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Abstract : Morphology of the seed cones of the Callitroideae is given. These cones are significantly less variable than those of the Cupressoideae in respect to the number of cone scales, and especially the formation of the distal end of the cone axis. They consist only of two whorls of cone scales. In some taxa the cone axis is developed into a so called columella, which however does not reach as far as the apical surface of the cone, being shorter than the scales. In the *Libocedrus* group and in *Diselma* only the distal whorl is fertile. Ovules of the Callitroideae are always inserted axillary. The cone scale is formed only by the bract scale. Non-axillary ovules do not exist. In contrast to the Cupressoideae, in *Actinostrobus* and *Callitris* (and perhaps also in *Fitzroya*) ovules of the distal whorl are developed slightly earlier than those of the lower ones.

Abstract : The conservation status of *Cupressus montana* a rare cypress species of the highest mountain range of Baja California is critically reviewed according to the available information.

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Cover photo : *Fitzroya cupressoides* in its natural habitat in Chile.
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Morphology and morphogenesis of the seed cones of the Cupressaceae - part III Callitroideae

Summary

Cone morphology of the subfamily Callitroideae (*Austrocedrus*, *Pilgerodendron*, *Libocedrus*, *Papuacedrus*, *Fitzroya*, *Diselma*, *Widdringtonia*, *Callitris*, *Actinostrobus* and *Neocallitropsis*) is given and diagrams for typical cones were drawn. Cones of the Callitroideae are significantly less variable than cones of the Cupressoideae in respect of the number of cone scales, and especially the formation of the distal end of the cone axis. They consist only of two whorls of cone scales. Sterile distal cone scales are never present. Within some taxa the cone axis is developed as a so called columella, which is however not involved in forming the surface of the cone. Within *Widdringtonia*, *Fitzroya*, *Callitris, Actinostrobus* and probably also in *Neocallitropsis*, both whorls of cone scales are regularly fertile. Within taxa of the *Libocedrus* group and in *Diselma* as well only the distal whorl is fertile. As in the Cupressoideae, spiral phyllotaxis is absent. In the Callitroideae, decussate, trimerous (e.g. *Fitzroya*, *Callitris*, *Actinostrobus*) and in some genera (*Callitris*, *Neocallitropsis*) also tetramerous states occur. The ovules are always inserted in an axillary position. Thus, the whole cone scale is formed by the bract scale only, as in the Cupressoideae. Non-axillary ovules, as they are developed in the Cupressoideae, do not exist. In contrast to the situation in most Cupressaceae, in *Actinostrobus* and *Callitris* (and perhaps also in *Fitzroya*) the ovules on the distal whorl are developed slightly earlier than those of the lower whorl.

1 Introduction

The following, exclusively southern hemisphere taxa of the Cupressaceae are placed within the subfamily Callitroideae: *Actinostrobus*, *Austrocedrus*, *Callitris*, *Diselma*, *Fitzroya*, *Libocedrus*, *Neocallitropsis*, *Papuacedrus*, *Pilgerodendron* and *Widdringtonia*. The southern hemisphere genus *Athrotaxis* does not belong to this subfamily but is in its own subfamily within the taxodiacous Cupressaceae (JAGEL & DÖRKEN 2014). The majority of the Callitroideae are genera with only few species and have comparably small distribution ranges. Currently, 33 species are placed within the Callitroideae. With 15 species, *Callitris* is the largest genus (FARJON 2005).

Within the Callitroideae the phyllotaxis is not uniform, and sometimes even not within a genus or a species. A spiral arrangement, as can be found in the taxodiaceous Cupressaceae, is never present on mature branches (though does occur in *Widdringtonia* seedlings). A decussate phyllotaxis is frequently developed. Whorls of three leaves are more frequent than in Cupressoideae, where they are only present within some species of *Juniperus*. Furthermore, in two species of the Callitroideae, whorls of four leaves are developed. As developed within the Cupressoideae, flattened branchlets with lateral and median leaves occur in some genera (*Libocedrus* s. str., *Papuacedrus*).

As in the other subfamilies of the Cupressaceae the majority of Callitroideae are monoecious, but the number of normally dioecious genera is somewhat higher (*Austrocedrus*, *Diselma*, *Fitzroya*). However, this character represents only the predominant distribution of the sexes; none of the genera is completely dioecious, and several species show occasional monoecious individuals (compare also e.g. PAGE 1990, GARDNER *et al.* 1999, JAGEL & STÜTZEL 2000). Such taxa can be described as trioecious (JAGEL & STÜTZEL 2000). Within taxa which are regularly monoecious, an individual plant can occasionally appear dioecious because of the lack of male flowers in some years, as is also described by FARJON (2005) for the genus *Widdringtonia* and by JAGEL & DÖRKEN 2015 for *Platycladus decussata* (Kom.) Jagel & Dörken.

Material was collected in several German botanic gardens and parks in Bochum, Bonn, Münster, Düsseldorf, Konstanz, the Grugapark in Essen, the Isle of Mainau (Konstanz, Germany), in the Palmengarten Frankfurt and in the private collection of Hubertus Nimsch (Bollschweil). All investigated specimens were cultivated under glass except *Austrocedrus* which is cultivated outdoors in the

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Palmengarten. Material of *Neocallitropsis* and *Papuacedrus* was not available for our investigations; data given by KRÜSSMANN (1983), JOHNS (1995), NIMSCH (2000) and FARJON (2005) was used for these.

In some species the terminal end of the cone axis is developed as a structure traditionally called a columella. This corresponds morphologically to the terminal piece we described in the taxodiaceous Cupressaceae and Cupressoideae, e.g. in *Chamaecyparis* and *Calocedrus* (JAGEL & DÖRKEN 2014, 2015), but it is smaller, and does not reach the periphery of the mature cone. Thus, this columella does not form part of the surface of the ripe cone. It can be divided or undivided, and is quite variable, not only within a single genus or species, but even between cones from a single individual plant.

2 Cone morphology of the Callitroideae

2.1 The *Libocedrus* group

The *Libocedrus* group consists of four genera; *Pilgerodendron* and *Austrocedrus* from South America, *Libocedrus* from New Zealand and New Caledonia, and *Papuacedrus* from the Moluccas to New Guinea. They are characterised by their small and simple cones with two decussate pairs of cone scales and four ovules per cone (fig. 3F). The seed cones mature in the first year. Their seeds are very asymmetrically winged (fig. 3D).

2.1.1 *Austrocedrus* Florin & Boutelje

The single species *Austrocedrus chilensis* (D.Don) Pic.Serm. & Bizzarri is distributed in the mountainous regions of Chile and Argentina. It is frequently said to be dioecious (e.g. CASTOR *et al.* 1996) or rarely monoecious (FARJON 2005). In the Palmengarten Frankfurt a monoecious individual exists. The cones are plagiotropic at pollination time (fig. 1A), the tips of the cone scales do not form a dome. The weakly developed tip of the cone axis remains hidden between the ovules (as in the other species of the *Libocedrus* group, see fig. 2B, arrow); a columella is not developed. The cone consists of two pairs of decussate cone scales. The basal pair is sterile; each distal cone scale carries two ovules and develops stronger than the lower ones at maturity (fig. 1F). The integument of the ovule is very asymmetrically developed at pollination time and does not completely enclose the nucellus (fig. 1B). When the pollination drops appear, they first form two drops, each ovule with the opposite ovule of the second fertile cone scale (fig. 1C). Subsequently the pollination drops fuse to a single large common drop (fig. 1D). The spine of the back side of the ripe cone scales is distinct in being very small (figs 1E, 1F).

2.1.2 *Pilgerodendron* Florin

Pilgerodendron is monoecious and comprises only *Pilgerodendron uviferum* Florin, which is distributed in rainy mountain regions of southern Argentina and Chile. Below the cones, two or three pairs of transitional leaves may be developed, which are more flattened and smaller than the typical scale leaves, having a broad margin. The morphology of the cones is quite similar to *Austrocedrus,* but differs in some conspicuous characters. The cones are erect at pollination time (fig. 2A) and keep this orientation while maturing (fig. 2F). At pollination time the tips of the cone scales are incurved, so that they cover each other and build a kind of dome which might protect the pollination drop against raindrops (fig. 2A). The collar of the micropyles is strongly asymmetrically enlarged at the inner side (figs 2C, 2D). Thus, a fusion of pollination drops of neighboured ovules to a single large one is supported.

As in *Austrocedrus* only the distal pair of cone scales carry two ovules in the axil of each cone scale. Some authors comment that in a number of cones, not all ovules mature. DALLIMORE & JACKSON (1966) reported mostly one, in rare cases two seeds per cone scale, while FLORIN (1930a) listed (3-) 4 seeds per cone. This is likely a consequence of their investigations being made with isolated cultivated plants where the fertilisation rate is lower than in individuals growing in natural habitats, as wild-collected cones examined consistently showed 4 seeds per cone (M. P. Frankis, *in litt.*).

Even at pollination time the basal, ventral part of the cone scale shows a bulge (fig. 2E). It becomes strongly enlarged while maturing and finally closes the cone. Thus, the distal parts of the cone scales are curved outwards and represent the characteristic spine (figs 2F, 3E). The described process of closing the cone is similar to those of the other Cupressaceae s. str., but in *Pilgerodendron* (as in the *Libocedrus* species) the spine is quite large in relation to the rest of the cone scale.

2.1.3 *Libocedrus* Endl.

The genus *Libocedrus* comprises five species: the New Caledonian *Libocedrus austrocaledonica* Brongn. & Gris, *Libocedrus chevalieri* J. Buchholz and *Libocedrus yateensis* Guillaumin; and the New Zealand *Libocedrus bidwillii* Hook.f. and *Libocedrus plumosa* (D. Don) Druce. A complete SEM-study of the cone development of *Libocedrus plumosa* was published by TOMLINSON *et al.* (1993). It shows a close structural similarity to the cones of *Pilgerodendron*. The young cones are erect and their scales forming a dome over the cone centre at pollination time (TOMLINSON *et al.* 1993: 652, fig. 11). The dorsal spine in the species of *Libocedrus* are conspicuous (figs 3A-C) and can be very long and slender, especially in the New Caledonian species (see NIMSCH 2015).

2.1.4 *Papuacedrus* H.L.Li

The single species *Papuacedrus papuana* (F.Muell.) H.L. Li is sometimes divided in two varieties, var. *papuana* and var. *arfakensis* (Gibbs) R.J.Johns. The species is distributed from the Moluccan islands to New Guinea. In Europe it is very rare in botanical collections; in Germany probably only in the Botanical Gardens of Bonn, which originates from the private collection of Hubertus Nimsch. So far, these plants are not fertile and thus, no material was available for our investigations. Drawings of the mature cones are given by JOHNS (1995) and FARJON (2005). They closely resemble the cones of the other genera in the *Libocedrus* group. The spines on their back are small.

2.2 *Fitzroya* Lindl.

The dioecious genus *Fitzroya* is widespread in rainforests of southern Chile and adjacent regions of Argentina. *Fitzroya cupressoides* (Molina) I.M.Johnst. is the single species. In Central Europe only female individuals are in cultivation, due to vegetative propagation of only one clone. From Great Britain it is reported that two individuals have also produced male pollen cones (DOYLE & SAXTON 1933); on one of these two individuals bisexual cones also developed. Within these cones several subsequent microsporophylls were inserted above the ovuliferous scales. More recently, a much wider gene base has been brought into cultivation by RBG Edinburgh (ALLNUTT *et al.* 1998, 1999, SHAW & HIRD 2014, M.F. GARDNER, pers. com.).

At pollination time the cones are plagiotropic or point downwards. The cone scales are inserted in whorls of three. One whorl of transitional leaves is developed below the cone, which is counted by some authors as part of it. The cone scales of the proximal whorl are sterile or develop only one ovule per cone scale (figs 4B, 4F). The distal whorl is always fertile. In the axils of each cone scale either three ovules are inserted in one row, or additionally a second row is developed with two or three ovules. In a row the ovules develop from outwards to inwards (centripetal). The second row of ovules develops later than the first. The development of ovules on the three cone scales of a whorl is not completely simultaneous (fig. 4A). That points out that in *Fitzroya* the elements of a whorl seem not to be arranged on exactly the same level. The ovules in the proximal whorl may develop earlier or later than those of the distal whorl and our investigations indicate that they only develop at roughly the same time. Alternating with the distal whorl of cone scales three globose structures are developed, in literature frequently considered as glands (fig. 4B). At maturity they secrete a fragrant resin (e.g. SAHNI & SINGH 1931). They develop later than the ovules.

At pollination time, the necks of the ovules extend and a distinct collar develops (compare JAGEL & STÜTZEL 2000). In the cone, these micropyle collars form four separate zones for the confluence of the four large pollination drops. One of these large drops is located in the centre of the cone built by the three central ovules of the distal cone scales. For the three other drops a lateral ovule of the distal cone scales corresponds with one lateral of the neighbouring cone scale and, if present, the single ovule of the proximal cone scale (figs 4B, 4C). The cone scales already show a distinct ventral bulge at pollination time (fig. 4C). *Fitzroya* cones mature in the first year (fig. 4D). The mature cones open widely (fig. 4E) and release the two- or three-winged seeds.

2.3 *Diselma* Hook.f.

Diselma is monotypic. The single dioecious species *Diselma archeri* Hook.f. is native in alpine regions of western Tasmania. The cones are inserted terminally on short shoots. A coherent orientation of the cones at pollination time is not detectable. The phyllotaxis in the vegetative parts as well as the arrangement of cone scales is decussate. At pollination time the scales of the two pairs of cone scales differ only slightly from the scale leaves. Transitional leaves are absent (figs 5D, 5E) or a single pair may exist. The two basal cone scales are sterile; in the axils of the two distal ones, two ovules develop on each scale (figs 5B, 5F), rarely three (fig. 5C). These observations are similar to those made by DOYLE (1934), who also reported about sterile basal cone scales and about three ovules per cone scale. Further investigations have to solve the question, if in exceptional cases the basal pair of cone scales is able to develop ovules as well. KRÜSSMANN (1983) reported that all cone scales develop two ovules, which might be a misinterpretation of mature cones. In nearly every young cone, the cone axis has a quite well developed columella, which is also still conspicuously recognisable in mature cones (compare drawings in e.g. DOYLE 1934 and FARJON 2005). The columella inhibits a pollination mechanism as in cones of the *Libocedrus* s. l. group. Thus, one-sided enlarged micropyles are also absent (figs 5B, 5C). The mature cones are only about 2-3 mm in length and thus representing the smallest conifer cones of the southern hemisphere and perhaps the smallest cone of all conifers (fig. 5E). A spine on the back of the cone scale is absent. Cones mature in the first year. Ovules as well as mature seeds show two or three more or less equal wings.

2.4 *Widdringtonia* Endl.

Within the South African genus *Widdringtonia* seven species were placed, which were described as quite well distinguishable (MOSELEY 1943). However in FARJON (1998, 2005, 2010), only four of them are still accepted: *Widdringtonia wallichii* Endl. (syn. *Widdringtonia cedarbergensis* J.A.Marsh), *Widdringtonia nodiflora* (L.) Powrie, *Widdringtonia whytei* Rendle and *Widdringtonia schwarzii* (Marloth) Mast. The latter was the main subject used in the investigations here.

Cones of *Widdringtonia* are produced on a fertile branchlet of the second order, which carries further branchlets of the third order, so that clusters of cones are formed. In contrast to all other Cupressaceae, the cone is directly inserted in the axil of a scale leaf of shoots in such a cluster (fig. 6D). The cones consist of two decussate pairs of cone scales, which follow each other closely due to a strong compression of the cone axis. Thus the cone scales are inserted at more or less at the same level and the ovules are placed in nearly the same plane (figs 6A, 6B). Each of the four cone scales is fertile. In *Widdringtonia schwarzii*, mostly three ovules are developed per cone scale (fig. 6F). However, in contrast to SAXTON (1910), four ovules per row were found from time to time. Furthermore, our research material has shown ovules inserted in a second row on the basal cone scales (fig. 6C, arrows). Ovules of the second row are developed later than those of the first row. The ovules of the proximal pair of cone scales develop somewhat earlier than those of the distal ones (fig. 6A). Within the cone up to 18-20 ovules develop. For *Widdringtonia nodiflora* even more ovules have been recorded (e.g. SAXTON 1909, MOSELEY 1943, FARJON 2005), so that it is possible that in these species several rows per cone scale develop as well. At the distal part of the cone, the cone axis terminates in an expanded, but flat tetragonal structure (fig. 6A).

At pollination time the cones already show a ventral swelling of the cone scales (fig. 6B). The pollination drops of adjacent ovules can merge to form a larger one. Mature cones are in no coherent orientation. The cones mature in the first year. The tip of the young cone scale is recognisable as a short spine on the back of the cone scale (fig. 6E). The seeds are unequally winged.

2.5 *Callitris* Vent.

Currently, 15 species are accepted in *Callitris*. All species are monoecious, and are native to Australia, Tasmania and New Caledonia. At pollination time cones are in a plagiotropic position at the end of small branchlets (fig. 7C), so that pollination drops are plagiotropic as well. A fusion of pollination drops was observed frequently. The cones consist of two whorls of three cone scales (figs 7B, 7F). The cone axis in the genus *Callitris* is developed as a more or less distinct columella which can be simple or three-parted; in *Callitris preissii* the edges of the columella are alternating to the distal whorl of cone scales. In the axil of a cone scale, several rows of ovules are inserted (in the investigated material of *Callitris preissii* mostly 3-4, fig. 7A). The inner row is developed first. The subsequent ones are developed gradually (centrifugally). Within a row ovules developed centripetally. Within the investigated cones of *Callitris preissii* the number of ovules per row on a cone scale of the same whorl was identical. Within the cone the development of ovules is different to all previously investigated taxa in this present study. The ovules of the distal cone scales develop earlier than those of the basal whorl (compare also TAKASO & TOMLINSON 1989). Within mature cones, it seems that all the strongly lignified cone scales are inserted in nearly the same plane. The cones open with six valves (fig. 7E). The distal cone scales are significant larger than those of the basal ones. At the tip of the cone scale a small spine is developed at the distal end. The seeds have two or three irregular wings.

