Bulletin of the *Cupressus* Conservation Project

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Cover photo: *Cupressus stephensonii*, cultivated, France, 18 September 2018. © CCP.

Bull. Cupressus Conservation Proj. 7 (2): 47-56. (2018-12) **D. Maerki**

Cupressus stephensonii pollen and seed cone phenology

Except for the most common species planted in urban areas where pollen release poses health concerns because of allergies (Hidalgo *et al.* 2003; Aboulaich *et al.* 2008), there is almost no information on cypress phenology for most species with regard to the pollination periods. Farjon (2005) is mute on this subject. Little (2005) is the only known author trying to give systematic data. Unfortunately the data are too often missing ("Phenology unknown"), while more seldom they are erroneous. When confronted with the investigation on the seed cone development of cypress species, one of the main problems resides in the fact that several populations have a very restricted area of occupancy and/or are very difficult to access, especially when it is necessary to carry observations over more than one year, and often even more than 24 months, from the pollen cone initiation to the opening of the mature seed cones (when the cones are not serotinous). Some species seem to pollinate during the same period (same season) whatever the climatic conditions or the differences in latitude or altitude (e.g. *Cupressus sempervirens* L.). Some first observations give hints that it may not be the case for every *Cupressus* species or that unusual climatic conditions (such the one over Europe during the winter 2015-2016 with very mild temperatures) could trigger shifts in the pollen cone initiation or in the pollination period. Usually botanical gardens display one specimen of one species and in the best cases, a few of them. Thus it is possible to record data on the pollination time of one tree, but not on the whole period during which the pollination of an entire population is occurring. This kind of information is very important to understand when there is a natural and phenological reproductive isolation of one population *versus* others, allowing over time a speciation process.

Currently there is no information on the necessary number of months after pollination for the seeds to begin being fertile. When the cones are not serotinous, seed cone opening is a clear indicator that the seeds are fully mature. Usually this seed cone opening happens only after 22 months. Before 12 months it is usually assumed that the seeds are not viable. On the other hand, seeds collected before cone opening proved once to be fertile (20 months after pollination and 4 months before cone opening). At maturity the seeds are usually a dark colour (brown or black, sometimes glaucous). During the maturing process, the seeds are light yellow turning light brown before becoming darker.

This article is the first of a series which will be published as observations continue.

On *Cupressus stephensonii* C.B.Wolf, Little (2005: 208) states: "Phenology unknown".

Wolf (1948: 125) in his diagnosis does not give information on the pollination period on the Cuyamaca Peak slope, the native habitat of *C. stephensonii*. He records: "Following pollination the cones soon turn from green to brown and attain a diam. of about 10 mm the first season." No date is given, but this observation fits the growth of the seed cones in spring.

Reveal (1978: 21) gives the following information: "In Cuyamaca cypress, pollination takes place in early fall, apparently before the end of September."

The observations reported here on *C. stephensonii* were made over several years on cultivated plants in the south of France at an altitude of ca. 600 m in a Mediterranean climate with oceanic influence. There are more than 200 specimens, with new trees starting to produce cones every year. The first trees were planted in July 2000. More specimens were planted during the following years and installation of new seedlings continues to this day. The first Cuyamaca Cypresses planted began to produce seed cones around 10-12 years after plantation, while some specimens planted later showed a shorter period between planting in the field and first seed cone production, with considerable differences between individuals. The seedlings spent usually 3-4 years in the nursery and are 30 to 60 cm high when planted out. Massive pollen release occurs from the beginning of July to mid-August with a maximum shift of two weeks between the years. Not all specimens are releasing their pollen at the same time, allowing a total pollination period of 4 to 5 weeks for a group of trees any given year. For instance one specimen still shrubby (1.6 m high, less than 0.8 m wide; see Fig.6) compared to its surrounding neighbours planted at the same time (to 5 m tall, several metres wide), began to pollinate at least one year before the others, and keeps pollinating every year one or even two weeks before the closest specimens.

Initiation of the pollen cones happens at the beginning of spring, between end of March and the middle of April. Just before pollen release the pollen cones have a marked quadrangular form, with the base larger than the distal end, the yellow pollen sacs protruding between the very light green scales, giving the cones the shape of a small step pyramid (see Figs 7 & 8). By mid-August all pollen cones are open and almost empty. After pollen release the scale colour turns from light green to light brown. The yellow colour seen from a distance is given by the pollen sacs when they are still closed and protruding between the scales. One specimen releases its pollen during a peak period varying between 5 to 8 days. In 2016 the last tree ended its pollen release around the 3 August. In 2015, pollen release happened with a shift one week later. In 2013 the pollen cones were all open in mid-August only. A few pollen grains can remain in the open cones depending on the wind exposure.

Fig. 1: Young seed cone in January. 2012-1-8.

During initiation, while still green, the seed cones are rather inconspicuous compared to some other species at the same stage (e.g. *C. macnabiana*). The seed cones are positioned on a peduncle on a branchlet grown the previous year from a main shoot. The first peduncle in a proximal position on that branchlet is typically more or less parallel to the main shoot with the seed cone pointing forward to the outside of the crown (Figs 1, 19 & 20). When there is more than one seed cone on a branchlet, the next peduncle is disposed either opposite to the first one or on the next even whorl of leaves (Fig. 20). Different dispositions were observed when the seed cones become more numerous on a branchlet. At pollination time the colour of the scales is variable from a dull yellow (Fig. 9), light brown to greyish (Fig. 12).

After pollination, the fertilised seed cones do not develop until the next spring, while any not pollinated are aborted. It is not possible to distinguish aborted cones from fertile ones before the end of the next winter. The top of the ovules are still visible between the bract-scales until April (Figs 1 & 21).

When the first year seed cones resume their development in spring they turn first to a dull light green and later to a brighter and darker colour (Fig. 21). Their size increases quickly from April. During summer, brown patches appear around the umbos until the cones get fully leathery and bright brown before fall. This colour change is hastened by direct sun exposure. Later the weathered cones become grey and some marks will appear (Fig.17) as the outer surface gets drier. Wolf (1948: 125): “At maturity the cones are a dull gray or brown, and the surface is somewhat roughened or warty”.

Diagram 1 (p. 49) summarises the seed cone phenology of *C. stephensonii*.

When seeds become viable, is still not tested for this species.

This seed cone development is quite unusual among the cypress species as several of them (the most common ones in cultivation) release their pollen in February-March (e.g. *C. sempervirens*, *C. glabra* Sudworth, *C. funebris* Endl., *C. macrocarpa* Gordon, *C. pygmaea* (Lemmon) Sargent, etc.), and the seed cones start their development immediately and quickly to attain their final size in the following months.

In the climatic conditions where *C. stephensonii* was observed for this research, it is the only New World *Cupressus* species beginning to release its pollen systematically in July.

C. stephensonii seed cones are actively serotinous[1], a known fire adaptation in a seasonally dry climate during summer like the Mediterranean one. The cones remain closed as long as they are vascularised. As with other species (e.g. *C. sempervirens*), it is often possible to see a few open cones on the branches when their vascularisation is interrupted. Extreme drought, extreme cold and/or excessive heat can have more or less the same effect as a fire, as can insect damage to the cone.

First described as a species by Wolf (1948), some authors reduced *C. stephensonii* to a synonym (Little 1953) or to a variety of *C. arizonica* Greene (Little 1966, 1970; Farjon 1998, 2001, 2005, 2010; Farjon & Filer 2013). Apart from the fact that the distribution ranges of both taxa are widely separated (by around 500 km), reproductive isolation is completely assured by the respective pollination periods which do not overlap at all. A **specific** barrier is thus established between the two taxa. There are other distinctive characters which separate *C. stephensonii* from *C. arizonica*, such as habit, size, growth rate, first production of cones, number of cotyledons, etc.

C. stephensonii is endemic on the Cuyamaca Peak west slope, San Diego County, California. Although it is adapted to fire, the population was reduced by several fires to only some 800 to 1000 trees by 2000. The Cedar fire in October 2003 then destroyed most of these. leaving about two dozen individuals on the King Creek slope and just about one hundred at a higher elevation where they are growing between rocks with minimal vegetation around them. The scarcity of the fuel preserved this limited population in 2003. The following years, regeneration happened at a very slow pace (contrary to what took place with *C. forbesii* at Coal Canyon, Orange County, California, where regeneration was immediately massive). Any new fire within the next years would put this species in danger of extinction in the wild, when there would not be enough time for the trees to produce new cones to reconstitute the seed load.

Some authors consider the population of *C. revealiana* (Silba) Bisbee in Baja California to be identical to *C. stephensonii* after examination of herbarium material. Not only does *C. revealiana* not release pollen in summer, but the seed cones show a completely different phenology and morphology in very similar environmental conditions (see Figs 3-5, 25-26 & 27-28 – Bisbee & Maerki 2012a, 2012b). Molecular analyses also confirm the species status of both *C. stephensonii* and *C. revealiana* (Adam *et al.* 2014; Terry *et al.* 2016).

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[1] By opposition to strongly serotinous, when the cones need fire to open (e.g. *C. forbesii*).

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Fig. 2: *Cupressus stephensonii* pollen cones. 2016-7-15. This specimen was the last one to release its pollen at the beginning of August in 2016. See close-up scans of the cones: Figs 7-8, p. 50.

Diagram 1: *Cupressus stephensonii* seed cone phenology from pollination to maturity

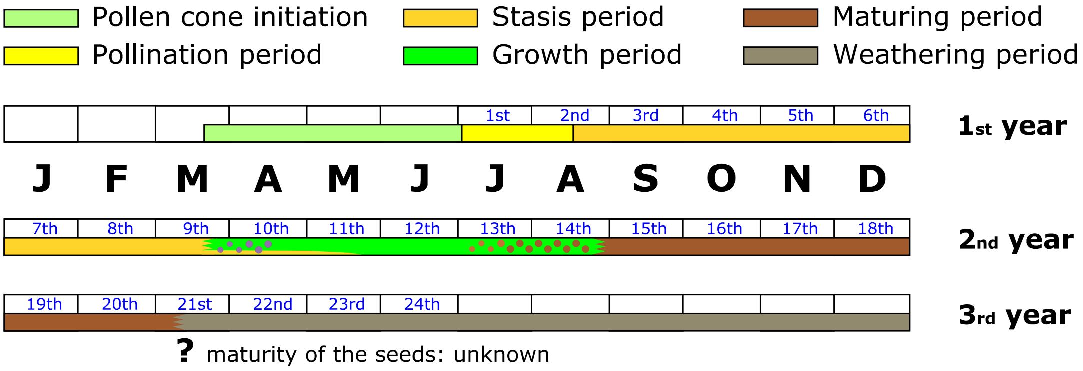
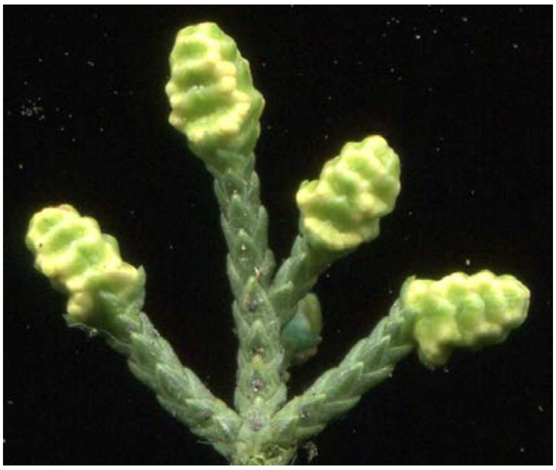


Fig. 3: *Cupressus stephensonii*, seed cones pollinated one year ago. 2016-7-9.

Fig. 4-5: *Cupressus revealiana* seed cone. Photos taken the same day as Fig. 3, showing the differences between the two species.

