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A revision of the Andean wax palms, *Ceroxylon* (Arecaceae)

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Abstract

The genus *Ceroxylon* is revised and twelve species are recognized. A total of 228 specimens from 19 herbaria were studied and field work was carried out in four countries. A list of 113 characters was explored in the specimens and described for each species. Additionally, leaf anatomy and pollen morphology (via Scanning Electron Microscopy, SEM) were examined for twelve and eleven species, respectively. SEM images were used to describe the surfaces of the leaf and fruit epicarp. Information on habitat, natural history, local names, uses and conservation status are incorporated after the morphological description of each species. A key for the identification of the species is provided and illustrations and distribution maps are included for all species.

Key words: leaf anatomy, morphology, pollen, wax palms

Resumen

Se hace una revisión del género *Ceroxylon*, en la cual se reconocen doce especies. Se examinó un total de 228 especímenes de 19 herbarios y se realizó trabajo de campo en cuatro países. Se exploró una lista de 113 caracteres en los especímenes y éstos se describen para cada especie. Adicionalmente, la anatomía foliar y la morfología polínica (por Microscopía Electrónica de Barrido MEB) se describen para doce y once especies, respectivamente. Imágenes por MEB son usadas para describir las superficies de la hoja y del epicarpio del fruto. Secciones que incluyen el hábitat, el conocimiento hasta la fecha sobre historia natural, nombres comunes, usos locales y finalmente el estado de conservación, se incorporan después de la descripción morfológica de cada especie. Una clave para la identificación de las especies, fotos y mapas de distribución, se incluyen para todas las especies.

Palabras clave: Palmas de cera, anatomía foliar, polen, morfología

Introduction

Ceroxyloideae Drude (1877: 632), one of the five subfamilies of Arecaceae, comprises three tribes (Dransfield *et al.* 2008): Ceroxyleae Satake (1962: 125; four genera), Cyclospatheae Cook (1902: 24; one genus), and Phytelepheae Horaninow (1847: 38; three genera). Ceroxyleae is characterized by the following suite of characters: dioecy, sheaths not forming crownshafts, peduncular bracts 3–5, and flowers scarcely dimorphic, solitary, and open before anthesis (Dransfield *et al*. 2008). It includes four genera of southern distribution: *Ceroxylon* Bonpl. ex DC. from South America, *Juania* Drude (1878: 40) from the Juan Fernández Islands, *Ravenea* Wendland ex Bouché (1878: 324) from Madagascar and the Comoro Islands, and *Oraniopsis* (Beccari) Dransfield, Irvine & Uhl (1985: 57) from Australia. Cyclospatheae, with its single genus *Pseudophoenix* H.Wendl., has a Caribbean distribution, whereas the genera of Phytelepheae, *Phytelephas* Ruiz & Pav., *Ammandra* O.F.Cook and *Aphandra* Barfod, are restricted to the lowlands of southern Central America and northwestern South America. Phytelepheae (formerly treated as a subfamily, Phytelephantoideae Drude has been revised by Barfod (1991), and Cyclospatheae by Zona (2002). Within Ceroxyleae, *Ravenea* has been revised by Beentje (1994), *Oraniopsis* by Dransfield *et al*. (1985) and *Juania* by Moore (1969). Here we present a taxonomic revision of the remaining genus, *Ceroxylon*.

Historical Survey

The subfamily Ceroxyloideae was formally erected by Uhl & Dransfield (1987), but the group dates back to Drude (1882), who recognized it at the rank of suborder as Ceroxylineae. Uhl & Dransfield recognized the subfamily primarily based on the combination of multiple peduncular inflorescence bracts, flowers never borne in triads, and a syncarpous and triovulate gynoecium. Three tribes were formerly recognized in Ceroxyloideae: Cyclospatheae O.F.Cook, Hyophorbeae Drude, and Ceroxyleae Satake, the last characterized by flowers that open early in development (Uhl & Dransfield 1987). With respect to this classification, Asmussen *et al*. (2006), using morphological and molecular data, suggested that the subfamily Phytelephantoideae should be included in Ceroxyloideae, while the tribe Hyophorbeae should be excluded and moved to subfamily Arecoideae. Hyophorbeae is now recognized as tribe Chamaedoreeae Drude (Dransfield *et al.* 2008). Phylogenetic studies by Asmussen *et al.* (2006), Trénel *et al.* (2007a, 2007b), and Baker *et al.* (2009) place *Ceroxylon* with *Ravenea* (including *Louvelia* Jumelle & H. Perrier (1912: 411)), *Juania*, and *Oraniopsis* in tribe Ceroxyleae.

The earliest record of *Ceroxylon* is that of J.C. Mutis, who, during the Real Expedición Botánica del Nuevo Reino de Granada (1783–1816), observed a wax-producing palm (Galeano 1985, Madriñán & Schultes 1995). But it was Bonpland who described the genus in 1804 (Bonpland & Humboldt 1804a, 1804b), with *Ceroxylon alpinum* Bonpl. ex DC. as the type species. A few decades later the genera *Klopstockia* H.Karst. and *Beethovenia* Engel were described, but they were later synonymized by Burret (1929). In total 36 specific epithets of *Ceroxylon* have been published.

Burret (1929) published the first and only synopsis of *Ceroxylon* to date. He accepted 17 species, and included descriptions of the new species, along with a key for identifying 11 of them. His classification was mainly based on pinna arrangement and orientation along the leaf rachis, the indumentum on the abaxial surface of the pinnae, the size of the palm (stem + crown) and the inflorescence, and the height of the corolla tube with respect to the length of the calyx lobes. One of the greatest taxonomic puzzles in the genus, the confusion of the type species, *C. alpinum*, with the parapatric *C. quindiuense* (H.Karst.) H.Wendl. was solved by Moore & Anderson (1976). The most recent taxonomic contribution has been the addition of several new species and range extensions (Galeano & Bernal 1982, 1983, Galeano 1995, Galeano *et al.* 2008).

The most recent taxonomic treatment of *Ceroxylon* was presented in the *Field guide to the palms of the Americas* (Henderson *et al.* 1995), in which the authors recognized 11 species and two subspecies, and included a brief but useful summary of field characters, geographic range and habitat of each. Most recently, Trénel *et al*. (2007a, 2007b, 2008) made significant contributions to the study of evolution in Ceroxyleae. Trénel *et al*. (2007a) provided a biogeographic hypothesis, supported by a phylogeny based on DNA sequences from three plastid and two nuclear regions. They proposed a time frame for evolution of the genus, according to which mid-Tertiary dispersal is proposed as an explanation for the distribution patterns of the subfamily Ceroxyloideae. This biogeographic scenario represents the only attempt so far to use molecular dating methods to test biogeographic hypotheses in the subfamily. The second work (Trénel *et al.* 2007b), though not yet formally published, included a partially resolved species-level phylogeny of *Ceroxylon*, based on three plastid and two nuclear regions. In this study, two species (*C. echinulatum* Galeano and *C. ventricosum* Burret) are recovered as paraphyletic assemblages, and one species (*C. parvum* Galeano) is recovered as polyphyletic involving two disjunct groups in Ecuador and Bolivia. The third paper (Trénel *et al.* 2008) provided decisive evidence in support of the hypothesis that *C. alpinum* subsp. *ecuadorense* Galeano and *C. echinulatum* form a clinal species. This conclusion is based on analysis of nuclear microsatellites, distribution of individuals over a more or less contiguous area of gene flow at the Amotape-Huancabamba pass, and a strong genetic clustering among five populations of *C. echinulatum* with one of *C. alpinum* subsp. *ecuadorense*. This finding also complements the phylogeny of the genus (Trénel *et al.* 2007b) in which *C. alpinum* subsp. *ecuadorense* is recovered as a group nested in a paraphyletic *C. echinulatum*. Trénel *et al.* (2007b) also reported that *C. quindiuense* is nested in *C. ventricosum*, based on AFLP data.

In this paper, we provide a taxonomic revision of the genus that includes complete morphological descriptions, a key, compilation of all the observations pertaining to natural history and biology of the species, and their uses, and an evaluation of the conservation status of the species.

Morphology

We collected data in the field and from 228 specimens from the following herbaria: AAU, B, BH, COL, HUA, JBSC, K, LE, LPB, MER, MERC, MO, NY, P, QCA, QCNE, SCZ, US, USM.

Roots:—The roots of *Ceroxylon* are densely packed in a subterranean root cone. Roots are branched several times, and vary in density and diameter, owing probably to opportunistic development (Tomlinson 1990). The young root axes are 0.8–1.0 cm diam., shiny cream-colored, but brown and rough with age. Stilt roots are never present, but the most superficial roots become occasionally exposed due to soil erosion on steep slopes.

Stems:—All species of *Ceroxylon* are solitary and pleonanthic, consistent with Corner's architectural model (Hallé *et al.* 1978). The stem is unarmed, covered with a layer of wax, and ranges from 3–60 m tall and 6–60 cm diameter, holding the record for the tallest free-standing palms in the world (*C. quindiuense*, Fig. 29). The leaf scars are dark and smooth. The wax layer can be thin and the stem appears green or brownish, as in *C. vogelianum* (Engel) H.Wendl. or *C. parvum* (Fig. 1a), or thick, giving the stem a silvery-white appearance (as in *C. quindiuense* and *C. ventricosum*) (Fig. 1b). Under the wax cover, the surface of the stem is usually green. Leaf scars are parallel and horizontal towards the base and become overlapping and oblique towards the apex (Fig. 1b).

FIGURE 1. Trunk color due to thickness of the layer of wax. **a)** *Ceroxylon vogelianum*; **b)** two stems of *C. quindiuense*; note oblique scars (apex of stem, right) vs. horizontal scars (middle of stem, left). Note places where the wax has peeled off, revealing the green surface of the stem.

Leaves:—The shape of the crown in mature specimens of *Ceroxylon* is a consistent diagnostic character for each species. It can be spherical, hemispherical, or funnel-shaped (Fig. 2); and can be dense, with numerous leaves (up to 30, Fig. 2c), or sparse and diffuse (as few as eight, Fig. 2b). Leaf abscission is complete, except in three species (*C. pityrophyllum* (Mart.) Mart. ex H.Wendl., *C. ceriferum* (H.Karst.) Pittier, and *C. parvum*) with 1–3 marcescent leaves. The juveniles of most species have erect leaves that form a funnel-shaped crown (Fig. 3). The leaves of the young individuals are generally larger and have more pinnae than those of adult palms. Leaves are reduplicately pinnate, as a result of the division of the leaf primordium along the abaxial folds (Dransfield *et al.* 2008). In the axil of each adult leaf there is an inflorescence bud, which is basally adnate to its subtending leaf. The leaf sheath splits adaxially and does not form a crownshaft; it has shortly fibrous margins and terminates in a gradual transition to the petiole. The petiole is woody, adaxially flat and sometimes slightly elevated at the center, and abaxially convex, with smooth but sharp margins. The rachis is adaxially flattened for ½–⅓ of its length, where it forms a hastula-like projection (Fig. 4) that can be an appressed flat appendix, a loose, but rigid triangular projection or just a short protuberance; the distal portion of the rachis is triangular in transverse section, with a sharp adaxial ridge, and slightly rounded abaxially. The rachis may be straight or arched, and sometimes is twisted 90 degrees near apex, and then the apical pinnae are held in a vertical position, a character that can be used to recognize some species.
The pinnae are linear, usually with oblique apices and equilateral bases; in *C. parvifrons* (Engel) H.Wendl. and *C. ceriferum* they are closely folded, especially near the base. Depending on the species, the pinnae are either regularly distributed or in groups, and inserted in one or several planes (Fig. 5). When the pinnae are regularly arranged in one plane, they can be completely pendulous, or horizontally spreading, or erect. Pinnae arrangement and angle of insertion are rather constant characters within species; when the pinnae spread in one plane the abaxial angle formed between the pinnae of either side is characteristic. When the pinnae are grouped, the distance between the groups may vary along the rachis, with groups closer at the leaf base and tip and more distant at the middle. Grouped pinnae may be oriented in highly or slightly divergent planes, but the proximal pinna of each group is always ascendant and forms an acute angle with respect to the rachis, resulting in a superposition of the proximal pinna over the rest of the pinnae of the group. Pinnae may be stiff all along their length or slightly bent downwards at the middle or beyond. Sometimes, the 5–7 apical pinnae appear united along their margins, but this varies within species.

FIGURE 2. Characteristic shape of crown in different species. **a)** Funnelled, with erect leaves (*Ceroxylon parvifrons);* **b)** Funnelled to unordered (*C. vogelianum*); **c)** Hemispherical (*C. sasaimae*).

FIGURE 3. Crown shapes at different developmental stages. Palm at left, juvenile, with erect leaves in a funnel-shaped crown; palms at right, adults, with spreading leaves forming hemispheric crowns, in *Ceroxylon quindiuense*. Photo: K. Mejía.

FIGURE 4. Leaf hastula-like projection in *Ceroxylon*. **a)** *C. echinulatum*; **b)** *C. peruvianum*. Photos: Jean-Christophe Pintaud.

FIGURE 5. Arrangement of pinnae. **a)** Regularly arranged pinnae, oriented in one plane (*Ceroxylon echinulatum*); **b)** Irregularly arranged pinnae, oriented in several planes (*C. vogelianum*).

Inflorescences:—Inflorescences are interfoliar, unisexual, solitary, and usually several inflorescences develop more or less simultaneously; staminate inflorescences are hanging at anthesis; pistillate inflorescences are erect when immature and pendulous at maturity. The inflorescences are panicles, branched usually up to third order, and consist of a peduncle, a prophyll, several peduncular bracts, and a rachis that bears numerous first-order branches. The prophyll is bicarinate and closed adaxially for 3–8 cm; there are (4–)6–7 leathery peduncular bracts, arranged in ½ phyllotaxy, increasing in size distally, except for the last one, which is considerably smaller. Each inflorescence branch is subtended by a membranaceous and tightly appressed bract; the rachillae are markedly sinuous or zig-zag. The pistillate inflorescences are larger and stouter than the staminate ones, have stiffer branches inserted on the rachis at a broader angle, and remain erect during a longer period of time (Fig. 6a). Staminate inflorescences are usually smaller, and the branches are drooping, forming a very acute angle with the rachis (Fig. 6b–c). Both pistillate and staminate inflorescences are white to cream-colored during anthesis, but pistillate inflorescences turn green as fruits ripen, while the staminate turn yellow and finally wilt.

The peduncle, prophyll, and bracts are always covered by a thick layer of fibrous scales that consist of a small (0.1–0.2 mm) base, and a degraded limb that interlocks with the adjacent scales, thus forming a cream to brownish mesh (white, in *C. echinulatum*). The rachis is glabrescent in all the species except *C. alpinum*, in which the indumentum of the peduncle continue along the rachis.

Flowers:— Flowers are unisexual and solitary throughout the rachillae, pedicellate, subtended by a minute, triangular bract, and arranged in ½–⅓ phyllotaxy. Flowers are open from very early in development, probably due to the pressure of the developing stamens and staminodes and the rapidly expanding apical dome (Uhl & Moore 1980). This character is one of the most important synapomorphies for tribes Ceroxyleae and Phytelepheae. Flowers are 3.5–9.0 mm long and only dimorphic in their sexual organs. The tripartite calyx is briefly connate with triangular lobes; the corolla is tripartite, connate to varying degrees and has

linear, elliptical or ovate lobes ending in a well-defined acumen. Occasionally some flowers appear with 4–5 sepals and/or 4–5 petals (observed in *C. quindiuense, C. echinulatum,* and *C. ceriferum*; see Fig. 7i); the androecium in both staminate and pistillate flowers is 6–19 parted depending on the species. Staminate flowers have 1–2(–3) episepalous and 1–4(–5) epipetalous stamens (Uhl & Moore 1980), with 1.5–2.0 mm long filaments, sometimes broadened at the base (Fig. 17), and dorsifixed, versatile anthers with the connective not extended (except in *C. alpinum*); in some species the stamens exceed the height of the corolla; the gynoecium is minute, trifid. The pistillate flowers have fully developed staminodes, usually with sagittate anthers and morphologically similar to functional stamens, but with abortive pollen; the number of staminodes corresponds to the number of stamens in each species; the gynoecium is syncarpous, trilocular, triovulate, but usually two ovules abort; the stigmas are apical and recurved at anthesis, and become basal during fruit development. The ovules are pendulous and hemianatropous (Dransfield *et al.* 2008).

FIGURE 6. Inflorescences of *Ceroxylon*. **a)** Pistillate inflorescence (*C. ceriferum*); **b)** staminate inflorescence (*C. ceriferum*); **c)** staminate inflorescence (*C. vogelianum*).

Fruits:—The fruit is globose, 1-seeded or occasionally 2-seeded, red to orange-red at maturity, with a smooth or ornamented epicarp, a fleshy, yellowish mesocarp and a thin endocarp. The seeds are globose, brown, with a basal hilum and a conspicuously branching raphe; the endosperm is homogeneous and the embryo is basal.

The fruit epicarp was studied in detail, as it is a useful taxonomic character to recognize species (Figs. 8–9). The fruits of twelve species were photographed under a dissecting scope, and of these, four were also studied under SEM (Fig. 16). The epicarp is smooth in two species (*C. sasaimae* Galeano, *C. parvifrons*), minutely warted in four species (*C. amazonicum* Galeano, *C. quindiuense, C. ventricosum, C. ceriferum*), echinate to densely tuberculate in two species (*C. peruvianum* Galeano, Sanín & K.Mejía, *C. echinulatum*), scarcely warted in two species (*C. parvum, C. pityrophyllum*), warted due to the projection of lenticels in one species (*C. alpinum*), and reticulate sulcate in one species (*C. vogelianum*).

Germination and Seedling:—Germination and seedlings of *Ceroxylon* have been described by Henderson & Stevenson (2006). Germination is adjacent-ligular. The eophyll is entire, plicate along the veins and covered with a wooly indumentum along both sides of the midribs and veins, and on the abaxial surface of the lamina (Fig. 10).

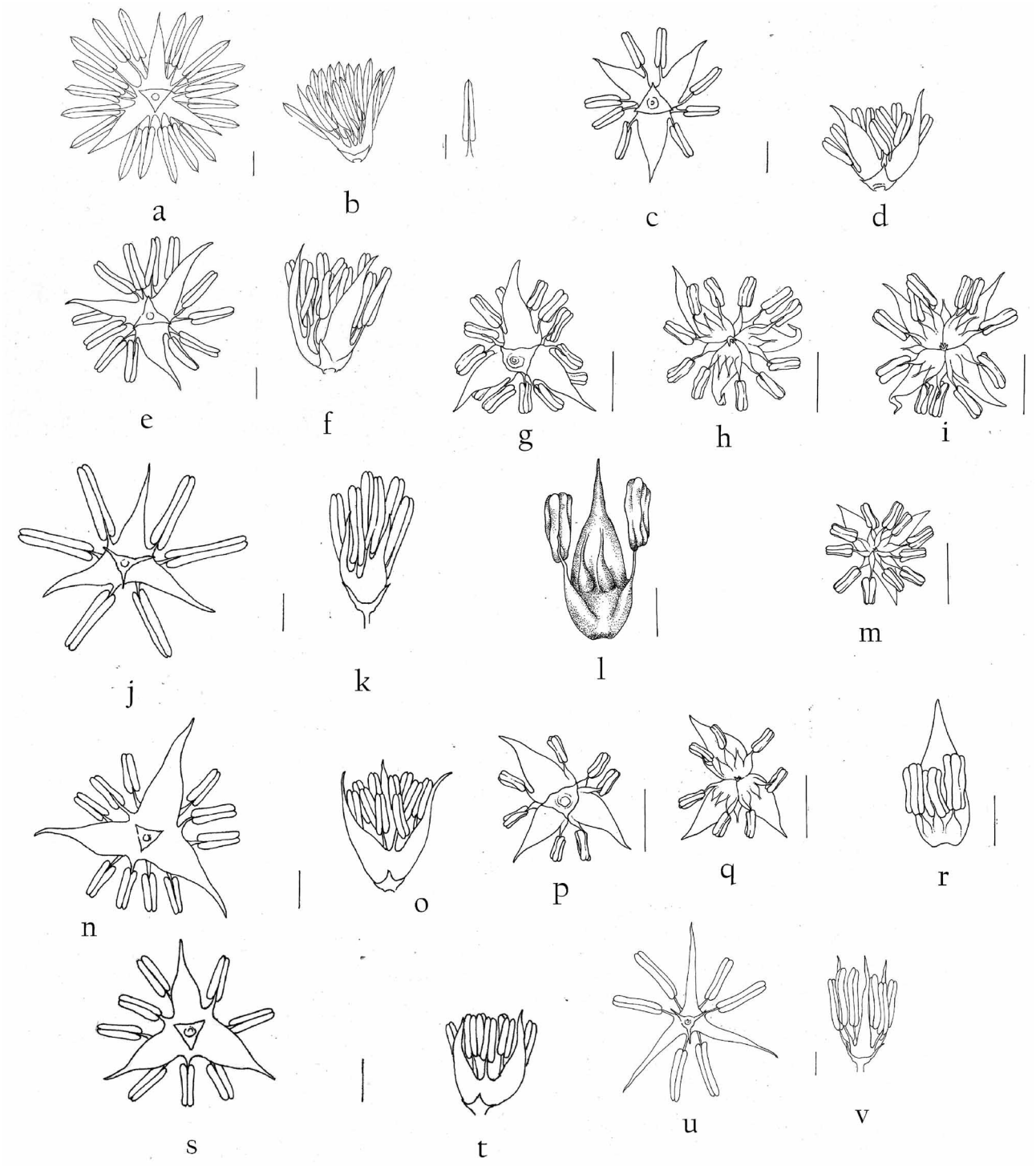

FIGURE 7. Variation in flower morphology in *Ceroxylon*. **a)** *C. alpinum*, bottom view; **b)** *C. alpinum*, lateral view, and detail of a stamen; **c)** *C. ceriferum*, bottom view; **d)** *C. ceriferum*, lateral view; **e)** *C. amazonicum*, bottom view; **f)** *C. amazonicum*, lateral view; **g)** *C. quindiuense*, bottom view; **h)** *C. quindiuense*, top view (Peru); **i)** *C. quindiuense*, top view of a flower with 4 petals; **j)** *C. pityrophyllum*, bottom view; **k)** *C. pityrophyllum*, lateral view; **l)** *C. quindiuense*, detail of a petal; **m)** *C. quindiuense*, top view (Colombia); **n)** *C. echinulatum*, bottom view; **o)** *C. echinulatum*, lateral view; **p)** *C. peruvianum*, bottom view; **q)** *C. peruvianum*, top view; **r)** *C. peruvianum*, detail of a petal; **s)** *C. parvifrons*, bottom view; **t)** *C. parvifrons*, lateral view; **u)** *C. vogelianum*, bottom view; **v)** *C. vogelianum*, lateral view. Illustrations by Eduard Martínez. Scale: bar = 1mm in **v**; bar = 2 mm in **a)**, **b)**, **d)**, **f)**, **k)**, **l)**, **o)**, **r)**, and **t)**; bar = 5 mm in **g), h)**, **i)**, **m)**, **p),** and **q)**.

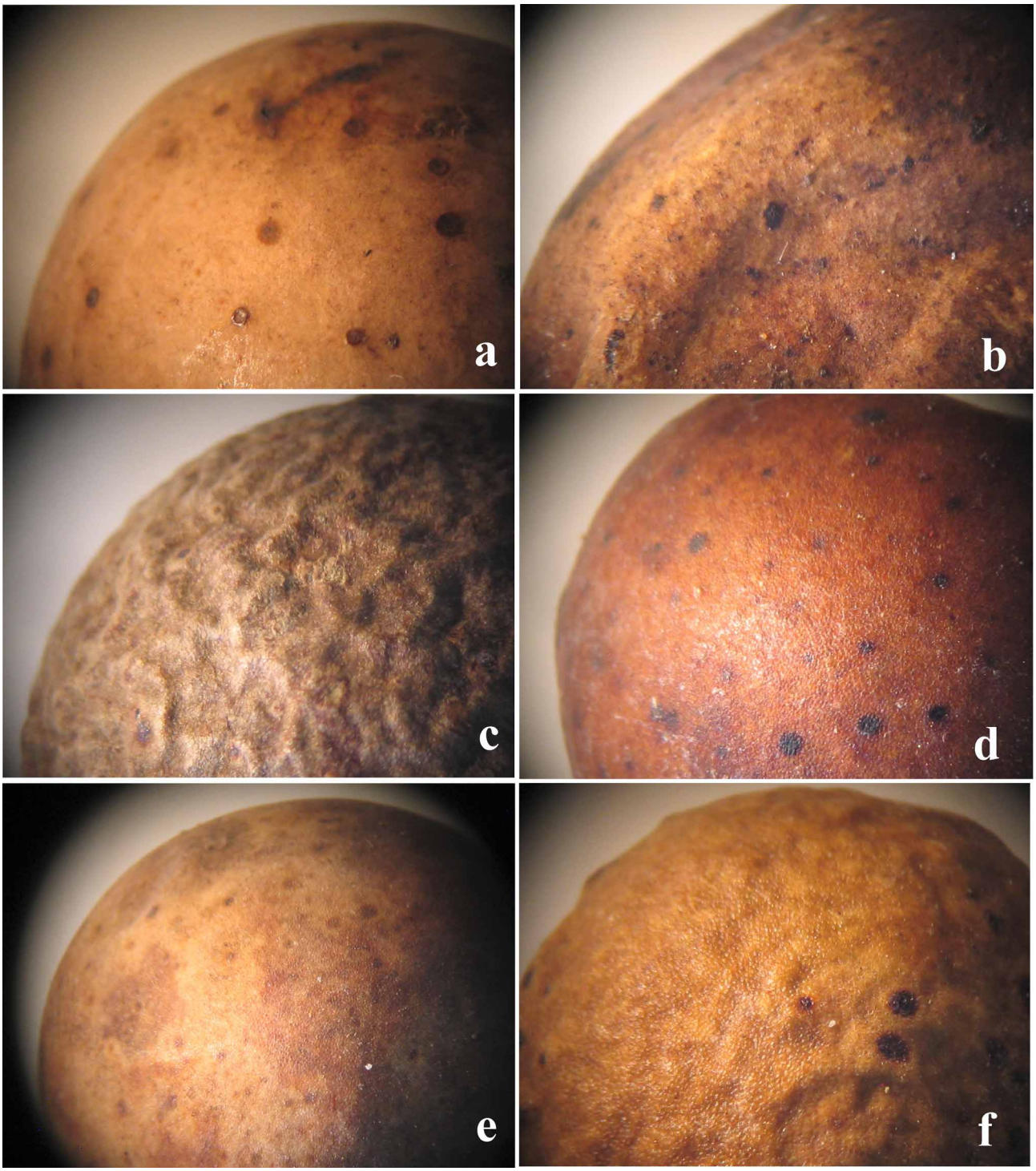

FIGURE 8. Fruit surface in species of *Ceroxylon*. **a)** smooth (*C. sasaimae, Galeano & Bernal 686*); **b)** smooth (*C. parvifrons, Duque 702*); **c)** minutely warted (*C. amazonicum, Balslev 62538*); **d)** minutely warted (*C. quindiuense, Bernal & Galeano 53*); **e)** minutely warted (*C. ventricosum, Balslev 62542*); **f)** minutely warted (*C. ceriferum, Wessels-Boer 2442*).

