Bulletin of the *Cupressus*
Conservation Project

Contents

Volume 4 Number 2

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Abstract : Morphology and ontogeny of seed cones of the Cupressoideae are presented. In this group the seed scale is completely reduced to the axillary ovules. The cone scale is not a fused bract/seed scale complex. Within derived Cupressoideae, high numbers of ovules (which are inserted in more than one row) are frequent. The rows are developed centrifugally and can be regarded as ascending accessory shoots. The fertile zone is shifted in distal parts of the cone by reducing sterile distal elements. In the most derived taxa, ovules are no longer inserted axillary, but terminally at the cone axis or alternate to the terminal cone scales. No argument was found for supporting a systematic splitting of *Cupressus* into two or more genera. Significant differences exist between cones of *Juniperus* section *Sabina* and *Juniperus* section *Juniperus*, suggesting a separation into two genera, *Sabina* and *Juniperus*. *Juniperus drupacea* is placed basal within section *Juniperus*. *Fokienia hodginsii* is best regarded as a member of the genus *Chamaecyparis* (*Chamaecyparis hodginsii* (Dunn.) Rushforth), and *Microbiota decussata* as a species of *Platycladus*. The new combination *Platycladus decussata* (Kom.) Jagel & Dörken (≡ *Microbiota decussata* Kom.) is given.

D. Maerki

Abstract : A new *Cupressus* hybrid is described from a cultivated plant. This tree is producing cones very different from those of the mother tree and which cannot be related to any known species.

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Cover photo : *Cupressus vietnamensis* in its natural habitat in northern Vietnam.
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Morphology and morphogenesis of the seed cones
of the Cupressaceae - part II
Cupressoideae

Summary

The cone morphology of the Cupressoideae genera *Calocedrus*, *Thuja*, *Thujopsis*, *Chamaecyparis*, *Fokienia*, *Platycladus*, *Microbiota*, *Tetraclinis*, *Cupressus* and *Juniperus* are presented in young stages, at pollination time as well as at maturity. Typical cone diagrams were drawn for each genus. In contrast to the taxodiaceous Cupressaceae, in Cupressoideae outgrowths of the seed-scale do not exist; the seed scale is completely reduced to the ovules, inserted in the axil of the cone scale. The cone scale represents the bract scale and is not a bract-/seed scale complex as is often postulated. Especially within the strongly derived groups of the Cupressoideae an increased number of ovules and the appearance of more than one row of ovules occurs. The ovules in a row develop centripetally. Each row represents one of ascending accessory shoots. Within a cone the ovules develop from proximal to distal. Within the Cupressoideae a distinct tendency can be observed shifting the fertile zone in distal parts of the cone by reducing sterile elements. In some of the most derived taxa the ovules are no longer (only) inserted axillary, but (additionally) terminal at the end of the cone axis or they alternate to the terminal cone scales (*Microbiota*, *Tetraclinis*, *Juniperus*). Such non-axillary ovules could be regarded as derived from axillary ones (*Microbiota*) or they develop directly from the apical meristem and represent elements of a terminal short-shoot (*Tetraclinis*, *Juniperus*). *Fokienia hodginsii* is here regarded as a member of the genus *Chamaecyparis* and *Microbiota decussata* as a species of *Platycladus*; hence, the new combination *Platycladus decussata* (Kom.) Jagel & Dörken (≡ *Microbiota decussata* Kom.) is given. The cone morphology of *Thuja* and *Thujopsis* shows conspicuous similarities and seem to be closely related. No supporting arguments could be found for a systematic splitting of *Cupressus* into different genera. Very obvious differences exist between the cones of *Juniperus* section *Sabina* and *Juniperus* section *Juniperus* that would support a separation in the two genera *Sabina* and *Juniperus*. It seems that *Juniperus drupacea* is placed at a basal position within section *Juniperus*. Thus, it could be treated at least formally into its own section.

1   Introduction

In part one of this series (JAGEL & DÖRKEN 2014) the cones of the taxodiaceous Cupressaceae (= "Taxodiaceae") were treated. In this part the mostly northern hemisphere taxa of the Cupressaceae s. str., in the subfamily Cupressoideae, will be treated. Part three (JAGEL & DÖRKEN in prep.) will focus on the southern hemisphere Callitroideae.

Within living Cupressoideae a spiral phyllotaxis is absent on adult branches as well as in the reproductive structures. It occurs only on seedlings of some genera. In most Cupressoideae leaves are decussate, only some taxa of *Juniperus* have whorls of three leaves. Within Cupressoideae the cone size is quite variable. Certain *Juniperus* species and *Microbiota* have the smallest coniferous cones of the northern hemisphere. In contrast cones of most *Cupressus* species are quite large (e.g. *Cupressus sempervirens*). Pollination drops of all Cupressoideae species are freely exposed to the airflow, so that they are easily visible from outside. The majority of Cupressoideae is monoecious; only within *Juniperus* do dioecious species exist. Within Cupressoideae the extremely variable number of ovules and seeds, from one ovule per cone scale (e.g. *Juniperus recurva*) to about 30 in *Cupressus*, is a conspicuous feature. Furthermore the arrangement of ovules in more than one row is important, a trait that is otherwise only rarely developed within taxodiaceous Cupressaceae (Sequoioideae) and for several genera of the Callitroideae. To analyse the arrangement of the seeds in a cone it is important to investigate the cones at pollination time or even better at an earlier point.

For systematics and also for identifying the taxa, the number of seeds in mature cones has limited relevance. However, in taxon descriptions this criterion is frequently used. Especially within taxa developing many ovules per cone scale, the number of seeds in mature cones is significantly less. Reasons

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for this are that not all ovules are successful in pollen capture, or pollen of other Cupressaceous genera being caught which can cause the withdrawal of the pollination drop which will not be secreted again, so that fertilisation does not take place. In some species pollination drops of neighbouring ovules can fuse to a larger one to increase the chance of pollen capture. However, when this occurs some of the ovules cannot be supplied with pollen (DÖRKEN & JAGEL 2014).

Material was collected in several German botanic gardens and parks at Bochum, Bonn, Dortmund, Münster Frankfurt a.M., Göttingen, Düsseldorf, the Grugapark in Essen, the Isle of Mainau (Konstanz), in the Palmengarten Frankfurt, in the living collection of Hubertus Nimsch (Bollschweil), in several public parks in Bochum and in garden centres in Bochum. Material of *Juniperus drupacea* was also collected in its natural habitat in the Parnon Mountains in the Peloponnese in Greece. The individuals of *Fokienia*, *Tetraclinis*, *Juniperus oxycedrus* and *Calocedrus macrolepis* were cultivated under glass.

2 Cone morphology of the Cupressoideae

2.1 *Calocedrus* Kurz

The monoecious genus *Calocedrus* comprises four species. Three Asian taxa *Calocedrus macrolepis* Kurz, *Calocedrus formosana* (Florin) Florin and *Calocedrus rupestris* Aver., T.H. Nguyên & P.K. Lôc as well as the North American *Calocedrus decurrens* (Torr.) Florin. *Calocedrus rupestris* from Vietnam was just described in 2004 (AVERYANOV *et al.* 2004, cf. also AVERYANOV *et al.* 2005).

Below the *Calocedrus* cones, 2-3 pairs of transitional leaves are developed. The arrangement of the decussate, fertile cone scales and ovules within the cone is more variable than first expected. The majority of cones consist of 3-4 pairs of cone scales. The most basal and most distal pairs are sterile. Two ovules are inserted in the axils of each fertile cone scale (figs 1A-1D, 2D). Differing from the common type, some cones developed two fertile pairs of cone scales. Within this cone-type the distal fertile scales develop a single median ovule each. A distinct terminal piece is always developed (figs 1A-1D), which consists of the tip of the cone axis and sometimes as well of a pair of not completely developed cone scales.

At pollination time the cones are plagiotropic or pointed slightly downwards (fig. 1F). A fusion of pollination drops was not observed. When a pollination drop has caught pollen grains, the pollination drop is drawn back. The pollen grains germinate and the micropyle closes by outgrowths of the inner wall. The exines of the pollen grains remain outside (fig. 1E). Mature cones are pendulous (fig. 2A). The basal sterile cone scales only become slightly thickened. The fertile pair of cone scales develops strongly. In contrast to the majority of Cupressaceae, they become more elongated than thickened. Thus, the cone scales become plate-like, on their abaxial side with a small prickle at the distal end, representing the tip of the cone scale (fig. 2B). The terminal piece fuses with the sterile pair of cone scales to a more or less three-parted plate. In its dimensions it reaches the sizes of the two fertile cone scales (fig. 2B). The cones mature in the first year and are long ovate in shape. Seeds of *Calocedrus* species are unequally winged (fig. 2C).

2.2 *Thuja* L.

Today five monoecious taxa are placed in the genus *Thuja*. The southwestern Chinese taxon *Thuja sutchuenensis* Franch., which was assumed to be extinct, has been rediscovered recently (XIANG *et al.* 2002). *Thuja koraiensis* Nakai is also native in East Asia (northeast China and Korea) as well as *Thuja standishii* Carrière (Japan: Honshu, Shikoku). The other two species, *Thuja plicata* Donn ex D.Don and *Thuja occidentalis* L. are native in North America.

Cones of *Thuja* consist of 3-5 decussate pairs of cone scales, preceded by 1-2 pairs of transitional leaves. Mostly the distal cone scales are sterile (figs 2F, 3F). Usually a distinct terminal piece is developed, which is formed by the tip of the cone axis and an incompletely developed pair of cone scales (fig. 2E). The ovules of the basal fertile cone scales are developed earlier as the distal ones (figs 2E, 2F). Usually three ovules develop in the axils of the basal cone scales, in smaller cones only two (frequently so in *Thuja occidentalis*). The number of ovules per cone scale decreases in the more distal scales (figs 2E, 3F). If three ovules are developed in a row, the outer ones develop first (centripetal). The development of a second row of ovules was found in some very young cones of *Thuja koraiensis* (fig. 2F, arrows).

At pollination time, cones are plagiotropic or slightly downwards pointed (figs 3A, 3B). After pollination they change their position significantly and turn about 90° in an upright position (fig. 3C). The cone scales

elongate strongly as in *Calocedrus* species. Mature cones are elongated and ovate, with a tiny prickle on the abaxial side in distal parts of the cone scales (fig. 3E). The cone scales do not get as strongly lignified as in most other cupressaceous taxa. They are leathery and remain more or less flexible. The cones mature in the first year. The flat seeds have distinct and equal wings.

2.3 *Thujopsis* Siebold & Zucc.

Thujopsis is monotypic. The single species *Thujopsis dolabrata* (Thunb. ex L.f.) Siebold & Zucc. is monoecious and native to Japan.

At pollination time cones are in a plagiotropic or slightly downward pointed position (fig. 4C). In contrast to *Thuja*, mature cones remain in this position and do not turn in an upright orientation (fig. 4D). Some fusion of pollination drops was observed. The cones consist of 3-5 decussate pairs of cone scales. In rare cases the most distal pair of cone scales is sterile (figs 4A, 4C, 4F). Transitional leaves are absent. Usually five ovules per cone scale are developed in the middle part of the cone. In this case three ovules develop in the first row and two in the second row (figs 4A, 4F). Furthermore in about 10% of the investigated cones in young stages one ovule develops in a third row. In general the distal fertile cone scales develop less ovules than the basal ones (figs 4A, 4B, 4F). In the distal part of the cone a terminal piece is less frequently developed as in *Thuja* (fig. 4B). Commonly two fertile cone scales can be found at the cone tip. At maturity cones of *Thujopsis* become strongly thickened and lignified (figs 4D, 4E). The cone scales are wedge-shaped at the base. The mature cone is more or less angular (fig. 4E) and therefore differs significantly from cones of *Thuja* (fig. 3E). *Thujopsis* cones mature in the first year. The seeds are winged, with equal wings.

2.4 *Chamaecyparis* Spach

Today six (or seven – see discussion below) species are included in the monoecious genus *Chamaecyparis*: *Chamaecyparis formosensis* Matsum., *Chamaecyparis taiwanensis* Masam. & S.Suzuki, *Chamaecyparis obtusa* (Siebold & Zucc.) Endl. and *Chamaecyparis pisifera* (Siebold & Zucc.) Endl. from East Asia and *Chamaecyparis lawsoniana* (A. Murray) Parl. and *Chamaecyparis thyoides* (Kunth) Endl. from North America. *Chamaecyparis funebris* (Endl.) Franco and *Chamaecyparis nootkatensis* (D. Don) Spach were placed in *Chamaecyparis* for a long time as well (e.g. KRÜSSMANN 1983, FARJON 1998), but are now placed in *Cupressus* (part 2.9).

At pollination time cones are plagiotropic or slightly downwards pointed. Fusion of pollination drops was not observed (fig. 5C). The cone consists of 4-5 pairs of decussate cone scales. The most basal pair is often sterile, or develops only 2 ovules per scale. Subsequent cone scales are fertile. The distal pair is generally sterile (figs 5A, 5F), and often fused with the rudimentary cone axis in a terminal piece. During early development of ovules, their number on facing cone scales is always the same. Normally in the middle of the cone the highest number of ovules per cone scale is developed. In most cases the number of ovules per cone scale is even-numbered. Within the investigated material the highest number was six. Ovules are obviously developed in one row and, in contrast to other Cupressaceae, develop from inwards to outwards (centrifugally). However, as the SEM of young cones distinctly show, this is not the case (JAGEL 2001, JAGEL & STÜTZEL 2001a). If four ovules are developed, they are inserted in two rows with two ovules in each row (fig. 5A, arrows at ovules of the second row), if six ovules are developed they are arranged in three rows. Uneven numbers of ovules per cone scale normally result from the abortion of single ovules. In only very rare cases a third median ovule is developed within a row (fig. 5B, arrow). This observation is important, because this ovule develops later than the outwards ones and reflects the centripetal development of the ovules within a row.

At maturity the cones remain in the plagiotropic position they had at pollination. The terminal piece develops as a distinct terminal shield (figs 5D, 5E). In a more or less central position on the back side of the mature cone scale the former scale-tip is developed as a tiny prickle (fig. 5E). The cones mature in the first year. The seeds are flat and winged.

2.5 *Fokienia* A. Henry & H.H. Thomas

Fokienia is monotypic. The single taxon *Fokienia hodginsii* A.Henry & H.H.Thomas is monoecious and native in China, Laos and Vietnam. The orientation of cones and pollination drops (fig. 6B), the structure

of cone scales (fig. 6D) and the distinct terminal piece (figs 6A, 6D) correspond to the situation as it is represented in *Chamaecyparis*. However, *Fokienia* cones are somewhat larger in size (at maturity about 1.5-2.5 cm) and they consist of more cone scales (up to 6-7 pairs of cone scales). In the investigated cones more than two ovules per cone scale could not be found (figs 6A, 6F). This might be a result of the limited material available; however, this number is also given by HENRY (1911) and FARJON (2005). The cones mature in the first year. The two wings of the seed are very unequal in size (fig. 6E).

2.6 *Platycladus* Spach

Platycladus is monoecious with a single species native in East Asia, *Platycladus orientalis* (L.) Franco. The genus was placed for a long time within *Thuja*, however they are not closely related.

At pollination time cones are plagiotropic or slightly downwards pointed. They often spread at an angle of 90° from the erect branches (fig. 7B). The number of the decussate cone scales and the arrangement of the ovules are quite variable (see JAGEL & STÜTZEL 2001b). Large cones consist of three fertile and two sterile pairs of cone scales. Small cones have only one fertile pair of cone scales, with only a single ovule per cone scale. In some cones abnormal large ovules were found (fig. 7A, arrow). Here two ovules have not completely separated during development and have a common integument. In the most common cone type two ovules were developed in the axils of each basal cone scale while the distal ones develop only one (figs 7C, 7F). Ovules of the lower cone scales develop earlier than those of the distal ones. The most basal and most distal pairs of cone scales are sterile. A terminal piece is not produced. Cones get closed by a ventral bulge of the cone scales, which later get strongly lignified. Each mature cone scale has a distinctly developed backward hooked spike (fig. 7E). Cones mature in the first year. The seeds are ovate and have no wings (fig. 7D).

2.7 *Microbiota* Kom.

