

MORPHOLOGY AND AFFINITIES OF *PINUS CANARIENSIS*

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ABSTRACT. A morphological and leaf anatomical description is given of the endemic Canary Island Pine *Pinus canariensis*; its affinities and possible evolutionary history are discussed.

INTRODUCTION

Pinus canariensis C. Smith, the Canary Island Pine, is endemic to the western Canary Islands of La Palma, Hierro, Tenerife, and Gran Canaria. In these areas the pine forms a tall semi-open, park-like community over the dry and often rocky topography, typically with few other trees or undershrubs. The once extensive natural forests have been widely felled for timber, substantially reducing its former range and many of the largest trees have disappeared. However, good native stands can still be found containing trees of all ages especially on La Palma. Here impressive natural forests flank the Caldera de Taburiente above about 1200 m (directly above the laurel forest belt), are present over much of the southern mountainous spine of the island (descending in places to perhaps 500 m), and are abundant within the Caldera itself. The forest reaches its highest limits at about 2000 m.

Although phytosociological and silvicultural aspects of the pine have been studied by Ceballos & Ortuño (1951), existing morphological descriptions are mostly brief and incomplete. An opportunity to study and collect material of it on the islands of La Palma, Hierro and Gran Canaria showed the existence of wider variation in morphology than previously indicated and it was felt that a fuller description would provide a more complete source of reference.

***Pinus canariensis* C. Smith in Buch, Besch. Canar. Ins. 159 (1825). Fig. 1.**

Mature trees 25–40 m or more in height, 1–2 m basal diameter, normally single-trunked with an irregularly branching habit*; crown spreading and irregularly rounded with branches ascending to broadly spreading, usually also with at least some of the lower branches persisting and widely spreading. *Foliage* with a characteristic somewhat weeping habit. *Bark* of trunk thick, somewhat soft, fissured into scaly plates, breaking readily into thin irregular flakes, grey to rich red-brown or deep red in colour. *Young trees* conical in shape with \pm regularly whorled branches, their bark thin, smooth, grey to red-brown in colour.

Young shoots glabrous, prominently ridged, yellowish at first becoming buff-brown in second year, mostly 6–13 mm diameter. *Branchlets* long, usually freely branched, often drooping or pendulous with upcurving tips, somewhat brittle, pale reddish-brown in colour, rough with persistent scale

* Individuals reaching 60–65 metres with a basal diameter of up to 2.66 metres have been reported by Ceballos & Ortuño (1951). Old trees at high altitudes often do not exceed 12–18 metres and have multiple trunks with low level branches persisting.



FIG. 1. *Pinus canariensis* C. Smith: a, shoot orientated in approximately natural position showing developing female cones (Page 9052); b, shoot with mature male inflorescence (Page 9051); c, mature female cone after opening; d, seed showing characteristic undulate markings on wing; e, bud-scale showing characteristic fimbriate-ciliate margins.

bases for several years. *Winter buds* large, ovoid, acute. *Bud scales* persisting 1-3 years, lanceolate, with free and often reflexed tips on bud, becoming strongly reflexed and usually circinnate after growth of the shoot, 10-16 × 4-5 mm, pale brown in colour with an often somewhat darker red-brown centre, shining, with conspicuous, usually whitish, 2-3 mm free, fimbriate or ciliate margins (fig. 1e). *Mature leaves* persisting 1-3 years, in fascicles of three, densely crowded on branchlets, flexible, spreading, arcuate and often somewhat pendulous, 15-30 cm or more × 0.5-1.3 mm, grass green, shining, with 2-4 lengthwise narrow white stomatal bands on the broad face of each leaf and 1-3 similar bands on each narrow leaf face, the three angles minutely serrulate with numerous fine low closely-spaced distally pointing acute teeth, tips of leaves flexible, acuminate. *Fascicle sheath* long (10-20 mm), persistent, grey-green to greenish brown.

