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Cover photo : *Cupressus tortulosa*, Isola Madre, Italy (see pp. 104 & 140). – 28.5.2014. © CCP

Bull. CCP 3 (3): 99-115. (12.2014) **D. Maerki**

Two distinct Himalayan cypress species *Cupressus tortulosa* and *Cupressus cashmeriana* with additional comparison to *Cupressus torulosa*

In a previous article (Maerki 2013b), the trees grown in France, Italy and Switzerland under the label *Cupressus cashmeriana* Carrière were investigated. It was discovered that the cypresses grown in France are different from those cultivated in Italy, which better match the material collected by Griffith in Bhutan and described by him under the name *Cupressus tortulosa*. A summary of the main differences has been proposed (Maerki, 2013b: 49-50) together with analysis of Carrière's protologue (1867) and discussion of the correct origin of the French plants in "Tibet" (now Arunachal Pradesh in India). The scope of the present article is to detail these differences with new observations and statistical data.

Cupressus torulosa D.Don, *Cupressus tortulosa* and *Cupressus cashmeriana* are all growing west to east on the southern slopes of the Himalaya in well separated distribution ranges[1]; west Nepal, and Himachal Pradesh and Uttarakhand in India, for *C. torulosa*, Bhutan for *C. tortulosa* and Arunachal Pradesh (India) for *C. cashmeriana*. All populations of each species are scattered in different valleys. It is quite likely that the compartmentalisation of these populations over several millions years allowed speciation processes from a common ancestor. There are also lots of planted trees near temples, monasteries and fortresses whose origins are not recorded. Several wild stands are very difficult to access, sometimes almost impossible above high cliffs, and are still in need of investigation; further taxa could possibly yet be discovered. So far only the three above mentioned species were already described in the 19th century. Unfortunately the exact origins of the material introduced in that century and currently still cultivated in Europe are poorly recorded, and the different names brought a lot of confusion until quite recently. New well documented introductions from western Bhutan, but from cultivated trees, occurred only in 1975 by Grierson and Long, by Ern in 1982 and by Keith Rushforth in 1985. Rushforth also introduced *Cupressus tortulosa* from the wild trees growing on the western side of the Pele La below Norbding in May 1987. In 2006 and 2008 he was the only author also to visit the wild stands of cypress in Arunachal Pradesh.

The statistical data and observations on different trees cultivated in France, Switzerland and Italy belonging to the three southern slope Himalayan species are summarised in tables 3 to 5 (pages 103 and 104). One specimen of *Cupressus torulosa* more than a century old was studied for comparison.

Morphology : statistical data

Cone size : although there is much variability, an obvious difference between *Cupressus cashmeriana* and the two other species exists. The Arunachal Pradesh species has the longest cones, to more than 30 mm, and the average length is more or less equivalent to the maximum length of the other taxa. Moreover the smaller cones of *Cupressus cashmeriana* have a clear majority of aborted seeds. Inside the trees attributed to *Cupressus tortulosa*, the variability between the different trees is important with the smallest cones belonging to the 150 years old Isola Madre tree[2]. The index length × max. width × min. width gives the volume of the orthogonal parallelepiped in which the cone is included. The volume thus defined shows an obvious difference between *Cupressus cashmeriana* and the other two species.

Cone shape : the shape of the cones show meaningful differences. An index[3] enables one to put into evidence these differences. It is calculated using three measurements: length of the cone, maximum width and minimum width. The ratio length/max. width gives information on the cone shape with elongated: >1.10 ; ovoid: between 1.10 and 1.07 ; subglobose: between 1.06 and 1.03 ; globose between 1.02 and 0.98 ; flattened: <0.98. The ratio max. width/min. width, always equal to or above 1.00, shows the regularity (close to 1.00, rounded in section) or the irregularity of the cone diameter (away from

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[1] The gap between *C. torulosa* and *C. tortulosa* is ~600 km, between the latter and *C. cashmeriana* at least 60 km. More investigation of the wild trees in eastern Bhutan is necessary. Shorter distances between other *Cupressus* species are known, e.g. between *C. macrocarpa* and *C. goveniana* (< 3 km) or between *C. stephensonii* and *C. forbesii* (< 10 km).

[2] Worth noting that the cones were collected on the lowest branches, with several containing mostly aborted seeds. The seed cones observed in September 2014 at 15 m high look bigger. See fig. 3.

[3] Meaning of index: a number derived from a formula, used to characterise a set of data.

1.00, ellipsoid or flattened in section). Combined these two ratios allow a meaningful comparison between the cones of different species on a statistical basis and add information to the absolute size of the cones. *Cupressus cashmeriana* has the most elongated cones, often quadrangular in section, instead of rounded.

Cone scales : the number of scales – although not as reliable as the previous characters – allows the use of statistical analysis to distinguish between the different species. *Cupressus cashmeriana* has 10 to 14 scales (see fig. 23 & 26 for cones with 14 scales), with a majority of cones with 12 scales. The average number of scales per cone for trees of this species is always above 11. Based on the oldest specimens (trees #5 and #7) and on the one with a recorded origin (tree #8), the average number of scales/cone for *Cupressus tortulosa* is below 11, with a range of 8 to 12 scales per cone and a majority of cones with 10 scales (with only one exception, tree #6). The data for the young specimens are less homogenous, but in a similar range. *Cupressus torulosa* has a more important percentage of its cones with 10 scales/cone.

Seeds per cone : the statistical data allow to distinguish clearly between *Cupressus cashmeriana* and the two other species. The lower number of seeds is found in *Cupressus torulosa* with less than 100 seeds per cone. *Cupressus tortulosa* shows a wide range of variability between 72 [4] to 120 seeds per cone on average, while *Cupressus cashmeriana* has on average always more than 150 seeds per cone. Raddi *et al*. (2013) confirm the present observations on *Cupressus tortulosa*. They found 110 seeds per cone on average with a sample of 100 cones.

Cotyledon size : the data on the length of the cotyledons appear in table 1. Cotyledons of *Cupressus cashmeriana* are smaller than those of *Cupressus tortulosa*.

Table 1 : Length of Cotyledons

		Length		
	Sample size	Average	Max.	Min.
		Mm		
Cupressus tortulosa	33	**12.1**	14.9	10.0
Cupressus cashmeriana	16	**7.4**	9.4	4.6

Cotyledon number : see table 2. The result of cotyledon observations from cultivated trees is rather confusing. In *Cupressus torulosa*, wild origin seeds (Kalamuni, Uttarakhand, India) give 100% of seedlings with 2 cotyledons, while seeds of cultivated origin (England and Italy) give a small amount of seedlings with 3 cotyledons (fig. 44). As already noted by Silba (2013), the data mentioned by Farjon (2005, 2010, 2013) of (2-)3-4 cotyledons are erroneous, as they are mainly based on Hill and De Fraine (1908: sample of 12 seedlings, nine with 3 cotyledons, two with 4 and one with 5), cited by Camus (1914). They clearly belong to *Cupressus lusitanica*, a species widely cultivated on the lower hills of the Himalaya, and an invasive species in India, several times confused with *Cupressus torulosa* (see Maerki 2013b, fig. 1 and Farjon 2013). All references give only 2 cotyledons for *Cupressus cashmeriana* [5]. The problem is that no source is ever cited, for instance no mention is made if the origin of the seeds is wild or cultivated, from trees grown in Europe or in Asia. More disturbing is the fact that the statistics are not constant when collecting seeds in different years, suggesting cotyledon number could be affected by environmental conditions. Until verification can be done with seeds of wild origins, the data presented here is the best available. A further hypothesis is that the *Cupressus torulosa* grown in Europe has an origin other than Kalamuni and represent a variety of it or a new taxon.

Table 2 : number of cotyledons

	torulosa			*tortulosa*		*Cashmeriana*				
	wild	cultivated tree #4		cultivated tree #3		cultivated tree #7			cultivated tree #8	
Number of cotyledons	**2**	**2**	**3**	**2**	**3**	**2**	**3**	**4**	**2**	**3**
number of seedlings	120	84	12	54	15	92	18	4	76	6
percent	**100%**	**87.5%**	**12.5%**	**78.3%**	**21.7%**	**80.7%**	**15.8%**	**3.5%**	**92.7%**	**7.3%**
sample size	**120**	**96**		**69**		**114**			**82**	

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[4] The lowest numbers belong to trees of completely unknown origin, except tree #6 (Hillier nursery, but source?).

[5] In previous works (e.g. Eckenwalder 2009, Farjon 2005, 2010, DP.Little 2005), with a few exceptions (e.g. Rushforth 1987), *Cupressus cashmeriana* was understood as including both *Cupressus cashmeriana* and *Cupressus tortulosa*.

Morphology : other observations

Foliage : the foliage is quite often deceptive when it comes to distinguish between different cypress species, because it is a very variable and highly adaptative character depending on the climatic conditions. Here all three taxa have their ultimate shoots disposed in flat sprays (fig. 16). *Cupressus torulosa* has the most distinguishable foliage as it is the only one with monomorphic appressed green adult leaves. *Cupressus tortulosa* commonly has dark green foliage with appressed needles. The strong glaucous and thinner leaves of the Isola Madre tree belong to a cultivar [6] rarely found in the wild populations, whereas glaucous foliage is a common feature in *Cupressus cashmeriana*. This shared [7] leaf character of a free apex is at the origin of the confusion between the two species of the eastern part of southern Himalaya.

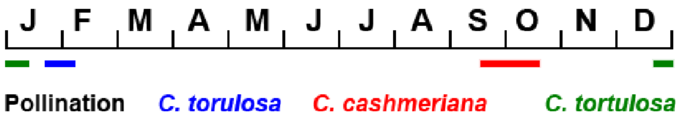
Seedlings : (photos, p. 110) the seedlings show well marked differences, both in growth rate and shape of the leaves at different times. *Cupressus torulosa* has the slowest growth and displays very early (already after one growing season) intermediate foliage with flattened dimorphic leaves. Adult foliage appears when the plant is between 40 and 60 cm high. *Cupressus tortulosa* displays intermediate growth rate, and *Cupressus cashmeriana* has the fastest growth rate. *Cupressus cashmeriana* keeps juvenile foliage for a longer period than *Cupressus tortulosa* which presents intermediate foliage with flattened shoots during the second growing season, similar to the intermediate foliage of *Cupressus torulosa*. This observation could explain the reduction by Carrière (1867) of *Cupressus corneyana* Carrière (1855 – a synonym of *Cupressus tortulosa*) to a variety of *Cupressus torulosa*. He could observe the development of the foliage of young trees and confusion is possible at some different stages when considering only this character.

Physiology

Serotiny : while both *Cupressus torulosa* and *tortulosa* open their cones soon after maturity, the seed cones of *Cupressus cashmeriana* remain closed as long as they are vascularised [8]. Exceptional weather conditions like a drought or a hard frost stressing the tree can trigger the opening of the cones and seeds release. In northern Italy, cone opening on *Cupressus tortulosa* happens in January exactly two years after pollination. In the same conditions the seed cones of *Cupressus torulosa* open in late summer.

Hardiness : the hardiness of these species decreases from west to east, *Cupressus torulosa* being hardier than *C. tortulosa*, and *C. tortulosa* being hardier than *C. cashmeriana*. The mature specimen growing in Geneva suffered from the two weeks cold wave of February 2012 (low to -12°C with no temperature above freezing during this period), and lost its leader while most of the cones opened.

Phenology



Pollination : *Cupressus tortulosa* sheds its pollen at the end of December to the start of January. Pollen cones observed in September are only in their initialisation phase (see fig. 5, 9 & 10), when *Cupressus cashmeriana* begins to release its pollen (in September-October – see fig. 27 & 28). No difference was observed in either Paris or Geneva or in the south of France [9]. As well no difference was observed on the different specimens of *Cupressus tortulosa* growing in Italy or Switzerland. In the Arboretum de Chèvreloup, France, *Cupressus torulosa* was observed releasing its pollen at the end of January.

Molecular analysis

To this date, only one series of genetic analysis has been conducted on French specimens of *Cupressus cashmeriana* using amplified fragment length polymorphism (AFLP). Material of several trees from

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[6] In fact this cultivar is retaining its intermediary foliage when adult.

[7] Between a species and the cultivar of another species.

[8] Like many other *Cupressus* species, e.g. *C. sempervirens*, *C. bakeri, C. macnabiana*, *C. stephensonii*, etc.

[9] By comparison, *Cupressus sempervirens* pollination dates between Morocco (Aboulaïch 2008), Spain (Hidalgo 2003, 2010), France and Switzerland (pers. obs.) do not vary significantly, occuring in February. Data about pollination periods are scarce in the literature, except for the most common species.

Italy, France and Switzerland was sent in June 2011 to Dr. R.Adams for analysis. Results are still pending.

AFLP : for his thesis, Bachelier (2003) collected material of all three species from botanical gardens and arbotera in southern France. *Cupressus tortulosa* was represented under the label of *Cupressus torulosa* var. *corneyana*[10], Ern collection from 1982.

Bachelier concluded from these AFLP tests : "Les taxons de l'Ancien Continent, par contre, sont très bien hiérarchisés. A l'intérieur de ce groupe se rencontrent successivement, de manière distincte, les sous-groupes suivants :

- *Cupressus funebris*,
- *Cupressus duclouxiana*,
- *Cupressus gigantea* et *Cupressus chengiana*,
- *Cupressus torulosa* var. *corneyana*,
- *Cupressus torulosa* avec inclus distinctement *Cupressus cashmeriana*,
- le sous-groupe méditerranéen, très bien isolé [..]"[11], but not reproduced here.

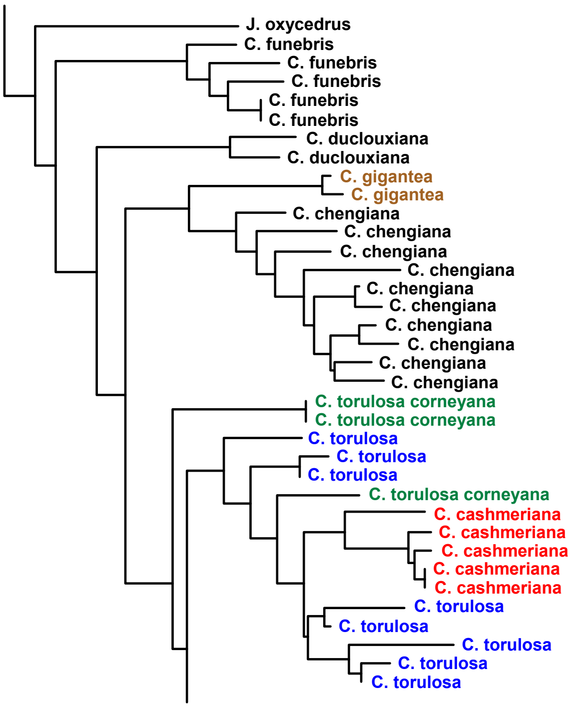

Fig. 1 : Bachelier (2003: fig. 36 in part), with colour additions.

The result shows that *Cupressus cashmeriana* is closer to *Cupressus torulosa* than to *Cupressus tortulosa* and also that there could be more than just one species of cypress currently under the labels *Cupressus torulosa* and *Cupressus tortulosa*[12].

Conclusion

From these observations on living plants, taking into account morphology with statistical data, physiology, phenology, biogeography and molecular analysis, there is enough evidence, despite the extreme variability of some characters, to justify the treatment proposed here, that is to distinguish at least three cypress species along the southern slopes of the Himalayan range : *Cupressus torulosa*, *Cupressus tortulosa* and *Cupressus cashmeriana*.

As all these results were obtained from cultivated trees in Europe[13], several with an unrecorded source, more investigations are needed with material collected in the wild populations to understand the origins of these specimens. For instance it is likely that most introductions from Bhutan were also from cultivated trees growing around fortresses or monasteries, and the wild origin of these plants is still not known with certainty. It is even possible that some of them are hybrids.

