



Hunt Institute for Botanical Documentation  
5th Floor, Hunt Library  
Carnegie Mellon University  
4909 Frew Street  
Pittsburgh, PA 15213-3890  
Telephone: 412-268-2434  
Email: [huntinst@andrew.cmu.edu](mailto:huntinst@andrew.cmu.edu)  
Web site: [www.huntbotanical.org](http://www.huntbotanical.org)

The Hunt Institute is committed to making its collections accessible for research. We are pleased to offer this digitized item.

#### *Usage guidelines*

We have provided this low-resolution, digitized version for research purposes. To inquire about publishing any images from this item, please contact the Institute.

#### *Statement on harmful and offensive content*

The Hunt Institute Archives contains hundreds of thousands of pages of historical content, writing and images, created by thousands of individuals connected to the botanical sciences. Due to the wide range of time and social context in which these materials were created, some of the collections contain material that reflect outdated, biased, offensive and possibly violent views, opinions and actions. The Hunt Institute for Botanical Documentation does not endorse the views expressed in these materials, which are inconsistent with our dedication to creating an inclusive, accessible and anti-discriminatory research environment. Archival records are historical documents, and the Hunt Institute keeps such records unaltered to maintain their integrity and to foster accountability for the actions and views of the collections' creators.

Many of the historical collections in the Hunt Institute Archives contain personal correspondence, notes, recollections and opinions, which may contain language, ideas or stereotypes that are offensive or harmful to others. These collections are maintained as records of the individuals involved and do not reflect the views or values of the Hunt Institute for Botanical Documentation or those of Carnegie Mellon University.

#### *About the Institute*

The Hunt Institute for Botanical Documentation, a research division of Carnegie Mellon University, specializes in the history of botany and all aspects of plant science and serves the international scientific community through research and documentation. To this end, the Institute acquires and maintains authoritative collections of books, plant images, manuscripts, portraits and data files, and provides publications and other modes of information service. The Institute meets the reference needs of botanists, biologists, historians, conservationists, librarians, bibliographers and the public at large, especially those concerned with any aspect of the North American flora.

Hunt Institute was dedicated in 1961 as the Rachel McMasters Miller Hunt Botanical Library, an international center for bibliographical research and service in the interests of botany and horticulture, as well as a center for the study of all aspects of the history of the plant sciences. By 1971 the Library's activities had so diversified that the name was changed to Hunt Institute for Botanical Documentation. Growth in collections and research projects led to the establishment of four programmatic departments: Archives, Art, Bibliography and the Library.

CORRECTIONS TO BE MADE IN THIS MANUSCRIPT

- I) The name of Manihot isoloba ssp. isoloba should be changed as Manihot rubricaulis ssp. isoloba; and Manihot isoloba ssp. rubricaulis should be changed as Manihot rubricaulis ssp. rubricaulis.
- II) The name of Manihot Websterae should be changed as Manihot Websteri.

Section 1. FRUTICOSAE D. J. Rogers & S. G. Appan, sect. nov.

DIAGNOSIS: Frutices aut frutices vineae similia, glabrae; capsulae minutae, minus 1.75 cm longa; semina parva, minus 1.5 cm longa.

Shrubs (decumbent, sprawling, erect or arborescent) or vines. Plant parts almost completely glabrous without any pubescence. FRUITS small, less than 1.75 cm long from base to apex. SEEDS small, less than 1.5 cm long; caruncle usually prominent.

DISTRIBUTION AND ECOLOGY: This section flourishes throughout the range of the North American segment of the genus Manihot as against section Arboreae which flourishes only in the central region of Mexico (Plate 6). One member of section Fruticosae - M. rhomboidea ssp. rhomboidea, overlaps the entire domain of section Arboreae, however the sub-shrubs of M. rhomboidea ssp. rhomboidea occupy different ecological niches in contrast to the tree species of section Arboreae. The gene pool of this subspecies appears to be richly endowed with immense potential genetic variability, which enables it to rapidly make available gene combinations exhibiting high fitness to various ecological pockets in the mountainous domain of this taxon (elaborated in the discussions of this taxon). Members of section Fruticosae manifest ecologically diverse adaptations. They flourish as members of different types of vegetation such as savanna, prairies and desert; whereas section Arboreae is predominantly adapted to forest vegetation.

DISCUSSION: In the subgraphs (Fig. 11) the section Fruticosae cluster and section Arboreae cluster develop inter-sectional connections at a low "C-value" of .681 ("level" 28). By "level" 30 both the clusters integrate into one cluster.

The distribution pattern (section Arboreae occupying the central region and section Fruticosae flourishing in the expanses extending in all directions from this central area) and the specialized ecological adaptations of members of section Fruticosae would tend to support a hypothesis that section Arboreae represents the nucleus from which evolutionary divergence occurred, molding new adaptive gene combinations which colonized the expanses radiating in all directions from the domain of section Arboreae. However these indications will have to be re-considered following the study of the South American segment of the genus, when an integrated analysis, of the genus as a whole, would be possible.

KEY TO THE SPECIES OF SECTION FRUTICOSAE:

- A. Bracts and bracteoles foliaceous (Plate 9 K); fruit pedicels ascending, held at an angle of about 45° to the rachis of the infructescence (Plate 9 E); lamina deeply cleft, lamina less than 0.5 cm wide from base of sinus to petiole attachment point (Plate 9 F).....1. M. PRINGLEI
- AA. Bracts and bracteoles non-foliaceous (Plate 12 D) or semi-foliaceous (Plate 12 E), never foliaceous; fruit pedicels not ascending, held horizontally or curved downwards; lamina not deeply cleft, lamina more than 0.5 cm wide from base of sinus to petiole attachment point.
- B. Leaf venation camptodromous (Plate 19 B); apex of secondary and tertiary lobes rounded (Plate 19 C).
- C. Tall erect shrubs (Plate 12 A) more than 1.0 m tall; petiole attachment basal; staminate tepal lobes erect or slightly reflexed at anthesis (Plate 27 B).

- D. Staminate buds auriculate (Plate 10 C); leaf lobe margin repand (Plate 10 D).....2. M. AURICULATA
- DD. Staminate buds campanulate (Plate 12 D) or conical (Plate 16 H); leaf lobe margin entire (Plate 16 G), or pandurate (Plate 13 N), never repand.
- E. Inflorescence a panicle; leaves with more than 3 major lobes (with the rare exception of a few cultivars of M. esculenta).
- F. Cultivated, not found growing wild; nodes on stem distinctly enlarged (Plate 1 E); wax pattern of mature abaxial leaf surface farinose.....3. M. ESCULENTA
- FF. Populations wild, not cultivated; nodes not enlarged; wax pattern of mature abaxial leaf surface smooth or stubby.
- G. Leaf lobes oblong (Plate 13 R) or oblong pandurate (Plate 13 Q), never linear; wax pattern of mature abaxial leaf surface stubby; inflorescence a profusely branched panicle (Plate 12 C).....4. M. AESCULIFOLIA
- GG. Leaf lobes linear (Plate 14 B), never oblong or oblong pandurate; wax pattern of mature abaxial leaf surface smooth; inflorescence a sparsely branched panicle (Plate 14 G)...5 & 6. M. ISOLOBA
- EE. Inflorescence a raceme; leaves with 3 major, 2 smaller, and 2 more minute lobes (Plate 19 A).
- H. Leaf lobes obovate (Plate 16 G) or obovate pandurate (Plate 16 E); distal end of capsules rounded or projected but never depressed; fruit dehiscence septicial (Plate 35 G); seeds oblong (Plate 16 L); arborescent shrubs (more than 1.5 m tall), or clambering vine-like shrubs.
- I. Staminate buds conical (Plate 16 H); racemes very short, usually less than 5.0 cm long, never longer than 8.0 cm; arborescent shrubs more than 1.5 m tall (Plate 16 B).....7. M. OAXACANA

- II. Staminate buds campanulate (Plate 18 O); racemes usually longer than 5.0 cm; clambering vine-like shrubs (Plate 17 A).....8. M. CHLOROSTICTA
- HH. Leaf lobes rhomboid (Plate 19 D) or rhomboid pandurate (Plate 19 C); distal end of capsules depressed (Plate 19 J) fruit dehiscence loculicidal (Plate 21 M); seeds rotund (Plate 19 G); medium-sized (less than 1.5 cm tall) slender-branched shrubs.....9. M. DAVISIAE
- CC. Sprawling subshrubs, less than 1 m tall (Plate 23 J); petiole attachment peltate (Plate 23 M); staminate tepal lobes prominently reflexed at anthesis (Plate 22 C).....11. M. RHOMBOIDEA\*
- BB. Leaf venation craspedodromous (with the rare exception of some forms of M. rhomboidea ssp. rhomboidea); (Plate 20 E); apex of secondary and tertiary lobes attenuate (Plate 20 E) or cuspidate (Plate 28 J) never rounded.
- J. Leaf lobes long (more than 12.0 cm); petiole attachment basal; distal end of capsules depressed; fruit dehiscence loculicidal; seeds large, more than 1.25 cm long; erect shrubs (Plate 20 A).....10. M. ANGUSTILOBA
- JJ. Leaf lobes short (less than 12.0 cm); petiole attachment peltate; distal end of capsules rounded or projected, never depressed; fruit dehiscence septical; seeds small, less than 1.25 cm long; decumbent or sprawling shrubs.
- K. Petiole attachment narrowly peltate (lamina base less than 0.5 cm wide); staminate buds campanulate or slightly constricted in the middle; staminate tepal lobes prominently reflexed at anthesis; seeds oblong; sprawling shrubs (Plate 25 C).
- L. Inflorescence a raceme; secondary leaf lobe apices attenuate; distribution mostly south of the Tropic of Cancer...11 & 12. M. RHOMBOIDEA
- LL. Inflorescence a subspicate raceme; secondary leaf lobe apices often dilated; distribution mostly north of the Tropic of Cancer.....13. M. SUBSPICATA

\* This condition occurs rarely in M. rhomboidea ssp. rhomboidea. This taxon predominantly has craspedodromous leaf venation (BB of this key).

- KK. Petiole attachment widely peltate (lamina base more than 0.5 cm wide); staminate buds distinctly constricted in the middle (Plate 27 D); staminate tepal lobes only slightly reflexed at anthesis; seeds round; decumbent shrubs (Plate 27 A).....  
.....14. M. WALKERAE

1. MANIHOT PRINGLEI Watson, Proc. Amer. Acad. 25:148. 1894.

NOMENCLATRURAL TYPE: Syntype (GH): C. G. Pringle 3558 !

ILLUSTRATIONS: Plates 9 and 38

VERNACULAR NAMES: None known.

SYNOPSIS OF GROSS MORPHOLOGY: More or less erect, tall shrubs (Plate 9 D) 3.0-4.0 m tall; dichotomously and trichotomously branching. ROOTS numerous, prominently swollen (Plate 9 L), elongated, 0.5-1.0 m long, shallow; epidermis relatively smooth, brown (5 YR 4/5)\*, lenticels oriented along horizontal lines; subepidermis light tan, somewhat yellowish; cortex whitish, soft, somewhat pulpy, with a very weak smell of HCN. Young STEMS glabrous, greenish grey-brown; mature stems glabrous, light grey, lenticels vertically oriented. LEAVES alternate; stipules deciduous, glabrous; petioles about 15.0 cm. long, occasionally longer, terete, glabrous, greenish, reddish (7.5 R 4/11)\* towards the base; lamina non-peltate, ventral surface deep green, glabrous, dorsal surface pale green, glabrous, abaxial surface was pattern smooth; venation camptodromous, veins on the ventral surface green, glabrous, on the dorsal surface reddish (7.5 R 4/11)\*, glabrous; palmately 7 or 9 lobed (Plate 9 F); median lobes oblong pandurate (Plate 9 B), rarely oblong entire lobed (Plate 9 C), usually about 12.0 cm long, apex acuminate, the base of the lobe very narrowly constricted, less than 0.25 cm across, lamina between the base of sinus and petiole

---

\* Color designations used are those of the Nickerson Color Fan, Amer. Hort. Council.

attachment point less than 0.5 cm wide; lowest lobes about half as long as median lobes, more or less similar in shape to median lobes. INFLORESCENCE a monoecious, terminal, subspicate/corymbose raceme, (Plate 9 K), about 30.0 cm in length, the lower half of the rachis usually devoid of flowers, all parts glabrous; bracteoles prominently foliaceous, lanceolate, apex acuminate, often as long as 3.0 cm, 0.5 cm wide, margin distinctly serrate, veins on dorsal and ventral surfaces purplish, bractlets foliaceous, purplish veined, often as long as 2.0 cm, 0.3 cm wide. PISTILLATE FLOWERS restricted to the base of the upper half of the inflorescence, borne on long straight ascending pedicels (Plate 9 E), held at an angle of about 45° to the rachis, the lowermost pedicel often 5.0-7.0 cm long, subsequent pedicels decreasing gradually in length towards the apical end of the inflorescence, creating more or less a corymbose type of inflorescence, pistillate tepals about 1.6 cm long, reddish (2.5 R 4/10)\* externally, greenish yellow (2.5 GY 9/8)\* internally, cleft down to base into 5 lobes, lobes oblong lanceolate, tapering, disc very prominent, fleshy, staminodes often present around the disc, pistil about 0.7 cm long, ovary ovate ellipsoid, the trifid stigma moderately lobed and lobulate. STAMINATE flowers almost tubular, slightly constricted in the middle, tepals about 1.8 cm long, reddish (2.5 R 4/10)\* externally, greenish yellow (2.5 CY 9/8)\* internally, cleft nearly 1/3 way down into 5 lobes, lobes not prominently reflexed at anthesis, disc yellowish (5 Y 9/9)\*, 10 lobed, stamens 10, didynamous, superior whorl about 1.3 cm long, inferior whorl about 1.2

cm long. FRUIT pedicels long, straight, ascending, 3.0-7.0 cm long; capsules ovate ellipsoid (Plate 9 J) about 1.5 cm long from base to apex, disc at the base very prominent, stigma scar at the apex distinctly pointed, fruit surface more or less smooth, perceptibly 6 ribbed, ribs very dark maroon (2.5 R 3/7)\*, greenish in between ribs; fruit dehiscence septicial splitting into 6 carpels. SEEDS oblong (Plate 9 P), about 1.25 cm long, basal end gently curved inside (Plate 9 O), caruncle moderately prominent. Seedlings at early stages have a characteristic swollen hypocotyl region (Plate 9 N).

DISTRIBUTION AND ECOLOGY: (Plate 38). MEXICO: Tamaulipas and San Luis Potosi, along the southern and southwestern slopes of Sierra de Tamaulipas and the eastern slopes of Sierra Madre Oriental, in a more or less crescent shaped area bordering the plains surrounding Tampico, at 300-2000 m. Growing in dense woods (Crutchfield & Johnston s.n.) and amidst dry scrub vegetation (Webster 11229), invariably in limestone based soil. Rogers, Appan & Rogers 528 was colonizing a disturbed habitat on unconsolidated sandy red lateritic soil dumped after road construction in a mixed broad leaf oak forest with Dioon edule, Croton sp., Solanum shrubs and scattered palms (Plate 9 A, D & M). This ability to colonize disturbed habitats is manifested by most of the species of Manihot.

The general region appears to receive an annual rainfall of about 1500 mm.\* The mean precipitation and temperature\*\* recorded at Tampico, the weather station nearest to the geographical range of M. Pringlei is given in Table 2.

PHENOLOGY: Flowering in May-September; fruiting in May-September.

DISCUSSION: As indicated by the "SKYLINE" (Plate 8) and subgraphs (Fig. 10), M. Pringlei is a distinct species. It is the last species to join the section Fruticosae cluster. It represents a fairly homogeneous population, forming a maximally connected cluster at a high "C-value" of .938, indicative of very little intraspecific phenotypic variation.

The species manifests several distinct morphological features, such as the narrowly constricted lobe bases and the deeply cleft sinuses between lobes; the characteristic inflorescence - a subspicate/corymbose raceme with large foliaceous bracts and bractlets, etc. The striking resemblance of its tuberos roots to that of the cultivated species M. esculenta, especially in the shape, color and texture of root epidermis; and the absence of strong smell of HCN in

---

\*These general indications of the precipitation of the geographical range of each of the taxa in this study, are based on the available data recorded at weather stations located within or near the range of the respective species. This picture synthesized from insufficient sample location data, will have to be taken, for the time being, for what it is worth, in the absence of any other means of projecting a more accurate picture.

\*\*The figures represent the mean for the 10 year period 1951-1960, given in World Weather Records, U. S. Dept. of Commerce Weather Bureau.

the root cortex, is significant. Rogers (1965) suggested that M. Pringlei may be considered for a role as one of the putative wild progenitors of M. esculenta. In a recent field trip to Northeastern Mexico, it was discovered (Rogers & Appan, unpublished) that the northern limits of commercial cultivation of cassava in Mexico extends as far north as Gomez Farias, Tamaulipas, which is near the northern end of the range of M. Pringlei. All these indications strongly support the possibility that the ancestral genes of M. esculenta, particularly the sweet types, may have been drawn from the gene pool represented by, or ancestral to, M. Pringlei.

SPECIMENS EXAMINED: MEXICO. Tamaulipas: [1] <sup>\*</sup> E. Palmer 266, vicinity of Victoria, 1907, (A2 <sup>\*\*</sup> = F,F,NY,UC,US,US,US); [2] G. L. Webster 11229, 15 miles SW of Ciudad Victoria, 9 June 1962, (A2 = NO,NO); [3] D. J. Rogers, S. G. Appan & R. Rogers 528, 13.5 miles SW of Ciudad Victoria on road to Juamave, 21 June 1968, (A3 = NO); [4] R. L. Dressler 1913, Sierra de Tamaulipas/Rancho Las Yucas, 20 July 1957, (A2 = MO); [5] J. Crutchfield & M. C. Johnston s.n., 3 miles SE of Gomez Farias, 26 September 1960, (A1 = TEX). San Luis Potosi: [6] C. A. Purpus 5465, Minas de San Rafael, May 1911, (A2 = F,MO,NY,UC); [7] C. G. Pringle 3558, Lime Stone Hills/Las Canoas, 15 July 1890, (A2-GH); [7] C. G. Pringle 3826, Lime Stone Hills/Las Canoas, 14 August 1891, (A2 = A,F,MICH,MICH,MO,NY,UC,US,US,W);

---

\* This serial number corresponds to the number representing this collection in distribution maps.

\*\* This "member" represents the cited herbarium sheets in the computer Similarity-Graph-Clustering-Analysis, the results of which are depicted in the subgraphs (Figures 10 & 11) and the "SKYLINE" (Plate 8).

[8] L. A. Kenoyer A-198, Valles, 3 September 1938, (A1 = F, MICH).

Tamaulipas: [9] K. Reiche 1072, S Victoria, September 1926, (A2 =

M). Unknown: [10] Collector name illegible, W/O locality, W/O date,

(A2 = MO 1771289).

2. MANIHOT AURICULATA McVaugh, Brittonia 13: 190. 1961.

NOMENCLATURAL TYPE: Holotype (MICH): R. McVaugh 15283 1

ILLUSTRATIONS: Plates 10 and 39.

VERNACULAR NAMES: None known.

SYNOPSIS OF GROSS MORPHOLOGY: Arborescent shrubs/low trees, about 6.0 m tall, diameter at base about 6.0 cm, with long weak trailing branches. ROOTS not seen. Young STEMS glabrous; mature stems glabrous, greyish brown. LEAVES alternate; stipules deciduous, glabrous; petioles 15.0-20.0 cm long, terete, glabrous; lamina non-peltate, dorsal and ventral lamina surfaces glabrous, abaxial surface was pattern smooth; venation camptodromous, midribs dorsal and ventral sides glabrous; palmately 5 lobed, 3 major and 2 slightly smaller lobes; (Plate 10 A); median lobes oblong, about 14.0 cm long and about 5.0 cm wide (Plate 10 D), margin broadly sinuate, apex acuminate; lowest lobes about half as long as median lobes, slightly reflexed downwards. INFLORESCENCE a long raceme, monoecious, (Plate 10 B), about 15.0 cm in length, all parts glabrous; bracteoles non-foliaceous, margin smooth; bractlets non-foliaceous. PISTILLATE FLOWERS restricted to the base of the inflorescence, borne on short (about 1.0 cm long) pedicels, tepals and pistils not seen. STAMINATE BUDS characteristically auriculate (Plate 10 C), tepals pale yellowish, about 1.7 cm long, 5 lobed, disc 10 lobed, stamens didynamous, longer ones about 1.3 cm in length, shorter ones about 0.8 cm, anthers .30-.35 cm long. FRUITS and SEEDS not seen.

DISTRIBUTION AND ECOLOGY: (Plate 39) MEXICO: Nayarit, along the western slopes of Sierra Madre Occidental, at about 500 m. This species is insufficiently represented in this study, and further collections are required to adequately portray its geographical and ecological limits. McVaugh 15283 was collected from the lower forested slopes of a steep rocky ravine near Tepic, growing amid Ficus, Ceiba, Inga, Euphorbia pulcherrima, etc. It appears that this species is sympatric with M. aesculifolia.

The region receives an annual rainfall of about 750 mm. The mean precipitation and temperature recorded at Mazatlan, the weather station nearest to the geographical range of this species are given in Table 2.

PHENOLOGY: Flowering in July; fruiting - no data.

DISCUSSION: This species is characterized by its unique auriculate, staminate tepal, a character not occurring in any other Manihot species in this study. It resembles M. aesculifolia with respect to several morphological characters and in the subgraphs (Fig. 10) the M. auriculata cluster merges with the M. aesculifolia cluster at a fairly high "C-value" of .833 ("level" 20). It would be desirable to confirm by cytogenetic investigations the existence of intrinsic reproductive barriers between these two sympatric species. The phenotypic resemblance and the sympatric distribution suggest a mutational mode of origin for M. auriculata arising from M. aesculifolia. The apparent highly endemic distribution of M. auriculata, if verified, would strengthen this hypothesis. As it is, there is no evidence, for or against, the possibility of the single collection

representing M. auriculata being a sporadic mutant. It may be necessary to re-examine the taxonomic status of this species when sufficient distributional and cytogenetic data become available.

SPECIMENS EXAMINED: MEXICO. Nayarit: [1] \* R. McVaugh 15283, Mirador Del Aguila/ca. 14 miles N of Tepic, 10 July 1957, (B1 \*\* = MICH; B2 = MICH).

---

\* This serial number corresponds to the number representing this collection in distribution maps.

\*\* This "member" represents the cited herbarium sheets in the computer Similarity-Graph-Clustering-Analysis, the results of which are depicted in the subgraphs (Figs. 10 & 11) and the "SKYLINE" (Plate 8).

4. MANIHOT AESCULIFOLIA (H.B.K.) Pohl, Pl. Bras. Ic. Descr. 1:55. 1827; Muell. Arg. in DC. Prodr. 15(2): 1065. 1866; Pax & Hoffmann, Pflanz. 44(iv.147.ii):58. 1910; Standley, Contr. U.S. Natl. Herb. 23:645. 1923; Croizat, J. Arnold Arbor. 23:218. 1942.

NOMENCLATURE TYPE: Humboldt & Bonpland s.n. (non vidi).

HOMOTYPIC SYNONYMS: Janipha aesculifolia H.B.K. Nov. gen. & sp. 2:107. Pl. 109. 1817; Jatropha aesculifolia Steud. Nomencl. ed. 2.I. 799. 1840.

