



Bulletin of the *Cupressus* **Conservation Project**

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This Bulletin is edited by the **Cupressus Conservation Project**, a non-profit organisation based in Geneva, Switzerland. It deals mainly with *Cupressus* species, but accepts manuscripts on other conifer species, as well as on the phylogeny and the evolution of gymnosperms. Emphasis is given to threatened and endangered taxa. Manuscripts are accepted in the following languages : English, French, German, Spanish, Italian and Russian. The Bulletin is peer reviewed.

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Cover photo : *Juniperus drupacea* in its natural habitat between Agios Johannis and the Malevis monastery, Peloponnese, Greece. © CCP

John SILBA

1961-2015

It is with much sadness that we were informed of the death of John Silba in his sleep on the 14 May 2015. John contributed to this Bulletin with several articles on *Cupressus* species. Lastly he sent us a new article currently under review. Two months ago he informed us that he was planning to revise his 1984 *International Census of the Coniferae* for 2016. We address to his mother our deep and sincere condolences.

Silba on Tecate Peak, looking for *Cupressus forbesii* during his trip with Jeff Bisbee to southern California, San Diego County, California, 5 January 2013.



Silba looking at a *Pinus torreyana* cone, Torrey Pines State Park, San Diego County, California, 6 January 2013.



Keith Rushforth: "I always found his comments on *Cupressus* needed careful consideration."

Jeff Bisbee: "John was a very determined person. Somewhat opinionated, but very passionate about his work."

Tom Cox: "John was not without controversy but he did an awful lot in terms of conifers."

Photos by J.Bisbee. More photos are available here: www.cupressus.net/Silba.html

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Juniperus drupacea in the Peloponnese (Greece)

Trip report and range map, with notes on phenology,
phylogeny, palaeontology, history, types and use

During three too short stays¹ in Greece we went to examine the *Juniperus drupacea* Labill. populations on the Peloponnese². During every successive visit we took the opportunity to explore further the distribution of this species which is quite different by his cone size and structure from any other juniper worldwide. In 2002-2003 the distribution map – although completed recently with two outside small localities³ – was far from complete. Mainly it followed the few paved roads into the mountain ranges. The highest altitude tree was thought to be not higher than 1500 m. The two main stands were located around the Malevis monastery, to the north of the Parnon range and its highest summit (Megali Tourla, 1935 m), and around Kosmas to the south. To access the most remote areas of the Parnon range between these two localities a 4x4 vehicle is mandatory.

A hypothesis was made of a possible continuous range between the Malevis and Kosmas populations along the slopes of the Parnon range. The aim of these trips was to explore the limits of the distribution range in all directions and to draw an updated range map. And likewise take the opportunity to learn more about this species which is rather rare in cultivation despite the fact that it is a beautiful tree, albeit slow growing.

Other conifers observed on the Parnon range included *Abies cephalonica* Loudon, usually mixed with *Juniperus drupacea* or in pure stands, *Pinus halepensis* Mill. in pure stands, *Pinus nigra* subsp. *nigra* var. *caramanica* (Loudon) Rehder in pure stands, scattered naturalised *Pinus brutia* Ten., scattered *Juniperus deltoides* R.P.Adams, and *Juniperus communis* subsp. *alpina* Gaudin at the highest altitudes. Coastal species include *Juniperus phoenicea* L. and *Juniperus macrocarpa* Sibth. & Sm.

Altitudinal distribution : below 600 m, only a very few individuals are found, e.g. along a stream when a seed likely floated down the slope of the mountain. Between 600-800 m, *Juniperus drupacea* is rare and scattered in the vegetation. The majority of the trees are growing between 800-1400 m, becoming rarer above 1500 m. They are found in pure forest, mainly open (for instance between Agios Johannis and Malevis), but also in closed forest (under the Malevis monastery), or together with *Abies cephalonica* (above the Malevis monastery). The highest individuals were found as shrubs just below a summit at 1780 m. This is so far the highest altitude recorded for this species in Greece. While driving on the dirt road leading by the north side to the plateau (ca.1650 m) just below the summit of the Megali Tourla (1935 m), we had unfortunately to return when facing a coming storm; the last recorded *Juniperus drupacea* was spotted at 1560 m. Photos posted on Panoramio on Google Earth show that it is also present as scattered shrubs on the plateau and on the first slopes of the Megali Tourla (~1700 m).

Between Malevis and Kosmas : a continuous distribution between these two localities was not found. On the western side of the Parnon, its distribution is interrupted by pure *Pinus nigra* forests. On the eastern side, the junipers become rarer from Sitená to Kastanitsa and disappear altogether around the later village, so that there is a gap in the distribution range just south to the Megali Tourla mountain.

On the western slope, the junipers reappear around Polidroso either as scattered trees or patches of groves becoming more extensive while heading south. When taking the road leading to Sparta, the trees become rarer again, to be almost absent below 800 m. This is also the case on the road to Kallithea.

On the eastern side of the range, at much higher altitudes (1300-1500 m), except for pure forest of *Abies cephalonica*, *Juniperus drupacea* is again present on the high roads to Platanaki. Around Agios Vassilios at a somewhat lower altitude the trees are scattered, except for a population which burned recently. Then on the road from Platanaki to Kosmas the trees are constantly present, some rather

¹ First trip: 26-27 October 2002 with MPF; second trip: 30 April-4 May 2003; third trip: 26 September-1st October 2003. These three successive trips allowed observations of the phenology for a period of almost one year.

² As noted by all articles on *Juniperus drupacea*, the Greek population – the only one in Europe – is separated from the larger stands in Turkey by a distance of about 800 km in a straight line.

³ The first one to the north of the Malevis (some 18 km away), the second one on the slopes of the Taygetes mountains to the west (maps 1 & 2).

limited in height in pure stands on shallow soils (with some dry stumps), some taller and mixed with firs on better soils and exposures.

South of Kosmas : the populations south of Kosmas are less investigated, at least in published articles, except for the trees along the road to Geraki in the south and the ones close to the road to Leonidio. Several dirt roads south of Kosmas allowed access to mixed forests of *Juniperus drupacea* and *Abies cephalonica* (a fir was measured to 23 m high). On the slopes between Filatika and the Korompelia summit (1535 m) is a pure and large open forest of *Juniperus drupacea* (fig. 33 & 34). As others trees were observed above Karitsa to the north, the stand looks continuous from Filatika (890 m) to the Karitsa heights (1000 m). Although the trees are not as high as the ones further north from Malevis to Kosmas, this population is certainly one of the most extensive. Below Karitsa, along a periodic stream, individual trees were seen at 510, 390 and 340 m. To the south-east of Filatika the altitude gets lower and only a few trees were seen, disappearing around Kounoupia. Between Kounoupia and Kremasti, on a dirt road, very scattered trees are found above 800 m. Arriving at Kremasti, individual trees or scattered small groves appear below 800 m (fig. 16). East of Kremasti a forest of *Juniperus drupacea* is again present above 900 m, while the trees are only scattered below that altitude. On the road from Kremasti to Peleta, the trees become very rare. In 2010, collections were made by A.Boratynski and G.Iszkuło along that road at 945 m, 5.6 kilometres before Peleta, as well as closer to Kremasti (see map 3, p. 34 for the collection details). The southernmost *Juniperus drupacea* was located about 2 km southeast of Kremasti.

West of Malevis : the next village to the west of the Malevis monastery is Agios Petros. It is separated from the Parnon by a stream and in the immediate vicinity of that place, the vegetation is quite different, obviously less dry than around Malevis. On the road to Vourvoura to the north-west small *Juniperus drupacea* are found. They are very scattered in open fields covered with grasses. To the south, on the hills above Agios Petros few medium sized trees are found at the crest line. The road leads back to the west side of the Parnon range. Unfortunately at the end of April 2003, because of snow and fallen trees across the path it was not possible to follow that road.

Taygetes range : in a “narrow gorge” “below Anavriti” is the last population discovered in the Peloponnese (Tan *et al.*, 1999). We went to check it. By possibly misunderstanding the details of its location (between 350 and 650 m), we could not find it while driving up and down that narrow road on the very steep slope. Our first *Juniperus drupacea* was seen on the side of the road at 770 m while arriving on the plateau, 1.5 km before Anavriti. The next day, more small junipers (2 to 3 m high) were found above the first one on the hill with the telecommunication station (fig. 17). South of Anavriti more trees were found, very scattered (fig. 18), some much bigger than the first mentioned here on the Taygetes range. The largest population could not be approached because of the difficult terrain (fig. 19). The altitude range of the observed specimens varied between 750 and 1090 m. Although explored, no *Juniperus drupacea* was found north of Anavriti. See also A.Boratyński & G.Iszkuło, fig. 47, p. 34.

Northernmost population : on the road from Kougeika to Achladokampos, at unusual low altitudes for *Juniperus drupacea* in Greece (350-550 m) are few scattered medium sized trees (fig. 31-32).

Last population : on the road from Agios Petros to Tripoli, after Krasti, we spotted some trees in the distance which could be *Juniperus drupacea*. The identity of these trees needs confirmation.

The result of all observations is displayed on the distribution range maps (p. 32 to 34).

Several questions about the phenology and the regeneration of *Juniperus drupacea* remained open. Very little can be found in the literature outside of Turkey.

Phenology : during the second trip, we had the opportunity to be present while pollen was being shed (fig. 23 & 35). We can assume safely that pollination begins in the second half of April and extends through May, depending on the local meteorological conditions (Spring 2003 was particularly cold with a snow storm) and altitude. The seed cones at pollination time are inconspicuous between the scale leaves (fig. 35 & 46). Five months later the cones are still very small and twelve months later the cones are only some 5 mm large and green (fig. 35). The cones resume growth during the second year, quickly attaining their final dimensions. At 24 months after pollination the cones are still firmly attached to their shoot (fig. 10-12). They remain on the

branches for another five to six more months. Cones pollinated in April-May 2003 only fall in September to October 2005 during the third growing season⁴.

Without monthly germination tests it is not possible to know when exactly the seeds become viable. They are likely already fertile while still on the trees. It is also unknown how long the seeds keep their germination capacity.

Gürlevik & Gültekin (2008) detail the conditions for germinating the seeds of *Juniperus drupacea* in nursery conditions. The results are improved by a mechanical pre-treatment (cracking the seed coat) or to a lesser extent by a warm stratification. Germination can be delayed for several months and up to two years.

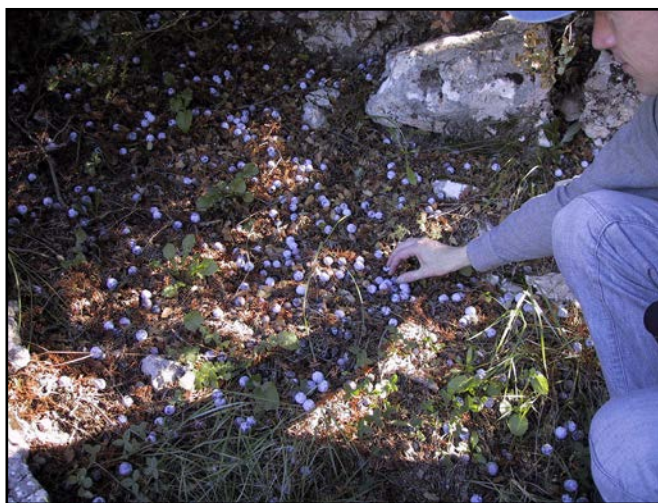
Regeneration : in English literature, the following questions are still without satisfactory answers :

1. How are the seeds dispersed?
2. Which animals eat the drupes, when and how?
3. Is it necessary that the cones be eaten to germinate?
4. What are the requirements for a successful germination in natural conditions?

After submitting those questions to N. Gürlevik, some interesting explanations were obtained (*in litt.*):

“As far as I know, fleshy outer part of the drupes of this species are consumed in nature by mammals such as goats, wild hogs and rodents. Central hard nut which contains the seeds is usually not eaten at all or it goes through the digestion system of the animals without complete digestion. But this is based on field observations of local people and foresters and I am not aware of any scientific information specifically on its consumption by animals. However, fleshy fruit is traditionally used by local people to produce highly nutritious fruit syrup (pekmez⁵).”

Although there are usually specimens of all ages at most places, we only observed regeneration with very young seedlings at a very few places. Three altogether! The first place was below the Malevis monastery under a complete shade. Despite the massive presence of cones on the ground in October (photo, right), only very few seedlings were present. The second place was south of Agios Petros. The seedlings grew just at the limit of the crowns of the parent trees. The last place was south of Kremasti, at the southernmost locality. Here there was a massive regeneration under the crown of a mature tree, with just a couple of other trees in close vicinity.



As noted earlier, the cones can float down along a temporary stream and a few trees were observed at unusually low altitudes on the banks of rivers.

