



Bulletin of the *Cupressus* Conservation Project

No 13

Volume 6 No 1 — 31 January 2017

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The conservation of the true Cypresses is a major concern. Several species and several populations are endangered or critically endangered. Most if not all of them have a restricted or quite restricted distribution range in the wild. The taxonomical treatment has a direct link to their conservation status. The IUCN policy is put under scrutiny.

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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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Reference : *Bull. CCP*.

Prices : online pdf version : free access ;

printed version : 30 CHF or 26 Euro per issue. Airmail shipping worldwide included. Publication is irregular.

Payment after delivery. After one's subscription, the next issues will be sent automatically, unless cancellation of the subscription takes place before shipping. www.cupressus.net/subscription.html

Web site : www.cupressus.net – Bulletin web site : www.cupressus.net/bulletin.html

Online PDF Version : ISSN 2235-400X

Bulletin No 13

Cover photo: *Cupressus sempervirens*, cultivated, France. Colours after pollen has been shed (2 April 2010). © CCP

Recent developments in the taxonomy of the genus *Cupressus* and consequences for their conservation

Until recently the true cypresses were a much neglected genus. They have little economic value compared to other conifers such as the pines, firs, spruces, larches and douglas-firs, as most of the cypresses do not grow so tall or fast; they are not hardy everywhere, their timber is less valuable because it has too many knots (they need heavy pruning to be knot-free). Only in tropical or subtropical climates are they exploited in plantations (inter-tropical Africa, New-Zealand – mainly *Cupressus lusitanica* Miller and *Cupressus macrocarpa* Gordon). Until the very end of the 20th century few articles were dedicated to this group of species. Few questions were answered. A discovery in the north of Vietnam triggered research and a new understanding of this genus. Some of the most important articles dedicated to the taxonomy of the genus *Cupressus* during the last 16 years are reviewed.

The conservation of the true Cypresses is a major concern. Several species and several populations are endangered or critically endangered. Most if not all of them have a restricted or quite restricted distribution range in the wild. The taxonomical treatment has a direct link to their conservation status. The IUCN policy is put under scrutiny.

Nootka Cypress: *Cupressus* or *Chamaecyparis* ?

An article by Michael Frankis (1993) raised this very important question. The Nootka Cypress was discovered by Menzies and described by D. Don under *Cupressus nootkatensis* in 1824. Spach (1841) transferred it to his new genus *Chamaecyparis* considering the flattened foliage and the small cones. But this new combination was erroneous from the start. In the original diagnosis of the genus *Chamaecyparis*, Spach wrote: “Floraison vernale. Maturité annuelle.”¹ That is in one growing season, while the Nootka Cypress mature its cones in more than 12 months (up to 18 months depending on the climatic conditions). Until 1993, following Spach, this species was quite generally treated as a *Chamaecyparis* species. The article by Frankis details the significant characters of Nootka Cypress and compares them with the other *Cupressus* and *Chamaecyparis* species. The characters reviewed are the maturity of the cones in two growing seasons, the scale shapes, the seed scars, the smell of the leaves and the hybrids. Based on these convincing arguments, the conclusion was unambiguous: Nootka Cypress belongs to the genus *Cupressus*.

Fig. 1: *Cupressus nootkatensis*.



¹ “Pollination in Spring. Yearly maturity.” Page 331.

Vietnam Cypress

A new conifer species was discovered in the north of Vietnam in September 1999 by two Vietnamese botanists Vũ Văn Cần and Lê Văn Châm during a survey aiming at creating a nature reserve. During the same year, this taxon was described by the authors of the discovery as *Thuja quanbaensis* (Vũ Văn Cần *et al.* 1999). The diagnose in Vietnamese language is complete and to the point, but very unfortunately there was no Latin description (see appendix A, and B and C for the French and English translations respectively). According to the Code of Nomenclature the proposed Latin name was thus not validly published².

In 2002, Farjon – after having rejected a first sample as nothing special – described this taxon as a new genus *Xanthocyparis* Farjon & T.H. Nguyễn (type: *X. vietnamensis* Farjon & T.H. Nguyễn) and linked it to the Nootka Cypress, proposing a new combination, *Xanthocyparis nootkatensis* (D. Don) Farjon & D.K. Harder. Quite unfortunately, he did not acknowledge the real discoverers of this new plant (see Appendix D for the description of the actual discovery, by Averyanov 2002, and Appendix E for the story told by Farjon 2008). The Nomenclatural Code and the validation of Latin names are one thing, the discovery of a new taxon is a fact of history and science and nobody can act as if what happened did not happen and as if the Vietnamese description was never written. To support his new genus, Farjon (2002) discarded the 1993 analysis by Frankis (and later by Jagel & Stützel 2001) in the following way:

“There has been debate concerning the placement of *C. nootkatensis* in either genus, with some authors arguing for inclusion in *Cupressus* based on characters of the ovuliferous cones (Frankis, 1993; Jagel & Stützel, 2001). Recent cladistic evidence based on molecular data (matK gene) gives only weak support for its inclusion in *Cupressus* (Gadek *et al.*, 2000); similar evidence using a combined data set (matK + non-molecular data) does not and places it as a sister group to *Cupressus* + *Juniperus* with stronger bootstrap support (Gadek *et al.*, 2000).”

Not only did Farjon ignore much of Frankis’ arguments (there is more than just the “ovuliferous cones”), he also turned the conclusion by Gadek *et al.* upside down as it is already mentioned in their abstract:

“*Chamaecyparis nootkatensis* falls within *Cupressus*, clustering with a robust clade of New World species.”

Further Gadek wrote (Gadek *et al.* 2000: 1054 – emphasis added):

“The morphological distinctiveness of this species, which has been responsible for the difficulty in placing it satisfactorily in a taxonomy, has again been influential here. **Support for a separate genus is certainly lacking in the molecular data**, and despite the differences in its morphology, it appears that *Chamaecyparis nootkatensis* should be returned to *Cupressus*. Hybrids are recorded to have arisen in cultivation between *Chamaecyparis nootkatensis* and *Cupressus lusitanica*, *C. arizonica* var. *arizonica* and *C. arizonica* var. *glabra* (Krüssmann, 1985), and this fact has been used by some authors to submerge the genera (e.g., Bartel, 1993). Since it is, however, the only species of *Chamaecyparis* to hybridize with *Cupressus*, the occurrence of these so-called intergeneric hybrids is in full accord with **our conclusion that *Chamaecyparis nootkatensis* is in fact a member of the genus *Cupressus*.**”

Another problem arose two years later as Little (2004) pointed to the fact that the combination *Xanthocyparis nootkatensis* was invalid because of the priority rule: Ørsted published the genus *Callitropsis* in 1865 as a monotypic genus with the new combination *Callitropsis nootkatensis*. Then Little (2006) transferred all New World Cypress in this resurrected genus *Callitropsis*, generating 17 new combinations.

The same year, Farjon (Mill & Farjon 2006) asked to conserve *Xanthocyparis* against *Callitropsis*. One of the developed arguments was that the combination *Callitropsis nootkatensis* was not formally adopted and validated by Ørsted:

“Neither *Chamaecyparis nootkatensis* nor *Thujopsis borealis* was explicitly said to be the type of *Callitropsis* by Ørsted, and neither was recombined under *Callitropsis* by him. The latter point is important since Little & al. (l.c.: 1879) have incorrectly written (**bold emphasis ours**) “The genus *Callitropsis* non *Callitropsis* sensu Compton (1922), **with *C. nootkatensis* (D. Don) Ørest.** [sic] **designated as its type**, was described in 1865 [sic].” but Ørsted never actually made this combination as required by Art. 33.1.”

In fact it was validly published by Ørsted, in a second text overlooked by Mill & Farjon (Maerki & Frankis 2012). Very quickly the Nomenclatural Committee accepted conservation of *Xanthocyparis* against *Callitropsis* (Brummitt 2007). The presented justifications were far from convincing; for instance:

“*C. nootkatensis* (which was always seen as doubtfully placed in *Cupressus*)”

With the facts known in 2007, this affirmation was not only completely wrong, it is also out of place when dealing with a nomenclatural question.

² Vienna Code 36.1 (Melbourne code 39.1): “In order to be validly published, a name of a new taxon (algae and fossils excepted) published between 1 January 1935 and 31 December 2011, inclusive, must be accompanied by a Latin description or diagnosis or by a reference (see Art. 38.13) to a previously and effectively published Latin description or diagnosis (...).”

“There is a further significant argument. The horticulturally important Leyland cypress, formerly known as *×Cupressocyparis*, has now been re-named as *×Cuprocyparis* in order to make as little change as possible for users of Latin names. This has apparently been swallowed without too much resistance by the horticultural world, and indeed by those in the legal profession for whom it causes problems.”

Again this was questionable in 2007 and is still very questionable now. The result of a Google search with “*Cuprocyparis leylandii*” gives today 4’630 hits (2.6.2016 – decreasing), while with “*Cupressocyparis leylandii*” there are 128’000 pages found (increasing). Moreover when typing “*Cuprocyparis leylandii*”, the search engine automatically suggests to try “*Cupressocyparis leylandii*”. In fact this hybrid was originally described as *Cupressus ×leylandii* and there is no reason to consider it as an intergeneric hybrid (see below for a further discussion on hybrids and their meaning). There is no intergeneric hybrids known among conifers and there is no argument to accept one artificially here. Finally:

“This taxonomy [Little’s taxonomy] has been strongly refuted by Farjon, one of the present proposers, in *Taxon* 56: 639-641. 2007. (...) If anyone should accept the taxonomy of Little, they will apparently need to make 19 new combinations in *Xanthocyparis*.”

We deal in Appendix F with the Letter to the Editor written by Farjon and referenced here by Brummitt. This “strongly refuted” taxonomy of Little is once again out of place when dealing with nomenclature. Several other authors chose other ways to use Little’s propositions and get rid of *Xanthocyparis nootkatensis*. They were able to resurrect *Callitropsis nootkatensis*, threatening even more the stability of the nomenclature by multiplying the synonyms, which is the very first result of that decision to conserve *Xanthocyparis*.

In 2009, Debreczy *et al.* published an article in which *Xanthocyparis vietnamensis* was reduced to a monospecific genus, and validated again *Callitropsis nootkatensis* together with all other new combinations under this genus. As this decision is based on taxonomical considerations, the Nomenclature Committee will not have a word to say. The case was far from closed. The consequences of the discovery of the Vietnam Cypress not only damaged the nomenclature by a series a mistakes – that is for the negative side, but it also triggered new research, especially on molecular analysis and phylogeny as well as new observations, bringing a flow of new data – the positive side.

Fig. 2: *Cupressus vietnamensis*, cultivated, Paris, France.



New World Cypresses

The consequences of the new information from molecular analyses can be summarised like this:

- The genus *Chamaecyparis* resolves as definitively well separated from the genus *Cupressus*³.
- *Juniperus* is closely related to the cypresses.
- Inside the genus *Cupressus* appear two distinct clades separating the old world and the new world species (except with the Vietnam species in the new world group).
- Following a suggestion by Little (2006), the cypresses were split into three genera by Debreczy (2009), *Cupressus*, *Xanthocyparis*, *Callitropsis*, and in four genera by Bartel with addition of the new genus *Hesperocyparis* Bartel & R.A. Price (Adams *et al.* 2009), regrouping here all species from the new world, except *Callitropsis nootkatensis*.

Several authors do not recognise these splits. *Xanthocyparis vietnamensis* was first reunited to *Cupressus* by Xiang & Li in May 2005. Unfortunately the basionym was not cited properly⁴ and their publication of this new combination was not valid under the nomenclatural code. In July 2005 Silba did it correctly, and thus we have *Cupressus vietnamensis* (Farjon & T.H. Nguyễn) Silba. Rushforth also wrote an article before 2005 acknowledging this very transfer to *Cupressus*, but it was only published in 2007.

In 2011, Christenhusz, Reveal, Farjon⁵, Gardner, Mill & Chase published a major review article *A new classification and linear sequence of extant gymnosperms*. On *Cupressus*, they wrote (p. 65):

“Note:—Adams *et al.* (2009) showed that *Cupressus* formed two clades: the Old World clade of *Cupressus* was sister to *Juniperus*, whereas the New World clade of *Cupressus* (*Hesperocyparis*) included *Xanthocyparis vietnamensis* and *Callitropsis nootkatensis*. However, Mao *et al.* (2010) showed that *Cupressus* in its broad sense including *Xanthocyparis* and *Callitropsis* is monophyletic with weak support. 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*.”

Adams (2012, 2014) published new data with the same cladogram as in Mao, that is a monophyletic genus *Cupressus* (but still split under *Callitropsis*, *Xanthocyparis* and *Hesperocyparis*).

Fig. 3: *Cupressus macrocarpa*. In herbaria *Cupressus sempervirens* is often confused with *C. macrocarpa* because *sempervirens* cones are often as large as or larger than *C. macrocarpa* cones.



³ Until 2002, Farjon listed *Cupressus nootkatensis* under *Chamaecyparis* (Farjon 1998, 2001).

⁴ Xiang & Li cited the complete article with the basionym, instead of the exact page on which the basionym is mentioned.

⁵ Although signing as co-author, Farjon keeps *Xanthocyparis* as a two-species genus on his online database and in his most recent book (Farjon 2013).

Christopher Earle from the conifer.org website (USA) recognises only one *Cupressus* genus. He explained his reasons clearly as follow:

“I have chosen here to broadly define *Cupressus*, and to reduce *Hesperocyparis*, *Callitropsis* and *Xanthocyparis* to synonymy, for two principal reasons. First, it isn’t possible to distinguish *Hesperocyparis* from the old world *Cupressus* on the basis of morphology; the distinction is made by applying a complex analytical algorithm to a large molecular data set. I do not know of any other case where someone has tried to assert the existence of two separable genera on the basis of such an abstract, artificial process. Second, and perhaps even more important, it is not necessary to subdivide *Cupressus*. Although the species occupy very diverse ecological settings, ranging from dominant trees of the temperate rainforest to shrubby trees of the high mountains and subtropical deserts, yet still if you confine your gaze to their cones and foliage, then they all resemble each other much more than any of them resembles another genus in the Cupressaceae. Breaking apart *Cupressus* makes about as much sense as breaking apart *Juniperus*, or any other large conifer genus for that matter. It could be done, but it would be inconsistent with the existing norms for distinguishing between genera within the Cupressaceae.”

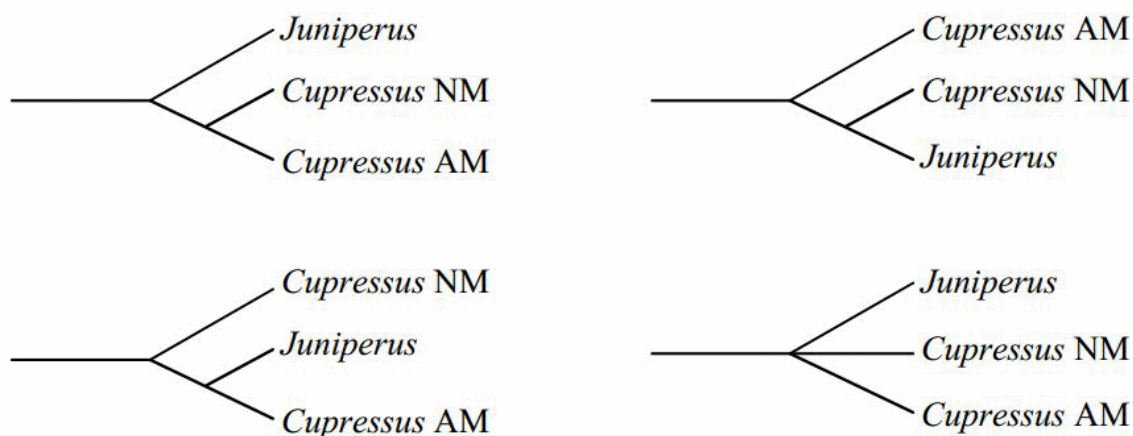
In addition to Gadek, Earle and Christenhusz *et al.*, Rushforth and Frankis (England), Jagel and Dörken (Germany), Lamant and Bauny (France) – among others – are authors keeping all the true cypresses in a unique genus *Cupressus*. This is also the choice here. Farjon (2009) does not recognise *Hesperocyparis* and explains his arguments in an article: *Do we have to chop up the cypresses?* (see appendix G).

