate terminal microsporangiophore bearing four (A), five (B), six (C), eight (D & E) or nine (F) microsporangia.



Fig. 6: Torreya californica.

Cross section of the distal part of two (A-C & D-F) typical shaped pollen cones; the terminal perisporangiate microsporangiophore is supplied with two (A-C) or four (D-F) collateral vascular bundle strands, each enters the cone axis in separate strands; a huge resin duct is developed in the central distal part of the perisporangiate microsporangiophore as is also developed in the scutellum of the lower hyposporangiate ones.



Fig. 7: Torreya californica.

Top view of anomalous pollen cones showing two (A & B), three (C & D) or four (E & F) hyposporangiate microsporangiophores instead of the typical perisporangiate terminal microsporangiophore.



Fig. 8: Torreya californica,

Cross section of the distal part of two (A-C & D-F) anomalous shaped pollen cones; instead of the usually developed perisporangiate microsporangiophore four hyposporangiate ones are formed; each microsporangiophore is supplied with one collateral vascular bundle strand.



Fig. 9: Cephalotaxus harringtonii.

A-E: Top view of a typical shaped pollen cones terminating with a perisporangiate microsporangiophore that is varying strongly in size, shape and in the number of microsporangia. **F:** Cross section of a terminal perisporangiate microsporangiophore; this microsporangiophore is supplied with two collateral vascular bundles (arrow).



Fig. 10: Cephalotaxus harringtonii.

A-E: Top view of anomalous pollen cones showing two (A-B), three (C & D) or four (E) hyposporangiate microsporangiophores instead of the typical perisporangiate terminal microsporangiophore. **F:** Cross section of a terminal hyposporangiate microsporangiophore; the microsporangiophore is supplied with a single collateral vascular bundle (arrow).



Fig. 11: Cross sections of lateral microsporangiophores in different Taxaceae.

The hyposporangiate microsporangiophores of *Torreya californica* (**A**) and *Cephalotaxus harring-tonii* (**B**) are supplied with a single collateral vascular bundle (arrow); the perisporangiate microsporangiophores of *Pseudotaxus chienii* (**C**) and *Taxus baccata* (**D & E**) are supplied with 2 vascular bundles (arrows). **F:** *Taxus baccata*, anomalous hyposporangiate microsporangiophore.



Fig. 12: Cephalotaxus harringtonii, proliferated pollen cones.

Due to the lack of a terminal pollen cone the cone axis can continue growing. Pollen cones are inserted in the axils of the inner bud scales. A-C: If the internodes of the fertile inner bud scales are not expanded the pollen cones are arranged closely to each other. D-F: If the internodes of the fertile inner bud scales are expanded the pollen cones are arranged distantly from each other at the shoot axis. E & F: Detail of D. E: Basal part of a pollen cone. F: Fertile inner bud scales with well developed internodes.



Fig. 13: Possible evolutionary scenarios for microsporangiophores in the investigated Taxaceae.

For a better overview the true dimensions among the different cones were not respected in this scheme.

Jeff Bisbee

Bull. CCP 5 (1): 22-25. (4.2016)

Torreya californica CALIFORNIA NUTMEG







Photos:

Page 91: West of Yosemite Valley, Yosemite National Park, California.

Page 92: West of Yosemite Valley, Yosemite National Park, California.

Page 93, top row, left: Largest recorded living *Torreya californica*, Swanton Road, Santa Cruz Mountains, California. Height measured in 1992: 29 m.

Page 93, top row, right: Hetch Hetchy Valley, Yosemite National Park, California.

Page 93, bottom row, left: Mayacamas Mountains, Mendocino County, California.

Page 93, bottom row, right: American River, Placer County, California.

Page 94: West of Yosemite Valley, Yosemite National Park, California..

Bull. CCP 5 (1): 26-30. (4.2016)

Taxus brevifolia PACIFIC YEW

Photos:

Page 95, top: Green and White Mountain, Siskiyou Mountains, Siskiyou County, California.

Page 96, top-right; page 97, top-left; page 99: Skillman Flat, Nevada County, California.

Page 99, bottom-right: Pasqualli Road, Nevada County, California.

All other photos: Marble Mountains, Siskiyou County, California.

BOOK REVIEW

 - 'An Atlas of the World's Conifers, An Analysis of their Distribution, Biogeography, Diversity and Conservation Status'

by A. Farjon & D. Filer, Brill Publishers, Leiden, Netherlands

How to do new with old.

Until now, there are only quite a few books or monographs dealing with conifers and displaying meaningful distribution range maps. The following works are the most interesting ones:

• Geographic distribution of the pines of the world (Critchfield & Little, 1966).