Statistical data and analyses will be needed to match the current described species with the wild populations growing in Bhutan, India and Nepal and to understand if there are more taxa than the currently accepted ones.

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[10] As stated above, a later synonym by Carrière (1867) of his *Cupressus corneyana*.

[11] "The old world taxa, on the other hand, are very well hierachised. Inside this group the following subgroups are distinctly met : * *Cupressus funebris*, * *Cupressus duclouxiana*, * *Cupressus gigantea* and *Cupressus chengiana*, * *Cupressus torulosa* var. *corneyana*, * *Cupressus torulosa* including distinctly *Cupressus cashmeriana*, * the Mediterranean subgroup, very well isolated [..]"

Note that *Cupressus gigantea* does not cluster with *Cupressus torulosa*, but with *Cupressus chengiana* and thus the merging of this species into a variety of *Cupressus torulosa* by Farjon (2005, 2010) is not justified (see Maerki 2013a).

[12] Unfortunately there is no record of the wild origins of these "*Cupressus torulosa*" and of several of the *Cupressus tortulosa*.

[13] Several of these species were first described (D.Don, Carrière) from introduced plants, so that it was a necessity to start this study on the southern Himalayan cypresses with that cultivated material (trees #2, 5, 7 & 8 are more than one century old).

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Table 3		**Tsenden**	***Cupressus cashmeriana***			
Statistical data		Farjon 2005 as *C."cashmeriana"*	Paris #1	Nice Oldest tree #2	Antibes #3	Geneva #4
Cones	Shape		*1.10-1.06*	*1.09-1.06*	*1.08-1.08*	*1.08-1.09*
		(sub)globose to ovoid	ovoid, often quadrangular in section			
	Length	(10-)12-21 mm	12.9-**26.4** mm	11.7-28.6 mm	13.7-**26.3** mm	13.7-**31.8** mm
	Average	***?***	***20.1 mm***	***21.7***	***23.0 mm***	***22.1 mm***
	Width	10-19 mm	11.2-23.3 mm	11.1-**23.9** mm	15.3-24.7 mm	11.5-27.2 mm
	Average	*?*	*17.8 mm*	*19.4 mm*	*20.5 mm*	*20.6 mm*
	Scales #	8-10	10-12	10-12-14	10-12	10-12-14
	%	?	40%-60%	35.4%-63.1%-1.5%	32.7%-67.3%	44.8%-52.8%-2.4%
	Average	***?***	***11.20***	***11.18***	***11.22***	***11.07***
			10 (39.8%) - 12 (58.6%) - 14 (1.5%)			
	Index	?	**6.36**	**8.14**	**9.65**	**8.68**
	Serotiny	parting scales	Serotinous			
	Sample #	?	20	65	49	127
	Seeds/cone (avg.)	***?***	***176***	***183***	***185***	***168***
	min.-max.		113-218	133-232	126-231	106-216
	Seeds/scale (avg.)	*?*	***15.6***	***16.5***	***16.2***	***15.5***
	min.-max.		*11.2-18.8*	*11.9-21.2*	*12.6-21.0*	*12.1-18.2*
	Sample #	?	14	62	21	40
Foliage	Colour		Glaucous-grey			
Pollen relase		?	Before December			September-October

Table 4
Statistical data

		Tsenden - ***C.tortulosa***				
			Italy			France
		Farjon 2005 as *C."cashmeriana"*	Isola Madre #5	Young tree #6	Old tree #7	Young tree #8
Cones	Shape		*0.97-1.11*	*1.07-1.07*	*0.99-1.07*	*1.05-1.05*
		(sub)globose to ovoid	globose to slightly subglobose			
	Length	(10-)12-21 mm	8.8-**15.6** mm	10.6-**18.9** mm	15.2-**22.6** mm	12.5-16.7 mm
	Average	***?***	***13.0 mm***	***14.7 mm***	***18.6 mm***	***14.7 mm***
	Width	10-19 mm	8.3-15.5 mm	6.2-14.7 mm	14.1-22.7 mm	11.1-16.1 mm
	Average	*?*	*12.8 mm*	*17.2 mm*	*18.3 mm*	*13.7 mm*
	Scales #	8-10	8-10-12	10-12	8-10-12	10-12
		?	6.5%-71%-22.6%	25.5%-74.5%	5%-74.3-20.7%	51.2%-48.8%
	Average	***?***	***10.26***	***11.26***	***10.05***	***10.79***
			8 (2.3%) - 10 (50.3%) - 12 (47.4%)			
	Index	?	**2.11**	**2.61**	**6.24**	**2.75**
	Serotiny	parting scales	not serotinous			
	Sample #	?	31	141	101	43
Seeds/cone (avg.)		**?**	**119**		**104**	**120**
	min.-max.		107-131		50-141	72-159
Seeds/scale (avg.)		?	***9.9***		***10.3***	***11.2***
	min.-max.		*8.9-10.9*		*5.0-13.8*	*7.2-15.5*
	Sample #	?	2		118	43
Foliage	Colour		Glaucous-blue	Glaucous-green	Glaucous-green	Green
Pollen relase		?			January	
Origin		?	W.B. Pentland	Hillier nursery	W.B. Pentland	H. Ern

Table 5
Statistical data

		Tsenden - ***C.tortulosa***				***C.torulosa***
			Italy		Switzerland	Italy
		Farjon 2005 as *C."cashmeriana"*	Young tree #9	Young tree #10	Young tree #11	Old tree #12
Cones	Shape		*0.96-1.05*	*1.02-1.05*	*1.03-1.07*	*1.0-1.06*
		(sub)globose to ovoid	globose to slightly subglobose			regular, globose
	Length	(10-)12-21 mm	10.6-**17.0** mm	13.3-**19.8** mm	10.3-**20.8** mm	12.7-**20.9** mm
	Average	***?***	***12.8 mm***	***16.7 mm***	***16.6 mm***	***18.0 mm***
	Width	10-19 mm	11.2-16.8 mm	12.3-18.8 mm	11.2-20.0 mm	12.8-20.8 mm
	Average	*?*	*13.0 mm*	*15.9 mm*	*15.6 mm*	*17.5 mm*
	Scales #	8-10	8-10-12	8-10-12	8-10-12	8-10-12
		?	16.7%-62.5%-20.8%	1.9%-48.1%-50%	3.8%-71.2-25%	5.1%-81.8%-13.1%
	Average	***?***	***10.08***	***10.77***	***10.54***	***9.99***
			8 (5.5%) - 10 (60.1%) - 12 (34.4%)			
	Index	?	**2.17**	**4.24**	**4.04**	**5.52**
	Serotiny	parting scales	not serotinous			not serotinous
	Sample #	?	24	52	52	99
Seeds/cone (avg.)		**?**			**72**	**69**
	min.-max.				50-89	47-96
Seeds/scale (avg.)		?			***6.8***	***7.0***
	min.-max.				*5.0-8.7*	*4.7-9.6*
	Sample #	?			26	64
Foliage	Colour		Glaucous-blue	Glaucous-green	Glaucous-green	Green
Pollen relase		?				January (France)
Origin		?	(Isola Madre ?)	unknown	unknown	unknown

Appendix : photos

Cover page : *Cupressus tortulosa*, Isola Madre, tree #5 (the # refers to the trees of tables 3-5, statistical data), foliage and cones close to the top. Note the yearly cones still green, the open cones pollinated in January 2012 and the greener than glaucous foliage colour. – 28.5.2014.

Fig. 2 : *Cupressus tortulosa*, Isola Madre, tree #5. – 28.5.2014.
The seed which gave rise to this famous tree was received in 1862 by the Borromeo family, owners of the islands of the same name on Lago Maggiore, in northern Italy. This tree was first struck by a lightning which cut its leader. Before this happened, the cypress had a conical shape. From that day it developed a broad rounded crown, with numerous lower branches taking the aspect and size of real trunks. The fate of this beautiful tree was almost sealed when on the night of the 26 June 2006, a most powerful "tromba di aria" (tornado) uprooted this almost 150 years old tree. Several other trees on the island where uprooted or their trunks broken. It was decided to rescue this almost unique monument in western Europe. Lead by GianCarlo Giustina and by a company specialising in tree care, the cypress was hauled up back into place and secured with cables. Eight years later, the tree is recovering and producing lot of cones, the foliage slowly filling the gaps left by the broken branches. The photo shows the side with the most damage, the tree having fallen in the direction of the photographer. Two saplings raised from cuttings are planted at its base.

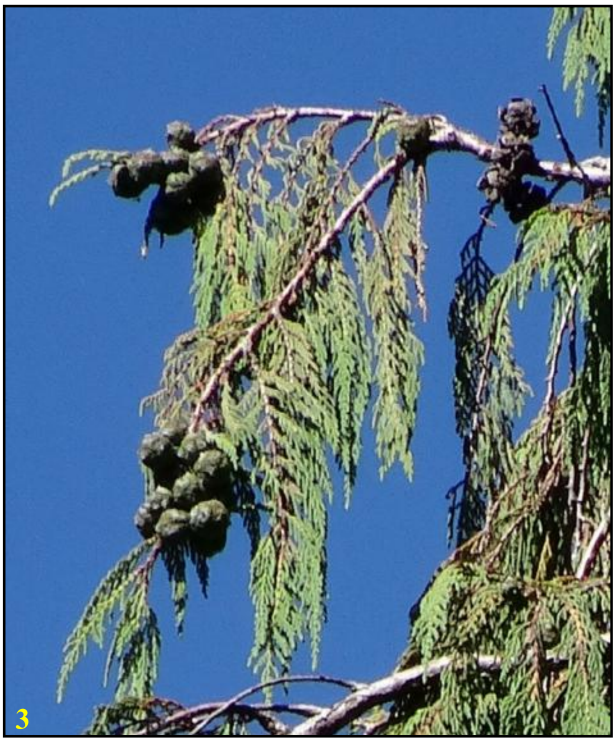


Fig. 3 : Detail of cover photo.

Fig. 4 & 5 : *C.tortulosa*, Isola Madre, tree #5. – 11.9.2014. Fig. 5 (below) shows pollen cone initialisation. Phenophase 1.

Fig. 6 : *C.tortulosa*, tree #7, 10.9.2014. Note the similarities between the two trees.

Fig. 7 : *Cupressus tortulosa*, tree #7. – 6.9.2012. Note the 8 months old green cones. The cones of the previous year – light brown – are still closed, while the older cones are all open. Compare with cover photo.

Fig. 8 : *Cupressus tortulosa*, tree #10. 10.9.2009.

Fig. 9 : *Cupressus tortulosa*, tree #9. 11.9.2011. Note the pollen cones in their initialisation phase.

Fig. 10 : *Cupressus tortulosa*, seed and pollen cones. Tree #10. The pollen cones are in phenophase 2c. 4.11.2007.

Fig. 11 : *Cupressus tortulosa*, mature seed cones. Tree #10. The seed cones older than 2 years are all open and their seeds have been released. Compare with fig. 13 and 25. 6.9.2012.

Fig. 12 : *Cupressus tortulosa*, foliage with immature seed cones. Tree #11. 12.4.2008.

Fig. 13 : *Cupressus cashmeriana*, foliage with mature seed cones all closed. Tree #2. 6.8.2013.

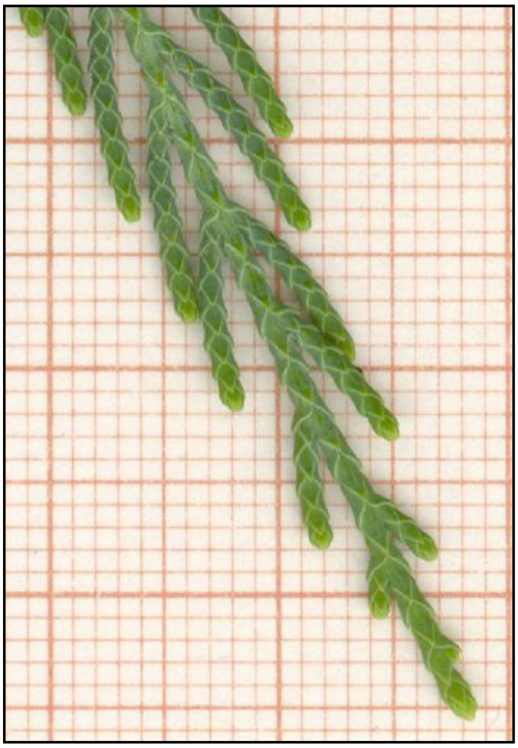


Fig. 14 : *Cupressus tortulosa*. Tree #10. Note the less appressed leaves, contrary to the cultivar tree of Isola Madre. 4.11.2007.

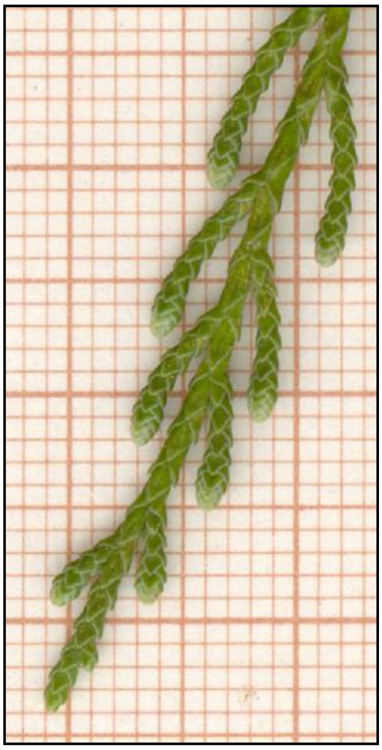


Fig. 15 : *Cupressus tortulosa*. Tree #7. Note the pollen cones still in their initialisation phase (phenophase 1b), while at this date (4.11.2007) *Cupressus cashmeriana* has already released its pollen.

Scale given by the millimetre paper.

Fig. 16 : Comparison of foliage between *Cupressus torulosa* and *Cupressus tortulosa*. 10.2010. From left to right : 1) *Cupressus torulosa*, note the monomorphic green leaves closely appressed on the shoot (#12). – 2) *Cupressus tortulosa*, tree #7. – 3) *Cupressus tortulosa* (no statistical data). Note the dimorphic leaves more or less appressed on the shoot. – 4) *Cupressus tortulosa*, tree #5, Isola Madre. Dimorphic leaves with a free apex, glaucous cultivar form.