Phylogeny: molecular analyses

The next question is to try to sort out the relationships discussed by Christenhusz *et al.* The authors mention two studies, the ones by Adams *et al.* (2009) and by Mao *et al.* (2010). But there are however more than these two papers. Three groups are identified: *Juniperus*, *Cupressus* Old World and *Cupressus* New World. What are the phylogenetic relationships between them according to the results currently available?

With three groups, there are four hypotheses for their phylogeny. They are summarised here (fig. 4).

Fig. 4: Possible phylogenies *Cupressus-Juniperus*.



- NM: New World
- AM: Old World

Hypothesis 1: A monophyletic *Cupressus*

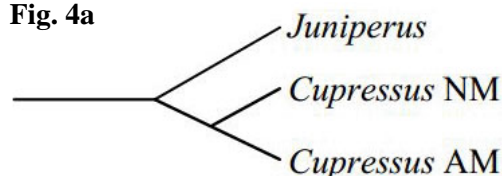
This hypothesis is supported by the following molecular analyses:

- *petN-psbM* ^{Adams 2009}
- *trnD-trnT* + *trnS-trnG* + *trnL-trnF* ^{Xu 2010}
- *rbcL* + *matK* + *psbB* + *petB-D* + *rps4* + *trnL-F* ^{Mao 2010}
- *matK* ^{Yang 2012}
- nrDNA + cpDNA ^{Terry 2012 + Adams 2014}

Other arguments:

- Morphology: the cones are very different and allow immediate distinction of the two genera.
- Phenology: all cypresses are monoecious, most of junipers are dioecious.
- Fossil data (a) ^{Mao 2010}

Fig. 4a



Hypothesis 2: *Cupressus* OW splitting first

This hypothesis is supported by the following molecular analyses:

- nrITS ^{Little 2006, Adams 2009}
- ITS + 4CL + *CnABI3* + *petN-psbM* ^{Adams 2009}
- Fossil data (b) ^{Mao 2010}

Hypothesis 3: *Cupressus* NW splitting first

This hypothesis is supported by the following molecular analyses:

- *NEEDLY* intron2 ^{Little 2006}
- Molecular + morphological combination ^{Little 2006}
- *ABI3* ^{Adams 2009}
- *LEAFY* full length ^{Yang 2012}
- *NEEDLY* full length ^{Yang 2012}
- *LEAFY* + *NEEDLY* + *matK* + *rps3* ^{Yang 2012}
- *rps3* shows *Cupressus funebris* grouped together with the *Juniperus*. ^{Yang 2012}
- 4CL shows *C. nootkatensis* and *vietnamensis* grouped together with old world cypresses. ^{Adams 2009}

Hypothesis 4: Common ancestor

This hypothesis is supported by the following molecular analyses:

- *matK* + *rbcL* + *trnL* ^{Little 2006}
- nrDNA + mtDNA + cpDNA ^{Mao 2010}

An example of molecular analyses: *Cupressus revealiana* vs. *Cupressus montana*

To confirm the status of *Cupressus revealiana* as a valid species (Bisbee & Maerki 2012), Adams *et al.* (2014: 77) published the following cladogram with *Cupressus revealiana* and *Cupressus montana* (treated under *Hesperocyparis*) with cpDNA results.

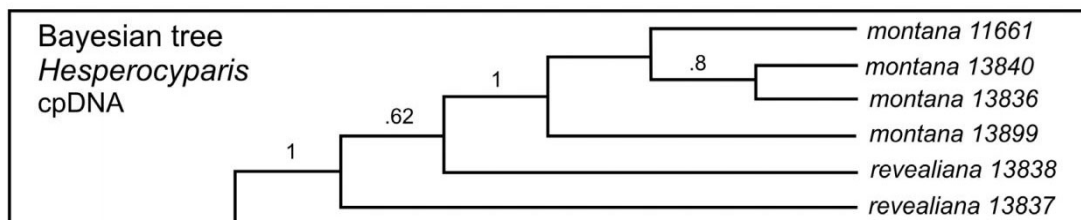


Fig. 5: Cladogram *Cupressus montana* vs. *Cupressus revealiana*, cpDNA.

In morphological, physiological, phenological, ecological, biogeographic (Bisbee & Maerki 2012) and leaf oil characteristics (Adams *et al.* 2014), both taxa are very distinct species easy to separate. They can already be distinguished easily as seedlings (article in preparation). But the result of the cpDNA analysis shows a paraphyletic *Cupressus revealiana*. The cause of this aberrant result (perhaps insufficient, or non representative samples, or erroneous mathematical model, or all of them) is not explained nor investigated. The result must be questioned and repeated (it is just rejected), while the data from the leaf oils are acknowledged.

Phylogeny: a provisional conclusion

Although molecular analyses⁶ are a very useful tool for decrypting or confirming relationships between taxa, the results presented here are more than problematic due to their contradictions. Currently, no conclusion can be drawn unilaterally. The monophyly of *Cupressus* is conversely assured by several physiological, phenological and morphological characters and also by several molecular analyses. Until this monophyly is disproved by unequivocal data, a conservative treatment should be the rule⁷.

⁶ Questions about the pertinence of the algorithms used and the pertinence of the parsimony principle are seldom asked. Is evolution parsimonious? Is it a refutable proposition? Here with the judicious choice of a definite molecular data set, it is possible to support any phylogeny between the three identified groups.

⁷ So far only very partial, contestable results are able to bring a different issue. Fossil record about a common ancestor is currently absent so that any hypothesis would be impossible to test.

Evolution

The vast majority if not all of the wild cypress populations occupy small and isolated areas away from each other. This distribution favours divergence and speciation processes. Cypressess are shade intolerant and often eliminated by taller trees growing faster (there are exceptions). They are adapted to sites where other species are not able to grow (podzolic and serpentine soils, arid or desert conditions).

Cupressus nootkatensis shows the widest natural area of occupancy (Pacific coast from Alaska to northern California from sea level to 1600m altitude inland). In the same region, Vancouver Island, a closely related species dating from Upper Cretaceous was found, *Thuites corpulentus* Bell (1957). This fossil species was renamed to *Chamaecyparis corpulenta* by McIver (1994). When a new fossil was found in the Axel Heiberg Island and described as *Chamaecyparis eureka* Kotyk (Kotyk *et al.* 2003), *Chamaecyparis corpulenta* was reviewed at the same time and considered close to [*Chamaecyparis*] *nootkatensis*. As the debate on the taxonomical place of Nootka Cypress had barely started at this time, the authors did not transfer *Ch. corpulenta* to *Cupressus*.⁸ With the placement of the Nootka Cypress in *Cupressus*, supported also by the evidence currently presented (and see Carrière below), this fossil taxon is here transferred:

***Cupressus corpulenta* (Bell) Maerki, comb. nova.**

Basionym: *Thuites corpulentus* Bell in *Geol. Surv. Canada, Mem.* 293: 35, Plate 18, Fig. 8. 1957.

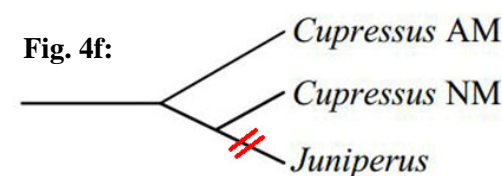
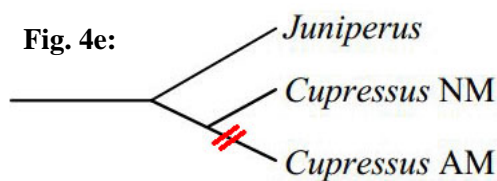
Synonym: *Chamaecyparis corpulenta* (Bell) McIver in *Canad. J. Bot.* 72: 1788. 1994.

As with the different results of molecular analysis, every hypothesis is supported by some parts of the genotype, which can contradict each other. How does one decide which analysis best reconstructs the real phylogeny? Are the data available on evolution – how scarce and ambiguous – able to give useful information? The characteristics of *Cupressus nootkatensis* and the related fossil *Cupressus corpulenta*, are basal to *Cupressus* (a position confirmed by the place of the former in cladograms), a hypothesis can be made that the area of diffusion of the genus lies in northwest America and northeast Asia (further supported by the ranges of other primitive species *Cupressus vietnamensis*, *C. funebris* and *C. tonkinensis*), and that the split between old world and new world cypresses is more recent than the emergence of *Juniperus*. This last genus is part of a co-evolution with birds. The first junipers could be as old as the first flying dinosaurs or pterosaurs. Attractive seeds coats (drupes, arils) are known from a variety of genera (Ephedraceae, Taxaceae) since the Mesozoic. *Mesocyparis*, considered as a sister group of *Cupressus*, is also present in NE Asia and NW America.

If for the ancestor of the old world cypresses was affected by one or several important mutations (following a possible bottleneck reduction (marked in the figure in red), molecular analysis results may show a mistaken phylogeny and erroneously support in this example the hypothesis #2 above – fig. 4b.

This reasoning is also valid the other way round (fig. 4f). The problem in this case is that the junipers, unlike cypresses, are a very successful genus with a little more than a hundred taxa⁹ according to Adams, wide distribution ranges for several species and adaptations to a variety of climates and soils, to drought and altitude. In that case a bottleneck reduction would be unlikely for the genus.

Most juniper populations are abundant. Thanks to very effective avian dispersal, the pool and the flow of genes are far greater than for any cypress species, and isolation less likely except on islands and through time. After the glaciation periods in the Quaternary, *Juniperus communis* var. *alpina* for instance returned very quickly on mountain slopes after the retreat of the glaciers, while no cypress was even able to return at all to continental Europe. As the genus *Cupressus* can be dated back to Cretaceous time, the origin of the junipers could be as old as the diversification of avian dinosaurs in late Jurassic or early Cretaceous.



⁸ “The taxon *Chamaecyparis corpulenta* should, therefore, be removed from *Chamaecyparis*, but resolution of the nomenclatural issues concerning the *Cupressus nootkatensis* clade is beyond the scope of this paper, so that formal transfer of *Chamaecyparis corpulenta* awaits further neobotanical research.” (Kotyk *et al.* 2003: 123.)

⁹ 76 species, 32 varieties, 8 formas (Adams 2014: 24).

Cypress hybrids

Four cultivated hybrid cypress species are known:

- 1) *Cupressus ×leylandii* Dallimore & Jackson: *C. nootkatensis* × *C. macrocarpa*
- 2) *Cupressus ×notabilis* (A.F. Mitch.) Silba: *C. nootkatensis* × *C. glabra*
- 3) *Cupressus ×ovensii* (A.F. Mitch.) Silba: *C. nootkatensis* × *C. lusitanica*
- 4) *Cupressus glabra* × *C. pygmaea*¹⁰

A fifth hybrid *Cupressus ×hybrida* A.Camus, as *C. sempervirens* × *C. macrocarpa*, was described by Camus (1924), but has not been verified.

Camus observed this hybrid on the Mediterranean coast close to Saint-Tropez in the south of France, describing a specimen with intermediate characters between both parents (Camus 1924, 1925). As these observations are already almost one century old, with no herbarium material or even a drawing left, and because the tree was cut down, no investigation or verification is now possible. There is a strong need for further research of potential hybrid cypresses between old and new world species.

Carrière (1861: 15) on the concept of species wrote on hybrids and taxonomy:

« Aussi, toutes les fois que la fécondation peut s'opérer entre espèces considérées comme appartenant à des genres différents et que leurs produits sont indéfiniment féconds, cela prouve tout simplement que notre système de classification est vicieux, que nous avons considéré comme appartenant à des genres distincts des espèces du même genre, et qui, de plus, sont très-semblables entre elles. »

[Also, every time that fertilisation can take place between species considered to belong to different genera and that their products are indefinitely fertile, this proves simply that our classification system is bad, that we have considered as belonging to distinct genera species of the same genus, and which, moreover, are very similar between them.]

Fig. 6: *Cupressus ×notabilis*.



¹⁰ Frank Callahan, pers. comm.; Adams *et al.* 2012.

On this principle this unequivocally means that all new world *Cupressus* species belong to the same genus. Should the observation by Camus of a hybrid between new world and old world cypresses be confirmed – between *Cupressus sempervirens* and *Cupressus macrocarpa*, or between any other species of the two worlds – the monogeneric status of the true cypresses under *Cupressus* will be affirmed without contestation under Carrière's principle. There is little doubt that hybrids currently remain the best genetic test to show how close two species are, far better than any short DNA sequence, for such hybridisation test implies the whole genomes of the taxa and proves their compatibility.

Taxonomy & conservation: *Cupressus* species

There is an obvious and important link between taxonomy and conservation. The accuracy of the descriptions of the different species is necessary to take meaningful decisions on their protection when necessary. Any taxon not recognised – considered for instance as synonym of another species – could be judged not worthy of protection. Within the genus *Cupressus*, there are several examples:

- *Cupressus tonkinensis* is considered by some authors (IUCN Red List 2013, Farjon 2005, 2010, Farjon & Filer 2013) as an exotic *Cupressus torulosa* or *lusitanica*, neither of them being considered as a threatened species, and thus not listed on the Red List, and with no international recognition. Quite unfortunately *Cupressus tonkinensis* is the most endangered of all cypress species: the only remaining wild specimens hang on a cliff and cannot compete on a normal soil (Pham Van The *et al.* 2013).
- *Cupressus revealiana* is considered (IUCN 2013 and Farjon 2005, 2010, Farjon & Filer 2013) as synonym of *Cupressus stephensonii*, species itself **Critically Endangered** (as a variety – IUCN 2013). In fact these are two distinct species, both in danger of extinction in their natural habitat. The extinction of one of them would not be identical with the extinction of one population, but of a whole species.
- *Cupressus tortulosa* vs. *Cupressus cashmeriana*: IUCN (2013) and Farjon (2005, 2010, Farjon & Filer 2013) consider *Cupressus tortulosa* Griff. as synonym of *Cupressus cashmeriana* Carrière, although these two species differ by their morphology, physiology, phenology, hardiness and biogeography. The distribution range of *Cupressus cashmeriana* appears very narrow and the species would best be considered as **Critically Endangered**, while the IUCN classifies its broader concept of *Cupressus cashmeriana* only as **Near Threatened**.

Fig. 7: *Cupressus tonkinensis*. This cone shows affinities with new world species and *Cupressus vietnamensis* in the low number of scales and shape.



Cupressus tortulosa occupies areas very difficult to access and at least five populations are known. As Griffith descriptions are based on cultivated specimens, the taxonomical position of all these wild populations needs to be confirmed.

Fig. 8: *Cupressus tortulosa*, cultivated, France.



Fig. 9: *Cupressus cashmeriana*, cultivated, France.



Fig. 10: *Cupressus dupreziana*, Tassili, Algeria.



- *Cupressus dupreziana* & *Cupressus atlantica*: these two taxa cannot hybridise; pollen of *Cupressus dupreziana* A. Camus is diploid, while that of *Cupressus atlantica* Gaussen is haploid, as are the ovules. A specific barrier is thus established (Pichot *et al.* 2008). The IUCN Red List (2013) following Farjon (2005, 2010, Farjon & Filer 2013) does not consider this physiological character and treats them as varieties of the same species. Their conservation status is the following:

- *Cupressus dupreziana*: **Endangered**
- *Cupressus dupreziana* var. *dupreziana*: **Critically Endangered**
- *Cupressus dupreziana* var. *atlantica*: **Critically Endangered**

The extinction of one variety has not the same importance as the extinction of one irreplaceable species. Based on morphology, physiology and biogeography, the treatment by the *Cupressus* Conservation Project follows logically:

- *Cupressus dupreziana*: **Critically Endangered** (the number of trees is diminishing.)
- *Cupressus atlantica*: **Critically Endangered** (Maerki & Lamant 2014.)
- For the detailed conservation status list as treated by the *Cupressus* Conservation Project compared to the IUCN list, see Appendix H.