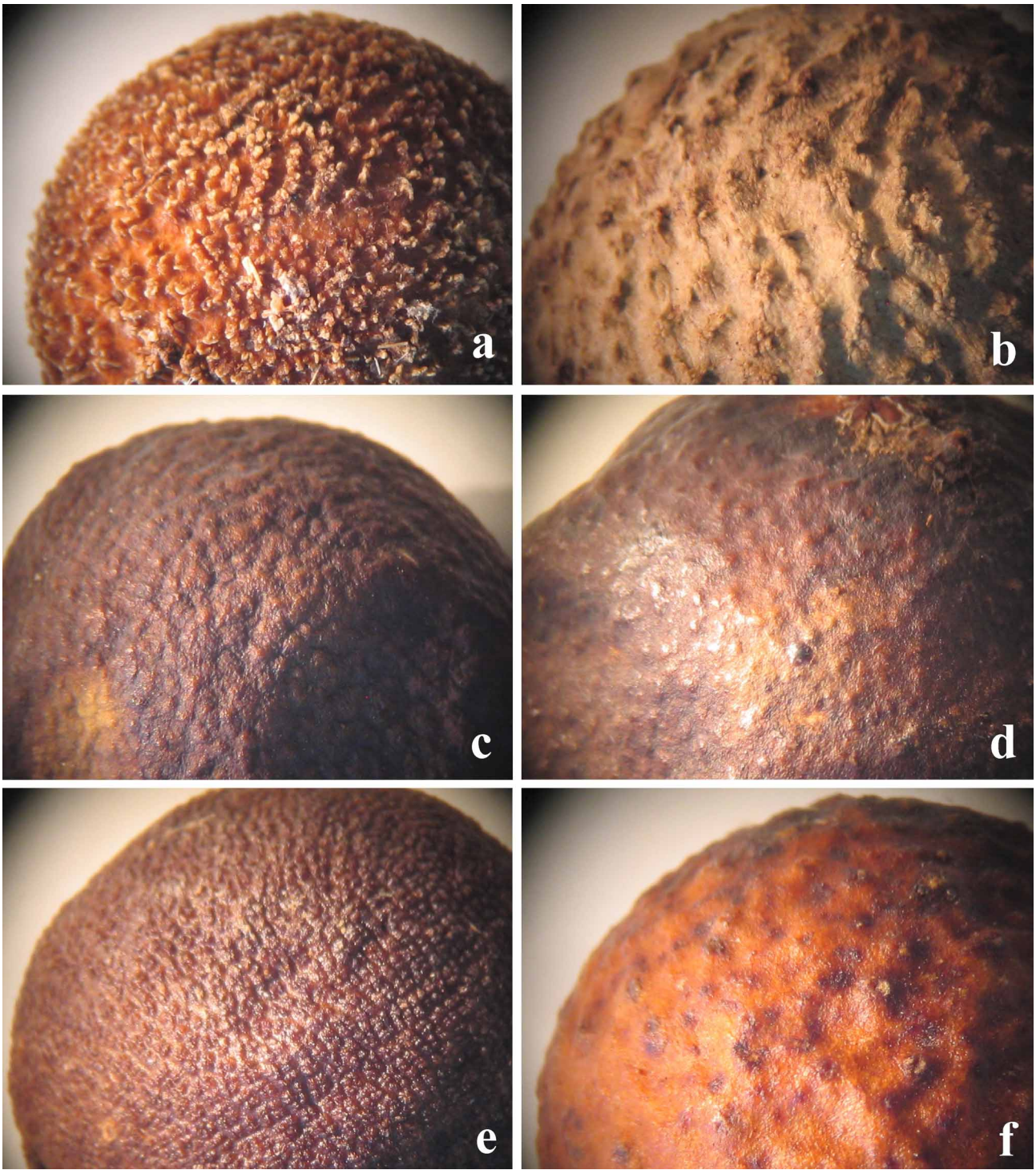

FIGURE 9. Fruit surface in species of *Ceroxylon*. **a)** echinate to densely tuberculate (*C. echinulatum, Dodson 14843*); **b)** echinate to densely tuberculate (*C. peruvianum, Millán 1488*); **c)** irregular, scattered warts (*C. parvum, Balslev 62529*); **d)** irregular, scattered warts (*C. pityrophyllum, Nee & Vargas 38268*); **e)** reticulate sulcate (*C. vogelianum, Smith 8202);* **f)** warted due to the projection of lenticels (*C. alpinum, Wessels-Boer 2447*).

FIGURE 10. Seedlings of *Ceroxylon*. **a)** Entire eophyll; **b)** many growing in cultivation in Sasaima, Cundinamarca (Colombia; *C. sasaimae*).

Indumentum:—The stem in *Ceroxylon* is covered by a layer of wax secreted by the epidermal cells; this wax can be scraped off without affecting the stem. According to Webster (1913), the wax of *C. alpinum* (as *C. andicola*) consists of two thirds resin and one third wax. The leaves bear waxy scales, that are variable in size and shape and that adhere to the epidermis through a thick, sclerenchymatic base (Fig. 11). The leaf scales are elliptical to linear, with darker and thicker bases (compared to the scale limb), and they are arranged in rows along the veins. The sheath, petiole, rachis, and midribs are covered with a lepidote indumentum on both the adaxial and the abaxial surfaces; however the adaxial scales are usually early deciduous, especially those of midrib, and rachis. The pinnae are only covered by scales on the abaxial surface. The scales of the sheath and petiole are adpressed, elliptical to oblong, 0.7–7.0 × 0.3–1.0 mm, mid-fixed to the surface through an elliptical, yellowish to brownish, 0.3–0.6 mm long base, and bordered by a fibrous to floccose margin. The sheath of *C. amazonicum* bears scales with irregularly-shaped rather than elliptical bases. The limbs of these scales often disintegrate partially with age, leaving behind the persistent bases. The indumentum of the rachis is much like that of the sheath and petiole, but the scales are usually arranged in narrow rows of 0.3–0.5 mm, and are also deciduous on the adaxial surface, usually more so towards the base. The midribs are covered by distinct, linear, thin, fragile, 0.6–9.0 mm, translucent, white, cream coloured to yellowish or brownish scales, mostly arranged in single rows, easily detached by scraping, with 0.3–0.4 mm wide bases and shortly fibrous margins. The abaxial surface of the pinnae is covered by elliptical, white, cream, yellowish, greyish or ferrugineous scales, that have either 0.1–0.3 mm wide bases (e. g., *C. vogelianum*), or very conspicuous, thick, waxy, 0.4–0.8 mm wide bases (e. g., *C. echinulatum*) that adhere tightly to the leaf surface. The margin of these scales is usually shortly fibrilous to floccose, and the texture is thin, smooth (e. g., *C. parvifrons*), or soft, and padded (*C. quindiuense*). Scales are arranged along leaf veins, in parallel rows 0.1–0.3 mm wide that

can be closely adjacent, overlapping, or not touching and exposing the leaf epidermis in between. The indumentum is conspicuous in young organs but is early deciduous. The most important characters of the indumentum are shape and size of the scale base, and size, texture and arrangement of the scales.

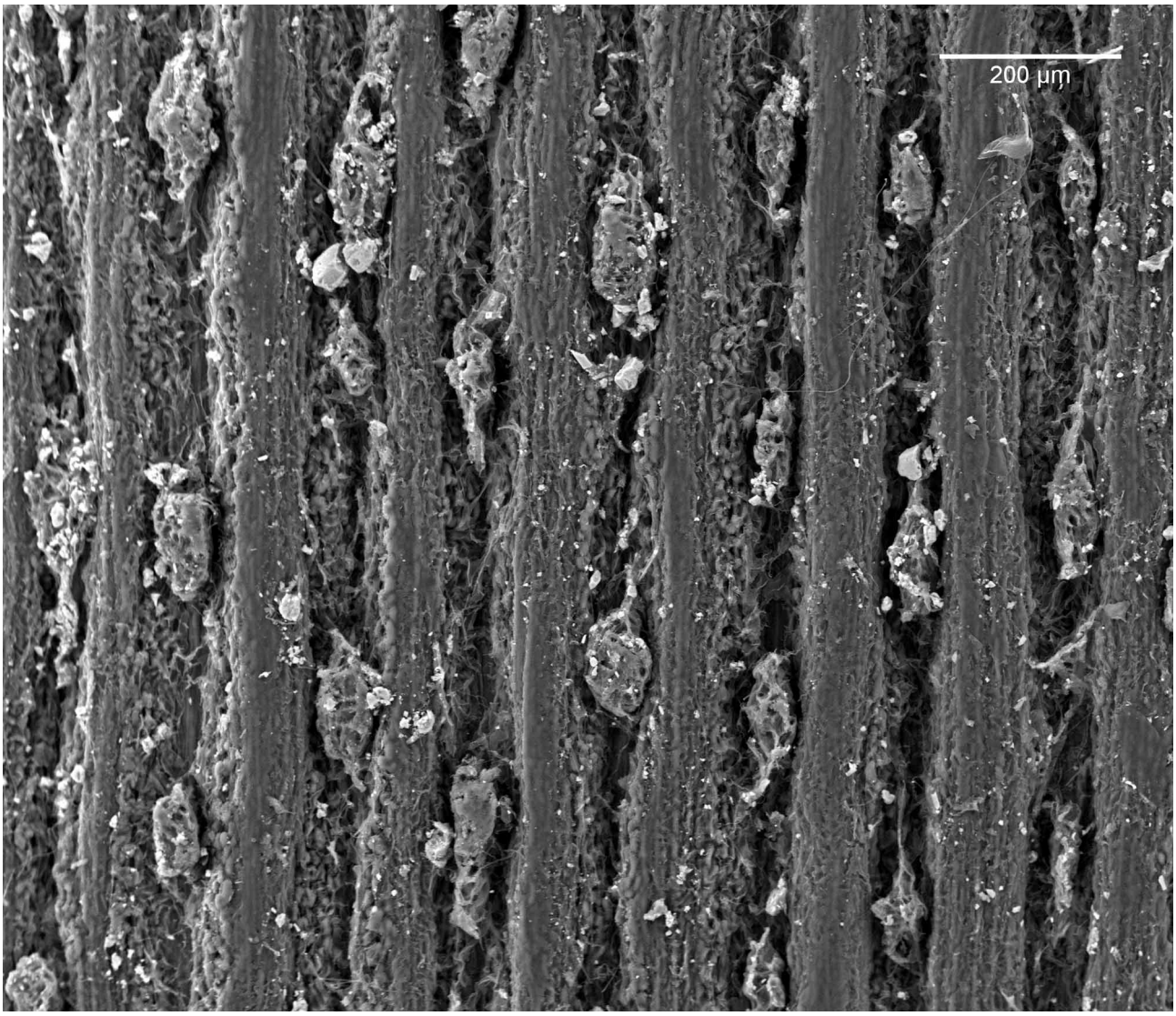

FIGURE 11. SEM image of indumentum on the abaxial surface of the pinnae in *Ceroxylon echinulatum* (*Balslev et al. 62089*).

Anatomy

Leaves:—Tomlinson (1961) described the foliar anatomy of *Ceroxylon* as unique among palms for its finely ribbed lamina and the structure of the upper and lower epidermis. He included a detailed analysis of the indumentum (scales), epidermis, stomata, hypodermis, chlorenchyma, fibres, veins, midrib, comissures and expansion cells, based on observations of only one species (*C. alpinum*, as *C. andicola*).

For the current revision, transverse sections (TS) of the middle portion of central pinnae were examined in each of the twelve species of the genus (Fig. 12). In four species SEM images of the abaxial surface of the pinnae were prepared to observe stomata (Fig. 13). The leaf sections were prepared in accordance with the protocol of Martens & Uhl (1980). Prior to sectioning, all material was softened in a glycerine-alcohol solution (50%–50%) for 45 days. For observations of the surface of pinnae, sections of dried material were coated with an Au/Pd solution.

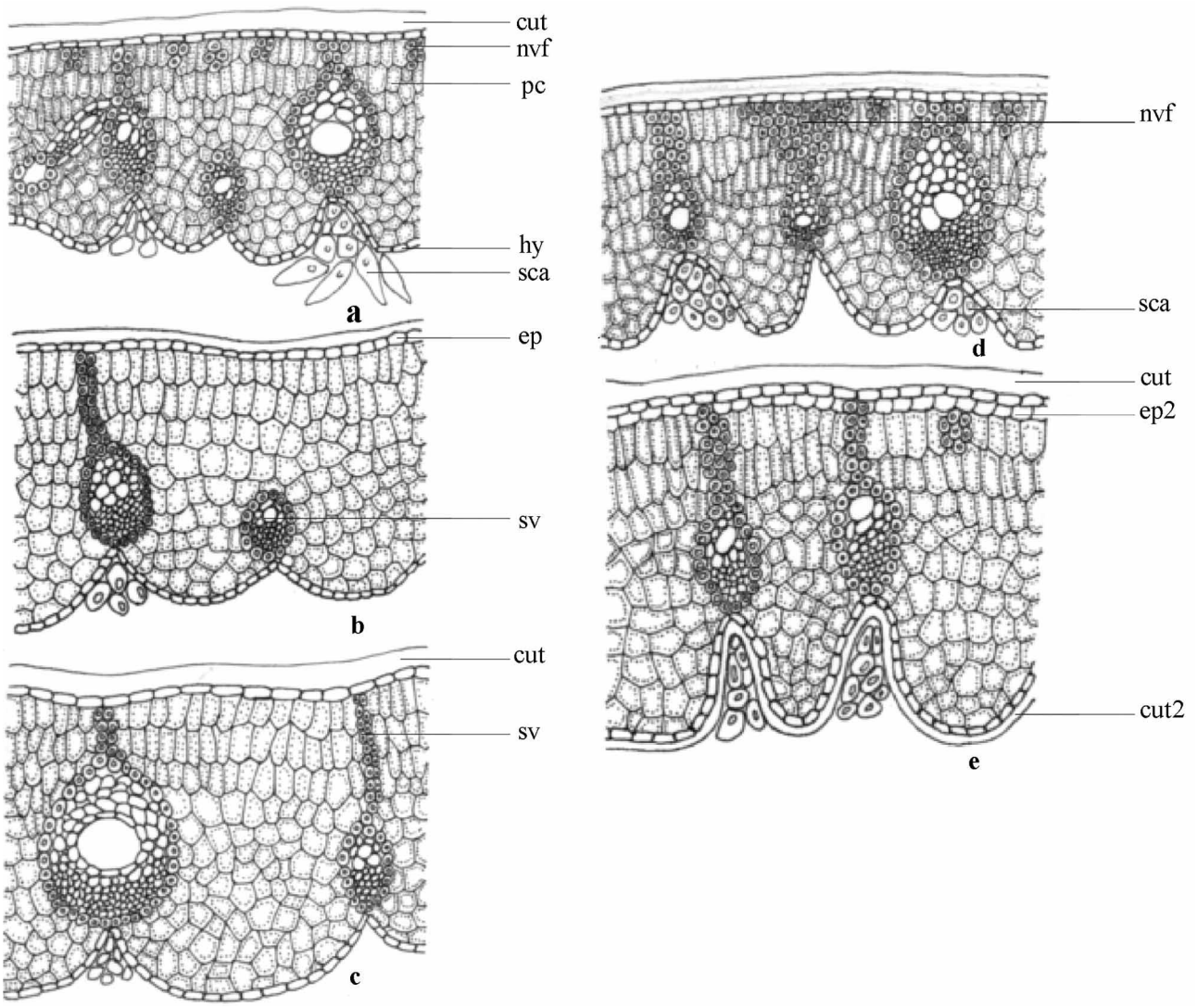

FIGURE 12. Leaf Anatomy. Cut = cuticle, cut2 = abaxial cuticle, ep = one-layered epidermis, ep2 = 2 layered epidermis, sca = scale, nvf = non vascular fiber, pc = palisade cells, hy = hypodermis, sv = secondary vein and associated fibres. **a)** *Ceroxylon amazonicum* (*Balslev 62538)*; **b)** *C. echinulatum* (*Balslev et al.62512*); **c)** *C. parvum* (*Balslev 62529*); **d)** *C. quindiuense (Fairchild* 53); **e)** *C. vogelianum* (*Bernal 1372*).

The thickness of the adaxial cuticle is variable among the species (Fig. 12). An abaxial cuticle was only observed in one species, *C. vogelianum* (Fig. 12e), and it was thinner than the adaxial cuticle on the same TS. Among the Ceroxyleae, *Ravenea* also has an abaxial cuticle. The epidermis is composed of rectangular cells that are thickened on the external side; it is sometimes two-layered, but this can vary even in the same TS. The hypodermis resembles the epidermis morphologically, but is always one-layered. The stomata are very similar among species, and are scattered in the exposed spaces between the rows of scales (Fig. 13). The subsidiary cells overlap the guard cells, which are sunken (Tomlinson 1961; Tomlinson *et al.* 2011). The scales are attached through sclerenchyma to the hypodermis above the fibrous sheath of the vein, so scales are always adhered along veins (Fig. 11). The row of sclerenchyma then opens to a thin layer of waxy, dead parenchyma which constitutes the limb of the scale. The fibres are scattered in bundles adjacent to the epidermis, or on the ridge in between veins, and in massive (*C. quindiuense,* Fig. 12d) to thin (*C. parvum,* Fig. 12c) lamellae that run from the vein sheath to the epidermis. The secondary veins are always attached in this way to the epidermis, but the tertiary or smaller veins can be connected or, as in some species (*C. echinulatum, C. amazonicum, C. ventricosum,* Fig. 12b) free from the epidermis, with layers of intervening mesophyll cells. The fibrous sheaths always have a point of contact with the hypodermis, and it is at this point that the scales are attached. The palisade cells are slightly elongated in TS but still clearly differentiated from the rest of the

mesophyll. Tannins are visible in mesophyll cells and in the parenchyma within the vascular bundles. The midribs are stiff due to the massive cylinder of sclerenchyma surrounding the vascular bundle (Fig. 12a–e). Expansion cells are located abaxially on each side of the midrib, with a thick row of sclerenchyma below.

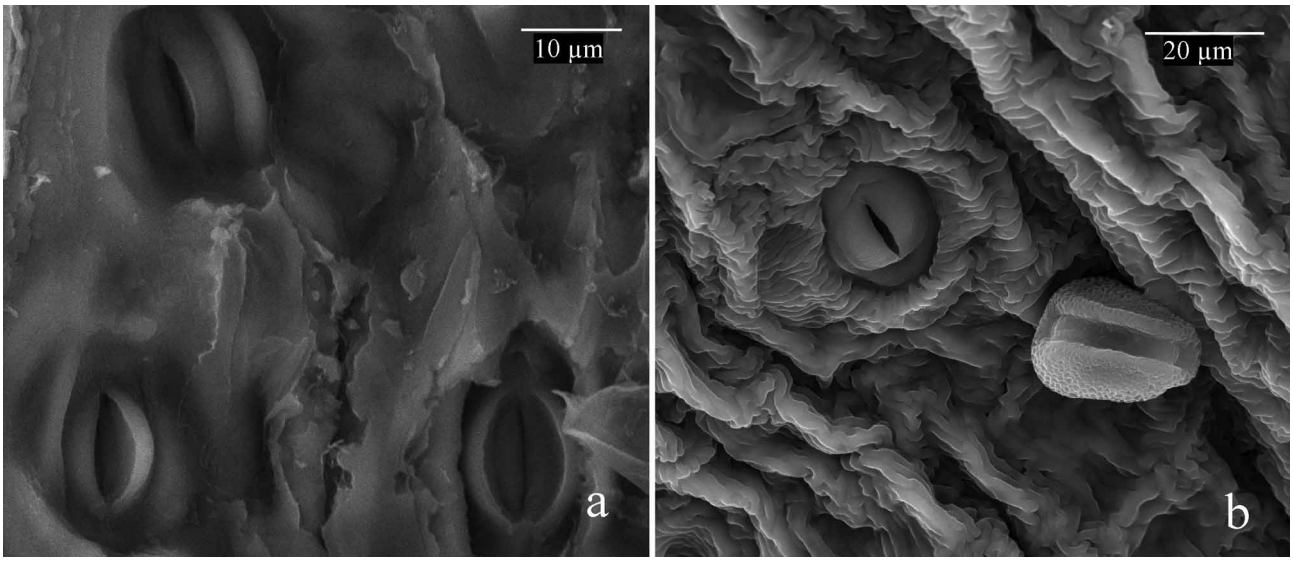

FIGURE 13. Leaf surface in species of *Ceroxylon*. **a)** stomata arranged in an unorderly manner, 4000 (*C. ceriferum*, *Wessels-Boer 2432*); **b)** stoma on petal (*C. ceriferum*, *Wessels-Boer 2443*).

Flowers:—Floral anatomy of *Ceroxylon* was studied by Uhl (1969, 1988), and by Uhl & Moore (1980). Staminate flowers have up to 7 to 9 vascular trunk bundles entering the floral axis, none of which supply the sepals. The bundles divide and vascularize the petals, the androecium and the gynoecium. Both the petal and stamen bundles are surrounded by a sheath of fibres like the leaf veins; anthers have a 4-layered endothecium. With regard to polyandry, Uhl & Moore (1980) concluded that the increase in number of stamens (6 to 19) occurs first in the position opposite to the petals, and then opposite to the sepals, which is related to the greater number of veins supplying the petals in *Ceroxylon*. Pistillate flowers have poorly vascularized sepals (0–5 bundles) and petals with more vascular and fibrous bundles (3–5 first order and several second order), as described by Uhl & Moore (1980). The flowers of *Ceroxylon*, *Ravenea* and *Juania* differ histologically in the following: *Ceroxylon* has raphide containing idioblasts and fibrous bundles; *Ravenea* lacks idioblastic substances; and *Juania* has tannin-rich cells and raphide idioblasts in the petals and in the walls of the gynoecium locules. The ovules are hemi-anatropous to anatropous, with a two-layered integument; the carpel margins are free in *Ceroxylon* and *Ravenea* and the three genera have conduplicately folded carpels (Uhl 1969). Uhl (1969) considered that the gynoecium of *Ceroxylon* is the least specialized among the three mentioned genera, due to a lesser degree of carpel fusion, and the almost anatropous ovules.

Palynology

Pollen grains from herbarium specimens were treated according to the protocol of Ferguson *et al.* (1988): all the samples were coated with Au/Pd (8:2) in a sputter SDC–050 (Balzers Brand) under pre-vaccuum conditions (<10–1 torr). Images were taken with a FEI QUANTA 200 Scanning Electron Microscope set at 30.0 KV, and at 50×, 2000×, 4000×, 8000×. Measurements were performed with the ImageJ (Rasband 2011: http://rsbweb.nih.gov/ij/) software package. Three grains and ten replicates were measured for each species.

Pollen types:—The pollen of Ceroxyloideae has received much attention (Sowunmi 1972, Thanikaimoni 1970a, 1970b, Ferguson *et al.* 1988, Barfod 1988, Dransfield *et al.* 2008). Within the tribe, pollen of *Ravenea* was studied by Ferguson *et al.* (1988), pollen of *Oraniopsis* and *Juania* was described in Uhl & Dransfield (1987), Dransfield *et al.* (2008), Thanikaimoni (1970a, 1970b), and later discussed by Ferguson & Harley

(1993). Pollen of *Ceroxylon* was first studied by Thanikaimoni (1970a, 1970b; *C. quindiuense*), then by Dransfield *et al.* (2008; *C. alpinum, C. quindiuense, C. vogelianum*). This is the first revision of pollen morphology that includes all of the species in the genus except one, *C. parvum*, for which staminate flowers were not available.

Ceroxylon pollen varies in shape, aperture and exine ornamentation (Figs. 14–15). The size of the pollen of all of the species falls in the range of 20–35 μ, which is small to medium sized according to Walker & Doyle's (1975) scale of palm pollen sizes. The exine is semitectate, reticulate (with differences in the size of the lumina or in the configuration of the muri), and the ambit is elliptical, globular, or asymmetric, or one of these in mixed condition with triangular ambit; the aperture is monosulcate, or trichotomosulcate (always as a mixed condition with monosulcate; *C. quindiuense*, *C. ventricosum*, *C. echinulatum*; Fig 15a–d). The trichotomosulcate aperture is considered to be derived from the symmetric monosulcate type, which is considered basal in monocots (Penet *et al.* 2004), and is widely distributed in Ceroxyloideae and Arecoideae. The associated ambits are the oldest in the fossil record, found from the Gallic Epoch (Early Cretaceous, 131–97 Ma; Harley & Baker 2001). In Ceroxyloideae, *Pseudophoenix sargentii* H.Wendl. ex Sargent also has both trichotomosulcate and monosulcate apertures (Machado 2003).

Even though pollen characters were not very divergent, some variation could be observed that is summarized here:

a) Ambit globular (in mixed condition with triangular), monosulcate and trichotomosulcate apertures, reticulate exine: *C. pityrophyllum.*
b) Ambit globular, monosulcate, and exine incomplete reticulate to gemmate reticulate: *C. vogelianum*.
c) Ambit irregular, monosulcate, exine reticulate, lumina narrow: *C. parvifrons,C. peruvianum, C. amazonicum, C. sasaimae*.
d) Ambit elliptical (boat-shaped), monosulcate or occasionally including triangular ambit and tricotomosulcate aperture, reticulate, lumina wide: *C. alpinum*, *C. quindiuense, C. ventricosum, C. ceriferum, C. echinulatum*.

Measurements supporting these differences are provided in Table 1, and SEM images of ten of the twelve species are provided in Figs. 14–15 (the pollen of *C. amazonicum* is not shown due to its similarity to that of *C. parvifrons*; pollen of *C. parvum* was not available) .

TABLE 1. Pollen grain measurements (in μm) for 11 species of *Ceroxylon.*

Species	Ambit	Size (μm) *	Exine sculpturing	Exine breadth (μm)
C. alpinum	Elliptical	29.6 1.8/ 17.7 0.2	Reticulate	0.6 0.4
C. amazonicum	Irregular-Globose	20.9 3.6	Reticulate	0.5 0.3
C. ceriferum	Elliptical		Reticulate	1.4 0.5
C. echinulatum	Elliptical -Triangular	32.9 0.8 / 20.1 0.5 – 20.7 1.0 / 21.0 0.9	Reticulate	1.6 0.7
C. parvifrons	Irregular-Globose	21.3 1.6	Reticulate	0.5 1.0
C. parvum	-	-	-	-
C. peruvianum	Irregular-globose	22.4 3.0	Reticulate	0.7 0.3
C. pityrophyllum	Globose	27.2 1.3	Reticulate	2.9 1.3
C. quindiuense	Elliptical -Triangular	33.9 1.0 / 19.1 0.4 – 21.7 0.6 / 21.1 0.9	Reticulate	1.2 0.4
C. sasaimae	Irregular-Globose	20.9 2.0	Reticulate	0.5 0.8
C. ventricosum	Triangular	29.5 1.0/ 20.5 0.6	Reticulate	1.0 0.2
C. vogelianum	Globose	24.9 1.6	Incomplete-reticulate	(open)

* When one measurement is provided = diameter (globular pollen); when two measurements are provided = longer axis/ shorter axis (elliptical); when four measurements are provided long axis/ shorter axis – side/height (elliptical-triangular ambits as a mixed condition).