Fig. 6 (left): One of the first Cuyamaca Cypress to release its pollen in July. 2016-7-9.



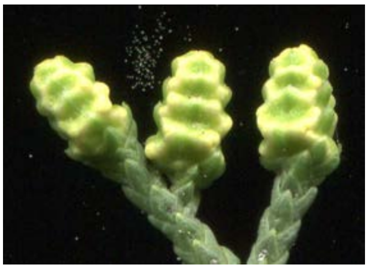


Fig. 7 & 8 (on the right): Pollen cones at pollination time (dots are pollen grains). 2016-7-22.

Fig. 9: Seed cones showing pollination drops. 2013-8-10.

Fig. 10-11: Pollen cones after pollen was shed. 2010-8-10.

Fig. 12: Seed cones after pollination. 2010-8-10.

Fig. 13 (middle right): One year seed cones and pollen cones still closed. 2013-8-4.

Fig. 14 (right): Seed cones and pollen cones. While the proximal pollen cones are already open and have changed colour, the distal ones are still closed. 2013-8-4.

Fig. 15: *Cupressus stephensonii* seed cones beginning to change their colour. 2013-8-4.
Fig. 16: Same cones as Fig. 15 eleven days later. 2013-8-15.

Fig. 17 (right): Seed cone of *C. stephensonii* two full years after pollination. The seeds were still not fully mature as shown by their light brown colour. 2016-8-15.

Fig. 17a (left): Seeds of *C. stephensonii* from a cone collected in July 2018. Mature seeds have a darker brown colour.

Fig. 18: Seed cones of *Cupressus stephensonii* at the end of the pollination period. The number of pollen and seed cones is increasing with the growth of the tree. 2016-8-15.

Fig. 19: *Cupressus stephensonii* first seed cones, in winter. Note the seed cones pointing in the same direction, parallel to the main shoot. Peduncles with 9 to 11 pairs of decussate leaves. 2008-12-23.

Fig. 20: Close-up of Fig. 19, showing more details.

Fig. 21: *Cupressus stephensonii*, seed cones nine months after pollination. 2018-4-18. On the left, a yellow aborting cone.

Fig. 22: *C. stephensonii* one year old cone and inconspicuous seed cones two months after pollination. 2018-9-19.

Fig. 23: *Cupressus stephensonii* covered with pollen cones. 2016-7-15. Note the other trees with few or no pollen cones.

Fig. 24: Same tree as on the previous photo, with empty pollen cones. 2016-9-4.

Fig. 25: Empty pollen cones of *Cupressus stephensonii*. 2016-9-4.

Fig. 26: At the same date as the previous photo: pollen cones of *Cupressus revealiana* still in their initiation stage. Note the difference in the branching patterns. 2016-9-4.

Fig. 27: *Cupressus revealiana* seed cones. 2016-9-2. Note the closed yellow pollen cones and the light brown aborted seed cones. Planted 2010-10.

Fig. 28: *C. stephensonii* seed cones on a sapling. First cones smaller than the cones on mature trees. 2016-9-2. Planted 2009-7.

Fig. 29: *Cupressus glabra* whose seeds were sold as *Cupressus stephensonii* in 2010. Note that the pollen cones are still in their initiation stage. Photograph taken the same day as the ones above (2016-9-2).

Cf. in this issue:
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J. Malone

Cupressus revealiana El Rincon, Sierra Juarez, Baja California Sur, Mexico: trip report

In November 2016 a trip was made by myself and Alan Rockefeller to the Sierra Juarez of Baja California, Mexico to visit the little-known population of *Cupressus revealiana* (Silba) Bisbee. Little information regarding this population was available in the literature and very few photographs were available online. Jeff Bisbee, who had formerly visited the Arroyo that runs southwest of the Mesa which main population of this grove grows on, had pointed out the region and area of the Sierra Juarez where this species is known to occur. The main population was reported to occur mainly on top of a Mesa – one of two mesas which together form a small "valley" between them – easily and clearly distinguished from both topographical maps and Google Maps Terrain View. Though Jeff had not personally visited the main population up on top of the Mesa, he had seen quite a few trees which were growing in the arroyo that serves as the main drainage of this Mesa, which is to the north/northeast of what constitutes the main road (a very rough one!) into the “valley” which exists between the two mesas.

There is a small ranch house located at the end of the road, right on the arroyo. We spoke to the man there, and like most Mexicans I have encountered on this trip, he was rather welcoming and friendly and did not seem to have a problem at all letting us into the gate (which was locked) which led to the small road that parallels the arroyo that the cypresses grow in. There is also a cypress or two growing near the ranch house. The man in the ranch house seemed to be aware of the rare nature of the trees and know that they were somewhat remarkable.

Fig. 1: *Cupressus revealiana*, 1st year cones. 2016-11-16.

We drove up the road past the gate a ways, maybe a mile or two, at which point the road became quite rocky and unpleasant to drive on anymore; here we pulled off the road into the scrub best we could and parked. At this point we were seeing quite a few cypresses growing in the arroyo, which indicated to us that there were many more up ahead, since water (i.e. running creeks and streams) is the only effective seed transport mechanism for most North American Cypress species. The “bread crumb trail” of cypresses in the wash seemed to indicate that the main population was located further up the creek, to the northeast, up on top of the mesa. We got out of the truck and walked, staying to the right.

It also became apparent that there was a trail – whether made by cattle or by the ranchers – which seemed to veer towards the right drainage (there were two drainages at this point as we slowly ascended up the arroyo. One drainage splits off and up to the left, the other off and up to the right. It was also apparent that the majority of cypresses were off to the right, with virtually none in the drainage off to the left (none were apparent, though there may indeed be more off to the left, which was geographically north – the drainage to the right was geographically northeast).

The trail climbs the center ridge which comprises the “fork” separating the two drainages and then circles around and proceeds to the east/south-east, finally opening up to a small meadow/basin area comprised of a bushy *Artemisia* species and bunchgrasses, with some rather large and exceptionally looking cypress trees on the margins of the small meadow/depression. It is to the west of this meadow that the top of the mesa “spills over” and drains to the valley below and to the west via a gulch which is flanked on both sides on the way down by cypresses. This geographical situation is visible via Google satellite map of the top of the south Mesa. The elevation of the “meadow” area on top of the Mesa is roughly 1200 meters.

Proceeding south down the dry creek-bed on top of the Mesa, cypresses become very abundant, along with oaks, namely *Quercus peninsularis*. The geology here is a red, intrusive igneous rock (almost a type of red granite) apparently fairly rich in iron, and the walls of the small canyon are comprised of large boulders of this material. Further south down the drainage, there are cypresses of varying ages, some very large and some rather small. Estimates would likely put the number of trees at > 3000, all appearing healthy, as opposed to some of the trees down in the valley appearing parched, sparse or dying.

Though there is a man-made trail up into the main grove of cypresses on top of the Mesa, human presence here seems to be minimal, and the overall area is rather pristine and undisturbed. We had traveled a bit further south down the creek-bed on top of the Mesa, seeing that the mesa gradually seemed to descend before (presumably) dropping off on the east side. We turned around as the sun would soon be down and watched a very beautiful sunset in a pink and orange sky from atop the Mesa before descending again through the scrub back to the arroyo and the truck.

Overall this is a very healthy population of trees, up on top of the Mesa, with a somewhat sparse, more stressed population growing in the arroyo down below. It would be interesting to see if there is also a small population of trees on the Mesa directly to the North, as well.

Fig. 2: *Cupressus revealiana*, in the bed of an irregular stream. 2016-11-16.

Fig. 3: *Cupressus revealiana*. 2016-11-16.

Fig. 4: *Cupressus revealiana*. 2016-11-16.

Fig. 5: *Cupressus revealiana*. 2016-11-16.

Fig. 6: *Cupressus revealiana*, 1st year cones. 2016-11-16.

Fig. 7: *Cupressus revealiana*. 2016-11-16. The main population of cypresses is up above this spill off. Being that water is the main dispersal mechanism for cypress seed and this small spill off is where most of the water drains off the Mesa – providing the most seasonal moisture – quite a few trees are evidence here. This was one of our main hints that there would be a much larger population on the Mesa just above the spill off.

Fig. 8: *Cupressus revealiana* are present in the wash. 2016-11-16.

Figs 9 to 19: These pictures were taken on top of the Mesa, where the main population of cypresses occurs, along with *Quercus peninsularis* and a species of sagebrush (*Artemisia* sp). There were easily 3000 trees or more here.

Fig. 10: *Cupressus revealiana*. 2016-11-16.

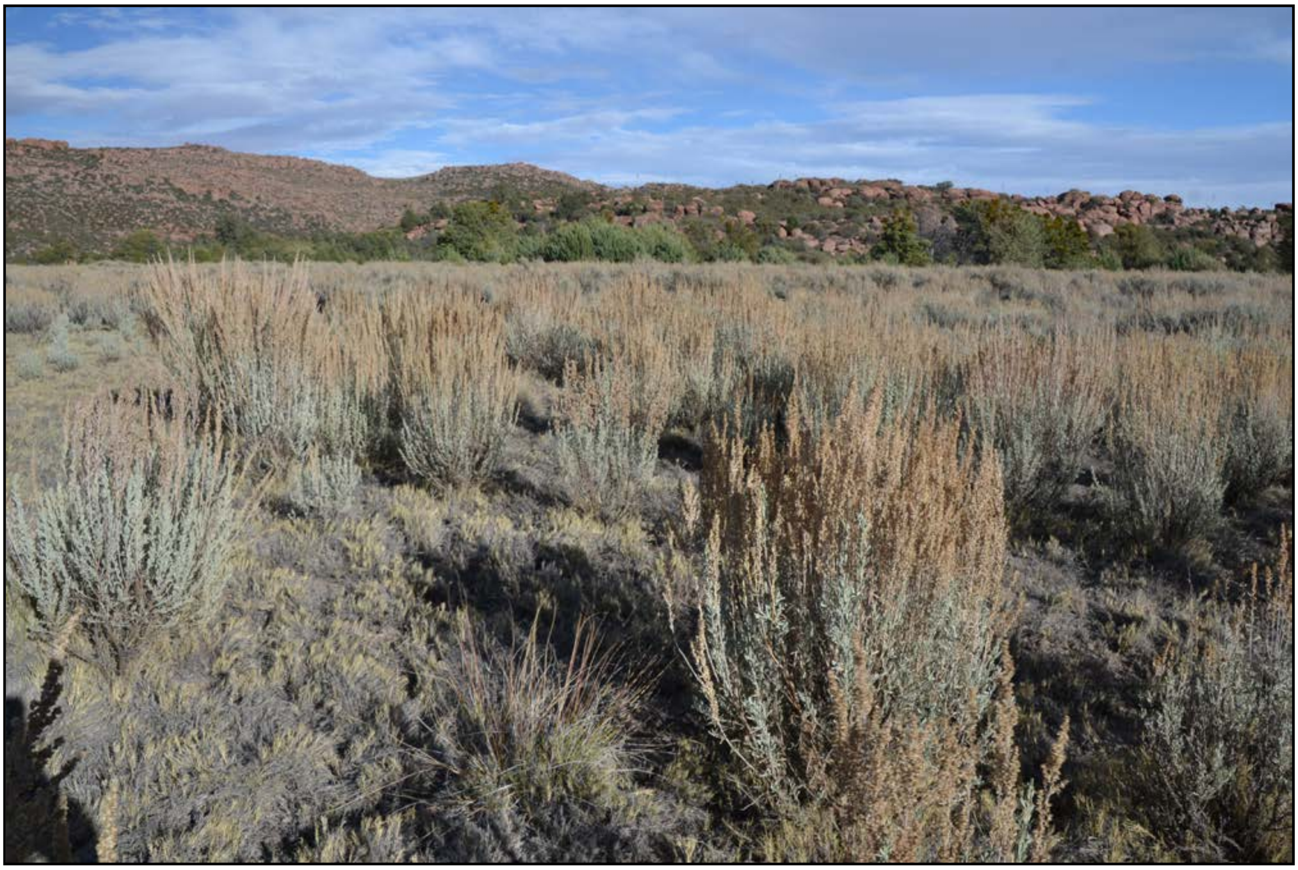

Fig. 11: Sagebrush species in the foreground and *Cupressus revealiana* in the background. 2016-11-16.