HETEROTYPIC SYNONYMS: Manihot intermedia Weatherby, Proc. Amer. Acad. 45:427. 1910. (Contr. Gray Herb. 2:427. 1910); Pax & Hoffmann, Pflanz. 44(iv.147.ii): 101. 1910; Standley, Contr. U.S. Natl. Herb. 23:643. 1923; Croizat, J. Arnold Arbor. 23:221. 1942. Nomenclature type: Syntypes: (ARIZ, ARIZ, F,GH,MICH,MO,UC,US): C. G. Pringle 13938 !

Manihot olfersiana Pax, Pflanz. 44(iv.147.ii):55. 1910; McVaugh, Brittonia 13:193. 1961; Manihot palmata var. multifida Muell. Arg. in DC. Prodr. 15(2):1062. 1866. ex parte; in Pl. Bras. 11(2):459. 1874. ex parte. Nomenclature type: Uhde 1176. (non vidi).

Manihot gualanensis Blake, Contr. U.S. Natl. Herb. 24:13. 1922. Nomenclature type: Holotype (US): Blake 7688 ! Isotypes (F,US).

ILLUSTRATIONS: Plates 12,13,40,41,42,43,44,45,46 and 47.

VERNACULAR NAMES: Yuca sylvestre. Tonduz 13977 (Costa Rica); Maxon, Harvey & Valentine 7107 and 7192 (Nicaragua); Rogers 504

(Yucatan, Mexico). Yuca de monte. Tonduz 13977; Echeverria 4158  
 (Costa Rica). Yuca. Standley 11481 (Nicaragua). Yuca cimarrona.  
 Maxon, Harvey & Valentine 7107 (Nicaragua); Calderon 776 (El Salvador);  
 Steyermark 51316 (Guatemala); Matuda 16375 (Chiapas, Mexico). Yquilla.  
 Steyermark 51316 (Guatemala). Chichput. Lundell & Lundell 7737  
 (Quintana Roo, Mexico). Batul. Novelo 114 (Yucatan, Mexico). Tacote.  
 Rogers 510 (Jalisco, Mexico).

USES: Some collections such as J. A. Steyermark 51316 and C. L. Lundell & A. A. Lundell 7737 are reported to have edible roots.

SYNOPSIS OF GROSS MORPHOLOGY: Erect tall shrubs (Plate 12 A and 13 M), up to 7.0 m tall, trunk at base about 10.0 cm in diameter. ROOTS prominently swollen, large; epidermis brown, rough and flaky; subepidermis creamy white. Young STEMS green, glabrous, internally white; mature stems greyish brown, glabrous; all parts have white latex. Young apical foliage (Plate 12 F) yellowish green to dark reddish purple (10 P 3/9)\*. LEAVES alternate; stipules deciduous, glabrous; petioles about 20.0 cm long, terete, glabrous, pure green or with various degrees of pigmentation such as green with bluish cast at base and apex, moderately reddish (2.5 R 4/10)\* throughout, or dark red throughout; lamina non-peltate, silvery beneath, deep green above (2.5 G 5/9)\*, abaxial surface wax pattern stubby with a characteristic microscopic pulverulence; venation camptodromous; palmately 5-9 lobed; median lobes 15.0-30.0 cm in length, 4.0-10.0 cm in width, oblong entire lobed (Plate 13 O) or oblong pandurate

---

\*Color designations used are those of the Nickerson Color Fan, Amer. Hort. Counc.

(Plate 13 N), the primary constriction of pandurate lobes differing considerably in depth and width (Plate 13 P to 13 V), apex acute to acuminate, bristle pointed, base of lobe usually 0.75-2.0 cm across, rarely less; lowest lobes about half as long, and more or less similar in shape, to median lobes. INFLORESCENCE monoecious usually a large profusely branched terminal panicle (Plate 12 C), often as long as 45.0 cm, occasionally shorter and less profusely branched, all parts glabrous; bracteoles non-foliaceous (Plate 12 D) or semi-foliaceous (Plate 12 E), in the latter case as long as 2.0 cm, linear, margin smooth; bractlets non-foliaceous. Pistillate flowers not restricted to the base of the inflorescence but occurring from the base up to almost the apex, interspersed with staminate flowers, tepals about 1.2 cm long, cleft down to base into 5 lobes, lobes lanciolate-oblong, about 0.4 cm wide, disc fleshy entire, pistil about 0.6 cm long, ovary sub-globose, glabrous, the trifid stigma much lobed and lobulate. STAMINATE flowers campanulate, often pendulous, tepals about 1.3 cm long, color varies from pure greenish yellow to various degrees of purple pigmentation, different types occurring together often in the same local population, cleft 1/3 way down into 5 lobes, lobes oblong obtuse, not prominently reflexed at anthesis, disc 10 lobed, depressed and fleshy; stamens 10, didynamous, superior whorl about 0.9 cm long, inferior whorl about 0.7 cm long. INFRUCTESCENCE usually a long cluster of fruits (Plate 12 G), characteristic of this species, fruit pedicles about 1.0 cm long, slightly curved downwards; capsules almost globular (Plate 12 H), about 1.5 cm long from base to apex, surface green, slightly tuberculate, without ribs, apex rounded; fruit dehiscence septicidal splitting into 6 carpels.

SEEDS oblong, (Plate 12 K), about 1.25 cm long, relatively thin and flat (Plate 12 L), dorsal side with conspicuous horizontal stripes; caruncle moderately prominent, broad.

DISTRIBUTION AND ECOLOGY: (Plates 40-47), MEXICO: Sinaloa, Nayarit, Jalisco, Colima, Michoacan, Guerrero, Mexico, Vera Cruz, Oaxaca, Chiapas, Yucatan and Quintana Roo Territory; BRITISH HONDURAS: GUATEMALA: HONDURAS: EL SALVADOR: NICARAGUA: COSTA RICA and PANAMA. Occurring in the interior region of the west and east facing coastal belts, usually along the foothills and lower slopes of the mountains, to about 1300 m, rarely in the plains. Along the west coast, from Sinaloa to Guerrero, M. chlorostica flourishes in the front of the coastal belt and M. aesculifolia is at the rear, towards the foothills, with possibly a little overlap where the two longitudinal ranges meet. At the boundary between the states of Michoacan and Guerrero the geographical range of this species penetrates from the coastal region, deeply towards the interior along the Iguala Canyon, in the shape of a limb, and at the extreme end extends up along the mountain slopes to an altitude of about 1300 m (Plate 43 E). The range of this species represented in Plate 37 appears fragmented into disjunct segments because this distribution map is based on the collections which were available for this study. Ecologically there is no reason for this species not to flourish in the gaps between the segments, and further collections from these areas would enable us to update this distribution map. The range should be expected to be in the form of two longitudinal strips: 1) from Sinaloa towards south along the west coast, and 2) from Vera Cruz

towards south along the east coast; with possibilities for the two strips to merge and interbreed at several locations across shallow mountain ranges in the region between Tehuantepec sinus and Panama.

Towards the south, the species flourishes in heavy rainfall areas with 2500 mm annual precipitation, in dense wet forests and thickets. In the Yucatan area with relatively drier climate it flourishes in steep banks of cenotes (limestone sinks with water at bottom. Karst topography), localized and not spreading far beyond the cenote margins. Towards the north with lower rainfall it grows in dry thorn forest vegetation dominated by Acacia, Cnidocolus, Coccoloba, Randia, etc.; or at the edge of savannas in grassy second growth thickets (Plate 12 A). At altitudes as high as 1000 m it flourishes in steep mountain sides in oak and bamboo zones (Plate 12 B). It seems to be capable of growing in varied soil types such as sand, loam, limestone based lateritic soil, clay, etc., and like many other Manihot species has the ability to colonize disturbed areas such as road cuts, fire denuded patches, etc.

The southern regions of the range receive a mean annual rainfall of about 2500 mm, while towards the north, the rainfall decreases to about 1000 mm. The weather data of several stations located within or very near the range of this species, viz., Tapachula, Progreso, Merida, Campeche, Coatzacoalcos, Acapulco, Manzanillo and Mazatlan, are given in Table 2.

PHENOLOGY: Flowering in May - August, rarely up to October, towards the north flowering begins a little later, by about June; fruiting

in June - December.

DISCUSSION: The population delineated as M. aesculifolia in this study remained split into 4 species, prior to this study:

M. gualanensis, M. intermedia, M. olfersiana and M. aesculifolia. 268 herbarium specimens representing the above 4 taxa were described with respect to the 50 morphological characters employed in this study, and as the subgraphs (Fig. 10) depict, there are only 12 distinct morphological types (D-1 to D-12), all the rest of the 268 being identical to some one of these 12. Of these 12, all except one (D-12) form a cluster with several "internal connections" at a very high "C-value" of .940 ("level" 9); the "connectedness" progressively increasing and forming a maximally connected cluster at a fairly high "C-value" of .857 ("level" 17). At this "level" the cluster has a significant moat too, as depicted in the "SKYLINE" (Plate 8). These indications strongly suggest that this is a single interbreeding population and not four independent closed gene pools. The characters on the strength of which this population was split into 4 "species", are not stable features occurring exclusively in these 4 so called species populations. M. gualanensis was considered to have deeply pandurate leaf lobes (Plate 13 N) as against M. aesculifolia which was believed to have usually entire, occasionally shallowly pandurate, lobes (Plate 13 O). Rogers 504 collected from Yucatan peninsula, the region hitherto believed to be the home range of M. aesculifolia, confirms that both types of lobes occur in the same plant, usually the apical leaves being non-pandurate, and the lower ones pandurate (Plate 12 F). Herbarium specimens

prepared from apical shoots were identified in the past as M. aesculifolia while others were identified as M. gualanensis. As early as 1942, Croizat felt that these two may be conspecific.

M. intermedia was believed to be characterized by its purplish tinged tepals and bristly bracteoles. A critical study of the geographical distribution of these two characters proves that these two features occur in many other places outside the Iguala Canyon area (what was believed to be the home range of M. intermedia). The tepal pigmentation appears to be an ecotypic phenomenon, manifested in several other specimens collected at higher altitudes. In one local population (Rogers 510) segregation in the progeny into pigmented and nonpigmented phenotypes was observed, indicating that the gene pool possesses the gene combinations for producing pigmented as well as nonpigmented flowers. Possibly the high altitude populations are homozygous for pigmented flowers, the low altitude populations homozygous for nonpigmented flowers, and the bridging population apparently heterozygous.

The type of M. olfersiana was not seen, but from the description, it seems to be identical to M. aesculifolia except for the inflorescence which was described as a raceme. It should be pointed out here that it was not uncommon to incorrectly describe a sparsely branched panicle as a raceme. The inflorescence of M. intermedia was described as a raceme in the original description, but the cited specimens when examined, turned out to be sparsely branched panicles and not racemes.

The distribution pattern, which emerged after the precise location of the 86 collections, representing the 4 "species", were

plotted on a topographical base map (Plates 40-47), does not tend to render any support for these 4 "species" to be independent closed gene pools; on the contrary it strongly suggests the possibility of these constituting a single interbreeding population.

The cluster representing M. esculenta in the subgraphs (Fig. 10), becomes connected to the M. aesculifolia cluster at a "C-value" of .854 and by .820 ("level" 21) both clusters completely integrate. Rogers (1965) noted the strong morphological similarity of these species, and suggested the possibility of M. aesculifolia being one of the putative wild progenitors to M. esculenta. Some M. aesculifolia collections are reported to have edible roots which are cooked and eaten. It is practically impossible to distinguish the M. aesculifolia leaves in some collections from M. esculenta leaves, without microscopic examination; but even a fragment of M. aesculifolia leaf can be positively indentified by its characteristic microscopic pulverulence, stubby, waxy, blunt-tipped projections about 500 to a cm on the abaxial surface of leaves. This diagnostic feature of M. aesculifolia has not been observed in any M. esculenta leaf examined so far.\*

At "level" 23 ("C-value" .770) M. isoloba joins M. aesculifolia cluster and at "level" 29 ("C-value" .673) M. Pringlei is connected to M. aesculifolia. Rogers (1965) suggested that M. isoloba and M. Pringlei are also potential candiates (besides M. aesculifolia)

---

\* Several M. esculenta leaves have so far been examined, and they predominantly have a characteristic farinose wax pattern, rarely smooth, but never stubby.

to qualify as progenitors of M. esculenta, and the subgraph connections endorse the close phenotypic similarity between these four species.

Steyermark 51316 (represented in subgraphs by D 12) stands out as a "satellite" of a well connected cluster in the subgraphs at "level" 21. Some of the leaves of this collection are hastate in outline with attenuate basal lobules terminating in a spinelike projection which is an extension of a vein. This craspedodromous venation is characteristic of M. rhomboidea ssp. microcarpa occurring in this general area. It would be interesting to investigate the possible occurrence of hybridization between these two species in this area. This specimen was collected from a steep valley, surrounded by 2200 m high mountain ranges (Plate 45 I), which could have provided partial isolation for such unusual gene combinations to remain sheltered and preserved.

Another collection, Schott 518, (represented in the subgraphs by D 11) stands out as an anomalous form at "level" 9 (Fig. 10). This is unusual because several other collections from the same general area are represented as typical forms of M. aesculifolia in the subgraphs. The leaves of the collection (Plate 12 I) have a vague resemblance to M. carthaginensis a native species of Colombia, and the inflorescence (Plate 12 J) more or less resembles M. oaxacana. Further field studies would throw more light on this anomaly.

SPECIMENS EXAMINED: MEXICO. Sinaloa: [1]\* H. S. Gentry 6101,

---

\* This serial number corresponds to the number representing this collection in distribution maps.

Palmar/50-70 miles N of Guamuchil, 22 August 1941, (D6\*\* = ARIZ, MICH, MO,NY); [2] D. J. Rogers 520, 18 kilometers N of Culiacan, 10 July 1966, (D7 = NO); [3] E. Palmer 1536, Culiacan, August - September 1891, (D8 = F,NY,US,US); [4] T. S. Brandegee s.n., Culiacan, 30 August 1904, (D8 = GH,N,UC 110153); [5] D. J. Rogers 521, 30 miles N of Mazatlan, 11 July 1966, (D4 = NO); [6] J. N. Rose 1611, between Rosario and Colomas, 12 July 1897, (D6 = GH); [7] J. N. Rose 3204, foothills of Sierra Madre/near Colomas, July 1897, (D6 = US). Nayarit: [8] C. Feddema 1007, ca 15 kilometers SE of San Blas/along road to Miramar, 26 August 1959, (D8 = US); [9] R. McVaugh 15355, 2 miles SE of Las Varas/road to Mazatan, 12 July 1957, (D8 = MICH). Unknown: [10] M. Galeotti 3735, Torullo/illegible, 1840, (D8 = P). Jalisco: [11] D. J. Rogers 510, 16 kilometers SW of Autlan, 29 July 1963, (D4 = NO). Colima: [12] R. C. Jancey 335, 6 miles N of Manzanillo, July 1965, (D6 = NO); [13] R. C. Jancey 334, 3 miles N of Manzanillo, July 1965, (D6 = NO). Jalisco: [14] D. J. Rogers 515, ca 22 kilometers W of Tecalitlan, 31 July 1963, (D5 = NO). Michoacan: [15] G. B. Hinton et al 13972, Coalcoman, 21 July 1939, (D5 = GH,NA,NY,US). Guerrero: [16] G. B. Hinton et al 6468, Pungarabato/Coyuca, 20 August 1934, (D9 = BM,F,MO,NY,US); [17] G. B. Hinton et al 6264, Pungarabato, 9 July 1934, (D5 = BM,GH). Mexico: [18] G. B. Hinton 4555, Bejuco, 19 August 1933, (D5 = BM,GH); [19] G. B. Hinton 1207, Chorrera, 30 July 1932, (D1 = BM,MO); [20] G. B. Hinton 4374, Ypericones, 26 July 1933,

---

\*\* This "member" represents the cited herbarium sheets in the computer similarity-graph-clustering analysis, the results of which are depicted in the subgraphs (Figs 10 & 11) and the "SKYLINE" (Plate 8).

(D1 = BM,GH). Guerrero: [21] G. B. Hinton 10376, Cundanchico, 2 July 1937, (D5 = F,GH,NY,UC,US); [22] C. G. Pringle 13938, Iguala Canyon, 29 July 1907, (D1 = ARIZ,ARIZ,F,GH,MICH,MO,UC,US); [23] Y. Mexia 8778, Temisco/Barranca de La Suriana, 9 November 1937, (D2 = ARIZ,F,MICH,MO,MO,NY,U,UC,UC,US); [24] G. E. Crisman & W. D. Willis 206, 5 miles N of Ocotito, 13 June 1954, (D5 = TEX); [25] H. H. Rusby 2, Limon Mt., 28 July 1910, (D6 = NY,US). Nera Cruz: [26] C. A. Purpus 8448, Baranca de Panoaya, July 1919, (D9 = GH,NY,UC,US); [27] C. A. Purpus 8484, Baranca de Panoaya, July 1919, (D9 = MO,MO); [28] C. A. Purpus 6112, Banos del Carrizal, August 1912, (D6 = UC). Oaxaca: [29] L. Williams 9867, Almoloya, July 1937, (D6 = F,MICH); [30] E. W. Nelson 2852, between Topana Oaxaca and Tonalá Chiapas, July-August 1895, (D6 = F,US,US). Chiapas: [31] R. M. Laughlin 1125, El Chorreadero, 21 June 1966, (D4 = NO); [32] R. C. Jancey 327, 20 miles S of Tonalá, July 1965, (D9 = NO); [33] R. C. Jancey 328, 20 miles S of Tonalá, July 1965, (D9 = NO); [34] R. C. Jancey 329, 20 miles S of Tonalá, July 1965, (D9 = NO); [35] E. Matuda 16375, Cacaluta/Escuintla, 14 June 1947, (D6 = F,MICH); [36] E. Matuda 4813, between Mazapa and Motozintla, 19 July 1941, (D6 = F,NY). Yucatan: [37] W. C. Steere 1947, Champoton/Campeche, July 1932, (D9 = F,MICH); [38] Schott 518, Merida, June-July 1865, (D11 = BM,F,MO,US,US); [39] G. F. Gaumer 1142, Progreso, W/O date, (D6 = EM,F,F,GH,MICH,MO,NY); [40] N. S. Novelo 114, Merida, August 1939, (D9 = NA); [41] C. L. Lundell & A. A. Lundell 7473, Chichen Itza off Kaula Road, June-July 1938, (D6 = A,F,MICH,US); [42] W. C. Steere 1673, Chichen Itza, 29 June 1932, (D6 = F,MICH); [43] R. C. Jancey 320, 10 miles NE of Piste, June 1965, (D6 = NO); [44] R. C. Jancey 321, 10 miles NE of Piste,

June 1965, (D6 = NO); [45] R. C. Jancey 322, 10 miles NE of Piste,  
 June 1965, (D6 = NO); [46] R. C. Jancey 323, 10 miles NE of Piste,  
 June 1965, (D6 = NO); [47] R. C. Jancey 324, 10 miles NE of Piste,  
 June 1965, (D6 = NO); [48] R. C. Jancey 325, 10 miles NE of Piste,  
 June 1965, (D6 = NO); [49] R. C. Jancey 326, 10 miles NE of Piste,  
 June 1965, (D6 = NO); [50] D. J. Rogers 504, E edge of Valladolid/  
 steep banks of Cenote, 18 July 1963, (D7 = NO); [51] G. F. Gaumer &  
 Sons 23394, Orchidia, December 1916, (D9 = F,MO). Quintana Roo Terri-  
 tory: [52] C. L. Lundell & A. A. Lundell 7848, Quintana Roo/Coba/  
 along Dzitnup Trail, June-July 1938, (D6 = MICH); [53] C. L. Lundell  
 & A. A. Lundell 7737, Quintana Roo/Coba, June-July 1938, (D6 = MICH).  
 BRITISH HONDURAS. El Cayo: [54] P. H. Gentle 2539, Vaca, 1 May 1938,  
 (D6 = A,F,MICH). GUATEMALA. Huehuetenango: [55] J. A. Steyermark  
 51316, trail between Democracia and Santa Ana, 25 August 1942, (D12 =  
 F,F,US). El Quiche: [56] J. I. Aguilar 1373, W/O locality, 1942,  
 (D6 = F). Schitepeques: [57] J. A. Steyermark 47778, S of Alotenango,  
 19 June 1942, (D10 = F,NY); [58] J. A. Steyermark 47779, S of Alote-  
 nango, 19 June 1942, (D6 = F). Santa Rosa: [59] P. C. Standley  
 79452, S of Guazacapan, 6 December 1940, (D6 = F). Chiquimula: [60]  
P. C. Standley 74305, Quebrada Shusho, 14 October 1940, (D6 = F);  
 [61] P. C. Standley 73736, near divide on road from Zacapa to Chiqui-  
 mula, 9 October 1940, (D6 = F). Zacapa: [62] P. C. Standley 73783,  
 between Zacapa and Chiquimula, 9 October 1940, (D6 = F); [63] P. C.  
 Standley 73669, vicinity of Zacapa, October 1940, (D6 = F); [64]  
P. C. Standley 73683, vicinity of Zacapa, October 1940, (D7 = F).  
 Izabal: [65] S. F. Blake 7688, Gualan, 26 May 1919, (D6 = F,US,US).

Unknown: [66] O. F. Cook & C. B. Doyle 311, W/O locality, 6 June 1904, (D6 = US). HONDURAS. Santa Barbara: [67] C. Thieme 5473, San Pedro Sula, June 1887, (D9 = US). Cortes: [68] W. N. Bangham 300, San Pedro Sula, 10 August 1929, (D9 = A,F); [69] H. Johansen 38, La Lima, 31 August 1929, (D6 = F,US). EL SALVADOR. San Salvador: [70] S. Calderon 776, La Chaera/San Salvador, 1922, (D9 = GH,NY,US). Unknown: [71] F. Choussy 73, Finca San Nicolas, 1923, (D9 = US). NICARAGUA. Chinadega: [72] W. R. Maxon, A. D. Harvey & A. T. Valentine 7107, Ameya, June 1923, (D6 = US,US); [73] W. R. Maxon, A. D. Harvey & A. T. Valentine 7192, Ameya, June 1923, (D6 = NY,US,US,US); [74] P. C. Standley 11481, vicinity of Chichigalpa, July 1947, (D9 = F,US). Jinotega: [75] P. C. Standley 9657, vicinity of Jinotega, June-July 1947, (D9 = F). Managua: [76] H. A. Garnier s.n., Sierra de Managua, W/O date, (D6 = F 1248277). Granada: [77] P. Levy 41, Envirns de Granada, June 1869, (D6 = P,P). Zelaya: [78] P. C. Standley 19836, vicinity of El Ricroe, April-May 1949, (D6 = F). COSTA RICA. Guanacaste: [79] O. F. Cook & C. B. Doyle 648, W/O locality, 22 May 1903, (D6 = US); [80] A. D. Tonduz 13977, Dans Les Broussailles a Nicoya, May 1900, (D6 = BM,US). Puntarenas: [81] R. W. Holm & H. H. Iltis 250, vicinity of Cascajal, 5 July 1949, (D3 = BM,F,MO,P). Unknown: [82] A. M. Brenes 3993, San Ramon/Rio Cacao, 24 June 1924, (D9 = F); [83] J. A. Echeverria 4158, Camino a Concepcion a Su Mateo/ illegible, July 1945, (D9 = F,UC); [84] H. Pittier & Th. Durand 6579, W/O locality, W/O date, (D9 = US). PANAMA. Canal Zone: [85] E. L. Tyson 4108, Farfan Beach area, 29 May 1966, (D6 = MO). Unknown: [86] S. Hayes 717, common about Paraiso, 4 June 1862, (D6 = BM,K).

5 & 6. MANIHOT ISOLOBA Standley emend. D. J. Rogers & S. G. Appan.

