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Phylogenetic Significance of Interspecific Hybridization in *Jatropha* (Euphorbiaceae)

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ABSTRACT. *Jatropha* is a morphologically diverse genus of 160–175 species of trees, shrubs, rhizomatous subshrubs, and geophytes, distributed primarily in the seasonally dry tropics. The results of attempted interspecific hybridization of 20 species in eight of the ten sections support the previously suggested phylogenetic relationships of various taxa; decrease in ability to cross corresponds with evolutionary advancement, which is indicated by morphological reductions including dioecy, drastic shifts in growth habit, and/or changes in ploidy level. Except for the dioecious species, these plants have an autoxenogamous breeding system and moderate to well-defined interspecific differences in floral mechanisms. Related species show largely a high degree of unilateral compatibility (genetic incongruity) and may be separated by preferential fertilization, rather than incompatibility, whereas more phylogenetically distant taxa are separated by actual incompatibility barriers. Geographical isolation notwithstanding, related species are capable of gene exchange within wide limits under artificial conditions; phylogenetic relationships may be inferred by crossability of the taxa.

Jatropha L. is a morphologically diverse genus of 160–175 species of trees, shrubs, rhizomatous subshrubs, or geophytes, each having a narrow geographical range in seasonally dry tropical regions. Successful artificial hybridization between two of the commonly cultivated species, *J. curcas* L. and *J. integerrima* Jacq., was reported by Rupert et al. (1970). Knowledge of this partially fertile hybrid prompted Dehgan and Webster (1979) to attempt a new classification of the genus, which resulted in recognition of two subgenera, ten sections, and ten subsections. *Jatropha curcas* was placed in *J.* subg. *Curcas* (Adans.) Pax, sect. *Curcas* (Adans.) Griseb., and *J. integerrima* was assigned to subg. *Jatropha*, sect. *Polymorphae* Pax. In addition, subg. *Jatropha* included all African (except for two species), Indian (except for one species), South American, and Antillean, and two relict North American, taxa. Subgenus *Curcas* included all of the Mexican, one Costa Rican, two African, and one Indian species. This revision was based on similarities and differences in gross morphological attributes of reproductive structures and on the basic premise that species of *Jatropha* have limited dispersibility and are consequently geographically restricted.

In agreement with McVaugh (1945) and Wilbur (1954), Dehgan and Webster (1979) considered *J. curcas* the most primitive member of the genus because (among other characteristics) it has palmately lobed leaves, arborescent growth habit, and occasional hermaphroditic flowers. Evolution was thought to have proceeded toward specialization in vegetative structure, culminating in a facultatively annual growth habit in sect. *Jatropha* and in rhizomatous-shrub habit concomitant with polyploidy ($2n = 4x = 44$) in sect. *Mozinna* (subg. *Curcas*). These changes were associated with reduction in reproductive structures in both subgenera. The evolutionary trends of the monotelic inflorescence (Troll 1964) showed formation of a highly symmetrical, compound, dichasium in subg. *Jatropha* [sect. *Peltatae* (Pax) Dehgan & Webster]; the co-florescence, which results from primary branching of the main-florescence, was reduced to a single pistillate flower in sect. *Collenucia* (Chiov.) Chiov. In subg. *Curcas*, however, inflorescences were drastically reduced to a few (or solitary) terminal or lateral flowers together with a gradual change from monoecy to dioecy. The evolution of the flower in subg. *Jatropha* resulted in reduction and rearrangement of stamens (from ten to eight, uni- or biseriate, monodelphus or free) without change in the number of locules of the fruit, while in subg. *Curcas* (except sect. *Curcas*) the number and arrangement of stamens remained unchanged, but the locules of the fruit and stigma lobes were progressively reduced from three to one. These reductions and modifications coincided with south to north latitude and increasing aridity (cf. diagram in Dehgan, 1982).

The proposed phylogenetic classification of the genus (Dehgan and Webster 1979) has been substantiated by comparative microscopic examination of various anatomical and morphological features (Dehgan and Craig 1978; Dehgan 1980, 1982). This paper reports the implications of interspecific hybridization in elucidation of the phylogeny and confirmation of the species relationships within the genus.

Materials and Methods

The plants were either field-collected by the author or received as seeds or cuttings. These were propagated and grown in insect-free greenhouses until flowering at which time hybridization trials were initiated. Emasculation proved not to be necessary despite self-compatibility in all but one of the monoecious species (*J. moranii* Dehgan & Webster). The reason for this was the lag of anthesis of staminate flowers, as well as the absence of insect vectors for pollen transfer. Hand-pollination involved rubbing dehisced anthers on stigmatic surfaces, which are usually receptive immediately after anthesis. The total number of pollinations was limited by the scarcity of pistillate flowers in all taxa and particularly those of subg. *Curcas*. If fruit enlargement was noted 7–10 days after pollination, cheesecloth bags were placed over the fruit to avoid loss of seeds.

Fluorescence light microscopy, using decolorized aniline blue (Martin 1959) was employed to observe pollen tube growth and penetration when fruit enlargement was not observed or pollen-stigma interaction caused abscission of the inflorescence or the flowers. Pollen viability was estimated using Alexander's (1969) stain. Somatic chromosome numbers of parental taxa were reported earlier (Dehgan and Webster 1979); counts for the hybrids were made from young leaves (Baldwin 1939).

Results

Comparative vegetative and floral morphology of parental species and F_1 hybrids are summarized in table 1 and illustrated in figures 1–33. The results of attempted interspecific crosses are presented in figure 34. Seed parents are mentioned first throughout the paper.