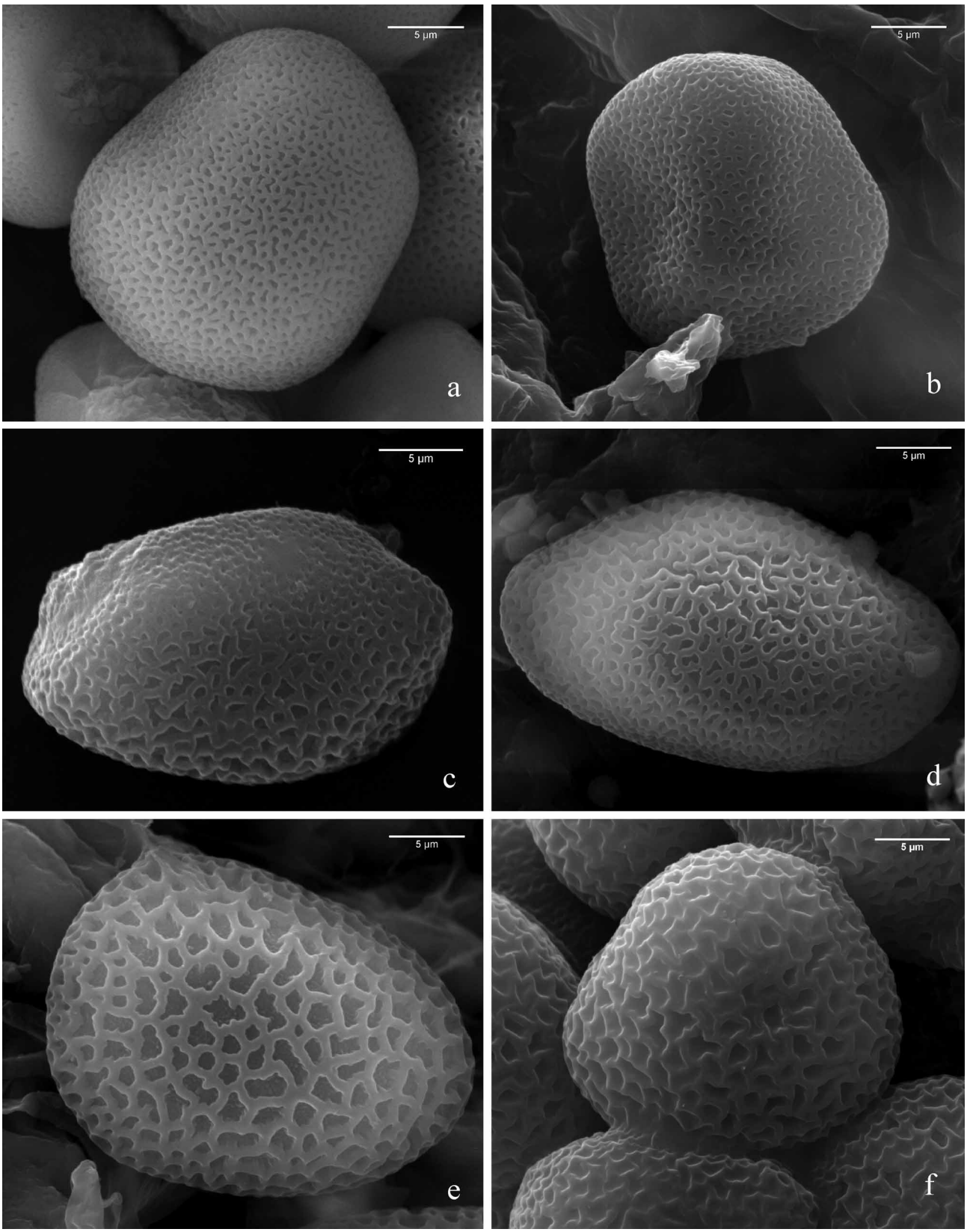

FIGURE 14. SEM images of pollen morphology in *Ceroxylon* (8000). **a)** *C. parvifrons* (*Bernal & Galeano 1424*); **b)** *C. sasaimae* (*Galeano et al. 7513*) ; **c)** *C. peruvianum* (*Millán et al. 1498*); **d)** C. *alpinum* (*Wessels-Boer 2448*); **e)** *C. ventricosum* (*Cuatrecasas 11576*)*;* **f)** *C. ceriferum* (*Wessels-Boer 2443*).

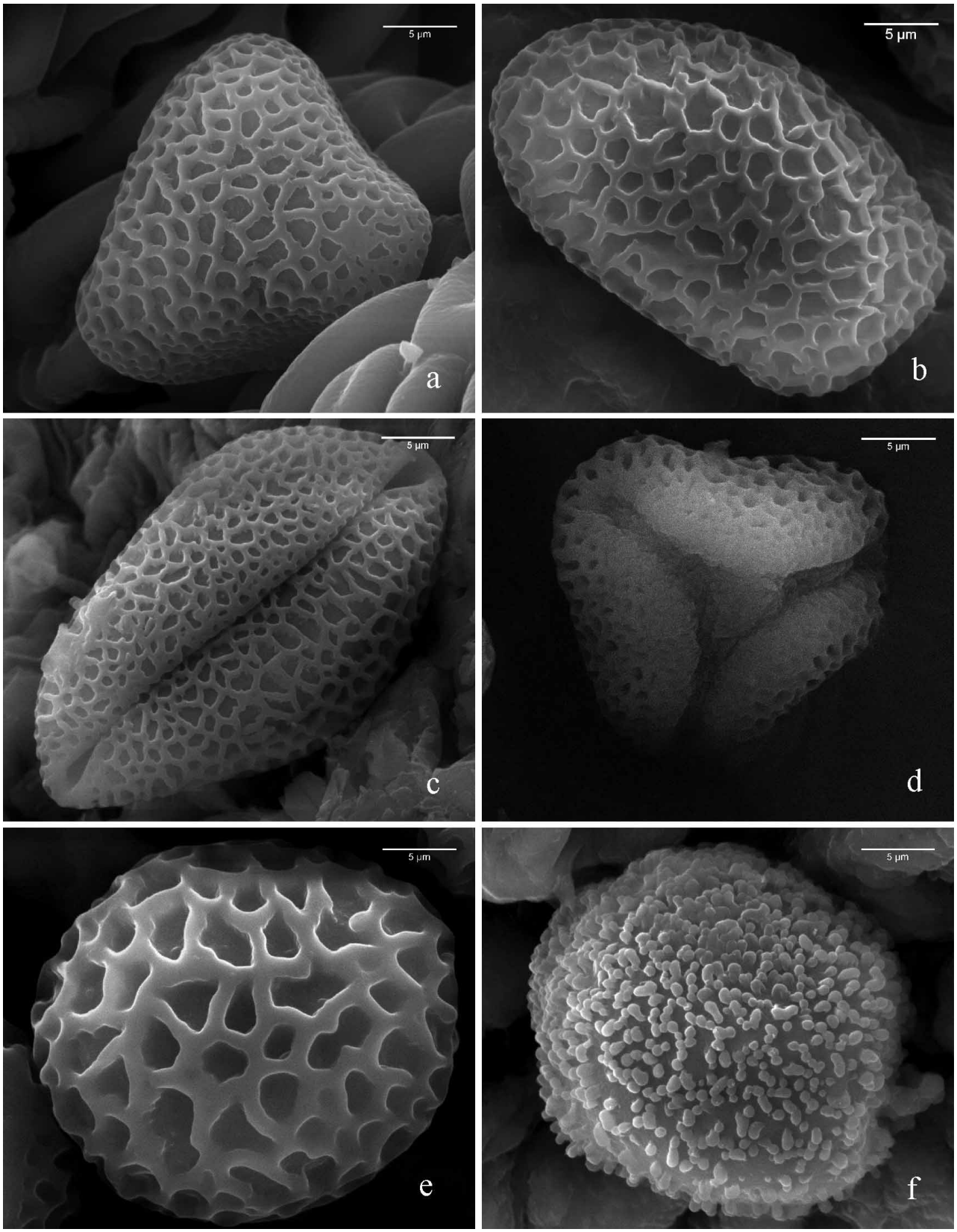

FIGURE 15. SEM images of pollen morphology in *Ceroxylon* (8000). **a)** *C. echinulatum* (*Palacios 9544)* ; **b)** *C. echinulatum* (*Balslev et al. 62512*); **c)** *C. quindiuense* (*Jaramillo-Mejía s.n.*, Colombia)*;* **d)** *C. quindiuense* (*Mejía et al. 4301*,Peru); **e)** *C. pityrophyllum* (*Henderson & Solomon 761*); **f)** *C. vogelianum* (*Galeano & Bernal1337*).

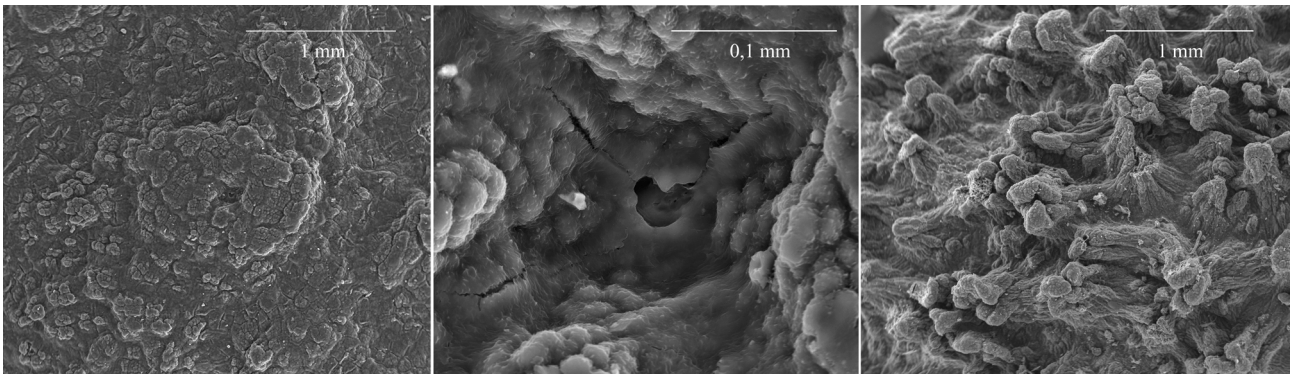

FIGURE 16. SEM images of the surface of the fruits, to show different nature of the warted epicarps. **a)** wart corresponding to the projection of a lenticel (*C. alpinum* (*Wessels-Boer 2447*)); **b)** close up of the protuberance on a), showing the lenticel at the center (*C. alpinum* (*Wessels-Boer 2447*)); **c)** echinate surface of the epicarp, with no projected lenticels (*C. echinulatum* (*Dodsonet al.14843*)).

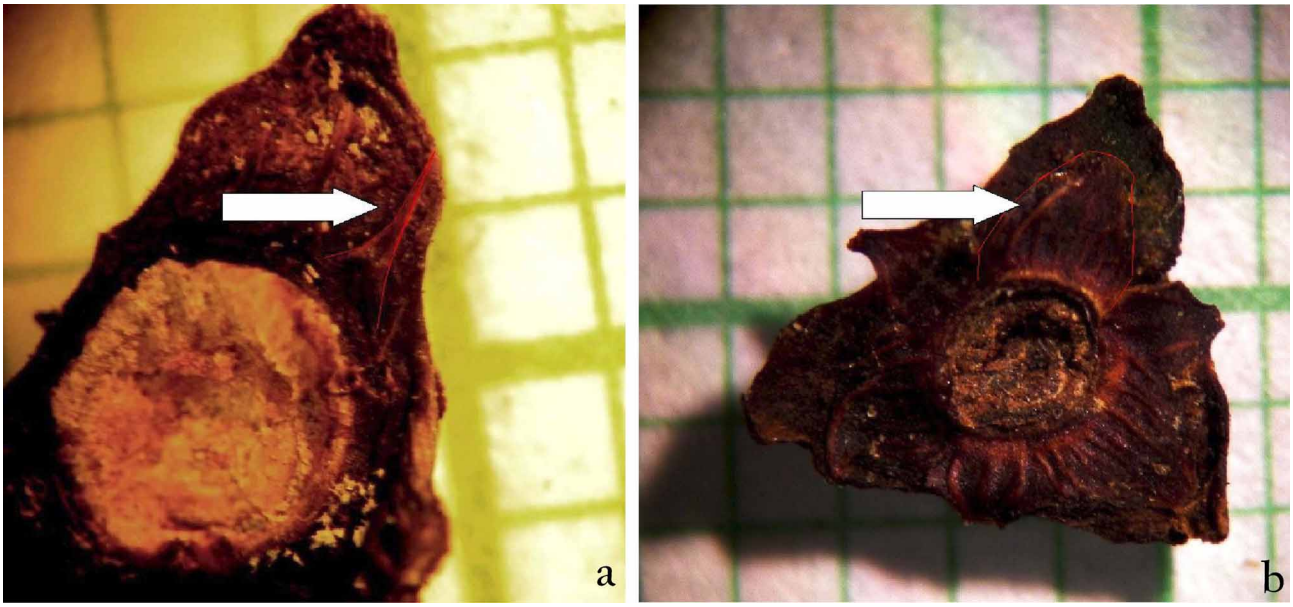

FIGURE 17. Fruiting perianth staminodial filament base. **a)** narrow (*C. peruvianum* (*Smith & Vasquez 4854*)); **b)** wide (*C. pityrophyllum* (*Nee & Vargas 38446*)).

Distribution

Ceroxylon is distributed from 11° 10' N in Distrito Federal, Venezuela, to 18°52' S in Cochabamba, Bolivia; and from 76° 30' W in Valle del Cauca, Colombia, to 63°55'W in Cochabamba, Bolivia. It occurs along the slopes and high inter-Andean valleys of the Central and Northern Andes, from the Cordillera de la Costa (Venezuela) to the three cordilleras of Colombia, and South to Ecuador (east and west slopes), Peru, and to the Department of Santa Cruz in Bolivia, from 900 m to 3500 m (Fig. 18–20). The individual species have a restricted elevation range; *C. amazonicum*, for example, is found only between 800–1200 m. Eight species have elevation ranges of 2000–2500 m, corresponding to montane cloud forest.

Another factor that determines the distribution of *Ceroxylon* is humidity. Although no quantitative studies have been carried out to correlate this factor with *Ceroxylon* distributions, palm stands are never found in xeric conditions. For example, *C. ceriferum* is restricted to the moist western slopes facing the Caribbean on the Sierra Nevada de Santa Marta but it does not occur in the drier forests of the eastern face; *C. pityrophyllum*

is never present in the dry forest but some scarce individuals dwell in transitional to humid montane forests. Cultivated seedlings perform better at high humidity levels. *Ceroxylon* palms are always found in humid or moist, montane forests or surviving in pastures. The only exception to this distribution is *C. parvifrons* which can grow at up to 3500 m elevation.

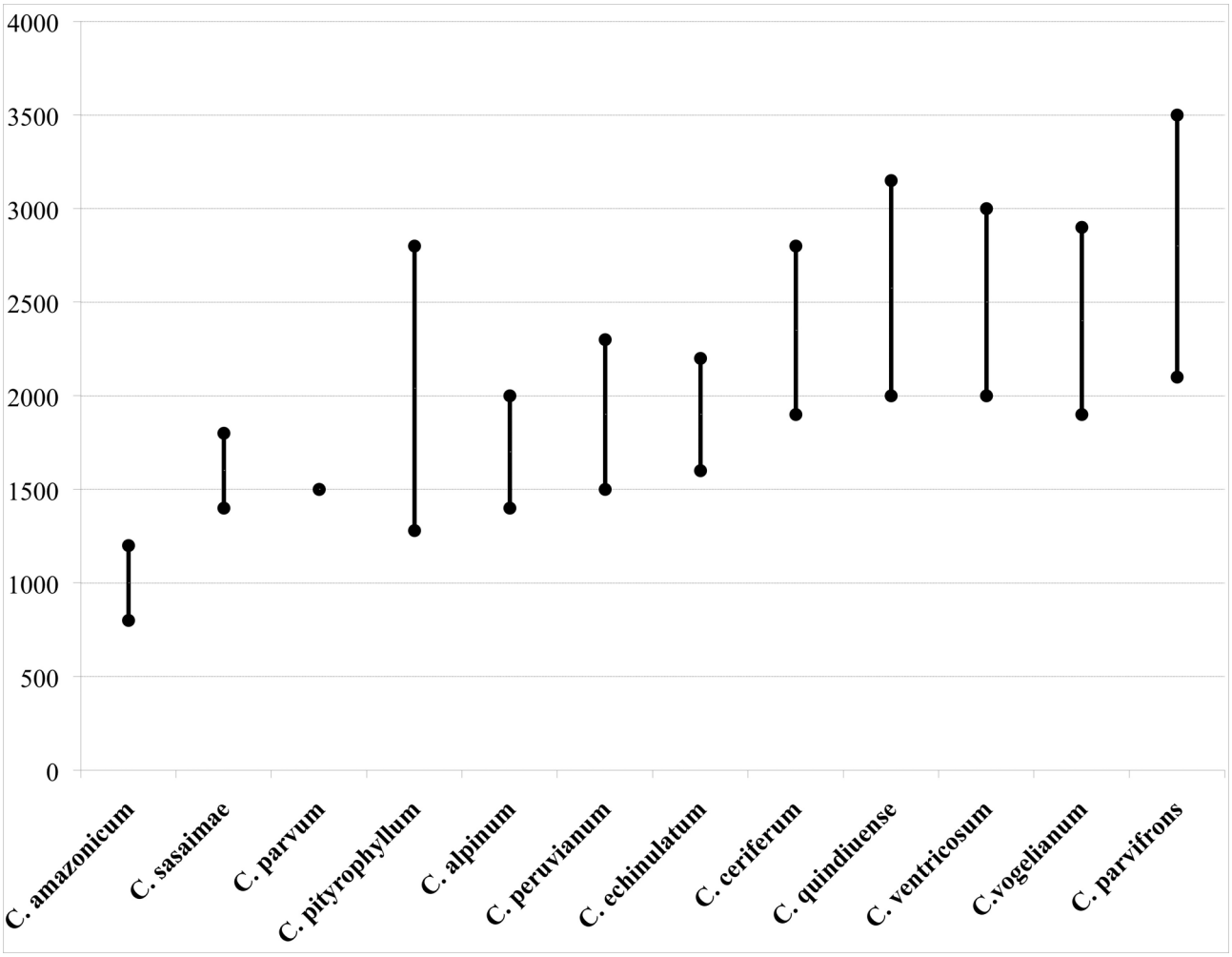

FIGURE 18. Altitudinal ranges of the species of *Ceroxylon* (y-axis = meters).

Reconstructing the biogeographic history of *Ceroxylon* is complicated for several resasons: 1) the ranges of all the species of *Ceroxylon* are probably relictual and hardly a fair representation of their past distributions; as 90% of the Andean forests have been eradicated (Henderson *et al.* 1991), most individuals of *Ceroxylon* are found in highly reduced populations surrounded by large pastures or eroded terrains where no palms persist, 2) collections of *Ceroxylon* are still incomplete, especially around the lake Titicaca area, the eastern slopes of the Peruvian Andes, and around the Táchira Deflection in southwestern Venezuelan. This is due in part to the difficulties of collecting these species, because of their size. Their dioecious nature, and the fact that an individual seldom carries fruits and flowers at the same time, means that a complete collection comprising staminate and pistillate flowers, as well as fruits, will require the collection from at least three individuals and usually several field campaigns. However, even if some sampling gaps remain, the present study encompasses field work done over more than 20 years, which has covered many previously unexplored localities. For this resason, no new species are expected in Venezuela, Colombia, Ecuador, and northern Peru.

Trénel *et al.* (2007b) put forward a comprehensive theory on the biogeography of subfamily Ceroxyloideae. In that study, 5.5 Kb of DNA from three plastid and two nuclear genomic regions were used to

reconstruct a phylogeny for which divergence times were estimated. Tribe Ceroxyleae was found to include two clades, one comprising *Ravenea* and the other *Oraniopsis, Juania* and *Ceroxylon*. Dating suggested that the Eocene–Oligocene was a geologic period of major radiation. Disjunctions in tribe Ceroxyleae most like arose during the mid-Tertiary which is too recent for the formerly proposed Cretaceous (Godwanan) vicariance to have occurred. Trénel *et al*. (2007b) suggest that repeated trans-oceanic dispersal events were involved. Ceroxyleae are, in general, adapted to cool hardy environments and therefore, the authors hypothesized that if Eocene ancestors exhibited similar ecological characteristics, austral intercontinental dispersal could have been possible.

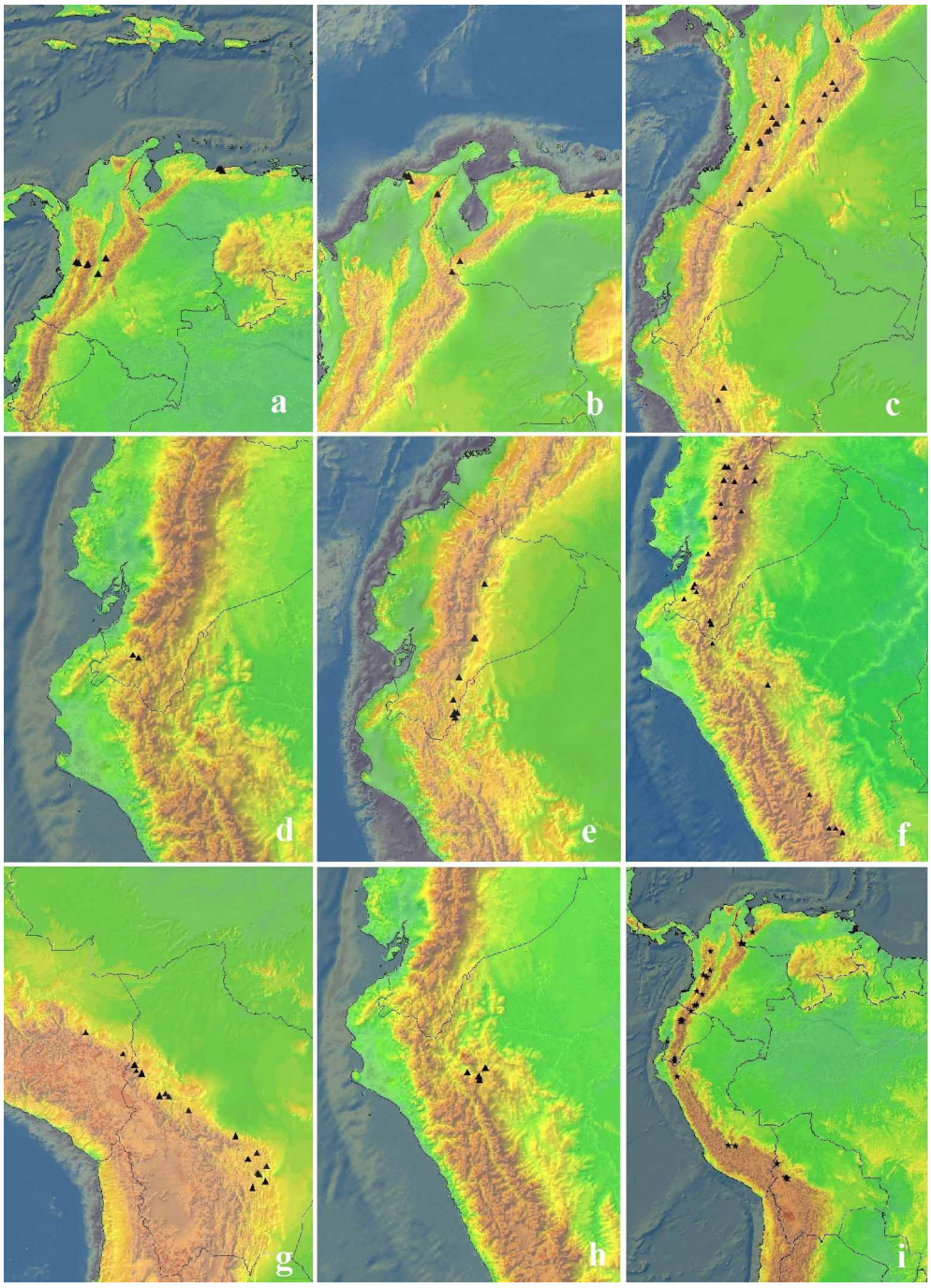

FIGURE 19. Geographical distribution of *Ceroxylon* species. **a)** *C. alpinum*; **b)** *C. ceriferum*; **c)** *C. quindiuense*; **d)** *C. parvum*; **e)** *C. amazonicum*; **f)** *C. echinulatum*; **g)** *C. pityrophyllum*; **h)** *C. peruvianum*; **i)** *C. parvifrons.*

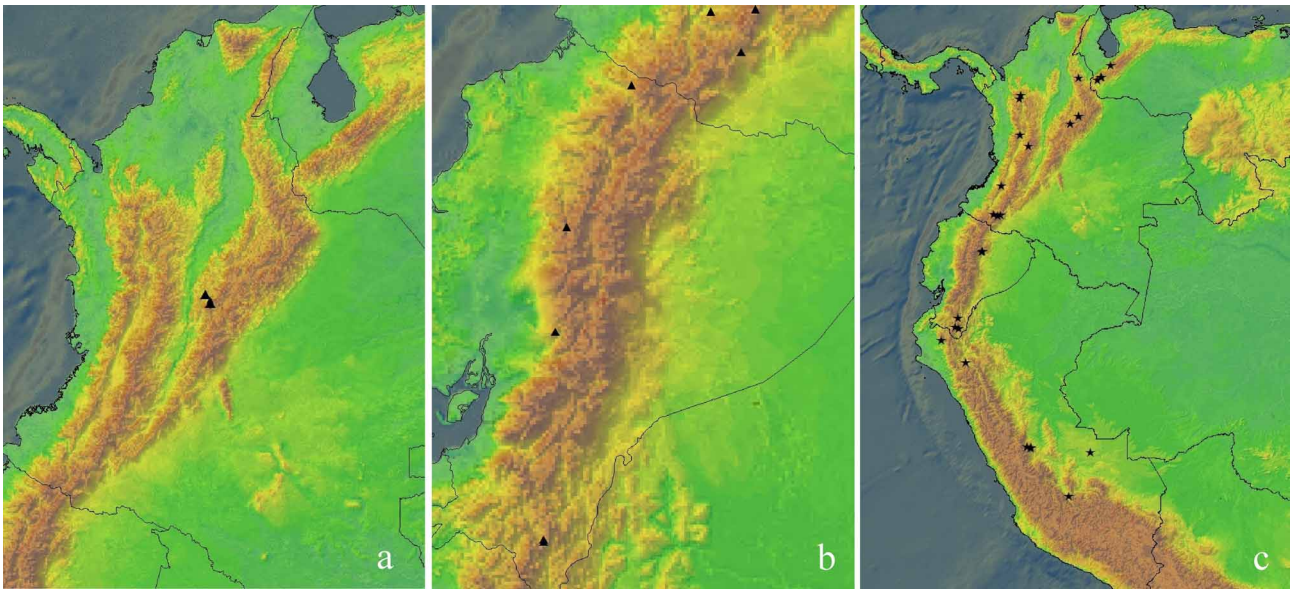

FIGURE 20. Geographical distribution of *Ceroxylon* species. **a)** *C. sasaimae*; **b)** *C. ventricosum*; **c)** *C. vogelianum*.

Ecology and floral biology

Demography:—Vergara-Chaparro (2002) evaluated various remnant populations of *C. alpinum* in Salento, Quindío Department (Colombia), with the use of Lefkovitch matrices to estimate the growth rate of the population. Individuals were found to produce 0.9 leaves per year in the seedling stage, 2.3 during the establishment phase, 7 during the mature-vegetative phase, and up to 11 during the mature-reproductive phase. The last phase was accompained by an abrupt reduction in stem diameter and in internode length: 0–5 m tall palms grew 55.7 cm per year, while 35–40 m tall palms grew 20.5 cm per year. She estimated that it took a palm 57 years to start producing a stem, 83 years to reach the reproductive phase, and 140 years to grow up to 25 m; life expectancy was estimated at 213 years. The ratios among sexes were balanced in the populations studied, and the reproductive cycles were annual, with the main flowering of both sexes occuring around September and fruit maturation seven months thereafter. Each adult produced 4–12 inflorescences per year and each infructescence 2000–3000 fruits; not all inflorescences matured simultaneously, so fruits were available during much of the year.

Rudas (1998) studied the life cycle and demography of a population of *C. sasaimae*, and found that the total number of adults summed to about 100, with an effective population size of less than 50 individuals, due to dioecy. For this reason, and the high level of degradation of the natural habitats this species was categorized as Critically Endangered, according to the 2001 IUCN Red List Categories and Criteria, version 3.1 (Galeano & Bernal 2005). Paredes-Ruiz (1995) studied the population structure and some aspects of growth and development of a population of *C. echinulatum* in the Province of Napo (Ecuador): leaf production per year in adults was estimated at 2.74 (SD = 0.86) in the forest and 2.85 (SD = 1.14) in pastures, and the production of pistillate and staminate inflorescences was 3 (sd = 2) per year, regardless of whether the individuals were growing in pastures or in the forest. Individuals growing in open pastures produced significantly more leaves per year, attained greater heights and had substantially lower regeneration rates, as can be expected in areas used for livestock grazing. The flowering cycles were annual, the main event occuring in September–January (staminate) and October–November (pistillate), suggesting an extended pollen offer throughout the whole flowering season.

Girón-Vanderhuck *et al*. (2001) studied the population structure of *C. quindiuense* in the Central Andes of Colombia and estimated leaf production in seedlings at 4.5 per year and at 3.92 in adults; flowering was also annual with the main event occurring in March–April, and occasionally in November.

Floral biology:—A detailed study of the floral biology of *Ceroxylon* species has not been completed to date. Knudsen *et al.* (2001) found that the pistillate and staminate flowers of *C. echinulatum* (as C. *alpinum* subsp. *ecuadorense*) emitted high levels of unsaturated aliphatic hydrocarbons, with 80% similarity to those emitted by *Mauritia flexuosa*, and *Wettinia maynensis*, suggesting adaptations to pollinators with comparable sensory preferences. The dominance of these closely related volatile compounds in floral scent, regardless of the sex of the plant, is usually associated with beetle pollination (Knudsen *et al*. 2001). Kirejtshuk & Couturier (2009) presented an overview of species of the genus *Mystrops* Murray, 1864 (Nitidulidae beetles) collected on male inflorescence of *C. quindiuense* in Peru, including the description of several new species of *Mystrops*.