Fig. 12: Mistletoes on *Cupressus revealiana*. 2016-11-16.

Fig. 13: *Cupressus revealiana*. 2016-11-16.

Fig. 14: View down the wash on top of the mesa. 2016-11-16.

Fig. 15: Local geology here is some sort of intrusive igneous rock, apparently very iron-rich. 2016-11-16.

Fig. 16: *Cupressus revealiana*, trunk and spreading branches. 2016-11-16.

Fig. 17: *Cupressus revealiana*. 2016-11-16.

Fig. 18: *Cupressus revealiana*. 2016-11-16.

Fig. 19: *Cupressus revealiana*. 2016-11-16.

Fig. 20: *Cupressus revealiana*, 1st year cones. 2016-11-16.

Fig. 21: *Cupressus revealiana*. 2016-11-16.

Fig. 22: *Cupressus revealiana*, mature seed cones. 2016-11-16.

Fig. 23: *Cupressus revealiana*, with the author. Altitude: 1450 m. 2016-11-17.

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D. Maerki

Misidentified *Cupressus stephensonii* specimens

As part of a continuing survey of cultivated *Cupressus* species, several specimens labelled *Cupressus stephensonii* C.B.Wolf were found to be wrongly identified.

* A row of a few "*Cupressus stephensonii*" specimens in a research field close to Firenze are *C. macnabiana*.

* One tree at the Faculté d'Orsay close to Paris is likely *C. sargentii*, and certainly not *C. stephensonii*.

* Plants grown from a batch of seeds purchased from Sandeman Seeds in March 2010 with the label *C. stephensonii* are not this species, but were identified mainly as *C. glabra* Sudworth (Figs 2-3). Among the saplings grown from this lot of seeds are other specimens which cannot be classified as *C. glabra*. Although the habit (crown shape, branching pattern and colour) is exactly the same as the *C. glabra* saplings mentioned here, the seed cones show completely different features. If the seeds were collected on the same tree, the only explanation of such different cones is that the source of the seeds is a tree in a botanical garden and these individuals grown from seeds are hybrids (Figs 4-5).

* A specimen labelled *C.* [*arizonica* var.] *stephensonii* at Bedgebury Pinetum, Kent, UK, is *C. revealiana* (Figs 6-12; cf. Figs 13-15).

Fig. 1: *Cupressus glabra*, cultivated, 40 metres from sapling of Fig. 2.

All photos on this page: 2016-9-22.

Figs 2-5: Different cones shapes and colours from the same seed lot sold by Sandeman Seeds in 2010.

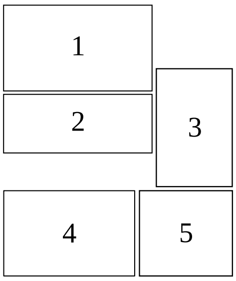

Fig. 2: This sapling is identified as *Cupressus glabra*, the cone, the foliage and the habit showing the same characteristics as the tree in fig. 1 planted some 40 metres away. **Fig. 3:** These cones are within *C. glabra* variability. **Figs 4-5:** The leathery bright brown colour is the only character which matches the one of *C. stephensonii*, but not the one of *C. glabra*; pollen cones are still in their initiation stage in September.

Figs 6 to 10: *Cupressus revealiana* labelled as *Cupressus stephensonii* at Bedgebury Pinetum, England. 2017-4-22.

The poor health of that specimen (more than two thirds of the tree is without leaves, many dry branches) could explain the absence of pollen and seed cones. See identification illustrations on the next two pages.

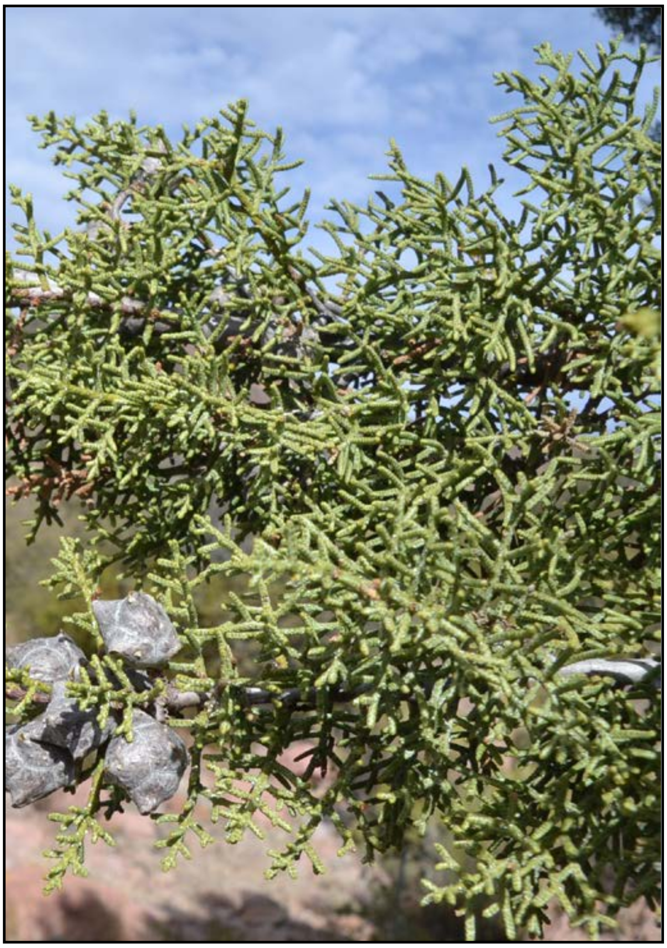

Fig. 11 (p. 72, top) : Foliage of *Cupressus revealiana*, Bedgebury Pinetum. 2017-4-22.

Fig. 12 (p. 72, bottom) : Exfoliating bark of *Cupressus revealiana*, Bedgebury Pinetum. 2017-4-22.

Fig. 13 (above, left) : Detail of foliage of *Cupressus revealiana*, wild, El Rincon, Baja Californica, Mexico.
© Joey Malone (see Fig. 1, p. 57).

Fig. 14 (above, right) : Foliage of *Cupressus stephensonii*, wild, Cuyamaca Peak, San Diego County, California, USA.
© Joey Malone

Worth noticing is the difference in the branching pattern of the foliage of both species.
See also Figs 25 & 26, p. 55 and Figs 27 & 28, p. 56.

Fig. 15: Bark of *Cupressus revealiana*, El Rincon, Baja California, Mexico.
© Jeff Bisbee.

For more comparisons between these species, visit the following web page:
http://www.pinetum.org/JeffCUrevealiana.htm

See also: *Cupressus revealiana* (Silba) Bisbee, *comb. nova* validation as a new *Cupressus* species, with notes on identification and distribution of other nearby cypress species. *Bull. Cupressus Conservation Proj.* 1: 3-15 & Addendum. *Bull. Cupressus Conservation Proj.* 1: 46-47.

Comments on the article: ‘Is *Cupressus sempervirens* native in Italy?’ by Bagnoli *et al.*

To try to answer to such a topic objectively, it is necessary to find arguments in favour of the hypothesis in discussion as well as against it. In the Bagnoli *et al.*'s article however, the arguments mainly sustain a positive answer to the question and some information pointing to another direction are not really being taken into account.

The conclusion of the article by Bagnoli *et al.* (2009) reads as follow:

> The data reveal a new interpretation of the history of cypress distribution characterized by ancient eastern populations (Turkey and Greek islands) and a mosaic of recently introduced trees and remnants of ancient, depauperate populations in the central Mediterranean range.

Further:

> The combined analysis of molecular data and palaeobotanical records reported in this study highlights a different history of cypress compared to the current one based entirely on human introduction (Pignatti 1982). Summarizing, the genetic data clearly distinguish two main groups, in the eastern and central Mediterranean, respectively, with significant differences in levels of genetic diversity and population structure. The differences between them may be the effect of either human activity and/or a combination of historically low effective population sizes and long-term disjunction of natural populations. The palaeobotanical data, indicating that *Cupressus* was present in Italy in the Pliocene, Pleistocene and Holocene, support the hypothesis that some of the genetic differences found between the Italian and eastern populations are due to a separation that occurred millions of years ago.

The discussion considers genetic and fossil data. They run as follows:

Genetic data: samples were collected in Turkey, in Greece, in Tunisia and throughout Italy. The analyses give a mosaic of different genetic diversities in Italy while in Greece and Turkey (wild populations) the variation of the genetic diversity parameters is progressive, showing a cline. Between Italy on one side and Turkey and Greece on the other side, there is no real match of these genetic diversity parameters. Few alleles are present in Italy which could not be found further east in the Greek and Turkish wild populations. The conclusion is that *Cupressus sempervirens* L. in Italy cannot come alone from introduced seeds collected abroad, but that a remnant survived through the last glaciations after a separation of several millions years.

Fossil data: *Cupressus* species fossils were found in Via Flaminia near Rome, dating from some 450,000 years before present (Follieri & Magrì 1961).

The overall interpretation of these data is that *C. sempervirens* should be native in Italy, even if introductions are also assumed.

Are the presented arguments really conclusive? Unfortunately it appears that some data have been discarded meanwhile some hypotheses or interpretations are quite debatable. It is necessary to present the important data and pertinent arguments which are contradicting the native hypothesis and which were not taken into account.

Critical analysis of the fossil data: in Via Flaminia not only fossils of a *Cupressus* species were found, though the state of the remains does not allow determining the species [1]. Among the other conifer fossils the following genera were found: *Abies*, *Amentotaxus*, *Cephalotaxus*, *Juniperus*, *Pinus*, *Taxodium*, *Taxus*, and *Torreya* (Follieri & Magrì 1961). Among the angiosperms, worth mentioning are: *Persea*, *Pterocarya*, and *Zelkova*. Between 450,000 before present and today, the Riss and Würm glaciations changed for long periods the climate in Europe. The Riss glaciation showed the most important ice extension. The Rhone glacier went as far as Lyon (France) and permanent glaciers were

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[1] By answering positively to the title question, the authors are assuming that these fossil remains are *Cupressus sempervirens*, when they can be another species, for instance closer to *C. atlantica* or a completely different taxon adapted to moister climatic conditions (like *C. nootkatensis*, *C. funebris*, *C. tortulosa* or *C. benthamii* – what the presence of *Taxodium*, *Zelkova*, and *Pterocarya* species – among other taxa – implies).

present on the Apennines [2]. As the Mediterranean Sea did not allow vegetation to retreat further south, many species not hardy in the new humidity and temperature conditions went extinct on the continent [3]. Some could find refuge stations in the southernmost localities. The case of *Abies* is very interesting as it is quite likely that it could retreat to Calabria and Sicily in the extreme south of Italy, and colonise back the peninsula to the Alps soon after the end of the glaciations [4]. Molecular data show a continuous genetic variation from south to north (Saltocyannes 1999b). Among the conifers *Amentotaxus*, *Cephalotaxus*, *Taxodium*, and *Torreya* became extinct. Of these four genera, only *Amentotaxus* is less hardy than *Cupressus* when considering *C. sempervirens* and the extant species of this genus in Taxaceae. *Taxodium* is frost hardier, but less drought tolerant (at least as saplings), while the two other genera *Cephalotaxus* and *Torreya* are certainly as frost hardy [5] as *Cupressus sempervirens*, and even shade tolerant, when the later is not. Thus, they could have found a further protection resource as understory trees, but were unable to make use of that capacity and became extinct in Europe. Also both genera have edible drupes or seeds which can be dispersed by animals – an important advantage for survival, when no animal disperser is known for the Euro-Mediterranean cypresses [6]. Two of the three angiosperms genera mentioned above also became extinct in Italy. A *Zelkova* species was found quite recently in Sicily; *Zelkova sicula* is a relict species present on a very small area comprising two populations [7], immediately classified as Critically Endangered and put under strict protection. Considering all these gymnosperm and angiosperm genera, there is no evidence to acknowledge the fact that a *Cupressus* species could have resisted the cold climatic conditions better than the other genera which could not come back by natural dispersion [8]. *Cupressus sempervirens* is adapted to a Mediterranean climate. 450,000 years ago the climate around Roma was quite different.