Unilateral compatibility was the rule for all but *J. curcas* × *integerrima* (fig. 22). In the reciprocal crosses and a large number of other crosses, seeds with a normal embryo were formed but the endosperm aborted. In at least two crosses, *J. integerrima* × *multifida* L. and *J. hernandiifolia* Vent. × *gossypiifolia* L., the entire inflorescence abscised within 24–48 hours after pollination. Examination of pollinated stigmas revealed that in both cases the pollen had germinated and penetrated the stylar tissue. Extensive formation of callose in both the pollen tube and the pollen itself was apparent in these crosses. In attempted crosses in which the fruit actually enlarged and seeds with embryo were formed, but endosperm aborted, and in crosses or hand-pollinated selfs that produced viable seeds, the pollen tube penetration was complete and could be seen reaching the ovary. Seed set of 100% was not uncommon in selfed as well as some of the cross-pollinated flowers (table 1). Flowers tagged but not hand-pollinated produced no seeds, except for the rare hermaphrodite flowers of *J. curcas*.

Although pollen fertility was high in most hybrids (table 1), only two of the hybrids, *J. curcas* × *integerrima* (but not the reciprocal) and *J. curcas* × *macrorhiza* Benth. (figs. 21–22) produced seed and F_2 progeny. In both cases seed set was low (only five seeds from 28 pollinations and three seeds from 17 pollinations, respectively), and plants segregated for vegetative and floral characters.

Young leaves of all hybrids had a chromosome number of $2n = 22$. Progenies of two attempted crosses involving *J. curcas* and two species of sect. *Peltatae* [*J. cathartica* Terán & Berland (fig. 8) and *J. podogrica* Hook. (fig. 9)], however, had $2n = 3x = 33$. These were nearly sterile as shown by 5% and 4% stainable pollen, respectively. Except for an increase in stem thickness and leaf size, they are indistinguishable from *J. curcas* (fig. 12) in their floral and vegetative morphology (data not included in table 1).

As a general rule, all F_1 hybrids, except *J. curcas* × *multifida* (fig. 28), were more vigorous than their parental species and flowered earlier.

Small size of the chromosomes (2–4 μm fide Rupert et al. 1970) and the apparent brief time lapse in meiotic stages (even when flower buds were collected at 1-hour intervals over a 24-hour period) rendered study of chromosomal behavior impracticable.

Discussion

Although this work presents the outcome of nearly 16 years of research, the results may at first appear insufficient for drawing convincing conclusions. When combined with morphological, autoecological, and evolutionary observations, however, the evidence in support of phylogenetic affinities between the various sections becomes more evident. Data presented in previous papers (Dehgan and Craig 1978; Dehgan and Webster 1979; Dehgan 1980, 1982) indicated *J. curcas,* a geographically widespread species with closely allied taxa in Meso-America, Africa, and India, to be the most primitive member of the genus. Most successful crosses involved *J. curcas* as the maternal parent, which suggests its primitiveness. The degree of specialization of other taxa in relation to *J. curcas,* which has been established on the basis of modifications of growth habit (Dehgan and Webster 1979), can therefore be substantiated by the ease or difficulty with which crosses are possible. The results of such hybridizations suggest a stepwise alteration of the genetic make up with respect to the development of barriers to interspecific compatibility.

Barriers to interspecific compatibility are weak between *J. curcas* and species of sect. *Polymorphae* Pax, as indicated by several hybrid combinations (fig. 34) as well as reciprocal backcrosses. Such hybrids also possess a high percentage of stainable pollen (table 1). The same may be said of subsect. *Capenses* Dehgan & Webster of sect. *Tuberosae* Pax (figs. 4–5). An interbreeding alliance indicating close phylogenetic affinity among *J. curcas* (a widespread small tree of the world tropics), *J. integerrima* (fig. 3), and *J. macrorhiza* (fig. 1) of sect. *Polymorphae* (a shrubby Cuban species and a geophyte from Arizona and northern Mexico, respectively), and *J. capensis* (fig. 4) of sect. *Tuberosae* (a South African relict shrub with an above-ground caudex and a subterranean tuber) may be established. Neither geographical isolation nor extensive morphological diversification, particularly with respect to growth habit, have produced strong barriers to interspecific compatibility. Thus, these taxa appear to be phylogenetically related.

A somewhat stronger compatibility barrier has developed between *J. curcas* and the species of sect. *Peltatae* (figs. 6–9), however. Interspecific cross-pollination between these taxa results in either production of seeds with normal embryo but aborted endosperm, sterile hybrids (?) with triploid chromosome numbers, or hybrids with low pollen viability and abortion of pistillate flowers as well as a general lack of vigor [e.g., *J. curcas* × *multifida* (fig. 28)]. From a phylogenetic standpoint, species of sect. *Peltatae* have evolved further than species of sect. *Polymorphae* and *Tuberosae* and are, therefore, more distantly related to *J. curcas.*

Because viable hybrids between *J. gossypiifolia* [a facultative annual (fig. 10)] or *J. excisa* Griseb. var. *pubescens* Lourt. & O'Donn. (fig. 11) and any other species were not obtained (cf. fig. 34), and fruit enlargement did not occur in a majority of the attempts, it is reasonable to assume the greatest phylogenetic distance between these taxa and *J. curcas.* It is not expected for a facultative annual such as *J. gossypiifolia* to cross with arborescent taxa such as *J. curcas, J. integerrima, J. capensis,* and *J. moranii* (fig. 14).

According to Grant (1975), the effect of the action of genes that control growth habit are modified by environmental conditions. The gene determining a given developmental sequence will have one phenotypic expression under one set of environmental conditions and a different expression under other conditions. *Jatropha macrorhiza* (fig. 1), a relict species in the northern part of Mexico and southern Arizona probably has undergone modifications in growth habit to adapt to the harsh environment of that area. In this case, perhaps, phenotypic expression as a result of gene-environment interaction is exhibited as a geophytic growth habit. *Jatropha integerrima* (fig. 3), a related species, while maintaining close genetic propinquity, has developed an evergreen, multibranched-shrub habit apparently as a response to the higher annual rainfall in Cuba. In contrast, *J. gossypiifolia* (fig. 10) has become totally reproductively isolated from its congeners. This is probably because of a high rate of genetic recombination associated with a shift to facultative annual condition (particularly because it produces more than one generation per year). Such high potential rate of genetic recombination would provide greater opportunities for the rapid evolution of an isolating mechanism that would preserve adaptive gene combinations. Reproductive isolation of *J. gos-*

TABLE 1. Characteristics of eleven *Jatropha* species and their successful artificial hybrids: nine species that failed to cross are excluded (cf. fig. 34). NA denotes data not available or not applicable; * = dioecious species.

