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## Pollen cone structure of the *Libocedrus s.l.* (Callitroideae, Cupressaceae) and its systematic implications for a controversial genus complex

### Abstract

A *Papuacedrus arfakensis* tree in the living collection of one of the authors (HN) first formed pollen cones in 2018. This event was used for a detailed morpho-anatomical study of the pollen cones, with two major aims: first, a detailed documentation of the pollen cone structure of *P. arfakensis*; second, a comparison of those data with those of the other three genera of the *Libocedrus s.l.* group to check whether there are any unique pollen cone features that clearly distinguish and separate the four genera *Austrocedrus*, *Libocedrus*, *Papuacedrus* and *Pilgerodendron* from each other.

According to our data, pollen cones within the *Libocedrus s.l.* group only show minor variation. They differ only slightly in the number of microsporangiphores per cone, the number of microsporangia per microsporangiphore and the dimensions of the microsporangia. Previously two major diagnostic differences were recognised in the group; the spiral or whorled arrangement of the microsporangiphores of *Papuacedrus*, and the larger number of microsporangia per microsporangiphore in *Pilgerodendron* than in the other taxa. These differences were emphasized and used to split *Libocedrus s.l.* in four distinct genera. However, in our material, all pollen cones of *Papuacedrus* had a decussate arrangement of microsporangiphores, as is also the case for all other taxa within the *Libocedrus s.l.* group. In our *Pilgerodendron* cones the number of microsporangia per microsporangiphore was not significantly increased compared to the other genera. Thus, the pollen cone structure is more or less similar throughout the entire *Libocedrus s.l.* group, as was previously shown also for the seed cone structure and for the majority of vegetative traits. Thus, the differences in the reproductive as well as vegetative structures are not sufficient enough to justify the systematic treatment of *Austrocedrus*, *Libocedrus*, *Papuacedrus* and *Pilgerodendron* as four distinct genera.

**Keywords:** pollen cones, morphology, systematic, microsporangia, microsporangiphores.

### Introduction

In 2018 a tree of *Papuacedrus arfakensis* cultivated in the living collection of HUBERTUS NIMSCH (Bollschweil, St. Ulrich, Freiburg im Breisgau, Germany) entered its reproductive phase and cones were produced for the first time. So far, only pollen cones have been produced. This fits well with the normal gender development in monoecious Cupressaceae. When individuals enter the reproductive phase, they exclusively produce pollen cones first, and then with increasing age later seed cones. It remains to be seen how the situation will develop in the next years: does the tree remain exclusively male, or will there be seed cones in addition?

This event is used now as an opportunity to investigate the structure of *Papuacedrus arfakensis* pollen cones in detail, and to compare them with pollen cones of other taxa belonging to the *Libocedrus s.l.* group (*Austrocedrus*, *Libocedrus* and *Pilgerodendron*). The aim of this study is not only a simple comparison of the pollen cone structure, but additionally to verify if the results are reliable enough to give statements about the systematic relationships within the *Libocedrus s.l.* group, which are still controversial and not finally resolved.

The evergreen coniferous genus *Papuacedrus* H.L.Li is native to Papua New Guinea, New Guinea and the East-Moluccas, where it occurs between (620-)900-3600(-3800) m above sea level (FARJON 2005). This genus belongs to the Cypress family (Cupressaceae). Within the Cupressaceae, *Papuacedrus* is a member of the exclusively southern hemisphere subfamily Callitroideae. The

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genus comprises only two taxa. Depending on the systematic view, they are treated either as two distinct species or both are treated as two subspecies (compare FARJON 2005, 2020; ECKENWALDER 2009; DÖRKEN & NIMSCH 2018, 2019). *Papuacedrus* and the three genera *Austrocedrus* FLORIN & BOUTELJE (one taxon; Chile and Argentina), *Libocedrus* ENDL. (five taxa; New Zealand and New Caledonia) and *Pilgerodendron* FLORIN (one taxon; southern Argentina and Chile) form a small, but complex cluster, comprising just few quite similar species. However, their systematic relationships are still controversial. Due to a very similar structure in the vegetative and also the reproductive parts, which show nearly no significant differences between the taxa, a systematic re-inclusion of all taxa into an enlarged genus *Libocedrus s.l.* could be justifiable, as mentioned by JAGEL & DÖRKEN 2015 who investigated the seed cones of the *Libocedrus s.l.* group.

Of the four genera belonging to the *Libocedrus s.l.* group only *Austrocedrus* is hardy enough in Central Europe to survive outdoors in protected and climatic mild conditions. In the forest arboretum Freiburg-Günterstal (Germany), *Pilgerodendron* is also cultivated; it has survived there outdoors, well protected by the canopy of the forest trees, for the last 20 years. However, all four genera are only rarely cultivated in common where they can be studied together, with *Austrocedrus* and *Pilgerodendron* the most “frequently” grown. In comparison, *Libocedrus* is only rarely cultivated. JOHNS (1995) describes *Papuacedrus* outside of Papua New Guinea as “*it is not known to be cultivated outside New Guinea*”. There are however, just a few, rare individuals, cultivated as pot plants in some special collections. Thus, it is not surprising that in particular for *Papuacedrus* only comparatively little data exists, especially about its reproductive structures. Even such basic features such as the distribution of the genders is still an open question. JOHNS (1995) describes the genus as basically dioecious, however he reports about single monoecious specimens which were found in its natural habitat on the Owen Stanley Mountains in Papua New Guinea. In contrast, KRÜSSMANN (1983), DE LAUBENFELS (1988), PAGE (1990) and ECKENWALDER (2009) describe the genus as monoecious. Also FARJON (2010) describes *Papuacedrus* as monoecious, however with an important additional note “*monoecious, often appearing dioecious*”. This is in accordance with the majority of existing herbarium specimens of *Papuacedrus*, where male and female vouchers were often collected from the same individual (JOHNS 1995). It could be shown that if the gender distribution is actually dioecious, then the majority of individuals are functionally often male, and the functionally exclusively female individuals represent the exception (JOHNS 1995). It could be conceivable that the general gender distribution is dioecious, however cones of both gender are not produced every year, so that there are male and female years, leading to the impression of dioecy. However, to solve this question without doubt additionally further *in situ* studies are necessary. Depending on the few *ex situ* cultivated individuals and the fact that most of them do not produce cones, reliable statements about the true gender distribution are not possible.

## Material und Methods

### Material

To investigate the morpho-anatomical structure, 20 mature pollen cones of each of the following species were collected shortly before pollen release. Material of *Papuacedrus arfakensis* was from the private living collection of HUBERTUS NIMSCH, Bollschweil, St. Ulrich, Germany; material of *Austrocedrus chilensis*, *Libocedrus bidwillii* and *Pilgerodendron uviferum* was collected in the Palmengarten, Frankfurt am Main, Germany; *A. chilensis* outdoors, *L. bidwillii* and *P. uviferum* in the sub-antarctic house. Herbarium vouchers of *Papuacedrus papuana* seed cones were provided by WOLF STIEGLITZ (curator of the cone collection in the Bot. Garden Wuppertal, Germany).

## Methods

Freshly collected material was photographed and then fixed in FAA (100 ml FAA = 90 ml ethanol 70% + 5 ml acetic acid 96% + 5 ml formaldehyde solution 37%) before being stored in 70% ethanol. The anatomy was studied from sections using the classical paraffin technique and subsequent astrablue/safranin staining (GERLACH 1984). Macrophotography was done with 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).

## Special terms

**Microsporangiophore:** because the identity of the coniferous pollen sac carrying structure is not finally resolved, the terms “sporophyll” or “microsporophyll” are not used, because homologies that are *a priori* applied to it should be avoided. Thus, the neutral term “microsporangiophore” (carrier of the pollen sacs) is used instead.

**Microsporangium (pollen sac):** structure developed on a microsporangiophore producing the pollen grains.

**Pollen cone:** the pollen producing “male” cones; in the majority of conifers unbranched structures usually with numerous pollen sacs (microsporangia) carrying structures (microsporangiophores). Pollen cones of all conifers are non-woody and dry out during or shortly after pollen release; dry and empty pollen cones are quickly abscised.

**Seed cone:** the ovule producing “female” cones. Within all conifers they are compound, inflorescence-like structures or can be regarded as being derived from such once; in the majority of species they become woody. After seed release the empty seed cones of some species remain, at time for several years, on the tree, while in others they abscise quickly or slowly.

**Scutellum:** small phylloid, distal structure, developed on the stalk of a microsporangiophore.

**Cone:** the more or less compact reproductive structures of conifers. The “male” cones producing the pollen are called pollen cones, the “female” cones producing the ovules, are called seed cones.

## Results

### Pollen cones of *Papuacedrus arfakensis*

The pollen cones are simple, unbranched, cone structures. They are developed densely on the previous year's small lateral, scale-leaved branchlets. The pollen cones are exclusively terminal; lateral axillary cones were not found (Fig. 1A-B). They are in an upright or plagiotropic position (Fig. 1A-B). The stalk of the cone is very short and does not elongate even at maturity, so the pollen cones are more or less sessile. (Fig. 1C). The mature pollen cones are about 5-15 mm long and 2-3 mm in diameter.

The pollen cone consists of a central cone axis, which bears 4-8(-10) pairs of microsporangiophores (Fig. 1C). There are 1-2 pairs of green, sterile, scaly transitional leaves developed below the first pair of fertile microsporangiophores (Fig. 1C). Bracts are absent in the cone (Fig. 1C). Microsporangiophores are decussately arranged (Figs 3 & 4). However some cones had an apparent spiral or whorled arrangement of microsporangiophores (Figs 1C, 1E & 2A). This non-decussate arrangement was mostly observed in small pollen cones with a very short cone axis, or in larger cones showing a very high number of microsporangiophores. In both cases, there is a lack of space on the cone axis and the microsporangiophores are densely arranged. Thus, maturing microsporangia push the stalks of adjacent microsporangiophores laterally out of their original position so that it appears that the microsporangiophores are in a spiral or whorled arrangement. However, the insertion points of the stalks at the cone axis clearly indicate the original decussate formation on the cone axis as illustrated clearly in Figs 3 & 4. Thus, the apparently spiral or whorled arrangement is just a result of bent microsporangiophore stalks which are so strongly curved that the distal parts (scutellum and microsporangia) get shifted out of their original decussate position. This clearly demonstrates the importance of anatomical sections as illustrated in Fig. 3 & 4. Without such anatomical sections, the actual decussate arrangement could not be proven in mature cones showing non-decussate microsporangiophores. When more material is available, additional developmental studies of earliest ontogenetic stages should be carried out, to show clearly the actual position of the microsporangiophore primordia.



There is a concentric vascular bundle in centre of the cone axis with inner xylem and an outer phloem. The xylem and phloem are not separated by any cambium, and endodermis is also absent. In the centre a distinct mark is developed. The concentric vascular bundle strand gets strongly interrupted by the leaf traces of the lateral microsporangiophores (Fig. 2B). The central vascular bundle strand is surrounded by a monomorphic, parenchymatic cortex, which is rich in cellulose. Sclerenchyma and resin ducts are absent (Fig. 2B).

All microsporangiophores are hyposporangiate, and consist of a central stalk, an adaxial terminal, phylloid-like green scutellum and abaxial microsporangia (Figs 1C, 1E & 2C-F). The scutellum has a triangular to slightly rhombic shape and a skinny, hyaline margin. It is about 1.8-2.3 mm long and 1.5-2.5 mm in diameter (Figs 1E & 2C-D). The scutelli of the distal microsporangiophores are however significantly smaller (Figs 2A & 2D); in some cases they were entirely reduced. These distal microsporangiophores consist only of the stalk and the abaxial microsporangia (Fig. 2A). On the lower side of the stalk there are (2-)3-4(-5) roundish, yellow microsporangia, which are developed in a single row (Tab.1). The microsporangiophores in the middle of the cone have the highest number of microsporangia (Fig. 2C). Distal microsporangiophores often develop just 2 microsporangia (Fig. 2D). The microsporangia are about 0.4-0.8(-1) mm in diameter (Figs 2C-F & 5). The distal scutellum and the microsporangia are always free and not fused to each other (Figs 2E & 5A). Mature microsporangia open via a stomium that represents a predefined line of dehiscence, which consists of flat and thin walled parenchymatic cells (Fig. 5B). The other cells of the microsporangia wall are large sized with distinct U-shaped wall thickenings (Fig. 5C).

There is only one collateral vascular bundle supplying the microsporangiophore, with the xylem located adaxially, and the phloem abaxially. This vascular strand is not branched. The vascular bundle has a closed structure; the xylem and phloem are not separated by any cambium. A vascular bundle sheath, controlling the exchange between the bundle strand and the surrounding tissue, is also absent. Within the majority of microsporangiophores, there is a resin duct below the vascular bundle (Fig. 2F).

In early developmental stages, the scutelli are imbricate and cover the developing microsporangia. Thus, they play an important role in protecting the young microsporangia, as protecting bud scales surrounding the cone are generally absent (Fig. 1D). Just shortly before pollen release, the cone axis elongates so that the microsporangia become exposed. The elongation of the cone axis is however not caused by cell division, but the consequence of pumping water into the cells, which elongates the cells. This elongation ensures that the microsporangia become best exposed to the ambient airflow and that pollen grains are released best out of the microsporangia (Fig. 1E). After pollen release, the pollen cones dry out quickly and are soon abscised.

### Pollen cones of *Austrocedrus*, *Libocedrus* and *Pilgerodendron*

As well as *Papuacedrus arfakensis*, pollen cones of *Austrocedrus chilensis*, *Libocedrus bidwillii* and *Pilgerodendron uviferum* were investigated. The results clearly indicate that their structure is broadly similar to that of *Papuacedrus*. They only differ slightly in the number of microsporangiophores per cone, in the number of microsporangia per microsporangiophore, and in the diameter of microsporangia (Table 1).

**Table 1:** Morphometric data of pollen cones developed in *Austrocedrus chilensis*, *Libocedrus bidwillii*, *Papuacedrus arfakensis* and *Pilgerodendron uviferum*; data based on 20 investigated pollen cones per species (d = decussate; h = hyposporangiate; t = terminal).

Taxa	pollen cones			Microsporangiophores			microsporangia		
	position	length [mm]	diameter [mm]	structure	arrangement	number per cone	number per microsporangiophore	diameter [mm]	arrangement
<i>A. chilensis</i>	t	5-15	2-3	h	d	10-12(-20)	(2-)3-4(-5)	0.5-0.6(-0.8)	single row
<i>L. bidwillii</i>	t	5-15	2-3	h	d	8-12(-20)	(2-)3-4(-6)	0.5-0.6(-0.8)	single row
<i>Pa. arfakensis</i>	t	5-15	2-3	h	d	8-16(-20)	(2-)3-4(-5)	0.4-0.8(-1)	single row
<i>Pi. uviferum</i>	t	5-15	2-3	h	d	8-12(-24)	(2-)2-4(-6)	0.5-0.6(-1)	single row

## Discussion

As already discussed in JAGEL & DÖRKEN (2015), the existing genus concept of the *Libocedrus s.l.* group seems to be more likely geographically motivated than being based on reliable distinct morpho-anatomical differences. The vegetative structure of *Pilgerodendron* (Figs 6D & 7D) differs from the other three genera by a different foliage and arrangement of lateral branchlets. In *Pilgerodendron* the decussate small needle leaves are monomorphic and are spreading distinctly from the shoot axis (Fig. 7D). Furthermore, the shoots are not two-dimensional flattened but three-dimensionally arranged (Fig. 6D; DÖRKEN & NIMSCH 2018, 2019). In *Austrocedrus* (Figs 6A & 7A), *Libocedrus* (Figs 6B & 7B) and *Papuacedrus* (Figs 6C & 7C) the leaves are scaly and show a distinct leaf dimorphism with lateral and facial leaves, which are strongly adpressed to the shoot axis. Additionally the shoots are two-dimensionally flattened (DÖRKEN & NIMSCH 2018, 2019). Further structural differences in the vegetative body can be found in the wood anatomy (PEIRCE 1937). For example, within the *Libocedrus s.l.* group, *Papuacedrus* has the largest tracheids and also the largest cross-field pits (FARJON 2005). Furthermore, the four genera differ slightly in the formation and arrangement of stomata, the size of the epidermis cells and the formation of the cuticle (FLORIN 1930b; FLORIN 1951; FLORIN & BOUTELJE 1954), which could be interpreted as adaptations to the distinct and different local climatic conditions.

Even in times of molecular phylogenies, the reproductive structures are of great systematic importance. The structure of these should either be so similar, or so distinct, that they could allow a clear definition of a genus or separation from others. Previous investigations of seed cones have already shown that they are structurally quite similar within the *Libocedrus s.l.* group. The seed cones consist of two decussate pairs of cone scales. The distal pair is always significantly larger than the lower one (Fig. 8). Only the distal pair of cone scale is fertile and produces two ovules per cone scale. When only a single ovule is formed, the second one is mostly aborted in the earliest ontogenetic stages. In all taxa, the central columella, which represents the tip of the cone axis (DÖRKEN & JAGEL 2017), is visible as a small, pointed tip. The mature seed cones differ only marginally in the size and formation of the dorsal umbo developed on the back of the cone scales (Fig. 8), which can differ not only markedly between the currently commonly accepted different genera of the *Libocedrus s.l.* group, but also within species of a same genus. This is well illustrated by the accepted species in the genus *Libocedrus s.str.*, where strong variations are observed (TOMLINSON *et al.* 1993; CASTOR *et al.* 1996; JAGEL 2001; JAGEL & DÖRKEN 2015, NIMSCH & DÖRKEN 2020). For example in the New Caledonian *Libocedrus* species, the umbo of *L. chevalieri* is quite short and only slightly exceeds the cone scales (Fig. 10), compared to the very long umbo of *L. austrocaledonica* which significantly exceeds the length of the cone scale (Fig. 11). The lengths of the umbos of *L. yateensis* (Fig. 9), are more or less intermediate between *L. chevalieri* and *L. austrocaledonica* (NIMSCH & DÖRKEN 2020). Additionally, in *L. austrocaledonica* and *L. yateensis* the length of the umbos of the lower sterile pair of the cone scales is broadly similar to these of the upper fertile pair of the cone scales. In *L. chevalieri* however, the lengths of the umbos of the fertile and sterile pairs of cone scales are less similar (compare drawings in FARJON 2005, 2010 and descriptions in NIMSCH & DÖRKEN 2020).