2.6 *Actinostrobus* Miq.

Three quite similar species are placed within the monoecious genus *Actinostrobus* which are native to a small coastal region of SW Australia. Cones of *Actinostrobus* differ from those of the closely related genus *Callitris* in the large number of distinct transitional leaves. These are counted by several authors in their entirety as cone scales, because at maturity they cover the lower part of the cone (fig. 9A). However, the cone in the proper sense consists of two whorls of cone scales (figs 8E, 8F). At pollination time the cone is plagiotropic (fig. 8C). The cone axis ends in a distinctly developed columella (figs 8A-C, 8F). FARJON (2005) indicated that there are 4-6 ovules within a whorl and 8-12 seeds per cone. The exact arrangement of the ovules is not given. Within the single very young cone which was available for our investigations, each of the three distal cone scales carries two ovules (figs 8A, 8B). The basal whorl developed only a single ovule per cone scale (fig. 8B). However, this ovule has a different shape to those of the distal cone scales. It is larger, broader and flatter. Also in a cone at pollination time (fig. 8C), at the position of such an "ovule" a scale-like structure is developed, which is obviously not a well developed ovule. In FARJON (2005) a drawing of *Actinostrobus arenarius* C.A.Gardner shows on one whorl much larger scars of the released seeds. Further investigations should show whether this is a regular ovule or perhaps an aborted one or a deformed structure. The number of seeds is normally nine although it is possible that on both whorls more ovules may develop. In general, mature cone scales do not show a dorsal spine or appendages (figs 8D-F). Mature cones open with 6 valves similar in size (fig. 8F), which seem to be placed all at the same level (fig. 8E). The seeds have three wings.

2.7 *Neocallitropsis* Florin

The single species of the monoecious genus is *Neocallitropsis pancheri* (Carrière) de Laub., native in New Caledonia. It is one of the rarest conifers of the world and is endangered in its natural habitats (NIMSCH 2000). A special character of *Neocallitropsis* is its unusual phyllotaxis with leaves in whorls of four, so that eight rows of leaves are developed on mature branches. The tetramerous cones are inserted terminally at the end of short branchlets. They consist of two tetramerous whorls of cone scales. The cone scales of the basal whorl are larger than those of the distal whorl (figs 9C, 9D). In the centre of the cone a short pyramidal columella is developed (FARJON 2005). Following FARJON (2005) the basal cone scales develop a single ovule each, while the distal ones develop 1-2 ovules, that could result in a diagram as the one shown in fig. 9E. 1-4 (NIMSCH 2000) or 1-2(-4) (FARJON 2005) seeds per cone are described in the literature, so that the arrangement shown in fig. 9F is plausible as well. The tips of the cone scales grow up to large spreading spines (figs 9C, 9D). These spines represent the same structure described in e.g. *Callitris* or *Libocedrus* spines (compare fig. 3E). The cones mature in the year of pollination; at maturity they are between 1-1.5 cm long. Mature seeds are three or four edged (FARJON 2005).

3 Discussion

In respect of the number of cone scales, the cones of the Callitroideae are significantly less variable than those of the taxodiaceous Cupressaceae and Cupressoideae. More than two fertile whorls of cone scales do not exist, and in our definition all cones consist of two whorls of cone scales. We count as cone scales only those which become strongly enlarged and lignified as they mature. However, in *Actinostrobus* transitional leaves below the cone scales can be quite conspicuous. Corresponding to the phyllotaxis, cones of the Callitroideae are more variable than those of the Cupressoideae. In addition to dimerous cones (*Widdringtonia, Diselma, Libocedrus* s. l.) trimerous (*Fitzroya, Callitris, Actinostrobus*) and tetramerous cones (*Callitris macleyana* and *Neocallitropsis pancheri*) exist. Moreover, some taxa show a certain intraspecific variability, and such as in *Callitris* species and *Fitzroya*, variations in phyllotaxis within the species can occur within the vegetative part as well as in the cones (DOYLE 1934, GARDNER *et al.* 1999, FARJON 2005).

3.1 Distribution of ovules within a cone

Within the Callitroideae, the ovules are always axillary. Thus, the whole cone scale is formed by the bract scale only as is the case in the Cupressoideae. Non-axillary ovules as developed in *Juniperus* and *Platycladus decussata* are absent, as well as cone scales alternating with the ovules as are developed in *Juniperus* section *Juniperus* and in *Tetraclinis*. The three terminal "glands" in *Fitzroya* might be interpreted as such non-axillary ovules. Following the anatomical investigations of SAHNI & SINGH (1931) the "glands" are quite similar to a "naked nucellus". But if they represent such a terminal whorl of non-axillary ovules, the ovules would develop earlier than the axillary ovules of the lower cone scales (compare JAGEL 2001, SCHULZ *et al.* 2003, JAGEL & STÜTZEL 2003, JAGEL & DÖRKEN 2015). This is not the case. Thus, the late development gives evidence for the hypothesis that they represent transformed sterile cone scales. SAHNI & SINGH (1931) saw in it a structure comparable to the three-parted columella developed in *Callitris*.

TOMLINSON *et al.* (1993) described the mature ovules in *Libocedrus plumosa* as alternating to the "fertile bracts", because they could not be clearly associated with the cone scales. Thus, they compared them with the alternating arrangement of ovules in *Juniperus* section *Juniperus*. To our mind, there is no support for such an interpretation in the photographs taken in Tomlinson's study. The axillary origin of the ovules in TOMLINSON *et al.* (1993) proves their association to the cone scales and there is no evidence for a secondary shift.

The tendency to dislocate the fertile zone to the distal part of the cone as observed in the Cupressoideae (compare fig. 16 in JAGEL & DÖRKEN 2015) is also observable within the Callitroideae. Sterile cone scales at the end of the cone are absent; the columella is mostly weakly developed or nearly completely reduced. In most cases the tip of the cone axis is so strongly suppressed that the ovules of different whorls could get in contact at the tip of the cone (e.g. *Libocedrus* s. l., *Widdringtonia*). Within the *Libocedrus*-group and also in *Diselma* only the distal pair of cone scale is fertile. In species of the genera *Widdringtonia*, *Fitzroya*, *Callitris* and in *Actinostrobus* and probably in *Neocallitropsis* as well, the lower whorl of cone scale is fertile as well. Within the genera *Callitris, Actinostrobus* and *Fitzroya* the number of ovules is significantly higher on the distal cone scales than on the lower whorl. As morphogenetic investigation of *Actinostrobus* and *Callitris* shows (compare also TAKASO & TOMLINSON 1989) the support of the distal cone scales is so strong that the ovules develop earlier than those of the lower whorl. Following the results of the present study this might also be the case in *Fitzroya*. This developmental order does not occur in either the Cupressoideae or the "Taxodiaceae". The evolutionary drives for such a shifting of the fertile zone to the distal end of the cone might be explained by an optimisation of the pollination process.

3.2 Phylogenetic relationships

The systematic division of the genus ***Libocedrus*** s. l. into the genera ***Austrocedus, Libocedrus*** s. str., ***Pilgerodendron*** and ***Papuacedrus*** is strongly motivated geographically. The development of the cones within the different genera is structurally quite similar, especially in mature cones. They show only differences in proportions of the cone, e.g. the position and length of the spine on the back of the cone scale, as it can be seen in our pictures and in illustrations given e.g. by KRÜSSMANN 1983, TOMLINSON *et al.* 1993 (*Libocedrus*), JOHNS 1995 (*Papuacedrus*), CASTOR *et al.* 1996 (*Austrocedrus*), NIMSCH 2015a (New Zealand *Libocedrus* species), NIMSCH 2015b (New Caledonian *Libocedrus* species) and FARJON (2005). They correspond, apart from the number of transitional leaves, to the cone diagram of *Libocedrus* shown in fig. 3F.

Differences in the foliage (e.g. non-flattened shoots in *Pilgerodendron*), the wood-anatomy (PEIRCE 1937), the cuticle of the leaf (FLORIN 1930 b, FLORIN & BOUTELJE 1954) and also in the structure of the pollen cones (FLORIN 1930b, LI 1953) are also cited as arguments for separating the genus

Libocedrus s. l. The main criterion for the formation of the genus *Papuacedrus* (LI 1953), the spiral arrangement of the microsporophylls in the male cones (which would be the only case within the Cupressaceae s. str.) was disproved a short time later by FLORIN & BOUTELJE (1954). The high number of up to 10 microsporangia per microsporophyll was especially highlighted in *Pilgerodendron* (FLORIN 1930a). This might be quite characteristic for the species, but is not sufficient for establishing a separate genus in our opinion.

In particular, the cones of *Pilgerodendron* and *Libocedrus* s. str. are structurally identical, including the young stages at pollination time (erect cones with dome-like structure, built by the cone scale tips). Thus, some authors as e.g. ECKENWALDER (2009) includes *Pilgerodendron* in the genus *Libocedrus* as *Libocedrus uvifera* (D. DON) PILGER. Our study strongly supports this placement. In *Austrocedrus*, however, the orientation of the cone at pollination time differs from the latter ones in being plagiotropic. As a consequence, a dome-like structure is not developed. It seems, that such a structure is not necessary in *Austrocedrus* because it would not protect against raindrops. Unfortunately, observations of young cones of *Papuacedrus* are lacking.

The distribution of a stretched genus *Libocedrus* s. l. (in this case with eight species) over several continents suggests, that it would reflect the most primitive group within the recent Callitroideae. This is also supported by molecular studies, where *Libocedrus* s. l. represents the sister group to all other Callitroideae (YANG *et al.* 2012). A small, scale- and seed-poor cone (only two ovules per cone scale) can be interpreted as the primitive condition of the Callitroideae cone. Some more derived groups show a markedly higher number of ovules per cone scales, especially numerous in the genus *Callitris*. As in the case of some of the derived genera of the Cupressoideae (e.g. *Cupressus*), an increase of ovules within a cone by the increase of ovules per cone scale, partly by developing several rows of ovules, can be observed.

The northern hemisphere genus *Calocedrus*, which was earlier placed within *Libocedrus* (e.g. JACKSON 1946, NEGER & MÜNCH 1952, KRÜSSMANN 1955), shows only superficially similar cones. They differ markedly in the distribution of the ovules within the cone, as well as in the development of a distinct terminal piece in the centre of the cone, which consists of the terminal cone axis and the distal pair of cone scales (JAGEL & DÖRKEN 2015).

The genera ***Callitris***, ***Actinostrobus*** and ***Neocallitropsis*** are closely related; some genetic work even suggests the first two should be merged (PIGGIN & BRUHL 2010). *Actinostrobus* cones are small *Callitris*-style cones, however with less ovules. In the structure and also in respect to the arrangement of the ovules, large structural differences do not exist between the two genera. In both trimerous cones are developed, which develop more ovules on the distal cone scales than on the basal ones. In both genera a more or less distinct columella is developed. The most obvious difference between cones of both genera is the high number of distinct transitional leaves developed at the base of *Actinostrobus* cones. However, if the ovules on the lower cone scales in *Actinostrobus* are not well developed ovules but other structures, it could perhaps count as a structural difference between *Actinostrobus* and *Callitris*. Due to the tetramerous whorls of the cone scales in *Neocallitropsis* the cones are conspicuously different, but they are similar to those of *Callitris maclayana*, where both trimerous and tetamerous cones occur. Cones of *Fitzroya* are normally trimerous, but less frequent tetramerous cones are occasionally developed (DOYLE 1934). In *Neocallitropsis pancheri* at least in the vegetative parts trimerous whorls occur (SCHNECKENBURGER 1999) and in the generally decussate *Pilgerodendron* sometimes trimerous whorls occur in the vegetative part (DE LAUBENFELS 1965). Against this background, using the position of the cone scales as a single character for distinguishing a genus in this group is worthy of discussion. The cones of *Neocallitropsis*, however, seem to represent a strongly reduced cone with only few seeds or it could be an ancient form. To solve the phylogenetic relationships, morphogenetic investigations would surely be quite helpful, to solve the exact number, distribution and development of ovules within the cone. However, this could not be examined due to the lack of adequate research material.

The genera ***Widdringtonia***, ***Fitzroya*** and ***Diselma*** are closely related following the results of several research groups. On the base of the cone morphology this is, however, less plausible. In molecular family-trees *Diselma* is the sister group of *Fitzroya* (e.g. GADEK *et al.* 2000, YANG *et al.* 2012). Also some morphological and anatomical investigations place them in a special relationship (e.g. DOYLE 1934, DE LAUBENFELS 1965, OLADELE 1983a, 1983b). In *Diselma*, for example, at least in the vegetative parts trimerous whorls of leaves are sometimes found (FARJON 2005). However, this postulated relationship is based on features of the foliage, the structure of the cone consisting of valvate cone scales (instead of imbricate ones) and the three-winged seeds. These features are not relevant (see also DE LAUBENFELS 1965) because they cannot separate both genera clearly from the other ones of the Callitroideae. Nevertheless, DE LAUBENFELS (1965) regarded both genera as closely related, based on their cotyledons and the phyllotaxis of the subsequent leaves, and the *Diselma* cone as a reduction of the *Fitzroya* cone. However, so strongly a reduced cone as is developed in *Diselma* can theoretically be derived in different directions.

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We are grateful to all visited Botanical Gardens for the generous providing of research material, especially the botanical gardens of Bonn Duesseldorf and the Palmengarten Frankfurt. For the technical support by preparing some of the SEM-pictures we are thankful to Dr. MICHAEL LAUMANN and Mrs. LAURETTA NEJEDLI (Elektron Microscopy Centre, Department of Biology, University of Konstanz). Furthermore we thank Prof. Dr. THOMAS STÜTZEL (Ruhr-University Bochum); some of the work was done at his chair for *Evolution und Biodiversität der Pflanzen*, and we are grateful for the several discussions on the topic. Furthermore we thank HUBERTUS NIMSCH (Bollschweil, Germany) and BERNARD SUPRIN (New Caledonia) for giving us the permission to use their photos of *Neocallitropsis*.

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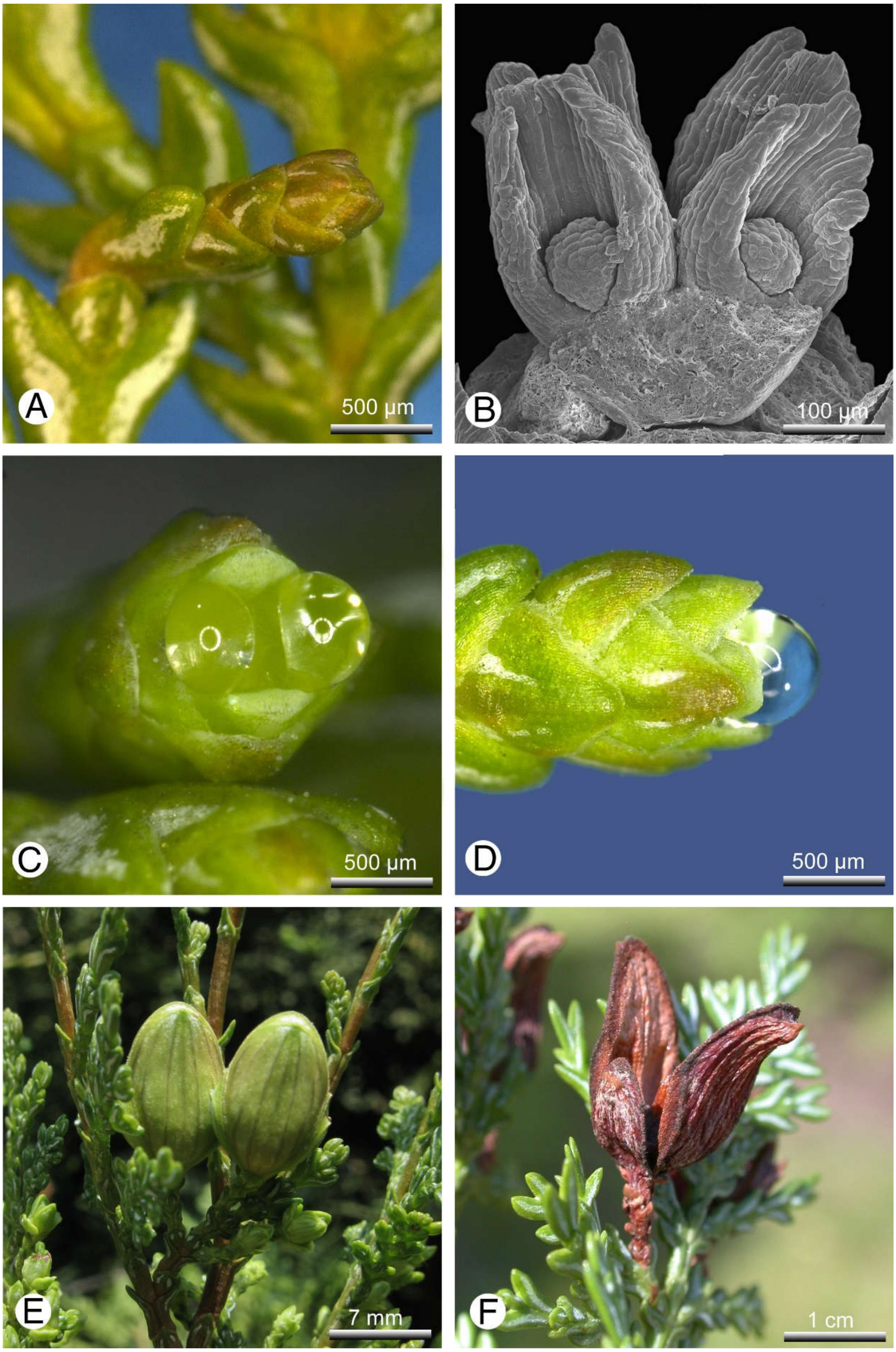

Fig. 1: Cone morphology of *Austrocedrus chilensis*.