Here and there (north-west of Agios Petros [fig. 6], north of Kremasti [fig. 16], south of Anavriti [fig. 18], etc.), there are very scattered individuals, when a stream is unable to explain such distribution. The cones were necessarily carried away and up a slope by animals, either after they fell from the trees or after they were eaten directly from the branches. The size of the drupes suggests that they are eaten – as mentioned above – by mammals and not by birds. The hard nut is

⁴ These field observations are confirming the data provided by Lemoine-Sébastien (1968: 24).

In mid-April 2015, A.Jagel, during his visit to the Peloponnese, confirmed that male cones were ready to release their pollen (pers. comm.), while at the same time in Montpellier (altitude 50 m) the cones were already completely open and mostly empty (pers. observ.).

⁵ See appendix page 13.

quite likely an adaptation protecting the seeds from the teeth of such mammals as goats and wild boar.

At one place under a tree, we found drupes half eaten. It is evidence that some rodents are feeding on the cones. It has been reported that if the drupe is not removed, the germination can be delayed by one or two more years (Gültekin *et al.*, 2004).

In an arboretum in Montpellier where several mature *Juniperus drupacea* are growing, among which one single female tree, significant regeneration occurred around the mother tree. The soil is shaded by surrounding tall trees and almost bare, except for some very small and low shrubs also regenerating. As nowhere else in the park such seedlings are to be found, the conclusion is that the seeds in that case are not dispersed by animals. This observation matches also the cases seen in Greece.

Phylogeny : Adams (2014) claimed “[t]his species in the monotypic section, *Caryocedrus*, is thought to be the most primitive of the junipers [...]” All cladograms based on molecular analysis place *Juniperus drupacea* at the base of the section *Juniperus* (Mao 2010, Adams 2013). Lemoine-Sébastien – in comparative studies of the pollen and seed cones of several species of *Juniperus* (1967a, 1967b, 1968) – came to the same conclusion, viewing the unique structure of the pollen cone as primitive. The position of the ovules in the seed cone shows a structure different from the other junipers. All these observations justify fully according to Jagel and Dörken (2015) the placement of this taxon in its own section. Antoine and Kotschy (1854: 249-250) placed this species in its own genus *Arceuthos* with the following arguments :

Diese von Labillardier in „Plant. Syr. Docad. II., p. 14, t. 8.“ als *Juniperus drupacea* aufgeführte Species musste, da nun zu den Untersuchungen ein vorzügliches Material benutzt werden konnte, ihrer hervorragend verschiedenen Charaktere wegen, von *Juniperus* getrennt und als eigene Gattung aufgestellt werden.⁶

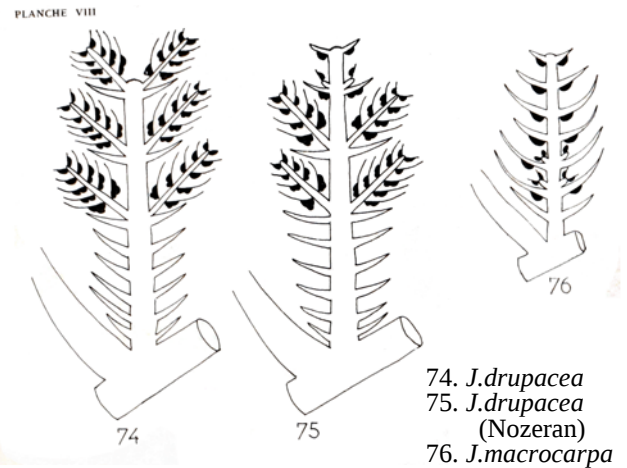
Later Antoine (1857) proposed to split the genus *Juniperus* in three genera: *Arceuthos*, *Juniperus* and *Sabina*. For consistency this treatment should be adopted by the authors who are already splitting the genus *Cupressus*. There are many more differences between *Juniperus drupacea* and the other junipers than between for instance *Cupressus sempervirens* and *Cupressus macrocarpa*, which are very often confused, for instance on herbarium sheets.

Evolving on its own, *Juniperus drupacea* has developed some unique features:

- Unlike all junipers (and true cypresses), *Juniperus drupacea* seed cones mature in three years (or more exactly in 3 growing seasons) instead of two, while all remaining species of the Cupressaceae s.str. mature their seed cones within one year.
- The ovuliferous cones – like all members of section *Juniperus* – have only 1 to 3 seeds per cone in an axillary terminal position (and exceptionally in a non axillary terminal position when there is only one seed per cone); many species of *Juniperus* section *Sabina* and all *Cupressus* have more seeds and all in lower axillary positions (like the other taxa of the Cupressaceae s.str. except *Tetraclinis articulata*). The evolutionary trend in the genus *Juniperus* points to a reduced number of seeds per cone, a trend well observed in section *Sabina*, when species like *Juniperus phoenicea* or *Juniperus flaccida* can have more than 10 seeds per cone and *Juniperus monosperma* or *Juniperus squamata* only one – few examples among several others (Jagel & Dörken 2015). The logical conclusion is that the ovuliferous cones of *Juniperus drupacea* are not primitive.
- The nut inside which the seeds are enclosed is not a primitive character, but a derived one, which is found in no other conifer taxon. The information forwarded by Gürlevik (see above) explains the selection of this unique character: the nut protects the seeds from the teeth of the mammals which are attracted by the drupe. Obviously wild boar or sheep have to wait for the cones to fall on the ground to eat them. Cracking the nut partially and the passing through the digestive system will favour the germination.

⁶ “This species, listed by La Billardiére in “Plant. Syr. Docad. II., p. 14, t. 8.” as *Juniperus drupacea*, has – since now an excellent material could be used for the investigations – to be separated from *Juniperus*, because of its outstanding different characters, and to be established in its own genus.”

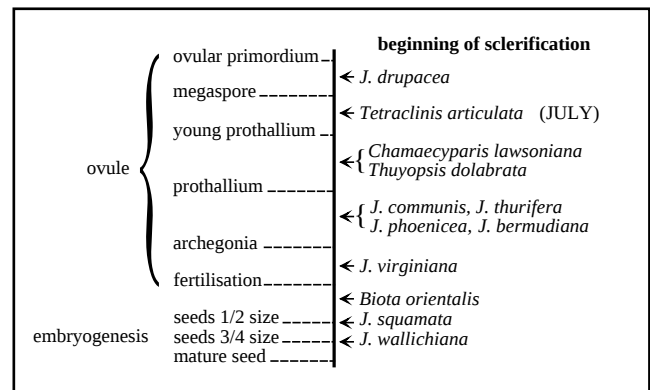
- The pollen cone is different from all species of the other sections. The link between *Juniperus drupacea* and the members of section *Juniperus* is shown by *Juniperus macrocarpa* which presents an intermediary structure of the pollen sacs (Lemoine-Sébastien, 1967a, 34, plate 8 – reproduced here on the right). Lemoine-Sébastien mentions an atavism or a primitive structure. The problem is that this arrangement is unique among *Cupressus* and *Juniperus* species and it is difficult to view it as basal in the Cupressaceae s.str.⁷. Evolution working backwards raises several interesting questions. Nozeran & Grauvogel-Stamm (1971) did not conclude in either way :



The ♂ structure of *Cephalotaxus* enables to understand the evolutionary sequence from branched to non-branched structures in the course of phylogeny; therefore, the «unbranched cone» state could be, according to the particular case, either archaic, or derived from branched structures, and accordingly more evolved.

In lower Trias both structures – simple and compound cones – already existed (Grauvogel-Stamm, 1978), so that it would be necessary to look into the Paleozoic to find evidence of the most primitive structure and which one derived from the other or if they appeared concomitantly and independently. Grauvogel-Stamm (1978: 184) gives the description of the pollen cone of the genus *Walchia* Sternberg – a conifer from the Carboniferous-Permian periods – as a simple one. The fertile scale of *Willsiostrobus* Grauvogel-Stamm & Schaaerschmidt (Trias) is peltate with abaxial pollen sacs. Among the *Juniperus* species, only the taxa of section *Sabina* have peltate scales.

- Sclerification of the ovule of *Juniperus drupacea* begins at a very early stage, contrary to all other junipers. Lemoine-Sébastien (1970: 25) summarises a series of observations on several species of Cupressaceae in the diagram on the right (translated from French).



Palaeontology : the distribution range is limited nowadays to the East Mediterranean area (Greece, Turkey, Syria and Lebanon).

More investigations are necessary to understand its biogeography. As its still rather wide but discontinuous distribution shows, it has the characteristics of a relict species. According to Rerolles (1885) *Juniperus drupacea* was present during the early Pliocene (around 5 mya) in Cerdagne (southern side of east Pyrenees). According to Palamarev (1967) its fossils were found in south-west Bulgaria from lower Oligocene (~ 33 mya) and according to Stefanov & Jordanov (1935) in upper Pontien-lower Dacien deposits (~ 5.5 mya) close to Sofia. Quaternary glaciations were the cause of the extinction in Europe of many conifer taxa, while a few others found a refuge in the Middle East⁸. Such is likely the case of *Juniperus drupacea*.

⁷ The Taxodiaceae pollen cones show the same simple structure as the Cupressaceae s.str., although their distribution is different: the cones are in fascicles in *Cunninghamia* and *Taiwania*, alternate in *Metasequoia* and *Taxodium*.

⁸ The list of conifer genera which disappeared from Europe during the last million years is impressive (Palamarev & al. 2005) : *Cedrus*, *Pseudotsuga*, *Tsuga*, *Cephalotaxus*, *Torreya*, *Amentotaxus*, *Sciadopitys*, *Athrotaxis*, *Taiwania*, *Sequoia*, *Sequoiadendron*, *Cryptomeria*, *Cunninghamia*, *Glyptostrobus*, *Taxodium*, *Platycladus*, *Thuja*, *Chamaecyparis*, *Cupressus*. Only the genera *Cedrus* and *Cupressus* – likewise *Juniperus drupacea* – found refuge in the Middle East (or northern Africa). But neither genus could come back, unless cultivated by humans.

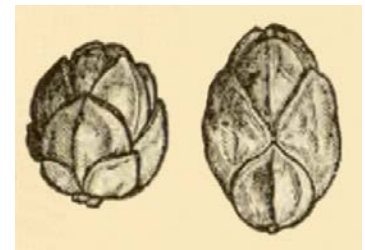
If the distribution range certainly shrank because of the climatic conditions, the co-evolution with any animal is difficult to assess: mammals expanded only since 65 million years, but herbivorous dinosaurs could have been at the origin of this species unless it is determined one way or the other that it could not be that old. All above mentioned innovations would support a more recent evolution than usually thought.

History : the first historical mention of *Juniperus drupacea* was done by Pierre Bellon in 1553, after a trip through the Ottoman empire, from Egypt to Istanbul. While on Mount Taurus (1547) he could observe this species which he called “genévrier majeur” [major juniper] :

Partants d’Adena, allions entre occident & septentrion. La campagne nous dura iusques à midy : puis commençames à monter le mont Taurus. Nous campasmes & dormimes en l’endroit ou la nuit nous surprint, & pource que le temps estoit serain, & qu’il faisoit froid, coupasmes plusieurs petits Platanes, Andrachnes, Nerions, Arbousiers, & feismes bon feu d’un Carroubier sec. Le lendemain long temps auant iour nous commençames à monter la montaigne fort difficile. A la summité de laquelle ie trouuay des Geneuriers maieurs, qui croissent hault comme Cypres, dont la semence est douce, & grosse comme vne noix resembants quasi à vne galle. Les habitants du pays les mangent, chose que i ay apperceu par les noyaux que i’alloye amassant ça & la le long du chemin, qui auoient esté iectez de ceux qui en auoyent mangez le dessus. Les noyaux sont si durs qu’on ne les peult rompre sinon à grands coups de marteau[, longs & gros comme vne petite oliue (1555)]. C’est l’arbre le plus singulier apres le Cedre, qui soit sur le mont Taurus, aussi est il tousiours verd. [L’on verra son naif portraict & description au liure qu’auons intitulé de Arboribus perpetua fronde virentibus, c’est-à-dire des arbres de perpetuelle verdure. (1555)]⁹

In the mentioned book published the same year (1553) written in Latin, Bellon does not give the promised description.

Clusius (1601: 37), after Bellon, under the caption *Habhel fructus*, published the first accurate drawing of two *Juniperus drupacea* seed cones. It is reproduced here on the right and Clusius explained : “cujus fructus *Abhel* toto Oriente notissimus, pilularum Cupressi magnitudine, colore rufo in nigrum declivi.”¹⁰ In a second book, Clusius (1605) is summarising in Latin what Bellon wrote in 1553, noting that he could not find the description promised by Bellon¹¹.