The results of these pollen cone investigations also show no significant differences between the four currently accepted genera. The dimensions and the structure of mature pollen cones are more or less identical throughout all investigated species and show only marginal differences. Pollen cones of all four genera represent unbranched uniaxial structures, carrying exclusively decussately arranged hyposporangiate microsporangioophores. However, unlike our results, GIBBS (1917) and LI (1953) described microsporangioophores of *Papuacedrus* as spirally arranged, which if correct is not only a distinct and unique character within the *Libocedrus s.l.* group, but additionally also within the entire Cupressaceae *s.str.* (= subfamilies Cupressoideae and Callitroideae). In contrast to the Cupressaceae *s.l.* (= subfamilies Cunninghamioideae, Athrotaxoideae, Taiwanoideae, Sequoioideae and Taxodioideae), microsporangioophores of Cupressaceae *s.str.* are not spirally arranged. In the majority of species they are in decussate pairs; only in some *Juniperus* species (mostly in species of

section *Juniperus*, e.g. *J. communis*, and of section *Caryocedrus* (*J. drupacea*) and in *Actinostrobus* and *Callitris* species, they are arranged in alternating whorls of three (FARJON 2005, 2010; ECKENWALDER 2009; DÖRKEN 2019; DÖRKEN & STÜTZEL 2019), and e.g. in *Neocallitropsis* also whorls of 4 are developed (FARJON 2005, ECKENWALDER 2009). With the pollen cones investigated by FLORIN (1951) and FLORIN & BOUTELJE (1954), or in our material, a spiral arrangement of microsporangiophores in *Papuacedrus* was not found. However, FLORIN (1951), as well as FLORIN & BOUTELJE (1954) and KRÜSSMANN (1983), describe the microsporangiophores in whorls of four. FLORIN & BOUTELJE (1954: 26 & 30) describe them as “being arranged in whorls of four instead of decussately” (p. 26) and as “in pairs, of which two always appeared to be at the same level” (p. 30). Also RUSHFORTH (1987: 143) describes the position of microsporangiophores in whorls of four, and writes explicitly that they are not decussate: “set in whorls of 4, not in decussate pairs”. FARJON (2005: 433, 2010: 536) describes the position of microsporangiophores of *Papuacedrus* as decussate or in whorls of four “decussate or in whorls of 4”. However here differences between the two species *P. papuana* and *P. arfakensis* are mentioned, *P. papuana* – decussate or whorled, *P. arfakensis* exclusively whorled. In contrast to that, DE LAUBENFELS (1988) and ECKENWALDER (2009: 360) describes the position as decussate. DE LAUBENFELS (1988: 444) – with *papuana* under *Libocedrus* – writes: “The New Guinea species was separated on the basis of spirally placed microsporophylls. In fact, simple opposite decussate pollen cones occur alongside crowded cones whose microsporophylls appear to be whorled or perhaps spirally placed” as is also shown in a line drawing in that publication (1988: 446, Fig. 89, C). The same drawing showing opposite microsporangiophores is also presented in JOHNS (1995: 69). ECKENWALDER (2009: 360) writes “8-10 alternating pairs of pollen scales often arranged like four or five aligned quartets or so crowded as to appear irregular”. Our results are in accordance with the findings of DE LAUBENFELS (1988) and ECKENWALDER (2009). When having a closer look at the leaf traces entering the microsporangiophores, it is clearly visible that there are always only two and not four opposite leaf traces leaving the concentric bundle of the cone axis in the same plane and enter the stalk of each microsporangiophore (Figs 3 & 4). If the microsporangiophores would have been in whorls of four, then four vascular bundles should leave the concentric bundle of the cone axis in the same plane. This finding clearly show that the arrangement of microsporangiophores is in decussate pairs. However, the subsequent microsporangiophores are, due to a lack of space, often developed closely to the lower pair so that it seems that the microsporangiophores are arranged in whorls of four. DE LAUBENFELS (1988) and ECKENWALDER (2009) describe that in pollen cones with a very dense arrangement of microsporangiophores or a very short cone axis the microsporangiophores are apparently in a spiral or whorled arrangement. Our results strongly support these findings of DE LAUBENFELS (1988) and ECKENWALDER (2009). Pollen cones with a very short cone axis are more or less roundish or nearly globose. In consequence, space within these pollen cones is therefore very restricted and the microsporangiophores in these pollen cones are much more densely arranged than in pollen cones showing the typical longer cone axis. Due to the continuously increasing size of the developing microsporangia in combination with the lack of space, stalks of neighboured microsporangiophores can easily be pushed out of their original position, so that their arrangement finally seems to be spirally or whorled. However, a close look at the insertion points of the stalks at the cone axis clearly show the true arrangement, that is, also in these cones, decussate pairs (Figs 3 & 4).

In regard to the problematic decussate vs whorled arrangement of microsporangia FARJON (2005) pursued another interesting idea. In Cupressaceae the phyllotaxis in vegetative parts (= foliage) corresponds always to that of the reproductive units (= cones). Mature individuals of *Papuacedrus* have a decussate leaf arrangement however, in juveniles also whorls of four leaves occur. FARJON (2005) describes a correlation between the arrangement of leaves (decussate vs whorled), the type of foliage (juvenile vs mature) and the position of the microsporangiophores (decussate vs whorled). FARJON describes the position as basically decussate. A whorled arrangement of microsporangiophores can be only found on branchlets still showing the juvenile foliage with leaves arranged in whorls of four. Such a shift in the phyllotaxis can be also observed in numerous seedlings of *Cupressus* with juvenile needle leaves, which are arranged in whorls of four before

shifting to the mature type of foliage with decussate scale leaves (personal observations). In other taxa, e.g. *Callitris macleayana*, a similar shift can be observed; the juvenile needle leaves are arranged in whorls of four, the mature scale leaves however in whorls of three (DÖRKEN *et al.* 2019). When regarding the microsporangiophores as pollen producing leaves in the sense of a sporophyll, this is a strong argument supporting the idea that there is no difference in the leaf arrangement between vegetative and reproductive part, because the leaf arrangement on vegetative branchlets correspond to the arrangement of microsporophylls on the cone axis. This idea fits well to the situation here: the pollen cones with their decussate microsporangiophores were developed on exclusively scale leaved branches showing a decussate phyllotaxis.

If the arrangement of microsporangiophores is actually decussate as it is demonstrated in this study or if it is whorled as suggested by FLORIN (1951), FLORIN & BOUTELJE (1954), KRÜSSMANN (1983) and FARJON (2005, 2010), it can finally be solved by ontogenetic studies dealing with the earliest developmental stages and the formation of the primordia of the microsporangiophores at the cone axis.

In the studied pollen cones no evidence for a spiral arrangement of microsporangiophores as described by GIBBS (1917) and LI (1953) was found. Our results agree with FLORIN & BOUTELJE (1954) that the postulated relationship between the Taxodiaceae (at that time still regarded as a distinct family, today merged into the Cupressaceae as 5 subfamilies, Cunninghamioideae, Athrotaxoideae, Taiwanoideae, Sequoioideae and Taxodioideae) and *Papuacedrus*, as suggested by LI (1953), is not supported.

The pollen cones within the *Libocedrus s.l.* group only differ slightly in the number of microsporangiophores per cone, the number of microsporangia per microsporangiophore, and the size of the microsporangia (Tab. 1). In one of the latest conifer phylogenies (YANG *et al.* 2022) the four *Libocedrus s.l.* genera are split into 3 tribes – tribe 1: Papuacedreae Y.YANG, *trib. nov.* (only *Papuacedrus*), Tribe 2: Austrocedreae Y.YANG, *trib. nov.* (only *Austrocedrus*) and tribe 3: Libocedreae H.L.LI (*Libocedrus* and *Pilgerodendron*) with *Papuacedrus* as sister to *Austrocedrus* and *Libocedrus* sister to *Pilgerodendron*. A high number of microsporangiophores (8-30) in *Papuacedrus* is mentioned as one of the main morphological features distinguishing the Austrocedreae from the Papuacedreae. However, in our investigated material of *Papuacedrus arfakensis* the number of microsporangiophores per pollen cone was 8-16(-20) and is therefore in accordance with the other genera of the *Libocedrus s.l.* group (Tab. 1) and not significantly higher than in the other taxa (*Austrocedrus chilensis* 10-12(-20), *Libocedrus bidwillii* 8-12(-20), and *Pilgerodendron uviferum* 8-12(-24)). In our material the highest number of microsporangiophores per pollen cone (with up to 24) was actually found in *Pilgerodendron*. Additionally in this phylogeny, the microsporangiophores of *Papuacedrus* are described as “peltate microsporophylls”. In none of our investigated pollen cones peltate microsporangiophores were found; all had throughout a hyposporangiate structure as is the case for all other species of the *Libocedrus s.l.* group (Tab. 1). Thus, in our results, the structure of the pollen cones, and in particular the number of microsporangiophores per cone and the type of microsporangiophore, could not be used as a reliable argument to justify this split into two new described tribes Austrocedreae and Papuacedreae. This is notable in the respect that in other conifer genera the structural differences of pollen cones can be much more distinct. For example in *Juniperus* (Cupressaceae: Cupressoideae), the pollen cones of *J. drupacea* (Sect. *Caryocedrus*) are compound and “inflorescence”-like, while in all other *Juniperus* species, they are simple and therefore “flower”-like. Additionally the number of microsporangiophores and the number of inserted microsporangia per microsporangiophore vary distinctly and this not only between the distinct *Juniperus*-species, but also within a species and even within a single pollen cone (compare LEMOINE-SÉBASTIAN 1967 & DÖRKEN 2019).

FLORIN (1930a) and FARJON (2005, 2010) mention a significant higher amount of microsporangia per microsporangiophore in *Pilgerodendron*, which would be a distinct feature to distinguish *Pilgerodendron* from the rest of the *Libocedrus s.l.* species. FLORIN (1930a) mentions 6(-4-8),



exceptional up to 10 microsporangia per microsporangiphore, FARJON (2005, 2010) says 4-8(-10). This high number of microsporangia per microsporangiphore was not found in our investigated material. Our results with 3-4(-5) microsporangia per microsporangiphore are more like those of LI (1953), who mentioned 4-8 microsporangia per microsporangiphore. Despite FARJON (2005, 2010) mentioning a high number of microsporangia per microsporangiphore, the microsporangiphore he has drawn (FARJON 2005: 454, Fig. 122-7, up) with just 4 microsporangia, corresponds well with the situation in our available material. This high number of microsporangia per microsporangiphores mentioned by FLORIN (1930a) and FARJON (2005, 2010) is remarkable, because FLORIN describes *Pilgerodendron uviferum* pollen cones as 2 mm in diameter, FARJON as 2-2.5 mm. Our investigated microsporangia are 0.5-0.6(-1) mm in diameter. This means, if there are 10 microsporangia per microsporangiphore, a possible total cone diameter of up to 1 cm would be obtained. This high number of microsporangia per microsporangiphore in cones showing total cone diameter of maximum 2.5 mm as mentioned by FLORIN and FARJON could therefore only be realised if the size of each microsporangium were strongly reduced, or the hyposporangiate structure could be replaced by a perisporangiate one, with microsporangia developed all around the stalk of the microsporangiphore (as can be found in some Taxaceae like *Taxus* and *Pseudotaxus*; WILDE 1975; MUNDY 2000; MUNDY & MUNDY 2001; DÖRKEN *et al.* 2011; DÖRKEN & NIMSCH 2016). However, perisporangiate microsporangiphores were not found in any of our investigated *P. uviferum* pollen cones. A further possibility to increase the number of microsporangia per microsporangiphore is an arrangement in more than one row as can be found in some *Juniperus* species (in Cupressaceae *s.str.*) (DÖRKEN 2019). For example in *J. drupacea* there are up to 11 microsporangia per microsporangiphore developed in 3 rows on the lower side of the stalk. But in our investigation of *P. uviferum* pollen cones, microsporangia were always inserted in a single abaxial row, parallel to the lower margin of the adaxial scutellum. Thus, it remains open, how the high number of microsporangia per microsporangiphores described in FLORIN (1930a) and FARJON (2005, 2010) were developed, without exceeding the cone diameter of 2-2.5 mm. This clearly indicates that further investigation is needed in this respect, ideally with material collected *in situ*.

## Conclusion

Following the results of JAGEL & DÖRKEN (2015, seed cones) and the present study, the lack of distinct morpho-anatomical differences in the vegetative and reproductive structures in the four species *A. chilensis*, *Papuacedrus papuana*, *P. afarkenensis* and *Pilgerodendron uviferum*, they are returned to the genus *Libocedrus*:

- *Libocedrus chilensis* (D.DON) ENDL. (1847) [basionym *Thuja chilensis* D.DON (1832)]
- *Libocedrus papuana* F.MUELL. (1891)
- *Libocedrus arfakensis* GIBBS (1917)
- *Libocedrus uvifera* (D.DON) PILG. (1926) [basionym *Juniperus uvifera* D.DON (1828)]

The total number of species in the *Libocedrus* genus rises to 9 with:

- *Libocedrus bidwillii* HOOK. (1864)
- *Libocedrus austrocaledonica* BRONGN. & GRIS (1872)
- *Libocedrus plumosa* (D.DON) DRUCE (1917) [bas. *Dacrydium plumosum* D.DON (1828)]
- *Libocedrus chevalieri* J.BUCHHOLZ (1949)
- *Libocedrus yateensis* GUILLAUMIN (1949)

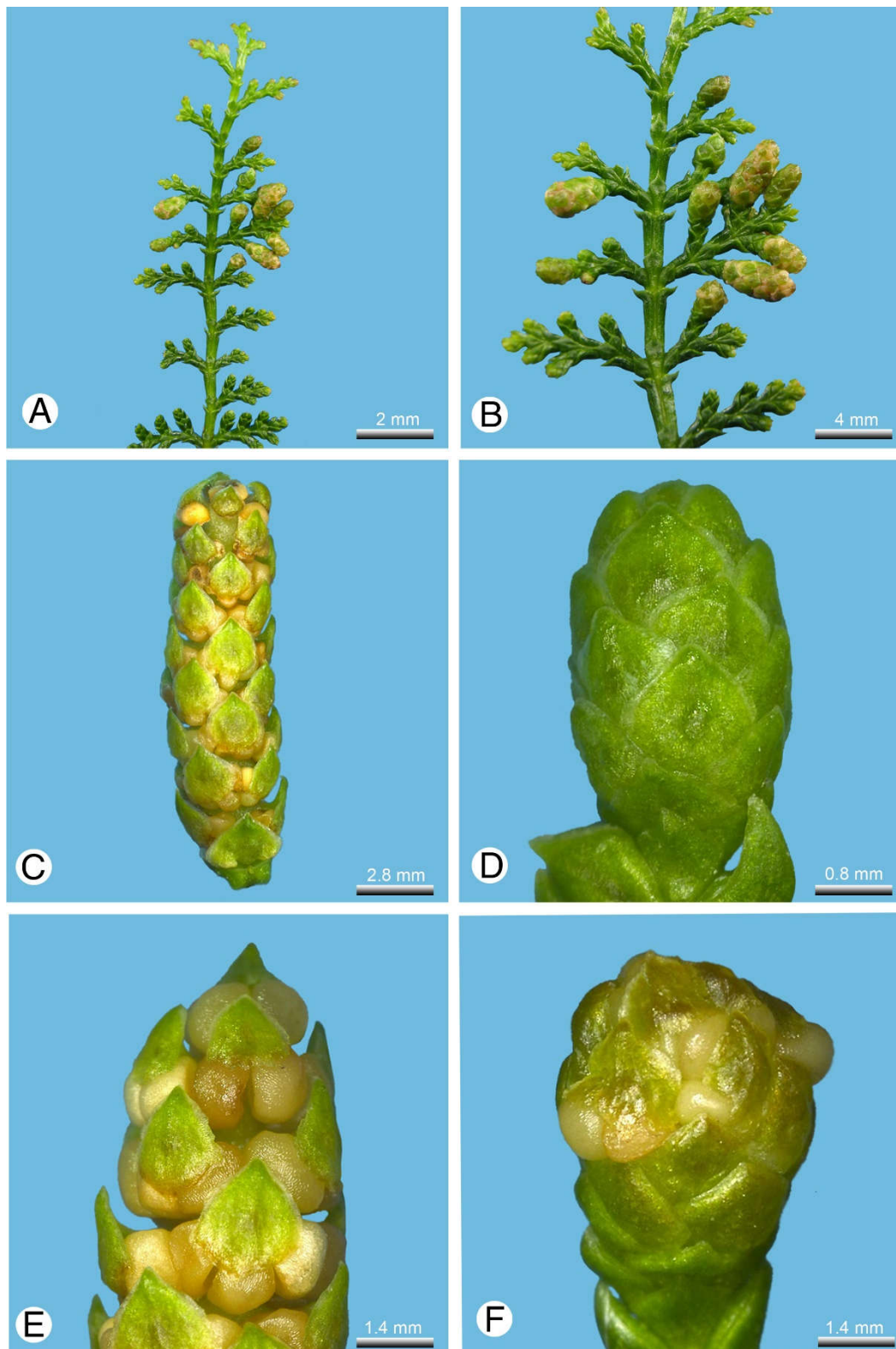
In this study the widely accepted genus names were used for clarity, pending circulation of the study. From now on, they should be regarded as synonyms.

## Acknowledgements

We thank the Palmengarten Frankfurt am Main (Germany) and WOLF STIEGLITZ, curator of the cone collection presented in the Bot. Garden Wuppertal (Germany) for generously providing research material and Dr. MICHAEL LAUMANN and Dr. PAAVO BERGMANN (Electron Microscopy Center, Universität Konstanz) for technical support (paraffin technique). We also thank the website [endemia.nc](http://endemia.nc) and the photographers of New Caledonia R. AMICE, A. LESPES, D. & I. LÉTOCART, B. SUPRIN for providing the images of Figs 9-11, for the photo gallery and for giving their agreement to use them.