SYNOPSIS OF GROSS MORPHOLOGY: Erect caespitose shrubs, 1.0-5.0 m tall with many slender stems arising from a woody base; foliage borne at the tip of the twigs. ROOTS not seen. Young STEMS glaucous; mature stems glaucous, reddish brown; latex present. LEAVES alternate; stipules deciduous, glabrous; petioles 6.0-12.0 cm long, occasionally longer, glabrous, terete; lamina non-peltate, deep green or ashy blue green in color, dorsal and ventral lamina surfaces and midribs glabrous, abaxial surface wax pattern smooth; venation camptodromous; palmately 5-9 lobed (Plates 14 A and 15 A); median lobes 6.0-10.0 cm long, occasionally as long as 17.0 cm, 0.75-2.0 cm wide, narrowly linear with almost parallel sides (Plate 14 B and 14 E), occasionally a shallow constriction present little below the apical end (Plate 14 D and 14 F), apex acute to acuminate, bristle tipped, sinuses between lobes prominently calloused, giving a "rooster's foot" appearance to leaves; lowest lobes about half as long as median lobes with a characteristic 'S' shaped bend (Plate 14 C). INFLORESCENCE a monoecious, axillary, few flowered, panicle (Plate 15 B) with sparse branching so that it sometimes appears like a raceme, 5.0-7.0 cm long, occasionally as long as 15.0 cm, all parts glabrous; bracteoles non-foliaceous (Plate 14 H), or semi-foliaceous (Plate 14 G), in the latter case up to 1.25 cm in length, margin smooth; bractlets non-foliaceous. PISTILLATE FLOWERS restricted to the base of the inflorescence, borne, usually on branched peduncles, pedicels 2.0-4.0 cm long, tepals yellowish green, sometimes with an ashy blue green tinge, 0.8-1.2 cm long. cleft to the base into 5

lobes, lobes 0.3-0.4 cm wide, lanceolate-oblong, disc fleshy, entire, pistils 0.4-0.6 cm long. ovary subglobose, glabrous, the 3 divisions of the stigma moderately lobed and lobulate. STAMINATE FLOWERS campanulate, tepals greenish yellow, sometimes with an ashy blue green tinge, 0.9-1.3 cm long, cleft 1/3 way down into 5 lobes, lobes oblong obtuse, not prominently reflexed at anthesis, disc fleshy, 10 lobed, stamens 10, didynamous, the longer ones about 0.9 cm long, shorter ones 0.7 cm long, filaments and anthers cream colored. FRUIT pedicels 2.0-4.0 cm long, almost straight; capsules ovate-ellipsoid (Plate 14 I and 15 C), 1.2-1.75 cm long from base to apex, surface slightly tuberculate, ribs not prominent, apex rounded, fruit dehiscence septicial, splitting into 6 carpels. SEEDS oblong, 0.9-1.2 cm long (Plate 14 J), surface finely pitted (Plate 14 K); caruncle moderately prominent, trapeziform (Plate 15 E).

KEY TO THE SUBSPECIES of *Manihot isoloba*.

- A. Fruits larger, over 1.5 cm in length; seeds longer, over 1.0 cm in length (Plate 14).....5. *M. isoloba* ssp. *isoloba*
- AA. Fruits smaller, less than 1.5 cm in length; seeds shorter, less than 1.0 cm in length (Plate 15)....6. *M. isoloba* ssp. *rubricaulis*

5. MANIHOT ISOLOBA Standley subsp. ISOLOBA D. J. Rogers & S. G. Appan, stat.nov.

NOMENCLATURE TYPE: Holotype (F): H. S. Gentry 2372 !. Isotypes (ARIZ,MO,UC,US).

BASIONYM: *Manihot isoloba* Standley, Publ. Field Mus. Nat. Hist. Bot. Ser. 17:197. 1937; Croizat, J. Arnold Arbor. 23:223. 1942.

ILLUSTRATIONS: Plates 14 and 48.

VERNACULAR NAMES: Pata de Gallo (Rooster's foot). Gentry 2372 (Chihuahua, Mexico); Gentry 6583 (Sinaloa, Mexico).

DIAGNOSIS: This typical subspecies differs from the ssp. rubricaulis with respect to the size of fruits and seeds. The fruits are relatively larger (Plate 14 I), more than 1.5 cm in length (from base to apex). The seeds are also bigger (Plate 14 J), over 1.0 cm in length. The leaf lobes are generally wider, mostly not less than 1.0 cm in width (Plate 14 D).

DISTRIBUTION AND ECOLOGY: (Plate 48). MEXICO: Sonora, Chihuahua and Sinaloa, along the west facing, and occasionally on the east facing slopes of the Sierra Madre Occidental, at about 1000-2750 m. The mountain ranges in this area are not very tall, and as some specimens have been collected from altitudes as high as 2500 m, it appears very likely that the western slope and the eastern slope populations are contiguous, thus the population capping the mountain and extending down to about 1000 m on either side.

On the more moist western slopes, this subspecies flourishes in pine-oak forests, in steep moist canyon slopes; and on the relatively drier eastern slopes, near Parral, it grows on arid rocky slopes, under xeric conditions.

Some of the areas along the eastern boundary of the range of this subspecies, receive a mean annual rainfall of less than 250 mm, 95% of which is received during June - September, the rest of the year being practically dry. The mean temperature is as low as 8°C

in January and as such this species exhibits a remarkable tolerance to prolonged drought and severe cold. The weather data recorded at Chichuahua, a station near the range, are given in Table 2.

DISCUSSION: In the subgraphs (Fig. 10) this subspecies forms a fairly homogeneous cluster at "level" 9, and subsequently merges with ssp. rubricaulis cluster at a fairly high "C-value" of .938 ("level"10), and forms a maximally connected cluster at the same "level". The cluster then remains distinct with a high "moat", till "level" 23 when it is connected to the linear lobed form (C-3) of M. esculenta. Cytogenetic investigations on the phylogenetic relationship between M. isoloba and the linear lobed cultivars of M. esculenta would be rewarding inasmuch as M. isoloba represents the only wild species in the genus Manihot, with linear, leaf lobes. If M. isoloba proves to have close genetic affinity with the cultivated species M. esculenta, it would open up avenues for the plant breeder to explore possibilities of transferring its remarkable drought resistance and cold tolerance potentials, to the cultivated species.

This subspecies is connected at "level" 23 to the entire lobed form of M. Davisiae, represented in subgraphs by I-1. This entire lobed form, discussed in detail in connection with M. Davisiae, is unique and stands out as a "satellite" of M. Davisiae cluster at "level" 14 (Fig. 10). They grow in a region adjoining the range of ssp. isoloba and their possible role as a bridging population in the evolutionary history is an aspect to be investigated cytogenetically.

SPECIMENS EXAMINED: MEXICO. Sonora: [1] S. S. White 3103, Canon de Bavispe, July - August 1940, (E2\*\* = ARIZ,GH,MICH); [2] S. S. White 3647, Piedra Parada, September 1940, (E2 = GH,MICH); [3] S. S. White 2930, La Palmita between Granados and Bacadehuachi, 7 July 1940, (E1 = GH,MICH,NA); [4] S. S. White 2758, Canon de Los Apaches/N of Aribabi, 6 September 1939, (E2 = MICH); [5] F. Shreve 6753 A, Santa Margarita Mountains/6 miles E of Mina Verde, 23 September 1934, (E2 = ARIZ,MICH); [6] C. H. Muller 3696, Nacore Chico/slopes above El Rio Bonito, 7 October 1939, (E2 = NA,UC). Chihuahua: [7] H. Lesueur 1249, Rio Aros, 6 August 1937, (E3 = F,GH,MO,TEX,UC,US); [8] C. H. T. Townsend & C. M. Barber 404, Sierra Madres/20 miles SW of Chuichupa, 5 September 1899, (E1 = BM,P,F,NY); [9] M. E. Jones s.n., Guayanopa Canyon/Sierra Madre Mountains, 24 September 1903, (E2 = POM 86336,POM 86338); [10] H. S. Gentry 2372, Guasaremos/Rio Mayo, 10 August 1936, (E2 = ARIZ,F,MO,UC,US). Sonora: [11] H. S. Gentry 1468, Bakachaka/Rio Mayo, 6 July 1935, (E3 = ARIZ,F,MO,UC,US). Chihuahua: [12] I. W. Knobloch 1335, vicinity of Areonapuchie/slopes of Barranca de Urique, 23 August 1954, (E2 = MICH). Sinaloa: [13] H. S. Gentry 6583, Quebrado de Mansana/Sierra Surotato, September 1941, (E2 = ARIZ,GH,MICH,MO,NY). Chihuahua: [14] Gentry, Correl & Arquelles 18083, Rio San Juan Valley, 29 October 1959, (E2 = US).

---

\* This serial number corresponds to the number representing this collection in distribution maps.

\*\* This "member" represents the cited herbarium sheets in the computer similarity-graph-clustering analysis, the results of which are depicted in the subgraphs (Figs. 10 & 11) and the "SKYLINE" (Plate 8).

## 6. MANIHOT ISOLOBA Standley subsp. RUBRICAULIS (I. M. Johnston)

D. J. Rogers & S. G. Appan, stat. nov.

NOMENCLATURE TYPE: Holotype (GH): E. Palmer 224 l. Isotypes (F, BM, NY, UC, US, US).

BASIONYM: Manihot rubricaulis I. M. Johnston, Contr. Gray Herb. 68: 90. 1923; Croizat, J. Arnold Arbor. 23:222. 1942.

ILLUSTRATIONS: Plates 15 & 48.

VERNACULAR NAMES: None known.

DIAGNOSIS: This ssp. differs from the typical ssp. isoloba, with respect to the size of fruits and seeds. The fruits are relatively smaller, less than 1.5 cm in length from base to apex (Plate 15 C). The seeds are also shorter (Plate 15 E), less than 1.0 cm in length. The leaf lobes are generally narrower, mostly less than 1.0 cm in width (Plate 15 A).

DISTRIBUTION AND ECOLOGY: (Plate 48) MEXICO: Sinaloa and Durango, along the western and eastern slopes of Sierra Madre Occidental.

PHENOLOGY: No data.

DISCUSSION: M. rubricaulis was described by I. M. Johnston as a new species, on the basis of a single collection; Palmer 224, the type. Croizat (1942) cited one more collection, Brandegee, s.n., and pointed out that M. rubricaulis is quite near M. isoloba. I. M. Johnston designated this taxon as rubricaulis in view of its characteristic reddish stem. This feature is also present in the other

population hitherto considered as M. isoloba. The 7 sheets representing the two collections of M. rubricaulis form a homogeneous cluster at "level" 9 in the subgraphs (Fig. 10). At a very high "C-value" of .938 ("level" 10) this cluster merges with M. isoloba cluster and forms a maximally connected cluster at the same "level". Though M. rubricaulis is insufficiently represented in this study, its close overall phenotypic similarity to M. isoloba, indicated by the subgraphs; and the geographical distribution, are strongly suggestive that these two taxa are not independent closed gene pools. The northerly and southerly ranges, and the few phenotypic characters (discussed in the diagnosis) which consistently separate these two taxa, bespeak these two being two semi-isolated populations. As such, they have been designated as subspecies, but the taxonomic status will have to be re-examined when sufficient cytogenetic and distributional data become available.

SPECIMENS EXAMINED: MEXICO. Sinaloa: [15] T. S. Brandege <sup>\*</sup>s.n., vicinity of Culiacan/Cerro Colorado, 1 November 1904, (F3 <sup>\*\*</sup> = UC 110152). Durango: [16] E. Palmer 224, city of Durango and vicinity, 1896, (F1 = BM,GH,GH,NY,UC,US,US; F2 = F).

---

\* This serial number corresponds to the number representing this collection in distribution maps.

\*\* This "member" represents the cited herbarium sheets in the computer similarity-graph-clustering analysis, the results of which are depicted in the subgraphs (Figs. 10 & 11) and the "SKYLINE" (Plate 8).

7. MANIHOT OAXACANA D. J. Rogers & S. G. Appan, spec.nov.

NOMENCLATURE TYPE: Holotype (NY): D. J. Rogers 505. Isotypes (F,K,MEXU,MO,UC,US,W).

ILLUSTRATIONS: Plates 16, 49 and 50.

VERNACULAR NAMES: None known.

SYNOPSIS OF GROSS MORPHOLOGY:

Frutices 2.0 - 5 m altae, glabrae; folia septemloba, lobus medianus ca. 10.0 cm longus, ca. 4.0 c m latis; inflorescentia racemosa, brevis, ca. 5.0 cm longa; flores staminati conici; capsulae ca. 1.5 cm longae; semina ca. 0.9 cm longa.

Arborescent shrubs, 2.0-5.0 m tall (Plate 16 A), trunk diameter about 10.0 cm, branching begins above the middle, dichotomously and trichotomously branching, branches with a tendency to spread out. All parts of the plant with strong odor of HCN. ROOTS

slightly swollen (Plate 16 C); epidermis rough, strong brown (5 YR 4/5)\*; subepidermis white. Young STEMS glabrous, strong brown (5 YR 4/5)\*, internally light yellow green (7.5 GY 9/4)\*; mature stems brownish grey; latex cream colored. Young foliage at apex strong yellow green (7.5 GY 6/8)\*. LEAVES alternate, stipules deciduous glabrous; petioles generally 10.0-15.0 cm long, terete, dull red green with some olive shading; lamina non-peltate, ventral surface deep green, glabrous; dorsal surface pale green, glabrous, midribs and major veins prominent, abaxial surface wax pattern finely farinose; venation camptodromous; palmately 7 lobed, 3 major, 2 smaller and often 2 minute lobes (Plate 16 D); median lobes usually about 10.0 cm long and about 4.0 cm wide, obovate pandurate (Plate 16 E), occasionally obovate entire lobed (Plate 16 G), the primary constriction of pandurate lobes shallow (Plate 16 E) to deep (Plate 16 F), apex varies from almost truncate with an acute conical tip in the middle (Plate 16 F), to acuminate (Plate 16 G). Plants begin to flower when about 1.0 m tall; INFLORESCENCE a short monoecious, axillary raceme (Plate 16 H), usually about 5.0 cm long, never longer than 8.0 cm, pedicels comparatively longer at base, gradually decreasing in length towards apex, giving the inflorescence a more or less conical shape, all parts glabrous; bracteoles non-foliaceous, less than 0.3 cm in length, margin smooth; bractlets non-foliaceous. PISTILLATE FLOWERS restricted to the base of the inflorescence, borne on 1.0-2.0 cm long pedicels, tepals externally brilliant yellow-green (2.5 GY 9/8)\*, cleft to the base into 5 lobes,

---

\* Color designations used are those of the Nickerson Color Fan, Amer. Hort. Council.

lobes lanceolate-oblong, disc fleshy, entire, brilliant yellow green (2.5 GY 9/8)\*, ovary subglobose, entire, the three divisions of the stigma moderately lobed and lobulate. STAMINATE FLOWERS characteristically conical (Plate 16 H), often as long as 1.8 cm, tepals brilliant yellowish green (Plate 16 I) externally (2.5 GY 9/8)\*, cleft 1/3 of the way down into 5 lobes, lobes tapering, acuminate, disc 10 lobed, brilliant yellowish green (2.5 GY 9/8)\*, stamens 10, didynamous, filaments and anthers white. FRUIT pedicels 1.0-2.0 cm long, slightly curved downwards; capsules more or less globular (Plate 16 J), about 1.5 cm long from base to apex, surface slightly rugose, with 6 very small wings, apex rounded, fruit dehiscence septicidal, splitting into 6 carpels. SEEDS oblong, about 0.9 cm long (Plate 16 L), carunculate end bluntly acute (Plate 16 K), caruncle moderately prominent.

DISTRIBUTION AND ECOLOGY: (Plates 49 and 50). MEXICO: Oaxaca. Flourishes in the plains and foothills surrounding Juchitan and Tehuantepec, and upstream on both sides of Rio Tehuantepec; to 150 m. It appears that the range of this species extends upwards as high as 1000 m, towards the headwaters of Rio Tehuantepec. Webster, Miller & Miller 11641, collected at an altitude of 870 m, may represent an ecotypic form of this taxon, but the poor condition of the specimen does not render critical comparisons possible. Similarly Conzatti 2413, collected from Quiotepec, Cuicatlan (Plate 50) at an altitude of 700 m resembles M. oaxacana, but positive identification has not been possible due to the poor condition of the specimen. Further collections from these areas will confirm the possibility of the range of this species extending along the northeastern

foothills of the Sierra Madre del Sur, up to Cuicatlan which is on the periphery of the range of Manihotoides pauciflora.

In the typical habitat along the foothills near Juchitan and Tehuantepec, large self-seeding colonies are common. Grows under partial shade (Plate 16 A) in a relatively undisturbed vegetation composed of thorny leguminous trees, shrubs, cacti, etc. Appears to be adapted to grow in several soil types such as sandy (King 1213), loose limestone with coarse friable reddish-brown soil mantle (Rogers 507), metamorphic rock (Webster, Miller & Miller 12955), and lateritic soil on non-calcareous rocks (Webster, Miller & Miller 11641).

Rainfall of the area about 1000 mm. The weather station at Salina Cruz, a location within the geographical range of this species, records a mean annual rainfall of 1055 mm (Table 2). Practically all the rain is received during the five month period of June - October, the rest of the year being comparatively dry. This species, like M. chlorosticta, appears to be adapted to tolerate very heavy rains during June - October and survive with very little moisture the rest of the year.

DISCUSSION: This species was confused in the past with M. chlorosticta, the former is an arborescent shrub while the latter is a clambering vine. There are several other features which characterize M. oaxacana such as the very short raceme, conical brilliant yellow flowers, smaller fruits and seeds, etc. Besides, the geographical ranges of these two species are disjunct and consequently there is little likelihood of interbreeding. This Oaxaca population represents a closed gene pool in itself and as such a distinct biological species. Rogers (1965) discovered and defined this

population as an undescribed species, based on field study observations. The specific epithet denotes the distribution which is confined only to the state of Oaxaca.

In the subgraphs (Fig. 10) M. oaxacana cluster joins M. chlorosticta cluster at "level" 17 ("C-value" .857) and soon both the clusters integrate tightly. The general ecological habitat of both these species is very similar, both flourishing along the coastal belt. All these suggest that these two species are very closely related. Without cytogenetic data it is unsound to hypothesize; nevertheless it seems obvious that M. oaxacana and M. chlorosticta once belonged to the same ancestral gene pool, eventually splitting and diverging into two closed gene pools. The M. oaxacana population, occupying a pocket confined by mountain barriers, is strongly suggestive of the possibility of a segment of the ancestral gene pool being restrained to evolve independently in isolation.

SPECIMENS EXAMINED: MEXICO. Oaxaca: [1] G. L. Webster, K. Miller & L. Miller 12955, 12 miles E of Juchitan, 11 August 1962, (G1\*\* = NO, NO); [2] D. J. Rogers 505, 17 kilometers ENE of Juchitan, 22 July 1963, (G5 = NO); [3] R. M. King 1213, Isthmus of Tehuantepec/2-4 kilometers E of Tehuantepec, 1 July 1959, (G2 = NY, TEX, UC, US); [4] R. M. King 366, Isthmus of Tehuantepec/5.5 kilometers E of

---

\* This serial number corresponds to the number representing this collection in distribution maps.

\*\* This "member" represents the cited herbarium sheets in the computer similarity-graph-clustering analysis, the results of which are depicted in the subgraphs (Figs. 10 & 11) and the "SKYLINE" (Plate 8).

Juchitan, 2 July 1958, (G4 = US); [5] D. J. Rogers 506, 7-8 kilometers WNW of Tehuantepec, 23 July 1963, (G4 = NO); [6] D. J. Rogers 507, 10 kilometers WNW of Tehuantepec, 23 July 1963, (G2 = NO); [7] G. L. Webster, K. Miller & L. Miller 13007, 8 miles W of Tehuantepec, 12 August 1962, (G2 = NO,NO); [8] R. M. King 737, Isthmus of Tehuantepec/10-15 miles NW of Tehuantepec, 26 July 1958, (G3 = US); [9] C. A. Purpus 7353, San Geronimo, July 1914, (G3 = UC); [10] G. L. Webster, K. Miller & L. Miller 11641, 70 miles SE of Oaxaca, 22 June 1962, (NONE<sup>\*</sup> = NO); [11] C. Conzatti 2413, Quicotepec, Cuicatlan, 21 June 1909, (NONE<sup>\*</sup> = F).

---

\*These specimens were not represented in the computer similarity-graph-clustering analysis, on account of the poor condition of the specimens.

8. MANIHOT CHLOROSTICTA Standley & Goldman, Contr. U.S. Natl. Herb.  
13:375. 1911.

NOMENCLATURAL TYPE: Holotype (US): E. W. Nelson & E. A. Goldman  
7401 l. Isotype (F).

HETEROTYPIC SYNONYMS:

Manihot colimensis Croizat, J. Arnold Arbor. 23:221. 1942. Nomen-  
clatural type: Holotype (A): R. S. Ferris 6140 l. Isotypes (F,US).

Manihot mobilis Standley, Amer. Midl. Naturalist 36:177. 1946. Nomen-  
clatural type: Holotype (F): Wm. C. Leavenworth & H. Hoogstraal  
1556 l.

ILLUSTRATIONS: Plates 17,18,51,52,53 and 54.

VERNACULAR NAME: Cuadrado. Ortega 6345 (Sinaloa, Mexico).

SYNOPSIS OF GROSS MORPHOLOGY: Clambering vines or vinelike decum-  
bent shrubs (Plate 17 A), up to about 5.0 m high, the trunk at the  
base about 10.0 cm in diameter, soon dividing into slender smooth  
long branches about 3.0 m in length, vigorous, turgescens and scan-  
dent, forming rather heavy masses on other vegetation. ROOTS not  
seen. Young STEMS greenish grey, glabrous; mature stems greyish  
with reddish brown tinge, glabrous; latex present. Young foliage at  
apex yellowish green. LEAVES alternate; stipules deciduous, gla-  
brous; petioles about 8.0 cm long, terete, glabrous, dark reddish;  
lamina non-peltate, deep green above, pale green beneath, abaxial  
surface wax pattern finely farinose; venation camptodromous; pal-  
mately 5-7 lobed, 3 major, 2 smaller, often 2 more minute lobes

(Plate 18 H & I); median lobes show considerable variation in size and shape (Plate 18 J,K,L&M), length varies from 5.0-12.0 cm, width 2.0-6.0 cm, obovate entire lobed (Plate 18 J) or obovate pandurate (Plate 18 L), the primary constriction of pandurate lobes varies considerably with respect to depth, width and sinuosity, apex acute to more or less acuminate; lowest lobes about 1/4 as long as median lobes. INFLORESCENCE a monoecious few flowered raceme (Plate 17 B), mostly axillary, about 8.0 cm in length; all parts glabrous; bracteoles non-foliaceous, less than 0.3 cm in length, purplish, margin smooth; bractlets non-foliaceous. PISTILLATE FLOWERS restricted to the base of the inflorescence, in most of the cases one of the pistillate flowers comes out from the very base of the inflorescence (Plate 17 B) and appears as if directly connected to the stem, pedicels usually long, sometimes as long as 5.0 cm, tepals lemon yellow, without any purplish pigmentation, cleft down to the base into 5 lobes, lobes oblong-lanceolate, about 1.0 cm long and about 0.3 cm wide, disc fleshy, entire, lemon yellow, pistil about 0.6 cm long, ovary subglobose, glabrous, the three divisions of the stigma moderately lobed and lobulate, cream colored. STAMINATE flowers campanulate (Plate 18 O), tepals about 1.4 cm long, lemon yellow without any purplish pigmentation, cleft 1/3 way down into 5 lobes, lobes oblong-obtuse, not prominently reflexed at anthesis, disc fleshy, 10 lobed, lemon yellow, stamens 10, didynamous, longer whorl about 1.0 cm long, shorter whorl about 0.8 cm long. filaments and anthers cream colored. FRUIT pedicels usually long, up to about 5.0 cm, robust, very slightly curved, in most of the cases one of the pistillate flowers at the very base of the inflorescence develops

into a lone fruit, and as such the fruits appear to come off directly from the stem. Capsules ovate ellipsoid (Plate 17 C), 1.25-1.75 cm long from base to apex, surface coarsely tuberculate, perceptibly 6 ribbed, apex slightly pointed, fruit dehiscence septicidal. SEEDS oblong, 1.25-1.5 cm long (Plate 17 D & E), caruncle moderately prominent, trapeziform (Plate 17 F & G).