Types : In 1791, La Billardièrre wrote a detailed botanical description of *Juniperus drupacea*¹². He did not cite Mount Taurus like Bellon, but Mount Casius also in Turkey¹³, where he collected samples. Farjon (2005), reproduced by Adams (2014), is mentioning : “Type: Turkey, Hatay, Jebel Akra, *J. J. H. de la Labillardiere*^[14] s. n. (holotype G-DEL?, n.v.; isotypes FI, K).” La Billardièrre’s description is accompanied by a plate: this illustration constitutes one of the syntypes (see Plate n° 3, bottom right). As there are three known herbarium sheets from La Billardièrre collection

⁹ “Leaving Adena, went between west and north. The countryside lasted us until midday : then began to climb mount Taurus. We camped and slept at the place where the night surprised us and because the weather was fine and because it was cold, cut several small plane trees, Greek strawberry trees, oleanders, strawberry trees, and made good fire with a dry carob tree. The next day, long time before day we began to climb the very difficult mountain. At the summit of which I found major junipers, which grow as tall as cypress, from which the seed is sweet and as big as a nut looking almost like a gall. The inhabitants of the country eat them, thing that I saw with the nuts that I went collecting here and there along the path, which had been thrown by those who had eaten the top. The nuts are so hard that it is not possible to break them unless with big hammer blows[, long and big like a small olive (ed. 1555 addition)]. It is the most singular tree after the Cedar which is on mount Taurus, is it too always green. [We will see its naïve portrait and description in the book we named de Arboribus perpetua fronde virentibus, that is of trees perpetually green.” (ed. 1555 addition)]

¹⁰ “Whose fruit *Abhel* is very well known throughout all East, of the size of a cypress cone, declining from a red colour to black.”

¹¹ This text is reproduced by La Billardièrre in his protologue (cf. Plate n° 1).

¹² See Plate n° 1.

¹³ Close to the Syrian border. Keldağ in Turkish, Djebel el Aqraa (with various spellings) in Arabic. In 1791, the whole region was part of the Ottoman Empire. The description as Syria comes from French understanding of the geography of the region, which dates from the Roman Empire.

¹⁴ The author name’s spelling on *Icones Plantarum rariorum* is “JACOBO-JULIANO LA BILLARDIERE”.

and as far as it was not done before, it is necessary to lectotypify one of the sheets. The Kew specimen bears the autograph mention by La Billardièrre of *Juniperus drupacea* and the reference to the protologue (“*ic. pl. Syr.*”) [see Plate n° 4a]. The Geneva specimen was examined on 10 December 2014. It has the manuscript mention: “*Juniperus / Syrie / Labillardière*” [see Plate n° 4b]. This herbarium sheet is not part of the Delessert herbarium (Farjon: “G-DEL?”). There was no mention that it belongs to a type. The isotype mention was added after identifying La Billardièrre handwriting. The Florence specimen is accompanied by the complete manuscript protologue by La Billardièrre (cf. Plate n° 3) like it was later printed in *Icones Plantarum Syriae rariorum, Decas Secunda* (cf. Plate n° 1). Chiara Nepi, curator of the Florence herbarium, explains (pers. comm.):

“Labillardière's collection was bought by P.B. Webb – the owner of the homonymous herbarium kept here – in 1834. The collection contains almost all the holotypes of the species described by Labillardière from Australia and New Calidonia, as well as those he described from the Lebanon, etc. The type material is often provided with the autographical description of the plant.”

The Florence Herbarium hosts hundreds of La Billardièrre types. The presence of the manuscript description induces the following designation :

Lectotypus (hic designatus) : Keldağ [“monte Cassio” (“djebel Lacara”)], Hatay Province, Turkey, *J.J. La Billardièrre s.n.*, FI 207064 (cf. Plate n° 2 & 3c).

Isotypes : • K000089312 (cf. Plate n° 4a).

• G00430252 (cf. Plate n° 4b).

Syntype : • *Ic. Pl. Syr.* Plate 8 (= FI 207065 – cf. Plate n° 3d).

Acknowledgments

To sort out the lectotype of *Juniperus drupacea* among the different herbarium materials, the collaboration of Chiara Nepi, Head Curator of the Botanical Section (FI), Natural History Museum, University of Florence, was essential, and we want to thank her wholeheartedly, not forgetting Egildo Luccioli who took the photographs of the type specimen and Marco Bazzani who forwarded our request. Adam Boratynski provided more information after a new trip to the Peloponnese in 2010, and herbarium specimens, which helpfully allowed to complete the range map. Michelle Price, curator of the conifer herbarium (G), as usual brought useful advice and support to our research. N. Gürlevik supplied the necessary information to understand dispersal, germination and regeneration of this species in natural conditions. It would be worth translating several articles currently available only in Turkish.

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Appendix : production of pekmez in Turkey.



The cones are collected on dry mountain slopes between 800 and 1000 m. Once the cones have been brought home, it is necessary to wait two days for the drupes to dry.



The drupes are separated from the seeds. While sugar will be added, 100 kilos of drupes will give 10 kilos of molasses.



Water is eliminated from the cones after 4 days. In 12 hours the boiling process will be over.

The *Juniperus drupacea* molasses is known to be good for anemia and for adjusting the amount of sugar in the blood; other reported healing benefits are for bronchitis, cough, mouth sores, tuberculosis, nephritis, psoriasis, nausea, lung and liver.



Juniper molasses is heavily produced and consumed in Kahramanmaraş, Osmaniye, Hatay, Mersin and Antalya regions.

Source:
<http://fotogaleri.bugun.com.tr/koza-laktan-gelen-sifa-andiz-pekmezi-fotogaleri-1305609/4>



JUNIPERUS DRUPACEA.

Dioecia monadelphia.

Char. essent. MASC. amenti. calyx squamæ ; *Cor.* nulla. *Stam.* 3....

FOEM. Cal. 3-partitus , *petala* 3. *Styli* 3. *Bacca* 3-sperma , tribus tuberculis calycis inæqualis.

♀. Foliis ternis , patentibus , acutis , drupâ triplo brevioribus , nuce 3-loculari.

Caulis frutescens , erectus , ramosior , ramis patentibus , ramuli triquetri.

Folia terna , patentia , sessilia , lanceolata , acuta , suprâ lineâ duplici subglauca.

Flores masculos fœmineosque non vidi.

15

Drupa testacea , rore glauco adpersa , foliis sæpè triplo longior , magna , subrotunda , tuberculis 6 sæpius 9 retusis angulata , exsculptaque.

Nux subovata , magna , trilocularis , loculis parvis , durissima , supernè lineis tribus excavata ; *nuclei* solitarii , ovato-oblongi , pelliculâ loculorum fundo affixi.

Habitat in monte Cassio quem Arabi vocant djebel lacara.

Observatio.

Hæc est fortè *Juniperus major* *Petr. Bellon. observat. lib. 2 , p. 162 in carol. clus. exotic. libris decem , in-fol.* de quâ sic loquitur.

„ In monte Tauro Juniperos majores in cupressi altitudinem as-
„ surgentes invenimus , fructu dulci , nucis ferè magnitudine et
„ gallæ quodam modo similes , quo indigenæ vescuntur , ut ex
„ nucleis hinc indè à nobis in itinere collectis , et ab his qui
„ pulpam exederant , abjectis , observabamus. Ii sunt longitudine
„ et crassitudine nuclei olivæ , adeo duri , ut solo mallei ictu frangi
„ quirent. Inter reliquas arbores in Tauro monte nascentes , post
„ cedrum , primas obtinet , perpetuòque viret. Ejus vera delineatio
„ et descriptio invenietur in libro cui titulum fecimus *de arboribus*
„ *perpetuâ fronde virentibus.* „

Hoc libro consulto , mihi observandum est ut et observat ipse clusius , quæ hactenùs vidi Bellonii exemplaria de coniferis , neque delineationem , neque descriptionem *Juniperi majoris* habent.

Explicatio tabulæ.

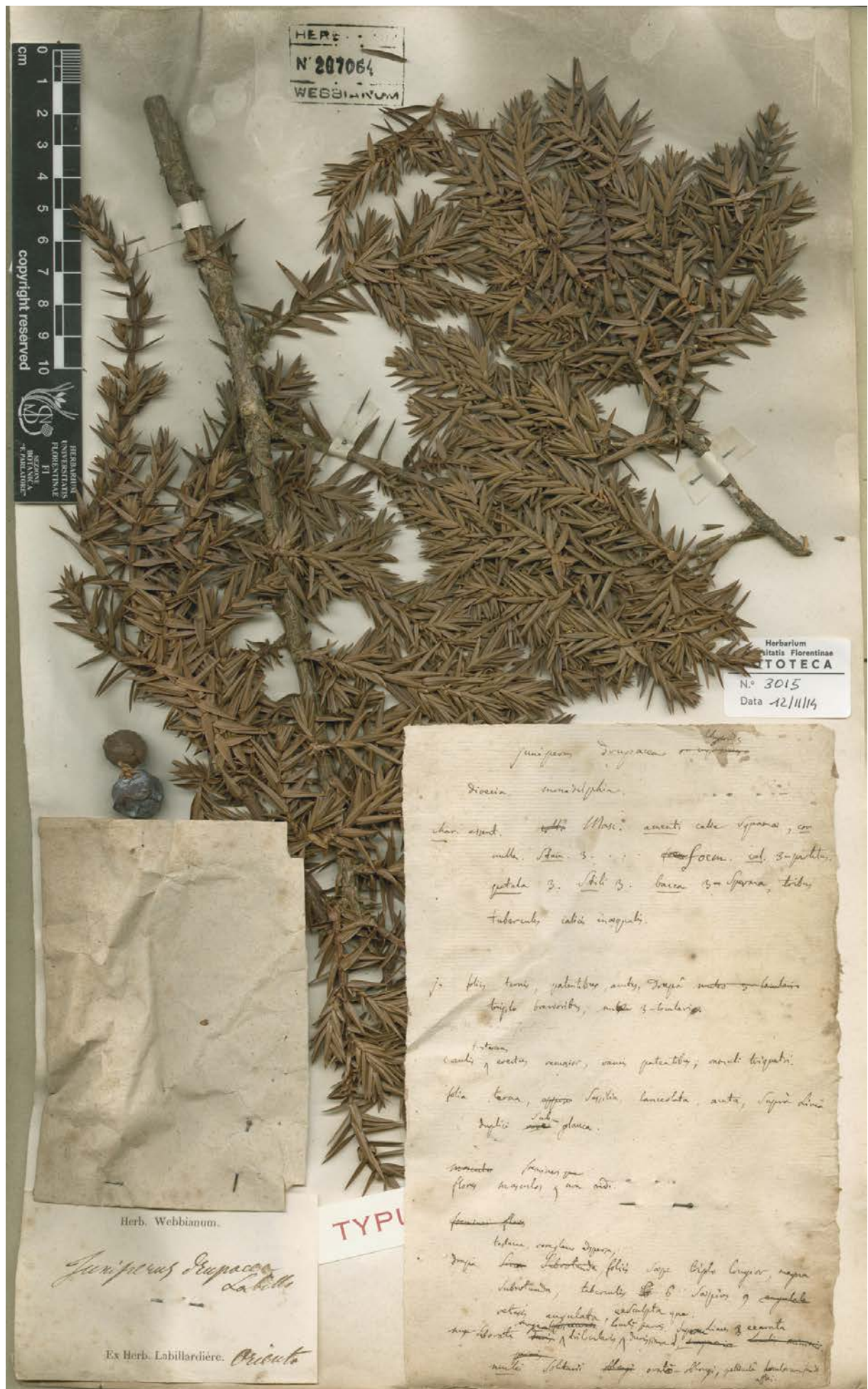
1. Ramus fructibus onustus. 2. Fructus. 3. Nux. 4. Nux transversè sectus. 5. Nucleus. *Omnia naturali proportionè.*

Plate n° 1 : Protologue of *Juniperus drupacea*. J.J. La Billardière, *Icones Plantarum Syriae rariorum, Secunda Decas*, 1791, p. 14-15, Plate 8.

Plate n° 2, p. 15 : Lectotype of *Juniperus drupacea*. (FI 207064)

Herb. Webbianum,
Ex Herb. Labillardière.

© FI Herbarium,
Botanical Section,
Natural History
Museum, University of
Florence, Italy.



HERB. N° 207064 WECHERLIN

Herb. Weidmann.

Juniperus communis L.

Ex Herb. Lohmeyer, Altona

TYPUS

HERBARIUM
N° 207063
WEDDELINUM

Juniperus drupacea.

Herbarium
Universitatis Copenhagen
BOTANICA
N° 3015/4
Dato 12/11/14

Plate n° 3, p. 16 : Lectotype of *Juniperus drupacea*.

© FI Herbarium.

3a & 3b, top of plate : manuscript protologue by La Billardière, showing the two sides of the sheet. Cf. printed text on Plate n° 1.

3c, bottom left : lectotype with the manuscript and a sheet of paper removed.

3d, bottom right : illustration by P.J. Redouté (FI 207065) attached to the lectotype.

Identical to Plate 8 of *Icones Plantarum Syriae rariorum, Decas Secunda*.

As such, one of the syntypes.

Photos of plates 2 & 3 by Egildo Luccioli, FI Herbarium, Natural History Museum, University of Florence, Italy.