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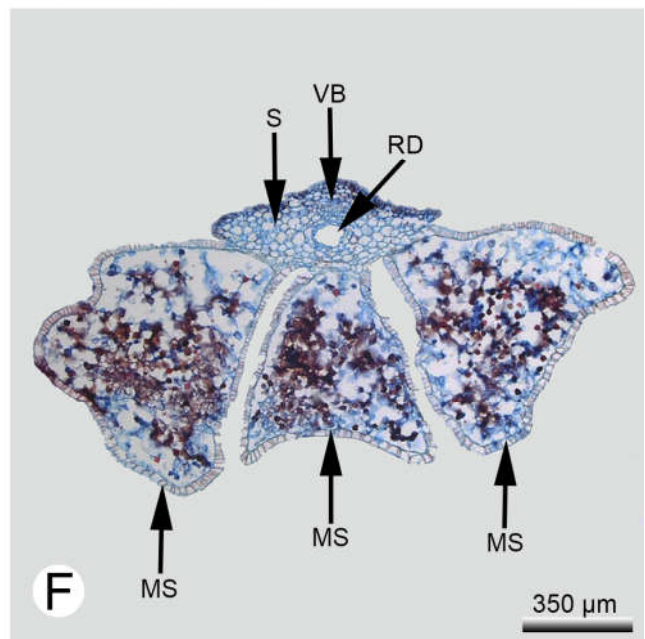
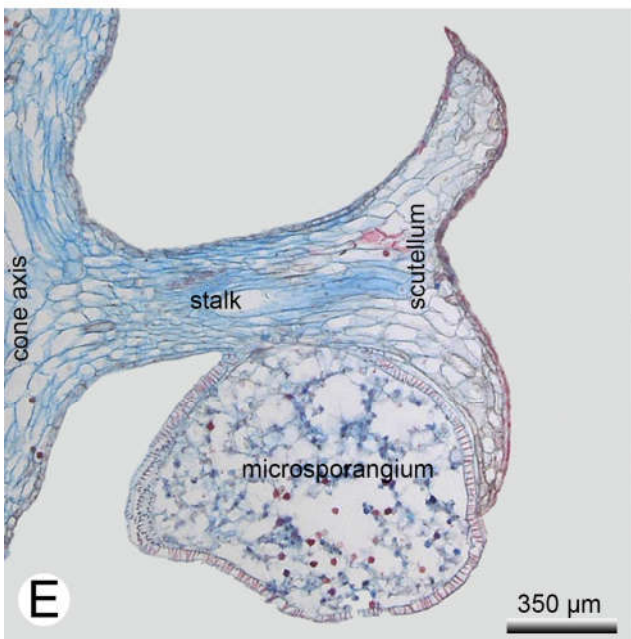
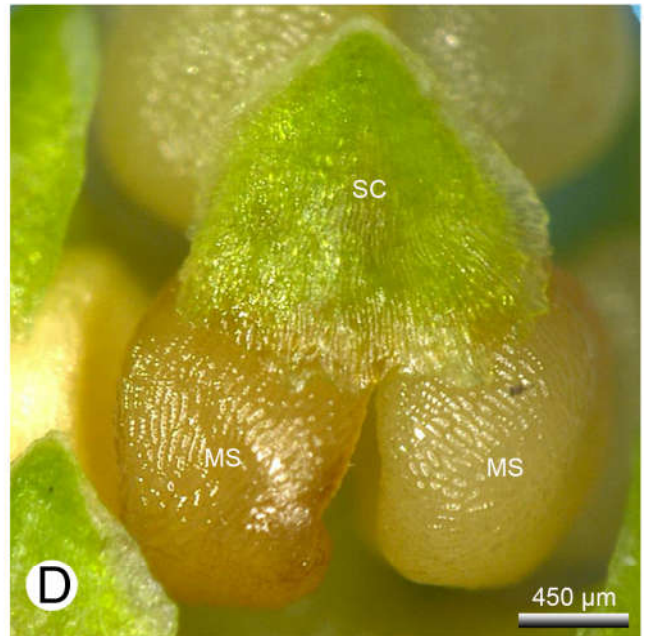
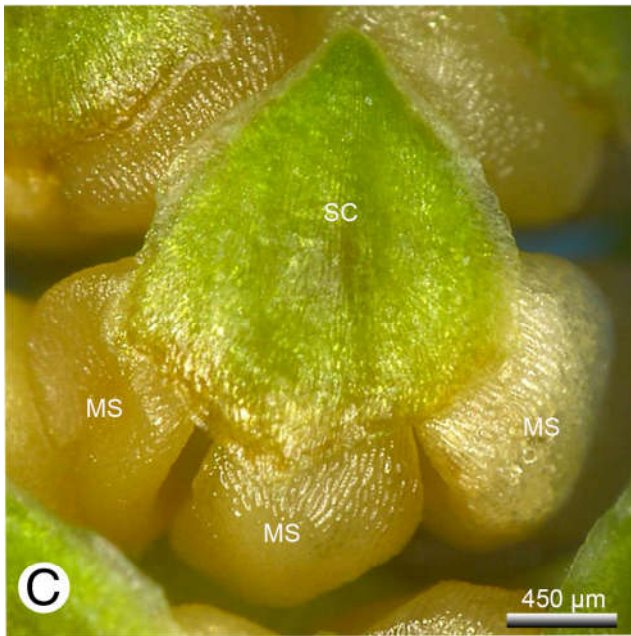
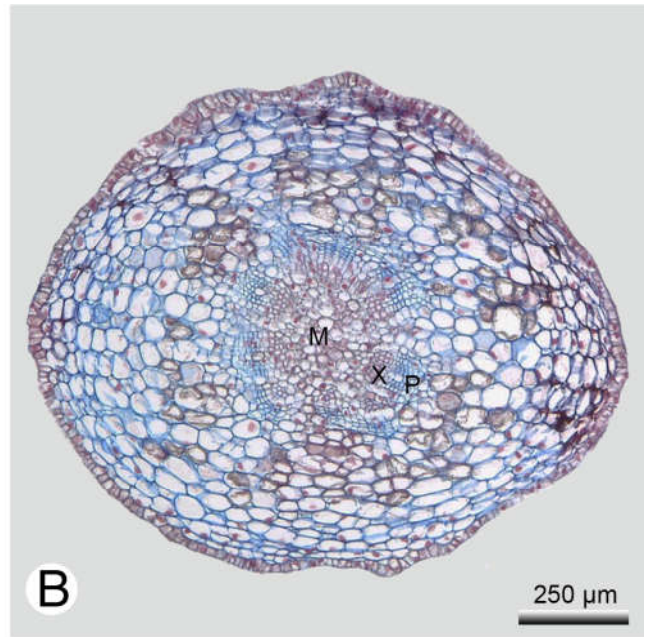
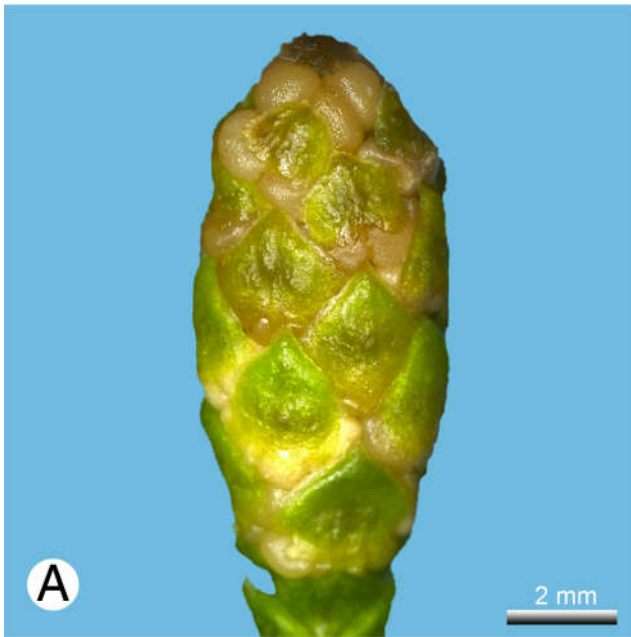


**Fig. 1:** *Papuacedrus arfakensis*, morphology of pollen cones (PC).

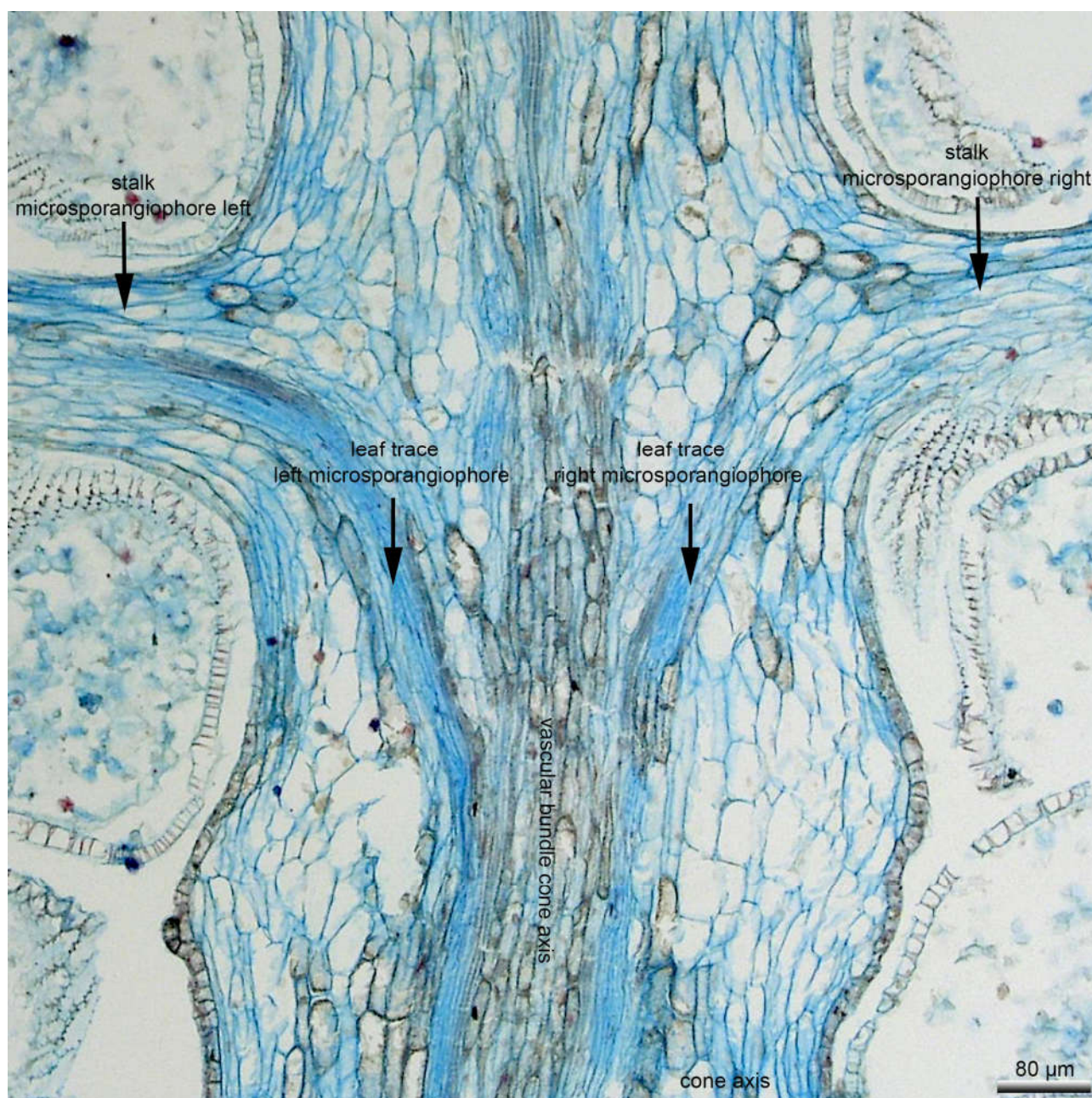
**A:** Fertile lateral branchlet; PC terminal on short, last year's branchlets. **B:** Detail of A. **C:** Mature PC with a high number of microsporangioophores; due to a lack of space on the cone axis the maturing microsporangia have pushed the stalks of adjacent microsporangioophores laterally out of their original position. **D:** Juvenile PC; scutelli imbricate and cover the microsporangia. **E:** Distal part of the mature PC illustrated in C, with spreading microsporangioophores. **F:** PC with a reduced cone axis; microsporangioophores seem to be in a spiral arrangement due to a lack of space within the cone because the maturing microsporangia push the stalks of the microsporangioophores out of their original position.

Images: V.M. DÖRKEN.









**Fig. 3:** *Papuacedrus arfakensis*, longitudinal section of a pollen cone showing the decussate microsporangiophores; the collateral leaf traces of the microsporangiophores are leaving the concentric stem bundle at the same level. Image: V.M. DÖRKEN.

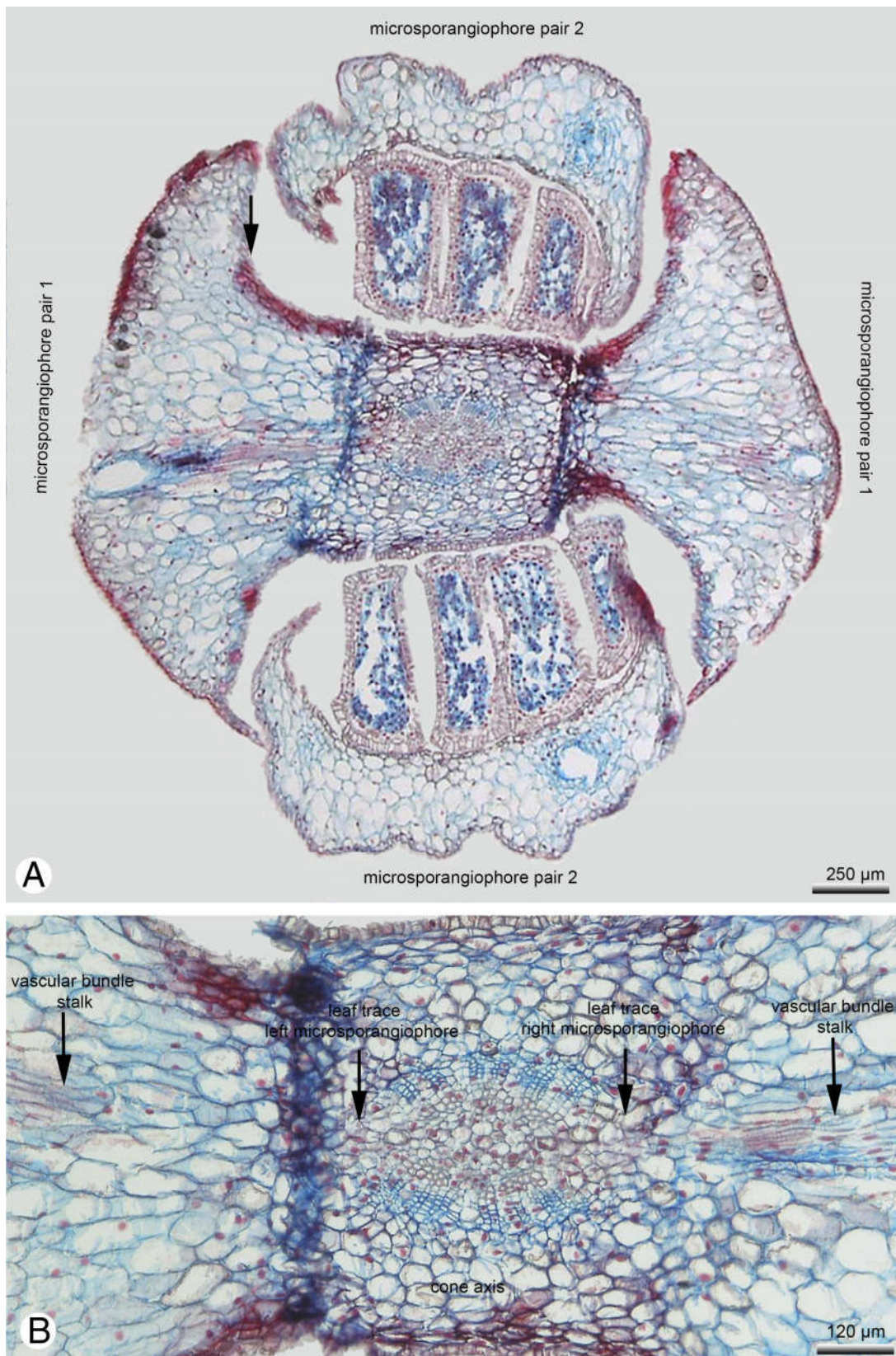
**Fig. 2 (p. 12):** *Papuacedrus arfakensis*, morphology and anatomy of microsporangiophores.

A: Pollen cone with a short cone axis and densely arranged microsporangiophores; maturing microsporangia push the stalks of adjacent microsporangiophores laterally out of their original position so that it seems that the microsporangiophores are in a spiral or whorled arrangement; scutelli of distal microsporangiophores strongly or entirely reduced. B: Cross section in the middle of the cone axis, showing the concentric stem bundle which is strongly interrupted by the leaf traces of the microsporangiophores. C: Microsporangiophore from the middle of the cone; there are three microsporangia. D: Distal microsporangiophore with a small scutellum, only two microsporangia. E: Longitudinal section of a microsporangiophore. F: Cross section of a microsporangiophore; the stalk of the microsporangiophore is carrying three microsporangia.

M = mark; MS = microsporangium; P = phloem; RD = resin duct; S = stalk; SC = scutellum; VB = vascular bundle; X = xylem.

Images: V.M. DÖRKEN.

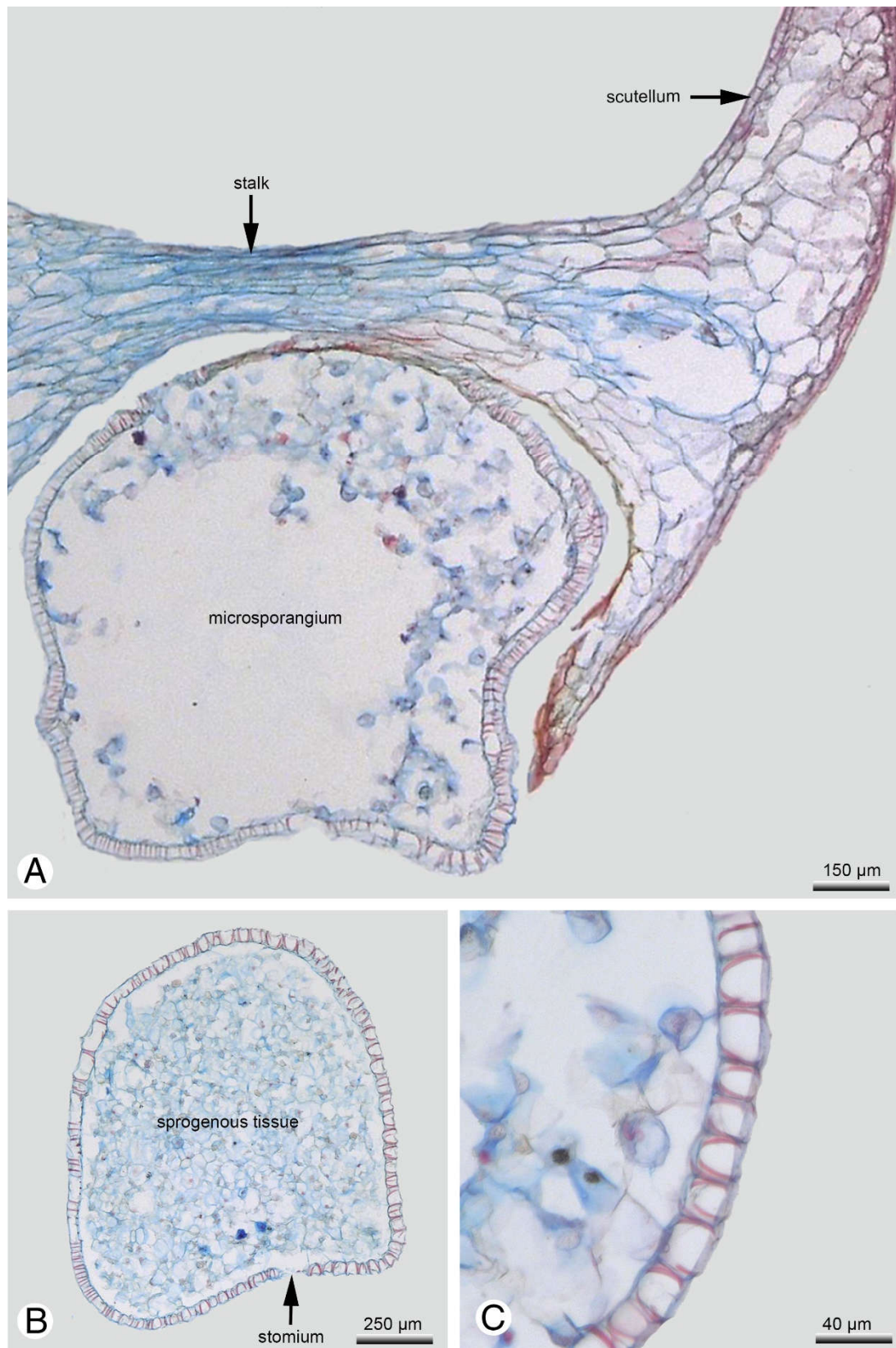




**Fig. 4:** *Papuacedrus arfakensis*, cross section of a pollen cone.

**A:** Overview showing the decussate microsporangiophores. **B:** Detail of the pollen cone axis (cross section) showing the two leaf traces of the decussate microsporangiophores leaving the concentric stem bundle at the same level.

Images: V.M. DÖRKEN.

