A review of the nineteenth-century literature on the wax palms of the genus Ceroxylon is presented, together with the available information on the biology, systematics, economic uses, ornamental value, and conservation status of the species in this genus.

The wax palms of the genus Ceroxylon are spectacular representatives of the palm family, Palmae. They grow at altitudes up to 3150 m, often in populations of hundreds of thousands of individuals, and their trunks reach 60 m in height. Travellers and naturalists, who for the last 200 years have visited the wax palm forests on the steep slopes of the Colombian central Andes, have admired their magnificence and referred to them extensively in their writings. Known as a source of an excellent wax, these palms have attracted the attention of chemists and industrialists alike.

The genus Ceroxylon comprises eleven species distributed throughout the northern Andes from Venezuela to Bolivia. The genus is a member of a small, relatively ancient lineage, and its species are widely scattered throughout the southern hemisphere.

The tallest and most populous species of wax palms, the Quindío wax palm Ceroxylon quindiuense (Karsten) Wendland, has been adopted as Colombia’s national tree and is
now protected by law. However, Ceroxylon quindiuense and other species of wax palms are threatened with extinction due to disturbance of their natural habitats, which interrupts their life cycles and increases their susceptibility to attack by pathogens. We here present an up-to-date review of the literature on wax palms.

Although the bibliography may appear extensive, the great majority of these references date from the nineteenth century and are mainly of historical interest. After almost two centuries, from the introduction of the wax palms to western science and their great admiration by naturalists, very little has been published about the basic biology of these palms. We hope this will soon change, for any effort to conserve these species will have to be based upon detailed knowledge of their biology.

THE PRINCES OF THE “PRINCIPE”

The first written account of the wax palm of which we have knowledge dates back to 1599, where in a military guide and description of the Indies by the Spanish captain Bernardo de Vargas Machuca (1892: II, 107), he mentions a tree that bears tallow. Several missionaries and explorers later commented on the wax produced by these palms and its properties (for a review of pre-Linnean references see Patiño, 1976: 189–190).

1 In the introduction to her excellent paper on the wax palms, Miriam L. Bombard, (1937:304) wrote: "...the wax palms with which we are here concerned are not only beautiful columnar trees but are probably the most remarkable palms in the world. They far exceed the most hopeful anticipations of the palm enthusiast; they are princes of the Príncipes." 2 Here the date appears as Sep. 12; it is corrected in the Spanish translation (Hernández de Alba, 1969–1975: I, 77–86). The latter was written in response to a letter sent to Mutis by Linnaeus fil. in 1777 (Uppsala, 6 November), when, due to the extreme illness of his father, the younger Linnaeus decided to contact his father's correspondents abroad and so continue with his father's work (for a translation of the letter from Latin to Spanish by Mutis himself, see his diary (Mutis, 1857–1868: I, 359–362)).
near the town of Guaduas on the Eastern Cordillera, he requested a sample, receiving an inflorescence, an infructescence with ripened fruits, some leaves, and wax. The "History of the Palms" to which Mutis made reference, not only in his letter to Linneaus fil. but elsewhere in his diary, probably corresponds to a manuscript written not long after 1793, and found among the documents of the Expedición Botánica in Madrid (Mutis, 1957–1958: II, 89). However, this text was apparently not written by Mutis but by an unidentified author known as ‘El Cura de los Teguas.’ It contains a description of 36 palms identified only by their local names, with indications of their uses, among which is a short description of the "Palma de Cera" (for annotated texts of the manuscript see Gredilla, 1911: 649–668; Patiño, 1985: 175–187). Among the plates of the Expedición Botánica, now housed at the Real Jardín Botánico in Madrid, are three plates of Ceroxylon, two in colour and one monochrome. These have been published together with a detailed account of the genus by G. Galeano in the recent folio sized volumes of the Flora de la Real Expedición Botánica del Nuevo Reyno de Granada (Galeano-Garcés and Bernal-González, 1985).