Taxonomy & conservation: *Juniperus macrocarpa* (Greece)

Juniperus macrocarpa Sibth. & Sm. is considered by some authors (IUCN Red List 2013, Farjon 2005, 2010, Farjon & Filer 2013) as a subspecies of *Juniperus oxycedrus* L., despite clear morphological, physiological, ecological and geographic differences. This taxon never grows away from the sea and is often very close to the shore on sand or gravel, even at altitudes below 2m. The species was described from a Greek specimen. There is no recent study to understand if it is the same species throughout the currently admitted range from east to west of the Mediterranean area. The distribution range map published by Adams (2014) is not up-to-date. Some localities are missing (Algeria, Tunisia), while some others represent *Juniperus oxycedrus* (continental France; Cadaquès area, Spain). More verifications are needed.

The IUCN Red List 2013 classifies *Juniperus macrocarpa* as **Least Concern**. Unfortunately this juniper with an extremely scattered distribution is threatened by new buildings on the coast lines, by tourism, by sand extraction, by sea level rise, by privatisation of the coastal areas in Greece following the economic crisis and overall by the general absence of protection with only a few exceptions.

Fig. 11: *Juniperus macrocarpa*, Greece.





Fig. 12: *Juniperus macrocarpa*, cones, Greece. **Fig. 13:** *J. macrocarpa* growing with *J. phoenicea*, Greece.



Taxonomy – conclusion

- The taxonomy of the cypresses is difficult due to great variability in characters, especially among the New World species. Unlike other groups, the cypresses are still very little studied despite several recent molecular analyses. More than one work – such as the monograph on *Cupressaceae* by Farjon (2005) – shows factual errors and a general ignorance of cypress phenology and physiology.
- The taxonomy of the cypresses must be based on morphological, physiological, phenological, ecological, geographic, paleontological and molecular data, treated when possible on a statistical basis. So far the most important dataset in one work – although still far from complete – was provided by Little (2005).
- Currently no definitive conclusion can be drawn from molecular analysis on the genealogy of the cypresses and the junipers, as the results are too contradictory between the different genes studied. Considering all data available, there is no reason to view the genus *Cupressus* as non monophyletic, especially when taking into account the following two points.
- Among conifers, no intergeneric hybrids are known.
- One can discard the principle stated by Carrière, but it will remain a classification based on a personal opinion not supported by a logical and reasonable method.
- Some *Cupressus* taxonomies¹¹ are faulty when two taxa which cannot hybridise naturally are placed as varieties of the same species¹² or in synonymy¹³ and when two species which can hybridise are placed in two different genera.¹⁴
- Current interest in the genus *Cupressus* is very recent and will quite likely display important developments in the near future.

Conservation – conclusion

- A better taxonomy is needed, leading to motivated and better decisions on species conservation. Observations on the phenology of the cypresses are dramatically missing.
- Today the *Cupressus* Conservation Project distinguishes 33 well supported species of *Cupressus*.
- The list of threatened species (that is Critically Endangered [CR], Endangered [EN] or Vulnerable [VU] categories of the IUCN) consists of 15 taxa out of 26 according to the IUCN, while **24 species of 33 are threatened** as determined by the *Cupressus* Conservation Project. Seven of these species are not recognised by Farjon and are not listed by the IUCN. Out of these seven species, five are evaluated here as Critically Endangered and one as Endangered (see Appendix H).
- To this day populations are not taken into consideration by the IUCN. Unfortunately many *Cupressus* populations are in danger of extinction, even if the involved species as a whole is not threatened. Such critically endangered populations are to be found especially among *Cupressus abramsiana*, *Cupressus arizonica*, *Cupressus forbesii*, *Cupressus sargentii*, *Cupressus sempervirens* and *Cupressus torulosa*.
- The reduction of several species to the rank of variety makes them disappear of the lists: according to the IUCN Red List 2013, there is zero “species” of *Cupressus* under the **Critically Endangered** status! (And only two *Juniperus*.)

Photo credits

Fig. 1 & 3: © Rick Fencil

Fig. 7: © Dennis Stevenson

Fig. 10: © Messaoud Ramdani

Other photos: © *Cupressus* Conservation Project

¹¹ Like Farjon’s one.

¹² See above the case about *Cupressus dupreziana* and *Cupressus atlantica*. To be added *Cupressus stephensonii/arizonica*.

¹³ See above the cases of *Cupressus tonkinensis/lusitanica*, *Cupressus stephensonii/revealiana* and *Cupressus tortulosa/cashmeriana*. To be added *Cupressus abramsiana/butanoensis*.

¹⁴ See above the cases of the different hybrids with *Cupressus nootkatensis* as one parent.

Appendix A: Vu Van Can, Vu Van Dung and Le Van Cham. 1999. Discovery of a new species of Cupressaceae, *Thuja quanbaensis* sp. nov., from a limestone area in Ha Giang province. In: Le Sau (ed.) *Protection and sustainable development of forest and biodiversity in limestone areas of Vietnam*. Forest Inventory and Planning Institute, Hanoi, Vietnam. (Vietnamese; French and English versions, p. 17-18.)

**PHÁT HIỆN MỘT LOÀI MỚI THUỘC HỌ HOÀNG ĐÀN (Cupressaceae):
CÂY CHÉ - *Thuja quanbaensis* sp. nov.,
Ở VÙNG NÚI ĐÁ VÔI TỈNH HÀ GIANG**

Vũ Văn Cần, Vũ Văn Dũng và Lê Văn Châm
Viện Điều tra Quy hoạch Rừng

(photo)

Loài cây mới phát hiện
Tên : Ché - *Thuja quanbaensis* sp. nov
ảnh : **Vũ Văn Dũng**

Trong đợt điều tra thám thực vật núi đá để xây dựng khu BTTN Bát Đại Sơn ở xã Thanh Vân, huyện Quản Bạ, tỉnh Hà Giang (23/9/99 – 27/9/99), chúng tôi đã phát hiện một loài mới thuộc chi Trắc Bách (*Thuja* L.) của hệ thực vật Việt Nam.

Dưới đây chúng tôi mô tả và xác định tên khoa học cho loài mới này :

- Tên khoa học : *Thuja quanbaensis* sp. nov.
- Tên phổ thông : Trắc bách quản bạ
- Tên địa phương : Ché (Hơ-mông)

Cây gỗ thường xanh, chiều cao 7-10m, đường kính ngang ngực 30-40cm, phân cành thấp, khoảng 1,5-2m.

Vỏ dày 2-3mm ; vỏ ngoài xám trắng, nứt dọc thành đường nhỏ ; vỏ trong phớt hồng ; thịt vỏ màu trắng, có nhựa gồm nhiều lớp mỏng, dai.

Lá có 2 dạng :

Lá sinh dưỡng hình giải, mọc vòng trên cành non tròn, có cạnh, 4 chiếc một đốt, dài 2,7-3cm, rộng 2mm, đầu có mũi nhọn sắc, gốc không cuống, mép nguyên, mặt trên lục nhẵn, mặt dưới có 2 giải lõm khí màu trắng chạy song theo chiều dài phiến lá, ngăn cách bởi gân giữa và mép lá, ba giải màu lục có chiều rộng gần bằng nhau.

Lá sinh sản hình mũi khoan, mọc đối chéo nhau trên cành con dẹt, xếp thành mặt phẳng, dài 2-5mm, đầu có mũi nhọn sắc.

Nón đực chưa biết. Nón cái mọc đơn đầu cành con ngắn, hình trứng ngược, chiều cao 1,2cm, đường kính 1cm, khi chín hoá [hóa?] gỗ, nê 4-6 mảnh, nếu 6 mảnh thì có 2 mảnh nhỏ nằm phía gốc quả, màu nâu, mảnh có 1 mô nhỏ ngắn, mỗi quả chứa 5-7 hạt ; hạt dạng trứng, cao 6mm, rộng 5mm, có cánh hẹp, màu nâu, nhẵn.

Loài này gần với Trắc bách *Thuja orientalis* L., khác bởi 4 lá dạng giải mọc vòng của Trắc bách chỉ tồn tại trong vòng 1 tuổi, cây trên 1 tuổi chuyển thành lá dạng vảy hoàn toàn. Hạt Trắc bách không có cánh, còn hạt Ché có cánh.

Tiêu bản gốc C658, C662, C663, C664 - HNF. Người lấy : Lê Văn Châm, Vũ Văn Cần. Nơi lấy : xã Thanh Vân, Quản Bạ, Hà Giang 25/9/1999.

Cây hỗn giao với các loài cây gỗ như Sam kim hỉ (*Pseudotsuga brevifolia*), Trai lý (*Garcinia paucinervis*), Sam hạt đỏ (*Taxus chinensis*) trên núi đá, độ cao khoảng 1000m, địa phận thôn Má Hồng, xã Thanh Vân, huyện Quản Bạ, tỉnh Hà Giang.

Gỗ màu vàng, rất thơm, mịn, bền, đẹp, ít nứt nẻ, cong vênh, khả năng chống mối mọt mục đều cao, dễ gia công, chịu chôn. Trước đây dùng làm quan tài quý.

Cây quý hiếm. Đề nghị xếp vào Sách Đỏ Việt Nam, tình trạng E.

* Sau một tháng, đoàn khảo sát của Giáo sư Phan Kế Lộc, trường Đại học Quốc gia Hà Nội cũng tìm được mẫu của loài trên trong cùng khu vực.

**DÉCOUVERTE D'UNE NOUVELLE ESPÈCE DE LA FAMILLE DES
CUPRESSACÉES (Cupressaceae):
ARBRE CHÉ - *Thuja quanbaensis* sp. nov.,
DANS LA RÉGION DES MONTAGNES CALCAIRES
DE LA PROVINCE HA GIANG**

Vũ Văn Cần, Vũ Văn Dũng et Lê Văn Châm
Institut de Planification Forestière

(photo)

Espèce de plante récemment découverte

Nom : Ché - *Thuja quanbaensis* sp. nov.

photo : **Vũ Văn Dũng**

Lors de l'exploration de la couverture végétale des montagnes rocheuses pour l'établissement de la réserve naturelle Bát Đại Sơn dans la commune Thanh Vân, district Quán Bạ, province Hà Giang (23/9/99 – 27/9/99), nous avons découvert une nouvelle espèce de la branche des thuyas [Trắc Bách] (*Thuja* L.) de la flore du Vietnam.

Ci-après nous avons décrit et déterminé le nom scientifique de cette nouvelle espèce:

- Nom scientifique: *Thuja quanbaensis* sp. nov.

- Nom commun: Thuya de Quan Ba

- Nom local: Ché (Hmông)

L'arbre est habituellement vert, haut de 7-10 m, son diamètre au niveau de la poitrine est 30-40 cm, sa ramification est basse, environ 1,5-2 m.

L'écorce est épaisse 2-3 mm ; l'écorce extérieure est gris blanc, les fissures sont verticales en petits sillons ; l'écorce intérieure est légèrement rosée ; la pulpe de l'écorce est blanche, avec de la résine comportant plusieurs couches fines, coriaces.

Les feuilles sont de 2 types :

La feuille végétative est en forme de ruban, pousse circulairement sur les branches jeunes et rondes, a des arêtes, 4 feuilles sur un entre-nœud, d'une longueur de 2,7-3 cm, d'une largeur de 2 mm, l'extrémité a un bout pointu et acéré, la base n'a pas de pétiole, le bord est entier, la face supérieure est verte et lisse, la face inférieure comporte 2 bandes de stomates blancs sur la longueur de la limbe foliaire, séparées par la nervure médiane et le bord de la feuille, les trois bandes vertes sont de largeur à peu près égale.

La feuille reproductive est en forme de mèche [à bois plate] de perceuse, pousse à l'opposé et en diagonale sur la jeune branche plate, se disposant en surface plane, d'une longueur de 2-5 mm ; l'extrémité a un bout pointu et acéré.

Le cône mâle n'est pas encore connu. Le cône femelle pousse sur une extrémité de jeune branche courte, en forme d'œuf inversé, d'une hauteur de 1,2 cm, d'un diamètre de 1 cm, lorsqu'il mûrit et se transforme en bois, il se fissure en 4-6 écailles, si ce sont 6 écailles, 2 petites écailles se trouvent à la base du fruit, de couleur brune, l'écaille possède 1 mucron petit et court, chaque fruit contient 5-7 graines ; la graine est ovoïde, d'une hauteur de 6 mm, d'une largeur de 5 mm, avec des ailes étroites, de couleur brune, lisse.

Cette espèce est proche du *Thuja orientalis* L. ; la différence de 4 feuilles en forme de ruban poussant circulairement du thuya n'existe que pendant un an, l'arbre de plus d'un an passe complètement aux feuilles en forme d'écaille. La graine de ce thuya n'a pas d'aile, alors que la graine du Ché a des ailes.

Échantillons originaux C658, C662, C663, C664 - HNF. Collecteurs : Lê Văn Châm, Vũ Văn Cần. Lieu de collection : commune Thanh Vân, district Quán Bạ, Hà Giang 25/9/1999.

L'arbre se rencontre avec d'autres types d'arbres comme le douglas à petite feuilles [Sam kim hi] (*Pseudotsuga brevifolia*), le tembusu [Trai lý] (*Garcinia paucinervis*), l'if à arilles rouges (*Taxus chinensis*) sur les montagnes rocheuses, à une altitude d'environ 1000 m, sur le territoire du hameau Má Hồng, commune Thanh Vân, district Quán Bạ, province Hà Giang.

Le bois est jaune, très odorant, lisse, solide, plat, se fissurant, se gondolant rarement, ses aptitudes à supporter les termites, les perce-bois et le pourrissement sont également élevées, il est facile à travailler, supporte l'enfouissement. Dans le passé il était utilisé pour fabriquer des cercueils précieux.

L'arbre est rare et précieux. Il est proposé de le classer dans le Livre Rouge du Vietnam, statut E.

* Un mois après, l'équipe d'exploration du Professeur Phan Kế Lộc, Université Nationale de Hanoi a également découvert des spécimens de cette espèce dans la même région.

**DISCOVERY OF A NEW SPECIES
OF THE CUPRESSACEAE FAMILY (Cupressaceae):
CHÉ TREE - *Thuja quanbaensis*, sp. nov.,
IN THE REGION OF THE LIMESTONE MOUNTAIN
OF THE HA GIANG PROVINCE**

Vũ Văn Cẩn, Vũ Văn Dũng and Lê Văn Châm
Institute of Forest Planning

(photo)

Recently discovered plant species
Name: Ché - *Thuja quanbaensis* sp. nov.
Photo: Vu Van Dung

During the exploration of the vegetation cover of the rocky mountains for the establishment of the natural reserve of Bát Đại Sơn in Thanh Vân municipality, Quận Bạ district, Hà Giang province (23/09/99 to 27/09/99), we have discovered a new species of the branch of the thuyas [Trắc Bách] (*Thuja* L.) in the flora of Vietnam.

Below we have described and determined the scientific name of this new species:

- Scientific name: *Thuja quanbaensis* sp. nov.
- Common name: Quan Ba thuja
- Local Name: Ché (Hmong)

The tree is usually green, 7 to 10 m high, its diameter at breast height is 30-40 cm, branching is low, about 1.5-2 m.

The bark is 2-3 mm thick; the outer bark is gray white, the fissures are vertical in small furrows; the inner bark is slightly pinkish; bark pulp is white, with resin having several thin layers, tough.

The leaves are of 2 types:

The vegetative leaf is strip-shaped, grows circularly on and round the young shoots, has edges, 4-leaf on a node, with a length of 2.7 to 3 cm, a width of 2 mm, the extremity has a pointed and sharp end, the base has no petiole, the board is full, the upper surface is smooth and green, the underside has 2 white stomata bands on the length of the leaf blade, separated by the median rib and the edge of the leaf, the three green stripes have an width approximately equal.

Reproductive leaf is [wood spade] drill bit shaped, grows in opposition and diagonally on the young flat shoot, organizing itself in a flat plane, with a length of 2-5 mm, the extremity has a pointed and sharp end.

The male cone is not yet known. The female cone grows on one extremity of a young short shoot, inverted egg-shaped, with a height of 1.2 cm, a diameter of 1cm, when it matures and turns into wood, it crack open in 4-6 scales, if there are 6 scales, 2 small scales are at the base of the fruit, brown in colour, the scale has 1 umbo small and short, each fruit contains 5-7 seeds; seed is oval (ovoid) with a height of 6 mm, a width of 5 mm, with narrow wings, brown, smooth.