Microbiota is monotypic. *Microbiota decussata* Kom. is native to alpine regions in East Siberia. It is not dioecious, as formerly stated, but monoecious (see VAN HOEY SMITH 1979, 1982, ZAMJATNIN 1963). However, many plants in culture show only a weak tendency to produce male flowers. In a garden centre in Bochum an individual with female as well as male flowers was found and planted into the Botanical Garden Bochum. But in the following years it only produced female cones.

The tiny seed cones are plagiotropic or slightly downward pointed at pollination time (fig. 8C). They consist of 2-3 decussate pairs of cone scales (figs 8A, 8F). The majority of the cones develop only one ovule, which is placed in an obviously terminal position, though a few develop two ovules. As the morphogenetic studies showed, the developing ovule could be in true terminal position of the cone axis from the beginning (fig. 8A) or it is first developed in the axil of a cone scale (fig. 8B). During further development the ovule shifts the rudimentary cone-axis in a lateral position and is not detectable in older stages (see also JAGEL & STÜTZEL 2001b). Thus this position could be termed as pseudoterminal. In spite of the strongly reduced cone, six different cone types could be found concerning the number and arrangement of ovules (JAGEL & STÜTZEL 2001b). Within 30 % of the cones the ovule was clearly inserted in the axil of a cone scale and a terminal sterile pair at the cones end. In rare cases cones with two ovules were found, which has not been reported before (compare JAGEL 2001, JAGEL & STÜTZEL 2001b). The cone gets closed by a strongly ventral bulge of the cone scale. Compared to their small size with about 4.5 mm in length the cone scales build a large prickle at the abaxial side (figs 8D, 8E). Cones mature in the first year. The seeds are ovate and have no wings (fig. 8D).

2.8 *Tetraclinis* Mast.

The genus *Tetraclinis* is represented by one monoecious species *Tetraclinis articulata* (Vahl) Mast., which is native in the Atlas mountains of NW Africa, from Morocco to Tunisia, on Malta and very locally in southeast Spain.

The fertile short-shoots are oriented plagiotropic before and at pollination time (fig. 9C). Already at this time the cone scales have a distinct ventral bulge. Fusion of pollination drops from neighbouring ovules was observed. Two pairs of transitional leaves are developed. The cone consist consequently of two pairs of cone scales. Sometimes they follow so closely at the cone axis that this is described as a tetramer whorl (e. g. DALLIMORE & JACKSON 1966, KRÜSSMANN 1972, PAGE 1990). This is not the case as ontogenetic

studies clearly show (JAGEL & STÜTZEL 2003). A terminal piece does not exist, only sometimes a short rudimentary cone-axis is detectable. Normally, six ovules per cone are developed (figs 9A, 9B, 9F), matching the data given in most literature. Due to the orientation of the seed wings it seems that three ovules are placed in the axils of the lower pair of cone scales. Data presented in literature are conflicting in this respect. KRÜSSMANN (1972) describes only the distal pair of cone scales as fertile. Then two or three ovules would be inserted at each cone scale. It is conspicuous that the frequently developed two ovules in the terminal region of the cone are seemingly inserted between the distal pair of cone scales. In several works data about the insertion of the ovules are not at all given (e.g. PILGER 1926, DALLIMORE & JACKSON 1966, PAGE 1990), which shows that the arrangement of the ovules is problematic. The developmental sequence of ovules and their exact orientation was solved by JAGEL (2001) (see also JAGEL & STÜTZEL 2003). It was shown that in over 90% of the cones with six ovules, the basal two cone scales carry two axillary ovules. The remaining two ovules are not inserted in the axil of cone scales, but alternate with them and thus they are in a terminal position. This explains why the ovules of the distal cone scales develop earlier than the basal ones (figs 9A, 9B). Next to this type of cone, some specimens were found with three ovules in the axils of the two basal cone scales, which develop centripetal. In even more rare cases the distal cone scales were fertile and each of them developed only a single ovule. In such a case the two terminal ovules are additionally developed above them.

Mature closed cones are cube-shaped and are placed more or less in an upright position (fig. 9D). The two distal cone scales are smaller than the basal ones. Mature cone scales are concave at their back. The former tip of the cone scale is developed as a small backward thorn in the distal third at the abaxial side (fig. 9E). Cones mature in the first year. The seeds have equal wings larger than the seed itself.

2.9   *Cupressus* L.

The genus *Cupressus* is monoecious. The number of species varies distinctly depending on the different systematic point of view between the different authors. FARJON (2005) suggests 17 species, the CUPRESSUS CONSERVATION PROJECT (2014) 33 species. The species are both extremely variable and similar to each other, so species delimitation is much disputed. Furthermore hybridisation appears to be frequent as well. *Cupressus* s. l. as it is treated here comprises also the species which were recently placed in other genera as *Xanthocyparis* Farjon & T.H.Nguyên (FARJON *et al.* 2002), *Callitropsis* Oerst. (LITTLE 2006), *Hesperocyparis* Bartels & R.A.Price (ADAMS *et al.* 2009) and *Neocupressus* de Laub. (DE LAUBENFELS 2009). The two species *Cupressus nootkatensis* D.Don and *Cupressus funebris* Endl., which were placed in *Chamaecyparis* for a long time, also belong to the genus *Cupressus* (JAGEL & STÜTZEL 2001a). The ontogeny of young cones and cones at pollination times of the following species were investigated in the present study: *Cupressus arizonica* Greene, *Cupressus bakeri* Jeps., *Cupressus duclouxiana* B.Hickel, *Cupressus funebris* Endl., *Cupressus nootkatensis* D.Don and *Cupressus sempervirens* L.

At pollination time cones are in a plagiotropic position (fig. 10C). Mature cones remain more or less in the same position. They consist species-specific of 2-7 decussate pairs of fertile cone scales. In the basal part of the cone a varying number of sterile cone scale pairs are developed. The distal ones, however, are mostly fertile. A terminal piece is absent (figs 10A, 10B, 10E, 10F, 11D, 11F). The size of the different *Cupressus* cones, the number of ovules per cone scale and the number of seeds per cone all vary considerably. *Cupressus nootkatensis* has very small cones and in most cones only two scales are fertile (figs 10B, 10E). Some ovules in a second row are developed in rare cases (JAGEL & STÜTZEL 2001a). Cones of *Cupressus vietnamensis* are fairly similar (fig. 10D). Cones of *Cupressus arizonica* and *Cupressus duclouxiana*, however, have mostly three fertile pairs of cone scales (fig. 10F), those of *Cupressus sempervirens* mostly six. In most species ovules are developed in a huge number, which are inserted in several rows in the axil of the cone scales. The innermost row (placed towards the cone-axis) develops first, the others follow successively in the direction towards the cone scale tip (centrifugally) (fig. 10A). Within a row the ovules develop from outwards to inwards (centripetally, fig. 10B). In cones with a very large number of ovules they are very closely packed and the rows and the order of development are sometimes difficult to see. *Cupressus* cones mature in the second year, between 14-25 months after pollination. They get strongly lignified and become globose (e.g. *Cupressus arizonica*, fig. 11A, *Cupressus vietnamensis*, fig. 11C, fig. 17 [p. 88] and *Cupressus nootkatensis*, fig. 11E, fig. 18 [p.88]) or ovate (e.g. *Cupressus sempervirens*, fig. 11B). Each cone scale is shield like and carries a more or less conspicuous spike on its back. The seeds are winged, but only with rudimentary wings. The number of mature seeds in such species is significantly

less than the number of initially developed ovules, because constantly several ovules do not get pollinated and abort.

2.10 *Juniperus* L.

Within the living Cupressaceae *Juniperus* is the largest genus. Due to its great variability of species and subspecies the number of species varies extremely widely in the literature. FARJON (1998) suggests 45 species, ADAMS & SCHWARZBACH (2013) about 75 species. *Juniperus* can be either monoecious or dioecious. However, dioecy in several species is not completely manifested, so that within species regarded as dioecious, monoecious individuals occur. The genus is native on all continents of the northern hemisphere, and one species, *Juniperus procera* Hochst. ex Endl., is native a short distance into the southern hemisphere in Africa (compare KERFOOT 1966). The determination of the *Juniperus* species is difficult, because large *Juniperus* collections are rare making it difficult to make direct comparisons of diagnostic features. In central European gardens several *Juniperus* species and especially their cultivars are represented, which can differ markedly from their wild forms. Traditionally the genus is subdivided into three sections: section *Sabina,* section *Juniperus* (= section *Oxycedrus*) and section *Caryocedrus*. A common feature of all *Juniperus* species is the development of the so-called Juniper "berries" (figs 12E, 13C, 14E, 15C). The cone scales do not become ligneous while maturing, but remain more or less fleshy for dispersal by animals. Detailed morphogenetic investigations of the *Juniperus* cones have been done by LEMOINE-SÉBASTIAN 1968a, 1968c, SCHULZ 2001 and SCHULZ *et al.* 2003).

2.10.1 Section *Sabina* Spach (= *Sabina* Mill.)

About 60 species are placed within section *Sabina* (ADAMS & SCHWARZBACH 2013). The taxa are species specific monoecious or dioecious. Investigations of young cones and those at pollination time have been done especially of *Juniperus chinensis* L., *Juniperus excelsa* M.Bieb., *Juniperus phoenicea* L., *Juniperus squamata* Lamb. and *Juniperus virginiana* L.

Most species of section *Sabina* develop scale-leaves. They are decussate or in whorls of three; the phyllotaxis can change within an individual shoot of an individual plant. Thus, in e.g. *Juniperus squamata* cones with scales in whorl of two can appear next to cones with scales in whorl of three on the same branch. Young plants and also branches of older individuals can develop needle-leaves (e.g. *Juniperus chinensis*). These needle-leaves differ from those developed within section *Juniperus* by the decurrent leaf bases. The cones consist of 1-4 pairs or trios of cone scales. The number of fertile cone scales varies considerably. In *Juniperus chinensis* often only one fertile pair of cone scales exist (figs 12C, 12D, 12F), in *Juniperus phoenicea*, however, up to three whorls of fertile cone scales (figs 13B, 13D). At the end of the cone axis a fertile or a sterile whorl of cone scales can be developed. Mostly, the ovules develop in the axil of the cone scale, within the investigated species 1-3 ovules per cone scale. They are arranged in one row. A second row of ovules was not found. Additionally, terminal ovules exist, which were developed directly in a terminal position. At the tip of a cone with a whorl of two scales of *Juniperus chinensis* two ovules were observed, that might be alternating to the distal pair of cone scales (compare SCHULZ *et al.* 2003). Within the investigated taxa of section *Sabina* a particular case is represented by *Juniperus squamata*, where only one single terminal ovule develops (figs 13E, 13F). From morphogenetic investigation this ovule is developed terminal and not initially inserted in the axil of a cone scale (SCHULZ *et al.* 2003).

At pollination time cones of section *Sabina* are in a plagiotropic or downward position (figs 12A, 12B, 13A), except in *Juniperus squamata*. At this point of time the cone scales show already a ventral swelling (fig. 12C). Pollination drops of neighbouring ovules can fuse to larger ones. After pollination maturing cones were closed by a strong swelling of the cone scales. The cones mature in the first year (e.g. *Juniperus virginiana*) or in the second year (e.g. *Juniperus chinensis*). At maturity cones do not open and the seeds do not get released; seed wings are absent. The seeds often show more or less sharply developed ridges.

2.10.2 Section *Juniperus*

Following ADAMS & SCHWARZBACH (2013) 14 species are included within section *Juniperus* (= section *Oxycedrus* Spach). All of them are dioecious. Investigation of young cones and those at pollination time was done on *Juniperus communis* L., *Juniperus conferta* Parl., *Juniperus oxycedrus* L. and *Juniperus rigida* Siebold & Zucc.

The species of section *Juniperus* have needle-leaves arranged in whorls of three. These leaves are distinctly separated from the shoot axis. In contrast to the leaves developed in taxa of section *Sabina*, the leaf base is not decurrent. Only a few leaves directly below the cones are scale-like. A distinct feature within section *Juniperus* is the arrangement of ovules within the cone. They are not developed axillary, but inserted alternating with the uppermost cone scales (figs 14B, 14C, 14F). Within the investigated species the cones consisted of 1-2 pairs of cone scales, which have to be described as sterile, because the ovules cannot be associated with them. In the morphogenetic investigations in rare cases some additional ovules could be observed in the axils of the cone scales below the alternating ovule-whorl. In very rare cases an additional second terminal ovule-whorl was found, alternating with the regular one. (SCHULZ *et al.* 2003). At pollination time cones of section *Juniperus* are arranged on the branch without a specific orientation (figs 14A, 14B). A fusion of pollination drops was not observed. The cones mature in the first or second year.

2.10.3 Section *Caryocedrus* Endl. (= *Arceuthos* Antoine & Kotschy)

Only one dioecious taxon *Juniperus drupacea* Labill., native in Greece, Turkey, Lebanon and Syria, is placed within this section. Phyllotaxis and structure are similar to section *Juniperus*. The cones consist of three whorls of three cone scales (fig. 15F). In the most cases the ovules are inserted in the axils of the three cone scales of the distal whorl, sometimes on the six cones scales of the uppermost two whorls (fig. 15A), one ovule per cone scale (see also LEMOINE-SÉBASTIAN 1968a, 1968c). The three ovules are initially not fused with each other. Furthermore some cones were found which only developed a single terminal ovule (fig. 15B). Mature cones are unusually large, about 2-3.5 cm in diameter. They distinctly show the edges of the cone scales which fuse with each other (fig. 15C) at maturity. They mature in the second or third year. In mature cones the three ovules fuse to a hard nut-like "stone" (figs 15D, 15E, compare also e.g. NEGER & MÜNCH 1952), which has obviously not been observed in other *Juniperus* species.

3 Discussion

3.1 Proportions of bract and seed scales

In none of the living Cupressoideae could outgrowths of the seed-scales be found, compared to some Cupressaceae (*Athrotaxis* and *Cunninghamia*) where they are still developed. Vegetative elements of a seed scale are never present. Within this subfamily the ovules are never inserted on a scale but mostly in the axils of the bract scales, or in a few taxa they develop terminally at the cone-axis or in a terminal whorl. Thus, the cone scale exclusively represents the bract scale, and is not a fusion product of bract and seed scales. Thus, the bract/seed scale complex, which is generally supposed to be developed within all living Cupressaceae s. l., does not exist in the Cupressoideae. The seed scale is strongly reduced and only represented by the ovules.

3.2 Arrangement of ovules within the cones and their developmental sequence

A further phylogenetic derived feature, which can be only found elsewhere in taxa of the subfamily Sequoioideae, is the development of ovules in more than one row. The ovules always develop in the same order; within a cone the developmental sequence follows at a short distance from proximal to distal, within a row from outwards to inwards (centripetally), and the innermost row of ovules, which is located directly at the cone axis, always develops first, the other ones develop successively outwards (centrifugally). In most cases, more ovules are developed within the first row than in the subsequent rows. As shown in JAGEL & DÖRKEN (2014) several rows of ovules can be understood as ascending accessory short shoots. Each of the short shoots is reduced to the ovules, a shoot axis no longer being detectable. The only genus where a centrifugal development of the ovules within a row seems to exist is *Chamaecyparis*. However, *Chamaecyparis* represents an exceptional case, where several rows of ovules develop, but each of them bears only two ovules.

Additional to the axillary ovules, non-axillary ovules exist within three genera of the Cupressoideae, *Microbiota*, *Tetraclinis* and *Juniperus*. Within *Juniperus* section *Juniperus* it is the rule. The morphogenetic investigations in *Microbiota* showed that the terminal ovule could have been primarily developed in an axillary position. During the secondary growing processes, the ovule is shifted towards the

tip of the cone-axis into a subterminal position, and the tip of the cone axis is no longer visible in older cones (compare JAGEL & STÜTZEL 2001b).