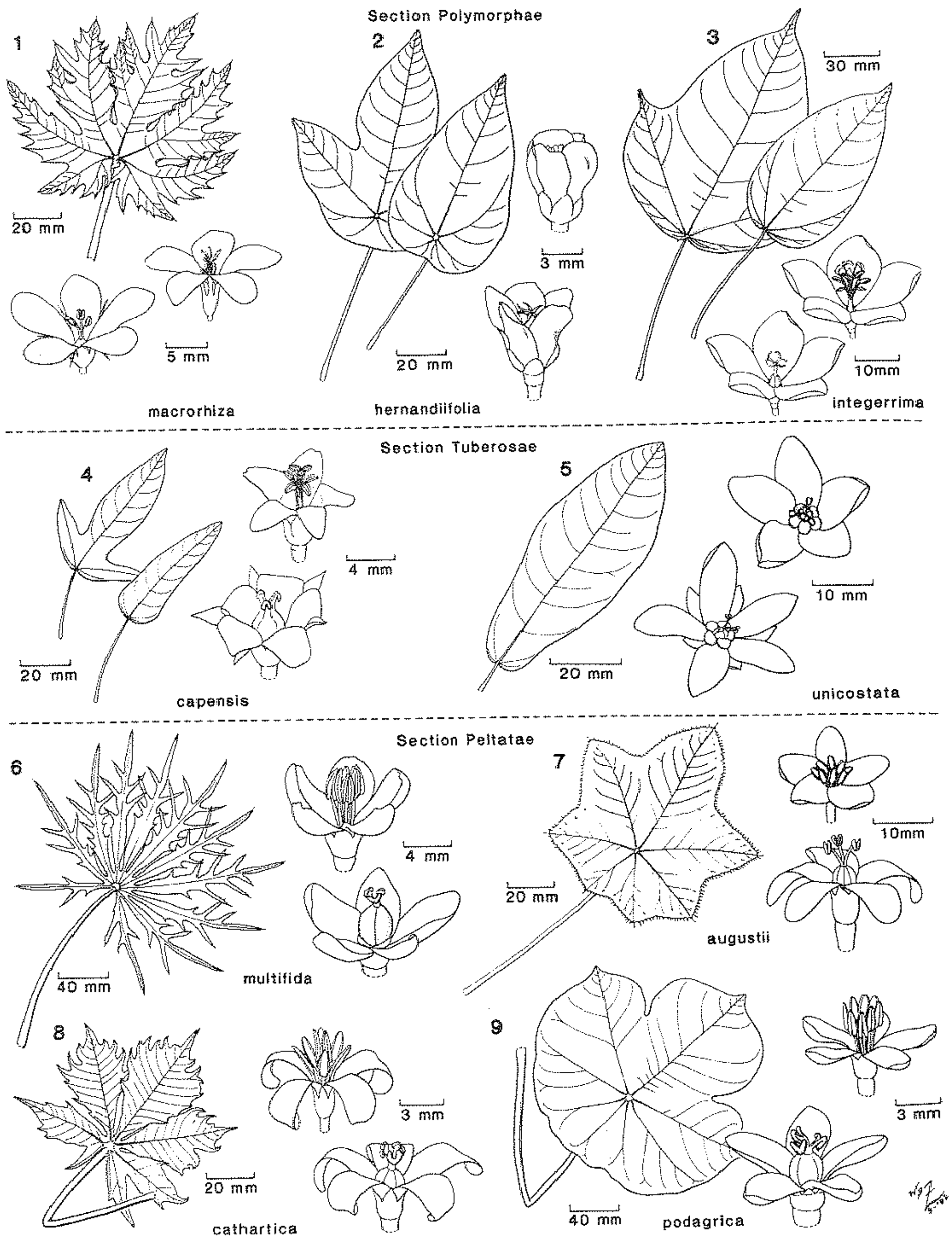
	Species or hybrid	Voucher number	Origin	Number of flowers pollinated	Number of seeds obtained	% germinated	Pollen: Stainable	Pollen: Average diam. in µm	Flower: Color	Flower: Average cup diam. (mm) (♂-♀)
1.	*J. curcas* (self)	B63.017	India	12	29	96.5	96.8	83.5	greenish-white	7–11
2.	× *integerrima*			8	8	50.0	66.2	89.0	pink	12–15
3.	× *macrorhiza*			7	21	100.0	63.0	84.5	white	11–14
4.	× *capensis*			10	6	100.0	28.0	86.0	greenish-white	7–12
5.	× *multifida*			11	2	100.0	12.0	83.0	pink	NA–13
6.	× *cordata**			5	5	100.0	NA	NA	NA	NA
7.	× *cinerea**			9	3	66.6	NA	NA	NA	NA
8.	*J. integerrima* (self)	B67.280	Cuba	10	30	100.0	98.8	86.6	pink to scarlet	26–32
9.	× *curcas*			56	9	16.0	18.6	89.9	pink	12–15
10.	*J. macrorhiza* (self)	B74.075	Arizona	10	30	40.0	100.0	78.3	pinkish-white	24–33
11.	× *integerrima*			6	18	100.0	38.0	82.0	light pink to dk. red	31–38
12.	× *capensis*			8	18	50.0	15.5	79.8	light pink	13–21
13.	× *moranii*			5	5	100.0	12.0	81.5	pink	14–24
14.	*J. capensis* (self)	B67.045	S. Africa	12	36	100.0	93.0	81.5	greenish white	8–12
15.	× *integerrima*			8	7	71.4	19.0	92.8	pink	15–25
16.	*J. multifida* (self)	B67.282	Barbados	10	30	93.3	92.2	84.7	red	11–16
17.	*J. cathartica* (self)	B67.524	Texas	22	65	32.3	98.0	79.6	dark red	13–17
18.	× *podagrica*			6	14	14.2	16.0	86.8	red	12–NA
19.	*J. podagrica* (self)	B59.318	Panama	25	74	100.0	92.5	78.8	red	10–16
20.	*J. moranii* (self)	B75.052	Baja Calif.	9	0	0.0	89.0	73.0	white	9–12
21.	*J. cordata**	B76.006	Mexico	3	6	83.3	82.5	69.0	yellowish-white	4–9
22.	× *cinerea**			3	1	100.0	18.0	79.0	red	10–NA
23.	*J. cinerea**	B74.020	Baja Calif.	6	11	91.6	81.4	72.0	red	6–9
24.	*J. cardiophylla**	B74.072	Arizona	4	4	100.0	98.0	69.0	pinkish-white	5–7
25.	× *moranii*			4	1	100.0	NA	NA	whitish-pink	4–NA