This species is close to *Thuja orientalis* L.; the difference of 4 leaves, ribbon shaped, growing circularly of the thuya exists only for one year, the tree of more than one year passes completely to scale-like leaves. The seed of this thuya has no wing, when the seed of Ché has wings.

Original samples C658, C662, C663, C664 - UFH. Collectors: Lê Văn Châm, Vũ Văn Cẩn. Place of collection: Thanh Vân municipality (commune), Quận Bạ district, Hà Giang 25/09/1999.

The tree is found with other species of trees such as the small leaves douglas [Sam kim hi] (*Pseudotsuga brevifolia*), the Trai lý (*Garcinia paucinervis*), the red aril yew (*Taxus chinensis*) on rocky mountains at an altitude of about 1000 m, on the territory of the hamlet Má Hồng, Thanh Vân municipality, Quận Bạ district, Hà Giang province.

The wood is yellow, very fragrant, smooth, solid, flat, is cracking, rarely gondolant, its ability to withstand termites, wood borers and decay are high, it is easy to work with, support landfill. In the past it was used to make precious coffins.

The tree is rare and precious. It is proposed to classify it in the Red Book of Vietnam, E status.

* A month later, the exploration team of Professor Phan Ke Loc, Hanoi National University also found specimens of this species in the same region.

Appendix D: Averyanov (2002: 32-33), on the discovery of *Cupressus vietnamensis*.

“For the first time *Xanthocyparis vietnamensis* was found by staff members of Forest Inventory and Planning Institute of the Ministry of Agriculture and Rural Development of Viet Nam in 25 September 1999 during wood inventory works in Ha Giang Province. This tree was discovered by Vietnamese foresters Le Van Cham and Vu Van Can near Thanh Van village in Quan Ba District of Ha Giang Province. They collected herbarium materials (*Le Van Cham, Vu Van Can, C658, C662, C663, and C664*), which were reported to be housed at the Herbarium of the Forest Inventory and Planning Institute in Hanoi (HNF). New tree species was compared with species of *Thuja* L. and reported under the name *Thuja quanbaensis* V.V. Can, V.V. Dung et L.V. Cham (V.V. Can, V.V. Dung, L.V. Cham, 1999). Unfortunately the description of this outstanding new discovery was not accompanied with Latin diagnosis and proposed name according to formal rules of botanical nomenclature can not be naturally accepted. Two weeks later *Xanthocyparis vietnamensis* was independently found by N.T. Hiep, L. Averyanov and P. Cribb during field works according to international exploration program of U.S.A. National Geographic Society and American Orchid Society on investigation of the flora of limestone areas of the northern Viet Nam. This species was discovered along tops of limestone ridge near Sing Xuoi Ho village in Can Ti Municipality of the same district of Ha Giang Province in 12 October 1999. It was observed as occasional co-dominant of the second stratum of the primary forest. Vietnamese botanists Dr. N.T. Hiep and Prof. P.K. Loc were first specialists who expected generic specificity of the plant on the base of study of collected herbarium samples (*N.T. Hiep, L. Averyanov, P. Cribb, NTH 3594*), young cones and few old seeds. One and two years later special trips was undertaken for studies of presumably new gymnosperm genus with support of U.S.A. National Geographic Society and U.S.A. National Science Foundation under management of staff member of Missouri Botanical Garden Dr. D.K. Harder. During April 2000 and February 2001 international group of botanists collected large herbarium materials in three geographical points of Bat Dai Son mountains in Quan Ba District (D.K. Harder et al., DKH 4977, DKH 6090, DKH 6091, DKH 6224) for special detailed investigation. Duplicates of these collections were sent to Royal Botanic Garden, Kew for attention of Dr. A. Farjon, who proposed name *Xanthocyparis vietnamensis* and managed appropriate description of this new genus and species.”

Appendix E: Farjon (2008: 47-49), on the discovery of *Cupressus vietnamensis*.

“In the far north of Vietnam [... t]he ridges and summits are riddled with holes and fissures, but support very little soil, and it is here that more than ten species of conifer have been found, among them the new genus and species, which I named *Xanthocyparis vietnamensis*. This species was serendipitously discovered in 1999 by my colleague, the great orchid specialist at Kew, Phil Cribb. These peaks are an orchid paradise, and he was looking for rare slipper orchids (*Paphiopedilum*) in the company of Vietnamese and Russian botanists. Sitting under this unfamiliar conifer high up on a ridge, Phil took a small branch and presented it to Nguyen Tien Hiep, one of Vietnam's leading botanists, asking if he recognized it. Nobody recognized it, so they took some photographs and a specimen, and Phil gave them to me back in Kew with the same question. There was not much to go by, so I thought it was perhaps an aberrant specimen (poor growing conditions) of a well-known conifer in the region. But more material was collected so I could compare it better. The tree had, strangely, two very different types of leaves on the same branches, juvenile and adult. These are normally separated between seedlings and mature trees¹⁵. The small seed cones were also unusual, but reminiscent of a well-known species on the northwestern coast of North America. Another expedition, led by Dan Harder, then at the Missouri Botanical Garden, went to the area. This time they collected plenty of material and I could do some serious work. We eventually jointly published the finding in the journal *Novon*: a new genus and species in Cupressaceae (Farjon et al. 2002).”

¹⁵ This character is very common on several species of junipers (for instance *Juniperus chinensis*) and can also be observed on some other cypresses like *Cupressus funebris* and *Cupressus sempervirens*.

Fig. 14: *Cupressus sempervirens* growing in the shade and showing adult and juvenile foliage on the same shoot.



Appendix F: Comments on Farjon (2007): Letters to the Editor: *In defence of a conifer taxonomy which recognises evolution.*

The main argument presented deals with a supposed opposition between a phylogenetic and an evolutionary taxonomy of the genus *Cupressus*. If the aim of cladistics is to establish the closest relationships between the different taxa and to look for the common ancestors of the different species or groups of species, the reconstruction of evolutionary histories follows automatically. If there is a difference, it lies in the data and the methods used, not in the desired results. If there is a difference, it lies in the acceptance or the refusal of paraphyletic taxa. Farjon unnecessarily despises the cladistic approach¹⁶. He actually discusses the recent article by Little (2006) where the New World cypresses, including *Cupressus vietnamensis* and *Cupressus nootkatensis*, are transferred into *Callitropsis*. Little is proposing an evolutionary scenario according to Fig. 4c (p. 72 above), that is with Old World *Cupressus* and *Juniperus* having a common ancestor away from the New World cypresses. Farjon is accepting these results without any criticism stating that a *Cupressus* species at the origin of the junipers is “very plausible” between “several possible pathways of evolution” (p. 640). The problem here is that the common ancestor is not known at all, and all possible hypotheses cannot be verified, not even tested, except with a time machine. Fossils are simply lacking. Farjon goes on by making unsupported assertions like on the speed of evolution of the junipers compared to the cypresses. In this respect too, the fossil evidence is lacking altogether. He is presenting *Cupressus* as a “conservative genus, now mostly represented by relict species in relict populations and with comparatively little morphological variation.” The different species not only show a great genetic variability at the population level, but they are also adapted to quite different climates and edaphic conditions, from the tallest *Cupressus tortulosa* in Bhutan in monsoon climate to the pygmy cypress on the Mendocino podzolic soil, from the very moist climate of the Pacific north-western coast of America to the arid conditions of Arizona or even the desert conditions of the Sahara, from coastal level to some 3'000 metres altitude. The limits are their absence of resistance to cold and the concurrence by other trees. Cypresses are not present where winter temperatures go regularly below -15°C for long periods or where other trees will outcompete them (they are shade intolerant). Comparatively there is much less morphological variability in several conifer genera (*Abies*, *Picea*, etc.).

In passing, it must be noted that the only significant morphological difference asserted in Little's paper between Old and New World *Cupressus* (2 and > 2 cotyledons) is incorrect: the latter values have been observed in *C. chengiana* and in *C. torulosa*, both from Asia (Farjon, 2005). There are no morphological or anatomical differences that justify this generic separation.

Unfortunately these statements are not correct. First, several cotyledon numbers given by Farjon (2005) are wrong. Not only are the sources of the published data not mentioned, not only do these numbers not rely on statistics (the sample sizes are never indicated), but they are more than once mistaken, as for the above two species:

- The number of cotyledons of *Cupressus torulosa* from a wild known origin (close to the locality of the type specimen) is always two with a sample size of several hundreds of seedlings (Silba 2013, Maerki 2014). Only from seeds collected on *Cupressus torulosa* cultivated in Italy were a few seedlings observed with three cotyledons. The origin of these cultivated trees is unknown. It is a fact that Farjon was not able to identify a cultivated *Cupressus lusitanica* specimen and that he confused it with a *Cupressus torulosa* specimen, while being confident of his identification from the origin of the seed alone (Farjon 2013).
- The number of cotyledons observed on *Cupressus chengiana* seedlings was only two (sample size: a little less than one hundred – personal observations).

Second, there are morphological differences between the Old and New World cypresses, apparently unknown by Farjon. Articles in preparation will deal in detail with this point.

Finally as Farjon is accepting the cladogram presented by Little, the naming of the different branches is no more a matter of evolution (the basal hypothesis is that the cladogram depicts the evolution), but a matter of accepting or refusing paraphyletic groups, that is the power of naming the groups according to one's prejudice, and this choice being accepted or not by the community of botanists. The main problem with phylogenetic reconstructions based on molecular data is that the material consists only of extant taxa. This point will be dealt accordingly with the comments on the following article. The main provisional conclusion here is that – contrary to the bold affirmation by Brummitt – Little's taxonomy is not “strongly refuted” at all¹⁷, especially as Farjon is accepting blindly the results proposed by that author. It is even less “refuted” as the proposal by Brummitt himself to rename all New World species into *Xanthocyparis* fully acknowledges Little's taxonomy, only with another genus name, that is a pure nomenclatural transfer.

¹⁶ “the dogmatic insistence on monophyletic taxa”; “strict adherence to a spurious dictum, more appropriate to a religious sect than to science”; all charges against cladistics are devoid of pertinence.

¹⁷ If to speak of refutation, what is currently refuted is the theory of the “missing link” between the genera *Cupressus* and *Chamaecyparis* represented by *Cupressus vietnamensis* ([Kew Press Release, no date](#), retrieved and saved on 29.4.2016).

Appendix G: Comments on Farjon (2009): *Do we have to chop up the cypresses?*

This question is very surprising as Farjon was the first one to “chop up” the genus *Cupressus* by creating his own genus *Xanthocyparis*. This first splitting of the true cypresses induced the subsequent ones.

Once again Farjon tries to justify keeping together the Old World and the New World cypresses under *Cupressus* still with the notable exception of *vietnamensis* and *nootkatensis*. As in his previous article of 2007, he is opposing cladistics and evolution. The main difference is that he is here commenting an article by Adams *et al.* (2008) where the supposed evolution scheme is represented by Fig. 4b (p. 72 above), with Old World cypresses splitting first from the two other groups. In that case, when *Cupressus vietnamensis* and *Cupressus nootkatensis* appear basal in all cladograms based on molecular analyses, it would be more than likely as a hypothesis that the junipers would have evolved from a basal *Cupressus* with small cones. To be logical, Farjon should have advocated an origin of the junipers within *Xanthocyparis*, and not from a *Cupressus*.

Farjon accepts the cladogram by Adams (he does not try to criticise it or to show that it is only one hypothesis among others with all the consequences for the pertinence of the results of the molecular analyses) as he accepted the one by Little so as to be able to develop his argument. These two diagrammatic reconstructions contradict themselves. One key feature of the scientific method is the principle of non-contradiction. It is possible to make as many hypotheses as one will judge necessary so as to test them, but how to bring an argument on one supposition in the absence of verification? It is like building hypothesis on hypothesis. This could go on and on without end, but has little to do with science. The two cladograms are mutually incompatible; each one is the refutation of the other. One of the arguments by Farjon reads like this:

If birds evolved from certain bipedal carnivorous dinosaurs (only a hypothesis), only cladists would insist that birds are dinosaurs. Birds learned to fly better than any other group of vertebrates ^[18] and they were enormously successful and became extremely diverse and ubiquitous as a result. They are as a result now very different from their ancestors, the dinosaurs. On a small scale, the hypothesis here presented, *Juniperus* evolved from *Cupressus*, is implying exactly the same scenario.

Bakker is a palaeontologist and he is famous for reviewing the classical ideas about dinosaurs and especially their physiology. In his book *The Dinosaur Heresies* (1987: 462), his conclusion is very clear:

Let the Dinosauria stand proudly alone, a Class by itself. They merit it. And let us squarely face the dinosauriness of birds and the birdness of the Dinosauria. When the Canada geese honk their way northward, we can say: “The dinosaurs are migrating, it must be spring!”

The data for the inclusion of the Aves into the Dinosauria are massive and convincing ¹⁹. If there is one researcher caring about evolution, it's Bakker. Is it possible to hold the same reasoning at the class level and at the genus level, when the scales are so different? If we would follow Farjon's comparative argument, it would be necessary to merge the junipers into the cypresses as “juniperian” cypresses and create new names for all the extant taxa currently classified under *Juniperus*. There is more to it. Recently the Taxodiaceae ²⁰ were merged into the Cupressaceae, for otherwise the former group of species would be paraphyletic. The consensus here among taxonomists is to refuse a paraphyletic family. If paraphyly is accepted in one case (for *Cupressus*) and refused in another case, it would mean to apply a double standard to the classification. As we have shown, there is currently no reasonable argument to discard a monophyletic genus *Cupressus*.

With its conclusion Farjon only makes clear that he is accepting a paraphyletic *Cupressus* genus:

My conclusion is therefore, that we are justified to adopt the hypothesis that *Juniperus* evolved from *Cupressus* and that we can continue to recognize both genera as previously circumscribed.

As shown by Jagel & Dörken (2015), this hypothesis – contrary to what Farjon affirms – is not supported by the seed cone ontology. The common ancestor is not known and could well have been a taxon now extinct, like Malejeff's *Protocupressus*. This hypothesis is as much justified if not more (cf. potential hybrids among *Cupressus*). In that case the molecular data are confusing and are not able to resolve alone the phylogeny. In some cases there is a limit to what the investigation on only extant taxa can bring: the history of the **successive** mutations and of possible **reversals** is lost. Cladistics does care about evolution and does care to name monophyletic groups. The applied methodology is constant and rigorous, that is: not arbitrary, but only if the data are foolproof. This has still to be demonstrated.

¹⁸ What about bats and Pterosauria?

¹⁹ A feathered tyrannosaurid has been discovered recently: *Yutyrannus huali*. The inclusion of the Aves into the Dinosauria was quite recently confirmed by the study of *Limusaurus*.

²⁰ The Taxodiaceae are basal among the Cupressaceae *s.l.*; by comparison it is like if the Dinosauria would have been merged into the Aves. The immediate consequence is that the taxonomy of the Cupressaceae does not reflect evolution, but only the nomenclatural rules and their priority.

Appendix H: Conservation status of the *Cupressus* species.