Within *Tetraclinis* and the species of *Juniperus* section *Juniperus*, the terminal ovules are not derived from a primary axillary position. This result is in contrast to former opinions. However this had been assumed at a time when cones in *Juniperus* were regarded as flowers, and the cone scales as being macrosporophylls (e.g. KUBART 1905, RENNER 1907). With this background it was not understood how ovules could be developed without a sporophyll. However, a postulated secondary shifting of ovules could not be observed anywhere (compare SCHULZ 2001, SCHULZ *et al.* 2003); the ovules were not secondary shifted in such a position. They develop directly from the apical meristem. As short shoots, reduced to the ovules, are inserted in the axils of the bract scales, this is also realised at the end of the cone-axis. In this case a terminal strongly reduced fertile short shoot determinates the growth of the cone axis (SCHULZ 2001, JAGEL 2001, SCHULZ *et al.* 2003, JAGEL & STÜTZEL 2003). Thus, terminal as well as axillary ovules are explainable. Within cones, where axillary ovules develop additionally, it is conspicuous that the terminal ones develop first. This obviously contrasts with the general developmental sequence within a cone from proximal to distal. However, it could be explained because the apical meristem has a slight developmental time advantage in comparison to the axillary meristems of a cone scale.

In *Tetraclinis* terminal ovules were not observed before the investigations of JAGEL (2001). They are not as conspicuous as in *Juniperus*. Cone scales of *Tetraclinis* are decussate, so that the non-axillary, alternating ovules come to lie above the cone scales and not between them as in *Juniperus*. In addition, in *Tetraclinis* axillary ovules exist as well carried by the proximal cone scales (JAGEL & STÜTZEL 2003). Such an existence of axillary and non-axillary ovules in a cone appears also in rare cases of cones in *Juniperus* (SCHULZ & al. 2003).

A morphological series within the Cupressoideae shows the tendency to dislocate the fertile zone of the cone in more distal parts (fig. 16). Therefore the terminal piece and/or the sterile cone scales get more and more reduced. Within strongest derived genera of the Cupressoideae more frequently fertile distal cone scales or pseudoterminal or terminal ovules (*Microbiota, Tetraclinis, Juniperus*) are developed at the tip of the cone-axis. Due to the reduction of the sterile elements at the tip of the cone, the proliferations found quite frequently in cones of several taxodioidaceous Cupressaceae, are mostly impossible in the Cupressoideae (and in the Callitrioideae as well). In Cupressoideae such a case could obviously only be found till now in the relatively primitive species *Chamaecyparis formosensis* (LI 1972).

3.3   Phylogenetic relationships within the Cupressoideae

Summarising species to a higher systematic rank as e.g. sections or genera is mostly subjective. Nowadays, results of morphological as well as anatomical studies are often critically checked with the results of published molecular investigations. This is important to see if such a potential taxon is monophyletic and therefore legitimate. However, even today molecular studies in the same groups can have contradictory results (e.g. LITTLE 2006 and ADAMS *et al.* 2009) and especially in groups which are quite difficult to determinate as in *Cupressus* and *Juniperus*. The critical view about which species were involved within such investigations may be a factor. In the present study only female cones were included. Thus, the conclusions about the definition of higher-ranking taxa are limited. However, it should be expected that the reproductive parts have more relevance than the vegetative ones (especially foliar features), because changes in the generative part of a plant could have a directly influence on the propagation of a taxon. In the following similarities/differences between the female cones are discussed, especially in respect to the question, how our results fit to the general accepted opinion about the interfamiliar systematic and to molecular cladograms.

Due to the similarities within the cones, ***Calocedrus*** was often placed within *Libocedrus* s. l. in former times (e.g. NEGER & MÜNCH 1952, JACKSON 1946, KRÜSSMANN 1955). That this similarity is only superficial could be shown in the morphogenetic investigations of young cones, which showed a high variability of the ovule arrangements on the one hand. On the other hand the development of the distinct terminal plate in *Calocedrus* is a fundamental difference to the cones of the *Libocedrus* group, which never develop sterile cone scales or a terminal piece at the distal end of the cone (JAGEL & DÖRKEN in prep.). With a small number of ovules per cone scale and a distinct terminal piece *Calocedrus* represents primitive features within cone morphology.

These cones have similarities with those of **Thuja**. Nearly all molecular studies show a basal position of *Thuja* within living Cupressoideae. *Thuja* also shows a terminal piece which, however, does not so strongly dominate the cone morphology as those developed in *Calocedrus*. Cone scales of *Thuja* are always significantly longer than thick, and relatively flat. Their lignification is not as strong as in the more derived genera of the Cupressoideae. In morphogenetic investigations a second row of ovules could be found in *Thuja*, a feature which is not found in *Calocedrus*. However, this suggests a relationship with **Thujopsis**, where two rows of ovules are common. On the first view cones of *Thuja* and *Thujopsis* are not quite similar at either pollination time or maturity. However, in respect to the number and insertion patterns of the ovules, *Thujopsis* cones representing in principle a large, seed rich *Thuja* cone. In comparision with *Thuja*, a trend is recognisable in *Thujopsis* to develop fertile cone scales at the distal end of the cones and to reduce increasingly the terminal piece. Mature cones of *Thujopsis* have a completely different shape to those of *Thuja*. Furthermore the cone scales are strongly lignified in *Thujopsis*. Also the change of orientation of the cone after pollination to an upright position is absent in *Thujopsis*. In molecular analyses *Thujopsis* represents the sister clade to *Thuja* (e.g. YANG *et al.* 2012).

Due to the globose shape of the cones and the shield-like cone scales the cones of **Chamaecyparis** are quite similar to those of *Cupressus*. Thus, both taxa were regarded as closely related for a long time, while the size of the cones and the structure of the branches have been regarded as the main differences. Problematical taxa with cones intermediary in size and in addition with somewhat flattened branchlets as represented in *Cupressus nootkatensis* and *Cupressus funebris* remain. Traditionally they were often placed in *Chamaecyparis*. However, in detailed morphological and anatomical analyses it has been shown that these similarities are just superficial, and *Cupressus nootkatensis* and *Cupressus funebris* clearly belong to *Cupressus* (JAGEL & STÜTZEL 2001a). Cones of *Cupressus nootkatensis* fit quite well in a morphological series with other *Cupressus* species and agree in all relevant features with each other (e.g. absence of a terminal piece, fertile cone scales at the cone tip, appearance of several rows of ovules, fusion of pollination drops). In contrast *Chamaecyparis* is characterized by the special arrangement of the ovules (see above). Also the molecular analyses show that *Chamaecyparis* and *Cupressus* are not closely related to each other (e.g. YANG *et al.* 2012). **Fokienia hodginsii** is so closely related to *Chamaecyparis* that it should be treated as *Chamaecyparis hodginsii* (Dunn) Rushforth (RUSHFORTH 2007); genetic studies also place it within *Chamaecyparis* (MAO *et al.* 2010). Within the cones and also in the vegetative parts no fundamental structural differences exist (see also JAGEL & STÜTZEL 2001a). *Fokienia* always develops just two ovules per cone scale, so that the developmental sequence of ovules as is characteristic in *Chamaecyparis* could not be observed.

Cones of **Platycladus** differ in fundamental features from those of *Thuja*, in which it had been placed for a long time. However, a close relationship does not exist (JAGEL & STÜTZEL 2001b), which has also been supported by molecular studies (e.g. GADEK *et al.* 2000, YANG *et al.* 2012). A terminal piece is absent and maturing cones get strongly lignified. The shape of cones and the cone scales are different as well. Furthermore *Platycladus* cones do not change their orientation after pollination and the ripe seeds are oval and have no seed wings. A morphological reduction line from *Platycladus* to **Microbiota** could be shown (JAGEL & STÜTZEL 2001b). The arrangement of the ovules in the cones shows that the *Microbiota* cones just represent small *Platycladus* cones. Furthermore the two taxa agree in the ovate, wingless seeds. *Microbiota* represents obviously an alpine relative of *Platycladus*. Taking these results into account, we propose the following new combination:

Platycladus decussata (Kom.) Jagel & Dörken, **comb. nova**.
Basionym: *Microbiota decussata* Kom. in Bot. Mater. Gerb. Glavn. Bot. Sada R.S.F.S.R. 4: 180. 1923.
Lectotype: Russia, Far Eastern Federal District, Primorsky Krai, Olginsky District, Mt. Zamo-Dynza, ["in monte Zamo-dinzsa non procul a fossis Sutschanensibus"], 12 July 1921, *I. K. Schischkin 158* (LE) (designated by Farjon 2005).

The question remains open to know if *Microbiota* is the more primitive or the more derived taxon. The development of a pseudoterminal ovule has to be regarded as a derived feature.

The genus **Cupressus** appears to be a phylogenetically modern taxon, at least as it is represented by its recent taxa. This is expressed by the high number of ovules in most species and the several very similar species as well as hybridisation between them. Currently, some authors divide *Cupressus* into two or more

different genera. FARJON *et al.* (2002) described a new genus *Xanthocyparis* based on the newly discovered Vietnamese species, *Xanthocyparis vietnamensis* Farjon & Hiep. They also transferred *Cupressus nootkatensis* (Alaska to northern California) into *Xanthocyparis*, as *Xanthocyparis nootkatensis* (D.Don) Farjon & D.K.Harder. Structural differences in the reproductive structures to separate this genus from *Cupressus* do not exist. The presence of needle leaves instead of scale leaves on adult branchlets has been described as a significant feature of *Xanthocyparis vietnamensis*. However, such needle leaves are known from several other cupressaceous taxa e.g. in *Juniperus chinensis*, where they are not uncommon. These leaves are important for horticultural selections as well, and a huge amount of needle-leafed cultivars exist. The needle leaves of *Xanthocyparis vietnamensis* could be perhaps regarded as a diagnostic feature to separate *Cupressus vietnamensis* from *Cupressus nootkatensis*, because further differences between the two species are difficult to find (compare data given by FARJON *et al.* 2002). As mentioned above, and explained by JAGEL & STÜTZEL (2001a) in detail, cones in *Cupressus nootkatensis* are representing undoubtedly a small *Cupressus* cone. As the cones of *Xanthocyparis vietnamensis* were described by FARJON *et al.* (2002) as more or less identical to those of *Xanthocyparis nootkatensis*, the species also has to be placed logically within *Cupressus*, and treated as *Cupressus vietnamensis* (Farjon & T. H. Nguyên) Silba (SILBA 2005). According to the molecular analyses by YANG *et al.* (2012), *Cupressus vietnamensis* and *Cupressus nootkatensis* are placed at the base of the new world *Cupressus* species, however, they do not represent a monophyletic pair.

The results of molecular analyses of the genus *Cupressus* are conflicting. They often led to nomenclatural changes, although diagnostic non molecular features are not given for them. Following LITTLE (2006) *Cupressus* has a paraphyletic origin. According to that study, *Juniperus* has evolved out of the new world clade of *Cupressus*. As a consequence of this, he placed all new world *Cupressus* species into the genus *Callitropsis* (type species *C. nootkatensis*). ADAMS *et al.* (2009) placed *Cupressus nootkatensis* in the genus *Callitropsis*, but all other new world *Cupressus* species in a newly described genus *Hesperocyparis*. Following morphological features DE LAUBENFELS (2009) placed the new world *Cupressus* species (excluding *Cupressus nootkatensis*) in the new genus *Neocupressus*, though according to the rules of botanical nomenclature this genus name is illegitimate. The number of cotyledons, differences in the characteristics of the subsequent leaves (development of monomorphous leaves versus lateral-/median leaves), as well as the structure of the branchlets were used by DE LAUBENFELS (2009) as explanation. In their molecular studies MAO *et al.* (2010) came to the result that *Cupressus* s. l. is monophyletic and represents the sister group to *Juniperus*. In the old world clades as well as in the new world clades of *Cupressus*, the species developing small, simple cones with fewer seeds are placed in a basal position. Furthermore it is observed that the Asian *Cupressus vietnamensis* is located at the base of the new world clade.

In this present study the genus *Cupressus* senso lato is maintained. Thus, intergeneric hybrids (× *Cupressocyparis* Dallim. = × *Cuprocyparis* Farjon = × *Neocupropsis* de Laub.) do not exist. No strong morphological differences separating the new world *Cupressus* species from the old world ones have been found. Also the listed data of DE LAUBENFELS (2009) are not usable in individual cases.

The obviously common feature of all ***Juniperus*** species is the fleshy berry-like cone. Its general structure is, however, quite variable, and the differences in cone morphology between section *Juniperus* and section *Sabina* are obviously so distinct, that the genus *Juniperus* could be split into two genera. Differences in the cone morphology are distinctly visible throughout the morphogenesis of the cone and at pollination time. Rare cases of cone types allow the construction of a hypothetical ancestral *Juniperus* cone with axillary ovules in the basal parts and non-axillary ovules at the terminal end. Such a "complete" cone could be the base for developed cones of section *Juniperus* on one hand with non-axillary ovules and cones of section *Sabina* on the other hand with mostly axillary ovules. Actually such a cone exists in *Tetraclinis articulata* and in some types of *Juniperus drupacea* (LEMOINE-SÉBASTIAN 1968c).

The basis for the exceptional position of *Juniperus drupacea* is the description by ANTOINE & KOTSCHY (1854) of its own genus *Arceuthos*. The unusual large sized mature cones played an important role, as well as the three ovules which fuse to a stone-like structure (e.g. PILGER 1931). Moreover the structure of the male reproductive structures is quite remarkable. In contrast to all other *Juniperus* species (and also all Cupressaceae species), it is not a simple male flower which develops from a bud, but a whole branched structure (compare LEMOINE-SÉBASTIAN 1968b, MAERKI & FRANKIS 2015).

The phyllotaxis corresponds to those of section *Juniperus*. However, the obviously most frequent axillary arrangement of ovules is quite untypical for section *Juniperus*. The formation of a "stone" is obviously absent in all other *Juniperus* species. Thus it can be regarded as an autapomorphy, and is therefore not helpful for relationship analyses. Following the molecular tree given by MAO *et al.* (2010) and ADAMS *et al.* (2013), which contains nearly all *Juniperus* species, *Juniperus drupacea* represents the sister group of the section *Juniperus*, which could support the placement in a separate section *Caryocedrus*.

Acknowledgments

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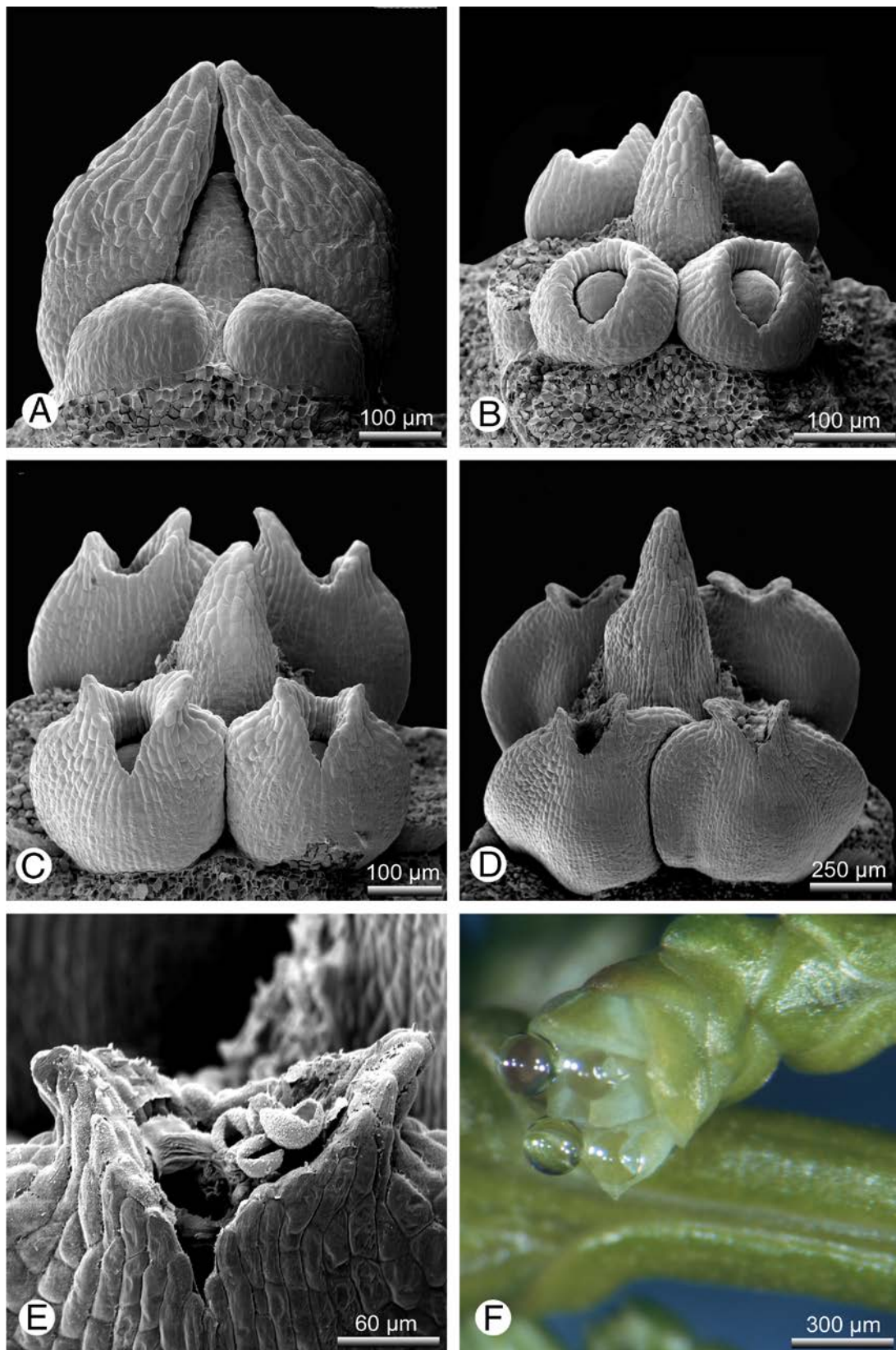
Fig. 1: Cone morphology of *Calocedrus*.