TABLE 1. Continued.

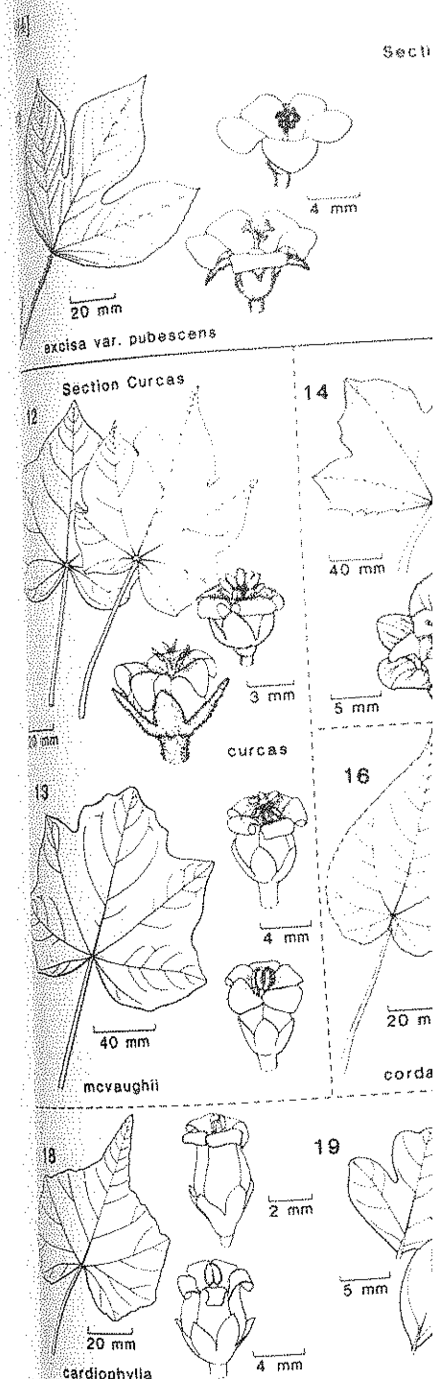
	Petal: Configuration	Petal: Attitude	Petal: Length (mm) (♂-♀)	Sepal: Configuration	Sepal: Length (mm) (♂-♀)	Number of stamens	Number of styles and locules	Leaf: Shape	Leaf: Glands	Growth habit
1.	coherent	reflexed	6–9	± imbricate in ♂	4–7	10	3	± lobed	–	tree
2.	± imbricate	reflexed	12–14	± distinct	4–5	10	3	shallowly lobed	–	small tree
3.	± coherent	reflexed	10–12	distinct	6–8	9 (10)	3	lobed	–	caudiciform shrub
4.	coherent in ♂	reflexed	8–14	distinct	7–9	10 (9)	3	lobed	–	large shrub
5.	free	± straight	NA–12	distinct	NA–4	9 (10)	NA	deeply lobed	–	small tree
6.	NA	NA	NA	NA	NA	NA	NA	lobed	+	small tree
7.	NA	NA	NA	NA	NA	NA	NA	lobed	–	small tree
8.		straight	14–17	distinct	3–4	10	3	lobed to entire	–	large tree
9.					4–9	10	3	entire to shallowly lobed	–	small tree

TABLE 1. Continued.