It was not until the beginning of the nineteenth century that the wax palms were to become fully known to western science through the combined efforts of Friedrich Wilhelm Heinrich Alexander von Humboldt and Aimé-Jacques-Alexandre Bonpland. In October 1801, Humboldt and Bonpland crossed the Central Andes of Colombia through the road constructed by Buenaventura two decades earlier. This road had seriously deteriorated due to heavy oxen and mule traffic and lack of maintenance. Furthermore, the covered bridges over the rivers San Juan and Coello, as well as the shelters along the road, conveniently spaced every 2–3 hours of travel, had been destroyed by an uprising in 1781 by the people of Ibagué, who were unhappy with the high tolls (Humboldt, 1982: 78/83a, 113/114a).

It nevertheless offered a unique travel experience, a detailed description of which Humboldt provided not only in his diaries but also in his fine account entitled Le Passage du Quindiu (Humboldt, 1810: 13–19, pl.V). Here the wax palms are mentioned only in passing, his attention being concerned mainly with other aspects of the road.

Detailed information on the wax palms was first presented in a memoir read by Bonpland at the Institut de France on November 4, 1804 (interestingly, in the minutes of this meeting the genus name was spelled Keraxylon [Delambre, 1913]). The memoir, later reviewed by the members of the Institut, Jacques-Julien-Houtou de Labillardière and Jean-Baptiste Antoine-Pierre Monnet de Lamarck (1913), consisted of a short account of the sexual characters of the genus, its affinities, a description of the locality where the plant was collected, its habit, and notes on the wax obtained from it. The first published version of the memoir was a summary written by Augustin-Pyramus de Candolle, who referred to the first known species of the genus as Ceroxylon alpinum just as Bonpland had in the verbal address (Candolle, 1804). Later, Humboldt and Bonpland (1805) published a second version of the memoir in which the species epithet was changed to andicola. Notwithstanding, the correct citation for the genus and species is Ceroxylon Bonpland ex DC. and Ceroxylon alpinum Bonpland ex DC. (see Moore 1961; Moore and Anderson, 1976). Various remarks made in the memoir must have struck Bonpland’s contemporaries. The maximum recorded altitude — 2825 m — at which these palms were observed exceeded by 1000 m the maximum altitude of any other palm known at the time. Furthermore, the minimum recorded temperature of their surroundings was of 6°C–7.5°C, with a mean daily temperature of 13.8°C. The height of the tallest individuals — 58 m, exceeding the tallest trees in their surroundings by 10 m — meant that they were the tallest plants then known.

Footnotes:
1. There seems to be an error in the temperatures reported in Bonpland’s memoir in both the Bulletin des Sciences as well as in Plantae Equinoxales, where 17°C was given for the low, and 19–20°C for the mean. Later Humboldt (1849: note 18, pp. 152–154), in the annotations to the growth form ‘Palmes’ of his Physognomik der Gewachse, reports the new figures with no indication of the previous error. The actual temperatures at these altitudes in the Equator are more in line with the ones presented here. In the same publication, Humboldt extends the maximum elevation at which wax palms grow to 4200 m. This he learned from a note written by Francisco José de Caldas, a Colombian scientist, in an annotated translation of Humboldt’s Essai sur la géographie des plantes. Here, Caldas reports having collected the wax palms in the Paramo of Guanacaxa (the old route across the central Andes, south of the Quindío Pass) (Caldas in Humboldt, 1985: note 1, p. 133). Humboldt, not knowing the true altitude of this locality, refers to it lies just below the lower limit of the snow line which he had recorded for the equator at 4900 l 90 m. In a later note in the same text, Caldas gives the altitudinal limits of the wax palm as 1500–3500 m (ibid., note 6, p. 115). Measurements in the original were given French feet and °Réaumur (1 Fr. Foot = 1.0665 Engl. feet = 0.3236 m; °Réaumur = 1.2°C).

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The next tallest trees were specimens of *Eucalyptus*, recorded by Labilladière from Tasmania, as reaching 48 m.\(^5\)

A quarter of a century after Humboldt and Bonpland’s voyage, the French geologist/agronomist/chemist Jean-Baptiste-Joseph-Dieudonné Boussingault, crossed the Central Cordillera through the Quindío Pass, collecting wax from the palms for chemical analysis.\(^6\) When arriving at the locality of ‘Las Cruces’ (alt. 2663 m, temp. 13.5°C) on the 27 of May 1827, he wrote: “From this station, the view rests on a green horizon where the gigantic wax palm (*Ceroxylon*) rises in numerous groups like white columns. From afar these parallel columns give the effect of masts of sail boats anchored in a harbor” (Boussingault, 1892–1903: IV, 154, our translation).