		IUCN ²¹		CCP	
		as species	as variety	species	as population
1	<i>abramsiana</i>	/	EN	EN	CR
2	<i>arizonica</i>	LC		LR	EN/CR
3	<i>atlantica</i>	/	CR	CR	
4	<i>austrotibetica</i>	not listed ¹	not listed	CR	
5	<i>bakeri</i>	VU		LR	EN
6	<i>benthamii</i>	/	NT	VU	
7	<i>butanoensis</i>	not listed ²	not listed	CR	
8	<i>cashmeriana</i>	not listed ¹	not listed	CR	
9	<i>chengiana</i> ²²	VU		EN	CR
10	<i>duclouxiana</i>	DD		EN	
11	<i>dupreziana</i>	EN	CR	CR	
12	<i>forbesii</i>	/	EN	VU	CR
13	<i>funnebris</i>	DD		EN	
14	<i>gigantea</i>	/	VU	EN	
15	<i>glabra</i>	/	NT	LR	
16	<i>goeniana</i>	EN	EN	CR	
17	<i>guadalupensis</i>	EN	EN	EN	
18	<i>lindleyi</i>	not listed ¹	not listed	DD	
19	<i>lusitanica</i>	LC	LC	DD	
20	<i>macnabiana</i>	LC		LR	EN
21	<i>macrocarpa</i>	VU		EN	
22	<i>montana</i>	/	CR	EN	
23	<i>nevadensis</i>	/	EN	EN	
24	<i>nootkatensis</i>	LC		LR	
25	<i>pygmaea</i>	not listed ¹	not listed	EN	
26	<i>reveliana</i>	not listed ²	not listed	CR	
27	<i>sargentii</i>	VU		LR	CR
28	<i>sempervirens</i>	LC		LR	
29	<i>stephensonii</i>	/	CR	CR	
30	<i>tonkinensis</i>	not listed ¹	not listed	CR	
31	<i>tortulosa</i>	NT ³		VU	
32	<i>torulosa</i>	LC	LC	VU	CR
33	<i>vietnamensis</i>	EN		CR	

Summary		IUCN		CCP	
		sp.	var.	sp.	pop.
CR	Critically Endangered	0	4	10	6
EN	Endangered	4	4	10	3
VU	Vulnerable	4	1	4	
NT	Near Threatened	1	2		
LR	Lower Risk			7	
LC	Least Concern	6	2		
DD	Data Deficient	2		2	
		17	13	33	9

¹ as synonym of another species

² as synonym of another variety

³ as *Cupressus cashmeriana*

²¹ From the IUCN available [list downloaded on the 26 April 2016](#).

²² *Cupressus jiangensis* Zhao is a synonym of *Cupressus chengiana* (article in preparation).

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Addendum: the present article takes its origin in a presentation done at the 5th *International Conference on Juniperus thurifera* held in Marrakech, Morocco from 30.4 to the 4.5.2014. Since that date, two further significant articles have been published:

- Terry, R.G. & R.P. Adams (2015). A molecular re-examination of phylogenetic relationships among *Juniperus*, *Cupressus*, and the *Hesperocyparis-Callitropsis-Xanthocyparis* clades of Cupressaceae. *Phytologia* 97: 67-75.
- Terry, R.G., M.I. Pyne, J.A. Bartel & R.P. Adams (2016). A molecular biogeography of the New World cypresses (*Callitropsis*, *Hesperocyparis*; Cupressaceae). *Plant Syst. Evol.* 302: 1-22. [DOI 10.1007/s00606-016-1308-4]

The first article presents arguments for a paraphyletic genus *Cupressus* (fig. 4b, Old World cypresses splitting first) based mainly on some nuclear DNA, but only to stress the contradictions and difficulties to evaluate the molecular data while taking into account other material. The conclusions we drew about Adams *et al.* 2014 article (see p. 72 above) are also valid for this more recent contribution.

Indeed the conclusion of the first article is very interesting: “Results presented here suggest a complex evolutionary history in which molecular processes in addition to possible ancient hybridization have obscured J-C-HCX^[23] relationships.” The different results conflict each other. It is easier to question the material and its supposed evolution than the methods. Although molecular analyses work fine in the majority of cases and give useful information, there could be some limits to use mathematical algorithms in some cases like the present one. The hybridisation hypothesis is the “*deus ex machina*” invoked to save the methods, be it Maximum Likelihood or Bayesian and the parsimony principle, and first of all not to evaluate them. Is evolution following a mathematical path which can be reconstructed from extant taxa? When dealing with conflicting results from molecular data, this is the kind of questions which should be answered before drawing any conclusions or building new hypotheses about a “complex evolutionary history”. It could show that evolution is not straightforward, is not parsimonious as the molecular data models necessarily imply.

Here is the summary of the cladograms presented in the three Terry *et al.* articles:

Fig. 4a: 2012: fig.2; 2016: fig.1; 2016: fig.4; 2016: fig.7.

Fig. 4b: 2015: fig.3; 2015: fig.4; **2015: fig.5.**

Fig. 4c: 2012: fig.1; 2015: fig.2.

Fig. 4d: 2015: fig.1.

It is not explained why apparently the same data give two different results (here highlighted in bold blue characters): “50 % majority-rule consensus tree resulting from Bayesian analysis of combined chloroplast and nuclear sequences, including 230 binary characters resulting from simple indel coding of length mutations.” (2012: 1995) and “50% majority-rule consensus tree generated from Bayesian analysis of all data”, that is “nuclear and cp data” (2015: 72). Nor are explained the contradictions of the different cladograms drawn from the different molecular analyses, taken alone or combined.

The second article takes into account evolution and biogeography. It shows – like a previous article (Terry *et al.*, 2012) – a monophyletic genus *Cupressus* (fig. 4a), with *Juniperus* splitting first in the Cretaceous and a more recent diversification of the NW cypresses. This second result was already reached by Bachelier (2003) in his thesis. Bachelier demonstrated by the use of AFLP and by studying the branching patterns of the cypresses (except *Cupressus nootkatensis*, still widely considered as a *Chamaecyparis* at that time) that the Old World cypresses are well distinguished from one another while the relationships between the New World ones are impossible to sort out. The resulting cladograms show unresolvable contradictions.

The multidisciplinary approach of Terry *et al.* (2016) is very fruitful and bears interesting first results, which support the taxonomical treatment advocated here for species *versus* varieties.

²³ For *Juniperus* – *Cupressus* – *Hesperocyparis* – *Callitropsis* – *Xanthocyparis*.

Cypprès de Nootka : *Chamaecyparis* ou *Cupressus* ?

(Traduction de l'anglais de l'article de 1993, *Newslett. Conifer Soc. Australia* 12: 9-10.)

Le cypprès de Nootka est classé comme *Chamaecyparis nootkatensis* (D. Don) Spach dans tous les textes modernes au milieu de 6-7 autres espèces, *Chamaecyparis formosensis*, *Chamaecyparis henryae* *, *Chamaecyparis lawsoniana*, *Chamaecyparis obtusa*, *Chamaecyparis pisifera*, *Chamaecyparis taiwanensis* and *Chamaecyparis thyoides* (* syn. *Chamaecyparis thyoides* subsp. *henryae*).

Cette classification est basée sur trois caractères du cypprès de Nootka par lesquels il ressemble à ces autres espèces de *Chamaecyparis* : petits cônes s'ouvrant à maturité, 2-5 graines par écaille de cône, et des rameaux disposés dans un plan. Les espèces du genre *Cupressus* d'un autre côté ont habituellement des cônes qui restent fermés pendant plusieurs années, 5-18 graines par écaille, et des rameaux diversifiés (s'embranchant sur deux plans, et non un seul). Mais s'agit-il de la meilleure classification et ces trois caractères sont-ils tous pleinement valides ?

Le meilleur test de classification réside dans une similarité génétique, seulement mesurable dans un laboratoire ADN coûtant des millions de dollars, mais est aussi reflétée de manière plus visible dans la phénologie reproductive et la morphologie, dans la composition chimique et les hybridations. Que montre le cypprès de Nootka en prenant en compte ces caractéristiques ? Est-ce qu'il ressemble aux espèces du genre *Chamaecyparis* davantage qu'aux espèces du genre *Cupressus* dans ces cas aussi ?

Phénologie. Les graines de toutes les espèces du genre *Cupressus* arrivent à maturité en deux ans. Les graines de toutes les espèces du genre *Chamaecyparis* arrivent à maturité en un été, au bout d'environ 6-8 mois. A l'exception du cypprès de Nootka : ses graines arrivent à maturité en deux ans.

Écailles du cône. Les cônes du cypprès de Nootka ont quatre (rarement six) écailles qui s'ouvrent en s'écartant largement avec une extrémité distincte, autour d'une columelle (plus ou moins comme le genre *Callitris*); les écailles possèdent aussi un très proéminent mucron. Aucune autre espèce de *Chamaecyparis* ne montre ces caractéristiques. La plupart des espèces de *Cupressus* ne montrent pas ces structures non plus, mais quelques unes, particulièrement *Cupressus lusitanica* ¹, le montrent occasionnellement. Un mucron proéminent est un caractère commun à beaucoup d'espèces du genre *Cupressus*. Aucun autre cypprès (de l'un ou l'autre genre) n'a quatre écailles comme nombre le plus fréquent.

Dispersion des graines. Les cônes du genre *Chamaecyparis* s'ouvrent et relâchent leurs graines dès qu'ils sont mûrs. Le cypprès de Nootka fait de même. La plupart des espèces du genre *Cupressus* ne le font pas, mais quelques uns le font (par exemple, *Cupressus himalaica*, *Cupressus funebris*), et d'autres montrent de la variabilité, quelques individus le font et d'autres non (par exemple *Cupressus lusitanica*). La non dispersion des graines est une adaptation aux feux de forêt (voir mon article sur les pins adaptés au feu, *Newslett. Conifer Soc. Australia* 9: 8, 1991) et n'a pas de signification utile pour la classification.

Taille du cône. Les cônes du cypprès de Nootka sont plus petits que la plupart des espèces du genre *Cupressus*, mais ne sont pas plus petits que ceux du *Cupressus funebris* ou du *Cupressus himalaica*, et plusieurs autres espèces de *Cupressus* peuvent avoir des cônes aussi petits, bien qu'habituellement quelque peu plus grands.

Graines. Les graines des espèces du genre *Cupressus* ont une large cicatrice à l'endroit où elles étaient attachées à l'écaille, et la cicatrice correspondante sur l'écaille est bien visible. Les graines des espèces de *Chamaecyparis* ont une petite cicatrice et ne laissent pas une cicatrice évidente sur l'écaille – à l'exception du cypprès de Nootka, qui présente une large cicatrice.

Analyse de la résine. Bien qu'une analyse chimique complète demande un grand laboratoire, le nez peut fournir une analyse simple et rapide, mais valable. Quand les rameaux sont broyés, toutes les espèces du genre *Chamaecyparis* ont une odeur assez semblable aisément perçue comme typique, à l'exception d'une seule : le cypprès de Nootka. Celui-ci a une odeur très différente de ceux-là, âcre et désagréable, et très similaire à l'odeur du *Cupressus bakeri*.

Hybrides. Trois hybrides sont connus qui impliquent le cypprès de Nootka. Ils comprennent tous des espèces du genre *Cupressus*, *Cupressus macrocarpa*, *Cupressus glabra*, *Cupressus lusitanica* ; bien qu'aucun croisement intentionnel n'ait encore connu de succès, une hybridation naturelle n'est clairement

¹ Caractère aussi observé depuis sur *Cupressus arizonica* et *Cupressus macnabiana*. [D. Maerki, pers. obs.]

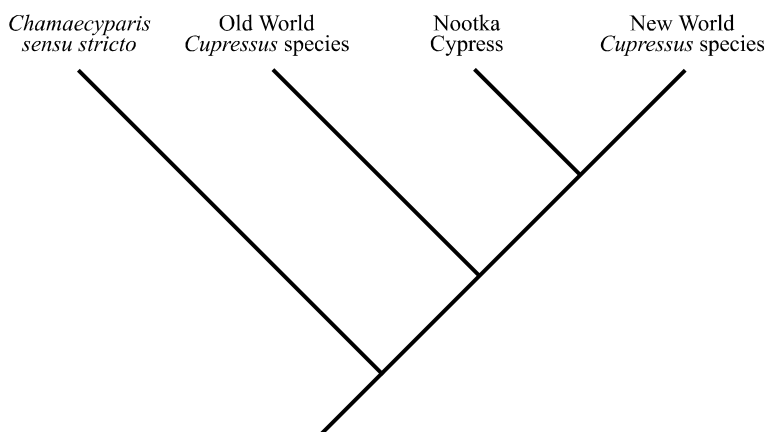
pas difficile, car ces hybrides sont représentés par au moins une vingtaine de clones. Le premier de ces trois hybrides est bien sûr l'infâme cyprès de Leyland, cet affreux poison des banlieues britanniques (voir *CSA Newsletter* 10: 11, 1991). Aucun hybride du cyprès de Nootka avec n'importe quelle autre espèce du genre *Chamaecyparis* n'existe, ni aucun autre *Chamaecyparis* ne s'est croisé avec aucun autre *Cupressus*.

A noter qu'un croisement cyprès de Nootka × faux cyprès de Lawson mentionné par Dallimore and Jackson (*Handbk. Coniferae* 4th ed., 1966) est une erreur : voir Hunt, *J. Roy. Hort. Soc.* 99: 361, 1974. Krüssmann (*Man. cult. Conif.*, 1985) cite faussement le parent mâle du clone de cyprès de Leyland 'Stapehill' comme étant le faux cyprès de Lawson : l'analyse de la résine a prouvé la filiation pollinique du cyprès de Nootka malgré l'éloignement du parent femelle de tout cyprès de Nootka (Mitchell, *Conif. Brit. Isles*, 1972).

Feuillage dans un plan. Plusieurs espèces du genre *Cupressus* ont aussi des rameaux disposés dans un plan : *Cupressus torulosa*, *Cupressus himalaica*, *Cupressus funebris*, aussi bien qu'une variété de *Cupressus lusitanica*, var. *benthamii*. A noter que ceux-ci sont majoritairement les mêmes qui ont les cônes qui s'ouvrent à maturité : en quoi diffèrent-ils des autres espèces de cyprès plus typiques ? Ils poussent tous dans des régions avec une plus forte humidité estivale et davantage de précipitations que la plupart des autres espèces, suggérant que les rameaux disposés dans un plan sont une adaptation à des climats humides et n'indique pas nécessairement une relation génétique. Ceci peut être confirmé par d'autres genres des Cupressaceae : dans les climats humides des rameaux disposés dans un plan, et des rameaux diversifiés dans les climats plus secs. Que le *Cupressus lusitanica* ait comme variétés des rameaux plats et diversifiés montre combien ce caractère est sans importance : les deux variétés sont autrement presque impossibles à distinguer, de sorte qu'il n'y a pas de bonne raison d'utiliser la forme des rameaux même comme distinction spécifique, et encore moins au niveau générique.

Cela laisse le nombre de graines par écaille comme la seule raison restante de placer le cyprès de Nootka dans le genre *Chamaecyparis*. La valeur de ce caractère est inconnue, et peut simplement être due à la difficulté de disposer les graines à l'intérieur d'un si petit cône. Inversement, le poids des évidences tirées de la phénologie, de la morphologie des écailles des cônes, de l'odeur et des hybridations suggèrent toutes qu'il est mieux placé dans le genre *Cupressus*, laissant *Chamaecyparis* comme un genre très bien défini, facilement distingué par sa chimie différente et sa phénologie de développement des cônes en une saison. Une analyse ADN complète devrait être faite de façon à prouver ou à réfuter cela. Le transfert dans le genre *Cupressus* ne nécessite pas une nouvelle combinaison ; il a d'abord été décrit comme *Cupressus nootkatensis* [D. Don](#), avant que *Chamaecyparis* ne soit séparé comme un nouveau genre en 1842.

Si le cyprès de Nootka est ainsi placé dans le genre *Cupressus*, à quelle espèce est-il le plus étroitement apparenté ? Cette question est plus difficile. Les jeunes plants de toutes les espèces américaines du genre *Cupressus* ont 3-5 cotylédons à pointe acérée, alors que les espèces de l'ancien monde en ont deux à pointe obtuse (Silba, *Phytologia* 52: 349-61, 1983) comme chez les espèces de *Chamaecyparis*. Le cyprès de Nootka a deux cotylédons obtus, et ainsi il peut être plus proche des espèces de l'ancien monde ; par l'aspect général du feuillage de l'arbre entier, il ressemble sans doute le plus au *Cupressus himalaica*. Mais ses cônes ont un mucron proéminent, ce qui est davantage un caractère des espèces américaines ; ils ressemblent le plus à ceux de l'espèce mexicaine *Cupressus lusitanica*, le cyprès qui possède le plus communément un petit nombre d'écailles qui s'écartent en s'ouvrant, et une columelle. Le *Cupressus bakeri*, avec l'odeur du feuillage la plus proche, est aussi américain, comme le sont toutes les espèces avec lesquelles le cyprès de Nootka s'est hybridé. Une phylogénie possible qui pourrait rendre de compte de toutes ces observations est présentée ci-dessous.



Taxonomic note on *Cupressus funebris*

Abstract

Quite recently a new combination was proposed by de Laubenfels for *Cupressus funebris* linking this species to the genus *Xanthocyparis* with the specific epithet of *pendula* Thunb. As *Cupressus pendula* Thunb. is a cultivar form of *Platycladus orientalis*, the synonymy with *Cupressus funebris* is taxonomically erroneous.