Female cones deflexed or pendent on the shoot when mature, sub-terminal, usually solitary or in pairs, rarely in clusters, 9-20 × 5-8 cm, ellipsoid-ovoid before opening, 9-20 × 9-12 cm, broadly ovoid or ovoid-conic after opening, 80-160 gm fresh weight, sessile or shortly (5-20 mm) pedunculate, cone normally breaking from distal end of peduncle without loss of cone scales, opening in autumn of 2nd year or spring of 3rd year (fig. 1a, c). *Apophyses* of cone scales more or less quadrato-rhombic, usually wider than long, pyramidal, up to about 24 mm lateral diameter, lustrous to sub-lustrous, nut-brown when mature, apex somewhat variable, low rounded to 2-3 mm obtusely prominent, red-brown to pale grey in colour, non-resinous. *Cone scales* hard and woody, 3-5 mm thick, 25-45 mm in length, 15-20 mm in breadth, the concealed portion pale brown in colour, sub-lustrous. *Female cones at end of one year*, ellipsoidal-fusiform, greenish, slightly glaucous, with brownish or purple-brown prominent tips to each scale, the scales with small resin patches; female cones at end of two years rather narrowly ovoid, greenish-grey to greenish-red, each scale with purple-grey tips. *Seed* ± obovoid, 10-14 × 5-8 mm, grey-brown or blackish, winged; wing broadly adnate to the seed, 12-25 mm in length, 6-11 mm in depth, with a more or less straight spine and circuate keel, membranous, translucent, lustrous, pale buff-brown with conspicuous lengthwise undulate deep brown lines, particularly densely marked along the spine, becoming pale towards the keel (fig. 1d). *Male cones* ovoid-ellipsoid, c 15 × 7 mm, greenish yellow before opening, elongating to 30 mm or more and turning red-bronze when open, clustered into large inflorescences, maturing March-April. *Pollen* yellow. *Inflorescences* large, sub-terminal, cylindrical, up to 10 × 6-7 cm, containing up to about 150 male cones (fig. 1b).

Seedlings with 7-10 cotyledons, the cotyledons up to 65 mm in length, mid-green in colour with slight glaucous bloom. *Hypocotyl* reddish or purplish-brown with faint glaucous bloom; stem of young shoot 1.5-3.0 mm diameter, greenish-white to pale violet in colour with a distinct glaucous bloom; first true (juvenile) leaves 12-15 mm long, becoming 50 mm within 4-5 cm of cotyledons. *Juvenile leaves* long persistent, and produced for many years, 30-80 × 0.5-1.5 mm, dorsiventrally flattened, with one (or occasionally two) low central keels on the ventral surface, distinctly glaucous throughout, each lateral edge of the leaf and ventral keel sparsely serrulate with irregularly scattered low distally pointing acute teeth, tips of leaves with a short flexible mucronate apex.

The Canary Island Pine can thus be recognised by its long grass-green somewhat weeping mature foliage, fringed bud scales, glaucous long-persistent juvenile leaves, large male inflorescences and female cones, and seed wings with characteristic undulate markings.

LEAF ANATOMY (Fig. 2)

Epidermis a single layer of thick walled cells. Stomata frequent on all surfaces of the leaf. *Hypodermis* conspicuous, continuous around outer periphery of leaf, strongly developed especially in each lateral edge of leaf, and with conspicuous inward extensions into the mesophyll (usually two on each of the inner leaf surfaces and 2-4 on the outer surface), some reaching to endodermis, outer cells with thick walls, inner cells with progressively less thickening. *Resin canals* usually two, external in position, one in each lateral edge of the leaf or with one or both on the leaf's outer periphery, persisting the length of the leaf, external in position and touching the hypodermis; sheathing cells of resin canals with uniformly thin walls. *Mesophyll* with large cells and abundant shallow peg-like infoldings. Endodermis of large rounded cells with uniformly thin walls. *Stelar region* elliptical-obovate in section, up to twice as broad as deep. *Vascular bundles* two in each leaf, situated closely together and sometimes touching at the base, occupying about two-thirds of the total stelar region.

