REVISION OF CHLOROPHORA (MORACEAE) IN AMERICA

R. C. KAASTRA

Instituut voor Systematische Plantkunde, Utrecht

1. INTRODUCTION

After several pre-Linnean mentions (see: BUREAU 1873), the name *Morus tinctoria* for plants belonging to the present genus *Chlorophora* was first validly published by LINNAEUS (1753). Later combinations were made under *Broussonetia* Ventenat by KUNTH (1817), under *Fusticus* Rafinesque by RAFINESQUE (1838), and under *Maclura* Nuttall by D. DON ex STEUDEL (1841). Rafinesque (l.c.) based the genus *Sukaminea* on *Morus tinctoria* L., without mentioning any species. GAUDICHAUD (1830) established the genus *Chlorophora*, based on *Morus tinctoria* L. Sp. Pl. 1753. The valid combination *Chlorophora tinctoria* (L.) was made by Bentham, who added the African *Morus excelsa* Welwitsch to *Chlorophora* (BENTHAM et HOOKER 1880). Recently CORNER (1962) made the combination *Maclura tinctoria* again, when reducing the genera *Cudrania* Trécul, *Cardiogyne* Bureau, and *Chlorophora* Gaudichaud to sections of *Maclura* Nuttall. Beside *C. tinctoria* several other species were described, e.g. *Maclura chlorocarpa* Liebmann, *Maclura affinis* Miquel, *Maclura mora* Grisebach, *Chlorophora mollis* Fernald. Especially Bureau (l.c.) and HASSLER (1919) distinguished several infraspecific taxa.

WOODSON, SCHERY et coll. (1960) distinguished only one American *Chlorophora* species, *C. tinctoria*. It seemed worth-while to investigate with ample material how many species and infraspecific taxa there are.

2. MATERIAL

About 830 herbarium specimens were studied from the following herbaria: Chicago Natural History Museum (F); Conservatoire et Jardin Botaniques, Genève (G); Rijksherbarium, Leiden (L); Instituto Miguel Lillo, Tucumán (LIL); Botanische Staatssammlung, München (M); Missouri Botanical Garden, St. Louis (MO); The New York Botanical Garden, New York (NY); Muséum National d'Histoire Naturelle, Laboratoire de Phanérogamie, Paris (P); Divisão de Botânica do Museu Nacional, Rio de Janeiro (R); Jardim Botânico, Rio de Janeiro (RB); Botanical Museum and Herbarium, Utrecht (U); U.S. National Museum, Washington, D.C. (US); Instituto Botánico, Caracas (VEN).

3. TYPIFICATION AND CONCEPTS OF LINNAEUS

In the Linnean herbarium there is a specimen under the name *Morus tinctoria*

(Savage's Cat. nr. 11112.10). – This name was originally *Morus tinctoria* but later the epithet was deleted and changed by Linnaeus to *zanthoxylon*, and finally again changed to *tinctoria*. – It consists of a part of a juvenile sterile twig with axillary spines and serrate-dentate oblong leaves with truncate-rotundate bases.

This specimen, however, was not used by Linnaeus for preparing the description of *Morus tinctoria* in Species Plantarum 1753. It was probably acquired by him between 1755 and 1767 (JACKSON 1912). Though this is not indicated on the herbarium sheet, according to the IDC micro-edition, the specimen came probably from Browne's herbarium of Jamaican plants which Linnaeus bought in 1758; see STEARN (1957 p.122). By the protologue of *Morus tinctoria*, however, the true type can be traced. Linnaeus, in his Sp. Pl.: 986. 1753, cited under *M. tinctoria* three previous publications: "Sloan. jam. hist. 2.p.3.t.158" (1725); "Raj. Dendr. 14" (1704); "Pluk. alm. 596. t. 239.f.3." (1692).

Plukenet's figure represents a twig with axillary spines and dentate-serrate ovate-oblong leaves. This does not agree with Linnaeus's description of *M. tinctoria*: "foliis ovatis hirsutis". The descriptions by Sloane of "Morus fructu viridi, ligno sulphureo tinctorio" in his Jam. Hist. and in Ray's Dendr. do not contradict Linnaeus's description and contain all elements of it. Plate 158.f.1 in Sloane's Jam. Hist. 2. (1725) of a male unarmed branch with entire leaves fully agrees with Linnaeus's description of *Morus tinctoria*. This picture therefore is to be regarded as the lectotype of *M. tinctoria* L. Sp. Pl. 1753.

In his Syst. Nat. 2 (ed. 10). 1759 Linnaeus described *Morus zanthoxylon* as follows: "foliis ovato-oblongis glabris, spinis axillaribus. Pluk. phyt. 239.f.3". Plukenet's figure (see above) agrees with this description by Linnaeus, though Linnaeus did not make any mention of the dentate-serrate leaf margin. It is not impossible that Linnaeus studied the herbarium specimen Savage, Cat. nr. 11112.10 for the preparation of the Syst.Nat. (ed. 10). Yet it is better not to choose this specimen as the type of *Morus zanthoxylon* on account of its hardly ovate but oblong leaves. Therefore Plukenet's plate is to be regarded as the type of *M. zanthoxylon* L.

The description of *M. tinctoria* in Sp.Pl. (ed. 2). 1763 must have been based on the herbarium specimen of Linnaeus, as shown by the changes with regard to earlier descriptions. Without mentioning *M. zanthoxylon*, Linnaeus cited Plukenet's illustration as a synonym of *M. tinctoria*, but with a question-mark.

In the Mantissa (1771) Linnaeus expressed as his opinion that *M. tinctoria* L. Sp. Pl. 1753 and *M. zanthoxylon* L. Syst. Nat. (ed. 10) belong to one and the same species: *M. tinctoria* ("duae hic plantae mixtae monente Millero"). This must be the reason why Linnaeus changed the name on his herbarium sheet.

4. TAXONOMY

The leaf outline and margin play an important role in many descriptions. The outline, however, is extremely variable and forms a continuum from elliptic via ovate to subrotundate, the leaf bases and apices varying independently. The margin varies from subentire via sinuate to lacerate. Frequently different leaf

types occur on the same branch or tree, e.g. *Leonard & Leonard 13129* st. (Haiti). Lacerate leaves seem to occur only in shrubby specimens or may be borne on root shoots. They are never found on fertile branches and have only been found in the West Indies.