Phenology and fruit development:—In *C. alpinum*, seven months pass from the time of pollination to the complete ripening of the fruit. Fruit maturation is more or less synchronized within the same area, but differs in timing between areas (Brown 1976). According to Brown & Delascio (1987), the seeds of *C. ceriferum* take 6–24 months to germinate. Local informants report that the fruits of *C. echinulatum* mature each year during November–December. In Ecuador, the locals report that *C. ventricosum* fruits only every 6–7 years (Doyle 233, *in scheda*). In some populations fruits may be available during most of the year.

Seed dispersers and interactions with local fauna:—Mejía-Londoño (1999) reported the following bird species as fruit dispersors of *C. alpinum*: sickle-winged guan (*Chamaepetes goudotii*), golden-headed quetzal (*Pharomachrus auriceps*), blue-crowned motmot (*Momotus momota*), toucanetes (*Aulachorhynchus haematopygus*, *A. prasinus*) as well as a single species of bat: *Artibeus jamaicencis*. The following were reported by the same author as potential dispersors: tawny-breasted tinamou (*Nothocercus julius*), chestnut wood quail (*Odonthophorus hyperythrus)*, masked trogon (*Trogon personatus*), red-ruffed fruitcrow (*Pyroderus scutatus*), green jay (*Cyanocorax yncas*), thrushes (*Turdus ignobilis* and *T. fuscater*). In Venezuela, the fruits are consumed by the groove-billed toucanet (*Aulacorhynchus sulcatus*; Brown 1976).

The fruits of *C. quindiuense* are eaten by birds like thrushes (*Turdus* spp.), green jays (*Cyanocorax yncas*), emerald toucanets (*Aulacorhynchus prasinus*) and by parrots (*Hapalopsitaca fuertesii*, *H. amazonina*), including the critically endangered yellow-eared parrot (*Ognorrhynchus icterotis*), which is closely associated with this species (Galeano & Bernal 2005)

Ceroxylon ceriferum is important for wildlife, especially birds. According to C. Olaciregui (pers. comm.), in the Sierra Nevada de Santa Marta, Colombia, the dead stems of *C. ceriferum* are used as nesting sites by the Santa Marta parakeet (*Pyrrhura viridicata*), the scarlet-fronted parakeet (*Aratinga wagleri*), and the strong-billed woodcreeper (*Xiphocolaptes promeropirhynchus*). The latter species also forages on beetles on the stems and among the pinnae. Toucans (*Aulacorhynchus prasinus lautus* and *A. sulcatus calorhynchus*), the sickle-winged guan (*Chamaepetes goudoti sanctaemartae*), and the golden quetzal (*Pharomachrus fulgidus festatus*) feed on the fruits of this species.

Karsten (1856) reported that the spectacled bear (*Tremarctos ornatus*) fed on the palm heart of a wax palm in Volcán de Chiles, Colombia, and Llamosas *et al*. (2003) reported this use for *C. ceriferum* in Venezuela. Henderson *et al.* (1995) describes that it climbs up the stems of the lower individuals to reach the crown

Uses

Ceroxylon palms have been mainly used for either ceremonial (religious) purposes, or for house and fence construction. Both activities are destructive and unsustainable. Other minor uses are fruit consumption by livestock (especially pigs), and usage of the cooked basal part of the peduncle of immature inflorescences for human consumption (Borchsenius *et al.* 1998); the fruits of *C. echinulatum* (Borchsenius & Moraes 2006) and *C. vogelianum* (Van der Eyden 2004) are reported to be eaten by humans; *C. parvifrons* is used for thatch in Bolivia (Moraes 2004). In the past, the stem wax of *C. quindiuense* was exploited and sold in local and international markets (Boussingault 1849). Locally it was used mainly for producing candles, a practice that stopped with the advent of electricity. Wax extraction persisted until World War II, when artificial wax replaced it (Brown 1976). Yet, as late as 1945–1946, Colombian statistics reported wax export to France as an

important activity (Pérez-Arbeláez 1956). In Peru (Ocol, Amazonas), wax extraction persists today. Palms are felled every year during October to make torches and candles that are lit during the local festivities.

Conservation

The conservation status of species of *Ceroxylon* has not been globally addressed. The Red Lists of endangered species are issued by national agencies, and *Ceroxylon* occurs in five countries (Bolivia, Peru, Ecuador, Colombia, Venezuela). Ecuador and Colombia are the only countries to have published Red Lists for palms (Borchsenius & Skov 1999, Galeano & Bernal 2005). Of the seven species of *Ceroxylon* occurring in Colombia, four are under threat. Of these, one is endemic and Critically Endangered (CR; *C. sasaimae*), and three are non-endemic, and Endangered (EN; *C. alpinum, C. quindiuense*, *C. ventricosum*). In Ecuador, Borchsenius & Skov (1999) categorized *C. echinulatum*, *C. ventricosum*, and *C. amazonicum* as Vulnerable, but the last has later been re-categorized as Endangered (Valencia *et al.* 2000). The conservation status of the species in Bolivia (two species), and Peru (six species) is unknown.

The most important threats to all *Ceroxylon* species are: a) habitat loss due to forest clearing processes; b) low regeneration rates due to cultivation and cattle farming; c) leaf extraction for religious festivities. Forest clearing for agriculture and cattle farming has severely reduced most populations of *Ceroxylon*, in some cases to a few individuals. These activities prevent seedlings from developing; thus, not only are population sizes reduced, but regeneration is severely hampered. Additionally, in many areas, the developing leaves of the remaining individuals were extracted for use during Palm Sunday, affecting growth and reproduction, and sometimes causing the death of the palms. Although this activity is banned in Colombia and discouraged in other countries, it still continues to threaten some *Ceroxylon* species, especially *C. ceriferum*, *C. parvifrons*, *C. quindiuense*, and *C. alpinum*.

Ceroxylon species have life history traits that make the design of conservation strategies especially challenging. All of the species are dioecious, most are expected to be long-lived (as observed in *C. alpinum*, and *C. echinulatum*), and all are adapted to a specific elevation range, precipitation regime, and soil drainage. All of these factors must be considered in the development of conservation strategies for each of the twelve species.

Taxonomic treatment

Ceroxylon Bonpland ex De Candolle (1804: 239). Type:— *Ceroxylon alpinum* Bonpl. ex DC.

Klopstockia Karsten (1847: t. I. fig. 6). Lectotype (designated by Moore 1963):— *K. cerifera* H.Karst. (=*Ceroxylon ceriferum* (H. Karst.) Pittier).

Beethovenia Engel (1865: 677). Type:— *B. cerifera* Engel (= *Ceroxylon ceriferum* (H.Karst.) Pittier).

Tall to medium-sized, solitary, unarmed, dioecious, pleonanthic palms. **Stem** erect, smooth, covered by a layer of wax, with conspicuous leaf scars. **Leaves** pinnate, numerous in crown; sheath leathery, open, not arranged in a crownshaft; petiole channeled adaxially, rounded abaxially; rachis adaxially flat but turning narrowing towards apex ending as a ridge (triangular in cross-section), glabrescent, rounded and covered by grey tomentum abaxially; pinnae regularly arranged along the rachis in one plane, or clustered in groups and oriented in several planes, horizontal or pendulous, linear-lanceolate, acute, with a prominent midrib, adaxial surface usually smooth and glossy or shiny, abaxial surface covered by a white or yellowish to brown tomentum of waxy scales. **Inflorescences** interfoliar, 2–6 (–8), in different stages of development, solitary in the axil of each leaf, branched up to second, third or fourth order; peduncle elongate; prophyll tubular, bicarinate, flattened, incompletely encircling the peduncle abaxially and open apically; peduncular bracts 4–7, inserted near the base of the peduncle, the lower ones open apically, the upper one beaked, completely enclosing the inflorescence in bud and opening abaxially at anthesis, and sometimes with an additional

smaller, thinner bract inserted distally on the peduncle; prophyll and peduncular bracts covered by thick indumentum of light brown scales; rachillae flexuous or zig-zag, glabrous or covered with indumentum, subtended by short, triangular bracts. Staminate and pistillate inflorescences can be distinguished from afar, the staminate being smaller and with adpressed rachillae close and somewhat drooping at anthesis. Pistillate inflorescences massive, with upright rachis and spreading, loosely inserted rachillae. Pistillate inflorescences green from the beginning of fruiting stage, and staminate inflorescences cream-coloured, turning yellowish after anthesis, and then brown and dry. **Flowers** open from early in development, solitary, pedicellate. Sepals 3, basally connate, acute to acuminate; petals 3, fleshy, briefly connate basally and shortly adnate to the bases of the antesepalous stamen/staminode filaments, acute to long-acuminate; stamens/staminodes 6–19, filaments awl-shaped, straight from early in development, anthers/abortive anthers basifixed, bifid basally, apically bifid or long-acuminate; pistil trifid, smooth to warty, pistillode minute. **Fruits** globose, 1.5–2.5 cm diam., red to orange-red; epicarp smooth, verrucose, reticulate or covered with prominent, irregular and acute bulges; mesocarp fleshy with few fibres; endocarp thin and papyraceous, loose from the seed; seed globose, light brown, with basal hilum, raphe branches slightly visible; endosperm homogeneous; embryo lateral near the base. Eophyll elliptic to narrowly lanceolate, covered with silver scales on abaxial surface.

Ceroxylon includes 12 species distributed throughout the Andes, in Venezuela, Colombia, Ecuador, Peru and Bolivia. Most of the species grow in moist, premontane to montane forest, commonly from 1400 to 3200 m, but one species grows in tropical rain forest at 800–1200 meters and another grows up to 3500 m (Fig. 18).

Key to the species of *Ceroxylon*

1 Pinnae regularly arranged (not in groups) 2
- Pinnae arranged in groups 7
2. Exocarp smooth or with subtle and scattered protuberances visible to the naked eye 3
- Exocarp furrowed, warty or covered with prominent, irregular and acute bulges 6
3. Leaf rachis twisted towards the apex, the distal pinnae therefore appearing vertically oriented; pinnae horizontal and straight to pendulous in the basal part of the leaf 4
- Leaf rachis not rotated; pinnae pendulous or erect 5
4. Leaves 8–14, petiole ~ 50 cm long; stamens or staminodes (7–)8–10(–12); at (1900–)2200–2800 m … *C. ceriferum*
- Leaves 16–22, petiole short (<15 cm); stamens or staminodes 11–13; at 800–1200 m ..... *C. amazonicum*
5. Palm **(**13–)20–45(–60) m tall, 25–40 cm diam.; stem and abaxial surface of pinnae silvery white, pinnae pendulous; stamens or staminodes 9–12(–17); rachis straight ..... *C. quindiuense*
- Palm 4–12(–17)m tall, (6–)10–30(–35) cm diam.; stem greyish, brown-grayish or brown; pinnae with abaxial surface brown-ferrugineous, pinnae erect; stamens or staminodes 6–11; rachis arched upwards (but not rotated) .... *C. parvifrons*
6. Exocarp densely covered with prominent, irregularly distributed and pointed bulges (warted to echinate); stamens or staminodes 9–12, anther connective not elongated; rachis and rachilla of the inflorescence glabrescent; leaf rachis not rotated; pinnae pendulous ..... *C. echinulatum*
- Exocarp with scattered warts that coincide with the raised lenticels; stamens 9–19, anther connective elongated; rachis and rachilla of inflorescence densely lepidote; rachis rotated towards apex; pinnae horizontal to slightly pendulous, forming an angle on the abaxial side close to 75° ..... *C. alpinum*
7. Exocarp smooth or with subtle and scattered protuberances visible to the naked eye 8
- Exocarp densely covered with prominent, irregular and acute bulges (echinate), densely warty or furrowed 11
8. Palm 3–15 m tall; stem green to brown, covered with a thin layer of wax; pinnae in several planes; stamens and staminodes 6–11 9
- Palm (8–)20–35 m tall; stem white or brown-greenish to grayish; pinnae in slighlty divergent planes; stamens and staminodes 9–11 10
9. Stamens and staminodes 6, filament base wide (1–1.3 mm); anthers 4.0–6.0 mm ..... *C. pityrophyllum*
- Stamens and staminodes (6–)9–11, filament base narrow; anthers 2.0–2.2 mm ..... *C. parvum*
10. Stem silvery white, 20–60 cm diam., covered with a thick layer of wax; petiole 30–59 cm long; crown hemispherical in outline; (1800–)2000–3000 m ..... *C. ventricosum*
- Stem brown-greenish to grayish, 17–30 cm diam., covered with thin layer of wax; petiole absent or short (<15 cm); crown spherical in outline; 1400–1800 m ..... *C. sasaimae*
11. Exocarp reticulate sulcate; stem green or brown; stamens and staminodes 6; central pinnae narrow (~2.2–3.5 cm) ..

..... *C. vogelianum*

- Exocarp densely covered with irregular and acute bulges; stem white; stamens and staminodes 12–15; central pinnae wide (3.5–5.0 cm) ..... *C. peruvianum*

1. *Ceroxylon alpinum* Bonpland ex De Candolle (1804: 240). *Ceroxylon andicolum* Humboldt & Bonpland (1805: 2). *Iriartea andicola* (Humb. & Bonpl.) Sprengel (1825: 623). Type:— COLOMBIA. Quindío, *A.Humboldt & A. Bonpland 1844* (holotype P!).

Ceroxylon ferrugineum von Regel (1879: 163). Type:— COLOMBIA. Quindío: Salento–Tambores, March 1986, *E. André 2563* (holotype P, n.v., isotypes K!, NY!).

Ceroxylon andicolum var. *occidentale* R.B.White ex Fawcett (1898: 39). Type:—COLOMBIA, Valle del Cauca, road from El Dovio to La Selva, in remnant of forest beside road, 22 nov 1974, H. E. Moore et al. 10203 (neotype (designated here) COL!, isoneotype BH!)

Figs. 7a–b, 9f, 14d, 18, 21.

Stem 8–21 m tall, 19–30 cm in diam., internodes covered with thin layers of wax, white at the base, grey to brown towards the apex. **Leaves** 17–20(–25) in hemispheric crown; sheath 75–125 cm long, densely covered with thick, eventually deciduous tomentum of white scales; petiole (10–)20–30 cm long, 4.5–7.0 cm wide apically, adaxial surface concave to flattened, margins acute, glabrescent, abaxial surface convex, densely covered with thick, deciduous scales or their broken bases, indumentum more persistent towards the margins; rachis 194–270 cm long, adaxially flattened in ⅔–¾ of its length, twisted 90° on distal portion thereby holding the pinnae in a vertical position, abaxial surface covered with an indumentum resembling that of the petiole; pinnae 90–110 on each side, regularly arranged in one plane, horizontal to slightly pendulous, in the latter case forming an angle (abaxially) close to 75°, abaxial surface covered with elliptical, membranaceous, white scales, becoming gradually more scattered with age, midrib covered with one row of translucent, deciduous scales, pinnae at the extreme proximal end filiform, 22–41(–62) × 0.2–0.3(–1.4) cm, 10th pinna from base 52–74 × 1–2 cm, middle pinnae 49–80 × 3.5–5.5 cm, 2.3–5.5 cm apart, apical pinnae (15–)24–31 × 0.5–1.0 cm, usually free, rarely united along the margins. **Staminate inflorescences**: peduncle ca. 80 cm long, covered with pale brown floccose scales; peduncular bracts 7, the longest 75 × 11 cm, leathery, covered with deciduous indumentum, only persisting towards margins; rachis 80–90 cm long, with ca. 56 first order branches, each subtended by a 0.5–1.5 mm membranaceous acuminate bract; rachis and branches covered with thick layer of persistent, white to cream indumentum of floccose scales; longest branches near base 37 cm long. **Pistillate inflorescences** up to five in various stages of development; peduncle 1.0–1.7 m long, 2.6–3.0 cm wide at apex, covered with pale brown, floccose, deciduos scales; prophyll covered with thick, brownish to yellowish, floccose; peduncular bracts 6–7, 22–148 × 11 cm, and an additional bract smaller, more distally inserted, about 8 cm, all bracts leathery, covered with thick indumentum like that of the prophyll; rachis 84–123 cm, with 54–62 first order branches, all branches subtended by a 0.5–2.0 mm, membranaceous, acuminate bract; longest branches 38–72 cm; rachis and first order branches densely covered with white and ferrugineous, persistent membranaceous scales. **Staminate flowers:** sepals 3, triangular-acuminate, apex narrow, 1.0–1.5 mm, connate basally for ⅓–½ their length, not reaching or exceeding edge of corolla tube; petals 3, ovate–acuminate to subulate, 4–8 mm, basally connate for 0.4–1.5 mm, apex long-acuminate, acumen 1–2 mm; stamens 10–17(–19), exserted, 3–6(–9) antesepalous, and 3–9(–10) antepetalous, filaments 1.0–2.5 mm, anthers basifixed, 4–7 mm, connective exceeding theca in length by 0.2–0.4 mm. **Pistillate flowers:** sepals 3, elliptical-acuminate, 1–2 mm long, connate for approx. ½ their length, reaching or exceeding edge of corolla tube; petals 3, elliptical-subulate, 4–5 mm long, basally connate for up to 1 mm, acumen narrow, 1 mm long; staminodes 12–16, 0.5 mm long, with thick filaments, abortive anthers

1.5–2.0 mm long. **Fruits** globose, orange-red when ripe, 1.6–2.0 cm diam., exocarp with raised lenticels appearing as scattered warts; perianth with triangular–acuminate sepals, 1.0–1.8 mm long, connate basally for 0.5–1.0 mm, lobes reaching edge of corolla tube, petals elliptical-subulate, 4–9 mm long, widened at base, acumen 1–3 mm long, connate basally for 0.7–1.0 mm. **Seeds** ca. 1 cm diam.

FIGURE 21. *Ceroxylon alpinum.* **a)** habit, in the front *C. alpinum*, in the back, *C. quindiuense*; **b), c)** habitat; Valle de Cocora, Quindío, Colombia. Photos provided by Rodrigo Bernal.

Distribution and habitat:—Premontane wet forest from 1400 to 2000 m, in the Andes of Venezuela (Distrito Federal, on the northwestern slopes of the Cordillera de La Costa, Aragua, and Táchira) and Colombia (western slope of the Eastern Cordillera, and eastern and western slopes of the Central and Western Cordilleras), (Fig. 19a).

Local names:—Chonta (Quindío, Colombia); palma bendita (Venezuela); palma de cera (Quindío, Valle del Cauca, Colombia; Venezuela); palma real (Valle del Cauca, Colombia).

Uses:—The young leaves have traditionally been used in religious processions on Palm Sunday, a practice that has been abandoned by law in Colombia (Galeano & Bernal 2005). The stems are used as fencing around houses and farms, and to build walls. The fruits are consumed by pigs.

Conservation status:—The vast majority of the montane forest within the range of this species has been destroyed or fragmented by coffee plantations or pastures. According to the IUCN criteria (Version 3.1) this species is Endangered (EN) in Venezuela (Llamosas *et al.* 2003), as well as in Colombia. In the latter country it is estimated that natural populations have been reduced more than 80% in the last 210 years (Galeano & Bernal 2005). Moreover, in one of the best conserved populations genetic erosion has been detected in seedlings (Gaitán-Solís 2003). A demographic study revealed that the maximum age of palm individuals

growing under natural conditions is 160 years and up to 213 years in one particular case (Vergara-Chaparro 2002). On average they developed an aerial stem at the approximate age of 57 years and started flowering when they were approximately 83 years old.

Notes:—*Ceroxylon alpinum* is characterized by its regularly arranged, horizontal pinnae, inflorescence axes with reddish indumentum, staminate flowers with large and exserted anthers with a projected connective, and a warty fruit exocarp, with raised lenticels (Fig. 9f, 16a–b).*C. alpinum* subsp. *ecuadorense* described from the western Andes of Ecuador (Galeano 1995), is here included in *C. echinulatum*; see comments under that species. This decision is supported by phylogenetic analyses based on molecular data (Trénel *et al.* 2007b, 2008).

The name *Ceroxylon andicolum* var. *occidentale* was published by Fawcett based on a description sent to him from Colombia by Robert B. White. The description was accompanied by a few seeds but apparently no specimen was ever made. White cited a locality "60 miles South of Cali, in the Valley of Cajamarca"; this locality is actually 114 km north of Cali, near the town of El Dovio, where the neotype was collected.

Specimens examined:—COLOMBIA. **Cundinamarca:** Sasaima, Road to Guaduas, km 64, 1720 m, 18 April 1985, G. *Galeano & R. Bernal 687* (pist.fl., fr.) (COL); on road between Bogotá and Honda, ca. 1880 m, 4 September 1970, *H. E. Moore & R. E. Diets IV 9864* (BH, COL); Guaduas, Road from La Cabaña to Chaguaní, slope towards Chaguaní, 1700 m, 3–4 October 1998, *R. Bernal & G. Galeano 2320* (st.fl.) (COL). **Quindío:** Salento, 1700–1900 m, 25–31 July 1922, *E. Killip 9049* (fr.) (US); toward R. Boquía, 1600–1700 m, 25–28 August 1922, *T. Hazen 10149* (US); 1 km east of Calarcá on road between Armenia and Ibagué, 1780–1830 m, 16 November 1974, *H. E. Moore et al. 10191* (st.fl., mat.fr.) (BH, COL, K, NY, US); no locality, no date, *Purdie 46* (st.fl.) (K, P). **Valle:** Cordillera Occidental, West slope, river basin of the Albán, El Zancudo, 1480–1540, 21 October 1946, *J. Cuatrecasas 22485* (MO); municipality of Argelia, road from Argelia to La Florida, 5 km from Argelia, 1 km before the Inspección de La Palma, 1560 m, 11 April 1989, *R. Bernal & W. Devia 1550* (st.fl.) (COL). VENEZUELA. **Distrito Federal:** Colonia Tovar, s.d., *A. Fendler 7466* (fl., fr.) (NY); 1854–1855, A. Fendler, s.n. (pist.fl., immat.fr.) (K, NY); *Karsten, sn.* (LE!), rich forested seaward slopes along quebrada leading towards "Portachuelo" above Hacienda El Limón, 5.8 km below junction at Geremba of Junquito–Colonia Tovar road, 1750–1800 m, 24 October 1963, J. *Steyermark 91772* (st.fl.) (BH, NY). Along road between El Limón and El Junquito-Colonia Tovar, 10°30' N 67°20' W, 1600, 7 March 1968, J.G. *Wessels-Boer et. al 2447* (mat.fr.), *2448* (st.fl.) (NY, MERC).

2. *Ceroxylon amazonicum* Galeano (1995: 398). Type:— ECUADOR. Zamora–Chinchipe: 11 Km East of Zumbi on the road to Paquisha, 03°55' S, 78°43' W, 1100 m, 18 May 1987, *H. Balslev et al. 62538* (fr.) (holotype QCA!, isotypes AAU!, COL!, K!, QCNE!).

Figs. 7e–f, 8c, 12a, 18, 22.

Stem 8–12(–20) m tall, 12–25 cm diam., internodes covered with thin layer of wax, whitish to greyish. **Leaves (**14–)19–22, in dense, hemispheric crown; sheath 104 cm long, covered with thick, light brown indumentum; petiole 10–15 cm long, 3.5–7.5 cm wide apically, adaxial surface flat and slightly elevated at center, glabrescent, abaxially covered with thick layer of persistent, brownish scales, with a stout, elongated, hammer-shaped base and a fibrous limb that projects upwards; rachis 203–290 cm long, twisted 90° on distal portion thereby holding the pinnae in a vertical position, adaxially flattened in about ½ of its length and ending in a well-defined 2 mm hastula-like projection, glabrescent with remnants of scales near the margins, abaxially convex, covered with oblong, adpressed, white, membranaceous scales; pinnae 83–106 on each side, regularly arranged in one plane, horizontal and straight to pendulous in the basal part of the leaf and straight toward the apex, abaxial surface and midrib covered with yellowish scales, with age falling to reveal the surface in some areas; the most basal filiform pinnae 37–51 × 0.2–0.6 cm, basal pinnae (10th from base and below) 59–60 × 1.2–1.8 cm, middle pinnae 50.0–83.5 × 4.2–5.0 cm, apical pinnae 24–42 × 1.5–2.0 cm,

sometimes the apical pinnae united along the margins. **Staminate inflorescences** 5–7 at a time; peduncle 67 cm long, 2.5 cm wide at apex, glabrescent; prophyll 41 cm long, 6 cm wide at base; peduncular bracts 5–6, up to 160 cm long, 5–8 cm wide, with an additional smaller bract inserted near the base of the peduncle, prophyll and peduncular bracts covered by thick indumentum of light brown, fibrous scales; rachis 77–103 cm long, with 97–98 branches, each subtended by a 0.5–2.0 cm long, membranaceous, acuminate bract, rachis and branches glabrescent, longest branches 50 cm. **Female inflorescences** 6–7 at a time; peduncle 124 cm long, 2.7 cm wide at apex; prophyll 45 cm long, 10–11 cm wide at base; peduncular bracts 5, to 153 cm long, an additional, 5 cm bract inserted 5 cm below rachis base; rachis 120 cm long, with ca. 92 branches, longest branches 59 cm; prophyll, peduncle, bracts and base of rachis covered with persistent, light brown to yellowish indumentum, rachillae glabrous. **Staminate flowers:** sepals 3, broadly triangular, 1.0–1.5 mm long, connate in 0.1 mm (ca. 1/10 of total length), exceeding total length of the corolla tube; petals 3, elliptical to long acuminate, 5–7 mm long, connate in 1.0–1.5 mm; stamens 9–12(–13), 3–6 episepalous, and 6–7 epipetalous, filaments 1.0–1.5 mm long, anthers 2.0–3.5 mm long, anther connective not projected. **Pistillate flowers:** sepals 3, broadly triangular-acuminate, 1.0–1.5 mm long, connate for 0.6–1.0 mm (1/2–2/3 of the total length), not reaching edge of corolla tube; petals 3, elliptical-acuminate, 5.0–6.5 mm long, connate up to 1.2 mm, acumen narrow, 1.0–1.5 mm long; staminodes 12, 1 antesepalous, 2–3 antepetalous, filaments 1 mm long, abortive anthers 0.9–1.2 mm long; pistil green, trifid, 2–3 mm diam. **Fruits** globose, orange-red when ripe, 1.7–2.0 cm diam., exocarp smooth. **Seeds** 1.3–1.5 cm diam.

FIGURE 22. *Ceroxylon amazonicum.* **a)** habit; see *Iriartea deltoidea* behind; **b)** habitat, grown together with *Wettinia maynensis.*

Distribution and habitat:—Only known from the southeastern slopes of the Ecuadorian Andes (Morona–Santiago and Zamora–Chinchipe), at 820–1200 m, most common around 1000 m. It grows in premontane to tropical rain forest on clayey soils, among typical Amazonian vegetation, which includes palms like *Iriartea deltoidea* Ruiz & Pav., *Wettinia maynensis* Spruce and *Oenocarpus bataua* Mart. On the sites found, it was growing on pastures and forest remnants, with some secondary regeneration after cultivation in Shuar pastures and homegardens. The low elevation and surrounding vegetation is very unusual for the palms of this genus (Fig. 19e).

Local names:—Ramo (Ecuador), paik (*Shuar*, Ecuador).

Uses:—No uses have been recorded.

Conservation status:—*Ceroxylon amazonicum* was considered Vulnerable by Borchsenius & Skov (1999), and later Endangered, mainly due to deforestation (Valencia *et al.* 2000).

Notes:—*Ceroxylon amazonicum* is diagnosed by its dense crown and leaves with regularly inserted and horizontal pinnae, staminate flowers with 9–12(–13) stamens (Fig. 7e–f), and smooth fruits. It is also the species that grows at lowest elevation.