• The distribution of forest trees in California (Griffin & Critchfield, 1972).

• Atlas of the gymnosperms of China (Ying, Chen & Chang, 2003).

These atlases are covering only a small part of the conifer world, either a genus or a State or a country as indicated by their respective titles. Until now there was no atlas covering all living conifer taxa. This work is filling undoubtedly a gap. But is it worth the name of 'atlas'? Unfortunately at first

sight the reduced maps are very deceptive and the text is occupying too much place at the cost of the quality and the size of the maps.

Herbarium sheets

The book is claiming to represent some 37,000 herbarium sheets. This way of mapping the conifer distribution ranges raises several methodological questions some of which are indeed mentioned in the introduction. Although quite impressive, this number of sheets does not account for the numerous duplicates in different herbaria, as well as for the different collectors who visited the same places. Another problem is given that many sheets date from more than a century ago. They tell us where the species was recorded then, but do not inform us if it is still there now. Logging, fires, roads, agricultural fields or buildings could have eradicated more than one stand, even for recent collections.

One example: *Podocarpus celatus*, Bolivia, *A.Antezana & et al. 322A*, 2004, 15°05'12"S, 68°29'32"W¹ was collected on the side of a road (as it is often the case). This species of *Podocarpus* is a valuable timber tree. Consequently every 'pino de monte' near a road is likely felled illegally in the first five years after the construction of the (unpaved) road.

Often it is not obvious, and sometimes impossible to know if the specimen on the herbarium sheet was collected on a wild or cultivated tree. Of course cultivated trees should be excluded; otherwise it would be necessary to map all trees growing in arboreta and botanical gardens, all the trees used as wind breaks or ornaments, an impossible and useless task. Some maps analysed below show that some cypress distribution ranges are mapped with both cultivated and wild trees.

Another problem is misidentification of specimens. Unfortunately this happens in this 'atlas'. For instance *Cupressus torulosa* D.Don is confused with specimens of four different taxa: *Cupressus gigantea* Cheng & Fu, *Cupressus tortulosa* Griffith, *Cupressus duclouxiana* Hickel in Camus and *Cupressus lusitanica* Miller, a new world species. Some dry material can be difficult to identify, but it is more worrying when a living *Cupressus lusitanica* is identified as a *Cupressus torulosa* (Farjon 2013).

On some herbarium sheets available online the exact locality is hidden as a mean of protection for the involved taxon. These cases where the information is not made public are not discussed. On the other hand it is true that the lack of precision of these maps would make rather difficult to trace back a population in the wild when this population has a narrow habitat, such as several *Cupressus* species.

Maps

The 728 maps are drawn thanks to a computer program and the distribution ranges are represented by dots. Thus – and except where several collections were made in different parts of one population – there is no indication if the stand is small or large or if there is only one tree or a few trees. The major problem is that several localities are not represented at all, because they are not present on any herbarium sheet or because the available information is insufficient to determine them. The distribution ranges are not only flawed by cultivated specimens and misidentified taxa, but also by the omission of several populations.

An atlas by definition is a collection of maps. Any cartographer will not be happy with the maps printed here for several reasons. The size of the maps poses a problem. They are so small² that it is more than once

D. Maerki

¹ <u>http://www.tropicos.org/Name/25600052?tab=specimens</u>

² Quite usually as large as one column, except for representing a genus or a family throughout their ranges.

impossible to understand which locality exactly is represented. Every scientific work shall give the opportunity to access and verify the data. Here they are not part of this opus. Instead we are sent back to an internet site and a database. The map backgrounds are retrieved from <u>http://www.naturalearthdata.com</u>. In the introduction, the authors explain that there was the choice between the following map scales: "1:10'000'000, 1:50'000'000 and 1:10'000'000 [sic ³]" and that the authors chose the larger scale. True it is the larger scale of the three, but it is still a very small scale. And this scale is not even kept on any map of the 'atlas' or only by chance.

To be readable maps should follow certain rules. Every map should have a title, a legend, a scale and geographic coordinates. In this 'atlas', the geographic coordinates are completely absent. The scales not only are not mentioned on any map, but they vary following the very extension of the distribution range, not allowing for instance to estimate the distances separating the different localities. The legend should explain the signs present on the map, using the sign itself drawn on the map. Here the legend is only textual and some colours are confusing such as for the *Cupressus arizonica* range map, when the different taxa are displayed using the following colours: black, red, pink, orange and blue (blue should have been reserved for seas, lakes and rivers especially when the blue colour is not so different). The problem is the same on the *Pinus strobiformis* map, where blue dots could be confused with lakes when the map scale is so small as 1:22'870'000 to represent all Mexico (see below p. 36).