Another feature which was used for differentiation is the indument of leaves, branches, etc. It varies from nearly glabrous to densely pilose and is often strigose and/or hirtellous but may also be pubescent (e.g. *R. S. Williams s.n.* ♀, Bolivia). It is not a distinctive feature; e.g. *Chlorophora mollis* Fernald is only a densely hairy extreme of a continuum. The venation at the lower surface of the leaf in several plants is of a lighter colour than the intervenium. HASSLER (1919) made use of this feature when distinguishing his Paraguayan ssp. *zanthoxyla*. This ssp. was also said to be characterized by a somewhat thicker lamina. Such plants do indeed occur in Paraguay, but these features have also been found in plants from other areas and are not consistently linked. The ssp. *zanthoxyla* Hassler therefore does no longer earn recognition.

The above-mentioned examples of the variability and continuity of some features, which is actually much more extensive, permits to distinguish only one species, *C. tinctoria*. This agrees with the idea of Woodson, Schery et coll. (l.c.). Beside the type ssp. there can be distinguished only ssp. *mora* (Griseb.) Hassler.

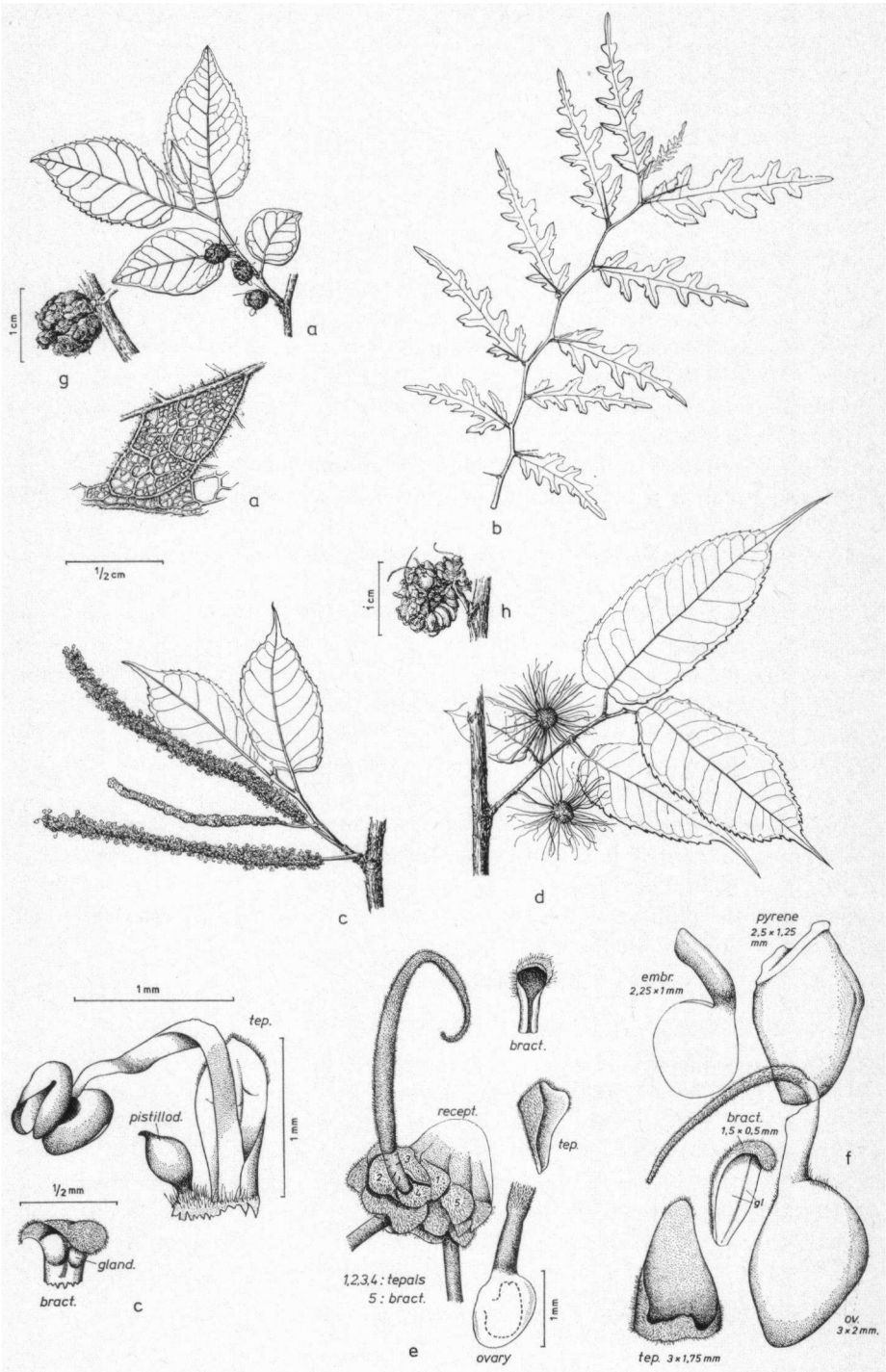
The concept of Corner (l.c.) about the taxonomic rank of *Chlorophora* and its generic position is divergent. In my opinion *Chlorophora* is to be maintained as a genus, not to be reduced to a section of *Maclura*. The main reasons for this are the longer stipules, the spicate male inflorescences, the presence of lithocysts, and the accumbent embryos of *Chlorophora*. These features are not found in the other sections of *Maclura* which Corner distinguished; see also a forthcoming paper on this subject (KAASTRA, in prep.).

Chlorophora or *Maclura brasiliensis* (Martius) and *C. scandens* Standley et Williams, described in the past, are heterotypic synonyms of the same taxon. They must be excluded from *Chlorophora* because of a large number of differences, e.g. the globose staminate inflorescence, the absence of lithocysts, the non-sessile flowers; see the above-mentioned paper (in prep.).

CHLOROPHORA TINCTORIA

Chlorophora tinctoria (Linnaeus) Gaudichaud in Freycinet ex Bentham et Hooker, Gen. Pl. 3: 363. 1880; Gaudichaud, Botanique in Freycinet, Voyage Uran. Physic.: 509. 1830 ("1826")*. – *Morus tinctoria* L. Sp. Pl.: 986. 1753; Sp. Pl. (ed. 2): 1399–1400. 1763; Sp. Pl. (ed. 3 Vienna): 1399. 1764; Miller, Gard. Dict. (ed. 8): nr. 5. 1768; L. Mant. 2: 495. 1771; Houttuyn, Nat. Hist. 2(3): 288–291. 1774; Poiret in Lamarck et Poiret, Encycl. Méth. Bot. 4: 379–380. 1797; L. Sp. Pl. 4 (ed. 5, "4", Willd.): 371. 1805; Persoon, Syn. Pl. 2: 558. 1807. – *Broussonetia tinctoria* (L.) Kunth in Humboldt et Bonpland, Nov.