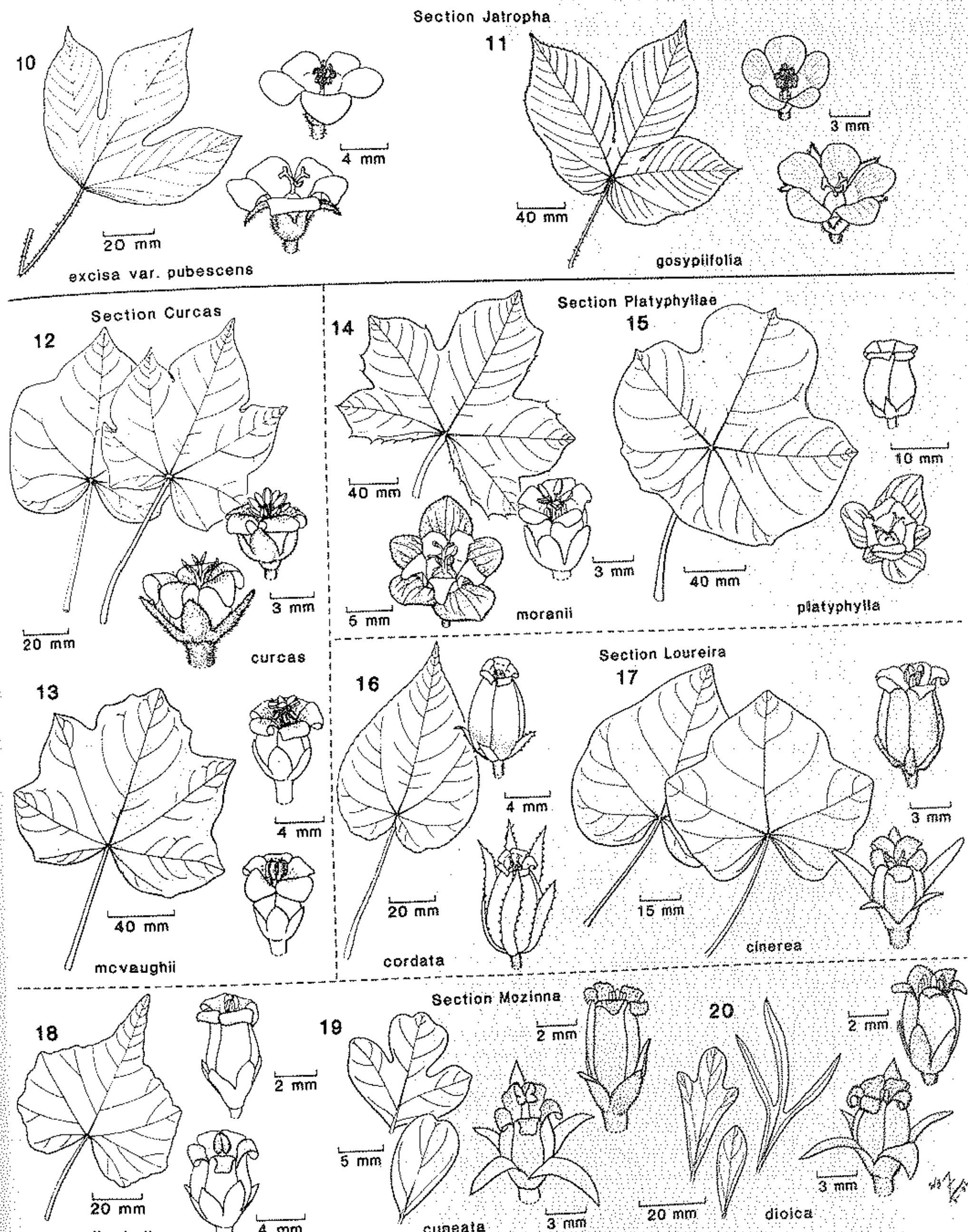
	Petal			Sepal		Number of stamens	Number of styles and locules	Leaf		
	Configuration	Attitude	Length (mm) (♂–♀)	Configuration	Length (mm) (♂–♀)			Shape	Glands	Growth habit
1.	coherent	reflexed	6–9	± imbricate in ♂	4–7	10	3	± lobed	–	tree
2.	± imbricate	reflexed	12–14	± distinct	4–5	10	3	shallowly lobed	–	small tree
3.	± coherent	reflexed	10–12	distinct	6–8	9 (10)	3	lobed	–	caudiciform shrub
4.	coherent in ♂	reflexed	8–14	distinct	7–9	10 (9)	3	lobed	–	large shrub
5.	free	± straight	NA–12	distinct	NA–4	9 (10)	NA	deeply lobed	–	small tree
6.	NA	NA	NA	NA	NA	NA	NA	lobed	+	small tree
7.	NA	NA	NA	NA	NA	NA	NA	lobed	–	small tree
8.	imbricate	straight	14–17	distinct	3–4	10	3	lobed to entire	–	large tree
9.	± imbricate	reflexed	12–15	± distinct	4–9	10	3	entire to shallowly lobed	–	small tree
10.	free to imbricate	straight	14–15	distinct (divided)	7–9	8	3	deeply lobed	–	geophyte
11.	free	± reflexed	16–19	distinct	6–11	9 (10)	3	lobed	–	caudiciform subshrub
12.	free	± straight	9–14	distinct	6–9	8	3	entire to deeply 3-lobed	–	caudiciform subshrub
13.	± imbricate	reflexed	11–17	± imbricate	5–7	9 (10)	3	lobed	+	subshrub
14.	± imbricate	reflexed in ♀	7–10	distinct	4–11	8	3	entire to 3-lobed	–	small caudiciform
15.	free to imbricate	reflexed	12–15	distinct	3–5	10 (9)	3	± entire to 3-lobed	–	small caudiciform
16.	± free	straight in ♀	6–9	distinct	2–3	8	3	divided	–	small tree
17.	free	reflexed in ♀	9–11	distinct	2–3	8	3	± divided or deeply lobed	–	geophyte
18.	free	± straight	8–NA	distinct	3–NA	NA	3	deeply lobed	–	small shrub
19.	free	straight	7–11	distinct	2–3	8(±12)	3	peltate-lobed	–	caudiciform shrub
20.	free	reflexed	8–13	imbricate in ♂	5–14	10	3	lobed	+	subshrub
21.	coherent	± reflexed	8–12	± imbricate	3–12	10	2	unlobed to ± lobed	+	small tree
22.	coherent	reflexed	10–13	imbricate	4–10	10	NA	lobed	+	shrub
23.	coherent	± reflexed	8–11	± imbricate	3–5	10	2	entire to ± lobed	±	shrub
24.	coherent	± reflexed	8–11	± imbricate	3–5	10	1	unlobed-crenate	–	rhizomatous shrub
25.	coherent	reflexed	NA–9	free in ♀	NA–60	NA	2 (1)	unlobed-crenate	–	subshrub



