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Carpoxylon macrospermum

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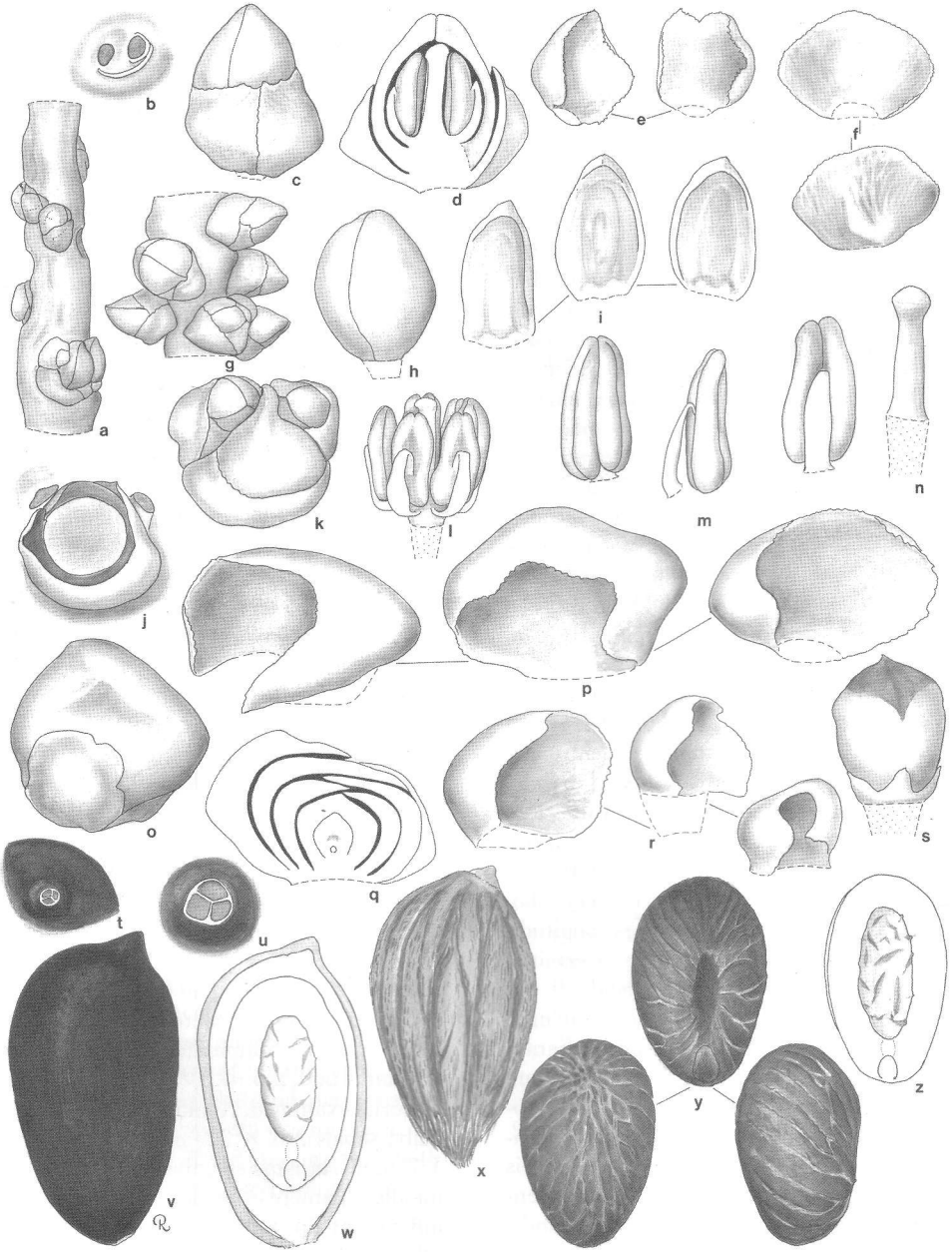
When "Genera Palmarum" went to press in 1986, *Carpoxylon* was known from fruit only. Since lack of information made it impossible to include the genus in the hierarchy of the classification, it was placed in an "Incertae Sedis" group along with the Madagascar genus *Masoala*. The rediscovery of *Carpoxylon*, described in the accompanying paper (Dowe 1989), allows us to provide here a complete description of the genus and its one species and to consider further the relationships of this unusual palm.

Carpoxylon H. A. Wendland & Drude, Linnaea 39: 177. 1875. Type: **C. macrospermum** H. A. Wendland & Drude. (Fig. 1, Cover Photo; see also Fig. 1, accompanying paper, p. 65).