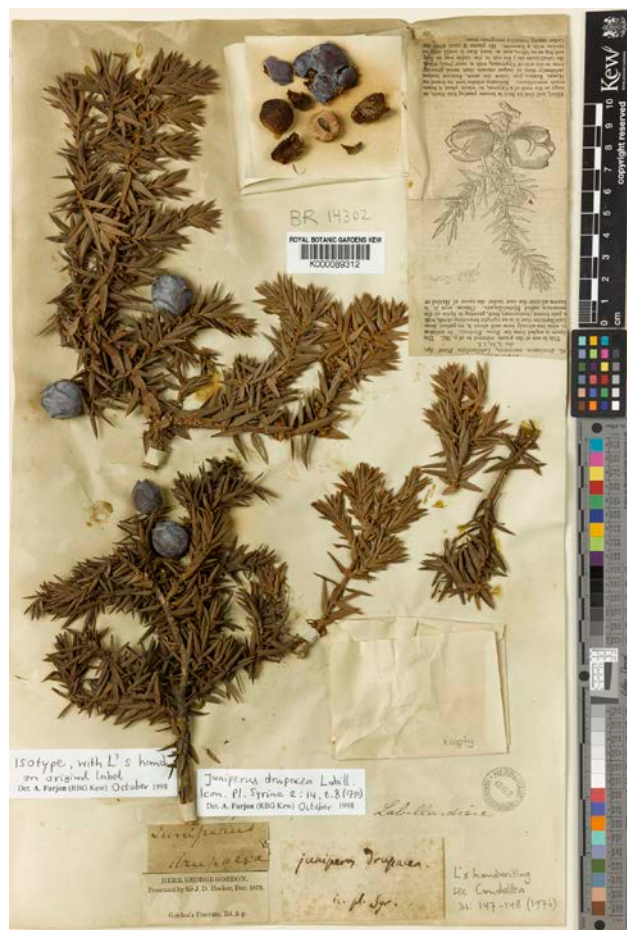


Plate 4a : *Juniperus drupacea*
© Kew herbarium, Royal Botanic Gardens, UK. (K000088095)

Plate 4b : *Juniperus drupacea*
© CJB Geneva Herbarium, Switzerland. (G00430252)

Although there is no doubt that this specimen is from La Billardière's collection, it is not sure if the attached label is from his own handwriting.

Analysis by Chiara Nepi, curator of the Head Curator of the Botanical Section (FI), Natural History Museum, University of Florence:

"I'm not entirely sure [the] label is in Labillardière's handwriting. It's true that it was written with more care than notes on the specimens (please, see also our website and look for the so many specimens by Labillardière). For example, the capital letters "L" and "S" are very similar as well as "p", but "s" and moreover "r" are different. Then I think that Labillardière signed as La Billardière, in fact see H. M. Burdet, 1979, *Auxilium ad botanicorum graphicem*. So, I have some doubt on [the] label, even though its differences from the verified Labillardière's handwritings may depend on the age, the place, the will of a good handwriting, etc. [so that there is] some incertitude..."





Fig. 1 & 2: Between Agios Johannis and the Malevis monastery, one of the best known stands.

Next page, right column: **Fig. 4:** Bark structure of a mature specimen. **Fig. 5:** Along the road.

Fig. 6: Very scattered *Juniperus drupacea* to the north-west of Agios Petros

Fig. 7: Small grove above Agios Petros where regeneration was taking place very close to the mature trees.

Fig. 8: Forest above the Malevis monastery with *Abies cephalonica*.



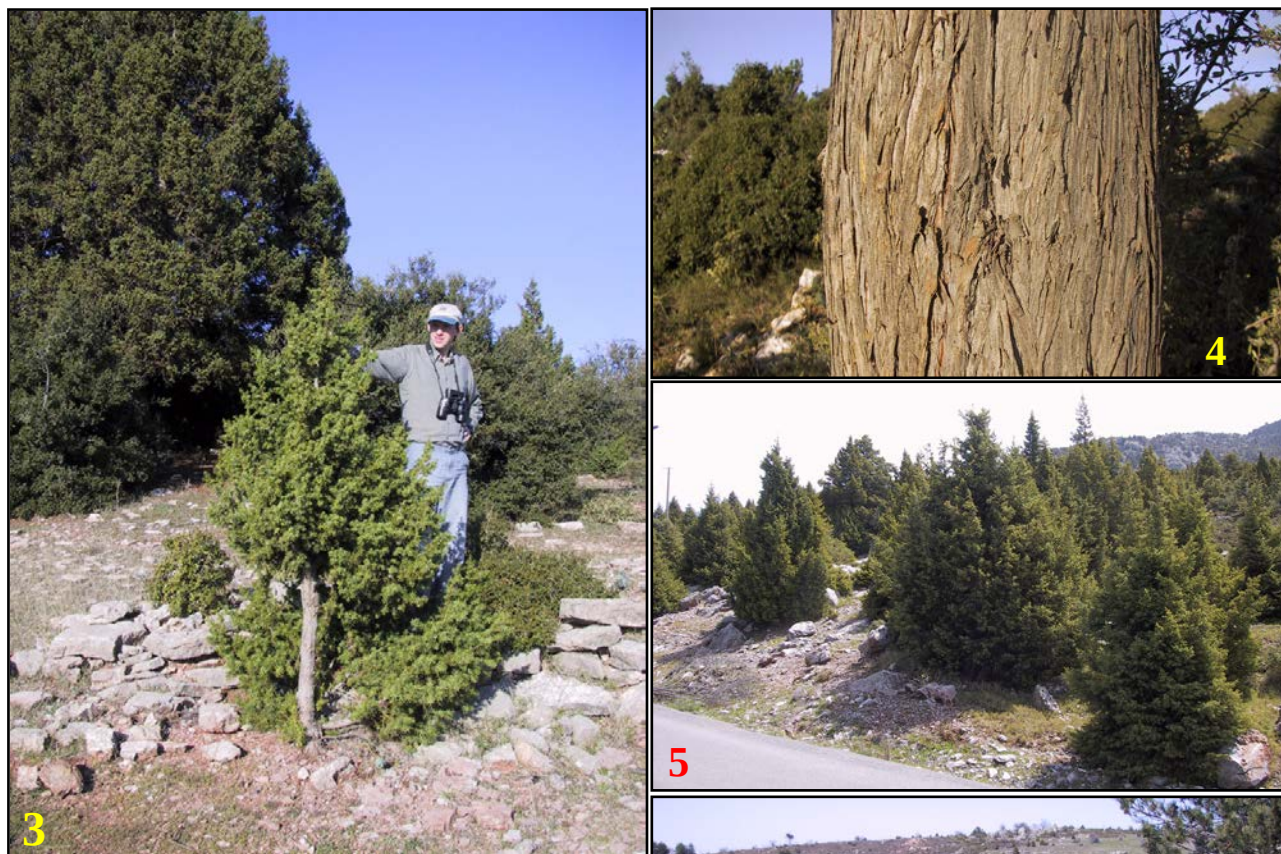


Fig 3: Sapling testifies for regeneration.

Fig. 9: One of the biggest trees below the Malevis monastery, measured to 16m high with a girth of 180 cm at 1 m from the ground.





10

Fig. 10: Seed cones: the one year old cones are still green, while the cones ready to be pollinated are inconspicuous between the leaves at the tip of the branchlets. Fig. 10, 11 & 12: 1 May 2003.

Fig.11: Pollen cones ready to shed their pollen in the following days.



11



12

Fig. 12: Two years old seed cones.

Fig. 13: Young tree browsed by goats.

Fig. 14: Beautiful specimen with a full crown. *A.cephalonica* in the background.



13



14



15

Fig. 15: Pollen cones in October.

Fig. 16: Small isolated grove below Kremasti.

Fig. 17 to 19: Anavriti populations (see text).



16



17





Fig. 20 & 21: Slopes above Karitsa with *Abies cephalonica* in the background.





Fig. 22: On limestone suffering from drought, N. of Kosmas. **Fig. 23:** Pollen release on 4 May 2003.





Fig. 24, 25 & 26: The highest specimens of *J. drupacea* were found on a summit of the Parnon range at 1780m altitude together with *Pinus nigra*, *J. oxycedrus* and *J. communis* subsp. *alpina*.





Fig. 27 & 28 : Different tree sizes in the open forest between Agios Johannis and Malevis.





Fig. 29 : Field on a Parnon slope above Malevis. **Fig. 30** : cones still on the tree.





Fig. 31 & 32: The northernmost locality of *J. drupacea* in Greece with very scattered trees.





Fig. 33 & 34: Korompelia summit (1535m) above Filatika.
Fig. 34: View from the summit.

Fig. 33: Summit in centre.
 Photos 33 & 34 © George Giannopoulos.





Fig. 34: Greece : Peloponnese, Arcadia Pref. Slopes of Parnon Mountain, near Malevis Monastery ; 37° 20'N - 22° 25' E, 918m alt. Three cones showing variation in the density of the white wax coating, also one (lower left) with the wax removed to show the ground colour. (M.P. Frankis)

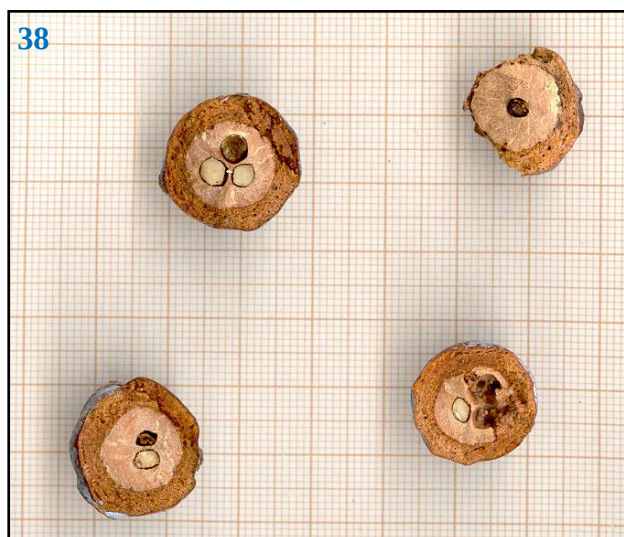


Fig. 35 : Shoot with seed cones from three generations at pollination time. New cones are inconspicuous at the top, while one year old cones are light green and still small and two years old cones with almost mature size.



Fig. 36: Male cones ready to shed their pollen or already releasing it (top right) – end of April, begin of May.

Fig. 37: (left) some cones have nine scales, rather than the usual six ; (right) unusually large cone, 28mm. (M.P. Frankis)

Fig. 38: Mature seed cones cut in half to display the seed cavities; they usually are three, but odd cones can come with only two or even one seed cavity; not all seed cavities are full with a viable seed ; it is possible to see aborted seeds in some of the seed cavities. Note the woody hard kernel surrounded by the fleshy part of the cone.

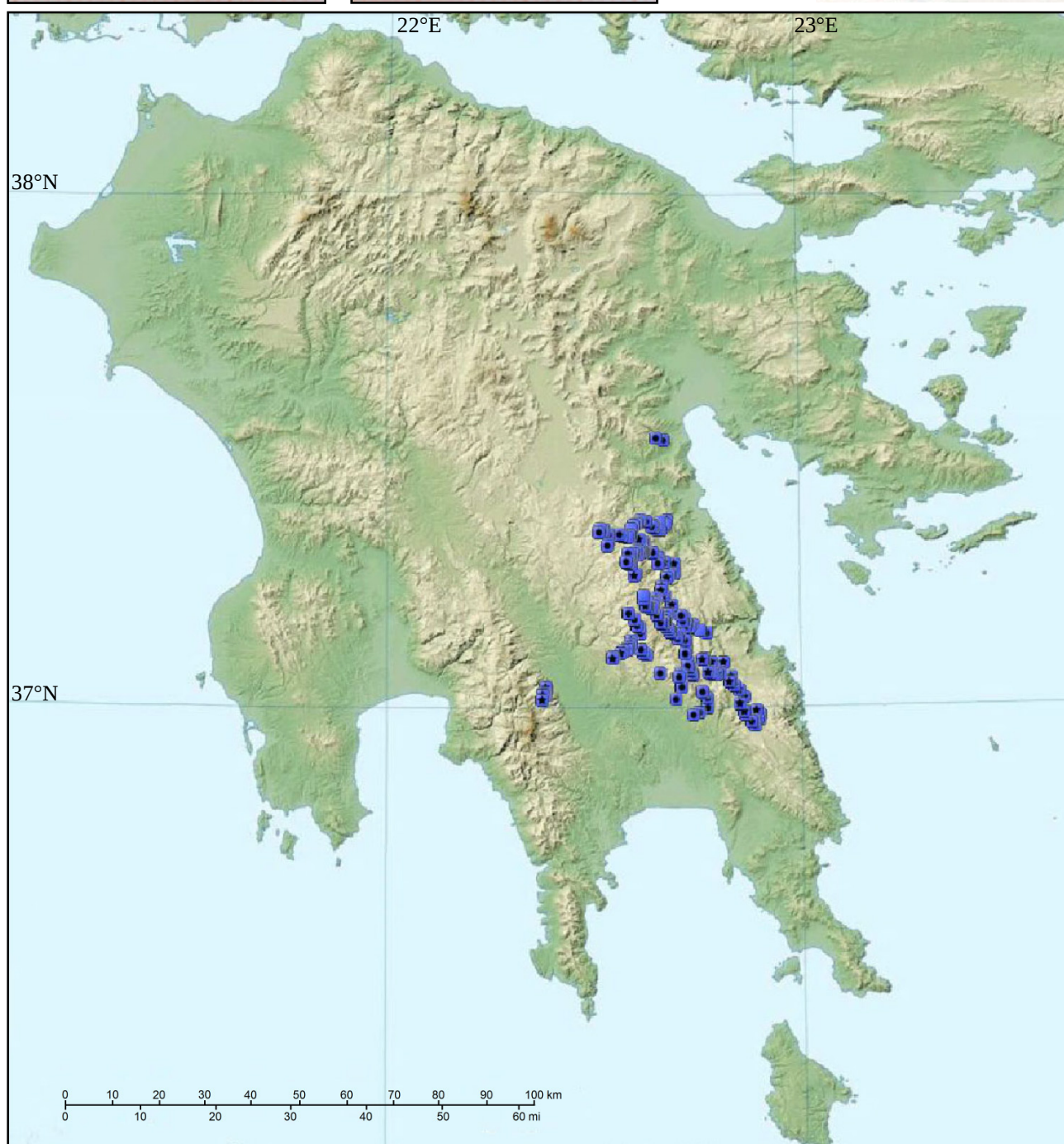
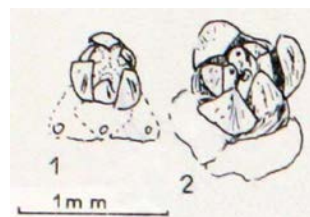
On fig. 35, 36 and 38, the size of the samples is given by the millimetre paper.