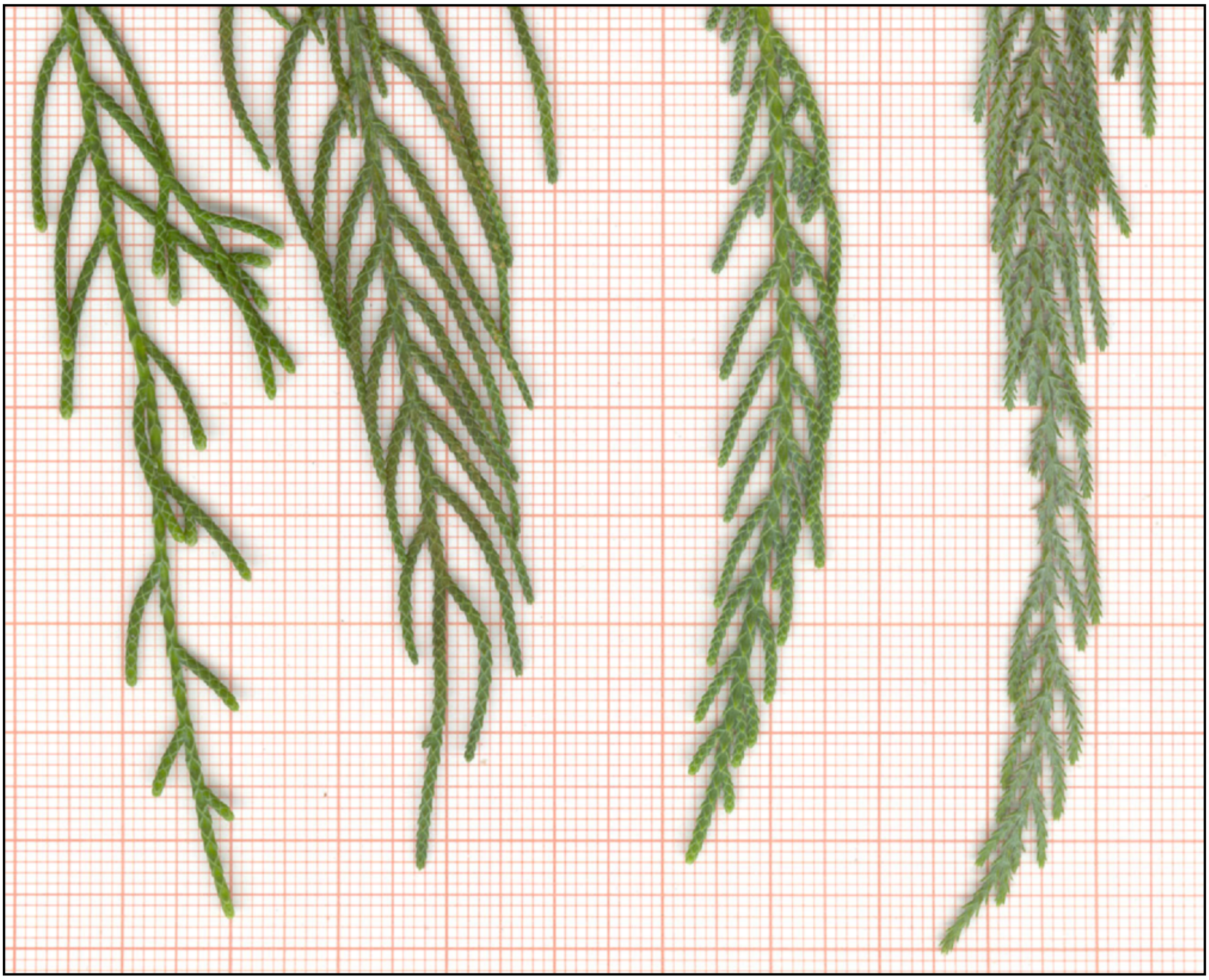


Fig. 17 : *Cupressus tortulosa* seedling. – 8.9.2012. **Fig. 18 :** *Cupressus cashmeriana* seedling. – 8.9.2012. Both seedlings are during their second year of growth. The seeds germinated at the same time. Note the differences between the size and the length of the juvenile needles. The tubes give the scale : their diameter at the top is 6.7 cm. (From seeds of trees #7 & #3.)

Fig. 19 : Side by side *Cupressus tortulosa* and *torulosa* of same height, but not same age (*torulosa* is older). Note the differences of the juvenile and intermediate foliage with *torulosa* almost entirely with intermediate foliage. (#7 & #12.)

Fig. 20 : Side by side *Cupressus tortulosa* and *cashmeriana* of about same height, but not same age (*tortulosa* is older). Note the differences in the foliage with only juvenile foliage on *cashmeriana*. (#7 & #3.)

Fig. 21 : Older *Cupressus cashmeriana* seedling still with juvenile foliage. (#3.)

Fig. 22 : *Cupressus cashmeriana*. Tree #3.Young seed cone 5 to 6 months after pollination. 24.3.2011.

(top right) **Fig. 23a, b & c :** *Cupressus cashmeriana*. Pollen cone. Tree #4. Bigger cone (> 3cm) found with 14 scales.
(right) **Fig. 24 :** *C. cashmeriana*. Pollen cones with 12 scales. #4.

Fig. 25 : *Cupressus cashmeriana*, mature seed cones. Only when they are not vascularised do the scales open.

Fig. 26 : *Cupressus cashmeriana*. Seed cone with 14 scales. Tree #4.

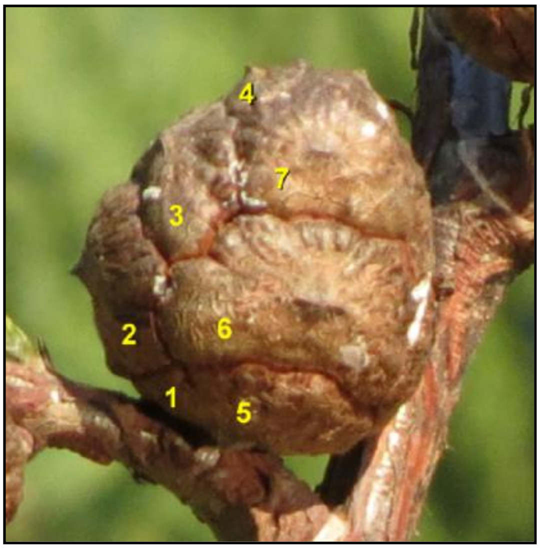
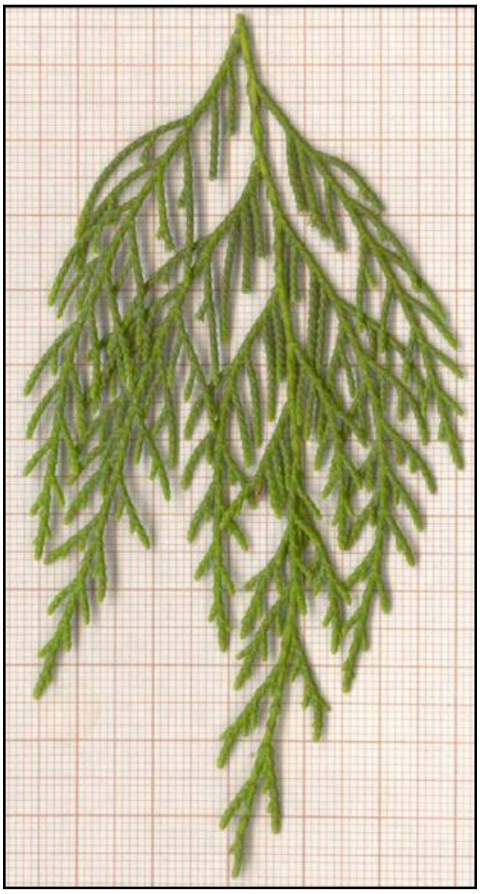


Fig. 27 : *Cupressus cashmeriana*, seed cone. Tree #4. Note the droplet on one of the ovules. 18.10.2011.

Fig. 28 : *Cupressus cashmeriana*, (left) pollen cones. Tree #4. Almost all cones have already released their pollen. 18.10.2011.

Fig. 29 & 30 : *Cupressus cashmeriana*, seed cones. Tree #4. After pollination. 29.11.2011.

Fig. 31 : *Cupressus cashmeriana*, mature seed cones. Tree #2.



(left) **Fig. 32 :** *Cupressus tortulosa*, flattened shoot with green leaves. Tree #11. 13.4.2008. On the branchlets of the upper part of the shoot, note that the pollen cones already have fallen.

(centre) **Fig. 33 :** *Cupressus tortulosa*, leaves, detail. Tree #11. 13.4.2008.

Fig. 34 : *Cupressus tortulosa*, seed cones, before and after maturity. Tree #11. 13.4.2008.

(right) **Fig. 35 :** *Cupressus tortulosa*, seed cones, Isola Madre. Tree #5. Note the similarities with the cones of tree #11. The smaller cones have mainly aborted seeds. *Scale 1:1*. Compare with fig. 23 & 24.

(below) **Fig. 36 :** *Cupressus tortulosa*, pollen cones. Tree #7. Phenophase 3f, near to flowering. 22.12.2012.© Francesco.

Fig. 37 : *Cupressus tortulosa*, seed cones. Tree #7. 23.4.2012. Compare with fig. 22 – taken one month earlier. *C.tortulosa* is about 2 months late in the cone development. © Francesco.

Fig. 38 : *C.tortulosa*,
Isola Madre. Tree #5.
Fig. 39 : *C.cashmeriana*.
Tree #2.
Fig. 40 : *C.tortulosa*.
Tree #11.
Fig. 41 : *C.tortulosa*.
Tree #10. ***All scales 1:1***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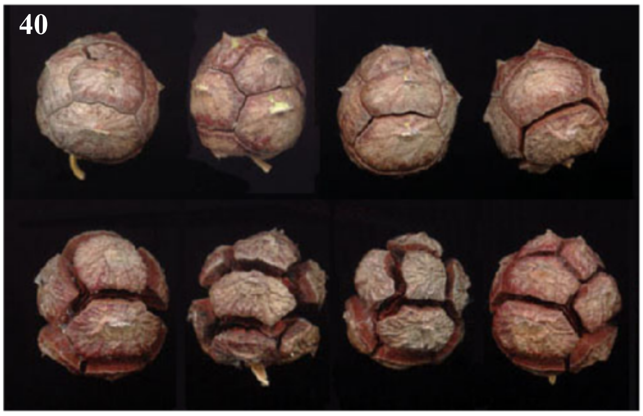
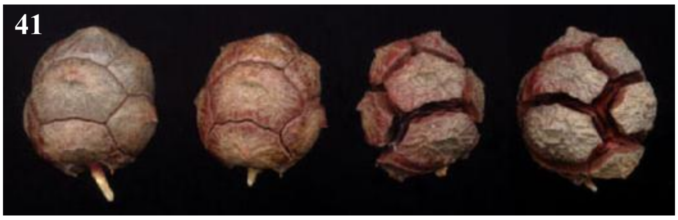

40


41


42

Fig. 42 : *Cupressus torulosa*. Tree #12.
Note the white wax on the seed cones.

Fig. 43 : *Cupressus torulosa*. Tree #12.
Seed cones. – *Scale 1:1*.
First row up : weathered mature cones.
Second row : mature cones.
Third row : immature cones with wax.

Fig. 44 : *Cupressus torulosa*. Seedlings from
tree #12. A few seedlings display 3 cotyledons.
Note the obtuse apex of the cotyledons.

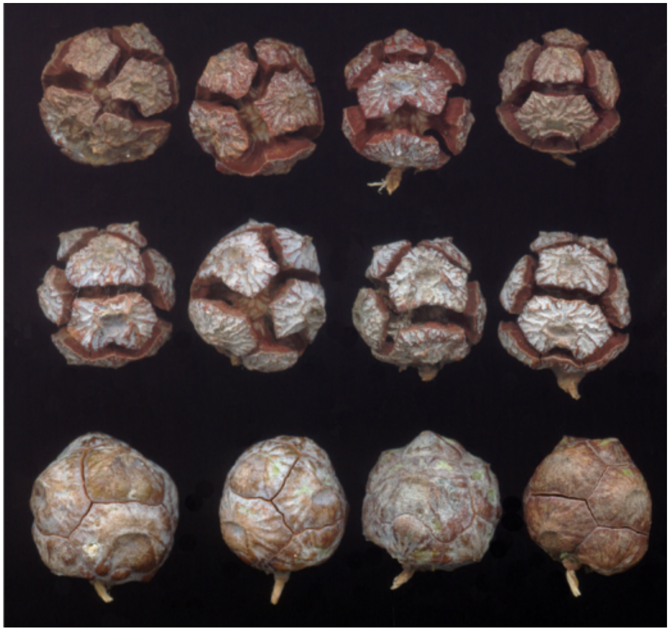


Fig. 45 : *Cupressus tortulosa*, tree #9. First year cones not yet fully developed. Compare with fig. 3. 28.5.14.

Key to native cypresses of the southern Himalaya.

1a. Cones serotinous, often longer than 25 mm, attached to the branches
for several years, on average more than 150 seeds/cone .... ***Cupresssus cashmeriana***

1b. Cones not serotinous, smaller than 25 mm, usually falling in
the year following cone opening, less than 150 seeds/cone..2

2a. Cones often covered with glaucous wax in the first year, always less
than 100 seeds/cone, slow growth during the 2 first years,
intermediate leaves already the first year, leaves monomorphic ....***Cupressus torulosa***

2b. Cones never covered with wax, from 50 to 150 seeds/cone, quick growth from
the start, intermediate leaves only from the second year or later, leaves dimorphic...................... ***Cupressus tortulosa***

Note on the epitypification of *Cupressus tortulosa* Griff.

D. Maerki

Following the publication of the article : *Typification of* Cupressus tortulosa *Griff.* [Bull CCP 3 (2) :69-75], Kanchi Gandhi (IPNI & Harvard University Herbaria) courteously drew our attention to a correctable error in the formulation concerning the designation of the epitype. He stated: "Since *Cupressus pendula* Griff. (1848) and *C. tortulosa* Griff. (1854) are nomenclatural synonyms, whatever typification is done to one name automatically applies to the other name." In order to remove any ambiguity in the formulation of the epityfication, the following presentation is added:

Cupressus pendula Griff., Itin. Pl. Khasyah Mts.: 131. 1848 [non Thunb., Fl. Jap.: 265. 1784].
Lectotype: Bhutan: Dewangiri [now Deothang], Samdrup Jongkhar District, 6.I.1838, *Griffith 27*
(K! [K000088093]) (designated by Maerki, 2014).
Epitype (hic designatus): s.l., s.d., *Griffith 1001/1* (P! [P06489919]).

The application of the two treated names comes down to the following nomenclatural formulation:

Cupressus tortulosa Griff., Not. Pl. Asiat. 4: 26. 1854.
≡ *Cupressus pendula* Griff., Itin. Pl. Khasyah Mts.: 131. 1848 [non Thunb., Fl. Jap.: 265. 1784].
Lectotype: Bhutan: Dewangiri [now Deothang], Samdrup Jongkhar District, 6.I.1838, *Griffith 27*
(K! [K000088093]).
Epitype: s.l., s.d., *Griffith 1001/1* (P! [P06489919]).

Cupressus cashmeriana Neotype

Figures 1 to 3 : *Cupressus cashmeriana* Carrière **Neotypus**, sheets 1/3, 2/3 and 3/3.

© Herbier MNHN, Paris, France.
Collection : Plantes vasculaires (P).

1) P02088769
2) P02088792
3) P02088793

Collector : *Y.Pauthier s.n.*, 20 December 2011.

Designated by D.Maerki (2013), Which name for the Tsenden? *Bull. CCP* 2 (2): 54.

Notes : on sheet 1/3, the cones are one year and a couple of months old and still immature as the yellow colour inside the cones testifies ; on sheets 2/3 and 3/3 the pollen cones are empty after pollen release in September-October ; on sheet 2/3 small blue seed cones soon after fertilisation are visible attached to the shoots, and the mature small – quite untypical – seed cone detached from the branch contains mainly aborted seeds.

D. Maerki

1

2

3

Bull. CCP 3 (3): 117-136. (12.2014)

A. Jagel [1] & V.M. Dörken [2]

Morphology and morphogenesis of the seed cones of the Cupressaceae - part I
Cunninghamioideae, Athrotaxoideae, Taiwanioideae, Sequoioideae, Taxodioideae

Summary

Seed cone morphology of the basal Cupressaceae (*Cunninghamia*, *Athrotaxis*, *Taiwania*, *Metasequoia*, *Sequoia*, *Sequoiadendron*, *Cryptomeria*, *Glyptostrobus* and *Taxodium*) is presented at pollination time and at maturity. These genera are named here taxodiaceous Cupressaceae (= the former family Taxodiaceae, except for *Sciadopitys*). Some close relationships exist between genera within the Sequoioideae and Taxodioideae. Seed cones of taxodiaceous Cupressaceae consist of several bract-/seed scale-complexes. The cone scales represent aggregation of both scale types on different levels of connation. Within *Cunninghamia* and *Athrotaxis* the bulges growing out of the cone scales represents the distal tip of the seed scale, which has been fused recaulescent with the adaxial part of the bract scale. In *Athrotaxis* a second bulge, emerging on the distal part of the cone scale, closes the cone. This bulge is part of the bract scale. Related conditions are found in the seed cones of *Taiwania* and Sequoioideae, but within these taxa bract- and seed scales are completely fused with each other so that vegetative parts of the seed scale are not recognizable. The ovules represent the only visible part of the seed scale. Within taxodiaceous Cupressaceae the number of ovules is increased compared to taxa of other conifer families. It is developed most distinctly within the Sequoioideae, where furthermore more than one row of ovules appears. The rows develop centrifugally and can be interpreted as short-shoots which are completely reduced to the ovules in the sense of ascending accessory shoots. Within the Taxodioideae the vegetative, visible parts of the seed scale can be interpreted as serial accessory shoots. Later they fuse with the bract scale.