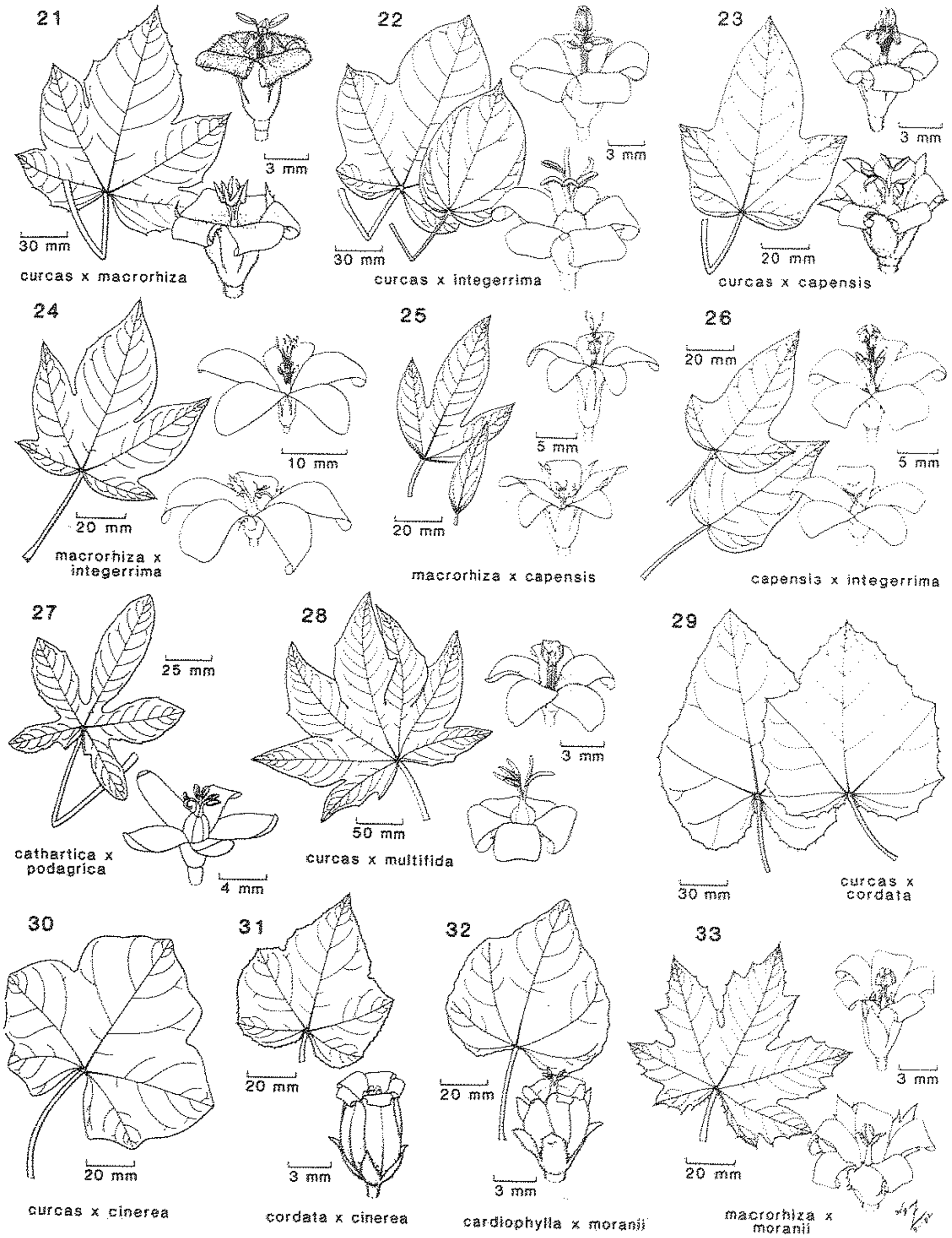
FIGS. 1–9. Leaves and flowers of species in *Jatropha* subg. *Jatropha*. 1–3. Sect. *Polymorphae*. 1. *J. macrorhiza* Benth. (B74.075—Arizona). 2. *J. hernandiifolia* Vent. (B67.281—Jamaica). 3. *J. integerrima* Jacq. (B67.280—Cuba). 4–5. Sect. *Tuberosae*. 4. *J. capensis* (L.f.) Sonder. (B67.045—S. Africa). 5. *J. unicostata* Balf. (B67.471—Socotra). 6–9. Sect. *Peltatae*. 6. *J. multifida* L. (B74.157—New Guinea). 7. *J. augustii* Pax & Hoffm. (B74.056—Peru). 8. *J. cathartica* Terán & Berland (B67.471—Texas). 9. *J. podagrica* Hook. (B74.011—Puerto Rico).



FIGS. 10–20. Leaves and flowers of spe
pubescens Lourteig & O'Donnell (B74.166—
Curcas. 12–13. Sect. *Curcas*. 12. *J. curcas* L.
Mexico). 14–15. Sect. *Platyphyllae*. 14. *J.*
phylla Muell. Arg. (B69.300—Mexico). 16
Mexico). 17. *J. cinerea* (Ortega) Muell. A
Muell. Arg. (B74.071—Arizona). 19. *J. c*
Sessé (B74.058—Mexico).



FIGS. 10–20. Leaves and flowers of species in *Jatropha*. 10–11. Sect. *Jatropha*. 10. *J. excisa* Griseb. var. *pubescens* Lourteig & O'Donnell (B74.166—Argentina). 11. *J. gossypiifolia* L. (B74.016—India). 12–20. Subg. *Curcas*. 12–13. Sect. *Curcas*. 12. *J. curcas* L. (B68.286—Senegal). 13. *J. mcvaughii* Dehgan & Webster (B74.232—Mexico). 14–15. Sect. *Platyphyllae*. 14. *J. moranii* Dehgan & Webster (B75.052—Baja California). 15. *J. platyphylla* Muell. Arg. (B69.300—Mexico). 16–17. Sect. *Loureira*. 16. *J. cordata* (Ortega) Muell. Arg. (B72.129—Mexico). 17. *J. cinerea* (Ortega) Muell. Arg. (B74.008—Mexico). 18–20. Sect. *Mozinna*. 18. *J. cardiophylla* Muell. Arg. (B74.071—Arizona). 19. *J. cuneata* Wiggins & Rollins (B74.026—Baja California). 20. *J. dioica* Sessé (B74.058—Mexico).