There is some interest to compare the fate of the two genera *Cedrus* and *Cupressus*. Where cedars are present, cypresses are not far away: in northwestern Africa, *Cedrus atlantica* and *Cupressus atlantica*; in the eastern Mediterranean area, *Cedrus libani* and *Cupressus sempervirens*; in western Himalaya, *Cedrus deodara* and *Cupressus torulosa*. Both genera were still present in Italy during the Pleistocene [9]. Because of the glaciations and the associate cooling of the climate, *Cedrus* became extinct on the Italian peninsula (Magri 2012; Follieri 2010; Svenning 2003). The date is subject to discussion. It likely happened after the Mindel glaciation (Magri *et al.* 2017; Magri 2012). For instance in the province of Salerno (Campania), “Tsuga, along with *Cedrus*, *Zelkova* as well as a few grains of *Pterocarya* and *Taxodium* type have been recorded between 0.58 and 0.43 Ma”[10] (Bertini 2010: 16). The extant *Cedrus*

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[2] The Fontegreca locality was in the immediate vicinity of the Montagne del Matese glacier to the east and the Monte Greco glacier to the north (see Giraudi 2011: 212, Fig. 17.1). A *C. sempervirens* grove could not survive in such periglacial conditions (see Map 2). Fontegreca means “Greek spring”. It gives a clue to who brought the cypresses, which – unlike most other cultivated trees in Italy – are resistant to *Seiridium* canker. As their shape (horizontal branches) is also different from most cypresses present in Italy, their possible origin is to be researched as far as Turkey or even Iran (see also note 15).

[3] As demonstrated by Svenning (2003), cold was the determinant factor for tree extinctions on continental Europe. A few drought hardier genera, although affected by the decrease of the temperatures, survived as relictual populations, often on islands (like *Zelkova*).

[4] *Abies alba* is hardy to USDA zone 4, -29 to -34°C.

[5] The species from China of both genera grow under a very moist monsoon climate. *Torreya californica*, as a Californian endemic, grows in a Mediterranean climate with a dry summer season, but also thrives under much moister conditions, while *T. taxifolia* is restricted to a riparian habitat in climate with a higher rainfall than California.

[6] Little is known about the way cypress species are dispersed through time and space in natural conditions. There is only one example with cones being browsed by squirrels (and possibly birds): *Cupressus macnabiana* (Frank Callahan, pers. comm. as well as pers. observation).

[7] The two populations are triploid, and are analysed as hybrids, with a different origin for each population (Christe *et al.* 2014). Other *Zelkova* species are hardy to at least zone 6. By comparison *Cupressus sempervirens* is fully hardy only in zone 8.

[8] Unlike the genera *Abies* and *Zelkova*, there is no relict cypress population in the south of Italy (Calabria or Sicily). The genus *Pinus* is worth a mention. *Pinus heldreichii* is known from one relict population in Calabria (apart from another one in the Balkans). Although very hardy further north, it did not manage to colonise the rest of Italy.

[9] The genus *Cedrus* (as well as the genus *Cupressus*) was also present on the Iberian and Balkan Peninsulas and “underwent a strong reduction” “in the course of the Pleistocene”, before disappearing (Magri 2012: 57).

[10] *Tsuga* which is even hardier than *Cedrus* or *Cupressus* (though less drought tolerant), also became extinct in Europe (Svenning 2003).

species are hardier [11] than *Cupressus sempervirens*, but even this fact did not help that genus to survive the last glaciations in continental Europe. Thus the conclusion looks unavoidable: if Mediterranean *Cedrus* taxa are cold hardier than *Cupressus sempervirens* and went extinct in Italy (and in all continental Europe), it is possible to conclude that this was also the fate of the latter, if it was ever present in Italy. Similarly the genus *Cupressus* disappeared from the European continent at the end of the Pleistocene.

In addition to climatic conditions (see note 1), the next argument against *C. sempervirens* being ever present in Italy [12] – even before the glaciations – comes from biogeographic considerations. Taking into account the data of Table 1, the species present in Italy mostly – if not all – belong to the western Mediterranean area and are distinct from the species of the eastern part. Adding all these new observations not mentioned by Bagnoli *et al.*, it follows that the most probable hypothesis concerning the fossil wood remains found in Italy is that they belonged to another *Cupressus* species than *sempervirens*.

Critical analysis of the genetic data: here a preliminary remark is necessary. In the study by Bagnoli *et al.*, several wild populations of *Cupressus sempervirens* are missing: Cyrenaica (Libya), Cyprus, east Turkey (the easternmost sample comes from Manavgat, 31°44' East longitude), Syria, Lebanon (Phoenicia), Jordan, and Iran (see Map 1 [after Browicz & Zieliński 1982], where the Tunisian population is not considered as native). In the article the Tunisian population is referenced as Makthar. There is no information indicating if the samples come from the ancient Roman city – where the trees are cultivated – or if they come from one of the three small populations considered as wild or naturalised (and described as var. *numidica* Trab. [13]). These populations are away from Makthar and are known under other locality names. Also missing are cultivated *C. sempervirens* from France, Spain and North Africa[14]. In a previous article dealing with a comparison between the Greek cultivated and wild populations (Papageorgiou *et al.* 2005), the authors found the very same overall results, i.e. lower diversity in introduced populations, using the same analysis tools.

Cupressus sempervirens is part of the Italian landscape since antiquity, especially in Tuscany. The Etruscans, established in this province at least since the 9th century before present, already cultivated this tree and it is known from archaeology that this civilisation had commercial contacts with Greece and Phoenicia (Lajard 1854). During the Roman Empire, commercial links developed throughout of the Mediterranean region *(Mare Nostrum)* and several Roman cities were installed also in Cyrenaica in North Africa. More recently in historical times, since the apparition of Christianity, pilgrimages and crusades formed a continuous link with Syria and Phoenicia setting further opportunities to import seeds or plants from the eastern Mediterranean region. Thus introductions from one or several of the localities not part of the Bagnoli *et al.* study not only cannot be excluded, but are probable. For the main argument – if not the only one – in favour of a native Italian cypress is that a few alleles found in current trees are absent in the Greek and west Turkish area.

The authors state that some genotypes present in Italy are rare or absent in the "eastern part" of the *sempervirens* range, forgetting that several disjunct populations were not investigated at all. Considering other conifer species like *Abies cilicica*, *Cedrus libani* or *Juniperus drupacea*, studies have shown that there are genetic differences between the Greek-western Turkish populations and the ones further east [15] (Boratyńska *et al.* 2015; Scaltsoyiannes 1999a; Sobierajska *et al.* 2016). Some populations have even been given a different taxonomic status like *Abies cilicica* subsp. *isaurica*, *Cedrus libani* var. *stenocoma* and *Cedrus libani var. brevifolia*. Moreover if an allele is rare in a natural population, it could escape

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[11] Sakai (1983: 2330) gives for the three *Cedrus* species a hardiness range from -15° to -24°C and the same data for four *Cupressus* species without mentioning which ones. Comparing *Cedrus libani* var. *stenocoma* in Turkey, the hardiest taxon of the genus, to *Cupressus sempervirens*, the cedar grows to a higher altitude than the cypress; it has also proved hardier (to nealy -30°C) in cultivation. Additionaly, cypresses, unlike Pinaceae, do not form buds to resist cold temperatures and display a continuous growth when the meteorological conditions allow it.

[12] See Maerki 2018, this issue p. 81.

[13] Should the studied material come from the wild population, the genetic results could confirm the validity of this taxon.

[14] In Rushforth *et al.* (2003), an analysis was performed on *Cupressus sempervirens* using RAPDs. The result reads: "*Cupressus sempervirens* samples from Iran (native) and the cultivated strict form (Spain) were found to be nearly identical."

[15] Not to speak of the Libyan *Cupressus* population.

collection, especially when this collection is limited (only two wild sites with a sample size > 30: Rhodes, Samos).

Another problem with the Italian samples is the lack of information about the origin of the selected trees which are either cultivated or naturalised. In Italy cypresses were selected since antiquity for the quality of their wood, for their shape, and possibly for the size of their cones. They were considered as sacred and funeral trees (Lajard 1854), much valued for their wood, resistant to decay. The owner of a *cupressetum* was made rich by this fact alone (Lajard 1854: 286). Few specimens are very old, although *Cupressus sempervirens* is known – like most Eurasian cypress species – to live for centuries, if not for millennia [16].

As mentioned, the results of the genetic analyses show a mosaic pattern from Tunisia to northern Italy. Throughout this range four genetic clusters are distinguished while there is only one for the Greek-Turkish populations. The only way to explain such a pattern inside a native Italian cypress hypothesis is to consider not one refuge, but at least three in Italy and the fourth one in Tunisia. The main problem is that there is no evidence of such refuges unless the Tunisian population could be considered as such, if not introduced. Part of the article's conclusion admits that most of the Italian cypresses were introduced, but fails to investigate from where. Considering the absence of any trace of a refuge and the absence of a relict population, the limited material put under analysis, the "remnant" hypothesis finds no real support.

On the contrary, a more complete approach tilts the balance in favour of the invalidation of the hypothesis of the extant *C. sempervirens* being native in Italy.

To support the hypothesis of a *Cupressus* species native in Italy it would be necessary to discover cypress remains not only from the interglacial period Riss-Würm, but also present after the Würm glaciation and before the Neolithic period. And it would be necessary that these remains could be identified as *C. sempervirens*.

Finally the last edition of the *Flora d'Italia* (Pignatti *et al.* 2017: 84 [17]) as well as two updated checklists by Bartolucci *et al.* (2018) and Galasso *et al.* (2018) also consider that *C. sempervirens* is an exotic species in Italy.

Addendum: In Sekewicz *et al.* (2018), molecular analyses on east Turkey (Taurus Mountains) and Lebanon populations of *C. sempervirens* confirms the above hinted differences with the Greek origins (Crete, Rhodes, etc).

Table 1: Comparison of the distribution of some extant species throughout the Mediterranean region.

West Mediterranea	**Central Mediterranea**	**East Mediterranea**
Spain, Morocco, Algeria	Italy	Greece, Turkey
Abies pinsapo / *numidica*	*Abies nebrodensis* / *alba*	*Abies cephalonica* / *cilicica*
Cedrus atlantica [18]	–	*Cedrus libani* / *brevifolia* [19]
Cupressus atlantica	*Cupressus* sp.? (450,000 years ago)	*Cupressus sempervirens*
–	–	*Juniperus drupacea*
Juniperus willkommii	*Juniperus willkommii*	*Juniperus macrocarpa*
Juniperus oxycedrus	*Juniperus oxycedrus* / (*deltoides*)	*Juniperus deltoides*
Juniperus thurifera	–	*Juniperus excelsa* / *foetidissima*
Pinus halepensis	*Pinus halepensis*	*Pinus brutia* / (*halepensis* - introduced?)
Pinus pinaster, *pinea*	*Pinus pinaster*	(*Pinus pinea* - introduced)
Pinus salzmanii [20]	*Pinus italica* / *corsicana* [21]	*Pinus caramanica* [22]
Tetraclinis articulata	*Tetraclinis articulata* (Malta!)	–
–	*Zelkova sicula* (Sicily)	*Zelkova abelicea* (Crete)

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[16] The oldest *Cupressus sempervirens* has an estimated age of 4,000 years.