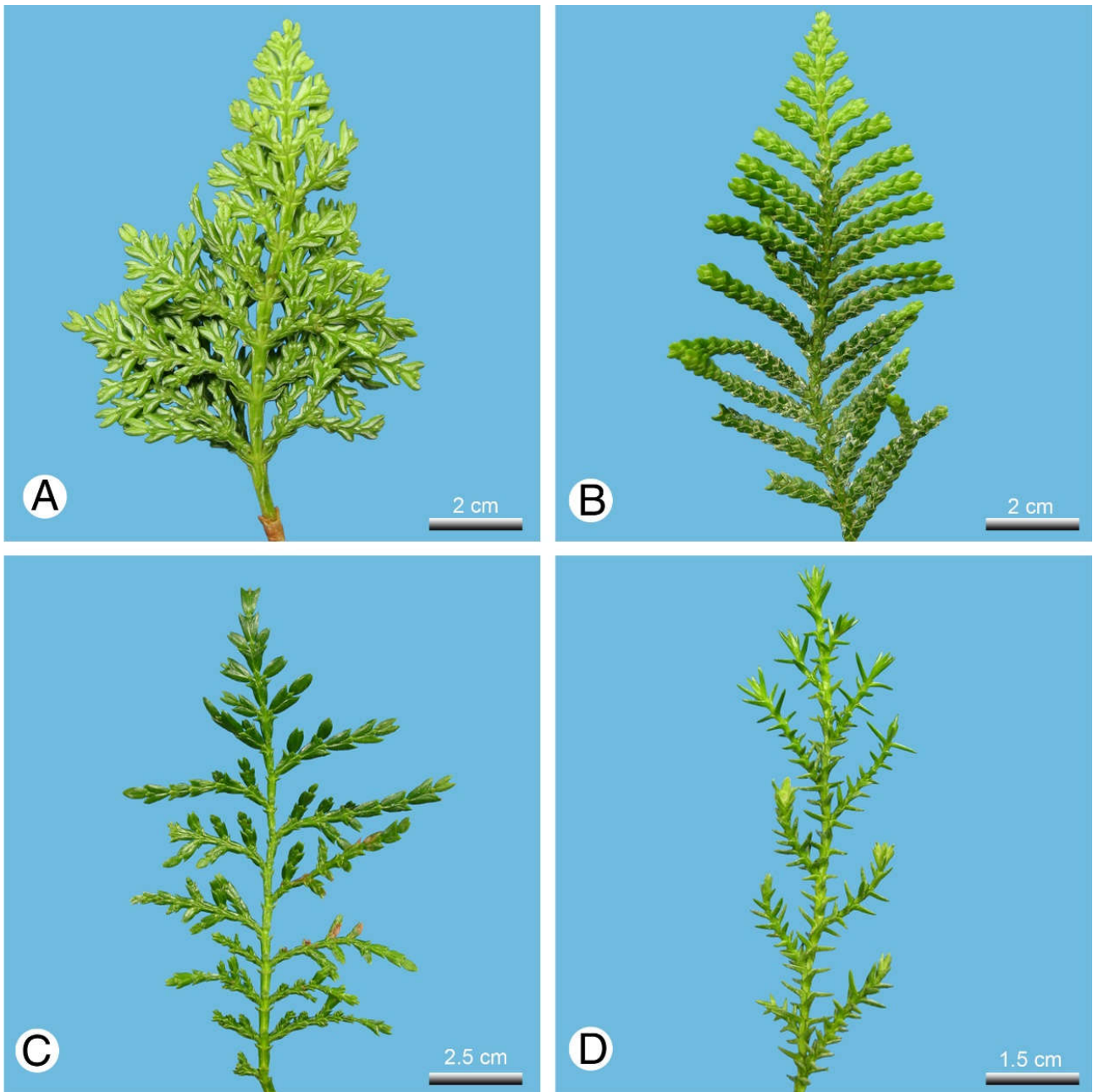


**Fig. 5:** *Papuacedrus arfakensis*, anatomy of microsporangia.

**A:** Scutellum and microsporangia are always free and never fused to each other. **B:** Cross section of a juvenile microsporangium; thin walled cells mark the later line of dehiscence (arrow). **C:** Detail of the microsporangium wall; cells with U-shaped wall thickenings.

Images: V.M. DÖRKEN.





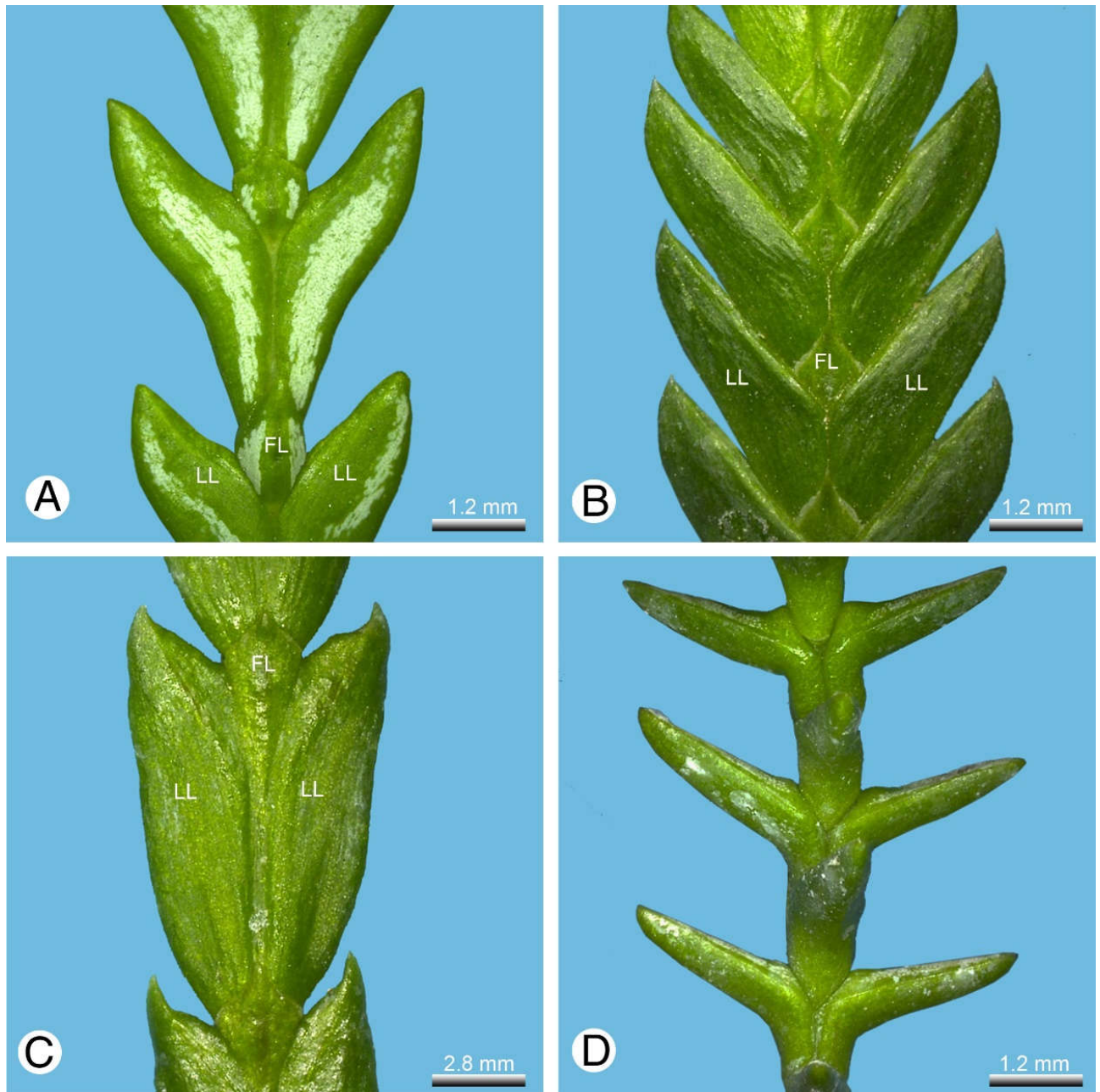
**Fig. 6:** Lateral shoots morphology of the *Libocedrus s.l.* group.

**A:** *Austrocedrus chilensis*. **B:** *Libocedrus plumosa*. **C:** *Papuacedrus arfakensis*. **D:** *Pilgerodendron uviferum*.

Lateral shoots of the genera *Austrocedrus* (A), *Libocedrus* (C) and *Papuacedrus* (D) two-dimensional flattened; in *Pilgerodendron* (G) three-dimensional spreading.

Images: V.M. DÖRKEN.



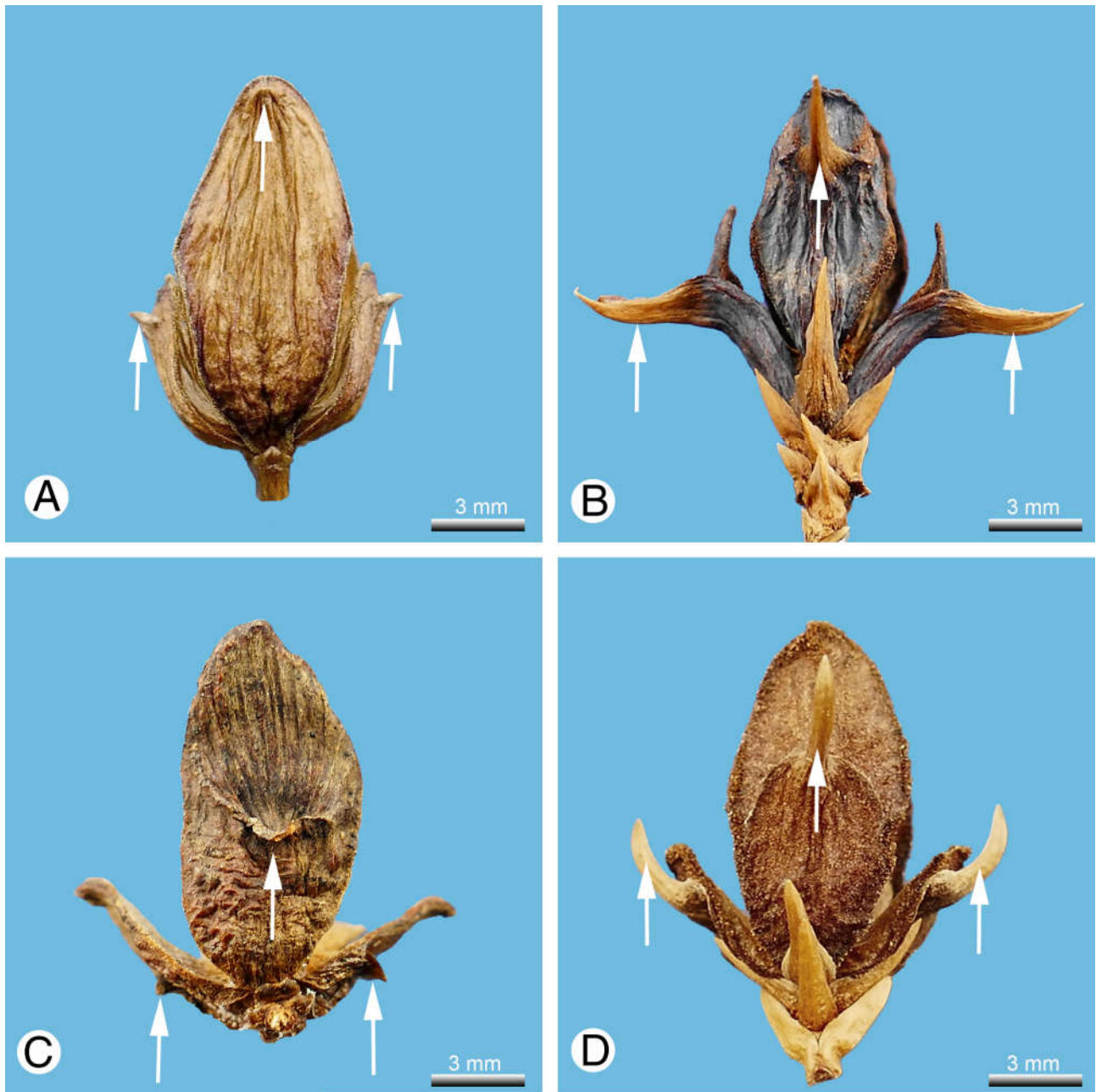


**Fig. 7:** Leaf morphology of the *Libocedrus* s.l. group.

**A:** *Austrocedrus chilensis*. **B:** *Libocedrus plumosa*. **C:** *Papuacedrus arfakensis*. **D:** *Pilgerodendron uviferum*.

*Austrocedrus* (B), *Libocedrus* (B) and *Papuacedrus* (C) with dimorphic scale leaves, that can be distinguished in facial (FL) and lateral leaves (LL); *Pilgerodendron* (H) monomorphic, small spreading needle leaves (FL = facial leaves; LL = lateral leaves).

Images: V.M. DÖRKEN.



**Fig. 8:** Seed cones of the *Libocedrus s.l.* group; seed cones more or less uniformly shaped; they mainly differ by the formation of the dorsal umbo developed on the back of the cone scales (arrows). See discussion p. 6.

**A:** *Austrocedrus chilensis*; **B:** *Libocedrus plumosa*; **C:** *Papuacedrus papuana*; **D:** *Pilgerodendron uviferum*.

Images: V.M. DÖRKEN.





**Fig. 9:** *Libocedrus yateensis*, seed cone displaying its long umbos. © A. LESPES, [Parc provincial de la Rivière Bleue](#), New Caledonia.

All photos on this page were obtained thanks to [endemia.nc](#) and their photographers.

**Fig. 10:** *Libocedrus chevalieri*, seed cone with shorter umbos. © R. AMICE, New Caledonia.



**Fig. 11:** *Libocedrus austrocaledonica*, seed cones. © D. & I. LÉTOCART, New Caledonia.





## ***Libocedrus* photo gallery (1) South America and New Zealand**



**Fig. 1:** Seed cones of *Libocedrus plumosa*, cultivated. Natural habitat: New Zealand      © A. Jagel





**Fig. 2:** Seed cones of *Libocedrus bidwillii*, cultivated. Natural habitat: New Zealand      © A. Jagel





**Fig. 3:** Seed cones of *Libocedrus chilensis*, cultivated. Natural habitat: Chile, Argentina.

© A. Jagel





**Fig. 4:** Seed cones of *Libocedrus uvifera*, cultivated. Natural habitat: Chile, Argentina.

© A. Jagel



## ***Libocedrus* photo gallery (2) New Caledonia**

The website [endemia.nc](http://endemia.nc) is the most important source for the fauna and flora of New Caledonia. The link under each *Libocedrus* Latin name opens the record of the species on [endemia.nc](http://endemia.nc). [Contact](#).

### ***Libocedrus chevalieri***







**Fig. 2:** Habitat (tree in centre). Mont Humboldt. Alt. 1550-1620 m. 2005.02.10-11. © R. Amice.

**Fig. 3:** Tree. Architecture. Mont Humboldt. Alt. 1550-1620 m. 2005.02.10-11. © R. Amice.



**Fig. 1 (p. 24):** Trees. Mont Humboldt. Alt. 1500-1600 m. 2005.02.10-11. © R. Amice.





**Fig. 4:** Shrub in its habitat. Mont Humboldt. © B. Suprin.

**Fig. 5:** Branches with shoots. Mont Humboldt. © B. Suprin.







**Fig. 6:** Branch with shoots. Mont Humboldt. Alt. 1550-1620 m. 2005.02.10-11. © R. Amice.





**Fig. 7:** Shoots. Mont Humboldt. Alt. 1550-1620 m. 2005.02.10-11. © R. Amice.

**Fig. 8:** Close-up of shoots. Mont Humboldt. Alt. 1550-1620 m. 2005.02.10-11. © R. Amice.







**Fig. 9:** Old pollen cones after pollen release (brown) and immature pollen cones before pollen release (light pinkish-green). Mont Humboldt. Alt. 1550-1620 m. 2005.02.10-11. © R. Amice.

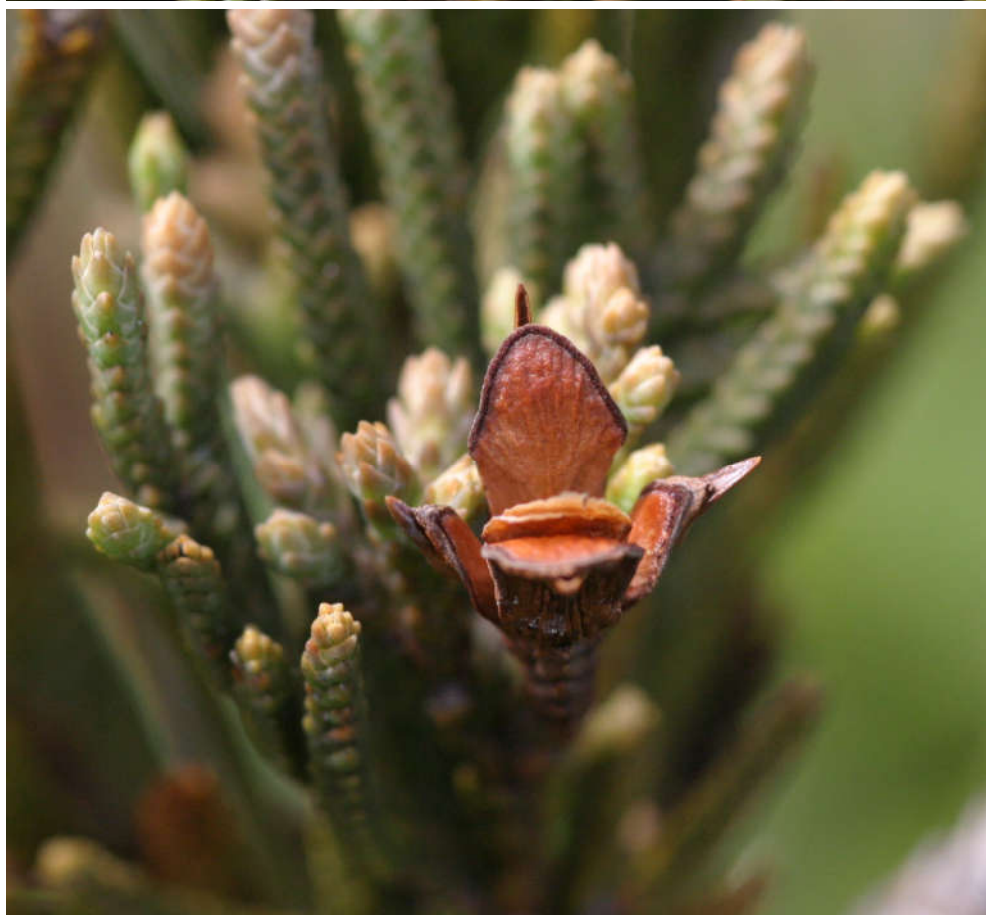
**Fig. 10:** Close-up of pollen cones after after pollen release (right), and an immature seed cone (left). Mont Humboldt. Alt. 1550-1620 m. 2005.02.10-11. © R. Amice.