In a recent article published in Novon (December 2015), de Laubenfels transferred *Cupressus pendula* Thunb. (Cupressaceae) as *Xanthocyparis pendula* (Thunb.) de Laub. & Husby, and synonymised *Cupressus funebris* Endl. under this name. De Laubenfels justifies this new combination by the following remark:

Given that the two types do indeed represent the same species, the names are heterotypic synonyms, with the name *Cupressus pendula* having priority. *Cupressus funebris* (Endlicher, 1847) does not differ from *C. pendula*, although Endlicher treated *C. pendula* as *Biota pendula* (Thunb.) Endl. (Endlicher, 1847: 49), not *B. orientalis* (L.) Endl.

The problem with this, is that the type of *Cupressus pendula* Thunberg (1783) and the type of *Cupressus funebris* Endlicher (1847) (see herbarium sheets, figs 1 & 2) are clearly in different genera. Thunberg did not see the cones and he described the plant only by its foliage¹ which is not typical for *Thuja orientalis* L. (the name under which this species was known at the end of the 18th century). It is now known to be a cultivar of *Platycladus orientalis* (L.) Franco², currently known under the name 'Filiformis Pendula'. Endlicher (1847: 46-50) studied the cones and the seeds, and proposed two new combinations *Biota orientalis* (= Linnaeus' *Thuja orientalis*) and *Biota pendula* (= Thunberg's *Cupressus pendula*) and he gave the same basic description for the cones and seeds of the genus, while distinguishing both taxa by their foliage only. Unfortunately the leaves of most Cupressaceae are quite variable (hence the huge number of cultivars) and often useless to establish phylogenetic relationships or even to identify a taxon. This was the case here.

The cones and seeds of *Platycladus orientalis* cannot be confused with any cypress cone or seed. Contrary to all *Cupressus* seeds, *Platycladus* seeds are ovate and have no wing (Endlicher 1847, Jagel & Dörken 2015). Gordon (1858: 117) made a similar mistake by classifying *Cupressus corneyana* Carrière (currently *Cupressus tortulosa* Griffith) under *Juniperus chinensis* for the very reason that he did not observe any cones³. In his supplement to *The Pinetum* (1862: 23), he admitted his error and commented:

I have to thank Mr. Robert Pince, of the great Exeter Nursery, for cone-bearing specimens of this Cypress, and for first drawing my attention to having placed it among the Cypress-like Junipers in the Pinetum; a circumstance which arose from the plant never having previously produced cones in England, and to the neglect of that infallible rule, "Wherefore by their fruits ye shall know them."

Wise advice indeed.

Even in the absence of the cones, the suggestion that the types of *Cupressus pendula* and *Cupressus funebris* are the same taxon is very surprising as their foliage is completely different (figs 1-4): the pendulous form is useless taxonomically. Already in a previous article, de Laubenfels proposed a taxonomy based mainly on the cypress foliage when this is one of the most adaptable characters influenced by climatic conditions. Thus he already published a new combination linking *Cupressus funebris* with *Callitropsis* Ørsted⁴ while hesitating to add also *Cupressus benthamii* (de Laubenfels 2012). All these species together with *Cupressus nootkatensis*, *Cupressus vietnamensis*, *Cupressus tonkinensis*, *Cupressus cashmeriana* and *Cupressus tortulosa* have dimorphic adult leaves, and shoots disposed in flat sprays. These cypresses of both eastern and western hemispheres are adapted to climates with high rainfalls and humidity.

¹ "*Cupressus pendula* : foliis oppositis, ovatis, ramulis dichotomis, pendulis." (Thunberg 1783: 40.) A description which could fit several different Cupressaceae species. In *Flora Japonica* (Thunberg 1784: 265-266), the description is more complete, but still insufficient for a proper identification: "*Crescit* in montibus Fakoniae, ubi semel inveni, non vero florentem. Arbor orgyalis altitudinis vel ultra, erecta, tota glabra. Rami alterni, laxi, aphylli, valde ramulosi. Ramuli dichotomi, filiformes, foliis tecti, longi, patuli, laxi, omnino penduli. Folia decussata, imbricata, ovata, acuta, apice parum patula, brevissima. Singularis et pulchra arbor ramulis suis longissimis, dichotomis et dependentibus maxima copia, facillime ab ómnibus aliis huius ordinis sempervirentibus distinguitur."

² The current accepted name. The genus *Platycladus* was described by Spach in 1841.

³ "How Mr. Knight could have mistaken it for a Cypress, is a mystery."

⁴ Contrary to what he is affirming in the article in discussion, *Callitropsis funebris* is a legitimate name at the condition that *Xanthocyparis vietnamensis* (the type of the genus) will be treated as monospecific (cf. IAPT International Code of Nomenclature for algae, fungi, and plants (Melbourne Code) Art. 14.6, Ex. 5.)

Moreover, *Cupressus funebris* does not correspond with Farjon *et al.*' (2002) diagnosis of the genus *Xanthocyparis*. The cones of that genus are defined as composed of a "[b]ract-scale complexes in 2 (sometimes 3) decussate pairs" while *Cupressus funebris* regularly has 4 pairs, and also with more seeds on each scale.

In conclusion therefore, the new combination proposed by de Laubenfels & Husby cannot be considered justified. *Cupressus funebris* is safely kept inside the 'true cypress' genus (cf. Christenhusz *et al.* 2011).

Acknowledgements

Dr. Mats Hjertson, Curator of the vascular plants herbarium at the Museum of Evolution, Botany Section, Uppsala University, Sweden and Jacek Wajer, Curator of Seed Plants Natural History Museum in London (BM), UK are wholeheartedly thanked for their help.

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Fig. 1: *Cupressus pendula*, C.P.Thunberg s.n.
© UPS Herbarium (UPS-THUNB No. 22566).

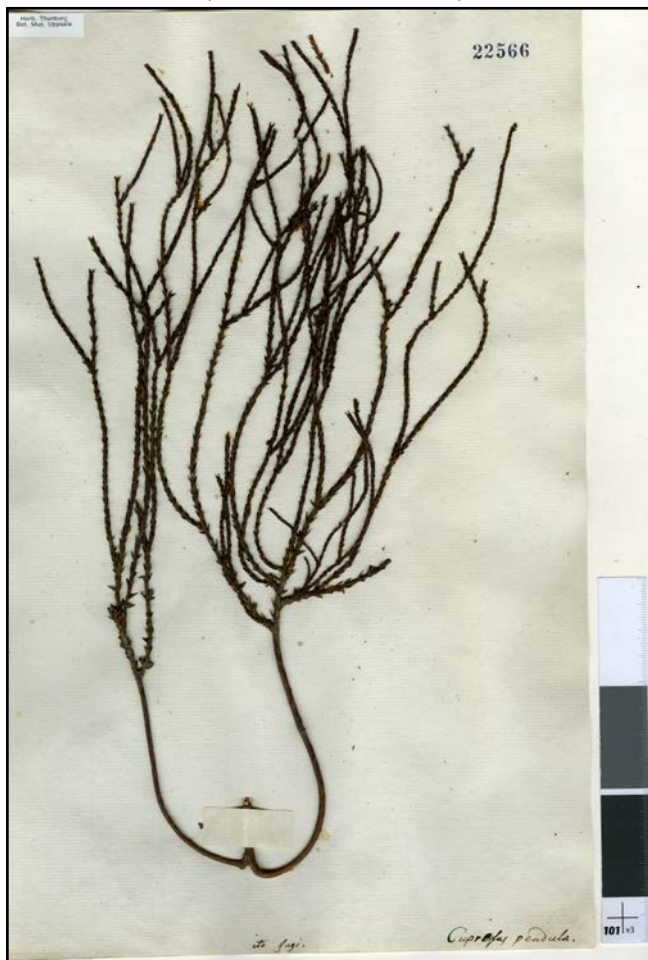


Fig. 2: *Cupressus funebris*, Staunton s.n.
© The Natural History Museum, London (BM000546886).





Fig. 3: *Platycladus orientalis* 'Filiformis Pendula', Winter colour, cult., Switzerland.

Fig. 4: *Cupressus funebris*, cult., France.



**Pollen cone anomalies
in *Pinus sylvestris* and *Tsuga canadensis* (Pinaceae):
can they give new insights in the evolution
of microsporangiophores in conifers?**

Abstract

In several pollen cones of *Pinus sylvestris* and *Tsuga canadensis*, in addition to the typical hyposporangiate microsporangiophores forming usually two microsporangia, several anomalous multisporangiate and perisporangiate microsporangiophores were also found. The results of the morpho-anatomical investigations clearly show that the adaxial scutellum is formed by strongly reduced adaxial microsporangia, which became sterile and scale-like. Thus, the adaxial scutellum does not represent the tip of a possible microsporophyll. It could be also shown that the microsporangia are not formed by the scutellum, but are formed by the central stalk of the microsporangiophore. Especially in distal microsporangiophores the scutellum is nearly always strongly reduced or completely absent. In anomalous terminal microsporangiophores found in *Tsuga canadensis* the stalk produced 1-3 distal microsporangia, but a scutellum was not developed. No evidence was found supporting the idea that the hyposporangiate type of microsporangiophores in Pinaceae is derived from a perisporangiate ancestral condition. The results deliver several supporting arguments that the microsporangia bearing structure corresponds to a microsporophyll. However, it still leaves open which part of the coniferous microsporangiophore is homologous to which part of a microsporophyll.

Key words: cone, evolution, conifers, *Pinus*, *Tsuga*, sporangiophore.

1 Introduction

In Pinaceae the male reproductive structures are arranged in compact strobili, the so called “pollen cones”. All pinaceous pollen cones are unbranched structures consisting of a central cone axis and several spirally inserted sporangiophores (e.g. Lotsy 1911; Krüssmann 1955, 1983; Coulter & Chamberlain 1917; Sporne 1965; Dallimore & Jackson 1966; Mirov 1967; Liu 1971; Farjon 1984, 1990, 2005, 2010; Eckenwalder 2008). Within pinaceous pollen cones, bracts and terminal microsporangiophores are always lacking (e.g. Pilger 1926; Farjon 1990; Mundry 2000). Branched pollen cones as developed in some Taxaceae and Cupressaceae (e.g. Lemoine-Sebastian 1967; Wilde 1975; Mundry & Mundry 2001; Farjon 2005; Eckenwalder 2009; Dörken *et al.* 2011; Schulz *et al.* 2014) are always absent in Pinaceae. Among extant Pinaceae the pollen cones differ significantly in size and shape from each other. Pollen cones in e.g. *Cathaya argyrophylla* are column-like, up to 70 mm long and consisting of 97-152 hyposporangiate microsporangiophores (Dörken & Nimsch 2015a). Pollen cones in e.g. *Tsuga canadensis*, however, are about 5-7 mm long and consist of 10-14 hyposporangiate microsporangiophores.

Within pollen cones of extant Conifers two different types of microsporangiophores are developed:

(1) perisporangiate, radial sporangiophores, with sporangia all around a central stalk;

(2) hyposporangiate, dorsiventral sporangiophores, with sporangia only on the abaxial side of a central stalk and an adaxial scutellum. The majority of extant Conifers are hyposporangiate. In Pinaceae only hyposporangiate sporangiophores are developed with always two abaxial microsporangia. Perisporangiate microsporangiophores as developed within Taxaceae (e.g. Wilde 1972; Mundry & Mundry 2001; Dörken *et al.* 2011; Schulz *et al.* 2014; Dörken & Nimsch 2015b) are always absent in Pinaceae. Even today the “true nature” of coniferous microsporangiophores is still discussed controversially; two conflicting major hypotheses exist:

(1) all microsporangiophores are homologous structures; the hyposporangiate (dorsiventral) type is derived from a perisporangiate one (e.g. Wordsell 1901; Dupler 1919; Dluhosch 1937);

(2) perisporangiate microsporangiophores represent a radial synangium consisting of several dorsiventral reduced microsporangiophores (e.g. Thomson 1940; Wilde 1975; Mundry & Mundry 2001;

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Dörken *et al.* 2011; Dörken & Nimsch 2015b). For Taxaceae it could be shown that the perisporangiate microsporangiophores represent radial synangia, consisting of several fused hyposporangiate microsporangiophores (Dörken & Nimsch 2015b). When regarding only typical shaped pollen cones and microsporangiophores, it is nearly impossible to make suggestions about the evolutionary pathway of pinaceous pollen cones and their sporangiophores. By chance several anomalous pollen cones in *Pinus sylvestris* and *Tsuga canadensis* were found, for example cones terminating with a microsporangiophore or cones forming multisporangiate microsporangiophores with a varying number of microsporangia instead of the typical two. Some of the anomalies seem to be quite helpful for suggesting evolutionary scenarios. The morpho-anatomical investigations will focus mainly on the question do the microsporangiophores correspond to microsporophylls and if so which parts in microsporangiophores and microsporophylls are homolog to each other. Furthermore the investigations should solve if the central stalk or the adaxial scutellum is responsible for producing the microsporangia. Investigations will be done with SEM and paraffin technique.

2 Material & Methods

2.1 Material

To exclude the possibility that the detected anomalies were random artifacts depending on genetic mutations or disturbances in the physiology of a single individual, pollen cones were collected from 10 different trees per species and also from different branches within the crown. Typical and anomalous pollen cones of *Pinus sylvestris* L. were collected from trees growing on the campus of the University of Konstanz (Germany). *Tsuga canadensis* (L.) Carrière was collected from trees cultivated in the Botanic Garden of the Ruhr-University Bochum (Germany), the Heinrich-Heine University Düsseldorf (Germany) and also on the Isle of Mainau (Konstanz, Germany).

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 pollen cones were examined with an AURIGA ZEISS TM. Microphotography was accomplished using 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 coniferous microsporangiophores as microsporophylls. Here I avoid using the term “sporophyll” or “microsporophyll” for the sporangia bearing structure as otherwise a homology that is applied to it would be introduced *a priori*. In general it is also still unclear which parts within the microsporangiophore can be regarded as homologous to which part of a leaf. Thus, the green adaxial scale-like structure in hyposporangiate microsporangiophores will be termed as scutellum and not as “phylloid rest” as is frequently done.

3 Results

Different types of pollen cone anomalies were found which can be classified into two morphological groups.

3.1 Anomalous multisporangiate microsporangiophores

3.1.1 *Pinus sylvestris*

Pollen cones of *Pinus sylvestris* consist of several spirally arranged hyposporangiate microsporangiophores. Each microsporangiophore consists usually of two abaxial sporangia and a distinct adaxial scutellum (fig. 1). Within 8.5% of the 300 investigated pollen cones, microsporangiophores bearing more than the usual two sporangia were found (figs 2E & F). They are developed in all regions of the pollen cone, but most frequently in distal parts (figs 2B-F). The majority of the multisporangiate microsporangiophores had three sporangia (figs 2A-D). The sporangia and the adaxial scutellum are similar in size and shape to these formed in typical bisporangiate microsporangiophores. Anomalous multisporangiate microsporangiophores bearing four sporangia were only found in most distal parts of

the pollen cones close to the tip of the cone axis (figs 1E & F). The scutellum of these microsporangiophores is deeply notched into two halves. Each of the halves is fused with two microsporangia (fig. 1F). The sporangia have the same dimensions as those of typical microsporangiophores.

3.1.2 *Tsuga canadensis*

Typical pollen cones of *Tsuga canadensis* consist of a varying number of spirally arranged, hyposporangiate microsporangiophores, each of them bearing two sporangia and a small adaxial scutellum (fig. 3). The scutellum is generally quite small (figs 3A-E). In 7% of the 300 investigated pollen cones, also some lateral microsporangiophores showing 3 fertile sporangia (fig. 4) were found. The adaxial scutellum is nearly completely reduced. These anomalous microsporangiophores are supplied with a single collateral vascular bundle strand.