* The dates of effective publication differing from dates as appearing in publications are according to STAFLEN (1967).


1 cm
g
a
a
b
1/2 cm
1 cm
h
c
d
1 mm
tep.
pistillod.
1 mm
1/2 mm
gland.
bract.
c
recept.
bract.
tep.
1,2,3,4 : tepals
5 : bract.
1 mm
ovary
e
pyrene
2,5 × 1,25 mm
embr.
2,25 × 1 mm
bract.
1,5 × 0,5 mm
gl
f
ov.
3 × 2 mm.
tep. 3 × 1,75 mm

Gen. Sp. 2: 32–33. 1817; Sprengel, Syst. Veg. 3 (ed. 16): 901. 1826 (pro parte); Martius, Fl. Regensb. 24, Beibl.: 9–10. 1841. – *Fusticus tinctoria* (L.) Rafinesque, New Fl. Amer. 3: 45. 1838 ("1836"). – *Fusticus vera* Rafinesque, op. cit.: 45 (nom. superfl.). – *Fusticus tataiba* Rafinesque, op cit.: 45–46 (nom. superfl.). – *Maclura tinctoria* (L.) D. Don ex Steudel, Nomencl. 2 (ed. 2): 87. 1841; Endlicher, Gen. Pl. Suppl. 4(2): 34. 1848 ("1847"); Bureau in DC. Prodr. 17: 228. 1873; Corner, Gard. Bull. Singapore 19: 236. 1962. – Lectotype (first chosen here): Sloane, Hist. Jam. 2: *t. 158. f.l.* 1725.

Morus zanthoxylon L. Syst. Nat. 2 (ed. 10): 1266. 1759; Jacquin, Select. Amer. Hist.: 247–248 et *t. 180. f. 55.* 1763; Miller, Gard. Dict. (ed. 8): nr. 8. 1768. – *Fusticus xanthoxylon* (L.) Rafinesque, New Fl. Amer. 3:45. 1838 ("1836"). – *Broussonetia xanthoxylon* (L.) Martius, Fl. Regensb. 24, Beibl.: 10. 1841; Herb. Bras.: 250. 1841. – *Maclura xanthoxylon* (L.) Endlicher, Gen. Pl. Suppl. 4(2): 34. 1848 ("1847"). – *Maclura tinctoria* (L.) Steudel var. *xanthoxylon* (L.) Bureau in DC. Prodr. 17:230. 1873. – *Chlorophora tinctoria* (L.) Bentham et Hooker var. *xanthoxylon* (L.) Chodat, Bull. Herb. Boissier II 3: 349. 1903; idem ssp. *zanthoxyla* (L.) Hassler, Annuaire Conserv. Jard. Bot. Genève 21:113. 1919; idem ssp. *zanthoxyla* (L.) Hassler var. *zanthoxyla*, op. cit.: 114 (var. "*xanthoxylon*"). – Type: Plukenet, Phytographia 3, Appendix, *t. 239. f. 3*, 1692.

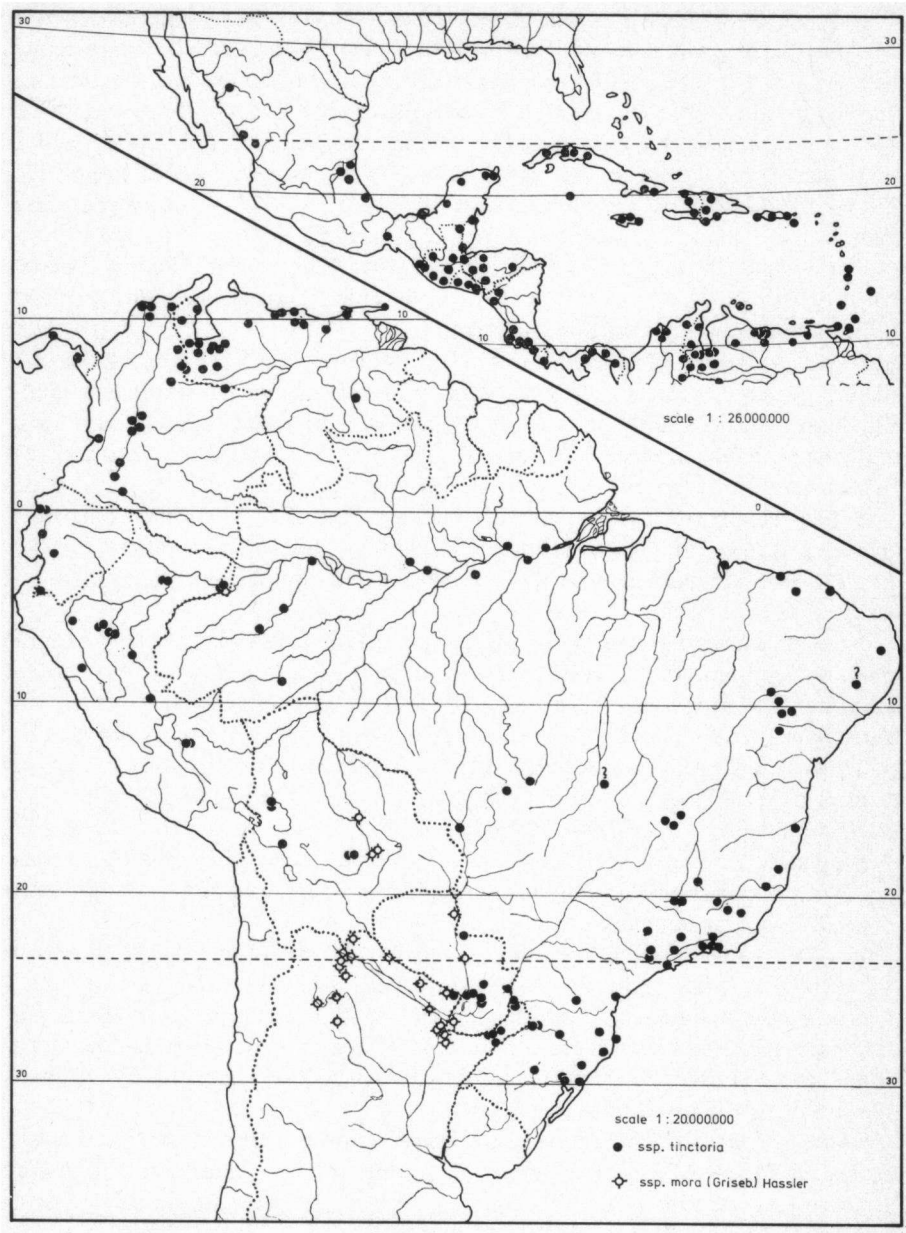
Broussonetia plumerii Sprengel, Syst. Veg. 3 (ed. 16): 901. 1826. – *Maclura plumerii* (Sprengel) D. Don ex Steudel, Nomencl. 2 (ed. 2): 87. 1841, erroneously written as "*plumiera*"; cf. URBAN (1920 p.9: foot-note). – *Morus plumerii* Burman ex Steudel, l.c. (nom. inval. pro syn., erroneously written as "*plumiera*" cf. URBAN (1920 p.9: foot-note). – Type: Plumier msc. ex Burman, Pl. Amer. fasc. 9: *t. 204.* 1759.