When there is more than one taxon on a map, for instance with two varieties, the species is represented with black dots and the variety with red dots. On the other hand, if only one taxon is present, the dots are generally black, except if this species is endangered. In that case the dots are sometimes red. The same colour should have the same meaning throughout the different maps of the atlas, but here it is obviously not the case with the red colour acquiring at least two different meanings.

The map backgrounds reflect the different altitudes, but no legend is presented and the number of different colours – from yellow to white through different tints of green with shaded areas to represent the relief – does not help the reader. The State borders in grey are difficult to see at higher altitudes, not to speak of the province borders which are on several maps confused with the backgrounds especially if the scale is reduced (cf. Mexico, India or China maps). No State name is presented. True, they would be useful only if the State borders were really always easily visible.

By comparison all the distribution range maps in the three atlases mentioned in the introduction are displayed using all the place available on one full page (even on two pages for the Chinese atlas) and respect the rules for best readability even if using few colours or in black & white ⁴.

Taxonomy

The taxonomy is Farjon's. There is a lot to say about the different choices and opinions of the author, choices which are not supported here at least for the *Cupressus* genus ⁵. It is only necessary to point to the fact that his numerous misidentifications (see below a first list of such herbarium misidentifications, Appendix 1) and incomplete studies of more than one taxon⁶ of *Cupressus* casts a serious doubt on the quality of the distribution ranges as they are represented.

The case of *Cupressus torulosa* has been mentioned above, which will be dealt in details elsewhere. Three maps and their comments are examined here in detail, two *Cupressus* and one *Pinus*.

Cupressus "cashmeriana" (p. 191)

The main problem is the confusion between *Cupressus tortulosa* Griffith and *Cupressus cashmeriana* Carrière so that we have *a priori* two undistinguished taxa on the same map. The map and the comments to the map are examined here in details.

Map

See Map 1. The map is representing indistinctly wild cypress populations together with several cultivated trees. In Sikkim, as mentioned by Farjon, there are only planted specimens of *Cupressus tortulosa*. But one of the trees – at least – is not a "*cashmeriana*", but again a *Cupressus lusitanica*. The dots in Bhutan are *Cupressus tortulosa*, but no distinction is made between cultivated specimens and wild stands. East of Bhutan, in Arunachal Pradesh, there is the only currently known wild population of *Cupressus cashmeriana*. The

³ Instead of "1:110'000'000".

⁴ For example, Bisbee 2014, pages 32 & 33, with maps adapted from Critchfield & E.Little 1966, with the help of Frankis and using several colours for a better readability (see appendix 2).

⁵ As co-author Farjon signed an article keeping *Xanthocyparis* into *Cupressus* (Christenhusz *et al.*, 2011): "Until resolution of the phylogenetic position of *Cupressus* is achieved, we take a conservative option and maintain *Cupressus* in a broad sense, including *Callitropsis*, *Hesperocyparis* and *Xanthocyparis*." In the "atlas", this last genus is presented on its own. Where is the coherence?

⁶ Farjon's taxonomy relies mainly on dry herbarium specimens, when all aspects of one taxon shall be examined and compared: physiology, phenology, ecology, edaphic and climatic conditions, geography, genetic and above all morphology of live specimens, and not dead dry ones.

second dot is quite likely something else, planted. The dot near Trulung in south-east Xizang (Tibet) is a wild *Cupressus austrotibetica* Silba, another misidentification by Farjon (see Appendix 1). The geographic coordinates of that last dot are also not correct.

Map 1 : It is not possible to give a title to this map considering its lack of coherence.

Text

It is necessary to quote some parts of the text exactly to point to the inaccuracies and mistakes.

"*Cupressus cashmeriana* was first known from plants and seeds collected by William Griffith in Bhutan in 1838 and brought to Europe, where in Paris E. Carrière who described and named it, working with cultivated plants sourced from England, got its provenance wrong and reported it to be native in Kashmir (Farjon, 1994)."

This is very unfortunately part of Farjon's myth as to the origin of Carrière's species. Carrière described Griffith's cypress, the Cypress of Bhutan under *Cupressus corneyana* Carrière. This plant was available already in 1850 at the Knight & Perry nurseries. There is no way to trace back *Cupressus cashmeriana* Carrière from England, when the glaucous cultivar of *Cupressus tortulosa* with similar foliage as *Cupressus cashmeriana* was introduced only in 1894 at Kew, and *Cupressus cashmeriana* itself only in 2006 by Rushforth. Carrière never reported it as native in Kashmir, but correctly gave its origin as Tibet, now Arunachal Pradesh in India (for details, see Maerki 2013, 2014).