3.2 Formation of an anomalous terminal microsporangiophore

3.2.1 *Tsuga canadensis*

In typical pollen cones, the microsporangiophores are developed exclusively lateral at the cone axis (fig. 5), so that the apex of the cone axis can still be observed as a small tip (fig. 5C). In 8% of the 300 investigated pollen cones a terminal microsporangiophore was developed at the end of the cone axis (fig. 6). Most of the terminal microsporangiophores are perisporangiate. All sporangia are fertile. Apart to the perisporangiate type some terminal microsporangiophores were found consisting only of a stalk and 1 (figs 6E & F) or 2 (fig. 6D) sporangia. A scutellum is not developed.

4 Discussion

Within Conifers the morphological identity of the microsporangium-bearing structure is still controversial. Even defining a clear border between the different parts within the microsporangiophores e.g. between the central stalk and the scutellum is very difficult. Thus, it is still quite problematic to determine if the microsporangiophores are displaying homologous structures among all extant Conifers (Schulz *et al.* 2014). Several authors regard the microsporangiophores in Conifers as reduced fertile leaves. Thus they are often called “microsporophylls” (e.g. Lotsy 1911; Krüssmann 1955, 1983; Coulter & Chamberlain 1917; Sporne 1965; Dallimore & Jackson 1966; Mirov 1967; Liu 1971; Farjon 1984, 2005, 2010; 1990; Eckenwalder 2009). However, the terminal position of microsporangiophores at the cone axis as found in some anomalous shaped pollen cones of *Tsuga canadensis* would exclude a leaf character for this structure, because leaves are always developed as lateral organs at the apex and can therefore never be developed terminal. However, they can be shifted by secondary growing processes out of the primary lateral position into a terminal one. Within mature pollen cones it cannot be recognized if the terminal position is the original one or if the sporangiophore has secondarily been shifted out of its original lateral position into the terminal one. This can only be solved in ontogenetic studies, but these anomalies are too rare, so that ontogenetic studies are nearly impossible. Such anomalous terminal microsporangiophores were described also for other coniferous groups, e.g. *Podocarpus* (Dörken & Nimsch 2015c). Terminal microsporangiophores are usually absent in Pinaceae, but typical for pollen cones of *Cephalotaxus* and *Torreya* (Taxaceae). In both *Cephalotaxus* and *Torreya* the terminal perisporangiate microsporangiophore represents a radial synangium consisting of 2-4 fused hyposporangiate microsporangiophores that get in physical contact and finally fuse to a single radial structure (Dörken & Nimsch 2015b). Depending on the number of hyposporangiate microsporangiophores that are involved in forming the perisporangiate terminal microsporangiophore the number of vascular bundle strands supplying the microsporangiophore varies strongly. Thus, the perisporangiate microsporangiophores in Taxaceae do not represent a peltate-like microsporophyll (Dörken & Nimsch 2015b). The anomalous perisporangiate terminal microsporangiophores found in *Tsuga canadensis* are quite different from that. In *Tsuga canadensis* the perisporangiate microsporangiophore are supplied by only a single collateral vascular bundle strand as is typical for hyposporangiate microsporangiophores. There is no evidence to regard the anomalous perisporangiate microsporangiophores of *Tsuga canadensis* as a Taxaceae-like radial synangium. Thus, two completely different development pathways are distinguishable between perisporangiate microsporangiophores of Taxaceae on one side and the anomalous perisporangiate ones in *Tsuga canadensis* on the other side. The results clearly show that in *Tsuga canadensis* the third adaxial microsporangium does not belong to a possible second, fused microsporangiophore. Here the central stalk developed a further fertile microsporangium instead of an adaxial scutellum. This explains why only a single collateral vascular

bundle is developed within the anomalous perisporangiate sporangiophores of *Tsuga canadensis*. The collateral structure of the vascular bundle indicates that the sporangia bearing structure has to be a leaf and excludes a shoot- or synangium-character. It remains, however, open, which part of the microsporangiophore belongs to which part of the leaf.

Within extant Conifers forming hyposporangiate microsporangiophores the number of microsporangia developed per sporangiophore varies strongly between the different systematic groups. Among e.g. Pinaceae, Sciadopityaceae and Podocarpaceae the microsporangiophores are always bisporangiate as is also the case for some taxa within Cupressaceae (e.g. *Athrotaxis* and some *Cupressus* species). However, in most Cupressaceae and Taxaceae the number of sporangia developed per hyposporangiate microsporangiophore varies strongly not only between the different taxa, also even within a single pollen cone (Farjon 1984, 1990, 2010). In several of the investigated pollen cones of *Pinus sylvestris* (fig. 2) and *Tsuga canadensis* (fig. 4) also several multisporangiate sporangiophores bearing 3 or 4 microsporangia, were inserted lateral at the cone axis. Within *Tsuga canadensis* the number of anomalous multisporangiate microsporangiophores was especially high. Such multisporangiate microsporangiophores are also described for other Pinaceae e.g. *Picea asperata* (Mundry 2000) and *Cathaya argyrophylla* (Dörken & Nimsch 2015a). Within several of the lateral anomalous *Tsuga canadensis* microsporangiophores showing 3 instead of the usually 2 sporangia, the additional third fertile one is developed exactly in the position where usually the scutellum would be formed. It seems that in Pinaceae the scutellum is formed by a reduced microsporangia that becomes sterile and scale-like. This is conforming to the results of earlier studies on microsporangiophores in *Pseudotaxus* (Taxaceae). Dörken & Nimsch (2015b) found apart from the typical perisporangiate microsporangiophores, several anomalous hyposporangiate ones with a distinct adaxial scutellum that is varying strongly in size and shape. It could be shown that in these anomalous hyposporangiate microsporangiophores the adaxial scutellum is formed by strongly reduced adaxial microsporangia, which became sterile. This explains why the abaxial microsporangia are not attached to the adaxial scutellum but exclusively to the central stalk. In this case the adaxial scutellum does not represent the tip of a possible microsporophyll. Some of the detected multisporangiate microsporangiophores of *Pinus sylvestris* are representing a fusion product of 2 hyposporangiate microsporangiophores that were fused laterally to each other so that the adaxial scutellum is still developed (figs 2E & F). Thomson (1940) observed such fusions at or near the apex of the pollen cones in all coniferous families. Such fusions are representing a simple contact parastichy of directly neighboured microsporangiophores and not of ontogenetic subsequent microsporangiophores. Their fusion takes place in earliest ontogenetic stages favoured by the broad bases of the central stalk of the microsporangiophores and due to a lack of space in distal parts of the cone axis. First, within a parastichy the primordia of directly neighboured microsporangiophores get in physical contact. Secondary, they fuse completely with each other so that the fusion product has only a single very broad stalk and also a very broad but conspicuously notched scutellum (figs 2E & F). Each half of the scutellum belongs to one of the involved microsporangiophores. Such contact parastichys are also random accidental artifacts and therefore without evolutionary relevance.

Apart from the strongly varying number of sporangia per microsporangiophore, the size and shape of the scutellum varies significantly between extant Conifers. Within the investigated anomalous multisporangiate microsporangiophores of *Tsuga canadensis* and *Pinus sylvestris* the central sporangia are not fused with the scutellum as is a typical feature for microsporangiophores forming usually more than 2 sporangia (e.g. several Cupressaceae). The central sporangia are exclusively attached to the stalk, as is also the case in the investigated *Pinus sylvestris* (figs 2A-D) and *Tsuga canadensis* (figs 2A-E). Especially at microsporangiophores developed in distal parts of the pollen cone the scutellum is mostly completely reduced so that only stalked microsporangia are formed (figs 6D-F). This clearly indicates that microsporangia are not formed by the scutellum but by the central stalk of the microsporangiophore. This idea is supported by anomalous terminal microsporangiophores of *Tsuga canadensis*, consisting of only a stalk and distal sporangia. Especially the anomalous microsporangiophores consisting of a central stalk terminating with a single microsporangium demonstrate quite well that the scutellum is not needed for forming the microsporangia (figs 6E & F).

5 Acknowledgements

I am grateful to Dr. Michael Laumann and Mrs. Lauretta Nejedly (SEM-Center, Department of Biology, University of Konstanz, Germany) for technical support (SEM and paraffin technique). Furthermore I thank all visited Botanic Gardens for generous providing of research material.

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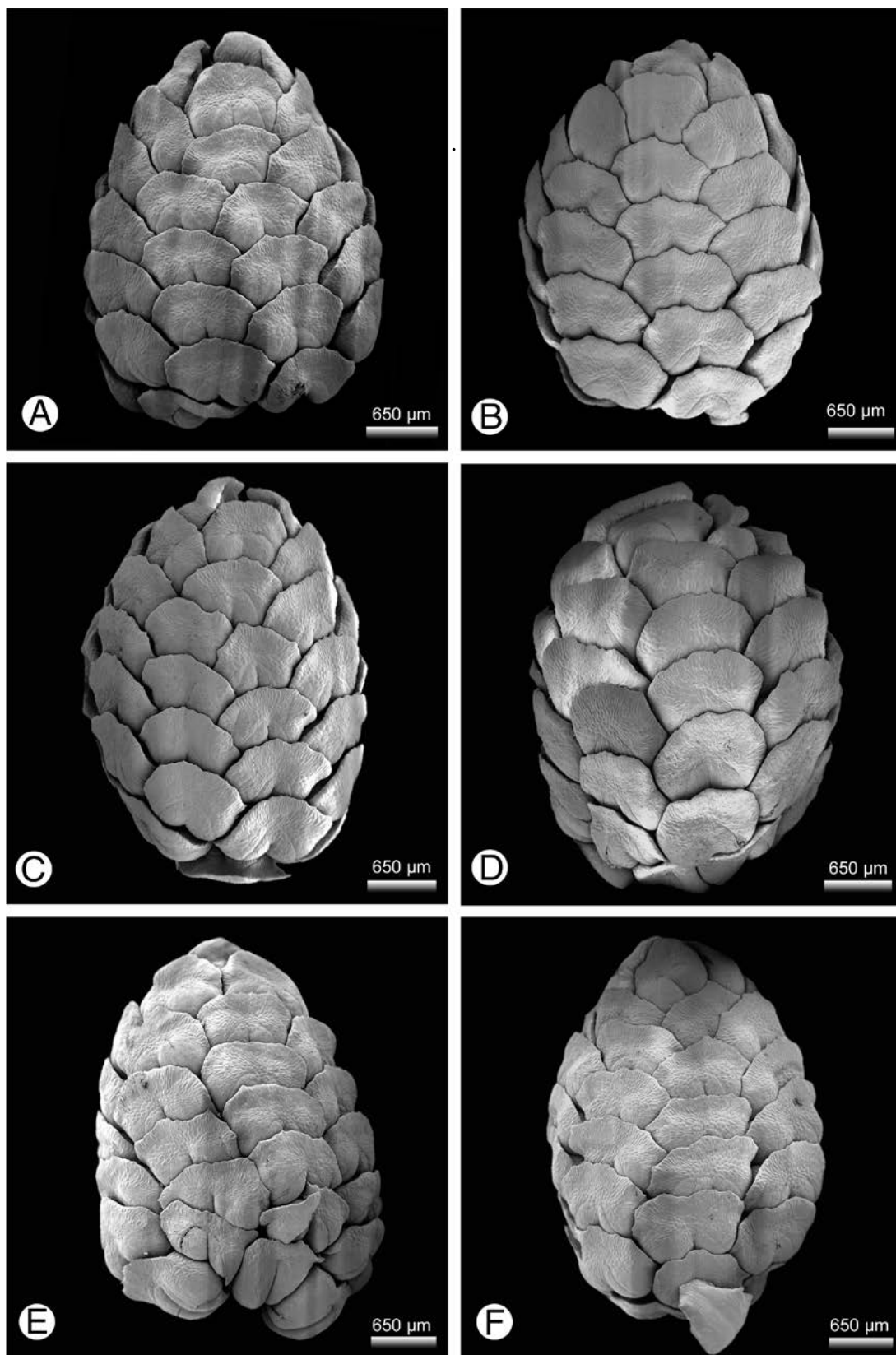


Fig. 1: *Pinus sylvestris*.

Lateral view of typical pollen cones carrying several spirally arranged hyposporangiate microsporangioophores; each sporangioophore with two sporangia and a distinct adaxial scutellum.

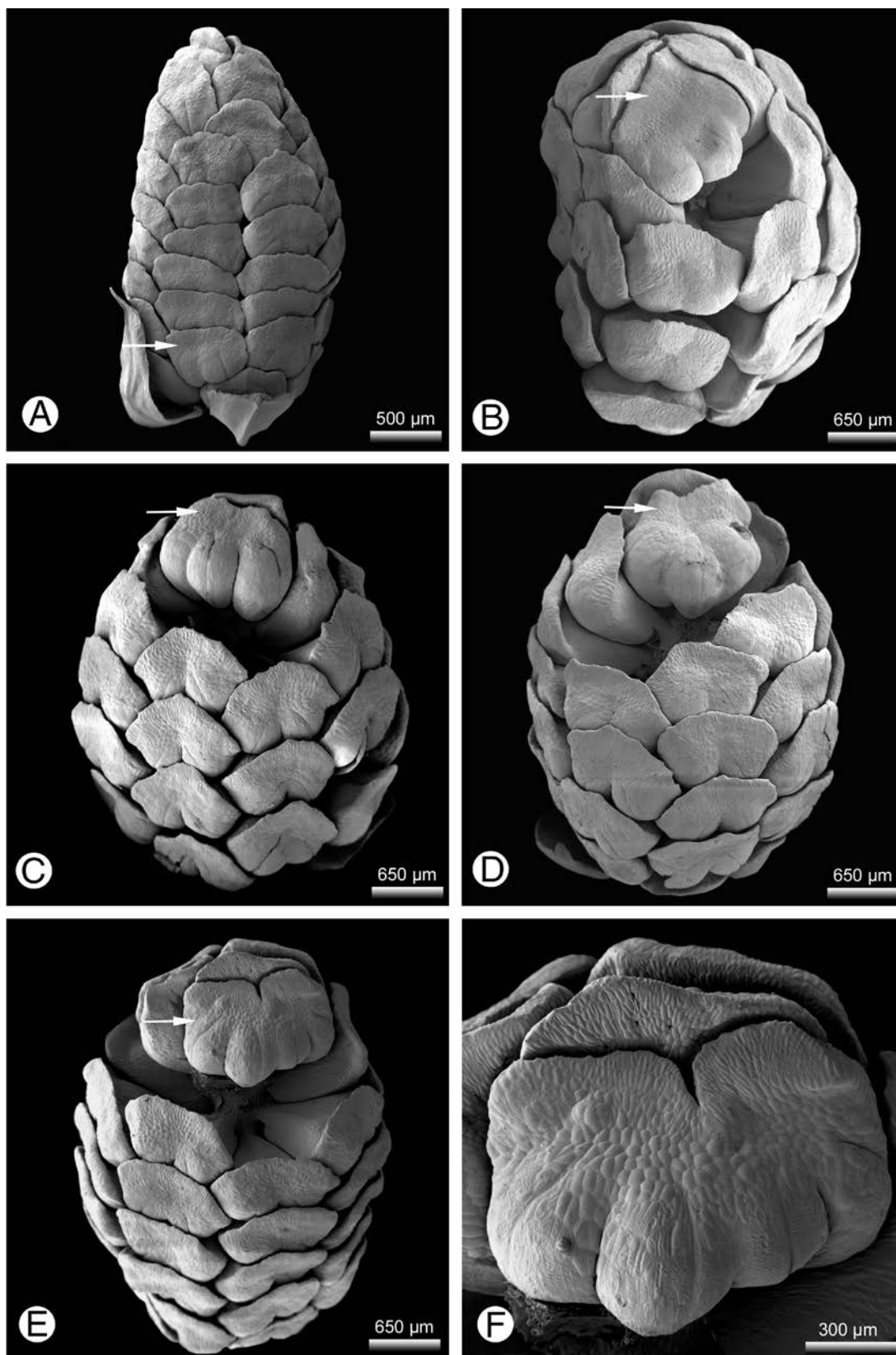


Fig. 2: *Pinus sylvestris*.

Pollen cones with anomalous multisporangiate microsporangiophores showing three (**A-D**) or four (**E & F**) sporangia and a distinct scutellum; scutellum at microsporangiophores with four sporangia deeply notched (**E & F**); for a better overview some microsporangiophores removed.