A: *Calocedrus decurrens*, young cone with developing ovules, integument still not developed (SEM-picture, terminal piece and distal sterile cone scales present, fertile cone scale removed). **B:** *Calocedrus decurrens*, young cone with developing ovules, beginning of the integument-development (SEM-picture, terminal piece present, cone scales removed). **C:** *C. decurrens*, young cone with developing ovules, micropyles of ovules becoming two-lipped (SEM-picture, terminal piece present, cone scales removed). **D:** *Calocedrus decurrens*, cone at pollination time (SEM-picture, terminal piece present, cone scales removed). **E:** *Calocedrus decurrens*, micropyle of an ovule after resorption of the pollination drop, the exines of the germinated pollen grains remains at the rim of the micropyle (SEM-picture). **F:** *Calocedrus formosana*, cone with pollination drops in natural orientation.
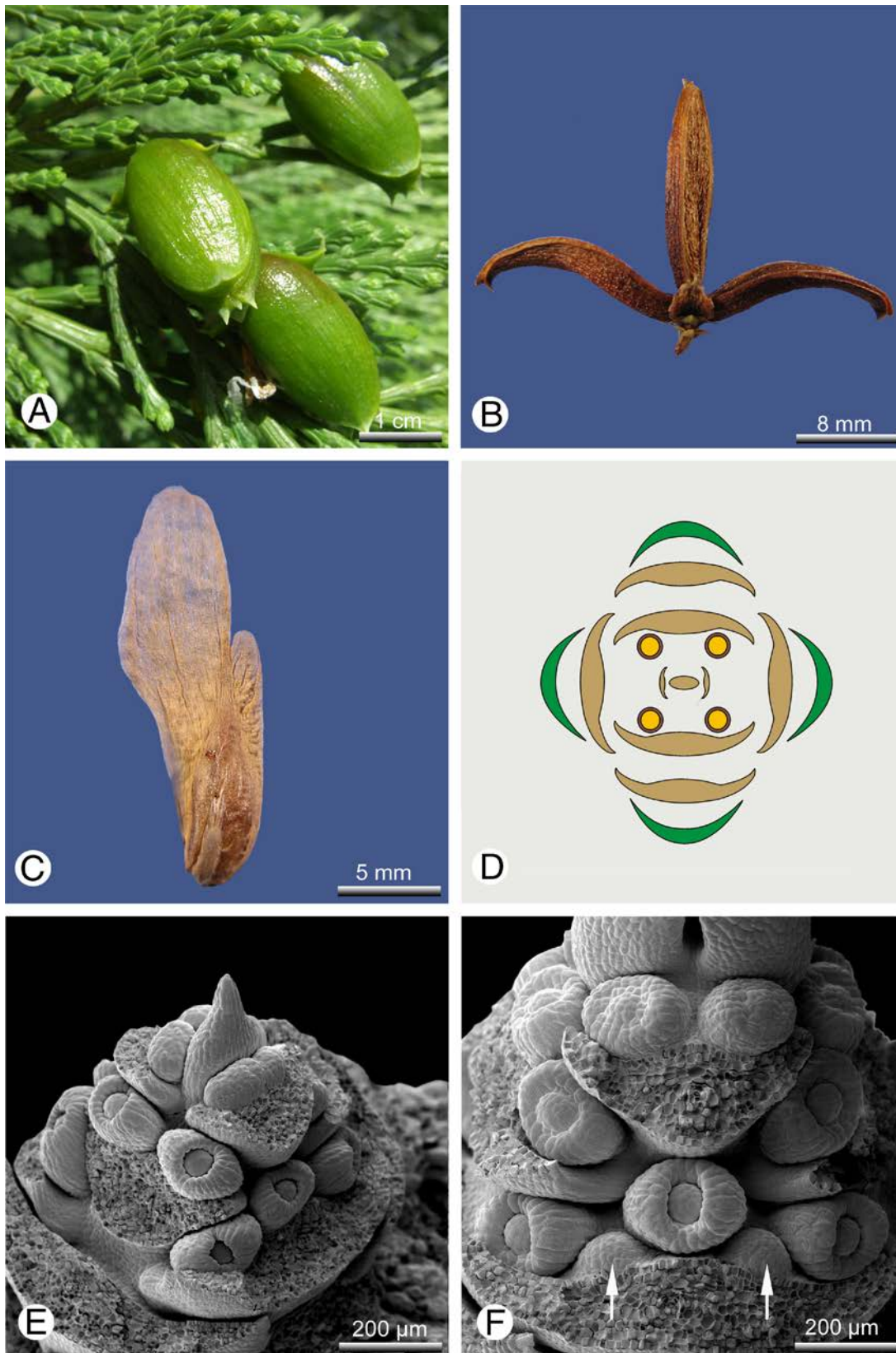
Fig. 2: Cone morphology of *Calocedrus decurrens* and *Thuja koraiensis*.

A: *Calocedrus decurrens*, immature pendulous cones on a branch. **B:** *Calocedrus decurrens*, mature open cone in lateral view with two prominent cone scales and a central plate. **C:** *Calocedrus decurrens*, unequally winged seed. **D:** *Calocedrus*, Typical cone diagram according to fig. 1, A to D (brown = cone scales, dark green = leaves). **E:** *Thuja koraiensis*, young cone with developing ovules; ovules develop from proximal to distal in the axils of the cone scales; cone ending in a terminal piece (SEM-picture, cone scales removed). **F:** *Thuja koraiensis*, young cone with developing ovules, arrows marking two ovules in a second row.
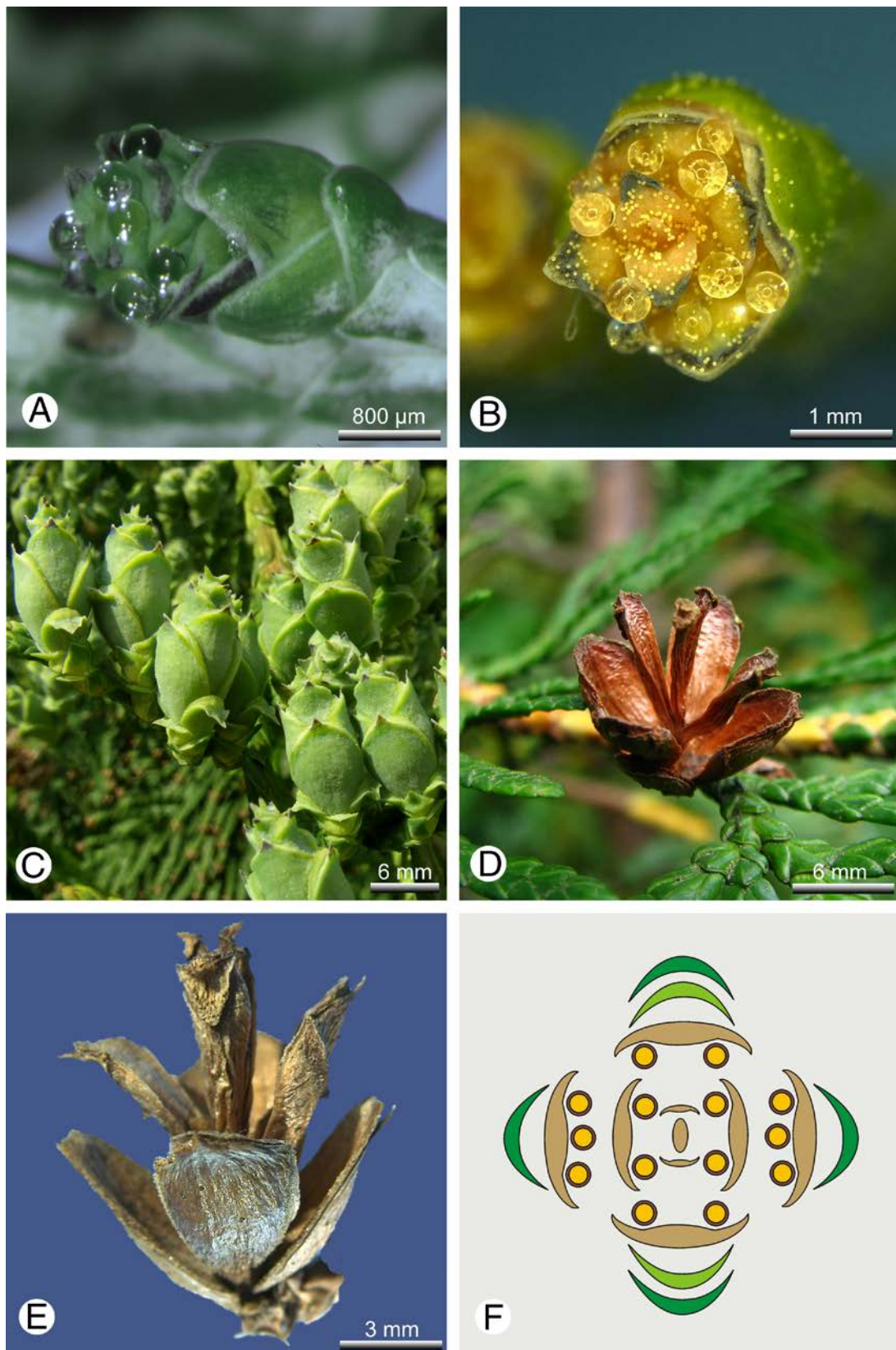
Fig. 3: Cone morphology of *Thuja*.

A: *Thuja koraiensis*, cone with pollination drops in the natural orientation. **B:** *Thuja plicata,* cone with pollination drops just have been pollinated before resorption of the drops. **C:** *Thuja plicata,* immature cones on a branch in erect position. **D:** *Thuja occidentalis,* mature cone on a branch in erect position; **E:** *Thuja plicata,* mature open cone in lateral view. **F:** Typical cone diagram (brown = cone scales, light green = transitional leaves, dark green = leaves).
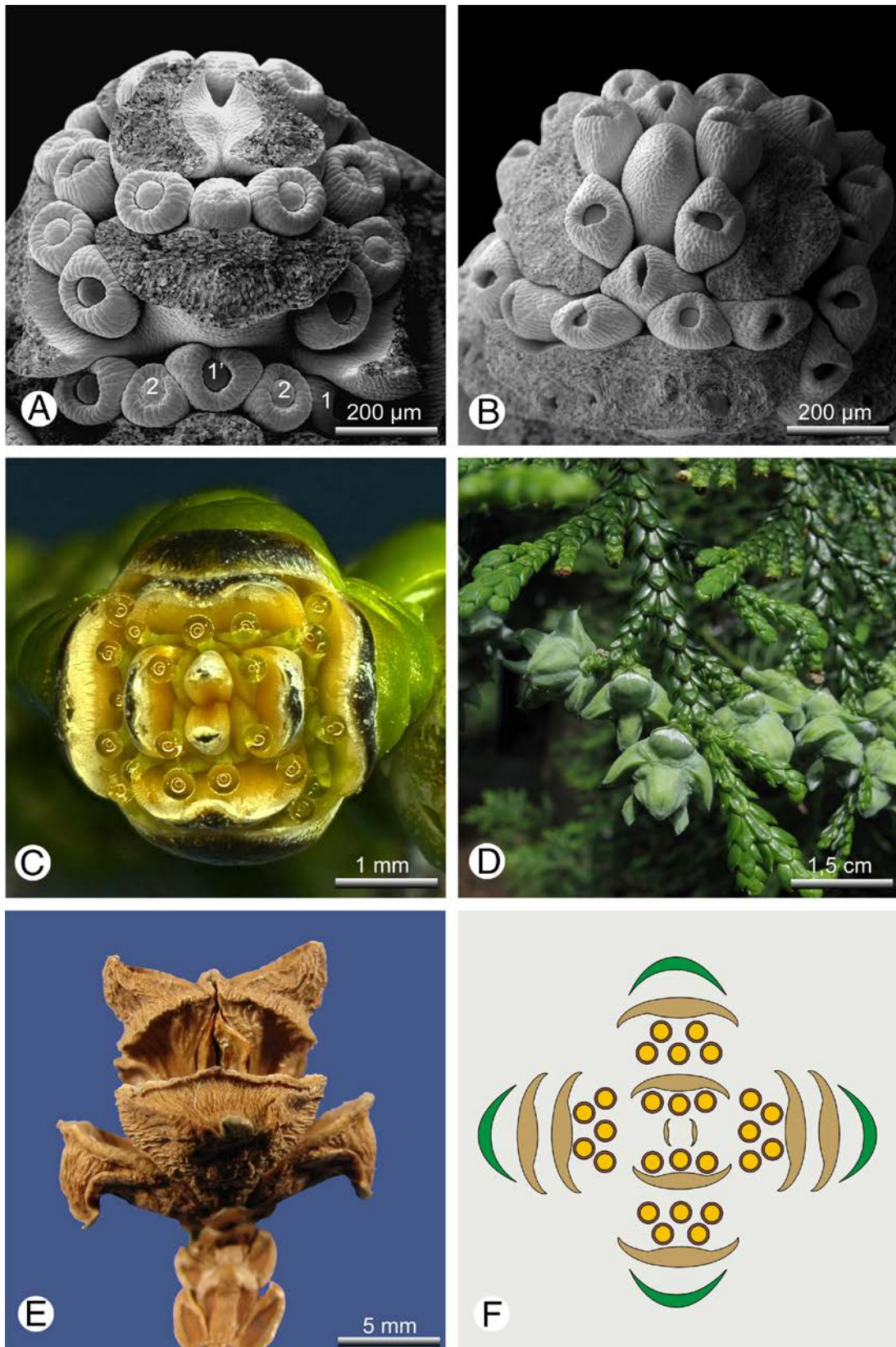
Fig. 4: Cone morphology of *Thujopsis dolabrata*.