[17] « Il cipresso, originario dell'Oriente (Egeo, Anatolia, Libano, Cirenaica), è stato introdotto in It. In epoca certo antichissima, forse già dagli Etruschi (che secondo la tradiz., confermata da ricerche recenti, sarebbero anch'essi originari di quella zona), e si è in seguito straodinariam. diffuso così da venire a costituire uno stabile componente della nostres vegetaz. »

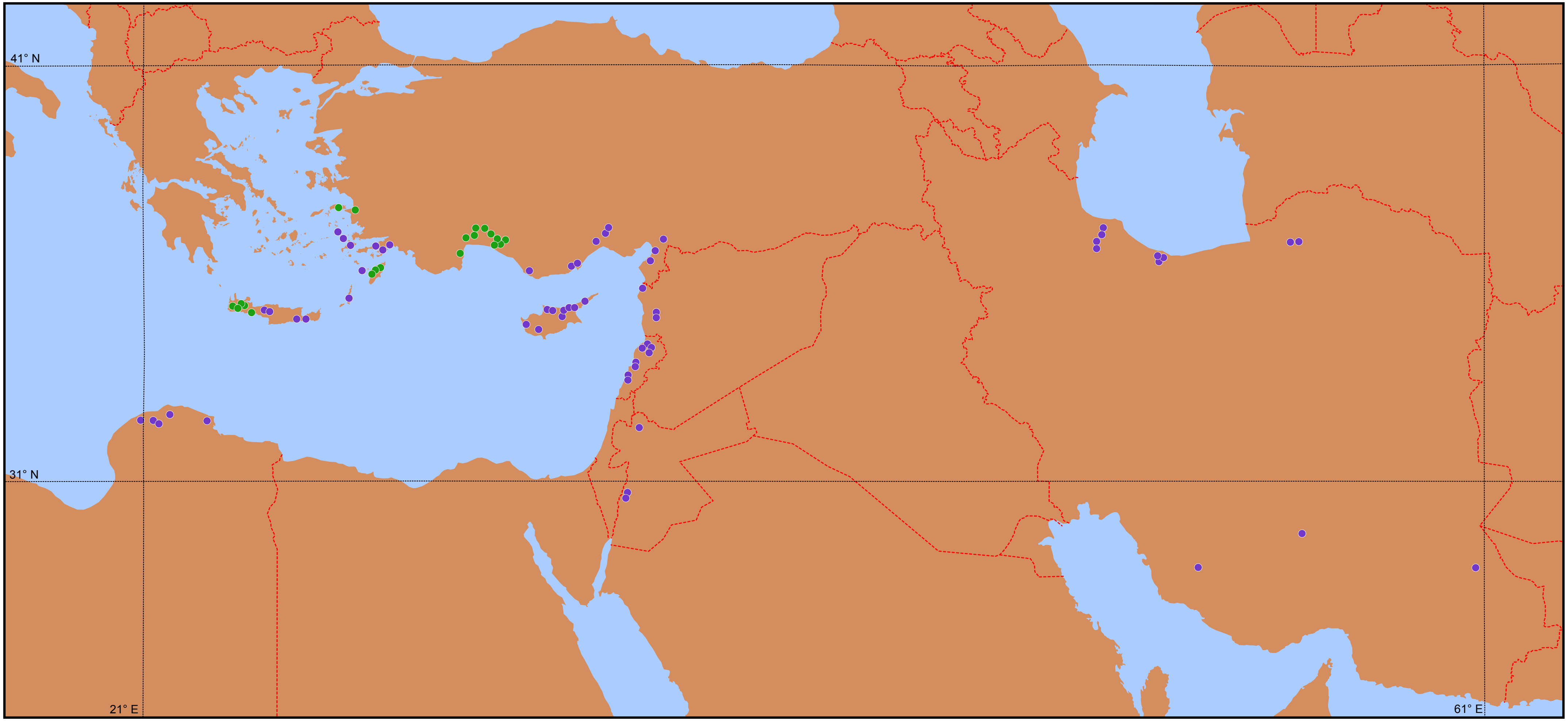
[18] Best treated as *Cedrus libani* subsp. *atlantica*.

[19] Best treated as *Cedrus libani* [subsp. *libani*] var. *stenocoma* and *Cedrus libani* [subsp. *libani*] var. *brevifolia*.

[20] Best treated as *Pinus nigra* subsp. *salzmanii*.

[21] Best treated as *Pinus nigra* [subsp. *salzmanii*] var. *corsicana* and *Pinus nigra* [subsp. *nigra*] var. *italica*.

[22] Best treated as *Pinus nigra* [subsp. *nigra*] var. *caramanica*.



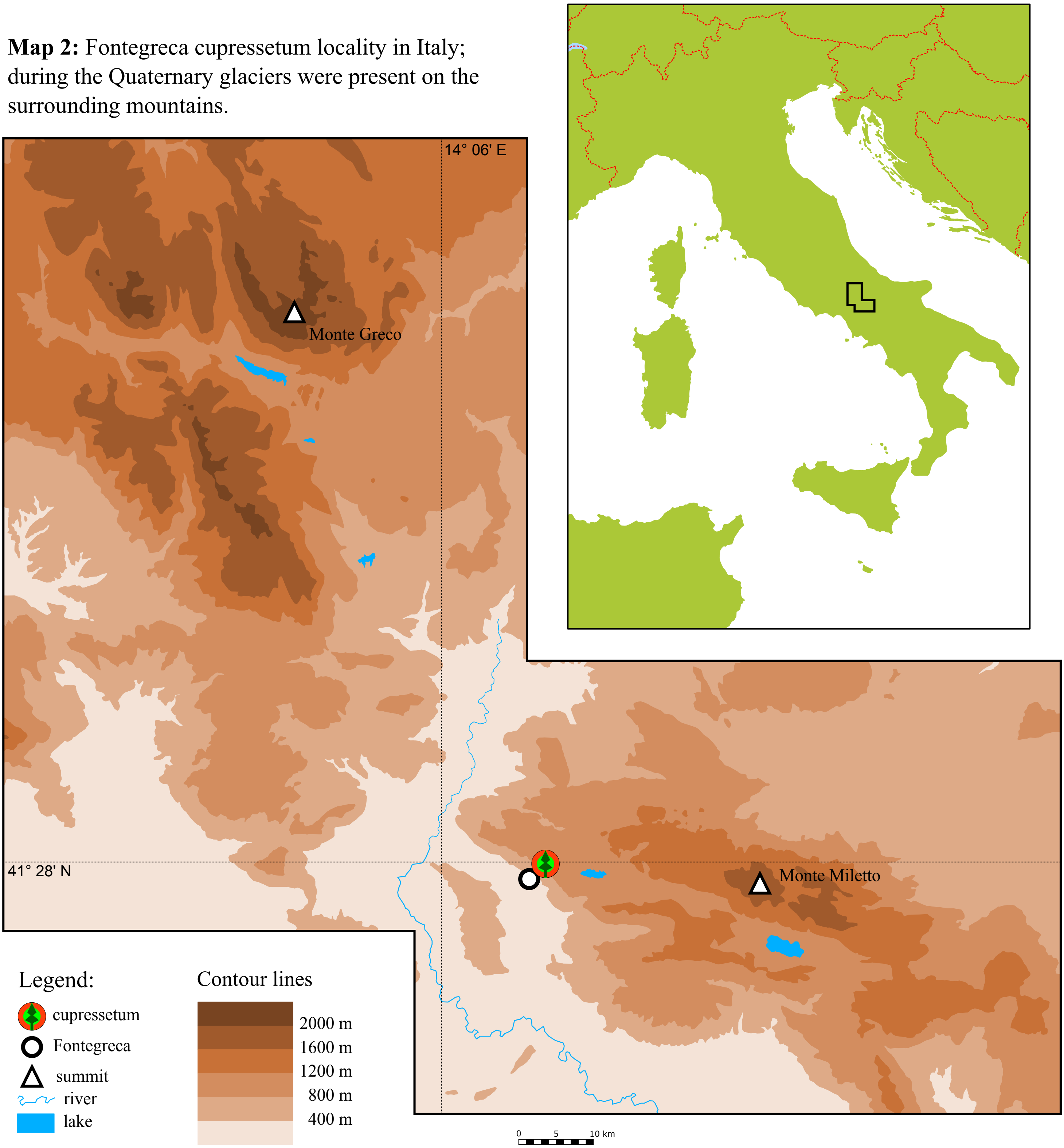
Map 1: Distribution range of *Cupressus sempervirens* wild populations.

Legend: ● *Cupressus sempervirens* localities studied in Bagnoli *et al.*, 2009.
● *Cupressus sempervirens* localities not studied in Bagnoli *et al.*, 2009.
State borders

Scale: ~1:14'700'000

Map and distribution range after Browicz & Zieliński, 1982.

Map 2: Fontegreca cupressetum locality in Italy; during the Quaternary glaciers were present on the surrounding mountains.



Monte Greco: 2.283 m., Appennino Abruzzese mountain chain.

Monte Miletto: 2.050 m., Matese mountain range.

Giraudi 2008: 218, conclusions.
"If the Alpine glaciation nomenclature and their chronology is considered (Hughes et al., 2006, 2007), it can be stated that [glacial] sediments were deposited during a pre-Mindel glacial phase, during two Rissian glacial phases and in two Würmian phases."

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Bull. Cupressus Conservation Proj. 7 (2): 81. (2018-12) **D. Maerki**

A new *Cupressus* fossil species in Italy

Considering the geological and climatological history of Italy during the Pleistocene and the data presented in Maerki & Frankis (2018), a new fossil species is described here from details of wood anatomy.

Cupressus italica Maerki, *sp. nova* (fossil).

Material: wood remains from Via Flaminia near Roma, Italy (Follieri & Magrì 1961, Follieri 2010) dated 450,000 years before present.

Holotype: illustration in Follieri (2010: 40): Fig. 2-15, showing a cross-field with 1-4 cupressoid pits.

Diagnosis: the Via Flaminia *Cupressus* fossil wood presents cross fields with 1-4 cupressoid pits (Follieri 2010: 40, Fig. 2-15) and rays 1-15(-20)-cells high (Follieri 2010: 40, Fig. 2-14). This combination of these key anatomical wood characters of *C. italica* is unique among analysed *Cupressus* species. All 16 species studied by Román-Jordán *et al.* (2016: 54-55, Tab. 1 [1]) have cross fields with 1-2 cupressoid pits, except for *C. vietnamensis* with 1-5 pits; on the other hand *C. vietnamensis* has rays only 1-10-cells high, when several *Cupressus* species have 1-15 [2] or 1-20 [3] cells.

Geographically the closest extant *Cupressus* species is *C. sempervirens* with wild populations in Crete (Greece) and in Cyrenaica (Libya). It is described as “a typical Mediterranean tree” (Follieri 2010: 42), that is adapted to a mild humid winter and a warm dry summer. *Cupressus italica* was found together with several fossil genera which are characteristic of a much moister climate (in particular *Taxodium*, *Amentotaxus*, *Cephalotaxus*, and *Torreya* [4] and *Zelkova* and *Pterocarya* among angiosperms). Like those genera, *Cupressus italica* became extinct during the Riss or Würm glaciations, the last ones of the Pleistocene[5].

As the tree was native in Italy, the name *italica* records this origin.

Further exploration of the type locality for potential cone and foliage fossils would be very desirable.