A: Plagiotropic cone just before pollination time. **B:** Ovules at pollination time, the integuments are very asymmetrically developed, not completely enclosing the nucellus (SEM-image, cone scales removed). **C:** Cone at pollination time with two pollination drops at an early stage. The drops are formed by the lateral ovules of each cone scale with the drops of the opposite cone scale. **D:** Cone at pollination time with one single pollination drop built by the four ovules. **E:** Immature erect cones on a branch. **F:** Mature open cone on a branch, the dorsal spines are only weekly developed.

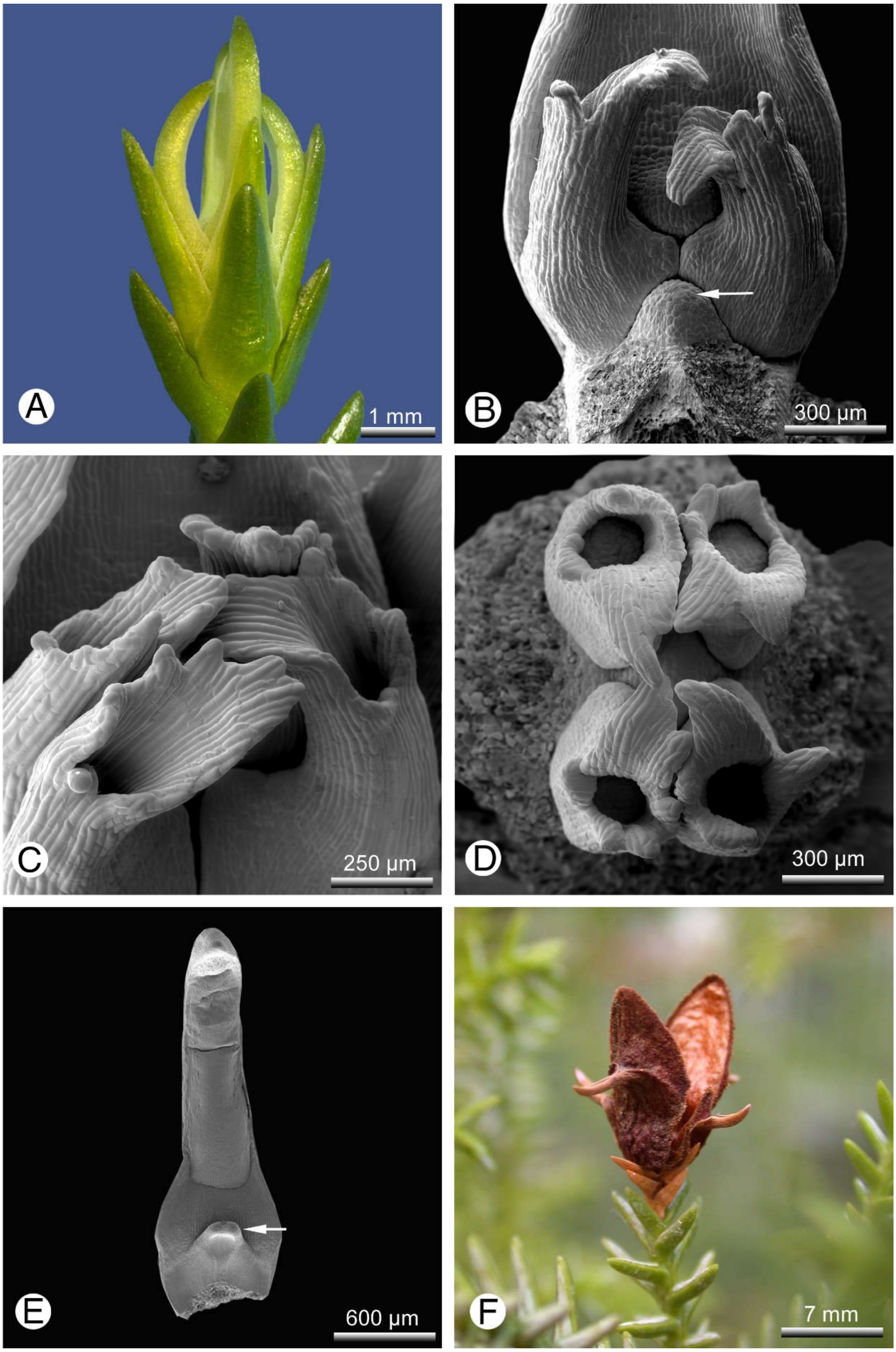

Fig. 2: Cone morphology of *Pilgerodendron uviferum*.

A: Cone at pollination time in erect position, the tips of the four cone scales form a dome covering the cone centre. **B:** Cone scale with two ovules at pollination time, the tip of the cone axis developed as a small hump. **C:** The tips of the ovules are asymmetrically prolonged to the centre supporting the development of a common drop, lateral view (SEM-image, cone scales removed). **D:** The tips of the ovules are asymmetrically prolonged to the centre supporting the development of a common drop, top view (SEM-image, cone scales removed). **E:** Cone scale just after pollination, beginning of the growth of the ventral swelling (arrow) which closes the cone (SEM-image). **F:** Mature cone with distinct dorsal spines, the distal pair of cone scales is larger than the proximal one.

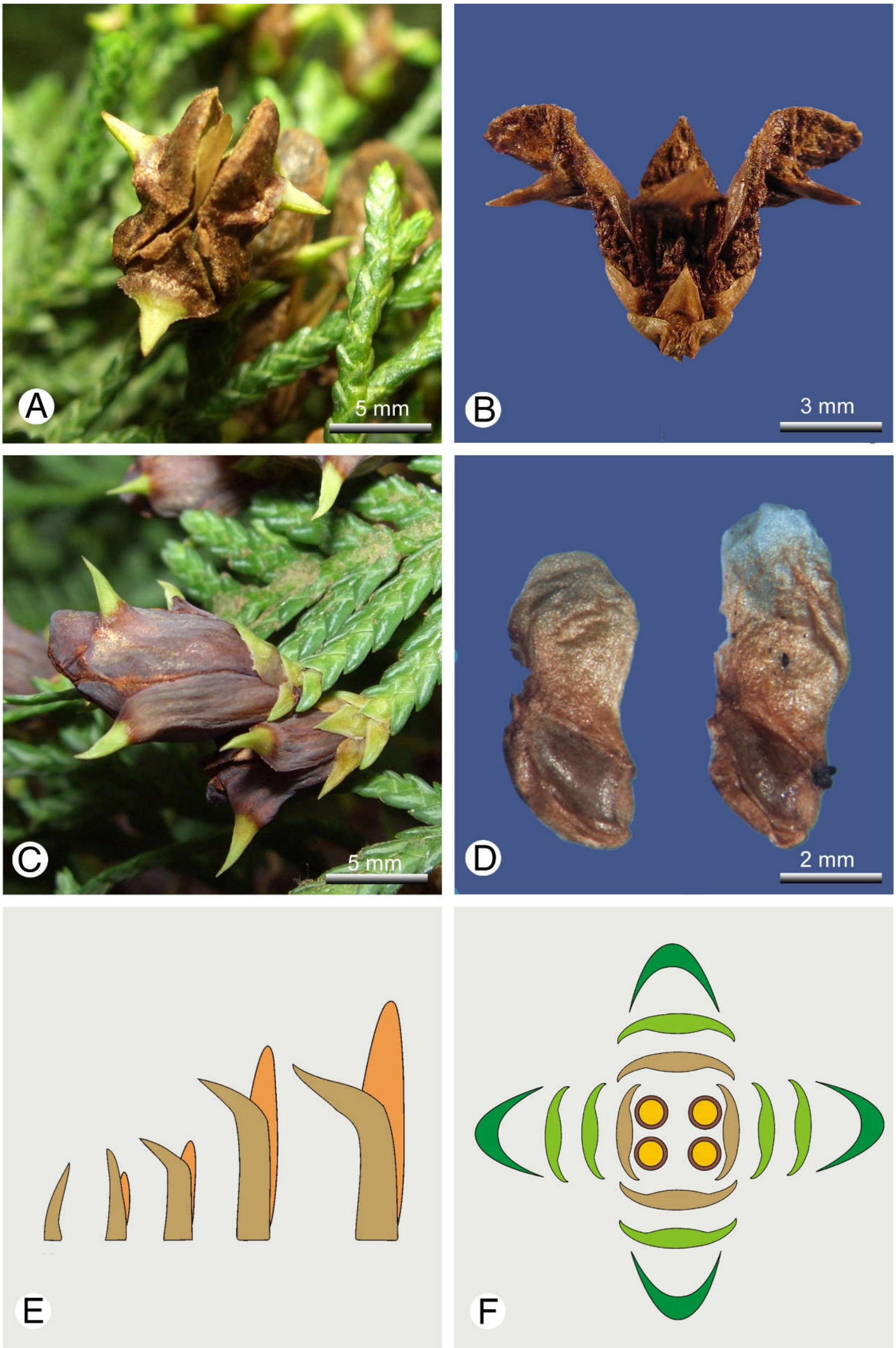

Fig. 3: Cone morphology of *Libocedrus* s. str.

A: *Libocedrus bidwillii*, mature cone on a branch with distinct dorsal spines, top view. **B:** *Libocedrus bidwillii*, mature cone, lateral view. **C:** *Libocedrus plumosa*, immature cone on a branch with distinct dorsal spines. **D:** *Libocedrus bidwilli*, asymmetrically winged seeds. **E:** Schematic drawing of the cone scale morphogenesis from pollination time until maturity, development of the dorsal spine (brown), ventral swelling (orange). **F:** Typical cone diagram of the species of the *Libocedrus* group (brown = cone scales, light green = transitional leaves, dark green = leaves).

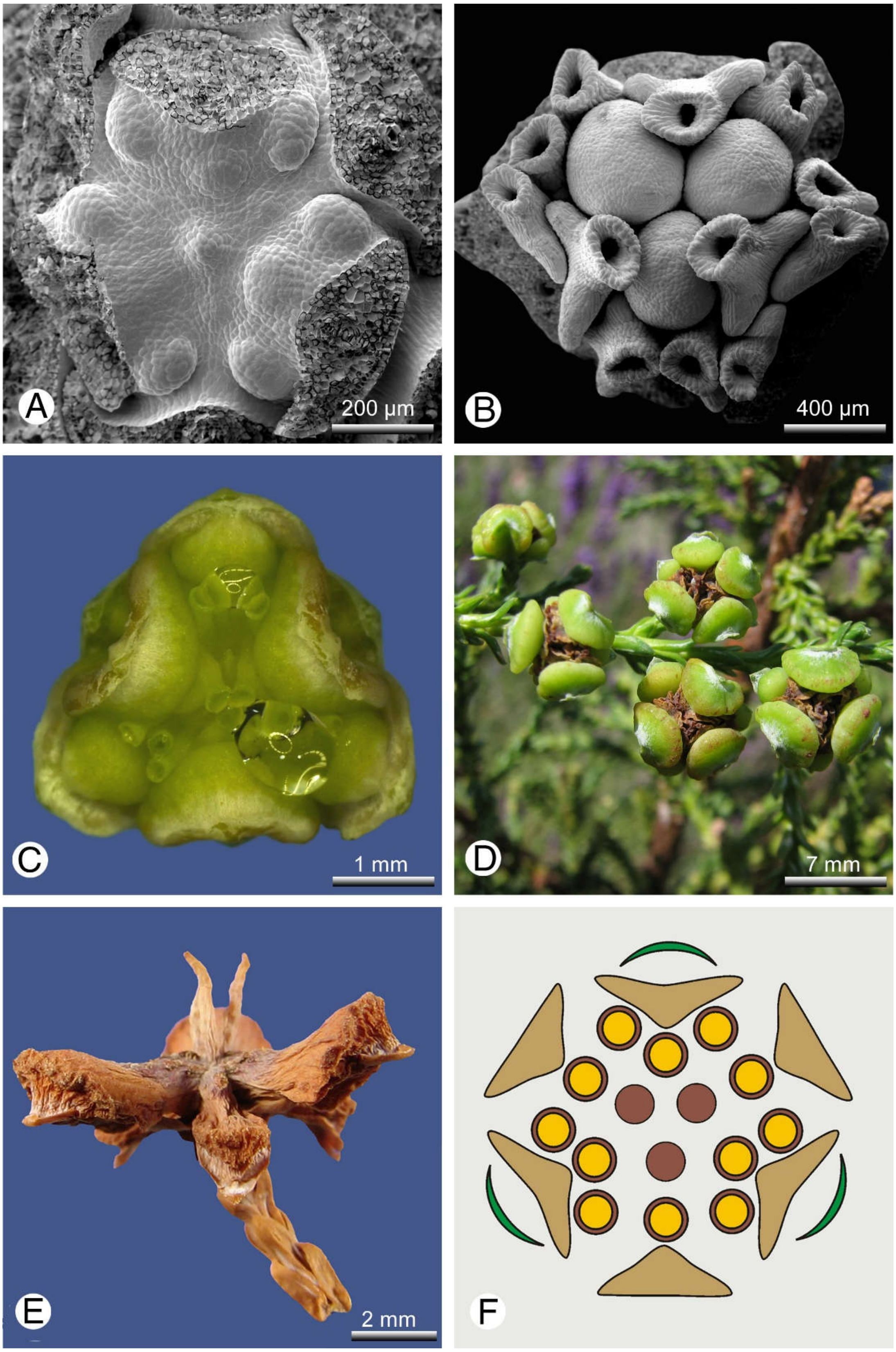

Fig. 4: Cone morphology of *Fitzroya cupressoides*.

A: Young cone, first stadium of ovule development. The development of the ovules of a whorl is slightly asynchronous (SEM-image, cone scales removed). **B:** Young cone with three ovules in the axils of each distal cone scale and one in the axils of each proximal cone scale, the micropyles of the central ovules of the distal cone scales growing towards the cone centre; above the cone scales three globose structures follows, the so called glands (SEM-image, cone scales removed). **C:** Cone at pollination time, four zones for common drops are built by the long necks to the ovules. **D:** Immature cones on a branch. **E:** Open mature cone in lateral view. **F:** Typical cone diagram corresponding to B (dark brown = "glands", light brown = cone scales, green = leaves).

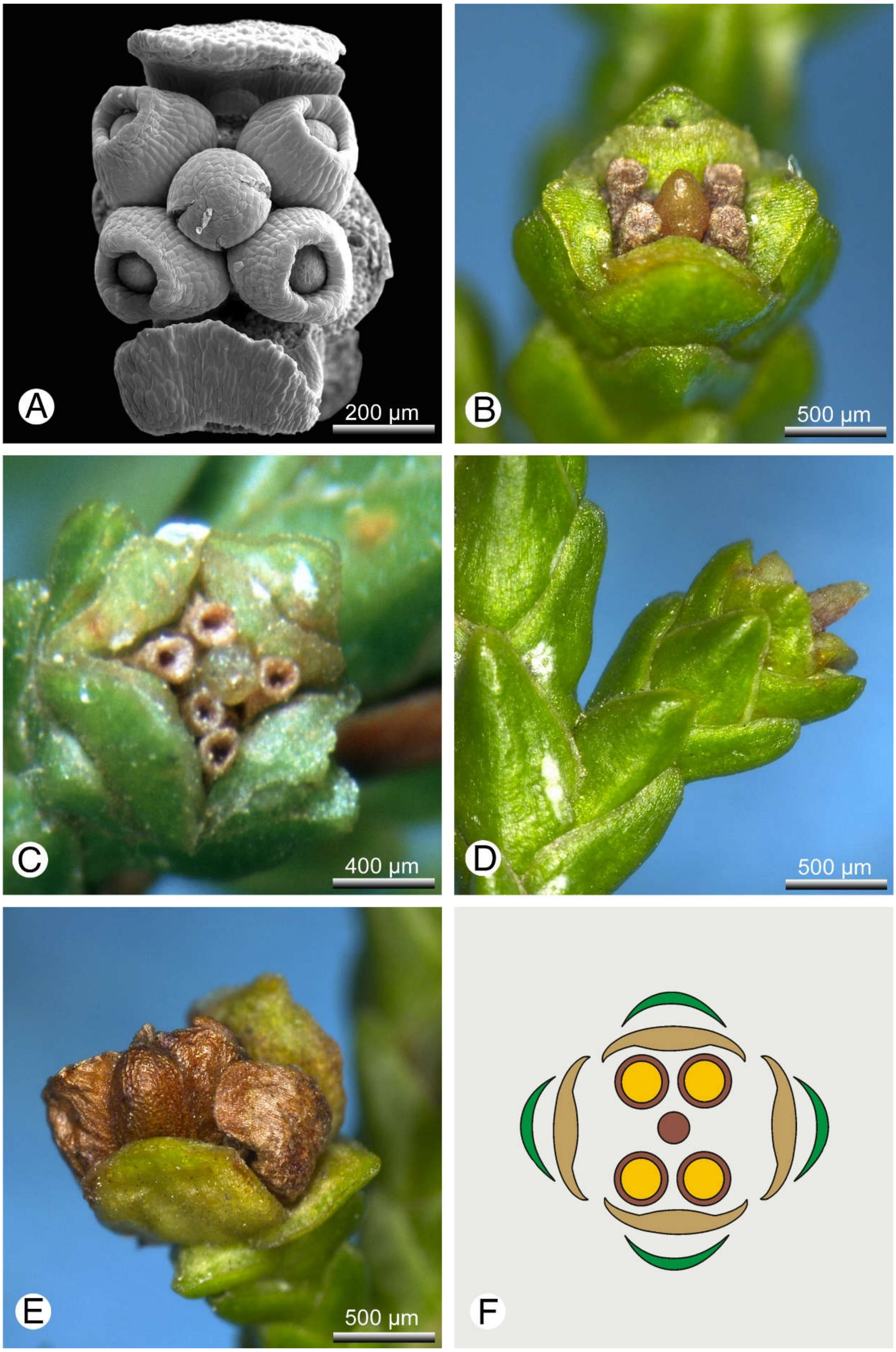

Fig. 5: Cone morphology of *Diselma archeri*.