A: Young cone: ovules develop from a proximal to a distal position in the axils of the cone scales and centripetally within a row; proximal cone scales with two rows of ovules, distal end with two sterile cone scales (SEM-picture, cone scales removed). **B:** Young cone with fertile cone scale at the distal end and a terminal piece (SEM-picture, cone scales removed). **C:** Cone with pollination drops, top view. **D:** Immature cones on a branch. **E:** Mature cone in lateral view. **F:** Cone diagram according to A (brown = cone scales, dark green = leaves,).
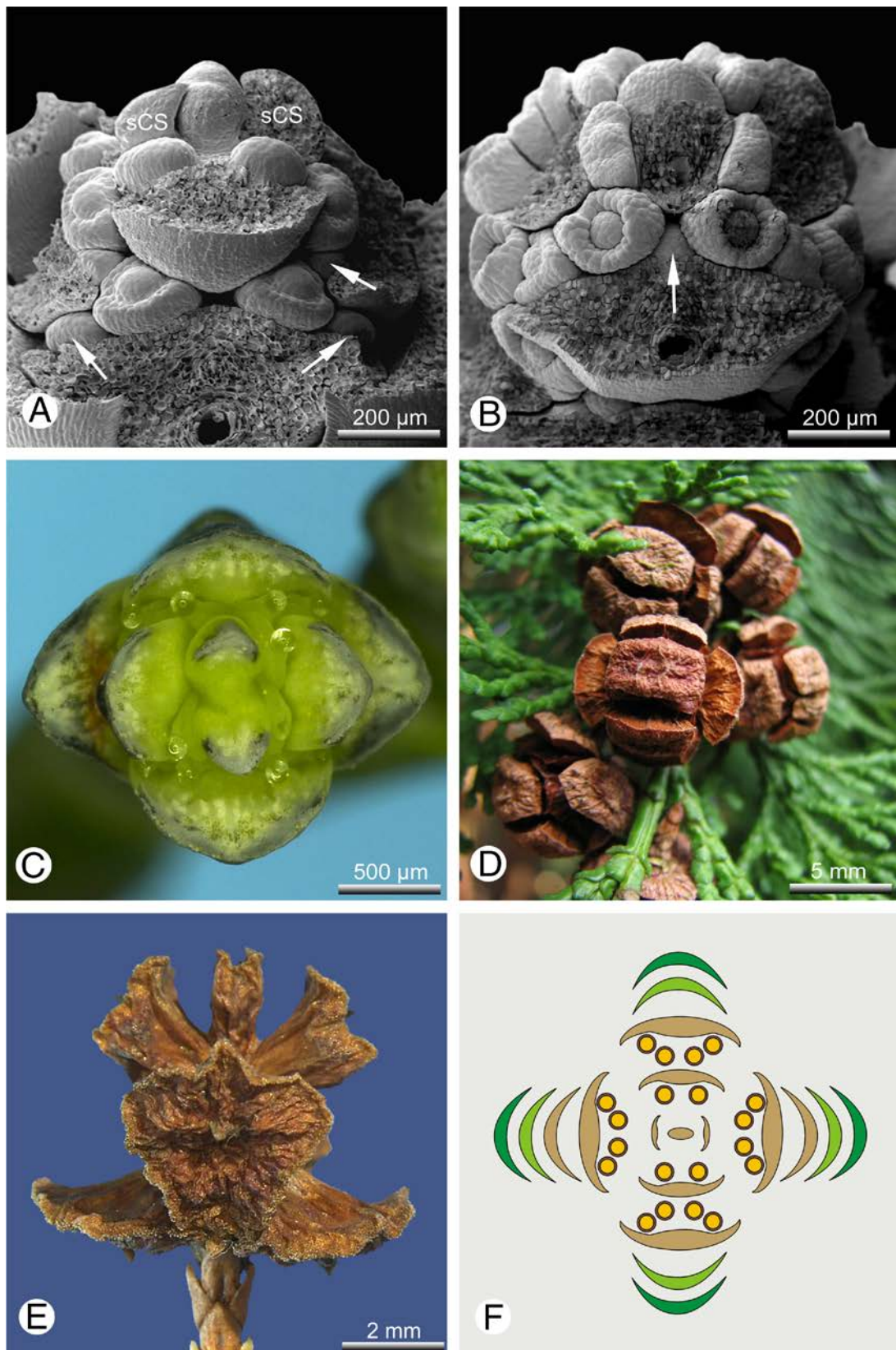
Fig. 5: Cone morphology of *Chamaecyparis*.

A: *Chamaecyparis lawsoniana*, young cone with developing ovules; the lower and middle fertile cone scales develop 4 ovules, the outer ones (arrows) develop later than the inner ones, they are inserted in the second row; sterile pair of cone scales (sCs) and terminal piece (T) at the cones end (SEM-picture, cone scales removed). **B:** *Chamaecyparis obtusa*, young cone with developing ovules; rare case with a developing median ovule in the second row (arrow). **C:** *Chamaecyparis lawsoniana*, cone with pollination drops, top view. **D:** *Chamaecyparis obtusa*, mature cones on a branch, top view of the shield-like terminal piece. **E:** *Chamaecyparis lawsoniana*, mature cone in lateral view with terminal piece. **F:** Typical cone diagram according to A (brown = cone scales, light green = transitional leaves, dark green = leaves).
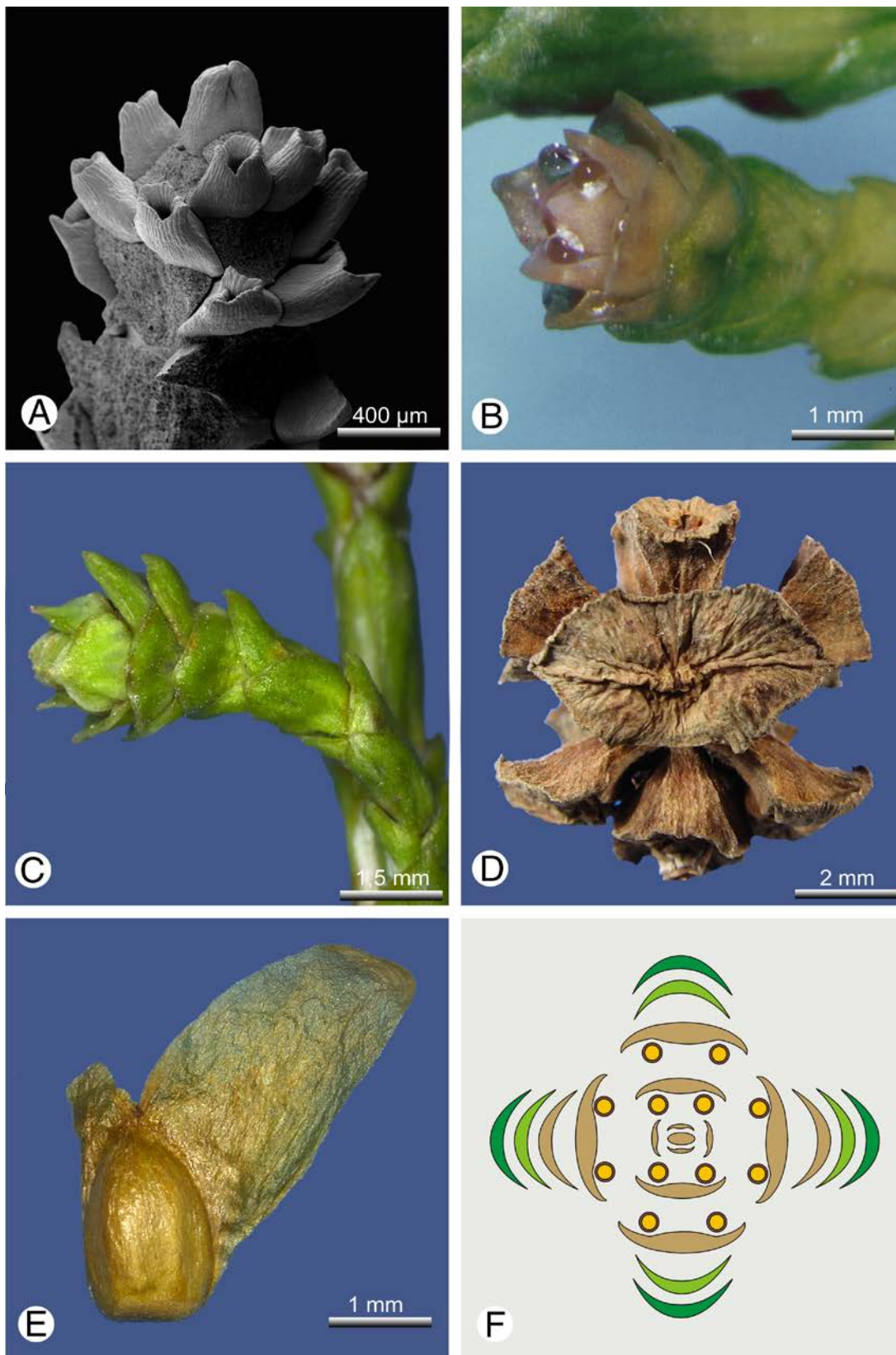
Fig. 6: Cone morphology of *Fokienia hodginsii*.

A: Cone at pollination time, each cone scale with two axillary ovules; a distinct terminal piece is developed at the distal end of the cone; (SEM-picture, cone scales removed). **B:** Cone with pollination drops in natural orientation. **C:** Young cone after pollination in natural orientation. **D:** Mature cone in lateral view with a shield-like terminal piece. **E:** Unequally winged seed. **F:** Typical cone diagram according to A (brown = cone scales, light green = transitional leaves, dark green = leaves).
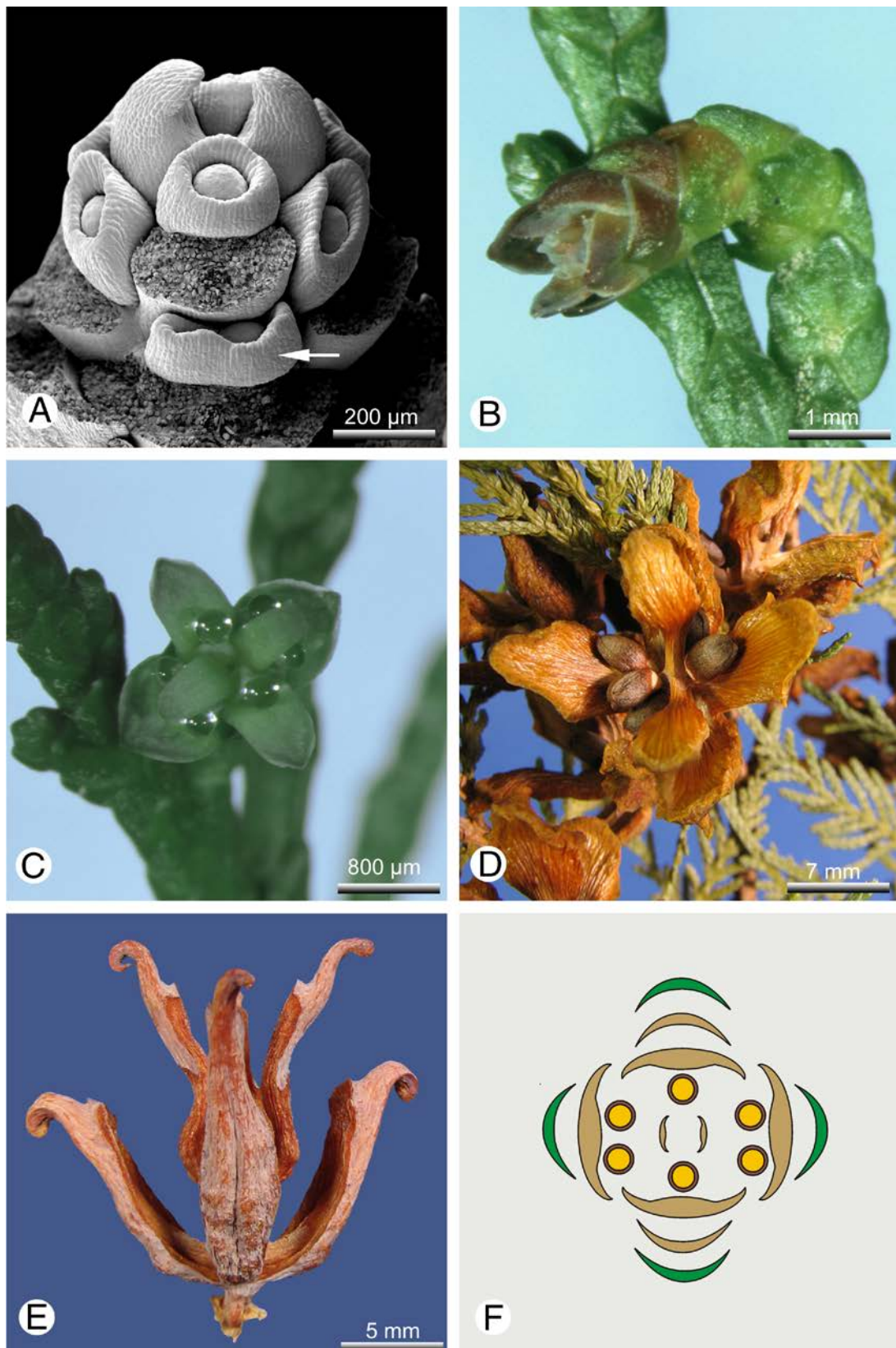
Fig. 7: Cone morphology of *Platycladus orientalis*.

A: Young cone with developing ovules and a sterile pair of cone scales at the cones end; ovules develop axillary from proximal to distal, one abnormal large ovule on the lowest fertile cone scale (arrow) (SEM-picture, proximal cone scales removed). **B:** Cone at pollination time in natural orientation. **C:** Cone with pollination drops with sterile cone scales at the cones end, top view. **D:** Mature open cone with wingless seeds. **E:** Mature cone in lateral view with prominent dorsal prickles. **F:** Typical cone diagram according to C (brown = cone scales, dark green = leaves).
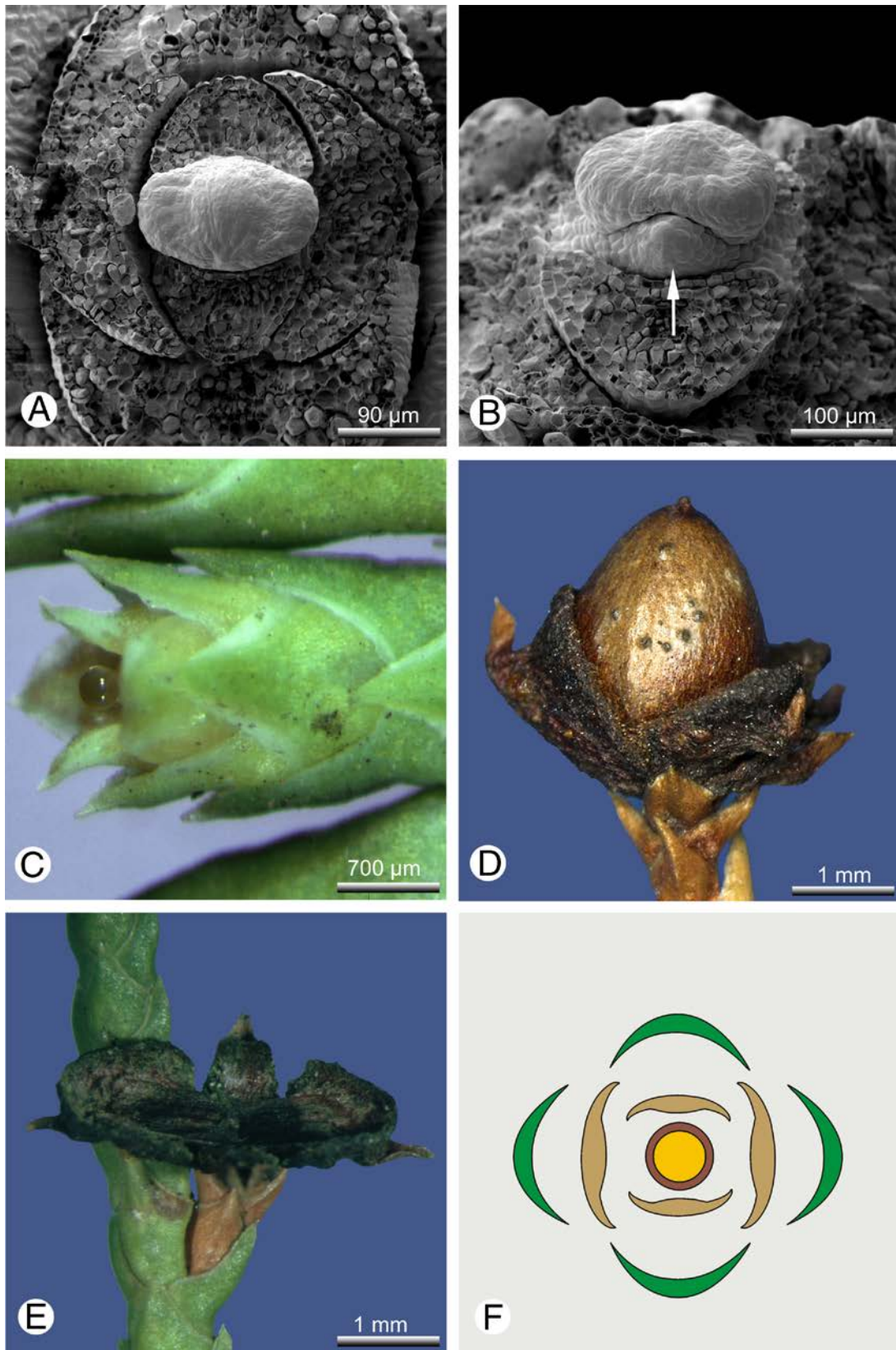
Fig. 8: Cone morphology of *Microbiota decussata*.