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[1] *Cupressus vietnamensis*, *C. nootkatensis*, *C. bakeri*, *C. macnabiana*, *C. goveniana*, *C. sargentii*, *C. macrocarpa*, *C. guadalupensis*, *C. arizonica*, *C. lusitanica*, *C. funebris*, *C. duclouxiana*, *C. tortulosa* (as *C. cashmeriana*), *C. torulosa*, *C. dupreziana*, *C. sempervirens*.

[2] *C. nootkatensis*, *C. macrocarpa*, *C. arizonica*, *C. lusitanica*, *C. funebris*, *C. duclouxiana*, *C. dupreziana*.

[3] *C. tortulosa*, *C. torulosa*, *C. sempervirens*.

[4] “The macrofossil flora from the Tufi grigi indicates that around 450 ka *Amentotaxus* and *Cephalotaxus*, nowadays occupying pluvial areas of China and Japan, lived in the surroundings of Rome together with *Taxodium* and *Torreya*, now populating swampy areas in North America [...].” (Follieri 2010: 39. – About *Torreya*, see also previous article in this issue, p. 75, note 5.)

[5] With the exception of *Zelkova*, where two relict small populations, named *Z. sicula* Di Pasq., Garfi & Quézel were found in Sicily from 1991.

Bull. Cupressus Conservation Proj. 7 (2): 82-91. (2018-12) **V. Pietzsch**[1] **& V. M. Dörken**[2]

Morphological and anatomical investigation of seed cones of *Cupressus glabra* (Cupressaceae): evolutionary aspects

Abstract

Within this study, the morphological and anatomical features of *Cupressus glabra* Sudw. seed cones were investigated, focused on the vascular supply to cone scales and ovules. These investigations should help towards a better understanding of the branching pattern both within seed cones of *C. glabra* and within in the primitive cupressaceous seed cones in general. Seed cones of *C. glabra* are strongly reduced and compact structures. They typically lack sterile distal elements, so that all terminal cone scales are usually fertile, and the apex of the cone axis is not visible. The ovules are arranged in up to four axillary rows. Each row, which can be understood as a descending accessory shoot, consists of several ovules. Within a bract/seed scale complex the cone scale and its axillary ovules are each supplied by an own vascular bundle. The vascular bundle strands of the cone scale and of the ovules do not fuse and enter the concentric stem bundle of the cone axis in separate strands. This situation corresponds quite well to the situation of a bract carrying a fertile axillary shoot. It seems that the seed scale was entirely reduced to its ovules, with no further vegetative structures belonging to it were visible. These results suggest the original cupressaceous seed cone was a more open and looser structure, which became strongly reduced to form the highly condensed compact seed cones of the extant *Cupressus* taxa.

Keywords: *Cupressus*, seed cone, morphology, anatomy, vasculature, evolution.

1 Introduction

The reproductive structures of conifers are arranged in compact, unisexual cones. The staminate male ones are called pollen cones; the female, ovuliferous ones, seed cones. Seed cones of extant conifers consist of two types of cone scales, the bract scale and the seed scale, both together are forming the bract/seed scale complex (e.g. Coulter & Chamberlain 1917; Pilger 1926; Florin 1951, 1954; Schweitzer 1963; Stützel & Röwekamp 1999). The seed cones consist species specific of one up to several hundred bract/seed scale complexes. The bract scale, which carries the axillary seed scale, corresponds to a leaf, whereas the seed scale represents a reduced and modified, fertile axillary shoot carrying the ovules. Thus, the coniferous seed cones are compound, polyaxial, inflorescence-like structures (e.g. Schuhmann 1902; Herzfeld 1914; Sporne 1965; Stewart & Rothwell 1993; Escapa *et al.* 2008; Taylor *et al.* 2009; Bateman *et al.* 2011; Rothwell *et al.* 2011; Rudall *et al.* 2011; Spencer *et al.* 2015; Dörken & Rudall 2018). This understanding of the coniferous seed cone structure is based on a concept originating from the morphology of Pinaceae seed cones and from the fossil record. Among extant conifers, the formation of the bract and seed scales as two distinct structures is only visible within Pinaceae and Sciadopityaceae, even at maturity in both families (e.g. Takaso & Tomlinson 1991; Mundry 2000; Dörken & Rudall 2018). Within all other extant coniferous families, the bract/seed scale complex became greatly modified and reduced. However, the evolutionary pathway leading to the compact seed cones of extant conifers is still highly controversial.

Unlike Pinaceae and Sciadopityaceae, only one type of cone scale can be found within cupressaceous seed cones. The bract and seed scales as two distinct structures are not visible, neither at pollination time nor at maturity. Among modern Cupressaceae *s.str.* (Cupressoideae and Callitroideae), all vegetative parts of the seed scale have been entirely reduced so that only the ovules remain, which can be understood as representing the only visible structures of the seed scale. Thus, the visible cone scale in Cupressaceae *s.str.* is represented exclusively by the bract scale (e.g. Page 1990; Farjon 2007, 2010; Gadek *et al.* 2000; Dörken 2012a, 2012b; Groth *et al.* 2011; Jagel &

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Dörken 2014, 2015a, 2015b; Dörken & Jagel 2017; Dörken & Rudall 2018), which carries the ovules always in an axillary position and never on its adaxial surface (Jagel & Dörken 2015a, 2015b). In their early ontogenetic stages a weakly developed, axillary bulge-like primordium is developed, forming the ovules. This could be interpreted as representing the rudimentary seed scale. In most of the derived Cupressaceae *s.str.*, the ovules are inserted in one or more successively developed rows in the axil of a cone scale. Within a row the single ovules develop centrifugally, whereas each row develops centripetally (Jagel & Dörken 2015a, 2015b). Each row of these axillary ovules is interpreted as an accessory descending fertile short shoot (e.g. Jagel 2001a, 2001b; Dörken 2012b; Jagel & Dörken 2015a, 2015b; Dörken *et al.* 2017) lacking any visible, sterile vegetative parts of the shoot axis. Thus, the seed scale can be understood as entirely reduced to its ovules.

However, among the basal taxa belonging to the Cupressaceae *s.l.* (the members of the former Taxodiaceae family), the bract and seed scale are completely fused to each other and form a common type of cone scale, which carries the ovules on its adaxial surface. However, within this fusion product, it is still unclear which exact portion of the cone scale belongs to the bract and which part belongs to the seed scale. Within some Cupressaceae *s.l.*, in the earliest ontogenetic stages weakly developed tongue-like structures on the upper surface of the cone scales are developed. They can be interpreted as vegetative parts of the seed scale as is the case in e.g. *Cunninghamia* and *Athrotaxis*. This indicates that in basal Cupressaceae the cone scale represents a fusion product of both bract and seed scale (Schulz & Stützel 2007; Jagel & Dörken 2014; Dörken & Rudall 2018).

In this study the morphology and anatomy of *Cupressus glabra* Sudw. seed cones were investigated. The study is focused on the formation of the vasculature within the seed cone and should help to answer the question if additional to the ovules further, however, sterile structures, can be found, which could be interpreted as belonging to the seed scale. The results should help towards a better understanding of the original branching pattern within *Cupressus* seed cones.

2 Material and Methods

Material

Cupressus glabra (Cupressaceae *s.str.*) is a monoecious, evergreen tree species, native to southern USA and northern Mexico. The investigated seed cones were collected by one of the authors (VMD) at pollination time on 12.04.2010-04-12 from a tree cultivated in the Botanic Garden of the Ruhr-University, Bochum (Germany).

Methods

Freshly collected material was immediately fixed in FAA (100 ml FAA = 90 ml 70% ethanol + 5 ml acetic acid + 5 ml formaldehyde solution 37%), thereupon being stored in 70% ethanol. The anatomy of the cones was studied from serial sections using the classical paraffin technique and subsequent astra blue/safranin staining (Gerlach 1984). Microphotography was accomplished with a digital microscope (Keyence VHX 500F) equipped with a high-precision VH mounting stand with X-Y stage and bright-field illumination (Keyence VH-S5).

3 Results

3.1 Morphology of wild-type seed cone

Seed cones are inserted terminally on short lateral shoots. They are in a more or less plagiotropic to upright position at pollination time (Fig. 1A) and at maturity as well. The seed cones consist of only a single type of cone scales (Fig. 1B). At pollination time the seed cones are about 4 mm in length and about 3 mm in width. The ovules do not exceed the cone scales. The seed cones consist of (2-)3-4 pairs of decussate fertile cone scales (Fig. 1B). Below the fertile cone scales two pairs of sterile decussate transitional leaves are developed (Fig. 3C). Sterile distal cone scales are usually absent. Sometimes the rudimentary apex of the cone axis is still visible as a small, central columella. Typically, the apex of the cone axis is completely used up, while the distal pair of scales is developed (Fig. 1E).

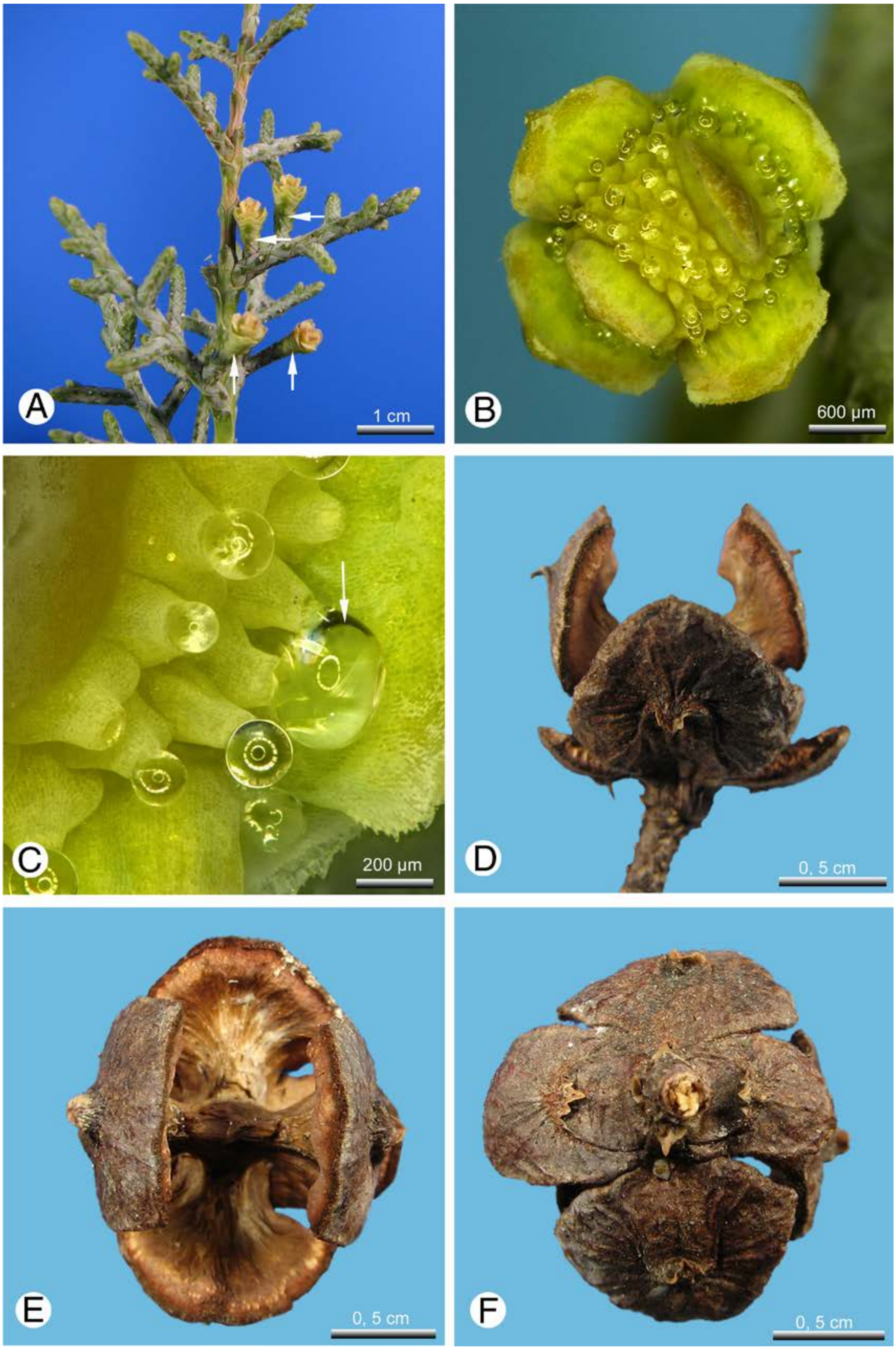

Fig. 1: *Cupressus glabra*, seed cone morphology.