A: Young cone with two fertile cone scales, two ovules in the axils of each, and a distinct columella (SEM-image, lower cone scales removed). **B:** Cone shortly after pollination time with four ovules and a distinct columella. **C:** Cone shortly after pollination time, with three ovules in the axil of one cone scale. **D:** Cone shortly after pollination time with distinct columella, lateral view. **E:** Mature cone. **F:** Typical cone diagram, corresponding to A and B (dark brown = columella, light brown = cone scales, green = leaves).

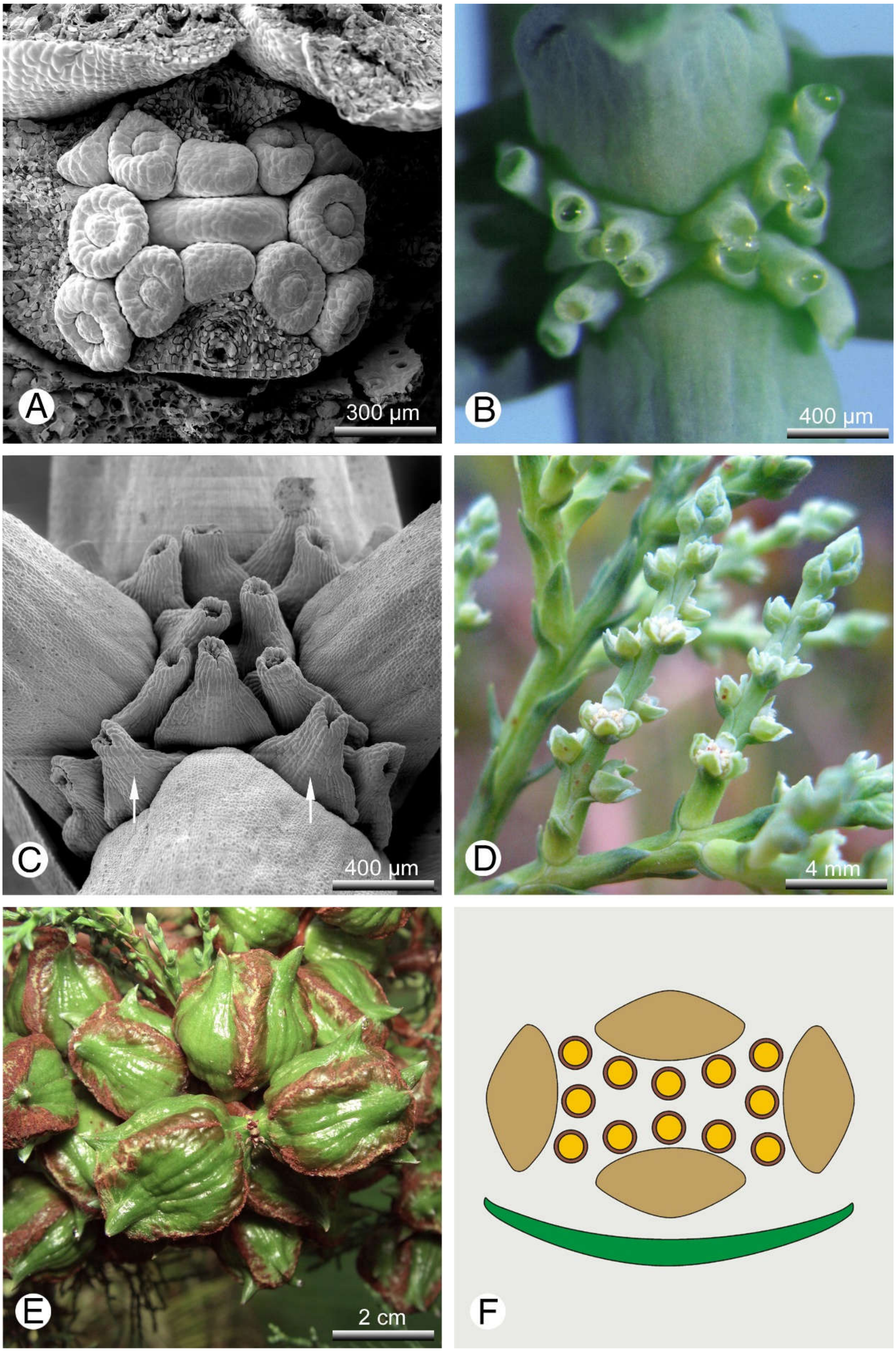

Fig. 6: Cone morphology of *Widdringtonia schwarzii.*

A: Young cone, ovules develop in the axils of the cone scales, the ovules of the proximal scales first, the three ovules in a row centripetally; in the centre of the cone the elongate shallow tip of the cone (SEM-image, cone scales removed). **B:** Cone at pollination with retrieving pollination drops. **C:** Cone at pollination time, the proximal cone scales with a second row (arrows) (SEM-image). **D:** Detail of the clustered arrangement of the cones at pollination time. **E:** Immature cones clustered on a branch. **F:** Cone diagram, corresponding to A (brown = cone scales, green = leaves).

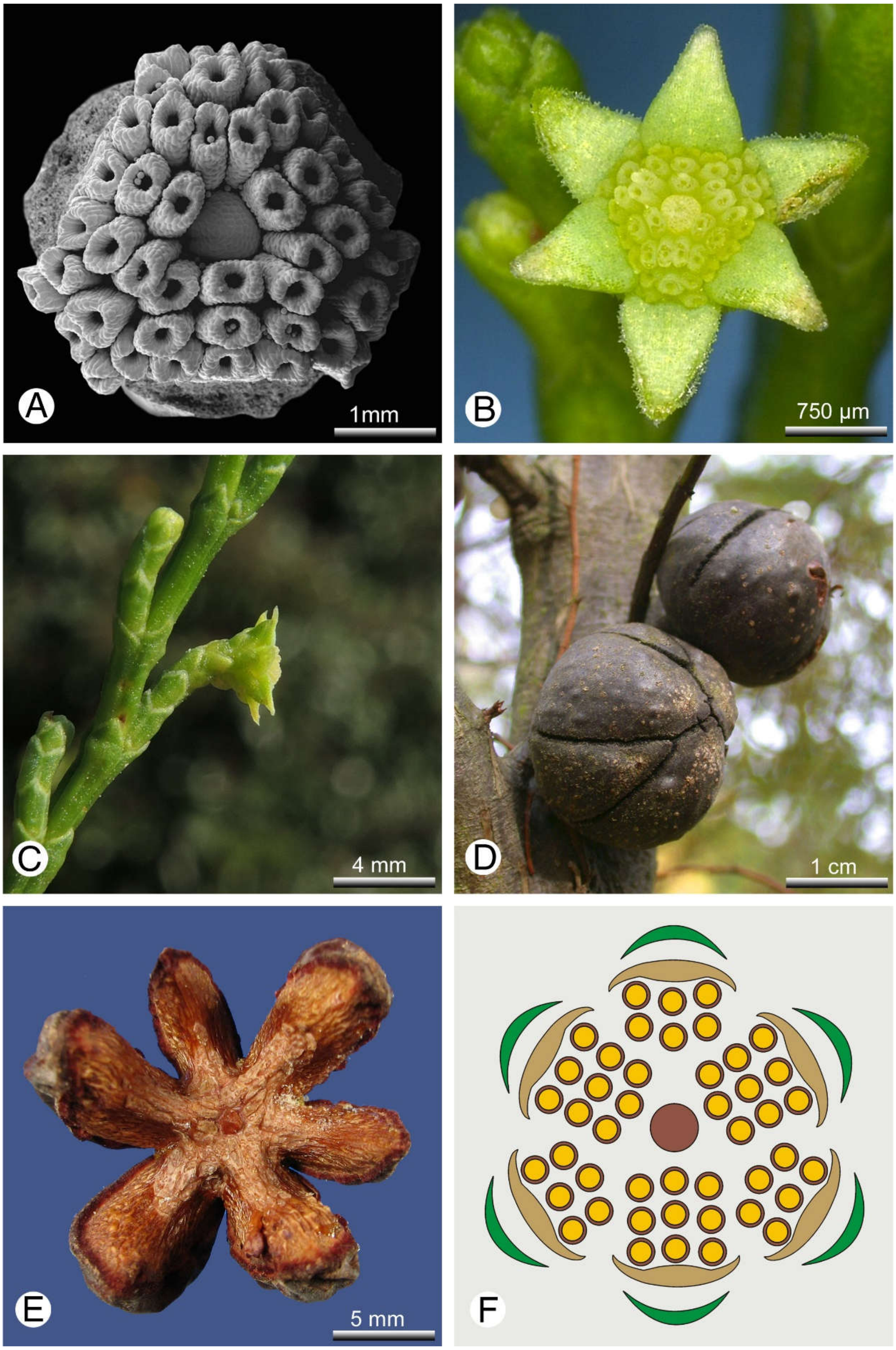

Fig. 7: Cone morphology of *Callitris preissii*.

A: Trimerous cone at pollination time with columella and two whorls of cone scales. The upper cone scales bear more ovules than the lower ones. **B**: Cone at pollination time. **C:** Cone at pollination time in plagiotropic orientation. **D:** Mature cones on a branch. **E:** Mature open cone with small columella, top view. **F:** Cone diagram corresponding to A (dark brown = columella, light brown = cone scales, green = leaves).

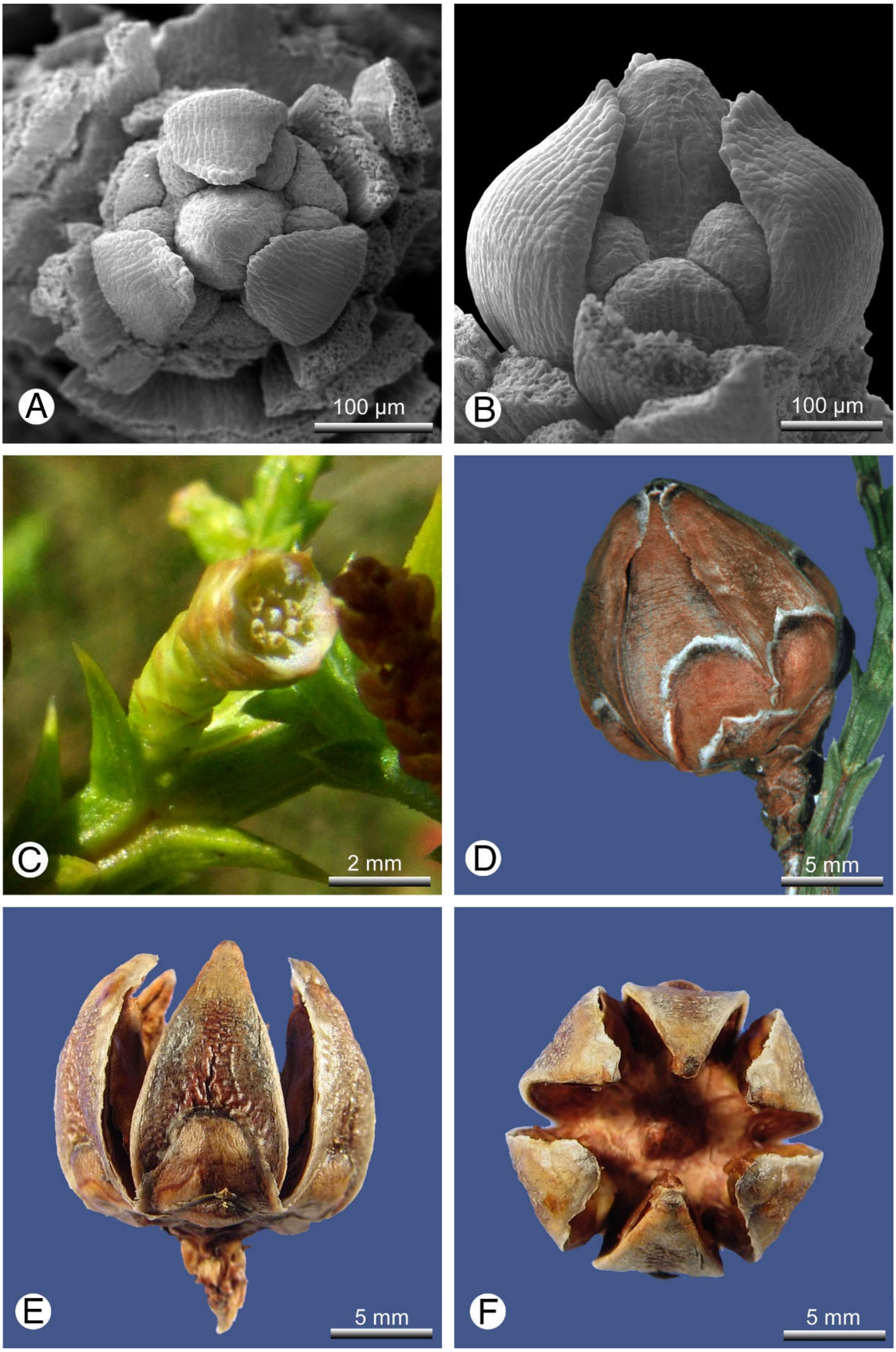

Fig. 8: Cone morphology of *Actinostrobus pyramidalis*.

A: Top view of a young, trimerous cone at pollination time. The very young ovules are developed axillary in each of the six cone scales, the upper cone scales develop two ovules each, the lower cone scale a single ovule, which is larger than the other ovules. A distinct columella is developed (SEM-image, lower cone scales removed). **B:** Young cone of A in lateral view. **C:** Cone at pollination time in plagiotropic orientation. **D:** Closed mature cone on a tree. **E:** Open mature cone, lateral view. **F:** Open mature cone, top view.

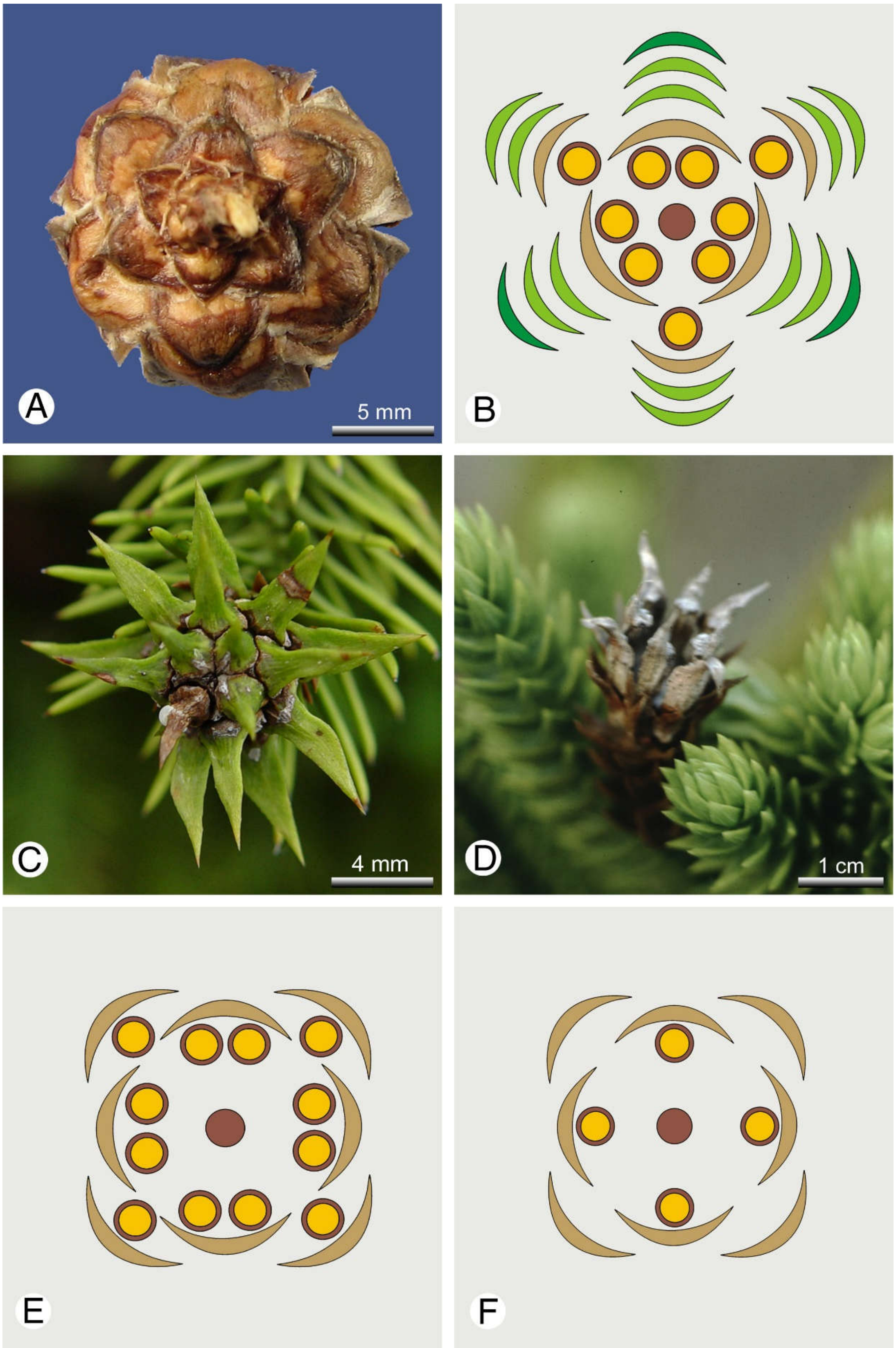

Fig. 9: Cone morphology of *Actinostrobus pyramidalis* and *Neocallitropsis pancheri*.