A: Young cone with ovule developing in terminal position (SEM-picture, cone scales removed). **B:** Young cone with terminal ovule developing in the axil of a cone scale. During further development the ovule shifts the rudimentary cone-axis (arrow) in a lateral position (SEM-picture, cone scales removed). **C:** Cone with pollination drop in natural orientation. **D:** Mature cone with distinct dorsal prickles on the back sides of the cone scales and an oval, wingless seed. **E:** Mature open empty cone. **F:** Typical cone diagram according to A (brown = cone scales, dark green = leaves).
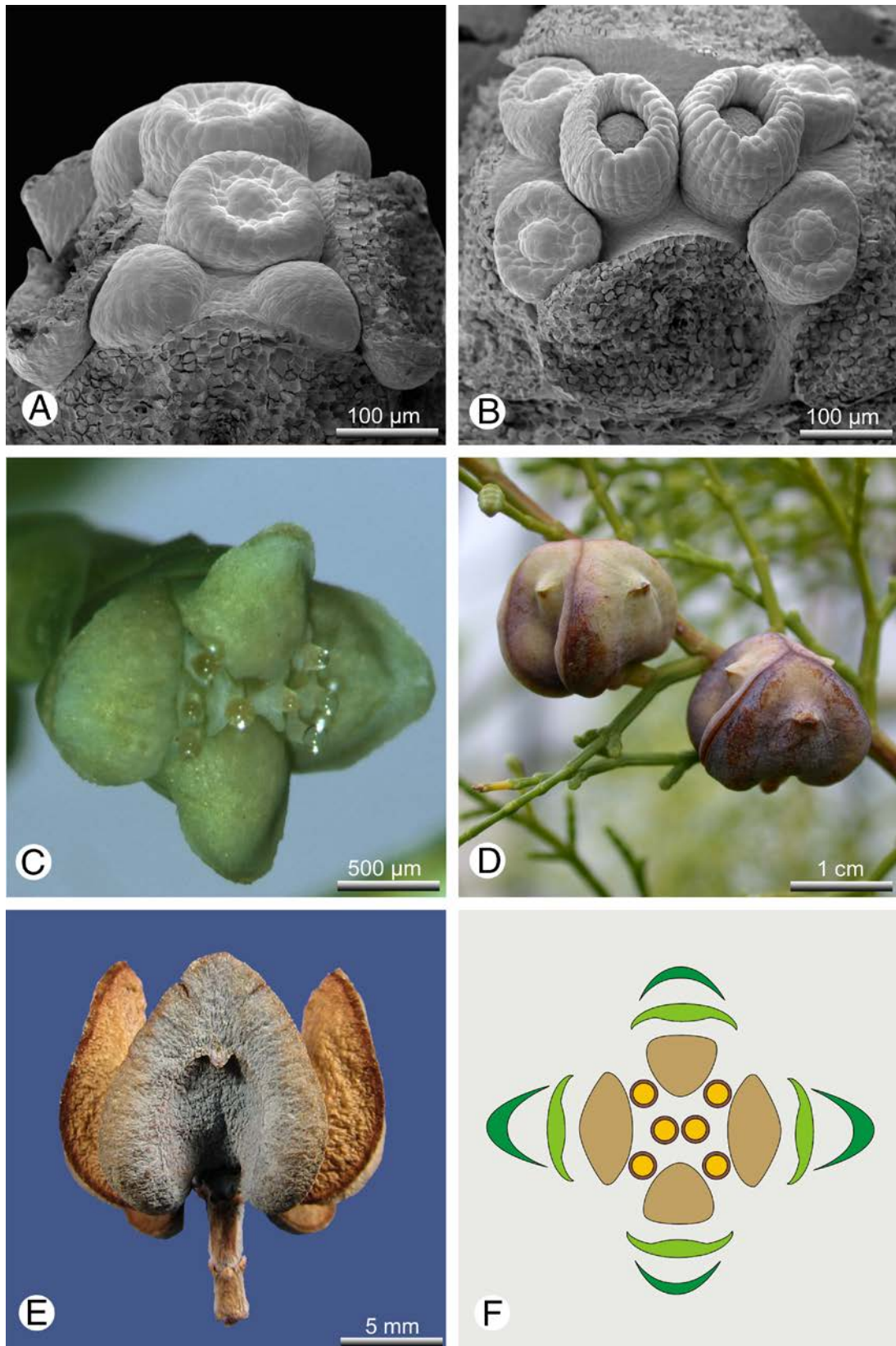
Fig. 9: Cone morphology of *Tetraclinis articulata*.

A & B: Young cone with developing ovules in different stages of development; the terminal ovules develop earlier than the axillary ovules (SEM-picture, cone scales removed). **C:** Cone with pollination drops in natural orientation. **D:** Closed mature and erect cones on a branch. **E:** Mature cone in lateral view. **F:** Typical cone diagram according to A, B and C (brown = cone scales, light green = transitional leaves, dark green = leaves).
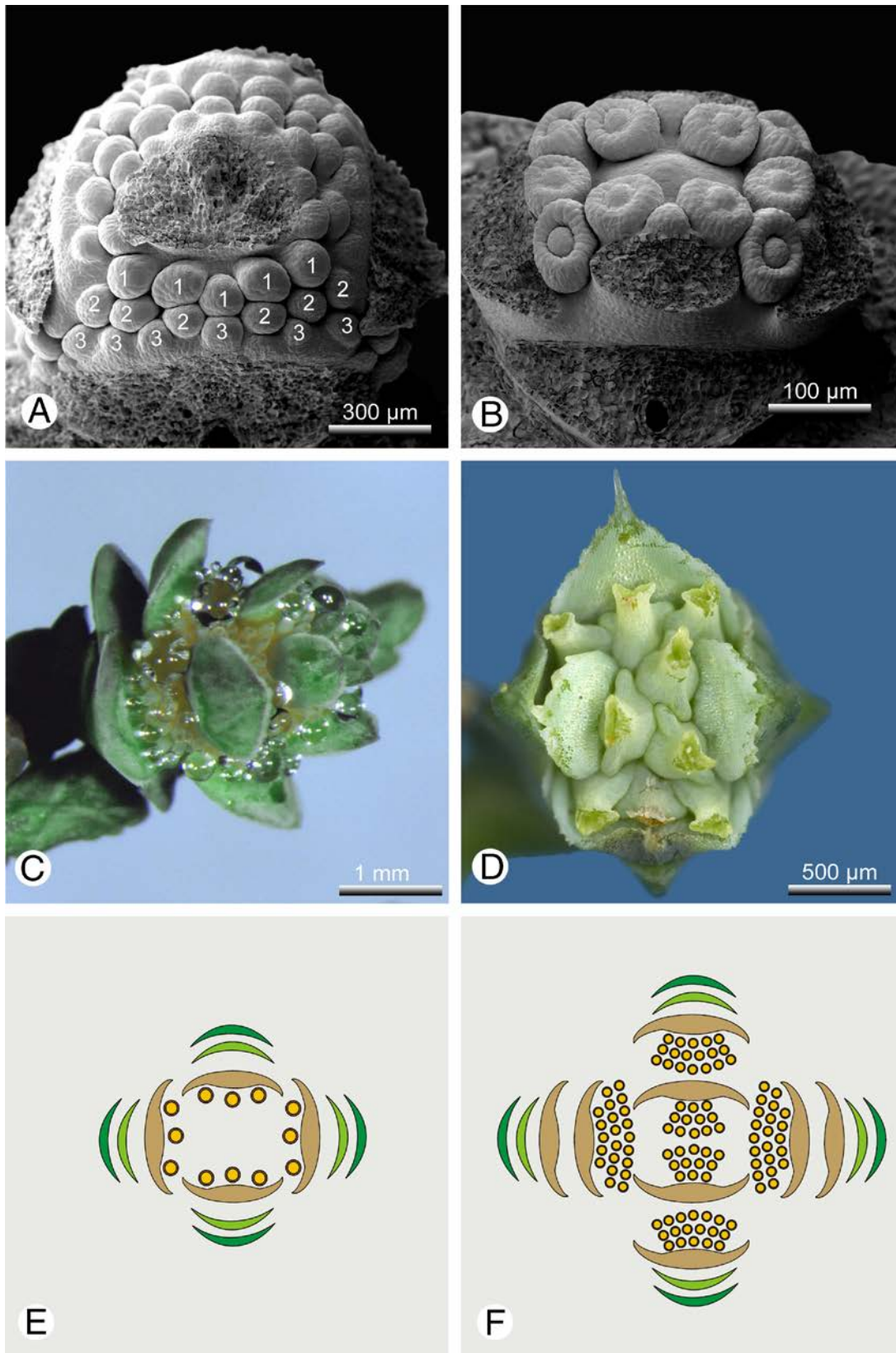
Fig. 10: Cone morphology of *Cupressus*.

A: *Cupressus douclouxiana*, young cones with several developing ovules in several rows, those of one with three rows marked with numbers (SEM-picture, cone scales removed). **B:** *Cupressus nootkatensis*, young cone with three ovules per cone scale, developing in centripetal order. **C:** *Cupressus sempervirens*, cone with pollination drops, some of them fuse to a larger one. **D:** *Cupressus vietnamensis*, cone at pollination time, top view. **E:** *Cupressus nootkatensis*, typical cone diagram according to B (brown = cone scales, light green = transitional leaves, dark green = leaves). **F:** *Cupressus arizonica*, typical cone diagram (brown = cone scales, light green = transitional leaves, dark green = leaves).
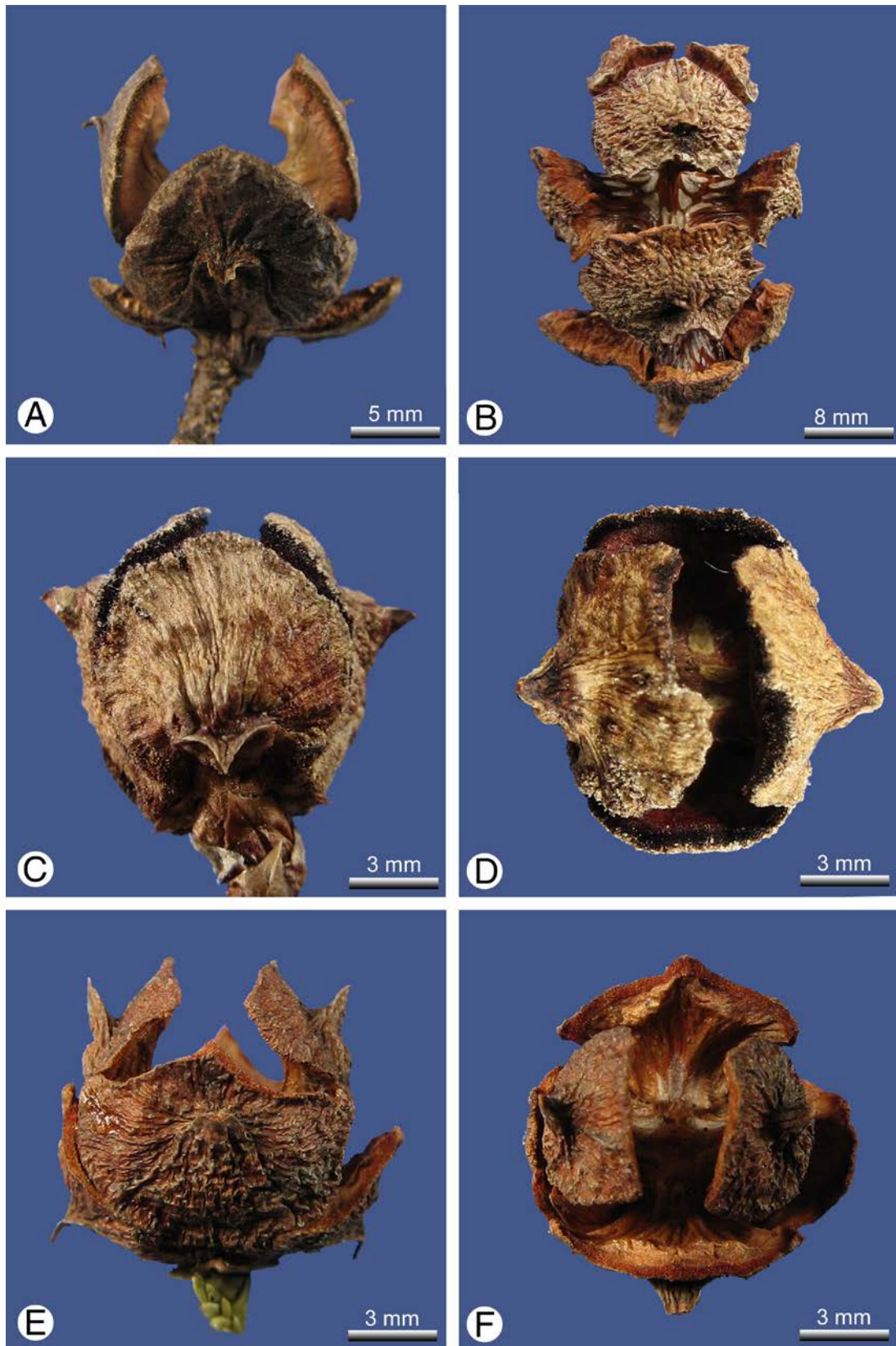
Fig. 11: Cone morphology of *Cupressus*.

A: *Cupressus arizonica*, mature cone in lateral view. **B:** *Cupressus sempervirens*, mature cone in lateral view. **C:** *Cupressus vietnamensis*, mature cone in lateral view. **D:** *Cupressus vietnamensis*, mature cone in top view. **E:** *Cupressus nootkatensis*, mature cone in lateral view. **F:** *Cupressus nootkatensis*, mature cone in top view.
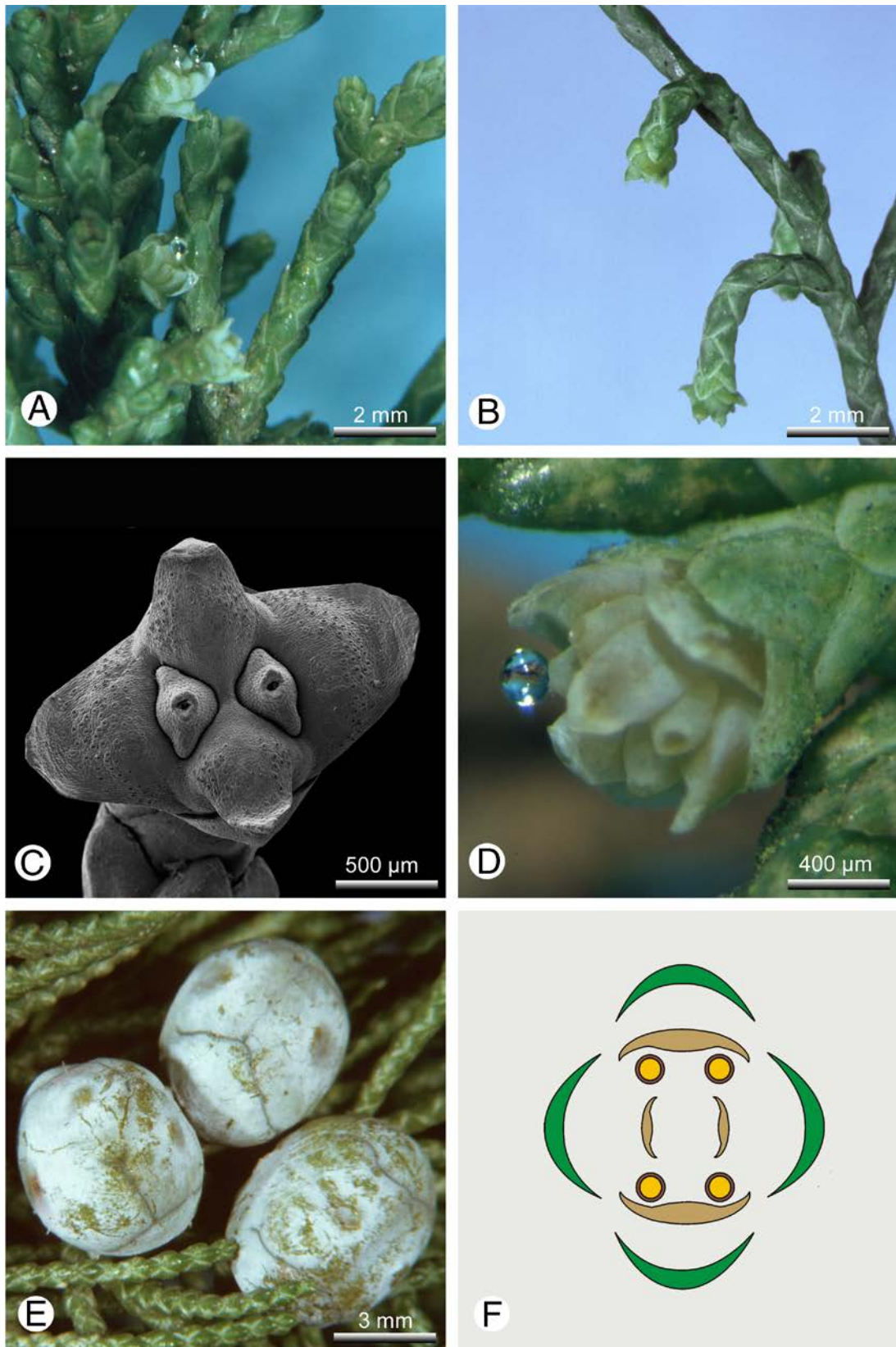
Fig. 12: Cone morphology of *Juniperus* section *Sabina.*