DISTRIBUTION AND ECOLOGY: (Plates 51 to 54). MEXICO: Baja California, Sinaloa, Jalisco, Colima, Michoacan, and Guerrero, along the coastal belt between the sea and the mountain ranges; 0-250 m, occasionally up to 500 m. It flourishes in a variety of ecological habitats such as on cliffs facing ocean as a member of a low spiny vegetation composed of Mimosa xanti, Jatropha cinerea, Melochia tomentosa, etc; between the beach and coastal lagoons; in heavy clay soils of coastal plains in thorn forest vegetation; on low rocky hills (about 50 m) as a member of low deciduous woodland vegetation comprised of various legumes, Bursera, Cordia, Jatropha, etc.; on basaltic hill slopes in short tree forest; occasionally on rocky slopes and ravines of gypsum and slate at altitudes of about 500 m in deciduous woodland with Juliania, Cephalocereus, Cyrtocarpa, Cassia, etc. The range of this species is parallel to that of M. aesculifolia, along the west coast, and it appears that M. chlorosticta is abundant towards the ocean, and M. aesculifolia flourishing at the back of the coastal belt towards the mountains; the two overlapping in the middle common territory. At the boundary between the states of Michoacan and Guerrero, the range extends interior in the form of a limb (Plate 54) along the canyon of

Rio de Tepalcatepec. At the extreme end of the limb the species extends up along the mountain slopes, in the Tancitaro region. One collection (Leavenworth and Hoogstraal 1532) was growing at an altitude of 750 m.

The southern region of the range receives a mean annual rainfall of about 1500 mm and towards the north about 1000 mm. The weather data of 3 stations located within the range of this species, Acapulco, Manzanillo, and Mazatlan, are given in Table 2. Practically all the rain is received during the five month period of June-October, with the rest of the year being drier.

PHENOLOGY: Flowering in June - December; fruiting in July - January.

DISCUSSION: Prior to this study this population remained split into three species: M. chlorosticta, M. colimensis and M. mobilis. 83 specimens representing these 3 species were compared with respect to 50 morphological characters, and in the subgraphs (Fig. 10) all form a completely connected cluster at a very high "C-value" of .938, indicating that there is very close overall phenotypic similarity between the 83 specimens. The high degree of polymorphism of leaves, manifested by most of the species of Manihot, can lead to erroneous decisions in species delimitations, especially when the decisions are based on the study of few herbarium specimens, and not supplemented by actual field studies. Rapid and efficient techniques and tools, such as the ones employed in this study, were not available to earlier botanists, and critical comparisons of large number of specimens with respect to numerous phenotypic characters, were practically impossible. M. mobilis was described as a new species,

on the basis of 2 collections and this taxon was believed to be characterized by its entire lobed leaves (Plate 18 M), in contrast to the pandurate leaves (Plate 18 L) of M. chlorosticta and M. colimensis. Field observations carried out as a part of this study proved that both types occur in the same plant. Rogers 511 and 512 confirm the occurrence of both types of leaves in the same twig.

M. colimensis was believed to be characterized by its longer seed (Plate 17 D), in contrast to the shorter seed (Plate 17 E) of M. chlorosticta. A critical examination of the seed size in this study confirmed that the size varies from short (1.25 cm) to long (1.5 cm), and both types occur mixed in what was believed to be M. chlorosticta population as well as in M. colimensis population.

The distribution pattern does not give any support to the possibility of the 3 "species" being 3 independent closed gene pools; on the contrary, it is strongly indicative of these being segments of a single interbreeding population.

The Baja California segment is separated from the mainland segment by a wide strip of sea, but the close phenotypic resemblance does not show even the slightest indication of any restriction to free interbreeding between the disjunct segments.

The population at the extreme interior end of the Rio de Tepalcatepec canyon appears to have only a limited access to the main segment, with consequent restriction to free interbreeding. Plate 54 E shows that this area is covered all around by tall mountains except for a small passage at the southern extremity through which the river flows into the sea. At "level" 9 (Fig. 10) in the subgraphs, H-1 which represents some specimens collected

from this area stands out as a "satellite". Ecologically this canyon population seems to have developed the genetic potential to colonize higher altitudes. One specimen was collected at this canyon at an altitude of 1200 m, while 500 m appears to be the upper limit for the main segment of this species occurring along the sea coast. At Apatzingan area, this canyon population appears to be sympatric with M. tomatophylla, an aspect of some evolutionary significance discussed in detail in connection with M. tomatophylla.

At "level" 22 in the subgraphs, H-8 acts as a distinct "articulator" between M. chlorosticta and M. rhomboidea. H-8 represents 4 collections (Ortega 7024 and 6345; Ferris & Mexia 5218; and Rose 3266) from the Mazatlan area. These four specimens possess the characteristic craspedodromous venation of M. rhomboidea (Plate 18 N). It is significant that these 4 specimens have been collected from widely dispersed localities, spread over a distance of over 100 miles, indicating that this is not an occurrence of sporadic hybridization but on the contrary, what seems to be a case of interspecific gene combination(s) becoming genetically fixed and flourishing as a self sustaining colony. This region represents the northern most extremity of the range of M. rhomboidea and as such, possibly this population may have evolutionary significance, representing ancestral forms.

The subgraphs (Fig. 10) indicate the close phenotypic similarity between M. chlorosticta and M. oaxacana; the 2 clusters joining at a "C-value" of .857 and becoming a maximally connected cluster at .820.

SPECIMENS EXAMINED: MEXICO. Baja California: [1] J. R. Hastings & R. M. Turner 64-355, 33 miles N of Cabo San Lucas, 17 October 1964, (H6\*\* = UC); [2] E. W. Nelson & E. A. Goldman 7401, San Jose Del Cabo, 6 January 1906, (H7 = F,US); [3] T. S. Brandegee 550, San Jose del Cabo, September 1890, (H7 = GH,UC,US); [4] C. Grabendorfer 550, San Jose del Cabo, 1899, (H7 = UC); [5] T. S. Brandegee s.n., San Jose del Cabo, November 1902, (H7 = UC 110154); [6] C. A. Purpus 517, San Jose del Cabo, January - February 1901, (H7 = UC). Sinaloa: [7] H. S. Gentry 7085, Maraton/12 miles W of Culiacan, 21 September 1944, (H6 = A,F,NY,UC,US); [8] H. S. Gentry 5026, Cerro E of Culiacan, 23 November 1939, (H6 = ARIZ,MICH,MO,NA,NY); [9] J. G. Ortega 7273, W/O locality, 1934, (H7 = F); [10] J. G. Ortega 7024, W/O locality, 1933, (H8 = F); [11] J. G. Ortega 6345, Mazatlan/Villa Union/Escamillas, August 1926, (H8 = GH,UC); [12] R. S. Ferris & Y. Mexia 5218, vicinity of Labrades, 21 September 1925, (H8 = A); [13] J. N. Rose 3266, between Rosario and Concepcion, 28 July 1897, (H8 = US). Jalisco: [14] R. McVaugh & W. N. Koelz 1695, near Playa de Cuastecomate, December 1959, (H6 = MICH,US). Colima: [15] R. McVaugh 15875, Bahia de Santiago, 29 July 1957, (H6 = MICH); [16] D. J. Rogers 511, Playa de Santiago/7 kilometers W of Manzanillo, 30 July 1963, (H4 = NO); [17] R. McVaugh 15638, Playa de Santiago, 22 July 1957, (H6 = MICH, TEX); [18] D. P. Gregory & G. Eiten 321, ca 5 miles WNW of Manzanillo City, 11 July 1956, (H6 = MICH,MO,NY); [19] E. Palmer 1027, Manzanillo,

---

\* This serial number corresponds to the number representing this collection in distribution maps.

\*\* This "member" represents the cited herbarium sheets in the computer similarity-graph-clustering analysis, the results of which are depicted in the subgraphs (Figs. 10 & 11) and the "SKYLINE" (Plate 8).

December 1890, (H5 = US); [20] E. Palmer 1027 A, Manzanillo, December 1890, (H5 = BM,NY,US); [21] R. S. Ferris 6140, vicinity of Manzanillo, 28 November 1925, (H4 = A,F,US); [22] D. J. Rogers 512, 16 kilometers SSW of Colima on highway 110, 30 July 1963, (H4 = NO); [23] R. McVaugh & W. N. Koelz 1553, 11 miles SSW of Colima on Manzanillo Road, December 1959, (H6 = MICH,US); [24] G. M. Emrick 140, Tecoman, November 1906, (H5 = F); [25] G. M. Emrick 156, Tecoman, November 1906, (H5 = F). Michoacan: [26] Wm. C. Leavenworth & H. Hoogstraal 1556, Tancitaro region/between Apatzingan and La Majada, 13 August 1941, (H2 = F); [27] Wm. C. Leavenworth & H. Hoogstraal 1532, Canyon between Acahuato and Apatzingan, 14 August 1941, (H1 = F,MO,NY); [28] Wm. C. Leavenworth 451, bank of Rio Apatzingan/2 miles S of Apatzingan, 5 August 1940, (H3 = F,GH). Guerrero: [29] Hinton et al 10345, Petatlan, 20 June 1937, (H4 = GH,K,NY,US); [30] G. B. Hinton et al 10939, Atoyac, 19 November 1937, (H4 = K,MICH,MO,NY,UC,US,US); [31] E. Palmer 272, Acapulco and vicinity, W/O date, (H7 = GH,US); [32] L. H. MacDaniels 212, Acapulco, 24 August 1935, (H6 = F).

9. MANIHOT DAVISIAE Croizat, J. Arnold Arbor. 23:225. 1942.

NOMENCLATURE TYPE: Holotype (US). Lemmon s.n. !. Isotype (BM).

ILLUSTRATIONS: Plates 19 and 55.

VERNACULAR NAMES: None known.

SYNOPSIS OF GROSS MORPHOLOGY: Erect shrubs, 1.0-3.0 m tall, caespitose, woody at the base. ROOTS not seen. Young STEMS glabrous; mature stems glabrous, greyish brown. LEAVES alternate, stipules deciduous, glabrous; petioles usually about 10.0 cm long, terete, glabrous; lamina non-peltate, dorsal and ventral surfaces glabrous, abaxial surface wax pattern smooth; venation camptodromous (Plate 19 B); palmately 7 lobed, 3 major, 2 smaller and often 2 more minute lobes (Plate 19 A); median lobes usually about 10.0 cm long, rhomboid entire lobed (Plate 19 D) or rhomboid pandurate (Plate 19 C), 3.0-4.0 cm wide, rarely narrower (Plate 19 E), pandurate lobes usually with a prominently dilated apical lobule, apex acuminate. INFLORESCENCE, a monoecious axillary raceme (Plate 19 F), usually short, about 8.0 cm in length, occasionally longer, all parts glabrous; bracteoles non-foliaceous, less than 0.3 cm in length, margin smooth; bractlets non-foliaceous. PISTILLATE FLOWERS restricted to the base of the inflorescence, borne on short (about 1.5 cm long) pedicels, tepals not seen. STAMINATE FLOWERS companulate (Plate 19 F) about 1.2 cm long, tepals yellowish-green without any purplish pigmentation, cleft 1/3 way down into 5 lobes, lobes oblong-obtuse, not prominently reflexed at anthesis, disc fleshy, 10 lobed, stamens 10 didynamous, longer ones about 0.8 cm long, shorter about 0.6 cm long,

filaments and anthers cream colored. FRUIT pedicels about 1.5 cm long, slightly curved downwards; capsules depressed globular, about 1.5 cm long from base to apex (Plate 19 J), surface nearly smooth without wings, apex depressed; fruit dehiscence loculicidal splitting into 3 parts, the commissural sutures not disjoining. SEEDS almost rotund (Plate 19 H), about 1.25 cm long; basal end prominently bulged in contrast to the tapering carunculate end (Plate 19 I), caruncle not prominent (Plate 19 G).

DISTRIBUTION AND ECOLOGY: (Plate 55). USA: Arizona; MEXICO: Sonora, Chihuahua and Sinaloa; usually at high altitudes, in the Santa Catalina mountains, Baboquivari mountains and northern regions of the Sierra Madre Occidental; but at the southern end of the range this species descends to sea level. M. Davisiae appears to be sympatric with M. angustiloba almost over its entire range with the possible exception of the Baja California area, where no M. Davisiae specimens have been collected so far. Croizat (1942) in the original description stated that M. Davisiae and M. angustiloba are altitudinally isolated, the former occupying higher elevations, the latter lower regions. Due to lack of sufficient ecological data it was not possible to accurately determine whether any altitudinal segregation of these two species is prevalent in the mountains. However, in the lowland area near the coast, around Los Mochis in Sinaloa, both the species seem to flourish at the same altitude, and in the subgraphs there are indications of considerable genetic exchange between these 2 taxa in this common territory (discussed in detail below). The range of M. Davisiae as delimited in this study

extends all the way down to about 25° latitude in Mexico, and as such M. Davisiae is not truly a relic species occurring in a narrowly localized area in the Arizona mountains as stated by Croizat (1942). At higher altitudes it grows on rocky volcanic slopes in thorn forests, on tropical forest slopes, etc.

The general region seems to receive a very low mean annual rainfall of about 350 mm. This species growing in the northernmost extremity of the range of the genus, tolerates very low mean temperatures, as low as 8° C in January. The weather data of 2 stations within the range of this species, Tucson and Guaymas, are given in Table 2.

PHENOLOGY: Flowering in July - August; fruiting in August - September.

DISCUSSION: Leaf polymorphism is commonly prevalent in Manihot species and as such leaf outline will have to be employed with caution when used as a taxonomic character. At the southernmost extremity of the range of M. Davisiae some forms (Gentry 14293; Gentry 2450) occur which not only possess completely entire lobed leaves (Plate 19 D), but also characteristically mottled seeds (Plate 19 H), in contrast to the normal Davisiae seeds (Plate 19 I). I-1 representing these specimens in the subgraphs (Fig. 10), stands out as a "satellite" at "level" 14. At "level" 23 it is connected to M. isoloba. Geographically, the area where these forms grow is adjoining the range of M. isoloba. Cytogenetic investigations may throw more light on the possibility of these forms constituting a bridging population in the ancestral history linking M. Davisiae

and M. isoloba. When the two clusters representing the two sections of Manihot join together in the subgraphs (Fig. 11, "level" 28), one of the connections is between this entire lobed form and M. caudata. The possible significance of this is discussed in connection with M. caudata.

At "level" 9, I-7 and J-1 form a small cluster of their own. I-7 and J-1 represent the morphologically mixed forms (Davisiae + angustiloba) growing in the lowland coastal plains around Los Mochis, where the two species are sympatric. At level 14, the [I-7 + J-1] cluster brings together M. Davisiae cluster and M. angustiloba cluster, thus acting as a linking population between the two species. The subgraph indications supported by the sympatric distribution, are strongly suggestive of this population being an ancestral stock from which M. Davisiae and M. angustiloba diverged. It may also be hypothesized that at this lowland common territory, the altitudinal isolation (believed to be existing between these two species at high altitudes) breaks down resulting in genetic exchange between these two taxa. Whatever the case may be, this exemplifies the potential of taximetric methods to aid in the formulation of working hypotheses for efficiently designing cytogenetic investigations.

The presence of certain collections such as White 542, where the same collection has both M. Davisiae specimens as well as M. angustiloba specimens, prevents completely ruling out the possibility that these two species may merely be two segregating forms of one interbreeding gene pool. It may be pointed out that field investigations carried out as a part of this study confirmed that M. mexicana and M. rhomboidea, hitherto considered as 2 different

species, are nothing but two segregating phenotypic forms in the progeny occurring mixed together in the same local population. Adequate field studies of M. Davisiae could not be carried out at the present time, and it may become necessary to revise its taxonomic status when more field data become available.

SPECIMENS EXAMINED: USA. Arizona: [1] <sup>\*</sup>R. H. Peebles 8796, Baboquivari Mountains, 3 August 1932, (I6 <sup>\*\*</sup> = ARIZ,ARIZ,F,GH,US); [2] Thorner s.n., Santa Catalina Mountains/Soldiers Canyon, 14 August 1910, (I2 = ARIZ 70287, POM 282626); [3] L. A. Davis s.n., Sabino Canyon Trail/Santa Catalina Mountains, 15 August 1942, (I3 = A -); [4] J. A. Harris 16475, The Basin/Santa Catalina Mountains, 5 August 1916, (I4 = NY); [5] Livingston & Thorner s.n., Santa Catalina Mountains Carillos Rance, 11 August 1906, (I4 = ARIZ 70288); [6] Lemmon Herb. 70 3055, Santa Catalina Mountains, 27 August 1883, (I4 = UC); [7] J. G. Lemmon s.n., Santa Catalina Mountains, 27 August 1883, (I6 = BM -,US 62129); [8] Millsbaugh Herb. 3055, W/O locality, 27 August 1883, (I6 = F); [9] Livingston & Thorner s.n., Santa Catalina Mountains, 12 August 1906, (I4 = ARIZ 70289,POM 282627). MEXICO. Sonora: [10] S. S. White 542, Santa Rosa Canyon/near Bavispe, 17 July 1938, (I5 = ARIZ); [11] I. L. Wiggins & R. C. Rollins 221, 2.5 miles E of main highway between La Palma and Cienequita, 1 September 1941, (I7 = ARIZ,MICH,MO,NY,US). Chihuahua: [12] H. S. Gentry 2450,

\* This serial number corresponds to the number representing this collection in distribution maps.

\*\* This "member" represents the cited herbarium sheets in the computer similarity-graph-clustering analysis, the results of which are depicted in the subgraphs (Figs. 10 & 11) and the "SKYLINE" (Plate 8).

Sawakoa/Rio Mayo, 25 August 1936, (I1 = ARIZ). Sinaloa: [13] H. S. Gentry 14293, Cerros Del Fuerte/18-24 miles N of Los Mochis, 25 September 1954, (I1 - US); [14] U. T. Waterfall 12808, 2 miles E and 14 miles N of Los Mochis, 17 August 1956, (I6 = MICH,US).

10. MANIHOT ANGUSTILOBA (Torrey) Muell. Arg. emend. D. J. Rogers & S. G. Appan.

NOMENCLATURE TYPE: Lectotype (MO): C. Wright 1811. Isolectotypes (GH, NY, US).

HOMOTYPIC SYNONYMS:

Janipha manihot H.B.K. var. angustiloba Torrey in Emory's Rept. U.S. Mex. Bound. Surv. 2:199. 1859. Pro parte.

Manihot angustiloba (Torrey) Muell. Arg. in DC. Prodr. 15 (2):1073. 1866. Pro parte; Pax & Hoffmann, Pflanzenr. 44(iv. 147. ii):83.

1910. Pro parte; Croizat, J. Arnold Arbor. 23:223. 1942. Pro parte; McVaugh, Brittonia 13(2):189. 1961. Pro parte.

Manihot acutiloba Weatherby, Proceed. Amer. Acad. 45:427. 1910. Pro parte.

ILLUSTRATIONS: Plates 20, 21 and 56.

VERNACULAR NAMES: Pico gallo. Carter 5126 (Baja California, Mexico).

SYNOPSIS OF GROSS MORPHOLOGY: Erect caespitose shrubs, 1.0-3.0 m tall, frequently branched, often forming clumps from tuberous root stocks (Plate 20 A). Very strong odor of HCN on all plant parts. ROOTS prominently swollen (Plate 20 C), about 0.5 m long, fusiform; epidermis light brown, slightly rough to rough, subepidermis tan to white; cortex white; vascular strands yellow. Young STEMS glabrous, moderate reddish brown (2.5 R 3/7)\*, terete, glabrous; lamina

---

\* Color designations used are those of the Nickerson Color Ran, Amer. Hort. Council.

non-peltate, dorsal and ventral surfaces glabrous, abaxial surface wax pattern smooth; venation craspedodromous (Plate 20 E); palmately 7 lobed, 3 major, 2 smaller and often 2 more minute lobes (Plate 20 D); median lobes usually more than 12.0 cm long, hastate (Plate 21 H), occasionally the basal lobules poorly developed (Plate 21 I), or absent (Plate 21 J), lobe and lobule apices acuminate terminating in a spine like point, an extension of a vein (Plate 20 E), very often a smaller lobulet present below the basal lobule, lamina margin above the basal lobule sinuate, entire, or incised into small falcate lobulets; lowest lobes about 1/4 as long as median lobes, attenuate. INFLORESCENCE a monoecious, axillary raceme (Plate 21 L), usually about 12.0 cm long, occasionally shorter, all parts glabrous; bracteoles non-foliaceous, margin smooth; bractlets non-foliaceous. PISTILLATE FLOWERS borne on branched peduncles at the base of the inflorescence (Plate 21 L), tepals greenish yellow without purplish pigmentation, about 1.5 cm long, cleft to the base into 5 lobes oblong-lanceolate, disc fleshy, entire, yellowish, pistil about 0.9 cm long, ovary sub-globose to slightly elongated, glabrous, the three divisions of stigma clearly divided, each well lobed and lobulate. STAMINATE FLOWERS campanulate, often as long as 1.8 cm, tepals brilliant yellowish green (2.5 GY 8/9)\*, cleft 1/3 way down into 5 lobes, lobes oblong, not prominently reflexed at anthesis, disc fleshy, yellowish, 10 lobed, stamens 10, didynamous, longer ones about 1.1 cm long, shorter ones about 0.9 cm long, filaments and anthers white. FRUIT pedicels 1.0-2.5 cm long, slightly curved downwards; capsules depressed globose (Plate 21 N), about 1.5 cm long from base to apex, surface very slightly

tuberculate, without ribs, apex depressed; fruit dehiscence loculicidal (Plate 21 M), splitting into 3 parts, the commissural sutures not disjoining. SEEDS almost rotund, about 1.25 cm long (Plate 20 F), the basal end prominently bulged in contrast to the tapering carunculate end (Plate 20 G); caruncle not prominent.

DISTRIBUTION AND ECOLOGY: (Plate 56). USA: Arizona and doubtfully in New Mexico; MEXICO: Sonora, Chihuahua, Sinaloa and Baja California; usually at about 1000-2000 m, in the Santa Catalina Mountains, Baboquivari Mountains, and the northern regions of Sierra Madre Occidental, but towards the southern end of the range it descends to sea level and flourishes in lowlands. A small segment of the population occurs in the Sierra de la Giganta in Baja California. This species appears to be sympatric, almost over its entire range, with M. Davisiae. It grows in various habitats such as on exposed rocky slopes; along rocky ridges; clinging in rock crevices; on basaltic hill slopes; in oak woodland; in oak grassland; on open slopes in short tree forests; in upper tropical forests; in volcanic slopes in coastal thorn forest; on loose sandstone rocky surfaces near sea level among various legumes, organ pipe cacti, Simmondsia, etc. (Plate 20 B).