1 Introduction

Among recent conifers, seed cones of Cupressaceae are those with the most variable form, a fact that leads to the great number of the genera accepted in this family. Cupressaceous seed cones have been the subject of several publications, but mostly only mature cones were used in the studies. At the end of the 1930s the investigation of female reproductive structures of Cupressaceae came more or less to a deadlock after several fundamental works had been published (e.g. PILGER 1926, HIRMER 1936, PROPACH-GIESELER 1936). Electron microscopy resulted in several important works on the "Taxodiaceae" (e.g. TAKASO & TOMLINSON 1989a, 1990, 1991, 1992, JAGEL 2001, FARJON & ORTIZ GARCIA 2003) and for the Cupressaceae *s. str.* (e.g. TAKASO & TOMLINSON 1989b, TOMLINSON *et al.* 1993, JAGEL 2001, JAGEL & STÜTZEL 2001a, 2001b, 2003, SCHULZ *et al.* 2003, SCHULZ & STÜTZEL 2007). Molecular studies to understand the phylogeny of the family have been carried out (e.g. BRUNSFELD *et al.* 1994, KUSUMI *et al.* 2000, GADEK *et al.* 2000, QUINN *et al.* 2002, YANG *et al.* 2012). How far morphological studies about the seed cones are supported by such molecular generated trees is the one subject of the present three-part series. The aim of these studies is not the construction of a diagnostic identification key or the complete illustration of the seed cones of each taxon. For this purpose several detailed works have been published recently, e.g. KINDEL 2004, SCHULZ 2006 or FARJON 2005, 2010a, 2010b. Several of the identification criteria used are suitable to identify taxa, but they are not necessarily usable for taxonomic classification as well. They are often only describing variations in proportions, sizes and numbers of e.g. scales or ovules. Thus, the present publication series focuses on the structural differences and similarities of cupressaceous seed cones.

An exact definition of delimitation of the seed cone is essential, because in literature it is defined variously. In the present study we only count elements as a part of the seed cone which develop strongly while maturing and become lignified. Leaves which represent intermediates in form and/or

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coloration between the cone scales and normal (scale) leaves at pollination time, are here called transitional leaves.

The very variable number of ovules per cone scale and the high number of them in several groups is typical for Cupressaceae cones. These show considerable intraspecific as well as interspecific variability. For correct analyses of the exact place and the developmental order of the ovules SEM-investigations of very young ontogenetic developmental stage are essential. In this context exceptional cone types can be important for the understanding of the cone morphology.

In the present study morphogenetic investigations were predominantly done in genera for which sufficient investigations do not currently exist. Within the Cupressaceae *s. str.* there are some large gaps in the literature whilst in the "Taxodiaceae" some important studies were published by authors with different aims and thus may not be directly comparable. These studies have been evaluated in the present study. As mentioned before, it is important to emphasise that investigations of mature cones alone are not sufficient for the understanding of their evolution. During cone maturation, a considerable number of ovules fail, and the proportions within the cone can change as well as the insertion point of the ovules. Regarding only mature cones can lead to misinterpretations, because essential evidences for interpreting important evolutionary steps are no longer visible. Also the orientation of cones at pollination time and maturity, and the secretion of pollination drops are extremely variable among Cupressaceae. This is, however, discussed in detail by DÖRKEN & JAGEL (2014) and will only briefly be mentioned here within the taxon descriptions.

Today the Cupressaceae *s. l.* comprises 30 genera (FARJON 2010a). Within this group, typical features of the cones are the increased number of ovules per cone scale (unlike the two in Pinaceae, or the one in Araucariaceae) and the structure of the seed-wings (if they are developed). The wings originate from the integument and not from seed scale tissue as is typical for seeds of pinaceous taxa. Cupressaceous pollen grains are not saccate, always lacking air bladders.

Part one of this compilation comprises the genera of the former family "Taxodiaceae"; parts two and three will deal with the subfamilies of the Cupressaceae *s. str.*, the mostly northern hemisphere Cupressoideae and the southern hemisphere Callitroideae.

2 Cone morphology of taxodiaceous Cupressaceae

The "Taxodiaceae" as a single distinct coniferous family is no longer sustainable, as it is paraphyletic and does not represent the sister group of the Cupressaceae *s. str.* (e.g. HART 1987, BRUNSFELD *et al.* 1994, GADEK *et al.* 2000, QUINN *et al.* 2002, YANG *et al.* 2012). Thus, in the present study the somewhat cumbersome phrase "taxodiaceous Cupressaceae" is used. In the past, *Sciadopitys* was also associated with this group, but today it is placed in the separate family Sciadopityaceae. With only 14 extant taxa, the species of the taxodiaceous Cupressaceae represent only a small group.

The taxodiaceous Cupressaceae represent phylogenetically the oldest part of the family. All of them represent tertiary relicts, which are only native in very small relict areas today (except *Taxodium*). The modern group of Cupressaceae *s. str.* has developed from a derived branch of this group (e.g. YANG *et al.* 2012). Distinct features in morphology and anatomy that could clearly separate the taxodiaceous Cupressaceae from the Cupressaceae *s. str.* do not exist. Until the discovery of *Metasequoia glyptostroboides* with its decussate orientation of leaves and cone scales (following TAKASO & TOMLINSON 1992 it is bijugate), the spirally arrangement of leaves was regarded as such a differential feature. Among taxodiaceous Cupressaceae some genera seem to be strongly separated from the others, however, others are so closely related, that they could be grouped within one subfamily or genus. Therefore several monotypic subfamilies for the more isolated genera were established (e.g. KUSUMI *et al.* 2000, YANG *et al.* 2012). All taxodiaceous Cupressaceae are monoecious. The majority of the genera are distributed in the northern hemisphere, with only *Athrotaxis* having an exclusively southern hemispheric distribution.

Material was collected in German botanic gardens and parks at Bochum, Bonn, Münster, and Düsseldorf, the Grugapark in Essen, the Isle of Mainau (Konstanz, Germany), and in the Palmengarten Frankfurt; that of *Athrotaxis, Taiwania*, and *Glyptostrobus* was cultivated under glass.

2.1 *Cunninghamia* R. Br. – Cunninghamia (Cunninghamioideae)

Today two species are often distinguished within the genus *Cunninghamia*, one of them is native in China, *C. lanceolata* (Lamb.) Hook., the other, *C. konishii* Hayata, has been described from Taiwan, and later discovered in Vietnam and some Chinese localities as well. However the taxonomic rank of *C. konishii* is controversial, with genetic data showing the two are not monophyletic with respect to each other and should be merged (LU *et al.* 1999). For individuals in German cultivation, the given diagnostic features seem to be quite doubtful.

At pollination time the cones are oriented strictly downward (fig. 1A). This orientation does not change while maturing (figs 1E, 1F). Several scale leaves are inserted at the peduncle (= the cone carrying short-shoot). The basal as well as the terminal cone scales are sterile. Each cone scale has a stalk-like base and carries normally three ovules. On the scales of the distal parts of the cone often only two occur, in the central part rarely four (fig. 1C). The ovule primordia develop on the base of the cone scales, not in their axils (fig. 1B). Investigations of cone development by FARJON & ORTIZ GARCIA (2003) show that the middle one of the three ovules on a cone scale develop later than the lateral ones (centripetally). Each ovule developed on a distinct tongue-like outgrowth, shifting the ovules in an inverse position.

At pollination time the cone opens and the ovules with their pollination drops get into a strictly vertical downward position (figs 1C, 1D). A fusion of neighboring pollination drops could not be observed. After pollination the cone closes by a strong extension of the cone scale, but without an excessive growth in girth. A ventral bulge is not developed. Mature cones are roundish to broad ovate (fig. 1E). The cone scales are not as strongly lignified as in the most other Cupressaceae genera. They remain more or less leathery and flexible and the cone is not solidly closed. The cones mature in the year of pollination. They frequently show a terminal proliferation in form of a short leafy shoot (fig. 1F). The lifespan of this shoot is, however, strongly correlated with the development of the cone; after releasing the seed the shoot dies. The seeds of *Cunninghamia* have two small wings.

2.2 *Athrotaxis* D. Don – Tasmanian Redwoods (Athrotaxoideae)

Athrotaxis comprises two or three species, *A. cupressoides* D.Don and *A. selaginoides* D.Don, and *A. laxifolia* Hook. which is sometimes regarded as a hybrid between the first two (e.g. ELLIOT 1951, BRENNAN *et al.* 1957, FARJON 1998, 2010a). *Athrotaxis* is distributed in western Tasmania. From each species cones were observed at pollination time. Investigations of the earliest ontogenetic stages were performed on material of *A. laxifolia*.

The cones develop at the end of leafy short-shoots carrying 15-20 spirally arranged scale leaves. About 10 transitional leaves precede the cone. The winged ovules are inserted in one row. Each row consists mostly of three to five ovules. Investigations of early ontogenetic stages show that the ovules do not develop in the axils of the cone scale but on the basal parts of their plane. Before or during the time of integument development, the ovules are still in an upright position. With a continuing development they get shifted distally on the scale and change into an inverse position. During this process a seed scale bulge is developed on which the bases of the ovules insert (figs 2B, 2E). At least in *Athrotaxis laxifolia* this bulge seems not to be built on each cone scale (fig. 2D). The situation is quite similar to that of *Cunninghamia* (fig. 1B), but the obvious difference in *Athrotaxis* is the distinct continuous bulge carrying the ovules. In *A. laxifolia* the investigation could not clearly solve if the ovules of a cone scale develop simultaneously or centripetally. This might possibly be a result of the hybridogenous origin of this taxon and it seems that several ovules stagnate at diverse point of time during development. The developmental series should therefore been also checked at the postulated parental species.

The upper two terminal cone scales are often sterile. The most distal cone scales do not separate completely from the cone-axis in most cases. Thus a terminal piece is often developed (fig. 2A). At pollination time the cones are in a more or less downward orientation (fig. 2B). They keep this position at maturity (fig. 2F).

Just before pollination the ovules are already in an inverse position due to the seed scale bulge. At pollination time the cone scales curve outwards to open the cone and the ovules with their pollination drops turn into a vertical downward position (fig. 2A). A fusion of neighboring pollination drops was not observed. Soon after pollination the seed scale bulges degenerate. The cones are closed by a ventral bulge which develops in the part of the cone scale distal from the seed cone bulge. Mature cones are roundish to ovate (figs 2C, 2F) maturing in the first year. The seeds have small wings.

2.3 *Taiwania* Hayata – Taiwan Redwood (Taiwanioideae)

The genus *Taiwania* is monotypic. The single species, *T. cryptomerioides* HAYATA, is native to Taiwan, southwestern China, and northern Vietnam. For the present study only receptive and mature cones, which had already released the seeds, were available (see also JAGEL & KNOPF 2007).

Cones develop terminally at short-shoots, carrying only a few scale leaves. At pollination time the cones are upright oriented (fig. 3A, 3B, 3C) and are more or less cylindrical. They consist of 14-20 spirally set cone scales. Only those in the middle of the cone are fertile, the basal and distal scales are sterile. Two erect ovules develop per cone scale. They do not develop in the axils of the cone scale but on the basal parts of the cones scales (FARJON & ORTIZ GARCIA 2003). Apart from the ovules no other structures are detectable on the cone scale at pollination time, which seems to be also the case for subsequent young developmental stages of the cone (FARJON & ORTIZ GARCIA 2003). In one illustration of the cited publication one of the cone scales shows a small bulge, but this structure seems to represent an aborted ovule—this cone scale carried only one ovule. At pollination time the cone scales are slightly spreading so that the pollination drops of the erected ovules are exposed to the airflow (fig. 3C). After pollination the cone closes by enlargement growth of the cone scale but without a ventral bulge. The cone scales become lignified but remain more or less flat. While maturing, the seeds are dislocated to more distal parts of the cone scales (fig. 3F) so that the seeds are turned into an inverse position. Thus, the development of the cone scale in this aspect is similar to Sequoioideae (fig. 10C); however, cones of *Taiwania* do not get closed by a ventral bulge of the cone scale. At maturity the cones still keep the upright orientation (figs 3D, 3E). Mature cones are broad-ovate, about 2 cm long and 1.5 cm wide (fig. 3D). The cones mature within one year. The seeds are uniformly winged.

2.4 The *Sequoia*-group – Redwoods (Sequoioideae)

The genera *Metasequoia, Sequoia* and *Sequoiadendron* are quite similar to each other, so that only one taxon will be treated here in detail. On account of the similarities the three taxa are placed in the subfamily Sequoioideae, which is also supported by molecular trees (e.g. KUSUMI *et al.* 2000, YANG *et al.* 2012).

2.4.1 *Metasequoia* Hu & W.C. Cheng – Dawn Redwood (Sequoioideae)

Metasequoia consists of only one recent species, the deciduous *Metasequoia glyptostroboides* Hu & W.C. Cheng, which is native to small relict areas of central China. Ontogenetic studies of the cone development have been done by TAKASO & TOMLINSON (1992), therefore only supplementary investigations were performed here.

Receptive cones are erect (fig. 4A). Pollination takes place long before sprouting of the leaves. The bud scales remain at the base of the peduncle for a long time. Subsequent leaves are strongly reduced green transitional leaves which lead into the decussate cone scales. Only the cone scales in the middle of the cones are fertile. The terminal and basal scales are always sterile. At pollination time, the small cones are cylindrical in shape and slightly tetragonal (fig. 4A). The pollination drops are not displayed on the surface of the cone but within it (fig. 4B). A fusion of pollination drops was not observed.

The ovules are not inserted axillary, but on the basal parts of the cone scales. Each cone scale carries several ovules inserted in one row (fig. 4C). Ovules develop centripetally (TAKASO & TOMLINSON 1992). The cones as well as the ovules are in an upright orientation while pollination time (fig. 4A, 4B), no further outgrowths of the cone scales are detectable at pollination time (fig. 4C). After pollination the cone closes by a strong development of the ventral bulge on the distal part of the cone scale. The bases of the ovules are dislocated in more distal parts of the cone scale while maturing. Thus, the seeds turn into an inverse position. The tip of the young cone scale is now shifted in the center of the mature cone scale (fig. 10D). In very rare cases the cones can show proliferations in different intensities (fig. 4E) (DÖRKEN 2011). After pollination the peduncle strongly elongates, sometimes up to the 4 or 5 times of the original length. While maturing the roundish or ovate cones change their orientation from upright to downward (fig. 4D). The cones mature in the year of pollination and are abscised as a whole in autumn or winter. The seeds are winged. The seed wings surround the seed nearly all around (fig. 4F).

2.4.2 *Sequoia* Endl. – Coast Redwood (Sequoioideae)

Sequoia sempervirens is native to coastal areas of California and Oregon in the USA. The cones are similar to those of *Metasequoia* (fig. 4) in accordance with their orientation and general structure, but differ in the spiral arrangement of the scales (figs 5A, 5F). The cone consists of about 25 cone scales. The distal and the basal scales are sterile. The ovules are inserted in mostly two rows on the basal part of the cone scales (figs 5C, 5D). The second row develops later than the first one (centrifugal) (fig. 5C), sometimes the ovules of the second row degenerate (5E). Compared to *Metasequoia, Sequoia* develops more ovules per cone scale. At pollination time the ovules are deeply hidden within the cone (fig. 5B). Mature cones are roundish or ovate (fig. 5F) maturing in the year of pollination. The seeds have small wings.