A: *Juniperus chinensis*, branches with cones with pollination drops. **B:** *Juniperus chinensis*, cones at pollination time in downward pointed orientation. **C:** Cone at pollination time with two ovules on one pair of fertile cone scales and a sterile terminal pair (SEM-picture). **D:** Cone at pollination time with pollination drop with four ovules on one fertile pair of cone scales. **E:** *Juniperus chinensis*, mature cones. **F:** cone diagram according to D (brown = cone scales, dark green = leaves).
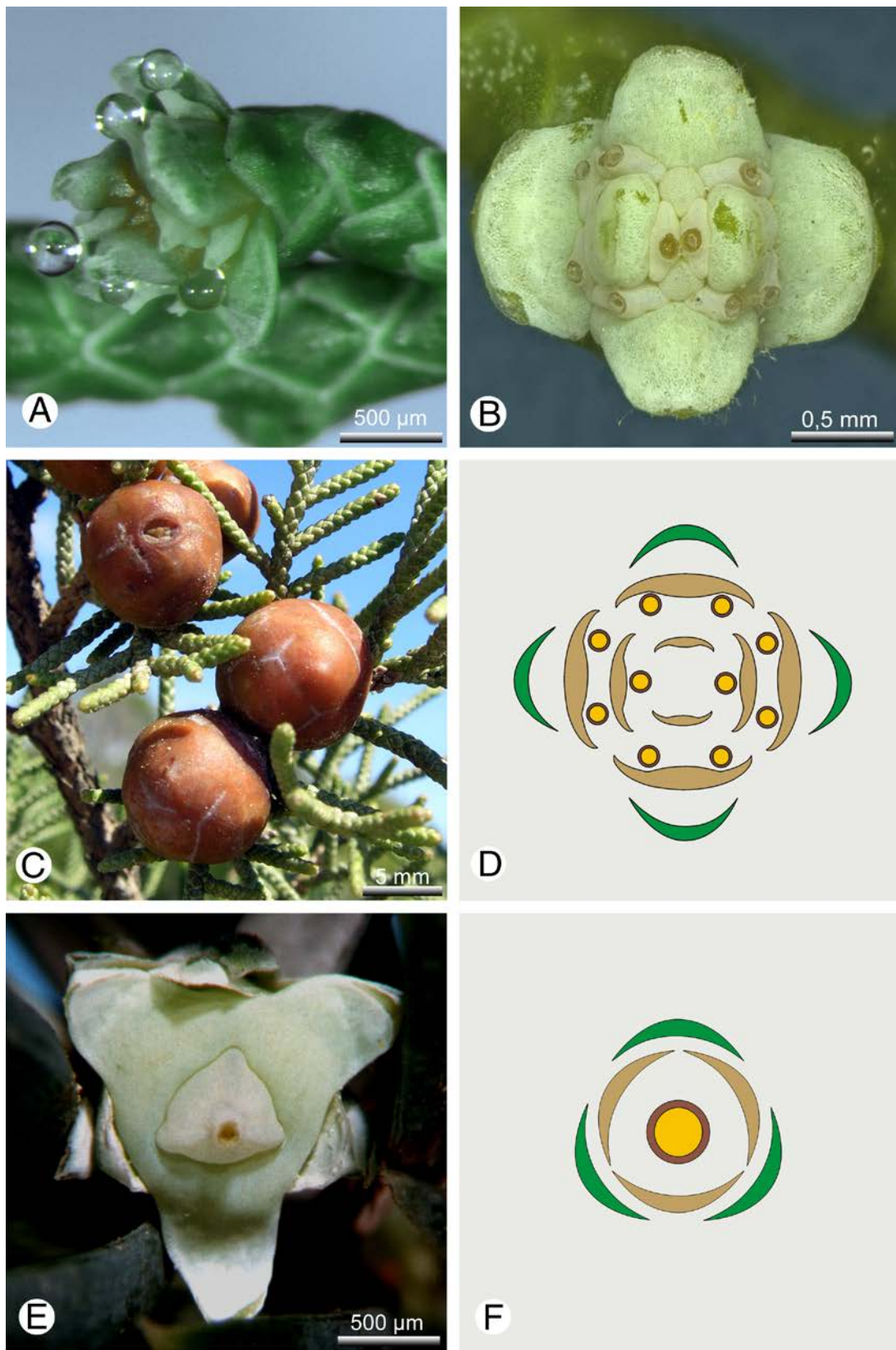
Fig. 13: Cone morphology of *Juniperus* section *Sabina*.

A: *Juniperus phoenicea*, cone with pollination drops. **B:** *Juniperus phoenicea*, cone at pollination time with three fertile pairs of cones scales. **C:** *Juniperus phoenicea*, mature cones. **D:** Cone diagram according to B (brown = cone scales, dark green = leaves). **E:** *Juniperus squamata*, cone with scales in a whorl of three at pollination time with a single terminal ovule. **F:** *Juniperus squamata*, cone diagram according to E (brown = cone scales, dark green = leaves).
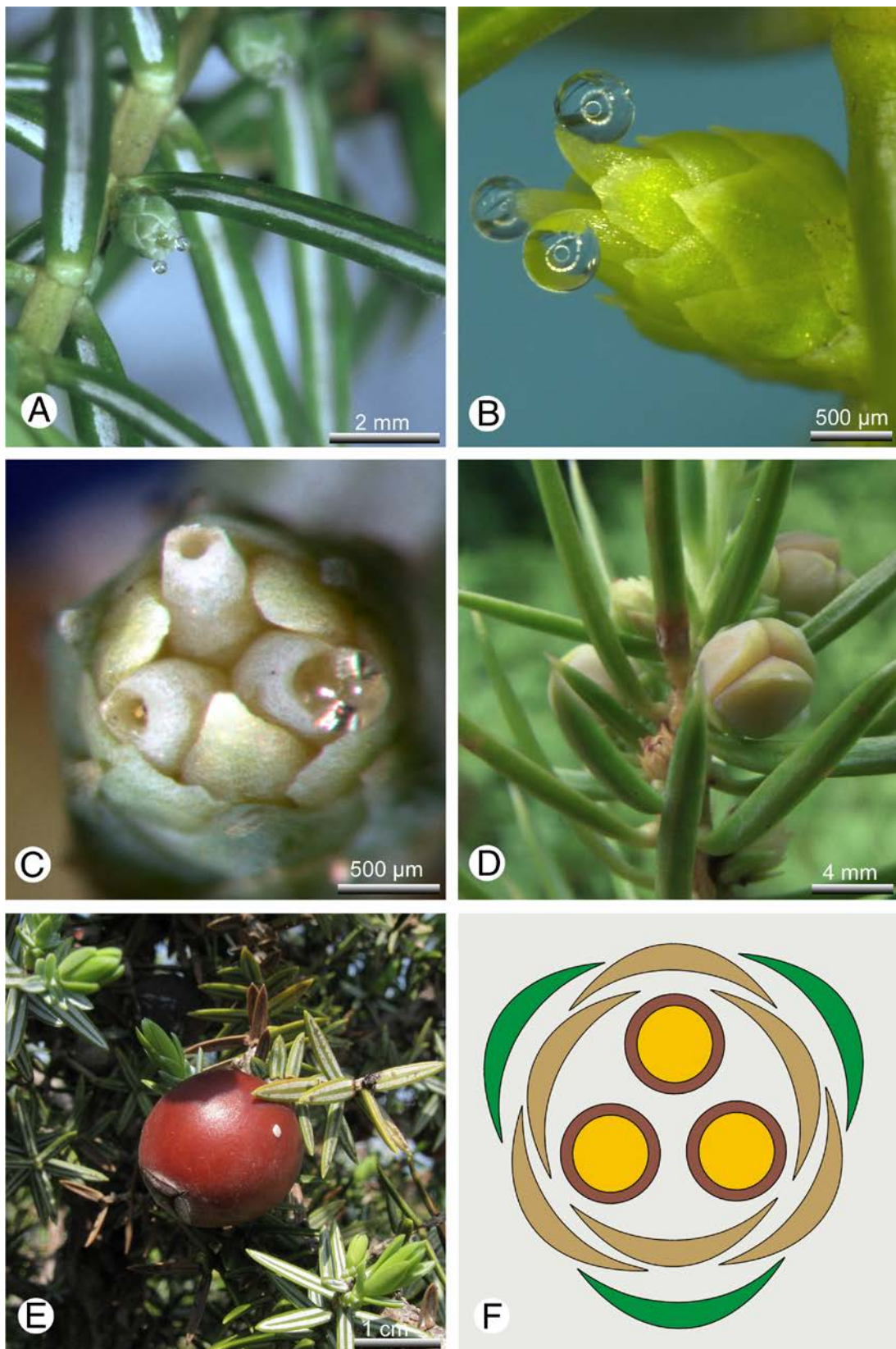
Fig. 14: Cone morphology of *Juniperus* section *Juniperus*.

A: *Juniperus rigida*, cone with pollination drops. **B:** *Juniperus communis*, cone with pollination drops in lateral view. **C:** *Juniperus communis*, cone at pollination time, the three non-axillary ovules visible. **D:** *Juniperus conferta*, immature cone on a branch. **E:** *Juniperus macrocarpa*, mature cone on a branch. **F:** Section *Juniperus*, typical cone diagram of section *Juniperus*, according to B and C (brown = cone scales, dark green = leaves).
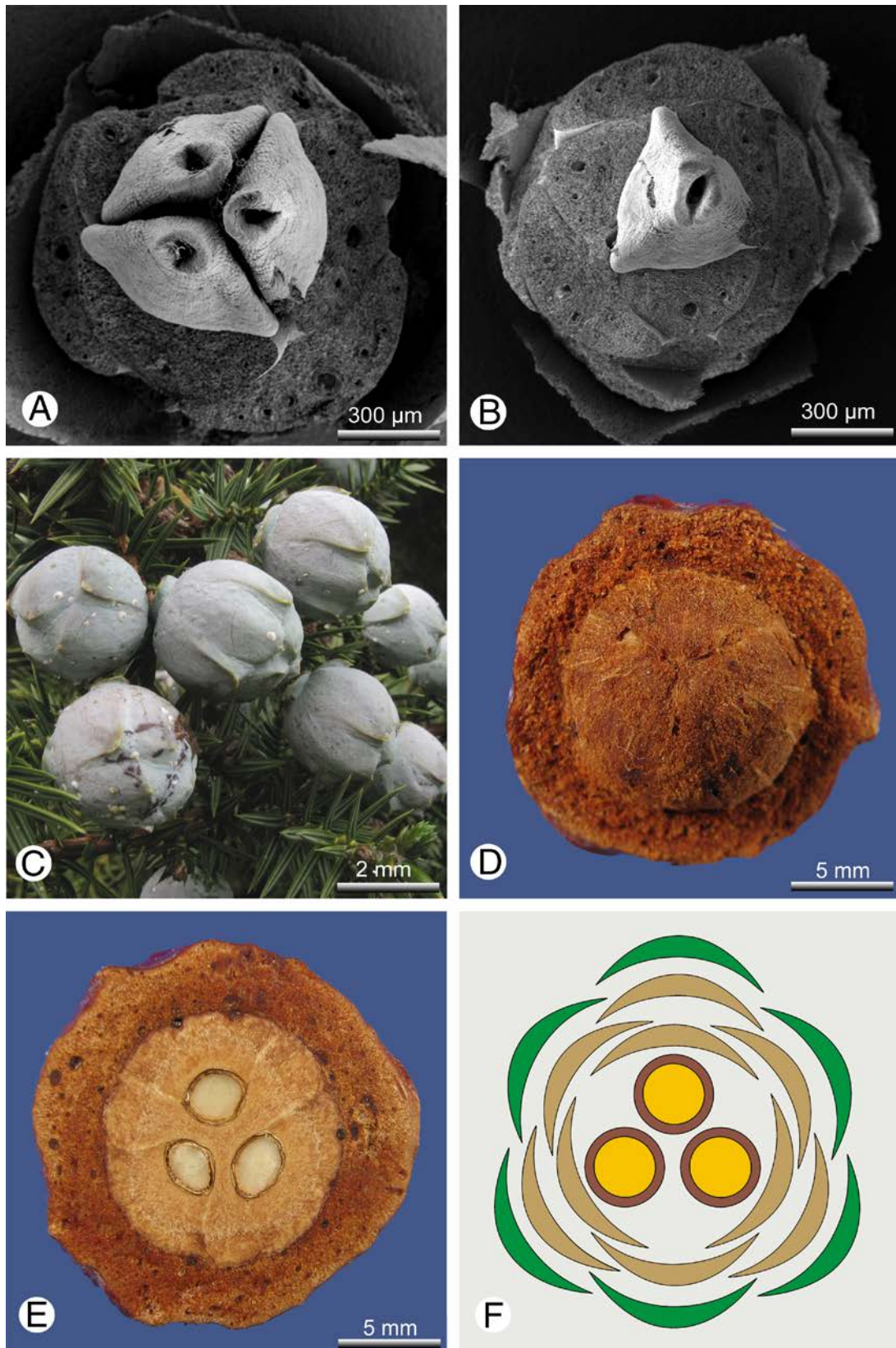
Fig. 15: Cone morphology of *Juniperus* section *Caryocedrus*, *Juniperus drupacea*.