Specimens examined:—ECUADOR. **Morona-Santiago:** road from Macas to Sucua, km 3, 02° 18' S, 78° 08' W, 1000 m, 14 July 1985, *H. Balslev & A. Henderson 60654* (fr.) (AAU); Parque Nacional de Sangay, Dormono sector at Macas, 02° 17' S, 78° 10' W, ca. 1000 m, 16 January 1987, *A. Barfod et al. 60154* (st.fl.) (AAU, COL, QCA). Northern and eastern slopes of Cordillera de Cutucú, 02° 15'S, 78° 00'W, 600–1700 m, 22–26 August 1996, *H. Balslev et al. 6452* (juvenile) (AAU). **Zamora-Chinchipe:** Nangaritza River, 5 min. in canoe down from Miazi military station, 04° 15' S, 78° 41' W, 1000 m, 23 October 1991, *B. Bergmann & M. Ruíz 97896* (sterile) (AAU, QCA); Cantón Nangaritza Shaimi, in front of military building, right margin of Nangaritza river, 04°18'S, 78°34'W, 930 m, 27 October 1991, *W. Palacios et al. 8745* (st.fl.) (COL, MO, QCA, QCNE); Nangaritza, Nangaritza river, ca. 500 m to SE from village of Yayu, 4° 23' S, 78° 40' W, 910–940 m, 16 November 2002, *J. Vormisto & A.Byg 656, 657* (seedling, juvenile) (AAU); Nangaritza, Nangaritza river, 4° 16'S, 78° 37' W, 800–900 m, 3 December 2002, *J. Vormisto & A. Byg 678* (sterile) (AAU).

3. *Ceroxylon ceriferum* (Karsten) Pittier (1926: 10). *Klopstockia cerifera* Karsten (1847: t. I. fig. 6). *Ceroxylon klopstockia* Martius (1849: 314), *nom. illeg*., *Iriartea klopstockia* (Martius) Watson (1885: 338), *nom. illeg*. Type:—VENEZUELA. Cordillera de la Costa, up from Caracas, 1500–2500 m, *Karsten, s.n.* (st.fl.) (lectotype LE, designated by Imchanitzkaja (1987)).

Beethovenia cerifera Engel (1865: 677). Type:— VENEZUELA. Táchira: La Grita, río Uribante, 2000–2650 m, *Engel*, s.d. (lectotype LE, designated by Imchanitskaja (1987)).

Ceroxylon schultzei Burret (1929: 846). Type:— COLOMBIA. Sierra Nevada de Santa Marta, San Lorenzo, 2200 m, *Schultze 811* (holotype B!).

Figs. 6a–b, 7c–d, 8f, 13, 14f, 18, 19b, 23.

Stem 7–10(–25)m tall, 14.5–28.0 cm diam., silverish, covered with a rather thin layer of wax. **Leaves** 8–12, horizontal or ascendant and arched, in a hemispheric crown, sometimes with on old leaf hanging; sheath 67–120(–180) cm long, 5.0–6.5 cm wide at apex, covered with thick, brownish, persistent indumentum; petiole 15–50 × 4.5–5.0 cm, wide, adaxially concave to flat on top, glabrescent, or with persistent, scale bases and some remnant scales towards margins, rounded abaxially, covered with appressed, grey-brownish scales; rachis 180–330 cm long, twisted 90° on distal portion thereby holding the pinnae in a vertical position, adaxially flattened in ⅓–⅔ of its length, then sharp, without a notorious hastula-like projection, the surface glabrescent with scarce remnants of scales, abaxially covered with thick and whitish indumentum; pinnae 86–116 on each side, regularly arranged in one plane, horizontal and straight to pendulous in the basal part of the leaf , the apices equilateral to briefly inequilateral by 0.2–0.5 cm, adaxial midrib and surface glabrous, abaxial midrib covered with one row of deciduous, translucent, thin, 1–7 mm scales, surface covered with silvery white to cream or brown, membranaceaous scales, immersed in furrows, arranged in closely adjacent, 0.1–0.3 mm wide rows, hiding leaf surface; the most basal filiform pinnae16–48 × 0.2–0.9 cm, basal pinnae (10th from base) 40–64 × 0.6–2.1 cm, middle pinnae 57–91 × 2.4–5.5 cm, (0.7–)1.8–2.8(–4.0) cm apart, apical pinnae 17–25 × 0.2–0.8 cm, never united along margins. **Staminate inflorescences** 1 or 2 at one time, erect; peduncle 83–96 cm long, covered with light–brown indumentum; prophyll 34–36 cm long, 13–14 cm wide; peduncular bracts 6–7, 46–167 × 7–12 cm, covered with persistent, brown to light–brown indumentum, and an additional, smaller, more distally inserted, membranaceous bract; rachis 44–73 cm long, with 52–75 branches, rachis and branches glabrescent, longest branches 34–36 cm long. **Pistillate inflorescences** 2–8 at one time, erect in flower, becoming arched and pendulous in fruit; peduncle 90–143 cm long, 1.6–3.0 cm wide at apex, toward

the base covered with persistent, woolly, light brown indumentum, glabrescent and green toward the apex; prophyll 25–42 cm long, 9–12 cm wide at base; peduncular bracts 6, 38–169 × 7–11 cm, and an additional, smaller, more distally inserted, 9–25 cm bract, all bracts covered with thick, brown or grey indumentum; rachis 49–90(–120) cm long, with 45–72 branches, subtended by a 0.5–3.2 mm long, membranaceous, acuminate bract, longest branches near the base, 26–49 cm, rachis and branches glabrescent. **Staminate flowers:** sepals 3 (–5), elliptical-acuminate, 1.0–1.5 mm, connate in 0.5 mm (⅓–½ of total length), reaching or exceeding edge of corolla tube; petals 3, elliptical-acuminate to alleznate, 3.5–6.0 mm, including a 1–2 mm acumen, connate in 0.5–1.0 mm; stamens (7–)8–10(–12), 3–6 antisepalous, and 3–6(–9) antipetalous, filaments 1.8–2.0 mm, inserted at basal 2/5–3/5 portion of anther, anthers 2.0–2.2 mm long, connective not projected. **Pistillate flowers:** sepals 3, elliptical-acuminate, 1.0–1.5 mm long, connate in 0.8–1.0 mm (½–⅔ of the total length), not reaching edge of corolla tube; petals 3, elliptical-subulate, 4–5 mm, including a narrow, 1 mm acumen, connate up to 1 mm; staminodes 9–12, with very thick, 0.5 mm filaments, and abortive anthers 1.5–2.0 mm. **Fruits** globose, orange-red when ripe, 1.4–1.5 cm diam., exocarp minutely granulose; fruiting perianth with sepals triangular-acuminate, 1–2 mm, connate in 0.5–1.0, lobes reaching or exceeding edge of corolla tube; petals elliptical-subulate, 3.5–5.0 mm long, including an acumen of 1(–2) mm long, widened at base, connate in 0.8–1.5 mm. **Seeds** ca. 1 cm diam.

FIGURE 23. *Ceroxylon ceriferum.* **a)** habit, Santa Marta, Colombia in the back; **b)** crown, note the small number of leaves and how the rachis rotates distally; **c)** habitat, Sierra Nevada de Santa Marta, Colombia; **d)** staminate palm.

Distribution and habitat:—In Venezuela, on the Cordillera de la Costa (Aragua, Miranda, Distrito Federal, Táchira), most commonly on the South slopes that head to the continent, and on the highest crests, and in Colombia, on the Northwestern side of the Sierra Nevada de Santa Marta (Magdalena, Guajira) and Serranía de Perijá (Cesar; Fig. 19b), in montane rain forest, at (1900–)2200–2800 m (Fig. 18), usually forming groups of many individuals.

Local names:—Palma de cera, palma de ramo (Colombia), siri (Arhuaco, Colombia), ramo bendito (Venezuela).

Uses:—In Colombia and Venezuela the young leaves are cut and used on Palm Sunday during the Holy Week. The stems are also used as columns, or split and used for walls in houses.

Conservation status:—In Venezuela, *C. ceriferum* has been recorded as Endangered according to the IUCN criteria, mainly due to the extraction of leaves for use during Palm Sunday in Holy Week, and demographic studies on this species have been seriously recommended (Llamosas *et al.* 2003). In Colombia the habitat of *C. ceriferum* has been altered to some extent, and the formerly large and healthy populations are today dramatically reduced. Fortunately, there are some areas of reserve that have been established in the last 20 years that protect some parts of the population. According to general observations, only populations on the steepest terrains have a well developed structure, including different size classes, while those on the flat terrains consist of mostly old individuals with few seedlings and juveniles, since those areas were cutoff more than 20 years ago for agricultural purposes, and only the adults that were already present were left standing. The offspring that is present now at the area was probably produced by the aldult individuals that attained sexual maturity in the last two decades.

Notes:—*Ceroxylon ceriferum* is diagnosed by having a crown with few leaves arched and twisted 90° on distal portion thereby holding the pinnae in a vertical position (Fig 23b) by its regularly arranged pinnae, almost horizontal and straight, small staminate flowers with 7 to 12 stamens (Fig. 7c–d), and fruit with exocarp minutely granulose (Fig. 8f).

Karsten first proposed the name *Klopstockia cerifera* in 1847, in his monograph on the vegetative organs of palms, in which he included an illustration of a seedling. He sent a detailed description of the palm to Martius, who published it under the name *Ceroxylon klopstockia*, citing Karten's letter and monograph. As Karsten's binomial is validly published, Martius' *Ceroxylon klopstockia* is illegitimate, being a superfluous name based on the same type.

Specimens examined:—COLOMBIA. **Cesar:** Serranía de Perijá, Municipality of Manaure, "El Cinco", Finca Vistahermosa, Southeast of the road, 72° 57' W, 10° 26' N, 2235 m alt., 14 November 1993, *M.Pardo et al. 277* (st.fl.) (COL); up from Los Eucaliptos, 3 km along road, 72° 57' W, 10° 26' N, 2640 m alt., 16 November 1993, *M.Pardo et al. 378* (st.fl.) (COL). **Guajira:** Cerro Pintado, El Espejo region, 2700 m, 12 November 1985, *H. Cuadros 2360* (pist.fl.) (MO). **Magdalena:** Municipality of Santa Marta, corregimiento Minca, vereda Bellavista, Sierra Nevada de Santa Marta, Cerro Kennedy,11°05'N 74°01'W, 2620 m, 14 January 1989, *A. Gentry & H. Cuadros 64664* (immat.fr.) (NY, MO); Cuchilla de San Lorenzo, near La Lagunita, on the way to Cerro Kenedy, 2475 m, January–1917, *M. T. Dawe* 703 (st.fl.) (K); 5 July 1920, *M. T. Dawe 795* (pist.fl., immat.fr.) (K); "Cleveland", above hacienda Cinncinati, ca. 2100 m, 5 August 1946, *M. B.Foster & E. Smith 1416* (st.fl.) (COL); between Cerro Quemado and Cerro San Lorenzo, 2600–2800 m, 17 April 1959, *Romero-Castañeda 7779* (immat.fr.) (COL); 2595 m alt., 11° 06' 38'' N, 74° 03' 06.6'' W, 2 November 2008, *G. Galeano et al. 7583* (mat.fr.) (COL, HUA), *G. Galeano et al. 7584* (st.fl.) (COL), *7585* (pist.fl., immat.fr.) (COL); Cebolleta, 2400 m, 2 February 1959, *Romero-Castañeda 7211* (st.fl.) (COL), *7218* (fr.) (COL).VENEZUELA. **Distrito Federal:** between El Junquito and Colonia Tovar, ca. 67° 15' W, 10° 25' N, cloud forest, 2300 m, 6 March 1968, G. *Wessels Boer et al. 2442* (immat.fr.) (NY), 2443 (st.fl.) (NY); 2000 m, 1 October 1963, *J. Steyermark 91612* (fr.) (BH, NY); 2400 m, 12 February 1966, *J. Steyermark 94797* (st.fl.) (US); Colonia Tovar, XI–1852, *M. Moritz 1672* (st.fl.) (BM, P); cloud forest on ridge West of El Junquito, 4 April 1962, *J. Steyermark* 90867 (pist.fl.) (NY). **Táchira**: source of the Quininarí River, near "Las Copas", at the base of la Peña de Pata de Judío, 15 km South of San Vicente de la Revancha, 30 km South of Alquitrana, Southeast of Santa Ana, 2400 m, 21 January 1968, *J. Steyermark et al. 101256* (fr.) (BH); 25 km S

of Delicias. (aprox.) 07°25' N 72° 30' W, 2450 m, 3 March 1968, *Wessels-Boer et al. 2436* (fr.) (NY) (MERC); Páramo de Zumbador, along road from La Grita to Táriba, 72° 5’ W, 7° 55´N, disturbed cloud forest, 2500 m, 2 March 1968, G. *Wessels Boer et al. 2433* (st.fl., fr.) (NY).

4. *Ceroxylon echinulatum* Galeano (1995: 399). Type:— ECUADOR. Napo: Road Quito-Tena, between Baeza and Cosanga, 00° 32'S, 78° 52'W, 1900 m alt., 6 May 1987, *H. Balslev et al. 62488* (fr.) (holotype QCA!, isotypes AAU!, COL!, QCNE!).

Ceroxylon alpinum Bonpl. ex DC. subsp. *ecuadorense* Galeano (1995: 395). Type:— ECUADOR**.** Pichincha: Road Quito–Santo Domingo, 4 Km to the E of Tandapi, 00° 25' S, 78° 47' W, 1600 m, 12 May 1987, *H. Balslev et al. 62512* (st.fl.) (holotype QCA!, isotypes AAU!, COL!, QCNE!).

Figs. 4a, 5a, 7n–o, 9a, 15a–b, 16c, 17a, 18, 19f, 24.

Stem 5–20(–25) m tall, 15–30 cm diam., white at base and turning green towards apex, covered with thin layer of wax. **Leaves** 7–15(–23), in a hemispheric crown; sheath 50–150 cm long, margins fibrous, abaxial surface covered with cream, floccose, lepidote indumentum, exhibiting a gradual transition to petiole; petiole 62–75(–85) cm long, 6.0–8.5 wide at apex, adaxial surface concave, waxy, glabrescent, margins acute, abaxial surface densely covered with persistent, cream-colored, 1–2 mm scales, with conspicuous, waxy, yellowish, 0.2–0.4 mm bases, and arranged in adjacent or interlocked rows, 0.3 mm wide; rachis 272–335 cm long, adaxially flattened in about ½ of its length, ending in a well-defined, 1–2 mm hastula-like projection, glabrescent to densely covered with light-yellow indumentum, abaxial surface covered (specially towards apex), with either persistent, yellowish, thick, waxy, 0.3–0.6 mm bases, or the whole scales appearing as white, linear threads and wooly fibres; pinnae 55–118 on each side, regularly arranged in one plane, slightly or completely pendulous, adaxial midrib glabrescent with visible scale base scars, abaxial midrib covered with persistent, linear, translucent scales, surface densely covered with persistent, padded, cream scales, shortly revealing leaf surface every 5–8 rows; the most basal filiform pinnae 20.5 cm × 0.6 cm, basal pinnae (10th from base) 39–78 × 0.6–3.0 cm, middle pinnae 89–115 × 3–4.5 cm, 1.5–4.0 cm apart, apical pinnae 13–49(–72) × 0.2–1.0 cm, the 5 apical pinnae sometimes joined at the tip. **Staminate inflorescences** 3 at one time; peduncle with scale base scars or scarce fibres of degraded scales; prophyll plus 4–6 peduncular bracts covered with very thin, translucent, fragile, scarce scales; rachis 84–123 cm long, with 65–100 branches, each subtended by a membranaceous acuminate bract, rachis and branches glabrescent, longest branches. **Pistillate inflorescences** 2–8 at one time; peduncle (60–)114–166 cm long, 3.0–3.5 cm wide at apex; prophyll 41–58 cm long, 12–14 cm wide at base; peduncular bracts 5, inserted at basal half of peduncle, 75–223 cm long, with a 6th smaller, distal one, 25–30 cm long, inserted near apex of peduncle, largest bracts 200–223 cm long; rachis 110–147 cm long, with (36–)63–85 branches, each subtended by a 0.5–2.8 cm long, membranaceous bract, longest branches 55–105 cm long; prophyll, peduncle, bracts and base of rachis covered with persistent, cream-colored scales, rachillae glabrous. **Staminate flowers:** sepals 3, triangular, acuminate, 1–2 mm long, connate in 0.3–0.5 mm (⅓–½ of total length), not reaching edge of corrolla tube; petals 3, elliptical to triangular, very long-acuminate, 5.5–8.0 mm long, including an acumen of 1.5–2.5 mm long, connate in 1.3–2.0 mm; stamens (9–)10–11(–12), 2–6 antisepalous stamens, and 6–9(–10) antipetalous stamens, filaments 1.0–1.5 mm long, anthers 2–3 mm long, anther connective not projected. **Pistillate flowers:** sepals 3, broadly triangular-acuminate, 1.0–1.5 mm long, connate in 0.6–1.0 mm (½–⅔ of total length), not reaching edge of corolla tube; petals 3, elliptical-acuminate, 5.0–6.5 mm long, including an acumen of 2–3 mm long, connate up to 1.2–2.0 mm; staminodes 9–11, 1 antisepalous, 2–3 antipetalous, filaments 1 mm long, abortive anthers 0.9–1.2 mm long, pistil green, trifid, 2–3 mm diam. **Fruits** globose, turning red when ripe, 1.3–2.2 cm diam., exocarp densely covered with prominent, irregular and acute bulges; fruiting perianth with very broadly

triangular sepals of 1.0–1.5 mm long, connate in 0.4–0.5, lobes not reaching or barely reaching edge of corolla tube, petals elliptical-acuminate, widened at base, connate in 0.7–1.0 mm.

FIGURE 24. *Ceroxylon echinulatum.* **a, b.** habit, former *C. alpinum* subsp. *ecuadorense*, in Ecuador near Tandapi (**a.** Photo: Jean-Christophe Pintaud); **c.** Habitat, in Ecuador, Napo, carretera Baeza–Tena.

Distribution and habitat:—Western and eastern Andes in Ecuador and Eastern Andes in Peru (Fig. 19f), in humid premontane and lower montane forest, at 1600–2200 m (Fig. 18), in pastures, coffee plantations, crop plots, and remnant forests. It forms populations of hundreds of individuals and apparently it was very abundant in the past. On the eastern Andes of Ecuador there are still extensive populations, especially of old individuals that are left standing in the middle of pastures, but regeneration is usually very abundant near forest patches left along streams (Borchsenius, pers. comm.)

Local names:—Ramito, palma de ramo, palma real, pumbo (Ecuador).

Uses:—The stems are used for building houses and fences. In the western and eastern Andes in Ecuador, the young leaves are used in religious processions on Palm Sunday (Borchsenius *et al.* 1998, Svenning & Balslev 1998, Borchsenius & Moraes 2006). The basal portion of the peduncle of young inflorescences is edible, and is cooked and added to salads (according to an informant in Valladolid, *A. Barfod et al. 60173, in scheda*). The fruits are eaten by pigs, and for this reason palms are often left standing on pastures (Borchsenius *et al.* 1998). The wax covering the stems was formerly used in Ecuador to make candles (*J. Steyermark 54130, in scheda*). Pintaud & Anthelme (2008) reported the use of this species in northern Peru as a source of wood for house construction and of fruits and infructescences for animal nutrition.

Conservation status:—*Ceroxylon echinulatum* was considered, according to the IUCN, Vulnerable in Ecuador, mainly due to deforestation and the cutting of young leaves for Palm Sunday (Borchsenius & Skov 1999, Valencia *et al.* 2000). Concerning the Western populations of this species, Svenning & Balslev (1998) have mentioned that although it is common in some areas, the survival of this species is threatened by the deforestation of its natural habitat. Pintaud & Anthelme (2008) consider that the destructive use of the stems of this species for house and fence construction, along with habitat loss due to forest clearing, is severely diminishing natural populations. These authors report the use of this species in agroforestry systems and its cultivation for wood extraction as a sustainable alternative that is already being implemented in the Upper Urumba Valley of northern Peru.

Notes:—This species now includes the former *C. alpinum* subsp. *ecuadorense* Galeano. The white indumentum of the peduncular bracts supporting this arrangement. Molecular studies (Trénel *et al.* 2007b)

presented the well-supported monophyly of these two entities according to AFLP, and a 6-gene data set (including PRK, *matK*, *trnD-trnT*, *ndhF*, and ITS), and also by finding active gene flow between these two populations. The evidence suggests that cline divergence and Quaternary dispersal have maintained the biological continuum between the populations of the morphotype described as *C. alpinum* subsp. *ecuadorense* and *C. echinulatum* in Ecuador (Trénel *et al.* 2008).

Ceroxylon echinulatum is diagnosed by its very long petiole, leaves arched with pinnae regularly arranged, slightly to completely pendulous; staminate flowers with 9–12 stamens (Fig. 7n–o) and very long-acuminate petals, and fruits with exocarp densely covered with prominent, irregular and acute bulges (Fig. 9a).

Specimens examined:—ECUADOR**. El Oro:** forests up from Paccha, 1920 m, 26 August 1943, *J. A. Steyermark 54130* (fr.) (F). **Napo:** Road Quito–Tena, via Baeza, 1860 m, 3 August 1984, *C. Dodson et al. 14843* (fr.) (AAU, MO); Cosanga, Mr. H. Erazo's Hacienda, secondary forest bosque near pastures, 0°37'S 77°52'W, 1900 m, 17 August 1992, *Paredes & Erazo 100* (pist.fl.) (QCA), *Paredes & Erazo 101* (st.fl.) (QCA), *Paredes & Erazo 102* (st.fl.) (QCA); Road Baeza–Tena, km 13,5 km before Cosanga, pastures along road, 0°32'16"S 77°52'45"W, 2000 m, 7 January 2004, *Borchsenius et al. 625* (immat.fr.) (AAU). **Zamora-Chinchipe:** Road Valladolid–Palanda , Km 2, 79° 08' W; 4° 34' S, 1900 m, 22 January 1987, *A. Barfod et al. 60173* (fr.) (AAU, COL, MECN, QCA); km 1.6, pastures, steep slopes along road plus shrubs, 04°33' 43" S 79°08'22"W, 1600 m, 11 January 2004, *Borchsenius et al. 639* (immat.fr. from ground) (AAU). **Pichincha:** Road Quito–Puerto Quito, on deviation towards Mindo, 00° 02' S, 78° 45' W, 1700 m, 10 May 1986, *H. Balslev et al. 62089* (st.fl.) (AAU). PERU. **Amazonas:** Rodríguez de Mendoza, Mariscal Benavides, Izcuchaca, 06°19' S 77°31' W, 1880 m, August 29 1998. *R. Vásquez & J. Campos 25311* (immat.fr.) (NY, MO). **Huánuco:** Provincia Leoncio Prado, Distrito Rupa–Rupa, Carretera a Aguaytia, en la divisoria por la entrada de la propiedad de la UNAS, 9º12'5.7" S 75º48'55" W, 1683 m, 6 July 2005, *B. Millán et al.* 1400 (immat.fr.) (USM). **Pasco:** Province Oxapampa, Río Yanachaga drainage, Hacienda Yanachaga, 10°32' S 75°32' W, 2280 m. 27 May 1983. *D. N. Smith & G. Pretel* 4197 (immat.fr.) (NY, MO); Río Yamaquizu Valley, Los Chacos, 2–9 km from the Oxapampa–La Merced road, 10°34' S 75°22' W, 2040–2160 m, 29 May 1883, *D.N. Smith 4215* (mm.fr.) (NY, MO); Oxapampa, outskirts of town, 11 September 1998, *A. Henderson et al. 3019* (pist.fl.) (NY); Parque Nacional Yanachaga Chemillén, parte Baja de la Quebrada San Alberto, 10°32' S 72° 21' W, 1900–2150 m, 27 March 2003. *A. Monteagudo et al. 4834* (immat.fr.) (NY, MO); 20 Km NE of Villa Rica on Road to Cacazu, 10°45'S 75° 10'W, 1600 m, 4 July 1988, *Gentry et al. 63244* (immat.fr.) (USM, MO).

5. *Ceroxylon parvifrons* (Engel) Wendland in Kerchove de Denterghem (1878: 239). *Klopstockia parvifrons* Engel (1865: 674). Type:—VENEZUELA. Mérida: páramo Tambur bei Iaji, 2650–3350 m, *F. Engel s.d.* (holotype B, destroyed, lectotype, here designated LE!).

Ceroxylon latisectum Burret (1929: 844). Type:— PERU. Amazonas: Province Luya, between Congón and Conila, 2950 m, 1 July 1915, *A. Weberbauer 7161* (fr.) (holotype B!, isotype US!, F(n.v.)).

Ceroxylon sclerophyllum Dugand (1953: 4). Type:— COLOMBIA. Norte de Santander: Tamá páramo, samaria slope, 2600–2900 m, 29 October 1941, *J. Cuatrecasas et al. 12734* (holotype COL!).

Ceroxylon mooreanum Galeano & R. Bernal (1982: 180). Type:— COLOMBIA. Antioquia: municipality of Bello, San Félix Inspection, Road to Alto Los Baldíos, ca. 2400 m, 12 August 1980, *G. Galeano & R. Bernal 213* (holotype COL!, isotype HUA!).

Figs. 2a, 7s–t, 8b, 14a, 18, 19i, 25.

FIGURE 25. *Ceroxylon parvifrons*. **a)** habit Páramo de Tamá, Norte de Santander, Colombia; **b)** habitat, at same locality; **c)** abaxial surface of leaf, note ferrugineous color of indumentum, and stiffness of pinnae; **d)** habit, note crown variations with respect to a), (former *C. mooreanum*), San Félix, Antioquia, Colombia; **e)** staminate inflorescence.

Stem 4–12(–17) m tall, (6–)10–30(–35) cm diameter, usually cylindrical, less frequently very thick at the base and thinner toward the apex, greyish, brown-grayish or brown, covered with a very thin layer of wax. **Leaves** (8–)12–15(–17), erect, arched, in a hemispheric or funnel-shaped crown; sheath 45–90(–104) cm long, covered with thick indumentum of intermixed, membranous, whitish to light-brown, more or less deciduous scales; petiole (13–)21–69(–90) cm long, (1.8–)2.5–6.0 cm wide at base, adaxially glabrescent, with ferrugineous, linear, translucent, very long (2–9 mm) scales, surface covered with brown, stiff, scales; rachis (80–)100–180(–270) cm long, notoriously arched, adaxially flattened in ¼–½ of its length, ending in a well-defined, 0.1–2.0 mm hastula-like projection, distal portion of adaxial surface of rachis covered with white,

deciduous scales, and abaxial surface covered with deciduous brown, thin, scales; pinnae (34–)49–84(–96) on each side of rachis, regularly and very closely inserted, arranged in one plane, erect, firm, leathery, plicate, apex inequilateral by 0.5–3.0 cm, adaxially dark green, smooth with the midrib prominent, covered with floccose, deciduous, scales and persistent scale bases, abaxial midrib covered with linear, translucent, brownish scales, surface covered with thick brown-ferugineous, or rarely yellowish scales; the basal filiform pinnae (14–)21–61 × 0.2–1.0 cm, basal pinnae (10th from base) (26–)37–86 × 1.0–1.6(–2.4) cm, middle pinnae (31–)46–94 × (1.5)3.5–5.5 cm, 1.5–3.5 cm appart, apical pinnae (10–)22–33 × 0.8–1.2 cm, usually free, usually free, rarely the apical 5–7 pinnae united along the margins. **Staminate inflorescences** with peduncle 84–100 cm long, covered with scale base scars or scarce fibres of degraded limb scales; prophyll 35 cm long; peduncular bracts 4–6, 40–114 cm long, covered with very thin indumentum of translucent, fragile scales; rachis 28–37 cm long, with 39–56 branches, each subtended by a membranaceous, acuminate bract; rachis and branches glabrescent; longest branches 13–25 cm long. **Pistillate inflorescences** 2–5at one time; peduncle (72–)106–248 cm long, (1.0–)1.5–3.5 cm wide at apex, covered with ferrugineous, persistent, brownish indumentum; prophyll (18–)30–53 cm long, 5–15 cm wide at base; peduncular bracts 4–6, 29–285 cm long, and sometimes an additional, smaller, more distally inserted, 11 cm bract, all bracts covered with floccose, very thin and fragile, brown indumentum; rachis 29–97 cm long, with 34–58 branches, each subtended by a 0.5–2.0 mm long, membranous, acuminate bract; longest branches (12–)28–60 cm long; rachis and branches glabrescent. **Staminate flowers:** sepals 3, ovate–acuminate, 1.0–1.5 mm, connate in 0.4 mm (⅓–½ of total length), not reaching total length of corolla tube; petals 3, ovate–acuminate, 4–6 mm, including an acumen of 1.5 mm, connate in 1.5–2.0 mm, apex very long-acuminate; stamens (6–)8–11, 3–5 antisepalous stamens, and 3–6 antipetalous stamens, filaments 1.5–2.0 mm, inserted at basal 2/5–3/5 portion of anther, anthers 2–3 mm, anther connective not projected. **Pistillate flowers:** sepals 3, triangular-acuminate, 1.0–1.2 mm, connate in 0.8–1.0 mm (½–⅔ of total length), not reaching corolla tube; petals 3, ovate–acuminate, 3.5–5.0 mm, including an acumen of 1.3–1.5 mm, connate up to 1 mm; staminodes 6–11, with very thick filaments of 1.5–2.0 mm, abortive anthers 1.0–1.5 mm; pistil trifid, 2–3 mm diam. **Fruits** globose, orange-red when ripe, 1.3–2.2(–2.5) cm diam., exocarp smooth; fruiting perianth with sepals triangular-acuminate, 1.0–1.5 mm long, connate in 0.3–1.0, lobes not reaching or reaching the corolla tube; petals ovate-acuminate, 2.5–4.5 mm long, including an acumen of 1.0–1.5 mm long, widened at base, connate in 0.3–1.0 mm. **Seeds** 1–2 cm diam.