Hermann Karsten, a German botanist who travelled in South America between 1844–1856, played an important role in the history of the wax palms. Having discovered three species of wax palms with their inflorescences enclosed by several spathes, he described them in the new genus *Kloptstockia* — the description and illustration of *Ceroxylon* by Humboldt and Bonpland clearly showed one spathe only — (Karsten, 1856). In 1854, he visited the Quindío Pass in the company of the Colombian botanist José Jerónimo Triana. There, he found a species that differed from *Ceroxylon alpinum* not only in the generic characters but in other respects. This species he named *Kloptstockia quindiuensis* (Karsten, 1859). Thus Karsten had increased the number of species of wax palms known to four; he registered a record high elevation for the wax palms (he reported the species *Kloptstockia utilis* Karsten in the páramo of Chiles in Colombia close to the border with Ecuador at 4100 m\(^6\)\(^3\)), and made a new analysis of the wax.

One further noteworthy figure in the early development of our knowledge of the wax palms was Édouard François André. Well known throughout Europe as a gardener and landscaper, André was the editor of Linden’s journal *L’Illustration Horticole* between the years 1870–1880. He came to know the wax palms in 1874, when writing a note accompanying an illustration of a young specimen of *Ceroxylon alpinum* in the collections of Jean Jules Linden in Ghent. The plant was grown from seeds collected by Linden himself during his own expeditions to Colombia (1840–1844) (André, 1874). Between 1875–1876, André led an expedition to tropical America sponsored by the French Ministère de l’Instruction Publique, the aim of which was to “collect plants, minerals, and animals in Colombia, Ecuador, and Peru, as well as to contribute in filling the gaps that still exist in the science of those regions” (André, 1879). From this expedition André published various works, including the official report (ibid.), as well as a magnificent account with beautiful engravings of the journey that appeared in various fascicles of the popular *Le Tour du Monde* (1877–1883), and later a short paper on the wax palms (1878). He carefully reviewed the writings of Humboldt and Bonpland, and like Karsten noticed inconsistencies between what these two naturalists had described and what he had observed in the field. This led him to describe a smaller species of *Ceroxylon* found growing around the town of Salento, Quindío, as *Ceroxylon ferrugineum* (André, 1877–1883: 37, 101). *Ceroxylon ferrugineum* André, the ‘Salento wax palm’ of Bornhard (1943), is now a synonym of *Ceroxylon alpinum*.

The findings of Karsten and André began to cast doubt on the identity of the palm collected and described by Humboldt and Bonpland and a series of nomenclatural changes followed. The German botanist Herman Wendland reduced the genus *Kloptstockia* to synonymy under the

\(^5\) Bonhard (1937), correctly states that the sequoias were not then widely known by western scientists, the genus being described only in 1847, although Archibald Menzies had discovered them in 1796.

\(^6\) Boussingault was part of a French mission (later known as *The Zea mission*), hired by the Colombian scientist and politician, Francisco Antonio Zea, to create educational centers in the recently established Republic of Colombia. He was accompanied by the zoologist François Desiré Boulin, the entomologist Jacques Bourdon, the botanist Justin Marie Goudot, and the Peruvian chemist Mariano de Rivero y Usatriz (Patiño, 1965: 112–113; Díaz-Piedrahita, 1991: 57–58).

\(^6\) Gloria Galeano (pers. comm.) on a recent visit to this locality was unable to find the palms reported here. The maximum altitude she has recorded for any species of palms is 3150 m in southern Colombia for *Ceroxylon parvifrons* (Engel) Wendland and Genoma weberbaueri Dammex Burrett (Henderson et al., 1995).
COLOMBIA'S NATIONAL TREE: THE WAX PALM Ceroxylon quindiuense AND ITS RELATIVES

earlier name Ceroxylon (Wendland, 1860). Further taxonomic work clarified the confusion over the identity of the two species of Ceroxylon found in the Quindío Pass (Engel, 1865 [origin of the generic name Beethovenia, now another synonym of Ceroxylon]; Burret, 1929; Dugand, 1940, 1953; Dugand-Gnecce, 1976; Galeano-Garcés and Bernal-González, 1983). Bonnard (1937, 1943) thoroughly reviewed this nineteenth-century taxonomic controversy and the detailed traveller's accounts made then. The work by Harold E. Moore, Jr., and Anthony B. Anderson, who reviewed the relevant literature and collected both species in the field, offers a definitive solution to the puzzle (Anderson, 1976; Moore and Anderson, 1976). There are indeed two species of Ceroxylon in the Quindío Pass with various morphological differences, each growing at different altitudes. The taller of the two, Ceroxylon quindiuense, lives in lower montane wet forest at altitudes of 2000–3100 m, while the smaller one, Ceroxylon alpinum, is found in pre-montane wet forest between 1500 and 2000 m.