Maclura sempervirens Tenore, Cat. Hort. Bot. Neap. 1845: 87. – Type and original descr. not seen but according to Bureau "descriptione huic varietati (= *Maclura tinctoria* (L.) Steudel var. *subcuneata* Bureau in DC. Prodr. 17: 229. 1873) optime congruit".

Maclura chlorocarpa Liebmann, Kongel. Danske Vidensk.-Selsk. Skr. Naturvidensk. Math. Afd. 2: 314. 1851. – *Maclura tinctoria* (L.) Steudel var. *chlorocarpa* Bureau in DC. Prodr. 17:229, 1873. – Syntypes: *Liebmann s.n.* ♂, Mexico, banks of river Tecolutla near Paso del Correo; ♀, Mexico, between Jalapa and Mirador (non vidi).

Maclura polyneura Miquel in Martius, Fl. Bras. 4 (1): 154–155. 1853. – *Maclura tinctoria* (L.) Steudel var. *polyneura* (Miquel) Bureau in DC. Prodr. 17:230. 1873. – *Chlorophora tinctoria* (L.) Bentham et Hooker ssp. *zanthoxyla* (L.) Hassler var. *zanthoxyla* f. *polyneura* (Miquel) Hassler, Annuaire Conserv. Jard. Bot. Genève 21:114. 1919. – Type: *Pohl s.n.* ♂, Brazil, Minas Gerais, Conçeião (M; isotypes L, U).

Plate 1. *Chlorophora tinctoria* ssp. *tinctoria*: from *Leonard et Leonard 11630* (US; *fig.* b), *Vargas 8535* (LIL; *fig.* c), *Woytkowski 35079* (LIL; *fig.* d), *Schwarz 7368* (LIL; *fig.* e), *Spruce s.n.*, Nov.–March 1849–1850 (NY; *fig.* f), and *Pittier 74* (NY; *fig.* h).
C. tinctoria ssp. *mora*: from *Pedersen 856* (US; *fig.* a), and *Rodriguez 117* (LIL; *fig.* g).



Map 1. Distribution of *Chlorophora tinctoria*.

Maclura affinis Miquel in Martius, Fl. Bras. 4(1): 155–156. 1853. – *Maclura tinctoria* (L.) Steudel var. *affinis* (Miquel) Bureau in DC. Prodr. 17:230. 1873. – *Chlorophora tinctoria* (L.) Bentham et Hooker ssp. *zanthoxyla* (L.) Hassler var. *affinis* (Miquel) Hassler, Annuaire Conserv. Jard. Bot. Genève 21: 113–114. 1919. – Syntypes: *Luschnath s.n.* ♀, Brazil (non vidi); *Schornbaum s.n.* ♂, Brazil (non vidi); *Ruiz et Pavón s.n.* ♀, ♂, Peru, loco non ind. (MA, non vidi; isosyntype F!).

Maclura subintegerrima Miquel in Martius, Fl. Bras. 4(1): 157. 1853. – *Maclura tinctoria* (L.) Steudel var. *subintegerrima* (Miquel) Bureau in DC. Prodr. 17: 228–229. 1873. – Type: *W. Hooker s.n.* ♀, Jamaica, loco non ind. (U; isotype P).

Maclura velutina Blume, Mus. Bot. 2:82. 1856 ("1852"). – Lectotype (first chosen here): *Wydler s.n.* ♀, Porto Rico, loco non ind. (L); paratype: *Wydler 291* ♀, Porto Rico (G).

Maclura sieberi Blume, Mus. Bot. 2: 83. 1856 ("1852"). – Type: *Sieber 105* ♀, Trinidad (L; isotypes G, MO).

Maclura tinctoria (L.) Steudel var. *subintegerrima* (Miquel) Bureau subvar. *quercina* Bureau in DC. Prodr. 17:229. 1873. – Lectotype: *Bertero s.n.* st., Santo Domingo (G–DC? non vidi; part of lectotype (seen by Bureau) P; isotype M).

Maclura tinctoria (L.) Steudel var. *subcuneata* Bureau in DC. Prodr. 17:229. 1873. – Lectotype (first chosen here): *Bonpland s.n.* ♀, Colombia, Santa Fé de Bogotá (P); paratypes: *Holton 234* ♂ and *250* ♀, Colombia, supra Honda, Rio Seco (NY).

Maclura tinctoria (L.) Steudel var. *chlorocarpa* (Liebmann) Bureau subvar. *sinuata* Bureau in DC. Prodr. 17:229. 1873. – Type: *Bonpland 37* st., Venezuela (P? non vidi).

Maclura tinctoria (L.) Steudel var. *ovata* Bureau in DC. Prodr. 17:229. 1873. – *Chlorophora tinctoria* (L.) Bentham et Hooker var. *ovata* (Bureau) Chodat, Bull. Herb. Boissier II 3:349. 1903 (excl. coll. cit. Hassler 7329 ♀ et 7329a ♂). – *Chlorophora tinctoria* (L.) Bentham et Hooker ssp. *eutinctoria* Hassler (nom. illeg. ex art. 24 et 26 Int. Code Bot. Nomencl. (ed. 1972)) f. *ovata* (Bureau) Hassler, Annuaire Conserv. Jard. Bot. Genève 21:115. 1919 (nom. inval. ex art. 34 (3) Int. Code Bot. Nomencl. (ed. 1972)). – Lectotype (first chosen here): *Gaudichaud 1068* ♀, Brazil, Rio de Janeiro (P; isotypes G, L, NY, P).

Maclura tinctoria (L.) Steudel var. *xanthoxylon* (L.) Bureau subvar. *lobata* Bureau in DC. Prodr. 17:230. 1873. – Type: *Plée s.n.* st., Venezuela, Maracaibo (P).