FIGS. 21–33. Leaves and flowers of artificial hybrids of species in various sections of *Jatropha*. 21. *J. curcas × macrorhiza*. 22. *J. curcas × integerrima*. 23. *J. curcas × capensis*. 24. *J. macrorhiza × integerrima*. 25. *J. macrorhiza × capensis*. 26. *J. capensis × integerrima*. 27. *J. cathartica × podogarica*. 28. *J. curcas × multifida*. 29. *J. curcas × cordata*. 30. *J. curcas × cinerea*. 31. *J. cordata × cinerea*. 32. *J. cardiophylla × moranii*. 33. *J. macrorhiza × moranii*.

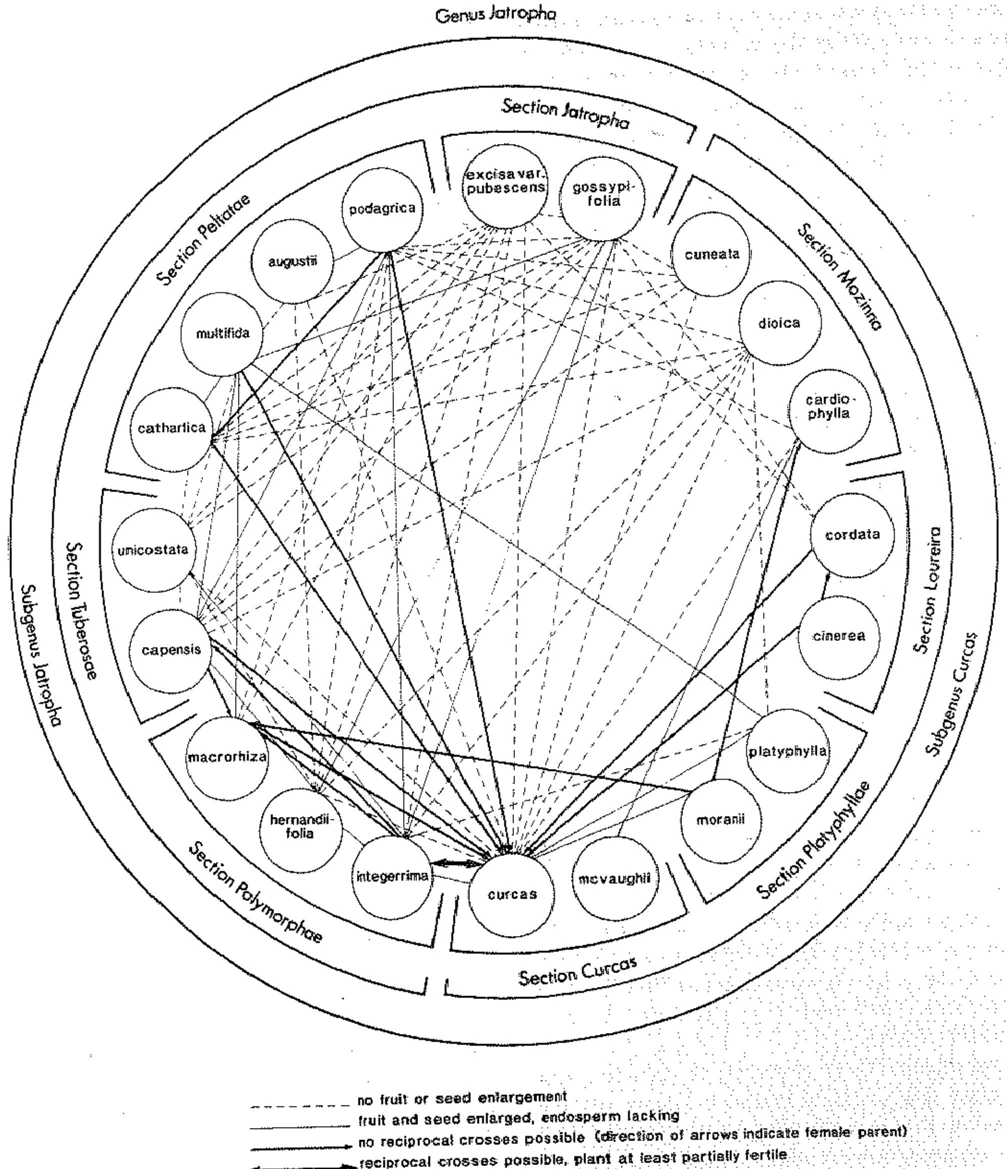


FIG. 34. Crossability of 20 species in the two subgenera and eight of the ten sections of *Jatropha*. Arrangement of the diagram is based on phylogenetic positioning of the taxa by Dehgen and Webster (1979). Primitive species at the base, advanced species at the top. Reciprocal crosses were attempted in all combinations.

sypiifolia and its allied taxa is probably indicative of their advanced position within the genus.