A RADIATION OF A VERY ANCIENT LINEAGE

The genus Ceroxylon (including Klopotockia and Beethovenia) is now known to have eleven species, although at least twice this number of names have been proposed which are either invalidly published, synonyms of previously described species, or names of uncertain applicability (Galeano, 1995; Moraes et al., 1995). The genus is closely related to Juania and Oraniopsis. Juania, has one species, J. australis (Martius) Drude ex J. D. Hooker (originally described as Ceroxylon australis Martius), from the Juan Fernández Islands, Chile, and Oraniopsis, with one species, O. appendiculata (Bailey) Dransfield, Irvine and Uhl, from NW Queensland, Australia. These three genera are in turn closely related to Ravenea (including Louvelia), with 17 species respectively, from Madagascar and the Comoro Islands (Moore, 1969; Tomlinson, 1969; Uhl, 1969; Dransfield et al., 1985; Uhl and Dransfield, 1987; Beentje, 1994).

The distribution pattern of this group of palms is not an uncommon one among plants (Smith, 1973; Thorne, 1973; Raven and Axelrod, 1974). The fragmentation of a previously broad west-gondwanan distribution following the break-up of South America and Africa in the lower Cretaceous (± 110–130 mybp), may have resulted in the separation of Ravenea/Louvelia species from Ceroxylon. Subsequently there was extinction in mainland Africa and eastern South America (Moore, 1973). On the other hand, the amphi-pacific relationship shown by Oraniopsis, Juania and Ceroxylon, suggests the existence of a more recent Antarctic migration route that existed sometime between the late Cretaceous and early Tertiary (± 65 mybp) (Thorne, 1973). Both scenarios indicate an early origin of this lineage with subsequent radiation in the Malagasy region and the Andes of South America.

“A FOREST ABOVE A FOREST”

The little we know about the biology of these palms comes from anecdotal evidence scattered in the literature and provided by naturalists who saw the palms only briefly in the field. An exception are the observations of the palms in their native habitat over an extended period by August Braun (1976). These observations relate to a population of Ceroxylon klopotockia Martius (a synonym of Ceroxylon ceriferum (Karsten) Wendland) found growing near Caracas, Venezuela, in the cloud forests of Avila at altitudes between 1650 and 2100 m. He presents information on the different stages in the life cycle of this species, which we summarize here, complemented with some observations from other sources.

Seeds from ripe fruits germinate under controlled conditions in six months, the proportion of germinating seeds highest between 8 and 13 months after sowing, and a few seeds remain dormant for up to two years.
(see also Braun, 1968). In the first year of growth, a single, undivided, photosynthetic leaf is produced (for detailed drawings of the germinated seed see Karsten, 1847: pl. 1 fig. 6, for Ceroxylon ceriferum; Mora-Osejo, 1984: fig. 5, for Ceroxylon quindiuense). From the second year onwards three leaves are produced every year. During the second year, the leaves are still undivided. In the third year, the leaves are cleft. From the fourth year onwards the leaves are pinnate, beginning with three to four pairs of pinnae and reaching the mature stage of 120 pairs of pinnae by the 15th year. During this time, the palms have invested most of their resources in radial growth of the stem, establishing the final stem diameter for the palm of about 30 cm. Ceroxylon quindiuense also takes 15 years in establishment (Francisco Sánchez, pers. comm.). Only after the 15th year does the stem of the palm start elongation. Three leaves are shed every year, each leaving a conspicuous ring on the stem. These rings may be equally spaced along the stem, but regions of shorter or longer internodal length are common. The crown generally consists of 9–18 leaves. Using the number of leaf rings to establish the age of the individuals (three rings/year + 15 years stem establishment + five years for the crown), Braun determined the minimum age of reproductive individuals to be 80 years.