"It is sometimes difficult to discern from information on herbarium labels whether the tree from which the specimen was collected grew in natural habitat, while some planted trees may not have been far removed from an indigenous population. This influences the accuracy of our map, which is the best estimate of natural distribution we are able to give based on these data."

This kind of statement relying mainly if not only on herbarium sheets will not allow displaying any meaningful map. It confines to guess work. In Bhutan it is very obvious where the cultivated trees and where the wild populations of *Cupressus tortulosa* are: the latest are away from any inhabited place and accessed with extreme difficulties. The locality data exist and only a blind collection of herbarium sheets could led to a "best estimate" which results in this insufficient and incorrect distribution range map mixing altogether several species as well as cultivated and wild specimens.

Cupressus arizonica (p. 79)

The subject here is not to discuss the taxonomical choice made⁷ as whether to treat as species or as varieties⁸ the different taxa represented on the following map under *Cupressus arizonica*, but only the correctness of the information presented.

Map

See Map 2. The two blue dots representing *Cupressus montana* are hardly visible for someone not familiar with the distribution range of this species. More worrying is the localisation of the *Cupressus "stephensonii* in

⁷ Except when this very point is put into discussion in the 'atlas' (see below).

⁸ Only to mention the fact that according to several molecular analyses the lumbering of all these taxa as varieties of *Cupressus arizonica* makes the group polyphyletic.

northern Baja California" (in fact a completely different taxon *Cupressus revealiana* – both in purple dots): it is at least 100 km off target. It would be a good point for the protection of this critically endangered species, if only the correct details were not given in the text. The *glabra* population (red dots) seems smaller than the *nevadensis* one (orange dots) when it is just the opposite that is correct both in term of number of trees and in extension of the distribution ranges. One *nevadensis* locality does not represent a wild population. Several populations of *arizonica* (black dots) are missing and some localities are not *arizonica*. Someone will claim that those are only "minor errors", but when added together they show a quite insufficient picture of the ranges of these taxa.

Map 2 : Cupressus arizonica and its varieties according to Farjon⁹.

Scale ~1:30'000'000

Text

Three taxa from California are mentioned in the 'atlas' under *Cupressus arizonica*, when there should have been four.

"The three Californian varieties have very limited distributions well separated from each other and perhaps because of this have been described and named as separate species."

Although biogeography is an important element, especially when the seed dispersion is fairly limited, there are other very obvious reasons to treat these taxa at the species level. Wolf (1948) wrote the most complete report on the new world cypresses after visiting almost all stands known at his time. His work was never surpassed until now even with the help of molecular analyses. For instance he described *Cupressus stephensonii* as botanically different from *Cupressus forbesii, arizonica* and *glabra*. Moreover this taxon releases its pollen in July and this fact alone – while not allowing a natural hybridisation with any other *Cupressus* with different pollination periods – raises a species barrier.

"Finally, var. *montana* occurs in several localities in the Sierra San Pedro Martir, the highest mountain complex in Baja California. Most of these Californian varieties form 'groves' or (sub)populations of trees of tens to thousands of individuals associated with few other trees, but var. *montana* occurs at higher altitudes in the zone of mixed conifer forest and is therefore more difficult to find. Var. *montana* and var. *stephensonii* are listed as Critically Endangered (CR) and var. *nevadensis* as Endangered (EN) on the IUCN Red List. Fire hazards are the main threat, increased by human interference with the environment."

This is the "analysis" of the conservation status of three cypress taxa... in less than one line. For each of them the importance of its population is as much as a guess, when it is not utterly underestimated 10^{10} .

Cupressus montana is not difficult to find because it is in a mixed conifer forest, when this forest is an open one, with scattered trees among the rocks (see photos, Bisbee 2012), but because this population is away from any paved or dirt road and necessitates several hours of hiking on a difficult terrain, even when the target is known with precision. If fires represent a threat, it cannot be left unreported that these species, except *Cupressus montana*, are fire adapted. And that fire is necessary for the regeneration of the populations. The hazard consists in small intervals between two fires, when the regenerating young trees have not had the time to develop a meaningful stock of seeds and when there is already sufficient fuel to allow the fire to spread again. Such was the case for instance on Tecate Peak for *Cupressus forbesii*. This population is now very close to extinction.

⁹ Note that the borders of the Mexican provinces are not discernible.

¹⁰ About the IUCN conservation status of *Cupressus montana* assessed by Farjon and the alleged 250 remaining specimens of that species, see Maerki 2015.