**Fig. 11(top):** Immature seed cones.  
Mont Humboldt.  
Alt. 1550-1620 m.  
2005.02.10-11.  
© R. Amice.



**Fig. 12:** Mature seed cone showing the seeds inside.  
Mont Humboldt.  
Alt. 1550-1620 m.  
2005.02.10-11.  
© R. Amice



*Libocedrus austrocaledonica*



**Fig. 13:** Crown habit. Mont Paéoua. 2008.09.10. © D. & I. Létocart.



**Fig. 14:**  
Foliage with  
two immature  
seed cones  
(green) and one  
old seed cone  
(brown).  
Montagne des  
Sources.  
Alt. 1000 m.  
2004.10.16.  
© R. Amice





**Fig. 15:** Foliage and habit of a young tree. Montagne des Sources. Alt. 1000 m. 2004.10.16. © R. Amice.

**Fig. 16:** Close-up of the foliage. Montagne des Sources. Alt. 1000 m. 2004.10.16. © R. Amice.







**Fig. 17:** Foliage with immature seed cones. Montagne des Sources. Alt. 1000 m. 2004.10.16. © R. Amice.

**Fig. 18:** Close-up of immature seed cones. Montagne des Sources. Alt. 1000 m. 2004.10.16. © R. Amice.







**Fig. 19:** Immature seed cones. 2008.09.10. © D. & I. Létocart.



**Fig. 20:** Dry seed cones.  
Montagne des Sources.  
Alt. 1000 m.  
2004.10.16.  
© R. Amice.





**Fig. 21:** Immature pollen cones. Paéoua. Alt. 1000 m. 2016.06.16. © R. Amice.

**Fig. 22:** Foliage. Koghi. 2007.01.28. © R. Amice.







**Figs 23 & 24:** Tree. Rivière Bleue. Alt. 800 m. 2010.09.08. © R. Amice.









**Fig. 25:** Foliage. Upper crown.  
Rivière Bleue. Alt. 800 m.  
2010.09.08.  
© R. Amice.

**Fig. 26:** Foliage. Koghi.  
2007.01.28.  
© R. Amice.





*Libocedrus yateensis*



**Fig. 27:** Shrub. Rivière Bleue. 2002.04.18. © D. & I. Létocart.









**Fig. 29:** Shrub. Rivière Bleue. Alt. 200 m. 2005.06.04. © R. Amice.

**Fig. 28 (p. 40):** Tree. Rivière Bleue. Alt. 200 m. 2005.06.04. © R. Amice.





**Fig. 30:** Seedling. Rivière Bleue. Alt. 200 m. 2005.06.04.  
© R. Amice.



**Fig. 31:** Trunk. Rivière Bleue. Alt. 200 m.  
2005.06.04. © R. Amice.

**Fig. 32:** Foliage. Rivière Bleue. Alt. 200 m. 2005.06.04. © R. Amice.







**Fig. 33:** Foliage. Rivière Bleue. Alt. 200 m. 2005.06.05. © R. Amice.

**Fig. 34:** Foliage. Rivière Bleue. Alt. 200 m. 2005.06.05. © R. Amice.







**Figs 35 & 36:** Seed cones (possibly two aborted conelets). © [Parc de la Rivière Bleue](#). Photos A. Lespès.







**Figs 37 & 38:** Immature seed cones. © [Parc de la Rivière Bleue](#). Photos A. Lespès.







**Fig. 39:** Immature seed cone. © [Parc de la Rivière Bleue](#). Photo A. Lespès.

**Fig. 40:** Seed cones and seeds. Scale 1.5x. © [Parc de la Rivière Bleue](#). Photo A. Lespès.







**Fig. 41:** Seeds. Scale 3x.  
 © [Parc de la Rivière Bleue](#).  
 Photo A. Lespès.



**Fig. 42:** Seed cones. Scale ~2.6x.  
 © [Parc de la Rivière Bleue](#).  
 Photos A. Lespès.





**Fig. 43:** Foliage of a sapling. Rivière Bleue. Alt. 200 m. 2005.06.05. © R. Amice.

**Fig. 44:** Immature pollen cones. Rivière Bleue. Alt. 200 m. 2005.06.05. © R. Amice.







**Fig. 45:** Mature pollen cones. Rivière Bleue. 2010.07.15. © D. & I. Létocart.





**Fig. 46:** Close-up of mature pollen cones. Rivière Bleue. 2010.07.16. © D. & I. Létocart.

**Fig. 47:** Foliage, adaxial side. Rivière Bleue. 2002.04.09. © D. & I. Létocart.





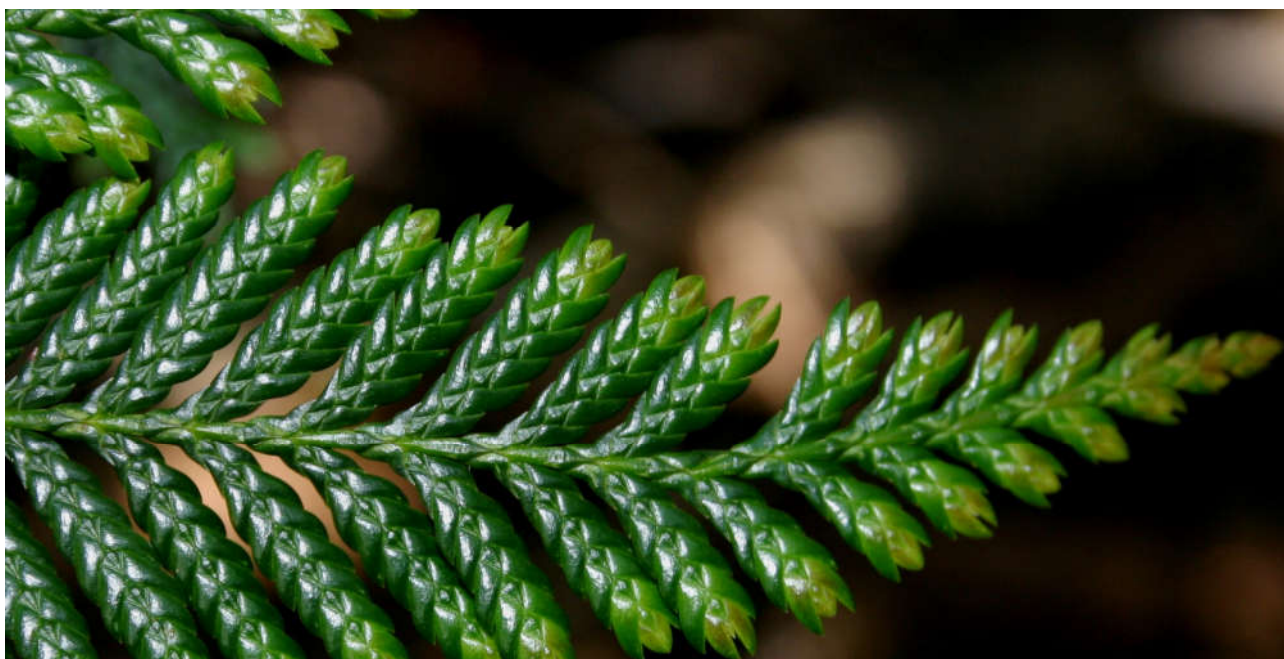


**Foliage comparison of the three New Caledonian *Libocedrus* species.**

**Fig. 48 (top):**  
*L. chevalieri*.  
© R. Amice.

**Fig. 49 (middle):**  
*L. austrocaledonica*.  
© R. Amice.

**Fig. 50 (bottom):**  
*L. yateensis*.  
© R. Amice.





## Morphology, anatomy and systematics of *Pseudotaxus* (Taxaceae, Coniferales) – *Taxus*-like, but not a *Taxus*

### Abstract

*Pseudotaxus* is an endangered (IUCN status: vulnerable) monotypic Chinese coniferous genus belonging to the Taxaceae. At first glance, the sole species *Pseudotaxus chienii* appears quite similar to *Taxus*: it was first described as *Taxus chienii*. However, there are some distinct morphological features distinguishing *P. chienii* from *Taxus*. Superficially, the white aril is a striking difference to the red or orange *Taxus* aril, but is not the most important difference. More significant in distinguishing them are the branched pollen cones in *Pseudotaxus*. In addition there are numerous foliar features distinguishing both genera. Compared to *Taxus*, the leaves of *Pseudotaxus* are rigid, have a sharply-pointed leaf tip, a free petiole, and the stomatal bands marked by two longitudinal white wax bands with monocyclic stomata, whilst epidermal papillae are absent from the stomatal bands. The vegetative and reproductive structures of *P. chienii* are investigated in regards to species identification and systematics. Depending on the results, *Taxus* and *Pseudotaxus* share some common features but there are also numerous features distinguishing them which justify the treatment as two distinct, but closely related genera.

### Introduction

*Pseudotaxus* W.C.Cheng is a monotypic coniferous genus in the family Taxaceae, comprising only the southeastern Chinese species *Pseudotaxus chienii* (W.C.Cheng) W.C.Cheng ( $\equiv$  *Taxus chienii* W.C.Cheng), which was discovered in 1934 (ECKENWALDER 2009; FARJON 2010; DÖRKEN & NIMSCH 2018, 2019). It is rarely cultivated outside its natural Chinese habitat. At first glance, its morphology appears very similar to the closely related genus *Taxus* (ECKENWALDER 2009, FARJON 2010, DÖRKEN & NIMSCH 2018, 2019). One of the most striking differences between the genera is the colour of the aril, white in *Pseudotaxus*, red or orange in *Taxus* (ECKENWALDER 2009; FARJON 2010; DÖRKEN & NIMSCH 2018, 2019; DÖRKEN *et al.* 2019). The similarities of *Pseudotaxus* and *Taxus* indicate a close relationship between the genera as is suggested both on morpho-anatomical (e.g. GHIMIRE & HEO, 2014; GHIMIRE *et al.* 2014; ELPE *et al.* 2017, 2018) as well as in genetic studies (e.g. CHENG *et al.* 2000). Thus, it is not too surprising that it was initially treated as *Taxus chienii* W.C.Cheng. In 1947, CHENG created the new genus *Pseudotaxus* for it, an action repeated by FLORIN in 1948 as *Nothotaxus* (*nomen superfluum*), because of differences in the vegetative (epidermis and stomata) as well as in the reproductive structures (colour of the aril and branching pattern of pollen cones).

The major aim of this study is to find out if there are more reliable morpho-anatomic features, that distinguish both genera from each other. Therefore, the morphology and anatomy of leaves and cones of both genders were investigated with different methods.

### Material und Methods

#### Material

Material of *Pseudotaxus chienii* was collected in the private living collection of Hubertus Nimsch, Bollschweil, St. Ulrich, Germany; material of *Taxus baccata* was collected from trees growing in the forests on the campus of the University of Konstanz, Germany.

#### Methods

Freshly collected material was photographed and then fixed in FAA (100 ml FAA = 90 ml ethanol 70% + 5 ml acetic acid 96% + 5 ml formaldehyde solution 37%) before being stored in 70% ethanol. The anatomy was studied from sections using the classical paraffin technique and subsequent astrablue/safranin staining (GERLACH 1984). Macrophotography was done with a digital camera (Canon PowerShot IS2) and microphotography with a digital microscope (Keyence VHX 500F) equipped with a

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high-precision VH mounting stand with X-Y stage and bright-field illumination (Keyence VH-S5). For scanning electron microscopy (SEM) analysis, the FAA-material was dehydrated in formaldehyde dimethyl acetal (FDA) for 24 hours (GERSTBERGER & LEINS 1978) and later 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.

### Special terms

**Microsporangiophore:** because the identity of the coniferous pollen sac carrying structure is not finally resolved, the terms “sporophyll” or “microsporophyll” are not used, because homologies that are *a priori* applied to it should be avoided. Thus, the neutral term “microsporangiophore” (carrier of the pollen sacs) is used instead.

**Microsporangium (pollen sac):** structure developed on a microsporangiophore producing the pollen grains.

**Pollen cone:** the pollen producing “male” cones; in the majority of conifers unbranched structures usually with numerous pollen sacs (microsporangia) carrying structures (microsporangiophores). Pollen cones of all conifers are non-woody and dry out during or shortly after pollen release; dry and empty pollen cones are quickly abscised.

**Seed cone:** the ovule producing “female” cones. Within all conifers they are compound, inflorescence-like structures or can be regarded as being derived from such once; in the majority of species they become woody. After seed release the empty seed cones of some species remain, at time for several years, on the tree, while in others they abscise, some quickly, some slowly.

**Scutellum:** small phylloid, distal structure, developed on the stalk of a microsporangiophore.

**Cone:** the more or less compact reproductive structures of conifers. The “male” cones producing the pollen are called pollen cones, the “female” cones producing the ovules, are called seed cones.

### Systematics

The genus *Pseudotaxus* belongs to the Yew family Taxaceae, which also comprises the genera *Taxus* with 7 north hemispheric species, *Amentotaxus* with 5 species distributed in China, Taiwan, India and Vietnam, *Austrotaxus* with a single south hemispheric species in New Caledonia and *Torreya* with 6 species in N-America and SE-Asia. The systematic position of *Cephalotaxus* is still controversial today. Depending on the systematic view, it is part of the Taxaceae (ECKENWALDER 2009; FARJON 2010; LESLIE *et al.* 2012; GHIMIRE & HEO 2014; ELPE *et al.* 2017, 2018; DÖRKEN & NIMSCH 2018, 2019; DÖRKEN *et al.* 2011, 2019) or it is placed in the monogeneric distinct family Cephalotaxaceae (DALLIMORE & JACKSON 1966; PAGE 1990; HAO *et al.* 2008; PAN *et al.* 2011; YI *et al.* 2013; BYKOWSKA & KLIMKO 2018; MAJEED 2019). Cephalotaxaceae has also been treated as a trigeneric family, with *Amentotaxus*, *Cephalotaxus*, and *Torreya* (RUSHFORTH 1987).

Also the systematic position of the Taxaceae has been controversial for a long time. In earlier days it was treated in the distinct order “Taxales” (FLORIN 1948), because the typical coniferous bract/seed scale complex is absent or only hardly visible due to strong reduction of the female cones, in *Taxus* and *Pseudotaxus* often to a single ovule. The results of both numerous morpho-anatomic and molecular phylogenetic studies, show no doubt today, that Taxaceae belongs to the Pinales (syn. “Coniferales”), which are the largest group within living gymnosperms. In most recent phylogenies Taxaceae is placed as sister to the Cypress family Cupressaceae (e.g. CHAW *et al.* 2000; QUINN *et al.* 2002; BURLEIGH & MATTHEWS 2004; DÖRKEN *et al.* 2011; COLE *et al.* 2017).

The Taxaceae *s.str.* are formed by two tribes, 1) Taxeae (*Austrotaxus*, *Taxus* and *Pseudotaxus*) and 2) Torreyaee (*Amentotaxus* and *Torreya*). The genus *Cephalotaxus* is regarded either as sister to the Taxaceae *s.str.* (ELPE *et al.* 2018), or within Torreyaee as sister to *Amentotaxus* and *Torreya* (LESLIE *et al.* 2012; GHIMIRE & HEO 2014); additionally, GHIMIRE & HEO 2014 found *Austrotaxus* as basal, sister to all the rest of the family. Within the Taxaceae, *Taxus* is consistently the sister of *Pseudotaxus* (LESLIE *et al.* 2012; GHIMIRE & HEO 2014; ELPE *et al.* 2017, 2018). The genus *Pseudotaxus* comprises only the SE Chinese species, *P. chienii* (DÖRKEN & NIMSCH 2018, 2019).

### Distribution

*Pseudotaxus* is a Chinese tertiary relict plant (FU *et al.* 1999). It has a scattered distribution pattern, in a quite large geographical area (FU *et al.* 1999; LIU *et al.* 2021) with a focus in the



southern parts of the SE-Chinese Province Zhejiang (ECKENWALDER 2009). The distribution in the provinces Guangdong, C-Guangxi, NW-Hunan and SW-Jiangxi is sporadic as it is restricted to suitable narrow high ridges. Consequently not only in horticulture, but also in its natural habitat, this species is rare and highly threatened. *Pseudotaxus* occurs in quite diverse habitats with a great heterogeneity of the biotic and abiotic environmental factors (LI 2020; LIU *et al.* 2021). In its main distribution area, there is a humid to subtropical climate, which is strongly influenced by the monsoon. *Pseudotaxus* occurs as single shrub or tree or in small groups disjunct in the understory of deciduous or evergreen mountain forests in about 900-1400 m above sea level. The annual mean temperature is about 12-15°C, the annual mean precipitation 1800-2000 mm, the air humidity about 80% (FU & JIN 1992). In genetic studies it could be shown that the adaptive genetic variation of local populations is significant and responses in most cases to abiotic and biotic stress factors (e.g. LIU *et al.* 2021), which can vary due to the distinct environmental heterogeneities existing between the different populations (LI 2020; LIU *et al.* 2021).

According to the IUCN (International Union for Conservation of Nature and Natural Resources) *Pseudotaxus* belongs to the category Vulnerable.

## Morphology and anatomy

*Pseudotaxus* is an evergreen shrub of mostly just up to four metres in height; only in rare cases is it a small tree up to eight metres. However, these tree-like individuals usually have numerous stems without a dominant leading trunk. The dormancy buds are ovate with a distinct tip. There are numerous dry, brownish spreading bud scales showing a distinct midrib (Fig. 1B; cf. difference to *Taxus*, Fig. 9B), where the buds are inconspicuous, ovate, with green bud scales strongly appressed on each other.

The needle leaves are up to 2.5 cm long and 4.5 mm broad. They are helically set but distichously arranged. When sprouting, the new leaves are yellow-green. They turn to dark green while maturing (Figs 1A & E). The lamina is slightly convex. In comparison to the soft leaves of *Taxus*, the needles of *Pseudotaxus* are markedly ridged, and show a short pointed and acute tip (Fig. 1C; cf. difference to *Taxus*, Fig. 9C). There are two distinct white bands on the abaxial surface, marking the stomata fields (Figs 1A, D-E; cf. difference to *Taxus*, Fig. 9D). *Pseudotaxus* is strictly hypostomatic (Figs 1E & F), and stomata are exclusively developed abaxially, as in all the other Taxaceae (ELPE 2018). There are 23-28 abaxial stomatal rows (cf. difference to *Taxus*, only 13-15), which are arranged in two longitudinal bands. The stomata fields are separated by the raised, green midrib. The stomata fields of *Pseudotaxus* (Figs 1F & 2A) are free of epidermal papillae (in ELPE *et al.* 2017 called cellular protuberances) as in *Austrotaxus* and *Amentotaxus* (ELPE *et al.* 2017), whereas in *Taxus* (Fig. 9E) as well as in *Torreya* numerous epidermal papillae are developed. While in the other taxaceous genera the presence or absence of epidermal papillae is a constant feature throughout each genus, in *Cephalotaxus* there is some variation. In some species papillae are developed, in others they are absent (ELPE *et al.* 2017). Another important difference between *Pseudotaxus* and *Taxus* is in the type of stomata. In *Pseudotaxus* they are monocyclic, showing just a single ring of isodiametric shaped subsidiary cells surrounding the guard cells of the stomata (Fig. 2B), a feature which is also developed in *Torreya* and *Amentotaxus* (ELPE *et al.* 2017). However, in *Taxus* the stomata are amphicyclic (Fig. 9F), as in *Austrotaxus* and *Cephalotaxus* (ELPE *et al.* 2017). There are four subsidiary cells surrounding the guard cells of the stomata, two elongated lateral ones and two polar ones (Fig. 9F). The short petiole is kneed and strongly appressed to the shoot axis (Fig. 1D), a distinct difference to *Taxus*, which has leaf bases strongly fused to the shoot axis (Fig. 9D). In *Pseudotaxus* the lamina is spreading more or less right-angled from the petiole (Fig. 1D). The leaf is supplied by a single vascular bundle strand (Figs 2C & E), which forms a distinct midrib, visible on both leaf surfaces as a longitudinal ridge. It is more prominently raised on the adaxial surface than on the abaxial surface. A thick cuticle covers the epidermis (Fig. 2D). The epidermis cells are thick walled and rich in phenolic substances (visible as the dark, intensive staining). A hypodermis is absent (Fig. 2D). The mesophyll is dimorphic with palisade parenchyma located towards the upper light exposed surface and spongy parenchyma placed towards the shaded lower surface (Figs 2C & D). In the collateral vascular bundle strand



xylem is located towards adaxial and phloem towards abaxial (Fig. 2E). A transfusion tissue consisting of sclerenchymatic cells is well developed on both lateral sides of the vascular bundle strand (Fig. 2E). The leaves of *Pseudotaxus* lack a resin duct below the vascular bundle (Figs 2C & E) as in *Austrotaxus* and *Taxus*. In *Torreya* and *Amentotaxus* (tribe Torreyaee) a distinct resin duct is placed below the bundle strand, as also in *Cephalotaxus* (ELPE *et al.* 2018).