2.4.3 *Sequoiadendron* J. Buchholz – Giant Sequoia (Sequoioideae)

Sequoiadendron giganteum is native to the Sierra Nevada of California in the USA. The structure of the *Sequoiadendron* cone correlates more or less with the cones of *Sequoia*, but differs from them in the higher amount of ovules per cone scale (fig. 6C) and the regular appearance of a third row of ovules (fig. 6C). With twelve ovules per cone scale *Sequoiadendron* has shown the highest number of ovule among all investigated taxodiaceous Cupressaceae. At pollination time cones and ovules are erect (fig. 6A, 6B). Mature cones are broad ovate (fig. 6D, 6F) and significantly larger than those of *Sequoia*. While maturing the tip of the cone scale is shifted in the center of the cone scale (fig. 6E). The cones mature in the year after pollination, so that the cones remain for at least two years on the tree, and often far longer. The flat seeds have distinct wings.

2.5 The *Taxodium*-group (Taxodioideae)

The genera *Cryptomeria*, *Glyptostrobus* and *Taxodium* show distinct structural similarities and were therefore placed in the subfamily Taxodioideae.

2.5.1 *Cryptomeria* D. Don – Sugi (Taxodioideae)

Cryptomeria is with one Japanese taxon *C. japonica* (Thunb. ex L. F.) D. Don monotypic (FARJON 2005). Early ontogenetic stages were investigated by TAKASO & TOMLINSON (1989a).

Several spirally inserted small needle leaves are located on the fertile short shoot. These leaves are followed by several transitional leaves leading over to the cone scales. At pollination time the cones resemble a showerhead and are oriented downwards (fig. 7A). The cone scales are inserted on a strongly condensed cone-axis so that they are inserted in nearly one plane (fig. 7B). The basal and distal cone scales are sterile. In the distal end of the cone a rudimentary cone-axis can be observed.

At pollination time the pollination drops are freely exposed to the airflow (fig. 7D). Several pollination drops can coalesce to form a larger one. The ovules are not inserted on the scales, but in their axils. Three or two ovules develop in a single row (fig. 7C). Even in early stages of development small teeth-like structures are detectable, mostly three to five (fig. 7C). Their number does not always correspond to the number of ovules. They develop in the axil of the cone scale between the ovules and the bract scale. While maturing the teeth grow strongly and take part in closing the cone. They are rising distinctly out of the mature cone (figs 7E, 7F). Their basal part is now strongly fused with the bract scale. While maturing the cones change their orientation about 180° in a vertical upright position (fig. 7E). The cones mature within one year. A short terminal proliferation of the cone-axis can often be observed. In very rare cases male flowers could be observed at such a shoot (fig. 7F). The seeds are narrowly winged.

2.5.2 *Glyptostrobus* Endl. – Chinese Swamp-cypress (Taxodioideae)

Glyptostrobus is a southeast Chinese and Vietnamese monotypic genus. The single taxon, *Glyptostrobus pensilis* (Staunton ex Don) K. Koch, is deciduous and abscises all leafy short-shoots at the end of the vegetation period. Ontogenetic studies of early stages of cone development were done by TAKASO & TOMLINSON (1990).

Pollination takes place before the leafy short shoots sprout. The cones are inserted on strongly condensed short-shoots. They are also showerhead-like (figs 8A, 8B), similar to of *Cryptomeria*. However, in *Glyptostrobus* the cone-axis is not as strongly condensed. Mature cones are roundish or ovate in shape (figs 8D, 8E, 8F). Contrasting to the situation in *Cryptomeria,* the receptive cones are not oriented vertical downwards but more or less plagiotropic (fig. 8A). Two (occasionally three) ovules are inserted per cone scale. After pollination the cones change into an upright position (fig. 8D).

Even at pollination time a small tooth-like structure is developed on the abaxial side of the ovule in the axil of the bract scale similar to the conditions in *Cryptomeria*. These structures strongly develop at maturity and take part in closing the cones. At maturity they are more or less fused to the half with the bract scale and show a varying number of bulges, so they develop a shell-like appearance (fig. 8E). Following TAKASO & TOMLINSON (1990) the cone development shows a prominent difference to *Cryptomeria*. The tooth-like structures inserted in the axil of the cone scale develop even later than in *Cryptomeria*. The cones of *Glyptostrobus* mature in the year of pollination. The seeds have distinct wings.

2.5.3 *Taxodium* Rich. – Baldcypress (Taxodioideae)

The genus *Taxodium* comprises two or three species native in the southern USA and Mexico. *Taxodium ascendens* Brongn. is often treated as a variety of *T. distichum* (L.) Rich. Both taxa are deciduous. The third species, *Taxodium mucronatum* Ten., is semi-evergreen. Early ontogenetic stages were investigated by TAKASO & TOMLINSON (1990).

Taxodium cones at pollination time (figs 9A, 9B, 9C) resemble more or less those of *Glyptostrobus* (fig. 8). At pollination time the cones are not placed in a coherent orientation, but are arranged more or less depending of the given branching system, so that the cones often have a plagiotropic orientation. Several cones are developed closely to each other at the shoot axis (figs 9A, 9E). They mature within one year. Mature cones are roundish or ovate (figs 9D, 9E). They disintegrate at maturity to the single cone scales (fig. 9E), a feature that is unique among recent Cupressaceae *s. l.* The seeds are irregularly angular and have no wings. The disintegrating cones and the missing seed wings are likely related to the water-dispersal of the species.

3 Discussion

Recognising phylogenetic relationships between the genera of the taxodiaceous Cupressaceae could be quite difficult, because the recent taxa represent only a small spectrum of a former much larger diversity. Several of these living fossils are isolated taxa of a particular developmental series, and most of the connecting links had died out (e.g. MEYER 2005, MOMOHARA 2005, LEPAGE *et al.* 2005). Based on the knowledge about the morphology and ontogeny of cones some of the taxa can be grouped, such as the Sequoioideae and the Taxodioideae, which are also supported by genetic data (BRUNSFELD *et al.* 1994, GADEK *et al.* 2000, KUSUMI *et al.* 2000, QUINN *et al.* 2002, YANG *et al.* 2012).

3.1. The cone scale: proportions of bract scale and seed scale

The coniferous bract scale is interpreted as a complex of a modified bract (bract scale) carrying in its axil a reduced and condensed short-shoot (the seed scale). The seed scale carries the ovules. Thus, the coniferous seed cone corresponds to the definition of an inflorescence (e.g. SCHUMANN 1902, HERZFELD 1914, PILGER 1926, FLORIN 1951, 1954, SCHWEITZER 1963). The fundamental knowledge about the structure of the cone scale was primarily gained from palaeobotanic investigations and research into living Pinaceae, which was later extended to the Cupressaceae. Thus, the cupressaceous cone scale was regarded for a long time as a complete fusion product of the bract scale with the seed scale. Only a different intensity of the fusion was differentiated (e.g. HEGI 1981, PAGE 1990). Within such a postulated bract-/seed scale-complex the complete adaxial part of the cone scale represents the seed scale (e.g. AASE 1915, PILGER 1926, FLORIN 1951). How far this is the correct interpretation will be discussed here for the taxodiaceous Cupressaceae. In contrast to the situation in the genera of Cupressaceae *s. str.* (JAGEL & DÖRKEN, in prep.), in taxodiaceous Cupressaceae the majority of the more or less distinct vegetative part on the cone scale has to be interpreted in fact as the seed scale. However, the ontogenetic investigations clearly show, that in some taxa the ovules are inserted distinctly in the axil of the cone scale, e.g. in the Taxodioideae. On the other hand the vegetative outgrowths of the upper surface of the cone scale in some taxodiaceous Cupressaceae are pointing to the distal part of the cone scale representing the bract scale, what will be explained more detailed in the following.

In ***Cunninghamia*** and ***Athrotaxis*** the fusion process of the basal parts of the seed scale and the cone scale has already taken place before the ovules develop. Here the ovules are inserted very closely to the cone-axis, but without any doubt on the basal part of the cone scale and not in its axil. The basal, upper (= adaxial) part of the cone scale has therefore to be interpreted as seed scale at least to the point of the insertion of the ovules (fig. 10A, 10B), because ovules could never be developed by a bract scale. Thus the ovule-carrying short-shoot is shifted on the upper surface of the bract scale in the sense of recaulescence. The bulge on the cone scale in *Athrotaxis* and the three tongue-like structures at the base of each ovule in *Cunninghamia* could be interpreted as the tips of the seed scale. These represent the only visible part of the seed scale, the rest is completely fused with the bract scale (figs. 10A, 10B). Such outgrowths possibly support the optimal orientation of the pollination drops (DÖRKEN & JAGEL 2014). However, they do not take part in closing the cone and degenerate after pollination. Maturing cone scales of *Cunninghamia* remain more or less flat (fig. 10A). In contrast to this, cones in *Athrotaxis* get closed by a bulge developing on the distal part of the cone scale (fig. 10B). Due to its topology (distally to the seed scale bulge) this swollen part can only be interpreted as a part of the bract scale. In this case no parts of the seed scale are involved in closing the cone, as it was earlier supposed to be. In *Cunninghamia* and *Athrotaxis* the low number of ovules, the stalked cone scales, the visible distal parts of the seed scale and the weakly lignified cone scales might represent the most primitive conditions within seed cones in recent Cupressaceae.

Cunninghamia, *Athrotaxis* and *Taiwania* are placed at the base of Cupressaceae in most morphological as well as in phylogenetic trees, although the order is not always the same (e.g. STEFANOVIC 1998, KUSUMI *et al.* 2000, QUINN *et al.* 2002, YANG *et al.* 2012). Among recent Cupressaceae *Cunninghamia* seems to be the most basal taxon.

In ***Taiwania*** and the genera of the **Sequoioideae** (*Sequoia*, *Sequoiadendron*, *Metasequoia*) the ovules are also developed at the base of the cone scale and not in their axils. Further outgrowths of the cone scale, which could be interpreted as parts of the seed scale, are absent (figs 10C, 10D).

Among these taxa only the basal, adaxial part represents the seed scale. But this is so closely fused with the cone scale, that it is not visible as a separate structure. The visible part of the seed scale is merely represented by the ovules. While in *Taiwania* the cones mainly close by growth in the elongation of the cone scales (fig. 10C), in the *Sequoia*-group the cone close by a strongly developed ventral bulge of the cone scale (fig. 10D).

Due to the structural similarity of cone morphology, especially the axillary position of the ovules and the tooth-like seed scale structures, ***Cryptomeria***, ***Glyptostrobus*** and ***Taxodium*** can be regarded as closely related. The tooth-like structures, developing between the ovules and the bract scale, strongly develop while maturing and fuse later with the bract scale, finally representing the major part of the cone scale (fig. 10E). TAKASO & TOMLINSON (1989b) regard a problem in interpretation the tooth-like structure of *Cryptomeria* as seed scale, because the teeth develop later than the ovules and therefore could not carry ovules. However, this does not have to be a contradiction with the interpretation as a seed scale, because the axillary tissue represents the seed scale in total (compare also SCHWEITZER 1963) and the ovule need not be carried by the teeth. Postulating that this axillary parenchyma is able to develop accessory shoots as is also realised in the vegetative parts of *Metasequoia*, the totality of the typical teeth can be regarded as a secondary shoot, in the sense of an ascending accessory shoot. Within such a branching system, the seed scale consists of two axillary structures, the first developed short shoot being represented merely by the ovules. The second one, which develops somewhat later, is sterile and develops the teeth (fig. 10E).

3.2 Increasing number of ovules per cone scales

Within Cupressaceae the strongly increased number of ovules per cone scale in several genera is a derived feature within this group. In the other conifer families more than two ovules per cone scale do not occur except in *Sciadopitys*. In the more derived taxa of the Sequoioideae group, several rows of ovules develop (figs 5D, 6C). In several genera of the modern subfamilies Cupressoideae and Callitroideae this feature is even more strongly developed (JAGEL & DÖRKEN, in prep.). Within a row the ovules develop centripetally. This corresponds to the development of reproductive structures on a short-shoot from proximal to distal. The development of several rows in the *Sequoia*-group corresponds with the disappearance of the visible, vegetative part of the seed scale. It seems therefore possible, that within the Sequoioideae the abaxial meristematic groups (e.g. in a second row) develops ovules instead of the vegetative outgrowths, which appear in the same places in the Taxodioideae. The second row of ovules develops later than the first one and can therefore be regarded as an accessory shoot. In this case the seed scale consists of two fertile short-shoots, which develop one after another. Each of them is reduced to the ovules.

Sciadopitys was formerly placed in the monogeneric subfamily Sciadopityoideae within the Taxodiaceae (e.g. PILGER 1926). Due to several morphological and genetic studies this is no longer accepted today. In molecular family trees *Sciadopitys* does even represent a sister group to the Cupressaceae. Both families are separated by the Taxaceae (STEFANOVIC 1998, QUINN *et al.* 2002, RAI *et al.* 2008, YANG *et al.* 2012, LESLIE *et al.* 2012). In contrast to Cupressaceae *s. l.*, the bract-/seed scale-complex which is taken as a basis of the primitive coniferous seed cone is still distinctly developed in *Sciadopitys*. In *Sciadopitys* the seed scale is decisively involved in closing the cone (TAKASO & TOMLINSON 1991). Even at maturity the seed scale is still visible from outside.

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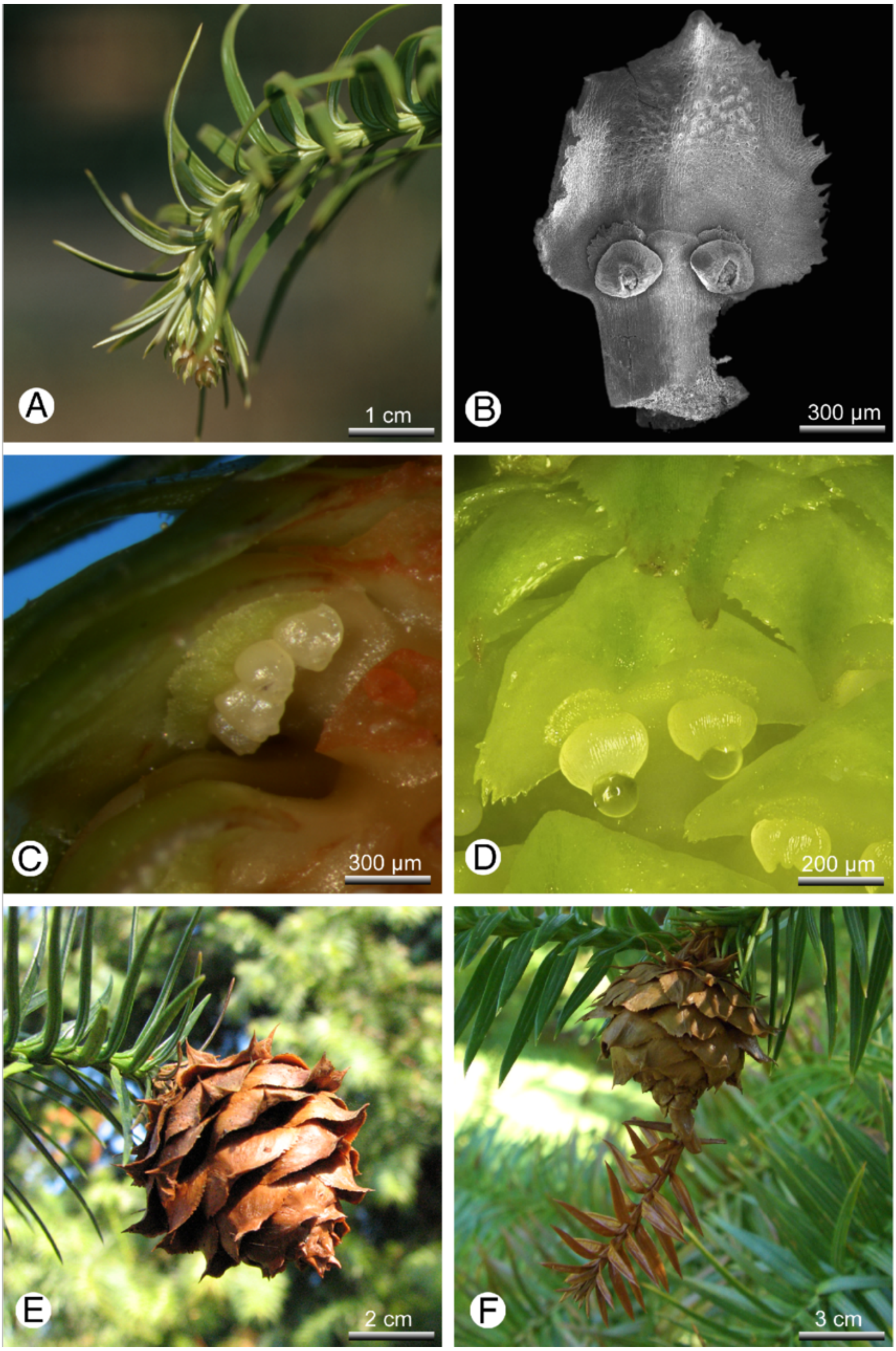

Fig. 1: Seed cone morphology of *Cunninghamia lanceolata*.