Moderate, solitary, unarmed, pleonanthic, monoecious palm. Stem erect, longitudinally fissured, swollen basally and with a boss of adventitious roots, prominently ringed with slightly sunken leaf scars, internodes short. Leaves regularly pinnate, spreading but arched towards the tips, neatly abscising; sheaths forming a crownshaft, crownshaft glossy, glabrous to lightly scaly, splitting opposite the petiole; petiole short, wider proximally, ridged adaxially, rounded abaxially; rachis flexible, broadly ridged adaxially at base, narrowly ridged distally, rounded abaxially, extending beyond the apical leaflets in a flexible tip; leaflets subopposite, in one rank, apically and basally inserted at right angles to the rachis, more obliquely inserted at midleaf, leaflets single fold, erect, linear, tapering to an irregularly rounded, more or less bifid tip, stiff, coriaceous, horizontal to erect, glabrous adaxially, with numerous punctate scales abaxially, midveins most prominent, marginal veins next largest, two other pairs of large veins conspicuous, transverse veinlets not evident. Inflorescences infrafoliar, branched to three orders basally, to one order distally, branches stiffly spreading; peduncle short, stout, elliptical in cross-section; prophyll completely encircling the peduncle at insertion, tubular, two-keeled, tapering distally, splitting abaxially, tomentose; peduncular bracts 2, the first inserted shortly above the prophyll, the second an equal distance above the first, both tubular, complete, tapering to rather short pointed tips, glabrous, caducous; scars of 2–3 incomplete bracts above the inner peduncular bract; rachis about twice as long as the peduncle, rachis bracts low, ridgelike in slitlike cavities, subtending ca. 10 primary branches; primary branches stout, dorsiventrally flattened, with a short bare part and two large lateral pulvini at the base, bearing very shallow bracts, each in a slitlike cavity, subtending rachillae; rachillae angled, tapering, also with basal pulvini, rachilla bracts shallow, rounded, subtending triads of flowers for about one-third their length, paired staminate flowers with some intermingled solitary staminate flowers above the triads, and solitary staminate flowers distally, in triads one staminate flower often distal and one lateral to the pistillate flower, flowers lateral to each other in staminate dyads, rachilla ending in a short bare portion; first bracteole surrounding the pistil-



Carpoxylon macrospermum. a, portion of rachilla in bud ×1⅓; b, scars of staminate dyad ×3⅓; c, staminate bud ×6⅔; d, staminate bud in vertical section ×6⅔; e, two stminate petals ×6⅔; f, staminate petal in two views ×6⅔; g, portion of rachilla with staminate buds ×2⅔; h, staminate bud sepals removed ×6⅔; i, staminate petals ×6⅔; j, scars from floral triad ×3⅔; k, triad ×3⅔; l, androecium ×6⅔; m, stamen in three views ×6⅔; n, pistillode ×6⅔; o, young pistillate bud ×6⅔; p, pistillate sepals ×6⅔; q, pistillate bud in vertical section ×6⅔; r, pistillate petals ×6⅔; s, gynoecium with staminodes ×6⅔; t, end of stigma ×1; u, end of stigma enlarged ×3; v, fruit ×⅔; w, fruit in vertical section ×⅔; x, endocarp ×⅔; y, seed in three views ×⅔; z, seed in vertical section ×⅔.

late flower large, rounded, coriaceous, the second smaller and more shallow. Staminate flowers very asymmetrical in bud, rounded or pointed apically; sepals 3, distinct, irregular, imbricate basally, keeled, prominently ridged when dry; petals 3, distinct, valvate, tips thickened, ridged when dry; stamens 6, filament slender, inflexed at tip, anthers more or less sagittate basally, slightly bifid apically, dorsifixed just below the middle, latrorse, versatile, connective tanniniferous; pollen elliptic in polar view with finely reticulate tectate exine; pistillode elongate, slightly longer than anthers in bud, tip enlarged, rounded. Pistillate flowers in young bud, irregular, rounded; sepals 3, distinct, very broadly imbricate, extremely thick basally; petals 3, very broadly imbricate, thick basally, tips thick, valvate; staminodes joined in a shallow ring with about 5 broad toothlike tips; gynoecium irregularly obovoid, unilocular, uniovulate, stigmas 3, fleshy, ovule erect at stage studied, ? anatropous. Fruit obovoid to ellipsoidal, red at maturity, stigmatic remains eccentrically apical, epicarp smooth, wrinkled basally when mature, mesocarp thick, with close packed longitudinal fibers, endocarp rather thick, whitish, bony, longitudinally ridged, large operculum over embryo. Seed obovoid, raphe elongate, branches longitudinal, endosperm homogeneous. Germination adjacent ligular, eophyll bifid.