Chlorophora mollis Fernald, Contr. Gray Herb. New Series 28:52. 1904. – Type: *Rose et Hough 4672* ♀, Mexico, Oaxaca, Tomellin Cañon (GH?; isotypes NY, US).

Chlorophora tinctoria (L.) Bentham et Hooker var. *acuminatissima* Huber, Bol. Mus. Paraense Hist. Nat. 5:332. 1909. (nom. inval. ex art. 34 (3) Int. Code Bot. Nomencl. (ed. 1972)); idem var. *acuminatissima* Huber f. *glabrescens*

Huber, l.c. (nom. inval. ex art. 32 (3) Int. Code Bot. Nomencl. (ed. 1972)). – Type: not precisely indicated.

Chlorophora tinctoria (L.) Bentham et Hooker ssp. *zanthoxyla* (L.) Hassler var. *zanthoxyla* f. *miqueliana* Hassler, Annuaire Conserv. Jard. Bot. Genève 21:114. 1919. – Type: *Hassler 3368* ♀, Paraguay, Cordillera de Altos (G – Hassler, non vidi; isotypes G-Delessert, L, MO, NY).

Chlorophora tinctoria (L.) Bentham et Hooker ssp. *zanthoxyla* (L.) Hassler var. *zanthoxyla* f. *tataiiba* Hassler, l.c. – Lectotype (first chosen here): *Hassler 12125* ♂, Central Paraguay, near lake Ypacaray (G – Hassler, non vidi; isotypes F, G-Delessert, L, LIL, MO, NY, US, Z).

Dioecious tree up to 30 m tall, sometimes shrubby. Branches with grey-yellow bark, conspicuously lenticellate; twigs often hirtellous or puberulous, becoming glabrous; unarmed or provided with axillary, solitary or sometimes paired, (almost) straight, to 3.5 cm long spines with small stipules at the base.

Leaves distichous, variable, mostly (narrowly) elliptic to (narrowly) ovate, rarely obovate or rotundate, to 8.5 × 19 cm, papyraceous but sometimes pergamentaceous; base subequal or unequal, truncate, cordate or subacute; apex mostly acuminate or caudate, sometimes acute or premorse and sometimes besides with mucronate tip; margin subentire or dentate-serrate, sometimes with one or more semi-circular incisions or lacerate; veins in each half of blade differing in number, 7–17 per side; more or less sparsely or densely strigose, or subglabrous, beneath sometimes more or less curled-hirtellous and somewhat paler than above. Petioles sulcate or not, 2–15 (20) mm, puberulous. Stipules (narrowly) ovate to (narrowly) triangular, dorsally puberulous and sparsely strigose, connate in the leaf axil, 2.5–11 mm long, enclosing the branchlets for one half to three quarters of their circumference but caducous, leaving a distinct scar.

Staminate inflorescences spicate, 4–7 × 30–125 mm, axillary, mostly solitary but sometimes 2–4 together on a short side-branchlet, densely set with sessile flowers, intermingled with bracts; peduncles 2–19 mm, pilosellous-pilose; bracts broadly spathulate or depressed-triangular, sometimes two connate, to 1 mm long, with glands, apex more or less cucullate, fimbriate; tepals elliptic to broadly elliptic or spathulate to broadly ovate, about 1.5 mm long, without glands, apex subacute, near the base somewhat connate, concave, thin, fimbriate, dorsally hirtellous-puberulous; stamens in bud incurvate, at anthesis exserted and recurved; filaments at anthesis about twice as long as the tepals and near the base adnate to them; anthers with broadly elliptic thecae, somewhat laterally extrorse; pistillode narrowly ovoid to ellipsoid, compressed, to 1 mm long, pilosellous-puberulous, with an uncinate apex.

Pistillate inflorescences capitate, axillary, mostly solitary, subglobose, mostly somewhat longer than broad, 3–8 (13) mm long, in fruit 6–18 mm; peduncles velutinous, 2–15 mm, in fruit 2–20 mm; flowering heads densely crowded with sessile flowers intermingled with bracts; bracts narrowly spathulate or obtrul-

late to narrowly spathulate, about 1–2 mm long, with (rarely without) glands, cucullate, more or less carinate, fimbriate, apex hoary velutinous or not; tepals obovate to shortly spathulate, to 3 mm long, cucullate, carinate, fimbriate, asymmetric, mostly with glands, somewhat connate near the bases; styles sublateral, mostly single and undivided but sometimes at the base bifid, the longer part of the style including the filiform stigma 5–18 mm long, the smaller part, if any, 0.5 mm or longer but always shorter than the tepals; ovary obovoid, oblique, 1.2–2.2 mm long, lens-shaped, apex barbate, margins puberulous-strigose; ovule one, pendulous; pyrene to 4 mm; embryo curvate with flat cotyledons and long accumbent radicle.

In the upper epidermis of the leaves there are lithocysts projecting downward into the mesophyll. These are easily recognized by microscope as pyramids on the surface when putting a shortly boiled piece of a leaf on a slide, without making sections. Leaves and flower parts often bear microscopic multicellular glandular hairs.

The plants are dioecious but bisexual flowers occur in *Krug 2833* (Brazil, São Paulo).

Though the flowers are mostly 4-merous, 5-merous flowers also occur exceptionally: *Schreiter 11443* ♂ and *Meyer 15.021* ♂ (Argentina, Salta, Orán).

The male inflorescence may bear a sterile longitudinal groove. Notably the specimens from Peru have long slender catkins.

The female inflorescence is mostly subglobose but elongates somewhat in fruit. This indicates the relationship with African Chlorophoras with oblong female heads, see CORNER (1962).

The presence of two yellow glandular parts in bracts and tepals is a conspicuous feature, but systematically not reliable. This tissue does not occur in all bracts and perianth segments, though rather frequently in bracts and in female tepals. In male tepals it does not occur, except in one specimen in which some glandular tissue could be found in some of the tepals: *Hassler 7329a* ♂ (Paraguay, near Concepcion).

KEY TO THE SUBSPECIES

All veins and veinlets on the lower surface of the leaves prominent; bracts in pistillate inflorescences not velutinous, tepals of pistillate flowers hardly ever velutinous; style incl. stigma 3–7 mm . . . . . ssp. **mora**

Smallest veinlets on the lower surface of the leaves not prominent; bracts and tepals of pistillate flowers hoary velutinous; style incl. stigma 7–18 mm . . . . . ssp. **tinctoria**

subspecies **tinctoria**

Leaf blade narrowly to broadly elliptic to more or less narrowly ovate, 0.7–8.5 × 1.2–19 cm; veins 7–17 per side, mostly 13–14; petioles terete to somewhat compressed, more or less sulcate, 2–15(20) mm long; on the lower surface of

leaves always non-prominent veinlets visible.