A-C: At pollination time; **D-F:** At maturity; **A:** Position of seed cones within the branching system; **B:** Top view of a seed cone with several pollination drops; **C:** Fusion of pollination drops of adjacent ovules (arrow); **D:** Open seed cone in lateral view, the tip of the cone scale visible as a distinct dorsal prickle; **E:** Open seed cone in top view, with a weakly developed central columella; **F:** Open seed cone from below.

Within each cone scale, the ovules are inserted in up to four rows (Fig. 1C). Within a row several ovules are developed. The ovules are always inserted axillary and never on the surface of the cone scale. Within a seed cone the second and third pair of cone scales in the middle part of the cone develops the highest number of ovules (Fig. 1C). Due to a lack of space within the seed cone the ovules are always inserted closely to each other. As a result, the ovules of the distal cone scales accumulate all together on a convex plain at the tip of the cone (Fig. 1B).

At pollination time the cone scales are spreading widely, so that the necks of the micropyles and the pollination drops are freely exposed to the airflow (Figs 1B & 1C). A fusion of pollination drops of adjacent ovules is common and occurs between neighboured ovules within the same row, but also between ovules from different rows. This fusion allows the formation of a significantly larger pollination drop and increases the success in pollen capture (Fig. 1C). The cone scales are strongly covered with a thick cuticle, enabling the large pollination drops to lean on its surface which allows a further increase of the pollination drop size (Fig. 1C).

After successful pollination, the seed cones close rapidly by a strong ventral swelling of the cone scales. The ventral bulge is formed by a strongly swollen tissue rich in water, which finally is so strongly developed that the cones get closed rapidly after pollination and the ovules can develop well protected within the cone. Due to this ventral swelling the tip of the cone scale is shifted onto the back of the cone scale, visible as a short backward dorsal umbo (Figs 1D to 1F). In addition, resin secretions from the cone scales help to seal the maturing cones. At maturity, the cone dries out and the cone scales shrink (Figs 1D to 1F), so that the winged seeds are freely exposed and can be dispersed from the opened cone by the wind. Once opened, the seed cone cannot close again.

3.2 Anatomy of wild type seed cones

The cone axis shows a concentric stem bundle with inner xylem and peripheral phloem (Fig. 2B). The xylem and phloem are not separated from each other by any cambium. In the centre of the cone axis a large section of pith is developed (Fig. 2B). Collateral leaf traces in an opposite arrangement leave the concentric stem bundle and enter the cone scales in basal parts (Figs 3A & 3B), where they branch several times dichotomously (Fig. 3B). Each of the vascular strands ends blindly in the tissue of the cone scale. They do not fuse (Fig. 3D). Within the fertile cone scales, an additional bundle strand is developed supplying the ovules (Figs 2C, 3D & 3F). However, not all ovules have a vascular supply. Only the lowest row located directly on the cone scale shows a vascular supply, which is lacking in the distal rows. However, within the lowest row only the outer ovules, which are those developed first and are the oldest ones within the row, have a vascular supply in the form of a distinct strand of vascular bundle (Fig. 3E). The inner ovules within this row lack a direct connection to a vascular bundle and are supplied by a cell-to-cell transport. Thus, within a fertile bract/seed scale complex, at least two vascular bundles are developed (Fig. 3), which enter the concentric stem bundle of the seed cone in separate strands (Figs 2C & 3D). Fusion of the vascular bundles of the cone scale and the ovules does not occur.

3.3 Anatomy of teratological seed cone

In addition to the wild type of seed cones with decussate cone scales, some teratological seed cones show cone scales in trimerous whorls were found (Fig. 2D). Here an abrupt change in the phyllotaxis from decussate vegetative scale leaves (Fig. 2A) to the trimerous arranged cone scales took place (Fig. 2D). All other features are similar to the normal type of seed cones.

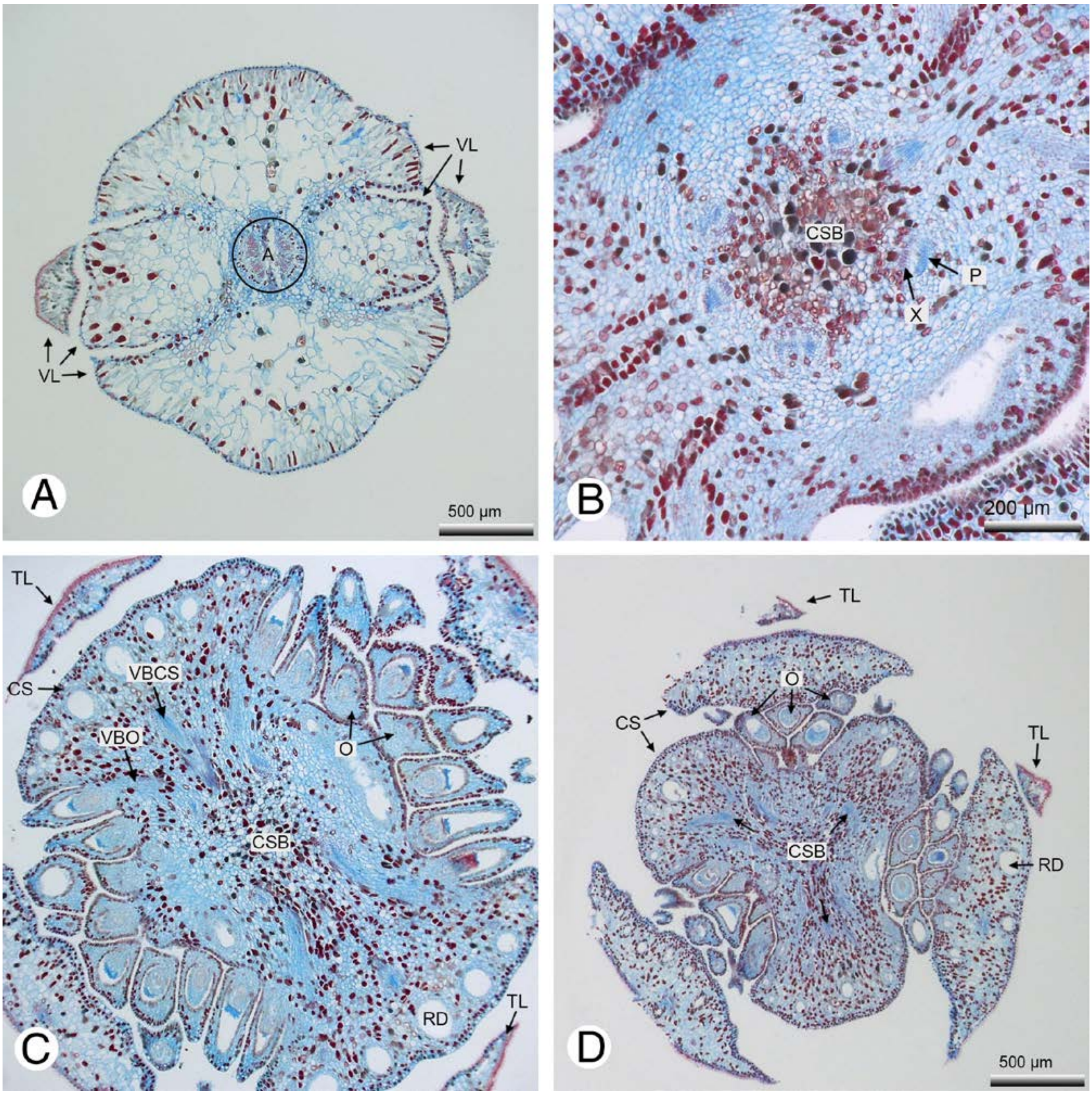

Fig 2: *Cupressus glabra*, anatomy of seed cones at pollination time, I.

A: Sterile leaves below the fertile cone scales in a decussate arrangement at the shoot axis; **B:** Detail of the central cone axis showing a concentric vascular stem bundle with inner xylem and peripheral phloem and a large central pith; **C:** Cone scales and ovules supplied by their own vascular bundle; **D:** Trimerous arranged cone scales, each supplied by a collateral vascular bundle; the vascular bundles of the cone scales come out of the concentric stem bundle in more or less the same plane (arrows).

A = axis, CS = cone scale, CSB = concentric stem bundle, O = ovule, P = phloem, TL = transitional leaf , VB = vascular bundle, VBCS = vascular bundle of the cone scale, VBO = vascular bundle of the ovules, VL = vegetative leaf , X = xylem.

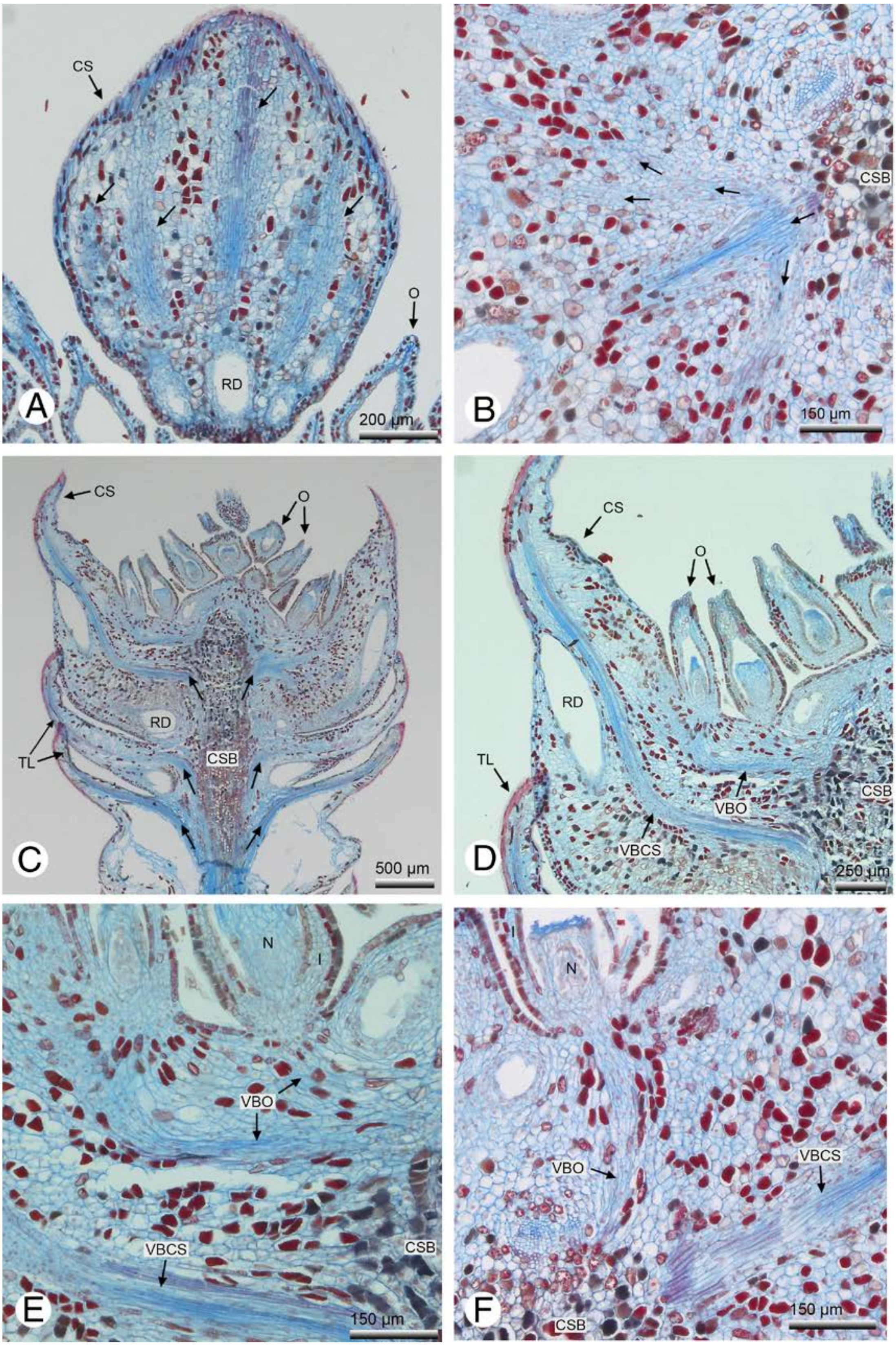

Fig. 3: *Cupressus glabra*, anatomy of seed cones at pollination time, II.