In most general texts or encyclopedias, the Taxaceae are described as dioecious (DALLIMORE & JACKSON 1966; GIFFORD & FOSTER 1989; PAGE 1990; COLE *et al.* 2017; ELPE *et al.* 2017), including *Pseudotaxus* (RUSHFORTH 1987; ECKENWALDER 2009; FARJON 2010). However our own experience based on six investigated individuals of *Pseudotaxus* have shown that the sex expression is not strictly dioecious as mentioned in this literature. The plants we investigated over a period of ten years showed a tendency to be functional either “male” or “female”, however with a distinct variation between years. There were “female” plants which developed in one year exclusively seed cones and, in the subsequent year, also pollen cones in addition to seed cones; or in other years, even only just pollen cones. The situation in basically “male” individuals was more or less comparable to that of basically “female” individuals. In one year exclusively pollen cones were produced, in other years additional to pollen cones also some seed cones (and this even on the same branch), and in some years these individuals turned to exclusively “female”. A similar phenomenon was also observed for Central European *Taxus baccata*. According to this, the genera *Pseudotaxus* and *Taxus* are not as strictly dioecious as frequently mentioned, because in addition to functional exclusively “male” and “female” individuals, “bisexual” ones also exist, and that sex expression can change markedly between years. These findings are in accordance with KRÜSSMANN (1983), who described *Taxus* as usually dioecious, rarely monoecious. MAERKI (2022) reported about a monoecious *Pseudotaxus* specimen.

As in all other conifers, the reproductive structures of *Pseudotaxus* are arranged in compact cones, the “male”, pollen producing cones are called pollen cones, the “female” ovuliferous cones, seed cones. The cones of both sexes are always developed in an axillary position, in the axil of a typical shaped green needle leaf (Figs 2B & D). No terminal cones were observed. The majority of cones are developed on last year’s lateral branchlets. They are placed on the lower side of the branchlets in a downward position (Figs 3A, 6A-B). The pollination drops, the receptive structure for pollen grains in seed cones, are always in a strictly downward position.

In *Pseudotaxus*, the pollen cones have a very short stalk, more or less sessile (Figs 3B-C), a difference to *Taxus* with its longer stalked pollen cones (Fig. 10A) The pollen cones consist of numerous pollen sac carrying structures, called microsporangiophores. *Pseudotaxus* microsporangiophores have a perisporangiate structure and consist of a central stalk, a shield-like terminal scutellum and numerous pollen sacs (= microsporangia) developed all around the stalk (Figs 3E-F). At a first glance, the pollen cone structure of *Pseudotaxus* (Fig. 3) and of *Taxus* appears quite similar (Fig. 10A); however there is one important striking difference. In *Taxus* the perisporangiate microsporangiophores are placed directly on the cone axis, and bracts are always absent (Fig. 10A). In *Pseudotaxus* however, the microsporangiophores are always inserted in the axil of a small scaly bract, showing a large skinny hyaline margin and a green central part. Thus, pollen cones of *Taxus* are simple unbranched structures, which correspond in total to a single flower, while *Pseudotaxus* pollen cones are compound and correspond to an inflorescence, and each bract-microsporangiophore-complex to a lateral flower (Fig. 3D; DLUHOSCH 1937; DUPLER 1919; WILDE 1944, 1975; KRÜSSMANN 1983; MUNDY & MUNDY 2001; DÖRKEN *et al.* 2011; DÖRKEN & NIMSCH 2016). In expanded morpho-anatomical studies it was found that each axillary perisporangiate microsporangiophore corresponds to a lateral, or axillary pollen cone, however strongly reduced. Thus, it is assumed that the pollen cone structure of *P. chienii* is derived from an ancestor showing, instead of axillary perisporangiate microsporangiophores, fully developed lateral pollen cones, similar to those developed within species of *Cephalotaxus* (DÖRKEN *et al.* 2011; DÖRKEN & NIMSCH 2016). This would explain the strictly axillary position of microsporangiophores in *Pseudotaxus*. If the perisporangiate microsporangiophores represented just simple pollen producing leaves in the sense of “microsporophylls”, such an axillary position would



not be possible, because ontogenetically a leaf can never be inserted in the axil of a leaf. Leaves are always formed as lateral structures on the shoot apex. In this regard, *Taxus* pollen cones, which are always free of bracts, could represent a progression of the *Pseudotaxus* situation. By a simple reduction of the *Pseudotaxus* microsporangiphore bract, the simple flower-like *Taxus* pollen cone is formed. In this case, the *Taxus* pollen cone is derived from a compound, inflorescence-like ancestor (DÖRKEN *et al.* 2011; DÖRKEN & NIMSCH 2016).

At pollination time, when the pollen grains are released, the bracts within *Pseudotaxus* pollen cones are strongly spreading, so the microsporangiphores – in particular the microsporangia – are best exposed to the ambient airflow, and the pollen grains can be efficiently shed from the cones. In immature pollen cones, the bracts are imbricate and cover the microsporangiphores entirely. Because *Pseudotaxus* pollen cones are not developed in a bud, the bracts within the cone carry out the protective function of the missing bud scales to protect the developing microsporangiphores (Fig. 3C). Thus, externally, only the bracts are visible during the early development of the cone.

The non-saccate pollen grains are spheroidal but slightly irregular in shape (Fig. 5), they are about 25-30 µm in diameter. The outer surface of the pollen grain (exine) is, as typical for Taxaceae, microverrucate-orbiculate. The density of the globose to oval orbicules is very high (Fig. 5). Earlier studies on pollen grains in Taxaceae have shown that they are useful to distinguish between the taxaceous genera, depending on the pollen grain size and the surface structure of the exine. BYKOWSKA & KLIMKO (2018) who investigated the pollen grains of *Cephalotaxus*, *Torreya* and *Taxus*, showed that pollen grains of *Cephalotaxus* and *Torreya* are significantly larger than these of *Taxus* and have a distinctly lower density of orbicules. In *Taxus* they were smaller and had many more orbicules. They also demonstrated that within *Taxus*, the exine sculpturing was so similar that it is not a good diagnostic feature for species identification. Interestingly, the structure of the exine sculpturing in *Pseudotaxus* is quite similar to *Taxus*. Compared to the images of *Taxus* presented in Figs 3-5 in BYKOWSKA & KLIMKO (2018), it seems that the density of orbicules is slightly higher in *Pseudotaxus* (Fig. 5). Comparing with the data on *Taxus* pollen grain size in PILCHER (1968) and BYKOWSKA & KLIMKO (2018), *Pseudotaxus* pollen grains, about 25-30 µm in diameter, are more or less the same size as in *Taxus*.

Due to the strong reduction of the seed cone, a distinct bract/seed scale complex (as is typical in many other coniferous groups, e.g. Pinaceae or Sciadopityaceae) is absent or hardly visible in Taxaceae (MUNDRY 2000; GHIMIRE *et al.* 2014). Mature seed cones of *Pseudotaxus* are 5-8 mm long and 4-5 mm broad. There are 7-8 pairs of imbricate decussate membranaceous scale leaves at the stalk of the seed cone, similar to the situation in *Taxus* (DÖRKEN *et al.* 2019). At pollination time, these scale leaves surround the ovule nearly entirely, so that only the micropyle remains free. These scale leaves are persistent, and remain below the aril in mature cones as green scales (Figs 7A-B). In *Taxus*, however they dry out and become brownish (Fig. 10D). In most cases there is just a single ovule per seed cone in *Pseudotaxus* (Figs 7A-B); two ovules are exceptional (Fig. 6D). The ovules are supplied by two collateral vascular bundle strands (Fig. 6E). At maturity, they are surrounded by a fleshy white, cup-like aril (Figs 6A-B & 7B-E; cf. difference to *Taxus*, aril of all species are red or orange, Fig. 10C). The aril and the seed are free and not fused to each other. The mature aril is as long as the seeds or slightly longer. The distal part of the cup-shaped aril has an unlobed distal collar (Fig. 7D), as is also typical for *Taxus* (Fig. 10C). In the beginning, the aril is initially thin and green. As the seed cones mature, the aril becomes fleshy and changes to white. The aril formation starts after pollination time, and the first time that the juvenile aril is visible, about 2-3 months after pollination, it is still flat and greenish, visible between the scale leaves (Fig. 6a). After the aril has exceeded the scale leaves, the further development progresses faster.

Our investigations of *Pseudotaxus* seed cones – in particular about the origin of the aril – have shown that the aril is formed by the uppermost pair of scale leaves developed on the stalk of the cone (Fig. 6F). In the earliest ontogenetic stages, the primordia of these leaves are physically in contact and fuse subsequently to form a ring-like structure, which later grows apically and surrounds the seed cup-like and becomes fleshy. A detailed study is presented in DÖRKEN *et al.* 2019. In some rare cases these two lateral primordia forming the aril do not become fused or only



fuse partly to each other, so that the mature aril consists of 2 free halves or a cup like aril with a distinct two-lobed collar (Fig. 7E). Such arils are also described in DÖRKEN *et al.* (2019) and MAERKI (2022). The formation of the aril represents an adaptation to seed dispersal by birds, as in *Taxus* (FARJON, 2007; DÖRKEN & HETZEL 2017; DÖRKEN *et al.* 2019). Due to this, the mature seed cones of *Pseudotaxus* and *Taxus* are structurally quite similar to each other. In both, the aril is strongly fleshy, cup-like and not fused to the seed. In *Pseudotaxus* the surface of the aril is smooth and weakly covered with short cylindrical cellular protuberances (Fig. 7F); in *Taxus* there are numerous densely developed irregularly shaped cellular protuberances (Fig. 10E). As in *Taxus*, the cones mature in the year of pollination.

The seeds are ovate and brownish and 0.5-1 cm in length (Fig. 8A). There is a large ovate hilum at the base of the seed. The hilum is surrounded by a swollen collar like ring (Fig. 8B). Even on mature seeds the micropyle is still visible (Figs 8A & C). The testa is characterised by longitudinal cells showing distinctly raised cell walls (Fig. 8D). In *Taxus*, the testa is smooth with numerous small flat holes (Fig. 10F).

## Conclusion

In summary, *Pseudotaxus* and *Taxus* appear quite similar to each other at first glance, but numerous distinct distinguishing characteristics exist which are summarised in Table 1 (p. 59). From the results gained in the present study, the treatment of *Pseudotaxus* as a distinct monotypic genus is justified. Despite the fact that there are numerous distinct morpho-anatomical differences between *Taxus* and *Pseudotaxus*, there are also numerous common features which both taxa share. Thus, we strongly support the systematic treatment of the two genera as distinct taxa but as closely related sister groups in the tribe Taxeae.

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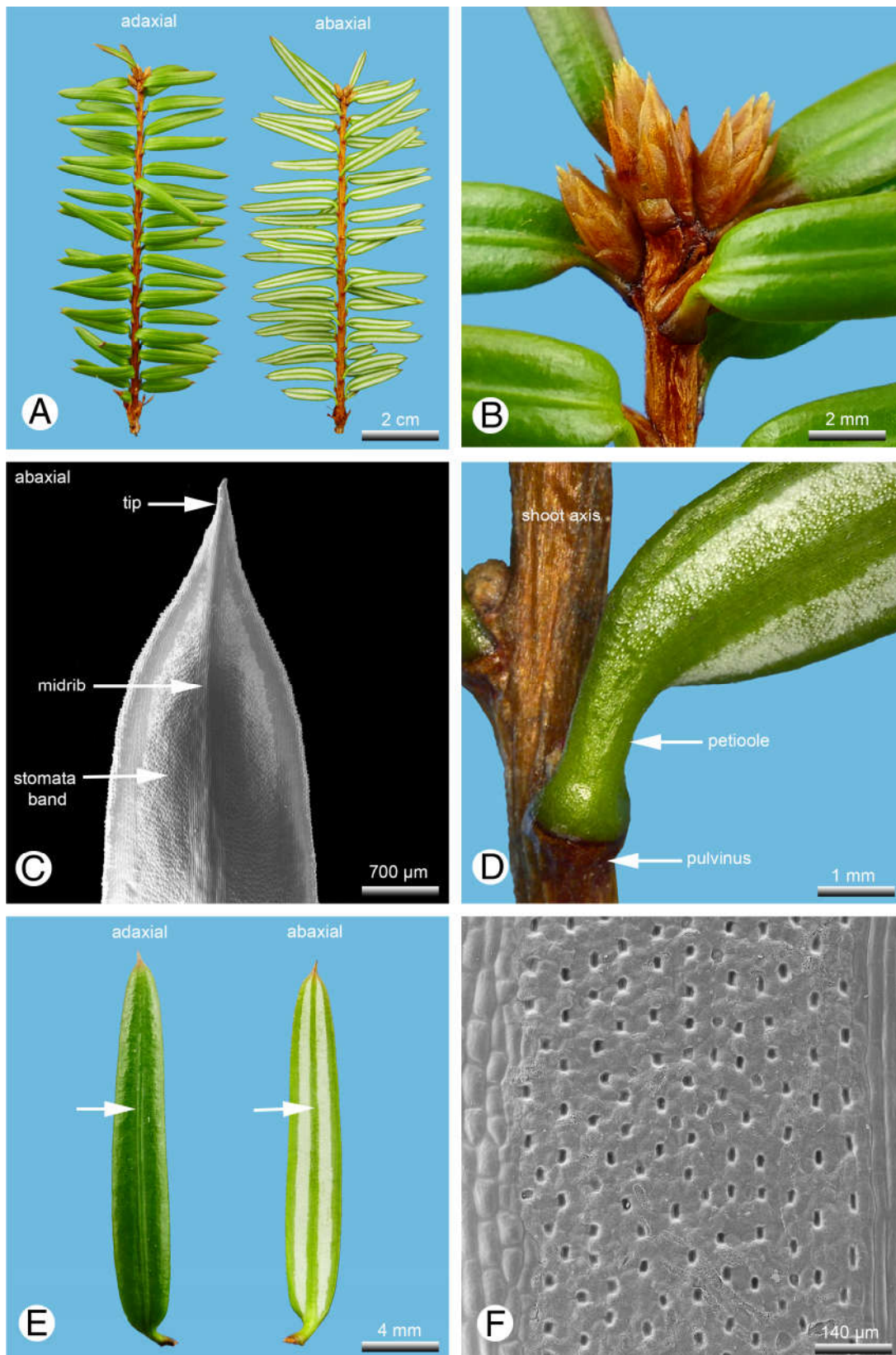
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**Table 1:** Distinguishing characters between *Taxus* and *Pseudotaxus*.

feature	<i>Taxus</i>	<i>Pseudotaxus</i>
<b>Bud</b>		
Shape	ovate or roundish (Fig. 9B)	ovate, pointed tip (Fig. 1B)
bud scales	green, strongly appressed (Fig. 9B)	brown, dry & spreading (Fig. 1B)
<b>needle leaf</b>		
structure	soft	Rigid
adaxial colour	dark green (Fig. 9A)	shiny dark green (Figs 1A, B & E)
abaxial colour	bright green (Figs 9A & D)	2 longitudinal white wax bands (Figs 1A, D & E)
Tip	not acute (Fig. 9C)	pointed and acute (Fig. 1C)
Petiole	decurent on the green shoot (Fig. 9D)	not decurent on the brown [non.photosynthetic] shoot (Fig. 1D)
Base	adnate to the shoot axis (Fig. 9D)	appressed to the shoot axis (Fig. 1D)
<b>stomata</b>		
Type	amphicyclic (Fig. 9F)	monocyclic (Fig. 2B)
total number of rows	13-15	23-28
papillae between stomata	present (Fig. 9E)	absent (Figs 1F, 2A)
<b>pollen cone</b>		
structure	simple (Fig. 10A)	compound (Fig. 3D)
Stalk	long (Fig. 10A)	very short (Figs 3B & D)
bracts in the pollen cones	absent (Fig. 10A)	present (Fig. 3D)
<b>seed cone</b>		
scale leaves on stalks of mature cones	dry & brownish; apex rounded (Fig. 10D)	green; apex acute (Fig. 7B)
<b>Seed</b>		
Colour	black	brown
Testa	smooth with numerous small holes (Fig. 10F)	longitudinal cells with raised walls (Fig. 8D)
<b>Aril</b>		
Colour	orange or red (Figs 10C & D)	white (Figs 7B-E)
surface	numerous irregularly shaped cellular protuberances (Fig. 10E)	few short cylindric cellular protuberances (Fig. 7F)



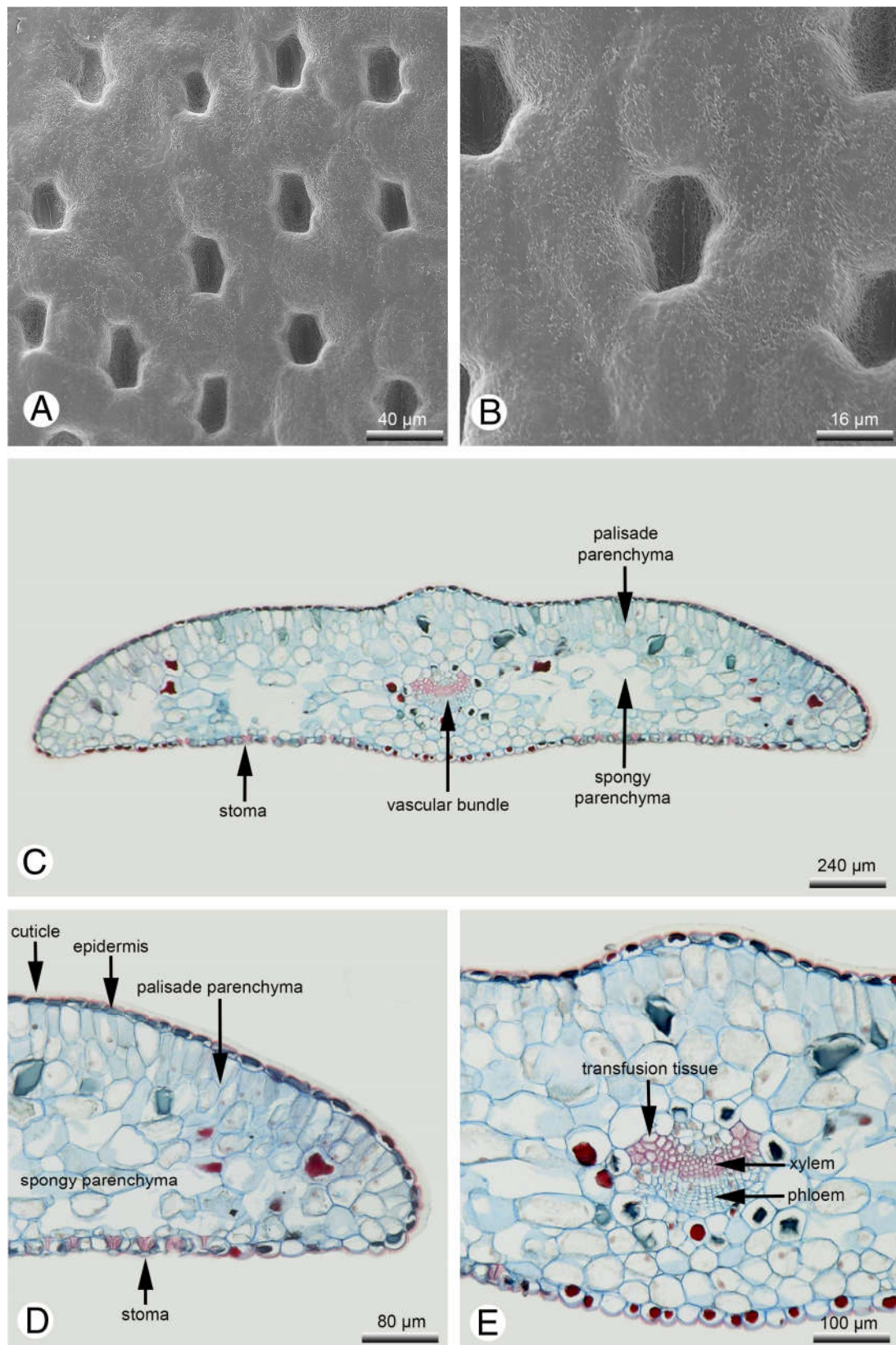


**Fig. 1:** *Pseudotaxus chienii*. Vegetative structures; morphology of shoots and leaves.

**A:** Ad- and abaxial view of a last year's shoot. **B:** Vegetative buds. **C:** Leaf tip pointed and acute. **D:** Leaf base. **E:** Ad- and abaxial view of a leaf showing a well developed midrib on both sides. **F:** Abaxial stomata field.