Staminate inflorescences with peduncles of 2–19 mm, mostly about 10 mm; catkins 30–125 mm long.

Pistillate inflorescences with peduncles of 2–13 mm, in fruit to 20 mm; length of flowering heads at anthesis 3–8 (13) mm, later to 18 mm; bracts narrowly spathulate, 1–2 mm, velutinous; style including the stigma 7–18 mm.

Flowering from September to December and from February to March (in Venezuela, Colombia and Ecuador to May), incidentally also in other months; in Central America from May to October, in the Antilles from April to September.

Distribution: tropical America, from 30° S.L. (Brazil, Rio Grande do Sul) to 26° N.L. (Mexico, Sinaloa), map 1. A very widespread subspecies but not found in all areas: not native in the Andes and in the Guyanas, only introduced in former British Guyana. Abundant in the Antilles but absent from the Bahamas and Florida.

From sea-level to 1600 m, often below 1000 m. Mostly in primary or secondary forests, wet or dry; often found on riverbanks. Also in pastures, xerophytic and savanna thickets of Central America.

Use: the tree of 4–30 m, often 8–12 m, has a trunk diameter of 40–60 (100) cm. The wood is yellow and very durable. For its very important uses as dyewood, e.g. for camouflage-dressing, furniture-wood and for its medicinal uses see STANDLEY (1922) and STANDLEY & STEYERMARK (1946).

Vernacular names: see BUREAU (1873); Central American names: Standley (l.c.).

Geographically selected specimens from the studied material:

Mexico: Yucatán, Suitun, *G. F. Gaumer & Sons 23302* ♀ (F, G, MO, NY, US). **Br. Honduras:** San Antonio, *P. Gentle 143* ♂ (F). **Guatemala:** Along Honduras road, Gualan, *C. C. Deam 6378* ♀ (F, MO, NY). **Honduras:** dep. Yoro, near Progreso, *Standley 55024* st. (F, US). **Nicaragua:** Momotombo, *C. L. Smith 113* ♂, ♀ (F, NY). **Costa Rica:** prov. Puntarenas, vic. Palmar, Norte de Osa, *P. H. Allen 5601* ♂, ♀ (F, G, US). **Panama:** Progreso, Chiriquí, *Cooper & Slater 237* st. (F, MO, US).

Cuba: prov. Oriente, Bayate, *E. L. Ekman 6407* ♀ (F, G, NY, US). **Gr. Cayman:** 0.4 mile S.E. of Old Man Village, *Proctor 27982* ♀ (U). **Jamaica:** vic. of Hampstead, *Proctor 8678* ♂ (LIL, NY). **Haiti:** Tortue Island, vic. of La Vallée, *E. C. Leonard & G. M. Leonard 11630* st. (NY, US). **Santo Domingo:** prov. Barahona, Barahona, *M. Fuertes 190* ♂ (F, G, L, LIL, M (♀), MO, NY, US, Z). **Puerto Rico:** Vieques Island, Cerra Encanta, *J. A. Shaver 2542* st. (NY, US). **St. Croix:** Jerusalem estate, *A. E. Ricksecker 482* ♀ (F, MO, NY, US). **Martinique:** loco non ind., *Plée 848* ♂ (P, U). **St. Lucia:** Soufrière, *J. S. Beard 526* ♂, ♀ (LIL, MO, NY). **Barbados:** Bush Hall, St. Michael, *J. R. Borell 194* ♂, ♀ (NY). **Grenada:** Pointe Saline, *P. Beard 1330* ♀ (US). **Curaçao:** loco non ind., *I. Boldingh 4702* ♀ (NY, U).

Tobago: Rockley Valley, *W. E. Broadway 4072* ♂ (F, G, L, U, Z). **Trinidad:** loco non ind., *Sieber 105* ♀ (G, L, MO; type of *Maclura sieberi* Blume). **Brazil:** Amazonas, basin of Rio Juruá, Marapota, mun. Carauary, *B. A. Krukoff 4570* ♀ (F, G, M, MO, NY, U); Pará, near Santarem, *R. Spruce s.n. (1705?)* ♂, ♀ (G, P, NY); Ceará/Piauí, loco non ind., *Gardner 2002* ♀ (G, L, P); Bahia, near Jacobina, *Blanchet 3301* ♂ (G, L, P, NY); Mato Grosso, Caceres, *F. C. Hoehne 4657* ♂ (R); Minas Gerais, 4.5 km road to São Miguel, *Y. Mexia 5329* ♀ (F, G, MO, NY, U, Z); Rio de Janeiro, loco non ind., *Gaudichaud 1086* ♀ (G, L, P, NY; lectotype of *Maclura tinctoria* (L.) Steudel var. *ovata* Bureau); Paraná, Foz do Iguassú, *G. J. Schwarz*

7368 ♀ (LIL); Rio Grande do Sul, Butterberg, near Montenegro, *B. Rambo 49143* ♂ (LIL). **Paraguay:** Centurion, between Río Apa and Aquidaban, 22–23° lat., *K. Fiebrig 4394* ♂ (G,L,M, US, Z); Cordillera de Altos, *K. Fiebrig 411* ♂ (F, G, L, M).

Venezuela: D. F., foot of Curucutí Valley, *Pittier 12453* ♀ (F, G, L, M, MO, NY, VEN); D. F., near El Zigzag, between Caracas and Puerto Cabello, *Pittier 74* ♀ (G, NY); La Guaira, *I. Boldingh 3932* ♂ (U). **Colombia:** Sta. Marta, *H. H. Smith 425* ♂, ♀ (F, L, MO, NY, U); region of Barranquilla, *Bro. Elias 1246* ♂ (F, US). **Ecuador:** prov. Loja, between Puente Boquerón and Gonzanamá, *E. Asplund 18085* ♀ (NY, R). **Peru:** dep. San Martín, prov. San Martín, Tarapoto, close to Chilcay river, *F. Woytkowski 35079* ♀ (F, LIL, MO); dep. Cuzco, prov. Convención, Idma, *C. Vargas 8535* ♂ (LIL, MO). **Bolivia:** region of Mapiri, San Carlos, *O. Buchtien 647* ♀ (G, MO, NY, Z).

Argentina: Formosa, dep. Pilcomayo, Estancia Riacho Negro, *I. Morel 3926* ♂ (LIL); Misiones, Posadas, *T. Meyer 5642* ♀ (LIL, U).