Distribution and habitat:—Widely distributed throughout the Andes from Venezuela (Mérida, Táchira) and Colombia to Ecuador, Peru and Bolivia (Fig. 19i), in wet montane forest, at 2100–3150(–3500) m (Fig. 18), usually found above 2600 m. Sometimes it forms populations of several individuals. Among the species of *Ceroxylon* and all palms it grows at the highest elevations in the world (3500 m in Ecuador; Borchsenius & Moraes 2006).

Local names:—Ramo, palma ramo, palma real (Colombia), ramos, palma real (Ecuador), palma de cera (Venezuela).

Uses:—The young leaves are traditionally cut to be used on Palm Sunday during Easter. In Ecuador, the wax from the stem was used for making candles (Borchsenius *et al.* 1998).

Conservation status:—In Venezuela, *C. parvifrons* has been categorized as Endangered according to the IUCN criteria, mainly due to habitat destruction caused by deforestation practices for agricutural purposes (Llamosas *et al*. 2003). In Colombia it was categorized as Nearly Threatened (NT; Galeano & Bernal 2005) because, although it is a species that is widely distributed along the country—therefore not fitting into a threat category, deforestation processes in the Andes are so vast that populations are expected to have been severely diminished. It is strongly emphasized that complete, and updated information on the conservation status of this species is necessary.

Notes:—This species is surprisingly constant in its morphology. It is easily recognized from a distance by its markedly arched leaves with ascending pinnae, resulting in a obovoid to fountain-shaped crown, its very stiff pinnae, and its smooth and large fruits (up to 2.5 cm). In spite of this morphological stability there are populations with stouter individuals, both in Ecuador (Zamora-Chinchipe, Loja) and in Colombia (Quindío, Huila, Tolima), but apparently this trait is not correlated with special ecological factors. Some individuals may

also be smaller than usual, with slender stems and smaller leaves, but this reduction in size is apparently associated with very exposed, windy habitats on mountain ridges.

Specimens examined:—BOLIVIA. **La Paz:** Prov. Nor Yungas, eastern slopes of the Cordillera Real (ca. 65 km) to the East of la Paz, on the road Unduavi-Coroico, 21 January 1975, *A. Anderson 2* (pist.fl., immat.fr.) (COL, K, US); en camino de Chupispata a Caranavi,16º17'21" S 67º48'19"W, 2722 m, 5 September 2007, *J. Roca, L.R. Moreno, O. Moreno 345* (sterile.) (LPB); a 5 km from Chuspipata towards La Paz, 2720 m, 14 July 1987, *M. Moraes & H. Balslev 850* (AAU, COL, LPB, US); Franz Tamayo, Parque Nacional Madidi, Keara, campamento Tocoaque, 14º37'05"S68º57'06"W, 2340 m, 6 November 2007, *A. Araújo-Murakami & A. Fernández 3996* (immat.fr.) (LPB); Madidi, Piñalito, 29 Km en línea recta al este de Apolo por el camino a San José de Uchupiamonas, trayecto 3,5 km, 14º29'40"S 68º16'30"W, 1900–2496 m, 16 July 2002, *A. Fuentes, R Alvarez, A. Araújo, H. Pariamo, F. Bascopé & M. Villanueva 5031* (juv.) (LPB); entre Tokoake y Chunkani, 14º37'52" S 68º57'37" W, 2673 m, 27 June 2005, *A. Fuentes, E. Cuevas y R. Cuevas 8858*, (inmat.fr.) (LPB); Provincia B. Saavedra, ANMI Apolobamba, Ininlaa, subiendo e Sita por senda de Incienseros, 15º11'41"S 68º38'36" W, 2200 m, 27 April 2005, *A. Fuentes, R. Cuevas, E. Cuevas & H. Pariamo 7416* (veg.) (LPB). COLOMBIA. **Antioquia:** Municipality of Belmira, El Páramo farm, 3060–3130 m, 21 April 1993, *D. Tuberquia & R. Fonnegra 174* (immat.fr.) (COL, HUA). **Cauca:** "El Ramal" to Riosucio, West of Popayán, 1800–2000 m, 3 July 1922, F. Pennell & E. Killip 8266 (st.fl.) (NY, US). **Huila**: between Paletará and Istmos, Istmos cabin, "Planada Achupayal de pericos", 2780 m, 21 October 1987, *A. Duque 702* (fr.) (COL). **Norte de Santander:** municipality of Toledo, track to Páramo de Tamá, Samaria region, 2500–2600 m, 21 March 1987, *R. Bernal & G. Galeano 1357* (st.fl., fr.) (AAU, BH, COL, FTG, NY); municipality of Herrán, Parque Natural Nacional Tamá, Orocué sector, towards Alto del Pesebre, 2650–3020 m, 2 April 1987, *G. Lozano et al. 5554* (fr.) (COL). **Putumayo:** Road Pasto–Sibundoy, Vereda Santa Clara, 10 km West of Santiago, 2870 m, 22 February 1988, *R. Bernal & G. Galeano 1424* (st.fl.) (AAU, BH, COL, HUA, K, NY); road El Encano-Sibundoy, down from the Páramo de Quilinsayaco, 3100 m, 13 June 2000, *R. Bernal et al. 2472* (seedling) (COL). **Tolima:** "Perales, on the Quindío," 1918, *M. T. Dowe 795* (NY). **Quindío**: municipality of Salento, Alto Quindío, La Marina, 3150 m, October 1992, *W. Vargas 676* (fr.) (COL). **Valle:** Los Farallones de Cali, Pance river basin, East slope, Cuchilla Hato Viejo, 3000 m, 25 August 1991, *E. Calderón 100B* (seedling) (COL); municipality of Tuluá, 2–3 km from Santa Lucía to Alto La Italia, Central Cordillera, 2950–3130 m, 7 March 1988, *R. Bernal et al. 1437* (fr.) (COL). ECUADOR. **Azuay:** West of Patul, 3 km between Huahualcay and Patul river, below Pasas de Piglión, 2670–3275 m, 19 May 1943, *J. Steyermark 52632* (seedling) (US). EL ORO: between Curtincapa and Guagra Uma, 8 miles northeast of Curtincapa on southwest slopes leading to Chapel, 1500–2895 m, 6 August 1943, *J. Steyermark 53916* (fr.) (F). **Bolívar:** Guaranda, Comuna Matiaví–Salinas, Bosque protector Peña Blanca, 01°22'S 79°05'W, 2150–2650 m, 23 January 1994, *A.Alvarez et al. 1135* (immat.fr.) (QCNE, MO); Bosque Protector Mashallingo, Recinto El Arrayán, 01°22'S 79°04'W, 3200 m. 27 January 1994, *Alvarez et al. 1271* (immat.fr.) (QCNE, MO). LOJA: Parque Nacional Podocarpus, Cajanúma, at Casa Predesur, 04°09'S 79°09'W, 3000 m, 23 February 1985, *S.Laegaard 53624* (juv.) (AAU); Loja–Las Palmas, Cerro El Tambo, just S of Cerro Villonaco, roadside and secondary forest,04°04'S 79°14'W, 2570–3020 m, 23 July 1990, *P. Jorgensen et al. 92089* (immat.fr.) (QCA); Nudo Sabanilla, S of Yangana, 4°23'S 79°10'W, 2330 m, 20 August 1982, *Clements 2375* (immat.fr.) (QCA); km 14–15 (S of Loja), 04°25'S 79°10'W, 2300–2350 m, 10 August 2000, *H. Balslev 6524* (infr.) (QCNE, MO). **Pichincha:** New road Quito–Santo Domingo, ca. 1 km W of Aloág, hacienda Gualilagna de Lasso, 2800 m, 21 May 1987, *H. Balslev et al. 62547, 62548* (pist.fl., fr.) (AAU, COL, QCA); Quito, Eufrasia school, cultivated, 2860 m, 6 July 1983, *A. Arguello & E. Fegan 304* (bare infr.) (QCA); Cantón Ruminiahui, Parroquia Amaguaña, Pasochoa protector forest, very moist montane forest, on the way to the summit of the Pasochoa, 00° 27' S 78° 28' W, 2800–3500 m, 7 February 1988, *C. Cerón & R. Alarcón 3554* (old infl.) (MO); 10 September 1988, *C. Cerón & R. Alarcón 4840* (sterile) (MO); Pasochoa west slope in Pasochoa protector forest, 78° 25' W 00° 25' S, 3000 m, 30 May 1987, *U. B. Mathiesen 62561* (AAU). **Zamora-Chinchipe:** Loja–Zumba road, 10 Km North of Valladolid, 79°10'W 04° 29'S, 2450 m, 16 May 1987, *H. Balslev et al. 62533* (fr.) (AAU, COL, QCA, QCNE); Yangana–Valladolid road, Km 13, 04 °25 S

79°10 W, ca. 2200 m, 21 January 1987, *A. Barfod et al. 60164* (pist.fl.) (AAU, COL, MECN, QCA); Road Loja–Zamora km 20, at San Francisco Field Station, north–facing slopes towards quebrada San Francisco, 03°58'S 79°03'W, 2300 m, 3 August 2000, *H. Balslev 6498* (juv.) (QCNE, QCA, AAU); Parque Nacional Podocarpus, road Yangana–Valladolid, km 21, wet montane forest, 79° 09' W 04° 28' S, 2650–2750 m, 2 December 1988, *J. E. Madsen et al. 75834* (AAU). PERU. **Cajamarca:** Province Cutervo, Madre Mía, between El Suro and La Flor, NE of the Parque, 2400 m, 25 June 1992, *I. Sanchez Vega & A. Miranda 6336* (immat.fr.) (CPUN, NY); lower edge of Cutervo National Park, 10–15 Km N of San Andrés de Cutervo, montane cloud forest, 06°10'S 78°40'W, 2200–2250,11 February 1988, *A. Gentry et al. 61492* (mat.fr.) (USM, MO). **Amazonas:** Bongará, 5 hours driving from Celendín to Leymebamba, 3000 m, 20 October 1990, *F.Kahn & F. Moussa 2966* (fr.) (USM), *2967* (fr.) (MHNSM, MO). **Cuzco:** Province La Convención, Distr. Echarati, E to Río Apurimac NE to Pueblo Libre, up Mountain of Anchihuay & Bellavista, S cordillera Vilcabamba, 12°51' S 73° 30' W, 2445 m, 3 August 1998, *P.Núñez et al. 23230* (immat.fr.) (USM, US).

6. *Ceroxylon parvum* Galeano (1995: 403). Type:—ECUADOR. Road Chaguapamba-Loja, 12 km West of Olinedo, 3° 55' S, 79° 40' W, 1500 m, 15 May 1987, *H. Balslev et al. 62529* (fr.) (holotype QCA!, isotypes AAU!, COL!, QCNE!).

Figs. 9c, 12c, 18, 19d, 26.

Stem 2.5–6.0 m tall, 9–28 cm diam, white at base and turning green towards apex, covered with a very thin layer of wax. **Leaves** 11, in a dense, spherical crown, with dead leaves hanging; sheath 78 cm long, adaxially glabrescent, abaxially covered with a deciduous layer of scales; petiole 10 cm long, covered with indumentum like that of the sheath; rachis 168 cm long, adaxially flattened in ½ of its length, glabrescent, abaxial surface covered with deciduous, membranous scales; pinnae 102–109 on each side, arranged in groups of 2–6, abaxial surface and midrib covered with elliptical, yellowish, 1 mm scales, with 0.3–0.5 mm bases, and arranged in adjacent 0.25 mm wide rows. **Staminate inflorescences** not seen. **Female inflorescences** 4 at one time; peduncle 133 cm long, 1.5 cm wide at apex; prophyll 30 cm long, 7.5 cm wide at base; peduncular bracts 5, 47–155 cm long; rachis 65 cm long, with ca. 55 branches, each subtended by a 0.2–0.6 cm membranous bract; longest branches 31 cm long; prophyll, peduncle, bracts and base of rachis covered with brown, persistent, lepidote indumentum, rachillae glabrous. **Pistillate flowers:** sepals 3, broadly–triangular–acuminate, 1.0–1.5 mm long, connate in 0.6–1.0 mm (½–⅔ of total length), not reaching corolla tube, petals 3, elliptical-acuminate, 5.0–6.5 mm long, including an acumen of 2–3 mm long, connate up to 1.2–2.0 mm; staminodes (7–)9–11, 1 antisepalous, 2–3 antipetalous, filaments 1 mm long, abortive anthers 0.9–1.2 mm long, pistil green, trifid, 2–3 mm diam. **Fruits** globose, orange-red when ripe, 1–2 cm diam., exocarp smooth to slightly warted; fruiting perianth with sepals triangular-acuminate, 1.0–1.5 mm long, connate in 0.3–1.0, lobes not reaching or reaching the corolla tube; petals ovate-acuminate, connate in 0.3–0.7 mm long, widened at base. **Seeds** 1.0–1.2 cm diam.

Distribution and habitat:—Southwestern cordillera of the Ecuadorian Andes (Fig. 19d), at 1500 m elevation, in premontane forests. It is only known as isolated individuals, not forming large populations, and usually kept standing on pastures.

Notes:—This species ressembles *C. pityrophyllum*, and some specimens that had been determined as *C. parvum* are here placed under *C. pityrophyllum*. However, *C. parvum* has slender filaments (of the staminodes), and staminodes that vary in number from 7–11, whereas *C. pityrophyllum* has broad-based filaments of the staminodes (Fig. 17b), and stamens and staminodes are always six in number. Apparently, *C. parvum* is a species that does not form large stands, while *C. pityrophyllum* does. It grows far from *C. pityrophyllum*, and only on the Western slopes of the Ecuadorian Andes.

Specimens examined:—ECUADOR. **El Oro.** Road Loja–Machala, km 13 past Olmedo. Pastures and scrubs in ravines. 3° 54' 28" S 79° 39' 32" W, 1530 m, 12 January 2004, *F. Borchsenius et al. 649* (st.fl.) (AAU).

FIGURE 26. *Ceroxylon parvum.* **a)** habit, note dense crown with spherical outline; **b)** stem, note thin layer of wax; **c)** leaf and infructescence.

7. ***Ceroxylon peruvianum*** Galeano, Sanín & Mejía (2008: 65).Type:— PERU. Department of Amazonas: Province Bongará, District Jazán, Pedro Ruiz trail to Gocta Falls, 06°03'0.4" S 77°53'18.2" W, 1800 m, 14 November 2007, B. Millán, J.C. Pintaud & L. Noblick 1488 (mat.fr.) (holotype USM!, isotypes, COL!, AAU!).

Figs. 4b, 7p–r, 9b, 14c, 18, 19h, 27.

Stem 8–12 m tall, 20–26 cm diameter, silver to light grey with thin layer of wax. **Leaves** 13–21, in a hemispheric crown; sheath 130–168 cm long, 5–7 cm wide at apex, with scarcely fibrous margins, covered with white tomentum; petiole 25–60 cm long, 3.5–8.0 cm wide, flat to convex, green and with scarce indumentum above, convex and densely covered with white to light brown tomentum below; rachis 240–362 cm long, adaxially flattened in ca. ⅔ of its length, abaxially covered with thick, white tomentum; pinnae 96–140 on each side, irregularly arranged in groups of 2–6, inserted in several planes, usually the proximal pinnae ascendant, the distal descendent, pinnae stiff up to the middle of their length, then pendulous, apex slightly asymmetric, midrib prominent, adaxial surface glabrous, glossy, dark olive green, abaxial surface covered with thin, white to yellowish indumentum, sometimes revealing the pinnae surface in between files; lowermost, filiform pinnae 7.0–41.5 × 0.2–1.0 cm, basal pinnae (10th pair, from base) 37–51 × 0.8–1.3 cm, middle pinnae 63–93 × 3.5–5.0 cm, apical pinnae 21–46 × 0.7–3.0 cm, 2–9 apical pinnae united along margins. **Staminate inflorescences:** peduncle 48–67 cm long, 4 cm wide at base; peduncular bracts 149.0–169.5 × 23–27 cm; rachis 81–102 cm long, with 72–99 branches, the longest branches up to 42 cm long. **Pistillate inflorescences** 144 cm in the fruiting stage; peduncle 62–90 cm long, 5.7 cm wide at apex; prophyll 31 cm long; peduncular bracts up to 118–220 cm long; rachis 77–134 cm, with 61–78 first order branches, the longest ones 79 cm long. **Staminate flowers**: sepals 3, ovate, 1 mm long, connate for ½ their length, lobes reaching ½ to the total height of the corolla tube; petals 3, ovate-acuminate, 4–7 mm long, including a 1 mm acumen, connate up to 1.0–1.5 mm (1/6–1/4 of their length); stamens 12–15, 3–9 episepalous and 6–9 epipetalous, filaments 1.0–1.5 mm long, anther 2.0–2.2 mm long, round at apex**. Pistillate flowers** not seen. **Fruits** globose, 2.0–2.3 cm long, 2.0–2.2 cm wide, green turning red when ripe, mature exocarp densely

covered with irregular and acute bulges; fruiting perianth with a persistent calyx about 1 mm long, reaching ½ the total height of the corolla tube; petals 4–5 mm long, connate for up to 2 mm (⅓–½ their length). **Seeds** ca. 1.5 cm diam.

FIGURE 27. *Ceroxylon peruvianum.* **a)** habitat, near Pedro Ruiz, Amazonas, Peru; **b)** habit, at town of San Carlos, Province Amazonas.

Distribution and habitat:—Eastern slopes of the northern Peruvian Andes (Fig. 19h), in humid premontane to montane forest at 1500–2300 m (Fig. 18), in areas currently heavily deforested to establish agricultural activities, where it remains as isolated individuals on forest fragments or in the middle of the farms.

Local names:—Pona (Peru)**.**

Uses:—Cultivated as an ornamental plant, in towns and farms. The stems are used for posts, fences and house construction; the leaves are occasionally used for thatching and the fruits are fed to pigs (Galeano *et al.* 2008).

Notes:—*Ceroxylon peruvianum* is very distinctive in its irregularly arranged pinnae (Fig. 4b), combined with staminate flowers bearing 12–15 stamens (Fig. 7p–r), and the exocarp densely covered with acute bulges (Fig. 9b).

Specimens examined:—PERU. **Amazonas:** Province Bongará, District San Carlos, cultivated in the town of San Carlos, 05°57’51.1” S, 77°56’50.4” W, 1830 m, 15 November 2007, *B. Millán et al. 1497* (mat.fr.) (USM); cultivated in the town of San Carlos, 05°57’57.8” S 77°56’37.2” W, 1880 m, 15 November 2007, *B. Millán et al. 1498* (st.fl.) (AAU, COL, NY, P, USM); same locality, 15 November 2007, *B. Millán et al. 1499* (immat.fr.) (AAU, COL, NY, P, USM); Province Bongará, District Jazán, cultivated near way to San Pablo, Pedro Ruiz road Chachapoyas, 06º03’31.8” S, 77º55’38.28” W, 1569 m, 16 March 2006, *B. Millán & J.C. Pintaud 1354* (immat.fr.) (USM); same locality, 16 March 2006, *B. Millán & J.C. Pintaud 1356* (seedling) (USM). Province Bongará, road from Pedro Ruiz to Moyobamba, km 12, October 1990, *F. Kahn and F. Moussa 2704* (immat.fr.) (USM). Province Bongará, Road Pedro Ruiz to Moyobamba, km 340–350, Buenos Aires, 5° 45’S 77° 47’W, 2300 m, 30 August 1983, *D. Smith & S. Vásquez 4854* (mat.fr.) (MO, USM); District Yambrasbamba, Anexo Vilcaniza, por la carretera destapada que va a Corosha, a 3 km de la carretera Pedro Ruiz-Tarapoto, 05°47’11,1” S 77°52’51,2” W, 1702 m, 21 October 2009, *M.J. Sanín, N. Vega y S.L. Vega-Güivín 05* (fr.) (USM, COL).

8. *Ceroxylon pityrophyllum* (Martius) Martius ex Wendland in Kerchove de Denterghem (1878: 239). *Cocos pityrophylla* Martius in d'Orbigny (1847: 99). Type:—BOLIVIA. Yungas, vertiente Este de la Cordillera de La Paz, cima de la montaña cerca a Carcuata, entre Carcuata y Cescueta, ca. 2600 m, *d'Orbigny, s.n.* (holotype, P lost). Neotype (designated here):—BOLIVIA. Department La Paz: Provincia Inquisivi, Comunidad Choquetanga, Valle Chimu, Valle lateral al Río Chimu, 16º48'S 67º15'W, 3000 m, 26 January 1994, *N. Salinas 2440*, (neotype LPB!).

Ceroxylon weberbaueri Burret (1929: 848). Type:—PERU. Puno: between Tambo Yuncacocha and Tambo Cachicachi (road from Sandía to Chunchusmayo), 1800–2000 m, 8 June 1902, *A. Weberbauer 1157* (holotype B, destroyed). Neotype (designated by Pintaud *et al.* 2010): PERU. Región Puno: Prov. Sandía, Dist. San Juan del Oro, loc. Siyacunga, 14°14'18.8"S, 69°10'40.2"W, 1775 m, 23 March 2010, (st.fl.), *B. Millán & F. Kahn 1701* (neotype USM!).

Figs. 7j, 9d, 15e, 17b, 28

Stem 4–20(–22) m tall, 9.9–30.0(–40.0) cm diam., green, covered with a very thin layer of wax. Leaves 12–20(–25), in a spheric crown, often grayish and with persistent, dried hanging leaves; sheath 40–124 cm long, 3.8 cm wide at apex, petiole 10–105 cm long, adaxially flat and slightly raised in the middle, green, glabrescent towards the middle, lepidote towards margins, abaxially covered with thick layer of persistent, yellowish stiff scales; rachis arched, 130–290 cm long, adaxially flattened in 1/2–3/5 of its length, ending in a well-defined 0.6 m hastula-like projection, that appears as if leaned to one side, glabrescent, abaxially convex, covered with scales like those on petiole; pinnae (47–)85–134 on each side, pinnae disposition and insertion variable, arranged in groups of 2–8(–13), and separated by 2.5–5.5 cm, inserted in many planes, or sometimes in very slightly divergent planes, sometimes pinnae inserted regularly on the basal and/or distal third of the rachis and in one plane, and sometimes almost regularly arranged in juveniles, the adaxial surface glabrous, the midrib bearing some persistent scale bases, the abaxial surface and midrib covered with yellowish linear; the most basal filiform pinnae 15–32 × 0.2–0.5 cm, basal pinnae (10th from base) 32–63 × 0.6–1.0 cm; middle pinnae 41–83 × 2.2–4.0 cm, apical pinnae 15–60 × 0.2–2.0 cm, the apical pinnae sometimes united along margins. **Staminate inflorescences** 3–4 at one time, with a peduncle 40–121 cm long, glabrescent; prophyll 40 cm long, peduncular bracts 5–7, (24–)37–188 cm long, 6–8 cm wide; rachis 52.5–76.0 cm long, with 56 branches, rachis and branches glabrescent, longest branches 27–42 cm long. **Pistillate inflorescences** 4–8 at one time; peduncle 69–185 cm long, 2 cm wide at apex; prophyll 17–45 cm long; peduncular bracts 4–6(–8), 37–180 cm long; rachis 47–93 cm long, with 33–50 branches, each subtended by a 0.2–0.6 cm long, membranaceous bract, longest branches 21–54 cm long; prophyll, peduncle and bracts covered with persistent, brown to ferrugineous scales, rachillae glabrous. **Staminate flowers:** sepals 3, elliptic, acuminate, 0.9–1.5 mm long, connate in 0.3 mm (1/3–1/5 of total length), not reaching the total length of corolla tube; petals 3, elliptic, long-acuminate, 4.5–6.0 mm long, including an acumen of 0.4–1.5 mm, connate in 2.0 mm, thin and membranaceous; stamens 6, conspicously exserted from the petals, alternating one antesepalous stamen, and one antepetalous stamen, filaments 1.0–1.5 mm long, very thick and swollen at base (triangular; Fig. 17), inserted at basal ¼ to center of anther, anthers 4.7–7.0 mm long, anther connective not projected. **Pistillate flowers:** sepals 3, broadly triangular, acuminate, 1.0–1.5 mm long, connate in 0.5–0.8 mm (½–⅓ of total length), not reaching the corolla tube; petals 3, elliptic, acuminate, 3.5–5.0 mm long, connate up to 1.2–1.5 mm, acumen narrow, 1 mm long; staminodes 6, alternating 1 antisepalous, 1 antipetalous, filaments 1 mm long, with very broad bases like filaments of stamens, abortive anthers 2.0–2.2 mm long. **Fruits** subglobose, orange-red when ripe, 1.7–1.9 cm diam., exocarp smooth when fresh and minutely verrucose when dry, with conspicuous black lenticels in maturation, sometimes the other 2 carpels developed to some point; fruiting perianth with sepals 1.0–1.5 mm long, connate in 0.5–0.8, lobes not reaching corolla tube, petals very wide at base, 3.5–5.0 cm including a 1 mm acumen, connate in 1–2 mm, staminodes 6, filaments very broad-based, and anthers caducous. **Seeds** 1.2–1.4 cm diam.

FIGURE 28. *Ceroxylon pityrophyllum*. **a)** habitat (forest fragments), near Postrervalle, Province Vallegrande, Department Santa Cruz, Bolivia); **b)** size of anthers (smallest ruler division = 0,5 mm; *Canqui et al. 351*; Photo: Ana Patricia Antezana); **c)** habit, Province Vallegrande, Department Santa Cruz, Bolivia; **d)** some variations in pinnae aggregation; **e–f)** habitat, cloud forest, same Province.

Distribution and habitat:—Known from the Andes in Bolivia (La Paz, Cochabamba, Santa Cruz and Chuquisaca) and Southeastern Andes of Peru (regions Cuzco and Puno; Fig. 19g), at 1285–2800 m, on slopes in patches of cloud (Fig. 28a, e–f), semi-deciduous, or deciduous forest (in the Yungas humid forest, the deciduous mountain Chaco forest, and the Tucumano-Boliviano forest). It is often observed along with *Parajubea* (Kessler & *al*. 5683, *in scheda*), with *Podocarpus parlatorei* Pilg., *Ternstroemia asymmetrica* Rusby, or in cloud forests disturbed by grazing, or in transitional forests between cloud forest and dry forests, mixed with *Podocarpus* sp., *Anadenanthera colubrina* (Vell.) Brenan and other Fabaceae and Myrtaceae; above limits of subtropical deciduous dry forests (Vargas & al. 2270, *in scheda*), Lauraceae, Myrtaceae and *Dictyocaryum lamarckianum* (Mart.) H. Wendl. (Paniagua & *al*. 5869, *in scheda*), but never in dry forest (Nee & Vargas 38268, *in scheda*). It can form populations of over several hundred trees along ridgetop (Nee & Vargas 38268, *in scheda*), but is mostly seen as scattered sub-canopy individuals. In Perú, it is conserved in cultivated plots and favored in shade coffee plantations, where it can be more abundant than in natural conditions (F. Kahn *et al*., *in scheda*). Nevertheless, most of the natural habitat is being rapidly converted to pastures and cultivation farms (Nee & Solomon 30324, *in scheda*).