A: Receptive cone in the natural downward pointed orientation. **B:** Cone scale at pollination time with two ovules inserted on tongue-like structures; a third ovule between both aborted at a very early developmental stage. **C:** Cone scale with four ovules in the natural, downward pointed orientation at pollination time. **D:** Cone scale with two ovules with pollination drops. **E:** Mature cone. **F:** Mature cone with terminal proliferation.

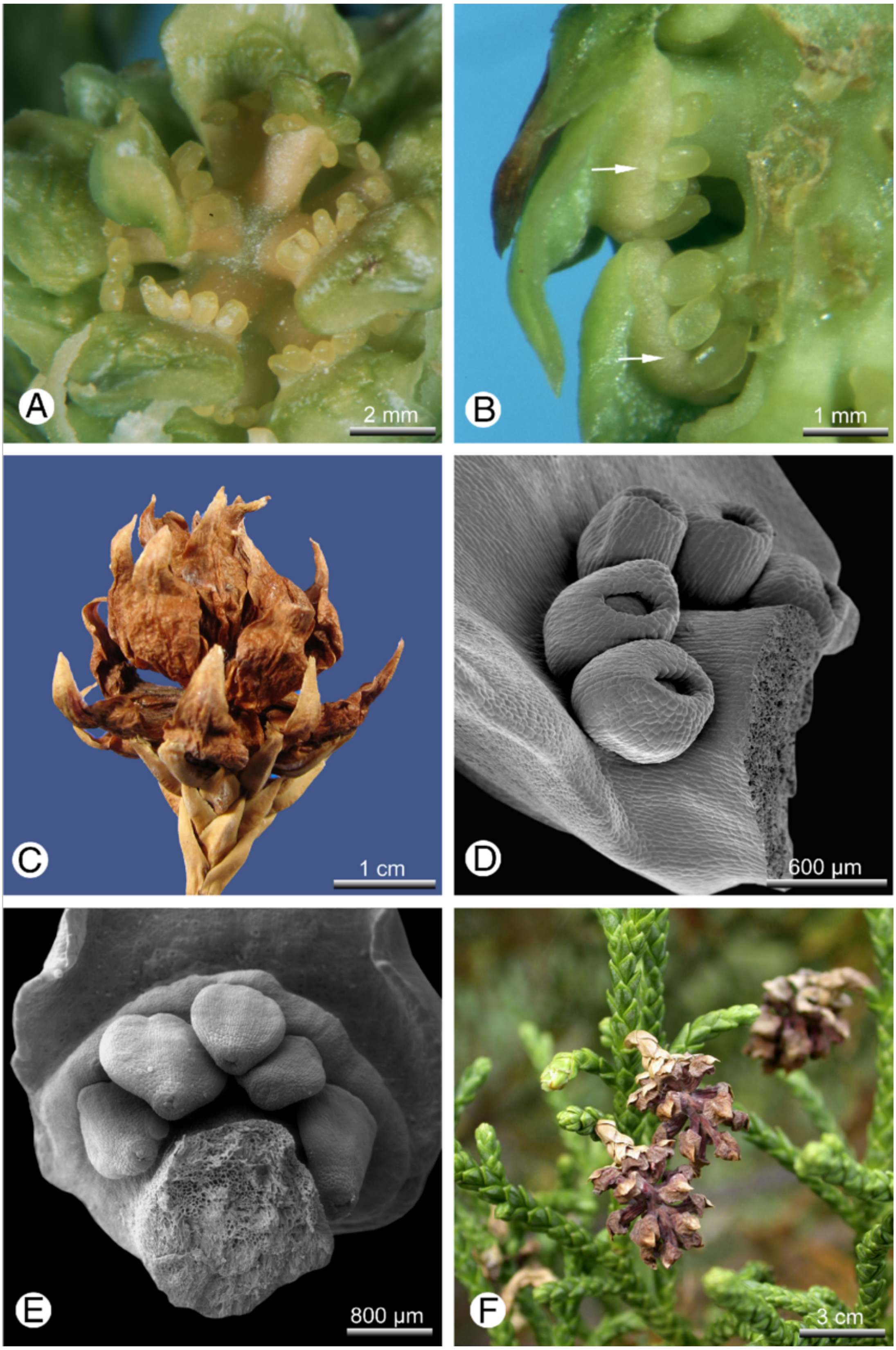

Fig. 2: Seed cone morphology of *Athrotaxis*.

A: *A. selaginoides*, top view of an open cone at pollination time. **B**: *A. laxifolia*, seed scales in the natural, downward pointed orientation, ovules inserted on a small seed cone bulge (arrows). **C**: *A. selaginoides*, mature cone. **D:** *A. laxifolia*, cone scale with young ovules, a seed-scale-bulge is not developed (SEM). **E**: *A. laxifolia*, cone scale with young seed just after pollination, seeds inserted on a seed cone bulge (SEM). **F:** *A. laxifolia*, mature seed cones.

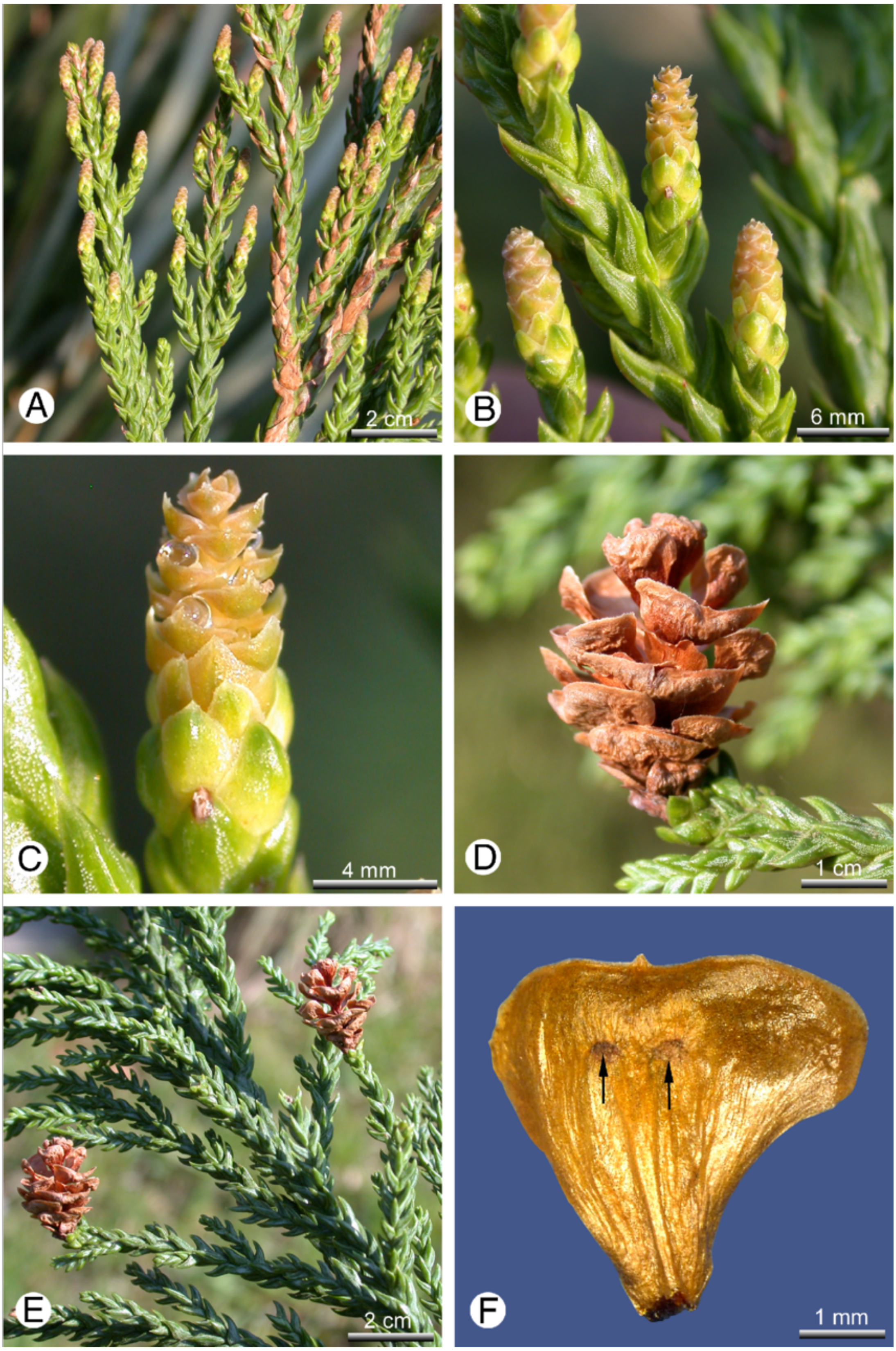

Fig. 3: Seed cone morphology of *Taiwania cryptomerioides*.

A: Fertile branch with several erect cones. **B:** Detail of A. **C:** Cone with pollination drops in the natural, erect orientation. **D & E:** Mature cones in lateral view in the natural erect orientation. **F:** Mature cone scale: the application point of the maturing seeds (arrows) were shifted in the distal part of the cone scale, thus the seeds turn into an inverse position.

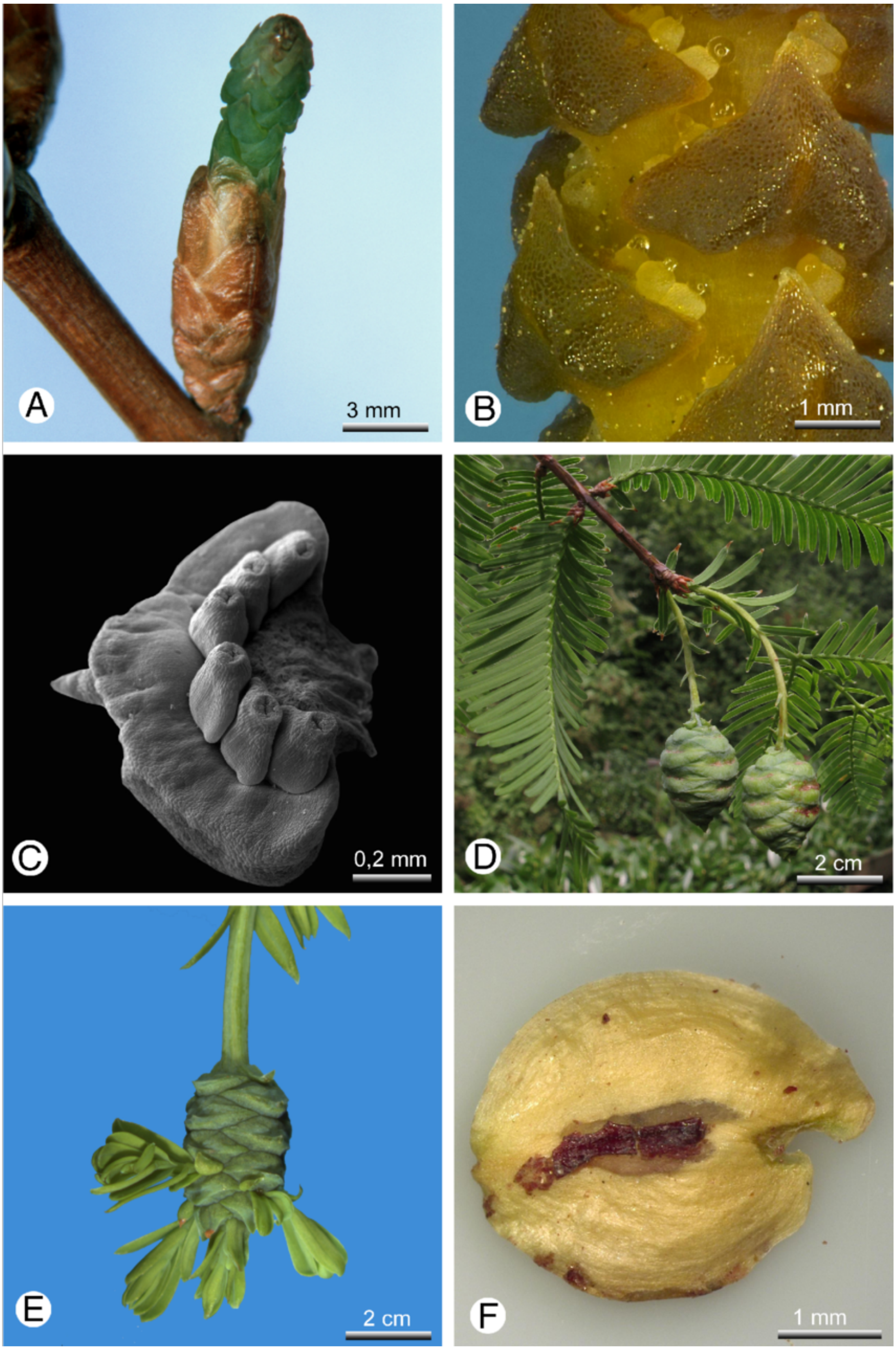

Fig. 4: Seed cone morphology of *Metasequoia glyptostroboides*.

A: Receptive cone in the natural erect orientation. **B**: Pollination drops are exposed within the cone. **C:** Cone scale at pollination time, ovules inserted in one row (SEM). **D**: Maturing cones in the natural, downward pointed orientation, **E:** Rare specimen with strongly proliferated seed cone. **F:** Winged seed.