The region seems to receive a very low annual rainfall of about 350 mm. This species, like M. Davisiae, grows in the northernmost extremity of the range of the genus, and is adapted to tolerate very low mean temperatures, as low as 8° C in January. Despite such, or perhaps due to such, conditions, the species seems to have an admirable capacity to store enormous quantities of carbohydrates

in its roots (Plate 20 C); a quality worth exploiting from a plant breeding point of view. The weather data of three stations within the range of the species, Tucson, Guaymas, and La Paz, are given in Table 2.

PHENOLOGY: Flowering in June - September, fruiting in August - October.

DISCUSSION: This taxon has had a complex taxonomic history (Table 1). In 1866 Muell. Arg. raised the status of Janipha Manihot H.B.K. var. angustiloba to that of a species and described it as Manihot angustiloba (Torrey) Muell. Arg. At that time it encompassed several taxa which were later designated as independent species, viz., M. subspicata, M. mexicana, M. microcarpa, and M. parvicocca. In 1872 Muell. Arg. separated M. microcarpa from M. angustiloba. In 1923 I. M. Johnston described M. mexicana as a separate species and according to his concept, the M. subspicata population (discovered and delimited as a new species in this study) was a part of M. mexicana. In 1942 Croizat described M. parvicocca as a separate species thus removing it from M. microcarpa. McVaugh in 1961 lumped M. microcarpa and M. parvicocca. He also merged Johnston's M. mexicana with M. angustiloba. As clarified in this study M. angustiloba is a closed gene pool in itself, and all the other taxa which at various time have been taken out of it or put back into it are entities which are taxonomically distinct from M. angustiloba.

The subgraphs (Fig. 10) present interesting indications of the relationship between M. angustiloba and M. Davisiae. At "level" 14, J-1 acts as a distinct "articulator" between the clusters

representing these two species. J-1 (Plate 21 K) represents specimens growing in the lowlands near the coast, where the range of this species descends from its usual high altitude mountain habitat. At this region the species shares common territory with M. Davisiae. The possible biological significance of this population is hypothesized in the discussions of M. Davisiae.

At "level" 21 M. angustiloba cluster is connected to M. rhomboidea cluster, and K-1 acts as an "articulator". K-1 represents a M. rhomboidea ssp. rhomboidea specimen (Rose 1608), collected from the northernmost extremity of the geographical range of this taxon, a point nearest to the southern boundary of the range of M. angustiloba. The subgraph indications supported by the distribution pattern, are strongly suggestive of an evolutionary divergence to have occurred from M. rhomboidea population towards the north, resulting in an offshoot developing into an independent closed gene pool - M. angustiloba. Material from the locality of Rose 1608 will be very valuable for a cytogenetic investigation of this hypothesis.

SPECIMENS EXAMINED: USA. Arizona: [1] F. A. Thackery 487, Baboquivari Flat/ Pima County, 17 July 1928, (J3<sup>\*</sup> = ARIZ, MO, NA, NY); [2] W. T. Swingle s.n., Baboquivari Mountains/Allison Dam/Pima County, 10 July 1931, (J3 = NA 75350); [3] F. W. Gould & H. S. Haskell 3248, Baboquivari Mountains/Fresnal Canyon/Pima County, 1 September 1945,

---

\* This serial number corresponds to the number representing this collection in distribution maps.

\*\* This "member" represents the cited herbarium sheets in the computer similarity-graph-clustering analysis, the results of which are depicted in the subgraphs (Figs. 10 & 11) and the "SKYLINE" (Plate 8).

- (J5 = ARIZ,UC); [4] T. H. Kearney & R. H. Peebles 14928, below Baboquivari Canyon/Pima County, 31 August 1940, (J5 = A,ARIZ,GH,NY,US); [5] L. N. Goodding 6548, Sycamore Canyon, 17 August 1937, (J3 = ARIZ); [6] L. N. Goodding 6549, Sycamore Canyon/Santa Cruz County, 16 July 1938, (J3 = ARIZ,NA); [7] Lemmon 3054, Santa Catalina Mountains, 17 August 1883, (J5 = BM,GH,UC); [8] G. J. Harrison & T. H. Kearney 7983, Rincon Mountains, 2 August 1931, (J5 = POM); [9] R. H. Peebles & T. H. Kearney 8742, Rincon Mountains, 31 July 1932, (J5 = GH,MICH,UC); [10] C. G. Pringle 127, Foothills of Santa Rita Mountains, 17 July 1881, (J5 = MO); [11] C. G. Pringle 76, Foothills of Santa Rita Mountains, 8 September 1884, (J5 = GH); [12] G. J. Harrison, T. H. Kearney & C. Hope 8904, Florida Canyon/Santa Rita Mountains, 20 August 1932, (J5 = ARIZ,F); [13] G. J. Harrison, T. H. Kearney & W. Hastings 6031, Nogales, 15 September 1929, (J5 = ARIZ); [14] R. H. Peebles, G. J. Harrison & T. H. Kearney 4584, Nogales, 7 August 1927, (J4 = ARIZ,US); [15] R. H. Peebles, G. J. Harrison & T. H. Kearney 5588, Patagonia Mountains, 18 August 1928, (J5 = ARIZ); [16] T. H. Kearney & R. H. Peebles 14816, Patagonia Mountains/Santa Cruz County, 24 August 1940, (J5 = ARIZ,POM); [17] L. N. Goodding 5370, Mule Mountains, 22 September 1939, (J5 = ARIZ); [18] L. N. Goodding 35-57, Coyote Mountains/Quinlin Pass/Pima County, 2 August 1957, (J5 = ARIZ); [19] R. A. Darrow, F. W. Gould, W. S. Phillips & L. M. Pultz 1937, Carr Canyon, 9 September 1944, (J5 = ARIZ). MEXICO. New Mexico: [20] C. Wright 1811, W/O locality, 1851, (J5 = GH,MO,NY,US). Chihuahua: [21] A. Schott III 8, Sierra

\* The precise locality of collection of this is in question. The local is recorded in the herbarium label as "N. Mexico". This may be interpreted as Northern Mexico or New Mexico.

los Janos camp/illegible, 30 June 1855, (J5 = F,F,NY,NY). Sonora:  
 [22] S. S. White 3013, Rio de Bavispa, 25 July 1940, (J5 = MICH);  
 [23] S. S. White 542, Santa Rosa Canyon/near Bavispe, 17 July 1938,  
 (J5 = GH,MICH); [24] I. L. Wiggins 7056, along Rio Magdalena, 9  
 September 1934, (J5 = US); [25] I. L. Wiggins 7155, 20 miles SE of  
 Magdalena, 12 September 1934, (J5 = A,MICH,US); [26] F. Shreve 6371,  
 Bajada/S of Las Trincheras, 2 September 1933, (J5 = ARIZ,ARIZ,F);  
 [27] H. S. Gentry 17802, San Bernardo/Rio Mayo, 13 September 1959,  
 (J5 = US). Chihuahua: [28] H. S. Gentry 2371, Guasaremos/Rio Mayo,  
 10 August 1936, (J6 = ARIZ,F,MO,NA,UC,US). Sonora: [29] I. L. Wig-  
gins & R. C. Rollins 221, 2.5 miles E of main highway between La Palma  
 and Cienequita, 1 September 1941, (J1 = UC); [30] E. Palmer 233,  
 Guaymas, 1887, (J1 = BM,NY,US,US); [31] H. S. Gentry 14282, Cerro/  
 ca 10 miles S of Ciudad Obregon, 22 September 1954, (J1 = US). Sina-  
 loa: [32] D. J. Rogers 519, vicinity of Topolobampo/18 miles SW of  
 Los Mochis, 10 July 1966, (J1 = NO); [33] J. R. Hastings & R. M.  
Turner 64-134, near Yacht Hotel/Topolobampo, 5 October 1964, (J1 =  
 ARIZ); [34] E. Palmer 222, Topolobampo, September 1897, (J1 = ARIZ,  
 MICH,US). Baja California: [35] A. Carter 4982, Sur Sierra de La  
 Giganta, 19 September 1965, (J6 = UC); [36] A. Carter 5126, Sur  
 Sierra de La Giganta, 4 October 1965, (J6 = UC).

11 & 12. MANIHOT RHOMBOIDEA Muell. Arg. emend. D. J. Rogers & S. G. Appan.

SYNOPSIS OF GROSS MORPHOLOGY: Sprawling shrubs (Plate 23 J), about 0.5 m tall, branching from base onwards, branches slender, weak. ROOTS prominently swollen (Plate 23 J), napiform, often as long as 25.0 cm; epidermis dark brown, rough; subepidermis white; with strong smell of HCN. Young STEMS glabrous; mature stems greyish brown, often with deep reddish tinge, glabrous, latex present. LEAVES alternate, stipules deciduous, glabrous; petioles usually about 6.0 cm long, occasionally as short as 3.0 cm, glabrous, terete, greenish or purplish tinged; lamina very narrowly peltate, ventral surface glabrous, color varying from pure green to various degrees of purplish tinge, dorsal surface glaucous, occasionally silvery, abaxial surface wax pattern smooth; venation camptodromous or craspedodromous; palmately 7 lobed, 3 major, 2 smaller and often 2 more minute lobes; median lobes show tremendous variation in size and shape, length varies from 3.0 - 15.0 cm, width 0.5 - 5.0 cm, shape varies from rhomboid entire lobed (Plate 23 L), or rhomboid pandurate (Plate 23 M) to hastate (Plate 23 K) or gladiate (Plate 24 C), with several combinations of these shapes also occurring (Plate 23 O, P & Q), often in the same local population, apex acute to acuminate; lowest lobes about 1/4 as long as median lobes, attenuate (Plate 23 K). INFLORESCENCE a monoecious raceme, two kinds present in the population, a short axillary raceme (Plate 22 C) less than about 10.0 cm in length, (flowers occurring from base up to the apex, pistillate flowers being restricted to the base), the other type a long

terminal raceme (Plate 22 D), often as long as 25 cm, (the lower half of the rachis completely devoid of flowers, pistillate flowers occurring at the base of the upper half of rachis); peduncles and pedicels glabrous, pure green or purplish tinged, bracteoles non-foliaceous less than 0.3 cm in length, glabrous, margin smooth; bractlets non-foliaceous, glabrous. PISTILLATE FLOWERS when occurring at the very base of the inflorescence - borne on pedicels about 2.0 cm long, slightly curved downwards, (Plate 22 C), when occurring at the base of the upper half of the rachis - borne on pedicels about 2.0 cm long with a characteristic downward bend, almost at a right angle (Plate 22 D), tepals about 1.1 cm long, pure greenish yellow to various degrees of purplish tinged, cleft to the base into 5 lobes, lobes oblong-lanceolate, disc orange yellow (Plate 22 C), fleshy, entire, pistil about 0.5 cm long, ovary greenish, glabrous, subglobose to slightly elongated, the 3 divisions of the stigma clearly divided down to base and relatively long-lobed and lobulate, cream colored. STAMINATE FLOWERS about 1.5 cm long, campanulate, (Plate 24 E), sometimes almost conical (Plate 22 C), tepals greenish yellow to various degrees of purplish tinged, cleft 1/3 way down into 5 lobes, lobes oblong-obtuse or tapering, very prominently reflexed at anthesis (Plate 22 C), disc orange yellow, fleshy, 10 lobed, stamens 10, didynamous, longer ones about 1.1 cm long, shorter ones about 0.9 cm long, fully exerted out at anthesis (Plate 22 A), filaments greenish white, anthers pale yellow. FRUIT pedicels slightly curved downwards (Plate 22 F) in case of fruits occurring at the very base of the inflorescence, or bent down almost at a right angle (Plate 24 F) in case of fruits occurring at the base of the upper

half of the rachis; capsules almost globular, about 1.0 cm or less in length from base to apex, surface more or less tuberculate (Plate 24 F), without ribs, apex rounded; fruit dehiscence septicial splitting into 6 carpels. SEEDS oblong, 0.5 - 0.8 cm in length; caruncle moderately prominent, trapeziform (Plate 22 H and 24 H).

THE BIOLOGICAL NATURE OF MANIHOT RHOMBOIDEA GENE POOL: The species M. rhomboidea is an ideal material for a population genetic study of preservation of genetic variability within an interbreeding population achieved by maintaining several heterozygous loci in the gene pool, thus storing immense potential genetic variability for rapidly making available gene combination exhibiting high fitness to specific ecological environments occurring within the geographic range of this species. The high degree of heterozygosity is evident from the enormous phenotypic segregation occurring among the progeny in local populations. The segregating phenotypes are so different morphologically that herbarium taxonomists working without field data, designated the different types as distinct species. M. rhomboidea, M. mexicana, M. ludibunda, M. microcarpa, M. parvicocca are all species designations applied to various phenotypes of this single gene pool. Field observations carried out as a part of this study exposed the fallacy of designating the segregating phenotypes as species and confirmed the high degree of heterozygosity preserved in this gene pool. Rogers 508 is a documentary evidence of this, and this collection represents a single local colony, where phenotypes resembling M. rhomboidea, M. mexicana and M. ludibunda were present.

The dwarf shrubs of this species seem to have a relatively

shorter life cycle which could enable the population to turn out progenies at quick succession. This might be a very significant factor in enabling the population to rapidly increase the frequency of genotypes possessing maximum fitness to a given ecological niche. The monoecious inflorescence typical of the genus Manihot, with difference in the time of maturity of staminate and pistillate flowers, aids in insuring high degree of outcrossing.

The mountainous terrain of this species has numerous, ecologically variable, semi-isolated pockets in ravines, valleys, canyons, etc., and it appears that the species has developed this remarkable genetic system which is apparently ideally suited to flourish in such terrain. The overwhelming success of this genetic system is evident in what this species has been able to accomplish by way of colonizing vast expanses; the greatest, for any single species in this study. Some examples of the numerous ecologically different habitats this taxon has been able to colonize are given in the discussion of the distribution and ecology of M. rhomboidea ssp. rhomboidea.

KEY TO THE SUBSPECIES OF MANIHOT RHOMBOIDEA:

- A. Leaf lobes rhomboid, rhomboid pandurate, hastate or a combination of these 3 shapes but never gladiate (Plates 22 and 23). Staminate tepals green or with various degrees of reddish or purplish pigmentation.....11. M. rhomboidea ssp. rhomboidea
- AA. Leaf lobes gladiate with or without falcate ascending lobules near base (Plate 24). Staminate tepals totally green with no purplish or reddish tinge.....12. M. rhomboidea ssp. microcarpa

11. MANIHOT RHOMBOIDEA Muell. Arg. Subsp. RHOMBOIDEA D. J. Rogers & S. G. Appan, comb. nov.

NOMENCLATORIAL TYPE: Sesse (hb. Boiss), non vidi.

BASIONYM: Manihot rhomboidea Muell. Arg. Linnaea 3:205. 1865; in DC. Prodr. 15 (2):1064. 1866; Millspaugh, Field Mus. Publ. Bot. 1:375. 1898; Pax & Hoffmann, Pflanzenr. 44(iv.147.ii):55. 1910; Standley, Contr. U.S. Natl. Herb. 23:645. 1923; Croizat, J. Arnold Arbor. 23: 219. 1942.

HETEROTYPIC SYNONYMS:

Manihot mexicana I. M. Johnston, Contr. Gray Herb. 68:90. 1923; Croizat, J. Arnold Arbor. 23:220. 1942. Nomenclatorial type: Holotype (GH): P. Goldsmith 120 l. Isotype (US).

Manihot ludibunda Croizat, J. Arnold Arbor. 23:219. 1942. Nomenclatorial type: Holotype (NY): C. Seler & E. Seler 2814 !. Isotype (US).

ILLUSTRATIONS: Plates 22, 23, 57 and 58.

VERNACULAR NAMES: Yuca cimarrona. Steyermark 51474 (Guatemala).

DIAGNOSIS: This typical subspecies differs from the ssp. microcarpa with respect to leaf lobe outline and pigmentation of various plant parts. The median lobes are rhomboid (Plate 23 L), rhomboid pandurate (Plate 23 M), or hastate (Plate 23 K), with several combinations of these 3 forms (Plate 23 O, P & Q), also occurring, but never gladiate or gladiate with falcate basal lobules. In addition to pure greenish forms, this subspecies also has forms showing various

degrees of reddish or purplish pigmentation in several plant parts such as stems, petioles, ventral lamina surface, midribs, peduncles, pedicels, tepals of pistillate and staminate flowers, etc. The gene pool of the other subsp. microcarpa is devoid of genetic mechanisms manifesting purplish or reddish pigmentation, in most of the plant parts, especially in staminate tepals which are always totally greenish yellow.

DISTRIBUTION AND ECOLOGY: (Plates 57 & 58). MEXICO: Sinaloa, Aguascalientes, Guanajuato, Queretaro, Jalisco, Colima, Michoacan, Mexico, Morelos and Puebla. This possesses a remarkable capacity to colonize a variety of ecological habitats within an altitudinal range of about 300 - 2000 m. It has been collected from habitats such as limestone scrub land with legumes and organ pipe cacti (Plate 22 B); rough rocky mountain sides with dry shrubs including Ipomoea, Bursera, Cnidoscolus, etc.; arid hillsides with scrub forest; steep eroded ravines in gray calcareous conglomerate soil; precipitous rocky slopes in oak forest with a few pines intermixed; mountain summits amid deciduous woodland; flood plains and bluffs of wooded ravines; pasture lands among large boulders; steep treeless hills; ungrazed areas with dense grass cover, etc. It is undoubtedly the most successful taxon in this study, a rich gene pool with the versatility to adapt itself to a variety of habitats within a wide ecological amplitude.

This subspecies is sympatric over the entire range of the section Arboreae; however it occupies very specific ecological niches in contrast to the tree species of section Arboreae.

The annual rainfall of the region varies from 500 - 1000 mm. The weather data recorded at Guadalajara, Morelia, Mexico City and Puebla - stations located more or less along the southwestern border of the range of this subspecies as well as stations Guanajuato and Leon - located with the range of this subspecies are given in Table 2.

PHENOLOGY: Flowering in June - September, fruiting in July - October.

DISCUSSION: The three major phenotypic forms of the subspecies rhomboidea, the rhomboidea form (Plate 23 L), the mexicana form (Plate 23 K) and the ludibunda form (Plate 23 M) appear as three peaks in the "SKYLINE" (Plate 8), with several intermediate forms in between the peaks. In the subgraphs (Fig. 10) these three major forms can be seen to form three small clusters at a high "C-value" of .940, with several intermediate forms joined to these as "satellites" and "chains". Subsequently these three clusters are connected to each other and also with the subspecies microcarpa cluster, at a high "C-value" of .900, and soon they form a maximally connected cluster, at "level" 15 ("C-value" .891). This indicates the close phenotypic similarity between these forms. A study of the geographical distribution of these forms shows that they do not have any geographical integrity of their own, all the forms occur scattered and interspersed over the entire range of this subspecies. There are several collections where two or more of these forms are represented in the same collection, indicating that such forms grow together in the same local population. All these evidence strongly suggest that M. rhomboidea, M. mexicana, and M. ludibunda are

nothing but morphological variants; as such they have been synonymised, and the oldest name rhomboidea has been chosen to represent this subspecies.

The close phenotypic similarity of this subspecies with the other subspecies microcarpa is evident in the subgraphs (Fig. 10). However, there are few morphologic characters which consistently differentiate these two populations (described in the morphological diagnosis of these subspecies) indicating that there is only limited interbreeding between these two populations. Nevertheless these two populations do not seem to represent 2 closed gene pools. There are clear cut signs of genetic exchange between these two populations along the line where these two meet, as evident from the frequent occurrence of forms which are morphologically more or less intermediate between these two subspecies, in the region where they merge. These two populations are therefore assumed to be partially isolated segments of one single closed gene pool, and as such designated as two subspecies of one biological species.

A peculiar situation is created by a few specimens of ssp. rhomboidea, which were previously designated as M. ludibunda. These specimens grow in the middle of the geographical range of ssp. microcarpa, in a deep valley surrounded by high mountains which appear as if they are sheltering this small disjunct subset of ssp. rhomboidea population (Plate 58). These ludibunda specimens (represented in the subgraphs by K-12 and K-13) form a completely connected cluster with ssp. rhomboidea specimens (represented in the subgraphs by K-11) at a high "C-value" of .940. This and the subsequent behavior of these specimens in the subgraphs, indicate the close morphological

similarity of the ludibunda specimens to ssp. rhomboidea specimens, but they do not show such strong similarity to ssp. microcarpa. The situation looks very peculiar and unexplainable, a disjunct ssp. rhomboidea colony, situated in the midst of the domain of ssp. microcarpa, but apparently protected by mountains all around from any genetic contact with members of ssp. microcarpa. Further field studies and cytogenetic investigations would be necessary to throw more light on this.

In the subgraphs, K-1 stands out as a "satellite" at level 16 and acts as a distinct "articulator" at "level" 21. The evolutionary significance of this specimen is discussed in connection with M. angustiloba.

SPECIMENS EXAMINED: MEXICO. Sinaloa: [1] <sup>\*</sup>J. N. Rose 1608, between Rosario and Colomas, 12 July 1897, (K1 <sup>\*\*</sup> = US). Aguascalientes: [2] J. N. Rose & R. Hay 6201, near city of Aguascalientes, 20 August 1901, (K6 = F,US). Guanajuato: [3] A. Duges 8, Guanajuato, September 1903, (K3 = GH); [4] A. Duges 203, Guanajuato, 1900, (K3 = GH). Queretaro: [5] J. N. Rose & J. S. Rose 11190, near Queretaro, August 1906, (K3 = F,NY,US). Jalisco: [6] R. McVaugh 17615, ca 1 mile SW of San Juan de Los Lagos, 1 September 1958, (K10 = MICH; K-15 = MICH); [7] F. C. Weintraub & J. Roller 122, 5 miles S of

---

\* This serial number corresponds to the number representing this collection in distribution maps.

\*\* This "member" represents the cited herbarium sheets in the computer Similarity-Graph-Clustering-Analysis, the results of which are depicted in the subgraphs (Figs. 10 & 11) and the "SKYLINE" (Plate 8).