Fig. 44 : Seed cone two years after pollination. May 2003.

Fig. 45 : Seed cone two years and a half after pollination. October 2003.

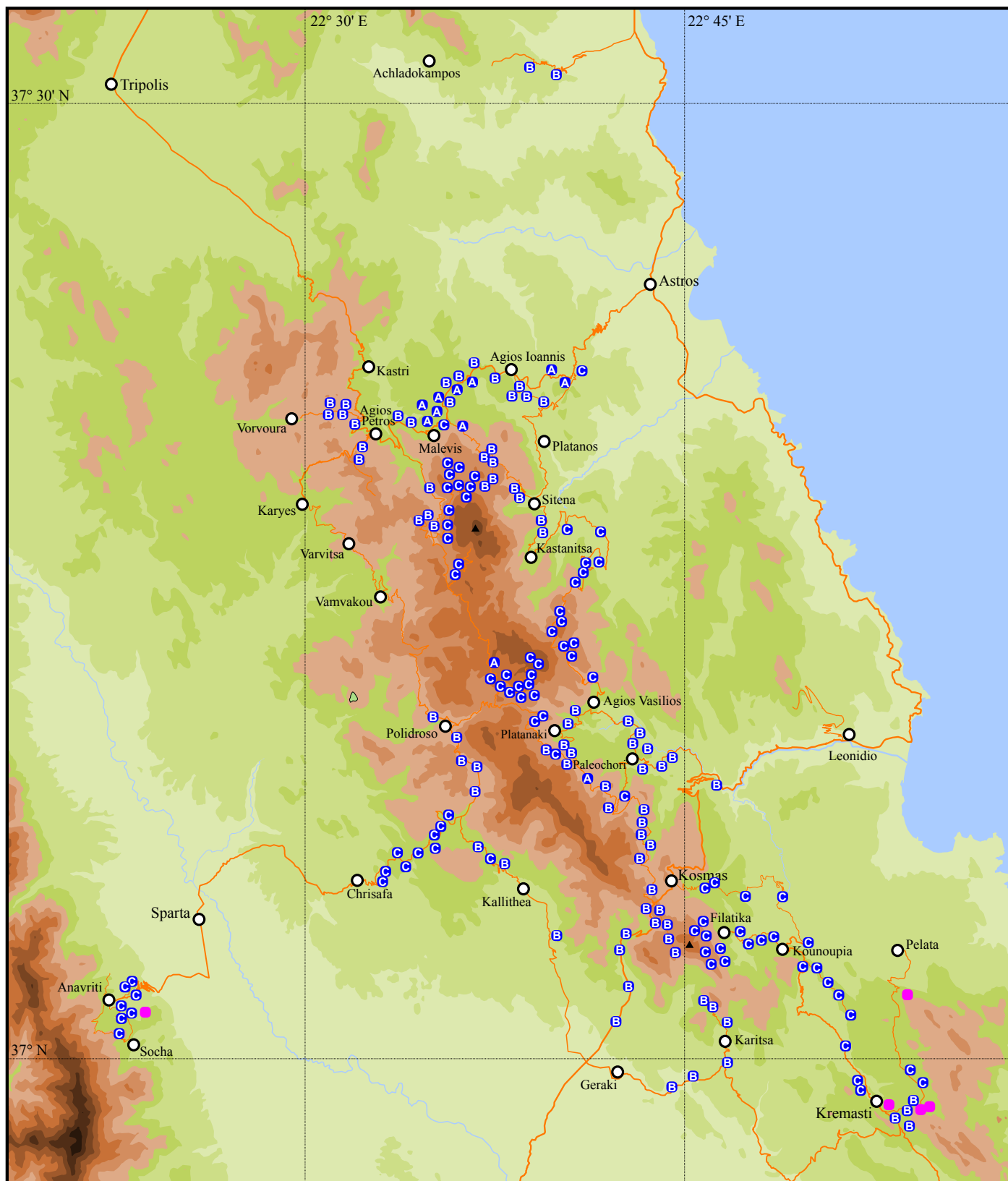
Fig. 46 :
Ovule
initiation.
Lemoine,
1968: 380,
Pl. CCV.



Map 1 : Distribution range of *Juniperus drupacea* in Peloponnese, Greece, based on personal observations in 2002 and 2003 (MPF, DM).

Background map : NASA SRTM3 v.2 – public domain.

Scale : 1:1'412'000. Legend : ■, ●, ★ Presence of *Juniperus drupacea*. (See map 2 for details.)



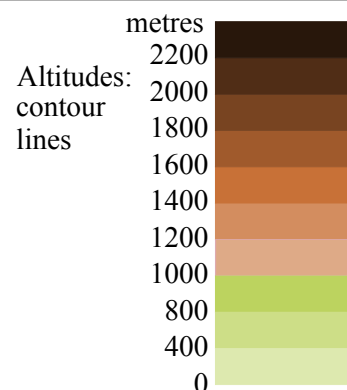
Map 2 : Distribution range of *Juniperus drupacea* in the Peloponnese.

Scale : 1:340'000

Legend :

- town
- Ⓐ First trip
- Ⓑ Second trip
- Ⓒ Third trip
- A.Boratynski & G.Iszkuło

- ▲ summit
- road
- river
- sea



Observation and collection notes by A.Boratyński & G.Iszkuło, June 2010.

Juniperus drupacea in Madara Mt. (on herbarium erroneously included into Parnon). SE of Kremasti along the road to Peleta:

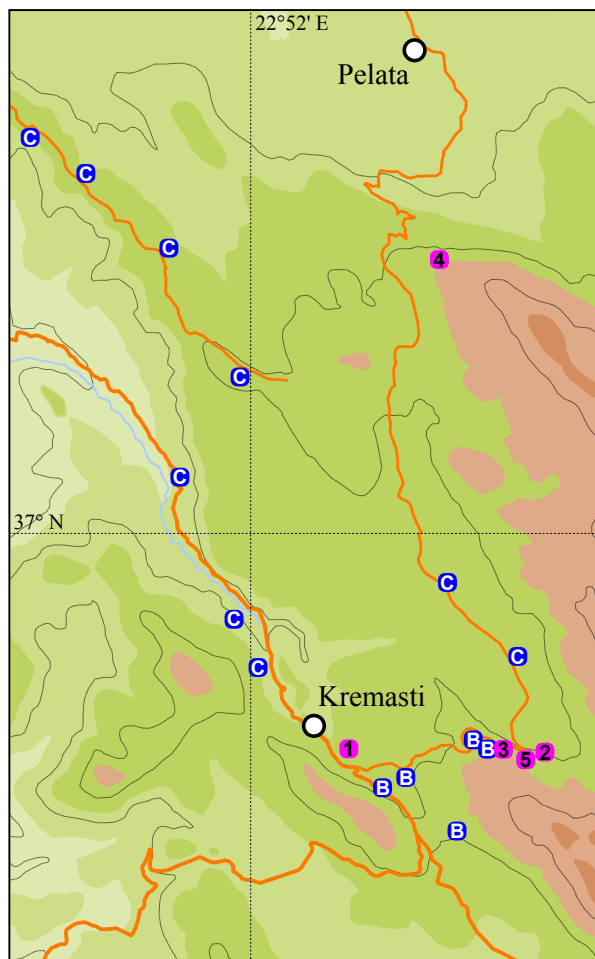
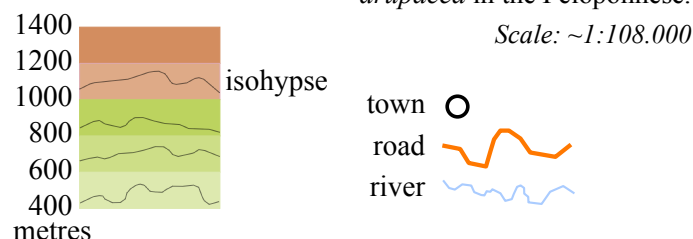
❶ Slopes above the road, single trees among the maquis and pastures: N36°58'22", E22°52'54", alt. 860 m, in observ. A.Boratyński, G. Iszkuło, 23 June 2010.

❷ On the calcareous rocks above the road (SE slope), on the edge of an *Abies cephalonica* forest, group of trees: N36°58'29", E22°54'27", alt. about 920m, in observ. A.Boratyński, G.Iszkuło, 23 June 2010.

❸ N slopes covered with sparse *Abies cephalonica* forest (limestones), single, dispersed individuals of *Juniperus drupacea*: N36°58'30", E22°54'15", alt. about 950m, in observ. A.Boratyński, G.Iszkuło, 23 June 2010.

❹ N slopes of the mount, dispersed individuals on the edge of *Abies cephalonica* forest: N37°01'53", E22°53'40", alt. about 1000m, in observ. A.Boratyński, G.Iszkuło, 23 June 2010.

Map 3 : The southernmost populations of *Juniperus drupacea* in the Peloponnese.



Herbarium sheets: © Herbarium Dendrologiae Institut, Academia Scientiarum Polona.

S of Kremasti, N36°58'23", E22°52'52", 858 m alt., lg. Boratyński, Iszkuło, 10.22.01. (Not reproduced here).

Fig. 47: Anavriti, N37°01'18", E22°23'43", 890 m alt., 24.6.2010, lg. Boratyński, Iszkuło, 10.28.01.



Fig. 48: ❹ E of Kremasti, N36°58'27", E22°54'24", 916 m alt. 23.6.2010, lg. Boratyński, Iszkuło, 10.23.01.



Comparison of three *Cupressus* species seedlings

Cupressus sempervirens, *Cupressus dupreziana* and *Cupressus torulosa*

All seedlings are eight to ten months old. Although the height of the different individuals of the three species is not uniform, same size seedlings (11.5-12 cm) were chosen for a better comparison of the leaf morphologies and the plant shapes. The photos speak by themselves.

All species display at this stage a glaucous juvenile foliage.

Cupressus sempervirens has the shortest leaves quite different from *Cupressus dupreziana*.

Cupressus torulosa shows already intermediate flattened foliage on the upper lateral shoots.



All *Cupressus torulosa* seedlings show the same pattern of growth with a leaning top and drooping long lateral shoots, while these same shoots in *Cupressus sempervirens* are straight and quickly present a reduced length toward the top. The longest cotyledons belong to *Cupressus dupreziana* and the shortest to *Cupressus torulosa*. The fact is that the seedlings of some *Cupressus* species are quite regular in their characteristics and can be identified at this early stage.

Fig. 1: *Cupressus sempervirens*.

Fig. 2: *Cupressus dupreziana*.

Fig. 3: *Cupressus torulosa*.

All photos at the same scale. Tube Ø 4 cm. The medium is not at the same level in all tubes.

Origin of the seeds: *Cupressus sempervirens*, Turkey, wild origin; *Cupressus dupreziana*, CJB Geneva, cultivated; *Cupressus torulosa*, northern Italy, cultivated.