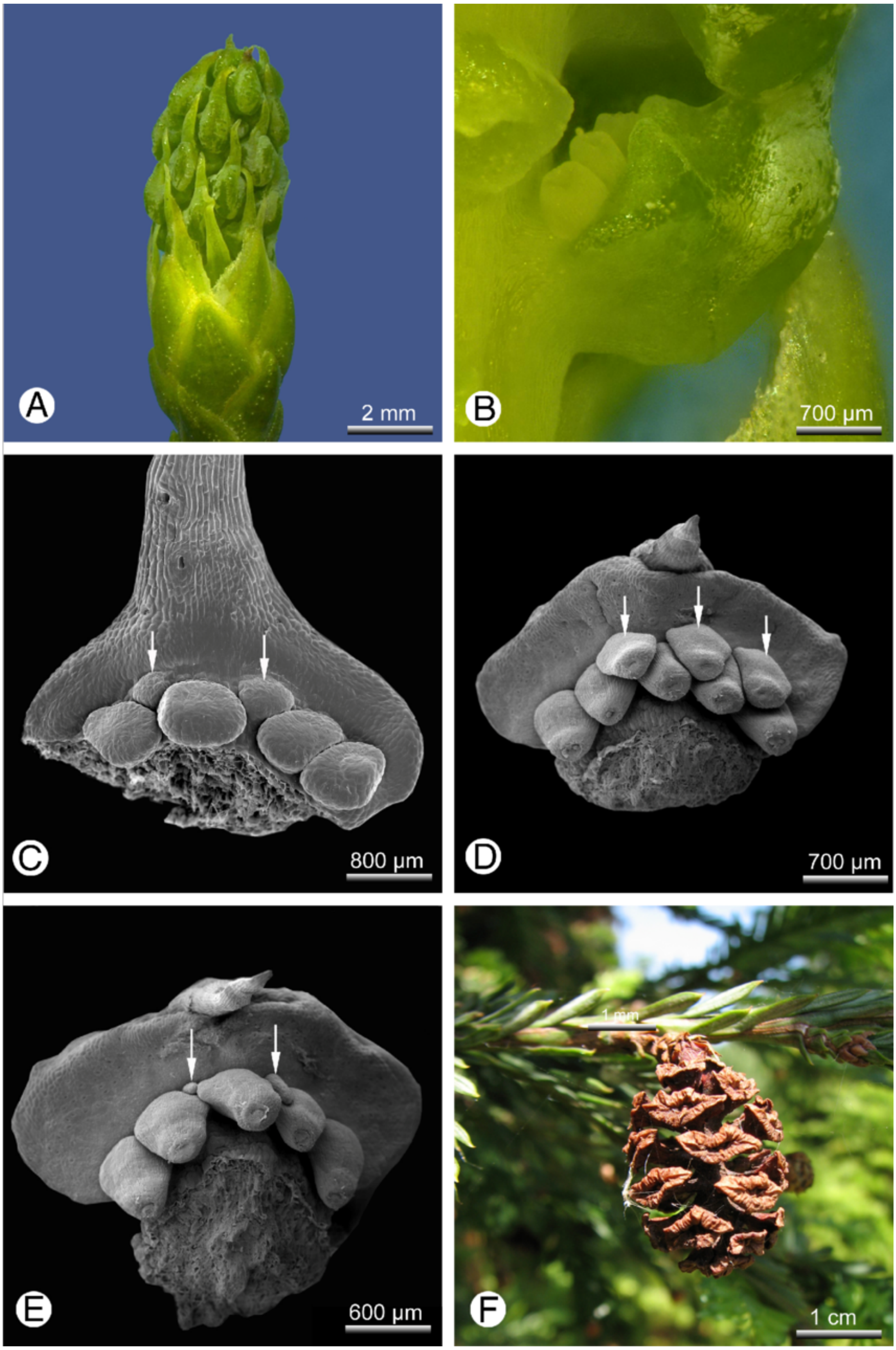

Fig. 5: Seed cone morphology of *Sequoia sempervirens*.

A: Receptive seed cone in the natural, erect orientation. **B:** Ovules and pollination drops developed deeply within the cone. **C:** Young cone scale, the second row of ovules (arrows) develops later than the first one (SEM). **D:** Cone scale at pollination time with a second row of ovules (arrows) (SEM). **E:** Cone scale at pollination time, the second row of ovules is aborted (arrows) (SEM). **F:** Mature cone with several spirally arranged cone scales.

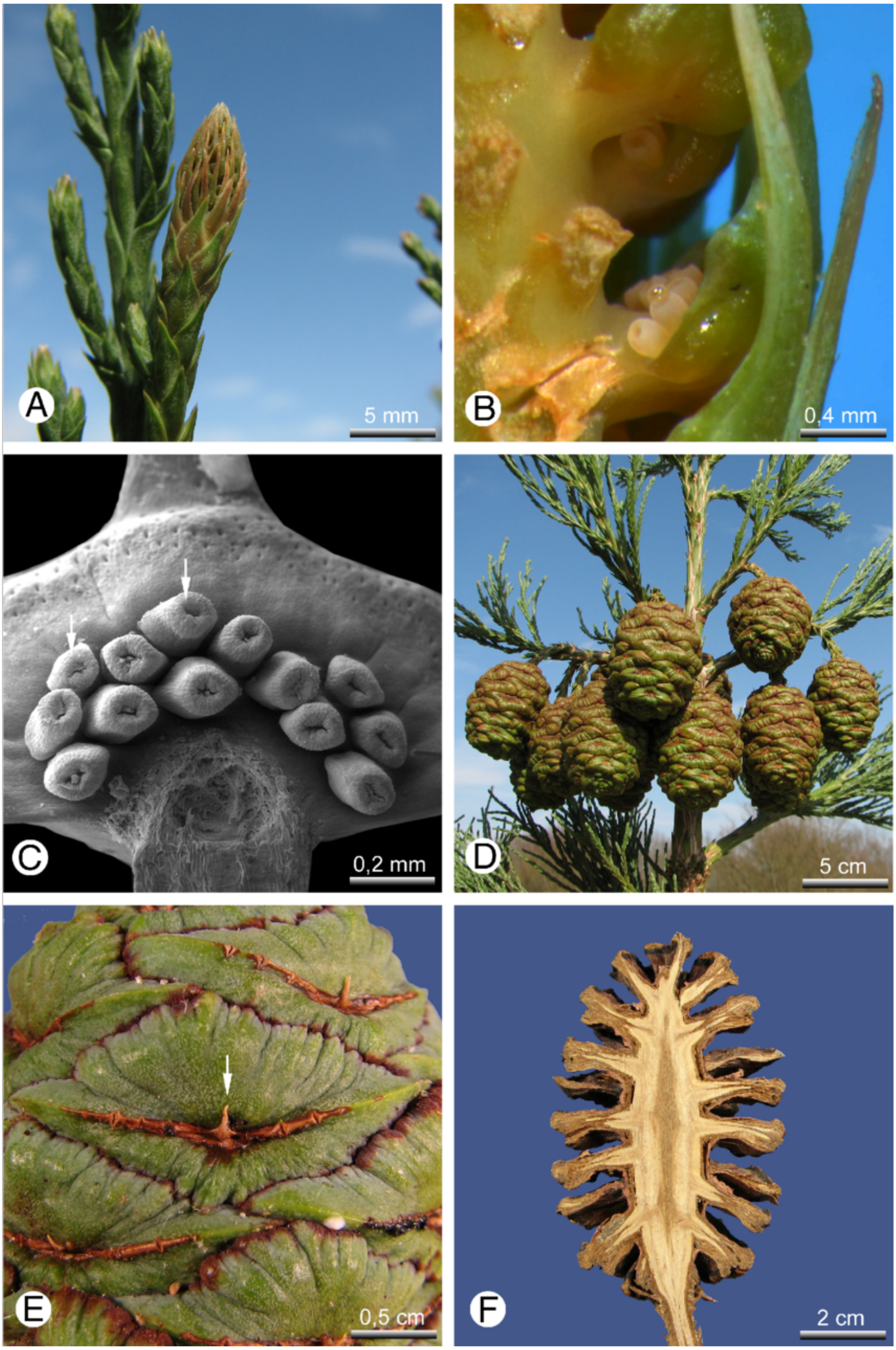

Fig. 6: Seed cone morphology of *Sequoiadendron giganteum.*

A: Receptive seed cones in the natural, erect orientation. **B:** Ovules and pollination drops developed deeply within the cone. **C:** Cone scale with a third row of ovules (arrows). **D:** Mature seed cones are downward oriented. **E:** Detail of a mature cone scale from outside; due to the ventral bulge developed on the adaxial side, the tip of the young cone scale is shifted to the middle of the mature cone scale. **F:** Longitudinal section of a ripe cone; the drying out of the cone scales opens the cones.

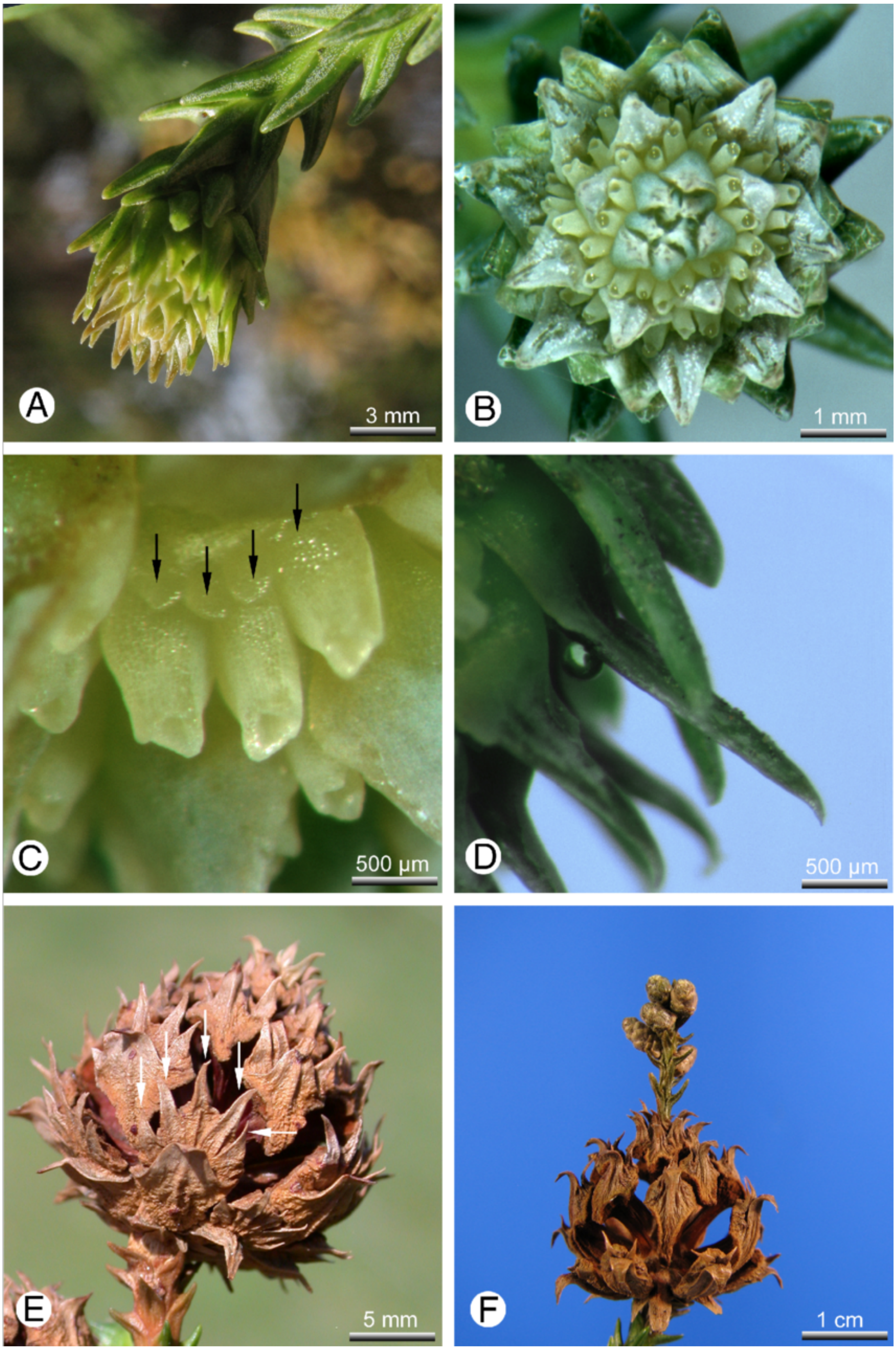

Fig. 7: Seed cone morphology of *Cryptomeria japonica*.

A: Cone at pollination time in the natural, downward pointed orientation. **B:** View onto the showerhead-like receptive cone with pollination drops. **C:** Three ovules and tooth-like structures (arrows) in the axil of a bract scale (bract scale removed). **D:** Pollination drop in lateral view. **E:** Mature cone in lateral view with strongly developed teeth of the seed scale (arrows). **F:** Rare mature cone with terminal proliferation carrying pollen cones.

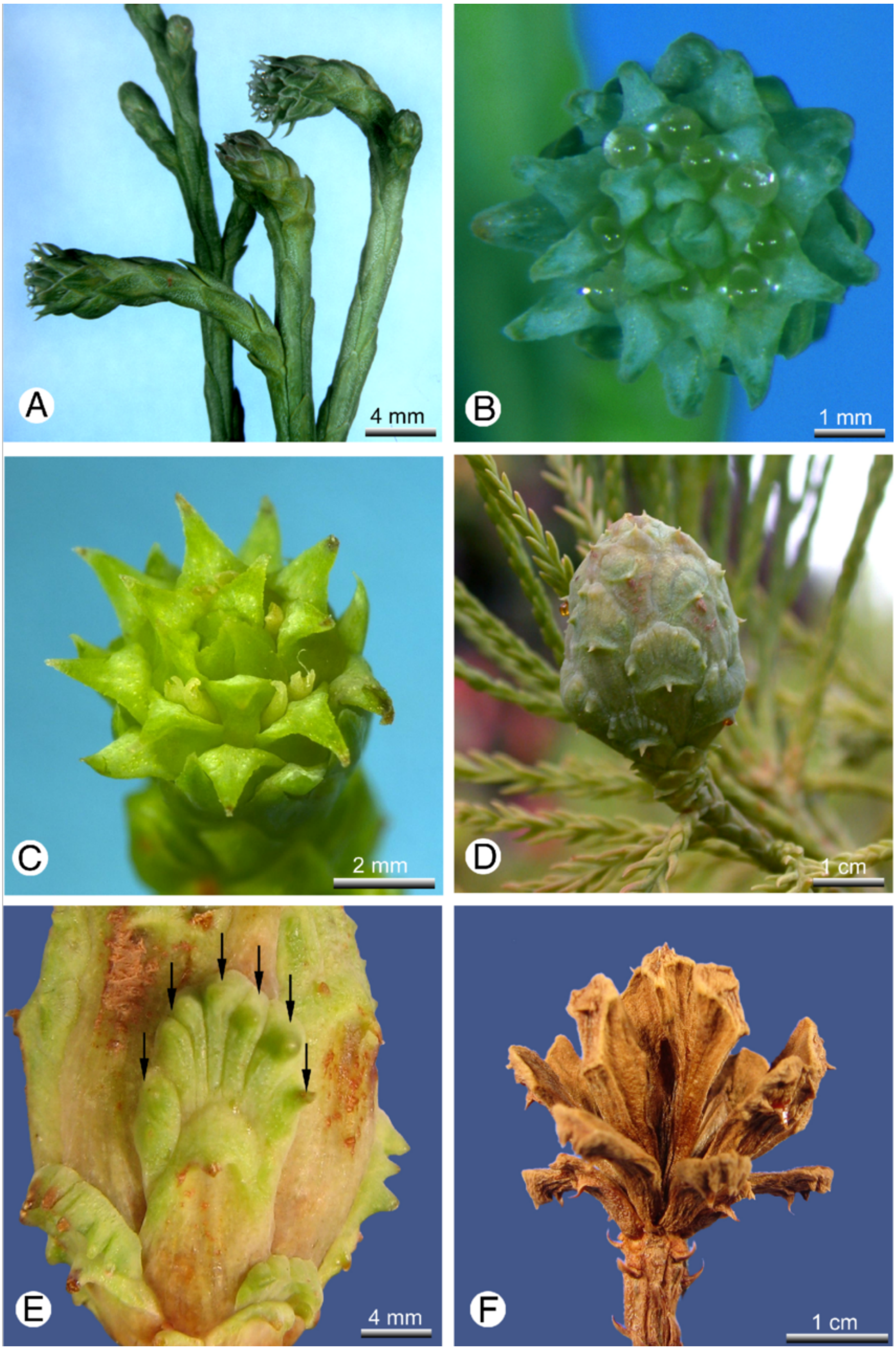

Fig. 8: Seed cone morphology of *Glyptostrobus pensilis*.

A: Cones with pollination drops in the natural, plagiotrop orientation. **B:** Receptive cone with pollination drops. **C:** Cone just after pollination. **D:** Immature cone in the natural, erect orientation. **E:** Cone scale with teeth-like outgrowths of the seed scale (arrows). **F:** Open mature cone.