Yahualica along road to Tepatitlan, 22 July 1955, (K3 = MICH); [8] C. G. Pringle 11318, slopes of Barranca of Guadalajara, 19 July 1902, (K3 = F,US); [9] E. W. D. Holway 513, Guadalajara, 12 October 1896, (K15 = F); [10] C. G. Pringle 5159, bluffs of Baranca/near Guadalajara, 12 September 1891, (K3 = GH); [11] E. Palmer 142=156, Baranca, June - July 1886, (K3 = BM,GH,NY,US,US,US); [12] A. C. Faberge s.n., 12 miles E of Guadalajara, July 1963, (K3 = TEX 220410); [13] R. McVaugh 13298, near El Molino/ca 25 miles SW of Guadalajara, 1 October 1952, (K10 = MICH); [14] P. Goldsmith 120, hillside of Zapotlan, 1905, (K4 = GH,US); [15] R. L. Wilbur & C. R. Wilbur 1743, 10 miles S of Autlan towards La Resolana, 15 July 1949, (K7 = MICH,US); [16] R. L. Wilbur & C. R. Wilbur 2088, ca 15 miles SE of Autlan, 1 August 1949, (K14 = MICH,MICH,US). Colima: [17] R. McVaugh 15531, 10 miles SSW of Colima on Manzanillo Road, 18 July 1957, (K7 = MICH); [18] R. McVaugh 15571, 11 miles SSW of Colima on Manzanillo Road, 19 July 1957, (K9 = MICH). Michoacan: [19] Wm. C. Leavenworth & H. Hoogstraal 1548, Apatzingan/canyon below Acahuato, 14 August 1941, (K10 = F,MO); [20] Bro. G. Arsene 5272, vicinity of Morelia/Punguato, 18 August 1910, (K15 = BM,US; K3 = MO,NY); [21] Arsene s.n., Morelia, June 1912, (K3 = F 416882); [22] M. Galeotti 3734, Cordillera, 1840, (K15 = F). Mexico: [23] G. B. Hinton 6188, Acatitlan, 19 June 1934, (K4 = BM,F,NY,US); [24] G. B. Hinton 4349, Acatitlan, 21 July 1933, (K16 = BM,GH; K7 = F); [25] G. B. Hinton 940, Puerto Salitre, 2 July 1932, (K3 = BM); [26] G. B. Hinton 4220, Tenayac, 14 July 1933, (K11 = ARIZ,BM,MO,US; K3 = F); [27] G. B. Hinton 4437, Tenayac, 17 August 1933, (K9 = BM,F,US). Morelos: [28] L. A. Kenoyer s.n., Tepoztlan, 16 July 1938, (K10 = MICH -). Puebla: [29]

F. Miranda 2092, Amatitlan, 25 July 1942, (K6 = GH); [30] D. J. Rogers 508 individual sheets numbered A to I, 47 kilometers NW of Acatlan on Highway 190, 25 July 1963, (K12 = NO 508; K8 = NO 508, 508 B, 508 H, 508 I; K9 = NO 508, 508 E; K7 = NO 508 A, 508 C, 508 D, 508 G; K17 = NO 508 F); [31] G. L. Webster, K. Miller & L. Miller 13080 individual sheets numbered A to C, 29.5 miles NW of Acatlan, 18 August 1962, (K17 = NO). Unknown: [32] Sesse & Mocina 30856, W/O locality, W/O date, (K3 = F); [33] Sesse, Mocino, Castillo & Maldonado 4222, W/O locality, W/O date, (K3 = F); [34] Sesse, Mocino, Castillo & Maldonado 4218, W/O locality, W/O date, (K16 = F); [35] Sesse, Mocino, Castillo & Maldonado 4573, W/O locality, W/O date, (K16 = F); [36] Pavon Herb. 34163, W/O locality, W/O date, (K16 = F); [37] C. Jurgensen 582, Sierra San Pedro Nolasco, 1843, (K3 = BM). GUATEMALA. Huehuetenango: [38] J. A. Steyermark 51474, between Nenton and Miramar, 29 August 1942, (K13 = F); [39] I. E. Melhus & G. J. Goodman 3652, below San Antonio Huisia, 29 September 1944, (K13 = F); [40] C. Seler & E. Seler 2814, Uaxackanal, 13 July 1896, (K12 = NY,US); [41] J. A. Steyermark 50614, Cerro Pix Pix, 15 August 1942, (K9 = F).

12. MANIHOT RHOMBOIDEA Muell. Arg. Subsp. MICROCARPA (Muell. Arg.)  
D. J. Rogers and S. G. Appan, comb. nov.

NOMENCLATORIAL TYPE: Holotype (M): Karwinsky s.n. 1. Isotypes (F,G).

BASIONYM: Manihot microcarpa Muell. Arg. Flora 55:42. 1872; Pax & Hoffmann, Pflanzenr. 44(iv 147 ii):76. 1910; Croizat, J. Arnold Arbor. 23:223. 1942; McVaugh, Brittonia 13(2):191. 1961.

HETEROTYPIC SYNONYMS: Manihot parvicocca Croizat, J. Arnold Arbor. 23:219. 1942; McVaugh, Brittonia 13(2):191, 1961. Nomenclatural type: Holotype (A): E. Matuda 1665 l. Isotypes (MICH,MO,NY,US).

ILLUSTRATIONS: Plates 24, 59 and 60.

VERNACULAR NAMES: None known.

DIAGNOSIS: This subspecies differs from the typical ssp. rhomboidea with respect to leaf lobe outline and pigmentation of plant parts. This ssp. can be easily distinguished by its characteristic gladiate leaf lobes, with (Plate 24 B) or without (Plate 24 D) falcate ascending lobules near the base. The lobes are never rhomboid or rhomboid pandurate. This ssp. is also characterised by the total absence of reddish to purplish pigmentation in staminate tepals, unlike the other ssp. rhomboidea. Purplish pigmentation is also lacking in most of the other plant parts with the possible exception of stems.

DISTRIBUTION AND ECOLOGY: (Plates 59 & 60). MEXICO: Nayarit, Jalisco, Colima, Michoacan, Mexico, Guerrero, Morelos, Oaxaca and Chiapas; GUATEMALA; EL SALVADOR; HONDURAS; and NICARAGUA. Grows within 300 - 2000 m. Ecologically this subspecies is very similar to the other subspecies rhomboidea, but ssp. rhomboidea is sympatric over the entire range of section Arboreae, while ssp. microcarpa is allopatric, not overlapping the range of any Manihot species. The range of ssp. microcarpa is the longest among the taxa in this study, extending from 13° N in Nicaragua to 22° N in Nayarit, Mexico, indicating its adaptability to flourish within such a wide latitudinal range.

The annual rainfall of the region varies from 500 - 1000 mm. The weather data recorded at Guadalajara, Morelia, Mexico City and Puebla, stations located more or less along the northeastern border of the range of this subspecies, and the station Oaxaca which is within the range of this subspecies are given in Table 2.

PHENOLOGY: Flowering in April - August, fruiting in May - September. The flowering and fruiting season of this subspecies begins and ends a little earlier compared to the other subspecies rhomboidea.

DISCUSSION: The justifications for designating this population as one of the subspecies of M. rhomboidea are elaborated in the discussions of M. rhomboidea ssp. rhomboidea.

M. microcarpa and M. parvicocca are merely two morphologic variants. McVaugh (1961) recognized this and synonymized these two species. M. microcarpa forms (Plate 24 C) represented by L-1, L-2, L-3 & L-4 in the subgraphs and M. parvicocca forms (Plate 24 B) represented by L-5, L-6 & L-7, merge together and form one maximally connected cluster at a very high "C-value" of .920 indicating the close morphologic similarity between these two. A critical study of the geographical distribution of these two forms proves that independently they do not have any geographical integrity, and both the forms occur interspersed all over the range of this subspecies. The type collection of M. parvicocca (Matuda 1665) itself is an example where both these forms occur together in a single collection indicating that they are morphologic forms occurring either in the same plant, or in the same local population.

SPECIMENS EXAMINED: MEXICO. Nayarit: [1]\* C. Feddema 909, 3 miles NE of Puga, 22 August 1959, (L1 = US); [2] R. McVaugh 13386, 10 miles SE of Tepic, 6 October 1952, (L6 = MICH); [3] R. McVaugh 16580, ca 10 miles SE of Tepic, 30 August 1957, (L2 = MICH). Jalisco: [4] R. M. Zingg 10, mountains near Bolanos, 1935, (L2 = F); [5] J. N. Rose & W. Hough 4751, near Tequila, July 1899, (L2 = US); [6] E. Plamer 142=156, Rio Blanco, June - July 1886, (L1 = GH,NY); [7] R. McVaugh 18128, Puente San Pedro/5 miles SW of Tecalitlan, 22 September 1958, (L2 = MICH,US); [8] R. McVaugh 15954, ca 11 miles N of bridge of Rio Chichuatlan, 1 August 1957, (L1 = MICH). Colima: [9] R. McVaugh 15531, 10 miles SSW of Colima on Manzanillo Road, 18 July 1957, (L4 = MICH,MICH); [10] R. McVaugh 15486, ca 18 miles E of Colima at kilometers 189, 17 July 1957, (L3 = MICH). Michoacan: [11] G. B. Hinton et al 15072, Barroloso, 7 August 1939, (L1 = NA, NY,US). Mexico: [12] G. B. Hinton 4467, Ixtapan, 1 August 1933, (L2 = F; L6 = BM,GH,US). Guerrero: [13] G. B. Hinton et al 8029, Chacamero, 8 July 1935, (L2 = GH,MICH,NY,US); [14] G. B. Hinton et al 9090, Placeras Mesa, 14 July 1936, (L5 = MICH; L7 = NY,US); [15] G. B. Hinton et al 10488, Mesa Quisle, 11 July 1937, (L6 = GH,MICH,NY,UC); [16] C. L. Ryan & H. A. Floyd 11, Agua del Obispo, 10 June 1954, (L2 = TEX); [17] D. F. Herald & E. E. Clark 349, 1 mile N of Acahuiztla, 27 June 1954, (L6 = TEX). Morelos: [18] Knechtel 507, Cuernavaca, W/O date, (L1 = W); [19] E. Lyonnet 301,

\* This serial number corresponds to the number representing this collection in distribution maps.

\*\* This "member" represents the cited herbarium sheets in the computer Similarity-Graph-Clustering-Analysis, the results of which are depicted in the subgraphs (Figs. 10 & 11) and the "SKYLINE" (Plate 8).

Cuernavaca, May - June 1929, (L2 = NY,US); [20] M. Martinez 15088,  
 Cuernavaca, August 1946, (L2 = MO); [21] L. A. Kenoyer s.n., Cuen-  
 navaca, 16 July 1938, (L2 = ARIZ 70285); [22] L. A. Kenoyer s.n.,  
 Tepoztlan, 16 July 1938, (L2 = MICH -). Unknown: [23] Karwinsky  
s.n., W/O locality, W/O date, (L1 = F 683365,G -,M -); [24] Sesse,  
Mocino, Castillo & Maldonado 4224, W/O locality, W/O date, (L2 =  
 F). Oaxaca: [25] M. Galeotti 3794, Brunneis, W/O date, (L6 = F);  
 [26] M. Ghiesbreght s.n., W/O locality, 1842, (L2 = P 66 140/64).  
 Chiapas: [27] E. W. Nelson 2899, top of ridge back of Tonola, 10  
 August 1895, (L1 = GH,US); [28] E. Matuda 1665, Siltepec, 8 August  
 1937, (L1 = A,MICH,MO; L7 = NY,US); [29] E. Matuda 4392, near  
 Siltepec, 9 July 1941, (L3 = A,NY); [30] C. A. Purpus 9322, Haci-  
 enda Menserrate, September 1923, (L2 = UC); [31] C. A. Purpus  
10213, mountains near Mouserrate, May 1925, (L6 = NY,UC,US). GUA-  
 TEMALA. Huehuetenango: [32] J. A. Steyermark 50866, along Rio  
 Cuilco, 18 August 1942, (L7 = F); [33] J. A. Steyermark 50614,  
 Cerro Pix Pix, 15 August 1942, (L7 = F). El Quiche: [34] J. I.  
Aguilar 1546, W/O locality, 1942, (L2 = F). Baja Verapas: [35]  
H. Pittier 132, Cuesta de Cachil, April 1905, (L2 = NY,US). Izabal:  
 [36] C. C. Deam 6097, W/O locality, 1 June 1909, (L6 = F). EL  
 SALVADOR. Unknown: [37] S. Calderon 1023, Cerro Dela Olla, 1922,  
 (L6 = GH,NY). HONDURAS. Francisco Morazan: [38] J. V. Rodriguez  
1528, Santa Ines, 4 November 1943, (L6 = F); [39] L. O. William  
 & A. R. Molina 10116, Las Mesas, 21 July 1946, (L2 = F,MICH,MO).  
 NICARAGUA. Unknown: [40] T. Morley 745, 43 miles towards Managua,  
 1 August 1946, (L6 = F,UC,US).

13. MANIHOT SUBSPICATA D. J. Rogers & S. G. Appan, spec. nov.

NOMENCLATURAL TYPE: Holotype (NY): D. J. Rogers, S. G. Appan & R. Rogers 529. Isotypes (F,K,MEXU,MO,US,W).

HOMOTYPIC SYNONYMS:

Janipha manihot H.B.K. var. angustiloba Torrey in Emory's Rept. U.S. Mex. Bound. Surv. 2:199. 1859. Pro parte.

Manihot mexicana I. M. Johnston, Contr. Gray Herb. 68:90. 1923. Pro parte; Croizat, J. Arnold Arbor. 23:221. 1942. Pro parte.

ILLUSTRATIONS: Plates 25, 26 and 61.

VERNACULAR NAMES: Palo mulato, Edwards 411 (Nuevo Leon, Mexico)

SYNOPSIS OF GROSS MORPHOLOGY:

Frutices ca. 1 m altae, ramis laxis, glabrae; folia septemloba lobis medianibus 6.0 - 10.0 cm longibus; inflorescentia subspicato-racemosa ca. 25 cm longa; capsulae ca. 1.5 cm longae; semina ca. 1.0 cm longa.

Weak stemmed, sprawling shrubs, (Plate 25 C), about 1.0 m tall, many branched from base, branches lax, slender, irregularly zig zag (Plate 25 D), often leaning on other vegetation. ROOTS prominently swollen, penetrating 0.3-1.0 m deep, of various shapes, napiform (Plate 25 F), fusiform (Plate 25 I), or irregularly swollen (Plate 25 E); epidermis more or less smooth, dark greyish brown; subepidermis tan to white; cortex white, spongy with strong smell of HCN. Young STEMS glabrous, greenish brown; mature stems glabrous, dark greyish brown, lower stems with prominent lenticels. LEAVES alternate; stipules deciduous, glabrous, petioles terete, 5.0-10.0 cm long, rarely longer, glabrous, dark red (10 R 3/4)\* above, greenish beneath; lamina very narrowly peltate (Plate 26 Q), rarely widely peltate (Plate 26 M); dorsal and ventral lamina surfaces and midribs glabrous, abaxial surface wax pattern smooth; venation craspedodromous (Plate 26 T); palmately 7 lobed, 3 major, 2 smaller and often 2 more minute lobes (Plate 26 N); median lobes 6.0-10.0 cm long, rarely longer, hastate (Plate 26 N), the apex of the basal lobules sometimes dilated, not narrowly attenuate (Plate 26 P), terminating in a spine like point (Plate 26 T), lamina margin above the basal lobules nearly entire (Plate 26 N), sinuate (Plate 26 Q), or incised into small pointed lobulets (Plate 26 P), the apical region of median lobes often slightly dilated (Plate 26 R & S), apex acuminate, bristle pointed; lowest lobes about 1/4 as long as median lobes, attenuate (Plate 26 T). INFLORESCENCE a monoecious subspicate terminal raceme (Plate 25 G), tall and erect (Plate 25 I), about 25.0 cm in length,

---

\* Color designations used are those of the Nickerson Color Fan, Amer. Hort. Council.

the lower half of the rachis devoid of flowers, all parts glabrous; bracteoles non-foliaceous, less than 0.3 cm in length, margin smooth or serrate; bractlets non-foliaceous. PISTILLATE FLOWERS restricted to the base of the upper half of the inflorescence, borne on pedicels 1.0-2.0 cm in length with a characteristic bend downwards almost at a right angle (Plate 25 L), tepals about 1.2 cm in length, greenish yellow externally and internally, cleft to the base into 5 lobes, lobes oblong lanceolate, disc fleshy, entire, bright orange, pistil about 0.6 cm long, ovary sub-globose, yellowish green, the trifid stigma moderately lobed and lobulate, cream colored. STAMINATE FLOWERS campanulate to almost conical (Plate 26 U), more or less sessile, pedicels less than 0.5 cm in length, tepals about 1.3 cm long, reddish (5 R 4/12)\* externally, greenish white internally, cleft 1/3 way down into 5 lobes, lobes more or less tapering, moderately reflexed at anthesis (Plate 25 H), disc bright orange, 10 lobed, fleshy, stamens 10, didynamous, longer ones about 0.9 cm, shorter ones 0.7 cm, filaments and anthers cream colored. FRUIT pedicels 1.0-2.0 cm long, with a characteristic downward bend at almost a right angle (Plate 26 V); capsules about 1.5 cm long from base to apex, ovate ellipsoid (Plate 25 K), surface fairly smooth, ribs not prominent, apex rounded; fruit dehiscence septicial, splitting into 6 carpels. SEEDS oblong, about 1.0 cm long (Plate 25 J), basal and carunculate ends smoothly rounded; caruncle prominent, trapeziform.

DISTRIBUTION AND ECOLOGY: (Plate 61). MEXICO: Coahuila, Nuevo Leon and Tamaulipas; along eastern slopes of Sierra Madre Oriental. Usually growing at about 200-700 m, but towards the southern end of its

geographical range the species grows in low lands in the coastal plains, adjacent to or possibly slightly overlapping the range of M. Walkerae.

This species characteristically grows close to and in the shade of other shrubs, thus protected by the taller shrubs. The savannah type habitat supports tall shrubs and medium sized trees such as Cordia boissieri, lechuguilla, thorny legumes, etc. This species is a relatively infrequent member of the vegetation. Towards the southern extremity of the range it grows in prairies with very shallow reddish sandy loam, amidst low Calliandra shrubbery and scattered mottes of taller brush. Usually grows in limestone based, loose and rocky soil. Like many other Manihot species this exhibits the potential to colonize disturbed areas, such as in soil dumped after road construction, eroded ravines etc.

The area receives a very low mean annual rainfall of 300-500 mm. The weather data of two stations within the range of this species, Monclova and Monterrey, are given in Table 2.

PHENOLOGY: Flowering in April - September; fruiting in June - September.

DISCUSSION: This species was confused in the past with M. mexicana. As clarified in this study, M. mexicana is merely one of the morphologic variants of M. rhomboidea ssp. rhomboidea. The range of M. subspicata is widely disjunct from the range of M. rhomboidea ssp. rhomboidea, and consequently there is little likelihood of interbreeding. This disjunct population is therefore assumed to be a closed gene pool and as such described as a new species. The specific

epithet is for the characteristic subspicate inflorescence.

The subgraphs (Fig. 10) present interesting indications of the direction of the affinities of this new species. At "level" 16 the M. subspicata cluster is connected to M. rhomboidea cluster. The number of connections progressively increases, but all the connections are only with the mexicana forms of M. rhomboidea ssp. rhomboidea. Biosystematic studies would confirm the possibilities of a segment of the M. rhomboidea gene pool, possibly the mexicana gene combinations, deviating towards north and evolving into this new closed gene pool - M. subspicata.

At "level" 25 M. Walkerae joins M. subspicata. Several connections are made through "level" 27, all of them being only with M. subspicata. In as much as M. Walkerae shows no affinity to any taxa other than M. subspicata, even at a low "C-value" of .729, M. subspicata represents the only likely ancestor to M. Walkerae. Comparative studies of chromosome morphology and other cytogenetic investigations, would throw light on the phylogenetic relationship between these two taxa. The southern end of the geographical range of M. subspicata is adjoining or possibly slightly overlapping the range of M. Walkerae. This might be an ideal place to look for material for cytogenetic studies.

SPECIMENS EXAMINED: MEXICO. Coahuila: [1]<sup>\*</sup> E. G. Marsh 1163,

---

\* This serial number corresponds to the number representing this Collection in distribution maps.

Muzquiz, April 1938, (M4\*\* = F,TEX). Nuevo Leon: [2] M. T. Edwards 411, Rancho Resendes/Lampazos, 29 June 1937, (M2 = F,MO,TEX). Tamaulipas: [3] H. Lesueur 246, mountains W of Bustamante, August 1938, (M2 = ARIZ,F,TEX). Nuevo Leon: [4] D. J. Rogers, S. G. Appan & R. Rogers 525, Mamulique Pass; just off old highway Milestone 1051, 18 June 1968, (M1 = NO); [5] D. J. Rogers, S. G. Appan & R. Rogers 526, summit of Mamulique Pass; 38 miles N of Monterrey, 19 June 1968, (M6 = NO); [6] J. Crutchfield & M. C. Johnston 5460 A, Mamulique Pass/23 miles S of Sabinas Hidalgo, 4 May 1960, (M3 = TEX); [7] A. E. Perkins & J. M. Hall 3565, Nuevo Leon/road from Monterrey to Nuevo Laredo, 12 April 1939, (M2 = F); [8] J. Gregg 198, Monterrey, 24 June 1848, (M2 = MO). Tamaulipas: [9] J. Crutchfield & M. C. Johnston 5523, 16 miles E of San Fernando-Santander Jiminez highway on road to Lareto, 15 September 1960, (M2 = TEX); [10] D. J. Rogers, S. G. Appan & R. Rogers 529, ca 5 miles E of Casas; 33 miles E of Ciudad Victoria, 21 June 1968, (M1 = NO); [11] J. Crutchfield & M. C. Johnston 5784 E, 5 miles E of Casason Victoria-Sotolamarina highway, 28 September 1960, (M2 = TEX); [12] L. A. Kenoyer C 142, S of Victoria, 14 August 1940, (M2 = GH); [13] D. J. Rogers, S. G. Appan & R. Rogers 533, 26 miles S of Ciudad Victoria, 26 June 1968, (M5 = NO); [14] J. Graham & M. C. Johnston 4721 B, 26 miles S of Victoria, 15 November 1959, (M4 = TEX); [15] H. H. Bartlett 10613, summit of Cerro de La Tamaulipeca, 26 July 1930, (M2 = MICH); [16] H. H. Bartlett 13695, summit of Cerro de La Tamaulipeca, 4 July 1931, (M2 = MICH,MICH).

---

\*\* This "member" represents the cited herbarium sheets in the computer Similarity-Graph-Clustering-Analysis, the results of which are depicted in the subgraphs (Figs. 10 & 11) and the "SKYLINE" (Plate 8).

14. MANIHOT WALKERAE Croizat, Bull. Torrey Bot. Club 69:452-457.  
1942.

NOMENCLATRURAL TYPE: Holotype (A): E. J. Walker (E. J. Parks) s.n. 1.  
Isotypes (A,A).

ILLUSTRATIONS: Plates 27, 28 and 62.

VERNACULAR NAMES: None Known.

SYNOPSIS OF GROSS MORPHOLOGY: Decumbent shrubs (Plate 27 A), about 0.5 m tall, profusely branching, branches slender, prostrate, long, weak (Plate 28 I). ROOTS prominently enlarged, carrot shaped, about 10.0 cm long; epidermis very dark brown, rough with bands of laterally oriented corky strips; cortex white with strong smell of HCN; tuberous roots reported to possess adventitious buds (used as propagating material, Walker 1003). Young STEMS glabrous, greenish brown; mature stems glabrous, greyish brown. LEAVES alternate; stipules setaceous, deciduous, glabrous; petioles slender, firm usually 7.0-10.0 cm long, glabrous, terete, ventral surface dark dull red, dorsal surface greenish; lamina widely peltate (Plate 28 M), over 0.5 cm wide at the region between the petiole attachment point and the lamina margin at the base of the leaf, ventral lamina deep green, dorsal lamina markedly glaucescent, abaxial surface wax pattern smooth; venation craspedodromous (Plate 28 K); palmately 5 lobed, 3 major and 2 smaller lobes (Plate 28 K); median lobes ovate-ellipsoid to more or less parabolical, pandurate (Plate 28 J), rarely entire lobed (Plate 28 L), usually 5.0-10.0 cm long, the basal lobule apex abruptly dilated, cuspidate, terminating in a spine-like point, an extension of a vein

(Plate 28 O), lamina margin above and below the basal lobule incised, often deeply, into lobulets which also terminate in spine-like extensions of veins (Plate 28 J), apex acute to acuminate; the sinuses on either side of the median lobe with a characteristically flat base forming an almost  $45^\circ$  angle to the median lobe mid rib (Plate 28 K); lowest lobes about half as long as median lobes, apex cuspidate. INFLORESCENCE a monoecious, axillary, subspicate, raceme (Plate 27 C), 5.0-10.0 cm long, all parts glabrous; bracteoles non-foliaceous, less than 0.3 cm long, glabrous, margin serrate; bractlets non-foliaceous glabrous. PISTILLATE FLOWERS restricted to the very base of the inflorescence, borne on (about 1.5 cm long) pedicels which appear as if attached directly to the stem and dissociated from the inflorescence per se (Plate 27 E), tepals about 1.1 cm long, light purplish streaked externally, cleft to the base into 5 lobes, lobes oblong lanceolate, disc fleshy, entire, several staminodes present around the disc, pistil about 0.6 cm long, ovary sub-globose, the trifold stigma well lobed and lobulate. STAMINATE FLOWERS almost tubular (Plate 27 C), distinctly constricted in the middle, tepals about 1.2 cm long, light purplish streaked externally (Plate 27 B), cleft  $1/3$  of the way down into 5 lobes, lobes oblong, tapering, not prominently reflexed at anthesis, disc fleshy, 5 lobed, stamens 6-10 (6, 7 and 8 observed, 10 reported in original description), superior whorl about 0.9 cm long, inferior whorl about 0.7 cm long, filaments and anthers cream colored. FRUIT pedicels slightly curved downwards about 1.5 cm long, pistillate pedicels being attached to the very base of the inflorescence the fruits appear as if connected directly to the stem (Plate 27 F); capsules almost globular, about 1.0 cm

long from base to apex, surface sparingly but manifestly verruculose and rugose, ribs not prominent; fruit dehiscence septicial splitting into 6 carpels. SEEDS rotund (Plate 27 H), about 0.8 cm long; caruncle very prominent (Plate 27 G), large in comparison to seed size, about 0.2 cm long and about 0.4 cm broad, cream colored, slightly cleft and 2 lipped in front.