Morphology and anatomy of pollen cones and pollen in *Podocarpus gnidioides* Carrière (Podocarpaceae, Coniferales)

Abstract

Podocarpus gnidioides is one of the rarest *Podocarpus* species in the world, and can rarely be found in collections; fertile material especially is not readily available. Until now no studies about its reproductive structures do exist. By chance a 10-years-old individual cultivated as a potted plant in the living collection of the second author produced 2014 pollen cones for the first time. Pollen cones of *Podocarpus gnidioides* have been investigated with microtome technique and SEM. Despite the isolated systematic position of *Podocarpus gnidioides* among the other New Caledonian Podocarps, it shows no unique features in morphology and anatomy of its hyposporangiate pollen cones and pollen. Both the pollen cones and the pollen are quite small and belong to the smallest ones among recent *Podocarpus*-species. The majority of pollen cones are unbranched but also a few branched ones are found, with one or two lateral units each of them developed from different buds, so that the base of each lateral cone-axis is also surrounded by bud scales. This is a great difference to other coniferous taxa with branched pollen cones e.g. *Cephalotaxus* (Taxaceae), where the whole “inflorescence” is developed from a single bud. It could be shown, that the pollen presentation in the erect pollen cones of *Podocarpus gnidioides* is secondary. However, further investigations with more specimens collected in the wild will be necessary.

Key words: Podocarpaceae, *Podocarpus*, morphology, pollen, cone

1 Introduction

Podocarpus gnidioides is an evergreen New Caledonian shrub, reaching up to 2 m in height (DE LAUBENFELS 1972; FARJON 2010). In older literature it is described as extinct in nature and only recorded from the original collection. Thus, *Podocarpus gnidioides* was regarded as a doubtful taxon (KRÜSSMANN 1983) and its systematic position among recent Podocarpaceae was therefore unclear for a long time. However, today some stable populations (figs 6 & 7) are well known in the south of the Baie de St. Vincent in South New Caledonia (ECKENWALDER 2009). Therefore the present conservation state of *Podocarpus gnidioides* is described as “near threatened” (THOMAS 2010). Thus, enough vegetative material was available to solve the systematic position of *Podocarpus gnidioides* based on molecular and also on foliar data (internal and external microscopic leaf characters). Following current cladistic analyses of Podocarpaceae *Podocarpus gnidioides* is placed within the Australis clade. Thus, *Podocarpus gnidioides* is closely related to the New Zealand taxa *Podocarpus acutifolius*, *Podocarpus cunninghamii*, *Podocarpus hallii*, *Podocarpus totara* (subclade Australis I) and to *Podocarpus nivalis* from New Zealand, *Podocarpus alpinus* and *Podocarpus lawrencei* from Australia (subclade Australis II) (KNOPF *et al.* 2011, fig. 4). *Podocarpus gnidioides* has no close affinities to the other taxa native in New Caledonian as e.g. *Podocarpus decumbens*, *Podocarpus longifoliolatus*, *Podocarpus lucienii*, *Podocarpus novae-caledoniae*, *Podocarpus polyspermus* and *Podocarpus sylvestris* (ECKENWALDER 2009). Within the Australis clade *Podocarpus gnidioides* is a sister taxon to the Australis I and Australis II subclades.

Podocarpus gnidioides is rare in cultivation and material (vegetative and fertile) is hardly available. Thus, currently only limited data about morphology and anatomy especially about its cones are available. *Podocarpus gnidioides* is dioecious as is also the case for nearly all other *Podocarpus*

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species (DALLIMORE & JACKSON 1966; DEL FUEYO 1996; ECKENWALDER 2009; FARJON 2010). A line drawing in DE LAUBENFELS (1972) is one of the rare illustrations of the pollen cones of *Podocarpus gnidioides* that exist. A 10-years-old male individual cultivated as a potted plant and overwintered in a temperate house in the private living collection of HUBERTUS NIMSCH, Bollschweil, St. Ulrich (Germany), started forming pollen cones for the first time in spring 2014. This was taken as an opportunity to investigate the morphology and anatomy of pollen cones and pollen of *Podocarpus gnidioides* in detail.

2 Material & Methods

2.1 Material

21 pollen cones were collected on 5.5.2014 shortly before anthesis. As typical for conifers the pollen cone development is simultaneous within an individual and all material that was available has been collected in a more or less the same late ontogenetic stage. Thus, ontogenetic studies about the pollen cone development could not be done.

2.2 Methods

Freshly collected material was photographed and then fixed in FAA (100 ml FAA = 90 ml 70% ethanol + 5 ml acetic acid 96% + 5 ml formaldehyde solution 37%) before being stored in 70% ethanol. The cone-anatomy was studied from serial sections using the classical paraffin technique and subsequent astrablue/safranin staining (GERLACH 1984). For SEM-analysis the FAA-material was dehydrated in formaldehyde dimethyl acetal (FDA) for at least 24 hours (GERSTBERGER & LEINS 1978) and critical point dried. Sputter coating was done with a Sputter Coater SCD 50 Baltec (BALZERS). The specimens were examined with an AURIGA ZEISS TM. Macrophotography was accomplished using a digital camera (CANON POWERSHOT IS2) and microphotography with a digital microscope (KEYENCE VHX 500F) equipped with a high-precision VH mounting stand with X-Y stage and bright field illumination (KEYENCE VH-S5).

2.3 Special terms

The term “sporophyll” or “microsporophyll” is avoided for the sporangia bearing structure in conifers. Otherwise this would introduce *a priori* a homology with the terminology applied. They are termed here as “sporangiphore” or “microsporangiphore”. The small green scale developed adaxial at the central stalk of hyposporangiate sporangiphores is called “scutellum”.

3 Results

3.1 Morphology and anatomy of pollen cones

On lateral shoots pollen cones are developed in distal parts of the last year's growth (figs 1A, 1C, 2A). They are inserted solitary in the axil of a typical needle-leaf (figs 1A, 1C). The pollen cone is surrounded by 13-17 small persisting bud scales (fig. 2C, 2E). The majority of the bud scales are small triangular, green and about 1 mm long and 1 mm wide (figs 2C, 2E). Only the inner bud scales can sometimes show the appearance of a typical needle-leaf (figs 1E, 1F), however they are strongly reduced in size. Ripe cones are erect and between 10-25 mm long and 2-2.5 mm wide (fig. 2A). The stalk is between 5-8 mm long and 1-1.5 mm in diameter (figs 2C, 2D). The cones consist of 83-126 densely spirally set hyposporangiate microsporangiphores (fig. 2B). Perisporangiate microsporangiphores were not found. Microsporangiphores are developed even shortly below the apex and the apex can still be recognised as a small tip (figs 4A, 4B, 4C, 4D). Even the most distal microsporangiphores are fertile (fig. 3D). In one of the investigated cones the cone-axis terminates with a microsporangiphore (figs 4E, 4F). The scutellum of this terminal microsporangiphore is quite short and roundish, peltate-like (figs 4E, 4F). The vascular bundle strand of the cone-axis terminates blindly in the distal part of the scutellum of the terminal microsporangiphore (figs 4E, 4F).

A typical microsporangiophore consists of a central stalk about 1 mm long, 2 abaxial sporangia each about 0.4-0.5 mm in diameter and an adaxial green more or less triangular, slightly serrate, upright scutellum 0.5-0.7 mm long and 0.8-1 mm wide (fig. 3A, 3B, 3C). The ripe sporangia are parallel to the central stalk of the microsporangiophore (fig. 3A). The scutellum of the most distal microsporangiophores is strongly elongated, and about 1.1-1.8 mm long and 0.8-1 mm wide (figs 3D, E). Especially in the scutellum of the most distal sporangiophores a huge resin duct is developed (fig. 4E). The microsporangia and the scutellum are strongly fused with each other (figs 3C, 3E). The scutellum is attached in an angle of nearly 80° to the stalk and also fused with the sporangia (fig. 3C). In young cones, the scutellum of the microsporangiophores are covering the sporangia of the more distal microsporangiophores. Before anthesis nearly only the phylloid part is visible externally. The cone-axis elongates strongly at anthesis and the microsporangia are freely exposed to the airflow. Within the sporangiophore no intercellular spaces are developed (figs 3C, 3E).

For better pollen release microsporangiophores diverge distally from each other at anthesis. At pollination time each microsporangium opens along a median, longitudinal preformed line (fig. 3A left) and releases the pollen grains over a period of 7-13 days. The release of the pollen starts even when the cone is not already completely open. The majority of pollen grains are collected first on the upper surface of the lower microsporangiophores especially on the scutellum. From here the pollen is taken secondary by the airflow, when the cone-axis has reached its final length. After releasing the pollen the cones dry out and are abscised as a unit.

The majority of cones are unbranched. Only some pollen cones are branched structures, showing 1-2 lateral axillary units in the basal part (fig. 2B). Each of these lateral units is inserted in the axil of a green triangular bud scale of the terminal cone. The lateral units are originated from a separate bud (figs 1E, 1F). Thus also at the base of the lateral cones persisting bud scales develop (figs 2E, 2F). In the investigated cones only the most basal bud scales were fertile – the distal ones were always sterile. The vascular bundle strand of the lateral cone and the fertile bud scale enter the vascular bundle strand of the axis of the terminal cone in separate strands (fig. 2F). They do not fuse. In the anomalous branched pollen cones the development of the terminal pollen cone is hurrying ahead to the lateral cones.

3.2 Morphology of pollen

The pollen grains are bisaccate (figs 5A, 5B, 5C). Their overall length including the sacchi varies between 40-50 µm. The corpus is elliptic and varies between 27-36 µm x 20-26 µm (fig. 5C). The sacchi are broadly attached at the corpus (figs 5A, 5B). They are between 15-20 µm in diameter and between 10-12 µm in height. The two sacchi are attached at an obtuse angle to the corpus, ranging between 110°-130° (fig. 5A). The outer surface of the sacchi is covered with several tiny papillae and has several perforations (figs 5A, 5B, 5E). The corpus has a strongly rugulate, thick sculpturing without perforations (figs 5C, 5D). The leptoma is 18-24 µm long and 8-13 µm wide. Its surface is fossulate. Perforations are absent (figs 5B, 5F).

4 Discussions

In its vegetative parts *Podocarpus gnidioides* differs significantly from the other taxa of the subclade Australis especially in some morpho-anatomical characters of the leaf, e.g. by forming a double layered hypodermis and lacking of hypodermal fibres between the abaxial stomata rows (KNOPF *et al.* 2011). When regarding the morpho-anatomical data of the pollen cones *Podocarpus gnidioides* complies with those of the other taxa of subclade Australis. Despite the relative isolated systematic position of *Podocarpus gnidioides* among the other New Caledonian *Podocarpus* species, its pollen cones do not have special features that are exclusively presented in this taxon. They show all features typical for pollen cones among *Podocarpus*.

Typical pollen cones of *Podocarpus gnidioides* are unbranched structures limited in growth and carrying several hyposporangiate sporangiophores, which are inserted directly at the cone-axis as is also the case in all other *Podocarpus* species (e.g. KRÜSSMANN 1983, DALLIMORE & JACKSON 1966, MUNDRY 2000, MUNDRY & MUNDRY 2001, FARJON 2010, DÖRKEN *et al.* 2011) and in nearly all other coniferous taxa. Most authors regard the coniferous microsporangiophores as microsporophylls and thus, unbranched pollen cones fulfill the definition of “flowers”. However, also some of the investigated pollen cones of *Podocarpus gnidioides* had a branched structure developing 1 or 2 lateral units in the basal part, each of them developed from different buds, so that the base of each lateral cone-axis is also surrounded by bud scales. This is a great difference to other coniferous taxa showing branched pollen cones e.g. *Cephalotaxus* (Taxaceae). In *Cephalotaxus* the whole “inflorescence” is developed from a single bud. Thus, bud scales are only developed at the base of the stalk of the complete cone.

The microsporangiophores of *Podocarpus gnidioides* differ from other coniferous microsporangiophores by lacking intercellular spaces, which are distinctly developed for example in microsporangiophores of *Pinus* (MUNDRY 2000). The change in the orientation of maturing microsporangia and their final position is quite different among recent conifers, sometimes even within a genus. MUNDRY (2000) has shown that in *Podocarpus macrophyllus* the young developing microsporangia are first orientated parallel to the stalk, perhaps due to a lack of space within the young, developing cone. In late ontogenetic states, when the cone-axis elongates, the sporangia turn in a more or less vertical position to the stalk. The orientation of ripe microsporangia of *Podocarpus gnidioides* differs strongly from *Podocarpus macrophyllus*. In *Podocarpus gnidioides* even the ripe sporangia are orientated parallel to the central stalk of the microsporangiophore. In this respect *Podocarpus gnidioides* is quite similar to *Pinus*. In *Pinus* young sporangia are developed parallel to the central stalk and keep this position also at maturity. It seems that in *Podocarpus gnidioides* this position is caused due to the lack of space even within ripe cones. For a successful release of the airborne pollen a vertical position of sporangia as developed in *Podocarpus macrophyllus* is more favourable. The microsporangia open along a preformed longitudinal line which is also more or less vertical to the central stalk and thus well exposed to the airflow. Thus a huge amount of pollen can be released by the microsporangia. In this respect the parallel orientation of microsporangia as developed in *Podocarpus gnidioides* (fig. 3A) or *Pinus* is not so favourable. The sporangia also open along a longitudinal preformed line, which is developed, however, parallel to the central stalk of the sporangiophore (fig. 3A) and therefore in some parts deeply placed within the cone. Thus, only a small amount of pollen can be released from the sporangia by the wind. In taxa with parallel orientated microsporangiophores the pollen is presented secondary. The released pollen is first collected especially on the adaxial side of the scutellum of the lower microsporangiophores. From here the pollen is taken by the wind.