A: *Actinostrobus pyramidalis*, mature cone, view from below, with conspicuous transitional leaves. **B:** Cone diagram, corresponding to 8A and 8B (dark brown = columella, light brown = cone scales, light green = transitional leaves, dark green = leaves). **C:** *Neocallitropsis pancheri*, nearly mature tetramerous cone on a branch (© B. Suprin). **D:** *Neocallitropsis pancheri*, open mature tetramerous cone on a branch after releasing the seeds (© H. Nimsch). **E:** *Neocallitropsis pancheri*, hypothetical cone diagram with one ovule on each proximal cone scale and two on each distal cone scale **F:** *Neocallitropsis pancheri*, hypothetical cone diagram with one ovule on each distal cone scale (dark brown = columella, ligh brown = cone scales).

Bull. CCP 4 (3): 109-115. (12.2015)

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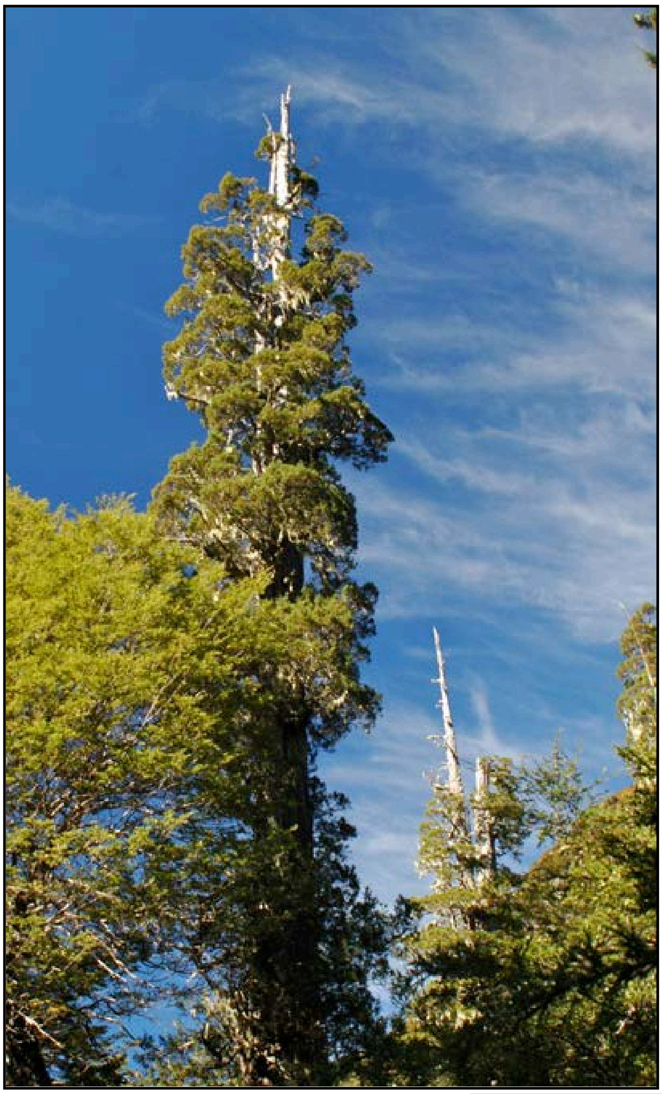
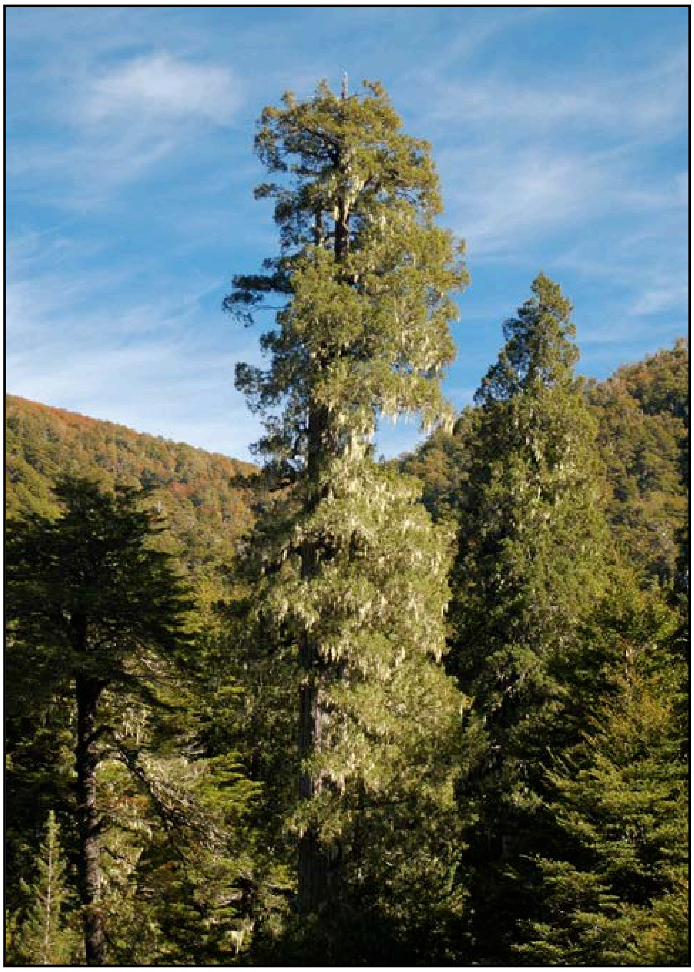
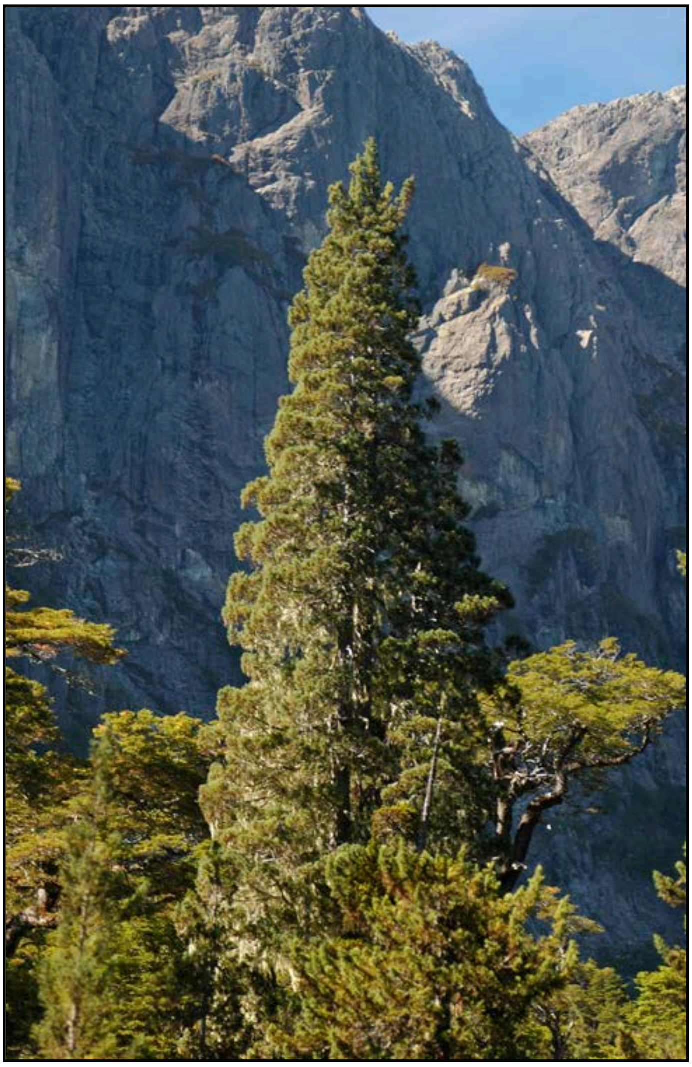
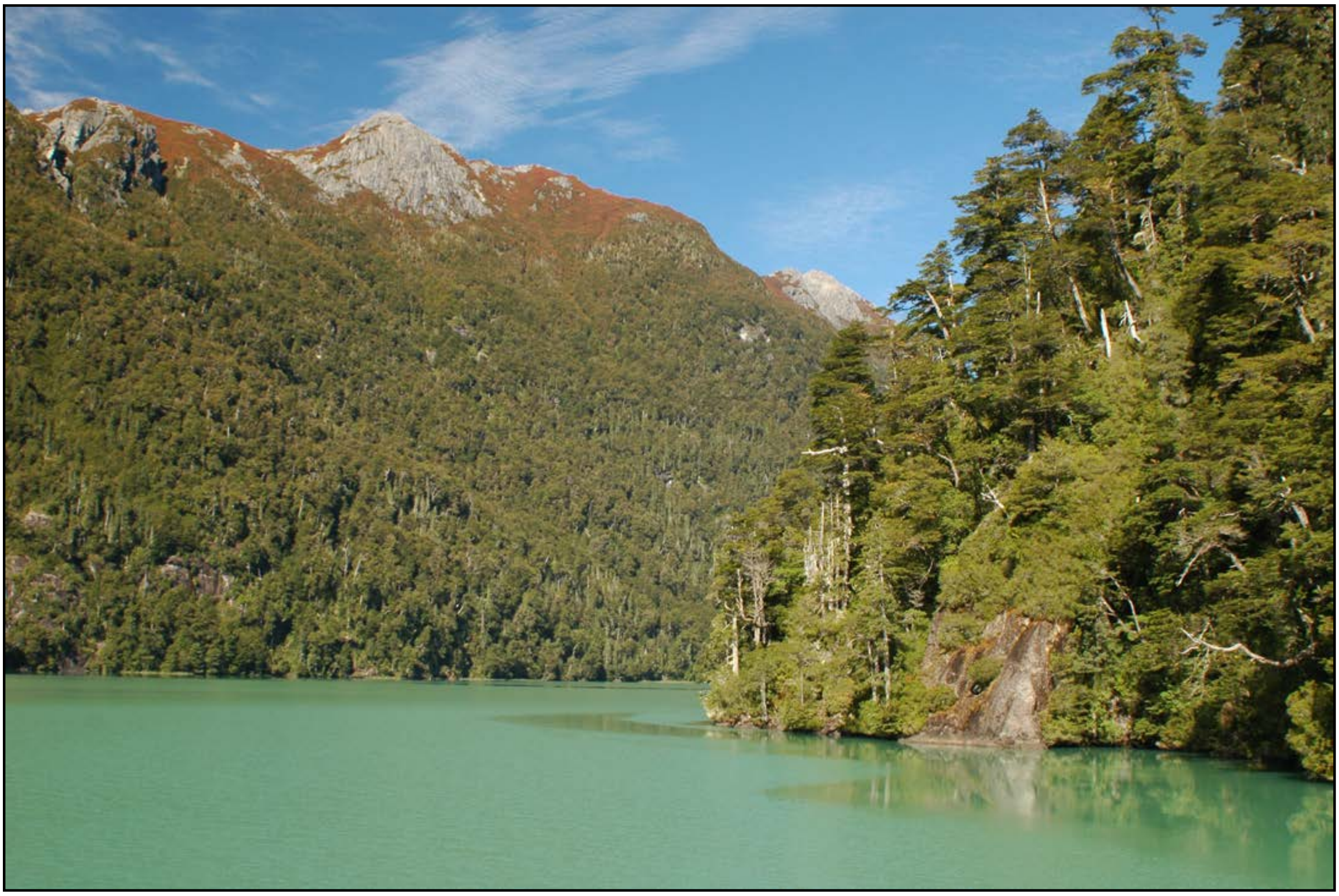
Fitzroya cupressoides (Molina) I.M.Johnst. 1924

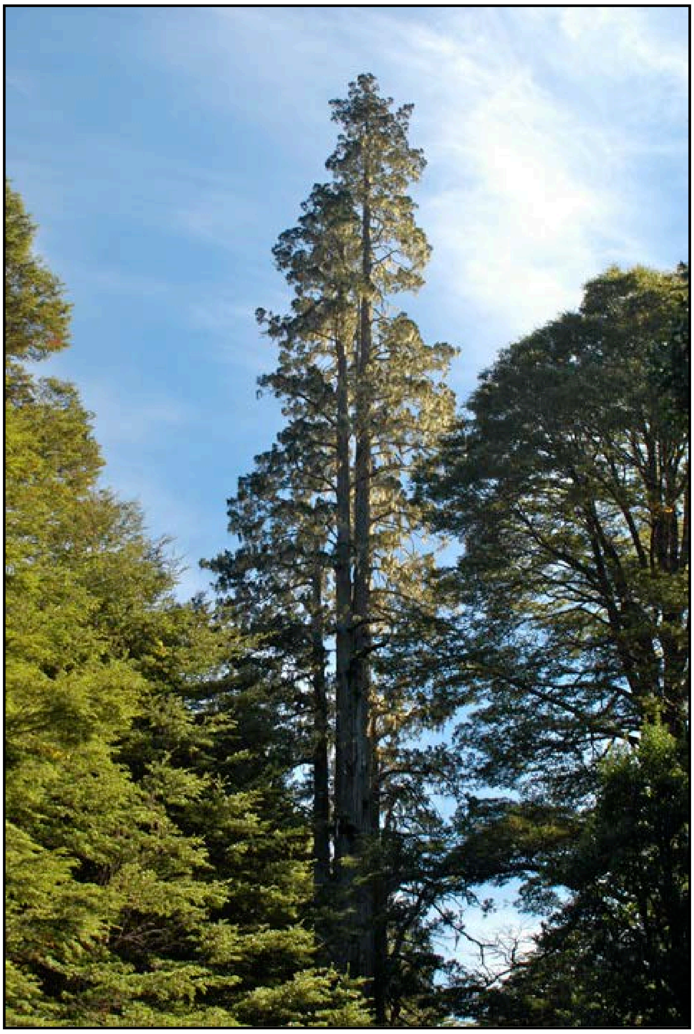
Puerto Blest on Lago Nahuel Huapi, and Laguna Frias, Argentina.