Local names:—Palma amarilla, palma real, palmera (Bolivia), vicuña palmito, morona (Peru).

Uses:—The young leaves are cut for Palm Sunday during the Holy Week, and the stems are used for posts, water canals, and thatching in home construction.

Conservation status:—This aspect has not been evaluated, but in Bolivia the species often grows in isolated forest fragments (Fig 28a).

Notes:—*Ceroxylon pityrophyllum* is very distinct in its large anthers (the largest in the genus, and almost twice the size that in other species; Fig. 28b). It ressembles *C. parvum* in its habit and hanging dry leaves; nevertheless, *C. parvum* has (6–) 9–11 slender staminodial filaments instead of six stamens and staminodes with swollen bases (Fig. 17b).

The habit of *C. pityrophyllum* can also resemble that of *C. vogelianum*, particularly in the case of slender individuals (Fig 28c), but the texture of the fruit exocarp (smooth to minutely verrucose in *C.pityrophyllum*, whereas always furrowed in *C. vogelianum*), and the length of the anthers (4.5–7 mm in *C.pityrophyllum* (Fig. 28b), while 2–2.5 mm in *C. vogelianum*), are key characters for distinguishing these species apart.

All the specimens from Bolivia that have been previously identified as *C. parvum* (Galeano 1995) or *C. vogelianum* belong in fact to *C. pityrophyllum*. *C. parvum* appears to be restricted to south-western Ecuador while *C. vogelianum* extends from Venezuela to southern Peru (Cuzco).

Ceroxylon pityrophyllum is morphologically very variable: it varies in size from 4 to 22 m tall; the wax on the stem and abaxial surface of the leaves can be thin or very thick; the leaf rachis arching and flexible or stiff and horizontal, and the orientation and disposition of the pinnae in 2 or in many planes, and almost regular (or even regular in juveniles) to conspicuously grouped. However, the reproductive characters such as the stamen number, the size of the anthers, the width of the staminodial filaments, and the texture of the fruit exocarp, are always constant characters throughout its geographic distribution.

Regarding the confusion with the name *C. pityrophyllum*, causing its designation as *Species dubia* by Burret (1929) and its exclusion as "Uncertain names" in Henderson *et al*. (1995), the following statements can be put forward. The holotype (of the name *Cocos pityrophylla* Martius) lost in P does not belong to the genus *Cocos*, as Govaerts & Dransfield (2005), and Glassman (1972) suggest. The corrections made by Martius, who saw the type, "pinnis … subtus squamilus parvis lanceolatis albidis", can only refer to *Ceroxylon*, not *Cocos*. Even though Burret (1929) explains that the observation "infrafoliar inflorescences, and rachis branched only to first order" could only be an error, he does not exclude the possibility of this being *Cocos*; therefore his designation of the species as *species dubia*. On the basis of recent observations in the area, the only genus growing in or near the type locality that combines the characteristics mentioned by Martius (1847; abaxial surface of pinnae pale, lepidote, inflorescences infrafoliar, rachis branched to first order) is *Ceroxylon*.

Lastly, many specimens of *C. pityrophyllum* from Bolivia had been determined as *C. vogelianum*, based on several premises: the first, that *C. vogelianum* actually grew in Bolivia, the second, that the staminate flowers with six stamens and the grouped pinnae inserted in many planes were characters found together only

in this species. Fieldwork in several departments has been carried out, and all of the collections of *Ceroxylon* from Bolivia have now been revised, not one belonging to *C. vogelianum* (see discussion above).

Ceroxylon weberbaueri Burret still grows in its type locality in Peru (Pintaud *et al.* 2010), area which forms an ecological continuum with the type locality of *C. pityrophyllum* in La Paz. All of the recent collections from both localities are the same species, and correspond to the original descriptions for both names. Therefore, the decision of which name to keep was taken regarding the date of publication (1847 vs. 1929).

Specimens examined:—BOLIVIA: **Chuquisaca**. Provincia Luis Calvo, Municipio Villa Vaca Guzmán, Comunidad Entierrillos, Parque Nacional y Área Natural de Manejo Integrado Serranía de Iñao, sendero de subida a la Laguna de Iñao, 19º32'36.8"S 63º54'99.6"W, 1700–1800 m, 27 November 2009, *J. Orías, F. Borchsenius, MJ. Sanín, R. Millanes, D. Andrade y L. Terrazas, s.n.* (fr.) (HSB, COL). **Cochabamba**: José Carrasco Torrico, 3 Km de Siberia hacia Karahuasi, 17º48'S 64º41'W, 2400 m, 18 October 1996, *M. Kessler, J. González & A. Acebey 9130* (LPB); Provincia Chapare, Cantón El Sillar, Km 87, 1830 m, 16 March 1991, *L. R. Moreno & O. Moreno 84* (immat.fr) (USZ, JBSC, NY). **La Paz**: Province Franz Tamayo, Parque Nacional Madidi, Senda Apolo-San José de Uchupiamonas, 5 Km antes de llegar a Río 3 de Mayo, 14º34'74"S 68º20'23" W, 1735 m, 30 December 2002, *T. Miranda, C. Maldonado, F. Canqui, R. Alvarez, J. Tito 302* (LPB); Senda Apolo-San José de Uchupiamonas, Piñalito, 14º32'12"S 68º19'29"W, 2239 m, 25 April 2003, *F. Canqui, E. Alvarez & J. Tito 351* (st.fl.) (LPB); Mojos, Carjata, sobre la senda a Queara, 14º34'14"S 68º54'4"W, 1656 m, 7 May 2007, *L. Cayola, N. Chapi, G. Chive, F. Andia & T. Alvarez 2866* (sterile) (LPB); Carjata, 14º34'05" 68º54'01"W, 1712 m, 30 June 2005, *A. Fuentes, E. Cuevas, R. Cuevas & Darte 9173* (veg) (LPB); Piedra Blanca, 10,4 Km en línea recta al S de Pata, sobre el camino a Santa Cruz del Valle Ameno, 14º38'40"S68º37'24"W, 1915 m, 11 November 2003, *N. Paniagua, A. Fuentes, L. Cayola, S. Whiteheat, R. Cuevas, C. Cuevas, E. Cuevas, L. Cuevas 5869* (LPB); Province Nor Yungas, 10 km N of Caranavi on road from town, 15°40'S 67°39'W, 1500 m, 6 December 1985, *A. Henderson & J. Solomon 523* (mat.fr.) (COL, K, NY); 10 km N (ca. 5 by air) of Caranavi on road from town, (aprox.) 15°47'S 67°32'W, 1400 m, 1 November 1984, *M. Nee & J. Solomon 30324* (immat.fr.) (holotype, LPB; Isotypes, NY!, MO); 3.6 Km NE of Chuspipata on road to Yolosa, 16º17'S 67º48'W, 2800 m, 24 September 1986, *J. Solomon 15641* (LPB); Province Sud Yungas, 39 Km de la Plazuela a La Paz, 16º38'S 67º 34'W, 2150 m, 29 September 1995, *M. Kessler, J. González, K. Bach, S. Hohnwald 5683* (LPB). **Santa Cruz**: Province Vallegrande, Alto Seco, one hour walk south of town in cloud forest, 64° 05'W, 18° 50' S, 1900 m, 13 May 1988, *A. Henderson, M. Moraes & M. Saldias 761* (st.fl.) (COL, LPB, NY); Loma Larga a 60 Km al sur de Vallegrande, NW de Loma Larga, 18º45'20"S63º54'28"W, 1851 m, 8 April 2006, *R. Hurtado 695* (LPB); 62 Km de Vallegrande a Masicuri, 2000 m, 9 July 1995, *M. Kessler, J. González, K. Bach, S. Hohnwald 5208* (LPB); 4 Km de Loma Larga a Masicuri, 18º47'S 63º53'W, 1800 m, 4 April 1996, *M. Kessler, Jiménez & T. Krömer 6298* (LPB); Loma Larga, camino a Masicuri 18º45'19"S 63º54'12"W, 2030 m, 15 April 2006, *L. Moreno & O. Moreno 349* (JBSC); Los Sitanos, 75 Km S of Vallegrande, 18°52'S 63°57'W, 1400 m, 28 December 1989, *I.G. Vargas 360* (mat.fr.) (NY,); 1 Km by road S of Chujllas, 18°48'S 64°01'W, 2125 m, 26 December 1989, *M. Nee & I. Vargas C. 38446* (NY); Postrer Valle, 4 km S from town, on the way to the waterfall of the electric central, 18°32'S 63°40'W, 1750 m, 14 May 1988, *M. Moraes, A. Henderson & M. Saldias 1052* (pist.fl., immat.fr.) (COL, LPB, NY); Localidad Aguaditas, entre Khazamonte y Los Sitanos, 18º43'S 64º01' W, 2580 m, 1 May 1989, *I. Vargas 175* (LPB); Provincia La Florida, Samaipato, Yungas de Mairana, 2500–2600 m, 10 March 1990, *L. R. Moreno 28* (NY); 5 Km SW of Yerba Buena, top of Ridge of upper reaches of Quebrada Agua Blanca, 18°01'S 64°03'W, 1900–1950 m, 23 December 1989, *M. Nee & I.G. Vargas 38268* (mat.fr.); La Chapa, ca. 5 km E de la Yunga, 18°06'S63°55' W, ca. 2200 m, 29 June 1996, *M. Saldias & L. Orozco 4216*, (NY); Parque Nacional Amboró, Santa Rosa de Lima 5 kmW, between Santa Rosa and Rio La Pajcha, 17°52.5'S 64°12.5'W, 1670–1800 m, 3–5 May 1993, *I.G. Vargas, J. Belalcazar & J. Erihsson 2270* (st.fl.) (NY, US); Parque Nacional Amboró, 8 Km by air NE of Mairana, along trails on and near ridgetop, 5.5 Km N of Campamento "La Yunga" park station, 18º03.5'S 63º55'W, 2300 m, 30 March 2002, *M. Nee, M. Sundue, M. Mendoza & A. Arbeláez de Churchill 5206* (NY); Province La Florida, Las Yungas de la Negra, Km 85, Road

Santa Cruz–Cochabamba, 1600 m, 9 August 1982, *M.J. Balick, D.C Daly & S. López-Pérez 1376* (immat.fr.) (NY). PERU. **Cuzco**: Provincia Quispicanchi, en laderas cerca al río Araza, cerca de 48 km en la carretera de Quincemil a Urcos, 1680 m, 12 June 1960, *H. Moore et al. 8602* (pist.fl.) (BH, USM); Región Puno, Prov. Sandía, San Juan del Oro, 14°14'19,1"S, 69°, 10', 40,5"W, 1758 m, 10 November 2009, *F. Kahn, J. C. Pintaud, M. Machahua 4478* (USM).

9. *Ceroxylon quindiuense* (Karsten) Wendland (1860:70). *Klopstockia quindiuensis* Karsten (1859: 1). Lectotype (designated by Moore & Anderson (1976)):—COLOMBIA. Karsten, Fl. Columb. 1: pl. 1, fig. B, 4.

Ceroxylon floccosum Burret (1929: 851). Type:—COLOMBIA. Antioquia: Angostura, 3000–3350 m, June 1880, *W. Kalbreyer 1932* (holotype B, destroyed). Neotype (here designated): Colombia. San José de la Montaña, Vereda Valmaría, valley of San Andrés river, 2600 m, 16 December 1979, *R.Bernal & G. Galeano 53* (mat.fr.) (neotype COL!).

Figs. 1b, 3, 7g–i, 7l–m, 8d, 12d, 15c–d, 18, 19c, 29

Stem (13–)20–45(–60) m tall, 25–40 cm diam., white, with prominent leaf scars, covered with a very thick layer of wax. **Leaves** 14–20, in a dense, hemispheric crown; sheath 70–120(–176) cm, covered with thick, light brown indumentum; petiole (29–)44–80 cm long, 8.5–10.0 cm wide at the apex, abaxially covered with white indumentum of deciduous scales with persistent, thick, waxy bases; rachis 185–350(–540) cm long, adaxially flattened in ½–⅔ of its lenght, 2 mm hastula-like projection, glabrescent, abaxial surface covered with thick indumentum of white to cream, fibrous scales; pinnae 70–128 on each side, regularly arranged in one plane, completely pendulous, adaxial surface glossy, olive–green but appearing grayish from a distance, the midrib covered with persistent scale base scars, abaxial surface and midrib densely covered with persistent, linear, white to cream, padded scales, never revealing the surface beneath in age; the most basal filiform pinnae 34–56 × 0.3–0.4 mm, basal pinnae (10th from base) 49–130 × 1.1–2.0 cm, middle pinnae 70–154 × (3.2–)4.4–6.0 cm, apical pinnae 41–62 × 0.7–2.5 cm, free. **Staminate inflorescences** 1–2 at one time; peduncular bracts 6–7, with an additional smaller bract inserted at base of peduncle; rachis 102 cm long, with about 91 branches, each subtended by a small, membranaceous, acuminate bract, rachis and branches glabrescent, longest branches 42 cm long. **Pistillate inflorescences** 2–5 at one time; peduncle 150–280 cm long, 4 cm wide at apex, covered with scattered, brown, eroded, appressed scales; prophyll 35–70 cm long, 17 cm wide; peduncular bracts 5–7, prophyll and peduncle bracts covered with persistent, brown to ferrugineous scales; rachis 90–163 cm long, with 63–76 branches, each subtended by a 0.2–2.0 cm long, membranous bract, longest branches 68–80 cm long; rachis and rachillae glabrous. **Staminate flowers:** sepals 3(–4), broadly triangular, 1.0–1.2 mm long, connate for 0.4 mm (⅓–½ of total length), reaching or exceeding total length of corolla tube; petals 3(–5), elliptical, long-acuminate, 4–7 mm long, including an acumen of 1.0–1.5(–3.5) mm long, connate for 1 mm; stamens 9–12(–17), 3–6 antisepalous stamens, and 3–9(–11) antipetalous stamens, filaments 1.0–3.5(–4.5) mm long, inserted at basal central portion of anther, anthers 2.2 mm long, anther connective not projected. **Pistillate flowers:** sepals 3, broadly-triangular-acuminate, 1.5 mm long, connate for 1 mm (⅔ of total length), not reaching corolla tube, petals 3, elliptical-acuminate, 4.0–7.5 mm long, connate for up to 1 mm, acumen narrow, 2–3 mm long; staminodes 12, 1–2 antisepalous, 2–3 antipetalous, filaments 3 mm long, abortive anthers 1.2 mm long, pistil trifid, 2–3 mm diam. **Fruits** globose, orange-red when ripe, 1.6–2.0 cm diam., exocarp very minutely warted; fruting perianth with sepals 1–2 mm long, connate in 0.2–0.5 mm, lobes reaching or exceeding corolla tube. **Seeds** ca.1 cm diam.

Distribution and habitat:—Disjunct, with populations in the Andes of Colombia, along the central and eastern Cordillera (near the border with Venezuela), scarcely on the western Cordillera, and elsewhere forming populations in the Andes of northern Peru (Fig. 19c). It grows in humid montane forest, usually at 2000–3000 m, rarely up to 3150 m (Fig. 18). It usually forms large and dense populations, many of which remain on pastures and forest remnants, especially on very steep slopes.

FIGURE 29. *Ceroxylon quindiuense*. **a)** habitat; note the person standing besides for scale (Palm height = 52 m), **b), c), d)** habitat, note how dense populations grow (Central Cordillera, Colombia); **e)** detail of contemporaneous infructescences in different levels of maturity; **f)** detail of staminate inflorescence (Peru). Photos **a)**–**e)** by Rodrigo Bernal; **f)** by Kémber Mejía.

Local names:—Palma de cera, palma de ramo (Colombia).

Uses:—Since 1985, *C. quindiuense* is the national tree of Colombia (Galeano & Bernal 2005). Until few years ago**,** the young leaves were cut in large quantities to be used on Palm Sunday during Easter. This practice had become widely commercial, threatening the species, but has been reduced severely in the last few years as a result of law enforcement and widespread campaign. The stems are cut and used for posts, houses and fencing, or split to cover indoor walls. In Colombia, the extraction of wax covering the stems was an economically important activity during the XIXth century, since it was used for manufacturing candles and matches, which were sold at local markets. In order to extract the wax, locals climbed up the stem, but most

commonly they felled the palm. Indigenous peoples sold the wax in small "cakes" (Boussingault 1849). The death of hundreds of palms was caused by this practice (Galeano & Bernal 2005). Still today in Peru (Amazonas), adult individuals are felled and layed on black cloths, then pounded untill the waxy litter covering the trunk gathers on the cloths as small flakes. These flakes are molten and combined with beeswax to impregnate on linens which are twisted to make torches for outdoor lighting. Also in Peru, the populations of this species are being widely harvested for housing and posts, and the stem ripped for covering indoor walls (Galeano *et al.* 2008). *C. quindiuense* is cultivated as ornamental in Colombia.

Conservation status:—*Ceroxylon quindiuense* is known to have been a very abundant species in Colombia until the beginning of the last century, and even if some large populations persist in the Central Cordillera, it has been classified as Endangered (EN; Galeano & Bernal 2005). Most of the forests where this species grows have been turned into pastures, and while hundreds of adult palms are still left standing, the young seedlings do not grow. Besides that, the cutting of young leaves for Palm Sunday during many years, caused the death of many individuals, and a delay in normal growth of the palms. Additionally, in the last decade a new and unknown disease has been causing the death of many adult palms (Cardozo & Guzmán 1993). In Peru, although a formal evaluation has not been made, it is believed that the situation does not differ substantially from the Colombian one (Galeano *et al.* 2008).

Notes:—*Ceroxylon quindiuense* is diagnosed by its robust and white stem, its regularly arranged, completely pendulous and silverish pinnae, staminate flowers with 9–12(–17) stamens (anther connective not projected), and minutely warted fruits. These characters are constant even among the two very widely disjunct Peruvian and Colombian populations, with very slight variations in flower size (Fig. 7g–i) that may be due to sampling effects.

Specimens examined:—COLOMBIA. **Antioquia:** Municipality of Guarne, Vereda Mejía, ca. 2300 m, 15 August 1979, *R. Bernal & G. Galeano 1* (COL); 1 Km NE of Guarne, ca. 2100 m, 26 August 1979, *R. Bernal & G. Galeano 5* (mat.fr.) (COL). Municipality of Yarumal, Corregimiento Llanos de Cuivá, sobre la Finca la Argentina, Área Protectora de Humedales, 121 km NE of Medellín on the road to Atlantic Coast on pluvial montane forest, 2865 m, 1 March 2010, *M.J. Sanín & R. Callejas 8* (sterile) (HUA).**Boyacá:** municipality of Duitama, Vereda Santa Elena, farm La Sierra, forest near La Rusia river, *Quercus* forest, 2450 m, 13 November 1997, *J. Betancur et al. 7600* (juvenile) (COL). **Caldas:** Manizales, Neighborhood Palermo, 2150 m, 14 November 1986, *B. Villegas 1* (st.fl.) (COL). **Caquetá:** Florencia–Suaza road, km 45, 1° 45' 18" N 75° 44' 57" W, 2432 m, 24 February 2002, *W. Malagón 33* (juvenile) (COL). **Cundinamarca:** Municipality of Granada, Vereda San José, 2700 m, 16 June 1987, *G. Morales et al. 953* (immat.fr.) (COL); Bogotá, 2640 m, cultivated, 5 June 1941, *Jaramillo s.n.*(COL). **Meta:** Road from San Juanito and the National Natural Park (PNN) Chingaza, 18 September 1997, *E. Acero 39* (juvenile) (COL). **Quindío**: "montañas del Quindío", *Karsten, s.n.* (st.fl.) (L). **Risaralda:** Municipality of Pereira, Ucumarí Reserve, up from La Pastora, 2610 m alt., 10 October 1989, *O. Rangel et al. 5237* (juvenile) (COL). **Santander:** municipality of Charalá, place El Bogotacito, after El Taladero, El Carmen–Virolín road, 2300 m, 23 September 1994, *J. Betancur et al. 5830* (juvenile) (COL). **Tolima:** "provincia de Mariquita, Páramo del Quindío", 3000 m, 1851–1857, *Triana 720* (st.fl.) (BM, P); *J.Triana 723* (US); Quindío–Las Cruces, 9 March 1876, *E.André 2426* (st.fl.) (K, NY); along road from Cajamarca and summit of Divide, 2438 m, 27–28 March 1939, *E.Killip & Varela 34540* (fr.) (COL, US); 2970 m, 27–28 March 1939, *E.Killip & Varela 34687* (COL); between Fresno and Manizales, Km 57, 29 September 1941, *D.Fairchild 53* (fr.) (COL); "La Ceja" to "Agua Bonita", old Quindío trail, 2500–3100 m, 2 August 1922, *E. Killip & Hazen 9525* (US); Bermellón River, slopes near road Ibagué–La Línea, 2000 m, 18 November 1974, *H.E. Moore et al. 10193* (fr.) (BH, COL, K, NY, US). Municipality of Roncesvalles, Vereda Cucuanita, Finca El Reflejo, 04º00'09,8"N 75º36'38,9" W, 2600 m, 13 April 2010. *M.J. Sanín et al. 9* (mat.fr.) (COL, HUA). **Valle**: Near Mares, on road Cali–Buenaventura, ca. 2000 m, 22 June 1944, *E.Killip et al. 39175* (COL, US); slopes up from Tenerife, ca. 3000 m, 15 September 1970, *H.E. Moore & Dietz 9879* (pist.fl.) (BH, COL); valley of the Bugalagrande river, slope of Barragán, over Quebrada de Los Osos, towards Los Cauchos, 3000 m, 21 April 1946, *J.Cuatrecasas 20964* (st.fl.) (BH, MO); Western Cordillera, Los Farallones, NW slope of Quebrada del Ratón, El Diamante mine, 2950–3000 m, 29–30 July 1946, *J.*

Cuatrecasas et al. 21748 (BH); municipality of Tuluá, 2–3 km of Santa Lucía, towards the Alto (summit) of La Italia, Central Cordillera, 2950–3130 m, 17 March 1988, *R.Bernal et al. 1436* (fr.) (COL). PERU. **Amazonas:** Province Chachapoyas, District Leimebamba, road to the Archeological Museum, 06°45'14.7" S 77°48'3.7" W, 2523 m, 13 November 2007, *B. Millán et al. 1487* (immat.fr.) (AAU, COL, P, USM); locality Ocol, 06°15'48" S 77° 34'41" W, 2373 m, 20 September 2007, *K. Mejía et al. 4301* (st.fl.) (USM); 06°15'45.5" S 77° 34'06" W, 2244 m, 28 October 2009, *M.J. Sanín & J.C. Pintaud 7* (immat. fr.) (USM); District Molinopampa, locality Puma Armana near Ocol, 06º15'27.72" S 77º34'24.54" W, 2360 m, 16 March 2006, *B. Millán & J.C. Pintaud 1352* (immat.fr.) (USM). **Cajamarca:** Province Santa Cruz, District Pulán, locality El Molino, 10º49'46,6"S 63º46'14,9"W, 2132 m, 18 October 2009, *M.J. Sanín et al. 2* (sterile) (USM); Province Santa Cruz, District Pulán, Locality Succhapampa, Farm of Segundo Santacruz, 06º43'51,5"S 78º57'01,6"W, 2389 m, 19 October 2009, *M.J. Sanín et al. 3* (immat.fr.) (USM).

10. *Ceroxylon sasaimae* Galeano (1995: 404). Type:—COLOMBIA. Cundinamarca: Municipio de Sasaima, carretera a Guaduas, km 64, 5°20'N, 74°23'W, 1720 m alt., 18 April 1985, *G. Galeano & R. Bernal 686* (st.fl., fr.) (holotype COL!).

Figs. 2c, 8a, 10, 14b, 18, 20a, 30.

Stem 8–15(–20)m tall, 17–30 cm diam., brown-greenish to grayish, covered by a very thin layer of wax. **Leaves** 16–26, in a very dense and nearly spherical crown; sheath 73–90(–121) cm long, margins fibrous, abaxial surface covered with thick, light-brown, scaly indumentum; petiole 0–15 cm long, 4–8 wide at apex, adaxial surface glabrescent, margins acute, abaxially covered with deciduous, appressed, often eroded scales; rachis 206–300 cm long, adaxially flattened about ⅔ of its length, hastula-like projection 1–5 mm long, adaxially and abaxially glabrescent to scarcely covered with an indumentum of persistent but eroded, yellowish scales; pinnae 93–120 on each side, slightly irregularly arranged in groups of 1–8 pinnae, the groups separated by 3–5 cm, the pinnae straight and rigid through their length and inserted at slightly divergent angles, inequilateral by 3 cm at the apex, adaxial midrib with scale base scars or persistent, yellowish, minute bases, adaxial surface glabrous, glossy green and covered with a layer of clear translucent wax, abaxial midrib and surface covered with persistent, linear, translucent, cream-colored to brownish, scales; the basal, filiform pinnae 6–45 × 0.2–0.7 cm, basal pinnae (10th from base) 23–80 × 0.5–2.0 cm, middle pinnae 52–78 × 3.2–5.0 cm, apical pinnae 10–28(–50) × 0.5–1.0 (–2.0) cm, sometimes, the 2–3 apical pinnae connate along margins. **Staminate inflorescences** peduncle ca. 77 cm long, 2 cm wide at apex; prophyll 39 cm long, 10–11 cm wide; peduncular bracts 7, 53–188 cm long; rachis 100–115 cm long, with 72–125 branches; rachis and branches glabrescent, longest branches 36–42 cm long; prophyll, peduncle, bracts and base of rachis covered with deciduous, ferrugineous, fibrous scales with minute bases; rachillae glabrous. **Pistillate inflorescences** 4–5(–14) at different stages of development; peduncle 85–102(–155) cm long, 1.5–2.0 cm wide at apex; prophyll 28–32 cm long, 10 cm wide at base; peduncular bracts 6, 43–180(–252) cm long, one 7th bract incomplete, ca. 40 cm long., inserted toward the apex of the peduncle; rachis 76–132 cm long, with 90–100(–125) branches, each subtended by a 0.2–0.6 cm membranaceous bract, longest branches 23–32 cm long; prophyll, peduncle, bracts and base of rachis covered with persistent, brown to ferrugineous scales; rachillae glabrous. **Staminate flowers:** sepals 3, triangular-acuminate, 1.0–1.5 mm long, connate in 0.3–0.5 mm (⅓–½ of the total length), not reaching total length of the corolla tube; petals 3, lanceolate and long-acuminate, 5.5–7.0 mm long, including an acumen of 1.5–2.5 mm long, connate in 1.3–1.8 mm; stamens 9–11(–12), 2–6 antisepalous stamens, and 6–10 antipetalous stamens, filaments 1.0–1.5 mm long, inserted at basal central portion of anther, anthers 2.2–3.5 mm long, anther connective not projected. **Pistillate flowers:** sepals 3, broadly-triangular-acuminate, 1.0–1.5 mm long, connate in 0.6–1.0 mm (½–⅔ of total length), not reaching corolla tube; petals 3, elliptical-acuminate, 5–6.5 mm long, including an acumen of 2–3 mm long,

connate up to 1.2–2.0 mm; staminodes 9–11, 1 antisepalous, 2–3 antipetalous, filaments 1 mm long, abortive anthers 0.9–1.2 mm long, pistil trifid, 2–3 mm diam. **Fruits** globose, orange-red when ripe, 1.5–1.8 cm diam., exocarp smooth; fruiting perianth with sepals very broadly triangular, 1.0–1.5 mm long, connate in 0.2–0.5, lobes reaching corolla tube, petals elliptical-acuminate, widened at base, connate in 0.3–0.5 mm, staminodes 9–11. **Seeds** ca.1.2 cm diam.

FIGURE 30. *Ceroxylon sasaimae.* **a)** habit; **b)** climber descending with male inflorescence.