A,C-E: Longitudinal sections; **B & F:** Cross sections; **A:** The fertile bract/seed scale complex supplied with a collateral vascular bundle which branches several times (arrows); **B:** Dichotomous branching pattern of vascular bundles supplying the cone scale; **C:** Overview of a whole seed cone; **D-F:** A distinct separate vascular bundle supplying the ovules of the lowest row located directly at the cone scale; within this row only the outermost ovules are connected to the vascular bundle, the innermost ovules are supplied by a cell-to-cell transport. CS = cone scale, CSB = concentric stem bundle, I = integument, N = nucellus, O = ovules, TL = transitional leaves, VBO = vascular bundle of the ovule, VBCS = vascular bundle of the cone scale.

4 Discussion

4.1 Seed cone morphology and anatomy

Conifer seed cones are characterized by the presence of the bract/seed scale complex. The bract scale represents a leaf carrying axillary a fertile short shoot, the seed scale, which produces the ovules (e.g. Schuhmann 1902; Herzfeld 1914; Sporne 1965; Stewart & Rothwell 1993; Escapa *et al.* 2008; Taylor *et al.* 2009; Bateman *et al.* 2011; Rothwell *et al.* 2011; Rudall *et al.* 2011; Spencer *et al.* 2015; Dörken & Rudall 2018). However, this bract scale/seed scale complex became variably modified within the different coniferous groups so that in some taxa bract and seed scale are fused to each other e.g. within Araucariaceae or Cupressaceae *s.l.*, while in other groups e.g. Cupressaceae *s.str.* the seed scale is strongly reduced, and the visible cone scale represents the bract scale (e.g. Page 1990; Farjon 2007, 2010; Gadek *et al.* 2000; Dörken 2012a, 2012b; Groth *et al.* 2011; Jagel & Dörken 2014, 2015a, 2015b; Dörken & Jagel 2017; Dörken & Rudall 2018). In previous studies on seed cones ontogeny it is suggested that among Cupressaceae *s.str.* the seed scale was continuously reduced to their ovules (Jagel & Dörken 2015a, 2015b). Only within basal species of Cupressaceae *s.l.* such as in the subfamilies *Cunninghamioideae* and *Athrotaxoideae*, tongue like structures below the ovules are visible until pollination time. These structures could be interpreted as vegetative parts of the seed scale. Within other basal Cupressaceae *s.l.* such as the subfamilies Taiwanioideae, Sequoioideae and Taxodioideae, the seed scale is fused to the upper surface of the bract scale, thus within these subfamilies the ovules are inserted on the upper surface of the cone scale (Jagel 2001a; Jagel & Dörken 2014; Schulz & Stützel 2007; Dörken *et al.* 2017; Dörken & Rudall 2018). In modern Cupressaceae *s.str.*, subfamilies Cupressoideae and Callitroideae, ovules are never inserted on the upper surface of the cone scale but always axillary. Compared to the basal Cupressaceae *s.l.* within the modern Cupressaceae *s.str.* the number of ovules per cone scale is strongly increased so that within *Cupressus* or *Callitris* up to four rows of ovules per cone scale are developed (Jagel & Dörken 2015a, 2015b). For the modern Cupressaceae *s.str.* it is suggested that the seed scales are completely reduced to their ovules and each row of ovules can be regarded as a descending accessory short shoot (e.g. Jagel 2001a, 2001b; Dörken 2012b; Jagel & Dörken 2014; Schulz & Stützel 2007; Dörken *et al.* 2017; Dörken & Rudall 2018). In addition to the increase in the number of ovules per cone scale a second major evolutionary trend within Cupressaceae is the dislocation of the fertile zone into apical parts of the seed cone so that sterile apical elements as can be found frequently in the basal taxa of Cupressaceae *s.l.* are always absent, maybe as an important improvement within the pollination mechanism to increase the success in pollen capture (Dörken & Jagel 2014). In basal Cupressaceae *s.l.*, only the cone scales in the middle of the seed cones are fertile while the basal and apical ones are sterile, so that in most basal taxa a sterile terminal piece is formed consisting of the tip of the cone axis and several sterile, incompletely separated cone scales (Jagel & Dörken 2015a). Among *Cupressus*, as one of the most modern and derived cupressaceous taxa, no sterile apical elements are developed, except in rare cases the apex of the cone axis is visible as a small central columella. Only among *Cupressus* species such as *C. vietnamensis* and *C. nootkatensis*, which are regarded as the most primitive extant species among the genus, the tip of the cone axis is frequently visible in the form of a distinct central columella, in more derived *Cupressus* species, however, only occasionally. Only in few derived *Cupressus* species, a distal pair of sterile and fused cone scales are found frequently as in e.g. *C. sempervirens*.

Our study of *C. glabra* seed cones clearly shows that the ovules, which are developed in up to four rows, are always located axillary and never on the cone scale surface (Figs 2C, 2D, 3C & 3D). Except for the small axillary buldge, no further structures or tissues were found which could be interpreted as representing vegetative parts of the seed scale. Investigation of the vasculature showed that each fertile bract/seed scale complex is supplied by more than one vascular bundle strand (Fig. 3A). There is always one collateral bundle strand supplying the cone scale and a further axillary one supplying the lowest row of ovules (Figs 2C, 3C-F). However, not all ovules within an axillary row have a vascular supply, only the oldest, outer ovules have a vascular connection, the younger central ovules are supplied by a cell-to-cell transport as is also the case for all distal rows of ovules (Figs 3E & 3F). The vascular bundle strands supplying the cone scale and the axillary one supplying the ovules do not fuse before entering the concentric stem bundle (Figs 2C, 3D & 3F). This branching pattern of the vasculature within a bract/seed scale complex is quite similar to that occurring in vegetative parts of the crown, as Dörken (2012) showed for *Metasequoia* and *Sequoia*. In these taxa in the vegetative part of the crown accessory short shoots are developed in the axil of a long shoot leaf (= bract). The bract and the axillary short shoots have a distinct separate vascular supply; the bract is supplied by a collateral vascular bundle, each accessory shoot with a concentric one. These vascular bundles do not fuse before entering the stem bundle of the long shoot, a type of vasculature which is quite similar to the one found in the fertile bract-seed scale complexes of the investigated *C. glabra*. This kind of vascular supply that Dörken (2012) described for the vegetative, sterile parts of *Metasequoia* and *Sequoia* gives strong support for the idea that each row of ovules within the *Cupressus* seed cone could be regarded as an accessory ovuliferous short shoot, whose axis, however, became greatly reduced to the ovules, so that finally no visible vegetative structures which could be interpreted as belonging to the seed scale could be found. Thus, the *Cupressus* seed cone could be regarded as representing a strongly reduced and condensed compound structure, which might have originated from a former more open and loose inflorescence, whose lateral, accessory fertile shoots became greatly reduced to their ovules.

4.2 Phyllotaxis within the cone

Within cupressaceous seed cones different types of cone scale arrangements can be found. Most of the basal Cupressaceae *s.l.* show helically arranged cone scales, e.g. all species of Cunninghamioideae, Athrotaxoideae, Taiwanioideae, Taxodioideae and most Sequoioideae (except *Metasequoia*). Within the derived modern Cupressaceae *s.str.*, the situation is much more diverse. Species of the subfamily Callitroideae show a large variability regarding the arrangement of cone scales which can be arranged in decussate pairs or in trimerous or occasionally tetramerous whorls, whereas cone scales of Cupressoideae are mostly decussate, except many *Juniperus* species showing cone scales in whorls of three (Krüssmann 1955, 1983; Dallimore & Jackson 1966; Farjon 2005, 2010; Eckenwalder 2009; Jagel & Dörken 2014, 2015a, 2015b). However, Jagel (2001b) described also for *Cupressus* seed cones consisting exceptionally of trimerous whorls of cone scales. The interpretation of these anomalous trimerous whorls is quite difficult. It may not to be a change in the phyllotaxis from decussate to whorled, but could be caused by an abortion of a basal cone scale, which leads to a dislocation and shift of the subsequent cone scales into a secondary, apparently “whorled” position. Within the investigated anomalous trimerous seed cone it seems that the vascular bundles supplying the cone scales would come out of the stem bundle of the cone axis all in the same plane as it would be common for typical shaped node showing trimerous whorls of leaves. However, it should be considered that if one of the basal cone scales was aborted in its primordial stage there would be no need to develop a vascular bundle for it, a fact that could lead to the impression that the distal vascular bundles supplying the three distal most cone scales are all in the same plane.

5 Conclusions

The investigation of *C. glabra* seed cones were focused on vasculature supplying the cone scales and the ovules. It was found that the cone scale and the inserted axillary rows of ovules were each supplied by its own vascular bundle strand, which gives strong support for the idea that the several axillary rows of ovules per cone scale can be regarded as descending accessory fertile shoots (= seed scales), which, however, got reduced to their ovules. Except to the vascular bundle strand supplying the lowest row of ovules, no additional visible vegetative structures were found that could be explained as belonging to the seed scale. This finding gives rise to the hypothesis that the former cupressaceous seed cone was a more open and loose branched structure, before it became greatly reduced to the compact structures typical of extant species.

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Addendum to the book review *Handbook of the World's Conifers*, 2nd edition, by A. Farjon.

See Maerki. D. (2017). Book review. *Bull. Cupressus Conservation Proj.* 6: 71-72.

The following photograph appears in the two editions of volume one, p. 333 in the 1st ed. and p. 343 in the 2nd ed., with the caption:

"**Figure 99**. *Cupressus torulosa* var. *torulosa* seed cones"

The cones and the foliage represented on the photo are however typical of *Cupressus lusitanica*. The cones are immature.

There is no information on the locality or on the date of the photo or if the specimen is cultivated or wild, but

see Maerki, D. (2017). Mislabelled *Cupressus* specimens at Kew, *Bull. Cupressus Conservation Proj.* 6: 72-73.

For comparison here are two photos of cultivated *Cupressus torulosa* and a series of cones from a third specimen.

Fig. 1: *Cupressus torulosa* immature cones, Lago Maggiore, Italy. 2012-9-21.

Noteworthy are the cone shapes and sizes, the number of cone scales, the umbo differences, the ultimate shoots disposed in flat sprays with a very different branching pattern, and the grey older shoots versus brown ones. A typical depression on some scales is visible in Fig. 1.

Fig. 2 (below): *Cupressus torulosa* immature cones with foliage, Villa Thuret, Antibes, France. 2008-7-25.

Fig. 3: *Cupressus torulosa* immature cones with foliage, Lago di Como, Italy. 2009-9-10.