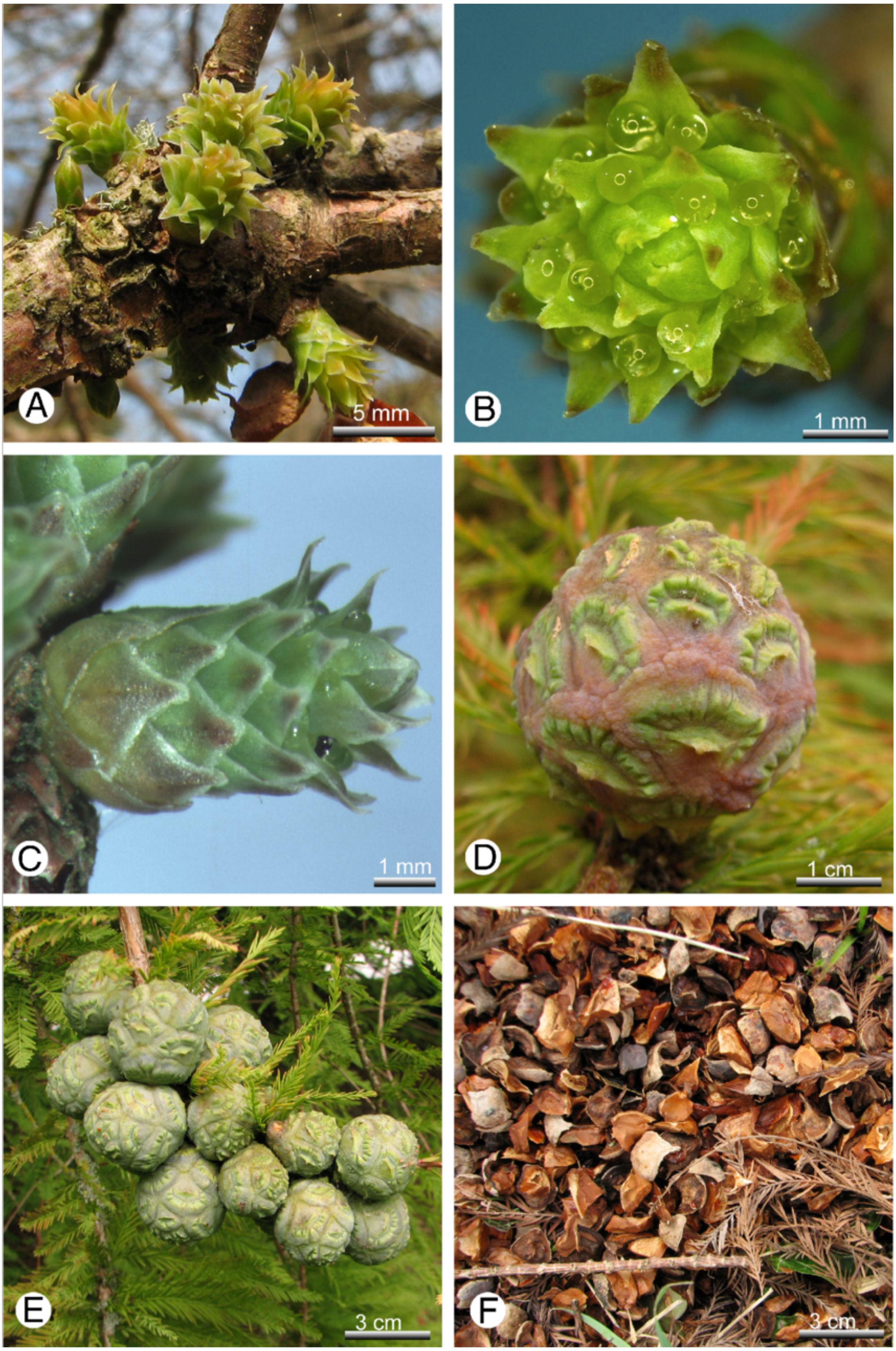

Fig. 9: Seed cone morphology of *Taxodium distichum*.

A: Receptive cones with pollination drops, top view. **B:** Receptive cones with pollination drops, lateral view. **C:** At pollination time cones arranged in an irregular position on the branch. **D:** Immature cone on a branch. **E:** Seed cones are often developed in clusters. **F:** After disintegration of the ripe cones, several cone scales are covering the ground.

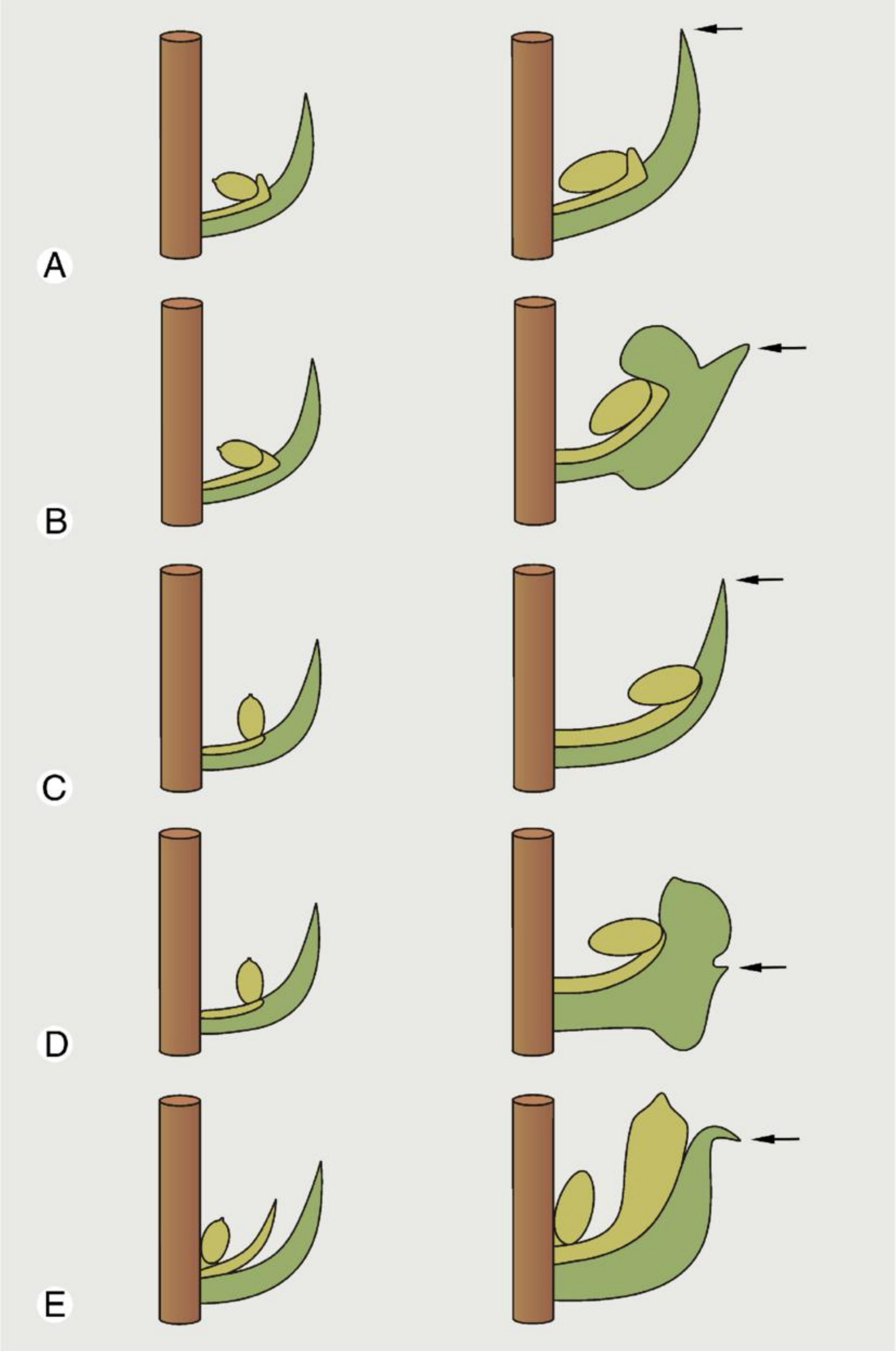

Fig. 10: Development of the bract/seed scale complex in taxodiaceous Cupressaceae, schematic, **left:** cone at pollination time; **right:** cone at maturity; arrow marking the tip of the bract scale; bright green = parts of the seed scale; dark green = parts of the bract scale. **A:** *Cunninghamia*, at pollination time ovules already in an inverse position, bract scales remains flat. **B:** *Athrotaxis*, ovules already in an inverse position at pollination time; bract scale with a strongly developed distal bulge when maturing. **C:** *Taiwania*, ovules erect at pollination time, seeds inverted at maturity, bract scale without a distal bulge. **D:** Sequoioideae: ovules erect at pollination time, seeds inverted at maturity, bract scale with a distinct distal bulge. **E:** Taxodioideae, ovules and seeds erect, inserted in the bract scale axil together with the tooth-like structures, seed scale consisting of two short-shoots, tooth-like structures of the seed scale and the bract-scale strongly swollen at maturity.

BULLETIN of the *CUPRESSUS* CONSERVATION PROJECT
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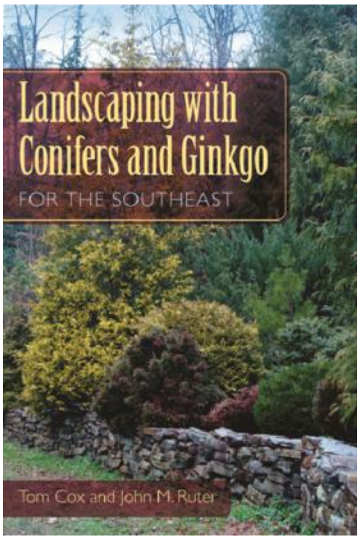
D. Maerki

BOOK REVIEW

– '**Landscaping with Conifers and Ginkgo** for the Southeast'

by **Tom Cox** & **John M. Ruter**



16.4.2013, University Press of Florida, 296 pp.
ISBN: 978-0-8130-4248-0
Soft cover. $29.95

The purpose and the scope of this book are perfectly described by its title: to provide advice on which conifers to use in the south-eastern US climate, that is warm and moist summer, with freezing temperatures going down occasionally to -15°C (hardiness zone 8) in winter. Not all species will like these conditions. In fact this kind of climate favours several diseases especially for plants adapted to drought, and it is not fit for most high altitude trees. Usually it is necessary to wait at least 30 years before being reasonably confident that a species will thrive – or let alone survive – at any given locality. Here Tom Cox [1], with co-author John Ruter [2], thanks to his experience of managing an arboretum since 1990, is providing a thorough list of conifer species. For any botanical garden or arboretum this kind of information is important, for it will help to decide which species to introduce in priority. Obviously in Georgia the exotic origins to privilege are from similar climates like those of southern China and Japan and likely some localities in Mexico.

Cupressus glabra 'Blue Ice'
Cox Arboretum, Georgia, USA.

The book is divided in four parts: planting advice, pests and diseases (in two different chapters), a list of conifer species and their cultivars, and several interesting and useful appendices.

After the introduction, the chapter *Cultural Practices* gives a lot of meaningful and detailed instructions on how to plant and care about the newly acquired conifer seedlings or saplings. Whatever the advice, gardeners will seldom agree with everything. There are many different kinds of soil and certainly with their experience the authors know which is the best advice in their local condition, that is with a heavy clay soil. The following recommendation (page 8): "If a plant is going to adapt to our soil, then the best way to acclimate it is to get the roots spreading into native soil from Day One", is excellent for any type of soil. Except for a heavy clay soil, I will not recommend to dig a planting hole twice as wide as the root ball as it is preferable that the native soil will be least disturbed. A too large planting hole will require more watering as the disturbed soil will become dry more quickly than the undisturbed soil. About fertilisers, I think that they are useless or even counterproductive, except in very special cases, for instance when it is necessary to promote root growth. For a healthy tree, there should be a balance between the roots and the foliage. Fertilisers will boost the shoot and foliage growth, eventually weakening the tree in case of storm or snow. In nature no chemical fertiliser is available. The last disagreement is on the use of such chemical like glyphosate. In no case I would recommend it. There are alternative means like mulching or special fabrics. Once established a tree will care itself by shading the place.

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[1] Former president of the American Conifer Society, owner of the Cox Arboretum in Georgia.
[2] Professor of Horticulture at the University of Georgia.

The *Pests* and *Diseases* chapters are targeting the health problems encountered in the south-east USA and are to the point, with an illustration for almost every kind of damage cited. To be noted that the use of the imidachloprid systemic insecticide is controversial and that miticides are useless in a non degraded environment. In the wild, carnivorous mites will soon control much better the mites which feed on conifer leaves. In nursery conditions, the problem is real.

The main part of the book is dedicated to the different conifer species and their cultivars adapted to the south-east region. The species are sorted by their alphabetical Latin names. Here at the *Cupressus* Conservation Project, we are least interested by cultivars and most interested by endangered conifer species, and of course by the genus *Cupressus*. To each his own. So several cultivars[3] are presented, and surely the local gardeners will find this choice interesting to be able to accommodate not too big plants around their house.

Cupressus funebris , Cox Arboretum, Georgia, USA.

It is a pleasure to see American authors acknowledging the genus name *Cupressus* for the new world species. Giving its original Latin name of *Cupressus nootkatensis* to the Nootka Cypress (unfortunately here as "Alaska-cedar"[4] for the common name instead of D.Don choice) allows to describe the cultivated hybrids as *Cupressus* hybrids and not intergeneric ones. Further (page 99), the description of the taxonomic mess for this genus is correct: "Depending on which taxonomist one goes with, the exact number of species and varieties can be a moving target. Much of the disagreement appears to stem from variation in and among relictual populations that have been historically subject to an array of naming and classification schemes. Probably no conifer genus has engendered more taxonomic treatment." Twenty-four taxa of Cupressus are mentioned here, nine less than the species recognised by the CCP.

Unsurprisingly the number of cypress taxa presented is fairly low: 5 species and 3 hybrids. Most Californian species for instance do not do well in south-eastern climate as already experienced in Texas (Lovett Pinetum in Angelina County). At the Tifton arboretum (nine taxa mentioned), *Cupressus macrocarpa* and *Cupressus dupreziana*[5] were "removed due to poor health" (page 272).

Six appendices complete the volume: Heat Zone and Hardiness Zone maps, Conifer sizes, Selection of conifers based on landscape application, Nursery sources and conifer gardens in the South, Growth data for conifers at Tifton arboretum, Georgia. In the list of species growing in full shade, the following genera shall be added: *Cephalotaxus*, *Taxus*, *Torreya*. They are understory taxa with an initial slow growth. As seedlings, several *Abies* and *Picea* species are adapted to such conditions too, but only a few species of those two genera will thrive in the south-eastern climate. Aside the nursery list, seed sources would have been welcome too.

Despite being critical on some details, 'Landscaping with Conifers and Ginkgo for the Southeast' is highly recommended for any person caring to enrich his garden with conifers as well as for botanic gardens and arboreta which will find safe advice for developing their collection.

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[3] For instance, there are 24 cultivars listed for *Cryptomeria japonica*, 13 for *Chamaecyparis obtusa* and 8 for *Cupressus glabra*, when every wild type is described on one page or less, but always with interesting observations.

[4] The common name cedar shall be kept for the genus *Cedrus*, which is a Pinaceae, not a Cupressaceae. For the same reason as one would not call a whale a fish.

[5] And please, not *Cupressus sempervirens* var. *dupreziana as Cupressus sempervirens* and *Cupressus dupreziana* cannot hybridise.

Cupressus tortulosa. Isola Madre. Fresh seeds received in 1862. The instructions recommended sowing them immediately. Note the changing colour of the foliage depending on the light. The photo is taken from the north-east corner of the square. The unbalanced crown is the result of the fall of the tree on the left. A panel explains the rescue work that was engaged immediately after the fall of the tree in June 2006. 25.8.2014.