Distribution: One species rediscovered 30 November 1987 on Espiritu Santo, Vanuatu where growing in silty alluvium on the edge of a small stream. The population may have been planted (see accompanying article), thus the wild location is uncertain. The original description mentions the mountains of the Vanuatu Islands.

Carpoxylon macrospermum H. A. Wendland & Drude, Linnaea 39: 177, Plate 1, Fig. 3. 1875. Type: Vanuatu, fruit only,? in GOET, not found.

Stem erect to 18 m, ca. 35 cm diam. DBH, base enlarged, 50 cm in diam., leaf scars whitish, prominent, internodes 7 cm long near base to 2 cm long distally. Leaves regularly pinnate, 3.5–4.0 m long; crownshaft green, 1.5–2.0 m long, somewhat larger in diam. towards base; petiole 25 cm long or less, wider proximally; rachis wide to 6.5 cm at base, 4.5 cm wide in middle, 4.0 cm wide distally, extending beyond apical leaflets in a flexible tip about 12 cm long; leaflets about 70 on each side of rachis, proximal ones 114 × 1.5 cm, mid-leaflets 122 × 3.2 cm, distal ones 36 × 1.5 cm. Inflorescences infrafoliar; peduncle stout, elliptical in cross-section, about 14 cm long, 4 cm diam.; prophyll 70 cm long, about 8 cm wide, peduncular bracts two, the first inserted ca. 5 cm above the prophyll, the second 5 cm above the first, each 70 × 7 cm tapering to a woody tip ca. 5 cm long; scars of two to three incomplete bracts above the inner peduncular bract; rachis ca. 36 cm long, rachis bracts subtending 10 primary branches; primary branches stout, lower ones to 2 cm wide with a basal bare portion 7–8 cm wide; rachillae stout, ca. 5 mm diam. and 30–40 cm long, tapering, also with basal pulvini, bearing spirally arranged, rather distant triads, 1.5–1.0 cm apart, for about one-third their length, rachillae much reduced in diam. to 2–3 mm distally, first bracteole surrounding the pistillate flower shallow, 2–4 mm high, rounded, coriaceous, evident in fruiting rachillae, second bracteole smaller and more shallow. Staminate flowers very irregular in bud, 2.5–4.5 × 2.0 mm in young material examined, rounded or pointed apically; sepals 2.5 × 3.0 mm; petals 2.9 × 1.7 mm; stamens six, dorsifixed near the middle, filaments slender, 1.5 mm long, inflexed at tip; anthers 2.0 mm long; pistillode 2.0 mm long. Pistillate flowers studied in very young bud, 2 × 6 mm, irregular; sepals various in size, about 4 × 2 mm; petals imbricate, also not completely developed and varying in size, about 3 × 2 mm; staminodes 0.5 mm high; gynoecium obovoid, 2 mm high × 1.5 mm wide. Fruit slightly obovoid to ellipsoidal, 6 ×

3.5 cm, stigmatic remains eccentrically apical; epicarp thin, mesocarp 2 mm thick with large fibers, endocarp 3–4 mm thick, thicker basally, longitudinally ridged, bony below ridges, operculum circular, large. Seed large, ellipsoidal, 4 × 2.5 cm, raphe fibers abundant, extending laterally, little anastomosing, endosperm homogeneous with central cavity; embryo basal. Germination adjacent ligular, eophyll bifid.

Discussion

Carpoxylon, then known only from fruit, was put in Areceae Incertae Sedis in "Genera Palmarum" (Uhl and Dransfield 1987). The newly collected material allows a subtribal placement. The large operculum over the embryo places the genus clearly in Subtribe Iguanurinae of the Areceae, where it appears most closely related to *Clinostigma*. This relationship is further supported by preliminary cladistic studies of Iguanurinae; using a data base of 32 characters, *Carpoxylon* and *Clinostigma* are indicated as sister genera (Uhl and Dransfield unpubl.). *Carpoxylon* differs from *Clinostigma* in lacking stilt roots, in the stiffly ascending rather than the pendulous pinnae of most species of *Clinostigma*, in two rather than a single peduncular bract, in inflorescence branches stiff and spreading rather than more or less pendulous, and in a ridged, bony rather than a thin crustaceous endocarp. Species of *Clinostigma* are poorly known as are those of other genera of Iguanurinae; more field studies are needed and may change the circumscription of *Carpoxylon*. A revised "Key to the Iguanurinae," with *Carpoxylon* now included follows:

Key to the Genera of the Iguanurinae

1. Prophyll completely encircling the peduncle at insertion, leaving a circular scar when caducous; stamens 6 or more 2
1. Prophyll incompletely encircling the peduncle at insertion, open abaxially, leaving an incomplete scar upon falling; stamens always 6 20
2. Seed irregularly ridged, furrowed and sculptured with adherent fibers ..... *Alsmithia*
2. Seed ± small, not ridged or sculptured 3
3. Staminate flowers borne in vertically oriented pairs sunken in distinct depressions distally, smaller than and lateral to pistillate flowers proximally on the rachillae; fruit large, with apical stigmatic remains. Fiji ..... *Neoveitchia*
3. Staminate flowers borne in horizontally oriented pairs distally, lateral to pistillate flowers proximally on the rachillae; fruit moderate, rarely large with apical, lateral, or basal stigmatic remains 4
4. Inflorescence interfoliar; fruit covered with prominent corky warts; stigmatic remains basal in fruit 5
4. Inflorescence interfoliar, or infrafoliar, fruit smooth or merely pebbled to granulose when dry; stigmatic remains various 6
5. Peduncular bract inserted near the base of the peduncle; fruit more than 2.5 cm in diameter. Marquesas Islands ..... *Pelagodoxa*
5. Peduncular bract inserted at the apex of the peduncle; fruit 1.5 cm in diameter or less. New Guinea ..... *Sommieria*
6. Flowers borne in laterally compressed pits, the staminate on long, hairy pedicels; fruit with stigmatic remains lateral in lower ¼; seeds ridged and grooved. Southern India and Nicobar Islands ..... *Bentinckia*
6. Flowers sessile or impressed in the rachillae but neither in laterally compressed pits nor the staminate with hair covered pedicels; stigmatic remains apical to basal; seeds smooth 7
7. Leaflets several-ribbed with praemorse apices or leaf blades, when not divided laterally, with toothed margins; inflorescences usually interfoliar; triads shallowly to deeply sunken in depressions in the rachillae. Malay Peninsula, Borneo, Java, Sumatra ..... *Iguanura*
7. Leaflets 1-ribbed with acute or acuminate apices; inflorescences various; triads superficial 8
8. Seed with ruminate endosperm 9
8. Seed with homogeneous endosperm 12
9. Leaf sheaths splitting opposite the petiole, not forming a prominent crownshaft; inflorescences interfoliar, at least in bud, sometimes infrafoliar at anthesis or in fruit; the peduncle elongate, prominent, usually as long as the rachis or longer. Philippines to Micronesia, New Guinea, Solomon Islands ..... *Heterospathe*
9. Leaf sheaths tubular, forming a prominent crownshaft; inflorescence infrafoliar; peduncle usually much shorter than the rachis 10
10. Inflorescence lacking branches adaxially except at the apex, branched to 1 order only and the lower branches ± ascending, not divaricate from the rachis at a 90° angle; fruit black at maturity. Mascarene Islands ..... *Dictyosperma*