Images: V.M. DÖRKEN



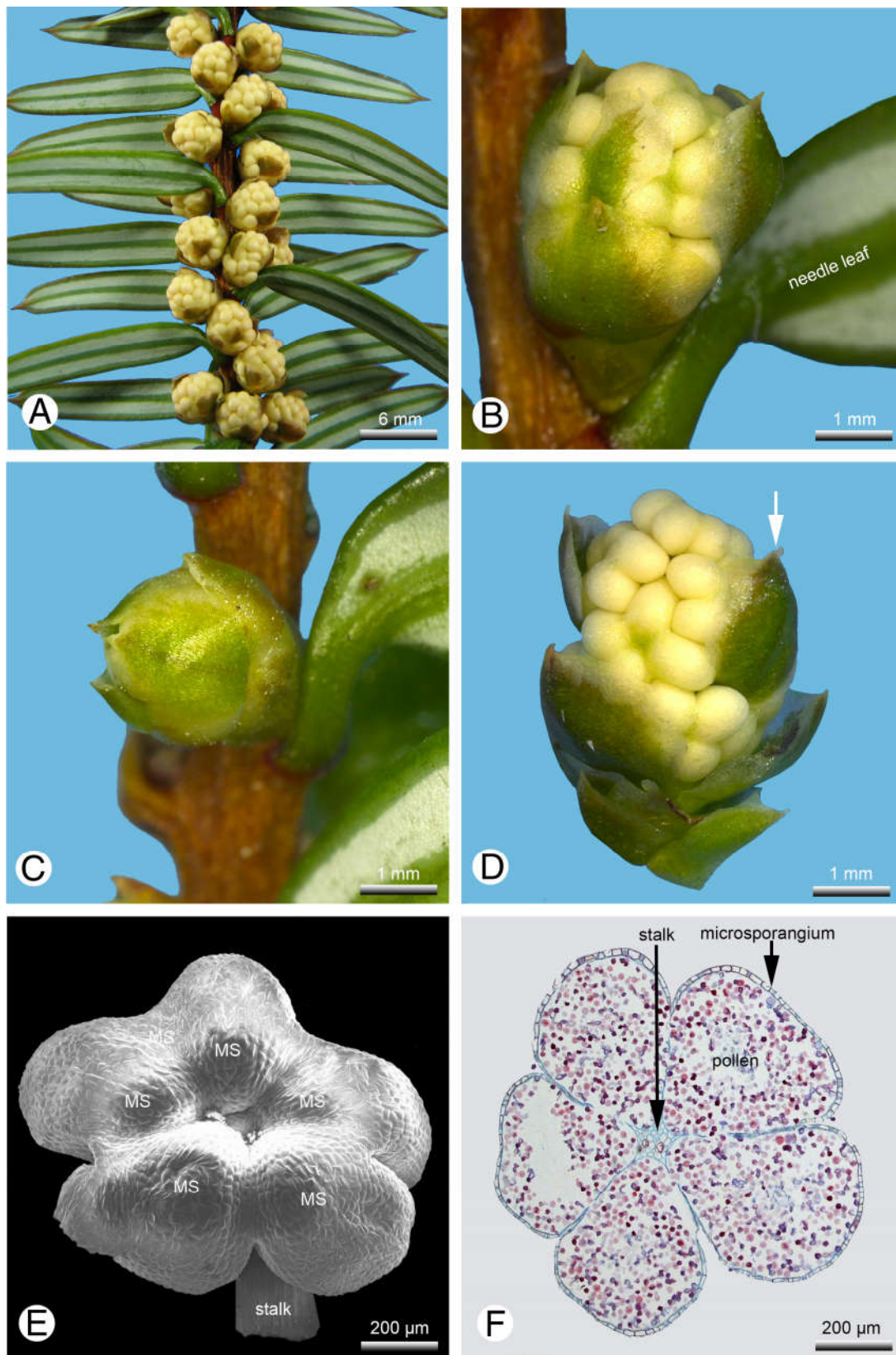


**Fig. 2:** *Pseudotaxus chienii*. Vegetative structures; morphology and anatomy of leaves.

**A:** Abaxial stomata fields showing no epidermal papillae. **B:** Monocyclic stoma. **C:** Cross section of a leaf showing the bifacial structure. **D & E:** Details of C. **D:** Detail of the different leaf tissues. **E:** Detail of the vascular bundle.

Images: V.M. DÖRKEN



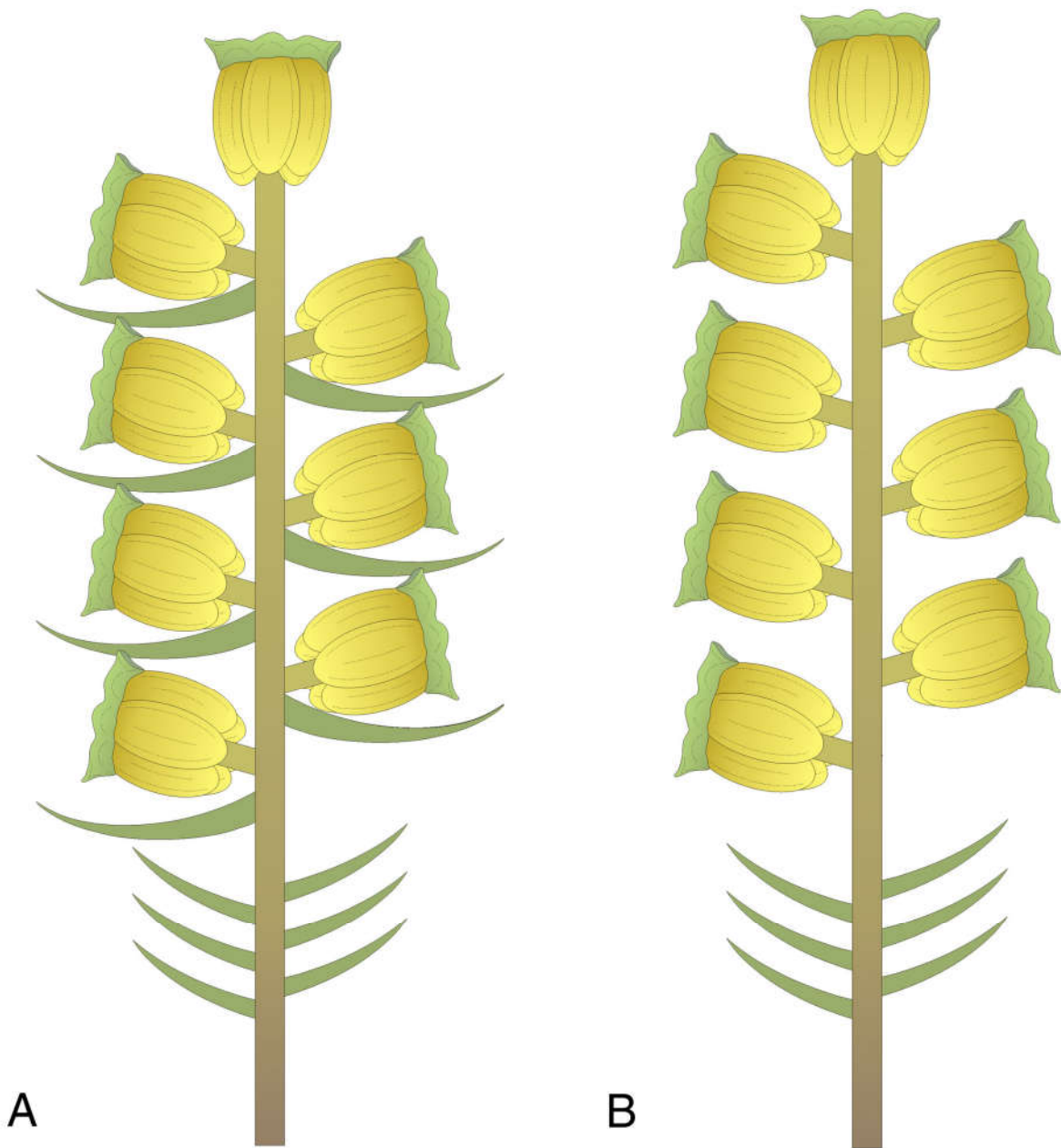


**Fig. 3:** *Pseudotaxus chienii*. Reproductive structures: morphology and anatomy of pollen cones.

**A:** Abaxial pollen cones. **B:** Pollen cones axillary. **C:** Immature pollen cone; the microsporangiophores are covered by their bracts; bud scales are absent. **D:** Mature pollen cone; bracts of the microsporangiophores are spreading; **E:** Perisporangiate microsporangiophore (SEM-image); **F:** Cross section of a perisporangiate microsporangiophore.

Images: V.M. DÖRKEN



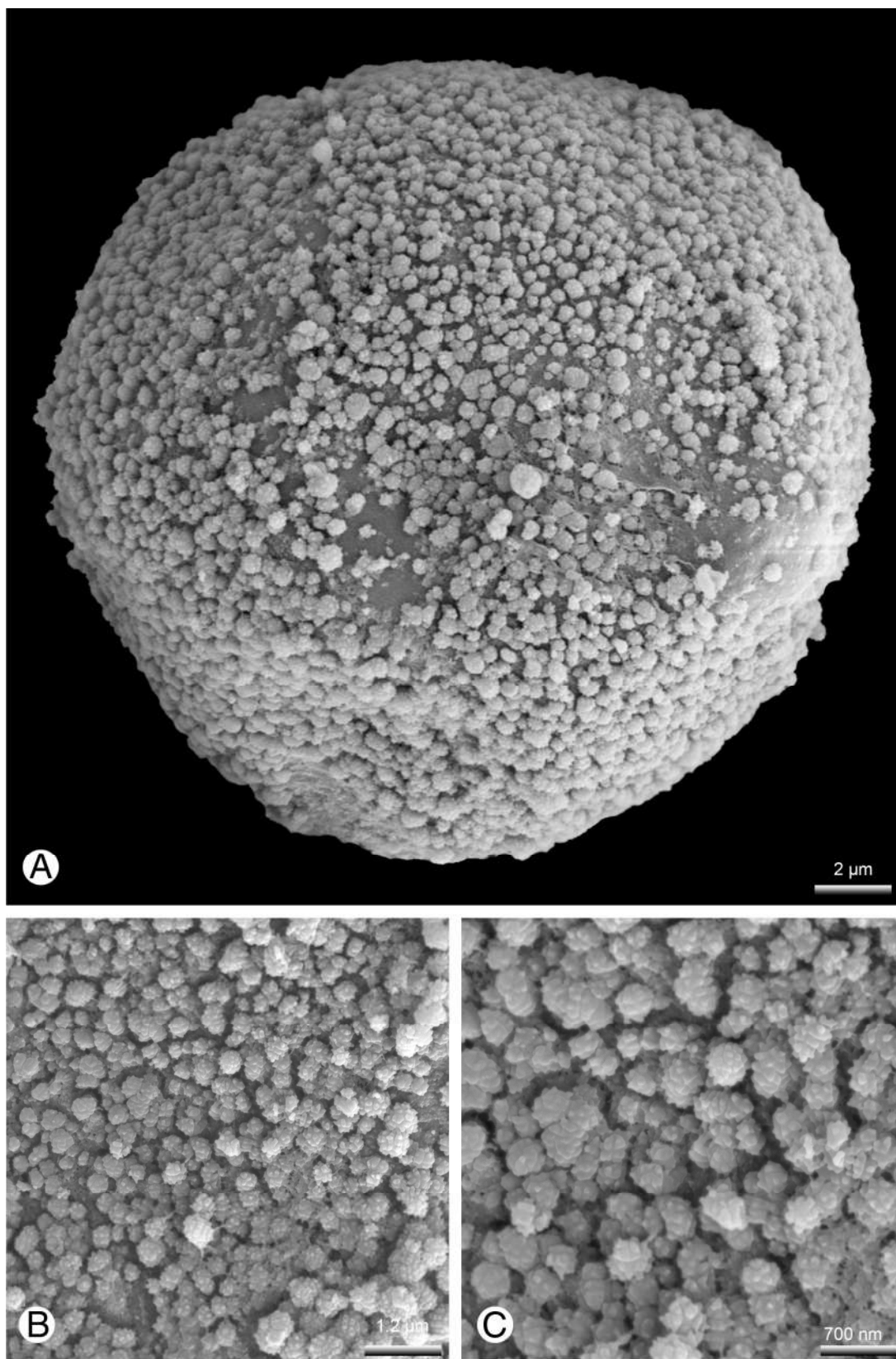


**Fig. 4:** Schematic drawing of pollen cones.

**A:** Compound pollen cone of *Pseudotaxus chienii*, the microsporangioophores are inserted in the axil of a scaly bract; **B:** Simple pollen cone of *Taxus baccata*; bracts within the cone are absent.

Drawings: V.M. DÖRKEN

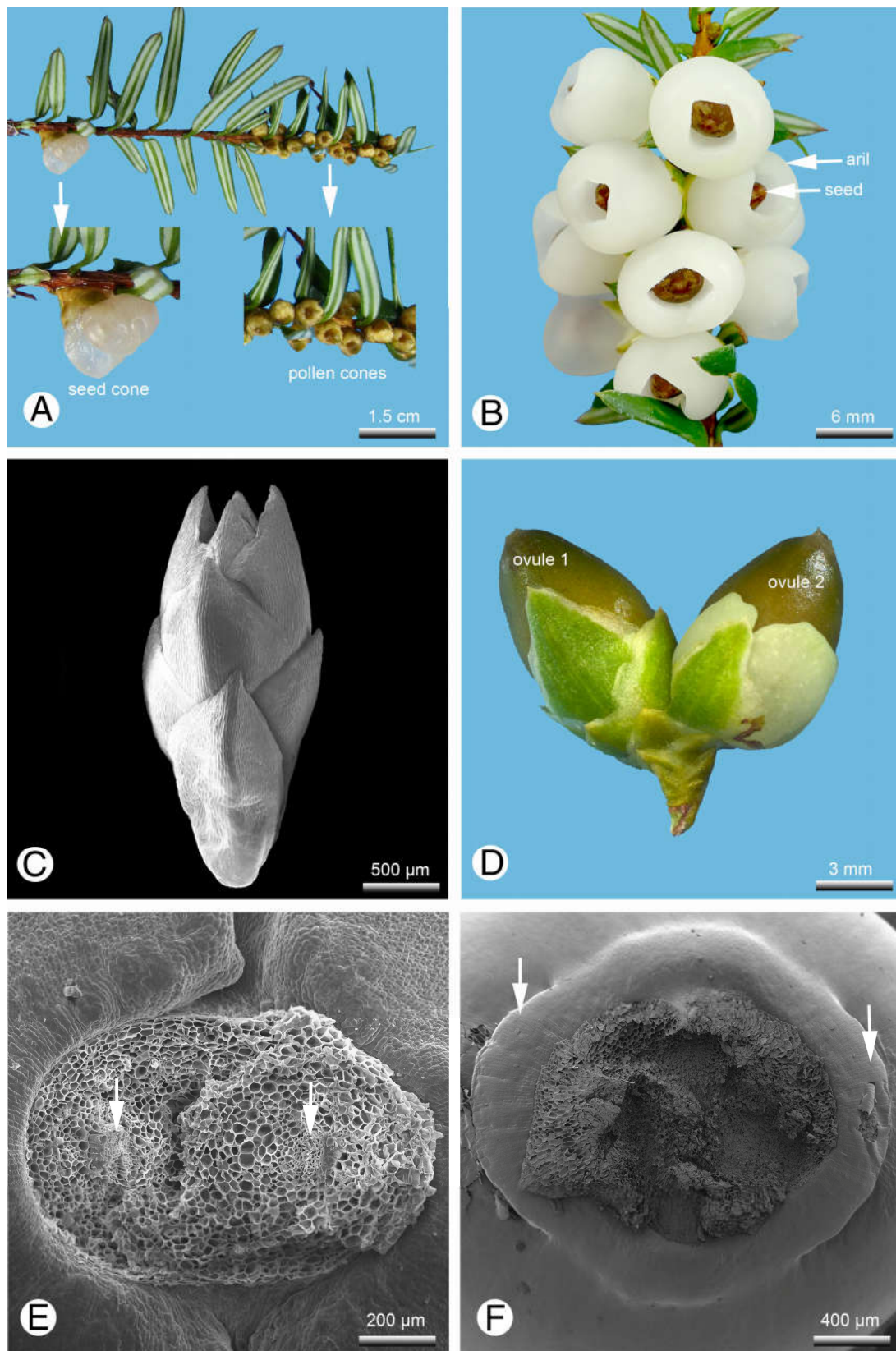




**Fig. 5:** *Pseudotaxus chienii*. Reproductive structures; morphology of pollen grains (SEM-images).  
**A:** Pollen grain. **B & C:** Pollen grain with microverrucate-orbiculate exine sculpturing showing a very high density of global to oval orbicules (SEM-image).