All species of Ceroxylon are believed to be dioecious (Gloria Galeano, pers. comm.), although the description of Humboldt and Bonpland mentions the plants having separate inflorescences with pistillate flowers and staminate/hermaphrodite flowers on the same plant (Humboldt and Bonpland, 1805). Karsten (1856) described the plants as being dioecious, polygamo-dioecious, or monoecious, as is indeed common in various other species of palms (Andrew Henderson, pers comm.); detailed information on the breeding systems of these palms is still lacking. Braun calculated a slightly skewed sex ratio in the populations he examined of 60% staminate and 40% pistillate individuals.

The plants do not bloom every year, but when in bloom, each plant produces three to five inflorescences maturing at approximately one week intervals. Braun reported pollination to be mediated by wind, whereas Galeano and Bernal have observed melyrid beetles on the staminate inflorescences of Ceroxylon mooreanum Galeano and Bernal (Galeano and Bernal, pers. comm. in Henderson, 1986). After pollination, the fruits require 8–12 months for maturation. An individual infructescence of Ceroxylon quindiuense can produce 6000 ripe fruits, a season’s harvest of Ceroxylon alpinum fruits weighing 360 kg. (Francisco Sánchez pers. comm.; Duke, 1977). The ripened fruits of Ceroxylon ceriferum are harvested by toucans (Aulacorhynchus) who eat the pericarp and disperse the seed. Reports of other visitors to these palms, either dispersing seed or obtaining food from the solid endosperm, include squirrels (Sciurus) (Humboldt and Bonpland, 1805), caciques (Icteria), jays (Cyanocarax yncas), thrushes (Turdus furocastor), guans (Cracidae), macaws (Ara militaris), the rare yellow-eared parrot (Oghnorhynchos icterotis), spectacled bears (Tremarctus ornatus), the páramo tapir (Tapirus pinchaque), agoutis (Dasypodica fuliginosa), peccaries (Tayassu sp.), and coatis (Nasua nasua and Nasua olivacea) (Haerencia Verde, 1991; Palomino-Ortiz, 1991; Galeano-Garcés and Bernal-González, 1984; Moraes et al., 1995). Among the birds, the smaller ones (caciques) eat the pericarp from the fruit on the tree and dispose of the seed close to the mother tree, while the larger ones (toucans and guans) ingest the fruit and defecate the seeds elsewhere (Sandra Arango, pers. comm.).

There is no information on population densities and demography of the different species in their natural habitats, apart from partial data presented by Braun (1976) and an indication of the abundance of palms in forests of varying degrees of disturbance in the region of the Quindio Pass (Palomino-Ortiz, 1991).

THE WAX PALM’S FORMER GIFTS TO MANKIND

The wax produced on the trunks and leaves has been discussed at length by almost all naturalists concerned with the history of the wax palms. Their observations relate to means of collecting the wax, yields, market, uses, properties, and chemical constitution. From the review made by Patino (1976) of the pre-Linnean literature relating to the wax palms, we learn that the wax was locally used then to make torches and candles.

The nineteen-century references offer somewhat more detailed information on the wax. A drawing by
Andre shows how the wax was collected in a non-destructive way by the local inhabitants of the Quindio Pass (Figure 7). Nevertheless, the most common way of harvesting was by felling the trees. The thickness of the wax he reported as being only 0.3-0.5 mm. He gave figures of up to 12 kg of wax from each palm, and a single person was capable of collecting wax from 8-10 trees per month, so obtaining 50-60 kg of wax. The product was sold in Ibague at 2.45 Fr/kg in 1876, while the English naturalist William Purdie, who visited the region between 1843-1847, quoted the price as 1.36 pence or 0.2 reales/kg (Purdie in Seeman, 1856). The wax was used for making torches that gave abundant light and resin with a faint, agreeable odour and some smoke (Andre, 1877-1883: 37, 101).