A: Cone with scales in whorls of three at pollination time with three axillary ovules (SEM-picture, cone scales removed). **B:** Cone at pollination time with a terminal ovule (SEM-picture, cone scales removed). **C:** Ripe cones on a branch at natural site (Parnon, Peloponnese, Greece). **D:** Mature cone, cone scales partly removed, view of the "stone", built of the adnate seeds. **E:** Mature cone in cross section with the "stone" built by the three seeds. **F:** Typical cone diagram according to A (brown = cone scales, dark green = leaves).
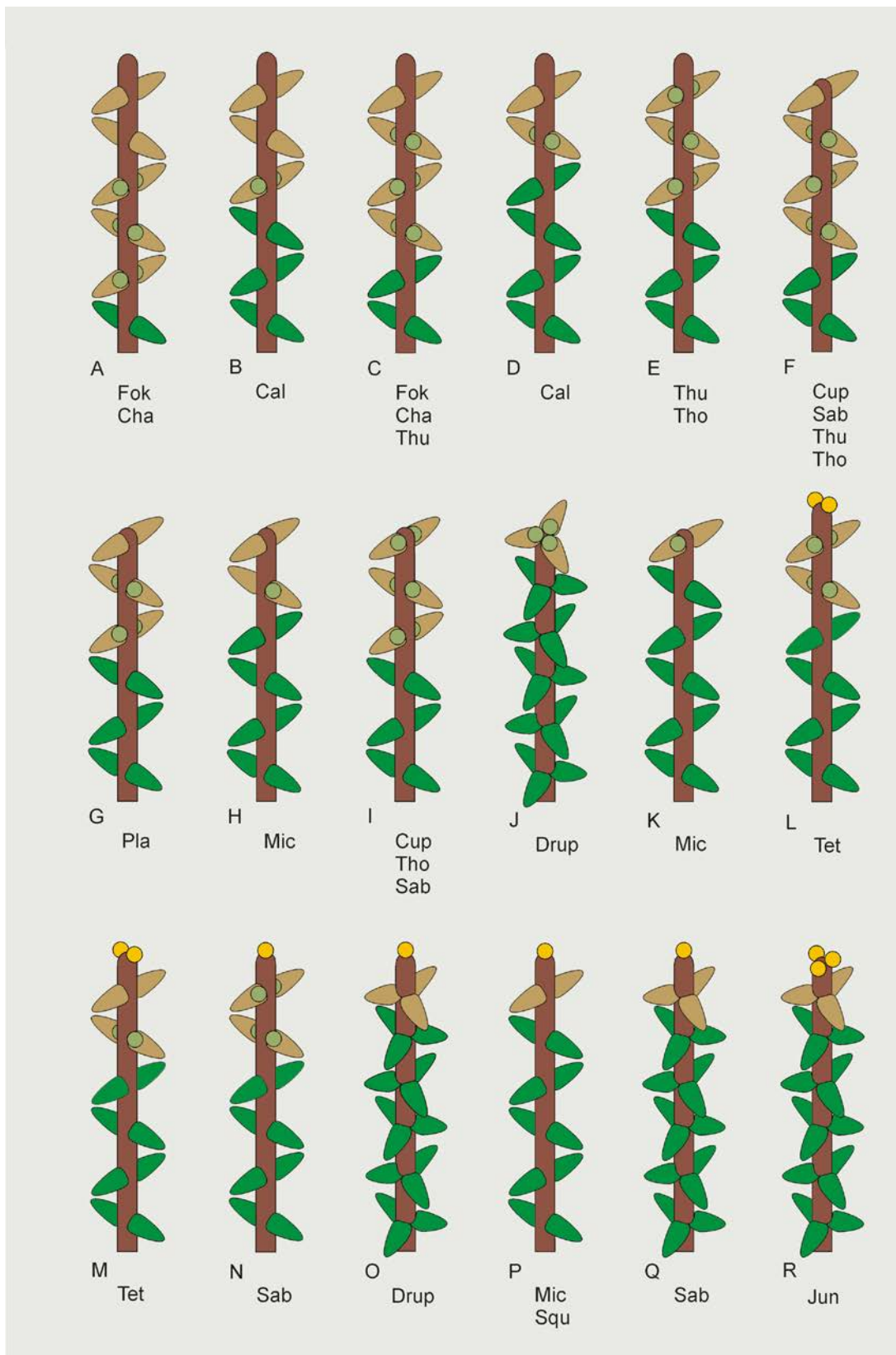
Fig. 16: Morphological series of the cones of Cupressoideae and their fertile zone.

Terminal sterile cone scales and the terminal piece are increasingly reduced; the ovules are located more and more to the cone's tip. In more derived taxa non-axillary ovules occur; dark brown = cone axis, light brown = cone scales, light green = axillary ovules, yellow = non-axillary ovules, dark green = leaves; (Cal = *Calocedrus*; Cha = *Chamaecyparis*; Cup = *Cupressus*; Dru = *Juniperus drupacea*; Fok = *Fokienia*; Jun = *Juniperus* section *Juniperus*; Mic = *Microbiota*; Pla = *Platycladus* Sab = *Juniperus* section *Sabina*; Squ = *Juniperus squamata*; Tet = *Tetraclinis*; Tho = *Thujopsis*; Thu = *Thuja*).

D. Maerki

A new cypress hybrid
Cupressus ×symbolica

The story begins with a tree planted in the 1980s. It was thriving and began to produce an abundance of cones covered the first year with an almost completely white wax. These cones were unusual in the sense that they had well developed umbos and a high number of scales, mostly 10 or 12. Tentatively this tree of unknown origin, purchased from an unknown nursery and without a name was identified as a hybrid (fig. 5, 6, 10-13). It undoubtedly belongs to the New World cypresses, but cannot fit in any known species considering all its characters [1]. To try to get a better idea, seeds were collected from the tree on the 6 January 2002 and sown. One seedling displayed an unusual quick growth, outgrowing even a *Cupressus lusitanica* Miller planted a couple of years earlier in the same field. In 2008, it began to produce seed cones (fig. 7-9), and these cones are quite different to those of the mother tree. Instead of being cylindrical in shape, the seed cones are rounded, more globose to ovoid, with a larger base; they are also heavier; instead of presenting a well developed umbo, it is reduced at maturity; and instead of showing a white wax during the first year, they have a green tint. It is known that the variability of most characters within all *Cupressus* species is very high. This poses serious problems to identify a lone cultivated tree of unknown origin when its description is restricted to few characters like the foliage or the bark, especially when several species are sharing the same characteristics. This applies to cones as well. In our case though, it is highly unlikely that the well marked differences between the cones of the mother and those of its offspring could be explained by cone variability inside one species, especially had it been a case of self-pollination (table 2). The F1 cones (fig. 1, 2, 7-9) have a mixture of characteristics which – as for the mother tree – cannot be attributed to any current species. The difficulty is to find the tree which provided the pollen as this mother tree had no known equivalent in the area at the time of pollination. The closest cypresses were two *Cupressus ×leylandii* Dallimore & A.B.Jackson, and two *Cupressus glabra* Sudworth (distance: c. 15 m – see fig. 12 & 13 where one is visible in the background). At some distance there are several *Cupressus sempervirens* L. (120 m) and other *Cupressus glabra*, and much farther away a *Cupressus macrocarpa* Hartw. (2.5 km). Foliage samples of the mother tree and of the F1 offspring were sent in July 2011 to Dr. R. P. Adams for molecular analysis (results still pending), which should confirm the hybrid origin of this specimen. Considering the current observations, I make the hypothesis that it is a hybrid, and that the putative father is a *Cupressus glabra*, although another species cannot be completely excluded, but is much less likely.

The following description is given:

Cupressus ×symbolica [2] Maerki, ***nothospecies nova***.
Parents: unknown *Cupressus* hybrid (♀)×*Cupressus glabra* (♂).
Seed cones: [sample size: 50 cones] shape: globose to ovoid; size: length: 21.2-33.4 mm, average 25.3 mm, width: 20.9-31.6 mm, average: 25.1 mm; scales 6-10, average 7.9; seeds/cone [32]: 105-167, average: 141, average number of seeds/scale: 17.9; umbo: variable, very small to small the first year, more or less disappearing after maturity, depression below most (a feature present in several species of new world cypresses); colour: green the first year, browning gradually during the first growing season, turning grey when weathered; serotiny: active [3]; peduncle: length variable, to 13.4 mm.

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[1] A hybrid originating in cultivation in India cannot be excluded. The putative parents are *C. lusitanica* (white wax on seed cones and spreading branches – this species almost certainly one of the parents), with either *C. macrocarpa* (absence of resin dots on leaves, high number of cone scales) or *C. arizonica* (white wax on seeds cones with well marked umbos, absence of resin dots on leaves). That the tree suffered marked cold damage in 2012 is further evidence for *C. lusitanica*.

[2] Meaning of *symbolica*: in ancient Greece the word σύμβολο [symbol] meant "sign of recognition". When two parties (guests, cities) met, they would cut an object in half and when meeting a second time the holders of the two parts of the object will reassemble the object as a sign of recognition of their previous agreement. If our observations are correct, the hybrid described here will quite likely appear in the future as a symbol, that is, a sign of recognition to keep united the new world and the old world cypresses under the genus *Cupressus*.

[3] Active serotiny: the seed cones remain closed as long as they are vascularised.

Fig. 1: *Cupressus ×symbolica*, seed cones.

Fig. 2: Bark at 1 m. high.

Fig. 3: Mother tree bark.

Pollen cones: light green before maturity, yellow before releasing their pollen; quadrangular in section. *Leaves*: dark green, not glaucous, adpressed on the shoot, not glandular, resin dots absent.

Shoots: quadrangular in section, quite irregular in their disposition; several (ultimate) branchlets in a plane, others in two perpendicular planes.

Branches: lower branches perpendicular to the trunk, spreading almost horizontally, higher branches at an angle and spreading straight.

Bark: red-brown, with black patches, turning greyish-green; exfoliating in scales; girth at 100 cm: 47 cm.

Growth: (at 11 years old) 6.8 metres (laser measurement), quick growth, faster than *Cupressus lusitanica* in the same local conditions.

Habit: broad conical shape.

Holotype: cultivated, France, 23.2.2014, *Maerki 14.054* (**G [G00199185]**). **Hic designatus.**

Fig. 4: *Cupressus ×symbolica*, top branches.

Appendix: photos

Fig. 5: Mother tree. One year old cones showing the white wax and 10 to 12 scales on each cone.

Fig. 6: Mother tree. Cones beginning to be weathered.

Fig. 7: Immature cones showing their green colour without any wax. 7 July 2008.

Fig. 8 & 9: Mature cones already weathered with scales still closed. 23 December 2013.
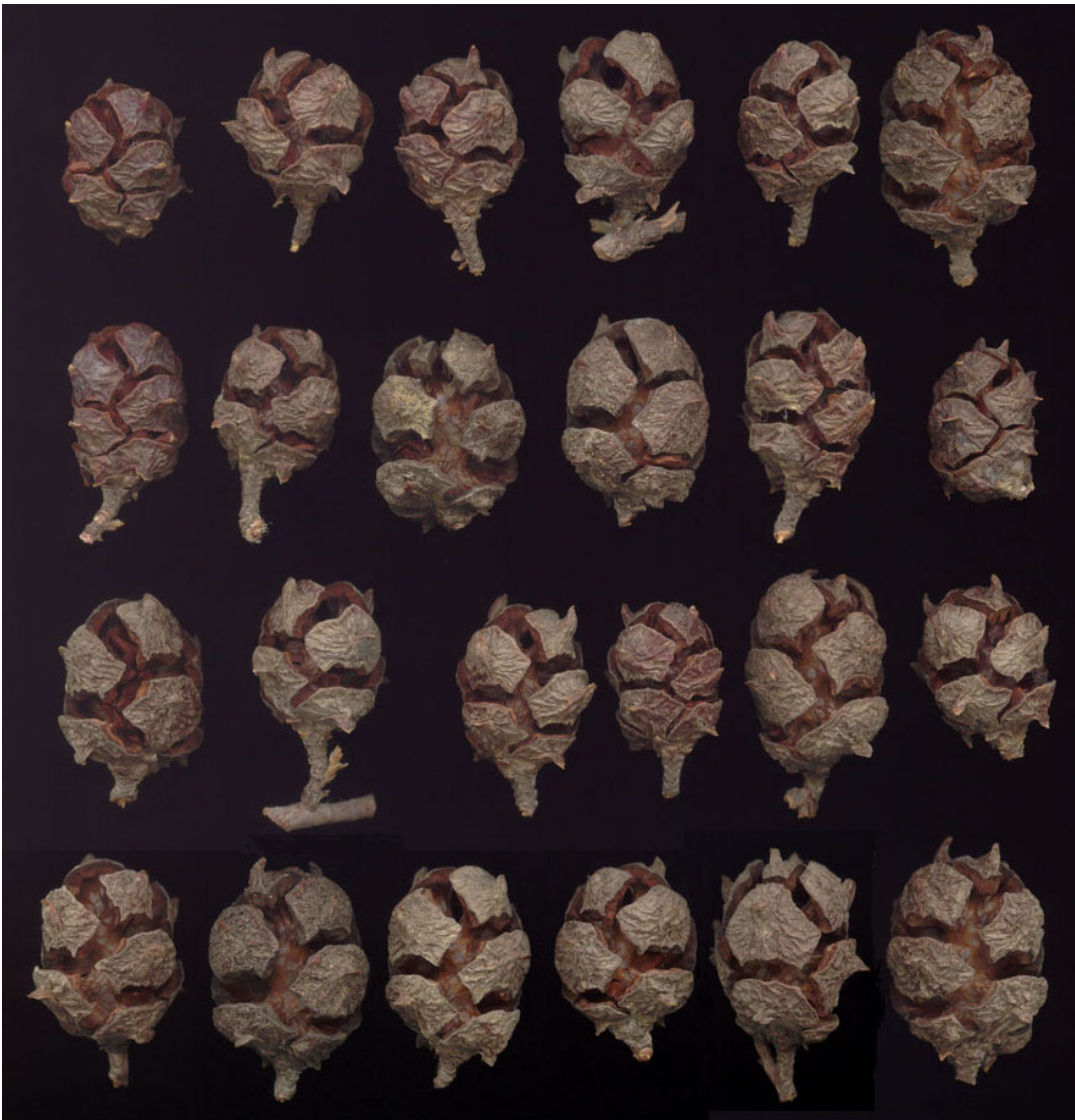
Fig. 10: Series of cones of the mother tree. Same scale as fig. 1.
Fig: 11: Wide spreading branches with cones covered with wax and others already weathered.

Fig. 12 & 13: Mother tree. To the right in the background is a *Cupressus glabra* as putative pollen parent.

Table 1: Summary of some discriminating characters of the trees or species discussed here.

Characters	Mother tree	symbolica	lusitanica	glabra	arizonica	macrocarpa	leylandii
Seed cone scales mostly 8	more	*	less	(*)	(*)	more	less
Wax on immature seed cones	*		(*)	*	*		
Green immature seed cones		*	(*)	(*)	(*)	*	*
Max seed cone length > 30 mm		*		(*)		*	
Higher number of seeds/cone	*	*		(*)		*	
Umbo	*	small	(*)	(*)	(*)		small
Spreading branch pattern	*	*	*			*	(*)
Bark: reddish, smooth, scaly		*		*			
Resin dots on leaves			(*)	*			
Ultimate branchlets in a flat spray		(*)					*

* Feature regularly or always present in the species.
(*) Feature irregularly present in the species.
Empty cell: feature not present in the species or tree. **Fig. 14:** *Cupressus ×symbolica*: leader with cones.

Fig. 15: *Cupressus ×symbolica*: cones with detail of ultimate shoots. Glandular leaves, but without resin dots. **Fig. 16:** *Cupressus ×symbolica*: wide spreading shoots. 10 August 2014.

Table 2: Statistical data of the seed cones: mother tree and *Cupressus ×symbolica*.

Mother tree   Sample size: 50

	A	B	C	D	E	F		Number of scales/cone				
								8	9	10	11	12
Average	24.05	19.97	1.21	18.94	1.06	10.6		8	9	10	11	12
Maximum	28.6	23.7	1.4	22.5	1.1	12	#	3	0	27	4	16
Minimum	19.2	15.3	1.1	14.6	1	8	%	6	0	54	8	32

Cupressus ×symbolica   Sample size: 50

	A	B	C	D	E	F		Number of scales/cone				
								6	7	8	9	10
Average	25.28	25.92	0.97	24.2	1.07	7.92		6	7	8	9	10
Maximum	33.4	31.6	1.1	29.3	1.2	10	#	3	4	39	2	2
Minimum	21.2	23.1	0.9	20.9	1	6	%	6	8	78	4	4

	Cupressus ×symbolica Sample size: 32		**Mother tree** Sample size: 14	
	Seeds/cone	Seeds/scale	Seeds/cone	Seeds/scale
Average	141	17.9	115	12.2
Maximum	167	20.9	148	16.0
Minimum	105	14.0	81	8.1

A = Length of the cones
B = Maximum width of the cones
C = A/B: relation length/max. width
D = Minimum width of the cones

E = B/D: relation max. width/min. width
F = Number of scales
The relations A/B and B/D give information on the shape of the cones.

Average PP Index A*B*D: **mother tree = 9.10**; *Cupressus ×symbolica* = **15.85**.
The PP Index gives the volume of the orthogonal parallelepiped in which the cone is included.

Fig. 16: *Cupressus ×symbolica*: cones turned brown by fall (cf. fig. 15). 26 October 2014.

Fig. 17: *Cupressus ×symbolica*: the trunk displays the initial red colour of the bark turning to greyish-green. Note the branching pattern with branches spreading almost horizontally from the trunk. Seed cones open when not vascularised (for instance on dry branches, but not only), but still usually closed on living branches. 1.1.2015.

Fig. 17: *Cupressus vietnamensis*, seed cone.
Fig. 18: *Cupressus nootkatensis*, mature seed cone.