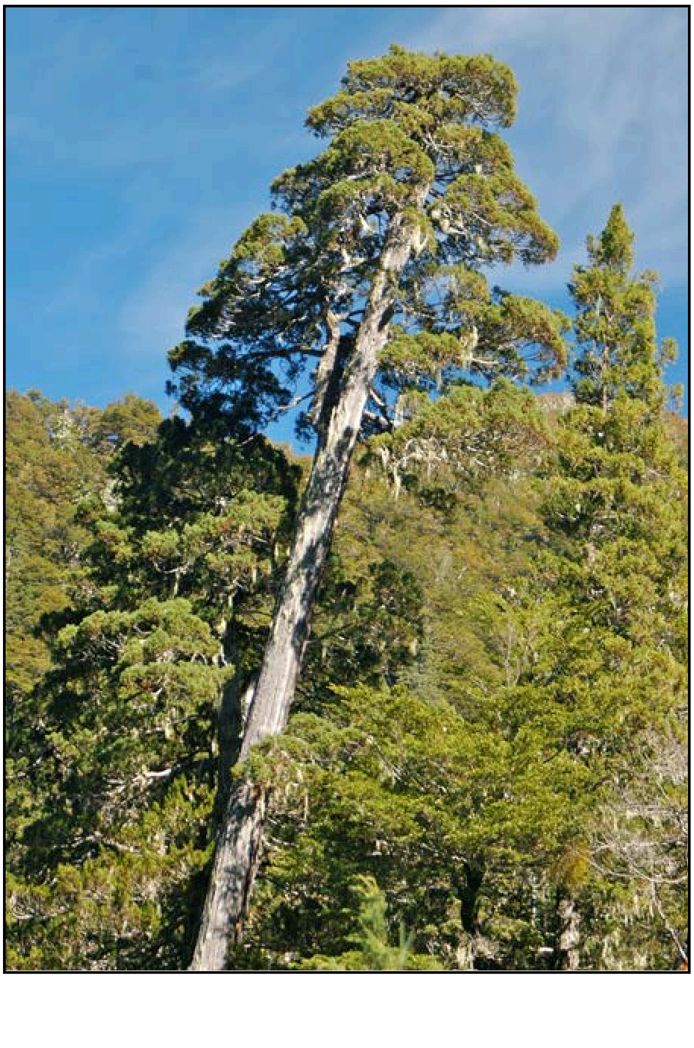


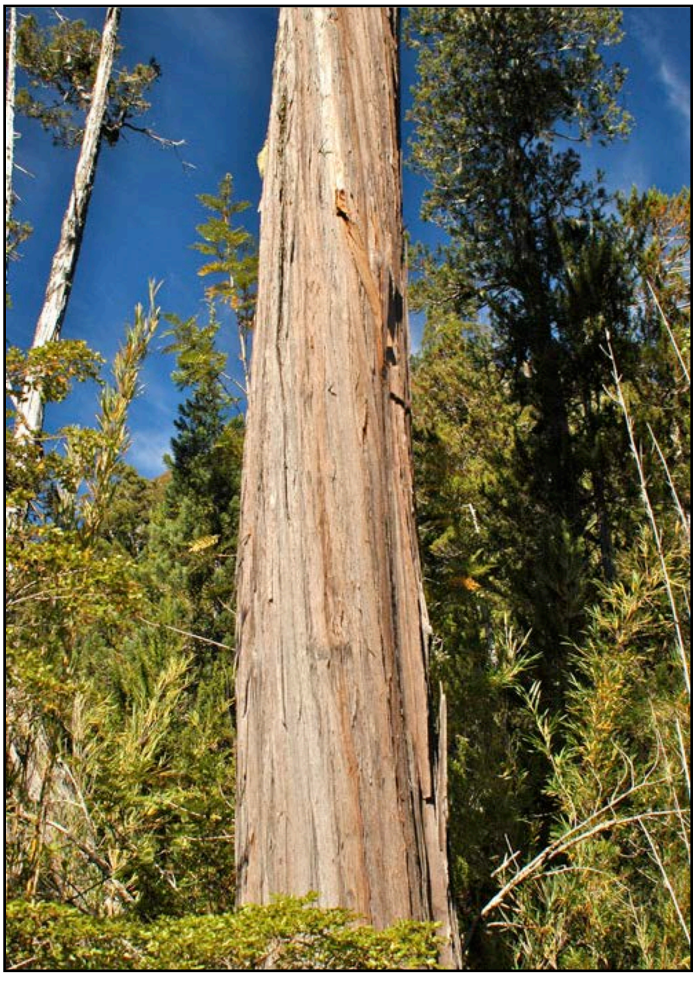










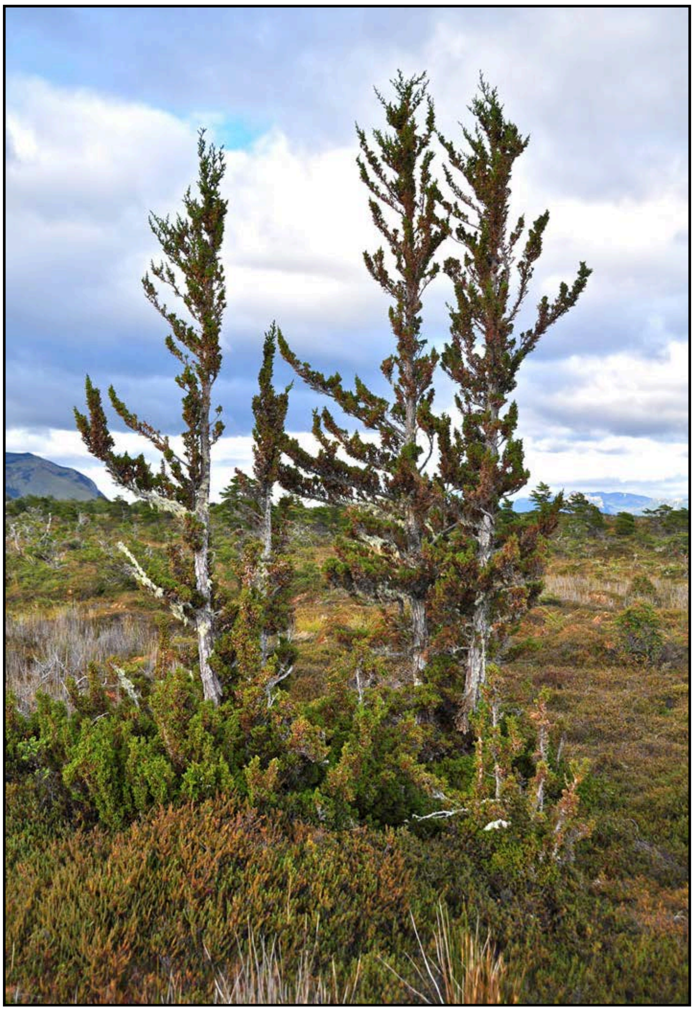


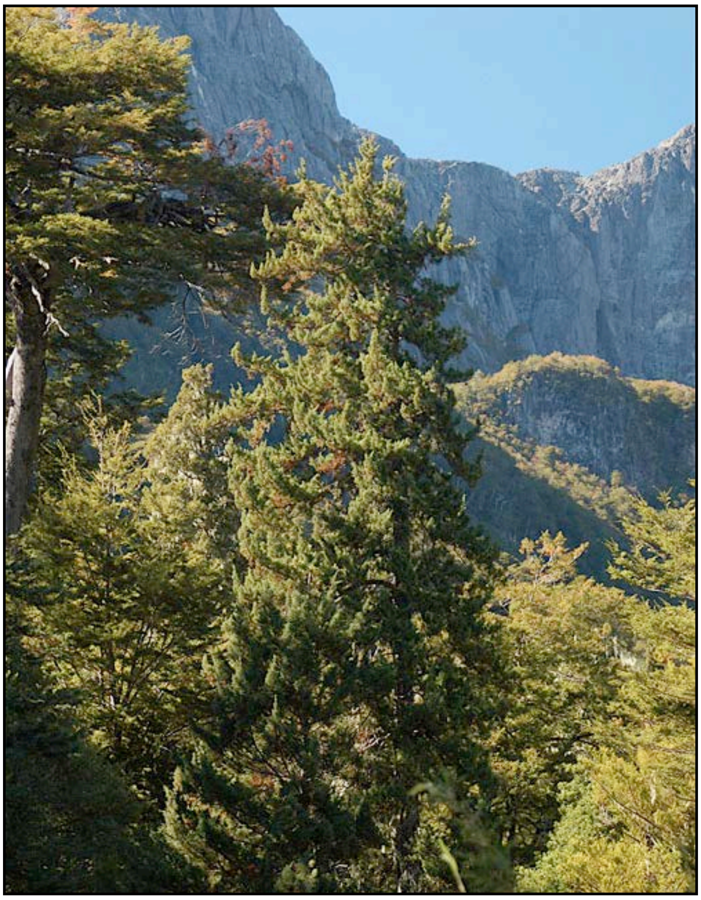
Bull. CCP 4 (3): 116-123. (12.2015)

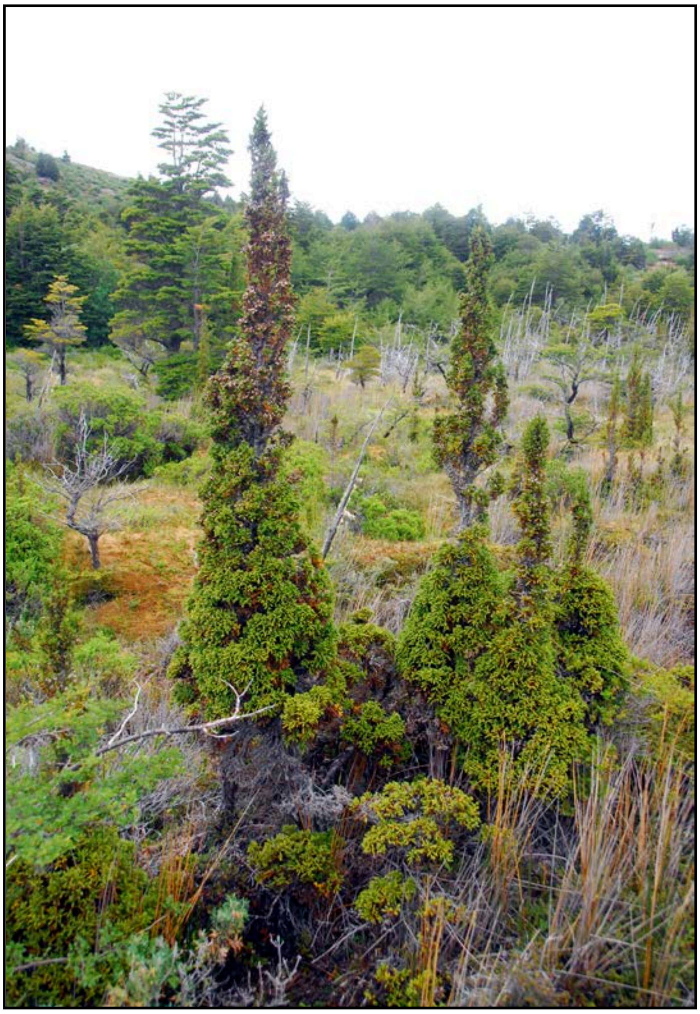
Jeff Bisbee

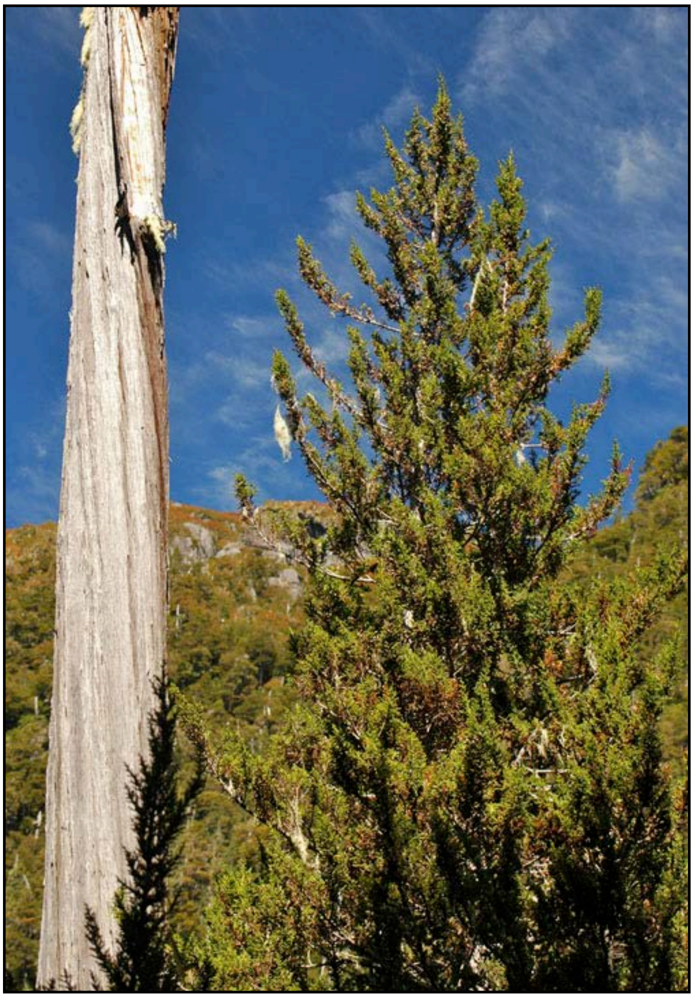
Libocedrus uvifera (D.Don) Pilg. 1926

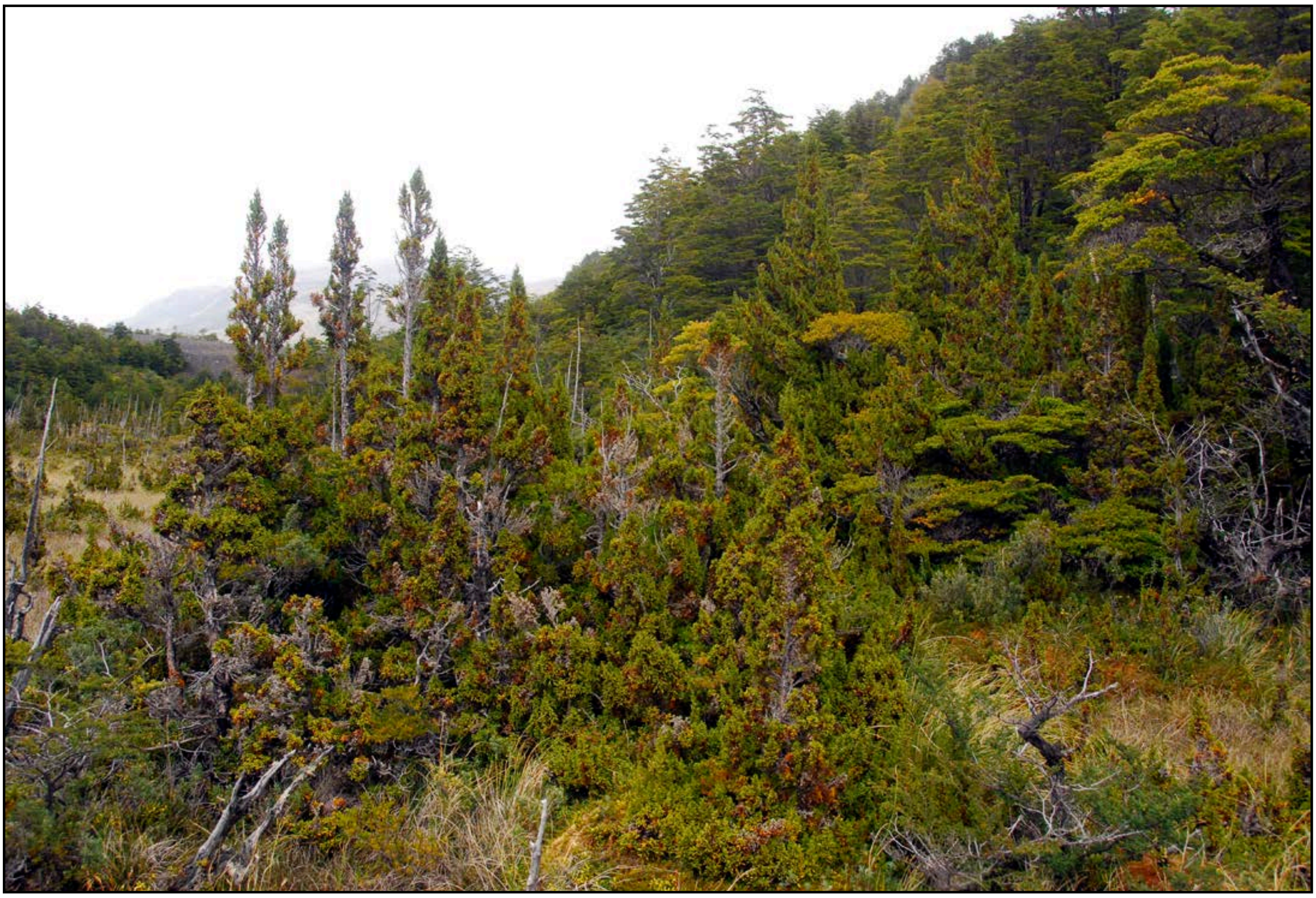
Puerto Natales and Torres del Paine National Park, Chile; Laguna Frias, Puerto Blest, Argentina (details see p. 123).
















Libocedrus uvifera (p. 116-123)

Puerto Natales and Torres del Paine National Park, Chile; Laguna Frias, Argentina.

Page 116: Laguna Frias; Puerto Natales; Puerto Natales
Page 117: Puerto Natales
Page 118: Puerto Natales; Laguna Frias; Puerto Natales
page 119: Puerto Natales; Puerto Natales; Laguna Frias; Puerto Natales
Page 120: Puerto Natales
Page 121: Laguna Frias
Page 122: Puerto Natales
Page 123: Puerto Natales

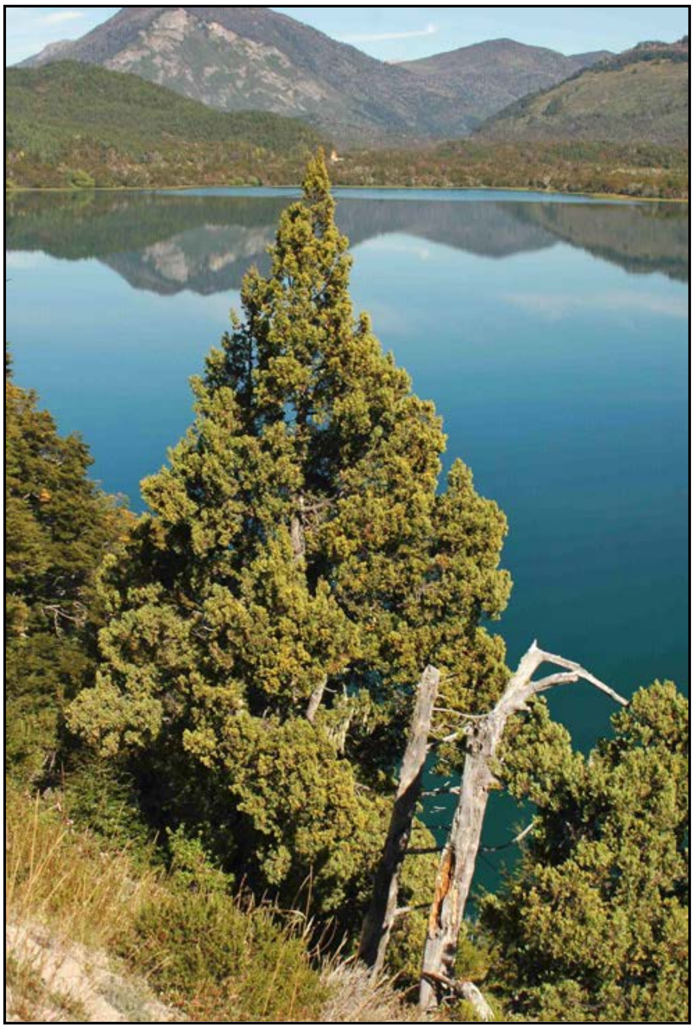
Austrocedrus chilensis (p. 124-132)

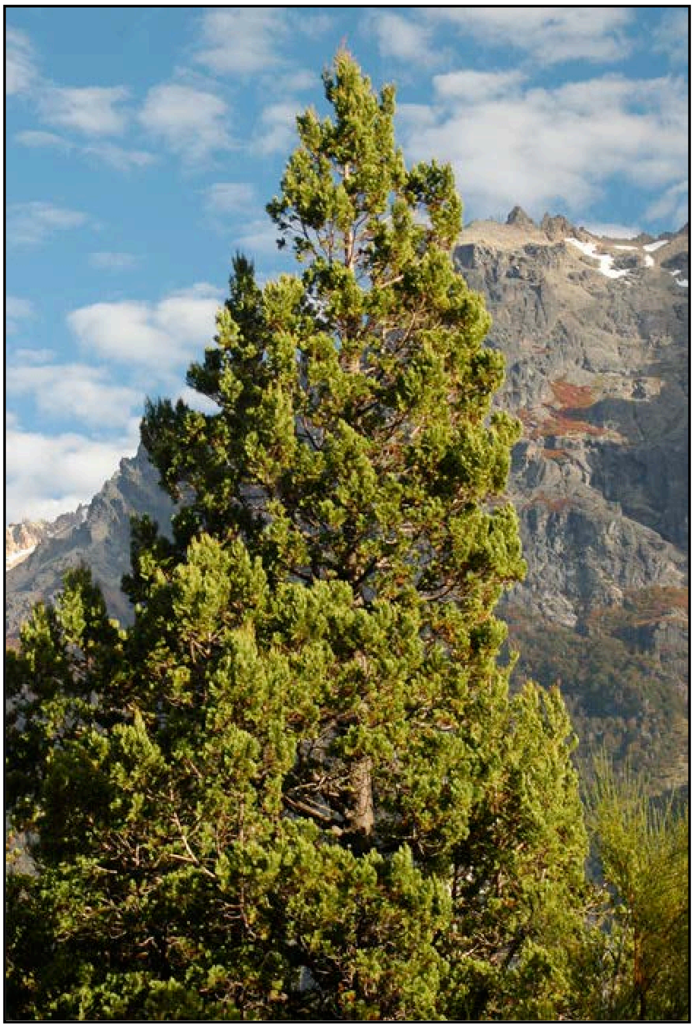
Siete Lagos, Lago Mascardi and Bariloche, Argentina; Conguillío, Chile.