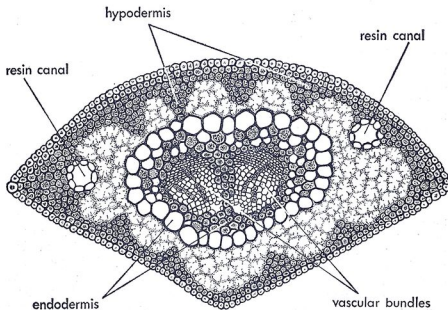


FIG. 2. Leaf anatomy of *Pinus canariensis*: T.S. of typical leaf showing conspicuous hypodermis with inward extensions, resin canals, mesophyll, endodermis with uniform walls and position of vascular bundles.

PRESENT DAY AFFINITIES

Pinus canariensis is the only species of 3-needled pine in the west of the Old World. Its only near relative, although more than 5000 miles distant, appears to be *P. roxburghii* Sargent (*P. longifolia* Roxb.) of the monsoon belt of the outer Himalayas, occurring from Nepal and Bhutan to West Pakistan at elevations of 450–2300 m (fig. 3). Most authors have placed *P. canariensis* and *P. roxburghii* in a bitypic group (Shaw, 1914; Pilger, 1926; Critchfield & Little, 1966; Mirov, 1967) clearly distinct from all other pines.

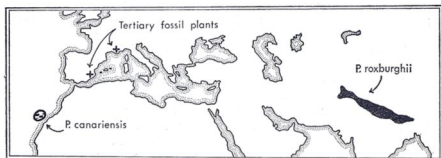


FIG. 3. Present distribution of *Pinus canariensis* and *P. roxburghii* and location of their Tertiary fossil allies.

P. roxburghii can be distinguished from *P. canariensis* by the more prominent umbos of the mature female cones, the more numerous resin ducts (2–6) in the leaves, a hypodermis somewhat less strongly developed and penetrating in patches into the mesophyll usually not as far as the endodermis, the thickened outer walls of the endodermal cells and typically more distantly-separated vascular strands. According to Hudson (1960), the two species also differ in certain details of wood anatomy: *P. roxburghii* has smaller diameter radial resin canals (44–51 μm cf. 60–73 μm in *P. canariensis*), fewer cells in the height of the rays in TLS (23–27 cf. 31–38 in *P. canariensis*), nearly smooth walls to the ray tracheids, and more numerous biseriate bordered pits in RLS.

The two species are undoubtedly very closely allied. Both are subtropical montane species growing at similar elevations under semi-arid conditions, each often forming pure forests (Meusel & Schubert, 1971). Both become large trees of similar general habit with open spreading crowns. In both species the bark of the mature trees is grey to reddish, thick, fissured, and shed in plates. Like *P. canariensis*, the leaves of *P. roxburghii* are borne in threes, and are long, slender, flexible, and light green with finely toothed margins and a persistent long basal sheath. In both, the leaves persist about two years, and the female cones are large and generally similar. The attachment of the seed wing is similar in both species, and both have the characteristic lengthwise undulate markings. In leaf section, the hypodermis in each species is conspicuous, and resin canals are present in an external position with typically one in each lateral corner of the leaf.

ORIGIN AND EVOLUTION

Although three-needled pines are absent from the native flora of Europe today, various species of pines of this type have been widespread in western Eurasia in the past and are known from fossil beds of the Tertiary.

The distribution of the genus *Pinus* in Europe during the Tertiary has been considered by Ferguson (1967). From beds of Paleocene-Eocene age, three-needle pines have been reported from Austria and the Paris basin of France. In the Oligocene such pines clearly occurred in Hungary, Germany, northern Italy and southern France, whilst by the Miocene they appear to have become both more abundant and wide-ranging and are known from Europe as far north as southern Russia (approx. lat. 51°N), as well as Romania, Yugoslavia, Hungary, Austria, Switzerland, Germany, Italy, and France. Although less numerous in the Pliocene than the Miocene, such pines persisted in Europe and their distribution seems to have been similar or slightly more southerly: Bulgaria, Romania, northern Italy, southern Germany, southern France and Portugal.