DISTRIBUTION AND ECOLOGY: (Plate 62). USA: Texas; MEXICO: Tamaulipas; flourishing in the lowland coastal plains on sandy loam prairies, growing up through protective thorn shrubs. Towards the southern extremity of the range this species appears to be adjacent or possibly slightly overlapping the range of *M. subspicata*.

The area receives a fairly well distributed rainfall of about 600 mm per year. The weather data of Brownsville, a station within the geographical range of this species, are given in Table 2. Introduced plants have formed a self sustaining colony at the University of Texas at Austin, which is 30° N, with mean temperature as low as 7° C in January. The plants prefer lime based alkaline soils.

PHENOLOGY: Flowering in April - September; fruiting in July - September.

DISCUSSION: This is a very distinct species forming a completely connected cluster (Fig. 10) at a very high "C-value" of .940, and thereafter, on account of an enormous moat, stays distinct till a low "C-value" of .734 when it is connected to *M. subspicata*. *M. Walkerae* shows no affinity to any other taxa till a very low "C-value" of .734 ("level" 25), and at this level it forms several

connections, all of them with M. subspicata. These subgraph indications and the geographical distribution patterns are strongly suggestive of M. Walkerae population possibly evolving as an offshoot of M. subspicata, diverging towards the north and developing into an independent closed gene pool.

In the original description of this species Croizat cites M. carthagenensis Muell. Arg. and Janipha loeflingii Torrey as synonyms of M. Walkerae. They are misidentifications and not synonyms.

SPECIMENS EXAMINED: USA. Texas: [1]<sup>\*</sup> D. J. Rogers 522, University of Texas/Austin, 31 August 1967, (N3<sup>\*\*</sup> = NO); [2] B. H. Wornock & P. A. Barkley 147, University of Texas campus, 7 June 1943, (N2 = MO,UC,US); [3] E. J. Walker 1003, La Joya, April 1940, (N2 = GH); [4] H. B. Parks s.n., Mission, 1940, (N2 = A -, A -, A -, A -); [5] A. Schott 52, Ringgold Barracks/Bravo del Norte, 2 June 1853, (N2 = F,F,NY,NY). MEXICO. Tamaulipas: [6] C. G. Pringle 2243, near Matamoros, 31 July 1888, (N1 = GH); [7] M. C. Johnston 5363 B, Rancho Loreto, 26 April 1960, (N2 = TEX); [8] J. Crutchfield & M. C. Johnston 5572 B, Papalote de Mirandena, 16 September 1960, (N2 = TEX).

---

\* This serial number corresponds to the number representing this collection in distribution maps.

\*\* This "member" represents the cited herbarium sheets in the computer Similarity-Graph-Clustering-Analysis, the results of which are depicted in the subgraphs (Figs. 10 & 11) and the "SKYLINE" (Plate 8).

Section 2. ARBOREAE D. J. Rogers & S. G. Appan, sect. nov.

DIAGNOSIS:

Arbores, pubescentes; capsulae grandes, plus 1.75 cm longa;  
semina grandia plus 1.5 cm longa.

Trees, as tall as 10.0 m. Many plant parts such as, stems, petioles, lamina, midribs, peduncles and pedicels of inflorescence, in some cases even tepals and ovaries are pubescent, in contrast to the almost total absence of pubescence in plant parts of section Fruticosae. FRUITS large, more than 1.75 cm long from base to apex. SEEDS large, more than 1.5 cm long, caruncle not prominent in contrast to the seed size.

DISTRIBUTION AND ECOLOGY: This section flourishes in the central region of Mexico (Plate 6), in the midst of the domain of section Fruticosae. Ecologically the species of this section (except M. tomatophylla) seem to be adapted to flourish at higher altitudes in the approximate range of 500 - 2000 m, as members of forest type of vegetation.

DISCUSSION: Conforming to the general trend among seed plants, the tree species of this section have larger fruits and seeds. The weather data recorded at stations within or near the domain of this section viz., Guadalajara, Guanajuato and Morelia (Table 2) indicate that the region receives an annual rainfall of about 1000 mm. The precipitation/evaporation ratio of the domain would be more than 1

for supporting the forest type of vegetation.

The subgraphs (Fig. 11) indicate that the populations representing the species of this section are homogeneous showing very little intraspecific phenotypic variation, their individual domain is also relatively smaller. This would seem to indicate that many of the species of section Fruticosae showing considerable intraspecific phenotypic variation and ability to flourish over widespread areas are more successful than species of section Arboreae. If the evolutionary patterns of genus Manihot are not exceptional to the general trends among angiosperms, the species of section Arboreae being trees tend to be more primitive than the species of section Fruticosae. The distribution pattern would tend to support such a contention.

KEY TO THE SPECIES OF SECTION ARBOREAE:

- A. Leaves with more than 3 lobes (Plate 29 D); capsules sub-globose (Plate 29 G); inflorescence a panicle (Plate 29 B), (M. tomatophylla and M. Websteriae inflorescences not seen).
- B. Petiole attachment peltate; bases of leaf lobes more than 0.25 cm across; lamina not deeply cleft, lamina more than 0.5 cm wide from base of sinus to petiole attachment point; leaf lobes obovate (Plate 29 F) or obovate pandurate (Plate 31 D); fruit pedicels more than 1.0 cm long; seeds oblong (Plate 31 I).
- C. Leaf lobes entire, never pandurate; fruit dehiscence septicial.
- D. Leaf apices prominently caudate (Plate 29 F); petioles, peduncles, pedicels, bracteoles and bractlets glabrous; lenticels on mature stem dense and pronounced.....15. M. CAUDATA
- DD. Leaf apices acute (Plate 30 D); petioles, peduncles, pedicels, bracteoles and bractlets sparsely pubescent; lenticels on mature stem sparse and not pronounced.....16. M. MICHAELIS
- CC. Leaf lobes pandurate (Plate 31 C); fruit dehiscence loculicidal.....17. M. TOMATOPHYLLA

- BB. Petiole attachment basal; bases of leaf lobes less than 0.25 cm across (Plate 32 A); lamina very deeply cleft, lamina less than 0.5 cm wide from base of sinus to petiole attachment point; leaf lobes oblong (Plate 32 A); fruit pedicels less than 1.0 cm long (Plate 32 B); seeds rotund (Plate 32 C).....  
.....18. M. WEBSTERAE
- AA. Leaves constantly 3 lobed (Plate 33 A); capsules conical, distal end tapering (Plate 34 E); inflorescence a raceme (Plate 34 D).
- E. Ovary tomentose.....19. M. FOETIDA
- EE. Ovary glabrous.....20. M. CRASSISEPALA

15. MANIHOT CAUDATA Greenman, Proc. Amer. Acad. 39:82. 1903.

NOMENCLATURE TYPE: Syntypes: C. G. Pringle 8687 ! (F,F,GH,MO,NY,UC, US,W) and E. Palmer 201 ! (US).

ILLUSTRATIONS: Plates 29, 63, 64 and 65.

VERNACULAR NAMES: None known.

SYNOPSIS OF GROSS MORPHOLOGY: Trees, about 10.0 m tall, the main trunk with a diameter of about 30.0 cm supporting an umbrella-like spreading, thick foliated canopy (Plate 29 A); branches usually bearing foliage at the summits; trunk covered with greyish brown cortex. Young STEMS light reddish brown, shiny, sparsely pubescent; mature stems glabrous, reddish brown, epidermis peeling off. Young foliage at apex strong yellow green (5 GY 6/8)\*. LEAVES alternate; stipules deciduous, sparsely pubescent; petioles generally about 15.0 cm long, glaucous, terete, occasionally very slightly canaliculate, dark red (2.5 R 3/7)\*; lamina narrowly peltate, ventral surface dark green (5 G 3/4)\*, abaxial surface wax pattern finely farinose; venation camptodromous; palmately 5 lobed, 3 major and 2 smaller lobes, (Plate 29 D); median lobes obovate entire (Plate 29 F), usually about 13.0 cm long. 6.0 cm wide, occasionally as long as 25.0 cm and as wide as 10.0 cm, apex abruptly caudate-acuminate, terminating in a bristle which is occasionally as long as 2.0 cm; lowest lobes slightly smaller than median lobes, conspicuously non-symmetric, curved up. INFLORESCENCE a monoecious, axillary panicle, usually many branched, 15.0 -

---

\* Color designations used are those of the Nickerson Color Fan, Amer. Hort. Counc.

25.0 cm long; peduncles, pedicels and young buds coated with ashy-blue glaucescence; bracteoles non-foliaceous (Plate 29 B), occasionally semi-foliaceous and as long as 4.0 cm (Plate 29 C), glaucous, margin smooth; bractlets non-foliaceous, glaucous. PISTILLATE FLOWERS restricted to the base of the inflorescence, borne on 2.0 - 4.0 cm long pedicels, tepals about 1.4 cm long, greenish yellow, often glaucous externally, cleft down to base into 5 lobes, lobes oblong-lanceolate, tapering, disc prominent, fleshy, entire, staminodes often present around the disc, pistil about 0.9 cm long, ovary sub-globose to slightly elongated, the trifid stigma moderately lobed and lobulate. STAMINATE FLOWERS companulate, tepals greenish yellow, often glaucous, about 1.6 cm long, cleft 1/3 way down into 5 lobes, lobes oblong-obtuse, not prominently reflexed at anthesis, disc fleshy shallowly 10 lobed, stamens 10, didynamous, superior whorl about 1.1 cm long, inferior whorl about 0.9 cm long, filaments and anthers pale yellowish. FRUIT pedicels 2.0 - 4.0 cm long, almost straight; capsules ovate-ellipsoid, about 2.25 cm long (Plate 29 G) from base to apex, surface very slightly rugose, glaucous, perceptibly 6 ribbed, apex slightly pointed; fruit dehiscence septicidal, splitting into 6 carpels. SEEDS oblong, about 1.5 cm long, flattened and conspicuously ribbed along the lateral edges (Plate 29 H); caruncle not prominent (Plate 29 I).

DISTRIBUTION AND ECOLOGY: (Plates 63-65). MEXICO: Michoacan, Guanajuato, Zacatecas and doubtfully in Chihuahua. Abundant on the rocky slopes above the south shore of Lake Chapala (Plate 29 A), at about 1500 m; in the volcanic hills near Monte Leon, west of Lake Chapala; and also towards the north in Guanajuato and Zacatecas.

Palmer 201, cited as a syntype is reported to have been collected from Chihuahua. It seems unlikely that the range of this species extends all the way north to Chihuahua, however, there is a close phenotypic affinity (indicated by the subgraphs) between M. caudata and the two species growing in Chihuahua, M. Davisiae and M. isoloba. Further field studies would be necessary to delimit the complete range of this species.

The area receives a mean annual rainfall of about 1000 mm. The weather data of one station located within or near the range of this species, Guadalajara, are given in Table 2.

PHENOLOGY: Flowering in June - July; fruiting in June - August.

DISCUSSION: This species forms a homogeneous cluster in the subgraphs (Fig. 11), at a very high "C-value" of .918. At "level" 19 it is connected to M. michaelis, at "level" 24 M. tomatophylla joins M. caudata, and at "level" 26 all the three species form a maximally connected cluster. These three species have adjoining ranges, and their close phenotypic affinity is clearly reflected in the subgraphs. M. michaelis and M. tomatophylla seem to be very narrowly localized, while M. caudata has spread over a large area. Evidently M. caudata is the most successful species among these three. The fact that this species is being used as fence row plants (Rogers 509; McVaugh 15037) is a proof of its adaptation to easy propagation, rapid establishment, ability to withstand adverse conditions and also to resist insect and disease infestation. These are qualities worth investigating from a plant breeding point of view.

M. caudata is the primary species linking section Arboreae

with section Fruticosae. At "level" 28 (Fig. 11) there are several connections between M. caudata and the two species in section Fruticosae - M. Davisiae and M. isoloba; indicating that M. caudata is the closest member of section Arboreae to section Fruticosae. There is a striking similarity in the ecological adaptations of M. caudata and the two species of section Fruticosae - M. Davisiae and M. isoloba. The latter two are adapted to higher altitudes unlike most of the other species in section Fruticosae. High altitude habitat is a quality shared by almost all the species in section Arboreae.

The subgraph connection of M. caudata with I-1 (representing the entire lobed forms of M. Davisiae) as well as with M. isoloba at "level" 28 (Fig. 11) further supports what has been already discussed in connection with M. Davisiae, that I-1 represents a very critical subset of the M. Davisiae gene pool, from an evolutionary point of view.

Though the distribution map depicts M. caudata to be sympatric with M. rhomboidea ssp. rhomboidea, there is no doubt that these two represent very distinct gene pools. M. rhomboidea ssp. rhomboidea being a very short sprawling shrub, occupies quite a different ecological niche than the tree species M. caudata. The subgraphs show absolutely no affinity between these two taxa.

SPECIMENS EXAMINED: MEXICO. Michoacan: [1] <sup>\*</sup>D. J. Rogers 509, S

---

\* This serial number corresponds to the number representing this collection in distribution maps.

shore of Lago Chapala, 28 July 1963, (O1\*\* = NO); [2] R. McVaugh 15037, S shore of Lake Chapala/5 miles E of Jalisco Line, 24 June 1957, (O3 = MICH,MICH); [3] C. G. Pringle 8687, Volcanic Hills/Monte Leon, 21 August 1902, (O2 = F,F,GH,MO,NY,UC,US; O3 = W). Guanajuato: [4] H. H. Rusby 178, Empalme de Gonzales/Guanajuato, 18 June 1910, (O2 = NY,US). Zacatecas: [5] J. N. Rose 2499, San Juan Capistrano, August 1897, (O2 = GH). Chihuahua: [6] E. Palmer 201, SW Chihuahua, 1885, (O2 = US).

---

\*\* This "member" represents the cited herbarium sheets in the computer Similarity-Graph-Clustering-Analysis, the results of which are depicted in the subgraphs (Figs. 10 & 11) and the "SKYLINE" (Plate 8).

16. MANIHOT MICHAELIS McVaugh, Brittonia 13:190. 1961.

NOMENCLATURE TYPE: Holotype (MICH): R. McVaugh 15502 1.

ILLUSTRATIONS: Plates 30 and 66.

VERNACULAR NAMES: None known.

SYNOPSIS OF GROSS MORPHOLOGY: Trees, about 10.0 m tall (Plate 30 A), trunk diameter at base about 20.0 cm, frequently branched above the middle from a single trunk, branches usually ascending, sometimes reclining. ROOTS not prominently swollen (Jancey 331); epidermis rough, brownish grey; subepidermis creamy white. Young STEMS pubescent, light reddish brown; mature stems sparsely pubescent, reddish brown to greyish brown, internally creamy white. LEAVES alternate, stipules deciduous, sparsely pubescent; petioles generally about 15.0 cm long, occasionally longer, terete, green, occasionally reddish, sparsely pubescent; lamina narrowly peltate, ventral surface green (2.5 G 5/9)\*, glabrous, dorsal surface glaucous, light green (7.5 G 8/6)\*, abaxial surface wax pattern finely farinose; venation camptodromous; palmately 5 lobed, 3 major and 2 smaller lobes (Plate 30 C); median lobes obovate, entire (Plate 30 D), generally about 12.0 cm long, about 5.0 cm wide, juvenile plants have much larger foliage, apex acute; lowest lobes slightly smaller than median lobes, conspicuously non-symmetric, curved up. INFLORESCENCE a monoecious axillary panicle, sparsely branched (Plate 30 E), about 10.0 cm long; peduncles

---

\* Color designations used are those of the Nickerson Color Fan, Amer. Hort. Council.

and pedicels sparsely pubescent; bracteoles greenish white, non-foliaceous, sparsely pubescent; bractlets non-foliaceous, sparsely pubescent. PISTILLATE FLOWERS restricted to the base of the inflorescence, borne on pedicels 2.4 - 4.0 cm long, tepals about 1.1 cm long, yellowish green, cleft down to base into 5 lobes, lobes oblong lanceolate, disc fleshy, entire, pistile about 0.6 cm long, ovary sub-globose, glabrous, the trifid stigma moderately lobed and lobulate. STAMINATE FLOWERS campanulate (Plate 30 F), tepals about 1.2 cm long, yellowish green, cleft 1/3 way down into 5 lobes, lobes oblong obtuse, disc fleshy, 10 lobed, stamens 10, didynamous, the superior whorl about 0.8 cm long, the inferior whorl about 0.7 cm long, filaments and anthers cream colored. FRUIT pedicels 2.4 - 4.0 cm long, almost straight (Plate 30 G); capsules ovate-ellipsoid, about 2.0 cm long (Plate 30 H) from base to apex, surface more or less smooth, often glaucous, perceptibly 6 ribbed, apex slightly pointed; fruit dehiscence septicidal, splitting into 6 carpels. SEEDS oblong, about 1.5 cm long, flattened and conspicuously ribbed along the lateral edges, caruncle not prominent.

DISTRIBUTION AND ECOLOGY: (Plate 66). MEXICO: Colima and Jalisco.

As far as known, this species is narrowly localized in the region around Colima city, growing at about 300 - 1750 m, in flood plains (Plate 30 B) and bluffs of wooded ravines (Plate 30 A), on both sides of Rio Tuxpan, Rio de Colima, and Rio de Armenia, the vegetation including Astronium, Brosimum, etc.

The weather data of the station nearest to the range of this species, Manzanillo, are given in Table 2.

PHENOLOGY: Flowering in July; fruiting in July.

DISCUSSION: In the subgraphs (Fig. 11), the cluster representing this species is connected to M. caudata at "level" 19, and both together form a maximally connected cluster at "level" 21, indicating the close similarity of these two taxa. At "level" 27 M. Websterae is connected to M. michaelis. This phenotypic affinity between M. Websterae and M. michaelis signifies the possibility of the ranges of these 2 species delineated in this study, being incomplete, and most likely to be extending towards each other.

When the 2 sections of Manihot join together at "level" 28 (Fig. 11), there are inter-sectional connections between M. caudata and M. tomatophylla, but M. michaelis stays apart without any connections to section Fruticosae. This indicates that M. michaelis is very likely to be the youngest taxon of the three, possibly having originated from gene combinations drawn from the existing gene pool of M. caudata or ancestral to it.

SPECIMENS EXAMINED: MEXICO. Colima: [1] R. C. Jancey 330, near summit of first mountain pass W of Colima, July 1965, (P2<sup>\*\*</sup> = NO); [2] R. C. Jancey 331, near summit of mountain pass/12 miles W of Colima, July 1965, (P2 = NO); [3] R. C. Jancey 332, near summit of mountain pass/12 miles W of Colima, July 1965, (P2 = NO); [4] R. C. Jancey 333, near summit of mountain pass/12 miles W of Colima, July 1965, (P2 = NO); [5] M. E. Jones 127, Colima, 2 July 1892, (P2 =

---

\* This serial number corresponds to the number representing this collection in distribution maps.

\*\* This "member" represents the cited herbarium sheets in the computer Similarity-Graph-Clustering-Analysis, the results of which are depicted in the subgraphs (Figs. 10 & 11) and the "SKYLINE" (Plate 8).

POM); [6] D. J. Rogers 513, 30 kilometers E of Colima, 30 July 1963, (P1 = NO); [7] R. McVaugh 15502, 18 miles E of Colima/near Rio Tuxpan bridge, 17 July 1957, (P2 = MICH). Jalisco: [8] D. J. Rogers 514, 32 kilometers E of Colima, 31 July 1963, (P1 = NO).

17. MANIHOT TOMATOPHYLLA Standley, Amer. Midl. Naturalist 36:178.  
1946.

NOMENCLATURE TYPE: Holotype (F): Wm. C. Leavenworth & H. Hoogstraal  
1402 l. Isotypes: (F, MICH, MO, NY).

ILLUSTRATIONS: Plates 31 and 67.

VERNACULAR NAMES: None known.

SYNOPSIS OF GROSS MORPHOLOGY: Trees, about 10.0 m tall (Plate 31 A), trunk diameter at base about 30.0 cm (Plate 31 B), successive dichotomous and trichotomous branching beginning at a height of about 1.5 m, branches many, erect, forming a more or less obovate crown supported by a main trunk, latex present. ROOTS not seen. Young STEMS glabrous, greyish brown with reddish tinge; mature stems glabrous, reddish brown, usually with white dot-like lenticels, bark on older stems light grey to silvery grey, warty. LEAVES alternate; stipules deciduous, glabrous; petioles about 15.0 cm long, occasionally longer, terete, sometimes slightly canaliculate, glabrous, bright red; lamina narrowly peltate, ventral surface deep green, glabrous, dorsal surface with distinct ashy-blue glaucescence, abaxial surface wax pattern finely farinose; venation camptodromous; palmately 5-7 lobed, 3 major, 2 slightly smaller and often 2 more smaller lobes (Plate 31 F); median lobes obovate pandurate (Plate 31 D), about 13.0 cm long, about 4.0 cm wide, primary constriction short (Plate 31 E), to as long as about 4.0 cm (Plate 31 C), margin within the constriction usually rounded without any secondary constrictions, apex obtuse to truncate, mucronate; lowest lobes in case of 5 lobed leaves -

slightly smaller than median lobes, conspicuously non-symmetric, curved up, in case of 7 lobed leaves - about 1/4 as long as median lobes, obtuse. INFLORESCENCE not seen. FRUIT pedicels 2.0 - 5.0 cm long, more or less straight (Plate 31 G), glaucous; capsules fleshy, ovate ellipsoid, about 2.5 cm long from base to apex, prominently 6 ribbed (Plate 31 H), ribs wavy, platelike, usually with a sharp edge, fruit surface prominently verruculose, glaucous, apex pointed; dehiscence loculicidal, splitting into 3 parts, the 3 commissural sutures not disjoining. SEEDS oblong, about 1.75 cm long (Plate 31 I & J), carunculate end acutely pointed, ventral surface with a prominent furrow along the middle, lateral edges prominently ribbed, surface shiny, brownish orange with fine black mottlings; caruncle not prominent, very small in contrast to the seed size.

DISTRIBUTION AND ECOLOGY: (Plate 67). MEXICO: Michoacan. As far as known, narrowly localized in the region of Apatzingan, growing at about 400 m and less. Grows on edges of dry canyons, on banks of dry arroyos, on low hills supporting sparse woodlands comprising Cordia, Amphipterygium, Cercidium, Caesalpinia platyloba, etc. (Plate 31 A & B).