Images: V.M. DÖRKEN



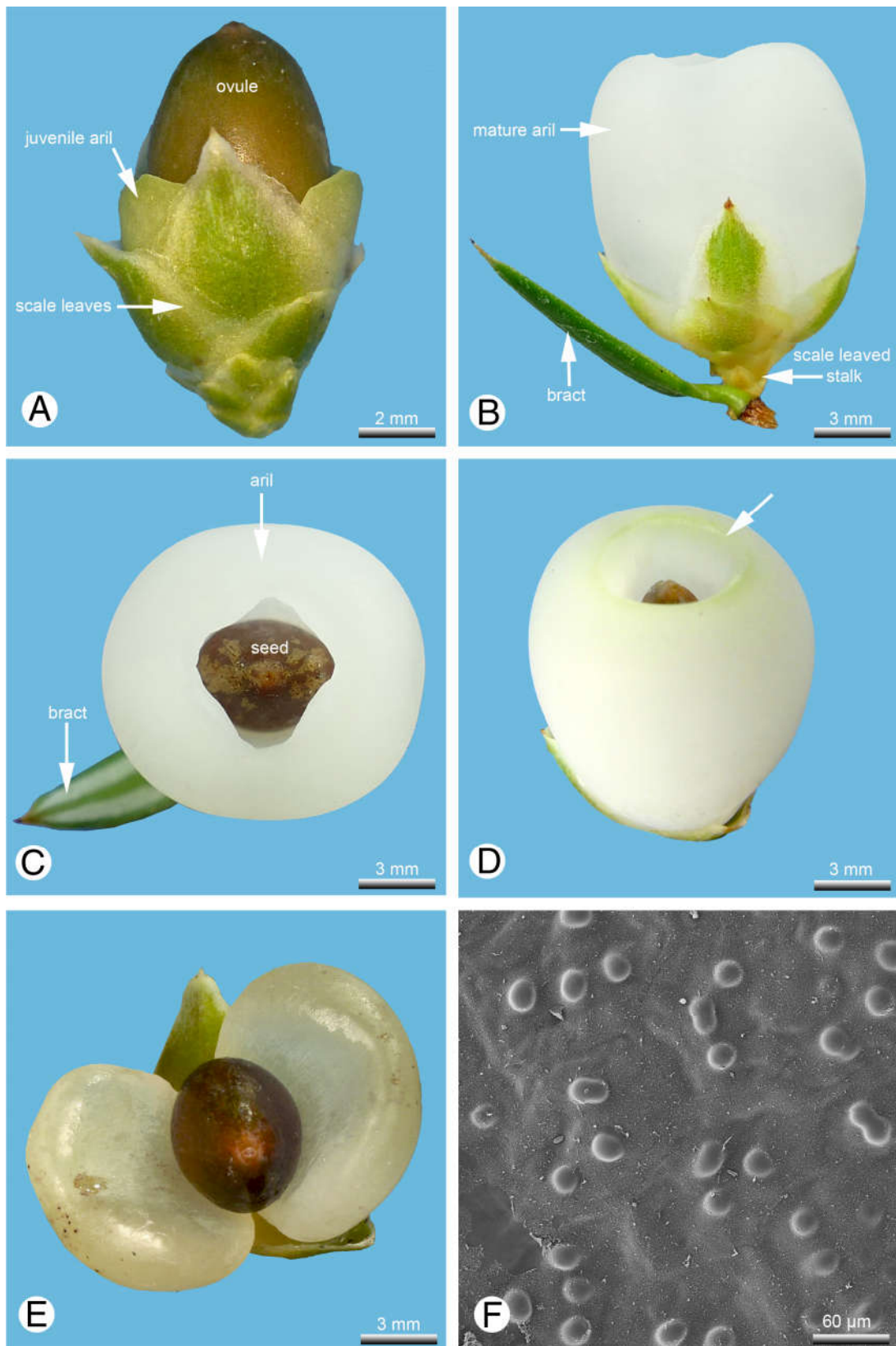


**Fig. 6:** *Pseudotaxus chienii*. Reproductive structures; morphology of seed cones.

**A:** Last year's shoot with a basal seed cone and several distal pollen cones. **B:** Abaxial seed cones. **C:** Immature seed cone; the ovule is covered by the scale leaves of the stalk. **D:** Seed cone with two instead of the typical single ovule. **E:** Basal part of an ovule showing two vascular bundles (arrows) supplying the ovule (SEM-image). **F:** The aril is formed by two lateral primordia (arrows) developed below the ovule (SEM-image).

Images: V.M. DÖRKEN

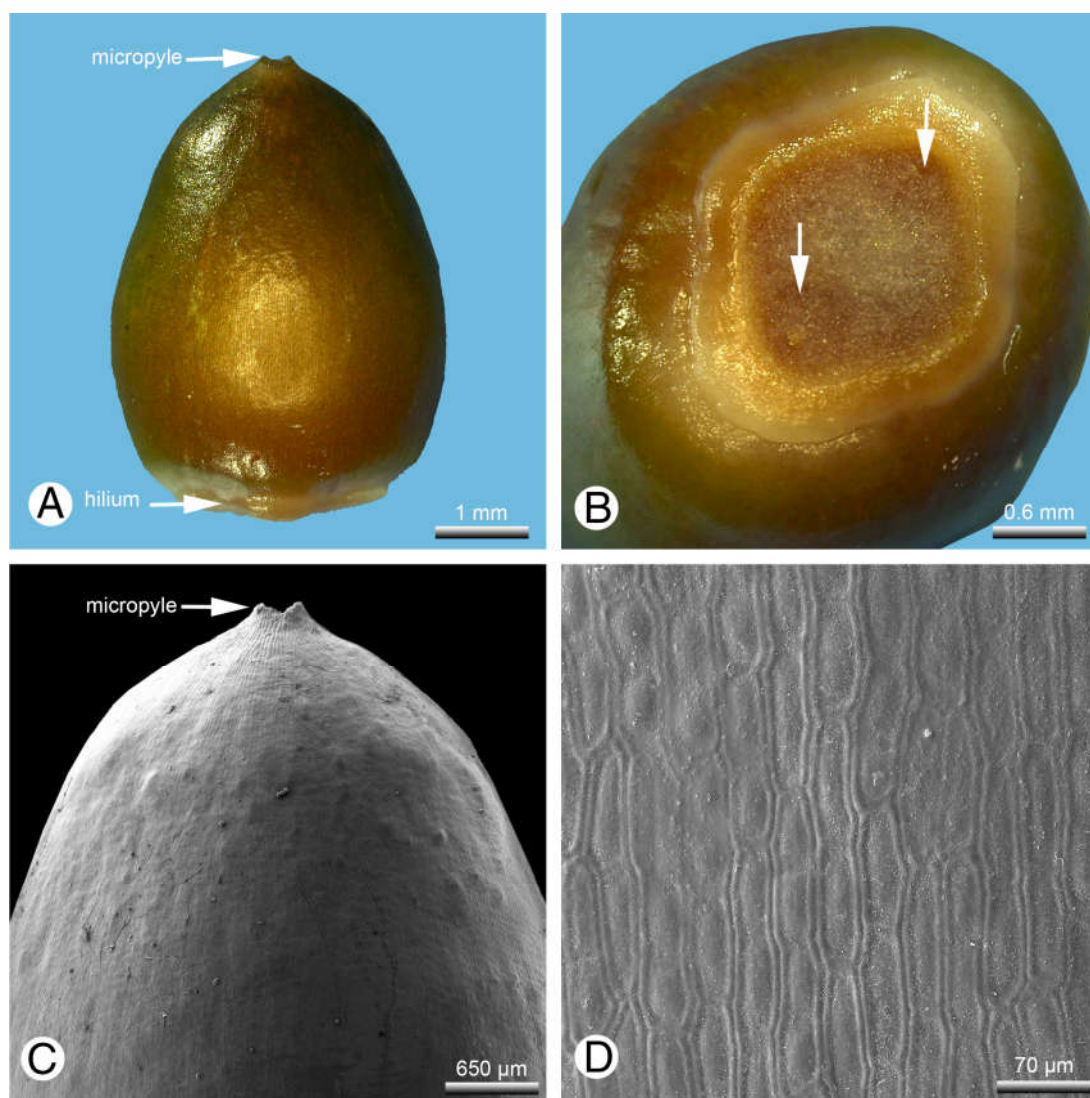




**Fig. 7:** *Pseudotaxus chienii*. Reproductive structures; morphology of seed cones.

**A:** Immature seed cone; about three month after pollination the aril is visible the first time.  
**B-E:** Mature seed cones. **B:** Lateral view. **C:** Top view; seed and aril not fused. **D:** Lateral view; aril with an unlobed distal collar. **E:** Anomalous seed cone; aril consists of two free halves.  
**F:** Microsculpturing of the outer aril surface (SEM-image).

Images: V.M. DÖRKEN

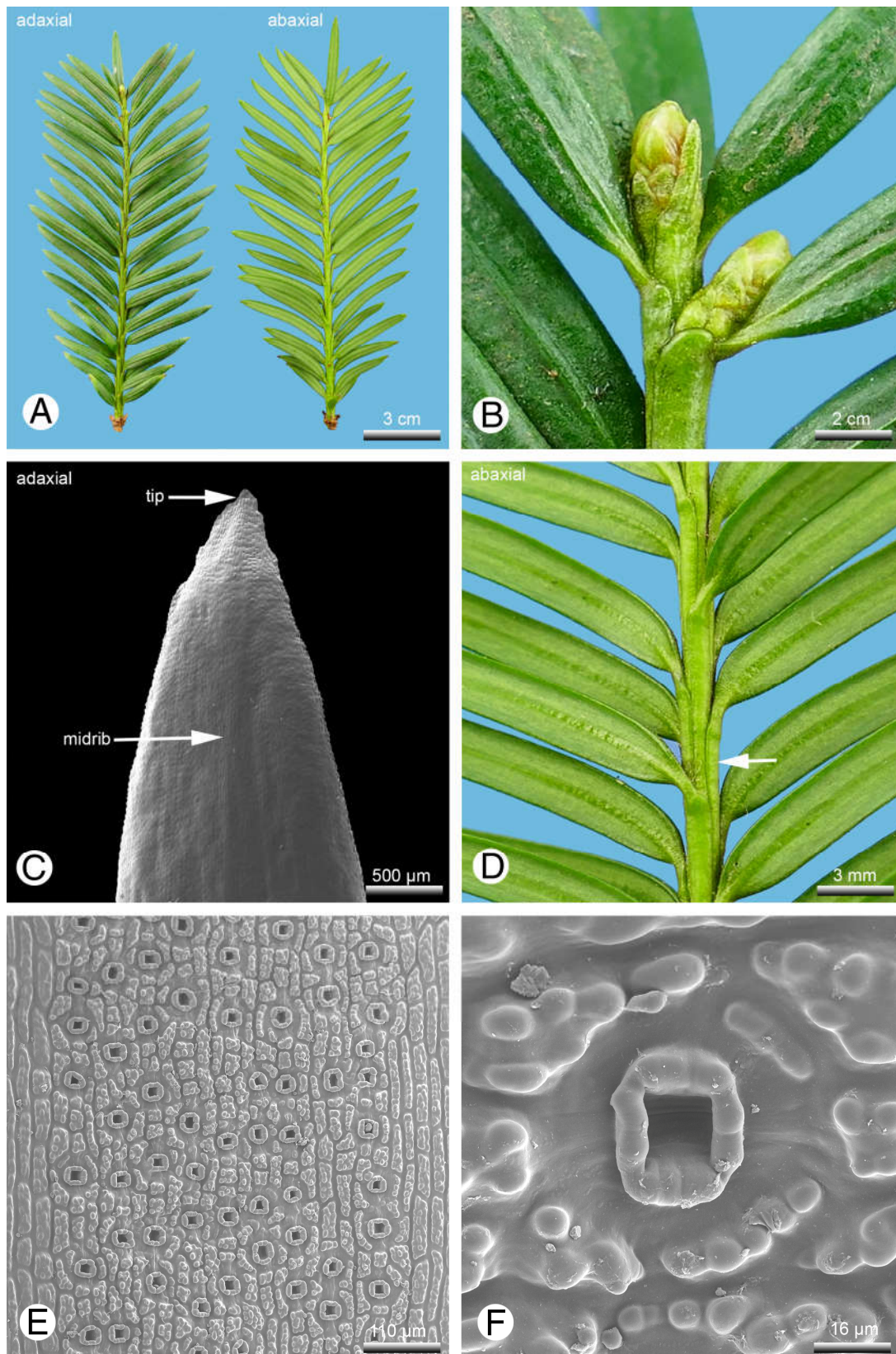


**Fig. 8:** *Pseudotaxus chienii*. Reproductive structures; morphology of seeds.

**A:** Mature seed in lateral view. **B:** Hilum; there are two collateral vascular bundles supplying the seed. **C:** Distal part of the seed showing the micropyle (SEM-image). **D:** Microsculpture of the testa (SEM-image).

Images: V.M. DÖRKEN

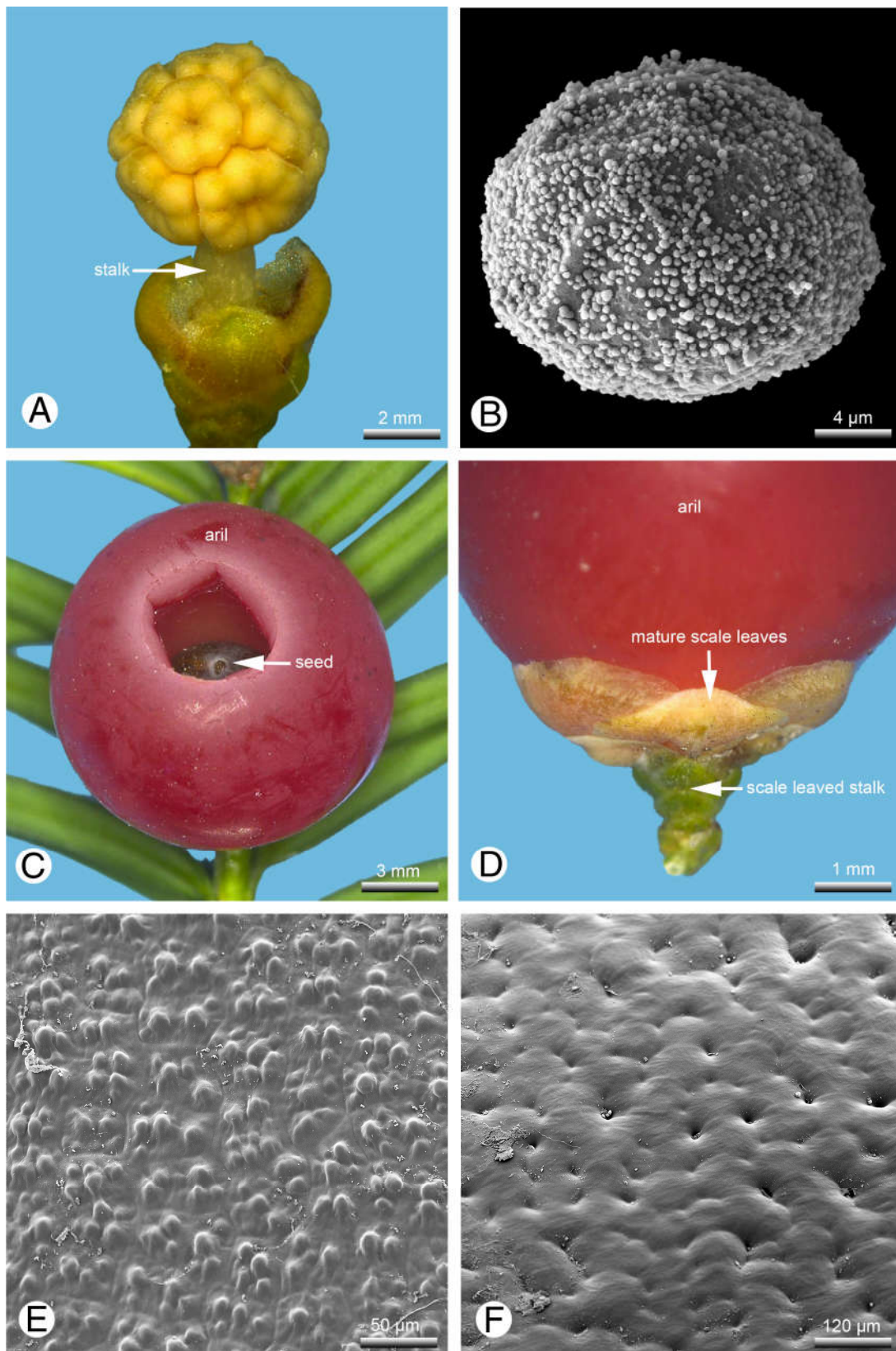




**Fig. 9:** *Taxus baccata*. Distinguishing characters of *Taxus* and *Pseudotaxus*.

**A:** Ad- and abaxial view of a last year's shoot; abaxial leaf surfaces without conspicuous wax markings. **B:** Vegetative buds roundish and appressed. **C:** Leaf tip pointed but not acute. **D:** Leaf bases fused to the stem. **E:** Stomata placed between numerous epidermal papillae. **F:** Amphicyclic stomata.

Images: V.M. DÖRKEN



**Fig. 10:** *Taxus baccata*. Distinguishing characters of *Taxus* and *Pseudotaxus*.

**A:** Pollen cone long stalked and simple; bracts within the pollen cone absent. **B:** Pollen grain with microverrucate-orbiculate exine sculpturing (SEM-image). **C:** Mature seed cone with red aril. **D:** At maturity the scale leaves on the stalk of the seed cone are dry and brown. **E:** Surface of the aril with numerous densely arranged epidermal papillae (SEM-image). **F:** Surface of the testa smooth with numerous small holes (SEM-image).

Images: V.M. DÖRKEN



## Observation of a monoecious *Pseudotaxus chienii* specimen

*Pseudotaxus chienii* is commonly considered to be dioecious species (Dallimore & Jackson 1966: 557; L.K.Fu 1992: 138; Farjon 2010: 927). The *China Plant Red Data Book* (L.K.Fu 1992: 138) is concerned by the poor regeneration of this species in its natural habitat; this rare species shows “a scattered distribution. Its rarity and inadequate pollination of female trees in forests have had a remarkable effect in preventing regeneration.”

Contrary to conifers raised from seeds, plants propagated by grafting or cuttings collected on a mature specimen can produce reproductive pollen and/or seed cones very early. This is what happened with a potted specimen of *Pseudotaxus chienii* in southwestern France.

These photos were taken at the beginning of November, showing mature seed cones with their typical white arils on lower branches and pollen cones in their initial phase, along several of the upper shoots.

*Flora of China* (1999: 91) gives information on the phenology of the reproductive timeline: “Pollination late Mar[ch]–May, seed maturity Oct[ober].”



**Fig. 1:** Shoot of *Pseudotaxus chienii* shoot, adaxial side, showing the pollen cones from above. Cultivated.

All photos:  
2022.11.06



**Fig. 2:** The same shoot from the abaxial side; the axillary positions of the pollen cones are clearly visible.





**Fig. 3:** Details of the shoot with the pollen cones. Notice their pyriform shape and the acute, spine-tipped leaves.



**Fig. 4 & 5:** Seeds cones on the same plant. Notice the split arils of some cones.



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## **Pollen cone structure of the *Libocedrus s.l.* (Callitroideae, Cupressaceae) and its systematic implications for a controversial genus complex ..... 2**

V.M. Dörken & H. Nimsch

**Abstract :** According to our data, pollen cones within the *Libocedrus s.l.* group only show minor variation. These differences were emphasized and used to split *Libocedrus s.l.* in four distinct genera. In our material, all pollen cones of *Papuacedrus* had a decussate arrangement of microsporangioophores, as is also the case for all other taxa within the *Libocedrus s.l.* group. The pollen cone structure is more or less similar throughout the entire *Libocedrus s.l.* group, as was previously shown also for the seed cone structure and for the majority of vegetative traits. Thus, the differences in the reproductive as well as vegetative structures are not sufficient enough to justify the systematic treatment of *Austrocedrus*, *Libocedrus*, *Papuacedrus* and *Pilgerodendron* as four distinct genera.

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A. Jagel

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## **Observation of a monoecious *Pseudotaxus chienii* specimen ..... 70**

D. Maerki

**Abstract :** Commonly considered to be dioecious, pollen and seed cones were observed on a single *P. chienii* specimen.

## **Editorial**

The scientific method relies on the verification of previous research and not taking anything for granted without this practice being applied systematically. This means that the argument of citing an authority cannot be used to justify theories or taxonomies based on results that can be disproved by carefully observed data.

This issue presents two articles that challenge in whole or in part previous observations that seemed firmly established. In the first case, a study of the anatomy of pollen cones shows that those of *Libocedrus arfakensis* do not deviate from the structure common to this genus; in the second, it is observed that *Pseudotaxus chienii* is not only dioecious as presented in the literature to this date, but can show monoecious specimens. Cases of monoecious specimens or individuals changing sex are already known among the Taxaceae.

This Bulletin is edited by the **Cupressus Conservation Project**, a non-profit organisation based in Geneva, Switzerland. It deals mainly with *Cupressus* species, but accepts manuscripts on other species of conifers. Emphasis is given to threatened and endangered taxa. Manuscripts are accepted in the following languages: English, French, German, Spanish, Italian and Russian. The Bulletin is peer reviewed.

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