As well as leaf impressions, Tertiary fossil pines from many of these and other localities contain numerous cones either isolated or attached to shoots and leaves. Although many new fossil species have been published—Ferguson listing c. 140 species of *Pinus* from the European Tertiary, including c. 70 from the Miocene—the actual number of 'good' species seems likely to be less than those described. Clearly these fossils, many of which were described in the 19th century, should be subjected to a modern revision based on critical examination of original material, but on the basis of the available descriptions it seems likely that one aggregate of species which existed in southern Europe as late as the Pliocene was of long-leaved, large-coned, three-needle species of which *P. canariensis* and *P. roxburghii* may be their nearest living members. Particularly noteworthy in this connection are plants described from the Pliocene deposits of southern France (especially the Rhône valley) (Saporta, 1865, 1868; Depape, 1922). Here, leaves, shoots, buds and female cones are preserved, many in the state of organic connection with one another, which have suggested affinities close to the living *P. canariensis*—*roxburghii* group. Amongst these fossils, species described under *P. resurgens* Sap. had 12+ cm long leaves with a persistent sheath, finely serrulate margins, with large cones borne on short pedicels, claimed to be of similar general shape to those of *P. canariensis* and with a similar umbo. Others from southern France described under *P. sterrolepis* Sap. and *P. trichophylla* Sap. (the latter existing as numerous imprints and having leaves 17–20 cm in length) were compared by Saporta (1865) with the living *P. roxburghii*, whilst specimens described under *P. lophocarpa* Sap. were compared with both *P. canariensis* and *P. roxburghii*. Another specimen attributed by Saporta (1868) to an affinity with the *P. canariensis*—*roxburghii* group, described as *P. matheronii* Sap., was a shoot with attached foliage which had a well-preserved large solitary oblong-conic winter bud with acute apex and lanceolate scales, and long (15–18 cm) serrulate-margined leaves.

Another Tertiary fossil pine suggested to have close affinities with the living *P. roxburghii* and *P. canariensis* was described by Lindley & Hutton (1837) from the Pliocene of Murcia, SE Spain. This plant had cones six or more inches in length and three inches broad, many details of which were considered identical with those of *P. canariensis*, whilst others approached those of

P. roxburghii. Although many of these fossils are somewhat ill-defined and perhaps variable in morphology, it is significant to note that it is possible in *P. canariensis* today to find considerable variation in leaf length and size and shape of the cones. The possibility thus seems strong that many of these Pliocene fossil species, likened by their authors to the *P. canariensis-roxburghii* group, may represent a single broad species-alliance which may have been widespread in southern Europe at the time. Depape (1928) also noted similarities between some of the Pliocene pines of Saint-Marcel (44°N) and *P. canariensis*, and also observed that they occur as fossils associated with several other species (notably Lauraceous trees and ferns such as *Woodwardia radicans*) whose affinities lie closely with the modern laurel forests of the Canary Islands. Depape theorised that forests of these pines, similar to those of *P. canariensis* in the Canary Islands today, occupied some of the higher elevations of the topography of Pliocene southern France. *P. canariensis* is thus in all probability a living survivor of a pine type which had already evolved by the late Tertiary. At this time forests of this pine, presumably much like those of *P. canariensis* today, were probably extensive over parts of southern Europe and perhaps extended further eastwards towards the present-day Himalayas. At the two extreme ends of its former range, forests survived after the extinction of the plant from the intermediate areas, leaving the modern *P. canariensis* and *P. roxburghii* remote from one another, but each little changed in morphology from their Tertiary progenitor.

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