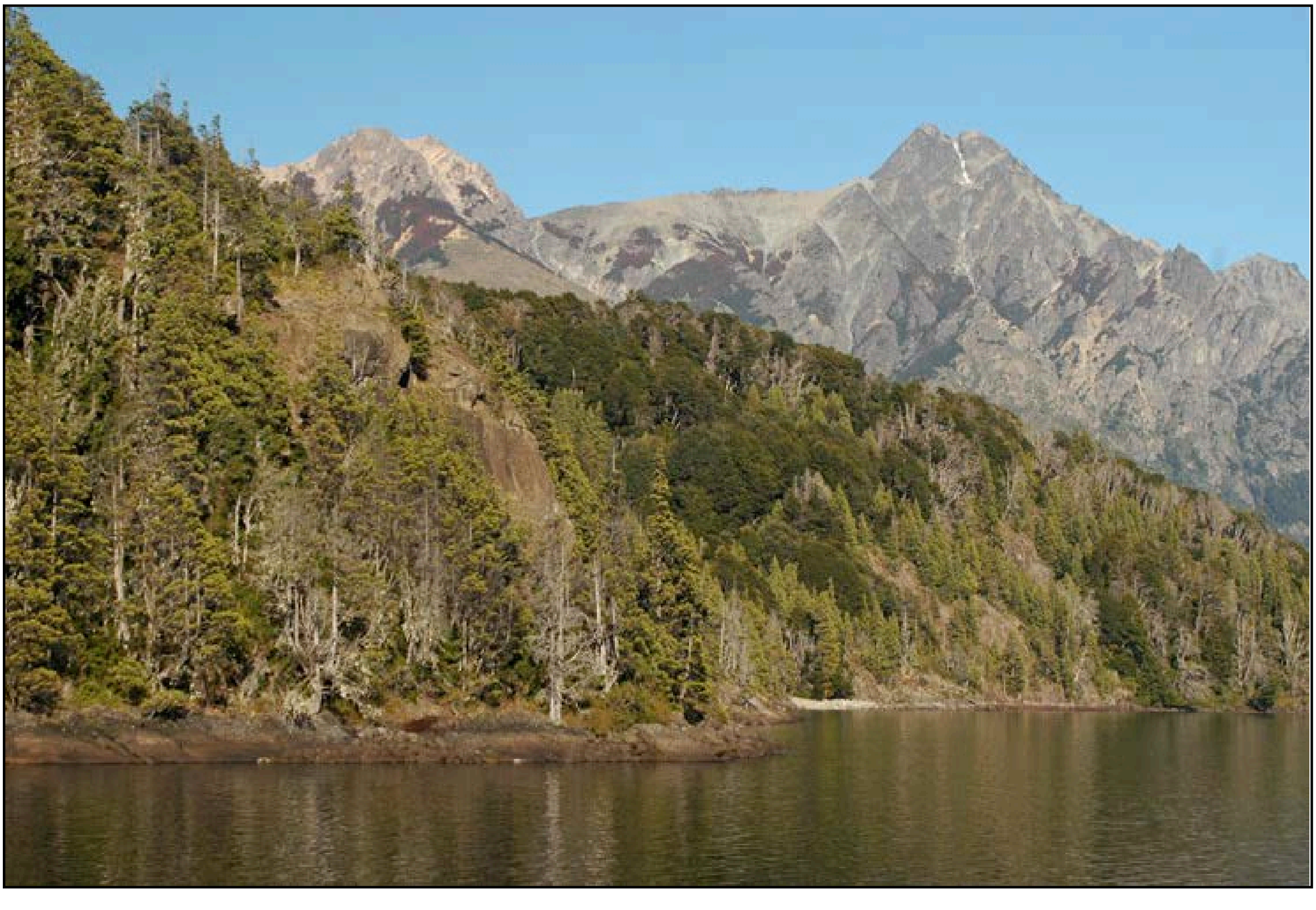
Page 124: Siete Lagos; Lago Mascardi; Siete Lagos
Page 125: Conguillío; Bariloche
Page 126: Conguillío
page 127: Bariloche
Page 128: Siete Lagos; Bariloche
Page 129: Siete Lagos; Bariloche; Bariloche; Conguillío
Page 130: Lago Mascardi
Page 131: Lago Mascardi; Siete lagos; Bariloche
Page 132: Siete Lagos

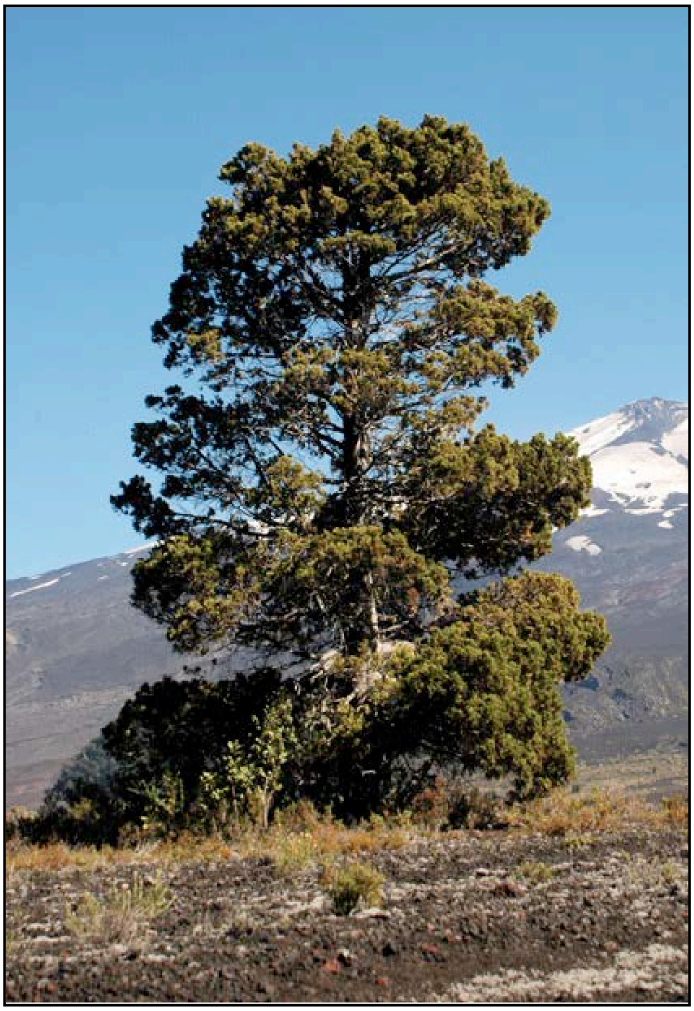
Austrocedrus chilensis (D.Don) Pic. Serm. & Bizzarri 1978

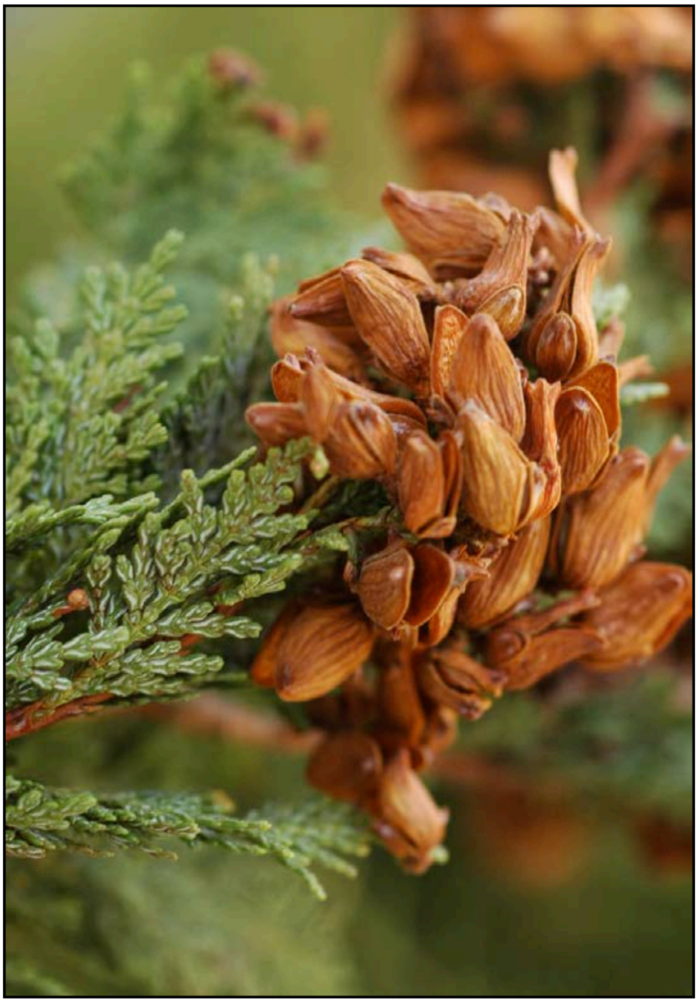
Lago Mascardi, Bariloche and Siete Lagos, Argentina; Conguillío, Chile (details see p. 123).