Note: references to Z (Botanischer Garten und Institut für Systematische Botanik der Universität Zürich) and some of the references to M and G were kindly communicated by Mr. C. C. Berg, who visited these herbaria by a grant of the WOTRO organization.

subspecies **mora**

Chlorophora tinctoria (L.) Gaudichaud in Freycinet ex Bentham et Hooker ssp. **mora** (Grisebach) Hassler, Annuaire Conserv. Jard. Bot. Genève 21:114–115. 1919. – *Maclura mora* Grisebach, Abh. Königl. Ges. Wiss. Göttingen Phys. Cl. 24:86.1879 (excl. synonyma). – *Ioxylon*[1] *mora* (Grisebach) O. Kuntze, Rev. Gen. Pl. 3(3): 294. 1898. – *Chlorophora mora* (Grisebach) Lillo in Venturi et Lillo, Contr. Conocim. Arb. Argentina: 63. 1910. – ? *Chlorophora tinctoria* (L.) Bentham et Hooker var. *mora* (Grisebach) Lillo, Bol. Mus. Cien. Nat. Univ. Tucumán 6:10. 1925 (publ. not seen; cf. Lilloa 1: 16. nr. 23. 1937). – Type: *Lorentz et Hieronymus 479* ♂, ♀?, Argentina, Orán (B, non vidi, indicated as type according to photogr. in MO; isotype ex herb. Kuntze in NY (2 ×)).

Maclura trilobata N. Rojas Acosta, Bull. Acad. Int. Géogr. Bot. 24:211. 1914. – Type: not indicated, from Argentina, Col. Benitez, along Rio Salado.

Chlorophora reticulata Herzog, Meded. Rijks-Herb. 27:73. 1915. – Type: *Herzog 1526* st., Bolivia, Pampa near Santa Cruz (L; isotype M).

Leaf blade more or less ovate, sometimes rotundate, 0.8–4 × 1–8 (11) cm; veins 7–15 per side, mostly 9–10; petioles terete, mostly not sulcate, 2–12 (16) mm; on the lower surface of leaves all veins and veinlets which are visible with low magnification, prominent and often densely strigose.

Staminate inflorescences with peduncles of 2–4 mm, catkins 35–41 mm long.

Pistillate inflorescences with peduncles of 1–4 mm, in fruit to 8 mm, flowering heads 2–5 mm, in fruit to 9 mm long; bracts obtrullate to shortly spathulate, about 0.7 mm long, subglabrous, not velutinous; tepals to 1.7 mm long, rotundate, hardly ever velutinous, at most somewhat pubescent near the margins: style including the stigma 3–7 mm (in a cultivated specimen to 10 mm).

Flowers from September to November, rarely to February.

Distribution: Northern Argentina, Paraguay, and Bolivia, in the Gran Chaco

[1] *Ioxylon* or *Joxylon* are typographic errors for *Toxylon*; see Greene, Pittonia 2: 122. 1890; cf. Kuntze, Rev. Gen. Pl. 3(2): 113. 1898.

especially along the borders of the Chaco, e.g. in Orán; see map 1. Allopatric with the type subspecies. In "bosques", sometimes in campos. To 750 m altitude.

Use: the tree of 4–30 m, mostly 8–10 m, has a trunk of about 50–80 cm diameter. The yellow (-rose?) wood is/was used for making carts and bridges and is used by carpenters. The ripe inflorescences seem to be edible (LILLO, 1910), but are small and consist for the greater part of hard pyrenes!

Vernacular names. Spanish: mora (Orán, Corrientes; mora colorada (Chaco, Salta); mora amarilla (Chaco); mora de la pampa (Bolivia). Guarany: tatá-yŷbá-saŷyú ("yellow fire branch") or tatá-yŷbá-pŷitá (Chaco); tatá-yŷbá (Corrientes); see LILLO (1910). The Guarany name tatá-yŷbá ("fire branch") is also an often reported vernacular name for the ssp. *tinctoria* in Brazil, and some authors based an epithet on it.

Specimens studied:

Bolivia: Andrés Ibanez, dep. Sta. Cruz, Los Arroy(it)os, *I. Peredo* ♀ (LIL); Pampa de Sta. Cruz, *Herzog 1526* st. (L, M; photo MO, NY); type of *Chlorophora reticulata* Herzog; Cercado, dep. Sta. Cruz, Urubó, *Steinbach 2828* ♂ (LIL).

Paraguay: Fuerte Olimpo, *T. Rojas 13.652a* ♀ (LIL); prope Concepcion, *Hassler 7329* ♀ (G, L, MO, NY); idem, *Hassler 7329a* ♂ (G, L, LIL, MO, NY, P); dep. Pilar, Curupayty, *T. Meyer 15.946* ♀ (LIL); Santisima Trinidad, Monte Avenida Artigas, *T. Rojas 12945a* ♀ (cult.?; F, LIL); Asunción, *T. Rojas 12945* ♂ (cult.; F).

Argentina: Jujuy, Ledesma, *Lillo 10845*? ♀ (LIL, U, US); idem, *Venturi 5396* ♂ (F, LIL, US, Z); Ledesma, El Sauzal, *Lillo (7243 inst. Lillo)* st. (US); idem, *Lillo 10828*? st. (LIL); Jujuy, Praile Pintado, *Pastrana 9157* ♀ (LIL); Jujuy, dep. San Pedro, La Mendieta, *Schreiter 11444* ♀ (F, LIL, U).

Salta, dep. Orán, loco non ind., *Lorentz et Hieronymus s.n.* st. (NY; isotype of *Maclura mora* Grisebach); *idem 479* ♂, ♀? (photogr. of specimen in B: MO; type of *Maclura mora* Grisebach); idem, *Rodriguez 1002* ♀ (LIL); *idem 1031* ♂(LIL); Orán, Cedral, *Rodriguez? (coll. non indicated) 1002* ♀ (LIL); Orán, Embarcación (Río Bermejo), *Schreiter 26* ♂ (F); *idem 5026* ♂ (LIL); *idem 11351* ♂ (LIL): idem *Venturi 5041* ♂ (F); Orán, Orán, *T. Meyer 4959* st. (F, LIL); Orán, Río Piedras, *Rodriguez 14* ♂ (F, LIL, US); *idem 117* ♀ (LIL); Orán, Abra Grande, *Venturi 5551* ♀ (F, LIL); Orán, Tartagal, *Schreiter 3412* ♀ (LIL); *idem 11443* ♂ (F, LIL, U); idem, *T. Meyer 15. 021* ♂ (LIL); Orán, Urundel, *T. Meyer 12.681* ♀ (LIL).