Interspecific crosses in subg. *Curcas* follow a pattern similar to those in subg. *Jatropha*. Analogous to *J. gossypiifolia*, no crosses are possible between *J. cuneata* Wiggins & Rollins (fig. 19) or *J. dioica* Sessé (fig. 20) of sect. *Mozinna* (Ortega) Pax and species of other sections (fig. 34). These two species represent the end product of an evolutionary reduction series associated with polyploidy ($2n = 4x = 44$), dioecy, and rhizomatous growth habit. *Jatropha cardiophylla* (Torrey) Muell. Arg. (fig. 29), the only diploid species in sect. *Mozinna*, crosses with other taxa in the subgenus (e.g., *J. moranii*; fig. 30). Ease of crossability between the more closely related taxa is exemplified by *J. curcas* × *cordata* (fig. 29) and *J. curcas* × *cinerea* (fig. 30). This occurs despite a shift to dioecy in sect. *Loureira* (Cav.) Muell. Arg. ex Pax, to which *J. cordata* (Ortega) Muell. Arg. and *J. cinerea* (Ortega) Muell. Arg. are assigned. In general, as the interspecific compatibility decreases, phylogenetic distance increases. This agrees with Pandey's (1978, 1979) hypothesis that with increasing phylogenetic distance the effect of the S gene complex diminishes and incongruity dominates to produce interspecific incompatibility.

The distinction made by Hoogenboom (1973, 1975) between "incompatibility" and "incongruity", seems to be applicable to interspecific pollen-stigma behavior in *Jatropha*. Incongruity, when interpreted in terms of nonmatching partners, is a plausible explanation for unilateral compatibility (matching partners). In the pistil of a particular species with a certain barrier capacity, only pollen with all matching penetration genes can function (Hoogenboom 1973; Heslop-Harrison 1975). Conversely, matching penetration genes may be present, but "preferential fertilization" (Grant 1975) may be responsible for the lack of endosperm in crosses in which the seed is seemingly normal and the embryo is formed. In such cases, pollen germination and penetration is normal, but fusion of one of the male gametes and the polar nuclei probably does not occur, hence endosperm is not produced. If this behavior is considered to be partial compatibility, then the relationship between the various sections becomes clearer.

Incompatibility in concert with phylogenetic distance reach a point at which crosses are not possible, that is, either fruit enlargement does not occur or flowers and/or inflorescences abscise following pollination. The antigen-antibody hypothesis of Lewis and Crowe (1958) and Nettancourt (1977) is perhaps applicable here as evidenced by excessive formation of callose in the pollen tubes.

The implications of compatibility between related species and incompatibility, incongruity, or preferential fertilization among more distantly related taxa can also be illustrated under natural conditions. Dehgan and Webster (1978) reported the existence of only one hybrid complex in Mexico (the *J. cinerea-canescens* complex), despite the sympatric occurrence of several species of subg. *Curcas*. Pax (1910) alluded to possible natural hybrids in South American species of sect. *Jatropha*. However, a hybrid complex, here referred to as the *J. integerrima-hastata* complex (possibly involving more than two species), occurs in Cuba and the nearby West Indian Islands. When selfed, the so-called *J. integerrima* progenies segregate as to flower size and color (light pink to dark red) as well as leaf size and shape (entire to three-lobed). Because Mendelian ratios, with respect to specific characters, are not detectable and simple dominance is not exhibited, the conclusion is inevitable that considerable heterozygosity exists in the genotype of the parental species. Most likely we are observing the outcome of repeated crossing and backcrossing (introgression) with the resulting proliferation of intergrading taxonomic entities [cf. Siebert (1947) on *Hevea*].

In certain cases, in which artificial hybridization of two sympatric species (e.g., *J. cordata* × *cinerea*, fig. 31) is possible under greenhouse conditions but no such hybrids are found in the wild, ethological factors such as pollinator specificity need to be examined. In this particular example flowering times coincide (pers. obs.) but flower color differs considerably in the two species. *Jatropha cordata* (fig. 16) has yellowish-white to white flowers; *J. cinerea* (fig. 17) has pink to red. Furthermore, the glands of the calyx lobes are prominent in *J. cordata* and lacking in *J. cinerea*. This may be sufficient reason for pollinator(s) of one species not to visit the other [see Dehgan and Webster (1979) for a discussion of pollination syndromes in *Jatropha*], consequently, cross-pollination is not likely to occur and such hybrids have not been observed.

Basic chromosome number in *Jatropha* has remained constant ($x = 11$ fide Dehgan and Webster 1979) but minimal structural differentiation similar to that in such woody temperate genera as *Ceanothus, Quercus, Pinus, Eucalyptus,* and *Ribes* (Grant 1971, 1975) may have occurred. These changes have not been sufficient, however, to cause interspecific incompatibility in the closely related but geographically isolated taxa in *Jatropha*. In the more distantly related species, interspecific incompatibility and hybrid inviability similar to that in such tropical genera as *Theobroma* (Addison and Tavares 1952) and *Hibiscus* (Menzell and Wilson 1969) is apparent. Considering the autoxenogamous breeding system (Dehgan and Webster 1979), incidence of polyploidy, and variations in growth habit, it is not surprising to find *Jatropha* falling into an intermediate geographic and evolutionary position between woody tropical and temperate groups. Thus, it seems appropriate to add a sixth pattern of species relationships (the *Jatropha* pattern) to the five recognized by Grant (1971:100–101). Species of *Jatropha* may be described as woody plants of uniform basic chromosome number with an autoxenogamous breeding system. Floral mechanisms have moderate to well-defined interspecific differences. Related species are separated largely by incongruity and/or preferential fertilization rather than incompatibility. In contrast, phylogenetically distant taxa are largely separated by actual genetic incompatibility barriers. Geographical isolation notwithstanding, the species are otherwise capable of gene exchange within relatively wide limits when brought together under artificial conditions.

Phylogenetic arrangement of the genus as was presented by Dehgan and Webster (1979) is therefore justified by interspecific crossability of the species as well as by morphology and anatomy. Further indication that *J. curcas* is perhaps the most primitive member of the genus is evidenced by its retention of the ability to interbreed (as maternal parent) with species of both subgenera. Establishment of the subgeneric limits is also well-supported because only one hybrid (*J. macrorhiza* × *moranii*, fig. 33), other than those involving *J. curcas*, has been possible between them.

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