Distribution and habitat:—Known until 2010 only from the eastern Cordillera in Colombia (Fig. 20a), in a small area completely transformed to agricultural land, corresponding to humid premontane forest zone, at 1400–1800 m (Fig. 18). However, in 2011 it was surprinsingly discovered in the wild by Bernal & Manrique (in press), at 144 km northwest from the known locality, in a 2800 hectare forest patch, though it is unclear what percentage of this patch is actually covered by the population of *C. sasaimae*. The total known population from Sasaima has been estimated in no more than 100 adult individuals, that grow in the middle of coffee and fruit plantations, where regeneration is abundant but is removed during cultivation labors (Galeano & Bernal 2005). Only scattered individuals survive as seedlings and juveniles in the fallow land. Therefore, it is crucial to search this species in other forest remnants that meet its requirements to determine its actual population.

Local name:—Palma de cera, palma real, palma de ramo (Cundinamarca, Colombia).

Uses:—The young leaves were cut in large quantities to be used as Palm Sunday during Easter (Galeano 1995). Currently, this practice is prohibited and people are growing palms from seeds to sell them for ornamental purposes.

Conservation status:—Because of its restricted distribution, the low number of adults and the deforestation of the habitat in the whole area, *C. sasaimae* was considered as Critically Endangered (CR), according to the UICN criteria (Galeano & Bernal 2005).

Notes:—*Ceroxylon sasaimae* is diagnosed by its very dense and almost sphaerical crown of leaves with very short or absent petiole (Fig. 2c), pinnae irregularly arranged in groups, rigid through their length and inserted at slightly divergent angles, male flowers with 9–12 stamens, and smooth fruits.

Specimens examined:—COLOMBIA. **Cundinamarca:** Municipio Sasaima, vereda Santa Ana, Finca El Tolima, ca. 5°10' N, 74°25' W, 1600 m, 27 October 1993, *G. Galeano & R. Bernal 3980* (mat.fr.) (AAU, COL, HUA, K, NY); municipio San Francisco, 1 km from the town toward the road Bogotá–La Vega, 1700 m, 3–4 October 1998, *R. Bernal & G. Galeano 2311* (sterile) (COL); municipio La Vega, km 45 on the road Bogotá–La Vega, ca. 1700 m, 04°58'04'' N, 74°18'48.8'' W, 25 February 2006, *G. Galeano et al. 7451* (mat.fr.) (COL, AAU); municipio San Francisco, vereda El Arrayán, Finca El Recuerdo, 1694 m, 04°58'13.9'' N, 74°18'27.6'' W, 25 February 2006, *G. Galeano et al. 7452* (juvenile) (COL, AAU); *7453* (immat.fr.) (COL, AAU); *7454* (mat.fr.) (COL, AAU); vereda Arrayán Bajo, Finca El Pino, 4°58'13" N 74°18'27" W, 1690 m, 2 March 2008, *G. Galeano et al. 7513* (st.fl.) (COL, HUA, AAU); municipio Supatá, near the town, on the road San Francisco–Supatá, 1870 m, 05°03'15''N, 74°14'16'' W, 25 February 2006, *G. Galeano et al. 7455* (COL, AAU).

11. ***Ceroxylon ventricosum*** Burret (1929: 847). Type:— ECUADOR. Andes de Quito, in forest near Chillanes, 2600 m, *P.L. Sodiro 18717* (holotype B, destroyed). Neotype (here designated): ECUADOR. Bolívar: 13 km South of Chillanes, Hacienda Tiquibuso, 02°00' S, 79°02' W, 2350 m, 20 May 1987, *H.Balslev et al. 62542* (mat.fr.) (neotype QCA!, isoneotypes AAU!, COL!, QCNE!).

Figs. 8e, 14e, 18, 20b, 31.

Stem 6–25(–35) m tall, 20–44(–60) cm diam., white at base and turning green towards apex, covered with thick layer of wax. **Leaves** 16–20, in a dense, hemispheric crown; sheath 100–150 cm long, abaxially covered with thick layer of persistent yellowish or brownish, degraded scales; petiole 30–59 cm long, 6–10 cm wide at the apex; rachis 250–334 cm long, twisted 90° on distal portion thereby holding the pinnae in a vertical position, adaxially flattened in 1/3–1/5 of its length, hastula-like projection 1 mm long, glabrescent, abaxial surface covered with appressed, white, translucent scales that are often degraded; pinnae 118–151 on each side, arranged toward the middle of the leaf in groups of 2–4(–7), very close to each other, oriented in slightly divergent planes, but basal and apical pinnae regularly arranged or tending to a disposition at regular intervals, the terminal half of each pinnae pendulous, abaxial surface covered with long, yellowish scales; the basal, filiform pinnae 21–39 × 0.2–0.3 mm, basal pinnae (10th from base) 39–86 × 0.8–1.5 cm, middle pinnae 76–115 × (2.5–)3.4–6.2 cm, apical pinnae 17–38 × 0.3–1.0 cm, free. **Staminate inflorescences** peduncle glabrescent; prophyll 41 cm long; peduncular bracts various, with an additional smaller bract inserted at the base of peduncle; rachis 79 cm long, with 93 branches, each subtended by a subulate membranaceous, acuminate bract 0.2–3.0 cm long; longest branches 31 cm long; rachis and branches glabrescent. **Pistillate inflorescences:** peduncle 199–240 cm long, 4.0 cm wide at the apex; prophyll 62 cm long; peduncular bracts 5, up to 206 cm long, and an additional, 7 cm bract inserted more distally on the peduncle; rachis 87–141 cm long, with 64–87 branches, each subtended by a 0.2–2.0 cm membranous bract, longest branches in basal half, 39–63 cm long; prophyll, peduncle and bracts covered with persistent, brown to ferrugineous, fibres of interlocked scales, rachis and rachillae glabrous. **Staminate flowers:** sepals 3, broadly triangular, 1.0–1.1 mm long, connate in 0.3 mm (⅓ of total length), not reaching to exceeding total length of corolla tube; petals 3, elliptical, long-acuminate, 5–6 mm long, including an acumen of 1 mm long, connate in 1.0–1.5 mm; stamens 9–11, 3–6 antisepalous stamens, and 3–8 antipetalous stamen, filaments 1.5–2.5 mm long, inserted at ⅔ basal portion of anther, anthers 2.0–2.5 mm long, anther connective not projected. **Pistillate flowers:** sepals 3, broadly triangular-acuminate, 1.5 mm long, connate for 0.6–1.0 mm (½–⅔ of total length), not reaching corolla tube, petals 3, elliptical-acuminate, 4.0–6.5 mm long, including an acumen of 2–3 mm long, connate up to 1.2–2.0 mm; staminodes 9–11, 1 antisepalous, 2–3 antipetalous, filaments 1 mm long, abortive anthers

0.9–1.2 mm long, pistil trifid, 2–3 mm diam. **Fruits** globose, orange-red when ripe, 1.5–1.8 cm diam., exocarp smooth; fruiting perianth with sepals elliptical-acuminate, 1.0–1.5 mm long, connate in 0.2, lobes exceeding corolla tube, petals 3, elliptical-acuminate, connate in 0.8 mm. **Seeds** ca. 1.3 cm diam.

FIGURE 31. *Ceroxylon ventricosum.* **a)** habit, Valladolid (Ecuador); **b, c)** habit, Chillanes (Ecuador); **c), d)** habit, cultivated in Quito (Ecuador); **e)** leaf; **f)** habitat, Chillanes (Ecuador).

Distribution and habitat:— Grows from the South of Colombia (Central Cordilllera, western slope in Cauca and Eastern slopes of the Andes in Putumayo) to the south-east of Ecuador (Fig. 20b), in moist montane forest or kept on pastures, at (1800–)2000–3000 m, usually above 2500 m (Fig. 18). It is commonly found forming stands of hundreds of individuals. It is also cultivated as ornamental in Ecuador (Borchsenius *et al.* 1998).

Local names:—Palma de cera (Colombia, Ecuador), läme (*Nasa*, Colombia), palma real (Putumayo, Colombia; Carchi, Ecuador), palma de tambán, tambán, palma de ramos (Ecuador).

Uses:—The split stems are used for fencing and house construction. The fruits are fed to pigs that are set loose on the palm stands during the fruiting season, and because of this, the palms are protected in the pastures and in the forest.

Conservation status:—According to the IUCN criteria, considered Vulnerable (VU) in Ecuador (Borchsenius & Skov 1999) and endangered (EN) in Colombia (Galeano & Bernal 2005), because of habitat reduction and the small size of the populations.

Notes:—*Ceroxylon ventricosum* is characterized by its massive, robust and white stem, by its leaves twisted 90° on distal portion thereby holding the pinnae in a vertical position, the pinnae pendulous and arranged in hardly discernible groups toward the middle of the leaves, staminate flowers with 9–11 stamens and smooth fruits. The best way to distiguish it from *C. quindiuense* is in its grouped pinnae spreading in various planes, whereas, *C. quindiuense* has regularly arranged, pendulous (in one plane) pinnae.

Specimens examined:—COLOMBIA. **Cauca:** Cordillera Central, Western slopes, headwaters of Río Palo, Santo Domingo creek, left slope, forests, 2750–2850 m, 14 December 1944, *J. Cuatrecasas 19322* (st.fl., pist.fl., immat.fr.) (BH, US); between Tacueyó and Huila (Tagala), January 1906, *C. B. Doyle 233* (st.fl.) (US). **Putumayo:** Valle de Sibundoy, Vereda Tonjoy, 2550 m, 13 January 2000, *R. Bernal et al. 2477* (fr.) (COL); Valle del Sibundoy, extremo Este, Junto a San Francisco, 2200 m, 1 Jaunuary 1941, *J. Cuatrecasas 11576* (st.fl.) (COL). ECUADOR. **Bolívar:** Jamirán, church of Chillanes, 6 November 1943, *M. Acosta Solís 6743* (mat.fr.) (F), *6763* (st.fl.) (F); Urcu–Corral, 2600–3000 m, 3 November 1943, *M. Acosta Solís 6621* (st.fl.) (F). **Carchi:** Cantón Espejo, km 5 of surveyed road, Maldonado to Tulcán, ca. 3000 m, 1 August 1935, *I. Mexia 7564* (pist.fl.) (BH, US). **Cotopaxi:** Cantón Pilalo, on the way to the summit of Cerro Puchuato, cloud forest, moist low montane forest (00°55ºS, 79°09º W), 1800–2500 m, 5 December 1987, *C. Cerón & S. Villavicencio 2830* (st.fl.) (AAU, MO). **Zamora-Chinchipe:** Loja–Zumba road, 6 km South of Yangana, 2020 m, 79°10’ W, 04°24’ S, 17 May 1987, *H. Balslev et al. 62536* (st.fl.) (AAU, COL, QCA, QCNE).

12. *Ceroxylon vogelianum* (Engel) Wendland in Kerchove de Denterghem (1878: 239). *Klopstockia vogeliana* Engel (1865: 673). Type:—COLOMBIA. Zwischen Magdalena und Catatumbo, bei Ocaña, Bergregion, 2000–2650 m, *F. Engel, s.n.* (holotype B, destroyed). Neotype (here designated):—COLOMBIA. Norte de Santander: municipio de Ábrego, 60 km on the road to Villacaro, 2600 m, 26 March 1987, *R. Bernal & G. Galeano 1372* (neotype COL!, isoneotypes AAU!, BH!, HUA!, NY!, K!).

Ceroxylon coarctatum (Engel) Wendland in Kerchove de Denterghem (1878: 238). *Klopstockia coarctata* Engel (1865: 676). Lectotype (designated by Imchanitzkaja 1987):— VENEZUELA. Prov.Táchira: bei La Grita, hohe Gebirgsrücken, am Fuße des paramo, *F. Engel, s.n.* (LE!).

Ceroxylon crispum Burret (1929: 849). Type:—PERU. Prov. Huanuco: Berge zwischen Chinchao und Acomayo, 2800 m, 4 September 1913, *A. Weberbauer 6825* (fr.). (holotype B, destroyed, lectotype (here designated) F!).

Ceroxylon verruculosum Burret (1929: 850). Type:—PERU. Junín, Prov. Tarma: Berge westlich von Huacapistana, 2700 m, 20 January 1903, *A. Weberbauer 2284* (fr.) (holotype B, destroyed). Neotype (here designated):—PERU. Junín: Chuquisiunca, near Huacapistana, 37 km east of Tarma, on road to La Merced, 2700–3000 m, 30 January 1975, *Anderson 6* (neotype BH!).

Ceroxylon hexandrum Dugand (1953: 1). Type:—COLOMBIA. Putumayo: Valle del Sibundoy, 2200 m, 1 January 1941, *J. Cuatrecasas 11574* (holotype COL!).

Ceroxylon flexuosum Galeano & R. Bernal (1982: 178). Type:—COLOMBIA. Antioquia: Municipio de Bello, Inspección San Félix, road to Alto Los Baldíos, ca. 2400 m, 27 September 1980, *Galeano & Bernal 257* (holotype COL!, isotype HUA!).

Figs. 1a, 2b, 5b, 6c, 7u–v, 9e, 12e, 15f, 18, 20c, 32.

Stem 3–13(–17) m tall, 12–25 cm diameter, rarely flexuous toward the apex, green to silverish, covered with a very thin layer of wax. **Leaves** 6–18, in a very variable but always untidy, hemispheric crown; sheath (32–)50–90(–130) cm long, 2.5 cm wide; petiole (15–)24–75 cm long, 2–5 cm wide at apex, adaxially glabrescent with remnant of scales, abaxially with brown-grayish indumentum, sometimes almost glabrescent; rachis (38–)77–140(–210) cm long, adaxially flattened in basal ½ of its lenght that end in a small almost unconspicuous hastula-like projection, glabrescent, abaxial surface convex, covered with scales degraded into flexuous

threads, and persistent 0.2–0.6 mm elliptical bases, arranged in adjacent, 0.2–0.3 mm wide rows; pinnae 46–80(–129) on each side of rachis, arranged in groups of 2–10 pinnae, separated by 2.0–6.5(–12.0) cm, and inserted in divergent planes, specially towards the base and the middle of the leaf, adaxial surface glabrescent, abaxial surface and midrib covered with elliptical to linear, very thin and narrow, translucent, cream scales, the basal, filiform pinnae 8.5–50 × 0.2–0.5 mm, basal pinnae (10th from base) 20–58(–89) × 0.7–2.2 cm, middle pinnae 23–75(–95) × (1.1–)2.2–3.5(–4.5) cm, apical pinnae 11–37 × 0.1–0.8 cm, not connate along margins. **Staminate inflorescences** 5–7 at one time, peduncle 125 cm long, 2.5 cm wide at apex; prophyll 26 cm; peduncular bracts at least 6, 54–106 × 5–8 cm, with an additional smaller, 7 cm bract inserted at the apex of the peduncle; rachis 34.5 cm long, with about 40 branches, each subtended by a 0.5–3.0 cm long, thin and narrow, membranaceous, acuminate bract, rachis and branches glabrescent, longest branches near base, 15.5–33.0 cm long. **Pistillate inflorescences** 1–5 at one time; peduncle 77–150(–248) cm long, 2.0–4.0 cm wide at apex; prophyll 17–45 cm long; peduncular bracts 5–7, 25–187 × 4–13 cm; rachis (22–)52–62(–100) cm long, with ca. 31–53 branches, each subtended by a 0.2–1.5 cm membranous bract, longest branches in basal half, (12–)20–51 cm long; prophyll, peduncle, bracts and base of rachis covered with persistent, brown to ferrugineous, intermixed fibres of interlocked scales with minute round, 0.1 mm bases, arranged in troughs formed in between veins, rachillae glabrous. **Staminate flowers:** sepals 3, elliptical-long acuminate, 0.8–1.5 mm long, connate for 0.2 mm (1/4–1/7 of total length), reaching or almost reaching the total length of corolla tube; petals 3, elliptical-long acuminate like sepals, 4.5–5.5 mm long, connate in 1.0–1.5 mm, acumen 1.5–2.5 mm long; stamens 6, alternating 1 antisepalous, and 1 antipetalous stamen, filaments 1.0–1.5 mm long, inserted at basal 2/5 to central portion of anther, anthers 1.6–2.5 mm long, anther connective not projected;pistillode trifid, minute. **Pistillate flowers:** sepals 3, broadly-triangular, narrowly acuminate, 1.0–1.5 mm long, connate for 0.4–0.7 mm (½ of total length), not reaching corolla tube, petals 3, elliptical, very narrowly acuminate to subulate, 5–6 mm long, connate for up to 1.0–2.0 mm, acumen narrow, 1.5–2.0 mm long; staminodes 6, 1 antisepalous, 1 antipetalous, filaments 1.5 mm long, broad at base, then narrowing at tip, abortive anthers 0.9–1.2 mm long, pistil green, trifid, 2–3 mm diam. **Fruits** globose, orange-red when ripe, 1.6–2.0 cm diam., exocarp reticulate sulcate, furrowed; perianth persistent, sepals in a swollen coriaceous ring around pedicel, 0.8–1.5 mm high, not reaching total height of the corolla tube, petals elliptical-acuminate, 3–6 cm long, including a 1–2 mm acumen, connate in 1.0–1.5 mm, staminodes with very thick filaments that are broadened at base, and with no remaining abortive anthers at this point. **Seeds** 1.1–1.6 cm diam.

Distribution and habitat:—*Ceroxylon vogelianum* is widely distributed through the Andes from Venezuela to Colombia, Ecuador, and Peru (Fig. 20c), in humid montane forest, at (1900–)2200–2900 m (Fig. 18). Although it is one of the most common palms of the high tropical Andes, it never forms extense stands, and is commonly sparse on mountain ridges.

Local names:—Palma de ramo, chile (Santander, Colombia), chonta (fruit; Antioquia, Colombia), palma de ramo criolla (Boyacá, Colombia); gallinazo, palma negra (Norte de Santander, Colombia), palma de cera (Venezuela).

Uses:—The new leaves are cut for Palm Sunday during Easter, and the stems are used to build fences and houses.

Conservation status:—In Venezuela, *C. vogelianum* has been recorded as Endangered (EN) according to the IUCN criteria, mainly due to deforestation practices along the Andes (Llamosas *et al.* 2003). In Colombia the species was only considered Near Threatened (NT; Galeano *et al.* 2005) because of its wide distribution, but more studies need to be done related to the population dynamics and reproductive biology of this species, as it is expected to be endangered due to the deforestation process due to agricultural activity in the Andes of Colombia.

Notes:—*Ceroxylon vogelianum* is, together with *C. parvifrons*, the most frequent and widely distributed species of *Ceroxylon*. It is unmistakable by its small size, with slender, usually greenish or brownish stem (Fig. 1a), leaves ascending (Fig. 2b), with pinnae arranged in groups and inserted in very divergent planes (Fig. 5b), staminate flowers with 6 stamens on slender filaments (Fig. 7u–v), and fruits with the very characteristic reticulate sulcate exocarp (Fig. 9e).

FIGURE 32. *Ceroxylon vogelianum.* **a, b, c)** habit; **d)** immature infructescence; **e)** aspect of former *Ceroxylon flexuosum* (Colombia)**.**

The specimens from Bolivia that had been determined as *C. vogelianum* actually correspond to *C. pityrophyllum* (see comments under this species), therefore *C. vogelianum* is not found in this country, although several texts report it.

Specimens examined:—COLOMBIA. **Antioquia:** Municipality of San José, vereda Valmaría, Hacienda La María, valley of the San Andrés River, tributary to Cauca River, ca. 2600 m, 15 October 1979, *R. Bernal & G. Galeano 52* (fr.) (COL); Municipality of Peque, Vereda La Tumba (Road Uramita–Peque, Km 45–48), 2500–2650 m, 2 April 1983, *R. Bernal & G. Galeano 566* (fr.) (COL). **Boyacá:** Municipality of Arcabuco, 3 km on the Road to La Palma, 2700 m, March 1987, *R. Bernal & G. Galeano 1337* (fr.) (COL). **Cauca:** El Tambo, PNN Munchique, Road La Cabaña de La Romelia–El Observatorio, 2° 38’ N, 76° 54’, 2600–2700 m, 22 June 2001, *R. Bernal et al. 2871* (immat.fr.) (COL). **Huila-Caquetá:** Eastern Cordillera, on the dividing range, in Gabinete, 2300–2450 m., 22 March 1940, *J. Cuatrecasas 8508* (st.fl.) (COL). **Nariño:** Municipality of Pasto, Corregimiento Encano, Vereda Santa Teresita, 11 May 2003, *N. Rodríguez & J. Castro 1* (fr.) (COL, PSO). **Norte de Santander:** 60 km from Ábrego on the Road to Villacaro, 2600 m, 26 March 1978, *R. Bernal & G. Galeano 1372* (fr.) (COL). **Putumayo:** South side of the Laguna de la Cocha, quebrada de Santa Lucía, 2850 m alt., 8 January 1941, *J. Cuatrecasas 11842* (immat.fr.) (COL); Sibundoy, 2400 m alt., 28 October 1946, *M. B. & R. Foster 1961* (immat.fr.) (BH, COL); Sibundoy valley, 1 km S of Sibundoy, ca. 2200 m, 14 August 1963, *M.L. Bristol 1302* (mat.fr.) (BH); Sibundoy Valley, Santiago, Vereda Tonjoy, 2500 m, 13 June 2000, *R. Bernal et al. 2475*, 2478 (fr.) (COL). **Quindío:** Municipality of Salento, Vereda Cocora, Farm La Botánica, 5 June 1996, *W. Vargas 3210* (immat. fr.) (COL). **Risaralda:** Municipality of Santuario, Vereda "Las Colonias", 400 m up from the camp, 2910 m, 2 February 1983, *J. Torres et al. 1472* (sterile) (COL).

Santander: Corregimiento de Virolín, Farm "La Sierra", 2500–2600 m, 17 May 1976, *G. Lozano et al. 2598* (immat.fr.) (COL). **Valle:** Farallones de Cali, river beds of River Pance, East slopes, Cuchilla del Hato Viejo, 2800 m, 25 August 1991, *E. Calderón 98A* (st.fl.) (COL). ECUADOR. **Loja:** Loja–Zamora road, 2–7 km W of the pass, disturbed montane forest, 79° 10' W, 3° 59' S, 2400–2700 m, 17 June 1979, *A. B. Lojtnant & U. Molau 15029* (immat. fr.) (AAU). **Napo:** Cerro de Huacamayas, 32 km South of Baeza along road to Tena, montane forest (77°51' W, 00°40' S), 1950 m, 4 May 1986, *H. Balslev & A. Henderson 62085* (st.fl.) (AAU); road Baeza–Tena, 9 km S of Cosanga, Cordillera of Huacamayos, steep slopes with shruby vegetation and scattered large trees, 2200 m, 8 May 1987, *H. Balslev et al. 62506* (mat.fr.) (AAU, COL). **Santiago-Zamora:** Along quebrada Honda, vicinity of rancho Achupallas, 2500–2700 m, 10 October 1943, *J. Steyermark 54580* (st.fl.) (AAU). **Zamora-Chinchipe:**Yangana–Valladolid road km 28, 79° 07´W 04° 29´ S, wet montane forest recently cut and burned, 2500 m, 24 January 1987, *A. Barfod et al. 60178* (mat.fr.) (AAU, COL, MECN, QCA). PERU. **Cuzco:** La Convención, Echarati, East Río Apurimac, NE of Pueblo Libre, up mountain of Anchihuay & Bellavista, South of Cordillera Vilcabamba, 2445 m, 12º51'S 73º30'W, 3 August 1998, *P. Núñez et al. 23471,23689* (USM, US). **Huánuco:**On west-facing steep slopes 1.8–4 km below Carpish (Acomayo side) on road from Acomayo to Chinchao, 2550–2700 m, 24 April 1960, *H. E. Moore et al. 8326* (fr.) (BH). **Pasco:** Oxapampa–Cerro de Pasco road, 20–30 km of Oxapampa, at 2000–2500 m, ca. 10° 40' S, 75° 55´W, 3 March 1983, *A. Gentry et al. 39939* (immat.fr.) (MO); Province Oxapampa, District Huancabamba, Cordillera Yanachaga, ridge SE of Cooperativa 3 de Mayo, 10° 27' S, 75° 26' W, ca. 2000 m, 24 May 1989, *A. Henderson et al. 1035* (fr.) (COL, NY).VENEZUELA. **Estado Lara:** Cloud forest, 9° 47' N, 69° 33´ W, between Cubiro and Escalera, 10–15 km SE of Cubiro, Distrito Menez., 1600–2000 m , 7 July 1974, *J. Steyermark et al. 110243* (fr.) (BH); **Táchira:** Road El Delgadito–Pregonero near las Helicias,aprox. 8°05'N 71°53'W, 2650 m, 1 March 1968, *J.G. Wessels-Boer et al. 2429* (mat.fr.) (NY, MER) *2430*(mat.fr.) (NY, MER).

Doubtful names and excluded taxa

Ceroxylon interruptum (Karsten) Wendland (1860: 70). *Klopstockia interrupta* Karsten (1856: 252). Karsten's description is very crude and the species was not associated with a specific locality, or a specimen. In the Leningrad Herbarium (LE), where Karsten's material was deposited, no specimens were found that could be used as a lectotype (Imchanitzkaya 1987).

Ceroxylon utile (Karsten) Wendland (1860: 70). *Klopstockia utilis* Karsten (1856: 252). There is no specimen that can be associated with this name in the Leningrad herbarium (LE; Imchanitzkaya 1987) and both the description and the locality are completely insufficient to relate this name to a specific *Ceroxylon* species.

Ceroxylon australe Martius (1849: 314) = *Juania australis* (Martius) Drude ex Hooker (1884: 57).

Ceroxylon niveum Wendland in Kerchove de Denterghem (1878: 239) = *Allagoptera caudescens* (Martius) Kuntze (1891: 726).

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Appendix 1. List of cited specimens

Numerical list of taxa

1. *C. alpinum* Bonpl. ex DC.
2. *C. amazonicum* Galeano
3. *C. ceriferum* (H.Karst.) Pittier
4. *C. echinulatum* Galeano
5. *C. parvifrons* (Engel) H.Wendl.
6. *C. parvum* Galeano
7. *C. peruvianum* Galeano, Sanín & Mejía
8. *C. pityrophyllum* (Mart.) Mart. ex H. Wendl.
9. *C. quindiuense* (H.Karst.) H.Wendl.
10. *C. sasaimae* Galeano
11. *C. ventricosum* Burret
12. *C. vogelianum* (Engel) H.Wendl.

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C. amazonicum (Barfod 60174; Borchsenius *et al.* 638; Palacios *et al.* 8745)
C. ceriferum (Wessels-Boer *et al.* 2443)
C. echinulatum (Balslev *et al*. 62089; 62512; Palacios 9544)
C. parvifrons (Bernal 213; 1424)
C. peruvianum (Millán *et al.* 1498)
C. pityrophyllum (Henderson 761)
C. quindiuense (Mejía *et al.* 4301; Triana 720; Karsten s.n.; Jaramillo-Mejía *s.n.*; Cuatrecasas 11576)
C. sasaimae (Galeano *et al.* 7513)
C. ventricosum (Balslev 62536; Cuatrescasas 19322)
C. vogelianum (Anderson 6; Galeano & Bernal 1337; H. Balslev & A. Henderson 62085)

Fruit exocarp SEM images

C. alpinum (Wessels-Boer 2447)
C. echinulatum (*Dodsonet al.*14843)
C. vogelianum (*Bernal & Galeano 1372*)

Leaf Anatomy

C. alpinum (Wessels-Boer *et al*. 2448)
C. amazonicum (Balslev 62538)
C. ceriferum (Wessels-Boer *et al.* 2432; 2442; 2443)
C. echinulatum (Balslev *et al*. 62089; 62488; 62512; 62844)
C. parvifrons (Balslev 62548; Balslev 62533; Bernal 1357; Bernal 1424)
C. parvum (Balslev 62529)
C. peruvianum (Smith 4854)
C. pityrophyllum (Nee & Solomon 30324)
C. quindiuense (Fairchild 53; Bernal s.n.; B. Millán *et al.* 1487)
C. sasaimae (Galeano *et al.* 7514)
C. ventricosum (Balslev 62536)
C. vogelianum (Bernal & Galeano 1372)