The *Cupressus* Conservation Project rates *Cupressus montana* as Endangered. This species not only occupies a very extensive area, but its best protection lies in its isolation so that the "human interference" is at its minimum. Regeneration is happening without a fire while the cones are releasing their seeds at maturity. There is no record of a recent fire in this range.

Pinus strobiformis (p. 106)

See map 3, p. 38. The map displays three taxa: *Pinus strobiformis, Pinus ayacahuite* and *Pinus ayacahuite* var. *veitchii*, and the text mentions a fourth one as *Pinus flexilis* var. *reflexa*. Again the discussion here will not be engaged on taxonomy (except to mention that *Pinus stylesii* is not recognised, see Bisbee 2014). The same defaults are present on that map as the ones mentioned for the *Cupressus* maps: indistinguishable blue dots for *Pinus ayacahuite* var. *veitchii*, wrong localities, missing localities. See appendix 2, page 38¹¹ to be able to compare the map of the 'atlas' with the map built with actual recent observations.

As illustrations there are several photos taken in the wild, but their size is not bigger than the map's while on every page there is an outside margin 4 cm wide.

Computers are wonderful tools to treat and analyse an important mass of data. With the appropriate software it is possible to create automatically hundreds of maps. The quantity is here, but what about their quality? What about the quality of the maps as well as quality of the data to build them? The distribution range maps of the different conifer taxa occupy the majority of the 512 pages of this 'atlas', but are more like vignettes and are of poor quality for the reasons presented above. Going through the pages and reading the comments there is nothing really new, almost nothing – save the errors – which cannot be found in previous works, let alone on Chris Earl website at <u>http://www.conifers.org</u>. Finally, what is the scope? How can the maps be used, if they can be used altogether?

Nothing will replace actual field work, especially when the populations are at risk to see parts or, in some cases, the totality of their range threatened by human activities or climate change. In that case a very approximate distribution range at a small scale is of no use. This 'atlas' is useful to get a big picture at a very small scale 12 , but it does not help – at least for the *Cupressus* species mostly put under scrutiny here – their conservation. This is due to a taxonomy based on insufficient observations, mostly limited to morphology of dry material without a single statistical analysis. The emphasis for conservation should be brought at the population level when in that case a much larger scale is necessary. This would need another atlas.

The title of this book should read "Atlas of conifer localities represented in some herbaria". The "analyses" mentioned in the subtitle do not go beyond generalities found elsewhere even with more details. For all the above enumerated reasons, this work does not meet a scientific standard let alone because it is practically impossible in most cases to verify the data reported on the maps when the sources are not part of the book and otherwise not easily available. In consequence we cannot recommend this 'atlas' ¹³.

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¹¹ Original full page map in Bisbee 2014, Map 2, p. 33.

¹² The most interesting parts are the ones on hot spots of conifer diversity, although these areas are already known for a long time without the help of computers. Hopefully they can be useful to convince governments and non profit organisations to take preservation actions if not already done.

¹³ If someone wants to propose a more positive review of that book, he will be welcome.

APPENDIX 1: Samples of herbarium sheets misidentified by Farjon.

K000088095 C.G.Trevor s.n., 3.1934 K000088107 K.Haridasan 0193, 18.8.1993 NY-00621791 Eberhardt 5073, s.d. P01637415 J.Bornmüller n° 1392, 8.1900 P01642281 Castellini s.n., 2.10.1905 P01654116 Poilane 12.290, 1924 ou 1925 P06489695 A.Chevalier 38.578, 12.9.1918 P06489696 Mignucci s.n., 6.1922 P06489698 A.Chevalier 29.662, 19.12.1913 P06489699 Pételot s.n., s.d. E00009189 SSY 207, 30.5.1992 etc.

APPENDIX 2: Comparison of two distribution range maps for *Pinus strobiformis* and relative species. Note the missing population of *Pinus reflexa* at the NM-TX border and the cultivated specimens at low altitudes.

In the 'atlas', the file format of the background is a bitmap (pixels). Unlike vector maps this format does not allow to resize the drawings without a loss of quality.

Map 3: Atlas, p.106.

Farjon's determination: *Cupressus cashmeriana* (aff.) *Cupressus torulosa Cupressus torulosa Cupressus funebris Cupressus aff. funebris Cupressus lusitanica Cupressus lusitanica* In fact:

Cupressus lusitanica Cupressus lusitanica Cupressus tonkinensis Cupressus lusitanica Cupressus tonkinensis Cupressus sempervirens Cupressus tonkinensis Cupressus tonkinensis Cupressus tonkinensis Cupressus tonkinensis Cupressus tonkinensis Cupressus tonkinensis Cupressus duclouxiana

Map 4: Bisbee 2014: 33.

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