The number of microsporangiophores in pollen cones of *Podocarpus gnidioides* (83-126) is slightly lower compared to closely related taxa. In this respect, pollen cones, e.g. of *Podocarpus totara* with 100-120 microsporangiophores, are quite similar to *Podocarpus gnidioides* (WILSON & OWENS 1999). In other *Podocarpus* species with large pollen cones the number of inserted microsporangiophores can reach up to 284 (SCHULZ *et al.* 2014). Thus, with only 83-126 microsporangiophores per pollen cone *Podocarpus gnidioides* has one of the smallest pollen cones among recent *Podocarpus* species.

Each microsporangium produces several bisaccate pollen grains as in all other *Podocarpus*-species (e.g. SPORNE 1965; TOMLINSON *et al.* 1991; OWENS *et al.* 1998; GELBART & VON ADERKAS 2002; FERNANDO *et al.* 2010; LESLIE 2010). The bisaccate pollen grains correlate well with the downward facing micropyles and secretion of a pollination drops. The sacchi help the pollen grains floating upward in the pollination drops. Thus the pollination mechanism in *Podocarpus* is similar to several Pinaceae, e.g. *Cedrus*, *Pinus* or *Picea*, albeit with a different seed cone morphology (e.g. SPORNE 1965; TOMLINSON *et al.* 1991; OWENS *et al.* 1998; GELBART & VON ADERKAS 2002; FERNANDO 2010; LESLIE 2010).

Podocarpus pollen grains are quite variable especially concerning the overall length, size, shape and sculpturing of the corpus and the width of the leptoma. Compared to pollen grains of other taxa among the subclade Australis the pollen of *Podocarpus gnidioides* with an overall length of 45 µm (average), a corpus length of 23 µm (average) and a leptoma 10.5 µm (average) in width are significantly smaller. Only the pollen grains of the New Zealand species *Podocarpus acutifolius* are quite similar to *Podocarpus gnidioides* in their dimensions (overall length 54 µm, corpus length 26 µm; width of the leptoma 13 µm) (POCKNALL 1981). The feature of a strongly rugulate sculpturing of the corpus is quite common among the taxa of subclade Australis, e.g. the New Zealand species *Podocarpus acutifolius*, *Podocarpus hallii* and *Podocarpus totara* (POCKNALL 1981). However this feature is also developed in not closely related *Podocarpus*-species such as the south American *Podocarpus nubigena* and *Podocarpus parlatorei* (DEL FUEYO 1996). Also the perforations in the surface of the sacchi are not a specific feature of *Podocarpus gnidioides* or exclusively developed among taxa of the subclade Australis. Such perforations are also developed in other not closely related taxa as e.g. *Podocarpus neriifolius*, *Podocarpus gracilior* or *Podocarpus macrophyllus* (e.g. VASIL & ALDRICH 1970; TIWARI *et al.* 2012). Thus, the pollen of *Podocarpus gnidioides* does not show features that are exclusively developed in this taxon.

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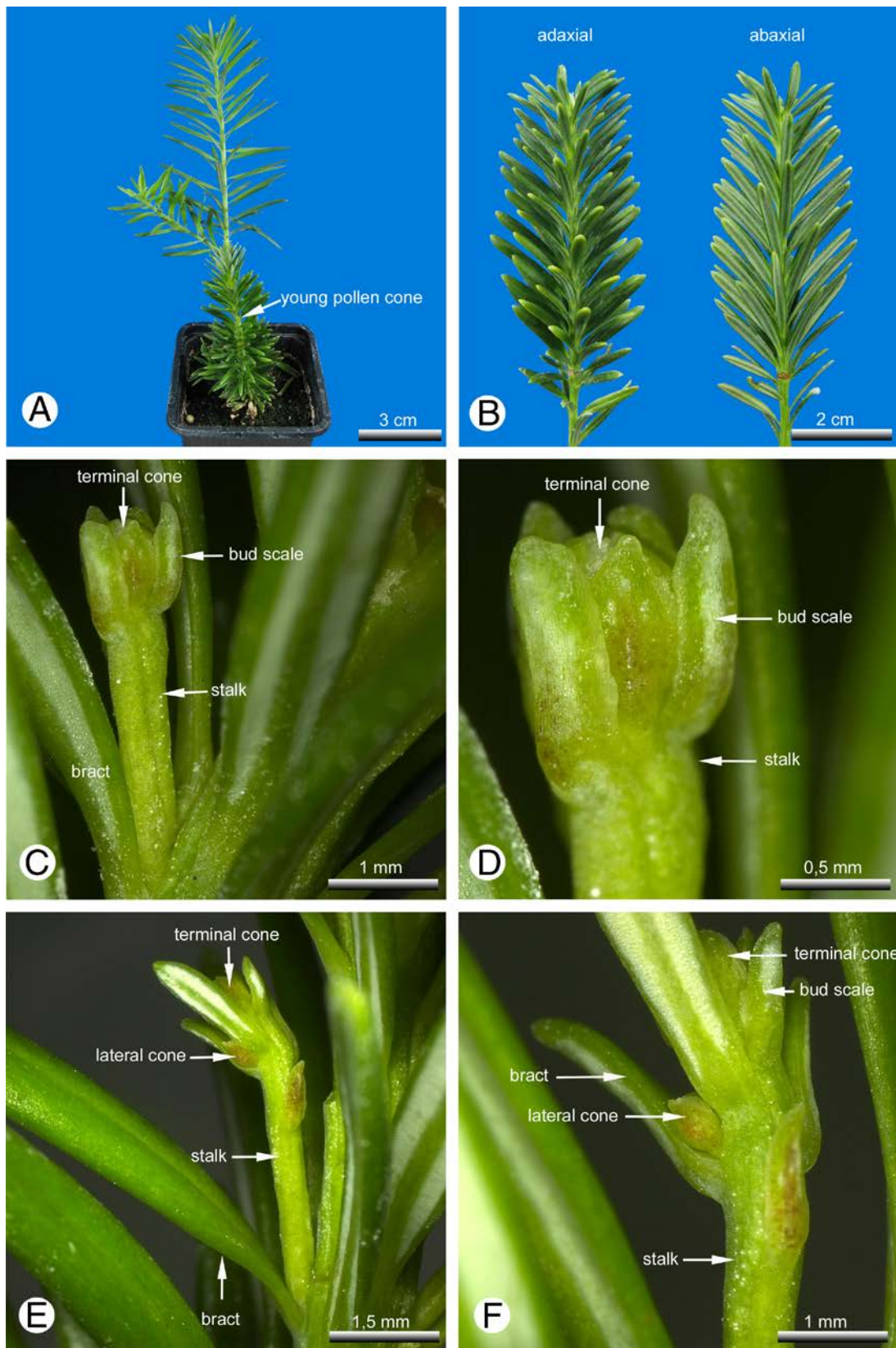


Fig. 1: *Podocarpus gnidioides*, young pollen cones and foliar details.

A: Habitus of a 2-years-old individual produced from cuttings collected from a 10 years old individual. **B:** Detail of a lateral shoot with the typical densely arranged needle-leaves. **C-F:** Young pollen cones developed at the individual illustrated in A. **C & D:** Unbranched pollen cone; the terminal pollen cone is surrounded by bud scales. **D:** Detail of C. **E & F:** Compound pollen cone; the terminal and the lateral pollen cone originate from different buds. **F:** Detail of E.

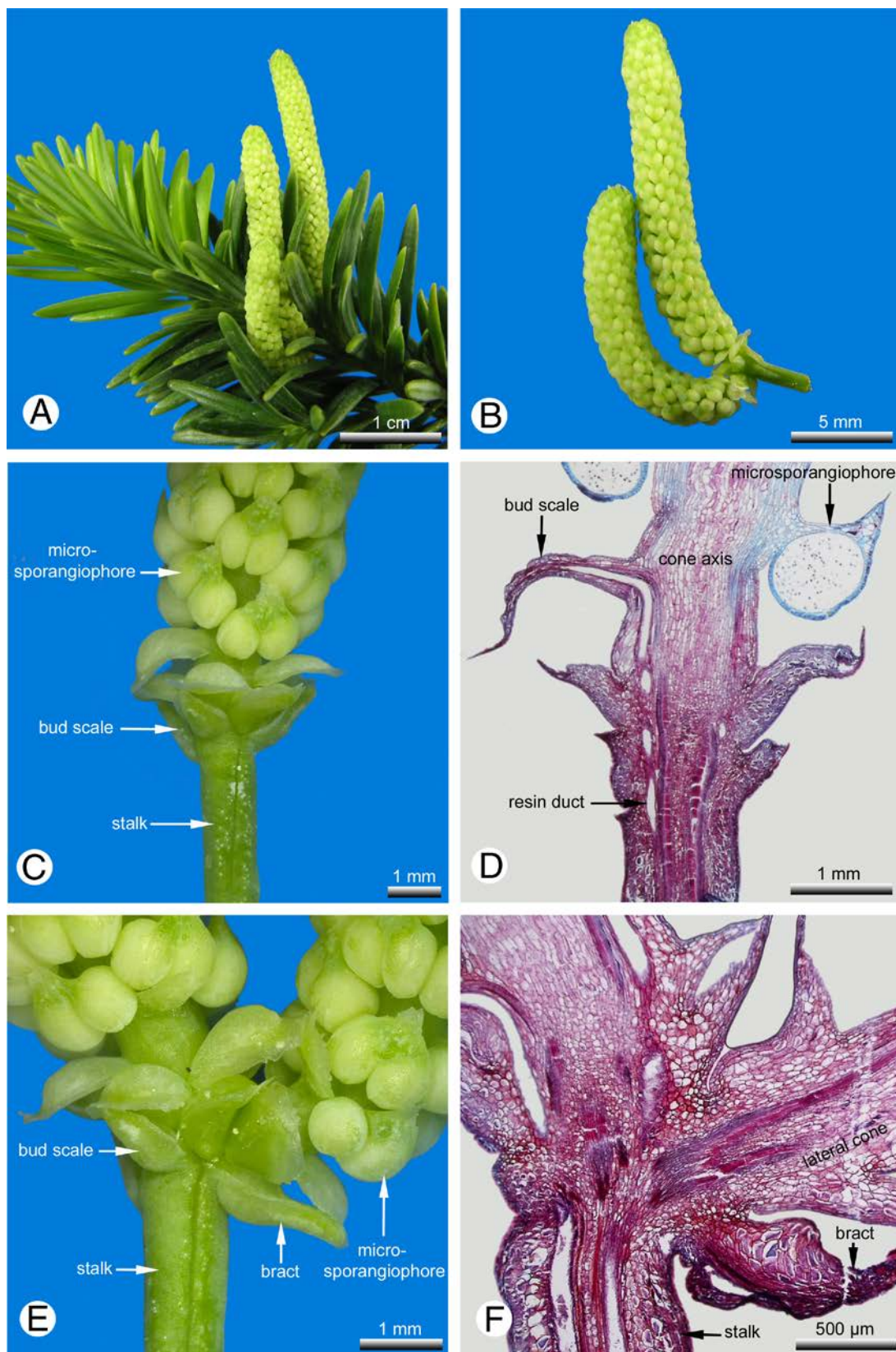


Fig. 2: *Podocarpus gnidioides*, morphology and anatomy of ripe pollen cones.

A: Pollen cones are erect at anthesis. **B:** Detail of a branched pollen cone. **C:** Base of an unbranched pollen cone with several persisting bud scales. **D:** Cross section of C. **E:** Base of a branched pollen cone; in one of the bud scales a lateral cone is inserted. **F:** Cross section of E.