Rainfall data of the habitat - not available.

PHENOLOGY: Flowering - no data; fruiting in August - September.

DISCUSSION: This distinct species with characteristic leaves having truncate lobe apices, forms a homogeneous cluster in the subgraphs (Fig. 11), at a very high "C-value" of .918, and stays inactive with a significant "moat", till a low "C-value" of .755 when it joins

M. caudata cluster.

M. tomatophylla is one of the 2 species linking the two sections of Manihot at "level" 28 in the subgraphs (Fig. 11), by establishing a connection with M. chlorosticta. In the Apatzingan region the geographical ranges of these 2 species are adjoining or slightly overlapping. Among the species of section Arboreae, M. tomatophylla is the only lowland species, all the others are growing at higher elevations, and as such, the phenotypic similarity between M. tomatophylla and M. chlorosticta, coincides with their similarities in the ecological adaptations also.

SPECIMENS EXAMINED: MEXICO. Michoacan: [1] R. McVaugh 17951, between San Juan de Los Platanos and Amatlan, 17 September 1958, (Q2\*\* = MICH,US); [2] D. J. Rogers 516, 6 kilometers W of Apatzingan, 1 August 1963, (Q2 = NO); [3] Wm. C. Leavenworth & H. Hoogstraal 1402, Tancitaro region/Apatzingan/near La Majada, 9 August 1941, (Q2 = F,F,MICH,MO,NY); [4] D. J. Rogers 517, ca 5 miles N of Nueva Italia, 1 August 1963, (Q2 = NO).

---

\* This serial number corresponds to the number representing this collection in distribution maps.

\*\* This "member" represents the cited herbarium sheets in the computer Similarity-Graph-Clustering-Analysis, the results of which are depicted in the subgraphs (Figs. 10 & 11) and the "SKYLINE" (Plate 8).

18. MANIHOT WEBSTERAE D. J. Rogers & S. G. Appan, spec. nov.

NOMENCLATURE TYPE: Holotype (DAV): G. L. Webster, K. Miller & L. Miller 13074. Isotype (PUL).

ILLUSTRATIONS: Plates 32 and 68.

VERNACULAR NAMES: None known.

SYNOPSIS OF GROSS MORPHOLOGY:

Arbores ca. 5.0 m alti, pubescentes; folia penta- vel septemloba lobis medianibus ca. 11.0 cm longibus, ca. 3.0 cm latibus; inflorescentia non visa; capsulae ca. 2.25 cm longae; semina ca. 1.5 cm longa.

Trees, about 5.0 m tall. ROOTS not seen. Young STEMS light reddish brown, pubescent; mature stems dark reddish brown, pubescent. LEAVES alternate; stipules deciduous, pubescent; petioles about 10.0 cm long, terete, sometimes slightly canaliculate, pubescent; lamina

non-peltate, ventral surface green, sparsely pubescent, dorsal surface light green, sparsely pubescent, abaxial surface wax pattern smooth; venation camptodromous, midribs dorsal and ventral sides sparsely pubescent; palmately 5-7 lobed (Plate 32 A); median lobes about 11.0 cm long, about 3.0 cm wide, oblong-obovate, broadest at about 2/3 way up from the base, tapering into an acuminate apex, terminating in a bristle about 0.75 cm long, lamina margin entire, base of lobe narrowly constricted, less than 0.25 cm across, sinuses in between lobes very deep, lamina between the base of sinuses and petiole attachment point less than 0.5 cm wide; lowest lobes slightly smaller than and more or less similar in shape to median lobe. INFLORESCENCE not seen. FRUIT pedicels very short, less than 1.0 cm long, almost straight; capsules globose, about 2.25 cm long (Plate 32 B) from base to apex, surface glaucous green, slightly tuberculate, ribs not prominent, apex rounded; fruit dehiscence septicial, splitting into 6 carpels. SEEDS oblong (Plate 32 C & D), about 1.5 cm long, carunculate end acutely pointed, ventral side with a prominent ridge along the middle, surface not shiny, sometime warty, light brownish orange, with fine black mottlings, caruncle very small, practically absent.

DISTRIBUTION AND ECOLOGY: (Plate 68). MEXICO: Puebla, in the region of Izucar de Matamoros, at about 1500 m, on limestone hills. Weather data of the station nearest to the range of this species, Mexico City, are given in Table 2.

PHENOLOGY: Flowering - no data; fruiting in August.

DISCUSSION: The single collection representing this species is phenotypically very distinct from all the other taxa. In the subgraphs (Fig. 11), M. Websterae cluster remains apart till as low a "C-value" as .714 ("level" 27), when it joins M. michaelis and subsequently with M. caudata. Such marked phenotypic distinctness practically rules out any possibility of this specimen being anything other than a population sample representing an undescribed closed gene pool. Further field studies are needed to outline its geographic range boundaries and ecological adaptations and limits. It should be expected that the domain of this species is larger than is shown in Plate 7, probably extending towards the range of M. michaelis. M. Websterae plants should be looked for in the region between Matamoros and Colima. This species can be easily distinguished from its close relatives M. michaelis and M. caudata by its characteristic non-peltate leaf (Plate 32 A), extremely constricted lobe bases, and the short fruit pedicel (Plate 32 B). The markedly constricted lobe base is a distinctive feature of the genus Manihotoides, whose domain is adjoining that of M. Websterae. It would be desirable to compare the floral morphology of M. Websterae and Manihotoides pauciflora. At "level" 28 (Fig. 11), M. Websterae cluster is connected to M. foetida as well as M. crassisepala, both growing in the neighborhood of M. Websterae.

SPECIMENS EXAMINED: MEXICO. Puebla: [1]<sup>\*</sup> G. L. Webster & K. Miller & L. Miller 10374, 8 miles SE of Izucar de Matamoros, 18 August

---

\*This serial number corresponds to the number representing this collection in distribution maps.

1962, (R1<sup>\*\*</sup> = NO).

---

\*\* This "member" represents the cited herbarium sheets in the computer Similarity-Graph-Clustering-Analysis, the results of which are depicted in the subgraphs (Figs. 10 & 11) and the "SKYLINE" (Plate 8).

19. MANIHOT FOETIDA (H.B.K.) Pohl, Fl. Bras. ic. et descr. 1:55. 1827; Muell. arg. in DC. Prodr. 15(2):1067. 1866; Pax & Hoffmann, Pflanzennr. 44 (iv.147.ii):28. 1910.

NOMENCLATURE TYPE: Humboldt s.n. (non vidi).

HOMOTYPIC SYNONYMS: Janipha foetida H.B.K. Nov. gen et spec. pl II: 84. 1817; Jatropha foetida Steud. Nomencl. ed. 2. I:799. 1840.

ILLUSTRATIONS: Plates 33 and 69.

VERNACULAR NAMES: Mercymarona (Pax & Hoffmann 1910).

SYNOPSIS OF GROSS MORPHOLOGY: Tall trees. ROOTS not seen. Young STEMS light reddish brown, pubescent; mature stems reddish brown, glaucous. LEAVES alternate; stipules deciduous, pubescent; petioles about 9.0 cm long, terete, pubescent; lamina non-peltate, ventral surface green, pubescent, dorsal surface light green, pubescent, abaxial surface wax pattern smooth; venation camptodromous; lamina non-peltate, 3 lobed (Plate 33 A); median lobes obovate, margin entire, about 8.0 cm long, about 0.5 cm wide, base of lobe more than 3.0 cm across, apex abruptly tapering into an acute point, sinuses on either side of the median lobes narrowly cuneate; lowest lobes slightly smaller than median lobes, non-symmetric, gently curved up, a major vein (in addition to the midrib) present along the base of the lowest lobe. INFLORESCENCE a monoecious axillary, few flowered raceme (Plate 33 B), 4.0 - 7.0 cm long with a strong disagreeable smell, peduncles and pedicels tomentose; bracts and bracteoles not seen. PISTILLATE FLOWERS restricted to the base of the inflorescence, borne on short pedicels (less than 1.0 cm long), tepals

yellowish green, tomentose, about 1.0 cm long, cleft down to base into 5 lobes, lobes oblong tapering, disc fleshy entire; pistil about 0.6 cm long, ovary tomentose, the trifid stigma short and moderately lobed and lobulate. STAMINATE FLOWERS campanulate (Plate 33 C), tepals about 1.1 cm long, yellowish green, tomentose, cleft 1/3 way down into 5 lobes, lobes oblong obtuse, disc fleshy, 10 lobed, stamens 10, didynamous, superior whorl about 0.7 cm long, inferior whorl about 0.6 cm long, filaments and anthers cream colored. FRUIT pedicels about 1.0 cm long; capsules 3.0 - 4.0 cm long from base to apex, distinctly conical (Plates 33 D & E), narrowly tapering towards the apex. SEEDS large (Plates 33 F & G), oblong, about 2.5 cm long, surface shiny, dark brown, with inconspicuous black mottlings; caruncle extremely small in contrast to the seed size.

DISTRIBUTION AND ECOLOGY: (Plate 69). MEXICO: Mexico, in the region of Temascaltepec, southwest of Mexico City, at about 900 m.

The weather data of the station nearest to the range of this species, Mexico City, are given in Table 2.

PHENOLOGY: Flowering in June; fruiting in June.

DISCUSSION: In the subgraphs (Fig 11) this species joins M. crassise-pala at a "C-value" of .891, which indicates the close phenotypic similarity between these 2 species. Due to insufficient representation, the geographical ranges of these 2 species delineated in this study are far from complete. However, the distribution of the few collections available for this study indicates that these 2 species are geographically very close to each other. It may be necessary to

re-examine the taxonomic status of these 2 species when ampler material becomes available.

At "level" 28 (Fig. 11) M. foetida is connected simultaneously to M. caudata and M. Websterae, indicating that M. foetida is very likely to have drawn or donated genetic material of these 2 species. Geographically M. foetida is between M. Websterae and M. caudata, and would therefore support such a hypothesis.

M. foetida has the largest seed among the species considered in this study, perhaps largest in the genus Manihot.

SPECIMENS EXAMINED: MEXICO. Mexico: [1]<sup>\*</sup> G. B. Hinton 3562, Limones, 6 March 1933, (S2<sup>\*\*</sup> = GH); [2] G. B. Hinton 4149, Naranjo/Temascaltepec, 20 June 1933, (S2 = A). Unknown: [3] Sesse, Mocino, Castillo & Maldonado 4229, W/O locality, W/O date, (S1 = F).

---

\* This serial number corresponds to the number representing this collection in distribution maps.

\*\* This "member" represents the cited herbarium sheets in the computer Similarity-Graph-Clustering-Analysis, the results of which are depicted in the subgraphs (Figs. 10 & 11) and the "SKYLINE" (Plate 8).

20. MANIHOT CRASSISEPALA Pax & K. Hoffmann, Pflanzenr. 44(iv. 147 ii):28. 1910

NOMENCLATRURAL TYPE: Kerber 185 (Photo of type at F,GH and NY seen).

ILLUSTRATIONS: Plates 34 and 70.

VERNACULAR NAMES: None known.

USES: Mature seeds are edible (Pax & Hoffmann, 1910).

SYNOPSIS OF GROSS MORPHOLOGY: Trees. ROOTS not seen. Young STEMS pubescent, greyish brown with reddish tinge; mature stems reddish brown, glaucous. LEAVES alternate, stipules deciduous, pubescent; petioles about 10.0 cm long, terete, glabrous, in some pubescent; lamina non-peltate, ventral surface green, glabrous, dorsal surface pale green, glabrous, abaxial surface wax pattern smooth; venation camptodromous; lamina non-peltate, 3 lobed (Plate 34 A); median lobes obovate (Plate 34 C), margin entire; about 10.0 cm long, about 5.0 cm wide, base of lobes more than 2.5 cm across, apex abruptly tapering into an acute point, sinuses on either side of the median lobes narrowly cuneate; lowest lobes slightly smaller than median lobes, nonsymmetric, gently curved up, a major vein (in addition to the mid rib) present along the base of the lowest lobe. INFLORESCENCE a monoecious few flowered axillary raceme (Plates 34 B & D), 4.0 - 8.0 cm long, peduncles and pedicels pubescent; bracteoles non-foliaceous, pubescent, margin smooth, bractlets non-foliaceous, pubescent. PISTILLATE FLOWERS restricted to the base of the inflorescence, borne on short pedicels, less than 1.5 cm long, tepals yellowish green,

very sparsely pubescent, about 1.0 cm long, cleft down to base into 5 lobes, lobes oblong tapering, disc fleshy, entire, pistil about 0.6 cm long, ovary glabrous, the trifid stigma short, moderately lobed and lobulate. STAMINATE FLOWERS campanulate, tepals about 1.1 cm long, yellowish green, very sparsely pubescent, cleft 1/3 way down into 5 lobes, lobes oblong obtuse, disc fleshy, 10 lobed, stamens 10, didymous, superior whorl about 0.7 cm long, inferior whorl about 0.6 cm long, filaments and anthers cream colored. FRUIT pedicels about 1.5 cm long; capsules about 2.25 cm long from base to apex, distinctly conical, narrowly tapering towards the apex, surface finely rugose, apex pointed, fruit dehiscence loculicidal, splitting into 3 parts, the 3 commissural sutures not disjoining (Plate 34 E). SEEDS not seen.

DISTRIBUTION AND ECOLOGY: (Plate 70). MEXICO: Mexico and Morelos, in the region between Yautepec near Cuernavaca to Temascaltepec, at about 900 - 1300 m.

The weather data of the station nearest to the range of this species, Mexico City, are given in Table 2.

PHENOLOGY: Flowering in June; fruiting in June.

DISCUSSION: The subgraphs (Fig. 11) indicate that this species is phenotypically very similar to M. foetida. As discussed in connection with M. foetida, the insufficient representation of M. crassise-pala and M. foetida in this study, precludes confidently delimiting these 2 as two independent closed gene pools. It may be necessary to re-examine the taxonomic status of M. crassise-pala, especially

its relationship with M. foetida, when sufficient material and field data become available.

In the original description of this species, the type local is reported as Colima. Photographs of the type are available, but it has not been possible to verify the label data with respect to the locality of collection. It seems highly unlikely that the range of this species extends to Colima, however further field studies would be necessary to delineate its complete range.

The note in the original description of this species indicates that the mature seeds are edible. This would be worth looking into from an economic point of view.

SPECIMENS EXAMINED: MEXICO. Mexico: [1] <sup>\*</sup>G. E. Hinton 3564, Limones; Temascaltepec, 3 June 1933, (T3 <sup>\*\*</sup>= GH). Morelos: [2] C. G. Pringle 11339, near Cuernavaca/Limestone Hills/Yautepec, 24 October 1902, (T1 = GH). Uncertain <sup>\*\*\*</sup>: [3] Kérber 185, W/O locality, 1880, (T2 = F, GH, NY).

---

\* This serial number corresponds to the number representing this collection in distribution maps.

\*\* This "member" represents the cited herbarium sheets in the computer similarity-graph-clustering analysis, the results of which are depicted in the subgraphs (Figs. 10 & 11) and the "SKYLINE" (Plate 8).

\*\*\* The precise locality of collection of this is uncertain. This is reported to have been collected from Colima, according to the original description, but it is doubtful that M. crassisejala's range extends to Colima.

II. MANIHOTOIDES D. J. Rogers & S. G. Appan, gen. nov.

TYPE SPECIES: Manihotoides pauciflora (T. S. Brandege) D. J. Rogers  
& S. G. Appan, gen. nov.

SYNOPSIS OF GROSS MORPHOLOGY:

Arbores; cortex fusco-castaneus; folia trisecta lobis medianis ca.  
2.0 cm longis, ca. 2.25 cm latis; inflorescentia uniflora; flos  
staminatus 2.0 - 2.5 cm longus; capsulae globosae diametro ca. 1.5  
cm; semina ca. 1.25 cm longa.

Low trees (Plate 35 A) about 2.5 m high, profusely branched  
from base onwards, branching not regularly dichotomous or trichoto-  
mous (as usually occurring in the species of Manihot) but very irreg-  
ular (Plate 35 D), forming a more or less "crookedly branched" tree,  
outer and basal branches often reclining, foliage characteristically  
borne on short, condensed stalks arising from branchlets (Plate 35  
B). ROOTS not seen. STEMS glabrous, smooth, shiny, succulent, dark  
greyish brown, castaneus. LEAVES alternate; stipules persistent,  
pubescent, 0.2 - 0.3 cm long; petioles about 3.0 cm long, occasionally  
longer, slender, greenish, glabrous, ventral surface shallowly canali-  
culate; lamina non-peltate, ventral surface green, glabrous, dorsal  
surface pale green, glabrous, abaxial surface wax pattern smooth;

venation camptodromous, midribs on ventral and dorsal sides glabrous; lamina so deeply cleft into lobes that the leaves appear ternately compound (Plate 35 C); median lobes obovate to nearly obcordate with a truncate apex, about 2.0 cm long, about 2.25 cm wide; base of lobes very narrowly constricted, leaving the midrib with a very narrow (rarely more than 0.1 cm wide) strip of lamina, which facilitates the lobes to droop down easily from an erect position to a pendent position (a xerophytic adaptation to avert exposure of lamina to direct sunlight); the two lateral lobes very similar in form to median lobes. INFLORESCENCE uniflorous (Plate 35 I), rarely 2 (Plate 35 H), monoecious, usually borne at the apex of the characteristic short stalks of this taxon, pedicels about 2.0 cm long, greenish, glabrous, bearing 2 non-foliaceous, pubescent bractlets, about 0.2 cm long. PISTILLATE TEPALS yellowish green, glabrous, about 1.8 cm long, cleft to base into 5 lobes, lobes oblong lanceolate, caducous, disc fleshy, entire, pistil about 0.8 cm long, ovary subglobose, glabrous, the trifid stigma moderately lobed and lobulate. STAMINATE FLOWERS nearly tubular (Plate 35 I), tepals usually 2.0 - 2.5 cm long, rarely shorter, yellowish green, glabrous, deeply cleft nearly to the base into 5 lobes, lobes oblong lanceolate, not prominently reflexed at anthesis, disc fleshy, shallowly 10 lobed, stamens 10, didynamous, superior whorl about 1.6 cm long, inferior whorl about 1.3 cm long, anthers dehiscent longitudinally, cream colored, about 0.3 cm long, dorsifixed, the point of attachment of filament little lower from middle, filaments cream colored. The lone FRUIT borne on pedicels 1.0 - 2.0 cm long; capsules more or less sub-globose (Plate 35 E), about 1.5 cm long from base to apex, surface slightly verruculose

(Plate 35 F), ribs not prominent, apex rounded, fruit dehiscence septicial (Plate 35 G), splitting into 6 carpels. SEEDS about 1.25 cm long, oblong, carunculate end tapering and acutely pointed (Plate 35 J & K), surface shiny, greyish with dark mottlings, caruncle not prominent, trapeziform.

DISTRIBUTION AND ECOLOGY: (Plates 6, 7 & 71). MEXICO: Puebla and Oaxaca. As far as known, narrowly localized in the upper and interior regions of the steep canyons formed by the tributaries of Rio Santo Domingo, southeast of Tehuacan City. Grows at altitudes of 1000 - 1800 m. The habitat is xerophytic with thorn scrub cactus cover on igneous and sedimentary rocks with friable light red soil (Plate 35 A).

DISCUSSION: This population was described and designated as a species of Manihot (Manihot pauciflora T. S. Brandegee) in 1910. In the computer aided similarity-graph-clustering analysis, the 13 specimens representing this population form a homogeneous cluster (Fig. 11) at a high "C-value" of .918 ("level" 12). This cluster then remains distinct, with an enormous "moat", till a very low "C-value" of .541 ("level" 30) when it gets connected to the cluster representing the genus Manihot, thus manifesting a remarkable phenotypic distinctness. The significant "moat" of this cluster reflected in the tall pillar like structure of this population in the SKYLINE (Plate 8) with a deep rift separating this from the populations of genus Manihot, indicates the significant lack of affinity between this population and the taxa of genus Manihot.

This population manifests several unique morphological attributes, which have not developed in any closed gene pool of genus Manihot. The characteristic uniflorous inflorescence (Plate 35 I) of this population (all the species of Manihot have many flowered inflorescence) is usually considered as a primitive character (Cronquist 1968). The simple leaves of this are markedly reduced with respect to number and size of lobes (Plate 35 C), and are morphologically unique. Such reduced leaf is also usually considered as a primitive feature. The foliage is borne characteristically on short condensed stalks arising from branchlets, a feature not occurring in any species of Manihot. (As early as 1923, Standley indicated that this taxon is very unlike other Manihot species, and the leaves resemble some species of Oxalis.) These and several other unique characters would tend to support a contention of primitiveness of this taxon, indicating that the divergence of this population from the ancestral Manihot gene pool(s) and the consequent closure of gene flow between the two, were perhaps relatively more primitive events compared to the period of evolution of species within the genus Manihot. Based on these indications this population has been raised to the status of a monotypic genus.

The re-establishment of the land connection between South American and North American continents was a fairly recent geological development, and the possible role it could have played in the evolution within the family Euphorbiaceae in the New World, needs to be investigated. Does the present population of Manihotoides represent a relic of a genus which once flourished in the northern side of the land connection? A critical biogeographic study of the

various genera in Euphorbiaceae would be inevitable to put genus Manihotoides in the proper phylogenetic perspective.

21. MANIHOTOIDES PAUCIFLORA (T. S. Brandegeee) D. J. Rogers & S. G.

Appan, gen. nov.

NOMENCLATURAL TYPE: Holotype (UC): C. A. Purpus 3418 l. Isotypes (F,MO,NY,UC,US).

BASIONYM: Manihot pauciflora T. S. Brandegeee, Univ. Calif. Publ. Bot. 4:89. 1910.

ILLUSTRATIONS: Plates 35 and 71.

VERNACULAR NAMES: None known.

SYNOPSIS OF GROSS MORPHOLOGY: Same as the monotypic generic description.

PHENOLOGY: Flowering June - August; fruiting June - August.

DISTRIBUTION AND ECOLOGY: Same as that of the genus.

SPECIMENS EXAMINED: MEXICO. Puebla: [1] <sup>\*</sup>C. A. Purpus 5841, Tehuacan, June 1912, (U1 <sup>\*\*</sup> = UC); [2] J. N. Rose, J. H. Painter & J. S. Rose 10114, near Tehuacan, August - September 1905, (U2 = US); [3] C. E. Smith s.n., Venta Salada/S of Tehuacan, September 1962, (U2 = NO -); [4] C. E. Smith, F. A. Peterson & N. Tejada 3563, Tehuacan area/near Coxcatlan on Cerro Ajuereado, July 1961, (U3 = F,TEX); [5] C. A. Purpus 3418, vicinity of San Luis Tultitlanapa/near Oaxaca, June 1908,

---

\* This serial number corresponds to the number representing this collection in distribution maps.

\*\* This "member" represents the cited herbarium sheets in the computer similarity-graph-clustering analysis, the results of which are depicted in the subgraphs (Figs. 10 & 11) and the "SKYLINE" (Plate 8).

(U3 = F,MO,NY,UC,UC,US). Oaxaca: [6] C. Conzatti 4130, Cuesta de San Bernardina, 25 May 1921, (U2 = US); [7] M. Kinnach & R. Moran 161, 4.8 miles beyond Teotitlan to Tecomavaca, 17 November 1959, (U3 = UC).

CORRECTIONS TO BE MADE IN THIS MANUSCRIPT

- I) The name of Manihot isoloba ssp. isoloba should be changed as Manihot rubricaulis ssp. isoloba; and Manihot isoloba ssp. rubricaulis should be changed as Manihot rubricaulis ssp. rubricaulis.
- II) The name of Manihot Websterae should be changed as Manihot Websteri.