Chemical analyses of the wax were carried out as early as 1805. The French chemist Joseph-Louis Proust commented that the wax was very similar to bee's wax and to that produced by various other plants including Myrica cerifera L., and the bloom on the fruit of Prunus (Proust in Humboldt and Bonpland, 1805). A wax sample was submitted to the chemist Nicolas-Louis Vauquelin for its analysis, who concluded that it was composed of two parts resin and one part wax, the latter being soluble in alcohol (Vauquelin in ibid.). Further details of this analysis were to be published in the Annales du Museum d'Histoire Naturelle, but they never appeared. Boussingault, working at the Escuela de Minas in Bogota in 1825, found that the constitution of the wax was quite different, and Humboldt, in a note accompanying Boussingault's paper, admits that the product he presented to Vauquelin may have included a portion of bee's wax mixed in by the people of Quindio (Boussingault, 1825). A detailed analysis of the chemical composition of the different constituents of the wax was later presented by Boussingault (1835). After collecting the wax, it was separated from impurities by mixing it in boiling water. Upon cooling, the impurities sank to the bottom, while the wax floated to the top. This wax melted at a temperature slightly higher than that of boiling water, and became strongly charged with electricity when rubbed. It was soluble in alcohol and ether. Two constituent parts could be separated by dissolving it in alcohol. After cooling, a white gelatinous mass was deposited; it had all the properties of a wax, melting at a temperature lower than that of boiling water, and containing an average of 81.4 %C, 12.3 %H, and 5.7 %O. The portion remaining soluble in the cold alcohol was a resin which became a crystalline white powder upon evaporation of the alcohol. A very bitter yellowish substance was also present in solution with the alcohol. The crystalline portion melted at a temperature higher than that of boiling water; it was soluble in hot alcohol, ether, and essential oils, and it contained an average of 83.4 %C, 11.5 %H, and 5.1 %O, corresponding to the formula C16H32O. A further portion was given the name Ceraxylon by the French chemist J. F. Bonastre (1828).

Karsten later reanalyzed the wax of Ceraxylon ceriferum; his results were similar, and he found that the bitter component which dissolved in the alcohol was chlorophyll (Karsten, 1847: fn. 1, pp. 39-40). Earlier this century, the Imperial Institute of Great Britain performed an analysis of the wax, concluding that it could be used as a substitute for carnauba wax from Copernica ceriferus Martius. Samples of the wax were presented to various companies for evaluation. Despite favourable results, the wax did not attain wide commercial use, probably due to lack of supply (Anonymous, 1917). The main industrial application of the wax was in the production of gramophone records (Willis, 1966: for further information on the wax see Poisson, 1904; Bonhard, 1945).

There appears to be no modern chemical analysis of the wax from these palms. Nevertheless, it is included with carnauba and caranday, obtained from species of Copernica from Argentina, Bolivia, and Paraguay, and caussia, from the marantaceous plant Calathea lutea (Aublet) G. Meyer, of the Amazon and other parts of tropical America respectively, as one of the finest and most useful of the vegetable waxes (Hill, 1952: 206-207; Scherry, 1952: 262-263; Markley, 1955; Hegnau, 1962: 406-407).

Apart from being a source of wax, the wax palms have been used in various other ways. The outer woody part of the stem is very durable after the removal of the soft pith and has been used locally to build houses, stables, and fences, as well as to make water pipes and channels. The long stems have also been used locally for power line and telegraph poles (Motiska

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*It is thus a saturated fatty alcohol probably equivalent to CH₃(CH₂)₉CH₂OH or any of its structural isomers; it is found also in other plants (Jack Taunton, pers. comm.).
et al., 1984; Bernal, 1989b). Humboldt and Bonpland suggested that the leaves could also be used to make hats, in the same way as the leaves of the palm Schleia butyracea (Mutis ex Linnaeus. fil.) Karsten ex Wendland were employed in the Orinoco. Also the filaments at the base of the petioles could be used as a source of fibre, like those of the areng de sucre (Arenga saccharifera Labillardière) from the Moluccas and the piassaba or chiqui-chiqui (Leopoldinia piassaba Wallace) of the Orinoco, Negro, Amazonas and Pará rivers (Humboldt and Bonpland, 1805). The unexpanded young leaves have been employed widely to make ornaments for the Christian ceremony of Palm Sunday.