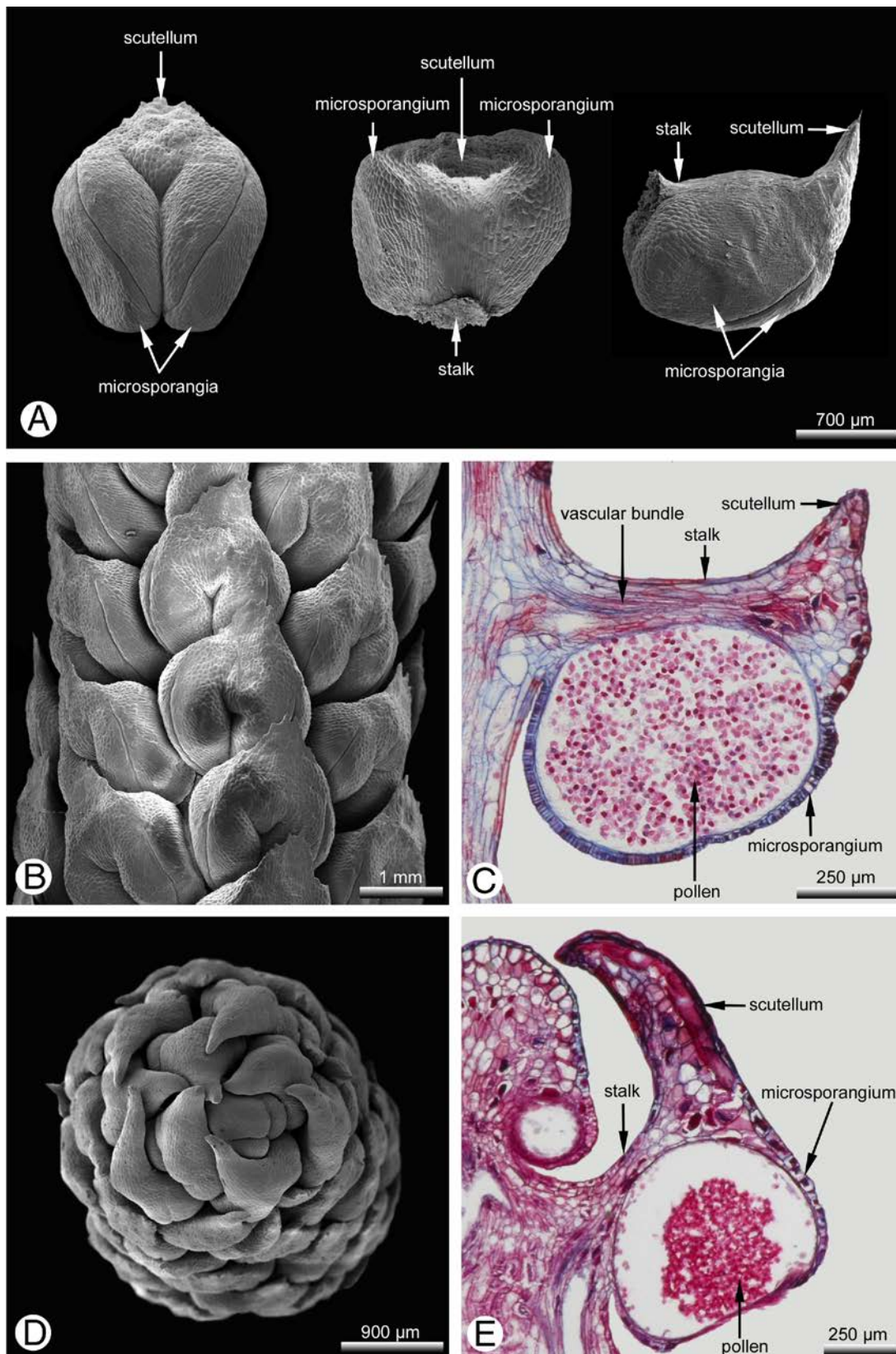


Fig. 3: *Podocarpus gnidioides*, morphology and anatomy of ripe pollen cones and ripe microsporangiochore.

A: Microsporangiochore in abaxial (left), adaxial (middle) and lateral view (right); sporangia are parallel to the central stalk. **B:** Microsporangiochore in the middle of the cone have a small scutellum. **C:** Cross section of a microsporangiochore in the middle part of the cone. **D:** In the distal part of the cone the scutella are strongly elongated. **E:** Cross section of a distal microsporangiochore.

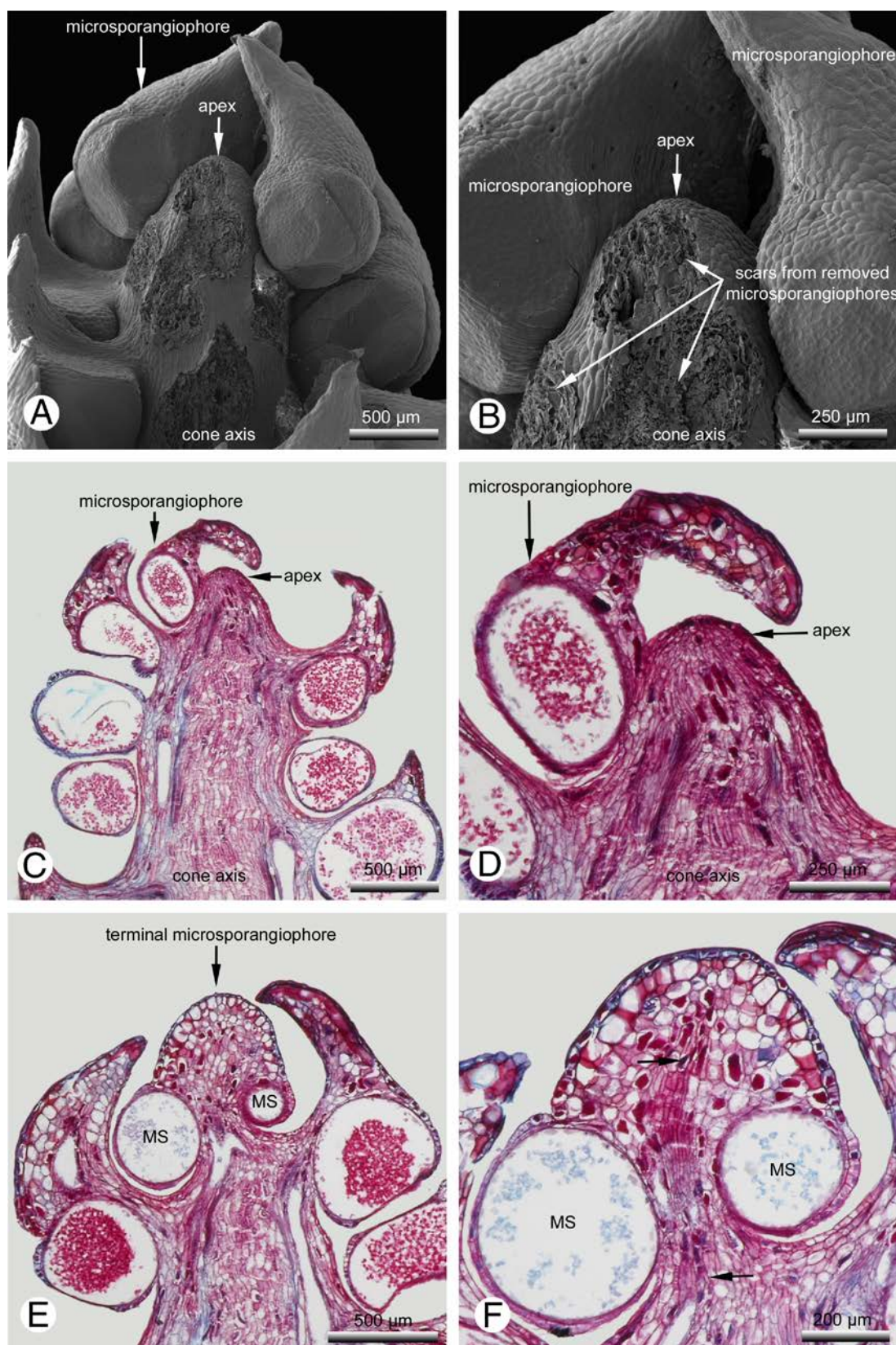


Fig. 4: *Podocarpus gnidioides*, details of the cone tip.

A-D: Typical pollen cones; the apex of the cone-axis is still recognizable; microsporangiophores are developed even shortly below the apex. **A & B:** Details with SEM. **C & D:** Longitudinal microtom sections of the distal part. **E & F:** Anomalous pollen cone terminating with a microsporangiophore; the scutellum rest is more or less peltate-like and carries two microsporangia (MS); the vascular bundle of the cone-axis (marked with arrows) ends blindly in the distal part of the scutellum. **F:** Detail of E; the sporangia of the terminal microsporangiophore are both fertile.

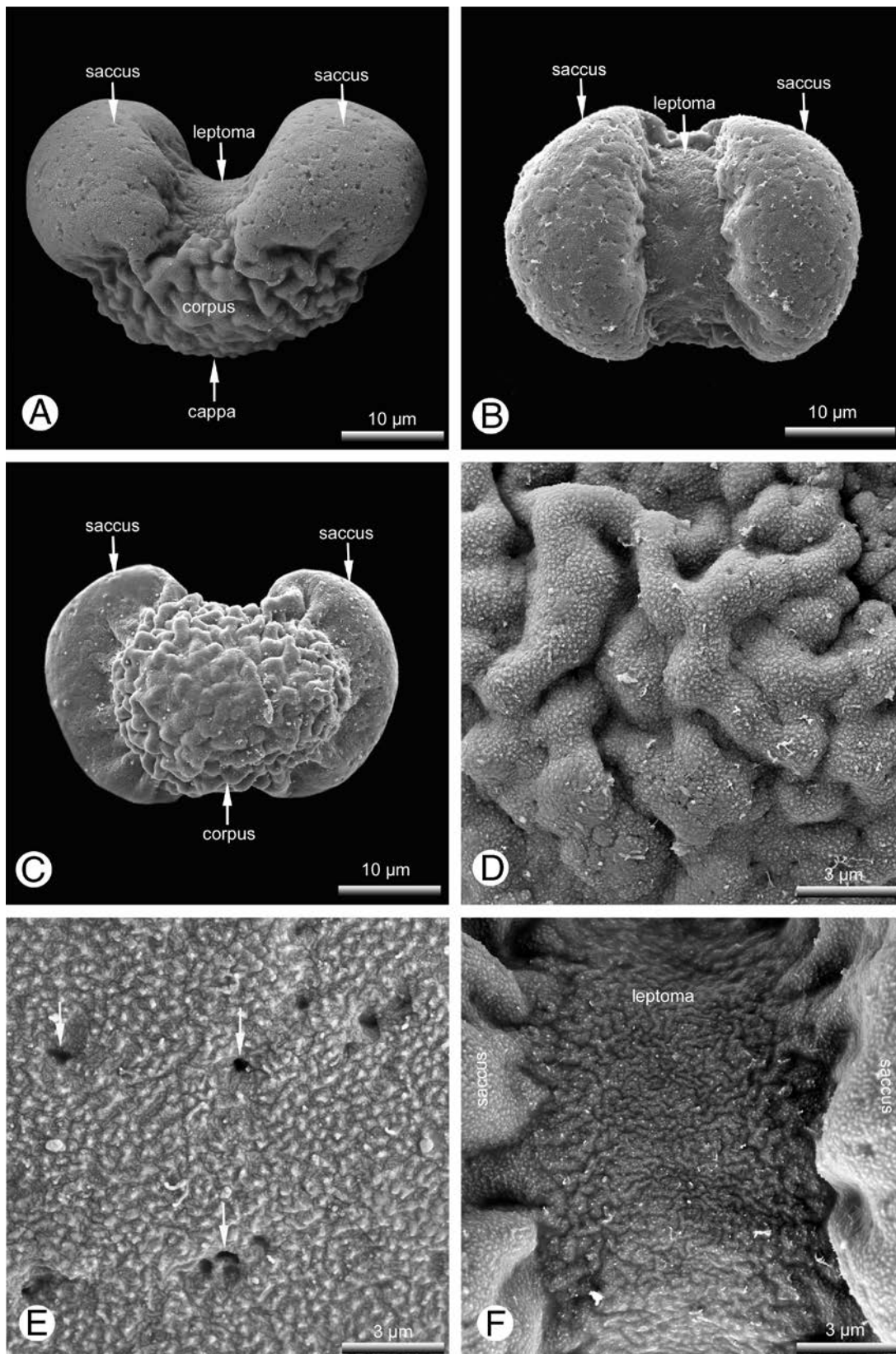


Fig. 5: *Podocarpus gnidioides*, pollen-morphology.

A-C: Overview of a bisaccate pollen grain. **A:** Equatorial view. **B:** Distal view. **C:** Proximal view. **D:** Detail of the corpus; surface strongly rugulate. **E:** Detail of the saccus; surface with several tiny papillae and perforations (some marked with arrows). **F:** Detail of the leptoma; surface fossulate.



Fig. 6: *Podocarpus gnidioides*, details of pollen cones and leaves.

A: Ripe pollen cones at anthesis. **B:** Young leaves are bright green.

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Fig. 7: *Podocarpus gnidioides* at its natural New Caledonian habitat on Mont-Dore, SE of Nouméa, at about 770 m above sea level; all photos taken in December 1995 by HN.

A: Mature shrub about 1.5 m high. **B:** *Araucaria muelleri* is also native in the same habitat. **C:** Foliar details of

Podocarpus gnidioides. **D:** Massive erosion of the soil caused by human activities is one of the main problems threatening *Podocarpus gnidioides*. **E:** Ripe seed cone carrying one seed. **F:** Young maturing seed cones, each with two seeds and an intensively red colored receptaculum.