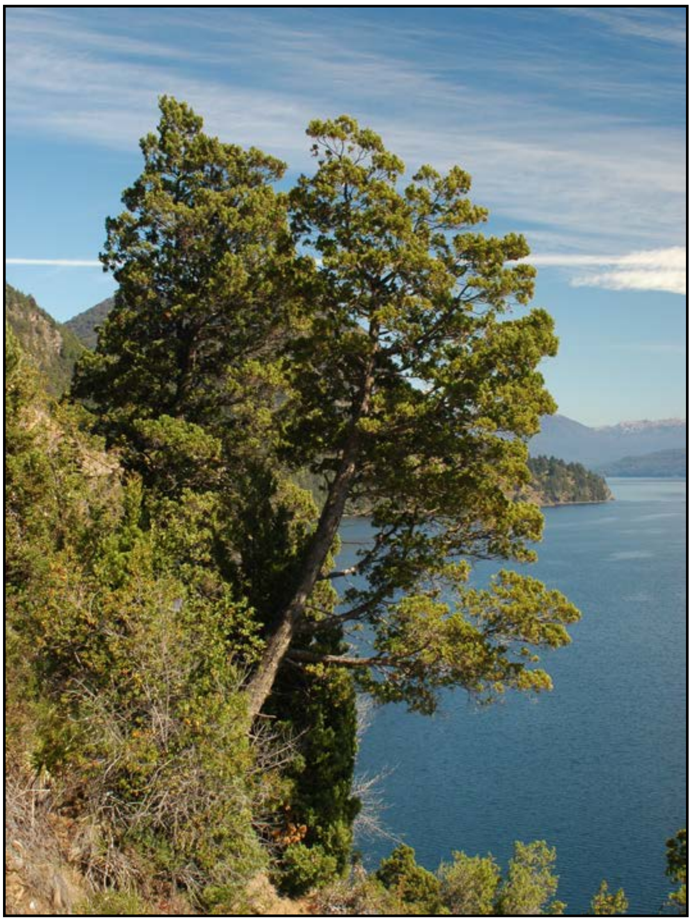


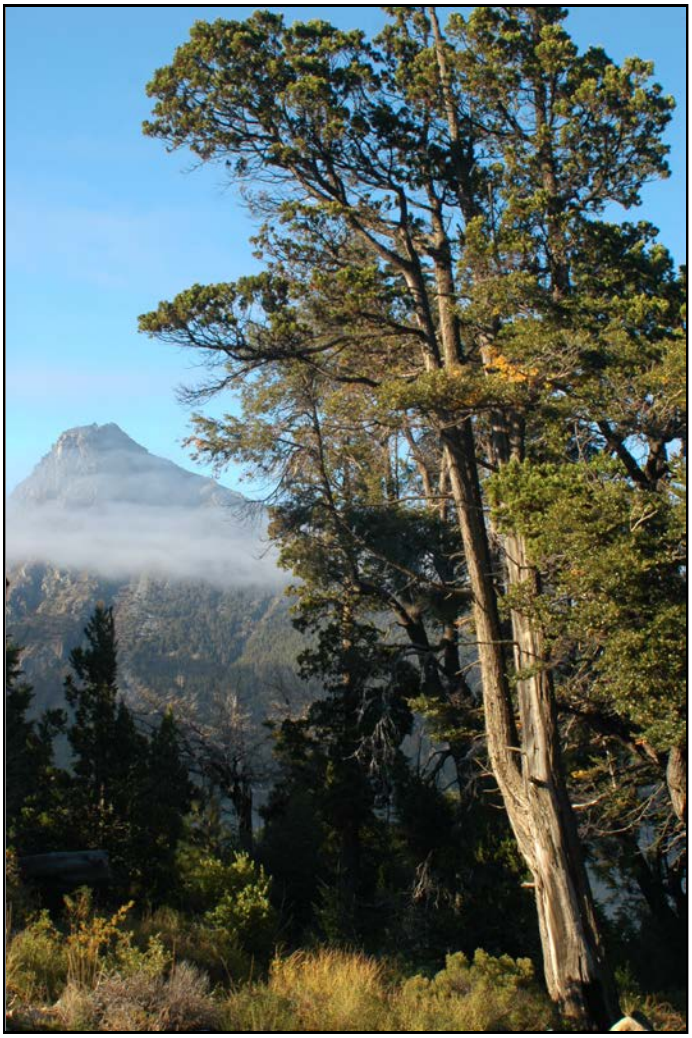


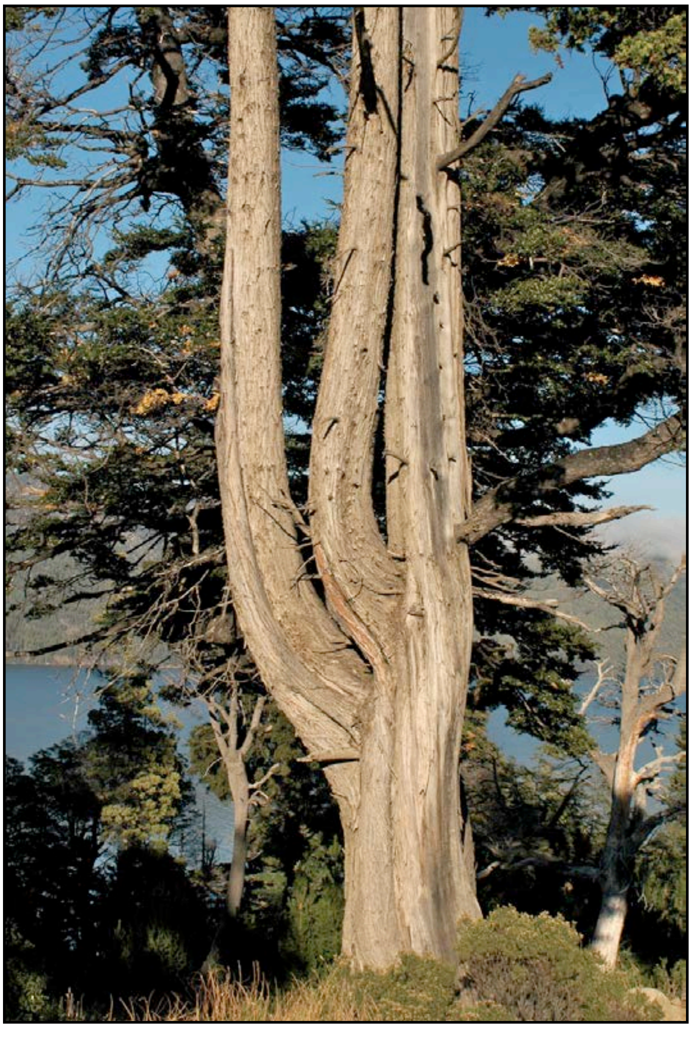


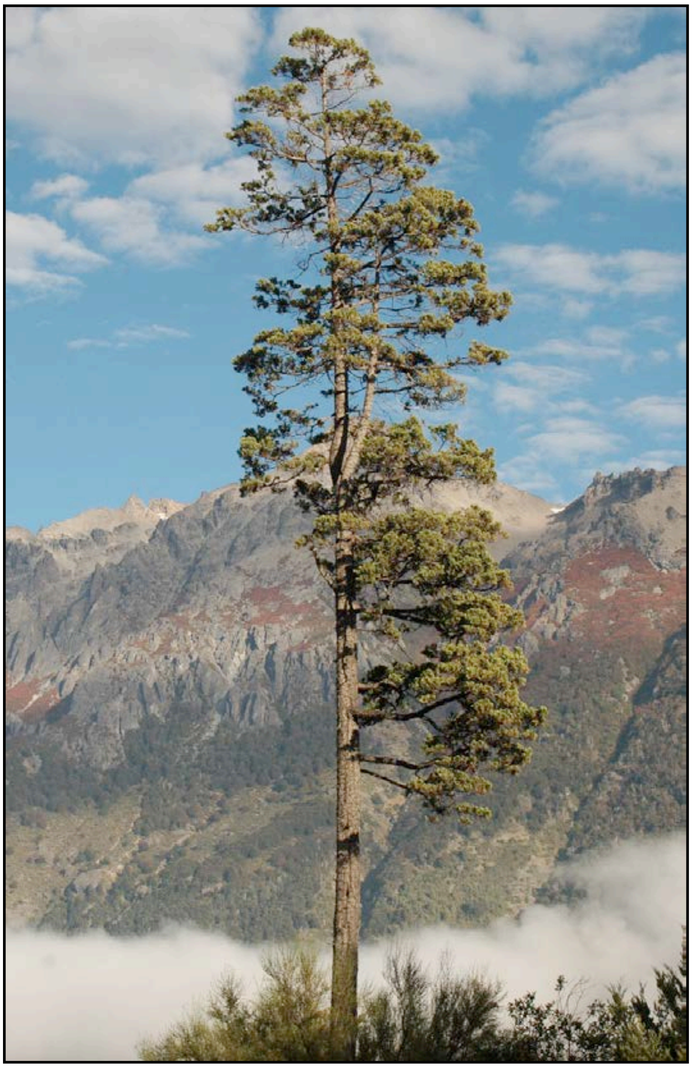


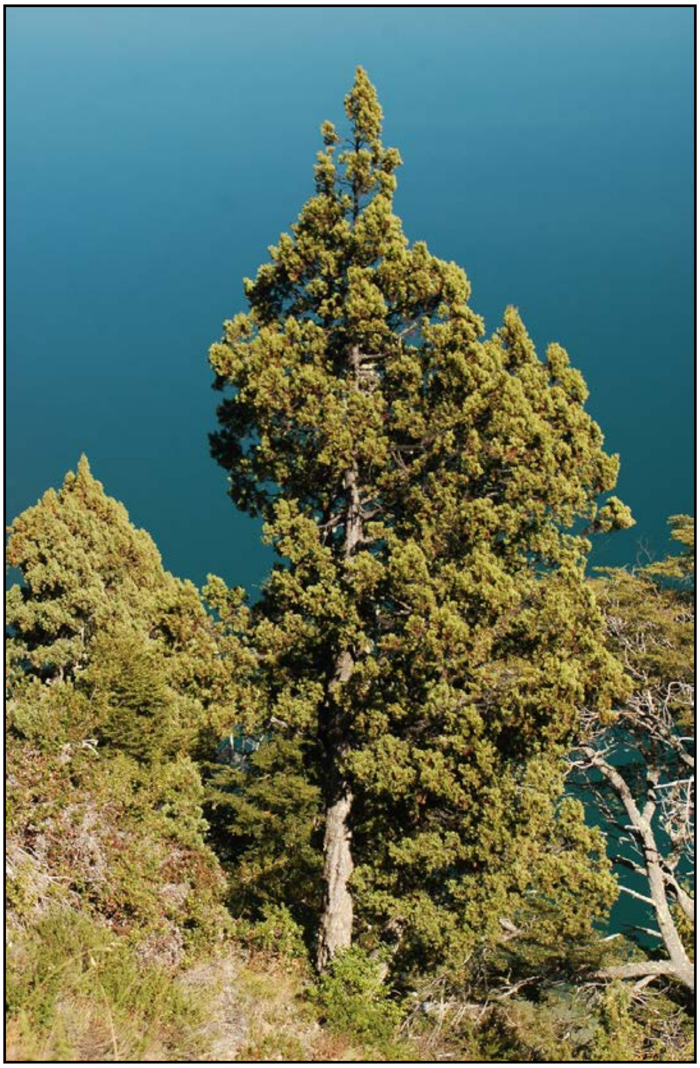


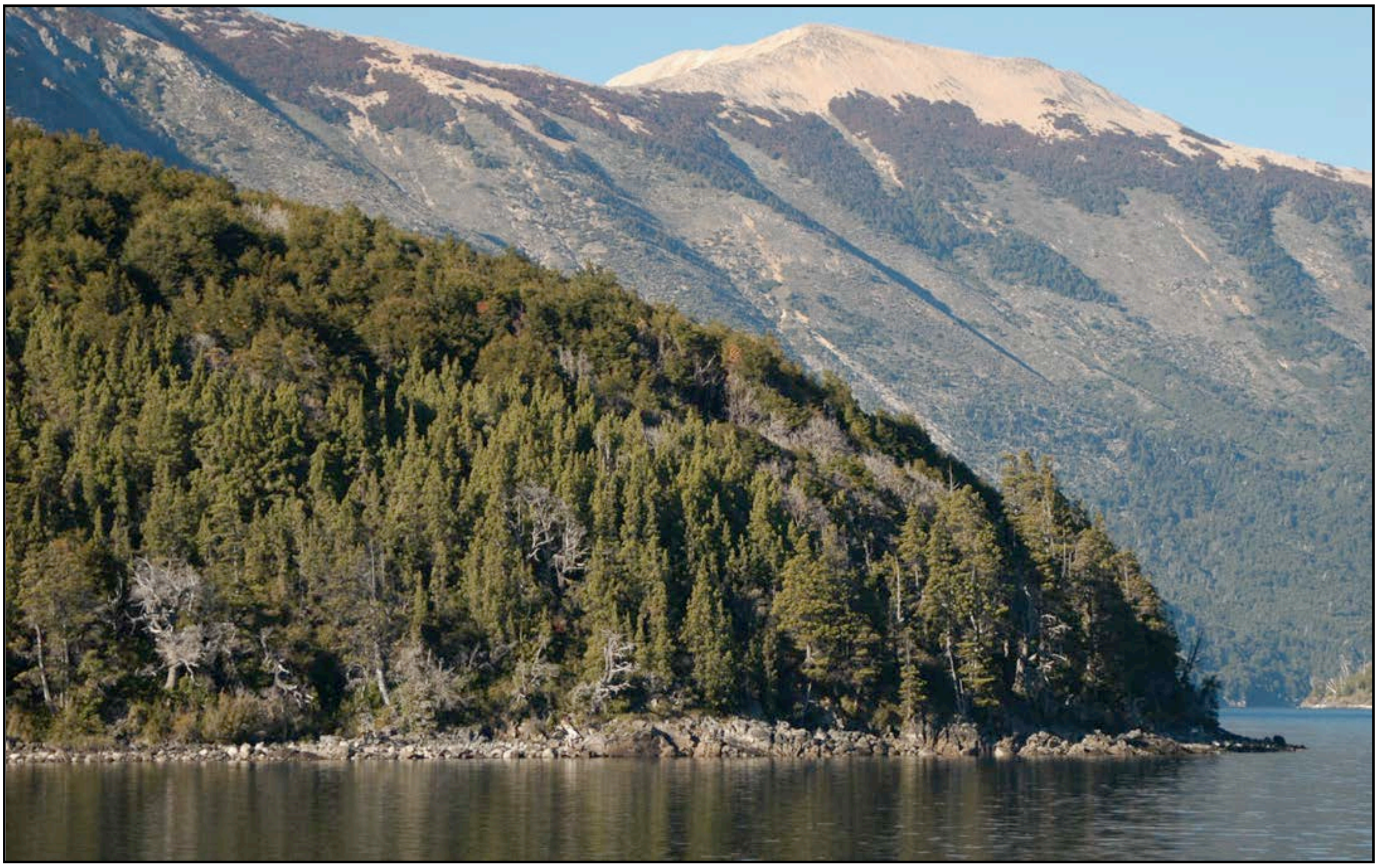












Bull. CCP 4 (3): 133-136. (12.2015)

D. Maerki

Note on the conservation status of *Cupressus montana*

Abstract

The conservation status of *Cupressus montana* a rare cypress species of the highest mountain range of Baja California is critically reviewed according to the available information.

Cupressus montana Wiggins grows on the slopes of the San Pedro Mártir mountains of northern Baja California (illustrations, see Bisbee 2012 and p. 136). This range culminates à 3095 metres at the Picacho del Diablo (highest summit of Baja California). A few authors (e.g. Farjon 2005, Farjon 2013) treat this taxon at a varietal rank of *Cupressus arizonica* Greene. Taking into account geography, phenology, physiology and cone and seedling morphology it is not only isolated, but also quite distinct from any other species (Bisbee & Maerki 2012). Investigations of molecular data by Adams *et al.* (2014) showed that it is different from the geographically closest cypress population in Baja California, *Cupressus revealiana* (Silba) Bisbee and acknowledged the species rank.

In 1998, the International Union for Conservation of Nature (IUCN) classified this taxon as vulnerable (VU) and in 2013 as critically endangered (CR) (Farjon 2013). The last assessment was done on the 22 March 2011 by A.Farjon and reviewed by P.Thomas at an unknown date. This conservation status (CR) is justified as follow:

> The estimated number of mature trees of this variety is fewer than 250, which would place it as Endangered under criterion D. However, the trees are extremely difficult to find and this number is therefore uncertain. Mapping the known occurrences from herbarium specimens is similarly difficult for a lack of fixed toponyms in the area, but most collections were made in a very small area around the summit Cerro de la Encantada. Therefore, the extent of occurrence (EOO) is likely to be much less than 100 km^2 (here calculated as 46 km² based on four map points of collected specimens) while there is a continuing decline inferred from unrestricted grazing. This places the taxon as Critically Endangered under the B criterion.

Except for the data present on a few herbarium specimens, no other source is given for the above justification. Herbarium sheets are often misleading and this is the case here. In fact all estimations presented are in error and some affirmations are also erroneous.

- The number of mature trees is in the thousands (J.Bisbee, pers. com.); it is “frequent and locally abundant” (Thorne *et al.* 2010).
- The trees are easily found once one knows where to go hiking.
- The extent of occurrence is more than 100 km². Using the distribution range map by Thorne *et al.* (Map 17, p. 49), the EOO is calculated to about 107 km², and the area of occupancy to about 30 km² (**Table 1**).
- The distribution range is mostly at high altitudes, above the other conifer species present on the San Pedro Mártir range. It is so remote that there is no human settlement or ranch with any sort of cattle (J.Bisbee, pers. com., 4 July 2015). Wild animals do not represent a threat. Young trees are observed (Bisbee 2012 and fig. 2, p. 136). There is perhaps confusion with *Cupressus atlantica* whose population is critically endangered because it is heavily grazed by goats.
- As shown by Thorne *et al.* (Map 1, p. 44) the toponyms in the area are well known and available. The most important ones are reproduced here on **Map 1**.
- The biggest population is around Picacho del Diablo (also known as Cerro de la Encantada). Some 91 disjoint groves (see **Table 1** for the details) are counted on the distribution range map by Thorne *et al.*, among which 19 have an area of at least 10 hectares.

The IUCN lists the following data:

Estimated area of occupancy (AOO) - km²:	16
Number of locations:	1
Lower elevation limit (metres):	1900
Upper elevation limit (metres):	2520
Range Map:	Click here to open the map viewer and explore range. (no map is available)

To be compared with the data given by Thorne *et al.* or computed here using their information:

Estimated area of occupancy (AOO) - km^2:	30 (area computed thanks to KML Tools Project.)
Number of locations:	91 groves which can be grouped in 9 localities (**Table 1**)
Lower elevation limit (metres):	1150 m, but mostly above 1900 m
Upper elevation limit (metres):	3025 m
Range Map:	Map 17 (see **Map 1** here)

The following assertions are unsupported as well as in contradiction with the “Current population trend” which is described as “unknown”:

> * Major Threat(s): Livestock is a threat to this variety: cattle are allowed to graze indiscriminately throughout the reserve, these cattle are damaging seedlings and preventing them from maturing.
> * Continuing decline of mature individuals: Yes
> * Continuing decline in area, extent and/or quality of habitat: Yes

Further:

> Population: There are few mature trees in the area from where it was originally described. Individuals that are present are hard to find amongst the other trees (mostly conifers). No numbers have been recorded in the literature.

The above description is unrealistic when compared with the lists of localities given by Thorne *et al.*:

“Cañón del Diablo (down to 1150 m), Arroyo de la Grulla, Cerro La Encantada [..] to summit of Picacho del Diablo (3095 m), [..] E of Corral Meadow on E escarpment and S along N-facing gullies on granite exposures to the primary population on Picacho del Diablo above Vallecitos, Los Llanitos, 2400 m [..]; locally on ridge extending out into E escarpment 5 km E of the northern end of La Encantada (2400–2600 m), and Cerro la Botella Azul, 2840 m.”

Only at the lowest altitudes of the range does *Cupressus montana* grow in mixed conifer forest. It is an impossible task to count from the ground so large and numerous a population in such remote and steep terrain. The only way would be through aerial colour photographs allowing discrimination between the different conifer genera.

> Use and Trade: This variety is used as an ornamental tree.

Except in selected botanical gardens and arboreta and in some private botanists’ gardens, this species is not in cultivation as an ornamental tree. K.Shaw and A.Hird list this taxon as present in only 23 *ex-situ* conifer collections, but without giving any information on the number of specimens. I am aware of only one mature specimen in France. It is more frequent in United Kingdom, but still very rare (Frankis, pers. com.).

The main threat for *Cupressus montana* is climatic change. As it is already the highest conifer in the San Pedro Mártir range, migration to higher altitudes will be impossible. The impact could be substantial, but is not immediate. Therefore the *Cupressus* Conservation Project evaluates this species as endangered (E).

Acknowledgements

I am quite thankful to J. Bisbee for his detailed reports, R. Fencl for his advice and support to help calculate the estimated different areas of the distribution range and M. P. Frankis for a very helpful discussion.

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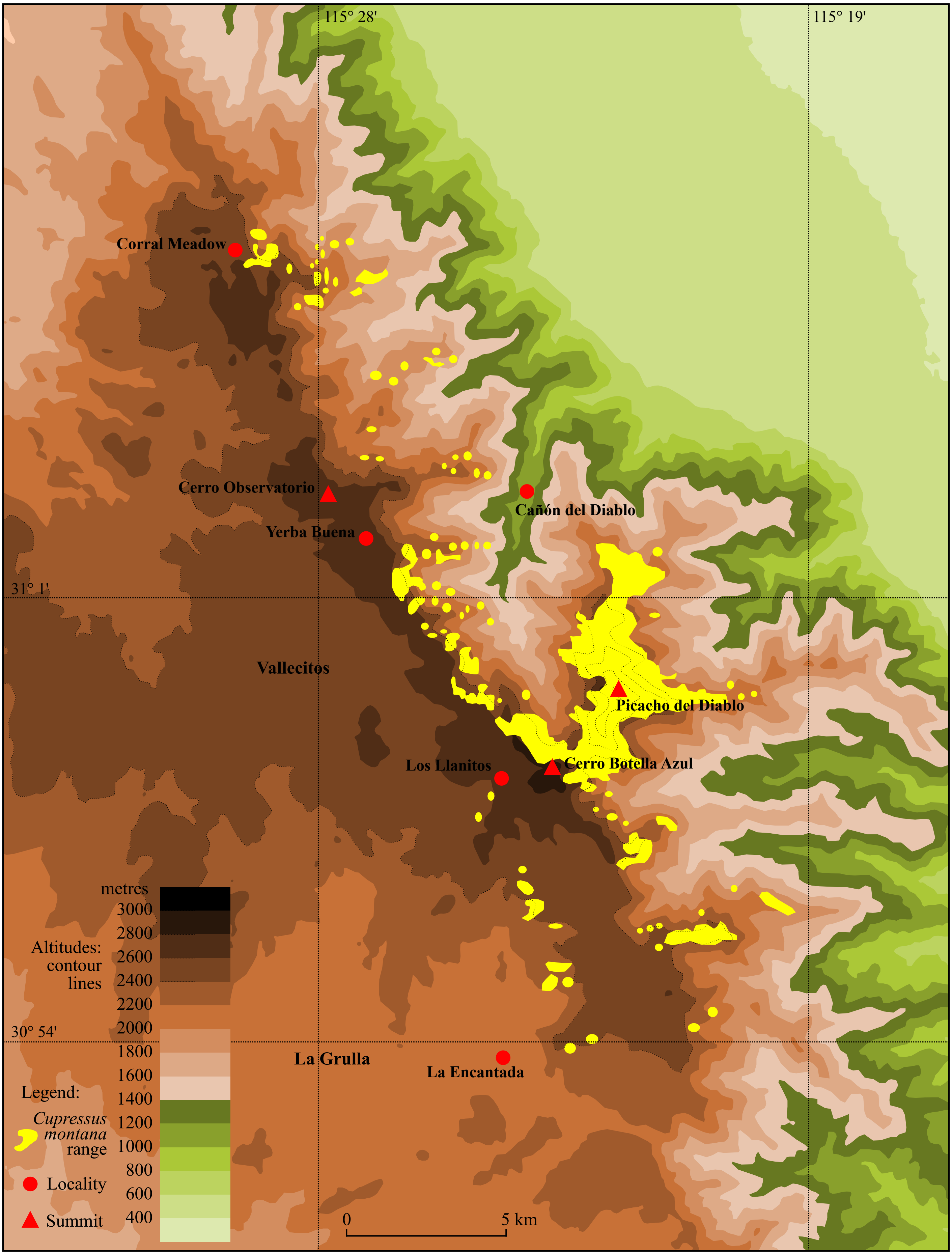
Map 1 (p. 135): Distribution range of *Cupressus montana* after Thorne *et al.*



Map 1: Distribution range of *Cupressus montana*, after Thorne *et al.* 2010.
In mixed conifer forest with *Pinus jeffreyi* and *Abies concolor* subsp. *lowiana*.

Scale: 1:143,000

Table 1:	**area** km²	**number of groves**
Total	**30.26581**	**91**
Main Range	17.12611	1
North Range	2.48380	17
South West Range	1.84593	11
South East Range	3.48570	16
South of North Range	0.52398	6
West Central Range	3.99417	26
Middle Range	0.46471	9
East Range	0.18776	3
North East Range	0.15365	2

Fig. 1 to 3: *Cupressus montana* in its natural habitat in the San Pedro Mártir mountain range (March 2011).

Note on all photos the rocky substrate.

The young tree on fig. 2 shows evidence that regeneration is taking place.

The cones of this species are releasing their seeds at maturity.

1
2 3

Photos by **Jeff Bisbee**.