WAX PALMS AS HORTICULTURAL GEMS

The wax palms have been in the horticulturists’ eyes ever since Humboldt and Bonpland discovered them and who even suggested that efforts should be made to cultivate the palm in Europe, where they thought it could easily be acclimatized (Humboldt and Bonpland, 1805). Later, naturalists such as Bussingault and André attempted to take seeds and live plants to Europe. Bussingault failed to keep his plants alive in the hot climates of the Magdalena valley (Bussingault, 1835). André, although not specifically referring to the wax palms, mentions having brought with him seeds and living plants, among which most certainly were some Ceroxylon (André, 1879). The first report of a Ceroxylon in Europe came in André’s description of Lindley’s specimen in Ghent. We have a report of a palm growing in 1888 in the Baron General Vincenzo Rocasoli’s gardens in Porto Ecole, Italy (Kyburz, 1989). Three different species of wax palms grew in Carl Schell’s garden in Brissago, Switzerland, in the 1980’s, but after a frost in the winter of 1985–1986, when the temperature dropped to −8 °C one of these died (ibid). A palm eight m tall was growing in the palm house at Kew in 1962 (Russell, 1962). The Sydney Botanic Gardens in Australia had in 1984 a specimen of Ceroxylon growing on the grounds (Fullington, 1985). Bornhard (1937) wrote a detailed analysis of the climatic conditions of various localities where the plants grew wild, and compared them with those of various localities in California and Oregon on the Pacific coast of the United States, where she suggested the palms could easily be acclimatized.

There are many reports in the American Palm Society Journal Principes of wax palms growing in California, and members of this Society have on various occasions travelled to Ecuador, Colombia and Venezuela in search of wax palms, collecting seeds and seedlings for cultivation abroad (Foster, 1974; Fullington, 1980; Motiska et al., 1984). Seeds of wax palms have also been advertised on various occasions between 1983 and 1988 in that journal with prices ranging from US$0.25–0.50 per seed (Anonymous, 1983, 1988). Among the various successful plantings in California are the individuals found in Oakland’s Bayside Bark, Ralph Velez’ garden, and what perhaps is the oldest individual growing in the USA., a palm grown from seed by Paulen Sullivan in 1967. By 1988 it had attained eight m in height (Vitkievicz, 1988; Tollefson, 1994). The most spectacular individuals are probably those currently growing ‘wild’ among the redwood forest in northern California, planted in 1978 by Garrin Fullington (Fullington, 1980; Ralph Velez, pers. comm.).

Wax palms have been widely cultivated as ornamentals in their countries of origin. In Bogotá, a large number of palms were planted in the Park of Independence in 1910, commemorating the 100th anniversary of the independence of Colombia (Dugand, 1970; Anonymous, 1971). Many specimens have been planted also in the Jardín Botánico ‘José Celestino Mutis’, whence seedlings and young individuals are constantly made available to adorn parks and public buildings. Eleven specimens were recently planted on the grounds of the Universidad Externado de Colombia to honor the judges who died during the assault on the Colombian Supreme Court in 1985 (Francisco Sánchez, pers. comm.).

Despite these rare successes in cultivation of wax palms in foreign lands, the palms are indeed very difficult to grow outside of their natural habitat.
Figure 1. "The princes of the Principes" (Bomhard, 1937: 304). Ceroxylon quindiuense on the eastern slopes of the Central Cordillera (the Quindío Pass), Tolima, Colombia. Photograph by S. Madriñán.
Figure 2. "The wax palms (Ceroxylon andicola) appear finally in all their majesty, their feet in the water, their heads in the clouds" (André, 1877-1883: 35, 222-224, pl. on p. 223).
Figure 3. "In [the] forests of beauty of mountain wilds, the Quindío hardly has rival. The groves of the wax palms are to the most sublime of all the realm of the plant world" (Thiermann, 1879; quoted by Bomhard, 1937). Photograph by S. Madriñán.
Figure 4. "The gigantic wax palm (Ceroxylon) rises in numerous group like white columns. From afar these parallel columns give the effect of masts of sail boats achored in harbor" (Boussingault, 1892–1903: IV, 154). Photograph by S. Madriñán.
Figure 5. Klopstockia quindiuensis Krst. (left) and Klopstockia cerifera Krst. (right), from a coloured folio-sized plate in Karsten's Florae Columbiae (1859: pl. I).
Figure 6. "They form forests (palmares) of columns which from afar look white like ivory, crowned by a sheaf of admirable leaves five to six meters and more in length. These forests are being diminished day by day." (André, 1877–1883: 35, 224). Photograph by S. Madriñán.
Figure 7. "[T]he only rational and honorable [method of harvesting] is to scrape the wax, while climbing the trees" (André, 1877–1883: 37, 100–101; pl. on p. 102).
Figure 8. Postage stamp issued by the Colombian postal service honoring the national tree of Colombia. Photograph by G. Romero.
They cannot stand temperatures above 20°C or below freezing, and need very high relative humidity. They grow well in containers and prefer clay soils on steep gradients (Francisco Sánchez, pers. comm.); G. Fullington's experience is that the palms should be planted in acidic and well aerated soils (1980).