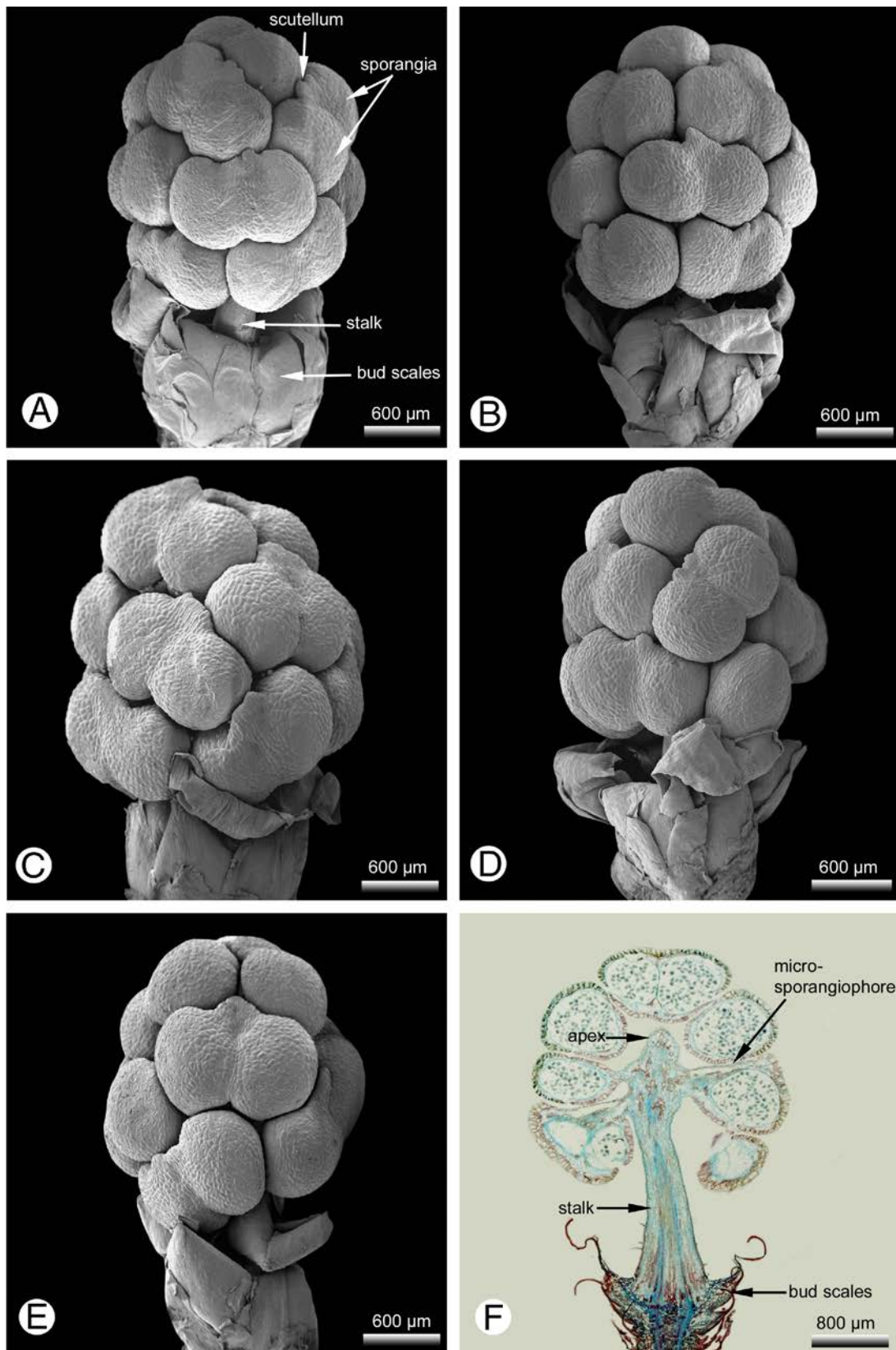


Fig. 3: *Tsuga canadensis*.

Typical pollen cones in lateral view; the cones consist of several hyposporangiate microsporangiophores; each with two microsporangia and a small adaxial scutellum (A-E); longitudinal section of a pollen cone (F).

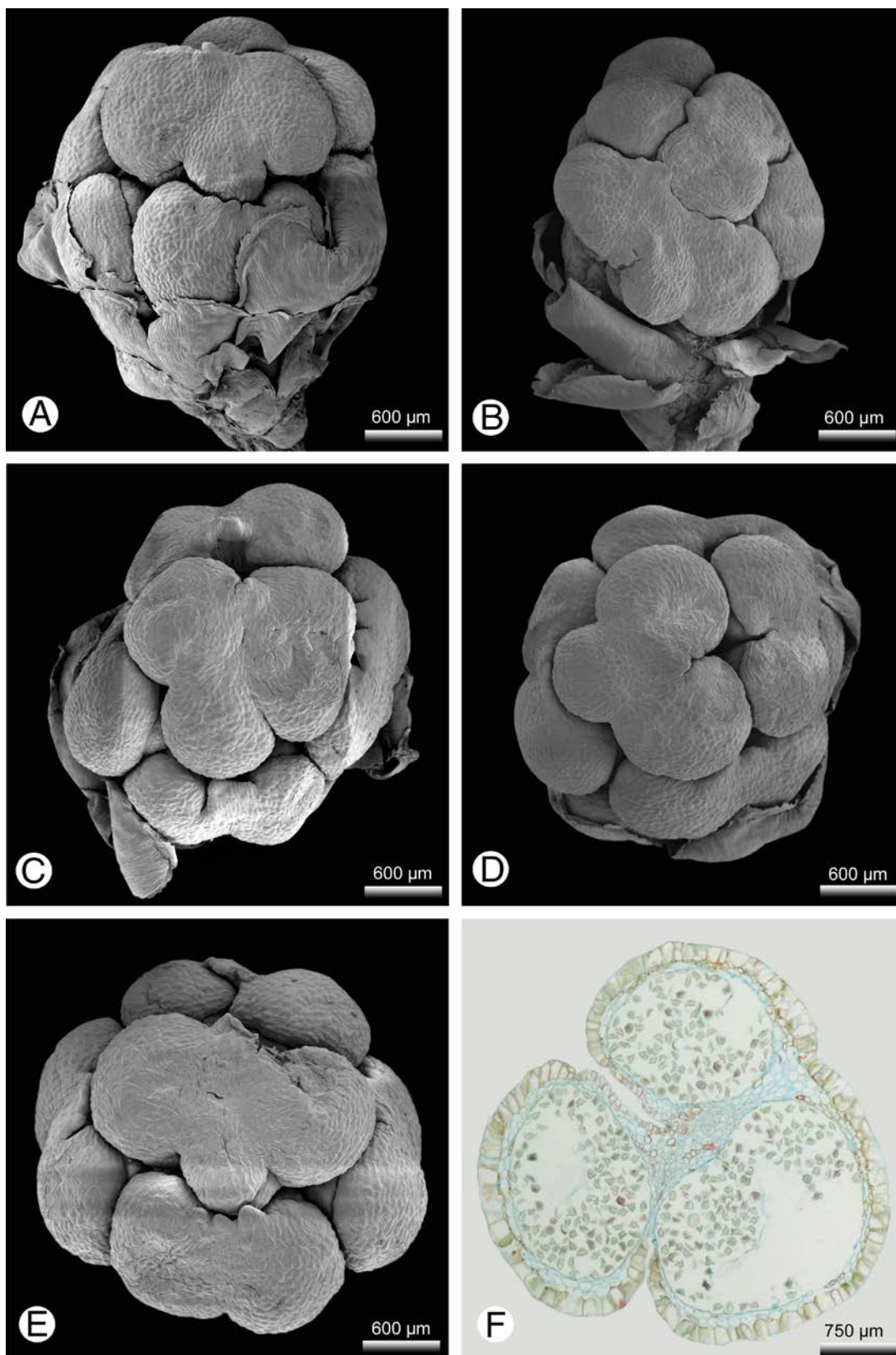


Fig. 4: *Tsuga canadensis*.

Pollen cones with anomalous microsporangiochophores showing three instead of the usual two sporangia (**A-E**); all 3 sporangia are fertile (**F**).

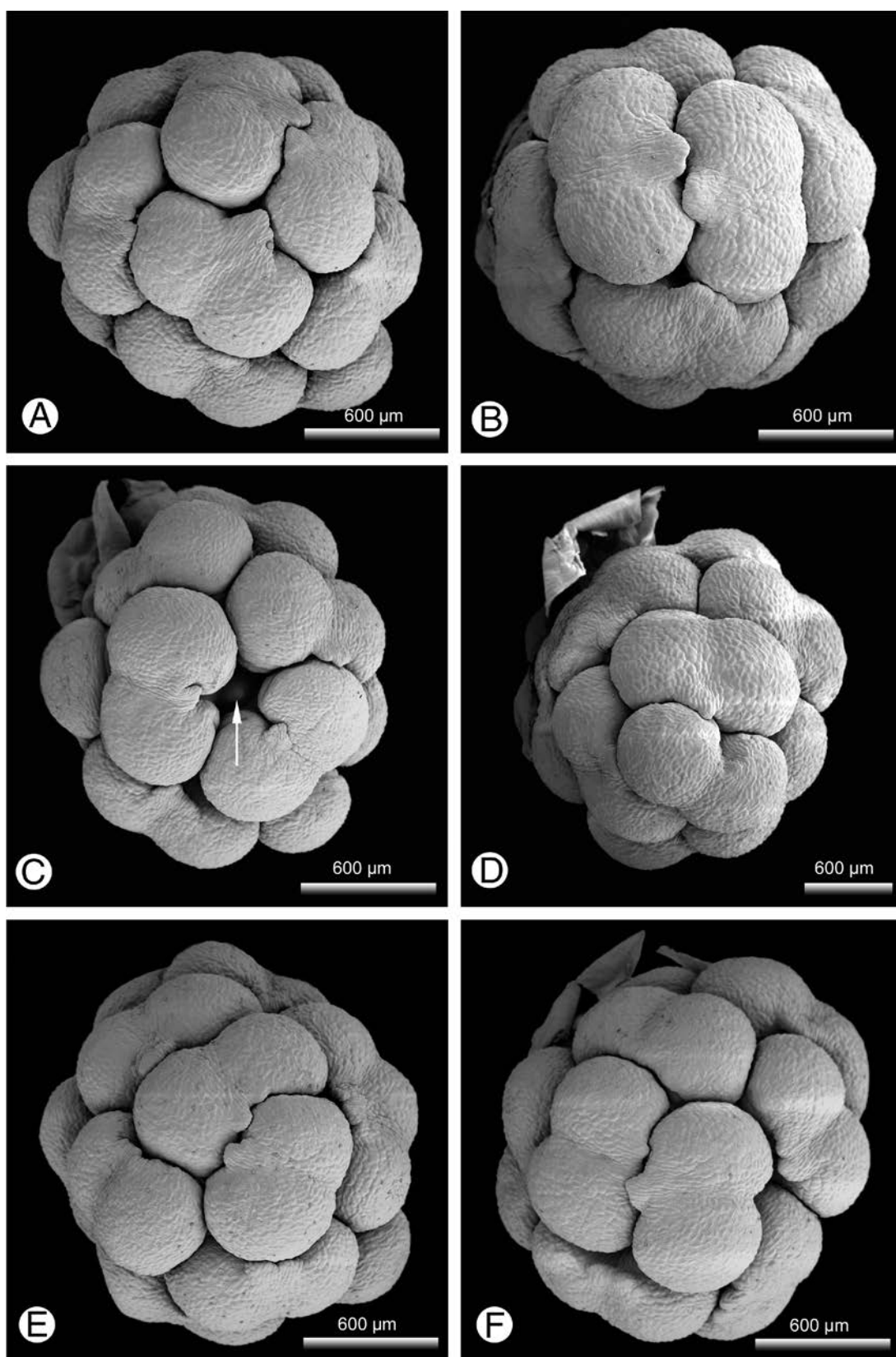


Fig. 5: *Tsuga canadensis*.

Top view of typical shaped pollen cones; a terminal microsporangiphore is always absent, sometimes the tip of the cone axis can be observed (C, arrow).

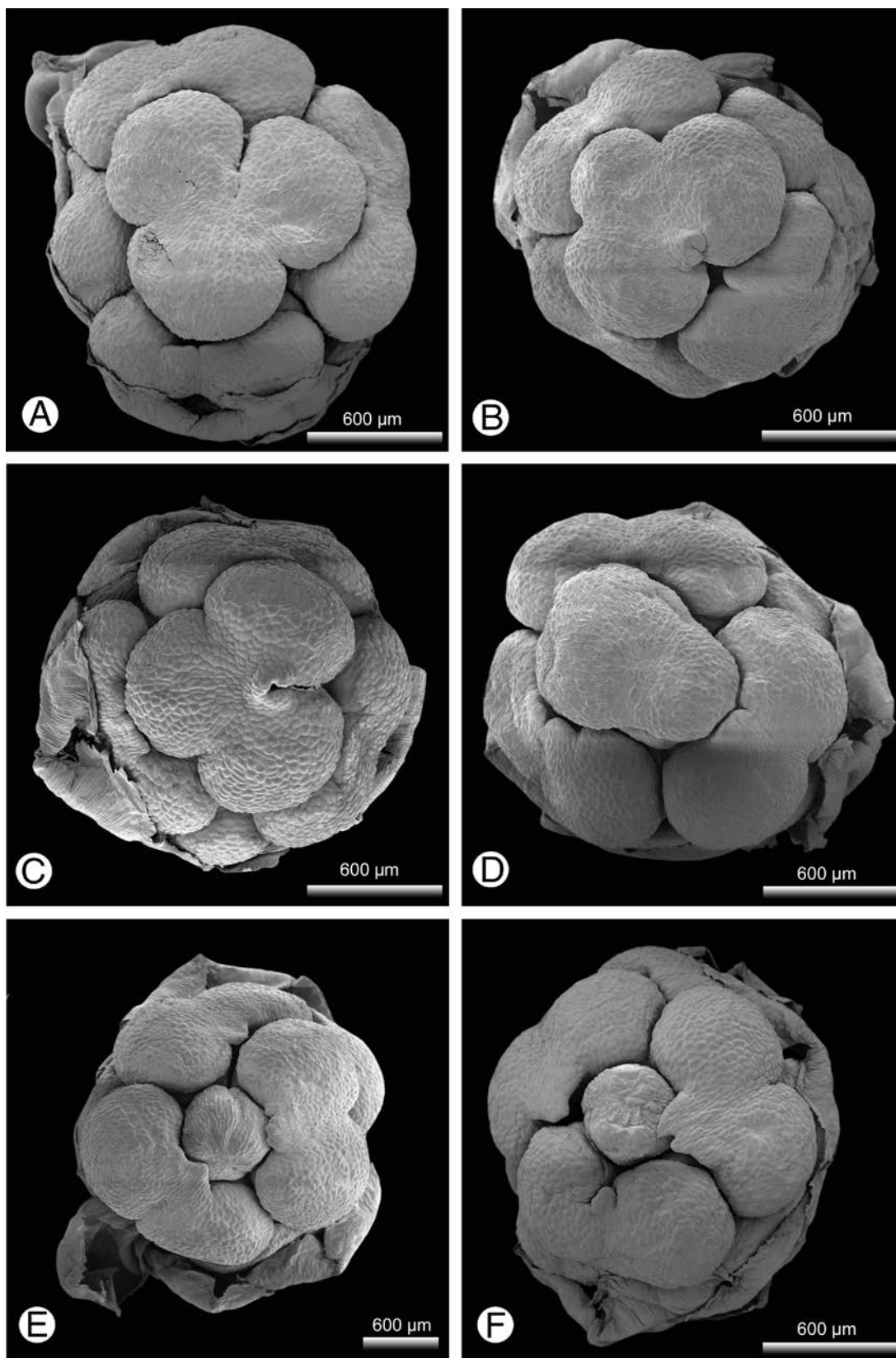


Fig. 6: *Tsuga canadensis*.

Anomalous shaped pollen cones terminating with a sporangiophore; within most of the microsporangiophores three sporangia are developed; the scutellum is strongly reduced (A-C); within microsporangiophores showing two (D) or one (E-F) sporangia, a scutellum is absent.