Formosa, Puerta El Colorado, Alta Río Bermejo, *T. Rojas 12127* ♀ (LIL); dep. Pilcomayo, Isla Puerta Elsa, *T. Rojas 12283* ♂ (F, LIL); idem, Buena Vista, *I. Morel 6.518* ♀ (LIL); idem, Ruta 86 al Km 79, *I. Morel 6.668* ♀ (LIL).

Chaco, Col. Benitez, *A. G. Sch(ulz) 1834* ♀ (LIL); Fontana, *T. Meyer 162* ♀ (LIL); *idem 3.185* ♀ (LIL); Communité Las Palmas, *P. Jórgensen 2159* ♀ (LIL, MO, US); Pte. Roca, *T. Meyer 1060* ♂ (LIL).

Corrientes, loc. non ind., *Bonpland s.n. (anno 1833)* st. (P); *idem (anno 1821)* st. (P); dep. San Cosme, Paraje Desaguadeso, *T. S. Ybarrola 921* ♂ (LIL); dep. Moburucuyá, C(B?)añada Paso B(C?)earios, *G. J. Schwarz 8650* ♂ (LIL); idem, Estancia "Sta. Teresa", *T. M. Pedersen 847* ♂ (G, MO, NY, U, US); idem, Estancia "Sta. Maria", *T. M. Pedersen 856* ♀ (G, MO, NY, U, US).

Tucumán, dep. Capital, Inst. Lillo, *T. Meyer 18.591* ♀ (cultiv.: LIL).

Though both subspecies are allopatric, (air-) pollination between them might take place, because of the relative proximity of their areas. Yet there are no intermediate plants which cannot be placed in one of them. Only one specimen,

Hassler 7329 ♀ (Paraguay, near Concepcion) has bracts and tepals velutinous; in its other features, e.g. the prominent leaf venation, it does not differ from ssp. *mora.*

DUBIOUS NAMES

Morus spinosa Herb. Mus. Gaudichaud, Botanique in Freycinet, Voyage Uran. Physic.: 508. 1830 ("1826") (nom. nud.). – *Morus spinosa* Herb. Mus. Par.? Steudel, Nomencl. 2 (ed. 2): 87. 1841 (pro syn.). – Probably based on a sterile specimen in herb. Vaillant, now in P, from St. Croix, which is a lacerate form of *C. tinctoria* ssp. *tinctoria.*

Morus tataiba Vellozo. Fl. Flum. Atlas 10: *t. 21.* 1835 ("1827") (nom. nud.; illustration cannot be determined with certainty, but may be *C. tinctoria*).

Fusticus glabra Rafinesque, New Fl. Amer. 3:44–45. 1838 ("1836"); on account of description possibly synonymous with *C. tinctoria*, but as it is reported from South Florida and Cuba this is at least partially uncertain.

EXCLUDED NAME

Broussonetia tinctoria Torrey, Ann. Lyceum Nat. Hist. New York 2: 246. 1828 = *Maclura pomifera* (Rafinesque) Schneider, Ill. Handb. Laubholzk. 1: 806. 1906.

ACKNOWLEDGEMENTS

Thanks are due to my teacher Mr. C. C. Berg, auctor intellectualis, for his critical suggestions and help, and for tracing the material. As a result of his visit to the herbaria G, M, P and Z, made possible through a WOTRO-grant, I could study many types.

Many thanks are also due to Dr. K. U. Kramer for his critical reading of the manuscript and for correcting the English text.

The drawings were made by miss E. M. Hupkens-van der Elst and Mr. T. Schipper.

The author is much indebted to the directors and keepers of the herbaria for the loan of the material.

REFERENCES

BENTHAM, G. et J. D. HOOKER (1880): *Genera Plantarum* **3**: 363. Reeve & Co, London.

BUREAU, Ed. (1873): *Moraceae*, in A. P. DE CANDOLLE: *Prodromus systematis naturalis regni vegetabilis etc.* **17**: 226–230. Masson, Paris.

CORNER, E. J. H. (1962):The classification of Moraceae. *Gard. Bull. Singapore* **19**: 187–252.

DON, D. ex E. G. STEUDEL (1841): *Nomenclator botanicus etc.* **2** (ed. 2): 87. Cotta, Stuttgart & Tübingen.

GAUDICHAUD-BEAUPRÉ, C. (1830; "1826"): *Botanique*, in L. de FREYCINET: *Voyage... Uranie et Physicienne:* 509. Ainé, Paris.

HASSLER, E. (1919): Moracearum Paraguariensium Conspectus. *Annuaire Conserv. Jard. Bot. Genève* **21**: 113–115.

JACKSON, B. D. (1912): *Index to the Linnean Herbarium etc.* 152 pp. Linnean Society, London.

KUNTH, C. S. (1817): *Botanique* Sect. 3. *Nova genera et species plantarum etc.* **2**, in F. H. A. VON HUMBOLDT et A. J. (G.) BONPLAND: *Voyage etc.*: 32–33. Paris (reprint Cramer, Weinheim. 1963).

LILLO, M. (1910): in S. VENTURI et M. LILLO: *Contribución al conocimiento de los árboles de la Argentina:* 63. Propriedad de los autores, Buenos Aires.

LINNAEUS, C. (1753): *Species Plantarum:* 986. Stockholm (facsimile Ray Society, London. 1957).

RAFINESQUE-SCHMALTZ, C. S. (1838; "1836"): *New flora and botany of North America etc.* Third part, New Sylva: 42–46. Philadelphia (facsimile Arnold Arboretum. 1946).

STAFLEU, F. A. (1967): Taxonomic literature. *Regnum Veg.* **52.**

STANDLEY, P. C. (1922): Trees and shrubs of Mexico. *Contr. U.S. Nation. Herb.* **23:** 203.

— & J. A. STEYERMARK (1946): Flora of Guatemala. *Fieldiana Bot.* **24**(4): 24.

STEARN, W. T. (1957): An introduction to the Species Plantarum and cognate botanical works of Carl Linnaeus. Introduction to C. LINNAEUS: *Species Plantarum* **1:** 1–176. Facsimile Ray Society, London.

URBAN, I. (1920): Plumiers Leben und Schriften etc. *Feddes Repert. Spec. Nov. Regni Veg. Beih.* **5:** 1–180.

WOODSON, R. E. Jr., R. W. SCHERY et collab. (1960): Flora of Panama 4(2): Moraceae. *Ann. Missouri Bot. Gard.* **47:** 116–118.

INDEX OF EXSICCATAE

On request available in offset-printing.