10. Inflorescence with branches spirally arranged, the lower branches abruptly divaricate at about a 90° angle from the rachis and again once- or twice-branched; fruit yellow, orange, or red 11
11. Stamens 6–9; pistillode prominent. Nicobar Islands, Malay Peninsula, Moluccas, New Guinea to the Solomon Islands ..... *Rhopaloblaste*
11. Stamens 15–30 or more; pistillode minute or lacking. New Guinea, Solomon Islands ..... *Actinorhytis*
12. Staminate flowers mostly larger than the pistillate; stamen filaments inflexed at the apex in bud; anthers dorsifixed, with elongate connective, not didymous 13
12. Staminate flowers mostly smaller than pistillate; stamen filaments erect in buds; anthers didymous 19
13. Stamens 12; fruit with basal stigmatic remains, lacking a shell of sclereids. New Caledonia ..... *Cyphokentia*
13. Stamens 6; fruit various 14
14. Endocarp minutely pitted; seed with lateral embryo. New Caledonia ..... *Alloschmidia*
14. Endocarp not pitted; seed with basal embryo 15
15. Leaf sheaths split opposite the petiole; inflorescence interfoliar. Lord Howe Island ..... *Lepidorrhachis*
15. Leaf sheaths forming a prominent crownshaft; inflorescence infrafoliar 16
16. Inflorescence densely tomentose; fruit with apical stigmatic residue. Ryukyu Islands ..... *Satakentia*
16. Inflorescence glabrous or at most minutely hairy; fruit with subapical to nearly basal stigmatic remains 17
17. Complete peduncular bracts two; endocarp hard, moderately thick, with longitudinal ridges. Vanuatu ..... *Carpoxylon*
17. Complete peduncular bracts one; endocarp thin or thick and prominently sculptured 18
18. Stilt roots usually developed; staminate flowers markedly asymmetrical, with short, trifid pistillode and acute sepals and petals; fruit lacking sclereids but with prominent, often greatly thickened fibers. New Ireland to Samoa ..... *Clinostigma*
18. Stilt roots not developed; staminate flowers symmetrical, with pistillode as long as stamens in bud and rounded sepals and petals; fruit with a layer of short sclereids beneath the exocarp. New Caledonia ..... *Moratia*
19. Fruit ellipsoidal, with basal stigmatic remains; sclereids lacking in mesocarp but tannin cells present. New Caledonia ..... *Brongniartikentia*
19. Fruit globose or nearly so, with lateral stigmatic remains; mesocarp with a shell of short sclereids beneath the exocarp 19
20. Leaf sheaths with minute scales, split opposite the petiole and not forming a crownshaft; peduncle short; fruit small, 1.4–1.6 cm in diameter, with tannin cells interior to sclereid layer. New Caledonia ..... *Clinosperma*
20. Leaf sheaths densely scaly, tubular and forming a prominent crownshaft; peduncle elongate; fruit large, ca. 3.2 cm in diameter, lacking tannin cells. New Caledonia ..... *Lavoixia*
21. Seed terete or 2-lobed in cross-section, ovoid, ellipsoidal, globose or rarely kidney-shaped in outline 21
21. Seed irregular in cross-section, externally angled or intricately ridged, furrowed, and sculptured 23
22. Fruit with apical stigmatic remains 22
22. Fruit with lateral stigmatic remains. New Caledonia ..... *Basselinia*
23. Stilt roots prominent and stout; pistillode of staminate flower shorter than stamens; fruit often curved apically. New Caledonia ..... *Campecarpus*
23. Stilt roots not prominently developed; pistillode of staminate flower longer than stamens, columnar; fruit straight. New Caledonia and Loyalty Islands ..... *Cyphophoenix*
24. Leaf sheaths split opposite the petiole in bud, not forming a prominent crownshaft; inflorescence among the leaves in bud, becoming infraoliar in fruit; peduncle elongate, much exceeding the rachis; prophyll and peduncular bract more or less persistent, at length marcescent; inflorescence branches with long bare basal portions, prominently swollen at the insertion, stiffly and divaricately 1-branched or the distal undivided. Fiji and New Caledonia ..... *Cyphosperma*
24. Leaf sheaths forming a prominent crownshaft; inflorescence infrafoliar; peduncle shorter than the rachis; prophyll and peduncular bracts caducous; inflorescence branches without a long basal bare portion, nor swollen at the insertion 24
25. Staminate flowers symmetrical; pistillode thick, columnar, longer than the stamens in bud, expanded into a broadly capitate apex; fruit subglobose with stigmatic remains lateral in upper third, the surface minutely granular-papillate. New Caledonia ..... *Veillonia*
25. Staminate flowers slightly to markedly asymmetrical, the pistillode elongate-conic to angled-columnar, shorter than the stamens in bud, not broadly capitate; fruit smooth or drying pebbled but not granular-papillose 25
26. Bracteoles surrounding the pistillate flower sepallike; anthers with locules not continuous but interrupted by sterile connectivelike areas; fruit drying densely pebbled and shouldered; mesocarp not readily separable from the stony, intricately sculptured, 4-angled endocarp with

dorsal groove, flanked by 2 ridges. New Caledonia ..... *Burretiokentia*

26. Bracteoles surrounding the pistillate flower very narrow, rarely (*P. dennisii*) with a slender process but never sepallike; locules of anthers continuous; fruit globose or subglobose or collapsing and drying wrinkled but not pebbled; mesocarp with a shining inner layer adjacent to and readily separated from the endocarp, endocarp sharply 4-angled to variously ridged and sculptured but always with a dorsal ridge. New Britain to Fiji ..... *Physokentia*

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