**COLOMBIA'S NATIONAL TREE**

The Colombian botanist and palm expert Prof. Armando Dugand suggested as early as 1949 that the Quindío wax palm, *Ceroxylon quindiuense*, be adopted as Colombia's national tree, and he continued to press for this idea (Dugand, 1970, 1972; Anonymous, 1971). In 1986, the Colombian Congress officially named *Ceroxylon quindiuense* as Colombia's national tree. Through this legislative decree, a conduit was created in which the government can assign funds to acquire lands in the Central Andes for the creation of reserves for the preservation of the wax palms in their natural habitat. Furthermore, the decree prohibits the felling of *Ceroxylon quindiuense* (Díaz-Piedrahita, 1987). In 1990, the Colombian postal service issued a stamp honoring the Quindío wax palm (Figure 8).

**A GIGANTIC TREE IN DANGER**

Little is known about the conservation status of the various species of *Ceroxylon* throughout their distributional range. The Colombian species are fortunate exceptions, thanks to the continued work of the Colombian botanists and palm experts, Rodrigo Bernal and Gloria Galeano (Galeano-Garcés and Bernal-González, 1984; Bernal, 1989a). Of the eleven currently accepted species, seven are found in Colombian territory, and two are endemic to that country (Galeano, pers. comm.). The major threat to the wax palms has been the disturbance of their natural habitats: Stands of wax palms are very common in pastures or in coffee plantations. Palomino-Ortiz (1991) provides a table of the area covered by different populations of *Ceroxylon quindiuense* and the degree of disturbance in the Tolima and Quindío region. Although the abundance of wax palms in such man-made habitats might suggest the persistence of numerous populations, this is misleading, for outside of their natural habitat, the life cycle of the palms is negatively affected. Without the surrounding forests, the other organisms with which the palms have close ecological interactions disappear. Furthermore, the palms in these cleared forests produce large quantities of viable seeds, however, these are unable to grow to mature reproductive individuals in the disturbed habitats because humidity and light regimes have drastically been changed (Moore and Anderson, 1976; Bernal, 1989b). Seeds in these disturbed habitats either fail to germinate, or those that do, survive poorly or are eaten by cattle.

A further agent of extinction has been the continued use of these palms, ever since the appearance of written accounts of them, in the Christian ceremony of Palm Sunday. The common names given to these palms in various countries — *palma de ramo, palma bendita* — refer to this widespread use. The religious ornaments for this ceremony are made from young, undeveloped leaves of various species of palms, none of which Jesus Christ could have used. These leaves are generally harvested from young individuals, the crowns of which are easily accessible. Dissection of the apical meristem of the palms signifies their almost certain death. R. Bernal, a strong advocate of the conservation of palms in Colombia, has called upon the leaders of the Catholic Church in Colombia to change their symbol (Bernal, 1989b).

A potentially disastrous phenomenon has been recently observed in populations of *Ceroxylon quindiuense* from the area of the Quindío Pass, where the highest densities of the wax palm are found. Since 1991 the palms in forest fragments in this area have been affected by an unknown disease that causes wilting of the crown (this usually occurring after fruiting) followed by death of the tree. In some fragments assayed 80% of the palms were affected. Although the agent is still unknown, preliminary studies indicate the presence of the beetle (*Xyleborus* sp.) and a fungus (*Ceratocystis* sp.), the former probably responsible for transmitting the latter which in turn may be the cause of the disease (Palomino-Ortiz, 1991). An urgent call for research has been released to the international scientific community by the Herencia Verde Foundation, which, together with other governmental and non-governmental agencies in Colombia and abroad, are
trying to stop the spread of this deadly disease (Herencia Verde, 1994). 

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